Taxonomy, phylogeny and evolution of freshwater *Hypocreomycetidae* (*Sordariomycetes*)

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Abstract

Hypocreomycetidae is a highly diverse group with species from various habitats. This subclass has been reported as pathogenic, endophytic, parasitic, saprobic, fungicolous, lichenicolous, algicolous, coprophilous and insect fungi from aquatic and terrestrial habitats. In this study, we focused on freshwater fungi of Hypocreomycetidae which resulted 41 fresh collections from China and Thailand. Based on morphological and phylogenetic analyses, we identified 26 species that belong to two orders (Hypocreales and Microascales) and six families (Bionectriaceae, Halosphaeriaceae, Microascaceae, Nectriaceae, Sarocladiaceae and Stachybotryaceae). Ten new species are introduced and 13 new habitats and geographic records are reported. Mariannaea superimposita, Stachybotrys chartarum and S. chlorohalonatus are recollected from freshwater habitats in China. Based on phylogenetic analysis of combined LSU, ITS, SSU, rpb2 and $tef1-\alpha$ sequences data, *Emericellopsis* is transferred to Hypocreales genera incertae sedis; Pseudoacremonium is transferred to Bionectriaceae; Sedecimiella is placed in Nectriaceae; Nautosphaeria and Tubakiella are excluded from Halosphaeriaceae and placed in Microascales genera incertae sedis; and Faurelina is excluded from Hypocreomycetidae. Varicosporella is placed under Atractium as a synonym of Atractium. In addition, phylogenetic analysis and divergence time estimates showed that Ascocodina, Campylospora, Cornuvesica and Xenodactylariaceae form distinct lineages in Hypocreomycetidae and they evolved in the family/ order time frame. Hence, a new order (Xenodactylariales) and three new families (Ascocodinaceae, Campylosporaceae and *Cornuvesicaceae*) are introduced based on phylogenetic analysis, divergence time estimations and morphological characters. Ancestral character state analysis is performed for different habitats of Hypocreomycetidae including freshwater, marine and terrestrial taxa. The result indicates that marine and freshwater fungi evolved independently from terrestrial ancestors. The results further support those early diverging clades of this subclass, mostly comprising terrestrial taxa and freshwater and marine taxa have been secondarily derived, while the crown clade (*Nectriaceae*) is represented in all three habitats. The evolution of various morphological adaptations towards their habitual changes are also discussed.

Keywords Ancestral character analysis \cdot Divergence time estimates \cdot Molecular clock analysis \cdot Morphology \cdot Phylogeny \cdot Freshwater fungi

Introduction

Hypocreomycetidae (*Sordariomycetes*) is an ecologically and morphologically diverse group. It comprises plant or human pathogens, endophytes, parasites, saprobes, fungicolous, lichenicolous, algicolous, coprophilous and insect fungi from various habitats, including freshwater, marine

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and terrestrial habitats (Maharachchikumbura et al. 2015; Hyde et al. 2017, 2020a). The members of *Hypocreomycetidae* have light-colored perithecia, nonamyloid or amyloid ascal rings, or those which lack apical rings and most taxa lack true paraphyses (Zhang et al. 2006). *Hypocreomycetidae* was established by Eriksson and Winka (1997) based on morphology and a single gene (SSU) phylogenetic analysis. Eriksson (2006) showed that *Hypocreomycetidae* formed a monophyletic clade within *Sordariomycetes* and four orders viz. *Coronophorales*, *Halosphaeriales*, *Hypocreales* and *Microascales* were accepted in *Hypocreomycetidae*.



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Coronophorales, Halosphaeriales and Hypocreales are monophyletic, while *Microascales* is paraphyletic. Zhang et al. (2006) updated the phylogenetic tree for *Sordariomycetes* using LSU, SSU, *tef1-a* and *rpb2* sequence data. Their analysis concurred with Eriksson (2006), except *Melanospora*, which formed a sister clade with *Coronophorales* and can be recognized as a distinct order. Thus, a new order *Melanosporales* was introduced to accommodate *Melanospora* (Zhang et al. 2006). Subsequently, Tang et al. (2007) accepted five orders in *Hypocreomycetidae*. In contrast, Hibbett et al. (2007) accepted only four orders in the subclass whereas *Halosphaeriales* was placed under *Microascales* based on phylogenetic analysis. Lumbsch and Huhndorf (2010) accepted four orders and 18 families in *Hypocreomycetidae*.

Boonyuen et al. (2011) and Réblová et al. (2011) introduced Savoryellales and Glomerellales in Hypocreomy*cetidae*, respectively. Maharachchikumbura et al. (2015) re-evaluated the classification of Sordariomycetes based on LSU, SSU, *tef*1- α and *rpb*2 sequence data. A new order, Falcocladiales, was added to Hypocreomycetidae; thus, seven orders and 30 families were accepted in this subclass (Maharachchikumbura et al. 2015). Consequently, Jones et al. (2015) introduced a new order Torpedosporales and Maharachchikumbura et al. (2016) placed Pleurotheciales in Hypocreomycetidae. Yang et al. (2016) introduced Fuscosporellales in the subclass. Hongsanan et al. (2017) and Hyde et al. (2017) showed that Conioscyphales, Fuscosporales, Pleurotheciales and Savoryellales formed a monophyletic clade, sister to Hypocreomycetidae. Therefore, these four orders were transferred to a newly introduced subclass Savoryellomycetidae. This was confirmed by Dayarathne et al. (2019) based on phylogenetic analysis and divergent time estimates. In addition, Parasympodiellales was assigned in *Hypocreomycetidae* and *Melanosporales* was placed under Coronophorales (Hernández-Restrepo et al. 2017; Hongsanan et al. 2017). Seven orders Coronophorales, Falcocladiales, Glomerellales, Hypocreales, Parasympodiellales, Torpedosporales and Microascales were accepted in Hypocreomycetidae based on both phylogenetic analysis and divergence time estimates (Hongsanan et al. 2017; Hyde et al. 2017, 2020a; Hernández-Restrepo et al. 2017). The recent treatment of *Hypocreomycetidae* was provided by Wijayawardene et al. (2022), who accepted eight orders (including Cancellidiales) and 38 families. Xiao et al. (2023) introduced a new family Polycephalomycetaceae in Hypocreales. Eight orders and 39 families are currently accepted in the Hypocreomycetidae (Wijayawardene et al. 2022). However, few orders and families remain polyphyletic; thus, this subclass needs to be revised (Hyde et al. 2020a; Huang et al. 2021).

The evolution study of *Hypocreomycetidae* is mainly focused on *Halosphaeriaceae* as this family comprises most

marine species with a few species from freshwater and terrestrial habitats (Sakayaroj et al. 2011; Jones et al. 2017, 2019). Several studies have discussed the evolution of morphological characters and the origin of *Halosphaeriaceae* (Sakayaroj et al. 2011; Jones et al. 2017, 2019). However, there is no specific studies on the evolution of *Hypocreomycetidae* especially for freshwater fungi.

Several studies have recommended the multiple origins of freshwater fungi and the evolution of freshwater ascomycetes from terrestrial habitats (Shearer 1993; Vijaykrishna et al. 2006; Hyde et al. 2021). Belliveau et al. (2005) investigated the evolution of aquatic hyphomycetes based on molecular data and their results demonstrated multiple origins of aquatic hyphomycetes. However, their study did not obtain any firm conclusions concerning their ancestors. It stated that the sexual and asexual morphs have concurrent adaptations to freshwater habitats as several sexual morphs of freshwater hyphomycetes have been reported on tree branches decaying in the water. However, the evolution of aquatic hyphomycetes, either terrestrial asexual or sexual morphs, is undetermined, and this needs further studies based on molecular and morphological data (Webster and Descals 1979; Webster 1992). Vijaykrishna et al. (2006) initially investigated the origin of freshwater ascomycetes based on the molecular clock, and their results stated that freshwater ascomycetes originated from terrestrial fungi with multiple and independent evolution. Freshwater ascomycetes have unique adaptations to survive in freshwater habitats; an example is the freshwater ascomycetes decompose lignocellulose in woody litter, softening the wood, which is thought to be a better adaptation for degrading wood in water-logged conditions. Another example is the unique morphological characters of freshwater ascomycetes, such as the asci with massive apical rings which help eject ascospores into the air and underwater to dispersal in freshwater. The appendages of ascospores can help the species to attached to the substrates in the running water (Ho and Hyde 2000; Hyde and Goh 2003; Vijaykrishna et al. 2006). However, these adaptions have also been found in terrestrial fungi, indicating that freshwater ascomycetes share a common ancestor with terrestrial ascomycetes (Shearer et al. 2009). Recently, Hyde et al. (2021) investigated the evolution of freshwater Diaporthomycetidae based on phylogenetic analysis and divergence time estimates; their result indicated that freshwater Diaporthomycetidae have evolved from terrestrial fungi and has evolved on several occasions.

Studies concluded that the fungi originated from aquatic habitats and then migrated to terrestrial habitats (Vijaykrishna et al. 2006; Beakes and Sekimoto 2009; Beakes et al. 2012; Jones et al. 2014). Vijaykrishna et al. (2006) made a conclusion based on the previous studies (e.g. Shearer 1993; Wong et al. 1998; Hyde and Wong 2000; Cai et al. 2003) that fungi may occur as pathogens, saprobes or endophytes on plants, then become adapted to the aquatic environment, when these plants invaded water. Some studies stated that fungi originated from the sea and then migrated to terrestrial habitats (Beakes and Sekimoto 2009; Jones et al. 2011, 2014). There is still controversial, and it would be interesting if further studies could focus on this. Hypocreomycetidae is widely distributed worldwide and has been reported in freshwater, terrestrial and marine environments. One-hundred and fifty-six Hypocreomycetidae species have been reported from freshwater habitats and are distributed in five orders viz. Coronophorales, Glomerellales, Hypocreales, Microascales and Torpedosporales (Calabon et al. 2021, 2022). Thus, studying the evolution of Hypocreomycetidae is important for understanding the possible transition and evolution of aquatic and terrestrial ascomycetes.

In this study, we aim to (1) investigate freshwater fungi in *Hypocreomycetidae* with fresh collections based on morphological and multi-gene phylogenetic analyses; (2) establish the divergence time of orders and families in *Hypocreomycetidae* based on molecular clock analyses and (3) explore the evolution of *Hypocreomycetidae* based on ancestral state analysis.

Materials and methods

Isolation and morphological examination

Samples (submerged woods) were collected from freshwater habitats (lakes and streams) in China and Thailand. The samples were brought to the laboratory in plastic bags. Sample incubation, observation and morphological studies were done following the methods outlined by Luo et al. (2018). Fungal species were isolated using single spore isolation following the method described in Senanayake et al. (2020). Germinating ascospores and conidia were transferred to fresh potato dextrose agar (PDA) media and incubated at room temperature for 2-4 weeks, and cultures were grown for 1-2 months. The cultures obtained from Thailand are deposited at the Mae Fah Luang University Culture Collection (MFLUCC) and the cultures obtained from China are deposited at the Kunming Institute of Botany Culture Collection (KUNCC). Herbarium specimens from China and Thailand were prepared following the methods provided by Luo et al. (2018), and the herbariums were deposited at Mae Fah Luang University (MFLU) and Herbarium of Cryptogams Kunming Institute of Botany Academia Sinica (Herb. KUN-HKAS) respectively. Facesoffungi and Index Fungorum numbers are registered as outlined in Jayasiri et al. (2015) and Index Fungorum (2023). The descriptions of the species are added to GMS database (Chaiwan et al. 2021).

DNA extraction, PCR amplification and sequencing

Genomic DNA was extracted from fungal mycelium or directly from the ascomatal tissue thalli of fungi as outlined by Wanasinghe et al. (2018). EZ gene[™] Fungal gDNA Kit (GD2416) was used to extract genomic DNA following the manufacturer's instructions. The primers are summarized in Table 1. The amplification reactions were performed in 25 µL of PCR mixtures containing 12.5 µL of 2×Power Taq PCR Master Mix (a premix and ready-to-use solution, including 0.1 Units/µL Taq DNA Polymerase, 500 µm dNTP Mixture each (dATP, dCTP, dGTP, dTTP), 20 mM Tris-HCl pH 8.3, 100 Mm KCl, 3 mM MgCl₂, stabilizer and enhancer), 1 µL of each primer, 1 µL DNA template and 9.5 µL nuclease-free water. PCR amplification was confirmed on 1% agarose electrophoresis gels stained with ethidium bromide. Purification and sequencing of PCR products were carried out using the above-mentioned PCR primers at Kunming Tsingke Biological Engineering Technology and Services Co., Ltd. (Kunming, P.R. China).

Sequence alignment and phylogenetic analyses

Sequences featuring a high degree of similarity were determined from a BLAST search for each gene to identify the closest matches with taxa in *Sordariomycetes*. The sequences were assembled using BioEdit and aligned with MAFFT v.7 online program (http://mafft.cbrc.jp/alignment/server/) (Katoh and Standleym 2013; Katoh et al. 2019) and final improvements were made when necessary, using BioEdit v7.2.3 (Hall 1999).

Maximum likelihood (ML) analysis was performed using RAxML-HPC v.8 (Stamatakis 2006; Stamatakis et al. 2008) on the XSEDE Teragrid of the CIPRES Science Gateway online flatform (Miller et al. 2010) with rapid bootstrap analysis, followed by 1000 bootstrap replicates. The final tree was selected amongst suboptimal trees from each run by comparing likelihood scores under the GTRGAMMA substitution model.

MP bootstrap analyses were performed with PAUP v4.0b10 (Swofford 2002). The analysis was performed using the heuristic search option with 1000 random taxa addition and tree bisection and reconnection (TBR) as the branch-swapping algorithm. All characters were unordered and of equal weight, and gaps were treated as missing data. Maxtrees were unlimited, branches of zero length were collapsed and all multiple, equally parsimonious trees were saved. Clade stability was assessed using a bootstrap (BT) analysis with 1000 replicates, each with 10 replicates of the random stepwise addition of taxa (Hillis and Bull 1993).

Bayesian analysis was performed by MrBayes v3.1.2 (Ronquist et al. 2012). The model of evolution was estimated by MrModeltest 2.2 (Nylander 2004). Posterior probabilities Table 1Information on loci andprimers used in this study

Loci	PCR primers (for- ward/reverse)	Sequences of primers	References	
acl1	acl1-230up	AGCCCGATCAGCTCATCAAG	Gräfenhan et al. (2011)	
	acl1-1220low	CCTGGCAGCAAGATCVAGGAGT		
act	ACT-512F	ATGTGCAAGGCCGGTTTCGC	Carbone and Kohn (1999)	
	ACT-783R	TACGAGTCCTTCTGGCCCAT		
cmd	CAL-228F	GAGTTCAAGGAGGCCTTCTCCC	Carbone and Kohn (1999)	
	CAL-737R	CATCTTTCTGGCCATCATGG		
his3	CYLH3F	AGGTCCACTGGTGGCAAG	Crous et al. (2004)	
	CYLH3R	AGCTGGATGTCCTTGGACTG		
ITS	ITS5	GGAAGTAAAAGTCGTAACAAGG	White et al. (1990)	
	ITS4	TCCTCCGCTTATTGATATGC		
LSU	LROR	ACCCG TGAACTTAAGC	Vilgalys and Hester (1990)	
	LR5	TCCTGAGGGAAACTTCG		
rpb1	Fa	CAYAARGARTCYATGATGGGWC ^d	O'Donnell et al. (2010)	
	G2R	GTCATYTGDGTDGCDGGYTCDCC		
rpb2	fRPB2-5f	GAYGAYMGWGATCAYTTYGG	Liu et al. (1999)	
	fRPB2-7cR	CCCATRGCTTGYTTRCCCAT		
SSU	NS1	GTAGTCATATGCTTGTCTC	White et al. (1990)	
	NS4	CTTCCGTCAATTCCTTTAAG		
<i>tef</i> 1-α	EF-1	ATGGGTAAGGARGACAAGAC	O'Donnell et al. (2010)	
	EF-2	GGARGTACCAGTSATCATG		
tub2	T1	AACATGCGTGAGATTGTAAGT	O'Donnell and Cigelnik (1997)	
	Bt2b	ACCCTCAGTGTAGTGACCCTTGGC	Glass and Donaldson (1995)	

(Rannala and Yang 1996) were performed by Markov Chain Monte Carlo Sampling (MCMC) in MrBayes v. 3.1.2. Six simultaneous Markov Chains were run for 1 billion generations, and trees were sampled every 1000 generation (resulting in 100,000 trees). The first 20,000 trees representing the burn-in phase of the analyses were discarded and the remaining 80,000 (post-burning) trees used for calculating posterior probabilities (PP) in the majority rule consensus tree.

Several recent studies have discussed the criteria to define a species (Boekhout et al. 2021; Chethana et al. 2021; Maharachchikumbura et al. 2021; Voigt et al. 2021). Maharachchikumbura et al. (2021) detailed the integrative approaches including morphological species concept (MSC), biological species concept (BSC), and Evolutionary/phylogenetic species concept (PSC) with chemotaxonomy and divergence time estimation for species delimitation in *Ascomycota*. In this study, the new species and families were established based on morphological characters, phylogenetic analysis and divergence time estimates. In addition, we also performed base pair comparison for the newly described taxa following Jeewon and Hyde (2016).

Calibration, divergence time and evolutionary rate estimations

This study used one secondary and a fossil calibration for the divergence time estimates. *Paleoophiocordyceps coccophagus*, a fossil of *Hypocreales*, which is similar to the asexual morph of *Hirsutella* and *Hymenostilbe* (Sung et al. 2007) that are synonyms of *Ophiocordyceps* (*Ophiocordycipitaceae*, *Hypocreales*; Quandt et al. 2014) was used to calibrate the *Ophiocordyceps* crown, using an exponential distribution (offset = 100, mean = 27.5, with 97.5% CI of 200 MYA) (Sung et al. 2008; Samarakoon et al. 2016). The crown age of *Sordariomycetes* with a normal distribution (mean = 250, SD = 40, with 97.5% CI = 338 MYA) was selected as a secondary calibration point (Hyde et al. 2017).

Divergence time estimates were carried out by BEAST v 1.8.4 (Drummond et al. 2012). Aligned sequence data were partitioned separately for LSU, ITS, SSU, *rpb2* and *tef*1- α dataset, and loaded to prepare an XML file constructed in BEAUti v1.8.0. The substitution models were selected based on jModeltest2.1.1; GTR + I + G for ITS

and LSU, TIM3+I+G for SSU, TrN+I+G for $tef1-\alpha$ and TIM2 + I + G for *rpb2*. However, the models TIM2, TIM3 and TrN were unavailable in BEAUti 1.8.4; thus, TN93 was selected by setting the "All Equal" for the base frequencies. An uncorrelated relaxed clock model (Drummond and Rambaut 2007) with a lognormal distribution of rates for each gene estimate was used for the analyses. We used a Yule tree prior, which assumes a constant speciation rate per lineage, and a randomly generated starting tree (Hyde et al. 2017). The analysis was run for 300 million generations and parameters were sampled every 30,000 generations. The effective sample sizes were checked in Tracer v.1.6 (Rambaut et al. 2013), and the acceptable values were greater than 200. Maximum clade creditability (MCC) trees were annotated using TreeAnnotator v1.8.0 and then visualized in FigTree v.1.4.2 (Rambaut 2014).

Ancestral character state analyses

Ancestral character state analysis (Thiyagaraja et al. 2020, 2021) was carried out to reconstruct the evolutionary relationship of habitual changes in *Hypocrealmycetidae*. The following states were established: freshwater, marine and terrestrial fungi. The platform Reconstruct Ancestral State in Phylogenies (RASP 3.2.1) was used to construct ancestral character analysis, using the Bayesian Binary MCMC based on the divergence time estimate tree (Yu et al. 2015, 2019). This approach was performed and visualized in RASP 3.2.1 using settings: 10 chains, a sampling frequency of 100, a temperature of 0.1, state frequencies fixed (JC), and among-site rate variation equal. The trees were edited using Microsoft PowerPoint 2013 and converted to jpeg files using Adobe Photoshop CS6 Extended 10.0 (Adobe Systems. U.S.A.).

Results

Phylogenetic analysis

The multi-gene dataset (LSU, ITS, SSU, rpb2 and $tef1-\alpha$) was used to reveal the relationships of orders and families in *Hypocreomycetidae* (Fig. 1). The alignment comprised 527 taxa from six subclasses (*Diaporthomycetidae*, *Hypocreomycetidae*, *Lulworthiomycetidae*, *Savoryellomycetidae*, *Sordariomycetidae* and *Xylariomycetidae*) of *Sordariomycetes* with four *Dothideomycetes* taxa as outgroup. The dataset comprised 4577 characters including gaps (LSU: 902 bp, ITS: 639 bp, SSU: 1010 bp, rpb2: 1072 bp, $tef1-\alpha$: 954 bp). The statistical analyses resulted in largely the same topology with high support for most branches in the ML and BI analyses and with similar overall topologies of order and family level relationships in agreement with previous work based

on ML and BI analyses (Hongsanan et al. 2017; Hyde et al. 2020a). Therefore, the best scoring RAxML tree is shown in Fig. 1, with a likelihood value of -189,870.011043.

The present phylogenetic analysis comprises 41 families including three new families (Ascocodinaceae, Campylosporaceae and Cornuvesicaceae). Most freshwater taxa in Hypocreomycetidae are included in the phylogenetic analysis except those species which lack sequence data in GenBank. Phylogenetic analysis showed that freshwater taxa are distributed in 10 families viz. Bionectriaceae, Campylosporaceae, Halosphaeriaceae, Juncigenaceae, Microascaceae, Nectriaceae, Reticulascaceae, Sarocladiaceae, Stachybotryaceae and Triadelphiaceae (Fig. 1). Our fresh collections clustered within two orders (Hypocreales and Microascales) and six families (Nectriaceae, Bionectriaceae, Stachybotryaceae, Sarocladiaceae, Halosphaeriaceae and Microascaceae) which represent 26 species including10 new species, 13 new records and 3 new collections. The acquired phylogenetic results are discussed where applicable in the notes below.

Molecular clock analysis

In recent years, divergence time estimates have been used in fungal taxonomic studies, especially in ranking higher taxa. Hyde et al. (2017) and Liu et al. (2017a) have recommended the range to recognize subclasses, orders, and families in the classes *Sordariomycetes* and *Dothideomycetes*. In *Sordariomycetes*, the stem ages of orders and families are recommended within 150–250 MYA and 50–150 MYA, respectively. According to the divergence time estimates (Fig. 2), the crown and stem ages of *Sordariomycetes* are 302 MYA and 323 MYA (Fig. 2), which are quite similar to Hyde et al. (2020a). The crown and stem ages of *Hypocreomycetidae* are 290 MYA and 302 MYA, respectively. The stem ages of all the orders in this subclass are listed in Table 2, including a new order *Xenodactylariales*. The phylogenetic analysis and divergence time estimates support all orders.

The stem ages of the orders are compared with previous studies (Hyde et al. 2017, 2020a). In our study, the stem ages of *Falcocladiales*, *Glomerellales*, *Hypocreales* and *Microascales* are similar to the previous studies (Table 2). However, the divergence time of *Coronophorales* and *Torpedosporales* are older than Hyde et al. (2017, 2020a) (Table. 1). The different fossils, models and substitution rate variation can cause different results of divergence times (Beimforde et al. 2014). Our study uses one fossil data (*Paleoophiocordyceps coccophagus* and a secondary calibration (crown age of *Sordariomycetes*). In contrast, Hyde et al. (2017) used one fossil datum (*Paleoophiocordyceps coccophagus*) and two secondary calibrations (the divergence time of *Sordariomycetes*) and Hyde et al.



Fig.1 Phylogenetic tree based on RAxML analyses of combined LSU, SSU, ITS, *tef*1- α and *rpb*2 sequence data. Maximum likelihood boot-strap \geq 75% (MLBS) and Bayesian posterior probabilities \geq 0.95 (PP) are indicated at the nodes. The freshwater species are in red and newly

obtained strains are in bold. The tree is rooted with Aureobasidium microstictum, Dothidea insculpta, D. sambuci and Pseudoseptoria collariana



Fig. 1 (continued)

(2020a) used two secondary calibrations (crown ages of *Sordariomycetes* and *Dothideomycetes*). In addition, Hyde et al. (2017) mentioned that the taxon sampling and number of base pair differences between fungal groups could affect the crown node age, and the crown node age can become older by including more taxa in the data set. Our analysis is focused on the subclass *Hypocreomycetidae* and the taxa were mostly selected from *Hypocreomycetidae*. In comparison, Hyde et al. (2017, 2020a) focused on the class *Sordariomycetes*. Thus, the divergence time of *Coronophorales* and *Torpedosporales* were different from that of Hyde et al. (2017, 2020a).

Ancestral character analysis

Savoryellomycetidae, Diaporthomycetidae, Sordariomycetidae, Lulworthiomycetidae and Xylariomycetidae show a terrestrial ancestor. Hypocreomycetidae also shares terrestrial as the common ancestor, whereas marine and freshwater taxa have independently evolved. Within the Hypocreales clade, the Stachybotryaceae clade comprised mostly freshwater taxa and clustered together with mostly terrestrial Incertae sedis species with terrestrial ancestor. Gliomastix represents marine, terrestrial and newly sequenced freshwater fungi which were recovered in the Bionectriaceae clade with several terrestrial and marine fungal genera. Clonostachys



Fig. 1 (continued)



Fig. 1 (continued)

and its sexual genus *Bionectria* mainly comprised terrestrial fungi except for two newly sequenced species which were reported from freshwater habitats. All these genera represent *Bionectriaceae* which formed a sister clade to the mostly marine fungal genera *Emericellopsis* with a marine ancestor which had high support. *Calcarisporiaceae*, *Clavicipitaceae*, *Cocoonihabitaceae*, *Cordycipitaceae*, *Flammocladiellaceae*, *Hypocreaceae*, *Niessliaceae*, *Ophiocordycipitaceae* and *Polycephalomycetaceae* show terrestrial ancestor and marine and freshwater taxa show independent evolution. The *Myrotheciomycetaceae* clade mostly comprises terrestrial fungi with terrestrial ancestors.

Cai et al. (2010) reported the first freshwater *Marian-naea* species and expected a large discovery of freshwater taxa (Cai et al. 2010; Hu et al. 2017). *Mariannaea humicola*

and *Mariannaea punicea* were recorded from soil (Lombard et al. 2015; Hu et al. 2017), while all other species, including our newly sequenced strains reported from freshwater habitats. *Thelonectria* are mostly saprobes in terrestrial habitats (Salgado-Salazar et al. 2016), while *T. discophora* (=*Nectria discophora*) was reported from aquatic (Shearer and Webster 1991) and terrestrial habitats (Zeng and Zhuang 2013). Our newly sequenced strains clustered together with terrestrial species of *Thelonectria* with freshwater ancestor and the node was not statistically supported. Throughout the *Nectriaceae* clade, several genera such as *Acremonium, Atractium, Fusicolla, Rodentomyces* and *Sedecimiella* comprised freshwater, marine or terrestrial species, while several clades represent all three habitats such as *Chaetopsina, Cosmospora, Neocosmospora* and *Volutella*. The basal clade of *Nectriaceae* are mostly





Fig. 1 (continued)

marine habitats which also shows terrestrial ancestor, and the freshwater and terrestrial habitats show independent evolution. The *Ophiocordycipitaceae* clade mainly comprised terrestrial fungi and several *Tolypocladium* species reported from marine habitats which together formed a clade with exclusively terrestrial *Niessliaceae* clade. *Clavicipitaceae* to *Hypocreaceae* clades comprised marine and terrestrial taxa with the ancestor of a terrestrial habitat. *Halosphaeriaceae*, one of the most prominent marine ascomycetous families, assigned within *Microascales* has a marine ancestor (Raghukumar 2017), which was also confirmed in our study.

Taxonomy

Sordariomycetes, Hypocreomycetidae

The recent treatment of *Hypocreomycetidae* was provided by Hyde et al. (2020a) and Wijayawardene et al. (2022), and are followed in the present study. We provided an updated phylogenetic tree for *Hypocreomycetidae* which includes 41 families and seven orders. Based on phylogenetic analysis and divergence time estimates, a new order (*Xenodactylariales*) and three new families (*Ascocodinaceae*,



Fig. 2 Ancestral character state reconstruction of terrestrial, freshwater and marine habitats in *Hypocreomycetidae* and maximum clade credibility (MCC) tree with divergence time estimates for *Hypocreomycetidae*. Multistate coding datasets analyzed with Bayesian Binary MCMC

approaches. Pie charts at terminals show the representative character and the internal nodes represent the marginal probabilities for each alternative ancestral area. The divergence time are shown at the nodes (MYA)



Fig. 2 (continued)



Fig. 2 (continued)



Fig. 2 (continued)



Fig. 2 (continued)

 Table 2
 Divergence times (MYA) of the orders in Hypocreomycetidae

Order	This study (Stem age)	Hyde et al. (2017)	Hyde et al. (2020a)
Coronophorales	246	196	196
Falcocladiales	193	196	196
Glomerellales	274	256	215
Hypocreales	274	231	229
Microascales	217	242	215
Torpedosporales	211	165	185
Xenodactylariales	211	-	-

Campylosporaceae, and *Cornuvesicaceae*) are introduced. Furthermore, the placements of several orders, families and genera are discussed and revised based on phylogenetic analysis. *Emericellopsis* and *Pseudoacremonium* are transferred to *Hypocreales* genera *incertae sedis* and *Bionectriaceae*, respectively; *Sedecimiella* is placed in *Nectriaceae*; *Nautosphaeria* and *Tubakiella* are excluded from *Halosphaeriaceae* and placed in *Microascales* genera *incertae sedis*; *Varicosporella* is placed under *Atractium* with synonymy of *A. aquatica* instead of *V. aquatica. Faurelina* is excluded from *Hypocreomycetidae*.

In this study, 41 fresh collections were made from freshwater habitats. Based on phylogenetic analysis and morphological characters, ten new species are introduced, and 13 new habitats and geographic records and 3 new collections are reported. Detailed descriptions and illustrations are provided.

Glomerellales Chadef. ex Réblová, W. Gams & Seifert, Stud. Mycol. 68: 170 (2011).

Glomerellales was established by Réblová et al. (2011) with three families viz. *Australiascaceae*, *Glomerellaceae* and *Reticulascaceae* based on multi-locus phylogenetic analysis. Two additional families *Plectosphaerellaceae* and *Malaysiascaceae* were subsequently added to this order by Maharachchikumbura et al. (2016) and Tibpromma et al. (2018). Currently, five families are accepted in *Glomerellales* (Hyde et al. 2020a). Members of *Glomerellales* have been reported as endophytes, pathogens, and saprobes from both terrestrial and aquatic habitats (Harter 1916; Rong and Gams 2000; Marsault and Peterson 2017; Cannon et al. 2012a; Jayawardena et al. 2020a). Freshwater species of the order are distributed in three genera (*Bertia, Cylindrotrichum* and *Kylindria*) in *Reticulascaceae* (Luo et al. 2019).

In our phylogenetic analysis, *Glomerellales* formed a monophyletic clade basal to *Hypocreomycetidae*; *Plectosphaerellaceae* is basal to *Glomerellales*; *Australiascaceae*, *Glomerellaceae* and *Malaysiascaceae* clustered together as a monophyletic clade and sister to *Reticulascaceae* (Fig. 1) with the stem ages of *Australiascaceae* (48 MYA), *Malaysiascaceae* (35 MYA), and *Glomerellaceae* (35 MYA) which fall within the genus status (Fig. 2). Hyde et al. (2021) mentioned the revision of *Malaysiascaceae* as the stem age of this family accord within genus level and our analysis also agree with Hyde et al. (2020a). Thus, the status of these three families may need further study. In addition, the genus *Ascocodinaea* formed a distinct lineage within *Glomerellales* (Fig. 1), and the divergence time estimates showed that the stem age of *Ascocodinaea* (96.8 MYA, Fig. 2) falls within the family level.

Ascocodinaceae D.F. Bao, K.D. Hyde & Z.L. Luo, *fam. nov.* Index Fungorum number: IF 900276; Facesoffungi number: FoF 13919.

Etymology: Named after the type genus, Ascocodinaea.

Type genus: Ascocodina C.D. Viljoen, M.J. Wingf. & K. Jacobs.

Fungicolous. Sterile setae and conidiophores abundant, arising from the host surface among perithecia. Sexual morph: Perithecia forming directly on the hymenial surface, gregarious, superficial to semi-immersed, gray to black, translucent brown in 3% KOH, ovoidal, with an acute apex, collapsing deeply by lateral pinching when dry, with stiff, erect, acute, unbranched, septate, black setae arising as modified cells of the surface of the upper half of the perithecium, thick-walled. Perithecial wall translucent brown by transmitted light, thin-walled cells of textura epidermoidea at the surface. perithecial apex formed of cells enlarged and arranged in files. Ostiolar canal periphysate; periphyses continuous with the paraphyses. Paraphyses abundant among, and overreaching, mature asci, infrequently branched, septate, slightly enlarged at the tip. Asci cylindrical, 8-spored; apex with a thin ring pierced by a pore. Ascospores uniseriate with overlapping ends, ellipsoidal to fusiform, slightly curved, multi-septate, central cells translucent brown and end cells hyaline, smooth-walled. Asexual morph: Conidiophores macronematous, mononematous, stiff, erect, unbranched, black, morphologically indistinguishable from the sterile setae, each bearing a single, terminal, integrated conidiogenous cell. Conidiogenous cells monophialidic, enteroblastic, proliferating percurrently or sympodially; tip not flared, with slight periclinal thickening at the conidiogenous locus. Conidia broadly ellipsoidal, cylindrical, or inequilateral, often slightly curved, 0-1-septate, hyaline, lacking a visible basal abscission scar, smooth-walled, held in a drop of hyaline slime at the tip of each conidiophore (Samuels et al. 1997).

Notes: Ascocodinaea was introduced by Samuels et al. (1997) to accommodate two fungicolous species, *Ascoco-dinaea polyporicola* and *A. stereicola* (type). Previously, the placement of *Ascocodinaea* was not well-resolved. *Ascocodinaea* was originally placed in *Lasiosphaeriaceae* (*Sordariales*), based on similar morphological characters

with Lasiosphaeriaceae, such as the dark, setose, pseudoparenchymatic ascomata and dematiaceous phialidic asexual morphs (Samuels et al. 1997). Réblová et al. (1999) transferred Ascocodinaea to Chaetosphaeriaceae based on characters of asci, ascospores and perithecial and the dictyochaeta-like asexual morph. Huhndorf et al. (2004) provided a phylogenetic analysis for Sordariales based on LSU sequence data and the result showed that the placement of Ascocodinaea is far from Lasiosphaeriaceae and had close affinities to Glomerella (Collectotrichum). Thus, Ascocodinaea was excluded from Lasiosphaeriaceae and treated as genus incertae sedis in Hypocreomycetidae (Lumbsch and Huhndorf 2007; Wijayawardene et al. 2012). Maharachchikumbura et al. (2015) placed Ascocodinaea in Glomerellales genera incertae sedis, which was accepted by later studies (Maharachchikumbura et al. 2016; Wijayawardene et al. 2017; Hyde et al. 2020a).

Only LSU sequence is available for *A. stereicola*; in our LSU phylogenetic analysis *Ascocodinaea stereicola* clustered as a distinct clade and sister to *Plectosphaerellacea*. In our multi-locus phylogenetic analysis, *Ascocodinaea stereicola* formed a distinct lineage within *Glomerellales* (Fig. 1). Currently, only *A. polyporicola* and *A. stereicola* are accepted to the genus, and sequence data of *A. polyporicola* were not available in the GenBank. However, *A. polyporicola* differs from *A. stereicola* in having larger ascospores, conidia and conidiophores, finer and much more intricately branched paraphyses (Samuels et al. 1997).

Morphologically, Ascocodinaea differs from Australiascaceae in having uniseriate ascospores with translucent brown central cells and hyaline end cells and broadly ellipsoidal, cylindrical, or inequilateral, 0-1-septate conidia. While, ascospores of Australiascaceae are biseriate, hyaline and conidia are ellipsoid to cylindrical-ellipsoidal, septate, aggregated in slime or in chains. Ascocodinaea can be easily distinguished from *Glomerellaceae* by the uniseriate, multi-septate, ascospores with translucent brown central cells and hyaline end cells. However, ascospores of Glomerellaceae are uni- to biseriate, hyaline and aseptate, in addition, conidia of Glomerellaceae sometimes have a filiform appendage, the base is rounded to truncate, sometimes with a prominent hilum, a character were not found in Ascocodinaea (Maharachchikumbura et al. 2016; Hyde et al. 2020a). Ascocodinaea differs from Reticulascaceae in having unbranched conidiophores and broadly ellipsoidal or inequilateral, 0-1-septate conidia, whereases, conidiophores of Reticulascaceae are branched or unbranched and conidia are pyriform to cylindrical, 1- or multi-septate. In addition, conidiogenous cells of Ascocodinaea have proliferating percurrent growth; this was not observed in Reticulascaceae (Réblová et al. 2011). Malaysiascaceae differs from Australiascaceae in having bi-seriate, hyaline ascospores that become 1-septate and pale brown after discharge. *Ascocodinaea* is different from *Plectosphaerellaceae* in having asci with a thin ring pierced by a pore and uniseriate with overlapping ends ascospores with translucent brown central cells and hyaline end cells. However, the asci of *Plectosphaerellaceae* lack an apical ring, and ascospores are irregularly arranged, hyaline or pale brown (Maharachchikumbura et al. 2016; Giraldo and Crous 2019).

Divergence time estimates showed that the stem age of *Ascocodinaea* is around 96.8 MYA which falls within the family range (Hyde et al. 2017). Therefore, a new family *Ascocodinaceae* is introduced to accommodate *Ascocodinaea* based on morphological and phylogenetic analyses and divergence time estimates.

Hypocreales Lindau, in Engler & Prantl, Nat. Pflanzenfam., Teil. I (Leipzig) 1(1): 343 (1897).

The most recent treatment of Hypocreales was provided by Hyde et al. (2020a) and Wijayawardene et al. (2022). Hyde et al. (2020a) listed 14 families under Hypocreales, while, Wijayawardene et al. (2022) accepted 15 families in the order where Cylindriaceae was additionally added. Earlier, Hyde et al. (2020a) placed Cylindriaceae in Xylariomycetidae. This was later confirmed by the analysis of Samarakoon et al. (2022). Hence, Cylindriaceae should be excluded from Hypocreales and placed in Xylariomycetidae. Xiao et al. (2023) recently introduced a new family *Polycepha*lomycetaceae to Hypocreales. Perera et al. (2023) provided an updated phylogenetic analysis of combined gene analysis of ITS, LSU, *rpb2*, *tef1-\alpha* and *tub2* for *Hypocreales* and accepted 17 families including three new families (Ijuhyaceae, Stromatonectriaceae and Xanthonectriaceae). Based on our phylogenetic analysis, the placements of a few genera, such as, Emericellopsis, Pseudoacremonium and Sedecimiella need further revisions. In our study, Pseudoacremonium and Sedecimiella are transferred to Bionectriaceae and Nectriaceae, respectively. Emericellopsis was excluded from Myrotheciomycetaceae and placed in Hypocreales genera incertae sedis. In our fresh collections, 39 freshwater strains were placed in Bionectriaceae, Nectriaceae, Sarocladiaceae and Stachybotryaceae within Hypocreales.

Bionectriaceae Samuels & Rossman, Stud. Mycol. 42: 15 (1999).

Bionectriaceae was introduced by Rossman et al. (1999) to accommodate 26 genera. The classification of *Bionectriaceae* has been revised and refined by several studies based on phylogenetic analyses (Rossman et al. 2001; Maharach-chikumbura et al. 2015, 2016; Wijayawardene et al. 2018). The recent treatment of *Bionectriaceae* was provided by Wijayawardene et al. (2022) with the acceptance of 47 genera. In our phylogenetic analyses, *Bionectriaceae* clustered with *Tilachlidiaceae*. *Tilachlidiaceae* was introduced by Lombard et al. (2015) and three genera *Psychronectria*,

Septofusidium and Tilachlidium, are accepted in the family. Our phylogenetic analysis suggests that Tilachlidiaceae may need to be revised and placed under Bionectriaceae (Fig. 1). In addition, our phylogenetic analysis showed that two Septofusidium species (S. berolinense and S. herbarum) and Pseudoacremonium sacchari clustered within Bionectriaceae (Fig. 1). Septofusidium was previously placed within Tilachlidiaceae (Lombard et al. 2015; Hyde et al. 2020a), recently, Perera et al. (2023) transferred it to Bionectriaceae based on phylogenetic analysis. However, the taxonomy of Septofusidium needs further studies, as Septofusidium is polyphyletic (Perera et al. 2023) and the type species lacks sequence data. Pseudoacremonium was placed in Hypocreales genera incertae sedis (Crous et al. 2014; Hyde et al. 2020a). Based on our phylogenetic analysis, Pseudoacremonium is transferred to Bionectriaceae.

In addition, our three fresh collections made from freshwater habitats and the phylogenetic analysis placed them in *Clonostachys* and *Gliomastix* within *Bionectriaceae*. The three fresh collections are identified as *Clonostachys rosea*, *Gliomastix masseei* and a new species *Clonostachys aquatica* based on phylogenetic analysis and morphological characters. *Clonostachys rosea*, and *Gliomastix masseei* were reported from freshwater habitats for the first time.

Clonostachys Corda, Pracht-Fl. Eur. Schimmelbild.: 31 (1839).

Clonostachys has a worldwide distribution and is commonly found in tropical and subtropical regions (Schroers 2001; Domsch et al. 2007). Species in the genus are saprobes, endophytes, plant pathogens and mycoparasites from various habitats including soil (Schroers 2001; Toledo et al. 2006; Zhang et al. 2008; Moreira et al. 2016). Clonostachys was linked to *Bionectria* by Rossman et al. (2013). Based on One Fungus–One Name concept, Rossman et al. (2013) synonymized Bionectria under Clonostachys by giving priority to older and frequently used name Clonostachys. The asexual morph of Clonostachys is characterized by penicillate, frequently sporodochial and, in many cases, dimorphic conidiophores (Schroers 2001). The sexual morph of Clonostachys is characterized by solitary to gregarious, subglobose or globose to ovoid, white, yellow, pale orange, tan, or brown perithecia with KOH- and LA- perithecial walls and narrowly clavate to clavate asci containing eight ascospores (Schroers 2001). There are more than 100 records of Clonostachys listed in Index Fungorum (2023), of which 65 species are commonly accepted (Rossman 2014; Lombard et al. 2015; Dao et al. 2016; Prasher and Chauhan 2017; Lechat and Fournier 2018, 2019, 2020a; Zeng and Zhuang 2022). In this study, a new species *Clonostachys aquatica* is introduced with detailed description and illustration and C. rosea was collected from freshwater habitat for the first time.

Clonostachys aquatica D.F. Bao, Z.L. Luo & K.D. Hyde *sp. nov.*

Index Fungorum number: IF 900263, Facesoffungi number: FoF 13920; Fig. 3

Etymology: Referring the fungus was collected from aquatic habitat.

Holotype: KUN-HKAS 125804.

Saprobic on submerged decaying wood. Sexual morph: Undetermined. Asexual morph: Colonies on natural substrate effuse, superficial, gregarious, velvety, white, shining. Mycelium superficial to semi-immersed, composed of hyaline, branched, smooth, septate hyphae. Conidiophores $75-105 \times 3-5 \ \mu m \ (\bar{x} = 90.2 \times 4.1 \ \mu m, n = 10)$, borne on aerial mycelium, macronematous, mononematous, penicillate, cylindrical, branched, septate, hyaline, smooth and thin-walled, bearing short branches in the upper part. Phialides 7–14×2–4 µm ($\bar{x} = 10.7 \times 3.0$ µm, n=25), in whorls of 2-4, hyaline, subulate to subcylindrical, swollen at the apex, smooth-walled. Conidia $(3-)4-5(-6) \times 2-3 \mu m$ $(\bar{x} = 4.6 \times 2.9 \ \mu m, n = 50)$, arranged in false heads on conidiogenous cells tips, solitary, ellipsoidal to obovoidal, rounded at both ends, hyaline, aseptate, smooth- and thin-walled.

Culture characteristics: Conidia germinating on PDA within 12 h. Colonies growing on PDA reaching 3 cm in 14 days at room temperature, surface effused, mycelium sparse, white.

Material examined: CHINA, Yunnan Province, on submerged decaying wood in Xingyun Lake, 12 July 2021, L.L. Li, L487 (KUN-HKAS 125804, holotype), ex-type culture, KUNCC 22–12454=CGMCC 3.24271.

GenBank numbers: ITS = OP876724, LSU = OP875077.

Notes: In our phylogenetic analysis, Clonostachys aquatica clustered sister to C. rossmaniae with 94%ML/98%MP/1.00PP support (Fig. 5). Morphologically, Clonostachys aquatica is similar to C. rossmaniae in having penicillate, branched hyaline conidiophores and one-celled, ellipsoidal to ovoidal, hyaline and similar size of conidia. However, C. aquatica is different from C. rossmaniae in having subulate to subcylindrical phialides which are swollen at the apex, while, phialides of C. rossmaniae are almost cylindrical, terminate, flask-shaped and the apex are not swollen (Schroers 2001). We also compared the base pair differences of ITS nucleotides between C. aquatica and C. rossmaniae and found 1.75% differences. Therefore, Clonostachys aquatica is introduced as a new species based on both morphological and phylogenetic analyses, as recommended by Chethana et al. (2021).

Clonostachys rosea (Link) Schroers, Samuels, Seifert & W. Gams, Mycologia 91(2): 369 (1999).

Index Fungorum number: IF 485209; Facesoffungi number: FoF 13921; Fig. 4

Saprobic on submerged decaying wood. **Sexual morph:** see Schroers et al. (1999). **Asexual morph:** Hyphomycetous. *Colonies* appearing as white patches on the host.



Conidiophores 61–100 × 3–5 µm ($\bar{x} = 80.7 \times 4.4$ µm, n = 20), arising from stroma, mononematous, monomorphic, hyaline, smooth-walled, penicillate, stipitate. *Penicilli* solitary to gregarious, not sporodochial, bi- or quater-verticillate; branches of the penicillus divergent, each branch terminating in metulae and adpressed phialides. *Phialides* 7–11×2–4 µm (\bar{x} =9.5×2.6 µm, n=15), in whorls of 2–6, narrowly flask-shaped, slightly tapering toward the apex, with visible periclinal thickening, collarettes inconspicuous, hyaline, smooth-walled. *Intercalary phialides* not observed. *Conidia* 5–6×2–3 µm (\bar{x} =5.3×2.7 µm, n=30), broadly ellipsoidal to oval, rarely minutely curved, ends broadly rounded, straight, aseptate, bi-guttulate, hilum laterally displaced, almost median or invisible, hyaline, smooth-walled.

Culture characteristics: Conidia germinating on PDA within 12 h. Colonies growing on PDA reaching 3.5 cm in 7 days at room temperature, surface effused, smooth, margin entire, initially white, becoming pale yellowish orange, reverse yellowish, orange at center.

Material examined: CHINA, Yunnan Province, on submerged decaying wood in Xihu Lake, 8 May 2021, S.P. Huang, L415 (KUN-HKAS 125782), living culture, KUNCC 22–12453.

GenBank numbers: ITS = OP876720.

Fig. 4 Clonostachys rosea (KUN-HKAS 125782) a, b Colonies on substrate. c-f Conidiophores and conidia. g-k Conidia. I Surface view of culture on PDA. m Reverse view of culture on PDA. Scale bars: $c-f=30 \mu m$, $g=20 \mu m$, $h-k=5 \mu m$



Notes: Clonostachys rosea was initially introduced as Gliocladium roseum by Bainier (1907). Schroers et al. (1999) found Clonostachys rosea quite different from other Gliocladium species in morphology, ecology, and DNA sequence data. Therefore, Gliocladium roseum was placed within Clonostachys and synonymized G. roseum under Clonostachys rosea. Clonostachys rosea has a cosmopolitan distribution and have been found in soil, insects, nematodes, win and as endophytes in different plants (Krauss et al. 2002; Verdejo-Lucas et al. 2002; Toledo et al. 2006; Mamarabadi et al. 2008; Viccini et al. 2009; Costa et al. 2012; Muvea et al. 2014; Sun et al. 2015a, b).

In our phylogenetic analysis, the new collection KUNCC 22–12453 clustered with *Clonostachys rosea* (Fig. 5). Our new isolate fits well with the description of *C. rosea* (Schroers et al. 1999). Therefore, we identified our new isolate as *C. rosea*, which has been reported from freshwater habitats for the first time.

Gliomastix Guég., Bull. Soc. mycol. Fr. 21: 240 (1905)

Gliomastix was introduced by Guéguen (1905), characterized by darkly pigmented phialoconidia. It is typified by Gliomastix murorum which was previously named as G. chartarum (Hughes 1958; Gams 1971). The placement of *Gliomastix* is controversial and debated by many authors (Gams 1971; Matsushima 1975; Domsch et al. 2007; Lechat et al. 2010; Kiyuna et al. 2011; Summerbell et al. 2011). Gams (1971) placed *Gliomastix* in a section of *Acremonium*. Matsushima (1975) placed Acremonium masseei and A. polychromum in Gliomastix and Lechat et al. (2010) linked G. fusigera with the sexual morph of Hydropisphaera bambusicola. Kiyuna et al. (2011) and Summerbell et al. (2011) revised and compiled the taxonomy of Gliomastix. Kiyuna et al. (2011) agreed with Gams's concept and accepted Gliomastix as a section of Acremonium. Furthermore, A. felinum was synonymized under Gliomastix felina and a new species A. tumulicola also was introduced. However, Summerbell et al. (2011) did not follow the Gams's concept and recognized Gliomastix as a distinct genus. Their phylogenetic analysis supported Gliomastix differs from previous morphological concepts by excluding several distantly related species e.g., Acremonium cerealis and A. inflatum. Maharachchikumbura et al. (2015) and Hyde et al. (2020a) followed the treatment of Summerbell et al. (2011) treated Gliomastix as a distinct genus in Bionectriaceae. Our

Fig. 5 Phylogenetic tree based on RAxML analyses of a combined ITS and tub2 dataset. Tree topology of the RAxML, MP and Bayesian analyses are similar. The tree is rooted to Fusarium acutatum (CBS 402.97) and Nectria cinnabarina (CBS 189.87). The combined gene analysis comprises 80 strains with 1123 characters after aligned including gaps (ITS: 497 bp, tub2: 626 bp), of which 469 were parsimonyinformative, 124 were parsimony-uninformative, and 530 characters were constant. The RAxML analysis of the combined dataset yielded the best scoring tree with a final ML optimization likelihood value of -12,821.753182. The matrix had 653 distinct alignment patterns, with 26.55% undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.211507, C = 0.281104, G = 0.249523,T = 0.257866; substitution rates AC=1.093935, AG=3.149063, AT = 1.106154, CG = 0.657912, CT = 3.704654, GT = 1.000000; gamma distribution shape parameter $\alpha = 0.311435$. Bootstrap support values for RAxML (blue) and MP (red) greater than 60% and Bayesian posterior probabilities (black) greater than 0.90 are given at each node



phylogenetic analysis also showed that *Gliomastix* formed a monophyletic clade within *Bionectriaceae* (Fig. 1), which agrees with Summerbell et al. (2011).

In this study, we collected a *Gliomastix* taxon which is identified as *G. masseei* based on both phylogenetic analysis and morphological characters. The new isolate was first time reported from freshwater habitats as well as from China.

Gliomastix masseei (Sacc.) Matsush., Icon. microfung. Matsush. lect. (Kobe): 76 (1975).

Index Fungorum number: IF 314510; Facesoffungi number: FoF 13922; Fig. 6

Saprobic on submerged decaying wood. Sexual morph: Undetermined. Asexual morph: Hyphomycetous. Colonies effuse, partly immersed, dark brown to black, velvety, hairy. Mycelium mostly immersed, partly superficial, consisting of septate, branched, smooth-walled, hyaline hyphae. Conidiophores $28-40 \times 2-3 \mu m$ ($\bar{x} = 34 \times 2.7 \mu m$, n = 20), micronematous, to semi-macronematous, cylindrical, hyaline to subhyaline, tractate and darker at the apex, Fig. 6 *Gliomastix masseei* (KUN-HKAS 125790) **a**, **b** Colonies on substrate. **c**–**f** Conidiophores and conidia. **g** Conidiophores. **h**–**n** Conidia. **o** Surface view of culture on PDA. **p** Reverse view of culture on PDA. Scale bars: **c**–**j**=10 μm, **k**–**n**=5 μm



aseptate, smooth, thin-walled. *Conidiogenous cells* polyblastic, terminal, determinate, subhyaline to pale brown, smooth. *Conidia* $6-8 \times 3-4 \mu m$ ($\bar{x} = 7.1 \times 3.5 \mu m$, n = 30), catenate, in branched chains, ellipsoid-fusiform, narrow and truncate at both ends, hyaline when young, brown to dark brown at maturity, darker at both ends, smooth, thickwalled, aseptate.

Culture characteristics: Conidia germinating on PDA within 24 h. Colonies growing on PDA reaching 5.0 cm in 7 days at room temperature, circular, with velvety to cotton, dense, greyish aerial mycelium, initially white, with light grey immersed hyphae, forming dark, grey, concentric rings.

Material examined: CHINA, Yunnan Province, on submerged decaying wood in Erhai Lake, 1 April 2021, S.P. Huang, L240 (KUN-HKAS 125790), living culture, KUNCC 22–12524.

GenBank numbers: ITS = OP876719, LSU = OP875073.

Notes: In our phylogenetic analysis, the newly obtained strain clustered with other strains of *Gliomastix masseei* (Figs. 1, 7). The morphology of our strain fits well with the description of *G. masseei* (Kiyuna et al. 2011). Thus, the new isolate is identified as *G. masseei*. *Gliomastix masseei*

has been reported from India, Italy and Japan. Our new isolate was collected from China which expands the geographical distribution of *G. masseei* (Kiyuna et al. 2011; Summerbell et al. 2011).

Septofusidium W. Gams, Cephalosporium-artige Schimmelpilze (Stuttgart): 147 (1971)

Septofusidium was introduced by Gams (1971) with S. elegantulum as the type. Currently, five species viz. Septofusidium berolinense, S. elegantulum, S. herbarum, S. stevensiae, S. variabile are included in the genus (Gams 1971; Samson 1974; Samuels 1989; Tan and Shivas 2022). The taxa have been reported as parasitic on foliicolous fungi (Gams 1971; Samson 1974; Samuels 1989). Lombard et al. (2015) initially provided phylogenetic analysis for Septofusidium and their result showed that Septofusidium berolinense and S. herbarum clustered with two strains of Tilachlidium brachiatum. They therefore introduced a new family Tilachlidiaceae to accommodate Septofusidium and Tilachlidium. However, all the families of Hypocreales were not considered in their phylogenetic analysis. Perera et al. (2023) showed that Septofusidium



Fig. 7 Phylogenetic tree based on RAxML analyses of a combined ITS and LSU dataset. Tree topology of the RAxML, MP and Bayesian analyses are similar. The tree is rooted to *Bionectria byssicola* (CBS 364.78) The combined gene analysis including 23 strains with 1526 characters after aligned including gaps (ITS: 626 bp. LSU: 900 bp), of which 151 were parsimony-informative, 82 were parsimony-uninformative and 1293 characters were constant. The RAxML analysis of the combined dataset yielded the best scoring tree with a final ML optimization likelihood value of -3922.297293.

berolinense and *S. herbarum* clustered within *Bionectriaceae*. Hence, they transferred *Septofusidium* to *Bionectriaceae* based on phylogenetic analysis. We obtained a similar result with Perera et al. (2023). However, the taxonomy of this genus needs further study, as *Septofusidium* is polyphyletic and sequence data of the type species *Septofusidium elegantulum* is lacking in GenBank.

Pseudoacremonium Crous, in Crous et al., Persoonia 32: 241 (2014)

Pseudoacremonium was introduced by Crous et al. (2014) and comprises a single species *P. sacchari* and is placed in *Hypocreales* genera *incertae sedis* (Crous et al. 2014; Hyde et al. 2020a). In our phylogenetic analysis, *P. sacchari* clustered as a sister taxon to *Septofusidium berolinense* within *Bionectriaceae* (Fig. 1). Thus, we transfer *Pseudoacremonium* to *Bionectriaceae*.

Nectriaceae Tul. & C. Tul. [as 'Nectriei'], Select. fung. carpol. (Paris) 3: 3 (1865)

Nectriaceae a highly diverse group with a worldwide distribution and it has higher diversity in warm temperate and tropical regions (Rossman et al. 1999; Rossman 2000; Chaverri et al. 2011; Schroers et al. 2011; Hyde et al. 2014; Lombard et al. 2015). Several authors have studied and

The matrix had 297 distinct alignment patterns, with 21.90% undetermined characters or gaps. Estimated base frequencies were as follows: A=0.242056, C=0.254477, G=0.285780, T=0.217687; substitution rates AC=1.319516, AG=1.218603, AT=1.905682, CG=0.505055, CT=5.019153, GT=1.000000; gamma distribution shape parameter α =0.049053. Bootstrap support values for RAxML (blue) and MP (red) greater than 75% and Bayesian posterior probabilities (black) greater than 0.95 are given at each node

revised the taxonomy of *Nectriaceae* (Petch 1938; Munk 1957; Dennis 1960; Kreisel 1969; Rossman et al. 1999; Lumbsch and Huhndorf 2010; Lombard et al. 2015; Maharachchikumbura et al. 2016). A recent treatment of Nectriaceae was provided by Wijayawardene et al. (2022), they accepted 70 genera in the family. Nectriaceae comprises mostly freshwater taxa of Hypocreomycetidae. In this study, we focused on the freshwater taxa in Nectriaceae, 25 fresh collections were made from freshwater habitats in China and Thailand. Phylogenetic analyses placed them in 11 genera (Aquanectria, Atractium, Cosmospora, Chaetopsina, Gliocladiopsis, Mariannaea, Neonectria, Neocosmospora, Paracremonium, Thelonectria and Volutella). Eight new species; Atractium fusiforme, Cosmospora cylindricospora, Mariannaea suae, M. yunnanensis, Neocosmospora aquatica, Neonectria aquatica, Thelonectria aquatica and Thelonectria cylindricospora, six new geographical and habitat records (Aquanectria penicillioides, Gliocladiopsis tenuis, Mariannaea dimorpha, Neocosmospora brevis, Paracremonium binnewijzendii and Volutella ciliata) are introduced with detailed description and illustration based on phylogenetic analysis and morphological characters.

Aquanectria L. Lombard & Crous, in Lombard, van der Merwe, Groenewald & Crous, Stud. Mycol. 80: 207 (2015)

Aquanectria was introduced by Lombard et al. (2015) to accommodate Flagellospora penicillioides (A. penicillioides) and Heliscus submersus (A. submersa) based on phylogenetic analysis. Subsequently, five additional species were introduced to Aquanectria. Currently, seven species are accepted in the genus (Gordillo and Decock 2019). Aquanectria is known to form both sexual and asexual morphs. The sexual morph is characterized by perithecial, superficial, ovate to subglobose, brown-orange to orange-red ascomata with papillate ostiolar region, 8-spored, cylindrical to clavate asci and ellipsoid to fusiform, hyaline, 1-septate ascospores; the asexual morphs of this genus are hyphomycetes that are characterized by erect, solitary, septate, hyaline, branched conidiophores with verticillate penicillus with 1-4 phialides, cylindrical, collarette phialides and filiform, curved to slightly sigmoid, aseptate to 1-septate, hyaline conidia (Lombard et al. 2015; Huang et al. 2018; Gordillo and Decock 2019).

Fig. 8 Aquanectria penicillioides (KUN-HKAS125807) **a–c** Appearance of ascomata on the host. d Section through ascoma. e, f Section of peridium in 3% KOH (arrowed in e and f, turning red dark to purple in 3% KOH). g section of peridium. h Paraphyses. i-l Asci. m Ascal apical ring. n-t Ascospores. Scale bars: $d-f = 50 \mu m$, $g = 30 \mu m$, $h - l = 20 \mu m$, g, $m - r = 10 \ \mu m$

C

25



Aquanectria species have been reported from China, Colombia, Ecuador, French Guiana, Singapore, the UK, and the USA (Lombard et al. 2015; Huang et al. 2018; Gordillo and Decock 2019). This study describes a new geographical and habitat record *Aquanectria penicillioides* based on morphological characteristics and phylogenetic evidence.

Aquanectria penicillioides (Ingold) L. Lombard & Crous, in Lombard, van der Merwe, Groenewald & Crous, Stud. Mycol. 80: 207 (2015).

Index Fungorum number: IF 810950; Facesoffungi number: FoF 05440; Fig. 8

Saprobic on submerged decaying wood. Sexual morph: Ascomata $165-220 \times 141-185 \ \mu m \ (\bar{x} = 192 \times 162.6 \ \mu m, n=8)$, perithecial, solitary or cespitose, superficial, pyriform or globose to subglobose, slightly papillate, yellow to orange, paler at the apex, KOH +, turning dark red to purple in 3% KOH. *Peridium* 22–35 µm (\bar{x} = 27.6 µm, n = 15), comprise two layers, outer layer comprises of orange *textura angularis* to *textura globulosa* cells; inner layer of hyaline to pale yellow *textura prismatica* cells. *Paraphyses* 6–13 µm (\bar{x} = 60.8 × 7.3 µm, n = 15), hyaline to subhyaline, septate, branched, smooth-walled. *Asci* 56–66 × 6–8 µm (\bar{x} = 60.8 × 7.3 µm, n = 30), unitunicate, 8-spored, cylindrical, with an apical ring. *Ascospores* 9–12 × 3–4 µm (\bar{x} = 10.6 × 3.5 µm, n = 30), 1–2-seriate, clavate to fusiform, gradually narrowing towards the ends, uniseptate, slightly constricted at septum, hyaline, guttulate, smooth-walled. **Asexual morph:** Undetermined.

Material examined: China, Yunnan Province, on submerged decaying wood in a stream, 12 May 2021, D.F. Bao, H360 (KUN-HKAS 125807).

GenBank numbers: ITS = OP876699, LSU = OP872569, tub2 = OQ025188, his3 = OQ064510, $tef1 - \alpha = OQ064517$.

Notes: Aquanectria penicillioides, the type species of Aquanectria, was originally introduced as Flagellospora



Fig. 9 Phylogenetic tree based on RAxML analyses of a combined *his3*, ITS, *tef*1- α and *tub*2 dataset. Tree topology of the RAxML, MP and Bayesian analyses are similar. The tree is rooted to *Dematiocla-dium celtidis* (CBS 115994). The combined gene analysis included 25 strains with 2269 characters after aligned including gaps (*his3*: 539 bp ITS: 548 bp, *tef*1- α : 546 bp, *tub*2: 636 bp), of which 496 were parsimony-informative, 228 were parsimony-uninformative and 1545 characters were constant. The RAxML analysis of the combined dataset yielded the best scoring tree with a final ML optimization likeli-

hood value of -10,069.552607. The matrix had 848 distinct alignment patterns, with 15.22% undetermined characters or gaps. Estimated base frequencies were as follows: A=0.220957, C=0.321481, G=0.230158, T=0.227403; substitution rates AC=1.910524, AG=3.670736, AT=1.710679, CG=0.917283, CT=6.457579, GT=1.000000; gamma distribution shape parameter α =0.221306. Bootstrap support values for RAxML (blue) and MP (red) greater than 70% and Bayesian posterior probabilities (black) greater than 0.95 are given at each node

penicillioides (Ingold 1942; Ranzoni 1956). Lombard et al. (2015) showed that *F. penicillioides* clustered with *Heliscus submersus* in a well-supported clade and sister to *Gliocladiopsis*. Therefore, a new genus *Aquanectria* was introduced to accommodate *F. penicillioides* and *H. submersus*, with the synonymization of *F. penicillioides* under *Aquanectria penicillioides* (Lombard et al. 2015).

Aquanectria penicillioides is characterized by perithecial, superficial, ovate to subglobose, brown-orange to orangered ascomata, with a papillate ostiolar region, cylindrical to clavate, 8-spored asci and ellipsoid to fusiform, hyaline, 1-septate ascospores. The new isolate fits well with the original description of *A. penicillioides* (Ranzon 1956). In our phylogenetic analysis, the new isolate KUN-HKAS 125807 clustered with *A. penicillioides* (CBS 257.54) with 100%ML /100%MP /1PP support (Fig. 9). Thus, we identified the new isolate as *A. penicillioides*. This species has been reported from freshwater habitats in the USA (Ingold 1942; Ranzoni 1956; Lombard et al. 2015). In this study, the new isolate was collected from freshwater habitat in China, it is a new record for China.

Atractium Link, Mag. Gesell. naturf. Freunde, Berlin 3(1–2): 10 (1809)

≡ Varicosporella Lechat & J. Fourn.

Sexual morphs: *Ascomata* on submerged wood, superficial, nonstromatic, obpyriform, pale orange, turing or not turning red or purple in 3% KOH, turning pale yellow in lactic acid. *Predium* composed of angular to flattened cells. *Hamathecium* composed of fugacious moniliform paraphyses. *Asci* 8-spored, cylindric-clavate with a J- flat- tened apical apparatus. *Ascospores* uniseriate, ellipsoid to fusiform, 1-septate, slightly constricted at septum, hyaline to paleyellow brown, ornamented with short sinuous ribs (Lechat and Fournier 2015). **Asexual morphs**: See Gräfenhan et al. (2011).

Notes: Atractium was established with A. stilbaster as the type species by Link (1809). Link (1825) reinterpreted the generic concept of Atractium to include the pale or colourful synnematous taxa with slimy conidial masses, usually with falcate, septate conidia. The genus was previously listed as a synonym of Fusarium (Wollenweber and Reinking 1935). However, Atractium has synnematous conidiophores which is different from *Fusarium*. Hence, Gräfenhan et al. (2011) proposed them as two distinct genera. In addition, the epitype of A. stilbaste (the type of Atractium) was designated by Gräfenhan et al. (2011), and they accepted three species (A. crissum, A. holubovae and A. stilbaster) in Atractium. Currently, 26 names of Atractium are listed in the Index Fungorum (2023), of which only three species are accepted in the genus while the placement of the other 23 species remains uncertain (Gräfenhan et al. 2011). Atractium species are commonly associated with water (Gräfenhan et al. 2011) and species in the genus have been found from Canada,

Germany, and the Philippines (Seifert 1985; Seifert et al. 1995; Sivichai et al. 2002; Fryar et al. 2004).

Atractium is only known by its asexual morphs and is characterized by synnematous conidiophores branching once or twice monochasial, 2-level verticillate, monoverticillate or irregularly biverticillate; monophialidic, hyaline, subulate conidiogenous cells and septate, clavate, obovoid or gently curved, rarely ellipsoidal, conidia with a rounded apical cell, and somewhat conical basal cell, lacking a differentiated foot, some species produce chlamydospores (Gräfenhan et al. 2011). In this study, a sexual species Varicosporella aquatica is transferred to Atractium and a new species Atractium fusiformis is introduced based on morphological and phylogenetic analyses. The morphological description of sexual morph of this genus is also provided.

Atractium aquatica (Lechat & J. Fourn) D.F. Bao, K.D. Hyde & Z.L. Luo, *comb. nov*.

 \equiv Varicosporella aquatica Lechat & J. Fourn., Ascomycete.org 7(1): 2 (2015).

Index Fungorum number: IF 900476; Facesoffungi number: FoF 13923;

Notes: Varicosporella was introduced by Lechat and Fournier (2015) with a single species *V. aquatica.* Phylogenetic analysis of Lechat and Fournier (2015) showed that *V. aquatica* grouped within *Nectriaceae* in a basal branch distant from extant genera. However, they did not include all the genera of *Nectriaceae* in their phylogenetic analysis. In our phylogenetic analysis, *V. aquatica* clustered with *Atractium* species within *Nectriaceae* (Fig. 11). Thus, we transferred *V. aquatica* to *Atractium*, and synonymized it under *A. aquatica* based on phylogenetic analysis.

Atractium aquatica is characterized by superficial, astromatic, obpyriform, orange ascomata, unitunicate cylindrical asci with a discoid refractive inamyloid apical apparatus, and ellipsoid with narrowly to broadly rounded ends, twocelled, pale brown ascospores ornamented with short sinuous ridges with fusarium-like asexual morph (Lechat and Fournier 2015). The morphology of this species fits well with Nectriaceae. Our phylogenetic analysis showed that A. aquatica clustered as a sister taxon to A. fusiformis. Atractium aquatica is similar to A. fusiformis in having pyriform, orange ascomata, uniseptate, cylindrical asci with an apical ring and two-celled, pale brown ascospores. However, A. aquatica differs from A. fusiformis in having ellipsoid with rounded ends ascospores and the ascospores wall are roughened by short, sinuous, brown, thick ribs, sometimes anastomosed. While ascospores of A. fusiformis are ellipsoid to fusiform, gradually narrowing towards the ends and ascospores walls are smooth when young, becoming verrucose with age. In addition, asci $(140-165 \times 17-20 \text{ vs.})$ $65-80 \times 7-10 \ \mu m$) and ascospores (21-24 $\times 8.5-10 \ (-11) \ vs.$ $10-14 \times 5-6 \ \mu\text{m}$) of A. aquatica are comparatively larger than those of A. fusiformis.

Fig. 10 Atractium fusiformis (KUN-HKAS 125815, holotype) **a**-**b** Appearance of ascomata on the host. **c** Vertical section of ascoma. **d** Section of peridium in 3% KOH. **e** Peridium. **f** Paraphyses. **g**-**k** Asci. **l** Apical ring of ascus. **m**, **o**-**t** Ascospores. **n** Germinating ascopore. **u** Surface view of culture on PDA. **v** Reverse view of culture on PDA. Scale bars: **c**-**d** = 50 μ m, **e** = 30 μ m, **f**-**k** = 20 μ m, **l**-**n** = 5 μ m



Atractium fusiformis D.F. Bao, K.D. Hyde & Z.L. Luo, sp. nov.

Index Fungorum number: IF 900264; Facesoffungi number: FoF 13924; Fig. 10

Etymology: Refers the fusiform ascospores of this fungus. Holotype: KUN-HKAS: 125,815.

Saprobic on submerged decaying wood. Sexual morph: Ascomata 100–150×85–160 µm ($\bar{x} = 125.6 \times 123.5$ µm, n = 10), perithecial, solitary or cespitose, superficial or with a minute stroma, globose to subglobose or pyriform, slightly papillate, yellow to orange, KOH +, turning to purple in the 3% KOH, surface smooth to slightly roughened. *Peridium* 19–25 µm (\bar{x} =22.2 µm, n=10) comprise orange to hyaline ells of *textura angular* to *textura prismatica* cells. *Paraphyses* 2–5 (\bar{x} =3.5 µm, n=15), hyaline to subhyaline, septate, branched, smooth-walled. *Asci* 65–80×7–10 µm (\bar{x} =72.4×8.5 µm, n=10), unitunicate, 8-spored, cylindrical, with an apical ring. *Ascospores* 10–14×5–6 µm (\bar{x} =11.8×5.4 µm, n=30), uniseriate, ellipsoid to fusiform, gradually narrowing towards the ends, uniseptate, slightly constricted at septum, hyaline when young, pale brown at maturity, guttulate, smooth-walled when young, becoming verrucose with age. **Asexual morph:** Undetermined.

Culture characteristics: Ascospore germinated on PDA media within 12 h. Colony reached 2.5–3 cm at room temperature for one week, circular, flat, with fluffy, dense, white mycelium, edge entire, reverse pale yellowish.

Material examined: CHINA, Yunnan Province, Yiliang County, on submerged decaying wood in a small stream, 16 May 2021, H.W. Shen, L525 (KUN-HKAS 125815, holotype), ex-type culture, KUNCC 22–12523 = CGMCC 3.24269; *ibid*, H387 (KUN-HKAS 125814, paratype), exparatype culture, KUNCC 22–12522. CHINA, Yunnan Province, Shizong County, on submerged decaying wood in a small stream, 12 May 2021, D.F. Bao, L731 (KUN-HKAS 125809, paratype), ex-paratype culture, KUNCC 22–12521. CHINA, Yunnan Province, Dali City, on submerged decaying wood in a Cibihu lake, 2 May 2021, S.P. Huang, L702 (KUN-HKAS 125789, paratype), ex-paratype culture, KUNCC 22–12452.

GenBank numbers: KUNCC 22–12523: ITS = OP876725, LSU = OP875078, *tub*2 = OQ025192. KUNCC 22–12522: ITS = OP876711, LSU = OP875067. KUKUNCC 22–12521: ITS = OP876729, LSU = OP875082, *tub*2 = OQ025196. KUNCC 22–12452: ITS = OP876727, LSU = OP875080, *tub*2 = OQ025195.

Notes: In this study, we introduce a new sexual species Atractium fusiformis in Atractium. Morphologically, A. fusiformis fits well with the generic concepts of Nectriaceae in having orange, orange-red, perithecial, globose to subglobose, pyriform ascomata, unitunicate, cylindrical or ellipsoidal asci with apical ring and uniseriate, hyaline to yellow, fusiform or ellipsoidal, septate ascospores (Hyde et al. 2020a). In the phylogenetic analysis, four newly obtained strains of Atractium fusiformis (KUNCC 22-12522, KUNCC 22-12523, KUNCC 22-12521 and KUNCC 22-12452) clustered together and sister to A. aquatica with low support (Fig. 11). However, A. fusiformis can be distinguished from A. aquatica in having ellipsoid with rounded ends ascospores and much larger asci and ascospores (Lechat and Fournier 2015). Thus, we introduce our new isolate as a new species based on both phylogeny and morphology.

Cosmospora Rabenh., Hedwigia 2: 59 (1862)

Cosmospora was established by Rabenhorst (1862) with *C. coccinea* as the type. The generic concept of *Cosmospora* was previously relatively broad, encompassing a great deal of asexual morph variability and the sexual morph usually with a small, orange or reddish KOH + and thin-walled perithecia, cylindrical asci with or without an apical ring, and 8-spored, uniseriate, 1-septate ascospores. Gräfenhan et al. (2011) strictly refined the generic concept of *Cosmospora* to include only the species growing on polypores and xylariaceous fungi and having acremonium-like or verticillium-like

asexual states. They accepted eight species in *Cosmospora*, 12 species were subsequently introduced to the genus. Currently, 20 species are accepted in the genus (Gräfenhan et al. 2011; Herrera et al. 2015; Zeng and Zhuang 2016; Luo et al. 2019; Lechat and Fournier 2021).

Species in *Cosmospora* are characterized by superficial, solitary to gregarious, orange-red to bright red, pyriform perithecia, cylindrical to narrowly clavate asci and ellipsoidal, multi-septate, verrucose or tuberculate, yellow–brown ascospores; ellipsoidal, oblong, clavate or allantoid and aseptate conidia (Gräfenhan et al. 2011; Herrera et al. 2015; Zeng and Zhuang 2016). This study introduces a new species *Cosmospora cylindricospora* based on phylogenetic and morphological analyses.

Cosmospora cylindricospora D.F. Bao, K.D. Hyde & Z.L. Luo, *sp. nov.*

Index Fungorum number: IF 900265; Facesoffungi number: FoF 13925; Fig. 12

Etymology: Referring to the cylindrical conidia of this fungus.

Holotype: KUN-HKAS 125785.

Saprobic on submerged decaying wood. Sexual morph: Undetermined. Asexual morph: Colonies effuse, white, shining, velvety, hairy. Mycelium partly superficial, composed of branched, septate, brown to dark brown, smooth hyphae. Conidiophores 58–90×4–6 μ m (\bar{x} =74.2×5 μ m, n =15) macronematous, mononematous, solitary, unbranched, straight or slightly flexuous, subhyaline to pale brown, paler towards the apex, 3–6-septate, smooth. Conidiogenous cells polyblastic, integrated, determinate, terminal, hyaline, denticulate, hyaline, smooth-walled. Conidia 92–124×4–5 μ m (\bar{x} =108×4.5 μ m, n=30), acrogenous, solitary, cylindrical, straight or slightly curved, tapering towards the apex, rounded at the apex, truncate at the base, hyaline, aseptate or sometimes with several pseudoseptate, with small guttules, smooth-walled.

Culture characteristics: Colonies on PDA reaching 4–4.5 cm diam. after three weeks at room temperature. Colony medium dense, circular, flattened to raised, surface slightly rough with hyphal tufts, edge entire, velvety to fluffy; from above, white to white yellowish at the margin, light green to yellowish green at the centre; from below, radiating outwards colony, white to cream at the margin, dark green at the middle, dark yellowish green at the centre.

Material examined: CHINA, Yunnan Province, Cangshan Mountain, on submerged decaying wood in a stream, 9 July 2021, J. He, L594 (KUN-HKAS 125785, holotype), ex-type culture, KUNCC 22–12662 = CGMCC 3.24270.

GenBank numbers: ITS = OP876700, LSU = OP872570, *tub2* = OQ025193, *rpb2* = OQ077584.

Notes: Cosmospora cylindricospora matches the generic concept of *Cosmospora* in having hyaline and aseptate conidia. However, *Cosmospora cylindricospora* is distinct



Fig. 11 Phylogenetic tree based on RAxML analyses of a combined ITS, LSU and *tub2* dataset. Tree topology of the RAxML, MP and Bayesian analyses are similar. The tree is rooted to *Neocosmospora haematococca* (CBS 119600 and CBS 101573). The combined gene analysis included 74 strains with 2037 characters after aligned, including gaps (ITS: 605 bp, LSU: 827 bp, *tub2*: 605 bp), of which 660 were parsimony-informative, 161 were parsimony-uninformative and 1216 characters were constant. The RAxML analysis of the combined dataset yielded the best scoring tree with a final ML opti-

from other species of the genus by its cylindrical, straight or slightly curved and longer conidia. *Cosmospora cylindricospora* shares similar morphological characteristics such as simple, unbranched conidiophores and hyaline, unicellular, smooth conidia with *C. khandalensis* and *C. lavitskiae*. However, *C. cylindricospora* differs from *C. khandalensis* and *C. lavitskiae* in having polyblastic conidiogenous cells and cylindrical, straight or slightly curved conidia with rounded apex and truncated base. Whereas conidiogenous cells of *C. khandalensis* and *C. lavitskiae* are monophialidic and conidia are ovoid to ellipsoidal or reniform (Sukapure

mization likelihood value of -22,438.740286. The matrix had 986 distinct alignment patterns, with 10.17% undetermined characters or gaps. Estimated base frequencies were as follows: A=0.233899, C=0.265503, G=0.269577, T=0.231020; substitution rates AC=1.264773, AG=2.524299, AT=1.254123, CG=0.974153, CT=4.563937, GT=1.000000; gamma distribution shape parameter α =0.220117. Bootstrap support values for RAxML (blue) and MP (red) greater than 70% and Bayesian posterior probabilities (black) greater than 0.95 are given at each node

and Thirumalachar 1966; Zhdanova 1966). In addition, our phylogenetic analysis showed that *C. cylindricospora* formed a distinct lineage within the genus (Fig. 13). Thus, *Cosmospora cylindricospora* is introduced as a new species and it is the second *Cosmospora* species reported from freshwater habitats in China.

Chaetopsina Rambelli, Atti Accad. Sci. Ist. Bologna, Cl. Sci. Fis. Rendiconti 3: 5 (1956).

Chaetopsina, a hyphomycetous genus, was introduced by Rambelli (1956) with *C. fulva* as the type species. Since then, many numbers of hyphomycetes species have been Fig. 12 Cosmospora cylindricospora (KUN-HKAS 125785, holotype) **a**, **b** Colonies on substrate. **c** Conidiophores and conidia. **d**–**f** Conidiophores. **g**–**j** Conidia. **k** Germinating conidium. **l** Surface view of culture on PDA. **m** Reverse view of culture on PDA. Scale bars: **c**–**k**=20 μm



introduced in *Chaetopsina* (Rambelli and Lunghini 1976; Sutton and Hodges 1976; 1979; Morgan-Jones 1979; Crane and Schoknecht 1982; Kirk 1985; Samuels 1985; Wingfield 1987; Holubova-Jechova 1990; Merli 1992; Zucconi and Rambelli 1993). Samuels (1985) described four sexual species of *Nectria* sensu lato having *Chaetopsina* asexual morphs. These species were later placed in a newly introduced genus *Chaetopsinectria* by Luo and Zhuang (2010a). Rossman et al. (2016) recommended the generic name *Chaetopsina* instead of *Chaetopsinectria* based on its priority, widespread use, and a greater number of names and this was accepted by later studies (Lechat and Fournier 2019, 2020b).

The sexual morph of *Chaetopsina* is characterized by perithecial, solitary, superficial, non-stromatic, obpyriform, red, becoming dark red in KOH ascomata with an acute apex, 8-spored, clavate asci with a simple apex or an apical ring and ellipsoid to fusiform, 1-septate, hyaline, smooth to striate ascospores. The asexual morphs are characterized by setiform, tapering towards acutely rounded apex, base bulbous, mostly flexuous, yellow–brown, turning red-brown in



Fig. 13 Phylogenetic tree based on RAxML analyses of a combined ITS, LSU and *tub2* dataset. Tree topology of the RAxML and MP analyses are similar. The tree is rooted to *Cosmosporella cavisperma* (CBS 172.31) and *C. olivacea* (KUMCC 17–0321). The combined gene of ITS, LSU and *tub2* analysis included 19 strains with 1977 characters after aligned including gaps (ITS: 591 bp, LSU: 901 bp, *tub2*: 585 bp), of which 173 were parsimony-informative, 110 were parsimony-uninformative and 1694 characters were constant. The RAxML analysis of the combined dataset yielded the best scoring

KOH, fertile in mid region, unbranched, verruculose conidiophores and the fertile region consisting of irregularly branched dense aggregated conidiogenous cells, conidiogenous cells are hyaline, mono- to polyphialidic, ampulliform to lageniform and conidia are subcylindrical, aseptate hyaline, smooth, with bluntly rounded ends and base rarely with flattened hilum (Rambelli 1956; Luo and Zhuang 2010a).

Currently, 27 species are included in *Chaetopsina* of which only 12 species have sequence data in GenBank. *Chaetopsina* species are widespread in tropical and neotropical areas and have been found on leaves, bark, dead palm leaves or ascomycetous stromata (Sutton and Hodges 1976; Rambelli and Lunghini 1976; Crane and Schoknecht 1982; Kirk 1985; Wingfield 1987; Merli 1992; Zucconi and Rambelli 1993; Lechat and Fournier 2019, 2020b). In this study, *Chaetopsina penicillate* was collected from freshwater habitats in China, and it is the first species of this genus reported from freshwater habitats.

tree with a final ML optimization likelihood value of -5471.730276. The matrix had 348 distinct alignment patterns, with 17.48% undetermined characters or gaps. Estimated base frequencies were as follows: A=0.225094, C=0.272713, G=0.272067, T=0.230126; substitution rates AC=1.175555, AG=3.331353, AT=1.155285, CG=1.079199, CT=7.475654, GT=1.000000; gamma distribution shape parameter α =0.020000. Bootstrap support values for RAxML (blue) and MP (red) greater than 60% and Bayesian posterior probabilities (black) greater than 0.95 are given at each node

Chaetopsina penicillata Samuels, Mycotaxon 22(1): 24 (1985).

Index Fungorum number: IF 105142; Facesoffungi number: FoF 13926; Fig. 14

Saprobic on decaying wood submerged in a lake. Sexual morph: Undetermined. Asexual morph: Colonies effuse, hairy, brown to dark brown, with a white to buff slimy conidial mass at the tip of conidiophores, shining. Mycelium partly immersed, composed brown, septate, branched smooth hyphae. Conidiophores $130-160 \times 7-10 \mu m$ ($\bar{x} = 146.9 \times 8.4 \mu m$, n = 25), macronematous, mononematous, reddish brown, paler towards the apex, septate, smooth-walled, arising from stromatic cells, each composed of a well-defined stipe and a complex penicillate head consisting of series of penicillate branches and terminating with conidiogenous cells and a head of slimy conidia. Conidiogenous cells $11-17 \times 2-5 \mu m$ ($\bar{x} = 14.1 \times 3.3 \mu m$, n = 30), polyblastic, hyaline to pale brown, parallel, obovoid, tapering towards apex, smooth-walled. Conidia $20-25 \times 7-9 \mu m$ Fig. 14 Chaetopsina penicillata (KUN-HKAS 102466). a, b Colonies on substrate. c, h Conidiogenous cells with conidia. d-g Conidiophores and conidia. i-m Conidia. n Germinating conidium. Scale bars: $c-h=30 \mu m$, $i=50 \mu m$, $j-n=10 \mu m$



 $(\bar{x}=22.8\times8.3 \,\mu\text{m}, n=43)$, solitary, slimy, straight, fusiform to clavate, gradually narrowing towards the ends, aseptate, hyaline, smooth-walled, guttulate.

Material examined: CHINA, Yunnan Province, on submerged decaying wood in Cibihu Lake, 20 July 2021, S.P. Huang, L701 (KUN-HKAS 102466), living culture, KUNCC 22–12664.

GenBank number: ITS = OP985128, LSU = OP985134.

Notes: In our phylogenetic analysis, the new collection KUNCC 22–12664 clustered with *Chaetopsina penicillata* with 100%ML/ 100%MP /1 PP support (Fig. 15). Morphologically, our new collection fits well with the original description of *C. penicillata* except the size of conidiophores. The conidiophores of our new collection are much shorter than the holotype (130–160 vs. 350–370 μ m) (Samuels 1985). We identified our new collection as *C. penicillata* based on both morphological characters and phylogenetic analysis. *Chaetopsina penicillata* was introduced by Samuels (1985) from terrestrial habitats in Ecuador, Jamaica and

New Zealand. This study provides the first report of *C. penicillata* from freshwater habitats in China.

Gliocladiopsis S.B. Saksena, Mycologia 46(5): 662 (1954)

Gliocladiopsis was established by Saksena (1954) with G. sagariensis as type species. The type species has been synonymized several times based on its morphological characteristics (Agnihothrudu 1959; Barron 1968; Crous and Wingfield 1993). Gliocladiopsis has been initially synonymized under Cylindrocarpon or Cylindrocladium (Agnihothrudu 1959; Barron 1968). Crous and Wingfield (1993) resurrected Gliocladiopsis based on its distinct characteristics of dense, penicillate conidiophores, and synonymized G. sagariensis under G. tenuis. Later, G. irregularis and G. sumatrensis were added to this genus (Crous and Peerally 1996; Crous et al. 1997). Lombard and Crous (2012) re-evaluated the taxonomy of Gliocladiopsis based on both phylogeny and morphology and the results showed that G. sagariensis and G. tenuis are distinct species, thus, G. sagariensis is reinstated as the type species for the genus;



Fig. 15 Phylogenetic tree based on RAxML analyses of a combined ITS, LSU, *rpb2*, *cmd*, *acl* and *his3*. Tree topology of the RAxML, MP and Bayesian analyses are similar. The tree is rooted to *Calostilbe striispora* (CBS 133491). The combined gene analysis included 44 strains with 4142 characters after aligned including gaps (ITS: 613 bp, LSU: 877 bp, *rpb2*: 861 bp, *cmd*: 474 bp, *acl*: 959 bp, *his3*: 358 bp), of which 952 were parsimony-informative, 461 were parsimony-uninformative and 2671 characters were constant. The RAxML analysis of the combined dataset yielded the best scoring tree with

in addition, five species were introduced in the genus. Consequently, 10 new species had since then been added in the genus (Liu and Cai 2013; Parkinson et al. 2017; Hyde et al. 2018; Zhai et al. 2019; Gordillo and Decock 2019; Perera et al. 2020). Currently, 19 species are included in the genus (Crous and Peerally 1996; Crous et al. 1997; Lombard and Crous 2012; Liu and Cai 2013; Parkinson et al. 2017; Hyde et al. 2018; Zhai et al. 2019; Gordillo and Decock 2019; Perera et al. 2020).

So far, only one sexual species (*G. pseudotenuis*) has been reported in *Gliocladiopsis*. *Gliocladiopsis pseudotenuis* was iniality introduced by Schoch et al. (2000) as *Glionectria tenuis* and it was incorrectly linked to the asexual morph of

a final ML optimization likelihood value of -31,301.685669. The matrix had 1548 distinct alignment patterns, with 51.88% undetermined characters or gaps. Estimated base frequencies were as follows: A=0.236102, C=0.265619, G=0.272345, T=0.225934; substitution rates AC=1.173873, AG=2.751368, AT=1.373236, CG=0.927145, CT=5.682462, GT=1.000000; gamma distribution shape parameter α =0.214794. Bootstrap support values for RAxML (blue) and MP (red) greater than 70% and Bayesian posterior probabilities (black) greater than 0.95 are given at each node

Gliocladiopsis tenuis. However, Phylogenetic analysis and morphological observations showed that it is a distinct species wihtin *Gliocladiopsis.* Therefore, Lombard and Crous (2012) provided a new name *Gliocladiopsis pseudotenuis* for *Glionectria tenuis.* The sexual morph of *Gliocladiopsis* is characterized by superficial, obovoid to broadly obpyriform ascomata that are turning red-brown in 3% KOH + with a dark red stromatic base, unitunicate, 8-spored, cylindrical, sessile asci with flattened apex and a refractive apical apparatus and uniseriate, hyaline, ellipsoidal, smooth, 1-septate ascospores that are becoming brown and verruculose with age; The asexual morphs are characterized by hyaline, penicillate conidiophores, which consist of a simple-septate Fig. 16 Gliocladiopsis tenuis (KUN-HKAS 125800) a, b Colonies on substrate. c-g, h Conidiophores and conidia. h Conidiogenous cells. i–m Conidia. Scale bars: c, d, i, $j=50 \mu m$, e–h, $k=30 \mu m$, l, $m=10 \mu m$



stipe bearing 2–4 successive whorls of branches subtending whorls of phialides and hyaline, cylindrical, 0–1-septate conidia accumulating in whitish to pale yellowish mucoid drops (Lombard and Crous 2012; Gordillo and Decock 2019).

Morphologies of *Gliocladiopsis* species are quite similar which make species identification very difficult. Thus, phylogeny is important to identify the *Gliocladiopsis* species. Of the 19 species, 14 have the sequence in the Gen-Bank. Therefore, sequence data of the other five species are required to understand the taxonomy of the genus better. *Gliocladiopsis* species have been isolated from soil, diseased plants root and asymptomatic rhizomes (Booth 1966; Crous et al. 1997; Dann et al. 2012; Parkinson et al. 2017; Li et al. 2008). Only two species *G. aquaticus* and *G. guangdongensis* were isolated from freshwater habitats. This study collected *Gliocladiopsis tenuis* from freshwater habitats in China for the first time.

Gliocladiopsis tenuis (Bugnic.) Crous & M.J. Wingf., Mycol. Res. 97(4): 446 (1993).



Fig. 17 Phylogenetic tree based on RAxML analyses of a combined *his3*, ITS, *tef1-* α , and *tub2* dataset. Tree topology of the RAxML, MP and Bayesian analyses are similar. The tree is rooted to *Dematiocla-dium celtidis* (CBS 115994). The combined gene analysis included 45 strains with 2221 characters after aligned including gaps (*his3*: 515 bp, ITS: 539 bp, *tef1-* α : 538 bp, *tub2*: 629 bp), of which 249 were parsimony-informative, 231 were parsimony-uninformative and 1741 characters were constant. The RAxML analysis of the combined dataset yielded the best scoring tree with a final ML optimization

Index Fungorum number: IF 359449; Facesoffungi number: FoF 06876; Fig. 16

Saprobic on submerged decaying wood in a lake. Sexual morph: Undetermined. Asexual morph: appearing as white masses on the substrate, becoming yellowish with age. Conidiophores 75–110×4–6 µm (\bar{x} =93×5.2 µm, n=16), penicillate, macronematous, mononematous, consisting of a stipe bearing a penicillate arrangement of fertile branches, hyaline, septate, branched, without stipe extensions and terminal vesicles. Conidiogenous cells apparatus with several series of hyaline, branched, smooth-walled branches. Phialides 9–14×3–4 µm (\bar{x} =11.4×3.4 µm, n=44), doliiform to cymbiform to cylindrical, arranged in terminal whorls of 3–6 per branch, with minute collarettes, central phialide frequently extending above the rest. Conidia 15–20×2–3 µm

likelihood value of -7798.259460. The matrix had 565 distinct alignment patterns, with 6.78% undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.218239, C = 0.323881, G = 0.229746, T = 0.228134; substitution rates AC = 1.311343, AG = 2.782041, AT = 1.439742, CG = 0.500710, CT = 5.688029, GT = 1.000000; gamma distribution shape parameter $\alpha = 0.183224$. Bootstrap support values for RAxML (blue) and MP (red) greater than 70% and Bayesian posterior probabilities (black) greater than 0.95 are given at each node

 $(\bar{x} = 17.1 \times 2.3 \text{ }\mu\text{m}, \text{ }n = 45)$, in chains, cylindrical with rounded ends, aseptate to 1-septate, hyaline, smooth-walled, straight.

Culture characteristics: Colonies on PDA reaching 3.5–4.0 cm diameter after 3 weeks at room temperature; colony from above, dense, circular, with edge entire, fluffy to floccose, with white tufts and black droplets, dark brown to black at the margin; reverse reddish-brown to dark brown.

Material examined: CHINA, Yunnan Province, on submerged decaying wood in Chenghai Lake, 28 May 2021, H.W. Shen, L603 (KUN-HKAS 125800), living culture, KUNCC 22–12663.

GenBank numbers: ITS = OP876701, tub2 = OQ025194, his3 = OQ064512, tef1- α = OQ064522.
Notes: In the phylogenetic analysis, the new isolate KUNCC 22–12663 clustered with the ex-type of *G. tenuis* (IMI 68205) and four extant strains of *G. tenuis* with 100% ML/ 100% MP/ 1 PP support (Fig. 17). Morphologically, the new isolate fits well with the original description of *G. tenuis* (Crous and Wingfield 1993), thus, we identified the new isolate as *G. tenuis* based on phylogenetic analysis and morphological characters.

Gliocladiopsis tenuis has been reported from terrestrial habitats in India, Indonesia, South-East Asia, Thailand and Vietnam (Crous and Wingfield 1993; Crous and Peerally 1996; Perera et al. 2020). In this study, the new collection was isolated from freshwater habitats for the first time and introduced as a new geographical record for China.

Mariannaea G. Arnaud ex Samson, Stud. Mycol. 6: 74(1974)

Mariannaea was formally established by Samson (1974) to accommodate *M. camptospora*, *M. elegans* and the variety *M. elegans* var. *punicea* and typified by *M. elegans*. The genus is characterized by branched, septate conidiophores with hyaline, flask-shaped phialides, 1–2-celled, hyaline conidia mostly forming imbricate chains or slimy

heads (Samson 1974; Samson and Bigg 1988; Samuels and Seifert 1991). The sexual morph of *Mariannaea* has been linked to *Nectria* (Samuels and Seifert 1991) and *Cosmospora* (Gräfenhan et al. 2011). However, *Cosmospora* and *Nectria* have been shown polyphyletic within *Nectriaceae*, while *Mariannaea* formed a monophyletic clade within *Nectriaceae*. Therefore, Gräfenhan et al. (2011) retained Mariannaea as a distinct genus in *Nectriaceae*.

The classification and species concept of *Mariannaea* were reviewed by Hu et al. (2017), they designated an epitype for *M. elegans* (the type species of *Mariannaea*) and accepted 15 species in the genus. Five new species were further introduced in the genus (Crous et al. 2019; Hyde et al. 2020b; Boonmee et al. 2021; Watanabe and Hirose 2021; Yang et al. 2021). Currently, 20 species are accepted in the genus (Index Fungorum 2023). This study collected five fresh collections from freshwater habitats in Yunnan Province. Two new species *M. yunnanense* and *M. suae*, as well as two new records are introduced based on phylogenetic analysis and morphological characters.

Mariannaea dimorpha Z.Q. Zeng & W.Y. Zhuang, Mycol. Progr. 13(4): 969 (2014).



Fig. 18 Mariannaea dimorpha (KUN-HKAS 125803). \mathbf{a} - \mathbf{b} Colonies on substrate. \mathbf{c} - \mathbf{e} Conidiophores. \mathbf{f} , \mathbf{h} Conidiogenous cells. \mathbf{g} - \mathbf{l} Conidia. Scale bars: \mathbf{c} =100 µm, \mathbf{d} - \mathbf{e} =50 µm, \mathbf{f} , \mathbf{h} =30 µm, \mathbf{g} , \mathbf{i} =20 µm, \mathbf{j} - \mathbf{l} =10 µm Fig. 19 Phylogenetic tree based on RAxML analyses of a combined ITS and LSU dataset. Tree topology of the RAxML, MP and Bayesian analyses are similar. The tree is rooted to Stachybotrys chartarum (CBS 129.13). The combined gene analysis included 56 strains with 1429 characters after aligned including gaps (ITS: 583 bp and LSU: 846 bp), of which 230 were parsimonyinformative, 89 were parsimony-uninformative and 1110 characters were constant. The RAxML analysis of the combined dataset yielded the best scoring tree with a final ML optimization likelihood value of -9021.203912. The matrix had 692 distinct alignment patterns, with 32.42% undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.242101, C=0.249327, G=0.274549, T = 0.234024; substitution rates AC = 1.654970, AG = 2.830985, AT=1.713621, CG=0.691184, CT = 6.463431, GT = 1.000000; gamma distribution shape parameter $\alpha = 0.165519$. Bootstrap support values for RAxML (blue) and MP (red) greater than 70% and Bayesian posterior probabilities (black) greater than 0.95 are given at each node



Index Fungorum number: IF 570079; Facesoffungi number: FoF 13927; Fig. 18

Saprobic on submerged decaying wood. Sexual morph: Undetermined. Asexual morph: Colonies on natural substrate superficial, scattered or gregarious, effuse, white, hairy, with glistening conidia. Mycelium composed of septate, branched, smooth, hyaline to brown hyphae. Conidiophores 230–450 × 12–14 μ m (\bar{x} = 338.7 × 13.1 μ m, n = 10), macronematous, mononematous, cylindrical, erect, straight or slightly flexouse, septate, hyaline when young, becoming orange brown at base and gradually paler towards apex, hyaline at the apex, smooth at the base, gradually verruculose towards the apex, branched, branching 1-2 levels verticillate, bearing short branches in the upper part with a terminal whorl of 5–7 phialides. Phialides $19-29 \times 3-5 \mu m$ $(\bar{x} = 23.9 \times 3.8 \ \mu m, n = 20)$, flask-like, hyaline to subhyaline, slightly swollen at base, tapering at apex, smooth when young, verruculose at maturity. Conidia 10-14×3-4 µm $(\bar{x} = 12.3 \times 3.5 \ \mu m, n = 30)$, oblong to fusiform, acuminate at apex, pointed at base, straight, (0)-1-septate, slightly constricted at septum, hyaline, smooth-walled.

Material examined: CHINA, Yunnan Province, on submerged decaying wood in Nanpan River, 12 July 2018, X. He, S1725 (KUN-HKAS 125803), living culture, KUNCC 22–12458.

GenBank numbers: ITS = OP876732, LSU = OP875086. Notes: Mariannaea dimorpha was introduced by Zeng and Zhuang (2014) with its sexual and asexual morphs. It was isolated on rotten bark from China. Phylogenetic analysis showed that our new isolate (KUNCC 22–12458) clustered with the holotype of *M. dimorpha* (Fig. 19). There are no differences in ITS region between these two species, we therefore identified our species as *M. dimorpha*. Our new isolate was collected from China and first reported from freshwater habitat.

Morphologically, our new isolate is similar to the holotype of *M. dimorpha* in having septate, hyaline conidiophores which branching 1–2 levels verticillate, phialidic conidiogenous cells and fusiform straight, (0)-1-septate,





hyaline, smooth-walled conidia (Zeng and Zhuang 2014). However, the conidiophores of our isolate are smooth at the base and gradually verruculose towards the apex and hyaline when young, becoming orange brown at the base and gradually became paler towards apex and the phialides are smooth when young, verruculose at maturity. However, these characters were not found from the holotype (Zeng and Zhuang 2014).

Mariannaea yunnanensis D.F. Bao, K.D. Hyde & Z.L. Luo, *sp. nov.*

Index Fungorum number: IF 900266; Facesoffungi number: FoF 13928; Fig. 20

Etymology: Referring to Yunnan Province, China, where the fungus was collected.

Holotype: KUN-HKAS 125786.

Saprobic on submerged decaying wood. Sexual morph: Undetermined. Asexual morph: Colonies on natural substrate superficial, effuse, white, hairy. Mycelium immersed, subhyaline to pale brown, composed of branched, septate hyphae. Conidiophores $220-330 \times 6-10 \mu m$ ($\bar{x} = 274.8 \times 7.8 \mu m$, n = 11), macronematous, mononematous, cylindrical, erect, straight or slightly flexouse, septate, smooth-walled, hyaline to subhyaline, branched, branching verticillately at 2–3 level verticillate, bearing short branches in the upper part with a terminal whorl of 3–6 phialides, and 1–2 lower nodes of 3–4 phialides. *Phialides* $12-23 \times 2-4 \mu m$ ($\bar{x} = 17.6 \times 3.1 \mu m$, n = 30), flask-like, hyaline, slightly swollen at base, tapering at apex, smooth-walled. *Conidia* $6-8 \times 3-4 \mu m$ ($\bar{x} = 7.1 \times 3.6 \mu m$, n = 30), ellipsoidal to fusiform, acuminate at apex, pointed at base, aseptate, hyaline, smooth and thin-walled.

Material examined: CHINA, Yunnan Province, on submerged decaying wood in a stream, 12 May 2021, D.F. Bao, B213 (KUN-HKAS 125786, holotype), ex-type culture, KUNCC 22–12455=CGMCC 3.24273; *ibid*, B215 (KUN-HKAS 125788, paratype), ex-paratype culture, KUNCC 22–12456=CGMCC 3.24272.

GenBank numbers: KUNCC 22–12455: ITS = OP876702, LSU = OP875058, *tub*2 = OQ025185. KUNCC 22–12456 ITS = OP876703, LSU = OP875059, *tub*2 = OQ025186.

Notes: In our phylogenetic analysis, two new isolates of *Mariannaea yunnanensis* (KUNCC 22–12455 and KUNCC 22–12456) formed a distinct lineage within *Mariannaea* which closed to *M. aquaticola*, *M. humicola*, *M. pinicola* and *M. samuelsii* (Fig. 19). *Mariannaea yunnanensis* resembles





M. aquaticola, M. humicola, M. pinicola and M. samuelsii in having macronematous, mononematous, cylindrical, erect, septate, hyaline conidiophores which bearing short branches on the upper part, phialidic, hyaline, smooth-walled conidiogenous cells and ellipsoidal to fusiform, aseptate conidia. However, the conidiophores of *M. aquaticola* has branches with whorls of 3-4 phialides, while, branch whorls of M. yunnanensis have 3-6 phialides (Cai et al. 2010). Mariannaea yunnanensis is different from M. humicola in having longer conidiophores (220-330 vs. 80-100 µm) and larger conidia $(6-8 \times 3-4 \text{ vs. } 4-6 \times 2-3 \mu\text{m})$ and the conidiophores with a terminal whorl of 3-6 phialides. Whereas conidiophores of *M. humicola* with a terminal whorl of 1-5 phialides (Lombard et al. 2015). Mariannaea yunnanensis can be distinguished from *M. pinicola* by its fewer terminal or intercalary whorls phialides (3-6 vs. 9) (Samuels and Seifert 1991). The conidiophores of Mariannaea yunnanensis are much longer than those of M. samuelsii (220-330 vs.100-200 µm). The conidiophores terminal whorl has 3-6 phialides and 1-2 lower nodes of 3-4 phialides in M. yunnanensis, while, terminal whorl has (2-)3-5 phialides and 1-2 lower nodes of 1-3 phialides in M. samuelsii (Gräfenhan et al. 2011).

Mariannaea suae D.F. Bao, K.D. Hyde & Z.L. Luo, sp. nov.

Index Fungorum number: IF 900267; Facesoffungi number: FoF 13929; Fig. 21

Etymology: "suae" (Lat.) in memory of the Chinese mycologist Prof. Hong-Yan Su (4 April 1967–3 May 2022). Holotype: KUN-HKAS 125787.

Saprobic on submerged decaying wood. Sexual morph: Undetermined. Asexual morph: Colonies on natural substrate superficial, scattered, effuse, white, hairy. Mycelium composed of branched, septate, hyaline to medium brown hyphae, smooth. Conidiophores 254–679×5–24 µm (\bar{x} = 466×13 µm, n = 10), macronematous, mononematous, single, cylindrical, erect, straight or slightly flexuous, septate, hyaline, smooth-walled, bearing short branches in the upper part with a terminal whorl of more than 10 phialides, branching one level verticillate. Phialides 16–23×1–2 µm (\bar{x} = 19.6×1.8 µm, n = 25), flask-like, cylindrical, hyaline, tapering towards apex, smooth-walled. Conidia 6–8×3–5 µm (\bar{x} = 6.8×4 µm, n = 30), ellipsoidal to oval, rounded at both ends, straight, aseptate, hyaline, guttulate, smooth-walled.

Material examined: CHINA, Yunnan Province, Cangshan Mountain on submerged decaying wood in a stream, 9 July 2021, J. He, B217 (KUN-HKAS 125787, holotype), ex-type culture, KUNCC 22–12525 = CGMCC 3.24274.

GenBank numbers: ITS = OP876704, LSU = OP875060.

Notes: Mariannaea suae is introduced here based on phylogenetic analysis and its distinct morphology. Mariannaea suae is unique in the genus by its conidiophores which bear short branches in the upper part with a terminal whorl of more than ten phialides, branching one level verticillate. While, conidiophores of other species less than ten phialides in the terminal whorl, and usually branching 1–3 levels verticillate (Cai et al. 2010; Gräfenhan et al. 2011; Zeng and Zhuang 2014; Lombard et al. 2015; Hu et al. 2017; Yang et al. 2021). In our phylogenetic analysis, *Mariannaea suae* formed a distinct lineage within *Mariannaea* (Fig. 19). Therefore, we introduce our new isolate as a new species based on phylogenetic and morphological analyses.

Mariannaea superimposita (Matsush.) Samuels [as 'superimpositus'], Mycologia 81(3): 353 (1989).

Index Fungorum number: IF 136166; Facesoffungi number: FoF 05444; Fig. 22

Saprobic on submerged decaying wood. Sexual morph: Undetermined. Asexual morph: Colonies on natural substrate superficial, scattered, effuse, white, hairy. Mycelium composed of septate, branched, smooth, hyaline to medium brown hyphae. Conidiophores 250-460×6-14 µm $(\bar{x} = 355.7 \times 9.8 \ \mu m, n = 10)$, macronematous, mononematous, simple, cylindrical, erect, straight or slightly flexouse, septate, hyaline when young, becoming orange brown at base and gradually paler towards apex, hyaline at apex, smooth-walled, branching 1-2 levels verticillate, bearing short branches in the upper part with 3-4 phialides in verticils. *Phialides* $21-31 \times 2-4 \mu m$ ($\bar{x} = 26 \times 3.2 \mu m$, n = 30), flask-like, hyaline, cylindrical, slightly swollen at base, tapering at apex, smooth-walled. Conidia 10-14×3-5 µm $(\bar{x} = 12.1 \times 3.6 \ \mu m, n = 30)$, ellipsoidal to fusiform, acuminate at apex, pointed at base, straight, or slightly curved, (0)-1-septate, slightly constricted at the septum, hyaline, smooth-walled.

Material examined: CHINA, Yunnan Province, Shizong County, on submerged decaying wood in a stream, 12 May 2021, D.F. Bao, H355 (KUN-HKAS 125808), living culture, KUNCC 22–12457.

GenBank numbers: ITS = OP876707, LSU = OP875063, *tub2* = OQ025187.

Notes: Matsushima (1975) initially introduced *Mariannaea superimposita* as *Penicillifer superimpositus*. It was later transferred to *Mariannaea* by Samuels (1989) and phylogenetic analysis also confirmed the placement of the species within *Mariannaea* (Nonaka et al. 2015). In the phylogenetic analysis (Fig. 19), our new isolate (KUNCC 22–12457) clustered with *Mariannaea superimposita* (CBS 113472 and CBS 124559). Morphologically, the new isolate is quite similar to *M. superimposita* (Matsushima 1975); we, therefore, identified our new isolate as *M. superimposita*.

Mariannaea superimposita has been reported from China, Japan and Venezuela (Matsushima 1975; Luo et al. 2019). In this study, the new isolate was recollected from freshwater habitats in China.





Neocosmospora E.F. Sm., Bull. U.S. Department of Agriculture 17: 45 (1899).

Neocosmospora was established by Smith (1899). Species in the genus are saprobes, endophytes, and plant and animal pathogens and are commonly found in soil, plant debris, living plant material, air and water (Sandoval-Denis et al. 2019; Guarnaccia et al. 2021). *Neocosmospora* is characterised by orange to red-brown, smooth-walled to coarsely warted perithecia, producing globose to ellipsoidal, 0–1-septate, distinctly ornamented (striate, cerebriform to spinulose), yellow golden brown ascospores; while asexual morphs produce distinctive very long and narrow, acremonium-like aerial monophialides (Sandoval-Denis et al. 2019).

Currently, 129 records of *Neocosmospora* are listed in Index Fungorum (2023). However, only *N. haematococca* has been reported from freshwater habitats. In this study, two species were collected from freshwater habitats. Based on multi-locus phylogenetic analysis and morphological characters, the species were identified as *N. aquatica* sp. nov. and *N. brevis*.





Neocosmospora aquatica D.F. Bao, K.D. Hyde & Z.L. Luo, *sp. nov.*

Index Fungorum number: IF 900268; Facesoffungi number: FoF 13930; Fig. 23

Etymology: Epithet refers to the collection from an aquatic habitat.

Holotype: KUN-HKAS 125810.

Saprobic on submerged decaying wood from freshwater habitats. **Sexual morph**: Undetermined. **Asexual morph**: *Colonies* on natural substrate superficial, effuse, gregarious, velvety, white. *Mycelium* superficial to semi-immersed, composed of hyaline, branched, smooth hyphae. *Conidiophores* 40–80×2–4 µm (\bar{x} =59.8×3.3 µm, n=20), borne on aerial mycelium, semi-macronematous to macronematous, mononematous, cylindrical, unbranched or irregularly laterally branched, aseptate, hyaline, smooth-walled, bearing terminal single phialides. *Conidiogenous cells* monophialidic, integrated, terminal, determinate, hyaline, subulate to subcylindrical, with a discrete flared collarette, smooth. *Conidia* 6–7×2–4 µm (\bar{x} =6.5×3 µm, n=32), arranged in false heads on phialide tips, ellipsoidal to obvoidal, hyaline, smooth- and thin-walled, aseptate.

Material examined: CHINA, Yunnan Province, Yiliang County, on submerged decaying wood in a stream, 16 May

Fig. 24 Phylogenetic tree based on RAxML analyses of a combined ITS, LSU, rpb2 and *tef*1- α , dataset. Tree topology of the RAxML and MP analyses are similar. The tree is rooted to Geejayessia atrofusca (NRRL 22316) and G. cicatricum (CBS 125552). The combined gene analysis including 147 strains with 3495 characters after aligned including gaps (ITS: 492 bp, LSU: 483 bp, *rpb2*: 1823 bp, *tef1-α*: 697 bp), of which 917 were parsimonyinformative, 349 were parsimony-uninformative and 2229 characters were constant. The RAxML analysis of the combined dataset yielded the best scoring tree with a final ML optimization likelihood value of -56,493.984935. The matrix had 1584 distinct alignment patterns, with 18.80% undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.238608, C = 0.274649, G = 0.260503,T = 0.226239; substitution rates AC=1.514461, AG=4.749211, AT = 1.456537, CG = 0.930417, CT = 9.220959, GT = 1.000000; gamma distribution shape parameter $\alpha = 0.258278$. Bootstrap support values for RAxML (blue) and MP (red) greater than 60% and Bayesian posterior probabilities (black) greater than 0.90 are given at each node



between *N. aquatica* and *N. parceramosa* for ITS and $tef1-\alpha$ gene regions revealed 1.8% and 1.2% differences respectively. Thus, the new isolate is introduced as a new species (Chethana et al. 2021; Pem et al. 2021).

Neocosmospora brevis Sand.-Den. & Crous, in Sandoval-Denis, Lombard & Crous, Persoonia 43: 119 (2019).

Index Fungorum number: IF 831176; Facesoffungi number: FoF 13931; Fig. 25

Saprobic on submerged decaying wood. Sexual morph: Undetermined. Asexual morph: Colonies on natural substrate superficial, effuse, gregarious, scattered, velvety, white, with a white slimy conidial mass on the conidiophores. Mycelium superficial to semi-immersed, composed of branched, hyaline, smooth hyphae. Conidiophores $100-140 \times 2-4 \mu m$ ($\bar{x} = 122.5 \times 3 \mu m$, n = 32), borne on aerial mycelium, semi-macronematous to macronematous, mononematous, cylindrical, unbranched or rarely branched, septate, hyaline to pale brown, smooth-walled, bearing terminal single phialides. Conidiogenous cells phialidic,

2021, H.W. Shen, H391 (KUN-HKAS 125810, holotype), ex-type culture, KUNCC 22–12459 = CGMCC 3.24275; *ibid*, H411 (KUN-HKAS 125811, paratype), ex-paratype culture, KUNCC 22–12460 = CGMCC 3.24276.

GenBank numbers: KUNCC 22–12459: ITS = OP876713, LSU = OP875069, *tef*1- α = OQ064518. KUNCC 22–12460: ITS = OP876716, LSU = OP875072, *tef*1- α = OQ064520.

Notes: In our phylogenetic analysis, *Neocosmospora* aquatica clustered as a sister taxon to *N. parceramosa* (Fig. 24). *Neocosmospora aquatica* resembles *N. parceramosa* in having simple, hyaline smooth-walled conidiophores, monophialidics, subulate to subcylindrical conidiogenous cells, with a discrete flared collarette and ellipsoidal, subcylindrical to clavate, hyaline, conidia that clustering in false heads at the tip of monophialides. However, *Neocosmospora aquatica* differs from *N. parceramosa* in having aseptate conidiophores and conidia. While, *N. parceramosa* has sepate conidiophores and conidia (Sandoval-Denis et al. 2019). In addition, nucleotide comparison





integrated, terminal, determinate, hyaline, $6-12 \times 3-4 \mu m$ ($\bar{x} = 9.1 \times 3.4 \mu m$, n = 30), cylindrical to subcylindrical, with a discrete flared collarettes, smooth. *Conidia* arranged in false heads on phialide tips, oval, ellipsoidal, clavate, with round ends, hyaline, smooth- and thin-walled, aseptate.

Material examined: CHINA, Yunnan Province, on submerged decaying wood in Chenghai Lake, 28 May 2021, S. Nuan, H314 (KUN-HKAS 125799), living culture, KUNCC 22–12461.

GenBank numbers: ITS = OP876705, LSU = OP875061, $tef1 - \alpha = OQ064516$.

Notes: *Neocosmospora brevis* was described by Sandoval-Denis et al. (2019), which was collected from soil–water polluted with diethyleneglycerol and ethylenglycerol, *Citrus sinensis* and a human eye in Belgium, Italy and the USA (Sandoval-Denis et al. 2019). In this study, a new isolate (KUNCC 22–12461) was identified as *Neocosmospora brevis* based on both phylogenetic and morphological analysis which was collected on submerged decaying wood from freshwater habitats in China. It is a new record for China.

In our phylogenetic analysis, the new isolate clustered with *Neocosmospora brevis* with significant support (Fig. 24). The nucleoide comparision of ITS and tef1- α between our new isolate (KUNCC 22-12461) and Neocosmospora brevis (CBS 130326) revealed 1 bp and 3 bp differences, respectively. Our new isolate is morphologically similar to the holotype of *N. brevis* in having cylindrical, unbranched or rarely branched, septate conidiophores, phialidic conidiogenous cells and oval, ellipsoidal straight or slightly curved, hyaline, smooth- and thin-walled microconidia, the macroconidia were not observed in the new isolate. However, our new isolate (KUNCC 22-12461) has longer conidiophores than the holotype $(100-140 \text{ vs. } 36.5-59 \mu \text{m})$ and aseptate conidia, while the holotype has 0-1(-2)-septate, which may due to their different hosts and habitats. The holotype of N. brevis was collected from soil-water with diethyleneglycerol and ethylenglycerol (Sandoval-Denis et al. 2019). However, our new isolate is a saprobe collected on submerged wood from freshwater habitats.

Neonectria Wollenw., Annls mycol. 15(1/2): 52 (1917).

Neonectria, is a cosmopolitan genus commonly distributed in tropical and temperate regions. The species occur as saprobes, pathogens and some species are isolated as soil inhabitants (Brayford 1993; Chaverri et al. 2011). Species of *Neonectria* sensu lato are characterised by subglobose to broadly obpyriform, smooth to roughened, red perithecia that are becoming dark red in 3% KOH, and with an acute to constricted apex that is sometimes knobby, the perithecial wall is ca. 50 μ m thick and generally composed of two regions, sometimes with an outer region that forms textura epidermoidea, that may or may not be covered with another region of cells; and the ascospores are hyaline, generally bicellular, rarely multi-cellular, and smooth or finely ornamented (Rossman et al. 1999; Chaverri et al. 2011).

Neonectria was linked to the asexual genus Cylindrocarpon. Neonectria and Cylindrocarpon was informally classified into several groups based on the combined morphology of asexual morph and sexual morph (Neonectria into five informal groups and Cylindrocarpon into four groups, Booth 1959, 1966; Brayford and Samuels 1993; Samuels and Brayford 1994). Phylogenetic analysis revealed that Neonectria and Cylindrocarpon are phylogenetically congeneric (Mantiri et al. 2001; Brayford et al. 2004; Seifert et al. 2003). Halleen et al. (2004) introduced a new asexual morph genus Campylocarpon to accommodate C. fasciculare, which is the first formal segregation from Cylindrocarpon. A taxonomic revision of Neonectria sensu lato was provided by Chaverri et al. (2011) based on multi-locus phylogenetic analysis, morphological characters and ecological data. Their phylogenetic analysis showed that five distinct highly supported clades that correspond to some extent with the informal Neonectria and Cylindrocarpon groups. Hence, three genera llyonectria, Rugonectria and Thelonectria were introduced to accommodate three Neonectria sensu lato informal groups. Currently, 55 Neonectria species epithets are listed in the Index Fungorum (2023). However, only N. lugdunensis has been reported from freshwater habitats. This study introduces a new freshwater species *Neonectria aquatica* based on phylogenetic analysis and morphological characters.

Neonectria aquatica D.F. Bao, K.D. Hyde & Z.L. Luo, sp. nov.

Index Fungorum number: IF 900269; Facesoffungi number: FoF 13932; Fig. 26

Etymology: Referring to the aquatic habitat of this fungus.

Holotype: KUN-HKAS 125779.

Saprobic on submerged decaying wood. Sexual morph: Undetermined. Asexual morph: Colonies appearing as white patches on the host, velvety, white, shinning. Mycelium superficial to semi-immersed, consisting of branched, hyaline, septate, smooth hyphae. Conidiophores borne on aerial mycelium, short, mononematous, cylindrical, loosely branched with branches terminating in several phialidies, hyaline, septate, smooth and thin-walled. Conidiogenous cells $17-31 \times 2-4 \ \mu m (\bar{x}=23.9 \times 3.2 \ \mu m, n=30)$, monophialidic, integrated, terminal, determinate, hyaline, cylindrical to subcylindrical, smooth-walled. Conidia $27-31 \times 6-8 \ \mu m$ ($\bar{x}=29 \times 7 \ \mu m, n=40$), acrogenous, solitary, cylindrical with round ends, uniseptate, straight or slightly curved, hyaline, slightly swollen at the apex, smooth- and thin-walled.

Material examined: CHINA, Yunnan Province, Cangshang Mountain, on submerged decaying wood in a stream, 1 March 2019, Z.Q. Zhang, S-3086 (KUN-HKAS 125779, holotype), ex-type culture, KUNCC 22–12462.





GenBank numbers: ITS = OP876733, LSU = OP875087, *tub2* = OQ025197.

Notes: In our phylogenetic analysis, Neonectria aquatica formed a basal clade to N. lugdunensis and N. obtusispora within Neonectria (Fig. 27). Neonectria aquatica is similar to N. lugdunensis and N. obtusispora in having short, mononematous, cylindrical conidiophores loosely branched with branches terminating in several phialidies and cylindrical, straight or slightly curved, hyaline, smooth-walled conidia (Luo and Zhuang 2010b). However, Neonectria aquatica can be distinguished from N. lugdunensis and N. obtusispora by having uniseptate, cylindrical conidia with round ends. While, N. lugdunensis has 0–1 septate conidia that are rounded at the distal end, with a lateral hilum (Luo and Zhuang 2010b) and conidia of *N. obtusispora* are 1-3 septate with rounded apex and somewhat pointed basal cell (Booth 1966). Therefore, we introduce our collection as a new species based on phylogenetic analysis and morphological characters following the guidelines of Chethana et al. (2021).

Paracremonium L. Lombard & Crous, in Lombard, van der Merwe, Groenewald & Crous, Stud. Mycol. 80: 233 (2015).

Paracremonium is an acremonium-like genus, was established by Lombard et al. (2015) with *P. inflatum* as the type species. Eight species were further introduced in the genus (Lynch et al.2016; Crous et al. 2017, 2021a; Zhang et al. 2017, 2021a; Al-Bedak et al. 2019; Ming et al. 2021).

Fig. 27 Phylogenetic tree based on RAxML analyses of a combined ITS, LSU, tef1- α and tub2 dataset. Tree topology of the RAxML, MP and Bayesian analyses are similar. The tree is rooted to Fusarium incarnatum (CBS 161.25) and F. equiseti (NL19-25,004). The combined gene analysis including 62 strains with 2872 characters after aligned including gaps (ITS: 567 bp, LSU: 831 bp, *tef*1-*α*: 819 bp, *tub*2: 655 bp), of which 865 were parsimonyinformative, 137 were parsimony-uninformative and 1870 characters were constant. The RAxML analysis of the combined dataset yielded the best scoring tree with a final ML optimization likelihood value of -18,747.693262. The matrix had 1202 distinct alignment patterns, with 20.40% undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.229010, C = 0.278072, G = 0.258275,T = 0.234642: substitution rates AC = 1.435040, AG = 2.735484, AT = 1.610328, CG = 0.862374, CT = 5.534221, GT = 1.000000; gamma distribution shape parameter $\alpha = 0.217640$. Bootstrap support values for RAxML (blue) and MP (red) greater than 70% and Bayesian posterior probabilities (black) greater than 0.95 are given at each node



Paracremonium is only known by the aseual morphs and characterized by hyaline, septate, branched hyphae which sometimes forming sterile coils from which conidiophores arise (Lombard et al. 2015). Species of *Paracremonium* are widely distributed and have been reported from Canada, California, China, India, Netherlands and Egypt (Lynch et al. 2016; Crous et al. 2017, 2021a; Al-Bedak et al. 2019; Zhang et al. 2021a; Ming et al. 2021). In this study, a new geographic record *Paracremonium binnewijzendii* is described.

Paracremonium binnewijzendii Houbraken, van der Kleij & L. Lombard, in Crous et al., Persoonia 39: 321 (2017).

Index Fungorum number: IF 823317; acesoffungi number: FoF 13933; Fig. 28

Saprobic on submerged decaying wood. Sexual morph: Undetermined. Asexual morph: colonies appearing as white patches on the host, effuse, superficial, gregarious, velvety, white. *Mycelium* superficial to semi-immersed, composed of hyaline, septate, branched, smooth, hyphae. *Conidiophores* borne on aerial mycelium, macronematous, mononematous, branched, hyaline, septate, smooth-walled, bearing branches on conidiophores with phialides in verticils, branching 1–2 levels verticillate, *Conidiogenous cells* $30-45 \times 2-3 \ \mu m \ (\bar{x}=38.9 \times 2.7 \ \mu m, n=20)$, phialidic, integrated, terminal, determinate, hyaline, cylindrical to subcylindrical, with a discrete flared collarettes, smooth-walled. *Conidia* 6–7×4–5 $\mu m \ (\bar{x}=6.5 \times 4.2 \ \mu m, n=30)$, arranged Fig. 28 Paracremonium binnewijzendii (KUN-HKAS 125796) a Colonies on substrate. **b–f** Conidiophores and conidia. **g**, **h** Conidiogenous cells with attached conidium. **i–o** Conidia. **p** Surface view of culture on PDA. **q** Reverse view of culture on PDA. Scale bars: **b-d**=30 μ m, **e**, **f**, **i**=20 μ m, **g**, **h**=10 μ m, **j–o=5** μ m



in false heads on conidiogenous cells tips, solitary, globose to subglobose, ellipsoidal, rounded at both ends, hyaline, aseptate, smooth- and thick-walled.

Culture characteristics: Colonies on PDA, 1.5–2 cm diam after one week at room temperature, margin regular, smooth surface, entire edge, cottony or woolly, whitish, well-defined edges with no pigmentation of the agar, reverse brown to dark yellow ate centre, pale yellow at the edge.

Material examined: CHINA, Yunnan Province, on submerged decaying wood in Chenghai Lake, 28 May 2021, L.L. Li, H372 (KUN-HKAS 125796), living culture, KUNCC 22–12526. CHINA, Yunnan Province, Cangshan Mountain, on submerged decaying wood in a stream, 1 March 2019, Z.Q. Zhang, S3093 (KUN-HKAS 125780), living culture, KUNCC 22–12463.

GenBank number: KUNCC 22–12526: ITS = OP876709, LSU = OP875065, *tub*2 = OQ025189. KUNCC 22–12463: ITS = OP876734, LSU = OP875088, *tub*2 = OQ025198.

Notes: In our phylogenetic analysis, our new isolate clustered with two strains of *Paracremonium binnewijzendii* with 100% ML/ 100% MP/ 1.00 PP support (Fig. 29). *Paracremonium binnewijzendii* was described by Crous et al. (2017), and is characterized by subcylindrical, hyaline, smooth, phialides with an inconspicuous collarette conidiogenous cells and aseptate, ellipsoidal, smooth conidia. Morphologically, our species is almost identical to the holotype of *P. binnewijzendii*, except the conidiophores of our new isolate that bear branches on conidiophores with phialides in verticils, branching 1–2 levels verticillate. Their morphological differences are probably due to the different growing environments and hosts. The holotype of *P. binnewijzendii* was collected in soil from stream embankment in the Netherlands. While, our new isolated was collected on submerged decaying wood from freshwater habitats in China, and it is a new record for China.

Sedecimiella K.L. Pang, Alias & E.B.G. Jones, in Pang, Alias, Chiang, Vrijmoed & Jones, Bot. Mar. 53(6): 495 (2010).

Sedecimiella was introduced with a single species S. taiwanensis by Pang et al. (2010). Sedecimiella taiwanensis is a mangrove-based marine fungus collected from Taiwan, China. Sedecimiella taiwanensis is placed in Hypocreales genera incertae sedis (Pang et al. 2010; Hyde et al. 2020a) and was characterized by orange to dark brown, pyriform



Fig. 29 Phylogenetic tree based on RAxML analyses of a combined ITS, LSU and *tub2* dataset. Tree topology of the RAxML, MP and Bayesian analyses are similar. The tree is rooted to *Nalanthamala vermoesenii* (CBS 230.48 and CBS 110893). The combined gene analysis included 23 strains with 2013 characters after aligned including gaps (ITS: 544 bp, LSU: 864 bp, *tub2*: 605 bp) of which 319 were parsimony-informative, 67 were parsimony-uninformative and 1627 characters were constant. The RAxML analysis of the combined dataset yielded the best scoring tree with a final ML optimization likeli-

with globose to subglobose venter, coriaceous, ostiolate ascomata, two-layered peridium, 16-spored, unitunicate, cylindrical asci with short pedicellate lacking an apical pore and globose, one-celled, hyaline ascospores. In our phylogenetic analysis, *Sedecimiella taiwanensis* clustered with two *Acremonium* species (*A. minutisporum* and *A. vitellinum*) within *Nectriaceae* (Fig. 1). We therefore place *S. taiwanensis* in *Nectriaceae*. However, the relationship between *S. taiwanensis* and the two species of *Acremonium* (*A. minutisporum* and *A. vitellinum*) needs to be resolved.

*Thelonectria*P. Chaverri & Salgado, in Chaverri, Salgado, Hirooka, Rossman & Samuels, Stud. Mycol. 68: 76 (2011).

Thelonectria was introduced to accommodate nectrialike sexual morph and a cylindrocarpon-like asexual morph (Brayford and Samuels 1993; Brayford et al. 2004; Chaverri et al. 2011; Salgado-Salazar et al. 2015, 2016). The genus is typified by *Thelonectria discophora* and is characterized by inconspicuous stromata, superficial, globose, subglobose, or pyriform to elongated and smooth or warty perithecia, a 2–3-layered perithecial wall and smooth, hyaline, 1-septate ascospores. The asexual morphs of *Thelonectria* are *Cylindrocarpon*-like and characterized by microconidia

hood value of—5662.553723. The matrix had 402 distinct alignment patterns, with 18.25% undetermined characters or gaps. Estimated base frequencies were as follows: A=0.231117, C=0.267958, G=0.280534, T=0.220391; substitution rates AC=1.209101, AG=2.644357, AT=1.498111, CG=0.870374, CT=7.193584, GT=1.000000; gamma distribution shape parameter α =0.160525. Bootstrap support values for RAxML (blue) and MP (red) greater than 70% and Bayesian posterior probabilities (black) greater than 0.95 are given at each node

rare, sometimes seen on natural substrata; chlamydospores rare, abundant in one species; conidiophores arising laterally from hyphae, irregularly branched conidiophores or forming fascicles; phialides cylindrical; macroconidia curved, often broadest at upper third, with rounded apical cells and flattened or rounded basal cells, (3-)5-7(-9)- septate, with inconspicuous hilum (Chaverri et al. 2011).

Thelonectria species are commonly found in temperate, subtropical and tropical regions and the taxa occur as saprobes on decaying bark, roots, dead or dying trees and soil (Guu et al. 2007; Chaverri et al. 2011; Salgado-Salazar et al. 2012, 2015). Currently, about 50 species are included in the genus (Index Fungorum 2023). This study introduces two new species of *Thelonectria* based on phylogenetic and morphological analyses.

Thelonectria aquatica D.F. Bao, K.D. Hyde & Z.L. Luo, *sp. nov.*

Index Fungorum number: IF 900270; Facesoffungi number: FoF 13934; Fig. 30

Etymology: Referring to the aquatic habitat of this fungus.

Holotype: MFLU 22-0254.

Fig. 30 Thelonectria aquatica (MFLU 22–0254, holotype). **a–b** Appearance of ascomata on the host. **c**, **d** Section through ascoma. **e** Section of peridium in 3% KOH. **f** Section through peridium. **g** Paraphyses, **h–i** Asci. **j** Ascal apical ring. **k–m** Ascospores. **n**, **o** Culture on PDA. Scale bars: **c–d**=100 μ m, **e**=50 μ m, **f**, **h**, **i**=30 μ m, **g**, **k–m**=10 μ m, **j**=15 μ m



Saprobic on submerged decaying wood. Sexual **morph**: Ascomata 155–285(–305) × 260–356(–378) µm $(\bar{x}=218.8\times 308.4 \,\mu\text{m}, n=5)$, perithecial, superficial or with base partially immersed in substratum on a minute stroma, solitary to gregarious, pyriform to subglobose, slightly papillate, yellow to orange, KOH-, with a darker red ostiolar area when dry, surface smooth to slightly roughened. Peridium 20–40 μ m (\bar{x} = 31.7 μ m, n = 11), comprises two layers, outer layer comprised orange cells of textura angularis to textura prismatica, sometimes with large textura globulosa cells; inner layer pale yellow to hyaline cells of textura prismatica. Paraphyses 4–8 μ m (\bar{x} = 6.0 μ m, n = 20), hyaline, septate, branched, smooth-walled. Asci $(86-)88.5-105(-115) \times 6-9 \ \mu m \ (\bar{x}=96.7 \times 7.5 \ \mu m, n=20),$ unitunicate, cylindrical, 8-spored, with an apical ring. Ascospores $12-14 \times 4-6 \ \mu m \ (\bar{x} = 12.6 \times 4.9 \ \mu m, n = 30)$, uniseriate, ellipsoid to broadly ellipsoid, uniseptate, slightly constricted at the septum, hyaline, guttulate, smooth. Asexual morph: Undetermined.

Culture characteristics: Ascospore germinated on PDA within 24 h. Colonies growing on MEA, reaching 2–2.5 cm in one week at room temperature. Mycelium superficial, circular, with entire margin, flat, smooth, from above white, from below dark yellowish at centre, white at the edge.

Material examined: THAILAND, Nakhon Phanom Province, on submerged decaying wood in a stream, 12 November 2018, D.F. Bao, B-170 (MFLU 22–0254, holotype), extype culture, MFLUCC 22–0169.

GenBank numbers: ITS = OP876736, LSU = OP875057.

Notes: In the phylogenetic analysis, two new isolates *Thelonectria aquatica* and *T. cylindricospora* clustered as sister taxa (Fig. 31). The nucleotide comparison between these species revealed 15 bp (2.7%) differences in the ITS gene region. We therefore identified them as two distinct species in *Thelonectria* as recommended by Jeewon and Hyde (2016).

Thelonectria aquatica is phylogenetically close to *T. beijingensis* (Fig. 31). *Thelonectria aquatica* is similar to

Fig. 31 Phylogenetic tree based on RAxML analyses of a combined act, ITS, LSU, act and *tef1-* α dataset. Tree topology of the RAxML and MP analyses are similar. The tree is rooted to Nectria cinnabarina (A.R. 4477). The combined gene analysis included 55 strains with 2812 characters after aligned including gaps (ITS: 571 bp, LSU: 822 bp, act: 584 bp, tef1- α : 835 bp), of which 531 were parsimony-informative, 237 were parsimony-uninformative and 2044 characters were constant. The RAxML analysis of the combined dataset yielded the best scoring tree with a final ML optimization likelihood value of -14,241.228239. The matrix had 859 distinct alignment patterns, with 27.68% undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.225983, C=0.284387, G=0.261256, T = 0.228374; substitution rates AC=1.159947, AG=2.128499, AT = 1.486238, CG = 1.120206, CT = 4.721893, GT = 1.000000; gamma distribution shape parameter $\alpha = 0.163203$. Bootstrap support values for RAxML (blue) and MP (red) greater than 70% are given at each node



the latter species in having superficial, subglobose to globose, orange red to red ascomata, two layers peridium, subcylindrical asci with an apical ring and uniseriate, fusiform-ellipsoid, uniseptate, hyaline, smooth ascospores. However, *T. aquatica* differs from *T. beijingensis* in having smaller ascomata $(155-285(-305) \times 260-356(-378))$ vs. $320-391 \times 305-385 \mu$ m) and ascospores $(12-14 \times 4-6)$ vs. $13-17 \times 4-7 \mu$ m) (Zeng and Zhuang 2013). In addition,

phylogenetic analysis also showed that they are distinct (Fig. 31).

Thelonectria cylindricospora D.F. Bao, K.D. Hyde & Z.L. Luo, *sp. nov.*

Index Fungorum number: IF 900271; Facesoffungi number: FoF 13935; Fig. 32

Etymology: Referring the cylindrical conidia of this fungus.

Fig. 32 Thelonectria cylindricospora (KUN-HKAS 125812, holotype). a Conidiomata on the host. b Conidiomata with conidia. c-f Conidiophores with conidia. g-j Conidia. k Surface view of culture on PDA. I Reverse view of culture on PDA. Scale bars: $d=30 \mu m$, $c-j=20 \mu m$



Holotype: KUN-HKAS 125812.

Saprobic on submerged decaying wood. Sexual morph: Undetermined. Asexual morph: Conidiomata stromatic, sporodochial, solitary, superficial, hyaline to pale brown. Conidiophores 10–22×2.5–3.5 μ m (\bar{x} =16×3 μ m, n=30), semi-macronematous, sometimes reduced to conidiogenous cells, branched, hyaline, septate, smooth-walled. Conidiogenous cells phialidic, terminal, hyaline. Conidia 41–49.5×5–7 μ m (\bar{x} =45.2×5.8 μ m, n=40), acrogenous, cylindrical with rounded ends, slightly curved, gradually become narrower towards both ends, hyaline, aseptate, guttulate, smooth-walled. *Culture characteristics*: Conidia germinating on PDA within 24 h. Colonies growing slowly on PDA medium, surface velvety, with entire edge, white, dense; center dark yellow, color decreasing from the center to periphery from below.

Material examined: CHINA, Yunnan Province, on submerged decaying wood in a stream, May 2021, H.W. Shen, H385 (KUN-HKAS 125812, holotype), ex-type culture, KUNCC22–12530=CGMCC 3.24277.

GenBank number: ITS = OP876710, LSU = OP875066.

Notes: In our phylogenetic analysis, T. cylindricospora clustered with T. aquatica, T. beijingensis and T. guangdongensis in a monophyletic clade within the genus (Fig. 31). Thelonectria cylindricospora resembles *T. beijingensis* in having branched, septate, hyaline conidiophores and phialidic, terminal, hyaline conidiogenous cells and cylindrical, curved, hyaline conidia. However, *T. cylindricospora* differs from *T. beijingensis* by its reduced and shorter conidiophores (10–22 vs. (28–)30–77(–80) µm) and and shorter conidia (41–49.5 vs. (59–)60–93(–93.5) µm). In addition, conidia of *T. beijingensis* are 0–3-septate, while conidia of *T. cylindricospora* are aseptate (Zeng and Zhuang 2013). *Thelonectria cylindricospora* can be distinguished from *T. guangdongensis* in having aseptate and shorter and wider conidia of *T. guangdongensis* are 2–5-septate (Zeng and Zhuang 2019).

Volutella Fr., Syst. mycol. (Lundae) 3(2): 458, 466 (1832)

Volutella was established by Fries (1832) with V. ciliata (Alb. & Schwein.) as the type species. Currently, 151 records of this genus are listed in the Index Fungorum (2023). However, few species have been revised and transferred to other genera such as Coccinonectria, Lectera, Koorchaloma, Pseudonectria, Scolecofusarium and Volutellonectria (Gräfenhan et al. 2011; Luo and Zhuang 2012; Cannon et al. 2012b; Lombard et al. 2015; Koukol et al. 2020; Crous et al. 2021b) and most species were seldom reported after their original descriptions; Hence the status of these species is still uncertain need to be revised (Gräfenhan et al. 2011). Only 11 species have sequence data in GenBank. Gräfenhan et al. (2011) revised the genus and accepted three species viz. Volutella ciliata, V. consors and V. citrinella in Volutella. Recently, seven additional species are introduced in the genus (Dubey and Pandey 2013; Zhang et al. 2017; Tibpromma et al. 2018; Perera et al. 2020; Lechat et al. 2022).

Luo and Zhuang (2012) established a sexual genus Volutellonectria (Vo.) with Vo. consors as the type and indicated that the asexual morph of this species is represented by Volutella (V.) minima. However, Gräfenhan et al. (2011) synonymised V. minima under Vo. Consors. In addition, they introduced a new species Vo. asiana and a new combination *Vo. ciliata* (= *V. ciliata*) in the genus. Lombard et al. (2015) pointed out that Volutellonectria is confusing in nomenclatural terms and should be replaced by Volutella, which has priority by date. And this treatment was accepted by later studies (Lechat et al. 2022; Perera et al. 2023). Most Volutella species are represented by their asexual morphs, only several species were known as sexual morphs: V. asiana, V. ciliata, V. citronella, V. consors, V. delonicis, V. minutissima, V. saulensis and V. thonneliana (Luo and Zhuang 2012; Perera et al. 2020, 2023; Lechat et al. 2022). The sexual morphs of Volutella are characterized by perithecial, solitary, superficial, obpyriform ascomata with an acute apex, turning dark red in 3% KOH and yellow in lactic acid, unitunicate,

clavate asci with an apical ring and uniseptate, hyaline, often smooth-walled ascospores (Luo and Zhuang 2012; Lechat et al. 2022). The asexual morphs of *Volutella* are characterized by discoid sporodochia with marginal setae, simple to verticillate conidiophores, compact and phialidic conidiogenous cells, and 1-celled, ovoid to oblong conidia; synasexual morph present in some species with two or more whorls of conidiogenous cells (Gräfenhan et al. 2011; Lombard et al. 2015; Tibpromma et al. 2018).

In this study, three fresh collections were collected from freshwater habitats, and were identified as *Volutella ciliata* based on both phylogenetic and morphological analyses. *Volutella ciliata* is the only *Volutella* species reported from freshwater habitats.

Volutella ciliata (Alb. & Schwein.) Fr., Syst. Mycol. 3: 467. 1832.

Index Fungorum number: IF 208513; Facesoffungi number: FoF 11027; Fig. 33

Saprobic on decaying wood submerged in a lake. Sexual morph: Undetermined. Asexual morph: Conidiomata 90–150 µm diam ($\bar{x} = 119.2 \mu m, n = 5$) superficial, solitary to gregarious, hyaline, with a white to buff slimy conidial mass in center, cupulate, setose. Conidiomatal setae $250-360 \times 5-7.5 \ \mu m \ (\bar{x} = 304.9 \times 6.4 \ \mu m, \ n = 25)$, cylindrical, subhyaline to hyaline, septate, unbranched, straight or slightly curved, tapering to apex, swollen terminally or intermediately, smooth-walled. Sporodochia sessile, globose, cream yellow, with several marginal setae. Conidiophores formed from the innermost layers of basal stroma, cylindrical, hyaline, branched or unbranched, septate, smooth-walled. Conidiogenous cells 9-13×1.5-2.5 µm $(\bar{x}=11.1\times2.1 \,\mu\text{m}, n=20)$, phialidic, cylindrical to subcylindrical, integrated, determinate, hyaline, gathered into a dense parallel layer, smooth-walled. Conidia 4-5.5×2-2.5 µm $(\bar{x} = 4.8 \times 2.4 \ \mu m, n = 50)$, forming slimy heads on sporodochium, ellipsoid with round ends, aseptate, hyaline, with small guttules.

Material examined: CHINA, Yunnan Province, Yiliang County, on submerged decaying wood in a stream, 16 May 2021, H.W. Shen, H318 (KUN-HKAS 125813), living culture, KUNCC 22–12532. CHINA, Yunnan Province, Yiliang County, on submerged decaying wood in a stream, 16 May 2021, H.W. Shen, H369 (KUN-HKAS 125816), living culture, KUNCC 22–12474. CHINA, Yunnan Province, Kunming City, on submerged decaying wood in a stream, 10 June 2021, X.G. Tian, L741 (KUN-HKAS 125801), living culture, KUNCC 22–12531.

GenBank numbers: KUNCC 22–12532: ITS = OP876706, LSU = OP875062, *cmd* = OQ025182, *acl* = OQ064513, *rpb2* = OQ077574. KUNCC 22–12474: ITS = OP876708, LSU = OP875064, *cmd* = OQ025183, *his3* = OQ064511, *acl* = OQ064514, *rpb2* = OQ077575. KUNCC 22–12531:

ITS = OP876730, LSU = OP875083, *cmd* = OQ025184, *acl* = OQ064515.

Notes: In our phylogenetic analysis, three new isolates (KUNCC 22–12532, KUNCC 22–12474 and KUNCC 22–12531) clustered with *Volutella ciliata* and two strains of *V. roseola* in a well-supported clade (Fig. 15). The two *V. roseola* strains (CBS 377.55 and CBS 128258) were provided by Vu et al. (2019) without detailed morphological descriptions. Thus, we doubt the two strains are

misidentified based on phylogenetic analysis. However, we are unable to revise these two strains as the morphology of these two strains are not available. Hence, further studies are required to resolve this problem based on morphological and phylogenetic analyses.

Phylogenetic analysis showed that our three new isolates clustered within *V. ciliata* clade. Morphologically, our new isolates fit well with the description of *V. ciliata* (Gräfenhan et al. 2011). Therefore, we identified the three new isolates

Fig. 33 Volutella ciliata (KUN-HKAS 125813). a, b Appearance of conidiomata on the host. c-f Squashed conidioma with setae. g-k Conidiophores, conidiogenous cells and developing conidia. l-r Conidia. s Surface view of culture on PDA. t Reverse view of culture on PDA. Scale bars: c=200 μ m, d=200 μ m, e-f=80 μ m, g-i=20 μ m, j, k=10 μ m, l=30 μ m, m-r=5 μ m







as *V. ciliata*, which is the first time of this species was collected from freshwater habitats.

Sarocladiaceae L. Lombard, in Crous et al., Persoonia 41: 343 (2018).

Sarocladiaceae was recently established by Crous et al. (2018). The family comprises two genera, *Parasarocladium* and *Sarocladium*, placed in *Hypocreales* (Crous et al. 2018; Hyde et al. 2020a). Phylogenetic analysis of Crous et al. (2018) showed that the family is sister to *Bionectriaceae*. While, Hyde et al. (2020a) showed that *Sarocladiaceae* is close to *Flammocladiellaceae*. In our phylogenetic analysis, *Sarocladiaceae* formed a sister clade to

Myrotheciomycetaceae with 86% ML/ 1.00 PP support values (Fig. 1). In this study, *Sarocladium kiliense* was collected from freshwater habitats for the first time in China.

Sarocladium W. Gams & D. Hawksw., Kavaka 3: 57 (1976) [1975].

Sarocladium was established with *S. oryzae* as the type by Gams and Hawksworth (1975). The genus is characterized by cylindrical, phialidic conidiogenous cells and the phialides arise solitarily from undifferentiated hyphae or conidiophores that are sparsely to densely branched, with ellipsoidal conidia formed in false heads (Summerbell et al. 2011; Ou et al. 2020). Summerbell et al. (2011) reviewed



Fig. 35 Phylogenetic tree based on RAxML analyses of a combined *act*, ITS and LSU dataset. Tree topology of the RAxML, MP and Bayesian analyses are similar. The tree is rooted to *Kiflimonium curvulum* (CBS 430.66). The combined gene analysis included 33 strains with 2230 characters after aligned including gaps (*act*: 795 bp, ITS: 573 bp and LSU: 862 bp), of which 338 were parsimony-informative, 198 were parsimony-uninformative and 1694 characters were constant. The RAxML analysis of the combined dataset yielded the best scoring tree with a final ML optimization likelihood

the taxonomy of *Sarocladium* and included the species that belong to the *A. bacillisporum* and *A. strictum* clades and accepted eight species in the genus. Since then, several new species have been introduced to the genus (Yeh and Kirschner 2014; Giraldo et al. 2015; Liu et al. 2017b; Crous et al. 2018; Ou et al. 2020). Currently, 30 species are included in the genus (Index Fungroum 2023).

Species of *Sarocladium* are distributed in many countries e.g., Canada, China, Egypt, Germany, India, Islands, Kenya, Solomon, Sri Lanka and USA, (Summerbell et al. 2011; Giraldo et al. 2012, 2015; Liu et al. 2017b; Crous et al.

value of -10,154.610543. The matrix had 668 distinct alignment patterns, with 23.12% undetermined characters or gaps. Estimated base frequencies were as follows: A=0.224695, C=0.284995, G=0.272715, T=0.217594; substitution rates AC=1.214019, AG=2.132685, AT=1.767746, CG=0.545386, CT=6.639778, GT=1.000000; gamma distribution shape parameter $\alpha=0.163723$. Bootstrap support values for RAxML (blue) and MP (red) greater than 70% and Bayesian posterior probabilities (black) greater than 0.95 are given at each node

2018). They have been reported as plant pathogens, endophytes, mycoparasites (Rivera-Varas et al. 2007), saprobes and a few are opportunistic human pathogens (Rivera-Varas et al. 2007; Yeh and Kirschner 2014; Giraldo et al 2015; Liu et al. 2017b; Crous et al. 2018; Ou et al. 2020).

Sarocladium kiliense (Grütz) Summerb., in Summerbell, Gueidan, Schroers, Hoog, Starink, Arocha Rosete, Guarro & Scott, Stud. Mycol. 68: 158 (2011)

Index Fungorum number: IF 519592; Facesoffungi number: FoF 05816; Fig. 34

Saprobic on decaying wood submerged in a lake. Sexual morph: Undetermined. Asexual morph: Conidiomata sporodochial, superficial, solitary to gregarious, hairy, velvety, brown with white conidia on the conidiomata, setose. Setae up to 400 um, cylindrical, septate, unbranched, flexuous, brown to dark brown, paler towards the apex, smoothwalled. Sporodochia globose, hyaline to subhyaline, with several marginal setae. Conidiophores formed from the innermost layers of basal stroma, reduced to conidiogenous cells, cylindrical, branched or unbranched, hyaline, aseptate, smooth-walled. Conidiogenous cells $10-13 \times 1-2 \mu m$ $(\bar{x} = 11.7 \times 1.6 \ \mu m, n = 30)$, phialidic, cylindrical to subcylindrical, determinate, integrated, hyaline, gathered into a dense parallel layer, smooth-walled. Conidia $5-7 \times 1-2 \,\mu m$ $(\bar{x}=5.9\times1.5 \,\mu\text{m}, n=45)$, narrower cylindrical, clavate, with round ends, aseptate, hyaline, guttulate, smooth-walled.

Material examined: CHINA, Yunnan Province, Dali City, on submerged decaying wood in Haixihai Lake, 22 July 2021, S.P. Huang, L965 (KUN-HKAS 125792), living culture, KUNCC 22–12465.

GenBank numbers: ITS = OP876731, LSU = OP875084. Notes: In our phylogenetic analysis, the new isolate KUNCC 22–12465 clustered with the ex-type strain of Sarocladium kiliense (Fig. 35). Sarocladium kiliense was originally described as Cephalosporium incoloratum by Sukapure and Thirumalachar (1965). It has been synonymized several times, as Acremonium incoloratum (Gams 1971) and Acremonium kiliense (Grütz 1925) based on morphological characters. Summerbell et al. (2011) initially provided the sequence data for this species and based on phylogenetic analysis, they transferred this species to Sarocladium as S. kiliense.

Sarocladium kiliense is ubiquitous, commonly found from soil, also isolated from man, cattle and maize (Sukapure and Thirumalachar 1965). In this study our new isolate was collected on submerged wood from freshwater habitats in China. Morphologically, the conidiogenous cells and conidia of our new isolate are identical to *S. kiliense*. We compared the base pairs differences for the ITS gene region which revealed 2 bp differences. We therefore identified our new isolate as *S. kiliense*, and it is a new record for China.

Stachybotryaceae L. Lombard & Crous, Persoonia 32: 283 (2014).

Stachybotryaceae was introduced by Crous et al. (2014) to accommodate Myrothecium, Peethamabra and Stachybotrys. The taxonomy of this family was revised by Lombard et al. (2016) based on morphological characters and multi-locus phylogenetic analysis. They accepted 33 genera in the family, including 21 new genera. While, Wijayawardene et al. (2018) accepted 36 genera. The last treatment of Stachybotryaceae was provided by Hyde et al. (2020a), and accepted 39 genera. Species in Stachybotryaceae are characterized by asexual morphs with mononematous to

sporodochial to synnematous conidiomata, usually with phialidic conidiogenous cells that produce 0–1-septate conidia in dark green dry chains or slimy masses. Only three species of *Stachybotryaceae* (*Koorchalomella salmonispora, Stachybotrys chartarum* and *S. chlorohalonata*) have been reported from freshwater habitats. In this study, two *Memnoniella* species viz. *Memnoniella echinate* and *M. oenanthes* were collected from freshwater habitats for the first time. *Stachybotrys chartarum* and *S. chlorohalonata* were recollected from freshwater habitats in China.

Memnoniella Höhn., Centbl. Bakt. ParasitKde, Abt. II 60: 16 (1923) [1924].

Memnoniella was introduced by Von Höhnel (1924) based on *M. aterrima*. It is characterized by macronematous, mononematous, unbranched conidiophores, phialidic conidiogenous cells with conspicuous collarettes, and unicellular, aseptate, smooth to verrucose conidia arranged in dry chains or slimy masses. The morphology of Memnoniella and Stachybotrys are similar and several studies have treated them as congeneric. (Jong and Davies 1976; Castlebury et al. 2004; Wang et al. 2015). However, Lombard et al. (2016) showed that Memnoniella species forming a well-supported clade distant to the Stachybotrys clade, hence, Memnoniella was resurrected as a distinct genus in Stachybotryaceae which was accepted by later studies (Doilom et al. 2017; Hyde et al. 2020a; Mapook et al. 2020; Samarakoon et al. 2021). Currently, 24 records of Memnoniella are listed in Index Fungorum (2023), of which 10 species were transferred to other genera viz. Brevistachys and Stachybotrys. In this study, we introduce two new habitat and geographic records of Memnoniella.

Memnoniella echinata (Rivolta) Galloway, Trans. Br. mycol. Soc. 18(2): 165 (1933).

Index Fungorum number: IF 263706; Facesoffungi number: FoF 09367; Fig. 36

Saprobic on submerged decaying wood. Sexual morph: undetermined. Asexual morph: hyphomycetous. Colonies on the substrate superficial, gregarious, velvety, black, hairy. Mycelium mostly immersed in the substratum, composed branched, septate, pale brown to brown, smooth-walled hyphae. Conidiophores $65-100 \times 3-5 \mu m$ ($\bar{x} = 82.3 \times 4.2 \mu m$, n = 15), macronematous, mononematous, cylindrical, simple, erect, straight or slightly flexuous, unbranched or rarely branched, verrucose at surface, thick-walled, often becoming roughened, especially towards the apex, septate, hyaline at the base, olivaceous brown to dark brown at the apex, bearing a crown of phialides at the tip. Conidiogenous cells $7-9 \times 3-5 \ \mu m \ (\bar{x} = 7.7 \times 4.0 \ \mu m, \ n = 25), \ monophialidic,$ determinate, terminal, discrete, obovoid, forming a more or less compact head, with peripheral ones somewhat curved, smooth, sub-hyaline when young, olivaceous brown with age. Conidia $3-4 \times 5-6 \mu m$ ($\bar{x} = 3.6 \times 5.3 \mu m$, n = 30), catenate, often aggregated as large glistening heads in black,

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Fig. 36 Memnoniella echinate (KUN-HKAS 125795). a-c Colonies on substrate. d-h Conidiophores and conidia. i Conidiogenous cells and conidia. j-m Conidia. n Surface view of culture on PDA. o Reverse view of culture on PDA. Scale bars: d-f=30 μ m, h, k-m=20 μ m, i, j=10 μ m

form in a long-chains, globose to subglobose, oval, verrucose at surface, aseptate, olivaceous brown to dark brown.

Culture characteristics: Colonies on PDA attaining 5 cm diam., within three weeks at room temperature, white in the beginning and brown to black with age, greyish white at middle, grey to brown at edge, circular, entire edge with raised on media surface, velvety.

Material examined: CHINA, Yunnan Province, on submerged decaying wood in Chenghai Lake, 28 May 2021, H.W. Shen, H406 (KUN-HKAS 125795), living culture, KUNCC 22–12529.

GenBank numbers: ITS = OP876714, LSU = OP875070, tub2 = OQ025191, $tef1-\alpha = OQ064519$, rpb2 = OQ077577.

Notes: During our investigation of freshwater fungi from China, a stachybotrys-like taxon was collected and identified as *Memnoniella echinata* based on morphology and phylogeny. Our collection fits well with *M. echinata* in having macronematous, mononematous, erect conidiophores,



Fig. 37 Phylogenetic tree based on RAxML analyses of a combined cmd, ITS, *rpb2*, *tef1-\alpha* and tub2 dataset. Tree topology of the RAxML, MP and Bayesian analyses are similar. The tree is rooted to Peethambara sundara (CBS 646.77 and CBS 521.96). The combined gene analysis included 81 strains with 2955 characters after aligned including gaps (cmd: 714 bp, ITS: 602 bp, *rpb*2: 721 bp, *tef*1-α: 545 bp, tub2: 368 bp), of which 1432 were parsimony-informative, 109 were parsimonyuninformative and 1414 characters were constant. The RAxML analysis of the combined dataset yielded the best scoring tree with a final ML optimization likelihood value of -39,090.972868. The matrix had 1736 distinct alignment patterns, with 31.48% undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.232711, C = 0.287296, G = 0.257431.T = 0.222563; substitution rates AC=1.239272, AG=3.467193, AT = 1.311736, CG = 0.931445, CT = 5.548817, GT = 1.000000; gamma distribution shape parameter $\alpha = 0.286873$. Bootstrap support values for RAxML (blue) and MP (red) greater than 70% and Bayesian posterior probabilities (black) greater than 0.95 are given at each node



monophialidic, discrete, determinate, terminal conidiogenous cells and globose to subglobose, olivaceous brown to dark brown, verrucose conidia (Lombard et al. 2016; Tennakoon et al. 2021). Phylogenetic analysis showed that the new collection clustered with four strains of *M. echinata* (Fig. 37). *Memnoniella echinata* has a worldwide distribution, commonly found in soil (Jarvis et al. 1998; Lombard et al. 2016; Tennakoon et al. 2021). Our collection was from submerged wood in freshwater habitats in China for the first time. *Memnoniella oenanthes* (M.B. Ellis) L. Lombard & Crous, in Lombard, Houbraken, Decock, Samson, Meijer, Réblová, Groenewald & Crous, Persoonia 36: 199 (2016).

Index Fungorum number: IF 816007; Facesoffungi number: FoF 13936; Fig. 38

Saprobic on submerged wood in a lake. Sexual morph: undetermined. Asexual morph: colonies on the substrate, superficial, scattered, black. Conidiophores $212-302 \times 6.5-10.5 \ \mu m \ (\bar{x}=257.3 \times 8.4 \ \mu m, n=10)$, cylindrical, solitary, erect, unbranched, straight or flexuous,

a

g

k

Fig. 38 Memnoniella oenanthes (KUN-HKAS 125794). a Colonies on substrate. **b**-e Conidiophores and conidia. **f**-h Conidiogenous cells and conidia. **i**-n Conidia. **o** Surface view of culture on PDA. **p** Reverse view of culture on PDA. Scale bars: **b**-e = 50 μ m, **f**=20 μ m, **g**-n = 10 μ m



m

n

septate, smooth, hyaline to subhyaline at the base, gradually becoming brown to dark brown towards the apex, bearing a crown of phialides at the tip. *Conidiogenous cells* $8.5-12.5 \times 2-4 \ \mu m (\bar{x}=10.5 \times 3.0 \ \mu m, n=20)$, in a single whorl at the apex of the conidiophore, monophialidic, determinate, terminal, ellipsoidal or obovoid, slightly curved, subhyaline to pale brown, smooth or slightly verrucose. Conidia 9–11×4–6 \mu ($\bar{x}=10.1 \times 5.4 \ \mu m, n=30$), solitary, reniform, ellipsoidal, curved, tapering at both ends, pale brown when young, dark brown to black at maturity, aseptate, verrucose.

Culture characters: Colonies on PDA slow growing, reaching 2.5–3.0 cm diam. after 2 weeks at room temperature, white to cream, or pale yellowish at the margins, cream at the centre, distinguished from the margin by white embossed hyphae with grey tufts in the centre; slightly radiating; reverse white cream at the margin, yellowish at the centre.

Material examined: CHINA, Yunnan Province, on submerged decaying wood in Chenghai Lake, 28 May 2021, H.W. Shen, H389 (KUN-HKAS 125794), living culture, KUNCC 22–12473.

GenBank numbers: ITS = OP876712, LSU = OP875068, *tub2* = OQ025190, *rpb2* = OQ077576.

Notes: Memnoniella oenanthes was reported as Stachybotrys oenanthes on dead stems of Oenanthe crocata by Ellis (1971). Lombard et al. (2016) re-evaluated the taxonomy of Stachybotriaceae based on phylogenetic analysis and morphological characters. The phylogenetic analysis showed that S. oenanthes clustered within Memnoniella. They, therefore, transferred S. oenanthes to Memnoniella as M. oenanthes.

Memnoniella oenanthes is characterized by erect, simple, 1-2 septate, solitary, smooth conidiophores, monophialidic, cylindrical or obovoid conidiogenous cells and reniform or ellipsoidal, smooth or verrucose conidia (Eills 1971, 1976; Wang et al. 2015). Our collection fits well with the description of *M. oenanthes* except the size of conidiophores and conidiogenous cells. The conidiophores of our collection are much longer (212–302 vs. 120–180 µm) and conidiogenous cells are smaller (8.5–12.5 × 2–4 vs.12–21 × 4–7 µm)

than the holotype (Ellis 1971, 1976). Phylogenetic analysis showed that our new collection clustered with *M. echinate* with good support (Fig. 37). Thus, we identified our new collection as *M. echinates* based on phylogeny and morphology. *Memnoniella echinate* has been reported as saprobes on the stems of *Euphorbia tirukalli* and *Oenanthe crocata* from Guernsey and India. In this study, our new isolate was collected from freshwater habitats in China and it is a new record for China.

Stachybotrys Corda, Icon. fung. (Prague) 1: 21 (1837).

The asexual genus *Stachybotrys* is ubiquitous distributed worldwide. Species in the genus are common in soil, plant litter (hay, straw, cereal grains, and decaying plant debris) and air and a few species have been found from damp paper, cotton, linen, cellulose-based building materials water-damaged indoor buildings, and air ducts from both aquatic and terrestrial habitats (Izabel et al. 2010; Lombard et al. 2016; Hyde et al. 2020a). *Stachybotrys* was established by Corda (1837) with *S. atrus* as the type. The genus was revised by Lombard et al. (2016), their phylogenetic analysis showed that *Stachybotrys* s.l. is poloyphyletic and it can

be segregated into ten genera, which is also supported by morphological observations. Hence, Lombard et al. (2016) refined the generic concept of *Stachybotrys* in a strict sense as conidiophores branching at the basal septum and the formation of thick-walled conidia sometimes bearing ornamentations.

Stachybotrys has been linked to the sexual genera Melanopsamma (Castlebury et al. 2004; Tang et al. 2007; Wang et al. 2015) and Ornatispora (Hyde and Goh 1999; Whitton et al. 2012; Wang et al. 2015). The sexual morph of M. pomiformis (type species) is linked to S. albipes and this was confirmed by ITS sequence analysis of Wang et al. (2015). Therefore, Wang et al. (2015) synonymized Melanopsamma under Stachybotrys. The sexual genus Ornatispora was introduced by Hyde and Goh (1999), they introduced O. taiwanensis with a Stachybotrys asexual state. In addition, Whitton et al. (2012) linked O. novaezelandiae to S. freycinetiae, and they found that O. nepalensis and O. taiwanensis have Stachybotrys asexual morphs. Morphologies of Ornatispora and Melanopsamma are similar, thus, Wang et al. (2015) synonymized Ornatispora under Stachybotrys.

Fig. 39 Stachybotrys chartarum (KUN-HKAS 125798). a, b Colonies on substrate. c–f Conidiophores. g-h Conidiogenous cells. i–k Conidia. Scale bars: c–f=50 μ m, g, h=20 μ m, i–k=10 μ m



The sexual morphs of *Stachybotrys* are characterized by perithecial, stromatic, ksubglobose to obpyriform, black ascomata with setae irregularly arranged over the surface, clavate, 8-spored asci with a refractive apical ring and cylindrical, 1-septate, subhyaline, verrucose, ascospores with slightly tapering apices, surrounded by a thick mucoid sheath (Lombard et al. 2015).

There are 88 records of *Stachybotrys* on Species Fungorum of which 33 species have DNA sequence data in GenBank. Recently, Samarakoon et al. (2021) introduced a new species *S. musae* on Banana. Currently, 88 species are included in the genus, of which, only *Stachybotrys char-tarum* and *S. chlorohalonatus* have been reported from freshwater habitats. In this study, we reported *S. chartarum* and *S. chlorohalonatus* from freshwater habitats again.

Stachybotrys chartarum (M.B. Ellis) L. Lombard & Crous, in Lombard, Houbraken, Decock, Samson, Meijer, Réblová, Groenewald & Crous, Persoonia 36: 199 (2016).

Index Fungorum number: IF 306362; Facesoffungi number: FOF01247; Fig. 39

Fig. 40 Stachybotrys chlorohalonata (KUN-HKAS 125806).
a, b Colonies on substrate.
c-i Conidiophores and conidia.
j-k Conidiogenous cells.
l-p Conidia. q Surface view of culture on PDA. r Reverse view of culture on PDA. Scale bars: c-e=50 μm, f-i=30 μm, j-p=10 μm Saprobic on decaying wood submerged in a lake. Sexual morph: Undetermined. Asexual morph: Colonies on the substrate, superficial, effuse, in groups, dark brown to black. Conidiophores $35-75.5 \times 3-5 \mu m$ ($\bar{x}=55.2 \times 3.7 \mu m$, n=25), macronematous, mononematous, single or in groups, verrucose, branched, straight to slightly flexuous, brown to olivaceous brown, septate, terminating with a crown of phialides at the apex. Conidiogenous cells $9.5-11 \times 3-5 \mu m$ ($\bar{x}=10.2 \times 3.9 \mu m$, n=15), monophialidic, terminal, discrete, in groups of 4–6 at the apex of each conidiophore, clavate to subclavate, reddish brown, with a minute collarette at the tip. Conidia $11-15 \times 6.5-15 \mu m$ ($\bar{x}=8.5 \times 13.5 \mu m$, n=30), acrogenous, globose to subglobose, verucose, aseptate, thick-walled, dark brown to black.

Material examined: CHINA, Yunnan Province, on submerged decaying wood in Chenghai Lake, 26 May 2021, H.W. Shen, H421 (KUN-HKAS 125798), living culture, KUNCC 22–12469. CHINA, Yunnan Province, on submerged decaying wood in Xihu Lake, 8 May 2021, S.P. Huang, L419 (KUN-HKAS 125781), living culture, KUNCC 22–12470. CHINA, Yunnan Province, on submerged decaying wood in Erhai Lake, 1 April 2021, S.P. Huang, L228 (KUN-HKAS 125791), living culture, KUNCC 22–12471. CHINA, Yunnan Province, on submerged decaying wood in Xihu Lake, 8 May 2021, S.P. Huang, L420 (KUN-HKAS 125783), living culture, KUNCC 22–12472.

GenBank numbers: KUNCC 22–12469: ITS = OP876717, *rpb2* = OQ077578. KUNCC 22–12470: ITS = OP876722, LSU = OP875075, *rpb2* = OQ077581. KUNCC 22–12471: ITS = OP876718, *rpb2* = OQ077579. KUNCC 22–12472: ITS = OP876723, LSU = OP875076, *rpb2* = OQ077582.

Notes: In our phylogenetic analysis, four new isolates clustered with *Stachybotrys chartarum* with 100% ML/ 99% MP/ 1.00 PP support (Fig. 37). Morphologically, our isolates fit well with the description of *S. chartarum*, such as macronematous, mononematous, simple, erect, verrucose conidiophores, monophialidic, terminal, discrete conidiogenous cells and verrucose, aseptate conidia (Ellis 1971; Jong and Davis 1976; Matsushima 1975; Elidemir et al. 1999; Whitton et al. 2001; Wang et al. 2015). However, the conidia of our new isolates are globose to subglobose, while *S. chartarum* has ellipsoidal conidia (Elidemir et al. 1999).

Stachybotrys chartarum has a worldwide distribution and is often found in soil. It is reported as plant and human pathogens, saprobes and endophytes from aquatic and terrestrial habitats (Ellis 1971; Matsushima 1975; Jong and davis 1976; Elidemir et al. 1999; Whitton et al. 2001; Wang et al. 2015; Lombard et al. 2016). Luo et al. (2019) firstly reported *S. chartarum* from freshwater habitats. In this study, we recollected *S. chartarum* from freshwater habitats in China.

Stachybotrys chlorohalonata B. Andersen & Thrane [as 'chlorohalonata'], in Andersen, Nielsen, Thrane, Szaro, Taylor & Jarvis, Mycologia 95(6): 1228 (2003).

Index Fungorum number: IF 626958; Facesoffungi number: FoF 05447; Fig. 40

Saprobic on decaying wood submerged in a lake. Sexual morph: Undetermined. Asexual morph: Colonies on the substrate, superficial, effuse, dark brown to black. Con*idiophores* $36.5-68 \times 3-4 \ \mu m \ (\bar{x} = 52.4 \times 3.5 \ \mu m, n = 20),$ macronematous, mononematous, branched, verrucose, branched, straight to slightly flexuous, subhyaline to hyaline at the base, gradually becoming brown to dark brown towards the apes, smooth or slightly verrucose at maturity, granulate on the surface, septate, terminating with a crown of phialides at the apex. Conidiogenous cells $7-9 \times 2-4 \mu m$ $(\bar{x}=7.9\times3.2 \,\mu\text{m}, n=20)$, monophialidic, discrete, determinate, terminal, clavate to subclavate, subhyaline when young, grey to greyish brown, smooth-walled, with conspicuous collarettes. Conidia $8-9 \times 5-8 \ \mu m \ (\bar{x} = 8.6 \times 6.4 \ \mu m, n = 50)$, acrogenous, ellipsoidal with round ends, verrucose, aseptate, guttulate, thick-walled, olive to dark brown or black.

Culture characteristics: Colonies on PDA reaching 3 cm diam, after 14 days at room temperature, white at first, irregular, raised, undulate, rough, after maturity, smooth at the margin, white from above, reverse cream to yellow at the margin, dark yellowish brown at centre.

Material examined: CHINA, Yunnan Province, on submerged decaying wood in Fuxian Lake, 12 July 2021, H.W. Shen, L496 (KUN-HKAS 125806), living culture, KUNCC 22–12467. CHINA, Yunnan Province, on submerged decaying wood in Fuxian Lake, 12 July 2021, H.W. Shen, L620 (KUN-HKAS 125805), living culture, KUNCC 22–12466. CHINA, Yunnan Province, on submerged decaying wood in Xihu Lake, 8 May 2021, S.P. Huang, L417 (KUN-HKAS 125784), living culture, KUNCC 22–12527. CHINA, Yunnan Province, on submerged decaying wood in Hixihai Lake, 22 July 2021, S.P. Huang, L713 (KUN-HKAS 125793), living culture, KUNCC 22–12468.

GenBank numbers: KUNCC 22-12467: LSU=OP875085, tef1- α =OQ064521, rpb2=OQ077583. KUNCC 22-12466: ITS=OP876726, LSU=OP875079, tef1- α =OQ064523, rpb2=OQ077585. KUNCC 22-12527: ITS=OP876721, LSU=OP875074, rpb2=OQ077580. KUNCC 22-12468: ITS=OP876728, LSU=OP875081, tef1- α =OQ064524, rpb2=OQ077586.

Notes: *Stachybotrys chlorohalonata* was introduced by Andersen et al. (2003) and isolated from cardboard on gypsum board. *Stachybotrys chlorohalonata* likely inhabits wet cellulose-containing materials such as fabric, hay, seaweed, grain, paper and soil and is found in Belgium, Denmark, Finland, Iraq, New Guinea, Spain and the USA. This study collected four fresh collections from freshwater habitats in China. Phylogenetic analysis showed that the four new isolates grouped with *S. chlorohalonata* (Fig. 37). With identical morphology to each, they were identified as *S. chlorohalonata*.

Hypocreales genera incertae sedis.

Emericellopsis J.F.H. Beyma, Antonie van Leeuwenhoek 6: 264 (1940) [1939].

Emericellopsis was described by Van Beyma (1940) with *E. terricola* as the type species. Since then, several species have been introduced worldwide in various habitats such as agricultural and forest soils, peat, rhizomes, prairies and freshwater-, estuarine- and marine-mud sediments (Stolk 1955; Gilman 1957; Mathur and Thirumalachar 1960, 1962; Backus and Orpurt 1961; Davidson and Christensen 1971; Zuccaro et al. 2004; Grum-Grzhimaylo et al. 2013). The placement of *Emericellopsis* has been revised several times by different authors. Emericellopsis was initially placed in Eurotiales (Van Beyma 1940). Phylogenetic analysis of *Emericellopsis* was firstly provided by Glenn et al. (1996) and placed in Hypocreales. Ogawa et al. (1997) set Emericellopsis in Hypocreaceae based on SSU and LSU sequence data. Subsequently, the genus was transferred to Bionectriaceae (Rossman et al. 1999, 2001; Grum-Grzhimaylo et al. 2013). Recently, Crous et al. (2018) transferred Emericellopsis to Myrotheciomycetaceae based on phylogenetic analysis. However, they did not include the type species of *Emericel*lopsis (E. terricola) in their phylogenetic analysis.

In our phylogenetic analysis, Emericellopsis did not cluster within Myrotheciomycetaceae. It grouped with an Acremonium clade (including four species, A. alternatum, A. charticola, A. sclerotigenum and A. tubakii) and an unverified clade which comprises four species (A. fusidioides, Bulbithecium hyalosporum, Hapsidospora irregularis, and Leucosphaerina arxii) within Hypocreales with high support (95%ML/ 1.00 PP, Fig. 1). We, therefore, exclude Emericellopsis from Myrotheciomycetaceae. Our phylogenetic analysis showed that *Bionectriaceae*, *Tilachlidiaceae*, Emericellopsis, an Acremonium clade (including four species, A. alternatum, A. charticola, A. sclerotigenum and A. tubakii) and an unverified clade (A. fusidioides, B. hyalosporum, H. irregularis, and L. arxii) formed a monophyletic clade within Hypocreales (Fig. 1). Thus, this clade may need further revision as to whether they should be combined in Bionectriaceae. However, based on our current phylogenetic analysis, we place Emericellopsis in Hypocreales genera incertae sedis.

Microascales Luttr. ex Benny & R.K. Benj., Mycotaxon 12(1): 40 (1980).

The last treatment of *Microascales* was provided by Wijayawardene et al. (2022) comprising seven families viz. *Ceratocystidaceae*, *Chadefaudiellaceae*, *Gondwanamycetaceae*, *Graphiaceae*, *Halosphaeriaceae*, *Microascaceae* and *Triadelphiaceae*. Our phylogenetic analysis, includes all the families of *Microascales* except *Chadefaudiellaceae* which lacks sequence data. Our phylogenetic analysis showed that *Ceratocystidaceae*, *Graphiaceae*, *Microascaceae* and *Triadelphiaceae* formed well-supported monophyletic clades

within Microascales (Fig. 1). While, Halosphaeriaceae is polyphyletic in our phylogenetic tree, the monotypic genera Nautosphaeria and Tubakiella are clustered out of Halosphaeriaceae (Fig. 1). Previous phylogenetic studies of Nautosphaeria and Tubakiella showed that the two genera always clustered together and were basal to Halosphaeriaceae (Sakayaroja et al. 2005a, b, 2011), while our phylogenetic analysis showed that Nautosphaeria and Tubakiella clustered together in an independent lineage within Microascales which is consistent with Hyde et al. (2020a). Hence, Nautosphaeria and Tubakiella are excluded from Halosphaeriaceae and placed in Microascales genera incertae sedis. In addition, our phylogenetic analysis showed that Cornuvesica species formed a monophyletic clade within Microascales (Fig. 1). Thus, a new family Cornuvesicaceae is introduced for Cornuvesica based on phylogenetic analysis, divergence time estimates and morphology.

Cornuvesicaceae D.F. Bao, K.D. Hyde & Z.L. Luo, *fam* . *nov*.

Index Fungorum number: IF 900272; Facesoffungi number: FoF 13937.

Etymology: Named after the type genus, Cornuvesica.

Type genus: *Cornuvesica* C.D. Viljoen, M.J. Wingf. & K. Jacobs.

On wood. Sexual morph: Ascomata superficial, scattered or in groups, dark, brown to black. Peridium firm, pseudoparenchymatous, textura epidermoidea to angularis. Ostiole hyphae convergent, compactly adhered to each other, pale brown to hyaline. Paraphyses terminating in obtuse apices, converging to form a narrow opening or slightly protruding beyond apical part of neck. Asci evanescent, deliquescing at an early stage. Ascospores falcate, straight or slightly curved, 1-septate, subhyaline, surrounded by hyaline sheath with both ends attenuated. Asexual morph: thielaviopsislike with two distinct ranges of conidial dimensions. Microconidiophores abundant, straight, unbranched or branched, hyaline or rarely pale brown, smooth, septate. Macro-conidiophores less common than those of smaller size, formed on hyphae originated from perithecium, straight, unbranched or branched, pale brown to brown, smooth-walled, septate. Micro-conidiogenous cells phialidic, collarette in distinct, hyaline or occasionally pale brown, discrete or integrated, intercalary or terminal, cylindrical gradually tapering to the apex. Macro-conidiogenous cells phialidic, collarette indistinct, pale brown, discrete or integrated, intercalary or terminal, cylindrical gradually tapering to the apex. Micro-conidia hyaline, oblong with truncate ends, aseptate, smooth-walled, in chains, endogenous. Macro-conidia hyaline, doliiform, aseptate, smooth-walled, in chains, endogenous (Viljoen et al. 2000; Marincowitz et al. 2015).

Notes: Cornuvesica was introduced by Viljoen et al. (2000) to accommodate *Ceratocystiopsis falcata*, originally placed in *Ceratocystis* (Wright and Cain 1961). A

phylogenetic analysis based on SSU sequence data showed that *Cornuvesica* clustered as a sister clade to *Ceratocystis* within *Microascales* (Hausner and Reid 2004). Therefore, *Cornuvesica* was placed in *Ceratocystidaceae* based on phylogenetic analysis (Réblová et al. 2011; de Beer et al. 2013a, 2014). Marincowitz et al. (2015) introduced three additional species in the genus. They reconstructed the phylogenetic analysis for *Cornuvesica* based on SSU and LSU sequence data and the result showed that *Cornuvesica* formed a monophyletic clade sister to *Ceratocystidaceae* within *Microascales*. Marincowitz et al. (2015) further placed *Cornuvesica* in *Microascales* genera *incertae sedis*. The placement of the genus was accepted by Hyde et al. (2020a) and Wijayawardene et al. (2020).

In our phylogenetic analysis, *Cornuvesica* formed a monophyletic clade grouping with *Ceratocystidaceae*,

Graphiaceae, Gondwanamycetaceae and two strains of Sporendocladia bactrospora (Microascales genera incertae sedis) (Fig. 1). Morphologically, Cornuvesica is known by both sexual and asexual morphs. Cornuvesica is different from Ceratocystidaceae in having falcate, straight or slightly curved, 1-septate, subhyaline ascospores. While, ascospores of Ceratocystidaceae are aseptate, hyaline and varied in shape, hat-shaped, ellipsoidal or elongate to slightly curved, with rounded ends, oblong, cylindrical or narrowly fusiform to spindle-shaped. Graphiaceae is only known by the asexual morphs. It is different from Cornuvesica in having macronematous, synnematous conidiophores, conidiogenous cells in whorls of two to six, with annellidic extensions and cylindrical to obovoid conidia often with a distinct basal frill. While Cornuvesica has two types of conidiophores which are mononematous, conidiogenous cells

a g

Fig. 41 Ascosacculus thailandicus (MFLU 22–0255, holotype). \mathbf{a} - \mathbf{b} Appearance of ascomata on the host. \mathbf{c} , \mathbf{d} Section through ascoma. \mathbf{e} - \mathbf{i} Asci. \mathbf{j} - \mathbf{m} Ascospores. \mathbf{n} Paraphyses. Scale bars: \mathbf{c} - \mathbf{d} = 50 µm, \mathbf{e} - \mathbf{h} = 30 µm, \mathbf{j} - \mathbf{n} = 15 µm of *Cornuvesica* are phialidic, collarette in distinct, discrete or integrated, intercalary or terminal and conidia are cylindrical to obovoid, often with a distinct basal frill. *Gondwanamycetaceae* is different from *Cornuvesica* in having hyaline, aseptate, fusiform to lunate or falcate or allantoid ascospores without sheath, mono-verticillate or penicillate conidiophores and cylindrical to allantoid, slimy conidia that are not in chains. Whereas, *Cornuvesica* has falcate or allantoid, 1-septate ascospores surrounded by hyaline sheath with both ends attenuated and *Cornuvesica* has two types of conidiophores which are mononematous, unbranched or branched and conidia are cylindrical to obovoid, often with a distinct basal frill.

In addition, *Cornuvesica* is phylogenetically distinct from *Ceratocystidaceae*, *Graphiaceae*, *Gondwanamycetaceae* (Fig. 1). The stem age of *Cornuvesicaceae* (209.88 MYA) falls within the family range (Hyde et al. 2017). Therefore, a new family *Cornuvesicaceae* is introduced to accommodate

Cornuvesica based on morphology, phylogeny and divergence time estimates.

Halosphaeriaceae E. Müll. & Arx ex Kohlm., Can. J. Bot. 50: 1951 (1972).

Halosphaeriaceae (Microascales, Hypocrealmycetidae) comprises 64 genera (Pang 2002; Jones et al. 2009, 2015, 2017, 2019; Maharachchikumbura et al. 2015; Wijayawardene et al. 2017, 2018, 2022; Hyde et al. 2020a). Species in the family are commonly found in marine habitats and few species are from freshwater and terrestrial habitats (Jones et al. 2009, 2015, 2017, 2019; Hyde et al. 2020a). In our phylogenetic analysis, *Halosphaeriaceae* is polyphyletic and the genera *Nautosphaeria* and *Tubakiella* clustered out of *Halosphaeriaceae* (Fig. 1). Thus, *Nautosphaeria* and *Tubakiella* are excluded from *Halosphaeriaceae* and placed in *Microascales* genera *incertae sedis* based on phylogenetic analysis.

Ascosacculus J. Campb., J.L. Anderson & Shearer, Mycologia 95(3): 545 (2003).

Fig. 42 Phylogenetic tree based on RAxML analyses of a combined LSU, SSU and ITS dataset. Tree topology of the RAxML, MP and Bayesian analyses are similar. The tree is rooted to Cylindrotrichum clavatum (CBS 125239) and C. gorii (DLUCC 0614). The combined gene analysis included 60 strains with 2607 characters after aligned including gaps (LSU: 1040 bp, SSU: 937 bp, ITS: 630 bp), of which 716 were parsimony-informative, 411 were parsimony-uninformative and 1480 characters were constant. The RAxML analysis of the combined dataset yielded the best scoring tree with a final ML optimization likelihood value of -19,573.549836. The matrix had 1232 distinct alignment patterns, with 37.17% undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.252490, C = 0.226587, G = 0.285624,T = 0.235299; substitution rates AC=1.161821, AG=1.973334, AT = 1.190076, CG = 1.054753, CT = 5.721411, GT = 1.000000; gamma distribution shape parameter $\alpha = 0.286939$. Bootstrap support values for RAxML (blue) and MP (red) greater than 70% and Bayesian posterior probabilities (black) greater than 0.95 are given at each node



Ascosacculus was introduced by Campbell et al. (2003) to accommodate two *Halosarpheia* species (*A. aquaticus* and *A. heteroguttulatus*) with *A. aquaticus* as the type species. The genus is known only by sexual moprs and it is characterized by immersed or superficial, globose to subglobose ascomata with long neck, 8-spored, thin-walled, early deliquescent asci, which lacking an apical pore and apical apparatus and fusiform to cylindrical, hyaline, 1-septate ascospores filled with many small guttules and having a hamate appendage at each apex that unfurls to form long, threadlike, sticky appendages (Campbell et al. 2003).

The genus currently comprises three species, and all three were reported from freshwater habitats (Wong et al. 1998; Campbell et al. 2003; Rosique-Gil et al. 2008; Luo et al. 2019). In this study, a new species *A. thailandicus* is introduced, which was collected from a freshwater habitat in Thailand.

Ascosacculus thailandicus D.F. Bao, K.D. Hyde & Z.L. Luo, sp. nov.

Index Fungorum number: IF 900273; Facesoffungi number: FoF 13938; Fig. 41

Etymology: Referring to Thailand, where species was collected.

Holotype - MFLU 22-0255.

Saprobic on decaying wood, submerged in freshwater habitats. Sexual morph: Ascomata 90-200 × 90-130 µm $(\bar{x} = 144.3 \times 109.3 \ \mu m, n = 5)$, immersed to semi-immersed, with a hyaline ostiole on the substrate, scattered, globose to subglobose or pyriform, papillate, hyaline to pale brown. Ostiole central, hyaline. Peridium 17-22 µm wide $(\bar{x} = 19.5 \ \mu m, n = 30)$, comprises two layers, outer layers composed of dark brown cells of textura angularis, inner layer composed rectangular to subglobose hyaline cells. Paraphyses 6–10 μ m (\bar{x} = 7.9 μ m, n = 15), hyaline, septate, constricted at the septa, branched, smooth-walled. Asci $65-80 \times 20-30 \ \mu m \ (\bar{x} = 72.1 \times 25.3 \ \mu m, n = 20), 8$ -spored, unitunicate, obovoid to broadly clavate, sessile to short pedicellate, without an apical ring. Ascospores 25-30×8-10 µm $(\bar{x}=28.6\times9.1 \ \mu m, n=30)$, bi-seriate, hyaline, fusiform to ellipsoidal, straight, with a supra-median primary septum, slightly constrict at the septum, guttulate, smooth-walled, with or without a sheath and appendages. Asexual morph: Undetermined.

Material examined: THAILAND, Nakhon Phanom Province, on submerged decaying wood in a small river, 12 November 2018, D.F. Bao, B-165 (MFLU 22–0255, holotype), ex-type culture, MFLUCC 22–0170.

GenBank numbers: ITS = OP876735, LSU = OP875056, SSU = OP985137, *tef*1- α = OQ064525.

Notes: In the phylogenetic analysis, *Ascosacculus thailandicus* clustered with *A. fusiformis* (MFLUCC 14–0036) with 93% ML/ 82% MP/ 0.98 PP support (Fig. 42). The nucleotide comparison of ITS region between the two

species revealed 5 bp differences. However, the two species differ. *Ascosacculus fusiformis* is characterized by unitunicate, cylindrical, pedicellate asci with a bilateral apical ring and uni-seriate, fusiform, 3-septate, hyaline, smooth-walled conidia with a thin mucilaginous sheath (Luo et al. 2019). While, *A. thailandicus* has obovoid to broadly clavate, sessile to short pedicellate asci and lacks an apical ring, ascospores are bi-seriate, hyaline, fusiform to ellipsoidal, uniseptate, and lack a mucilaginous sheath.

Ascosacculus fusiformis differs from the morphological concepts of the genus, such as having cylindrical, pedicellate asci with an apical ring, and uniseriate, fusiform, 3-septate conidia. Asci of other Ascosacculus species are obovoid to broadly cylindrical lacking an apical ring and ascospores are bi-seriate and uniseptate. Thus, we doubt the reliability of the sequence data of A. fusiformis. Currently, only three species are introduced in the genus and with the few taxa sampled, a clear understanding of the characters of Ascosacculus cannot be provided. Hence, further fresh collections are required to better understand this genus.

Microascaceae Luttr. ex Malloch, Mycologia 62(4): 734 (1970).

Microascaceae was introduced by Luttrell (1951) to accommodate Microascus which was originally placed in Ophiostomataceae (Nannfeldt 1932) or Eurotiaceae (Emmonas and Dodge 1931; Moreau and Moreau 1953; Doguet 1957). Malloch (1970) validated the family and accepted Kernia, Lophotrichus and Petriellidium in the family. Sandoval-Denis et al. (2016a, b) revised Microascaceae and proposed several new taxa and combinations under Microascaceae based on multi-locus phylogenetic analysis. The last treatment of *Microascaceae* was provided by Hyde et al. (2020a), and 23 genera accepted. Species in this family have a worldwide distribution and most species are saprobes in soil, dung or on decaying plant materials (Seifert and Gams 2011; Sandoval-Denis et al. 2016a, b; Hyde et al. 2020a), while a few species are opportunistic pathogens of humans (de Hoog et al. 2011; Sandoval-Denis et al. 2013, 2016a, b; Lackner et al. 2014). In our phylogenetic analysis, Microascaceae clustered basal to Microascales, and the stem age of Microascaceae is around 153 MYA, which falls within the family range (Hyde et al. 2017).

Parascedosporium Gilgado, Gené, Cano & Guarro, Int. J. Syst. Evol. Microbiol. 57(9): 2176 (2007).

Notes: Parascedosporium was established by Gilgado et al. (2007) with *P. tectonae* as the type. *Parascedosporium* is a polymorphic genus with two asexual morphs, one is characterized by solitary conidiophores with sympodial conidia emerging from denticulate conidiogenous cells. The second one showed the features typical of *Graphium* wich has annellidic conidiogenous cells (Gilgado et al. 2007; Lackner and de Hoog 2011).

Fig. 43 Parascedosporium putredinis (KUN-HKAS 125797). **a**, **b** Colonies on substrate. **c**-**e** Conidiophores and conidia. **f**-**i** Conidiogenous cells and conidia. **j**-**n** Conidia. **o** Surface view of culture on PDA. **p** Reverse view of culture on PDA. Scale bars: **c**-**e** = 300 μ m, **f**=30 μ m, **g**, **i**, **m**, **n**=20 μ m, **h**=10 μ m, **j**-**l**=5 μ m



Lackner and de Hoog (2011) examined the ex-type culture (CBS 127.84) of *Parascedosporium tectona* and their phylogenetic analysis based on ITS sequence data showed that *P. putredinis* clustered with *P. tectonae* and there were maximally two base pairs differences within the clade. Therefore, they considered *P. tectona* as a synonym of *P. putredinis*. Later, de Beer et al. (2013b) examined the holotype of *Parascedosporium tectona* (IMI 95673d) and accepted the treatment of Lackner and de Hoog (2011). Zhang et al. (2021b) introduced another species *P. sanyaense* which was initially placed in *Scedosporium*. Zhang et al. (2021b) showed that *Scedosporium sanyaense* clustered with *P. putredinis*. They therefore transferred *Scedosporium sanyaense* to *Parascedosporium* as *P. sanyaense*. There are three *Parascedosporium* species listed in the Index Fungorum (2023). In this study, *P. putredinis* was collected from freshwater habitats in China.

Parascedosporium putredinis (Corda) Lackner & de Hoog, IMA Fungus 2(1): 44 (2011).



Fig. 44 Phylogenetic tree based on RAxML analyses of a combined ITS and LSU dataset. Tree topology of the RAxML, MP and Bayesian analyses are similar. The tree is rooted to *Trichoderma viride* (DAOM JBT1003). The combined gene analysis included 35 strains with 1460 characters after aligned including gaps (ITS: 608 bp and LSU: 852 bp), of which 340 were parsimony-informative, 113 were parsimony-uninformative and 1007 characters were constant. The RAxML analysis of the combined dataset yielded the best scoring tree with a final ML optimization likelihood value of

-7620.970690. The matrix had 567 distinct alignment patterns, with 39.27% undetermined characters or gaps. Estimated base frequencies were as follows: A=0.240472, C=0.261313, G=0.275744, T=0.222471; substitution rates AC=1.665133, AG=2.568340, AT=2.153117, CG=1.775983, CT=5.631232, GT=1.000000; gamma distribution shape parameter α =0.208532. Bootstrap support values for RAxML (blue) and MP (red) greater than 70% and Bayesian posterior probabilities (black) greater than 0.95 are given at each node

Index Fungorum number: IF 519652; Facesoffungi number: FoF 04557; Fig. 43

Saprobic on submerged decaying wood. Sexual morph: Undetermined. Asexual morph: Colonies effuse on natural substrate, scattered, dark brown. Mycelium partly immersed in substrate, composed of septate, branched, dark brown, smooth-walled hyphae. Conidiophores $670-918 \times 13-25 \mu$ m ($\bar{x} = 794 \times 19.1 \mu$ m, n = 15), macronematous, synnematous, arising from a compact basal stroma, consisting of numerous individual conidiophores, erect, straight or flexuous, smooth-walled, dark brown, septate, with flaring conidiogenous head, containing a subhyaline to pale brown, mucoid conidial mass. *Conidiogenous cells* 16–24 \times 1.5–2 µm ($\bar{x} = 20 \times 1.5$ µm, n = 20), monoblastic, terminal, integrated, cylindrical, smooth-walled, hyaline to pale brown. *Conidia* 5–8 \times 3–4 µm ($\bar{x} = 6.3 \times 3.2$ µm, n = 30), acrogenous, solitary, subcylindrical to ellipsoidal, straight, rounded at both ends, aseptate, with small guttules, hyaline, smooth-walled.

Culture characteristics: Conidia germinated within 24 h on PDA, colonies grow rapidly on PDA at room temperature, reaching around 4 cm diam., after three weeks. Colonies on medium appear circular to irregular, medium dense, flat or effuse, with fimbriate edge, colonies from above and below

white to greyish, white at middle, cream to pale grey at edge; reverse pale grey to pale yellowish grey.

Material examined: CHINA, Yunnan Province, on submerged decaying wood in Chenghai Lake, 28 May 2021, H.W Shen, H407 (KUN-HKAS 125797), living culture, KUNCC 22–12464.

GenBank numbers: ITS = OP876715, LSU = OP875071.

Notes: Parascedosporium putredinis was introduced by Lackner and de Hoog (2011). The species has a world-wide distribution and is reported from living plant leaves, seeds of *Tectona grandis*, other plant debris and soil or dung in Czech Republic, France, Jamaica, Japan, Thailand and the United Kingdom. In our phylogenetic analysis, our newly obtained strain clustered with 13 strains of *P. putredinis* with 100% ML/ 100% MP/ 1.00 PP support (Fig. 44). Morphology of our new isolate is quite similar to the holotype (Lackner and de Hoog 2011). Therefore, we identified our new isolate as *P. putredinis* and introduced as a new geographical and habitat record.

Microascales genera incertae sedis

Gabarnaudia Samson & W. Gams, in Samson, Stud. Mycol. 6: 88 (1974).

Gabarnaudia was established by Samson (1974) with G. betae as the type species. Phylogenetic analysis of Hausner and Reid (2004) and de Beer et al. (2013b) showed that G. betae clustered within Sphaeronaemella (Melanconiellaceae, Diaporthomycetidae). Therefore, de Beer et al. (2013b, c) transferred G. betae to Sphaeronaemella. Gabarnaudia fimicola and G. humicola were also transferred to Sphaeronaemella (de Beer et al. 2013c). Currently, only G. cucumeris and G. tholispora are included in Gabarnaudia. Hyde et al. (2020a) and Wijayawardene et al. (2022) placed Gabarnaudia in Microascales genera incertae sedis. However, G. tholispora clustered with Calcarisporium arbuscula within the Hypocreales (de Beer et al. 2013c). Thus, de Beer et al. (2013b) doubted the reliability of sequence data of Gabarnaudia. In our phylogenetic analysis, G. tholispora clustered with Calcarisporium arbuscula within Hypocreales with 100%ML/1.00PP support (Fig. 1), consistent with de Beer et al. (2013b). Hence, the placement of G. tholispora needs further revision based on morphological characters and phylogenetic analysis. Gabarnaudia cucumeris was originally placed in Oospora, De Hoog et al. (1986) transferred it to Gabarnaudia based on morphological characters. However, de Beer et al. (2013c) mentioned that the status of this species is uncertain as the description of this species is not clear and lacks sequence data. Thus, the placement of Gabarnaudia needs revisions based on further morphological and phylogenetic analyses.

Nautosphaeria E.B.G. Jones, Transactions of the British Mycological Society 47 (1): 97 (1964).

Nautosphaeria was introduced by Jones (1964) with a single species N. cristaminuta. Nautosphaeria is characterized by spherical, hyaline to cream-colored ascomata, broadly clavate or ellipsoidal, pedunculate asci and onecelled, ellipsoidal, hyaline ascospores which possess a tuft of bristle-like appendages at each end and four tufts around the equator (Jones 1964). Previsous phylogenetic analysis showed that Nautosphaeria clustered with Tubakiella basal to Halosphaeriaceae (Sakayaroja et al. 2011). However, our phylogenetic analysis showed that N. cristaminuta clustered with Tubakiella galerita in a distinct clade within Microascales (Fig. 1). Hence, Nautosphaeria was excluded from Halosphaeriaceae. Divergence time estimates showed that the stem age of N. cristaminuta + T. galerita is around 181 MYA (Fig. 2). Both phylogenetic analysis and divergence time analysis suggested that N. cristaminuta and T. galerita can be transferred to a new family. However, the phylogenetic status of these two species is not stable. Hence, we place them in Microascales genera incertae sedis and further phylogenetic analysis is needed to clarify their placement.

Tubakiella Sakayaroj, K.L. Pang & E.B.G. Jones, Fungal Diversity 46: 97 (2011).

The monotypic genus *Tubakiella* was introduced with *T. galerita* by Sakayaroj et al. (2011), which was originally placed in *Remispora*. Sakayaroj et al. (2011) showed that two strains of *T. galerita* clustered with *Nautosphaeria cristaminuta* and *Haligena elaterophora* in a monophyletic clade basal to *Halosphaeriaceae*. Hence, Sakayaroj et al. (2011) established *Tubakiella* to accommodate *T. galerita* based on phylogenetic analysis. Hyde et al. (2020a) showed that *T. galerita* grouped with *N. cristaminuta* but clustered out of *Halosphaeriaceae*. Our phylogenetic analysis obtained a similar result (Fig. 1). Hence, *Tubakiella* is excluded from *Halosphaeriaceae* and placed in *Microascales* genera *incertae sedis*. Further phylogenetic studies are required to clarify the placement of *Tubakiella*.

Xenodactylariales D.F. Bao, K.D. Hyde & Z.L. Luo, ord. nov.

Index Fungorum number: IF 900274; Facesoffungi number: FoF 13939.

Type family: *Xenodactylariaceae* Crous, in Crous et al., Persoonia 41: 289 (2018).

Endophytic on plant tissue. *Mycelium* consists of smooth, hyaline, branched, septate, hyphae. *Conidiophores* reduced to conidiogenous cells on hyphae, erect to flexuous, hyaline, smooth-walled, with one to several denticulate apical loci. *Conidia* occurring in branched chains, hyaline, smooth-walled, subcylindrical, septate. (Adapted from Crous et al. 2018).

Notes: Xenodactylariaceae was introduced by Crous et al. (2018) with a single species *X. thailandica* which

was collected on leaves of unidentified vine in Thailand. Phylogenetic analysis of Crous et al. (2018) showed that *X. thailandica* formed a distinct lineage within *Hypocreales* and close to *Ophiocordycipitaceae*. However, Crous et al. (2018) placed the family in *Myrmecridiales, Diaporthomycetidae* (*Sordariomycetes*). Hyde et al. (2020a) showed that *Xenodactylariaceae* grouped within *Hypocreomycetidae* and close to *Torpedosporales*. Recently, a phylogenetic analysis of Hyde et al. (2021) found that *Xenodactylariaceae* did not cluster with members of *Diaporthomycetidae* and suggested excluding this family from *Diaporthomycetidae*.

In our phylogenetic analysis, *Xenodactylariaceae* grouped within *Hypocreomycetidae* as a distinct lineage close to *Torpedosporales* (Fig. 1) which is consistent with the analysis of Hyde et al. (2020a). *Xenodactylariaceae* has subcylindrical, hyaline, septate conidia that are in branched chains. These characters are quite different from *Torpedosporales*; Conidia of *Torpedosporales* are solitary and helicoid e.g. *Juncigenaceae* has single, brown, helicoid conidia and conidia of *Torpedosporaceae* are solitary, irregularly helicoid and muriform (Hyde et al. 2020a). In addition, falls within the order range (Hyde et al. 2017). Thus, we transfer the family to *Hypocreomycetidae* in a newly introduced order *Xenodactylariales* based on the phylogenetic analysis and divergence time estimates.

Hypocreomycetidae families incertae sedis.

Campylosporaceae D.F. Bao, K.D. Hyde & Z.L. Luo, *fam. nov.*

Index Fungorum number: IF 900275; Facesoffungi number: FoF 13940.

Type genus: *Campylospora* Ranzoni, Farlowia 4(3): 373 (1953).

Saprobic on submerged leaves or *endophytic* in plants. Sexual morph: Undetermined. Asexual morph: Colonies hyaline to pale brown hyphae including variously shaped inflated cells. Conidiophores lateral or rarely terminal or intercalary, cylindrical or somewhat nodose, mostly simple or rarely sparsely branched. Conidiogenous cells integrated, typically proliferating sympodially. Conidia tetraradiate, hyaline, composed of two parts, deltoid and allantoid, both with two diverging branches at the ends; deltoid triangular to pyramidal, basal cells with ends rounded; apical cells of both parts rounded; branches aseptate. (Fiuza and Gusmão 2013; Marvanová and Laichmanová 2014).

Notes: The aquatic hyphomycetous genus *Campylospora* was introduced by Ranzoni (1953) with *C. chaetocladia* as the type species. Two additional species viz. *C. filicladia* and *C. parvula* were subsequently introduced in the genus (Kuzuha 1973; Nawawi 1974). Recently, *C. brasiliensis* and *C. leptosome* were introduced in *Campylospora* (Fiuza and Gusmão 2013; Marvanová and Laichmanová 2014). Currently, five species are accepted in the genus. All *Campylospora* species have been reported from freshwater habitats

and are commonly found on submerged leaves or foams in stream. *Campylospora chaetocladia* and *C. parvula* have also been reported as endophytes from terrestrial habitats (Fisher and Petrini 1989; Sati and Belwal 2005). *Campylospora* species are widely distributed in worldwide e.g. Americas, Austria, Brazil, Ecuador, England, Hawaii, India, Malaysia, New Zealand, Peru, the South African Republic, Spain, Thailand, The USA and Venezuela (Nilsson 1962; Cowling 1963; Ranzoni 1979; Tubaki et al. 1983; Arambarri and Spinedi 1984; Aimer and Segedin 1985; Schoenlein-Crusius and Milanez 1990; Sridhar and Kaveriappa 1992; Matsushima 1993; Webster et al. 1994; Malosso 1995; Casas and Descals 1997; Schoenlein-Crusius 2002; Sakayaroj et al. 2005b; Cressa and Smits 2007; Smits et al. 2007; da Silva and Briedis 2009; Fiuza and Gusmão 2013).

Placement of Campylospora was unclear since it was established. Hyde et al. (2020a) and Wijayawardene (2022) place Campylospora in Hypocreomycetidae genera incertae sedis. In our phylogenetic analysis, Campylospora formed a monophyletic clade sister to Falcocladiaceae (the only family in Falcocladiales) within Hypocreomycetidae (Fig. 1). Our phylogenetic analysis suggests it can be introduced as a new family. In addition, the divergence time estimates showed that the stem age of Campylospora is 193.9 MYA which accords with the family level suggested by Hyde et al. (2017). Morphology of *Campylospora* is distinct in the subclass in having tetraradiate conidia, which are composed two parts of deltoid and allantoid, both with two diverging branches at the ends (Fiuza and Gusmão 2013; Marvanová and Laichmanová 2014). Hence, a new family Campylosporaceae is introduced to accommodate Campylospora based on phylogenetic analysis and divergence time estimates.

Excluded from Hypocreomycetidae

Faurelina Locq.-Lin., Revue Mycol., Paris 39(2): 127 (1975).

Faurelina was described by Locquin-Linard (1975) for several cleistothecial ascomycetes. The placement of *Faurelina* is controversial and has been changed many times by different authors (Locquin-Linard 1975; Parguey-Leduc and Locquin-Linard 1976; von Arx 1978; Cannon and Kirk 2007; Tang et al. 2007; Réblová et al. 2011; Maharachchikumbura et al. 2015; Wijayawardene et al. 2017; Hyde et al. 2020a). The last treatment of *Faurelina* was provided by Wijayawardene et al. (2022), and placed in *Chadefaudiellaceae* (*Microascales*).

Tang et al. (2007) firstly provided sequence data for a single strain of *Faurelina indica* (CBS 126.78) and this strain was similar to the type species of *Ceratocystis* (*C. fimbriata*). However, Réblová et al. (2011) doubted the reliability of
this strain. They studied and sequenced two strains of F. indica including the ex-type strain (CBS 126.78), and confirmed that the strain of Tang et al. (2007) was based on different fungus. In addition, phylogenetic analysis of Réblová et al. (2011) showed that the two strains of F. indica have relationship with Didymellaceae (Pleosporales, Dothideomycetes). Therefore, we exclude Faurelina from Chadefaudiellaceae (Microascales). However, Hyde et al. (2020a) and Wijayawardene et al. (2022) placed Faurelina in Chadefaudiellaceae (Microascales). Our study is in agreement with Réblová et al. (2011) excluded Faurelina from Chadefaudiellaceae (Microascales). In our preliminary phylogenetic analysis, F. fimigena and F. indica clustered out of the Sordariomycetes (thus Faurelina was excluded from our phylogenetic analysis). The blast result showed that these two species have higher similarity to Dothideomycetes rather than Sordariomycetes. Our result is consistent with Réblová et al. (2011). Hence, we suggest to exclude Faurelina from Chadefaudiellaceae (Microascales). However, the placement of Faurelina need further studies based on phylogenetic analysis and morphological characteristics.

Discussion

Evolution of Hypocreomycetidae

The evolution of fungi is still a matter of debate (Calabon et al. 2021), and transitions from aquatic to terrestrial habitats have been commonly postulated (Hibbett and Binder 2001). The basal clade of the kingdom *Fungi* is Chytrids, also known as lower fungi, and are mainly found in the freshwater habitats (Raghukumar 2017). They developed uniflagellate zoospores, which helps to disperse in water (Raghukumar 2017). The unicellular group of fungi are thought to have changed their lifestyles several times and developed into multicellular organisms in the terrestrial environment, resulting in Ascomycota and Basidiomycota (Raghukumar 2017). The initial colonizer of terrestrial environment faced harsh physical environment thus, they underwent macroevolutionary jump (Selosse and Le Tacon 1998). The initial terrestrial colonization was formed by the association of fungus and phototrophs (Selosse and Le Tacon 1998). In some lineages, mutualism with fungi was an ancestral feature (Selosse and Le Tacon 1998). The colonization of fungi on land is thought to have started with the establishment of arbuscular mycorrhiza-like symbioses between fungi belonging to Glomeromycota and plant roots (Redecker et al. 2000; Raghukumar 2017). The fungi facilitated nutrient intake of these earlier plants (Bidartondo et al. 2011). Later studies revealed that the earliest mycorrhizal symbiosis was formed between Mucoromycota with land plants or dual Mucoromycotina-Glomeromycotina partnerships with land plants (Strullu-Derrien et al. 2014; Rimington et al. 2015; Feijen et al. 2018). Terrestrial fungi may be originated directly from marine or freshwater (Little 1990; Berbee et al. 2017). However, the transition from marine to freshwater is difficult, based on its limited frequency in phylogenies (del Campo and Ruiz-Trillo 2013; Berbee et al. 2017).

Marine Ascomycota have independently derived from terrestrial and freshwater ascomycetes (Spatafora et al. 1998). They clustered as sister clades to terrestrial or freshwater species and several genera of Ascomycota contain terrestrial and freshwater species together with marine species (Raghukumar 2017). Primary marine Ascomycota species are assumed to be derived from the marine environment, and secondary marine species are assumed to have a terrestrial ancestor (Spatafora et al. 1998; Raghukumar 2017). The phylogenetic analyses conducted by Vijaykrishna et al. (2006) showed that freshwater taxa have derived from terrestrial habitats several times independently. The freshwater taxa could be moved from terrestrial when the associated plants invaded water or ran off rainwater and sediments (Vijaykrishna et al. 2006). Evidently, some freshwater Ascomycota mainly occur on bamboo and in many countries, bamboo grows near river banks (Vijaykrishna et al. 2006). Freshwater Ascomycota shows various adaptations to aquatic environments, such as enhanced mechanisms for dispersal and subsequent attachment in freshwater (Vijaykrishna et al. 2006) and various environments (Ruisi et al. 2007). The freshwater Sordariomycetes reported in this study mainly occur on decayed wood in submerged lakes, rivers and streams. Vijaykrishna et al. (2006) also stated the potential of aquatic fungi to degrade submerged substrates which help the survival in water-logged conditions. Goh and Hyde (1996) proposed four artificial groups of hyphomycetes based on occurrences, namely 1) ingoldian fungi, 2) aero-aquatic hyphomycetes, 3) terrestrial-aquatic hyphomycetes and 4) submerged-aquatic hyphomycetes. Aero-aquatic hyphomycetes are mainly reported from ponds, ditches, or slow-running streams. They are characterized primarily by conspicuous conidiophores which occur in submerged leaves or woody substrates under semi-anaerobic conditions. Our new collections of Clonostachys rosea, Gliomastix masseei and Memnoniella echinate show visible larger conidiophores and are reported from submerged decaying wood near the lakes.

Despite being one of the largest classes, freshwater *Sor-dariomycetes* account for more than 60% of total freshwater ascomycetes (Shearer and Raja 2013). Samarakoon et al. (2016) and Hongsanan et al. (2017) studied several subclasses of unitunicate fungi based on divergence time estimate analysis. Hyde et al. (2021) recently reviewed the evolution of freshwater *Diaporthomycetidae* based on molecular clock analyses. In addition, evolutionary studies have been mostly conducted for *Halosphaeriaceae* and

related orders such as *Koralionastetales* and *Lulworthiales* (Raghukumar 2017). In the study of Spatafora et al. (1998), marine *Halosphaeriales* (*Microascales*) species showed the independent evolution from terrestrial environment based on phylogenetic analyses. Further species of *Halosphaeriaceae* clustered as sister clades to terrestrial or freshwater species, and several genera of *Ascomycota* contain terrestrial and freshwater species together with marine species (Raghukumar 2017). As for accommodating freshwater, marine and terrestrial fungi, studying the evolution of *Hypocreomycetidae* are important for understanding the possible transition and evolution of aquatic and terrestrial ascomycetes.

In this study, we tried to address the possible evolutionary transitions of aquatic Hypocreomycetidae with broad taxon sampling. The result supports the transition of aquatic Hypocreomycetidae from terrestrial habitat to freshwater and marine habitats. Our finding concurred with the study of Vijaykrishna et al. (2006) who stated the evolution of freshwater ascomycetes form terrestrial habitats based on molecular phylogeny. Several molecular studies also stated the close association of several aquatic ascomycetes with terrestrial relatives (Liew et al. 2002). Shearer (1993) noted the evolution of aquatic hyphomycetes from terrestrial plantassociated or litter-associated fungi (Shearer 1993; Selosse et al. 2008), which was later supported in other ascomycetous fungi (Baschien et al. 2013). In the present study, the aquatic hyphomycetes, Clonostachys rosea, Gliomastix masseei and Memnoniella echinate were first reported from freshwater habitats. In contrast, previously they have been reported only in terrestrial habitats. However, we could not find a firm conclusion of the origin for these aquatic hyphomycetes. The early diverging clades of Hypocreomycetidae mostly comprise terrestrial fungi, while the marine and freshwater species show secondary independent evolution, represented by the order *Glomerellales* (Figs. 1, 2). The crown clade is represented by Nectriaceae (Hypocreales), which moderately comprises all three habitats with terrestrial ancestors. The following clades are represented by Coronophorales and Falcocladiales, which entirely include terrestrial fungi. The adjacent clade represents Torpedosporales which constitutes all three habitats, whereas a single species from the terrestrial habitat represents the next clade Xenodactylariales. Halosphaeriaceae (Microascales) clade mainly represents marine fungi, and only a few species show terrestrial and freshwater habitats that were secondarily derived. The representative families of Microascales, including Ceratocystidaceae, Cornuvesicaceae, Gondwanamycetaceae, Graphiaceae and Microascaceae, entirely accommodate terrestrial fungi, while Triadelphiaceae comprises a few freshwater fungi. The specific morphological adaptations observed among the representative species in various habitats were discussed under morphological adaptions of freshwater Hypocreomycetidae. However, no clear pattern in habitual transitions were observed within several lineages, and the absence of molecular data for several genera of the subclass renders the definitive conclusion. The details studies on fungal adaptation strategies, sexual and asexual connections, and their evolutionary changes can provide more information about their origin.

Divergence time estimates of *Hypocreomycetidae*

The divergence time estimates revealed that Hypocreomycetidae evolved during the early Permian (251-290 MYA) (Hyde et al. 2017, 2020a; Dayarathne et al. 2019). In this study, the estimated crown age of Hypocreomycetidae (290 MYA) is similar to previous studies and falls within the early Permian period (Hyde et al. 2017, 2020a; Dayarathne et al. 2019). However, previous studies used different methods to calibrate the evolution tree. Hyde et al. (2017) used fossil data (Paleoophiocordyceps coccophagus) and two secondary calibrations (the divergence time of Sordariomycetes and Leotiomycetes and crown age of Sordariomycetes). Dayarathne et al. (2019) used Paleoophiocordyceps coccophagus fossil data, and crown age of Sordariomycetes as secondary calibration and Hyde et al. (2020a) used two secondary calibrations (crown ages of Sordariomycetes and Dothideomycetes). In this study, we used Paleoophiocordyceps coccophagus fossil data and the crown age of Sordariomycetes as secondary calibration. The result showed that the stem and the crown age of Hypocreomycetidae are around 290 and 302 MYA, respectively. The crown ages of several orders in Hypocreomycetidae viz. Coronophorales (220 MYA), Glomerellales (218 MYA), Hypocreales (222 MYA), Microascales (249 MYA), and Torpedosporales (175 MYA) lie within the Jurassic period (251.9–201.3 MAY). The Jurassic period had a warm climate, which promoted the flourishing of gymnosperms and true ferns, and formed vast forests covering the world, which providing various hosts for fungi. In addition, during the mass extinction event, the death of animals or insect also provided nutrients for fungi to survive and diversify during this period.

Studies suggested that basal fungi originated from aquatic habitats and fungal territorialization occurred during the Cambrian, over 500 million years ago (MYA) (Taylor and Osborn 1996; Brundrett 2002; Wijayawardene et al. 2018). *Ascomycota* and *Basidiomycota* are divergent at a similar time with the fungal territorialization and evolved from terrestrial ancestors (Vijaykrishna et al. 2006; James et al. 2006; Liu et al. 2006; Lucking et al. 2009; Gueidan et al. 2011; Hyde et al. 2021). Based on the molecular clock and ancestral state analysis, freshwater taxa in *Hypocreomycetidae* have evolved from terrestrial ancestors (Fig. 2). They have divergent much later than the terrestrial taxa (Fig. 2).

The *Hypocreomycetidae* may evolved from terrestrial to freshwater habitats in two pathways: 1) fungi may occur initially as pathogens, endophytes or saprobes on plants and they develop adaptation for freshwater when plants invaded freshwater habitats, 2) freshwater fungi may on the branches, stems or leaves in riparian vegetation and these substrates fallen into streams, the fungi colonized and adapted to the freshwater habitats (Shearer 1993; Hyde et al. 2021). Most freshwater *Hypocreomycetidae* have been reported on submerged wood or leaves, supporting Sherear (1993). The evolution of morphological characters in freshwater fungi along the molecular study can provide more information for evolutionary strategies.

Morphological adaptions of freshwater *Hypocreomycetidae*

Fungi show morphological adaptation when they transit from land to aquatic habitats. Sherer (1993) proposed several morphological adaptations of freshwater Ascomycota such as ascospores with appendages or sheaths, which help the ascospores attaching the substrate and remain connected as the water moves (Aniptodera, Ceriospora, Ceriosporopsis and Halosarpheia) (Shearer and Crane 1980; Shearer 1993). Filiform-like ascospores become sigmoid shape in the water which expands the area of the orthogonal projection, while the long filamentary shape enhances entanglement with the matrix (Webster and Davey 1984; Webster 1987). Few genera also developed deliquescent asci, which facilitate the dispersal of ascospores. Massive apical rings of asci also help the strong ejection of ascospores (Hyde and Goh 2003). The asexual freshwater species show branched, tetraradiate, sigmoid, helicosporous, and multicellular air trapping conidia which facilitate the dispersal and attachment of conidia to substrata shapes (Sherer 1993). However, it is hard to conclude that these characteristics have been developed as either pre-adaptation or convergent evolution since these characteristics are also found in terrestrial species (Vijaykrishna et al. 2006).

In our phylogenetic analysis, freshwater *Hypocreomyceti*dae are mainly distributed in *Campylosporaceae*, *Halospha*eriaceae, *Nectriaceae* and *Reticulascaceae* and therefore, our discussion is mainly focused to these families.

The asexual genus *Campylospora* (*Campylosporaceae*) entirely composed of freshwater species. The taxa are characterized by tetraradiate and hyaline conidia composed of two parts, deltoid and allantoid, and both show diverging branches at the ends. The presence of tetraradiate with diverging branches is a typical character of freshwater fungi, which helps the conidia to attach to the substrate and dispersal (Read et al. 1992; Vijaykrishna et al. 2006).

Halosphaeriaceae is a well-studied family with most marine species and few species from freshwater and terrestrial habitats (Pang 2002; Jones et al. 2009, 2015, 2017, 2019; Maharachchikumbura et al. 2015; Wijayawardene et al. 2017, 2018). Molecular data showed that Halosphaeriaceae has a marine ancestor (Fig. 2), which developed morphological adaptations to marine habitats. Based on morphological characters, Vijaykrishna et al. (2006) divided Halosphaeriaceae into two groups: (1) species with early deliquescing asci and appendaged ascospores and (2) species with persistent asci, often with an apical apparatus and mostly with ascospores with polar filamentous unfurling appendages. However, deliquescing asci may not be a good adaptation as deliquescing asci are rarely found in freshwater species (Hyde et al. 2000). The second group are common in freshwater and marine habitats. Persistent asci with an apical apparatus may have the ability to facilitate strong ejection of ascospores and ascospores with polar filamentous unfurling appendages, which is important for dispersal and subsequent attachment in freshwater habitats (Goh and Hyde 1996). Jones (2006) assumed the ancestral ascospore lacked appendages or spore wall ornamentation. Sakavaroj et al. (2011) suggested that the appendages were lost several times during the evolution based on the phylogenetic analysis. However, ascospores of few species lack appendages when they release from the ascus, yet when the ascospores mounted in seawater, which produce apical appendages, but not in freshwater (Savoryella appendiculata, Halosarpheia aquatica, Thalespora appendiculata) (Jones and Hyde 1992; Hyde 1992; Jones 2006). Our phylogenetic analysis showed that freshwater fungi clustered with marine taxa in four clades (Fig. 1). Most freshwater Halosphaeriaceae species have ascospores with appendages, and only a few species lack appendages (e.g. Nais inornata). Thus, we assume that the appendages of these species may be lost during their evolution, as proposed by Sakayaroj et al. (2011).

Nectriaceae is an ecologically diverse group with species that have been found as endophytes, saprobes and pathogens of plants, and some are entomogenous, a few species are human pathogens (Hyde et al. 2020a). Nectriaceae comprises the mostly freshwater taxa of Hypocreomycetidae (Luo et al. 2019). Several freshwater species have also been reported from terrestrial habitats (e.g., Aquanectria penicillioides, Chaetopsina penicillata, Gliomastix masseei, Neocosmospora brevis and Volutella ciliata). Only a few species (e.g. Atractium aquatica and Mariannaea aquaticola) are restricted to freshwater habitats (Luo et al. 2019; Calabon et al. 2022). However, there are no special morphological adaptations have been reported in the freshwater Nectriaceae species except for a few which show apical rings (e.g., A. aquatica, Atractium fusiformis and Thelonectria aquatica), that help the ascospores to release into the water (Vijaykrishna et al. 2006).

Reticulascaceae comprises four genera, two genera (*Cylindrotrichum*; *Cylindrotrichum aquaticum*, *C. gorii*, *C. submersum* and *Kylindria*; *K. aquatica* and *K. chinensis*) include freshwater species but also encompass terrestrial species (Luo et al. 2019). Shearer (1993) mentioned that freshwater fungi adapt to aquatic habitats by their asexual morphs (e.g. hyphomycetes). *Cylindrotrichum* and *Kylindria* were reported in their asexual morphs (Maharachchikumbura et al. 2018; Luo et al. 2019). No definite morphological adaptations were observed among the species except *Kylindria aquatica*, which has conidia with a slimy mucilaginous coating around it (Maharachchikumbura et al. 2018). This indicates the independent evolution of morphological adaption from freshwater to terrestrial habitats.

Diversity of freshwater Hypocreomycetidae

Fungi are ubiquitous and have been found in all habitats. The number of fungi has been estimated between 2.2 and 3.8 million; however, only about 150,600 species of fungi and fungus-like taxa have been so far described (Hyde et al. 2020c; Phukhamsakda et al. 2022; Wijayawardene et al. 2020). Freshwater fungi as a unique ecological group of highly diverse fungi; since Shearer (1993) reported 288 ascomycetes species found in watery settings, and this number has now expanded to 3077 (Calabon et al. 2022). However, many species are yet to be discovered (Bao et al. 2021; Calabon et al. 2022).

Hypocreomycetidae are an ecologically diverse group with species found in various environments. Hu et al. (2013) reported 57 *Hypocreomycetidae* species from freshwater habitats in China, and Luo et al. (2019) documented 76 species. Bao et al. (2021) provided a checklist of freshwater fungi in Yunnan Province during 2015–2020 and listed 21 freshwater *Hypocreomycetidae* species, and most species were collected from submerged decaying wood. In the latest study of Calabon et al. (2022), 156 *Hypocreomycetidae* species have been reported from freshwater habitats, with most documented from Lotic habitats (river and stream) (Calabon et al. 2022). In this study, 26 *Hypocreomycetidae* species have been reported from lentic freshwater habitats (lakes). This indicates that freshwater *Hypocreomycetidae* is highly diverse not only in lotic habitats but also in lentic habitats.

Update of *Hypocreomycetidae* based on the current study

In this section, we provide an updated classification of *Hypocreomycetidae* based on current study and recent publications (Hyde et al. 2020a; Huang et al. 2021; Wijaya-wardene et al. 2022; Xiao et al. 2023; Perera et al. 2023).

Currently, *Hypocreomycetidae* comprises seven orders and 45 families. Herein, an updated outline of *Hypocreomyceti- dae* is provided.

Phylum ASCOMYCOTA Caval-Sm.

Subphylum PEZIZOMYCOTINA O.E. Erikss. & Winka.

Class Sordariomycetes O.E. Erikss. & Winka. Subclass Hypocreomycetidae O.E. Erikss. & Winka Coronophorales Nannf. Bertiaceae Smyk. Bertia De Not. Gaillardiella Pat. Ceratostomataceae G. Winter. Arxiomyces P.F. Cannon & D. Hawksw. Dactylidispora Y. Marín et al. Echinusitheca Y. Marín et al. Erythrocarpon Zukal. Gonatobotrys Corda. Harzia Costantin. Melanospora Corda. Microthecium Corda. Neotrotteria Sacc. Pseudomicrothecium Y. Marín et al. Pustulipora P.F. Cannon. Rhytidospora Jeng & Cain. Scopinella Lév. Setiferotheca Matsush. Syspastospora P.F. Cannon & D. Hawksw. Vittatispora P. Chaudhary et al. Chaetosphaerellaceae Huhndorf et al. Chaetosphaerella E. Müll. & C. Booth. Crassochaeta Réblová. Neochaetosphaerella Lar.N. Vassiljeva et al. Spinulosphaeria Sivan. Coronophoraceae Höhn. Coronophora Fuckel. Nitschkiaceae (Fitzp.) Nannf. Acanthonitschkea Speg. Biciliosporina Subram. & Sekar. Botryola Bat. & J.L. Bezerra. Fracchiaea Sacc. Groenhiella Jørg. Koch et al. Janannfeldtia Subram. & Sekar. Lasiosphaeriopsis D. Hawksw. & Sivan. Loranitschkia Lar.N. Vassiljeva. Nitschkia G.H. Otth ex P. Karst. Rhagadostoma Körb. Rhagadostomella Etayo. Tortulomyces Lar.N. Vassiljeva et al. Parasympodiellaceae Hern.-Restr. et al. Parasympodiella Ponnappa. Scortechiniaceae Huhndorf et al. Biciliospora Petr.

Coronophorella Höhn. Euacanthe Theiss. Neocryptosphaerella S.K. Huang & K.D. Hyde. Neofracchiaea Teng. Pseudocatenomycopsis Crous & L.A. Shuttlew. Pseudocryptosphaerella S.K. Huang & K.D. Hyde. Scortechinia Sacc. Scortechiniella Arx & E. Müll. Scortechiniellopsis Sivan. Tympanopsis Starbäck. Coronophorales genera incertae sedis. Papulaspora Preuss. Sphaerodes Clem. Tengiomyces Réblová. Falcocladiales R.H. Perera et al. Falcocladiaceae Somrithipol et al. Falcocladium S.F. Silveira et al. Glomerellales Chadef. ex Réblová et al. Ascocodinaceae D.F. Bao et al. Ascocodina C.D. Viljoen et al. Australiascaceae Réblová & W. Gams. Monilochaetes Halst. ex Harter. Glomerellaceae Locq. ex Seifert & W. Gams. Colletotrichum Corda. Malaysiascaceae Tibpromma & K.D. Hyde. Malaysiasca Crous & M.J. Wingf. Plectosphaerellaceae W. Gams et al. Acremoniisimulans Tibpromma & K.D. Hyde. Acrostalagmus Corda. Brunneochlamydosporium Giraldo López & Crous. Brunneomyces A. Giraldo, Gené & Guarro. Chlamydosporiella Giraldo López & Crous. Chordomyces Bilanenko et al. Furcasterigmium Giraldo López & Crous. Fuscohypha Giraldo López & Crous. Gibellulopsis Bat. & H. Maia. Lectera P.F. Cannon. Longitudinalis Tibpromma & K.D. Hyde. Musicillium Zare & W Gams. Musidium Giraldo López & Crous. Nigrocephalum Giraldo López & Crous. Paragibellulopsis Giraldo López & Crous. Paramusicillium Giraldo López & Crous. Phialoparvum Giraldo López & Crous. Plectosphaerella Kleb. Sayamraella Giraldo López & Crous. Sodiomyces A.A. Grum-Grzhim. et al. Stachylidium Link. Summerbellia Giraldo López & Crous. Theobromium Giraldo López & Crous. Verticillium Nees. Xenoplectosphaerella Jayaward., Phukhams. & K.D. Hyde.

Cylindrotrichum Bonord. Kylindria DiCosmo et al. Sporoschismopsis Hol-Jech. & Hennebert. Hypocreales Lindau. Bionectriaceae Samuels & Rossman. Acremonium Link. Anthonectria Döbbeler. Aphanotria Döbbeler. Battarrina (Sacc.) Clem. & Shear. Bryocentria Döbbeler. Bryotria Döbbeler & P.G. Davison. Chrysonectria Lechat & J. Fourn. Clibanites (P. Karst.) P. Karst. Clonostachys Corda. Dimerosporiella Speg. Fusariella Sacc. Geonectria Lechat & J. Fourn. Geosmithia Pitt. Gliomastix Guég. Gracilistilbella Seifert. Halonectria E.B.G. Jones. Heleococcum P.M. Jørg. Hydropisphaera Dumort. Laniatria Döbbeler & P.G. Davison. Lasionectria (Sacc.) Cooke. Lasionectriella Lechat & J. Fourn. Mycoarachis Malloch & Cain. Mycocitrus Möller. Nectriella Nitschke ex Fuckel. Nectriopsis Maire. Nigrosabulum Malloch & Cain. Ochronectria Rossman & Samuels. Ovicillium Zare & W. Gams. Ovicuculispora Etayo. Paracylindrocarpon Crous et al. Paranectria Sacc. Periantria Döbbeler & P.G. Davison. Peristomialis (W. Phillips) Boud. Periantria Döbbeler & P.G. Davison. Pronectria Clem. Protocreopsis Yoshim Doi. Pseudoacremonium Crous. Roumegueriella Speg. Selinia P. Karst. Septofusidium W. Gams. Stephanonectria Schroers & Samuels. Stilbocrea Pat. Synnemellisia N.K. Rao et al. Verrucostoma Hirooka et al.

Calcarisporiaceae Jing Z. Sun et al. *Calcarisporium* Preuss.

Verticimonosporium Matsush. Clavicipitaceae (Lindau) Earle ex Rogerson. Aciculosporium I. Miyake. Aschersonia Mont. Atkinsonella Diehl. Balansia Speg. Cavimalum Yoshim. Doi et al. Claviceps Tul. Collarina Giraldo et al. Commelinaceomyces E. Tanaka. Conoideocrella D. Johnson et al. Corallocytostroma Y.N. Yu & Z.Y. Zhang. Dussiella Pat. Ephelis Fr. Epichloë (Fr.) Tul. & C. Tul. Epicrea Petr. Helicocollum Luangsa-ard. Helminthascus Tranzschel. Heteroepichloë E. Tanaka et al. Keithomyces Samson, Luangsa-ard & Houbraken. Konradia Racib. Loculistroma F. Patt & Charles. Marquandomyces Samson, Houbraken & Luangsa-ard. Metapochonia Kepler et al. Metarhiziopsis D.W. Li et al. Metarhizium Sorokīn. Moelleriella Bres. Mycomalus A. Möller. Mycophilomyces Crous & M.J. Wingf. Myriogenospora G.F. Atk. Neobarya Lowen. Neocordyceps Kobayasi. Nigelia Luangsa-ard. Nigrocornus Ryley & Langdon. Orbiocrella D. Johnson et al. Papiliomyces Luangsa-ard, Samson & Thanakitp. Parepichloë J.F. White & P.V. Reddy. Periglandula U. Steiner et al. Petchia Thanakitp., Mongkols. & Luangsa-ard. Pochonia Bat. & O.M. Fonseca. Pseudomeria G.L. Barron. Purpureomyces Luangsa-ard, Samson & Thanakitp. Regiocrella Chaverri & K.T. Hodge. Romanoa Thirum. Rotiferophthora G.L. Barron. Samuelsia Chaverri & K.T. Hodge. Shimizuomyces Kobayasi. Sphaerocordyceps Kobayasi. Sungia Luangsa-ard, Samson & Thanakitp. Tyrannicordyceps Kepler & Spatafora. Ustilaginoidea Bref. Yosiokobayasia Samson, Luangsa-ard & Thanakitp. Cocoonihabitaceae W.Y. Zhuang & Z.Q. Zeng.

Cocoonihabitus W.Y. Zhuang & Z.Q. Zeng. Cordvcipitaceae Kreisel ex G.M. Sung et al. Akanthomyces Lebert. Amphichorda Fr. Ascopolyporus Möller. Beauveria Vuill. Beejasamuha Subram. & Chandrash. Blackwellomyces Spatafora & Luangsa-ard. Cordyceps (Fr.) Link. Coremiopsis Sizova & Suprun. Engyodontium de Hoog. Flavocillium H. Yu et al. Gamszarea Z.F. Zhang & L. Cai. Gibellula Cavara. Hevansia Luangsa-ard et al. Hyperdermium J. White et al. Leptobacillium Zare & W. Gams. Liangia H. Yu et al. Neotorrubiella Tasan., Thanakitp. & Luangsa-ard. Parengyodontium C.C. Tsang. Pseudogibellula Samson & H.C. Evans. Samsoniella Mongkols. et al. Simplicillium W. Gams & Zare. Flammocladiellaceae Crous et al. Flammocladiella Crous et al. Hypocreaceae De Not. Arachnocrea Z. Moravec. Dialhypocrea Speg. Escovopsioides H.C. Evans & J.O. Augustin. Escovopsis J.J. Muchovej & Della Lucia. Hypocreopsis P. Karst. Hypomyces (Fr.) Tul. & C. Tul. = *Cladobotryum* Nees. = Sibirina G.R.W. Arnold. Kiflimonium Summerb., J.A. Scott, Guarro & Crous. Lichenobarva Etayo et al. Mycogone Link. Protocrea Petch. Rogersonia Samuels & Lodge. Sepedonium Link. Sphaerostilbella (Henn.) Sacc. & D. Sacc. = *Gliocladium* Corda. Sporophagomyces K. Põldmaa & Samuels. Stephanoma Wallr. Trichoderma Pers. =*Aphysiostroma* Barrasa et al. =Hypocrea Fr. = Podocrea (Sacc.) Lindau. = Podostroma P. Karst. =*Pseudohypocrea* Yoshim. Doi. = Sarawakus Lloyd. Ijuhyaceae R.H. Perera, E.B.G. Jones, Maharachch., &

K.D. Hyde.

Ijuhya Starbäck = Peristomialis (W. Phillips) Boud. Kallichroma Kohlm. & Volkm.-Kohlm. Myrotheciomycetaceae Crous. Leucosphaerina Arx. Myrotheciomyces Crous. Trichothecium Link. Nectriaceae Tul. & C. Tul. Albonectria Rossman & Samuels. Allonectella Petr. Aphanocladium W. Gams. Aquanectria L. Lombard & Crous. Atractium Link. = Varicosporella Lechat & J. Fourn. Baipadisphaeria Pinruan. Bisifusarium L. Lombard et al. Calonectria De Not. Calostilbe Sacc. & Syd. Campylocarpon Halleen et al. Chaetonectrioides Matsush. Chaetopsina Rambelli. Chrysonectria Lechat & J. Fourn. Cinnamomeonectria Salgado & P. Chaverri. Coccinonectria Lombard & Crous. Corallomycetella Henn. Corallonectria C. Herrera & P. Chaverri. Corinectria C. González & P. Chaverri. Cosmospora Rabenh. Cosmosporella S.K. Huang et al. Curvicladiella Decock & Crous. Cyanochyta Höhn. Cyanonectria Samuels & Chaverri. Cyanophomella Höhn. Cylindrocladiella Boesew. Cylindrodendrum Bonord. Dacryoma Samuels. Dactylonectria L. Lombard & Crous. Dematiocladium Allegr. et al. Fusarium Link. Fusicolla Bonord. Geejayessia Schroers et al. Gliocephalotrichum J.J. Ellis & Hesselt. Gliocladiopsis S.B. Saksena. Globonectria Etayo. Ilyonectria P. Chaverri & C. Salgado. Longinectria O. Savary, M. Coton, E. Coton & J.L. Jany. Luteonectria Sand.-Den., L. Lombard, Schroers & Rossman. Macroconia (Wollenw.) Gräfenhan et al. Macronectria Salgado & P. Chaverri. Mariannaea G. Arnaud ex Samson. Microcera Desm. Nalanthamala Subram.

Nectria (Fr.) Fr. Neocalonectria Crous. Neocosmospora E.F. Sm. Neonectria Wollenw. Nothofusarium Crous, Sand.-Den. & L. Lombard. Ophionectria Sacc. Pandanaceomyces Tibpromma & K.D. Hyde. Paracremonium L. Lombard & Crous. Payosphaeria W.F. Leong. Penicillifer Emden. Persiciospora P.F. Cannon & D. Hawksw. Pleiocarpon L. Lombard & D. Aiello. Pleogibberella Sacc. Pleurocolla Petr. Pseudoachroiostachys Tibpromma & K.D. Hyde. Pseudocosmospora C. Herrera & P. Chaverri. Pseudonectria Seaver. Rectifusarium Lombard et al. Rugonectria P. Chaverri & Samuels. Sarcopodium Ehrenb. Scolecofusarium L. Lombard, Sand.-Den. & Crous. Sedecimiella K.L. Pang et al. Setofusarium (Nirenberg & Samuels) Crous & Sand.-Den. Stylonectria Höhn. Thelonectria P. Chaverri & C.G. Salgado. =Neothyronectria Crous & Thangavel. Thyronectria Sacc. =*Allantonectria* Earle. =Neothyronectria Crous & Thangavel. =Pleonectria Sacc. = Sulcatistroma A.W. Ramaley. =Thyronectroidea. Tumenectria Salgado & Rossman. Varicosporellopsis Lechat & J. Fourn. Vesicladiella Crous & M.J. Wingf. Volutella Fr. Xenoacremonium Lombard & Crous. Xenocylindrocladium Decock et al. Xenogliocladiopsis Crous & W.B. Kendr. Xenoleptographium Marinc. et al. Xenonectriella Weese. Niessliaceae Kirschst. Atronectria Etayo. Circinoniesslia Samuels & M.E. Barr. Cryptoniesslia Scheuer. Eucasphaeria Crous. Malmeomyces Starb. Melchioria Penz. & Sacc. Miyakeomyces Hara. Myrmaeciella Lindau. Myrtacremonium Crous. Neoeucasphaeria Crous. Niesslia Auersw.

=*Hyaloseta* A.W. Ramaley. Nitschkiopsis Nannf. & R. Sant. Paraniesslia K.M. Tsui et al. Pseudohyaloseta Tibpromma & K.D. Hyde. Pseudonectriella Petr. Pseudorhynchia Höhn. Rosasphaeria Jaklitsch & Voglmayr. Taiwanascus Sivan & H.S. Chang. Trichosphaerella E. Bommer et al. Valetoniella Höhn. Valetoniellopsis Samuels & M.E. Barr. Polycephalomycetaceae Y.P. Xiao, Y.B Wang, T.C. Wen, H. Yu & K.D. Hyde. Perennicordyceps Matočec & I. Kušan. Pleurocordyceps Y.J. Yao et al. Polycephalomyces Kobayasi. Ophiocordycipitaceae G.H. Sung et al. Drechmeria W. Gams & H.B. Jansson. Hantamomyces Crous. Harposporium Lohde. Hirsutella Pat. Hymenostilbe Petch. Ophiocordyceps Petch. Paraisaria Samson & B.L. Brady. Purpureocillium Luangsa-ard et al. Tolypocladium W. Gams. Sarocladiaceae L. Lombard. Parasarocladium Summerb. et al. Sarocladium W. Gams & D. Hawksw. Stachybotryaceae L. Lombard & Crous. Achroiostachys L. Lombard & Crous. Albifimbria L. Lombard & Crous. Albosynnema E.F. Morris. Alfaria Crous et al. Alfariacladiella Crous & R.K. Schumach. Brevistachys L. Lombard & Crous. Capitofimbria L. Lombard & Crous. Cymostachys L. Lombard & Crous. Didymostilbe Henn. Digitiseta Gordillo & Decock. Dimorphiseta L. Lombard & Crous. Globobotrys L. Lombard & Crous. Grandibotrys L. Lombard & Crous. Gregatothecium L. Lombard & Crous. Hyalinostachys C.G. Lin & K.D. Hyde. Inaequalispora L. Lombard & Crous. Kastanostachys L. Lombard & Crous. Koorchalomella Chona et al. Melanopsamma Niessl. Memnoniella Höhn. Myrothecium Tode. Myxospora L. Lombard & Crous. Neomyrothecium L. Lombard & Crous.

Paramyrothecium L. Lombard & Crous. Parasarcopodium Mel'nik et al. Parvothecium L. Lombard & Crous. Peethambara Subram. & Bhat. Pseudoornatispora Tibpromma & K.D. Hyde. Septomyrothecium Matsush. Sirastachys L. Lombard & Crous. Smaragdiniseta L. Lombard & Crous. Stachybotrys Corda. Striatibotrys L. Lombard & Crous. Striaticonidium L. Lombard & Crous. Tangerinosporium L. Lombard & Crous. Virgatospora Finley. Xenomyrothecium L. Lombard & Crous. Xepicula Nag Raj. Xepiculopsis Nag Raj. Stromatonectriaceae R.H. Perera, E.B.G. Jones, Maharachch., & K.D. Hyde. Stromatonectria Jaklitsch & Voglmayr. Tilachlidiaceae Lombard & Crous. Psychronectria J. Pawłowska et al. Tilachlidium Preuss. Xanthonectriaceae R.H. Perera, E.B.G. Jones, Maharachch., & K.D. Hyde. Bullanockia Crous. Xanthonectria J. Fourn. & P.-A. Moreau. Hypocreales genera incertae sedis. Acremoniopsis Giraldo et al. Berkelella (Sacc.) Sacc. Bryonectria Döbbeler. Bulbithecium Udagawa & T Muroi. Cephalosporiopsis Peyronel. Chondronectria Etayo et al. Cylindronectria Etayo. Diploöspora Grove. Emericellopsis J.F.H. Beym. Gynonectria Döbbeler. Hapsidospora Malloch & Cain. Haptospora G.L. Barron. Illosporiopsis D. Hawksw. Illosporium Mart. Leptobarya Etayo. Lichenopenicillus Etayo. Metadothella Henn. Munkia Speg. Neomunkia Petr. Peloronectria Möller. Pseudoidriella Crous & R.G. Shivas. Pseudomeliola Speg. Rodentomyces Doveri et al. Roselliniella Vain. Saksenamyces A.N. Rai & P.N. Singh. Stanjemonium W. Gams et al.

Stilbella Lindau. Ticonectria Döbbeler. Trichonectria Kirschst. Tilakidium Vaidya et al. Microascales Luttr. ex Benny & Kimbr. Ceratocystidaceae Locq. ex Réblová et al. Ambrosiella Brader ex Arx & Hennebert. Berkelevomvces W.J. Nel et al. Bretziella Z.W. de Beer et al. Ceratocystis Ellis & Halst. Chalaropsis Peyronel. Davidsoniella Z.W. de Beer et al. Endoconidiophora Münch. Huntiella Z.W. de Beer et al. Meredithiella McNew et al. Phialophoropsis L.R. Batra emend. T.C. Harr. Thielaviopsis Went. Cornuvesicaceae D.F. Bao et al. Cornuvesica C.D. Viljoen et al. Chadefaudiellaceae Faurel & Schotter ex Benny & Kimbr. Chadefaudiella Faurel & Schotter. Gondwanamycetaceae Réblová et al. Custingophora Stolk. Knoxdaviesia M.J. Wingf et al. Graphiaceae De Beer. Graphium Corda. Halosphaeriaceae E. Müll & Arx ex Kohlm. Alisea J. Dupont & E.B.G. Jones. Amphitrite S. Tibell. Aniptodera Shearer & M. Miller. Aniptosporopsis (K.D. Hyde) K.L. Pang. Anisostagma K.R.L. Petersen & Jørg. Koch. Antennospora Meyers. Appendichordella R.G. Johnson et al. Arenariomyces Höhnk. Ascosacculus J. Campbell, J.L. Anderson & Shearer. Bathyascus Kohlm. Carbosphaerella I. Schmidt. Ceriosporopsis Linder. Chadefaudia Feldm.-Maz. Corallicola Volkm.-Kohlm. & Kohlm. Corollospora Werderm. Cucullosporella K.D. Hyde & E.B.G. Jones. Ebullia K.L. Pang. Gesasha Abdel-Wahab & Nagah. Haiyanga K.L. Pang & E.B.G. Jones. Haligena Kohlm. Halosarpheia Kohlm. & E. Kohlm. Halosphaeria Linder. Halosphaeriopsis T.W. Johnson. Havispora K.L. Pang & Vrijmoed. Iwilsoniella E.B.G. Jones.

Kitesporella Jheng & K.L. Pang. Kochiella Sakav. et al. Lautisporopsis E.B.G. Jones et al. Lignincola Höhnk. Limacospora Jørg. Koch & E.B.G. Jones. Luttrellia Shearer. Magnisphaera J. Campb. et al. Marinospora A.R. Caval. Moana Kohlm. & Volkm.-Kohlm. Morakotiella Sakay. Naïs Kohlm. Natantispora J. Campb. et al. Neptunella K.L. Pang & E.B.G. Jones. Nereiospora E.B.G. Jones et al. Nimbospora Jørg. Koch. Nohea Kohlm. & Volkm.-Kohlm. Oceanitis Kohlm. Ocostaspora E.B.G. Jones et al. Okeanomyces K.L. Pang & E.B.G. Jones. Ondiniella E.B.G. Jones et al. Ophiodeira Kohlm. & Volkm.-Kohlm. Panorbis J. Campb. et al. Paraaniptodera K.L. Pang et al. Phaeonectriella R.A. Eaton & E.B.G. Jones. Pileomyces K.L. Pang & Jheng. Praelongicaulis Jones et al. Pseudolignincola Chatmala & E.B.G. Jones. Remispora Linder. Saagaromyces K.L. Pang & E.B.G. Jones. Sablicola E B.G. Jones et al. Thalassogena Kohlm. & Volkm.-Kohlm. Thalespora Chatmala & E.B.G. Jones. Tinhaudeus K.L. Pang et al. Tirispora E.B.G. Jones & Vrijmoed. Toriella Sakay. et al. Trailia G.K. Sutherl. Trichomaris Hibbits et al. Tunicatispora K.D. Hyde. Microascaceae Luttr. ex Malloch. Acaulium Sopp. Brachyconidiellopsis Decock et al. Canariomyces Arx. Cephalotrichum Link. Doratomyces Corda. Echinobotryum Corda. Enterocarpus Locq.-Lin. Fairmania Sacc. Gamsia M. Morelet. Kernia Nieuwl. Lomentospora Hennebert & B.G. Desai. Lophotrichus R.K. Benj. Microascus Zukal. Parascedosporium Gilgado et al.

Petriella Curzi. Pseudallescheria Negroni & I. Fisch. Pseudoscopulariopsis M. Sandoval-Denis et al. Rhinocladium Sacc. & Marchal. Scedosporium Sacc. ex Castell. & Chalm. Scopulariopsis Bainier. Wardomyces F.T. Brooks & Hansf. Wardomycopsis Udagawa & Furuya. Yunnania H.Z. Kong. Triadelphiaceae Y.Z. Lu et al. Synnematotriadelphia Chuaseehar et al. Triadelphia Shearer & J.L. Crane. Microascales genera incertae sedis. Bisporostilbella Brandsb. & E.F. Morris. Cephalotrichiella Crous. Cornuvesica C.D. Viljoen et al. Gabarnaudia Samson & W. Gams. Nautosphaeria E.B.G. Jones. Tubakiella Sakayaroj, K.L. Pang & E.B.G. Jones. Sporendocladia G. Arnaud ex Nag Raj & W.B. Kendr. Torpedosporales E.B.G. Jones et al. Etheirophoraceae Rungjindamai et al. Etheirophora Kohlm. & Volkm.-Kohlm. Swampomyces Kohlm. & Volkm. Juncigenaceae E.B.G. Jones et al. Elbamvcella A. Poli. Fulvocentrum E.B.G. Jones & Abdel-Wahab. Juncigena Kohlm Kohlm. et al. Khaleijomyces Abdel-Wahab. Marinokulati E.B.G. Jones & K.L. Pang. Torpedosporaceae E.B.G. Jones & K.L. Pang. Torpedospora Meyer. Xenodactylariales D.F. Bao et al. Xenodactylariaceae Crous. Xenodactylaria Crous. Hypocreomycetidae families incertae sedis. Campylosporaceae D.F. Bao et al. Campylospora Ranzoni. Hypocreomycetidae genera incertae sedis. Dendroclathra Voglmayr & G. Delgado.

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Declarations

Conflict of interest The authors declare no conflict of interest.

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