bioRxiv preprint doi: https://doi.org/10.1101/2022.07.05.498902; this version posted July 9, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

# Outline and divergence time of subkingdom Mucoromyceta: two new phyla, five new orders, six new families and seventy-three new species

Heng Zhao<sup>1,2,3</sup>, Yu-Cheng Dai<sup>1#</sup>, Xiao-Yong Liu<sup>2,3#</sup>

<sup>1</sup> Institute of Microbiology, School of Ecology and Nature Conservation, Beijing Forestry University, Beijing 100083, China
<sup>2</sup> College of Life Sciences, Shandong Normal University, Jinan 250358, China
<sup>3</sup> State Key Laboratory of Mycology, Institute of Microbiology, Chinese Academy of Sciences, Beijing 100101, China
# Corresponding Author: Yu-Cheng Dai, yuchengdai@bjfu.edu.cn; and Xiao-Yong Liu, 622001@sdnu.edu.cn

#### Abstract

Zygomycetes are phylogenetically early diverged, ecologically diverse, industrially valuable, agriculturally beneficial, and clinically pathogenic fungi. Although new phyla and subphyla have been constantly established to accommodate specific members and a subkingdom, Mucoromyceta, was erected to unite core zygomycetous fungi, their phylogenetic relationships have not been well resolved. Taking account of the information of monophyly and divergence time estimated from ITS and LSU rDNA sequences, the present study updates the classification framework of the subkingdom Mucoromyceta from the phylum down to the generic rank: six phyla (including two new phyla Endogonomycota and Umbelopsidomycota), eight classes, 15 orders (including five new orders Claroideoglomerales, Cunninghamellales, Lentamycetales, Phycomycetales and Syncephalastrales), 41 families (including six new families Circinellaceae, Gongronellaceae, Protomycocladaceae, Rhizomucoraceae, Syzygitaceae and Thermomucoraceae), and 121 genera. The taxonomic hierarchy was calibrated with estimated divergence times: phyla 810–639 Mya, classes 651–585 Mya, orders 570–400 Mya, and families 488–107 Mya. Along with this outline, 71

1

genera are annotated and 73 new species are described. In addition, three new combinations are proposed. In this paper, we update the taxonomic backbone of the subkingdom Mucoromyceta and reinforce its phylogeny. We also contribute numerous new taxa and enrich the diversity of Mucoromyceta.

**Key words:** Early-diverging fungi, Zygomycetes, Phylogenomics, New taxa, Endogonomycota, Umbelopsidomycota

#### Introduction

As an early-diverging group of fungi, zygomycetes are considered an evolutionary transition from ancestral aquatic zoosporic chytrids to terrestrial nonflagellated higher fungi (Spatafora et al. 2016, Voigt et al. 2021), playing a critical role at the dawn of terrestrial life (Berbee et al. 2017). They are ecologically diverse, including pathogens of animals and plants, parasites on other fungi, mycorrhizal symbionts, endophytes, and decomposers of organic matter (Domsch et al. 1980, Yao et al. 1996, Kamei 2000, Zheng et al. 2009, Benny et al. 2014, Rashmi et al 2019, Wagner et al. 2020, Voigt et al. 2021). It is well-known that some zygomycetous fungi are used not only to synthesize industrially valuable products such as glucoamylase, laccase, lipase, polygalacturonase, pectinase, proteases, β-carotene, carotenoids, chitosan, fatty acids, biodiesel, progesterone and testosterone, but also to ferment traditional foods like Asian soybean-based staples and European cheese (Davoust & Persson 1992, Papp et al. 2009, Liu & Voigt 2010, Hermet et al. 2012, Hong et al. 2012, Kristanti et al. 2016, Kosa et al. 2018, Zoghi et al. 2019, de Carvalho Tavares et al. 2020, Luo et al. 2020, Jia et al. 2021, Sandmann 2021, Zhao et al. 2021a). Many species are agriculturally useful, being able to solubilize phosphate, degrade metalaxyl, and promote crop growth (Doilom et al. 2020, Li et al. 2020, Martins et al. 2020, Ozimek & Hanaka 2021). A few species are widely applied in pharmaceutical industries (Abrashev et al. 2021). Several species are also model organisms for dimorphism, drug metabolism/biotransformation, phototropism/light-growth response, and forcible ejection (Page 1964, Schulz et al. 1974, Galland & Lipson 1985, Khale & Deshpande 1992, Sepuri & Vidyavathi 2008). However, some zygomycetes are still notorious for

infecting humans and causing deadly diseases, such as the mucormycosis during the COVID-19 pandemic (Kwon-Chung 2012, Cheng *et al.* 2017, Morin-Sardin *et al.* 2017, Hallur *et al.* 2021, Mahalaxmi *et al.* 2021).

Zygomycetous fungi are characterized by 1) fast growing mycelia, 2) coenocytic aseptate filamentous hyphae except for irregular septa with age or at the point of branching, 3) asexual intercalary or terminal chlamydospores as well as sporangiospores in a sack such as multi-spored sporangia, one to multi-spored sporangiola, and one to few-spored merosporangiola, and 4) sexual zygospores or azygospores in a zygosporangium or sporocarp (Berbee *et al.* 2017). Zygomycetes were once classified in the phylum Zygomycota (Moreau 1952), though it is invalid and illegal because of a lack of Latin diagnosis or description (Liu & Voigt 2010, Turland *et al.* 2018). Half a century later, the phylum Zygomycota was rejected by Hibbett *et al.* (2007) and its members were assigned to the phylum Glomeromycota and four subphyla *incertae sedis*, viz.,

Entomophthoromycotina, Kickellomycotina, Mucoromycotina and Zoopagomycotina. Due to a paraphyletic grade relationship to the Dikarya in a genome-scale phylogeny, they were reclassified in two monophyletic phyla Mucoromycota and Zoopagomycota (Spatafora *et al.* 2016). The former phylum accommodated the core members of traditional zygomycetous fungi, comprising three subphyla Glomeromycotina, Mortierellomycotina and Mucoromycotina (Spatafora *et al.* 2016). Recently, it was further raised to the subkingdom rank as Mucoromyceta accommodating Calcarisporiellomycota, Glomeromycota, Mortierellomycota and Mucoromycota (Tedersoo *et al.* 2018). However, the subkingdom was still a paraphyletic grade to the subkingdom Dikarya rather than a monophyletic clade, and the placement of the Glomeromycota and Mortierellomycota was incongruent among several studies (James *et al.* 2006, Oehl *et al.* 2011a, b, c, Spatafora *et al.* 2016, Tedersoo *et al.* 2018, Wijayawardene *et al.* 2020).

Nowadays, it is more and more popular to incorporate divergence time in ranking fungal taxa, especially in Basidiomycota (Hyde *et al.* 2017, Zhao *et al.* 2017, He *et al.* 2019, Wang *et al.* 2021a). Zygomycetous fossil evidence has been accumulated recently, making it possible to date the molecular evolution within zygomycetes (Batra *et al.* 1964, Baxter 1975, Taylor & Alexander 2005, Krings *et al.* 2011, 2018, Taylor *et al.* 2014, Gan *et al.* 2021). The present study adopts molecular clock hypothesis for further refining the Mucoromyceta with a hierarchical outline from class to genus.

3

Since the 1780's, a total of 792 species has been proposed for the subkingdom Mucoromyceta, though much less than those in the subkingdom Dikarya

(https://nmdc.cn/fungarium/fungi/worldfungi, accessed on November 12, 2021, Fig. 1 and Table S1). Voigt *et al.* (2021) supposed that species in Mucoromyceta could be significantly higher than what was known to exist. Inspiringly, new species have been described in the subkingdom (Hurdeal *et al.* 2021, Nguyen *et al.* 2021, Zhao *et al.* 2021b, Zong *et al.* 2021) at an accelerated pace after the inflection point around the year of 2000 on the trend curve of species number (Fig. 1), which is due to advances in molecular phylogeny (Dai *et al.* 2015, Voigt *et al.* 2021). In this paper we describe new species in the subkingdom Mucoromyceta, along with the proposal of an updated higher-rank taxonomic framework. The internal transcribed spacer (ITS) region of the ribosomal RNA gene (rDNA) has been recommended as a universal fungal DNA barcode for identification at the species rank (Schoch *et al.* 2012, Nilsson *et al.* 2014). In the present study, all new species are identified with a combination of morphological traits and ITS rDNA sequences.

#### **Materials and Methods**

#### Strains and culture conditions

Samples including soil, plant debris, leaves, rotten wood, flowers, macrofungi, paper and animal dung were collected, and strains were isolated according to methods described previously (Zhao *et al.* 2021b, Zong *et al.* 2021). In brief, approximately 1 g of sample was suspended and shaken with sterilized water. About 200 µL of the suspension was then incubated at room temperature with potato dextrose agar (PDA: 20 g / L glucose, 200 g / L potato, 20 g / L agar, pH7), and examined daily with a stereo microscope (SMZ1500, Nikon Corporation, Japan). Selective antibiotics (100 mg / mL streptomycin sulfate, and 100 mg / mL ampicillin) were added to the PDA medium to inhibit bacterial growth. Living and dried cultures for nomenclatural types were deposited in the China General Microbiological Culture Collection Center, Beijing, China (CGMCC) and the Herbarium Mycologicum Academiae Sinicae, Beijing, China (HMAS), respectively. Living cultures numbered

with initial acronyms "XY" were preserved in both Shandong Normal University and Beijing Forestry University.

# Morphology and growth temperature tests

Pure cultures were established with PDA or synthetic mucor agar (SMA: 20 g / L dextrose, 2 g / L asparagine, 0.5 g / L KH<sub>2</sub>PO<sub>4</sub>, 0.25 g / L MgSO<sub>4</sub>·H<sub>2</sub>O, 0.5 mg / L thiamin chloride, 20 g / L agar, pH7) or malt-extract agar (MEA: 20 g / L malt-extract, 20 g / L agar, pH7) for morphological observation. Strains were incubated inversely at 20 °C, 27 °C or 30 °C for two weeks, and examined and photographed daily under a light microscope (Axio Imager A2, Carl Zeiss, Oberkochen, Germany). Colonies reaching 90 mm in diameter within three days were referred to as 'fast growing', and if more than seven days as 'slow growing'. Colony colors were taken from Ridgway (1912). The sizes of microscopic features were measured with a software platform (Leica Application Suite v4.5, Leica Microsystems Inc., Buffalo Grove, Illinois, USA). In order to determine the maximum growth temperature, strains were initially cultivated at 25 °C for two days, and then the temperature was gradually increased by a gradient of 1 °C until the colony stopped growing.

# DNA extraction, amplification and sequencing

Cultures were grown at 27 °C for one week on PDA plates. For Sanger sequencing and whole genomic sequencing (WGS), cell total DNAs were extracted from the fungal thalli following the instruction of the GO-GPLF-400 kit (GeneOnBio Corporation, Changchun, China). The internal transcribed spacer of the ribosomal DNA (ITS rDNA) was amplified with the primer pairs LR5M (5'-GCT ATC CTG AGG GAA ACT TCG-3') and NS5M (5'-GGC TTA ATT TGA CTC AAC ACG G-3'; Zhao *et al.* 2021b). The polymerase chain reaction (PCR) program was performed as follows: an initial temperature at 95 °C for 5 min; then 30 cycles of denaturation at 95 °C for 1 min, annealing at 55 °C for 45 s and extension at 72 °C for 1 min; and a final extra extension at 72 °C for 10 min. The PCR products were sequenced with the primers ITS4 and ITS5 (White *et al.* 1990). Sanger sequencing of the PCR products was conducted by BGI Tech Solutions Beijing Liuhe Co., Limited (https://www.bgi.com/, Beijing, China). For WGS, total DNAs were applied to the HiSeq

4000 platform (https://www.illumina.com, Illumina Inc., California, USA) with Novogene Co., Ltd. (https://novogene.com/, Beijing, China).

#### Phylogenomic and phylogenetic analyses

De novo assembly, manual proofreading and target extraction for ITS rDNA sequences were carried out with Geneious 9.0.2 (http://www.geneious.com, Kearse et al. 2012). Assembled sequences were then submitted to GenBank under accession numbers in Table 1. The ITS rDNA dataset containing sequences retrieved from GenBank was realigned locally with AliView 3.0 (Larsson 2014) and MAFFT 7 (Katoh et al. 2019), and then was manually proofread. The annotated genome sequences were then submitted to GenBank under accession numbers in Table 2. The whole proteome was obtained from the annotated genome with Gffread v0.12.4 (Pertea & Pertea 2020), and 192 clusters of orthologous proteins (COPs) were retrieved with HMMER 3.3.1 (http://hmmer.org/download.html) and Trimal 1.4.4 (Sanchez et al. 2011) according to the method by Spatafora et al. (2016). Phylogenetically informative protein markers followed James et al. (2013). Phylogenomic and phylogenetic analyses were carried out following the methods by Nie et al. (2020a, b), using the PROTGAMMALGX model with 100 bootstrap replications. Phylogenetic analyses were carried out following the methods by Nie et al. (2020a, b), including Maximum Likelihood (ML) and Bayesian Inference (BI) implemented in RAxML version 8 (Stamatakis 2014) and MrBayes 3.2.7a (Ronquist et al. 2012), respectively. Maximum Likelihood analysis was performed using the GTRGAMMA model with 1,000 bootstrap replications. For BI analysis, eight cold Markov chains ran simultaneously for two million generations with the GTR + I + G model, sampling every 1,000 generations and removing the first 25% sampled trees as burn-in. In the BI analyses, Markov Chain Monte Carlo (MCMC) chains ran until the convergence met and the standard deviation fell below 0.01. The phylogram was viewed and modified with FigTree version 1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/).

#### **Molecular dating**

A set of ITS and LSU rDNA sequences retrieved from GenBank database, was used to infer the divergence time within the Mucoromyceta (Table 2). The divergence time was estimated with BEAST 2.6.5 (Bouckaert *et al.* 2014). A BEAST XML input file was generated with BEAUti v2 implemented in the BEAST 2.6.5. The estimation of rates of evolutionary changes at amino acid sites was performed by ModelTest 3.7 (Posada & Crandall 1998) using the GTR substitution model. The relaxed clock model with a log-normal distribution was used. A Yule model was selected as prior, assuming a constant speciation rate with no extinction (Barraclough & Nee 2001) and an offset age with a gamma distributed prior (scale = 10, shape = 1.0). The divergence time analysis was calibrated using two fossil fungi and three molecular divergence estimates. The two fossil fungi were 1) Protoascon missouriensis L.R. Batra et al. in the Middle Pennsylvanian sub-epoch (approximately 315-307 Mya) which is remarkably similar to Absidia spinosa Lendn. or A. spinosa var. azygospora Boedijn in azygosporangia and appendages (Boedijn 1958, Batra et al. 1964, Baxter 1975, Taylor & Alexander 2005, Taylor et al. 2014), and 2) Jimwhitea circumtecta M. Krings & T.N. Taylor which is the most persuasive fossil representative of the Endogone and was discovered from the Middle Triassic epoch (roughly 247-237 Mya; Krings et al. 2011, Taylor et al. 2014). The three molecular divergence estimates were as follows: 1) Although some molecular studies suggested that zygomycetous fungi appeared at the Precambrian super eon (1.4–1.2 Gya), the conservative estimate of 800 Mya or so during the Proterozoic eon was adopted herein (Berbee & Taylor 2001, Heckman et al. 2001, Blair 2009); 2) The crown age of Mucoromycota was set to 560 Mya with 95 % HPD of 183–735 Mya (Tedersoo et al. 2018). 3) Glomeromycota was set to differentiate 642 Mya with 95 % HPD of 597-720 Mya (Tedersoo et al. 2018). The analysis ran for 200 million generations, logging states every 1,000 generations. Log files were mixed with Tracer v1.7.2 (Rambaut & Drummond 2013) and checked for convergence. Finally, a maximum clade credibility (MCC) tree was summarized with TreeAnnotator 1.8.2 (within BEAST), removing the first 20 % of states as burn-in, and annotating clades with more than 0.8 posterior probability.

#### Results

#### Phylogenomics, phylogenetics and molecular dating in Mucoromyceta

We sequenced the genomes of 12 strains of 12 species in 6 genera for phylogenomic analyses (Table 2). We also downloaded the published genomes of 44 strains of 42 species in 29 genera including an outgroup from *Smittium culicis* Tuzet & Manier ex Kobayasi in the phylum

Zoopagomycota, and all of these retrieved genomes are freely available for public use in accordance with the usage policy in the GenBank database and the Joint Genome Institute (JGI) portal MycoCosm database (Table 2). Unfortunately, genomes on Calcarisporiellomycota are unavailable. Phylogenetic analyses and molecular dating were conducted based on ITS and LSU rDNA sequences of 170 strains of 165 species in 98 genera (accounting for 81 %, 98 / 121) in the Mucoromyceta and that of an outgroup in Neurospora crassa Shear & B.O. Dodge. The most optimal model of BI was GTR + I + R, and the average standard deviation of split frequencies was 0.009026. Topology of ML tree was selected to represent the phylogenetic relationship of Mucoromyceta (Fig. 3). The phylogenomic (Fig. 2) and phylogenetic analyses (Fig. 3) suggest an identical taxonomic backbone of the subkingdom Mucoromyceta: four accepted phyla (Calcarisporiellomycota, Glomeromycota, Mortierellomycota and Mucoromycota) and two new phyla (Endogonomycota phyl. nov. and Umbelopsidomycota *phyl. nov.*). These results also provide a strong phylogenetic resolution for the phylum, class, order and family in the subkingdom Mucoromyceta, proposing five new orders (Claroideoglomerales ord. nov., Cunninghamellales ord. nov., Lentamycetales ord. nov., Phycomycetales ord. nov. and Syncephalastrales ord. nov.) and six new families (Circinellaceae fam. nov., Gongronellaceae fam. nov., Protomycocladaceae fam. nov., Rhizomucoraceae fam. nov., Syzygitaceae fam. nov. and Thermomucoraceae fam. nov.).

The taxonomic hierarchy above is dated with estimated divergence times: phyla 810–639 Mya, classes 651-585 Mya, orders 570-400 Mya, and families 488-107 Mya (Fig. 4 and Table 4). The six phylum clades are supported with high posterior probabilities (PP): Glomeromycota (810 Mya / PP = 1.0), Mortierellomycota (777 Mya / PP = 0.9), Calcarisporiellomycota (748 Mya / PP = 1.0), Endogonomycota *phyl. nov.* (708 Mya / PP = 1.0), Mucoromycota (639 Mya / PP = 1.0), and Umbelopsidomycota *phyl. nov.* (639 Mya / PP = 1.0).

We accepted the phylum Glomeromycota, and three classes Archaeosporomycetes (585 Mya / PP = 0.9), Glomeromycetes (585 Mya / PP = 0.9) and Paraglomeromycetes (651 Mya / PP = 1.0) were described (Schüßler et al. 2001, Oehl et al. 2011a, b, c). The Archaeosporomycetes contained one class Archaeosporales (585 Mya / PP = 0.9) and three families (Ambisporaceae 401 Mya / PP = 1.0 and Archaeosporaceae 401 Mya / PP = 1.0, while Geosiphonaceae absent). The Glomeromycetes held four classes (Claroideoglomerales 539 Mya / PP = 1.0, Diversisporales 400 Mya / PP = 1.0 and Glomerales 478 Mya / PP = 1.0). The

Claroideoglomerales comprised one family Claroideoglomeraceae with 539 Mya / PP = 1.0. The Diversisporales consisted of five families (Acaulosporaceae 285 Mya, Diversisporaceae 333 Mya / PP = 1.0, Pacisporaceae 285 and Sacculosporaceae 288, while Entrophosporaceae absent). The Gigasporales comprised four families (Gigasporaceae 107 Mya / PP = 1.0, Racocetraceae 107 Mya / PP = 1.0 and Scutellosporaceae 134 Mya / PP = 1.0, while Dentiscutateae absent). The Glomerales was one family described (Glomeraceae 478 Mya / PP = 1.0 and mean crown age of Glomeraceae 276 Mya / PP = 1.0). The Paraglomeromycetes included one class (Paraglomerales 651 Mya / PP = 1.0) and two families (Paraglomeraceae 483 Mya / PP = 1.0).

The Mortierellomycota comprised one class (Mortierellomycetes), one order (Mortierellales) and one family Mortierellaceae (mean stem age 777 Mya / PP = 0.9, mean crown age 268 Mya / PP = 1.0).

The Calcarisporiellomycota accommodated one class, one order and one family Calcarisporiellaceae (mean stem age 728 Mya / PP = 1.0, mean crown age 111 Mya /PP = 1.0).

The Endogonomycota contained one class, one order and two families Endogonaceae (mean stem age 708 Mya / PP = 1.0, mean crown age 326 Mya / PP = 1.0) and Densosporaceae (data unavailable).

The Mucoromycota held one class (Mucoromycetes 639 Mya with a 1.0 PP support). The Mucoromycetes evolved into five orders (Cunninghamellales 504 Mya, Lentamycetales 570 Mya / PP =1.0, Mucorales 519 Mya / PP =1.0, Phycomycetales 543 Mya / PP =1.0 and Syncephalastrales 504 Mya). The Cunninghamellales consisted of three families (Absidiaceae 403 Mya / PP = 1.0, Cunninghamellaceae 403 Mya / PP = 1.0 and Gongronaceae 440 Mya / PP =1.0). The Lentamycetales was monotypic with 570 Mya / PP = 0.8 and mean crown ages 299 Mya / PP =1.0. The monotypic Mucorales diverged into five families (Backusellaceae 437 Mya / PP =1.0, Mucoraceae 387 Mya / PP =1.0, Pilobolaceae 337 Mya / PP =1.0, Rhizopodaceae 237 Mya / PP =1.0, and Syzygitaceae 237 Mya / PP =1.0). The Phycomycetales contained three families (Phycomycetaceae 399 Mya / PP = 1.0, Radiomycetaceae 399 Mya / PP = 1.0, and Saksenaeaceae 488 Mya / PP = 1.0). Syncephalastromycetales held seven families (Circinellaceae 391 Mya, Lichtheimiaceae 354 Mya, Protomycocladaceae 454 Mya / PP = 1.0, Rhizomucoraceae 340 Mya /

PP = 0.8, Syncephalastraceae 340 Mya / PP = 0.8, Thermomucoraceae 354 Mya, and Mycocladaceae data unavailable).

The Umbelopsidomycota consisted of one class (Umbelopsidomycetes), one order (Umbelopsidales) and two families (Pygmaeomycetaceae 434 Mya / PP =1.0 and Umbelopsidaceae 434 Mya / PP =1.0).

# New taxa at high ranks

Comprehensively considering morphological features, divergence dating and monophyletic concept, a total of thirteen new taxa, including two phyla, five orders and six families, are proposed herein.

# New phyla

Endogonomycota H. Zhao, Y.C. Dai, B.K. Cui, F. Wu & X.Y. Liu, phyl. nov.

#### Fungal Names: FN570870.

*Type: Endogone* Link, Mag. Gesell. naturf. Freunde, Berlin 3(1–2): 33, 1809. *Diagnosis*: Mycelium well-known to be ectomycorrhizal with plants or sometimes saprobic. Sporangiospores absent. Chlamydospores present or absent. Zygospores always formed in sporocarps.

Umbelopsidomycota H. Zhao, Y.C. Dai, B.K. Cui, F. Wu & X.Y. Liu, phyl. nov.

# Fungal Names: FN570871.

Type: Umbelopsis Amos & H.L. Barnett, Mycologia 58(5): 807, 1966.

*Diagnosis*: Colonies frequently sectoring due to a possible genetic instability. Aerial hyphae so degenerated that the colonies are a thin layer of sporangiophores. Sporangiophores arising mainly from substrate hyphae and rarely from aerial hyphae. Sporangia one- or multi-spored, subglobose to globose, typically pigmented, resulting in reddish or ochraceous colonies. Collars and columellae obvious or degenerated. Sporangiospores globose, subglobose, teardrop-shaped, angular or irregular. Chlamydospores present in substrate hyphae. Zygospores unknown.

# New orders

Claroideoglomerales H. Zhao, Y.C. Dai, B.K. Cui, F. Wu & X.Y. Liu, ord. nov.

# Fungal Names: FN571005.

Type: Claroideoglomus C. Walker & A. Schüßler, 2010.

*Diagnosis*: Spores single, commonly in soil or rarely in plant roots. Subtending hyphae hyaline to white, and rarely subhyaline, conspicuously bill-shaped. Spores with one to four layers, with a pore closure at the base which allowing spore to germinate from the structural layer, or from an adherent innermost (semi-)flexible layer, or from both layers.

Cunninghamellales H. Zhao, Y.C. Dai, B.K. Cui, F. Wu & X.Y. Liu, ord. nov.

# Fungal Names: FN570873.

*Type: Cunninghamella* Matr., Annls Mycol. 1(1): 46, 1903.

*Diagnosis*: Sporangiophores arising from substrate and aerial hyphae, or from stolons. Rhizoids always present, finger-like or root-like. Stolons present. Apophyses present. Asexual reproduction by either sporangia or sporangiola. Sporangia pyriform to globose, multi-spored. Sporangiola borne on pedicels on vesicles, with spines all over the surface, containing one smooth sporangiospore. Chlamydospores unknown. Zygospores if present, always with appendages.

Lentamycetales H. Zhao, Y.C. Dai, B.K. Cui, F. Wu & X.Y. Liu, ord. nov.

# Fungal Names: FN570874.

Type: Lentamyces Kerst. Hoffm. & K. Voigt, Pl. Biol. 11(4): 550, 2009.

*Diagnosis*: Colonies slow growing. Maximum growth temperatures < 30 °C. Sporangiophores erect, unbranched, without whorls. Sporangia spherical to subpyriform, multi-spored. Columellae spherical to hemispherical, without terminal appendages. Sporangiospores ovoid to cylindrical. Rhizoids present. Stolons present. Apophyses present. Projections absent. Zygospores without appendages. Phycomycetales H. Zhao, Y.C. Dai, B.K. Cui, F. Wu & X.Y. Liu, ord. nov.

# Fungal Names: FN570875.

Type: Phycomyces Kunze, Mykologische Hefte (Leipzig) 2: 113, 1823.

*Diagnosis*: Asexual reproduction by either multi-spored sporangia or uni-spored sporangiola, with walls either deliquescent or persistent. Apophyses typically present. Zygospores if present, with suspensors opposed.

Syncephalastrales H. Zhao, Y.C. Dai, B.K. Cui, F. Wu & X.Y. Liu, ord. nov.

# Fungal Names: FN570876.

Type: Syncephalastrum J. Schröt., Krypt.-Fl. Schlesien (Breslau) 3.1(9–16): 217, 1886.

*Diagnosis*: Sporangiophores arising from aerial or substrate hyphae, unbranched, simple branched or sympodially branched. Rhizoids present or absent. Stolons present or absent. Sporangia multi-spored, columellate, either apophysate or nonapophysate. Chlamydospores absent or scarcely produced. Zygospores if present, with suspensors opposed.

# New families

Circinellaceae H. Zhao, Y.C. Dai, B.K. Cui, F. Wu & X.Y. Liu, fam. nov.

# Fungal Names: FN570878.

Type: Circinella Tiegh. & G. Le Monn., Annls Sci. Nat., Bot., sér. 5 17: 298, 1873.

*Diagnosis*: Most recently originated in the Syncephalastrales clade in phylogenetic divergence time analyses. Sporangiophores arising from substrate and aerial hyphae, simple or branched, main stem straight and lateral branches circinate, curved or twisted. Terminal sporangia always subglobose to globose, multi-spored. Lateral sporangia subglobose to globose, uni- to multi-spored. Apophyses present. Sporangiospores often ovoid to ellipsoid. Chlamydospores sometimes present in substrate hyphae. Zygospores if known, ornamented, pigmented, heterothallic or homothallic, with suspensors opposed. Gongronellaceae H. Zhao, Y.C. Dai, B.K. Cui, F. Wu & X.Y. Liu, fam. nov.

#### Fungal Names: FN570879.

Diagnosis: Gongronella Ribaldi, Riv. Biol. 44: 164, 1952.

*Description*: Basal in the Cunninghamellales clade in phylogenetic and divergence time analyses. Sporangiophores arising from substrate and aerial hyphae, erect to curved, unbranched. Sporangia globose. Zygospores if known, ornamented, pigmented, heterothallic, with suspensors opposed.

Protomycocladaceae H. Zhao, Y.C. Dai, B.K. Cui, F. Wu & X.Y. Liu, fam. nov.

#### Fungal Names: FN570880.

Type: Protomycocladus Schipper & Samson, Mycotaxon 50: 487, 1994

*Diagnosis*: Basal in the order Syncephalastrales clade in phylogenetic and divergence time analyses. Sporangiophores arising from substrate hyphae, sympodially branched. Apophyses present. Sporangia apophysate, smooth, pyriform and multi-spored, walls deliquescent. Zygospores ornamented, homothallic, with suspensors opposed.

Rhizomucoraceae H. Zhao, Y.C. Dai, B.K. Cui, F. Wu & X.Y. Liu, fam. nov.

#### Fungal Names: FN570881.

Type: Rhizomucor Lucet & Costantin, Rev. gén. Bot. 12: [81], 1900.

*Diagnosis*: Next to the Protocladaceae clade and the Syncephalastraceae clade in the Syncephalastrales group in phylogenetic and divergence time analyses. Rhizoids always present. Sporangiophores arising from hyphae, branched. Apophyses absent. Sporangia columellate and multi-spored. Chlamydospores sometimes present. Zygospores ornamented, with opposed suspensors and a pigmented zygosporangial wall. Mesophilic and thermophilic.

Syzygitaceae H. Zhao, Y.C. Dai, B.K. Cui, F. Wu & X.Y. Liu, fam. nov.

#### Fungal Names: FN571006.

Type: Syzygites Ehrenb., Sylv. mycol. berol. (Berlin): 25, 1818.

*Diagnosis*: Sporangiophores arising directly from substrate hyphae, umbel or dichotomously branched. Sporangia subglobose to globose, columellate, few-spored or multi-spored, deliquescent-

walled. Sporangiospores globose to ovoid, spinose-walled. Zygospores ornamented, with suspensors opposed.

Thermomucoraceae H. Zhao, Y.C. Dai, B.K. Cui, F. Wu & X.Y. Liu, fam. nov.

# Fungal Names: FN571007.

*Type: Thermomucor* Subrahm., B.S. Mehrotra & Thirum., Georgia J. Sci. 35(1): 1, 1977. *Diagnosis*: Sporangiophores arising from stolons and rhizoids, branched. Sporangia globose, columellate, multi-spored, and apophysate. Sporangiospores subglobose, smooth-walled. Zygospores produced from aerial hyphae, with opposed suspensors and a smooth zygosporangial wall. Homothallic and thermophilic.

# Outline of the subkingdom Mucoromyceta

Subkingdom Mucoromyceta Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov 2018

Phylum Calcarisporiellomycota Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel,

T. May, M. Ryberg & Abarenkov 2018

**Class Calcarisporiellomycetes** Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov 2018

**Order Calcarisporiellales** Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov 2018

Family Calcarisporiellaceae Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T.

May, M. Ryberg & Abarenkov 2018

Calcarisporiella de Hoog 1974

Echinochlamydosporium X.Z. Jiang, H.Y. Yu, M.C. Xiang, X.Y. Liu & Xing Z. Liu 2011

Phylum Endogonomycota H. Zhao, Y.C. Dai, B.K. Cui, F. Wu & X.Y. Liu, phyl. nov.

Class Endogonomycetes Doweld 2014

Order Endogonales Jacz. & P.A. Jacz. 1931
Family Densosporaceae Desirò, M.E. Sm., Bidartondo, Trappe & Bonito 2017
Densospora McGee 1996
Family Endogonaceae Paol. 1889
Bifiguratus Torr.-Cruz & Porras-Alfaro 2017
Endogone Link 1809
Jimgerdemannia Trappe, Desirò, M.E. Sm., Bonito & Bidartondo 2017
Peridiospora C.G. Wu & Suh J. Lin 1997
Sclerogone Warcup 1990
Vinositunica Koh. Yamam., Degawa & A. Yamada 2020

# Phylum Glomeromycota C. Walker & A. Schüßler 2001

Class Archaeosporomycetes Sieverd., G.A. Silva, B.T. Goto & Oehl 2011 Order Archaeosporales C. Walker & A. Schüßler 2001 Family Ambisporaceae C. Walker, Vestberg & A. Schüßler 2007 Ambispora C. Walker, Vestberg & A. Schüßler 2007 Family Archaeosporaceae J.B. Morton & D. Redecker 2001 Archaeospora J.B. Morton & D. Redecker 2001 Family Geosiphonaceae Engl. & E. Gilg 1924 Geosiphon F. Wettst. 1915 Class Glomeromycetes Caval.-Sm. 1998 Order Claroideoglomerales H. Zhao, Y.C. Dai, B.K. Cui, F. Wu & X.Y. Liu, ord. nov. Family Claroideoglomeraceae C. Walker & A. Schüßler 2010 Claroideoglomus C. Walker & A. Schüßler 2010 Order Diversisporales C. Walker & A. Schüßler 2004 Family Acaulosporaceae J.B. Morton & Benny 1990 Acaulospora Gerd. & Trappe 1974 Kuklospora Oehl & Sieverd. 2006 Tricispora Oehl, Sieverd., G.A. Silva & Palenz. 2011 Family Diversisporaceae C. Walker & A. Schüßler 2004

bioRxiv preprint doi: https://doi.org/10.1101/2022.07.05.498902; this version posted July 9, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

Corymbiglomus Błaszk. & Chwat 2012

Desertispora Błaszk., Kozłowska, Ryszka, Al-Yahya'ei & Symanczik 2018

Diversispora C. Walker & A. Schüßler 2004

Otospora Oehl, Palenz. & N. Ferrol 2008

Redeckera C. Walker & A. Schüßler 2010

Sieverdingia Błaszk., Niezgoda & B.T. Goto 2019

Family Entrophosporaceae Oehl & Sieverd. 2006

Entrophospora R.N. Ames & R.W. Schneid. 1979

Family Pacisporaceae C. Walker, Błaszk., A. Schüßler & Schwarzott 2004

Pacispora Sieverd. & Oehl 2004

Family Sacculosporaceae Oehl, Sieverd., G.A. Silva, B.T. Goto, Sánchez-Castro & Palenz.

Sacculospora Oehl, Sieverd., G.A. Silva, B.T. Goto, Sánchez-Castro & Palenz. 2011

Order Gigasporales S.P. Gautam & U.S. Patel 2007

Family Dentiscutataceae Sieverd., F.A. Souza & Oehl 2009

Dentiscutata Sieverd., F.A. Souza & Oehl 2009

Family Gigasporaceae J.B. Morton & Benny 1990

Gigaspora Gerd. & Trappe 1974

Intraornatospora B.T. Goto, Oehl & G.A. Silva 2012

Paradentiscutata B.T. Goto, Oehl & G.A. Silva 2012

Family Racocetraceae Oehl, Sieverd. & F.A. Souza 2009

Cetraspora Oehl, F.A. Souza & Sieverd. 2009

Racocetra Oehl, F.A. Souza & Sieverd. 2009

Family Scutellosporaceae Sieverd., F.A. Souza & Oehl 2009

Bulbospora Oehl & G.A. Silva 2014

Scutellospora C. Walker & F.E. Sanders 1986

Order Glomerales J.B. Morton & Benny 1990

Family Glomeraceae Piroz. & Dalpé 1989

Dominikia Błaszk., Chwat & Kovács 2014

Epigeocarpum Błaszk., B.T. Goto, Jobim, Niezgoda & Marguno 2021

Funneliformis C. Walker & A. Schüßler 2010

Funneliglomus Corazon-Guivin, G.A. Silva & Oehl 2019

Glomus Tul. & C. Tul. 1844

Halonatospora Błaszkowski, Niezgoda, B.T. Goto & Kozłowska 2018

Kamienskia Błaszk., Chwat & Kovács 2014

Microdominikia Oehl, Corazon-Guivin & G.A. Silva 2019

Microkamienskia Corazon-Guivin, G.A. Silva & Oehl 2019

Nanoglomus Corazon-Guivin, G.A. Silva & Oehl 2019

Oehlia Błaszk., Kozłowska, Niezgoda, B.T. Goto & Dalpé 2018

Rhizophagus P.A. Dang. 1896

Sclerocarpum B.T. Goto, Błaszk., Niezgoda, A. Kozłowska & Jobim 2019

Silvaspora Błaszk., Niezgoda, B.T. Goto, Crossay & Magurno 2021

Class Paraglomeromycetes Oehl, G.A. Silva, B.T. Goto & Sieverd. 2011

Order Paraglomerales C. Walker & A. Schüßler 2001

Family Paraglomeraceae J.B. Morton & D. Redecker 2001

Innospora Błaszk., Kovács, Chwat & Kozłowska 2017

Paraglomus J.B. Morton & D. Redecker 2001

Family Pervetustaceae Błaszk., Chwat, Kozłowska, Symanczik & Al-Yahya'ei 2017

Pervetustus Błaszk., Chwat, Kozłowska, Symanczik & Al-Yahya'ei 2017

Phylum Mortierellomycota Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T.

May, M. Ryberg & Abarenkov 2018

**Class Mortierellomycetes** Doweld 2013

Order Mortierellales Caval.-Sm. 1998

Family Mortierellaceae Luerss. 1877

Actinomortierella Chalab 1968

Aquamortierella Embree & Indoh 1967

Benniella Vandepol & Bonito 2020

Dissophora Thaxter 1914

Entomortierella Vandepol & Bonito 2020

Gamsiella Benny & M. Blackwell 2004

Gryganskiella Vandepol, Stajich & Bonito 2020 Linnemannia Vandepol & Bonito 2020 Lobosporangium M. Blackwell & Benny 2004 Lunasporangiospora Vandepol & Bonito 2020 Modicella Kanouse 1936 Mortierella Coemans 1863 Necromortierella Vandepol & Bonito 2020 Podila Stajich, Vandepol & Bonito 2020 Phylum Mucoromycota Doweld 2001 **Class Mucoromycetes** Doweld 2001 Order Cunninghamellales H. Zhao, Y.C. Dai, B.K. Cui, F. Wu & X.Y. Liu, ord. nov. Family Absidiaceae Arx 1982 Absidia Tiegh. 1878 Chlamydoabsidia Hesselt. & J.J. Ellis 1966 Halteromyces Shipton & Schipper 1975 Family Cunninghamellaceae Naumov ex R.K. Benj. 1959 Cunninghamella Matr. 1903 Family Gongronellaceae H. Zhao, Y.C. Dai, B.K. Cui, F. Wu & X.Y. Liu, fam. nov. Gongronella Ribaldi 1952 Hesseltinella H.P. Upadhyay 1970 Order Lentamycetales H. Zhao, Y.C. Dai, B.K. Cui, F. Wu & X.Y. Liu, ord. nov. Family Lentamycetaceae K. Voigt & P.M. Kirk 2012 Lentamyces Kerst. Hoffm. & K. Voigt 2008 **Order Mucorales** Dumort 1829 Family Backusellaceae K. Voigt & P.M. Kirk 2012 Backusella Hesselt. & J.J. Ellis 1969 Family Mucoraceae Fr. 1821 Actinomucor Schostak. 1898 Ambomucor R.Y. Zheng & X.Y. Liu 2014

bioRxiv preprint doi: https://doi.org/10.1101/2022.07.05.498902; this version posted July 9, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

- Benjaminiella Arx 1981
- Blakeslea Thaxt. 1914
- Chaetocladium Fresen. 1863
- Choanephora Curr. 1873
- Cokeromyces Shanor 1950
- Dicranophora J. Schröt. 1886
- Ellisomyces Benny & R.K. Benj. 1975
- Gilbertella Hesselt. 1960
- Helicostylum Corda 1842
- Hyphomucor Schipper & Lunn 1986
- Isomucor J.I. Souza, Pires-Zottar. & Harakava 2012
- Kirkiana L.S. Loh, Kuthub. & Nawawi 2001
- Kirkomyces Benny 1996
- Mucor Fresen. 1850
- Mycotypha Fenner 1932
- Nawawiella L.S. Loh & Kuthub. 2001
- Parasitella Bainier 1903
- Pilaira Tiegh. 1875
- Pirella Bainier 1882
- Poitrasia P.M. Kirk 1984
- Rhizopodopsis Boedijn 1959
- Thamnidium Link 1809
- Tortumyces L.S. Loh 2001
- Family Pilobolaceae Corda 1842
- Pilobolus Tode 1784
- Utharomyces Boedijn ex P.M. Kirk & Benny 1980

#### Family Rhizopodaceae K. Schum. 1894

- Rhizopus Ehrenb. 1821
- Family Syzygitaceae H. Zhao, Y.C. Dai, B.K. Cui, F. Wu & X.Y. Liu, fam. nov.
- Sporodiniella Boedijn 1959

bioRxiv preprint doi: https://doi.org/10.1101/2022.07.05.498902; this version posted July 9, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

# Syzygites Ehrenb. 1818

Order Phycomycetales H. Zhao, Y.C. Dai, B.K. Cui, F. Wu & X.Y. Liu, ord. nov.

#### Family Phycomycetaceae Arx 1982

*Phycomyces* Kunze 1823

Spinellus Tiegh. 1875

#### Family Radiomycetaceae Hesselt. & J.J. Ellis 1974

Radiomyces Embree 1959

#### Family Saksenaeaceae Hesselt. & J.J. Ellis 1974

Apophysomyces P.C. Misra 1979

Saksenaea S.B. Saksena 1953

Order Syncephalastrales H. Zhao, Y.C. Dai, B.K. Cui, F. Wu & X.Y. Liu, ord. nov.

Family Circinellaceae H. Zhao, Y.C. Dai, B.K. Cui, F. Wu & X.Y. Liu, fam. nov.

Circinella Tiegh. & G. Le Monn. 1873

Fennellomyces Benny & R.K. Benj. 1975

Phascolomyces Boedijn ex Benny & R.K. Benj. 1976

Thamnostylum Arx & H.P. Upadhyay 1970

Zychaea Benny & R.K. Benj. 1975

Family Lichtheimiaceae Kerst. Hoffm., Walther & K. Voigt 2009

Dichotomocladium Benny & R.K. Benj. 1975

Lichtheimia Vuill. 1903

Family Mycocladaceae Kerst. Hoffm., Discher & K. Voigt 2007

Mycocladus Beauverie 1900

Family Protomycocladaceae H. Zhao, Y.C. Dai, B.K. Cui, F. Wu & X.Y. Liu, fam. nov.

Protomycocladus Schipper & Samson 1994

Family Rhizomucoraceae H. Zhao, Y.C. Dai, B.K. Cui, F. Wu & X.Y. Liu, fam. nov.

Rhizomucor Lucet & Costantin 1900

Family Thermomucoraceae H. Zhao, Y.C. Dai, B.K. Cui, F. Wu & X.Y. Liu, fam. nov.

Thermomucor Subrahm., B.S. Mehrotra & Thirum. 1977

# Family Syncephalastraceae Naumov ex R.K. Benj. 1959

Syncephalastrum J. Schröt. 1886

Phylum Umbelopsidomycota H. Zhao, Y.C. Dai, B.K. Cui, F. Wu & X.Y. Liu, *phyl. nov.*Class Umbelopsidomycetes Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T.
May, M. Ryberg & Abarenkov 2018
Order Umbelopsidales Spatafora, Stajich & Bonito 2016
Family Pygmaeomycetaceae E. Walsh & N. Zhang 2020 *Pygmaeomyces* E. Walsh & N. Zhang 2020
Family Umbelopsidaceae W. Gams & W. Mey. 2003
Umbelopsis Amos & H.L. Barnett 1966

#### Notes of genera in Mortierellomycota, Mucoromycota and Umbelopsidomycota

In this study, we describe 73 new species, propose three new combinations and present 43 Chinese new record species. These 119 species belong to Mortierellomycota, Mucoromycota and Umbelopsidomycota. These three phyla accommodate 71 genera in total, and therefore we provide herein notes for all these genera.

1. Absidia Tiegh., Annls Sci. Nat., Bot., sér. 6 4(4): 350, 1878

*Absidia* is the type of the family Absidiaceae and typified by *A. reflexa* Tiegh. (van Tieghem 1876). Members of the genus always produce sporangiophores from stolons, form rhizoids between sporangiophores, and develop sporangia which are pyriform, with deliquescent walls, and apophysate (Benny *et al.* 2001). Columellae are mainly conical, subglobose and applanate, commonly with apical projections (van Tieghem 1876, Hoffmann *et al.* 2007). Some species produce zygospores within zygosporangia, and their opposite suspensory cells possess appendages (Hoffmann *et al.* 2007, Hoffmann 2010). Currently, it contains 51 species (Zhao *et al.* 2022b). This genus is distributed worldwide in soil (Rafhaella *et al.* 2020), herbivorous dung and rotten plants (van Tieghem 1876), and particularly in the mycangia of ambrosia beetles (*A. psychrophilia* Hesselt. & J.J. Ellis; Hesseltine & Ellis 1964, Kaitera *et al.* 2019) as well as the body surface of bats (*A. stercoraria* Hyang B. Lee, H.S. Lee & T.T.T. Nguyen; https://bccm.belspo.be/content/remarkable-fungal-biodiversity-northern-belgium-bats). Some species of the genus are industrially relevant. The α-galactosidase from *A. reflexa* was used to yield rubusoside derivatives (Kitahata *et al.* 1989). Laccase from *A. spinosa* Lendn. is used for the biotransformation of cresol red (Kristanti *et al.* 2016). *A. repens* Tiegh. yields chitosan (Davoust & Persson 1992). In total, 15 new taxa are described herein.

#### 2. Actinomortierella Chalab., Nov. sist. Niz. Rast., 1968 (5): 129, 1968

*Actinomortierella* is the type of the family Actinomortierellaceae and typified by *A. capitata* (Marchal) Vandepol & Bonito (Vandepol *et al.* 2020). It was once treated as a section in the genus *Mortierella* by Gams (1977), but resurrected as a separate genus by Vandepol *et al.* (2020). Short branches grow on the apical inflation of sporangiophores. Terminal sporangia form on both stem and lateral sporangiophores. Chlamydospores are absent (Vandepol *et al.* 2020). Currently, it contains three species *A. ambigua* (B.S. Mehrotra) Vandepol & Bonito, *A. capitata* and *A. wolfii* (B.S. Mehrotra & Baijal) Van- depol & Bonito. Members are distributed in soil (Mehrotra *et al.* 1963). Cultures have been recorded in Fiji, India, New Zealand, North America, and the UK. *A. wolfii* is a well-known pathogen of animals (Munday *et al.* 2006, 2010, Davies *et al.* 2010), but also reported to be associated with human invasive diseases (Layios *et al.* 2014). However, another species, *A. capitata*, is useful as being able to promote crop growth (Li *et al.* 2020). This paper newly records this genus in Yunnan, China.

#### 3. Actinomucor Schostak., Ber. Dt. Bot. Ges. 16: 155, 1898

Actinomucor is typified by *A. elegans* (Eidam) C.R. Benj. & Hesselt. (Benjamin & Hesseltine 1957). The genus is closely related to *Mucor*, but differs in sporangiophores, stolons and rhizoids (Benjamin & Hesseltine 1957). Currently, only the type species is accepted in the genus (Zheng & Liu 2005). This species is a pathogen of mucormycosis (Davel *et al.* 2001, Tully *et al.* 2009, Mahmud *et al.* 2012, Trobisch *et al.* 2020). It produces glutaminase (Lu *et al.* 1996) and is widely used to ferment soybean food (Han *et al.* 2001), which in turn benefits human health (Yin *et al.* 2021). It also secretes proteases and lipases for biodegrading polylactic acid / polybutylene adipate-coterephthalate (Jia *et al.* 2021).

#### 4. Ambomucor R.Y. Zheng & X.Y. Liu, Mycotaxon 126: 99, 2014

*Ambomucor* is typified by *A. seriatoinflatus* X.Y. Liu & R.Y. Zheng and is characterized by simultaneously having two kinds of sporangia, fertile and aborted. Currently, it contains three species, *A. clavatus* X.Y. Liu & R.Y. Zheng, *A. ovalosporus* R.Y. Zheng & X.Y. Liu and *A. seriatoinflatus* (Zheng & Liu 2014, Liu & Zheng 2015). All these three species are reported from China in soil (Romero-Olivares *et al.* 2019). *A. seriatoinflatus* is found to synthesize sialidases which are widely applied in food and pharma industries (Abrashev *et al.* 2021).

#### 5. Apophysomyces P.C. Misra, Mycotaxon 8(2): 377, 1979

Apophysomyces is typified by A. elegans P.C. Misra, K.J. Srivast. & Lat and is characterized by pyriform sporangia, and conspicuous funnel- or bell-shaped apophyses (Misra & Lata 1979, Khuna et al. 2019, Li et al. 2020). Currently, it contains six species (Misra & Lata 1979, Li et al. 2020). All species of Apophysomyces are found in soil, decayed vegetation and detritus. At least four species, A. elegans, A. mexicanus A. Bonifaz et al., A. ossiforms E. Álvarez et al. and A. variabilis
E. Álvarez et al., are reported to cause mucormycosis (Chakrabarti et al. 2010, Guarro et al. 2011, Bonifaz et al. 2014, Khuna et al. 2019, Martínez-Herrera et al. 2020). Apophysomyces species are the second common agents of mucormycosis in India (Chander et al. 2021).

#### 6. Aquamortierella Embree & Indoh 1967

*Aquamortierella* is typified by *A. elegans* Embree & Indoh (Misra & Lata 1979). The genus is characterized by sporangiospores discharging under water, and reniform (kidney-shaped) to allantoid (sausage-shaped) sporangiospores (Embree & Indoh 1967). Currently, it includes the type species only (www.indexfungorum.org; accessed 5 August 2021), but no living culture is available. This species is isolated from midge larvae in a freshwater stream in New Zealand (Embree & Indoh 1967).

# 7. Backusella Hesselt. & J.J. Ellis, Mycologia 61: 863, 1969

*Backusella* is the type of the family Backusellaceae and typified by *B. circina* J.J. Ellis & Hesselt. (Ellis & Hesseltine 1969). The genus is characterized by many sporangiola-bearing lateral branches

on the stem of the sporangiophores which in turn produce multi-spored sporangia (Ellis & Hesseltine 1969). In recent years, the species number of *Backusella* has been dramatically increasing, especially from Australia and Korea (Nguyen *et al.* 2021, Urquhart *et al.* 2021). Currently, 29 species are recorded in Index Fungorum (www.indexfungorum.org; accessed 5 August 2021). However, only two species, *B. circina* and *B. lamprospora* (Lendn.) Benny & R.K. Benj., are recorded in China (Zheng *et al.* 2013). Species of the genus inhabit mainly in soil, litter and herbivore dung. Two species, *B. circina* and *B. lamprospora*, are recorded as agents of mucormycosis (Zheng *et al.* 2013, Panthee *et al.* 2021). *B. lamprospora* has capacity to produce beta-carotene (Papp *et al.* 2009) and is also a potential oleaginous fungus (Zhao *et al.* 2021a). In this paper, we present three new species and four new Chinese records.

8. Benniella Vandepol & Bonito, in Vandepol et al., Fungal Diversity 104: 281, 2020

*Benniella* is typified by *B. erionia* Liber & Bonito (Vandepol *et al.* 2020). It was erected in honor of Gerald Benny's significant contributions on Mortierellaceae (Vandepol *et al.* 2020). Aerial hyphae are abundant in this genus, near the agar surface, producing slight rings with age (Vandepol *et al.* 2020). Currently, it contains the type species only (www.indexfungorum.org; accessed 5 August 2021).

#### 9. Benjaminiella Arx, Gen. Fungi Sporul. Cult., Edn 3 (Vaduz): 60, 1981

*Benjaminiella* is typified by *B. poitrasii* (R.K. Benj.) Arx (basionym *Cokeromyces poitrasii* R.K. Benj.; von Arx 1970). The genus produces sporangiola on relatively long, unbranched, curved to twisted pedicels, which in turn form on the entire surface of fertile vesicles (von Arx 1970, Kirk 1989, Benny *et al.* 1985). The fertile vesicles are produced at the terminal of the sporangiophores (von Arx 1970, Kirk 1989, Benny *et al.* 1985). The pedicels and sporangiola are released as a unit when dehiscence occurs at a circumscissile zone, leaving denticles regularly scattered on the surface of the vesicles (von Arx 1970, Kirk 1989, Benny *et al.* 1985). Zygosporangia are homothallic, pigmented and ornamented (von Arx 1970, Benny *et al.* 1985). Kirk 1989). Currently, the genus includes three species which are commonly isolated from soil and rat dung, and sometimes are pathogens of humans (Gade *et al.* 2017). *B. poitrasii* is a well-known model of a dimorphic fungus and contains a large number of chitin synthase (Khale & Deshpande 1992, Chitnis *et al.* 2002).

#### 10. Blakeslea Thaxt., Bot. Gaz. 58: 353, 1914

*Blakeslea* is typified by *B. trispora* Thaxt. (Thaxter 1914). The genus is characterized by two types of sporangia on separate sporangiophores (Kirk 1984, Zheng & Chen 1986). Three species are currently accepted in the genus (www.indexfungorum.org; accessed 5 August 2021). They are commonly collected from soil and fallen flowers of cucurbitaceous or malvaceous plants (Ho & Chang 2003). *B. trispora* is used industrially for producing carotenoids (Luo *et al.* 2020).

#### 11. Chaetocladium Fresen., Beitr. Mykol. 3: 97, 1863

*Chaetocladium* is typified by *C. jonesiae* (Berk. & Broome) Fresen. (Benny & Benjamin 1976). In *Chaetocladium*, uni-spored sporangiola have a separable sporangial wall (Benny & Benjamin 1976, Benny *et al.* 2001). The sporangiola are borne on pedicels which grow on vesicles (Benny & Benjamin 1976, Benny *et al.* 2001). Fertile hyphae produce two or three branches from one point, and branches usually end in a sterile spine (Benny & Benjamin 1976, Benny *et al.* 2001). Zygospores are formed between opposite suspensors, which are more or less equal (Benny & Benjamin 1976, Benny *et al.* 2001). Two species, *C. brefeldii* Tiegh. & G. Le Monn. and *C. jonesiae*, are accepted (www.indexfungorum.org; accessed 5 August 2021). Species of *Chaetocladium* are facultative parasites on other mucoralean fungi (Benny & Benjamin 1976, Benny *et al.* 2001).

# 12. Chlamydoabsidia Hesselt. & J.J. Ellis, Mycologia 58(5): 761, 1966

*Chlamydoabsidia* is typified by *C. padenii* Hesselt. & J.J. Ellis (Hesseltine & Ellis 1966). The genus differs from *Absidia* by large, pigmented, fusiform, multiseptated chlamydospores formed on aerial hyphae (Hesseltine & Ellis 1966). It includes the type species only (www.indexfungorum.org; accessed 5 August 2021).

#### 13. Choanephora Curr., J. Linn. Soc., Bot. 13: 578, 1873

*Choanephora* replaced the synonym *Cunninghamia* and is typified by *Choanephora infundibulifera* (Curr.) D.D. Cunn. (basionym *Cunninghamia infundibulifera* Curr.; Kirk 1984). The genus produces multi-spored sporangia and uni-spored sporangiola at separate sporangiophores (Kirk

1984). In contrast to those in the genus *Blakeslea*, sporangiola in *Choanephora* are uni-spored, forming on fertile heads and lacking suture in the sporangial wall (Kirk 1984). There are no really separable walls in the uni-spored sporangiola (Kirk 1984). Two species, *C. cucurbitarum* and *C. infundibulifera*, are accepted in *Choanephora* so far (www.indexfungorum.org; accessed 5 August 2021). They cause a blossom blight in gourd, pumpkin, pepper, okra, and other cucubits. (Agrios 2005, Saroj *et al.* 2012).

# 14. Circinella Tiegh. & G. Le Monn., Annls Sci. Nat., Bot., sér. 5 17: 298, 1873

*Circinella* is the type of the family Circinellaceae and typified by *C. umbellata* Tiegh. & G. Le Monn. (Hesseltine & Fennell 1955). The genus is characterized by sporangiophores bearing circinate branches that terminate in globose apophysate persistent-walled sporangia (Hesseltine & Fennell 1955). Nowadays, nine species are accepted in this genus (www.indexfungorum.org; accessed 5 August 2021), and two of them were described from China (Zheng *et al.* 2017). Species of the genus can be used as microbial biosensors, and in the biotransformation of progesterone and testosterone (Alpat *et al.* 2008, Zoghi *et al.* 2019). In this paper, we present one new species from China.

# 15. Cokeromyces Shanor, Mycologia 42(2): 272, 1950

*Cokeromyces* is typified by *C. recurvatus* Poitras and is characterized by pedicellate sporangiola originating from a globoid enlargement at the hyphal terminal (Shanor *et al.* 1950). Pedicles are elongate and non-deciduous (Shanor *et al.* 1950, Benny & Benjamin 1976, Kirk 1984). Sporangiola are columellate, multi-spored, globose, persistent-walled, smooth (Shanor *et al.* 1950, Benny & Benjamin 1976, Kirk 1984). Sporangiospores are variable in shape, globose, ovoid, or irregular (Shanor *et al.* 1950, Benny & Benjamin 1976, Kirk 1984). Sporangiospores are variable in shape, globose to subglobose, with dark walls and opposed suspensors, homothallic (Shanor *et al.* 1950, Benny & Benjamin 1976, Kirk 1984). The sole species, *C. recurvatus*, is accepted in the genus, and it causes mucormycosis (Tsai *et al.* 1997).

# 16. Cunninghamella Matr., Annls Mycol. 1(1): 46, 1903

*Cunninghamella* is the type of the order Cunninghamellales and the family Cunninghamellaceae and typified by *C. africana* Matr. (Zheng & Chen 2001). The genus is characterized by terminal vesicles bearing uni-spored sporangiola, which are surrounded by spines (Zheng & Chen 2001). A worldwide monographic on a combination of morphology, maximum growth temperature, mating compatibility and molecular systematics was conducted and consequently 15 species/varieties were accepted (Zheng & Chen 2001). Subsequently, four species, *C. bigelovii* Z.H. Xin, Y. Hui Zhao & Hui Wang, *C. gigacellularis* A.L. Santiago, C.L. Lima & C.A.F. de Souza, *C. guizhouensis* Zhi.Y. Zhang, Y.F. Han & Z.Q. Liang and *C. globospora* H. Zhao & X.Y. Liu, were described in the genus (Guo *et al.* 2015, Hyde *et al.* 2016, Zhang *et al.* 2020, Zhao *et al.* 2021b). Species of *Cunninghamella* are found in soil, plant material, animal material and cheese. Some members of the genus are endophytic (Zhao *et al.* 2014). Fatty acids in the genus are dominantly composed of oleic acid (Zhao *et al.* 2014). In addition to being a common contaminant, *Cunninghamella* spp. are agents of zygomycosis (Robinson *et al.* 1990). Conversely, *Cunninghamella* spp. are also a microbial model for drug metabolism/biotransformation (Sepuri & Vidyavathi 2008). In this paper, six new species are described, and one new combination is proposed within the genus.

# 17. Dichotomocladium Benny & R.K. Benj., Aliso 8(3): 338, 1975

*Dichotomocladium* is typified by *D. elegans* Benny & R.K. Benj. (Benny & Benjamin 1975). Based on molecular data, the genus was once treated as a member of Lichtheimiaceae, closely related to *Lichtheimia* (Hoffmann *et al.* 2009b). It is distinguished from *Lichtheimia* by dichotomously branched fertile hyphae, sporangiola, sterile spines and absence of giant cells (Benny & Benjamin 1975, 1993, Hoffmann *et al.* 2009b). It contains five species (Hoffmann *et al.* 2009b) which are coprophilous and rarely found (Benny & Benjamin 1975, 1993).

#### 18. Dicranophora J. Schröt., Jber. Schles. Ges. Vaterl. Kultur 64: 184, 1886

*Dicranophora* is typified by *D. fulva* J. Schröt. and is characterized by two types of sporangia, treelike sporangiospores, yellow colonies, pronounced anisogamy, zygospores with irregular creviced, homothallism (Voglmayr & Krisai-Greilhuber 1996). Currently, it contains the type species only (Voglmayr & Krisai-Greilhuber 1996) which grows on rotting boletes in Austria (Voglmayr & Krisai-Greilhuber 1996).

# 19. Dissophora Thaxt., Bot. Gaz. 58: 361, 1914

*Dissophora* is typified by *D. decumbens* Thaxt. and is characterized by fertile hyphae abruptly differentiated from slender creeping vegetative hyphae, and by sporangiophores continuously arising as buds from fertile hyphae (Thaxter 1914). The uni- or two-spored sporangiola are similar to those in *Mortierella* (Thaxter 1914). Currently, it includes four species (www.indexfungorum.org; accessed 5 August 2021). Most species of the genus are found in soil except *D. decumbens* which was originally isolated from wood mouse (*Apodemus sylvaticus*) dung (Thaxter 1914).

# 20. Ellisomyces Benny & R.K. Benj., Aliso 8(3): 330, 1975

*Ellisomyces* is typified by *E. anomalus* (Hesselt. & P. Anderson) Benny & R.K. Benj.; basionym is *Thamnidium anomalum* Hesselt. & P. Anderson (Hesseltine & Anderson 1956). Sporangiophores arise from the substrate hyphae, producing bifurcate or trifurcate apical branches with multi-spored, columellate, persistent-walled, and globose sporangiola (Benny & Benjamin 1975). Zygospores are surrounded by an undulate wall and produced between opposed, approximately equal suspensors (Benny & Benjamin 1975). Currently, it includes the type species only (Benny & Benjamin 1975).

21. Entomortierella Vandepol & Bonito, in Vandepol et al., Fungal Diversity 104: 281, 2020

*Entomortierella* is typified by *E. lignicola* (G.W. Martin) Vandepol & Bonito (basionym *Haplosporangium lignicola* G.W. Martin) and is characterized by globose, smooth or spiny sporangiospores, as well as spiny chlamydospores in some species (Vandepol *et al.* 2020). Currently, it includes five species (Vandepol *et al.* 2020). These species are usually associated with insects and widely distributed in soil, roots and rotten plants (Vandepol *et al.* 2020). They are also associated with soil bacteria (Telagathoti *et al.* 2021).

# 22. Fennellomyces Benny & R.K. Benj., Aliso 8(3): 328, 1975

*Fennellomyces* is typified by *F. linderi* (Hesselt. & Fennell) Benny & R.K. Benj. (basionym *Circinella linderi* Hesselt. & Fennell) and is characterized by swellings immediately below a large terminal sporangium (Benny & Benjamin 1975). Four species are accepted (www.indexfungorum.org; accessed 5 August 2021), and they are found in rat dung and poplin fabric (Benny & Benjamin 1975).

#### 23. Gamsiella (R.K. Benj.) Benny & M. Blackw., Mycologia 96(1): 147, 2004

*Gamsiella* typified by *G. multidivaricata* (R.K. Benj.) Benny & M. Blackw. was previously treated as a subgenus in *Mortierella* (Gams 1976, 1977, Benny & Blackwell 2004). The genus is characterized by repeatedly divaricately branched sporangiophores, two-spored sporangiola on long slender pedicels, and terminal globose ornamented chlamydospores (Benjamin 1978, Benny & Blackwell 2004). Currently, it includes two species (Vandepol *et al.* 2020). Previously, strains of the genus were isolated from detritus taken from a rotten stump (Benjamin 1978). In this paper, we describe a new species of *Gamsiella*, which is found in soil.

# 24. Gilbertella Hesselt., Bull. Torrey bot. Club 87: 24, 1960

*Gilbertella* is typified by *G. persicaria* (E.D. Eddy) Hesselt. (basionym *Choanephora persicaria* E.D. Eddy) and is characterized by sporangia with a longitudinal suture on their persistent walls (Hesseltine 1960, Benny 1991). Currently, it contains the type species only. This species is a potential new source of oleic acid (Shah *et al.* 2021) and also a post-harvest soft rot pathogen of fruits and vegetables (Guo *et al.* 2012, Pinho *et al.* 2014, Cruz-Lachica *et al.* 2015). Most recently, it has been isolated from human stool (Huët *et al.* 2020).

#### 25. Gongronella Ribaldi, Riv. Biol. 44: 164, 1952

*Gongronella* is the type of the family Gongronellaceae and typified by *G. urceolifera* (Ribaldi 1952, Hesseltine & Ellis 1964). The characteristic of *Gongronella* is a distinct swollen apophysis (Ribaldi 1952, Hesseltine & Ellis 1964, Doilom *et al.* 2020). A total of twelve species are accepted in the genus (Hesseltine & Ellis 1964, Doilom *et al.* 2020). *Gongronella butleri* (Lendn.) Peyronel & Dal

Vesco is well-known in chitosan industry (Tan *et al.* 1996, Babu *et al.* 2015). *Gongronella* spp. were found to be among phosphate-solubilizing (Doilom *et al.* 2020) and metalaxyl degrading fungi (Martins *et al.* 2020). A species of *Gongronella* was found capable of inducing overproduction of laccase in *Coprinopsis cinerea* (Schaeff.) Redhead, Vilgalys & Moncalvo (Hu *et al.* 2019) and *Panus rudis* Fr. (Wei *et al.* 2010). In this paper, two new species are described from China.

# 26. Gryganskiella Vandepol & Bonito, in Vandepol et al., Fungal Diversity 104: 282, 2020

*Gryganskiella* is typified by *G. cystojenkinii* (W. Gams & Veenb.-Rijks) Vandepol & Bonito 2020 (basionym *Mortierella cystojenkinii* W. Gams & Veenb.-Rijks; Vandepol *et al.* 2020). The genus was established in honor of Andrii Gryanskyi, a Ukrainian-American mycologist who has made a great contribution to the Mucoromycota (Vandepol *et al.* 2020). Unique characteristics are not described for this genus, though some are really remarkable, including smooth, ellipsoid to cylindrical sporangiospores, and lightly pigmented, Light Brown, ochre or orange chlamydospores (Vandepol *et al.* 2020). Currently, it includes two species (Vandepol *et al.* 2020).

# 27. Halteromyces Shipton & Schipper, Antonie van Leeuwenhoek 41: 337, 1975

*Halteromyces* is typified by *H. radiatus* Shipton & Schipper and is characterized by dumbbellshaped, apophysate, sporangia with deliquescent walls (Shipton & Schipper 1975). Currently, it contains the type species only (Shipton & Schipper 1975). Strains of the species were isolated from mud in a mangrove forest (Shipton & Schipper 1975).

# 28. Hesseltinella H.P. Upadhyay, Persoonia 6(1): 111, 1970

*Hesseltinella* is typified by *H. vesiculosa* H.P. Upadhyay and is characterized by sporangia which are multi-spored, spiny, on pedicels on versicles that originate from multi-vesiculate sporangiophores (Upadhyay 1970, Young 1987, Benny & Benjamin 1991). Currently, it contains the type species only (Upadhyay 1970). Strains of the species were isolated from soil samples (Upadhyay 1970, Young 1987).

# 29. Helicostylum Corda, Icon. Fung. (Prague) 5: 18, 1842

*Helicostylum* is typified by *H. elegans* Corda (Corda 1842). The main stem of the sporangiophores produces larger, multi-spored, sporangia with deliquescent walls, while the lateral branches bear smaller, persistent, and pedicellate sporangia, as well as verticillate or pseudo-verticillate borne spines (Corda 1842, Benny 1995b). Two species have been described in this genus (Benny 1995b). *H. pulchrum* (Preuss) Pidopl. & Milko is a psychrotolerant fungus, gowning on refrigerated meat (Spatafora *et al.* 2016).

# 30. Hyphomucor Schipper & Lunn, Mycotaxon 27: 83, 1986

*Hyphomucor* is typified by *H. assamensis* (B.S. Mehrotra & B.R. Mehrotra) Schipper & Lunn (basionym *Mucor assamensis* B.S. Mehrotra & B.R. Mehrotra; Schipper 1986a). Sporangiophores are sympodially branched. Sporangia are apophysate and subglobose (Schipper 1986a). Sporangial walls are dry and powdery (Schipper 1986a). Sporangiospores are subglobose (Schipper 1986a). Currently, it contains the type species only (Schipper 1986a).

31. Isomucor J.I. Souza, Pires-Zottar. & Harakava, Mycologia 104(1): 233, 2012

*Isomucor* is typified by *I. trufemiae* J.I. Souza, Pires-Zottar. & Harakava (de Souza *et al.* 2012). It was established based on molecular data and unique morphological traits (de Souza *et al.* 2012). The genus produces lateral branches bearing multi-spored sporangiola and sporangia as well as uniformly septate hyphae (de Souza *et al.* 2012). It contains two species, *I. fuscus* (Berk. & M.A. Curtis) J.I. Souza, Pires-Zottar. & Harakava, and *I. trufemiae* (de Souza *et al.* 2012). In this paper, *I. trufemia* is recorded from China for the first time.

# 32. Kirkiana L.S. Loh, Kuthub. & Nawawi, Mucoraceous Fungi from Malaysia (Kuala Lumpur): 76, 2001

*Kirkiana* is typified by *K. ramosa* L.S. Loh, Kuthub. & Nawawi (Loh *et al.* 2001). Currently, it contains the type species only (Loh *et al.* 2001). However, no cultures and sequences are available.

#### 33. Kirkomyces Benny, Mycologia 87(6): 922, 1995

*Kirkomyces*, formerly named *Kirkia*, is typified by *K. cordense* (B.S. Mehrotra & B.R. Mehrotra) Benny (Benny 1995a, b). The genus is characterized by the absence of spine-like fertile branches and a higher optimal growth temperature than that of *Helicostylum* (Benny 1995a, b). Currently, it contains the type species only (Benny 1995a, b).

# 34. Lentamyces Kerst. Hoffm. & K. Voigt, Pl. Biol. 11(4): 550, 2009

*Lentamyces* is the type of the order Lentamycetales and the family Lentamycetaceae. It is typified by *L. parricidus* (Renner & Muskat ex Hesselt. & J.J. Ellis) Kerst. Hoffm. & K. Voigt (basionym *Absidia parricida* Renner & Muskat; Hoffmann & Voigt 2009). The genus is characterized by a slow growth and a maximum growth temperature < 30 °C (Hoffmann & Voigt 2009). It contains four species so far (www.indexfungorum.org; accessed 5 August 2021).

# 35. Lichtheimia Vuill., Bull. Soc. Mycol. Fr. 19: 126, 1903

*Lichtheimia* is the type of the family Lichtheimiaceae (Hoffmann & Voigt 2009, Hoffmann 2010). It is typified by *L. corymbifera* (Cohn) Vuill. (basionym *Mucor corymbifer* Cohn; Hoffmann & Voigt 2009, Hoffmann 2010). Most species of the genus formerly belonged to *Absidia* (Hoffmann & Voigt 2009, Hoffmann 2010). The genus is differentiated from *Absidia* by a maximum growth temperature of above 37 °C (Hoffmann & Voigt 2009, Hoffmann 2010). Currently, seven species are accepted (www.indexfungorum.org; accessed 5 August 2021). Interestingly, some species, such as *L. corymbifera* and *L. ramosea* (Zopf) Vuill., are well-known as pathogenic fungi causing mucormycosis, and are widely distributed in foods and the environment (Gomes *et al.* 2011, André *et al.* 2014, Schwartze & Jacobsen 2014). In this study, two new species are illustrated from Chinese soil samples.

36. Linnemannia Vandepol & Bonito, in Vandepol et al., Fungal Diversity 104: 282, 2020

*Linnemannia* is typified by *L. hyalina* (Harz) Vandepol & Bonito (basionym *Hydrophora hyalina* Harz; Vandepol *et al.* 2020). It was set up in honor of Germaine Linnemann for his contribution to the family Mortierellaceae (Vandepol *et al.* 2020). Most members of the genus usually produce

ellipsoid, spherical to cylindrical sporangiospores (Vandepol *et al.* 2020). Chlamydospores are irregular, with various brown shades (Vandepol *et al.* 2020). Sexual reproduction is heterothallic (Vandepol *et al.* 2020). Currently, it includes eleven species (www.indexfungorum.org; accessed 5 August 2021).

# 37. Lobosporangium M. Blackw. & Benny, Mycologia 96(1): 144, 2004

*Lobosporangium* replaced the synonym *Echinosporangium* and is typified by *Lobosporangium transversale* (Malloch) M. Blackw. & Benny (basionym *Echinosporangium transversale* Malloch; Benny & Blackwell 2004). The genus is characterized by coenocytic and anastomosing mycelia, forming 3–4 dichotomies at lateral branches, terminating with a cylindrical sporangium and several spines (Benny & Blackwell 2004). Currently, it contains the type species only (Benny & Blackwell 2004).

# 38. Lunasporangiospora Vandepol & Bonito, in Vandepol et al., Fungal Diversity 104: 283, 2020

*Lunasporangiospora* is typified by *L. chienii* (P.M. Kirk) Vandepol & Bonito (basionym *Mortierella chienii*) and is characterized by smooth and lunate sporangiospores (Vandepol *et al.* 2020). It accommodates two species, *L. chienii* and *L. selenospora* (W. Gams) Vandepol & Bonito (Vandepol *et al.* 2020). They were found in mushroom compost and forest soil (Vandepol *et al.* 2020).

# 39. Modicella Kanouse, Mycologia 28(1): 60, 1936

*Modicella* is typified by *M. malleola* (Harkn.) Gerd. & Trappe (basionym *Endogone malleola* Harkn.) and is characterized by truffle-like fruitbodies, namely sporocarps which consist of smooth, thin-walled and hyaline sporangia (Kanouse 1936). Phylogenetic analysis demonstrated that *Modicella* was monophyletic in Mortierellales (Smith *et al.* 2013). Apart from the type species, the other two species in the genus are *M. albostipitata* J.A. Cooper and *M. reniformis* (Bres.) Gerd. & Trappe (Cooper & Park 2020).

#### 40. Mortierella Coem., Bull. Acad. R. Sci. Belg., Cl. Sci., sér. 2 15: 536, 1863

Mortierella is the type of the phylum Mortierellomycota, the class Mortierellomycetes, the order Mortierellales and the family Mortierellaceae (Tedersoo et al. 2018). It is typified by M. polycephala Coem. (Coemans 1863). The genus is characterized by sporangiophores enlarging at the base and shrinking sharply towards top (Coemans 1863). Some colonies are zonate and some look like rounded to slightly pointed rosette petals (Gams 1976, 1977). A few species even grow flat on the surface of the solid media (Gams 1977, Vandepol et al. 2020). Four types of spores are observed in this genus, including asexual sporangiospores, chlamydospores, stylospores and sexual zygospores, while one or more types of spores are absent in some members (Gams 1977, Vandepol et al. 2020). Currently, it encompasses more than 110 species, the largest genus in the phylum Mortierellomycota (www.indexfungorum.org; accessed 5 August 2021). Species of the genus are widely distributed in soils, plant debris, living plant roots, mosses and insect guts (Gams 1977, Domsch et al. 1980). Mortierella seems to be the most commonly isolated Mucoromyceta genus from soil and is highly associated with soil bacteria (Telagathoti et al. 2021). Some species of the genus accumulate large amounts of polyunsaturated fatty acids, especially arachidonic acid, attracting widespread interest (Zhao et al. 2021a). Mortierella species can be endophytic and plant growth promoting (Ozimek & Hanaka 2021).

#### 41. Mucor Fresen., Beitr. Mykol. 1: 7, 1850

*Mucor* is the type of the subkingdom Mucoromyceta, the phylum Mucoromycota, the class Mucoromycetes, the order Mucorales and the family Mucoraceae (Tedersoo *et al.* 2018). It is a conserved genus with the explicitly conserved type *M. mucedo* Fresen. (Appendix III; Turland *et al.* 2018). The genus is characterized by fast growth, luxuriant aerial and substrate hyphae, usually unbranched sporangiophores, non-apophysate, zygospores with opposed suspensors, and are heterothallic or homothallic (Schipper 1978a). Species of *Mucor* are distributed all over the world, and commonly collected in soil and dung (Walther *et al.* 2013). It accommodates more than 100 species, the largest genus in the phylum Mucoromycota (www.indexfungorum.org; accessed 5 August 2021). In practice, *Mucor* seems to be the second most common genus of the Mucoromyceta isolated from soil. Some species are widely used in fermentation and

34

biotransformation (Hong *et al.* 2012). Several species are used in the pharmaceutical industry for podophyllotoxin, kaempferol (Huang *et al.* 2014), and stearidonic acid (Khan *et al.* 2019), and some species are well-known pathogens causing mucormycosis (Chibucos *et al.* 2016, Panthee *et al.* 2021).

# 42. Mycocladus Beauverie, Annls Univ. Lyon, Ser. 2 3: 162, 1900

*Mycocladus* is the type of the family Mycocladaceae (Hoffmann *et al.* 2007). It is typified by *M. verticillatus* Beauverie and is characterized by relatively high optimum and maximum growth temperatures (37–42 °C and 53 °C, respectively), abundantly giant cells, stolons and rhizoids, and apophysate sporangia with deliquescent walls (Hoffmann *et al.* 2007). Several species described in this genus, have been transferred to *Absidia* and *Lichtheimia* (Beauverie 1900, Hoffmann *et al.* 2007, Hoffmann *et al.* 2009b). Currently, it contains the type species only (Hoffmann *et al.* 2009b).

# 43. Mycotypha Fenner, Mycologia 24(2): 196, 1932

*Mycotypha* is typified by *M. microspora* Fenner and is characterized by cylindrical vesicles and two distinct kinds of denticles (Benny *et al.* 1985). Three species are recorded in the genus. They are distributed in Finland, India, Japan, USA and Zimbabwe (Benny & Benjamin 1976, Benny *et al.* 1985). *M. microspora* was found to induce the aggregation of firebrats (*Thermobia domestica*), a fast-moving brownish insect frequently living indoors in warm environments (Woodbury & Gries 2013). *M. africana* R.O. Novak & Backus and *M. microspora* are traditional dimorphic fungi (Schulz *et al.* 1974) and have been most recently reported as new pathogens causing mucormycosis (Trachuk *et al.* 2018).

44. Nawawiella L.S. Loh & Kuthub., Mucoraceous Fungi from Malaysia (Kuala Lumpur): 73, 2001

*Nawawiella* is typified by *N. apophysa* L.S. Loh & Kuthub. (Loh *et al.* 2001). It contains the type species only (Loh *et al.* 2001). However, no cultures and sequences are available for the species.

45. Necromortierella Vandepol & Bonito, in Vandepol et al., Fungal Diversity 104: 284, 2020

*Necromortierella* is typified by *N. dichotoma* (Linnem. ex W. Gams) Vandepol & Bonito (basionym *Mortierella dichotoma* Linnem. ex W. Gams) and is characterized by sporangiophores irregularly dichotomously branched and tapering towards the apex quickly, ellipsoid to cylindric sporangiospores, and elongated or irregular chlamydospores (Vandepol *et al.* 2020). Currently, it contains the type species only (Vandepol *et al.* 2020). This species has a necrotrophic and mycophilic life mode (Vandepol *et al.* 2020).

#### 46. Parasitella Bainier, Bull. Soc. Mycol. Fr. 19(2): 153, 1903

*Parasitella* is typified by *P. parasitica* (Bainier) Syd. (basionym *Mucor parasiticus* Bainier) and is characterized by mycoparasitic behavior, sporangiophores from substrate hyphae *in vitro* and from aerial hyphae *in vivo*, subglobose to globose sporangia, apophysate, with a columella and moist wall, multi-spored, zygospores, and is heterothallic (Schipper 1978b). Currently, it contains the type species only (Schipper 1978b). The species is parasitic on other Mucoraceae such as *Absidia glauca* Hagem (Schipper 1978b).

# 47. Phascolomyces Boedijn ex Benny & R.K. Benj., Aliso 8(4): 417, 1976

*Phascolomyces* is typified by *P. articulosus* Boedijn ex Benny & R.K. Benj. (Benny & Benjamin 1976). The genus is allied to *Cunninghamella*, and characterized by chlamydospores which form on substrate hyphae, swollen vesicles on the side of sporangiophores, sporangiola which are pedicellate, globose to subglobose, columellate and uni-spored (Benny & Benjamin 1976). Currently, it contains the type species only (Benny & Benjamin 1976).

# 48. Phycomyces Kunze, Mykologische Hefte (Leipzig) 2: 113, 1823

*Phycomyces* is the type of the order Phycomycetales and the family Phycomycetaceae. It is typified by *P. nitens* (C. Agardh) Kunze (basionym *Ulva nitens* C. Agardh; Benjamin & Hesseltine 1959). The genus is characterized by sporangia which are non-apophysate, multi-spored and borne on exceedingly long, unbranched, bluish or metallic sporangiophores, zygospores which are *Mucor*-like and produce dichotomously branched, darkened spines and appendages (Benjamin &
Hesseltine 1959, Bergman *et al.* 1969). The dried thalli in test tubes looks like a bunch of hair, wellknown as a hairy fungus (Benjamin & Hesseltine 1959, Bergman *et al.* 1969). This genus accommodates three species, *P. blakesleeanus* Burgeff, *P. microspores* Tiegh. and *P. nitens* (C. Agardh) Kunze (Benjamin & Hesseltine 1959, Bergman *et al.* 1969). Among these species, *P. blakesleeanus* is well-known as a model organism for phototropism and light-growth response (Galland & Lipson 1985).

## 49. Pilobolus Tode, Schr. Ges. Naturf. Freunde, Berlin 5: 46, 1784

*Pilobolus* is the type of the family Pilobolaceae and typified by *P. crystallinus* (F.H. Wigg.) Tode (basionym *Hydrogera crystallina* F.H. Wigg.; www.indexfungorum.org; accessed 5 August 2021). The genus is characterized by trophocytes which give rise to positively phototropic sporangiophores, sporangia which are produced on a huge swelling and are violently discharged (Page 1962, Hu *et al.* 1989, Viriato 2008, Lee *et al.* 2018). It accommodates 15 species (www.indexfungorum.org; accessed 5 August 2021). Members of the genus are cosmopolitan and coprophilous and are also known as model organisms for the forcible ejection of entire ripe sporangia (Page 1964, Page & Kennedy 1964).

#### 50. Pilaira Tiegh., Annls Sci. Nat., Bot., sér. 6 1: 51, 1875

*Pilaira* is typified by *P. cesatii* Milko (basionym *Ascophora cesatii* Coem., an illegitimate name) and is characterized by sporangiophores which are simple or branched, and sporangia which have cutinized walls, and are apophysate, columellate and multi-spored. It accommodates nine species (Zheng & Liu 2009, Liu *et al.* 2012, Urquhart *et al.* 2017).

# 51. Pirella Bainier, Étud. Mucor., (Thèse, Paris) (Paris): 83, 1882

*Pirella* is typified by *P. circinans* Bainier and is characterized by sporangiophores which produce simultaneously terminal multi-spored sporangia and lateral several-spored sporangiola. Lateral branches are twisted and contorted (Benny & Schipper 1992). Zygospores are globose to compressed, with a pigmented and ornamented wall (Benny & Schipper 1992). It accommodates

two species *P. circinans* and *P. naumovii* (Milko) Benny & Schipper (Benny & Schipper 1992). *P. circinans* has been isolated from China once (Liu 2004).

52. Podila Stajich, Vandepol & Bonito, in Vandepol et al., Fungal Diversity 104: 284, 2020

*Podila*, in honor of Gopi Podila, is typified by *P. minutissima* (Tiegh.) Vandepol & Bonito (basionym *Mortierella minutissima*; Vandepol *et al.* 2020). It seems there are no characteristics unique to this genus because species of the genus produce various types of sporangiospores, chlamydospores, and zygospores. Species are distributed in forest and agricultural soil, plant roots, compost, animal dung and municipal waste (Vandepol *et al.* 2020). It accommodates seven species all transferred from *Mortierella* (Vandepol *et al.* 2020).

# 53. Poitrasia P.M. Kirk, Mycol. Pap. 152: 51, 1984

*Poitrasia* is typified by *P. circinans* (H. Nagan. & N. Kawak.) P.M. Kirk (basionym *Blakeslea circinans*) and is characterized by tong-like suspensors (Kirk 1984). Currently, it contains the type species only (Kirk 1984) which was originally isolated from soil but also found to be a marine fungus with a phytotoxicity activity (Huang *et al.* 2018). It produces protease and keratinase (Agrawal *et al.* 2021).

## 54. Protomycocladus Schipper & Samson, Mycotaxon 50: 487, 1994

*Protomycocladus* is the type of the family Protomycocladaceae. It is typified by *P. faisalabadensis* (J.H. Mirza *et al.*) Schipper & Samson (basionym *Mucor faisalabadensis et al.*). The genus is characterized by the multi-spored sporangia that are apophysate, columellate and obpyriform (Mirza *et al.* 1979, Schipper & Samson 1994). Currently, it contains the type species only (Schipper & Samson 1994).

# 55. Pygmaeomyces E. Walsh & N. Zhang, Mycologia 113(1): 141, 2021

*Pygmaeomyces* is the type of the family Pygmaeomycetaceae and typified by *P. thomasii* E. Walsh & N. Zhang (Walsh *et al.* 2021). The genus is characterized by microchlamydospores which are hyaline, globose to subglobose, and distinguished from its most closely related genus *Umbelopsis* 

by producing colonies without pigmentation, sporangiophores and sporangiospores (Walsh *et al.* 2021). Currently, it contains two species which are associated with plant roots (Walsh *et al.* 2021).

## 56. Radiomyces Embree, Am. J. Bot. 46: 25, 1959

*Radiomyces* is the type of the family Radiomycetaceae and typified by *R. spectabilis* Embree (Embree 1959, Benny & Benjamin 1991). The genus is characterized by two levels of vesicles, the single main vesicle proliferating several secondary vesicles which in turn produce pedicles and unior several-spored sporangiola. Its zygospores are *Mucor*-like, except for simple or branched appendages (Embree 1959, Benny & Benjamin 1991). Three species are accepted in the genus (www.indexfungorum.org; accessed 5 August 2021), and they are coprophilous but are thermotolerant and pathogenic to mice (Kitz *et al.* 1980).

# 57. Rhizopodopsis Boedijn, Sydowia 12(1-6): 220, 1958

*Rhizopodopsis* is typified by *R. javensis* Boedijn and is characterized by sporangiophores which directly arise from a long erect hyphal branch, by sporangia which are apophysate, columellate and multi-spored, by sporangiospores which are globose to elongated, and by zygospores which are *Mucor*-like and homothallic (Boedijn 1958). Currently, it contains the type species only (Boedijn 1958).

## 58. Rhizomucor Lucet & Costantin, Rev. Gén. Bot. 12: 81, 1900

*Rhizomucor* is the type of the family Rhizomucoraceae and typified by *R. parasiticus* (replaced synonym *Mucor parasiticus* Lucet & Costantin, competing homonym non *M. parasiticus* Bainier; Schipper 1979). The genus differs from *Mucor* by rhizoids, and from *Thermomucor* by nonapohysate sporangia and rough zygospores (Subrahmanyam *et al.* 1977, Schipper 1979). It accommodates six species (Lucet and Costantin 1900, Zheng *et al.* 2009). *Rhizomucor* is a cosmopolitan genus and found in soil, decayed fruit and vegetables, fermenting and composting organic matter. All species in this genus produce lipase (Li *et al.* 2018), also cause mucormycosis in humans (Lukacs *et al.* 2004).

59. Rhizopus Ehrenb., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 10: 198, 1821

*Rhizopus* is type genus of the family Rhizopodaceae and typified by *R. nigricans* Ehrenb. which is an illegitimate name and synonymized with *R. stolonifer* (Ehrenb.) Vuill. (basionym *Mucor stolonifer* Ehrenb; Zheng *et al.* 2007). The genus is characterized by deep gray to blackish colonies, abundant rhizoids on hyphae and stolons, solitary or more often in a group, sporangia dark, round, apophysate and columellate, sporangiospores striped and of various shapes and sizes, zygospores or azygospores hyaline, globose to broadly ovoid (Zheng *et al.* 2007). It accommodates twelve species (Li *et al.* 2016, Zheng *et al.* 2007). Species of *Rhizopus* are distributed worldwide in soil and air. They play key roles in industrial, agricultural, and medical applications as fermentation agents, and some species cause diseases in plants, humans and animals (Zheng *et al.* 2007, Cheng *et al.* 2017, Yao *et al.* 2018, Ju *et al.* 2020).

#### 60. Saksenaea S.B. Saksena, Mycologia 45(3): 434, 1953

*Saksenaea* is type genus of the family Saksenaeaceae (Ellis & Hesseltine 1974) and typified by *S. vasiformis* S.B. Saksena (Saksena 1953). The genus is characterized by flask-shaped or variform sporangia with a long neck (Saksena 1953). It accommodates six species which often cause mucomycosis in humans (Saksena 1953, Labuda *et al.* 2019).

## 61. Spinellus Tiegh., Annls Sci. Nat., Bot., sér. 6 1: 66, 1875

*Spinellus* is typified by *S. fusiger* (Link) Tiegh. (basionym *Mucor fusiger* Link; Zycha *et al.* 1969) and is characterized by unbranched sporangiophores, apophysate and multi-spored, spinose zygospores, and a facultative parasitism on fungi (Zycha *et al.* 1969, Overton 1997). Six species are reported in the genus so far (www.indexfungorum.org, accessed 5 August 2021).

## 62. Sporodiniella Boedijn, Sydowia 12(1-6): 336, 1959 [1958]

*Sporodiniella* is typified by *S. umbellata* Boedijn and is characterized by umbel-branched sporangiophores, and spinose sporangiospores (Boedijn 1958). Currently, it contains only the type species which is a facultative parasite on insect larvae in the tropics (Boedijn 1958, Chien & Hwang 1997).

## 63. Syncephalastrum J. Schröt., Krypt.-Fl. Schlesien (Breslau) 3.1(9-16): 217, 1886

*Syncephalastrum* is type genus of the class Syncephalastromycetes, the order Syncephalastrales and the family Syncephalastraceae. It is typified by *S. racemosum* Cohn ex J. Schröt. (Benjamin 1959). The genus is characterized by cylindrical merosporangia, rough or dark-walled zygosporangia, and opposed, more or less equal suspensors (Benjamin 1959). It accommodates five species (www.indexfungorum.org; accessed 5 August 2021). They are a group of fungi pathogenic to humans (Pavlovic & Bulajic 2006, Rao *et al.* 2007, Irshad *et al.* 2020). In this study, four new species are described from China.

#### 64. Syzygites Ehrenb., Sylv. Mycol. Berol. (Berlin): 25, 1818

*Syzygites* is typified by *S. megalocarpus* Ehrenb. and is characterized by columellate and few-spored sporangia, dichotomously branched sporangiophores, and homothallic zygospores (Kovacs & Sundberg 1999). In addition, its spinose sporangiospores are similar to those of *Sporodiniella* (Ekpo & Young 1979). Currently, it contains the type species only (Kovacs & Sundberg 1999). In nature, this species is parasitic on fleshy fungi (Kovacs & Sundberg 1999).

## 65. Thamnidium Link, Mag. Gesell. Naturf. Freunde, Berlin 3(1-2): 31, 1809

The monotypic *Thamnidium* is typified by *T. elegans* Link and is characterized by sporangia with deliquescent walls and persistent-walled sporangiola, primary sporangiophores and lateral dichotomous branchlets (Benny 1992). As a psychrophilic fungus, *T. elegans* is isolated from soil and cold-storage meat (Brooks & Hansford 1923), and it releases proteases and collagenolytic enzymes for colonizing meat (Dashdorj *et al.* 2016).

## 66. Thamnostylum Arx & H.P. Upadhyay, Gen. Fungi Sporul. Cult. (Lehr): 247, 1970

*Thamnostylum* is typified by *T. piriforme* (Bainier) Arx & H.P. Upadhyay (basionym *Helicostylum piriforme* Bainier) and is characterized by producing spherical to pyriform apophysate sporangia and pyriform apophysate sporangiola (von Arx 1970, Upadhyay 1973, Benny & Benjamin 1975). It accommodates four species (von Arx 1970). *T. lucknowense* (J.N. Rai, J.P. Tewari & Mukerji) Arx & H.P. Upadhyay is found to be an agent of rhino-orbital mucormycosis (Xess *et al.* 2012).

67. Thermomucor Subrahm., B.S. Mehrotra & Thirum., Georgia J. Sci. 35(1): 1, 1977

*Thermomucor* is typified by *T. indicae-seudaticae* Subrahm., B.S. Mehrotra & Thirum. and is characterized by apophysate sporangia and unusually smooth zygospores (Subrahmanyam *et al.* 1977, Schipper 1979). Currently, it contains the type species only (Schipper 1979). This species is a human pathogen and synthesizes cellulases, glucoamylase, pectinase, and protease (Subrahmanyam & Lakshmi 1993, Kumar & Satyanarayana 2007, Merheb-Dini *et al.* 2012, Martins *et al.* 2019, de Carvalho Tavares *et al.* 2020, Pereira *et al.* 2020).

68. Tortumyces L.S. Loh, Mucoraceous Fungi from Malaysia (Kuala Lumpur): 80, 2001

*Tortumyces* is typified by *T. fimicola* L.S. Loh (Loh *et al.* 2001). It accommodates two species, *T. cameronensis* L.S. Loh and *T. fimicola* (Loh *et al.* 2001). However, their cultures and sequences are unavailable so far.

69. Umbelopsis Amos & H.L. Barnett, Mycologia 58(5): 807, 1966

*Umbelopsis* is type genus of the phylum Umbelopsidomycota, the class Umbelopsidales and the family Umbelopsidaceae. It is typified by *U. versiformis* Amos & H.L. Barnett (Amos & Barnett 1966). The genus differs from its allied genus *Mortierella* in having small but distinct columellae and ochraceous to reddish colonies (Meyer & Gams 2003, Wang *et al.* 2013, 2014, 2015). Currently, 18 species are accepted in the genus (von Arx 1982, Yip 1986, Meyer & Gams 2003, Wang *et al.* 2014, 2015, Crous *et al.* 2017, Wijayawardene *et al.* 2018, Yuan *et al.* 2020). They are distributed worldwide in soil and are also endophytic (Qin *et al.* 2018). Some species of the genus are used for lipid production (Gardeli *et al.* 2017, Zhao *et al.* 2021a).

70. Utharomyces Boedijn ex P.M. Kirk & Benny, Trans. Br. Mycol. Soc. 75(1): 124, 1980

*Utharomyces* is typified by *U. epallocaulus* Boedijn and is similar to *Pilobolus* in having sporangiophores that arise from a trophocyte in the substrate hyphae and with subsporangial swellings but differs in sporangia which are not violently discharged (Boedijn 1958, Kirk & Benny 1980, Hu *et al.* 1989). Currently, it contains the type species only (Kirk & Benny 1980).

71. Zychaea Benny & R.K. Benj., Aliso 8(3): 334, 1975

*Zychaea* is typified by *Z. mexicana* Benny & R.K. Benj. and is characterized by sporangiola which are pedicellate, and sporangiospores which are globose to subglobose, uni-spored or multi-spored, ovoid to ellipsoid (Benny & Benjamin 1975). Currently, it contains the type species only (Benny & Benjamin 1975). Strains of the species were isolated from dung (Benny & Benjamin 1975).

#### Taxonomy of new species and new combinations

In the present study, we describe 73 new species in the Mortierellomycota, Mucoromycota and Umbelopsidomycota (Table 1). Besides, three new combinations are elevated from a variety status (Table 1). All these new taxa are illustrated below.

1. Absidia alpina H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 17.

Fungal Names: FN570882.

*Etymology: alpina* (Lat.) refers to the mountain environment where the type was collected. *Holotype:* HMAS 351506.

*Colonies* on MEA at 27 °C for 10 days, slow growing, reaching 65 mm in diameter, irregular concentrically zonate with ring, white at first, gradually becoming Light Brown to Sudan Brown. *Hyphae* hyaline at first, brown when mature, aseptate when juvenile, septate with age,  $3.0-15.5 \,\mu\text{m}$  in diameter. *Stolons* branched, hyaline to brownish, smooth, with few septa. *Rhizoids* root-like, always unbranched, with a septum at the top. *Sporangiophores* erect or slightly bent, 1-5 in whorls, often monopodial, rarely simple unbranched, hyaline, with a septum  $11.5-18.0 \,\mu\text{m}$  below apophyses,  $35.0-300.0 \,\mu\text{m}$  or more in length and  $2.5-5.0 \,\mu\text{m}$  in width. *Sporangia* subglobose, smooth, multi-spored, hyaline when young, brown when old,  $12.5-30.0 \,\mu\text{m}$  long and  $16.0-28.0 \,\mu\text{m}$  wide, walls deliquescent. *Apophyses* distinct, slightly pigmented,  $3.0-6.0 \,\mu\text{m}$  high,  $4.0-7.0 \,\mu\text{m}$  wide at the base, and  $6.5-15.0 \,\mu\text{m}$  wide at the top. *Collars* present or absent, and distinct if present. *Columellae* subglobose to ellipsoid, hyaline, smooth, some with a  $3.0-7.5 \,\mu\text{m}$  projection at the apex,  $10.0-18.5 \,\mu\text{m}$  long and  $12.5-20.0 \,\mu\text{m}$  wide. *Zygospores* absent. *Chlamydospores* absent.

Material examined: China, Yunnan Province, Dali, Huacong Mountain, 26°25'21"N,

99°53'41"E, from soil sample, 28 October 2021, Heng Zhao (holotype HMAS 351506, living exholotype culture CGMCC 3.16104).

GenBank accession number: OL678133.

*Notes: Absidia alpina* is closely related to *A. ampullacea* T.K. Zong *et al.* based on phylogenetic analysis of ITS rDNA sequences (Fig. 5). However, morphologically *A. ampullacea* differs from *A. alpina* by ovoid to subglobose sporangiospores, sympodially-branched and swollen sporangiophores.

 Absidia ampullacea T.K. Zong, H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 18. Fungal Names: FN570883.

*Etymology: ampullacea* (Lat.) refers to the species having ampulliform swollen hyphae and sporangiophores.

Holotype: HMAS 350295.

*Colonies* on MEA at 27 °C for 10 days, slow growing, reaching 90 mm in diameter, irregularly zonate, white at first and then Saccardo's Olive. *Hyphae* hyaline at first, becoming brown when mature, sometimes ampulliform-shaped swollen, 6.0–16.5 µm in diameter. *Stolons* branched, hyaline, smooth, septate, 4.0–9.0 µm in diameter. *Rhizoids* finger-like, mostly twice or more repeatedly, with a septum at the base. *Sporangiophores* erect or slightly bent, 1–6 in whorls, unbranched, simple branched, monopodial, or sympodial, hyaline, with a septum 14.5–21.5 µm below apophyses, sometimes a swelling beneath sporangium, 30.0–320.0 µm long and 2.5–5.5 µm wide. *Sporangia* globose to pyriform, smooth, multi-spored, 17.5–37.5 µm long and 17.5–45.0 µm wide, walls deliquescent. *Apophyses* distinct, bell-shaped, slightly pigmented, 4.0–9.5 µm high, 2.5–8.0 µm wide at the base, and 9.5–20.0 µm wide at the top. *Collars* distinct. *Columellae* hemispherical, hyaline, smooth, occasionally with a 0.5–2.0 µm verrucous projection at the apex, 8.5–22.5 µm long and 10.5–24.0 µm wide. *Sporangiospores* ovoid or subglobose, 3.0–4.5 µm long and 2.5–4.0 µm wide. *Zygospores* absent. *Chlamydospores* absent. No growth at 30 °C.

Material examined: China, Beijing, 40°3'49"N, 116°1'26"E, from soil sample, 31 December

2019, Xiao-Yong Liu (holotype HMAS 350295, living ex-holotype culture CGMCC 3.16054).

GenBank accession number: MZ354138.

Notes: See the notes in Absidia alpina.

 Absidia biappendiculata (Rall & Solheim) T.K. Zong, H. Zhao, Y.C. Dai & X.Y. Liu, comb. et stat. nov., Fig. 19.

Fungal Names: FN570884.

Basionym: *Absidia spinosa* var. *biappendiculata* Rall & Solheim, Mycologia, 56(1), 99. 1964. [MB no.: 348993].

Holotype: CBS 187.64.

Colonies on MEA at 27 °C for 6 days, reaching 90 mm in diameter, regularly zonate, white at first and becoming Pale Mouse Gray with age. Hyphae hyaline to slightly pigmented, 5.5-11.0 µm in diameter. Stolons branched, hyaline, smooth, septate, 3.5-5.5 µm in diameter. Rhizoids root-like, tapering at the end, with a septum at the base. Sporangiophores erect or slightly bent, 1–5 in whorls, unbranched or simple branched, monopodial, and sympodial forms absent, hyaline, with a septum 11.0-17.0 µm below apophyses, 65.0-210.0 µm long and 2.5-5.0 µm wide. Sporangia globose to pyriform, smooth, multi-spored, 16.0–29.0 µm long and 15.5–27.0 µm wide, walls deliquescent. Apophyses distinct, slightly pigmented, 3.5–9.0 µm high, 2.5–4.5 µm wide at the base, and 8.0–20.0 µm wide at the top. Collars distinct if present. Columellae hemispherical to subglobose, hyaline, smooth, sometimes with a 3.0-7.0 µm spinous projection at the apex, occasionally with two projections, or with a conical projection in some of smaller columellae, 7.5-19.0 µm long and 8.5-20.0 µm wide. Sporangiospores cylindrical to ovoid, slightly constricted in the center, hyaline, smooth, 3.5–4.5 µm long and 2.0–2.5 µm wide. Zygospores globose, brown to Dark Brown, rough, 33.0-66.0 µm in diameter. Suspensor with appendages, mostly two, nearly equal, parallel or nearly so, sometimes only one, hyaline or brown, 14.0-27.0 µm in diameter. Chlamydospores absent. No growth at 35 °C.

*Material examined*: USA, Wyoming, Albany County, from leaves of *Comandra pallida*, August 1960, G. Rall (NRRL 3033, isotype CBS 187.64, isotype HMAS 350310)

GenBank accession number: MZ354153

*Notes: Absidia biappendiculata* was previously regarded as a synonym of *A. spinosa*. However, morphologically *A. spinosa* differs from *A. biappendiculata* by wider sporangiophores (5.0–10.5 μm wide vs. 2.0–2.5 μm wide), producing one projection on columellae only (Hesseltine & Ellis 1964, Rall & Solheim 1964).

4. Absidia brunnea T.K. Zong, H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 20.

Fungal Names: FN570885.

*Etymology: brunnea* (Lat.) refers to the species having brown colonies on MEA. *Holotype:* HMAS 350296.

*Colonies* on MEA at 27 °C for 10 days, slow growing, reaching 90 mm in diameter, obversely regularly concentrically zonate with ring, white at first and then Sayal Brown or Snuff Brown. *Hyphae* hyaline at first, becoming brown when mature,  $6.0-17.5 \mu m$  in diameter. *Stolons* branched, hyaline, smooth, septate,  $3.5-10.0 \mu m$  in diameter. *Rhizoids* rarely branched, with a septum at the base. *Sporangiophores* erect or slightly bent, 1-7 in whorls but mostly 4-6, unbranched, simple branched or monopodial, rarely sympodial, hyaline, with a septum  $11.0-17.0 \mu m$  below apophyses, sometimes a swelling beneath sporangium, occasionally branched at the swelling,  $50.0-420.0 \mu m$  long and  $3.0-6.5 \mu m$  wide. *Sporangia* globose to pyriform, smooth, multi-spored,  $17.5-38.0 \mu m$  long and  $19.0-34.5 \mu m$  wide, walls deliquescent. *Apophyses* distinct, funnel-shaped, slightly pigmented,  $3.0-10.0 \mu m$  high,  $2.5-7.5 \mu m$  wide at the base, and  $10.0-20.0 \mu m$  wide at the top. *Collars* distinct. *Columellae* hemispherical, hyaline, smooth, always with a  $2.5-6.0 \mu m$  clavate projection at the apex,  $7.0-18.5 \mu m$  long and  $10.5-24.0 \mu m$  wide. *Sporangiospores* hyaline, smooth, two kinds, cylindrical to ovoid,  $3.0-4.0 \mu m$  long and  $2.0-2.5 \mu m$  wide; ovoid with vacuoles,  $4.0-7.0 \mu m$  long and  $3.0-5.0 \mu m$  wide. *Zygospores* absent. *Chlamydospores* absent. No growth at  $35 \circ$ C.

*Material examined*: China, Qinghai Province, Xining, Huangzhong County, from soil sample, 2 August 1999, Long Wang (holotype HMAS 350296, living ex-holotype culture CGMCC 3.16055).

GenBank accession number: MZ354139.

*Notes: Absidia brunnea* is closely related to *A. soli* V.G. Hurdeal *et al.* based on phylogenetic analysis of ITS rDNA sequences (Fig. 5). However, morphologically *A. soli* differs from *A. brunnea* by sporangiophores up to 6 in whorls, septa distantly below apophyses (21.5–37.5  $\mu$ m vs. 11.0–17.0  $\mu$ m), and cylindrical sporangiospores without a vacuole (Hurdeal *et al.* 2021). Moreover, *A. soli* physiologically differs from *A. brunnea* by a slightly higher maximum growth temperature (37 °C vs. 35 °C).

 Absidia chinensis T.K. Zong, H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 21. Fungal Names: FN570886. Etymology: chinensis (Lat.) refers to China where the type was collected.

#### Holotype: HMAS 350297.

Colonies on MEA at 27 °C for 9 days, slow growing, reaching 90 mm in diameter, obversely regularly concentrically zonate with ring, white at first and then Drab Gray or Snuff Brown. Hyphae hyaline at first, becoming brown when mature, generally swollen, 6.0-15.5 µm in diameter. Stolons branched, hyaline, smooth, septate, 3.5–11.0 µm in diameter. Rhizoids coralliform, mostly simple or two-branched, with a septum at the base. Sporangiophores erect or slightly bent, 1-5 in whorls, mostly unbranched or simple branched, rarely monopodial, sympodial form absent, hyaline, with a septum 13.0–22.0 µm below apophyses, generally a swelling beneath sporangium, sometimes branched at the swelling, 45.0–220.0 µm long and 2.5–6.0 µm wide. Sporangia globose or pyriform, smooth, multi-spored, 15.0-39.5 µm long and 15.0-37.5 µm wide, walls deliquescent. Apophyses distinct, bell-shaped or hourglass-shaped, slightly pigmented, 3.5-7.0 µm high, 2.5-5.5 μm wide at the base, and 6.0–15.5 μm wide at the top. Collars present or absent, but distinct if present. Columellae spherical or hemispherical, hyaline, smooth, always with a 2.0-5.5 µm papillary projection at the apex, 5.0–15.5 µm long and 7.5–17.5 µm wide. Sporangiospores cylindrical to ovoid, hyaline, smooth, 3.5–4.5 µm long and 2.0–2.5 µm wide. Zygospores subglobose, brown or Dark Brown, rough, 37.0-90.0 µm long and 36.0-80.0 µm wide. Suspensor unequal, parallel to subparallel, brown, the larger one 27.0–44.0 µm in diameter, the smaller one mostly 20.0-33.0 µm in diameter. Chlamydospores absent. No growth at 31 °C.

*Materials examined*: China. Yunnan Province, Jinghong, Mengla County, from soil sample, 4 July 1994, Gui-Qing Chen (holotype HMAS 350297, living ex-holotype culture CGMCC 3.16056). Sichuan Province, Ngawa, Jiuzhaigou County, from soil sample, 23 May 1994, Gui-Qing Chen (living culture CGMCC 3.16057).

GenBank accession numbers: MZ354140 and MZ354141.

*Notes: Absidia chinensis* is closely related to *A. xinjiangensis* H. Zhao, Y.C. Dai & X.Y. Liu based on phylogenetic analysis of ITS rDNA sequences (Fig. 5). However, morphologically *A. xinjiangensis* differs from *A. chinensis* by the absence of zygospores and projections.

 Absidia cinerea T.K. Zong, H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 22. Fungal Names: FN570887.

Etymology: cinerea (Lat.) refers to the species having gray colonies on MEA.

#### Holotype: HMAS 350303.

Colonies on MEA at 27 °C for 5 days, reaching 90 mm in diameter, regularly concentrically zonate with ring, white at first and then Pale Mouse Gray. Hyphae hyaline at first, becoming brown when mature, 5.5–14.5 µm in diameter. Stolons branched, hyaline, smooth, septate, 3.5–7.0 µm in diameter. *Rhizoids* branch-shaped and tapering at the end, mostly two branches arising at a place, with a septum at the base. Sporangiophores erect or slightly bent, 1-7 in whorls, unbranched, simple branched or monopodial arising from stolons, mostly sympodial arising from aerial mycelia, hyaline, with a septum 11.0–17.0 µm below apophyses, 50.0–150.0 µm long and 2.5–5.0 µm wide. Sporangia globose to pyriform, smooth, multi-spored, 7.0–27.5 µm long and 7.0–25.0 µm wide, walls deliquescent. Apophyses distinct, bell-shaped or funnel-shaped, slightly pigmented, 2.0-7.5 μm high, 2.5–5.5 μm wide at the base, and 6.0–12.5 μm wide at the top. Collars present or absent, but distinct if present. Columellae hemispherical, hyaline, smooth, always with a 1.3-5.0 µm rodshaped or needle-like projection at the apex, 5.0–14.0 µm long and 7.0–15.0 µm wide. Sporangiospores cylindrical, slightly constricted in the center, hyaline, smooth, 4.5–6.0 µm long and 2.0-2.5 µm wide. Zygospores globose, brown to Dark Brown, rough, 36.0-81.0 µm in diameter. Suspensor mostly one, rarely unequal two, brown, with 8-13 appendages on a single suspensor, 17.0-33.0 µm in diameter. Chlamydospores absent. No growth at 35 °C.

*Material examined*: China, Beijing, 40°21′30″N, 116°6′27″E, from soil sample, 31 December 2019, Xiao-Yong Liu (holotype HMAS 350303, living ex-holotype culture CGMCC 3.16062). *GenBank accession number*: MZ354146.

*Notes*: *Absidia cinerea* is closely related to *A. pseudocylindrospora* Hesselt. & J.J. Ellis and *A. stercoraria* Hyang B. Lee *et al.* based on phylogenetic analysis of ITS rDNA sequences (Fig. 5). However, morphologically *A. pseudocylindrospora* differs from *A. cinerea* by shorter cylindrical sporangiospores (2.5 µm long vs. 4.5–6.0 µm long), rhizoids rarely septate, and arising in whorls of up to 11 (Hesseltine & Ellis 1961). *A. stercoraria* differs from *A. cinerea* by rhizoids poorly developed and arising in whorls of up to 5 (Li *et al.* 2016). Moreover, physiologically, *A. pseudocylindrospora* has a maximum growth temperature of 37 °C, but neither *A. cinerea* nor *A. stercoraria* can grow above 35 °C.

 Absidia digitula T.K. Zong, H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 23. Fungal Names: FN570888. Etymology: digitula (Lat.) refers to the species having finger-like rhizoids.

Holotype: HMAS 350299.

*Colonies* on MEA at 27 °C for 9 days, slow growing, reaching 90 mm in diameter regularly flower-shaped zonate, white at first and then becoming Snuff Brown. *Hyphae* hyaline at first, becoming brown when mature, sometimes swollen, 8.0–18.0  $\mu$ m in diameter. *Stolons* branched, hyaline or Light Brown, smooth, septate, 4.0–9.5  $\mu$ m in diameter. *Rhizoids* finger-like, mostly twice or more repeatedly, with a septum at the base. *Sporangiophores* erect or slightly bent, 1–6 in whorls, unbranched, not generally simple branched, each sporangiophore in whorls, rarely monopodial or sympodial, hyaline or Light Brown, with a septum 14.5–25.5  $\mu$ m below apophyses, occasionally a swelling beneath sporangium, 60.08–470.0  $\mu$ m long and 3.5–8.5  $\mu$ m wide. *Sporangia* globose to pyriform, smooth, multi-spored, 24.0–64.0  $\mu$ m long and 26.5–48.5  $\mu$ m wide, walls deliquescent. *Apophyses* distinct, slightly pigmented, 5.5–13.5  $\mu$ m high, 4.5–8.5  $\mu$ m wide at the base, and 12.5–21.0  $\mu$ m wide at the top. *Collars* distinct if present. *Columellae* hemispherical, hyaline, smooth, sometimes with a 4.0–9.0  $\mu$ m clavate projection at the apex, occasionally with two projections, slightly bulbous at the end, 10.5–22.0  $\mu$ m long and 11.5–30.0  $\mu$ m wide. *Sporangiospores* globose, hyaline, smooth, non-uniform in shape, 3.0–5.0  $\mu$ m in diameter. *Zygospores* absent. *Chlamydospores* absent. No growth at 32 °C.

*Material examined*: China, Xinjiang Auto Region, Ili, Qapqal Xibe Country, Wusun Mountain, from soil sample, 14 June 2002, Xue-Wei Wang (holotype HMAS 350299, living ex-holotype culture CGMCC 3.16058).

GenBank accession number: MZ354142.

*Notes: Absidia digitula* is closely related to *A. turgida* T.K. Zong & X.Y. Liu based on phylogenetic analysis of ITS rDNA sequences (Fig. 5). However, morphologically *A. turgida* differs from *A. digitula* by sporangiophores singly or in whorls of up to 4, one projection on the columellae only, and variably shaped sporangiospores such as globose, cylindrical, or irregular (Zong *et al.* 2021).

 Absidia jiangxiensis H. Zhao, T.K. Zong, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 24. Fungal Names: FN570889.

*Etymology: jiangxiensis* (Lat.) refers to the locality of Jiangxi Province, China, where the type was collected.

#### Holotype: HMAS 351507.

Colonies on MEA at 27 °C for 5 days, reaching 68 mm in diameter, higher in the centre than at margin, white at first becoming Dark Citrine when mature. Hyphae hyaline at first, becoming Light Brown when mature, 7.0–17.0 µm in diameter. Stolons branched, hyaline to Light Brown, smooth, septate, 3.5–8.5 µm in diameter. *Rhizoids* root-like, rarely branched, hyaline, septate. Sporangiophores erect or slightly bent, 1–6 in whorls, unbranched, simple, monopodial or sympodial, hyaline to Light Brown, with a septum 10.5–22.5 µm below apophyses, 25.0–280.0 µm long and 3.0-6.0 µm wide. Sporangia globose to pyriform, smooth, multi-spored, 16.5-48.0 µm long and 16.5-44.0 µm wide, walls deliquescent. Apophyses distinct, funnel-shaped, slightly greenish, 6.0–15.0 µm high, 3.0–7.5 µm wide at the base, and 10.0–20.0 µm wide at the top. Collars distinct if present. Columellae subspherical to hemispherical, sometimes conical, hyaline, smooth, 10.0–30.0 µm long and 10.5–34.0 µm wide, one projection present on apex of columellae, occasionally two, papillary, rod-like or blunt, 2.5-6.5 µm long. Sporangiospores ovoid to cylindrical, sometimes globose to subglobose, hyaline, smooth, uniform, 3.5-4.5 µm long and 2.5-3.0 µm wide. Zygospores globose, brown to Dark Brown, rough, 40.0–85.0 µm in diameter. Suspensor mostly one, sometimes two, particularly unequal, hemispherical, brown, 17.0–36.0 µm in diameter. Appendages derived from larger one. Homothallic. Chlamydospores absent. No growth at 31 °C.

*Material examined*: China, Jiangxi Province, Lushan, from soil sample, 1 October 2013, Xiao-Yong Liu (holotype HMAS 351507, living ex-holotype culture CGMCC 3.16105).

GenBank accession number: OL678134.

*Notes: Absidia jiangxiensis* is closely related to *A. jindoensis* Hyang B. Lee & T.T.T. Nguyen based on phylogenetic analysis of ITS rDNA sequences (Fig. 5). However, morphologically *A. jindoensis* differs from *Absidia jiangxiensis* by hemispherical, sometimes subglobose columellae with one projection and a collarette (Wanasinghe *et al.* 2018).

 Absidia nigra (Hesselt. & J.J. Ellis) T.K. Zong, H. Zhao, Y.C. Dai & X.Y. Liu, comb. et stat. nov., Fig. 25.

Fungal Names: FN570890.

Basionym: *Absidia cylindrospora* var. *nigra* Hesselt. & J.J. Ellis, Mycologia, 56(4): 595, 1964. [MB no.: 353238]

#### Holotype: NRRL 3060.

*Colonies* on MEA at 27 °C for 9 days, slow growing, reaching 62 mm in diameter, regularly zonate, white at first becoming Light Drab. *Hyphae* hyaline at first, becoming brown when mature, sometimes swollen, 8.0–18.5  $\mu$ m in diameter. *Stolons* branched, hyaline, smooth, septate, 4.0–8.5  $\mu$ m in diameter. *Rhizoids* finger-like, short, mostly twice or repeatedly, with a septum at the base. *Sporangiophores* erect or slightly bent, 1–5 in whorls, unbranched, simple, rarely monopodial or sympodial, hyaline, with a septum 11.5–21.0  $\mu$ m below apophyses, sometimes a swelling beneath sporangium, 60.0–380.0  $\mu$ m long and 2.5–6.5  $\mu$ m wide. *Sporangia* globose to pyriform, smooth, multi-spored, 17.0–46.5  $\mu$ m long and 16.5–38.5  $\mu$ m wide, walls deliquescent. *Apophyses* distinct, slightly greenish, 3.5–8.5  $\mu$ m high, 3.3–5.9  $\mu$ m wide at the base, and 9.5–18.5  $\mu$ m wide at the top. *Collars* distinct if present. *Columellae* spherical or ovoid to hemispherical, hyaline, smooth, sometimes with a 1.5–5.0  $\mu$ m clavate or slightly swollen projection at the apex, 8.5–19.0  $\mu$ m long and 2.0–2.5  $\mu$ m wide and globose, 4.0–9.0  $\mu$ m in diameter. *Zygospores* absent. *Chlamydospores* absent. No growth at 31 °C.

*Materials examined*: USA, Wisconsin, from soil sample, 1940 (holotype NRRL 3060, isotype CBS 127.68, isotype HMAS 350309). China. Jilin Province, Jiaohe, from soil sample, 1 September 1991, Feng-Yan Bai (HMAS 350300, living culture CGMCC 3.16059); Inner Mongolia Auto Region, Arxan, from soil sample, 16 August 1991, Feng-Yan Bai (HMAS 350301, living culture CGMCC 3.16060).

GenBank accession numbers: MZ354143, MZ354144 and MZ354152

*Notes: Absidia nigra* was previously synonymized with *A. cylindrospora* Hagem (Hesseltine & Ellis 1964), however, this does not receive any support either phylogenetically or morphologically (Fig. 5). Phylogenetically, *A. nigra* is closer to *A. chinensis* rather than *A. cylindrospora*. Physiologically, strains of *A. nigra* and *A. cylindrospora* are not compatible (Hesseltine and Ellis 1964). Morphologically, *A. cylindrospora* differs from *A. nigra* by producing cylindrical sporangiospores only, while there are two types of sporangiospores in *A. nigra* (Hesseltine & Ellis 1964).

# Absidia oblongispora T.K. Zong, H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 26. Fungal Names: FN570891.

*Etymology: oblongispora* (Lat.) refers to the species having oblong sporangiospores. *Holotype*: HMAS 350302.

*Colonies* on MEA at 27 °C for 10 days, slow growing, reaching 90 mm in diameter, slightly irregularly concentrically zonate with ring, white at first and then becoming Pale Mouse Gray to Light Drab. *Hyphae* hyaline at first, becoming brown when mature,  $5.5-11.5 \mu m$  in diameter. *Stolons* branched, hyaline, smooth, with few septa near the base of sporangiophores,  $4.0-9.5 \mu m$  in diameter. *Rhizoids* root-like, branched repeatedly, with a septum at the base. *Sporangiophores* erect or slightly bent, 1-5 in whorls, mostly unbranched, rarely simple or monopodial, sympodial form absent, hyaline, with a septum 9.5–16.0 µm below apophyses, occasionally with a septum at the base,  $33.0-300.0 \mu m$  long and  $3.0-5.5 \mu m$  wide. *Sporangia* globose, smooth, multi-spored,  $13.5-31.0 \mu m$  in diameter, walls deliquescent. *Apophyses* distinct, slightly greenish,  $3.5-6.5 \mu m$  high,  $3.5-7.5 \mu m$  wide at the base, and  $7.0-19.0 \mu m$  wide at the top. *Collars* present or absent, but distinct if present. *Columellae* mostly conical, rarely hemispherical, hyaline, smooth, always with a  $3.0-7.5 \mu m$  bulbous projection at the apex,  $7.0-15.0 \mu m$  long and  $2.5-3.0 \mu m$  wide. *Sporangiospores* oblong, hyaline, smooth, uniform,  $3.5-4.5 \mu m$  long and  $2.5-3.0 \mu m$  wide. *Zygospores* absent. *Chlamydospores* absent. No growth at  $32 \circ C$ .

Material examined: China, Yunnan Province, Jinghong, Mengla County, from soil sample, 4 July 1994, Gui-Qing Chen (holotype HMAS 350302, living ex-holotype culture CGMCC 3.16061). GenBank accession number: MZ354145.

*Notes*: *Absidia oblongispora* is closely related to *A. heterospora* Y. Ling based on phylogenetic analysis of ITS rDNA sequences (Fig. 5). However, morphologically *A. heterospora* differs from *A. oblongispora* by wider columellae (10.5–34 μm vs. 8.5–16.5 μm in diameter) and two types of sporangiospores (Hesseltine & Ellis 1964).

11. *Absidia purpurea* H. Zhao, T.K. Zong, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 27.

Fungal Names: FN570892.

*Etymology: purpurea* (Lat.), refers to the species having pale purple colonies, hyphae and stolons.

Holotype: HMAS 351508.

*Colonies* on MEA at 27 °C for 8 days, slow growing, reaching 90 mm in diameter, regularly concentrically zonate with ring, higher at margin than in center, white at first and then becoming

Pale Quaker Drab. *Hyphae* hyaline at first, becoming violet-blue when mature,  $5.0-15.5 \mu m$  in diameter. *Stolons* branched, hyaline, smooth, septate,  $3.5-6.5 \mu m$  in diameter. *Rhizoids* root-like, tapering at the end, septate. *Sporangiophores* erect or slightly bent, 1-5 in whorls, unbranched, simple or monopodial, never sympodial, hyaline, with a septum  $14.0-28.5 \mu m$  below apophyses,  $75.0-285.0 \mu m$  long and  $3.5-5.5 \mu m$  wide. *Sporangia* mostly globose, occasionally pyriform, smooth, multi-spored,  $19.0-42.0 \mu m$  in diameter, walls deliquescent. *Collars* distinct if present. *Apophyses* distinct, funnel-shaped, slightly greenish,  $4.5-6.0 \mu m$  high,  $3.0-5.5 \mu m$  wide at the base, and  $9.5-15.0 \mu m$  wide at the top. *Columellae* subspherical to hemispherical, hyaline, smooth, without projection,  $9.0-24.0 \mu m$  long and  $13.0-24.0 \mu m$  wide. *Sporangiospores* ovoid or cylindrical, hyaline, smooth,  $3.0-5.0 \mu m$  long and  $2.5-4.0 \mu m$  wide. *Zygospores* absent. *Chlamydospores* absent. No growth at  $30 \,^\circ$ C.

*Material examined*: China, Yunnan Province, Lincang, from soil sample, 22 April 2021, Heng Zhao (holotype HMAS 351508, living ex-holotype culture CGMCC 3.16106).

GenBank accession number: OL678135.

*Notes: Absidia purpurea* is closely related to *A. multispora* T.R.L. Cordeiro *et al.* based on phylogenetic analysis of ITS rDNA sequences (Fig. 5). However, morphologically *A. multispora* differs from *A. purpurea* by producing projections and abortive sporangia, sporangiospores variably shaped, including globose, subglobose, ellipsoid, cylindrical, short-cylindrical, and even irregular, and branched (single or in whorls of 2(–4) vs. 1–5 in whorls; Cordeiro *et al.* 2020).

 Absidia sympodialis T.K. Zong, H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 28. Fungal Names: FN570893.

*Etymology: sympodialis* (Lat.) refers to the species having sympodial sporangiophores. *Holotype*: HMAS 350305.

*Colonies* on MEA at 27 °C for 6 days, reaching 90 mm in diameter, regularly zonate, white at first and then Cedar Green. *Hyphae* hyaline at first, becoming Light Brown when mature, 9.0–19.0 μm in diameter. *Stolons* branched, hyaline, smooth, with few septa near the base of sporangiophores, 6.5–12.5 μm in diameter. *Rhizoids* fibrous-root-shaped, tapering at the end, branched mostly repeatedly, with a septum at the base. *Sporangiophores* erect or slightly bent, 1–6 in whorls, unbranched, simple, monopodial or sympodial, hyaline or Light Brown, with a septum 7.5–17.5 μm below apophyses, 90.0–630.0 μm long and 4.5–10.5 μm wide. *Sporangia* globose to

pyriform, smooth, multi-spored, 20.0–63.0  $\mu$ m long and 18.5–63.0  $\mu$ m wide, walls deliquescent. *Apophyses* distinct, slightly pigmented, 6.0–13.7  $\mu$ m high, 6.0–14.1  $\mu$ m wide at the base, and 12.0– 31.0  $\mu$ m wide at the top. *Collars* present or absent, but distinct if present. *Columellae* spherical, ovoid to hemispherical or chestnut-shaped, hyaline, smooth, sometimes with a 2.0–4.0  $\mu$ m papillary or pointed projection at the apex, 8.0–40.0  $\mu$ m long and 9.5–39.0  $\mu$ m wide. *Sporangiospores* globose, hyaline, smooth, uniform, 2.5–3.5  $\mu$ m in diameter. *Zygospores* absent. *Chlamydospores* absent. No growth at 33 °C.

*Materials examined*: China. Shaanxi Province, Hanzhong, Foping County, from soil sample, 13 October 2002, Xue-Wei Wang (holotype HMAS 350305, living ex-holotype culture CGMCC 3.16064). Beijing, 40°1′32″N, 116°8′54″E, from soil sample, 31 December 2019, Xiao-Yong Liu (living culture CGMCC 3.16063).

GenBank accession numbers: MZ354148 and MZ354147.

*Notes*: *Absidia sympodialis* is closely related to *A. virescens* T.K. Zong *et al.* based on phylogenetic analysis of ITS rDNA sequences (Fig. 5). However, morphologically *A. virescens* differs from *A. sympodialis* by root-like rhizoids, hemispherical columellae, and whorls of sporangiophores (6 vs. 4). In addition, *A. virescens* produces sporangiospores which are non-uniform in size and columellae with two projections, some projections up to 6.5 µm in length, whereas the sporangiospores of the new species are uniform in size, and both columellae have only one projection less than 5.0 µm in length.

 Absidia varians T.K. Zong, H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 29. Fungal Names: FN570894.

*Etymology: varians* (Lat.) refers to the species having various projections on columellae. *Holotype:* HMAS 350306.

*Colonies* on MEA at 27 °C for 5 days, slow growing, reaching 90 mm in diameter, regularly zonate, white at first and then Pale Green-Blue Gray. *Hyphae* hyaline to slightly brownish, 8.5–12.0 μm in diameter. *Stolons* branched, hyaline, smooth, septate, 5.0–8.5 μm in diameter. *Rhizoids* root-like, multi-branched, aseptate. *Sporangiophores* erect or slightly bent, 1–4 in whorls but mostly 2–3 borne from stolons, unbranched, simple, monopodial or sympodial, hyaline, with a septum 13.5–19.0 μm below apophyses, 100.0–480.0 μm long and 4.5–9.0 μm wide. *Sporangia* subglobose to ellipsoid, smooth, multi-spored, 26.0–58.0 μm long and 22.5–50.0 μm wide, walls deliquescent.

54

Apophyses distinct, 6.0–12.0  $\mu$ m high, 5.5–11.0  $\mu$ m wide at the base, and 10.5–22.5  $\mu$ m wide at the top. *Collars* distinct if present. *Columellae* spherical or hemispherical, hyaline, smooth, always with several kinds of projections at the apex, mostly one, occasionally two, bulbous swelling, papillary, clavate or spinous, 11.0–30.5  $\mu$ m long and 12.5–35.0  $\mu$ m wide. *Sporangiospores* globose, ovoid, short cylindrical, hyaline, smooth, 3.0–4.0  $\mu$ m long and 2.0–3.0  $\mu$ m wide. *Zygospores* absent. *Chlamydospores* absent. No growth at 29 °C.

*Material examined*: China, Yunnan Province, Dehong, Mangshi, 24°32′36″N, 98°40′29″E, from soil sample, 30 April 2021, Heng Zhao (holotype HMAS 350306, living ex-holotype culture CGMCC 3.16065).

GenBank accession number: MZ354149.

*Notes: Absidia varians* is closely related to *A. glauca* Hagem based on phylogenetic analysis of ITS rDNA sequences (Fig. 5). However, morphologically *A. glauca* differs from *A. varians* by globose sporangiospores (Ellis & Hesseltine 1965, Schipper 1990). Besides, *A. varians* is morphologically similar to *A. repens* Tiegh. by sharing different types of projections on the columellae. However, *A. repens* differs from *A. varians* by olive-gray colonies and two types of sporangiospores (Hesseltine & Ellis 1966).

 Absidia virescens T.K. Zong, H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 30. Fungal Names: FN570895.

*Etymology: virescens* (Lat.) refers to the species having a greenish colony on MEA. *Holotype*: HMAS 350307.

*Colonies* on MEA at 27 °C for 6 days, reaching 90 mm in diameter, regularly disc-shaped, white at first and then Ring Elm Green. *Hyphae* hyaline at first, becoming brown when mature, 6.0–11.5 µm in diameter. *Stolons* branched, hyaline, smooth, with few septa near the base of sporangiophores, 4.5–9.0 µm in diameter. *Rhizoids* root-like, branched mostly twice or three times, with a septum at the base. *Sporangiophores* erect or slightly bent, 1–4 in whorls, mostly unbranched or simple, rarely monopodial or sympodial, hyaline, with a septum 10.0–22.5 µm below apophyses, occasionally with a septum at the base, sometimes a swelling beneath sporangium, 75.0–480.0 µm long and 5.5–11.5 µm wide. *Sporangia* globose to pyriform, smooth, multi-spored, 15.5–51.5 µm long and 15.5–45.5 µm wide, walls deliquescent. *Apophyses* distinct, sometimes slightly greenish, 5.5–14.0 µm high, 6.5–15.5 µm wide at the base, and 12.5–25.5 µm wide at the top. *Collars* 

present or absent, but distinct if present. *Columellae* spherical or ovoid to hemispherical, hyaline, smooth, sometimes with one or two  $3.0-6.5 \mu m$  projections at the apex,  $10.5-40.5 \mu m$  long and  $11.5-45.0 \mu m$  wide. *Sporangiospores* mostly globose, occasionally subglobose, hyaline, smooth,  $3.0-5.5 \mu m$  in diameter, but mostly  $3.0-3.5 \mu m$  in diameter. *Zygospores* absent. *Chlamydospores* absent. No growth at  $32 \ C$ .

*Materials examined*: China, Yunnan Province. Xishuangbanna, from soil sample, 9 July 1994, Gui-Qing Chen (holotype HMAS 350307, living ex-holotype culture CGMCC 3.16067). Kumming, from soil sample, 27 August 1995, Ying-Lan Guo (living culture CGMCC 3.16066).

*GenBank accession numbers*: MZ354151 and MZ354150.

Notes: See notes of Absidia sympodialis.

15. Absidia xinjiangensis H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 31.

Fungal Names: FN570896.

*Etymology: xinjiangensis* (Lat.) refers to the locality of Xinjiang Auto Region, China, where the type was collected.

Holotype: HMAS 351509.

*Colonies* on MEA at 27 °C for 7 days, slow growing, reaching 45 mm in diameter, irregular concentrically zonate with ring, white at first and then gradually becoming Light Brown. *Hyphae* hyaline at first, brown when mature, aseptate when juvenile, septate with age, 2.5–13.5  $\mu$ m in diameter. *Stolons* branched, hyaline, brownish, smooth, with septa. *Rhizoids* coralliform, branched or unbranched. *Sporangiophores* erect or slightly bent, 1–4 in whorls, often monopodial, simple, unbranched, rarely sympodial, hyaline, sometimes with one septum or two septa 12.0–22.0  $\mu$ m below apophyses, 25.0–170.0  $\mu$ m long and 2.5–6.0  $\mu$ m wide. *Apophyses* distinct, 3.5–7.0  $\mu$ m high, 3.5–6.0  $\mu$ m wide at the base, and 5.0–11.0  $\mu$ m wide at the top. *Sporangia* subglobose to ellipsoid, multi-spored, hyaline when young, brownish with age, 14.5–26.5  $\mu$ m long and 13.5–24.0  $\mu$ m wide, walls deliquescent. *Columellae* hemispherical, subglobose to globose, clavate, hyaline and brownish, smooth, 6.0–17.0  $\mu$ m long and 6.5–17.5  $\mu$ m wide. *Collars* usually absent, and rarely distinct if present. *Sporangiospores* always cylindrical to ellipsoid, or rarely irregular, subhyaline, smooth, 3.0–6.0  $\mu$ m long and 2.5–5.0  $\mu$ m wide. *Zygospores* absent. *Chlamydospores* absent.

*Material examined*: China, Xinjiang Auto Region, Altay, Burqin Country, 28°37'1"N, 87°2'58"E, from soil sample, 31 October 2021, Heng Zhao (holotype HMAS 351509, living exholotype culture CGMCC 3.16107).

GenBank accession number: OL678136.

Notes: See notes of Absidia chinensis.

16. Backusella dichotoma H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov. Fig. 32.

Fungal Names: FN570897.

*Etymology: dichotoma* (Lat.) refers to the species producing a dichotomous form of azygospores.

Holotype: HMAS 351510.

Colonies on PDA at 27 °C for 7 days, reaching 90 mm in diameter, less than 5 mm high, flat, granulate, initially white, soon becoming Sudan Brown to Brussels Brown, irregular at margin. Odor none. Hyphae sparse, hyaline, aseptate at first, septate with age, 2.5–9.5 µm in diameter. Rhizoids absent. Stolons absent. Sporangiophores arising directly from substrate mycelia, usually with large terminal sporangia, erect, forming lateral circinate branches, bent or curved, simple or divided once to several times. Terminal sporangia subglobose to globose, hyaline or brownish, smooth, multi-spored, more than 10 sporangiospores per sporangium, walls deliquescent. Lateral circinate branches simple or sympodial, ending with a multi-spored sporangiolum or a unisporangiolum. Lateral sporangiola globose, with numerous spines, hyaline, containing 2-6 sporangiospores, or rarely uni-spored, 10.5–28.5 µm in diameter, walls deliquescent. Apophyses absent. Collars absent. Columellae hyaline, always hemispherical in terminal sporangia, 16.0-25.5  $\mu$ m long and 14.5–23.5  $\mu$ m wide, always conical or hemispherical in lateral sporangiola, 5.5–11.5 μm long and 6.5–12.5 μm wide. Sporangiospores globose, subglobose or ovoid, hyaline, with droplets, 11.0–15.5 µm long and 10.5–13.5 µm wide. Azvgosporangia mostly globose, occasionally subglobose, initially hyaline, soon becoming Light Brown to black, with conical projections on walls, 51.0–104.0 µm in diameter. Suspensor cells erect, bent, usually dichotomous, Light Brown. Chlamydospores absent. Zygospores absent.

*Materials examined*: China. Yunnan Province, Lincang, Cangyuan Country, from soil sample, 22 July 2021, Heng Zhao (holotype HMAS 351510, living ex-holotype culture CGMCC 3.16108, and living culture XY07504).

GenBank accession numbers: OL678137 and OL678138.

*Notes: Backusella dichotoma* is closely related to *B. psychrophila* Urquhart & Douch based on phylogenetic analysis of ITS rDNA sequences (Fig. 6). However, morphologically *B. psychrophila* differs from *B. dichotoma* by producing collars, variably shaped sporangiospores, including globose, broadly ellipsoid to ellipsoid, and the absence of azygospores (Urquhart *et al.* 2021).

17. Backusella moniliformis H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 33.

Fungal Names: FN570898.

*Etymology: moniliformis* (Lat.) refers to the species having moniliform chlamydospores in the substrate hyphae.

Holotype: HMAS 351511.

Colonies on PDA at 27 °C for 5 days, reaching 90 mm in diameter, 15 mm high, floccose, white, irregular at margin. Odor none. Hyphae flourishing, aseptate at first, septate with age, hyaline, 4.5–13.5 µm in diameter. Rhizoids absent. Stolons absent. Sporangiophores arising directly from substrate hyphae, usually with a large terminal sporangium, erect or slightly curved, forming lateral circinate branches, simple or divided once. Terminal sporangia mostly globose, occasionally subglobose, rough with spines, Light Brown to black, multi-spored with more than 30 sporangiospores per sporangium, 51.0–61.5 µm in diameter, walls deliquescent. Lateral circinate branches simple or sympodial, ending with multi-spored sporangiola or uni-sporangiola. Lateral sporangiola globose, with spines, usually multi-spored with 3-20 sporangiospores and Light Brown to black, rarely uni-spored and yellow to Light Brown, 22.0–43.5 µm in diameter, walls deliquescent. Apophyses absent. Collars usually absent, rarely small if present. Columellae frequently hemispherical or conical, hyaline or brownish, 17.0–27.5 µm long and 18.0–26.5 µm wide. Sporangiospores subglobose to globose, ovoid, hyaline, with droplets, 7.5-13.0 µm long and 5.5–12.0 um wide. *Chlamydospores* abundant in substrate hyphae, moniliform when young, becoming ovoid, subglobose or globose when mature, hyaline, with droplets, 9.5–21.0 µm long and 11.5–15.5 µm wide. Zygospores unknown.

*Material examined*: China, Shaanxi Province, Baoji, 107°46'40.03"E, 37°0'0.51"N, from soil sample, 1 October 2013, Xiao-Yong Liu (holotype HMAS 35151, living ex-holotype culture CGMCC 3.16109).

GenBank accession number: OL678139

*Notes: Backusella moniliformis* is closely related to *Backusella* "group X" Urquhart & Douch based on phylogenetic analysis of ITS rDNA sequences (Fig. 6). However, morphologically *Backusella* 'group X' differs from *B. moniliformis* by the variably shaped columellae, including globose, ellipsoid and applanate, and the absence of chlamydospores (Urquhart *et al.* 2021).

18. Backusella ovalispora H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 34.

Fungal Names: FN570899.

Etymology: ovalispora (Lat.) refers to the species having ovoid sporangiospores.

Holotype: HMAS 351512.

Colonies on PDA at 27 °C for 3 days, fast growing, reaching 90 mm in diameter, 20 mm high, cottony, initially white, gradually becoming Grayish White. Odor none. Hyphae branched, hyaline, aseptate at first, septate with age, 4.5–18.0 µm in diameter. Rhizoids absent. Stolons absent. Sporangiophores arising from substrate or aerial hyphae, frequently tapering slightly toward the sporangia, usually with a large terminal sporangium, straight or slightly curved, and then forming lateral circinate branches, bent or curved, simple or divided once to several times successively and terminating in a sporangiolum. Terminal sporangia mostly globose, occasionally subglobose, hyaline or pigmented, smooth, multi-spored, usually with more than 50 sporangiospores per sporangium, 52.5–89.5 µm in diameter, walls deliquescent. Lateral circinate branches simple, ending with a multi-spored sporangiolum or rarely with a uni-sporangiolum. Lateral sporangiola mostly globose, occasionally subglobose, smooth, hyaline, three to fifteen sporangiospores per sporangiolum, 16.0-37.0 µm in diameter, walls deliquescent. Apophyses absent. Collars frequently absent, rarely small. Columellae always globose or subglobose in terminal sporangia, usually conical, subglobose, globose or depressed globose in lateral sporangiola, hyaline or brown, 6.0–59.5 μm long and 7.0-60.5 μm wide. Sporangiospores with striations, mainly ovoid, rarely irregular, 8.5–18.5 um long and 7.0–16.0 um wide. Chlamvdospores absent. Zvgospores absent.

*Materials examined*: China, Guangxi Auto Region, Fangchenggang, 21°44'27"N, 108°3'29"E, from soil sample, 15 July 2021, Heng Zhao (holotype HMAS 351512, living ex-holotype culture CGMCC 3.16110, and living culture XY07481).

GenBank accession numbers: OL678140 and OL678141.

*Notes: Backusella ovalispora* is closely related to *B. gigacellularis* J.I. Souza *et al.* based on phylogenetic analysis of ITS rDNA sequences (Fig. 6). However, morphologically *B. gigacellularis* 

differs from *B. ovalispora* by abundant giant cells, ellipsoid, cylindrical and rarely pyriform columellae, ellipsoid sporangiospores, and multi-spored sporangiola consisting of 3–4 sporangiospores (de Souza *et al.* 2014).

19. Circinella homothallica H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 35.

Fungal Names: FN570831.

*Etymology: homothallica* (Lat.) refers to the species producing zygospores by homothallism. *Holotype:* HMAS 249879.

*Colonies* on PDA at 27 °C for 9 days, slow growing, reaching 50 mm in diameter, carpet-like, initially white, soon becoming Mars Yellow, irregular at margin. *Hyphae* branched, aseptate when juvenile, septate with age, 4.5–10.5 µm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* always laterally circinate, and apically erect. *Sporangia* globose to ellipsoid, smooth, 17.0–43.0 µm long and 14.5–43.5 µm wide, walls deliquescent. *Apophyses* present. *Collars* always present. *Columellae* globose to conical, smooth, 8.0–31.5 µm long and 11.0–29.5 µm wide. *Projections* sometimes present. *Sporangiospores* ellipsoid, 5.5–8.5 µm long and 2.5–4.5 µm wide. *Chlamydospores* absent. *Zygospores* homothallic, hyaline when juvenile, gradually brownish with age, surrounded by droplets, 53.0–90.0 µm long and 55.0–89.0 µm wide.

*Material examined*: China, Hainan Province, Shihuashui Cave, from soil sample, 12 November 2020, Jia-Jia Chen (holotype HMAS 249879, living ex-holotype culture CGMCC 3.16026).

GenBank accession number: MW580599.

*Notes*: *Circinella homothallica* is distinguished from all other species of the genus by producing zygospores through a homothallic mating. Bainier (1903) first reported zygospores in *Circinella*, however, zygospores have not been observed by any other researchers (Hesseltine & Fennell 1955, Zheng *et al.* 2017). *C. homothallica* is closely related to *C. mucoroides* Saito based on phylogenetic analysis of ITS rDNA sequences (Fig. 7). However, morphologically *C. mucoroides* differs from *C. homothallica* by producing globose, shortly ovoid sporangiospores, ovoid, cylindrical, or pyriform columellae, lacking projections (Zheng *et al.* 2017).

20. Cunninghamella arrhiza H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 36.

Fungal Names: FN570900.

*Etymology: arrhiza* (Lat.) refers to the species rarely producing rhizoids. *Holotype*: HMAS 351513.

*Colonies* on PDA at 27 °C for 5 days, reaching 90 mm in diameter, more than 20 mm high, initially white, gradually becoming Light Gray, floccose, irregular at margin. *Hyphae* flourishing, branched, aseptate when young, septate when old, 1.5–12.0 µm in diameter. *Rhizoids* infrequent, root-like, always branched. *Stolons* present. *Sporangiophores* arising from aerial hyphae, erect, straight, always broadening upwards, unbranched or simple branched, in pairs, monopodial, but never verticillate. *Septa* absent. *Vesicles* subglobose, clavate, hyaline or subhyaline, rough, sometimes with brownish tints, 7.0–36.5 µm long and 5.0–29.5 µm wide. *Apophyses* present. *Pedicels* 3.0–4.5 µm long. *Sporangiola* borne on pedicels on vesicles, globose with thick spines, 7.5–13.0 µm in diameter. *Chlamydospores* absent. *Zygospores* unknown.

*Materials examined*: China. Hunan Province, Changsha, 28°8'4"N, 112°57'19"E, from soil sample, 28 August 2021, Heng Zhao (holotype HMAS 351513, living ex-holotype culture CGMCC 3.16111). Beijing, 40°39'35"N, 117°16'35"E, from soil sample, 31 July 2021, Heng Zhao (living culture XY08047).

GenBank accession numbers: OL678142 and OL678143.

*Notes*: *Cunninghamella arrhiza* is closely related to *C. guizhouensis* Zhi.Y. Zhang *et al.* based on phylogenetic analysis of ITS rDNA sequences (Fig. 7). However, morphologically *C. guizhouensis* differs from *C. arrhiza* by producing monopodial and verticillate sporangiophores, and globose to subglobose versicles (Zhang *et al.* 2020).

21. Cunninghamella guttata H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 37.

Fungal Names: FN570901.

*Etymology: guttata* (Lat.) refers to the species producing lipid droplets in sporangiola. *Holotype:* HMAS 351514.

*Colonies* on PDA at 27 °C for 6 days, reaching 90 mm in diameter, 15 mm high, initially white, becoming Drab Gray with age, floccose, in reverse regular at margin. *Hyphae* branching, aseptate when young, rarely septate with age, 4.5–20.5 µm in diameter. *Rhizoids* abundant, root-like, branched. *Stolons* present. *Sporangiophores* arising from stolons or aerial hyphae, erect, straight or bent, 0–4 branched, single, in pairs or 3 or 4 verticillate, often broadening upwards. *Septa* if present, often at the upper part of the sporophores. *Vesicles* subglobose or globose, usually hyaline or subhyaline, sometimes with brownish tints, 13.5–40.5 µm long and 12.5–40.5 µm wide. *Apophyses* present. *Pedicels* 2.0–3.0 µm long. *Sporangiola* borne on pedicels on vesicles, ovoid,

with droplets when young, subhyaline or hyaline,  $9.0-12.5 \mu m$  long and  $7.5-9.0 \mu m$  wide, mostly globose, occasionally subglobose, dark, with a few spines,  $8.5-15.0 \mu m$  in diameter.

Chlamydospores absent. Zygospores unknown.

*Material examined*: China, Beijing, 40°30'29.16"N, 116°48'29.34"E, from soil sample, 28 July 2021, Heng Zhao (holotype HMAS 351514, living ex-holotype culture CGMCC 3.16112).

GenBank accession number: OL678144.

*Notes: Cunninghamella guttata* is closely related to *C. varians* H. Zhao *et al.* based on phylogenetic analysis of ITS rDNA sequences (Fig. 8). However, morphologically *C. varians* differs from *C. guttata* by producing two types of sporangiola (ovoid or globose vs. mostly globose, occasionally subglobose), and short pedicels (1.0–1.5 µm long vs. 2.0–3.0 µm long).

22. Cunninghamella irregularis H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 38.

Fungal Names: FN570902.

Etymology: irregularis (Lat.) refers to the colonies having an irregular margin.

Holotype: HMAS 351515.

*Colonies* on PDA at 27 °C for 7 days, slow growing, reaching 70 mm in diameter, 10 mm high, initially white, gradually becoming Light Gray, floccose, irregular at margin. *Hyphae* flourishing, branched, aseptate when young, septate when old, 3.0–13.5 µm in diameter. *Rhizoids* abundant, root-like, always branched, sometimes swollen. *Stolons* present. *Sporangiophores* arising from aerial hyphae, erect, straight, or few slightly bent, always broadening upwards, unbranched, or simple branched, in pairs, sympodial, but never verticillate. *Septa* if present, usually one to several below the vesicles on the sporangiophores. *Vesicles* ovoid, subglobose, globose and rarely clavate, even irregular, rough, hyaline, sometimes with brownish tints, 3.0–40.0 µm long and 2.5–34.5 µm wide. *Apophyses* present. *Pedicels* short, usually less than 3.0 µm long. *Sporangiola* borne on pedicels on vesicles, two types: with thick spines, ovoid, 10.0–12.5 µm long and 8.0–10.5 µm wide, and globose, 9.0–16.5 µm in diameter. *Chlamydospores* absent. *Zygospores* unknown.

*Materials examined*: China, Inner Mongolia Auto Region. Xilingol, Erenhot, 43°24'53"N, 112°7'55"E, from soil sample, 31 July 2021, Heng Zhao (holotype HMAS 351515, living exholotype culture CGMCC 3.16113, and living culture XY07657); Ulanqab, Chahar, 41°50'8"N, 113°4'10"E, from soil sample, 31 July 2021, Heng Zhao (living culture XY07683).

GenBank accession numbers: OL678145, OL678146 and OL678147.

*Notes: Cunninghamella irregularis* is closely related to *C. varians* H. Zhao *et al.* based on phylogenetic analysis of ITS rDNA sequences (Fig. 8). However, morphologically *C. varians* differs from *C. irregularis* by verticillate sporangiophores.

23. Cunninghamella nodosa (R.Y. Zheng) H. Zhao, Y.C. Dai & X.Y. Liu, comb. et stat. nov., Fig. 39.

Fungal Names: FN570903.

Basionym: *Cunninghamella echinulata* var. *nodosa* R.Y. Zheng, in Zheng & Chen, Mycotaxon 80: 35, 2001 [MycoBank no.: 474177]

Holotype: HMAS 80705

Colonies on SMA at 27 °C for 6 days, reaching 90 mm in diameter, 10 mm high, white at first, finally Avellaneous or Colonial Buff, in reverse Yellowish Cream, initially floccose, soon granulate. Hyphae branched, aseptate when young, septate with age, 3.5–14.0 µm in diameter. Stolons sometimes present. Rhizoids common, simple or repeatedly branched. Sporangiophores arising from stolons, sometimes opposite rhizoids, or directly from aerial hyphae, erect, stolon-like, straight or recumbent, verticillate or pseudoverticillate, mostly simple, occasionally in pairs, rarely repeated, typically short and 10.0–75.0 µm long, occasionally reaching 250.0 µm long, usually broadening upwards, sometimes with nodulous swellings, 7.5-25.0 µm in diameter. Septa sometimes in sporangiophores. Vesicles forming on the top of the main axes of sporangiophores, slightly depressed-globose, subglobose, 22.5–70.0 µm in diameter, or forming on lateral branches, usually globose, occasionally broadly ovoid, 8.5–27.5 µm in diameter, smooth and hyaline, occasionally proliferating. Pedicels numerous, arising over entire surface of vesicles, 2.5-4 µm long. Sporangiola borne on pedicels on vesicles, globose, broadly ellipsoid, ovoid or bluntly pointed at one end, hyaline, 6.0–17.5 µm long 5.5–13.5 µm wide, or borne singly or intermixed with the hyaline ones on the same vesicle, globose, dark, 11.5–17.5 µm in diameter, exclusively monosporous, all evidently echinulate and with long thick spines. Sporangiospores detachable, but usually remaining within the sporangiola, similar in shape and size to the sporangiola, spineless, tuberculate, hyaline. Chlamydospores absent. Zygosporangia mostly globose, occasionally subglobose, Dark Brown when mature, with pointed wart-like projections,  $26.5-53.5 \,\mu\text{m}$  in diameter. Zygospores heterothallic, mainly globose, rarely broad ellipsoid, hyaline, usually very thick-walled, smooth or slightly crenulate, with indistinct ridges, 23.0–48.0 µm in diameter.

Suspensors equal, not inflated, 12.5–35.5 µm in long and 9.0–29.5 µm wide, slightly attenuated or typically remaining straight or broadening toward the base, aseptate or septate at the basal part, not incrusted and hyaline or sometimes incrusted and brownish (Zheng and Chen 2001).

*Material examined*: China, Beijing, from flower sample, 28 May 2021, Gui-Qing Chen, 15 August 1986, (holotype HMAS 80705, living ex-holotype CGMCC 3.5628).

GenBank accession number: AF346407.

*Notes: Cunninghamella nodosa* was initially established as a variety of *C. echinulata* (Zheng and Chen 2001). However, morphologically *C. nodosa* has two intergrading kinds of sporangiophores and dark giant sporangiola in old cultures, being distinguished from these three allied species by processing nodulous sporophores, proliferating vesicles, long and slender pedicels (Zheng and Chen 2001).

24. Cunninghamella regularis H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 40.

Fungal Names: FN570904.

*Etymology: regularis* (Lat.) refers to the species having uniform shape and size of sporangiola. *Holotype:* HMAS 351516.

*Colonies* on PDA at 27 °C for 4 days, fast growing, reaching 90 mm in diameter, more than 20 mm high, initially white, soon becoming Light Gray, floccose. *Hyphae* flourishing, branched, aseptate when young, septate with age, 3.5–12.0 µm in diameter. *Rhizoids* abundant, root-like or finger-like, branched or unbranched. *Stolons* present. *Sporangiophores* arising from stolons or aerial hyphae, erect, straight or slightly bent, often broadening upwards, mainly unbranched and simple branched, abundant when borne laterally, very rarely dichotomous, in pairs or sympodial. *Septa* if present, at the upper part of the sporangiophores. *Vesicles* ovoid or globose, hyaline or pigmented, rough, sometimes with brownish tints, 8.5–27.0 µm long and 7.5–28.0 µm wide. *Apophyses* present. *Pedicels* 4.5–7.5 µm long. *Sporangiola* borne on pedicels on vesicles, globose, hyaline when young, brown or black when old, with few spines, 6.5–10.0 µm in diameter. *Chlamydospores* absent. *Zygospores* unknown.

*Materials examined*: China, Yunnan Province, Lincang, Cangyuan Country, from soil sample, 22 July 2021, Heng Zhao (holotype HMAS 351516, living ex-holotype culture CGMCC 3.16114, and living culture XY07510, XY07512 and XY07516).

GenBank accession numbers: OL678148, OL678149, OL678150 and OL678151.

*Notes: Cunninghamella regularis* is closely related to *C. binariae* Naumov based on phylogenetic analysis of ITS rDNA sequences (Fig. 8). However, morphologically *C. binariae* differs from *C. regularis* by the variably shaped sporangiola, ovoid to ellipsoid, globose and lacrymoid, compared to only one type of sporangiola in *C. regularis* (Zheng & Chen 2001). Moreover, in *C. binariae*, sporangiophores are pseudoverticillate and verticillate, while they are absent in *C. regularis* (Zheng & Chen 2001).

25. Cunninghamella subclavata H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 41.

Fungal Names: FN570905.

*Etymology: subclavata* (Lat.) refers to the species being similar to *Cunninghamella clavata*. *Holotype*: HMAS 351517.

*Colonies* on PDA at 27 °C for 4 days, fast growing, reaching 90 mm in diameter, 20 mm high, at first white, finally Light Gray. *Hyphae* flourishing, branched, aseptate when young, septate with age, 4.5–17.0 µm in diameter. *Rhizoids* abundant, root-like, always branched. *Stolons* present. *Sporangiophores* arising from aerial hyphae, erect, straight, always broadening upwards, unbranched or simple branched, in pairs, sympodial or dichotomous. *Septa* absent. *Vesicles* ovoid or globose on main sporangiophores, clavate or subclavate on lateral sporangiophores, hyaline, rough, sometimes with brownish tints, 9.5–33.5 µm long and 7.5–29.5 µm wide. *Apophyses* present. *Pedicels* 1.5–4.0 µm long. *Sporangiola* borne on pedicels on vesicles, globose, hyaline when young, Light Brown with age, with many thin (10.0–17.0 µm in diameter) spines on the surface. *Chlamydospores* absent. *Zygospores* unknown.

*Materials examined*: China, Yunnan Province, Xishuangbanna, 21°55'70"N, 101°16'16"E, from soil sample, 31 July 2021, Heng Zhao (holotype HMAS 351517, living ex-holotype culture CGMCC 3.16115, and living culture XY07766).

GenBank accession numbers: OL678152 and OL678153.

*Notes*: *Cunninghamella subclavata* is closely related to *C. clavata* R.Y. Zheng & G.Q. Chen based on phylogenetic analysis of ITS rDNA sequences (Fig. 8). However, morphologically *C. clavata* differs from *C. subclavata* by longer pedicels (2.5–11.0 µm long vs. 1.5–4.0 µm long), and typically clavate vesicles (Zheng & Chen 1998, 2001).

26. Cunninghamella varians H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 42.

Fungal Names: FN570906.

*Etymology: varians* (Lat.) refers to the species producing sporangiola of various shapes and sizes.

Holotype: HMAS 351518.

*Colonies* on PDA at 27 °C for 7 days, reaching 70 mm in diameter, 10–15 mm high, initially white, soon becoming Drab Gray, floccose, reverse irregular at margin. *Hyphae* branched, aseptate when young, septate when old, 2.5–15.0 µm in diameter. *Rhizoids* frequent, root-like, branched. *Stolons* present. *Sporangiophores* arising from stolons or aerial hyphae, erect, straight or recumbent, sometimes slightly broadening upwards in main axes, branched solitarily, in pairs, sympodially or 2–5 verticillate, variable in length, 11.5–251.5 µm in long. *Vesicles* ovoid or globose, usually hyaline, sometimes with brownish tints, 6.0–44.0 µm long and 5.0–40.0 µm wide. *Septa* often below the vesicles in the sporangiophores if present. *Apophyses* present. *Pedicels* 1.0–1.5 µm long. *Sporangiola* borne on pedicels on vesicles, two types: ovoid or globose, 7.0–14.5 µm long and 6.5–12.5 µm wide, and dark, exclusively globose, with thick (11.0–21.0 µm in diameter) spines. *Chlamydospores* absent. *Zygospores* unknown.

*Materials examined*: China, Jiangsu Province, Xinghua, 33°8'5"N, 120°6'14"E, from soil sample, 28 May 2021, Heng Zhao (holotype HMAS 351518, living ex-holotype culture CGMCC 3.16116, and living culture XY06999).

*GenBank accession numbers*: OL678154 and OL678155. *Notes*: See notes of *Cunninghamella irregularis*.

27. Gamsiella globistylospora H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 43. Fungal Names: FN570907.

*Etymology: globistylospora* (Lat.) refers to the species having globose stylospores. *Holotype*: HMAS 351519.

*Colonies* on PDA at 20 °C for 10 days, slow growing, reaching 90 mm in diameter, less than 5 mm high, broadly lobed and zonate, white, irregular margin and Pale Chalcedony Yellow. *Hyphae* branched, dense in the center, 1.5–5.0 µm in diameter. *Stylospores* borne on aerial hyphae, mostly globose, occasionally subglobose, abundant after two weeks, terminal and intercalary, with droplets, subhyaline to hyaline when young, gradually becoming light brow to black with age, smooth, 12.0–42.0 µm in diameter. *Rhizoids*, *stolons*, *collar*, *columellae*, *sporangia*, *sporangiospores*, *sporangiospores*, *chlamydospores* and *zygospores* absent.

Material examined: China, Tibet Auto Region, Linzhi, Bome County, from soil sample, 28

August 2021, Heng Zhao (holotype HMAS 351519, living ex-holotype culture CGMCC 3.16117). *GenBank accession number*: OL678156.

Notes: Gamsiella globistylospora is closely related to *G. stylospora* (Dixon-Stew.) Vandepol & Bonito based on phylogenetic analysis of ITS rDNA sequences (Fig. 9). However, morphologically *G. stylospora* differs from *G. globistylospora* by stylospores bearing spines (Dixon-Stewart 1932, Vandepol *et al.* 2020).

 Gongronella chlamydospora H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 44. Fungal Names: FN570908.

*Etymology: chlamydospora* (Lat.) refers to the species producing chlamydospores in substrate hyphae.

Holotype: HMAS 351520.

*Colonies* on PDA at 27 °C for 11 days, slow growing, reaching 90 mm in diameter, floccose, first white, gradually becoming Drab Gray. *Hyphae* flourishing, branched, aseptate when juvenile, septate with age, 2.5–5.5  $\mu$ m in diameter. *Rhizoids* and *stolons* present. *Sporangiophores* arising from substrate hyphae or stolons, erect, straight, or bent, unbranched or simple branched, hyaline, slightly constricted at the top, sometimes one septum below the apophysis. *Sporangia* globose, multi-spored, hyaline or subhyaline, 8.5–17.0  $\mu$ m in diameter. *Apophyses* urn-shaped to subglobose, hyaline or subhyaline, 6.0–12.0  $\mu$ m long and 6.0–10.0  $\mu$ m wide. *Collars* present. *Columellae* ovoid to depressed subglobose, hyaline, smooth, 3.0–5.5  $\mu$ m long and 3.5–6.5  $\mu$ m wide. *Sporangiospores* ellipsoid, reniform or irregular, 2.0–3.0  $\mu$ m long and 1.0–2.0  $\mu$ m wide. *Chlamydospores* in substrate hyphae, mostly globose, occasionally irregular, abundant, 2.0–3.0  $\mu$ m in diameter. *Zygospores* unknown.

*Material examined*: China, Jiangxi Province, Nanchang, from soil sample, 28 October 2013, Xiao-Yong Liu (holotype HMAS 351520, living ex-holotype culture CGMCC 3.16118).

GenBank accession number: OL678157.

*Notes*: *Gongronella chlamydospora* is closely related to *G. butleri* (Lendn.) Peyronel & Dal Vesco based on phylogenetic analysis of ITS rDNA sequences (Fig. 10). However, morphologically *G. butleri* differs from *G. chlamydospore* by larger columellae (4–11 µm in diameter vs. 3.0–5.5 µm long and 3.5–6.5 µm wide), larger sporangia (7–32 µm in diameter vs. 8.5–17.0 µm in diameter),

larger chlamydospores (4–9 μm in diameter vs. 2.0–3.0 μm in diameter; Hesseltine & Ellis 1964). In addition, zygospores are produced in *G. butleri*, but not in *G. chlamydospora* (Hesseltine & Ellis 1964).

29. Gongronella multispora H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 45.

Fungal Names: FN570909.

*Etymology: multispora* (Lat.) refers to the species having multiple sporangiospores. *Holotype*: HMAS 351521.

*Colonies* on PDA at 27 °C for 10 days, slow growing, reaching 80 mm in diameter, less than 10 mm high, floccose, first white, gradually becoming Yellowish Glaucous, crusty in reverse, Picric Yellow. *Hyphae* flourishing, branched, aseptate when juvenile, septate with age, 2.0–5.0 µm in diameter. *Rhizoids* rarely present, root-like. *Stolons* present. *Sporangiophores* arising from substrate hyphae or stolons, erect, straight, or slightly bent, unbranched or simple branched, sympodial, 2–3 in whorls and swollen on the base, slightly constricted at the top, often with one septum to several septa below the apophyses. *Sporangia* globose, multi-spored, hyaline or subhyaline, 12.0–17.0 µm in diameter. *Apophyses* pyriform to subglobose, hyaline, 8.0–12.0 µm long and 7.0–9.5 µm wide. *Collars* absent. *Columellae* degenerated, hemispherical, hyaline, smooth, 2.0–4.5 µm long and 2.0–4.0 µm wide. *Sporangiospores* variably shaped, ellipsoid, fusiform, cylindrical, reniform subglobose to globose, or irregular, 2.5–3.5 µm long and 1.5–2.5 µm wide. *Chlamydospores* absent. *Zygospores* unknown.

*Material examined*: China, Beijing, from soil sample, 28 October 2021, Zhi-Kang Zhang (holotype HMAS 351521, living ex-holotype culture CGMCC 3.16119).

GenBank accession number: OL678158.

*Notes: Gongronella multispora* is closely related to *G. chlamydospora* H. Zhao *et al.* based on phylogenetic analysis of ITS rDNA sequences (Fig. 10). However, morphologically *G. chlamydospora* differs from *G. multispora* by producing globose chlamydospores on the top of substrate hyphae.

30. Lichtheimia alba H. Zhao, T.K. Zong, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 46.

Fungal Names: FN570910.

Etymology: alba (Lat.) refers to the species forming white colonies.

Holotype: HMAS 351522.

*Colonies* on MEA at 30 °C for 8 days, slow growing, reaching 60 mm in diameter, floccose, flat, regular at margin, always white, sporulating profusely yet with sparse aerial hyphae. *Hyphae* hyaline at first, becoming slightly brownish with age,  $5.0-11.0 \mu$ m wide. *Stolons* branched, hyaline or slightly brownish, smooth,  $3.5-7.5 \mu$ m in diameter. *Rhizoids* infrequent because of the proliferation of substrate hyphae. *Sporangiophores* erect or slightly bent, never curved or circinate, solitary or in pairs, never in whorls, unbranched, simple, monopodial or sympodial, hyaline, sometimes with a septum  $15.0-60.0 \mu$ m below apophyses,  $50.0-260.0 \log$  and  $2.5-6.5 \mu$ m wide. *Apophyses* sometimes distinct, funnel-shaped,  $6.0-22.0 \mu$ m in diameter at the widest point. *Sporangia* globose to ellipsoid, occasionally subpyriform, smooth, multi-spored,  $13.5-40.0 \log$ and  $13.5-38.5 \mu$ m wide, walls deliquescent. *Collars* short if present. *Columellae* spherical to hemispherical, or spatulate, hyaline, smooth, without projections,  $8.0-35.0 \log$  and  $8.0-32.0 \mu$ m wide. *Sporangiospores* mostly globose, occasionally subglobose, hyaline, smooth, uniform,  $3.5-5.0 \mu$ m wide. *Collars* and  $2.5 - 6.5 \mu$ m wide. *Collars* and  $2.5 - 6.5 \mu$ m wide.

*Material examined*: China, Beijing, 1 October 2013, from soil sample Xiao-Yong Liu (holotype HMAS 351522 living ex-holotype culture CGMCC 3.16120).

GenBank accession number: OL678159.

Notes: Lichtheimia alba is closely related to L. corymbifera (Cohn) Vuill., L. ornata (A.K. Sarbhoy) Alastr.-Izq. & Walther and L. romosa (Zopf) Vuill. based on phylogenetic analysis of ITS rDNA sequences (Fig. 11). However, physiologically L. corymbifera, L. ornata and L. romosa can grow above 43 °C (Hoffmann 2010).

31. Lichtheimia globospora H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 47.

Fungal Names: FN570829.

*Etymology: globospora* (Lat.) refers to the species having globose sporangiospores. *Holotype*: HMAS 249878.

*Colonies* on PDA at 27 °C for 8 days, slow growing, reaching 90 mm in diameter, floccose, initially white, becoming Yellow Ocher with age. *Hyphae* simple branched, aseptate when juvenile, septate with age, with irregularly swollen giant cells, surrounded by liquid droplets, 3.0–20.0 µm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from aerial hyphae, not or simple branched, erect, bent or circinate, 50.5–95.5 µm long. *Sporangia* irregular or subglobose,

Dark Brown, rough, 19.5–30.5 μm long and 16.0–35.0 μm wide, walls deliquescent. *Apophyses* obvious, 3.5–12.5 μm long and 2.5–11.5 μm wide. *Collars* present. *Columellae* brown, variable, bell-shaped, 4.0–12.5 μm long and 6.5–11.5 μm wide. *Projections* always present, one or two, cylindrical or irregular. *Sporangiospores* hyaline or pigmented, globose, 5.0–7.5 μm in diameter. *Chlamydospores* absent. *Zygospores* absent.

*Material examined*: China, Hainan Province, Shihuashui Cave, from soil sample, 12 November 2020, Jia-Jia Chen (holotype HMAS 249878, living ex-holotype culture CGMCC 3.16025)

GenBank accession number: MW580598.

*Notes*: *Lichtheimia globospora* is closely related to *L. hyalospora* (Saito) Kerst. Hoffm. *et al.* based on phylogenetic analysis of ITS rDNA sequences (Fig. 11). However, morphologically *L. hyalospora* differs from *L. globospora* by producing stolons and rhizoids, regularly pyriform sporangia, longer columellae (up to 42.0 µm long vs. 4.0–12.5 µm long), and hemispherical columellae (Hoffmann *et al.* 2009b).

32. Modicella abundans H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 48.

Fungal Names: FN570911.

*Etymology: abundans* (Lat.) refers to the species having abundant chlamydospores. *Holotype*: HMAS 351523.

*Colonies* on PDA at 20 °C for 3 days, fast growing, reaching 90 mm in diameter, devoid of visible growth rings, white to Light Gray, with dense aerial mycelia at edge. *Hyphae* flourishing, white, branched, 2.5–4.5  $\mu$ m in diameter. *Rhizoids* rarely present, branched, thinner than hyphae, less than 2  $\mu$ m in diameter. *Stolons* present. *Sporangiophores*, sporangia, and sporangiospores absent even after one month of growth. *Chlamydospores* variable, ovoid, ovoid, ellipsoid, subglobose, in chains, hyaline or subhyaline, simple branched, 1.5–3.0  $\mu$ m long and 1.5–2.0  $\mu$ m wide. *Zygospores* and *sporocarps* unknown.

*Material examined*: China, Anhui Province, Hefei, Lu'an, 115°43'24"E, 31°27'36"N, from soil sample, 28 May 2021, Heng Zhao (holotype HMAS 351523, living ex-holotype culture CGMCC 3.16121).

GenBank accession number: OL678160.

*Notes*: In this paper, we isolated a culture from a soil sample, which phylogenetically is closer to *Modicella* based on the ITS rDNA sequences (Fig. 12). We describe it as *Modicella abundans*. It

is characterized by chlamydospores in chains and by an absence of sporangiospores or sporocarps. These characteristics are unique in members of *Modicella* (Smith *et al.* 2013, Cooper & Park 2020).

33. Mortierella amphispora H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 49.

Fungal Names: FN570912.

Etymology: amphispora (Lat.) refers to the species having two kinds of sporangiospores.

Holotype: HMAS 351524.

*Colonies* on PDA at 20 °C for 7 days, slow growing, reaching 90 mm in diameter, broadly lobed and concentrically zonate, with dense aerial mycelia in two weeks, white, irregular at margin. *Hyphae* flourishing, branched, 3.0–8.5 µm in diameter. *Rhizoids* rarely present, root-like, branched. Stolons present. Sporangiophores arising from aerial hyphae, erect, usually unbranched, occasionally simple branched, monopodial, generally constricted at the top. *Sporangia* mostly globose, occasionally subglobose, hyaline or subhyaline, smooth, multi-spored or uni-spored, 14.0– 24.5 µm in diameter, walls deliquescent. *Apophyses* absent. *Collars* absent. *Columellae* degenerated. *Sporangiospores* ovoid or globose, hyaline with a large droplet, or subhyaline with very small droplets, 9.5–15.0 µm long and 8.0–11.5 µm wide. *Chlamydospores* bearing in aerial hyphae, elongate, subhyaline, 16.0–27.5 µm long and 10.5–19.0 µm wide. *Zygospores* unknown.

*Materials examined*: China, Yunnan Province. Diqing, Pudacuo National Park, 27°49'40"N, 99°57'45"E, from soil sample, 24 October 2021, Heng Zhao (holotype HMAS 351524, living exholotype culture CGMCC 3.16122, and living culture XY08653). Lijiang, Ninglang Country, 27°31'23"N, 100°44'32"E, from soil sample, 24 October 2021, Heng Zhao (living culture XY08796).

GenBank accession numbers: OL678161, OL678162 and OL678292.

*Notes: Mortierella amphispora* is closely related to *M. longigemmata* Linnem. based on phylogenetic analysis of ITS rDNA sequences (Fig. 13). However, morphologically *M. longigemmata* differs from *M. amphispora* by shorter sporangiospores (5–9 µm in long vs. 9.5–15.0 µm long), larger chlamydospores (up to 60 µm in diameter vs. 16.0–27.5 µm long and 10.5–19.0 µm wide), and the absence of rhizoids (Zycha *et al.* 1969).

34. Mortierella annulata H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 50.

Fungal Names: FN570913.

Etymology: annulata (Lat.) refers to the species producing rings of colonies.

#### Holotype: HMAS 351525.

*Colonies* on PDA at 20 °C for 7 days, reaching 90 mm in diameter, broadly lobed and concentrically zonate, with dense aerial mycelia along the growth ring, white, irregular at margin. *Hyphae* flourishing, branched, 2.5–10.5 μm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from aerial hyphae, erect or slightly bent, unbranched or monopodial, usually swollen at the bottom and constricted at the top. *Sporangia* mostly globose, occasionally subglobose, hyaline when young, greenish when old, persistent-walled, 15.0–33.5 μm in diameter. *Apophyses* absent. *Collars* absent. *Columellae* degenerated. *Sporangiospores* ellipsoid, reniform, subglobose, globose or irregular, hyaline or subhyaline, always with droplets, 14.5–21.0 μm long and 9.5–12.5 μm wide. *Chlamydospores* absent. *Zygospores* unknown.

*Material examined*: China, Yunnan Province, Diqing, Pudacuo National Park, 27°49'40"N, 99°57'45"E, from soil sample, 24 October 2021, Heng Zhao (holotype HMAS 351525, living exholotype culture CGMCC 3.16123).

GenBank accession number: OL678163.

*Notes: Mortierella annulata* is closely related to *M. gemmifera* M. Ellis based on phylogenetic analysis of ITS rDNA sequences (Fig. 13). However, morphologically *M. gemmifera* differs from *M. annulata* by producing zygospores on malt agar, and sporangiophores sometimes branched cymosely (Ellis 1940).

35. Mortierella cylindrispora H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 51.

Fungal Names: FN570914.

*Etymology: cylindrispora* (Lat.) refers to the species having cylindrical sporangiospores. *Holotype*: HMAS 351526

*Colonies* on PDA at 20 °C for 9 days, slow growing reaching 90 mm in diameter, forming rosettes of dense lobes, white, with dense aerial mycelia. *Hyphae* flourishing, white, branched, aseptate when young, septate when old, 2.0–6.5 µm in diameter. *Rhizoids* present, root-like. *Stolons* present, abundant, simple branched, slightly thin. *Sporangiophores* arising from aerial or substrate hyphae, erect, unbranched, very long. *Sporangia* subglobose or globose, smooth, 15.0–24.5 µm long and 15.0–26.5 µm wide, walls deliquescent. *Apophyses* and *Collars* absent. *Columellae* degenerated. *Sporangiospores* ellipsoid or cylindrical, hyaline, 9.0–16.0 µm long and 4.5–8.0 µm wide. *Chlamydospores* absent. *Zygospores* unknown.
*Material examined*: China, Jiangsu Province, Lianyungang, 119°30'1"E, 34°38'10"N, from soil sample, 28 May 2021, Heng Zhao (holotype HMAS 351526, living ex-holotype culture CGMCC 3.16124).

GenBank accession number: OL678164.

*Notes: Mortierella cylindrispora* is closely related to *M. zychae* Linnem. based on phylogenetic analysis of ITS rDNA sequences (Fig. 13). However, morphologically *M. zychae* differs from *M. cylindrispora* by wider sporangia (30–35 μm wide vs. 5.0–26.5 μm wide), shorter sporangiospores (9.2 μm long vs. 9.0–16.0 μm long), and globose to oblong chlamydospores in the aerial hyphae (Linnemann 1941).

36. Mortierella floccosa H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 52.

Fungal Names: FN570915.

Etymology: floccosa (Lat.) refers to the species having floccose colonies.

Holotype: HMAS 351527.

*Colonies* on PDA at 20 °C for 15 days, slow growing, reaching 90 mm in diameter, broadly lobed and concentrically zonate, floccose, white. *Hyphae* simply branched, hyaline, 1.5–3.0 µm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from aerial hyphae, erect, unbranched, usually swollen at bottom and tapering very slightly from the bottom upwards. *Sporangia* mostly globose, occasionally subglobose, hyaline, smooth, multi-spored, 6.5–11.5 µm in diameter, walls deliquescent. *Apophyses* absent. *Collars* present. *Columellae* degenerated. *Sporangiospores* ovoid, cylindrical, fusiform or oblong, hyaline, with some droplets, 2.0–4.5 µm long and 1.0–2.0 µm wide. *Chlamydospores* regular, subglobose or globose, hyaline, always with droplets, 4.5–9.5 µm long and 3.0–9.5 µm wide. *Zygospores* absent.

*Material examined*: China, Jiangsu Province, Lianyungang, 34°38'9"N, 119°29'58"E, from soil sample, 28 May 2021, Heng Zhao (holotype HMAS 351527, living ex-holotype culture CGMCC 3.16125).

GenBank accession number: OL678165.

*Notes: Mortierella floccosa* is closely related to *M. alpina* Peyronel based on phylogenetic analysis of ITS rDNA sequences (Fig. 13). However, morphologically *M. alpina* differs from *M. floccosa* by producing rhizoids and the absence of chlamydospores (Zycha *et al.* 1969), while rhizoids are absent and chlamydospores are present in *M. floccosa*.

37. Mortierella fusiformispora H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 53.

Fungal Names: FN570828.

*Etymology: fusiformispora* (Lat.) refers to the species having fusiform sporangiospores. *Holotype*: HMAS 249877.

*Colonies* on PDA at 20 °C for 10 days, slow growing, reaching 60 mm in diameter, crust-like, white, reverse Pale Yellow-Orange Light to Orange-Yellow. *Hyphae* simple branched, aseptate when juvenile, septate with age, 1.0–4.5 µm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from aerial hyphae, erect or bent. *Sporangia* contained in a droplet of water, globose or sub-globose, smooth, 5.0–8.0 µm long and 5.5–7.5 µm wide, walls deliquescent. *Apophyses* absent. *Collars* present. *Columellae* degenerated. *Sporangiospores* fusiform, hyaline, smooth, with one or two droplets, 3.0–4.0 µm long and 1.5–2.5 µm wide. *Chlamydospores* absent. *Zygospores* absent.

*Materials examined*: Antarctica, Fields Peninsula, from soil sample, 27 May 2020, Ze Liu (holotype HMAS 249877, living ex-holotype culture CGMCC 3.16029, and living culture CGMCC 3.16030).

GenBank accession numbers: MW580602 and MW580603.

*Notes: Mortierella fusiformispora* is closely related to *M. alliacea* Linnem. based on phylogenetic analysis of ITS rDNA sequences (Fig. 13). However, morphologically *M. alliacea* differs from *M. fusiformispora* by the presence of chlamydospores and the absence of sporangiospores (Gams 1977).

38. Mortierella lobata H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 54.

Fungal Names: FN570916.

Etymology: lobata (Lat.) refers to the species having lobate colonies.

Holotype: HMAS 351528.

*Colonies* on PDA at 20 °C for 7 days, slow growing, reaching 70 mm in diameter, broadly lobed and concentrically zonate, with dense aerial mycelia in two weeks, white, irregular at margin *Hyphae* sparse in one week, flourishing in two weeks, branched, hyaline, 1.5–6.0 µm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores*, sporangia, and sporangiospores absent even after one month. *Chlamydospores* mainly globose, occasionally subglobose, 6.0–13.5 µm in

diameter, rarely ovoid or irregular, 8.0–20 μm long and 6.5–13.5 μm wide, subhyaline or Light Brown, sometimes with papillate appendages, always with droplets. *Zygospores* unknown.

*Material examined*: China, Beijing, 115°25'54"E, 39°58'6"N, 6 July 2021, from soil sample, Heng Zhao (holotype HMAS 351528, living ex-holotype culture CGMCC 3.16126).

GenBank accession number: OL678166.

*Notes: Mortierella lobata* is closely related to *M. seriatoinflata* H. Zhao *et al.* based on phylogenetic analysis of ITS rDNA sequences (Fig. 13). However, morphologically *M. seriatoinflata* differs from *M. lobata* by a faster growth rate under the same conditions (90 mm in diameter vs. 70 mm in diameter) and producing sporangiospores.

39. Mortierella macrochlamydospora H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 55.

Fungal Names: FN570917.

*Etymology: macrochlamydospora* (Lat.) refers to the species having big chlamydospores. *Holotype*: HMAS 351529.

*Colonies* on PDA at 20 °C for 7 days, slow growing, reaching 55 mm in diameter, scaly and white, reverse regular and Baryta Yellow. *Hyphae* sparse, white, branched, aseptate when young, septate when old, 2.0–7.5 µm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from aerial hyphae, erect, unbranched, aseptate. *Sporangia* mostly globose, occasionally subglobose, persistent-walled, smooth, 14.5–30.0 µm in diameter. *Apophyses* absent. *Collars* absent. *Columellae* degenerated. *Sporangiospores* mostly globose, occasionally subglobose, 2.0–3.5 µm in diameter. *Chlamydospores* abundantly produced in media, mostly globose, occasionally subglobose, 22.0–67.0 µm in diameter. *Zygospores* absent.

*Materials examined*: China, Inner Mongolia Auto Region, Hulun Buir, Genhe County, 122°15'48"E, 52°8'21"N, from plant debris, 30 Mar 2018, Peng-Cheng Deng (holotype HMAS 351529, living ex-holotype culture CGMCC 3.16127, and living culture XY04275).

GenBank accession numbers: OL678167 and OL678168.

*Notes: Mortierella macrochlamydospora* is closely related to *M. macrocystis* W. Gams based on phylogenetic analysis of ITS rDNA sequences (Fig. 13). However, morphologically *M. macrocystis* differs from *M. macrochlamydospora* by larger chlamydospores (20.0–300.0 µm in diameter vs. 22.0–67.0 µm in diameter; Gams 1961, 1977).

40. Mortierella microchlamydospora H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 56.

Fungal Names: FN570918.

*Etymology: microchlamydospora* (Lat.) refers to the species having the small chlamydospores. *Holotype*: HMAS 351530.

*Colonies* on PDA at 20 °C for 6 days, reaching 90 mm in diameter, broadly lobed and concentrically zonate, white, with dense aerial mycelia at edge. *Hyphae* flourishing, white, branched, aseptate when young, septate when old, sometimes swollen, 0.5–5.5 µm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores*, s*porangia*, s*porangiospores* absent after one month of incubation. *Chlamydospores* globose or subglobose or irregular, hyaline or subhyaline, sometimes with spines, obviously thick-walled when mature, 9.5–17.5 µm long and 10–13.5 µm wide. *Zygospores* unknown.

*Materials examined*: China. Yunnan Province, Dehong, Mangshi, 98°40'3"E, 24°32'38"N, from soil sample, 28 May 2021, Heng Zhao (holotype HMAS 351530, living ex-holotype culture CGMCC 3.16128). Beijing, 115°25'54"E, 39°58'6"N, from soil sample, 30 June 2021, Heng Zhao (culture XY07258); 115°34'1"E, 39°47'49"N, from soil sample, 30 June 2021, Heng Zhao (culture XY07283).

GenBank accession numbers: OL678169, OL678170 and OL678171.

*Notes*: We isolated three strains (XY06926, XY07258, XY07283) from China, which are closely related to the strain CBS 510.63 in ITS rDNA phylogeny (Fig. 13). The CBS 510.63 was identified as *M. exigua* Linnem. Two other strains of *M. exigua* CBS 655.68 (type of *M. sterilis* B.S. Mehrotra & B.R. Mehrotra) and CBS 358.76, were also deposited in GenBank with ITS rDNA sequences. According to the protologue of *M. exigua*, the sporangiophores are 300  $\mu$ m long, gradually narrowing, from 5  $\mu$ m to 1.5  $\mu$ m wide; the sporangia are globose with deliquescent walls, the sporangiospores are globose or ovoid, 4–7  $\mu$ m in diameter, and the chlamydospores are globose or hemispherical, 20  $\mu$ m in diameter (Linnemann 1941). In this study, we proposed *M. microchlamydospora* for these three Chinese strains based on their distinctive characteristics, viz., the absence of sporangiophores, sporangia and sporangiospores and the presence of chlamydospores which are globose, irregularly shaped, 9.5–17.5  $\mu$ m long and 10–13.5  $\mu$ m wide. Consequently, we treated the strain CBS 510.63 as *M. microchlamydospora* rather than *M. exigua*.

41. Mortierella mongolica H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 57.

Fungal Names: FN570919.

*Etymology: mongolica* (Lat.) refers to the Inner Mongolia Auto Region, China, where the type was collected.

Holotype: HMAS 351531.

*Colonies* on PDA at 20 °C for 12 days, slow growing, reaching 80 mm in diameter, lobed and scaly, white, reverse Pale Yellow-Orange. *Hyphae* flourishing, white, branched, sometimes swollen, aseptate when young, septate when old,  $1.5-6.0 \mu m$  in diameter. *Sporangia* infrequent, subglobose to globose, hyaline or subhyaline, smooth, several-spored,  $9.0-11.5 \mu m$  long and  $8.0-12.5 \mu m$  wide, walls deliquescent. *Apophyses* and *Collars* absent. *Columellae* degenerated. *Sporangiospores* ovoid, hyaline,  $3.5-6.5 \mu m$  long and  $3.0-3.5 \mu m$  wide. *Chlamydospores* ovoid or globose, hyaline or subhyaline appendages,  $9.0-21.0 \mu m$  long and  $9.5-15.0 \mu m$  wide. *Zygospores* unknown.

*Materials examined*: China, Inner Mongolia Auto Region. Zhalantun, 121°39'26''E, 47°37'45''N, from soil sample, 7 March 2018, Yu-Chuan Bai (holotype HMAS 351531, living exholotype culture CGMCC 3.16129); Arxan, 119°41'16''E, 47°18'26''N, from soil sample, 29 January 2018, Yu-Chuan Bai (living culture XY03534).

GenBank accession numbers: OL678172 and OL678173.

*Notes: Mortierella mongolica* is closely related to *M. antarctica* Linnem. based on phylogenetic analysis of ITS rDNA sequences (Fig. 13). However, morphologically *M. antarctica* differs from *M. mongolica* by subglobose sporangiospores, and globose chlamydospores (Zycha *et al.* 1969, Gams 1977).

42. Mortierella seriatoinflata H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 58.

Fungal Names: FN570920.

*Etymology: seriatoinflata* (Lat.) refers to the species having chains of swellings in the hyphae. *Holotype*: HMAS 351532.

*Colonies* on PDA at 20 °C for 7 days, reaching 90 mm in diameter, broadly lobed and concentrically zonate, white, with some aerial mycelia mainly in center, sparse growth within one week but abundant within two weeks. *Hyphae* simply branched, hyaline, producing a chain of swellings in both aerial and substrate hyphae, 1.0–7.0 µm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from aerial hyphae, erect or slightly bent, unbranched, tapering slightly from bottom upwards. *Sporangia* contain droplets, mostly globose, occasionally

subglobose, hyaline or subhyaline, 15.0–30.0 μm in diameter, walls deliquescent or persistent. *Apophyses* absent. *Collars* absent. *Columellae* degenerated. *Sporangiospores* ovoid or subglobose, hyaline, with some droplets, 5.5–11.5 μm long and 4.5–8.5 μm wide. *Chlamydospores* absent. *Zygospores* absent.

*Materials examined*: China. Beijing, 115°25'54"E, 39°58'6"N, from plant debris sample, 6 July 2021, Heng Zhao (holotype HMAS 351532, living ex-holotype culture CGMCC 3.16130). Anhui Province, Chuzhou, Quanjiao Country, 117°55'8"E, 32°0'25"N, from soil sample, 28 May 2021, Heng Zhao (living culture XY06985). Germany, from forest soil sample, G. Linnemann (living culture CBS 314.52).

GenBank accession numbers: OL678174, OL678175 and MH868591.

*Notes*: Two strains XY07264 and XY06985 from China are grouped together with CBS 314.52, which was treated as *Mortierella gamsii* Milko based on phylogenetic analysis of ITS rDNA sequences (Fig. 13). However, type strain of *M. gamsii*, CBS 749.68, is distantly related to these three strains. Therefore, the identification of CBS 314.52 was incorrect. Historically, CBS 314.52 was initially a syntype of *M. spinosa*, but it is incongruent with the typical features of *M. spinosa* Linnem., such as collars and columellae (Linnemann 1941). Consequently, *M. seriatoinflata* was proposed for CBS 314.52 and two Chinese strains.

43. Mortierella sparsa H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 59.

Fungal Names: FN570921.

Etymology: sparsa (Lat.) refers to the species having sparse aerial hyphae.

Holotype: HMAS 351533.

*Colonies* on PDA at 20 °C for 7 days, slow growing, reaching 60 mm in diameter, radial, broadly lobed, initially white, then Baryta Yellow. *Substrate hyphae* swollen. *Aerial hyphae* sparse, 1.5–5.0 µm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from aerial hyphae, erect, unbranched, aseptate. *Sporangia* mostly globose, occasionally subglobose, hyaline or subhyaline, smooth, 15.5–20.0 µm in diameter, walls deliquescent. *Apophyses* and *collars* absent. *Columellae* degenerated. *Sporangiospores* ellipsoid, cylindrical or ovoid, hyaline or subhyaline, 3.0–4.0 µm long and 2.0–2.5 µm wide. *Chlamydospores* absent. *Zygospores* absent.

*Materials examined*: China. Heilongjiang Province, Mohe Country, 52°29'27''N, 122°31'41''E, from leaves sample, 21 January 2018, Peng-Cheng Deng (holotype HMAS 35153, living ex-

holotype culture CGMCC 3.16131); Huma Country, 52°21′23″N, 123°59′15″E, from leaves sample, 6 February 2018, Peng-Cheng Deng (living culture XY03860). Inner Mongolia Auto Region, Argun, 51°53′57″N, 120°54′33″E, from leaves sample, 8 April 2018, Peng-Cheng Deng (living culture XY04406).

GenBank accession numbers: OL678176, OL678177 and OL678291.

Notes: Mortierella sparsa is closely related to *M. basiparvispora* W. Gams & Grinb., *M. jenkinii* (A.L. Sm.) Naumov and *M. parvispora* Linnem. based on phylogenetic analysis of ITS rDNA sequences (Fig. 13). However, morphologically *M. basiparvispora* and *M. parvispora* differ from *M. sparsa* by subglobose to globose of sporangiospores (Gams 1976, 1977). *M. jenkinii* differs from *M. sparsa* by producing lemon-shaped chlamydospores (Gams 1977).

44. Mortierella varians H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 60.

Fungal Names: FN570922.

*Etymology: varians* (Lat.) refers to the species having various sporangiospores in shape. *Holotype:* HMAS 351534.

*Colonies* on PDA at 20 °C for 7 days, slow growing, reaching 80 mm in diameter, broadly lobed zonate or umbrella-shaped, white. *Hyphae* sparse when young, flourishing when old, white, branched, septate with age, 1.5–13.5 µm in diameter. *Rhizoids* root-like, simple branched, slightly thin. *Sporangiophores* arising from aerial hyphae, erect or slightly bent, unbranched, aseptate. *Sporangia* subglobose or globose, hyaline or subhyaline, smooth, 20.5–37.5 µm long and 22.0–36.0 µm wide, walls deliquescent. *Apophyses* and *Collars* absent. *Columellae* degenerated. *Sporangiospores* variable, ovoid or ellipsoid or globose or subglobose, 5.0–14.0 µm long and 4.0–8.0 µm wide. *Chlamydospores* irregular or subglobose or ovoid, 9.0–15.0 µm long and 7.0–13.0 µm wide. *Zygospores* absent.

*Materials examined*: China, Tibet Auto Region, Naqu, from soil sample, 21 Dec 2020, Heng Zhao (holotype HMAS 351534, living ex-holotype culture CGMCC 3.16132, and living culture XY05920).

GenBank accession numbers: OL678178 and OL678179.

*Notes*: *Mortierella varians* is closely related to *M. acrotona* W. Gams based on phylogenetic analysis of ITS rDNA sequences (Fig. 13). However, morphologically *M. acrotona* differs from *M. varians* by sporangia containing 1–4 sporangiospores which are variable in size (11–24 μm in

diameter; Gams 1976), while sporangia contain abundant sporangiospores which are stable in size (17–20 µm in diameter) in *M. varians*.

45. Mucor abortisporangium H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 61.

Fungal Names: FN570923.

*Etymology: abortisporangium* (Lat.) refers to the species having sporangia failing to mature. *Holotype:* HMAS 351535.

*Colonies* on PDA at 27 °C for 7 days, reaching 80 mm in diameter, first white, gradually becoming Cinnamon-Drab, floccose, irregular at margin. *Hyphae* flourishing, branched, aseptate when juvenile, septate with age, 2.0–10.0 μm in diameter. *Rhizoids* absent. *Stolons* absent. *Stolons* absent. *Sporangiophores* arising from substrate and aerial hyphae, erect or slightly curved, unbranched. *Fertile sporangia* globose, smooth, 19.0–30.0 μm in diameter, walls deliquescent. *Aborted sporangia* laterally formed on aerial hyphae, hyaline. *Apophyses* absent. *Collars* absent. *Columellae* subglobose or globose, hyaline, 11.0–25.5 μm long and 10.5–24.0 μm wide. *Sporangiospores* fusiform or ellipsoid, with droplets, 4.5–5.5 μm long and 2.0–3.0 μm wide. *Chlamydospores* produced in substrate hyphae, in chains, cylindrical, ellipsoid, ovoid, subglobose, globose or irregular, 5.0–22.5 μm long and 6.5–15.5 μm wide. *Zygospores* unknown.

*Material examined*: China, Guangxi Auto Region, Guigang, from soil sample, 16 September 2021, Heng Zhao (holotype HMAS 351535 living ex-holotype culture CGMCC 3.16133).

GenBank accession number: OL678180.

*Notes: Mucor abortisporangium* is closely related to *M. radiatus* H. Zhao *et al.* based on phylogenetic analysis of ITS rDNA sequences (Fig. 14). However, morphologically *M. radiatus* differs from *M. abortisporangium* by a slower growth rate (60 mm within 10 days vs. 80 mm within 7 days), abundant chlamydospores borne in the substrate hyphae and aerial hyphae (in substrate hyphae only in *M. abortisporangium*).

46. Mucor amphisporus H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 62.

Fungal Names: FN570924.

*Etymology: amphisporus* (Lat.) refers to the species producing two types of sporangiospores. *Holotype:* HMAS 351536.

*Colonies* on PDA at 27 °C for 9 days, slow growing, reaching 60 mm in diameter, more than 20 mm high, floccose, white, reverse Light Yellow. *Hyphae* flourishing, always unbranched,

substrate hyphae abundant, usually swollen, 9.5–23.5 μm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from substrate and aerial hyphae, erect or slightly bent, unbranched, generally constricted. *Sporangia* globose, Light Brown to black, smooth, 38.0–77.5 μm in diameter, walls deliquescent. *Apophyses* absent. *Collar* distinct and large. *Columellae* subglobose and globose, brownish, smooth, 17.0–58.5 μm long and 11.5–57.5 μm wide. *Sporangiospores* of two kinds: cylindrical and constricted in the middle, 5.5–9.5 μm long and 2.5–4.0 μm wide, and globose, 4.0–6.0 μm in diameter. *Chlamydospores* absent. *Zygospores* unknown.

*Materials examined*: China, Inner Mongolia Auto Region. 42°27'45"N, 113°5'15"E, from soil sample, 29 July 2021, Heng Zhao (holotype HMAS 351536, living ex-holotype culture CGMCC 3.16134); 42°59'17 "N, 112°29'34"E, from soil sample, 29 July 2021, Heng Zhao (living culture XY07649).

GenBank accession numbers: OL678181 and OL678182.

*Notes: Mucor amphisporus* is closely related to *M. zychae* Baijal & B.S. Mehrotra based on phylogenetic analysis of ITS rDNA sequences (Fig. 14). However, morphologically *M. zychae* differs from *M. amphisporus* by larger sporangiospores (12–31.5 µm long and 5.2–15.7 µm wide vs. 5.5–9.5 µm long and 2.5–4.0 µm wide), smaller columellae (17.5–35 µm long and 14–25.5 µm wide vs. 17.0–58.5 µm long and 11.5–57.5 µm wide), producing conical columellae and various-shaped sporangiospores, including globose, broadly ellipsoid and reniform (Baijal & Mehrotra 1965).

47. Mucor breviphorus H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 63.

Fungal Names: FN570925.

*Etymology: breviphorus* (Lat.) refers to the species having short lateral sporangiophores. *Holotype:* HMAS 351537.

*Colonies* on PDA at 27 °C for 12 days, slow growing, reaching 65 mm in diameter, less than 5 mm high, initially white, gradually becoming Pale Yellow-Orange with age, granulate, regular at margin. *Hyphae* flourishing, simply branched, aseptate when juvenile, septate with age, 5.5–19.5 µm in diameter. *Substrate hyphae* abundant, always swollen. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising directly from substrate hyphae, erect or recumbent, long or short, unbranched, simply branched or sympodial, always septate below columellae, slightly constricted on the top. *Sporangia* mostly globose, occasionally pigmented, multi-spored, 17.0–52.5 µm in diameter, walls deliquescent but rough. *Apophyses* absent. *Collars* present, always distinct, rarely

small. *Columellae* hemispherical or globose, hyaline, smooth, 13.0–42.5  $\mu$ m long and 13.0–36.5  $\mu$ m wide. *Sporangiospores* mainly ovoid or fusiform, rarely subglobose, globose or irregular, 4.0–10.5  $\mu$ m long and 2.5–7.5  $\mu$ m wide, or 7.0–8.5  $\mu$ m in diameter. *Chlamydospores* absent. *Zygospores* unknown.

*Material examined*: China, Yunnan Province, Diqing, Deqen County, 28°27'38"N, 98°46'15"E, from soil sample, 10 October 2021, Heng Zhao (holotype HMAS 351537, living ex-holotype culture CGMCC 3.16135).

GenBank accession number: OL678183.

*Notes: Mucor breviphorus* is closely related to *M. heilongjiangensis* H. Zhao *et al.* based on phylogenetic analysis of ITS rDNA sequences (Fig. 14). However, morphologically *M. heilongjiangensis* differs from *M. breviphorus* by a faster growth rate (90 mm in diameter with 7 days vs. 65 mm in diameter with 12 days), smaller sporangia (18.0–32.0 µm in diameter vs. 17.0– 52.5 µm in diameter), ellipsoid to reniform sporangiospores, and producing chlamydospores.

48. Mucor brunneolus H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 64.

Fungal Names: FN570926.

Etymology: brunneolus (Lat.) refers to the species having pale brown sporangia.

Holotype: HMAS 351538.

*Colonies* on PDA at 27 °C for 4 days, fast growing, reaching 90 mm in diameter, more than 10 mm high, floccose, initially white, soon becoming Sulphur Yellow. *Hyphae* flourishing, unbranched, 4.6–16.0 µm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from substrate hyphae, erect or bent, unbranched. *Sporangia* globose, hyaline when young, Pale Brown when old, smooth, 40.5–63.0 µm in diameter, walls deliquescent. *Apophyses* absent. *Collar* small, or absent. *Columellae* conical, ovoid, subglobose and globose, hyaline or subhyaline, smooth, 15.5–40.0 µm long and 14.0–40.0 µm wide. *Sporangiospores* mainly fusiform, rarely ovoid and cylindrical, hyaline, 2.5–7.0 µm long and 1.0–3.5 µm wide. *Chlamydospores* absent. *Zygospores* unknown.

*Material examined*: China, Guangxi Auto Region, Fangchenggang, 21°44'46"N, 108°5'13"E, from soil sample, 22 July 2021, Heng Zhao (holotype HMAS 351538, living ex-holotype culture CGMCC 3.16136).

GenBank accession number: OL678184.

Notes: Mucor brunneolus is closely related to *M. irregularis* Stchigel (replaced synonym *Rhizomucor variabilis* var. *variabilis*) based on phylogenetic analysis of ITS rDNA sequences (Fig. 14). However, morphologically *M. irregularis* differs from *M. brunneolus* by sporangiospores and columellae which are both variable and irregular in shape and size, and producing rhizoids and stolons (Zheng & Chen 1991, Alvarez *et al.* 2011).

49. Mucor changshaensis H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 65.

Fungal Names: FN570927.

*Etymology: changshaensis* (Lat.) refers to Changsha, Hunan Province, China, where the type was collected.

Holotype: HMAS 351539.

*Colonies* on PDA at 27 °C for 8 days, slow growing, reaching 90 mm in diameter, first light yellow, soon becoming Strontian Yellow, floccose, granulate, irregular at margin. *Hyphae* flourishing, branched, aseptate when juvenile, septate with age, 4.5–15.0 µm in diameter. *Rhizoids* present, root-like, branched. *Stolons* present. *Sporangiophores* arising from substrate or aerial hyphae, erect or bent, unbranched or repeatedly branched, sometimes slightly constricted at the top. *Sporangia* globose, Light Brown to black, smooth, 23.5–52.0 µm in diameter, walls deliquescent. *Apophyses* absent. *Collars* always present. *Columellae* subglobose to globose, hyaline, 10.0–28.5 µm long and 10.5–28.0 µm wide. *Sporangiospores* ovoid to subglobose, 4.0–7.0 µm long and 3.0–5.0 µm wide. *Chlamydospores* abundant in substrate hyphae, in chains, variable in shape, cylindrical, ellipsoid, ovoid or irregular, 8.5–20.0 µm long and 7.0–16.5 µm wide, or globose, 8.5–14.0 µm in diameter. *Zygospores* unknown.

*Materials examined*: China. Hunan Province, Changsha, 28°8'4"N, 112°53'10"E, from soil sample, 28 August 2021, Heng Zhao (holotype HMAS 351539, living ex-holotype culture CGMCC 3.16137, and living culture XY07965).

GenBank accession numbers: OL678185 and OL678186.

*Notes: Mucor changshaensis* is closely related to *M. atramentarius* L. Wagner & G. Walther based on phylogenetic analysis of ITS rDNA sequences (Fig. 14). However, morphologically *M. atramentarius* differs from *M. changshaensis* by larger sporangia (up to 90 µm in diameter vs. 23.5–52.0 µm in diameter), subglobose to globose sporangiospores, and the absence of chlamydospores (Wagner *et al.* 2020). 50. Mucor chlamydosporus H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 66.

Fungal Names: FN570928.

Etymology: chlamydosporus (Lat.) refers to the species having chlamydospores.

Holotype: HMAS 351540.

*Colonies* on PDA at 27 °C for 7 days, slow growing, reaching 70 mm in diameter, floccose, initially white, becoming Pale Yellow-Orange when mature. *Hyphae* flourishing, branched, aseptate when juvenile, septate with age, 3.5–13.5 µm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from substrate hyphae, erect, simple and unbranched, or sympodial, septate, slightly constricted. *Fertile sporangia* always terminal on sporangiophores, subglobose or globose, walls deliquescent. *Aborted sporangia* laterally formed on aerial hyphae, globose, hyaline, smooth, 10.0–53.0 µm in diameter. *Apophyses* absent. *Collars* rarely present. *Columellae* mostly globose, occasionally subglobose, smooth, 7.5–24.0 µm in diameter. *Projections* absent. *Sporangiospores* ellipsoid or ovoid, 4.0–7.5 µm long and 2.5–3.5 µm wide. *Chlamydospores* irregular, 10.5–16.0 µm long and 8.5–13.5 µm wide. *Zygospores* absent.

*Materials examined*: China. Hebei Province, Shijiazhuang, 38°43'16"N, 113°50'39"E, from soil sample, 14 Jan 2021, Tong-Kai Zong (holotype HMAS 351540, living ex-holotype culture CGMCC 3.16138). Yunnan Province, Chuxiong, 25°18'53"N, 101°25'17"E, from soil sample, 14 October 2021, Heng Zhao (living culture XY08211 and XY08225).

GenBank accession numbers: OL678187, OL678188 and OL678189.

*Notes: Mucor chlamydosporus* is closely related to *M. fluvii* Hyang B. Lee *et al.* based on phylogenetic analysis of ITS rDNA sequences (Fig. 14). However, morphologically *M. fluvii* differs from *M. chlamydosporus* by smaller sporangia (8.0–45 µm in diameter vs. 10.0–53.0 µm), bigger columellae (9.5–31.5 µm in diameter vs. 7.5–24.0 µm in diameter; Wanasinghe *et al.* 2018).

51. Mucor donglingensis H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 67.

Fungal Names: FN570929.

*Etymology: donglingensis* (Lat.) refers to Dongling Mountain, Beijing, China, where the type was collected.

Holotype: HMAS 351541.

*Colonies* on PDA at 27 °C for 5 days, fast growing, reaching 90 mm in diameter, floccose, first white, soon becoming Naphthalene Yellow to Citron Yellow. *Hyphae* flourishing, branched, 6.5–

16.5 μm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from substrate hyphae, erect, unbranched, slightly constricted at the top. *Sporangia* globose, hyaline when young, brown when old, smooth, 39.5–55.0 μm in diameter, walls deliquescent. *Apophyses* absent. *Collars* absent. *Columellae* globose to subglobose, hyaline or subhyaline, 19.5–49.5 μm long and 20.0–44.5 μm wide. *Sporangiospores* oblong to ovoid, hyaline or subhyaline, 2.5–8.0 μm long and 1.0–4.5 μm wide. *Chlamydospores* abundantly in substrate hyphae, in chains, ellipsoid, oblong, ovoid, subglobose, globose or irregular, 11.0–33.5 μm long and 6.5–15.5 μm wide, or 15.0–24.5 μm in diameter. *Zygospores* unknown.

*Materials examined*: China. Beijing, Dongling Mountain, 115°25'48"E, 39°22'12"N, from plant debris sample, 28 August 2021, Heng Zhao (holotype HMAS 351541, living ex-holotype culture CGMCC 3.16139). Yunnan Province, Diqing, Deqen Country, 98°46'15"E, 28°27'38"N, from soil sample, 9 October 2021, Heng Zhao (living culture XY08501).

GenBank accession numbers: OL678190 and OL678191.

*Notes: Mucor chlamydosporus* is closely related to *M. fluvii* based on phylogenetic analysis of ITS rDNA sequences (Fig. 14). However, morphologically *M. fluvii* differs from *M. donglingensis* by simple or sympodial sporangiophores, and one or two septa below the sporangia (Crous *et al.* 2018).

52. Mucor floccosus H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 68.

Fungal Names: FN570930.

Etymology: floccosus (Lat.) refers to the species having floccose colonies.

Holotype: HMAS 351542.

*Colonies* on PDA at 27 °C for 7 days, reaching 90 mm in diameter, broadly lobed and concentrically zonate, first white, gradually becoming Light Gray, floccose. *Hyphae* flourishing, branched, aseptate when juvenile, septate with age, 3.0–13.0 µm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from aerial hyphae, erect, straight or bent, unbranched, slightly expanded at the top. *Sporangia* globose, hyaline when young, brown when old, smooth, 19.5–43.5 µm in diameter, walls deliquescent. *Apophyses* absent. *Collars* absent. *Columellae* hemispherical or depressed globose, hyaline, smooth, 9.0–23.5 µm long and 11.0–26.0 µm wide. *Sporangiospores* fusiform or ellipsoid, 4.0–7.5 µm long and 1.0–4.0 µm wide. *Chlamydospores* in

aerial hyphae, hemispherical, subglobose, globose, or irregular, 9.5–19.0 μm long and 5.5–15.0 μm wide. *Zygospores* unknown.

*Materials examined*: China, Hunan Province, Changsha, 28°8'4"N, 112°53'10"E, from soil sample, 28 August 2021, Heng Zhao (holotype HMAS 351542, living ex-holotype culture CGMCC 3.16140, and living culture XY07967).

GenBank accession numbers: OL678192 and OL678193.

Notes: Mucor floccosus is closely related to *M. rhizosporus* H. Zhao *et al.* and *M. pernambucoensis* C.L. Lima *et al.* based on phylogenetic analysis of ITS rDNA sequences (Fig. 14). However, morphologically *M. rhizosporus* differs from *M. floccosus* by abundant chlamydospores in rhizoids, Pale Yellow-Orange colonies, and ovoid to oblong columellae. *M. pernambucoensi* differs from *M. floccosus* by sympodially-branched sporangiophores (de Lima *et al.* 2018).

53. Mucor fusiformisporus H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 69.

Fungal Names: FN570931.

Etymology: fusiformisporus (Lat.) refers to the species having fusiform sporangiospores.

Holotype: HMAS 351543.

*Colonies* on PDA at 27 °C for 4 days, fast growing, reaching 90 mm in diameter, 10 mm high, floccose, granulate, initially white, soon becoming Marguerite Yellow, reverse regular at margin. *Hyphae* flourishing, branched, aseptate when juvenile, septate with age, 4.0–21.5 µm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from aerial or substrate hyphae, erect or bent, unbranched. *Sporangia* globose, hyaline when young, Light Brown to Dark Brown when old, smooth, multi-spored, 15.0–40.5 µm in diameter, walls deliquescent. *Apophyses* absent. *Collars* usually absent and occasionally small. *Columellae* subglobose or globose, hyaline or subhyaline, smooth, 8.0–37.5 µm long and 8.5–32.0 µm wide. *Sporangiospores* fusiform, hyaline or subhyaline, smooth, 3.0–7.0 µm long and 1.5–3.5 µm wide. *Chlamydospores* absent. *Zygospores* unknown.

*Materials examined*: China. Zhejiang Province, Hangzhou, 30°07'15"N, 119°58'46"E, from soil sample, 4 June 2021, Jia-Jia Chen (holotype HMAS 351543, living ex-holotype culture CGMCC 3.16141). Yunnan Province, Dali, from soil sample, 28 October 2021, Heng Zhao (living culture XY08153 and XY08154). Zhejiang Province, Hangzhou, from soil sample, 10 October 2021, Heng Zhao (living culture XY08117). GenBank accession numbers: OL678194, OL678195, OL678196 and OL678197.

*Notes: Mucor fusiformisporus* is closely related to *M. donglingensis* H. Zhao *et al.* and *M. souzae* C.L. Lima *et al.* based on phylogenetic analysis of ITS rDNA sequences (Fig. 14). However, morphologically *M. donglingensis* differs from *M. fusiformisporus* by chlamydospores that are variable in shape. *M. souzae* differs from *M. fusiformisporus* by sporangiospores that are variable in shape, including ellipsoid, ellipsoid to fusoid, reniform and irregular, and by simple or sympodial sporangiophores (Crous *et al.* 2018).

54. Mucor heilongjiangensis H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 70.

Fungal Names: FN570932.

*Etymology: heilongjiangensis* (Lat.) refers to Heilongjiang, a province in China, where the type was collected.

Holotype: HMAS 351544.

*Colonies* on PDA at 27 °C for 7 days, reaching 90 mm in diameter, more than 10 mm high, broadly lobed and concentrically zonate, floccose, initially white, gradually becoming Pinkish Cinnamon to Verona Brown. *Hyphae* flourishing, always unbranched when young, branched when old, 2.0–15.5 µm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from substrate and aerial hyphae, erect, unbranched, sometimes slightly expanded at the top. *Sporangia* globose, hyaline when young, Light Brown to brown when old, smooth, 18.0–32.0 µm in diameter, walls deliquescent. *Apophyses* absent. *Collars* usually absent, occasionally present but small. *Columellae* subglobose, globose, ellipsoid, or pyriform, hyaline or subhyaline, sometimes pigmented, smooth, 6.0–29.5 µm long and 5.0–21.5 µm wide. *Sporangiospores* usually ellipsoid, occasionally reniform, 3.5–10.0 µm long and 2.5–6.0 µm wide. *Chlamydospores* abundant in substrate hyphae, in chains, ellipsoid, ovoid, subglobose, globose or irregular, 5.0–18.0 µm long and 5.5–15.5 µm wide. *Zygospores* unknown.

*Materials examined*: China, Heilongjiang Province, Heihe, 48°4'37"N, 127°6'54"E, from soil sample, 18 April 2018, Ze Liu (holotype HMAS 351544, living ex-holotype culture CGMCC 3.16142, and living culture XY05057).

*GenBank accession numbers*: OL678198 and OL678199. *Notes*: See notes of *Mucor breviphorus*.

55. Mucor hemisphaericum H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 71.

Fungal Names: FN570933.

*Etymology: hemisphaericum* (Lat.) refers to the species having hemispherical columellae. *Holotype*: HMAS 351545.

*Colonies* on PDA at 27 °C for 4 days, fast growing, reaching 90 mm in diameter, floccose, irregular at margin, first white, soon becoming Ivory Yellow. *Hyphae* flourishing, always unbranched and aseptate when young, branched and septate when old,  $1.5-23.5 \mu m$  in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from substrate and aerial hyphae, erect or slightly bent, unbranched, occasionally slightly expanded at the top. *Sporangia* globose, hyaline when young, Light Brown to brown when old, smooth,  $17.5-42.5 \mu m$  in diameter, walls deliquescent. *Apophyses* absent. *Collars* usually absent, small if present. *Columellae* hemispherical or depressed globose, hyaline or subhyaline,  $5.5-20.5 \mu m$  long and  $6.0-20.0 \mu m$  wide. *Sporangiospores* ovoid,  $3.5-7.5 \mu m$  long and  $1.5-3.5 \mu m$  wide. *Chlamydospores* abundant in substrate hyphae, in chains, variable in shape, cylindrical, ellipsoid, oblong, ovoid, subglobose, globose or irregular,  $9.0-23.5 \mu m$  long and  $7.0-16.5 \mu m$  wide, or  $9.0-16.5 \mu m$  in diameter. *Zygospores* unknown.

*Material examined*: China, Tibet Auto Region, Rikaze, Yadong County, from soil sample, 22 August 2021, Heng Zhao (holotype HMAS 351545, living ex-holotype culture CGMCC 3.16143). *GenBank accession number*: OL678200.

*Notes: Mucor hemisphaericum* is closely related to *M. merdicola* C.A.F. de Souza & A.L. Santiago based on phylogenetic analysis of ITS rDNA sequences (Fig. 14). However, morphologically *M. merdicola* differs from *M. hemisphaericum* by the wider columellae (30.0–35.0 μm wide vs. 6.0–20.0 μm wide) and sympodially branched sporangiophores (Li *et al.* 2016).

56. Mucor homothallicus H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 72.

Fungal Names: FN570934.

*Etymology: homothallicus* (Lat.) refers to the species producing zygospores by homothallism. *Holotype*: HMAS 351546.

*Colonies* on PDA at 25 °C for 9 days, slow growing, reaching 55 mm in diameter, 10 mm high, floccose, granulate, lobed at edge, initially white, then becoming Light Black, reverse irregular at margin. *Hyphae* flourishing, branched, aseptate when juvenile, septate with age, 5.0–17.0 µm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from aerial hyphae, erect or

slightly bent, unbranched. *Sporangia* globose, smooth, Light Brown or Dark Brown, 10.0–22.5 μm in diameter, walls deliquescent. *Apophyses* absent. *Collars* absent. *Columellae* oblong, subglobose and globose, hyaline or subhyaline, smooth, 6.0–13.5 μm long and 6.5–14.5 μm wide. *Sporangiospores* ellipsoid or subglobose, 7.0–11.0 μm long and 3.0–7.0 μm wide. *Chlamydospores* absent. *Zygospores* homothallic, mainly globose, hyaline when juvenile, gradually Dark Brown with age, surrounded by liquid droplets, finally Light Brown, hyaline or subhyaline, 39.0–80.0 μm in diameter.

*Materials examined*: China, Jiangsu Province, Lianyungang, 34°38'9"N, 119°29'58"E, from soil sample, 28 May 2021, Heng Zhao (holotype HMAS 351546, living ex-holotype culture CGMCC 3.16144, and living culture XY06967).

GenBank accession numbers: OL678201 and OL678202.

*Notes: Mucor homothallicus* is closely related to *M. endophyticus* (R.Y. Zheng & H. Jiang) J. Pawłowska & Walthe based on phylogenetic analysis of ITS rDNA sequences (Fig. 14). However, morphologically *M. endophyticus* differs from *M. homothallicus* by abundant rhizoids, collars, subglobose, ovoid, limoniform, or irregular chlamydospores, larger sporangia (38.0–80.0 µm in diameter vs. 10.0–22.5 µm in diameter), larger columellae (19.0–50.5 µm long and 18.0–46.0 µm or 13.5–37.0 µm in diameter vs. 6.0–13.5 µm long and 6.5–14.5 µm wide), and sporangiospores variable in shape, including narrowly to broadly ellipsoid, ovoid, subglobose, triangular, allantoid, and irregular (Zheng & Jiang 1995, Hoffmann *et al.* 2013).

57. Mucor hyalinosporus H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 73.

Fungal Names: FN570935.

*Etymology: hyalinosporus* (Lat.) refers to the species having hyaline chlamydospores. *Holotype*: HMAS 351547.

*Colonies* on PDA at 27 °C for 7 days, reaching 70 mm in diameter, initially white, soon becoming Sea-Foam Yellow, floccose, broadly lobed. *Hyphae* flourishing, firstly mainly in the center, then abundant throughout when old, 1.5–4.5 µm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising directly from substrate or aerial hyphae, erect or slightly bent, unbranched, always septate, slightly constricted on the top. *Sporangia* mostly globose, occasionally subglobose, brown when older, smooth, 13.0–31.0 µm in diameter. *Apophyses* absent. *Collars* absent, walls deliquescent. *Columellae* conical to cylindrical, hyaline or subhyaline, smooth, 9.5– 21.0  $\mu$ m long and 9.5–17.0  $\mu$ m wide. *Sporangiospores* fusiform, hyaline, with droplets, 4.5–7.5  $\mu$ m long and 2.0–4.0  $\mu$ m wide. *Chlamydospores* borne on substrate hyphae, in chains, moniliform, ovoid, globose, rarely irregular, hyaline, with droplets, 10.5–20.5  $\mu$ m long and 10.0–17.5  $\mu$ m wide. *Zygospores* unknown.

*Material examined*: China, Beijing, from soil sample, 28 October 2021, Heng Zhao (holotype HMAS 351547, living ex-holotype culture CGMCC 3.16145).

GenBank accession number: OL678203.

Notes: Mucor hyalinosporus is closely related to M. subtilissimus Oudem. based on phylogenetic analysis of ITS rDNA sequences (Fig. 14). However, morphologically M. subtilissimus differs from M. hyalinosporus by producing collars (Hurdeal et al. 2021).
58. Mucor lobatus H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 74.

Fungal Names: FN570936.

Etymology: lobatus (Lat.) refers to the species having lobate colonies.

Holotype: HMAS 351548.

*Colonies* on PDA at 27 °C for 6 days, reaching 80 mm in diameter, 10 mm high, floccose, lobed, initially white, soon becoming Baryta Yellow, reverse irregular at margin and Capucine Yellow. *Hyphae* flourishing, unbranched or simply branched, aseptate, 7.5–19.5 µm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from substrate hyphae, erect or bent, unbranched, aseptate, sometimes slightly constricted, very long. *Sporangia* globose, subhyaline, smooth, brown, 36.5–70.0 µm in diameter, walls deliquescent. *Apophyses* absent. *Collars* absent. *Collars*

*Materials examined*: China. Jiangsu Province, Yancheng, 33°41'55"N, 120°23'38"E, from soil sample, 28 May 2021, Heng Zhao (holotype HMAS 351548, living ex-holotype culture CGMCC 3.16146). Hubei Province, Huanggang, 30°59'46"N, 114°32'18"E, from soil sample, 31 May 2021, Heng Zhao (culture XY07029).

GenBank accession numbers: OL678204 and OL678203.

*Notes: Mucor lobatus* is closely related to *M. fusiformis* Walther & de Hoog, *M. hiemalis* Wehmer, and *M. japonicus* (Komin.) Walther & de Hoog based on phylogenetic analysis of ITS

rDNA sequences (Fig. 14). However, morphologically *M. fusiformis*, *M. hiemalis* and *M. japonicus* differ from *M. lobatus* by producing zygospores (Hesseltine *et al.* 1959, Schipper 1986b, Walther *et al.* 2013).

**59.** *Mucor moniliformis* H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 75.

Fungal Names: FN570937.

*Etymology: moniliformis* (Lat.) refers to the species having moniliform chlamydospores. *Holotype*: HMAS 351549.

*Colonies* on PDA at 27 °C for 5 days, reaching 90 mm in diameter, 10 mm high, floccose, granulate, initially white, soon becoming Buff-Yellow, reverse irregular at margin. *Hyphae* flourishing, branched, aseptate when juvenile, septate with age, 4.0–23.5 µm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from aerial or substrate hyphae, erect or slightly bent, simple branched, somewhere slightly constricted, 6.0–13.5 µm in diameter. *Sporangia* globose, hyaline when young, Light Brown or Dark Brown when old, smooth, 18.0–64.5 µm in diameter, walls deliquescent. *Apophyses* absent. *Collar* distinct present, or absent. *Columellae* subglobose and globose, hyaline or subhyaline, smooth, 15.0–30.5 µm long and 17.0–32.0 µm wide. *Sporangiospores* ovoid, hyaline or subhyaline, 3.5–5.5 µm long and 2.5–3.5 µm wide. *Chlamydospores* abundantly in substrate hyphae, in chains, ellipsoid, ovoid, subglobose, globose or irregular, 5.5–17.0 µm long and 7.0–15.5 µm wide. *Zygospores* unknown.

*Materials examined*: China. Zhejiang Province, Hangzhou, 30°07'15"N, 119°58'47"E, from soil sample, 4 June 2021, Jia-Jia Chen (holotype HMAS 351549, living ex-holotype culture CGMCC 3.16147). Hubei Province, Tianmen Mountain, from soil sample, 22 July 2021, Heng Zhao (living culture XY07458).

GenBank accession numbers: OL678206 and OL678207.

*Notes: Mucor moniliformis* is closely related to *M. brunneolus* H. Zhao *et al.* based on phylogenetic analysis of ITS rDNA sequences (Fig. 14). However, morphologically *M. brunneolus* differs from *M. moniliformis* by unbranched sporangiophores and fusiform sporangiospores.

60. Mucor orientalis H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 76.

Fungal Names: FN570938.

*Etymology: orientalis* (Lat.) refers to the locality of the holotype, Anhui Province, East Asia. *Holotype:* HMAS 351550.

*Colonies* on PDA at 27 °C for 7 days, reaching 90 mm in diameter, initially white, soon becoming Wax Yellow, floccose, granulate, regular at margin. *Hyphae* flourishing, simply branched, aseptate when juvenile, septate with age, 7.0–31.0 µm in diameter. *Substrate hyphae* abundant, 7.0–25.0 µm in diameter. *Substrate hyphae* abundant. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising directly from substrate or aerial hyphae, erect or recumbent, mainly unbranched, sometimes septate, slightly constricted, long or short. *Fertile sporangia* always terminally borne on the main axes, mostly globose, occasionally subglobose, light yellow to brown, smooth, 38.0–56.5 µm in diameter, walls deliquescent. *Aborted sporangia* borne laterally or intercalarily on sporangiophores. *Apophyses* absent. *Collars* sometimes present, always distinct, occasionally large. *Columellae* mostly globose, occasionally subglobose, hyaline, smooth, 17.0– 49.5 µm in diameter. *Sporangiospores* ovoid, ellipsoid, fusiform or irregular, 3.0–5.5 µm long and 2.0–3.5 µm wide. *Chlamydospores* arising from substrate hyphae, moniliform. *Zygospores* unknown.

*Material examined*: China, Anhui Province, Hefei, Lu'an, 31°27'36"N, 115°43'24"E, from soil sample, 28 May 2021, Heng Zhao (holotype HMAS 351550, living ex-holotype culture CGMCC 3.16148).

GenBank accession number: OL678208.

*Notes: Mucor orientalis* is closely related to *M. orantomantidis* Hyang B. Lee *et al.* based on phylogenetic analysis of ITS rDNA sequences (Fig. 14). However, morphologically *M. orantomantidis* differs from *M. orientalis* by producing zygospores and chlamydospores (Phookamsak *et al.* 2019).

61. Mucor radiatus H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 77.

Fungal Names: FN570939.

Etymology: radiatus (Lat.) refers to the species having radiating colonies.

Holotype: HMAS 351551.

*Colonies* on PDA at 27 °C for 10 days, slow growing, reaching 60 mm in diameter, radiating, initially white, gradually becoming Light Brown, floccose, irregular at margin. *Hyphae* flourishing when old, branched, 2.5–9.0 µm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from substrate or aerial hyphae, erect or curved, unbranched. *Fertile sporangia* always borne terminally on main axes, globose, smooth, 19.0–34.5 µm in diameter, walls deliquescent. *Aborted* 

*sporangia* mainly forming laterally or intercalary on sporangiophores, globose, monopodial, hyaline, thick-walled, 10.5–13.0 µm in diameter. *Apophyses* absent. *Collars* absent. *Columellae* forming between two aborted sporangia, subglobose to globose, hyaline, 12.5–26.5 µm long and 12.5–25.5 µm wide. *Sporangiospores* two types: mainly fusiform, with droplets, 3.5–5.5 µm long and 1.5–3.0 µm wide; and globose (rare), 3.0–5.0 µm in diameter. *Chlamydospores* abundantly produced on substrate hyphae and rarely on aerial hyphae, in chains, cylindrical, ellipsoid, ovoid or irregular when young, mostly globose, occasionally subglobose when old, 11.0–18.0 µm in diameter. *Zygospores* unknown.

*Materials examined*: China, Yunnan Province, Chuxiong, Mouding Country, 25°18'44"N, 113°12' 40"E, from soil sample, 30 September 2021, Heng Zhao (holotype HMAS 351551, living ex-holotype culture CGMCC 3.16149, and living culture XY08167).

*GenBank accession numbers*: OL678209 and OL678210. *Notes*: See notes of *Mucor abortisporangium*.

62. Mucor rhizosporus H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 78.

Fungal Names: FN570940.

*Etymology: rhizosporus* (Lat.) refers to the species producing chlamydospores in the rhizoids. *Holotype:* HMAS 351552.

*Colonies* on PDA at 27 °C for 7 days, slow growing, reaching 80 mm in diameter, first white, gradually becoming Pale Yellow-Orange, floccose, irregular at margin. *Hyphae* flourishing, branched, aseptate when juvenile, septate with age, 2.5–11.5 µm in diameter. *Rhizoids* abundant, root-like, branched, swollen, always producing chlamydospores. *Stolons* present, abundant. *Sporangiophores* arising from substrate and aerial hyphae, erect, unbranched. *Sporangia* globose, smooth, 22.0–37.5 µm in diameter, walls deliquescent. *Apophyses* absent. *Collars* always absent. *Columellae* ovoid to oblong, hyaline, 13.5–31.5 µm long and 10.0–22.5 µm wide. *Sporangiospores* fusiform or ellipsoid, 5.0–6.0 µm long and 2.0–3.0 µm wide. *Chlamydospores* produced in aerial hyphae and rhizoids; abundant in rhizoids, in chains, variable in shape when young, globose or subglobose when old, in aerial hyphae, cylindrical, ellipsoid, ovoid, subglobose to globose or irregular, 10.0–19.5 µm long and 8.0–13.5 µm wide. *Zygospores* unknown.

*Material examined*: China, Guangxi Auto Region, Nanning, from soil sample, 29 August 2021, Heng Zhao (holotype HMAS 351552, living ex-holotype culture CGMCC 3.16150). GenBank accession number: OL678211.

*Notes: Mucor rhizosporus* is closely related to *M. pernambucoensis* C.L. Lima *et al.* based on phylogenetic analysis of ITS rDNA sequences (Fig. 14). However, morphologically *M. pernambucoensis* differs from *M. rhizosporus* by larger sporangiospores (4.5–14.5 µm long and 2.5–5 µm wide vs. 5.0–6.0 µm long and 2.0–3.0 µm wide), sympodially branched sporangiophores, variable columellae, and neither rhizoids nor stolons (de Lima *et al.* 2018).

63. Mucor robustus H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 79.

Fungal Names: FN570941.

Etymology: robustus (Lat.) refers to the species having robust hyphae.

Holotype: HMAS 351553.

*Colonies* on PDA at 27 °C for 7 days, reaching 80 mm in diameter, granulate, broadly lobed and zonate, initially white, gradually becoming Maize Yellow. *Hyphae* unbranched or simple branched, robust, hyaline, 14.0–77.0 µm in diameter, substrate hyphae abundant, root-like, branched. *Rhizoids* and *stolons* absent. *Sporangiophores* arising directly from substrate hyphae, erect to curved, unbranched, simple branched, or repeatedly unbranched, rarely with septa at the base on sporangiospores, generally constricted on the top, very long or short. *Sporangia* mostly globose, occasionally subglobose multi-spored, brown to black, 33.0–160.0 µm in diameter, walls deliquescent. *Columellae* hemispherical, conical, subglobose to globose, hyaline or subhyaline, rough, sometimes with pigment, 14.5–109.0 µm long and 16.0–105.5 µm wide. *Apophyses* absent. *Collar* usually absent, small if present. *Sporangiospores* ovoid to globose, 4.0–7.0 µm long and 3.5–6.0 µm wide. *Chlamydospores* absent. *Zygospores* unknown.

*Materials examined*: China, Xinjiang Auto Region, Altay, Burqin Country, 48°39'29"N, 87°2'9"E, from soil sample, 31 October 2021, Heng Zhao (holotype HMAS 351553, living exholotype culture CGMCC 3.16151, and living culture XY08976 and XY09024).

GenBank accession numbers: OL678212, OL678213 and OL678214.

*Notes*: *Mucor robustus* is closely related to *M. aligarensis* B.S. Mehrotra & B.R. Mehrotra, *M. flavus* (Mart.) Fr. and *M. rongii* F.R. Bai & C. Cheng based on phylogenetic analysis of ITS rDNA sequences (Fig. 14). However, morphologically *M. aligarensis* differs from *M. robustus* by larger sporangiospores (6.6–15.4 µm long and 5.5–11 µm wide vs. 4.0–7.0 µm long and 3.5–6.0 µm wide; Mehrotra & Mehrotra 1969). *M. flavus* differs from *M. robustus* by fusiform sporangiophores

(https://www.mycobank.org). *M. rongii* differs from *M. robustus* by broadly ellipsoid to cylindrical or rather irregular sporangiospores (Bai *et al.* 2021).

64. Mucor sino-saturninus H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 80.

Fungal Names: FN570942.

*Etymology: sino-saturninus* (Lat.) refers to the species being like *Mucor saturninus* but occurring in China.

Holotype: HMAS 351554.

*Colonies* on PDA at 27 °C for 7 days, slow growing, reaching 80 mm in diameter, broadly lobed, initially white, gradually becoming Ochraceous-Tawny to Dresden Brown, granulate. *Hyphae* unbranched or simple branched, hyaline, 7.5–43.5 µm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising directly from substrate or aerial hyphae, erect or bent, simple branched, sympodial, septate usually at the base and sometimes one to several below sporangia, generally constricted on the top, sometimes swollen below sporangia. *Sporangia* mostly globose, occasionally subglobose, brownish, with spines, 23.0–105.0 µm in diameter, walls deliquescent. *Apophyses* absent. *Collars* always present, distinct. *Columellae* subglobose to globose, hyaline, rough or smooth, 16.0–37.5 µm long and 14.5–37.0 µm wide. *Sporangiospores* ovoid to globose, subhyaline, 4.5–10.5 µm long and 3.0–7.0 µm wide. *Chlamydospores* absent. *Zygospores* unknown.

*Materials examined*: China, Yunnan Province, Diqing, Deqen Country, 98°46'15"E, 28°27'38"N, from soil sample, 19 October 2021, Heng Zhao (holotype HMAS 351554, living exholotype culture CGMCC 3.16152, and living culture XY08556).

GenBank accession numbers: OL678215 and OL678216.

*Notes: Mucor sino-saturninus* is closely related to *M. saturninus* Hagem based on phylogenetic analysis of ITS rDNA sequences (Fig. 14). However, morphologically *M. saturninus* differs from *M. sino-saturninus* by larger columellae (35–100 μm long and 25–90 μm wide vs. 16.0–37.5 μm long and 14.5–37.0 μm wide) and broadly ellipsoid sporangiospores (Hagem 1910).

65. Syncephalastrum breviphorum H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 81. Fungal Names: FN570943.

*Etymology: breviphorum* (Lat.) refers to the species having short lateral sporangiophores. *Holotype*: HMAS 351555.

*Colonies* on PDA at 27 °C for 6 days, reaching 90 mm in diameter, zonate, scaly, floccose, initially white, soon becoming Buckthorn Brown, reverse irregular at margin. *Hyphae* flourishing, branched, hyaline or slightly pigmented, aseptate at first, septate with age, 5.5–15.5 µm in diameter. *Rhizoids* root-like or finger-like, branched. *Stolons* present. *Sporangiophores* arising from aerial hyphae, erect, bent, even curved, simple or sympodially branched, abundant, and shorter when laterally branched. *Vesicles* globose to subglobose, subtended or irregular, rough, hyaline to subhyaline, sometimes with one septum to two septa, 12.5–21.5 µm in diameter, or 17.5–35.0 µm long and 19.0–29.0 µm wide. *Merosporangia* borne over entire surface of merosporangia, containing a single row of 3–5 sporangiospores, frequently five-spored, 10.6–16.5 µm long and 2.0–4.0 µm wide. *Apophyses* absent. *Collars* absent. *Columellae* degenerated. *Sporangiospores* striated, variable shape, mainly globose, 3.0–5.0 µm in diameter, sometimes subglobose, ovoid, cylindrical or ellipsoid, 3.0–4.5 µm long and 2.5–3.5 µm wide. *Chlamydospores* absent. *Zygospores* unknown.

*Materials examined*: China, Fujian Province, Fuzhou, Fujian Academy of Agricultural Sciences, from paper sample, 1 October 2013, Xiao-Yong Liu (holotype HMAS 351555, living exholotype culture CGMCC 3.16153, and living culture XY06838).

GenBank accession numbers: OL678217 and OL678218.

*Notes: Syncephalastrum breviphorum* is closely related to *S. contaminatum* A.S. Urquhart & A. Idnurm based on phylogenetic analysis of ITS rDNA sequences (Fig. 15). However, morphologically *S. contaminatum* differs from *S. breviphorum* by globose sporangiospores and frequently four-spored merosporangia (Urquhart & Idnurm 2020).

66. Syncephalastrum elongatum H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 82.

Fungal Names: FN570944.

Etymology: elongatum (Lat.) refers to the species having long merosporangia.

Holotype: HMAS 351556.

*Colonies* PDA at 27 °C for 6 days, reaching 90 mm in diameter, scaly, floccose, granulate, initially white, soon becoming Clay Color, reverse irregular at margin. *Hyphae* flourishing, branched, aseptate at first, septate with age, hyaline or slightly pigmented,  $3.5-24.0 \mu m$  in diameter. *Rhizoids* rare, root-like or finger-like. *Sporangiophores* arising from aerial hyphae, erect, bent, even curved, simple branched or unbranched, shorter and always curved when laterally branched, sometimes septate,  $4.5-13.5 \mu m$  in wide. *Vesicles* subglobose, globose or subtended, rough, hyaline

or Light Brown, 8.5–60.5 μm long and 10.0–45.0 μm wide. *Merosporangia* borne on entire surface of vesicles, containing a single row of 4–18 sporangiospores, frequently more than ten-spored, 11.5–51.5 μm long and 3.0–4.0 μm wide. *Apophyses* present. *Collars* absent. *Columellae* degenerated. *Sporangiospores* with striation, variable shape, subglobose, 3.0–5.5 μm in diameter, sometimes subglobose, ovoid, cylindrical or ellipsoid, 3.5–5.5 μm long and 2.5–3.5 μm wide. *Chlamydospores* absent. *Zygospores* unknown.

*Material examined*: China, Fujian Province, Fuzhou, Fujian Academy of Agricultural Sciences, from paper sample, 1 October 2013, Xiao-Yong Liu (holotype HMAS 351556, living exholotype culture CGMCC 3.16154).

GenBank accession number: OL678219.

*Notes*: *Syncephalastrum elongatum* is closely related to *S. verruculosum* P.C. Misra based on phylogenetic analysis of ITS rDNA sequences (Fig. 15). However, morphologically *S. verruculosum* differs from *S. elongatum* by merosporangia (13.0–23.0 µm long and 4.0–7.0 µm wide, containing a single row of 2–6 sporangiospores vs. 11.5–51.5 µm long and 3.0–4.0 µm wide, containing a single row of 4–18 sporangiospores), and the absence of rhizoids (Misra 1975).

67. Syncephalastrum simplex H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 83.

Fungal Names: FN570945.

*Etymology: simplex* (Lat.) refers to the species having simple branching of the sporangiophores.

Holotype: HMAS 351557.

*Colonies* on PDA at 27 °C for 7 days, reaching 90 mm in diameter, lobed, floccose, granulate, initially white, soon becoming Clove Brown, reverse irregular at margin. *Hyphae* flourishing, branched, aseptate when juvenile, septate with age, 5.5–14.5 µm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from aerial hyphae, erect, slightly bent, simple branched, or unbranched, 2.5–11.5 µm wide. *Vesicles* subglobose, globose or irregular, rough, hyaline to Light Brown, some with septa, 6.5–28.5 µm long and 7.5–28.0 µm wide. *Merosporangia* borne on entire surface of vesicles, containing a single row of 3–9 sporangiospores, mainly four- to five-spored. *Apophyses* present. *Collars* absent. *Columellae* degenerated. *Sporangiospores* with striation, variable shape, mainly globose, 3.5–6.5 µm in diameter, subglobose, ovoid or ellipsoid, 3.0–7.5 µm long and 2.5–5.5 µm wide. *Chlamydospores* absent. *Zygospores* unknown.

*Material examined*: China, Hubei Province, Shennongjia National Nature Reserve, from soil sample, 1 October 2013, Xiao-Yong Liu (holotype HMAS 351557, living ex-holotype culture CGMCC 3.16155).

GenBank accession number: OL678220.

Notes: Syncephalastrum simplex is closely related to S. monosporum R.Y. Zheng et al. based on phylogenetic analysis of ITS rDNA sequences (Fig. 15). However, morphologically S. monosporum differs from S. simplex by the absence of rhizoids or stolons (Zheng et al. 1988).

68. Syncephalastrum sympodiale H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 84.

Fungal Names: FN570946.

*Etymology: sympodiale* (Lat.) refers to the species having sympodial branching of the sporangiophores.

Holotype: HMAS 351558.

*Colonies* on PDA at 27 °C for 7 days, reaching 80 mm in diameter, small scaly, floccose, granulate, initially white, gradually becoming Buckthorn Brown to Dresden Brown, reverse irregular at margin. *Hyphae* flourishing, branched, hyaline, aseptate at first, septate when old, 3.5–16.5 µm in diameter. *Rhizoids* mostly root-like or finger-like, rarely unbranched. *Sporangiophores* arising from aerial hyphae, erect, bent, even curved, usually sympodial, unbranched, or simple branched, sometimes with one septum or two septa blow apophyses, shorter and always curved when laterally branched, 4.5–11.5 µm in wide. *Vesicles* mainly subglobose or globose, rarely subtended or irregular, rough, hyaline or Light Brown, 9.0–35.0 µm long and 8.5–30.5 µm wide. *Merosporangia* borne over entire surface of vesicles, containing a single row of 2–7 sporangiospores, frequently five- or six-spored, 6.0–19.5 µm long and 2.5–4.0 µm wide. *Apophyses* present. *Collars* absent. *Columellae* degenerated. *Sporangiospores* with striation, variable shape, mainly globose, 4.0–6.0 µm in diameter, sometimes subglobose, ovoid or ellipsoid, 4.0–6.0 µm long and 3.0–5.0 µm wide. *Chlamydospores* absent. *Zygospores* unknown.

*Materials examined*: China. Beijing, from soil sample, 1 October 2013, Xiao-Yong Liu (holotype HMAS 351558, living ex-holotype culture CGMCC 3.161536, and living culture XY06803). Hubei Province, Shennongjia National Nature Reserve, from mushroom sample, 1 October 2013, Xiao-Yong Liu (living culture XY06811).

GenBank accession numbers: OL678221, OL678222 and OL678223.

*Notes*: *Syncephalastrum sympodiale* is closely related to *S. elongatum* H. Zhao *et al.* and *S. verruculosum* P.C. Misra based on phylogenetic analysis of ITS rDNA sequences (Fig. 15). However, morphologically *S. verruculosum* differs from *S. sympodiale* by longer merosporangia (11.5–51.5 µm long vs. 6.0–19.5 µm long), the absence of sympodially branched sporangiophores and rhizoids. And *S. verruculosum* differs from *S. sympodiale* by larger vesicles (45–90 µm in diameter vs. 9.0–35.0 µm long and 8.5–30.5 µm wide), no sympodially branched sporangiophores, and the absence of rhizoids (Misra 1975).

69. Umbelopsis brunnea H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 85.

Fungal Names: FN570832.

Etymology: brunnea (Lat.) refers to the species having brown colonies.

Holotype: HMAS 249876.

*Colonies* on PDA at 27 °C for 9 days, slow growing, reaching 70 mm in diameter, thin pancake-like, concentrically zoned, regular at margin, initially white, becoming Antique Brown to Amber Brown with age, reverse smooth. *Hyphae* branched, aseptate when juvenile, always irregularly septate with age, 2.0–5.0  $\mu$ m in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangia* globose, pigmented, smooth, 10.5–15.5  $\mu$ m in diameter, walls deliquescent. *Apophyses* absent. *Collars* absent. *Columellae* hemispherical to cylindrical, smooth, 1.5–2.5  $\mu$ m long and 2.0–2.5  $\mu$ m wide. *Projections* absent. *Sporangiospores* subglobose, smooth, 2.0–3.0  $\mu$ m in diameter. *Chlamydospores* absent. *Zygospores* absent.

*Materials examined*: China. Heilongjiang Province, Yichun, 48°14'11"N, 129°15'45"E, from soil sample, 23 Dec 2017, Mei-Lin Lv (holotype HMAS 249876, living ex-type culture CGMCC 3.16023). Inner Mongolia Auto Region, Hulun Buir, Genhe County, 48°14'11"N, 129°15'45"E, from soil sample, 23 Dec 2017, Mei-Lin Lv and Xiao Ju (living culture CGMCC 3.16024).

GenBank accession numbers: MW580596 and MW580597.

*Notes: Umbelopsis brunnea* is closely related to *U. globospora* H. Zhao *et al.* based on phylogenetic analysis of ITS rDNA sequences (Fig. 16). However, morphologically *U. globospora* differs from *U. brunnea* by Mouse Gray colonies and degenerated columellae.

70. Umbelopsis chlamydospora H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 86. Fungal Names: FN570947.

Etymology: chlamydospora (Lat.) refers to the species having chlamydospores.

## Holotype: HMAS 351559.

*Colonies* on PDA at 25 °C for 9 days, slow growing, reaching 45 mm in diameter, white at first, gradually becoming Pale Salmon Color to Seashell Pink, granulate, flat, velvety. *Hyphae* branched, aseptate when juvenile, septate with age, sometimes with swellings, 1.0–4.5 µm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from aerial or substrate hyphae, erect, sometimes bent, mainly unbranched and simple branched or sympodial, hyaline, with a septum below sporangium. *Sporangia* globose, pink, smooth, multi-spored, 10.0–16.5 µm in diameter, walls deliquescent. *Apophyses* absent. *Collars* absent or present. *Columellae* subglobose to globose, smooth, 3.0–8.0 µm long and 3.5–10.0 µm wide. *Sporangiospores* ellipsoid, ovoid, 2.0–4.0 µm long and 1.5–2.5 µm wide. *Chlamydospores* globose, 30.0–53.5 µm in diameter. *Zygospores* absent.

*Material examined*: China, Beijing, from soil sample, 10 October 2013, Xiao-Yong Liu (holotype HMAS 351559, living ex-holotype culture CGMCC 3.16157).

GenBank accession number: OL678224.

*Notes*: *Umbelopsis chlamydospora* is closely related to *U. heterosporus* C.A. de Souza *et al.* based on phylogenetic analysis of ITS rDNA sequences (Fig. 16). However, morphologically *U. heterosporus* differs from *U. chlamydospora* by a faster growth rate (75 mm in diameter for 7 days vs. 45 mm in diameter for 9 days) and variable shape and size of sporangiospores, including ellipsoid 4.5–9  $\mu$ m long and 1.5–4  $\mu$ m wide, cylindrical 4.5–8  $\mu$ m long and 2.5–4  $\mu$ m wide, reniform, 3.5–7.5  $\mu$ m long and 2.5–4  $\mu$ m wide, angular, 2.5–6  $\mu$ m in diameter, and irregular, 5–11  $\mu$ m long and 3.5–5  $\mu$ m wide (Yuan *et al.* 2020).

71. Umbelopsis crustacea H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 87.

Fungal Names: FN570948.

*Etymology: crustacea* (Lat.) refers to the species having a crusty texture to the colonies. *Holotype*: HMAS 351560.

*Colonies* on PDA at 27°C for 12 days, slow growing, reaching 35 mm in diameter, less than 0.10 mm high, broadly lobed and concentrically zonate, irregular at margin, white at first, gradually becoming La France Pink to Peach Red, granulate, crusty. *Hyphae* simple branched, always swollen, aseptate when juvenile, frequently septate with age, 2.5–10.0 µm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from substrate or aerial mycelia, erect, unbranched,

simple branched or sympodial, hyaline, sometimes with one septum to several septa below sporangiophores, or aseptate. *Sporangia* globose, hyaline when young, red when old, smooth, multi-spored, 8.0–15.0 µm in diameter, walls deliquescent. *Apophyses* absent. *Collars* present or absent, distinct if present. *Columellae* hemispherical or degenerated, hyaline, subhyaline or pigmented, 1.5–2.5 µm long and 2.5–6.5 µm wide. *Sporangiospores* angular or irregular, subhyaline or hyaline, 2.0–5.0 µm long and 2.0–3.5 µm wide. *Chlamydospores* absent. *Zygospores* unknown.

*Materials examined*: China. Inner Mongolia Auto Region, Arxan, 119°41'16"E, 47°18'26"N, from soil sample, 29 January 2018, Yu-Chuan Bai (holotype HMAS 351560, living ex-holotype culture CGMCC 3.16158); Zhalantun,120°56'52"E, 47°32'23"N, from soil sample, 29 January 2018, Yu-Chuan Bai (living culture XY03542). Heilongjiang Province, Yichun, 129°23'58"E, 48°48'21"N, form soil sample, 28 March 2018, Yu-Chuan Bai (culture XY03944).

GenBank accession numbers: OL678225, OL678226 and OL678227.

*Notes: Umbelopsis crustacea* is closely related to *U. autotrophica* (E.H. Evans) W. Gams based on phylogenetic analysis of ITS rDNA sequences (Fig. 16). However, morphologically *U. autotrophica* differs from *U. crustacea* by globose sporangiospores (Evans 1971, Meyer & Gams 2003).

72. Umbelopsis globospora H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 88.

Fungal Names: FN570949.

*Etymology: globospora* (Lat.) refers to the species having globose sporangiospores. *Holotype*: HMAS 351561.

*Colonies* on PDA at 27°C for 12 days, slow growing, reaching 90 mm in diameter, less than 5 mm high, zonate, white at first, gradually becoming Mouse Gray, granulate, flat, velvety, regular at margin, forming sectors because of the whitish hyphae upon old sporulation layer. *Hyphae* branched, 1.5–5.0 µm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from substrate mycelia, erect, sometimes bent, simple branched several times, hyaline, sometimes with one septum on branches of sporangiophores, swollen at the basal part, slightly constricted. *Sporangia* globose, smooth, hyaline when young, pigmented when old, smooth, multi-spored, 8.0–13.0 µm in diameter, walls deliquescent. *Apophyses* absent. *Collars* absent. *Columellae* degenerated. *Sporangiospores* mostly globose, occasionally subglobose, subhyaline or hyaline, 1.5–2.5 µm in diameter. *Chlamydospores* absent. *Zygospores* unknown.

*Material examined*: China, Zhejiang Province, Quzhou, Gutian Mountain Nature Reserve, from soil sample, 10 October 2020, Heng Zhao (holotype HMAS 351561, living ex-holotype culture CGMCC 3.16159).

GenBank accession number: OL678228.

Notes: See notes of Umbelopsis brunnea.

73. Umbelopsis gutianensis H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 89.

Fungal Names: FN570950.

*Etymology: gutianensis* (Lat.) refers to the Gutian Mountain Nature Reserve, Zhejiang Province, China, where the type was collected.

Holotype: HMAS 351562.

*Colonies* on PDA at 27°C for 12 days, slow growing, reaching 40 mm in diameter, broadly lobed and concentrically zonate, irregular at margin, white at first, afterwards becoming Brazil Red at the edge, velvety. *Hyphae* simple branched, aseptate when juvenile, septate with age, 2.5–6.5 μm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from substrate mycelia, erect or bent, unbranched or simple branched, hyaline, always swollen on branches. *Sporangia* globose, hyaline when young, red when old, smooth, multi-spored, 8.0–12.5 μm in diameter, walls deliquescent. *Apophyses* absent. *Collars* absent. *Columellae* degenerated. *Sporangiospores* angular, subhyaline or hyaline, 3.0–4.0 μm long and 2.0–3.0 μm wide. *Chlamydospores* absent. *Zygospores* unknown.

*Materials examined*: China, Zhejiang Province, Quzhou, Gutian Mountain Nature Reserve, from soil sample, 16 March 2021, Heng Zhao (holotype HMAS 351562, living ex-holotype culture CGMCC 3.16160, and living culture XY06604, XY06605).

GenBank accession numbers: OL678229, OL678230 and OL678231.

*Notes: Umbelopsis gutianensis* is closely related to *U. changbaiensis* Y.N. Wang *et al.* based on phylogenetic analysis of ITS rDNA sequences (Fig. 16). However, morphologically *U. changbaiensis* differs from *U. gutianensis* by depressed globose columellae, and by bearing collars (Wang *et al.* 2014).

74. Umbelopsis oblongispora H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 90. Fungal Names: FN570951.

Etymology: oblongispora (Lat.) refers to the species having oblong sporangiospores.

## Holotype: HMAS 351563.

*Colonies* on PDA at 25 °C for 9 days, slow growing, reaching 45 mm in diameter, white at first, gradually becoming Pale Salmon Color to Seashell Pink, granulate, flat, velvety. *Hyphae* branched, aseptate when juvenile, septate with age, sometimes with swellings, 1.0–4.5 µm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from aerial or substrate hyphae, erect, sometimes bent, mainly unbranched and simple branched or sympodial, hyaline, with a septum below sporangium. *Sporangia* globose, pink, smooth, multi-spored, 10.0–16.5 µm in diameter, walls deliquescent. *Apophyses* absent. *Collars* absent or present. *Columellae* subglobose to globose, smooth, 3.0–8.0 µm long and 3.5–10.0 µm wide. *Sporangiospores* variable, oblong, ellipsoid, cylindrical, reniform, ovoid, or irregular, 2.0–4.0 µm long and 1.5–2.5 µm wide. *Chlamydospores* globose, 30.0–53.5 µm in diameter. *Zygospores* absent.

*Material examined*: China, Zhejiang Province, Quzhou, Gutian Mountain Nature Reserve, from soil sample, 16 March 2021, Heng Zhao (holotype HMAS 351563, living ex-holotype culture CGMCC 3.16161).

GenBank accession number: OL678232.

*Notes: Umbelopsis oblongispora* is closely related to *U. gibberispora* M. Sugiy. *et al.* based on phylogenetic analysis of ITS rDNA sequences (Fig. 16). However, morphologically *U. gibberispora* differs from *U. oblongispora* by two types of chlamydospores: subglobose to globose macrochlamydospores, and variably shaped microchlamydospores (Sugiyama *et al.* 2003).

75. Umbelopsis septata H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 91.

Fungal Names: FN570952.

*Etymology: septata* (Lat.) refers to the species having hyphae with abundant septa with age. *Holotype:* HMAS 351564.

*Colonies* on PDA at 27°C for 12 days, slow growing, reaching 70 mm in diameter, less than 5 mm high, white at first, gradually becoming Smoke Gray, granulate, velvety, broadly lobed and concentrically zonate, irregular at margin, forming sectors because of the whitish hyphae upon old sporulation layer. *Hyphae* branched, sometimes swollen, aseptate when juvenile, frequently septate with age, 1.5–8.0 µm in diameter. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from substrate or aerial mycelia, erect, sometimes bent, hyaline, simple branched or unbranched, sometimes with a septum on branches of sporangiophores. *Sporangia* globose, hyaline when young,

Light Brown when old, smooth, multi-spored, 11.5–16.5 µm in diameter, walls deliquescent. *Collars* absent. *Apophyses* absent. *Columellae* degenerated. *Sporangiospores* globose to subglobose, subhyaline or hyaline, 2.0–3.0 µm long and 1.5–3.0 µm. *Chlamydospores* absent. *Zygospores* unknown.

*Material examined*: China, Zhejiang Province, Quzhou, Gutian Mountain Nature Reserve, from soil sample, 16 March 2021, Heng Zhao (holotype HMAS 351564, living ex-holotype culture CGMCC 3.16162).

GenBank accession number: OL678233.

*Notes: Umbelopsis septata* is closely related to *U. globospora* H. Zhao *et al.* based on phylogenetic analysis of ITS rDNA sequences (Fig. 16). However, morphologically *U. globospora* differs from *U. septata* by a faster growth rate at the same condition (90 mm in diameter vs. 70 mm in diameter), and simple or several-time branched sporangiophores.

76. Umbelopsis tibetica H. Zhao, Y.C. Dai & X.Y. Liu, sp. nov., Fig. 92.

Fungal Names: FN570953.

*Etymology: tibetica* (Lat.) refers to the Tibet Auto Region, China, where the type was collected.

Holotype: HMAS 351565.

*Colonies* on PDA at 27 °C for 12 days, slow growing, reaching 45 mm in diameter, thin pancake-like, concentrically zoned, regular at margin, white at first, gradually becoming light red. *Hyphae* abundant, simple branched, aseptate when juvenile, septate with age,  $1.5-7.5 \mu m$  in diameter, swollen and containing droplets in substrate hyphae. *Rhizoids* absent. *Stolons* absent. *Sporangiophores* arising from substrate hyphae, erect, simple branched, hyaline, always swollen on branches. *Sporangia* globose, hyaline when young, brown when old, smooth, multi-spored, with one septum to several septa below sporangium,  $13.0-18.5 \mu m$  in diameter, walls deliquescent. *Apophyses* absent. *Collars* present, distinct. *Columellae* subglobose to ovoid, hyaline, smooth, 4.0-7.0 µm long and 5.5–9.0 µm wide. *Sporangiospores* always ovoid to globose, rarely irregular, subhyaline or hyaline,  $2.0-3.0 \mu m$  long and  $1.5-2.5 \mu m$  wide. *Chlamydospores* in substrate hyphae, hyaline, abundant, irregular when young, globose when old,  $26.5-47.5 \mu m$  in diameter. *Zygospores* unknow. *Materials examined*: China, Tibet Auto Region, Linzhi, Bome County, from soil sample, 28 August 2021, Heng Zhao (holotype HMAS 35156, living ex-holotype culture CGMCC 3.16163, and living culture XY07881 and XY07882).

GenBank accession numbers: OL678234, OL678235 and OL678236.

*Notes*: *Umbelopsis tibetica* is closely related to *U. wigerinckiae* Sand.-Den. based on phylogenetic analysis of ITS rDNA sequences (Fig. 16). However, morphologically *U. wigerinckiae* differs from *U. tibetica* by umbellately branched sporangiospores, pink, coral to red sporangia, and smaller chlamydospores (5–10 µm in diameter vs. 26.5–47.5 µm in diameter; Crous *et al.* 2017).

## Species new to China

Along with these new species and new combinations above, we found the following 43 species belonging to Mucoromyceta for the first time in China (Table 1).

 Absidia caerulea Bainier [as 'cærulea'], Bull. Soc. Bot. Fr. 36: 184, 1889 Materials examined: China, Guangdong Province, Guangzhou, South China Agricultural University, from flower sample, 1 October 2013, Xiao-Yong Liu (living cultures XY00608 and XY00729).

GenBank accession numbers: OL620081 and OL620082.

 Absidia koreana Hyang B. Lee, Hye W. Lee & T.T. Nguyen, in Ariyawansa et al., Fungal Diversity 75: 248, 2015

Materials examined: China. Fujian Province, Kulangsu, from soil sample, 1 October 2013,

Xiao-Yong Liu (living culture XY00816). Hubei Province, Shennongjia National Nature Reserve,

from soil sample, 1 October 2013, Xiao-Yong Liu (living culture XY00596).

GenBank accession numbers: OL620083 and OL620084.

 Absidia pararepens Jurjević, M. Kolařík & Hubka, in Crous et al., Persoonia 44: 351, 2020 Materials examined: China. Beijing, from soil sample, 1 October 2013, Xiao-Yong Liu (living cultures XY00631 and XY00615). Tibet Auto Region, Naqu, from soil sample, 16 Nov 2020, Heng Zhao (Living culture XY05899).

GenBank accession numbers: OL620085, OL620086 and OL620087.

 Actinomortierella ambigua (B.S. Mehrotra) Vandepol & Bonito, in Vandepol et al., Fungal Diversity, 2020

Material examined: China, Yunnan Province, Dehong, 98°40'3"E, 24°32'38"N, from soil

sample, 28 May 2021, Heng Zhao (living culture XY06923).

GenBank accession number: OL620101.

 Backusella dispersa (Hagem) Urquhart & Douch, in Urquhart et al., Persoonia 46: 16, 2020 Material examined: China, Xinjiang Auto Region, Ili, 43°47'4"N, 81°51'55"E, from soil

sample, 28 October 2021, Heng Zhao (living culture XY08806).

GenBank accession number: OL620088.

 Backusella locustae Hyang B. Lee, S.H. Lee & T.T.T. Nguyen, in Wanasinghe et al., Fungal Diversity 89: 213, 2018

Material examined: China, Hunan Province, Changsha, 28°8'4"N, 112°57'19"E, from soil

sample, 28 August 2021, Heng Zhao (living culture XY07940).

GenBank accession number: OL620089.

 Backusella oblongielliptica (H. Nagan., Hirahara & Seshita ex Pidopl. & Milko) Walther & de Hoog, Persoonia 30: 41, 2013

Materials examined: China. Yunnan Province, Dali, from soil sample, 28 October 2021, Heng

Zhao (living culture XY08152). Zhejiang Province, Quzhou, Gutian Mountain Nature Reserve,

from soil sample, 27 October 2021, Heng Zhao (living cultures XY08767 and XY08768).

GenBank accession numbers: OL620090, OL620091 and OL620092.

- Backusella tuberculispora (Schipper) Walther & de Hoog, Persoonia 30: 41, 2013
   Materials examined: China, Yunnan Province, Lincang, Cangyuan County, from soil sample,
- 22 July 2021, Heng Zhao (living cultures XY07548 and XY7557). GenBank accession numbers: OL620093 and OL620094
- Cunninghamella antarctica Caretta & Piont., Sabouraudia 15(1): 6, 1977
   Materials examined: China. Anhui Province, Chuzhou, Quanjiao Country, 32°0'25"N,

117°55'8"E, from soil sample, 28 May 2021, Heng Zhao (living culture XY07003). Gansu

Province, Lanzhou, from soil sample, 31 May 2021, Heng Zhao (living culture XY07050).

*GenBank accession numbers*: OL620095 and OL620096.

 Dissophora globulifera (O. Rostr.) Vandepol & Bonito, in Vandepol et al., Fungal Diversity, 104: 279, 2020

Material examined: China, Xinjiang Auto Region, Ili, Zhaosu County, 43°13'58"N,

- 81°10'45"E, from soil sample, 30 October 2021, Heng Zhao (living culture XY08870).*GenBank accession number*: OL620097.
- Gongronella namwonensis Hyang B. Lee, A.L. Santiago & H.J. Lim, in Crous et al., Persoonia
   44: 395, 2020

Material examined: China, Zhejiang Province, Hangzhou, from soil sample, 14 August 2021,

Heng Zhao (living culture XY08131).

GenBank accession number: OL620098.

12. *Isomucor trufemiae* J.I. Souza, Pires-Zottar. & Harakava, in Souza *et al.*, *Mycologia* 104(1): 236, 2012

Materials examined: China, Yunnan Province, Lincang, Cangyuan Country, from soil sample,

- 22 July 2021, Heng Zhao (living cultures XY07543 and XY7554). GenBank accession numbers: OL620099 and OL620100.
- Mortierella bainieri Costantin, Bull. Soc. Mycol. Fr. 4(3): 152, 1889 [1888]
   Material examined: China, Yunnan Province, Diqing, Pudacuo National Park, 27°49'40"N,
- 99°57'45"E, from soil sample, 28 October 2021, Heng Zhao (living culture XY08661).

GenBank accession number: OL620102.

- Mortierella beljakovae Milko, Nov. sist. Niz. Rast. 10: 83, 1973
   Material examined: China, Heilongjiang Province, Mohe Country, 122°28'47"E, 52°19'16"N,
- from plant debris sample, 27 January 2018, Peng-Cheng Deng (living culture XY03433). GenBank accession number: OL620103.
- Mortierella chlamydospora (Chesters) Plaäts-Nit., in Plaäts-Niterink et al., Persoonia 9(1): 91, 1976

*Materials examined*: China. Zhejiang Province, Wenzhou, Nanyandang Mountain, from soil sample, 22 July 2021, Jia-Jia Chen (living culture XY07448). Guangxi Auto Region, Guigang, from soil sample, 14 August 2021, Heng Zhao (living culture XY08109).

- GenBank accession numbers: OL620104 and OL620105.
- 16. Mortierella cystojenkinii W. Gams & Veenb.-Rijks, Persoonia 9(1): 137, 1976

bioRxiv preprint doi: https://doi.org/10.1101/2022.07.05.498902; this version posted July 9, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

Materials examined: China. Heilongjiang Province, Huma Country, 122°48'58"E, 52°4'23"N,

from plant debris sample, 6 February 2018, Peng-Cheng Deng (living cultures XY03876 and

XY03882). Inner Mongolia Auto Region, Zhalantun, 121°39'26"E, 47°37'45"N, from soil sample,

27 March 2018, Yu-Chuan Bai (living culture XY03898).

GenBank accession numbers: OL620106, OL620107 and OL620108.

17. Mortierella epicladia W. Gams & Emden, Persoonia 9(1): 133, 1976
 Materials examined: China, Yunnan Province, Dehong, Mangshi, 98°40'3"E, 24°32'38"N,

from soil sample, 28 May 2021, Heng Zhao (living cultures XY06924 and XY06927). *GenBank accession numbers*: OL620109 and OL620110.

 Mortierella fluviae Hyang B. Lee, K. Voigt & T.T.T. Nguyen, in Hyde et al., Fungal Diversity 80: 255, 2016

*Material examined*: China, Heilongjiang Province, Heihe, 127°6'54"E, 48°4'37"N, from soil sample, 4 April 2018, Ze Liu (living culture XY04370).

GenBank accession number: OL620111.

 Mortierella lignicola (G.W. Martin) W. Gams & R. Moreau, Annls Sci. Univ. Besançon, Sér. 2, Méd. Pharm. 3: 103, 1960

Material examined: China, Yunnan Province, Chuxiong, 25°18'53"N, 101°25'17"E, from soil

sample, 28 September 2021, Heng Zhao (living culture XY08224).

GenBank accession number: OL620112

20. Mortierella longigemmata Linnem., Mucorales (Lehre): 199, 1969

Materials examined: China, Yunnan Province. Diqing, Pudacuo National Park, 27°49'40"N,

99°57'45"E, from soil sample, 19 October 2021, Heng Zhao (living cultures XY08599 and

XY08601). Yuxi, Ailao Mountain, from soil sample, 25 July 2021, Heng Zhao (living culture XY07567).

GenBank accession numbers: OL620113, OL620114 and OL620115.

21. Mortierella nantahalensis C.Y. Chien, Mycologia 63(4): 826, 1971

Materials examined: China. Guangxi Auto Region, Fangchenggang, 21°44'46"N, 108°5'13"E,

from soil sample, 22 July 2021, Heng Zhao (living culture XY07486), Hainan Province, Limu

Mountain, from soil sample, 30 December 2021, Jia-Jia Chen (living culture XY06017).

GenBank accession numbers: OL620116 and OL620117.
Mortierella rishikesha B.S. Mehrotra & B.R. Mehrotra, Zentbl. Bakt. ParasitKde, Abt. II 118: 184, 1964 [1963]

Material examined: China, Beijing, 39°45'49"N, 115°36'34"E, from soil sample, 9 July 2021,

Heng Zhao (living culture XY07315).

GenBank accession number: OL620118.

- Mortierella schmuckeri Linnem., Arch. Mikrobiol. 30: 263, 1958
   Materials examined: China, Beijing, 39°52'11"N, 115°59'46"E, from soil sample, 12 July
- 2021, Heng Zhao (living culture XY07412); 40°27'37"N, 117°1'14"E, from soil sample, 13 July
- 2021, Heng Zhao (living culture XY07419).

GenBank accession numbers: OL620119 and OL620120.

24. Mortierella sclerotiella Milko, Nov. sist. Niz. Rast.4: 160, 1967

Material examined: China, Inner Mongolia Auto Region, Arxan, 119°41'16"E, 47°18'28"N,

from soil sample, 29 January 2018, Yu-Chuan Bai (living culture XY03528). GenBank accession number: OL620121.

- Mortierella turficola Y. Ling, Rev. gén. Bot. 42: 743, 1930
   Material examined: China, Heilongjiang Province, Mohe Country, 122°28'47"E, 52°19'16"N,
- from plant debris sample, 21 January 2018, Peng-Cheng Deng (living culture XY03346). GenBank accession number: OL620122.
- Mucor aligarensis B.S. Mehrotra & B.R. Mehrotra, Sydowia 23(1–6): 183, 1970 [1969]
   Material examined: China, Yunnan Province, Yuxi, Ailao Mountain, from soil sample, 25 July
- 2021, Heng Zhao (living culture XY07583). GenBank accession number: OL620123.
- Mucor atramentarius L. Wagner & G. Walther, in Wagner et al., Persoonia 44: 87, 2019
   Material examined: China, Tibet Auto Region, Ngari, Coqen County, from soil sample, 28
- May 2021, Heng Zhao (living culture XY06751). GenBank accession number: OL620124.
- Mucor bainieri B.S. Mehrotra & Baijal, Aliso 5(3): 237, 1963
   Material examined: China, Yunnan Province, Dali, 26°24'45"N, 99°53'41"E, from soil sample,
- 28 October 2021, Heng Zhao (living culture XY08747).

GenBank accession number: OL620125.

29. Mucor fuscus (Berk. & M.A. Curtis) Berl. & De Toni, in Berlese et al., Syll. Fung. (Abellini)7(1): 204, 1888

Materials examined: China, Tibet Auto Region, Lhasa, Damxung County, from soil sample, 28

- May 2021, Heng Zhao (living cultures XY06718 and XY06719). GenBank accession numbers: OL620126 and OL620127.
- Mucor fluvii Hyang B. Lee, S.H. Lee & T.T.T. Nguyen, [as 'fluvius'], in Wanasinghe et al., Fungal Diversity 89: 220, 2018

Materials examined: China, Zhejiang Province, Wenzhou, Nanyandang Mountain, from soil

sample, 22 July 2021, Jia-Jia Chen (living cultures XY07446 and XY07447).

GenBank accession numbers: OL620128 and OL620129.

 Mucor griseocyanus Hagem, Skr. VidenskSelsk. Christiania, Kl. I, Math.-Natur.(no. 7): 28, 1908

Materials examined: China, Tibet Auto Region, Linzhi, Gongbujiangda County, from soil

sample, 28 May 2021, Heng Zhao (living cultures XY06685 and XY06697).

GenBank accession numbers: OL620130 and OL620131.

32. Mucor lusitanicus Bruderl., Bull. Soc. Bot. Genève, 2 sér. 8: 276, 1916

Materials examined: China. Beijing, 39°47'49"N, 115°34'1"E, from dung sample, 6 July 2021,

Heng Zhao (living cultures XY07298 and XY07299). Shandong Province, Dongying, 37°45'23"N,

118°29'22"E, from soil sample, 30 December 2020, Heng Zhao (living cultures XY06042 and

XY06074).

GenBank accession numbers: OL620132, OL620133, OL620134 and OL620135.

Mucor minutus (Baijal & B.S. Mehrotra) Schipper, Stud. Mycol. 10: 24, 1975
 Materials examined: China. Hubei Province, Tianmenshan, form soil sample, 22 July 2021,

Heng Zhao (living culture XY07460). Yunnan Province, Dehong, Mangshi, 98°40'3"E,

24°32'38"N, from soil sample, 28 May 2021, Heng Zhao (living cultures XY06939 and XY06940). *GenBank accession numbers*: OL620136, OL620137 and OL620138.

34. Mucor mucedo Fresen., Beitr. Mycol. 1: 7, 1850

*Materials examined*: China, Beijing, 39°46'39"N, 115°28'57"E, from soil sample, 6 July 2021, Heng Zhao (living cultures XY07301 and XY07302).

GenBank accession numbers: OL620139 and OL620140.

35. Mucor nanus Schipper & Samson, Mycotaxon 50: 477, 1994

Materials examined: China. Beijing, 39°30'19"N, 115°58'28"E, from soil sample, 6 July 2021,

Heng Zhao (living culture XY07221). Hubei Province, Shiyan, Danjiangkou, 39°46'39"N,

- 111°8'16"E, from soil sample, 31 May 2021, Heng Zhao (living culture XY07037). *GenBank accession numbers*: OL620141 and OL620142.
- 36. Mucor nidicola A.A Madden, Stchigel, Guarro, Deanna A. Sutton & Starks, Int. J. Syst. Evol. Microbiol. 62(7): 1712, 2012

Material examined: China, Yunnan Province, Dali, 25°42'6"N, 100°9'19"E, from soil sample,

28 October 2021, Heng Zhao (living culture XY08161).

GenBank accession number: OL620143.

 Mucor pseudocircinelloides L. Wagner & G. Walther, in Wagner et al., Persoonia 44: 91, 2019 Materials examined: China, Shanxi Province, Shuozhou, Youyu Country, 10°2'40"N,

112°35'7"E, from soil sample, 1 August 2021, Heng Zhao (living cultures XY07713 and

XY07714).

GenBank accession numbers: OL620144 and OL620145.

- Mucor silvaticus Hagem, Skr. VidenskSelsk. Christiania, Kl. I, Math.-Natur. (no. 7): 31, 1908
   Materials examined: China, Inner Mongolia Auto Region, Hulun Buir, Genhe County,
- 122°15'48''E, 52°8'22''N, from plant debris sample, 4 April 2018, Peng-Cheng Deng (living cultures XY04328 and XY04329).

GenBank accession numbers: OL620146 and OL620147.

 Mucor stercorarius Hyang B. Lee, P.M. Kirk & T.T.T. Nguyen, in Tibpromma et al., Fungal Diversity 83: 110, 2017

Material examined: China, Anhui Province, Hefei, Lu'an, 116°0'28"E, 31°45'27"N, from soil

sample, 28 May 2021, Heng Zhao (living culture XY07007).

GenBank accession number: OL620148.

- 40. Mucor variicolumellatus L. Wagner & G. Walther, in Wagner et al., Persoonia 44: 92, 2019
   Materials examined: China, Beijing, 40°29'46"N, 117°4'5"E, from rotten tree sample, 6 July
- 2021, Heng Zhao (living cultures XY07369 and XY07370). *GenBank accession numbers*: OL620149 and OL620150.
- 41. Umbelopsis gibberispora M. Sugiy., Tokum. & W. Gams, Mycoscience 44(3): 220, 2003

Material examined: China, Zhejiang Province, Quzhou, Gutian Mountain Nature Reserve,

from soil sample, 28 May 2021, Heng Zhao (living culture XY06667).

GenBank accession number: OL620151.

42. Umbelopsis ovata (H.Y. Yip) H.Y. Yip, Trans. Br. Mycol. Soc. 86(2): 334, 1986 Materials examined: China, Heilongjiang Province, Muhe Country, 122°38'47"E, 52°40'1"N, from plant debris sample, 17 April 2018, Peng-Cheng Deng (living cultures XY03175 and XY03176).

GenBank accession numbers: OL620152 and OL620153.

 Umbelopsis sinsidoensis Hyang B. Lee & T.T.T. Nguyen, in Wanasinghe et al., Fungal Diversity 89: 223, 2018

*Material examined*: China, Zhejiang Province, Quzhou, Gutian Mountain Nature Reserve, from soil sample, 25 January 2021, Heng Zhao (living culture XY06194).

GenBank accession number: OL620154

### Discussion

Since Hibbett *et al.* (2007) abolished the phylum Zygomycota, the phylogeny of early diverging fungi has been undergoing drastic changes. Spatafora *et al.* (2016) proposed a phylum-level framework based on genomic data, accepting two phyla and six subordinate subphyla, Mucoromycota (Glomeromycotina, Mortierellomycotina and Mucoromycotina) and Zoopagomycota (Entomophthoromycotina, Kickxellomycatina and Zoopagomycotina). Depending on the phylogeny of 18S and 28S rDNA sequences, these phyla and subphyla were raised to subkingdoms (Mucoromyceta, Zoopagomyceta) and phyla (Entomophthoromycota, Glomeromycota, Kickxellomycota, Mucoromycota and Zoopagomycota), respectively, along with a novel phylum Calcarisporiellomycota being erected (Tedersoo *et al.* 2018). In this paper, we sharpened our focus on the subkingdom Mucoromyceta, and looked further into its inner relationship by a time-scaled phylogenetic tree in concert with the monophyly concept. The results suggest that the divergence time of phyla in Mucoromyceta is earlier than 639 Mya, falling in the time interval revealed in other studies (Table 4; Gueidan *et al.* 2011, Chang *et al.* 

2015, Tedersoo *et al.* 2018). Consequently, two new phyla are proposed (Fig. 2, 3, 4), namely Umbelopsidomycota and Endogonomycota. The former morphologically differs from Mucoromycota and Mortierellomycota by degenerated aerial hyphae and a large quantity of substrate-borne sporangiophores which produce a thin layer of colonies, and by abundant pigmented sporangia which cause reddish or ochraceous colonies, as well as a frequently occurring sectoring due to a possible genetic instability (Meyer & Gams 2003, Wang *et al.* 2013, 2014, 2015). Besides, it is physiologically different from its allied phylum Mortierellomycota by the inability to synthesize arachidonic acid (Zhao *et al.* 2021a). The later phylum Endogonomycota differs from all other phyla in the subkingdom Mucoromyceta by forming ectomycorrhizae with plants, by producing sexual spores (zygospores) in sporocarps rather than zygosporangia, and by producing asexual chlamydospores but not sporangiospores (Yao *et al.* 1996, Desirò *et al.* 2017, Yamamoto *et al.* 2020).

Some secondary ranks were validly introduced in the subkingdom Mucoromyceta, including subphyla, viz., Glomeromycotina, Mucoromycotina, Kickxellomycotina, Mortierellomycotina and Calcarisporiellomycotina (Hibbett *et al.* 2007, Hoffmann *et al.* 2011, Spatafora *et al.* 2016, Tedersoo *et al.* 2018), and subfamilies, viz., Absidioideae, Chaetocladioideae, Choanephoroideae, Cokeromycetoideae, Cunninghamelloideae, Dichotomocladioideae, Dicranophoroideae, Gilbertelloideae, Lichtheimioideae, Mycotyphoideae, Rhizomucoroideae, Kirkomycetoideae, Mucoroideae and Thamnidioideae (Voigt & Kirk 2015). In this taxonomic hierarchy of six phyla of the subkingdom Mucoromyceta, viz., Calcarisporiellomycota, Endogonomycota, Glomeromycota, Mortierellomycota, Mucoromycota and Umbelopsidomycota, we followed the principal ranks of taxa, without dealing with any secondary ranks.

In basal fungi, studies of divergence times have focused mainly on ranks above class (Chang *et al.* 2015, Tedersoo *et al.* 2018). For the first time, taking the subkingdom Mucoromyceta as a case, we established a minimum age range of earlier than 639 Mya, earlier than 585 Mya, 651–400 Mya and 570–107 Mya, for phyla, classes, orders, and families, respectively (Fig. 4, Table 4 and 5). The results suggest that Mucoromyceta contains six phyla (two new phyla, Endogonomycota and Umbelopsidomycota), eight classes, 15 orders (five orders, Claroideoglomerales, Cunninghamellales, Lentamycetales, Phycomycetales and Syncephalastrales), 41 families (six new families, Circinellaceae, Gongronellaceae, Protomycocladaceae, Rhizomucoraceae, Syzygitaceae

113

and Thermomucoraceae) and 121 genera. In details, 1) Calcarisporiellomycota comprises one class, one order, one family and two genera; 2) Endogonomycota includes one class, one order, two families and seven genera; 3) Glomeromycota diverges into three classes, six orders, 16 families and 41 genera; 4) Mortierellomycota accommodates one class, one family and 14 genera; 5) Mucoromycota contains one classes, five orders, 19 families and 55 genera, including five new orders, six new families and one revived family; 6) Umbelopsidomycota consists of one class, one order, two families and two genera. In addition, most families of Mucoromycota, such as Backusellaceae, Lentamycetaceae, Phycomycetaceae, Pilobolaceae, Radiomycetaceae, Rhizopodaceae and Saksenaeaceae were phylogenetically and morphologically well-supported, by other authors (von Arx 1982, Benny *et al.* 2001, O'Donnell *et al.* 2001, Voigt & Wöstemeyer 2001, Hoffmann *et al.* 2013). This updated classification is vigorously supported by molecular dating analyses, except for the Choanephoraceae and Mycotyphaceae which are yet unique in traditional morphological characteristics (Benny *et al.* 1985, Benny 1991, Hoffmann *et al.* 2013).

In this study, we accepted the Glomeromycota as the phylum rank (Schüßler *et al.* 2001, Tedersoo *et al.* 2018), rather than the subphylum erected by Spatafora *et al.* (2016). And Glomeromycota divided into three classes, five orders and 14 families by Oehl *et al.* (2011a, b, c). In this study, the phylogenetic analyses and divergence time analyses suggest that its class, order and family ranks are well supported, while the family Claroideoglomeraceae is raised up to a newly order Claroideoglomerales in the Glomeromycetes. Moreover, the divergence time of higher taxa of Glomeromycota provided in our study (Fig. 4 and Table 4), class rank: mean stem divergence time earlier than 585 Ma, order rank: mean stem divergence time earlier than 400 Ma and family rank: mean stem divergence time during 107–539 Ma.

In the past decades, a great step has been made for the phylogenetic relationship within Mucorales and Mortierellales based on morphology, multi-loci and genomic phylogeny (Gams 1976, 1977, Zheng *et al.* 2007, Hoffmann *et al.* 2009a, 2013, Wagner *et al.* 2013, Walther *et al.* 2013, Vandepol *et al.* 2020). However, the results of the MCC tree (Fig. 4) suggest the genus *Mucor* is polyphyletic. For instance, *Mucor abundans*, *M. azygosporus*, *M. indicus*, *M. luteus*, *M. mucedo* and *M. silvaticus* are located in different clades, causing difficulties in defining the boundaries of the genus. This implies that it is necessary to resolve the polyphyletic genus into different genera including new monophyletic genera (Wanger *et al.* 2013). A perfect example was

114

to re-circumscribe the genera of *Absidia*, *Lentamyces* and *Lichtheimia* based on a combination of physiological, phylogenetic and morphological characters (Hoffmann *et al.* 2007, Hoffmann and Voigt 2009, Hoffmann 2010). Another example is that of Vandepol *et al.* (2020), where 14 genera were accepted in Mortierellaceae by multiple genes recalled from genomics with some new genera being established to resolve the polyphyly. Although the ITS rDNA was recommended as the fungal DNA barcode (Schoch *et al.* 2012, Nilsson *et al.* 2014), it evolved too fast (White *et al.* 1990) to be aligned across families and higher taxa. Therefore, we strongly suggest that multiple markers, i.e., physiological, phylogenetic, phylogenomic, morphological data and divergence time, should be considered comprehensively as much as possible when dealing with taxa at the generic level for basal or early diverging fungi.

Other eight genera with an uncertain taxonomic position in the Catalogue of Life or Index Fungorum are classified into definite families in this study. In detail, *Ambomucor* is assigned to the family Mucoraceae, *Densospora* is assigned to the family Densosporaceae, *Echinochlamydosporium* is assigned to the family Calcarisporiellaceae, *Intraornatospora* and *Paradentiscutata* are assigned to the family Gigasporaceae, *Modicella* is assigned to the family Mortierellaceae, and a new family Syzygitaceae was proposed to accommodate the genera *Sporodiniella* and *Syzygites*.

Currently, it is a common requirement to delineate fungal species using genealogical concordance and phylogenetic species recognition (GCPSR; Taylor *et al.* 2000, Hibbett & Taylor 2013). Species in major genera such as *Absidia* (Hurdeal *et al.* 2021, Zong *et al.* 2021), *Apophysomyces* (Alvarez *et al.* 2010), *Backusella* (Urquhart *et al.* 2021, Nguyen *et al.* 2021), *Cunninghamella* (Zheng & Chen 2001) and *Rhizopus* (Zheng *et al.* 2007, Liu *et al.* 2008) were characterized by unique morphological features and molecular data, making it easy to add new species. However, early morphological studies left a number of species complexes and cryptic species, especially in the species-rich genera like *Mortierella* and *Mucor* (Petkovits *et al.* 2011, Hoffmann *et al.* 2013, Wagner *et al.* 2013, 2020). This problem hinders studies on the diversity of basal fungal species. An important progress has been made in resolving the *Mucor circinelloides* complex based on five genes, phenotypic features, mating behaviors and maximum growth temperatures (Schipper 1976, Wagner *et al.* 2020). In brief, we are looking forward to better solving

the species identification and definition in the subkingdom Mucoromyceta, providing a solid foundation for further studies.

Although studies on Chinese Mucoromyceta began relatively late, there are currently 308 species recorded (Fig. 1 and Table S1), accounting for nearly 40 % of the 792 species recorded worldwide (https://nmdc.cn/fungarium/fungi/chinadirectories, November 12, 2021). However, 46 type strains originated from China only (less than 6 %, Table 6), far less than those in the USA (126) and close to those in India (51), Brazil (46), and Germany (44). In mainland China, Prof. Zheng's team has long been devoted to the systematic study on Mucoromyceta, particularly Absidia (Zhao et al. 2021b, 2022a, b, Zong et al. 2021), Actinomucor (Zheng & Liu 2005), Ambomucor (Zheng & Liu 2014, Liu & Zheng 2015), Backusella (Zheng et al. 2013), Blakeslea (Zheng & Chen 1986), Circinella (Zheng et al. 2017), Cunninghamella (Liu et al. 2001, Zheng & Chen 2001, Zhao et al. 2021b,), Mortierella (Chen 1992a, b), Mucor (Pei 2000a, b, Zheng 2002), Pilaira (Liu et al. 2012, Zheng & Liu 2009), Pilobolus (Hu et al. 1989), Pirella (Liu 2004), Rhizomucor (Zheng et al. 2009), Rhizopus (Zheng et al. 2007, Liu et al. 2008), Syncephalastrum (Zheng et al. 1988), and Umbelopsis (Wang et al. 2013, 2014, 2015). In Taiwan of China, Prof. Ho's team also contributed a large number of species in Mucoromyceta, including Absidia (Ho et al. 2004, Hsu et al. 2009, Hsu & Ho 2010), Blakeslea (Ho & Chen 2003), Circinella (Ho 1995a), Chaetocladium (Ho et al. 2008), Gongronella (Ho & Chen 1990), Lichtheimia (Yang et al. 2012), Rhizopus (Ho 1988, 1995b, Ho & Chen 1994), and *Thamnidium* (Ho 2002). In the current study, we further explored the Mucoromyceta in China and found 73 species new to science and 43 species new to China. Our results increase the diversity of basal fungi in China and the world as well. To sum up with these taxa proposed herein, a total of six phyla, eight classes, 15 orders, 41 families, 121 genera an 868 species belonging to Mucoromyceta in the world are outlined. Specifically, six phyla, seven classes, 13 orders, 32 families, 56 genera and 426 species are recorded in China. We believe more taxa in Mucoromyceta will be described from China when sampling from different ecosystems, as has occurred in the Ascomycota and Basidiomycota (Wu et al. 2020, 2022, Zheng et al. 2020, Dai et al. 2021, Wang et al. 2021b, Liu et al. 2022).

### Acknowledgments

We thank the following scholars for their help with sampling and culture isolation: Yu-Chuan Bai and Peng-Cheng Deng (North Minzu University), Meng Zhou, Hong-Ming Zhou, Shun Liu, Xiao-Wu Man, Chang-Ge Song and Tai-Min Xu (Beijing Forestry University), Ya-Ning Wang, Jing Yang, Mao-Qiang He, Yue Zhang, Jie Li, Xiao-Ling Liu, Gui-Qing Chen, Feng-Yan Bai, Xue-Wei Wang (Prof.), Xue-Wei Wang (Ph.D. student), Xin-Yu Zhu and Long Wang (Institute of Microbiology, Chinese Academy of Chinese), Xiao Ju (Nanjing Agricultural University), Zhi-Kang Zhang (Ludong University), Ze Liu, Xiang Sun and Qi-Ming Wang (Hebei University), Zhong-Dong Yu (Northwest A&F University), Yan-Yan Long (Guangxi Academy of Agricultural Sciences), Nian-Kai Zeng (Hainan Medical University), Ze-Fen Yu and Min Qiao (Yunnan University), Pei-Wu Cui (Hunan University of Chinese Medicine), Jun-Feng Liang (Chinese Academy of Forestry), Yan-Feng Hang (Guizhou University), Wang-Qiu Deng (Guangdong Institute of Microbiology), Pu Liu, Li-Ying Ren (Jilin Agricultural University), Biao Xu (Tarim University), Rafael F. Castañeda-Ruiz (Academia de Ciencias de Cuba, Cuba), Kerstin Voigt (Friedrich Schiller University Jena, Germany), Manfred Binder (Clark University, USA), and Timothy Y. James (Michigan University, USA), Nicolas Corradi and Mathu Malar C (University of Ottawa, USA), and Francis Michel Martin (Head of Department at French National Institute for Agriculture, Food, and Environment, France).

### Author contributions

Heng Zhao is responsible for sample collection, culture isolations, identifications and descriptions, data analyses, drafting and editing the manuscript; Yu-Cheng Dai and Xiao-Yong Liu for funding acquisition, conceiving this study, and improving the manuscript.

# Data availability

All sequences have been deposited at GenBank database. All the trees have been deposited at TreeBase (Added when revised).

## **Compliance with ethical standards**

Conflict of interest: All authors declare no conflict of interest. Consent to participate: All authors agreed to participate in this research. Consent for publication: All authors read and approved submitted manuscript.

## Funding

This study was supported by the National Natural Science Foundation of China (Grant Nos. 31970009 and 32170012), the Second Tibetan Plateau Scientific Expedition and Research Program (STEP, Grant No. 2019QZKK0503), and the Third Xinjiang Scientific Expedition and Research Program (STEP, Grant No. 2021XJKK0505).

# Legends



**Fig. 1.** Trends in accumulative number of species of Mucoromyceta recorded in the world and China.

bioRxiv preprint doi: https://doi.org/10.1101/2022.07.05.498902; this version posted July 9, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.



**Fig. 2.** A Maximum Likelihood phylogenomic tree illustrating relationships within subkingdom Mucoromyceta based on 192 clusters of orthologous proteins. New taxa proposed in the present

study are in red. Maximum Likelihood bootstrap values ( $\geq$ 50%) are indicated along branches. Phyla are highlighted in different colors. A scale bar in the upper left indicates substitutions per site.

bioRxiv preprint doi: https://doi.org/10.1101/2022.07.05.498902; this version posted July 9, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.



**Fig. 3.** A Maximum Likelihood phylogenetic tree illustrating relationships within subkingdom Mucoromyceta based on ITS and LSU rDNA sequences, with *Neurospora crassa* as outgroup. New taxa proposed in the present study are in red. Maximum Likelihood bootstrap values ( $\geq$ 50%) / Bayesian Inference Posterior Probabilities ( $\geq$ 0.80) are indicated along branches. Taxa are highlighted in different colors. A scale bar in the upper left indicates substitutions per site.



-1000 -750 -500 -250 0

**Fig. 4.** Time-scaled Bayesian maximum clade credibility phylogenomic tree inferred from ITS and LSU rDNA sequences for the subkingdom Mucoromyceta, with *Neurospora crassa* as outgroup Estimated mean divergence time (Mya) and posterior probabilities (PP) > 0.8 are annotated at the internodes. The 95 % highest posterior density (HPD) interval of divergence time estimates are marked by horizontal blue bars. New taxa proposed in the present study are in red.



**Fig. 5.** Maximum Likelihood phylogenetic tree of *Absidia* based on ITS rDNA sequences, with *Cunninghamella polymorpha* as outgroup. Thirteen new species, *A. alpina*, *A. ampullacea*, *A. brunnea*, *A. chinensis*, *A. cinerea*, *A. digitula*, *A. jiangxiensis*, *A. oblongispora*, *A. purpurea*, *A. sympodialis*, *A. xinjiangensis*, *A. varians*, *A. virescens*, and two new combinations, *A. biappendiculata* and *A. nigra*, are in shade. Maximum Likelihood (ML) bootstrap values ( $\geq$ 50%) of each clade are indicated at nodes. A scale bar in the upper left indicates substitutions per site.

bioRxiv preprint doi: https://doi.org/10.1101/2022.07.05.498902; this version posted July 9, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.



**Fig. 6.** Maximum Likelihood phylogenetic tree of *Backusella* based on ITS rDNA sequences, with *Mucor indicus* as outgroup. Three new species, *B. dichotoma*, *B. moniliformis* and *B. ovalispora*, are in shade. Maximum Likelihood (ML) bootstrap values ( $\geq$ 50%) of each clade are indicated at nodes. A scale bar in the upper left indicates substitutions per site.



**Fig. 7.** Maximum Likelihood phylogenetic tree of *Circinella* based on ITS rDNA sequences, with *Thamnostylum piniforme* as outgroup. One new species, *C. homothallica*, is in shade. Maximum Likelihood (ML) bootstrap values ( $\geq$ 50%) of each clade are indicated at nodes. A scale bar in the upper left indicates substitutions per site. Double slashes indicate branch lengths shortened ten-fold to facilitate visualization.

bioRxiv preprint doi: https://doi.org/10.1101/2022.07.05.498902; this version posted July 9, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.



**Fig. 8.** Maximum Likelihood phylogenetic tree of *Cunninghamella* based on ITS rDNA sequences, with *Mucor janssenii* as outgroup. Six new species, *C. arrhiza*, *C. guttata*, *C. irregularis*, *C. regularis*, *C. subclavata*, *C. varians*, and one combination, *C. nodosa*, are in shade. Maximum Likelihood (ML) bootstrap values ( $\geq$ 50%) of each clade are indicated at nodes. A scale bar in the upper left indicates substitutions per site. Double slashes indicate branch lengths shortened five-fold to facilitate visualization.



**Fig. 9.** Maximum Likelihood phylogenetic tree of *Gamsiella* based on ITS rDNA sequences, with *Actinomortierella* as outgroup. One new species, *G. globistylospora*, is in shade. Maximum

Likelihood (ML) bootstrap values ( $\geq$ 50%) of each clade are indicated at nodes. A scale bar in the upper left indicates substitutions per site.



**Fig. 10.** Maximum Likelihood phylogenetic tree of *Gongronella* based on ITS rDNA sequences with *Absidia cylindrospora* as outgroup. Two new species, *G. chlamydospora* and *G. multispora*, are in shade. Maximum Likelihood (ML) bootstrap values ( $\geq$ 50%) of each clade are indicated at nodes. A scale bar in the upper left indicates substitutions per site. Double slashes indicate branch lengths shortened five-fold to facilitate visualization.

bioRxiv preprint doi: https://doi.org/10.1101/2022.07.05.498902; this version posted July 9, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.





bioRxiv preprint doi: https://doi.org/10.1101/2022.07.05.498902; this version posted July 9, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.



**Fig. 12.** Maximum Likelihood phylogenetic tree of *Modicella* based on ITS rDNA sequences, with *Actinomortierella* as outgroup. One new species, *M. abundans*, is in shade. Maximum Likelihood (ML) bootstrap values ( $\geq$ 50%) of each clade are indicated at node. A scale bar in the upper left indicates substitutions per site.

bioRxiv preprint doi: https://doi.org/10.1101/2022.07.05.498902; this version posted July 9, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.



**Fig. 13.** Maximum Likelihood phylogenetic tree of *Mortierella* based on ITS rDNA sequences, with *Mucor abundans* as outgroup. Twelve new species, *M. amphispora*, *M. annulata*, *M. cylindrispora*, *M. floccosa*, *M. fusiformispora*, *M. lobata*, *M. macrochlamydospora*, *M. microchlamydospora*, *M. mongolica*, *M. seriatoinflata*, *M. sparsa* and *M. varians*, are in shade, Maximum Likelihood (ML) bootstrap values ( $\geq$ 50%) of each clade are indicated at nodes. A scale bar in the upper left indicates substitutions per site. Double slashes indicate branch lengths shortened ten-fold to facilitate visualization.

bioRxiv preprint doi: https://doi.org/10.1101/2022.07.05.498902; this version posted July 9, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.



**Fig. 14.** Maximum Likelihood phylogenetic tree of *Mucor* based on ITS rDNA sequences, with *Umbelopsis changbaiensis* as outgroup. Twenty new species, *M. abortisporangium*, *M. amphisporus*, *M. breviphorus*, *M. brunneolus*, *M. changshaensis*, *M. chlamydosporus*, *M. donglingensis*, *M. floccosus*, *M. fusiformisporus*, *M. heilongjiangensis*, *M. hemisphaericum*, *M. homothallicus*, *M. hyalinosporus*, *M. lobatus*, *M. moniliformis*, *M. orientalis*, *M. radiatus*, *M. rhizosporus*, *M. robustus* and *M. sino-saturninus*, are in shade. Maximum Likelihood (ML) bootstrap values ( $\geq$ 50%) of each clade are indicated at nodes. A scale bar in the upper left indicates substitutions per site. Double slashes indicate branch lengths shortened ten-fold to facilitate visualization.



**Fig. 15.** Maximum Likelihood phylogenetic tree of *Syncephalastrum* based on ITS rDNA sequences, with *Circinella angarensis* as outgroup. Four new species, *S. breviphorum*, *S. elongatum*, *S. simplex* and *S. sympodiale*, are in shade. Maximum Likelihood (ML) bootstrap values

 $(\geq 50\%)$  of each clade are indicated at nodes. A scale bar in the upper left indicates substitutions per site. Double slashes indicate branch lengths shortened ten-fold to facilitate visualization.



**Fig. 16.** Maximum Likelihood phylogenetic tree of *Umbelopsis* based on ITS rDNA sequences, with *Mucor janssenii* as outgroup. Eight new species, *U. brunnea*, *U. chlamydospora*, *U. crustacea*, *U. globospora*, *U. gutianensis*, *U. oblongispora*, *U. septata* and *U. tibetica*, are in shade. Maximum Likelihood (ML) bootstrap values ( $\geq$ 50%) of each clade are indicated at nodes. A scale bar in the upper left indicates substitutions per site. Double slashes indicate branch lengths shortened ten-fold to facilitate visualization.



Fig. 17. Morphologies of *Absidia alpina* ex-holotype CGMCC 3.16104. a, b. Colonies on MEA (a. obverse, b. reverse); c–e. Sporangia; f. Columellae; g. Rhizoids; h. Sporangiospores. — Scale bars: c–f. 10 μm, g. 20 μm, h. 5 μm.



**Fig. 18.** Morphologies of *Absidia ampullacea* ex-holotype CGMCC 3.16054. **a**, **b**. Colonies on MEA (**a**. obverse, **b**. reverse); **c**. Sporangia; **d**. Columellae; **e**, **f**. Swelling on sporangiophores and hyphae; **g**. Rhizoids; **h**. Sporangiospores. — Scale bars: **c**, **d**, **g**. 10 μm, **e**, **f**. 20 μm, **h**. 5 μm.



Fig. 19. Morphologies of *Absidia biappendiculata* ex-holotype CBS 187.64. a, b. Colonies on MEA (a. obverse, b. reverse); c. Sporangia; d. Columellae; e. Rhizoids; f. Sporangiospores; g–i.
Zygospores. — Scale bars: c, d. 10 μm, f. 5 μm, e, g–i. 20 μm.



Fig. 20. Morphologies of *Absidia brunnea* ex-holotype CGMCC 3.16055. a, b. Colonies on MEA (a. obverse, b. reverse); c. Sporangia; d. Columellae; e, f. Swellings on sporangiophores; g. Rhizoids; h. Sporangiospores. — Scale bars: c–g. 10 μm, h. 5 μm.



Fig. 21. Morphologies of *Absidia chinensis* ex-holotype CGMCC 3.16056. a, b. Colonies on MEA (a. obverse, b. reverse); c. Sporangia; d. Columellae; e. Swellings in sporangiophores; f. Rhizoids;
g. Sporangiospores; h–j. Zygospores. — Scale bars: c, d, f, h–j. 10 μm, e. 20 μm, g. 5 μm.



**Fig. 22.** Morphologies of *Absidia cinerea* ex-holotype CGMCC 3.16062. **a**, **b**. Colonies on MEA (**a**. obverse, **b**. reverse); **c**. Sporangia; **d**. Columellae; **e**. Sporangiospores; **f**. Sporangiophores in whorls; **g–i**. Zygospores. — Scale bars: **c–e**. 5 μm, **f–i**. 20 μm.



Fig. 23. Morphologies of *Absidia digitula* ex-holotype CGMCC 3.16058. a, b. Colonies on MEA (a. obverse, b. reverse); c. Sporangia; d. Swellings in hyphae; e. Columellae; f. Rhizoids; g. Sporangiospores. — Scale bars: c, e. 10 μm, d, f. 20 μm, g. 5 μm.



Fig. 24. Morphologies of *Absidia jiangxiensis* ex-holotype CGMCC 3.16105. a, b. Colonies on MEA (a. obverse, b. reverse); c. Sporangia; d. Sporangiospores; e–h. Columellae; i. Rhizoids; j–l. Zygospores. — Scale bars: c, e–i. 10 μm, d. 5 μm, j–l. 20 μm.


**Fig. 25.** Morphologies of *Absidia nigra* ex-holotype CGMCC 3.16059. **a**, **b**. Colonies on MEA (**a**. obverse, **b**. reverse); **c**. Sporangia; **d**. Columellae; **e**. Swellings in sporangiophores; **f**. Rhizoids; **g**. Sporangiospores. — Scale bars: **c**–**f**.10 μm, **g**. 5 μm.



Fig. 26. Morphologies of *Absidia oblongispora* ex-holotype CGMCC 3.16061. a, b. Colonies on MEA (a. obverse, b. reverse); c. Sporangia; d. Columellae; e. Rhizoids; f. Sporangiospores. —
Scale bars: c–e. 10 μm, f. 5 μm.



**Fig. 27.** Morphologies of *Absidia purpurea* ex-holotype CGMCC 3.16106. **a**, **b**. Colonies on MEA (**a**. obverse, **b**. reverse); **c**. Sporangia; **d**, **e**. Columellae; **f**. Sporangiospores; **g**. Rhizoids. — Scale bars: **c**, **g**. 20 μm, **d**, **e**. 10 μm, **f**. 5 μm.



Fig. 28. Morphologies of *Absidia sympodialis* ex-holotype CGMCC 3.16064. a, b. Colonies on MEA (a. obverse, b. reverse); c. Sporangia; d. Columellae; e. Sympodial sporangiophores; f. Rhizoids; g. Sporangiospores. — Scale bars: c, e, f. 20 μm, d. 10 μm, g. 5 μm.



**Fig. 29.** Morphologies of *Absidia varians* ex-holotype CGMCC 3.16065. **a**, **b**. Colonies on MEA (**a**. obverse, **b**. reverse); **c**. Sporangia; **d–f**. Columellae; **g**. Rhizoids; **h**. Sporangiospores. — Scale bars: **c–f**. 10 μm, **g**. 20 μm, **h**. 5 μm.



Fig. 30. Morphologies of *Absidia virescens* ex-holotype CGMCC 3.16067. a, b. Colonies on MEA (a. obverse, b. reverse); c. Sporangia; d. Monopodial sporangiophores with columellae; e. Rhizoids;
f. Sporangiospores. — Scale bars: c, e. 10 μm, d. 20 μm, f. 5 μm.



Fig. 31. Morphologies of *Absidia xinjiangensis* ex-holotype CGMCC 3.16107 a, b. Colonies on MEA (a. obverse, b. reverse); c. Sporangia; d, e. Columellae; f. Monopodial sporangiophores; g. Sporangiospores. — Scale bars: c–e, g. 5 μm, f. 10 μm.



Fig. 32. Morphologies of *Backusella dichotoma* ex-holotype CGMCC 3.16108. a, b. Colonies on PDA (a. obverse, b. reverse); c–e. Azygospores; f. Columellae of terminal sporangia; g.
Sporangiospores. — Scale bars: c–g. 10 μm.



Fig. 33. Morphologies of *Backusella moniliformis* ex-holotype CGMCC 3.16109. a, b. Colonies on PDA (a. obverse, b. reverse); c. Lateral uni-spored sporangiolum; d. Lateral uni-spored sporangiolum; e. Columellae; f. Chlamydospores; g. Sporangiospores. — Scale bars: c–g. 5 μm.



**Fig. 34.** Morphologies of *Backusella ovalispora* ex-holotype CGMCC 3.16110. **a**, **b**. Colonies on PDA (**a**. obverse, **b**. reverse); **c**. Sporangiospores; **d**. Lateral multi-spored sporangiola; **e**. Lateral uni-spored sporangiolum; **f**, **g**. Columellae — Scale bars: **c**–**g**. 10 μm.



Fig. 35. Morphologies of *Circinella homothallica* ex-holotype CGMCC 3.16026. a, b. Colonies on PDA (a, obverse, b, reverse); c, Columellae with a projection and collars; d, e. Circinate lateral sporangiophores; h. Sporangiospores; g–i. Zygospores. — Scale bars: c–i, 10 μm.



**Fig. 36.** Morphologies of *Cunninghamella arrhiza* ex-holotype CGMCC 3.16111. **a, b.** Colonies on PDA (**a.** obverse, **b.** reverse); **c.** Sporangiola; **d–f.** Sporangiophores showing characteristic branching patterns with vesicles; **g.** Rhizoids. — Scale bars: **c–f.** 10 μm, **g.** 20 μm.



Fig. 37. Morphologies of *Cunninghamella guttata* ex-holotype CGMCC 3.16112. a, b. Colonies on PDA (a. obverse, b. reverse); c. Sporangiophores showing characteristic branching patterns; d.
Rhizoids; e, f. Sporangiola. — Scale bars: c, e. 10 μm, d. 20 μm, f. 5 μm.



**Fig. 38.** Morphologies of *Cunninghamella irregularis* ex-holotype CGMCC 3.16113. **a, b.** Colonies on PDA (**a.** obverse, **b.** reverse); **c–e.** Sporangiophores showing characteristic branching patterns with vesicles; **f.** Rhizoids; **g.** Sporangiola. — Scale bars: **c–g.** 10 μm.



Fig. 39. Morphologies of *Cunninghamella nodosa* ex-holotype CGMCC 3.5628. a, b. Colonies on PDA (a. obverse, b. reverse); c–e. Sporangiophores showing characteristic branching patterns; f. Sporangiola. — Scale bars: c–f. 10 μm.



**Fig. 40.** Morphologies of *Cunninghamella regularis* ex-holotype CGMCC 3.16114. **a**, **b**. Colonies on PDA (**a**. obverse, **b**. reverse); **c**. Rhizoids; **d**, **e**. Sporangiophores showing characteristic branching patterns; **f**. Lateral branches of sporangiophores with sporangiola; **g**. Sporangiola. — Scale bars: **c**. 20 μm, **d**–**g**. 10 μm.



Fig. 41. Morphologies of *Cunninghamella subclavata* ex-holotype CGMCC 3.16115. a, b. Colonies on PDA (a. obverse, b. reverse); c–e. Sporangiophores showing characteristic branching patterns; f. Sporangiola. — Scale bars: c–f. 10 μm.



Fig. 42. Morphologies of *Cunninghamella varians* ex-holotype CGMCC 3.16116. a, b. Colonies on PDA (a. obverse, b. reverse); c–g. Sporangiophores showing characteristic branching patterns; h. Sporangiola. — Scale bars: c–h. 10 μm.



**Fig. 43.** Morphologies of *Mortierella globistylospora* ex-holotype CGMCC 3.16117. **a**, **b**. Colonies on PDA (**a**. obverse, **b**. reverse); **c**, **f**. Stylospores on the intercalarily produced; **d**, **e**. Stylospores terminally produced. — Scale bars: **c**–**f**. 10 μm.



Fig. 44. Morphologies of *Gongronella chlamydospora* ex-holotype CGMCC 3.16118. a, b.
Colonies on PDA (a. obverse, b. reverse); c. Chlamydospores; d. Simple branches of sporangiophores; e. Columellae; f. Sporangiospores. — Scale bars: c, f. 5 μm, d, e. 10 μm.



Fig. 45. Morphologies of *Gongronella multispora* ex-holotype CGMCC 3.16119. a, b. Colonies on PDA (a. obverse, b. reverse); c–e. Sporangia; f. Columellae with apophyses; g. Sporangiophores showing branches; h. Sporangiospores. — Scale bars: c, d, h. 5 μm, e, f. 10 μm, g. 20 μm.



Fig. 46. Morphologies of *Lichtheimia alba* ex-holotype CGMCC 3.16120. a, b. Colonies on MEA (a. obverse, b. reverse); c. Sporangia; d. Columellae; e, f. Sporangiophores branched; g. Sporangiospores. — Scale bars: c, d. 10 μm, e, f. 20 μm, g. 5 μm.



Fig. 47. Morphologies of *Lichtheimia globospora* ex-holotype CGMCC 3.16025. a, b. Colonies on PDA (a. obverse, b. reverse); c, d. Giant cells in aerial hyphae; e, f. Columellae and collars; g. Sporangiospores. — Scale bars: c. 20 μm, d–g. 10 μm.



**Fig. 48.** Morphologies of *Modicella abundans* ex-holotype CGMCC 3.16121. **a, b.** Colonies on PDA (**a.** obverse, **b.** reverse); **c, d.** Chlamydospores. — Scale bars: **c, d.** 10 μm.



Fig. 49. Morphologies of *Mortierella amphispora* ex-holotype CGMCC 3.16122. a, b. Colonies on PDA (a. obverse, b. reverse); c. Sporangiospores; d, e. Sporangiophores with sporangia; f. Chlamydospores; g. Degenerated columellae without collars; h. Rhizoids. — Scale bars: c, e, h. 20 μm, d, f, g. 10 μm.



**Fig. 50.** Morphologies of *Mortierella annulata* ex-holotype CGMCC 3.16123. **a**, **b**. Colonies on PDA (**a**. obverse, **b**. reverse); **c–f**. Sporangiospores; **g**, **h**. Sporangia; **i**. Sporangiophores without collars and columellae. — Scale bars: **c–f**. 5 μm, **g–i**. 10 μm.



Fig. 51. Morphologies of *Mortierella cylindrispora* ex-holotype CGMCC 3.16124. a, b. Colonies on PDA (a. obverse, b. reverse); c. Sporangia; d. Sporangiospores with hyphae. — Scale bars: c, d. 10 μm.



Fig. 52. Morphologies of *Mortierella floccosa* ex-holotype CGMCC 3.16125. a, b. Colonies on
PDA (a. obverse, b. reverse); c, d. Sporangiophores with collars; e. Sporangia; f. Chlamydospores;
g. Sporangiospores. — Scale bars: c, e. 10 μm, d, f, g. 5 μm.



Fig. 53. Morphologies of *Mortierella fusiformispora* ex-holotype CGMCC 3.16029. a, b. Colonies on PDA (a, obverse, b, reverse); c. Immature sporangia; d. Collars (red arrow) and sporangiophores; e. Sporangiospores showing one or two pigmented spots inside. — Scale bars: c, e. 5 μm, d. 10 μm.



Fig. 54. Morphologies of *Mortierella lobata* ex-holotype CGMCC 3.16126. a, b. Colonies on PDA (a. obverse, b. reverse); c, d. Chlamydospores. — Scale bars: c. 5 μm, d. 10 μm.



Fig. 55. Morphologies of *Mortierella macrochlamydospora* ex-holotype CGMCC 3.16127. a, b.
Colonies on PDA (a. obverse, b. reverse); c. Hyphal swellings; d. Chlamydospores; e. Sporangia; f.
Sporangiospores. — Scale bars: c–f. 10 μm.

bioRxiv preprint doi: https://doi.org/10.1101/2022.07.05.498902; this version posted July 9, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.



**Fig. 56.** Morphologies of *Mortierella microchlamydospora* ex-holotype CGMCC 3.16128. **a**, **b**. Colonies on PDA (**a**. obverse, **b**. reverse); **c**. Hyphae branched; **d**, **e**. Chlamydospores. — Scale bars: **c**. 20 μm, **d**, **e**. 5 μm.



**Fig. 57.** Morphologies of *Mortierella mongolica* ex-holotype CGMCC 3.16129. **a, b.** Colonies on PDA (**a.** obverse, **b.** reverse); **c, f.** Chlamydospores; **d.** Sporangia; **e.** Sporangiospores. — Scale bars: **c–f.** 5 μm.



**Fig. 58.** Morphologies of *Mortierella seriatoinflata* ex-holotype CGMCC 3.16130. **a, b.** Colonies on PDA (**a.** obverse, **b.** reverse); **c.** Sporangia; **d, e.** Swellings in hyphae; **f.** Sporangiospores. — Scale bars: **c, f.** 10 μm, **d, e.** 20 μm.



Fig. 59. Morphologies of *Mortierella sparsa* ex-holotype CGMCC 3.16131. a, b. Colonies on PDA (a. obverse, b. reverse); c. Sporangia; d. Sporangiophores; e. Swellings in substrate hyphae. —
Scale bars: c. 20 μm, d, e. 10 μm.



Fig. 60. Morphologies of *Mortierella varians* ex-holotype CGMCC 3.16132. a, b. Colonies on
PDA (a. obverse, b. reverse); c. Rhizoids; d. Sporangia; e. Chlamydospores; f. Sporangiospores. —
Scale bars: c, f. 20 μm, d, e. 10 μm.



Fig. 61. Morphologies of *Mucor abortisporangium* ex-holotype CGMCC 3.16133. a, b. Colonies on PDA (a. obverse, b. reverse); c. Aborted lateral sporangia; d. Sporangia; e. Columellae; f. Chlamydospores; g. Sporangiospores. — Scale bars: c–g. 10 μm.



**Fig. 62.** Morphologies of *Mucor amphisporus* ex-holotype CGMCC 3.16134. **a**, **b**. Colonies on PDA (**a**. obverse, **b**. reverse); **c**. Sporangia; **d**. Substrate hyphae with swollen; **e**, **f**. Columellae with collar; **g**. Sporangiospores. — Scale bars: **c**–**f**. 20 μm, **g**. 5 μm.


Fig. 63. Morphologies of *Mucor breviphorus* ex-holotype CGMCC 3.16135. a, b. Colonies on PDA (a. obverse, b. reverse); c. Sporangia; d. Columellae with collars; e. Sympodial sporangiophores; f. Swellings in substrate hyphae; g. Sporangiospores. — Scale bars: c–e. 20 μm, f, g. 10 μm.



Fig. 64. Morphologies of *Mucor brunneolus* ex-holotype CGMCC 3.16136. a, b. Colonies on PDA (a. obverse, b. reverse); c. Sporangiospores; d. Sporangia; e–g. Columellae. — Scale bars: c. 5 μm, d. 20 μm, e–g. 10 μm.



Fig. 65. Morphologies of *Mucor changshaensis* ex-holotype CGMCC 3.16137. a, b. Colonies on PDA (a. obverse, b. reverse); c. Sporangia; d, e. Columellae with collars; f. Rhizoids; g. Chlamydospores; h. Sporangiospores. — Scale bars: c–e, g, h. 10 μm, f. 50 μm.



Fig. 66. Morphologies of *Mucor chlamydosporus* ex-holotype CGMCC 3.16138. a, b. Colonies on PDA (a. obverse, b. reverse); c. Chlamydospores formed in aerial hyphae; d. Immature fertile sporangia; e. Aborted sporangia; f. Columellae; g. Sporangiospores. — Scale bars: c–f. 20 μm, g. 10 μm.



Fig. 67. Morphologies of *Mucor donglingensis* ex-holotype CGMCC 3.16139. a, b. Colonies on
PDA (a. obverse, b. reverse); c. Sporangiospores; d. Sporangia; e, f. Columellae; g, h.
Chlamydospores. — Scale bars: c. 5 μm, d–h. 10 μm.



Fig. 68. Morphologies of *Mucor floccosus* ex-holotype CGMCC 3.16140. a, b. Colonies on PDA (a. obverse, b. reverse); c. Sporangiospores; d. Sporangia; e, f. Columellae without collar; g. Chlamydospores. — Scale bars: c. 5 μm, d–g. 10 μm.



Fig. 69. Morphologies of *Mucor fusiformisporus* ex-holotype CGMCC 3.16141. a, b. Colonies on PDA (a. reverse, b. obverse); c. Sporangia; d–f. Sporangiospores with columellae; g. Sporangiospores. — Scale bars: c. 20 μm, d–f. 10 μm, g. 5 μm.



Fig. 70. Morphologies of *Mucor heilongjiangensis* ex-holotype CGMCC 3.16142. a, b. Colonies on PDA (a. obverse, b. reverse); c. Sporangia; d–f. Columellae; g. Chlamydospores; h. Sporangiospores. — Scale bars: c–f, h. 10 μm, g. 20 μm.



Fig. 71. Morphologies of *Mucor hemisphaericum* ex-holotype CGMCC 3.16143. a, b. Colonies on PDA (a. obverse, b. reverse); c. Chlamydospores; d. Sporangia; e–g. Columellae with small collars;
h. Sporangiospores. — Scale bars: c. 20 μm, d–h. 10 μm.



**Fig. 72.** Morphologies of *Mucor homothallicus* ex-holotype CGMCC 3.16144. **a**, **b**. Colonies on PDA (**a**. obverse, **b**. reverse); **c**, **d**. Zygospores; **e**. Sporangia; **f**. Columellae; **g**. Sporangiospores. — Scale bars: **c**. 100 μm, **d**–**g**. 10 μm.



Fig. 73. Morphologies of *Mucor hyalinosporus* ex-holotype CGMCC 3.16145. a, b. Colonies on PDA (a. obverse, b. reverse); c, d. Sporangia; e. Chlamydospores; f–h. Columellae without collar;
i. Sporangiospores. — Scale bars: c, d, f–h. 10 μm, e. 10 μm, i. 5 μm.



Fig. 74. Morphologies of *Mucor lobatus* ex-holotype CGMCC 3.16146. a, b. Colonies on PDA (a. obverse, b. reverse); c. Sporangiospores; d. Immature sporangia; e, f. Columellae with sporangiophores. — Scale bars: c. 10 μm, d–f. 20 μm.



Fig. 75. Morphologies of *Mucor moniliformis* ex-holotype CGMCC 3.17147. a, b. Colonies on
PDA (a. obverse, b. reverse); c. Sporangia; d. Columellae with collars; e. Sporangiophores; f, g.
Chlamydospores; h. Sporangiospores. — Scale bars: c, e. 20 μm, d, f, g. 10 μm, h. 5 μm.



**Fig. 76.** Morphologies of *Mucor orientalis* ex-holotype CGMCC 3.16148. **a**, **b**. Colonies on PDA (**a**. obverse, **b**. reverse); **c**. Chlamydospores; **d**. Fertile sporangia; **e**, **f**. Aborted sporangia on sporangiophores; **g**. Sporangiospores; **h**, **i**. Columellae with collars. — Scale bars: **c**–**i**. 20 μm.



Fig. 77. Morphologies of *Mucor radiatus* ex-holotype CGMCC 3.16149. a, b. Colonies on PDA (a. obverse, b. reverse); c. Sporangia; d. Aborted lateral sporangia with swellings in hyphae; e.
Columellae; f-h. Chlamydospores; i. Sporangiospores. — Scale bars: c, e-g. 10 μm, d. 20 μm, h, i. 5 μm.



Fig. 78. Morphologies of *Mucor rhizosporus* ex-holotype CGMCC 3.16150. a, b. Colonies on PDA (a. obverse, b. reverse); c. Chlamydospores at rhizoids; d. Chlamydospores in aerial hyphae; e.
Sporangia; f. Columellae; g. Sporangiospores. — Scale bars: c–f. 10 μm, g. 5 μm.



Fig. 79. Morphologies of *Mucor robustus* ex-holotype CGMCC 3.16151. a, b. Colonies on PDA (a. obverse, b. reverse); c, d. Sporangia; e–g. Sporangiophores with columellae; h. Substrate hyphae; i. Sporangiospores. — Scale bars: c–g. 20 μm, h. 50 μm, i. 10 μm.



Fig. 80. Morphologies of *Mucor sino-saturninus* ex-holotype CGMCC 3.16152. a, b. Colonies on PDA (a. obverse, b. reverse); c. Sporangiophores branched; d. Swellings below sporangia; e, f. Columellae with collars; g. Sporangiospores. — Scale bars: c–f. 20 μm, g. 10 μm.



**Fig. 81.** Morphologies of *Syncephalastrum breviphorum* ex-holotype CGMCC 3.16153. **a**, **b**. Colonies on PDA (**a**. obverse, **b**. reverse); **c**. Merosporangia; **d**–**f**. Sporangiophores with branched and vesicles; **g**. Rhizoids; **h**, **i**. Sporangiospores. — Scale bars: **c**, **e**–**h**. 10 μm, **d**. 20 μm, **i**. **5** μm.



Fig. 82. Morphologies of *Syncephalastrum elongatum* ex-holotype CGMCC 3.16154. a, b.
Colonies on PDA (a. obverse, b. reverse); c–f. Sporangiophores with branched and vesicles; g.
Rhizoids; h, i. Sporangiospores. — Scale bars: c–i. 10 μm.



**Fig. 83.** Morphologies of *Syncephalastrum simplex* ex-holotype CGMCC 3.16155. **a**, **b**. Colonies on PDA (**a**. obverse, **b**. reverse); **c**, **d**. Vesicles; **e**. Sporangiophores; **f**, **g**. Sporangiospores. — Scale bars: **c**–**g**. 10 μm.



Fig. 84. Morphologies of *Syncephalastrum sympodiale* ex-holotype CGMCC 3.16156. a, b.
Colonies on PDA (a. obverse, b. reverse); c. Merosporangia; d–g. Sporangiophores with branches and vesicles; h, i. Sporangiospores; j. Rhizoids. — Scale bars: c, g, j. 20 μm, d–f, h. 10 μm, i. 5 μm.



**Fig. 85.** Morphologies of *Umbelopsis brunnea* ex-holotype CGMCC 3.16023. **a**, **b**. Colonies on PDA (**a**, obverse, **b**, reverse); **c**. Sporangiospores; **d**, **e**. Sporangia; **f**. Columellae; **g**. Hyphal branches showing irregular septate. — Scale bars: **c**, **d**, **f**. 5 μm, **e**, **g**. 10 μm.



Fig. 86. Morphologies of *Umbelopsis chlamydospora* ex-holotype CGMCC 3.16157. a, b. Colonies on PDA (a. obverse, b. reverse); c. Sporangiospores; d. Sporangia; e, f. Chlamydospores; g. Sporangiophores. — Scale bars: c. 5 μm, d–e. 10 μm, g. 20 μm.



Fig. 87. Morphologies of *Umbelopsis crustacea* ex-holotype CGMCC 3.16158. a, b. Colonies on PDA (a. obverse, b. reverse); c. Sporangiospores; d. Sporangia; e. Columellae with collars; f. Columellae with septa. — Scale bars: c, e, f. 5 μm, d. 10 μm.



Fig. 88. Morphologies of *Umbelopsis globospora* ex-holotype CGMCC 3.16159. a, b. Colonies on PDA (a. obverse, b. reverse); c. Sporangiospores; d. Sporangia; e. Degenerated columellae; f. Sporangiophores. — Scale bars: c–e. 10 μm, f. 5 μm.



Fig. 89. Morphologies of *Umbelopsis gutianensis* ex-holotype CGMCC 3.16160. a, b. Colonies on PDA (a. obverse, b. reverse); c. Sporangiospores; d. Sporangia; e. Sporangiophores. — Scale bars:
c–e. 10 μm.



**Fig. 90.** Morphologies of *Umbelopsis oblongispora* ex-holotype CGMCC 3.16161. **a, b.** Colonies on PDA (**a.** obverse, **b.** reverse); **c.** Sporangiospores; **d.** Sporangia; **e.** Columellae with collars; **f.** Chlamydospores; **g.** Sporangiophores. — Scale bars: **c**–**g.** 10 μm.



Fig. 91. Morphologies of *Umbelopsis septata* ex-holotype CGMCC 3.16162. a, b. Colonies on
PDA (a. obverse, b. reverse); c. Sporangiospores; d. Sporangia; e. Hyphae with septa; f.
Sporangiophores. — Scale bars: c–f. 10 μm.



Fig. 92. Morphologies of *Umbelopsis tibetica* ex-holotype CGMCC 3.16163. a, b. Colonies on PDA (a. obverse, b. reverse); c. Sporangiospores; d. Sporangia; e. Columellae with collars; f. Chlamydospores; g. Sporangiophores. — Scale bars: c. 5 μm, d–h. 10 μm.

**Table 1.** Information of new species and Chinese new record species reported in this study. \* New species proposed herein are in bold, new combinations herein are underlined. \*\* T represents exholotype.

Species*	Strains**	Substrate	Locality	GenBank
				accession Nos.
				of ITS rDNA
Absidia alpina	CGMCC 3.16104 <sup>T</sup>	soil	Yunnan, China	OL678133
A. ampullacea	CGMCC 3.16054 <sup>T</sup>	soil	Beijing, China	MZ354138
<u>A. biappendiculata</u>	NRRL 3033	leaves	Wyoming, USA	MZ354153
A. brunnea	CGMCC 3.16055 <sup>T</sup>	soil	Qinghai, China	MZ354139

A. caerulea	XY00608	flower	Guangdong, China	OL620081
	XY00729	flower	Guangdong, China	OL620082
A. chinensis	CGMCC 3.16056 <sup>T</sup>	soil	Yunnan, China	MZ354140
	CGMCC 3.16057	soil	Sichuan, China	MZ354141
A. cinerea	CGMCC 3.16062 <sup>T</sup>	soil	Beijing, China	MZ354146
A. digitula	CGMCC 3.16058 <sup>T</sup>	soil	Xinjiang, China	MZ354142
A. jiangxiensis	CGMCC 3.16105 <sup>T</sup>	soil	Jiangxi, China	OL678134
A. koreana	XY00816	soil	Hubei, China	OL620083
	XY00596	seed	Hubei, China	OL620084
<u>A. nigra</u>	NRRL 3060 <sup>T</sup>	soil	Wisconsin, USA	MZ354143
	CGMCC 3.16059	soil	Jilin, China	MZ354144
	CGMCC 3.16060	soil	Inner Mongolia, China	MZ354152
A. oblongispora	CGMCC 3.16061 <sup>T</sup>	soil	Yunnan, China	MZ354145
A. pararepens	XY00631	soil	Beijing, China	OL620085
	XY00615	soil	Beijing, China	OL620086
	XY05899	soil	Tibet, China	OL620087
A. purpurea	CGMCC 3.16106 <sup>T</sup>	soil	Yunnan, China	OL678135
A. sympodialis	CGMCC 3.16064 <sup>T</sup>	soil	Shaanxi, China	MZ354148
	CGMCC 3.16063 <sup>T</sup>	soil	Beijing, China	MZ354147
A. xinjiangensis	CGMCC 3.16107 <sup>T</sup>	soil	Xinjiang, China	OL678136
A. varians	CGMCC 3.16065 <sup>T</sup>	soil	Yunnan, China	MZ354149
A. virescens	CGMCC 3.16067 <sup>T</sup>	soil	Yunnan, China	MZ354151
	CGMCC 3.16066 <sup>T</sup>	soil	Yunnan, China	MZ354150
Actinomortierella	XY06923	soil	Yunnan, China	OL620101
ambigua				
Backusella	CGMCC 3.16108 <sup>T</sup>	soil	Yunnan, China	OL678137
dichotoma				
	XY07504	soil	Yunnan, China	OL678138
B. dispersa	XY08806	soil	Xinjiang, China	OL620088
B. locustae	XY07940	soil	Hunan, China	OL620089

B. moniliformis	CGMCC 3.16109 <sup>T</sup>	soil	Shanxi, China	OL678139
B. ovalispora	CGMCC 3.16110 <sup>T</sup>	soil	Guangxi, China	OL678140
	XY07481	soil	Guangxi, China	OL678141
B. oblongielliptica	XY08152	soil	Yunnan, China	OL620090
	XY08767	soil	Zhejiang, China	OL620091
	XY08768	soil	Zhejiang, China	OL620092
B. tuberculispora	XY07548	soil	Yunnan, China	OL620093
	XY7557	soil	Yunnan, China	OL620094
Circinella	CGMCC 3.16026 <sup>T</sup>	soil	Hainan, China	MW580599
homothallica				
Cunninghamella	XY07003	soil	Anhui, China	OL620095
antarctica				
	XY07050	soil	Gansu, China	OL620096
C. arrhiza	CGMCC 3.16111 <sup>T</sup>	soil	Hunan, China	OL678142
	XY08047	soil	Beijing, China	OL678143
C. guttata	CGMCC 3.16112 <sup>T</sup>	soil	Beijing, China	OL678144
C. irregularis	CGMCC 3.16113 <sup>T</sup>	soil	Inner Mongolia, China	OL678144
	XY07683	soil	Inner Mongolia, China	OL678146
	XY07657	soil	Inner Mongolia, China	OL678147
<u>C. nodosa</u>	AS. 3.5628 <sup>T</sup>	flower	Beijing, China	AF346407
C. regularis	CGMCC 3.16114 <sup>T</sup>	soil	Yunnan, China	OL678148
	XY07510	soil	Yunnan, China	OL678149
	XY07512	soil	Yunnan, China	OL678150
	XY07519	soil	Yunnan, China	OL678151
C. subclavata	CGMCC 3.16115 <sup>T</sup>	soil	Yunnan, China	OL678152
	XY07766	soil	Yunnan, China	OL678153
C. varians	CGMCC 3.16116 <sup>T</sup>	soil	Jiangsu, China	OL678154
	XY06999	soil	Jiangsu, China	OL678155
Dissophora	XY08870	soil	Xinjiang, China	OL620097
globulifera				

Gamsiella	CGMCC 3.16117 <sup>T</sup>	soil	Tibet, China	OL678156
globistylospora				
Gongronella	CGMCC 3.16118 <sup>T</sup>	soil	Jiangxi, China	OL678157
chlamydospora				
G. multispora	CGMCC 3.16119 <sup>T</sup>	soil	Beijing, China	OL678158
G. namwonensis	XY08131	soil	Zhejiang, China	OL620098
Isomucor trufemiae	XY07543	soil	Yunnan, China	OL620099
	XY07544	soil	Yunnan, China	OL620100
Lichtheimia alba	CGMCC 3.16120 <sup>T</sup>	soil	Beijing, China	OL678159
L. globospora	CGMCC 3.16025 <sup>T</sup>	soil	Hainan, China	MW580598
Modicella abundans	CGMCC 3.16121 <sup>T</sup>	soil	Anhui, China	OL678160
Mortierella	CGMCC 3.16122 <sup>T</sup>	soil	Yunnan, China	OL678161
amphispora				
	XY08653	soil	Yunnan, China	OL678162
	XY08796	soil	Yunnan, China	OL678292
M. annulata	CGMCC 3.16123 <sup>T</sup>	soil	Yunnan, China	OL678163
M. bainieri	XY08661	soil	Yunnan, China	OL620102
M. beljakovae	XY03433	soil	Heilongjiang, China	OL620103
M. chlamydospora	XY07448	soil	Zhejiang, China	OL620104
	XY08109	soil	Guangxi, China	OL620105
M. cylindrispora	CGMCC 3.16124 <sup>T</sup>	soil	Jiangsu, China	OL678164
M. cystojenkinii	XY03898	soil	Inner Mongolia, China	OL620106
	XY03876	plant debris	Heilongjiang, China	OL620107
	XY03882	plant debris	Heilongjiang, China	OL620108
M. epicladia	XY06924	soil	Yunnan, China	OL620109
	XY06927	soil	Yunnan, China	OL620110
M. floccosa	CGMCC 3.16125 <sup>T</sup>	soil	Jiangsu, China	OL678165
M. fluviae	XY04370	soil	Heilongjiang, China	OL620111
M. fusiformispora	CGMCC 3.16029 <sup>T</sup>	soil	Fields Peninsula, Antarctica	MW580602
	CGMCC 3.16030	soil	Fields Peninsula, Antarctica	MW580603

M. lignicola	XY08224	soil	Yunnan, China	OL620112
M. lobata	CGMCC 3.16126 <sup>T</sup>	soil	Beijing, China	OL678166
M. longigemmata	XY07567	soil	Yunnan, China	OL620113
	XY08599	soil	Yunnan, China	OL620114
	XY08601	soil	Yunnan, China	OL620115
М.	CGMCC 3.16127 <sup>T</sup>	plant	Inner Mongolia, China	OL678167
macrochlamydospora		debris		
	XY04275	plant	Inner Mongolia, China	OL678168
		debris		
М.	CGMCC 3.16128 <sup>T</sup>	soil	Yunnan, China	OL678169
microchlamydospora				
	XY07258	soil	Beijing, China	OL678170
	XY07283	soil	Beijing, China	OL678171
M. mongolica	CGMCC 3.16129 <sup>T</sup>	soil	Inner Mongolia, China	OL678172
	XY03534	soil	Inner Mongolia, China	OL678173
M. nantahalensis	XY07486	soil	Guangxi, China	OL620116
	XY06017	soil	Hainan, China	OL620117
M. rishikesha	XY07315	soil	Beijing, China	OL620118
M. schmuckeri	XY07412	soil	Beijing, China	OL620119
	XY07419	soil	Beijing, China	OL620120
M. sclerotiella	XY03528	soil	Inner Mongolia, China	OL620121
M. seriatoinflata	CGMCC 3.16130 <sup>T</sup>	plant	Beijing, China	OL678174
		debris		
	XY06985	soil	Anhui, China	OL678175
	CBS 314.52	soil	Germany	MH868591
M. sparsa	CGMCC 3.16131 <sup>T</sup>	leaves	Heilongjiang, China	OL678176
	XY03860	leaves	Heilongjiang, China	OL678291
	XY04406	leaves	Inner Mongolia, China	OL678177
M. turficola	XY03346	plant debris	Heilongjiang, China	OL620122
M. varians	CGMCC 3.16132 <sup>T</sup>	soil	Tibet, China	OL678178

	XY05920	soil	Tibet, China	OL678179
Mucor	CGMCC 3.16133 <sup>T</sup>	soil	Guangxi, China	OL678180
abortisporangium				
M. aligarensis	XY07583	soil	Yunnan, China	OL620123
M. amphisporus	CGMCC 3.16134 <sup>T</sup>	soil	Inner Mongolia, China	OL678181
	XY07649	soil	Inner Mongolia, China	OL678182
M. atramentarius	XY06751	soil	Tibet, China	OL620124
M. bainieri	XY08747	soil	Yunnan, China	OL620125
M. breviphorus	CGMCC 3.16135 <sup>T</sup>	soil	Yunnan, China	OL678183
M. brunneolus	CGMCC 3.16136 <sup>T</sup>	soil	Guangxi, China	OL678184
M. changshaensis	CGMCC 3.16137 <sup>T</sup>	soil	Hunan, China	OL678185
	XY07965	soil	Hunan, China	OL678186
M. chlamydosporus	CGMCC 3.16138 <sup>T</sup>	soil	Hebei, China	OL678187
	XY08211	soil	Yunnan, China	OL678188
	XY08225	soil	Yunnan, China	OL678189
M. donglingensis	CGMCC 3.16139 <sup>T</sup>	plant	Beijing, China	OL678190
		debris		
	XY08501	soil	Yunnan, China	OL678191
M. floccosus	CGMCC 3.16140 <sup>T</sup>	soil	Hunan, China	OL678192
	XY07967	soil	Hunan, China	OL678193
M. fluvii	XY07446	soil	Zhejiang, China	OL620126
	XY07447	soil	Zhejiang, China	OL620127
M. fuscus	XY06718	soil	Tibet, China	OL620128
	XY06719	soil	Tibet, China	OL620129
M. fusiformisporus	CGMCC 3.16141 <sup>T</sup>	soil	Jiangsu, China	OL678194
	XY08153	soil	Yunnan, China	OL678195
	XY08154	soil	Yunnan, China	OL678196
	XY08117	soil	Zhejiang, China	OL678197
M. griseocyanus	XY06685	soil	Tibet, China	OL620130
	XY06697	soil	Tibet, China	OL620131

M. heilongjiangensis	CGMCC 3.16142 <sup>T</sup>	soil	Heilongjiang, China	OL678198
	XY05057	soil	Heilongjiang, China	OL678199
M. hemisphaericum	CGMCC 3.16143 <sup>T</sup>	soil	Tibet, China	OL678200
M. homothallicus	CGMCC 3.16144 <sup>T</sup>	soil	Jiangsu, China	OL678201
	XY06967	soil	Jiangsu, China	OL678202
M. hyalinosporus	CGMCC 3.16145 <sup>T</sup>	soil	Beijing, China	OL678203
M. lobatus	CGMCC 3.16146 <sup>T</sup>	soil	Jiangsu, China	OL678204
	XY07029	soil	Hubei, China	OL678205
M. lusitanicus	XY06042	soil	Shandong, China	OL620132
	XY06074	soil	Shandong, China	OL620133
	XY07298	dung	Beijing, China	OL620134
	XY07299	dung	Beijing, China	OL620135
M. minutus	XY06939	soil	Yunnan, China	OL620136
	XY06940	soil	Yunnan, China	OL620137
	XY07460	soil	Hubei, China	OL620138
M. moniliformis	CGMCC 3.16147 <sup>T</sup>	soil	Zhejiang, China	OL678206
	XY07458	soil	Hubei, China	OL678207
M. mucedo	XY07301	soil	Beijing, China	OL620139
	XY07302	soil	Beijing, China	OL620140
M. nanus	XY07037	soil	Hubei, China	OL620141
	XY07221	soil	Beijing, China	OL620142
M. nidicola	XY08161	soil	Yunnan, China	OL620143
M. orientalis	CGMCC 3.16148 <sup>T</sup>	soil	Anhui, China	OL678208
М.	XY07713	soil	Shanxi, China	OL620144
pseudocircinelloides				
	XY07714	soil	Shanxi, China	OL620145
M. radiatus	CGMCC 3.16149 <sup>T</sup>	soil	Yunnan, China	OL678209
	XY08167	soil	Yunnan, China	OL678210
M. rhizosporus	CGMCC 3.16150 <sup>T</sup>	soil	Guangxi, China	OL678211
M robustus	CGMCC 3.16151 <sup>T</sup>	soil	Xinjiang, China	OL678212

	XY08976	soil	Xinjiang, China	OL678213
	XY09024	soil	Xinjiang, China	OL678214
M. silvaticus	XY04328	plant debris	Heilongjiang, China	OL620146
	XY04329	plant debris	Heilongjiang, China	OL620147
M. sino-saturninus	CGMCC 3.16152 <sup>T</sup>	soil	Yunnan, China	OL678215
	XY08556	soil	Yunnan, China	OL678216
M. stercorarius	XY07007	soil	Anhui, China	OL620148
M. variicolumellatus	XY07369	rotten wood	Beijing, China	OL620149
	XY07370	rotten wood	Beijing, China	OL620150
Syncephalastrum	CGMCC 3.16153 <sup>T</sup>	paper	Fujian, China	OL678217
breviphorum				
	XY06838	paper	Fujian, China	OL678218
S. elongatum	CGMCC 3.16154 <sup>T</sup>	paper	Fujian, China	OL678219
S. simplex	CGMCC 3.16155 <sup>T</sup>	soil	Hubei, China	OL678220
S. sympodiale	CGMCC 3.16156 <sup>T</sup>	soil	Beijing, China	OL678221
	XY06803	soil	Beijing, China	OL678222
	XY06811	mushroom	Beijing, China	OL678223
Umbelopsis brunnea	CGMCC 3.16023 <sup>T</sup>	soil	Heilongjiang, China	MV580596
	CGMCC 3.16024	soil	Inner Mongolia, China	MV580597
U. chlamydospora	CGMCC 3.16157 <sup>T</sup>	soil	Beijing, China	OL678224
U. crustacea	CGMCC 3.16158 <sup>T</sup>	soil	Inner Mongolia, China	OL678225
	XY03542	soil	Inner Mongolia, China	OL678226
	XY03944	soil	Heilongjiang, China	OL678227
U. gibberispora	XY06667	soil	Zhejiang, China	OL620151
U. globospora	CGMCC 3.16159 <sup>T</sup>	soil	Zhejiang, China	OL678228
U. gutianensis	CGMCC 3.16160 <sup>T</sup>	soil	Zhejiang, China	OL678229
	XY06604	soil	Zhejiang, China	OL678230
	XY06605	soil	Zhejiang, China	OL678231
U. oblongispora	CGMCC 3.16161 <sup>T</sup>	soil	Zhejiang, China	OL678232
U. ovata	XY03175	soil	Heilongjiang, China	OL620152

	XY03176	soil	Heilongijang, China	OL620153
TT			71	01 (79222
U. septata	<b>UGMUU 3.16162</b> <sup>4</sup>	SO11	Znejiang, Unina	UL0/8233
U. sinsidoensis	XY06194	soil	Zhejiang, China	OL620154
U. tibetica	CGMCC 3.16163 <sup>T</sup>	soil	Tibet, China	OL678234
	XY07881	soil	Tibet, China	OL678235
	XY07882	soil	Tibet, China	OL678236

**Table 2.** The genomic information used for molecular dating in this study. \* SRA NCBI stands forSequence Read Archive, National Center for Biotechnology Information, US National Library ofMedicine.

Species	Strains	BioSample	SRA NCBI*	Reference
Absidia glauca	CBS 101.48	SAMEA3923633	ERS1110767	(Ellenberger et al. 2016)
Acaulospora morrowiae	CL551	SAMEA8911292	ERS6594176	
Ambispora gerdemannii	MT106	SAMEA8911308	ERS6594192	
A. leptoticha	FL130A	SAMEA8911307	ERS6594191	
Apophysomyces elegans	B7760	SAMN02351510	SRS478092	
A. trapeziformis	B9324	SAMN02351504	SRS478090	
Backusella circina	CGMCC3.15908	SAMN28403603		This study
B. lamprospora	CGMCC3.15922	SAMN28403604		This study
Cetraspora pellucida	FL966	SAMEA8911298	ERS6594182	
Choanephora	KUS-F282377	SAMN04532838		
cucurbitarum Claroideoglomus candidum	CCK_pot_B_6-9	SAMEA8911304	ERS6594188	
Cokeromyces recurvatus	B5483	SAMN02370952	SRS489494	
Cunninghamella elegans	B9769	SAMN02351511	SRS478097	
Dentiscutata erythropus	MA453B	SAMEA8911297	ERS6594181	
Dissophora decumbens	CBS 301.87	SAMN23435287		This study
D. globulifera	CBS 858.70	SAMN23461011		This study
Diversispora eburnea	AZ414A	SAMEA8911293	ERS6594177	
Endogone sp.	FLAS-F59071	SAMN09071421	SRS5707057	(Chang et al. 2019)
Entomortierella lignicola	CBS 207.37	SAMN23441792		This study
---------------------------	--------------	--------------	------------	----------------------------
E. parvispora	CBS 304.52	SAMN23437757		This study
Funneliformis caledonium	UK204	SAMEA8911289	ERS6594173	
F. mosseae	87-	SAMEA8911288	ERS6594172	
	6_pot_B_2015			
Gamsiella multidivaricata	CBS 227.78	SAMN23437755		This study
Geosiphon pyriformis	V1.0			(Malar <i>et al.</i> 2021,
				2022)
Gigaspora margarita	BEG34	SAMEA6235760	ERS4035453	
G. rosea	DAOM194757			(Morin et al. 2019)
Hesseltinella vesiculosa	NRRL 3301	SAMN02745228	SRS710783	(Mondo et al. 2017)
Jimgerdemannia	AD002	SAMN09071422	SRS5707054	(Chang et al. 2019)
flammicorona				
J. flammicorona	GMNB39	SAMN05444478		(Chang et al. 2019)
J. lactiflua	OSC166217	SAMN10169340		(Chang et al. 2019)
Lichtheimia corymbifera	FSU 9682	SAMEA2189700	ERS339162	(Schwartze et al. 2014)
L. ramosa	FSU 6197	SAMN05179542	SRS1468292	(Linde et al. 2014)
Linnemannia amoeboidea	CBS 889.72	SAMN19911466	SRS9293840	(Yang et al. 2022)
Mortierella indohii	CBS 720.71	SAMN23441793		This study
M. microzygospora	CBS 880.97	SAMN23441791		This study
M. parazychae	CBS 868.71	SAMN23441790		This study
M. rishikesha	CBS 652.68	SAMN23437756		This study
Mucor circinelloides	1006PhL	SAMN00103456	SRS074119	(Lee et al. 2014)
M. lusitanicus	CBS 277.49	SAMN00120579		(Corrochano et al. 2016)
M. saturninus		SAMN16393843		
Paraglomus brasilianum	BR232B	SAMEA8911306	ERS6594190	
P. occultum	IA702	SAMEA8911305	ERS6594189	
Parasitella parasitica	CBS 412.66	SAMEA278055	ERS550304	(Ellenberger et al. 2016)
Podila clonocystis	CBS 357.76	SAMN23461012		This study
Racocetra persica	MA461A	SAMEA8911300	ERS6594184	
Rhizophagus cerebriforme	DAOM 227022			(Morin et al. 2019)

R. clarus	RCL21	SAMD00190756		
R. irregularis	DAOM 197198			(Morin et al. 2019)
Rhizopus arrhizus	GL8	SAMN14162349		(Nguyen et al. 2020)
R. arrhizus	GL4	SAMN14162309		(Nguyen et al. 2020)
R. microsporus	ATCC 52813	SAMN06821222	SRS2140116	(Horn <i>et al.</i> 2015)
Phycomyces blakesleeanus	NRRL 1555	SAMN00189023		(Corrochano et al. 2016)
Smittium culicis	GSMNP	SAMN04489870		(Wang et al. 2016)
Syncephalastrum monosporum	B8922	SAMN02370995	SRS489641	
Thermomucor indicae- seudaticae	HACC 243	SAMN03070115	SRS702596	
Umbelopsis isabellina	WA0000067209	SAMN16393839		(Takeda et al. 2014)
U. vinacea	WA0000051536	SAMN16393840	SRS7563300	

## Table 3. GenBank accession numbers of sequences used in this study. "T" represents

ex-nolotype.				
Species	Strains	GenBank acc	GenBank accession nos.	
		ITS	LSU	
Absidia cylindrospora	CBS 100.08	JN205822	JN206588	
Absidia glauca	CBS 101.08 <sup>T</sup>	NR_111658	NG_058550	
Absidia repens	CBS 115583 <sup>T</sup>	NR103624	HM849706	
Acaulospora alpina	pMK114-32	FR681930	FR681930	
Acaulospora entreriana	W5476 <sup>T</sup>	NR_121441		
Acaulospora spinosa	pMK038-15	FR750152	FR750152	
Actinomucor elegans	CBS 100.13	MH854612	MH866137	
Actinomucor elegans	CBS 111559	AY243955	AF157173	
Ambispora fennica	W4752	FR750157	FR750157	
Ambispora granatensis	JEP-2010	FN820280		
Ambomucor seriatoinflatus	CGMCC 3.6665 <sup>T</sup>	AY743664	AY743664	
Apophysomyces elegans	CBS 476.78 <sup>T</sup>	NR_149336	JN206536	
Apophysomyces mexicanus	CBS 136361 <sup>T</sup>	HG974255	HG974256	

Archaeospora ecuadorianaW6483 TNR_168426Archaeospora trappeiAtt178-3FR750035FR750035Backusella circinaCBS 128.70 TMH859516MH871298Backusella lamprosporaCBS 118.08 TNR_145291MH866110Benjaminiella multisporaCBS 421.70 TNR_103645JN206410Benjaminiella voungiiCBS 103.89 TNR_103644NG_069814Benniella sp.J.122MW580775MH873958Blakeslea trisporaCBS 564.91 TMH862277MH873958Bulbospora minimaG36KJ944324Calcarisporiella thermophilaCBS 279.70 TNR_153863AB617741Cetraspora armeniacaCe-8MG459217MG459217Chaetocladium brefeldiiCBS 137.28MH854954MH866440Chaetocladium brefeldiiCBS 172.67 TNR_153872NG_070364Choanephora infundibuliferaCBS 107.13MH854617JN206513Circinella muscaeCBS 107.13MH854617JN20650Claroideoglomus haminnii251-101KP191488KP191482Claroideoglomus haminniiSV_421MT765715MT65715Claroideoglomus haminnii162-41KP191492KP191492Corymbiglomus corymbiglomus100-4KP060297KP60297Cunninghamella echinulataCBS 156.28 TJN206589HM849702				
Archaeospora trappeiAtt178-3FR750035FR750035Backusella circinaCBS 128.70TMH859516MH871298Backusella lamprosporaCBS 118.08TNR_145291MH866110Benjaminiella multisporaCBS 421.70TNR_103645JN206410Benjaminiella multisporaCBS 103.89TNR_103644NG_069814Benjaminiella sp.JL122MW580775Blakeslea trisporaCBS 564.91TMH862277MH873958Bulbospora minimaG36KJ944324CalcarisporiellaCBS 279.70TNR_153863AB617741thermophilaCBS 137.28MG459217MG459217Cetraspora helveticaSAF15TNG_075173MH866440Chlamydoabsidia padeniiCBS 137.28MH854954MH866440Choanephora infimdibultiferaCBS 107.13MH854617JN206513Circinella muscaeCBS 107.13MH854617JN206513Claroideoglomus drummondii251-101KP191488KP191482Claroideoglomus hanumondii251-101KP191482KP191482Claroideoglomus walkeri162-41KP191492KP191492Cokeromyces recurvatusCBS 158.50NR_071712HM8496997Corymbiglomus corymbiglomus100-4KP00297KF060297Cunninghamella echimulataCBS 156.28TJN205895HM849702	Archaeospora ecuadoriana	W6483 <sup>T</sup>	NR_168426	
Backusella circinaCBS 128.70°MH859516MH871298Backusella lamprosporaCBS 118.08°NR_145291MH866110Benjaminiella multisporaCBS 103.89°NR_103645JN206410Benjaminiella youngiiCBS 103.89°NR_103644NG_069814Benniella sp.JL122MW580775MH873958Blakeslea trisporaCBS 564.91°MH862277MH873958Bulbospora minimaG36KJ944325Bulbospora minimaG35KJ944324CalcarisporiellaCBS 279.70°NR_153863AB617741thermophilaCBS 172.87°NR_153863AB617741Cetraspora armeniacaCe-8MG459217MG459217ChacarisporiellaCBS 172.67°NR_153872NG_070364ChaonephoraCBS 172.67°NR_153872NG_070364ChoanephoraCBS 153.51JN206236JN206513infimdibuliferaCBS 153.51MH854617JN206513Circinella muscaeCBS 171.3MH854517JN206513Claroideoglomus120-81MH85752MH869090ClaroideoglomusASV_421MT765715MT765715lamellosum162-41KP191482KP191492Corymbiglomus100-4KF060297KF060297corymbiforme100-4KF060297KF060297	Archaeospora trappei	Att178-3	FR750035	FR750035
Backusella lamprosporaCBS 118.08 <sup>T</sup> NR_145291MH866110Benjaminiella multisporaCBS 421.70 <sup>T</sup> NR_103645JN206410Benjaminiella youngiiCBS 103.89 <sup>T</sup> NR_103644NG_069814Benniella sp.JL122MW580775MH873958Blakeslea trisporaCBS 564.91 <sup>T</sup> MH862277MH873958Bulbospora minimaG36KJ944325Bulbospora minimaG35KJ944324CalcarisporiellaCBS 279.70 <sup>T</sup> NR_153863AB617741thermophilaCBS 137.28MH8549217MG459217Cetraspora helveticaSAF15 <sup>T</sup> NG_075173NG_075173Chaetocladium brefeldiiCBS 137.28MH854954MH866440Chlamydoabsidia padeniiCBS 153.51JN206236JN206513infindibuliferaCBS 153.51JN206236JN206513Circinella muscaeCBS 107.13MH854617JN206550Claroideoglomus120-81KP191482KP191488drummondii251-101KP191482KP191482Claroideoglomus hanlinii251-101KP191482KP191482Claroideoglomus walkeri162-41KP191492KP191492Corymbigforme100-4KF060297KF060297Corymbiforme100-4KF060297KF060297	Backusella circina	CBS 128.70 <sup>T</sup>	MH859516	MH871298
Benjaminiella multisporaCBS 421.70 <sup>T</sup> NR_103645JN206410Benjaminiella youngiiCBS 103.89 <sup>T</sup> NR_103644NG_069814Benniella sp.JL 122MWS80775Blakeslea trisporaCBS 564.91 <sup>T</sup> MH862277MH873958Bulbospora minimaG36KJ944325Bulbospora minimaG35KJ944324Calcarisporiella thermophilaCBS 279.70 <sup>T</sup> NR_153863AB617741Cetraspora armeniacaCe-8MG459217MG459217Cetraspora armeniacaCe-8MG459217MG6_075173Chaetocladium brefeldiiCBS 137.28MH854954MH866440Chlamydoabsidia padeniiCBS 172.67 <sup>T</sup> NR_153872NG_070364Circinella muscaeCBS 107.13MH854617JN206513Circinella umbellataCBS 145.56MH857552MH869090Claroideoglomus drummondii251-101KP191482KP191482Claroideoglomus hanlinii251-101KP191482KP191482Claroideoglomus walkeri162-41KP191492KP191492Corymbiglomus corymbiglomusCBS 155.50NR_077172HM849699Corymbiglomus corymbiglorme100-4KF060297KF060297Cunninghamella echinulataCBS 156.28 <sup>T</sup> JN205895HM849702	Backusella lamprospora	CBS 118.08 <sup>T</sup>	NR_145291	MH866110
Benjaminiella youngiiCBS 103.89°NR_103644NG_069814Benniella sp.JL122MW580775Blakeslea trisporaCBS 564.91°MH862277MH873958Bulbospora minimaG36KJ944325Bulbospora minimaG35KJ944324Calcarisporiella thermophilaCBS 279.70° Cetraspora armeniacaNR_153863AB617741Cetraspora armeniacaCe-8MG459217MG459217Cetraspora helveticaSAF15°NG_075173Chaetocladium brefeldiiCBS 137.28MH854954MH866440Chlamydoabsidia padeniiCBS 172.67°NR_153872NG_070364Choanephora infundibuliferaCBS 153.51MH854954MH86090Circinella muscaeCBS 107.13MH854617JN206513Circinella umbellataCBS 145.56MH85752MH869090Claroideoglomus harumondii251-101KP191482KP191482Claroideoglomus hanlinii251-101KP191482KP191482Claroideoglomus walkeri162-41KP191492KP191492Corymbiglomus corymbiglomusCBS 158.50NR_077172HM849699Corymbiglomus corymbiforme100-4KF060297KF060297Cunninghamella echinulataCBS 156.28°JN205895HM849702	Benjaminiella multispora	CBS 421.70 <sup>T</sup>	NR_103645	JN206410
Benniella sp.JL 122MWS80775Blakeslea trisporaCBS 564.91"MH862277MH873958Bulbospora minimaG36KJ944325Bulbospora minimaG35KJ944324CalcarisporiellaCBS 279.70"NR_153863AB617741thermophilaCe-8MG459217MG459217Cetraspora armeniacaCe-8MH854954MH866440Chaetocladium brefeldiiCBS 137.28MH854954MH866440Chaanydoabsidia padeniiCBS 172.67"NR_153872NG_070364ChoanephoraCBS 153.51JN206236JN206513infundibuliferaCBS 107.13MH854617JN206550Circinella muscaeCBS 145.56MH857552MH869090ClaroideoglomusJ20-81KP191482KP191482drummondii251-101KP191482KP191482Claroideoglomus hanlinii251-101KP191482KP191482Claroideoglomus walkeri162-41KP191492KP191492Cokeromyces recurvatusCBS 158.50NR_07172HM849699CorymbiglomusCBS 158.50NR_07172HM849699CorymbiformeCBS 158.28"JN205895HM849702	Benjaminiella youngii	CBS 103.89 <sup>T</sup>	NR_103644	NG_069814
Blakeslea trisporaCBS 564.91 <sup>T</sup> MH862277MH873958Bulbospora minimaG36KJ944325Bulbospora minimaG35KJ944324CalcarisporiellaCBS 279.70 <sup>T</sup> NR_153863AB617741thermophilaCBS 279.70 <sup>T</sup> NR_153863AB617741Cetraspora armeniacaCe-8MG459217MG459217Cetraspora helveticaSAF15 <sup>T</sup> NG_075173Chaetocladium brefeldiiCBS 137.28MH854954MH866440Chlamydoabsidia padeniiCBS 172.67 <sup>T</sup> NR_153872NG_070364Choanephora infundibuliferaCBS 107.13MH854617JN206513Circinella muscaeCBS 107.13MH854617JN206550Claroideoglomus drummondii251-101KP191482KP191482Claroideoglomus hamellosumASV_421MT765715MT765715Claroideoglomus walkeri162-41KP191492KP191492Corymbiglomus corymbiforme100-4KF060297KF060297Cunninghamella echinulataCBS 156.28 <sup>T</sup> JN205895HM849702	Benniella sp.	JL122	MW580775	
Bulbospora minimaG36KJ944325Bulbospora minimaG35KJ944324Calcarisporiella (hermophilaCBS 279.70° CBS 279.70°NR_153863AB617741Cetraspora armeniacaCe-8MG459217MG459217Cetraspora helveticaSAF15°NG_075173Chaetocladium brefeldiiCBS 137.28MH854954MH866440Chlamydoabsidia padeniiCBS 172.67°NR_153872NG_070364Choanephora infundibuliferaCBS 153.51NR_02036MH86040Circinella muscaeCBS 107.13MH854617JN206513Claroideoglomus drummondiiCBS 145.56MH857552MH869090Claroideoglomus hanlinii251-101KP191488KP191488Claroideoglomus hamellosum162-41KP191492KP191492Claroideoglomus walkeri162-41KP191492KP191492Corymbiglomus corymbiformeCBS 158.50NR_077172HM849699Corymbiglomus corymbiformeCBS 156.28°JN205895HM849702	Blakeslea trispora	CBS 564.91 <sup>T</sup>	MH862277	MH873958
Bulbospora minimaG35KJ944324Calcarisporiella thermophilaCBS 279.70TNR_153863AB617741Cetraspora armeniacaCe-8MG459217MG459217Cetraspora helveticaSAF15TNG_075173Chaetocladium brefeldiiCBS 137.28MH854954MH866440Chlamydoabsidia padeniiCBS 172.67TNR_153872NG_070364Choanephora infundibuliferaCBS 173.51NN206236MB2050Circinella muscaeCBS 107.13MH854617JN206513Claroideoglomus drumnondiiCBS 145.56MH857552MH869090Claroideoglomus hanlinii251-101KP191488KP191488Claroideoglomus walkeri162-41KP191492KP191492Claroideoglomus walkeri162-41KP191492KP191492Corymbiglomus corymbiformeD0-4KF060297KF060297Cunninghamella cehinulataCBS 156.28TJN205895HM849702	Bulbospora minima	G36		KJ944325
Calcarisporiella thermophilaCBS 279.70°NR_153863AB617741thermophilaCBS 279.70°NR_153863AB617741Cetraspora armeniacaCe-8MG459217MG459217Cetraspora helveticaSAF15°NG_075173Chaetocladium brefeldiiCBS 137.28MH854954MH866440Chlamydoabsidia padeniiCBS 172.67°NR_153872NG_070364Choanephora infundibuliferaCBS 153.51JN206236JN206513Circinella muscaeCBS 107.13MH854617JN206550Claroideoglomus drumnondiiCBS 145.56MH857552MH869090Claroideoglomus hanlinii251-101KP191488KP191482Claroideoglomus hanliniiASV_421MT765715MT765715Iamellosum162-41KP191492KP191492Cokeromyces recurvatusCBS 158.50NR_077172HM849699Corymbiglomus corymbiforme100-4KF060297KF060297Cunninghamella echinulataCBS 156.28°JN205895HM84702	Bulbospora minima	G35		KJ944324
thermophilaCBS 279.70°NR_153863AB617/41thermophilaCeraspora armeniacaCe-8MG459217MG459217Cetraspora helveticaSAF15 <sup>T</sup> NG_075173Chaetocladium brefeldiiCBS 137.28MH854954MH866440Chlamydoabsidia padeniiCBS 172.67 <sup>T</sup> NR_153872NG_070364ChoanephoraCBS 172.67 <sup>T</sup> NR_153872NG_070364ChoanephoraCBS 153.51JN206236JN206513infundibuliferaCBS 107.13MH854617JN206550Circinella muscaeCBS 145.56MH857552MH869090Claroideoglomus120-81KP191488KP191488drummondii251-101KP191482KP191482Claroideoglomus hanlinii251-101KP191482KP191482Claroideoglomus walkeri162-41KP191492KP191492Cokeromyces recurvatusCBS 158.50NR_077172HM849699Corymbiglomus100-4KF060297KF060297Cunninghamella echinulataCBS 156.28 <sup>T</sup> JN205895HM849702	Calcarisporiella		ND 1529/2	AD(17741
Cetraspora armeniacaCe-8MG459217MG459217Cetraspora helveticaSAF15TNG_075173Chaetocladium brefeldiiCBS 137.28MH854954MH866440Chlamydoabsidia padeniiCBS 172.67TNR_153872NG_070364ChoanephoraCBS 172.67TNR_153872NG_070364ChoanephoraCBS 153.51JN206236JN206513infundibuliferaCBS 107.13MH854617JN206550Circinella muscaeCBS 145.56MH857552MH869090Claroideoglomus120-81KP191488KP191488drummondii251-101KP191482KP191482Claroideoglomus hanlinii251-101KP191482KP191482Claroideoglomus walkeri162-41KP191492KP191492Cokeromyces recurvatusCBS 158.50NR_077172HM849699Corymbiglomus $100-4$ KF060297KF060297Cunninghamella echinulataCBS 156.28TJN205895HM849702	thermophila	CBS 279.70 <sup>2</sup>	NR_153863	AB01//41
Cetraspora helveticaSAF15TNG_075173Chaetocladium brefeldiiCBS 137.28MH854954MH866440Chlamydoabsidia padeniiCBS 172.67TNR_153872NG_070364ChoanephoraCBS 153.51JN206236JN206513infundibuliferaCBS 107.13MH854617JN206550Circinella muscaeCBS 145.56MH857552MH869090Claroideoglomus120-81KP191488KP191488drummondii251-101KP191482KP191482Claroideoglomus hanlinii251-101KP191482KP191482Claroideoglomus walkeri162-41KP191492KP191492Cokeromyces recurvatusCBS 158.50NR_077172HM849699Corymbiglomus100-4KP600297KP60297Cunninghamella echinulataCBS 156.28TJN205895HM849702	Cetraspora armeniaca	Ce-8	MG459217	MG459217
Chaetocladium brefeldii         CBS 137.28         MH854954         MH866440           Chlamydoabsidia padenii         CBS 172.67 <sup>T</sup> NR_153872         NG_070364           Choanephora         CBS 153.51         NR_153872         NG_070364           infundibulifera         CBS 153.51         JN206236         JN206513           Circinella muscae         CBS 107.13         MH854617         JN206550           Circinella umbellata         CBS 145.56         MH857552         MH869090           Claroideoglomus         120-81         KP191488         KP191488           drummondii         251-101         KP191482         KP191482           Claroideoglomus hanlinii         251-101         KP191482         KP191482           Claroideoglomus hanlinii         251-101         KP191482         KP191482           Claroideoglomus hanlinii         251-101         KP191482         KP191492           Iamellosum         6BS 158.50         NR_077172         HM849699           Cokeromyces recurvatus         CBS 158.50         NR_077172         HM849699           Corymbiglomus         100-4         KF060297         KF060297           Cunninghamella echinulata         CBS 156.28 <sup>T</sup> JN205895         HM849702	Cetraspora helvetica	$SAF15^{T}$		NG_075173
Chlamydoabsidia padenii         CBS 172.67 <sup>T</sup> NR_153872         NG_070364           Choanephora $BB 153.51$ $JN206236$ $JN206513$ infundibulifera         CBS 107.13         MH854617 $JN206550$ Circinella muscae         CBS 145.56         MH857552         MH869090           Claroideoglomus         CBS 145.56         MH857552         MH869090           Claroideoglomus         120-81         RP191488         RP191488           drummondii         251-101         KP191482         KP191482           Claroideoglomus hanlinii         251-101         KP191482         KP191482           Claroideoglomus hanlinii         251-101         KP191482         KP191482           Claroideoglomus hanlinii         251-101         KP191482         KP191482           Claroideoglomus walkeri         162-41         KP191492         KP191492           Cokeromyces recurvatus         CBS 158.50         NR_077172         HM849699           Corymbiglomus         100-4         KF060297         KF060297           Cunninghamella echinulata         CBS 156.28 <sup>T</sup> JN205895         HM849702	Chaetocladium brefeldii	CBS 137.28	MH854954	MH866440
Choanephora infundibulifera $CBS 153.51$ $JN206236$ $JN206513$ Circinella muscae         CBS 107.13         MH854617         JN206550           Circinella muscae         CBS 107.13         MH857552         MH869090           Circinella umbellata         CBS 145.56         MH857552         MH869090           Claroideoglomus drummondii $120-81$ $KP191488$ $KP191488$ Claroideoglomus hanlinii         251-101         KP191482         KP191482           Claroideoglomus hamellosum $ASV_421$ MT765715         MT765715           Claroideoglomus walkeri         162-41         KP191492         KP191492           Cokeromyces recurvatus         CBS 158.50         NR_077172         HM849699           Corymbiglomus corymbiforme $100-4$ $KF060297$ $KF060297$ Cunninghamella echinulata         CBS 156.28 <sup>T</sup> JN205895         HM849702	Chlamydoabsidia padenii	CBS 172.67 <sup>T</sup>	NR_153872	NG_070364
infundibuliferaJN206236JN206313infundibuliferaCBS 133.51JN206513Circinella muscaeCBS 107.13MH854617JN206550Circinella umbellataCBS 145.56MH857552MH869090Claroideoglomus120-81KP191488KP191488drummondii251-101KP191482KP191482Claroideoglomus hanlinii251-101KP191482KP191482ClaroideoglomusASV_421MT765715MT765715lamellosum162-41KP191492KP191492Cokeromyces recurvatusCBS 158.50NR_077172HM849699Corymbiglomus100-4KF060297KF060297Cunninghamella echinulataCBS 156.28 <sup>T</sup> JN205895HM849702	Choanephora	ODC 152 51	<b>D</b> 120(22)	<b>NI20(512</b>
Circinella muscae         CBS 107.13         MH854617         JN206550           Circinella umbellata         CBS 145.56         MH857552         MH869090           Claroideoglomus         120-81         KP191488         KP191488           drummondii         251-101         KP191482         KP191482           Claroideoglomus hanlinii         251-101         KP191482         KP191482           Claroideoglomus         ASV_421         MT765715         MT765715           lamellosum         162-41         KP191492         KP191492           Cokeromyces recurvatus         CBS 158.50         NR_077172         HM849699           Corymbiglomus         100-4         KF060297         KF060297           Cunninghamella echinulata         CBS 156.28 <sup>T</sup> JN205895         HM849702	infundibulifera	CBS 153.51	JN206236	JIN206513
Circinella umbellataCBS 145.56MH857552MH869090Claroideoglomus $120-81$ $KP191488$ $KP191488$ drummondii $251-101$ $KP191482$ $KP191482$ Claroideoglomus hanlinii $251-101$ $KP191482$ $KP191482$ Claroideoglomus $ASV_421$ $MT765715$ $MT765715$ lamellosum $162-41$ $KP191492$ $KP191492$ Cokeromyces recurvatusCBS 158.50 $NR_077172$ $HM849699$ Corymbiglomus $100-4$ $KF060297$ $KF060297$ Cunninghamella echinulataCBS 156.28 <sup>T</sup> $JN205895$ $HM849702$	Circinella muscae	CBS 107.13	MH854617	JN206550
Claroideoglomus drummondii120-81KP191488KP191488Claroideoglomus hanlinii251-101KP191482KP191482Claroideoglomus lamellosum $ASV_421$ MT765715MT765715Claroideoglomus walkeri162-41KP191492KP191492Cokeromyces recurvatusCBS 158.50NR_077172HM849699Corymbiglomus corymbiforme $100-4$ KF060297KF060297Cunninghamella echinulataCBS 156.28 <sup>T</sup> JN205895HM849702	Circinella umbellata	CBS 145.56	MH857552	MH869090
$I20-81$ KP191488KP191488 $drummondii$ $Claroideoglomus hanlinii$ $251-101$ $KP191482$ $KP191482$ $Claroideoglomus$ $lamellosum$ $ASV_421$ $MT765715$ $MT765715$ $Claroideoglomus walkeri$ $162-41$ $KP191492$ $KP191492$ $Cokeromyces recurvatus$ $CBS 158.50$ $NR_077172$ $HM849699$ $Corymbiglomus$ $corymbiforme$ $100-4$ $KF060297$ $KF060297$ $Cunninghamella echinulata$ $CBS 156.28^T$ $JN205895$ $HM849702$	Claroideoglomus	120.01	<b>ZD101400</b>	<b>UD101400</b>
Claroideoglomus hanlinii251-101KP191482KP191482Claroideoglomus lamellosum $ASV_421$ $MT765715$ $MT765715$ Claroideoglomus walkeri162-41KP191492KP191492Cokeromyces recurvatusCBS 158.50NR_077172HM849699Corymbiglomus corymbiforme $100-4$ $KF060297$ $KF060297$ Cunninghamella echinulataCBS 156.28 <sup>T</sup> JN205895HM849702	drummondii	120-81	KP191488	KP191488
Claroideoglomus lamellosumASV_421MT765715MT765715Claroideoglomus walkeri162-41KP191492KP191492Cokeromyces recurvatusCBS 158.50NR_077172HM849699Corymbiglomus corymbiforme100-4KF060297KF060297Cunninghamella echinulataCBS 156.28 <sup>T</sup> JN205895HM849702	Claroideoglomus hanlinii	251-101	KP191482	KP191482
IamellosumASV_421MT/65/15MT/65/15 $Claroideoglomus walkeri$ 162-41KP191492KP191492 $Cokeromyces recurvatus$ CBS 158.50NR_077172HM849699 $Corymbiglomus$ $corymbiforme$ 100-4KF060297KF060297 $Cunninghamella echinulata$ CBS 156.28 <sup>T</sup> JN205895HM849702	Claroideoglomus	A GV 421	NTT(5715	
Claroideoglomus walkeri162-41KP191492KP191492Cokeromyces recurvatusCBS 158.50NR_077172HM849699Corymbiglomus corymbiforme100-4 $KF060297$ $KF060297$ Cunninghamella echinulataCBS 156.28 <sup>T</sup> JN205895HM849702	lamellosum	ASV_421	M11/05/15	M1/03/13
Cokeromyces recurvatusCBS 158.50NR_077172HM849699Corymbiglomus corymbiforme100-4KF060297KF060297Cunninghamella echinulataCBS 156.28TJN205895HM849702	Claroideoglomus walkeri	162-41	KP191492	KP191492
Corymbiglomus corymbiforme100-4KF060297KF060297Cunninghamella echinulataCBS 156.28 <sup>T</sup> JN205895HM849702	Cokeromyces recurvatus	CBS 158.50	NR_077172	HM849699
corymbiformeIOO-4KF060297KF060297Cunninghamella echinulataCBS 156.28TJN205895HM849702	Corymbiglomus	100.4	VE0/0207	VE0(0207
<i>Cunninghamella echinulata</i> CBS 156.28 <sup>T</sup> JN205895 HM849702	corymbiforme	100-4	KF000297	KFU0U29/
	Cunninghamella echinulata	CBS 156.28 <sup>T</sup>	JN205895	HM849702

Cunninghamella globospora	CGMCC 3.16020 <sup>T</sup>	MW264073	MW264132
Desertispora omanana	D73	KF154770	KF154770
Dichotomocladium elegans	CBS 714.74 <sup>T</sup>	JN205839	JN206555
Dichotomocladium	CBS 440.76 <sup>T</sup>	JN205843	NG_059082
Disugnophong fulya	NIDDI 22204		AE157196
	NKKL 22204	12076001	AF15/100
Dissophora aecumbens	CBS 301.87	JA9/0001	HQ007334
Dissophora ornata	CBS 348.77	MH861074	MH872843
Diversispora celata	BEG 231 <sup>1</sup>		NG_070483
Diversispora clara	1.11	FR873632	FR873632
Dominikia bernensis	FO310	HG938304	HG938304
Dominikia difficilevidera	279-8	KR105649	KR105649
Echinochlamydosporium variabile	LN07-7-4 <sup>T</sup>	EU688962	EU688963
Ellisomyces anomalus	CBS 243.57 <sup>T</sup>	MH857709	MH869249
Endogone botryocarpus	Е-14001 <sup>т</sup>		NG_068251
Endogone corticioides	NC0024744		LC107372
Endogone pisiformis	NC0024232		LC107366
Entomortierella lignicola	CBS 207.37 <sup>T</sup>	NR_145301	NG_070276
Entomortierella parvispora	CBS 304.52 <sup>T</sup>	JX975859	MH868582
Fennellomyces	CDC 200 0/	<b>B</b> 100 50 4 4	
heterothallicus	CBS 290.86	JN205844	MH8/364/
Fennellomyces linderi	CBS 158.54 <sup>T</sup>	NR_164085	HM849723
Funneliformis caledonium	BEG20	FN547496	FN547496
Funneliformis mosseae	BEG12		FN547474
Funneliformis pilosus	7P	MT376718	MT376718
Gamsiella multidivaricata	CBS 227.78 <sup>T</sup>	MH861129	MH872890
Gigaspora albida	FL713-L2		JF816995
Gigaspora decipiens	DSU-55	ON081653	
Gigaspora decipiens	URMFMA15		MT967282

Gigaspora margarita	W5792	FR750040	FR750040
Gigaspora rosea	DAOM194757	FN547591	FN547591
Gilbertella persicaria	CBS 190.32	MH855278	MH866729
Glomus macrocarpum	Att1495-0	FR750368	FR750368
Glomus macrocarpum	W5288	FR750530	FR750530
Gongronella butleri	CBS 216.58	MH859014	MH869292
Gongronella namwonensis	CNUFC WW2-12 <sup><math>T</math></sup>	NR_175640	MN658482
Gryganskiella cystojenkinii	CBS 696.70	MH859910	MH871704
Gryganskiella fimbricystis	CBS 943.70 <sup>T</sup>	MH860013	MH871799
Halteromyces radiatus	CBS 162.75 <sup>T</sup>	NR_145293	NG_057938
Helicostylum elegans	CBS 169.57	AB113013	JN206471
Helicostylum pulchrum	CBS 259.68	JN206054	MT523864
Hesseltinella vesiculosa	CBS 197.68 <sup>T</sup>		JN206610
Hyphomucor assamensis	CBS 415.77 <sup>T</sup>	MH861081	MH872849
Innospora majewskii	1	KY630229	KY630229
Intraornatospora	-11		<b>NIO71072</b>
intraornata	clone 1		JIN9/10/3
Isomucor trufemiae	CCIBt 2328 <sup>T</sup>	HQ592190	NG_060268
Jimgerdemannia ambigua	G-14001		LC431096
Jimgerdemannia		01/220101	01/220101
flammicorona	GMNB39	OM238191	OM238191
Kamienskia bistrata	G-14001	KJ564137	KJ564137
Kirkomyces cordense	NRRL 22618		AF157196
Lentamyces parricidus	CBS 174.67 <sup>T</sup>	NR_103651	NG_067380
Lentamyces zychae	FSU 5797	EF030529	EU736309
Lichtheimia corymbifera	CBS 479.75 <sup>T</sup>	NR_111413	FJ719444
Lichtheimia ornata	CBS 958.68	MH859253	MH870981
Linnemannia amoeboidea	CBS 889.72 <sup>T</sup>	NR_111579	
Linnemannia gamsii	CBS 749.68 <sup>T</sup>	NR_152954	NG_070584

Lobosporangium	CBS $357.67^{T}$		MH870693
transversale	010 337.07		1111070075
Lunasporangiospora chienii	CBS 124.71	MH860031	MH871813
Lunasporangiospora	CBS 811 68 <sup>T</sup>	NR 145296	NG 057800
selenospora	CD5 011.00	NK_145250	NG_057677
Microdominikia litorea	ASV_425	MT765719	MT765719
Microkamienskia divaricata	240-10 <sup>T</sup>	KX758126	KX758126
Microkamienskia peruviana	clone 1	MK903005	MK903005
Modicella malleola	Т	KF053135	KF053131
Modicella reniformis		KF053136	KF053132
Mortierella indohii	CBS 720.71 <sup>T</sup>	NR_111561	NG_042545
Mortierella microzygospora	CBS 880.97 <sup>T</sup>	NR_111569	NG_042553
Mortierella parazychae	CBS 868.71 <sup>T</sup>	MH860387	NG_057895
Mortierella polycephala	CBS 293.34	JX976050	JX976137
Mortierella rishikesha	CBS 652.68 <sup>T</sup>	NR_111564	NG_042548
Mucor abundans	CNS 338.35 <sup>T</sup>	MH855716	MH867228
Mucor azygosporus	CBS 292.63 <sup>T</sup>	NR_103639	JN206497
Mucor indicus	CBS 226.29 <sup>T</sup>	MH855050	NG_057878
Mucor luteus	CBS 243.35 <sup>T</sup>	NR_120224	HM849685
Mucor mucedo	CBS 144.24	MH854782	MH866285
Mucor silvaticus	CBS 249.35	MH855666	MH867180
Mycotypha africana	NRRL 2978		AF157201
Mycotypha indica	CBS 245.84 <sup>T</sup>	NR_160167	NG_064135
Necromortierella dichotoma	CBS 221.35 <sup>T</sup>	NR_111568	MH867165
Neurospora crassa	OR74A	HQ271348	AF286411
Oehlia diaphana	Od_2	MG836667	MG836667
Pacispora franciscana	Att599-7		FR750219
Pacispora scintillans	O18	OK184925	OK184925
Paradentiscutata bahiana	spore 1		JN971069
Paradentiscutata maritima			JN971079

Paraglomus	C21		IV122772	
pernambucanum	021		JA122/72	
Paraglomus	C26		IV100777	
pernambucanum	620		J2X144	
Parasitella parasitica	CBS 412.66 <sup>T</sup>	JN206027	JN206438	
Pervetustus simplex	MENA166	ON033169	ON033169	
Phascolomyces articulosus	CBS 113.76	JX665039	JN206547	
Phycomyces blakesleeanus	CBS 112.20 <sup>T</sup>	MH854683	MH866200	
Phycomyces nitens	CBS 149.24	MH854786	MH866290	
Pilaira anomala	CBS 131.23	MH859777	MH866256	
Pilobolus umbonatus	CBS 425.50	MH856700	MH868216	
Pirella circinans	CBS 962.68 <sup>T</sup>	NR_103637	NG_057933	
Pirella naumovii	CBS 524.68	NR_155626	JN206474	
Podila clonocystis	CBS 357.76 <sup>T</sup>	NR_111570	NG_042554	
Podila humilis	CBS 222.35	NR_077209	NG_070522	
Poitrasia circinans	CBS 153.58 <sup>T</sup>	NR_145288	NG_057934	
Protomycocladus			MI1072(00	
faisalabadensis	CBS 661.86		MH8/3099	
Pygmaeomyces pinuum	PP16-P31	MN017034	MN017099	
Pygmaeomyces thomasii	PP16-P25	MN017031	MN017096	
Racocetra crispa	CMPC739.2	KX529097	KX529097	
Racocetra tropicana	86-8600	GU385897	GU385897	
Radiomyces embreei	CBS 205.77	JN206291	HM849663	
Radiomyces spectabilis	CBS 255.60 <sup>T</sup>		MH869529	
Redeckera megalocarpum	FL130		MT832215	
Rhizomucor miehei	CBS 182.67 <sup>T</sup>	NR_164370	NG_057880	
Rhizomucor pusillus	CBS 354.68 <sup>T</sup>	JN206312	NG_057879	
Rhizophagus intraradices	FL208	FR750126	FR750126	
Rhizophagus irregularis	MUCL 43205	FR750116	FR750116	
Rhizophagus prolifer	MUCL 41827	FN547501	FN547501	

Rhizopus arrhizus	CBS 112.07 <sup>T</sup>	NR_103595	HM849659
Rhizopus microsporus	CBS 699.68	MH859203	MH870925
Sacculospora baltica	E101-7	KX355820	KX355820
Sacculospora felinovii	Gf6	KX345943	KX345943
Saksenaea oblongispora	CBS 133.90 <sup>T</sup>	NR_137569	HM849694
Saksenaea vasiformis	NRRL 2443	FR687327	HM776679
Sclerocarpum amazonicum	Sa8	MK036784	MK036784
Sieverdingia tortuosa	G14-2	JF439096	JF439096
Spinellus fusiger	CBS 405.63	JN206298	MH869929
Sporodiniella umbellata	CBS 195.77	JN206372	JN206405
Syncephalastrum	CPS 122 12	MH854610	MH966125
nonosporum	CBS 122.12	MI1034010	WI1000133
Syncephalastrum	CPS 202 65	MU858577	MH970214
acemosum	CB3 502.05	WII 1050577	WIII070214
Syzygites megalocarpus	CBS 372.39	JN206369	JN206401
Fhamnidium elegans	CBS 642.69	MH859391	MH871163
Fhamnostylum piriforme	CBS 316.66 <sup>T</sup>	NR_164081	JN206544
Thermomucor indicae-	$CPS 104 75^{T}$	ND 111662	NG 057860
eudaticae	CB3 104.75	NK_111005	NG_037809
Umbelopsis longicollis	CBS 209.32 <sup>T</sup>	NR_119919	NG_042542
Umbelopsis ovata	CBS 499.82 <sup>T</sup>	KC489501	NG_058033
Umbelopsis ramanniana	CBS 129589	MH865437	MH876898
Umbelopsis vinacea	CBS 212.32 <sup>T</sup>	MH855292	JN206570
Utharomyces epallocaulus	CBS 112.81 <sup>T</sup>	NR_160160	MH873072
<sup>7</sup> inositunica ingens	F-15001		LC431108
Vinositunica radiata	B-13001		LC431103
Zychaea mexicana	CBS 441.76 <sup>T</sup>	NR_154478	MH872761

 Table 4. Inferred divergence time of higher taxa in subkingdom Mucoromyceta. \* New taxa

 proposed in the present study are in bold. \*\* Means of mean crown age (Mya). "–" represents the

 absence of divergence time in this study.

Phyla	Classes	Orders	Families	Means
				of
				stem
				age
				(Mya)
Calcarisporiellomycota	Calcarisporiellomycetes	Calcarisporiellales	Calcarisporiellaceae	748
			Calcarisporiellaceae	111
			(crown)**	
Endogonomycota	Endogonomycetes	Endogonales		708
			Densosporaceae	_
			Endogonaceae	708
			Endogonaceae	326
			(crown) **	
Glomeromycota				810
	Archaeosporomycetes			585
		Archaeosporales		585
			Ambisporaceae	401
			Archaeosporaceae	401
			Geosiphonaceae	_
	Glomeromycetes			585
		Claroideoglomerales*		539
			Claroideoglomeraceae	539
		Diversisporales		400
			Acaulosporaceae	285
			Diversisporaceae	333
			Entrophosporaceae	_
			Pacisporaceae	285

			Sacculosporaceae	288
		Gigasporales		400
			Dentiscutataceae	_
			Gigasporaceae	107
			Racocetraceae	107
			Scutellosporaceae	134
		Glomerales		478
			Glomeraceae	478
			Glomeraceae (crown)	276
			**	
	Paraglomeromycetes			651
		Paraglomerales		651
			Paraglomeraceae	483
			Pervetustaceae	483
Mortierellomycota	Mortierellomycetes	Mortierellales	Mortierellaceae	777
			Mortierellaceae	268
			(crown) **	
Mucoromycota				639
	Mucoromycetes			639
		Cunninghamellales*		504
			Absidisceae	403
			Cunninghamellaceae	403
			Gongronellaceae*	440
		Lentamycetales*		570
			Lentamycetaceae	570
			Lentamycetaceae	299
			(crown)**	
		Mucorales		519
			Backusellaceae	437
			Mucoraceae	387

			Pilobolaceae	337
			Rhizopodaceae	237
	*		Syzygitaceae*	327
		Phycomycetales*		543
			Phycomycetaceae	399
			Radiomycetaceae	399
			Saksenaeaceae	488
		Syncephalastrales*		504
			Circinellaceae*	391
			Lichtheimiaceae	354
			Mycocladaceae	_
			Protomycocladceae*	454
			Rhizomucoraceae <sup>*</sup>	340
			Thermomucoraceae <sup>*</sup>	354
			Syncephalastraceae	340
Umbelopsidomycota	Umbelopsidomycetes	Umbelopsidales		639
			Pygmaeomycetaceae	434
			Umbelopsidaceae	434

**Table 5.** A comparison of estimated fossil age and inferred divergence time of the five phyla in the subkingdom Mucoromyceta in different studies. \* New taxa proposed in the present study are in bold.

Phyla	Inferred mean of stem age (Mya)	References	
Calcarisporiellomycota	748	This study	
	626	(Tedersoo et al. 2018)	
Endogonomycota*	708	This study	
Glomeromycota	810	This study	
	610	(Redecker et al. 2000)	
	590	(Berbee & Taylor 2001)	
	725	(Berney & Pawlowski 2006)	

	720	(Lucking et al. 2009)
	510	(Gueidan et al. 2011)
	520	(Gaya et al. 2015)
	511	(Chang et al. 2015)
	642	(Tedersoo et al. 2018)
Mortierellomycota	777	This study
	727	(Tedersoo et al. 2018)
	511	(Chang et al. 2015)
Mucoromycota	639	This study
	610	(Berbee & Taylor 2001)
	510	(Gueidan et al. 2011)
	520	(Gaya et al. 2015)
	578	(Chang et al. 2015)
	626	(Tedersoo et al. 2018)
Umbelopsidomycota*	694	This study

**Table 6.** The origin of taxonomic types in Mucoromyceta

Countries	Types	Percentage	Countries	Types	Percentage
		(%)			(%)
USA	126	15.9	Japan	18	2.3
India	51	6.4	Republic of Korea	18	2.3
Brazil	46	5.8	Colombia	14	1.8
China	46	5.8	Malaysia	13	1.6
Germany	44	5.6	Spain	12	1.5
France	41	5.2	Cuba	11	1.4
Poland	40	5.1	Netherland	10	1.3
Australia	30	3.8	Unknown	87	11.0
Switzerland	21	2.7	Other countries	146	18.4
UK	19	2.4			

Table S1. Species publication years, types origin, and record time in China.

## References

- Abrashev R, Krumova E, Petrova P, *et al.* (2021). Distribution of a novel enzyme of sialidase family among native filamentous fungi. *Fungal Biology* 125:412–425. https://doi.org/10.1016/j.funbio.2020.12.006
- Agrawal S, Nandeibam J, Devi I (2021). Danger of exposure to keratinophilic fungi and other dermatophytes in recreational place in the northeast region of India. *Aerobiologia* 37:755–766. https://doi.org/ 10.1007/S10453-021-09719-2
- Agrios GN (2005). Plant pathology, 5th ed. Academic Press. San Diego, CA. USA.
- Alpat S, Alpat SK, Çadırcı BH, et al. (2008). A novel microbial biosensor based on Circinella sp. modified carbon paste electrode and its voltammetric application. Sensors and Actuators B: Chemical 134:175–181. https://doi.org/10.1016/j.snb.2008.04.044
- Alvarez E, Cano J, Stchigel AM, et al. (2011). Two new species of Mucor from clinical samples. Medical Mycology 49:62–72. https://doi.org/10.3109/13693786.2010.499521
- Alvarez E, Stchigel AM, Cano J, et al. (2010). Molecular phylogenetic diversity of the emerging mucoralean fungus Apophysomyces: proposal of three new species. Revista Iberoamericana de Micologia 27:80–89. https://doi.org/10.1016/j.riam.2010.01.006
- Amos RE, Barnett HL (1966). Umbelopsis versiformis, a new genus and species of the imperfects. Mycologia 58:805– 808.
- André LDA, Hoffmann K, Lima DX, et al. (2014). A new species of Lichtheimia (Mucoromycotina, Mucorales) isolated from Brazilian soil. Mycolgical Progress 13:343–352. https://doi.org/10.1007/s11557-013-0920-8
- Babu AG, Kim SW, Adhikari M, et al. (2015). A new record of *Gongronella butleri* isolated in Korea. *Mycobiology* 43:166–169. https://doi.org/10.5941/MYCO.2015.43.2.166
- Bai FR, Yao S, Cai CS, et al. (2021). Mucor rongii sp. nov., a new cold-tolerant species from China. Current Microbiology 78:2464–2469. https://doi.org/10.1007/s00284-021-02494-w
- Baijal U, Mehrotra B (1965). Species of Mucor from India 2. Sydowia 19:204–212.
- Bainier G (1903). Sur quelques especes de Mucorinées nouvelles ou peu connues. Bull Soc Mycol France 19:153–172.
- Barraclough T, Nee S (2001). Phylogenetics and speciation. *Trends in Ecology and Evolution* 16:391–399. https://doi.org/10.1016/S0169-5347(01)02161-9
- Batra LR, Segal RH, Baxter RW (1964). A new Middle Pennsylvanian fossil fungus. *American Journal of Botany* 51:991–995. https://doi.org/10.1002/j.1537-2197.1964.tb06728.x
- Baxter RW (1975). Fossil fungi from America Pennsylvanian coal balls. *The University of Kansas Paleontological Contributions* 7:1–6.
- Beauverie J (1900). Mycocladus verticillatus. Ann Univ Lyon 3:162-180.
- Benjamin CR, Hesseltine CW (1957). The genus *Actinomucor*. *Mycologia* 49:240–249. https://doi.org/10.1080/00275514.1957.12024635
- Benjamin CR, Hesseltine CW (1959). Studies on the genus *Phycomyces*. *Mycologia* 5:751–771. https://doi.org/10.1080/00275514.1959.12024858
- Benjamin RK (1959). The merosporangiferous mucorales. *Aliso: A Journal of Systematic and Evolutionary Botany* 4:321–433.
- Benjamin RK (1978). Gamsiella, a new subgenus of Mortierella (Mucorales: Mortierellaceae). Aliso: A Journal of Systematic and Evolutionary Botany 9:157–170.
- Benny GL (1991). Gilbertellaceae, a new family of the Mucorales (Zygomycetes). *Mycologia* 83:150–157. https://doi.org/10.1080/00275514.1991.12025991
- Benny GL (1992). Observations on Thamnidiaceae (Mucorales) 5. Thamnidium. Mycologia 84:834-842.

https://doi.org/10.1080/00275514.1992.12026214

- Benny GL (1995a). *Kirkomyces*, a new name for Kirkia Benny. *Mycologia* 87:922. https://doi.org/10.1080/00275514.1995.12026615
- Benny GL (1995b). Observations on Thamnidiaceae 7. *Helicostylum* and a new genus *Kirkia*. *Mycologia* 87:253–264. https://doi.org/10.1080/00275514.1995.12026527
- Benny GL, Benjamin RK (1975). Observations on Thamnidiaceae (Mucorales). New taxa, new combinations, and notes on selected species. *Aliso: A Journal of Systematic and Evolutionary Botany* 8:301–351.
- Benny GL, Benjamin RK (1976). Observations on Thamnidiaceae (Mucorales) 2. Chaetocladium, Cokeromyces, Mycotypha, and Phascolomyces. Aliso: A Journal of Systematic and Evolutionary Botany 8:391–424.
- Benny GL, Benjamin RK (1991). The Radiomycetaceae (Mucorales; Zygomycetes) 3. A new species of *Radiomyces*, and cladistic analysis and taxonomy of the family; with a discussion of evolutionary ordinal relationships in Zygomycotina. *Mycologia* 83:713–735. https://doi.org/10.2307/3760429
- Benny GL, Benjamin RK (1993). Observations on Thamnidiaceae (Mucorales) 6. Two new species of Dichotomocladium and the zygospores of D. hesseltinei (Chaetocladiaceae). Mycologia 85:660–671. https://doi.org/10.2307/3760511
- Benny GL, Blackwell M (2004). Lobosporangium, a new name for Echinosporangium Malloch, and Gamsiella, a new genus for Mortierella multidivaricata. Mycologia 96:143–149. https://doi.org/10.1080/15572536.2005.11833004
- Benny GL, Humber RA, Morton JB (2001). Zygomycota: zygomycetes. In: McLaughlin DJ, McLaughlin EG, Lemke PA (eds) Systematics and evolution, 1st edn. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 113–146.
- Benny GL, Humber RA, Voigt K (2014). Zygomycetous fungi: phylum entomophthoromycota and subphyla kickxellomycotina, mortierellomycotina, mucoromycotina, and zoopagomycotina. In: Mclaughlin DJ, Spatafora JW (eds) Systematics and evolution, 2nd edn. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 209–250.
- Benny GL, Kirk PM, Samson RA (1985). Observations on Thamnidiaceae (Mucorales) 3. Mycotyphaceae fam. nov. and a re-evaluation of *Mycotypha* sensu Benny & Benjamin illustrated by two new species. *Mycotaxon* 22:119– 148.
- Benny GL, Schipper M (1992). Observations on Thamnidiaceae (Mucorales) 4. Pirella. Mycologia 84:52–63. https://doi.org/10.1080/00275514.1992.12026103
- Berbee ML, James TY, Strullu-Derrien C (2017). Early diverging fungi: diversity and impact at the dawn of terrestrial life. *Annual Review of Microbiology* 71:41–60. https://doi.org/10.1146/annurev-micro-030117-020324.
- Berbee ML, Taylor JW (2001). Fungal molecular evolution: gene trees and geologic time. In: McLaughlin DJ, McLaughlin EG, Lemke PA (eds) Systematics and evolution, 1st edn. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 229–245.
- Bergman K, Burke PV, Cerdá-Olmedo E, et al. (1969). Phycomyces. Bacteriological Reviews 33:99–157.
- Berney C, Pawlowski J (2006). A molecular time-scale for eukaryote evolution recalibrated with the continuous microfossil record. *Proceedings of the Royal Society B: Biological Sciences* 273:1867–1872. https://doi.org/10.1098/rspb.2006.3537.
- Blair J (2009). Fungi. In: Hedges SB, Kumar K (eds) The timetree of life, 1st edn. Oxford University Press, New York, pp 215–129.
- Boedijn KB (1958). Notes of the Mucorales of Indonesia. Sydowia 12:321-362
- Bonifaz A, Stchigel AM, Guarro J, et al. (2014). Primary cutaneous mucormycosis produced by the new species Apophysomyces mexicanus. Journal of Medical Mycology 52:4428–4431. https://doi.org/10.1128/JCM.02138-14
- Bouckaert R, Heled J, Kühnert D, et al. (2014). BEAST 2: a software platform for Bayesian evolutionary analysis.

PLoS Computational Biology 10:e1003537. https://doi.org/10.1371/journal.pcbi.1003537

- Brooks FT, Hansford CG (1923). Mould growths upon cold-store meat. *Transactions of the British Mycological Society* 8:113–142. https://doi.org/10.1016/S0007-1536(23)80020-1
- Chakrabarti A, Shivaprakash MR, Curfs-Breuker I, et al. (2010). Apophysomyces elegans: epidemiology, amplified fragment length polymorphism typing, and in vitro antifungal susceptibility pattern. Journal of Medical Mycology 48:4580–4585. https://doi.org/10.1128/JCM.01420-10
- Chander J, Singla N, Kaur M, et al. (2021). Apophysomyces variabilis, an emerging and worrisome cause of primary cutaneous necrotizing infections in India. Journal de Mycologie Médicale 31:101197. https://doi.org/10.1016/J.MYCMED.2021.101197
- Chang Y, Desirò A, Na H, *et al.* (2019). Phylogenomics of Endogonaceae and evolution of mycorrhizas within Mucoromycota. *New Phytologist* 222:511–525. https://doi.org/10.1111/nph.15613
- Chang Y, Wang S, Sekimoto S, et al. (2015). Phylogenomic analyses indicate that early fungi evolved digesting cell walls of algal ancestors of land plants. Genome Biology and Evolution 7:1590–1601. https://doi.org/10.1093/gbe/evv090
- Chen FJ (1992a). Haplosporangium a new record genus of Mucorales from China. Mycosystema 5:19–22.
- Chen FJ (1992b). Mortierella species in China. Mycosystema 5:23-64.
- Cheng Y, Gao Y, Liu XY, et al. (2017). Rhinocerebral mucormycosis caused by *Rhizopus arrhizus* var. tonkinensis. Journal de Mycologie Médicale 27:586–588. https://doi.org/10.1016/j.mycmed.2017.10.001
- Chibucos MC, Soliman S, Gebremariam T, *et al.* (2016). An integrated genomic and transcriptomic survey of mucormycosis-causing fungi. *Nature Communications* 7:1–11. https://doi.org/10.1038/ncomms12218
- Chien CY, Hwang BC (1997). First record of the occurrence of *Sporodiniella umbellata* (Mucorales) in Taiwan. *Mycoscience* 38:343–346. https://doi.org/10.1007/BF02464094
- Chitnis MV, Munro CA, Brown AJP, et al. (2002). The zygomycetous fungus, Benjaminiella poitrasii contains a large family of differentially regulated chitin synthase genes. Fungal Genetics and Biology 36:215–223. https://doi.org/10.1016/S1087-1845(02)00015-4
- Coemans E (1863). Quelques hyphomycetes nouveaux 1. *Mortierella polycephala* et Martensella pectinata. *Bulletin de l'Académie Royale des Sciences de Belgique Classe des Sciences* 2, ser 15:536–544.
- Cooper JA, Park D (2020). *Modicella albostipitata*, a new species of sporocarp-forming fungus from New Zealand (Mortierellaceae: Mortierellomycota). *Phytotaxa* 453:293–296. https://doi.org/10.11646/phytotaxa.453.3.11
- Corda A (1842). Incones fungorum hucusque cognitorum. Vol. 5. F. Ehrlich, Prague. pp 92.
- Cordeiro TRL, Nguyen TTT, Lima DX, *et al.* (2020). Two new species of the industrially relevant genus *Absidia* (Mucorales) from soil of the Brazilian Atlantic Forest. *Acta Botanica Brasilica* 34:549–558. https://doi.org/10.1590/0102-33062020abb0040
- Corrochano LM, Kuo A, Marcet-Houben M, *et al.* (2016). Expansion of signal transduction pathways in fungi by extensive genome duplication. *Current Biology* 26:1577–1584. https://doi.org/ 10.1016/j.cub.2016.04.038
- Crous PW, Cowan D, Maggs-Kolling G, *et al.* (2020). Fungal planet description sheets: 1112–1181. *Persoonia* 45:251–409. https://doi.org/10.3767/PERSOONIA.2020.45.10
- Crous PW, Wingfield MJ, Burgess TI, et al. (2017). Fungal planet description sheets: 625–715. Persoonia 39:270–467. https://doi.org/10.3767/persoonia.2017.39.11
- Crous PW, Wingfield MJ, Burgess TI, et al. (2018). Fungal planet description sheets: 716–784. Persoonia 40:240–393. https://doi.org/10.3767/persoonia.2018.40.10
- Cruz-Lachica I, Marquez-Zequera I, Garcia-Estrada RS, *et al.* (2015). First report of *Gilbertella persicaria* causing papaya fruit rot. *Plant Disease* 100:227–227. https://doi.org/10.1094/pdis-05-15-0607-pdn
- Dai YC, Cui BK, Si J, *et al.* (2015). Dynamics of the worldwide number of fungi with emphasis on fungal diversity in China. *Mycological Progress* 14:1–9. https://doi.org/10.1007/s11557-015-1084-5

- Dai YC, Yang ZL, Cui BK, *et al.* (2021). Diversity and systematics of the important macrofungi in Chinese forests. *Mycosystema* 40:770–805. https://doi.org/10.13346/j.mycosystema.210036
- Dashdorj D, Tripathi VK, Cho S, *et al.* (2016). Dry aging of beef: review. *Journal Animal Sciences and Technolology* 58:20. https://doi.org/10.1186/s40781-016-0109-1
- Davel G, Featherston P, Fernández A, et al. (2001). Maxillary sinusitis caused by Actinomucor elegans. Journal of Clinical Microbiology 39:740–742. https://doi.org/10.1128/JCM.39.2.740-742.2001
- Davies JL, Ngeleka M, Wobeser GA (2010). Systemic infection with *Mortierella wolfii* following abortion in a cow. *The Canadian Veterinary Journal* 51:1391–1393.
- Davoust N, Persson A (1992). Effects of growth morphology and time of harvesting on the chitosan yield of *Absidia* repens. Applied Microbiology and Biotechnology 37:572–575. https://doi.org/10.1007/BF00240727
- de Carvalho Tavares IM, Umsza-Guez MA, Martin N, *et al.* (2020). The improvement of grape juice quality using *Thermomucor indicae-seudaticae* pectinase. *Journal of Food Science and Technology* 57:1565–1573. https://doi.org/10.1007/s13197-019-04192-9
- de Lima CL, Lima DX, de Souza CA, et al. (2018). Description of Mucor pernambucoensis (Mucorales, mucoromycota), a new species isolated from the Brazilian upland rainforest. Phytotaxa 350:274. https://doi.org/10.11646/phytotaxa.350.3.6
- de Souza JI, Marano AV, Pires-Zottarelli CLA, *et al.* (2014). A new species of *Backusella* (Mucorales) from a Cerrado reserve in Southeast Brazil. *Mycological Progress* 13:981. https://doi.org/10.1007/s11557-014-0981-3
- de Souza JI, Pires-Zottarelli CL, Dos Santos JF, *et al.* (2012). *Isomucor* (Mucoromycotina): a new genus from a Cerrado reserve in state of Sao Paulo, Brazil. *Mycologia* 104:232–241. https://doi.org/10.3852/11-133
- Desirò A, Rimington WR, Jacob A, *et al.* (2017). Multigene phylogeny of Endogonales, an early diverging lineage offungi associated with plants. *IMA Fungus* 8:245–257. https://doi.org/10.5598/imafungus.2017.08.02.03
- Dixon-Stewart D (1932). Species of *Mortierella* isolated from soil. *Transactions of the British Mycological Society* 17:208–220.
- Doilom M, Guo JW, Phookamsak R, et al. (2020). Screening of phosphate-solubilizing fungi from air and soil in Yunnan, China: four novel species in Aspergillus, Gongronella, Penicillium, and Talaromyces. Frontiers in Microbiology 11:585215. https://doi.org/10.3389/fmicb.2020.585215
- Domsch KH, Gams W, Anderson TH (1980). Compendium of soil fungi. Volume 1. Academic Press (London) Ltd. https://doi.org/10.1016/0016-7061(82)90042-8
- Ekpo E, Young T (1979). Fine-structure of the dormant and germinating sporangiospore of *Syzygites megalocarpus* (Mucorales) with notes on *Sporodiniella umbellata*. *Microbios Letters* 10:63–68
- Ellenberger S, Burmester A, Wöstemeyer J (2016). Complete mitochondrial DNA sequence of the mucoralean fungus *Absidia glauca*, a model for studying host-parasite interactions. *Genome Announcements* 4:e00153–16. https://doi.org/10.1128/genomeA.00153-16
- Ellis JJ, Hesseltine CW (1965). The genus Absidia: globose-spored species. Mycologia 57:222-235.
- Ellis JJ, Hesseltine CW (1969). Two new members of the Mucorales. *Mycologia* 61:863–872. https://doi.org/10.1080/00275514.1969.12018810
- Ellis JJ, Hesseltine CW (1974). Two new families of Mucorales. Mycologia 66:87-95
- Ellis M (1940). Some fungi isolated from pinewood soil. *Transactions of the British Mycological Society* 24:87–97. https://doi.org/10.1016/S0007-1536(40)80022-3
- Embree RW (1959). *Radiomyces*, a new genus in the Mucorales. *American Journal of Botany* 46:25–30. https://doi.org/10.1002/j.1537-2197.1959.tb06977.x
- Embree RW, Indoh H (1967). *Aquamortierella*, a new genus in the Mucorales. *Bulletin of the Torrey Botanical Club* 94:464–467. https://doi.org/10.2307/2483563
- Evans EH (1971). Studies on Mortierella ramanniana 1. Relationship between morphology and cultural behaviour of

certain isolates. Transactions of the British Mycological Society 56:201-213

- Gade L, Hurst S, Balajee SA, et al. (2017). Detection of mucormycetes and other pathogenic fungi in formalin fixed paraffin embedded and fresh tissues using the extended region of 28S rDNA. Medical Mycology 55:385–395. https://doi.org/10.1093/mmy/myw083
- Galland P, Lipson ED (1985). Modified action spectra of photogeotropic equilibrium in *Phycomyces blakesleeanus* mutants with defects in genes *madA*, *madB*, *madC*, and *madH*. *Photochemistry and Photobiology* 41:331–335. https://doi.org/10.1111/j.1751-1097.1985.tb03493.x
- Gams W (1961). Eine neue Mortierella aus dem zentralalpinen Rothumus. Nova Hedwigia 3:69-71.
- Gams W (1976). Some new or noteworthy species of Mortierella. Persoonia 9:111-140.
- Gams W (1977). A key to the species of Mortierella. Persoonia 9:381-391.
- Gan T, Luo T, Pang K, *et al.* (2021). Cryptic terrestrial fungus-like fossils of the early Ediacaran Period. *Nature Communications* 12:1–12. https://doi.org/10.1038/S41467-021-20975-1
- Gardeli C, Athenaki M, Xenopoulos E, et al. (2017). Lipid production and characterization by Mortierella (Umbelopsis) isabellina cultivated on lignocellulosic sugars. Journal of Applied Microbiology 123:1461–1477. https://doi.org/10.1111/jam.13587
- Gaya E, Fernández-Brime S, Vargas R, et al. (2015). The adaptive radiation of lichen-forming Teloschistaceae is associated with sunscreening pigments and a bark-to-rock substrate shift. Proceedings of the National Academy of Sciences 112:11600–11605. https://doi.org/10.1073/pnas.1507072112
- Gomes MZ, Lewis RE, Kontoyiannis DP (2011). Mucormycosis caused by unusual mucormycetes, non-Rhizopus, -Mucor, and -Lichtheimia species. Clinical Microbiology Reviews 24:411–445. https://doi.org/10.1128/CMR.00056-10
- Guarro J, Chander J, Alvarez E, et al. (2011). Apophysomyces variabilis infections in humans. Emerging Infectious Diseases 17:134–135. https://doi.org/10.3201/eid1701.101139
- Gueidan C, Ruibal C, de Hoog G, *et al.* (2011). Rock-inhabiting fungi originated during periods of dry climate in the late Devonian and middle Triassic. *Fungal Biology* 115:987–996. https://doi.org/10.1016/j.funb.2011.04.002
- Guo J, Wang H, Liu D, et al. (2015). Isolation of *Cunninghamella bigelovii* sp. nov. CGMCC 8094 as a new endophytic oleaginous fungus from *Salicornia bigelovii*. *Mycological Progress* 14:1–8. https://doi.org/10.1007/s11557-015-1029-z
- Guo LW, Wu YX, Mao ZC, et al. (2012). Storage rot of dragon fruit caused by *Gilbertella persicaria*. Plant Disease 96:1826–1826. https://doi.org/10.1094/PDIS-07-12-0635-PDN
- Hagem O (1910). Neue untersuchungen über norwegische mucorineen. Annales Mycologici 8:265-286.
- Hallur V, Prakash H, Sable M, et al. (2021). Cunninghamella arunalokei a new species of Cunninghamella from India causing disease in an immunocompetent individual. Journal of Fungi 7:670. https://doi.org/10.3390/JOF7080670
- Han B, Rombouts FM, Nout MJR (2001). A Chinese fermented soybean food. International Journal of Food Microbiology 65:1–10. https://doi.org/10.1016/S0168-1605(00)00523-7
- He MQ, Zhao RL, Hyde KD, et al. (2019). Notes, outline and divergence times of Basidiomycota. Fungal Diversity 99:105–367. https://doi.org/10.1007/s13225-019-00435-4
- Heckman DS, Geiser DM, Eidell BR, *et al.* (2001). Molecular evidence for the early colonization of land by fungi and plants. *Science* 293:1129–1133. https://doi.org/10.1126/science.1061457
- Hermet A, Méheust D, Mounier J, et al. (2012). Molecular systematics in the genus Mucor with special regards to species encountered in cheese. Fungal Biology 116:692–705. https://doi.org/10.1016/j.funbio.2015.06.001
- Hesseltine CW (1960). *Gilbertella* gen. nov. (Mucorales). *Bulletin of the Torrey Botanical Club* 87:21–30. https://doi.org/10.2307/2483058

- Hesseltine CW, Anderson P (1956). The genus *Thamnidium* and a study of the formation of its zygospores. *American Journal of Botany* 43:696–703. https://doi.org/10.1002/j.1537-2197.1956.tb14434.x
- Hesseltine CW, Benjamin CR, Mehrotra BS (1959). The genus Zygorhynchus. Mycologia 51:173–194. https://doi.org/10.1080/00275514.1959.12024811
- Hesseltine CW, Ellis JJ (1961). Notes on mucorales, especially *Absidia*. *Mycologia* 53:406–426. https://doi.org/10.1080/00275514.1961.12017970
- Hesseltine CW, Ellis JJ (1964). The genus *Absidia*: *Gongronella* and cylindrical-spored species of *Absidia*. *Mycologia* 56:568–601. https://doi.org/10.1080/00275514.1964.12018145
- Hesseltine CW, Ellis JJ (1966). Species of *Absidia* with ovoid sporangiospores 1. *Mycologia* 58:761–785. https://doi.org/10.1080/00275514.1966.12018369
- Hesseltine CW, Fennell DI (1955). The genus *Circinella*. *Mycologia* 47:193–212. https://doi.org/10.1080/00275514.1955.12024444
- Hibbett DS, Binder M, Bischoff JF, *et al.* (2007). A higher-level phylogenetic classification of the fungi. *Mycological Research* 111:509–547. https://doi.org/10.1016/j.mycres.2007.03.004
- Hibbett DS, Taylor JW (2013). Fungal systematics: is a new age of enlightenment at hand? Nature Reviews Microbiology 11:129–133. https://doi.org/10.1038/nrmicro2963
- Ho HM (1988). The study of *Rhizopus stolonifer* isolated in Taiwan 2. Morphological study of *Rhizopus stolonifer*: asexual apparatus and zygosporogenesis. *Transactions of the Mycological Society of Republic of China* 3:73–81
- Ho HM (1995a). Notes on two coprophilous species of the genus *Circinella* (Mucorales) from Taiwan. *Fungal Science* 10:23–27
- Ho HM (1995b). Zygospore wall in early stage of *Rhizopus sexualis* (Mucoraceae): smooth or warted? *Fungal Science* 10:29–31
- Ho HM (2002). Notes on Zygomycetes of Taiwan 2: two Thamnidiaceae (Mucorales) fungi. Fungal Science 17:87-92
- Ho HM, Chang LL (2003). Notes on Zygomycetes of Taiwan 3: two *Blakeslea* species (Choanephoraceae) new to Taiwan. *Taiwania* 48:232–238. https://doi.org/10.6165/tai.2003.48(4).232
- Ho HM, Chen ZC (1990). Morphological study of *Gongronella butleri* (Mucorales) from Taiwan. *Taiwania* 35:259–263. https://doi.org/10.6165/tai.1990.35.259
- Ho HM, Chen ZC (1994). Post cleavage transformation of columella in *Rhizopus stolonifer* (Mucoraceae). *Botanical Bulletin of Academia Sinica* 35:249–259.
- Ho HM, Chuang SC, Chen SJ (2004). Notes on Zygomycetes of Taiwan 4: three *Absidia* species (Mucoraceae). *Fungal Science* 19:125–131.
- Ho HM, Chuang SC, Hsieh CY (2008). Notes on Zygomycetes of Taiwan 6: *Chaetocladium brefeldii* new to Taiwan. *Fungal Science* 23:21–25.
- Hoffmann K (2010). Identification of the genus Absidia (Mucorales, Zygomycetes): a comprehensive taxonomic revision. In: Gherbawy Y, Voigt K (eds) Molecular identification of fungi, 1st, edn. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 439–460.
- Hoffmann K, Discher S, Voigt K (2007). Revision of the genus *Absidia* (Mucorales, Zygomycetes) based on physiological, phylogenetic, and morphological characters; thermotolerant *Absidia* spp. form a coherent group, Mycocladiaceae fam. nov. *Mycological Research* 111:1169–1183. https://doi.org/10.1016/j.mycres.2007.07.002
- Hoffmann K, Pawłowska J, Walther G, *et al.* (2013). The family structure of the Mucorales: a synoptic revision based on comprehensive multigene-genealogies. *Persoonia* 30:57–76. https://doi.org/10.3767/003158513X666259
- Hoffmann K, Telle S, Walther G, *et al.* (2009a). Diversity, genotypic identification, ultrastructural and phylogenetic characterization of zygomycetes from different ecological habitats and climatic regions: limitations and utility

of nuclear ribosomal DNA barcode markers. In: Gherbawy Y, Mach R, Rai M (eds) Current advances in molecular mycology, 1st, edn. Nova Science Publishers, New York, pp 263–312.

- Hoffmann K, Voigt K (2009). Absidia parricida plays a dominant role in biotrophic fusion parasitism among mucoralean fungi (Zygomycetes): Lentamyces, a new genus for A. parricida and A. zychae. Plant Biology 11:537–554. https://doi.org/10.1111/j.1438-8677.2008.00145.x
- Hoffmann K, Voigt K, Kirk PM (2011). Mortierellomycotina subphyl. nov., based on multi–gene genealogies. *Mycotaxon* 115:353–363. https://doi.org/10.5248/115.353
- Hoffmann K, Walther G, Voigt K (2009b). Mycocladus vs. Lichtheimia: a correction (Lichtheimiaceae fam. nov., Mucorales, Mucoromycotina). Mycological Research 113:277–278.
- Hong SB, Kim DH, Lee M, et al. (2012). Zygomycota associated with traditional meju, a fermented soybean starting material for soy sauce and soybean paste. Journal of Microbiology 50:386–393. https://doi.org/10.1007/s12275-012-1437-6
- Horn F, Üzüm Z, Möbius N, et al. (2015). Draft genome sequences of symbiotic and nonsymbiotic Rhizopus microsporus strains CBS 344.29 and ATCC 62417. Genome Announcements 3:e01370-14. https://doi.org/10.1128/genomeA.01370-14
- Hsu TH, Ho HM (2010). Notes on Zygomycetes of Taiwan 8: three new records of *Absidia* in Taiwan. *Fungal Science* 25:5–11.
- Hsu TH, Ho HM, Chien C (2009). Taxonomic study of *Absidia* sensu lato in Taiwan. Asian Mycological Congress and 11th International Marine and Freshwater Mycology Symposium Abstract Book, pp 42.
- Hu FM, Zheng RY, Chen GQ (1989). A redelimitation of the species of Pilobolus. Mycosystema 2:1-133
- Hu J, Zhang Y, Xu Y, et al. (2019). Gongronella sp. w5 elevates Coprinopsis cinerea laccase production by carbon source syntrophism and secondary metabolite induction. Applied Microbiology and Biotechnology 103:411– 425. https://doi.org/10.1007/s00253-018-9469-4
- Huang J, Zhang X, et al. (2014). Mucor fragilis as a novel source of the key pharmaceutical agents podophyllotoxin and kaempferol. Pharmaceutical Biology 52: 237–1243. https://doi.org/10.3109/13880209.2014.885061
- Huang R, Gou J, Zhao D, et al. (2018). Phytotoxicity and anti-phytopathogenic activities of marine-derived fungi and their secondary metabolites. RSC Advances 8:37573–37580. https://doi.org/10.1039/c8ra08047j
- Huët MAL, Wong LW, Goh CBS, et al. (2020). First reported case of Gilbertella persicaria in human stool: outcome of a community study from Segamat, Johor, Malaysia. Brazilian Journal of Microbiology 51:2067–2075. https://doi.org/10.1007/s42770-020-00323-z
- Hurdeal VG, Gentekaki E, Lee HB, et al. (2021). Mucoralean fungi in Thailand: novel species of Absidia from tropical forest soil. Cryptogamie, Mycologie 42:39–61. https://doi.org/10.5252/CRYPTOGAMIE-MYCOLOGIE2021V42A4
- Hyde KD, Hongsanan S, Jeewon R, *et al.* (2016). Fungal diversity notes 367–490: taxonomic and phylogenetic contributions to fungal taxa. *Fungal Diversity* 80:1-270. https://doi.org/10.1007/s13225-016-0373-x
- Hyde KD, Maharachchikumbura SS, Hongsanan S, *et al.* (2017). The ranking of fungi: a tribute to David L. Hawksworth on his 70th birthday. *Fungal Diversity* 84:1–23. https://doi.org/10.1007/s13225-017-0383-3
- Irshad M, Nasir N, Hashmi UH, *et al.* (2020). Invasive pulmonary infection by *Syncephalastrum* species: two case reports and review of literature. *IDCases* 21:e00913 https://doi.org/10.1016/j.idcr.2020.e00913
- James TY, Kauff F, Schoch CL, *et al.* (2006). Reconstructing the early evolution of fungi using a six-gene phylogeny. *Nature* 443:818–822. https://doi.org/10.1038/nature05110
- James TY, Pelin A, Bonen L, et al. (2013). Shared signatures of parasitism and phylogenomics unite Cryptomycota and microsporidia. Current Biology 23:1548–1553. https://doi.org/10.1016/j.cub.2013.06.057
- Jia H, Zhang M, Weng Y, et al. (2021). Degradation of polylactic acid/polybutylene adipate-co-terephthalate by

coculture of *Pseudomonas mendocina* and *Actinomucor elegans*. *Journal of Hazardous Materials* 403:123679. https://doi.org/10.1016/j.jhazmat.2020.123679

- Ju X, Zhang MZ, Zhao H, *et al.* (2020). Genomic SNPs reveal population structure of *Rhizopus arrhizus*. *Mycosystema* 39:2285–2303. https://doi.org/10.13346/j.mycosystema.200105
- Kaitera J, Henttonen HM, Müller MM (2019). Fungal species associated with butt rot of mature Scots pine and Norway spruce in northern boreal forests of Northern Ostrobothnia and Kainuu in Finland. *European Journal of Plant Pathology* 154:541–554. https://doi.org/ 10.1007/s10658-019-01678-2
- Kamei K (2000). Animal models of Zygomycosis—*Absidia*, *Rhizopus*, *Rhizomucor*, and *Cunninghamella*. *Mycopathologia* 152:5–13.
- Kanouse BB (1936). Studies of two species of *Endogone* in culture. *Mycologia* 28:47–62. https://doi.org/10.1080/00275514.1936.12017117
- Katoh K, Rozewicki J, Yamada KD (2019). MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics* 20:1160–1166. https://doi.org/10.1093/bib/bbx108
- Kearse M, Moir R, Wilson A, et al. (2012). Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28:1647–1649. https://doi.org/10.1093/bioinformatics/bts199
- Khale A, Deshpande MV (1992). Dimorphism in *Benjaminiella poitrasii*: cell wall chemistry of parent and two stable yeast mutants. *Antonie van Leeuwenhoek* 62:299–307. https://doi.org/10.1007/BF00572598
- Khan MA, Yang J, Hussain SA, et al. (2019). Genetic modification of Mucor circinelloides to construct stearidonic acid producing cell factory. International Journal of Molecular Sciences 20:1683. https://doi.org/10.3390/ijms20071683
- Khuna S, Suwannarach N, Kumla J, et al. (2019). Apophysomyces thailandensis (Mucorales, Mucoromycota), a new species isolated from soil in northern Thailand and its solubilization of non-soluble minerals. MycoKeys 45:75–92. https://doi.org/10.3897/mycokeys.45.30813
- Kirk PM (1984). A monograph of the Choanephoraceae. Mycological Papers 152:1-61.
- Kirk PM (1989). A new species of Benjaminiella (Mucorales: Mycotyphaceae). Mycotaxon 35:121-125
- Kirk PM, Benny GL (1980). Genus Utharomyces Boedijn (Pilobolaceae: Zygomycetes). Transactions of the British Mycological Society 75:123–131. https://doi.org/10.1016/S0007-1536(80)80202-6
- Kitahata S, Ishikawa H, Miyata T, *et al.* (1989). Production of rubusoside derivatives by transgalactosylation of various α-galactosidases. *Agricultural and Biological Chemistry* 53: 2929–2934. https://doi.org/10.1271/bbb1961.53.2929
- Kitz DJ, Embree RW, Jr. Cazin. J (1980). *Radiomyces* a genus in the mucorales pathogenic for mice. *Sabouraudia* 18:115–121. https://doi.org/10.1080/00362178085380191
- Kosa G, Zimmermann B, Kohler A, et al. (2018). High-throughput screening of Mucoromycota fungi for production of low- and high-value lipids. *Biotechnology for Biofuels* 11:1–17. https://doi.org/10.1186/s13068-018-1070-7
- Kovacs R, Sundberg W (1999). Syzygites megalocarpus (Mucorales, Zygomycetes) in Illinois. Transations of the Illinois State Academy Science 92:181–190.
- Krings M, Harper CJ, Taylor EL (2018). Fungi and fungal interactions in the Rhynie chert: a review of the evidence, with the description of *Perexiflasca tayloriana* gen. et sp. nov. *Philosophical Transactions of the Royal Society B: Biological Sciences* 373:20160500. https://doi.org/10.1098/rstb.2016.0500
- Krings M, Taylor TN, Dotzler N (2011). The fossil record of the Peronosporomycetes (Oomycota). Mycologia 103:445– 457. https://doi.org/10.3852/10-278
- Kristanti RA, Zubir MMFA, Hadibarata T (2016) Biotransformation studies of cresol red by Absidia spinosa M15. Journal of Environmental Management 172:107–111. https://doi.org/10.1016/j.jenvman.2015.11.017
- Kumar P, Satyanarayana T (2007). Economical glucoamylase production by alginate-immobilized Thermomucor

*indicae-seudaticae* in cane molasses medium. *Letters in Applied Microbiology* 45:392–397. https://doi.org/10.1111/j.1472-765X.2007.02201.x

- Kwon-Chung KJ (2012). Taxonomy of fungi causing mucormycosis and entomophthoramycosis (zygomycosis) and nomenclature of the disease: molecular mycologic perspectives. *Clinical Infectious Diseases* 2012:54 Suppl 1 (Suppl 1):S8–S15. https://doi.org/10.1093/cid/cir864
- Labuda R, Bernreiter A, Hochenauer D, et al. (2019). Saksenaea dorisiae sp. nov., a new opportunistic pathogenic fungus from Europe. International Journal of Microbiology 2019:6253829. https://doi.org/10.1155/2019/6253829
- Larsson A (2014). AliView: a fast and lightweight alignment viewer and editor for large datasets. *Bioinformatics* 30:3276–3278. https://doi.org/10.1093/bioinformatics/btu531
- Layios N, Canivet J, Baron F, et al. (2014). Mortierella wolfii-associated invasive disease. Emerging Infectious Diseases 20:1591–1592. https://doi.org/10.3201/eid2009.140469
- Lee SC, Billmyre RB, Li A, *et al.* (2014). Analysis of a food-borne fungal pathogen outbreak: virulence and genome of a *Mucor circinelloides* isolate from yogurt. *MBio* 5:e01390-14. https://doi.org/ 10.1128/mBio.01390-14
- Lee SH, Nguyen TTT, Lee HB (2018). Isolation and characterization of two rare Mucoralean species with specific habitats. *Mycobiology* 46:205–214. https://doi.org/10.1080/12298093.2018.1509513
- Li F, Zhang S, Wang Y, *et al.* (2020). Rare fungus, *Mortierella capitata*, promotes crop growth by stimulating primary metabolisms related genes and reshaping rhizosphere bacterial community. *Soil Biology and Biochemistry* 151:108017. https://doi.org/10.1016/j.soilbio.2020.108017
- Li G, Fang X, Su F, et al. (2018). Enhancing the thermostability of *Rhizomucor miehei* lipase with a limited screening library by rational-design point mutations and disulfide bonds. *Applied Environmental Microbiology* 84:e02129–17. https://doi.org/10.1128/AEM.02129-17
- Li GJ, Hyde KD, Zhao RL, *et al.* (2016). Fungal diversity notes 253–366: taxonomic and phylogenetic contributions to fungal taxa. *Fungal Diversity* 78:1–237. https://doi.org/10.1007/s13225-016-0366-9
- Li S, Han R, Zhang H, *et al.* (2020). *Apophysomyces jiangsuensis* sp. nov., a salt tolerant and phosphate-solubilizing fungus from the Tidelands of Jiangsu Province of China. *Microorganisms* 8:1868. https://doi.org/10.3390/MICROORGANISMS8121868
- Linde J, Schwartze V, Binder U, et al. (2014). De novo whole-genome sequence and genome annotation of *Lichtheimia* ramosa. Genome Announcements 2:e00888-14. https://doi.org/ 10.1128/genomeA.00888-14
- Linnemann G (1941). Die Mucorineen-Gattung *Mortierella* Coemans. *Pflanzenforschung* 23:1–64. https://www.jstor.org/stable/43804972
- Liu F, Ma ZY, Hou LW, et al. (2022). Updating species diversity of *Colletotrichum*, with a phylogenomic overview. *Studies in Mycology* 101:1–56. https://doi.org/10.3114/sim.2022.101.01
- Liu XY (2004). *Pirella* (Thamnidiaceae, Mucorales), a new record genus for China. *Mycosystema* 23:301–302. https://doi.org/10.3969/j.issn.1672-6472.2004.02.023
- Liu XY, Huang H, Zheng RY (2001). Relationships within *Cunninghamella* based on sequence analysis of ITS rDNA. *Mycotaxon* 80:77–95.
- Liu XY, Huang H, Zheng RY (2008). Delimitation of *Rhizopus* varieties based on IGS rDNA sequences. *Sydowia* 60:93–112.
- Liu XY, Voigt K (2010). Molecular characters of zygomycetous fungi. In: Gherbawy Y, Voigt K (eds) Molecular identification of fungi. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 461–488
- Liu XY, Wang Y, Zheng RY (2012). Molecular phylogeny of *Pilaira* (Mucorales, Zygomycetes) inferred from ITS rDNA and pyrG sequences. *Sydowia* 64:55–66.
- Liu XY, Zheng RY (2015). New taxa of *Ambomucor* (Mucorales, Mucoromycotina) from China. *Mycotaxon* 130:165–171. https://doi.org/10.5248/130.165

- Liu ZB, Wu YD, Zhao H, *et al.* (2022). Outline, divergence times, and phylogeneticanalyses of Trechisporales (Agaricomycetes, Basidiomycota). *Frontier in Microbiology* 13:818358. https://doi.org/10.3389/fmicb.2022.818358
- Loh L, Nawawi A, Kuthubutheen A (2001). Mucoraceous fungi from Malaysia. Dissertation, University of Malaya
- Lu JM, Yu RC, Chou CC (1996). Purification and some properties of glutaminase from *Actinomucor taiwanensis*, starter of sufu. *Journal of the Science of Food and Agriculture* 70:509–514. https://doi.org/10.1002/(SICI)1097-0010(199604)70:4<509::AID-JSFA532>3.0.CO;2-7
- Lucet A, Costantin J (1900). *Rhizomucor parasiticus*. EspeA ce pathogeAne delhomme. *Revue GeAneArale de Botanique* 12:89–98.
- Lucking R, Huhndorf S, Pfister DH, *et al.* (2009). Fungi evolved right on track. *Mycologia* 101:810–822. https://doi.org/10.3852/09-016
- Lukacs B, Papp T, Nyilasi I, et al. (2004). Differentiation of *Rhizomucor* species on the basis of their different sensitivities to lovastatin. *Journal of Clinical Microbiology* 42:5400–5402. https://doi.org/10.1128/JCM.42.11.5400-5402.2004
- Luo W, Xue C, Zhao Y, et al. (2020). Blakeslea trispora photoreceptors: identification and functional analysis. Applied Environmental Microbiology 86:e02962–19. https://doi.org/10.1128/AEM.02962-19
- Mahalaxmi I, Jayaramayya K, Venkatesan D, et al. (2021) Mucormycosis: an opportunistic pathogen during COVID– 19. Environmental Research 111643. https://doi.org/10.1016/j.envres.2021.111643
- Mahmud A, Lee R, Munfus-McCray D, et al. (2012). Actinomucor elegans as an emerging cause of mucormycosis. Journal of Clinical Microbiology 50:1092–1095. https://doi.org/10.1128/JCM.05338-11
- Malar CM, Krüger M, Krüger C, et al. (2021). The genome of Geosiphon pyriformis reveals ancestral traits linked to the emergence of the arbuscular mycorrhizal symbiosis. Current Biology 31:1570–1577. https://doi.org/10.1016/j.cub.2021.01.058
- Malar CM, Wang Y, Stajich JE, *et al.* (2022) Early branching arbuscular mycorrhizal fungus *Paraglomus occultum* carries a small and repeat-poor genome compared to relatives in the Glomeromycotina. *Microbial Genomics* 8:000810. https://doi.org/10.1099/mgen.0.000810
- Martínez-Herrera E, Frías-De-León MG, Julián-Castrejón A, et al. (2020). Rhino-orbital mucormycosis due to Apophysomyces ossiformis in a patient with diabetes mellitus: a case report. BMC Infectious Diseases 20:1–4. https://doi.org/10.1186/s12879-020-05337-4
- Martins EDS, Gomes E, da Silva R, *et al.* (2019). Production of cellulases by *Thermomucor indicae-seudaticae*: characterization of a thermophilic β-glucosidase. *Preparative Biochemistry and Biotechnology* 49:830–836. https://doi.org/10.1080/10826068.2019.1625060
- Martins MR, Santos C, Soares C, et al. (2020). Gongronella eborensis sp. nov., from vineyard soil of Alentejo (Portugal). International Journal of Systematic and Evolutionary Microbiology 70:3475–3482. https://doi.org/10.1099/ijsem.0.004201
- Mehrotra BS, Baijal U, Mehrotra BR (1963). Two new species of *Moriterella* from India. *Mycologia* 55:289–296. https://doi.org/10.11646/zootaxa.4742.1.3
- Mehrotra BS, Mehrotra BR (1969). Two new species of Mucor from India 4. Sydowia 23:183-185
- Merheb-Dini C, Garcia GAC, Penna ALB, et al. (2012). Use of a new milk-clotting protease from Thermomucor indicae-seudaticae N31 as coagulant and changes during ripening of Prato cheese. Food Chemistry 130:859– 865. https://doi.org/10.1016/j.foodchem.2011.07.105
- Meyer W, Gams W (2003). Delimitation of *Umbelopsis* (Mucorales, Umbelopsidaceae fam. nov.) based on ITS sequence and RFLP data. *Mycological Research* 107:339–350. https://doi.org/10.1017/s0953756203007226
- Mirza J, Khan S, Begum S, *et al.* (1979). Mucorales of Pakistan. University of Agriculture, Faisalabad, Pakistan, pp 1–183.

Misra PC (1975). A new species of Syncephalastrum. Mycotaxon 3:51-54

- Misra PC, Srivastava KJ, Lata K (1979). *Apophysomyces*, a new genus of the Mucorales. *Mycotaxon* 8:377–382. https://doi.org/10.1080/00275514.1953.12024280
- Mondo SJ, Dannebaum RO, Kuo RC, *et al.* (2017). Widespread adenine N6-methylation of active genes in fungi. *Nature Genetics* 49:964–968. https://doi.org/10.1038/ng.3859
- Moreau F (1952). Les champignons, physiologie, morphologie développement ét systematique. Botany, Paris.
- Morin E, Miyauchi S, San Clemente H, et al. (2019). Comparative genomics of *Rhizophagus irregularis*, *R. cerebriforme*, *R. diaphanus* and *Gigaspora rosea* highlights specific genetic features in Glomeromycotina. New Phytologist 222:1584–1598. https://doi.org/10.1111/nph.15687
- Morin-Sardin S, Nodet P, Coton E, *et al.* (2017). *Mucor*: a Janus-faced fungal genus with human health impact and industrial applications. *Fungal Biology Reviews* 31:12–32. https://doi.org/10.1016/j.fbr.2016.11.002
- Munday JS, Laven RA, Orbell GMB, et al. (2006). Meningoencephalitis in an adult cow due to *Mortierella wolfii*. Journal of Veterinary Diagnostic Investigation 18:619–622. https://doi.org/10.1177/104063870601800620
- Munday JS, Wolfe AG, Lawrence KE, et al. (2010). Disseminated Mortierella wolfii infection in a neonatal calf. New Zealand Veterinary Journal 58:62–63. https://doi.org/10.1080/00480169.2010.65062
- Nguyen MH, Kaul D, Muto C, et al. (2020). Genetic diversity of clinical and environmental Mucorales isolates obtained from an investigation of mucormycosis cases among solid organ transplant recipients. *Microbial Genomics*, 6:mgen000473. https://doi.org/10.1099/mgen.0.000473
- Nguyen TTT, Voigt K, de Santiago ALCMA, *et al.* (2021). Discovery of novel *Backusella* (Backusellaceae, Mucorales) isolated from invertebrates and toads in Cheongyang, Korea. *Journal of Fungi* 7:513. https://doi.org/10.3390/jof7070513
- Nie Y, Cai Y, Gao Y, *et al.* (2020a). Three new species of *Conidiobolus* sensu stricto from plant debris in eastern China. *MycoKeys* 73:133–149. https://doi.org/10.3897/mycokeys.73.56905
- Nie Y, Yu DS, Wang CF, et al. (2020b). A taxonomic revision of the genus Conidiobolus (Ancylistaceae, Entomophthorales): four clades including three new genera. MycoKeys 66:55–81. https://doi.org/10.3897/mycokeys.66.46575
- Nilsson RH, Hyde KD, Pawłowska J, *et al.* (2014). Improving ITS sequence data for identification of plant pathogenic fungi. *Fungal Diversity* 67:11–19. https://doi.org/10.1007/s13225-014-0291-8
- O'Donnell K, Lutzoni FM, Ward TJ, *et al.* (2001) Evolutionary relationships among mucoralean fungi (Zygomycota): evidence for family polyphyly on a large scale. *Mycologia* 93:286–297. https://doi.org/10.1111/nph.15687
- Oehl F, da Sliva GA, Goto BT, *et al.* (2011a). Glomeromycota: two new classes and a new order. *Mycotaxon* 116:365–379. https://doi.org/10.5248/116.365
- Oehl F, da Sliva GA, Goto BT, *et al.* (2011b). Glomeromycota: three new genera and glomoid species reorganized. *Mycotaxon* 116:75–120. https://doi.org/ 10.5248/116.75
- Oehl F, Sieverding E, Palenzuela J, *et al.* (2011c). Advances in Glomeromycota taxonomy and classification. *IMA Fungus* 2:191–199. https://doi.org/10.5598/imafungus.2011.02.02.10
- Overton BE (1997). Notes on the genus *Spinellus* with comparisons to other Zygomycetes found in fungicolous associations with Basidiomycetes. Dissertation, Southern Illinois University at Carbondale
- Ozimek E, Hanaka A (2021). *Mortierella* species as the plant growth-promoting fungi present in the agricultural soils. *Agriculture* 11:7. https://doi.org/10.3390/AGRICULTURE11010007
- Page RM (1962). Light and the asexual reproduction of *Pilobolus*. *Science* 138:1238–1245. https://doi.org/10.1126/science.138.3546.1238
- Page RM (1964). Sporangium discharge in *Pilobolus*: a photographic study. *Science* 146:925–927. https://doi.org/10.1126/science.146.3646.925
- Page RM, Kennedy D (1964). Studies on the velocity of discharged sporangia of *Pilobolus kleinii*. Mycologia 56:363– 368. https://doi.org/10.1080/00275514.1964.12018119

- Panthee S, Hamamoto H, Nishiyama Y, et al. (2021). Novel pathogenic Mucorales identified using the silkworm infection model. *Journal of Fungi* 7:995. https://doi.org/10.3390/JOF7110995
- Papp T, Nagy G, Csernetics A, et al. (2009). Beta-carotene production by mucoralean fungi. Journal of Engineering, Annals of Faculty of Engineering Hunedoara 7:173–176.
- Pavlovic MD, Bulajic N (2006). Great toenail onychomycosis caused by *Syncephalastrum racemosum. Dermatology* Online Journal 12:7. https://doi.org/10.5070/D3794644t6
- Pei KQ (2000a). A new variety of *Mucor variosporus* and the validation of *M. luteus* Linnemann and *M. variosporus* Schipper. *Mycosystema* 19:10–12. https://doi.org/10.13346/j.mycosystema.2000.01.004
- Pei KQ (2000b). Three new records of *Mucor* from China. *Mycosystema* 19: 563–565. https://doi.org/10.3969/j.issn.1672-6472.2000.04.024
- Pereira WES, da Silva RR, de Amo GS, et al. (2020). A collagenolytic aspartic protease from Thermomucor indicaeseudaticae expressed in Escherichia coli and Pichia pastoris. Applied Biochemistry and Biotechnology 191:1258–1270. https://doi.org/10.1007/s12010-020-03292-z
- Pertea G, Pertea M (2020). GFF utilities: GffRead and GffCompare. *F1000Research* 9:304. https://doi.org/10.12688/f1000research.23297.1
- Petkovits T, Nagy LG, Hoffmann K, et al. (2011). Data partitions, Bayesian analysis and phylogeny of the zygomycetous fungal family Mortierellaceae, inferred from nuclear ribosomal DNA sequences. PLoS One 6:e27507. https://doi.org/10.1371/journal.pone.0027507
- Phookamsak R, Hyde KD, Jeewon R, et al. (2019). Fungal diversity notes 929–1035: taxonomic and phylogenetic contributions on genera and species of fungi. Fungal Diversity 95:1–273. https://doi.org/10.1007/s13225-019-00421-w
- Pinho DB, Pereira OL, Soares DJ (2014). First report of *Gilbertella persicaria* as the cause of soft rot of fruit of Syzygium cumini. Australasian Plant Disease Notes 9:143. https://doi.org/10.1007/s13314-014-0143-0
- Posada D, Crandall KA (1998). Modeltest: testing the model of DNA substitution. *Bioinformatics* 14:817–818. https://doi.org/10.1093/bioinformatics/14.9.817
- Prakash H, Rudramurthy SM, Gandham PS, et al. (2017) Apophysomyces variabilis: draft genome sequence and comparison of predictive virulence determinants with other medically important Mucorales. BMC Genomics 18:1–13. https://doi.org/10.1186/s12864-017-4136-1
- Qin D, Wang L, Han M, et al. (2018). Effects of an endophytic fungus Umbelopsis dimorpha on the secondary metabolites of host–plant Kadsura angustifolia. Frontiers in Microbiology 9:2845. https://doi.org/10.3389/fmicb.2018.02845
- Rafhaella T, Cordeiro L, Thuong T, et al. (2020). Two new species of the industrially relevant genus Absidia (Mucorales) from soil of the Brazilian Atlantic Forest. Acta Botanica Brasilica 34:1–10. https://doi.org/10.1590/0102-33062020abb0040
- Rall G, Solheim W (1964). A variety of *Absidia* isolated from *Comandra pallida*. *Mycologia* 56:99–102. https://doi.org/10.1080/00275514.1964.12018086
- Rambaut A, Drummond A (2013). Tracer v1. 5. http://beast.bio.ed.ac.uk/Tracer
- Rao CY, Kurukularatne C, Garcia-Diaz JB, et al. (2007). Implications of detecting the mold Syncephalastrum in clinical specimens of new orleans residents after Hurricanes Katrina and Rita. Journal of Occupational and Environmental Medicine 49:411–416. https://doi.org/10.1097/JOM.0b013e31803b94f9
- Rashmi M, Kushveer JS, Sarma VV (2019). A worldwide list of endophytic fungi with notes on ecology and diversity. *Mycosphere* 10:798–1079. https://doi.org/10.5943/mycosphere/10/1/19
- Redecker D, Kodner R, Graham LE (2000). Glomalean fungi from the Ordovician. *Science* 289:1920–1921. https://doi.org/10.1126/science.289.5486.1920
- Ribaldi M (1952). Sopra un interessante Zigomicete terricola: Gongronella urceolifera n. gen., n. sp. Riv Biol Gen, NS 44:157–166.

Ridgway R (1912). Color standards and color nomenclature. Washington, D. C., The author.

- Robinson BE, Stark MT, Pope TL, *et al.* (1990). *Cunninghamella bertholletiae*: an unusual agent of zygomycosis. *Southern Medical Journal* 83:1088–1091.
- Romero-Olivares AL, Meléndrez-Carballo G, Lago-Lestón A, *et al.* (2019). Soil metatranscriptomes under long-term experimental warming and drying: fungi allocate resources to cell metabolic maintenance rather than decay. *Frontiers in Microbiology* 10:1914. https://doi.org/10.3389/fmicb.2019.01914
- Ronquist F, Teslenko M, Van Der Mark P, et al. (2012). MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61:539–542. https://doi.org/10.1093/sysbio/sys029
- Saksena S (1953). A new genus of the Mucorales. *Mycologia* 45:426–436. https://doi.org/10.1080/00275514.1953.12024280
- Sanchez R, Serra F, Tarraga J, et al. (2011). Phylemon 2.0: a suite of web-tools for molecular evolution, phylogenetics, phylogenomics and hypotheses testing. Nucleic Acids Research 39:W470–W474. https://doi.org/10.1093/nar/gkr408
- Sandmann G (2021). Diversity and origin of carotenoid biosynthesis: its history of coevolution towards plant photosynthesis. *New Phytologist* 232:479–493. https://doi.org/10.1111/NPH.17655
- Saroj A, Kumar A, Qamar N, et al. (2012). First report of wet rot of Withania somnifera caused by Choanephora cucurbitarum in India. Plant Disease 96:293–293. https://doi.org/10.1094/PDIS-09-11-0801
- Schipper MAA (1976). On *Mucor circinelloides, Mucor racemosus* and related species. *Studies in Mycology* 12:1–40. https://doi.org/10.1016/S0007-1536(76)80201-X
- Schipper MAA (1978a). On certain species of Mucor with a key to all accepted species. Studies in Mycology 17:1-52.
- Schipper MAA (1978b). On the genera Rhizomucor and Parasitella. Studies in Mycology 17:53-71.

Schipper MAA (1979). *Thermomucor* (Mucorales). *Antonie van Leeuwenhoek* 45:275–280. https://doi.org/10.1007/BF00418590

- Schipper MAA (1986a). Hyphomucor, an new genus in the Mucorales for Mucor assamensis. Mycotaxon 27:83-86.
- Schipper MAA (1986b). Notes on Zygorhynchus species. Persoonia 13:97-105.
- Schipper MAA, Samson RA (1994). Miscellaneous notes on Mucoraceae. Mycotaxon 50:475-491.
- Schipper, MAA (1990). Notes on Mucorales-1. Observations on Absidia. Persoonia 14:133-149.
- Schoch CL, Seifert KA, Huhndorf S, et al. (2012). Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for Fungi. Proceedings of the National Academy of Sciences 109:6241–6246. https://doi.org/10.1073/pnas.1117018109
- Schüßler A, Schwarzott D, Walker C (2001). A new fungal phylum, the Glomeromycota: phylogeny and evolution. Mycological Research 105:1413–1421. https://doi.org/10.1017/S0953756201005196
- Schulz BE, Kraepelin G, Hinkelmann W (1974). Factors affecting dimorphism in *Mycotypha* (Mucorales): a correlation with the fermentation/respiration equilibrium. *Microbiology* 82:1–13. https://doi.org/10.1099/00221287-82-1-1
- Schwartze VU, Jacobsen ID (2014). Mucormycoses caused by *Lichtheimia* species. *Mycoses* 57:73–78. https://doi.org/10.1111/myc.12239
- Schwartze VU, Winter S, Shelest E, et al. (2014). Gene expansion shapes genome architecture in the human pathogen Lichtheimia corymbifera: an evolutionary genomics analysis in the ancient terrestrial mucorales (Mucoromycotina). PLoS Genetic 10:e1004496. https://doi.org/10.1371/journal.pgen.1004496
- Sepuri A, Vidyavathi M (2008). *Cunninghamella* a microbial model for drug metabolism studies a review. *Biotechnology Advances* 27:16–29. https://doi.org/10.1111/myc.12239
- Shah AM, Mohamed H, Zhang Z, et al. (2021). Isolation, characterization and fatty acid analysis of Gilbertella persicaria DSR1: a potential new source of high value single-cell oil. Biomass and Bioenergy 151:106156. https://doi.org/10.1016/J.BIOMBIOE.2021.106156

- Shanor L, Poitras AW, Benjamin RK (1950). A new genus of the Choanephoraceae. *Mycologia* 42:271–278. https://doi.org/10.1080/00275514.1950.12017831
- Shipton W, Schipper MAA (1975). *Halteromyces*, a new genus in the Mucorales. *Antonie van Leeuwenhoek* 41:337–342. https://doi.org/10.1007/BF02565068
- Smith ME, Gryganskyi A, Bonito G, et al. (2013). Phylogenetic analysis of the genus Modicella reveals an independent evolutionary origin of sporocarp-forming fungi in the Mortierellales. Fungal Genetics and Biology 61:61–68. https://doi.org/10.1016/j.fgb.2013.10.001
- Spatafora JW, Chang Y, Benny GL, *et al.* (2016). A phylum-level phylogenetic classification of zygomycete fungi based on genome-scale data. *Mycologia* 108:1028–1046. https://doi.org/10.3852/16-042
- Stamatakis A (2014). RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30:1312–1313. https://doi.org/10.1093/bioinformatics/btu033
- Stanke M, Waack S (2003). Gene prediction with a hidden Markov model and a new intron submodel. *Bioinformatics* 19:215–225. https://doi.org/10.1093/bioinformatics/btg1080
- Subrahmanyam A, Lakshmi BV (1993). *Thermomucor indicae-seudaticae* on human skin. *Mycoses* 36:201–202. https://doi.org/10.1111/j.1439-0507.1993.tb00750.x
- Subrahmanyam A, Mehrotra B, Thirumalachar M (1977). *Thermomucor*, a new genus of Mucorales. *Georgia Journal of Science* 35:1–4.
- Sugiyama M, Tokumasu S, Gams W (2003). Umbelopsis gibberispora sp. nov. from Japanese leaf litter and a clarification of Micromucor ramannianus var. angulisporus. Mycoscience 44:217–226. https://doi.org/10.1007/s10267-003-0105-4
- Takeda I, Tamano K, Yamane N, et al. (2014). Genome sequence of the Mucoromycotina fungus Umbelopsis isabellina, an effective producer of lipids. Genome Announcements 2:e00071-14. https://doi.org/10.1128/genomeA.00071-14
- Tan SC, Tan TK, Wong SM, *et al.* (1996). The chitosan yield of zygomycetes at their optimum harvesting time. *Carbohydrate Polymers* 30:239–242. https://doi.org/10.1016/S0144-8617(96)00052-5
- Taylor AF, Alexander I (2005). The ectomycorrhizal symbiosis: life in the real world. *Mycologist* 19:102–112. https://doi.org/10.1017/S0269-915X(05)00303-4
- Taylor JW, Jacobson DJ, Kroken S, et al. (2000). Phylogenetic species recognition and species concepts in fungi. Fungal Genetics and Biology 31:21–32. https://doi.org/10.1006/fgbi.2000.1228
- Taylor TN, Krings M, Taylor EL (2014). Fossil fungi. Academic Press, London
- Tedersoo L, Sánchez-Ramírez S, Kõljalg U, *et al.* (2018). High-level classification of the fungi and a tool for evolutionary ecological analyses. *Fungal Diversity* 90:135–159. https://doi.org/10.1007/s13225-018-0401-0
- Telagathoti A, Probst M, Peintner U (2021). Habitat, snow-cover and soil pH, affect the distribution and diversity of Mortierellaceae species and their associations to Bacteria. *Frontiers in Microbiology* 12:1817. https://doi.org/10.3389/FMICB.2021.669784
- Thaxter R (1914). New or peculiar Zygomycetes. 3: *Blakeslea*, *Dissophora*, and *Haplosporangium*, nova genera. *Botanical Gazette* 58:353–366.
- Trachuk P, Szymczak WA, Muscarella P, et al. (2018). A case of invasive gastrointestinal Mycotypha infection in a patient with neutropenia. Case Reports in Infectious Diseases 2018:5864175. https://doi.org/10.1155/2018/5864175
- Trobisch A, Marterer R, Gorkiewicz G, et al. (2020). Invasive mucormycosis during treatment for acute lymphoblastic leukaemia-successful management of two life-threatening diseases. Supportive care in cancer: official journal of the Multinational Association of Supportive Care in Cancer 28:2157–2161. https://doi.org/10.1007/s00520-019-04962-3
- Tsai T, Hammond L, Rinaldi M, et al. (1997). Cokeromyces recurvatus infection in a bone marrow transplant recipient.

Bone Marrow Transplantation 19:301–302.

- Tully CC, Romanelli AM, Sutton DA, et al. (2009). Fatal Actinomucor elegans var. kuwaitiensis infection following combat trauma. Journal of Clinical Microbiology 47: 3394–3399. https://doi.org/10.1128/JCM.00797-09
- Turland NJ, Wiersema JH, Barrie FR, et al. (2018). International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159. Glashütten: Koeltz Botanical Books. https://doi.org/10.12705/Code.2018
- Upadhyay H (1970). Soil fungi from north-east and north Brazil 8. Persoonia 6:111–117.
- Upadhyay H (1973). *Helicostylum* and *Thamnostylum* (Mucorales). *Mycologia* 65:733–751.

https://doi.org/10.1080/00275514.1973.12019489

- Urquhart AS, Coulon PM, Idnurm A (2017). *Pilaira australis* sp. nov. Mucorales, Mucoromycota isolated from emu faeces in Australia. *Phytotaxa* 329:277–283. https://doi.org/10.11646/phytotaxa.329.3.9
- Urquhart AS, Douch J, Heafield T, *et al.* (2021). Diversity of *Backusella* (Mucoromycotina) in south-eastern Australia revealed through polyphasic taxonomy. *Persoonia* 46:1–25. https://doi.org/10.3767/persoonia.2021.46.01
- Urquhart AS, Idnurm A (2020). *Syncephalastrum contaminatum*, a new species in the Mucorales from Australia. *Mycoscience* 61:111–115. https://doi.org/10.1016/j.myc.2020.02.003
- van Tieghem P (1876). Troisieme memoire sur les Mucorinees. *Annales des Sciences Naturelles Botanique*, Ser 6 4:312–398
- Vandepol N, Liber J, Desiro A, et al. (2020). Resolving the Mortierellaceae phylogeny through synthesis of multi-gene phylogenetics and phylogenomics. *Fungal Diversity* 104:267–289. https://doi.org/10.1007/s13225-020-00455-5
- Viriato A (2008). Pilobolus species found on herbivore dung from the São Paulo Zoological Park, Brazil. Acta Botanica Brasilica 22:614–620. https://doi.org/10.1590/S0102-33062008000300002
- Voglmayr H, Krisai-Greilhuber I (1996). Dicranophora fulva, a rare mucoraceous fungus growing on boletes. Mycological Research 100:583–590. https://doi.org/10.1016/S0953-7562(96)80012-8
- Voigt K, James TY, Kirk PM, et al. (2021). Early-diverging fungal phyla: taxonomy, species concept, ecology, distribution, anthropogenic impact, and novel phylogenetic proposals. *Fungal Diversity* 109:59–98. https://doi.org/10.1007/s13225-021-00480-y
- Voigt K, Kirk PM (2015). Index Fungorum no. 245. ISSN 2049–2375. Index Fungorum doi: http://www.indexfungorum.org/Publications/Index%20Fungorum%20no.245.pdf.
- Voigt K, Wöstemeyer J (2001). Phylogeny and origin of 82 zygomycetes from all 54 genera of the Mucorales and Mortierellales based on combined analysis of actin and translation elongation factor EF-1α genes. *Gene* 270:113–120. https://doi.org/10.1016/S0378-1119(01)00464-4

## von Arx JA (1970). The genera of fungi sporulating in pure culture. pp 1–288. https://doi.org/10.1002/fedr.19820930124

- von Arx JA (1982). On Mucoraceae s. str. and other families of the Mucorales. Sydowia 35:10-26.
- Wagner L, Stielow B, Hoffmann K, et al. (2013). A comprehensive molecular phylogeny of the Mortierellales (Mortierellomycotina) based on nuclear ribosomal DNA. *Persoonia* 30:77–93. https://doi.org/10.3767/003158513X666268
- Wagner L, Stielow JB, de Hoog GS, et al. (2020). A new species concept for the clinically relevant Mucor circinelloides complex. Persoonia 44:67–97. https://doi.org/10.3767/persoonia.2020.44.03
- Walsh E, Luo J, Khiste S, *et al.* (2021). Pygmaeomycetaceae, a new root-associated family in Mucoromycotina from the pygmy pine plains. *Mycologia* 113:134–145. https://doi.org/10.1080/00275514.2020.1803649
- Walther G, Pawłowska J, Alastruey-Izquierdo *et al.* (2013). DNA barcoding in Mucorales: an inventory of biodiversity. *Persoonia* 30:11–47. https://doi.org/10.3767/003158513X665070
- Wanasinghe DN, Phukhamsakda C, Hyde KD, et al. (2018). Fungal diversity notes 709–839: taxonomic and phylogenetic contributions to fungal taxa with an emphasis on fungi on Rosaceae. Fungal Diversity 89:1–236.

https://doi.org/10.1007/s13225-018-0395-7

- Wang K, Chen SL, Dai YC, et al. (2021a). Overview of China's nomenclature novelties of fungi in the new century (2000–2020). Mycosystema 40: 822–833. https://doi.org/10.13346/j.mycosystema.210064
- Wang XW, Jiang JH, Liu SL, et al. (2021b). Species diversification of the coniferous pathogenic fungal genus Coniferiporia (Hymenochaetales, Basidiomycota) in association with its biogeography and host plants. Phytopathology. https://doi.org/10.1094/PHYTO-05-21-0181-R
- Wang Y, White MM, Kvist S, et al. (2016). Genome-wide survey of gut fungi (Harpellales) reveals the first horizontally transferred ubiquitin gene from a mosquito host. *Molecular Biology and Evolution* 33:2544–2554. https://doi.org/10.1093/molbev/msw126
- Wang YN, Liu XY, Zheng RY (2013). Four new species records of Umbelopsis (Mucoromycotina) from China. Journal of Mycology 2013:970216. https://doi.org/10.1155/2013/970216
- Wang YN, Liu XY, Zheng RY (2014). Umbelopsis changbaiensis sp. nov. from China and the typification of Mortierella vinacea. Mycological Progress 13:657–669. https://doi.org/10.1007/s11557-013-0948-9
- Wang YN, Liu XY, Zheng RY (2015). Umbelopsis longicollis comb. nov. and the synonymy of U. roseonana and U. versiformis with U. nana. Mycologia 107:1023–1032. https://doi.org/10.3852/14-339
- Wei F, Hong Y, Liu J, et al. (2010). Gongronella sp induces overproduction of laccase in Panus rudis. Journal of Basic Microbiology 50:98–103. https://doi.org/10.1002/jobm.200900155
- White TJ, Bruns T, Lee S, *et al.* (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. pp. 315-322 In: PCR protocols: a guide to methods and applications, eds. Innis, MA, Gelfand DH, Sninsky JJ, and White TJ. Academ- ic Press, Inc., New York.
- Wijayawardene NN, Hyde KD, Al-Ani LKT, et al. (2020). Outline of fungi and fungus-like taxa. Mycosphere 11:1060– 1456. https://doi.org/10.5943/mycosphere/11/1/8
- Wijayawardene NN, Pawłowska J, Letcher PM, *et al.* (2018). Notes for genera: basal clades of fungi (including Aphelidiomycota, Basidiobolomycota, Blastocladiomycota, Calcarisporiellomycota, Caulochytriomycota, Chytridiomycota, Entomophthoromycota, Glomeromycota, Kickxellomycota, Monoblepharomycota, Mortierellomycota, Mucoromycota, Neocallimastigomycota, Olpidiomycota, Rozellomycota and Zoopagomycota). *Fungal Diversity* 92:43–129. https://doi.org/10.1007/s13225-018-0409-5
- Woodbury N, Gries G (2013). Firebrats, *Thermobia domestica*, aggregate in response to the microbes *Enterobacter cloacae* and *Mycotypha microspora*. *Entomologia Experimentalis et Applicata* 147:154–159. https://doi.org/10.1111/eea.12054
- Wu F, Yuan HS, Zhou LW, et al. (2020). Polypore diversity in South China. Mycosystema 39: 653–682. https://doi.org/10.13346/j.mycosystema.200087
- Wu F, Zhou LW, Vlasák J, et al. (2022). Global diversity and systematics of Hymenochaetaceae with poroid hymenophore. Fungal Diversity 113:1–192. https://doi.org/10.1007/s13225-021-00496-4
- Xess I, Mohapatra S, Shivaprakash MR, et al. (2012). Evidence implicating Thamnostylum lucknowense as an etiological agent of rhino-orbital mucormycosis. Journal of Clinical Microbiology 50:1491–1494. https://doi.org/10.1128/JCM.06611-11
- Yamamoto K, Degawa Y, Yamada A (2020). Taxonomic study of Endogonaceae in the Japanese islands: new species of Endogone, Jingerdemannia, and Vinositunica, gen. nov. Mycologia 112:309–328. https://doi.org/10.1080/00275514.2019.1689092
- Yang LW, Ho HM, Chien CY (2012). Notes on Zygomycetes of Taiwan 10: the genus *Lichtheimia* in Taiwan. *Fungal Science* 27:109–120.
- Yang Y, Liu XY, Huang B (2022). The complete mitochondrial genome of *Linnemannia amoeboidea* (W. Gams) Vandepol & Bonito (Mortierellales: Mortierellaceae). *Mitochondrial DNA Part B* 7:374–376. https://doi.org/10.1080/23802359.2022.2039080

- Yao LD, Ju X, James TY, *et al.* (2018). Relationship between saccharifying capacity and isolation sources for strains of the *Rhizopus arrhizus* complex. *Mycoscience* 59:409–414. https://doi.org/10.1016/j.myc.2018.02.011
- Yao YJ, Pegler DN, Young TW (1996). Genera of Endogonales. Royal Botanic Gardens, Kew.
- Yin LQ, Zhang YZ, Azi F, et al. (2021). Neuroprotective potency of Tofu bio-processed using Actinomucor elegans against hypoxic injury induced by cobalt chloride in PC12 Cells. Molecules 26:2983. https://doi.org/10.3390/MOLECULES26102983
- Yip HY (1986). Umbelopsis fusiformis sp. nov. from a wet sclerophyll forest and a new combination for Mortierella ovata. Transactions of the British Mycological Society 86:334–337. https://doi.org/10.1016/S0007-1536(86)80167-X
- Young T (1987). Morphology of the anamorph of *Hesseltinella vesiculosa*. *Transactions of the British Mycological Society* 89:392–396. https://doi.org/10.1016/S0007-1536(87)80126-2
- Yuan HS, Lu X, Dai YC, et al. (2020). Fungal diversity notes 1277–1386: taxonomic and phylogenetic contributions to fungal taxa. Fungal Diversity 104:1–266. https://doi.org/10.1007/s13225-020-00461-7
- Zhang ZY, Zhao YX, Shen X, et al. (2020). Molecular phylogeny and morphology of Cunninghamella guizhouensis sp. nov. (Cunninghamellaceae, Mucorales), from soil in Guizhou, China. Phytotaxa 455:31–39. https://doi.org/10.11646/phytotaxa.455.1.4
- Zhao H, Lv ML, Liu Z, *et al.* (2021a). High-yield oleaginous fungi and high-value microbial lipid resources from Mucoromycota. *BioEnergy Research* 14:1196–1206. https://doi.org/10.1007/s12155-020-10219-3
- Zhao H, Nie Y, Zong TK, *et al.* (2022a). Three new species of *Absidia* (Mucoromycota) from China based on phylogeny, morphology and physiology. *Diversity* 14:132. https:// doi.org/10.3390/d14020132
- Zhao H, Nie Y, Zong TK, et al. (2022b). Species diversity and ecological habitat of Absidia (Cunninghamellaceae, Mucorales) with emphasis on five new species from forest and grassland soil in China. Journal of Fungi 8:471. https://doi.org/10.3390/jof8050471
- Zhao H, Zhu J, Zong TK, *et al.* (2021b). Two new species in the family Cunninghamellaceae from China. *Mycobiology* 49:142–150. https://doi.org/10.1080/12298093.2021.1904555
- Zhao RL, Li GJ, Sanchez-Ramirez S, *et al.* (2017). A six-gene phylogenetic overview of Basidiomycota and allied phyla with estimated divergence times of higher taxa and a phyloproteomics perspective. *Fungal Diversity* 84:43–74. https://doi.org/10.1007/s13225-017-0381-5
- Zhao Y, Wang H, Liu T, et al. (2014). The individual lipid compositions produced by Cunninghamella sp. Salicorn 5, an endophytic oleaginous fungus from Salicornia bigelovii Torr. European Food Research and Technology 238:621–633. https://doi.org/10.1007/s00217-013-2141-4
- Zheng HD, Zhuang WY, Wang XC, et al. (2020). Ascomycetes from the Qilian Mountains, China Pezizomycetes and Leotiomycetes. Mycosystema 39: 1823–1845. https://doi.org/10.13346/j.mycosystema.200217
- Zheng RY, Chen GQ (1986). *Blakeslea sinensis* sp. nov., a further proof for retaining the genus *Blakeslea*. *Acta Mycologica Sinica*, Suppl I:40–55
- Zheng RY, Chen GQ (1991). A nonthermophilic *Rhizomucor* causing human primary cutaneous mucormycosis. *Mycosystema* 4:45–57
- Zheng RY, Chen GQ (1998). Cunninghamella clavata sp. nov., a fungus with an unusual type of branching of sporophore. Mycotaxon 69:187–198
- Zheng RY, Chen GQ (2001). A monograph of Cunninghamella. Mycotaxon 80:1-75
- Zheng RY, Chen GQ, Hu FM (1988). Monosporus varieties of Syncephalastrum. Mycosystema 1:35-52
- Zheng RY, Chen GQ, Huang H, et al. (2007). A monograph of Rhizopus. Sydowia 59:273.
- Zheng RY, Jiang HJM (1995). *Rhizomucor endophyticus* sp. nov., an endophytic zygomycetes from higher plants. *Mycotaxon* 56:455–466
- Zheng RY, Liu XY (2005). Actinomucor elegans var. meitauzae, the correct name for A. taiwanensis and Mucor

meitauzae (Mucorales, Zygomycota). Nova Hedwigia:419-432.

- Zheng RY, Liu XY (2009). Taxa of *Pilaira* (Mucorales, Zygomycota) from China. *Nova Hedwigia* 88:255–267. https://doi.org/10.1127/0029-5035/2009/0088-0255
- Zheng RY, Liu XY (2014). *Ambomucor* gen. & spp. nov. from China. *Mycotaxon* 126:97–108. https://doi.org/10.5248/126.97
- Zheng RY, Liu XY, Li RY (2009). More *Rhizomucor* causing human mucormycosis from China: *R. chlamydosporus* sp. nov. *Sydowia* 61:135–147.
- Zheng RY, Liu XY, Wang YN (2013). Two taxa of the new record genus *Backusella* from China. *Mycosystema* 32:330–341.
- Zheng RY, Liu XY, Wang YN (2017). *Circinella* (Mucorales, Mucoromycotina) from China. *Mycotaxon* 132:43–62. https://doi.org/10.5248/132.43
- Zheng RY. (2002). Zygorhynchus multiplex, a new species isolated from paddy soil. Mycotaxon 84 367-378.
- Zimin AV, Marçais G, Puiu D, *et al.* (2013). The MaSuRCA genome assembler. *Bioinformatics* 29:2669–2677. https://doi.org/10.1093/bioinformatics/btt476
- Zoghi M, Gandomkar S, Habibi Z (2019). Biotransformation of progesterone and testosterone enanthate by *Circinella muscae*. *Steroids* 151:108446. https://doi.org/10.1016/j.steroids.2019.108446
- Zong TK, Zhao H, Liu XL, et al. (2021). Taxonomy and phylogeny of four new species in Absidia (Cunninghamellaceae, Mucorales) from China. Frontiers in Microbiology 12:677836. https://doi.org/10.3389/fmicb.2021.677836
- Zycha H, Siepmann R, Linnemann G (1969). Mucorales: eine Beschreibung aller Gattungen und Arten dieser Pilzgruppe. Verlag von J. Cramer, pp 1–355