MYCOSPHERE 16(1): 4594–4662 (2025) www.mycosphere.org ISSN 2077 7019
https://doi.org/10.5943/mycosphere/16/1/34

ARTICLE

Updating taxonomy of *Conidiobolus* sensu lato: Proposal of a new family, a new genus, 23 new species and two new combinations

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Citation – Nie Y, Zhao H, Zhang MH, Lee HB, Chang Y, Liu XY, Huang B. 2025 – Updating taxonomy of *Conidiobolus* sensu lato: Proposal of a new family, a new genus, 23 new species and two new combinations. Mycosphere 16(1), 4594–4662, https://doi.org/10.5943/mycosphere/16/1/34

Abstract

Conidiobolus sensu lato entomophthoroid fungi comprise one of the most species-rich, diverse, and ecologically significant lineages in entomophthoroid fungi. Primarily saprophytic on fallen leaves and other organic debris, these fungi are also pathogenic to insects and can occasionally infect mammals, including humans, causing conidiobolomycosis. The recent increase in human infections underscores the urgency of a comprehensive taxonomic reassessment to understand disease origins better, develop preventive measures, and harness biocontrol potential. Molecular analyses have revealed the polyphyletic nature of this group, prompting its reclassification into three families and five genera. Although this revision provides clarity, the precise phylogenetic placement of *Microconidiobolus* remains unresolved. We herein performed a comprehensive phylogenomic analysis of *Conidiobolus* s.l., incorporating 43 newly sequenced genomes and divergence-time estimates based on multiple loci (nucLSU, *EFL*, and mtSSU). The results indicate that family-level lineages diverged approximately 281 million years ago (Mya), highlighting the deep evolutionary history of these fungi. *Microconidiobolus* was robustly placed as a sister group to *Conidiobolaceae*, with an estimated divergence time around 279 Mya, and was consequently raised to family rank. Integrating these molecular findings with morphological data, we propose an updated classification of four families (*Capillidiaceae*, *Conidiobolaceae*, *Microconidiobolaceae*, and *Neoconidiobolaceae*) and six genera (*Azygosporus*, *Callaghania*, *Capillidum*, *Conidiobolus* sensu stricto, *Microconidiobolus*, and *Neoconidiobolus*). Twenty-three new species (two in *Capillidium*, 16 in *Conidiobolus* s.s., and five in *Neoconidiobolus*) were described from China, and two new combinations were put into *Callaghania*. Additionally, comprehensive morphological keys to facilitate species identification were provided. Overall, this study constitutes a monographic treatment of *Conidiobolus* s.l., offering crucial insights into their taxonomy and into the early diversification of terrestrial fungi.

Keywords – Classification – Early-diverging fungi – Entomophthoromycotina – New taxa – Phylogenomics

Submitted: 12 September 2025; **Accepted:** 16 December 2025; **Published:** 30 December 2025
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Accepted by: Samantha C. Karunarathna

INTRODUCTION

The genus *Conidiobolus* (*Ancylistaceae*, *Entomophthorales*) was originally established by Brefeld (1884) to encompass *Co. utriculosus* and *Co. minor.* Clements & Shear (1931) designated *Co*. *utriculosus* as the type, while *Co*. *minor* is now synonymized with the type and widely accepted (Srinivasan & Thirumalachar 1967, King 1977, Nie et al. 2020a). Due to the lack of ex-type living culture of the type species *Co*. *utriculosus*, another widespread species *Co*. *coronatus*, was recently designated as neotype for the genus *Conidiobolus* (Möckel et al. 2022). Morphologically, the genus is characterized by the following features: (i) nuclei that are not stained with aceto-orcein and lack granular contents; (ii) simple conidiophores; (iii) globose to pyriform, multinucleate conidia; (iv) resting spores formed predominantly as zygospores within the hyphal axis; and (v) walled vegetative cells (Humber, 1997). Ecologically, members of *Conidiobolus* function as important saprotrophs in terrestrial ecosystems, particularly in the decomposition of fallen leaves, branches, and other organic detritus (Gryganskyi et al. 2012, 2013; Nie et al. 2012, 2020a). However, certain species occasionally infect insects and mammals, including humans, causing conidiobolomycosis (Vilela et al. 2010, Mendoza et al. 2014, Gryganskyi et al. 2022). Although human conidiobolomycosis was historically associated primarily with *Co. coronatus*, *Co. incongruus*, and *Neoconidiobolus lamprauges*, recent cases suggest a broader range of potential pathogenic species (Vilela & Mendoza 2018). Elucidating the pathogenic capabilities and ecological niches of *Conidiobolus* is therefore crucial for medical intervention.

Despite their prospective utility in managing insect pests, challenges remain due to biosafety concerns and difficulties maintaining stable growth in fluctuating natural environments (Gryganskyi et al. 2024). Intriguingly, *Co. coronatus* produces coronatin-1 and coronatin-2, which are enzymes with known insecticidal activity, further underscoring the group's potential for agricultural and industrial applications (Bogus et al. 2016, 2017). Yet, these same species can opportunistically infect mammals, emphasizing the delicate balance between beneficial and pathogenic traits. Therefore, a comprehensive and stable taxonomy is essential for the effective monitoring, management, and utilization of these fungi.

Historically, the genus *Conidiobolus* was recognized as polyphyletic (Ben-Ze'ev & Kenneth 1982, Jensen et al. 1998, Gryganskyi et al. 2013) and was subdivided into three subgenera based on secondary conidial types (Ben-Ze'ev & Kenneth 1982, Humber 1989). Later, molecular investigations (Bruns et al. 1991) led to the delineation of *Capillidium* (characterized by capilliconidia), *Conidiobolus* sensu stricto (producing microconidia), *Microconidiobolus* (forming small primary conidia, often < 20.0 μm, without capilliconidia or microconidia), and *Neoconidiobolus* (lacking capilliconidia or microconidia) (Nie et al. 2020a). Subsequently, *Azygosporus* was described to accommodate species producing azygospores (Cai et al. 2021), and a broader phylogenetic framework encompassing these five genera led to the recognition of three families: *Capillidiaceae*, *Conidiobolaceae*, and *Neoconidiobolaceae* (Gryganskyi et al. 2022). Nevertheless, taxonomic ambiguities remain. For instance, members of *Microconidiobolus* occupy contentious phylogenetic positions (Gryganskyi et al. 2022, Seto & James 2024), and taxa such as *Co. iuxtagenitus*, *Ca. adiaeretum*, and *Ca. bangalorense* suggest cryptic lineages that deviate from established morphological and phylogenetic boundaries (Waters & Callaghan 1989, Nie et al. 2022, 2023). To ensure clarity and terminological consistency throughout the text, we have adopted the term "*Conidiobolus* s.l." to refer to the aforementioned taxonomic units collectively.

Numerous mycologists have contributed to the characterization and description of *Conidiobolus* s.l. taxa. Drechsler, for example, documented 25 species from the United States (Drechsler 1952, 1953a, b, 1954, 1955a, b, c, 1956, 1957a, b, c, 1960, 1961, 1962, 1965), while 13 species were reported from India by Srinivasan & Thirumalachar (1961, 1962a, b, 1965, 1967, 1968a, b). King (1976a, b, 1977) then employed numerical taxonomy, recognizing 27 definitive species. Although certain species (*Co. iuxtagenitus*, *Co. margaritatus*, and *Co. thermophilus*) are readily diagnosed by morphological or physiological traits, most *Conidiobolus* s.l. display subtle diagnostic features, rendering them difficult to identify without molecular tools (Waters & Callaghan 1989, Huang et al. 2007, Waingankar et al. 2008). In particular, nucLSU and *EFL* loci

have proven instrumental in species delimitation (Nie et al. 2012; Goffre et al. 2020; Pawar et al. 2025; Wang et al. 2025).

Over the past decade, extensive collections from China have resulted in 17 *Conidiobolus* s.l. new species (Nie et al. 2012, 2016, 2017, 2018, 2020b, 2021, 2022, 2023, 2024, Cai et al. 2021), greatly enriching our understanding of the group's diversity. This expanded taxon sampling establishes a stronger foundation for reconstructing their evolutionary history, clarifying phylogenetic positions, and resolving long-standing systematic uncertainties.

Advances in phylogenomics that are exemplified by initiatives such as the 1000 Fungal Genomes Project (Shen et al. 2020, Li et al. 2021) have revolutionized the study of early-diverging fungi, as demonstrated by major taxonomic revisions in *Mucoromycota* and *Zoopagomycota* (Spatafora et al. 2016, Vandepol et al. 2020, Zhao et al. 2023). Similarly, divergence time estimations have proven useful in calibrating higher-ranking fungal clades and refining classifications in groups like the *Basidiomycota* (Zhao et al. 2017, He et al. 2019) and the lichenized fungi (Prieto et al. 2024), and meaningful in evaluating lower-ranking fungal groups like the *Chaetomiaceae* (Wang et al. 2022). For entomophthoroid fungi, estimates of *Entomophthoromycota*'s origins vary widely, from approximately 405 ± 90 million years ago (Gryganskyi et al. 2012) to more than 700 million years ago (Tedersoo et al. 2018). Against this backdrop, a comprehensive approach employing genome-scale data, broad taxon sampling, and morphological correlation is essential to untangle the phylogeny of *Conidiobolus* s.l. and is a critical step toward harnessing their ecological, pathogenic, and biocontrol potential.

Hence, in this study, we aim to 1) reveal the diversity of *Conidiobolus* s.l. in China, 2) to clarify their phylogenetic relationships using multi-locus and genomic data alongside divergence time estimation, and 3) to propose an updated taxonomic framework that addresses long-standing systematic ambiguities. By providing a more robust classification and deeper evolutionary perspective, our work lays the groundwork for future research on the biology, ecology, and pathogenicity of these important early-diverging fungi.

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MATERIALS AND METHODS

Strains, sampling, and isolation

Ex-type strains of *Conidiobolus* s.l. sequenced in this study were obtained from the American Type Culture Collection (ATCC; Manassas, USA), the China General Microbiological Culture Collection Center (CGMCC; Beijing, China), and the Research Center for Entomogenous Fungi (RCEF) at Anhui Agricultural University, Anhui Province, China (Table 1). Additional *Conidiobolus* s.l. strains were isolated from plant debris and soil samples collected in various National Forest Parks and National Nature Reserves across China.

Samples (2 × 2 cm) were excised with sterilized scissors and placed in pre-sterilized plastic bags. Once these samples were brought to the laboratory, isolations of *Conidiobolus* s.l. were conducted following modified methods of Drechsler (1952) and King (1976a), as outlined by Nie et al. (2012). Briefly, plant fragments or small soil lumps were distributed onto the inverted lid of a Petri dish containing potato dextrose agar (PDA: 20 g glucose, 200 g potato, 20 g agar, 1 L distilled water, pH 7) at 21 °C. When fungal growth resembling *Conidiobolus* s.l. was observed using a Nikon SMZ1500 stereomicroscope (Nikon, Japan), colonies were transferred to fresh PDA plates for purification and subsequent morphological and molecular analyses. All isolates were deposited at RCEF

Morphological observation

Fungal colonies were incubated on PDA at 21 °C for up to two weeks, and colony characteristics were monitored daily. Morphological observations followed King (1976a). Microstructures (mycelium, conidiophores, conidia, and resting spores) were examined with an Olympus BX51 light microscope (Olympus, Tokyo, Japan), and digital images were captured with an Olympus DP25 camera. Secondary conidia were induced on 2% water agar (2 g agar in 1 L distilled water). Measurements of morphological structures ($n \geq 30$ for each feature) were recorded.

DNA extraction, PCR amplification, and sequencing

Genomic DNA was extracted from one-week-old mycelia ground in liquid nitrogen using a cetyltrimethylammonium bromide (CTAB) protocol (Watanabe et al. 2010). Three loci of nucLSU, *EFL*, and mtSSU were targeted for phylogenetic analyses. The nucLSU region was amplified with primers LR0R (5'-ACC CGC TGA ACT TAA GC-3') and LR5 (5'-TCC TGA GGG AAA CTT CG-3') (Vilgalys & Hester 1990), *EFL* with EF983 (5'-GCY CCY GGH CAY CGT GAY TTY AT-3') and EF1aZ-1R (5'-ACA TCW CCG ACA CCC TTG ATC TTG -3') (Nie *et al.* 2012), and mtSSU with mtSSU1 (5'-GCW GCA GTG RGG AAT NTT GGR CAA T-3') and mtSSU2R (5'-GTR GAC TAM TSR GGT ATC TAA TC-3') for mtSSU (Zoller et al. 1999).

PCR conditions consisted of an initial denaturation at 94 °C for 3 min; 35 cycles of denaturation at 94 °C for 1 min, annealing (nucLSU at 55 °C, mtSSU at 54 °C, *EFL* at 57 °C) for 1 min, and extension at 72 °C for 1 min; plus a final extension at 72 °C for 10 min (Nie et al. 2022). Amplicons were purified and Sanger-sequenced (Shanghai Genecore Biotechnologies, China). Assembled sequences were deposited in GenBank under the accession numbers listed in Table 1.

In addition, whole-genome sequencing was performed for 43 *Conidiobolus* s.l. isolates (Table 2) using the Illumina HiSeq X Ten platform (Fuyu Biosciences, Beijing, China). Paired-end libraries (~300 bp inserts) were constructed with the AIR Paired-End DNA Sequencing Kit (Bioo Scientific, USA). Quality control of raw reads was assessed with FastQC v0.11.8 (Andrews 2010). Draft assemblies were generated using SOAPdenovo v2.04 (Luo et al. 2012) and annotated with funannotate v1.8.1 (Palmer & Stajich 2020). Predicted protein-coding genes were extracted via Gffread v0.12.4 (Pertea & Pertea 2020).

Phylogenomic and phylogenetic analyses

For phylogenomic analyses, the predicted proteomes of 25 additional fungal genomes were retrieved from GenBank, and the genome of *Zoophthora radicans* was obtained from the Joint Genome Institute (Table 2). Detailed genomic information is presented in Table S1. Three species of *Mucoromycota* (*Phycomyces blakesleeanus*, *Saksenaea vasiformis*, and *Umbelopsis ramanniana*) served as outgroups. Phylogenomic marker selection followed Vandepol et al. (2020), using 434 conserved single-copy genes built into HMM profiles via HMMER3 (Eddy 2011). Each HMM profile was searched against the annotated proteomes of all 69 fungal genomes. Multiple alignments were generated with hmmalign, trimmed using TRIMAL (Capella-Gutierrez et al. 2009), and concatenated into a supermatrix. A Maximum Likelihood (ML) phylogenomic tree was inferred in RAxML v8.1.17 (Stamatakis 2014) using the "-f a" algorithm with 100 rapid bootstrap replicates.

For multi-locus phylogenetic analyses, nucLSU, *EFL*, and mtSSU sequences (see Table 1 for details) were aligned individually with MAFFT v7 (Katoh et al. 2019) and edited in BioEdit v7.2.6 (Hall 1999). The three alignments were concatenated in SequenceMatrix 1.7.8 (Vaidya et al. 2011). Outgroups included ten species of *Mucoromycota*. ModelFinder (Kalyaanamoorthy et al. 2017) identified the optimal nucleotide substitution model using the Akaike Information Criterion (AIC). ML analysis was performed in IQ-TREE 2.3.6 (Nguyen et al. 2015), applying 1,000 ultrafast bootstrap replicates. Bayesian Inference (BI) was conducted with MrBayes v3.2.6 (Ronquist et al. 2012). Four Markov chains were run for 3 M generations, sampling every 100 generations, until the average standard deviation of split frequencies fell below 0.01. The initial 25% of sampled trees were discarded as burn-in, and posterior probabilities (PP) were calculated from the remaining trees. Resulting trees were visualized with FigTree v1.4 (Rambaut 2012) and finalized in iTOL (https://itol.embl.de/) and Adobe Illustrator CS6. The final alignment and ML trees were deposited in TreeBASE (Submission ID S31978.

Divergence time estimation

All taxa were included in a molecular dating analysis using the combined nucLSU, *EFL*, and mtSSU dataset (Table 1). Divergence time estimation was performed in BEAST 2.6.7 (Bouckaert et al. 2014). An XML input file was generated in BEAUTI v2 under a relaxed clock model (uncorrelated lognormal distribution) and Yule speciation prior, assuming no extinction (Barraclough & Nee 2001). ModelTest-NG v0.1.7 (Darriba et al. 2020) was used to select the best-fitting nucleotide substitution model, identifying GTR as the optimal model accounting for evolutionary rate heterogeneity across sites. The selection of fossil fungal calibration points followed established methodologies from previous studies on ascomycetes, basidiomycetes, and entomophthoroid fungi (Gryganskyi et al. 2012, Zhao et al. 2017, Samarakoon et al. 2022, Zhao et al. 2025).

Table 1 The species used in the phylogenetic and divergence time analyses.

Species	Strains	GenBank accession numbers			References
		nucLSU	*EFL*	mtSSU	
Absidia glauca	CBS 101.08 (T)	NG058550	–	–	Vitale et al. (2012)
Absidia repens	CBS 115583 (T)	HM849706	–	–	Vitale et al. (2012)
Azygosporus macropapillatus	CGMCC 3.16068	MZ542006	MZ555650	MZ542279	Cai et al. (2021a)
Azygosporus parvus	ATCC 14634 (T)	KX752051	KY402207	MK301192	Cai et al. (2021a)
Backusella circina	CBS 128.70 (T)	MH871298	–	–	Vu et al. (2019)
Basidiobolus haptosporus	ARSEF 261	JX242586	–	–	Gryganskyi et al. (2012)
Basidiobolus heterosporus	CBS 311.66	JX242587	–	JX242627	Gryganskyi et al. (2012)
Basidiobolus magnus	CBS 205.64	JX242588	–	JX242628	Gryganskyi et al. (2012)
Basidiobolus meristosporus	CBS 931.73	JX242589	–	JX242629	Gryganskyi et al. (2012)
Basidiobolus microsporus	CBS 130.62 (T)	JX242590	–	JX242630	Gryganskyi et al. (2012)
Basidiobolus omanensis	CBS 146281 (T)	MT831973	–	–	Al-Hatmi et al. (2021)
Basidiobolus ranarum	NRRL 34594	DQ273807	DQ275340	EF392490	James et al. (2006a)
Batkoa apiculata	ARSEF 3130	EF392404	–	EF392513	Gryganskyi et al. (2012)
Batkoa gigantea	ARSEF 214	JX242591	–	JX242631	Gryganskyi et al. (2012)
Batkoa major	ARSEF 2936	EF392401	–	EF392511	Gryganskyi et al. (2012)
Batkoa obscurus	CBS 182.60	JX242595	–	JX242635	Gryganskyi et al. (2012)
Batkoa pseudapiculata	ARSEF 395	EF392378	–	EF392508	Gryganskyi et al. (2012)
Callaghania adiaereta	CGMCC 3.15888	MN061284	MN061481	MN061287	Nie et al. (2020a)
Callaghania bangalorensis	ARSEF 449 (T)	DQ364204	–	DQ364225	Nie et al. (2020a)
Capillidium denaeosporum	ATCC 12940 (T)	JF816215	JF816228	MK301181	Nie et al. (2020a)
Capillidium heterosporum	RCEF 4430	JF816225	JF816239	MK301183	Nie et al. (2020a)

Species	Strains	GenBank accession numbers			References
		nucLSU	*EFL*	mtSSU	
Capillidium huangfushanense	**RCEF 7528 (T)**	**PV084580**	**PV107230**	**PV084628**	This article
Capillidium huangfushanense	**RCEF 7529**	**PV084581**	**PV107231**	**PV084629**	This article
Capillidium jinlanshanense	**RCEF 7931 (T)**	**PV084582**	**PV107232**	**PV084630**	This article
Capillidium jinlanshanense	**RCEF 7932**	**PV084583**	**PV107233**	**PV084631**	This article
Capillidium lobatum	ATCC 18153 (T)	JF816218	JF816233	MK301187	Nie et al. (2020a)
Capillidium pumilum	ARSEF 453 (T)	EF392383	–	EF392496	Nie et al. (2020a)
Capillidium rhysosporum	ATCC 12588 (T)	JN131540	JN131546	MK301195	Nie et al. (2020a)
Capillidium rugosum	CBS 158.56 (T)	MH869097	–	–	Vu et al. (2019)
Capillidium marcocapilliconidium	CGMCC 3.16169 (T)	OL830454	OL801337	OL830457	Nie et al. (2022a)
Capillidium jiangsuense	CGMCC 3.16168 (T)	OL830456	OL801339	OL830459	Nie et al. (2022a)
Conidiobolus amphitus	**RCEF 7939 (T)**	**PV084594**	**PV107244**	**PV084642**	This article
Conidiobolus amphitus	**RCEF 7940**	**PV084595**	**PV107245**	**PV084643**	This article
Conidiobolus bifurcatus	CGMCC 3.15889 (T)	MN061285	MN061482	MN061288	Nie et al. (2020b)
Conidiobolus brefeldianus	ARSEF 452 (T)	EF392382	–	EF392495	Nie et al. (2020a)
Conidiobolus chlamydosporus	ATCC 12242 (T)	JF816212	JF816234	MK301178	Nie et al. (2020a)
Conidiobolus coronatus	NRRL 28638	AY546691	DQ275337	–	James et al. (2006b)
Conidiobolus dabieshanensis	CGMCC 3.15763 (T)	KY398125	KY402206	MK301180	Nie et al. (2017)
Conidiobolus firmipilleus	ARSEF 6384	JX242592	–	JX242632	Gryganskyi et al. (2012)
Conidiobolus gonimodes	ATCC 14445 (T)	JF816221	JF816226	MK301182	Nie et al. (2020a)

Species	Strains	GenBank accession numbers			References
		nucLSU	*EFL*	mtSSU	
Conidiobolus hainanensis	**RCEF 7486 (T)**	**PV084600**	**PV107250**	**PV084648**	This article
Conidiobolus hainanensis	**RCEF 7487**	**PV084601**	**PV107251**	**PV084649**	This article
Conidiobolus hainanensis	**RCEF 7488**	**PV084602**	**PV107252**	**PV084650**	This article
Conidiobolus hippocrepiformis	**RCEF 7923 (T)**	**PV084603**	**PV107253**	**PV084651**	This article
Conidiobolus hippocrepiformis	**RCEF 7924**	**PV084604**	**PV107254**	**PV084652**	This article
Conidiobolus humicolus	ATCC 28849 (T)	JF816220	JF816231	MK301184	Nie et al. (2020a)
Conidiobolus incongruus	NRRL 28636	AF113457	–	–	Voigt et al. (1999)
Conidiobolus iuxtagenitus	ARSEF 6378 (T)	KC788410	–	–	Gryganskyi et al. (2013)
Conidiobolus iuxtagenitus	RCEF 4445	JX946695	JX946700	MK333391	Nie et al. (2020a)
Conidiobolus jiangxiensis	RCEF 7484 (T)	PP034291	PP035215	PP034295	Nie et al. (2024)
Conidiobolus khandalensis	ATCC 15162 (T)	KX686994	KY402204	MK301185	Nie et al. (2020a)
Conidiobolus kunmingensis	**RCEF 7945 (T)**	**PV084605**	**PV107255**	**PV084653**	This article
Conidiobolus kunmingensis	**RCEF 7946**	**PV084606**	**PV107256**	**PV084654**	This article
Conidiobolus lichenicolus	ATCC 16200 (T)	JF816216	JF816232	MK301186	Nie et al. (2020a)
Conidiobolus lii	**RCEF 4911**	**PV084607**	**PV107257**	**PV084655**	This article
Conidiobolus lii	**RCEF 7535 (T)**	**PV084608**	**PV107258**	**PV084656**	This article
Conidiobolus lunulus	CEP 788 (T)	MN956769	–	–	Goffre et al. (2020)
Conidiobolus longibasalis	**RCEF 7929 (T)**	**PV084609**	**PV107259**	**PV084657**	This article
Conidiobolus longibasalis	**RCEF 7930**	**PV084610**	**PV107260**	**PV084658**	This article
Conidiobolus longiconidiophorus	RCEF 6563 (T)	OQ540746	OQ550509	OQ540744	Nie et al. (2023)
Conidiobolus longivillosus	RCEF 7911 (T)	PQ659539	PQ670986	PQ659548	Wang et al. (2025)
Conidiobolus marcoconidius	RCEF 6918 (T)	PP034289	PP035213	PP034293	Nie et al. (2024)

Species	Strains	GenBank accession numbers			References
		nucLSU	*EFL*	mtSSU	
Conidiobolus marcosporus	ATCC 16578 (T)	KY398124	KY402209	MK301188	Nie et al. (2020a)
Conidiobolus macrozygosporus	**RCEF 7521 (T)**	**PV084611**	**PV107261**	**PV084659**	This article
Conidiobolus macrozygosporus	**RCEF 7522**	**PV084612**	**PV107262**	**PV084660**	This article
Conidiobolus megalotocus	CBS 139.57 (T)	MH869214	–	–	Vu et al. (2019)
Conidiobolus megalotocus var. *indicus*	ATCC 28854 (T)	MF616383	MF616385	MK301189	Nie et al. (2020a)
Conidiobolus mycophagus	ATCC 16201 (T)	JX946694	JX946698	MK301190	Nie et al. (2020a)
Conidiobolus mycophilus	ATCC 16199 (T)	KX686995	KY402205	MK301191	Nie et al. (2020a)
Conidiobolus oxyconidius	**RCEF 7937 (T)**	**PV084613**	**PV107263**	**PV084661**	This article
Conidiobolus oxyconidius	**RCEF 7938**	**PV084614**	**PV107264**	**PV084662**	This article
Conidiobolus pachyconidiophorus	**RCEF 7941 (T)**	**PV084615**	**PV107265**	**PV084663**	This article
Conidiobolus pachyconidiophorus	**RCEF 7942**	**PV084616**	**PV107266**	**PV084664**	This article
Conidiobolus pectiniformis	**RCEF 4923 (T)**	**PV084596**	**PV107246**	**PV084644**	This article
Conidiobolus pectiniformis	**RCEF 4925**	**PV084597**	**PV107247**	**PV084645**	This article
Conidiobolus planibasalis	**RCEF 7515 (T)**	**PV084598**	**PV107248**	**PV084646**	This article
Conidiobolus planibasalis	**RCEF 7516**	**PV084599**	**PV107249**	**PV084647**	This article
Conidiobolus polyspermus	ATCC 14444 (T)	MF616382	MF616384	MK301193	Nie et al. (2020a)
Conidiobolus polysporus	RCEF 7058 (T)	OQ540747	OQ550510	OQ540745	Nie et al. (2023)
Conidiobolus polytocus	ATCC 12244 (T)	JF816213	JF816227	MK301194	Nie et al. (2020a)
Conidiobolus proximus	**RCEF 7927 (T)**	**PV084617**	**PV107267**	**PV084665**	This article
Conidiobolus proximus	**RCEF 7928**	**PV084618**	**PV107268**	**PV084666**	This article
Conidiobolus pseudogonimodes	**RCEF 7933 (T)**	**PV084619**	**PV107269**	**PV084667**	This article

Species	Strains	GenBank accession numbers			References
		nucLSU	*EFL*	mtSSU	
Conidiobolus pseudogonimodes	**RCEF 7934**	**PV084620**	**PV107270**	**PV084668**	This article
Conidiobolus ramiconidiophorus	**RCEF 7523 (T)**	**PV084626**	**PV107276**	**PV084674**	This article
Conidiobolus ramiconidiophorus	**RCEF 7524**	**PV084627**	**PV107277**	**PV084675**	This article
Conidiobolus robustus	**RCEF 7943 (T)**	**PV084621**	**PV107271**	**PV084669**	This article
Conidiobolus robustus	**RCEF 7944**	**PV084622**	**PV107272**	**PV084670**	This article
Conidiobolus robustus	**RCEF 7947**	**PV084623**	**PV107273**	**PV084671**	This article
Conidiobolus shanxiensis	**RCEF 7935 (T)**	**PV084624**	**PV107274**	**PV084672**	This article
Conidiobolus shanxiensis	**RCEF 7936**	**PV084625**	**PV107275**	**PV084673**	This article
Conidiobolus srinivasanii	NFCCI 5839 (T)	PQ536954	PQ541123	PQ536953	Pawar et al. (2025)
Conidiobolus taihushanensis	CGMCC 3.16016 (T)	MT250086	MT274290	MT250088	Nie et al. (2020b)
Conidiobolus variabilis	CGMCC 3.16015 (T)	MT250085	MT274289	MT250087	Nie et al. (2020b)
Cunninghamella echinulata	CBS 156.28 (T)	HM849702	–	–	Vitale et al. (2012)
Endogone botryocarpus	E-14001 (T)	NG_068251	–	–	Yamamoto et al. (2020)
Endogone corticioides	NC0024744	LC107372	–	–	Yamamoto et al. (2017)
Entomophaga aulicae	ARSEF 172	EF392372	–	EF392487	Gryganskyi et al. (2012, 2022)
Entomophaga maimaga	ARSEF 1400	EF392395	–	EF392505	Gryganskyi et al. (2012, 2022)
Eryniopsis caroloniana	ARSEF 640	EF392387	–	EF392500	Gryganskyi et al. (2012, 2022)
Entomophthora grandis	ARSEF 6701	DQ481229	–	–	Gryganskyi et al. (2012, 2022)
Entomophthora scatophaga	ARSEF 6704	DQ481226	–	–	Gryganskyi et al. (2012, 2022)
Entomophthora muscae	ARSEF 3074	DQ273772	DQ275343	–	Gryganskyi et al. (2012, 2022)
Entomophthora planconiana	ARSEF 6252	GQ285878	–	–	Gryganskyi et al. (2012, 2022)

Species	Strains	GenBank accession numbers			References
		nucLSU	*EFL*	mtSSU	
Entomophthora schizophorae	ARSEF 5348	GQ285883	–	–	Gryganskyi et al. (2012, 2022)
Entomophthora syrphi	ARSEF 5595	DQ481230	–	–	Gryganskyi et al. (2012, 2022)
Erynia conica	ARSEF 1439	EF392396	–	EF392506	Gryganskyi et al. (2012, 2022)
Erynia ovispora	ARSEF 400	JX242601	–	JX242641	Gryganskyi et al. (2012, 2022)
Erynia rhizospora	ARSEF 1441	EF392397	–	EF392507	Gryganskyi et al. (2012, 2022)
Erynia sciarae	ARSEF 1870	EF392399	–	EF392509	Gryganskyi et al. (2012, 2022)
Furia americana	ARSEF 742	EF392389	–	–	Gryganskyi et al. (2012, 2022)
Furia gastropachae	ARSEF 5541	EF392407	–	EF392516	Gryganskyi et al. (2012, 2022)
Furia ithacensis	ARSEF 663	EF392388	–	EF392501	Gryganskyi et al. (2012, 2022)
Furia neopyralidarum	ARSEF 1145	EF392394	–	EF392504	Gryganskyi et al. (2012, 2022)
Furia pieris	ARSEF 781	EF392390	–	EF392502	Gryganskyi et al. (2012, 2022)
Furia virescens	ARSEF 1129	EF392393	–	EF392503	Gryganskyi et al. (2012, 2022)
Lichtheimia corymbifera	CBS 479.75 (T)	FJ719444	–	–	Garcia-Hermoso et al. (2009)
Massospora cicadina	ARSEF 374	EF392377	–	EF392492	Gryganskyi et al. (2012, 2022)
Microconidiobolus nodosus	ATCC 16577 (T)	JF816217	JF816235	MK333388	Nie et al. (2020a)
Microconidiobolus paulus	ARSEF 450 (T)	KC788409	–	–	Nie et al. (2020a)
Microconidiobolus terrestris	ATCC 16198 (T)	KX752050	KY402208	MK301199	Nie et al. (2020a)
Microconidiobolus undulatus	ATCC 12943 (T)	JX946693	JX946699	MK301201	Nie et al. (2020a)
Mucor abundans	CBS 388.35 (T)	MH867228	–	–	Vu et al. (2019)
Neoconidiobolus antarcticus	ARSEF 6913 (T)	DQ364207	–	DQ364227	Tosi et al. (2004)
Neoconidiobolus beijingensis	**RCEF 7517 (T)**	**PV084586**	**PV107236**	**PV084634**	This article
Neoconidiobolus beijingensis	**RCEF 7518**	**PV084587**	**PV107237**	**PV084635**	This article

Species	Strains	GenBank accession numbers			References
		nucLSU	*EFL*	mtSSU	
Neoconidiobolus couchii	ATCC 18152 (T)	JN131538	JN131544	MK301179	Nie et al. (2020a)
Neoconidiobolus flavozygosporus	**RCEF 7919 (T)**	**PV084588**	**PV107238**	**PV084636**	This article
Neoconidiobolus flavozygosporus	**RCEF 7920**	**PV084589**	**PV107239**	**PV084637**	This article
Neoconidiobolus pseudothromboides	RCEF 6692 (T)	ON391168	OL286957	ON310965	Nie et al. (2022b)
Neoconidiobolus kunyushanensis	CGMCC 3.15890 (T)	MN061286	MN061483	MN061289	Nie et al. (2021)
Neoconidiobolus lachnodes	ARSEF 700	KC788408	–	–	Gryganskyi et al. (2013)
Neoconidiobolus lamprauges	CBS 461.97	MH874268	–	–	Vu et al. (2019)
Neoconidiobolus microzygosporus	**RCEF 7925 (T)**	**PV084590**	**PV107240**	**PV084638**	This article
Neoconidiobolus microzygosporus	**RCEF 7926**	**PV084591**	**PV107241**	**PV084639**	This article
Neoconidiobolus mirabilis	CGMCC 3.17763 (T)	MH282852	MH282853	MK333389	Nie et al. (2018)
Neoconidiobolus muscoides	**RCEF 7921 (T)**	**PV084592**	**PV107242**	**PV084640**	This article
Neoconidiobolus muscoides	**RCEF 7922**	**PV084593**	**PV107243**	**PV084641**	This article
Neoconidiobolus nanodes	CBS154.56 (T)	MH869096	–	–	Vu et al. (2019)
Neoconidiobolus osmodes	ARSEF 79	EF392371	–	DQ364219	Chen and Huang (2018)
Neoconidiobolus osmodes	RCEF 4447	JN131539	JN131545	MK333392	Nie et al. (2020a)
Neoconidiobolus ovalisporus	**RCEF 7513 (T)**	**PV084584**	**PV107234**	**PV084632**	This article
Neoconidiobolus ovalisporus	**RCEF 7514**	**PV084585**	**PV107235**	**PV084633**	This article
Neoconidiobolus pachyzygosporus	CGMCC 3.17764 (T)	KP218521	KP218524	MK333390	Nie et al. (2018)
Neoconidiobolus sinensis	RCEF 4952 (T)	JF816224	JF816238	MK301196	Nie et al. (2012)
Neoconidiobolus stilbeus	RCEF 5584 (T)	KP218522	KP218525	MK301197	Nie et al. (2016)

Species	Strains	GenBank accession numbers			References
		nucLSU	*EFL*	mtSSU	
Neoconidiobolus stromoideus	ATCC 15430 (T)	JF816219	JF816229	MK301198	Nie et al. (2012)
Neoconidiobolus thromboides	ATCC 12587 (T)	JF816214	JF816230	MK301200	Nie et al. (2012)
Pandora blunckii	ARSEF 217 (T)	JX242602	–	–	Gryganskyi et al. (2012)
Pandora delphacis	ARSEF 459	EF392384	–	EF392497	Gryganskyi et al. (2012, 2022)
Pandora dipterigena	ARSEF 397	EF392380	–	EF392565	Gryganskyi et al. (2012, 2022)
Pandora kondoiensis	CBS 642.92	JX242603	–	JX242642	Gryganskyi et al. (2012)
Pandora neoaphidis	ARSEF 3240	EF392405	–	EF392514	Gryganskyi et al. (2012, 2022)
Rhizopus arrhizus	CBS 112.07 (T)	HM849659	–	–	Vitale et al. (2012)
Schizangiella serpentis	ARSEF 2237	EF392428	–	EF392488	Gryganskyi et al. (2012, 2022)
Umbelopsis longicollis	CBS 209.32 (T)	NG042542	–	–	Petkovits et al. (2011)
Zoophthora anglica	ARSEF 396	EF392379	–	EF392493	Gryganskyi et al. (2012, 2022)
Zoophthora lanceolata	ARSEF 469	EF392385	–	EF392498	Gryganskyi et al. (2012, 2022)
Zoophthora phalloides	ARSEF 2281	EF392400	–	EF392510	Gryganskyi et al. (2012, 2022)
Zoophthora radicans	ARSEF 388	JX242605	–	JX242644	Gryganskyi et al. (2012, 2022)

*****New species were shown in bold. ARSEF, ARS Entomopathogenic Fungus Collection (Ithaca, USA). ATCC, American Type Culture Collection (Manassas, USA). CBS, Westerdijk Fungal Biodiversity Institute (Utrecht, The Netherlands). CEP, Entomopathogenic Fungal Culture Collection of CEPAVE (La Plata, Buenos Aires, Argentina). CGMCC, China General Microbiological Culture Collection Center (Beijing, China). NFCCI, National Fungal Culture Collection of India. NRRL, ARS Culture Collection (Peoria, USA). RCEF, Research Center for Entomogenous Fungi (Hefei, China). "T" represents ex-type; "–" indicates unavailable sequences.

Table 2. The species used for phylogenomic analyses in this study

Species	Strains	Biosample	Type	References
Acaulopage tetraceros	T-All	SAMN10060497	No	Davis et al. (2019)
Azygosporus macropapillatus	CGMCC 3.16068	SAMN46815040	Yes	This study
Basidiobolus heterosporus	B8920	SAMN02371514	No	Tabima et al. (2020)
Basidiobolus meristosporus	CBS 931.73	SAMN02745972	Yes	Mondo et al. (2017)
Basidiobolus meristosporus	B9252	SAMN02371520	No	Tabima et al. (2020)
Basidiobolus ranarum	AG-B5	SAMN18260851	No	n/a
Callaghania adiaereta	CGMCC 3.15888	SAMN46815041	No	This study
Capillidium heterosporum	CGMCC 3.15857	SAMN12879746	No	Wang et al. (2020)
Capillidium huangfushanense	RCEF 7528	SAMN46815042	Yes	This study
Capillidium jiangsuense	RCEF 6545	SAMN46815043	Yes	This study
Capillidium jinlanshanense	RCEF 7931	SAMN46815044	Yes	This study
Capillidium macrocapilliconidium	RCEF 6553	SAMN46815045	Yes	This study
Capillidium rhysosporum	ATCC 12588	SAMN37911642	Yes	n/a
Cochlonema odontosperma	E-All	SAMN10060498	No	Davis et al. (2019)
Coemansia reversa	NRRL 1564	SAMN00631612	No	Chang et al. (2015)
Conidiobolus chlamydosporus	ATCC 12242	SAMN46815046	Yes	This study
Conidiobolus coronatus	NRRL 28638	SAMN00779232	No	Chang et al. (2015)
Conidiobolus hainanensis	RCEF 7486	SAMN46815049	Yes	This study
Conidiobolus hippocrepiformis	RCEF 7923	SAMN46815050	Yes	This study

Species	Strains	Biosample	Type	References
Conidiobolus incongruus	B7586	SAMN02371512	No	n/a
Conidiobolus jiangxiensis	RCEF 7484	SAMN46815051	Yes	This study
Conidiobolus kunmingensis	RCEF 7945	SAMN46815052	Yes	This study
Conidiobolus lichenicolus	ATCC 16200	SAMN46815053	Yes	This study
Conidiobolus lii	RCEF 7535	SAMN46815054	Yes	This study
Conidiobolus longibasalis	RCEF 7929	SAMN46815055	Yes	This study
Conidiobolus longiconidiophorus	RCEF 6563	SAMN46815056	Yes	This study
Conidiobolus macrozygosporus	RCEF 7521	SAMN46815057	Yes	This study
Conidiobolus macroconidius	RCEF 6918	SAMN46815058	Yes	This study
Conidiobolus mycophagus	ATCC 16201	SAMN46815060	Yes	This study
Conidiobolus oxyconidius	RCEF 7937	SAMN46815061	Yes	This study
Conidiobolus pachyconidiophorus	RCEF 7941	SAMN46815062	Yes	This study
Conidiobolus pectiniformis	RCEF 4923	SAMN46815047	Yes	This study
Conidiobolus planibasalis	RCEF 7515	SAMN46815048	Yes	This study
Conidiobolus polyspermus	ATCC 14444	SAMN46815063	Yes	This study
Conidiobolus polysporus	RCEF 7058	SAMN46815064	Yes	This study
Conidiobolus polytocus	ATCC 12244	SAMN46815065	Yes	This study
Conidiobolus proximus	RCEF 7927	SAMN46815066	Yes	This study
Conidiobolus pseudogonimodes	RCEF 7933	SAMN46815067	Yes	This study
Conidiobolus ramiconidiophorus	RCEF 7523	SAMN46815059	Yes	This study

Species	Strains	Biosample	Type	References
Conidiobolus robustus	RCEF 7943	SAMN46815068	Yes	This study
Conidiobolus shanxiensis	RCEF 7935	SAMN46815069	Yes	This study
Conidiobolus taihushanensis	CGMCC 3.16016	SAMN46815070	Yes	This study
Dimargaris cristalligena	RSA 1219	SAMN15720059	No	n/a
Entomophthora muscae	Berkeley	SAMN09621101	No	n/a
Furculomyces boomerangus	AUS-77-4	SAMN05412446	No	Wang et al. (2018)
Linderina pennispora	ATCC 12442	SAMN02744846	Yes	Mondo et al. (2017)
Martensiomyces pterosporus	CBS 209.56	SAMN02841237	Yes	Amses et al. (2022)
Microconidiobolus nodosus	ATCC 16577	SAMN46815071	Yes	This study
Microconidiobolus undulatus	ATCC 12943	SAMN46815072	Yes	This study
Neoconidiobolus beijingensis	RCEF 7517	SAMN46815073	Yes	This study
Neoconidiobolus flavozygosporus	RCEF 7919	SAMN46815074	Yes	This study
Neoconidiobolus kunyushanensis	CGMCC 3.15890	SAMN46815075	Yes	This study
Neoconidiobolus microzygosporus	RCEF 7925	SAMN46815076	Yes	This study
Neoconidiobolus muscoides	RCEF 7921	SAMN46815077	Yes	This study
Neoconidiobolus ovalisporus	RCEF 7513	SAMN46815078	Yes	This study
Neoconidiobolus pachyzygosporus	CGMCC 3.17764	SAMN46815079	Yes	This study
Neoconidiobolus stilbeus	RCEF 5584	SAMN46815080	Yes	This study
Neoconidiobolus stromoideus	ATCC 15430	SAMN46815081	Yes	This study
Neoconidiobolus thromboides	ATCC 12587	SAMN46815082	Yes	This study

Species	Strains	Biosample	Type	References
Neoconidiobolus thromboides	FSU 785	SAMN03003400	No	Amses et al. (2022)
Phycomyces blakesleeanus	NRRL 1555	SAMN00189023	No	n/a
Ramicandelaber brevisporus	CBS 109374	SAMN02841238	Yes	Amses et al. (2022)
Saksenaea vasiformis	B4078	SAMN02352517	No	Naranjo-Ortiz et al. (2022)
Smittium simulii	SWE-8-4	SAMN05412451	No	Wang et al. (2018)
Syncephalis plumigaleata	NRRL S24	SAMN05445192	No	Chang et al. (2022)
Thamnocephalis sphaerospora	RSA 1356	SAMN09741940	No	Ahrendt et al. (2018)
Umbelopsis ramanniana	AG	SAMN02745731	No	Amses et al. (2022)
Zoophagus insidians	Zi-All	SAMN10060500	No	Davis et al. (2019)
Zoophthora radicans	ATCC 208865	n/a	Yes	n/a

***** "n/a" indicates not applicable.

Table 3 Divergence time of families and genera of *Conidiobolus* s.l.

Families	Genera	Means of stem age (Mya)	Means of crown age (Mya)
Capillidiaceae		435	281
	Callaghania	281	163
	Capillidium	281	202
Conidiobolaceae		418	285
	Azygosporus	285	123
	Conidiobolus s.s.	285	214
Microconidiobolaceae	*Microconidiobolus*	418	279
Neoconidiobolaceae	*Neoconidiobolus*	435	303

Accordingly, two well-established fossil fungi were utilized as calibration points for divergence time estimation: 1) *Protoascon missouriensis* (315–307 Mya), which exhibits remarkable morphological similarity to extant *Absidia* species, particularly *A. spinosa* and *A. spinosa* var. *azygospora* (Baxter 1975, Taylor and Alexander 2005, Taylor et al. 2014), and 2) *Jimwhitea circumtecta* (247–237 Mya), which represents the most compelling fossil evidence for the genus *Endogone* (Krings et al. 2011, Taylor et al. 2014). Corresponding extant taxa (*Absidia* spp. and *Endogone* spp.) were included in the phylogenetic analysis to provide robust temporal constraints for calibrating the molecular clock. In addition, secondary calibration points were included based on the estimated mean crown ages of 225 Mya (with 95% HPD 150–300 Mya) for *Entomophthoraceae* (Gryganskyi et al. 2012) and 582 Mya (with 95% HPD 572–592 Mya Mya) for *Mucoromycota* (Zhao et al. 2023). The stem average ages were constrained using a gamma-distributed prior (scale = 10, shape = 1.0) with an offset. The chain was run for 200 M generations, logging every 1 000 steps, and convergence was assessed in Tracer v1.7.2 (Rambaut & Drummond 2013). The maximum clade credibility (MCC) tree was summarized with TreeAnnotator v1.8.2, omitting the first 20% of generations as burn-in. Node ages with posterior probabilities > 0.90 were mapped onto the resulting chronogram in FigTree v1.4.

RESULTS

Phylogenomic and phylogenetic analyses

Our phylogenomic inference based on 434 single-copy orthologs (Fig. 1) corroborated the previous multi-locus results (Nie et al. 2020a, Gryganskyi et al. 2022), yielding high bootstrap support for *Capillidiaceae*, *Conidiobolaceae*, *Neoconidiobolaceae*, and the newly proposed *Microconidiobolaceae*. Notably, *Microconidiobolaceae* received a bootstrap value of 98% in the phylogenomic tree, exceeding its support in the multi-locus analyses (85%/1.00, Fig. 2).

Given the limited genomic data available for *Entomophthoromycotina* species outside *Conidiobolus* s.l., we expanded our dataset by incorporating additional entomophthoroid fungi and recently described *Conidiobolus* s.l. species to construct a multi-locus phylogenetic tree. This expanded analysis confirmed our phylogenomic results, particularly regarding the phylogenetic placement of *Conidiobolus* s.l. within the entomophthoroid fungi. The concatenated multi-locus dataset (nucLSU, *EFL*, and mtSSU) comprised 1,470 aligned characters. GTR+F+R5 for nucLSU, *EFL*, and mtSSU was selected as the best-fit substitution model for both ML and BI analyses, yielding largely congruent topologies. The final BI run yielded an average standard deviation of split frequencies of 0.00721, indicating convergence. The resulting ML tree (Fig. 2) resolved all *Conidiobolus* s.l. taxa into four strongly supported clades *Capillidiaceae* (BS = 100%; PP = 1.00), *Conidiobolaceae* (BS = 100%; PP = 1.00), *Microconidiobolaceae* fam. nov. (BS = 85%; PP = 1.00), and *Neoconidiobolaceae* (BS = 100%; PP = 1.00).

To further investigate species boundaries, we conducted three separate phylogenetic analyses focusing on *Capillidium*, *Conidiobolus* sensu stricto, and *Neoconidiobolus*. Sequence alignments and phylogenetic trees for these genus-level analyses were deposited in TreeBASE (Submission IDs S31979, S31980, and S31981). All datasets comprised concatenated multi-locus sequences (nucLSU, *EFL*, and mtSSU), and phylogenetic reconstructions were performed using ML and BI approaches, producing largely congruent topologies.

The *Capillidium* dataset consisted of 1,719 aligned characters with best-fit substitution models of GTR+F+R3 for nucLSU, SYM+R2 for *EFL*, and TVM+F+R3 for mtSSU. BI convergence was adequate (average standard deviation of split frequencies = 0.00423). The ML tree (Fig. 5) shows the phylogenetic placement of two newly described *Capillidium* species.

The *Conidiobolus* s.s. dataset consisted of 1,710 aligned characters with best-fit substitution models of GTR+F+R4 for nucLSU and *EFL*, and GTR+F+R3 for mtSSU. BI convergence was adequate (average standard deviation of split frequencies = 0.00521). The ML tree (Fig. 8) shows the phylogenetic placement of 16 newly described *Conidiobolus* s.s. species.

The *Neoconidiobolus* dataset consisted of 1,644 aligned characters with best-fit substitution models of GTR+F+R3 for nucLSU and *EFL*, and TVM+F+R3 for mtSSU. BI convergence was

adequate (average standard deviation of split frequencies = 0.00996). The ML tree (Fig. 25) shows the phylogenetic placement of five newly described *Neoconidiobolus* species.

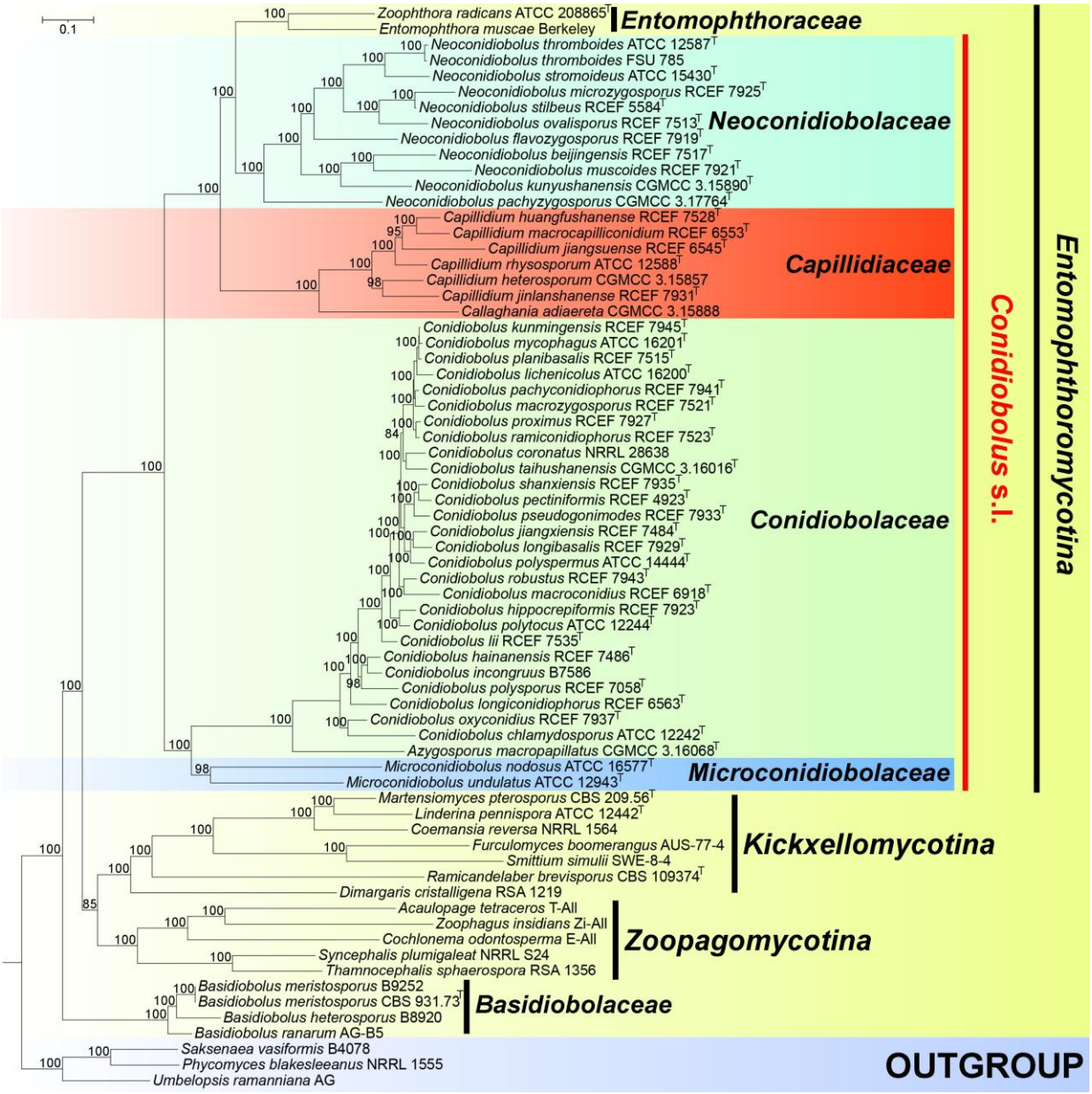

Figure 1 – A Maximum Likelihood phylogenomic tree of *Conidiobolus* s.l. based on 434 clusters of orthologous proteins. Three *Mucoromycota* fungi were selected as outgroups (Zhao et al. 2023). Maximum Likelihood bootstrap values (≥75 %) are indicated along branches. Scale bar indicates substitutions per site. Type taxa are indicated in the tree.

Divergence time estimation

A time-scaled MCC tree inferred from the combined nucLSU+*EFL*+mtSSU dataset for these taxa is shown in Fig. 3. Mean crown ages (and posterior probabilities > 0.90) suggest that the four families of *Conidiobolus* s.l. originated between 281 and 303 million years ago (Table 3): *Capillidiaceae* (281 Mya, PP = 1.00), *Conidiobolaceae* (285 Mya, PP = 1.00), *Microconidiobolaceae* (279 Mya, PP = 0.95), and *Neoconidiobolaceae* (303 Mya, PP = 1.00). *Batkoaceae* diverged more recently at ~127 Mya, whereas *Entomophthoraceae* arose around 246 Mya as sister to *Batkoaceae*. Taken together, these estimates indicate that family-level lineages within *Conidiobolus* s.l. originated in the Triassic to early Jurassic, underscoring their deep volutionary history.

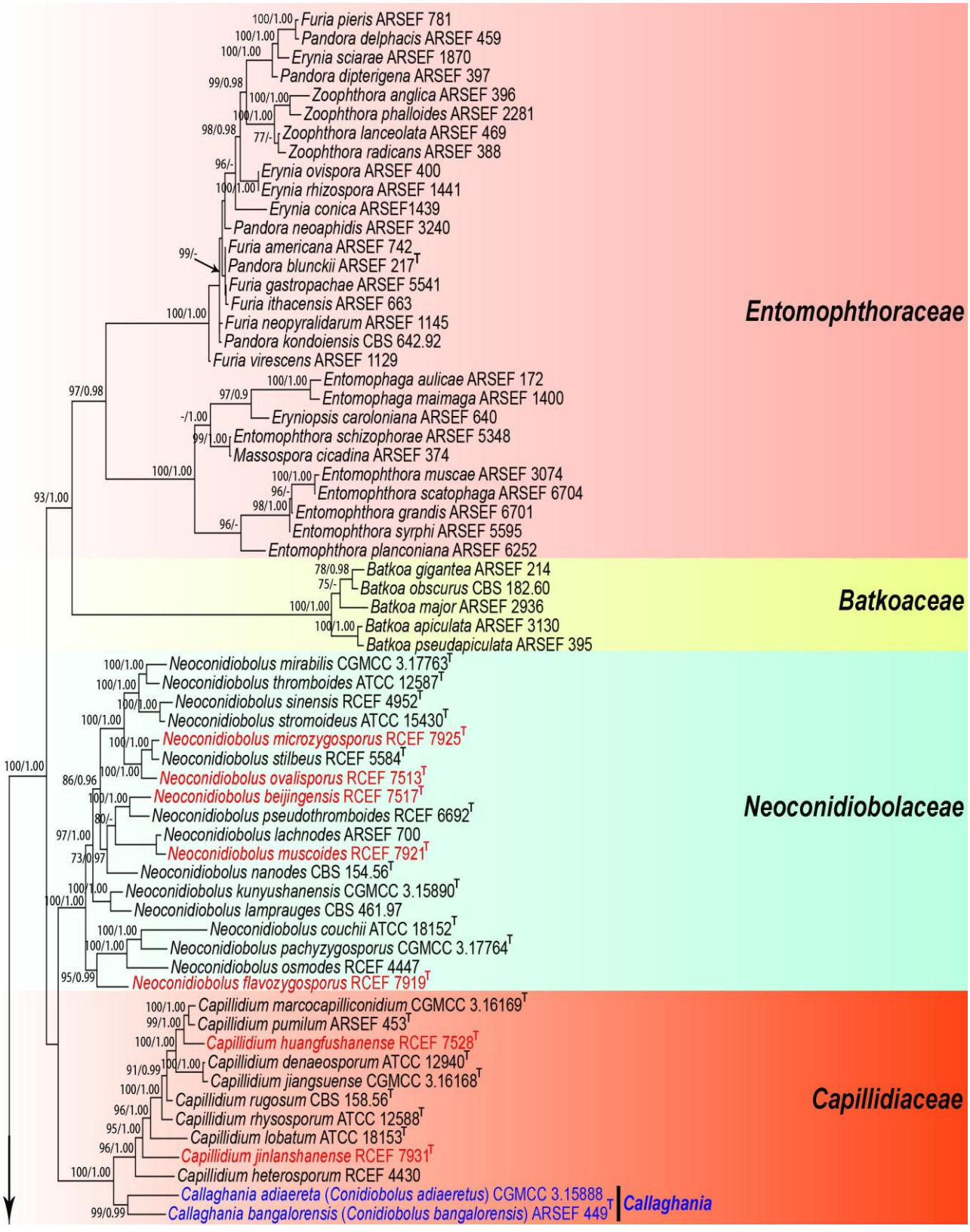

Figure 2 – Maximum Likelihood phylogenetic tree of *Conidiobolus* s.l. based on the sequences of nucLSU, *EFL*, and mtSSU (Table 1). Ten *Mucoromycota* fungi were selected as outgroups. Maximum Likelihood bootstrap values (≥ 70%) / Bayesian posterior probabilities (≥ 0.90) are indicated along each branch. The new family and new species are highlighted in red; the new genus and new combinations are indicated in blue. Type taxa are noted on the tree. The scale bar represents substitutions per site.

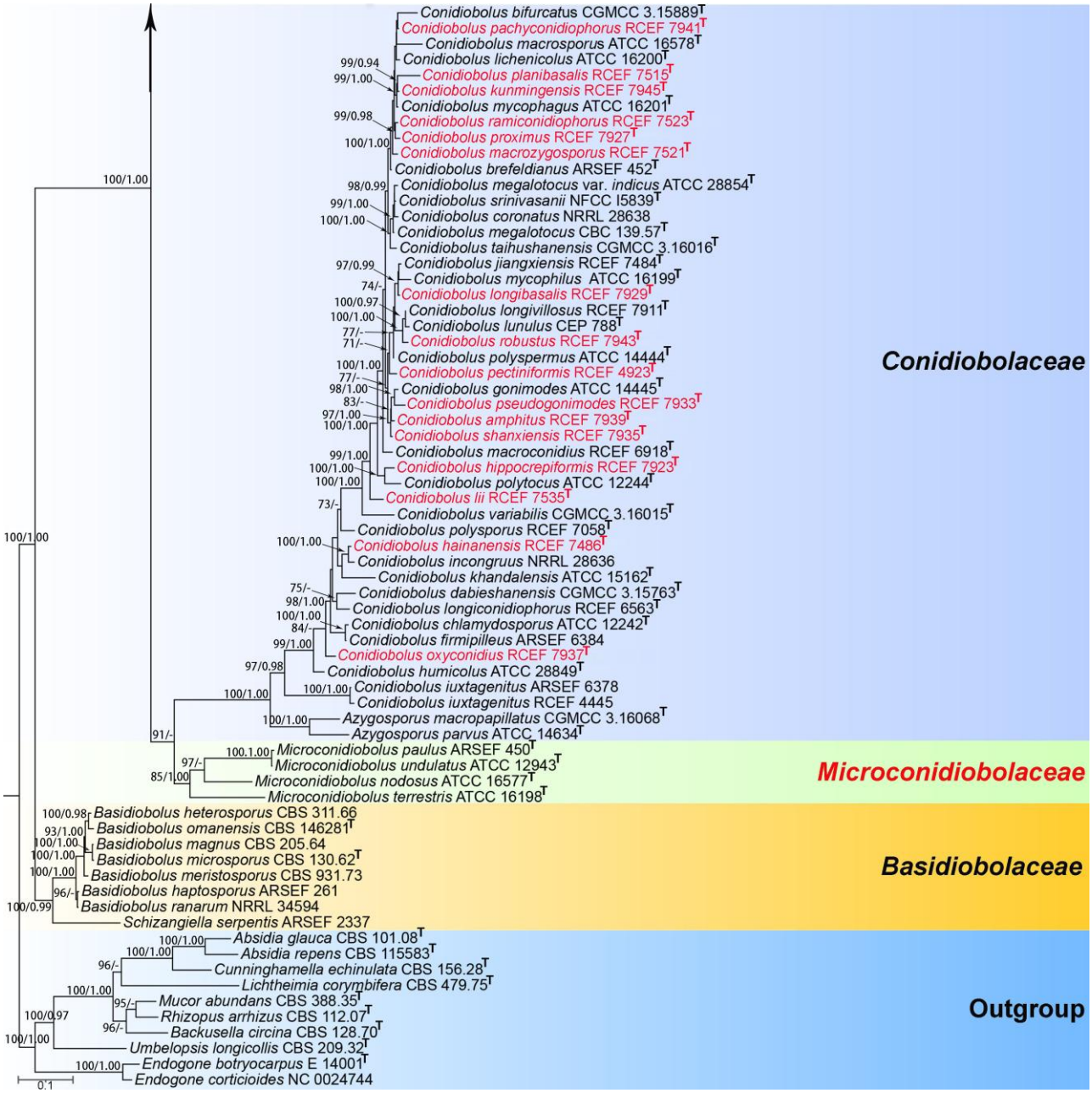

Figure 2 – Continued.

Taxonomy

Taxonomic outline of *Conidiobolus* s.l.
Family *Capillidiaceae* Y. Nie, Stajich, K.T. Hodge, J. Fungi 8(789): 6 (2022)
Callaghania B. Huang & Y. Nie, this article
Capillidium B. Huang & Y. Nie, MycoKeys 66: 62 (2020)
Family *Conidiobolaceae* B. Huang, Stajich, K.T. Hodge, J. Fungi 8(789): 7 (2022)
Azygosporus B. Huang & Y. Nie, MycoKeys 85: 165 (2021)
***Conidiobolus* sensu stricto** B. Huang & Y. Nie, MycoKeys 66: 65 (2020)
Family *Microconidiobolaceae* B. Huang & Y. Nie, this article
Microconidiobolus B. Huang, Y. Nie, MycoKeys 66: 72 (2020)
Family *Neoconidiobolaceae* X.Y. Liu, Stajich, K.T. Hodge, J. Fungi 8(789): 8 (2022)
Neoconidiobolus B. Huang & Y. Nie, MycoKeys 66: 70 (2020)

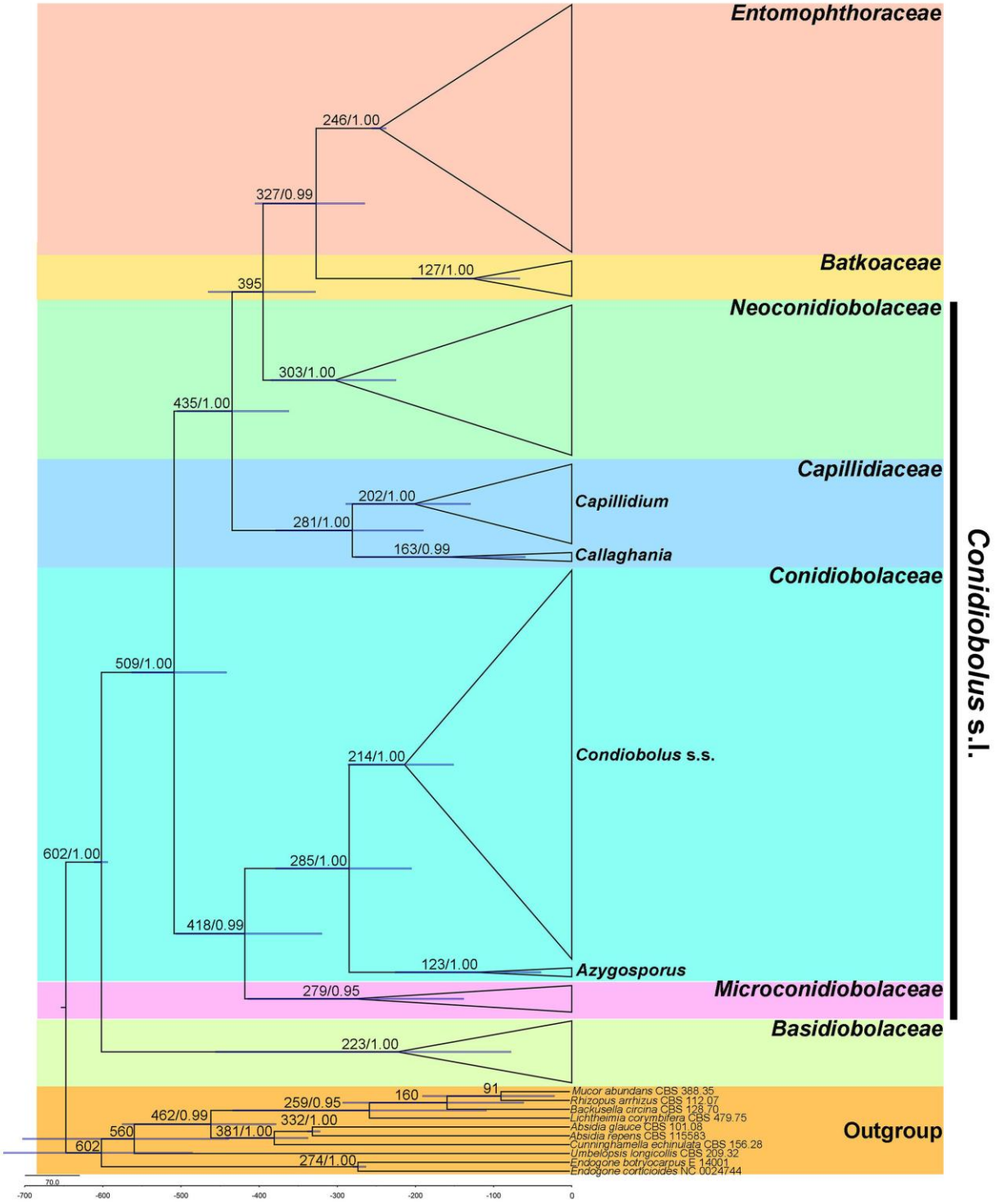

Figure 3 – A time-scaled Bayesian maximum clade credibility phylogenetic tree inferred from sequences of nucLSU rDNA, *EFL*, and mtSSU rDNA sequences for *Conidiobolus* s.l., with *Mucoromycota* as outgroup. Two fossil fungi (*Protoascon missouriensis* 307–315 Mya and *Jimwhitea circumtecta* 237–247 Mya) and two estimated mean crown ages (*Entomophthoraceae* 225 Mya and *Mucoromycota* 582 Mya) were used for calibrating the divergence time. The estimated mean divergence time (Mya) and the posterior probability (PP) value above 0.90 are annotated at each internode. The 95% highest posterior density (HPD) interval of divergence time estimates is marked by horizontal blue bars.

Proposal of a new family

Microconidiobolaceae B. Huang & Y. Nie, fam. nov.

MycoBank: MB857656; **Facesoffungi:** FoF17343

Etymology – Refers to small discharged primary conidia.

Type genus – *Microconidiobolus* B. Huang & Y. Nie, MycoKeys 66: 68 (2020)

Type species – *Microconidiobolus paulus* (Drechsler) B. Huang & Y. Nie, MycoKeys 66: 70 (2020) ≡ *Conidiobolus paulus* Drechsler, Bulletin of the Torrey Botanical Club 84 (1957) (basionym)

Description – Mycelia colorless, septate, branched. Primary conidiophores simply arising from hyphal cells, bearing a single primary conidium. Primary conidia forcibly discharged via papilla inverting, multinucleate (2–8 nuclei in average), colorless, globose to obovoid, usually small, mostly less than 20.0 μm. Replicative conidia globose, similar and smaller than primary conidia. Chlamydospores globose. Zygospores formed in axial alignment with conjugating segments, globose to ellipsoidal, smooth and yellowish.

Notes – The genus *Microconidiobolus* was originally established to include three species: *M. paulus*, *M. nodosus*, and *M. terrestris*, all of which produce smaller primary conidia compared to most *Conidiobolus* s.s. species (Nie et al. 2020a). The nuclei of entomophthoralean fungi exhibit greater morphological diversity than most other fungal groups; consequently, these features hold significant taxonomic value, particularly at suprageneric ranks (Humber 2012). In this study, we observed that the nuclei within the primary conidia of these three species range from 2 to 8, as confirmed by 4',6-diamidino-2-phenylindole (DAPI) staining (Fig. 4). Molecular phylogenetic analyses and phylogenomic data consistently place these species within a single clade (Figs. 1 and 2). The estimated mean crown age for this clade is approximately 279 million years, aligning with the divergence times observed for other families of *Conidiobolus* s.l. Based on these findings, we propose the recognition of this clade as a new family, *Microconidiobolaceae*.

Proposal of a new genus

Callaghania B. Huang & Y. Nie, gen. nov.

MycoBank: MB857657; **Facesoffungi:** FoF17344

Etymology – Refers to producing both microconidia and capilliconidia.

Type species – *Callaghania adiaereta* (Drechsler) B. Huang & Y. Nie = *Capillidium adiaeretum* (Drechsler) B. Huang & Y. Nie, MycoKeys 66: 63 (2020) ≡ *Conidiobolus adiaeretus* Drechsler, Journal of the Washington Academy of Science 43 (1953) (basionym)

Description – Colonies growing slowly on PDA at 21 °C. Mycelia colorless. Primary conidiophores simple, often possessing a pronounced dimensional contrast with mycelial filaments, bearing a single primary conidium. Primary conidia forcibly discharged, colorless, globose, pyriform to obovoid. Replicative conidia, exhibiting three kinds, the first one similar to but smaller than primary conidia, the second one (capilliconidia) arising from elongate and slender conidiophores, and the third one (microconidia) arising around the conidia from short sterigmatas. Chlamydospores formed within substrata, colorless, globose to ellipsoidal. Zygospores formed in axial alignment with conjugating two segments, globose to subglobose, smooth.

Notes – This genus is proposed to accommodate two species (*C. adiaereta* and *C. bangalorensis*) that produce both microconidia and capilliconidia (Callaghan et al. 2000). These distinctive morphological traits clearly set *Callaghania* apart from other genera in the family *Capillidiaceae*. Phylogenetic analyses robustly support the distinction of these species from other *Capillidiaceae* species (Fig. 5). We therefore establish the new genus *Callaghania* in honor of taxonomist A.A. Callaghan, who first identified these unique morphological features. As a result, *Capillidium bangalorense* (Sriniv. & Thirum.) B. Huang & Y. Nie is reclassified as *Callaghania bangalorensis* (Sriniv. & Thirum.) B. Huang & Y. Nie.

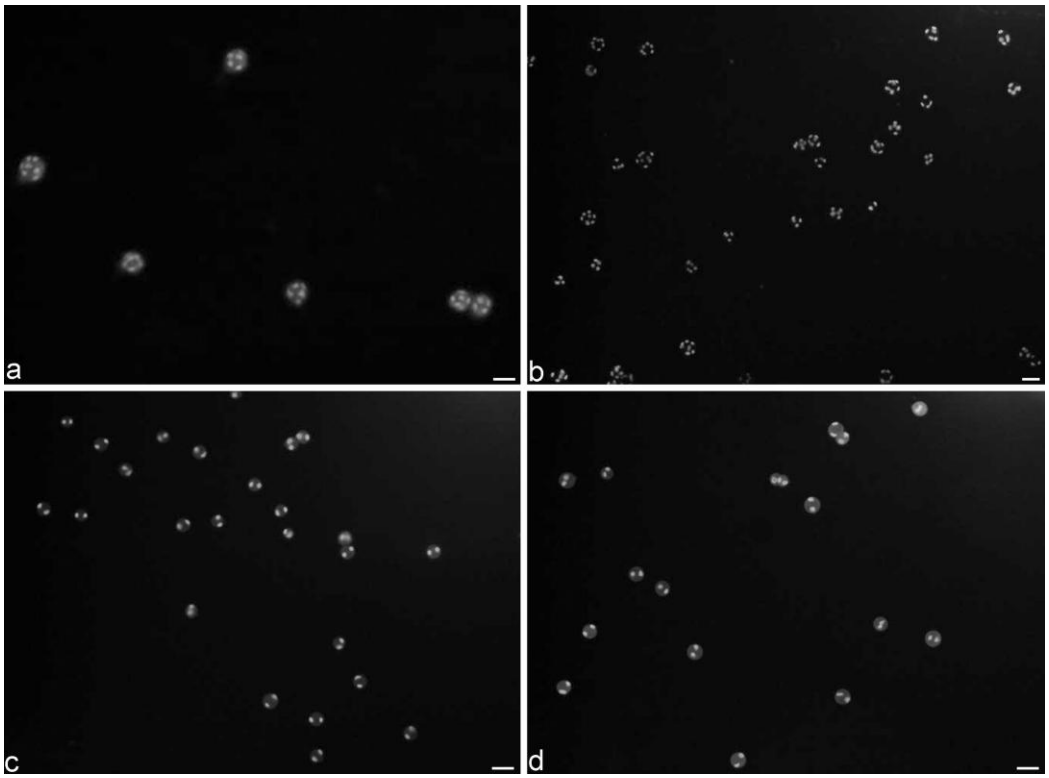

Figure 4 – a. 6–8 nuclei within the primary conidia of *M. nodosus* (ATCC 16577); b. 4–7 nuclei within the primary conidia of *M. undulatus* (ATCC 12943); c, d. two nuclei within the primary conidia of *M. terrestris* (ATCC 16198). Scale bars: a–d = 20 μm.

Description of the new species in China

Capillidium huangfushanense B. Huang & Y. Nie, sp. nov. Fig. 6

MycoBank: MB857658; **Facesoffungi:** FoF17345

Etymology – *huangfushanense* (Lat.) refers to the type locality, Huangfushan National Forest Park.

Known distribution – Anhui Province, China.

Material examined – CHINA, Anhui Province, Chuzhou City, Huangfushan National Forest Park, 32°20′ N, 118°1′ E, from plant debris, 29 Dec. 2021, *Y. Nie*, holotype HFS211229. Ex-type culture RCEF 7528. GenBank: nucLSU = PV084580; *EFL* = PV107230; mtSSU = PV084628.

Additional specimen examined – CHINA, Anhui Province, Chuzhou City, Huangfushan National Forest Park, 32°20′ N, 118°1′ E, from plant debris, 29 Dec. 2021, *Y. Nie*, culture RCEF 7529. GenBank: nucLSU = PV084581; *EFL* = PV107231; mtSSU = PV084628.

Description – Colonies on PDA at 21 °C for 3 d, white, reaching ca 15.0–17.0 mm in diameter, slightly yellowish after 12 d. Mycelia white, 5.0–9.0 μm wide, often unbranched when young. Primary conidiophores arising from hyphae, septate, smooth-walled, hyaline, 120.0–280.0 × 8.0–11.0 μm, without widening upwards near the tip, unbranched and producing a single primary conidium. Primary conidia forcibly discharged, papillate, solitary, globose to subglobose, smooth-walled, 26.0–37.0 × 22.0–31.0 μm. Papilla on primary conidia, conical, often broadly rounded, sometimes a little tapered, 1.5–8.0 × 7.0–12.0 μm. Secondary conidiophores arising from primary conidia, bearing a single replicative conidium similar to but smaller than the primary ones. Capillidiconidia not observed. Zygospores produced from the conjugation of adjacent segments of hyphae after 12 d, yellowish, intercalary, surface wrinkled or smooth, mostly globose, guttulate, 18.0–26.0 μm, with a 1.0–2.5 μm thick wall.

Notes – Morphologically, the size of primary conidia of *Ca. huangfushanense* is similar to *Ca. heterosporum* (primary conidia 9.0–30.0 × 10.0–35.0 μm), *Ca. macrocapilliconidium* (25.0–34.0 × 20.0–28.0 μm), and *Ca. rhysosporum* (18.0–30.0 × 22.0–36.0 μm) (Drechsler 1953, 1954, Nie et al.

2022). However, *Ca. heterosporum* has slender, branched conidiophores bearing multiple capilliconidia (2–6) at the apex and lacks resting spores. Meanwhile, *Ca. rhysosporum* has shorter primary conidiophores (40.0–100.0 μm) and larger zygospores (up to 31.0 μm); and *Ca. marcocapilliconidium* forms larger capilliconidia (25.0–37.0 × 14.0–17.0 μm). Although *Ca. huangfushanense* overlaps somewhat with *Ca. macrocapilliconidium* in conidial size, phylogenetic analysis supports recognizing it as a separate species (100% ML, 1.00 BYPP, Fig. 5). Sequence similarities between *Ca. huangfushanense* and *Ca. macrocapilliconidium* are 94.3% (nucLSU) and 91.4% (*EFL*).

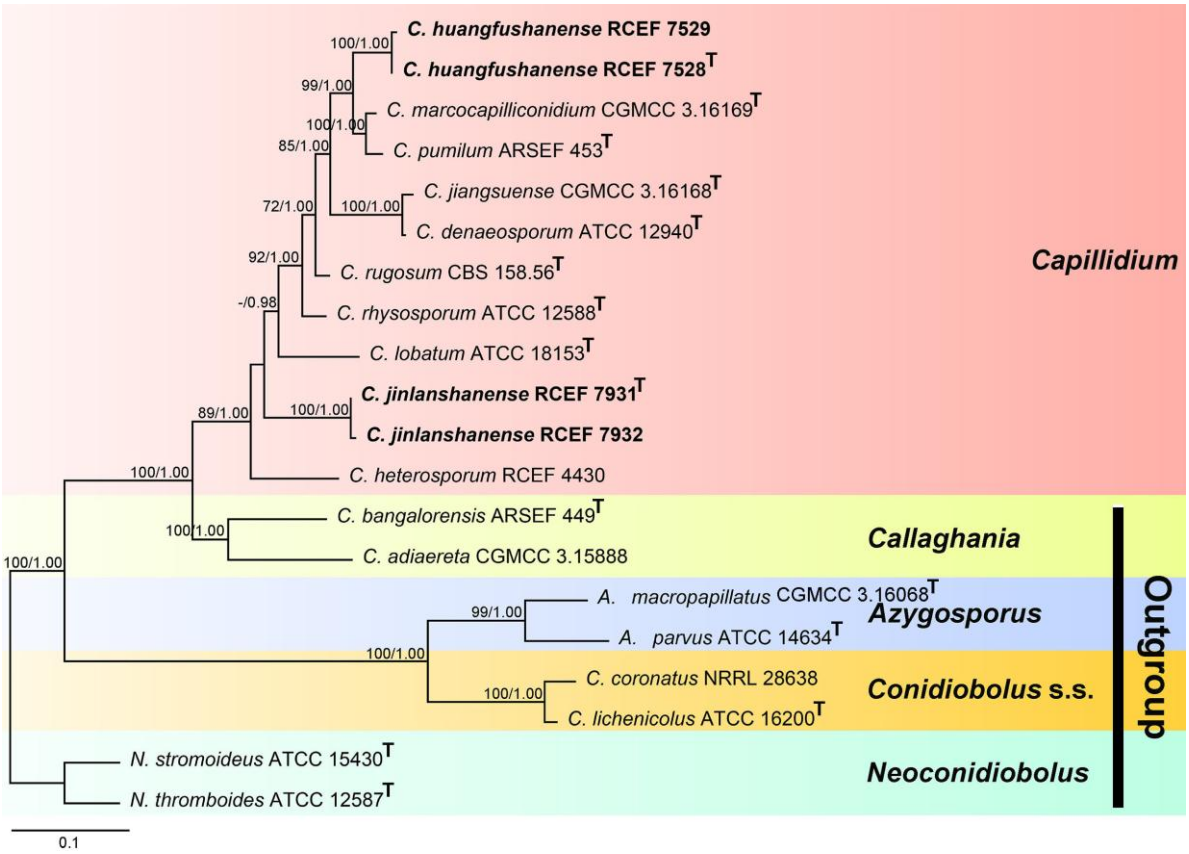

Figure 5 – Phylogenetic tree of the genus *Capillidium* based on nucLSU, *EFL*, and mtSSU loci. Two species of *Azygosporus*, two species of *Callaghania*, two species of *Condiobolus* s.s., and two species of *Neoconidiobolus* served as outgroups. Maximum Likelihood bootstrap values (≥70%) / Bayesian posterior probabilities (≥0.90) of clades are provided alongside the branches. The scale bar at the bottom left indicates the number of substitutions per site. New species are indicated in bold. Type taxa are noted on the tree.

Capillidium jinlanshanense B. Huang & Y. Nie, sp. nov. Fig. 7

MycoBank: MB857659; **Facesoffungi:** FoF17346

Etymology – *jinlanshanense* (Lat.), referring to the region where the fungus was collected.

Known distribution – Henan Province, China.

Typification – CHINA, Henan Province, Xinyang City, Jinlanshan National Forest Park, 31°43′ N, 115°23′ E, from mosses, 15 Mar. 2024, *Y. Nie*, holotype JLS2403151602. Ex-type culture RCEF 7931. GenBank: nucLSU = PV084582; *EFL* = PV107232; mtSSU = PV084630.

Additional specimens examined – CHINA, Henan Province, Xinyang City, Jinlanshan National Forest Park, 31°43′ N, 115°23′ E, from mosses, 15 Mar. 2024, *Y. Nie*, culture RCEF 7932. GenBank: nucLSU = PV084583; *EFL* = PV107233; mtSSU = PV084631.

Description – Colonies on PDA at 21 °C for 3 d, white, reaching ca 5.0 mm in diameter. Mycelia colorless, unbranched at the edge of colony, 4.5–9.0 μm wide, distended to form segments

when old. Primary conidiophores arising from hyphae, septate, smooth-walled, hyaline, 60.0–100.0 × 6.5–13.0 µm wide, 80.0 µm long on average, sometimes widening upward at the tip, producing a single primary conidium. Primary conidia forcibly discharged, papillate, solitary, hyaline smooth-walled, globose to subglobose, 24.0–30.0 × 19.0–25.0 µm, with a basal papilla, conical, 6.5–10.0 µm wide and 4.0–8.0 µm long. Secondary conidia arising from primary conidia, similar to but smaller than primary conidia. Capilliconidia not observed. Zygospores produced from the conjugation of adjacent segments of hyphae after 15 d, intercalary, guttulate, globose to ellipsoidal, smooth-walled, 17.0–26.0 µm long, 15.0–20.0 µm wide, with a 1.0–2.0 µm thick wall.

Notes – Due to the absence of both capilliconidia and microconidia in our initial observations, this species was morphologically misidentified as a *Neoconidiobolus* member (Nie et al. 2022a). However, phylogenetic inference places it in the *Capillidium* clade (100% ML, 1.00 BYPP; Fig. 5). Its consistent morphological characteristics and its unique, fully supported position in the tree justify its recognition as a new taxon within *Capillidium*. Sequence similarities between *Ca. jinlanshanense* and *Ca. heterosporum* are 89.3% (nucLSU) and 82.8% (*EFL*).

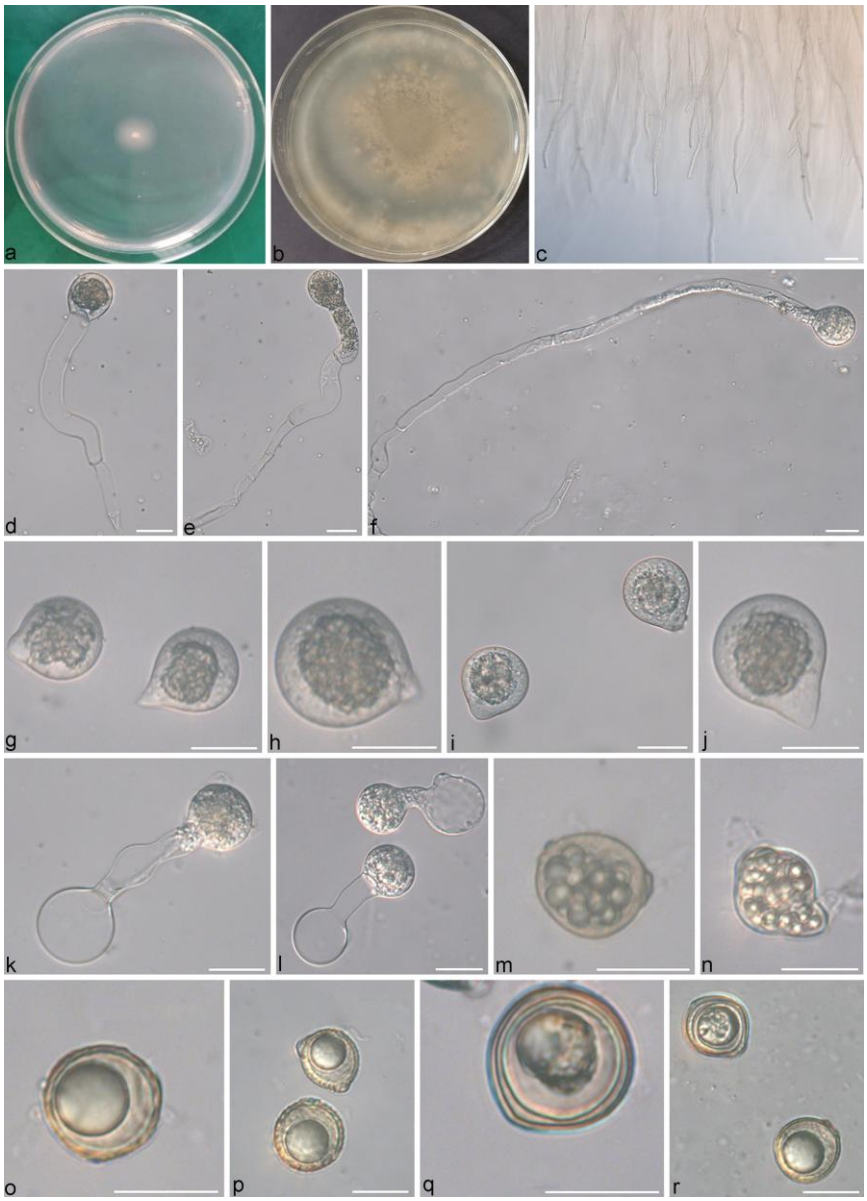

Figure 6 – ***Capillidium huangfushanense*** (RCEF 7528, ex-type). a Colony on PDA after 3 d at 21 °C. b Colony on PDA after 12 d at 21°C. c Mycelia unbranched at the edge of the colony. d–f Primary conidiophores bearing a single primary conidium. g–j Primary conidia. k, l Primary

conidia bearing a single secondary conidium. m, n Young zygospores. o–r Mature zygospores. Scale bars: b = 100 μm, c–r = 20 μm.

Conidiobolus amphitus B. Huang & Y. Nie, sp. nov. Fig. 9

MycoBank: MB857660 **Facesoffungi:** FoF17347

Etymology – *amphitus* (Lat.) refers to its two types of resting spores.

Known distribution – Jiangsu Province, China.

Typification – CHINA, Jiangsu Province, Yizheng City, Yangzhou Western Suburbs Forest Park, 32°32' N, 119°13' E, from plant debris, 15 July. 2024, *Y. Nie*, holotype JSYZ24071512. Ex-type culture RCEF 7939. GenBank: nucLSU = PV084594; *EFL* = PV107244; mtSSU = PV084642.

Additional specimen examined – CHINA, Jiangsu Province, Yizheng City, Yangzhou Western Suburbs Forest Park, 32°32' N, 119°13' E, from plant debris, 15 July. 2024, *Y. Nie*, culture RCEF 7940. GenBank: nucLSU = PV084595; *EFL* = PV107245; mtSSU = PV084643.

Description – Colonies on PDA at 21 °C for 3 d, white, reaching ca 9.0 mm in diameter. Mycelia white, 6.5–13.0 μm wide, mostly unbranched at the edge of colony. Distended to form segments when old. Primary conidiophores arising from hyphae, septate, smooth-walled, hyaline, sometimes widening upward near the tip, 30.0–135.0 × 5.0–10.0 μm, producing a single primary conidium. Primary conidia forcibly discharged, papillate, solitary, hyaline smooth-walled, globose, 26.0–32.0 × 22.0–29.0 μm, with a basal papilla, conical, 5.5–9.0 μm wide and 2.5–5.0 μm long. Secondary conidia arising from primary conidia, similar to but smaller than primary conidia. Microconidia not observed on PDA or 2% water agar. Chlamydospores formed after 5 d, globose, 22.0–36.0 μm. Zygospores produced from the conjugation of adjacent segment of hyphae, mostly globose, smooth-walled, 20.0–27.0 μm, with a 2.5–3.5 μm thick wall.

Notes – *Conidiobolus amphitus* resembles *Co. mycophilus* and *Co. polytocus* in primary conidium size but differs by having longer primary conidiophores and two distinct types of resting spores (chlamydospores and zygospores) (cf. Drechsler 1955c, Srinivasan & Thirumalachar 1965). Phylogenetically, *Co. amphitus* groups within *Conidiobolus* s.s. and is allied to *Co. shanxiensis* (100% ML, 1.00 BYPP, Fig. 8), but differs from *Co. shanxiensis* by its smaller primary conidia and larger zygospores. Sequence similarities between *Co. amphitus* and *Co. shanxiensis* are 97.6% (nucLSU) and 94.6% (*EFL*).

Conidiobolus hainanensis B. Huang & Y. Nie, sp. nov. Fig. 10

MycoBank: MB857663; **Facesoffungi:** FoF17350

Etymology – *hainanensis* (Lat.) refers to the type locality, Hainan Province, China.

Known distribution – Hainan and Zhejiang Province, China.

Typification – CHINA, Hainan Province, Sanya City, Linchunling Forest Park, 18°26′ N, 109°53′ E, from soil, 12 Nov. 2023, *Y. Nie*, holotype Hainan231112. Ex-type culture RCEF 7486. GenBank: nucLSU = PV084600; *EFL* = PV107250; mtSSU = PV084648.

Additional specimens examined – CHINA, Hainan Province, Sanya City, Linchunling Forest Park, 18°26′ N, 109°53′ E, from soil, 12 Nov. 2023, *Y. Nie*, culture RCEF 7487. GenBank: nucLSU = PV084601; *EFL* = PV107251; mtSSU = PV084649; CHINA, Zhejiang Province, Hangzhou City, Qiandaohu, 29°59′ N, 118°93′ E, from soil, 15 May. 2024, *Y. Nie*, ex-paratype RCEF 7488. GenBank: nucLSU = PV084602; *EFL* = PV107252; mtSSU = PV084650.

Description – Colonies on PDA at 21 °C for 3 d, white, reaching ca 11.0 mm in diameter. Mycelia colorless, 4.0–9.0 μm wide, unbranched when young. Single primary conidiophores arising from hyphae, septate, smooth-walled, hyaline, 40.0–195.0 × 6.5–12.0 μm, sometimes slightly widening upwards near the tip, unbranched and producing a single primary conidium. Primary conidia forcibly discharged, papillate, solitary, hyaline smooth-walled, globose, subglobose to oval, 24.0–36.0 × 22.0–33.0 μm. Papilla on primary conidia, often tapered, 2.0–5.0 × 4.0–9.0 μm. Secondary conidiohpore arising from primary conidia, usually unbranched and bearing a single replicative conidium, sometimes branched at the tip and bearing two replicative conidia.

Microconidia not observed. Azygospores formed in the middle region of the old hyphal segments after 10 d, mostly globose, sometimes elongate, 25.0–34.0 µm, with a 0.5–1.0 µm thick wall.

Notes – Phylogenetically, *Co. hainanensis* clusters within *Conidiobolus* s.s. and is most closely related to *Co. incongruus* (NRRL 28636). It differs from the latter by having smaller primary conidia (13.0–37.0 × 18.0–42.0 µm in *Co. incongruus*) and lacking zygospores (Drechsler 1960). Azygospores have not been previously documented in *Conidiobolus* s.s. (King 1977, Nie et al. 2020a), setting *Co. hainanensis* apart from other members of this lineage. Although the genus *Azygosporus* also produces azygospores, *Co. hainanensis* is phylogenetically distinct from *Azygosporus* species (100% ML, 1.00 BYPP, Fig. 8). Sequence similarities between *Co. hainanensis* and *Co. incongruus* is 96.7% (nucLSU)

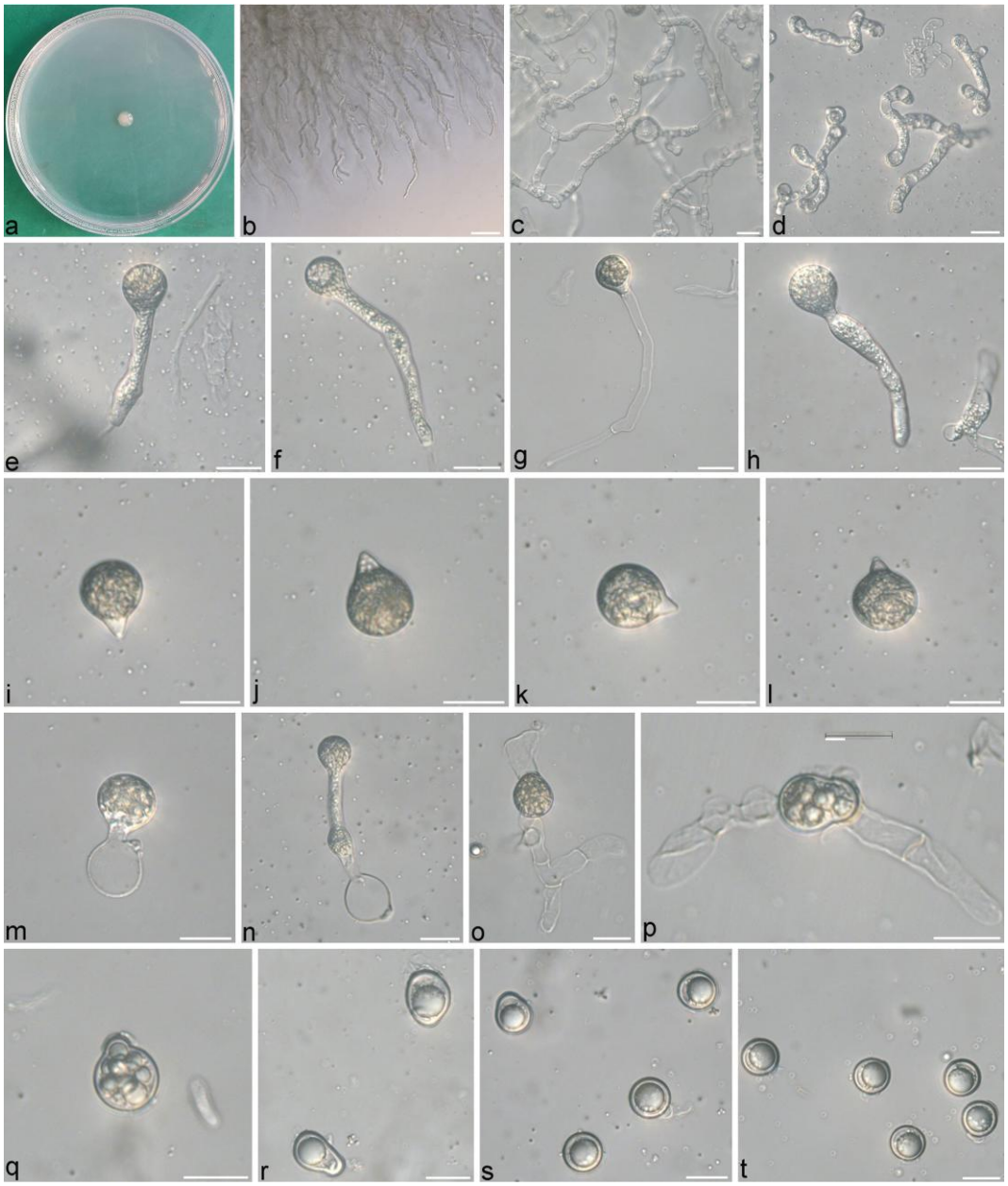

Figure 7 – ***Capillidium jinlanshanense*** (RCEF 7931, ex-type). a Colony on PDA after 3 d at 21 °C. b Mycelia unbranched at the edge of the colony. c, d Hyphae; e–h. Primary conidiophores bearing a single primary conidium. i–l Primary conidia. m, n Primary conidia bearing a single secondary conidium. o, p Zygospores formed in the same conjugating segments. q Immature zygospores. r–t Mature zygospores. Scale bars: b = 100 µm, c–t = 20 µm.

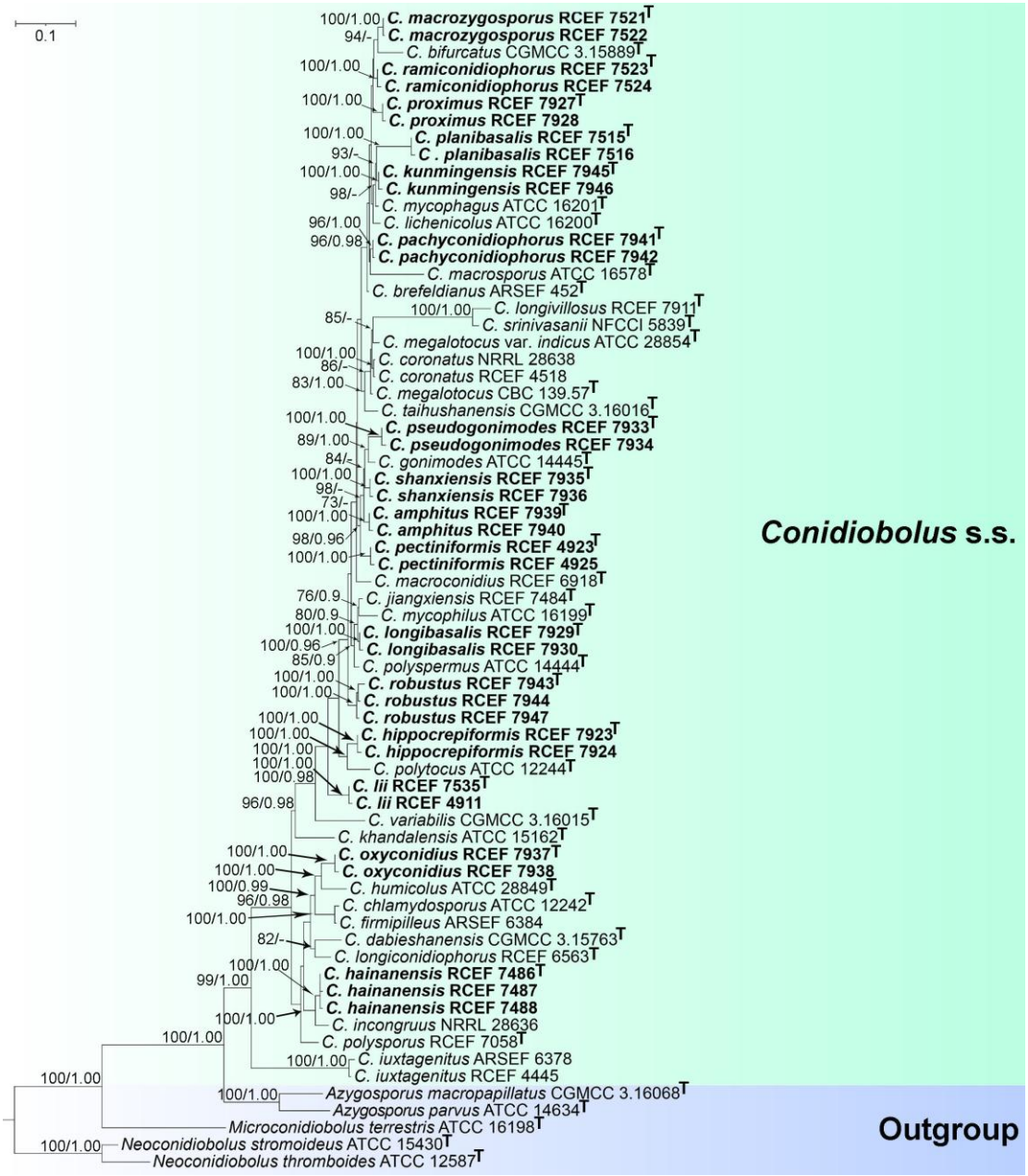

Figure 8 – Phylogenetic tree of the genus *Conidiobolus* s.s. based on nucLSU, *EFL*, and mtSSU loci. Two species of *Azygosporus*, one species of *Microconidiobolus*, and two species of *Neoconidibolus* served as outgroups. Maximum Likelihood bootstrap values (≥70%) / Bayesian posterior probabilities (≥0.90) of clades are provided alongside the branches. The scale bar at the top left indicates the number of substitutions per site. New species are indicated in bold. Type taxa are noted on the tree.

Conidiobolus hippocrepiformis B. Huang & Y. Nie, sp. nov. Fig. 11

MycoBank: MB857664; **Facesoffungi:** FoF17351

Etymology – *hippocrepiformis* (Lat.) refers to its horseshoe-shaped basal papilla of primary conidia.

Known distribution – Hunan Province, China.

Typification – CHINA, Hunan Province, Yueyang City, Dayunshan National Forest Parks, 29°26' N, 113°49' E, from plant debris, 13 Mar. 2024, *Y. Nie*, holotype DYS24031319. Ex-type culture RCEF 7923. GenBank: nucLSU = PV084603; *EFL* = PV107253; mtSSU = PV084651.

Additional specimen examined – CHINA, Hunan Province, Yueyang City, Dayunshan National Forest Parks, 29°26' N, 113°49' E, from plant debris, 14 Mar. 2024, *Y. Nie*, culture RCEF 7924. GenBank: nucLSU = PV084604; *EFL* = PV107254; mtSSU = PV084652.

Description – Colonies on PDA at 21 °C for 3 d, white, reaching ca 8.0 mm in diameter. Mycelia colorless, branched at the edge of colony, frequently distended to segment after 4 d, 5.5–15.0 µm wide. Primary conidiophores arising from hyphae, septate, smooth-walled, hyaline, 50.0–260.0 × 8.5–16.5 µm, usually arising from hyphal segments, without widening upward at the tip, producing a single primary conidium. Primary conidia forcibly discharged, papillate, solitary, hyaline smooth-walled, subglobose to oval, 31.0–41.0 × 23.0–35.0 µm, with a falcate, point, or horseshoe-shaped basal papilla 8.0–13.0 µm wide and 2.5–8.0 µm long. Secondary conidia arising from primary conidia, similar to but smaller than primary conidia. Triple or fourth replicated conidia commonly formed. Only two Microconidia arising from conidia, globose to subglobose, 12.0–17.0 × 10.0–17.5 µm. Chlamydospore spores formed after 25 d, globose, smooth, 24.0–37.0 µm.

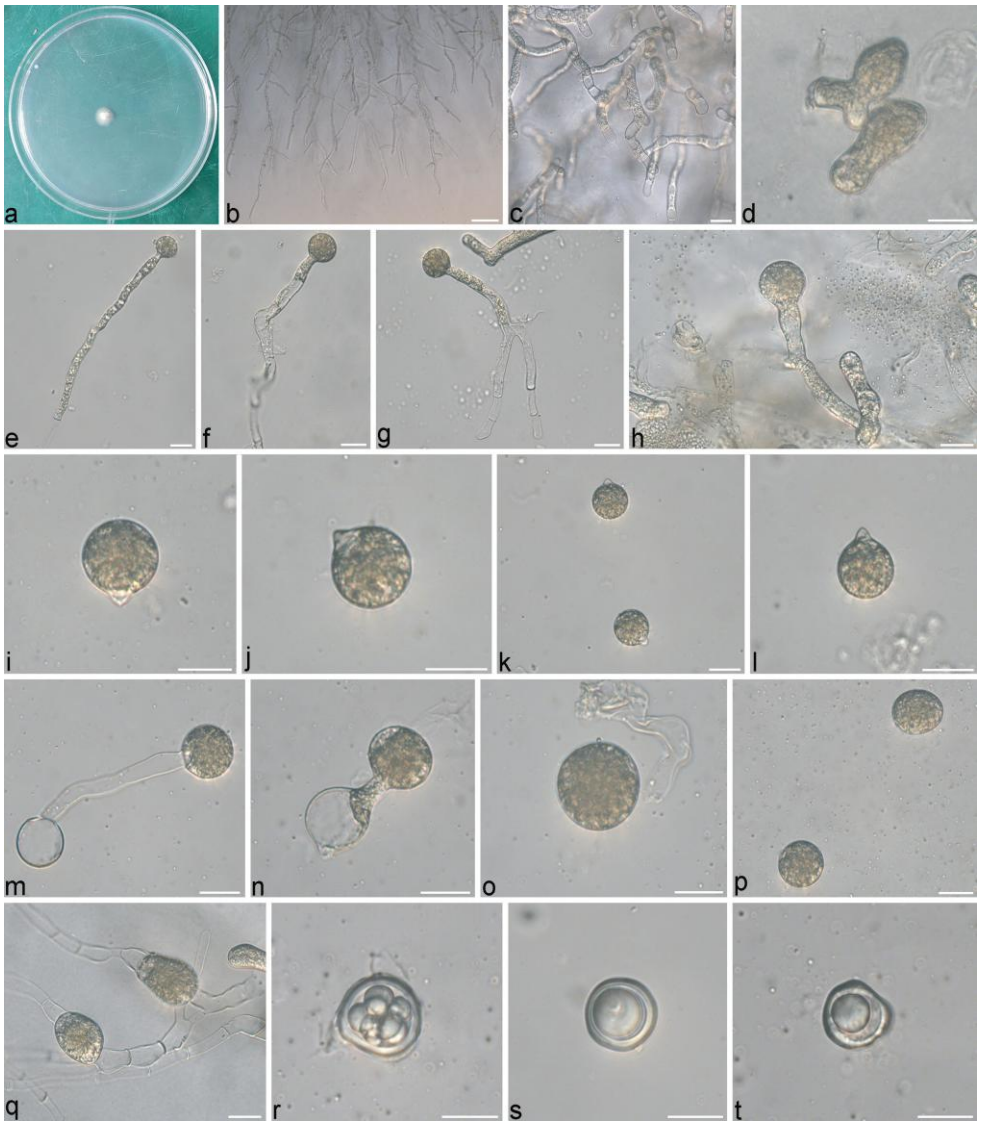

Figure 9 – ***Conidiobolus amphitus*** (RCEF 7939, ex-type). a Colony on PDA after 3 d at 21 °C. b Mycelia branched at the edge of the colony. c, d Mycelia. e–h Primary conidiophores bearing a single primary conidium. i–l Primary conidia. m, n Primary conidia bearing a single secondary conidium. o, p Chlamydospores. q Zygospores formed in one of the conjugating segments. R Immature zygospores. s, t Mature zygospores. Scale bars: b = 100 µm, c–t = 20 µm.

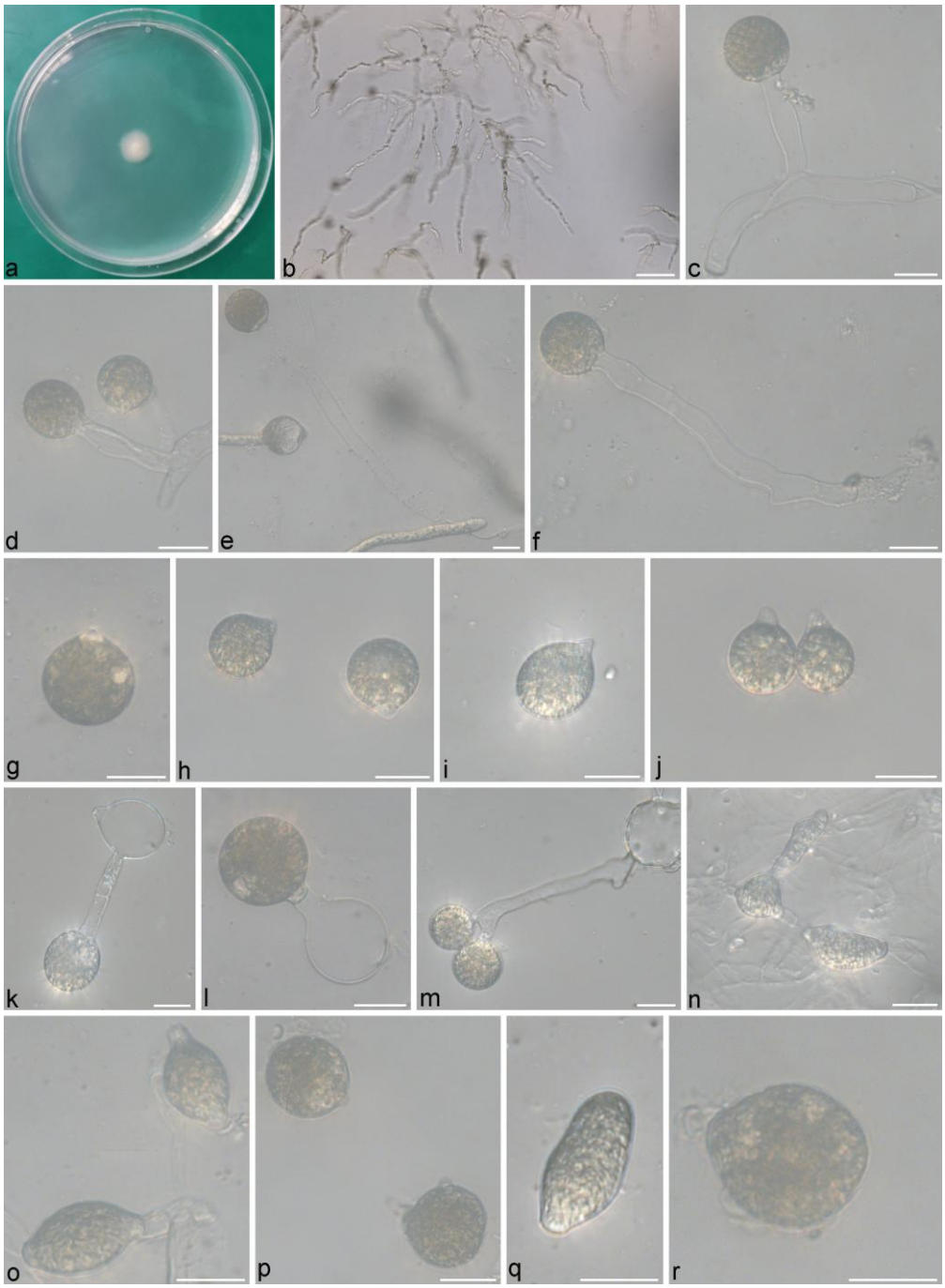

Figure 10 – ***Conidiobolus hainanensis*** (RCEF 7486, ex-type). a Colony on PDA after 3 d at 21 °C. b Mycelia unbranched at the edge of the colony. c–f Primary conidiophores bearing a single primary conidium. g–j Primary conidia. k, l Primary conidia bearing a single secondary conidium. m Secondary conidiophore branched at the tip and bearing two secondary conidia. n, o Young azygospores. p–r Mature azygospores. Scale bars: b = 100 μm, c–r = 20 μm.

Notes – Morphologically, *Co. hippocrepiformis* resembles *Co. humicolus* in having similarly sized primary conidia and chlamydospores (Srinivasan & Thirumalachar 1961). However, it differs by possessing a distinctive horseshoe-shaped basal papilla and larger microconidia. Phylogenetically, *Co. hippocrepiformis* is closely related to *Co. polytocus* (ATCC12244) with 100% ML and 1.00 BYPP, but differs in having larger primary conidia and unbranched primary conidiophores (Drechsler 1955c). Sequence similarities between *Co. hippocrepiformis* and *Co. polytocus* are 95.3% (nucLSU) and 94.1% (*EFL*).

Conidiobolus kunmingensis B. Huang & Y. Nie, sp. nov. Fig. 12

MycoBank: MB857665; **Facesoffungi:** FoF17352

Etymology – *kunmingensis* (Lat.) refers to the type locality, Kunming City, Yunnan Province, China.

Known distribution – Yunnan Province, China.

Typification – CHINA, Yunnan Province, Kunming City, Zhangjiaba Reservoir, 24°91' N, 102°45' E, from plant debris, 11 September. 2024, *Y. Yin*, holotype KM24091110. Ex-type culture RCEF 7945. GenBank: nucLSU = PV084605; *EFL* = PV107255; mtSSU = PV084653.

Additional specimens examined – CHINA, Yunnan Province, Kunming City, Zhangjiaba Reservoir, 24°91' N, 102°45' E, from plant debris, 11 September. 2024, *Y. Yin*, culture RCEF 7946. GenBank: nucLSU = PV084606; *EFL* = PV107256; mtSSU = PV084654.

Description – Colonies on PDA at 21 °C for 3 d, white, reaching ca 21.0 mm in diameter. Mycelia white, 8.5–14.0 μm wide, often unbranched at the edge of colony. Primary conidiophores arising from hyphae, septate, smooth-walled, hyaline, sometimes widening upward near the tip, 45.0–200.0 × 7.0–15.0 μm, producing a single primary conidium. Primary conidia forcibly discharged, papillate, solitary, hyaline smooth-walled, globose to subglobose, 36.0–53.0 × 31.0–45.0 μm, with a basal papilla 11.0–17.0 μm wide and 3.5–11.5 μm long. Secondary conidia arising from primary conidia, similar to but smaller than primary conidia. Microconidia arising around conidia, globose to slightly ellipsoidal, 14.5–22.0 × 12.0–18.0 μm. Zygospores produced from the conjugation of adjacent segment of hyphae after 5 d, globose to subglobose, smooth, colorless, 24.0–32.0 μm in diameter with a wall 1.5–3.5 μm thick.

Notes – Morphologically, the large primary conidia of *Co. kunmingensis* are reminiscent of *Co. macrosporus*, *Co. polyspermus*, *Co. polysporus*, and *Co. variabilis* (Drechsler 1961, Srinivasan & Thirumalachar 1965, Nie et al. 2020b, 2023). However, it differs from *Co. macrosporus* and *Co. polyspermus* by having longer primary conidiophores (50.0–100.0 μm in *Co. macrosporus* and 30.0–125.0 μm in *Co. polyspermus*) and smaller zygospores (26.0–40.0 μm in *Co. macrosporus* and 14.0–45.0 × 15.0–48.0 in *Co. polyspermus*), from *Co. variabilis* by the presence of zygospores and larger microconidia, and from *Co. polysporus* by unbranched primary conidiophores and larger microconidia. Phylogenetically, *Co. kunmingensis* is close to *Co. planibasalis* (RCEF7515, RCEF7516) but can be distinguished by its larger primary conidia, longer primary conidiophores, and smaller zygospores (100% ML, 1.00 BYPP, Fig. 8). Sequence similarities between *Co. kunmingensis* and *Co. planibasalis* are 97.2% (nucLSU) and 96.4% (*EFL*).

Conidiobolus lii B. Huang & Y. Nie, sp. nov. Fig. 13

MycoBank: MB857666; **Facesoffungi:** FoF17353

Etymology – *lii* (Lat.), named in honor of Prof. Zengzhi Li for his pioneering contributions to the study of entomophthoroid fungi in China.

Known distribution – Anhui Province, China.

Typification – CHINA, Anhui Province, Hefei City, Zipeng Mountain, 31°53' N, 117°06' E, from soil, 26 Feb. 2024, *Y. Yin*, holotype ZPS24022608. Ex-type culture RCEF 7535. GenBank: nucLSU = PV084608; *EFL* = PV107258; mtSSU = PV084656.

Additional specimen examined – CHINA, Anhui Province, Chuzhou City, Langya Mountain, 32°28' N, 118°29' E, from soil, 11 May. 2010, *Y. Nie*, ex-paratype RCEF 4911. GenBank: nucLSU = PV084607; *EFL* = PV107257; mtSSU = PV084655.

Description – Colonies on PDA at 21 °C for 3 d, white, reaching ca 11.0–13.0 mm in diameter. Mycelia colorless, 6.0–11.5 μm wide, usually branched when young. Primary conidiophores colorless, 40.0–125.0 × 6.0–10.5 μm, arising from hyphal segments and not widening upward, producing a single primary conidium. Primary conidia forcibly discharged, colorless, globose, subglobose to oval, 30.0–37.5 × 23.0–32.0 μm, with a prominent basal papilla 6.0–12.0 μm wide and 3.0–8.0 μm long. Secondary conidia arising from primary conidia, similar to but smaller than primary conidia. Microconidia not observed. Several zygospores often formed in the same conjugating segments after 3 d, globose, smooth, 16.5–24.0 μm in diameter with a wall 2.0–3.0 μm thick.

Notes – *Conidiobolus lii* is similar to *Co. humicolus* and *Co. iuxtagenitus* in the size of primary conidia and zygospores (Srinivasan & Thirumalachar 1961, Waters & Callaghan 1989). However, it differs from *Co. humicolus* in having shorter primary conidiophores and lacking chlamydospores, and from *Co. iuxtagenitus* in having longer primary conidiophores and lacking fusiform secondary conidia. Phylogenetically, *Co. lii* forms an independent clade within the *Conidiobolus* s.s. lineage (100% ML, 1.00 BYPP, Fig. 8).

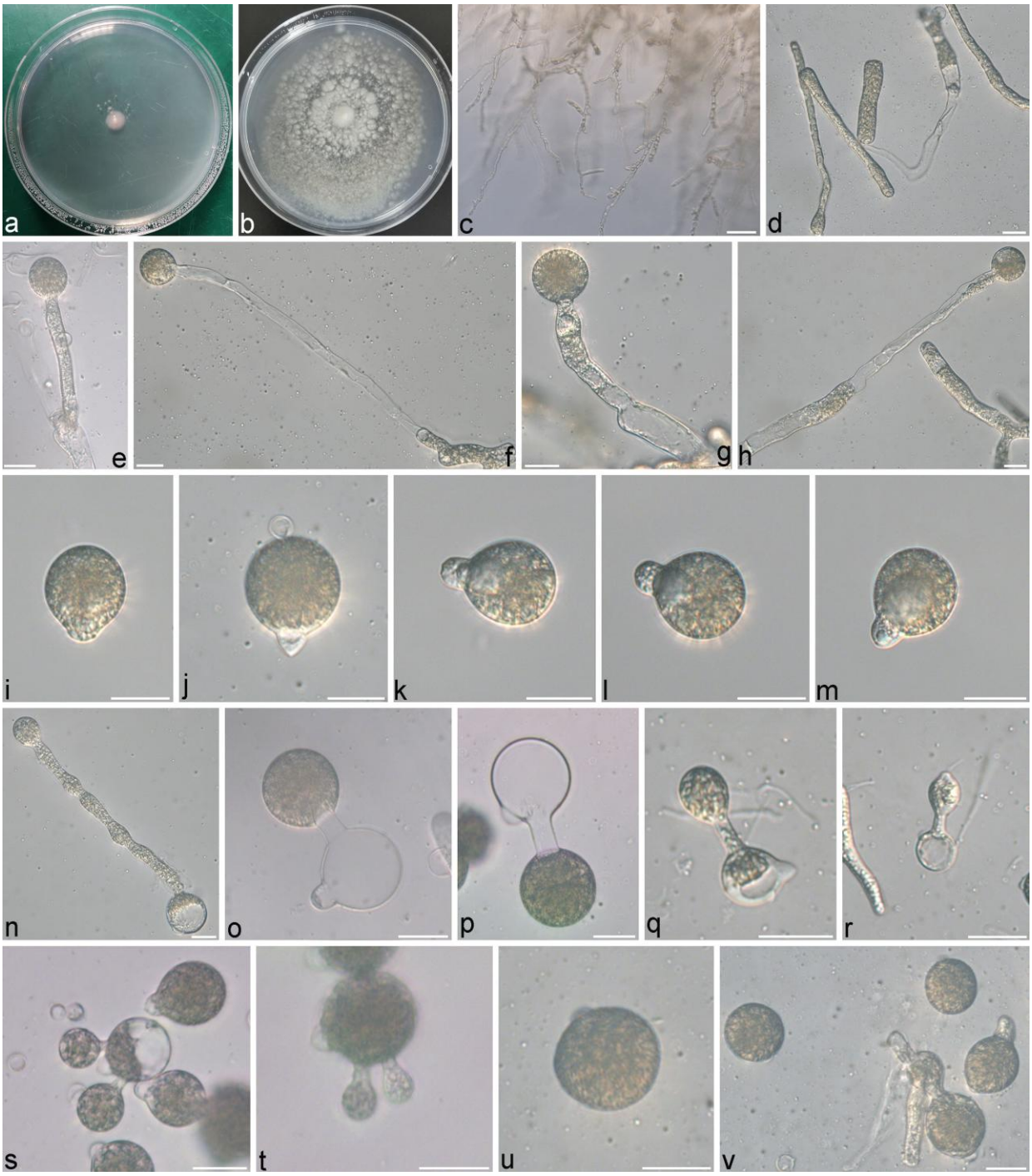

Figure 11 – ***Conidiobolus hippocrepiformis*** (RCEF 7923, ex-type). a Colony on PDA after 3 d at 21 °C. b Colony on PDA after 10 d at 21 °C. c Mycelia branched at the edge of the colony. d Hyphae segments. e–h Primary conidiophores bearing a single primary conidium. i–m Primary conidia. n–p Primary conidia bearing a single secondary conidium. q, r Triple or fourth replicated conidia.s, t Microconidia arising from a single conidium. u, v Chlamydospore. Scale bars: c = 100 µm, d–v = 20 µm.

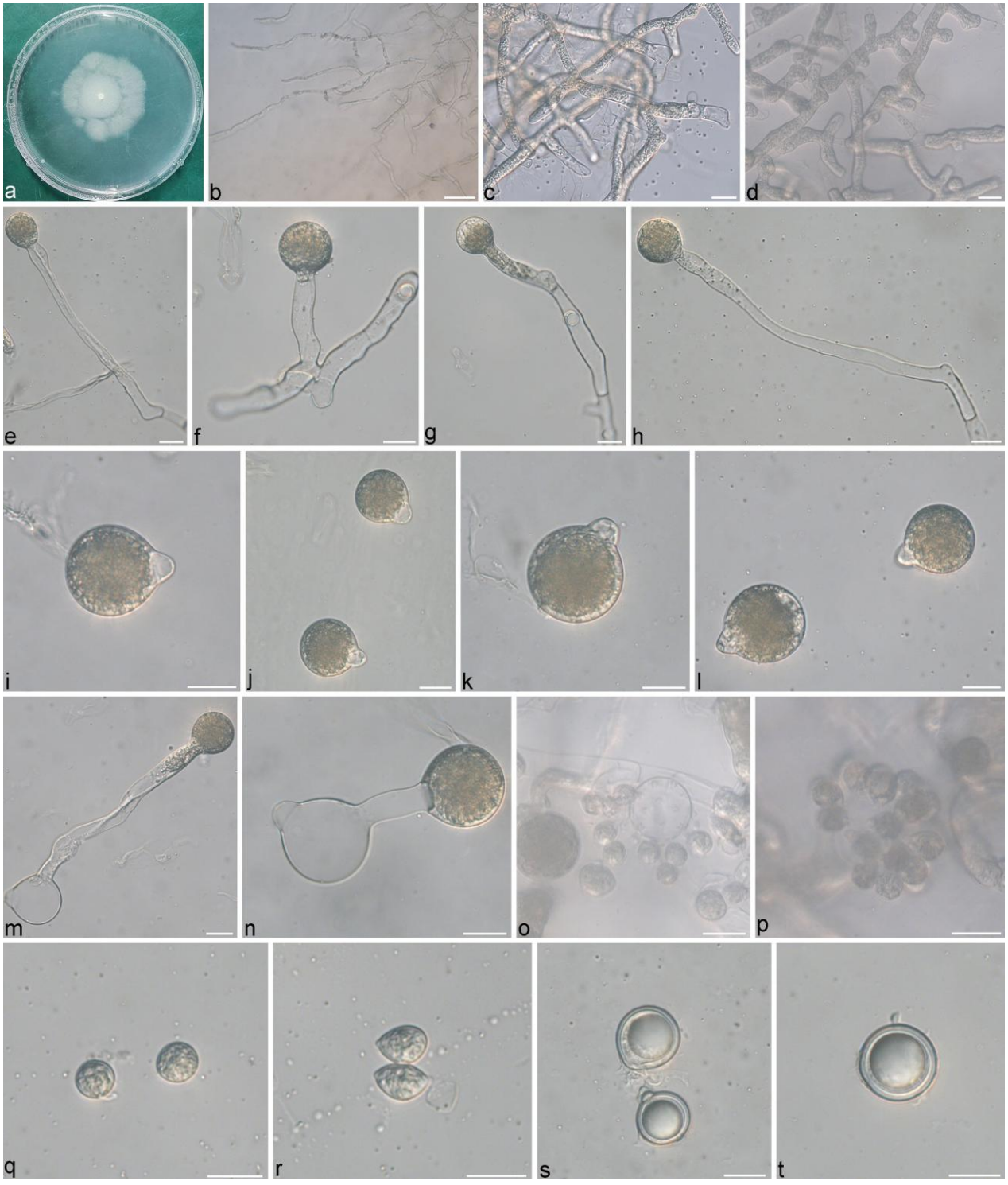

Figure 12 – ***Conidiobolus kunmingensis*** (RCEF 7945, ex-type). a Colony on PDA after 3 d at 21 °C. b Mycelia branched at the edge of the colony. c, d Mycelia. e–h Primary conidiophores bearing a single primary conidium. i–l Primary conidia. m, n Primary conidia bearing a single secondary conidium. o, p Microconidia arising from conidia. q, r Microconidia. s, t Zygospores. Scale bars: b = 100 μm, c–t = 20 μm.

Conidiobolus longibasalis B. Huang & Y. Nie, sp. nov. Fig. 14

MycoBank: MB857667; **Facesoffungi:** FoF17354

Etymology – *longibasalis* (Lat.) refers to the long base of primary conidia.

Known distribution – Henan Province, China.

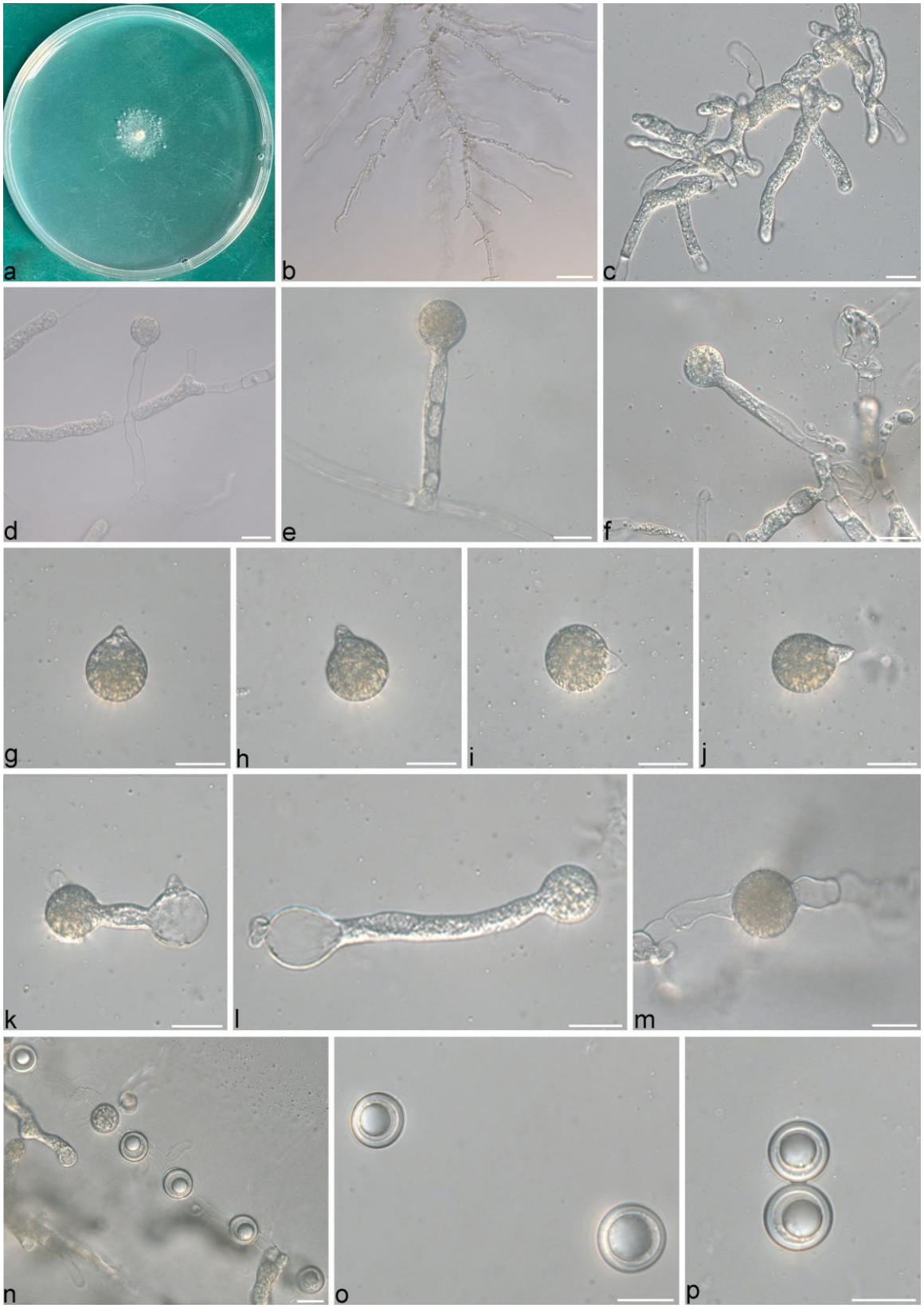

Figure 13 – ***Conidiobolus lii*** (RCEF 7535, ex-type). a Colony on PDA after 3 d at 21 °C. b Mycelia often branched at the edge of the colony. c Mycelia. d–f Primary conidiophores bearing a single primary conidium. g–j Primary conidia. k, l Primary conidia bearing a single secondary conidium. m, n Zygospores formed in the same conjugating segments. o, p Mature zygospores. Scale bars: b = 100 µm, c–p = 20 µm.

Typification – CHINA, Henan Province, Xinyang City, Jinlanshan National Forest Parks, 31°23′ N, 115°19′ E, from plant debris, 15 Mar. 2024, *Y. Nie*, holotype JLS2403151501. Ex-type culture RCEF 7929. GenBank: nucLSU = PV084609; *EFL* = PV107259; mtSSU = PV084657.

Additional specimen examined – Henan Province, Xinyang City, Jinlanshan National Forest Parks, 31°23′ N, 115°19′ E, from plant debris, 15 Mar. 2024, *Y. Nie*, culture RCEF 7930. GenBank: nucLSU = PV084610; *EFL* = PV107260; mtSSU = PV084658.

Description – Colonies on PDA at 21 °C for 3 d, white, reaching ca 14.0–18.0 mm in diameter. Mycelia white, 5.5–12.0 μm wide, usually branched at the edge of colony. Primary conidiophores colorless, without widening upward near the tip, 30.0–85.0 × 8.0–12.0 μm, producing a single primary conidium. Primary conidia forcibly discharged, colorless, subglobose, 30.0–42.0 × 23.0–33.0 μm, often with a long basal papilla 8.0–11.0 μm wide and 6.0–10.0 μm long. Secondary conidia arising from primary conidia, similar to but smaller than primary conidia, sometimes arising in pairs of two secondary conidia from a primary one. Microconidia formed at the initial growth stage, globose to slightly ellipsoidal, 11.0–17.5 × 10.0–15.0 μm. Zygospores formed in axial alignment with one or both conjugating segments after 3 d, globose, sometimes ellipsoidal, smooth, 26.0–44.0 μm long, 25.0–37.0 μm wide, with a 1.5–4.5 μm thick wall.

Notes – *Conidiobolus longibasalis* is similar to *Co. bifurcatus*, *Co. incongruus*, and *Co. margaritatus* in the sizes of its conidia and zygospores but differs in key traits: it has shorter primary conidiophores and larger microconidia than *Co. bifurcatus* (Nie et al. 2020b); lacks the chain-like conidial arrangement of *Co. margaritatus* (Huang et al. 2007); and features thicker-walled zygospores than *Co. incongruus* (Drechsler 1960). Although phylogenetically related to *Co. jiangxiensis* and *Co. mycophilus* with 80% ML and 0.90 BYPP, *Co. longibasalis* is easily distinguished by its long basal papilla and thicker zygospore walls (Nie et al. 2024).

Conidiobolus macrozygosporus B. Huang & Y. Nie, sp. nov. Fig. 15

MycoBank: MB857668; **Facesoffungi:** FoF17355

Etymology – *macrozygosporus* (Lat.) refers to its large zygospores.

Known distribution – Anhui Province, China.

Typification – CHINA, Anhui Province, Hefei City, Zipeng Mountain, 31°73' N, 117°02' E, from plant debris, 15 Jan. 2024, *Y. Yin*, holotype ZPS24011504. Ex-type culture RCEF 7521. GenBank: nucLSU = PV084611; *EFL* = PV107261; mtSSU = PV084659.

Additional specimen examined – CHINA, Anhui Province, Hefei City, Zipeng Mountain, 31°73' N, 117°02' E, from plant debris, 15 Jan. 2024, *Y. Yin*, culture RCEF 7522. GenBank: nucLSU = PV084612; *EFL* = PV107262; mtSSU = PV084660.

Description – Colonies on PDA at 21 °C for 3 d, white, reaching ca 10.0 mm in diameter. Mycelia white, 10.0–26.0 μm wide, usually unbranched when young. Primary conidiophores colorless, 40.0–350.0 × 14.0–24.0 μm, often arising from hyphal centre and widening upward near the tip, producing a single primary conidium. Primary conidia forcibly discharged, colorless, globose, subglobose to ellipsoidal, 43.0–60.0 × 35.0–54.0 μm, with a basal papilla 13.0–21.5 μm wide and 5.0–13.0 μm long. Secondary conidia often arising from primary conidia, similar to but smaller than primary conidia, sometimes two or three secondary conidia arising from primary conidia. Microconidia rarely observed at the initial growth stage. Zygospores formed in the same conjugating segments after 10 d, globose, smooth, 25.0–46.0 μm in diameter with a 4.5–8.0 μm thick wall.

Notes – *Conidiobolus macrozygosporus* is characterized by its large primary conidiophores and conidia, as well as thick-walled zygospores. It resembles *Co. incongruus*, *Co. polyspermus*, and *Co. taihushanensis* in producing large (> 45.0 μm) zygospores, but each of these species has smaller primary conidia and shorter primary conidiophores (Drechsler 1960, 1961, Nie et al. 2020b). Likewise, *Co. polyspermus* differs in having thinner zygospore walls. Phylogenetically, *Co. macrozygosporus* is separate from these species (100% ML, 1.00 BYPP, Fig. 8). Sequence similarities between *Co. macrozygosporus* and *Co. bifurcatus* are 96.0% (nucLSU) and 93.0% (*EFL*).

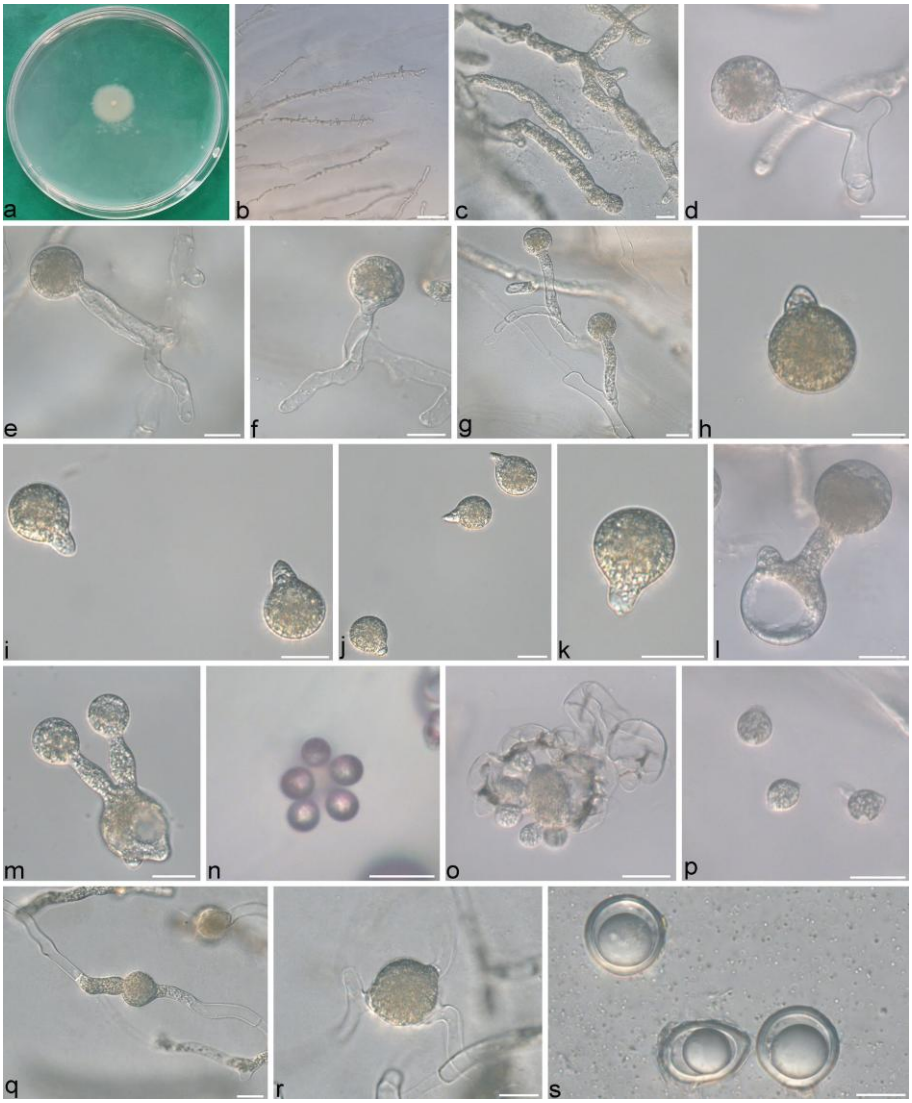

Figure 14 – ***Conidiobolus longibasalis*** (RCEF 7929, ex-type). a Colony on PDA after 3 d at 21 °C. b Mycelia unbranched at the edge of the colony. c Mycelia. d–g Primary conidiophores bearing a single primary conidium. h–k Primary conidia. l Primary conidia bearing a single secondary conidium. m Primary conidia bearing two secondary conidia. n, o Microconidia arising from a conidium. p Microconidia. q Zygospores formed in one of the conjugating segments. r Zygospores formed in axial alignment with both conjugating segments. s Mature zygospores. Scale bars: b = 100 µm, c–s = 20 µm.

Conidiobolus oxyconidius B. Huang & Y. Nie, sp. nov. Fig. 16

MycoBank: MB857670; **Facesoffungi:** FoF17357

Etymology – *oxyconidius* (Lat.) refers to the slightly sharpened outline of the primary conidia.

Known distribution – Jiangsu Province, China.

Typification – CHINA, Jiangsu Province, Yizheng City, Yangzhou Western Suburbs Forest Park, 32°42' N, 119°24' E, from plant debris, 15 July. 2024, *Y. Nie*, holotype JSYZ24071501. Ex-type culture RCEF 7937. GenBank: nucLSU = PV084613; *EFL* = PV107263; mtSSU = PV084661.

Additional specimen examined – CHINA, Jiangsu Province, Yizheng City, Yangzhou Western Suburbs Forest Park, 32°42' N, 119°24' E, from plant debris, 15 July. 2024, *Y. Nie*, culture RCEF 7938. GenBank: nucLSU = PV084614; *EFL* = PV107264; mtSSU = PV084662.

Description – Colonies on PDA at 21 °C for 3 d, white, reaching ca 10.0–14.0 mm in diameter. Mycelia white, colorless, 5.0–11.0 µm wide, unbranched at the edge of colony. Primary

conidiophores colorless, without widening upward near the tip, 35.0–150.0 × 6.0–11.0 µm, producing a single primary conidium. Primary conidia forcibly discharged, colorless, globose, subglobose to ellipsoidal, often growing slight sharp near the side of basal papilla, 29.0–34.0 × 20.0–29.0 µm, with a basal papilla 6.0–8.5 µm wide and 4.0–7.5 µm long. Secondary conidia arising from primary conidia, similar to but smaller than primary conidia. Microconidia not observed on PDA or 2% water agar. Resting spores not observed after 30 d.

Notes – *Conidiobolus oxyconidius* shares similarities in conidial size with *Co. brefeldianus*, *Co. iuxtagenitus*, and *Co. lichenicolus* (Couch 1939, Waters & Callaghan 1989, Srinivasan & Thirumalachar 1968a). It differs by having markedly longer primary conidiophores (35.0–150.0 µm vs. 30.0–50.0 µm in *Co. brefeldianus*, 30.0–60.0 µm in *Co. iuxtagenitus*, and 30.0–100.0 µm in *Co. lichenicolus*) and slightly pointed conidial apices. Phylogenetically, *Co. oxyconidius* is allied to *Co. humicolus* (ATCC 28849) with 100% ML and 1.00 BYPP, but differs from its absence of resting spores (Fig. 8). Sequence similarities between *Co. oxyconidius* and *Co. humicolus* are 96.7% (nucLSU) and 90.0% (*EFL*).

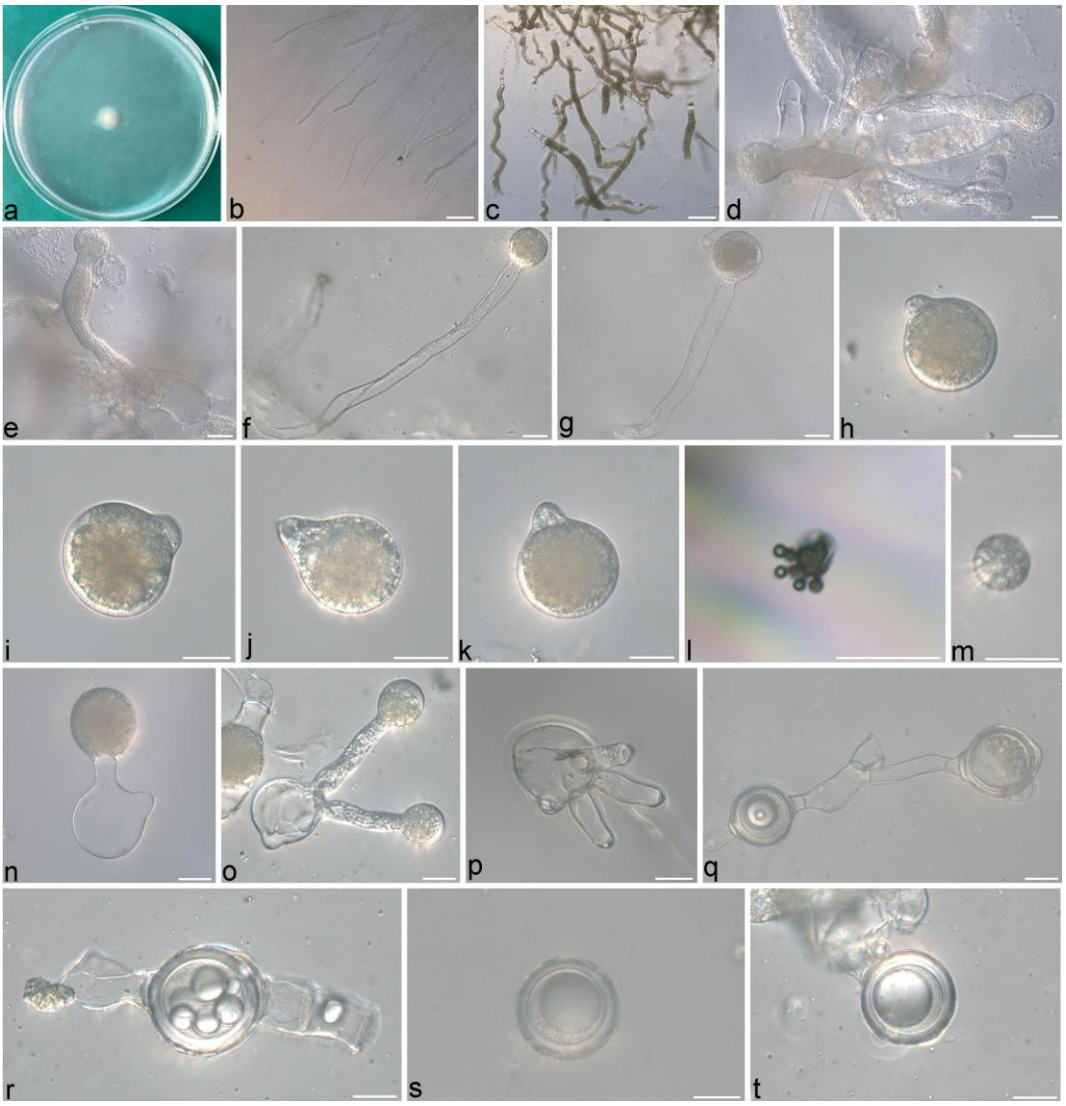

Figure 15 – ***Conidiobolus macrozygosporus*** (RCEF 7521, ex-type). a Colony on PDA after 3 d at 21 °C. b Mycelia unbranched at the edge of the colony. c Mycelia. d–g Primary conidiophores bearing a single primary conidium. h–k Primary conidia. l Microconidia arising from a conidium; m Microconidia. n Primary conidia bearing a single secondary conidium. o Two secondary conidium arising from a conidium. p A ghost of three secondary conidia arising from a conidium. q,

r Zygospores formed in the same conjugating segments. s, t Mature zygospores. Scale bars: b–c = 100 µm, d–t = 20 µm.

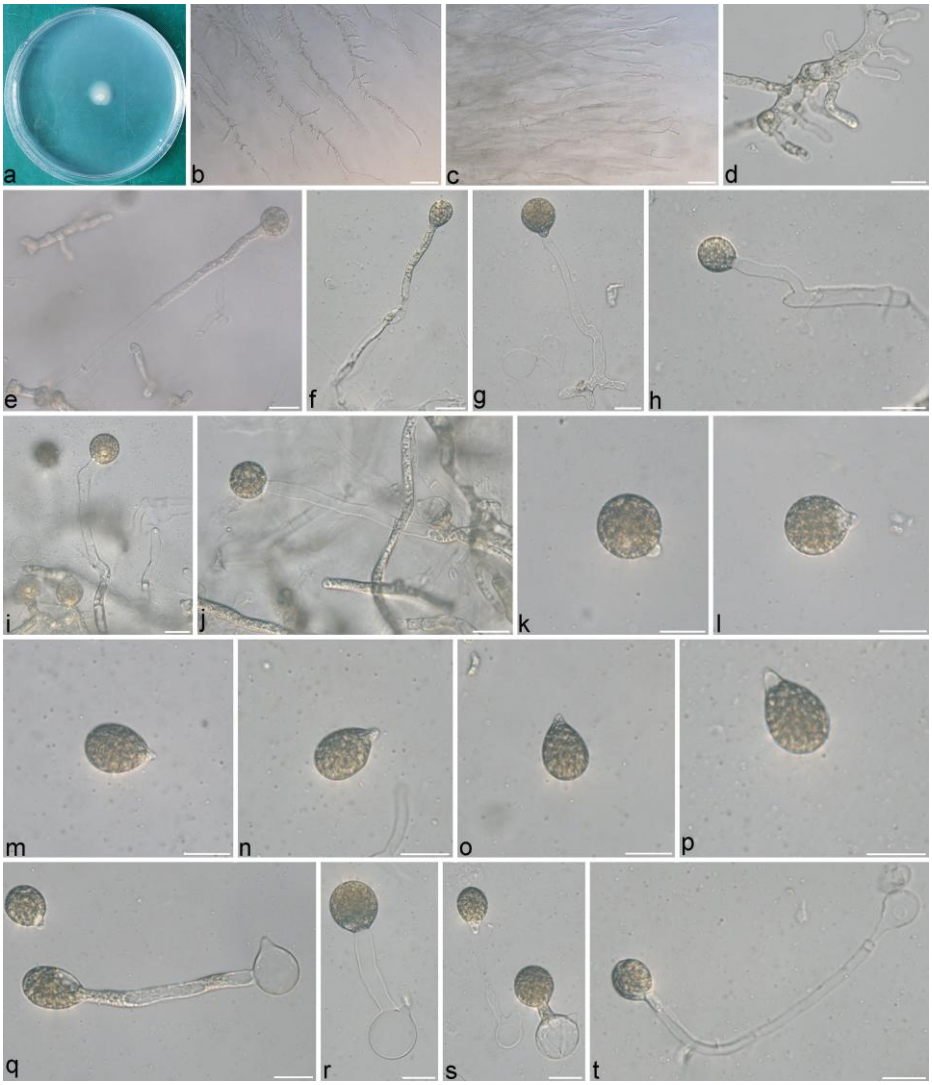

Figure 16 – ***Conidiobolus oxyconidius*** (RCEF 7937, ex-type). a Colony on PDA after 3 d at 21 °C. b, c Mycelia branched at the edge of the colony. d Mycelia. e–j Primary conidiophores bearing a single primary conidium. k–p Primary conidia. q–t Primary conidia bearing a single secondary conidium. Scale bars: b, c = 100 µm, d–t = 20 µm.

Conidiobolus pachyconidiophorus B. Huang & Y. Nie, sp. nov. Fig. 17

MycoBank: MB857671; **Facesoffungi:** FoF17358

Etymology – *pachyconidiophorus* (Lat.) refers to its thick primary conidiophores.

Known distribution – Jilin Province, China.

Typification – CHINA, Jilin Province, Changchun City, Jingyuetan National Forest Park, 43°79' N, 125°46' E, from plant debris, 3 August. 2024, *Y. Yin*, holotype CC24080302. Ex-type culture RCEF 7941. GenBank: nucLSU = PV084615; *EFL* = PV107265; mtSSU = PV084663.

Additional specimen examined – CHINA, Jilin Province, Changchun City, Jingyuetan National Forest Park, 43°79' N, 125°46' E, from plant debris, 3 August. 2024, *Y. Yin*, culture RCEF 7942. GenBank: nucLSU = PV084616; *EFL* = PV107266; mtSSU = PV084664.

Description – Colonies on PDA at 21 °C for 3 d, white, reaching ca 6.0 mm in diameter, many punctiform colonies around the central colony. Mycelia white, 6.0–11.0 µm wide, unbranched at the edge of colony. Distended to form segments when old. Primary conidiophores colorless, without widening upward near the tip, thick and robust, often wider than mycelia, 70.0–230.0 ×

10.0–17.0 µm, producing a single primary conidium. Primary conidia forcibly discharged, colorless, globose to subglobose, 35.0–48.0 × 29.5–39.0 µm, with a basal papilla 8.0–13.0 µm wide and 3.0–9.0 µm long. Secondary conidia arising from primary conidia, similar to but smaller than primary conidia. Secondary conidiophores sometimes formed a string of drum shaped structure and occupied near a half-length of secondary conidiophores. Microconidia not observed on PDA or 2% water agar. Zygospores formed in axial alignment, globose, smooth, 23.0–40.0 µm, with a 2.0–3.0 µm thick wall.

Notes – *Conidiobolus pachyconidiophorus* is distinctive for its thick, robust primary conidiophores. Morphologically, it recalls *Co. dabieshanensis*, *Co. margaritatus*, and *Co. megalotocus* but differs in key traits: it lacks chain-like conidia (as in *Co. margaritatus*), lacks chlamydospores (as in *Co. dabieshanensis*), and produces zygospores (unlike *Co. megalotocus*) (Drechsler 1956, Huang et al. 2007, Nie et al. 2017). In the phylogenetic tree (Fig. 8), *Co. pachyconidiophorus* forms a separate clade within *Conidiobolus* s.s. with 96% ML and 1.00 BYPP. Sequence similarities between *Co. pachyconidiophorus* and *Co. macrosporus* are 85.9% (nucLSU) and 97.1% (*EFL*).

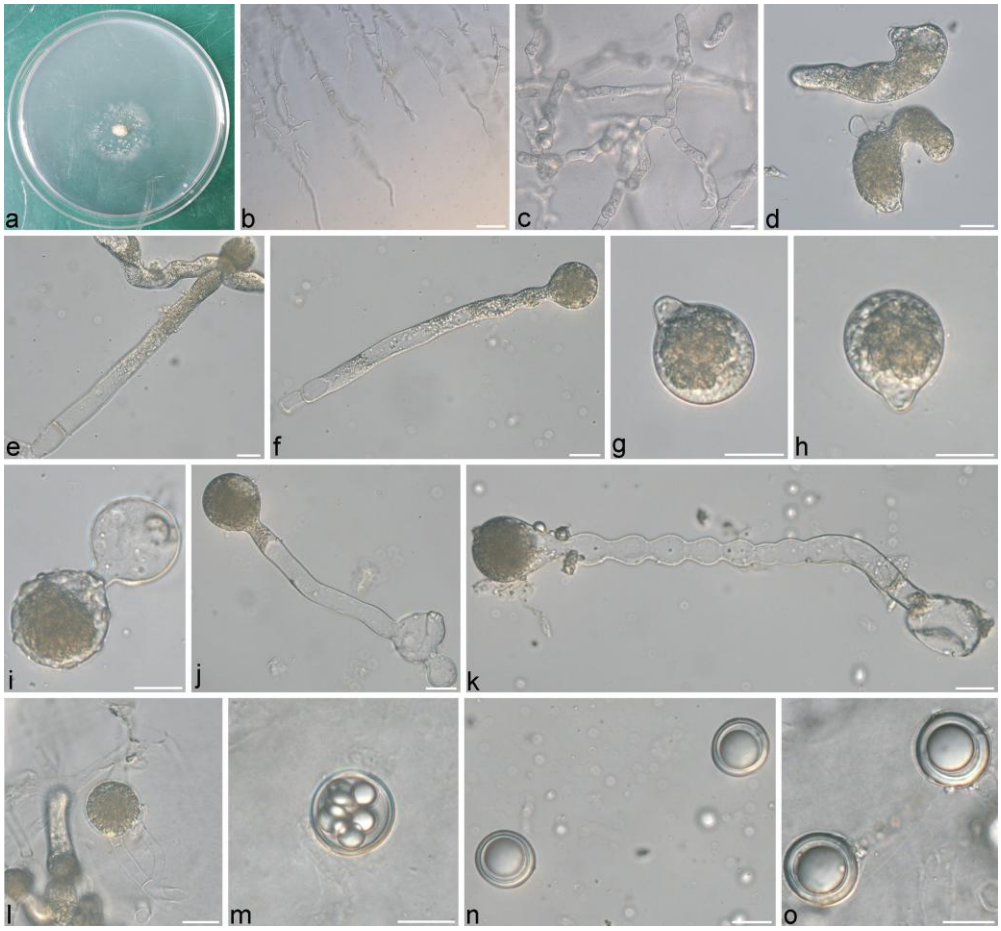

Figure 17 – ***Conidiobolus pachyconidiophorus*** (RCEF 7941, ex-type). a Colony on PDA after 3 d at 21°C. b Mycelia branched at the edge of the colony. c, d Mycelia. e, f Primary conidiophores bearing a single primary conidium. g, h Primary conidia. i–k Primary conidia bearing a single secondary conidium. l Zygospores formed in one of the conjugating segments. m Immature zygospores. n, o Mature zygospores. Scale bars: b = 100 µm, c–o = 20 µm.

Conidiobolus pectiniformis B. Huang & Y. Nie, sp. nov. Fig. 18

MycoBank: MB857661; **Facesoffungi:** FoF17348

Etymology – *pectiniformis* (Lat.), referring to the comb-shaped segments of the mycelium.

Known distribution – Anhui Province, China.

Typification – CHINA, Anhui Province, Shitai County, Baishiling Village, 30°09′ N, 117°52′ E, from plant debris, 11 May. 2010, *Y. Nie*, holotype BSL 100511. Ex-type culture RCEF 4923. GenBank: nucLSU = PV084596; *EFL* = PV107246; mtSSU = PV084644.

Additional specimen examined – CHINA, Anhui Province, Shitai County, Baishiling Village, 30°09′ N, 117°52′ E, from plant debris, 11 May. 2010, *Y. Nie,* culture RCEF 4925. GenBank: nucLSU = PV084597; *EFL* = PV107247; mtSSU = PV084645.

Description – Colonies on PDA at 21 °C for 3 d, white, reaching ca 15.0 mm in diameter. Mycelia white, 8.0–17.0 µm wide, unbranched when young, distended to form comb-like segments when old. Primary conidiophores arising from hyphae, short, 20.0–70.0 × 5.0–12.5 µm, unbranched and producing a single primary conidium. Primary conidia usually arising from primary conidiophores, sometimes directly arising from hyphae, globose, pyriform to obovoid, 25.0–40.0 × 20.0–30.0 µm, with tapering and pointed papilla, 1.5–6.0 × 6.0–11.0 µm. Secondary conidiophores arising from primary conidia, one or two, bearing similar replicative conidia to primary conidia. Microconidia produced readily, globose to subglobose, 11.0–15.5 × 9.0–14.0 µm. Resting spores not observed.

Notes – Morphologically, the new species *Co. pectiniformis* resembles *Co. firmipilleus*, *Co. gonimodes*, and *Co. iuxtagenitus* in the sizes of primary conidiophores and conidia (Drechsler 1953, 1961, Waters & Callaghan 1989). However, it differs in producing comb-like mycelial segments and primary conidia that may arise directly from hyphae. Phylogenetically, *Co. pectiniformis* is closely related to *Co. amphitus* (RCEF 7939 and 7940) with strong support (100% ML, 1.00 BYPP; Fig. 8), but can be distinguished by its comb-like mycelium and absence of zygospores.

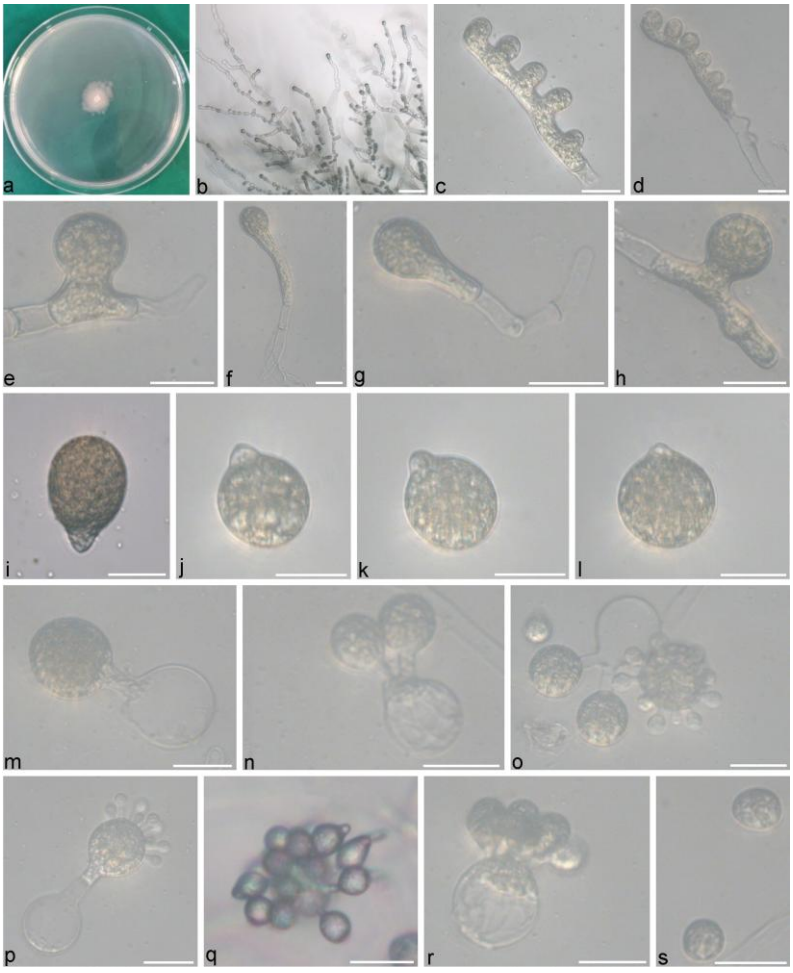

Figure 18 – ***Conidiobolus pectiniformis*** (RCEF 4923, ex-type). a Colony on PDA after 3 d at 21 °C. b Mycelia unbranched at the edge of the colony. c, d Hyphae form "comb" like segments. e, h Primary conidia directly from mycelium. f, g Primary conidiophores bearing a single primary

conidium. i–l Primary conidia. m Primary conidia bearing a single secondary conidium. n Primary conidia bearing two secondary conidia. o Primary conidia bearing two secondary conidia, microconidia arising from conidia. p Microconidia arising from secondary conidia. q, r. Microconidia arising from conidia. s. Microconidia. Scale bars: b = 100 μm, c–s = 20 μm.

Conidiobolus planibasalis B. Huang & Y. Nie, sp. nov. Fig. 19

MycoBank: MB857662; **Facesoffungi:** FoF17349

Etymology – *planibasalis* (Lat.) refers to the flat base of primary conidia.

Known distribution – Jiangxi Province, China.

Typification – CHINA, Jiangxi Province, Nanchang City, Aixihu Forest Wetland Park, 28°57′ N, 115°69′ E, from plant debris, 7 Dec. 2022, *Y. Nie*, holotype BWPU 221207-2. Ex-type culture RCEF 7515. GenBank: nucLSU = PV084598; *EFL* = PV107248; mtSSU = PV084646.

Additional specimen examined – CHINA, Jiangxi Province, Nanchang City, Aixihu Forest Wetland Park, 28°57′ N, 115°69′ E, from plant debris, 7 Dec. 2022, *Y. Nie*, culture RCEF 7516. GenBank: nucLSU = PV084599; *EFL* = PV107249; mtSSU = PV084647.

Description – Colonies on PDA at 21 °C for 3 d, white, reaching ca 14.0–15.0 mm in diameter. Mycelia white, 7.5–15.0 μm wide, usually unbranched when young. Primary conidiophores colorless, without widening upward near the tip, 30.0–75.0 × 10.0–13.0 μm, arising from hyphae and producing a single primary conidium. Primary conidia forcibly discharged, colorless, globose, 35.0–43.0 × 30.0–38.0 μm, often with a flat basal papilla 10.0–17.0 μm wide and 4.0–7.5 μm long. Secondary conidia arising from primary conidia, similar to but smaller than primary conidia. Microconidia not observed. Zygospores formed in axial alignment with one or both conjugating segments, globose, smooth, 28.0–40.0 μm in diameter with a 2.5–3.5 μm thick wall.

Notes – *Conidiobolus planibasalis* is distinctive for its flat basal papilla of primary conidia, a feature resembling that of *Co. eurypus* (Drechsler 1957b), although the latter has smaller primary conidia and lacks resting spores. Moreover, *Co. eurypus* was previously treated as a synonym of *Co. megalotocus* (King 1976b), and its taxonomic position remains to be clarified by molecular data. *Conidiobolus planibasalis* also produces two modes of sexual reproduction (zygospores in different conjugation patterns), a trait shared only by *Co. brefeldianus* and *Co. utriculosus*. It differs from both by having larger primary conidia and smaller zygospores (Brefeld 1884, Couch 1939, King 1977). Phylogenetically, *Co. planibasalis* is close to *Co. kunmingensis* (RCEF 7945 and 7946) with 93% ML, but differs in its shorter primary conidiophores and larger zygospores.

Conidiobolus proximus B. Huang & Y. Nie, sp. nov. Fig. 20

MycoBank: MB857672; **Facesoffungi:** FoF17359

Etymology – *proximus* (Lat.) refers to the short hyphal outgrowths formed on one or both sides of conjugating segments during zygospore development.

Known distribution – Hubei Province, China.

Typification – CHINA, Hubei Province, Xiaogan City, Xiaochang County, Shuangfengshan National Forest Parks, 31°22' N, 114°23' E, from plant debris, 12 Mar. 2024, *Y. Nie*, holotype SFS24031206. Ex-type culture RCEF 7927. GenBank: nucLSU = PV084617; *EFL* = PV107267; mtSSU = PV084665.

Additional specimen examined – CHINA, Hubei Province, Xiaogan City, Xiaochang County, Shuangfengshan National Forest Parks, 31°22' N, 114°23' E, from plant debris, 12 Mar. 2024, *Y. Nie*, culture RCEF 7928. GenBank: nucLSU = PV084618; *EFL* = PV107268; mtSSU = PV084666.

Description – Colonies on PDA at 21 °C for 3 d, white, reaching ca 14.0 mm in diameter. Mycelia white, 6.0–18.0 μm wide, usually branched at the edge of colony. Primary conidiophores colorless, without widening upward near the tip, 60.0–265.0 × 11.5–17.0 μm, producing a single primary conidium. Primary conidia forcibly discharged, colorless, subglobose to oval, 34.0–49.0 × 29.0–40.0 μm, often with a basal papilla 10.5–15.0 μm wide and 5.0–9.5 μm long. Secondary conidia arising from primary conidia, similar to but smaller than primary conidia. Microconidia not observed on PDA or 2% water agar. Zygospores formed in axial alignment after 3 d, mycelium

often formed on one side or both sides of the conjugating segments, globose, smooth, 30.0–39.0 µm, with a 2.5–4.0 µm thick wall.

Notes – *Conidiobolus proximus* is notable for the short mycelium formed on one or both sides of the conjugating segments during zygospore formation. In *Conidiobolus* s.s., a somewhat similar structure is known only in *Co. iuxtagenitus*, where it appears as a single beak-like swelling rather than the short hyphal outgrowths seen here (Waters & Callaghan 1989). Phylogenetically, *Co. proximus* is closest to *Co. ramiconidiophorus* (RCEF 7523 and 7524) from which it differs by having larger primary conidia and lacking digitately branched primary conidiophores.

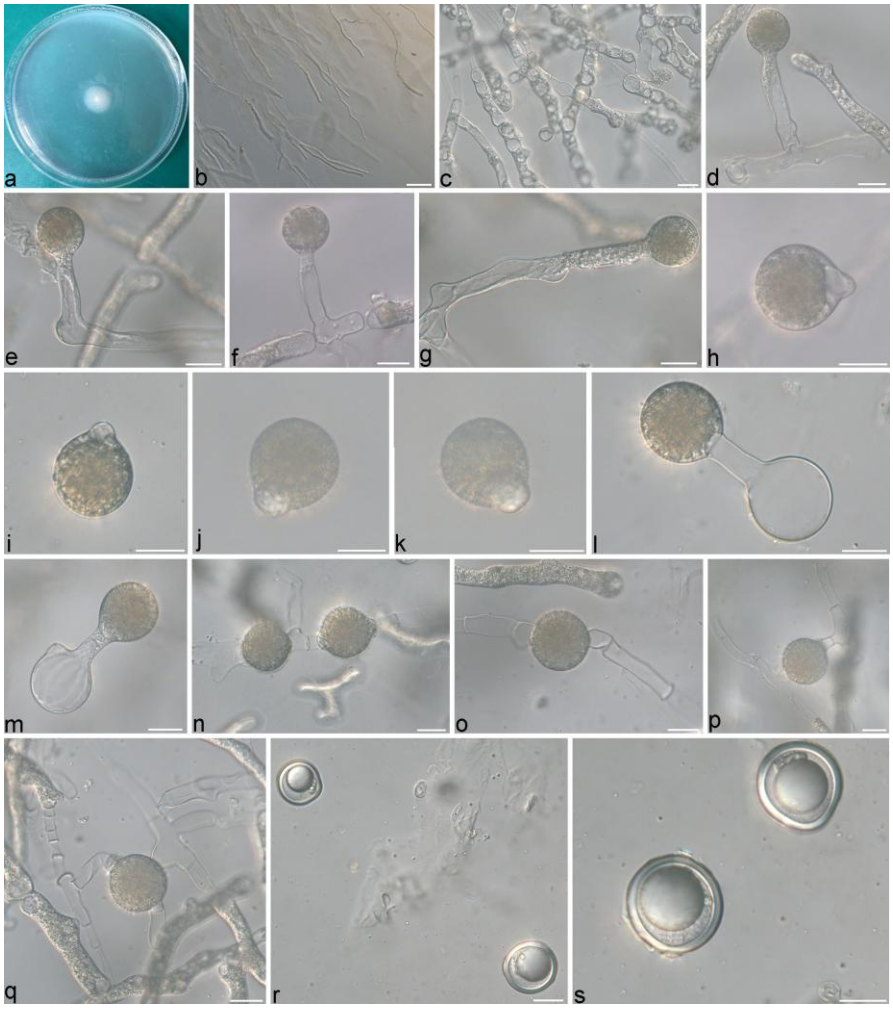

Figure 19 – ***Conidiobolus planibasalis*** (RCEF 7515, ex-type). a Colony on PDA after 3 d at 21 °C. b Mycelia unbranched at the edge of the colony. c Mycelia. d–g Primary conidiophores bearing a single primary conidium. h–k Primary conidia. l, m Primary conidia bearing a single secondary conidium. n, o Zygospores formed in one of the conjugating segments. p, q Zygospores formed in axial alignment with both conjugating segments. r, s Mature zygospores. Scale bars: b = 100 µm, c –s = 20 µm.

Conidiobolus pseudogonimodes B. Huang & Y. Nie, sp. nov. Fig. 21

MycoBank: MB857673; **Facesoffungi:** FoF17360

Etymology – *pseudogonimodes* (Lat.) refers to its similarity to *Conidiobolus gonimodes*.

Known distribution: Anhui Province, China.

Typification – CHINA, Anhui Province, Hefei City, Zipeng Mountain, 31°72' N, 117°01' E, from plant debris, 26 Feb. 2024, *Y. Yin*, holotype ZPS24022610. Ex-type culture RCEF 7933. GenBank: nucLSU = PV084619; *EFL* = PV107269; mtSSU = PV084667.

Additional specimen examined – CHINA, Anhui Province, Hefei City, Zipeng Mountain, 31°72' N, 117°01' E, from plant debris, 26 Feb. 2024, *Y. Yin*, culture RCEF 7934. GenBank: nucLSU = PV084620; *EFL* = PV107270; mtSSU = PV084668.

Description – Colonies on PDA at 21 °C for 3 d, white, reaching ca 6.0 mm in diameter. Mycelia white, 5.0–13.0 µm wide when young, unbranched at the edge of colony, frequently distended to segment after 5 d, 12.0–23.0 µm wide. Primary conidiophores colorless, without widening upward near the tip, 35.0–260.0 × 6.0–11.0 µm, producing a single primary conidium, sometimes branched at the tip and bearing two primary conidium. Primary conidia forcibly discharged, colorless, globose, subglobose to oval, 24.0–39.0 × 20.0–29.0 µm, often with a basal papilla 5.0–8.0 µm wide and 2.0–6.0 µm long. Secondary conidia arising from primary conidia, similar to but smaller than primary conidia. Microconidia not observed on PDA or 2% water agar. Zygospores formed in axial alignment after 7 d, globose, smooth, 18.0–27.0 µm, with a 2.0–3.0 µm thick wall.

Notes – *Conidiobolus pseudogonimodes* resembles *Co. gonimodes* (ATCC 14445) in morphology and clusters with it in phylogenetic analyses, but can be distinguished by its longer primary conidiophores and oval primary conidia (Drechsler 1961). In terms of conidial and zygospore dimensions, it is also similar to *Co. humicolus* (Srinivasan & Thirumalachar 1961), yet forms a separate clade from that species (100% ML, 1.00 BYPP, Fig. 8). Sequence similarities between *Co. pseudogonimodes* and *Co. gonimodes* are 96.9% (nucLSU) and 89.5% (*EFL*).

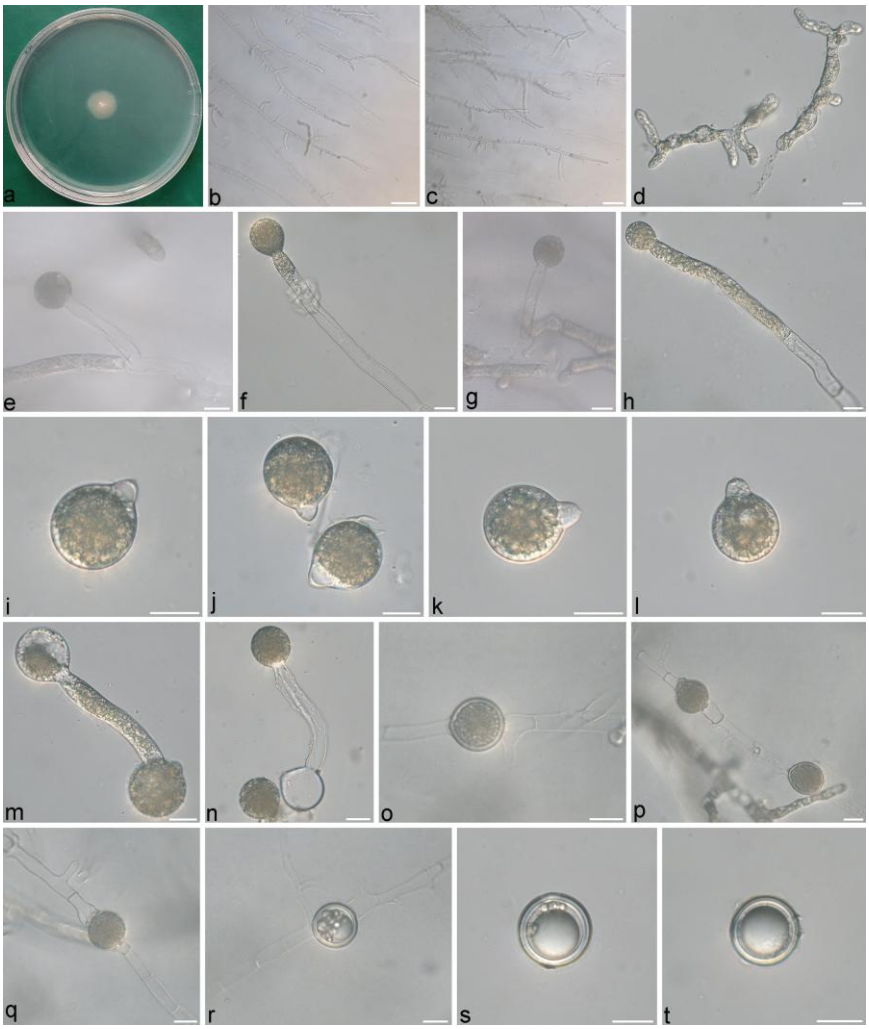

Figure 20 – ***Conidiobolus proximus*** (RCEF 7927, ex-type). a Colony on PDA after 3 d at 21 °C. b, c Mycelia unbranched at the edge of the colony. d Mycelia. e–h Primary conidiophores bearing a single primary conidium. i–l Primary conidia. m, n Primary conidia bearing a single secondary conidium. o–r Zygospores formed in one of the conjugating segments with short mycelium formed

at one side or both sides of the conjugating segments. s, t Mature zygospores. Scale bars: b, c = 100 μm, d–t = 20 μm.

Figure 21 – ***Conidiobolus pseudogonimodes*** (RCEF 7933, ex-type). a Colony on PDA after 3 d at 21 °C. b Mycelia unbranched at the edge of the colony. c, d Mycelia. e–h Primary conidiophores bearing a single primary conidium. i Primary conidiophores branched at the tip and bearing two primary conidia. j–m Primary conidia. n–p Primary conidia bearing a single secondary conidium. q, r Zygospores formed in one of the conjugating segments. s, t Mature zygospores. Scale bars: b = 100 μm, c–t = 20 μm.

Conidiobolus ramiconidiophorus B. Huang & Y. Nie, sp. nov. Fig. 22

MycoBank: MB857669; **Facesoffungi:** FoF17356

Etymology – *ramiconidiophorus* (Lat.) refers to multiple-branched primary conidiophores.

Known distribution – Yunnan Province, China.

Typification – CHINA, Yunnan Province, Wuding County, Kangzhao Village, 25°8′ N, 102°31′ E, from plant debris, 17 May. 2022, *Y. Nie*, holotype BWPU 220517. Ex-type culture RCEF 7523. GenBank: nucLSU = PV084626; *EFL* = PV107276; mtSSU = PV084674.

Additional specimen examined – CHINA, Yunnan Province, Wuding County, Kangzhao Village, 25°8′ N, 102°31′ E, from plant debris, 17 May. 2022, *Y. Nie* culture RCEF 7524. GenBank: nucLSU = PV084627; *EFL* = PV107277; mtSSU = PV084675.

Description – Colonies on PDA at 21 °C for 3 d, white, reaching ca 12.0 mm in diameter. Mycelia white, 6.5–15.0 µm wide, unbranched when young, branched moss-like when old. Primary conidiophores arising from hyphae, 88.0–265.0 × 7.5–15.0 µm, mostly unbranched and producing a single primary conidium, usually narrowing at the tip, sometimes branched at the base or tip and bearing two conidia at each branch, or digitally branched and bearing several conidia. Primary conidia forcibly discharged, globose, subglobose to obovoid, 31.0–45.0 × 25.0–38.0 µm. Papilla on primary conidia, small, 7.5–16.0 × 3.0–7.0 µm. Secondary conidiophores arising from primary conidia, bearing single or two replicative conidium. Microconidia not observed. Zygospores formed in axial alignment with conjugating segments after 14 d, mature zygospores smooth, globose, 29.0–43.0 µm in diameter, with a 3.3–5.5 µm thick wall.

Notes – Morphologically, the digitately branched conidiophores of *Co. ramiconidiophorus* resemble those of *Co. polysporus*, *Co. polytocus*, and *Co. taihushanensis* (Drechsler 1955c, Nie et al. 2020b, 2023). However, its primary conidia (31.0–45.0 × 25.0–38.0 µm) are larger than those of *Co. polytocus* (12.0–25.0 × 14.0–29.0 µm), smaller than those of *Co. polysporus* (42.0–55.0 × 33.0–45.0 µm), and comparable to *Co. taihushanensis* but with longer conidiophores and smaller zygospores. Phylogenetically, *Co. ramiconidiophorus* forms a distinct, fully supported lineage (100% ML, 1.00 BYPP) and is distant from the aforementioned species (Fig. 8).

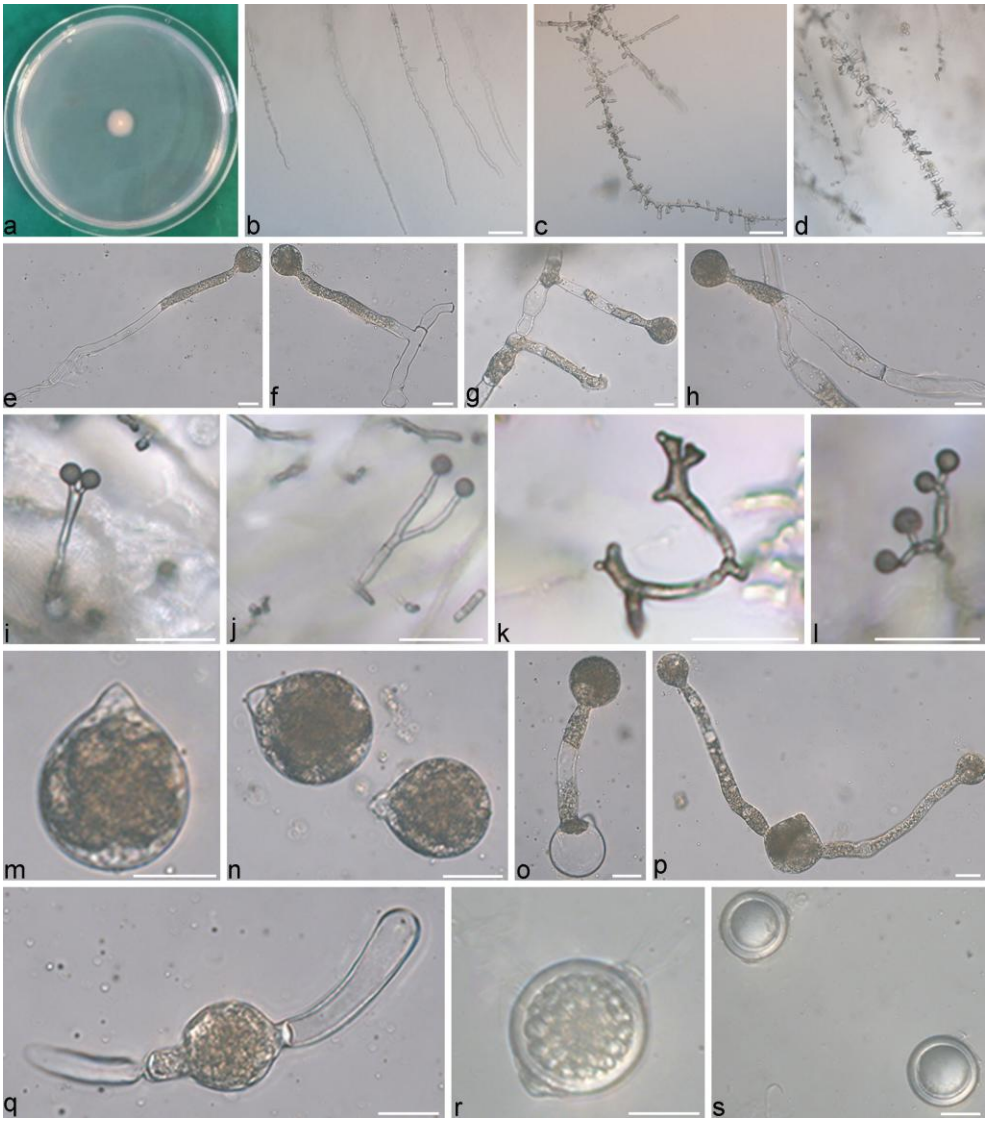

Figure 22 – ***Conidiobolus ramiconidiophorus*** (RCEF 7523, ex-type). a Colony on PDA after 3 d at 21 °C. b Mycelia unbranched at the edge of the colony. c, d Assimilative hyphae branched mosslike. e–h Primary conidiophores bearing a single primary conidium. i Primary conidiophores

branched at the tip and bearing two conidia at each branch. j Primary conidiophores branched at the base and bearing two conidia at each branch. k, l Primary conidiophores digitally branched and bearing several conidia. m, n Primary conidia. o Primary conidia bearing a single secondary conidium. p Primary conidia bearing two secondary conidia. q Zygospores formed between adjacent segments of the same hypha. r Young zygospores. s. Mature zygospores. Scale bars: b–d, i–l = 100 μm, e–h, m–s = 20 μm.

Conidiobolus robustus B. Huang & Y. Nie, sp. nov. Fig. 23

MycoBank: MB857674; **Facesoffungi:** FoF17361

Etymology – *robustus* (Lat.) refers to its robust cell structure.

Known distribution – Guizhou and Yunnan province, China.

Typification – CHINA, Guizhou Province, Tongren City, Fanjinshan National Nature Reserve, 27°89' N, 108°72' E, from plant debris, 13 August. 2024, *Y. Yin*, holotype GZ24081309. Ex-type culture RCEF 7943. GenBank: nucLSU = PV084621; *EFL* = PV107271; mtSSU = PV084669.

Additional specimens examined – CHINA, Guizhou Province, Tongren City, Fanjinshan National Nature Reserve, 27°89' N, 108°72' E, from plant debris, 13 August. 2024, *Y. Yin*, culture RCEF 7944. GenBank: nucLSU = PV084622; *EFL* = PV107272; mtSSU = PV084670. CHINA, Yunnan Province, Kunming City, Zhangjiaba Reservoir, 24°93' N, 102°37' E, from plant debris, 11 September. 2024, *Y. Yin*, ex-paratype RCEF 7947. GenBank: nucLSU = PV084623; *EFL* = PV107273; mtSSU = PV084671.

Description – Colonies on PDA at 21 °C for 3 d, white, reaching ca 31.0 mm in diameter. Mycelia white, 5.0–20.0 μm wide, unbranched at the edge of colony. Primary conidiophores colorless, sometimes widening upward near the tip, thick and robust, 40.0–300.0 × 12.0–21.0 μm, producing a single primary conidium, long primary conidiophores often bearing larger primary conidia than short primary conidiophores. Primary conidia forcibly discharged, colorless, globose, 41.0–67.0 × 31.0–56.0 μm, with a basal papilla 12.5–22.0 μm wide and 7.5–16.0 μm long. Secondary conidia arising from primary conidia, similar to but smaller than primary conidia. Microconidia frequently arising around conidia at the early growth stage, colorless, globose to ellipsoidal, some conical at the tips, 15.0–32.0 × 12.5–22.0 μm. Resting spores not observed.

Notes – *Conidiobolus robustus* is distinguished by its notably robust mycelia, conidiophores, conidia, and microconidia. Although it resembles *Co. marcoconidius* and *Co. coronatus* in forming large primary conidia, it lacks the characteristic of villose spores in *Co. coronatus* (Batko 1964); it differs from *Co. marcoconidius* in lacking zygospores and having much longer primary conidiophores (Nie et al. 2024). Phylogenetically, *Co. robustus* forms a distinct clade separate from other *Conidiobolus* s.s. taxa with 100% ML and 1.00 BYPP statistical support (Fig. 8).

Conidiobolus shanxiensis B. Huang & Y. Nie, sp. nov. Fig. 24

MycoBank: MB857675; **Facesoffungi:** FoF17362

Etymology – *shanxiensis* (Lat.) refers to Shanxi Province, where this fungus was collected.

Known distribution – Shanxi Province, China.

Typification – CHINA, Shanxi Province, Linfen City, Houma City, 35°69' N, 111°35' E, from plant debris, 23 June 2024, *M.H. Zhang*, holotype SXB24062310. Ex-type culture RCEF 7935. GenBank: nucLSU = PV084624; *EFL* = PV107274; mtSSU = PV084672.

Additional specimen examined – CHINA, Shanxi Province, Linfen City, Houma City, 35°69' N, 111°35' E, from plant debris, 23 June. 2024, *M.H. Zhang*, culture RCEF 7936. GenBank: nucLSU = PV084625; *EFL* = PV107275; mtSSU = PV084673.

Description – Colonies on PDA at 21 °C for 3 d, white, reaching ca 17.0 mm in diameter. Mycelia white, 5.0–12.0 μm wide, often branched at the edge of colony. Primary conidiophores colorless, without widening upward near the tip, 30.0–160.0 × 6.5–11.5 μm, producing a single primary conidium. Primary conidia forcibly discharged, colorless, mostly globose, sometimes oval, 23.0–40.0 × 20.0–33.0 μm, with a basal papilla 3.0–8.0 μm wide and 7.0–11.0 μm long. Secondary

conidia arising from primary conidia, similar to but smaller than primary conidia. Microconidia not observed on PDA or 2% water agar. Zygospores formed in axial alignment after 5 d, mostly globose, smooth, 13.0–25.0 μm, sometimes ellipsoidal, 23.0–29.0 × 20.0–23.0 μm, with a 1.0–3.0 μm thick wall.

Notes – Morphologically, *Conidiobolus shanxiensis* is closely related to *Co. mycophagus*, *Co. incongruus*, and *Co. taihushanensis* but differs by producing smaller zygospores (Drechsler 1960, Srinivasan & Thirumalachar 1965, Nie et al. 2020b). In phylogenetic analyses, it forms a separate branch from these species. While *Co. shanxiensis* clusters with *Co. pseudogonimodes* and *Co. gonimodes* (84% ML support), it is morphologically distinguishable from them: it possesses longer primary conidiophores (30.0–160.0 μm) compared to *Co. gonimodes* (20.0–80.0 μm) and smaller zygospores (13.0–25.0 μm) compared to *Co. pseudogonimodes* (18.0–27.0 μm).

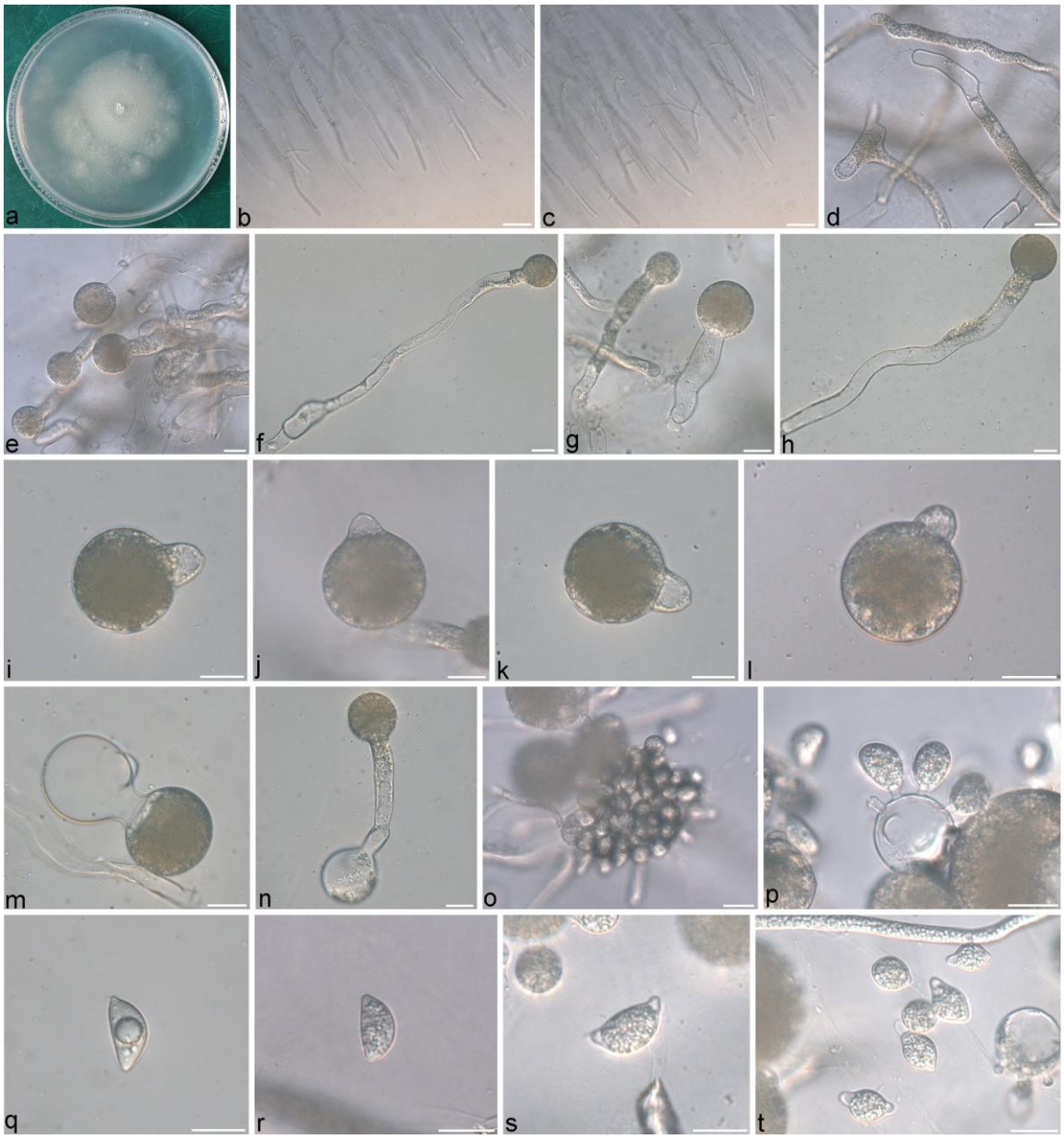

Figure 23 – ***Conidiobolus robustus*** (RCEF 7943, ex-type). a Colony on PDA after 3 d at 21 °C. b, c Mycelia branched at the edge of the colony. d Mycelia. e–h Primary conidiophores bearing a single primary conidium. i–l Primary conidia. m, n Primary conidia bearing a single secondary conidium. o, p Microconidia arising from conidia. q–t Microconidia. Scale bars: b–c = 100 μm, d–t = 20 μm.

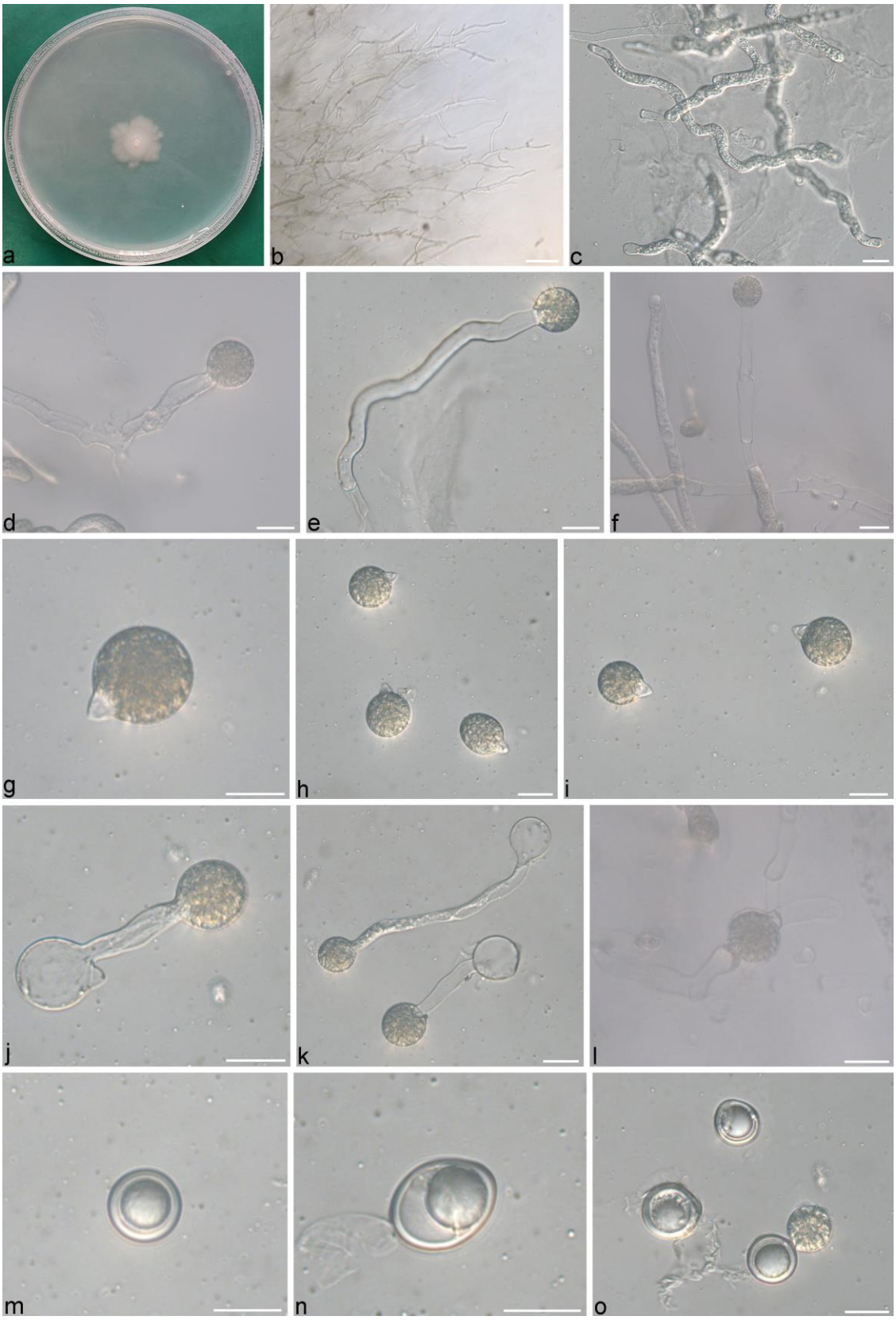

Figure 24 – ***Conidiobolus shanxiensis*** (RCEF 7935, ex-type). a Colony on PDA after 3 d at 21 °C. b Mycelia branched at the edge of the colony. c Mycelia. d–f Primary conidiophores bearing a single primary conidium. g–i Primary conidia. j, k Primary conidia bearing a single secondary conidium. l Zygospores formed in one of the conjugating segments. m–o Mature zygospores. Scale bars: b = 100 μm, c–o = 20 μm.

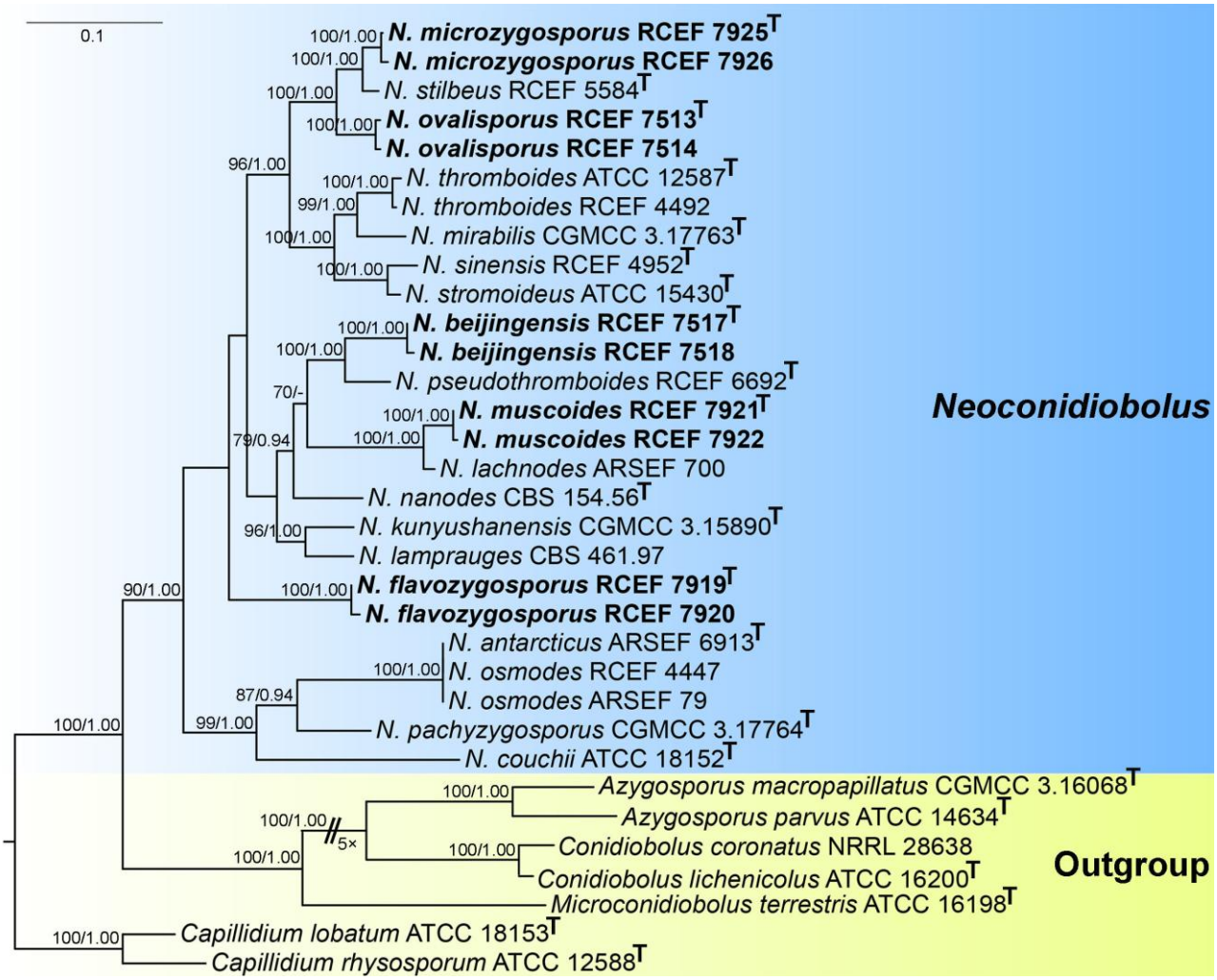

Figure 25 – Phylogenetic tree of the genus *Neoconidiobolus* based on nucLSU, *EFL*, and mtSSU loci. Two species of *Azygosporus*, two species of *Capillidium*, two species of *Conidiobolus* s.s., and one species of *Microconidiobolus* served as outgroups. Maximum Likelihood bootstrap values (≥70%) / Bayesian posterior probabilities (≥0.90) of clades are provided alongside the branches. The scale bar at the top left indicates the number of substitutions per site. New species are indicated in bold. Type taxa are noted on the tree.

Neoconidiobolus beijingensis B. Huang & Y. Nie, sp. nov. Fig 26

MycoBank: MB857676; **Facesoffungi:** FoF17363

Etymology – *beijingensis* (Lat.) refers to the type locality, Beijing City.

Known distribution – Beijing City, China.

Typification – CHINA, Beijing City, Beijing Olympic Forest Park, 40°02′ N, 116°39′ E, from soil, 21 Dec. 2023, *H. Zhao*, holotype BJ 231221-1. Ex-type culture RCEF 7517. GenBank: nucLSU = PV084586; *EFL* = PV107236; mtSSU = PV084634.

Additional specimen examined – CHINA, Beijing City, Beijing Olympic Forest Park, 40°02′ N, 116°39′ E, from soil, 21 Dec. 2023, *H. Zhao*, culture RCEF 7518. GenBank: nucLSU = PV084587; *EFL* = PV107237; mtSSU = PV084635.

Description – Colonies on PDA at 21 °C for 3 d, white, reaching ca 21.0 mm in diameter. Mycelia colorless, 3.0–5.0 µm wide, rarely branched when young, septate to segments when old. Primary conidiophores colorless, arising from hyphae, sometimes widening upward near the tip, 35.0–100.0 × 6.0–9.5 µm, unbranched and producing a single primary conidium. Primary conidia forcibly discharged, colorless, globose to subglobose, 21.0–28.0 × 18.0–24.0 µm, with a basal papilla 5.0–8.5 µm wide and 1.0–5.5 µm long. Secondary conidiophores single, arising from

primary conidia, bearing similar to but smaller replicative conidium than primary conidia. Zygospores formed between two contiguous segments of the same hyphae after 7 d, globose, smooth, 12.5–17.0 µm in diameter with a 1.5–3.0 µm thick wall.

Notes – *Neoconidiobolus beijingensis* is morphologically similar to species such as *N. flavozygosporus*, *N. lachnodes*, *N. mirabilis*, and *N. pesudothromboides*, all of which share comparable conidial sizes. However, it differs from *N. flavozygosporus*, *N. mirabilis*, and *N. pesudothromboides* in having shorter primary conidiophores and smaller zygospores (Nie et al. 2018, 2022b); from *N. lachnodes* by its longer primary conidiophores and absence of chlamydospores (Drechsler 1955b). Phylogenetically, *N. beijingensis* clusters with *N. pesudothromboides* with 100% ML and 1.00 BYPP statistical support (Fig. 25). Sequence similarities between *N. beijingensis* and *N. pesudothromboides* are 93.4% (nucLSU) and 85.4% (*EFL*).

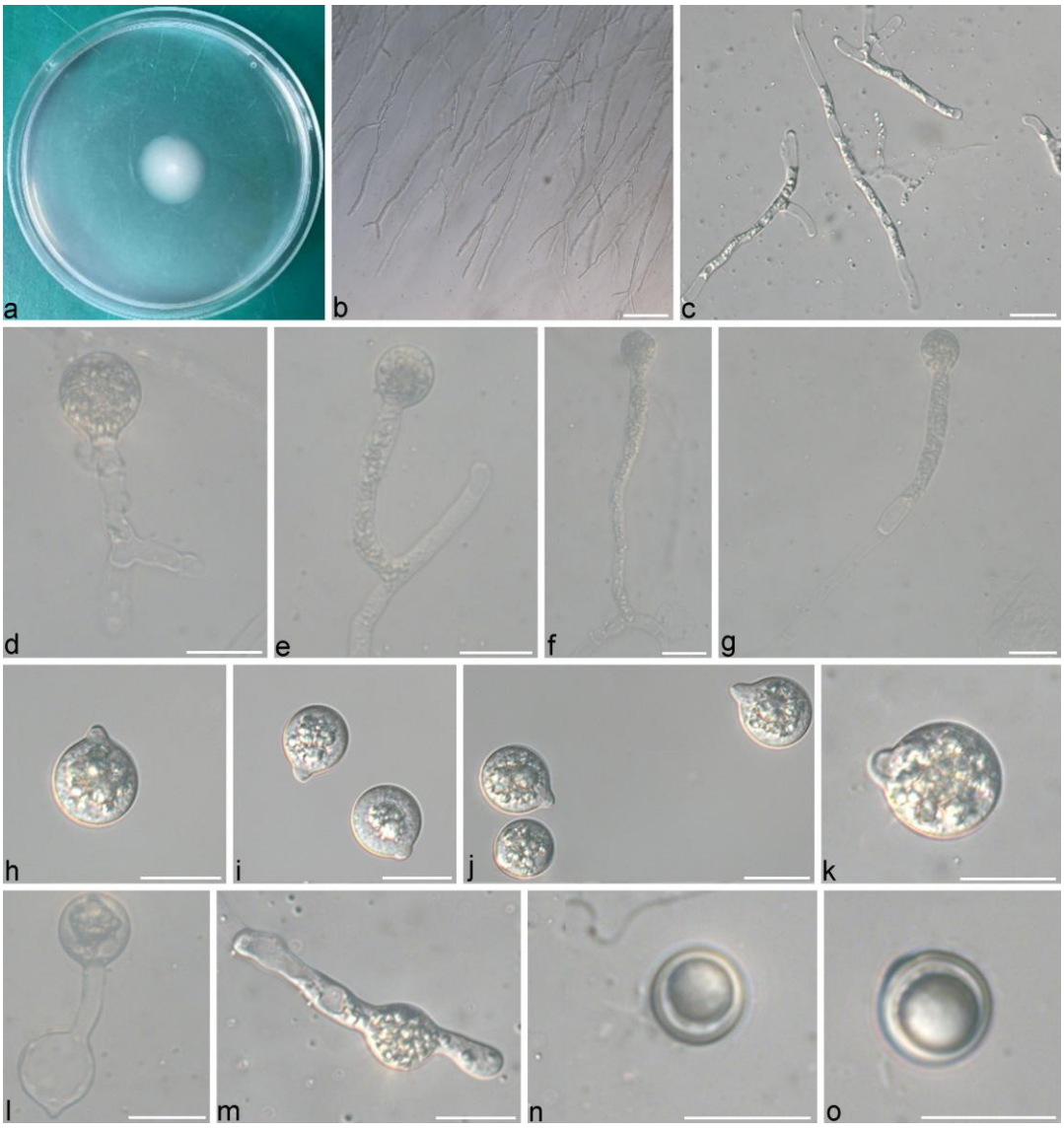

Figure 26 – ***Neoconidiobolus beijingensis*** (RCEF 7517, ex-type). a Colony on PDA after 3 d at 21 °C. b Mycelia unbranched at the edge of the colony. c Mycelia at the old colony. d–g Primary conidiophores bearing a single primary conidium. h–k Primary conidia. l Primary conidia bearing a single secondary conidium. m Zygospores formed between segments of the same hyphae. n, o. Mature zygospores. Scale bars: b = 100 µm, c–o = 20 µm.

Neoconidiobolus flavozygosporus B. Huang & Y. Nie, sp. nov. Fig. 27

MycoBank: MB857677; **Facesoffungi:** FoF17364

Etymology – *flavozygosporus* (Lat.) refers to its yellowish zygospores.

Known distribution – Henan Province, China.

Typification – CHINA, Henan Province, Xinyang City, Xin County, Jinlanshan National Forest Parks, 31°65' N, 114°83' E, from plant debris, 15 Mar. 2024, *Y. Nie*, holotype JLS24031508. Ex-type culture RCEF 7919. GenBank: nucLSU = PV084588; *EFL* = PV107238; mtSSU = PV084636.

Additional specimen examined – CHINA, Henan Province, Xinyang City, Xin County, Jinlanshan National Forest Parks, 31°65' N, 114°83' E, from plant debris, 15 Mar. 2024, *Y. Nie*, culture RCEF 7920. GenBank: nucLSU = PV084589; *EFL* = PV107239; mtSSU = PV084637.

Description – Colonies on PDA at 21 °C for 3 d, white, reaching ca 10.0–16.0 mm in diameter. Mycelia colorless, non-septate when young, distended to segment after 3 d, 8.0–24.0 μm wide, usually branched at the edge of colony. Colony yellowish at the positive and negative of culture. Primary conidiophores colorless, 40.0–190.0 × 7.0–9.5 μm, usually arising from hyphal segments, sometimes widening upward at the tip, producing a single primary conidium. Primary conidia forcibly discharged, colorless, subglobose, with a spherical structure in the centre of spore, 23.0–30.0 × 17.0–26.0 μm, with a flat or small basal papilla 6.5–11.0 μm wide and 2.5–6.0 μm long. Secondary conidia arising from primary conidia, similar to but smaller than primary conidia. Zygospores formed in the same conjugating segments after 5 d, globose, smooth, yellowish, 20.0–26.0 μm in diameter with a wall 2.5–4.0 μm thick.

Notes – Based on the dimensions of primary conidiophores, conidia, and zygospores, *N. flavozygosporus* is morphologically comparable to *N. pseudothromboides*. However, *N. flavozygosporus* differs in its broader hyphal segments and distinctly yellowish zygospores (Nie et al. 2022b). Despite some superficial similarities, it is phylogenetically distant from *N. pseudothromboides* and occupies a separate clade in the *Neoconidiobolus* lineage with 100% ML and 1.00 BYPP statistical support (Fig. 25).

Neoconidiobolus microzygosporus B. Huang & Y. Nie, sp. nov. Fig. 28

MycoBank: MB857678; **Facesoffungi:** FoF17365

Etymology – *microzygosporus* (Lat.) refers to its small zygospores.

Known distribution – Hunan Province, China.

Typification – CHINA, Hunan Province, Ningxiang City, Xiangshan National Forest Parks, 28°10' N, 112°36' E, from plant debris, 14 Mar. 2024, *Y. Nie*, holotype XS24031401. Ex-type culture RCEF 7925. GenBank: nucLSU = PV084590; *EFL* = PV107240; mtSSU = PV084638.

Additional specimen examined – CHINA, Hunan Province, Ningxiang City, Xiangshan National Forest Parks, 28°10' N, 112°36' E, from plant debris, 14 Mar. 2024, *Y. Nie*, culture RCEF 7926. GenBank: nucLSU = PV084591; *EFL* = PV107241; mtSSU = PV084639.

Description – Colonies on PDA at 21 °C for 3 d, white, reaching ca 11.0 mm in diameter. Mycelia colorless, often branched at the edge of colony, 5.5–11.0 μm wide. Primary conidiophores colorless, 35.0–90.0 × 5.0–10.5 μm, usually arising directly from hyphal, rarely widening upward at the tip, producing a single primary conidium. Primary conidia forcibly discharged, colorless, subglobose, 19.0–23.0 × 16.0–20.5 μm, with a basal papilla 3.0–7.0 μm wide and 1.0–3.0 μm long. Secondary conidia arising from primary conidia, similar to but smaller than primary conidia. Zygospores formed in the same conjugating segments after 10 d, globose, smooth, 8.5–20.5 μm in diameter with a wall 0.5–2.0 μm thick.

Notes – *Neoconidiobolus microzygosporus* is morphologically related to *N. kunyushanensis*, *N. lamprauges*, *N. pachyzygosporus*, and *N. stilbeus* owing to their similar conidial sizes. However, it differs from *N. kunyushanensis* and *N. pachyzygosporus* by having shorter primary conidiophores and smaller zygospores (Nie et al. 2018, 2021), from *N. lamprauges* by its smaller zygospores and more branched mycelium at the colony margin (Drechsler 1953a), and from *N. stilbeus* by lacking mycelial strands (Nie et al. 2016), although they cluster together in phylogenetic trees with 100%

ML and 1.00 BYPP (Fig. 25). Sequence similarities between *N. microzygosporus* and *N. stilbeus* are 96.4% (nucLSU) and 93.3% (*EFL*).

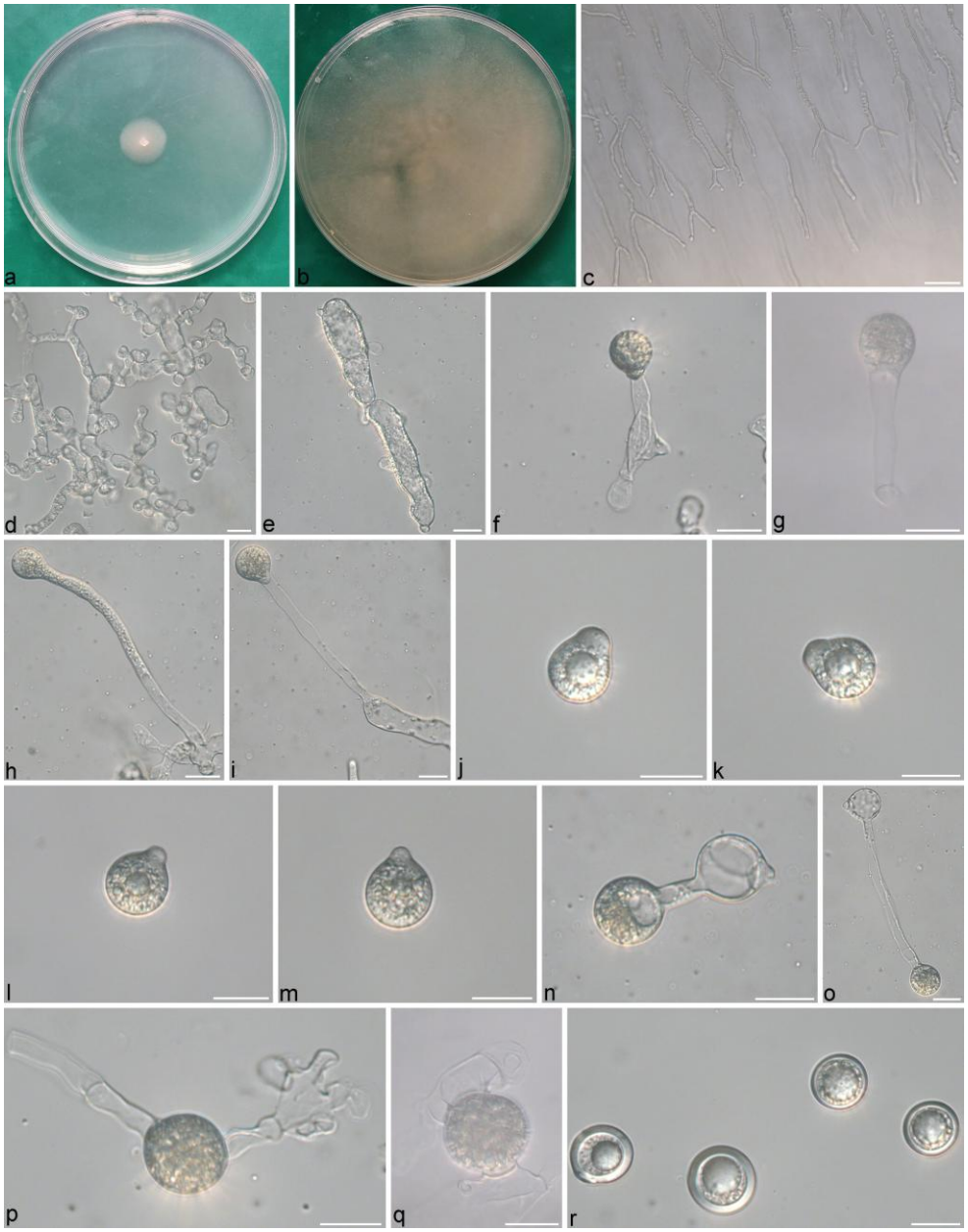

Figure 27 – ***Neoconidiobolus flavozygosporus*** (RCEF 7919, ex-type). a Colony on PDA after 3 d at 21 °C. b Colony on PDA after 12 d at 21°C. c Mycelia often branched at the edge of the colony. d, e Mycelia segments. f–i Primary conidiophores bearing a single primary conidium. j–m Primary conidia. n, o Primary conidia bearing a single secondary conidium. p, q Zygospores formed in the same conjugating segments. r. Mature zygospores. Scale bars: c = 100 µm, d–s = 20 µm.

Neoconidiobolus muscoides B. Huang & Y. Nie, sp. nov. Fig. 29

MycoBank: MB857679; **Facesoffungi:** FoF17366

Etymology – *muscoides* (Lat.) refers to the moss-like appearance of its mycelia.

Known distribution – Hubei Province, China.

Typification – CHINA, Hubei Province, Xiaogan City, Xiaochang County, Shuangfengshan National Forest Parks, 31°11' N, 114°13' E, from mosses, 12 Mar. 2024, *Y. Nie*, holotype SFS24031209. Ex-type culture RCEF 7921. GenBank: nucLSU = PV084592; *EFL* = PV107242; mtSSU = PV084640.

Additional specimen examined – CHINA, Hubei Province, Xiaogan City, Xiaochang County, Jiangjiawan Town, 31°09' N, 114°09' E, from mosses, 12 Mar. 2024, *Y. Nie*, culture RCEF 7922. GenBank: nucLSU = PV084593; *EFL* = PV107243; mtSSU = PV084641.

Description – Colonies on PDA at 21 °C for 3 d, white, reaching ca 17.0 mm in diameter. Mycelia colorless, usually branched at the edge of colony, frequently appearing pronouncedly vacuolated at the initial growth stage, 4.5–8.0 µm wide. Mycelia forms mosses-like shape after 4–5 d. Aerial hyphae form after 10 d, 3.0–5.0 µm wide. Primary conidiophores colorless, 80.0–130.0 × 5.0–11.0 µm, usually arising directly from hyphal, sometimes widening upward at the tip, producing a single primary conidium. Primary conidia forcibly discharged, colorless, globose to subglobose, 19.0–24.0 × 16.0–21.0 µm, with a basal papilla 4.0–8.0 µm wide and 1.5–5.0 µm long. Secondary conidia arising from primary conidia, similar to but smaller than primary conidia. Resting spores not observed after 30 d.

Notes – By virtue of its primary conidial size and copious aerial hyphae, *N. muscoides* is morphologically similar to *N. lachnodes* and *N. stilbeus*. It differs from *N. stilbeus* by lacking zygospores and mycelial strands (Nie et al. 2016). Although *N. muscoides* clusters phylogenetically with *N. lachnodes* (ARSEF 700) with strong support (100% ML, 1.00 BYPP, Fig. 25), it can be distinguished by its longer primary conidiophores and absence of chlamydospores (Drechsler 1955b). The nucLSU sequence similarity between *N. muscoides* and *N. lachnodes* is 93.6%.

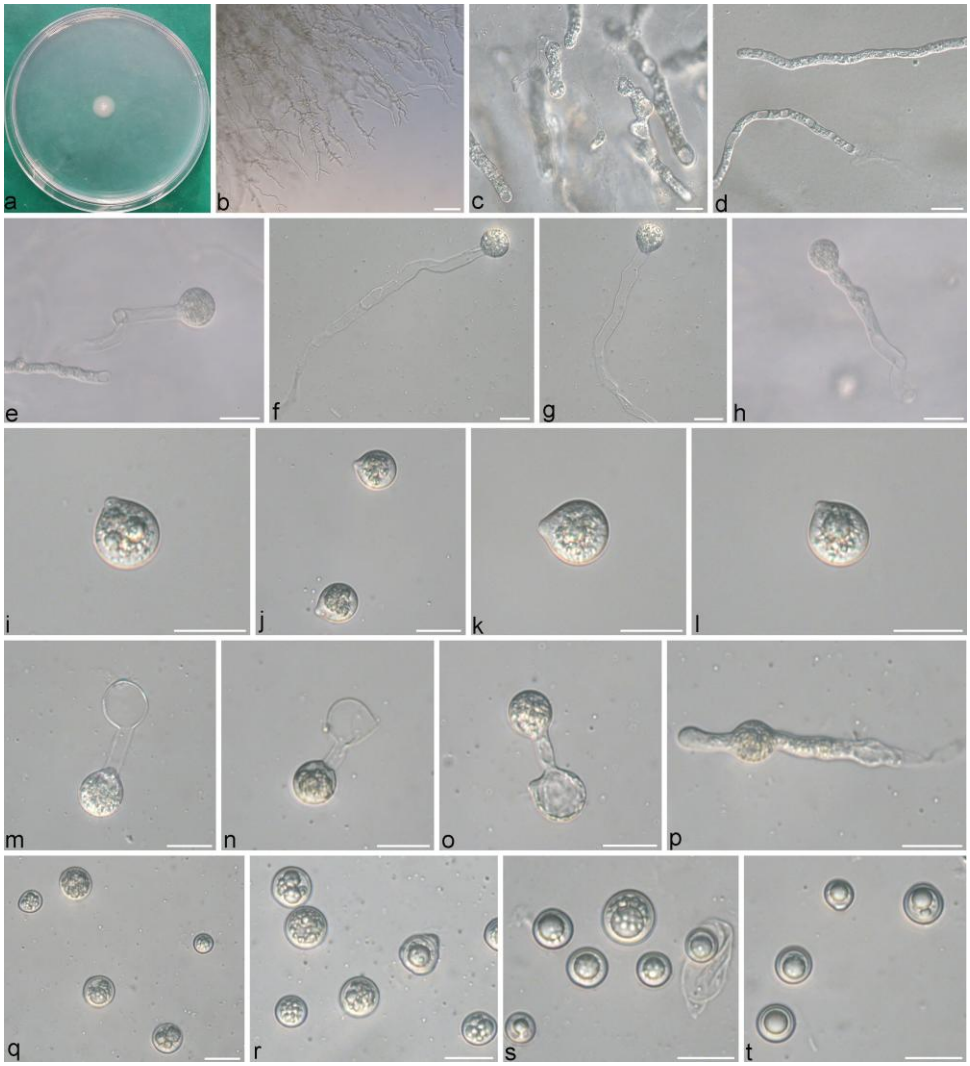

Figure 28 – ***Neoconidiobolus microzygosporus*** (RCEF 7925, ex-type). a Colony on PDA after 3 d at 21 °C. b Mycelia often branched at the edge of the colony. c, d Hyphae. e–h Primary conidiophores bearing a single primary conidium. i–l Primary conidia. m–o Primary conidia

bearing a single secondary conidium. p Zygospores formed in the same conjugating segments. q, r Immature zygospores. s, t Mature zygospores. Scale bars: b = 100 μm, c–t = 20 μm.

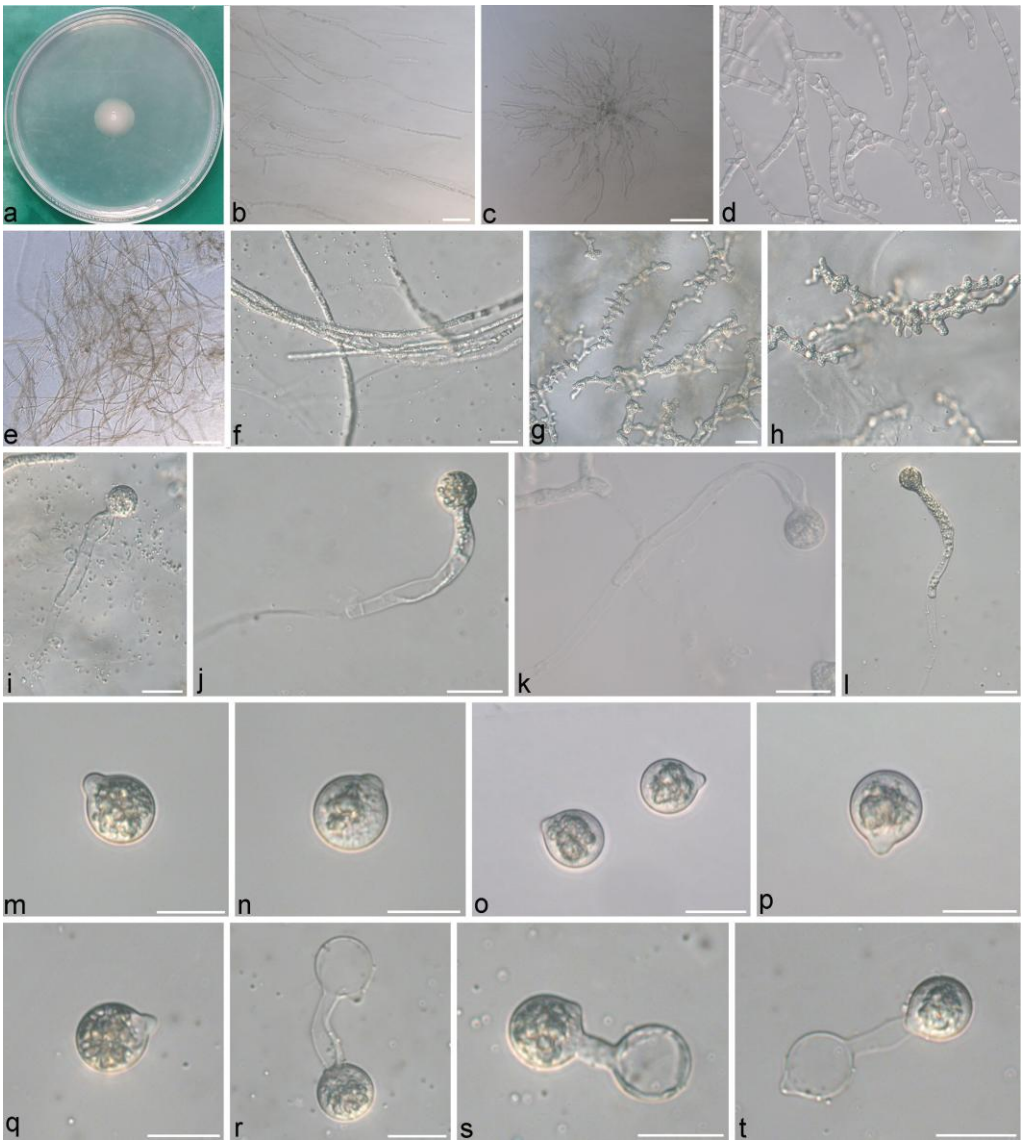

Figure 29 – ***Neoconidiobolus muscoides*** (RCEF 7921, ex-type). a Colony on PDA after 3 d at 21 °C. b Mycelia often branched at the edge of the colony. c, d Young mycelia. e, f Aerial hyphae. g, h Mosses-like mycelia. i–l Primary conidiophores bearing a single primary conidium. m–q Primary conidia. r–t Primary conidia bearing a single secondary conidium. Scale bars: b, c, e = 100 μm, d, f –t = 20 μm.

Neoconidiobolus ovalisporus B. Huang & Y. Nie, sp. nov. Fig. 30

MycoBank: MB857680; **Facesoffungi:** FoF17367

Etymology – *ovalisporus* (Lat.) refers to its oval primary conidia.

Known distribution – Beijing City and Jiangsu Province, China.

Typification – CHINA, Jiangsu Province, Jurong City, Tianwang Town, 31°42' N, 119°16' E, from plant debris, 24 Mar. 2023, *Y. Nie*, holotype JS23032401. Ex-type culture RCEF 7513. GenBank: nucLSU = PV084584; *EFL* = PV107234; mtSSU = PV084632.

Additional specimen examined – CHINA, Beijing City, Beijing Olympic Forest Park, 40°12′ N, 116°23′ E, from plant debris, 21 Dec. 2023, *H. Zhao*, ex-paratype RCEF 7514. GenBank: nucLSU = PV084585; *EFL* = PV107235; mtSSU = PV084633.

Description – Colonies on PDA at 21 °C for 3 d, white, reaching ca 12.0 mm in diameter. Mycelia white, 4.0–8.5 µm wide, unbranched when young. Primary conidiophores colorless, 27.0–115.0 × 5.0–9.0 µm, arising from hyphae without widening upward near the tip, producing a single primary conidium. Primary conidia forcibly discharged, colorless, mostly oval, sometimes subglobose, 17.0–23.0 × 15.0–18.0 µm, with a basal papilla 4.0–7.5 µm wide and 1.0–4.0 µm long. Secondary conidia arising from primary conidia with short or long secondary conidiophores, similar to but smaller than the primary conidia. Zygospores formed in the same conjugating segments, globose, smooth, 11.0–18.0 µm in diameter with a 1.0–2.0 µm thick wall.

Notes – Morphologically, *N. ovalisporus* is allied to *N. lamprauges* and *N. stilbeus* by virtue of similarly sized primary conidia and zygospores (Drechsler 1953a, Nie et al. 2016). However, *N. ovalisporus* differs from *N. lamprauges* in its oval primary conidia and lack of lustrous mycelium; the two species are also phylogenetically distant (Fig. 25). Despite clustering with *N. stilbeus*, *N. ovalisporus* lacks mycelial strands and displays distinctly oval conidia, setting it apart from *N. stilbeus*. Phylogenetically, *N. ovalisporus* is cluster with *N. microzygosporus* and *N. stilbeus* with 100% ML and 1.00 BYPP (Fig. 25).

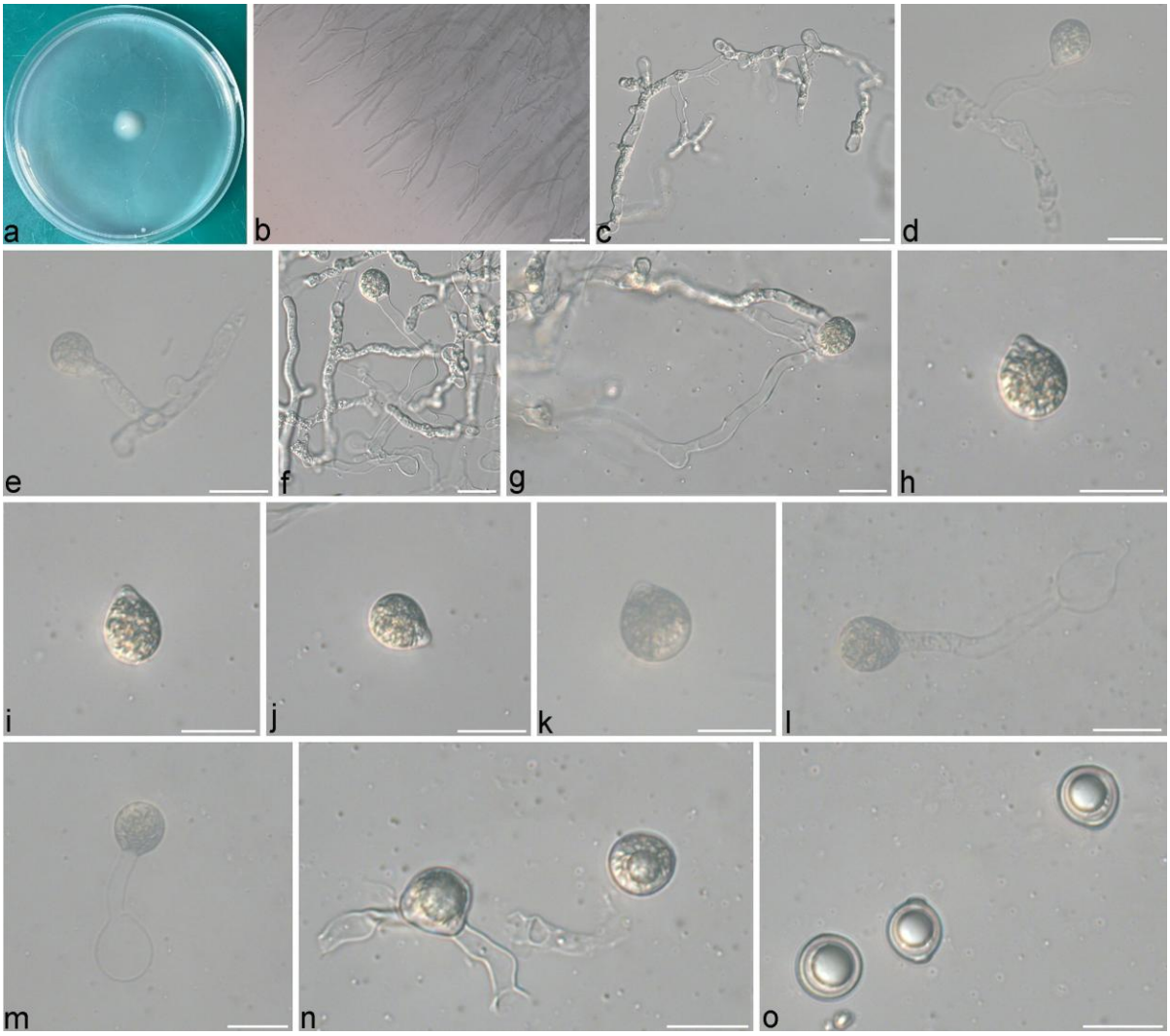

Figure 30 – ***Neoconidiobolus ovalisporus*** (RCEF 7513, ex-type). a Colony on PDA after 3 d at 21 °C. b Mycelia unbranched at the edge of the colony. c Mycelia. d–g Primary conidiophores bearing a single primary conidium. h–k Primary conidia with different shapes. l, m Primary conidia bearing a single secondary conidium. n Zygospores formed in the same conjugating segments. o. Mature zygospores. Scale bars: b = 100 µm, c–o = 20 µm.

Proposal of two new combinations

Callaghania adiaereta (Drechsler) B. Huang & Y. Nie, comb. nov.
MycoBank: MB857681

Basionym: *Conidiobolus adiaeretus* Drechsler, Journal of the Washington Academy of Science 43 (1953). MycoBank: MB119780.

Homotypic synonym: *Capillidium adiaeretum* (Drechsler) B. Huang & Y. Nie, MycoKeys 66: 63 (2020). MycoBank: MB831602.

Callaghania bangalorensis (Sriniv. & Thirum.) B. Huang & Y. Nie, comb. nov.
MycoBank: MB857682

Basionym: *Conidiobolus bangalorensis* Sriniv. & Thirum., Mycologia 59(4): 702 (1967). MycoBank: MB328748.

Homotypic synonym: *Capillidium bangalorense* (Sriniv. & Thirum.) B. Huang & Y. Nie, MycoKeys 66: 71 (2020). MycoBank: MB831607.

Morphological characteristics of *Conidiobolus* s.l.

In this study, we describe 23 new species, including two *Capillidium* species, 16 *Conidiobolus* s.s. species, and five *Neoconidiobolus* species. To better understand each species, we provide an updated index (Table S2) and identification keys for all recognized species in each genus.

Identification keys of *Conidiobolus* s.l. worldwide

Key to the species of *Azygosporus*

1a. Primary conidiophores longer, 37.0–150.0 μm, basal papilla prominent.....*A. macropapillatus* (Cai et al. 2021)
1b. Primary conidiophores shorter, 15.0–30.0 μm, basal papilla not prominent.....*A. parvus* (Drechsler 1962)

Key to the species of *Callaghanii*

1a. Primary conidia larger, up to 46.0 μm, chlamydospores produced .....*C. adiaereta* (Drechsler 1953a)
1b. Primary conidia smaller, less than 25.0 μm, zygospores produced ..... *C. bangalorensis* (Srinivasan & Thirumalachar 1967)

Key to the species of *Capillidium*

1a. Capilliconidia not observed.....2
1b. Capilliconidia produced.....3
2a. Primary conidiophores longer, 120.0–280.0 μm, primary conidia larger, 26.0–37.0 × 22.0–31.0 μm.....***C. huangfushanense***
2b. Primary conidiophores shorter, 80.0 μm, primary conidia smaller, 24.0–30.0 × 19.0–25.0 μm.....***C. jinlanshanense***
3a. Slender conidiophores branched at the base, bearing 2–6 terminal capilliconidia ..... *C. heterosporum* (Drechsler 1953b)
3b. Slender conidiophores unbranched at the base, bearing a single capilliconidium 4
4a. Resting spores of zygospores produced, yellowish, mostly wrinkled, sometimes smooth 5
4b. Resting spores not observed 6
5a. Primary conidia and zygospores larger, more than 30.0 μm 7
5b. Primary conidia and zygospores smaller, less than 25.0 μm.....*C. rugosum* (Drechsler 1955b)
6a. Primary conidia larger, more than 30.0 μm.....8

6b. Primary conidia smaller, less than 26.0 µm 9
7a. Capilliconidia up to 37.0 µm ..... *C. macrocapilliconidium* (Nie et al. 2022a)
7b. Capilliconidia less than 32.0 µm.....*C. rhysosporum* (Drechsler 1954)
8a. Capilliconidia larger, 17.0–32.0 × 10.0–15.0 µm, primary conidiophores longer, 50.0–240.0 µm.....*C. jiangsuense* (Nie et al. 2022a)
8b. Capilliconidia smaller, 10.0–18.0 × 6.0–10.0 µm, primary conidiophores shorter, 15.0–50.0 µm.....*C. denaeosporum* (Drechsler 1957c)
9a. Primary conidia larger, 21.0–26.0 × 20.0–24.0 µm, capilliconidia larger, 18.0–25.0 × 8.0–10.0 µm.....*C. lobatum* (Srinivasan & Thirumalachar 1968b)
9b. Primary conidia smaller, 9.0–18.0 × 7.3–14.0 µm, capilliconidia smaller, 8.8–12.0 × 5.0–7.5 µm..... *C. pumilum* (Drechsler 1955a)

Key to the species of *Conidiobolus* s.s.

1a. Villose resting spores produced.....2
1b. Villose resting spores not produced 5
2a. zygospores produced.....*C. srinivasanii* (Pawar et al. 2025)
2b. zygospores not produced.....3
3a. Villose longer, up to 15.0 µm.....*C. longivillosus* (Wang et al. 2025)
3b. Villose shorter, less than 10.0 µm.....4
4a. Microconidia globose, elliptical to half–moon shapes.....*C. lunulus* (Goffre et al. 2020)
4b. Microconidia globose to subglobose.....*C. coronatus* (Batko 1964)
5a. Primary conidiophores produced from cushion mycelia.....*C. lichenicolus* (Srinivasan & Thirumalachar 1968a)
5b. Primary conidiophores not produced from cushion mycelia.....6
6a. Each zygospore in a position separated by a short, but relatively constant, distance from a lateral conjugation outgrowth or beak.....*C. iuxtagenitus* (Waters and Callaghan 1989)
6b. Each zygospore in a position not separated by a short, but relatively constant, distance from a lateral conjugation outgrowth or beak.....7
7a. Primary conidiophores branched, produced more than two primary conidia.....8
7b. Primary conidiophores unbranched, produced a single primary conidium.....9
8a. Resting spores observed.....10
8b. Resting spores not observed.....11
11a. Primary conidiophores longer, 20.0–125.0 µm, primary conidia upto 44.0 µm.....*C. megalotocus* (Drechsler 1956)
11b. Primary conidiophores shorter, 20.0–30.0 µm, primary conidia smaller, less than 29.0 µm.....*C. polytocus* (Drechsler 1955c)
10a. Microconidia observed.....12
10b. Microconidia not observed.....13
12a Primary conidiophores longer, 68.0–270.0 µm, primary conidia larger, 42.0–55.0 × 33.0–45.0 µm.....*C. polysporus* (Nie et al. 2023)
12b. Primary conidiophores shorter, 20.0–80.0 µm, primary conidia smaller, 11.0–33.0 × 12.0–39.0 µm.....*C. gonimodes* (Drechsler 1961)
13a. Zgyospores larger, more than 29.0 µm.....14
13b. Zgyospores smaller, less than 27.0 µm.....***C. pseudogonimodes***
14a. Secondary conidiophores bearing two replicative conidium.....***C. ramiconidiophorus***
14b. Secondary conidiophores bearing one replicative conidium.....*C. taihushanensis* (Nie et al. 2020b)
9a. Primary conidiophores longer, more than 100.0 µm.....15
9b. Primary conidiophores shorter, less than 100.0 µm.....16
15a. Primary conidia larger, more than 40.0 µm.....17
15b. Primary conidia smaller, less than 40.0 µm.....18

17a. Microconidia observed.....19
17b. Microconidia not observed.....20
19a. Resting spores observed.....21
19b. Resting spores not observed.....22
21a. Only chlamydospores produced.....***C. hippocrepiformis***
21b. Only zygospores produced.....23
23a. Primary conidia larger, more than 50.0 μm.....24
23b. Primary conidia smaller, less than 42.0 μm.....25
24a. Two or three secondary conidia arising from primary conidia, zygospores larger, up to 46.0 μm.....***C. macrozygosporus***
24b. One secondary conidia arising from primary conidia, zygospores smaller, less than 40.0 μm.....26
26a. Primary conidiophores longer, 45.0–200.0 μm, zygospores smaller, 24.0 × 32.0 μm.....***C. kunmingensis***
26b. Primary conidiophores shorter, 50.0–200.0 μm, zygospores larger, 26.0 × 40.0 μm.....*C. macrosporus* (Srinivasan & Thirumalachar 1967)
25a. Primary conidiophores longer, 38.0–254.0 μm, zygospores smaller, 25.0 × 40.0 μm.....*C. bifurcatus* (Nie et al. 2020b)
25b. Primary conidiophores shorter, 30.0–130.0 μm, zygospores larger, 15.0–40.0 × 18.0–45.0 μm.....*C. incongruus* (Drechsler 1960)
22a. Microconidia larger, up to 32.0 μm.....***C. robustus***
22b. Microconidia smaller, less than 16.0 μm.....27
27a. Primary conidia larger, 25.0–40.0 × 31.0–55.0 μm.....*C. variabilis* (Nie et al. 2020b)
27b. Primary conidia smaller, 6.5–33.0 × 8.0–40.0 μm.....*C. firmipilleus* (Drechsler 1953b)
20a. Primary conidia larger, 45.0–67.0 × 42.0–58.0 μm.....*C. marcoconidius* (Nie et al. 2024)
20b. Primary conidia smaller, less than 49.0 μm.....28
28a. Resting spores not observed.....*C. longiconidiophorus* (Nie et al. 2023)
28b. Resting spores observed.....29
29a. Only chlamydospores produced.....*C. dabieshanensis* (Nie et al. 2017)
29b. Only zygospores produced.....30
30a. Primary conidiophores shorter, less than 130.0 μm.....*C. polyspermus* (Drechsler 1961)
30b. Primary conidiophores longer, more than 200.0 μm.....31
31a. Mycelia 6.0–18.0 μm, mycelium often formed near on one side or both side of conjugating segments.....***C. proximus***
31b. Mycelia 6.0–1q.0 μm, mycelium not formed near on one side or both side of conjugating segments.....***C. pachyconidiophorus***
18a. Resting spores not observed.....***C. oxyconidius***
18b. Resting spores observed.....32
32a. Azygospores produced.....***C. hainanensis***
32b. Azygospores not produced.....33
33a. Chlamydospores and zygospores produced.....34
33b. Only zygospores produced.....35
34a. Primary conidiophores shorter, 30.0–135.0 μm, primary conidia smaller, 26.0–32.0 × 22.0–29.0 μm.....***C. amphitus***
34b. Primary conidiophores longer, 40.0–200.0 μm, primary conidia larger, 23.0–34.0 × 26.0–38.0 μm.....*C. humicolus* (Srinivasan & Thirumalachar 1961)
35a. Microconidia observed.....*C. mycophagus* (Srinivasan & Thirumalachar 1965)
35b. Microconidia not observed.....36
36a. Primary conidiophores longer, 30.0–160.0 μm, zygospores globose to ellipsoidal.....***C. shanxiensis***
36b. Primary conidiophores shorter, 40.0–125.0 μm, zygospores globose.....***C. lii***
16a. Microconidia not observed.....37

16b. Microconidia observed.....38
37a. Zygspores larger, up to 40.0 µm.....***C. planibasalis***
37b. Zygspores shorter, less than 30.0 µm.....39
39a. Primary conidiophores longer, 30.0–95.0 µm, primary conidia larger, 30.0–41.0 × 24.0–36.0 µm.....*C. jiangxiensis* (Nie et al. 2024)
39b. Primary conidiophores shorter, 10.0–30.0 µm, primary conidia smaller, 15.0–18.0 × 17.0–21.0µm.....*C. khandalensis* (Srinivasan & Thirumalachar 1962b)
38a. Resting spores not observed.....***C. pectiniformis***
38b. Resting spores observed.....40
40a. Zygospores formed in axial alignment with one or both conjugating segments...*C. brefeldianus* (Couch 1939)
40b. Zygospores formed in axial alignment with one conjugating segments.....41
41a. Primary conidia larger, 30.0–42.0 × 23.0–33.0 µm, papilla longer, up to 11.0 µm.....***C. longibasalis***
41b. Primary conidia smaller, 20.0–26.0 × 25.0–30.0 µm, papilla shorter, less than 8.0 µm.....*C. mycophilus* (Srinivasan & Thirumalachar 1965)

Key to the species of *Microconidiobolus*

1a. Primary conidia globose to obovoid, larger than 12.0 µm, producing neither capilliconidia nor microconidia, chlamydospores or zygospores produced.....2
1b. Primary conidia small, less than 12.0 µm, resting spores not observed, only 2 nuclei within the primary conidia.....*M. terrestris* (Srinivasan & Thirumalachar 1968a)
2a. Primary conidiophores longer, 30.0–50.0 µm, primary conidia larger, 13.0–16.0 × 17.0–22.0 µm, only chlamydospores produced.....*M. nodosus* (Srinivasan & Thirumalachar 1967)
2b. Primary conidiophores shorter, 15.0–30.0 µm, primary conidia smaller, 4.0–14.0 × 5.0–19.0 µm, only zygosporus produced.....*M. paulus* (Drechsler 1957a)

Key to the species of *Neoconidiobolus*

1a. Forming mycelial strand with 2–6 aerial phototropic hyphae .....*N. stilbeus* (Nie et al. 2016)
1b. Not forming mycelial strand 2
2a. Primary conidiophores produced from cushion mycelia..... 3
2b. Primary conidiophores not produced from cushion mycelia..... 4
3a. Usually branched at edge mycelia, much shorter conidiophores (12.0–40.0 µm) produced .....*N. stromoideus* (Srinivasan & Thirumalachar 1962a)
3b. Rarely branched at edge mycelia, much longer conidiophores (32.5–110.0 µm) produced .....*N. sinensis* (Nie et al. 2012)
4a. Mycelia forms mosses–like shape, resting spores not observed.....***N. muscoides***
4b. Mycelia not forms mosses–like shape, resting spores produced.....5
5a. Primary conidia mostly oval.....***N. ovalisporus***
5b. Primary conidia without oval.....6
6a. Primary conidia oboviod.....7
6b. Primary conidia globose to subglobose.....8
7a. Azygospores produced.....*N. vermicola* (Mcculloch 1977)
7b. Zygospores produced.....9
9a. Primary conidia larger, 22.0–30.0 × 25.0–37.0 µm, zygospores larger, 13.0–37.0 µm.....*N. osmodes* (Drechsler 1954)
9b. Primary conidia smaller, 8.0–14.0 × 10.0–17.0 µm, zygospores smaller, 7.0–14.0 µm.....*N. nanodes* (Drechsler 1955b)

8a. Sepcially forming zygospores among two to four adjacent hyphal segments.....*N. mirabilis* (Nie et al. 2018)
8b. Forming zygospores among two adjacent hyphal segments.....10
10a. Zygospores with a thick double wall, more than 3.2 μm.....*N. pachyzygosporus* (Nie et al. 2018)
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11a. Zygospores larger, more than 25.0 μm.....12
11b. Zygospores smaller, less than 20.5 μm.....13
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18b. Primary conidia smaller, less than 23.0 μm, zygospores produced.....***N. microzygosporus***

DISCUSSION

Early attempts to classify *Conidiobolus* based on secondary conidial morphology (Ben-Ze'ev & Kenneth 1982, Humber 1989) provided a foundation for understanding its diversity but also revealed inconsistencies, particularly as more complex secondary conidia (e.g., microconidia and capilliconidia) were detected within single species (Callaghan et al. 2000). Subsequent molecular work employing nucLSU, SSU, *EFL*, and mtSSU (Nie et al. 2020a) led to the recognition of multiple new genera alongside *Conidiobolus* s.s., culminating in three family-level groupings (*Capillidiaceae*, *Conidiobolaceae*, *Neoconidiobolaceae*; Gryganskyi et al. 2022). Nonetheless, the precise placement of *Microconidiobolus*, which appears phylogenetically distinct from *Conidiobolus* s.s. and *Azygosporus*, remained contentious (Gryganskyi et al. 2022, Seto & James 2024). Equally problematic has been the reconciliation of certain taxa (e.g., *Co. iuxtagenitus*, *Ca. adiaeretum*, *Ca. bangalorense*) that display unusual morphological traits or ambiguous phylogenetic affinities (Waters & Callaghan 1989, Nie et al. 2022, 2023). These unresolved issues highlight the need for broader taxon sampling, more robust molecular markers, and genomic-scale analyses to elucidate evolutionary relationships in *Conidiobolus* s.l.

Increasingly, phylogenomic analyses are being used to elucidate the evolutionary history of fungi (de Beer et al. 2022, Li et al. 2023, Liu et al. 2024, Razaghi et al. 2024). Accordingly, our study significantly advances the classification of *Conidiobolus* s.l. by incorporating 43 newly sequenced genomes, along with multi-locus phylogenetic analyses and divergence time estimates. This holistic approach has addressed several long-standing taxonomic issues. First, we propose recognizing *Microconidiobolus* as a separate family, *Microconidiobolaceae*, based on its well-supported monophyly, distinctive morphological features, such as small primary conidia with countable nuclei, and its divergence time of approximately 279 Mya. This proposal aligns with the divergence times of other established families, reinforcing its evolutionary distinctiveness. Second, we introduce a new genus, *Callaghania*, within the *Capillidiaceae* to accommodate species that uniquely produce both microconidia and capilliconidia. Our phylogenomic and divergence-time

analyses consistently place *Callaghania* as a separate lineage within *Capillidiaceae*, which underscores its significant evolutionary divergence from other genera in the family.

Despite this progress, we observed instances where morphological characters did not align neatly with phylogenetic groupings. In *Conidiobolus* s.s., for example, species such as *Co. amphitus*, *Co. planibasalis*, and *Co. shanxiensis* have yet to exhibit the microconidia often considered diagnostic for that clade (Nie et al. 2024). A similar issue arose in *Capillidium*, where *Ca. huangfushanense* and *Ca. jinlanshanense*, which are expected to form capilliconidia, did not consistently produce them under laboratory conditions. Such inconsistencies may reflect either a narrow range of culture conditions that fail to induce certain spore forms or genuine phenotypic plasticity linked to genetic variation. High-quality genome sequencing and fine-scale comparative analyses will be crucial for deciphering the genetic underpinnings of these variable traits, thereby clarifying whether they reflect cryptic diversity or simply incomplete sampling of morphological states.

Previously considered a single species, *Conidiobolus coronatus* exhibits substantial morphological and genetic diversity. Our recent work suggests that cryptic species likely exist within this complex, a notion supported by the recent discovery of a fourth *Conidiobolus* species with villose conidia from China (Wang et al. 2025). We also propose developing unique taxonomic indices, such as maximum growth temperature and the length of villi around villose conidia, to further clarify the boundaries of the *Co. coronatus* complex. According to previous studies of other fungal complex species (McTaggart et al. 2021, Liu et al. 2022, Han et al. 2023), phylogenomic analyses based on a broader collection of strains from diverse geographical locations are necessary to resolve the full extent of diversity within this species.

Beyond *Conidiobolus* s.l., our nucLSU, *EFL*, and mtSSU phylogenies corroborate earlier studies in revealing distinct clades within the *Entomophthoraceae* (Gryganskyi 2012, Nie et al. 2020a). The subfamilies *Entomophthoroideae* and *Erynioideae* appear as two primary lineages, although genera such as *Erynia*, *Furia*, and *Pandora* sometimes exhibit unstable topologies (Keller & Petrini 2005, Humber 2012). The status of *Batkoaceae* remains uncertain herein, its divergence time (~127 Mya) suggests it may not warrant familial rank, echoing other recent findings (Seto & James 2024). Our results also confirm that *Basidiobolus*, historically placed variably within or outside the entomophthoroid fungi (Nagahama et al. 1995, Jensen et al. 1998, Spatafora et al. 2016, 2017, Davis et al. 2019, Wang et al. 2020, 2023), occupies a distinct position at the base of *Zoopagomycota*. Further taxon sampling and high-coverage genomic data will be needed to resolve fully its relationships to other early-diverging fungal lineages.

In line with our initial objectives (see Introduction), this study advances the taxonomy of *Conidiobolus* s.l. by integrating phylogenomics, multi-locus analyses, and divergence time estimations. We define a new family, *Microconidiobolaceae*, establish the genus *Callaghania* to house species exhibiting unique conidial forms, and describe 23 new species from China. Collectively, these findings refine our understanding of entomophthoroid fungal evolution, with divergence estimates placing family-level radiations between ~281 and 303 Mya. Beyond resolving longstanding taxonomic ambiguities, our updated classification and morphological index provide a robust framework for investigating the ecology, pathogenicity, and potential biocontrol applications of this important fungal group. Further research leveraging high-quality genomes and broader sampling will undoubtedly yield deeper insights into the evolutionary processes shaping *Conidiobolus* s.l. and early-diverging fungi more broadly across diverse ecological niches.

ACKNOWLEDGEMENTS

This study was supported by the National Natural Science Foundation of China (Nos. 32370007 and 31900008).

DECLARATION OF COMPETING INTEREST

The authors declare no conflicts of interest regarding this article.

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