DOI 10.12905/0380.sydowia75-2022-0013 Published online 29 November 2022

Honghemyces pterolobii, gen. et sp. nov. (Bezerromycetaceae, Tubeufiales), a new ascomycetous fungus from *Pterolobium macropterum* in Honghe, China

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Wanasinghe D.N., Bezerra J.D.P., Xu J. & Mortimer P.E. (2021) *Honghemyces pterolobii,* gen. et sp. nov. (Bezerromycetaceae, Tubeufiales), a new ascomycetous fungus from *Pterolobium macropterum* in Honghe, China. – Sydowia 75: 13–21.

This study introduces the new genus *Honghemyces* in the family Bezerromycetaceae (Tubeufiales) based on morphological features and multi-locus (ITS, LSU, SSU, *tef*1-α and *rpb*2) phylogenetic analyses. This fungus was found on dead twigs of *Pterolobium macropterum* (Fabaceae) during an expedition to Honghe County in China. Phylogenetically, *Honghemyces* and *Bezerromyces* are related genera in Bezerromycetaceae. *Honghemyces pterolobii* is morphologically characterised by the production of semi-immersed to superficial, subglobose and glabrous ascomata, clavate, short pedicellate asci with a minute ocular chamber, ellipsoidal, hyaline and three-septate ascospores and globose to subglobose chlamydospores forming a chain of a torulose-like structure.

Keywords: Dothideomycetes, Greater Mekong Subregion, microfungi, molecular phylogeny, taxonomy, Yunnan. – 1 new genus, 1 new species.

The order Tubeufiales was introduced by Boonmee et al. (2014) based on morphological features and multi-loci phylogenetic analyses. Currently, Tubeufiales includes 55 genera classified in three families, with known teleomorphic and anamorphic species (Hongsanan et al. 2020, Wijayawardene et al. 2020). Over the past few years, mycologists have worked on the taxonomy of Tubeufiales based on morphology, phylogenetic analyses and divergence time estimations (e.g., Liu et al. 2017, Lu et al. 2018, Hongsanan et al. 2020). Tubeufiaceous taxa generally have saprophytic modes of life in terrestrial and aquatic habitats, few species are reported as endophytes and they are also sources of bioactive molecules, especially the helicosporous members (Bezerra et al. 2017, Liu et al. 2017, Lu et al. 2018, Rashmi et al. 2019, Hongsanan et al. 2020).

The family Bezerromycetaceae was introduced to accommodate two genera viz. *Bezerromyces* and *Xiliomyces*, first isolated as endophytic fungi (Bezerra et al. 2017). In their paper, Bezerra et al. (2017) also proposed the order Bezerromycetales to accommodate this family. In the same year, based on divergence time estimates, Liu et al. (2017) treated Bezerromycetales as a synonym of Tubeufiales and placed Bezerromycetaceae in this order. The same treatment was adopted by Wijayawardene et al. (2020) who also accepted Bezerromycetaceae as a family of Tubeufiales. Based on multi-gene phylogenetic analyses and morphological features, Lu et al. (2018) transferred *Neorhamphoria* to Bezerromycetaceae, a genus first introduced *incertae sedis* of Tubeufiales (Boonmee et al. 2016). In the recent outline of families of Dothideomycetes, Hongsanan et al. (2020) treated these three genera in Bezerromycetaceae (Tubeufiales). Later, Crous et al. (2021) synonymized *Xiliomyces* under *Bezerromyces* and introduced one new species, *B. gobabebensis*, for a fungus found growing on the leaves of a succulent plant in the Central Namib Desert (Namibia).

Members of Bezerromycetaceae are known for their endophytic mode of life (*Bezerromyces*) on cacti in Brazil (Bezerra et al. 2017), growing on the leaves of a succulent plant in Namibia (Crous et al. 2021) and their saprophytic life mode (*Neorhamphoria*) on the dead wood of a Rosaceae species in Turkey (Boonmee et al. 2016). During fieldwork at the Centre for Mountain Futures (CMF) in Honghe

County (Yunnan, China), dead twigs of *Pterolobium macropterum* (Fabaceae), with fungal structures morphologically similar to Dothideomycetes, were collected. Based on micro-morphological features and multi-loci phylogenetic analyses, this fungus is proposed as a new genus of Bezerromycetaceae (Tubeufiales).

Materials and methods

Herbarium material and fungal strains

Fresh fungal materials were collected from dead twigs of *Pterolobium macropterum* from Honghe County (Yunnan, China) at the end of the dry season (December 2020). Single spore isolation was conducted following the methods described in Wanasinghe et al. (2021). Germinated spores were individually transferred to potato dextrose agar (PDA) plates and grown at 20 °C in daylight. Living cultures were deposited at the Kunming Institute of Botany Culture Collection (KUMCC), Kunming, China. Dry herbarium materials were stored in the herbarium of Cryptogams Kunming Institute of Botany, Academia Sinica (KUN-HKAS).

Morphological observations

The morphology of external and internal macro-/micro-structures were observed as described in Wanasinghe et al. (2020). In hand sections, the ascomata were mounted in distilled water and the following characteristics were evaluated and measured: ascomata diameter, height, colour and shape; width of peridium; and height and diameter of ostioles. Length and width (at the widest point) of asci and ascospores. Images were captured with a Canon EOS 600D digital camera fitted to a Nikon ECLIPSE Ni compound microscope. Measurements were made with the Tarosoft (R) Image Frame Work program, and images used for figures were processed with Adobe Photoshop CS5 Extended version 10.0 software (Adobe Systems, San José, CA, USA).

DNA extraction, PCR amplifications and sequencing

Genomic DNA was extracted from the axenic mycelium as described by Wanasinghe et al. (2017) and Phookamsak et al. (2017). Mycelia for DNA extraction from each isolate were grown on PDA for 3–4 weeks at 20 °C and total genomic DNA was extracted from approximately 150 ± 50 mg axenic mycelium scraped from the edges of the growing culture. Mycelium was ground to a fine powder with liquid nitrogen and DNA extracted using the Biospin Fungus Genomic DNA Extraction Kit-BSC14S1 (BioFlux, P.R. China) following the instructions of the manufacturer. DNA to be used as templates for polymerase chain reaction (PCR) were stored at 4 °C for use in regular work and duplicated at –20 °C for long-term storage.

The primers and PCR protocols for ITS (internal transcribed spacers) = ITS5/ITS4 (White et al. 1990), LSU (partial 28S large subunit rDNA) = LR0R/LR5 (Vilgalys & Hester 1990, Rehner & Samuels 1994), SSU (partial 18S small subunit rDNA) = NS1/NS4 (White et al. 1990), *tef*1 (translation elongation factor 1-α) = EF1-983F/EF1-2218R (Liu et al. 1999, Rehner & Buckley 2005), and *rpb*2 (RNA polymerase II second largest subunit) = fRPB2-5f/fRPB2-7cR (Sung et al. 2007) were conducted by following the methods of Wanasinghe et al. (2021). PCR was carried out at a volume of 25 µl, which contained 12.5 µl of 2 × Power Taq PCR MasterMix (Bioteke Co., China), 1 µl of each primer (10 µM), 1 µl genomic DNA and 9.5 µl deionized water. The amplified PCR fragments were sent to a commercial sequencing provider (BGI, Ltd Shenzhen, P.R. China). The nucleotide sequence data obtained were deposited in GenBank (Tab. 1).

Sequencing and sequence alignment

Sequences generated from different primers of the five genes were analysed with other sequences retrieved from GenBank (Tab. 1). Sequences with high similarity indices were determined from a BLAST search to find the closest matches with taxa in Dothideomycetes, according to Bezerra et al. (2017) and Maharachchikumbura et al. (2021). The multiple alignments of all consensus sequences as well as the reference sequences were automatically generated with MAFFT v. 7 (Katoh et al. 2019) and manually corrected where necessary using BioEdit v. 7.0.5.2 (Hall 1999).

The alignments were concatenated into a multilocus alignment that was subjected to maximum likelihood (ML) and Bayesian (BI) phylogenetic analyses.

The CIPRES Science Gateway platform (Miller et al. 2012) was used to perform RAxML and Bayesian analyses. ML analyses were made with RAxML-HPC2 on XSEDE v. 8.2.10 (Stamatakis 2014) using GTR+GAMMA swap model with 1000 bootstrap repetitions. The evolutionary models for Bayesian analysis was selected independently for each locus using MrModeltest v. 2.3 (Nylander 2004) under the Akaike Information Criterion (AIC) implemented in

Tab. 1. Taxa used in the phylogenetic analysis of Dothideomycetes and their corresponding GenBank numbers. Newly generated sequences in bold.

Species	Strain no	GenBank accession no.				
		ITS	LSU	SSU	TEF	RPB2
Bezerromyces brasiliensis	URM 7411	KX470390	KX518623	KX518627	KX518631	
Bezerromyces pernambucoensis	URM 7412	KX470391	KX518624	KX518628	KX518632	
Bezerromyces pseudobrasiliensis	URM 7413	KX470392	KX518625	KX518629	KX518633	
Bezerromyces pseudobrasiliensis	URM 7414	KX470393	KX518626	KX518630	KX518634	
Botryosphaeria dothidea	CBS 115476	KF766151	NG_027577	NG_062738	DQ767637	DQ677944
Botryosphaeria pseudoramosa	CGMCC3.18739	KX277989	MF410031	MF410229		MF410140
Botryosphaeria qingyuanensis	CGMCC3.18742	KX278000	MF410042	MF410240		MF410151
Botryosphaeria wangensis	CGMCC3.18744	KX278002	MF410044	MF410242		MF410153
Catinella olivacea	UAMH 10679	DQ915483	EF622212	DQ915484		
Diatrype disciformis	AFTOL-ID 927		DQ470964	DQ471012	DQ471085	DQ470915
Graphostroma platystoma	CBS 270.87	JX658535	DQ836906	DQ836900	DQ836915	DQ836893
Helicoma chiangraiense	MFLUCC 10-0115	JN865200	JN865188	JN865176	KF301551	
Helicoma fagacearum	MFLUCC 11-0379	KF301524	KF301532	KF301540	KF301553	
Holmiella junipericola	MFLUCC 18-0503	MH188902	MH188900	MH188901		
Holmiella junipericola	SQUCC 15186	MW077142	MW077151	MW077160	MW075769	
Holmiella juniperi-semiglobosae	MFLUCC 17-1955	MH188905	MH188903	MH188904		
Homortomyces combreti	CPC 19808	NR_120215	NG_059480			
Homortomyces tamaricis	MFLUCC 13-0441	NR_155161	NG_059495	KU870905		
Honghemyces pterolobii	**KUMCC 20-0218**	**MZ779210**	**MZ779214**	**MZ781483**	**MZ798163**	**MZ798159**
Honghemyces pterolobii	**KUMCC 21-0030**	**MZ779213**	**MZ779217**	**MZ781486**	**MZ798166**	**MZ798162**
Honghemyces pterolobii	**KUMCC 21-0031**	**MZ779212**	**MZ779216**	**MZ781485**	**MZ798165**	**MZ798161**
Honghemyces pterolobii	**KUMCC 21-0032**	**MZ779211**	**MZ779215**	**MZ781484**	**MZ798164**	**MZ798160**
Hysteropatella clavispora	CBS 247.34		AY541493	DQ678006	DQ677901	DQ677955
Hysteropatella elliptica	CBS 935.97		DQ767657	EF495114	DQ767640	DQ767647
Kirschsteiniothelia phoenicis	MFLUCC 18-0216	NR_158532	NG_064508	MG859979	MG994911	MG994912
Kirschsteiniothelia rostrata	MFLUCC 15-0619	NR_156318	NG_059790	NG_063633	MF953397	
Kirschsteiniothelia tectonae	MFLUCC 12-0050	NR_148089	KU764708			
Muripulchra aquatica	KUMCC 15-0276	KY320534	KY320551		KY320564	MH551058
Neodactylaria obpyriformis	CBS 142668		MK562751	MK562750		MK562752
Neodactylaria simaoensis	YMF 1.3984	MH379209	MH379210	MK562747	MK562748	MK562749
Neorhamphoria garethjonesii	MFLUCC 16-0210		KY405014	KY405013	KY405015	
Parawiesneriomyces syzygii	CBS 141333	KX228288	KX228339			
Patellaria atrata	CBS 958.97		GU301855	GU296181	GU349038	GU371726
Patellaria atrata	SQUCC 15290	MW077143	MW077152		MW075770	
Patellaria quercus	CPC 27232	NR_152540	NG_059696			
Pseudogliophragma indicum	MTCC 11985	KM052850	KM052851	KM052852		
Sordaria fimicola	AFTOL-ID 216	DQ518178	FR774289	AH007748	DQ518175	DQ368647
Speiropsis pedatospora	CBS 397.59	KR822200	KR869797			
Tubeufia chiangmaiensis	MFLUCC 11-0514	KF301530	KF301538	KF301543	KF301557	
Tubeufia guangxiensis	MFLUCC 17-0045	MG012025	MG012018		MG012004	MG012011
Tubeufia javanica	MFLUCC 12-0545	KJ880034	KJ880036	KJ880035	KJ880037	
Tubeufia paludosa	CBS 120503		GU301877	GU296203	GU349024	
Wiesneriomyces conjunctosporus	BCC 4027		KJ425449	KJ425440		
Wiesneriomyces conjunctosporus	BCC 18525		KJ425450	KJ425436		
Wiesneriomyces conjunctosporus	BCC 20803		KJ425453	KJ425439		
Wiesneriomyces conjunctosporus	BCC 40633		KJ425455	KJ425442		

both PAUP v. 4.0b10, and GTR+I+G was selected as the best fit model for all three analyses. MrBayes analyses were performed setting GTR+I+G, 2 M generations, sampling every 100 generations, ending the run automatically when standard deviation of split frequencies dropped below 0.01 with a burn-in fraction of 0.25. ML bootstrap values equal or greater than 75 % and the posterior probability in BI (BYPP) greater than 0.95 are given above each node of every trees. Phylograms were visualized with FigTree v1.4.0 program (Rambaut 2012) and reorganized in Microsoft power point (2007).

Results

Phylogenetic analysis

Evolutionary relationships of the studied fungi were evaluated in the phylogenetic analysis based on the combined SSU, LSU, ITS, *tef*1-α and *rpb*2 sequences of 44 representative strains of the Botryosphaeriales, Catinellales, Holmiellales, Homortomycetales, Kirschsteiniotheliales, Neodactylariales, Patellariales and Tubeufiales in Dothideomycetes. *Diatrype disciformis*, *Graphostroma platystoma* and *Sordaria fimicola* (Sordariomycetes) were used to root the tree. The final alignment contained a total of 4848 characters used for the phylogenetic analyses, including alignment gaps. The RAxML analysis of the combined dataset yielded a best scoring tree with a final ML optimization likelihood value of -33108.948117. The matrix had 2301 distinct alignment patterns, with 39.76 % undetermined characters or gaps. Parameters for the GTR + I + G model of the combined amplicons were as follows: estimated base frequencies; A = 0.247028, C = 0.24613, G = 0.27138, T = 0.235461; substitution rates AC = 1.441544, AG = 2.857473, AT = 1.459553, CG = 1.349518, CT = 7.122393, GT = 1.000; proportion of invariable sites I = 0.359806; gamma distribution shape parameter α = 0.538476. The Bayesian analysis ran 240000 generations before the average standard deviation for split frequencies reached below 0.01 (0.00906). The analysis generated 2401 trees (saved every 100 generations) from which 1801 were sampled after 25 % of the trees were discarded as burn-in. The alignment contained a total of 2306 unique site patterns.

There were no conflicts among the trees generated by the two different phylogenetic analyses of ML and BI. Sequences of *Honghemyces pterolobii* grouped in a clade (100 % ML and 1.00 BYPP, Fig. 1) containing *Bezerromyces brasiliensis*, *B. pernambucoensis*, *B. pseudobrasiliensis* and *Neorhamphoria garethjonesii* in Bezerromycetaceae, Tubeufiales. The new species subclade, based on four strains, was resolved as a monophyletic taxon in both ML and BI analyses with strong statistical support (100 % ML and 1.00 BYPP, Fig. 1).

Taxonomy

Honghemyces Wanas., J.D.P. Bezerra & Mortimer, **gen. nov.**
MycoBank no.: MB840852

Etymology. – The generic epithet refers to the "Honghe" County, Yunnan, China.

Description. – Saprobic on dead twigs and branches in terrestrial habitats. – Sexual morph: ascomata scattered, semi-immersed to superficial, subglobose, glabrous. – Peridium comprising cells of *textura angularis* to *textura globosa*. – Hamathecium comprising numerous, filamentous, branched, septate pseudoparaphyses. – Asci eight-spored, bitunicate, fissitunicate, clavate, with a pedicel, apically rounded with or without an ocular chamber. – Ascospores overlapping or crowded, ellipsoidal, hyaline, three-septate, constricted at the middle septum, with the ends remaining rounded, with or without a mucilaginous sheath. – Asexual morph: globose to subglobose chlamydospores forming a chain of a torulose-like structure.

Typus generis. – *Honghemyces pterolobii* Wanas. & J.D.P. Bezerra

Honghemyces pterolobii Wanas. & J.D.P. Bezerra, **sp. nov.** – Fig. 2.
MycoBank no.: MB840853

Etymology. – The specific epithet reflects the host genus *Pterolobium*.

Holotypus. – CHINA. Yunnan, Honghe Hani and Yi Autonomous Prefecture, Honghe County, 23.421068 N, 102.229128 E, 735 m, on dead twigs of *Pterolobium macropterum*, 08 December 2020, *leg.* D.N. Wanasinghe, DWHH04-2 (HKAS115910), ex-type culture, KUMCC 20-0218.

Description. – Saprobic on dead twigs of *Pterolobium macropterum* Kurz. (Fabaceae). – Sexual morph: ascomata (140)150–180(200) µm high (n=10), (150)165–200(220) µm diam. ($\bar{x}$ = 168.4 × 178.6 µm, n = 10), scattered, semi-immersed to superficial, subglobose, conical or irregular base, glabrous, fused with host tissues. – Peridium (8)10–15(17) µm wide (n = 15) at base, (12)15–25(28) µm wide (n = 15) at sides, comprising 2–3 layers, pigmented, reddish brown to dark brown, with thin-walled cells of *textura angularis* to *glo-*

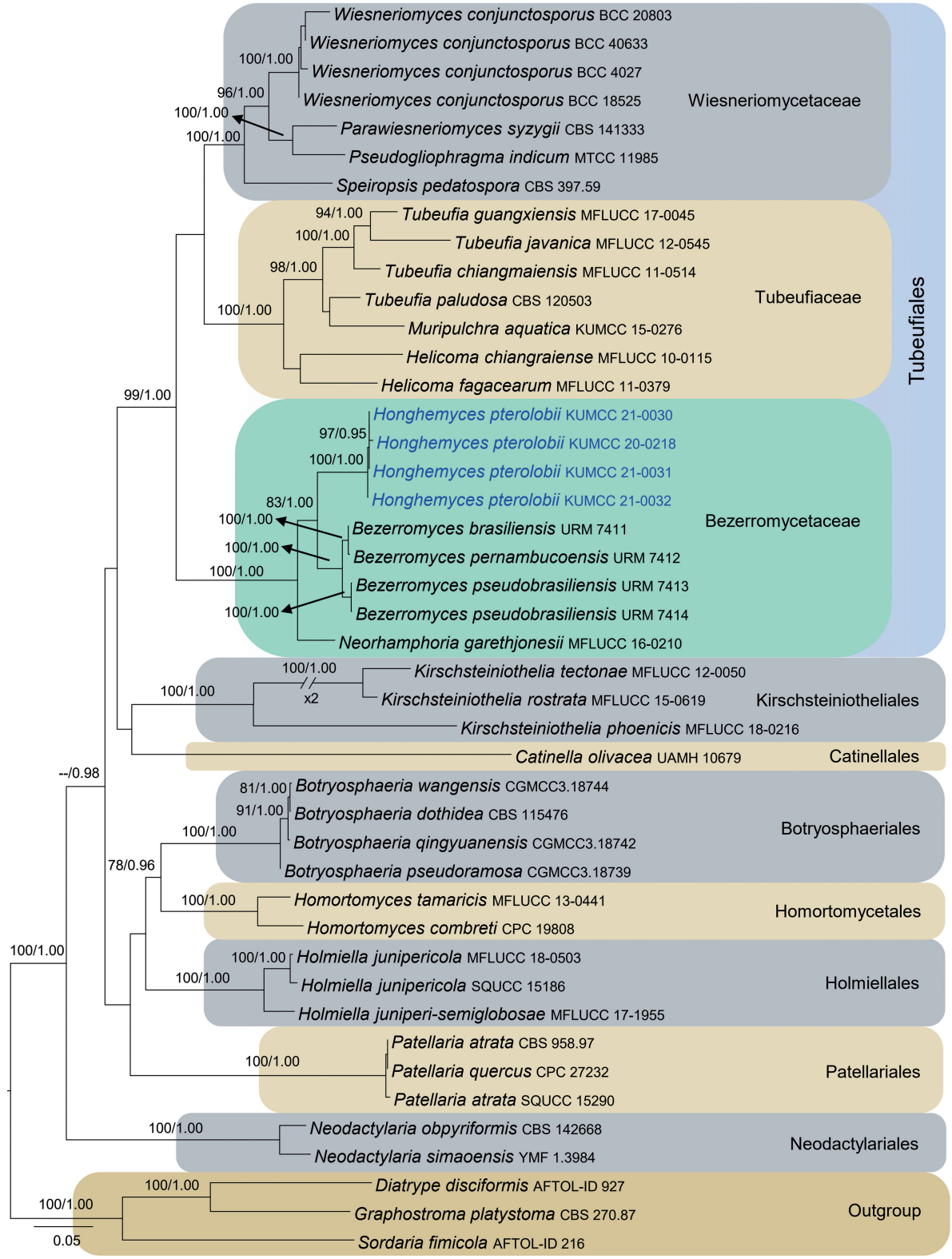

Fig. 1. RAxML tree based on a combined dataset of partial SSU, LSU, ITS, *tef*1-α and *rpb*2 DNA sequence analysis. Bootstrap support values for ML equal to or greater than 75 %, BYPP equal to or greater than 0.95 are shown as ML/BI above the nodes. The new isolates are in blue. The scale bar represents the expected number of nucleotide substitutions per site.

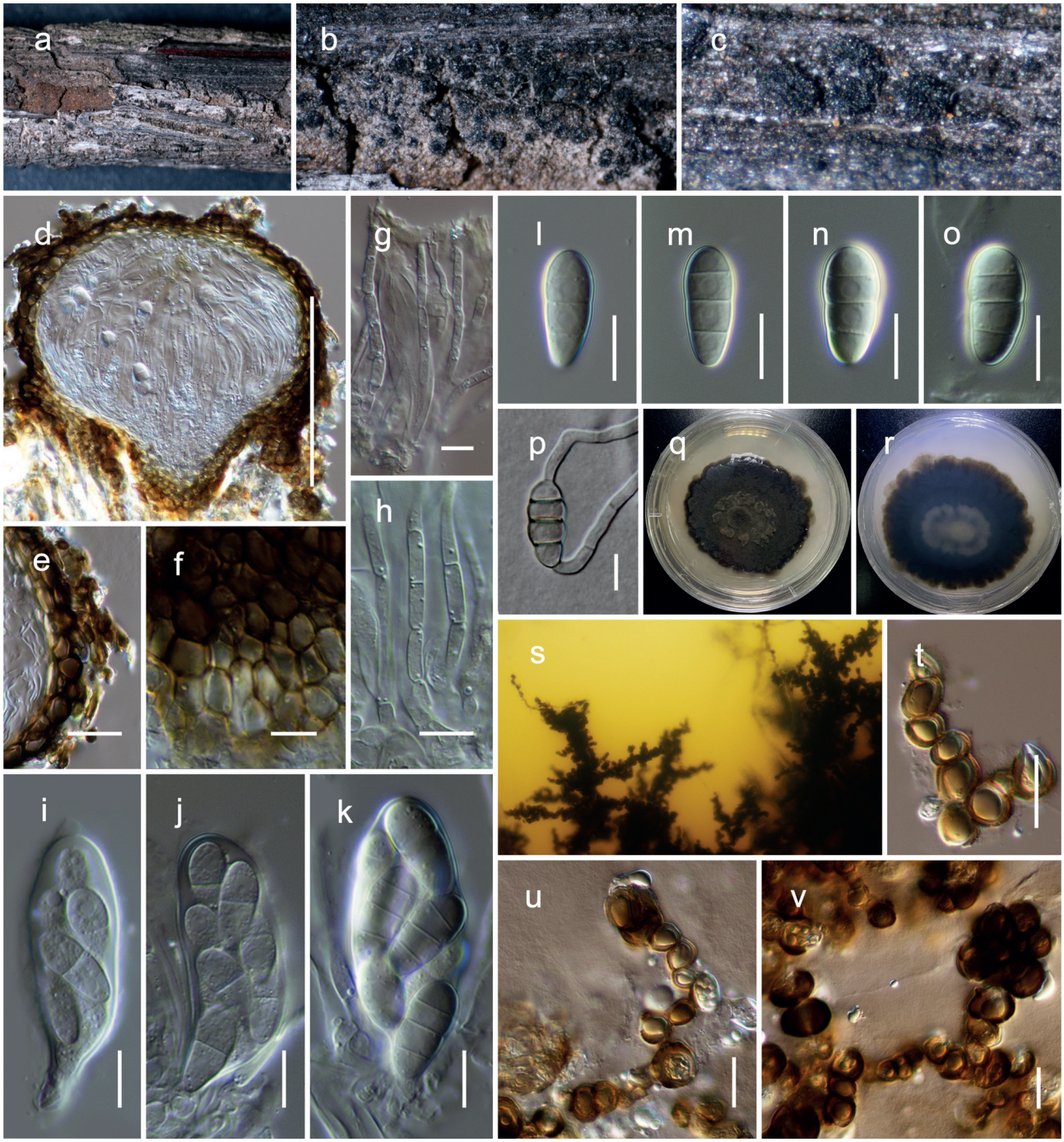

Fig. 2. *Honghemyces pterolobii* (HKAS115910, holotype) **A–C.** Ascomata on the dead woody twigs of *Pterolobium macropterum*; **D.** Vertical section of an ascoma; **E, F.** Cells of the peridium; **G, H.** Pseudoparaphyses; **I–K.** Asci; **L–O.** Ascospores; **P.** A germinated ascospore; **Q, R.** Colony on PDA (R from the bottom); **S–V.** Chlamydospores. Scale bars: D = 100 µm; E, T–V = 20 µm; F–O = 10 µm.

bosa. – Hamathecium comprising numerous, 2–3 µm (n=30) wide, filamentous, branched, septate pseudoparaphyses. – Asci (43)45–55(60) × (14)16–20(22) µm ($\bar{x}$ = 51.1 × 18 µm, n = 30), eight-spored, bitunicate, fissitunicate, clavate, with a short pedicel (10–15 µm long), apically rounded with a minute ocular chamber. – Ascospores (17)18–19.5(20) × (7.2)7.5–8.5(8.7) µm ($\bar{x}$ = 18.7 × 8.1 µm, n = 50), overlapping or crowded, ellipsoidal, hyaline, three-septate, constricted at the middle septum, with the up-

per part wider than the lower, and smooth-walled with guttules in each cell, conically rounded at both ends. – Asexual morph globose to subglobose, brown to dark brown chlamydospores forming a chain of a torulose-like structure.

Culture characteristics. – Colonies on PDA reaching 3 cm in diameter after 2 weeks at 20 °C; circular, with an undulate margin, creamy-whitish at the beginning, becoming dark olive at the centre and dark brown towards the margin after 4 weeks; slightly raised, and reverse dark olive green; hyphae producing chlamydospores after 6 weeks of incubation.

Known distribution. – Yunnan, China, on *Pterolobium macropterum*.

Material examined. – CHINA. Yunnan, Honghe Hani and Yi Autonomous Prefecture, Honghe County, 23.421068 N, 102.229128 E, 735 m, on dead twigs of *Pterolobium macropterum*, 08 December 2020, D.N. Wanasinghe, HH-D7Nb (HKAS115911), culture, KUMCC 21-0032; *ibid.* 23.421099 N, 102.233562 E, 601 m, DWHH18-03 (HKAS115912), culture, KUMCC 21-0031, *ibid.* 23.421377 N, 102.233610 E, 606 m, on dead twigs of an unknown host, DWHH19-04 (HKAS115913), culture, KUMCC 21-0030.

Notes. – *Honghemyces* has a saprotrophic life mode, differing from its phylogenetically related genus *Bezerromyces*, which has previously only been reported as comprising endophytes (Bezerra et al. 2017) and growing on leaves of a succulent (Crous et al. 2021). Colonies of the new genus *Honghemyces* grew faster than those of *Bezerromyces*, and produced glabrous and smaller ascomata (*Bezerromyces* has hairy ascomata), and smaller three-septate dimorphosporous ascospores (*Bezerromyces* has muriformly septate ascospores) (Bezerra et al. 2017). *Honghemyces* also has globose to subglobose chlamydospores, disposed in chains of a torulose-like structure, while *Bezerromyces* has multiseptate, globose to subglobose or ellipsoid to cylindrical chlamydospores (Bezerra et al. 2017). *Honghemyces pterolobii* morphologically resembles *Neorhamphoria garethjonesii* which differs by cup-shaped ascomata and phragmosporous to muriform ascospores and abscence of chlamydospores (Boonmee et al. 2016).

Key to genera in Bezerromycetaceae

1*. Hyaline ascospores 2
1. Pigmented ascospores ..... *Bezerromyces*
2 Apothecial ascomata, muriform ascospores .... *Neorhamphoria*
2. Pseudothecial ascomata, transversely septate ascospores ..... *Honghemyces*

Discussion

Tubeufiales members are mainly found as saprophytes in tropical and temperate environments, and some species have been reported as endophytes (Bezerra et al. 2017, Liu et al. 2017, Lu et al. 2018, Rashmi et al. 2019, Hongsanan et al. 2020). Among them, three genera are currently included in Bezerromycetaceae (Hongsanan et al. 2020). The description of *Honghemyces* is an important finding which will contribute to the understanding of lifestyles and distribution of taxa in this family. Sexual morphological characters and multi-marker (ITS, LSU, SSU, *tef*1-α and *rpb*2) phylogenetic analyses using sequences of the four species included in Bezerromycetaceae, along with representatives of the families Tubeufiaceae and Wiesneromycetaceae (Tubeufiales) and related orders of Dothideomycetes, confirmed that *Honghemyces* is a separate genus of Bezerromycetaceae, even when compared to *Bezerromyces* and *Neorhamphoria*, which are morphologically and phylogenetically related genera. Thus, we accept the three genera in Bezerromycetaceae viz. *Bezerromyces*, *Honghemyces* and *Neorhamphoria*.

Bezerromycetaceae is a family of fungi originally isolated as endophytes from the cactus *Tacinga inamoena* in the Caatinga forest (a tropical dry forest) in Brazil (Bezerra et al. 2017). Bezerra et al. (2017) introduced the morphologically well characterised teleomorphic species *Bezerromyces brasiliensis* and *B. pernambucoensis*, while *B. pseudobrasiliensis* was described based on multi-gene phylogenetic analyses while lacking defined sexual or asexual reproductive structures. Recently, Crous et al. (2021) introduced a new species in *Bezerromyces*, *B. gobabebensis*, found on leaves of a succulent plant in the Namib desert, in Namibia. The genus *Neorhamphoria* was introduced by Boonmee et al. (2016), as a genus *incertae sedis* of Tubeufiales, from a fungus found on dead wood of *Cotoneaster nummularius* (Rosaceae) in Turkey. Later, Lu et al. (2018) transferred *Neorhamphoria* to Bezerromycetaceae based on morphological features and phylogenetic inferences.

Morphologically, the *Bezerromyces* species are mainly characterised by 'superficial and immersed, globose to subglobose, smooth or hairy ascomata, bitunicate asci, and muriformly septate, ellipsoidal ascospores' (Bezerra et al. 2017). The monotypic genus *Neorhamphoria* has 'dark apothecial ascomata, broad cellular pseudoparaphyses, with bitunicate, broad-clavate asci, and hyaline, muriform ascospores' (Boonmee et al. 2016, Hongsanan et al.

2020). The main characteristics for introducing *Honghemyces pterolobii* as the type species of the new genus *Honghemyces*, of Bezerromycetaceae, are the teleomorph with glabrous ascomata; bitunicate asci with a short pedicel; ellipsoidal, hyaline and three-septate ascospores; and anamorphic globose to subglobose chains of chlamydospores.

Acknowledgements

Austin G. Smith at World Agroforestry (ICRAF), Kunming Institute of Botany, China, is thanked for English editing. Lu Wen Hua and Li Qin Xian are thanked for their invaluable assistance. Dhanushka Wanasinghe thanks CAS President's International Fellowship Initiative (PIFI) for funding his postdoctoral research (number 2021FYB0005), the National Science Foundation of China (NSFC) under the project code 32150410362 and the Postdoctoral Fund from Human Resources and Social Security Bureau of Yunnan Province. We acknowledge Kunming Institute of Botany, Chinese Academy of Sciences for providing the laboratories and instruments for molecular work.

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(Manuscript accepted 7 June 2022; Corresponding Editor: I. Krisai-Greilhuber)