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The Enigmatic Thelebolaceae (Thelebolales, Leotiomycetes): One New Genus *Solomyces* and Five New Species

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The family Thelebolaceae belongs to the order Thelebolales, class Leotiomycetes, and contains 22 genera. In this study, we introduce a new genus *Solomyces* gen. nov. in the family Thelebolaceae, which is supported by morphological observation and multilocus-based [internal transcribed spacers (ITS) + *LSU* and ITS + *LSU*+ *MCM7*+ *EF1A*+ *RPB2*] phylogenetic analysis. Maximum-likelihood and Bayesian phylogenetic inference analyses indicated that *Solomyces* is a distinct genus within this family. The new genus is compared against related Thelebolaceae genera, and its description and illustration are provided. This genus comprises one new species and one unnamed species (including two strains). We also report the addition of four new species – *Pseudogymnoascus shaanxiensis*, *Pseudogymnoascus guizhouensis*, *Pseudogymnoascus sinensis*, and *Geomyces obovatus* – in the family Thelebolaceae and present their morphological and phylogenetic characterizations.

Keywords: taxonomy, phylogeny, Thelebolales, new genus, new species

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INTRODUCTION

The class Leotiomycetes (Pezizomycotina) was erected by Eriksson and Winka (1997) to accommodate inoperculate discomycetes. Fungi in the class Leotiomycetes are ecologically diverse and include mycorrhizas, root and leaf endophytes, plant pathogens, aquatic and aeroaquatic hyphomycetes, mammalian pathogens, and saprobes (Johnston et al., 2019). Leotiomycetes currently comprises 19 orders and order-level clades, 54 families, and 13 family level clades (Ekanayaka et al., 2019; Karunarathna et al., 2020). Previously, however, this class included a wide range of taxa based on traditional morphological taxonomy (Korf, 1973; Spooner, 1987), and the current classification of Leotiomycetes is still largely based on morphologically defined taxa, especially at higher taxonomic levels (Johnston et al., 2019). Nevertheless, sexual or asexual morphs of many Leotiomycetes taxa are not recorded, and a few links between sexual and asexual morphs in Leotiomycetes have been confirmed (Sutton and Hennebert, 1995; Sati and Pathak, 2016; Ekanayaka et al., 2017; Johnston et al., 2019). Thelebolales, an order in the class Leotiomycetes, consists of Thelebolaceae and the *Alatospora–Miniancora* clade, in which some

genera (e.g., *Caccobius*, *Coprobolus*, and *Leptokalpion*) are erected based on their sexual, but not asexual, morphology (Wijayawardene et al., 2017).

Haeckel (1894) introduced the order Thelebolales; however, the taxonomy of this order has long been contentious. Some researchers believed that the order contained only one family (De Hoog et al., 2005), whereas others suggested that at least two families were involved (Ekanayaka et al., 2019; Johnston et al., 2019; Batista et al., 2020). The family Thelebolaceae is important in the order Thelebolales because of several species that can produce antifreeze proteins, ice-binding proteins, and some secondary metabolites with potential application values that offer valuable resources for biotechnological exploitation (Batista et al., 2020); the family was introduced by Eckblad (1968) and typified by the genus *Thelebolus* with *Thelebolus stercoreus* as the type species. Members of this family are characterized by absent, apothecial, or cleistothecial ascomata (Van Brummelen, 1985; Stchigel et al., 2001; De Menezes et al., 2017; Ekanayaka et al., 2019). During an extensive diversity survey of *Geomyces* and allied genera in China, we gathered a collection of fungal isolations. In this study, we introduced their morphological, cultural, and phylogenetic characterization and propose one new genus and five new species.

MATERIALS AND METHODS

Isolates and Morphology

Soil samples were obtained from Dali City, Yunnan Province; Guiyang City, Guizhou Province; Xi'an and Hanzhong City, Shaanxi Province; and Yichang City, Hubei Province, China. Samples were treated according to the method described by Zhang et al. (2019). Fungi were isolated using a modified baiting technique with chicken feathers as the substrate (Vanbreuseghem, 1952). The feathers were washed, thoroughly rinsed with distilled water, dried, cut into 2-cm fragments, and autoclaved. Plates containing soil material and sterile feathers were incubated at room temperature for 1 month. Fungi were isolated and purified using a conventional dilution technique described by Zhang et al. (2019), as follows: 2 g of soil sample was suspended in 9 ml of distilled water, and the prepared suspension was vortexed, diluted to 1:10,000, and cultured on Sabouraud's dextrose agar (SDA; 10 g of peptone, 40 g of dextrose, 20 g of agar, 1 L of ddH_2O) supplemented with chloramphenicol and cycloheximide. The plates were incubated at 25°C until fungal colony growth was observed. The axenic strains were then transferred to potato dextrose agar (PDA; Shanghai Bio-way Technology Co., Ltd., China) plates for purification. Dried holotypes were deposited in the Mycological Herbarium of the Institute of Microbiology, Chinese Academy of Sciences, Beijing, China (HMAS), or the Institute of Fungus Resources, Guizhou University (GZUIFR, formally the Herbarium of Guizhou Agricultural College; code, GZAC). Ex-type strains and other strains were deposited in the China General Microbiological Culture Collection Center (CGMCC) or the GZUIFR.

The pure strains were incubated on PDA at 25°C for 14 days in the dark to determine the macroscopic characteristics, diameters, and colony colors (surface and reverse). The characterization and measurement of fungal microscopic characteristics were performed in 25% lactic acid. Images were obtained using an optical microscope (OM, DM4 B, Leica, Germany) with differential interference contrast (DIC). The taxonomic descriptions and names of the new taxa were introduced into MycoBank[1] and Faces of Fungi[2].

DNA Extraction, PCR Amplification, and Sequencing

Total DNA was extracted using the BioTeke Fungus Genomic DNA Extraction kit (DP2032, BioTeke, Beijing, China) following the manufacturer's instructions. Total DNA was used for the amplification and sequencing of five fragments: ribosomal internal transcribed spacers (ITS; primers ITS1/ITS4) (White et al., 1990), the 28S LSU rRNA gene (primers LROR/LR7) (Vilgalys and Hester, 1990; Vilgalys and Sun, 1999), translation elongation factor 1 alpha (*EF1A*; primers 983F/2218R) (Rehner and Buckley, 2005), RNA polymerase II subunit 2 (*RPB2*; primers fRPB2-7cF/RPB2-3053b) (Liu et al., 1999; Reeb et al., 2004), and minichromosomal maintenance protein 7 (*MCM7*; primers MCM7-709/MCM7-1348) (Schoch et al., 2009). The PCR products were sequenced with the abovementioned primers at a commercial sequencing service provider (Shanghai Sangon Biological Engineering Technology & Services Co., Shanghai, China) in an ABI 3730xl DNA Analyzer, using the Sanger method. The consensus sequences were obtained using the SeqMan software v. 7 (DNASTAR Lasergene, Madison, WI, United States). Sequences generated in this study were deposited in GenBank (**Table 1**).

Phylogenetic Analyses

Sequence data were selected from data previously published by Crous et al. (2019), Ekanayaka et al. (2019), Johnston et al. (2019), and Minnis and Lindner (2013) and then downloaded from GenBank for molecular phylogenetic analyses (**Table 1**). Multiple sequence alignments for ITS, *LSU*, *MCM7*, *RPB2*, and *EF1A* were carried out using MAFFT v7.037b (Katoh and Standley, 2013). Sequence editing was performed with MEGA6 (Tamura et al., 2013). The concatenated ITS and *LSU*, and ITS, *LSU*, *MCM7*, *RPB2*, and *EF1A* sequences were assembled by SequenceMatrix v.1.7.8 (Vaidya et al., 2011). Gene concordance was assessed with the "hompart" command in PAUP4.0b10 (Swofford, 2002).

Sequence alignment and maximum-likelihood (ML) and Bayesian inference (BI) phylogenetic analyses were performed according to the methodology described by Zhang et al. (2019). Maximum-likelihood (ML) analyses were constructed with IQ-TREE v. 1.6.11 (Nguyen et al., 2015). The best-fit model of substitution for each locus was estimated using IQ-TREE's ModelFinder function (Kalyaanamoorthy et al., 2017) under the Bayesian information criterion (BIC). Bootstrap analysis was performed using the ultrafast bootstrap approximation (Minh et al., 2013) with 1,000 replicates, and bootstrap support (BS) ≥90% was considered as statistically significant. For

[1] www.Mycobank.org

[2] www.facesoffungi.org

TABLE 1 | List of strains used in the phylogenetic analysis.

Species	Strain	GenBank Accession				
		ITS	LSU	MCM7	RPB2	EF1A
Alatospora acuminata	CBS 104.88	MH862121	MH873811	NA	NA	NA
Alatospora constricta	CCM F-11302	KC834040	KC834017	NA	NA	NA
Alatospora pulchella	CCM F-502	KC834039	KC834019	NA	NA	NA
Antarctomyces pellizariae	UFMGCB 12416	KX576510	NA	NA	NA	NA
Antarctomyces psychrotrophicus	CBS 100573	MH874317	NA	NA	NA	NA
Cleistothelebolus nipigonensis	CBS 778.70	MH859938	MH871738	NA	NA	NA
Crinula caliciiformis	AFTOL-ID 272	KT225524	AY544680	NA	NA	NA
Epiglia gloeocapsae	CBS 126301	MH863968	MH875423	NA	NA	NA
	CBS 126302	MH863969	MH875424	NA	NA	NA
Geomyces auratus	CBS 108.14	KF039895	KF017864	KF017690	KF017746	KF017805
Geomyces obovatus	CGMCC 3.18491	MT509362	MT509376	MT534202	MT534216	MT534227
	CGMCC 3.18492	MT509363	MT509377	MT534203	MT534217	MT534228
Gorgomyces honrubiae	CCM F-12003	KC834057	KC834028	NA	NA	NA
	CCM F-12696	KC834058	NA	NA	NA	NA
Gymnostellatospora alpina	CBS 620.81	MH861383	MH873132	NA	NA	NA
	UAMH 9430	DQ117459	NA	NA	NA	NA
Holwaya mucida	NBRC 112552	LC425042	LC429385	NA	NA	NA
Leuconeurospora pulcherrima	CBS 343.76	KF049206	FJ176884	NA	FJ238367	FJ238409
Leuconeurospora polypaeciloides	UAMH 11459	KC884266	NA	NA	NA	NA
Leuconeurospora sp.	01NH01	JX270336	KF017814	KF017645	KF017699	KF017754
Leuconeurospora sp.	01NH04	JX270339	KF017815	KF017646	KF017700	KF017755
Leuconeurospora sp.	02NH04	JX270349	KF017817	KF017648	KF017702	KF017757
Leuconeurospora sp.	15PA04	JX270479	KF017841	KF017669	KF017725	KF017781
Miniancora allisoniensis	CCM F-30487	KC834064	NA	NA	NA	NA
Patinella hyalophaea	H.B. 9739	KT876978	KT876978	NA	NA	NA
Pseudeurotium ovale	CBS 531.71	MH860256	MH872019	NA	NA	NA
	CBS 460.69	MH859352	MH871109	NA	NA	NA
Pseudeurotium zonatum	CBS 329.36	AY129286	DQ470988	NA	DQ470940	DQ471112
	CBS 391.61	MH858096	MH869666	NA	NA	NA
Pseudogymnoascus appendiculatus	02NH11	JX270356	KF017819	KF017650	KF017704	KF017759
	07MA02	JX270402	KF017827	KF017658	KF017712	KF017767
Pseudogymnoascus bhattii	CBS 760.71	MH860337	MH872092	NA	NA	NA
	CBS 761.71	MH860338	MH872093	NA	NA	NA
	CBS 762.71	MH860339	MH872094	NA	NA	NA
Pseudogymnoascus destructans	20631-21	EU884921	KF017865	KF017691	KF017747	KF017806
Pseudogymnoascus guizhouensis	GZUIFR 376.1	MT509369	MT509383	MT534209	MT534223	MT534234
	GZUIFR 376.2	MT509370	MT509384	MT534210	MT534224	MT534235
	GZUIFR 376.3	MT509371	MT509385	MT534211	MT534225	MT534236
	GZUIFR 376.4	MT509372	MT509386	MT534212	MT534226	MT534237
Pseudogymnoascus lindneri	02NH05	JX270350	KF017818	KF017649	KF017703	KF017758
	LHU 158	MN542212	NA	NA	MN541384	MN541383
Pseudogymnoascus shaanxiensis	GZUIFR HZ5.7	MT509366	MT509380	MT534206	MT534220	MT534231
	GZUIFR CY1.8	MT509367	MT509381	MT534207	MT534221	MT534232
	GZUIFR 173.1	MT509368	MT509382	MT534208	MT534222	MT534233
	14PA06	JX270469	KF017839	KF017668	KF017723	KF017779
	RMF C 101	KF039896	KF017869	KF017695	KF017750	KF017810
Pseudogymnoascus roseus	05NY06	JX270385	KF017824	KF017655	KF017709	KF017764
	05NY08	JX270387	KF017825	KF017656	KF017710	KF017765
	05NY09	JX270388	KF017826	KF017657	KF017711	KF017766
	WSF 3629	KF039897	KF017870	KF017696	KF017751	KF017811

(Continued)

TABLE 1 | Continued

Species	Strain	GenBank Accession				
		ITS	LSU	MCM7	RPB2	EF1A
Pseudogymnoascus sinensis	CGMCC 3.18493	MT509364	MT509378	MT534204	MT534218	MT534229
	CGMCC 3.18494	MT509365	MT509379	MT534205	MT534219	MT534230
Pseudogymnoascus turneri	Ps5	MN542214	NA	NA	MN541382	MN541381
	LHU 121	MN542213	NA	NA	MN541380	MN541379
Pseudogymnoascus verrucosus	04NY16	JX270377	KF017822	KF017653	KF017707	KF017762
	24MN13	JX270621	KF017861	KF017687	KF017743	KF017802
	01NH08	JX270343	KF017816	KF017647	KF017701	KF017756
Pseudogymnoascus sp.	10NY09	JX270433	KF017830	KF017660	KF017715	KF017770
Pseudogymnoascus sp.	MN-Mycosel-7	KF039899	KF017872	KF017698	KF017753	KF017813
Pseudogymnoascus sp.	10NY10	JX270434	KF017831	NA	KF017716	KF017771
Pseudogymnoascus sp.	18VA08	JX270528	KF017848	KF017676	KF017731	KF017789
Pseudogymnoascus sp.	21IN01	JX270568	KF017854	KF017680	KF017737	KF017795
Pseudogymnoascus sp.	11MA05	JX270440	KF017833	KF017662	KF017718	KF017773
Pseudogymnoascus sp.	11MA07	JX270442	KF017834	KF017663	KF017719	KF017774
Pseudogymnoascus sp.	A07MA10	KF039893	KF017828	NA	KF017713	KF017768
Pseudogymnoascus sp.	24MN14	JX270622	KF017862	KF017688	KF017744	KF017803
Pseudogymnoascus sp.	18VA12	JX270532	KF017849	NA	KF017732	KF017790
Pseudogymnoascus sp.	18VA13	JX270533	KF017850	NA	KF017733	KF017791
Pseudogymnoascus sp.	12NJ13	JX270459	KF017838	KF017667	KF017722	KF017778
Pseudogymnoascus sp.	17WV06	JX270513	NA	KF017673	KF017729	KF017785
Ramgea ozimecii	CNF 2/9997	KY368752	KY368753	NA	NA	NA
Solomyces sinensis	CGMCC 3.18498	MT509373	MT509387	MT534213	NA	MT534238
	CGMCC 3.18499	MT509374	MT509388	MT534214	NA	MT534239
	CGMCC 3.18500	MT509375	MT509389	MT534215	NA	MT534240
Solomyces sp.	15PA02	JX270477	KF017840	NA	KF017724	KF017780
	17WV02	JX270509	KF017845	NA	KF017730	KF017786
Thelebolus balaustiformis	MUT 2357	NR_159056	NG_067559	NA	NA	NA
Thelebolus globosus	CBS 113940	MH862951	NG_067263	NA	NA	NA
Thelebolus spongiae	MUT 2359	MG813185	MG816493	NA	NA	NA

CBS, Westerdijk Fungal Biodiversity Institute, Utrecht, Netherlands; CGMCC, China General Microbiological Culture Collection Center, Beijing, China; GZUIFR, Guizhou University, Institute of Fungus Resources; CCM, Czech Collection of Microorganisms, Brno, Czechia; NBRC (IFO), Institute for Fermentation, Osaka, Japan; UAMH, UAMH Centre for Global Microfungal Biodiversity, Toronto, ON, Canada; MUT, Mycotheca Universitatis Taurinensis, Turin, Italy; NA, not available. DNA sequences for the new isolates were in blue.

Bayesian inference (BI), a Markov chain Monte Carlo (MCMC) algorithm was used to generate phylogenetic trees with Bayesian probabilities using MrBayes v.3.2 (Ronquist et al., 2012) for the combined sequence datasets. The selection of the best-fit nucleotide substitution model for each locus was calculated by the Akaike information criterion (AIC) with ModelTest v.3.7 (Posada and Crandall, 1998). After the BI analyses, both runs were examined with Tracer v.1.5 (Drummond and Rambaut, 2007) to determine burn-in and check for convergence.

Two multilocus phylogenies were analyzed to evaluate the various generic placements and establish the phylogenetic relationships in Thelebolaceae. The genus placement was evaluated based on a concatenated ITS and *LSU* dataset. This phylogeny was constructed to assess if *Solomyces* is a well-delimited genus. The second multilocus phylogeny was based on a concatenated alignment of ITS, *LSU*, *MCM7*, *RPB2*, and *EF1A* sequences and included 49 isolates of *Geomyces* and its allied genera. This analysis was performed to evaluate the generic boundaries and species groupings within the genera *Solomyces*, *Geomyces*, and *Pseudogymnoascus*. All the trees were displayed in FigTree 1.4.2[3] and edited in Microsoft Paint. DNA alignments have been deposited at TreeBASE.

RESULTS

Phylogenetic Analyses

The first concatenated matrix contains 1,220 nucleotides, i.e., 445 from the ITS and 775 from the *LSU*. The second concatenated alignment contained 2,808 nucleotides (ITS: 434, *LSU*: 806, *MCM7*: 503, *RPB2*: 437, and *EF1A*: 628). The best-fit evolutionary model for each locus in the two datasets is listed in **Table 2**. The tree topology of the Bayesian inference agrees with that of the ML tree (**Figures 1**, **2**). The phylogenies indicated that each genus clusters into a monophyletic clade (**Figure 1**). In

[3]http://tree.bio.ed.ac.uk/software/figtree

TABLE 2 | The best-fit evolutionary model in the phylogenetic analyses.

Dataset/phylogenetic analysis		Model				
		ITS	LSU	MCM7	RPB2	EF1A
First dataset	ML analysis	TIM2e + I + G4	K2P + R2			
	BI analysis	GTR + I + G	GTR + I + G			
Second dataset	ML analysis	TIM2e + R3	TPM2u + F + I	TNe + I + G4	TNe + I + G4	TIM2e + R3
	BI analysis	SYM + I + G	GTR + I	HKY + I + G	K80 + I + G	SYM + I + G

ML, maximum likelihood; BI, Bayesian inference.

the phylogenetic tree, the new genus *Solomyces* forms a well-supported (1 BYPP/100 MLBS) clade separated from other genera in Thelebolaceae (**Figure 1**). *Solomyces sinensis* represents a separate subclade and is located within the new genus near another unnamed species (includes two strains, 15PA02 and 17WV02, from Hibernacular soil). Furthermore, all the new species of *Pseudogymnoascus* and *Geomyces* are placed in a distinct branch.

Taxonomy

In this section, *Solomyces* Zhi.Y. Zhang, Y.F. Han and Z.Q. Liang, gen. nov. and five new species – *S. sinensis* Zhi.Y. Zhang, Y.F. Han and Z.Q. Liang, sp. nov.; *Geomyces obovatus* Zhi.Y. Zhang, Y.F. Han and Z.Q. Liang, sp. nov.; *Pseudogymnoascus guizhouensis* Zhi.Y. Zhang, Y.F. Han and Z.Q. Liang, sp. nov.; *Pseudogymnoascus shaanxiensis* Zhi.Y. Zhang, Y.F. Han and Z.Q. Liang, sp. nov.; and *Pseudogymnoascus sinensis* Zhi.Y. Zhang, Y.F. Han and Z.Q. Liang, sp. nov. – are described and illustrated. We also propose a new combination, *Gymnostellatospora bhattii* (Samson) Zhi.Y. Zhang, Y.F. Han and Z.Q. Liang, comb. nov. based on phylogenetic analyses.

Geomyces obovatus Zhi.Y. Zhang, Y.F. Han and Z.Q. Liang, sp. nov.

MycoBank number: MB 835718, Facesoffungi number: FoF 08691 (**Figure 3**).

Etymology: Referring to the obovoid conidia.

Holotype: permanently preserved in a metabolically inactive state, GZAC 20.8.

Description based on GZAC 20.8. Asexual: Colonies on PDA, reaching 28–30 mm in diameter after 14 days at 25°C, slightly felty to floccose, margin identified, khaki at center, and white at edge; reverse hazel. Aerial mycelium abundant, smooth and thin walled, septate, 0.5- to 2-μm wide. Racquet hyphae absent. Conidia abundant, normally terminal and intercalary conidia in a series of 1–4, rarely solitary on short stalk, smooth or echinulate, 3.0–5.0 × 2.5–4.0 μm (*av.* = 3.5 × 2.5 μm, *n* = 50). Terminal conidia obovoid, rarely subglobose; intercalary conidia alternate and pyriform, barrel or irregularly shaped.

Sexual morph: not observed.

Geographical distribution: China.

Material examined: China, Guizhou, Guiyang, Qianlingshan Park, 26°60′N, 106°69′E, from soil beside a road, September 2016, Zhi. Y. Zhang (GZAC 20.8 – holotype; CGMCC 3.18491 = GZUIFR QL20.8.1 – ex-type living cultures; ibid., CGMCC 3.18492 = GZUIFR QL20.8.2). The living cultures were kept in sterile 30% glycerol and deposited in a −80°C freezer.

Notes: The *Geomyces* was introduced by Traaen (1914), and several species have subsequently been described. Currently, the genus contains seven species (Traaen, 1914; Dal Vesco, 1957; Sigler and Carmichael, 1976; Hocking and Pitt, 1988; Li and Cui, 1989; Luo et al., 2016; Chen et al., 2017): *Geomyces auratus*, *Geomyces asperulatus*, *Geomyces vinaceus*, *Geomyces pulvereus*, *Geomyces laevis*, *Geomyces guiyangensis*, and *Geomyces fujianensis*. *G. asperulatus* and *G. vinaceus* likely belong to *Pseudogymnoascus* (Minnis and Lindner, 2013); *G. pulvereus* and *G. laevis* do not have any available sequence data; *G. pulvereus* lacks intercalary conidia (Hocking and Pitt, 1988), and *G. laevis* has oblong-elliptical or barrel-shaped intercalary conidia (Li and Cui, 1989). Only ITS sequences are available for *G. guiyangensis* and *G. fujianensis*, and the ITS data for CGMCC 3.18491 (the type strain of *G. obovatus*) show similarity to those of *G. guiyangensis* (strain G014512) (465/509; 91%, with 4 gaps) and *G. fujianensis* (strain G242) (464/526; 88%, with 11 gaps); however, the latter two species have no intercalary conidia (Luo et al., 2016; Chen et al., 2017). The proposed new species, *G. obovatus*, is morphologically and phylogenetically related to *G. auratus*, but they can be distinguished by their ITS (512/524; 97%, with three gaps), *LSU* (931/938; 99%, no gaps), *MCM7* (592/619; 95%, no gaps), *RPB2* (696/717; 97%, no gaps), and *EF1A* (843/855; 98%, with one gap) sequence data.

Gymnostellatospora bhattii (Samson) Zhi.Y. Zhang, Y.F. Han and Z.Q. Liang, comb. nov.

Basionym: *Pseudogymnoascus bhattii* Samson, *Acta Botanica Neerlandica* 21: 519. 1972.

Notes: This species was erected by Samson (1972) based on morphological characteristics. However, our phylogenetic analysis based on Thelebolaceae ITS and *LSU* data indicated that this species was closely related to *Gymnostellatospora* and separated from *Pseudogymnoascus*. Based on morphological characteristics, it was difficult to distinguish the closely related species, and even the genera, through traditional taxonomy, and modern phylogenetic methods were a very important adjunct. We therefore transferred *P. bhattii* to *Gymnostellatospora* and named the species *G. bhattii*.

Pseudogymnoascus guizhouensis Zhi.Y. Zhang, Y.F. Han and Z.Q. Liang, sp. nov.

MycoBank number: MB 835716, Facesoffungi number: FoF 08692 (**Figure 4**).

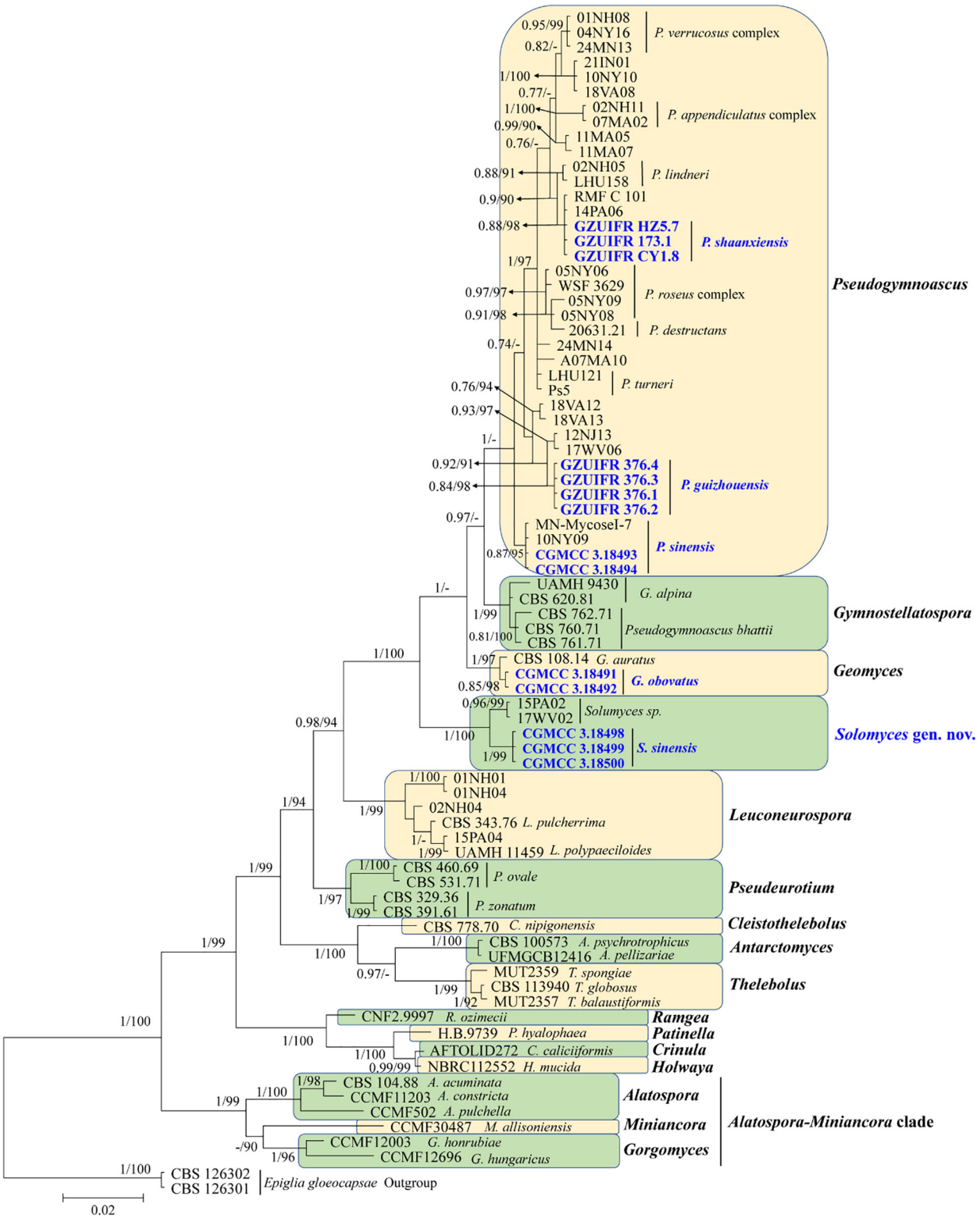

FIGURE 1 | Phylogenetic relationships among the genera in Thelebolales based on Bayesian inference and maximum-likelihood analyses of the concatenated internal transcribed spacers (ITS) and *LSU* dataset. Posterior probabilities ≥0.7 and maximum-likelihood bootstrap values ≥90% are shown above the internal branches. The new isolates are presented in bold and blue.

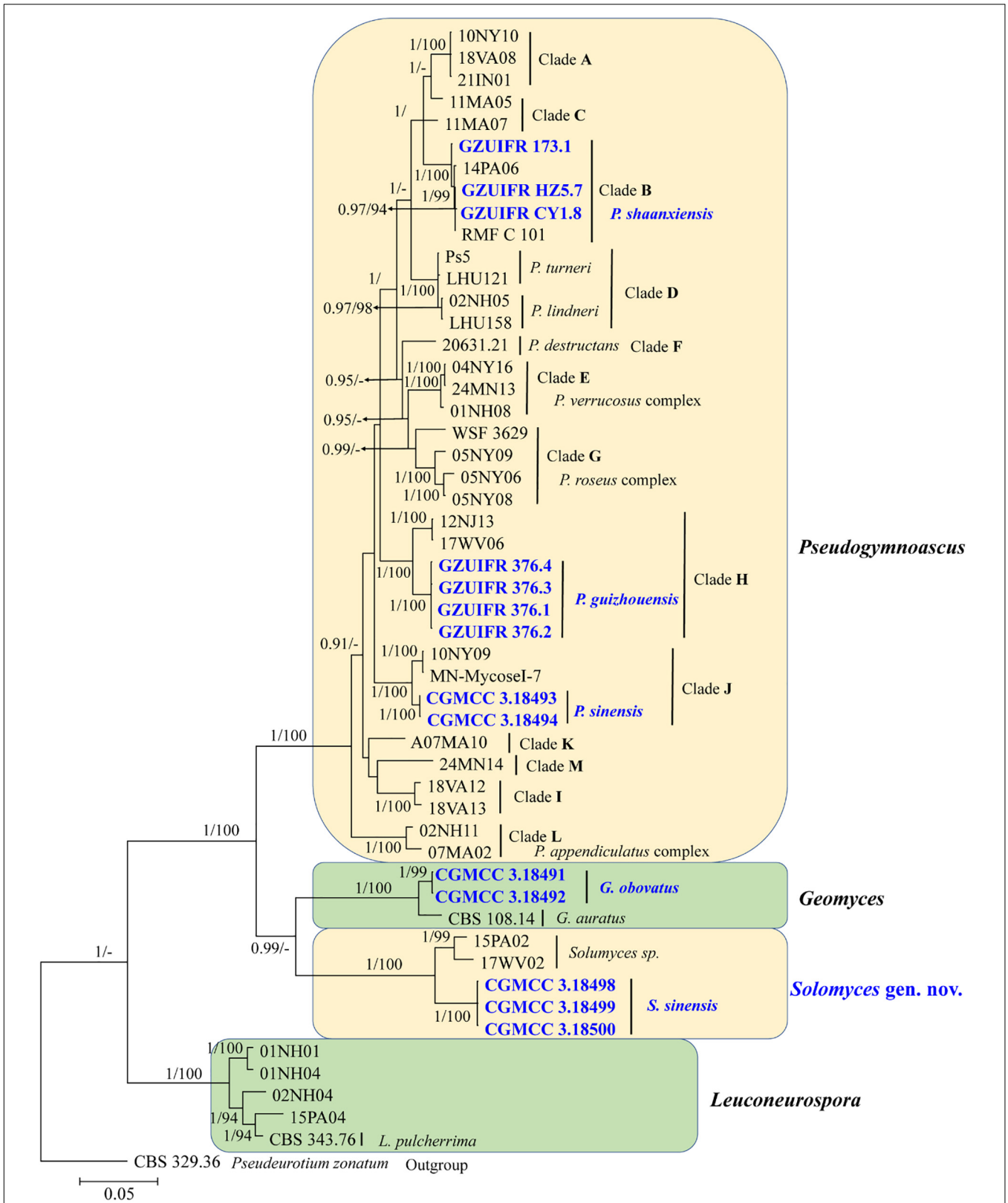

FIGURE 2 | The consensus tree from the Bayesian inference and *Geomyces* and its allied genera based on the ITS, *LSU*, *MCM7*, *RPB2*, and *EF1A* concatenated dataset. Posterior probabilities ≥0.7 and maximum-likelihood bootstrap values ≥90% are shown above the internal branches. The new isolates are presented in bold and blue.

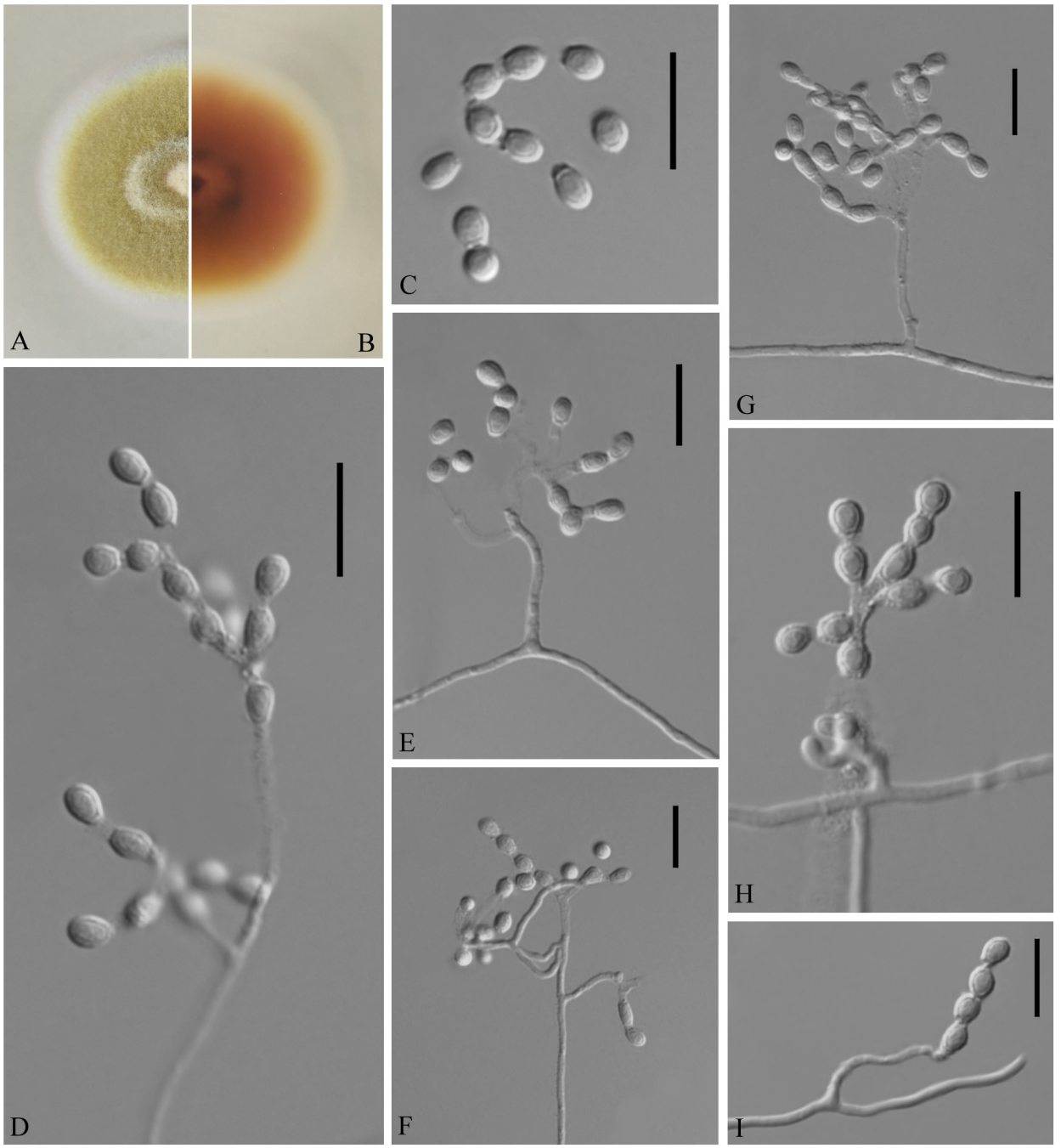

FIGURE 3 | *Geomyces obovatus* [from ex-holotype China General Microbiological Culture Collection Center (CGMCC) 3.18491]. **(A,B)** The front and reverse of a *G. obovatus* colony on potato dextrose agar (PDA) after 14 days at 25°C. **(C–I)** Conidiophores and conidia. Scale bars = 10 μm.

Etymology: Refers to the region from which the fungus was isolated.

Holotype: permanently preserved in a metabolically inactive state, GZAC 376.

Description based on GZAC 376. Asexual: Colonies on PDA, reaching 20–23 mm in diameter after 14 days at 25°C, elevate, powdery, floccose, margin identified, locally indented, pale purple at center and white at the edge, producing a clear exudate; reverse brown. Aerial mycelium abundant, smooth and thin walled, septate, 1.5- to 3.0-μm wide. Racquet hyphae absent. Conidia normally borne on verticillate branches, terminal, intergrading with intercalary conidia, sometimes borne laterally and solitary on hyphae, smooth walled or echinulate, obovoid, pyriform, subglobose or clavate, 3.0–5.5 × 3.0–3.5 μm (*av.* = 4.0 × 3.0 μm,

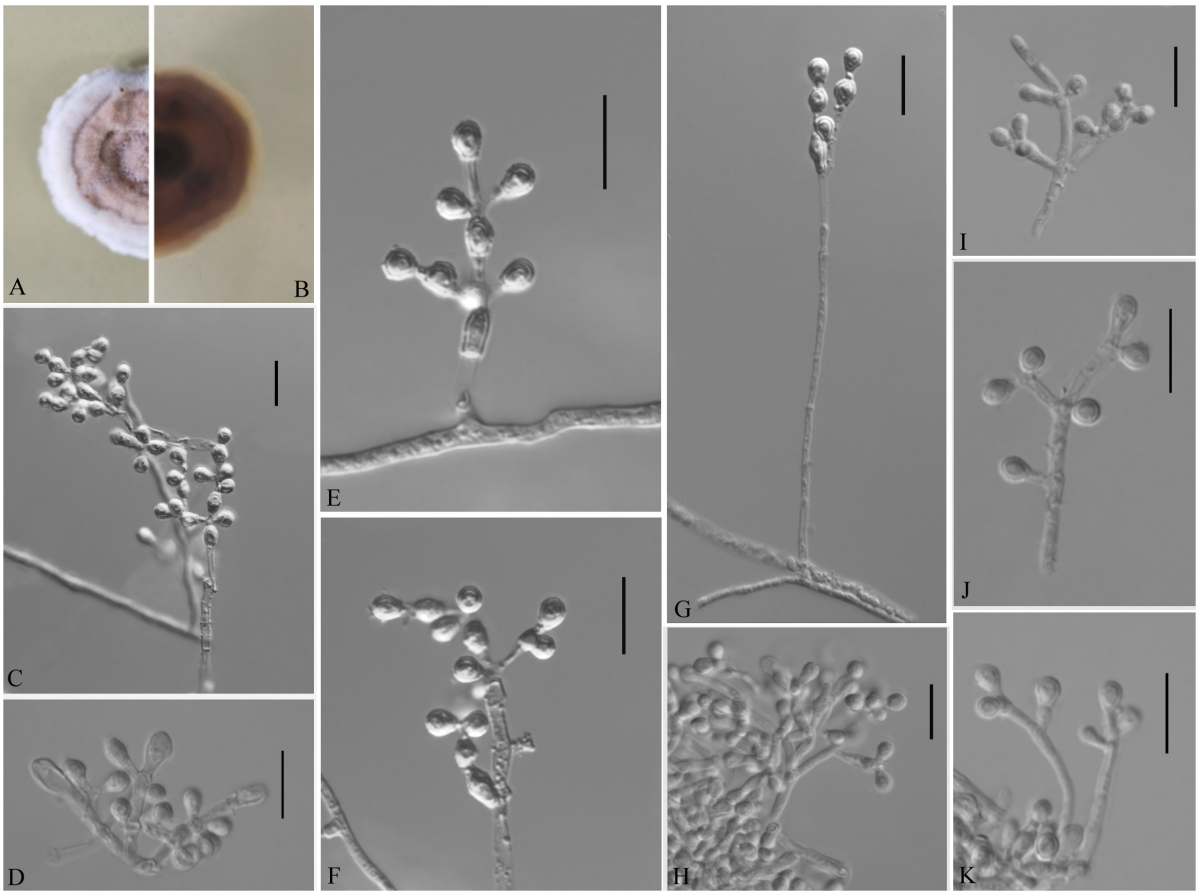

FIGURE 4 | *Pseudogymnoascus guizhouensis* [from ex-holotype Institute of Fungus Resources, Guizhou University (GZUIFR) 376.1]. **(A,B)** The front and reverse of a *P. guizhouensis* colony on PDA after 14 days at 25°C. **(C–K)** Conidiophores and conidia. Scale bars = 10 μm.

n = 50). Intercalary conidia are borne on the outer branches of the hyphae or verticillate hyphae, alternate, in series of 1–2, smooth walled or echinulate, cuneiform, barrel shaped, 3.5–6.0 × 3.0–3.5 μm (*av*. = 4.0 × 3.0 μm, *n* = 50).

Sexual morph: not observed.

Geographical distribution: China.

Material examined: China, Guizhou, Guiyang, Guizhou University, 26°45′N, 106°67′E, from epiphytic soil of *Cinnamomum camphora*, June 2019, Zhi. Y. Zhang (GZAC 376 – holotype; GZUIFR 376.1 – ex-type living culture; ibid., GZUIFR 376.2; ibid., GZUIFR 376.3; ibid., GZUIFR 376.4). The living cultures were kept in sterile 30% glycerol and deposited in a −80°C freezer.

Notes: Morphologically, *Pseudogymnoascus guizhouensis* is similar to *Pseudogymnoascus linderi*, *Pseudogymnoascus turneri* (both isolated from sediment), and *Pseudogymnoascus destructans* (isolated from a wing of a small brown bat, *Myotis lucifugus*), based on the obovoid and subglobose conidia. However, *P. guizhouensis* differs from *P. linderi* and *P. turneri* as it has cuneiform, barrel-shaped intercalary conidia (the intercalary conidia of *P. linderi* and *P. turneri* are globose to truncate) (Crous et al., 2019). *P. guizhouensis* can be distinguished from *P. destructans* by the size of conidia and intercalary conidia (4.0 × 3.0 μm vs. 5.0–12.0 × 2.0–3.5 μm, respectively) (Gargas et al., 2009). Phylogenetically, our isolates GZUIFR 376.1, GZUIFR 376.2, GZUIFR 376.3, and GZUIFR 376.4 cluster together very well and form a single clade separated from other *Pseudogymnoascus* species (**Figures 1**, **2**).

Pseudogymnoascus shaanxiensis Zhi.Y. Zhang, Y.F. Han and Z.Q. Liang, sp. nov.

MycoBank number: MB 835715, Facesoffungi number: FoF 08689 (**Figure 5**).

Etymology: Refers to Shaanxi, the province where the isolate was collected.

Holotype: permanently preserved in a metabolically inactive state, HMAS 255395.

Description based on HMAS 255395. Asexual: Colonies on PDA, reaching 21–23 mm in diameter after 14 days at 25°C, velvety to floccose, margins regular, white, producing a diffusible faint yellow pigment and clear exudates; reverse brown. Hyphae hyaline, smooth-walled, septate, 1.5- to 2.5-μm wide.

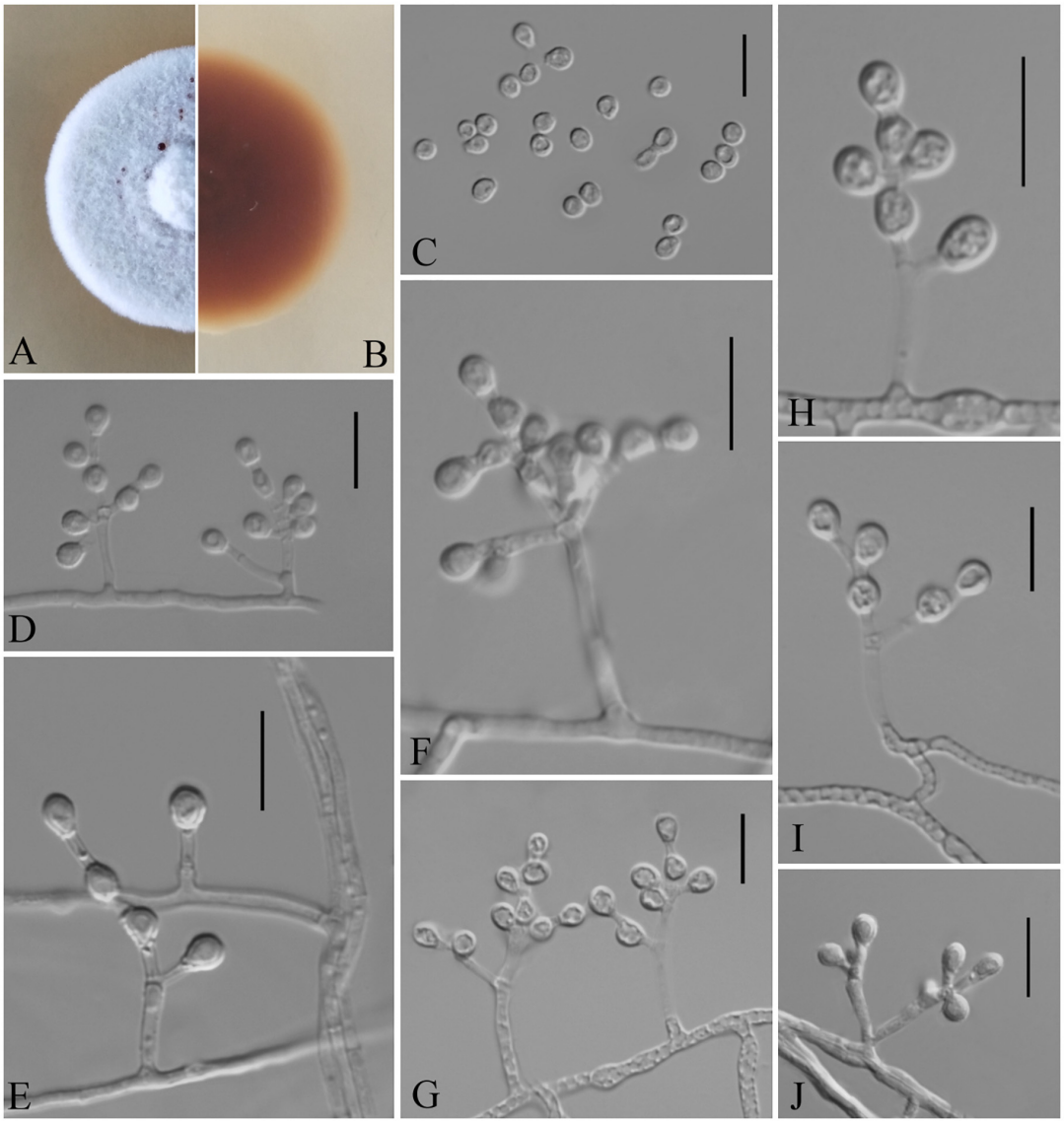

FIGURE 5 | *Pseudogymnoascus shaanxiensis* (from ex-holotype GZUIFR 173.1). **(A,B)** The front and reverse of a *P. shaanxiensis* colony on PDA after 14 days at 25°C. **(C)** Conidia. **(D–J)** Conidiophores and conidia. Scale bars = 10 μm.

Racquet hyphae absent. Conidia abundant, pyriform, sometimes subglobose, smooth 3.5–5.0 × 2.5–3.0 μm (*av.* = 4.0 × 3.0 μm, *n* = 50). Intercalary conidia subglobose, pyriform, or irregularly shaped, smooth, 3.5–4.0 × 3.0–4.0 μm (*av.* = 3.5 × 3.0 μm, *n* = 50). Terminal and lateral conidia on hyphae, short stalk or side branch, solitary, always forming verticillate and opposite branches with an acute angle to the axis near the apex.

Sexual morph: not observed.

Geographical distribution: China and America.

Material examined: China, Shaanxi, Xi'an, Xincheng district, 34°27′N, 108°95′E, from epiphytic soil of *Broussonetia papyrifera*, September 2018, Zhi. Y. Zhang (HMAS 255395 – holotype; GZUIFR 173.1 – ex-type living culture); Hanzhong, Shaanxi province, from epiphytic soil of *Trachycarpus fortunei*, September 2018, Zhi. Y. Zhang (GZUIFR HZ5.7); Yichang, Hubei province, from soil beside a park, September 2018, Zhi. Y. Zhang (GZUIFR CY 1.8). The living cultures were kept in sterile 30% glycerol and deposited in a −80°C freezer.

Notes: Morphologically, *P. shaanxiensis* resembles *Pseudogymnoascus appendiculatus* and *Pseudogymnoascus verrucosus* because of the pyriform conidia. However, *P. shaanxiensis* differs from *P. appendiculatus* and *P. verrucosus* based on its subglobose, pyriform intercalary conidia (the intercalary conidia of *P. appendiculatus* and *P. verrucosus*

are subglobose to elongate) (Rice and Currah, 2006). Phylogenetically, our isolates GZUIFR 173.1, GZUIFR HZ5.7, and GZUIFR CY 1.8 cluster with 14PA06 and RMF C 101 in a distinct subclade and are separated from other clades (**Figures 1**, **2**). Furthermore, since 2013 (Minnis and Lindner, 2013), isolates 14PA06 and RMF C 101 have remained an undescribed species owing to the lack of morphological characteristics. Therefore, we introduce *P. shaanxiensis* sp. nov. in this study.

Pseudogymnoascus sinensis Zhi.Y. Zhang, Y.F. Han and Z.Q. Liang, sp. nov.

MycoBank number: MB 835717, Facesoffungi number: FoF 08690 (**Figure 6**).

Etymology: In reference to China, the country where the type specimen was obtained.

Holotype: permanently preserved in a metabolically inactive state, HMAS 255394.

Description based on HMAS 255394. Asexual: Colonies on PDA, reaching 20–21 mm in diameter after 14 days at 25°C, powdery, floccose, margin identified, light pink at the center and pewter at the edge; reverse brown. Aerial mycelium abundant, smooth and thin walled, septate, 1- to 2-μm wide. Racquet hyphae absent. Conidia abundant, terminal and lateral conidia on hyphae, short stalk or side branches, sometimes forming verticillate and opposite branches with an acute angle to the axis near the apex, solitary, obovoid, 3.0–5.0 × 2.5–3.0 μm (*av.* = 4.0 × 2.5 μm, *n* = 50). Intercalary conidia are borne on the outer branches of the hyphae or verticillate hyphae, smooth walled, drum, obovoid, pyriform, or irregularly shaped, 3.0–4.5 × 2.5–5.0 μm (*av.* = 3 × 3 μm, *n* = 50).

Sexual morph: not observed.

Geographical distribution: China.

Material examined: China, Guizhou, Guiyang, the Affiliated Hospital of Guizhou Medical University, 26°59′N, 106°71′E, from soil beside a road, September 2016, Zhi. Y. Zhang (HMAS 255394 – holotype; CGMCC 3.18493 = GZUIFR K278.1 – ex-type living cultures; ibid., CGMCC 3.18494 = GZUIFR K278.2). The living cultures were kept in sterile 30% glycerol and deposited in a −80°C freezer.

Notes: Morphologically, *P. sinensis* is similar to *P. linderi* and *P. turner*, based on its obovoid conidia. However, *P. sinensis* differs from *P. linderi* and *P. turneri* as it has drum, obovoid, pyriform, or irregularly shaped intercalary conidia (the intercalary conidia of *P. linderi* and *P. turneri* are globose to truncate) (Crous et al., 2019). Phylogenetically, our isolates CGMCC 3.18493 and CGMCC 3.18494 cluster together very well and form a single clade separated from other *Pseudogymnoascus* species (**Figure 1**).

Solomyces Zhi.Y. Zhang, Y.F. Han and Z.Q. Liang, gen. nov.

MycoBank number: MB 835713; Facesoffungi number: FoF 08688.

Etymology: *Solo-* (from *Solum*), in reference to its isolation from soil.

Saprobic on soil. Asexual morph: *Conidia*: terminal and lateral conidia borne on hyphae, short protrusions, or side branches. Conidia solitary, sometimes 2 in chains, pyriform, sometimes subglobose. Intercalary conidia abundant, olivary, subglobose to globose. Sexual morph: Unknown.

Geographical distribution: China and America.

Type species: *Solomyces sinensis* Zhi.Y. Zhang, Y.F. Han and Z.Q. Liang.

Notes: *Solomyces* is introduced to accommodate *Solomyces sinensis* and another unnamed species (containing two strains, 15PA02 and 17WV02, from Hibernacular soil in Pennsylvania and West Virginia, respectively; Minnis and Lindner, 2013). The morphology of *Solomyces* species is similar to that of *Geomyces* and the asexual morphs of *Pseudogymnoascus*. However, *Geomyces* differ in having terminal and lateral conidia borne on hyphae, short protrusions or side branches; intercalary conidia barrel shaped, and conidiophores abundant, always forming verticillate and opposite branches with an acute angle to the axis near the apex (Van Oorschot, 1980; Chen et al., 2017). As can be seen in **Figures 1**, **2**, strains of these genera appear in distinct clades in a phylogeny based on multiple strains, thereby justifying the erection of the new genus *Solomyces*.

Solomyces sinensis Zhi.Y. Zhang, Y.F. Han and Z.Q. Liang, sp. nov.

MycoBank number: MB 835714, Facesoffungi number: FoF 08687 (**Figure 7**).

Etymology: In reference to China, the country where the type specimen was obtained.

Holotype: permanently preserved in a metabolically inactive state, HMAS 255397.

Description based on HMAS 255394. Asexual: Colonies on PDA, reaching 16–17 mm in diameter after 14 days at 25°C, elevate at the center, velvety to floccose, margins regular, pewter at the center and white at the edge, producing a diffusible faint yellow pigment and clear exudates; reverse brown. Aerial mycelium abundant, smooth and thin walled, septate, 1- to 2-μm wide. Terminal and lateral conidia borne on hyphae, short protrusions, or side branches. Conidia solitary, sometimes two in chains, pyriform, sometimes subglobose, smooth or rarely rough walled, ecru, 4.0–6.0 × 3.0–5.5 μm (*av.* = 5.5 × 4.0, *n* = 50). Intercalary conidia abundant, olivary, subglobose to globose, 4.0–7.0 × 3.0–5.5 μm (*av.* = 5.0 × 4.0, *n* = 50).

Sexual morph: not observed.

Geographical distribution: China.

Material examined: China, Guizhou, Guiyang, the Affiliated Hospital of Guizhou Medical University, 26°59′N, 106°71′E, from soil beside a road, September 2016, Zhi. Y. Zhang (HMAS 255397 – holotype; CGMCC 3.18498 = GZUIFR K277.1 – ex-type living cultures; ibid., CGMCC 3.18499 = GZUIFR K277.2; ibid., CGMCC 3.18500 = GZUIFR K277.3). The living cultures were kept in sterile 30% glycerol and deposited in a −80°C freezer.

Notes: *Solomyces sinensis* was isolated from soil in Guizhou Province, China. We did not compare morphological characteristics between *S. sinensis* and another two strains within *Solomyces* owing to the lack of morphological description of these two strains (Minnis and Lindner, 2013). However, *S.*

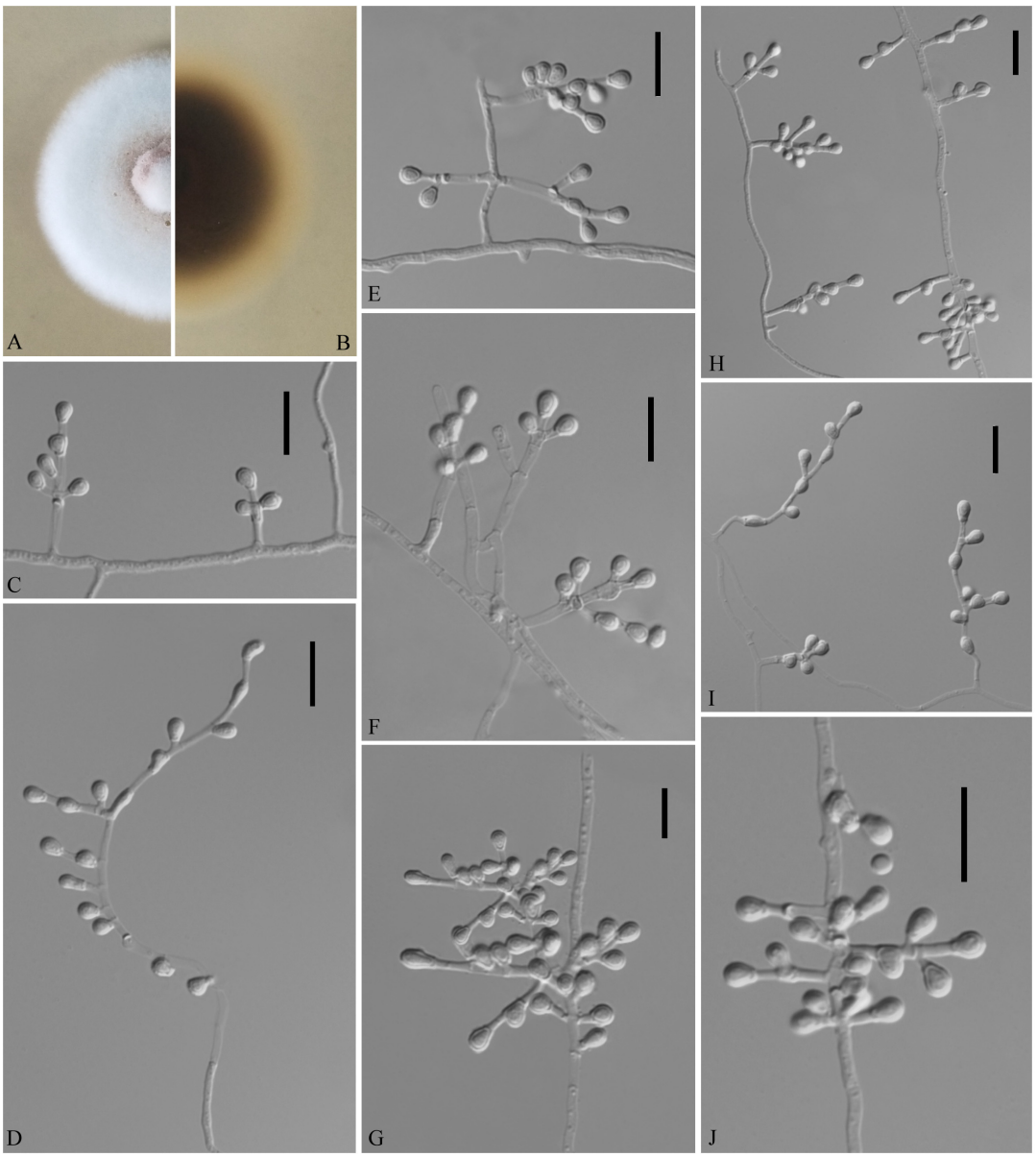

FIGURE 6 | *Pseudogymnoascus sinensis* (from ex-holotype CGMCC 3.18493). **(A,B)** The front and reverse of a *P. sinensis* colony on PDA after 14 days at 25°C. **(C–J)** Conidiophores and conidia. Scale bars = 10 μm.

sinensis is phylogenetically distinct from these strains with high statistical support (1.00 BYPP, 100% MLBS) (**Figures 1**, **2**).

DISCUSSION

In this study, *Solomyces* gen. nov. is introduced with an asexual morph. Five new species are also described. All the new taxa belong in the order Thelebolales, the members of which are ubiquitous in the environment. Several taxa belonging to this order have been isolated from tropical to arctic regions. They are often coprophilous and frequently isolated from freshwater and saline lakes (De Hoog et al., 2005). They have also been recorded from soils, epiphytic soils in tree holes (Chen et al., 2017), mine sediments (Crous et al., 2019), and sponges (Bovio et al., 2018). Thelebolales have been recorded as saprobic on dead plant material, rarely as plant-parasitic, and also as animal pathogens, e.g., the well-known white-nose disease of bats (Lorch et al., 2011). In addition, several members of Thelebolales are keratinophilic; i.e., they can invade and degrade keratin material (Saxena et al., 2005). All the proposed new taxa in our study were isolated using the baiting technique, a method specifically

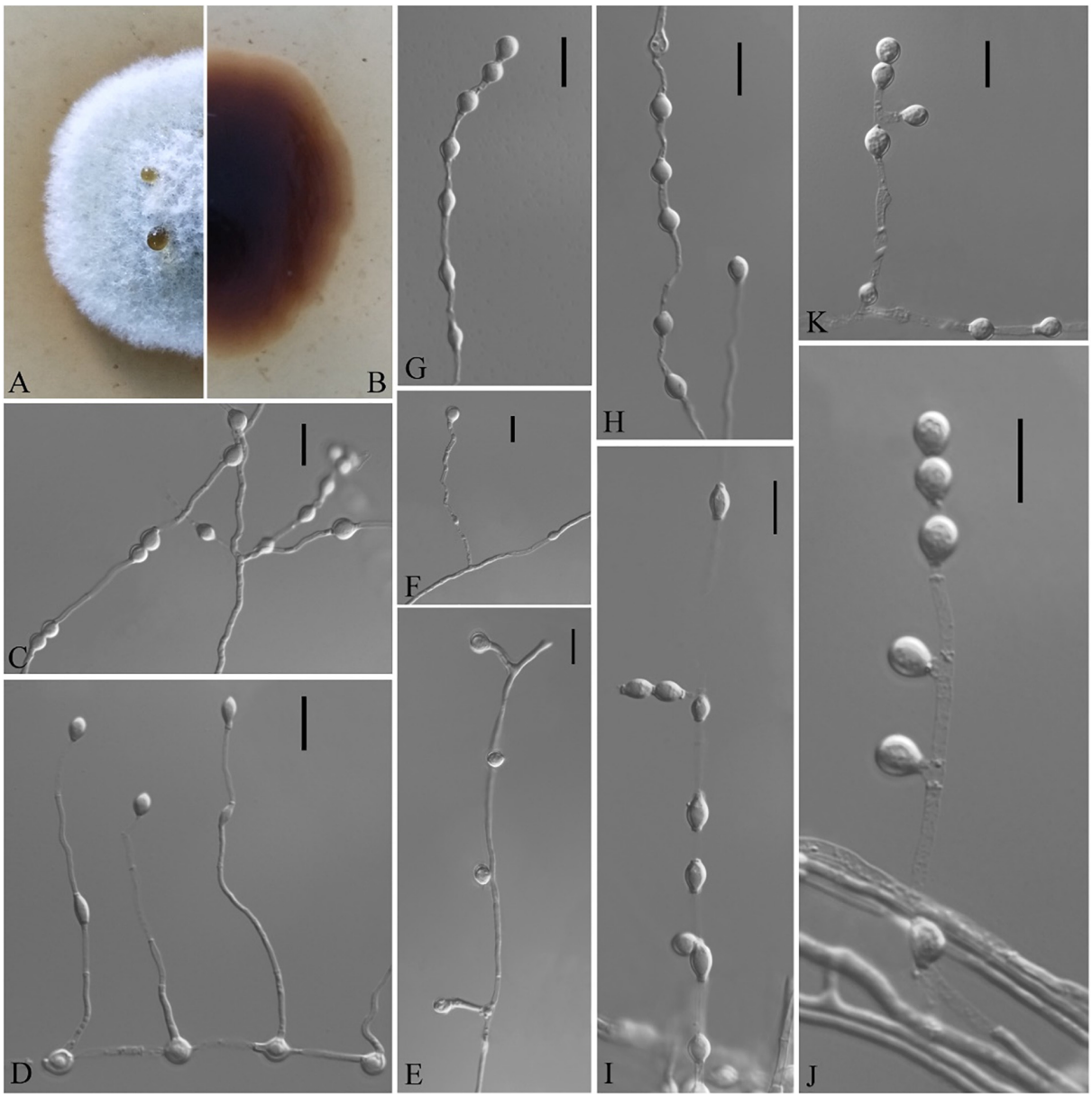

FIGURE 7 | *Solomyces sinensis* (from ex-holotype CGMCC 3.18498). **(A,B)** The front and reverse of a *S. sinensis* colony on PDA after 14 days at 25°C. **(C–K)** Conidiophores and conidia. Scale bars = 10 μm.

designed for the isolation of keratinophilic fungi. Consequently, additional studies are needed to assess whether our new taxa can also degrade keratin material.

Recent studies demonstrated that the Thelebolales comprise at least two families or groups (Ekanayaka et al., 2019; Johnston et al., 2019; Batista et al., 2020). Some studies have proposed that the Thelebolales consists of Pseudeurotiaceae and Thelebolaceae based on three distinct pieces of evidence (568 ITS sequences, 15 genes concatenated from 279 species, and a phylogenomic approach from 51 complete genomes) and on a phylogenomic approach, respectively (Johnston et al., 2019; Batista et al., 2020). The Thelebolaceae, represented by the *Thelebolus* and *Antarctomyces*, share a common ancestor with the family Pseudeurotiaceae, represented by the genus *Pseudogymnoascus* (Johnston et al., 2019; Batista et al., 2020). However, a different study indicated that Pseudeurotiaceae was nested within Thelebolaceae based on phylogenetic analysis and synonymized Pseudeurotiaceae under Thelebolaceae (Ekanayaka et al., 2019). The same authors discovered that several genera, previously classified as Leotiaceae and Leotiomycetes genera *incertae sedis*, clustered within Thelebolales as a sister clade to the Thelebolaceae and defined them as the *Alatospora–Miniancora* clade (Ekanayaka et al., 2019). The studies by Ekanayaka et al. contained more genus taxa in Thelebolales;

therefore, we continued the phylogenetic analysis in Thelebolales based on this study.

Recent reports have indicated that the Thelebolales contained 22 genera. However, because no ITS and *LSU* sequence data were available for *Ascophanus*, *Ascozonus*, *Caccobius*, *Coprobolus*, *Leptokalpion*, *Neelakesa*, and *Pseudascozonus* (Ekanayaka et al., 2019), we could not compare the phylogenetic relationships between these genera and *Solomyces*. In our phylogenetic analysis, our three isolates (CGMCC 3.18498, CGMCC 3.18499, and CGMCC 3.18500; *Solomyces sinensis*) and two isolates of Minnis and Lindner (2013) (15PA02 and 17WV02, from Hibernacular soil in Pennsylvania and West Virginia, respectively) formed an independent clade with strong statistical support (BYPP 1/MLBS 100%) and were close to *Geomyces*. Morphologically, the asexual stage of *Ascophanus*, *Ascozonus*, *Caccobius*, *Coprobolus*, *Leptokalpion*, *Neelakesa*, and *Pseudascozonus* is not recorded in the literature (Wijayawardene et al., 2017). Therefore, no morphological comparison can be done between these genera and *Solomyces*. However, *Solomyces* differs from Geomyces by terminal and lateral conidia borne on hyphae, short protrusions or side branches, olivary, subglobose to globose intercalary conidia, and absence of the forming verticillate and opposite branches with an acute angle to the axis near the apex of conidiophores (Sigler and Carmichael, 1976).

Based on morphological characteristics, it was difficult to distinguish closely related species, and even genera, using traditional taxonomy, and modern phylogenetic methods were a very important adjunct. Although Crous et al. (2019) described the new species, *P. linderi* and *P. turneri*, based on the similarity of morphological characteristics between these two new species and *P. bhattii*, they did not compare the phylogenetic relationship. Our phylogenetic analysis indicated that *P. bhattii* (type strain CBS 760.71) was nested within *Gymnostellatospora* (**Figure 1**), and we, therefore, transferred *P. bhattii* to the *Gymnostellatospora* and named it *G. bhattii*.

DATA AVAILABILITY STATEMENT

The sequences generated in this study can be found in GenBank. The accession numbers of the sequences deposited in GenBank are ITS: MT509362–MT509372, *LSU*: MT509376–MT509386, *MCM7*: MT534202–MT534212, *RPB2*: MT534216–MT534226, and *EF1A*: MT534227–MT534237.

AUTHOR CONTRIBUTIONS

YH and JH were responsible for conceptualization and funding acquisition. ZZ, CD, WC, QM, and XL were responsible for data acquisition. ZZ, CD, and WC did the formal analysis. ZZ wrote the first draft. YH and ZL wrote, reviewed, and edited the manuscript. All authors have read and agreed to the published version of the manuscript.

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