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Cyathus tongxinianus sp. nov. (Basidiomycota) from China

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Abstract

A new species of bird's nest fungus, *Cyathus tongxinianus*, is proposed based on a combination of morphological and molecular evidence. *Cyathus tongxinianus* is characterized by the cupulate to obconical basidiomata with the smooth outer and inner surface of the peridium, a dimitic hyphal system of peridium walls with generative hyphae having clamp connections, the presence of the fimbriate mouth, brown black to dark grey peridioles, a monomitic hyphal system bearing the generative hyphae with clamp connections, the presence of crystals, and sub-globose, thick-walled basidiospores (8.5–19.5 × 7.5–11). Sequences of ITS and nLSU rRNA markers of the studied samples were generated, and the phylogenetic analyses were performed with maximum likelihood, maximum parsimony and bayesian inference methods on two datasets (ITS+nLSU and ITS). The analyses showed that the new species clustered into the genus *Cyathus* within the family Nidulariaceae based on the ITS+nLSU phylogenetic tree. The phylogenetic analyses based on molecular data from ITS sequences showed that *C. tongxinianus* is sister to *C. annulatus*, and groups with *C. renweii.*

Key words: 1 new species, Molecular phylogeny, Nidulariaceae, Taxonomy, Wood-inhabiting fungi

Introduction

Fungi in the Nidulariaceae, otherwise known as 'bird's nest fungi', are among the least studied groups of Basidiomycota (Kraisitudomsook *et al*. 2021). Bird's nest fungi usually grow in decaying wood, on manure, or directly on soil. They have a cosmopolitan distribution and have a rich diversity related to the high diversity of plants growing in boreal, temperate, subtropical, and tropical regions (Brodie 1975, Shinners-Carnelley *et al*. 2002, Blenis & Chow 2005, Zhao *et al*. 2008; Kraisitudomsook *et al*. 2022). Bird's nest fungi are decomposers that absorb nutrients from dead organic materials (Wicklow *et al*. 1984), thus, they play an important role in recycling nutrients and decomposing plant debris in natural ecosystems (Kraisitudomsook & Smith 2020).

The genus *Cyathus* was first introduced by Haller (Haller 1768) and later was adopted by Persoon (Persoon 1801), typified by *C. striatus* (Huds.) Willd. (1787: 399). Due to their cup-like basidiomata resembling bird nests and lenticular periodioles resembling eggs, five genera viz. *Cyathus*, *Crucibulum* Tul. & C. Tul. (1844: 89), *Mycocalia* J.T. Palmer (1961: 58), *Nidula* V.S. White (1902: 271), and *Nidularia* Fr. (1817: 2), are commonly known as bird's nest fungi (Brodie 1975, Gómez & Pérez-Silva 1988, Zhao *et al.* 2008). This genus is characterized by having the deeper or cupped, inverted bell-shaped basidiomata covered with shaggy or tomentose hairs on the outside; peridium composed of three layers of tissues, filled with a number of dark-colored, small, hard lentil-shaped peridioles attached with funicular cords; and colorless, thin- or thick-walled, smooth basidiospores (Lloyd 1906, Brodie 1974, Brodie 1975, Brodie & Sharma 1980, Miller & Miller 1988, Das & Zhao 2012, 2013). Both MycoBank database (http://www.MycoBank.org; 25 April 2023) and Index Fungorum (http://www.indexfungorum.org; 25 April 2023) have registered

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207 specific and infraspecific names in the genus *Cyathus*, but the actual number of species has been estimated to be around 60 (Niranjan & Singh, 2021, Duan *et al.* 2022), of which 35 have been recorded from China (Zhou 2007, Duan *et al.* 2022).

The comprehensive molecular systematic studies on *Cyathus* were started in the last two decades (Matheny *et al.* 2006, Zhao *et al.* 2007, Kraisitudomsook *et al.* 2022). An overview of the phylogeny of Agaricales based on a multilocus analysis of a six-gene region supermatrix revealed that the family Nidulariaceae was close to Cystodermateae, in which *Cyathus striatus* and *Crucibulum laeve* (Huds.) Kambly (1936: 167) grouped together within the family Nidulariaceae (Matheny *et al.* 2006). Phylogenetic relationships among *Cyathus* were investigated with ITS and nLSU ribosomal DNA sequences datasets inferred from the neighbor-joining, maximum likelihood, maximum parsimony, and MrBayes analyses, showing that morphological characters and molecular data were incompatible. These include, for example, the peridium plications, variations in peridium hair anatomy, peridiole structure, and fruit-body color. However, the ITS and nLSU datasets supported the recognition of three infrageneric groups, herein named the ollum, pallidum, and striatum groups (Zhao *et al.* 2007). The phylogeny of *Cyathus* based on ITS and nLSU ribosomal DNA sequences showed that *C. cheliensis* F.L. Tai and C.S. Hung (1948: 161), *C. gansuensis* B. Yang, J. Yu & T.X. Zhou (2002: 313), and *C. megasporus* W. Ren & T.X. Zhou (1992: 25) were respectively accepted as synonyms of *C. limbatus* Tul. & C. Tul. (1844: 78), *C. pygmaeus* Lloyd (1906: 26), and *C. poeppigii* Tul. & C. Tul. (1844: 77). (Zhao *et al.* 2008). On the basis of the morphological and molecular data, Martín *et al.* (2015) studied on the affinities among *Cyathus* species, which showed that this group formed a monophyletic lineage with high support. Silva *et al.* (2016) carried out the phylogenetic reconstruction of *Cyathus* species based on an alignment of 641 nucleotides of the ITS region, and indicated that three new species as *C. batistae* M.M.B. Barbosa & Baseia (2016: 60), *C. apiculatus* M.M.B. Barbosa & Baseia (2016: 62), and *C. pedunculatus* M.A. Silva, M.M.B. Barbosa & Baseia (2016: 63) were proposed, and discussed the relationships with other species of *Cyathus*. Investigation considering four loci (ITS, nLSU, *TEF1*, and *RPB2*) revealed that Nidulariaceae was resolved as a monophyletic lineage with Squamanitaceae as a potential sister branch, and suggested that the species concepts needed to be revisited and refined. Additionally, it was suggested that some bird's nest fungi species had global geographical distributions, whereas others may have more limited ranges, and that basic morphological characteristics of bird's nest fungi had likely been lost or gained multiple times (Kraisitudomsook *et al.* 2021). The phylogenetic research based on five loci (ITS, nLSU, SSU, *TEF1*, and *RPB2*) revealed that a new genus *Retiperidiolia* Kraisit., Choeyklin, Boonprat. & M.E. Sm. (2022: 4) to accommodate this phylogenetically and morphologically unique fungus lineage, in which *Cyathus* formed a monophyletic lineage, sister to *Retiperidiolia* (Kraisitudomsook *et al.* 2022). The phylogenetic analyses based on ITS and nLSU sequences confirmed the monophyly of *Cyathus* with maximum support, and the infrageneric groups of the most recent classification were unchanged, but the clade striatum was found to be divided into four groups and three subgroups (Cruz *et al.* 2023). Recently, by using molecular systematics and morphology, one new species of *Cyathus* from China was introduced (Duan *et al.* 2022).

During the investigations on bird's nest fungi in China, we found a species of *Cyathus* that could not be assigned to any of the described species. The species is here described as *C. tongxinianus sp. nov.* based on the morphological characteristics and molecular phylogenetic analyses.

Materials and methods

Morphological studies

The fresh fruiting bodies of the bird's nest fungi were collected on 13th September 2000 from Horinger County of Nei Monggol Autonomous Region, China. The specimens were dried in an electric food dehydrator at 40 °C, then sealed and stored in an envelope bag and deposited in the herbarium of the Southwest Forestry University (SWFC), Kunming, Yunnan Province, China. The macro-morphological descriptions were based on field notes and photos taken in the field and lab. The macro-morphological descriptions follow Brodie (1975). The micro-morphological data were obtained from the dried specimens and observed under a Nikon Eclipse E100 light microscope (Zhao & Wu 2017). The color terms followed Kornerup and Wanscher (1978). Drawings were made with the aid of a fungus plotter (Wu *et al.* 2022). The measurements and drawings were made from slide preparations stained with Cotton Blue (0.1 mg aniline blue dissolved in 60 g pure lactic acid), Melzer's reagent (3 g potassium iodide, 1 g crystalline iodine, 44 g chloral hydrate, and 40 ml distilled water) and 5% potassium hydroxide. Spore size data, excluded 5% of the measurements from each end of the range, showing them in parentheses. The following abbreviations are used: KOH = 5% potassium hydroxide; CB = cotton blue; CB– = acyanophilous; IKI = Melzer's reagent; IKI– = non-amyloid and non-dextrinoid; L = mean spore length (arithmetic average of all spores); W = mean spore width (arithmetic average of all spores); Q = variation in the L/W ratios between the specimens studied; n = a/b [number of spores (a) measured from given number (b) of specimens].

DNA extraction, PCR amplification, sequencing and phylogenetic analyses

The CTAB rapid plant genome extraction kit-DN14 (Aidlab Biotechnologies Co., Ltd, Beijing, China) was used to obtain genomic DNA from the dried fungal specimens according to the manufacturer's instructions (Zhao & Wu 2017). The nuclear ribosomal ITS region was amplified with ITS5 and ITS4 primer pair (White *et al.* 1990). The nuclear LSU region was amplified with the LR0R and LR7 primer pair (http://lutzonilab.org/nuclear-ribosomal-dna/). The PCR procedure for ITS was as follows: initial denaturation at 95 °C for 3 min, followed by 35 cycles at 94 °C for 40 s, 58 °C for 45 s, and 72 °C for 1 min, and a final extension of 72 °C for 10 min. The PCR procedure for nLSU was as follows: initial denaturation at 94 °C for 1 min, followed by 35 cycles at 94 °C for 30 s, 48 °C for 1 min, and 72 °C for 1.5 min, and a final extension of 72 °C for 10 min. The PCR products were purified and sequenced at Kunming Tsingke Biological Technology Limited Company (Yunnan Province, China). All of the newly generated sequences were deposited in NCBI GenBank (https://www.ncbi.nlm.nih.gov/genbank/) (Table 1).

TABLE 1. List of species, specimens and GenBank accession numbers of sequences used in this study.

Species name	**Sample No.**	**Locality**	**GenBank accession No.**		**References**
			ITS	**nLSU**	
Crucibulum crucibuliforme	F-C0294427F	USA	-	MW600342	Kraisitudomsook *et al.* 2021
C. cyathiforme	Mushroom Observer 426306	USA	MW633046	-	Kraisitudomsook *et al.* 2022
C. laeve	UTC-0025855	USA	MT444042	MT444013	Kraisitudomsook *et al.* 2021
C. laeve	SWFC 21261	China	DQ463357	-	Zhao *et al.* 2007
C. parvulum	FLAS-F-66522	USA	-	MW600344	Kraisitudomsook *et al.* 2021
Cyathus africanus	DAOM 200370	Tanzania	DQ463347	-	Zhao *et al.* 2007
C. albinus	UFRN-Fungos 2239	Brazil	KY176371	-	Accioly *et al.* 2018
C. amazonicus	URM 80036	Brazil	KY495280	-	Accioly *et al.* 2018
C. annulatus	MichaelKuo-8200901	USA	MT444076	-	Kraisitudomsook *et al.* 2021
C. annulatus	DAOM 200366	Canada	NR_119588	NG_058740	Zhao *et al.* 2007
C. apiculatus	UFRN:Fungos 1448	Brazil	KT365516	-	Silva *et al.* 2016
C. aurantogriseocarpus	UFRN:Fungos:2798	Brazil	KX966026	-	Cruz *et al.* 2017
C. badius Kobayasi	KH:JPN15-1321	Japan	KX906250	-	Cruz *et al.* 2018
C. batistae	UFRN:Fungos 1449	Brazil	KT365515	-	Silva *et al.* 2016
C. berkeleyanus	SWFC 20789	China	DQ463355	-	Zhao *et al.* 2007
C. bulleri H.J.	DAOMC 195062	India	MK020156	-	Vats & Mishra 2021
C. canna Lloyd	CBS 370.80	Costa Rica	MH861275	-	Vu *et al.* 2019
C. colensoi Berk.	DAOM 200423	India	DQ463344	-	Zhao *et al.* 2007
C. crassimurus	DAOM 200372	Hawaii	DQ463350	-	Zhao *et al.* 2007
C. discoideus	AB 7831	China	KY652080	-	Cruz 2017
C. gansuensis	SWFC 20880	China	DQ463348	-	Zhao *et al.* 2007
C. gansuensis	69	China	KC869661	-	Cruz *et al.* 2018
C. gracilis	AB7873	Japan	KY652081	-	Cruz 2017
C. hookeri	SWFC 20799	China	DQ463346	-	Zhao *et al.* 2007
C. hortensis	UFRN:Fungos:1819	Brazil	KX906252	-	Cruz *et al.* 2018
C. ibericus	AH:48137	Spain	KX858597	-	Crous *et al.* 2016
C. ibericus	AH:48138	Spain	KX858598	-	Crous *et al.* 2016

......*continued on the next page*

TABLE 1. (Continued)

Species name	**Sample No.**	**Locality**	**GenBank accession No.**		**References**
			ITS	**nLSU**	
C. intermedius	UFRN:Fungos 1033	Brazil	KT365519	-	Silva *et al.* 2016
C. jiayuguanensis	SWFC 20846	China	DQ463341/ NR119585	-	Zhao *et al.* 2007
C. lijiangensis	CLZhao 27922	China	OQ846829	-	
C. lijiangensis	CLZhao 28033	China	OQ846828	-	
C. lignilantanae	MA Fungi 87327	Cape Verde	NR_154827	-	Cruz *et al.* 2018
C. limbatus	UFRN-Fungos 2238	Brazil	KY176373	-	Accioly *et al.* 2018
C. magnomuralis	UFRN:Fungos:1817	Brazil	KX906251	-	Cruz *et al.* 2018
C. minimus Pat.	AB7868	Japan	KY652082	-	Cruz 2017
C. novae-zeelandiae	PDD-76442	New Zealand	MT444096	MT444025	Kraisitudomsook *et al.* 2021
C. olla	BPI 727227	Canada	DQ463345	-	Zhao *et al.* 2007
C. olla	PDD-86833	New Zealand	MT444086	-	Kraisitudomsook *et al.* 2021
C. pallidus	KKUITN2	Thailand	KU202745	-	Sutthisa & Sanoamuang 2020
C. pallidus	KKUITN3	Thailand	KU202751	-	Sutthisa & Sanoamuang 2020
C. pallidus	NK-01	USA	MT444032	MT444006	Kraisitudomsook *et al.* 2021
C. parvocinereus	UFRN:Fungos:1814	Brazil	KX906253	-	Cruz *et al.* 2018
C. pedunculatus	UFRN:Fungos 403	Brazil	KT365518	-	Silva *et al.* 2016
C. poeppigii	cp-457	Brazil	KT962176	-	Silva *et al.* 2016
C. pyristriatu	MFLUCC:14-0770	Germany	KU865513	-	Richter *et al.* 2016
C. renweii	SWFC 201406	China	DQ463352	DQ463333	Zhao *et al.* 2007
C. setosus	DAOM 200815	Jamaica	DQ463349	-	Zhao *et al.* 2007
C. stercoreus	NK-08	USA	MT444037	-	Kraisitudomsook *et al.* 2021
C. stercoreus	DM4	Canada	KY706156	-	Hay *et al.* 2019
C. striatus	NK-61	England	MT444056	MT444020	Kraisitudomsook *et al.* 2021
C. subglobisporus	BBH-14815	USA	MT444063	-	Kraisitudomsook *et al.* 2021
C. subglobisporu	BBH18348	Thailand	EF613553	-	Zhao *et al.* 2008
C. tongxinatus	CLZhao 27588[a]	China	OQ676567	OQ861249	Present study
C. tongxinatus	CLZhao 28521	China	OQ859922		Present study
C. triplex Lloyd	SWFC 21077	China	DQ463353	-	Zhao *et al.* 2007
C. uniperidiolus	AMH:10196	India	MN398297	-	Boonmee *et al.* 2021
C. wenshanensis	CLZhao 20202	China	ON795104		Duan *et al.* 2022
Cystodermella cinnabarina	DBG-20996	USA	-	MW600359	Kraisitudomsook *et al.* 2021
C. cinnabarina	DBG-29008	USA	-	MW600358	Kraisitudomsook *et al.* 2021
Mycocalia denudata	CBS-494.85	Canada	MT444107	MW600347	Kraisitudomsook *et al.* 2021
M. denudata	K(M)141776	England	MT444100	OM831392	Kraisitudomsook *et al.* 2021
Nidula candida	UBCF23768	Canada	KC581303	-	Unpublished
N. niveotomentosa	SWFC 3000	China	DQ463358	-	Zhao *et al.* 2007
N. niveotomentosa	UBC:F19769	Canada	HQ604744	-	Silva *et al.* 2016
Nidularia deformis	CMP	Spain	MW248505	-	Olariaga *et al.* 2020
N. farcta	CBS-156.42	Sweden	MH856106	MW600352	Kraisitudomsook *et al.* 2021
N. pulvinata	FH-00822889	USA	MT444039	MT444010	Kraisitudomsook *et al.* 2021
Retiperidiolia aquaphila	UFRN:Fungos:2944	Brazil	MG836281	MG836282	Kraisitudomsook *et al.* 2022
R. reticulata	BBH-19922	Thailand	OM831397	OM831389	Kraisitudomsook *et al.* 2022

[a] is shown type material, holotype.

Sequencher 4.6 (GeneCodes, Ann Arbor, MI, USA) was used to assemble and edit the generated sequence reads. Sequences were aligned in MAFFT 7 (https://mafft.cbrc.jp/alignment/server/) using the “G-INS-I” strategy. The alignment was adjusted manually using AliView version 1.27 (Larsson 2014). The sequence alignment was deposited in TreeBase (submission ID 30354). *Cystodermella cinnabarina* (Alb. and Schwein.) Harmaja (2002: 45) was selected as an outgroup for phylogenetic analyses of combined ITS and nLSU sequences data (Kraisitudomsook *et al.* 2021). *Crucibulum laeve* and *Nidula niveotomentosa* (Henn.) Lloyd (1910: 455) were selected as an outgroup for the phylogenetic analysis of ITS sequence (Accioly *et al.* 2018).

Maximum parsimony (MP), Maximum Likelihood (ML) and Bayesian Inference (BI) analyses were applied to the combined three datasets. Approaches to phylogenetic analyses followed Zhao & Wu (2017). MP analysis was performed in PAUP* version 4.0b10 (Swofford 2002). All of the characters were equally weighted and gaps were treated as missing data. Trees were inferred using the heuristic search option with Tree Bisection and Reconnection (TBR) branch swapping and 1000 random sequence additions. Max trees were set to 5000, branches of zero length were collapsed and all most parsimonious trees were saved. Clade robustness was assessed using bootstrap (BT) analysis with 1000 replicates (Felsenstein 1985). Descriptive tree statistics tree length (TL), the consistency index (CI), the retention index (RI), the rescaled consistency index (RC), and the homoplasy index (HI) were calculated for each most-parsimonious tree generated. ML was inferred using RAxML-HPC2 through the Cipres Science Gateway (www.phylo.org) (Miller *et al.* 2009). Branch support (BS) for ML analysis was determined by 1,000 bootstrap replicates and evaluated under the gamma model.

The best-evolutionary model of each alignment was estimated using jModelTest (Guindon & Gascuel 2003; Posada 2008) under the Akaike information criterion. MrModeltest 2.3 (Nylander 2004) was used to determine the best-fit evolution model for the dataset for Bayesian Inference (BI). Bayesian Inference was performed with MrBayes 3.1.2 with a general time reversible (GTR+I+G) model of DNA substitution and a gamma distribution rate variation across sites (Ronquist & Huelsenbeck 2003). Four Markov chains were run for two runs from random starting trees for 500 thousand generations combined ITS and nLSU sequences (Fig. 1), or for 600 thousand generations for ITS (Fig. 2) with trees and parameters sampled every 100 generations. The first quarter of all the generations were discarded as burn-ins. A majority rule consensus tree of all remaining trees and posterior probabilities were calculated. Branches were considered significantly supported if they received a maximum likelihood bootstrap value (BS) of ≥70%, a maximum parsimony bootstrap value (BT) of ≥70%, or Bayesian posterior probabilities (BPP) of ≥0.95.

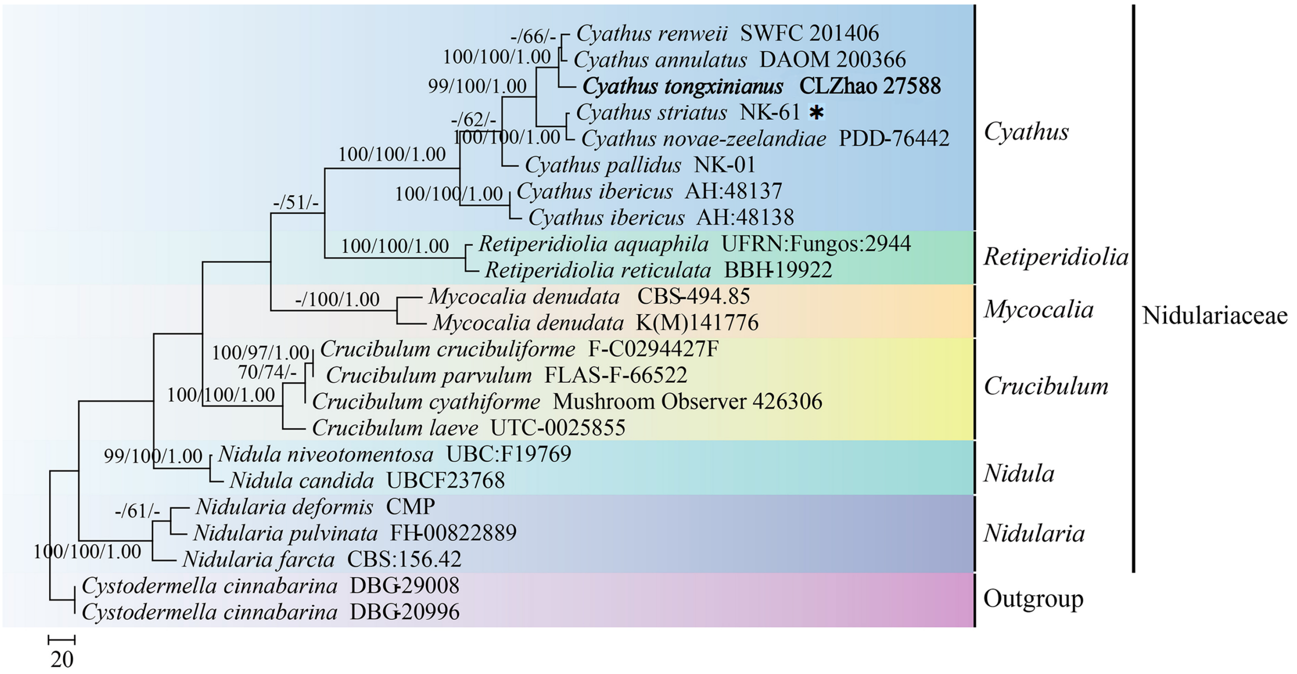

FIGURE 1. Maximum parsimony strict consensus tree illustrating the phylogeny of the new species of *Cyathus* and related genera in the family Nidulariaceae based on combined ITS and nLSU sequences dataset. Branches are labelled with maximum likelihood bootstrap values ≥70%, parsimony bootstrap values ≥50% and Bayesian posterior probabilities ≥0.95, respectively, Scale bar = 20. The new species is in bold, ✱ corresponds to type species.

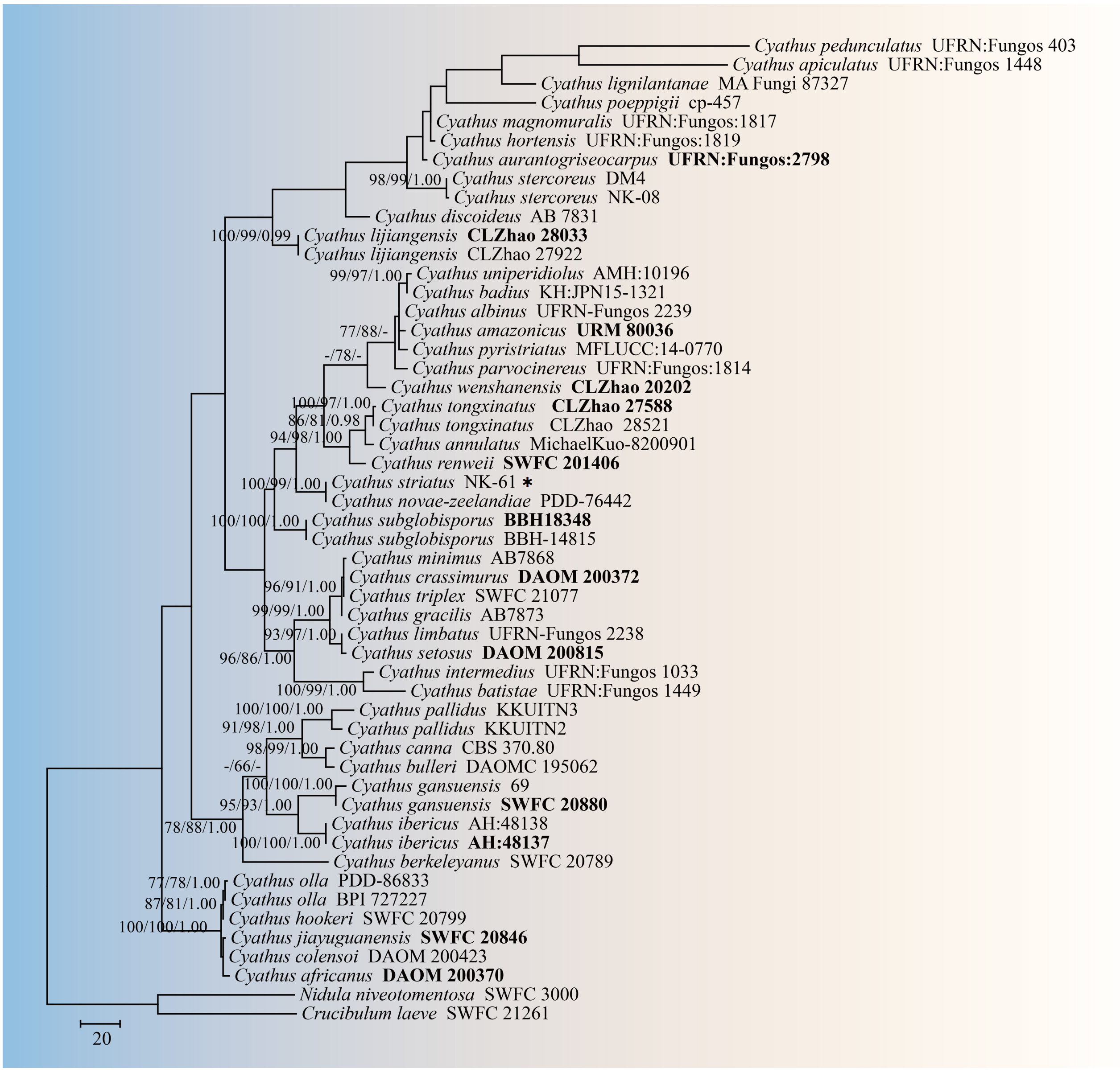

FIGURE 2. Maximum parsimony strict consensus tree illustrating the phylogeny of the new species and related species in *Cyathus* based on ITS sequences. Branches are labelled with maximum likelihood bootstrap values ≥70%, parsimony bootstrap values ≥50%, and Bayesian posterior probabilities ≥0.95, respectively. Scale bar = 20. Type specimen accessions are in bold, ✱ corresponds to type species.

Results

Molecular phylogeny

The combined ITS and nLSU dataset (Fig. 1) included sequences from 23 fungal specimens representing 20 species. The dataset had an aligned length of 1535 characters, of which 969 characters are constant, 100 are variable and parsimony-uninformative, and 466 are parsimony-informative. Maximum parsimony analysis yielded one equally parsimonious tree (TL = 1084, CI = 0.7076, HI = 0.2924, RI = 0.8119, RC = 0.5745). The best model for the combined ITS and nLSU dataset estimated and applied in the Bayesian analysis was GTR+I+G (lset nst = 6, rates = invgamma; prset statefreqpr = dirichlet (1,1,1,1). The bayesian analysis and ML analyses resulted in a similar topology to that of the MP analysis with an average standard deviation of split frequencies = 0.009958 (BI), and the effective sample size (ESS) across the two runs is double the average ESS (avg ESS) = 532.5. The phylogeny (Fig. 1) based on the combined ITS and nLSU sequences indicated that the species *Cyathus tongxinianus* was nested within the genus *Cyathus*.

The ITS dataset alone (Fig. 2) included sequences from 52 fungal specimens representing 44 species. The dataset had an aligned length of 887 characters, of which 347 characters are constant, 223 are variable and parsimony-uninformative, and 317 are parsimony-informative. Maximum parsimony analysis yielded 5000 equally parsimonious trees (TL = 1211, CI = 0.6474, HI = 0.3526, RI = 0.7855, RC = 0.5086). The best model for the ITS dataset estimated and applied in the Bayesian analysis was GTR+I+G (lset nst = 6, rates = invgamma; prset statefreqpr = dirichlet (1,1,1,1). The bayesian analysis and ML analyses resulted in a similar topology to that of the MP analysis with an average standard deviation of split frequencies = 0.009493 (BI), and the effective sample size (ESS) across the two runs is double the average ESS (avg ESS) = 165.5. The phylogenetic tree (Fig. 2) inferred from ITS sequences revealed that *Cyathus tongxinianus* was sister to *C. annulatus* H.J. Brodie (1970: 749) with supports (86% BS, 81% BT, 0.98% BPP), and nested with *C. renweii* T.X. Zhou and R.L. Zhao (2004: 245) with supports (94% BS, 98% BT, 1.00 BPP).

Taxonomy

Cyathus tongxinianus Z.Y. Duan & C.L. Zhao, ***sp. nov.*** Figs. 3, 4, 5, 6
MycoBank no.: MB 848643

***Diagnosis*:—**differs from other *Cyathus* species by its exoperidium with cream tomentum, smooth outer and inner surface, brown black peridioles with double-layered cortex, a monomitic hyphal system with clamped generative hyphae and ellipsoid-elongate, ovoid-elongate basidiospores measuring 8.5–19.5 × 7.5–11 µm.

Etymology*:—tongxinianus* (Lat.) in honour of the Chinese mycologist Prof. Tongxin Zhou.

***Holotype*:—**CHINA. Nei Monggol Autonomous Region, Hohhot, Horinger County, Nantianmen Forest Farm, E 112°25′, N 40°86′, on fallen branch of angiosperm, 13 September 2000, CLZhao 27588 (SWFC).

***Fruiting body*:—**cupulate to obconical, 4–10 mm in high, 3–5 mm in wide at the mouth, 0.1–0.2 mm in wide at the base, without expanding at the top or tapering abruptly at the base; *emplacement* clearly observed; *young fruit bodies* clavate, lightly brown (6D4), covered by the cream (5A3) hairs aggregated into tomentum or shaggy clusters; *exoperidium* slightly brown (6E4), tomentulose, external wall non-striate, covered with cream (4A2), irregular and flexible tufts of the hair; the hairy appearance composed by hyphae with clamp connections, yellowish brown, thick-walled (up to 0.5–2 µm thick), 3–8.5 µm in diameter; *endoperidium* silvery grey to greyish brown (6E4–7F3), smooth inside; *mouth* finely fimbriate; *peridium walls* consist of three different layers: (1) outer wall layer hyphal system dimitic, CB–, IKI–, tissues unchanged in KOH; generative hyphae with clamp connections, buff to pale brown, slight thick-walled, branched, 2.5–4.5 µm in diameter; skeletal hyphae yellowish to pale brown, thick-walled, unbranched, 3–5.5 µm in diameter; (2) inner wall layer, hyphal system dimitic, CB–, IKI–, tissues unchanged in KOH; generative hyphae with clamp connections, buff-yellow to pale brown, slight thick-walled, branched, 3.5–5 µm in diameter; skeletal hyphae buff-yellow to pale brown, thick-walled, unbranched, slightly curved, 4–6 µm in diameter; (3) middle layer, pseudoparechymatous, colorless.

***Peridioles*:—**angular to irregular, subglobose to broadly ellipsoid, brown black (6F5) to dark grey (8F1), surface irregular, wrinkled, tunica olivaceous buff (4C4), 1.3–2 × 1.2–1.8 mm; *cortex* double-layered; *funicular cord* present, funiculus hyphae with clamp connections, thick-walled, branched, yellowish brown, 1.5–4.5 µm in diameter; *hyphal system* of peridiole monomitic, generative hyphae with clamp connections, colorless, slightly thick-walled, frequently branched, with oil drops inside, 1–5 µm in diameter, CB–, IKI–, tissues unchanged in KOH; crystals present.

***Basidiospores*:—**subglobose, ellipsoid-elongate, ovoid-elongate to broadly ovoid, some irregular, hyaline, smooth, thick-walled (wall up to 0.5–2.5 µm thick), CB–, IKI–, with inclusions or oil-like globule, (8–)8.5–19.5(–20.5) × (7–)7.5–11(–11.5) µm, the range of the mean of length × the range of the mean of width = 14.13 × 9.22 µm, Q = 1.5–1.6 (n = 60/2). Basidia not observed.

***Additional specimen examined (paratype)*:—**CHINA. Nei Monggol Autonomous Region, Hohhot, Horinger County, Nantianmen Forest Farm, E 112°25′, N 40°86′, on fallen branch of angiosperm, 13 September 2000, CLZhao 28521 (SWFC).

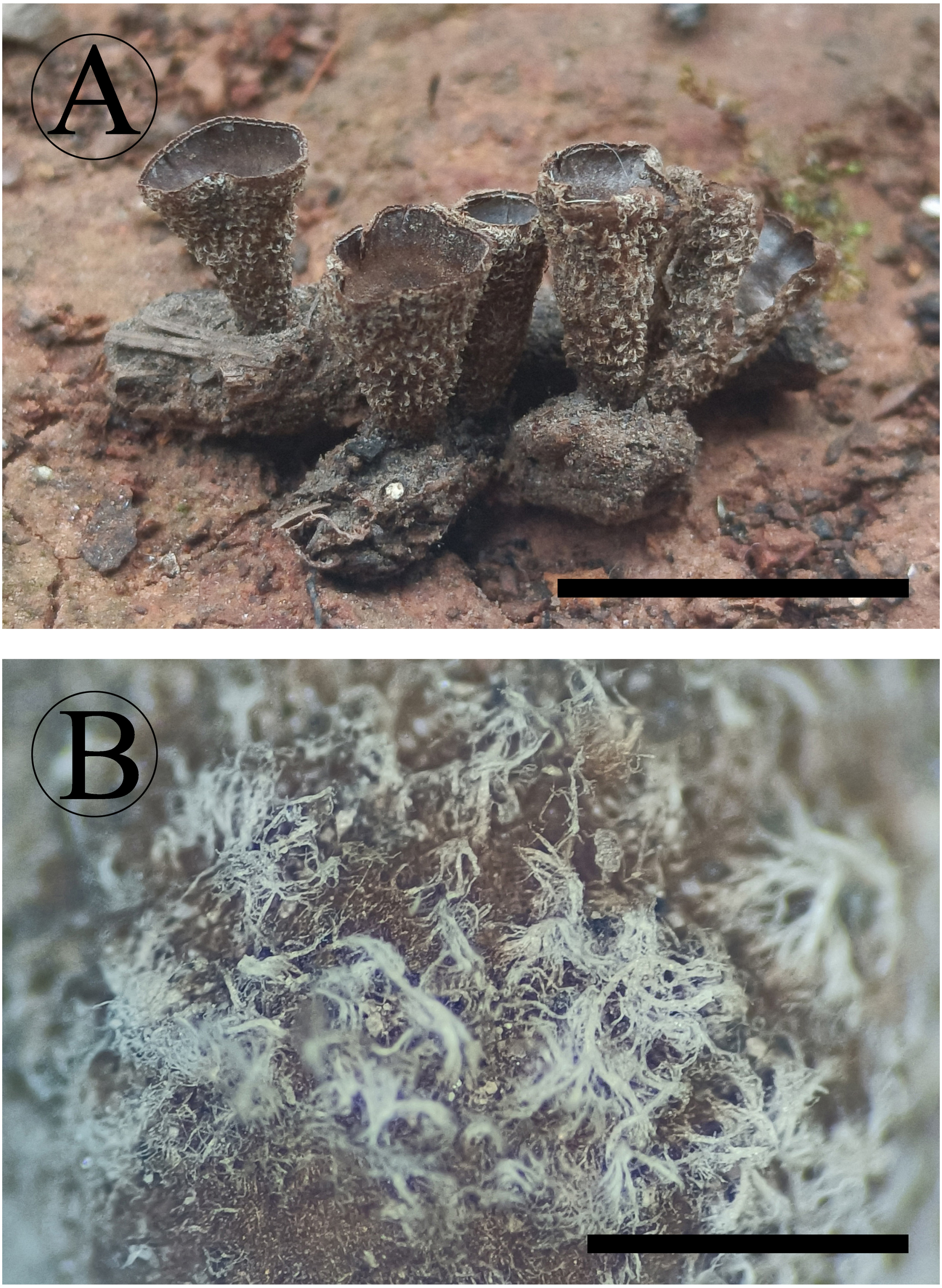

FIGURE 3. Basidiomata of *Cyathus tongxinianus* showing in (B) hairs of peridium. Bars: A = 1 cm, B = 1 mm (Holotype: CLZhao 27588). Photoplate by: Zi-Yan Duan.

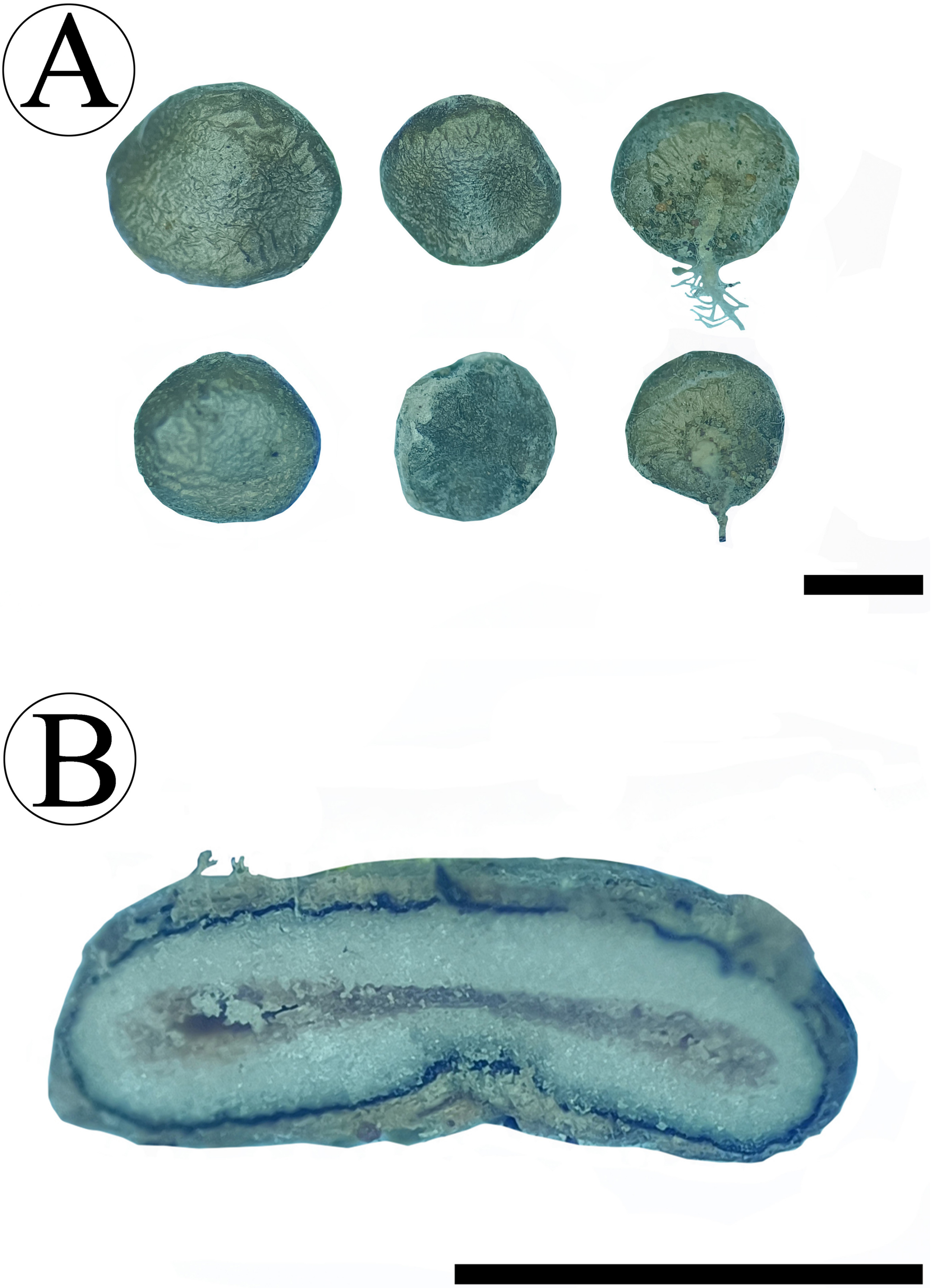

FIGURE 4. Peridioles of *Cyathus tongxinianus* showing in (B) a cross-section. Bars: A–B = 1 mm (Holotype: CLZhao 27588). Photoplate by: Zi-Yan Duan.

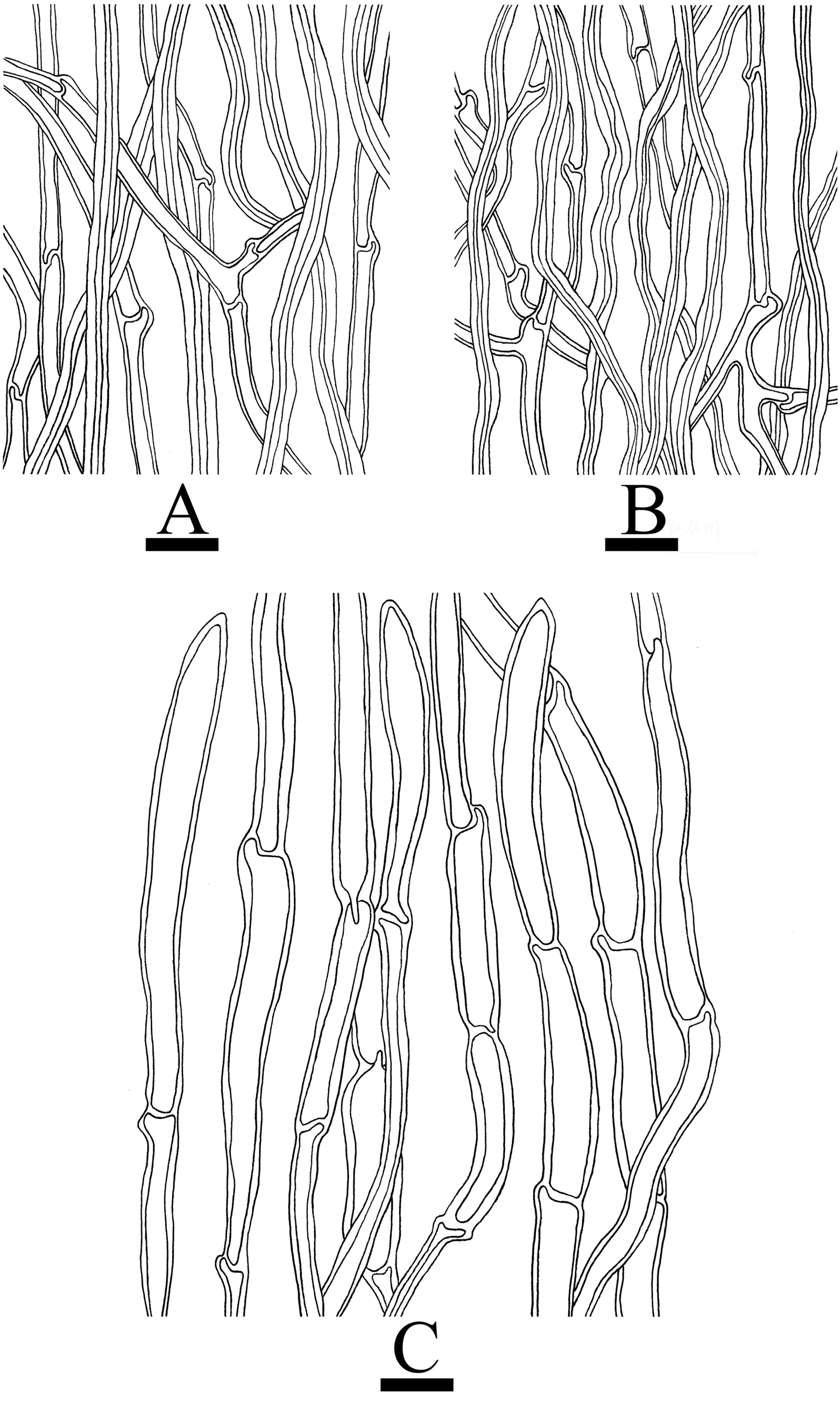

FIGURE 5. Microscopic structures of *Cyathus tongxinianus* (drawn from the holotype, CLZhao 27588). A: Outer wall of peridium. B: Inner wall of peridium. C: Structure of the hairs. Bars: A–C = 10 µm. Drawings by: Zi-Yan Duan.

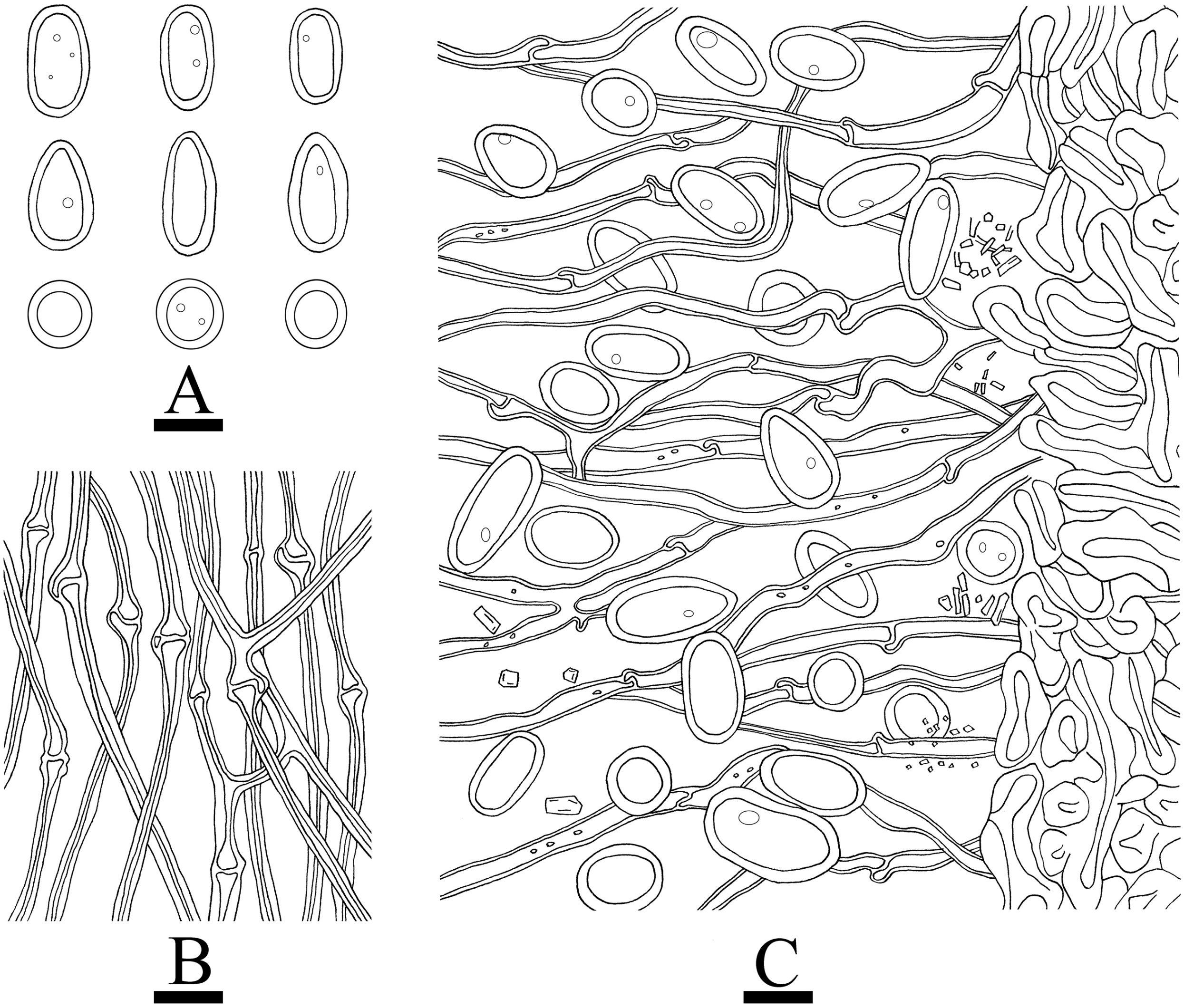

FIGURE 6. Microscopic structures of *Cyathus tongxinianus* (drawn from the holotype, CLZhao 27588). A: Basidiospores. B: Generative hyphae of the funicular cord. C: Internal structure of the peridiole. Bars: A–C = 10 µm. Drawings by: Zi-Yan Duan.

Discussion

In the present study, *Cyathus tongxinianus* is described as a new species based on phylogenetic analyses and morphological characteristics. Phylogenetically, the bird's nest fungi family revealed that Nidulariaceae was resolved as a monophyletic lineage with Squamanitaceae as a potential sister taxon, in which two genera *Cyathus* and *Crucibulum* formed independent and well-supported clade individually, and *Nidula* and *Nidularia* formed another clade, but each genus is polyphyletic (Kraisitudomsook *et al.* 2021). Additionally, Kraisitudomsook *et al.* (2022) proposed a new genus named *Retiperidiolia*. In the present study, based on ITS and nLSU (Fig. 1) datasets, we found that six taxa *Crucibulum*, *Cyathus*, *Mycocalia*, *Nidula*, *Nidularia,* and *Retiperidiolia* formed their own independent clades, and the new species, *Cyathus tongxinianus*, was nested within the genus *Cyathus* of the family Nidulariaceae. Based on ITS topology (Fig. 2), *C. tongxinianus* was sister to *C. annulatus* and then grouped with *C. renweii*. However, morphologically *C. annulatus* differs from *C. tongxinianus* by having the expanded peridium at the top, the presence of lip of peridium marked by a distinct deep-brown ring, and its wider basidiospores (15–19 × 15.5–17 µm, Brodie 1970); *C. renweii* differs in its conspicuous striations on the outer and inner surface of the peridium, and larger basidiospores (21–31 × 10.5–13.5 µm, Zhou *et al.* 2004).

Morphologically, six *Cyathus* species including *C. batistae*, *C. hortensis* R. Cruz & Baseia (2014: 175), *C. magnomuralis* R. Cruz & Baseia (2014: 177), *C. pedunculatus*, *C. poeppigii* and *C. lignilantanae* R. Cruz & M.P. Martín (2015: 165) are similar to *C. tongxinianus* by having peridioles with double-layered cortex. However, *C. batistae* differs by its expanded mouth of basidiomata, dark brown exoperidium, and smaller basidiospores (9–13 × 5–8 µm) with an apiculus (Silva *et al.* 2016); *C. hortensis* is distinguished by its basidiomata constricted abruptly at the base and forming a slender stipe, and larger basidiospores (17–34 × 13–20 µm; Cruz & Baseia 2014); *C. magnomuralis* is separated by having the dark blond exoperidium, and larger basidiospores (27–49 × 23–41 µm) with the small apiculus (Cruz & Baseia 2014); *C. pedunculatus* differs by its larger basidiospores (25–34 × 22–29 µm, Silva *et al.* 2016); *C. poeppigii* is distinguished by its basidiomata with incurved mouths and a slender stipe at the base, and larger basidiospores (30–45 × 18–30 µm, Zhao *et al.* 2006); and *C. lignilantanae* is separated by having the reddish brown exoperidium, conspicuously striations on the outer and inner walls of the peridium, brownish grey to greyish brown and larger peridioles (2.1–2.3 × 1.8–2 mm; Martín *et al.* 2015).

Three taxa *Cyathus hookeri* Berk. (1854: 204), *C. olla* (Batsch) Pers. (1801: 237) and *C. stercoreus* (Schwein.) De Toni (1888: 40) are similar to *C. tongxinianus* by having smooth peridium walls. However, *C. hookeri* differs by its basidiomata with short stipe, and single-cortex peridioles (Sharma 2016); *C. olla* is distinguished by its larger basidiomata (10–15 mm height, and 7–10 mm width), greyish exoperidium, pure silver peridioles, and smaller basidiospores (9.8–11.2 × 6.4–8 µm, Dorjey *et al.* 2013); and *C. stercoreus* differs by having both larger peridioles (2.4–3.1 × 1.8–2.6 µm) and basidiospores (30–41 × 25–31 µm, Gómez & Pérez-Silva 1988).

The family Nidulariaceae is a characteristic group of Agaricomycetes (Basidiomycota), previously studied based on morphological, phylogenetic, and cytological studies in China (Wu *et al.* 2020, Dai *et al.* 2021), but its knowledge is far to be complete (Xu *et al.* 2019, Huang *et al.* 2020, Ma *et al.* 2020, Wang *et al.* 2020, Cai *et al.* 2023, Yang *et al.* 2023, Yuan *et al.* 2023, Zhao *et al*. 2023). Therefore, the present work contributes to increasing the known fungal diversity of saprotrophs from China and pretends to encourage studies in the Nidulariaceae family.

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