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Morphological and molecular identification of three new resupinate species of *Hyphoderma* (Hyphodermataceae, Agaricomycetes) from East Asia

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Abstract

The genus *Hyphoderma* is one of the most important corticioid fungi worldwide, which causes white rot in wood and plays an important role in forest ecosystems and carbon cycle. In this study, three new wood-inhabiting fungal species, *H. marginatum*, *H. tropicum* and *H. yunnanense* are proposed based on a combination of the morphological and molecular evidence. *Hyphoderma marginatum* is characterized by the cracking, hard fragile basidiomata having smooth hymenial surface with the upwarping margin, a monomitic hyphal system with clamped generative hyphae, and cylindrical basidiospores. *Hyphoderma tropicum* is characterized by the resupinate basidiomata with tuberculate hymenial surface, presence of the moniliform cystidia, and ellipsoid to cylindrical basidiospores (6.5–7.5 × 3–4 µm), *Hyphoderma yunnanense* is characterized by the corneus basidiomata, presence of clamped septate cystidia, and ellipsoid to cylindrical basidiospores. Sequences of ITS and nLSU rRNA genes were used for phylogenetic analyses using maximum likelihood, maximum parsimony, and Bayesian inference methods. The three new species of *Hyphoderma* inferred from ITS sequences and form separate lineages within the genus.

Keywords: Basidiomycota, corticioid fungi, molecular systematics, wood-inhabiting fungi, Yunnan Province

Introduction

Hyphoderma Wallr. (1833: 576) (Hyphodermataceae, Polyporales) represents one of the most species-rich and taxonomically complicated genera among wood-inhabiting fungi typified by *H. setigerum* (Fr.) Donk. (1957: 15) (Donk 1957; Yurchenko & Wu 2015; Kirk *et al.* 2008). The species within the genus cause white rot (Wu 1997b), and is one of the most important fungal groups that plays a key role in the carbon cycle and the most efficient wood decomposers in the forest ecosystem (Floudas*et al.* 2012). The genus is characterized by resupinate to effuse-reflexed basidiomata with ceraceous consistency, and a smooth to tuberculate, grandinioid or odontioid hymenial surfaces, a monomitic hyphal system (rarely dimitic) with clamp connections on generative hyphae, presence of cystidia or not, suburniform to subcylindrical and cylindrical basidia, and ellipsoid to subglobose, smooth, thin-walled basidiospores (Wallroth 1833, Bernicchia & Gorjón 2010). Both MycoBank database (www.MycoBank.org; 10 March 2023) and Index Fungorum (www.indexfungorum.org; 10 March 2023) register 203 specific and infraspecific names in *Hyphoderma*. *Hyphoderma* species are extensively studied. Currently, about 110 species have been accepted worldwide (Donk 1957, Nakasone 2008, Wu *et al.* 2010, Baltazar *et al.* 2016, Martín *et al.* 2018, Ma *et al.* 2021, Guan & Zhao 2021a,b, Guan *et al.* 2021), including 31 species from China (Wu 1997a,b, Dai 2011, Yurchenko & Wu 2014a,b, Yurchenko & Wu 2015, Ma *et al.* 2021, Guan & Zhao 2021 a,b, Guan *et al.* 2021).

DNA sequence data has become a popular source of information for studying fungal speciation and biogeography (Petersen & Hughes 1999, 2007). The internal transcribed spacer (ITS) regions have been proposed as universal

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barcodes for fungi (Schoch *et al.* 2012, Blaalid *et al.* 2013, Kõljalg*et al.* 2013), and ITS sequences have proved useful in describing many fungal species (Irinyi *et al.* 2015, Vu *et al.* 2016). Molecular systematics has supported many existing lineages, changed the traditional attribution of a large number of fungal species, and found many new taxa.

The phylogenetic analyses of *Hyphoderma* were carried out based on the large subunit nuclear ribosomal RNA gene (nLSU) and ITS sequences. Based on molecular phylogenetic method, Langer (2002) revealed that all species of *Hyphoderma* did not cluster at the same position in a homobasidiomycete tree, and the analysis results showed that *H. praetermissum* (P. Karst.) J. Erikss. & Å. Strid (1975: 505) clustered with *Resinicium bicolor* (Alb. & Schwein.) Parmasto (1968: 98), whereas the other *Hyphoderma* species and several polypore species formed a hyphodermoid clade. Subsequently, the mycologists (Larsson *et al.* 2004) focused on the classification and evolution of the corticioid species based on the multi-gene datasets, which revealed that two species *H. praetermissum* and *H. guttuliferum* (P. Karst.) Donk (1962: 223) of were closely related to *Hyphodontia* species, *Hyphoderma* s. str. and *Hypochnicium* J. Erikss. (1958: 100) taxa were confirmed as sister group and positioned in the phlebioid clade. Nilsson *et al.* (2003) highlighted the phylo geography of *Hyphoderma setigerum* in the northern hemisphere based on the molecular, morphological and crossing tests, nine preliminary taxa were shown to exist inside the *H. setigerum* complex. Molecular systematics covering *Hyphoderma* taxa revealed the classification among the corticioid fungi and indicated that *H. obtusum* J. Erikss. (1958: 97) and *H. setigerum* clustered into Meruliaceae Rea and then grouped with genus *Hypochnicium polonense* (Bres.) Å. Strid (1975: 68), based on the ITS and nLSU sequences (Larsson 2007). Telleria *et al.* (2012) discussed the relationships between *Hyphoderma* and *Peniophorella* P. Karst. (1889: 427), in which species from *Hyphoderma* and *Peniophorella* grouped together and a new species, *H. macaronesicum* was proposed. Binder *et al.* (2013) presented the molecular studies employing multi-gene datasets (5.8S, nLSU, mitochondrial rRNA gene sequences (*mtSSU*), translation elongation factor 1-α (*TEF1*) gene, the second-largest subunit of RNA polymerase II (*RPB2*) and the largest subunit of RNA polymerase II) to investigate the phylogenetic relationships within the Polyporales, in which *H. cremeoalbum* (Höhn. & Litsch.) Jülich (1974: 80) and *H. setigerum* were nested into the residual polyporoid clade. Yurchenko & Wu (2014a) studied the *H. setigerum* complex and showed that *H. pinicola* Yurchenko & Sheng H. Wu (2014b: 2) represented a fifth species in this complex. Yurchenko & Wu (2015) reported that *H. moniliforme* (P.H.B. Talbot) Manjón, G. Moreno & Hjortstam (1988: 261) and *H. nemorale* K.H. Larss. (1998: 123), saprobically growing on wood, were recorded as new for mycobiota in China. Based on the various loci analysed, namely ITS, *IGS*, *RPB2* and *EF1-α*, *H. macaronesicum* included at least two separate species, one of which was newly described as *H. paramacaronesicum* Telleria, M. Dueñas, J. Fernández-López & M.P. Martín (2018: 64) (Martín *et al.* 2018). Salcedo *et al.* (2020) confirmed that *H. etruriae* Bernicchia (1993: 38) was not closely related to *H. capitatum* J. Erikss. & Å. Strid (1975: 461) and *H. orphanellum* (Bourdot & Galzin) Donk (1957: 15), and molecular analyses confirmed that these three species belonged to the order Hymenochaetales. Based on molecular systematics and morphology, nine new species of *Hyphoderma* from China were found and recorded (Ma *et al.* 2021, Guan & Zhao 2021a,b, Guan *et al.* 2021).

During investigations on wood-inhabiting fungi in the Yunnan–Guizhou Plateau of China, three additional *Hyphoderma* species were collected. To clarify the placement and relationships of the three species, we study carried out a phylogenetic and taxonomic study on *Hyphoderma*, based on the ITS and nLSU sequences.

Materials and methods

Morphological studies

Fresh fruiting bodies of the fungi growing on the angiosperm trunk were collected from the Puer,Wenshan and Kunming of Yunnan Province, P.R. China. The samples were photographed *in situ*. The fresh macroscopic details were recorded and the samples were transported to the field station where the basidiomata were dried by using an electronic food dryer at 45°C. Once dried, the specimens were carried in envelopes and sealed in zip lock plastic bags and labeled. The dried specimens were deposited in the herbarium of the Southwest Forestry University (SWFC), Kunming, Yunnan Province, P.R. China.The macro-morphological descriptions were based on field notes and photos captured in the field and lab. Color terminology follows Petersen (Petersen, 1996). The micro-morphological data were obtained from the dried specimens and observed under Nikon Eclipse E100 light microscope following Zhao and Wu (2017). Drawings were made with the aid of a fungus plotter. 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, aq. dest. 40 ml) and 5% potassium hydroxide. In presenting spore size data, 5% of the measurements excluded from each end of the range are shown 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, P.R. China) was used to obtain genomic DNA from the dried specimens. The nuclear ribosomal ITS region was amplified with primers ITS5 and ITS4 (White *et al.*, 1990). The nuclear nLSU region was amplified with primer pair LR0R and LR7 (Vilgalys & Hester 1990). 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, P.R. China). All newly generated sequences were deposited in NCBI GenBank (https://www.ncbi.nlm.nih.gov/genbank/). These sequences along with sequences from closely related taxa are given in Table 1.

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

Species name	Sample no.	GenBank accession no.		References
		ITS	**nLSU**	
Climacocystis borealis	FD-31	KP135308	KP135210	Justo *et al.* 2017
Diplomitoporus crustulinus	FD-137	KP135299	KP135211	Justo *et al.* 2017
D. crustulinus	Cui 17690	MW377289	MW377368	Liu *et al.* 2022
Hyphoderma amoenum	USO 286622	HE577030	—	Telleria *et al.* 2012
H. assimile	CBS:125852	MH863808	MH875272	Vu *et al.* 2019
H. cremeoalbum	NH 11538 (GB)	DQ677492	DQ677492	Larsson 2007
H. cremeoalbum	CLZhao 17007	OM985716	OM985753	Unpublished
H. crystallinum	CLZhao 9338*	MW917161	MW913414	Guan & Zhao 2021a
H. crystallinum	CLZhao 9374	MW917162	MW913415	Guan & Zhao 2021a
H. crystallinum	CLZhao 18459	MW917166	MW913419	Guan & Zhao 2021a
H. definitum	NH 12266 (GB)	DQ677493	—	Larsson 2007
H. fissuratum	CLZhao 6731	MT791331	MT791335	Ma *et al.* 2021
H. fissuratum	CLZhao 6726*	MT791330	MT791334	Ma *et al.* 2021
H. floccosum	CLZhao 17215	MW301687	MW293735	Guan & Zhao 2021b
H. floccosum	CLZhao 16492	MW301688	MW293734	Guan & Zhao 2021b
H. floccosum	CLZhao 17129*	MW301683	MW293733	Guan & Zhao 2021b
H. floccosum	CLZhao 17296	MW301686	MW293736	Guan & Zhao 2021b
H. granuliferum	KHL 12561	JN710545	JN710545	Yurchenko & Wu 2014a
H. incrustatum	KHL6685	—	AY586668	Yurchenko & Wu 2014a
H. litschaueri	NH 7603 (GB)	DQ677496	DQ677496	Larsson 2007
H. litschaueri	FP-101740-Sp	KP135295	KP135219	Floudas & Hibbett 2015
H. macaronesicum	TFC:Mic.15981	HE577027	—	Yurchenko & Wu 2014a
H. macaronesicum	MA:Fungi:16099Tell	HE577028	—	Yurchenko & Wu 2014a
H. marginatum	**CLZhao 3404***	**OM985717**	**OM985754**	**Present study**
H. medioburiense	NH 10950 (GB)	DQ677497	DQ677497	Larsson 2007
H. membranaceum	CLZhao 5844	MW917167	MW913420	Guan & Zhao 2021a

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TABLE 1. (Continued)

Species name	Sample no.	GenBank accession no.		References
		ITS	nLSU	
H. microporoides	CLZhao 6857*	MW917169	MW913422	Guan & Zhao 2021a
H. microporoides	CLZhao 8695	MW917170	MW913423	Guan & Zhao 2021a
H. moniliforme	Wu 0211-42*	KC928282	—	Yurchenko & Wu 2015
H. moniliforme	Wu 0211-46	KC928284	KC928285	Yurchenko & Wu 2015
H. moniliforme	CLZhao 10242	OM985718	OM985757	Unpublished
H. moniliforme	CLZhao 10176	MT246965	OM985756	Unpublished
H. mopanshanense	CLZhao 6498*	MT791329	MT791333	Ma *et al.* 2021
H. mopanshanense	CLZhao 6493	MT791328	MT791332	Ma *et al.* 2021
H. mopanshanense	CLZhao 6449	OM985720	OM985759	Unpublished
H. nemorale	TNM F3931	KJ885183	KJ885184	Yurchenko & Wu 2015
H. nemorale	Wu 9508-14*	**KC928280**	**KC928281**	Yurchenko & Wu 2015
H. nudicephalum	Wu9307_29	AJ534269	—	Nilsson *et al.* 2003
H. nudicephalum	Wu9508_225	AJ534268	—	Nilsson *et al.* 2003
H. nudicephalum	CLZhao 17839	OM985721	OM985760	Unpublished
H. obtusiforme	KHL 1464	JN572909	—	Yurchenko & Wu 2014b
H. obtusiforme	KHL 11105	JN572910	—	Yurchenko & Wu 2014b
H. obtusum	JS17804	—	AY586670	Yurchenko & Wu 2014b
H. occidentale	KHL 8477 (GB)	DQ677499	DQ677499	Larsson 2007
H. paramacaronesicum	MA:Fungi:87736	KC984399	—	Martín *et al.* 2018
H. paramacaronesicum	MA:Fungi:87737	KC984405	—	Martín *et al.* 2018
H. pinicola	TNM F13637*	KJ885181	KJ885182	Yurchenko & Wu 2014b
H. pinicola	Wu 0108-36	KC928278	KC928279	Yurchenko & Wu 2014b
H. prosopidis	ARIZ HHB 8479	HE577029	—	Yurchenko & Wu 2015
H. puerense	CLZhao 9476*	MW443045	—	Guan *et al.* 2021
H. puerense	CLZhao 9583	MW443046	MW443051	Guan *et al.* 2021
H. roseocremeum	NH10545	—	AY586672	Yurchenko & Wu 2014b
H. setigerum	FCUG1200	AJ534273	—	Nilsson *et al.* 2003
H. setigerum	FCUG 1688*	AJ534272	—	Nilsson *et al.* 2003
H. sinense	CLZhao 7963	MW301679	MW293730	Guan & Zhao 2021b
H. sinense	CLZhao 17811*	MW301682	MW293732	Guan & Zhao 2021b
H. subsetigerum	Wu9304_18	AJ534277	—	Nilsson *et al.* 2003
H. subtestaceum	CFMR:HHB11620	GQ409521	—	Yurchenko & Wu 2014b
H. tenuissimum	KUC20121102-21	KJ668522	—	Jang *et al.* 2016
H. tenuissimum	KUC11052	KJ714002	—	Jang *et al.* 2015
H. tenuissimum	CLZhao 7221*	MW443049	MW443054	Guan *et al.* 2021
H. tenuissimum	CLZhao 16210	MW443050	MW443055	Guan *et al.* 2021
H. transiens	NH 12304 (GB)	DQ677504	DQ677504	Larsson 2007
H. tropicum	**CLZhao 17308***	**OM985727**	**OM985768**	**Present study**
H. variolosum	CBS:734.91	MH862320	MH873992	Vu *et al.* 2019
H. variolosum	CBS:735.91	MH862321	MH873993	Vu *et al.* 2019
H. yunnanense	**CLZhao 8845***	**OM985728**	**OM985769**	**Present study**
Hypochnicium erikssonii	NH 9635 (GB)	—	DQ677508	Larsson 2007
H. geogenium	NH 10910 (GB)	—	DQ677509	Larsson 2007
H. geogenium	MA:Fungi 48308	FN552534	JN939576	Telleria *et al.* 2010

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TABLE 1. (Continued)

Species name	Sample no.	GenBank accession no.		References
		ITS	nLSU	
H. punctulatum	FP101698sp	KY948827	KY948860	Justo *et al.* 2017
H. cf. *sphaerosporum*	RLG15138sp	KY948803	KY948861	Justo *et al.* 2017
H. wakefieldiae	MA:Fungi 7675	FN552531	JN939577	Telleria *et al.* 2010
Physisporinus subcrocatus	Dai 15917*	KY131870	KY131926	Wu *et al.* 2017
P. subcrocatus	Dai 12800	KY131869	KY131925	Wu *et al.* 2017
P. tibeticus	Cui 9588	KY131873	KY131929	Wu *et al.* 2017
P. tibeticus	Cui 9518	KY131872	KY131928	Wu *et al.* 2017
Rigidoporus eminens	Dai 17200	MT279690	MT279911	Wu *et al.* 2017
R. undatus	Miettinen 13591*	KY948731	KY948870	Justo *et al.* 2017

* indicates type material (holotype).

The sequences were aligned in MAFFT version 7 (Katoh *et al.*, 2019) using the G-INS-i strategy. The alignment was adjusted manually using AliView version 1.27 (Larsson, 2014). The dataset was aligned first and then ITS and nLSU sequences were combined with Mesquite version 3.51. Alignment datasets were deposited in TreeBASE (submission ID 30077). *Climacocystis borealis* (Fr.) Kotl. & Pouzar (1958: 103) and *Diplomitoporus crustulinus* (Bres.) Domański (1970: 192) were selected as outgroup taxa for the phylogenetic analysis of the ITS+nLSU following a previous study (Justo *et al.* 2017), *D. crustulinus* was selected as an outgroup for the phylogenetic analysis of the ITS sequences.

Maximum parsimony (MP), Maximum Likelihood (ML) and Bayesian Inference (BI) analyses were applied to the combined three datasets. Approaches to phylogenetic analyses followed Zhao and 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 TBR branch swapping and 1000 random sequence additions. Maxtrees 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.* 2012). Branch support (BS) for ML analysis was determined by 1,000 bootstrap replicates and evaluated under the gamma model.

MrModeltest 2.3 (Nylander 2004) was used to determine the best-fit evolution model for each data set for Bayesian inference (BI), which was performed using MrBayes 3.2.7a with a GTR+I+G model of DNA substitution and a gamma distribution rate variation across sites (Ronquist *et al.* 2012). A total of 4 Markov chains were run for 2 runs from random starting trees for 2.7million generations for ITS+nLSU (Fig. 1), 1 million generations for ITS (Fig. 2) with trees and parameters sampled every 1000 generations. The first one-fourth of all generations was discarded as burn-in. The majority rule consensus tree of all remaining trees was calculated. Branches were considered as significantly supported if they received maximum likelihood bootstrap value (BS) ≥70%, maximum parsimony bootstrap value (BT) ≥70%, or Bayesian posterior probabilities (BPP) ≥0.95.

Results

Molecular phylogeny

The ITS+nLSU dataset included sequences from 72 fungal specimens representing 48 species. The dataset had an aligned length of 1931 characters, of which 1351 characters are constant, 91 are variable and parsimony-uninformative, and 489 are parsimony-informative. Maximum parsimony analysis yielded 90 equally parsimonious trees (TL = 3491, CI = 0.2796, HI = 0.7204, RI = 0.5942, RC = 0.1661). 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). Bayesian analysis and ML analysis resulted in a similar topology to MP analysis with an average standard deviation of split frequencies = 0.009620 (BI), and the effective sample size (ESS) across the two runs is the double of the average ESS (avg ESS) = 192. The phylogram based on the ITS+nLSU rDNA gene regions (Fig. 1) including three families within Polyporales, in which three new species of *Hyphoderma* fall into Hyphodermataceae.

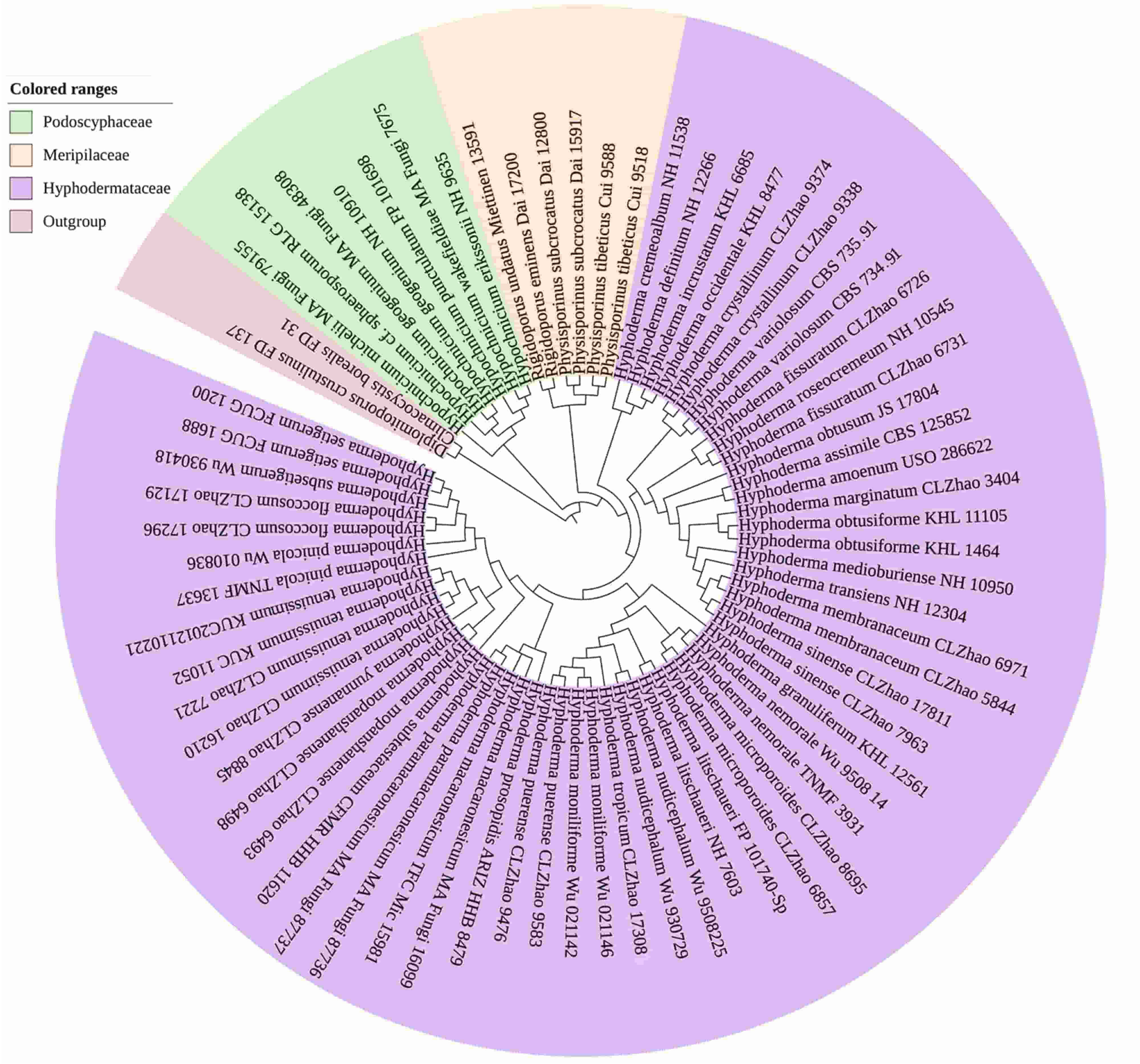

FIGURE 1. Maximum parsimony strict consensus tree illustrating the phylogeny of *Hyphoderma* and related genera in the order Polyporales based on ITS+nLSU sequences. The families represented by each color are indicated in the upper left of the phylogenetic tree.

The ITS dataset included sequences from 54 fungal specimens representing 34 species. The dataset had an aligned length of 671characters, of which 276 characters are constant, 50 are variable and parsimony uninformative, and 345 are parsimony informative. Maximum parsimony analysis yielded 8 equally parsimonious trees (TL = 2222, CI = 0.3258, HI = 0.6742, RI = 0.6035, and RC = 0.1966). The best model for the 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). Bayesian analysis and ML analysis resulted in a similar topology to MP analysis with an average standard deviation of split frequencies = 0.013877 (BI), and the effective sample size (ESS) across the two runs is the double of the average ESS (avg ESS) = 175.5. The phylogram inferred from the ITS sequences analysis (Fig. 2) indicated that three new species grouped into genus *Hyphoderma*, in which *H. marginatum* grouped with two taxa; *H. medioburiense* (Burt) Donk (1957: 15) and *H. obtusiforme* J. Erikss. & Å. Strid (1975: 493) and then closely grouped with *H. amoenum* (Burt) Donk (1957: 14), *H. assimile* (H.S. Jacks. & Dearden) Donk (1957: 15) and *H. fissuratum* C.L. Zhao & X. Ma. *Hyphoderma tropicum* clustered with *H. moniliforme* and *H. puerense* C.L. Zhao & Q.X. Guan (2021: 151). *Hyphoderma yunnanense* grouped with *H. tenuissimum* C.L. Zhao & Q.X. Guan (2021: 153), and then grouped closely with *H. floccosum* C.L. Zhao & Q.X. Guan (2021b: 455), *H. mopanshanense* C.L. Zhao (2021: 39), *H. nudicephalum* Gilb. & M. Blackw. (1988: 378), *H. pinicola*, *H. setigerum* and *H. subsetigerum* Sheng H. Wu.

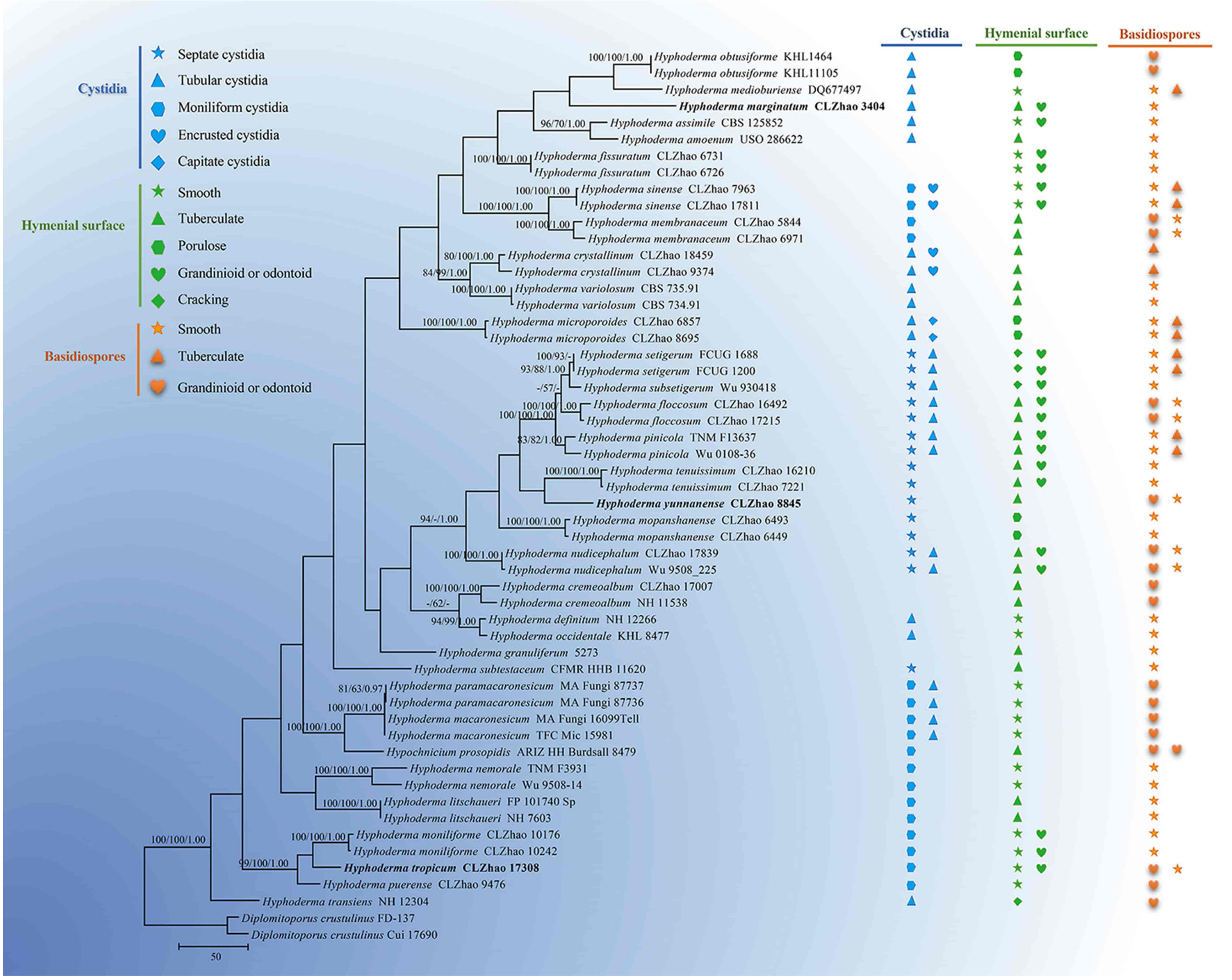

FIGURE 2. Maximum parsimony strict consensus tree illustrating the phylogeny of three new species and related species in *Hyphoderma* based on ITS sequences. Branches are labelled with maximum likelihood bootstrap values ≥70%, parsimony bootstrap values ≥50% and Bayesian posterior probabilities ≥0.95, respectively. Scale bar = 50. The new species are in bold.

Taxonomy

Hyphoderma marginatum Z.Y. Duan & C.L. Zhao, ***sp. nov.*** Figs. 3, 4

MycoBank no.: MB 847109

Etymology:—*marginatum* (Lat.) refers to the basidiomata with upwarping margin of the specimens.

Holotype:—CHINA. Yunnan Province, Puer, Zhenyuan County, Xieqipo Forestry Park, E101°5′54″, N25°00′50″, elev. 1500 m, on fallen angiosperm branch, 1 October 2017, CLZhao 3404 (SWFC).

Fruiting body:—annual, resupinate, adnate, membranous, without odor and taste when fresh, and up to 20 cm long, 2.5 cm wide, and 30–100 µm thick. Hymenial surface smooth, slightly cream when fresh, cream on drying, cracking, hard fragile. Margin sterile, narrow, upwarping, cream, up to 2 mm wide.

Hyphal structure:—Monomitic, generative hyphae with clamp connections,colorless, thin-walled, frequently branched, interwoven, 2.5–4.5 µm in diam, IKI–, CB–, tissues unchanged in KOH.

Hymenium:—Cheilocystidia cylindrical, slightly wider at the top, slightly constricted, thin-walled, 30–48.5 × 7.5–11.5 µm; basidia clavate to subcylindrical, slightly constricted in the base to somewhat sinuous, with 4 sterigmata and a basal clamp connection, 21–31.5 × 5–7 µm; basidioles in shape similar to basidia, but slightly smaller.

Basidiospores:—(8.5–)9–10(–10.5) × 3.5–4.5(–5) µm, L = 9.68 µm, W = 3.99 µm, Q = 2.42 (n = 30/1), cylindrical, colorless, thin-walled, smooth, with irregular vacuole inside, IKI–, CB–.

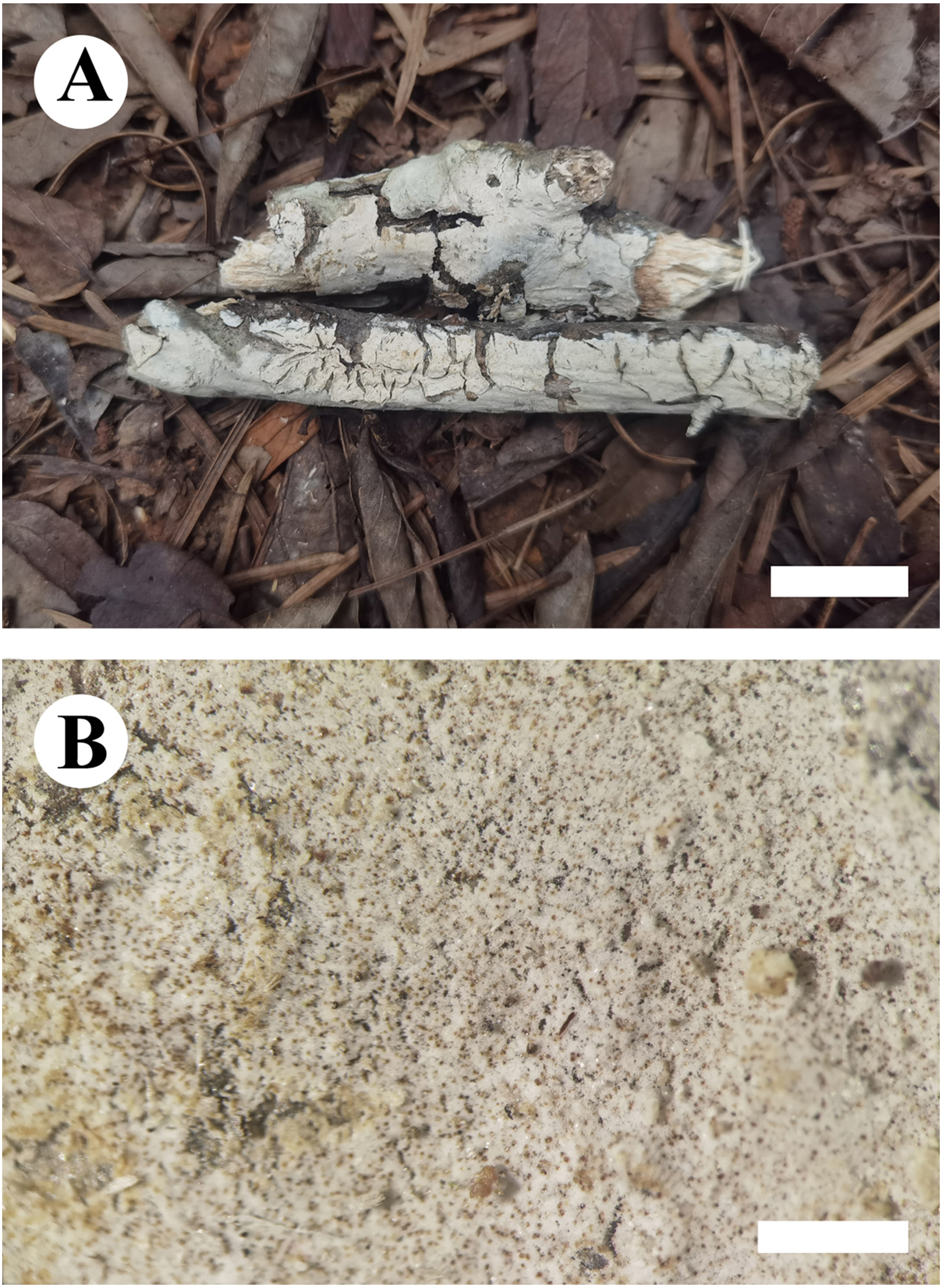

FIGURE 3. Basidiomata of *Hyphoderma marginatum*. Bars: A = 2 cm, B = 1 mm (Holotype: CLZhao 3404). Photo plate by: Zi-Yan Duan.

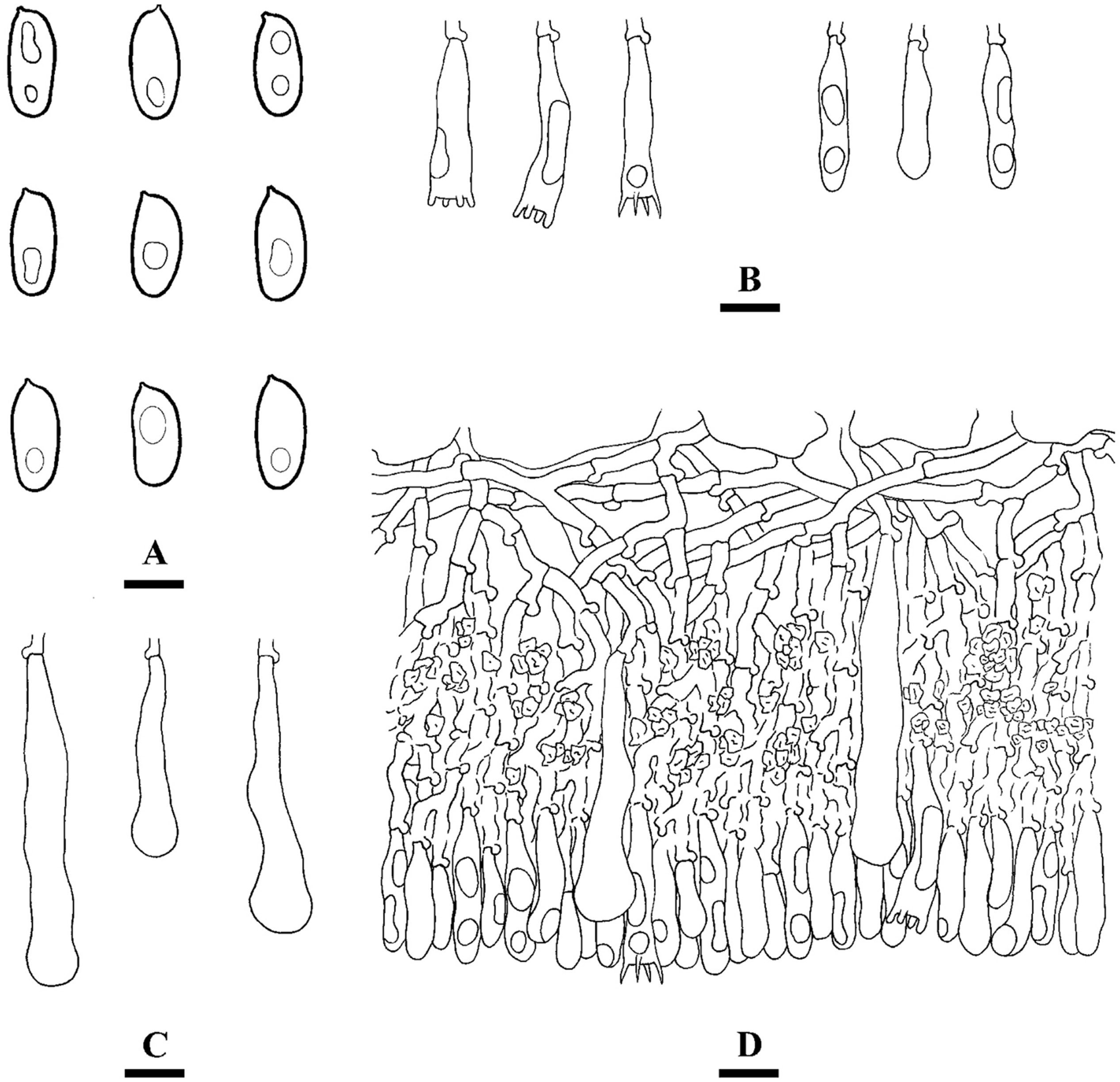

FIGURE 4. Microscopic structures of *Hyphoderma marginatum* (drawn from the holotype, CLZhao 3404). A: Basidiospores. B: Basidia and basidioles. C: Cystidia and cystidioles. D: Part of the vertical section of hymenium. Bars: A = 5 µm, B–D = 10 µm. Drawings by: Zi-Yan Duan.

Hyphoderma tropicum Z.Y. Duan & C.L. Zhao, ***sp. nov.*** Figs. 5, 6
MycoBank no.: MB 847192

Etymology:—*tropicum* (Lat.) refers to the locality (tropics) of the specimens.

Holotype:—CHINA. Yunnan Province, Wenshan, Wenshan National Nature Reserve, E 104°40′32″, N 23°19′32″, elev. 1258 m, on fallen angiosperm branch, 28 July 2019, CLZhao 17308 (SWFC).

Fruiting body**:—**annual, resupinate, adnate, soft coriaceous when fresh, hard coriaceous upon drying, without odor and taste when fresh, and up to 20 cm long, 3 cm wide, and 100–200 µm thick. Hymenial surface tuberculate, white to cream when fresh, cream on drying, cracking. Margin sterile, narrow, and white to cream, up to 1–2 mm wide.

Hyphal structure**:—**Monomitic; generative hyphae with clamp connections,colorless, thin-walled, frequently branched, interwoven, 2.5–5 µm in diam, IKI–, CB–, tissues unchanged in KOH.

FIGURE 5. Basidiomata of *Hyphoderma tropicum*. Bars: A = 2 cm, B = 1 mm (Holotype: CLZhao 17308). Photo plate by: Zi-Yan Duan.

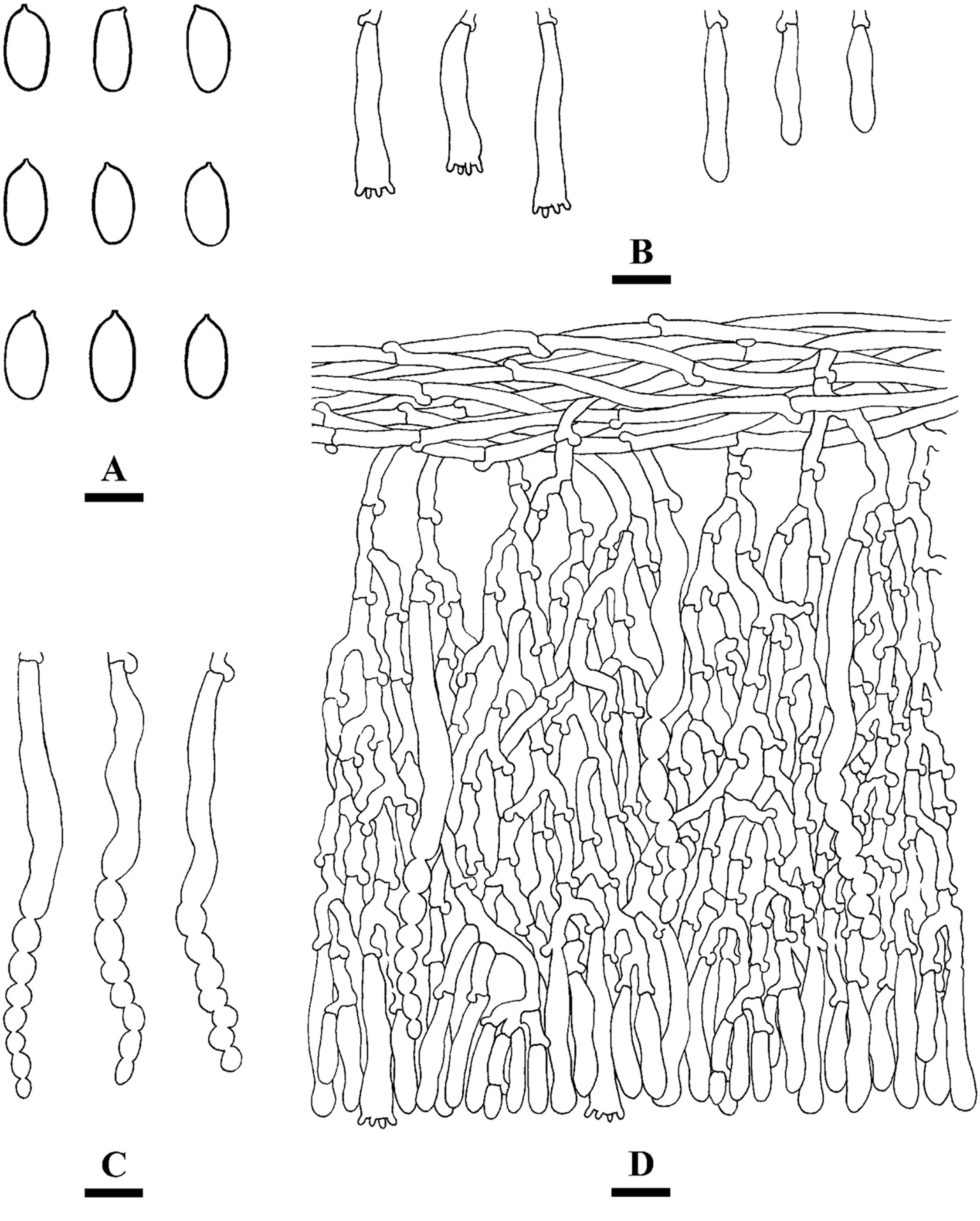

FIGURE 6. Microscopic structures of *Hyphoderma tropicum* (drawn from the holotype, CLZhao 17308). A: Basidiospores. B: Basidia and basidioles. C: Cystidia. D: Part of the vertical section of hymenium. Bars: A = 5 µm, B–D = 10 µm. Drawings by: Zi-Yan Duan.

***Hymenium*:—**Cystidia moniliform, thin-walled, 65–102.5 × 5.5–7.5 µm; basidia clavate, slightly constricted in the base to somewhat sinuous, with 4 sterigmata and a basal clamp connection, 29.5–38 × 4–6 µm; basidioles in shape similar to basidia, but slightly smaller.

***Basidiospores*:—**6.5–7.5(–8) × (2.5–)3–4 µm, L = 7.3 µm, W = 3.38 µm, Q = 2.16 (n = 30/1), ellipsoid to cylindrical, colorless, thin-walled, smooth, IKI–, CB–.

Hyphoderma yunnanense Z.Y. Duan & C.L. Zhao, ***sp. nov.*** Figs. 7, 8

MycoBank no.: MB 847111

Etymology:—*yunnanense* (Lat.) refers to the province (Yunnan Province, China) of the specimen.

Holotype:—CHINA. Yunnan Province, Kunming, Southwest Forestry University, E 102°45′55″, N 25°04′01″, elev. 1939 m, on fallen angiosperm trunk, 31 June 2018, CLZhao 8845 (SWFC).

***Fruiting body*:—**annual, resupinate, adnate, corneus when fresh, coriaceous upon drying, without odor and taste when fresh, and up to 8 cm long, 4 cm wide, and 50–150 µm thick. Hymenial surface tuberculate, slightly cream when fresh, cream to pale buff on drying. Margin sterile, narrow, white to pale cream, up to 1–2 mm wide.

***Hyphal structure*:—**Monomitic; generative hyphae with clamp connections,colorless, thin-walled, frequently branched, interwoven, 2.5–4.5 µm in diam, IKI–, CB–, tissues unchanged in KOH.

***Hymenium*:—**Cystidia cylindrical, with multiple clamped septa, encrusted with crystals, thin-walled, 63–124 × 7–10 µm; basidia clavate to subcylindrical, slightly sinuous, with 2 sterigmata and a basal clamp connection, 15.5–20 × 3.5–4.5 µm; basidioles in shape similar to basidia, but slightly smaller.

***Basidiospores*:—**(9.5–)10–11.5(–12) × 4–5.5(–6) µm, L = 10.71 µm, W = 4.8 µm, Q = 2.23 (n = 30/1), ellipsoid to cylindrical, colorless, thin-walled, smooth, with oil drops inside, IKI–, CB–.

Discussion

Phylogenetically, amplifying the nLSU, ITS, and *RPBl* genes, the family-level classification of Polyporales (Basidiomycota) revealed that four species of *Hyphoderma*; *H. macaronesicum*, *H. medioburiense*, *H. mutatum* (Peck) Donk (1957: 15), and *H. setigerum*, nested into Hyphodermataceae within the residual polyporoid clade (Justo *et al.* 2017). In this study, the phylogram (Fig. 1) inferred from the ITS+nLSU gene regions, four genera, *Hyphoderma*, *Hypochnicium*, *Physisporinus*, and *Rigidoporus*, were separated into three families within Polyporales, in which two genera *Physisporinus*, and *Rigidoporus* were members of Meripilaceae, and one genus; *Hypochnicium* clustered into Podoscyphaceae, and three new species of *Hyphoderma* located in Hyphodermataceae. Based on the ITS sequences, three new species grouped into *Hyphoderma* (Fig. 2), in which *H. marginatum* grouped with two taxa *H. medioburiense* and *H. obtusiforme* and then closely grouped with *H. amoenum*, *H. assimile* and *H. fissuratum*. *Hyphoderma tropicum* clustered with *H. moniliforme* and *H. puerense*. *Hyphoderma yunnanense* grouped with *H. tenuissimum*, and then grouped closely with *H. floccosum*, *H. mopanshanense*, *H. nudicephalum*, *H. pinicola*, *H. setigerum*, and *H. subsetigerum*. However, morphologically *H. amoenum*is is distinct from *H. marginatum* by the larger basidiospores (12–15 × 4–6 µm, Donk 1957); *H. assimile* differs from *H. marginatum* by having the tubular cystidia, and larger basidia (33–37 × 7–8 µm, Eriksson 1958); *H. medioburiense* is separated from *H. marginatum* by the larger cystidia (60–100 µm × 7–10 µm), longer basidia (30−40 µm × 7−8 µm), and larger basidiospores (11–15 µm × 4–5 µm, Burt 1925); *H. obtusiforme* differs from *H. marginatum* by its both larger cystidia (50–60 × 8–10 µm) and basidiospores (10–12 × 5–6 µm, Eriksson and Ryvarden 1975); *H. fissuratum* differs from *H. marginatum* by its generative hyphae present crystal (Ma *et al.* 2021). The species of *H. moniliforme* is distinguished from *H. tropicum* by its wider basidia (20–38 × 6–7.5 µm), and larger basidiospores (8–9 × 3.5–4 µm, Yurchenko & Wu 2015); *H. puerense* differs in its smooth to floccose hymenial surface (6–7.5 × 3–4.5 µm, Guan *et al.* 2021). The taxon, *H. floccosum* is separated from *H. yunnanense* by having a floccose hymenial surface, tubular cystidia and smaller basidiospores (6–9.5 × 3–4.5 µm, Guan & Zhao 2021b); *H. mopanshanense* another taxon differs in having the porulose to pilose hymenial surface (Ma *et al.* 2021); *H. nudicephalum* differs from *H. yunnanense* by the septocystidial (swollen up to 14 µm, Gilbertson & Blackwell 1988); *H. pinicola* differs from *H. yunnanense* by both larger basidia (25–28 × 5–6.5 µm) and basidiospores (13–16 × 4–4.5 µm, Yurchenko & Wu 2014b); *H. setigerum* differs from *H. yunnanense* by having the tubular cystidia, and larger basidia (25–30 × 6–7 µm, Bernicchia & Gorjón 2010); *H. subsetigerum* differs in having larger basidia (20–30 × 4.5–5.5 µm) and smaller basidiospores (6–8 × 2.8–3.2 µm, Wu 1997b); *H. tenuissimum* differs by having the wider basidia (17–31 × 4.5–8 µm) bearing 4 sterigmata (Guan *et al.* 2021).

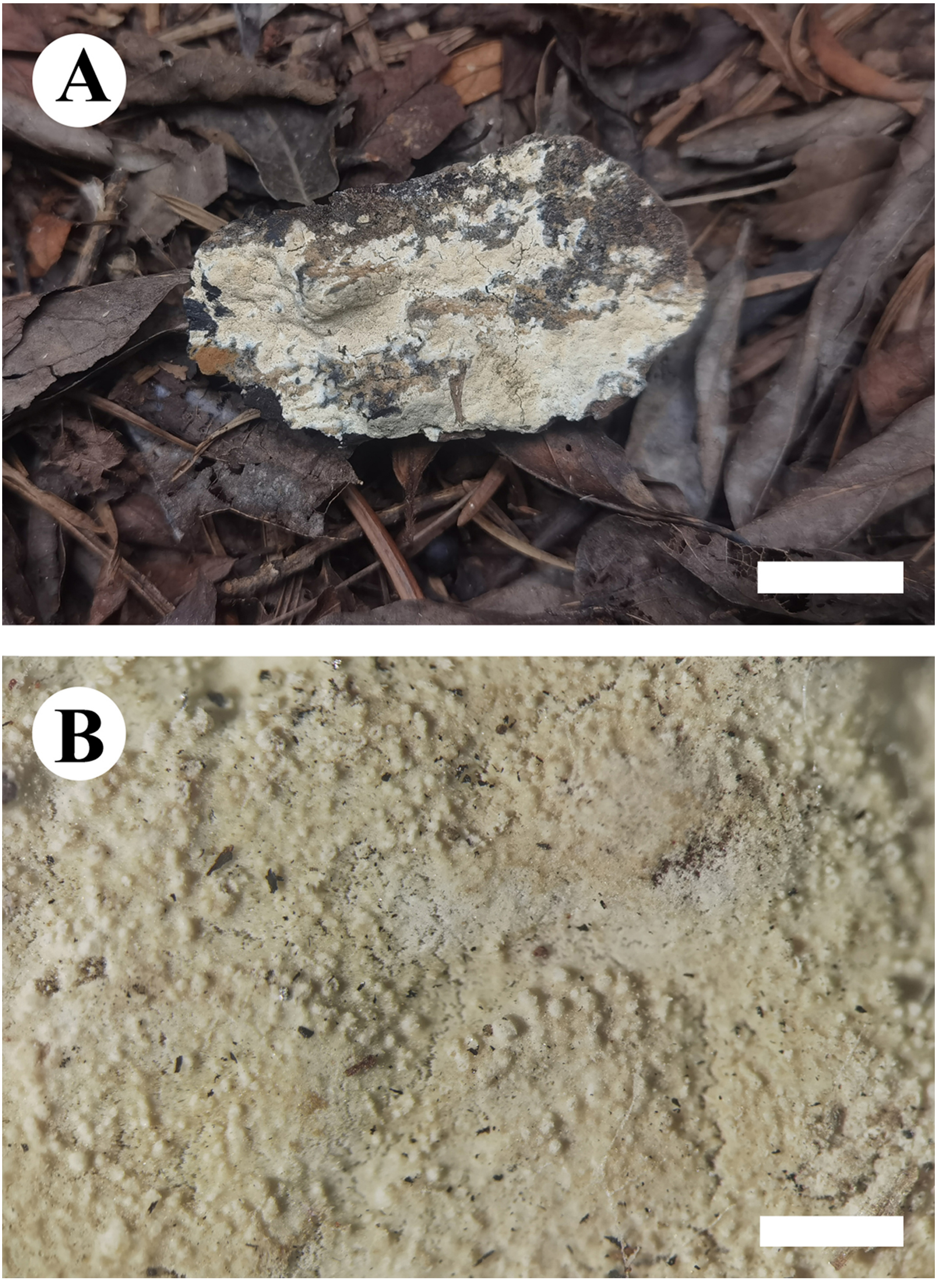

FIGURE 7. Basidiomata of *Hyphoderma yunnanense.* Bars: A = 1 cm, B = 1 mm (Holotype: CLZhao 8845). Photo plate by: Zi-Yan Duan.

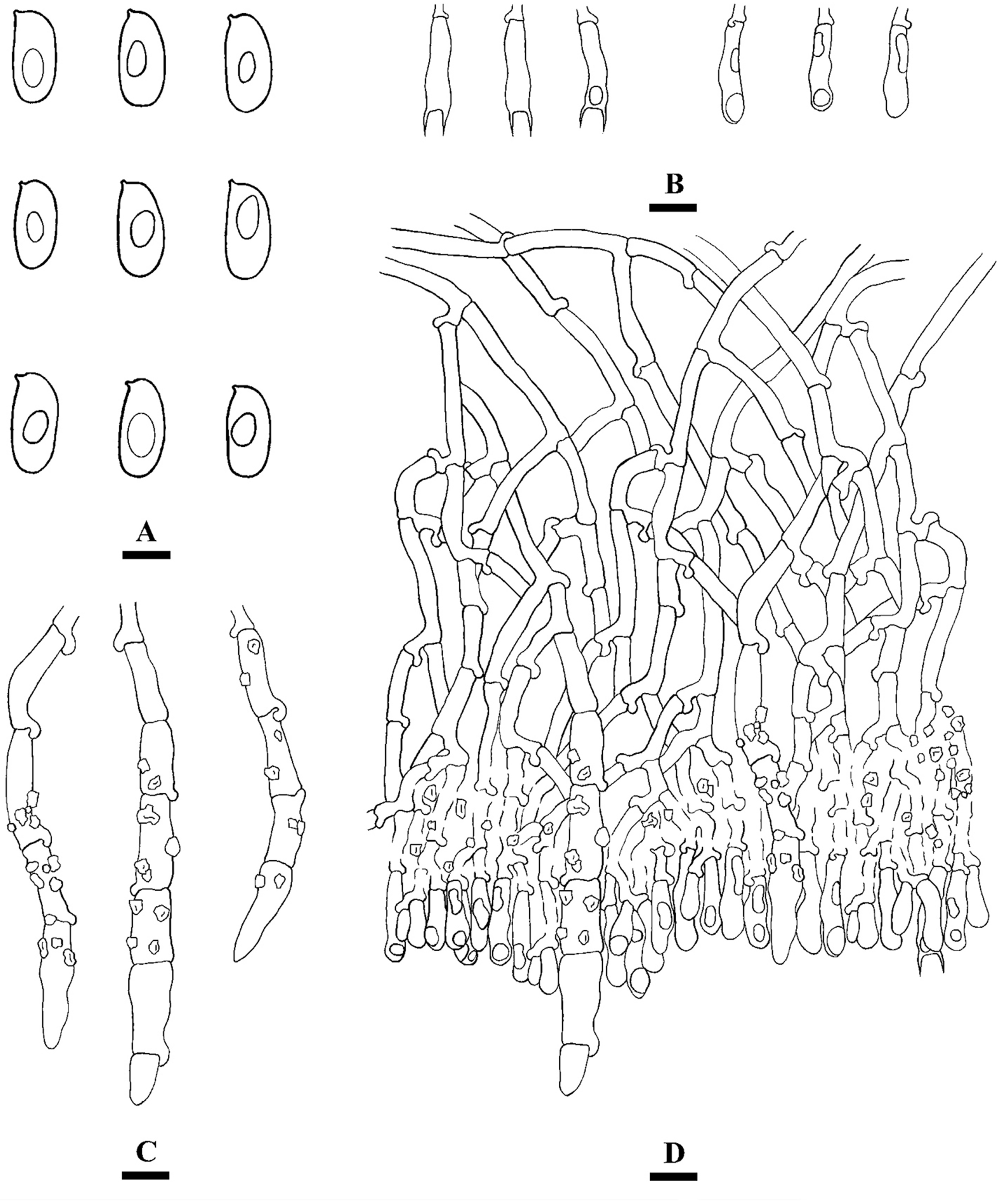

FIGURE 8. Microscopic structures of *Hyphoderma yunnanense* (drawn from the holotype, CLZhao 8845). A: Basidiospores. B: Basidia and basidioles. C: Cystidia. D: Part of the vertical section of hymenium. Bars: A = 5 µm, B–D = 10 µm. Drawings by: Zi-Yan Duan.

Morphologically, *H. marginatum* is similar to *H. obtusum*, *H. puerense* and *H. roseocremeum* (Bres.) Donk (1957: 15) in having a smooth hymenium and non-septate cystidia. However, *H. obtusum* is distinguished from *H. marginatum* by its the wider basidiospores (8–9 × 5–6.5 µm, Eriksson 1958); *H. puerense* differs from *H. marginatum* by the smaller basidiospores (6–7.5 × 3–4.5 µm, Guan *et al.* 2021); *H. roseocremeum*differs in having the larger tubular cystidia (80–100 × 6–9 µm, Donk 1957).

Hyphoderma membranaceum C.L. Zhao & Q.X. Guan (2021a: 8), *H. paramacaronesicum*, *H. prosopidis* prosopidis (Burds.) Tellería, M. Dueñas & M.P. Martín (2012: 1125) and *H. sinense* C.L. Zhao & Q.X. Guan (2021b: 454) are similar to *H. tropicum* by having the moniliform cystidia. However, *H. membranaceum* is distinguished from *H. tropicum* by both larger cystidia (28–60 µm × 6.5–10.5 µm) and basidiospores (11–13.5 × 4.5–5.5 µm, Guan & Zhao 2021a); *H. paramacaronesicum* differs in its both larger cystidia (70–124 µm × 8–13 µm), and basidiospores (12–15 µm × 5.5–7 µm, Martín *et al.* 2018); *H. prosopidis* differs from *H. tropicum* by the arachnoid to farinaceous hymenial surface and larger basidia (40−45 µm × 8−11 µm, Telleria *et al.* 2012); *H. sinense* differs in its having encrusted cystidia (18.5–38 µm × 6–11 µm) and larger basidiospores (8–11.5 µm × 3–5 µm, Guan & Zhao 2021b).

Wood-inhabiting fungi were generally found in dead tree trunks, inverted wood, and artificial wood products, which can secrete various biological enzymes degrading cellulose, hemicellulose and lignin in wood into simple inorganic substances, and they play a pivotal role in forest ecosystem and are important members of ecosystem decomposition (Dai 2011). Based on the morphological and phylogenetic method, a number of wood-inhabiting fungi were recorded in China (Wu *et al.* 2020, 2022, Dai *et al.* 2021, Luo & Zhao 2022, Zhao *et al.* 2023), *Hyphoderma* is one of the important representative groups of wood-inhabiting fungi (Bernicchia & Gorjón 2010), but the species diversity of this genus is still not well known in China, especially in subtropical and tropical areas of this country (Ma & Zhao 2021, Zong *et al*. 2021, Deng & Zhao 2022, Gu & Zhao 2022). The present will be useful to push the further research on fundamental research and applied research of fungi.

Acknowledgements

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