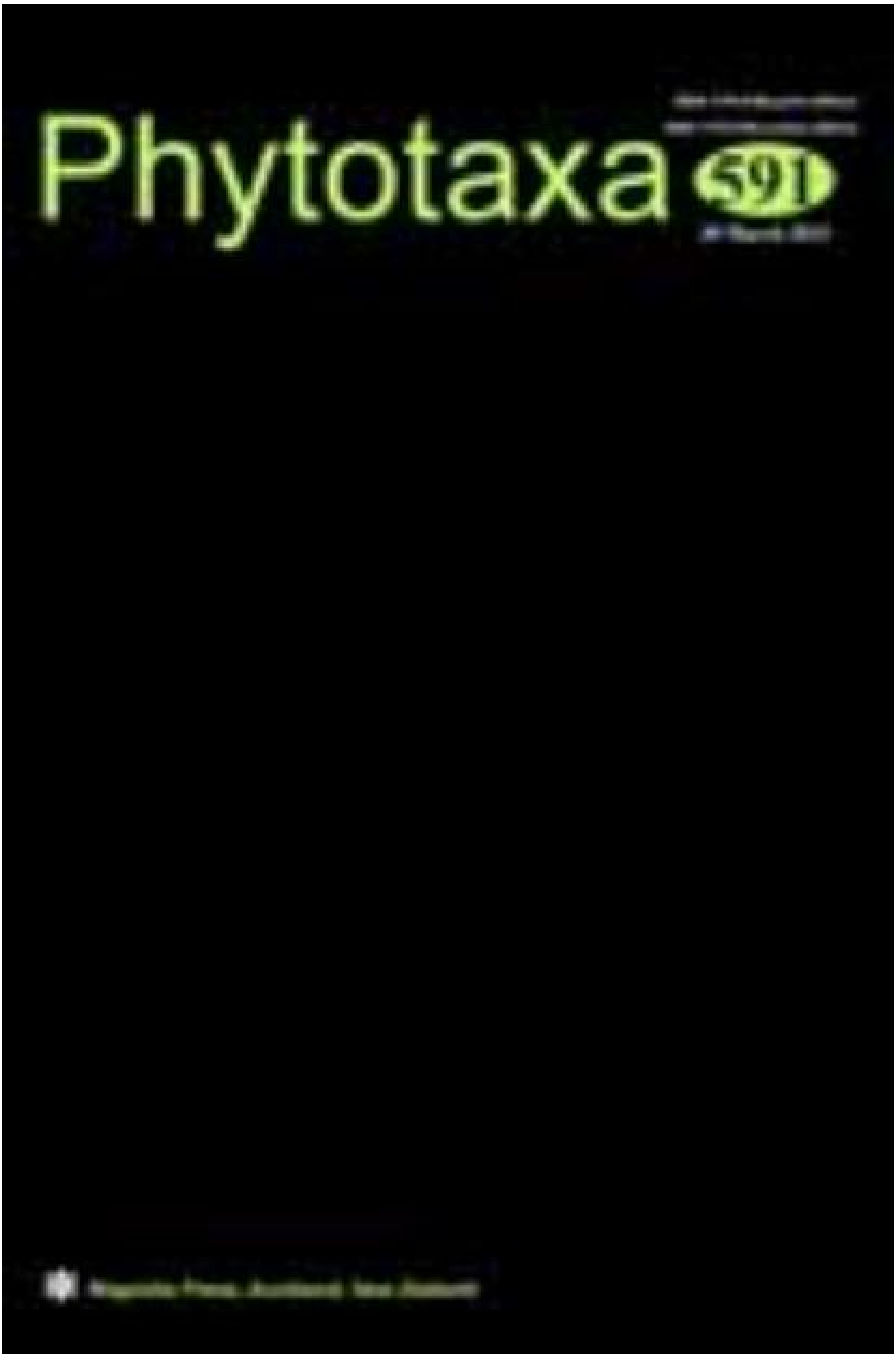

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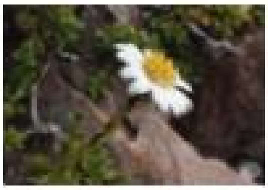

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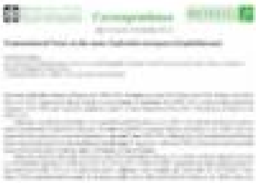

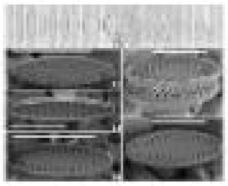

Phytotaxa 591 (1): 001–018
https://www.mapress.com/pt/
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Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

https://doi.org/10.11646/phytotaxa.591.1.1

Morphological and molecular identification for two new species of wood-inhabiting macrofungi (Basidiomycota) from Yunnan-Guizhou Plateau, China

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Abstract

Two new wood-inhabiting macrofungal species, *Coniophora yunnanensis* and *Resupinatus yunnanensis* are proposed based on a combination of morphological features and molecular evidence. *Coniophora yunnanensis* is characterized by annual basidiomata with odontoid hymenophore with olivaceous to brown hymenial surfaces, a monomitic hyphal system with simple septate generative hyphae, and yellowish basidiospores. While, *R. yunnanensis* is characterized by resupinate to cupulate basidiomata with greyish to greyish-brown hymenophore, a monomitic hyphal system with clamped generative hyphae and ellipsoid basidiospores measuring as 4.5–9 × 3.5–7 µm. The phylogenetic analyses based on molecular data of ITS+nLSU sequences showed that *C. yunnanensis* and *R. yunnanensis* nested within Agaricomycetidae, in which *C. yunnanensis* clustered into the family Coniophoraceae (Boletales), and *R. yunnanensis* grouped into family Pleurotaceae (Agaricales). The phylogenetic tree derived from ITS sequences revealed that *C. yunnanensis* grouped into genus *Coniophora*, in which it grouped with *C. marmorata*. Additionally, *R. yunnanensis* clustered into genus *Resupinatus* and then was sister to *R. conspersus*.

Keywords: Asia, Macrofungi, Molecular systematics, Taxonomy, Yunnan Province

Introduction

Fungal classification of the kingdom fungi has been updated continuously, with the frequent inclusion of data from DNA sequences and by using both fresh material and cultures, mycologists re-collect historic taxa and types to accomplish taxonomy and phylogeny in 20 phyla of fungi as Aphelidiomycota, Ascomycota, Basidiobolomycota, Basidiomycota, Blastocladiomycota, Calcarisporiellomycota, Caulochytriomycota, Chytridiomycota, Entomophthoromycota, Entorrhizomycota, Glomeromycota, Kickxellomycota, Monoblepharomycota, Mortierellomycota, Mucoromycota, Neocallimastigomycota, Olpidiomycota, Rozellomycota, Sanchytriomycota and Zoopagomycota (Wijayawardene *et al.* 2022). Basidiomycota constitute a major phylum of the kingdom fungi and is second in number of described species to Ascomycota (Wijayawardene *et al.* 2017). Recently, approximately 60 new genera have been recognized for agarics, 40 for boletes, and 50 for bracket fungi in Basidiomycota (Wijayawardene *et al.* 2020).

The genus *Coniophora* DC. (1815: 34) belonged to the family Coniophoraceae (Boletales, Basidiomycota), typified by *C. membranacea* DC. (1815: 34), is characterized by resupinate, membranaceous basidiom with a smooth to tuberculate hymenophore with a brown hymenial surface mainly a monomitic hyphal system with clamped generative hyphae, cylindrical basidia with 4-sterigmata, ellipsoid to ovoid or fusiform, smooth, thick-walled, pale yellowish to brownish, cyanophilous, variably dextrinoid basidiospores (Bernicchia & Gorjón 2010). Based on the Index Fungorum (www.indexfungorum.org; accessed on 19 December 2022), the genus *Coniophora* has 170 specific and registered names, but the legitimate number of species has reached 30 (Gersonde 1958, Ginns & Kokko 1976, Käärik 1979, Ginns 1982, Blanco *et al.* 2009). The genus *Resupinatus* Nees ex Gray (1821: 617) belonged to the family Pleurotaceae

Accepted by Samantha C. Karunarathna: 19 Mar. 2023; published: 30 Mar. 2023

(Agaricales, Basidiomycota), typified by *R. applicatus* (Batsch) Gray (1821: 617), is characterized by the resupinate basidiomata with lamellate, poroid or cyphelloid hymenophore, hyphal system monomitic, thin-walled, clamped, frequently branching from clamps, basidia clavate or subclavate, 2- or 4-spored, basidiospores colorless, thin-walled, smooth, globose or subglobose to oblong or cylindric, inamyloid (Mcdonald 2015, Bijeesh *et al*. 2020).The Index Fungorum (www.indexfungorum.org; accessed on 19 December 2022) have registered 84 specific and infraspecific names in *Resupinatus*, but the legitimate number of the species has reached 45 (Gray 1821, Redhead *et al*. 1987, Singer 1975, Bodensteiner *et al*. 2004, Consiglio & Setti 2018).

Recent pioneering researches according to genera *Coniophora* and *Resupinatus* were just the prelude to the molecular systematics of Basidiomycota. Molecular systematics and biological diversification of Boletales based on the multigene dataset (nuc-ssu, nuc-lsu, 5.8S, mt-lsu, atp6) revealed that *Coniophora* nested into the family Coniophoraceae, in which both families Coniophoraceae and Hygrophoropsidaceae grouped together within the order Boletales, and this study suggested that the ancestor of the Boletales was a resupinate or polyporoid saprotrophic fungus, producing a brown-rot (Binder & Hibbett 2006). Taxonomic and phylogenetic revision of *Coniophora* showed that *C. prasinoides* (Bourdot & Galzin) Bourdot & Galzin (1927: 361) and *C. opuntiae* Tellería (1984: 26) represented two different species, and two taxa *C. arachnoidea* Pat. (1912: 31) and *C. opuntiae* were as synonyms (Blanco *et al.* 2009). Majority rule consensus tree from Bayesian analysis indicated that the species of *Resupinatus* grouped into resupinatus clade, in which this monophyletic group also included members of *Asterotus* Singer (1943: 161) and the cyphelloid genus *Stigmatolemma* Kalchbr. (1882: 104) (Thorn *et al*. 2005). The genus *Resupinatus* was emended to include poroid (*R. porosus* M.P. Martín, Lodge & Thorn (2005: 1142)) or merulioid hymenophore species as *R. merulioides* Redhead & Nagas. (1987: 973) (Thorn *et al*. 2005). Phylogeny analysis of a supermatrix of three nuclear gene regions (ITS, nLSU and TEF1) showed that two sequences known as *Hohenbuehelia nigra* (Schwein.) Singer (1949: 256) were placed with strong support in the sister genus *Resupinatus* with the speceis *R. niger* (Schwein.) Murrill (1915: 242) (Consiglio & Setti 2018). Phylogenetic analysis of *Resupinatus* species inferred from nrITS sequences showed that a merulioid hymenophore taxon as *R. odoratus* C.K. Pradeep, C. Bijeesh & A.M. Kumar (2020: 170) was reported from Kerala State, India as a saprotrophic, lignicolous fungus (Bijeesh *et al.* 2020).

During the investigations on the wood-inhabiting fungi, we collected two new taxa of Basidiomycota from Yunnan Province that could not be assigned to any described species. We present morphological and molecular phylogenetic evidence that supports the two new species in *Coniophora* and *Resupinatus*, based on the internal transcribed spacer (ITS) regions and the large subunit nuclear ribosomal RNA gene (nLSU) sequences of ribosomal DNA gene.

Materials and methods

Morphological studies

Fresh fruiting bodies of the fungi were collected from Chuxiong, Honghe, Pu'er and Wenshan of Yunnan Province, P.R. China. 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, P.R. China. Macromorphological descriptions are based on field notes and photos captured in the field and lab. Colour terms follow Petersen (1996). Micromorphological data were obtained from the dried specimens when observed under a light microscope following Dai *et al.* (2015). The following abbreviations were used: KOH = 5% potassium hydroxide water solution, CB = Cotton Blue, CB– = acyanophilous, CB+ = cyanophilous, IKI = Melzer's reagent, IKI– = both inamyloid and indextrinoid, L = mean spore length (arithmetic average for all spores), W = mean spore width (arithmetic average for all spores), Q = variation in the L/W ratios between the specimens studied, and n = a/b (number of spores (a) measured from a given number (b) of specimens), Qm = the average of Q (arithmetic average for all spores).

Molecular procedures and phylogenetic analyses

CTAB rapid plant genome extraction kit-DN14 (Aidlab Biotechnologies Co., Ltd, Beijing) was used to obtain genomic DNA from dried specimens, according to the manufacturer's instructions that were slightly modified by grinding a small piece of the dried fungal specimen (30 mg) to powder with liquid nitrogen. The powder was transferred to a 1.5 mL centrifuge tube, suspended in 0.4 mL of lysis buffer, and incubated in a 65 °C water bath for 60 min. After that, 0.4 mL phenol-chloroform (24:1) was added to each tube and the suspension was shaken vigorously. After centrifugation at 13 thousand rpm for 5 min, 0.3 mL supernatant was transferred to a new tube and mixed with 0.45 mL binding buffer. The mixture was then transferred to an Adsorbing Column (AC) for centrifugation at 12,000 rpm for 0.5 min.

Then, 0.5 mL inhibitor removal fluid was added to the AC for centrifugation at 12 thousand rpm for 0.5 min. After washing twice with 0.5 mL washing buffer, the AC was transferred to a clean centrifuge tube, and 100 mL elution buffer was added to the middle of the adsorbed film to elute the genome DNA. The internal transcribed spacer region (ITS) was amplified with primer pairs ITS5 and ITS4 (White *et al.* 1990). The nuclear large subunit region (nLSU) was amplified with primer pairs LR0R and LR7 (https://sites.duke.edu/vilgalyslab/rdna_primers_for_fungi/). The PCR procedure for ITS was as follows: initial denaturation at 95 °C for 3 min, followed by 35 cycles of 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 of 94 °C for 30 s, 48 °C 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 directly sequenced at the Kunming Tsingke Biological Technology Limited Company, Kunming, Yunnan Province, China. All newly generated sequences were deposited in GenBank (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	LSU	
Agrocybe praecox	AFTOL-ID 728	AY818348	AY646101	Yang *et al.* 2005
Amylocorticium cebennense	HHB-2808	GU187505	GU187561	Binder *et al.* 2010
Anomoloma bombycina	L-6240	GU187508	GU187564	Binder *et al.* 2010
Anthracophyllum archeri	AFTOL-ID 973	DQ404387	AY745709	Matheny *et al.* 2006
Armillaria mellea	AFTOL-ID 449	AY789081	AY700194	Matheny *et al.* 2006
Aroramyces gelatinosporus	H4010	DQ218698	DQ218524	Hosaka *et al.* 2008
Asterophora lycoperdoides	CBS 170.86	AF357037	—	Hofstetter *et al.* 2002
Athelia arachnoidea	CBS 105.18	MH854664	MH866181	Vu *et al.* 2019
A. epiphylla	FP-100564	GU187501	GU187558	Binder *et al.* 2010
Austroboletus fusisporus	HKAS75207	JX889719	JX889720	Hosen *et al.* 2013
Austropaxillus statuum	Pst2	HM135659	HM135709	He *et al.* 2019
Blastosporella zonata	TJB8371	EU708340	EU708337	Halling *et al.* 2007
Boletellus projectellus	AFTOL-ID 713	AY789082	AY684158	Hosen *et al.* 2013
Boletinellus merulioides	AFTOL-ID 575	DQ200922	AY684153	Matheny *et al.* 2007
Boletus edulis	Be953	AY680988	AF456816	Leonardi *et al.* 2005
Bondarcevomyces taxi	Dai2524	DQ534575	DQ534672	Binder & Hibbett 2006
Borofutus dhakanus	HKAS73789	JQ928606	JQ928616	Hosen *et al.* 2013
Bothia castanella	MB03-053	DQ867110	DQ867117	Halling *et al.* 2007
Calostoma cinnabarinum	AFTOL-ID 439	AY854064	AY645054	Hosen *et al.* 2013
Callistosporium graminicolor	AFTOL-ID 978	DQ484065	AY745702	Matheny *et al.* 2006
Camarophyllopsis hymenocephala	AFTOL-ID 1892	DQ484066	DQ457679	Matheny *et al.* 2006
Catathelasma ventricosum	AFTOL-ID 1488	DQ486686	DQ089012	Matheny *et al.* 2006
Ceraceomyces borealis	L-8014	GU187512	GU187570	Binder *et al.* 2010
Clarkeinda trachodes	xml2014104	LT716022	KY418837	Zhao *et al.* 2017
Clavaria zollingeri	AFTOL-ID 563	AY854071	AY639882	Matheny *et al.* 2006
Clitocybula atroalba	AFTOL-ID 1529	DQ192179	DQ457659	Matheny *et al.* 2006
Clitopilus prunulus	AFTOL-ID 522	DQ202272	AY700181	Matheny *et al.* 2006
Chalciporus piperatus	HKAS50214	JQ928610	JQ928621	Hosen *et al.* 2013
Chlorophyllum agaricoides	AFTOL-ID 440	DQ200928	AY700187	Matheny *et al.* 2007
Coniophora arida	FP-104367	GU187510	GU187573	Zhao *et al.* 2018
C. arida	He 4658	MG763875	—	Zhao *et al.* 2018
C. cerebella	HK 8	GU187625	—	Binder *et al.* 2010

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TABLE 1. (Continued)

Species name	**Sample no.**	**GenBank accession no.**		**References**
		ITS	**LSU**	
C. cystidiophora	CBS 153.33	MH855390	—	Vu *et al.* 2019
C. hanoiensis	He 5197	MG763873	—	Zhao *et al.* 2018
C. hanoiensis	He 5202	MG763874	—	Zhao *et al.* 2018
C. marmorata	MUCL31667	GU187515	—	Binder *et al.* 2010
C. marmorata	P158	AJ518879	—	Schmidt *et al.* 2002
C. olivacea	FP-104386	GU187516	GU187572	Binder *et al.* 2010
C. opuntiae	AH 31855	FJ790314	—	Blanco *et al.* 2009
C. prasinoides	MA-Fungi 19417	AJ419197	—	He *et al.* 2019
C. puteana	VL298	JF440570	—	Lygis *et al.* 2014
C. yunnanensis	**CLZhao 3517**	**OP901836**	**OP904195**	**Present study**
C. yunnanensis	**CLZhao 3594**	**OP901837**	**OP904196**	**Present study**
Coprinellus curtus	SZMC-NL-2339	FM878016	FM876273	Nagy *et al.* 2011
Coprinopsis atramentaria	AFTOL-ID 1496	—	DQ457661	Matheny *et al.* 2006
Coprinus comatus	AFTOL-ID 626	AY854066	AY635772	Matheny *et al.* 2007
Corneriella bambusarum	DED5462	NR153878	NG060410	He *et al.* 2019
Corneroboletus indecorus	HKAS63126	—	KF112440	Wu *et al.* 2014
Cortinarius iodes	AFTOL-ID 285	—	AY702013	Matheny *et al.* 2006
Cortinarius renidens	OS582	KC842459	KC842529	He *et al.* 2019
Crepidotus applanatus	PBM 717	DQ202273	AY380406	Matheny *et al.* 2007
Cylindrobasidium laeve	AFTOL-ID 453	DQ205682	DQ234541	Matheny *et al.* 2007
Cystoagaricus strobilomyces	30-V-1997	AY176347	AY176348	Vellinga 2004
Dermoloma sp.	ECV4208	KU058494	KU058531	He *et al.* 2019
Entocybe trachyospora	ZRL20151426	LT716037	KY418852	Zhao *et al.* 2017
Entoloma pluteisimilis	C.20011208	—	GQ289180	Co-David *et al.* 2009
Flagelloscypha minutissima	CBS 823.88	AY571040	AY571006	Bodensteiner *et al.* 2004
Flammulaster sp.	PBM3449	HQ827176	HQ827177	Matheny *et al.* 2014
Flammulina velutipes	AFTOL-ID 558	AY854073	AY639883	Matheny *et al.* 2006
Gymnopus confluens	ZRL20151148	LT716054	KY418870	Zhao *et al.* 2017
Gyrodontium sacchari	He4157	MG763879	MH476327	Larsson *et al.* 2006
G. sacchari	MUCL40589	GU187522	GU187579	Binder *et al.* 2010
Harrya chromapes	HKAS50527	—	KF112437	Wu *et al.* 2014
Hebeloma cavipes	ZRL20151612	LT716034	KY418849	Zhao *et al.* 2017
Hohenbuehelia atrocoerulea	AMB 18084	KU355301	KU355388	Bijeesh *et al.* 2020
H. grisea	MCVE 27293	KU355329	KU355394	Consiglio & Setti 2018
H. tremula	AFTOL-ID 1503	DQ182504	DQ440645	Matheny *et al.* 2006
Hydnomerulius pinastri	MD312	GU187523	GU187580	Binder *et al.* 2010
Hygrophoropsis aurantiaca	AFTOL-ID 714	AY854067	AY684156	Binder *et al.* 2010
Hymenagaricus taiwanensis	AFTOL-ID 1383	DQ490633	DQ457680	Matheny *et al.* 2006
Hypsizygus ulmarius	JM/HW 25S	EF421105	AF042584	Moncalvo *et al.* 2000
Jaapia argillacea	CBS:252.74	NR 119766	NG042523	Binder *et al.* 2010
J. ochroleuca	KHL 8433	EU118637	EU118637	Larsson 2007
Lachnella villosa	AFTOL-ID 525	DQ097362	DQ097347	Binder *et al.* 2006
Lamelloclavaria petersenii	SAV F-3493	NR154119	NG060318	Birkebak *et al.* 2013
Leccinum aurantiacum	HKAS57390	JQ928611	JQ928625	Hosen *et al.* 2013

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TABLE 1. (Continued)

Species name	Sample no.	GenBank accession no.		References
		ITS	LSU	
Lentinula edodes	TMI1941	—	AF261557	Moncalvo *et al.* 2002
Lepiota cristata	ZRL20151133	LT716026	KY418841	Zhao *et al.* 2017
Leptosporomyces raunkiaeri	HHB-7628	GU187528	GU187588	Binder *et al.* 2010
Leucocoprinus fragilissimus	ZRL20151466	LT716029	KY418844	Zhao *et al.* 2017
Leucogyrophana mollusca	KHL 11160	EU118643	EU118643	Larsson 2007
Leucopaxillus alboalutaceus	LAS00/082	KJ417275	KJ417195	He *et al.* 2019
Megacollybia marginata	ZRL20151245	LT716049	KY418865	Zhao *et al.* 2017
Melanogaster rivularis	PAM08090514	NR132848	—	Rochet *et al.* 2010
Micropsalliota globocystis	ZRL2013465	LT716024	KY418839	Zhao *et al.* 2017
Mycaureola dilseae	BM17/85	DQ097364	DQ097348	Binder & Hibbett 2006
Naucoria escharoides	PBM1719	—	AY380405	Matheny 2005
Nolanea strictior	DUKE-JM96/10	EF421109	—	Hofstetter *et al.* 2007
Omphalotus olearius	AFTOL-ID 1718	DQ494681	DQ470816	Matheny *et al.* 2006
Parasola conopila	ZRL20151990	LT716064	KY418880	Zhao *et al.* 2017
Phlebopus portentosus	HKAS52855	—	JQ928622	Hosen *et al.* 2013
Phylloporus pelletieri	Pp1	DQ534566	AF456818	Binder & Hibbett 2006
Physalacria bambusae	CBS 712.83	DQ097367	DQ097349	Matheny *et al.* 2006
Piloderma fallax	S 12	GU187535	GU187591	Binder *et al.* 2010
Pisolithus tinctorius	AWW219	EU718114	EU718148	He *et al.* 2019
Pleuroflammula praestans	ZRL2015066	LT716043	KY418859	Zhao *et al.* 2017
Pleurotus eryngii	HIK153	HM998840	HM998804	Zervakis *et al.* 2014
P. ferulaginis	HIK132	HM998831	HM998794	Zervakis *et al.* 2014
Podoserpula ailaoshanensis	ZJL2015015	NR158915	NG060161	He *et al.* 2019
Porphyrellus porphyrosporus	AFTOL-ID 1779	DQ534563	DQ534643	Binder & Hibbett 2006
Porpoloma portentosum	REH5788	KJ417299	KJ417211	He *et al.* 2019
Psathyloma catervatim	PBM3420	HQ840663	HQ840664	Matheny *et al.* 2014
Pseudobaeospora sp.	ECV5553	KU058502	KU058539	He *et al.* 2019
Pseudomerulius curtisii	REH8912	GU187533	GU187589	Binder *et al.* 2010
Radulomyces copelandii	Dai 15061	KU535664	KU535672	Zhao *et al.* 2016
Radulotubus resupinatus	Cui 8383	KU535660	KU535668	Zhao *et al.* 2016
Resupinatus alboniger	TFB12417	KP026234	—	Petersen *et al.* 2015
R. alboniger	TENN62044	FJ596893	—	Hughes *et al.* 2009
R. applicatus	PB335	AY571059	AY571022	Bodensteiner *et al.* 2004
R. applicatus	PDD 95777	HQ533025	—	McDonald *et al.* 2015
R. conspersus	C61852	AY571061	—	Bodensteiner *et al.* 2004
R. europaeus	AMB 18076	KU355365	—	Consiglio & Setti 2018
R. europaeus	AMB 18078	KU355363	—	Consiglio & Setti 2018
R. griseopallidus	AMB 18277	MH137823	—	Bijeesh *et al.* 2020
R. griseopallidus	Blasco	MG553642	—	Bijeesh *et al.* 2020
R. hausknechtii	WU 7659	KU355370	—	Bijeesh *et al.* 2020
R. kavinii	AVM 3128	MG553643	—	Bijeesh *et al.* 2020
R. odoratus	TBGT17789	MT452498	—	Bijeesh *et al.* 2020
R. niger	RLG 10761	KY679146	KY679146	Consiglio & Setti 2018
R. niger	Roux 3740	KU355372	—	Unpublished

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TABLE 1. (Continued)

Species name	Sample no.	GenBank accession no.		References
		ITS	LSU	
R. poriiformis	GT 11034	MH137825	—	Consiglio & Setti 2018
R. poriiformis	CBS 327.91	AY571062	—	Bodensteiner *et al.* 2004
R. porosus	PR5832	DQ017063	—	Thorn *et al.* 2005
R. rouxii	ACAD 7603	KU355369	—	Consiglio & Setti 2018
R. rouxii	Z+ZT 971	MH137828	—	Consiglio & Setti 2018
R. striatulus	KR-M-053702	MW035051	—	Lotz-Winter *et al.* 2021
R. striatulus	KR-M-0091193	MW035047	—	Lotz-Winter *et al.* 2021
R. taxi	MO315409	MH558280	—	Bijeesh *et al.* 2020
R. trichotis	AVM 3173	MH137833	—	Consiglio & Setti 2018
R. trichotis	HMJAU2150	GQ142022	—	McDonald *et al.* 2015
R. violaceogriseus	PDD95788	HQ533014	—	McDonald *et al.* 2015
R. yunnanensis	**CLZhao 3802**	**OP901840**	**—**	**Present study**
R. yunnanensis	**CLZhao 7168**	**OP901838**	**—**	**Present study**
R. yunnanensis	**CLZhao 8651**	**OP901839**	**OP904197**	**Present study**
Retiboletus griseus	HKAS59460	JQ928613	JQ928626	Hosen *et al.* 2013
Royoungia boletoides	ACW 4137	—	DQ534663	Binder & Hibbett 2006
Serpula lacrymans	REG 383	GU187542	GU187596	Binder *et al.* 2010
Simocybe serrulata	AFTOL-ID 970	DQ494696	AY745706	Matheny *et al.* 2006
Spongiforma thailandica	DED7873	EU685113	EU685108	Desjardin *et al.* 2009
Strobilomyces floccopus	AFTOL-ID 716	AY854068	AY684155	Hosen *et al.* 2013
Tephrocybe ambusta	CBS452.87	AF357057	—	Hofstetter *et al.* 2002
Tricholoma palustre	AFTOL-ID 497	DQ494699	AY700197	Matheny *et al.* 2006
Tubaria confragosa	AFTOL-ID 498	DQ267126	AY700190	Matheny *et al.* 2007
Tylopilus felleus	HKAS54926	HQ326909	HQ326933	Li *et al.* 2011
Veloporphyrellus alpinus	HKAS57490	JX984526	JX984537	Li *et al.* 2014
Verrucospora flavofusca	AFTOL-ID 655	DQ241779	DQ470825	Matheny *et al.* 2006
Xanthoconium stramineum	3518	—	KF030353	Nuhn *et al.* 2013
Xerocomellus cisalpinus	PDD94421	JQ924296	JQ924322	Wu *et al.* 2014
Xerula sinopudens	ZRL20151504	LT716059	KY418875	Zhao *et al.* 2017

Sequencher 4.6 (GeneCodes, Ann Arbor, MI, USA) was used to edit the DNA sequence. Sequences were aligned in MAFFT 7 (http://mafft.cbrc.jp/alignment/server/) using the "G-INS-I" strategy and manually adjusted in BioEdit (Hall 1999). The sequence alignment was deposited in TreeBase (submission ID 30015). Phylogenetic analyses of genera *Coniophora* and *Resupinatus* were carried out, in which sequence of *Aroramyces gelatinosporus* (J.W. Cribb) Castellano (2000: 13) retrieved from GenBank was used as outgroup in ITS+nLSU (Fig. 1) analysis following He *et al.* (2019). Sequences of *Gyrodontium sacchari* (Spreng.) Hjortstam. (1995: 186) retrieved from GenBank were used as outgroups in Fig. 2 (ITS+nLSU) and analysis following Zhao *et al.* (2018). The sequence of *Hohenbuehelia atrocoerulea* (Fr.) Singer (1951: 255) retrieved from GenBank was used as outgroup in ITS+nLSU (Fig. 3) analysis following Bijeesh *et al.* (2020).

Maximum parsimony analysis was applied to ITS and ITS+nLSU dataset sequences. Approaches to phylogenetic analysis followed Zhao and Wu (2017), and the tree construction was performed in PAUP* version 4.0b10 (Swofford 2002). All characters were equally weighted and gaps were treated as missing data. Trees were inferred using the heuristic search option with TBR branch swapping and 1,000 random sequence additions. Max-trees were set to 5,000, branches of zero length were collapsed and all parsimonious trees were saved. Clade robustness was assessed using a bootstrap (BT) analysis with 1,000 replicates (Felsenstein 1985). Descriptive tree statistics tree length (TL), consistency index (CI), retention index (RI), rescaled consistency index (RC), and homoplasy index (HI) were calculated for each Maximum Parsimonious Tree generated. Sequences were also analyzed using Maximum Likelihood (ML) with

RAxML-HPC2 through the Cipres Science Gateway (www.phylo.org; Miller *et al.* 2009). Branch support (BS) for ML analysis was determined by 1000 bootstrap replicates.

MrModeltest 2.3 (Nylander 2004) was used to determine the best-fit evolution model for each data set for Bayesian Inference (BI). BI was calculated with MrBayes 3.2.7a with a general time reversible (GTR+I+G) model of DNA substitution and a gamma distribution rate variation across sites (Ronquist *et al.* 2012). Four Markov chains were run for 2 runs from random starting trees, for 6 million generations (Fig. 1), 0.32 million generations (Fig. 2) and 2 million generations (Fig. 3) and trees were sampled every 100 generations. The first one-fourth generations were discarded as burn-in. A majority rule consensus tree of all remaining trees was calculated. Branches are labeled with maximum likelihood bootstrap values equal to or above 70%, parsimony bootstrap values equal to or above 50% and Bayesian posterior probabilities equal to or above 0.95.

Results

Phylogenetic analyses

The ITS+nLSU dataset (Fig. 1) included sequences from 113 fungal specimens representing 112 species within the class Agaricomycetidae and one outgroup. The dataset had an aligned length of 3261 characters, of which 1350 characters were constant, 422 were variable and parsimony-uninformative, and 1489 were parsimony-informative. Maximum parsimony analysis yielded 61 equally parsimonious trees (TL = 18023, CI = 0.2090, HI = 0.7910, RI = 0.3044, RC = 0.0636). The best model for the ITS+nLSU dataset estimated and applied in the Bayesian analysis: was GTR+I+G. Bayesian analysis and ML analysis resulted in a similar topology as MP analysis, with an average standard deviation of split frequencies = 0.015999 (BI), and the effective sample size (ESS) across the two runs is double that of the average ESS (avg ESS) = 918. The phylogenetic tree (Fig. 1) inferred from ITS+nLSU sequences revealed that *C. yunnanensis* and *R. yunnanensis* nested within Agaricomycetidae, in which *C. yunnanensis* clustered into the family Coniophoraceae (Boletales), and *R. yunnanensis* grouped into family Pleurotaceae (Agaricales).

The ITS dataset (Fig. 2) included sequences from 16 fungal specimens representing 10 species of *Coniophora* and two outgroups. The dataset had an aligned length of 748 characters, of which 469 characters were constant, 117 were variable and parsimony-uninformative, and 162 were parsimony-informative. Maximum parsimony analysis yielded 3 equally parsimonious trees (TL = 510, CI = 0.7216, HI = 0.2784, RI = 0.6595, RC = 0.4759). The best model for the ITS dataset estimated and applied in the Bayesian analysis was GTR+I+G. Bayesian analysis and ML analysis resulted in a similar topology as MP analysis, with an average standard deviation of split frequencies = 0.007274 (BI), and the effective sample size (ESS) across the two runs is double that of the average ESS (avg ESS) = 456.5. The phylogenetic tree (Fig. 2) inferred from ITS sequences revealed that *Coniophora yunnanensis* grouped into the genus *Coniophora* and closely related to *C. marmorata* Desm. (1823: 18).

The ITS dataset (Fig. 3) included sequences from 27 fungal specimens representing 17 species of *Resupinatus* and an outgroup. The dataset had an aligned length of 679 characters, of which 330 characters were constant, 72 were variable and parsimony-uninformative, and 277 were parsimony-informative. Maximum parsimony analysis yielded 1 equally parsimonious tree (TL = 1291, CI = 0.4462, HI = 0.5538, RI = 0.4936, RC = 0.2202). The best model for the ITS dataset estimated and applied in the Bayesian analysis was GTR+I+G. Bayesian analysis and ML analysis resulted in a similar topology as MP analysis, with an average standard deviation of split frequencies = 0.009024 (BI), and the effective sample size (ESS) across the two runs is double that of the average ESS (avg ESS) = 180. The phylogenetic tree (Fig. 3) inferred from ITS sequences revealed that *Resupinatus yunnanensis* clustered into genus *Resupinatus* and sister to *R. conspersus* Thorn, Moncalvo & Redhead. (2006: 1148).

Taxonomy

Coniophora yunnanensis Y. Yang & C.L. Zhao, *sp. nov.* Figs. 1, 2, 4, 5

MycoBank no.: MB 847019

***Holotype*:—**CHINA. Yunnan Province, Pu’er, Jingdong County, Wuliangshan National Nature Reserve, E 100°31′10″, N 24°25′07″, elev. 1500 m, on the dead bamboo, 2 October 2017, CLZhao 3594 (SWFC!), GenBank No. (ITS OP901837; nLSU OP904196).

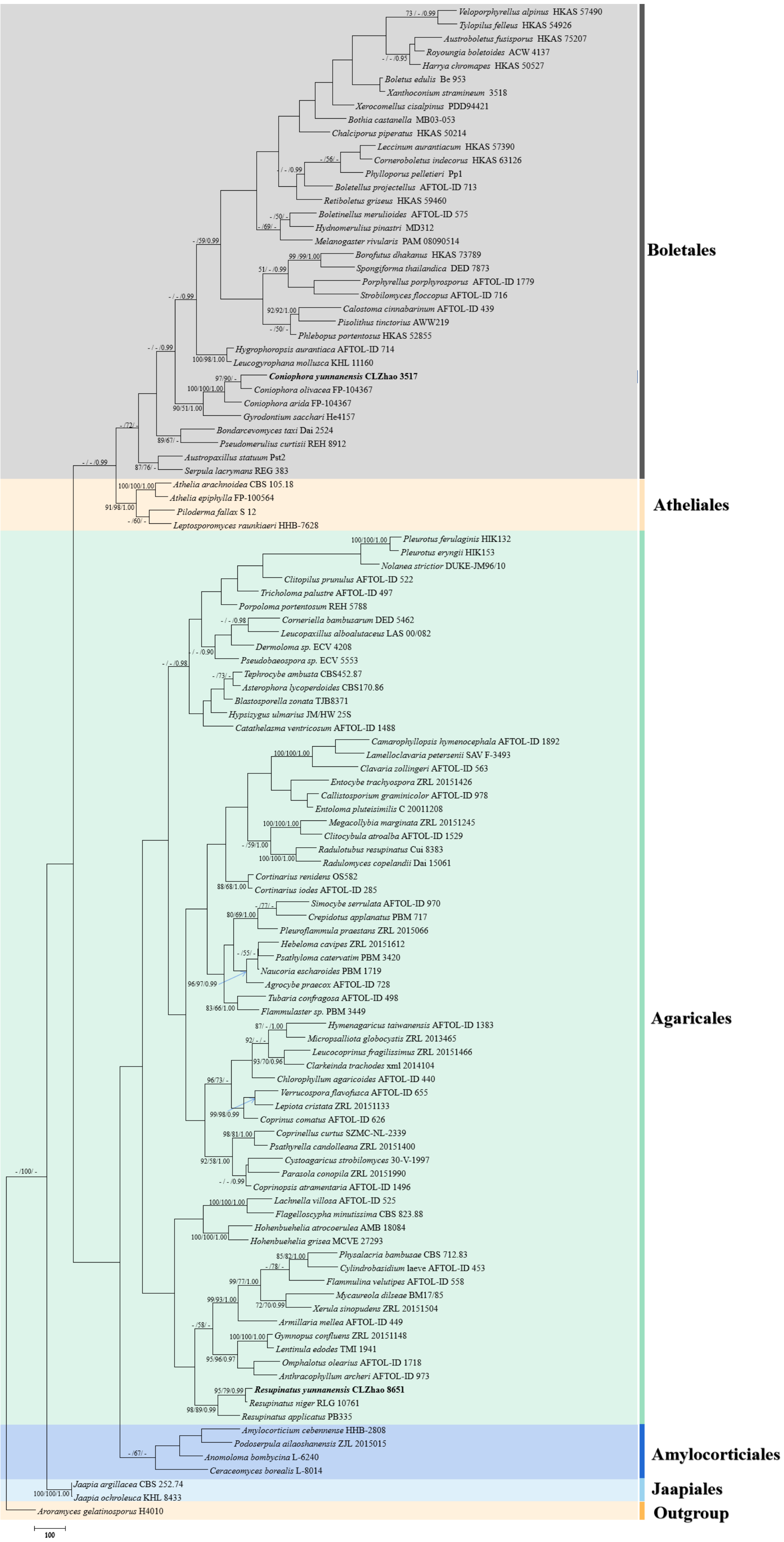

FIGURE 1. Maximum Parsimony strict consensus tree illustrating the phylogeny of two new species and related species in Agaricomycetidae based on ITS+nLSU sequences. Branches are labeled with maximum likelihood bootstrap values equal to or above 70%, parsimony bootstrap values equal to or above 50% and Bayesian posterior probabilities equal to or above 0.95. The new species are in bold.

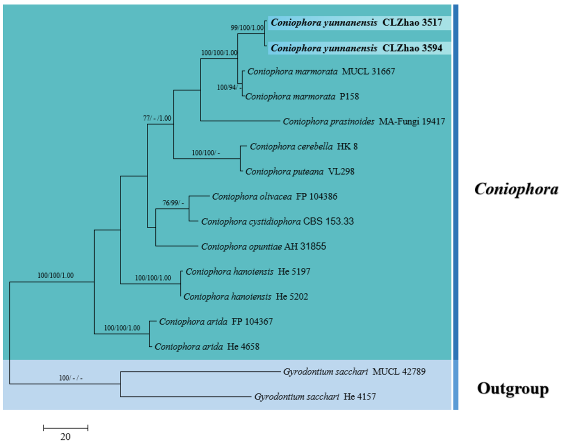

FIGURE 2. Maximum Parsimony strict consensus tree illustrating the phylogeny of the new species of *Coniophora* based on ITS sequences. Branches are labeled with maximum likelihood bootstrap values equal to or above 70%, parsimony bootstrap values equal to or above 50% and Bayesian posterior probabilities equal to or above 0.95.

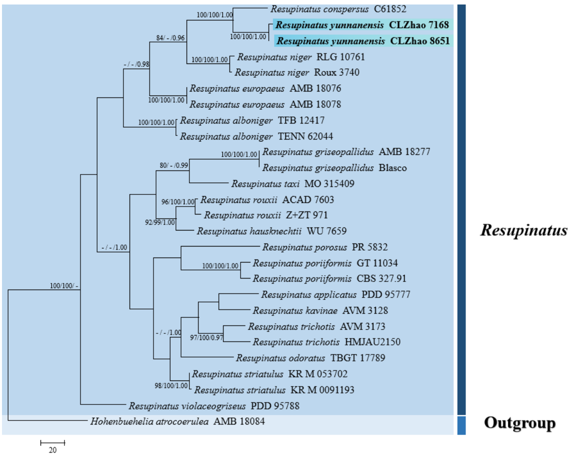

FIGURE 3. Maximum Parsimony strict consensus tree illustrating the phylogeny of the new species of *Resupinatus* based on ITS sequences. Branches are labeled with maximum likelihood bootstrap values equal to or above 70%, parsimony bootstrap values equal to or above 50% and Bayesian posterior probabilities equal to or above 0.95.

Etymology:—*yunnanensis* (Lat.): refers to the locality (Yunnan Province) of the type specimen.

***Basidiomata*:**—Annual, resupinate to effused, separable, soft ceraceous, without odor or taste when fresh, becoming hard corky upon drying, up to 10 cm long, 4 cm wide, 0.5–1 mm thick; hymenial surface odontoid, 100–500 µm long, olivaceous buff (4C4) when fresh, olivaceous buff (4C4) to greyish brown (5/6E4) drying; sterile margin indistinct and olivaceous buff (4C4).

***Hyphal structure*:**—Hyphal system monomitic; generative hyphae with simple septa, colorless, thin-walled, rarely branched, interwoven, 2.5–6 µm in diam; IKI–, CB–, tissues unchanged in KOH.

***Hymenium*:**—Cystidia and cystidioles absent; basidia cylindrical, constricted, 40–90 × 5–7 µm, with 4-sterigmata and a basal simple septum, basidioles dominant, in shape similar to basidia, but slightly smaller.

***Basidiospores*:**—Ovoid to broadly ellipsoid, smooth, thick-walled, pale yellowish, with oil drops, IKI–, CB–, (8–)8.5–12.5 × (5.5–)6.5–8.5 µm, L = 10.7 µm, W = 7.27 µm, Q = 1.46–1.53 (n = 60/2), Qm = 1.47.

***Additional specimen examined*:—**CHINA. Yunnan Province, Pu’er, Jingdong County, Wuliangshan National Nature Reserve, E 100°31′10″, N 24°25′07″, elev. 1500 m, on the dead bamboo, 2 October 2017, CLZhao 3517 (SWFC!), GenBank No. (ITS OP901836; nLSU OP904195).

Notes: Morphologically, *Coniophora arida* (Fr.) P. Karst. (1868: 370), *C. hanoiensis* Pat. (1907: 76), *C. olivacea* (Fr.) P. Karst. (1879: 162), and *C. puteana* (Schumach.) P. Karst. (1803: 397) are similar to *C. yunnanensis* by having ovoid to ellipsoid basidiospores. However, *C. arida* differs from *C. yunnanensis* by its wider basidia (40–70 × 7–10 µm), and presence of the hyphal strands (Bernicchia & Gorjón 2010); *C. hanoiensis* is separated from *C. yunnanensis* by its white to yellowish-brown hymenial surface and dimitic hyphal system (Ginns 1982); *C. olivacea* is distinguished from

C. yunnanensis by smooth hymenial surface, presence of the thick-walled septate cystidia and dextrinoid basidiospores (Bernicchia & Gorjón 2010); *C. puteana* is separated from *C. yunnanensis* by having the tabular, yellowish-brown, smooth basidiomata and brownish basidiospores (Bernicchia & Gorjón 2010).

Coniophora yunnanensis resembles *C. arachnoidea*, *C. fusispora* (Cooke & Ellis) Cooke (1889: 650) and *C. ladoi* Tellería (1991: 236) in having a odontoid hymenial surface. However, *Coniophora arachnoidea* is different from *C. yunnanensis* by brownish hymenophore and smaller basidiospores (6–8 × 4–5 µm) (Blanco *et al.* 2009); *C. fusispora* can be delimited from *C. yunnanensis* by its orange-yellow to brown hymenophore and longer basidiospores (14–20 × 5–8 µm) (Bernicchia & Gorjón 2010); *C. ladoi* is distinguished from *C. yunnanensis* by small basidiospores (5.5–7.5 × 3.5–4.5 µm) (Bernicchia & Gorjón 2010).

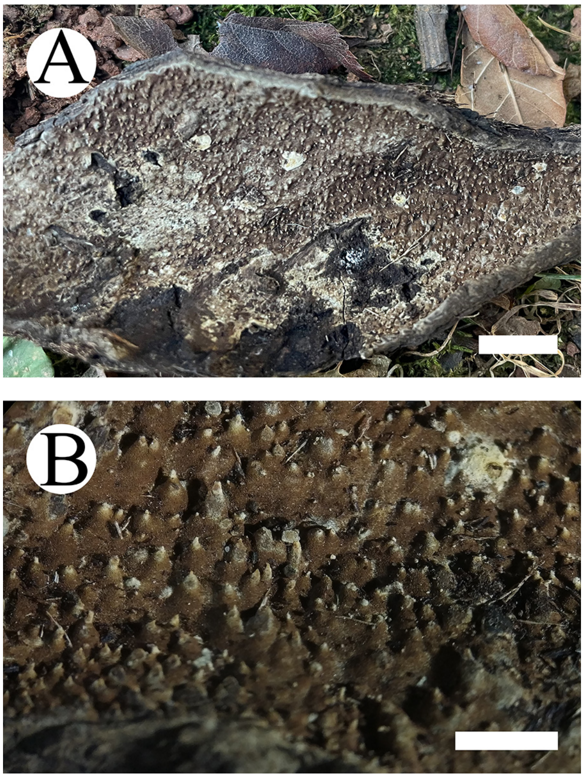

FIGURE 4. Basidiomata of *Coniophora yunnanensis*. Bars: A = 1 cm; B = 2 mm (holotype). Photos by: Yang Yang

Resupinatus yunnanensis Y. Yang & C.L. Zhao, *sp. nov.* Figs. 1, 3, 6, 7

MycoBank no.: MB 847020

***Holotype*:**—CHINA. Yunnan Province, Pu'er, Jingdong County, Taizhong Township, Xujiaba, Ailaoshan Ecological Station, E 100°53′41″, N 24°23′36″, elev. 1800 m, on the fallen branch of angiosperm, 24 August 2018, CLZhao 8651 (SWFC!), GenBank No. (ITS OP901839; nLSU OP904197).

***Etymology*:**—*yunnanensis* (Lat.): refers to the locality (Yunnan Province) of the type specimen.

***Basidiomata*:**—Annual, resupinate to cupulate, soft gelatinous when fresh, fragile when drying, up to 12 cm long, 3 cm wide, 0.5 mm thick, cups globose or depressed-globose, up to 150–500 µm in diameter, aggregated in groups, 3–6 per mm, buff (4A4) to slightly brown (5B/C7), covered in a dense mat of white hairs; hymenophore cyphelloid, buff (4A4) to slightly brown (5B/C7) when fresh, greyish (19C2) to pale mouse-grey (7C2) upon drying; sterile margin indistinct and slightly brown; subiculum felty, loosely attached to the substrate and densely packed, up to 200 µm thick.

***Hyphal structure*:**—Hyphal system monomitic; generative hyphae with clamp connections, colorless, thin-walled, branched, interwoven, 1.5–3.5 µm in diam; IKI–, CB–, tissues unchanged in KOH. presence of crystal encrusted branched hyphae with short finger-like projections at the tips.

***Hymenium*:**—Cystidia and cystidioles absent; basidia clavate, 12–36.5 × 4–8 µm, with 4-sterigmata and with a basal clamp connection, basidioles dominant, in shape similar to basidia, but slightly smaller.

***Basidiospores*:**—Ellipsoid, colorless, thin-walled, smooth, with oil drops, IKI–, CB–, 4.5–9(–9.5) × 3.5–7 µm, L = 6.68 µm, W = 4.72 µm, Q = 1.32–1.71 (n = 90/3), Qm = 1.42.

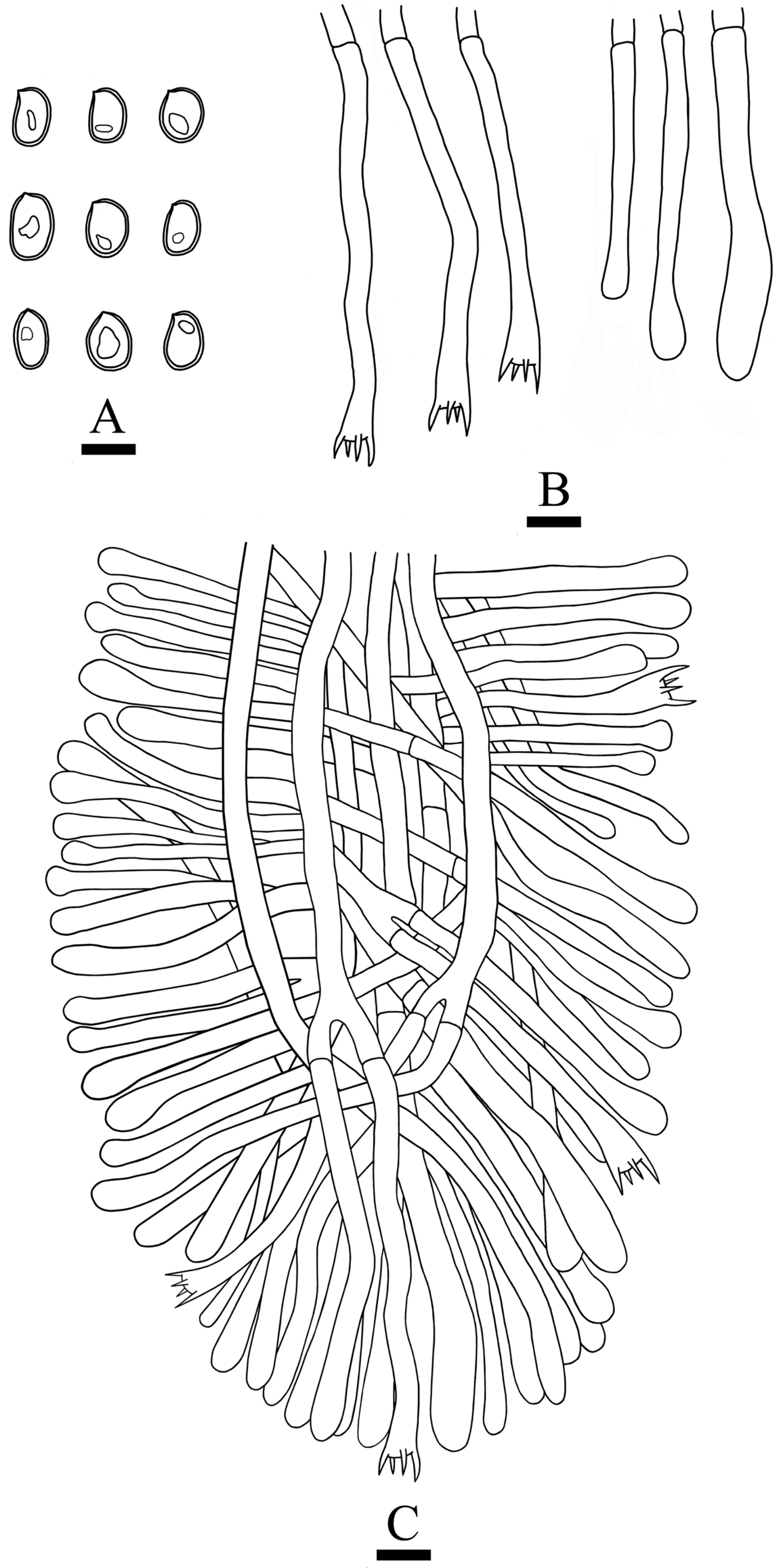

FIGURE 5. Microscopic structures of *Coniophora yunnanensis* (drawn from the holotype). A. Basidiospores. B. Basidia and basidioles. C. A section of hymenium. Bars: A–C = 10 µm. Drawings by: Yang Yang

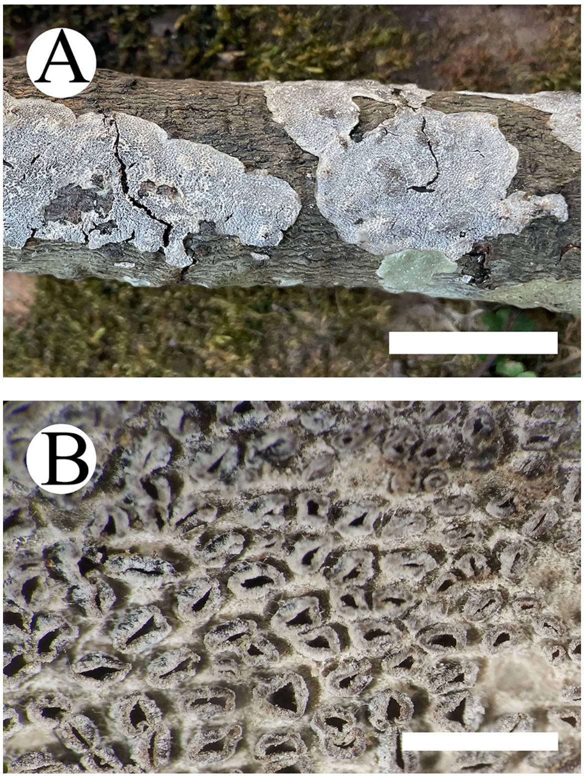

FIGURE 6. Basidiomata of *Resupinatus yunnanensis*. Bars: A = 2 cm, B = 1 mm (holotype). Photos by: Yang Yang

Additional specimens examined:—CHINA. Yunnan Province, Pu'er, Jingdong County, Taizhong Town, Ailaoshan, E 100°51′30″, N 24°25′42″, elev. 1800 m, on the fallen branch of angiosperm, 4 October 2017, CLZhao 3802 (SWFC!), GenBank No. (ITS OP901840); Chuxiong, Zixishan Forestry Park, E 101°24′06″, N 25°03′60″, elev. 2100 m, on the trunk of angiosperm, 1 July 2018, CLZhao 7168 (SWFC!), GenBank No. (ITS OP901838).

Notes: *Resupinatus alboniger* (Pat.) Singer, Beih. (1977: 17), *R. cinerascens* (Cleland) Grgur.(1997: 47), *R. hyalinus* (Singer) Thorn, Moncalvo & Redhead (2006: 1148) and *R. vinosolividus* (Segedin) J.A. Cooper (2012: 1) resemble *R. yunnanensis* by having the elliptical basidiospores. However, *Resupinatus alboniger* is distinguished from *R. yunnanensis* by the brown hymenophore and irregular finger-like cystidia (23–35 × 8–10 µm) (Gonou-Zagou *et al.* 2011); *R. cinerascens* differs in *R. yunnanensis* by having the grayish black hymenophore and diverticulate branching cystidia (19–35.5 × 2.5–6 µm) (Mcdonald 2015); *R. hyalinus* is separated from *R. yunnanensis* by having the surface hairs and finger-like cystidia (Mcdonald 2015); *R. vinosolividus* differs from *R. yunnanensis* by having the cheilocystidia at edge of basidiomata on top surface of gills (Mcdonald 2015).

Resupinatus yunnanensis resembles *R. applicatus* (Batsch) Gray (1821: 617), *R. huia* (G. Cunn.) Thorn, Moncalvo & Redhead (2006: 1148), *R. incanus* (Kalchbr.) Thorn, Moncalvo & Redhead (2006: 1148) and *R. poriaeformis* (Pers.) Thorn, Moncalvo & Redhead (2006: 1148) in having cupulate basidiomata. However, *Resupinatus applicatus* is different from *R. yunnanensis* by having the brown to black hymenophore with a lateral pseudostipe, diverticulate with finger-like cystidia and globose to subglobose basidiospores (Mcdonald 2015); *R. huia* can be delimited from *R. yunnanensis* by its simple septa generative hyphae and oblong basidiospores (Thorn *et al.* 2005); *R. incanus* differs from *R. yunnanensis* by grey to black basidiomata and oblong basidiospores (Thorn *et al.* 2005); *R. poriaeformis* is distinguished from *R. yunnanensis* by dark brown or grey basidiomata, diverticulate cystidia, and globose to subglobose basidiospores and tan to (Thorn *et al.* 2005).

Discussion

In the present study, two new species, *Coniophora yunnanensis* and *Resupinatus yunnanensis* are described based on phylogenetic analyses and morphological characteristics.

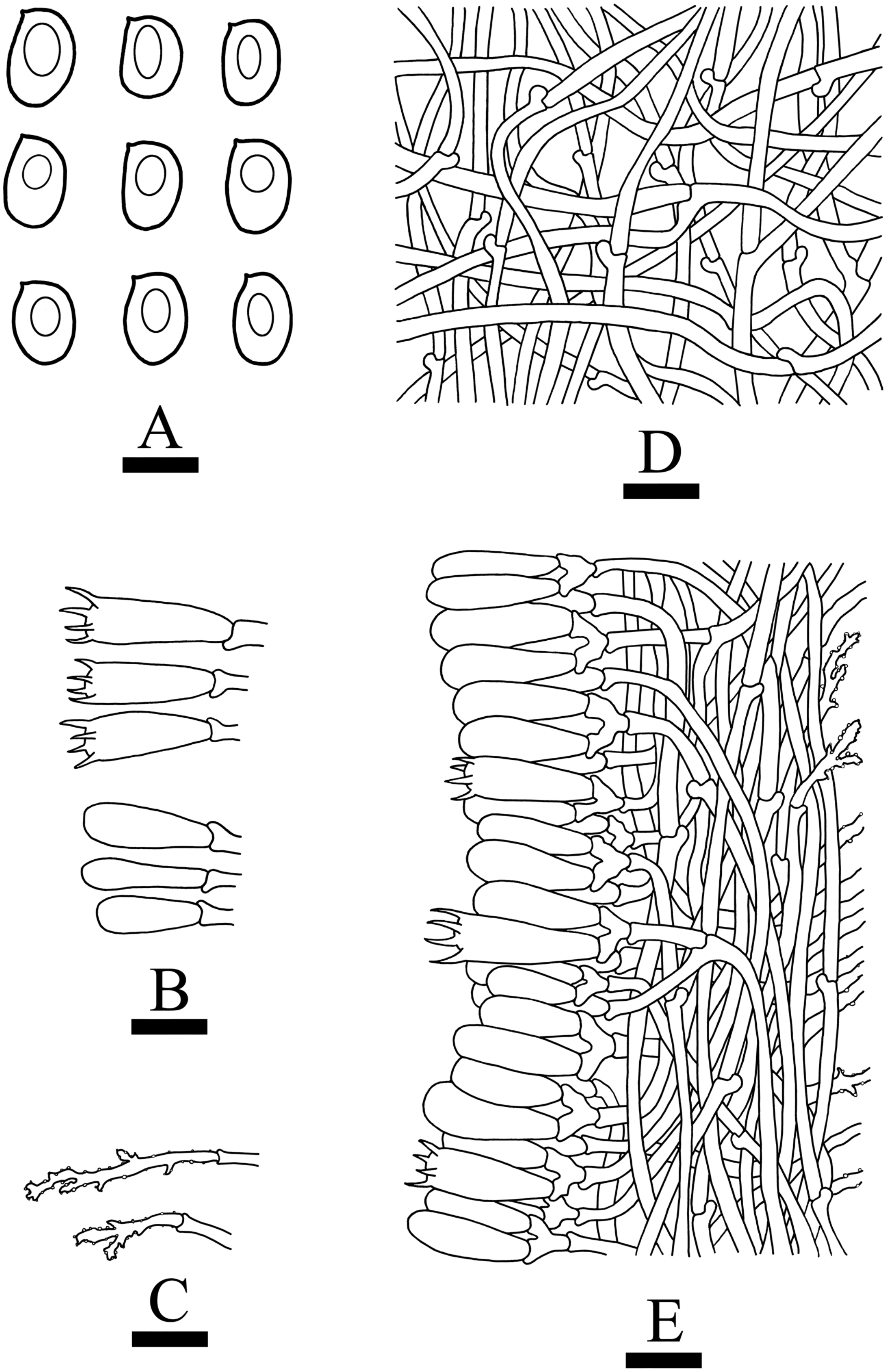

FIGURE 7. Microscopic structures of *Resupinatus yunnanensis* (drawn from the holotype). A: Basidiospores. B: Basidia and basidioles. C: The structure of some crystal encrusted branched hyphae on the cuticle of the fruit bodies. D: Hyphae from context. E: Section of hymenophore trama. Bars: A = 20 µm, B–E = 10 µm. Drawings by: Rong Li

An outline of all genera of Basidiomycota including three phylogenetic analyses with combined nLSU, SSU, 5.8S, RPB1, RPB2, and EF1 datasets for the subphyla Agaricomycotina, Pucciniomycotina and Ustilaginomycotina revealed that *Coniophora* nested into family Coniophoraceae Ulbr. (Boletales, Agaricomycetes) and *Resupinatus* Nees ex Gray (Agaricales, Agaricomycetes) clustered into family Pleurotaceae (He *et al.* 2019). In the present study, based on the ITS+nLSU data (Fig. 1), *C. yunnanensis* nested into the order Boletales, and *R. yunnanensis* clustered into the order Agaricales, in which the results are similar two previous topology research. The placement of all fungal genera form 19 phyla of fungi at the class-, order- and family-level showed that both genera *Coniophora* and *Resupinatus* grouped in Basidiomycota (Wijayawardene *et al.* 2020).

In our study, the phylogenetic research inferred from ITS sequences data (Fig. 2) revealed that *C. yunnanensis* grouped into genus *Coniophora*, in which it grouped with *C. marmorata* having the strong supports (BS = 97%, BP = 100%, BPP = 1). However, *C. marmorata* differs *C. yunnanensis* by having its dimitic hyphal system and presence of the hyphal strands, and the subglobose basidiospores (Ginns 1982). Furthermore, phylogeny within the *Resupinatus* showed that *R. yunnanensis* clustered into genus *Resupinatus* and then was sister to *R. conspersus* (BS = 100%, BP = 100%, BPP = 1). However, morphologically, *R. conspersus* is separated from *R. yunnanensis* by having the basidiospores inamyloid and oblong, without the oil drops (Mcdonald 2015).

In the geographical distribution and ecological importance, *Coniophora* and *Resupinatus* species are an extensively studied group (Bernicchia & Gorjón 2010, Mcdonald 2015), mainly distributed in Europe (e.g., Austria, Russia, France, Germany, Poland, UK, Netherlands, Portugal, Sweden, Italy, Denmark, Norway, Finland, Spain) and mainly found on hardwood, although a few species grow on coniferous wood. Many species of *Coniophora* were found in Europe, but only three species were reported in China, and none species of *Resupinatus* were described in this country (Dai 2011), in which we presumed that more specimens of *Coniophora* and *Resupinatus* were under sampled by the mycologists. The researches on the taxa related with wood-decaying fungi of *Coniophora* from China have been reported (Dai 2011), in which three *Coniophora* species were reported, *C. arida* (Fr.) P. Karst., *C. olivacea* (Fr.) P. Karst., and *C. puteana* (Schumach.) P. Karst. Further studies should focus on the relationships between the host and *Coniophora*, *Resupinatus* species, as well as trying to better understand the evolutionary directions between plant and two genera species. The researches on the phylogeny of *Coniophora* and *Resupinatus* as well as many fungal studies on the molecular systematics (Binder & Hibbett 2006, Thorn *et al*. 2005, Bijeesh *et al.* 2020), will be useful to push the further research on fundamental research and applied research of fungi. I believe more species of *Coniophora* and *Resupinatus* occur in subtropical and tropical Asia, because macrofungi are a well study group of wood-inhabiting fungi, and they are much rich in tropical China (Wu *et al.* 2020, Wang *et al.* 2021, Yuan *et al.* 2021, Luo & Zhao 2022, Zhao *et al.* 2023), and it is very possible the same phenomenon for *Coniophora* and *Resupinatus*.

Wood-inhabiting macrofungal fungi are an extensively studied group of Basidiomycota (Bernicchia & Gorjón 2010, Dai 2012, Ma & Zhao 2021, Wu *et al.* 2022). The taxa of *Coniophora* and *Resupinatus* are typical examples of wood-rotting fungi, which is an extensively studied (Schmidt *et al.* 2002, Blanco *et al.* 2009, Gonou-Zagou *et al.* 2011, Mcdonald 2015, Lotz-Winter 2021). So far, several studies on new wood-decaying fungi of *Coniophora* and *Resupinatus* from China have been reported (Dai 2011, 2012).

Acknowledgements

The research was supported by the National Natural Science Foundation of China (Project No. 32170004), the High-level Talents Program of Yunnan Province (YNQR-QNRC-2018-111) and the Science Foundation of Education Department of Yunnan Province (2023Y0724).

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