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Morphological characteristics and phylogenetic analyses reveal *Antrodia yunnanensis sp. nov.* (Polyporales, Basidiomycota) from China

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Abstract

A new polypore, *Antrodia yunnanensis*, collected from southwestern China, is described and illustrated based on morphological characteristics and molecular evidence. It is characterized by annual, resupinate basidiocarps with greyish blue to dark greyish blue pore surface upon drying, round to angular pores measuring 2–3 per mm, a dimitic hyphal system with clamped generative hyphae, subicular hyphae bearing fine crystals, and cylindrical, thin-walled, smooth basidiospores measuring 7–9.9 × 2.5–3.1 µm. Molecular phylogeny inferred from ITS and nLSU sequence data showed that samples of *A. yunnanensis* formed a distinctive lineage in *Antrodia* sensu lato, and it nested a sister group with *A. tropica*.

Keywords: brown-rot fungi, Fomitopsidaceae, phylogeny, polypore, taxonomy

Introduction

Antrodia P. Karst. (1879: 40), typified by *A. serpens* (Fr.) P. Karst. (1879: 40) (Karsten 1879; Runnel *et al.* 2019), is a large cosmopolitan genus in a wide sense. *Antrodia* sensu lato is characterized by an annual to perennial growth habit, resupinate to effused-reflexed basidiocarps, a dimitic hyphal system with clamped generative hyphae, and hyaline, thin-walled, usually cylindrical to oblong-ellipsoid basidiospores, which are negative in Melzer's reagent. Species in the genus cause a brown rot (Gilbertson & Ryvarden 1986; Bernicchia & Ryvarden 2001; Núñez & Ryvarden 2001; Dai & Niemelä 2002; Ryvarden & Melo 2014). Chen & Cui (2015) reported that more than 45 species had been accepted in the genus worldwide, of which 22 species were recorded from China. Then, several new species were subsequently discovered (Chen & Wu 2017; Kout *et al.* 2017; Yuan *et al.* 2017; Runnel *et al.* 2019).

Phylogenetically, *Antrodia* is polyphyletic and closely related to other brown rot genera, such as *Fomitopsis* P. Karst. (1881: 9), *Daedalea* Pers. (1801: 500), *Rhodofomes* Kotl. & Pouzar (1990: 235), and *Oligoporus* Bref (1888: 114) (Rajchenberg *et al.* 2011; Bernicchia *et al.* 2012; Cui 2013; Spirin *et al.* 2013b; Ortiz-Santana *et al.* 2013; Han *et al.* 2016). Taxa in *Antrodia* sensu lato were divided into three different genera: *Antrodia* sensu stricto, *Fibroporia* Parmasto (1968: 176) and *Amyloporia* Bondartsev & Singer (1941: 50) (Rajchenberg *et al.* 2011). Ortiz-Santana *et al.* (2013) investigated the phylogenetic relationships among members of the *Antrodia* clade based on ITS and nLSU sequences, and supported the segregation of the genus *Antrodia* sensu lato into *Antrodia* and *Fibroporia* as the monophyly of *Amyloporia* was not supported. Spirin *et al.* (2013b) studied *Antrodia* sensu stricto based on ITS and *tef1* data, and found that *Antrodia* sensu stricto contained species of the *Antrodia heteromorpha* complex, *A. macra* (1966: 339) and *A. mappa* (2013: 1567). *Antrodia heteromorpha* complex included four species: *A. heteromorpha* sensu stricto, *A. serpens*, *A. favescens* (2013: 1564) and *A. tanakae* (2013: 1572). Spirin *et al.* (2015) focused on species that are closely related to *Antrodia crassa* (1973: 8), and investigated their phylogeny and species delimitation

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using geographic, ecological, morphological and molecular data (ITS, nLSU and *tef1*). Their analyses distinguished four clades within *Antrodia crassa* group: *Antrodia pini-cubensis* clade, *Antrodia crassa* clade, *Antrodia sitchensis* clade and *Antrodia pinea* clade. Spirin *et al.* (2016) revised taxonomy of the *Antrodia malicola* group based on DNA, morphological, ecological, and geographic data, and reported that *Antrodia malicola* group was not related to *Antrodia* sensu stricto but constituted its own lineage within the large *Fomitopsis – Daedalea* clade. And five species were included in the *A. malicola* group: *Antrodia malicola* sensu stricto, *A. kuzyana* (2016: 6), *A. cyclopis* (2016: 5), *A. minuta* (2007: 150) and *A. tuvensis* (2016: 10). Then taxonomy and phylogeny of the *Antrodia serialis* group were revised with morphological, ecological, and geographic data, partial *tef1*, ITS and nLSU sequences, and 13 species discovered in boreal and temperate zones of the Northern Hemisphere were contained in this group (Spirin *et al.* 2017). Runnel *et al.* (2019) showed that a corticioid species with a smooth hymenophore, *Phlebia griseoflavescens* (Litsch.) J. Erikss. & Hjortstam (1981: 1121) [= *Antrodia griseoflavescens* (Litsch.) Runnel, Spirin & K.H. Larss. (2019: 877)], belonged to *Antrodia* sentu strito, and redefined *Antrodia* in morphology to encompass both poroid and corticioid species.

During investigations on brown rot fungi in southwestern China, one new species of *Antrodia* is discovered based on morphological characters and ITS and nLSU rDNA sequences, and its illustrated description is provided.

Materials and methods

Morphological studies.—The specimens studied were deposited at the herbaria of Langfang Normal University (LFNC) and Southwest Forestry University (SWFC). Macro-morphological descriptions were based on field notes. Color terms follow Petersen (1996). Micro-morphological data were observed and under light microscopy following Dai (2012). In the text the following abbreviations were used: KOH = 5% potassium hydroxide, CB = cotton blue, CB– = acyanophilous, IKI = Melzer's reagent, IKI– = both non-amyloid and non-dextrinoid, L = mean spore length (arithmetic average of all spores), W = mean spore width (arithmetic average of all spores), R = mean of L/W ratios, Q = variation in the L/W ratios between the specimens studied, n = number of spores measured from given number of specimens.

DNA extraction and sequencing.—A cetyl trimethylammonium bromide rapid plant genome extraction kit (Aidlab Biotechnologies Co., Ltd, Beijing) was used to extract total genomic DNA from dried specimens, and performed the polymerase chain reaction (PCR) according to the manufacturer's instructions with some modifications. The DNA was amplified with the primers: ITS4 and ITS5 for ITS (White *et al.* 1990), and LR0R and LR7 for nLSU (Vilgalys & Hester 1990). The PCR procedures followed Han *et al.* (2016). The PCR products were purified and sequenced at Beijing Genomics Institute (China), with the same primers. All newly generated sequences were deposited at GenBank (Table 1).

Sequences generated in this study were aligned with additional sequences downloaded from GenBank (Table 1) using ClustalX (Thompson *et al.* 1997) and manually adjusted in BioEdit (Hall 1999). Sequence alignment was deposited at TreeBase (http://purl.org/phylo/treebase; submission ID 26346).

TABLE 1. A list of species, specimens, and GenBank accession number of sequences used in this study.

Species	Sample no.	Locality	GenBank accession no.		References
			ITS	nLSU	
Amyloporia crassa	Teppo Helo 60707009	Finland	KC595890	KC595890	Ortiz-Santana *et al.* 2013
Am. hingganensis	Dai 3748	China	KC595893	KC595893	Ortiz-Santana *et al.* 2013
Am. sinuosa	Otto Miettinen 12407	Finland	JQ700270	JQ700270	Ortiz-Santana *et al.* 2013
Am. sordida	RLG 9497-T	—	EU232193	EU232289	unpublished
Am. xantha	Cui 11544	China	KR605817	KR605756	Han *et al.* 2016
Am. xantha	Cui 6947	China	KC951154	—	Cui & Dai 2013

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TABLE 1. (Continued)

Species	Sample no.	Locality	GenBank accession no.		References
			ITS	nLSU	
An. ferox	Vlasak 1209_75	USA	KT711011	KT711035	Spirin *et al.* 2015
An. heteromopna	Tuomo Niemela 2621	Canada	KC543149	KC543149	Spirin *et al.* 2013b
An. heteromopna	Dai 12755	USA	KP715306	KP715322	Chen & Cui 2015
An. huangshanensis	Dai 6082	China	JQ837943	MG787640	Cui 2013
An. huangshanensis	Cui 10277	China	KX958178	—	Yuan *et al.* 2017
An. hyalina	Viacheslav Spirin 2772	Russia	JQ700283	JQ700283	Ortiz-Santana *et al.* 2013
An. infirma	Tuomo Niemela 7637	Finland	KC595894	KC595894	Ortiz-Santana *et al.* 2013
An. infirma	Tuomo Niemela 7644	Finland	KC595895	KC595895	Ortiz-Santana *et al.* 2013
An. juniperina	SRM-403-T	USA	KC585285	KC585109	Ortiz-Santana *et al.* 2013
An. juniperina	FP-105489-Sp	USA	KC585282	KC585105	Ortiz-Santana *et al.* 2013
An. leucaena	Jorma Pennanen 927	Finland	JQ700278	JQ700278	Ortiz-Santana *et al.* 2013
An. leucaena	Dai 11398	China	KX958179	—	Yuan *et al.* 2017
An. macra	Jenni Hottola 2729	Finland	KC543135	KC543135	Spirin *et al.* 2013b
An. malicola	Otto Miettinen 10595.1	China	KC595896	KC595896	Ortiz-Santana *et al.* 2013
An. malicola	Cui 7754	China	KX958180	KX958184	Yuan *et al.* 2017
An. mappa	Tuomo Niemela 2669	Canada	KC543130	KC543130	Spirin *et al.* 2013b
An. mappa	Reijo Penttila 11756	Finnland	KC543113	KC543113	Ortiz-Santana *et al.* 2013
An. mellita	Viacheslav Spirin 3315	Russia	KC543140	KC543140	Spirin *et al.* 2013b
An. minuta	Viacheslav Spirin s.n.	Russia	KC595900	KC595900	Ortiz-Santana *et al.* 2013
An. minuta	Viacheslav Spirin 2680	Russia	KC595898	KC595898	Ortiz-Santana *et al.* 2013
An. primaeva	Otto Miettinen 177	Russia	JQ700272	JQ700272	Ortiz-Santana *et al.* 2013
An. pulvinascens	Otto Miettinen 7488	Finnland	JQ700274	JQ700274	Ortiz-Santana *et al.* 2013
An. ramentacea	Per Marstad 274-09	Norway	KC543138	KC543138	Ortiz-Santana *et al.* 2013
An. ramentacea	Dai 6118	China	KC951178	—	Cui & Dai 2013
An. serialiformis	Otto Miettinen 14816	USA	JQ700290	—	Spirin *et al.* 2013a
An. serialiformis	JK-2009a	USA	FJ788412	—	Kout & Vlasák 2009
An. serialis	Otto Miettinen 12401	Finnland	JQ700271	JQ700271	Ortiz-Santana *et al.* 2013
An. serialis	Dai 7626	China	KR605812	KR605751	Han *et al.* 2016

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TABLE 1. (Continued)

Species	Sample no.	Locality	GenBank accession no.		References
			ITS	nLSU	
An. serpens	P. Vampola s. n.	Slovakia	KC543143	KC543143	Spirin *et al.* 2013b
An. subserpens	Cui 8310	China	KP715310	KP715326	Chen & Cui 2015
An. subserpens	Dai 13233	China	KP715309	KP715325	Chen & Cui 2015
An. tanakae	Dai 11770	China	KR605815	KR605754	Han *et al.* 2016
An. tanakae	Yuan 1106	China	KP715313	KP715329	Chen & Cui 2015
An. taxa	TFRI 781	Taiwan	EU232191	EU232275	unpublished
An. taxa	TFRI 782	Taiwan	EU232192	EU232276	unpublished
An. tropica	Cui 6471	China	JQ837939	—	Cui 2013
An. tropica	Dai 13428	China	MG787605	MG787652	unpublished
An. tropica	Dai 13434	China	KX958181	KX958185	Yuan *et al.* 2017
An. uzbekistanica	Dai 17104	Uzbekistan	KX958182	KX958186	Yuan *et al.* 2017
An. uzbekistanica	Dai 17105	Uzbekistan	KX958183	KX958187	Yuan *et al.* 2017
An. variiformis	CBS 309.82	USA	DQ491418	AY515344	Kim *et al.* 2007
An. variiformis	FP-90100-Sp	USA	KC585311	KC585136	Ortiz-Santana *et al.* 2013
An. variiformis	VS8406_1LR	USA	KT995137	KT995159	Spirin *et al.* 2017
An. yunnanensis	**Han 1157**	**China**	**MT497886**	**MT497884**	**in the present study**
An. yunnanensis	**CLZhao 4566**	**China**	**MT497887**	**MT497885**	**in the present study**
Daedalea dickinsii	Yuan 2685	China	KP171201	KP171223	Han *et al.* 2015
D. dickinsii	Yuan 2707	China	KP171202	KP171224	Han *et al.* 2015
D. quercina	Dai 12152	Czech Republic	KP171207	KP171229	Han *et al.* 2015
D. quercina	Dai 12659	Finland	KP171208	KP171230	Han *et al.* 2015
Fibroporia albican	Cui 9464	China	KC456250	KR605758	Han *et al.* 2016
F. gossypium	Otto Miettinen 13991	Finland	KC595905	KC595905	Ortiz-Santana *et al.* 2013
F. vaillantii	FP-90877-R	USA	KC585345	KC585170	Ortiz-Santana *et al.* 2013
Fomitopsis cana	Dai 9611	China	JX435776	JX435774	Li *et al.* 2013
Fo. pinicola	Cui 10312	China	KR605781	KR605720	Han *et al.* 2016
Fo. pinicola	Cui 10405	China	KC844852	KC844857	Han *et al.* 2016
Fo. subtropica	Cui 10578	China	KR605787	KR605726	Han *et al.* 2016

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TABLE 1. (Continued)

Species	Sample no.	Locality	GenBank accession no.		References
			ITS	nLSU	
L. sulphureus	Dai 12826	Czech Republic	KR605819	KR605762	Han *et al.* 2016
Rhodofomes cajanderi	Cui 9879	China	KC507157	KC507167	Han & Cui 2015
R. incarnatus	Cui 10348	China	KC844848	KC844853	Han & Cui 2015
R. rosea	Cui 10520	China	KC507162	KC507172	Han & Cui 2015
R. rosea	Cui 10633	China	KR605782	KR605721	Han *et al.* 2016
R. subfeei	Cui 9229	China	KR605789	KR605728	Han *et al.* 2016
Rhodofomitopsis africana	MUCL 43284	Cameroon	DQ491422	—	Kim *et al.* 2007
Rh. cupreorosea	CBS 236.87	Costa Rica	DQ491400	AY515325	Kim *et al.* 2007
Rh. feei	JV 0610/K9-Kout	Mexico	KF999922	KF999926	Han & Cui 2015
Rh. feei	Oinonen 6011906	Brazil	KC844851	KC844856	Han & Cui 2015
Rh. feei	Ryvarden 37603	Venezuela	KC844850	KC844855	Han & Cui 2015
Rh. feei	Uotila 42928	Australia	KF999924	KF999928	Han & Cui 2015
Rh. lilacinogilva	Schigel 5193	Australia	KR605773	KR605712	Han *et al.* 2016

New sequences are shown in bold.

Sequences of *Laetiporus sulphureus* (Bull.) Murrill (1920: 11) obtained from GenBank were used as an outgroup to root trees following Yuan *et al.* (2017). Maximum parsimony analysis 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 1000 random sequence additions. Max-trees were set to 5000, branches of zero length were collapsed and all parsimonious trees were saved. Clade robustness was assessed using a bootstrap (BT) analysis with 1000 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 (MPT) generated. RAxML v.7.2.8 was used to construct a maximum likelihood (ML) tree with GTR+G+I model of site substitution including estimation of Gamma-distributed rate heterogeneity and a proportion of invariant sites (Stamatakis 2006). The branch support was evaluated with bootstrapping method of 1000 replicates (Hillis & Bull 1993). Phylogenetic trees were visualized using Treeview (Page 1996).

MrModeltest 2.3 (Posada & Crandall 1998; Nylander 2004) was used to determine the best-fit evolution model for each data set for Bayesian inference (BI). Bayesian inference was calculated with MrBayes3.1.2 with a general time reversible (GTR) model of DNA substitution and a gamma distribution rate variation across sites (Ronquist & Huelsenbeck 2003). Four Markov chains were run for 2 runs from random starting trees for 3 million generations 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 that received bootstrap support for maximum likelihood (BS), maximum parsimony (MP) and Bayesian posterior probabilities (BPP) greater than or equal to 75 % (BS and MP) and 0.95 (BPP) were considered as significantly supported, respectively.

Results

Taxonomy

Antrodia yunnanensis M.L. Han & Q. An, *sp. nov.* (Figs. 1–2)
MycoBank no.: MB 835655

FIGURE 1. A Basidiomata of *Antrodia yunnanensis* (from holotype). Scale bar: 6 mm.

Antrodia yunnanensis is characterized by annual, resupinate basidiocarps with greyish blue to dark greyish blue pore surface upon drying; round to angular pores measuring 2–3 per mm, a dimitic hyphal system with clamped generative hyphae, subicular hyphae bearing fine crystals, and cylindrical, thin-walled, smooth basidiospores measuring 7–9.9 × 2.5–3.1 µm.

Type.—**China**. Yunnan Province, Jingdong County, Wuliangshan Nature Reserve, 6 October 2017, on living angiosperm tree, *Han 1157* (holotype, LFNC!).

Etymology.—*Yunnanensis* (Lat.): referring to distribution of the species in Yunnan Province, southwestern China.

Basidiomata.—Basidiocarps annual, resupinate, adnate, easy to separate from substrate, corky, up to 11 cm long, 3.3 cm wide, 4.3 mm thick when fresh. Pore surface greyish blue to vinaceous when fresh, turning to greyish blue to dark greyish blue upon drying; pores round to angular, 2–3 per mm; dissepiments thin, entire. Sterile margin very narrow to almost lacking, concolorous with pore surface. Subiculum cream, corky, up to 3.5 mm thick. Tubes thin, concolorous with pore surface, corky, up to 0.8 mm long.

Hyphal structure.—Hyphal system dimitic; generative hyphae bearing clamped connections, generative hyphae and skeletal hyphae CB–, IKI–; tissues becoming mouse-grey in KOH.

Subiculum.—Generative hyphae hyaline, thin- to slightly thick-walled, occasionally branched, 2–3 µm in diam.; skeletal hyphae dominant, thick-walled with a narrow lumen to subsolid, rarely branched, straight to flexuous, interwoven, 2–4 µm in diam. All hyphae covered with fine crystals.

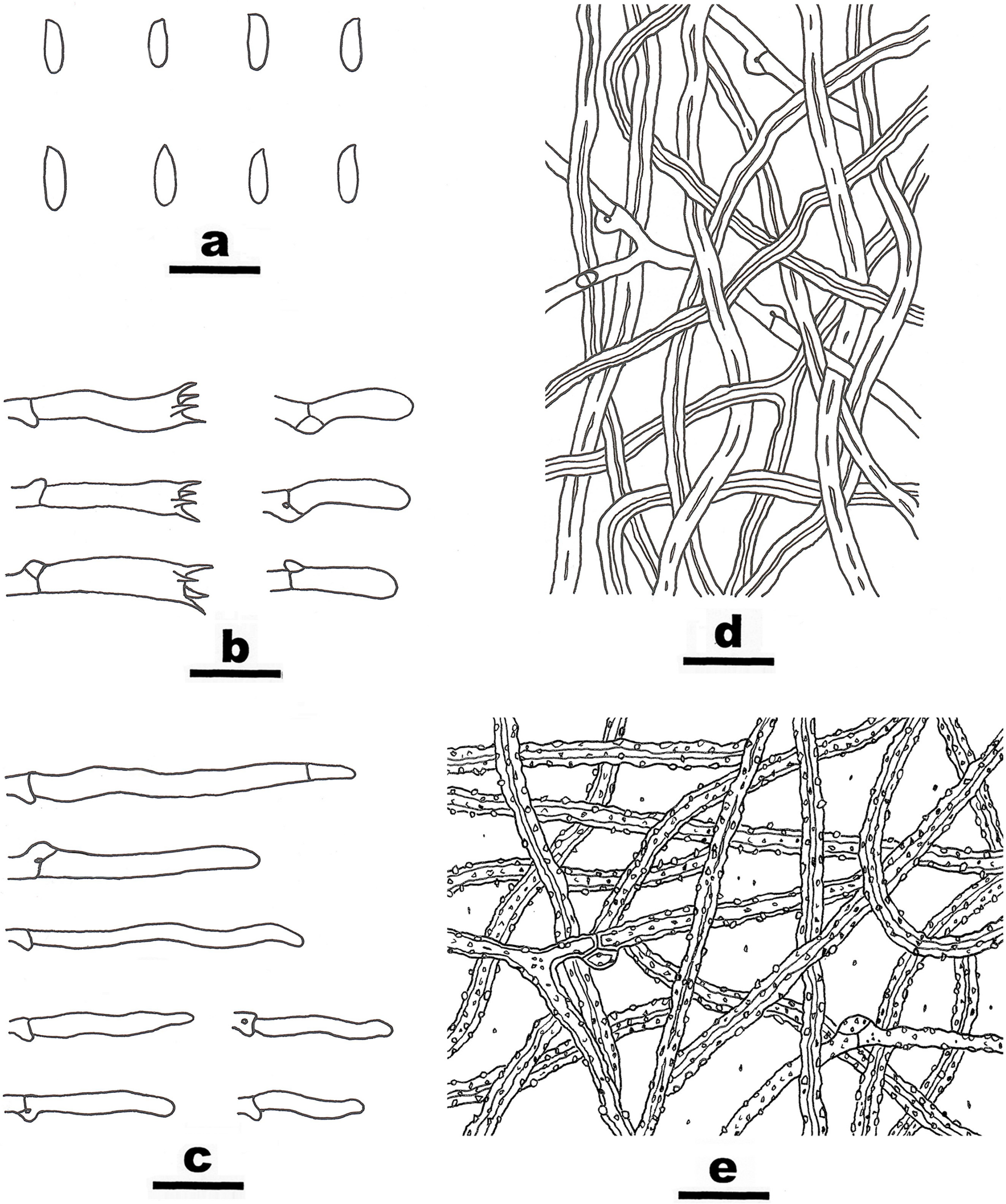

FIGURE 2. Microscopic structures of *Antrodia yunnanensis* (from holotype). a. Basidiospores. b. Basidia and basidioles. c. Cystidioles. d. Hyphae from trama. e. Hyphae from subiculum. Scale bars: a–e =10 µm.

Tubes.—Generative hyphae hyaline, thin-walled, occasionally branched, 2–3 µm in diam.; skeletal hyphae dominant, thick-walled with a narrow lumen to subsolid, rarely branched, straight to flexuous, interwoven, 2–3.5 µm in diam. Cystidia absent; cystidioles clavate, fusoid, sometimes with simple septa near to tips, thin-walled, 12–50 × 2–4 µm. Basidia infrequent, clavate, bearing four sterigmata and a basal clamp connection, 18–20 × 4–6 µm; basidioles dominant, in shape similar to basidia, but smaller.

Spores.—Basidiospores cylindrical, thin-walled, smooth, IKI–, CB–, 7–9.9(–10) × 2.5–3.1(–3.2) µm, L = 8.17 µm, W = 2.9 µm, Q = 2.82 (n = 20/1).

Type of rot.—Brown rot.

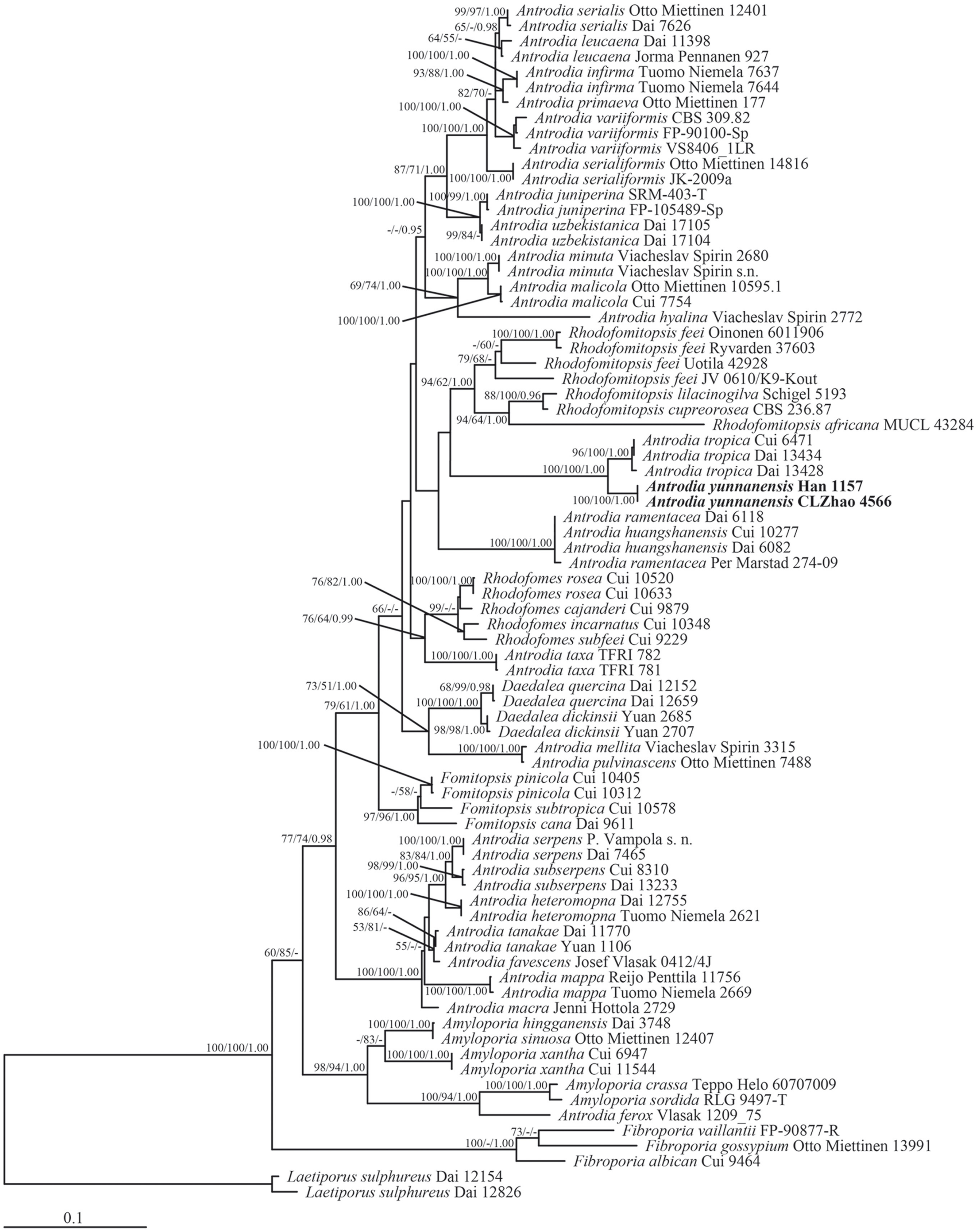

FIGURE 3. Maximum likelihood tree illustrating the phylogeny of *Antrodia yunnanensis* and related species based on combined ITS and nLSU sequence data. Branches are labeled with maximum likelihood bootstrap > 50%, parsimony bootstrap proportions > 50%, and Bayesian posterior probabilities > 0.95.

Additional specimen examined.—**China**. Yunnan Province, Jingdong County, Wuliangshan Nature Reserve, 6 October 2017, on living angiosperm tree, *CL Zhao 4566* (paratype, SWFC!).

Molecular phylogeny

The combined ITS and nLSU dataset included sequences from 78 fungal specimens or isolates representing 48 taxa and had an aligned length of 1529 characters, of which 923 characters are constant, 76 are variable and parsimony-uninformative, and 530 are parsimony-informative. Maximum parsimony analysis yielded three equally parsimonious trees (TL = 2323, CI = 0.424, RI = 0.773, RC = 0.328, HI = 0.576). Best model for the combined ITS and nLSU dataset estimated and applied in the Bayesian analysis was a GTR+I+G model. Bayesian analysis and ML analysis resulted in a similar topology as MP analysis, with an average standard deviation of split frequencies = 0.004417.

The ITS combined nLSU strict consensus tree (Fig. 3) generated by maximum likelihood, maximum parsimony and Bayesian analysis showed that two sampled specimens of *Antrodia yunnanensis* were grouped together and formed a highly supported lineage (BS = 100%, MP = 100%, BPP = 1.00), it is closely related to *A. tropica* B.K. Cui (2013: 226) with a full support (BS = 100%, MP = 100%, BPP = 1.00).

Discussion

Antrodia yunnanensis is described based on morphological features and molecular data. Phylogenetically, *A. yunnanensis* grouped with *A. tropica* and formed a highly supported lineage (Fig. 3). Morphologically, *A. tropica* and *A. yunnanensis* share annual, resupinate basidiomata, a dimitic hyphal system and similar size basidiospores (*A. tropica*: 8.3–10 × 2.5–3 µm), but *A. tropica* differs in greyish to pinkish buff pore surface, smaller angular pores (3–4 per mm), and lacking of cystidioles. In addition, hymenophoral trama of *A. tropica* is dominated by generative hyphae, and absence of crystal in subicular hyphae (Cui 2013).

Antrodia huangshanensis Y.C. Dai & B.K. Cui (2011: 16) and *A. ramentacea* (Berk. & Broome) Donk (1966: 339) also have annual, resupinate basidiocarps, and large pores (*A. huangshanensis*: 1–3 per mm, Cui *et al.* 2011; *A. ramentacea*: 1–2 per mm, Ryvarden & Melo 2014), and were neighbored to *A. yunnanensis* in the phylogenetic analysis (Fig. 3). But *A. huangshanensis* differs significantly in its white to cream pore surface, and smaller, cylindrical to allantoid basidiospores (5–6.5 × 1.6–2 µm, Cui *et al.* 2011). *A. ramentacea* differs from *A. yunnanensis* by generative hyphae dominant in the trama, and larger basidiospores (9–11 × 4.5–5 µm, Ryvarden & Melo 2014).

Morphologically, *Antrodia yunnanensis* reminds of two genera *Rhodofomes* and *Rhodofomitopsis* B.K. Cui, M.L. Han & Y.C. Dai (2016: 365), on the basis of its greyish blue to dark greyish blue pore surface and causing a brown rot. However, *Rhodofomes* is characterized by perennial, effused-reflexed to pileate or occasionally resupinate basidiocarps, smaller pores (more than 3 per mm), and mainly grow on gymnosperm wood; *Rhodofomitopsis* have effused-reflexed to pileate basidiocarps, and lack of cystidioles (Han *et al.* 2016). Phylogenetically, *Antrodia yunnanensis*, *Rhodofomes* and *Rhodofomitopsis* are distantly related. (Fig. 3).

Our results further confirm that *Antrodia* sensu lato is polyphyletic and nests with other brown rot fungal genera, such as *Fomitopsis*, *Daedalea* and *Rhodofomitopsis* in the antrodia clade (Cui 2013; Spirin *et al.* 2013b; Ortiz-Santana *et al.* 2013; Han *et al.* 2016; Cui *et al.* 2019; Runnel *et al.* 2019), though a better phylogenetic research of this group is needed based on more samples and more conserved gene markers.

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