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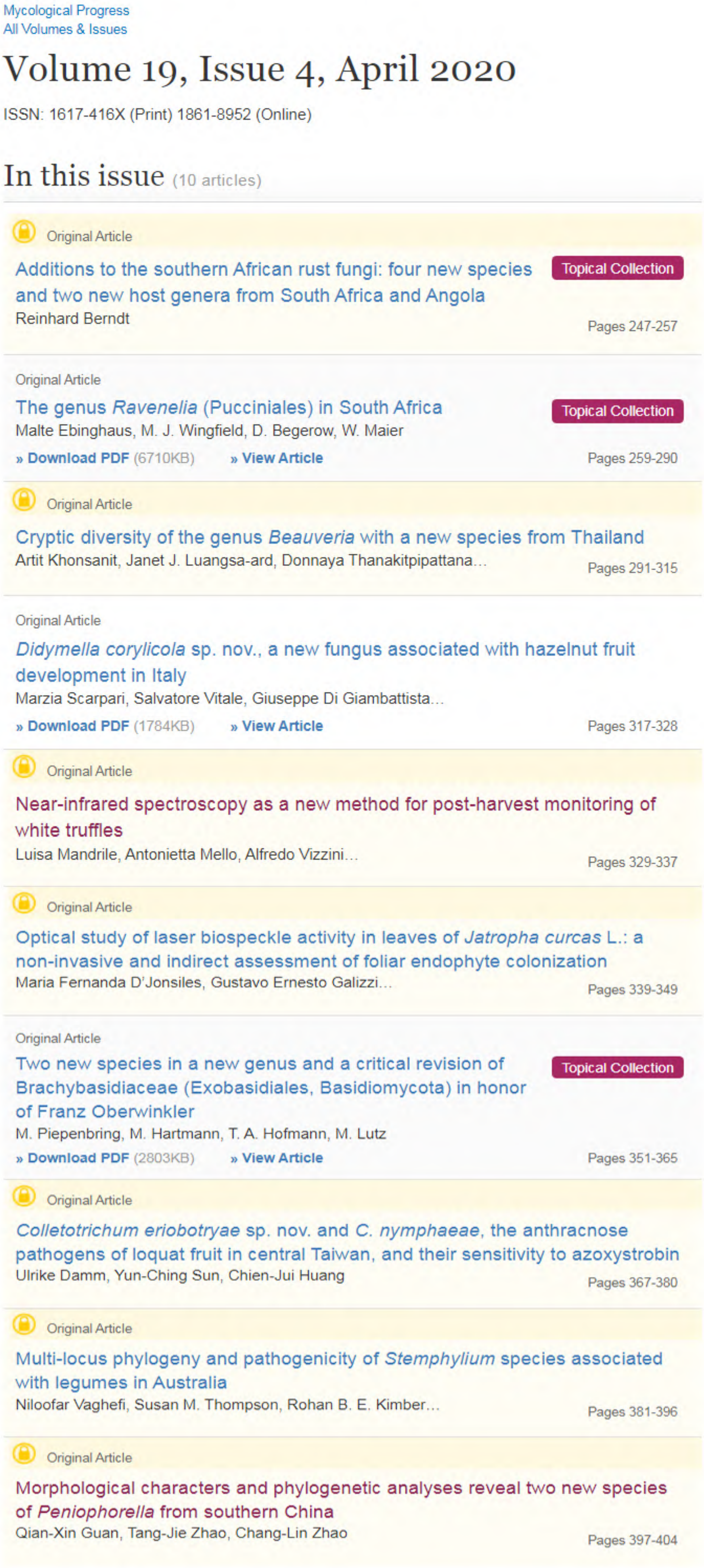

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ORIGINAL ARTICLE

Morphological characters and phylogenetic analyses reveal two new species of *Peniophorella* from southern China

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Abstract

Two new wood-inhabiting fungal species, *Peniophorella fissurata* and *P. yunnanensis*, are proposed based on a combination of morphological features and molecular evidence. *Peniophorella fissurata* is characterized by resupinate basidiomata with smooth to tuberculate hymenial surface, a monomitic hyphal system with clamped generative hyphae, fusiform cystidia, and allantoid, colorless, thin-walled, smooth basidiospores measuring 9–11 × 3–3.9 μm. *Peniophorella yunnanensis* is characterized by an annual basidiomata with grandinioid hymenial surface, a monomitic hyphal system with clamped generative hyphae, presence of three types cystidia, and ellipsoid, colorless, smooth, thin-walled basidiospores (8–9 × 4.7–5.5 μm). Sequences of ITS gene region of the studied samples were generated, and phylogenetic analyses were performed with maximum likelihood, maximum parsimony, and Bayesian inference methods. These phylogenetic analyses showed that *P. fissurata* was sister to *P. pubera*. *Peniophorella yunnanensis* formed a monomitic lineage and then grouped with *P. odontiiformis* and *P. rude*.

Keywords Hyphoderma · Phylogeny · Taxonomy · Wood-inhabiting fungi · Yunnan Province

Introduction

Peniophorella P. Karst. (Hyphodermataceae, Basidiomycota) is characterized by resupinate basidiomata with ceraceous to corneus consistency, smooth to tuberculate, and odontioid hymenophore with white to brownish-yellow hymenial surface. The hyphal system is monomitic with generative hyphae bearing clamp connections. Cystidia of several types as leptocystidia, gloeocystidia, and echinulated cells (echinocysts or stephanocysts) are present in some species. Basidiospores are cylindrical, ellipsoid or allantoid, smooth, thin-walled, IKI–, CB– (Karsten 1889; Bernicchia and Gorjón 2010) and was typed by *P. pubera* (Fr.) P. Karst. (1889). So far 20 species have been accepted in the genus worldwide (Karsten 1889; Donk 1957, 1962; Jülich 1974, 1978; Malençon 1982; Gilbertson and Blackwell 1984; Wu 1990; Boidin and Gilles 1991; Larsson 2007; Hjortstam and Ryvarden 2009; Duhem and Buyck 2011; Nakasone 2012; Duhem 2013; Prasher 2015).

Recently, molecular studies involving *Peniophorella* have been carried out (Larsson 2007; Miettinen and Larsson 2011; Telleria et al. 2012; Justo et al. 2017). Molecular phylogeny of *Hyphoderma* and the reinstatement of *Peniophorella* resulted in 19 new combinations in *Peniophorella* and *Peniophorella* species were nested into hymenochaetoid clade (Larsson 2007). Miettinen and Larsson (2011) revealed that *P. praetermissa* (P. Karst.) K.H. Larss. and *P. tsugae* (Burt) K.H. Larss. grouped together and clustered into Hymenochaetales. Telleria et al. (2012) studied *Hyphoderma* (Meruliaceae, Polyporales) and its discrimination from closely related taxa and revealed that eight *Peniophorella* species were closely grouped and were distinct from *Hyphoderma* s.s. Justo et al. (2017) did a revised family-level classification of the Polyporales (Basidiomycota) and proposed that 20 species should now be classified in *Peniophorella* in the Hyphodermataceae (Hymenochaetales).

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During studies on wood-inhabiting fungi in southern China, two additional taxa were found which could not be assigned to any described species. In this study, the authors expand samplings from the previous studies to examine taxonomy and phylogeny of two species within the genus *Peniophorella*, based on sequences of the internal transcribed spacer (ITS) region.

Materials and methods

Morphological studies

The specimens studied are deposited at the herbarium of Southwest Forestry University (SWFC), Kunming, Yunnan Province, P.R. China. Macromorphological or macromorphology descriptions are based on field notes. Color terms follow Petersen (1996). Micromorphological data were obtained from the dried specimens and observed under a light microscope following Dai (2012). The following abbreviations were used: KOH = 5% potassium hydroxide, CB = Cotton Blue, CB– = acyanophilous; 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, (n = a/b) = number of spores (a) measured from given number (b) of specimens.

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 with some modifications that a small piece of dried fungal specimen (about 30 mg) was ground 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 at 65 °C in a 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 13,000 rpm for 5 min, 0.3 mL of supernatant was transferred to a new tube and mixed with 0.45 mL of binding buffer. The mixture was then transferred to an adsorbing column (AC) for centrifugation at 13,000 rpm for 0.5 min. Then, 0.5 mL of inhibitor removal fluid was added in AC for a centrifugation at 12,000 rpm for 0.5 min. After washing twice with 0.5 mL of washing buffer, the AC was transferred to a clean centrifuge tube, and 100 mL elution buffer was added to the middle of adsorbed film to elute the genome DNA. ITS region was amplified with primer pair ITS5 and ITS4 (White et al. 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 products were purified and directly sequenced at Kunming Tsingke Biological Technology Limited Company. All newly generated sequences were deposited at GenBank (Table 1).

Sequencher 4.6 (GeneCodes, Ann Arbor, MI, USA) was used to edit the DNA sequences. 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 25288). Sequences of *Basidioradulum radula* (Fr.) Nobles and *Hypochnicium detriticum* (Bourdot) J. Erikss. & Ryvarden obtained from GenBank were used as an outgroup to root trees following Larsson et al. (2004) and Larsson (2007) (Fig. 1).

Maximum parsimony analysis was applied to the ITS dataset. Approaches to phylogenetic analyses followed Zhao and Wu (2017), and the tree construction procedure 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 treestatistics — 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. Datamatrix was also analyzed using Maximum Likelihood (ML) approach 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 3.1.2 (Ronquist and Huelsenbeck 2003). Four Markov chains run for 2 runs from random starting trees for 550, 000 generations (Fig. 1), and trees were sampled every 100 generations. The first one-fourth generations were 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 (BS) > 70%, maximum parsimony bootstrap (BT) > 50%, or Bayesian posterior probabilities (BPP) > 0.95.

Results

Molecular phylogeny

The ITS dataset (Fig. 1) included sequences from 38 fungal specimens representing 12 species. The dataset had an aligned

Table 1 List of species, specimens, and GenBank accession number of sequences used in this study

Species	Specimen no.	GenBank accession no. (ITS)	References
Basidioradulum radula (Fr.) Nobles	NH 9453	AF347105	Larsson et al. (2004)
Hypochnicium detriticum (Bourdot) J. Erikss. & Ryvarden	K.G. Nilsson	DQ677507	Larsson (2007)
Peniophorella echinocystis (J. Erikss. & Å. Strid) K.H. Larss.	KHL 6284	DQ677494	Larsson (2007)
Peniophorella fissurata C.L. Zhao	CLZhao 4539	MN864259	This study
Peniophorella fissurata	CLZhao 9421	MN864260	This study
Peniophorella fissurata	CLZhao 11412	MN864261	This study
Peniophorella fissurata	CLZhao 5848	MN864262	This study
Peniophorella guttulifera (P. Karst.) K.H. Larss.	NH 12012	DQ647501	Hallenberg et al. (2007)
Peniophorella guttulifera	NH 7813	DQ647502	Hallenberg et al. (2007)
Peniophorella odontiiformis (Boidin & Berthier) K.H. Larss.	TMIC 34389	DQ647496	Hallenberg et al. (2007)
Peniophorella odontiiformis	TMIC 50047	DQ647500	Hallenberg et al. (2007)
Peniophorella pertenuis (P. Karst.) Hallenb. & H. Nilsson	NH 15115	DQ647487	Hallenberg et al. (2007)
Peniophorella pertenuis	WU 960613	DQ647477	Hallenberg et al. (2007)
Peniophorella pertenuis	TMI 16118	DQ647484	Hallenberg et al. (2007)
Peniophorella pertenuis	NH 11063	DQ647485	Hallenberg et al. (2007)
Peniophorella pertenuis	NH 12429	DQ647486	Hallenberg et al. (2007)
Peniophorella pertenuis	NH 3868	DQ647479	Hallenberg et al. (2007)
Peniophorella praetermissa (P. Karst.) K.H. Larss.	NH 3494	DQ647453	Hallenberg et al. (2007)
Peniophorella praetermissa	NH 9815	DQ647454	Hallenberg et al. (2007)
Peniophorella praetermissa	AN 3031	DQ647463	Hallenberg et al. (2007)
Peniophorella praetermissa	NH 7827	DQ647460	Hallenberg et al. (2007)
Peniophorella praetermissa	NH 11451	DQ647455	Hallenberg et al. (2007)
Peniophorella praetermissa	NH 11803	DQ647456	Hallenberg et al. (2007)
Peniophorella pubera (Fr.) P. Karst.	NH 10380	DQ647504	Hallenberg et al. (2007)
Peniophorella pubera	NH 10512	DQ647505	Hallenberg et al. (2007)
Peniophorella pubera	EL 4439	DQ647503	Hallenberg et al. (2007)
Peniophorella pubera	NH 3950	DQ647506	Hallenberg et al. (2007)
Peniophorella pubera	NH 12069	DQ647507	Hallenberg et al. (2007)
Peniophorella pubera	FCUG 3126	GQ409535	Hallenberg et al. (2007)
Peniophorella rude (Bres.) K.H. Larss.	Wu 9307-39	DQ647499	Hallenberg et al. (2007)
Peniophorella rude	Wu 0104-3	DQ647495	Hallenberg et al. (2007)
Peniophorella subpraetermissa (Sheng H. Wu) K.H. Larss.	Wu 950627	DQ647493	Hallenberg et al. (2007)
Peniophorella yunnanensis C.L. Zhao	CLZhao 4810	MN864263	This study
Peniophorella yunnanensis	CLZhao 6113	MN864264	This study
Peniophorella yunnanensis	CLZhao 6128	MN864265	This study
Peniophorella yunnanensis	CLZhao 6137	MN864266	This study
Peniophorella yunnanensis	CLZhao 6144	MN864267	This study
Peniophorella yunnanensis	CLZhao 6132	MN864268	This study

length of 692 characters, of which 378 characters are constant, 29 are variable and parsimony-uninformative, and 285 are parsimony-informative. Maximum parsimony analysis yielded 8 equally parsimonious trees (TL = 668, CI = 0.662, HI = 0.338, RI = 0.890, RC = 0.609). 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 as MP analysis, with an average standard deviation of split frequencies = 0.009191 (BI).

The phylogenetic tree (Fig. 1) inferred from ITS sequences, demonstrated 10 species of *Peniophorella* and revealed that *P. fissurata* was sister to *P. pubera* (Fr.) P. Karst.; the branch of

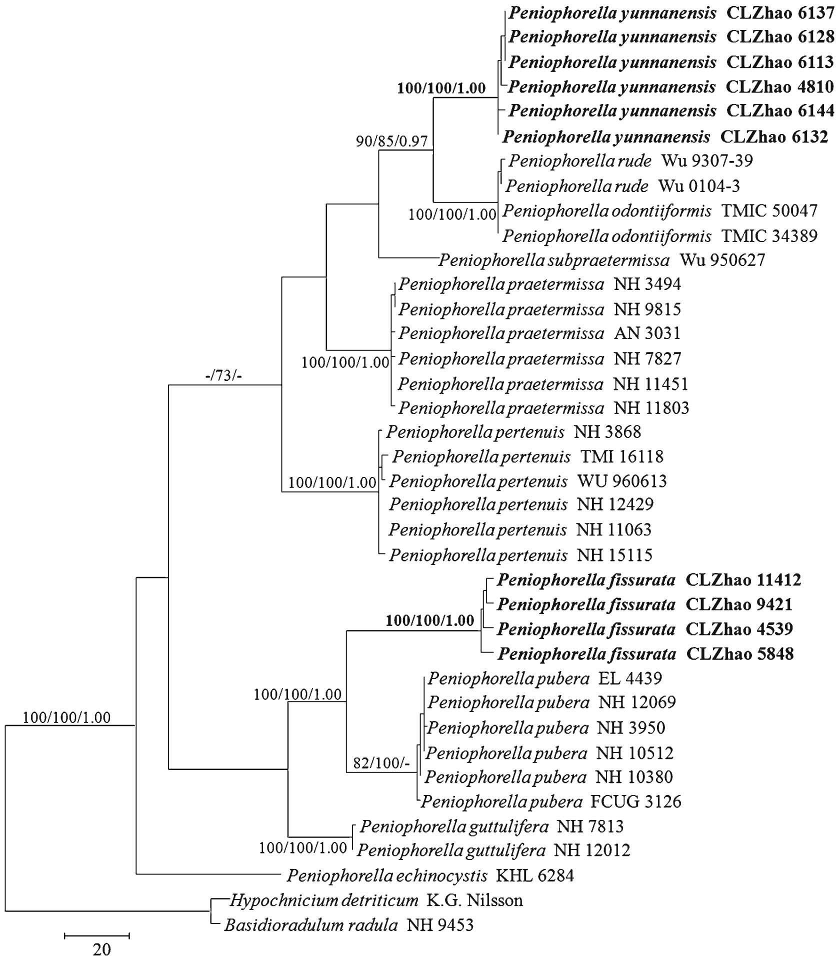

Fig. 1 Maximum Parsimony strict consensus tree illustrating the phylogeny of two new species and related species in *Peniophorella* based on ITS sequences. Branches are labelled with maximum likelihood bootstrap > 70%, parsimony bootstrap proportions > 50%, and Bayesian posterior probabilities >0.95, respectively, Scale bar = 20

P. fissurata has high support–100% BS, 100% BT and 1.00 BPP. *Peniophorella yunnanensis* grouped with *P. odontiiformis* (Boidin & Berthier) K.H. Larss. and *P. rude* (Bres.) K.H. Larss.

Taxonomy

Peniophorella fissurata C.L. Zhao, sp. nov. **(**Fig. 2 and Fig. 3)

MycoBank no.: MB 833813

Holotype: CHINA, Yunnan Province, Puer, Jingdong County, Wuliangshan National Nature Reserve, E 100°08′, N 24°04′, alt. round to 3000 m, on fallen branch of angiosperm, 4 Jan 2019, CLZhao 9421 (SWFC).

Etymology: *Fissurata* (Lat.)—referring to the cracking hymenial surface.

Fruiting body: Basidiomata annual, adnate, ceraceous, without odor or taste when fresh, becoming ceraceous to corneus upon drying, up to 20 cm long, 2.5 cm wide, 100–300 μm thick. Hymenial surface smooth to tuberculate, white to cream when fresh, turning cream to buff upon drying, cracking. The subiculum very thin, cream to buff.

Hyphal structure: Hyphal system monomitic, generative hyphae with clamp connections, colorless, thin-walled, branched, interwoven, 2–3.5 μm in diameter, IKI–, CB–; tissues unchanged in KOH.

Hymenium: Cystidia fusiform, 28–65 × 6.5–15 μm; basidia clavate to subclavate, constricted, with 4 sterigmata and a basal clamp connection, 19–30 × 5.5–9 μm.

Spores: Basidiospores allantoid, colorless, thin-walled, smooth, IKI–, CB–, 9–11(–11.5) × 3–3.9 μm, L = 9.95 μm, W = 3.46 μm, Q = 2.83–2.9 (*n* = 60/2).

Additional specimens examined: China, Yunnan Province, Wenshan, Malipo County, Pingzhai Forestry Farm, E 104°55′, N 24°12′, alt. 1250 m, on fallen branch of angiosperm, 18 Jan 2019, CLZhao 11412 (SWFC); Puer, Jingdong County, Wuliangshan National Nature Reserve, E 100°08′, N 24°04′, alt. round to 3000 m, on fallen angiosperm branch, 6 Oct 2017, CLZhao 4539 (SWFC); Zhenyuan County, Heping Town, Liangzizhai, E 101°10′, N 24°00′, alt. 3150 m, on fallen angiosperm branch, 15 Jan 2018, CLZhao 5848 (SWFC).

Peniophorella yunnanensis C.L. Zhao, sp. nov. **(**Fig. 4 and Fig. 5)

MycoBank no.: MB 833814

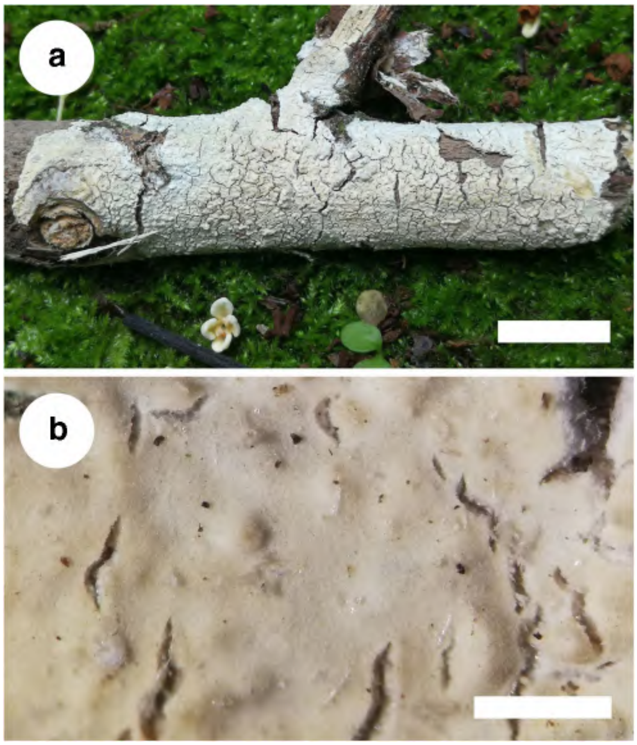

Fig. 2 Basidiomata of *Peniophorella fissurata* (holotype). Bars: A = 1 cm, B = 1 mm

Holotype: CHINA, Yunnan Province, Puer, Zhenyuan County, Heping Town, Damoshan, E 101°10′, N 24°00′, alt. 3150 m, on fallen branch of angiosperm, 16 Jan 2018, CLZhao 6137 (SWFC).

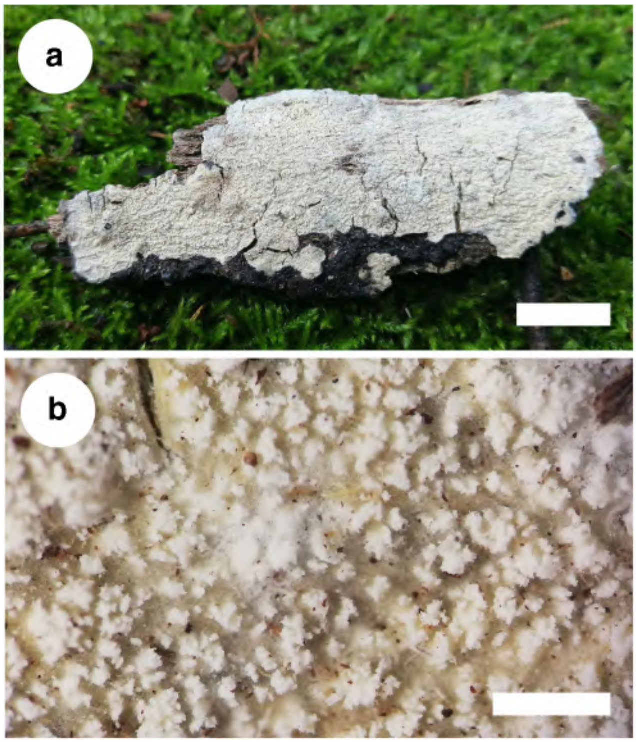

Fig. 4 Basidiomata of *Peniophorella yunnanensis* (holotype). Bars: A = 1 cm, B = 1 mm

Etymology: Yunnanensis (Lat.)—referring to the locality (Yunnan Province) of the type specimens.

Fruiting body: Basidiomata annual, adnate, ceraceous, without odor or taste when fresh, becoming corneus upon

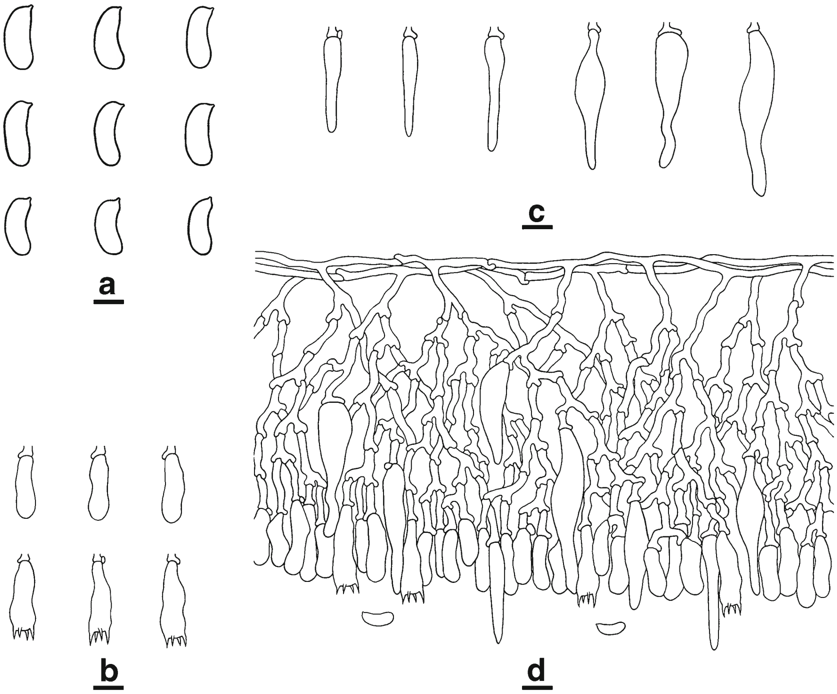

Fig. 3 Microscopic structures of *Peniophorella fissurata* (holotype). **a** Basidiospores. **b** Basidia and basidioles. **c** Cystidia. **d** A section of hymenium. Bars: A = 5 μm, B–D = 10 μm

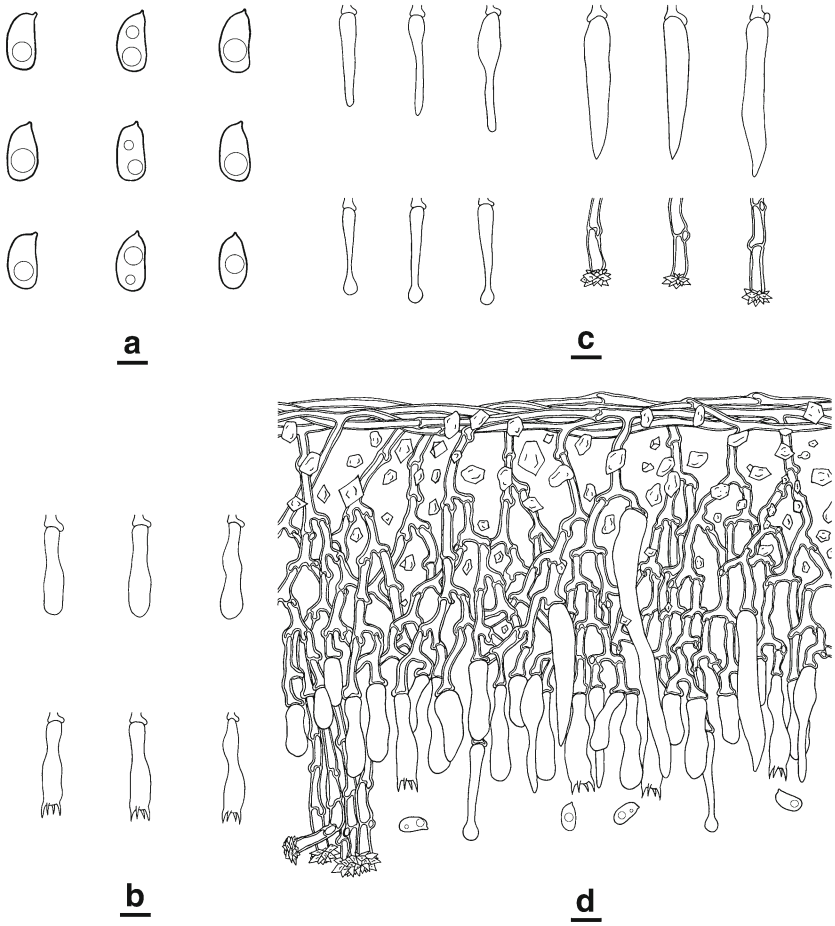

Fig. 5 Microscopic structures of *Peniophorella yunnanensis* (holotype). **a** Basidiospores. **b** Basidia and basidioles. **c** Cystidia. **d** A section of hymenium. Bars: A = 5 µm, B–D = 10 µm

drying, up to 10 cm long, 4 cm wide, 100–200 µm thick. Hymenial surface grandinioid, white to cream when fresh, turn to cream upon drying. The subiculum very thin, cream.

Hyphal structure: Hyphal system monomitic, generative hyphae with clamp connections, colorless, thick-walled, branched, interwoven, 2–4.5 µm in diameter, IKI–, CB–; tissues unchanged in KOH (Fig. 5).

Hymenium: Cystidia of three types: (i) fusiform cystidia smooth, thin-walled, 20–85 × 5.5–12.5 µm; (ii) capitate cystidia smooth, thin-walled, slightly constricted at the neck, with a globose head, 20–40 × 3–6 µm; (iii) asterocystidia thick-walled, with the apical part encrusted, 9–28 × 3–8.5 µm; basidia clavate, with 4 sterigmata and a basal clamp connection, 18.5–32.5 × 6–8.5 µm.

Spores: Basidiospores ellipsoid, colorless, smooth, thin-walled, with oil drops, IKI–, CB–, (7.5)8–9(−9.5) × 4.5–5.5 µm, L = 8.67 µm, W = 4.91 µm, Q = 1.69–1.84 (*n* = 60/2).

Additional specimens (paratypes) examined: China, Yunnan Province, Puer, Zhenyuan County, Heping Town, Damoshan, E 101°10′, N 24°00′, alt. 3150 m, on angiosperm trunk, 11 Jan 2018, CLZhao 4810 (SWFC), 16 Jan 2018, CLZhao 6113, CLZhao 6144 (SWFC), on fallen angiosperm branch, 16 Jan 2018, CLZhao 6128, CLZhao 6132 (SWFC).

Discussion

In the present study, two new species, *Peniophorella fissurata* and *P. yunnanensis* spp. nov., are described based on phylogenetic analyses and morphological characters.

Phylogenetically, *Peniophorella fissurata* is closely related to *P. pubera* in the rDNA (Fig. 1), and *P. yunnanensis* is grouped with *P. odontiiformis* and *P. rude*. But morphologically *P. pubera* differs from *P. fissurata* by having white to ochraceous hymenial surface, and thick-walled, strongly encrusted cystidia and ellipsoid basidiospores (Bernicchia and Gorjón 2010). *Peniophorella odontiiformis* differs from *P. yunnanensis* by odontioid hymenophore and subcylindrical basidiospores (Larsson 2007). *Peniophorella rude* has larger (9–10 × 5–7 µm) and ellipsoid basidiospores (Larsson 2007).

Morphologically, *Peniophorella allantospora* (Sheng H. Wu) K.H. Larss., *P. capitulata* (Boidin & Gilles) K.H. Larss., *P. flagellata* (G. Cunn.) K.H. Larss., *P. guttulifera* (P. Karst.) K.H. Larss., *P. incrustatissima* (Boidin & Gilles) K.H. Larss., *P. pallida* (Bres.) K.H. Larss. and *P. praetermissa* (P. Karst.) K.H. Larss. are similar to *P. fissurata* based on the smooth hymenophore and allantoid basidiospores. However, *Peniophorella allantospora* differs in its longer basidiospores

(11–13 μm, Larsson 2007); *P. capitulata* in its presence of stephanocysts (Larsson 2007); *P. flagellata* in its echinocysts (Larsson 2007); *P. guttulifera* in its larger, thick-walled and encrusted cystidia (Larsson 2007); *P. incrustatissima* in its encrusted cystidioles (Boidin and Gilles 1991; Larsson 2007); *P. pallida* in its whitish to ochraceous hymenial surface and presence of resinous brown matter in hymenium (Bernicchia and Gorjón 2010); *P. praetermissa* in its stephanocysts and wider basidiospores (8–12 × 4–5 μm, Bernicchia and Gorjón 2010).

Peniophorella comptopsis (Burds. & Nakasone) K.H. Larss. and *P. echinocystis* (J. Erikss. & Å. Strid) K.H. Larss. are similar to *P. yunnanensis* inferred from the grandinioid to odontioid hymenophore, but *P. comptopsis* is separated from *P. yunnanensis* by yellowish white to grayish yellow hymenial surface and smaller basidiospores (4.5–5.5 × 3–4 μm, Burdsall & Nakasone 1981). *Peniophorella echinocystis* differs from *P. yunnanensis* by having globose echinocysts and larger basidiospores (9–12 × 2.5–3 μm, Bernicchia and Gorjón 2010).

Wood-rotting fungi are an extensively studied group of Basidiomycota (Gilbertson and Ryvarden 1987; Núñez and Ryvarden 2001; Bernicchia and Gorjón 2010; Dai 2012; Ryvarden and Melo 2014), but the Chinese wood-rotting fungal diversity is still not well known, especially in subtropical and tropical areas, and many recently described taxa of this ecological group were from these areas (Cui et al. 2011; Zhao and Cui 2012; Cui 2013; Cui and Decock 2013; Li et al. 2013; Chen and Cui 2014; Bian et al. 2016; Zhou et al. 2016; Ma and Zhao 2019). Two new species in the present study are from subtropics, too. It is possible that new taxa will be found after further field studies and molecular analyses.

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