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Table of Contents

Article

Correspondence

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Morphological and molecular identification of a new species of *Perenniporia* (Polyporales, Basidiomycota) in North America

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Abstract

A new poroid wood-inhabiting fungal species, *Perenniporia bostonensis sp. nov*., is proposed based on morphological and molecular characters. The species is characterized by resupinate, cream to buff pore surface; a dimitic hyphal system with skeletal hyphae strongly dextrinoid, unbranched, interwoven and a distinct wide lumen; ovoid to broad ellipsoid, non-truncate, hyaline, distinct thick-walled, smooth, dextrinoid basidiospores, 3.5–4.5 × 3–4 µm. The internal transcribed spacer (ITS) and the large subunit (LSU) regions of nuclear ribosomal RNA gene sequences of the studied samples were generated, and phylogenetic analyses were performed with maximum likelihood, maximum parsimony and bayesian inference methods. The phylogenetic analysis based on molecular data of ITS+nLSU sequences showed that *P. bostonensis* recognized in *Perenniporia* sensu stricto. The new species formed a monophyletic lineage with a strong support (100% BS, 100% BP, 1.00 BPP) and was closely related to *P. bannaensis* and *P. koreana*. Both morphological and molecular characters confirmed the placement of the new species in *Perenniporia*.

Keywords: Phylogenetic analysis, Polypores, Taxonomy, Wood-rotting fungi

Introduction

Perenniporia Murrill is a large cosmopolitan genus characterized by poroid basidiomata, thick-walled, ellipsoid to distinctly truncate basidiospores, and cyanophilous and variable dextrinoid reactions and the genus has been considered a member of the Polyporaceae (Ryvarden 1991). The hyphal system of *Perenniporia* species is a di- or trimitic with clamp connections on generative hyphae, while the vegetative hyphae are cyanophilous and variably dextrinoid (Decock & Stalpers 2006). About 100 species have been accepted in the genus worldwide (Gilbertson & Ryvarden 1987, Hattori & Lee 1999, Núñez & Ryvarden 2001, Dai *et al*. 2002, 2011, Cui *et al*. 2007, Xiong *et al*. 2008, Choeyklin *et al*. 2009, Decock 2011, 2016, Decock *et al*. 2011, Ryvarden & Melo 2014, Jiang *et al*. 2015, Ji *et al*. 2017). Fifteen species were recorded from North America (Zhou *et al*. 2016).

Recently, the phylogenetic study of *Perenniporia* inferred from the combined data of the internal transcribed spacer (ITS) regions and the large subunit nuclear ribosomal RNA gene (nLSU) datasets have demonstrated that several monophyletic entities were well supported and could be recognized as distinct genera (Robledo *et al*. 2009, Zhao *et al*. 2013). Robledo *et al*. (2009) employed molecular study based on LSU and ITS DNA datasets and demonstrated that *Perenniporia* grouped with related genera *Abundisporus* Ryvarden, *Hornodermoporus* Teixeira, *Perenniporiella* Decock & Ryvarden and *Truncospora* Pilát by using ribosomal DNA sequences. Molecular studies employing the nuclear ribosomal LSU and ITS DNA sequence data has helped to investigate phylogenetic overview of the genus *Perenniporia* and suggested that it was polyphyletic (Zhao *et al*. 2013). Later, several new species were described based on ribosomal DNA sequences and nested within the *Perenniporia* (Zhao & Cui 2013, Jiang *et al*. 2015, Ji *et al*. 2017).

During investigations on the diversity of polypores in North America, an additional undescribed species corresponding to *Perenniporia* was found. To confirm the affinity of the undescribed species of *Perenniporia*, phylogenetic analysis was carried out based on the ITS and nLSU sequences.

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Materials and methods

Morphological studies.—The specimens studied are deposited at the herbarium of Southwest Forestry University (SWFC). Macro-morphological descriptions are based on field notes. Special colour terms follow Petersen (1996). Micro-morphological data were obtained from the dried specimens, and observed under a light microscope following Dai (2010). 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 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, amplification, sequencing 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 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 13 000 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 13 000 rpm for 0.5 min. Then, 0.5 ml 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 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 pairs ITS5 and ITS4 (White *et al*. 1990). Nuclear LSU region was amplified with primer pairs LR0R and LR7 (http://www.biology.duke.edu/fungi/mycolab/primers.htm). 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 1 min and 72 °C for 1.5 min, and a final extension of 72 °C for 10 min Chen *et al*. (2016). 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 sequence. Sequences were aligned in MAFFT 6 (Katoh & Toh 2008, 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 21826). Sequences of *Donkioporia expansa* (Desm.) Kotl. & Pouzar and *Pyrofomes demidoffii* (Lév.) Kotl. & Pouzar obtained from GenBank were used as outgroups to root trees following Zhao *et al*. (2013) in the ITS+nLSU analysis.

Maximum parsimony analysis was applied to the ITS+nLSU dataset sequences. Approaches to phylogenetic analysis followed Song *et al*. (2016), 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 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 (MPT) 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 for ML analysis was determined by 1000 bootstrap replicate.

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 8 million generations (ITS+nLSU), 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 (BP) and Bayesian posterior probabilities (BPP) greater than or equal to 75 % (BP) and 0.95 (BPP) were considered as significantly supported, respectively.

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

Species name	Sample no.	GenBank accession no.		References
		ITS	nLSU	
Abundisporus sclerosetosus	MUCL 41438	FJ411101	FJ393868	Robledo *et al*. (2009)
A. violaceus	MUCL 38617	FJ411100	FJ393867	Robledo *et al*. (2009)
Donkioporia expansa	MUCL 35116	FJ411104	FJ393872	Robledo *et al*. (2009)
Hornodermoporus latissima	Cui 6625	HQ876604	JF706340	Zhao *et al*. (2013)
H. martia	Cui 7992	HQ876603	HQ654114	Zhao *et al*. (2013)
H. martia	MUCL 41677	FJ411092	FJ393859	Robledo *et al*. (2009)
H. martia	MUCL 41678	FJ411093	FJ393860	Robledo *et al*. (2009)
Microporellus violaceo-cinerascens	MUCL 45229	FJ411106	FJ393874	Robledo *et al*. (2009)
Perenniporia africana	Cui 8674	KF018119	KF018128	Present study
P. africana	Cui 8676	KF018120	KF018129	Present study
P. aridula	Dai 12398	JQ001855	JQ001847	Zhao *et al*. (2013)
P. aridula	Dai 12396	JQ001854	JQ001846	Zhao *et al*. (2013)
P. bannaensis	Cui 8560	JQ291727	JQ291729	Zhao *et al*. (2013)
P. bannaensis	Cui 8562	JQ291728	JQ291730	Zhao *et al*. (2013)
P. bostonensis	CLZhao 144	MG491283	MG491286	Present study
P. bostonensis	CLZhao 2854	MG491284	MG491287	Present study
P. bostonensis	CLZhao 2854	MG491285	MG491288	Present study
P. cinereofusca	Dai 9289	KF568893	KF568895	Zhao *et al*. (2013)
P. cinereofusca	Cui 5280	KF568892	KF568894	Zhao *et al*. (2013)
P. corticola	Cui 1248	HQ848472	HQ848482	Zhao *et al*. (2013)
P. corticola	Dai 7330	HQ654094	HQ654108	Cui & Zhao (2012)
P. corticola	Cui 2655	HQ654093	HQ848483	Cui & Zhao (2012)
P. ellipsospora	Cui 10276	KF018124	KF018132	Present study
P. ellipsospora	Cui 10284	KF018125	KF018133	Present study
P. hainaniana	Cui 6364	JQ861743	JQ861759	Zhao & Cui (2013)
P. hainaniana	Cui 6365	JQ861744	JQ861760	Zhao & Cui (2013)
P. hainaniana	Cui 6366	JQ861745	JQ861761	Zhao & Cui (2013)
P. japonica	Cui 7047	HQ654097	HQ654111	Cui & Zhao (2012)
P. japonica	Cui 9181	JQ001856	JX141468	Zhao & Cui (2012)
P. koreana	KUC 200932	KJ156313	KJ156305	Jiang *et al*. (2015)
P. koreana	KUC 2008J-02	KJ156310	KJ156302	Jiang *et al*. (2015)
P. lacerata	Cui 7220	JX141448	JX141458	Zhao & Cui (2013)
P. lacerata	Dai 11268	JX141449	JX141459	Zhao & Cui (2013)
P. luteola	H 1308a	JX141456	JX141466	Zhao & Cui (2014)
P. luteola	H 1308b	JX141457	JX141467	Zhao & Cui (2014)
P. maackiae	Cui 8929	HQ654102	JF706338	Cui & Zhao (2012)
P. maackiae	Cui 5605	JN048760	JN048780	Cui & Zhao (2012)
P. macropora	Zhou 280	JQ861748	JQ861764	Zhao & Cui (2013)
P. medulla-panis	MUCL 49581	FJ411088	FJ393876	Robledo *et al*. (2009)
P. medulla-panis	MUCL 43250	FJ411087	FJ393875	Robledo *et al*. (2009)
P. medulla-panis	Cui 3274	JN112792	JN112793	Zhao *et al*. (2013)
P. nanlingensis	Cui 7620	HQ848477	HQ848486	Zhao & Cui (2012)
P. nanlingensis	Cui 7589	HQ848478	HQ848487	Zhao & Cui (2012)
P. pyricola	Cui 9149	JN048762	JN048782	Cui & Zhao (2012)

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TABLE 1. (Continued)

Species name	Sample no.	GenBank accession no.		References
		ITS	nLSU	
P. pyricola	Dai 10265	JN048761	JN048781	Cui & Zhao (2012)
P. rhizomorpha	Dai 7248	JF706330	JF706348	Zhao & Cui 2012
P. rhizomorpha	Cui 7507	HQ654107	HQ654117	Cui & Zhao (2012)
P. russeimarginata	Yuan 1244	JQ861750	JQ861766	Zhao & Cui (2013)
P. straminea	Cui 8718	HQ876600	JF706335	Cui & Zhao (2012)
P. straminea	Cui 8858	HQ654104	JF706334	Cui & Zhao (2012)
P. subacida	Dai 8224	HQ876605	JF713024	Zhao *et al*. (2013)
P. subacida	Cui 3643	FJ613655	AY336753	Zhao *et al*. (2013)
P. subacida	MUCL 31402	FJ411103	AY333796	Robledo *et al*. (2009)
P. subadusta	Cui 8459	HQ876606	HQ654113	Zhao *et al*. (2013)
P. substraminea	Cui 10177	JQ001852	JQ001844	Zhao *et al*. (2013)
P. substraminea	Cui 10191	JQ001853	JQ001845	Zhao *et al*. (2013)
P. subtephropora	Dai 10962	JQ861752	JQ861768	Zhao & Cui (2013)
P. subtephropora	Dai 10964	JQ861753	JQ861769	Zhao & Cui (2013)
P. tenuis	Wei 2783	JQ001858	JQ001848	Zhao *et al*. (2013)
P. tenuis	Wei 2969	JQ001859	JQ001849	Zhao *et al*. (2013)
P. tephropora	Cui 9029	HQ876601	JF706339	Cui & Zhao (2012)
P. tephropora	Cui 6331	HQ848473	HQ848484	Cui & Zhao (2012)
P. tibetica	Cui 9459	JF706327	JF706333	Zhao & Cui (2013)
P. truncatospora	Cui 6987	JN048778	HQ654112	Zhao & Cui (2012)
P. truncatospora	Dai 5125	HQ654098	HQ848481	Cui & Zhao (2012)
Perenniporiella chaquenia	MUCL 47647	FJ411083	FJ393855	Robledo *et al*. (2009)
Pe. chaquenia	MUCL 47648	FJ411084	FJ393856	Robledo *et al*. (2009)
Pe. micropora	MUCL 43581	FJ411086	FJ393858	Robledo *et al*. (2009)
Pe. neofulva	MUCL 45091	FJ411080	FJ393852	Robledo *et al*. (2009)
Pe. pendula	MUCL 46034	FJ411082	FJ393853	Robledo *et al*. (2009)
Pyrofomes demidoffii	MUCL 41034	FJ411105	FJ393873	Robledo *et al*. (2009)
Truncospora detrita	MUCL 42649	FJ411099	FJ393866	Robledo *et al*. (2009)
T. macrospora	Cui 8106	JX941573	JX941596	Zhao *et al*. (2013)
T. ochroleuca	Dai 11486	HQ654105	JF706349	Zhao *et al*. (2013)
T. ochroleuca	MUCL 39726	FJ411098	FJ393865	Robledo *et al*. (2009)
T. ochroleuca	MUCL 39563	FJ411097	FJ393864	Robledo *et al*. (2009)
T. ohiensis	Cui 5714	HQ654103	HQ654116	Zhao *et al*. (2013)
T. ohiensis	MUCL 41036	FJ411096	FJ393863	Robledo *et al*. (2009)
Vanderbylia delavayi	Dai 6891	JQ861738	KF495019	Zhao *et al*. (2013)
V. fraxinea	DP 83	AM269789	AM269853	Robledo *et al*. (2009)
V. fraxinea	Cui 7154	HQ654095	HQ654110	Zhao *et al*. (2013)
V. fraxinea	Cui 8885	HQ876611	JF706344	Zhao *et al*. (2013)
V. fraxinea	Cui 8871	JF706329	JF706345	Zhao *et al*. (2013)
V. robiniophila	Cui 5644	HQ876609	JF706342	Zhao *et al*. (2013)
V. robiniophila	Cui 7144	HQ876608	JF706341	Zhao *et al*. (2013)
V. robiniophila	Cui 9174	HQ876610	JF706343	Zhao *et al*. (2013)
V. vicina	MUCL 44779	FJ411095	AF518666	Robledo *et al*. (2009)

Results

Molecular phylogeny

The ITS+nLSU dataset included sequences from 87 fungal specimens representing 47 species. The dataset had an aligned length of 2091 characters, of which 1560 characters are constant, 90 are variable and parsimony-uninformative, and 441 are parsimony-informative. Maximum parsimony analysis yielded four equally parsimonious trees (TL = 2022, CI = 0.377, HI = 0.623, RI = 0.744, RC = 0.280). Best model for the ITS+nLSU dataset estimated and applied in the Bayesian analysis: GTR+I+G. Bayesian analysis and ML analysis resulted in a similar topology as MP analysis, with an average standard deviation of split frequencies = 0.005287 (BI).

The phylogeny (Fig. 1) inferred from ITS+nLSU sequences demonstrated that *Perenniporia bostonensis* recognized in *Perenniporia* sensu strict and it formed a monophyletic lineage with a strong support (100% BS, 100% BP, 1.00 BPP) and was closely related to *P. bannaensis* B.K. Cui & C.L. Zhao and *P. koreana* Y. Jang & J.J. Kim.

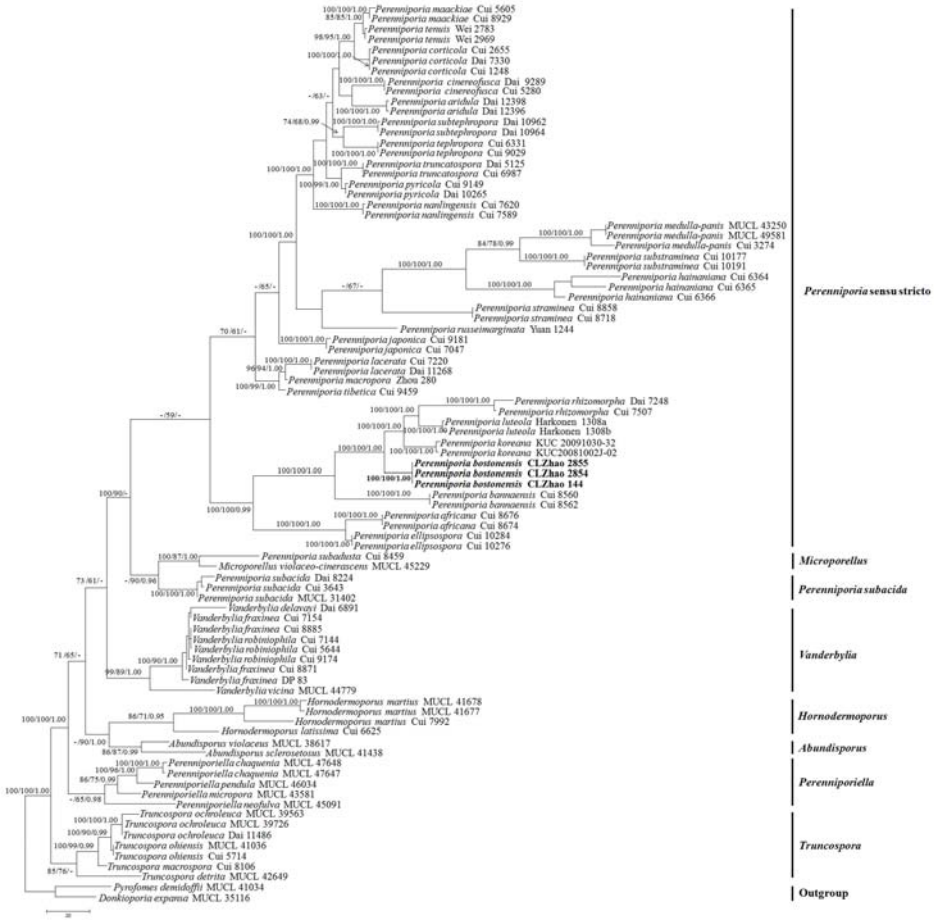

FIGURE 1. Maximum Parsimony strict consensus tree illustrating the phylogeny of *Perenniporia bostonensis* and related species based on ITS+nLSU sequences. Branches are labeled with maximum likelihood bootstrap higher than 70%, parsimony bootstrap proportions higher than 50% and Bayesian posterior probabilities more than 0.95 respectively.

Taxonomy

Perenniporia bostonensis C.L. Zhao, *sp. nov.* (Figs. 2, 3)

MycoBank no.: MB 824131

Type.—**USA**. MA, Boston, Blackstone Park, alt. 52 m, on fallen angiosperm branch, 27 July 2015, *CLZhao 144* (holotype, SWFC!)

FIGURE 2. Basidiomata of *Perenniporia bostonensis* (holotype). Scale bar: a–5 mm.

Etymology.—*Bostonensis* (Lat.): referring to the locality (Boston) of the type specimen.

Basidiomata.—Annual, resupinate, without odor or taste when fresh, becoming corky upon drying, up to 5 cm long, 3 cm wide, 2 mm thick at centre. Pore surface cream when fresh, cream to buff upon drying; pores angular, 4–6 per mm; dissepiments thin, entire. Sterile margin wide, grey white to pale brown, up to 1.5 mm wide. Subiculum cream, thin, up to 0.5 mm thick. Tubes cream to buff, corky, up to 1.5 mm long.

Hyphal structure.—Hyphal system dimitic; generative hyphae with clamp connections; skeletal hyphae strong dextrinoid, CB+; tissues unchanged in KOH.

Subiculum.—Generative hyphae infrequent, hyaline, thin-walled, unbranched, 2.5–3.5 µm in diam.; skeletal hyphae dominant, hyaline, thick-walled with a wide lumen, unbranched, interwoven, 3–5 µm in diam.

Tubes.—Generative hyphae infrequent, hyaline, thin-walled, unbranched, 2–3 µm in diam.; skeletal hyphae dominant, hyaline, thick-walled with a wide lumen, unbranched, interwoven, 3–4 µm. Cystidia absent, fusoid cystidioles present, hyaline, thin-walled, 8.5–12 × 2.5–4 µm; basidia barrel-shaped to clavate, with four sterigmata and a basal clamp connection, 11–15 × 7–9.5 µm; basidioles dominant, mostly pear-shaped, but slightly smaller than basidia.

Spores.—Basidiospores ovoid to broad ellipsoid, non-truncate, hyaline, distinct thick-walled, smooth, dextrinoid, CB+, (3.2–)3.5–4.5(–4.7) × (2.8–)3–4(–4.2) µm, L = 3.94 µm, W = 3.42 µm, Q = 1.01–1.13 (n = 180/3).

Additional specimens examined.—**USA**. MA, Boston, Blackstone Park, alt. 52 m, on fallen angiosperm branch, 27 July 2015, *CLZhao 2854, 2855* (paratypes, SWFC!).

Discussion

In the present study, a new species, *Perenniporia bostonensis*, is described based on phylogenetic analyses and morphological characters. In the ITS+nLSU analyses (Fig. 1), it formed a monophyletic lineage with a strong support (100% BS, 100% BP, 1.00 BPP) and then grouped with *P. bannaensis* and *P. koreana*. However, morphologically *P. bannaensis* differs from *P. bostonensis* by its smaller pores (6–8 per mm) and larger basidiospores (5.2–6 × 4–4.6 µm, Zhao *et al*. 2013). *Perenniporia koreana* is separated from *P. bostonensis* by having the grayish orange pore surface and the narrower lumen and larger basidiospores (6–7 × 3.9–5.2 µm, Jiang *et al*. 2015).

In the previous studies, three species (with non-truncate basidiospores), *Perenniporia bannaensis*, *P. luteola* B.K. Cui & C.L. Zhao and *P. rhizomorpha* B.K. Cui, Y.C. Dai & Decock grouped closely with generic species *P. medulla-panis* (Jacq.) Donk (with truncate basidiospores) (Zhao & Cui 2013, Zhao *et al.* 2013). However, in the present

study (Fig. 1), these species grouped with other four species (with non-truncate basidiospores): *P. africana* Ipulet & Ryvarden, *P. bostonensis*, *P. ellipsospora* Ryvarden & Gilb. and *P. koreana*, and then clustered with *P. medulla-panis* group. The different topology maybe results from the more taxa in the current study.

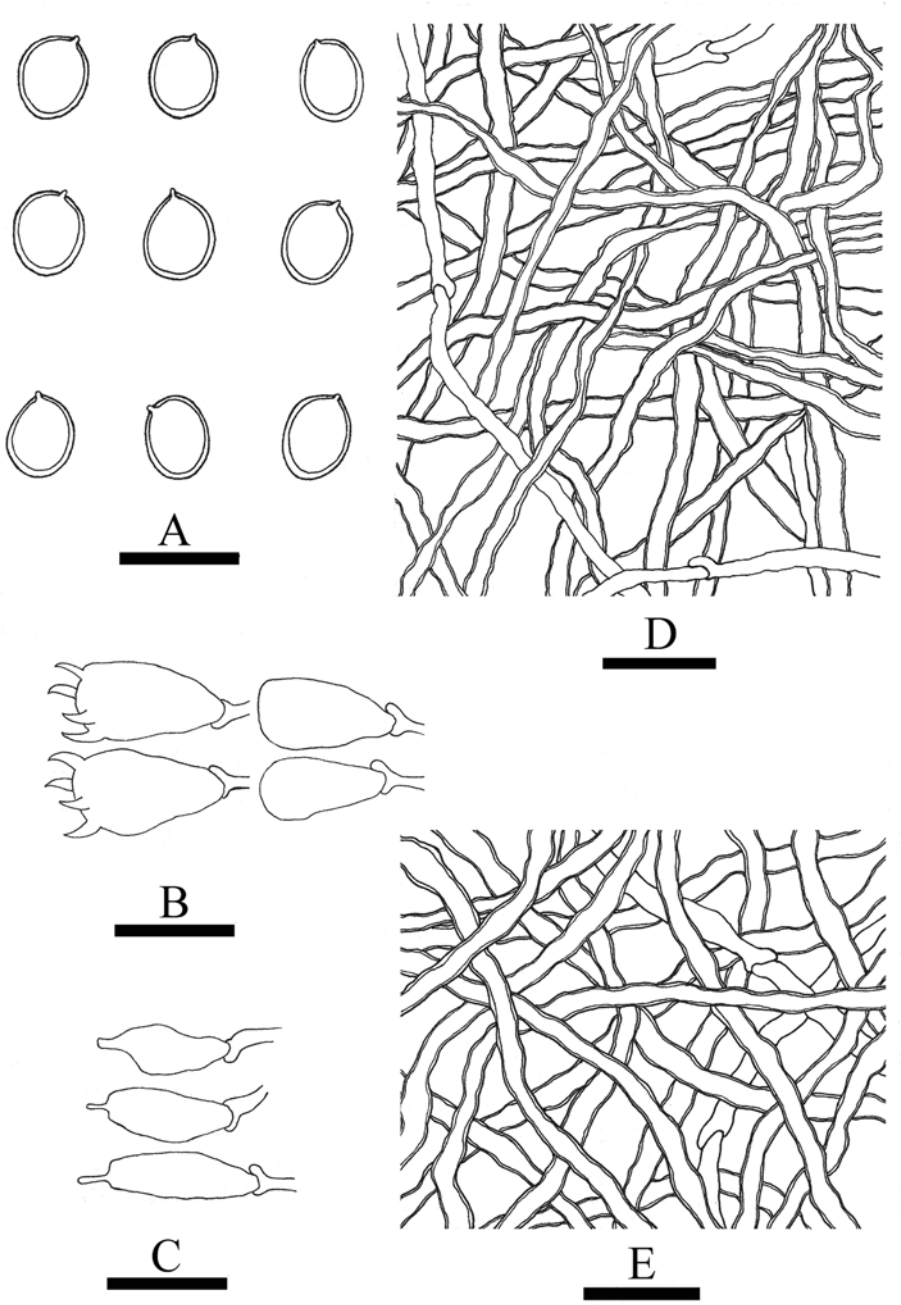

FIGURE 3. Microscopic structures of *Perenniporia bostonensis* (drawn from the holotype). a. Basidiospores. b. Basidia and basidioles. c. Cystidioles. d. Hyphae from trama. e. Hyphae from subiculum. Bars: a–5 μm; b–e–10 μm.

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