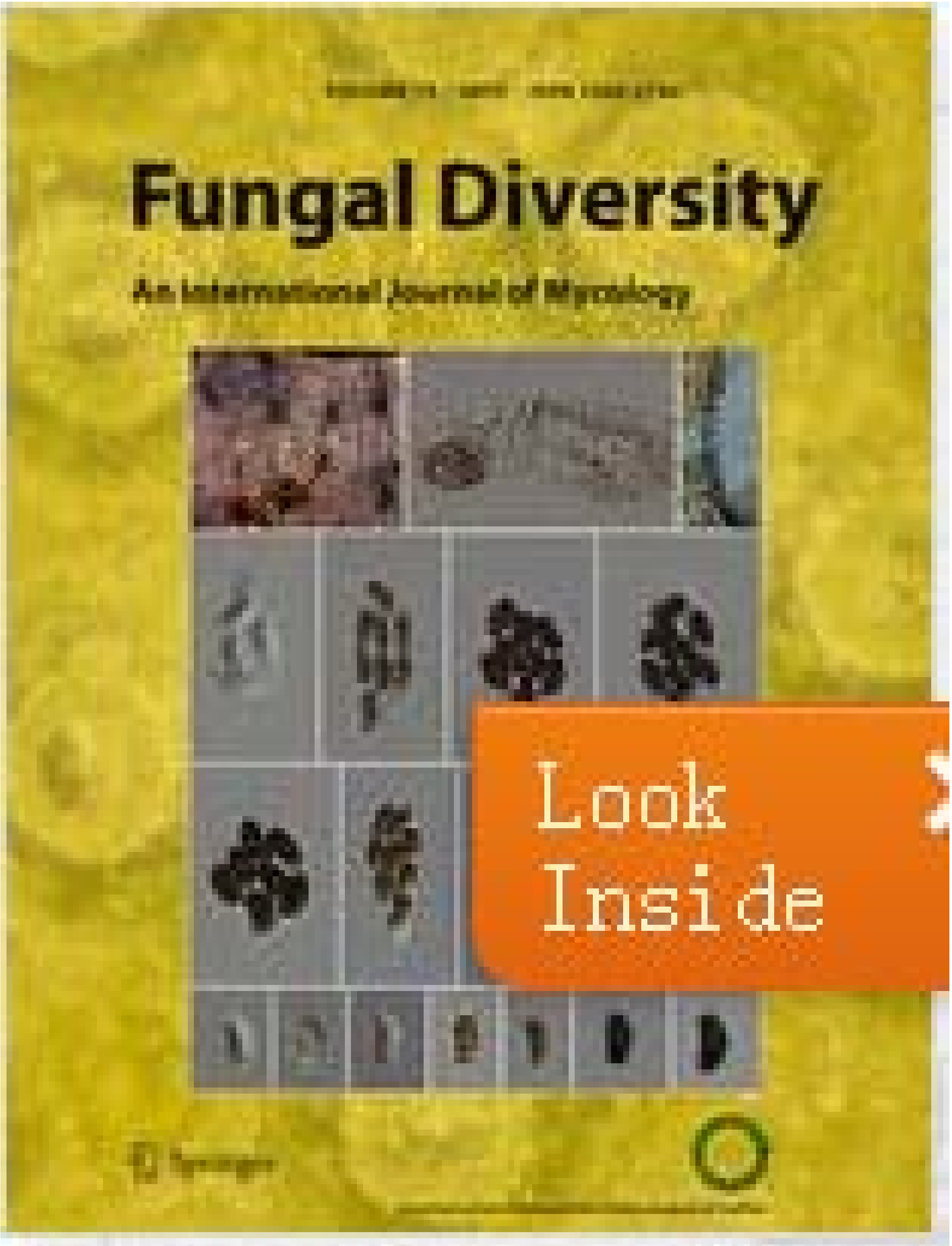
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New species and phylogeny of *Perenniporia* based on morphological and molecular characters

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Abstract Three new resupinate, poroid, wood-inhabiting fungi, *Perenniporia aridula*, *P. bannaensis* and *P. substraminea*, are introduced on the basis of morphological and molecular characters. Molecular study based on sequence data from the ribosomal ITS and LSU regions supported the three new species' positions in *Perenniporia* s.s., and all of them formed monophyletic lineages with strong support (100 % BP, 1.00 BPP). Phylogenetic analysis revealed seven clades for the 31 species of *Perenniporia* s.l. used in this study. Among them, *Perenniporiella* clustered with *Perenniporia ochroleuca* group, and then subsequently grouped with *Abundisporus*. In addition, the *P. ochroleuca* group, the *P. vicina* group, the *P. martia* group and *P. subacida* formed well supported monophyletic entities, which could be recognized as distinct genera, and they are not related to *P. medulla-panis* which belongs to *Perenniporia* s.s. clade. An identification key to 38 species of *Perenniporia* occurring in China is provided.

Keywords Phylogeny · ITS and nLSU · Polypore · Taxonomy · China

Introduction

Polypores are very important group of wood-inhabiting fungi because of their pathogenic and potential application in biomedical engineering and biodegradation (Younes et al. 2007; Dai et al. 2007, 2009; De Silva et al. 2012; Wang et al. 2012). *Perenniporia* Murrill (Polyporales, Basidiomycetes) is a large cosmopolitan polypore genus. The circumscription of *Perenniporia* has been broadly expanded in the last 20 years, and taxa in the genus are lignicolous and cause a white rot. *Perenniporia* species produce ellipsoid to distinctly truncate basidiospores, which are usually thick-walled and have cyanophilous and variably dextrinoid reactions; the hyphal structure is di- to trimitic with clamp connections on generative hyphae, and the vegetative hyphae can be cyanophilous and variably dextrinoid (Decock and Stalpers 2006). About 90 species have been described in or transferred to *Perenniporia* (Gilbertson and Ryvarden 1987; Ryvarden and Gilbertson 1994; Hattori and Lee 1999; Decock and Ryvarden 1999, 2000, 2011; Decock et al. 2000, 2001, 2011; Decock 2001a; Núñez and Ryvarden 2001; Dai et al. 2002, 2011; Cui et al. 2007; Xiong et al. 2008; Choeyklin et al. 2009; Dai 2010a; Cui and Zhao 2012). The preliminary phylogeny of *Perenniporia* s.l. was investigated with an analysis of nuclear ribosomal partial LSU and ITS DNA sequences data by Robledo et al. (2009). In their study, the differentiation of the hyphal system and the basidiospore morphology were outlined as critical features for the definition of genera in the *Perenniporia* complex.

During investigations on wood-inhabiting fungi in China, three undescribed species matching the concepts of *Perenniporia* were discovered and are introduced. Molecular data can be used to infer relationships amongst groups of morphologically similar basidiomycetes (Yang 2011; Cao et al. 2012; He and Dai 2012). The aims of this study are to 1) confirm the taxonomic affinity of the new species and 2) infer the evolutionary relationships among representative species of *Perenniporia* to establish if the genus is mono- or polyphyletic.

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Materials and methods

Morphological studies

The studied specimens were deposited at the herbaria of the Institute of Microbiology, Beijing Forestry University (BJFC) and the Institute of Applied Ecology, Chinese Academy of Sciences (IFP). The microscopic routine followed Dai (2010b). Sections were studied at magnification up to ×1000 using a Nikon Eclipse E 80i microscope and phase contrast illumination. Drawings were made with the aid of a drawing tube. Microscopic features, measurements and drawings were made from slide preparations stained with Cotton Blue and Melzer's reagent. Spores were measured from sections cut from the tubes. In presenting the variation in the size of the spores, 5 % of measurements were excluded from each end of the range, and were given in parentheses. In the text the following abbreviations were used: IKI = Melzer's reagent, IKI– = negative in Melzer's reagent, KOH = 5 % potassium hydroxide, CB = Cotton Blue, CB+ = cyanophilous, 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 = number of spores measured from given number of specimens. Special color terms followed Petersen (1996).

Molecular study and phylogenetic analysis

Molecular techniques followed Cui et al. (2008) and Dai et al. (2010). The fungal taxa used in this study are listed in Table 1. Phire Plant Direct PCR Kit (Finnzymes) procedure was used to extract total genomic DNA from the fruitbodies and for the polymerase chain reaction (PCR). DNA sequencing was performed at Beijing Genomics Institute. All newly generated sequences were submitted to GenBank and are listed in Table 1. In the study, sequence data of nuclear ribosomal RNA regions were used to determine the phylogenetic positions of the new species. The internal transcribed spacer (ITS) regions were amplified with the primers ITS4 and ITS5 (White et al. 1990), and the large subunit (nLSU) with the primers LR0R and LR7 (Pinruan et al. 2010).

Sequences were aligned with additional sequences downloaded from GenBank (Table 1) using BioEdit (Hall 1999) and ClustalX (Thomson et al. 1997). Alignment was manually adjusted to allow maximum alignment and to minimize gaps. Sequence alignment was deposited at TreeBase (http://purl.org/phylo/treebase/; submission ID 12083).

Maximum parsimony analysis was applied to the combined ITS and nLSU datasets. In phylogenetic reconstruction, sequences of *Donkioporia expansa* (Desm.) Kotl. & Pouzar and *Pyrofomes demidoffii* (Lév.) Kotl. & Pouzar obtained from GenBank were used as outgroup. The tree construction procedure was performed in PAUP* version 4.0b10 (Swofford 2002) as described by Jiang et al. (2011). 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 (MPT) generated.

MrMODELTEST2.3 (Posada and Crandall 1998; Nylander 2004) was used to determine the best-evolution for each data set for Bayesian inference (BY). 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 and Huelsenbeck 2003). Four Markov chains were run for 2 runs from random starting trees for 2 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 parsimony (MP) and Bayesian posterior probabilities (BPP) greater or equal than 75 % (MP) and 0.95 (BPP) respectively were considered as significantly supported.

Results

Taxonomy

Perenniporia aridula B.K. Cui & C.L. Zhao, **sp. nov.** (Figs. 1 and 2)

MycoBank: MB 800238

Type **China**. Yunnan Province, Yuanjiang County, on fallen angiosperm trunk, 9 June 2011 Dai 12396 (holotype in BJFC).

Etymology Aridula (Lat.): referring to the species growth in a xerothermic environment.

Fruiting body Basidiocarps perennial, resupinate, adnate, corky, without odor or taste when fresh, becoming hard corky upon drying, up to 18 cm long, 8.5 cm wide, 6.2 mm thick at centre. Pore surface cream when fresh, becoming cream to buff-yellow upon drying; pores round, 6–7 per mm; dissepiments thick, entire. Sterile margin more or less receding, cream-buff to pale salmon, up to 2 mm wide. Subiculum buff, thin, up to 0.6 mm thick. Tubes concolorous with pore surface, hard corky, up to 5.6 mm long.

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

Species name	Sample no.	GenBank no.		References
		ITS	LSU	
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
Microporellus violaceo-cinerascens	MUCL 45229	FJ411106	FJ393874	Robledo et al. 2009
Perenniporia aridula	Dai 12398	JQ001855[a]	JQ001847[a]	
P. aridula	Dai 12396	JQ001854[a]	JQ001846[a]	
P. bannaensis	Cui 8560	JQ291727[a]	JQ291729[a]	
P. bannaensis	Cui 8562	JQ291728[a]	JQ291730[a]	
P. corticola	Cui 2655	HQ654093	HQ848483	Zhao and Cui 2012
P. corticola	Cui 1248	HQ848472	HQ848482	Zhao and Cui 2012
P. corticola	Dai 7330	HQ654094	HQ654108	Cui et al. 2011
P. detrita	MUCL 42649	FJ411099	FJ393866	Robledo et al. 2009
P. fraxinea	DP 83	AM269789	AM269853	Guglielmo et al. 2007
P. fraxinea	Cui 7154	HQ654095	HQ654110	Zhao and Cui 2012
P. fraxinea	Cui 8871	JF706329	JF706345	Cui and Zhao 2012
P. fraxinea	Cui 8885	HQ876611	JF706344	Zhao and Cui 2012
P. japonica	Cui 7047	HQ654097	HQ654111	Zhao and Cui 2012
P. japonica	Cui 9181	JQ001856[a]	JQ001841[a]	
P. latissima	Cui 6625	HQ876604	JF706340	Zhao and Cui 2012
P. maackiae	Cui 8929	HQ654102	JF706338	Zhao and Cui 2012
P. maackiae	Cui 5605	JN048760	JN048780	Cui and Zhao 2012
P. martia	Cui 7992	HQ876603	HQ654114	Cui et al. 2011
P. martia	MUCL 41677	FJ411092	FJ393859	Robledo et al. 2009
P. martia	MUCL 41678	FJ411093	FJ393860	Robledo et al. 2009
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[a]	JN112793[a]	
P. ochroleuca	Dai 11486	HQ654105	JF706349	Zhao and Cui 2012
P. ochroleuca	MUCL 39563	FJ411097	FJ393864	Robledo et al. 2009
P. ochroleuca	MUCL 39726	FJ411098	FJ393865	Robledo et al. 2009
P. ohiensis	MUCL 41036	FJ411096	FJ393863	Robledo et al. 2009
P. ohiensis	Cui 5714	HQ654103	HQ654116	Zhao and Cui 2012
P. piceicola	Dai 4184	JF706328	JF706336	Cui and Zhao 2012
P. pyricola	Cui 9149	JN048762	JN048782	Cui and Zhao 2012
P. pyricola	Dai 10265	JN048761	JN048781	Cui and Zhao 2012
P. rhizomorpha	Cui 7507	HQ654107	HQ654117	Zhao and Cui 2012
P. rhizomorpha	Dai 7248	JF706330	JF706348	Cui and Zhao 2012
P. robiniophila	Cui 5644	HQ876609	JF706342	Zhao and Cui 2012
P. robiniophila	Cui 7144	HQ876608	JF706341	Zhao and Cui 2012
P. robiniophila	Cui 9174	HQ876610	JF706343	Zhao and Cui 2012
P. straminea	Cui 8718	HQ876600	JF706335	Cui and Zhao 2012
P. straminea	Cui 8858	HQ654104	JF706334	Cui and Zhao 2012
P. subacida	Dai 8224	HQ876605	JF713024	Zhao and Cui 2012
P. subacida	Cui 3643	FJ613655	AY336753	Zhao and Cui 2012
P. subacida	MUCL 31402	FJ411103	AY333796	Robledo et al. 2009
P. substraminea	Cui 10177	JQ001852[a]	JQ001844[a]	
P. substraminea	Cui 10191	JQ001853[a]	JQ001845[a]	

Table 1 (continued)

Species name	Sample no.	GenBank no.		References
		ITS	LSU	
P. tenuis	Wei 2783	JQ001858[a]	JQ001848[a]	
P. tenuis	Wei 2969	JQ001859[a]	JQ001849[a]	
P. tephropora	Cui 6331	HQ848473	HQ848484	Zhao and Cui 2012
P. tephropora	Cui 9029	HQ876601	JF706339	Zhao and Cui 2012
P. tibetica	Cui 9459	JF706327	JF706333	Cui and Zhao 2012
P. tibetica	Cui 9457	JF706326	JF706332	Cui and Zhao 2012
P. truncatospora	Cui 6987	JN048778	HQ654112	Cui et al. 2011
P. truncatospora	Dai 5125	HQ654098	HQ848481	Zhao and Cui 2012
P. vicina	MUCL 44779	FJ411095	FJ393862	Robledo et al. 2009
Pe. chaquenia	MUCL 47647	FJ411083	FJ393855	Robledo et al. 2009
Pe. chaquenia	MUCL 47648	FJ411084	FJ393856	Robledo et al. 2009
Pe. micropora	MUCL43581	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

[a] Sequences newly generated in this study

Hyphal structure Hyphal system trimitic; generative hyphae with clamp connections; skeletal and binding hyphae IKI–, CB+; tissues unchanged in KOH.

Subiculum Generative hyphae infrequent, hyaline, thin-walled, usually unbranched, 1.8–2.2 μm in diam; skeletal hyphae dominant, hyaline, thick-walled with a wide to narrow lumen, occasionally branched, interwoven, 2.7–3.2 μm in diam; binding hyphae hyaline, thick-walled, frequently branched, flexuous, interwoven, 0.9–1.9 μm in diam.

Tubes Generative hyphae infrequent, hyaline, thin-walled, unbranched, 1.5–2 μm in diam; skeletal hyphae dominant, hyaline, thick-walled with a wide lumen, frequently branched, interwoven, 2.1–2.7 μm; binding hyphae hyaline, thick-walled, frequently branched, interwoven, 1–1.5 μm in diam. Cystidia absent, fusoid cystidioles present, hyaline, thin-walled, 13.1–19.2×3.2–5 μm; basidia barrel-shaped to pear-shaped, with four sterigmata and a basal clamp connection, 11.5–17.2×8.7–10 μm; basidioles dominant, mostly pear-shaped, but slightly smaller than basidia.

Fig. 1 A basidiocarp of *Perenniporia aridula* (Dai 12396)

Spores Basidiospores ovoid to subglobose, truncate, hyaline, thick-walled, smooth, strongly dextrinoid, CB+, (6–)6–7(–7.1)×(5–)5.1–6(–6.1) μm, L=6.65 μm, W=5.61 μm, Q=1.17–1.20 (*n*=60/2).

Additional specimen examined (*paratype*) **China**. Yunnan Province, Yuanjiang County, on fallen bamboo, 9 June 2011 Dai 12398 (BJFC).

Remarks Perenniporia aridula is characterized by perennial, resupinate basidiocarps with cream to buff-yellow pore surface, a trimitic hyphal system with indextrinoid and inamyloid skeletal and binding hyphae, and its basidiospores are ovoid to subglobose, truncate, strongly dextrinoid and cyanophilous.

Perenniporia meridionalis Decock & Stalpers is similar to *P. aridula* in having perennial basidiocarps and basidiospore morphology (6–7.7×4.5–6.2 μm), but differs by having a dimitic hyphal system with dextrinoid skeletal hyphae, and presence of arboriform hyphae (Decock and Stalpers 2006).

Perenniporia rosmarini A. David & Malençon resembles *P. aridula* by having a trimitic hyphal system, and truncate and dextrinoid basidiospores (6.5–7.5×5.5–6.5 μm), but it differs in having tough to hard basidiocarps, white to isabelline pore surface and rarely branched skeletal hyphal (Ryvarden and Gilbertson 1994).

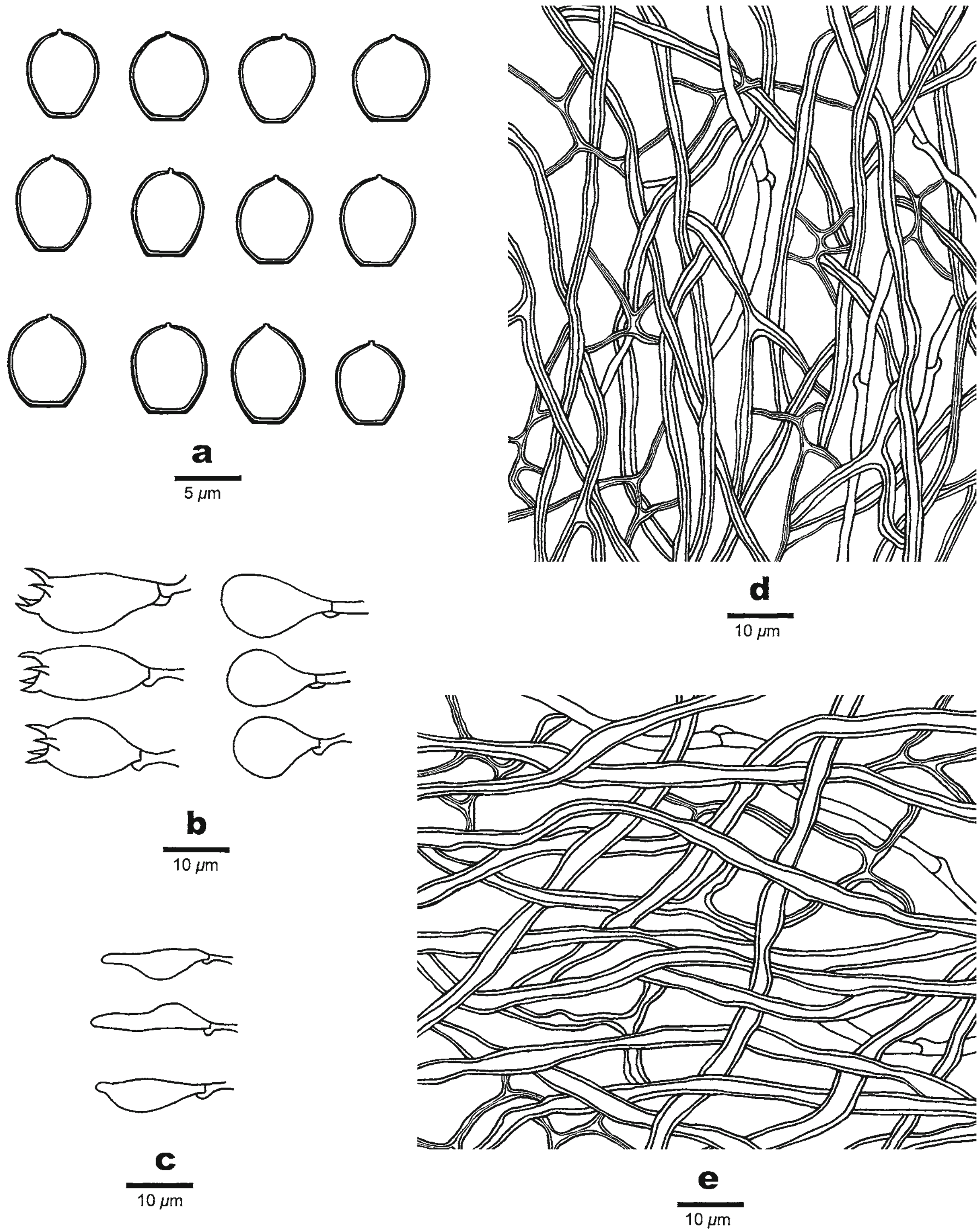

Fig. 2 Microscopic structures of *Perenniporia aridula* (from holotype). **a** Basidiospores; **b** Basidia and basidioles; **c** Cystidioles; **d** Hyphae from trama; **e** Hyphae from subiculum

Perenniporia tenuis (Schwein.) Ryvarden may be confused with *P. aridula* by sharing resupinate basidiocarps with cream to buff-yellow pore surface; however, *P. tenuis* is distinguished from *P. aridula* by larger pores (3–5 per mm), subparallel tramal hyphae, and ellipsoid and smaller basidiospores (5.5–6.5×4.5–5 μm, Dai et al. 2002).

Phylogenetically, *Perenniporia tephropora* (Mont.) Ryvarden was found to be close to *P. aridula* in the ITS + nLSU tree (Fig. 7); however, it has clay, grey to pale umber pore surface, and smaller basidiospores (4.2–5.2×3.2–4.2 μm), and its skeletal hyphae become black in KOH (Dai et al. 2002).

Perenniporia bannaensis B.K. Cui & C.L. Zhao, **sp. nov.** (Figs. 3 and 4)

MycoBank: MB 800240

Type **China**. Yunnan Province, Xi-Shuang-Banna, Mengla County, Wangtianshu Nature Reserve, on fallen angiosperm trunk, 2 November 2009 Cui 8560 (holotype in BJFC).

Etymology Bannaensis (Lat.): referring to the locality (Banna) of the type specimen.

Fruiting body Basidiocarps annual, resupinate, adnate, corky, without odor or taste when fresh, becoming hard corky upon drying, up to 10 cm long, 6.5 cm wide, 2 mm thick at centre. Pore surface cream to buff when fresh, becoming buff-yellow to pinkish buff upon drying; pores round to angular, 6–8 per mm; dissepiments thin, entire to distinctly lacerate. Sterile margin thin, cream-buff, up to 2 mm wide. Subiculum buff-yellow, thin, up to 0.3 mm thick. Tubes concolorous with pore surface, corky, up to 1.7 mm long.

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

Subiculum Generative hyphae infrequent, hyaline, thin-walled, usually unbranched, 2.5–3.9 μm in diam; skeletal hyphae dominant, hyaline, thick-walled with a wide lumen, unbranched, interwoven, 2–3.7 μm in diam.

Tubes Generative hyphae infrequent, hyaline, thin-walled, unbranched, 1.9–3.3 μm in diam; skeletal hyphae dominant, hyaline, thick-walled with a wide lumen, usually unbranched, interwoven, 2–3.4 μm. Cystidia absent, fusoid cystidioles present, hyaline, thin-walled, 15.5–21×5–6.5 μm; basidia barrel-shaped, with four sterigmata and a basal clamp connection, 11.5–15×5.9–8.2 μm; basidioles dominant, in shape similar to basidia, but slightly smaller.

Spores Basidiospores ellipsoid, hyaline, distinctly thick-walled, smooth, strongly dextrinoid, CB+, (5–)5.2–6(–6.4)×(3.9–)4–4.6(–4.8) μm, L=5.45 μm, W=4.22 μm, Q=1.27–1.32 (*n*=120/4).

Fig. 3 A basidiocarp of *Perenniporia bannaensis* (Cui 8560)

Additional specimens examined (*paratypes*) **China**. Yunnan Province, Xi-Shuang-Banna, Mengla County, Wangtianshu Nature Reserve, on fallen angiosperm trunk, 17 September 2007 Yuan 3665 & 3683 (IFP), 2 November 2009 Cui 8562 (BJFC).

Remarks Perenniporia bannaensis is characterized by annual and resupinate basidiocarps with buff-yellow to pinkish buff pore surface, a dimitic hyphal system with strongly dextrinoid and cyanophilous skeletal hyphae, and its basidiospores are ellipsoid, not truncate, distinctly thick-walled, strongly dextrinoid and cyanophilous, 5.2–6×4–4.5 μm.

Perenniporia chromatica (Berk. & Broome) Decock & Ryvarden and *P. bannaensis* share a dimitic hyphal system and dextrinoid basidiospores (5.2–6.7×4.1–5.9 μm), but the former differs in its larger pores (4–5 per mm) and having arboriform hyphae and truncate basidiospores (Decock and Ryvarden 1999).

Perenniporia ellipsospora Ryvarden & Gilb. may be confused with *P. bannaensis* in having annual basidiocarps, a dimitic hyphal system with unbranched skeletal hyphae, and non-truncate basidiospores, but it is distinguished from *P. bannaensis* in having a whitish to pale yellowish brown pore surface, larger pores (3–4 per mm) and smaller basidiospores (4–5.5×3–4 μm, Gilbertson and Ryvarden 1987).

Perenniporia subacida (Peck) Donk is similar to *P. bannaensis*, and both have non-truncate basidiospores and unbranched skeletal hyphae. However, *P. subacida* is distinguished from *P. bannaensis* by having distinctly perennial basidiocarps with ivory to yellowish pore surface, larger pores (5–6 per mm), and its basidiospores are slightly thick-walled and negative in Melzer's reagent (Núñez and Ryvarden 2001; Decock and Stalpers 2006).

Perenniporia subaurantiaca (Rodway & Cleland) P.K. Buchanan & Ryvarden is similar to *P. bannaensis* by a dimitic hyphal system, and non-truncate, strongly dextrinoid basidiospores; however, it differs by having a cream to greyish orange pore surface and larger basidiospores (7.2–9.5×4.2–5.5 μm; Decock et al. 2000).

Perenniporia bannaensis is closely related to *P. rhizomorpha* B.K. Cui et al. according to our rDNA phylogeny (Fig. 7), but the latter produces larger pores (4–6 per mm), cream to buff colored rhizomorphs and finely encrusted skeletal hyphae (Cui et al. 2007).

Perenniporia substraminea B.K. Cui & C.L. Zhao, **sp. nov.** (Figs. 5 and 6)

MycoBank: MB 800241

Type **China**. Zhejiang Province, Taishun County, Wuyanling Nature Reserve, on angiosperm stump, 22 August 2011 Cui 10177 (holotype in BJFC).

Etymology Substraminea (Lat.): referring to the species is slightly similar to *Perenniporia straminea*.

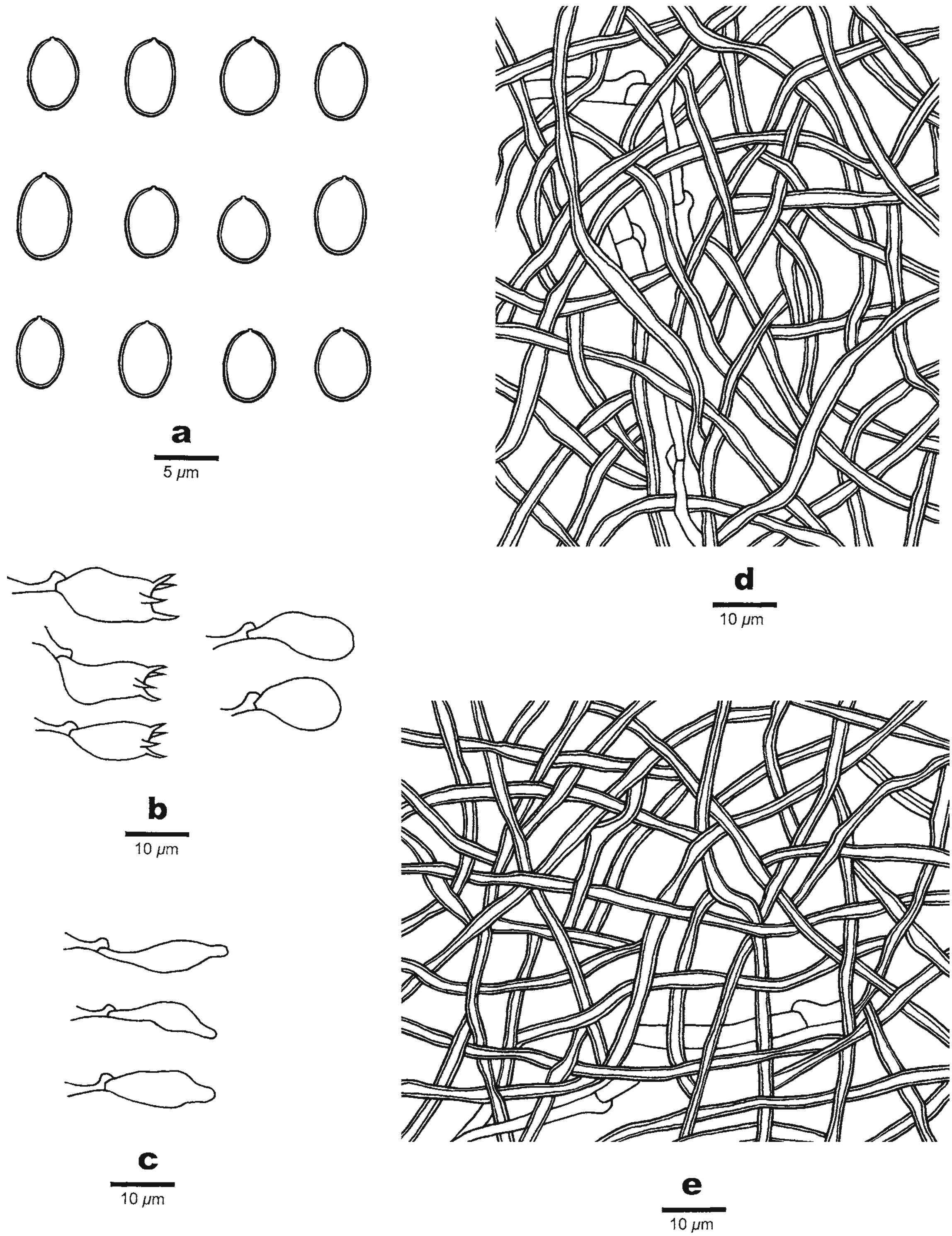

Fig. 4 Microscopic structures of *Perenniporia bannaensis* (from holotype). **a** Basidiospores; **b** Basidia and basidioles; **c** Cystidioles; **d** Hyphae from trama; **e** Hyphae from subiculum

Fruiting body Basidiocarps perennial, resupinate, adnate, corky, without odor or taste when fresh, becoming hard corky upon drying, up to 14.5 cm long, 9.5 cm wide, 5 mm thick at centre. Pore surface white to cream when fresh, becoming cream to pinkish buff upon drying; pores round, 9–12 per mm; dissepiments thin, entire. Sterile margin narrow, cream, up to 1 mm wide. Subiculum white to cream, thin, up to 0.2 mm thick. Tubes concolorous with pore surface, hard corky, up to 4.8 mm long.

Fig. 5 A basidiocarp of *Perenniporia substraminea* (Cui 10177)

Hyphal structure Hyphal system trimitic; generative hyphae with clamp connections; skeletal and binding hyphae IKI–, CB+; tissues unchanged in KOH.

Subiculum Generative hyphae infrequent, hyaline, thin-walled, usually unbranched, 1.5–2.6 μm in diam; skeletal hyphae dominant, hyaline, thick-walled with a wide lumen, occasionally branched, interwoven, 2–3.5 μm in diam; binding hyphae hyaline, thick-walled, frequently branched, flexuous, interwoven, 0.8–1.9 μm in diam.

Tubes Generative hyphae infrequent, hyaline, thin-walled, usually unbranched, 1.3–2 μm in diam; skeletal hyphae dominant, hyaline, thick-walled with a wide lumen, occasionally branched, interwoven, 1.8–2.2 μm; binding hyphae hyaline, thick-walled, frequently branched, interwoven, 0.8–1.5 μm in diam. Dendrohyphidia common at the dissepiments. Cystidia absent, fusoid cystidioles present, hyaline, thin-walled, 8–11.5×3–4.9 μm; basidia mostly pear-shaped, with four sterigmata and a basal clamp connection, 7.9–9.9×5.2–7 μm; basidioles dominant, in shape similar to basidia, but slightly smaller. Large rhomboid crystals abundant.

Spores Basidiospores ellipsoid, truncate, hyaline, thick-walled, smooth, strongly dextrinoid, CB+, (3–)3.1–3.8(–3.9)×(2.1–)2.4–3(–3.1) μm, L=3.43 μm, W=2.81 μm, Q=1.22–1.23 (*n*=60/2).

Additional specimen examined (*paratype*) China. Zhejiang Province, Taishun County, Wuyanling Nature Reserve, on fallen angiosperm trunk, 22 August 2011 Cui 10191 (BJFC).

Remarks Perenniporia substraminea is characterized by perennial and resupinate basidiocarps with white to cream pore surface, very small pores (9–12 per mm), a trimitic hyphal system with indextrinoid and inamyloid skeletal hyphae, small, ellipsoid and truncate basidiospores (3.1–3.8×2.4–3 μm), presence of both dendrohyphidia and large rhomboid crystals.

Morphologically, *Perenniporia substraminea* is similar to *P. straminea* (Bres.) Ryvarden in having small pores (8–9 per mm) and basidiospores (3.3–3.8×2.7–3.2 μm), but the latter has straw-colored, pale yellow to yellow pore surface, a dimitic hyphal system, and presence of arboriform skeleton-binding hyphae (Decock 2001a).

Perenniporia dendrohyphidia Ryvarden resembles *P. substraminea* by having whitish to cream-colored pore surface and dendrohyphidia, but differs in having larger pores (6–8 per mm), a dimitic hyphal system, and larger basidiospores (5.3–6.3×4.3–5.5 μm, Decock 2001b).

Perenniporia medulla-panis (Jacq.) Donk has whitish pore surface, and strongly dextrinoid basidiospores, it forms a sister group of *P. substraminea* in the phylogenetic study (Fig. 7), but it is different in larger pores (4–6 per mm) and larger basidiospores (4.5–5.5×3.5–4.5 μm, Decock and Stalpers 2006).

Perenniporia subdendrohyphidia Decock may be confused with *P. substraminea*, as they both produce dendrohyphidia and small basidiospores (4–4.8×2.8–3.3 μm); however, the former differs by its larger pores (5–7 per mm), and non-dextrinoid basidiospores (Decock 2001b).

Molecular phylogeny

The combined ITS + nLSU dataset included sequences from 62 fungal specimens representing 33 taxa. The dataset had an aligned length of 1709 characters in the dataset, of which, 1246 characters are constant, 100 are variable and parsimony-uninformative, and 353 are parsimony-informative. Maximum Parsimony analysis yielded 100 equally parsimonious trees (TL=1082, CI=0.416, RI=0.700, RC=0.291, HI=0.584), and a strict consensus tree of these trees is shown in Fig. 7. Bayesian analysis resulted in a same topology with an average standard deviation of split frequencies=0.007321.

Collections of the three new species all formed a well supported clade in the phylogenetic analysis as shown in the combined ITS + nLSU strict consensus tree (Fig. 7). *Perenniporia aridula* is placed in relation to *P. tephropora*; however, it represents a monophyletic entity with strong support (100 % BP, 1.00 BPP). *Perenniporia bannaensis* is phylogenetically closely related to, but distinct from *P. rhizomorpha* and *P. subacida* based on the ITS + nLSU data. Similarly, *P. substraminea* is phylogenetically closely related to *P. medulla-panis*.

Discussion

In the present study, analysis using the combined ITS and nLSU dataset produced a well-resolved phylogeny. 31 sampled species belonging to *Perenniporia* s.l. formed seven clades (Fig. 7), and most of these clades recovered by the

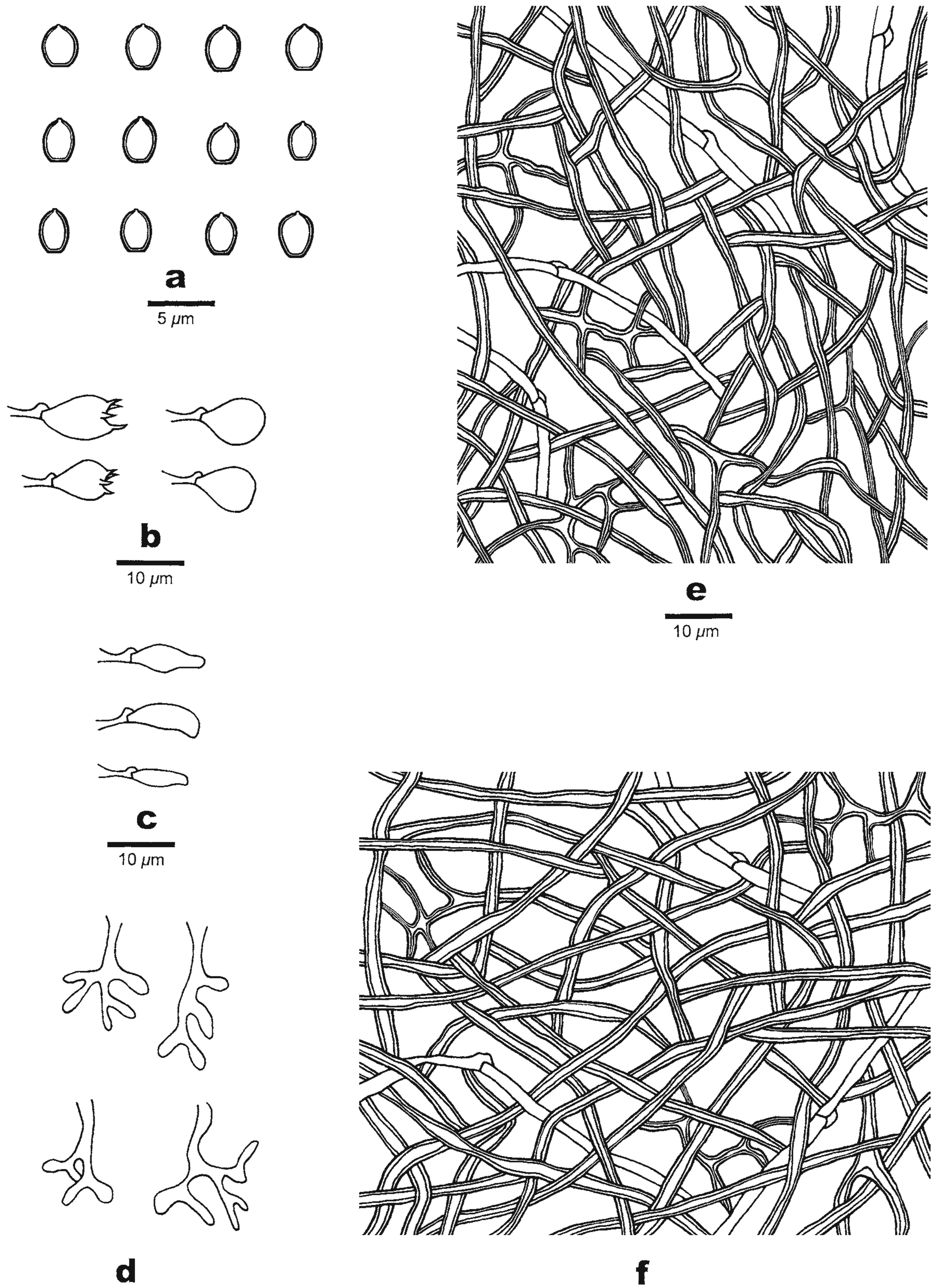

Fig. 6 Microscopic structures of *Perenniporia substraminea* (from holotype). **a** Basidiospores; **b** Basidia and basidioles; **c** Cystidioles; **d** Dendrohyphidia; **e** Hyphae from trama; **f** Hyphae from subiculum

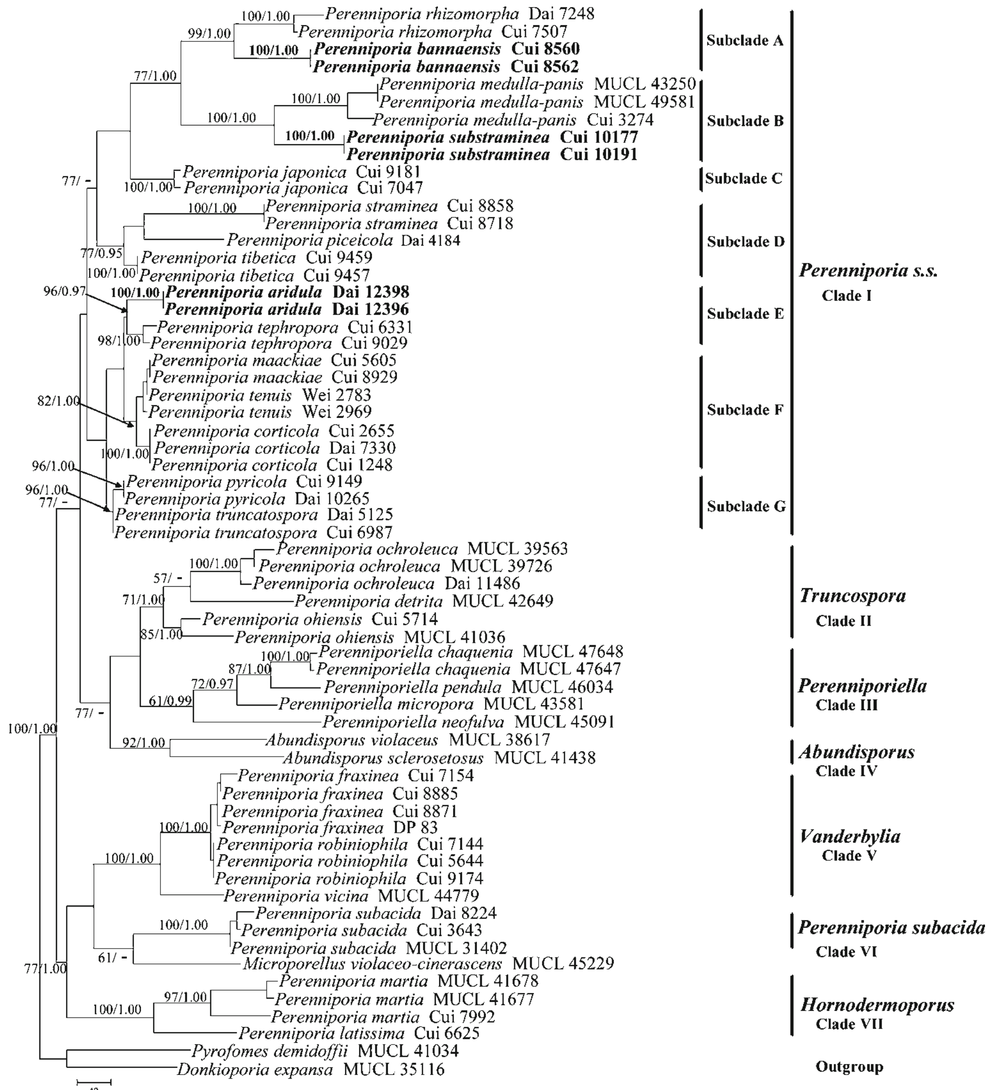

Fig. 7 Strict consensus tree illustrating the phylogeny of three new species and related species generated by Maximum Parsimony based on combined ITS + LSU sequences. Parsimony bootstrap proportions (before the/) higher than 50 % and Bayesian posterior probabilities (after the/) more than 0.95 were indicated along branches

combined ITS and nLSU dataset got strong bootstraps and Bayesian posterior probability supports.

Clade I is formed by species of *Perenniporia* s.s., and comprises seven subclades, subclade A includes *P. bannaensis* and *P. rhizomorpha*, and is characterized by species having resupinate basidiocarps, occasionally branched and strongly dextrinoid skeletal hyphae, and not truncate basidiospores. Subclade B includes *P. medulla-panis* and *P. substraminea*, and it is characterized by species having resupinate to effused-reflexed basidiocarps, frequently branched, indextrinoid skeletal hyphae, and truncate, strongly dextrinoid basidiospores. Subclade C is formed by *P. japonica* (Yasuda) T. Hatt. & Ryvarden, and it is characterized by species having resupinate basidiocarps with white to cream colored rhizomorphs, and a dimitic hyphal system with branched, dextrinoid skeletal hyphae, and truncate, dextrinoid basidiospores; *P. tibetica* B.K. Cui & C.L. Zhao and *P. rhizomorpha* also produce rhizomorphs, but they are not in the same clade (Fig. 7); our observation suggests that presence of rhizomorphs has evolved multiple times in the genus. Subclade D includes *P. straminea*, *P. piceicola* Y.C. Dai and *P. tibetica*, and is characterized by resupinate basidiocarps, branched, indextrinoid to slightly dextrinoid skeletal hyphae and truncate, dextrinoid basidiospores. Subclade E includes *P. aridula* and *P. tephropora*, and is characterized by resupinate basidiocarps, branched skeletal hyphae, and truncate, dextrinoid basidiospores. Subclade F includes *P. corticola* (Corner) Decock, *P. maackiae* (Bondartsev & Ljub.) Parmasto and *P. tenuis*, and it is characterized by resupinate basidiocarps with yellow pore surface and branched skeletal hyphae, and truncate, dextrinoid basidiospores; morphologically, a yellow pore surface is a key character to unify this group. Subclade G includes *P. pyricola* Y.C. Dai & B.K. Cui and *P. truncatospora* (Lloyd) Ryvarden, and is characterized by frequently branched, dextrinoid skeletal hyphae, and truncate, indextrinoid to dextrinoid basidiospores.

Clade II includes *Perenniporia detrita* (Berk.) Ryvarden, *P. ochroleuca* (Berk.) Ryvarden and *P. ohiensis* (Berk.)

Ryvarden, and it is characterized by smaller, pileate basidiocarps, indextrinoid to weakly dextrinoid skeletal hyphae, and larger, truncate, strongly dextrinoid basidiospores. Pilát (1953) established the genus *Truncospora* typified by *T. ochroleuca* (Berk.) Pilát to accommodate the species *P. ochroleuca*, but many mycologists considered *Truncospora* as a synonym of *Perenniporia* (Ryvarden 1972, 1991; Ryvarden and Johansen 1980; Gilbertson and Ryvarden 1987; Ryvarden and Gilbertson 1994; Dai et al. 2002). Decock and Ryvarden (1999) concluded that *P. detrita*, *P. ochroleuca* and *P. ohiensis* formed a morphologically homogeneous alliance, which could be recognized at the genus level, and the name *Truncospora* would be available. Phylogenetic analysis based on DNA sequences data by Robledo et al. (2009) showed that these three taxa formed a monophyletic clade distinct from *Perenniporia* s.s., and should be recognized at genus level (Decock 2011). In our study (Fig. 7), *Perenniporia ochroleuca* complex forms a monophyletic entity, and it was distinct from *Perenniporia* s.s., which may indicate that these three species could be recognized as a separate genus of *Truncospora* (MycoBank: MB 18685).

Clade III is formed by species in *Perenniporiella* Decock & Ryvarden. *Perenniporiella* was segregated from *Perenniporia* by Decock and Ryvarden (2003), characterized by pileate basidiocarps, a dimitic hyphal system, and non-truncate, weakly dextrinoid basidiospores. Preliminary phylogenetic relationship of *Perenniporiella* and *Perenniporia* was analyzed inferred from partial nuclear ribosomal LSU and ITS DNA sequences data (Robledo et al. 2009), which demonstrated that *Perenniporiella* formed a well supported monophyletic clade, and was distantly related to *Perenniporia* s.s. Our study (Fig. 7) confirmed that *Perenniporiella* is monophyletic, and it groups with *Perenniporia ochroleuca* complex by a weakly support (less than 50 % BP).

Clade IV is formed by species in *Abundisporus* Ryvarden, and this genus was established to include species with colored and non-dextrinoid basidiospores, and species in the genus were previously listed under *Loweporus* Wright or *Perenniporia* (Dai et al. 2002). Only two species of *Abundisporus* were included in our analysis (Fig. 7), and these two species formed a monophyletic lineage with strong support (92 % BP, 1.00 BPP). The *Abundisporus* clade (Clade IV) subsequently grouped with *Perenniporia ochroleuca* group (Clade II) and *Perenniporiella* clade (Clade III). This result is identified to the previous study by Robledo et al. (2009).

Clade V includes *Perenniporia fraxinea* (Bull.) Ryvarden, *P. robiniophila* (Murrill) Ryvarden and *P. vicina* (Lloyd) D.A. Reid, and species in this clade are characterized by pileate basidiocarps, strongly dextrinoid skeletal hyphae, and amygdaliform, non-truncate and strongly dextrinoid basidiospores. Reid (1973) established the genus *Vanderbylia* D.A. Reid to accommodate these species. But it was treated as a synonym of *Perenniporia* (Ryvarden 1991). Our analysis inferred from ITS combined LSU sequences data showed that *P. fraxinea*, *P. robiniophila* and *P. vicina* formed a well resolved monophyletic clade with strong support (100 % BP, 1.00 BPP), and it is distant from *Perenniporia* s.s., and could be recognized as a separate genus of *Vanderbylia* (MycoBank: MB 18722).

Clade VI includes *Perenniporia subacida*, this species was traditionally accepted in *Perenniporia*. Decock and Stalpers (2006) mentioned that it does not appear to belong to *Perenniporia*, and mainly by the unbranched skeletal hyphae, ellipsoid and non-truncate basidiospores. Its taxonomic position remains uncertain. Robledo et al. (2009) found that *P. subacida* is monophyletic and distinct from *Perenniporia* s.s. In our study, three sampled *P. subacida* specimens formed a well supported clade with a 100 % bootstrap value and 1.00 Bayesian posterior probability, and it weakly grouped with *Microporellus violaceo-cinerascens* (Petch) A. David & Rajchenb.

Clade VII includes *Perenniporia latissima* (Bres.) Ryvarden and *P. martia* (Berk.) Ryvarden, and it is characterized by large pileate basidiocarps, unbranched and strongly dextrinoid skeletal hyphae, oblong ellipsoid, truncate and strongly dextrinoid basidiospores, and presence of cystidia. Teixeira (1993) established *Hornodermoporus* Teixeira to accommodate *Perenniporia martia* complex. In our phylogenetic analysis, *P. martia* complex is resolved as a monophyletic lineage with a 100 % bootstrap value and 1.00 Bayesian post probability (Fig. 7), and it is distant from the *Perenniporia* s.s clade. This indicates that the *P. martia* complex could be recognized as *Hornodermoporus* (MycoBank: MB 27305) at the generic level.

Perenniporia s.l. in China was reviewed by Dai et al. (2002). Since then, several new species and new records in the genus were reported, and currently, 38 species have been recorded from the country (Cui et al. 2007; Xiong et al. 2008; Dai 2010a; Dai et al. 2011; Zhao and Cui 2012; Cui and Zhao 2012). As keys of *Perenniporia* species present in other areas of the world are available (Hattori and Lee 1999; Decock and Ryvarden 2000; Decock and Stalpers 2006; Choeyklin et al. 2009; Decock et al. 2011), we provide a key to the species of *Perenniporia* s.l. occurring in China.

Key to the species of *Perenniporia* s.l. (including *Hornodermoporus*, *Truncospora* and *Vanderbylia*) from China

1. Basidiocarps stipitate....................................*P. subadusta*
1. Basidiocarps sessile..2
2. Bsidipcarps resupinate...3
2. Bsidipcarps pileate...25
3. Basidiospores amyloid.....................................*P. hattorii*
3. Basidiospores inamyloid...4

4. Skeletal hyphae brownish to blackish in KOH................5
4. Skeletal hyphae hyaline in KOH.....................................6
5. Pores 4–6 per mm, basidiospores ellipsoid....*P. tephropora*
5. Pores 6–8 per mm, basidiospores amygdaliform.....*P. gomezii*
6. Basidiospores >8 μm in length.......................................7
6. Basidiospores <8 μm in length.....................................10
7. Pores <4 per mm...8
7. Pores >4 per mm...9
8. Cystidia present...*P. piceicola*
8. Cystidia absent..*P. isabelllina*
9. Pores 4–6 per mm; skeletal hyphae IKI– ......*P. phloiophila*
9. Pores 6–7 per mm; skeletal hyphae dextrinoid...*P. nanlingensis*
10. Basidiocarps with rhizomorphs...................................11
10. Basidiocarps without rhizomorphs..............................13
11. Basidiospores not truncate......................*P. rhizomorpha*
11. Basidiospores truncate...12
12. Pores 2–3 per mm...*P. tibetica*
12. Pores 6–7 per mm..*P. japonica*
13. Dendrohyphidia present at dissepimental edges..........14
13. Dendrohyphidia absent at dissepimental edges............15
14. Basidiospores >4 μm in length...........*P. dendrohyphidia*
14. Basidiospores <4 μm in length..............*P. substraminea*
15. Basidiospores not truncate..16
15. Basidiospores truncate...17
16. Basidiocarps perennial; basidiospores IKI– ....*P. subacida*
16. Basidiocarps annual; basidiospores strongly dextrinoid..*P. bannaensis*
17. Pore surface bright yellow-orange..............................18
17. Pore surface whitish to pale yellowish.........................21
18. On *Maackia,* basidiospores >5.5 μm in length....*P. maackiae*
18. On wood other than *Maackia*; basidiospores <5.5 μm in length..19
19. Pore surface violet to black in KOH ....*P. bambusicola*
19. Pore surface unchanged in KOH................................20
20. Basidiospores >3.3 μm in width..................*P. corticola*
20. Basidiospores <3.3 μm in width.................*P. straminea*
21. Basidiospores indextrinoid..............................*P. fergusii*
21. Basidiospores dextrinoid...22
22. Basidiocarps annual..*P. tenuis*
22. Basidiocarps perennial...23
23. Skeletal hyphae dextrinoid............................*P. pyricola*
23. Skeletal hyphae indextrinoid.......................................24
24. Pore surface whitish, pores 4–6 per mm...*P. medulla-panis*
24. Pore surface cream to buff-yellow, pores 6–7 per mm ....*P. aridula*
25. Basidiospores >9 μm in length....................................26
25. Basidiospores <9 μm in length...................................29
26. Basidiocarps annual, osseous....................*P. minutissima*
26. Basidiocarps perennial, not osseous............................27
27. Arboriform skeletal hyphae present at tubes.....*P. detrita*
27. Arboriform skeletal hyphae absent at tubes.................28
28. Pores 5–7 per mm, pileus light brown to blackish ....*T. ohiensis*
28. Pores 2–5 per mm, pileus cream to ochraceous ....*T. ochroleuca*
29. Basidiospores not truncate..30
29. Basidiospores truncate...33
30. Dichohyphidia present at dissepiments..........*P. delavayi*
30. Dichohyphidia absent at dissepiments.........................31
31. Basidiospores >8 μm in length.........................*V. vicina*
31. Basidiospores <8 μm in length...................................32
32. Basidiospores <5.3 μm in width, skeletal hyphae with large lumen in KOH....................................*V. fraxinea*
32. Basidiospores >5.3 μm in width, skeletal hyphae subsolid in KOH...*V. robiniophila*
33. Cystidia present...34
33. Cystidia absent..35
34. Basidiocarps annual, hyphal system dimitic.....*H. latissima*
34. Basidiocarps perennial, hyphal system trimitic....*H. martia*
35. Basidiospores dextrinoid...36
35. Basidiospores indextrinoid..37
36. Pores 7–8 per mm, skeletal hyphae strongly dextrinoid...*P. malvena*
36. Pores 4–6 per mm, skeletal hyphae weakly amyloid...*P. minor*
37. Basidiospores <5 μm in length.....................*P. contraria*
37. Basidiospores >5 μm in length............*P. truncatospora*

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