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Morphological and molecular identification of four new resupinate species of *Perenniporia* (Polyporales) from southern China

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Abstract: Four new resupinate species, *Perenniporia hainaniana*, *P. macropora*, *P. russeimarginata* and *P. subtrophopora*, are described as new from southern China on the basis of morphological and molecular examination. *Perenniporia hainaniana* is characterized by a perennial growth habit, cream to buff pore surface, a dimitic to trimitic hyphal system with amyloid skeletal hyphae and presence of dendrohyphidia. *Perenniporia macropora* is distinguished by an annual growth habit, large pores (2–3 per mm), a dimitic hyphal system with branched skeletal hyphae and presence of dendrohyphidia. *Perenniporia russeimarginata* differs from other species in the genus by a perennial growth habit, white to cream pore surface and reddish to reddish brown sterile margin. *Perenniporia subtrophopora* is characterized by a perennial growth habit, cream-buff to grayish buff pore surface, hymenophoral trama becoming black in KOH and a dimitic hyphal system with branched skeletal hyphae. Phylogenetic analysis inferred from the ITS and LSU-rDNA regions revealed eight clades for *Perenniporia* sensu lato with the four new species recognized in *Perenniporia* sensu stricto. The *Perenniporia ochroleuca* group, *P. vicina* group, *P. martia* group, *P. subacida*, *Microporellus*, *Perenniporiella* and *Abundisporus*, formed monophyletic entities respectively, and they are not related to *P. medulla-panis* (generic type), which belongs to *Perenniporia* sensu stricto. *Abundisporus*, *Microporellus* and *Perenniporiella* were widely applied as generic names. Other generic or clade names, *Hornodermoporus*, *Truncospora*, *Vanderbylia* and the *P. subacida* clade, have not been widely applied, but they are valid higher level taxa containing former species of *Perenniporia*. A key to genera and clades allied with *Perenniporia* sensu stricto and a key to species of *Perenniporia* are provided.

Key words: phylogeny, polypore, taxonomy, wood-inhabiting 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 and amyloid reactions. The genus has been considered a member of the Polyporaceae (Ryvarden 1991). The hyphal system of *Perenniporia* species is di- or trimitic with clamp connections on generative hyphae, while the vegetative hyphae are cyanophilous and variably dextrinoid or amyloid (Decock and Stalpers 2006). About 90 species have been accepted in the genus worldwide (Gilbertson and Ryvarden 1987; Ryvarden and Gilbertson 1994; Hattori and Lee 1999; Decock and Ryvarden 2000; Núñez and Ryvarden 2001; Dai et al. 2002, 2011; Cui et al. 2007; Xiong et al. 2008; Choeyklin et al. 2009; Dai 2010; Decock et al. 2011). Thirty-eight species have been recorded from China, including several species recently described based on morphological and molecular evidence (Dai et al. 2002, 2011; Cui et al. 2007; Xiong et al. 2008; Dai 2010, 2012; Cui and Zhao 2012; Zhao and Cui 2012; Zhao et al. 2013a).

Phylogenetic studies of *Perenniporia* inferred from nuclear ribosomal LSU and ITS DNA sequence data have demonstrated that several monophyletic entities are well supported and can be recognized as distinct genera (Robledo et al. 2009, Zhao et al. 2013a) within the polyporoid clade. Binder et al. (2005) divided the polyporoid clade into three main groups, the core polyporoid clade, the *Antrodia* clade and the phlebioid clade, together with some residual taxa not assigned to any group; however, no species of *Perenniporia* were included in that study. Miettinen and Rajchenberg (2012) found that *Perenniporia* clustered in the core polyporoid clade of the Polyporaceae. Zhao et al. (2013b) confirmed that *Perenniporia* was nested within the core polyporoid clade.

Four additional undescribed species corresponding to *Perenniporia* were found during investigations on the diversity of polypores in southern China. To confirm the affinity of the four new taxa of *Perenniporia*, phylogenetic analysis was carried out based on ITS and nLSU sequences.

MATERIALS AND METHODS

Morphological studies.—The studied specimens are deposited at the herbaria of the Institute of Microbiology, Beijing

Forestry University (BJFC), and the Institute of Applied Ecology, Chinese Academy of Sciences (IFP). Microscopic procedures follow Dai et al. (2010). Sections were studied at a magnification up to 1000× with a Nikon 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 are given in parentheses. In the text these abbreviations are 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. Color terms follow Petersen (1996).

DNA extraction and sequencing.—The fungal taxa used in this study are listed (TABLE I). A Phire Plant Direct PCR Kit (Finnzymes) procedure was used to extract total genomic DNA from fruit bodies and for polymerase chain reaction (PCR). DNA sequencing was performed at Beijing Genomics Institute. All newly generated sequences were submitted to GenBank and are listed (TABLE I). Sequence data of nuclear ribosomal RNA regions were used to determine the phylogenetic positions of the new species. The PCR products were sequenced by the primers ITS4 and ITS5 for ITS (White et al. 1990) and LR0R and LR7 for LSU (<http://www.biology.duke.edu/fungi/mycolab/primers.htm>).

Phylogenetic analysis.—Sequences generated for this study were aligned with additional sequences downloaded from GenBank (TABLE I) using BioEdit (Hall 1999) and Clustal X (Thompson et al. 1997). Before phylogenetic analysis, ambiguous sequences at the start and the end were deleted and gaps manually adjusted to optimize alignment. The sequence alignment was deposited at TreeBASE (<http://purl.org/phylo/treebase>; submission ID 13516). The best-fit model of nucleotide evolution was selected by hierarchical likelihood ratio tests (hLRT) in MrModeltest 2.3 (Posada and Crandall 1998, Nylander 2004). Maximum parsimony (MP) analysis and Bayesian inference was applied to the combined dataset of ITS and nLSU sequences, as in Zhao et al. (2013a). Sequences of *Donkioporia expansa* (Desm.) Kotl. & Pouzar and *Pyrofores demidoffii* (Lév.) Kotl. & Pouzar obtained from GenBank were used as outgroups to root trees following Zhao et al. (2013a).

Four Markov chains were run twice from random starting trees for 3 000 000 generations, sampling trees every 100 generations. The first 25% was discarded as burn-in. A majority rule consensus tree of all remaining trees was calculated. Maximum parsimony (MP) bootstrap proportions higher than 75% and Bayesian posterior probabilities (BPP) more than 0.95 were considered significant support.

RESULTS

Molecular phylogeny.—The combined ITS+nLSU dataset included sequences from 88 fungal specimens representing 47 taxa. The dataset had an aligned length of 2084 characters, of which 1378 are constant, 277 are variable and parsimony uninformative and 429 are parsimony informative. Maximum parsimony analysis yielded six equally parsimonious trees (TL = 1447, CI = 0.397, RI = 0.676, RC = 0.268, HI = 0.603). The best model for the combined ITS+nLSU partition was a GTR+I+G model. The Bayesian inference analysis resulted in a similar topology.

The phylogeny (FIG. 1) inferred from ITS+nLSU sequence data demonstrates eight major clades for 47 sampled species of *Perenniporia* sensu lato. Sampled specimens of four new species, *P. hainaniana* sp. nov., *P. macropora* sp. nov., *P. russeimarginata* sp. nov. and *P. subtephropora* sp. nov., form well supported lineages distinct from other species. All four are recovered in the *Perenniporia* sensu stricto clade. The clades of *Perenniporia ochroleuca* group, *P. vicina* group, *P. martia* group, *P. subacida* group, *Microsporellus* group, *Perenniporiella* group and *Abundisporus* group, formed monophyletic entities respectively, and they are not related to *P. medulla-panis* (Jacq.) Donk (type of *Perenniporia*), which is nested in the *Perenniporia* sensu stricto clade.

TAXONOMY

Perenniporia hainaniana B.K. Cui & C.L. Zhao, sp. nov. FIGS. 2, 3

MycoBank MB800565

Perenniporia hainaniana is characterized by perennial basidiocarps with a cream to buff pore surface, a dimitic to trimitic hyphal system with amyloid skeletal hyphae, broadly ellipsoid, truncate and dextrinoid basidiospores 4.0–4.5 × 3.0–4.0 μm and presence of dendrohyphidia.

Etymology: hainaniana (Lat.): referring to the locality (Hainan) of the type specimens.

Holotype: CHINA, HAINAN PROVINCE, Changjiang County, Bawangling Nature Reserve, on an angiosperm stump, 8 May 2009 *Cui 6364* (BJFC).

Basidiocarps perennial, resupinate, adnate, corky, without odor or flavor when fresh, becoming hard-corky upon drying, up to 15.5 cm long, 6 cm wide, 3 mm thick at center. Pore surface cream when fresh, becoming cream-buff upon drying; pores round, 5–6 per mm; dissepiments thin, entire. Sterile margin narrow, white to cream, up to 1 mm wide. Subiculum cream, thin, up to 0.2 mm thick. Tubes concolorous with pore surface, hard and corky, up to 3 mm long.

Hyphal system dimitic to trimitic; generative hyphae with clamp connections; skeletal hyphae

amyloid in Melzer's reagent, CB+; tissues unchanged in KOH. Generative hyphae in subiculum infrequent, difficult to find, hyaline, thin-walled, occasionally branched, 2.0–3.0 μm diam; skeletal hyphae in subiculum dominant, hyaline, thick-walled with a wide to narrow lumen, branched, interwoven, normally 3.0–4.0 μm diam; skeleto-binding hyphae present, hyaline, thick-walled, frequently branched, flexuous, interwoven, 1.0–1.5 μm diam. Generative hyphae in trama infrequent, difficult to find, hyaline, thin-walled, branched, 2.0–2.5 μm diam; skeletal hyphae in trama dominant, hyaline, thick-walled with a wide to narrow lumen, branched, interwoven, 2.5–3.5 μm wide; skeleto-binding hyphae present, hyaline, thick-walled, frequently branched, interwoven, 1.0–1.5 μm diam. Dendrohyphidia common at the dissepiments. Cystidia absent; fusoid cystidioles present, hyaline, thin-walled, 10–12 \times 3.7–4.8 μm ; basidia barrel- to pear-shaped, with four sterigmata and a basal clamp connection, 10.5–13.5 \times 5.0–8.0 μm ; basidioles in shape similar to basidia but slightly smaller. Basidiospores broadly ellipsoid, truncate, hyaline, thick-walled, smooth, dextrinoid, CB+, (3.5–) 4.0–4.5(–5) \times 3.0–4.0 μm , L = 4.3 μm , W = 3.6 μm , Q = 1.21–1.25 (n = 90/3).

Additional specimens examined: CHINA, HAINAN PROVINCE, Changjiang County, Bawangling Nature Reserve, on a fallen angiosperm trunk, 8 May 2009 Cui 6365 & 6366 (BJFC).

Comments: Morphologically *Perenniporia subdendrohyphidia* Decock is similar to *P. hainaniana* by having dendrohyphidia and similar basidiospores (4.0–4.8 \times 2.8–3.3 μm). However, this species produces a dimitic hyphal system with strongly dextrinoid skeletal hyphae and non-dextrinoid basidiospores (Decock 2001). *Perenniporia amylo-dextrinoidea* Gilb. & Ryvar-den may be confused with *P. hainaniana* morphologically in that they both produce amyloid skeletal hyphae and dextrinoid basidiospores; however *P. amylo-dextrinoidea* is an annual species with larger pores (3–5 per mm) and a dimitic hyphal system (Gilbertson and Ryvar-den 1987). *Perenniporia hattorii* Y.C. Dai & B.K. Cui is another species that has amyloid skeletal hyphae but differs from *P. hainaniana* by having amyloid and larger basidiospores (9.8–12.7 \times 5.8–7.2 μm) according to Dai et al. (2011).

Perenniporia macropora B.K. Cui & C.L. Zhao, sp. nov. FIGS. 2, 4
Mycobank MB800567

Perenniporia macropora is characterized by annual basidiocarps with cream to buff pore surface, large pores (2–3 per mm), a dimitic hyphal system with dextrinoid and branched skeletal hyphae, ellipsoid and truncate basidiospores (7.0–8.5 \times 5.5–6.5 μm) and presence of dendrohyphidia.

Etymology: *macropora* (Lat.): referring to the large pores.

Holotype: CHINA, GUANGXI AUTONOMOUS REGION, Ningming County, Nonggang Nature Reserve, on a fallen angiosperm branch, 8 Jul 2007 Zhou 407 (IFP).

Basidiocarps annual, resupinate, adnate, soft when fresh, becoming corky upon drying, up to 2.5 cm long, 1.5 cm wide, 1 mm thick at center. Pore surface cream when fresh, becoming cream-buff upon drying; pores angular, 2–3 per mm; dissepiments thin, entire. Sterile margin narrow, cream, up to 0.5 mm wide. Subiculum cream, thin, up to 0.2 mm thick. Tubes concolorous with pore surface, corky, up to 0.8 mm long.

Hyphal system dimitic; generative hyphae with clamp connections; skeletal hyphae dextrinoid, CB+; tissues unchanged in KOH. Generative hyphae in subiculum infrequent, difficult to find, hyaline, thin-walled, unbranched, 2.0–4.0 μm diam; skeletal hyphae in subiculum dominant, hyaline, thick-walled with a wide to narrow lumen, branched, interwoven, 2.5–3.5 μm diam. Generative hyphae in trama infrequent, difficult to find, hyaline, thin-walled, unbranched, 2.0–3.0 μm diam; skeletal hyphae in trama dominant, hyaline, thick-walled with a wide to narrow lumen, branched, interwoven, 2.0–3.0 μm wide. Dendrohyphidia present at the dissepiments. Cystidia absent; fusoid cystidioles present, hyaline, thin-walled, 16–17.5 \times 3.0–5.0 μm ; basidia barrel- to pear-shaped, with four sterigmata and a basal clamp connection, 15.5–21 \times 9.0–10.0 μm ; basidioles in shape similar to basidia but slightly smaller. Basidiospores ellipsoid to broadly ellipsoid, truncate, hyaline, thick-walled, smooth, dextrinoid, CB+, (6.5–) 7.0–8.5(–8.8) \times (5.0–) 5.5–6.5(–7) μm , L = 7.7 μm , W = 5.9 μm , Q = 1.24–1.37 (n = 90/3).

Additional specimens examined: CHINA, GUANGXI AUTONOMOUS REGION, Ningming County, Nonggang Nature Reserve, on fallen angiosperm branch, 7 Jul 2007 Zhou 280 & 297 (IFP).

Comments: *Perenniporia dendrohyphidia* Ryvar-den resembles *P. macropora* by having annual resupinate basidiocarps with a cream pore surface, dimitic hyphal system and presence of dendrohyphidia. However, *P. dendrohyphidia* differs in having smaller pores (6–8 per mm) and basidiospores (5.3–6.3 \times 4.3–5.5 μm , Decock 2001). *Perenniporia pyricola* Y.C. Dai & B.K. Cui may be confused with *P. macropora* in that they produce resupinate basidiocarps with cream-buff pore surface, a dimitic hyphal system with dextrinoid and branched skeletal hyphae and similar basidiospores (6.3–7.6 \times 4.8–6.5 μm); however, *P. pyricola* differs in its perennial basidiocarps and smaller pores (3–5 per mm, Dai 2010).

Perenniporia russeimarginata B.K. Cui & C.L. Zhao, sp. nov. FIGS. 2, 5
Mycobank MB800568

TABLE I. Species, specimens and GenBank accessions numbers of sequences in this study

Species	Sample no.	GenBank accession nos.	
		ITS	LSU
<i>Abundisporus sclerosetosus</i>	MUCL 41438	FJ411101 ^a	FJ393868 ^a
<i>A. violaceus</i>	MUCL 38617	FJ411100 ^a	FJ393867 ^a
<i>Donkioporia expansa</i>	MUCL 35116	FJ411104 ^a	FJ393872 ^a
<i>Microsporellus violaceo-cinereascens</i>	MUCL 45229	FJ411106 ^a	FJ393874 ^a
<i>Perenniporia aridula</i>	Dai 12398	JQ001855	JQ001847
<i>P. aridula</i>	Dai 12396	JQ001854	JQ001846
<i>P. bannaensis</i>	Cui 8560	JQ291727	JQ291729
<i>P. bannaensis</i>	Cui 8562	JQ291728	JQ291730
<i>P. contraria</i>	Knudsen 04-111	JQ861737	JQ861755
<i>P. corticola</i>	Cui 1248	HQ848472	HQ848482
<i>P. corticola</i>	Cui 2655	HQ654093	HQ848483
<i>P. corticola</i>	Dai 7330	HQ654094	HQ654108
<i>P. detrita</i>	MUCL 42649	FJ411099 ^a	FJ393866 ^a
<i>P. formosana</i>	Dai 5245	HQ876612	JX941590
<i>P. fergusii</i>	Gilbertson 16116	HQ876607	JF706337
<i>P. fraxinea</i>	DP 83	AM269789 ^a	AM269853 ^a
<i>P. fraxinea</i>	Cui 7154	HQ654095	HQ654110
<i>P. fraxinea</i>	Cui 8871	JF706329	JF706345
<i>P. fraxinea</i>	Cui 8885	HQ876611	JF706344
<i>P. hainaniana</i>	Cui 6364	JQ861743	JQ861759
<i>P. hainaniana</i>	Cui 6365	JQ861744	JQ861760
<i>P. hainaniana</i>	Cui 6366	JQ861745	JQ861761
<i>P. japonica</i>	Cui 7047	HQ654097	HQ654111
<i>P. japonica</i>	Cui 9181	JQ001856	JQ001841
<i>P. lacerata</i>	Cui 7220	JX141448	JX141458
<i>P. lacerata</i>	Dai 11268	JX141449	JX141459
<i>P. latissima</i>	Cui 6625	HQ876604	JF706340
<i>P. luteola</i>	H 1308a	JX141456	JX141466
<i>P. luteola</i>	H 1308b	JX141457	JX141467
<i>P. maackiae</i>	Cui 8929	HQ654102	JF706338
<i>P. maackiae</i>	Cui 5605	JN048760	JN048780
<i>P. macropora</i>	Zhou 407	JQ861746	JQ861762
<i>P. macropora</i>	Zhou 280	JQ861748	JQ861764
<i>P. macropora</i>	Zhou 297	JQ861747	JQ861763
<i>P. martia</i>	Cui 7992	HQ876603	HQ654114
<i>P. martia</i>	MUCL 41677	FJ411092 ^a	FJ393859 ^a
<i>P. martia</i>	MUCL 41678	FJ411093 ^a	FJ393860 ^a
<i>P. medulla-panis</i>	MUCL 49581	FJ411088 ^a	FJ393876 ^a
<i>P. medulla-panis</i>	MUCL 43250	FJ411087 ^a	FJ393875 ^a
<i>P. medulla-panis</i>	Cui 3274	JN112792	JN112793
<i>P. minor</i>	Cui 5782	HQ883475	HQ654115
<i>P. minor</i>	Cui 5738	HQ848475	HQ848485
<i>P. minutissima</i>	Cui 6053	JX978408	JX978409
<i>P. nanlingensis</i>	Cui 7620	HQ848477	HQ848486
<i>P. nanlingensis</i>	Cui 7589	HQ848478	HQ848487
<i>P. ochroleuca</i>	Dai 11486	HQ654105	JF706349
<i>P. ochroleuca</i>	MUCL 39563	FJ411097 ^a	FJ393864 ^a
<i>P. ochroleuca</i>	MUCL 39726	FJ411098 ^a	FJ393865 ^a
<i>P. ohiensis</i>	MUCL 41036	FJ411096 ^a	FJ393863 ^a
<i>P. ohiensis</i>	Cui 5714	HQ654103	HQ654116
<i>P. piceicola</i>	Cui 10460	JQ861742	JQ861758
<i>P. pyricola</i>	Cui 9149	JN048762	JN048782
<i>P. pyricola</i>	Dai 10265	JN048761	JN048781
<i>P. rhizomorpha</i>	Cui 7507	HQ654107	HQ654117

TABLE I. Continued

Species	Sample no.	GenBank accession nos.	
		ITS	LSU
<i>P. rhizomorpha</i>	Dai 7248	JF706330	JF706348
<i>P. robiniohila</i>	Cui 5644	HQ876609	JF706342
<i>P. robiniohila</i>	Cui 7144	HQ876608	JF706341
<i>P. robiniohila</i>	Cui 9174	HQ876610	JF706343
<i>P. russeimarginata</i>	Yuan 1225	JQ861749	JQ861765
<i>P. russeimarginata</i>	Yuan 1244	JQ861750	JQ861766
<i>P. russeimarginata</i>	Yuan 1262	JQ861751	JQ861767
<i>P. straminea</i>	Cui 8718	HQ876600	JF706335
<i>P. straminea</i>	Cui 8858	HQ654104	JF706334
<i>P. subacida</i>	Dai 8224	HQ876605	JF713024
<i>P. subacida</i>	Cui 3643	FJ613655	AY336753
<i>P. subacida</i>	MUCL 31402	FJ411103 ^a	AY333796 ^a
<i>P. subadusta</i>	Cui 8459	HQ876606	HQ654113
<i>P. substraminea</i>	Cui 10177	JQ001852	JQ001844
<i>P. substraminea</i>	Cui 10191	JQ001853	JQ001845
<i>P. subtephropora</i>	Dai 10962	JQ861752	JQ861768
<i>P. subtephropora</i>	Dai 10964	JQ861753	JQ861769
<i>P. tenuis</i>	Wei 2783	JQ001858	JQ001848
<i>P. tenuis</i>	Wei 2969	JQ001859	JQ001849
<i>P. tephropora</i>	Cui 6331	HQ848473	HQ848484
<i>P. tephropora</i>	Cui 9029	HQ876601	JF706339
<i>P. tianmuensis</i>	Cui 2648	JX141453	JX141463
<i>P. tianmuensis</i>	Cui 2759	JX141455	JX141465
<i>P. tibetica</i>	Cui 9459	JF706327	JF706333
<i>P. tibetica</i>	Cui 9457	JF706326	JF706332
<i>P. truncatospora</i>	Cui 6987	JN048778	HQ654112
<i>P. truncatospora</i>	Dai 5125	HQ654098	HQ848481
<i>P. vicina</i>	MUCL 44779	FJ411095 ^a	FJ393862 ^a
<i>Perenniporiella chaquenia</i>	MUCL 47647	FJ411083 ^a	FJ393855 ^a
<i>P. chaquenia</i>	MUCL 47648	FJ411084 ^a	FJ393856 ^a
<i>P. microspora</i>	MUCL43581	FJ411086 ^a	FJ393858 ^a
<i>P. neofulva</i>	MUCL 45091	FJ411080 ^a	FJ393852 ^a
<i>P. pendula</i>	MUCL 46034	FJ411082 ^a	FJ393853 ^a
<i>Pyrofomes demidoffii</i>	MUCL 41034	FJ411105 ^a	FJ393873 ^a

^aSequences downloaded from GenBank.

Perenniporia russeimarginata is characterized by perennial basidiocarps with a white to cream pore surface, distinct reddish brown sterile margin and a dimittic hyphal system with dextrinoid skeletal hyphae.

Etymology: *russeimarginata* (Lat.): referring to the reddish brown margin of basidiocarps.

Holotype: CHINA, YUNNAN PROVINCE, Chuxiong, Zixishan Nature Reserve, on fallen angiosperm trunk, 1 Aug 2005 Yuan 1225 (IFP).

Basidiocarps perennial, resupinate, adnate, soft when fresh, becoming corky upon drying, up to 8 cm long, 5 cm wide, 7 mm thick at center. Pore surface white to cream when fresh, becoming cream upon drying; pores round, 6–8 per mm; dissepiments thick, entire. Sterile margin distinct, reddish brown, up to 6 mm wide. Subiculum pinkish buff, thin, up to

0.5 mm thick. Tubes cinnamon-buff, slightly darker than pore surface, corky, up to 6.5 mm long.

Hyphal system dimittic; generative hyphae with clamp connections; skeletal hyphae dextrinoid, CB+; tissues unchanged in KOH. Generative hyphae in subiculum infrequent, difficult to find, hyaline, thin-walled, unbranched, 1.5–2.0 µm diam; skeletal hyphae in subiculum dominant, hyaline, thick-walled, branched, interwoven, 1.5–2.0 µm diam. Generative hyphae in trama infrequent, difficult to find, hyaline, thin-walled, unbranched, 1.0–1.5 µm diam; skeletal hyphae in trama dominant, hyaline, thick-walled, branched, interwoven, 1.0–2.0 µm. Cystidia absent; fusoid cystidioles present, hyaline, thin-walled, 11.0–12.5 × 2.5–3.0 µm; basidia pear-shaped, with four sterigmata and a basal clamp connection, 9.0 × 6.0–7.0 µm;

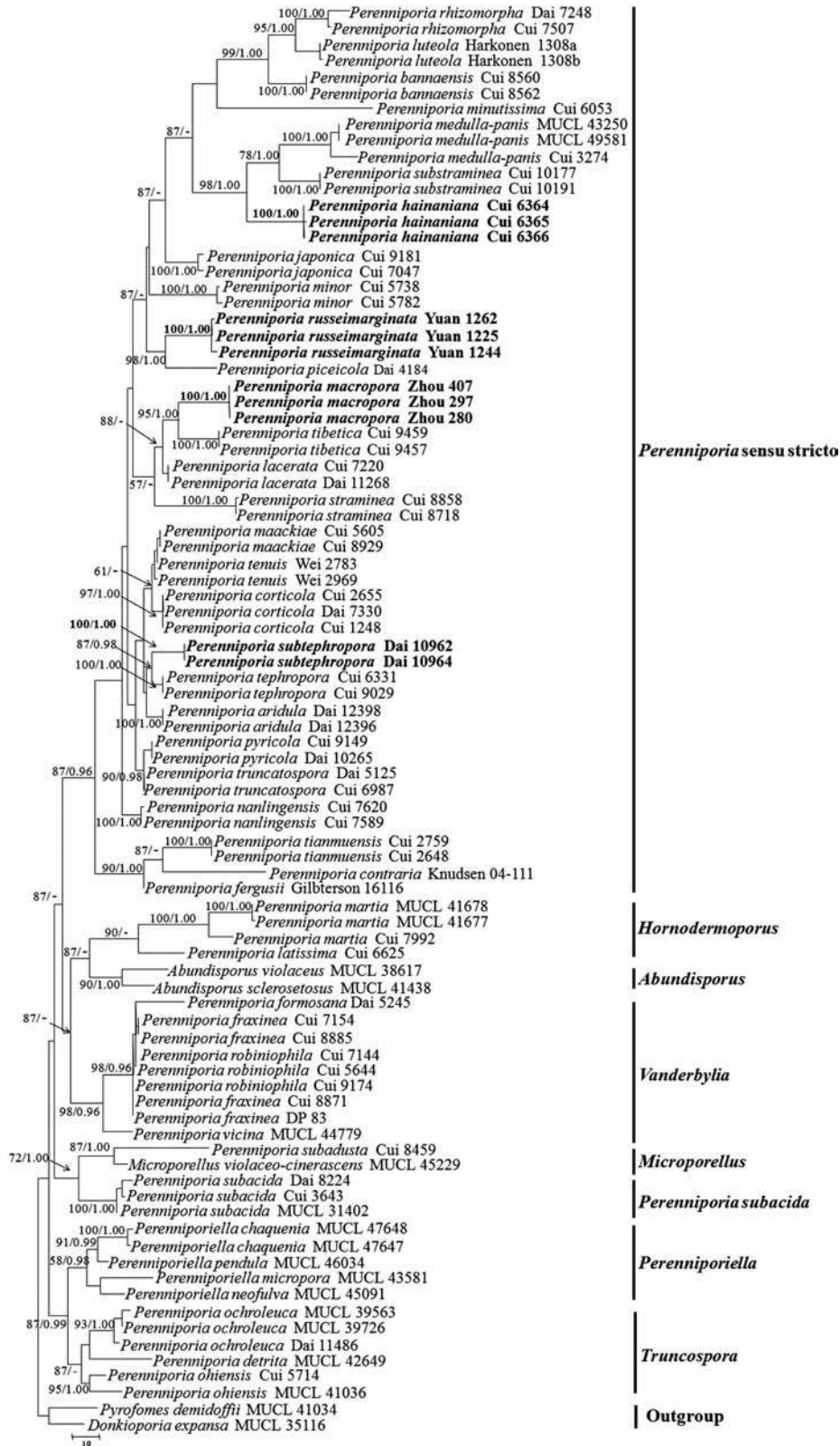


FIG. 1. One of the most parsimonious trees illustrating the phylogeny of four new *Perenniporia* species and related species based on ITS+nLSU sequences. Parsimony bootstrap proportions (before slash markers) higher than 50% and Bayesian posterior probabilities (after slash markers) more than 0.95 are indicated along branches.

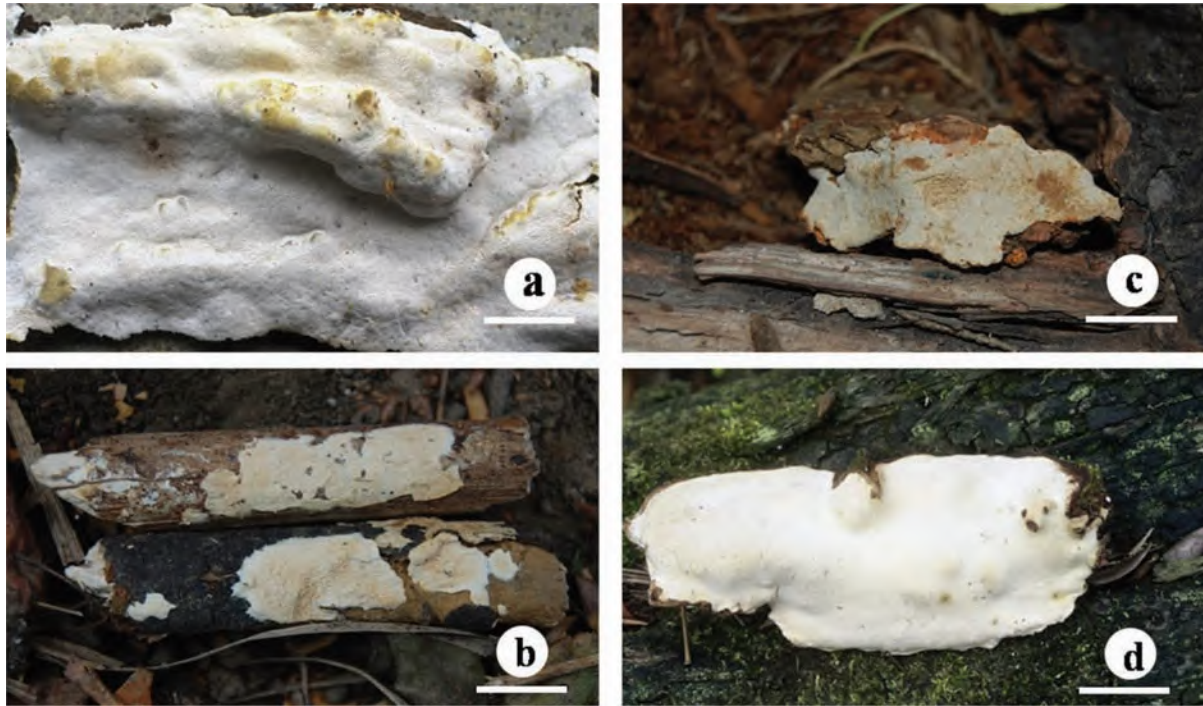


FIG. 2. Basidiocarps of the four new *Perenniporia* species. a. *P. hainaniana*. b. *P. macropora*. c. *P. russeimarginata*. d. *P. subtephropora*. Bars: a = 2 cm; b, c = 1 cm; d = 2 cm.

basidioles in shape similar to basidia but slightly smaller. Basidiospores ellipsoid, truncate, hyaline, thick-walled, smooth, dextrinoid, CB+, (3.5–)4.0–5.0 × (2.5–)3.0–4.0 μm, L = 4.4 μm, W = 3.3 μm, Q = 1.31–1.36 (n = 90/3).

Additional specimens examined: CHINA, YUNNAN PROVINCE, Chuxiong, Zixishan Nature Reserve, on fallen angiosperm trunk, 1 Aug 2005 Yuan 1244 & 1262 (IFP).

Comments: *Perenniporia alboferruginea* Decock was described recently from Cameroon, and it is similar to *P. russeimarginata* with its ferruginous red upper margin of basidiocarps and a dimitic hyphal system. This species differs from *P. russeimarginata* in having annual basidiocarps, larger pores (5–6 per mm) and indextrinoid basidiospores (4.5–5.8 × 3.0–4.0 μm, Decock et al. 2011). *Perenniporia medulla-panis* is similar to *P. russeimarginata* in that both produce resupinate basidiocarps with a white to cream pore surface when fresh, a dimitic hyphal system and truncate basidiospores; however, *P. medulla-panis* differs by its larger pores (4–6 per mm), nondextrinoid but variable amyloid skeletal hyphae, and larger basidiospores (4.5–5.5 × 3.5–4.5 μm, Decock and Stalpers 2006).

Perenniporia subtephropora B.K. Cui & C.L. Zhao,
sp. nov. FIGS. 2, 6
Mycobank MB 800569

Perenniporia subtephropora is characterized by perennial, resupinate basidiocarps with cream-buff to grayish buff pore surface, tubes becoming black in

KOH, a dimitic hyphal system with branched skeletal hyphae, and ellipsoid, truncate, hyaline to pale yellowish basidiospores.

Etymology: *subtephropora* (Lat.): referring to this species' similarity to *Perenniporia tephropora*.

Holotype: CHINA, GUANGDONG PROVINCE, Lianzhou County, Nanling Nature Reserve, on fallen angiosperm trunk, 16 May 2009 Dai 10962 (BJFC).

Basidiocarps perennial, resupinate, adnate, corky, without odor or flavor when fresh, becoming hard-corky upon drying, up to 12 cm long, 6.2 cm wide, 5.5 mm thick at center. Pore surface cream when fresh, becoming cream-buff to grayish buff upon drying; pores round, 6–8 per mm; dissepiments thin, entire. Sterile margin grayish brown, up to 1 mm wide. Subiculum clay-buff, thin, up to 1 mm thick. Tubes darker than pore surface, clay-buff, corky, up to 4.5 mm long, becoming black in KOH.

Hyphal system dimitic; generative hyphae with clamp connections; skeletal hyphae dextrinoid, CB+; tissues pale olivaceous to brown in KOH. Generative hyphae in subiculum infrequent, difficult to find, hyaline, thin-walled, occasionally branched, 3.0–4.0 μm diam; skeletal hyphae in subiculum dominant, hyaline to pale yellowish, thick-walled with a wide lumen, branched, interwoven, 2.5–4.0 μm diam. Generative hyphae in trama infrequent, difficult to find, hyaline, thin-walled, occasionally branched, 3.0–4.0 μm diam; skeletal hyphae in trama dominant, hyaline to pale yellowish, thick-walled with a wide to narrow lumen,

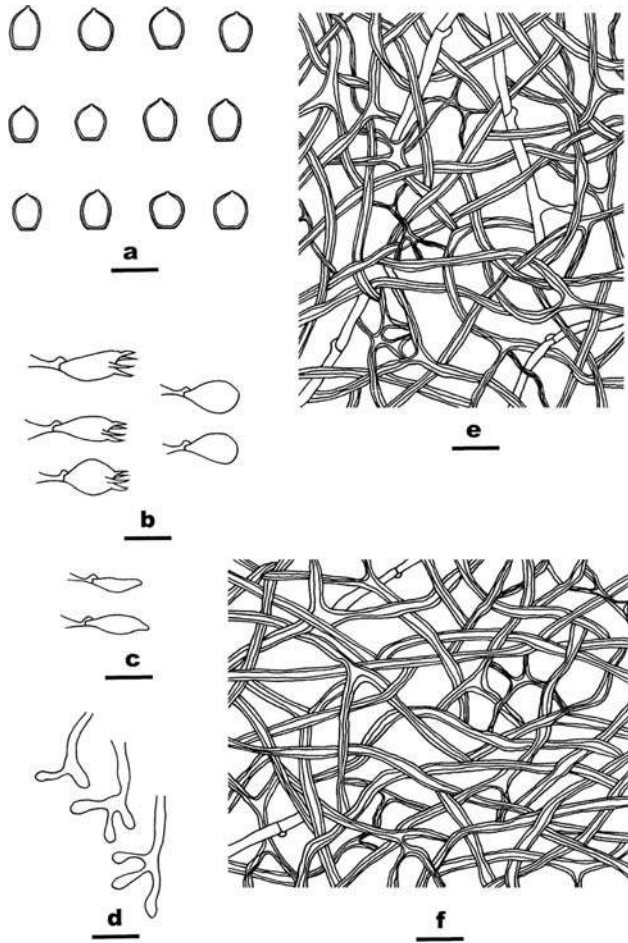


FIG. 3. Microscopic structures of *Perenniporia hainaniana* (drawn from the holotype). a. Basidiospores. b. Basidia and basidioles. c. Cystidioles. d. Dendrohyphidia. e. Hyphae from trama. f. Hyphae from subiculum. Bars: a = 5 μ m, b–f = 10 μ m.

branched, interwoven, 2.5–4.0 μ m. Cystidia absent; fusoid cystidioles present, hyaline, thin-walled, 13–22 \times 3.5–5.0 μ m; basidia clavate to pear-shaped, with four sterigmata and a basal clamp connection, 13.0–14.0 \times 7–7.5 μ m; basidioles in shape similar to basidia but slightly smaller. Large rhomboid crystals abundant. Basidiospores ellipsoid to broadly ellipsoid, truncate, hyaline to pale yellowish, thick-walled, smooth, dextrinoid, CB+, 4.0–5.0 \times (3.0–)3.5–4.5 μ m, L = 4.6 μ m, W = 3.8 μ m, Q = 1.17–1.26 (n = 60/2).

Additional specimen examined: CHINA, GUANGDONG PROVINCE, Lianzhou County, Nanling Nature Reserve, on angiosperm stump, 16 May 2009 *Dai 10964* (BJFC).

Comments: Morphologically *Perenniporia inflexibilis* (Berk.) Ryvarden is similar to *P. subtephropora* by producing smaller pores (6–8 per mm), a dimittic hyphal system with branched skeletal hyphae and truncate, hyaline to pale yellowish basidiospores. *Perenniporia inflexibilis* differs by having pileate

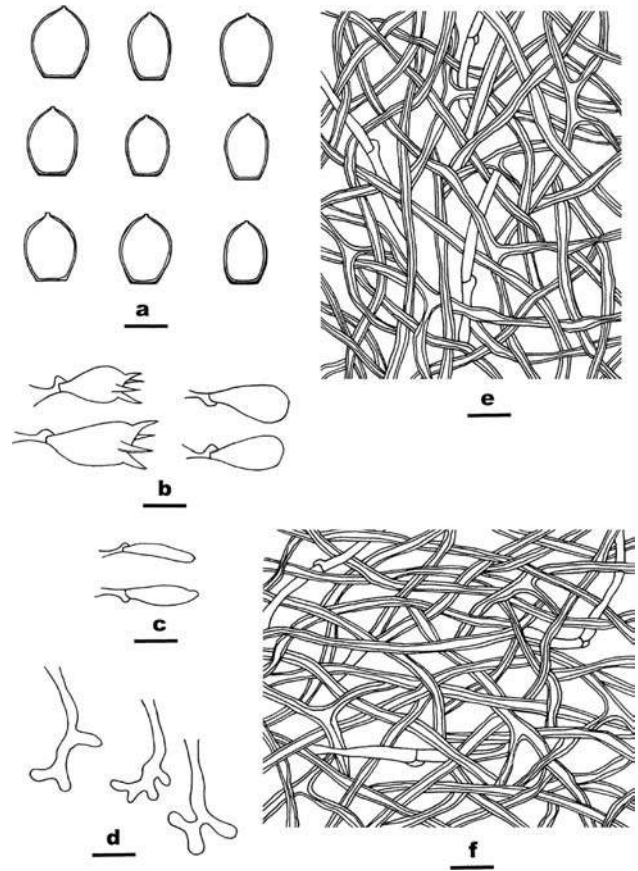


FIG. 4. Microscopic structures of *Perenniporia macropora* (drawn from the holotype). a. Basidiospores. b. Basidia and basidioles. c. Cystidioles. d. Dendrohyphidia. e. Hyphae from trama. f. Hyphae from subiculum. Bars: a = 5 μ m, b–f = 10 μ m.

basidiocarps and a gray to pale brown pore surface (Decock et al. 2002). *Perenniporia centrali-africana* Decock & Mossebo resembles *P. subtephropora* by having similar small pores (7–8 per mm) and basidiospores (4.8–6.0 \times 3.8–5.3 μ m). This species differs, however, by the pileate basidiocarps and a trimitic hyphal system (Decock and Mossebo 2001).

KEY TO GENERA AND CLADES ALLIED TO
PERENNIPORIA SENSU STRICTO

1. Context brown to fuscous, skeletal hyphae brown to black in KOH *Abundisporus*
1. Context cream to ochraceous, skeletal hyphae hyaline to ochraceous in KOH 2
2. Cystidia present 3
2. Cystidia absent 4
3. Pileus with a black crust, basidiospores truncate....
. *Hornodermoporus*
3. Pileus without a black crust, basidiospores not truncate *Microporellus*
4. Skeletal hyphae unbranched 5

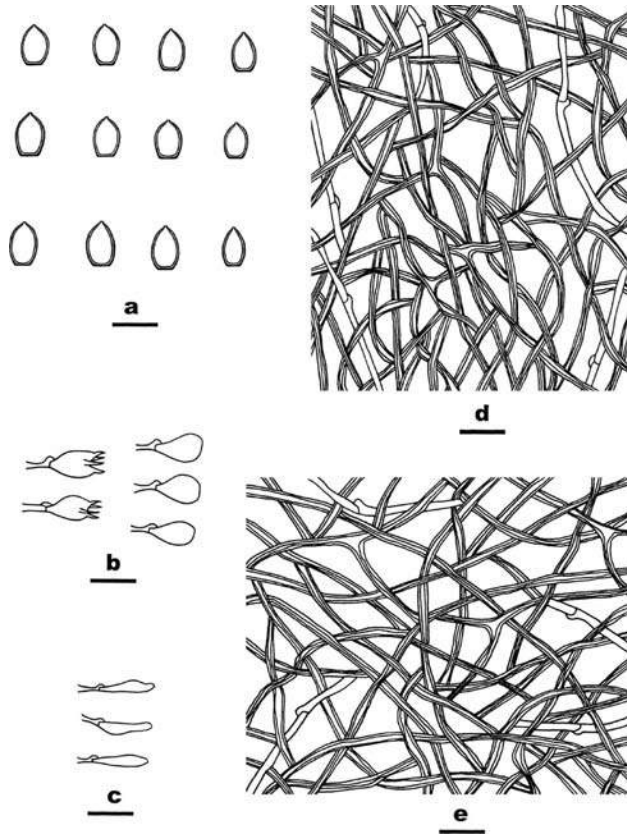


FIG. 5. Microscopic structures of *Perenniporia russeimarginata* (drawn from the holotype). a. Basidiospores. b. Basidia and basidioles. c. Cystidioles. d. Hyphae from trama. e. Hyphae from subiculum. Bars: a = 5 μ m, b–e = 10 μ m.

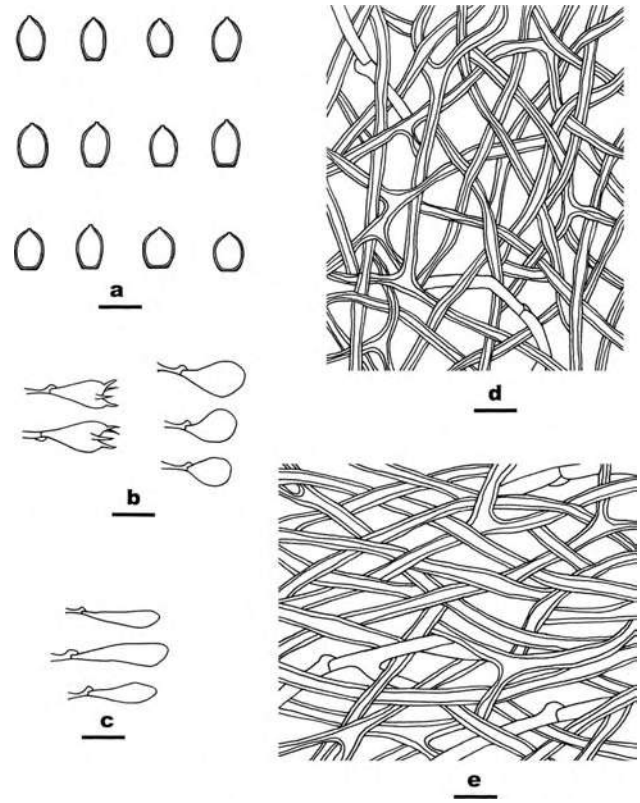


FIG. 6. Microscopic structures of *Perenniporia subtrophopora* (drawn from the holotype). a. Basidiospores. b. Basidia and basidioles. c. Cystidioles. d. Hyphae from trama. e. Hyphae from subiculum. Bars: a = 5 μ m, b–e = 10 μ m.

- 4. Skeletal hyphae branched 6
- 5. Basidiocarps pileate, basidiospores > 10 μ m long *Truncospora*
- 5. Basidiocarps resupinate, basidiospores < 10 μ m long *Perenniporia subacida*
- 6. Skeletal hyphae strongly dextrinoid, basidiospores amygdaliform *Vanderbylia*
- 6. Skeletal hyphae dextrinoid or not, basidiospores not amygdaliform 7
- 7. Basidiospores globose to subglobose, not truncate *Perenniporiella*
- 7. Basidiospores broadly ellipsoid to ellipsoid, truncate or not *Perenniporia sensu stricto*

KEY TO SPECIES OF *PERENNIPORIA* SENSU STRICTO INDICATED IN THE TREE

- 1. Basidiocarps resupinate 2
- 1. Basidiocarps pileate 23
- 2. Basidiospores truncate 3
- 2. Basidiospores not truncate 20
- 3. Dendrohyphidia present at dissepimental edges 4
- 3. Dendrohyphidia absent at dissepimental edges 6
- 4. Skeletal hyphae inamyloid *P. macropora* sp. nov.
- 4. Skeletal hyphae amyloid 5

- 5. Basidiospores > 4 μ m long *P. hainaniana* sp. nov.
- 5. Basidiospores < 4 μ m long *P. substraminea*
- 6. Skeletal hyphae brownish in KOH 7
- 6. Skeletal hyphae hyaline in KOH 8
- 7. Skeletal hyphae unbranched *P. tephropora*
- 7. Skeletal hyphae branched *P. subtrophopora* sp. nov.
- 8. Basidiospores > 8 μ m long 9
- 8. Basidiospores < 8 μ m long 10
- 9. Pores < 4 per mm *P. piceicola*
- 9. Pores > 4 per mm *P. nanlingensis*
- 10. Basidiocarps with rhizomorphs 11
- 10. Basidiocarps without rhizomorphs 12
- 11. Pores 2–3 per mm *P. tibetica*
- 11. Pores 6–7 per mm *P. japonica*
- 12. Pore surface bright yellow-orange 13
- 12. Pore surface whitish to pale yellowish 15
- 13. On *Maackia*; basidiospores > 5.5 μ m long *P. maackiae*
- 13. On wood other than *Maackia*; basidiospores < 5.5 μ m long 14
- 14. Basidiospores > 3.3 μ m wide *P. corticola*
- 14. Basidiospores < 3.3 μ m wide *P. straminea*
- 15. Sterile margin distinct reddish brown *P. russeimarginata* sp. nov.
- 15. Sterile margin whitish to cream-buff 16
- 16. Basidiocarps annual 17

16. Basidiocarps perennial 18
 17. Pores lacerate *P. lacerata*
 17. Pores entire *P. tenuis*
 18. Skeletal hyphae dextrinoid *P. pyricola*
 18. Skeletal hyphae indextrinoid 19
 19. Pore surface whitish, pores 4–6 per mm
 *P. medulla-panis*
 19. Pore surface cream to buff-yellow, pores
 6–7 per mm *P. aridula*
 20. Basidiocarps with rhizomorphs ... *P. rhizomorpha*
 20. Basidiocarps without rhizomorphs 21
 21. Pores > 6 per mm *P. bannaensis*
 21. Pores < 6 per mm 22
 22. Basidiospores > 6 µm long *P. luteola*
 22. Basidiospores < 6 µm long *P. fergusii*
 23. Basidiocarps osseous *P. minutissima*
 23. Basidiocarps corky, not osseous 24
 24. Basidiospores truncate 25
 24. Basidiospores not truncate 26
 25. Basidiospores indextrinoid, skeletal hyphae
 dextrinoid *P. truncatospora*
 25. Basidiospores dextrinoid, skeletal hyphae weakly
 amyloid *P. minor*
 26. Basidiocarps annual, basidiospores dextrinoid...
 *P. tianmuensis*
 26. Basidiocarps perennial, basidiospores indextrinoid
 *P. contraria*

DISCUSSION

Polypores are an 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; Wang et al. 2012). Most of these fungi also can decompose cellulose, hemicellulose and lignin in the plant cell walls and therefore play a key role in nutrient recycling in most forest ecosystems (Dai 2012). China has a large land area, including boreal, temperate, subtropical and tropical vegetation, and the diversity of polypores is rich (Dai 2012). Most parts of southern China have subtropical to tropical vegetation, but some temperate vegetation occurs in high mountains. The diversity of trees in southern China is high, and the climate is suitable for the growth of polypores. Polypore diversity in southern China has been extensively studied in the past 10 y, and many new species have been described (Dai et al. 2003, 2004, 2010, 2011; Cui and Dai 2006, 2008, 2011; Cui et al. 2009, 2011a, b, c; Du and Cui 2009; Dai 2010; Li and Cui 2010), including eight new species of *Perenniporia* (Dai et al. 2002, 2011; Cui et al. 2007; Cui and Zhao 2012; Zhao and Cui 2012; Zhao et al. 2013a). *Perenniporia* has high diversity in southern China, and four additional new species of *Perenniporia* are described from southern China in the present study.

The four new *Perenniporia* species, *P. hainaniana*, *P. macropora*, *P. russeimarginata* and *P. subtrophopora*, are described as new based on morphological differences and molecular phylogenetic analyses. Phylogenetically *P. hainaniana* clusters with *P. medulla-panis* (generic type) and *P. substraminea* B.K. Cui & C.L. Zhao. But morphologically *P. medulla-panis* produces a whitish pore surface, indextrinoid skeletal hyphae but amyloid in the lumen or close to the inner side of the wall and relatively larger basidiospores (4.5–5.5 × 3.5–4.5 µm); moreover *P. medulla-panis* lacks dendrohyphidia (Decock and Stalpers 2006). *Perenniporia substraminea* differs in smaller pores (9–12 per mm), indextrinoid and inamyloid skeletal hyphae, and smaller basidiospores (3.0–4.0 × 2.5–3.0 µm, Zhao et al. 2012a).

Perenniporia macropora is sister to *P. tibetica* B.K. Cui & C.L. Zhao with strong support (FIG. 1). Both species share similar pore size (2–3 per mm) and basidiospore size (6.7–8.7 × 5.3–6.8 µm), but the former differs in producing white to cream rhizomorphs (Cui and Zhao 2012); in addition, *P. tibetica* occurs at high elevations on the Tibetan Plateau, while *P. macropora* is found only in subtropical to tropical forest in southern China.

Perenniporia russeimarginata is closely related to *P. piceicola* Y.C. Dai based on the rDNA phylogeny (FIG. 1), and these two species group together. *P. piceicola* is distinguished morphologically by its larger pores (2–3 per mm) and basidiospores (11.0–14.0 × 5.4–7.5 µm, Dai et al. 2002); moreover, it has distinctly thick-walled and pyriform cystidia, and occurs on spruce (*Picea*) (Dai et al. 2002).

Perenniporia subtrophopora clusters with the *P. tephropora* (Mont.) Ryvarden, not unexpectedly, as well as with *P. aridula* B.K. Cui & C.L. Zhao. Morphologically *P. tephropora* differs in its gray to pale brown pore surface, larger pores (4–6 per mm) and unbranched skeletal hyphae (Gilbertson and Ryvarden 1987, Núñez and Ryvarden 2001). *Perenniporia aridula* differs from *P. subtrophopora* by having indextrinoid skeletal hyphae and bigger basidiospores (6.0–7.0 × 5.1–6.0 µm, Zhao et al. 2013a).

In the present study phylogenetic analysis inferred from the ITS and LSU-rDNA regions revealed eight clades (FIG. 1) within *Perenniporia* sensu lato with the four new species recognized in *Perenniporia* sensu stricto. The *P. ochroleuca* group, *P. vicina* group, *P. martia* group, *P. subacida* group, *Microporellus* group, *Perenniporiella* group and *Abundisporus* group form well supported monophyletic entities. These groups can be recognized as distinct genera in that they are distantly related to *P. medulla-panis*, which belongs to the *Perenniporia* sensu stricto clade and represents the type of *Perenniporia*. This result is similar to

Robledo et al. (2009) and Zhao et al. (2013a). *Abundisporus*, *Microporellus*, *Perenniporiella* have been widely applied as generic names; the other generic or clade names, including *Hornodermoporus*, *Truncospora*, *Vanderbylia* and the *P. subacida* clade, are not widely applied, but these are robust and solid higher level taxa containing former species of *Perenniporia*.

Perenniporia sensu stricto clade is formed by 55 fungal specimens representing 27 taxa (87% BP, 0.96 BPP; FIG. 1), and species in this clade usually have resupinate basidiocarps or occasionally pileate basidiocarps, dimitic hyphal system, branched and cyanophilous skeletal hyphae, which are indextrinoid to dextrinoid, and ellipsoid basidiospores, which are indextrinoid to dextrinoid. *P. medulla-panis* (type of *Perenniporia*) is recognized in this clade, and it has resupinate basidiocarps, dimitic hyphal system, frequently branched and indextrinoid skeletal hyphae, and truncate, strongly dextrinoid basidiospores. Decock et al. (2001) concluded that *P. contraria* (Berk. & M.A. Curtis) Ryvar den did not appear to belong to the core clade of *Perenniporia* and can be recognized separately. The phylogeny of *Perenniporia* sensu stricto was analyzed by Zhao et al. (2013a), and seven subclades of *Perenniporia* sensu stricto were recognized, but *P. contraria* group was not included in that phylogenetic analysis. Our present study shows that *P. contraria* clustered with *P. tianmuensis* B.K. Cui & C.L. Zhao and *P. fergusii* Gilb. & Ryvar den with strong support (90% BP, 1.00 BPP), and the *P. contraria* group belongs to the *Perenniporia* sensu stricto clade (FIG. 1). Morphologically the three species in *P. contraria* group have resupinate to pileate basidiocarps, dimitic hyphal system, strongly dextrinoid and cyanophilous skeletal hyphae, ellipsoid and non-truncate basidiospores; these characters could not separate them from other species of *Perenniporia* sensu stricto, so we treated *P. contraria* group belonging to *Perenniporia* sensu stricto for the time being.

Abundisporus Ryvar den was established to include species with brown to fuscous context, skeletal hyphae that are brown to black in KOH, pigmented and non-dextrinoid basidiospores. Species in the genus were classified under *Lowe porus* Wright or *Perenniporia* (Dai et al. 2002). In our phylogenetic analysis (FIG. 1), *Abundisporus* forms a monophyletic lineage and may be recognized as a distinct genus.

Perenniporiella Decock & Ryvar den was segregated from *Perenniporia* by Decock and Ryvar den (2003) based on its pileate basidiocarps, a dimitic hyphal system and non-truncate, weakly dextrinoid basidiospores. Preliminary phylogenetic relationship of *Perenniporiella* and *Perenniporia* inferred from partial nuclear ribosomal LSU and ITS DNA sequences data

was analyzed (Robledo et al. 2009, Zhao et al. 2013a), which demonstrated that *Perenniporiella* formed a well supported monophyletic clade and was distantly related to *Perenniporia* sensu stricto. The present study (FIG. 1) confirms that *Perenniporiella* is monophyletic.

Microporellus Murrill (1905) originally was described with *M. dealbatus* (Berk. & Curtis) Murrill as the type. *Microporellus* is characterized by pileate basidiocarps usually with a stipe, white to pale cream context, dimitic hyphal system with unbranched skeletal hyphae, presence of cystidia, subglobose basidiospores that are hyaline or faintly yellowish, slightly thick-walled, cyanophilous and occasionally slightly dextrinoid (Decock 2007). Robledo et al. (2009) and Zhao et al. (2013a) revealed that *Microporellus* was distinct from *Perenniporia* sensu stricto. *Perenniporia subadusta* (Z.S. Bi & G.Y. Zheng) Y.C. Dai was treated as a synonym of *M. violaceo-cinerascens* (Petch) A. David & Rajchenb. based on its morphological examination (Decock 2007). Our phylogenetic analysis shows that *Perenniporia subadusta* is clustered with *M. violaceo-cinerascens* and *Microporellus* group forms a monophyletic entity and could be recognized as a separate genus.

The *Perenniporia martia* group includes *P. latissima* (Bres.) Ryvar den and *P. martia* (Berk.) Ryvar den. Teixeira (1993) established *Hornodermoporus* Teixeira to accommodate *P. martia* (the type) and allies. *Hornodermoporus* is characterized by its large pileate basidiocarps, unbranched and strongly dextrinoid skeletal hyphae, oblong ellipsoid, truncate and strongly dextrinoid basidiospores and presence of cystidia. In our phylogenetic analysis, multiple samples of *P. martia* are resolved as a monophyletic lineage (FIG. 1) with *P. latissima* and are distant from *Perenniporia* sensu stricto. This indicates that the *P. martia* group could be recognized as *Hornodermoporus* at the generic level, a result also affirmed by Zhao et al. (2013a).

Pilát (1953) established the genus *Truncospora* Pilát typified by *T. ochroleuca* (Berk.) Pilát to accommodate the species *P. ochroleuca*, *P. ohiensis* (Berk.) Pilát, and *P. truncatospora* (Lloyd) S. Ito. *Truncospora* is characterized by its smaller, pileate basidiocarps, indextrinoid to weakly dextrinoid skeletal hyphae, and larger, truncate, strongly dextrinoid basidiospores. Many systematists have considered *Truncospora* a synonym of *Perenniporia* (Ryvar den 1972, 1991; Gilbertson and Ryvar den 1987; Ryvar den and Gilbertson 1994; Dai et al. 2002). Decock and Ryvar den (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 form a monophyletic group distinct from *Perenniporia* sensu stricto and should be recognized at genus level (Decock 2011). In our study (FIG. 1) the *P. ochroleuca* group forms a monophyletic entity and it is distinct from *Perenniporia* sensu stricto. Thus, *Truncospora* could be recognized as a good genus.

The *Perenniporia vicina* group includes *P. fraxinea* (Bull.) Ryvar den, *P. robinio phila* (Murrill) Ryvar den and *P. vicina* (Lloyd) D.A. Reid. These species 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 them, typified by *P. vicina*. However, Ryvar den (1991) treated *Vanderbylia* as a synonym of *Perenniporia*. Our phylogenetic analysis shows that the *P. vicina* group forms a well supported monophyletic group distinct from *Perenniporia* sensu stricto and could be recognized as a separate genus.

Perenniporia subacida (Peck) Donk traditionally was accepted in *Perenniporia*, however Decock and Stalpers (2006) concluded that this species did not appear to belong to *Perenniporia* based on the unbranched skeletal hyphae and ellipsoid and non-truncate basidiospores. Robledo et al. (2009) and Zhao et al. (2013a) found that *P. subacida* is monophyletic and distinct from *Perenniporia* sensu stricto. In the present study three sampled *P. subacida* specimens form a well supported clade with a 100% bootstrap value and 1.00 Bayesian posterior probability and it could be recognized as a distinct genus.

A few discrepancies between this and prior studies do exist. A molecular study of *Perenniporia* sensu lato based on sequence data from the ribosomal ITS and LSU regions carried out by Zhao et al. (2013a) uncovered seven clades for 31 species of *Perenniporia* sensu lato. In Zhao et al. (2013a) *Perenniporiella* clusters with the *P. ochroleuca* group, which is then sister to *Abundisporus*; in addition, the *P. subacida* group clusters with the *P. vicina* group. In the present work phylogenetic analysis uncovers eight clades for 47 species of *Perenniporia* sensu lato, *Abundisporus* clusters with the *P. martia* group, while the *P. subacida* group forms a separate lineage. To fully resolve the phylogeny for *Perenniporia* sensu lato, evolutionary information from more conserved gene markers likely will be required.

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