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Phylogeny and diversity of the morphologically similar polypore genera *Rigidoporus, Physisporinus, Oxyporus*, and *Leucophellinus*

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ABSTRACT

Rigidoporus and its morphologically similar genera *Physisporinus, Oxyporus*, and *Leucophellinus*, which include some forest pathogens and medicinal species, are very important groups of wood-decaying fungi. Species of these genera have not only ecological functions, but also economic importance. Phylogenetic and taxonomic studies on taxa in these genera were carried out. Inferred from phylogenies based on DNA sequences of the nuc rDNA ITS1-5.8S-ITS2 (internal transcribed spacer [ITS]) and D1–D2 domains of nuc 28S rDNA, 36 species sampled that traditionally belong to *Physisporinus, Rigidoporus, Leucophellinus*, and *Oxyporus* are nested mostly in eight lineages. Of these lineages, five (including four genera of *Physisporinus, Emmia, Flaviporus*, and *Flavodon* and one taxon "*R. hypobrunneus*") belong to Polyporales and three (including the genera *Rigidoporus, Bridgeoporus*, and *Leucophellinus*) belong to Hymenochaetales. *Rigidoporus* and *Oxyporus* are merged because the type species of both genera are nested in a single lineage within Hymenochaetales. Some taxon previously placed in *Ceriporia* and *Oxyporus* are transferred to *Emmia* and *Flavodon*, respectively, on the basis of current phylogeny. Utilizing a combination of the morphological and phylogenetic evidence, 16 new combinations in *Bridgeoporus, Emmia, Flaviporus, Flavodon, Rigidoporus*, and *Physisporinus* are proposed. Five new species, *Physisporinus crataegi, P. lavendulus, P. subcrocatus, P. tibeticus*, and *Rigidoporus submicroporus*, are recognized from China. Illustrated descriptions of these novel species are provided. Three taxa are treated at the generic level of *Physisporinus* because of limited samples.

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Hymenochaetales; phylogenetic analysis; Polyporales

INTRODUCTION

Polypores in the genera *Rigidoporus* Murrill, *Physisporinus* P. Karst., *Oxyporus* (Bourdot & Galzin) Donk, and *Leucophellinus* Bondartsev & Singer are one of the most important groups of wood-decaying fungi, growing on substrates from living trees to rotten wood and playing a critical role in the forest ecosystem (Gilbertson and Ryvarden 1987; Dai 2012; Ryvarden and Melo 2014). In addition, some species in these genera have economic importance, as some species, e.g., *Rigidoporus populinus* (Schumach.) Pouzar, *Oxyporus sinensis* X.L. Zeng, and *R. microporus* (Sw.) Overeem, are forest pathogens on angiosperm trees (Sinclair et al. 1987; Dai et al. 2007; Rajchenberg and Robledo 2013). Other species, e.g., *O. corticola* (Fr.) Ryvarden and *R. ulmarius* (Sow.) Imazeki, have medicinal properties (Boulet 2003; Dai et al. 2009). Moreover, *R. ulmarius*, which produces basidiocarps up to 1.5 m in diam, and *Bridgeoporus nobilissimus* (W.B. Cooke) Volk et al. (= *O. nobilissimus* W.B. Cooke), which has a basidiocarp up to 136 kg, are the largest basidiomycetes in Europe and North America, respectively (Gilbertson and Ryvarden 1987; Ryvarden and Melo 2014).

Rigidoporus, Physisporinus, Oxyporus, and *Leucophellinus* share similar morphological characters, including a monomitic hyphal structure, cyanophilous generative hyphae with simple septa, mostly broadly ellipsoid to globose basidiospores, and causing a white rot. These characters have resulted in a complex of species in which generic limits are difficult to define. Traditionally, *Oxyporus* is characterized by white to cream-colored and consistently corky basidiocarps, and usually the presence of hymenial cystidia. *Rigidoporus* has ochraceous to brownish and hard corky basidiocarps, and the presence of hyphoid cystidia. *Physisporinus* comprises seasonal and thin basidiocarps, which are soft or juicy when fresh but change to red or finally even to black and fragile when dry, and a lack cystidia (Gilbertson and Ryvarden 1987; Dai 1998; Niemelä 2005;

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Ryvarden and Melo 2014). *Leucophellinus* has thick-walled basidiospores, but otherwise the same hyphal structure as *Oxyporus* (Parmasto 1983; Dai 1998; Núñez and Ryvarden 2001).

Recently, phylogenetic analyses showed that some species of *Oxyporus* and *Rigidoporus* were nested in Hymenochaetales, but *Physisporinus* and several species of *Rigidoporus* were in Polyporales (Wagner and Fischer 2002; Larsson et al. 2006; Miettinen et al. 2012). However, all of these studies were based on limited species and sampling. As a result, there is almost no comprehensive analysis of the phylogeny of *Rigidoporus, Physisporinus, Leucophellinus*, and *Oxyporus*.

Based on broad sampling mostly from the Northern Hemisphere, phylogenetic analysis on species of *Rigidoporus, Physisporinus, Leucophellinus*, and *Oxyporus* and related genera were carried out. With the aid of morphological studies and phylogenetic analysis of the nuc rDNA ITS1-5.8S-ITS2 (internal transcribed spacer [ITS]) and D1–D2 domains of nuc 28S rDNA sequences, five new species are described and 16 new combinations are proposed. In addition, three samples of *Physisporinus* are treated as *Physisporinus* sp. 1, *Physisporinus* sp. 2, and *Physisporinus* sp. 3 because of there being a single specimen for each of these taxa.

MATERIALS AND METHODS

Specimens examined were deposited in the herbaria of the Institute of Microbiology, Beijing Forestry University (BJFC), National Museum Prague of Czech Republic (PRM), and the Institute of Applied Ecology, Chinese Academy of Sciences (IFP), as well as the private herbarium of J. Vlasák (JV). Macromorphological descriptions were based on field notes and herbarium specimens. Color terms followed Petersen (1996). Micromorphological data were obtained from dried specimens as observed under a light microscope following the methods of Dai (2010). Sections were studied at a magnification of up to ×1000 using a Nikon E 80i microscope with phase-contrast illumination (Tokyo, Japan). Drawings were made with the aid of a drawing tube. Microscopic characters, measurements, and drawings were made from slide preparations stained with Cotton Blue (CB) or Melzer's reagent (IKI). Basidiospores were measured from sections cut from the tubes. To represent variation in the size of spores, 5% of measurements were excluded from each end of the range and are given in parentheses. The following abbreviations are used: KOH = 5% potassium hydroxide; IKI– = both nonamyloid and nondextrinoid; CB– = acyanophilous; 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; and n (a/b) = number of spores (a) measured from given number (b) of specimens.

A cetyltrimethylammonium bromide (CTAB) rapid plant genome extraction kit (Aidlab Biotechnologies Co., Ltd., Beijing, China) was used to extract total genomic DNA from dried specimens following the manufacturer's instructions with some modifications (Chen et al. 2015, 2016). For polymerase chain reactions (PCRs), the DNA was amplified with the primers ITS4 and ITS5 for nuc rDNA ITS1-5.8S-ITS2 (ITS) (White et al. 1990), and LR0R and LR7 for D1–D2 domains of nuc 28S rDNA (28S) (Vilgalys and Hester 1990). The PCR profile for ITS was initial denaturation at 95 C for 3 min, followed by 35 cycles at 94 C for 40 s, 54 C for 45 s, and 72 C for 1 min, and a final extension at 72 C for 10 min. The PCR profile for 28S was initial denaturation at 94 C for 1 min, followed by 35 cycles at 94 C for 30 s, 50 C for 1 min, and 72 C for 1.5 min, and a final extension at 72 C for 10 min. PCR products were purified and sequenced in Beijing Genomics Institute, China, with the same primers.

Phylogenetic analysis was done as in Chen et al. (2016). Sequences were aligned with additional sequences downloaded from GenBank (SUPPLEMENTARY TABLE 1) using BioEdit (Hall 1999) and Clustal X (Thompson 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 20276).

Maximum parsimony analysis was applied to the combined data set of ITS and 28S sequences with PAUP* 4.0b10 (Swofford 2002). The sequences of *Exidiopsis calcea* (Pers.) K. Wells was used as the outgroup (Miettinen and Larsson 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 by bootstrap 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 generated.

MrModeltest 2.3 (Nylander 2004) was used to determine the best-fit evolution model for the combined data set of ITS and 28S sequences for estimating Bayesian inference (BI). BI was calculated with MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003). Four Markov chains were run for two runs from random starting trees for 3 000 000 generations for ITS+28S, and trees were sampled every 100 generations. The first one-fourth of the generations were discarded as

burn-in. Majority rule consensus tree of all remaining trees was calculated. Branches that simultaneously received bootstrap supports and Bayesian posterior probabilities (BPPs) greater than or equal to 75% and 0.95, respectively, were considered as significantly supported.

RESULTS

The ITS+28S data set included sequences from 139 fungal specimens representing 86 taxa. The data set had an aligned length of 2 116 characters, of which 1 011 characters are constant; 247 are variable and parsimony-uninformative, and 858 are parsimony-informative. Maximum parsimony analysis yielded 54 equally parsimonious trees (TL = 6724, CI = 0.302, RI = 0.787, RC = 0.238, HI = 0.698). The best model for the combined ITS +28S data set estimated and applied in the Bayesian analysis is as follows: GTR+I+G, lset nst = 6, rates = invgamma; prset statefreqpr = dirichlet (1,1,1,1). Both MP and BI trees resulted in similar topologies. Only the MP tree was provided. Both bootstrap values (≥50%) and BPPs (≥0.90) are shown at the nodes (FIG. 1).

The phylogeny (FIG. 1) inferred from ITS+28S sequences demonstrates seven major clades for 101 fungal samples of 66 taxa in Polyporales and 37 specimens of 19 taxa in the Hymenochaetales with high support (79% ML and BPPs = 1 for Polyporales, 97% ML and BPPs = 1 for Hymenochaetales). The 36 taxa sampled that traditionally belong to *Physisporinus, Rigidoporus, Leucophellinus*, and *Oxyporus* are nested mostly in eight lineages: five lineages (including the genera *Physisporinus, Emmia* Zmitr., Spirin & Malysheva, *Flaviporus* Murrill, and *Flavodon* Ryvarden and one taxon "*R. hypobrunneus*") belong to Polyporales, and three (including the genera *Rigidoporus, Leucophellinus*, and *Bridgeoporus*) belong to Hymenochaetales.

On the basis of the phylogenetic evidence and morphological characters (stated below), five new species are described and 16 new combinations are proposed.

TAXONOMY

Physisporinus crataegi F. Wu, Jia J. Chen & Y.C. Dai, sp. nov. FIGS. 2a, 3
MycoBank MB819191

Typification: CHINA. TIANJIN: Ji County, Panshan Forest Park, on stump of *Crataegus pinnatifida*, N40° 05′32″, E117°16′22″, 6 Aug 2015, *Dai 15497* (**holotype** BJFC 019602).

Etymology: Crataegi (Lat.): referring to the host tree genus *Crataegus*.

Basidiocarps annual, effused-reflexed, soft to juicy when fresh, without odor or taste, becoming fragile when dry. Pilei elongated, projecting up to 1 cm, 8 cm wide, and 5 mm thick at the base. Pileal surface cream and azonate when fresh, becoming buff yellow and glabrous with a distinct pellicle when dry; margin sharp, incurved when dry. Pore surface white when fresh, buff when bruised, buff to pinkish buff when dry; sterile margin very narrow to almost lacking; pores round to angular, 6–8 per mm; dissepiments thin, lacerate. Context buff, corky, azonate, up to 1 mm thick. Tubes concolorous with the pore surface, fragile, up to 4 mm long.

Hyphal system monomitic; hyphae simple septate, IKI–, moderately CB+, unchanged in KOH. Contextual hyphae hyaline, fairly thick-walled with a large lumen, rarely branched and frequently simple septate, slightly straight to flexuous, more or less interwoven, 4–6 µm diam. Tramal hyphae hyaline, thin- to slightly thick-walled with a wide lumen, occasionally branched, frequently simple septate, more or less straight, loosely interwoven to subparallel along the tubes, 2.5–4 µm diam; hymenial cystidia absent; cystidioles present, fusoid with a basal simple septum, thin-walled, smooth, 10–14 × 4–6 µm; basidia broadly clavate to barrel-shaped with four sterigmata and a simple basal septum, occasionally bearing a guttule, 11–13 × 5–6 µm; basidioles similar to basidia in shape, but smaller. Some hyphae at the dissepiment edge bearing crystals and resembling hyphoid cystidia. Basidiospores broadly ellipsoid to subglobose, hyaline, thin-walled, smooth, bearing a large guttule, IKI–, CB–, (4–)4.2–5(–5.2) × (3–)3.2–4.2 µm, L = 4.67 µm, W = 3.86 µm, Q = 1.2–1.23 (n = 60/2).

Type of rot: White rot.

Other material examined: CHINA. TIANJIN: Ji County, Panshan Forest Park, on stump of *Crataegus pinnatifida*, 6 Aug 2015, *Dai 15499* (**paratype** BJFC 019604).

Notes: Physisporinus crataegi is characterized by effused-reflexed and soft to juicy basidiocarps, lack of cystidia, broadly ellipsoid to subglobose and acyanophilous basidiospores, and growth on angiosperm wood (so far on *Crataegus*) in temperate forests. The resupinate part of *P. crataegi* is similar to *P. vitreus* (originally described from Europe) in having white and juicy basidiocarps, but *P. vitreus* has bigger pores (4–6 per mm) and larger and slightly cyanophilous basidiospores (5–6 × 4–5 µm; Niemelä 2005).

Phylogenetically, *Physisporinus crataegi* is closely related to *P. cinereus* (Núñez & Ryvarden) F. Wu et al. (= *Rigidoporus cinereus* Núñez & Ryvarden; FIG. 1). However, *P. cinereus* has a grayish, distinctly fibrillose pileus, larger pores (5–6 per mm), and larger and globose basidiospores (5–6 µm in diam; Núñez and Ryvarden 1999), whereas *P. crataegi* has a cream-colored, glabrous pileus with a distinct pellicle, smaller pores (6–8 per mm), and broadly ellipsoid to subglobose basidiospores (4.2–5 × 3.2–4.2 µm). In addition,

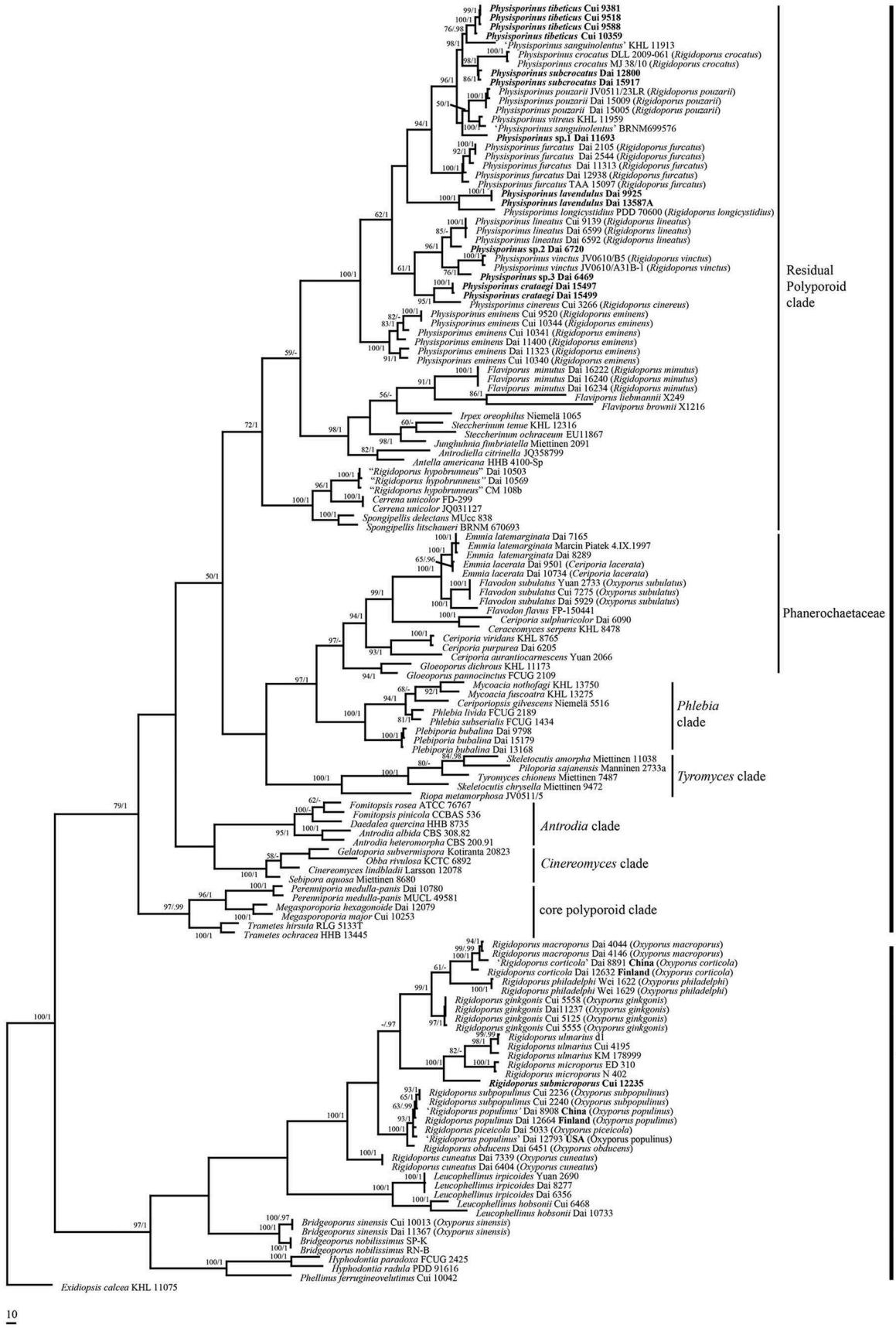

Figure 1. Strict consensus tree illustrating the phylogeny of *Rigidoporus, Oxyporus*, and *Physisporinus* and related species generated by maximum parsimony based on combined ITS+28S sequences. Branches are labeled with parsimony bootstrap proportions (before forward slash) higher than 50% and Bayesian posterior probabilities (after forward slash) more than 0.90.

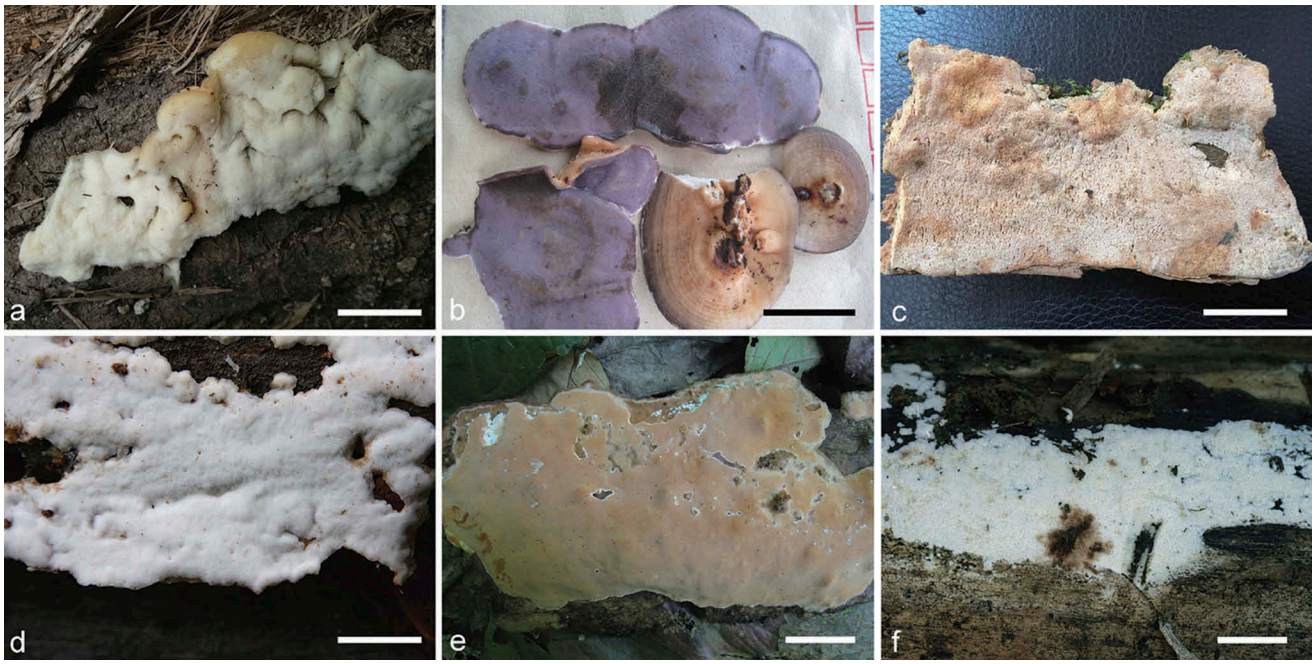

Figure 2. Basidiocarps of *Physisporinus* and *Rigidoporus* in China. a. *Physisporinus crataegi* (Dai 15499). b. *Physisporinus lavendulus* (Dai 13587A). c. *Physisporinus subcrocatus* (Dai 15937). d. *Physisporinus tibeticus* (Cui 9381). e. *Rigidoporus submicroporus* (Cui 12235). f. *Physisporinus* sp. 3 (Dai 6469). Bars: a–f = 2 cm.

the basidiocarp of *P. cinereus* becomes woody hard when dry, but it is fragile in *P. crataegi*.

Physisporinus lavendulus F. Wu, Jia J. Chen & Y.C. Dai, sp. nov. FIGS. 2b, 4
MycoBank MB819192

Typification: CHINA. HAINAN PROVINCE: Lingshui County, Diaoluoshan Forest Park, on fallen angiosperm branch, N18°55′17″, E109°58′08″, 13 Jun 2014, *Dai 13587A* (**holotype** BJFC 017326).

Etymology: Lavendulus (Lat.): referring to the lavender pore color when fresh.

Basidiocarps annual, pileate, sometimes with a rudimentary base at the center, corky when fresh, without odor or taste, becoming woody hard when dry. Pilei dimidiate to elongated, projecting up to 2 cm, 5 cm wide, and 5 mm thick at the center. Pileal surface cream, pinkish buff or grayish blue from center to margin and concentrically zonate when fresh, becoming pinkish buff to dark grayish blue, distinctly zonate and velutinate when dry; margin sharp, incurved when dry. Pore surface lavender when fresh, dark gray when bruised, blackish blue to black when dry; sterile margin very narrow to almost lacking; pores round to angular, 9–10 per mm; dissepiments thin, more or less entire. Context cream to buff, woody hard and azonate when dry, up to 2 mm thick. Tubes olivaceous buff, woody hard, up to 3 mm long.

Hyphal system monomitic; hyphae simple septate, IKI–, CB+, unchanged in KOH. Contextual hyphae hyaline, thick-walled with a large lumen, occasionally branched, frequently simple septate, more or less straight, loosely interwoven, 4–6 µm diam; hyphae at pileal surface composed of thick-walled, sometimes simple septate club-shaped or tubular hyphae, 50–100 × 8–10 µm. Tramal hyphae hyaline, thin- to slightly thick-walled with a wide lumen, occasionally branched and frequently simple septate, distinctly straight, parallel along the tubes, 4–5 µm diam; hyphoid cystidia present along trama, especially at the dissepiment edge, clavate, thick-walled, apically encrusted, up to 100 µm long and 6–8 µm diam in the widest part; hymenial cystidia absent; cystidioles present, mostly fusoid with a basal simple septum, pointed, thin-walled, smooth, 8–11 × 6–8 µm; basidia barrel-shaped to capitate with four sterigmata and a simple basal septum, 9–12 × 7–9 µm; basidioles in shape similar to basidia, but smaller. Basidiospores globose, hyaline, slightly thick-walled, smooth, sometimes bearing a small guttule, IKI–, moderately CB+, (4.1–)4.2–5(–5.1) × 4–5 µm, L = 4.65 µm, W = 4.52 µm, Q = 1.02–1.04 (n = 60/2).

Type of rot: White rot.

Other material examined: CHINA. HAINAN PROVINCE: Ledong County, Jianfengling Nature Reserve, on fallen angiosperm trunk, 1 Jun 2008, *Dai 9925* (**paratype** IFP 008123).

Notes: Physisporinus lavendulus is characterized by pileate basidiocarps, lavender to blackish pore surface, hyphoid cystidia in the trama and at the dissepiment edges, globose basidiospores and occurring in tropical

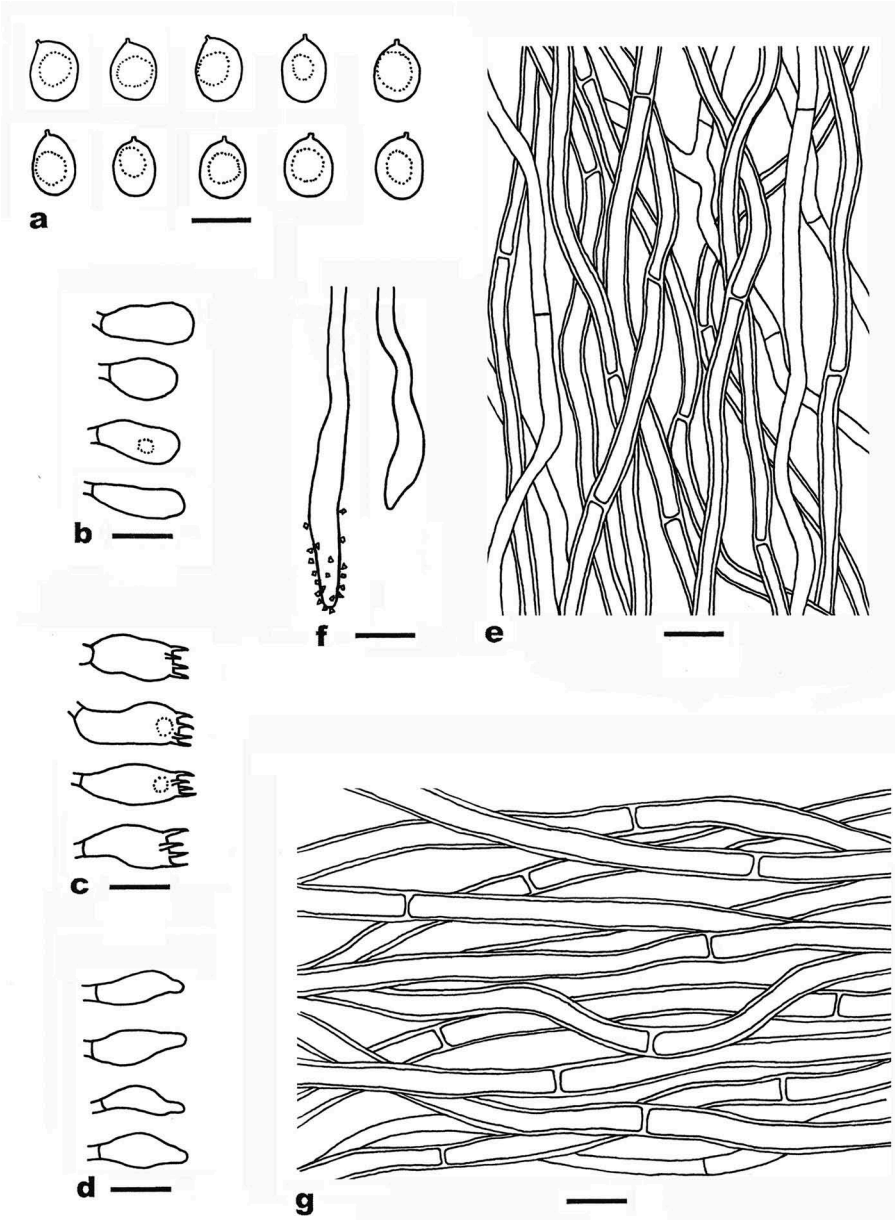

Figure 3. Microscopic characters of *Physisporinus crataegi* (drawn from the holotype). a. Basidiospores. b. Basidioles. c. Basidia. d. Cystidioles. e. Hyphae from trama. f. Hyphoid cystidia-like hyphae at the dissepiment edge. g. Hyphae from context. Bars: a = 5 µm; b–g = 10 µm.

forests. It may be confused with *Bjerkandera adusta* (Willd.) P. Karst. in the field, especially when both are old or dry because of pileate basidiocarps and dark pore surface. However, *B. adusta* has clamp connections and oblong-ellipsoid basidiospores and grows in temperate forests (Ryvarden and Melo 2014).

Tyromyces dacrydii Corner and *Oxyporus lilaceus* Corner were described from Malaysia and the Solomon Islands, respectively, and both have violaceous pores and lack clamp connections (Corner 1987, 1989). As mentioned by Hattori (2002), the holotype of *T. dacrydii* may be conspecific with *O. lilaceus*. Either way, *T. dacrydii* and *O. lilaceus* resemble *Physisporinus lavendulus* in having similar pores, but differ in having a dimitic hyphal system and the presence of hymenial cystidia and allantoid basidiospores that measure 2.5–3 × 0.5 µm (Hattori 2001, 2002).

Phylogenetically, *Physisporinus lavendulus* is closely related to *P. longicystidius* (P.K. Buchanan & Ryvarden) F. Wu et al. (= *Rigidoporus longicystidius* P.K. Buchanan & Ryvarden; FIG. 1). *Physisporinus longicystidius* has a resupinate to effused, reflexed and cartilaginous basidiocarp, a beige to ochraceous pore surface, the presence of hyphoid and apically pointed cystidia protruding into hymenium, and grows on *Nothofagus* in New Zealand (Buchanan and Ryvarden 2000), whereas *P. lavendulus* has a distinctly pileate and corky basidiocarp, lavender to

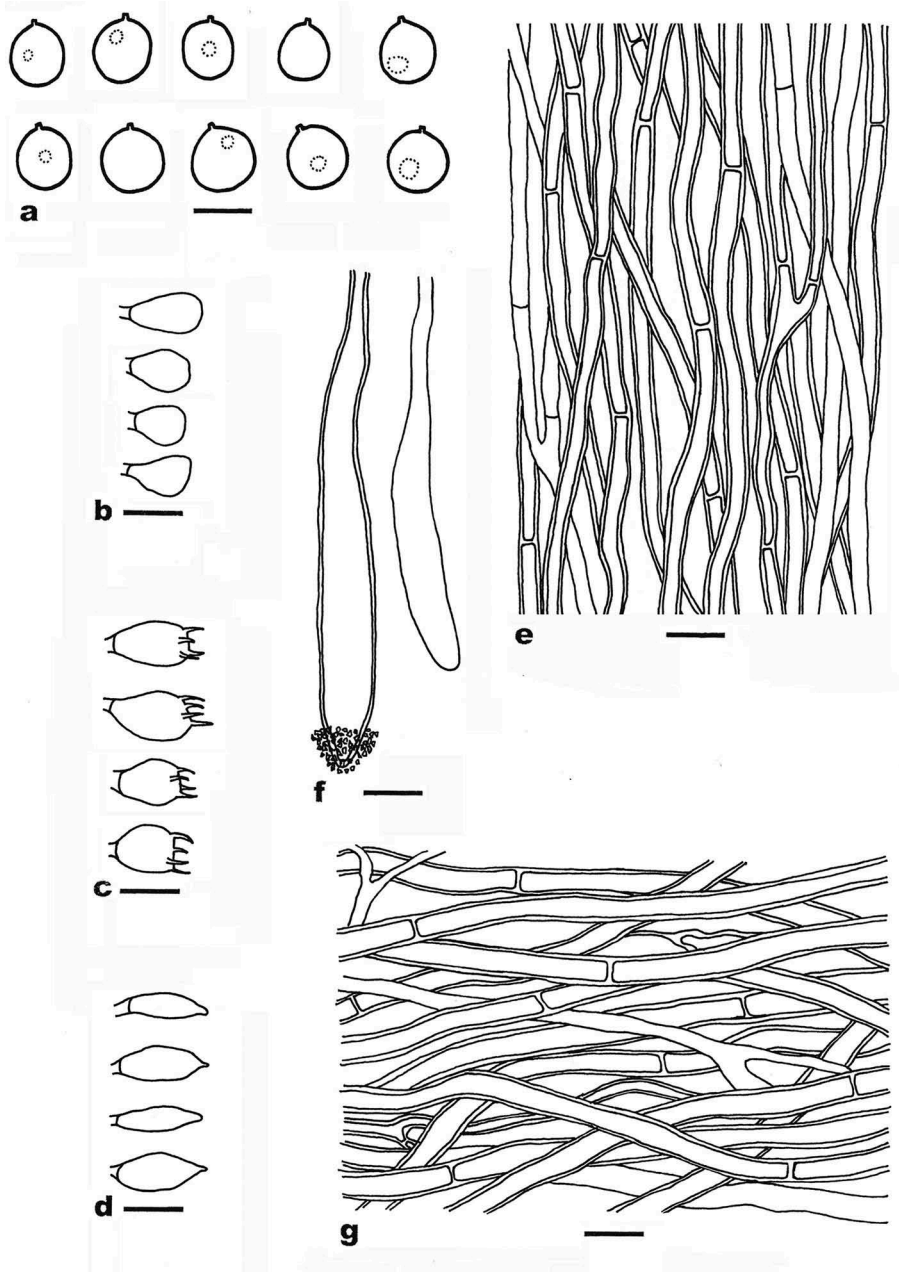

Figure 4. Microscopic characters of *Physisporinus lavendulus* (drawn from the holotype). a. Basidiospores. b. Basidioles. c. Basidia. d. Cystidioles. e. Hyphae from trama. f. Hyphoid cystidia. g. Hyphae from context. Bars: a = 5 µm; b–g = 10 µm.

blackish blue pores, hyphoid cystidia that do not protrude into hymenium, and grows on angiosperm wood rather than *Nothofagus*.

Physisporinus subcrocatus F. Wu, Jia J. Chen & Y.C. Dai, sp. nov. FIGS. 2c, 5

MycoBank MB819193

Typification: CHINA. XINJIANG AUTONOMOUS REGION: Yining, Gongliu County, West Tianshan Nature Reserve, on rotten wood of *Picea*, N43°12′18″, E83°02′35″, 13 Sep 2015, *Dai 15917* (**holotype** BJFC 020018).

Etymology: Subcrocatus (Lat.): referring to the similarity of *Rigidoporus crocatus*.

Basidiocarps perennial, resupinate, cushion-shaped, and distinctly receding from center to margin, leathery to corky when fresh, without odor or taste, becoming bone hard when dry, up to 15 cm long, 6 cm wide, and 7 mm thick at the center. Pore surface dark fawn to vinaceous brown when fresh, brownish vinaceous to fawn when dry; sterile margin present, buff yellow when fresh, cream when dry, up to 1.5 mm wide; pores round to angular, 5–7 per mm; dissepiments thin, more or less entire. Subiculum present in each tube layer, cream, corky, around 0.2 mm thick in each layer. Tubes distinctly stratified, wood hard to brittle,

pinkish buff, paler than pore surface, each tube layer up to 2 mm long.

Hyphal system monomitic; hyphae simple septate, IKI–, CB+, becoming slightly swollen in KOH. Contextual hyphae hyaline, thin- to thick-walled with a large lumen, occasionally branched, frequently simple septate, strongly flexuous, interwoven, 4–7 μm diam. Tramal hyphae hyaline, thin- to thick-walled with a wide lumen, frequently branched, simple septate, more or less straight, subparallel along the tubes, 4–6 μm diam; hymenial cystidia absent, fusoid cystidioles present; basidia barrel-shaped with four sterigmata and a simple basal septum, 11–13 × 7–8 μm; basidioles similar to basidia in shape, but smaller. Some hyphae at the dissepiment edge bearing crystals and resembling hyphoid cystidia. Basidiospores subglobose, hyaline, thin-walled, smooth, bearing a large guttule, IKI–, CB –, (5.0–)5.1–5.8(–6) × (4.1–)4.2–5.0(–5.1) μm, L = 5.41 μm, W = 4.63 μm, Q = 1.16–1.18 (n = 60/2).

Other materials examined: CHINA. XINJIANG AUTONOMOUS REGION: Yining, Gongliu County, West Tianshan Nature Reserve, on rotten wood of *Picea*, 13 Sep 2015, *Dai 15937* (**paratype** BJFC 020038). USA. CONNECTICUT: Colchester, Salmon River State Forest, on rotten wood of *Betula*, 23 Jul 2012, *Dai 12800* (**paratype** BJFC 013105).

Notes: Physisporinus subcrocatus is characterized by perennial, resupinate, and cushion-shaped basidiocarps,

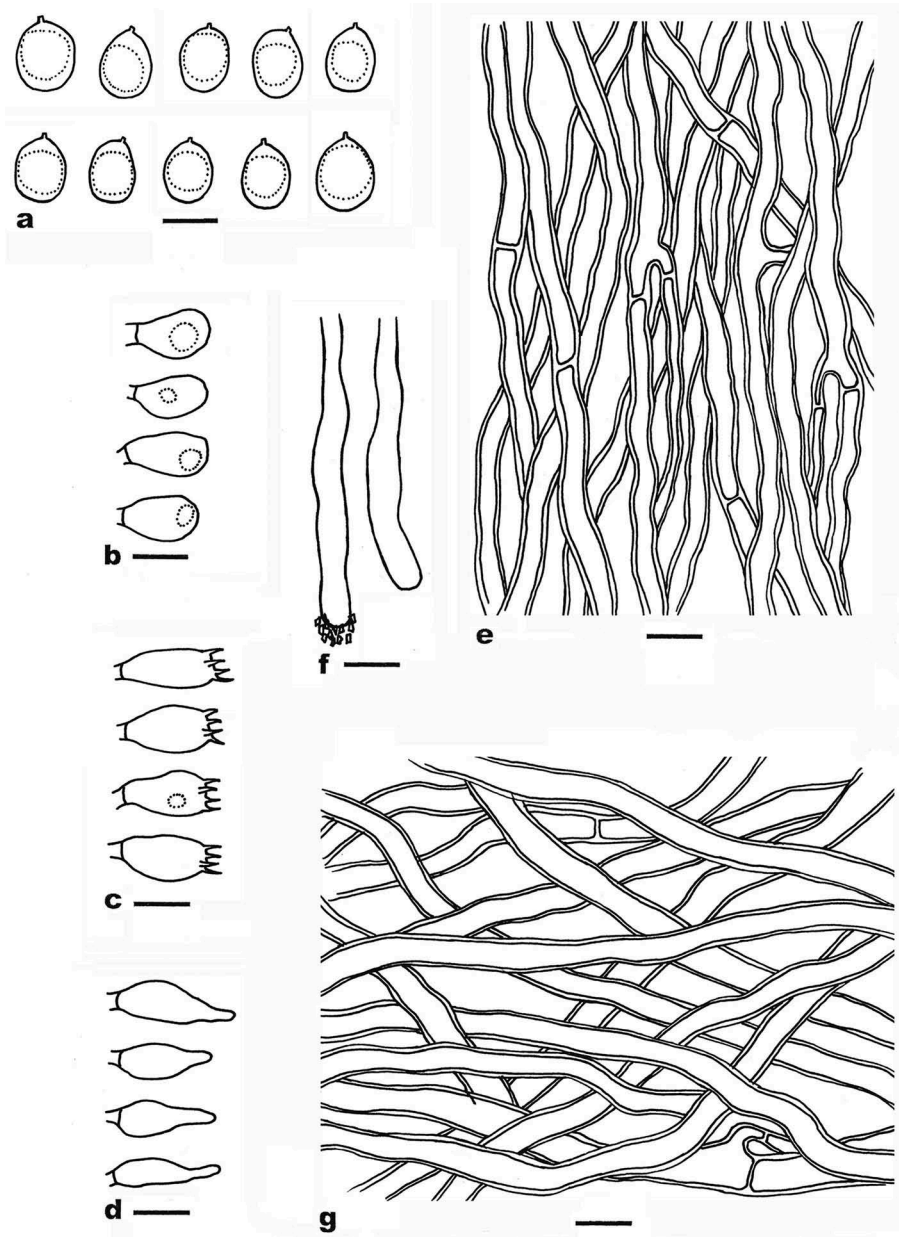

Figure 5. Microscopic characters of *Physisporinus subcrocatus* (drawn from the holotype). a. Basidiospores. b. Basidioles. c. Basidia. d. Cystidioles. e. Hyphae from trama. f. Hyphoid cystidia-like hyphae at the dissepiment edge. g. Hyphae from subiculum. Bars: a = 5 μm; b–g = 10 μm.

dark fawn to vinaceous brown pore surface, round to angular pores, presence of fusoid cystidioles, and subglobose basidiospores.

Physisporinus crocatus was originally described as *Poria crocata* Pat. from Tunisia (Lowe 1966). *Physisporinus nigrescens* Bres., described from Hungary, was treated as a synonym of *P. crocatus* by Gilbertson and Ryvarden (1987), and no similar species are known from Asia and North America. *Physisporinus subcrocatus* is very similar to *P. crocatus* in macromorphology, and the two species are phylogenetically closely related (FIG. 1), but the latter has smaller basidiospores that measure 4.4–5.2 × 4–4.5 µm (Niemelä 2005).

Physisporinus tibeticus F. Wu, Jia J. Chen & Y.C. Dai, sp. nov. FIGS. 2d, 6

MycoBank MB819194

Typification: CHINA. TIBET: Bayi County, Lulang, on fallen trunk of *Abies*, 17 Sep 2010, *Cui 9381* (**holotype** BJFC 008319).

Etymology: Tibeticus (Lat.): referring to the locality of the species in Tibet.

Basidiocarps annual, resupinate, soft to juicy when fresh, without odor or taste, becoming fragile to brittle when dry, up to 10 cm long, 5 cm wide, and 4.2 mm thick at the center. Pore surface snow white when fresh, yellowish brown when bruised, pinkish buff to buff yellow when dry, bruised portions becoming dark brown when dry; sterile margin very narrow to almost lacking; pores round to angular, 5–7 per mm; dissepiments thin, lacerate. Subiculum cream, corky, very thin, up to 0.2 mm thick. Tubes concolorous with the pore surface, fragile, up to 4 mm long.

Hyphal system monomitic; hyphae simple septate, IKI–, CB+, becoming slightly swollen in KOH. Contextual hyphae hyaline, thick-walled with a large lumen, rarely branched, frequently simple septate, more or less flexuous, loosely interwoven, 4–6 µm diam. Tramal hyphae hyaline, thin- to thick-walled with a wide lumen, rarely branched, frequently simple septate, more or less straight, loosely interwoven to subparallel along the tubes, slightly agglutinated, 3–5 µm in diam; hymenial cystidia absent; cystidioles present, fusoid with a simple basal septum, thin-walled, smooth, 10–15 × 5–6 µm; basidia broadly clavate to barrel-shaped with four sterigmata and a simple basal septum, occasionally bearing one or two small guttules, 11–14 × 6–7 µm; basidioles similar to basidia in shape, but smaller. Some hyphae at the dissepiment edge bearing crystals and resembling hyphoid cystidia. Basidiospores broadly ellipsoid, hyaline, thin-walled, smooth, bearing a big guttule, IKI–, CB–, (4.6–)4.8–5.5(–5.6) × (3.5–)3.7–4.3(–4.5) µm, L = 5.07 µm, W = 3.95 µm, Q = 1.28–1.29 (n = 60/2).

Type of rot: White rot.

Other materials examined: CHINA. TIBET: Bomi County, Lulang, on fallen trunk of *Pinus*, 20 Sep 2010, *Cui 9518* (**paratype** BJFC 008456) and *9588* (**paratype** BJFC 008526); YUNNAN PROVINCE: Lanping County, Tongdian, on rotten wood of *Pinus*, 19 Sep 2011, *Cui 10359* (**paratype** BJFC 011254).

Notes: Physisporinus tibeticus is characterized by resupinate basidiocarps, white pores when fresh, which become buff yellow when dry, lack of hyphoid cystidia and hymenial cystidia, and broadly ellipsoid, acyanophilous basidiospores. It grows on gymnosperm wood in boreal forests and is very similar to *P. vitreus* in morphology. However, *P. vitreus* has larger and slightly cyanophilous basidiospores (5–6 × 4–5 µm; Niemelä 2005). *Physisporinus tibeticus* also resembles *P. eminens* (Y.C. Dai) F. Wu et al. (= *Rigidoporus eminens* Y.C. Dai) in macromorphology, but the latter has smaller pores (7–8 per mm) and distinctly thick-walled hyphoid cystidia (Dai 1998).

Phylogenetically, *Physisporinus tibeticus* is closely related to *P. sanguinolentus* (Alb. & Schwein.) Pilát (FIG. 1). However, *P. sanguinolentus* has bigger pores (3–4 per mm) and basidiospores (5.2–6.1 × 4.4–5.2 µm; Niemelä 2005). In addition, fresh pores of *P. sanguinolentus* become bloody red when bruised (Ryvarden and Melo 2014), whereas those of *P. tibeticus* become yellowish brown.

Rigidoporus submicroporus F. Wu, Jia J. Chen & Y.C. Dai, sp. nov. FIGS. 2e, 7

MycoBank MB819195

Typification: CHINA. TIBET: Motuo County, on fallen angiosperm trunk, 20 Sep 2014, *Cui 12235* (**holotype** BJFC 017149).

Etymology: Submicroporus (Lat.): referring to the similarity of *Rigidoporus microporus.*

Basidiocarps perennial, resupinate, cushion-shaped, and distinctly receding from center to margin, leathery to corky when fresh, without odor or taste, becoming bone hard when dry, up to 20 cm long, 6 cm wide, and 5 mm thick at the center. Pore surface olivaceous buff when fresh, fawn when dry; sterile margin distinct, white when fresh, cream when dry, up to 0.5 mm wide; pores angular, 8–10 per mm; dissepiments thin, more or less entire. Subiculum cream, corky, up to 1 mm thick. Tubes distinctly stratified, wood hard to brittle, new tubes concolorous with the pore surface, old tubes cream, tube layer to 4 mm long.

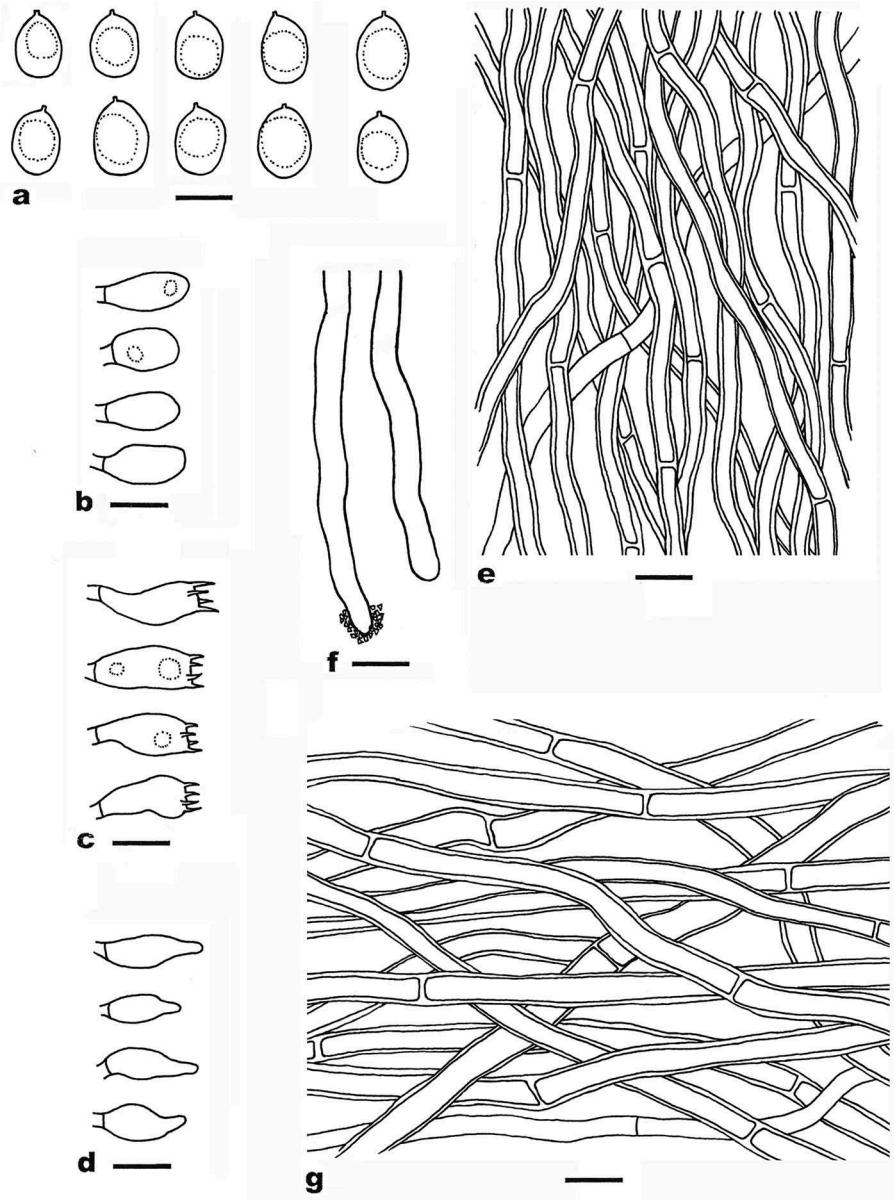

Figure 6. Microscopic characters of *Physisporinus tibeticus* (from holotype). a. Basidiospores. b. Basidioles. c. Basidia. d. Cystidioles. e. Hyphae from trama. f. Hyphoid cystidia-like hyphae at the dissepiment edge. g. Hyphae from subiculum. Bars: a = 5 μm; b–g = 10 μm.

Hyphal system monomitic; hyphae simple septate, IKI–, CB+, unchanged in KOH. Contextual hyphae hyaline, thick-walled with a large lumen, occasionally branched, frequently simple septate, strongly flexuous, interwoven, 4–5 μm diam. Tramal hyphae hyaline to pale yellowish, thin- to distinctly thick-walled with a narrow to wide lumen, rarely branched, frequently simple septate, more or less flexuous, interwoven, gelatinized, 3–5 μm diam; hymenial cystidia present, ventricose with a pointed tip, 15–21 × 7–8.5 μm; cystidioles absent; basidia barrel-shaped with four sterigmata and a simple basal septum, 6–7 × 3.5–4 μm; basidioles similar to basidia in shape, but smaller; irregular crystals abundant among trama. Big and irregular crystals present among trama and hymenium. Basidiospores subglobose, hyaline, thin-walled, smooth, IKI–, CB–, (3.1–)3.2–3.7(–3.8) × (2.7–)2.8–3.2(–3.3) μm, L = 3.41 μm, W = 2.99 μm, Q = 1.14 (n = 30/1).

Type of rot: White rot.

Notes: Rigidoporus submicroporus is described based on a single specimen, because the holotype is very large, well-developed, and in very good condition. *R. submicroporus* differs from other species in *Rigidoporus* by the presence of smooth, ventricose cystidia with a pointed tip, and small basidiospores that measure 3.2–3.7 × 2.8–3.2 μm. *R. submicroporus* is very similar to *R. microporus*, but the latter has pileate basidiocarps and larger basidiospores (3.5–5 ×

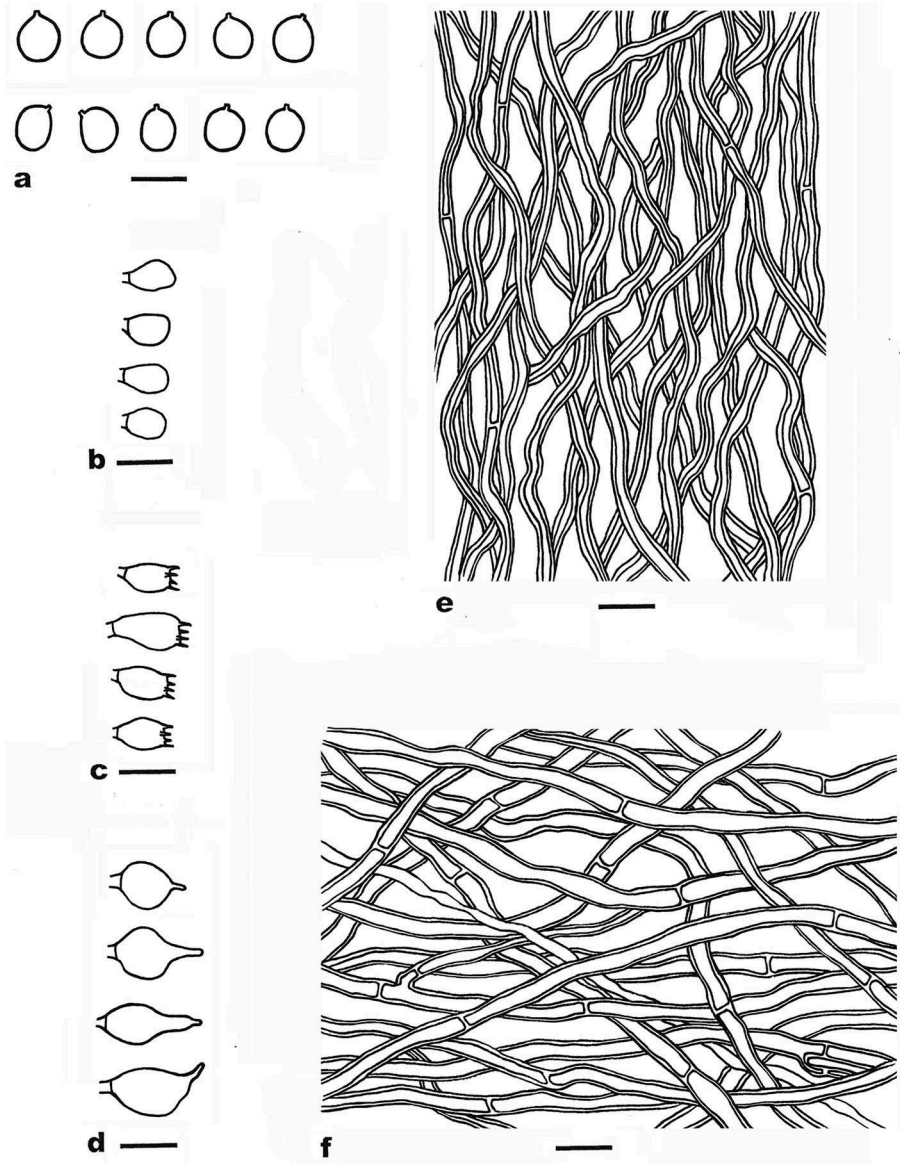

Figure 7. Microscopic characters of *Rigidoporus submicroporus* (from holotype). a. Basidiospores. b. Basidioles. c. Basidia. d. Cystidia. e. Hyphae from trama. f. Hyphae from subiculum. Bars: a = 5 µm; b–g = 10 µm.

3.5–4 µm; Gilbertson and Ryvarden 1987) and lacks cystidia. We consider the fusoid elements in the hymenium to be cystidia rather than cystidioles as in *R. submicroporus* because they are distinctly larger than the basidia (FIG. 7); however, such elements in other species of *Rigidoporus* are considered as cystidioles because they are almost the same size (FIGS. 3–6). In addition, phylogenetically, *R. submicroporus* forms a lineage that is independent from other lineages of *Rigidoporus* (FIG.1).

Combinations.—*Rigidoporus cinereus* Núñez & Ryvarden, *R. crocatus* (Pat.) Ryvarden, *R. eminens* Y.C. Dai, *R. furcatus* Núñez & Ryvarden, *R. lineatus* (Pers.) Ryvarden, *R. longicystidius* P.K. Buchanan & Ryvarden, and *R. pouzarii* Vampola & Vlasák are accepted in *Rigidoporus* (Corner 1987; Dai 1998; Núñez and Ryvarden 1999; Ryvarden and Melo 2014). In our phylogeny (FIG. 1), these species are nested within the *Physisporinus* clade rather than the *Rigidoporus* clade, so the following new combinations are proposed.

Physisporinus cinereus (Núñez & Ryvarden) F. Wu, Jia J. Chen & Y.C. Dai, comb. nov.
MycoBank MB819196

≡ *Rigidoporus cinereus* Núñez & Ryvarden, Fungal Divers 3:115. 1999 (Basionym).

Material examined: CHINA. FUJIAN PROVINCE: Wuyishan County, Wuyishan Nature Reserve, on rotten angiosperm wood, 23 Oct 2005, *Cui 3266* (BJFC 002171).

Physisporinus crocatus (Pat.) F. Wu, Jia J. Chen & Y.C. Dai, comb. nov.
MycoBank MB819197

≡ *Poria crocata* Pat., J Bot Paris 8:220. 1894 (Basionym).

Material examined: Estonia. PÄRNUMAA: Saarda, Veelikse, on rotten wood of *Alnus*, 17 Jul 1996, *Dai 2231* (H).

Physisporinus eminens (Y.C. Dai) F. Wu, Jia J. Chen & Y.C. Dai, comb. nov.
MycoBank MB819198

≡ *Rigidoporus eminens* Y.C. Dai, Ann Bot Fenn 35:144. 1998 (Basionym).

Materials examined: CHINA. HENAN PROVINCE: Neixiang County, Baotianman Nature Reserve, on rotten wood of *Quercus*, 23 Sep 2009, *Dai 11323* (BJFC 007469); JILIN PROVINCE: Erdao, Changbaishan Nature Reserve, on rotten wood of *Populus*, 9 Sep 2009, *Dai 11400* (BJFC 007305), Huadian County, Dongxing, on rotten wood of *Tilia*, 19 Oct 1993, *Dai 1728* (H); TIBET: Bomi County, Lulang, on fallen trunk of *Pinus*, 20 Sep 2010, *Cui 9520* (BJFC 008458); YUNNAN PROVINCE: Lanping County, Tongdian, on rotten wood of *Pinus*, 19 Sep 2011, *Cui 10340* (BJFC 011235), *10341* (BJFC 011236), and *10344* (BJFC 011239).

Physisporinus furcatus (Núñez & Ryvarden) F. Wu, Jia J. Chen & Y.C. Dai, comb. nov.
MycoBank MB819199

≡ *Rigidoporus furcatus* Núñez & Ryvarden, in Núñez et al., Fungal Divers 6:112. 2001 (Basionym).

Materials examined: CHINA. HENAN PROVINCE: Neixiang County, Baotianman Nature Reserve, on rotten angiosperm wood, 23 Sep 2009, *Dai 11313* (BJFC 007459); JILIN PROVINCE: Erdao, Changbaishan Nature Reserve, on rotten wood of *Larix*, 14 Sep 1995, *Dai 2105* (BJFC 001927), 16 Aug 1997, *Dai 2544* (H, IFP 015205); SICHUAN PROVINCE: Mianning County, Lingshansi, on fallen trunk of *Castanopsis*, 18 Sep 2012, *Dai 12938* (BJFC 013196). RUSSIA. PRIMORYE: On dead tree of *Alnus*, 12 Sep 1990, *TAA 15097* (**isotype** in O).

Physisporinus lineatus (Pers.) F. Wu, Jia J. Chen & Y. C. Dai, comb. nov.
MycoBank MB819200

≡ *Polyporus lineatus* Pers., in Gaudichaud-Beaupré in Freycinet,Voy. Uranie. Bot.:174. 1827 (Basionym).

Materials examined: CHINA. GUANGDONG PROVINCE: Guangzhou, Botanical Garden, on angiosperm wood, 5 Aug 2010, *Cui 9139* (BJFC 008077); JIANGSU PROVINCE: Nanjing, Zhongshanling, on stump of *Pinus*, 3 Jun 2005, *Dai 6592* (BJFC 002192), Zhongshan Botanical Garden, on living tree of *Magnolia*, 4 Jun 2005, *Dai 6599* (BJFC 002191); YUNNAN PROVINCE: Menglan County, Menglun, on angiosperm stump, 4 Aug 2005, *Dai 6720* (BJFC 002194).

Physisporinus longicystidius (P.K. Buchanan & Ryvarden) F. Wu, Jia J. Chen & Y.C. Dai, comb. nov.
MycoBank MB819201

≡ *Rigidoporus longicystidius* P.K. Buchanan & Ryvarden, N Z J Bot 38:259. 2000 (Basionym).

Materials examined: NEW ZEALAND. Paparoa National Park, Bullock Creek, on dead angiosperm wood, 25 Mar 1996, *Ryvarden 38613* and *Buchanan 96/114* (PDD 70600, **isotype** in O).

Physisporinus pouzarii (Vampola & Vlasák) F. Wu, Jia J. Chen & Y.C. Dai, comb. nov.
MycoBank MB819202

≡ *Rigidoporus pouzarii* Vampola & Vlasák, Czech Mycol 64:5. 2012 (Basionym).

Materials examined: CHINA. GUIZHOU PROVINCE: Suiyang County, Kuankuoshui Nature Reserve, on rotten wood of *Fagus*, 25 Nov 2014, *Y.C. Dai, Dai 15005* (BJFC 018118) and *15009* (BJFC 018122). CZECH REPUBLIC. RANSPURK: Lanzhot, on *Ulmus*, Nov 2015, *JV0511/23* (JV, PRM).

The type species of *Oxyporus* is *O. polulinus* (Schumach.) Donk. The type locality is St. Petersburg, Russia, but the type was destroyed, and a neotype was selected from Denmark (Donk 1933). *Rigidoporus microporus* is the type species of *Rigidoporus* (Murrill 1905; type locality: Cuba). In our phylogeny, both species are nested within a clade of Hymenochaetales (FIG. 1). Since *Rigidoporus* and *Oxyporus* have no distinct morphological differences, these two genera are merged with *Rigidoporus*, which has priority because it was published in 1905, and *Oxyporus* in 1933 (Murrill 1905; Donk 1933). Pouzar was of the same opinion and transferred several species of *Oxyporus* to *Rigidoporus* (Pouzar 1966). The following combinations are proposed.

Rigidoporus cuneatus (Murrill) F. Wu, Jia J. Chen & Y. C. Dai, comb. nov.
MycoBank MB819203

≡ *Coriolellus cuneatus* Murrill, N Am Fl (New York) 9(1):28. 1907 (Basionym).

Specimens examined: CHINA. FUJIAN PROVINCE: Wuyishan County, Wuyishan Nature Reserve, on rotten of *Cryptomeria*, 21 Oct 2005, *Y.C. Dai, Dai 7339* (BJFC 001348); ZHEJIANG PROVINCE: Lin'an County, Tianmushan Nature Reserve, on rotten wood of *Cryptomeria*, 16 Oct 2004, *Y.C. Dai, Dai 6404* (BJFC 001341).

Rigidoporus ginkgonis (Y.C. Dai) F. Wu, Jia J. Chen & Y.C. Dai, comb. nov.
MycoBank MB819205

≡ *Oxyporus ginkgonis* Y.C. Dai, Mycotaxon 92:346. 2005 (Basionym).

Specimens examined: CHINA. BEIJING: Botanical Garden, on rotten wood of *Ginkgo*, 9 Jul 2008, *B.K Cui, Cui 5555* (BJFC 003576), Summer Palace, on living tree of *Sabina*, 2 Jul 2008, *B.K Cui, Cui 5558* (BJFC 003579); JIANGSU PROVINCE: Nanjing, Zhongshan Botanical Garden, on angiosperm branch, 12 Sep 2009, *Y.C. Dai, Dai 11237* (BJFC 007210); SHANDONG PROVINCE: Pingyi County, Mengshan Forest Park, on stump of *Pinus*, 10 Aug 2007, *B.K. Cui, Cui 5125* (BJFC 003166).

Rigidoporus macroporus (Y.C. Dai & Y.L. Wei) F. Wu, Jia J. Chen & Y.C. Dai, comb. nov.
MycoBank MB819207

≡ *Oxyporus macroporus* Y.C. Dai & Y.L. Wei, in Dai, Wei & Wang, Ann Bot Fenn 41(5):325. 2004 (Basionym).

Specimens examined: CHINA. SICHUAN PROVINCE: Jiuzhai County, Jiuzhaigou Nature Reserve, on fallen trunk of *Tsuga*, 12 Oct 2002, *Y.C. Dai, Dai 4044* (BJFC 010373, **holotype**), on fallen trunk of *Picea*, 13 Oct 2002, *Y.C. Dai, Dai 4146* (BJFC 010375).

Rigidoporus piceicola (B.K. Cui & Y.C. Dai) F. Wu, Jia J. Chen & Y.C. Dai, comb. nov.
MycoBank MB819208

≡ *Oxyporus piceicola* B.K. Cui & Y.C. Dai, Mycotaxon 109:314. 2009 (Basionym).

Specimen examined: CHINA. QINGHAI PROVINCE: Huzhu County, Beishan Forest Park, on stump of *Picea*, 31 Aug 2003, *Y.C. Dai, Dai 5033* (IFP 003712, **holotype**).

Rigidoporus subpopulinus (B.K. Cui & Y.C. Dai) F. Wu, Jia J. Chen & Y.C. Dai, comb. nov.
MycoBank MB819210

≡ *Oxyporus subpopulinus* B.K. Cui & Y.C. Dai, in Cui, Huang & Dai, Mycotaxon 96:208. 2006 (Basionym).

Specimens examined: CHINA. QINGHAI PROVINCE: Xunhua County, Mengda Nature Reserve, on living tree of *Picea crassifolia*, 30 Aug 2005, *B.K. Cui, Cui 2313* (BJFC 001402, **holotype**); GANSU PROVINCE: Yuzhong County, Xinglongshan Nature Reserve, on base of living *Picea crassifolia*, 27 Aug 2005, *B.K. Cui, Cui 2236* (BJFC 001405) and *2240* (BJFC 001400).

Oxyporus subulatus Ryvarden and*O. sinensis* X.L. Zeng have previously been placed in *Oxyporus* (Hjortstam and Ryvarden 1982; Zeng 1992; Dai 2012; Ryvarden and Melo 2014). According to our phylogeny, the former species are nested within *Flavodon*, and the latter is nested within *Bridgeoporus* T.J. Volk et al. In addition, *Rigidoporus minutus* B.K. Cui & Y.C. Dai was originally described in *Rigidoporus* (Cui et al. 2009) but is closely related to *Flaviporus* Murrill phylogenetically. Moreover, *Ceriporia lacerata* N. Maek., Suhara & R. Kondo grouped with *Emmia latemarginata* (Durieu & Mont.) Zmitr., Spirin & Malysheva with a high support (100% ML and BPPs = 1) phylogenetically. Thus, the following four combinations are proposed.

Bridgeoporus sinensis (X.L. Zeng) F. Wu, Jia J. Chen & Y.C. Dai, comb. nov.
MycoBank MB819212

≡ *Oxyporus sinensis* X.L. Zeng, Mycotaxon 44:51. 1992 (Basionym).

Specimens examined: CHINA. GANSU PROVINCE: Erdao, Changbaishan Nature Reserve, on root of living *Populus ussuriensis*, 7 Oct 2009, *Y.C. Dai, Dai 11367* (BJFC 007286), 8 Aug 2011, *B.K. Cui, Cui 10013* (BJFC 010906).

Emmia lacerata (N. Maek., Suhara & R. Kondo) F. Wu, Jia J. Chen & Y.C. Dai, comb. nov.
MycoBank MB822111

≡ *Ceriporia lacerata* N. Maek., Suhara & R. Kondo, Mycotaxon 86:342. 2003 (Basionym).

Specimens examined: CHINA. HENAN PROVINCE: Xiuwu County, Yuntaishan, on fallen angiosperm trunk, 4 Sep 2009, *B.K. Cui, Cui 7275* (BJFC 005762); HUBEI PROVINCE: Shennongjia, Muyu, on fallen trunk of *Celtis*, 25 Sep 2004, *Y.C. Dai, Dai 5929* (BJFC 010379, IFP 003711); SHANXI PROVINCE: Zhouzhi County, Taibaishan Nature Reserve, on fallen angiosperm trunk, 25 Oct 2006, *H.S. Yuan, Yuan 2733* (BJFC 001406, IFP 003703).

Flaviporus minutus (B.K. Cui & Y.C. Dai) F. Wu, Jia J. Chen & Y.C. Dai, comb. nov.
MycoBank MB819217

≡ *Rigidoporus minutus* B.K. Cui & Y.C. Dai, in Cui, Dai & Li, Nova Hedwigia 88:190. 2009 (Basionym).

Specimens examined: CHINA. HAINAN PROVINCE: Wuzhishan County, Wuzhishan Nature Reserve, on rotten angiosperm wood, 15 Nov 2015, *Y. C. Dai, Dai 16222* (BJFC 020308), *16234* (BJFC 020320), and *16240* (BJFC 020326).

Flavodon subulatus (Ryvaren) F. Wu, Jia J. Chen & Y. C. Dai, comb. nov.
MycoBank MB822110

≡ *Oxyporus subulatus* Ryvarden, in Hjortstam and Ryvarden, Nord J Bot 2:280. 1982 (Basionym).

Specimens examined: CHINA. HENAN PROVINCE: Xiuwu County, Yuntaishan, on fallen angiosperm trunk, 4 Sep 2009, *B.K. Cui, Cui 7275* (BJFC 005762);

HUBEI PROVINCE: Shennongjia, Muyu, on fallen trunk of *Celtis*, 25 Sep 2004, *Y.C. Dai, Dai 5929* (BJFC 010379, IFP 003711); SHANXI PROVINCE: Zhouzhi County, Taibaishan Nature Reserve, on fallen angiosperm trunk, 25 Oct 2006, *H.S. Yuan, Yuan 2733* (BJFC 001406, IFP 003703).

DISCUSSION

On the basis of 80 samples from the Northern Hemisphere, mostly from Asia, species traditionally accepted in *Physisporinus, Rigidoporus, Leucophellinus*, and *Oxyporus* were analyzed on the basis of both morphology and phylogeny; five new species in *Physisporinus* and *Rigidoporus* are found and described, 16 new combinations in *Bridgeoporus, Emmia, Flaviporus, Flavodon, Physisporinus*, and *Rigidoporus* are proposed, and the phylogenetic relationships of these species are outlined.

Rigidoporus and *Oxyporus* were recombined because the type species of the two genera are nested within a clade in Hymenochaetales. In addition, the traditional taxa in *Rigidoporus* and *Oxyporus* were shown to be polyphyletic. The type species of *Rigidoporus* (*R. microporus*) belongs to Hymenochaetales, whereas seven species belong to Polyporales and were transferred to *Physisporinus*. Although *P. vinctus* (Berk.) Murrill was previously accepted as *Rigidoporus vinctus* (Berk.) Ryvarden in most publications (Ryvarden and Johansen 1980; Gilbertson and Ryvarden 1987; Núñez and Ryvarden 2001; Dai 2012), it belongs to *Physisporinus* in our phylogeny (FIG.1).

Most species of *Oxyporus* belong to Hymenochaetales and were transferred to *Rigidoporus*, but one species (*O. subulatus*) belong to Polyporales, and being closely related to *Flavodon*, it was combined with *Flavodon*.

On the basis of current phylogeny, it is even more difficult to clearly define *Physisporinus, Rigidoporus*, and *Oxyporus*, as some important morphological characters overlap in these genera. In addition, the current phylogeny is mostly based on samples from the Northern Hemisphere, and several species in these genera from the Southern Hemisphere are not included. Either we did not have voucher specimens or we failed to extract DNA. Thus, we are reluctant to define these genera until a phylogeny is carried out with additional species in these genera. In the future, more new species will be described from other continents (e.g., Vlasák's personal collections, not published), including the following three taxa that are treated only at the generic level because of limited materials.

Physisporinus sp. 1 (Dai 11693) was collected in southern China, and it grows on rotten angiosperm wood in a subtropical forests. Its pores are pinkish brown (5–6 per mm) and the basidiospores are broadly ellipsoid (4.8–5.2 (–5.5) × (3.8–)3.9–4.5(–4.7) µm, L = 4.99 µm, W = 4.06 µm, Q = 1.23 (n = 30/1). Although it resembles *P. crocatus*, it has a strongly agglutinated hyphal structure, and is phylogenetically related to *P. vitreus*.

Physisporinus sp. 2 (Dai 6720) was collected in southwest China, and it grows on angiosperm stump in a tropical forest. It is characterized by pileate basidiocarps with very small pores (9–11/mm), hyphoid and apically encrusted cystidia, and subglobose basidiospores that measure (4.2–)4.5–5.2(–5.5) × 4–4.9(–5) µm, L = 4.87 µm, W = 4.28 µm, Q = 1.13 (n = 30/1). This taxon is macromorphologically similar to *Rigidoporus microporus*, but phylogenetically related to *Physisporinus lineatus*, which has larger pores (6–8/mm) and basidiospores (5–6 µm diam; Ryvarden and Melo 2014).

Physisporinus sp. 3 (Dai 6469; FIG. 2f) was collected in eastern China, and it grows on fallen, decorticated trunks of *Populus* in a subtropical forests. It resembles *P. vitreus* in having similar pores (4–5 per mm) and basidiospores (5–6.2(–6.5) × (4.2–)4.5–5.1(–5.5) µm, L = 5.75 µm, W = 4.89 µm, Q = 1.18 (n = 30/1), and pores that become bloody red when bruised. However, it has capitate basidia and is phylogenetically related to *P. lineatus*.

It seems that *Physisporinus sanguinolentus, Rigidoporus corticola*, and *R. populinus* are the species complexes and that more taxa exist in these complexes. For example, two sequences '*Physisporinus sanguinolentus*' (KHL 11913 from Sweden and BRNM 699576 from Slovakia) are divided into different lineages in our phylogeny (FIG. 1).

On the basis of the ITS and 28S rDNA-based phylogeny (FIG. 1), *Rigidoporus minutus* is closely related to species of *Flaviporus* and distant from the type species of *Rigidoporus, R. microporus*. In addition, *R. minutus* is similar to *F. brownii* (Humb.) Donk and *F. liebmannii* (Fr.) Ginns in sharing tiny pores and basidiospores, although the former species has a monomitic hyphal system, and the latter two species have a dimitic hyphal structure. Therefore, in this paper, *Rigidoporus minutus* is combined as *Flaviporus minutus*.

Although *Rigidoporus hypobrunneus* (Petch) Corner forms as a distinct sublineage with *Cerrena unicolor* in our phylogeny with high support (96% ML and BPPs = 1; FIG. 1), *R. hypobrunneus* and *C. unicolor* have very different morphologies and ecologies. The former has a resupinate basidiocarp with small, regular pores, a monomitic hyphal system with simple septa,

subglobose basidiospores, and grows in subtropical to tropical areas. The latter has a pileate basidiocarp with daedaleoid pores, a dimitic hyphal system with clamp connections, ellipsoid basidiospores, and grows in temperate and boreal forests. Although it may be reasonable to establish an independent genus for *R. hypobrunneus*, we treat the species as '*Rigidoporus hypobrunneus*' for the time being, even though the species does not belong to *Rigidoporus*.

Emmia was recently established by the generic type as *E. latemarginata* (Durieu & Mont.) Zmitr., Spirin & Malysheva based on morphological characters only (Zmitrovich at al. 2006). The Asian and European samples of *E. latemarginata* formed a distinct clade in our phylogeny (FIG. 1). In addition, *Ceriporia lacerata* is closely related to *E. latemarginata* (FIG. 1). So we accept the genus *Emmia* and *Emmia lacerata* is proposed.

Flavodon flavus Ryvarden is analyzed is our phylogeny; surprisingly, *Ceriporia subulata* is closely related to *Flavodon* rather than *Emmia*. We have studied the morphology of *Flavodon flavus* (Klotzsch) Ryvarden (the generic type) and *Ceriporia subulata*. The former has a dimitic hyphal system and yellowish, hydnaceous hymenophore, whereas the latter has a monomitic and poroid to hydnoid hymenophore with cream to pale yellow color. However, both species have simple septated hyphae and similar cystidia and basidiospores. Although *Ceriporia subulata* has poroid hymenophore in juvenile, it becomes irpicoid and more or less yellowish when mature, so *Flavodon flavus* and *Ceriporia subulata* have similar morphology. We accept *Flavodon* and *Flavodon subulatus* is proposed.

There is another problem for definition of *Rigidoporus corticola* and *R. populinus*. The type localities of *Rigidoporus corticola* and *R. populinus* are in Sweden and Denmark, respectively. Samples from Finland (Dai 12632 for *R. corticola* and Dai 12664 for *R. populinus*) were analyzed, and distinct variations existed between European (Dai 12632) and Asian (Dai 8895) representatives for *R. corticola* and among the Northern Hemisphere materials (Dai 12664 from Finland, Dai 8098 from China, and Dai 12793 from USA) for *R. populinus* (FIG. 1). So these two taxa seem to be species complex, and samples outside of Europe are treated as "*Rigidoporus corticola*" and "*R. populinus*" in our phylogeny. Although *Rigidoporus populinus, R. subpopulinus*, and *R. piceicola* are very closely related in the phylogeny based on ITS and 28S, they have distinct difference in RPB2 (phylogeny is not shown).

Bridgeoporus nobilissimus was described as *Oxyporus nobilissimus* from the northwestern United States (Cooke 1949; Gilbertson and Ryvarden 1987). Cooke (1949) mentioned that the species causes a brown rot of *Tsuga heterophylla*, but Gilbertson and Ryvarden (1987) concluded that it is probably a white rot fungus. Burdsall et al. (1996) indicated that the species causes a brown rot and transferred it to *Bridgeoporus*. In our phylogenetic analysis, *Oxyporus sinensis* is nested within the *Bridgeoporus* clade. Furthermore, *O. sinensis* and *B. nobilissimus* are similar in morphology and ecology: both species producing large and pileate basidiocarps, the presence of hyphoid, thick-walled cystidia, and growing near the root collar of living trees or snags. *Bridgeoporus nobilissimus* occurs on coniferous trees (*Tsuga* and *Abies*), whereas *O. sinensis* lives on angiosperms (exclusively on *Populus ussuriensis*). *Oxyporus sinensis* is the second species described in the genus. The wood decay of *B. sinensis* seems to be white rot, although a culture from decayed wood is needed to confirm the rot type.

Leuocophellinus was originally established by Bondartsev and Singer (1941). Although it was invalidly published because it lacked a Latin diagnosis, it was later validated by Singer (1944). Two species are included in the genus, *L. hobsonii* (Berk. ex Cooke) Ryvarden (synonyms: *L. mollissimus* (Pat.) Parmasto, *Poria xylina* Lloyd) and *L. irpicoides* (Bondartsev ex Pilát) Bondartsev & Singer (Parmasto 1983; Ryvarden 1988; Dai and Niemelä 1995). These two species are rather similar, but *L. hobsonii* occurs on many angiosperm trees in tropical and subtropical areas and has pileate basidiocarps and basidiospores that measure 8–10 × 6–7 µm, whereas *L. irpicoides* grows mostly on trees of *Acer* in northeast Asia and has resupinate to effused-reflexed basidiocarps without a true cap and basidiospores that measure 6–8.5 × 5–6 µm (Corner 1987; Dai and Niemelä 1995; Dai 2012). Phylogenetically, the samples of these two species are nested mostly in an independent lineage (*Leuocophellinus*), so the genus is more likely related to *Rigidoporus* rather than *Physisporinus* (FIG. 1). We accept *Leucophellinus* as an independent genus because of its distinctly thick-walled and cyanophilous basidiospores.

Our phylogenetic analysis based on ITS and 28S demonstrated that the morphologically similar polypore genera *Rigidoporus, Physisporinus, Oxyporus*, and *Leucophellinus* are polyphyletic (FIG. 1). We accept the genera of *Physisporinus, Emmia, Flaviporus, Flavodon, Rigidoporus, Leucophellinus*, and *Bridgeoporus*, the former four genera belongs to Polyporales and the latter three genera belong to Hymenochaetales. *Oxyporus* is treated as a synonym of *Rigidoporus*.

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