

Global phylogeny and taxonomy of the wood-decaying fungal genus phlebiopsis (poly...

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Introduction

In 1978, *Phlebiopsis* Jülich was suggested for *Thelephora gigantea* Fr. that has effused, ceraceous basidiomata with a smooth to odontoid hymenophore, a monomitic hyphal system with colorless, partially agglutinated, simple-septate hyphae, lamprocystidia with thick, colorless walls, and basidiospores with colorless, thin, smooth walls that do not react in Melzer's reagent or cotton blue ([Jülich, 1978](#) ; [Bernicchia and Gorjón, 2010](#)). Over the next 40 years, 12 species with similar morphology were described in or transferred to the genus by [Hjortstam and Ryvarden \(1980\)](#) , [Jülich and Stalpers \(1980\)](#) , [Dhingra \(1987\)](#) , [Hjortstam \(1987\)](#) , [Gilbertson and Adaskaveg \(1993\)](#) , [Douanla-Meli and Langer \(2009\)](#) , [Wu et al. \(2010\)](#) , [Priyanka et al. \(2011\)](#) , [Kaur et al. \(2015\)](#) , and [Zhao et al. \(2018\)](#) .

Morphologically, *Phlebiopsis* is similar to *Scopuloides* (Masse) Höhn. & Litsch. and some species of *Phanerochaete* P. Karst based on the characteristics of lamprocystidia and simple-septate generative hyphae. It was traditionally placed in the *Phanerochaete sensu lato* group ([Rattan, 1977](#) ; [Burdsall, 1985](#)). Although [Burdsall \(1985\)](#) considered *Phlebiopsis* and *Scopuloides* to be synonyms of *Phanerochaete* , most researchers at the time recognized the genera as distinct ([Eriksson et al., 1978](#) , [1981](#) , [1984](#) ; [Jülich and Stalpers, 1980](#) ; [Wu, 1990](#)).

The generic circumscription of *Phlebiopsis* was expanded when molecular studies showed that *Phanerochaete crassa* (Lév.) Burds. and *Phlebiopsis gigantea* (Fr.) Jülich were closely related ([de Koker et al., 2003](#) ; [Greslebin et al., 2004](#) ; [Wu et al., 2010](#) ; [Floudas and Hibbett, 2015](#)). With the inclusion of

P. crassa, *Phlebiopsis* now also includes species with effused-reflexed, coriaceous basidiomata, a dimitic hyphal system, and lamprocystidia or skeletocystidia with light brown walls. In addition, based on both phylogenetic and morphological evidence, [Floudas and Hibbett \(2015\)](#) created *Phaeophlebiopsis* Floudas & Hibbett to accommodate *Phlebiopsis peniophoroides* Gilb. & Adask. and similar species with ceraceous, beige-brown basidiomata and subicula, lamprocystidia with brown walls, and small basidiospores. The limits of the *Phlebiopsis* clade were extended by [Miettinen et al. \(2016\)](#) who transferred six species into *Phlebiopsis*. The results of their phylogenetic study showed that the type species of *Castanoporus* Ryvardeen, *Merulius castaneus* Lloyd, was nested in a clade with *P. gigantea* and, therefore, a synonym of *Phlebiopsis*. Similarly, *Dentocorticium pilatii* (Parmasto) Duehm & Michel, *Lopharia papyrina* (Mont.) Boidin, *Phanerochaete brunneocystidiata* Sheng H. Wu, and *Phanerochaete laxa* Sheng H. Wu clustered in the *Phlebiopsis* clade, and were all transferred to the genus. Based on the morphological similarity of *Thelephora friesii* Lév., the type of *Hjortstamia* [Boidin and Gilles, 2003](#) to *L. papyrina* and *P. crassa*, they also transferred *T. friesii* to *Phlebiopsis*, thereby reducing *Hjortstamia* to a synonym of *Phlebiopsis*. *Phlebiopsis pilatii* (Parmasto) Spirin & Miettinen is unique in the genus for it has a dimitic hyphal system of simple-septate generative and microbinding (squeletto-ligatives) hyphae and finely branched hyphidia but lacks lamprocystidia or skeletal cystidia ([Larsen and Gilberston, 1977](#); [Duhem and Michel, 2009](#)).

With *Hjortstamia* and *Castanoporus* as synonyms, *Phlebiopsis* became a morphologically heterogeneous genus with effused, effused-reflexed or

pileate basidiomata with a membranous, ceraceous, corneous or coriaceous texture, hymenophore smooth to tuberculate, odontoid, or poroid, hyphal system monomitic or dimitic with a loose to compact subiculum, and typically with lamprocystidia or skeletocystidia with colorless to brown walls. In phylogenetic analyses of Phanerochaetaceae, *Phlebiopsis* species are in a clade sister to *Rhizochaete* Gresl., Nakasone & Rajchenb., *Hapalopilus* P. Karst. and *Phaeophlebiopsis*, but distant from *Phanerochaete sensu stricto* and *Scopuloides* ([Floudas and Hibbett, 2015](#) ; [Miettinen et al., 2016](#)).

Another genus of interest is *Australohydnum* Jülich for it is similar to *Phlebiopsis* by its warted, irpicoid to hydroid hymenophore, a dimitic hyphal system with colorless, encrusted skeletocystidia, and thin-walled, smooth basidiospores ([Jülich, 1978](#)). The morphological similarities between *Australohydnum* and *Phanerochaete sensu lato* were observed by [Hjortstam and Ryvarden \(1990\)](#) . In a limited study of *Irpex sensu stricto*, sequences of *A. dregeanum* (Berk.) Hjortstam & Ryvarden and *I. vellereus* Berk. & Broome (a possible synonym of *A. dregeanum*) clustered together in a clade sister to *Phanerochaete chrysosporium* Burds. and *Phanerochaete sordida* (P. Karst.) J. Erikss. & Ryvarden ([Lim and Jung, 2003](#)). However, the phylogenetic relationship of *Australohydnum* within the Phanerochaetaceae remained unknown ([Miettinen et al., 2016](#)).

Among the 24 names of *Phlebiopsis* recovered in Index Fungorum [1](#) (accessed on 21 January 2020), four species were transferred to *Phaeophlebiopsis* . Of the remaining 20 species, 11 were described originally from Asia ([Dhingra, 1987](#) ; [Wu, 2000](#) , [2004](#) ; [Priyanka et al., 2011](#) ; [Kaur et](#)

[al., 2015](#) ; [Zhao et al., 2018](#) ; [Xu et al., 2020](#)). More than 150 specimens of *Phlebiopsis* were collected by the corresponding author from China and Southeast Asia in recent years. Based on these specimens and sequences obtained from GenBank, the phylogenetic analyses and taxonomic study of *Phlebiopsis* and related taxa in the Phanerochaetaceae were undertaken. This study is a contribution to the understanding of the diversity and phylogenetic relationships of crust fungi in China.

Materials and Methods

Specimen Collection

Field trips for specimen collection in many kinds of Nature Reserves and Forest Parks in China and other countries were carried out by the authors. *In situ* photos of the fungi were taken with a Canon camera EOS 70D (Canon Corporation, Japan). Fresh specimens were dried with a portable drier (manufactured in Finland). Dried specimens were labeled and then stored in a refrigerator of minus 40°C for 2 weeks to kill the insects and their eggs before they were ready for morphological and molecular studies.

Morphological Studies

Voucher specimens are deposited at the herbaria of Beijing Forestry University, Beijing, China (BJFC), Centre for Forest Mycology Research, U. S. Forest Service, Madison, WI, United States (CFMR), National Museum of Natural Science, Taichung, Taiwan, China (TNM) and Beijing Museum of Natural History, Beijing, China (BJM). The Sri Lankan voucher specimens are deposited in the Faculty of Agriculture, University of Ruhuna, Kamburupitiya, Sri Lanka and the herbarium of Beijing Forestry University, Beijing, China (BJFC), and were studied under the material transfer agreement signed by <https://assignbuster.com/global-phylogeny-and-taxonomy-of-the-wood-decaying-fungal-genus-phlebiopsis-polyporales-basidiomycota/>

the two universities. Freehand sections were made from dried basidiomata and mounted in 2% (w/v) potassium hydroxide (KOH), 1% (w/v) phloxine, Melzer's reagent (IKI) or cotton blue (CB). Microscopic examinations were carried out with a Nikon Eclipse 80i microscope (Nikon Corporation, Japan) at magnifications up to 1000×. Drawings were made with the aid of a drawing tube. The following abbreviations are used: IKI-, neither amyloid nor dextrinoid; CB-, acyanophilous; L, mean spore length; W, mean spore width; Q, L/W ratio; n (a/b), number of spores (a) measured from number of specimens (b). Color codes and names follow [Kornerup and Wanscher \(1978\)](#).

DNA Extraction and Sequencing

A CTAB plant genomic DNA extraction Kit DN14 (Aidlab Biotechnologies Co., Ltd., Beijing, China) was used to extract total genomic DNA from dried specimens then amplified by the polymerase chain reaction (PCR), according to the manufacturer's instructions. The ITS1-5.8S-ITS2 region was amplified with the primer pair ITS5/ITS4 ([White et al., 1990](#)) using the following protocol: initial denaturation at 95°C for 4 min, followed by 34 cycles at 94°C for 40 s, 58°C for 45 s and 72°C for 1 min, and final extension at 72°C for 10 min. The nrLSU D1-D2 region was amplified with the primer pair LR0R/LR7 [2](#) employing the following procedure: initial denaturation at 94°C for 1 min, followed by 34 cycles at 94°C for 30 s, 50°C for 1 min and 72°C for 1.5 min, and final extension at 72°C for 10 min. DNA sequencing was performed at Beijing Genomics Institute, and the sequences were deposited in GenBank [3](#) ([Table 1](#)). BioEdit v. 7.0.5.3 ([Hall, 1999](#)) and Geneious Basic v. 11.1.15

([Kearse et al., 2012](#)) were used to review the chromatograms and for contig assembly.

TABLE 1

Species and sequences used in the phylogenetic analyses.

Phylogenetic Analyses

Two separate datasets, the concatenated ITS-nrLSU sequences of species in the Phanerochaetaceae and ITS only sequences of *Phlebiopsis* , were analyzed. *Ceraceomyces serpens* (Tode) Ginns and *Phlebia acerina* Peck were selected as an outgroup for the ITS-LSU dataset, whilst *Rhizochaete radicata* (Henn.) Gresl., Nakasone & Rajchenb. was used in the ITS dataset ([Floudas and Hibbett, 2015](#)). For the concatenated dataset, the sequences of ITS and nrLSU were aligned separately using MAFFT v. 7.4 ([Katoh et al., 2017](#)) with the G-INS-I iterative refinement algorithm, and optimized manually in BioEdit v. 7.0.5.3. The separate alignments were then concatenated using Mesquite v. 3.5.1 ([Maddison and Maddison, 2018](#)). The datasets were deposited in TreeBase [5](#) (submission ID: 26529 for Phanerochaetaceae ITS-LSU, 26530 for *Phlebiopsis* ITS).

Maximum parsimony (MP), maximum likelihood (ML) analyses and Bayesian inference (BI) were carried out by using PAUP * v. 4.0b10 ([Swofford, 2002](#)), RAxML v. 8.2.10 ([Stamatakis, 2014](#)), and MrBayes 3.2.6 ([Ronquist et al., 2012](#)), respectively. In MP analysis, trees were generated using 100 replicates of random stepwise addition of sequence and tree-bisection reconnection (TBR) branch-swapping algorithm with all characters given

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equal weight. Branch supports for all parsimony analyses were estimated by performing 1000 bootstrap replicates with a heuristic search of 10 random-addition replicates for each bootstrap replicate. In ML analysis, statistical support values were obtained using rapid bootstrapping with 1000 replicates, with default settings used for other parameters. For BI, the best-fit substitution model was estimated with jModeltest v. 2.1.7 ([Darriba et al., 2012](#)). Four Markov chains were run for five million and three million generations for the Phanerochaetaceae ITS-LSU and *Phlebiopsis* ITS datasets, respectively, until the split deviation frequency value was lower than 0.01. Trees were sampled every 100th generation. The first quarter of the trees, which represented the burn-in phase of the analyses, were discarded, and the remaining trees were used to calculate posterior probabilities (BPP) in the majority rule consensus tree.

Results

Phylogenetic Analyses

Forty-three ITS and 37 nrLSU sequences were generated for this study. The concatenated ITS-LSU dataset contained 101 ITS and 107 nrLSU sequences from 107 samples representing 86 Phanerochaetaceae taxa and the outgroup, while the ITS dataset contained 71 samples representing 21 *Phlebiopsis s. s.* taxa, a sample of *Irpex vellereus* and the outgroup ([Table 1](#)). The concatenated dataset had an aligned length of 2339 characters, of which 554 were parsimony-informative. MP analysis yielded one equally parsimonious tree (TL = 3603, CI = 0.360, RI = 0.695, RC = 0.250, HI = 0.640). The ITS dataset had an aligned length of 726 characters, of which 178 were parsimony-informative. MP analysis yielded 92 equally parsimonious

trees (TL = 658, CI = 0.579, RI = 0.870, RC = 0.504, HI = 0.421). jModelTest suggested GTR + I + G and HKY + G were the best-fit models of nucleotide evolution for the concatenated ITS-LSU and ITS datasets, respectively. The average standard deviation of split frequencies of BI was 0.009223 and 0.007710 at the end of the run. ML and BI analyses resulted in almost identical tree topologies compared to the MP analysis. The MP trees are shown in [Figures 1, 2](#) with the parsimony bootstrap values ($\geq 50\%$, first), Bayesian posterior probabilities (≥ 0.95 , second) and likelihood bootstrap values ($\geq 50\%$, third) labeled along the branches.

FIGURE 1

Phylogenetic tree from maximum parsimony analysis from the concatenated ITS and nrLSU sequences of Phanerochaetaceae taxa. Branches are labeled with parsimony bootstrap values ($\geq 50\%$, first), Bayesian posterior probabilities (≥ 0.95 , second) and likelihood bootstrap values ($\geq 50\%$, third). New species are set in bold.

FIGURE 2

Phylogenetic tree obtained from maximum parsimony analysis of ITS sequence data of *Phlebiopsis*. Branches are labeled with parsimony bootstrap values ($\geq 50\%$, first), Bayesian posterior probabilities (≥ 0.95 , second) and likelihood bootstrap values ($\geq 50\%$, third). New species are set in bold.

In the Phanerochaetaceae ITS-LSU tree ([Figure 1](#)), *Phlebiopsis* , *Phaeophlebiopsis* , *Hapalopilus* , and *Rhizochaete* formed a strongly supported clade (98/1/100). Within this clade, the *Phlebiopsis* species clustered together with relatively strong support values (69/1/98), and species of *Phaeophlebiopsis* , *Hapalopilus* and *Rhizochaete* were in the sister subclades. In the *Phlebiopsis* ITS tree ([Figure 2](#)), 24 lineages were resolved including 21 taxa of *Phlebiopsis* and ' *Irpex vellereus*. ' Samples of *P. crassa* were distributed in three distinct lineages. The six new species, *P. albescens* , *P. brunnea* , *P. cylindrospora* , *P. magnicystidiata* , *P. membranacea* and *P. sinensis* , formed distinct lineages.

Taxonomy

Phlebiopsis albescens Y. N. Zhao & S. H. He, sp. nov.

MycoBank: MB836023

Type – Sri Lanka, Avissawella, Salgala Forest, on fallen angiosperm twig, 3 March 2019, He 5805 (BJFC 030672, holotype; isotype in BJM).

Etymology – Refers to the white basidiomata.

Fruiting body – Basidiomata annual, resupinate, widely effused, closely adnate, inseparable from substrate, ceraceous to crustose, first as small patches, later confluent up to 15 cm long, 1 cm wide, up to 80 µm thick in section. Hymenophore smooth, white (6A1), orange white (6A2) to pale orange (6A3), unchanged in KOH, not cracking on drying; margin indistinct, concolorous with hymenophore. Context white.

Microscopic structures - Hyphal system monomitic; generative hyphae simple-septate. Subiculum indistinct to absent. Subhymenium well developed; hyphae colorless, thin- to slightly thick-walled, tightly agglutinated, 2. 5-4 μm in diam. Lamprocystidia abundant, conical, colorless to pale yellow, thick-walled, heavily encrusted with crystals along entire length, embedded or slightly projecting beyond hymenium, with one or two secondary septa, with a basal simple septum, 25-40 \times 8-12 μm (without encrustations). Basidia clavate to cylindrical, colorless, thin-walled, with a basal simple septum and four sterigmata, 10-16 \times 3-4. 5 μm ; basidioles numerous, similar to basidia but slightly smaller. Basidiospores oblong ellipsoid to short cylindrical, colorless, thin-walled, smooth, IKI-, CB-, 3. 5-5 \times 2-2. 2 (-2. 5) μm , $L = 4. 4 \mu\text{m}$, $W = 2. 1 \mu\text{m}$, $Q = 2. 1 (n = 30/1)$.

Distribution - Sri Lanka.

Notes - *Phlebiopsis albescens* ([Figure 3](#)) is characterized by thin, white to pale orange basidiomata, an indistinct subiculum, short lamprocystidia (<40 μm long) and basidia (<16 μm long), and small basidiospores (<5 μm long). *Phlebiopsis punjabensis* G. Kaur, Avn. P. Singh & Dhingra, from India, also has thin, white basidiomata and short lamprocystidia, 20-36 \times 7-9. 8 μm , but larger basidiospores, 5. 3-8. 5 \times 2. 5-4 μm ([Kaur et al., 2015](#)). Another species with short basidiospores, *P. yunnanensis* C. L. Zhao, from southern China, has thicker basidiomata, 100-500 μm thick, with a smooth to odontoid hymenophore, and ellipsoid basidiospores, 2. 5-3. 5 μm wide ([Zhao et al., 2018](#)). In the ITS phylogenetic tree ([Figure 2](#)), *P. albescens* formed its

lineage and was not closely related to any other species for current sequences.

FIGURE 3

Phlebiopsis albescens [from the holotype He 5805; scale bars: A = 1 cm, B-E = 10 μ m].(A) Basidiomata;(B) basidiospores;(C) basidia;(D) basidioles;(E) lamprocystidia.

***Phlebiopsis brunnea* Y. N. Zhao & S. H. He, sp. nov.**

MycoBank: MB836024

Type – Sri Lanka, Western Province, Mitirigala Nissarana Vanaya Forest Monastery, on fallen angiosperm branch, 4 March 2019, He 5822 (BJFC 030689, holotype; isotype in BJM).

Etymology – Refers to the brown context of basidiomata.

Fruiting body – Basidiomata annual, resupinate, widely effused, closely adnate, inseparable from substrate, coriaceous, developing as small patches then confluent, up to 20 cm long, 5 cm wide, up to 350 μ m thick in section. Hymenophore smooth, brownish gray (6C2–6D2), brownish orange (6C3) to grayish brown (6D3), unchanged in KOH, not cracking on drying; margin thinning out, indistinct, concolorous or darker than hymenophore. Context pale brown.

Microscopic structures – Hyphal system pseudodimitic; generative hyphae simple-septate. Subiculum well-developed, a non-agglutinated, loosely

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interwoven tissue; skeletocystidia (skeletal hyphae) brown, distinctly thick-walled, slightly encrusted, up to 120 μm long, 14 μm wide; hyphae colorless to pale yellowish brown, thick-walled, smooth, moderately branched at right angles, frequently septate, 2–5 μm in diam. Subhymenium thin; skeletocystidia as in subiculum but shorter and more heavily encrusted; generative hyphae colorless, thin- to thick-walled, moderately branched, frequently septate, loosely interwoven, 2–4.5 μm in diam. Lamprocystidia subulate to fusiform, colorless, thin- to thick-walled, distal end encrusted with small crystals, projecting up to 30 μm beyond hymenium, with an obtuse or acute tip, with a basal simple septum, 35–65 \times 7–12 μm . Basidia clavate to subcylindrical, colorless, thin-walled, with a basal simple septum and four sterigmata, 20–33 \times 4.5–6 μm ; basidioles numerous, similar to basidia but slightly smaller. Basidiospores oblong ellipsoid to subcylindrical, colorless, thin-walled, smooth, IKI-, CB-, 6.5–7.5 (–8) \times 3–3.6 (–4) μm , $L = 7.3 \mu\text{m}$, $W = 3.3 \mu\text{m}$, $Q = 2.2$ ($n = 30/1$).

Distribution – Sri Lanka.

Notes – *Phlebiopsis brunnea* ([Figure 4](#)) is characterized by a coriaceous basidiomata with a smooth hymenophore and brown context, abundant, brown skeletocystidia in the subiculum and subhymenium, lamprocystidia, and oblong ellipsoid to subcylindrical basidiospores. *Hjortstamia bambusicola* (Berk. & Broome) Hjortstam & Ryvarden is similar with its grayish brown hymenophore and pseudodimitic hyphal system with brown skeletocystidia but with narrower basidiospores (2.5–3 μm wide) and grows on bamboo in Australia ([Hjortstam and Ryvarden, 2005](#)). *Phlebiopsis*

brunneocystidiata (Sheng H. Wu) Miettinen has narrower lamprocystidia (5–8 µm wide) with brown walls and a host preference for Pandanaceae in Taiwan ([Wu, 2004](#)). Another similar species, *P. crassa* differs from *P. brunnea* by having effused-reflexed basidiomata with a more or less purple hymenophore and larger lamprocystidia, 50–120 × 8–20 µm ([Burdvall, 1985](#) ; [Hjortstam and Ryvarde, 1990](#)). *Phlebiopsis brunnea* formed weakly supported sister lineages to *P. brunneocystidiata* or *P. crassa* group B and C in the ITS-LSU and ITS trees, respectively ([Figures 1](#) , [2](#)).

FIGURE 4

Phlebiopsis brunnea (from the holotype He 5822; scale bars: A = 1 cm, B–E = 10 µm). (A) Basidiomata; (B) basidiospores; (C) lamprocystidia; (D) basidia and basidiole; (E) hyphae from subiculum.

***Phlebiopsis cylindrospora* Y. N. Zhao & S. H. He, sp. nov.**

MycoBank: MB836025

Type – China, Hainan Province, Lingshui County, Diaoluoshan Nature Reserve, on dead, small diameter bamboo, 2 July 2019, He 5984 (BJFC 030860, holotype; isotype in BJM).

Etymology – Refers to the cylindrical basidiospores.

Fruiting body – Basidiomata annual, resupinate, widely effused, closely adnate, inseparable from substrate, coriaceous, first as small patches, later confluent up to 20 cm long, 4 cm wide, up to 150 µm thick in section.

Hymenophore smooth, orange white (6A2), orange gray (6B2) to grayish
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orange (6B3), turning purple in KOH, not cracking on drying; margin thinning out, indistinct, slightly fimbriate, paler than or concolorous with hymenophore. Context gray.

Microscopic structures - Hyphal system monomitic; generative hyphae simple-septate. Subiculum distinct, a somewhat agglutinated, compact tissue, arranged more or less parallel to substrate; hyphae colorless, thick-walled, encrusted with yellow, resinous granules, infrequently branched, moderately septate, 2-4. 5 μm in diam. Subhymenium indistinct; hyphae thin- to slightly thick-walled, heavily encrusted with yellow, resinous granules, frequently septate, more or less agglutinated, 2-4 μm in diam. Lamprocystidia numerous, subfusiform, colorless, thick-walled, apically encrusted with small crystals, embedded or slightly projecting beyond hymenium, 20-36 (-40) \times 5-9 μm . Basidia clavate to subcylindrical, colorless, thin-walled, with a basal simple septum and four sterigmata, 12-16 \times 4-5 μm ; basidioles numerous, similar to basidia but slightly smaller. Basidiospores cylindrical, colorless, thin-walled, smooth, IKI-, CB-, (5-) 5. 5-7. 5 (-8) \times 1. 8-2. 8 (-3) μm , $L = 5. 9 \mu\text{m}$, $W = 2. 2 \mu\text{m}$, $Q = 2. 4-3. 1$ ($n = 90/3$).

Additional specimens examined - China, Hainan Province, Qiongzong County, Limushan Nature Reserve, on fallen angiosperm twig, 8 June 2016, He 3831 (BJFC 022333); on dead, small diameter bamboo, 8 June 2016, He 3882 (BJFC 022384, CFMR); Wuzhishan County, Wuzhishan Nature Reserve, on dead, small diameter bamboo, 10 June 2016, He 3926 (BJFC 022428); 30 June 2019, He 5922 (BJFC 030797), He 5932 (BJFC 030807), He 5936 (BJFC

030811) & He 5938 (BJFC 030813); Lingshui County, Diaoluoshan Nature Reserve, on dead, small diameter bamboo, 2 July 2019, He 5981 (BJFC 030857); 5 July 2019, He 6054 (BJFC 030930), He 6061 (BJFC 030937) & He 6063 (BJFC 030939); on fallen angiosperm branch, 5 July 2019, He 6038 (BJFC 030914). Thailand, Chiang Rai, Doi Pui, on rotten bamboo, 23 July 2016, He 4080 (BJFC 023521), He 4083 (BJFC 023524) & He 4094 (BJFC 023535, CFMR).

Distribution - China and Thailand.

Notes - *Phlebiopsis cylindrospora* ([Figure 5](#)) is characterized by pale-colored, smooth hymenophore that turns purple in KOH, a monomitic hyphal system with generative hyphae encrusted with yellow, resinous granules, small subfusiform lamprocystidia, cylindrical basidiospores, and habit on bamboo and woody angiosperms. It is similar to *P. punjabensis* that also has a pale-colored, smooth hymenophore and short lamprocystidia, but the latter species does not react with KOH and develops longer basidia (14–26 μm long), and slightly larger basidiospores (5.3–8.5 \times 2.5–4 μm , [Kaur et al., 2015](#)). *Phlebiopsis albescens* differs from *P. cylindrospora* by its white hymenophore that is unchanged in KOH and distinctly smaller basidiospores (3.5–5 \times 2–2.2 μm). The hymenophore in *P. friesii* (Lév.) Spirin & Miettinen turns purple in KOH also but is distinct from *P. cylindrospora* by having effused-reflexed basidiomata, a pseudodimitic hyphal system, and larger lamprocystidia, up to 80 \times 20 μm ([Hjortstam and Ryvarden, 1990](#)).

Although the phylogenetic trees ([Figures 1](#) , [2](#)) show that *P. cylindrospora* and *P. pilatii* are closely related, the latter species is distinct morphologically

for it lacks lamprocystidia and develops finely branched dendrohyphidia and larger basidiospores, 8–10 × 4–4.5 μm ([Parmasto, 1965](#) ; [Larsen and Gilberston, 1977](#) ; [Duhem and Michel, 2009](#)).

FIGURE 5

Phlebiopsis cylindrospora (from the holotype He 5984; scale bars: A = 1 cm, B–E = 10 μm). (A) Basidiomata; (B) basidiospores; (C) basidia and basidiole; (D) lamprocystidia; (E) hyphae from subiculum.

***Phlebiopsis magnicystidiata* Y. N. Zhao & S. H. He, sp. nov.**

MycoBank: MB836026

Type – China, Hunan Province, Guzhang County, Gaowangjie Nature Reserve, on dead angiosperm branch, 4 August 2018, He 5648 (BJFC 026710, holotype; isotype in BJM).

Etymology – Refers to the large lamprocystidia.

Fruiting body – Basidiomata annual, resupinate, widely effused, closely adnate, inseparable from substrate, ceraceous to coriaceous, up to 15 cm long, 5 cm wide, up to 400 μm thick in section. Hymenophore smooth to slightly odontoid with scattered tubercles, pruinose from projecting cystidia, grayish orange [6B(3–5)], brownish orange [6C(3–5)] to light brown [6D(4–6)], unchanged in KOH, sometimes sparsely and deeply cracked with age; margin thinning out, indistinct, concolorous with hymenophore. Context white.

Microscopic structures - Hyphal system monomitic; generative hyphae simple-septate. Subiculum indistinct to absent. Subhymenium thickening, well-developed; hyphae colorless, thin- to slightly thick-walled, frequently septate, slightly agglutinated, vertically arranged, 2-4.5 μm in diam. Lamprocystidia numerous, fusiform to subulate, colorless, thick-walled, heavily encrusted with crystals, embedded or projecting beyond hymenium up to 40 μm , with a basal simple septum, apex subacute, 40-80 \times (7-) 9-13 (-15) μm (without encrustations). Basidia clavate, colorless, thin-walled, with a basal simple septum and four sterigmata, 20-30 \times 5-6 μm ; basidioles numerous, similar to basidia but slightly smaller. Basidiospores broadly ellipsoid to subglobose, colorless, thin-walled, smooth, IKI-, CB-, 4.5-6.5 (-6.8) \times (3.5-) 3.8-4.8 μm , $L = 5.6 \mu\text{m}$, $W = 4.3 \mu\text{m}$, $Q = 1.3-1.4$ ($n = 60/2$).

Additional specimens examined - China, Yunnan Province, Mengla County, Wangtianshu Forest Park, on fallen angiosperm branch, 19 July 2014, He 20140719-18 (BJFC 019145); Taiwan Province, Taichung, Tunghai University, on dead branch of *Cassia siamea*, 5 August 1989, Wu 890805-1 (TNM F0022186).

Distribution - Hunan, Yunnan, and Taiwan Provinces in southern China.

Notes - *Phlebiopsis magnicystidiata* ([Figure 6](#)) is characterized by large lamprocystidia and broadly ellipsoid to subglobose basidiospores. It is morphologically similar to and phylogenetically closely related to *P.*

flavidoalba (Cooke) Hjortstam ([Figures 1](#) , [2](#)) that has smooth

hymenophore, slightly longer ellipsoid basidiospores (6-7.5 μm long) and a

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distribution in North and South America ([Burdvall, 1985](#) ; [Gilbertson and Blackwell, 1985](#)). *Phlebiopsis gigantea* and *P. magnicystidiata* have similar lamprocystidia but the former differs in its well-developed subiculum, narrowly ellipsoid basidiospores, $5-7 \times 2.5-3.5 \mu\text{m}$, and often occurs on gymnospermous wood in the North Hemisphere ([Eriksson et al., 1981](#) ; [Bernicchia and Gorjón, 2010](#)). Except for developing a distinct subiculum, *P. darjeelingensis* and *P. magnicystidiata* have similar sized lamprocystidia, basidia, and basidiospores ([Dhingra, 1987](#)). Reports of *P. flavidoalba* from India ([Rattan, 1977](#)) and Taiwan ([Wu, 1990](#)) need to be confirmed for they may be *P. magnicystidiata* instead.

FIGURE 6

Phlebiopsis magnicystidiata (A from He 20140719-18, B-E from the holotype He 5648; scale bars: A = 1 cm, B-E = 10 μm). (A) Basidiomata; (B) basidiospores; (C) basidia and basidiole; (D) lamprocystidia; (E) hyphae from subiculum.

***Phlebiopsis membranacea* Y. N. Zhao & S. H. He, sp. nov.**

MycoBank: MB836027

Type – China, Hainan Province, Qiongzong County, Limushan Nature Reserve, on dead, small diameter bamboo, 8 June 2016, He 3849 (BJFC 022351, holotype; isotype in BJM).

Etymology – Refers to the membranaceous basidiomata.

Fruiting body - Basidiomata annual, resupinate, widely effused, adnate, separable from substrate, membranaceous, up to 20 cm long, 5 cm wide, up to 250 μm thick in section. Hymenophore smooth, orange white (6A2), orange gray (6B2), grayish orange [6B(3-5)] to brownish orange [6C(3-5)], unchanged in KOH, sometimes sparsely and finely cracked with age; margin thinning out, fimbriate, concolorous with hymenophore. Context gray.

Microscopic structures - Hyphal system pseudodimitic; generative hyphae simple-septate. Subiculum well-developed, a non-agglutinated, loosely interwoven tissue; skeletocystidia abundant, fusiform to clavate, brown, thick-walled, smooth, with an acute or obtuse apex, embedded, (30-) 40-70 \times 8-15 μm ; hyphae colorless, moderately to distinctly thick-walled, smooth, rigid, frequently branched at right angles, frequently septate, 3-5 μm in diam. Subhymenium thin; hyphae colorless, thin-walled, smooth, somewhat agglutinated, interwoven, 2-4.5 μm in diam. Hymenial cystidia scattered, similar to skeletocystidia in shape and size but with paler, thinner walls, and sparse encrustations at apex. Basidia clavate, colorless, thin-walled, with a basal simple septum and four sterigmata, 15-22 \times 4-5 μm ; basidioles numerous, similar to basidia but slightly smaller. Basidiospores oblong ellipsoid to subcylindrical, colorless, thin-walled, smooth, IKI-, CB-, 4. 2-6. 2 (-6. 8) \times 2-3 (-3. 2) μm , $L = 5.5 \mu\text{m}$, $W = 2.6 \mu\text{m}$, $Q = 1.9-2.3$ ($n = 90/3$).

Additional specimens examined - China, Hainan Province, Qiongzong County, Limushan Nature Reserve, on dead, small diameter bamboo, 8 June 2016, He 3842 (BJFC 022344); Lingshui County, Diaoluoshan Nature Reserve, on dead, small diameter bamboo, 5 July 2019, He 6062 (BJFC 030938).

Distribution – Hainan Province, southern tropical China.

Notes – *Phlebiopsis membranacea* ([Figure 7](#)) is characterized by membranaceous basidiomata with well-developed subicula, brown, smooth, thick-walled skeletocystidia, without lamprocystidia, and habit on bamboo in tropical China. Like *P. membranacea* , *Hjortstamia novae-granatae* (A. L. Welden) Hjortstam & Ryvarde, from Columbia, grows on bamboo but its brown, smooth skeletocystidia are tubular in shape and its basidiospores are larger, 5.5–7 × 3–4 μm ([Hjortstam and Ryvarde, 1990](#)). *Phlebiopsis laxa* (Sheng H. Wu) Miettinen like *P. membranacea* has membranaceous basidiomata and loosely arranged subicular hyphae but differs in having lamprocystidia and larger basidiospores, 8–10 × 4–5 μm ([Wu, 2000](#)). In the phylogenetic trees ([Figures 1](#) , [2](#)), *P. membranacea* is sister to *P. laxa* , though their relationship is not strongly supported.

FIGURE 7

Phlebiopsis membranacea (A from He 3842, B–E from the holotype He 3849; scale bars: A = 1 cm, B–E = 10 μm). (A) Basidiomata; (B) basidiospores; (C) basidia and basidiole; (D) hymenial cystidia; (E) hyphae from subiculum.

***Phlebiopsis sinensis* Y. N. Zhao & S. H. He, sp. nov.**

MycoBank: MB836028

Type – China, Sichuan Province, Wanyuan County, Huaeshan Nature Reserve, on fallen angiosperm branch, 17 July 2013, He 4673 (BJFC 024192, holotype; isotype in BJM).

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Etymology - Refers to the distribution in China.

Fruiting body - Basidiomata annual, resupinate to effused-reflexed with reflexed edges elevated and incurved with age, loosely adnate, easily detached from substrate, coriaceous, first as small patches, later confluent up to 15 cm long, 5 cm wide, up to 300 μm thick in section. Pileus projecting up to 1.5 mm; upper surface gray, slightly sulcate. Hymenophore smooth, brownish orange [6C(3-5)], grayish brown [6(D-F)3] to brown [6E(4-6)], unchanged in KOH, sometimes finely cracked with age; margin thinning out, distinct, white to gray, silky, slightly fimbriate, up to 1 mm wide. Context gray to yellowish brown.

Microscopic structures - Hyphal system pseudodimitic; generative hyphae simple-septate. Tomentum and cortex (a dark line between the tomentum and subiculum) present. Subiculum well-developed, a non-agglutinated tissue; skeletocystidia brown, thick-walled, encrusted at apex, embedded, intermediate forms between skeletocystidia and lamprocystidia observed; hyphae colorless to pale yellow, moderately to distinctly thick-walled, smooth, rarely branched, moderately septate, easily separated, more or less parallel to substrate, 3-6 μm in diam. Subhymenium indistinct.

Lamprocystidia abundant, broadly fusiform to broadly subulate, usually with a long, curved stalk and resembling skeletocystidia, colorless to brown, thick-walled, heavily encrusted, 30-60 \times 8-13 μm , projecting up to 30 μm . Basidia clavate, colorless, thin-walled, with a basal simple septum and four sterigmata, 20-30 \times 4.5-5.5 μm ; basidioles numerous, similar to basidia but slightly smaller. Basidiospores oblong ellipsoid to subcylindrical,

colorless, thin-walled, smooth, IKI-, CB-, (5-) 5. 8-7. 8 (-8) × (2. 2-) 2. 5-3. 5 (-3. 8) μm, $L = 6. 4$ μm, $W = 2. 9$ μm, $Q = 2. 1-2. 4$ ($n = 90/3$).

Additional specimens examined - China, Gansu Province, Pingliang County, Kongtongshan Nature Reserve, on construction wood, 3 August 2015, He 2416 (BJFC 020870, CFMR); Hubei Province, Wufeng County, Houhe Nature Reserve, on dead angiosperm branch, 16 August 2017, He 5081 (BJFC 024599); Hunan Province, Yongshun County, Xiaoxi Nature Reserve, on dead angiosperm branch, 6 August 2018, He 5662 (BJFC 026724); Inner Mongolia, Chifeng, Aohan County, Daheishan Nature Reserve, on fallen *Quercus mongolia* branch, 3 September 2015, Tiezhi Liu et al. (CFSZ 10714), on fallen *Pinus tabuliformis* branch, 19 September 2016, Tiezhi Liu et al. (CFSZ 12436); Jiangxi Province, Ji'an County, Jinggangshan Nature Reserve, on dead *Rhododendron* branch, 11 August 2016, He 4295 (BJFC 023737, CFMR); Liaoning Province, Zhuanghe County, Xianrendong Forest Park, on dead *Quercus* branch, 5 August 2017, He 4665 (BJFC 024184); Shaanxi Province, Foping County, Foping Nature Reserve, on fallen *Betula* branch, 11 September 2013, He 1907 (BJFC 016374); Sichuan Province, Baoxing County, Fengtongzhai Nature Reserve, on fallen angiosperm trunk, 18 September 2012, He 20120918-3 (BJFC 014609).

Distribution - Gansu, Hubei, Hunan, Jiangxi, Liaoning, Shaanxi and Sichuan Provinces and Inner Mongolia Autonomous Region of China.

Notes - *Phlebiopsis sinensis* ([Figure 8](#)) is characterized by effused to effused-reflexed, coriaceous basidiomata with well-developed subicula, brown skeletocystidia, lamprocystidia, and a temperate distribution.

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Submembranaceous-pellicular basidiomata, narrower cystidia (5–8 µm wide), and a tropical distribution distinguish *P. brunneocystidiata* from *P. sinensis* ([Wu, 2004](#)). Both *P. crassa* and *P. sinensis* develop effused-reflexed basidiomata, but the former species has a purple-tinted hymenophore, larger lamprocystidia, 50–120 × 8–20 µm, and a tropical distribution ([Hjortstam and Ryvarden, 1990](#)). Although the ITS tree ([Figure 2](#)) shows that *P. sinensis* and *P. friesii* are sister taxa, *P. friesii* is distinct morphologically with a hymenophore that turns purple in KOH and has a dimitic hyphal system with colorless to yellow skeletal hyphae ([Hjortstam and Ryvarden, 1990](#)).

FIGURE 8

Phlebiopsis sinensis (from He 4673; scale bars: A = 1 cm, B–E = 10 µm). (A) Basidiomata; (B) basidiospores; (C) basidia and basidiole; (D) lamprocystidia; (E) hyphae from subiculum.

***Phaeophlebiopsis mussooriensis* (Priyanka, Dhingra & N. Kaur) Nakasone & S. H. He, comb. nov.**

MycoBank: MB836029

Synonym: *Phlebiopsis mussooriensis* Priyanka, Dhingra & N. Kaur, Mycotaxon 115: 255, 2011.

Notes – This species is characterized by a grayish yellow hymenophore, well-developed subiculum, thin-walled generative hyphae, lamprocystidia, and ellipsoid basidiospores ([Priyanka et al., 2011](#)). As mentioned in the protolog, *P. mussooriensis* is quite similar to *P. himalayensis*, now

Phaeophlebiopsis himalayensis (Dhingra) Zmitr., differing primarily in basidiospore size and color change of hymenophore in KOH. Based on [Priyanka et al.'s 2011](#) description, illustration, and comments, we propose the transfer of *P. mussooriensis* into *Phaeophlebiopsis*.

***Phlebiopsis bambusicola* (Berk. & Broome) Nakasone & S. H. He, comb. nov.**

MycoBank: MB836030

Synonyms: *Corticium bambusicola* Berk. & Broome, Transactions of the Linnaean Society of London 2: 64, 1882. *Peniophora bambusicola* (Berk. & Broome) Sacc., Sylloge Fungorum 6: 647, 1888. *Hjortstamia bambusicola* (Berk. & Broome) Hjortstam & Ryvar den, Synopsis Fungorum 20: 37, 2005.

Notes – This Australian species is known only from the type and is characterized by a grayish brown hymenophore, a dimitic hyphal system, large, brown skeletocystidia, lamprocystidia, narrowly ellipsoid to allantoid basidiospores, and a habit on bamboo ([Hjortstam and Ryvar den, 2005](#)). Although similar to *P. crassa*, *P. bambusicola* has narrower basidiospores, 2.5–3 µm broad and is restricted by host preference and distribution.

***Phlebiopsis dregeana* (Berk.) Nakasone & S. H. He, comb. nov.**

MycoBank: MB836031

Synonyms: *Corticium dregeanum* Berk., London Journal of Botany 5: 3, 1846. *Hymenochaete dregeana* (Berk.) Masee, Botanical Journal of the Linnean Society 27: 114, 1890. *Terana dregeana* (Berk.) Kuntze, Revisio generum plantarum 2: 872, 1891. *Lopharia dregeana* (Berk.) P. H. B. Talbot, Bothalia

6: 57, 1951. *Irpex dregeanus* (Berk.) P. H. B. Talbot, *Bothalia* 6: 344, 1954.
Australohydnum dregeanum (Berk.) Hjortstam & Ryvar den, *Synopsis Fungorum* 4: 61, 1990.

Notes – This is a poorly understood species that has been interpreted differently by various researchers. We take a narrow concept of *P. dreageana* based on studies of the type specimen and specimens restricted to Africa as described and illustrated by [Massee \(1891\)](#), [Talbot \(1951\)](#), [Reid \(1975\)](#), and [Hjortstam and Ryvar den \(1990\)](#). The ellipsoid basidiospores based on these studies are approximately 6.5–8 × 4–5 µm in size. Note that the cylindrical basidiospores illustrated by [Reid \(1975\)](#) are questionable for [Hjortstam \(1989\)](#) noted that basidia and spores were not observed in the type. [Hjortstam and Ryvar den \(1990\)](#) took a broad interpretation of *A. dreageanum* when they placed *Hydnum griseofuscescens* Reichardt from Australia and *Irpex vellereus* Berk. & Broome from Sri Lanka in synonymy; see below for further discussion of these two taxa. Although *A. dreageanum* has since been reported from India ([De, 1998](#), as *Oxyporus vellereus*), South Korea ([Lim, 2001](#) ; [Lim and Jung, 2003](#)), New Zealand ([Buchanan and Ryvar den, 2000](#)), Portugal ([Melo and Hjortstam, 2002](#)), Israel ([Tura et al., 2011](#)), and Italy ([Saitta et al., 2014](#)), the basidiospore size, when given, is significantly smaller than the African collections.

Sequences from authentic specimens of the species are not available at present, but ITS sequences labeled “ *Australohydnum dregeanum* ” in GenBank, from United States, Korea and Sri Lanka, formed a strongly

supported lineage within *Phlebiopsis* ([Figure 2](#)). The identity of the taxa in this lineage needs further study.

***Phlebiopsis griseofuscescens* (Reichardt) Nakasone & S. H. He, comb. nov.**

MycoBank: MB836032

Synonyms: *Hydnum griseofuscescens* Reichardt, Verhandlungen der Zoologisch-Botanischen Gesellschaft Wien 16: 374, 1866. *Irpex griseofuscescens* (Reichardt) D. A. Reid, Kew Bulletin 17 (2): 273, 1963. *Australohydnum griseofuscescens* (Reichardt) Jülich, Persoonia 10 (1): 138, 1978. *Irpex vellereus* Berk. & Broome, Journal of the Linnean Society. Botany 14: 61, 1875. *Xylodon vellereus* (Berk. & Broome) Kuntze, Revisio generum plantarum 3 (2): 541, 1898. *Hirschioporus vellereus* (Berk. & Broome) Teng, Zhong Guo De Zhen Jun [Fungi of China]: 761, 1963. *Oxyporus vellereus* (Berk. & Broome) A. Roy & A. B. De, J. Mycopathol. Res.: 41, 1998. *Phlebiopsis lacerata* C. L. Zhao, Phytotaxa 440 (4): 274, 2020. *Hydnochaete philippinensis* Lloyd (as “ *philippensis* ”), Mycological Writings 7 (67): 1154, 1922. *Trichaptum venustum* (Berk.) G. Cunn., Bulletin of the New Zealand Department of Scientific and Industrial Research 164: 97, 1965.

Specimens examined – Sri Lanka, Western Province, Ingiriya, Dombagaskanda Forest Reserve, on fallen angiosperm branch, 27 February 2019, He 5734 (BJFC 030601). China, Sichuan Province, Miyi County, Haita Village, on fallen *Quercus* trunk, 13 September 2015, Cui 12629 (BJFC 028408) & Cui 12637 (BJFC 028416).

Notes - *Hydnum griseofuscescens* was described from Australia and is the type of *Australohydnum* ([Jülich, 1978](#)). It is characterized by resupinate to effused-reflexed basidiomata with a hydroid, purplish brown hymenophore, a pseudodimitic hyphal system with simple-septate, colorless, generative hyphae, 4–9 µm broad, encrusted hymenial cystidia with colorless walls, and small ellipsoid basidiospores, 4–6 × 2.5–3 µm ([Reid, 1956](#) as *Irpex vellerus* , [Jülich, 1978](#)). We follow [Reid \(1956, 1963\)](#) who determined that *H. griseofuscescens* and *I. vellerus* , described from Sri Lanka, were synonyms after studying the types of both species. [Reid \(1967\)](#) also reported that *T. venustum* sensu [Cunningham \(1965\)](#) is *H. griseofuscescens* . Based on morphological studies and sequence analyses, we determined that *P. lacerata* described from southern China ([Xu et al., 2020](#)) is conspecific with *P. griseofuscescens* .

[Gilbertson and Adaskaveg \(1993\)](#) described and illustrated *I. griseofuscescens* from Hawaii, but this species lacks encrusted hymenial cystidia and has small basidiospores, 4–4.5 × 2–2.5 µm. Similarly, [De's \(1998\)](#) description of *O. vellerus* from India appears to represent a different species with a monomitic hyphal system of colorless to pale brown hyphae and cylindrical basidiospores, 5.2–7 × 2–3 µm. One of the specimens cited, VBMN 80451, is also at CBS, CBS 515.92, and its ITS sequence is available from GenBank (AF479670) as “ *Irpex vellerus* . ” This sequence was included in [Lim and Jung \(2003\)](#) and [Figure 2](#) , herein, where it is on a long branch, sister to *P. griseofuscescens* .

***Phlebiopsis novae-granatae* (A. L. Welden) Nakasone & S. H. He, comb. nov.**

MycoBank: MB836033

Synonyms: *Lopharia novae-granatae* A. L. Welden [as ‘*nova-granata*’], *Mycologia* 67: 540, 1975. *Porostereum novae-granatum* (A. L. Welden) Hjortstam & Ryvarden [as ‘*nova-granatum*’], *Synopsis Fungorum* 4: 41, 1990. *Phanerochaete novae-granatae* (A. L. Welden) Sheng H. Wu [as ‘*nova-granata*’], *Mycotaxon* 88: 375, 2003. *Hjortstamia novae-granatae* (A. L. Welden) Hjortstam & Ryvarden [as ‘*nova-granata*’], *Synopsis Fungorum* 25: 19, 2008.

Notes – Reported from Colombia on bamboo, this species is characterized by a pale brown hymenophore and smooth skeletocystidia but lacking lamprocystidia ([Welden, 1975](#) ; [Hjortstam and Ryvarden, 1990](#)). Because of its morphological similarity to *P. crassa* , the transfer of *P. novae-granatae* is proposed.

***Phlebiopsis crassa* Species Complex**

Specimens examined – *Phlebiopsis crassa* group A: Vietnam, Ho Chi Minh City, the Botanical Garden Padua, on fallen angiosperm trunk, 13 October 2017, He 5205 (BJFC 024723). Sri Lanka, Central Province, Kandy, Peradeniya Botanic Garden, on fallen angiosperm branch, 2 March 2019, He 5763 (BJFC 030630). China, Guangdong Province, Renhua County, Danxiashan Nature Reserve, on fallen angiosperm trunk, 4 June 2019, He 5855 (BJFC 030730, [Figure 9A](#)); Yunnan Province, Qiubei County, Puzhehei Nature Reserve, 17 November 2019, He 6300 (BJFC, [Figure 9C](#)), He 6301

(BJFC, [Figure 9D](#)), He 6303 (BJFC, [Figure 9B](#)) & He 6304 (BJFC); Ximeng County, Mengsuolongtan Forest Park, on fallen angiosperm branch, 15 April 2005, Wu 0504-22 (TNM F0018719).

FIGURE 9

Basidiomata of *Phlebiopsis crassa* s. l. (A–D : *P. crassa* group A, E–H : *P. crassa* group B; scale bars: A–H = 1 cm). (A) He 5855; (B) He 6303; (C) He 6300; (D) He 6301; (E) He 6266; (F) He 5866; (G, H) He 3349.

Phlebiopsis crassa group B: China, Guangdong Province, Renhua County, Danxiashan Nature Reserve, on fallen angiosperm branch, 4 June 2019, He 5866 (BJFC 030741, [Figure 9F](#)); Yunnan Province, Lushui County, Gaoligongshan Nature Reserve, on fallen angiosperm trunk, 29 November 2015, He 3349 (BJFC 021744, [Figures 9G, H](#)); Maguan County, Gulinqing Nature Reserve, on fallen angiosperm branch, 14 November 2019, He 6266 (BJFC, [Figure 9E](#)).

Phlebiopsis crassa group C: United States, Arizona, Pima County, Santa Rita Experimental Range, on *Fouquieria splendens*, 31 July 1976, K. K. Nakasone, KKN-86-sp (CFMR); Illinois, Coles County, Fox Ridge State Park, on hardwood, 24 September 1990, A. S. Methven, FP-1024996-sp (CFMR); Mississippi, Harrison County, Harrison Experimental Forest, on *Quercus* sp., 26 March 1976, H. H. Burdsall, Jr., HHB-8834-sp (CFMR).

Notes – Our phylogenetic analyses showed that samples of *P. crassa* group A from Vietnam, Sri Lanka and southern China formed a distinct lineage and

represent *P. crassa* s. s. , for the type was described from Vietnam ([Figures 1, 2](#)). Collections from southern China and Japan, group B, and the United States, group C, clustered into two lineages in the ITS tree ([Figure 2](#)). All three lineages of *P. crassa* are morphologically similar, however. Unraveling this species complex is beyond the scope of this study, involving a number of presumed synonyms of *P. crassa* ; see [Lentz \(1955\)](#) and Burdsall (1985).

***Phlebiopsis darjeelingensis* Dhingra, Nova Hedwigia 44: 222, 1987**

Synonyms: *Phanerochaete lamprocystidiata* Sheng. H. Wu, Mycotaxon 90: 426, 2004. *Phlebiopsis lamprocystidiata* (Sheng H. Wu) Sheng H. Wu & Hallenb., Fungal Diversity 42: 116, 2010.

Notes – Because *P. darjeelingensis* , from India, and *P. lamprocystidiata* , from Taiwan, are nearly identical in morphology — basidiomata ceraceous when fresh then corneous when dried, well-developed subiculum of compactly packed, colorless hyphae, and cystidia and basidiospores of similar shape and size ([Dhingra, 1987](#) ; [Wu, 2004](#)), we consider *P. lamprocystidiata* to be a later synonym of *P. darjeelingensis* . [Zmitrovich \(2018\)](#) transferred *Phlebiopsis lamprocystidiata* to *Phaeophlebiopsis* based on morphology, our phylogenetic analyses show that it belongs to *Phlebiopsis* s. s. , however.

Discussion

The generic limits of *Phlebiopsis* has expanded over the last 40 years since its introduction in 1978 to include significant morphological range in basidiomata habit and texture and hymenophore configuration with the aid of molecular phylogenetic methods ([Floudas and Hibbett, 2015](#) ; [Miettinen](#) <https://assignbuster.com/global-phylogeny-and-taxonomy-of-the-wood-decaying-fungal-genus-phlebiopsis-polyporales-basidiomycota/>

[et al., 2016](#) ; [Zhao et al., 2018](#) ; [Xavier de Lima et al., 2020](#) ; [Xu et al., 2020](#)). In this study, we emphasized sampling of *Phlebiopsis* taxa, and our overall results confirm those of [Floudas and Hibbett \(2015\)](#) , [Miettinen et al. \(2016\)](#) , and [Chen et al. \(2018b\)](#) . In [Figures 1](#) , [2](#) , *Phlebiopsis* , including the types of *Australohydnum* , *P. griseofuscescens* and *Hjortstamia* , *P. friesii* , formed a well-supported clade in the Phanerochaetaceae and is closely related to *Phaeophlebiopsis* , *Hapalopilus* and *Rhizochaete* . The genera *Phlebiopsis* and *Australohydnum* were published simultaneously ([Jülich, 1978](#)) but the former is favored to avoid unnecessary name changes. So, we propose that *Australohydnum* is a synonym of *Phlebiopsis* . Twenty-four lineages were resolved in the ITS tree of *Phlebiopsis* , among which 18 are accepted species, including the *P. crassa* species complex and six new species described herein. Further study is required to identify the taxa named *P. cf. dregeana* , *Irpex vellerus* , *Phlebiopsis* sp. FP-102937 and *Phlebiopsis* sp. ECS-1971.

Among the 24 names of *Phlebiopsis* in Index Fungorum (accessed on 21 January 2021), we accept 17 taxa in *Phlebiopsis s. s.* , including 11 that are supported by molecular data. Five taxa, *P. himalayensis* Dhingra, *P. mussooriensis* , *P. peniophoroides* Gilb. & Adask., *P. ravenelii* (Cooke) Hjortstam, and *P. roumegueri* (Bres.) Jülich & Stalpers were transferred to *Phaeophlebiopsis* based on morphology and sequence data. *Phlebiopsis lacerata* and *P. lamprocystidiata* are synonyms of *P. griseofuscescens* and *P. darjeelingensis* , respectively, as discussed above. Thus, 27 species of *Phlebiopsis* worldwide are accepted, including the six new species and four new combinations reported herein. An emended description of *Phlebiopsis*

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and an identification key to all species in the genus worldwide are presented below.

***Phlebiopsis* (Jülich) Nakasone & S. H. He, Emended**

Synonyms: *Castanoporus* [Ryvarden, 1991](#) Synopsis Fungorum 5: 121, 1991.

Hjortstamia [Boidin and Gilles, 2003](#) Bulletin de la Société Mycologique de France 118 (2): 99, 2003. *Australohydnum* Jülich, Persoonia 10 (1): 138, 1978.

Description: Basidiomata annual, resupinate, effused, effused-reflexed or pileate, ceraceous, membranaceous to coriaceous. Pilei, when present, tomentose, gray to brown. Hymenophore smooth, tuberculate, odontoid, hydroid to poroid, white, gray, grayish brown, purplish brown or brown, turning purple in KOH in two species. Hyphal system monomitric or dimitic; generative hyphae simple-septate, colorless or rarely pale brown, in dimitic species with skeletal or, in one species, micro-binding hyphae. Subiculum absent to well-developed, colorless, brown, agglutinated or not, compact to loosely interwoven. Skeletocystidia absent or present, colorless or brown, distinctly thick-walled, smooth or encrusted. Hymenial cystidia or lamprocystidia typically present, colorless or light brown, thick-walled, usually encrusted. Dendrohyphidia present in one species, colorless, thin-walled, smooth, branched. Basidia clavate or subcylindrical, with four sterigmata and a basal simple septum. Basidiospores cylindrical, ellipsoid, broadly ellipsoid or subglobose, colorless, thin-walled, smooth, negative in Melzer's reagent, acyanophilous.

Type species: *Phlebiopsis gigantea* (Fr.) Jülich

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Notes – The terminology relating to the cystidia observed in *Phlebiopsis* species is varied in the literature and thus confusing. There are up to three kinds of cystidia, but intermediate forms can develop to blur their distinctiveness. Lamprocystidia are found in most species of *Phlebiopsis* in the hymenium, often projecting, and may become embedded as the basidiomata thickens. They are typically conical or subfusiform with thick walls that are lightly to heavily encrusted in the upper half or apex. Skeletocystidia are found in dimitic or pseudodimitic species in which thick-walled hyphae in the subiculum curve toward the hymenium but remain embedded in the subiculum or subhymenium. The terminal ends may or may not be differentiated and usually lack encrustations. Hymenial cystidia are those structures that are similar to skeletocystidia but terminate in the hymenium and may be encrusted. In other cases, they are formed in the subhymenium and are smaller than lamprocystidia and not conical or heavily encrusted.

Key to 27 *Phlebiopsis* Species

1. Hymenophore poroid, irpicoid or hydroid..... 2
1. Hymenophore smooth, tuberculate or odontoid..... 4
2. Basidiomata resupinate; hymenophore poroid to irpicoid; on gymnosperms..... *P. castanea*
2. Basidiomata effused-reflexed; hymenophore hydroid; on angiosperms..... 3
3. Basidiospores 6. 5–8 × 4–5 μm..... *P. dregeana*

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3. Basidiospores 4. 5–6 × 2. 5–3 μm..... *P. griseofuscescens*
4. Dendrohyphidia present..... *P. pilatii*
4. Dendrohyphidia absent..... 5
5. Hyphal system pseudodimitic or dimitic..... 6
5. Hyphal system monomitic..... 13
6. Hymenophore turning purple in KOH..... *P. friesii*
6. Hymenophore unchanged in KOH..... 7
7. Basidiomata with well-developed pilei; skeletocystidia
absent..... *P. papyrina*
7. Basidiomata resupinate to effused-reflexed; skeletocystidia
present..... 8
8. Hymenophore without purple tints..... 9
8. Hymenophore with purple tint..... 12
9. Lamprocystidia none; basidiospores ≤ 6 μm
long..... *P. membranacea*
9. Lamprocystidia present; basidiospores ≥ 6 μm long..... 10
10. Basidiomata resupinate to effused-reflexed; from temperate
China..... *P. sinensis*

10. Basidiomata strictly resupinate; from tropical-subtropical Asia or Australia..... 11
11. Basidiospores 6–7 × 2. 5–3 μm; on bamboo; from Australia..... *P. bambusicola*
11. Basidiospores 6. 5–7. 5 × 3–3. 6 μm; on angiospermous wood; from Sri Lanka..... *P. brunnea*
12. Lamprocystidia brown to dark brown; South American species..... *P. amethystea*
12. Lamprocystidia colorless to pale brown; North American or Asian species..... *P. crassa s. l.*
13. Lamprocystidia none; skeletocystidia or hymenial cystidia present..... 14
13. Lamprocystidia present; skeletocystidia absent..... 15
14. Basidiospores 5. 5–7 × 3–4 μm; on bamboo; from Colombia..... *P. novae-granatae*
14. Basidiospores 3. 7–5. 5 × 2. 5–3. 3 μm; on hardwood; from New Zealand..... *P. afibulata*
15. Basidiospores > 8 μm long, > 4 μm broad..... *P. laxa*
15. Basidiospores < 8 μm long, <4 μm broad..... 16
16. Lamprocystidia small, generally <40 μm long..... 17

16. Lamprocystidia large, generally > 40 μm long..... 20
17. Hymenophore purple in KOH..... *P. cylindrospora*
17. Hymenophore unchanged in KOH..... 18
18. Basidiospores broadly ellipsoid, 3.5-4.5 \times 2.5-3.5 μm , $Q = 1.3$ *P. yunnanensis*
18. Basidiospores narrowly ellipsoid to cylindrical..... 19
19. Basidiospores 3.5-5 \times 2-2.2 μm *P. albescens*
19. Basidiospores 5.3-8.5 \times 2.5-4 μm *P. punjabensis*
20. Lamprocystidia brown; on Pandanaceae; from Taiwan..... *P. brunneocystidiata*
20. Lamprocystidia colorless; on other plants; from various locations..... 21
21. Subiculum indistinct to absent..... 22
21. Subiculum distinct to well-developed..... 24
22. Basidia with two sterigmata..... *P. bicornis*
22. Basidia with four sterigmata..... 23
23. Basidiospores 5.5-7.5 \times 3.5-4.5 μm ; from North and South America..... *P. flavidoalba*

23. Basidiospores 4.5–6.5 × 3.8–4.8 μm; from Asia..... *P. magnicystidiata*
24. Basidiospores narrowly ellipsoid to ellipsoid, ≤ 3 μm broad..... 25
24. Basidiospores broadly ellipsoid, ≥4 μm broad..... 26
25. Hymenophore smooth, pale orange to rosy; lamprocystidia 40–50 × 6–7 μm; basidiospores < 2.5 μm wide; from Argentina..... *P. erubescens*
25. Hymenophore smooth to tuberculate, pale white to gray; lamprocystidia 60–90 × 10–20 μm; basidiospores ≥ 2.5 μm wide; from Northern Hemisphere..... *P. gigantea*
26. Lamprocystidia < 10 μm wide; from South America..... *P. galochroa*
26. Lamprocystidia > 10 μm wide; from Asia..... *P. darjeelingensis*

Data Availability Statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/supplementary material.

Author Contributions

S-HH designed the research, collected most of the specimens, and wrote the text. Y-NZ performed the phylogenetic analyses and did most of the measurement, descriptions and illustrations. KN loaned and examined type specimens of some related species, and revised language of the text. C-CC provided with some specimens and sequences. S-LL helped in field trips and species illustrations. KLWK and H-XM helped in field trips and collected some specimens. M-RH collected some specimens and helped in specimen preservation. All authors contributed to the article and approved the submitted version.

Funding

Financial support was provided by the National Natural Science Foundation of China (Grant Nos. 31870011 and 31750001).

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Acknowledgments

We would like to express our deep appreciation to Profs. Sheng-Hua Wu (National Museum of Natural Science, Taiwan, China), Tie-Zhi Liu (Chifeng University, Inner Mongolia, China), and Bao-Kai Cui (Beijing Forestry University, Beijing, China) for allowing us to study their specimens.

Abbreviations

ITS, internal transcribed spacer; nrLSU, nuclear ribosomal large subunit; BJFC, herbarium of Beijing Forestry University, Beijing, China; CFMR, Centre for Forest Mycology Research, U. S. Forest Service, Madison, WI, United States; TNM, National Museum of Natural Science, Taichung, Taiwan, China; KOH, 2% (w/v) potassium hydroxide; IKI, Melzer's reagent; CB, cotton blue; IKI-, neither amyloid nor dextrinoid; CB-, acyanophilous; L, mean spore length; W, mean spore width; Q, L/W ratio, n (a/b), number of spores (a) measured from number of specimens (b); CTAB, cetyltrimethylammonium bromide; DNA, deoxyribonucleic acid; PCR, polymerase chain reaction; MP, maximum parsimony; ML, maximum likelihood; BI, Bayesian inference; TBR, tree-bisection reconnection; BPP, Bayesian posterior probability.

Footnotes

1. <http://www.indexfungorum.org/>
2. <http://www.biology.duke.edu/fungi/mycolab/primers.htm>
3. <https://www.ncbi.nlm.nih.gov/>
4. <http://mafft.cbrc.jp/alignment/server/>
5. <http://treebase.org/treebase-web/home.html>

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