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Phylogeny and taxonomy of *Ceriporia* and other related taxa and description of three new species

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ABSTRACT

Species of *Ceriporia* (Irpicaceae, Basidiomycota) are saprotrophs or endophytes in forest ecosystems. To evaluate the taxonomy and generic relationships of *Ceriporia* and other related taxa, we used morphology and multigene phylogenetic analyses based on sequence data from nuc rDNA internal transcribed spacer ITS1-5.8S-ITS2 (ITS) region, nuc 28S rDNA (28S), and RNA polymerase II largest subunit (*rpb1*). Our results show that *Ceriporia* sensu lato is polyphyletic and distributed across multiple clades in the Irpicaceae, Phanerochaetaceae, and Meruliaceae. Some species previously considered in *Ceriporia* are now recovered in *Meruliopsis*, resulting in four new combinations: *M. albomellea*, *M. crassitunicata*, *M. nanlingensis*, and *M. pseudocystidiata*. Two new species of *Meruliopsis* are described: *M. leptocystidiata* from northeast China and South Korea and *M. parvispora* from Taiwan. *Ceriporia arbuscula* is described as a new species from Taiwan. *Ceriporia mellita* and *Meruliopsis nanlingensis* are newly recorded from Japan and Taiwan, and *M. taxicola* is recorded from Taiwan for the first time.

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Leptoporus; phlebioid clade; Polyporales; systematics; wood-inhabiting fungi; 7 new taxa

INTRODUCTION

The polypore genus *Ceriporia* Donk belongs to the Irpicaceae Spirin & Zmitr. of the Polyporales Gäum. (Justo et al. 2017), with *Polyporus viridans* Berk. & Broome as its type species. Most species of *Ceriporia* are saprotrophs that cause white rot on well-decayed wood (Ryvarden and Melo 2017), but some species may be endophytic (Martin et al. 2015), thus playing important roles in the maintenance of forest ecosystems. Morphologically, *Ceriporia* is generally characterized by resupinate or rarely reflexed basidiocarps with variable colors, a monomitic hyphal system (a few species are dimitic), generative hyphae with simple septa or with rare clamps, presence or absence of cystidia, and thin-walled, ellipsoid, cylindrical, or allantoid basidiospores (Gilbertson and Ryvarden 1986; Pieri and Rivoire 1997; Jia et al. 2014; Ryvarden and Melo 2017).

Ceriporia encompasses around 80 taxa (Index Fungorum 2019), many of which were described worldwide during the past two decades from East Asia (Dai et al. 2002; Suhara et al. 2003; Jia and Cui 2011a, 2012; Jia et al. 2014; Miettinen et al. 2016; Yuan et al. 2017), Europe (Bernicchia and Niemelä 1998; Miettinen et al. 2016;

Spirin et al. 2016), North America (Miettinen et al. 2016; Spirin et al. 2016), Oceania (Cunningham 1947; Gilbertson and Hemmes 2004), and South America (Lindblad and Ryvarden 1999; Rajchenberg 2000; Ryvarden and Iturriaga 2003; Aime et al. 2007; Læssøe and Ryvarden 2010; Mata and Ryvarden 2010; Gomes-Silva et al. 2012; Soares et al. 2014; Miettinen et al. 2016).

Despite high species diversity, only a few *Ceriporia* species have been incorporated into phylogenetic studies (Kim and Jung 1999; Jia et al. 2014; Miettinen et al. 2016; Spirin et al. 2016; Yuan et al. 2017). Thus, the limits of *Ceriporia* and its phylogenetic relationships with other taxa remain unresolved to date. Kim and Jung (1999) reported the monophyly of *Ceriporia* based on five sequences of mitochondrial small subunit rDNA (mt SSU). By contrast, recent studies based on sequences from the nuc rDNA internal transcribed spacer ITS1-5.8S-ITS2 (ITS) region and nuc 28S rDNA (28S) have suggested that *Ceriporia* sensu lato is a polyphyletic group (Jia et al. 2014; Miettinen et al. 2016; Yuan et al. 2017).

Most *Ceriporia* species clustered with its type species in the Irpicaceae, but a few species also appeared in the Meruliaceae Rea or the Phanerochaetaceae Jülich (Floudas and Hibbett 2015; Miettinen et al. 2016).

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Miettinen et al. (2016) revised the genus concept of those species in Phanerochaetaceae, resulting in two segregated genera: *Phanerina* Miettinen and *Riopa* D.A. Reid. In addition, the amended concept of the genus *Phanerochaete* P. Karst. contains *Ceriporia inflata* B.S. Jia & B.K. Cui (Miettinen et al. 2016).

Recently, Justo et al. (2017) established a classification framework for the Polyporales based on sequences from ITS, 28S, and the gene encoding the RNA polymerase II largest subunit (*rpb1*). To better understand phylogenetic relationships and limits of *Ceriporia* and other related taxa, we expanded the molecular and taxonomic sampling, including new sequences of three loci (ITS, 28S, and *rpb1*) and new samples from East Asia. As a result, three new species are described and illustrated.

MATERIALS AND METHODS

Morphological studies.—All studied specimens were deposited at the herbarium of National Museum of Natural Science (TNM), Taichung, Taiwan. Two specimens collected from South Korea were deposited at the Seoul National University Fungus Collection (SFC), Seoul, South Korea. Abbreviations for herbaria followed Index Herbariorum (<http://sweetgum.nybg.org/ih/>). Free-hand thin sections of basidiocarps were mounted in 5% potassium hydroxide with 1% phloxine for observation and measurements, Melzer's reagent for checking amyloidity and dextrinoidity, and cotton blue (CB; Fluka 61335; Buchs SG, Switzerland) for determining cyanophily using a Leica DM2500 (Leica, Wetzlar, Germany) microscope at a magnification of up to 1000 \times . The following abbreviations are used: L = mean basidiospore length (arithmetic average for all basidiospores), W = mean basidiospore width (arithmetic average for all basidiospores), Q = variation in the L/W ratios between the specimens studied, n = number of measured basidiospores.

DNA extraction, PCR, and sequencing.—Dried specimens or mycelia grown on malt extract agar were broken into small pieces using liquid nitrogen and a TissueLyser II (Qiagen, Hilden, Germany). DNA was extracted using the Plant Genomic DNA Extraction Miniprep System (Viogene-Biotek, New Taipei, Taiwan) according to the manufacturer's instruction or a modified cetyltrimethylammonium bromide extraction protocol (Rogers and Bendich 1994). The ITS region was amplified using primers ITS1 or ITS1F and ITS4 or ITS4B (White et al. 1990; Gardes and Bruns 1993), 28S using LR0R and LR5 (Vilgalys and Hester 1990), and *rpb1* using RPB1-Af (Stiller and Hall 1997), RPB1-Int2f or RPB1-Int2.1f (Frøslev

et al. 2005), or RPB1-Int2.2f (Binder et al. 2010) and RPB1-Cr (Matheny et al. 2002) or RPB1-Int2.1r (Frøslev et al. 2005). The polymerase chain reaction (PCR) for the ITS and 28S regions followed Park et al. (2013) or as follows: initial denaturation at 95 C for 5 min, followed by 40 cycles at 94 C for 45 s, 53 C for the ITS region or 50 C for the 28S region for 45 s, and 72 C for 45 s, and a final extension at 72 C for 10 min; for the *rpb1*: initial denaturation at 94 C for 2 min, followed by 35 cycles at 94 C for 40 s, 60 C for 40 s, and 72 C for 2 min, and a final extension at 72 C for 10 min. PCR products were purified and Sanger sequenced by the MB Mission Biotech Company (Taipei, Taiwan) or Macrogen (Seoul, South Korea). Newly generated sequences were manually assembled using BioEdit 7.2.5 (Hall 1999), and their quality was checked based on five guidelines by Nilsson et al. (2012) before submitting to the DNA Data Bank of Japan (DDBJ)/European Molecular Biology Laboratory (EMBL)/GenBank.

Alignment and phylogenetic analyses.—Sequences were aligned using MAFFT 7.409 with the "G-INS-i" option for ITS, 28S, and *rpb1* (Katoh and Standley 2013) and, when necessary, manually adjusted in MEGA7 (Kumar et al. 2016). Some sequences were treated with gaps owing to missing data. A data set of combined ITS+28S+*rpb1* was used to investigate the systematic positions of *Ceriporia* species within the phlebioid clade of Polyporales. *Hyphoderma litschaueri* (Burt) J. Erikss. & Å. Strid and *H. mutatum* (Peck) Donk were chosen as outgroups for the three-gene data set following Wu et al. (2018). A second data set for combined ITS+28S, with a larger sampling of species and specimens, was used to infer interspecific relationships and taxonomy in clades recovered in the three-gene analysis. Two strains of *Byssomerulius corium* (Pers.) Parmasto were chosen as outgroups for the second data set. The references used to validate the sequences for both data sets were Jia et al. (2014), Floudas and Hibbett (2015), Miettinen et al. (2016), Spirin et al. (2016), Justo et al. (2017), Yuan et al. (2017), and Chen et al. (2018), and by BLAST search at the National Center for Biotechnology Information (NCBI) (SUPPLEMENTARY TABLE 1). Optimized sequence alignments were submitted to TreeBASE (submission ID 23585).

Partitioned Bayesian inference (BI) and maximum likelihood (ML) analyses were carried out using MrBayes 3.2.6 (Ronquist et al. 2012) and RAxML-HPC 8.0.2 (Stamatakis 2014) at the CIPRES Science Gateway (Miller et al. 2010). jModelTest 2.1.10 (Darriba et al. 2012) was used to test the evolutionary models for each gene region and the combined data sets based on the Akaike information criterion. BI

analyses were run for 10 million generations with four chains sampling every 100 generations. After the average standard deviation of split frequencies fell below 0.01, the first 25% of trees were discarded as burn-in, whereas remaining trees were used to construct the 50% majority-rule consensus phylogram with Bayesian posterior probabilities (BPPs). Tracer 1.7 was used to confirm that the average split deviation frequencies reached appropriate levels (Rambaut et al. 2018). ML analyses were performed under a GTRCAT model with 1000 bootstrap replicates yielding a best-scoring tree with proportional bootstrap values. Phylograms were visualized and edited in TreeGraph 2 (Stöver and Müller 2010) and Adobe Illustrator (Adobe Systems, San Jose, CA, USA).

RESULTS

We generated 63 new sequences representing 14 species and 23 specimens, of which 23 were from ITS, 22 from 28S, and 18 from *rpb1* (SUPPLEMENTARY TABLE 1). The ITS+28S+*rpb1* data set included 85 species and 99 sequences. The final alignment had 3463 positions including gaps, of which 42% were parsimony-informative. The ITS+28S data set included 40 species and 79 sequences. The final alignment had 1682 positions including gaps, of which 33% were parsimony-informative. For both data sets, the GTR+I+G model was estimated as the best model for each gene region. Phylograms obtained from ML and BI analyses resulted in similar topologies. Only the ML trees were shown. Both bootstrap values ($\geq 70\%$) and BPPs (≥ 0.9) are shown at internodes (FIGS. 1, 2).

Three well-supported clades were recovered corresponding to families Irpicaceae, Meruliaceae, and Phanerochaetaceae (FIG. 1). Species considered in *Ceriporia* sensu lato were recovered along with three highly supported clades within the Irpicaceae (100% ML and BPPs = 1 for clades I–III), three lineages in the Phanerochaetaceae, and a lineage with two specimens of *C. alachuana* (Murrill) Hallenb in the Meruliaceae (FIG. 1). Together, clades I and II formed a strongly supported clade dominated by numerous *Ceriporia* species.

Clade I recovered species previously included in *Ceriporia* and *Meruliopsis* Bondartsev, including the type species of *Meruliopsis*, *M. taxicola* (Pers.) Bondartsev (FIGS. 1, 2). Four species initially regarded as *Ceriporia* must be transferred to *Meruliopsis* according to the phylogenetic analysis in FIG. 2: *Ceriporia albomellea* Yuan Yuan, Jia J. Chen & X.H. Ji, *C. crassitunicata* Y.C. Dai & Sheng H. Wu, *C. nanlingensis* B.K. Cui & B.S. Jia, and *C. pseudocystidiata* B.S. Jia & Y.C. Dai. Additionally, specimens of two new species presented in this study,

Meruliopsis leptocystidiata and *M. parvispora* (described below), formed separate highly supported monophyletic groups.

Ceriporia viridans (Berk. & Broome) Donk, type species of the genus, was recovered in clade II. This clade was divided in three major subclades with high support: (i) the *C. viridans* group, which included *C. aurantiocarnescens* (Henn.) M. Pieri & B. Rivoire and *C. viridans* sensu lato, the latter a species complex; (ii) the *C. pierii* Rivoire, Miettinen & Spirin group, which included five species; and (iii) the *C. purpurea* (Fr.) Donk group, which included six species. Additionally, two specimens of a new species described below as *Ceriporia arbuscula* occurred in this clade. Some species that resembled *Ceriporia* were also recovered in this clade: *Candelabrochaete langloisii* (Pat.) Boidin, *C. septocystidia* (Burt) Burds., *Leptoporus mollis* (Pers.) Quél., and *Phanerochaete allantospora* Burds. & Gilb (FIGS. 1, 2).

In clade III, we recovered two lineages of *Ceriporia* (FIG. 1). One included a single sample of *C. cystidiata* Ryvarden & Iturr. from Thailand together with *Emmia* Zmitr., Spirin & Malysheva species. One sample of *Ceriporia sulphuricolor* Bernicchia & Niemelä from China appeared in a lineage with *Ceraceomyces serpens* (Tode) Ginns.

In the Phanerochaetaceae, the generic position of some species previously placed in *Ceriporia* was confirmed (FIG. 1), viz., *Phanerina mellea* (Berk. & Broome) Miettinen, *Phanerochaete inflata* (B.S. Jia & B.K. Cui) Miettinen, and *Riopa metamorphosa* (Fuckel) Miettinen & Spirin.

TAXONOMY

Ceriporia arbuscula C.C. Chen & Sheng H. Wu, sp. nov. FIGS. 3A, 4

Mycobank MB828034

Typification: TAIWAN. Nantou County, Aowanta, 23° 57'N, 121°10'E, 1200 m, on branch of *Pinus taiwanensis*, 28 Aug 2017, C.C. Chen, GC 1708-338 (holotype TNM F31793). GenBank: ITS = LC427008; 28S = LC427040; *rpb1* = LC427058.

Etymology: *arbuscula* (Latin), referring to subicular hyphae with short and tortuous side branches resembling an arbuscule.

Diagnosis: *Ceriporia arbuscula* is distinguished by yellowish brown to pale brown basidiocarps, the subicular hyphae with short and tortuous side branches, and presence of yellowish resin on the surfaces of tramal hyphae.

Description: Basidiocarps up to 0.7 mm thick and 1.5 cm wide, annual, resupinate, effuse, adnate, ceraceous; margin up to 1 mm wide, slightly paler than

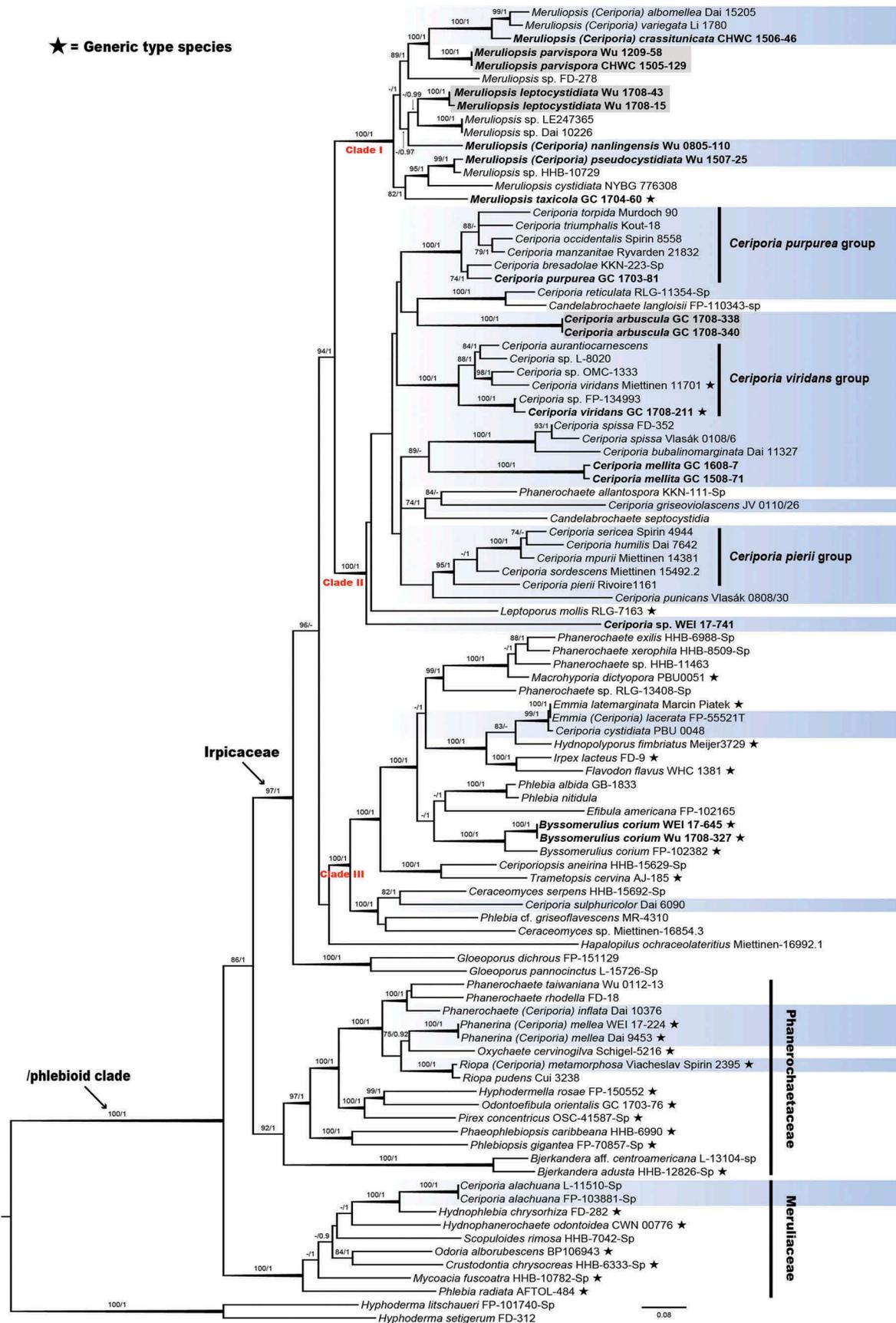


Figure 1. The phylogram inferred from maximum likelihood (ML) analyses using the combined ITS+28S+*rbp1* data set. Branches are labelled with ML bootstrap $\geq 70\%$ and BPPs ≥ 0.9 from Bayesian analyses. Thicken branches indicated both ML bootstrap $\geq 95\%$ and BPPs ≥ 0.99 from Bayesian analyses. Blue-shaded areas represent taxa of *Ceriporia* sensu lato in the phlebioid clade. Three new species are shown in gray boxes. Sequences newly generated in this study were shown in bold. Black stars (★) represent strains of generic type species. Bar = substitutions per site.

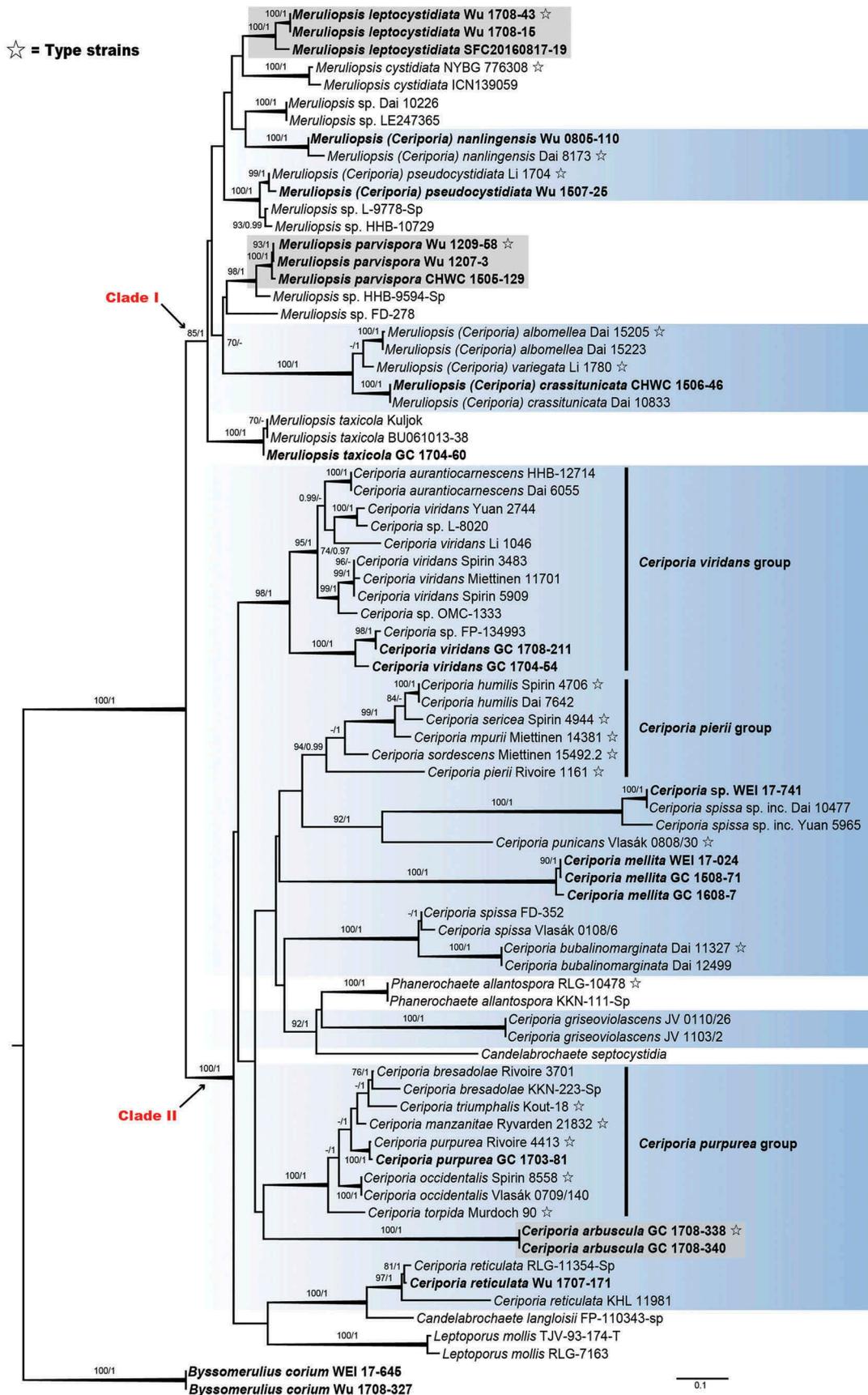


Figure 2. The phylogram inferred from maximum likelihood (ML) analyses using the combined ITS+28S data set. Branches are labeled with ML bootstrap $\geq 70\%$ and BPPs ≥ 0.9 from Bayesian analyses. Thicken branches indicated both ML bootstrap $\geq 95\%$ and BPPs ≥ 0.99 from Bayesian analyses. Blue-shaded areas represent taxa of *Ceriporia* sensu lato in clades I and II. Three new species are shown in gray boxes. Sequences newly generated in this study were shown in bold. White stars (☆) represent type strains. Bar = substitutions per site.



Figure 3. Basidiocarps of *Ceriporia* sensu stricto species in general and detailed views. A. *C. arbuscula* (GC 1708-338, holotype). B. *C. mellita* (GC 1608-7) in situ. Bars = 1 mm.

pore surface, very thin, usually indistinct. Pore surface yellowish brown to pale brown when dry; pores 4–6 per mm, round to angular; tubes up to 0.5 mm deep, concolorous with pore surface; dissepiments up to 125 μm thick, entire, sterile; subiculum thin, white. Hyphal system monomitic; hyphae simple-septate. Subicular hyphae 2–5 μm diam, strongly ramified, frequently with short and tortuous side branches, interwoven, colorless, thick-walled, anastomoses frequent. Tramal hyphae 2–4 μm diam, moderately ramified, interwoven, colorless, thick-walled, abundantly covered with yellowish resin, anastomoses frequent. Cystidia absent. Basidia 9–11 \times 3.5–4 μm , cylindrical to clavate, usually guttulate, 4-sterigmate. Basidiospores mostly 3–3.5 \times 1–1.5 μm [(2.5–)3–3.5 (–4.5) \times 1–1.5(–2) μm , L = 3.25 μm , W = 1.39 μm , Q = 2.33–2.34 (n = 30) (holotype)], cylindrical, slightly curved, colorless, thin-walled, smooth, inamyloid, nondextrinoid, cyanophilous, usually with one or a few oil drops.

Ecology and distribution: On dead branches of *Pinus taiwanensis*, Taiwan, Aug.

Other specimen examined: TAIWAN. Nantou County, Aowanta, 23°57'N, 121°10'E, 1200 m, on branch of *Pinus taiwanensis*, 28 Aug 2017, C.C. Chen, GC 1708-340 (TNM F31794).

Notes: Other *Ceriporia* have brownish basidiocarps and lack cystidia such as *C. albobrunnea* Ryvar den & Iturr., *C. angulata* Gomes-Silva, Ryvar den & Gibertoni, *C. ferruginicincta* (Murrill) Ryvar den, and *C. incrustata* M. Mata & Ryvar den (Ryvar den 2015). However, both *C. albobrunnea* and *C. angulata* differ from *C. arbuscula* in having larger pores and basidiospores [*C. albobrunnea*: 2–3 per mm, 4–4.5 \times 1.5 μm (Ryvar den and Iturriaga 2003); *C. angulata*: 2–3 per mm, 4–4.5 \times 1.7–2.2 μm (Gomes-Silva et al. 2012)]. Both *C. ferruginicincta* and *C. incrustata* differ from *C. arbuscula* in having smaller pores and ellipsoid basidiospores [*C. ferruginicincta*: 6–8 per mm, 3.5–5 \times 2–3 μm (Gilbertson and Ryvar den 1986); *C. incrustata*: 6–8 per mm, 3–3.5 \times 1.8–2 μm (Mata and Rivarden 2010)]. In addition, *C. arbuscula* is easily distinguished from other species of *Ceriporia* by the subicular hyphae with short and tortuous side branches.

Ceriporia mellita (Bourdot) Bondartsev & Singer, *Annales Mycologici* 39:50. 1941. **FIGS. 3B, 5**

Basidiocarps up to 1 mm thick and 4 cm wide, annual, resupinate, effuse, adnate, ceraceous to gelatinous; margin up to 1.5 cm wide, white when fresh, cream to pale ochraceous when dry, thinning out, usually cottony. Pore surface pale red when fresh, reddish brown to dark violet when

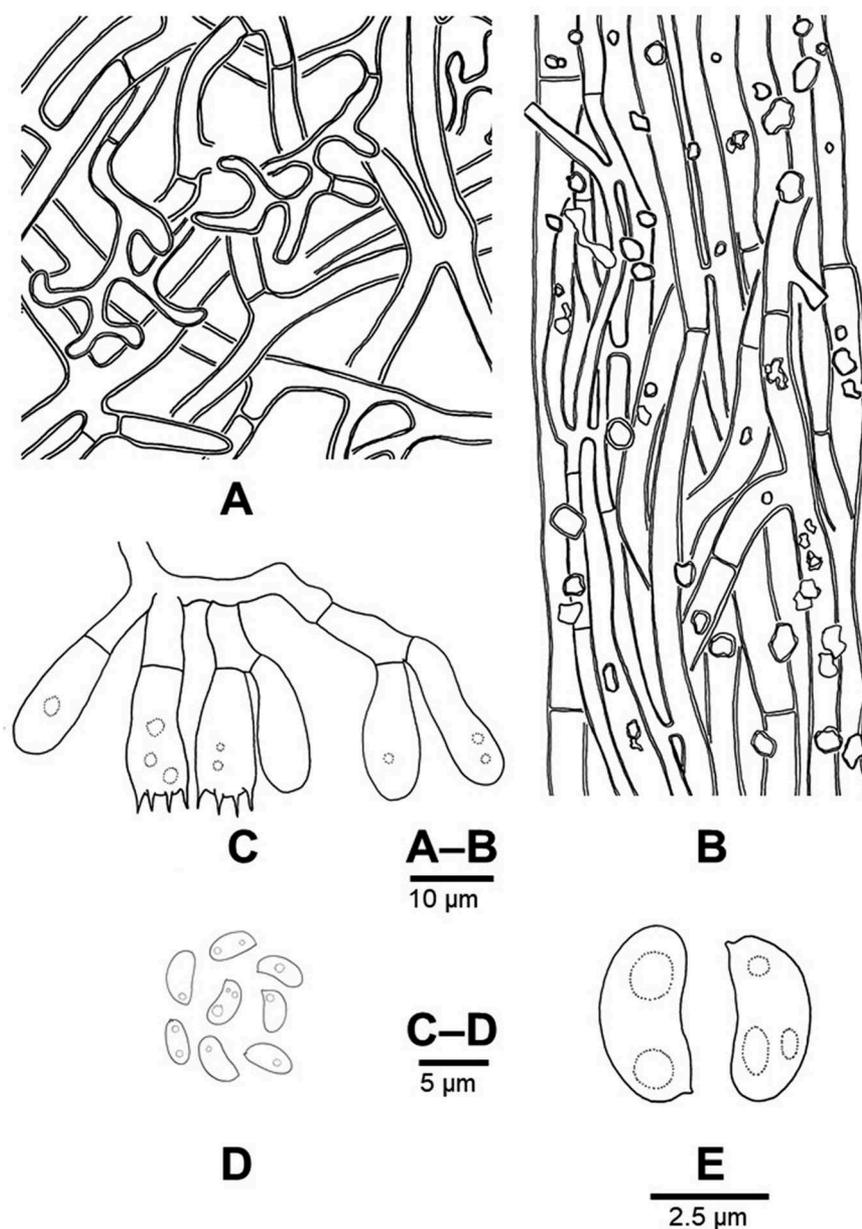


Figure 4. Micromorphological features of *Ceriporia arbuscula* (drawn from GC 1708-338, holotype). A. Hyphae from subiculum. B. Hyphae from tube trama. C. Basidia. D–E. Basidiospores. Bars: A–B = 10 μm ; C–D = 5 μm ; E = 2.5 μm .

dry; pores 4–5 per mm, round to angular; tubes up to 1.3 mm deep, concolorous with pore surface; dissepiments up to 250 μm thick, entire, sterile; subiculum thin, white to cream. Hyphal system monomitic; hyphae simple-septate. Subicular hyphae 2–6 μm diam, strongly ramified, interwoven, occasionally irregularly swollen, colorless, slightly thick- to thick-walled, anastomoses frequent. Tramal hyphae 2–4 μm diam, moderately ramified, interwoven, colorless, slightly thick- to thick-walled, anastomoses frequent. Cystidia absent. Hyphoid elements 14–36 \times 2.5–4.5 μm , frequently situated in the dissepiment edge of pore surface, clavate, colorless, thin-walled. Basidia 12–14 \times 4–5

μm , cylindrical to clavate, 4-sterigmate. Basidiospores mostly 5–6 \times 1.5–2 μm [(4.5–)5–6(–7) \times 1.5–2 μm , L = 5.4 μm , W = 1.69 μm , Q = 3.18–3.19 (n = 40) (GC 1608-7)], allantoid, colorless, thin-walled, smooth, inamyloid, non-dextrinoid, acyanophilous.

Ecology and distribution: On dead angiosperm (e.g., *Alnus*, *Eucalyptus*, *Fagus*, *Malus*, and *Populus*) and dead gymnosperm wood, or rotten bamboo, central Europe (France [type], Belgium, Czech Republic, Poland) and East Asia (Japan and Taiwan). Jan, Apr, Aug in East Asia.

Specimens examined: JAPAN. KYOTO PREFECTURE: Kyoto City, Kyoto Botanical Garden, 35°2'58"N, 135°45'

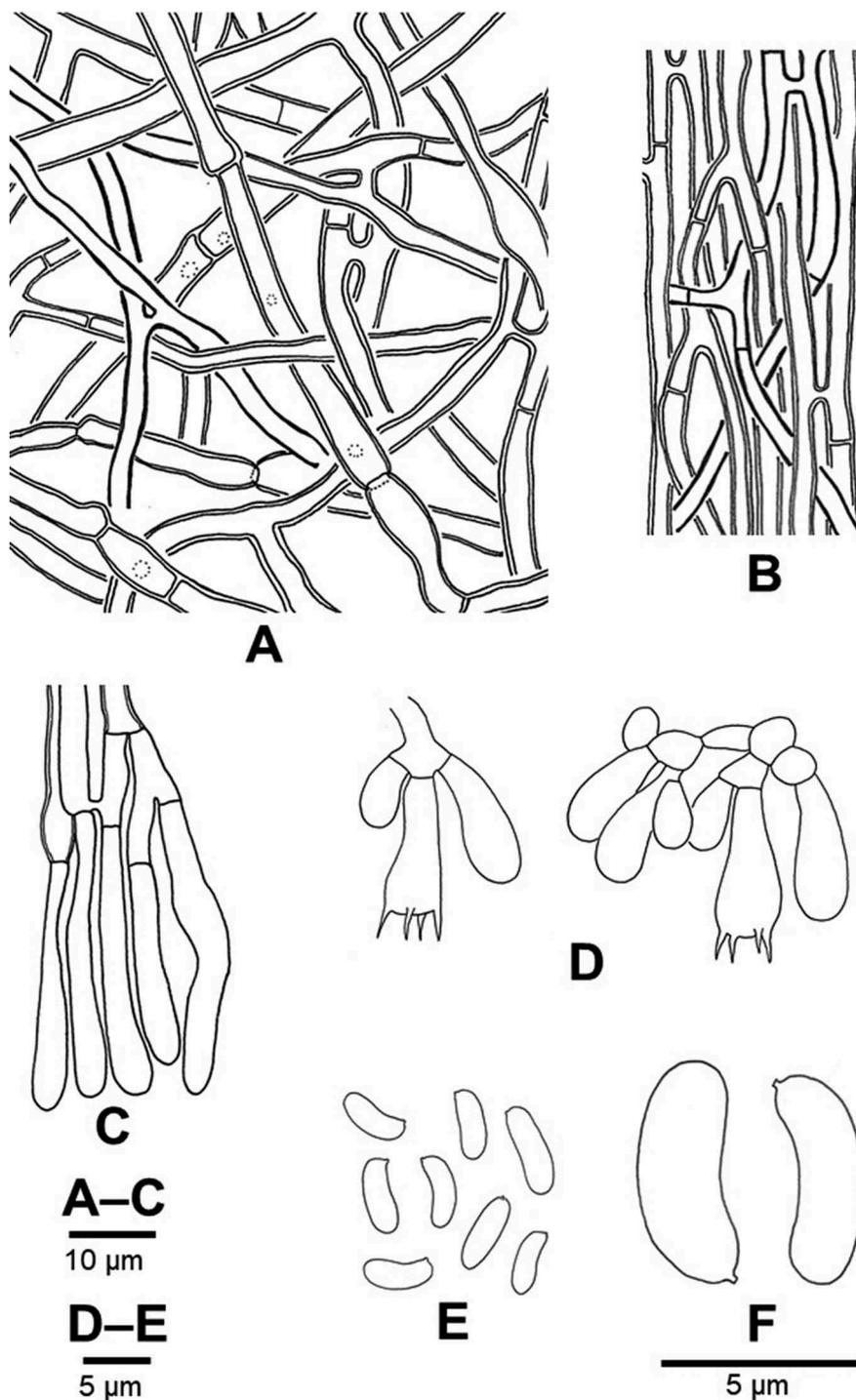


Figure 5. Micromorphological features of *Ceriporia mellita* (drawn from GC 1608-7). A. Hyphae from subiculum. B. Hyphae from tube trama. C. Hyphoid sterile elements from the dissepiment edge. D. Basidia. E-F. Basidiospores. Bars: A-C = 10 µm; D-F = 5 µm.

41°E, 77 m, on decorticated gymnosperm branch, 1 Aug 2016, C.C. Chen & C.L. Chen, GC 1608-7 (TNM F31790); *ibid.*, GC 1608-8 (TNM F31791). TAIWAN. New Taipei City, Chinshan District, Yangmingshan National Park, Yulu Historical Trail, 25°10'N, 121°35'E, 516 m, on angiosperm branch, 26 Aug 2015, C.C. Chen, C.

L. Wei, W.C. Chen & S. Lim, GC 1508-71 (TNM F29546); Gongliao District, Tatiehiao, on rotten bamboo culm, 27 Jan 2017, C.L. Wei, C.T. Wei & M.Y. Huang, WEI 17-024 (TNM F31792); Nantou County, Jenai Township, Aowanda National Forest Recreation Area, 23°57'11"N, 121°10'41"E, 1250 m, on angiosperm trunk, 28 Apr 2018,

C.L. Wei, WEI 18-042 (TNM F32431); *ibid.*, WEI 18-043 (TNM F32432).

Notes: Ryvarden and Gilbertson (1993) treated *Ceriporia mellita* as a synonym of *C. purpurea*. However, Pieri and Rivoire (1997) considered them to be two independent species. East Asian specimens of *C. mellita* fit well with previous reports such as Spirin et al. (2016) and Ryvarden and Melo (2017), except for the presence of hyphoid sterile elements in the dissepiment edge of pore surface (FIG. 5C). *Ceriporia mellita* is newly recorded from East Asia (Japan and Taiwan).

Meruliopsis albomellea (Yuan Yuan, Jia J. Chen & X.H. Ji) C.C. Chen & Sheng H. Wu, *comb. nov.*

MycoBank MB830642

Basionym: *Ceriporia albomellea* Yuan Yuan, Jia J. Chen & X.H. Ji, *Phytotaxa* 298:23. 2017.

Description: See Yuan et al. (2017).

Ecology and distribution: On rotten angiosperm wood, China (Hainan), May.

Specimen examined: CHINA. HAINAN PROVINCE: Qiongzong County, Limushan Nature Reserve, on rotten angiosperm wood, 30 May 2015, *Dai 15205* (**holotype** in BJFC).

Notes: *Meruliopsis albomellea* is characterized by buff yellow basidiocarps with a white and cottony margin, clavate cystidia, and oblong-ellipsoid basidiospores. Phylogenetically, *M. albomellea* is sister to *M. variegata* (B.S. Jia & Y.C. Dai) *Zmitr.* (FIGS. 1, 2). However, *M. variegata* differs from *M. albomellea* by the white to cream basidiocarps and variably shaped cystidia (clavate, fusoid, or lanceolate) with adventitious septa.

Meruliopsis crassitunicata (Y.C. Dai & Sheng H. Wu) C.C. Chen & Sheng H. Wu, *comb. nov.*

MycoBank MB830643

Basionym: *Ceriporia crassitunicata* Y.C. Dai & Sheng H. Wu, *Mycotaxon* 83:213. 2002.

Description: See Dai et al. (2002).

Ecology and distribution: On rotten angiosperm (e.g., *Alnus*) wood, China (Dai 2012) and Taiwan (Dai et al. 2002), Jun to Aug.

Specimens examined: TAIWAN. Nantou County, Yuchih Township, Lienhuachih, 23°56'N, 120°53'E, 700 m, on rotten angiosperm trunk, 5 Jun 2001, *S.H. Wu*, *Wu 0106-4* (**holotype** TNM F13430); 6 Aug 2018, *C.C. Chen & C.M. Hu*, *GC 1808-22* (TNM F32429); *ibid.*, *GC 1808-23* (TNM F32430); 23°55'N, 120°53'E, 715 m, on angiosperm branch, 23 Jun 2015, *W.C. Chen*, *C.C. Chen & C.L. Wei*, *CHWC 1506-46* (TNM F29222).

Notes: *Meruliopsis crassitunicata* is characterized by white to cream basidiocarps made up of distinctly thick-

walled hyphae and oblong-ellipsoid basidiospores. Phylogenetically, *M. crassitunicata* is closely related to *M. albomellea* and *M. variegata* (FIGS. 1, 2). These three species share similar basidiospores [*M. albomellea*: 3.1–3.8 × 1.7–2 μm (Yuan et al. 2017); *M. crassitunicata*: 3.4–4.1 × 1.6–2 μm (Dai et al. 2002); *M. variegata*: 3–4 × 1.6–2 (Jia et al. (2014)]. However, *M. albomellea* and *M. variegata* differ from *M. crassitunicata* in having smaller pores, and presence of cystidia.

Meruliopsis cystidiata (Ryvarden) P.E. Jung & Y.W. Lim, *Mycol Prog* 17:861. 2018.

Description: See Ryvarden (1987) and Jung et al. (2018).

Ecology and distribution: On dead bamboo and wood, Brazil, May to Jun.

Notes: This species was originally described as *Gloeoporus cystidiatus* from Brazil by Ryvarden (1987). Recently, Jung et al. (2018) sequenced the type material of *G. cystidiatus* (NYBG 776308) and transferred the species to *Meruliopsis* based on molecular phylogenetic results. Here, we also support this view. *Meruliopsis cystidiata* is characterized by resupinate or rarely effuse-reflexed basidiocarps with a purplish pore surface, presence of cystidia, and cylindrical to subballantoid basidiospores. Phylogenetically, *M. cystidiata* is closely related to the new species, *M. leptocystidiata* (FIG. 2), described below. However, *M. leptocystidiata* has resupinate basidiocarps with a white to cream pore surface, narrower cystidia, and ellipsoid basidiospores.

Meruliopsis leptocystidiata C.C. Chen & Sheng H. Wu, *sp. nov.* FIGS. 6A, 7

MycoBank MB830636

Typification: CHINA. LIAONING PROVINCE: Anshan City, Qianshan, 40°60'N, 123°08'E, 300 m, on rotten angiosperm branch, 1 Aug 2017, *S.H. Wu*, *Wu 1708-43* (**holotype** TNM F31795). GenBank: ITS = LC427013; 28S = LC427033; *rpb1* = LC427070.

Etymology: *leptocystidiata* (Latin), referring to leptocystidia, thin-walled cystidia originating from the hymenium.

Diagnosis: *Meruliopsis leptocystidiata* is characterized by white to cream basidiocarps, strongly encrusted subicular hyphae, ellipsoid basidiospores with one oily drop, and presence of leptocystidia without adventitious septa.

Description: Basidiocarps up to 1 mm thick and 2.5 cm wide, annual, resupinate, effuse, adnate, membranaceous; margin up to 0.8 cm wide, slightly paler than pore surface, thinning out, usually cottony to fimbriate, sometimes rhizomorphic. Pore surface white to cream when dry; pores 4–5 per mm, round; tubes up to 125 μm deep, concolorous with pore surface; dissepiments up to 250 μm thick, entire, with continuous hymenium; subiculum thin, white. Hyphal

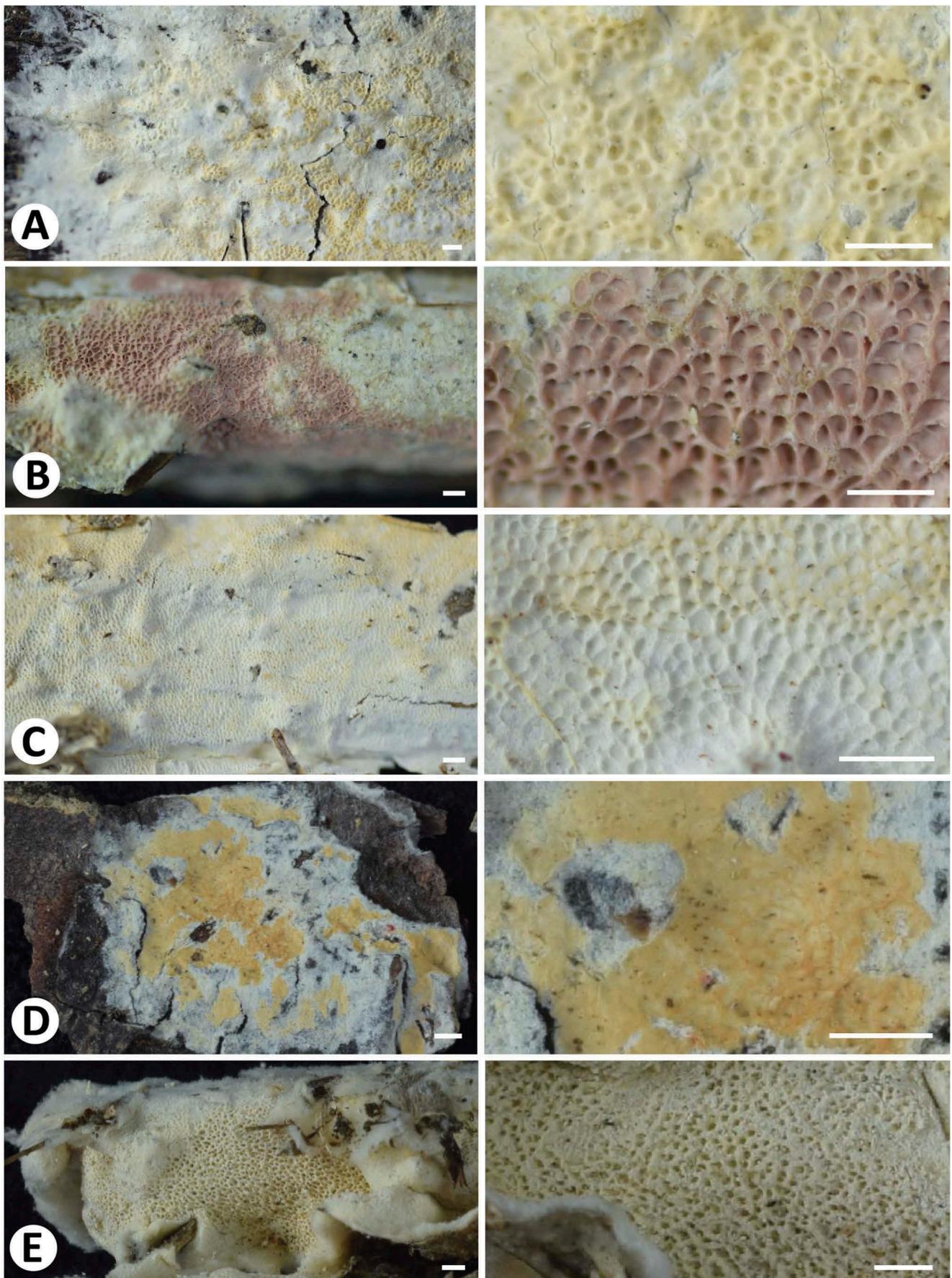


Figure 6. Basidiocarps of *Meruliopsis* species in general and detailed views. A. *M. leptocystidiata* (Wu 1708-43, holotype). B. *M. nanlingensis* (Wu 0805-110). C. *M. parvispora* (Wu 1209-58, holotype). D. *M. pseudocystidiata* (Dai 1704, holotype). E. *M. variegata* (Li 1780, holotype). Bars = 1 mm.

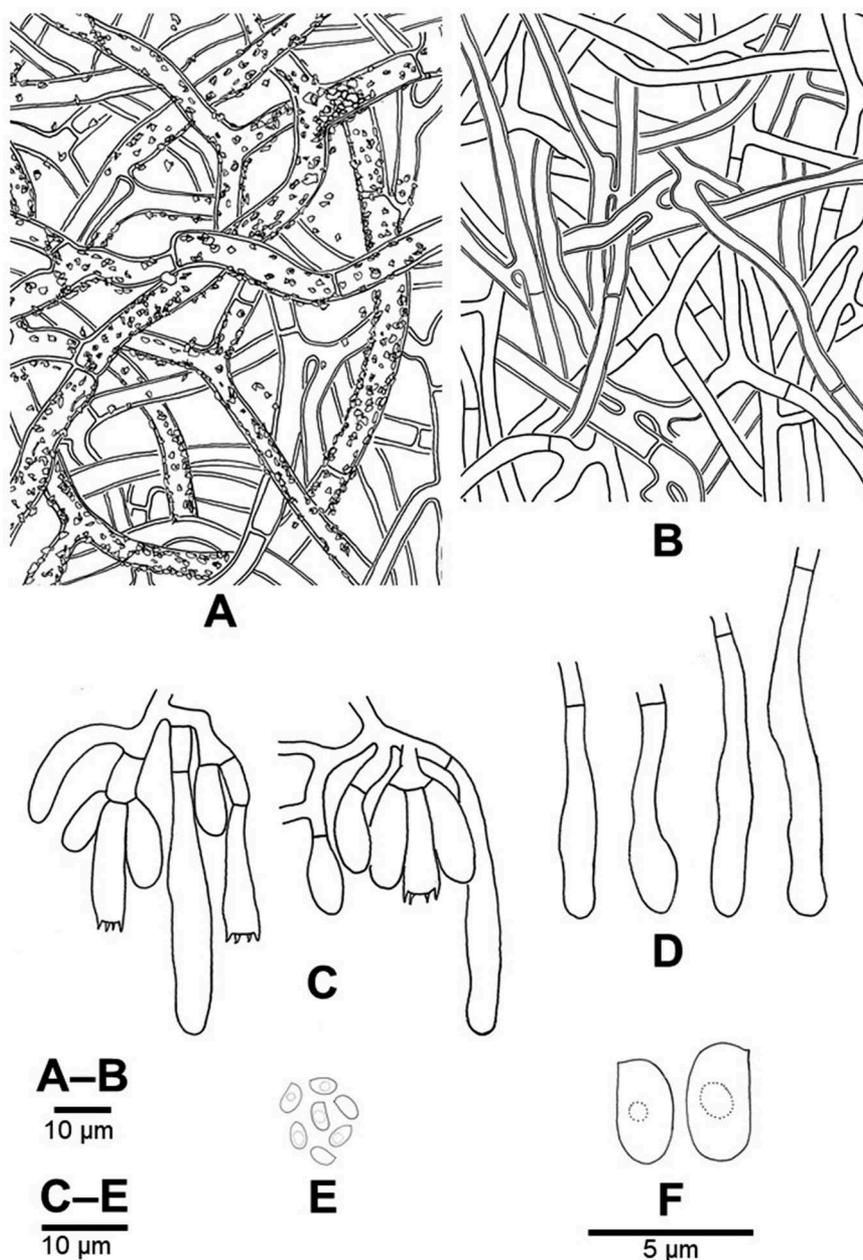


Figure 7. Micromorphological features of *Meruliopsis leptocystidiata* (drawn from Wu 1708-43, holotype). A. Hyphae from subiculum. B. Hyphae from tube trama. C. Hymenium (cystidia, basidia, and basidioles). D. Cystidia. E–F. Basidiospores. Bars: A–E = 10 μm ; F = 5 μm .

system monomitic; hyphae simple-septate. Subicular hyphae 3–6 μm diam, strongly ramified, interwoven, colorless, thick-walled, strongly encrusted, anastomoses occasional. Tramal hyphae 2–5.5 μm diam, strongly ramified, interwoven, colorless, slightly thick- to thick-walled, anastomoses occasional. Leptocystidia 24–40 \times 3.5–4.5 μm , numerous, projecting, usually cylindrical, occasionally clavate, colorless. Basidia 12–15 \times 3.5–4 μm , cylindrical to clavate, 4-sterigmate. Basidiospores mostly 3–4 \times 1.5–2 μm [3–4 \times 1.5–2 (–2.5) μm , L = 3.45 μm , W = 1.81 μm , Q = 1.9–1.91

(n = 30) (holotype); (3–)3.5(–4) \times 1.5–2(–2.5) μm , L = 3.6 μm , W = 1.9 μm , Q = 1.7–2.2 (n = 20) (SFC20180710-15); 3–3.5(–4) \times 1.5–2(–2.5) μm , L = 3.2 μm , W = 1.8 μm , Q = 1.8–2 (n = 20) (SFC20160817-19)], ellipsoid, colorless, thin-walled, smooth, inamyloid, nondextrinoid, cyanophilous, usually with one oily drop.

Ecology and distribution: On dead branches and trunks (*Quercus*, *Pinus*), China (Liaoning) and South Korea, Jul to Aug.

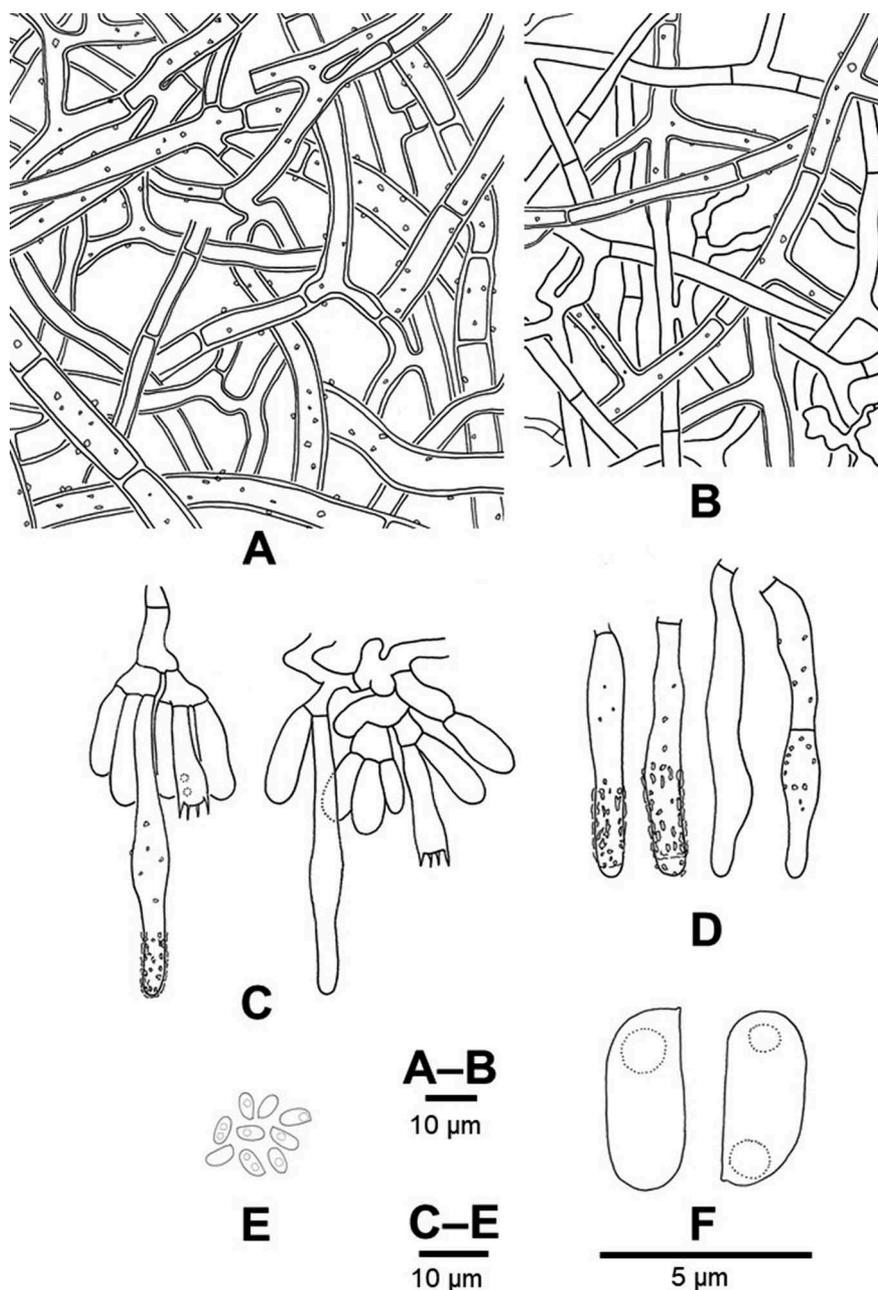


Figure 8. Micromorphological features of *Meruliopsis nanlingensis* (drawn from Wu 0805-110). A. Hyphae from subiculum. B. Hyphae from tube trama. C. Hymenium (basidia and basidioles). D. Cystidia. E–F. Basidiospores. Bars: A–E = 10 µm; F = 5 µm.

Other specimens examined: CHINA. LIAONING PROVINCE: Anshan City, Qianshan, 40°60'N, 123°08' E, 300 m, on angiosperm branch, 1 Aug 2017, S.H. Wu, Wu 1708-7 (TNM F31597); *ibid.*, Wu 1708-15 (TNM F31796); *ibid.*, Wu 1708-29 (TNM F31797); *ibid.*, Wu 1708-57 (TNM F31798). SOUTH KOREA. GYEONGGI-DO: Incheon, Ongjin-gun, Sindo, 37°52' N, 126°44' E, 100 m, on branch of *Quercus mongolica*, 17 Aug 2016, N.K. Kim & Y.W. Lim, SFC20160817-19 (SFC); GYEONGSANGBUK-DO: Chilgok-gun,

Namwon-ri, 35°78'N, 129°23'E, 158 m, on trunk of *Pinus densiflora*, 10 Jul 2018, A. Lupala & Y.W. Lim, SFC20180710-15 (SFC).

Notes: *Meruliopsis leptocystidiata* resembles *M. albomellea* and *M. variegata* in having a white to cream pore surface, presence of cystidia, and similar basidiospore size. However, *M. albomellea* has smaller pores (5–7 per mm; Yuan et al. 2017), and *M. variegata* bears wider cystidia with adventitious septa (Jia et al. 2014).

Meruliopsis nanlingensis (B.K. Cui & B.S. Jia) C.C. Chen & Sheng H. Wu, comb. nov. FIGS. 6B and 8 MycoBank MB830644

Basionym: *Ceriporia nanlingensis* B.K. Cui & B.S. Jia, Mycotaxon 116:458. 2011.

Basidiocarps up to 0.5 mm thick and 3 cm wide, annual, resupinate, effuse, adnate, membranaceous; margin up to 1 mm wide, white to cream, very thin, usually indistinct. Pore surface rose pink to grayish rose when fresh, rosy buff to buff when dry; pores 2–4 per mm, round to irregular; tubes up to 0.4 mm deep, concolorous with pore surface; dissepiments up to 125 μm thick, entire, with continuous hymenium; subiculum thin. Hyphal system monomitic; hyphae simple-septate. Subicular hyphae 3–8 μm diam, moderately ramified, loosely interwoven, colorless, slightly thick- to thick-walled, anastomoses frequent. Tramal hyphae 2–5 μm diam, moderately ramified, moderately interwoven, colorless, thin- to thick-walled, sometimes irregularly swollen, anastomoses occasional. Leptocystidia 30–42 \times 4–6 μm , numerous, projecting, clavate to subulate, slightly flexuous, with acute or blunt apex, colorless, often sparsely encrusted, occasionally with one adventitious septum. Basidia 15–21 \times 4.5–5 μm , cylindrical to clavate, 4-sterigmate. Basidiospores mostly 3.5–4 \times 1.5–2 μm [(3–)3.5–4 (–4.5) \times 1.5–2 μm , L = 3.92 μm , W = 1.78 μm , Q = 2.1–2.11 (n = 40) (*Wu 0805-110*)], narrowly ellipsoid to cylindrical, slightly curved, colorless, thin-walled, smooth, inamyloid, nondextrinoid, cyanophilous.

Ecology and distribution: On dead angiosperm wood, China (Hubei and Hunan) (Jia and Cui 2011a), Japan and Taiwan (this study), May to Sep.

Specimens examined: CHINA. HUNAN PROVINCE: Yizhang County, Mangshan Nature Reserve, on angiosperm twig, 26 Jun 2007, *Dai 8173* (holotype in BJFC). JAPAN. HONSHU: Yamanashi, Minami-tsuru-gun, Fuji-kawaguchiko-machi, Goten-niwa, 35°29'N, 138°38' E, 965 m, on angiosperm branch, 4 July 2008, *S.H. Wu, Wu 0807-5* (TNM F22057). TAIWAN. Taichung City, Hoping District, Anmashan Hiking Trail, 24°16'N, 121°00'E, 2250 m, on angiosperm branch, 10 May 1999, *S.H. Wu, S.W. Chou & Y.H. Chen, Wu 9905-21* (TNM F10523); 19 km of Dasyueshan Forestry Road, 6 May 2018, *C.C. Chen & C.M. Hu, GC 1805-14* (TNM F31800); 43 km of Dasyueshan Forestry Road, Anma Villa, 24°15'22"N, 120°59'59"E, 2250 m, on rotten wood, 22 May 2008, *S.H. Wu, S.Z. Chen & Y.T. Wang, Wu 0805-107* (TNM F22546); *Wu 0805-110* (TNM F22546); Henglingshan Trail, 24°14'03"N, 120°56'08"E, 1770 m, on angiosperm branch, 7 May 2017, *C.C. Chen, GC 1705-7* (TNM F32061); *ibid.*, *GC 1705-11* (TNM

F32062); *C.L. Wei, WEI 17-090* (TNM F32063); 24°14' 12"N, 120°55'08"E, 1400 m, 7 May 2017, *C.C. Chen, GC 1705-13* (TNM F32064).

Notes: *Meruliopsis nanlingensis* is characterized by the rose pink to grayish rose pore surface when fresh, presence of cystidia, and narrowly ellipsoid to cylindrical basidiospores. Morphological features of Japanese and Taiwanese specimens generally agree with the original description by Jia and Cui (2011a). However, our specimens have slightly larger pores (3–5 per mm; Jia and Cui 2011a) and sparse crystals on the cystidia (FIG. 7D). Also, the hymenium is continuous over the dissepiments, which was not mentioned in the protologue. Phylogenetically, one of our collections (*Wu 0805-110*) is clustered with the type strain (*Dai 8173*) of *M. nanlingensis* in a highly supported lineage (FIG. 2). This species is new to Japan and Taiwan.

Meruliopsis parvispora C.C. Chen & Sheng H. Wu, sp. nov. FIGS. 6C and 9 MycoBank MB830634

Typification: TAIWAN. Nantou County, Jenai Township, Huisun Forestry Station, 24°05'N, 121°03'E, 720 m, on angiosperm trunk, 16 Sep 2012, *S.H. Wu, Wu 1209-58* (holotype TNM F26829). GenBank: ITS = LC427017; 28S = LC427039; *rpb1* = LC427065.

Etymology: *parvispora* (Latin), referring to the small basidiospores.

Diagnosis: *Meruliopsis parvispora* is recognized by white to cream basidiocarps with small pores and small and narrowly ellipsoid to cylindrical basidiospores.

Description: Basidiocarps up to 0.25 mm thick and 4 cm wide, annual, resupinate, effuse, adnate, membranaceous; margin up to 1 cm wide, slightly paler than pore surface, thinning out, usually arachnoid to cottony. Pore surface white when fresh, white to cream when dried; pores 5–7 per mm, round to angular; tubes up to 125 μm deep, concolorous with pore surface; dissepiments up to 100 μm thick, entire, sterile; subiculum thin, white. Hyphal system monomitic; hyphae simple-septate. Subicular hyphae 2–4 μm diam, strongly ramified, interwoven, colorless, thick-walled, anastomoses frequent. Tramal hyphae 2–3 μm diam, moderately ramified, interwoven, colorless, slightly thick- to thick-walled, anastomoses frequent. Cystidia absent. Basidia 8–13 \times 3–4 μm , cylindrical to clavate, 4-sterigmate. Basidiospores mostly 2.5–3 \times 1–1.5 μm [2.5–3 (–3.5) \times 1–1.5 μm , L = 2.85 μm , W = 1.22 μm , Q = 2.13–2.14 (n = 30) (holotype)], narrowly ellipsoid to cylindrical, slightly curved, colorless,

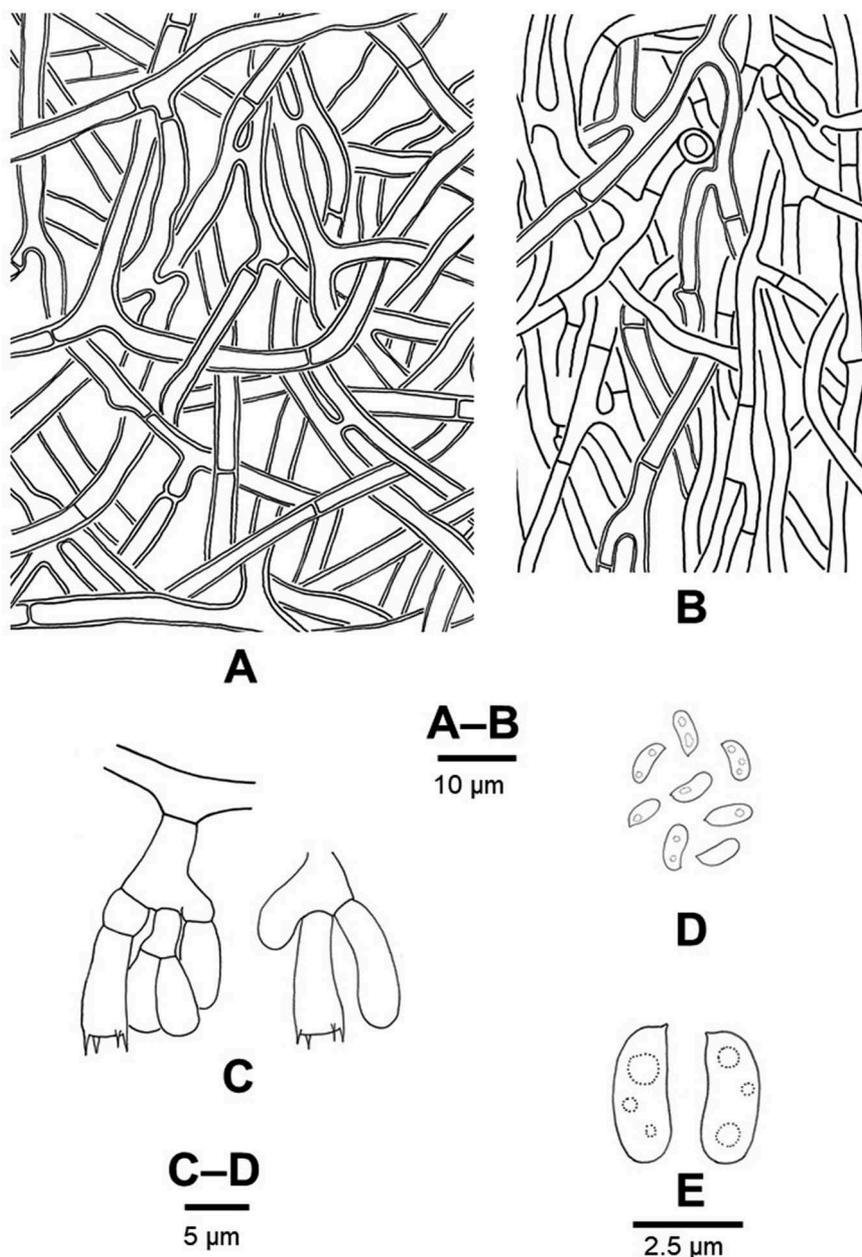


Figure 9. Micromorphological features of *Meruliopsis parvispora* (drawn from Wu 1209-58, holotype). A. Hyphae from subiculum. B. Hyphae from tube trama. C. Hymenium (basidia and basidioles). D–E. Basidiospores. Bars: A–B = 10 µm; C–D = 5 µm; E = 2.5 µm.

thin-walled, smooth, inamyloid, nondextrinoid, cyanophilous, usually with one or a few oily drops.

Ecology and distribution: On rotten angiosperm wood, Taiwan, Mar, May, Sep.

Other specimens examined: TAIWAN. Nantou County, Jenai Township, Huisun Forestry Station, 24°05'N, 121°03'E, 718 m, on angiosperm wood, 16 Sep 2012, W.C. Chen, CHWC 1209-26 (TNM F26829); Yuchih Township, Lienhuachih, 23°56'N, 120°53'E, 700 m, on rotten wood, 16 Jul 2012, S.H. Wu, Wu 1207-3 (TNM F31799); New Taipei City, Chinshan

District, Yangmingshan National Park, Yulu Historical Trail, 25°10'N, 121°35'E, 490 m, on angiosperm trunk, 19 May 2015, W.C. Chen, C.C. Chen & C.L. Wei, CHWC 1505-129 (TNM F29190); Pingxi District, Lingjiaoliao Mountain Trail, 25°02'01"N, 121°45'27"E, 210 m, on rotten wood, 23 March 2018, S.Z. Chen, C.C. Chen & C.L. Wei, Chen 3805 (TNM F32059); Chen 3812 (TNM F32060); Taipei City, Peitou District, Yangmingshan National Park, Shamaoshan, Dapu Hiking Trail Entrance, 25°08'N, 121°31'E, 340 m, on angiosperm branch,

24 May 2016, C.C. Chen & C.L. Wei, WEI 16-115 (TNM F30708).

Notes: The small pores and small basidiospores of *Meruliopsis parvispora* are reminiscent of *Ceriporia microspora* I. Lindblad & Ryvarden (6–8 per mm, 3–3.5 × 1.5–2 µm; Lindblad and Ryvarden 1999) and *C. incrustata* (6–8 per mm, 3–3.5 × 1.8–2 µm; Mata and Ryvarden 2010). However, *M. parvispora* differs from these two species in possessing slightly larger pores and smaller basidiospores.

Phylogenetically, *M. parvispora* is closely related to *M. albomellea*, *M. crassitunicata*, and *M. variegata*. These species share white to cream basidiocarps. However, *M. albomellea* and *M. variegata* differ from *M. parvispora* in presence of cystidia (Jia et al. 2014; Yuan et al. 2017). *Meruliopsis crassitunicata* differs from *M. parvispora* in having larger pores and basidiospores (3–4 per mm, 3.4–4.1 × 1.6–2 µm; Dai et al. 2002).

Meruliopsis pseudocystidiata (B.S. Jia & Y.C. Dai) C.C. Chen & Sheng H. Wu, comb. nov. FIG. 6D
Mycobank MB830645

Basionym: *Ceriporia pseudocystidiata* B.S. Jia & Y.C. Dai, Mycol Prog 13:86. 2014.

Description: See Jia et al. (2014).

Ecology and distribution: On rotten angiosperm and gymnosperm (e.g., *Abies* Mill. and *Pinus*) wood, China (Henan, Hunan, Jilin, and Yunnan) and South Korea (Jia et al. 2014; Jang et al. 2016), Jun to Aug.

Specimens examined: CHINA. HUNAN PROVINCE: Yizhang County, Mangshan Nature Reserve, on rotten angiosperm stump, 25 Jun 2007, Dai 1704 (**holotype** in BJFC); JILIN PROVINCE: Antu County, Erdaobaihe Town, Changbaishan, Dayangdi, 42°23'N, 128°06'E, 700 m, on rotten wood, 9 Aug 2016, S.H. Wu, Wu 1608-196 (TNM F30616); 800 m, on rotten trunk, 6 Jul 2015, S.H. Wu, Wu 1507-25 (TNM F29842); YUNNAN PROVINCE: Chuxiong Yi Autonomous Prefecture, Nanhua County, Tujie Town, 24°49'N, 100°46'E, 1915 m, on *Pinus* branch, 15 Aug 2017, C.C. Chen, GC 1708-315 (TNM F32214); *ibid.*, GC 1708-317 (TNM F32215).

Notes: *Meruliopsis pseudocystidiata* resembles *M. albostramineus* (Torrend) Jülich & Stalpers by the meruloid to poroid hymenophore, basidiospore size (*M. albostramineus*: 3.5–5.5 × 1.5–2 µm in Ginns [1976] and 4.5–6 × 1.5–2 µm in Bernicchia and Gorjón [2010]; *M. pseudocystidiata*: 3.7–4.3 × 1.6–1.8 µm in Jia et al. [2014]), and presence of tubular cystidia. Moreover, *M. albostramineus* is associated with brown rot (Ginns 1976).

Meruliopsis taxicola (Pers.) Bondartsev, Izv Akad Nauk Estonsk SSR, Ser Biol:274. 1959.

Description: See Ginns (1976) and Ryvarden and Melo (2017).

Ecology and distribution: Often on dead gymnosperm (especially *Pinus*) wood and also reported on dead angiosperm wood in North America. Widely distributed throughout Northern Hemisphere, also in New Zealand and Australia (Ryvarden and Melo 2017), occurring Apr to Oct.

Specimens examined: TAIWAN. Chiayi County, Yushan National Park, Nanhsi Forest Road, 23°28'N, 120°54'E, 2100 m, on branch of *Pinus taiwanensis*, 6 Oct 1992, S.H. Wu, Wu 9210-32 (TNM F14862); *ibid.*, 7 Oct 1992, S.H. Wu, Wu 9210-67 (TNM F14864); *ibid.*, 2250 m, on branch of *P. taiwanensis*, 14 Oct 1993, S.H. Wu & S.Z. Chen, Wu 9310-129 (TNM F1403); Miaoli County, Taian Township, Shei-Pa National Park, east line of Talu Forest Road, 24°29'47"N, 121°09'57"E, 1966 m, on gymnosperm branch, 22 Apr 2017, C.C. Chen, GC 1704-59 (TNM F32089); *ibid.*, GC 1704-60 (TNM F32090). SWEDEN. LAPLAND: Gällivare, the forest reserve “Jalkaskielas,” N of Mount Maisavare, 18 km ENE of Polcirkeln railway station, on *Picea abies* (L.) H. Karst., 31 July 1968, Erna & Åke Strid, 4759 (TNM F4616). USA. MICHIGAN: Marquette County, Elm Creek Trail, Huron Mountain Club, on *Tsuga canadensis* (L.) Carrière, 18 Aug 1976, H.H. Burdsall Jr., HHB 9070 (TNM F932).

Notes: *Meruliopsis taxicola* is newly reported from Taiwan. This species is somewhat similar to *Ceriporia purpurea* by the gelatinous and purplish basidiocarps but is distinguished from it by larger pores and smaller basidiospores (respectively 6–8 per mm and 5–8.4 × 1.7–2.3 µm in *C. purpurea*; Spirin et al. 2016). Morphological features of Taiwanese specimens fit well with descriptions by Ginns (1976) and Ryvarden and Melo (2017).

Meruliopsis variegata (B.S. Jia & Y.C. Dai) Zmitr., Folia Cryptogamica Petropolitana 6:98. 2018. FIG. 6E

Description: See Jia et al. (2014).

Ecology and distribution: On rotten angiosperm stump, China, Jun.

Specimen examined: CHINA. HAINAN PROVINCE: Yizhang County, Mangshan Nature Reserve, on rotten angiosperm stump, 26 Jun 2007, Li 1780 (**holotype** in BJFC).

Notes: *Meruliopsis variegata* was originally described from southern China by Jia et al. (2014). Recently, Zmitrovich (2018) transferred this species to *Meruliopsis* (viz., *M. variegata*), results of which are confirmed here (FIGS. 1, 2). *Meruliopsis variegata* is characterized by white to cream basidiocarps, cylindrical

to oblong-ellipsoid basidiospores, and variable cystidia (clavate, fusoid, or lanceolate) with adventitious septa.

DISCUSSION

The present study conducted a three-gene phylogenetic analysis of *Ceriporia* and other related taxa within the Irpicaceae, Meruliaceae, and Phanerochaetaceae. Major topologies of phylograms were consistent with modern classification frameworks (Miettinen et al. 2016; Justo et al. 2017). Some significant findings are summarized as follows: (i) *Ceriporia* sensu lato is a polyphyletic group, as has been previously suggested by Jia et al. (2014); (ii) *Meruliopsis* sensu lato is paraphyletic because some species previously considered in *Ceriporia* were recovered in *Meruliopsis*; and (iii) *Ceriporia arbuscula*, *Meruliopsis leptocystidiata*, and *M. parvispora* are described as new species from East Asia.

Meruliopsis, typified by *M. taxicola*, was considered a synonym of *Gloeoporus* Mont. by Ryvarden and Gilbertson (1993), Coelho et al. (2006), and Ryvarden and Melo (2017). However, phylogenetic studies did not support this viewpoint (Larsson 2007; Miettinen et al. 2016; Justo et al. 2017; Jung et al. 2018). Here, *Meruliopsis* is proposed to accommodate species in clade I because the type species was nested in this highly supported clade (FIGS. 1, 2) and *Meruliopsis* is the earliest priorable name available for clade I.

Meruliopsis (clade I) contains species with resupinate to effused-reflexed basidiocarps that are white to cream, buff yellow, pinkish to purplish, or reddish brown, and meruloid to poroid hymenophore. Microscopically, all species share monomitic hyphal system and simple-septate hyphae, and over half of them possess cystidia or cystidioles. The basidiospores are ellipsoid to cylindrical, or cylindrical to allantoid.

Few morphological differences exist, however, between *Meruliopsis* and *Ceriporia* sensu stricto, and some overlap was observed. For example, *Meruliopsis* is separated from *Ceriporia* mainly by the meruloid to poroid hymenophore with a continuous hymenium over the dissepiments (Ginns 1976; Chamuris 1988). However, some *Meruliopsis* species produce typical pores with sterile dissepiments, such as *M. crassitunicata* and *M. parvispora*. Besides, most *Meruliopsis* species possess cystidia or cystidioles (except for *M. crassitunicata* and *M. parvispora*), whereas only one species of *Ceriporia* possesses cystidia (viz., *C. bubalinomarginata* B.S. Jia & Y.C. Dai).

Clade II is very well supported and includes type species of *Ceriporia* and *Leptoporus* Qué. In clade II, *Leptoporus* has nomenclatural priority over *Ceriporia*. However, *Leptoporus* is a monotypic genus, and *Ceriporia* has considerably more species. To treat

Ceriporia in clade II as *Leptoporus* would result in dramatic number of name changes. Moreover, *Leptoporus* causes brown rot in wood (Ryvarden and Melo 2017), whereas *Ceriporia* causes white rot. At this moment, we suggest the following: (i) acknowledge *Ceriporia* as a paraphyletic group (in clade II) but retain its generic concept for the time being; and (ii) formally conserve *Ceriporia* against *Leptoporus* (in clade II) in the future.

In clade II (FIGS. 1, 2), the concept of *Ceriporia* expands to encompass resupinate species with a smooth hymenophore (e.g., *Candelabrochaete langloisii*, *C. septocystidia*, and *Phanerochaete allantospora*) and pileate species with a poroid hymenophore (e.g., *Leptoporus mollis*). Microscopically, these species share monomitic hyphal systems and allantoid basidiospores. *Candelabrochaete* Boidin was distinguished by the small clavate basidia, septate cystidia, and a loosely interwoven subiculum (Burdall 1984). However, *Candelabrochaete* is polyphyletic, and the type species, *C. africana* Boidin, is not nested in the phlebioid clade (Justo et al. 2017) and thus not included in this study. For the time being, it may be too early to make generic name changes for these species. Solving relationships among these taxa may require additional data.

Three subclades in clade II, namely, the *Ceriporia pierii*, *C. purpurea*, and *C. viridans* groups, are interpretable in terms of morphology (FIGS. 1, 2). The *C. pierii* group includes species with white, pale pink, or pale ochraceous basidiocarps with a minutely rhizomorphic margin, cylindrical to ellipsoid basidiospores (>2 µm in width), and fan-shaped crystals occurring among the subiculum. Also, the subicular hyphae are wider than the tramal hyphae (Miettinen et al. 2016). The *C. purpurea* group encompasses species with pink, reddish, or violet and gelatinous basidiocarps, allantoid to cylindrical basidiospores, and hyphae of nearly the same diameter in subiculum and trama (Spirin et al. 2016). The *C. viridans* group comprises *C. aurantiocarnescens* and *C. viridans* sensu lato with cream to cinnamon or orange basidiocarps and curved and cylindrical basidiospores (<2 µm in width). Like the *C. pierii* group, subicular hyphae are wider than tramal ones (Pieri and Rivoire 1997; Ryvarden and Melo 2017).

Ceriporia viridans sensu lato contains at least three genetically different lineages (FIG. 2). Among them, a lineage consisting of three European samples (Miettinen 11701, Spirin 5909, and Spirin 3483) may represent *C. viridans* sensu stricto, since this species was originally described from Britain and widespread in Europe (Pieri and Rivoire 1997; Ryvarden and Melo 2017). Other lineages contain non-European specimens

from East Asia or North America. Species delimitation within the *C. viridans* sensu lato is so far unresolved and waiting a thorough revision.

In clade III, two species of *Emmia* Zmitr. et al. and *C. cystidiata* were recovered in a clade, with very high support. *Emmia* was established merely based on morphological characters, with *E. latemarginata* as the type species (Zmitrovich et al. 2006). Subsequently, its generic status was supported by phylogenetic studies, and an additional species: *E. lacerata* (N. Maekawa, Suhara & R. Kondo) F. Wu, Jia J. Chen & Y.C. Dai (\equiv *Ceriporia lacerata* N. Maek., Suhara & R. Kondo) was accommodated (Zmitrovich and Malysheva 2014; Miettinen et al. 2016; Wu et al. 2017). *Emmia lacerata* is a common species in forest ecosystems and has been reported as the agent of human disease (Chowdhary et al. 2014). *Emmia* is characterized by resupinate basidiocarps with white to cream pore surface, simple-septate hyphae, presence or absence of encrusted cystidia, and ellipsoid basidiospores.

Ryvarden and Iturriaga (2003) recently described *Ceriporia cystidiata* from Venezuela, without providing DNA sequences from the type specimen. Later, Permpornsakula et al. (2016) redescribed and sequenced this species from Thailand based on a specimen (PBU 0048) that forms a lineage with *E. lacerata* and *E. latemarginata* with high support (FIG. 1). Morphologically, *C. cystidiata* also fits well with *Emmia* based on previous descriptions (Ryvarden and Iturriaga 2003; Permpornsakula et al. 2016). However, we refrain from concluding the generic placement of this species until more representative sequences are available.

Ceriporia sulphuricolor Bernicchia & Niemelä is a rare species hitherto known from the type locality in Italy (Bernicchia and Niemelä 1998) and temperate China (Jia and Cui 2011b). Phylogenetically, a specimen of *C. sulphuricolor* from China (Dai 6090) is closely related to *Ceraceomyces serpens* (Tode) Ginns (FIG. 1). At the moment, we are uncertain whether Dai 6090 represents the real *C. sulphuricolor*, since other representative sequences of this species are not available now.

Ceriporia alachuana is widespread in the southern United States, as well as in East Asia and Europe (Ryvarden and Melo 2017). Two specimens of *C. alachuana* from Florida (L-11510-Sp) and Maryland (FP-103881-Sp) of United States, respectively, form a lineage allied with the generic type of *Hydnophlebia* Parmasto within the Meruliaceae (FIG. 1), which is consistent with recent studies (Floudas and Hibbett 2015; Justo et al. 2017; Chen et al. 2018). Bernicchia and Niemelä (1998) have studied a duplicate of L-11510-Sp (as Lowe 11510 in their study) whose basidiospore size was measured

as $3.8\text{--}4.5 \times 2\text{--}2.3 \mu\text{m}$. This *C. alachuana* lineage seems to represent this species because its type locality is from Florida.

Ceriporia alachuana resembles *Hydnophlebia* in having resupinate basidiocarp, monomitic hyphae system with simple-septate hyphae, and ellipsoid basidiospores. However, the latter has hydroid hymenophore and cystidia (Ryvarden and Melo 2017; Telleria et al. 2017). According to their close relationship, *Ceriporia alachuana* should be phylogenetically congeneric with *Hydnophlebia*. For some genera of Agaricomycetes Doweld, poroid and hydroid species can be congeneric, e.g., *Sistotrema* Fr., *Sidera* Miettinen & K.H. Larss, and *Xylodon* (Pers.) Fr. (Miettinen and Larsson 2011). However, we refrain from transferring *C. alachuana* to *Hydnophlebia* until more comprehensive studies of this lineage are available.

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