

Two new species of *Ceriporia* (Irpicaceae, Basidiomycota) from Asia Pacific

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Abstract

Based on morphology and phylogeny of samples from Asia Pacific, two new species of *Ceriporia*, *C. eucalypti* sp. nov. and *C. sino-viridans* sp. nov., are described. *C. eucalypti* is characterized by resupinate and snow white fresh basidiocarps, abundant crystals and oily substances present in subiculum and trama, distinct allantoid basidiospores measuring $4\text{--}4.4 \times 1.1\text{--}1.4 \mu\text{m}$, and growing on wood of *Eucalyptus* in Australia. *C. sino-viridans* is characterized by white to flesh-pink fresh pores, ellipsoid to lunate basidiospores measuring $3\text{--}3.5 \times 1.7\text{--}2.2 \mu\text{m}$, and occurring in tropical China. Phylogenetically *C. eucalypti*, *C. sino-viridans*, *C. aurantiocarnescens* and *C. viridans* are related, but they can be distinguished by size of basidiospores. A key to accepted species of *Ceriporia* in China is provided.

Introduction

Ceriporia Donk, belonging to the Irpicaceae Spirin & Zmitr. of Polyporales (Justo et al. 2017), was established by Donk (1933) with *Polyporus viridans* Berk. & Broome (\equiv *C. viridans* (Berk. & Broome) Donk) as the type species. It is a poroid genus comprises species with seasonal, thin and resupinate basidiocarps which are soft when fresh and variable colors and fragile when dry. Microscopically species in the genus has a monomitric hyphal structure with simple septa on generative hyphae in most species, subicular hyphae usually distinctly thicker than tramal hyphae, lacking of cystidia in most species, and hyaline, thin-walled basidiospores which are negative in Cotton Blue and Melzer's reagent, and causing a white rot (Gilbertson and Ryvarden 1986; Jia et al. 2014; Ryvarden and Melo 2017; Chen et al. 2020).

The genus was at first considered monophyletic based on five sequences of mitochondrial small subunit rDNA (Kim and Jung 1999). Recently, more molecular data of *Ceriporia* were provided by phylogenetic analyses and the genus was treated as sensu lato (s.l.) based on the internal transcribed spacer (ITS) regions and nuclear large subunit (nrLSU) ribosomal RNA gene regions (Jia et al. 2014; Floudas and Hibbett 2015; Miettinen et al. 2016; Spirin et al. 2016; Justo et al. 2017; Yuan et al. 2017; Chen et al. 2020). Based on sequences from ITS, nrLSU, and the gene encoding the RNA polymerase II largest subunit (rpb1), three species of *Ceriporia* addressed in the Phanerochaetaceae Jülich were transferred to the recently proposed genera *Emmia* Zmitr. et al. (*E. lacerata* (N. Maek. et al.) F. Wu et al. \equiv *C. lacerata* N. Maek. et al.), *Phanerina* Miettinen (*P. mellea* (Berk. & Broome) Miettinen \equiv *C. inflata* B.S. Jia & B.K. Cui) and *Riopa* D.A. Reid. (*R. metamorphosa* (Fuckel) Miettinen & Spirin \equiv *C. metamorphosa* (Fuckel) Ryvarden & Gilb.) (Miettinen et al. 2016; Wu et al. 2017). With the aid of three loci (ITS, 28S, and rpb1), Chen et al. (2020) revised the part species concept of *Ceriporia* s.l. and *Meruliopsis* Bondartsev, resulting four new combinations: *M. albomellea* (Yuan Yuan et al.) C.C. Chen & Sheng H. Wu (\equiv *C. albomellea* Yuan Yuan et al.), *M. crassitunicata* (Y.C. Dai & Sheng H. Wu) C.C. Chen & Sheng H. Wu (\equiv *C. crassitunicata* Y.C. Dai & Sheng H. Wu), *M. nanlingensis* (B.K. Cui & B.S. Jia) C.C. Chen & Sheng H. Wu (\equiv *C. nanlingensis* B.K. Cui & B.S. Jia), and *M. pseudocystidiata* (B.S. Jia & Y.C. Dai) C.C. Chen & Sheng H. Wu (\equiv *C. pseudocystidiata* B.S. Jia & Y.C. Dai). For the being now, approximately 54 *Ceriporia* species have been recorded worldwide including 18 species from China (Jia et al. 2014; Spirin et al. 2016; Ryvarden and Melo 2017; Yuan et al. 2017; Ryvarden 2018, 2020; Chen et al. 2020).

During a study on wood-decaying fungi from Asia Pacific area, three specimens have seasonal and thin basidiocarps, a monomitic hyphal structure with simple septa on generative hyphae, and hyaline, thin-walled, ellipsoid or lunate to allantoid basidiospores. These characteristics correspond definition of *Ceriporia*, but no existing names are suitable for them. After phylogenetic analyses, these samples formed two independent lineages in *Ceriporia* clades. Based on both morphology and phylogeny, we describe them as two new species of *Ceriporia*, one is from tropical China and another from Australia.

Materials And Methods

Morphological studies

Specimens examined were deposited in the herbaria of the Institute of Microbiology, Beijing Forestry University (BJFC). Australian specimen will forward to Royal Botanic Gardens Victoria, Australia (MEL). Morphological descriptions are based on field notes and herbarium specimens. Microscopic analyses follow Dai (2010). In the description: KOH = 5% potassium hydroxide, IKI = Melzer's reagent, IKI- = neither amyloid nor dextrinoid, CB = Cotton Blue, CB+ = cyanophilous in Cotton Blue, CB- = acyanophilous, L = mean spore length (arithmetic average of all spores), W = mean spore width (arithmetic average of all spores), Q = variation in the L/W ratios between the specimens studied, n (a/b) = number of spores (a) measured from given number (b) of specimens. Colour terms are cited from Petersen (1996).

Molecular studies and phylogenetic analysis

A cetyl trimethylammonium bromide rapid plant genome extraction kit (Demeter Biotechnologies Co., Ltd, Beijing) was used to extract total genomic DNA from dried specimens, and performed the polymerase chain reaction (PCR) according to the manufacturer's instructions with some modifications (Cui et al. 2019). Two DNA gene fragments, ITS and nrLSU were amplified using the primer pairs respectively ITS5/ITS4 (White et al. 1990) and LR0R/LR7 (Vilgalys and Hester 1990). The PCR procedures for ITS and nrLSU followed Shen et al. (2019) in the phylogenetic analyses. DNA sequencing was performed at Beijing Genomics Institute, and the newly generated sequences were deposited in the GenBank database. Besides the sequences generated from this study (Table 1), other reference taxa for our phylogenetic analysis were selected from GenBank, Jia et al. (2014), Miettinen et al. (2016), and Chen et al. (2020). Sequences were aligned with BioEdit (Hall 1999) and ClustalX (Thompson et al. 1997). Alignment was manually adjusted to allow maximum alignment and to minimize gaps. Sequence alignment was deposited at TreeBase (<http://purl.org/phylo/treebase/>; submission ID 27658).

Table 1

A list of species, specimens, and GenBank accession numbers of sequences used in this study

Species name	Sample no.	Locality	GenBank accession no.	
			ITS	nLSU
<i>Bjerkandera adusta</i>	NBRC 4983	—	AB733156	AF287848
<i>Byssomerulius corium</i>	FP 102382	USA	KP135007	KP135230
<i>Candelabrochaete langloisii</i>	FP 110343sp	USA	KY948793	KY948886
<i>C. septocystidia</i>	AS 95	Sweden	EU118609	EU118609
Ceriporia alachuana	Dai 17769	Singapore	MW491773	MW491763
<i>C. alachuana</i>	FP 103881-Sp	USA	KP135341	KP135201
<i>C. arbuscula</i>	GC 1708 - 338	China	LC427008	LC427040
<i>C. aurantiocarnescens</i>	Dai 6055	China	JX623904	JX644043
<i>C. aurantiocarnescens</i>	Dai 17951	China	MW491774	MW491764
<i>C. bresadolae</i>	HK 18071	Russia	KX236469	KX236469
<i>C. bubalinomarginata</i>	Dai 11327	China	JX623953	JX644045
<i>C. bubalinomarginata</i>	Dai 17937	China	MW491775	MW491765
<i>C. cystidiata</i>	Dai 18323	Vietnam	MW491776	MW491766
<i>C. cystidiata</i>	Dai 18388	Vietnam	MW491777	MW491767
<i>C. cystidiata</i>	Dai 18500A	China	MW491778	MW491768
<i>C. cystidiata</i>	ROI 2	Thailand	KC570339	KU760725
<i>C. eucalypti</i>	Dai 18675	Australia	MW491779	MW491769
<i>C. excelsa</i>	Dai 3204	China	JX644056	—
<i>C. griseoviolascens</i>	JV 0110/26	Czech	KX236487	KX236487
<i>C. humilis</i>	Spirin 4706	Russia	KX752608	—
<i>C. manzanitae</i>	Ryvarde 21832	USA	KX236478	KX236478
<i>C. mpurii</i>	Miettinen 14381	Indonesia	KX752603	KX752603
<i>C. occidentalis</i>	Spirin 8558	USA	KX236475	KX236475
<i>C. pierii</i>	Rivoire 1161	France	KX752604	KX752604

New sequences are shown in bold.

Species name	Sample no.	Locality	GenBank accession no.	
			ITS	nLSU
<i>C. punicans</i>	JV 0808/30	USA	KX236479	KX236479
<i>C. purpurea</i>	Rivoire 4413	France	KX236461	KX236461
<i>C. reticulata</i>	KHL11981	Norway	JX109845	JX109845
<i>C. sericea</i>	Spirin 4944	Russia	KX752609	KX752609
<i>C. sino-viridans</i>	Dai 13617A	China	MW491780	MW491770
<i>C. sino-viridans</i>	Dai 13621A	China	MW491781	MW491771
<i>C. sordescens</i>	Miettinen 15492.2	USA	KX752606	KX752606
Dai 10477	China	KC182769	KC182781	
Dai 8110	China	KC182767	KC182784	
Dai 8168	China	KC182768	KC182785	
Yuan 5862	China	KC182771	KC182782	
Yuan 5965	China	KC182772	KC182783	
<i>C. spissa</i>	JV 0108/6	USA	KX236483	KX236483
<i>C. spissa</i>	PRM 915965	USA	GU594155	—
<i>C. sulphuricolor</i>	Dai 6090	China	JX623934	JX644066
<i>C. torpida</i>	Murdoch 90	Finland	KX236477	KX236477
<i>C. triumphalis</i>	Kout 18	Spain	KX236476	KX236476
<i>C. viridans</i>	Miettinen 11701	Netherlands	KX752600	KX752600
<i>C. viridans</i>	VS3843	Russia	KX236480	KX236480
<i>C. viridans</i>	VS5909	Finland	KX236481	KX236481
<i>Ceriporiopsis aneirina</i>	HHB 15629- Sp	USA	KP135023	KP135207
<i>C. gilvescens</i>	Niemelä 5516	Czech	HQ659222	HQ659222
<i>Emmia lacerata</i>	Dai 10734	China	JX623916	JX644068
<i>E. lacerata</i>	Dai 18520A	China	MW491782	MW491772

New sequences are shown in bold.

Species name	Sample no.	Locality	GenBank accession no.	
			ITS	nLSU
<i>E. latemarginata</i>	Piatek 4.IX.1997	Poland	KX752592	KX752592
<i>Gloeoporus dichrous</i>	KHL 11173	Norway	EU118627	EU118627
<i>Hyphoderma litschaueri</i>	FP 101740-Sp	USA	KP135295	KP135219
<i>H. setigerum</i>	FD 312	USA	KP135297	KP135222
<i>Hyphodermella corrugata</i>	MA Fungi 5527	Morocco	FN600372	JN939597
<i>H. rosae</i>	MA Fungi 22929	Spain	FN600391	JN939580
<i>Irpex lacteus</i>	FD-9	USA	KP135026	KP135224
<i>Leptoporus mollis</i>	RLG 7163	USA	EU402583	EU402583
<i>Macrohyporia dictyopora</i>	PBU 0051	Thailand	KC570331	KU760726
<i>Meruliopsis albomellea</i> (<i>Ceriporia albomellea</i>)	Dai 15205	China	KX494574	KX494578
<i>M. crassitunicata</i> (<i>C. crassitunicata</i>)	Dai 10833	China	JX623935	JX644064
<i>M. cystidiata</i> (<i>Gloeoporus cystidiatus</i>)	776308	Brazil	MG572749	MG572733
<i>M. leptocystidiata</i>	Wu 1708-43	China	LC427013	LC427033
<i>M. leptocystidiata</i>	Li 1011	China	JX623898	JX644049
<i>M. nanlingensis</i> (<i>Ceriporia nanlingensis</i>)	Yuan 5749	China	JX623940	JX644054
<i>M. parvispora</i>	Wu 1209-58	China	LC427017	LC427039
<i>M. pseudocystidiata</i> (<i>Ceriporia pseudocystidiata</i>)	Li 1704	China	JX623944	—
<i>M. tarda</i> (<i>Ceriporia tarda</i>)	Dai 10226	China	JX623945	—
<i>M. taxicola</i>	Kuljok 00/75	Sweden	EU118648	EU118648
<i>M. variegata</i> (<i>Ceriporia variegata</i>)	Li 1780	China	JX623936	JX644065
<i>Oxychaete cervinogilvus</i>	Schigel 5216	Australia	KX752596	KX752596
<i>Phanerina mellea</i> (<i>Ceriporia mellea</i>)	Dai 9453	China	JX623932	JX644059
<i>Phanerochaete affinis</i>	KHL 11839	Sweden	EU118652	EU118652

New sequences are shown in bold.

Species name	Sample no.	Locality	GenBank accession no.	
			ITS	nrLSU
<i>P. allantospora</i>	KKN 111-Sp	USA	KP135038	KP135038
<i>P. exilis</i>	HHB 6988	USA	KP135001	KP135236
<i>P. inflata</i> (<i>C. inflata</i>)	Cui 7712	China	JX623930	JX644063
<i>P. sordida</i>	KHL 12054	Norway	EU118653	EU118653
<i>Phlebia livida</i>	FCUG 2189	—	AF141624	AF141624
<i>P. subochracea</i>	KGN 162/95	Sweden	EU118656	EU118656
<i>P. tremellosa</i>	FCUG 1813	Sweden	AF141632	AF141632
<i>Pirex concentricus</i>	OSC 41587	USA	KP134984	KP135275
<i>Riopa metamorphosa</i> (<i>C. metamorphosa</i>)	Spirin 2395	Russia	KX752601	KX752601
<i>Riopa pudens</i>	Cui 3238	China	JX623931	JX644060
New sequences are shown in bold.				

Maximum parsimony analysis was applied to the combined dataset of ITS and nrLSU sequences with PAUP* version 4.0b10 (Swofford 2002). The sequences of *Hyphoderma litschaueri* (Burt) J. Erikss. & Å. Strid and *H. setigerum* (Fr.) Donk were used as the outgroups (Chen et al. 2020). All characters were equally weighted, and gaps were treated as missing data. Trees were inferred using the heuristic search option with TBR branch swapping and 1,000 random sequence additions. Max-trees were set to 5,000, branches of zero length were collapsed and all parsimonious trees were saved. Clade robustness was assessed by bootstrap analysis with 1,000 replicates (Felsenstein 1985). Descriptive tree statistics, tree length (TL), consistency index (CI), retention index (RI), rescaled consistency index (RC), and homoplasy index (HI) were calculated for each maximum parsimonious tree generated.

Maximum likelihood (ML) analysis and Bayesian inference (BI) methods were also used to analyze the combined ITS and nrLSU dataset. Substitution models suitable for each partition in both datasets were determined using Akaike Information Criterion implemented in MrMODELTEST2.3 (Nylander 2004). The General Time Reversible + proportion Invariant + Gamma (GTR + I + G) was the selected substitution model for each partition. RAxML v7.2.6 (Stamatakis 2006) was used for ML analysis. All parameters in the ML analysis used the default setting, and statistical support values were obtained using nonparametric bootstrapping with 1000 replicates. A Bayesian tree was inferred using MrBayes3.1.2 (Ronquist and Huelsenbeck 2003), with a general time reversible model of DNA substitution and an invgamma distribution rate variation across sites. Four Markov chains were run for two runs from random starting trees for 2,500,000 generations for ITS + nrLSU, and trees were sampled every 100 generations. The first one-fourth of the generations were discarded as burn-in. Majority rule consensus

tree of all remaining trees was calculated. Branches that received bootstrap values for MP, ML, and bayesian posterior probabilities (BPP) greater than or equal to 75% (MP), 75% (ML), and 0.90 (BPP) were considered as significantly supported. Tree was visualized in TreeView 1.6.6 (Page 1996).

Results

Molecular phylogeny

The ITS + nrLSU dataset included sequences from 81 fungal specimens representing 64 taxa. The dataset had an aligned length of 1,613 characters, of which 810 characters are constant, 170 are variable and parsimony-uninformative, and 633 are parsimony-informative. Maximum parsimony analysis yielded six equally parsimonious trees (TL = 4,324, CI = 0.329, RI = 0.652, RC = 0.215, HI = 0.671). BI, ML and MP analyses yielded similar tree topologies with an average standard deviation of split frequencies = 0.009281 and only the MP tree is shown (Fig. 1). Both bootstrap values ($\geq 50\%$) and BPPs (≥ 0.90) are shown at the nodes (Fig. 1).

The sequences of *Ceriporia eucalypti* clustered together with *C. aurantiocarnescens* (Henn.) M. Pieri & B. Rivoire with high support (76% ML and 0.99 BPPs, Fig. 1), then formed a distinct supported clade together with *C. sino-viridans* and *C. viridans* with modest support (67% ML and 1 BPPs).

Taxonomy

Ceriporia eucalypti Y.C. Dai & Jia J. Chen, sp. nov. (Figs. 2–3)

MycoBank no.: MB 838617

Ceriporia eucalypti is characterized by its annual, resupinate, snow white fresh basidiocarps, generative hyphae with simple septa, allantoid basidiospores measuring $4.0 - 4.4 \times 1.1 - 1.4 \mu\text{m}$ and a distribution in Australia.

Type. AUSTRALIA. Melbourne, Dandenong Ranges Botanical Garden, on rotten wood of *Eucalyptus*, 12.V.2018, Dai 18675 (holotype BJFC027144, isotype in MEL).

Etymology. *Eucalypti* (Lat.) referring to the host tree of *Eucalyptus*.

Rotting type. White rot.

Basidiocarps. Basidiocarps annual, resupinate, very soft when fresh, brittle when dry, up to 3 cm long, 1 cm wide, and 1.1 mm thick at center. Pore surface snow white when fresh, curry-yellow when dry; pores angular, 3–5 per mm; dissepiment thin, lacerate. Margin thin, cream to buff, cottony, up to 1 mm wide. Subiculum white, fragile when dry, up to 0.1 mm thick. Tubes concolorous with pore surface, brittle when dry, up to 1 mm long.

Hyphal structure. Hyphal system monomitic; generative hyphae with simple septa, IKI–, CB+; tissues unchanged in KOH.

Subiculum. Generative hyphae hyaline, thin- to thick-walled, frequently branched, interwoven, 4–6 µm in diam; abundant crystals and oily substances present among hyphae.

Tubes. Generative hyphae hyaline, thin-walled, frequently branched, subparallel along tube to loosely interwoven, slightly gelatinized, usually incrustated with irregular crystals, 2–4 µm in diam; cystidia and cystidioles absent; basidia barrel-shaped, with four sterigmata and a simple basal septum, 12–14 · 3–4 µm; basidioles in shape similar to basidia, but slightly smaller.

Spores. Basidiospores allantoid, hyaline, thin-walled, smooth, IKI–, CB–, sometimes bearing one or two guttules, (3.8–)4–4.4(–4.6) · 1.1–1.4(–1.5) µm, L = 4.2 µm, W = 1.2 µm, Q = 3.5 (n = 30/1).

Ceriporia sino-viridans Y.C. Dai & Jia J. Chen, sp. nov. (Figs. 4–5)

Mycobank no.: MB 838618

Ceriporia sino-viridans is distinguished from other species in the genus by its annual, resupinate, white to flesh-pink fresh basidiocarps, generative hyphae with simple septa, ellipsoid to lunate basidiospores measuring 3.0 – 3.5 × 1.7 – 2.2 µm and a distribution in China.

Type. CHINA. Hainan Prov., Baoting County, Diaoluoshan Forest Park, on dead basidiocarp of *Physisporinus vinctus*, 14.VI.2014, Dai 13617A (Holotype BJFC017356).

Etymology. *Sino-viridans* (Lat.) referring to the Chinese specimens similar to *Ceriporia viridans*.

Rotting type. White rot.

Basidiocarps. Basidiocarps annual, resupinate, very soft when fresh, brittle when dry, up to 8 cm long, 4 cm wide, and 1 mm thick at center. Pore surface white to flesh-pink when fresh, pinkish buff when dry; pores more or less circular, 4–6 per mm; dissepiment thin, lacerate. Margin thin, buff, cottony, up to 1 mm wide. Subiculum cream, fragile when dry, less than 0.1 mm thick. Tubes concolorous with pore surface, brittle when dry, up to 0.9 mm long.

Hyphal structure. Hyphal system monomitic; generative hyphae with simple septa, IKI–, CB+; tissues unchanged in KOH.

Subiculum. Generative hyphae hyaline, thin- to slightly thick-walled, frequently branched, interwoven, 6–8 µm in diam; irregular crystals present among hyphae.

Tubes. Generative hyphae hyaline, thin-walled, frequently branched, subparallel along tube or loosely interwoven, 3–5 µm in diam; cystidia and cystidioles absent; basidia short clavate to barrel-shaped, with

four sterigmata and a simple basal septum, 10–12 · 4–4.5 µm; basidioles in shape similar to basidia, but slightly smaller.

Spores. Basidiospores ellipsoid to lunate, hyaline, thin-walled, smooth, IKI–, CB–, (2.9–)3–3.5(–3.8) · (1.4–)1.7–2.2(–2.3) µm, L = 3.21 µm, W = 1.93 µm, Q = 1.66 (n = 60/2).

Additional specimen examined (paratype). CHINA. Hainan Prov., Baoting County, Diaoluoshan Forest Park, on rotten angiosperm wood, 14.VI.2014, Dai 13621A (BJFC017360).

Discussion

Phylogenetically *Ceriporia eucalypti* is related to *C. aurantiocarnescens*, *C. sino-viridans* and *C. viridans*, but the latter three species have wider basidiospores (4–4.4 · 1.1–1.4 µm in *C. eucalypti*, 3.5–4 · 1.8–2 µm in *C. aurantiocarnescens*, 3–3.5 · 1.7–2.2 µm in *C. sino-viridans* and 4–6 · 1.5–2 µm in *C. viridans*, Ryvarden & Melo 2017). *C. sino-viridans* differs from *C. aurantiocarnescens* and *C. viridans* by its shorter basidiospores (see above data).

Ceriporia eucalypti is similar to *C. alba* M. Pieri & B. Rivoire by sharing snow white pore surface and almost the same size of pores, but the latter species has bigger basidiospores (5.5–7 × 2–2.5 µm, Pieri and Rivoire 1997). Among species of *Ceriporia*, *C. eucalypti* resembles *C. albobrunnea* Ryvarden & Iturr. and *C. arbuscula* C.C. Chen & Sheng H. Wu by thin basidiospores (<1.5 µm wide). However, *C. albobrunnea* is different from *C. eucalypti* by its bigger pores (2–3 per mm), thick dissepiments and occurring in Venezuela (Ryvarden and Iturriaga 2003); *C. arbuscula* differs from *C. eucalypti* by its shorter basidiospores (3–3.5 × 1–1.5 µm, Chen et al. 2020).

Ceriporia sino-viridans is very similar to *C. viridans*, the latter species was originally described from UK and has a highly variable in micromorphology (Ryvarden 1984). However, *C. viridans* differs from *C. sino-viridans* by longer basidiospores (4–6 · 1.5–2 µm, Ryvarden and Melo 2017). The fresh basidiocarps of *C. sino-viridans* remind of *C. xylostromatoides* (Berk.) Ryvarden, but the latter species has subglobose basidiospores (4–5 · 3.5–4.5 µm, Ryvarden and Melo 2017).

Two specimens of *Ceriporia alachuana* (Murrill) Hallenb. respectively from Maryland (FP-103881-Sp) of United States and Singapore (Dai 17769), formed a lineage within the Meruliaceae Rea (Fig. 1). This lineage seems to represent *C. alachuana* because the species was originally described from United States. In our phylogeny, the sequences of the specimen Li 1011 which was originally identified as Chinese *C. alachuana* clustered together with that of *Meruliopsis leptocystidiata* with high support (100% MP, 1 BPPs). The ITS sequences of the specimen Li 1011 (GenBank Accession No. MG572749) showed 99.83% identity to that of the holotype *M. leptocystidiata* LC427013. Therefore, the Chinese samples previously treated as *C. alachuana* seem to be *M. leptocystidiata*.

Our phylogenetic tree is overall consistent with that presented by Miettinen et al. (2016) and Chen et al. (2020). Judging from our molecular analysis, *Ceriporia* is still a heterogeneous assemblage. It seems

more taxa are existed in the so-called ` *C. spissa* (Schwein. ex Fr.) Rajchenb.´. Moreover the taxonomic status of some *Ceriporia* species nested in Meruliaceae (e.g. *C.alachuana*) or the other genera (e.g. *C. cystidiata* Ryvarden & Iturr.) is needed to be confirmed. Therefore, a fully resolved phylogeny for *Ceriporia*, *Meruliopsis*, *Emmia* and their related genera requires evolutionary information from wider taxa samplings and more conserved gene markers. The studies on these taxa will be done in the coming papers.

Key to species of *Ceriporia* in China

- 1 Hyphal system dimitic————— *C. totara* (G. Cunn.) P.K. Buchanan & Ryvarden
- 1 Hyphal system monomitic————— 2
- 2 Cystidia present————— 3
- 2 Cystidia absent————— 6
- 3 Pores 6–8 per mm————— 4
- 3 Pores 1–5 per mm————— 5
- 4 Cystidia tubular and encusted————— *C. bubalinomarginata* B.S. Jia & Y.C. Dai
- 4 Cystidia clavate and non-encusted————— *C. cystidiata*
- 5 Cystidia present at the bottom of tube only; basidiospores > 2.9 µm wide—————
————— *C. mellea* (Berk. & Broome) Ryvarden
- 5 Cystidia present in all parts of the hymenium; basidiospores mostly < 2.9 µm wide—————
————— *C. purpurea* (Fr.) Donk
- 6 Basidiospores allantoid————— 7
- 6 Basidiospores oblong-ellipsoid to cylindrical, or cylindrical but a little curved————— 10
- 7 Pores brown, orange-brown to reddish-brown; basidiospores mostly > 5 µm long—————
————— *C. spissa*
- 7 Pores cream, buff, cinnamon, salmon, clay-pink or brownish vinaceous; basidiospores mostly < 5 µm long————— 8
- 8 Pores 5–8 per mm————— *C. aurantiocarnescens*
- 8 Pores 3–6 per mm————— 9

9 Basidiospores 4.0–4.4 × 1.1–1.4 μm	—————	<i>C. eucalypti</i>
9 Basidiospores 4–6 × 1.5–2 μm	—————	<i>C. viridans</i>
10 Basidiospores mostly > 5 μm long	—————	11
10 Basidiospores mostly <5 μm long	—————	12
11 Pores 2–3 per mm; tramal hyphae thin-walled	—————	<i>C. reticulata</i> (Hoffm.) Domański
11 Pores 3–4 per mm; tramal hyphae thin- to slightly thick-walled	—————	
—————	—————	<i>C. camaresiana</i> (Bourdot & Galzin) Bondartsev & Singer
12 Tramal hyphae interwoven	—————	<i>C. sulphuricolor</i> Bernicchia & Niemelä
12 Tramal hyphae parallel or subparallel along the tube	—————	13
13 Subicular hyphae thick-walled	—————	14
13 Subicular hyphae thin- to slightly thick-walled	—————	15
14 Basidiospores > 3.5 μm long	—————	<i>C. tarda</i> (Berk.) Ginns
14 Basidiospores < 3.5 μm long	—————	<i>C. arbuscula</i>
15 Pores 2–3 per mm	—————	<i>C. excels</i> Parmasto
15 Pores 3–6 per mm	—————	16
16 Basidiospores > 4.2 μm long	—————	<i>C. davidii</i> (D.A. Reid) M. Pieri & B. Rivoire
16 Basidiospores < 4.2 μm long	—————	17
17 Pores white to cream when dry	—————	<i>C. humilis</i> Spirin & Miettinen
17 Pores pinkish buff when dry	—————	<i>C. sino-viridans</i>

Declarations

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Declarations

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The authors declare that there are no conflicts of interest.

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All data generated or analysed during this study are included in this published article and its supplementary information files.

Code availability: Not applicable.

Authors' contributions:

Jia-Jia Chen, Wang Ya-Rong, Wang Chao-Ge performed the experiment, the data analyses and wrote the manuscript. Yu-Cheng Dai designed the experiments and helped perform the analysis with constructive discussions.

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Table

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

Species name	Sample no.	Locality	GenBank accession no.	
			ITS	nLSU
<i>Bjerkandera adusta</i>	NBRC 4983	—	AB733156	AF287848
<i>Byssomerulius corium</i>	FP 102382	USA	KP135007	KP135230
<i>Candelabrochaete langloisii</i>	FP 110343sp	USA	KY948793	KY948886
<i>C. septocystidia</i>	AS 95	Sweden	EU118609	EU118609
<i>Ceriporia alachuana</i>	Dai 17769	Singapore	MW491773	MW491763
<i>C. alachuana</i>	FP 103881-Sp	USA	KP135341	KP135201
<i>C. arbuscula</i>	GC 1708-338	China	LC427008	LC427040
<i>C. aurantiocarnescens</i>	Dai 6055	China	JX623904	JX644043
<i>C. aurantiocarnescens</i>	Dai 17951	China	MW491774	MW491764
<i>C. bresadolae</i>	HK 18071	Russia	KX236469	KX236469
<i>C. bubalinomarginata</i>	Dai 11327	China	JX623953	JX644045
<i>C. bubalinomarginata</i>	Dai 17937	China	MW491775	MW491765
<i>C. cystidiata</i>	Dai 18323	Vietnam	MW491776	MW491766
<i>C. cystidiata</i>	Dai 18388	Vietnam	MW491777	MW491767
<i>C. cystidiata</i>	Dai 18500A	China	MW491778	MW491768
<i>C. cystidiata</i>	ROI 2	Thailand	KC570339	KU760725
<i>C. eucalypti</i>	Dai 18675	Australia	MW491779	MW491769
<i>C. excelsa</i>	Dai 3204	China	JX644056	—
<i>C. griseoviolascens</i>	JV 0110/26	Czech	KX236487	KX236487
<i>C. humilis</i>	Spirin 4706	Russia	KX752608	—
<i>C. manzanitae</i>	Ryvarden 21832	USA	KX236478	KX236478
<i>C. mpurii</i>	Miettinen 14381	Indonesia	KX752603	KX752603
<i>C. occidentalis</i>	Spirin 8558	USA	KX236475	KX236475
<i>C. pierii</i>	Rivoire 1161	France	KX752604	KX752604
<i>C. punicans</i>	JV 0808/30	USA	KX236479	KX236479
<i>C. purpurea</i>	Rivoire 4413	France	KX236461	KX236461
<i>C. reticulata</i>	KHL11981	Norway	JX109845	JX109845
<i>C. sericea</i>	Spirin 4944	Russia	KX752609	KX752609
<i>C. sino-viridans</i>	Dai 13617A	China	MW491780	MW491770
<i>C. sino-viridans</i>	Dai 13621A	China	MW491781	MW491771
<i>C. sordescens</i>	Miettinen 15492.2	USA	KX752606	KX752606
' <i>C. spissa</i> '	Dai 10477	China	KC182769	KC182781
' <i>C. spissa</i> '	Dai 8110	China	KC182767	KC182784
' <i>C. spissa</i> '	Dai 8168	China	KC182768	KC182785
' <i>C. spissa</i> '	Yuan 5862	China	KC182771	KC182782
' <i>C. spissa</i> '	Yuan 5965	China	KC182772	KC182783
<i>C. spissa</i>	JV 0108/6	USA	KX236483	KX236483
<i>C. spissa</i>	PRM 915965	USA	GU594155	—
<i>C. sulphuricolor</i>	Dai 6090	China	JX623934	JX644066
<i>C. torpida</i>	Murdoch 90	Finland	KX236477	KX236477
<i>C. triumphalis</i>	Kout 18	Spain	KX236476	KX236476
<i>C. viridans</i>	Miettinen 11701	Netherlands	KX752600	KX752600
<i>C. viridans</i>	VS3843	Russia	KX236480	KX236480
<i>C. viridans</i>	VS5909	Finland	KX236481	KX236481
<i>Ceriporiopsis aneirina</i>	HHB 15629-Sp	USA	KP135023	KP135207
<i>C. gilvescens</i>	Niemelä 5516	Czech	HQ659222	HQ659222

<i>Emmia lacerata</i>	Dai 10734	China	JX623916	JX644068
<i>E. lacerata</i>	Dai 18520A	China	MW491782	MW491772
<i>E. latemarginata</i>	Piatek 4.IX.1997	Poland	KX752592	KX752592
<i>Gloeoporus dichrous</i>	KHL 11173	Norway	EU118627	EU118627
<i>Hyphoderma litschaueri</i>	FP 101740-Sp	USA	KP135295	KP135219
<i>H. setigerum</i>	FD 312	USA	KP135297	KP135222
<i>Hyphodermella corrugata</i>	MA Fungi 5527	Morocco	FN600372	JN939597
<i>H. rosae</i>	MA Fungi 22929	Spain	FN600391	JN939580
<i>Irpex lacteus</i>	FD-9	USA	KP135026	KP135224
<i>Leptoporus mollis</i>	RLG 7163	USA	EU402583	EU402583
<i>Macrohyporia dictyopora</i>	PBU 0051	Thailand	KC570331	KU760726
<i>Meruliopsis albomellea (Ceriporia albomellea)</i>	Dai 15205	China	KX494574	KX494578
<i>M. crassitunicata (C. crassitunicata)</i>	Dai 10833	China	JX623935	JX644064
<i>M. cystidiata (Gloeoporus cystidiatus)</i>	776308	Brazil	MG572749	MG572733
<i>M. leptocystidiata</i>	Wu 1708-43	China	LC427013	LC427033
<i>M. leptocystidiata</i>	Li 1011	China	JX623898	JX644049
<i>M. nanlingensis (Ceriporia nanlingensis)</i>	Yuan 5749	China	JX623940	JX644054
<i>M. parvispora</i>	Wu 1209-58	China	LC427017	LC427039
<i>M. pseudocystidiata (Ceriporia pseudocystidiata)</i>	Li 1704	China	JX623944	—
<i>M. tarda (Ceriporia tarda)</i>	Dai 10226	China	JX623945	—
<i>M. taxicola</i>	Kuljok 00/75	Sweden	EU118648	EU118648
<i>M. variegata (Ceriporia variegata)</i>	Li 1780	China	JX623936	JX644065
<i>Oxychaete cervinogilvus</i>	Schigel 5216	Australia	KX752596	KX752596
<i>Phanerina mellea (Ceriporia mellea)</i>	Dai 9453	China	JX623932	JX644059
<i>Phanerochaete affinis</i>	KHL 11839	Sweden	EU118652	EU118652
<i>P. allantospora</i>	KKN 111-Sp	USA	KP135038	KP135038
<i>P. exilis</i>	HHB 6988	USA	KP135001	KP135236
<i>P. inflata (C. inflata)</i>	Cui 7712	China	JX623930	JX644063
<i>P. sordida</i>	KHL 12054	Norway	EU118653	EU118653
<i>Phlebia livida</i>	FCUG 2189	—	AF141624	AF141624
<i>P. subochracea</i>	KGN 162/95	Sweden	EU118656	EU118656
<i>P. tremellosa</i>	FCUG 1813	Sweden	AF141632	AF141632
<i>Pirex concentricus</i>	OSC 41587	USA	KP134984	KP135275
<i>Riopa metamorphosa (C. metamorphosa)</i>	Spirin 2395	Russia	KX752601	KX752601
<i>Riopa pudens</i>	Cui 3238	China	JX623931	JX644060

New sequences are shown in bold.

Figures

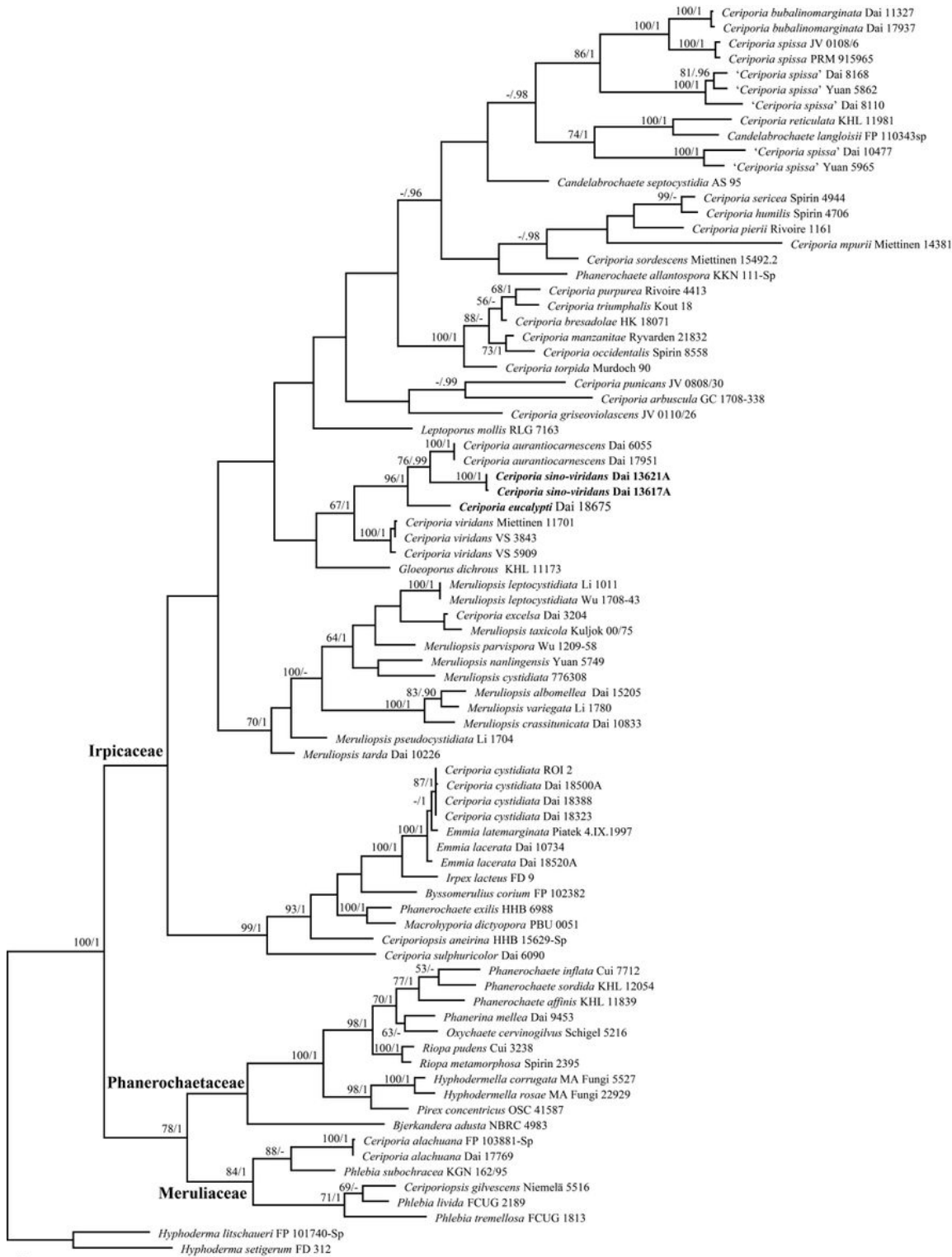


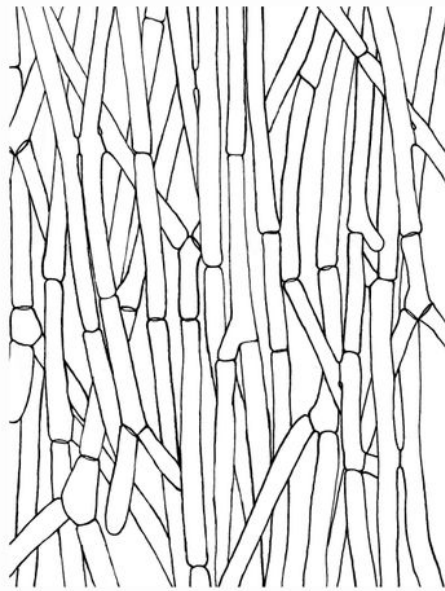
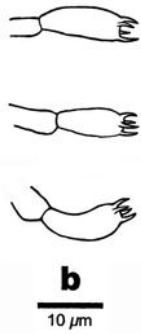
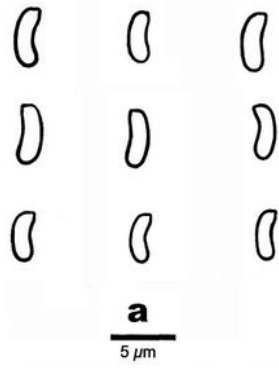
Figure 1

Phylogeny of *Ceriporia* and related species generated by maximum parsimony analysis based on combined ITS and nrLSU sequences. Branches are labeled with parsimony bootstrap values $\geq 50\%$ and Bayesian posterior probabilities ≥ 0.90 .

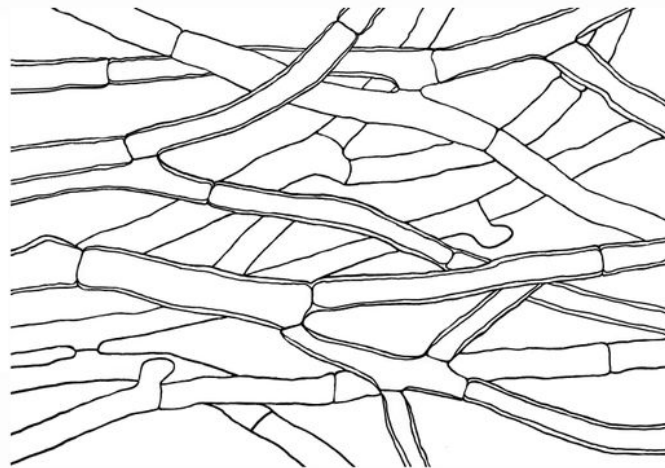


Figure 2

Basidiocarps of *Ceriporia eucalypti* (holotype, Dai 18675). Bar: 1 cm. Photo by Yu-Cheng Dai.



d
10 μm



e
10 μm

Figure 3

Microscopic structures of *Ceriporia eucalypti* (drawn from Dai 18675). a. Basidiospores. b. Basidia. c. Basidioles. d. Hyphae from trama. e. Hyphae from subiculum.

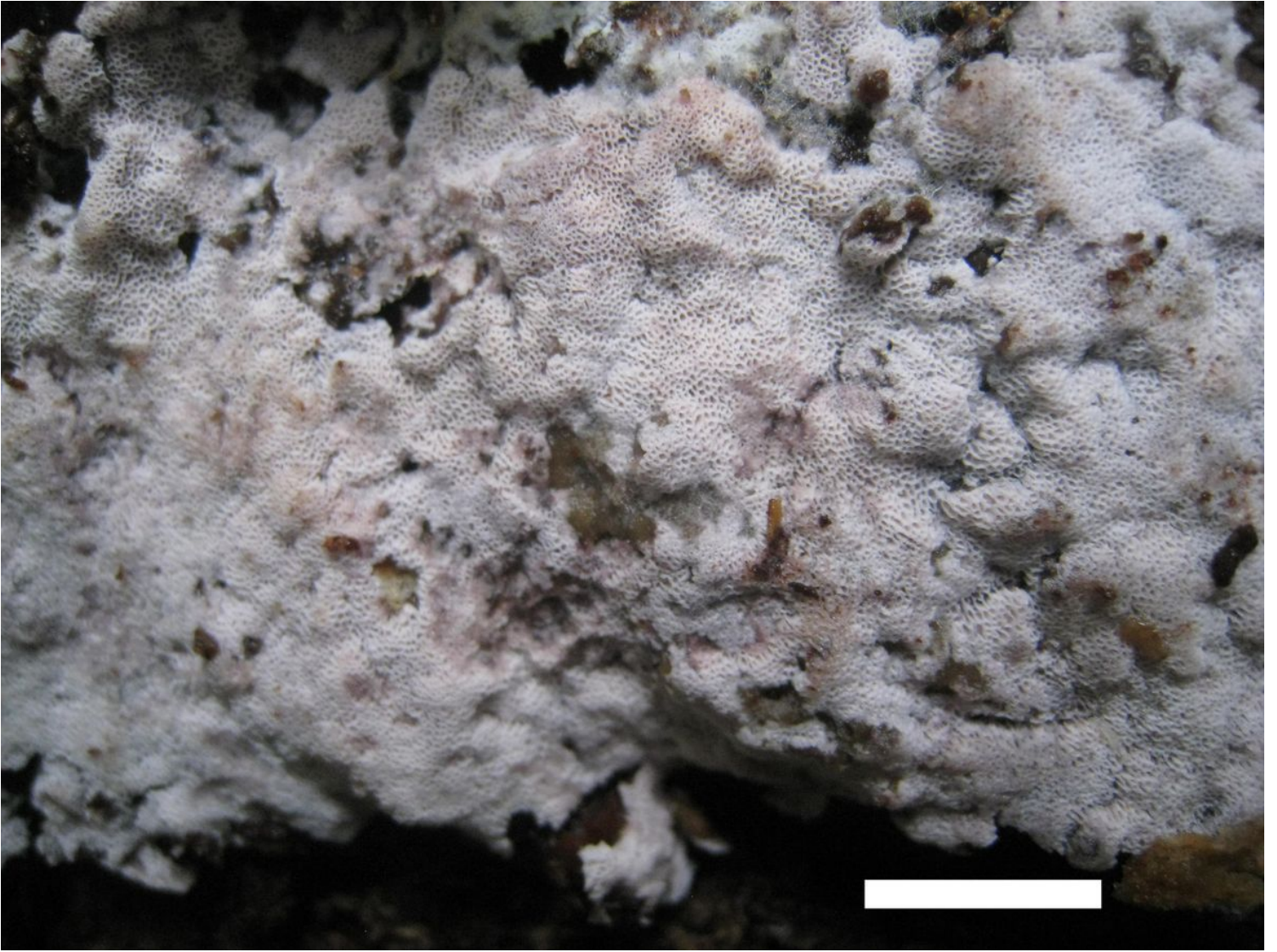


Figure 4

A basidiocarp of *Ceriporia sino-viridans* (holotype, Dai13617A). Bar: 1 cm. Photo by Yu-Cheng Dai.

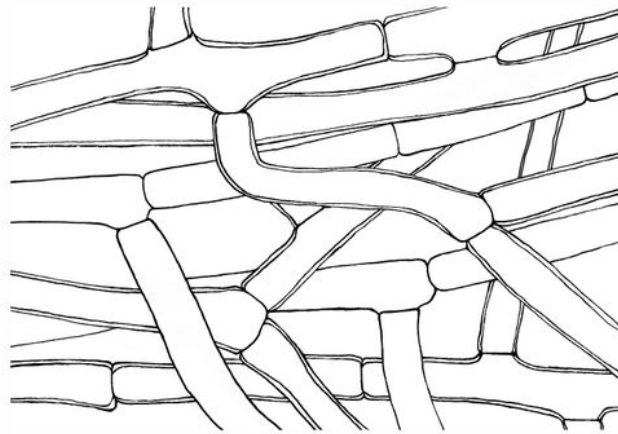
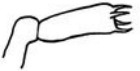
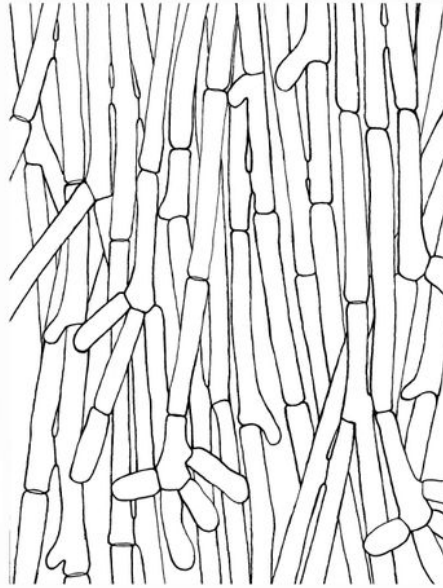
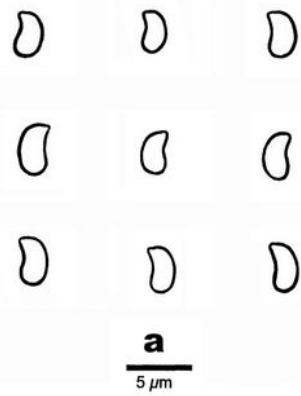


Figure 5

Microscopic structures of *Ceriporia sino-viridans* (drawn from Dai 13617A). a. Basidiospores. b. Basidia. c. Basidioles. d. Hyphae from trama. e. Hyphae from subiculum.