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ORIGINAL ARTICLE

Taxonomy and phylogeny of *Ceriporia* (Polyporales, Basidiomycota) with an emphasis of Chinese collections

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Abstract *Ceriporia* accommodates a kind of wood-inhabiting polypores producing resupinate basidiocarps and causing a white rot. More than 30 species of this genus have been described; however, only a few species were referred to molecular phylogeny. In this study, a total of 203 specimens of *Ceriporia* were studied morphologically, and the ITS and/or nLSU regions from 42 samples, representing 18 species, were sequenced for phylogenetic analysis. Based on both morphological and phylogenetic analyses, three new species of *Ceriporia*, *C. bubalinomarginata*, *C. pseudocystidiata* and *C. variegata*, are described and illustrated. An annotated identification key is provided for all 20 species of this genus thus far known in China. Our phylogeny shows that (1) *Ceriporia* is not monophyletic, (2) *C. spissa* and *C. viridans* as morphologically circumscribed are polyphyletic, (3) *C. inflata* is retained for both *C. inflata* and *C. jiangxiensis*, and (4) presence or absence of hymenial cystidia is not a useful character in delimiting species relationships in *Ceriporia*.

Keywords Phanerochaetaceae · ITS · nLSU · Wood-inhabiting fungi

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Introduction

Ceriporia Donk, belonging to the Phanerochaetaceae, the Polyporales, was established by Donk (1933) with *Polyporus viridans* Berk. & Broome as type. The species in this genus have an annual growth habit, cause a white rot, and produce resupinate basidiocarps with variable colors of poroid surface, a monomitic hyphal structure with simple septa on generative hyphae, and hyaline, thin-walled and usually cylindrical to oblong-ellipsoid basidiospores (Gilbertson and Ryvarden 1986; Ryvarden 1991; Ryvarden and Gilbertson 1993; Núñez and Ryvarden 2001). However, a few species with a dimitic hyphal structure, generative hyphae with clamps and cystidia have also been addressed in the genus, because of their similar growth habit and basidiospores (Buchanan and Ryvarden 1988; Pieri and Rivoire 1997; Ryvarden and Iturriaga 2003; Aime et al. 2007; Jia and Cui 2011). *Ceriporia* has a wide distribution, and 36 species have been recorded worldwide (Gilbertson and Ryvarden 1986; Buchanan and Ryvarden 1988; Ryvarden and Gilbertson 1993; Pieri and Rivoire 1997; Bernicchia and Niemelä 1998; Lindblad and Ryvarden 1999; Rajchenberg 2000; Dai et al. 2002; Suhara et al. 2003; Ryvarden and Iturriaga 2003; Gilbertson and Hemmes 2004; Aime et al. 2007; Læssøe and Ryvarden 2010; Mata and Ryvarden 2010; Jia and Cui 2011, 2012; Gomes-Silva et al. 2012). The identification of the species of *Ceriporia* is difficult, because there are only a few stable taxonomical characters and a single species might have even various pore surfaces in color.

Although phylogenetic analyses on many genera within Polyporales have been carried out (Decock and Stalpers 2006; Robledo et al. 2009; Bernicchia et al. 2012; Yuan and Wan 2012; Zhao and Cui 2012; Zhou and Qin 2012; Cui and Decock 2013), only a few species of *Ceriporia* were described with molecular supports (Kim and Jung 1999;

Table 1 Species used for phylogenetic analysis in this study with their vouchers and GenBank accession numbers

Species name	Voucher No.	GenBank No.	
		ITS	nLSU
Antrodia xantha (Fr.) Ryvarden	CBS 155.79	DQ491424	
A. xantha	P 289		AJ583430
Bjerkandera adusta (Willd.) P. Karst.	B 1	JX049389	
B. adusta	NBRC 104974	AB733157	
B. adusta	BRFM 965	JX082339	
B. sp.	M 127		HM595615
Ceriporia alachuana (Murrill) Hallenb.	Li 968	**JX623899**	
C. alachuana	Li 1011	**JX623898**	**JX644047**
C. alachuana	Li 1115	**JX623900**	**JX644050**
C. aurantiocarnescens (Henn.) M. Pieri & B. Rivoire	Yuan 975	**JX623901**	
C. aurantiocarnescens	Yuan 2066	**JX623902**	**JX644042**
C. aurantiocarnescens	Dai 6055	**JX623904**	**JX644043**
C. bubalinomarginata Y.C. Dai & B.S. Jia	Dai 11327	**JX623953**	**JX644045**
C. bubalinomarginata	Dai 12499	**JX623954**	**JX644043**
C. camaresiana (Bourdot & Galzin) Bondartsev & Singer	Cui 3238	**JX623931**	**JX644060**
C. crassitunicata Y.C. Dai & Sheng H. Wu	Dai 10833	**JX623935**	**JX644064**
C. crassitunicata	Dai 9995	**JX623905**	
C. excelsa S. Lundell ex Parmasto	Dai 3204		**JX644056**
C. inflata B.S. Jia & B.K. Cui	Dai 10376	**JX623929**	**JX644062**
C. inflata	Cui 7712	**JX623930**	**JX644063**
C. lacerata N. Maek., Suhara & R. Kondo	Li 449	**JX623918**	
C. lacerata	Dai 9501	**JX623908**	**JX644069**
C. lacerata	Dai 10734	**JX623916**	**JX644068**
C. lacerata	KUC 3018	DQ912694	
C. lacerata	SFFPS MZ-340 (Type)	AB091675	
C. mellea (Berk. & Broome) Ryvarden	Dai 9453	**JX623932**	**JX644059**
C. mellea	Dai 9667	**JX623933**	**JX644058**
C. nanlingensis B.K. Cui & B.S. Jia	Li 1670	**JX623939**	**JX644055**
C. nanlingensis	Dai 8107	**JX623938**	**JX644052**
C. nanlingensis	Yuan 5749		**JX644051**
C. pseudocystidiata Y.C. Dai & B.S. Jia	Cui 6878	**JX623943**	**JX644057**
C. purpurea (Fr.) Donk	Dai 6205	**JX623951**	**JX644046**
C. purpurea	Dai 6366	**JX623952**	**JX644047**
C. reticulata (Hoffm.) Domański	Li 1045	**JX623946**	
C. reticulata	Li 1316	**JX623947**	
C. spissa (Schwein. ex Fr.) Rajchenb.	Cui 8097	**KC182780**	
C. spissa	Dai 10477	**KC182769**	**KC182781**
C. spissa	Dai 8110	**KC182767**	**KC182784**
C. spissa	Dai 8168	**KC182768**	**KC182785**
C. spissa	Yuan 5862	**KC182771**	**KC182782**
C. spissa	Yuan 5965	**KC182772**	**KC182783**
C. spissa	PRM 915964	GU594154	
C. spissa	PRM 915965	GU594155	
C. sulphuricolor Bernicchia & Niemelä	Dai 6090	**JX623934**	**JX644066**
C. tarda (Berk.) Ginns	Dai 10226	**JX623945**	
C. variegata Y.C. Dai & B.S. Jia	Li 1780	**JX623936**	**JX644065**
C. viridans (Berk. & Broome) Donk	Yuan 2744	**KC182773**	

Table 1 (continued)

Species name	Voucher No.	GenBank No.	
		ITS	nLSU
C. viridans	Yuan 2747	**KC182778**	
C. viridans	Cui 8012	**KC182774**	
C. viridans	Yuan 5702	**KC182779**	
C. viridans	Li 1046	**KC182776**	
C. viridans	Dai 5183		**KC182786**
Ceriporiopsis gilvescens (Bres.) Domański	Tuomo Niemelä 5516 (H)		HQ659222
C. rivulosa (Berk. & M.A. Curtis) Gilb. & Ryvarden	T241i	JQ027728	
C. rivulosa	JLL-10602-sp	AY219363	
C. sp.	PRM 899297		JN592504
C. sp.	PRM 899300		JN592505
C. sp.	JV 0904/46		JN592507
Gloeoporus dichrous (Fr.) Bres.	KHL 11173 (GB)		EU118627
G. taxicola (Pers.) Gilb. & Ryvarden	GL 52	AM231907	
G. taxicola	O 146364	AM231903	
G. taxicola	GB 98		AY586656
G. taxicola	Kuljok 00/75 (GB)		EU118648
Hyphodermella corrugata (Fr.) J. Erikss. & Ryvarden	MA-Fungi 5527	FN600372	JN939597
H. corrugata	MA-Fungi 5529	FN600381	
H. corrugata	MA-Fungi 7653		JN939593
H. rosae (Bres.) Nakasone	MA-Fungi 1103	FN600384	
H. rosae	MA-Fungi 22929	FN600391	JN939580
H. rosae	MA-Fungi 24292		JN939589
Phanerochaete affinis (Burt) Parmasto	KHL 11839		EU118652
P. chrysosporium (Burds.) Hjortstam & Ryvarden	IFM 47473	AB361644	
P. chrysosporium	HN19	JQ796876	
P. sordida (P. Karst.) J. Erikss. & Ryvarden	xsd08107	FJ481018	
P. sordida	KHL 12054		EU118653
P. sordida	M 47		HM595608
Phlebia firma J. Erikss. & Hjortstam	K268 (GB)		EU118654
P. leptospermi (G. Cunn.) Stalpers	TTT 1607	HQ153413	
P. livida (Pers.) Bres.	MG 103	HQ153415	
P. livida	MG 104	HQ153416	
P. radiata Fr.	ATCC64658	FJ746663	
P. radiata	FPL6140		AF287885
P. subochracea (Alb. & Schwein.) J. Erikss. & Ryvarden	KGN 162/95 (GB)		EU118656
P. tremellosa (Schrad.) Nakasone & Burds.	BRFM 968	JX082340	
P. tremellosa	I 236	GU062266	
P. unica (H.S. Jacks. & Dearden) Ginns	K268 (GB)		EU118657

Newly submitted sequences are indicated in *bold*

Suhara et al. 2003). Larsson et al. (2004) and Binder et al. (2005) showed that *Ceriporia* was situated in the phlebioid clade of polyporoid clade. However, only two species of *Ceriporia*, isolating from each other, were included in the analyses (Larsson et al. 2004; Binder et al. 2005). Therefore, the overall picture of phylogenetic relationships among species of *Ceriporia* is unknown.

Wood-decaying fungi in subtropical China have been extensively studied, and many new species have been described recently (i.e. Wang et al. 2011; Yuan and Wan 2012; Cui 2013; He and Li 2013; Li and Cui 2013). However, there are still many unknown specimens of wood-decaying fungi from subtropical China. During the examination of the undetermined specimens from subtropical China, three undescribed species of *Ceriporia* were identified. To confirm the affinity of and infer the evolutionary relationships among the new taxa and other species of *Ceriporia*, phylogenetic analysis on this genus was performed based on the ribosomal internal transcribed spacer (ITS) regions and nuclear ribosomal large subunit (nLSU).

Materials and methods

Morphological study

The studied specimens are deposited at the herbaria of the Institute of Microbiology, Beijing Forestry University (BJFC), the Botanical Museum of the University of Oslo, Norway (O), Université Claude Bernard, France (LY), Museum of National Natural History, France (P), National Museum of Czech Republic (PRM), Landcare Research, New Zealand (PDD) and University of Guyana, Guyana (BRG). In the text, the following abbreviations are used: KOH=10 % potassium hydroxide, CB = Cotton Blue, CB+ = cyanophilous, CB– = acyanophilous, IKI = Melzer's reagent, IKI– = both inamyloid and indextrinoid, L = mean basidiospore length (arithmetic average of all basidiospores), W = mean basidiospore width (arithmetic average of all basidiospores), Q = variation in the L/W ratios between the specimens studied, n (a/b) = number of basidiospores (a) measured from given number (b) of specimens. Macro-morphological descriptions are based on the field notes. Special color terms follow Anonymous (1969) and Petersen (1996). Micro-morphological data were obtained from dried specimens. Sections were studied at magnification up to ×1000, using a Nikon Eclipse 80i microscope and phase contrast illumination. Drawings were made with the aid of a drawing tube. Microscopic features, measurements and drawings were made from slide preparations stained with CB, KOH and IKI. Basidiopores were measured from sections cut from the tubes. In presenting the variation in size of basidiospores, 5 % of the measurements were excluded from each end of the range, and are given in parentheses.

Molecular study

Phire® Plant Direct PCR Kit (Finnzymes, Finland) was used to directly amplify PCR products from herbarium specimens. A small piece of fruit body was incubated in 30 μl Dilution Buffer for 3 min at room temperature, and then 0.75 μl of the supernatant were used as template for a 30 μl polymerase chain reaction (PCR): initial denaturation at 98 °C for 5 min, followed by 39 cycles at 98 °C for 5 s, 59 °C (for ITS)/52 °C (for nLSU) for 5 s and 72 °C for 5 s, and a final extension of 72 °C for 1 min. DN14-CTAB A Large Number of Plant Genomic DNA Rapid Extraction Kit (Aidlab Biotechnologies Co., Ltd, China) was also used to extract total genomic DNA, according to manufacture's instructions, from herbarium specimens for subsequent PCR amplifications using Trans 2×EasyTaq PCR SuperMix with 1 μl of the supernatant as template for a 30 μl reaction system. The PCR procedure was as follows: initial denaturation at 94 °C for 1 min, followed by 35 cycles at 94 °C for 30 s, 54 °C (for both ITS and nLSU) for 1 min and 72 °C for 1.5 min, and a final extension of 72 °C for 10 min. Primer pair ITS5 and ITS4 (White et al. 1990) was used to amplify ITS sequences, while primers LROR and LR7 (http://www.biology.duke.edu/fungi/mycolab/primers.htm) were used to amplify nLSU region. The PCR products were directly sequenced in the Beijing Genomics Institute, China with the same primers as those in the amplifications. All newly generated sequences were submitted to GenBank (http://www.ncbi.nlm.nih.gov; Table 1).

Phylogenetic analysis

For the type species of *Ceriporia*, *C. viridans* (Berk. & Broome) Donk, has been evidenced in the phlebioid clade (Larsson et al. 2004; Binder et al. 2005), the ITS and nLSU sequences from other species in this clade were also downloaded from GenBank (Table 1) and included in phylogenetic analysis. Most of the vouchers of these sequences only have either ITS or nLSU sequences. Therefore, the ITS and nLSU sequences were not combined to analysis. *Antrodia xantha* (Fr.) Ryvarden, belonging to the Antrodia clade (Binder et al. 2005), was selected as outgroup. Two datasets, ITS and nLSU, were, respectively, aligned using ClustalX 1.83 (Chenna et al. 2003) with default parameters, and then manually edited using BioEdit 7.0.1 (Hall 1999) as necessary.

Maximum parsimony (MP) analysis was performed using PAUP* version 4.0b10 (Swofford 2002). Gaps in the alignments 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 automatically increase by 100, branches of zero length were collapsed and all parsimonious trees were saved. Clade stability was assessed by performing 1,000 bootstrap (BS) replicates (Felsenstein 1985). Descriptive tree statistics, tree length (TL), consistency index (CI), retention index (RI), rescaled consistency index (RC), homoplasy index (HI) were calculated for each tree generated.

The best-fit parameters for Bayesian inference (BI) of the two datasets were estimated with MrMODELTEST2.3 (Posada and Crandall 1998; Nylander 2004). Following these parameters, MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003) was used for BI, implementing by Markov chain Monte Carlo (MCMC) technique. Eight simultaneous Markov chains were run for 4,000,000 and 3,000,000 generations, respectively, for ITS and nLSU datasets, starting from random trees and keeping one tree every 100th generation. The first 25 % trees were discarded as the burn-in phase of

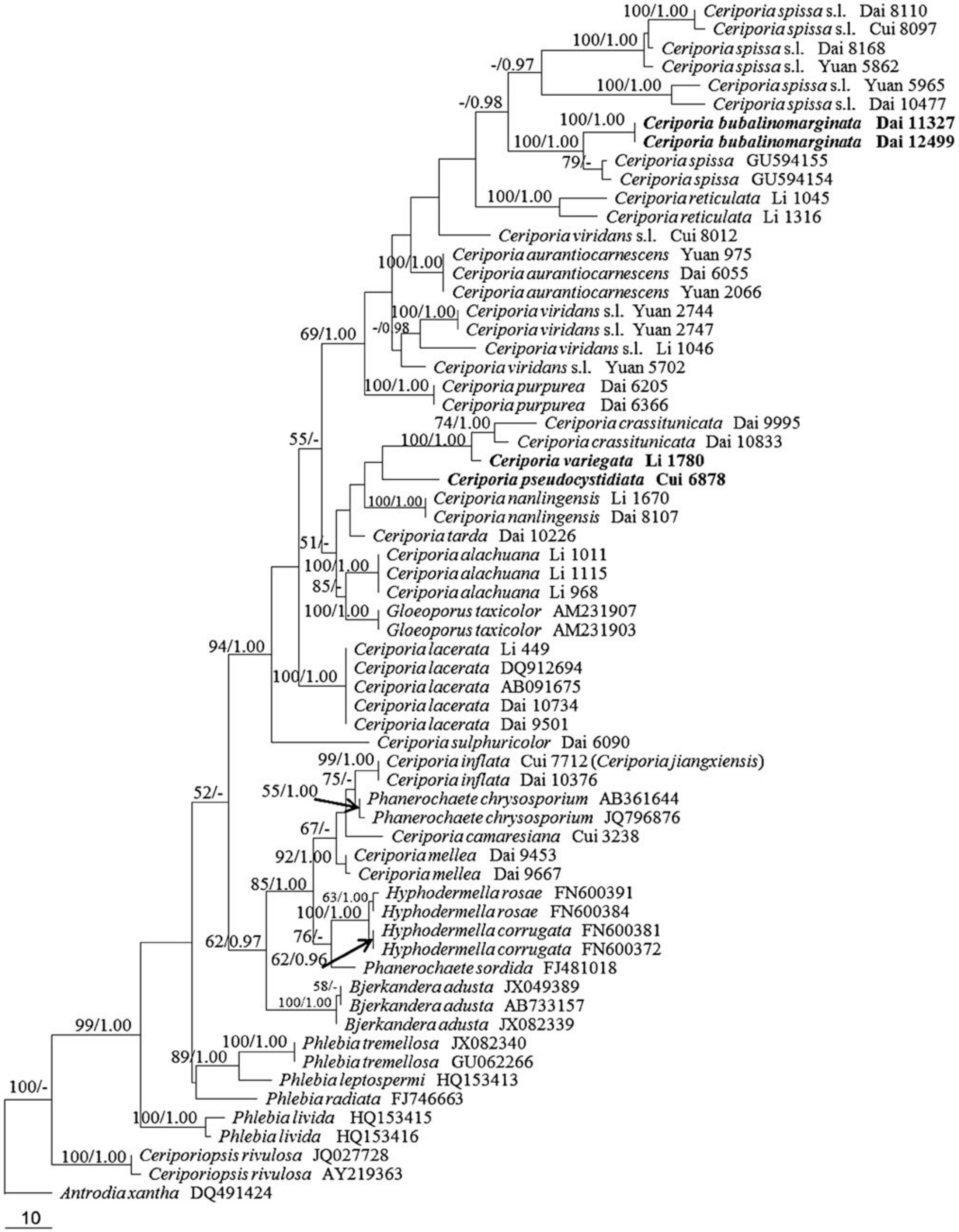

Fig. 1 Phylogeny of *Ceriporia* and some related species inferred from ITS sequences. Topology from MP analysis with BS (above 50 %) and BPP (above 0.95) from MP and BI analyses, respectively. New species described here are shown in *bold*

the analysis, while the remaining trees were used for calculating Bayesian posterior probabilities (BPPs) for each clade. Trees were figured in Treeview 1.6.6 (Page 1996).

Results

Molecular phylogeny

The ITS dataset, including 64 ITS sequences from 43 *Ceriporia* and 21 other related samples, resulted in a 710 character alignment with 416 parsimony informative characters. MP analysis yielded one MP tree (TL=806, CI=0.3018, RI=0.5995, RC=0.2209, HI=0.6982). Best model was estimated as GTR+G and was applied in BI, which resulted in average standard deviation of split frequencies=0.005700. The topologies from MP and BI trees were similar, and thus only the MP tree was presented with both BS values (above 50 %) and BPPs (above 0.95) at the nodes (Fig. 1).

The tree inferred from ITS dataset (Fig. 1) shows that not all species of *Ceriporia* formed a clade, while some species from other genera in the phlebioid clade were clustered together with the species of *Ceriporia*. At the species level, most species of *Ceriporia* previously identified by morphology were evidenced. However, both *Ceriporia spissa* (Schwein. ex Fr.) Rajchenb. and *C. viridans* were polyphyletic, while *C. inflata* B.S. Jia & B.K. Cui and *Ceriporia jiangxiensis* B.S. Jia & B.K. Cui were clustered together. In addition, one unknown clade (Dai 11327 & 12499) and two new branches (Li 1780 and Cui 6878) were formed by four Chinese specimens.

A total of 49 nLSU sequences from 29 *Ceriporia* and 20 other related samples were included in the nLSU dataset, which resulted in an alignment with 202 parsimony informative characters from total 1317 characters. MP analysis generated one MP tree (TL=685, CI=0.3847, RI=0.7609, RC=0.3044, HI=0.6153). GTR+I was estimated as best model and applied in BI, which resulted in average standard deviation of split frequencies=0.004475. MP and BI trees had similar topologies. Therefore, only the topology from MP tree was presented with both BS values (above 50 %) and BPPs (above 0.95) at the nodes (Fig. 2).

Like the ITS tree, the tree from nLSU dataset (Fig. 2) suggests that *Ceriporia* under the current circumscription is not a monophyletic genus and the concepts of certain species should be reevaluated. One unknown clade and two new branches of Chinese specimens in the ITS tree were also supported in the nLSU tree.

Taxonomy

Ceriporia bubalinomarginata B.S. Jia & Y.C. Dai, sp. nov. (Fig. 3)

MycoBank no.: MB 802906

Basidiocarps annual, resupinate. Pore surface clay-buff, orange brown, fawn to reddish brown when dry; pores angular, 6–7 per mm. Hyphal system monomitic; generative hyphae with simple septa. Cystidia clavate, hyaline, thin-walled, 21.8–26.6×2.8–4.1 μm. Basidiospores allantoid, hyaline, thin-walled, IKI–, CB–, 3.5–4.3×1–1.2 μm.

Type. CHINA. Henan Prov., Neixiang County, Baotianman Nat. Res., on rotten angiosperm wood, 23.IX.2009 Dai 11327 (holotype in BJFC).

Etymology. *Bubalinomarginata* (Lat.) refers to the cream to buff margin.

Fruitbody. Basidiocarps annual, resupinate, brittle when dry, up to 8.3 cm long, 5.4 cm wide, and 1.7 mm thick at center. Pore surface clay-buff, orange brown, fawn to reddish brown when dry; pores angular, 6–7 per mm; dissepiment thin, slightly lacerate. Margin thin, cream to buff, cottony, up to 3 mm wide. Subiculum cream to buff, fragile when dry, up to 0.4 mm thick. Tubes concolorous with pore surface, brittle when dry, up to 1.3 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, 2.6–4.5 μm in diam; tiny pale-yellow crystals present among hyphae.

Tubes. Generative hyphae hyaline, thin- to slightly thick-walled, frequently branched, parallel along the tubes, usually incrusted with orange-brown crystals, 2.2–3.6 μm in diam; cystidia present, clavate, hyaline, thin-walled, 21.8–26.6×2.8–4.1 μm; basidia clavate, with four sterigmata and a simple basal septum, 8.4–12.9×2.7–4 μm; basidioles in shape similar to basidia, but obviously smaller.

Spores. Basidiospores allantoid, hyaline, thin-walled, smooth, IKI–, CB–, (3.2–)3.5–4.3(–4.5)×1–1.2(–1.3) μm, L=3.93 μm, W=1.07 μm, Q=3.54–3.82 (*n*=60/2).

Type of rot. White rot.

Additional specimen examined (paratype). — CHINA. Sichuan Prov., Ya'an County, Mengding Mountain, on rotten angiosperm wood, 21.VIII.2011 Dai 12499 (BJFC).

Remarks. *Ceriporia bubalinomarginata* is characterized by its clay-buff, orange brown, fawn to reddish brown pore surface, cream to buff margin, small pores, narrowly allantoid basidiospores and clavate cystidia. It is similar to *Ceriporia spissa*, which, however, has larger basidiospores (4–6×1.5–2 μm) and lacks cystidia (Gilbertson and Ryvarden 1986). *Ceriporia subspissa* Aime & Ryvarden also has deep reddish brown pore surface and cystidia, but its pores are larger (4–5/mm) and its basidiospores are ellipsoid (4–4.5×2 μm, Aime et al. 2007). *Ceriporia purpurea* (Fr.) Donk resembles *C. bubalinomarginata* by similar pore surface and cystidia, but the former species has larger pores (3–4/mm) and basidiospores (5–6×2–2.5 μm, Ryvarden and Gilbertson 1993).

Ceriporia pseudocystidiata B.S. Jia & Y.C. Dai, sp. nov. (Fig. 4)

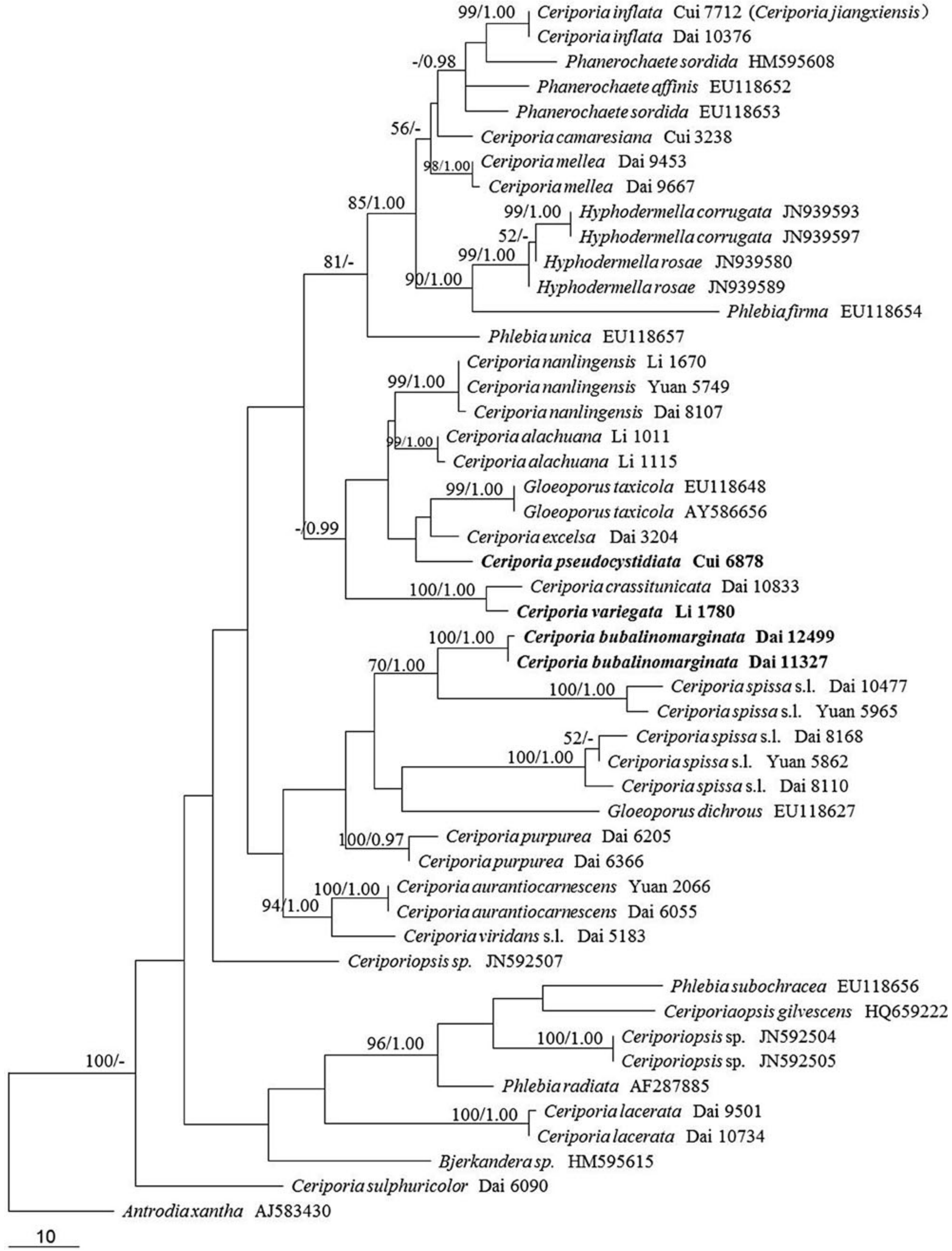

Fig. 2 Phylogeny of *Ceriporia* and some related species inferred from nLSU sequences. Topology from MP analysis with BS (above 50 %) and BPP (above 0.95) from MP and BI analyses, respectively. New species described here are shown in *bold*

MycoBank no.: MB 802907

Basidiocarps annual, resupinate. Pore surface buff-yellow to cinnamon-buff when dry; pores round to irregular, very shallow, 4–5 per mm. Hyphal system monomitic; generative hyphae with simple septa. Cystidia clavate, hyaline, mostly 25–54×3–6 μm, some up to 90 μm. Basidiospores allantoid, hyaline, thin-walled, IKI–, CB–, 3.7–4.3×1.6–1.8 μm.

Type. CHINA. Hunan Prov., Yizhang County, Mangshan Nat. Res., on rotten angiosperm stump, 25.VI.2007 Li 1704 (holotype in BJFC).

Etymology. Pseudocystidiata (Lat.) refers to resemblance with *Ceriporia cystidiata.*

Fruitbody. Basidiocarps annual, resupinate, brittle when dry, up to 5.5 cm long, 2.6 cm wide, and 0.25 mm thick at the centre. Pore surface buff-yellow to cinnamon-buff when dry; pores round to irregular, very shallow, 4–5 per mm; dissepiment thin, entire. Margin very thin, up to 3 mm wide, white, lanate. Subiculum white to cream, fragile, lanate, up to 0.2 mm thick. Tubes concolorous with pore surface, brittle when dry, up to 0.05 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, often at right angles, sometimes collapsed, interwoven, 2.8–5 μm in diam.

Tubes. Generative hyphae hyaline, thin-walled, some slightly thick-walled, moderately branched, interwoven, encrusted by abundant pale yellowish crystals, plenty of oily substance present along hyphae, 1.8–4.8 μm in diam; cystidia present, hyaline, clavate, mostly 25–54×3–6 μm, some up to 90 μm; basidia clavate, with four sterigmata and a simple basal septum, 13–17.5×3.4–5.2 μm; basidioles in shape similar to basidia, but smaller.

Spores. Basidiospores allantoid, hyaline, thin-walled, smooth, usually with two small guttules, IKI–, CB–, (3.5–)3.7–4.3×(1.4–)1.6–1.8(–1.9) μm, L=3.99 μm, W=1.7 μm, Q=2.3–2.41 (*n*=60/2).

Type of rot. White rot.

Additional specimen examined (paratype). CHINA. Henan Prov., Neixiang County, Baotianman Nat. Res., on fallen angiosperm trunk, 22.VIII.2006 Li 1010 (BJFC).

Remarks. Ceriporia pseudocystidiata is characterized by its very thin basidiocarps, allantoid basidiospores and presence of cystidia. *Ceriporia cystidiata* Ryvarden & Iturr. resembles *C. pseudocystidiata* by similar basidiospores and cystidia. The type material of *C. cystidiata* was studied. Its cystidia are not common, tubes lack oily substance, hyphae are constricted at septa and all hyphae are densely separated, while *C. pseudocystidiata* has plenty of cystidia and oily substance in tubes, and hyphae more sparsely septate and not constricted at septa. *C. pseudocystidiata* and *Ceriporia aurantiocarnescens* (Henn.) M. Pieri & B. Rivoire have similar basidiospores. The type material of the latter species has smaller pores (5–7 per mm) and thick-walled subicular hyphae, and lacks cystidia. *C. pseudocystidiata* is also similar to *Ceriporia subspissa* by similar basidiospore dimension. According to the type specimen of *C. subspissa*, its pores are deep reddish brown, cystidia are fusoid, and basidiospores are oblong-ellipsoid [(3.2–)3.3–4×(1.8–)1.9–2(–2.1) μm, L=3.71 μm, W=1.95 μm, Q=1.9 (*n*=30/1)].

Ceriporia variegata B.S. Jia & Y.C. Dai, sp. nov. (Fig. 5)

MycoBank no.: MB 802908

Basidiocarps annual, resupinate. Pore surface white when fresh, cream when dry; pores round to radially elongated, shallow, 4–6 per mm. Hyphal system monomitic; generative hyphae with simple septa. Cystidia variable in shape, clavate, fusoid or lanceolate, some with one or two septa, some collapsed near the tops, 25–60×4.8–8 μm. Basidiospores cylindrical to oblong-ellipsoid, hyaline, thin-walled, IKI–, CB–, 3–4×1.6–2 μm.

Type. CHINA. Hunan Prov., Yizhang County, Mangshan Nat. Res., on rotten angiosperm stump, 26.VI.2007 Li 1780 (holotype in BJFC).

Etymology. *Variegata* (Lat.) refers to the variable cystidia.

Fruitbody. Basidiocarps annual, resupinate, brittle when dry, up to 7.5 cm long, 5 cm wide, and 1 mm thick at centre. Pore surface white when fresh, cream when dry; pores round to radially elongated, shallow, 4–6 per mm; dissepiment thick, entire. Margin thinning out, cream, cottony, up to 0.5 mm wide. Subiculum cream, cottony when dry, up to 0.7 mm thick. Tubes concolorous with pore surface, brittle when dry, up to 0.3 mm thick.

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

Subiculum. Generative hyphae hyaline, slightly thick-walled with a wide lumen, frequently branched, loosely interwoven, usually covered by fine hyaline crystals, 2.4–7.3 μm in diam.

Tubes. Generative hyphae hyaline, thin- to slightly thick-walled, some distinctly thick-walled, occasionally branched, loosely interwoven, usually covered by fine hyaline crystals, 3–5.8 μm in diam; cystidia present, thin-walled, variable in shape, clavate, fusoid or lanceolate, some with one or two septa, some collapsed near the tops, 25–60×4.8–8 μm; cystidioles present; basidia clavate, with four sterigmata and a simple basal septum, 12.5–20.6×4.2–5.8 μm; basidioles in shape similar to basidia, but smaller.

Spores. Basidiospores cylindrical to oblong-ellipsoid, hyaline, thin-walled, smooth, sometimes bearing a small guttule, IKI–, CB–, 3–4(–4.1)×(1.4–)1.6–2 μm, L=3.56 μm, W=1.86 μm, Q=1.91 (*n*=30/1).

Type of rot. White rot.

Remarks. Ceriporia variegata is characterized by its white to cream pore surface and presence of variable cystidia.

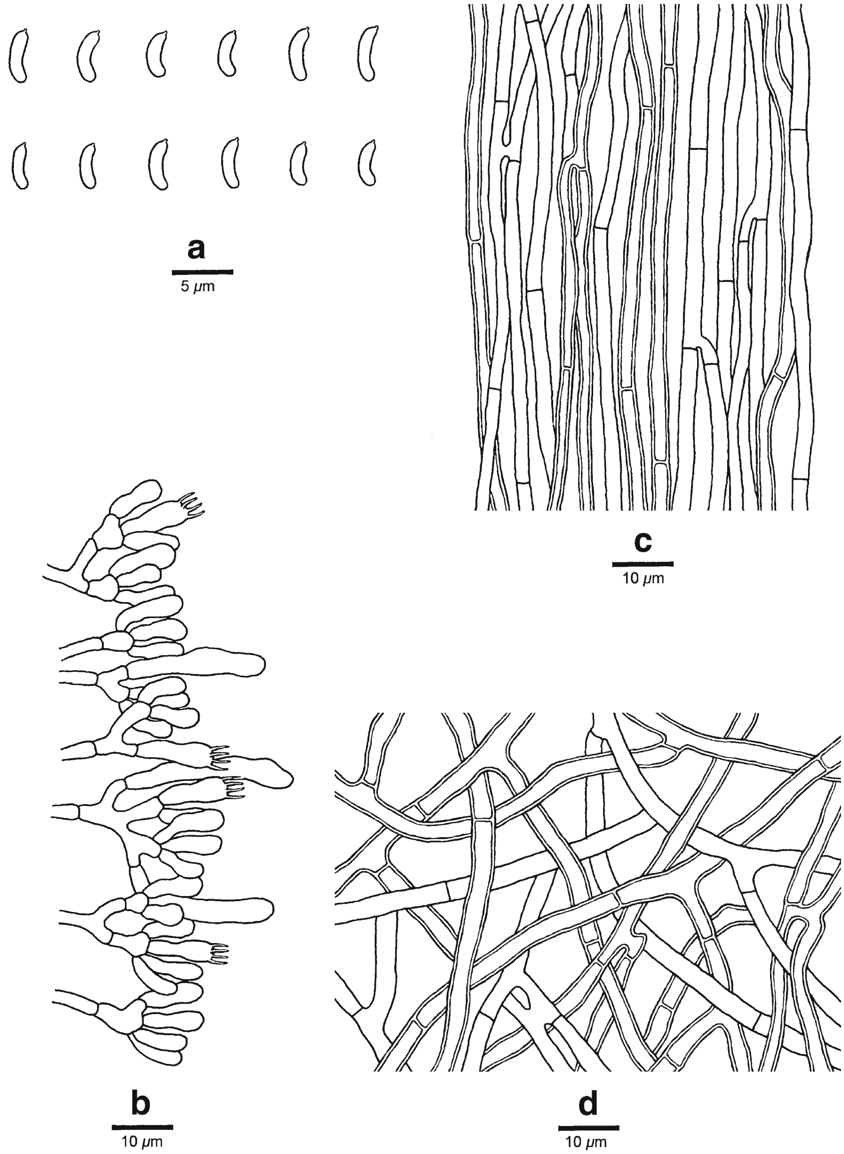

Fig. 3 Microscopic structures of *Ceriporia bubalinomarginata* (drawing from the holotype). **a** Basidiospores; **b** Hymenium (cystidia, basidia and basidioles); **c** Hyphae from tube trama; **d** Hyphae from subiculum

Ceriporia subspissa was recently described from Guyana by Aime et al. (2007), and it is similar to *C. variegata.* Type material of the former species was studied, and its pore surface is deep reddish brown, cystidia are lacking, but fusoid cystidioles are present. *C. aurantiocarnescens* and *C. variegata* share very similar basidiospores, but the former has salmon to brownish vinaceous pore surface, smaller pores (5–8 per mm), parallel tramal hyphae, and absence of cystidia (Pieri and Rivoire 1997).

Other studied specimens are presented in Supplementary material 1.

Key to species of *Ceriporia* so far found in China (see Supplementary material 2 for the size of their basidiospores)

1. Hyphal system dimitic .... *C. totara*
1. Hyphal system monomitic 2
2. Hyphae swollen in KOH .... *C. inflata*
2. Hyphae unchanged in KOH 3
3. Cystidia present 4
3. Cystidia absent 9
4. Cystidia variable in shape (clavate, fusoid, lanceolate, some with one or two septa, some collapsed near the tops) .... *C. variegata*
4. Cystidia relatively uniform in shape 5
5. Pores 6–7 per mm; basidiospores <1.4 μm wide .... *C. bubalinomarginata*
5. Pores 1–5 per mm; basidiospores >1.4 μm wide 6
6. Basidiospores >4.8 μm long 7
6. Basidiospores <4.8 μm long 8
7. Cystidia only present at the bottom of tube; basidiospores >2.9 μm wide .... *C. mellea*
7. Cystidia present in all parts of the hymenium; basidiospores mostly <2.9 μm wide .... *C. purpurea*
8. Basidiospores allantoid .... *C. pseudocystidiata*

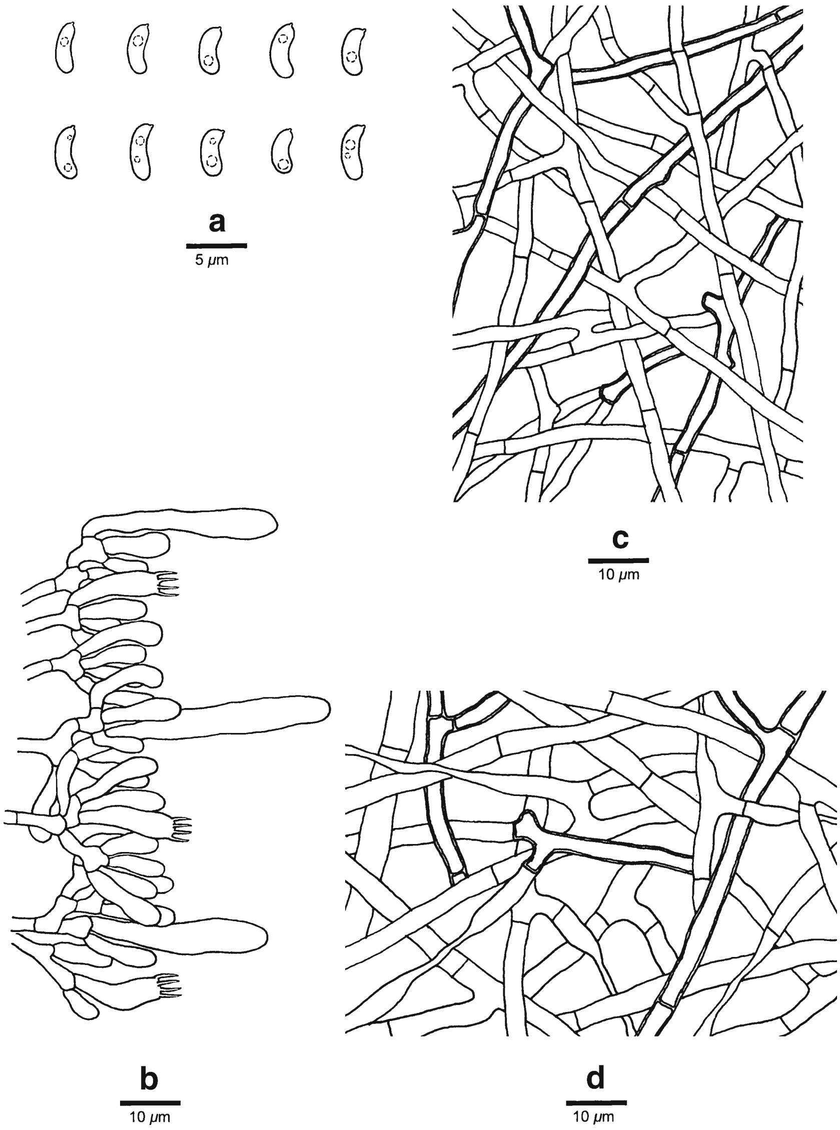

Fig. 4 Microscopic structures of *Ceriporia pseudocystidiata* (drawing from the holotype). **a** Basidiospores; **b** Hymenium (cystidia, basidia and basidioles); **c** Hyphae from tube trama; **d** Hyphae from subiculum

8. Basidiospores oblong-ellipsoid to cylindrical, or cylindrical but a little curved .... *C. nanlingensis*
9. Basidiospores allantoid 10
9. Basidiospores oblong-ellipsoid to cylindrical, or cylindrical but a little curved 12
10. Pores brown, orange-brown to reddish-brown; most of the basidiospores >5 μm long .... *C. spissa*
10. Pores cream, buff, cinnamon, salmon, clay-pink or brownish vinaceous; most of the basidiospores <5 μm long 11
11. Pores variable in color when fresh, buff when dry, 3–6 per mm .... *C. viridans*
11. Pores salmon, clay-pink or brownish vinaceous, 5–8 per mm .... *C. aurantiocarnescens*
12. Most of the basidiospores >5 μm long 13
12. Most of the basidiospores <5 μm long 14
13. Pores 2–3 per mm; tramal hyphae thin-walled .... *C. reticulata*
13. Pores 3–4 per mm; tramal hyphae thin- to slightly thick-walled .... *C. camaresiana*
14. Most of the basidiospores >2.5 μm wide ... *C. lacerata*
14. Most of the basidiospores <2.5 μm wide 15
15. Tramal hyphae interwoven 16
15. Tramal hyphae parallel or nearly parallel along the tube 18
16. Subicular hyphae clearly thick-walled .... *C. crassitunicata*
16. Subicular hyphae thin- to slightly thick-walled 17
17. Pores cream to buff; basidiospores narrow-ellipsoid, subicular hyphae 4.8–10.5 μm in diam .... *C. alachuana*
17. Pores sulphur; basidiospores ellipsoid, subicular hyphae 2–4 μm in diam .... *C. sulphuricolor*
18. Pores rose-pink to purple when fresh; subicular hyphae slightly thick- to thick-walled .... *C. tarda*

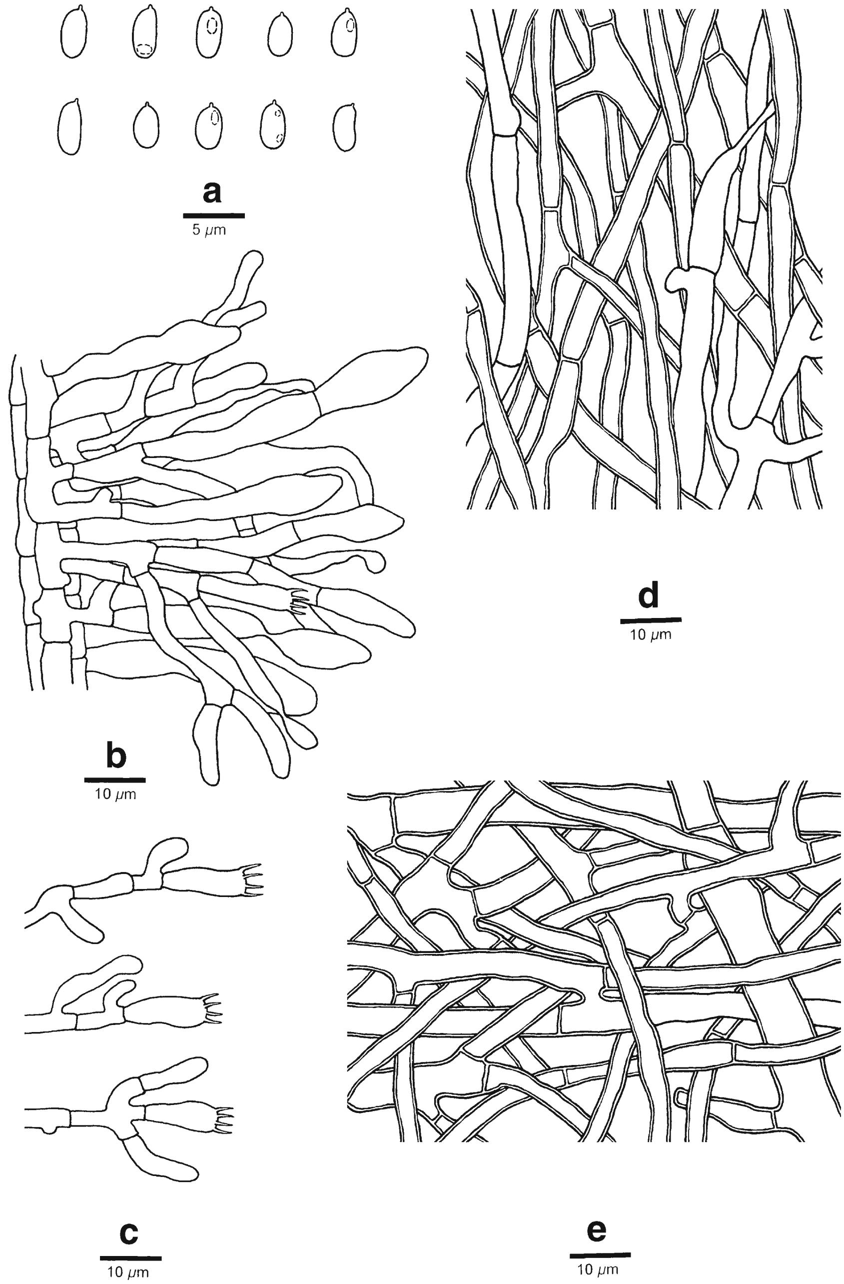

Fig. 5 Microscopic structures of *Ceriporia variegata* (drawing from the holotype). **a** Basidiospores; **b** Hymenium; **c** Basidia and basidioles; **d** Hyphae from tube trama; **e** Hyphae from subiculum

18. Pores cream, pinkish-buff or purplish when fresh; subicular hyphae thin- to slightly thick-walled 19
19. Tramal hyphae thin-walled, rarely branched, often as "Y" shapes .... *C. davidii*
19. Tramal hyphae thin- to slightly thick-walled, frequently branched, often as "H" shapes .... *C. excelsa*

Discussion

In this study, a total of 193 specimens of *Ceriporia* throughout China and 10 specimens out of China have been morphologically examined in detail, which made 20 species identified in China. Eighteen species of *Ceriporia*, including 17 from China, were sequenced here and referred to in our phylogeny. To the best of our knowledge, this is the most comprehensive study of *Ceriporia* for now.

Kim and Jung (1999) indicated that *Ceriporia* was a monophyletic genus based on phylogeny of nSSU sequences. Based on other genes, however, Larsson et al. (2004), Binder et al. (2005) and Wu et al. (2010) found that the sampled species of *Ceriporia* did not form a clade. Similarity, our phylogeny inferred from ITS and nLSU sequences (Figs. 1 and 2) indicates that *Ceriporia* is not a natural group.

Ceriporia has only a few morphological characters; therefore, it is hard to find the morphological differences of certain phylogenetic species. For example, six specimens identified as *C. spissa* in morphology represented at least four phylogenetic species in the ITS tree (Fig. 1). Likewise, five specimens known as *C. viridans* were distinguished as four phylogenetic species (Fig. 1). The nLSU tree showed a similar topology (Fig. 2). For now, we could not obtain any sequences from type specimens of *C. spissa* and *C. viridans*, so we treated the Chinese specimens as *C. spissa* s. l. and *C. viridans* s. l.

Even the size and shape of basidiospores, usually regarded as reliable characters (Ryvarden 1991), might be not stable in *Ceriporia*. *Ceriporia inflata* and *C. jiangxiensis* were described as two separate species because of their differences in shape of basidiospores as well as in the presence or absence of cystidia (Jia and Cui 2012); however, phylogenetic analysis showed that these morphological differences were not suitable to discriminate the two species, as they formed a terminal clade (Figs. 1 and 2) and in fact represented a single species. *C. inflata* has the priority to *C. jiangxiensis* (Jia and Cui 2012) and should be the legal name for this species.

With regard to hymenial cystidia, eight species, C. *bubalinomarginata*, *C. inflata*, *C. mellea*, *C. nanlingensis*, *C. pseudocystidiata*, *C. purpurea*, *C. totara* and *C. variegata*, produce this structure, but they were not clustered together (Figs. 1 and 2). Therefore, the presence or absence of cystidia was not supposed to be a useful character to reflect the interspecies relationships in *Ceriporia*.

Wu et al. (2010) advised to provide DNA sequences when describing a new species belonging to Phanerochaetaceae. The current study provides new ITS and/or nLSU sequences, the most popular molecular markers, for three new species of *Ceriporia* as well as those described previously. However, it is still very hard to fully solve the phylogeny of this genus. In future, taxon-samplings, including more species from other genera closely related *Ceriporia*, are needed to delimit *Ceriporia* into several smaller natural groups with the help of multi-locus phylogeny.

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