ORIGINAL ARTICLE

Molecular phylogeny and morphology reveal two new species of *Coltricia* (Hymenochaetaceae Basidiomycota) from China

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Abstract





Two new species of *Coltricia*, *C. subcinnamomea* and *C. subverrucata*, are described from China based on both morphological and molecular data. Phylogenetic analyses based on nuc rDNA ITS1-5.8S-ITS2, partial 28S rDNA and partial 18S rDNA, mt partial 12S rDNA, partial sequences of genes for RNA polymerase II subunits 1 and 2, and partial sequences of genes for EF-1 α confirmed the generic placement of the two new species. *Coltricia subcinnamomea* is characterized by stipitate, mesopodal basidiocarps, a slightly shiny pileal surface, 2–3 pores per mm, and broadly ellipsoid to subglobose basidiospores, 8.0–9.5 × 6.2–6.8 µm. *Coltricia subverrucata* is characterized by stipitate, mesopodal basidiocarps, a faintly concentrically zonate pileal surface with radiating lines, 0.5–2 pores per mm, strongly vertucose hyphae and broadly ellipsoid basidiospores, 7.8–9.0 × 6.0–7.0 µm.

Keywords Hymenochaetales · Phylogeny · Polypore · Taxonomy

Introduction

Coltricia Gray, typified by *C. perennis* (L.) Murrill, and *Coltriciella* Murrill, typified by *C. dependens*, are cosmopolitan genera of Hymenochaetales. Most species are terrestrial and a few have been found associated with plant roots, and presumably mycorrhizal (Tedersoo et al. 2007), while others are found on wood (that could only be a physical support in fact).

Coltricia is characterized by poroid and stipitate basidiocarps, a monomitic hyphal system lacking clamp connections and colored, ellipsoid to subglobose, smooth basidiospores (Dai 2010). The complex habitat and exceedingly closed morphology characteristics make this genus easy to be confounded with *Coltriciella*. *Coltriciella* differs from *Coltricia* by the ornamented vs smooth basidiospores (Ryvarden 1991), and molecular data indicated that the two genera were sister clades, forming a single lineage. However, the monophyly of each genus is still unresolved (Wagner and

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The two genera have been extensively studied worldwide; so far, 46 species are recognized in *Coltricia*, and 13 species in *Coltriciella* (Burdsall 1969; Gilbertson and Ryvarden 1986; Corner 1991; Masuka and Ryvarden 1993; Rajchenberg and Wright 1998; Núñez and Ryvarden 2000; Aime et al. 2003; Niemelä 2005; Ryvarden et al. 2006; Ryvarden 2007; Gomes-Silva et al. 2009; Baltazar et al. 2010; Dai 2010; Dai et al. 2010; Dai and Li 2012; Zhou and Tedersoo 2012; Valenzuela et al. 2012; Decock 2013; Ryvarden and Melo 2014; Bian and Dai 2015; Bian et al. 2016; Vasco-Palacios 2016; Bian and Dai 2017).

During investigations of *Coltricia* and *Coltriciella* in China, several collections of *Coltricia* were found that could not be assigned to any described species, also forming two distinct clades in multilocus phylogenetic inferences. They are described as *Coltricia subcinnamomea* and *Coltrica subverrucata*. An identification key of *Coltricia* and *Coltriciella* observed in China is provided.

Materials and methods

Morphological studies

The studied specimens are deposited in the herbarium of the Institute of Microbiology, Beijing Forestry University (BJFC).

Macromorphological descriptions were based on field notes and laboratory observations. Microscopic routine used in this study followed Dai (2010). Drawings were made with the aid of a drawing tube. Microscopic measurements were made from slide preparations stained with Cotton Blue and Melzer's reagent. Spores were measured from section cuts from tubes. In presenting variation in basidiospore size, 5% of measurements were excluded from each end of the range, and are given in parentheses. In the text, the following abbreviations were used: KOH = 5% potassium hydroxide, IKI =Melzer's reagent, IKI- = neither amyloid nor dextrinoid, CB = Cotton Blue, CB- = acyanophilic, L = mean basidiospore length (arithmetic average of all basidiospores), W = mean basidiospore width (arithmetic average of all basidiospores), O = variation in the ratios of L/W between specimens studied, n = number of basidiospores measured from given number of specimens. Color terms followed Kornerup and Wanscher (1978).

Molecular phylogeny

The collections and sequences of the two new species and other fungal taxa used in this study are listed in Table 1. Eighteen new sequences were generated for this study and deposited to GenBank. The methods of DNA extraction and amplification in this study followed Chen et al. (2016). The CTAB rapid plant genome extraction kit-DN14 (Aidlab Biotechnologies Co., Ltd., Beijing) was used to extract total genomic DNA from dried specimens according to the manufacturer's instructions. The primers ITS5/ITS4 for nuc rDNA ITS1-5.8S-ITS2 (ITS), LR0R/LR7 for nuc 28S rDNA (nLSU), NS1/NS4 for nuc 18S rDNA (nSSU), MS1/MS2 for mt 12S rDNA (mtSSU), RPB1-A_f/RPB1-C_r for RNA polymerase II subunit 1 gene (RPB1), fRPB2-5f/fRPB2-7cR for RNA polymerase II subunit 2 gene (RPB2), and EF1-983F/ EF1-1567F for EF-1 α (*TEF-1*) were used for PCR amplifications (Vilgalys and Hester 1990; White et al. 1990; Matheny 2005). The PCR products were sequenced in Beijing Genomics Institute, China, with the same primers. The newly generated sequences were deposited at GenBank.

For the phylogenetic analyses, the combined dataset of ITS, nLSU, nSSU, mtSSU, *RPB1*, *RPB2* and *TEF-1* included 73 sequences representing 31 taxa, in which 23 taxa of *Coltricia* and 6 taxa of *Coltriciella* are involved. *Fomitiporella chinensis* (Pilát) Y.C. Dai, X.H. Ji & Vlasák and *Inonotus griseus* L.W. Zhou were chosen as outgroup. Sequences were aligned with MAFFT (Katoh and Toh 2008), BioEdit (Hall 1999), and Clustal X (Thompson et al. 1997). Sequence alignments were deposited at TreeBASE (submission ID 25951, www.treebase.org). The best-fit evolutionary model was estimated using MrModeltest 2.3 (Posada and Crandall 1998) as GTR + I + G for the combined dataset.

Maximum parsimony (MP) analyses were applied to the combined dataset. The construction was performed in PAUP* version 4.0b10 (Swofford 2002). 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 1000 random sequence additions. Max-trees was set to 5000, branches of zero length were collapsed, and all parsimonious trees were saved. Clade robustness was assessed by a bootstrap (BT) analysis with 1000 replicates (Felsenstein 1985). Descriptive tree statistics, i.e., tree length (TL), consistency index (CI), retention index (RI), rescaled consistency index (RC), and homoplasy index (HI) were calculated for each maximum parsimonious tree (MPT) generated.

RAxML v.7.2.8 was used to construct maximum likelihood (ML) trees with the GTR + I + G model of site substitution including estimation of Gamma-distributed rate heterogeneity and a proportion of invariant sites (Stamatakis 2006). The branch support was evaluated with a bootstrapping method of 1000 replicates (Hillis and Bull 1993).

BI analyses were calculated with MrBayes3.1.2 with a general time reversible (GTR) model of DNA substitution and a gamma distribution rate variation across sites (Ronquist and Huelsenbeck 2003). Four Markov chains were run for 2 runs from random starting trees for 500,000 generations, and trees were sampled every 100 generations. The first 25% of sampled trees were set as burn-in. A majority rule consensus tree of all remaining trees was calculated. BS (bootstrap support for MP and ML) values and BPPs (Bayesian posterior probabilities for BI) simultaneously not less than 75% and 0.95, respectively, are shown at the nodes.

Results

The combined dataset had an aligned length of 7839 characters, of which 4233 characters are constant, 596 are variable and parsimony-uninformative, and 3010 are parsimony-informative. MP analysis yielded four equally most-parsimonious trees (TL = 13,236, CI = 0.456, RI = 0.754, RC = 0.344, HI = 0.544). Bayesian analysis and ML analysis resulted in a similar topology to MP analysis. The ML tree is provided in Fig. 1.

The sampled specimens of *C. subcinnamomea* and *C. subverrucata* nested within the "main" *Coltricia* lineage, forming two well-supported terminal clades (*C. subcinnamomea* 100% in MP, 100% in ML, 1.00 in BI; *C. subverrucata* 100% in MP, 100% in ML, 1.00 in BI).

According to the phylogeny analyses, the two new species are distinctive from the other sampled species.

Table 1 List of species, specimens, and GenBank accession numbers of sequences used in this study

Species name	Sample no.	GenBank acc	ession no.					
		ITS	nLSU	nSSU	mtSSU	RPB1	RPB2	TEF1
Coltricia abieticola	Cui 10265	KX364784	KX364803	KY693760	KY693822	KX364827	KX364875	_
C. abieticola	Cui 10321	KX364785	KX364804	KY693761	KY693823	KX364828	KX364876	KY693911
C. abieticola	Cui 12276	KU360673	KU360643	KY693762	KY693824	KX364829	KX364877	KY693912
C. abieticola	Cui 12312	KU360674	KU360644	KY693763	KY693825	KX364830	KX364878	
C. austrosinensis	Dai 13093	KU360670	KU360640	KY693764	KY693826	KX364824	KX364872	KY693913
C. austrosinensis	Dai 13098	KU360671	KU360640	KY693765	KY693827	KX364825	KX364873	
C. austrosinensis	Dai 13823	KU360672	KU360642	KY693766	KY693828	KX364826	KX364874	KY693914
C. cinnamomea	Cui 10494	KU360675	KJ000217	KY693767		KX364831	KX364879	_
C. cinnamomea	Cui 10505	KU360676	KU360645	KY693768	KY693829	KX364832	KX364880	KY693915
C. cinnamomea	Cui 12549	KY693728	KY693742	KY693769	KY693830	KY693882	KY693895	KY693916
C. cinnamomea	Cui 12584	KY693729	KY693743	KY693770	KY693831	KY693883	KY693896	KY693917
C. cinnamomea	Cui 12654	KY693730	KY693744	KY693771	KY693832	KY693884	KY693897	KY693918
C. cinnamomea	Cui 14175	_	KY693745	KY693772	KY693833	KY693885	KY693898	_
C. cinnamomea	Cui 14177	_	KY693746	KY693773	KY693834	KY693886	KY693899	_
C. cinnamomea	Cui 14262	KY693731	KY693747	KY693774	KY693835	KY693887	KY693900	KY693919
C. cinnamomea	Cui 14289	KY693732	KY693748	KY693775		KY693888	KY693901	_
C. crassa	Cui 9211	KU360677	KU360646	KY693776		KX364833	KX364881	KY693920
C. crassa	Cui 10255	KU360678	KU360647	KY693777	KY693836	KX364834	KX364882	KY693921
C. crassa	Dai 15163	KU360679	KU360648	KY693778	KY693837	KX364835	KX364883	KY693922
C. fragilissima	Dai 16636	KY693733	KY693749	KY693779			KY693902	_
C. focicola	Dai 16090	KX364786	KX364805			KX364836	KX364884	KY693923
C. hirtipes	Dai 16647	KY693734	KY693750		KY693838	KY693889	KY693903	_
C. kinabaluensis	Dai 13957	KX364787	KX364806	KY693780		KX364837	KX364885	KY693924
C. kinabaluensis	Dai 13958	KX364788	KX364807	KY693781	KY693839	KX364838	KX364886	KY693925
C. lateralis	Cui 12563	KX364789	KX364808	KY693782	KY693840	KX364839	KX364887	KY693926
C. lateralis	Dai 13564	KX364790	KX364809		KY693841	KX364840		KY693927
C. macropora	Cui 9019	KU360680	KJ000220	KY693783	KY693842	KX364841	KX364888	
C. macropora	Cui 9039	KU360681	KJ000221	KY693784	KY693843	—		KY693928
C. minima	Dai 15206	KU360682	KU360649	KY693785	KY693844	KX364842	KX364889	KY693929
C. minima	Dai 15222	KU360683	KU360650	KY693786	KY693845	KX364843	KX364890	KY693930
C. minor	Dai 16088	KU360684	KU360651	KY693787	KY693846	KX364844	KX364891	KY693931
C. montagnei	Cui 10169	KU360685	KU360652	KY693788	KY693847	KX364845	KX364892	KY693932
C. montagnei	Dai 12137	_	KX364810	KY693789	KY693848	KX364846	_	KY693933
C. perennis	Cui 10318	KU360686	KJ000224	KY693790	KY693849	KX364847	KX364893	KY693934
C. perennis	Cui 10319	KU360687	KU360653	KY693791	KY693850	KX364848	KX364894	KY693935
C. perennis	JV 0809/66	KX364791	KX364811	KY693792	KY693851	KX364849	KX364895	KY693936
C. pyrophila	Cui 10314	KU360689	KU360655	KY693793	KY693852	KX364850	KX364896	KY693937
C. pyrophila	Cui 10411	KU360690	KU360656	KY693794	KY693853	KX364851	KX364897	KY693938
C. pyrophila	Cui 12553	KX364792	KX364812	KY693795	KY693854	KX364852	KX364898	KY693939
C. rigida	Dai 13622a	KX364793	KX364813	KY693796	—	KX364853	KX364899	KY693940
C. rigida	Dai 16322	KX364794	KX364814	KY693797	KY693855	KX364854	KX364900	KY693941
C. strigosipes	Dai 15145	KX364795	KX364815	KY693798	KY693856	KX364855	KX364901	KY693942
C. strigosipes	Dai 15586	KU360692	KU360658	KY693799	KY693857	KX364856	KX364902	KY693943
C. strigosipes	Dai 15587	KU360693	KU360659	KY693800	KY693858	KX364857	KX364903	KY693944
C. subcinnamomea	Dai 17016	KY693740	KY693755	KY693810	KY693868	KY693892	KY693906	
C. subcinnamomea	Dai 17022	—	KY693756	KY693811	KY693869	KY693893	KY693907	—
C. subperennis	Dai 11625	KY693735	KY693753	KY693804	KY693862	KY693890	KY693904	KY693948

Table 1 (continued)

Species name	Sample no.	GenBank acc	ession no.					
		ITS	nLSU	nSSU	mtSSU	RPB1	RPB2	TEF1
C. subperennis	Dai 13095	KY693736	KY693754	KY693805	KY693863	KY693891	KY693905	
C. subverrucata	Dai 12919	MT174242 ^a	MT174235 ^a	MT174233 ^a	MT174240 ^a	_	_	MT133895 ^a
C. subverrucata	Dai 15600	MT174243 ^a	MT174236 ^a	MT174234 ^a	MT174241 ^a	MT133893 ^a	MT133894 ^a	MT133896 ^a
C. verrucata	Dai 15120	KU360694	KU360660	KY693801	KY693859	KX364858	KX364904	KY693945
C. verrucata	Dai 15125	KU360695	KU360661	KY693802	KY693860	KX364859	KX364905	KY693946
C. verrucata	Dai 16289	KU360696	KU360662	KY693803	KY693861	KX364860	KX364906	KY693947
C. weii	Cui 11011	KU360698	KU360664	KY693806	KY693864		KX364907	KY693949
C. weii	Cui 12624	KX364796	KX364816	KY693807	KY693865	KX364861	KX364908	KY693950
C. weii	Dai 13422	KX364797	KX364817	KY693808	KY693866	KX364862	KX364909	KY693951
C. wenshanensis	Dai 15585	KX364798	KX364818	KY693809	KY693867	KX364863	KX364910	KY693952
C. wenshanensis	Dai 18367	MT174244 ^a	MT174237 ^a					—
Coltriciella baoshanensis	Cui 8147	KX364799	KX364819			KX364864	KX364911	_
C. baoshanensis	Dai 13075	KX364800	KX364820	KY693812	KY693870	KX364865	KX364912	KY693953
C. dependens	Dai 10944	KY693737	KY693757	KY693813	KY693871		KY693908	_
C. dependens	Cui 9210	KY693738	KY693758	KY693814	KY693872	_	_	_
C. globosa	Cui 7545	KJ540930	KJ000226	KY693815	KY693873	KX364866	KX364913	KY693954
C. globosa	Dai 18420	MT174245 ^a	MT174238 ^a				—	_
C. globosa	Dai 18421	MT174246 ^a	MT174239 ^a	_	_	_	_	_
C. pseudodependens	Cui 8138	KJ540931	KJ000227	KY693816	KY693874	KX364867	KX364914	_
C. pseudodependens	Cui 12582	KX364801	KX364821	KY693817	KY693875	KX364868	KX364915	KY693955
C. pusilla	Dai 15168	KU360701	KU360667	KY693818	KY693876	KX364869	KX364916	KY693956
C. pusilla	Dai 15581	KY693739	KU360668	KY693819	KY693877		KY693909	KY693957
C. subglobosa	Dai 15158	KU360702	KU360669	KY693820	KY693878	_	KX364917	_
C. subglobosa	Yuan 6253	_	KX364822	KY693821	KY693879	KX364870	KX364918	_
Fomitiporella chinensis	Cui 11230	KX181309	KY693759	_	KY693880	KY693894	KY693910	KY693958
Inonotus griseus	Dai 13436	KX364802	KX364823	—	KY693881	KX364871	KX364919	KY693959

^a Newly generated sequences for this study

Taxonomy

Coltricia subcinnamomea L.S. Bian & Y.C. Dai, sp. nov. Fig. 2

MycoBank no.: MB 834952

Diagnosis: this species is characterized by stipitate, mesopodal basidiocarps, a slightly shiny pileal surface, 2–3 pores per mm, 11–14-µm-wide contextual hyphae and broadly ellipsoid to subglobose basidiospores, $8.0-9.5 \times 6.2 6.8 \mu m$ (average).

Holoype: CHINA. Shanxi Province: Qinshui County, Lishan National Nature Reserve, on ground, 24 Aug 2016, Dai 17016 (BJFC 023121).

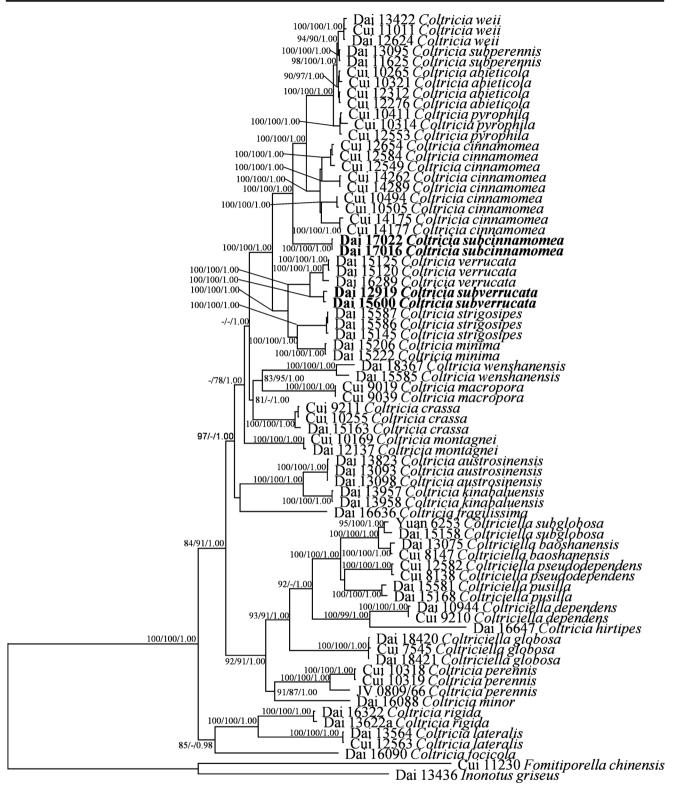
Etymology: *subcinnamomea* (Lat.): referring to similarity to *Coltricia cinnamomea*.

Basidiocarps: annual, centrally stipitate, solitary, soft, and without odor or taste when fresh, becoming soft corky when dry. Pilei more or less circular, flat to infundibuliform, up to 2 cm in diam and 3 mm thick at center. Pileal surface honey-

yellow to grayish brown when dry, hirsute in the center with bristles erected, velutinate to glabrous, slightly shiny, distinctly concentrically zonate and sulcate; margin thin and obtuse, curving down upon drying. Pore surface cinnamon-buff to yellowish brown upon drying; pores angular, 2–3 per mm; dissepiments thin, lacerate. Context fawn, leathery, up to 0.5 mm thick. Tubes buff-yellow, distinctly paler than context, fragile or slightly brittle when dry, up to 2 mm long. Stipe reddish brown, corky, finely velutinate, up to 1.5 cm long, 3 mm in diam.

Hyphal structure: hyphal system monomitic; generative hyphae simple septate; tissue darkening but otherwise unchanged in KOH.

Context: contextual hyphae cinnamon-buff to yellowish brown, thick-walled with a wide lumen, rarely branched, frequently simple septate, more or less straight, more or less regularly arranged, $11-14 \mu m$ in diam; hyphae in stipe similar to those in context, parallel along the main axe, rarely branched, sometimes collapsed, $10-14 \mu m$ in diam.

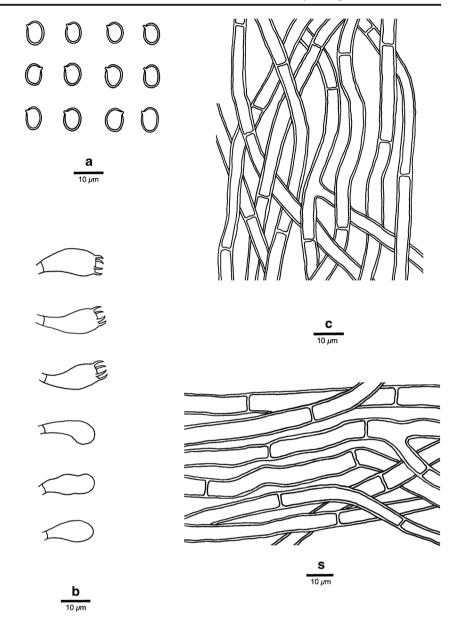


0.1

Fig. 1 Strict consensus tree illustrating the phylogeny based on the combined dataset. Branches are labeled with parsimony bootstrap proportions higher than 75%, maximum likelihood bootstrap higher than 75%, and Bayesian posterior probabilities more than 0.95

Tubes: tramal hyphae cinnamon-buff to yellowish brown, thin- to slightly thick-walled with a wide lumen, rarely branched, frequently simple septate, straight, subparallel along the tubes, 5–7 μ m in diam. Cystidia and cystidioles

Fig. 2 Microscopic structures of *Coltricia subcinnamomea* (drawn from the holotype). **a** Basidiospores. **b** Basidia and basidioles. **c** Hyphae from trama. **d** Hyphae from context



absent; basidia broadly clavate, thin-walled, with four sterigmata and a simple septum at the base, $15-20 \times 7-9 \mu m$; basidioles similar in shape but slightly smaller.

Spores: basidiospores broadly ellipsoid to subglobose, yellowish, thick-walled, smooth, IKI-, CB-, (6.2–)8.0– $9.5 \times (5.2-)6.2-6.8(-7.4) \mu m$, $L = 8.12 \mu m$, $W = 6.47 \mu m$, Q = 1.26-1.32 (n = 60/2).

Additional material (paratype) examined: CHINA. Shanxi Province, Qinshui County, Lishan National Nature Reserve, on ground, 24 Aug 2016, Dai 17022 (BJFC 023127).

Coltricia subverrucata L.S. Bian & Y.C. Dai, sp. nov. Figs. 3 and 4

MycoBank no.: MB 834953.

Diagnosis: this species is characterized by centrally stipitate basidiocarps, an indistinctly concentrically zonate pileal surface with radially aligned lines, 0.5–2 pores per mm, strongly verucose hyphae and broadly ellipsoid basidiospores, $7.8-9.0 \times 6.0-7.0 \mu m$ (average).

Holotype: CHINA. Guizhou Province, Lvyang County, Kuankuoshui National Nature Reserve, on ground of angiosperm forest, 27 Sep 2014, Dai 15600 (BJFC 019704).

Etymology: *subverrucata* (Lat.): referring to similarity to *Coltricia verrucata*.

Basidiocarps: annual, centrally stipitate, solitary, soft and without odor or taste when fresh, becoming soft corky when dry. Pilei more or less circular, flat to infundibuliform, up to 2.5 cm in diam and 2 mm thick at center. Pileal surface fawn to grayish brown when dry, velutinate, with indistinct concentric zones and radially aligned lines; margin thin and obtuse, curved down when dry. Pore surface honey-yellow to yellowish brown upon drying; pores angular, 0.5–2 per mm; dissepiments thin,



Fig. 3 Basidiocarps of *Coltricia subverrucata* (Dai 15600, holotype). Bar = 1 cm

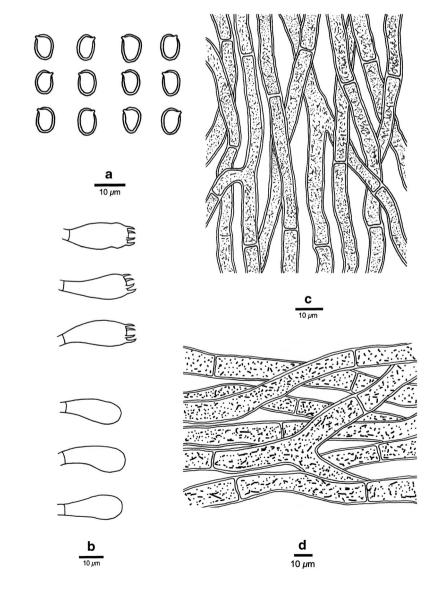
lacerate. Context deep olive, leathery, up to 0.5 mm thick. Tubes curry-yellow, distinctly paler than context, fragile or slightly brittle when dry, up to 1.5 mm long. Stipe reddish brown, corky, finely velutinate, up to 2.5 cm long, 2 mm in diam, swollen near the base.

Hyphal structure: hyphal system monomitic; generative hyphae simple septate; tissue darkening but otherwise unchanged in KOH.

Context: contextual hyphae yellowish brown to fawn, thickwalled with a wide lumen, occasionally branched, frequently simple septate, more or less straight, strongly vertucose, more or less regularly arranged, $17-20 \mu m$ in diam; hyphae in stipe similar to those in context, parallel along the main axe, rarely branched, sometimes collapsed, $17-20 \mu m$ in diam.

Tubes: tramal hyphae honey-yellow to yellowish brown, thinto slightly thick-walled with a wide lumen, occasionally branched, frequently simple septate, straight, strongly vertucose,

Fig. 4 Microscopic structures of *Coltricia subverrucata* (drawn from the holotype). **a** Basidiospores. **b** Basidia and basidioles. **c** Hyphae from trama. **d** Hyphae from context



subparallel along the tubes, 5–7 μ m in diam. Cystidia and cystidioles absent; basidia broadly clavate, thin-walled, with four sterigmata and a simple septum at the base, $20-25 \times 7-10 \mu$ m; basidioles similar in shape but slightly smaller.

Spores: basidiospores broadly ellipsoid, yellowish, thickwalled, smooth, IKI–, CB–, 7.8–9.0(–9.2) × (5.5–)6.0–7.0(– 7.5) μ m, *L* = 8.40 μ m, *W* = 6.40 μ m, *Q* = 1.31–1.32 (*n* = 60/2).

Additional material (paratype) examined: CHINA. Sichuan Province, Liangshan, Mianning County, Lingshan Temple, on ground of *Castanopsis* forest, 17 Sep 2012, Dai 12919 (BJFC 013183).

Discussion

Coltricia subcinnamomea has centrally stipitate basidiocarps, large pores, wide contextual hyphae, and broadly ellipsoid to subglobose basidiospores. These features are also shared by C. abieticola Y.C. Dai, C. austrosinensis L.S. Bian & Y.C. Dai and C. wenshanensis L.S. Bian & Y.C. Dai. However, C. abieticola has a duplex stipe and grows in conifer forest (Dai 2010). Coltricia austrosinensis can be distinguished by indistinct concentric zones, pale pore surface (buff-yellow), and distinctly narrower basidiospores $(8-10 \times 5.5-$ 6.5 µm; Bian et al. 2016). Coltricia wenshanensis has larger basidiocarps (up to 5 cm in diam), larger pores (0.5-2 per mm) and smaller basidiospores $(7.5-8 \times 6-7; Bian and Dai)$ 2017). Coltricia subcinnamomea shares C. cinnamomea these macromorphological characters, including the slightly shiny pileal surface. And the two species are closely related in the phylogenetic analyses (Fig. 1). However, C. cinnamomea has narrower contextual hyphae (up to 10 μ m in diam) and smaller basidiospores (6.9–8.1 × 5.5– 6.4 μ m, $L = 7.7 \mu$ m, $W = 6.0 \mu$ m, Niemelä 2005).

Coltricia subverrucata resembles C. crassa Y.C. Dai and C. montagnei (Fr.) Murrill in having centrally stipitate basidiocarps, large pores and broadly ellipsoid basidiospores. However, C. crassa has thicker basidiocarps (up to 2 cm at the base), paler pore surface (cream to buff-yellow), dendrohyphidia-like hyphae, and larger basidiospores (9- $12 \times 5.9-7$ µm; Dai 2010). Coltricia montagnei differs from C. subverrucata by larger basidiocarps (up to 12 cm wide and 1-2 cm thick), lamellate hymenophore, wavy margin, and distinctly longer but narrower basidiospores $(9-12 \times 5-$ 6 μm; Murrill 1920). Coltricia subverrucata is phylogenetically related to C. verrucata Aime, T.W. Henkel & Ryvarden (Fig. 1). Both species have vertucose hyphae, but C. vertucata has smaller pores (2-5 per mm), narrower contextual hyphae (8–13 μ m) and narrower basidiospores (7–9 × 5–6 μ m; Aime et al. 2003).

In the phylogenetic analyses of combined dataset (Fig. 1), *Coltricia* species are scattered into two lineages, with *Coltriciella* species placed in between. This questions the monophyly of *Coltricia* or the pertinence of keeping *Coltricia* and *Coltriciella* as distinct generic entities. *Coltriciella* was originally established for a species with tiny and pendent basidiocarps (Murrill 1904), a feature also shared by *Coltricia tsugicola* Y.C. Dai & B.K. Cui (Dai and Cui 2006; Vasco-Palacios 2016). With more and more species found, *Coltriciella* is hard to distinguish from *Coltricia* but for the ornamented basidiospores. The confounding of the two genera in morphology is also indicated by our phylogenetic analyses.

Key to species of Coltricia and Coltriciella in China

They to species of connect and connection in clinic
1 Basidiospores smooth2
1* Basidiospores finely ornamented or verrucose24
2 Hymenophore more or less concentrically lamellate
Coltricia montagnei
2* Hymenophore poroid
3 Basidiocarps pendentColtricia tsugicola
3* Basidiocarps erect
4 Basidiocarps laterally stipitate5
4* Basidiocarps eccentrically to centrally stipitate
5 Mature pilei < 0.5 cm in diam <i>Coltricia minor</i>
5* Mature pilei > 0.5 cm in diam6
6 Basidiocarps woody-hard; basidiospores subglobose to
globose, < 7 µm longColtricia rigida
6* Basidiocarps soft to corky; basidiospores ellipsoid to
broadly ellipsoid, > 7 μm long7
7 Basidiocarps up to 1 cm thick; basidiospores $8-10 \times 6-$
7 μmColtricia duportii
7* Basidiocarps up to 2 mm thick; basidiospores 7–8 \times
5.2–6 µm <i>Coltricia lateralis</i>
8 Stipe duplex; on fallen trunk of Abies
8 Stipe duplex; on fallen trunk of <i>Abies</i>
8 Stipe duplex; on fallen trunk of <i>Abies</i> <i>Coltricia abieticola</i> 8* Stipe homogeneous; on ground of mixed forests9
 8 Stipe duplex; on fallen trunk of <i>Abies</i> <i>Coltricia abieticola</i> 8* Stipe homogeneous; on ground of mixed forests9 9 Pores 0.5–3 per mm10
8 Stipe duplex; on fallen trunk of <i>Abies</i> <i>Coltricia abieticola</i> 8* Stipe homogeneous; on ground of mixed forests9 9 Pores 0.5–3 per mm10 9* Pores 3–6 per mm
 8 Stipe duplex; on fallen trunk of <i>Abies</i> <i>Coltricia abieticola</i> 8* Stipe homogeneous; on ground of mixed forests9 9 Pores 0.5–3 per mm10
8 Stipe duplex; on fallen trunk of <i>Abies</i> <i>Coltricia abieticola</i> 8* Stipe homogeneous; on ground of mixed forests9 9 Pores 0.5–3 per mm
 8 Stipe duplex; on fallen trunk of <i>Abies</i> <i>Coltricia abieticola</i> 8* Stipe homogeneous; on ground of mixed forests9 9 Pores 0.5–3 per mm
8 Stipe duplex; on fallen trunk of <i>Abies</i> <i>Coltricia abieticola</i> 8* Stipe homogeneous; on ground of mixed forests9 9 Pores 0.5–3 per mm
 8 Stipe duplex; on fallen trunk of <i>Abies</i> <i>Coltricia abieticola</i> 8* Stipe homogeneous; on ground of mixed forests9 9 Pores 0.5–3 per mm
 8 Stipe duplex; on fallen trunk of <i>Abies</i>
 8 Stipe duplex; on fallen trunk of <i>Abies</i> <i>Coltricia abieticola</i> 8* Stipe homogeneous; on ground of mixed forests9 9 Pores 0.5–3 per mm10 9* Pores 3–6 per mm17 10 Hyphae strongly vertucose11 10* Hyphae smooth12 11 Basidiocarps up to 1 cm in diam, pores 2–3 per mm; basidiospores 7.5–9 × 4.8–5 µm<i>Coltricia vertucata</i> 11* Basidiocarps up to 2.5 cm in diam, pores 0.5–2 per
 8 Stipe duplex; on fallen trunk of <i>Abies</i>
 8 Stipe duplex; on fallen trunk of <i>Abies</i>
 8 Stipe duplex; on fallen trunk of <i>Abies</i>
 8 Stipe duplex; on fallen trunk of <i>Abies</i>
 8 Stipe duplex; on fallen trunk of <i>Abies</i>
 8 Stipe duplex; on fallen trunk of <i>Abies</i>

14 Basidiospores oblong-ellipsoid, < 5.5 μm wide Coltricia focicola
14* Basidiospores broadly ellipsoid to subglobose, > 5.5 μm wide
15 Contextual hyphae > 10 μm wide Coltricia subcinnamomea
15* Contextual hyphae < 10 μm wide16
16 Stipe more or less uniform; basidiospores $7.5-8.2 \times$
6–6.8 μm <i>Coltricia wenshanensis</i>
16* Stipe up to 8 mm diam at the apex; basidiospores 8–
10×5.5 – $6.5 \ \mu m$ Coltricia austrosinensis
17 Stipe bearing numerous spinesColtricia strigosipes
17* Stipe smooth or velutinate
18 Growing in gymnosperm forests; basidiospores ellipsoid <i>Coltricia perennis</i>
18* Growing in angiosperm forests; basidiospores broadly
ellipsoid to globose19
19 Tramal hyphae 3–4 μm in diam20
19* Tramal hyphae 4–9 in diam21
20 Mature pilei > 1.5 cm in diam; basidiospores $7.8-9 \times$
5.2–6 μmColtricia subperennis
20* Mature pilei < 1.5 cm in diam; basidiospores $6-7 \times 4-$
5 μm <i>Coltricia minima</i> 21 Basidiospores < 4 μm wide <i>Coltricia pyrophila</i>
21 Basidiospores $< 4 \mu\text{m}$ wideConnet pyrophila 21* Basidiospores $> 4 \mu\text{m}$ wide
22 Pileal surface hyphae dichotomously branched
Coltricia well
22* Pileal surface hyphae unbranched
22* Pileal surface hyphae unbranched23 23 Mature pilei > 2 cm in diam; basidiospores 7–8 × 5.5– 6.5 μm <i>Coltricia cinnamomea</i>
22* Pileal surface hyphae unbranched23 23 Mature pilei > 2 cm in diam; basidiospores 7–8 × 5.5– 6.5 μm <i>Coltricia cinnamomea</i> 23* Mature pilei < 2 cm in diam; basidiospores 5.5–6.2 ×
 22* Pileal surface hyphae unbranched
22* Pileal surface hyphae unbranched23 23 Mature pilei > 2 cm in diam; basidiospores 7–8 × 5.5– 6.5 μm <i>Coltricia cinnamomea</i> 23* Mature pilei < 2 cm in diam; basidiospores 5.5–6.2 × 4.5–5.8 μm <i>Coltricia velutina</i> 24 Basidiocarps resupinate to effused-reflexed
22* Pileal surface hyphae unbranched

- 30* Pores 1–2 per mm; basidiospores 8.5–10.2 × 5–6 μm
 Coltriciella oblectabilis
 31 Basidiospores naviculate, 8–11 × 5–6.2 μm
- Coltriciella naviculiformis 31* Basidiospores subglobose to globose, 6–7 × 5.8–7 μmColtriciella globosa

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References

- Aime MC, Henkel TW, Ryvarden L (2003) Studies in neotropical polypores 15: new and interesting species from Guyana. Mycologia 95:614–619. https://doi.org/10.2307/3761937
- Baltazar JM, Ryvarden L, Gibertoni TB (2010) The genus *Coltricia* in Brazil: new records and two new species. Mycologia 102:1253– 1262. https://doi.org/10.3852/09-227
- Bian LS, Dai YC (2015) Coltriciella globosa and C. pseudodependens spp. nov. (Hymenochaetales) from southern China based on morphological and molecular characters. Mycoscience 56:190–197. https://doi.org/10.1016/j.myc.2014.06.001
- Bian LS, Dai YC (2017) Morphological and molecular evidence for three new species of *Coltricia* (Hymenochaetaceae, Basidiomycota) from southern China. Mycologia 109:64–74. https://doi.org/10.1080/ 00275514.2017.1286571
- Bian LS, Wu F, Dai YC (2016) Two new species of *Coltricia* (Hymenochaetaceae, Basidiomycota) from southern China based on the evidence from morphology and DNA sequence data. Mycol Prog 15:27. https://doi.org/10.1007/s11557-016-1173-0
- Burdsall HH (1969) A new polypore from the Eastern United States. Mycologia 61:647–651. https://doi.org/10.2307/3757257
- Chen JJ, Cui BK, Dai YC (2016) Global diversity and molecular systematics of *Wrightoporia* s.l. (Russulales, Basidiomycota). Persoonia 37:21–36. https://doi.org/10.3767/003158516x689666
- Corner EJH (1991) Ad Polyporaceas 7. Nova Hedwigia 101:1–175
- Dai YC (2010) Hymenochaetaceae (Basidiomycota) in China. Fungal Divers 45:131–343. https://doi.org/10.1007/s13225-010-0066-9
- Dai YC, Cui BK (2006) Two new species of Hymenochaetaceae from eastern China. Mycotaxon 94:341–347. https://doi.org/10.1016/ S0014-5793(01)02483-8
- Dai YC, Li HJ (2012) Type studies on *Coltricia* and *Coltriciella* described by E. J H Corner from Southeast Asia Mycoscience 53: 337–346. https://doi.org/10.1007/s10267-011-0174-8
- Dai YC, Yuan HS, Cui BK (2010) *Coltricia* (Basidiomycota, Hymenochaetaceae) in China. Sydowia 62:11–21
- Decock C (2013) Coltricia oboensis sp. nov. from the high elevation cloud forest of São Tomé. Cryptogam Mycol 34:175–181. https:// doi.org/10.7872/crym.v34.iss2.2013.175
- Felsenstein J (1985) Confidence intervals on phylogenetics: an approach using bootstrap. Evolution 39:783–791
- Gilbertson RL, Ryvarden L (1986) North American polypores 1. Abortiporus–Lindtneria, Fungiflora, Oslo
- Gomes-Silva AC, Ryvarden L, Gibertoni TB (2009) New and interesting species of Hymenochaetaceae from the Brazilian Amazonia. Mycol Prog 8:273–279. https://doi.org/10.1007/s11557-009-0606-4
- Hall TA (1999) Bioedit: a user-friendly biological sequence alignment editor and analysis program for windows 95/98/NT. Nucleic Acids Symp Ser 41:95–98

- Hillis DM, Bull JJ (1993) An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. Syst Biol 42:182– 192. https://doi.org/10.2307/2992540
- Katoh K, Toh H (2008) Improved accuracy of multiple ncRNA alignment by incorporating structural information into a MAFFT-based framework. BMC Bioinformatics 9:212. https://doi.org/10.1186/1471-2105-9-212
- Kornerup A, Wanscher JH (1978) Methuen handbook of colour, 3rd edn. Eyre Methuen, London
- Larsson K-H, Parmasto E, Fischer M, Langer E, Nakasone KK, Redhead SA (2006) Hymenochaetales: a molecular phylogeny for the hymenochaetoid clade. Mycologia 98:926–936. https://doi.org/10. 1080/15572536.2006.11832622
- Masuka A, Ryvarden L (1993) Two new polypores from Malawi. Mycologia Helvetica 5:143–148
- Matheny PB (2005) Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences. Mol Phylogen Evol 35:1–20. https://doi.org/10.1016/j.ympev.2004.11.014
- Murrill WA (1904) The Polyporaceae of North America: VII. The genera Hexagona, Grifola, Romellia, Coltricia and Coltriciella. Bull Torrey B Club 31:325–348. https://doi.org/10.2307/2478798
- Murrill WA (1920) Corrections and additions to the polypores of temperate North America. Mycologia 12:6–24. https://doi.org/10.2307/ 3753482
- Niemelä T (2005) Polypores, lignicolous fungi. Norrlinia 13:1-320
- Núñez M, Ryvarden L (2000) East Asian polypores 1. Ganodermataceae and Hymenochaetaceae. Synop Fungorum 13:1–168
- Posada D, Crandall KA (1998) Modeltest: testing the model of DNA substitution. Bioinformatics 14:817–818. https://doi.org/10.1093/ bioinformatics/14.9.817
- Rajchenberg M, Wright JE (1998) Two interesting polypore species (Hymenochaetales) from Argentina. Folia Cryptog Estonica 33: 119–122
- Ronquist F, Huelsenbeck JP (2003) MRBAYES 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572–1574. https://doi.org/10.1093/bioinformatics/btg180
- Ryvarden L (1991) Genera of polypores. Nomenclature and taxonomy. Synop Fungorum 5:1–363
- Ryvarden L (2007) Studies in Neotropical polypores 23. New and interesting wood-inhabiting fungi from Belize. Synop Fungorum 23:32– 50
- Ryvarden L, Melo I (2014) Poroid fungi of Europe. Synop Fungorum 31: 1–455

- Ryvarden L, Krisai-Greilhuber I, Hausknecht A (2006) Coltricia grandispora and Tyromyces vitellinus, two new polypores. Österr Z Pilzk 15:143–147
- Stamatakis A (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22:2688–2690. https://doi.org/10.1093/ bioinformatics/btl446
- Swofford DL (2002) PAUP*: phylogenetic analysis using parsimony (*and other methods), version 4.0b10. Sinauer Associates, Sunderland, Massachusetts
- Tedersoo L, Suvi T, Beaver K, Saar I (2007) Ectomycorrhizas of *Coltricia* and *Coltriciella* (Hymenochaetales, Basidiomycota) on Caesalpiniaceae, Dipterocarpaceae and Myrtaceae in Seychelles. Mycol Prog 6:101–107. https://doi.org/10.1007/s11557-007-0530-4
- Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG (1997) The Clustal_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Res 25:4876–4882. https://doi.org/10.1093/nar/25.24.4876
- Valenzuela R, Raymundo T, Cifuentes J, Esqueda M, Amalfi M, Decock C (2012) *Coltriciella sonorensis* sp. nov. (Basidiomycota, Hymenochaetales) from Mexico: evidence from morphology and DNA sequence data. Mycol Prog 11:181–189. https://doi.org/10. 1007/s11557-011-0740-7
- Vasco-Palacios AM (2016) Ectomycorrhizal fungi in Amazonian tropical forests in Colombia. geboren op 13 januari te Bogotá, Colombia
- Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. J Bacteriol 172:4238–4246. https://doi.org/10.1128/jb.172. 8.4238-4246.1990
- Wagner T, Fischer M (2002) Proceedings towards a natural classification of the worldwide taxa *Phellinus* s.l. and *Inonotus* s.l., and phylogenetic relationships of allied genera. Mycologia 94:998–1016. https:// doi.org/10.2307/3761866
- White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds) PCR protocols: a guide to methods and applications. Academic Press, San Diego
- Zhou LW, Tedersoo L (2012) Coltricia australica sp. nov. (Hymenochaetales, Basidiomycota) from Australia. Mycotaxon 122:123–128. https://doi.org/10.5248/122.123

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