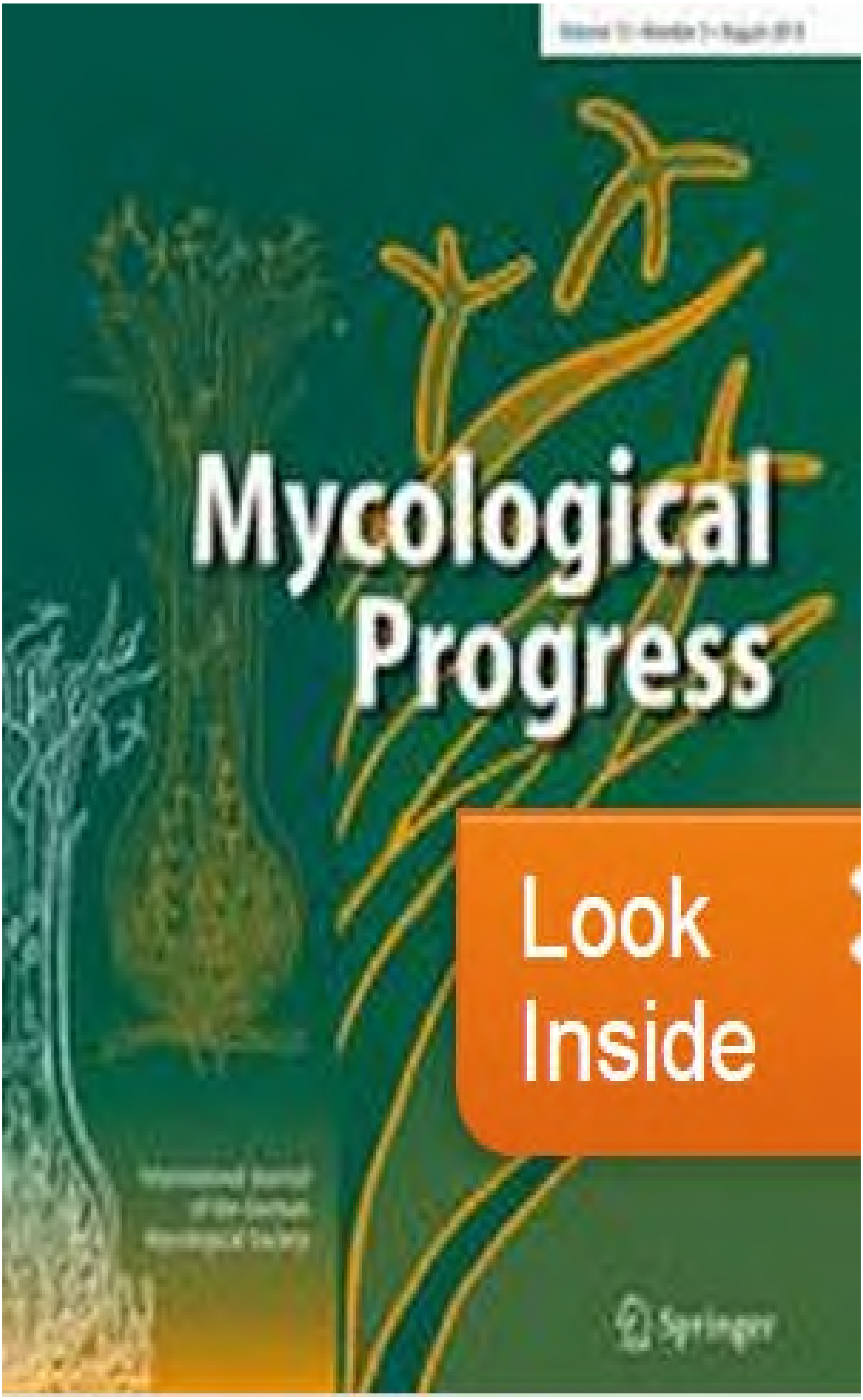
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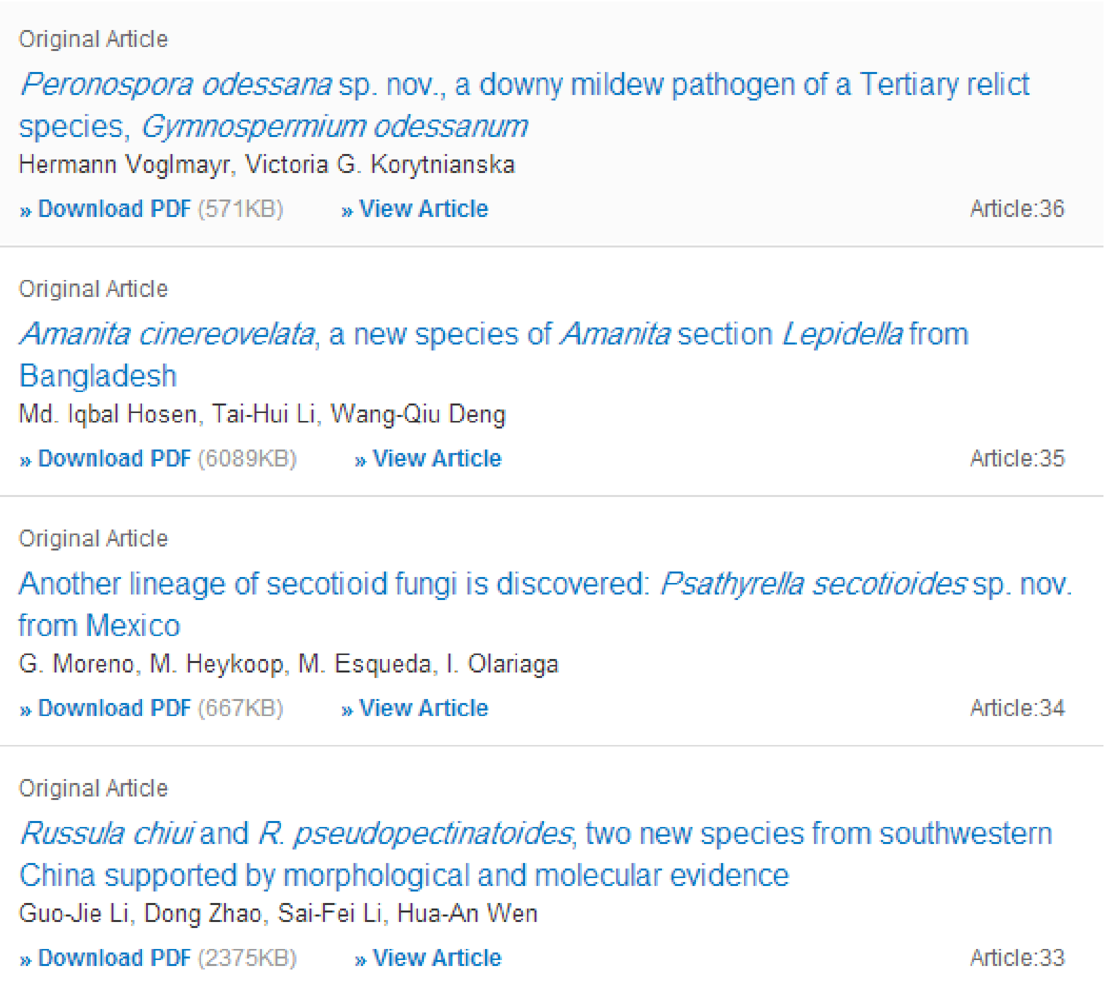

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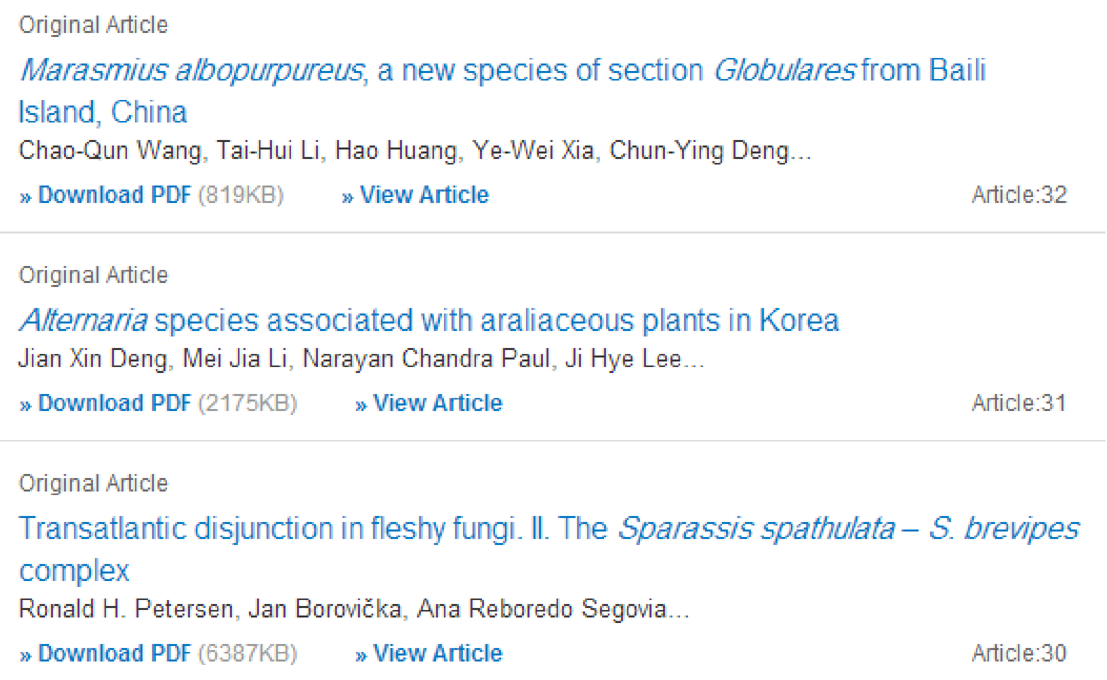

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ORIGINAL ARTICLE

Phylogeny and taxonomy of the genus *Abundisporus* (Polyporales, Basidiomycota)

Chang-Lin Zhao[1] · Hong Chen[1] · Jie Song[1] · Bao-Kai Cui[1]

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Abstract Phylogenetic and taxonomic studies of *Abundisporus* were carried out. Inferred from phylogenies based on DNA sequences of multiple loci including the internal transcribed spacer (ITS) regions, the large subunit nuclear ribosomal RNA gene (nLSU), the small subunit mitochondrial rRNA gene sequences (mtSSU) and the translation elongation factor 1-α gene (*tef1*), species falling under the current concept of *Abundisporus* represent a monophyletic lineage, which belongs to the core polyporoid clade. The genus is morphologically characterized by resupinate to pileate basidiocarps with pale umber to deep purplish brown or greyish to umber brown context; a dimitic hyphal structure with yellow to pale brown skeletal hyphae; pale yellowish, non-dextrinoid, ellipsoid basidiospores with slightly thick walls; and tissues that turn brown in KOH. Seven taxa have been recognized in the genus with both morphological and molecular evidence. A new species, *A. mollissimus*, is described here. The new species is characterized by its soft, perennial, effused-reflexed to pileate basidiocarp, a dimitic hyphal system with dextrinoid, cyanophilous and narrower skeletal hyphae, and ellipsoid basidiospores measuring 4–4.5 × 3–3.5 µm. Illustrated descriptions and a key to all species in this genus are provided.

Keywords Phylogenetic analysis · Polypore · Taxonomy · Wood-rotting fungi

Introduction

Abundisporus Ryvarden was established by Ryvarden (1998) and typified by *A. fuscopurpureus* (Pers.) Ryvarden. The genus is characterized by resupinate to pileate basidiocarps with pale umber to deep purplish brown or greyish to umber brown context and a dimitic hyphal structure with yellow to pale brown skeletal hyphae, and basidiospores of *Abundisporus* are ellipsoid, slightly thick-walled, pale yellowish and non-dextrinoid (Ryvarden 1998). Most species of *Abundisporus* were recorded in tropics and subtropical areas (Ryvarden 1998), although *A. pubertatis* (Lloyd) Parmasto and *A. quercicola* Y.C. Dai were reported in temperate areas (Dai 2012). Phylogenetic studies based on ITS and nLSU DNA sequence data have suggested that *Abundisporus* is monophyletic (Robledo et al. 2009). Recent studies showed that *Abundisporus* clustered in the core polyporoid clade of the Polyporaceae, sampling with only two species of *Abundisporus* (Miettinen and Rajchenberg 2012; Binder et al. 2013; Zhao et al. 2013).

Investigations on the diversity of wood-rotting fungi have been carried out recently in Hainan Province, which is a tropic island located in southern China, between 18°10'–20°10' N and 108°37'–111°05' E (Dai and Cui 2011; Dai et al. 2011; Cui 2013; Li and Cui 2013). During the surveys, an undescribed fungus of *Abundisporus* was identified, based on morphological characters and phylogenetic analysis of DNA sequences inferred from ITS, nLSU, mtSSU and *tef1*. It is described as *A. mollissimus* in this paper. Other species of *Abundisporus* were also studied for comparison. Illustrated

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descriptions and an identification key to species of *Abundisporus* are provided.

Materials and methods

Morphology

The studied specimens were deposited in the herbaria of the Beijing Forestry University (BJFC), the Botanical Museum (O), the Royal Botanic Gardens (K), the Farlow Herbarium (FH), the Université Catholique de Louvain (MUCL) and the Universidad de Córdoba (HUC). Macro-morphological descriptions are based on field notes. Special color terms follow Petersen (1996). Micro-morphological data were obtained from the dried specimens, and observed under a light microscope following Li et al. (2014). Sections were studied at a magnification of 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 cotton blue and Melzer's reagent. Spores were measured from sections cut from the tubes. In presenting the variation of spore size, 5 % of measurements were excluded from each end of the range, and are given in parentheses. The following abbreviations were used: KOH = 5 % potassium hydroxide, CB = cotton blue, CB– = acyanophilous, IKI = Melzer's reagent, IKI– = both non-amyloid and non-dextrinoid, 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 a given number (b) of specimens.

Molecular phylogeny

A CTAB rapid plant genome extraction kit (Aidlab Biotechnologies Co., Ltd, Beijing) was used to extract total genomic DNA from dried specimens and perform the polymerase chain reaction (PCR), according to the manufacturer's instructions (Chen et al. 2015). The ITS regions were amplified with primer pairs ITS5 and ITS4 (White et al. 1990). The nLSU regions were amplified with primer pairs LR0R and LR7 (http://www.biology.duke.edu/fungi/mycolab/primers.htm). The mtSSU regions were amplified with primer pairs MS1 and MS2 (White et al. 1990). Part of *tef1* was amplified with primer pairs EF1-983 F and EF1-2218R (Rehner and Buckley 2005). The PCR cycling schedule for ITS and mtSSU included an initial denaturation at 95 °C for 3 min, followed by 35 cycles at 94 °C for 40 s, 58 °C for ITS and 55 °C for mtSSU for 45 s and 72 °C for 1 min, and a final extension of 72 °C for 10 min. The PCR cycling schedule for nLSU and *tef1* included an initial denaturation at 94 °C for 1 min, followed by 35 cycles at 94 °C for 30 s, 48 °C for nLSU and 59 °C for *tef1* for 1 min and 72 °C for 1.5 min, and a final extension of 72 °C for 10 min. The PCR products were purified and sequenced at Beijing Genomics Institute China, with the same primers. All newly generated sequences were deposited in GenBank (Table 1).

Additional sequences were downloaded from GenBank (Table 1). All sequences were aligned using ClustalX (Thompson et al. 1997) and manually adjusted in BioEdit (Hall 1999). The missing sequences are coded as "N". Ambiguous nucleotides were coded as "N". The final concatenated sequence alignment was deposited in TreeBase (submission ID 17431).

Most parsimonious phylogenies were inferred from the ITS + nLSU and the combined multi-gene dataset of ITS + nLSU + mtSSU + *tef1*, and their combinability was evaluated with the incongruence length difference (ILD) test (Farris et al. 1994) implemented in PAUP* 4.0b10 (Swofford 2002), under a heuristic search and 1000 homogeneity replicates giving a P value of 1.000, much greater than 0.01, which means there is no discrepancy among the four loci in reconstructing phylogenetic trees. Phylogenetic analysis approaches followed Zhao et al. (2014, 2015), and the tree construction procedure 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 were set to 5000, branches of zero length were collapsed and all parsimonious trees were saved. Clade robustness was assessed using a bootstrap (BT) analysis with 1000 replicates (Felsenstein 1985). Descriptive tree statistics including tree length (TL), the consistency index (CI), retention index (RI), rescaled consistency index (RC), and homoplasy index (HI) were calculated for each maximum parsimonious tree (MPT) generated.

MrModeltest 2.3 (Posada and Crandall 1998; Nylander 2004) was used to determine the best-fit evolution model for each data set for Bayesian inference (BI). Bayesian inference was 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 two runs from random starting trees for 5 million generations (ITS + nLSU), for 10 million generations (ITS + nLSU + mtSSU + *tef1*) and trees were sampled every 100 generations. The initial 25 % of generations were discarded as burn-in. A 50 % majority rule consensus tree of all remaining trees was calculated. Branches that received bootstrap support for maximum parsimony (MP) and Bayesian posterior probabilities (BPPs) greater than or equal to 75 % (MP) and 0.95 (BPP) were considered as significantly supported, respectively.

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

Species name	Sample no.	GenBank accessions				References
		ITS	nLSU	mtSSU	*tef1*	
Abundisporus fuscopurpureus	Cui 8638	JN048771	JN048790	KF051024	KF181153	Present study
A. fuscopurpureus	Cui 10950	KC456254	KC456256	KF051025	KF181154	Present study
A. fuscopurpureus	Cui 10969	KC456255	KC456257	KF051026	KF181155	Present study
A. mollissimus	Cui 6257	JX141451	JX141461	KF051027	KF181156	Present study
A. mollissimus	Dai 10764	JX141452	JX141462	KF051028	KF181157	Present study
A. pubertatis	Dai 12140	JN048772	JN048791	KF051033	KF181127	Present study
A. pubertatis	Cui 5776	KC787565	KC787572	KF051029	KF181129	Present study
A. pubertatis	Cui 5774	KC787566	KC787573	KF051032	KF181126	Present study
A. pubertatis	Cui 8607	KC787567	KC787574	KF051057	KF181151	Present study
A. pubertatis	Dai 11310	KC787568	KC787575	KF051031	KF181125	Present study
A. pubertatis	Dai 11927	KC787569	KC787576	KF051034	KF181128	Present study
A. quercicola	Dai 3084	KC415907	KC415909	KF051035	—	Present study
A. roseoalbus	Dai 12272	KC787571	KC787578	KF051036	KF181130	Present study
A. roseoalbus	Dai 12269	KC415908	KC415910	KF051037	KF181131	Present study
A. sclerosetosus	MUCL 41438	FJ411101	FJ393868	—	—	Robledo et al. 2009
A. violaceus	MUCL 38617	FJ411100	FJ393867	—	—	Robledo et al. 2009
A. violaceus	Ryvarden 32807	KF018127	KF018135	KF051038	KF181132	Present study
A. violaceus	Ryvarden 10775	KF018126	KF018134	KF051058	KF181152	Present study
Amaurodon viridis	TAA149664	AM490942	AM490942	—	—	Miettinen and Rajchenberg 2012
Basidioradulum radula	NH 9453	AF347105	AF347105	AF026611	—	Larsson et al. 2004
Bjerkandera adusta	DAOM 215869	DQ060097	AF287848	AF026592	—	Hibbett et al. 2007
Boletopsis leucomelaena	AFTOLID 1527	DQ484064	DQ154112	DQ435797	—	Matheny et al. 2006
Byssomerulius corium	KHL 8593	AY463389	AY586640	—	—	Larsson et al. 2004
Ceraceomyces violascens	KHL 11169	EU118611	EU118612	—	—	Larsson 2007
Ceriporia viridans	KHL 8765	AF347109	AF347109	AF393084	—	Larsson et al. 2004
Ceriporiopsis aneirina	MUAF 888	EU340895	EU368503	EU368504	—	Tomšovský et al. 2009
Donkioporia expansa	MUCL 35116	FJ411104	FJ393872	—	—	Robledo et al. 2009
Globulicium hiemale	5444b	DQ873595	DQ873595	DQ873594	—	Larsson 2007
Gloeoporus dichrous	KHL 11173	EU118627	EU118627	AY986495	—	Larsson 2007
G. pannocinctus	FCUG 2109	AF141612	AF141612	—	—	Miettinen and Rajchenberg 2012
Grammetheliopsis subtropica	Cui 9035	JQ845094	JQ845097	KF051030	KF181124	Zhao et al. 2014
G. subtropica	Cui9041	JQ845096	JQ845099	KF051039	KF181133	Zhao et al. 2014
Hornodermoporus latissima	Cui 6625	HQ876604	JF706340	KF051040	KF181134	Zhao et al. 2014
H. martia	Cui 7992	HQ876603	HQ654114	KF051041	KF181135	Zhao et al. 2014
H. martia	MUCL 41677	FJ411092	FJ393859	—	—	Robledo et al. 2009
H. martia	MUCL 41678	FJ411093	FJ393860	—	—	Robledo et al. 2009
Hyphoderma capitatum	KHL 8464	DQ677491	DQ677491	—	—	Larsson 2007
H. orphanellum	NH 12208	DQ677500	DQ677500	—	—	Larsson 2007
Hyphodermella corrugata	KHL 3663	EU118630	EU118630	—	—	Larsson 2007
Megasporia cystidiolophora	Cui 2688	JQ780389	JQ780431	—	—	Li and Cui 2013
M. guangdongensis	Cui 9130	JQ314373	JQ780428	—	—	Li and Cui 2013
M. hengduanensis	Cui 8076	JQ780392	JQ780433	—	—	Li and Cui 2013
M. hexagonoides	He 2608	JQ314368	JQ314388	—	—	Li and Cui 2013
M. ellipsoidea	Cui 5222	JQ314367	JQ314390	—	—	Li and Cui 2013
Meruliopsis taxicola	Kuljok 00/75	EU118648	EU118648	—	—	Larsson 2007
Microporellus violaceo-cinerascens	MUCL 45229	FJ411106	FJ393874	—	—	Robledo et al. 2009

Table 1 (continued)

Species name	Sample no.	GenBank accessions				References
		ITS	nLSU	mtSSU	*tef1*	
M. violaceo-cinerascens	Cui 8459	HQ876606	HQ654113	KF051042	KF181136	Zhao et al. 2014
Perenniporia hainaniana	Cui 6364	JQ861743	JQ861759	KF051044	KF181138	Zhao et al. 2014
P. hainaniana	Cui 6365	JQ861744	JQ861760	KF051045	KF181139	Zhao et al. 2014
P. hainaniana	Cui 6366	JQ861745	JQ861761	KF494996	KF494981	Zhao et al. 2014
P. medulla-panis	MUCL 49581	FJ411088	FJ393876	—	—	Robledo et al. 2009
P. medulla-panis	MUCL 43250	FJ411087	FJ393875	—	—	Robledo et al. 2009
P. medulla-panis	Cui 3274	JN112792	JN112793	KF051043	KF181137	Zhao et al. 2014
P. subacida	Cui 10053	KF495006	KF495017	KF218321	KF286327	Zhao et al. 2014
P. substraminea	Dai 10781	KF495007	KF495018	KF494995	KF494983	Zhao et al. 2014
P. substraminea	Cui 10177	JQ001852	JQ001844	KF051046	KF181140	Zhao et al. 2014
P. substraminea	Cui 10191	JQ001853	JQ001845	KF051047	KF181141	Zhao et al. 2014
Perenniporiella chaquenia	MUCL 47647	FJ411083	FJ393855	—	HM467609	Robledo et al. 2009
P. chaquenia	MUCL 47648	FJ411084	FJ393856	—	HM467610	Robledo et al. 2009
P. micropora	MUCL43581	FJ411086	FJ393858	—	HM467608	Robledo et al. 2009
P. neofulva	MUCL 45091	FJ411080	FJ393852	—	HM467599	Robledo et al. 2009
P. pendula	MUCL 46034	FJ411082	FJ393853	—	HM467601	Robledo et al. 2009
Phanerochaete sordida	KHL 12054	EU118653	EU118653	—	—	Larsson 2007
Poriodontia subvinosa	H 10493	FN907920	FN907920	—	—	Miettinen and Larsson 2011
Pycnoporus cinnabarinus	AFTOL-ID 772	DQ411525	AY586703	U27059	—	Binder et al. 2013
Pyrofomes demidoffii	MUCL 41034	FJ411105	FJ393873	—	—	Robledo et al. 2009
Rickenella mellea	Lamoure 74	U66438	U66438	—	—	Miettinen and Larsson 2011
Trametes elegans	FP105679	JN164944	JN164799	FJ591058	JN164899	Justo and Hibbett. 2011
T. hirsuta	RLG5133T	JN164854	JN164801	AF042154	JN164891	Justo and Hibbett. 2011
Trichaptum abietinum	FCUG 2581	AF141636	AF141636	—	AJ309877	Binder et al. 2005
Truncospora detrita	MUCL 42649	FJ411099	FJ393866	—	—	Robledo et al. 2009
T. ochroleuca	Dai 11486	HQ654105	JF706349	KF051048	KF181142	Zhao et al. 2014
T. ochroleuca	MUCL 39726	FJ411098	FJ393865	—	—	Robledo et al. 2009
T. ochroleuca	Cui 5671	JX941584	JX941602	KF218309	KF286315	Zhao et al. 2014
T. ochroleuca	Cui 5673	JX941585	JX941603	KF218308	KF286314	Zhao et al. 2014
T. ohiensis	MUCL 41036	FJ411096	FJ393863	—	—	Robledo et al. 2009
T. ornata	Cui 5714	HQ654103	HQ654116	KF051056	KF181150	Zhao et al. 2014
Vanderbylia fraxinea	DP 83	AM269789	AM269853	—	—	Guglielmo et al. 2007
V. fraxinea	Cui 8871	JF706329	JF706345	KF051050	KF181144	Zhao et al. 2014
V. fraxinea	Cui 7154	HQ654095	HQ654110	KF218288	KF286294	Zhao et al. 2014
V. robiniophila	Cui 5644	HQ876609	JF706342	KF051051	KF181145	Zhao et al. 2014
V. robiniophila	Cui 7144	HQ876608	JF706341	KF051052	KF181146	Zhao et al. 2014
V. vicina	MUCL 44779	FJ411095	AF518666	—	—	Robledo et al. 2009
Vuilleminia comedens	T-583	AY463482	AY586725	AF518699	—	Larsson et al. 2004
Yuchengia narymica	Dai 6998	JN048775	JN048794	KF051055	KF181149	Zhao et al. 2014

Results

The ITS + nLSU dataset included sequences from 72 fungal specimens representing 56 taxa. The dataset had an aligned length of 2478 characters, of which 1481 characters are constant, 277 are variable and parsimony-uninformative, and 720 are parsimony-informative. Maximum parsimony analysis yielded 6 equally parsimonious trees (TL = 4274, CI=0.386, HI=0.614, RI=0.598, RC=0.239). The best model for the combined ITS + nLSU dataset estimated and applied in the Bayesian analysis is: GTR + I + G, lset nst = 6, rates = invgamma; prset statefreqpr = dirichlet (1,1,1,1). Bayesian analysis resulted in a similar topology as MP analysis, with an average standard deviation (SD) of split frequencies = 0.007613 (BI). Sequences of *Amaurodon viridis* (Alb. & Schwein.) J. Schröt., *Boletopsis leucomelaena* (Pers.) Fayod and *Vuilleminia comedens* (Nees) Maire obtained from GenBank were used as outgroups to root trees following Miettinen and Rajchenberg (2012).

The phylogeny (Fig. 1) inferred from ITS + nLSU sequences demonstrated thirteen major subclades for sampled species of the core polyporoid clade. The new species clustered into the *Abundisporus* lineage.

The four gene (ITS, nLSU, mtSSU and *tef1*) sequence datasets did not show any conflicts in tree topology for the reciprocal bootstrap trees, which allowed us to combine them. The number of characters, including gaps, for each locus alignment was as follows: 694 for ITS, 1421 for nLSU, 521 for mtSSU and 1020 for *tef1*. The combined dataset included sequences from 55 fungal specimens representing 29 taxa. The dataset had an aligned length of 3654 characters, of which 2626 were constant, 139 were variable but parsimony-uninformative, and 889 were parsimony-informative. Maximum parsimony analysis yielded 10 equally parsimonious trees (TL=2792, CI=0.544, HI=0.456, RI=0.782, RC=0.423). The best model for the combined ITS, nLSU, mtSSU and *tef1* partition was a GTR + I + G model. The Bayesian inference analysis resulted in a similar topology. Sequences of *Donkioporia expansa* (Desm.) Kotl. & Pouzar and *Pyrofomes demidoffii* (Lév.) Kotl. & Pouzar obtained from GenBank were used as outgroups to root trees following Zhao et al. (2014).

The phylogeny (Fig. 2) inferred from the combined ITS + nLSU + mtSSU + *tef1* sequence dataset resolved nine major clades for the sampled species of *Abundisporus* and related genera. Sampled specimens of the new species, *A. mollissimus*, formed a well-supported lineage distinct from other species.

Taxonomy

Abundisporus mollissimus B.K. Cui & C.L. Zhao, sp. nov. Figs. 3c, d, 4

MycoBank no.: MB 811607

Differs from other *Abundisporus* species by effused-reflexed to pileate and soft basidiocarps, narrower skeletal hyphae, and basidiospores measuring 4–4.5×33.5 μm.

Holotype. **CHINA**. Hainan Prov., Chengmai County, on fallen angiosperm trunk, 6 May 2009 *Cui 6257* (BJFC).

Etymology. mollissimus (Lat.): referring to the soft basidiocarps.

Fruitbody. Basidiocarps perennial, effused-reflexed to pileate, soft, without odor or taste when fresh, becoming soft corky upon drying. Pileus semicircular to conchate, projecting up to 1.5 cm, 3.5 cm wide and 3 mm thick at base. Pileal surface yellow brown to umber-brown, velutinate, concentrically zonate; margin acute, yellowish brown. Pore surface buff to buff-yellow when fresh, buff-yellow upon drying; pores round, 7–8 per mm; dissepiments thin, entire. Sterile margin narrow, cream to buff, up to 1 mm wide. Context dull brown, soft corky, thin, up to 1 mm thick. Tubes concolorous with porous surface, soft corky, up to 2 mm long.

Hyphal structure. Hyphal system dimitic; generative hyphae with clamp connections; skeletal hyphae dextrinoid, CB+; tissues becoming brownish in KOH.

Context. Generative hyphae infrequent, hyaline, thin-walled, usually unbranched, 1.5–2.5 μm in diameter; skeletal hyphae dominant, yellowish brown, thick-walled with a wide lumen, usually unbranched, flexuous, interwoven, 2.5–3 μm in diameter.

Tubes. Generative hyphae infrequent, difficult to find, hyaline, usually unbranched, 1–1.5 μm in diameter; skeletal hyphae dominant, yellowish brown, thick-walled with a narrow lumen, occasionally branched, strongly flexuous, interwoven, 2–3 μm in diameter. Cystidia absent, but fusoid cystidioles present, hyaline, thin-walled, 10–12×5–5.5 μm; basidia barrel-shaped to pear-shaped, with four sterigmata and a basal clamp connection, 11–13×6–7 μm; basidioles dominant, similar to basidia in shape but slightly smaller.

Spores. Basidiospores ellipsoid, yellowish, slightly thick-walled, smooth, non-dextrinoid, CB+, (3.5–)4–4.5(–5)×(2.5–)3–3.5 μm, L=4.3 μm, W=3.3 μm, Q=1.4–1.42 (n=60/2).

Type of rot. A white rot.

Additional specimen (*paratype*) *examined*: **CHINA**. Hainan Prov., Changjiang County, Bawangling Nature Reserve, on dead tree of *Xanthophyllum hainanense*, 8 May 2009 *Dai 10764* (BJFC).

Abundisporus fuscopurpureus (Pers.) Ryvarden, Belg. J. Bot. 131:154 (1999). Figs. 3a, b, 5

Basionym: *Polyporus fuscopurpureus* Pers.

Fruitbody. Basidiocarps perennial, pileate, corky, without odor or taste when fresh, becoming hard corky upon drying. Pilei applanate to slightly dimidiate or semicircular, projecting up to 5 cm, 9 cm wide and 2 cm thick at base. Pileal surface umber-brown to dark brown or black, smooth, with indistinct concentric zones; margin acute, white to pale brown. Pore surface pinkish to buff when fresh, greyish brown to orange-brown upon drying; pores round, 7–9 per mm; dissepiments thin, entire. Sterile margin narrow, greyish brown, up to 1 mm wide. Context clay-buff, corky, up to 2 mm thick. Tubes concolorous with pore surface, corky, up to 1.8 cm long.

Hyphal structure. Hyphal system dimitic; generative hyphae with clamp connections; skeletal hyphae dextrinoid, CB+; tissues becoming brownish in KOH.

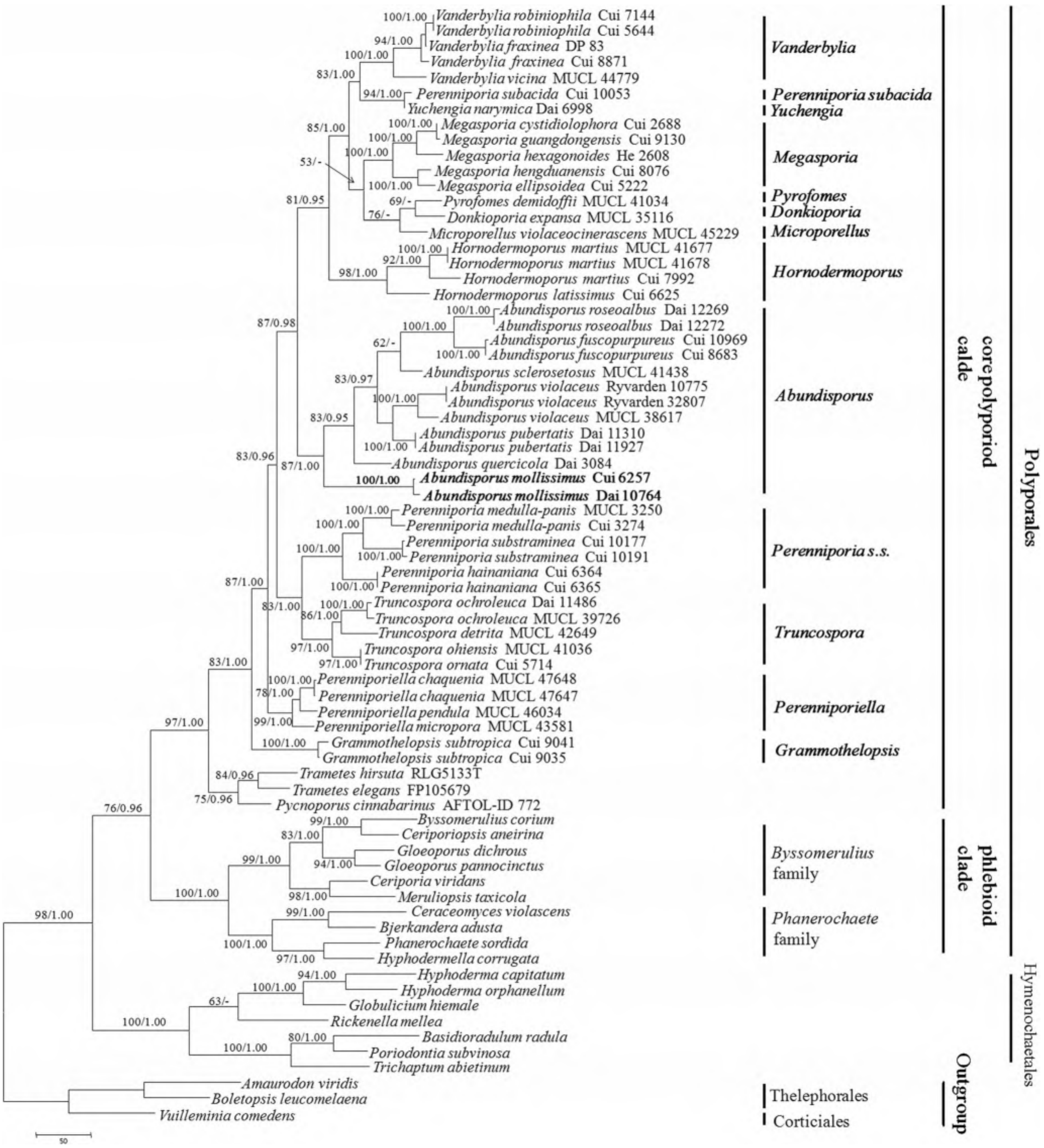

Fig. 1 Maximum parsimony strict consensus tree illustrating the phylogeny of *Abundisporus* species and related species based on ITS + nLSU sequences. Branches are labeled with parsimony bootstrap proportions higher than 50 % and Bayesian posterior probabilities more than 0.95, respectively. Clade names follow Miettinen and Rajchenberg (2012)

Context. Generative hyphae infrequent, hyaline, thin-walled, usually unbranched, 2.5–3.5 μm in diameter; skeletal hyphae dominant, yellowish brown, thick-walled with a wide lumen, branched, flexuous, interwoven, 3–4.5 μm in diameter.

Tubes. Generative hyphae infrequent, difficult to find, hyaline, thin-walled, usually unbranched, 2–2.5 μm in diameter; skeletal hyphae dominant, yellowish brown, thick-walled with a wide lumen, occasionally branched, flexuous, interwoven, 2–3.5 μm in diameter. Cystidia and cystidioles absent; basidia

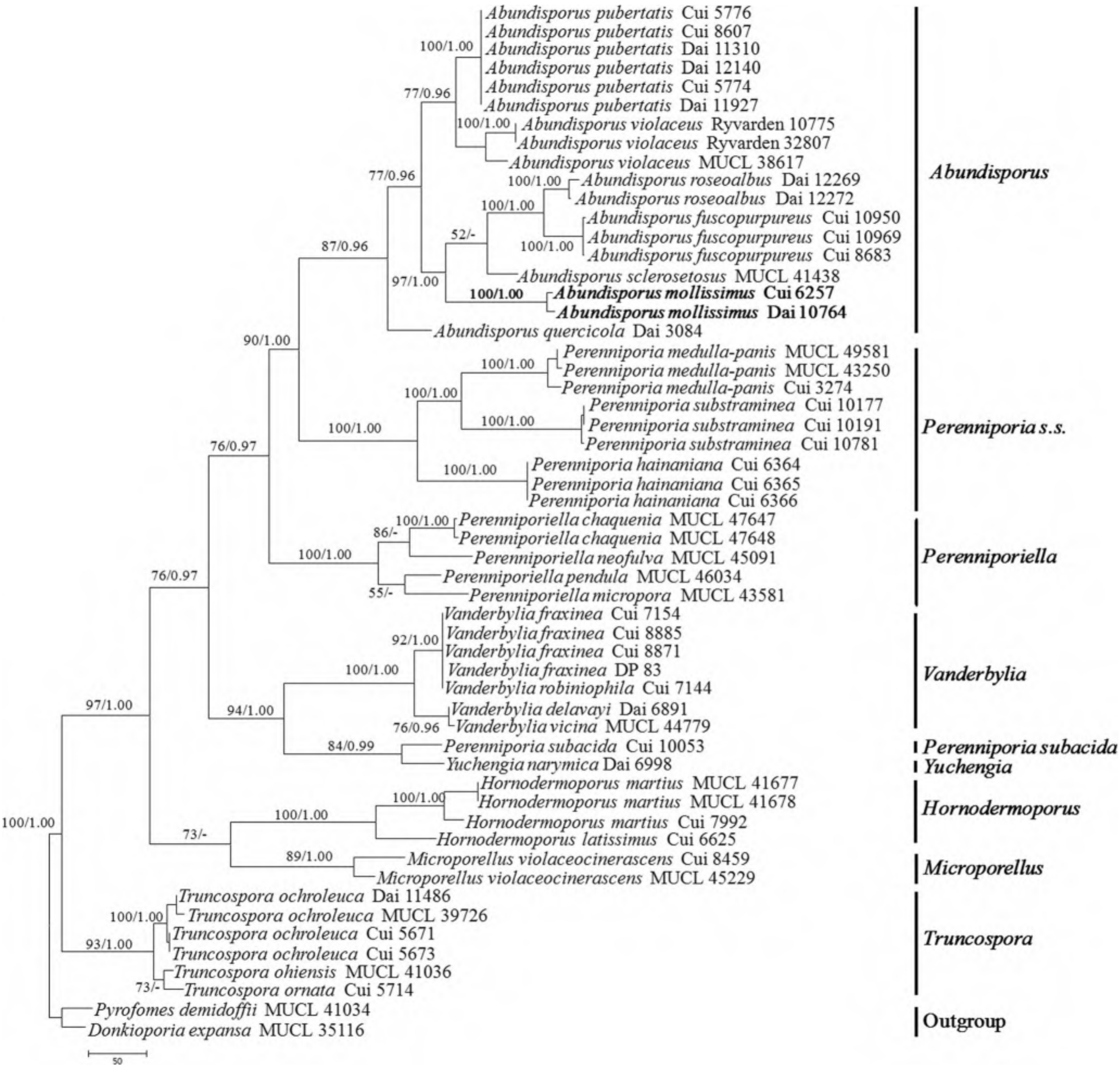

Fig. 2 Maximum parsimony strict consensus tree illustrating the phylogeny of *Abundisporus* species and related species based on the combined ITS+ nLS + mtSSU + *tef1* sequence dataset. Branches are labeled with parsimony bootstrap proportions higher than 50 % and Bayesian posterior probabilities more than 0.95, respectively. Clade names follow Zhao et al. (2014)

barrel-shaped to pear-shaped, with four sterigmata and a basal clamp connection, 12–16×6–10 μm; basidioles dominant, in shape similar to basidia, but slightly smaller.

Spores. Basidiospores ellipsoid, yellowish, slightly thick-walled, smooth, non-dextrinoid, CB–, (2–)2.5–3.3(–3.9)× (1.5–)1.7–2.1(–2.5) μm, L=2.8 μm, W=1.9 μm, Q=1.48–1.55 (n=240/8).

Type of rot. A white rot.

Specimens examined: **BRAZIL**. Parana State, San Mateus do Sul, Fazenda Durgo, on decayed branch, 24 August 1966 *TRTC 66.1489* (K); 19 August 1989 *No.1320* (O). **CAMEROON**. South West Prov., Korup National Park, on partly fallen trunk, 1 September 1996 *P.J. Roberts K 50* (K). **CHINA**. Hainan Prov., Lingshui County, Diaoluoshan Nature Reserve, on fallen angiosperm trunk, 10 November 2012 *Cui 10950* (BJFC); 11 November 2012 *Cui 10969*, *10975* (BJFC); Yunnan Prov., Mengla County, Wangtianshu Park, on fallen angiosperm trunk, 3 November 2009 *Cui 8638* (BJFC). **KENYA**. Coast Prov., Shimba Hills, on dead hardwoods, 12 October 1972 *Taylor 863* (O). **PAPUA NEW GUINEA**. Morobe Prov., Kui, Morobe District, on rotting wood, 7 February 1968 *FM 350* (K). **UGANDA**. Central Region, Mabira

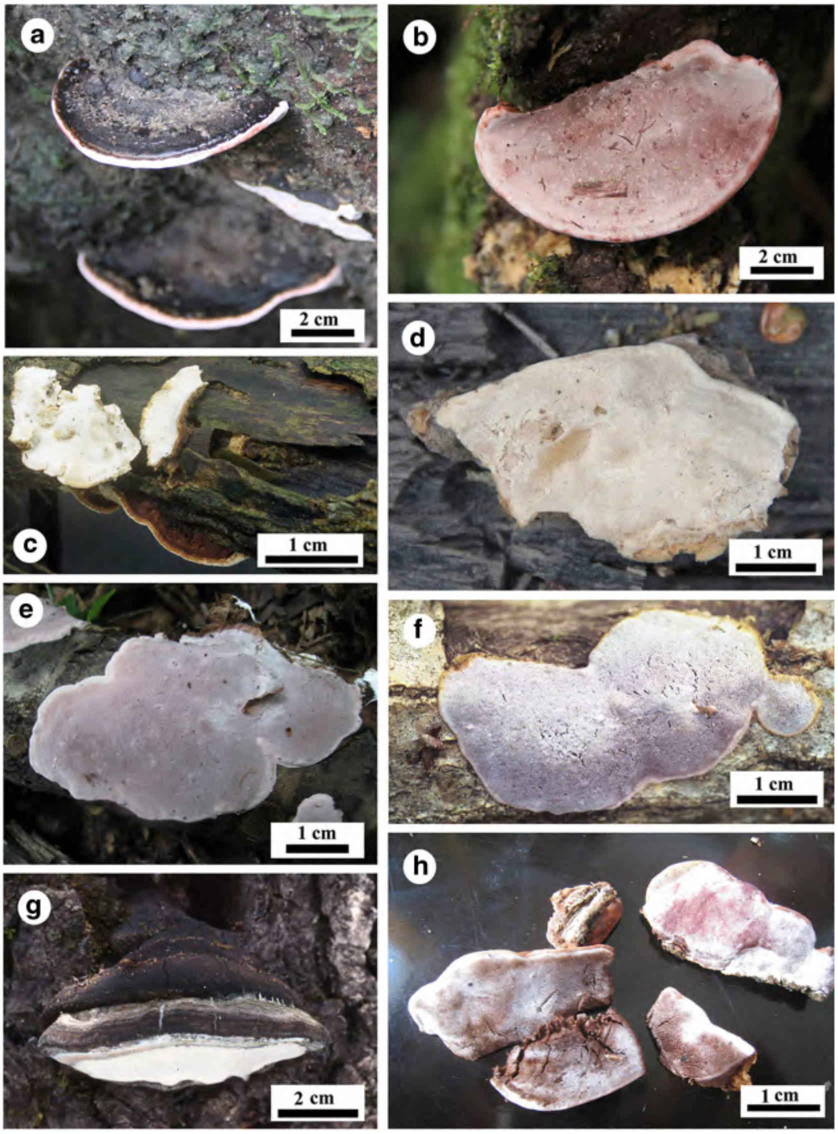

Fig. 3 Basidiocarps of the *Abundisporus* species. **a**–**b**. *A. fuscopurpureus*; **c**–**d**. *A. mollissimus*; **e**–**f**. *A. pubertatis*; **g**. *A. quercicola*; **h**. *A. roseoalbus*

Forest, Mulange, on fallen trunk, 10 April 1919 *Dümmer 4040* (K).

Abundisporus pubertatis (Lloyd) Parmasto, Karstenia 40:133 (2000). Figs. 3e, f, Fig. 6

Basionym: *Polyporus pubertatis* Lloyd.

Fruitbody. Basidiocarps perennial, resupinate to effused-reflexed, adnate, corky, without odor or taste when fresh, becoming hard corky upon drying. Pilei semicircular, projecting up to 2 cm, 3 cm wide and 1 cm thick at base. Pileal surface orange-brown to pale brown, smooth, concentrically zonate; margin obtuse, greyish brown. Pore surface brownish-vinaceous to greyish brown when fresh, orange-brown to pale brown upon drying; pores round to angular, 5–7 per mm; dissepiments thin, entire. Sterile margin narrow, greyish brown, up to 1.5 mm wide. Context dull brown, soft corky, thin, up to 2 mm thick. Tubes concolorous with pore surface, corky, up to 8 mm long.

Hyphal structure. Hyphal system dimitic; generative hyphae with clamp connections; skeletal hyphae non-dextrinoid, CB+; tissues becoming brownish in KOH.

Context. Generative hyphae infrequent, hyaline, thin-walled, usually unbranched, 3.5–5 μm in diameter; skeletal hyphae dominant, yellowish brown, thick-walled with a narrow to wide lumen, branched, more or less flexuous, interwoven, 3.5–5 μm in diameter.

Tubes. Generative hyphae infrequent, difficult to find, hyaline, thin-walled, usually unbranched, 2.5–3.5 μm in diameter; skeletal hyphae dominant, yellowish brown, thick-walled with a narrow to wide lumen, occasionally branched, more or less flexuous, interwoven, 3–4 μm in diameter. Cystidia absent, but cystidioles present, narrowly fusoid, thin-walled, smooth, 11–15 × 2–3 μm; basidia barrel-shaped, with four sterigmata and a basal clamp connection, 15–18 × 8–10 μm; basidioles dominant, mostly pear-shaped, smaller than basidia.

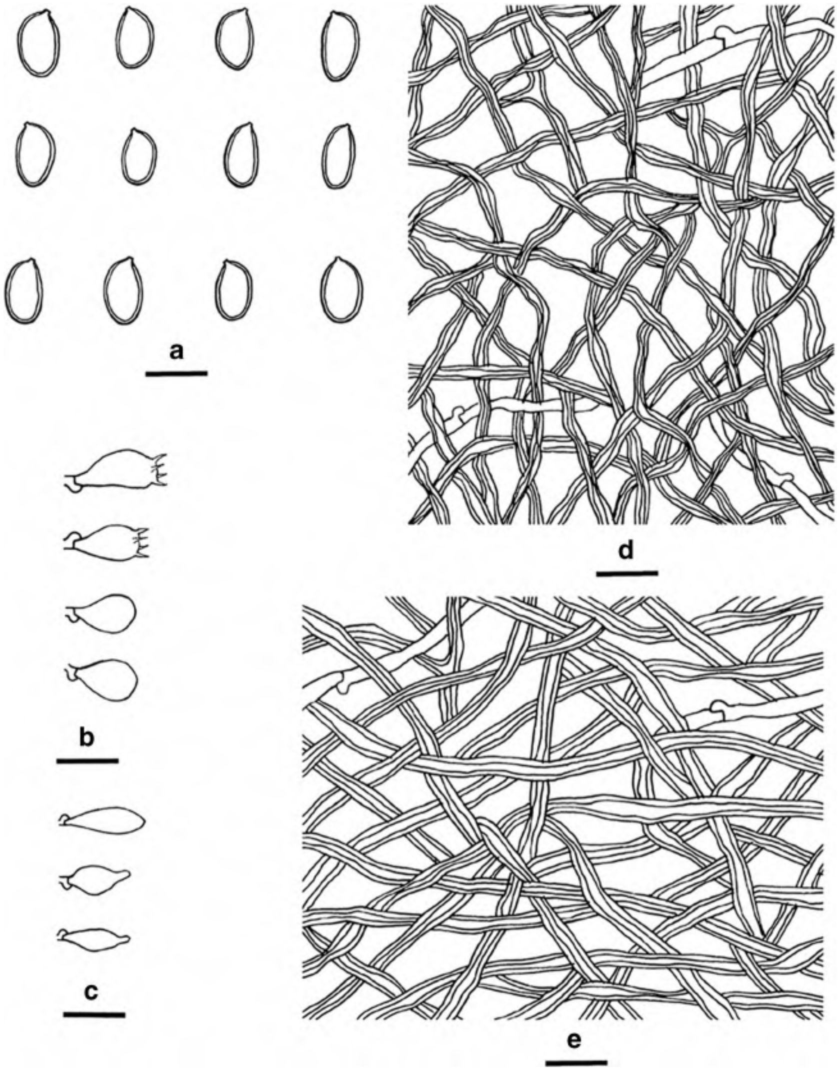

Fig. 4 Microscopic structures of *Abundisporus mollissimus* (drawn from the holotype). **a**. Basidiospores; **b**. Basidia and basidioles; **c**. Cystidioles; **d**. Hyphae from trama; **e**. Hyphae from context. Bars: **a**=5 μm; **b**–**e**=10 μm

Spores. Basidiospores ellipsoid, yellowish, slightly thick-walled, smooth, non-dextrinoid, CB–, (4–)4.2–5(–5.2)×2.5–3(–3.2) μm, L=4.41 μm, W=2.81 μm, Q=1.55–1.59 (n=120/4).

Type of rot. A white rot.

Specimens examined: **CHINA**. Anhui Prov., Huangshan, Huangshan Park, on fallen trunk of *Castanopsis*, 22 October 2010 *Dai 11927* (BJFC); Fujian Prov., Wuyishan County, Wuyi Mountains, on angiosperm stump, 19 October 2005 *Dai 7254* (BJFC); Henan Prov., Neixiang County, Baotianman Nature Reserve, on fallen trunk of *Quercus*, 23 September 2009 *Dai 11310* (BJFC); Hunan Prov., Shimen County, Hupingshan Nature Reserve, on living angiosperm tree, 15 August 2010 *Dai 12140* (BJFC); Liaoning Prov., Huanren County, Laotudingzi Nature Reserve, on fallen branch of *Quercus*, 1 August 2008 *Cui 5774*, *5776*, *5780* (BJFC); Yunnan Prov., Mengla County, Wangtianshu Park, on fallen angiosperm trunk, 03 November 2009 *Cui 8607* (BJFC).

Abundisporus quercicola Y.C. Dai, Ann. Bot. Fenn. 39:171 (2002). Figs. 3g, 7

Fruitbody. Basidiocarps perennial, pileate, solitary, becoming hard corky upon drying. Pilei ungulate, projecting up to 5 cm, 7 cm wide and 5 cm thick at base. Pileal surface dark grey to almost black, smooth, concentrically zonate; margin blunt, greyish black. Pore surface white when fresh, becoming ochraceous when dry; pores round, 5–7 per mm; dissepiments entire. Context dark brown, corky, up to 3 cm thick. Tubes dull brown, paler than context, corky, up to 2 cm long, a thin layer of context present between each annual tube layer.

Hyphal structure. Hyphal system dimitic; generative hyphae with clamp connections; skeletal hyphae dextrinoid, CB+; tissues darkening in KOH.

Context. Generative hyphae infrequent, thin-walled, usually unbranched, 2–3.5 μm in diameter; skeletal hyphae dominant, yellowish brown to rust brown, thick-walled with a wide lumen, frequently branched, flexuous, interwoven, 3–5 μm in diameter.

Tubes. Generative hyphae infrequent, difficult to find, hyaline, hyaline, thin-walled, usually unbranched, 2–2.5 μm in diameter; skeletal hyphae dominant, yellowish brown, thick-walled with a narrow to wide lumen, frequently branched,

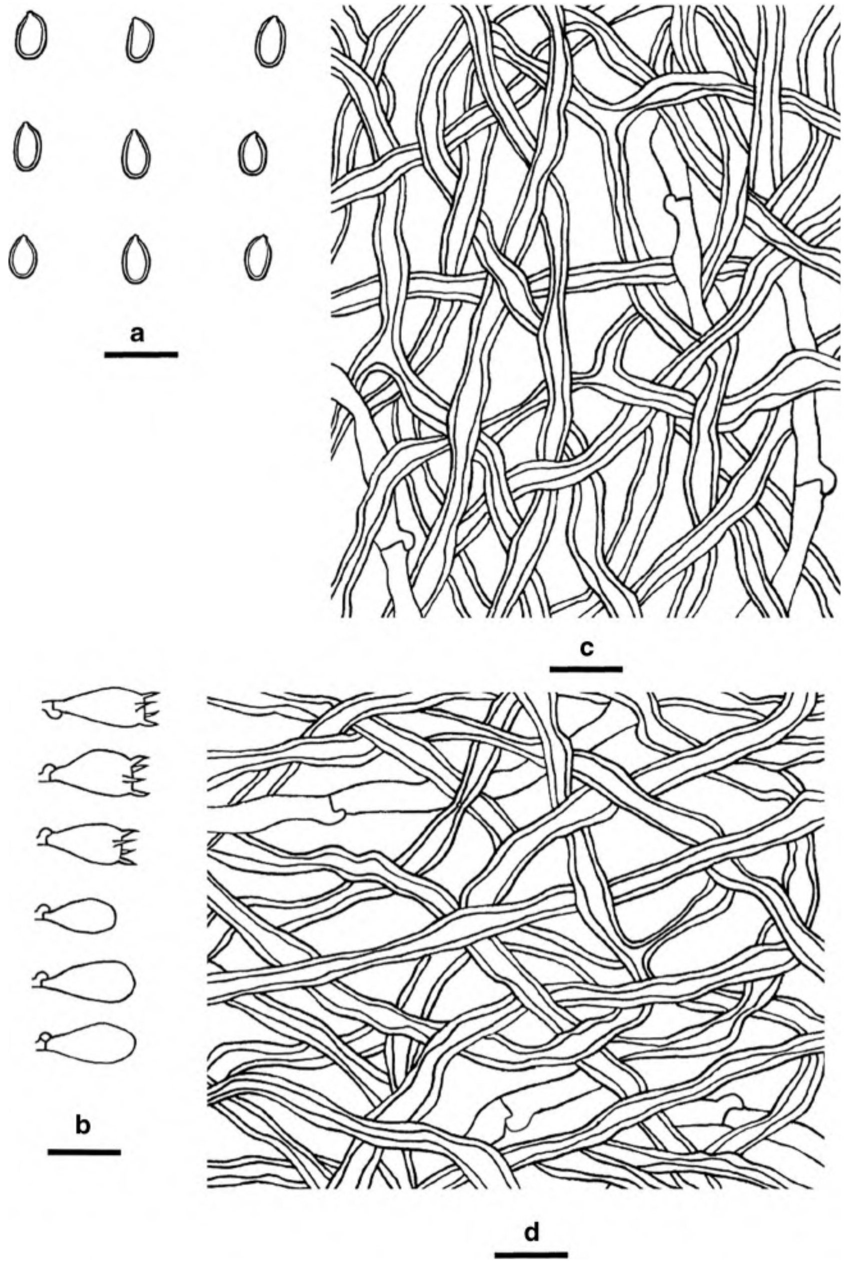

Fig. 5 Microscopic structures of *Abundisporus fuscopurpureus* (drawn from Cui 10969). **a**. Basidiospores; **b**. Basidia and basidioles; c. Hyphae from trama; d. Hyphae from context. Bars: a= 5 μm; b–d=10 μm

flexuous, interwoven, 3–4 μm in diameter. Cystidia and cystidioles absent; basidia barrel-shaped, with four sterigmata and a basal clamp connection, 14–19×9–12 μm; basidioles dominant, in shape similar to basidia, but slightly smaller.

Spores. Basidiospores narrowly ovoid, yellowish, slightly thick-walled, smooth, non-dextrinoid, CB+, (6–)6.5–8.5(–9)× (4–)4.2–5(–5.5) μm, L=7.6 μm, W=4.7 μm, Q=1.6 (n=30/1).

Type of rot. A white rot.

Specimen (*type*) *examined*: **CHINA**. Yunnan Prov., Lijiang, Sandaowan, on living tree of *Quercus*, 18 June 1999 *Dai 3084* (BJFC).

Abundisporus roseoalbus (Jungh.) Ryvarden, Belg. J. Bot. 131:154 (1999). Figs. 3h, 8

Basionym: *Polyporus roseoalbus* Jungh.

Fruitbody. Basidiocarps perennial, pileate, becoming hard corky upon drying. Pilei applanate to slightly conchate, projecting up to 2.5 cm, 4 cm wide and 1.5 cm thick at base. Pileal surface clay-buff to umber-brown; margin acute, pale brown. Pore surface pale, pinkish to buff when fresh, pinkish buff to greyish brown drying; pores round, 5–7 per mm; dissepiments thin, entire. Sterile margin narrow, greyish brown, up to 1 mm wide. Context clay-buff to orange-brown, soft corky, up to 3 mm thick. Tubes concolorous with pore surface, corky, up to 1.2 cm long.

Hyphal structure. Hyphal system dimitic; generative hyphae with clamp connections; skeletal hyphae dextrinoid, CB+; tissues becoming brown in KOH.

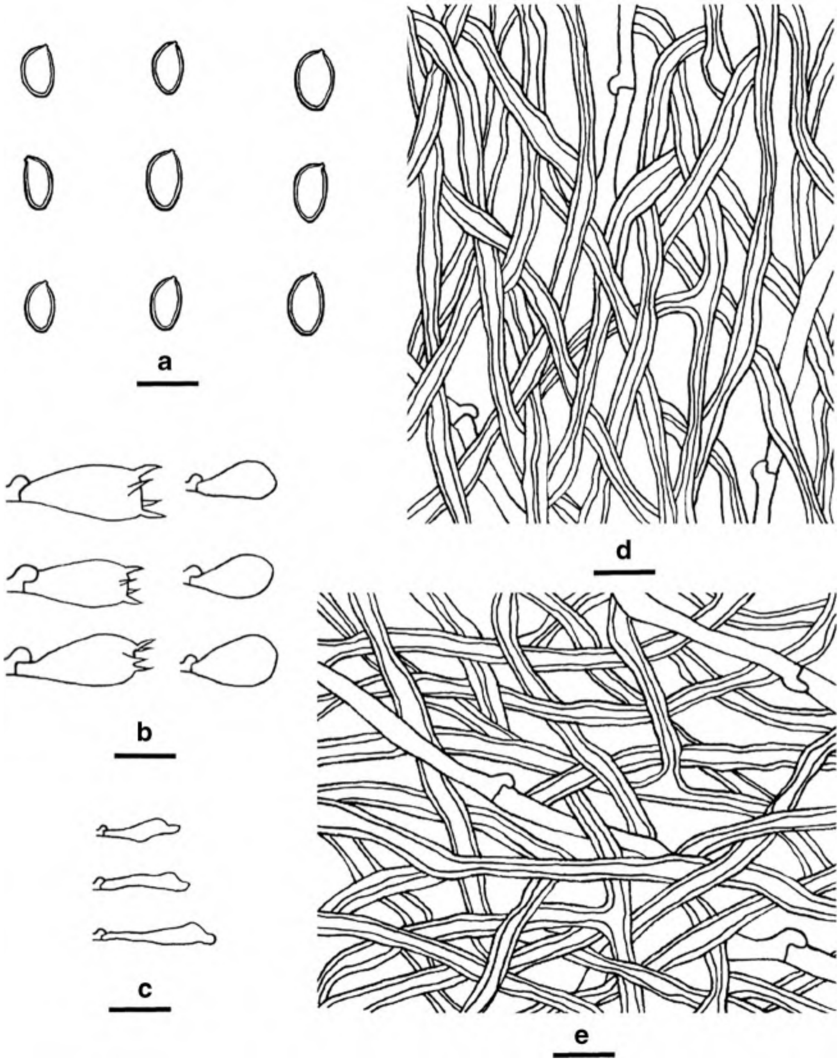

Fig. 6 Microscopic structures of *Abundisporus pubertatis* (drawn from Dai 11310). **a**. Basidiospores; **b**. Basidia and basidioles; **c**. Cystidioles; **d**. Hyphae from trama; **e**. Hyphae from context. Bars: **a**=5 µm; **b**–**e**=10 µm

Context. Generative hyphae infrequent, hyaline, thin-walled, usually unbranched, 2–3 µm in diameter; skeletal hyphae dominant, yellowish brown, thick-walled with a narrow to wide lumen, unbranched, slightly flexuous, interwoven, 3.5–5 µm in diameter.

Tubes. Generative hyphae infrequent, difficult to find, hyaline, hyaline, thin-walled, usually unbranched, 2–3.5 µm in diameter; skeletal hyphae dominant, yellowish brown, thick-walled with a narrow to wide lumen, unbranched, slightly flexuous, interwoven, 3–4 µm in diameter. Cystidia absent, but cystidioles present, narrowly fusoid to subulate, thin-walled, smooth, 8–10×1.5–2.5 µm; basidia barrel-shaped to pear-shaped, with four sterigmata and a basal clamp connection, 9–15×4.5–7.5 µm; basidioles dominant, in shape similar to basidia, but slightly smaller.

Spores. Basidiospores ellipsoid, yellowish, slightly thick-walled, smooth, non-dextrinoid, CB–, (3.5–)3.7–4.2(–4.5)×(2–)2.3–3(–3.2) µm, L=3.91 µm, W=2.49 µm, Q=1.39–1.53 (n=120/4).

Type of rot. A white rot.

Specimens examined: **CHINA**. Hainan Prov., Ledong County, Jianfengling Nature Reserve, on fallen angiosperm trunk, 12 May 2009 *Cui 6650* (BJFC); Yunnan Prov., Jinghong County, Sanchahe Nature Reserve, on fallen angiosperm trunk, 7 June 2011 *Dai 12269*, *12272* (BJFC). **COLUMBIA**. Magdalena, Sierra Nevada de Santa Marta, Reaerba Forestal San Lorenzo, 9 September 1985 *Ryvarden 16140* (HUC). **CUBA**. Orientali, on dead wood, 1 July 1856 *Wright 165* (type of *Polyporus subflexibilis* in FH). **TANZANIA**. Tanga Prov., Tanga District, Usambara Montains, on dead deciduous wood, 18 February 1973 *Ryvarden 10737* (HUC).

Abundisporus sclerosetosus Decock & Laurence, Cryptog. Mycol. 21:28 (2000). Fig. 9

Fruitbody. Basidiocarps perennial, pileate, solitary, becoming corky upon drying. Pilei applanate, slightly convex, semicircular, projecting up to 3.5 cm long, 5.5 cm wide, 1.3 cm thick at base. Pileal surface glabrous, smooth, light brown to

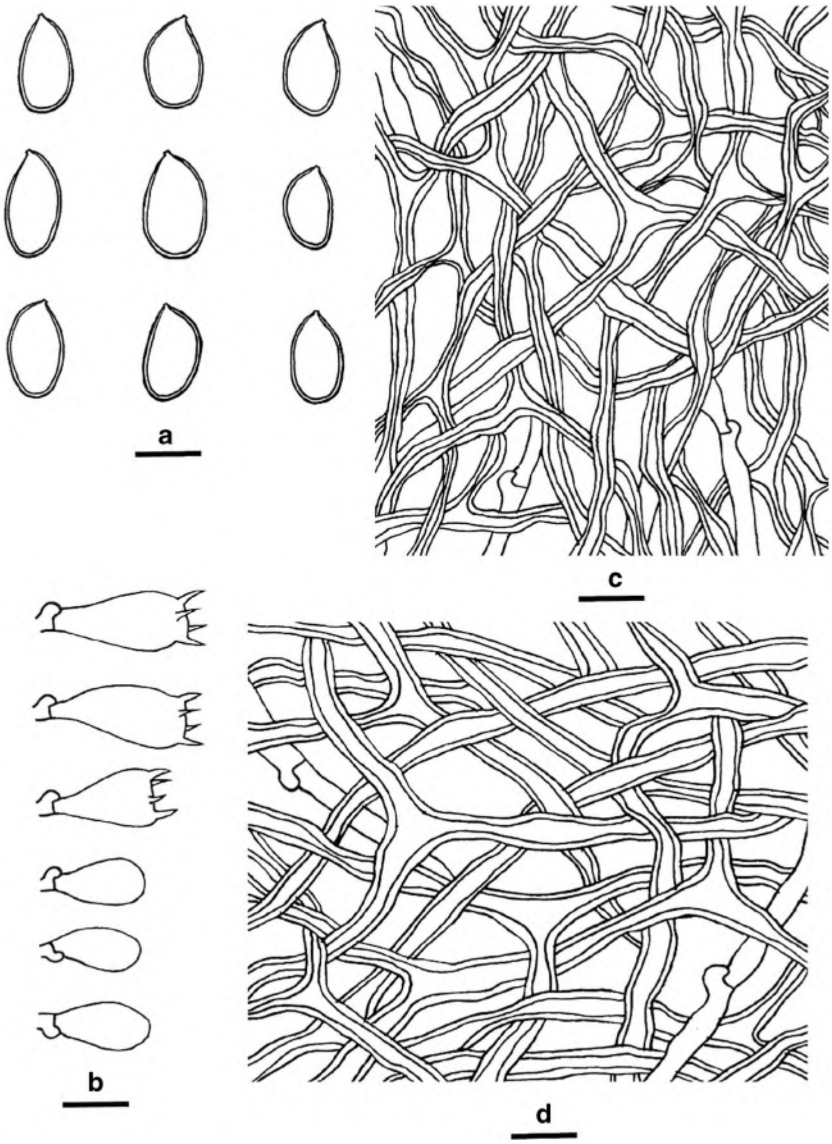

Fig. 7 Microscopic structures of *Abundisporus quercicola* (drawn from the holotype). **a**. Basidiospores; **b**. Basidia and basidioles; **c**. Hyphae from trama; **d**. Hyphae from context. Bars: **a**= 5 μm; **b**–**d**=10 μm

dark reddish brown; margin even, rounded, creamy to yellowish grey. Pore surface greyish white when fresh, light brown to dark brown on bruising; pores round, 7–8 per mm; dissepiments thin, entire. Sterile margin narrow, dark brown, up to 1 mm wide. Context greyish brown, corky, up to 7 mm thick. Tubes concolorous with pore surface, corky, up to 6 mm long.

Hyphal structure. Hyphal system dimitic; generative hyphae with clamp connections; skeletal hyphae dextrinoid, CB+; tissues becoming brown in KOH.

Context. Generative hyphae infrequent, hyaline, thin-walled, usually unbranched, 2–3.5 μm in diameter; skeletal hyphae dominant, yellowish brown, thick-walled with a narrow to wide lumen, frequently branched, interwoven, 3–5.5 μm in diameter.

Tubes. Generative hyphae infrequent, difficult to find, hyaline, thin-walled, usually unbranched, 2–3 μm in diameter; skeletal hyphae dominant, yellowish brown, thick-walled with a narrow to wide lumen, occasionally branched, interwoven, 3–5 μm in diameter. Setiform scleridioid hyphae variously shaped, with lageniform, apically pointed protuberance, thick-walled, yellowish to brownish, dextrinoid, cyanophilous, 20–40×5–9 μm. Cystidia and cystidioles absent; basidia clavate to pear-shaped, with four sterigmata and a basal clamp connection, 11.5–14×5.5–7.5 μm; basidioles dominant, in shape similar to basidia, but slightly smaller.

Spores. Basidiospores ellipsoid, yellowish, thick-walled, smooth, non-dextrinoid, CB–, (3–)3.2–3.5(–3.8)×(2–)2.3–2.6(–2.8) μm, L=3.45 μm, W=2.46 μm, Q=1.35 (n=30).

Type of rot. A white rot.

Specimen (*type*) *examined*: **SINGAPORE**. Bukit Timah Nature Reserve, on dead trunk of *Shorea*, August 1998 *MUCL 41438* (MUCL).

Abundisporus violaceus (Wakef.) Ryvarden, Belg. J. Bot. 131:154 (1999). Fig. 10

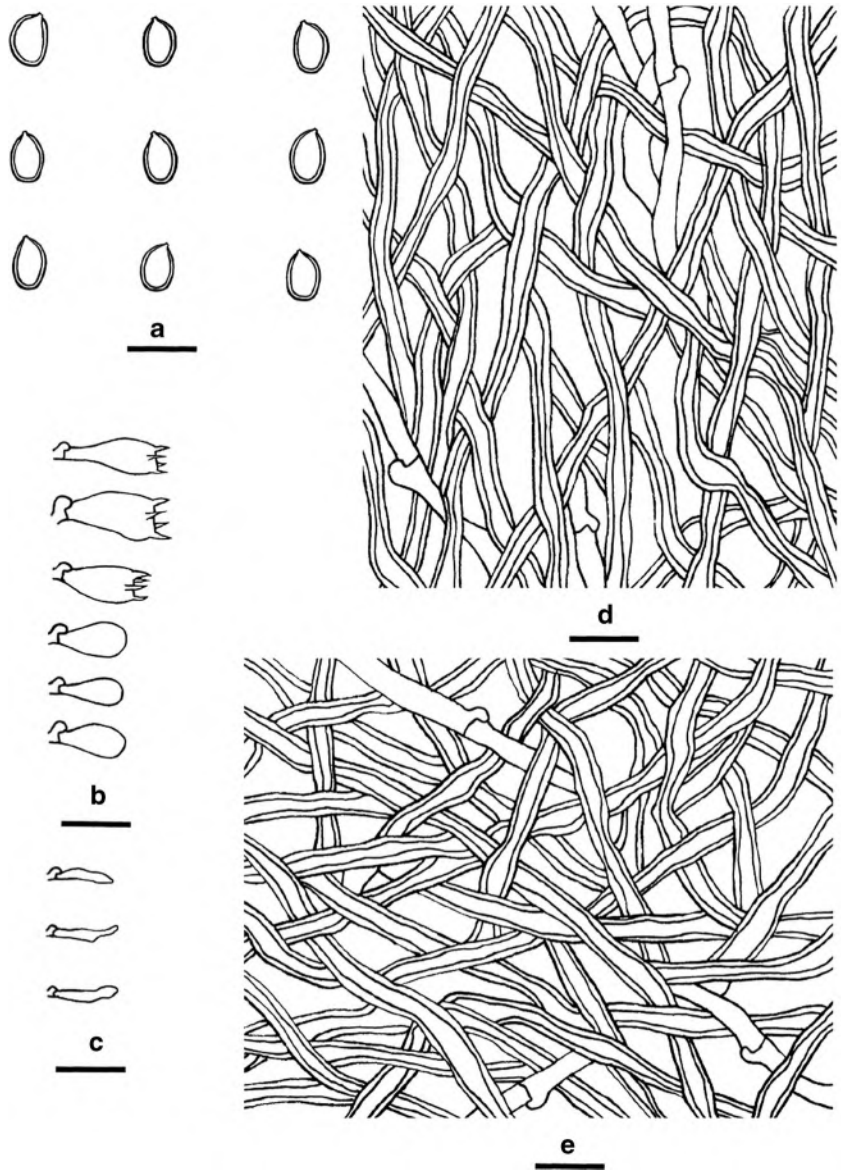

Fig. 8 Microscopic structures of *Abundisporus roseoalbus* (drawn from Dai 12269). **a**. Basidiospores; **b**. Basidia and basidioles; **c**. Cystidioles; **d**. Hyphae from trama; **e**. Hyphae from context. Bars: **a**=5 μm; **b**–**e**=10 μm

Basionym: *Polystictus violaceus* Wakef.

Fruitbody. Basidiocarps perennial, pileate, solitary or imbricate and laterally fused, becoming hard corky upon drying. Pilei dimidiate, slightly conchate or semi-triquetrous in section, projecting up to 5 cm long, 10 cm wide, 3 cm thick at base. Pileal surface ochraceous to violet, velutinate and azonate; margin acute, pink to violet. Pore surface ochraceous to pink when fresh, greyish brown drying; pores angular, 3–5 per mm; dissepiments thin, entire. Sterile margin narrow, greyish brown, up to 3 mm wide. Context pale brown, fibrous-cottony, up to 3 mm thick. Tubes concolorous with pore surface, corky, up to 2.7 cm long.

Hyphal structure. Hyphal system dimitic; generative hyphae with clamp connections; skeletal hyphae dextrinoid, CB+; tissues becoming brown in KOH.

Context. Generative hyphae infrequent, hyaline, thin-walled, usually unbranched, 2–4 μm in diameter; skeletal hyphae dominant, pale brown, thick-walled with a wide lumen, unbranched, subparallel, 4.5–5.5 μm in diameter.

Tubes. Generative hyphae infrequent, difficult to find, hyaline, thin-walled, unbranched, 2–3.5 μm in diameter; skeletal hyphae dominant, pale brown, thick-walled with a narrow to wide lumen, unbranched, subparallel, 3.5–5 μm in diameter. Cystidia and cystidioles absent; basidia barrel-shaped to pear-shaped, with four sterigmata and a basal clamp connection, 13–17×5.5–7 μm; basidioles dominant, in shape similar to basidia, but slightly smaller.

Spores. Basidiospores ellipsoid, yellowish, thick-walled, smooth, non-dextrinoid, CB–, (4.2–)4.5–5.1(–5.3)×(2.9–)3.1–3.5(–3.7) μm, L=4.79 μm, W=3.38 μm, Q=1.39–1.42 (n=90/3).

Type of rot. A white rot.

Specimens examined: **TANZANIA**. Tanga Prov., Magamba, on fallen trunk of *Podocarpus*, 21 February 1973

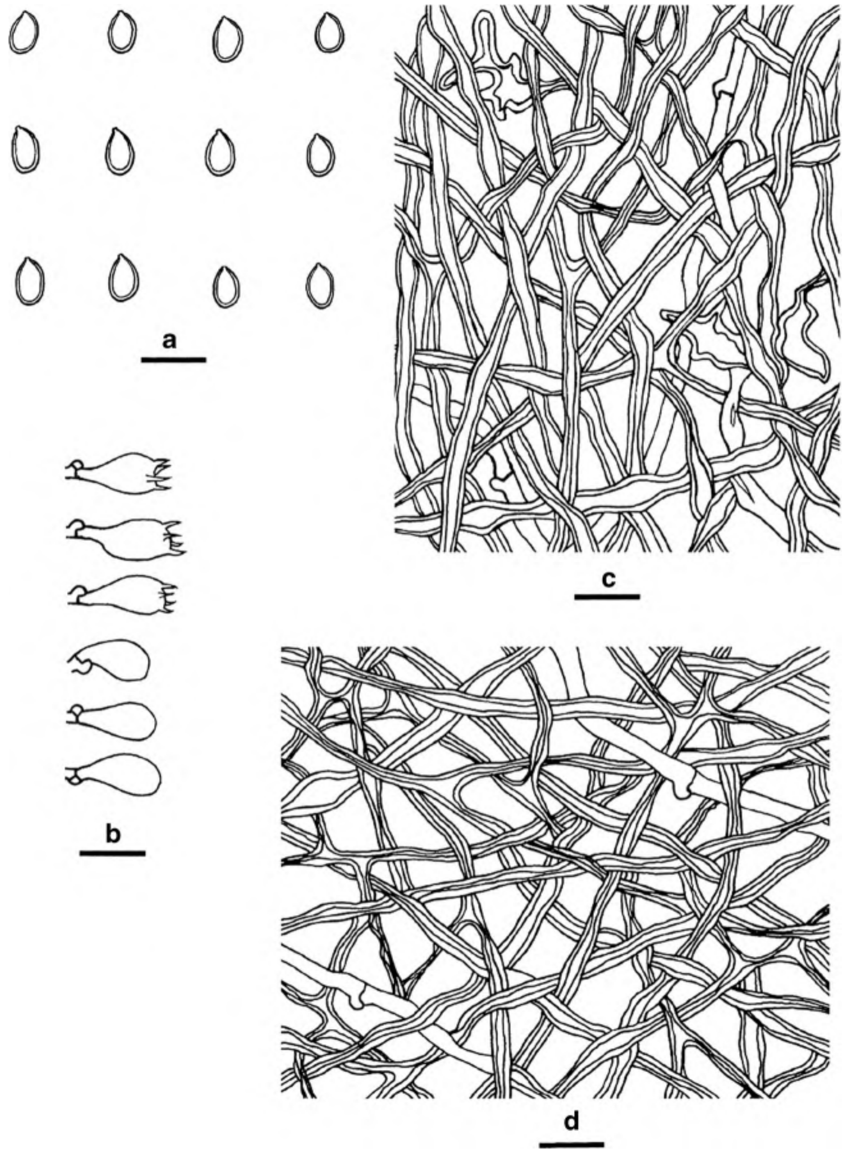

Fig. 9 Microscopic structures of *Abundisporus sclerosetosus* (drawn from MUCL 41438). **a**. Basidiospores; **b**. Basidia and basidioles; **c**. Hyphae from trama; **d**. Hyphae from context. Bars: **a**=5 µm; **b**–**d**=10 µm

Ryvarden 10775 (O). **ZIMBAWE**. Eastern Prov., Chimanimani Skyline Junction, on fallen angiosperm trunk, 18 Feb 1986 *Ryvarden 23642* (O); Manicaland Prov., Chinanimani Nat. Park main entrance, 2 Feb 1993 *Ryvarden 32807* (O).

Discussion

Current species of *Abundisporus* were initially treated under *Loweporus* Wright (Corner 1989; Ryvarden 1991, 1998). Ryvarden (1998) proposed *Abundisporus* for *A. fuscopurpureus*, *A. roseoalbus* and *A. violaceus* that formed a morphologically homogeneous alliance. Molecular phylogenetic analysis supported that *Abundisporus* sensu Ryvarden is monophyletic and suggested the genus as a clade distinct from the *Perenniporia* sensu stricto clade (Robledo et al. 2009; Zhao et al. 2013). Our results were consistent with previous studies on the systematics of *Abundisporus*. In the present study, multi-locus phylogenies based on sequences of ITS, nLSU, mtSSU and *tef1* confirmed the monophyly of *Abundisporus* and its affinities within the core polyporoid clade (Figs. 1, 2). Six previously described species and one new species have been recognized phylogenetically and morphologically.

Abundisporus mollissimus is described here based on morphology and molecular phylogeny. Phylogenetically (Figs. 1, 2), two samples of *A. mollissimus* formed a well supported clade (100 % MP, 1.00 B.P. and were distant from other species of *Abundisporus*. Morphologically, *A. mollissimus* is characterized by effused-reflexed to pileate and soft basidiocarps, narrower skeletal hyphae, and basidiospores measuring 4–4.5 × 3–3.5 µm. *Abundisporus quercicola* is similar to *A. mollissimus* in producing perennial basidiocarps and

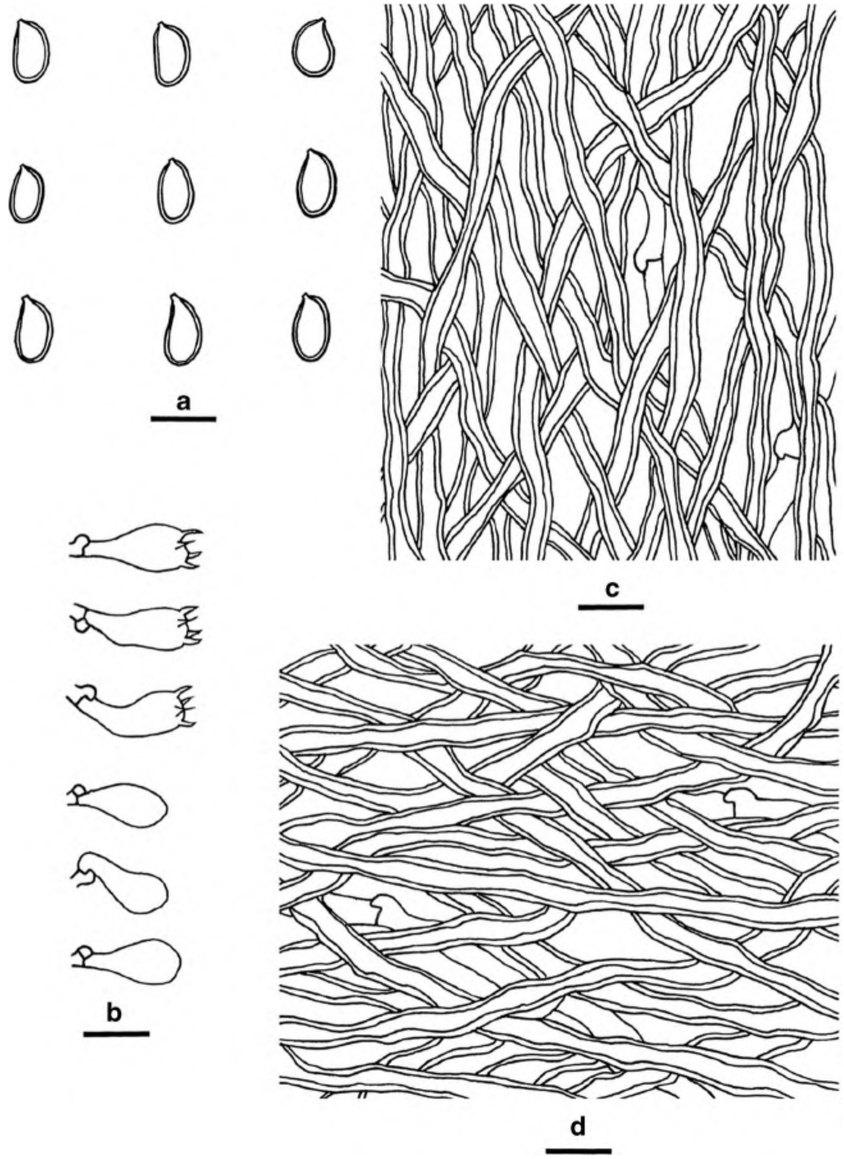

Fig. 10 Microscopic structures of *Abundisporus violaceus* (drawn from Ryvarden 23642). **a**. Basidiospores; **b**. Basidia and basidioles; **c**. Hyphae from trama; **d**. Hyphae from context. Bars: **a**=5 μm; **b**–**d**=10 μm

dextrinoid skeletal hyphae. However, *A. quercicola* is distinct from *A. mollissimus* in its large basidiospores (6.8–8.8×4.2–5 μm, Dai et al. 2002). *Abundisporus fuscopurpureus* is similar to *A. mollissimus* in producing perennial basidiocarps, similar pores (7–9 per mm) and dextrinoid skeletal hyphae. However, *A. fuscopurpureus* produces a distinctly pileate basidiocarp and smaller basidiospores (2.5–3×1.7–2 μm). *Abundisporus roseoalbus* and *A. mollissimus* produce similar basidiospores (3.7–4.2×2.3–3 μm), but *A. roseoalbus* is distinguished by its distinct pileate and corky basidiocarps and larger pores (5–7 per mm, Decock and Laurence 2000; Dai et al. 2002). *Abundisporus sclerosetosus* and *A. mollissimus* share similar pores (7–8 per mm); but it differs by having pileate basidiocarps and small basidiospores (3–3.7×2–2.6 μm; Decock and Laurence 2000). *Mollicarpus cognatus* (Berk.) Ginns is similar to *A. mollissimus* by sharing soft and effused reflexed basidiomata and broadly ellipsoid basidiospores, but it differs in its trimitic hyphal system, non-dextrinoid and acyanophilous skeletal hyphae, and thin-walled, acyanophilous basidiospores (Ginns 1984).

Abundisporus pubertatis was supported as a sister to *A. violaceus*, and grouped with *A. sclerosetosus* in the phylogenetic analysis (Fig. 1); morphologically, *A. pubertatis* and *A. violaceus* have similar basidiospores (4.2–5×2.5–3 μm in *A. pubertatis*; 4.5–5.1×3.1–3.5 μm in *A. violaceus*). However, *A. pubertatis* differs from *A. violaceus* by its resupinate to effused-reflexed basidiocarps and small pores (5–7 per mm, Ryvarden and Johansen 1980; Dai et al. 2002). *Abundisporus pubertatis* is similar to *A. sclerosetosus* in its smaller pores (5–7 per mm) and pale brown to dark brown pore surface. *Abundisporus pubertatis* differs from *A. sclerosetosus* in its non-dextrinoid skeletal hyphae, larger basidiospores (4.2–5×2.5–3 μm), and lack of scleridioid setiform elements (Decock and Laurence 2000). *Abundisporus quercicola* is separated from other *Abundisporus* species in the phylogenetic analysis (Figs. 1, 2). Morphologically, *A. quercicola* is distinct from all other *Abundisporus* species in its large basidiospores (6.8–8.8×4.2–5 μm, Dai et al. 2002).

Polyporus subflexibilis Berk. & M.A. Curtis was treated as a synonym of *A. roseoalbus* by Ryvarden (1998) due to its *Abundisporus*-like characters, such as 1) a chocolate or vinaceous brown pore surface, 2) small pores (7–9 per mm), 3) a dimitic hyphal structure with yellow to pale brown skeletal hyphae that swell in KOH solution, and 4) shorter, pale yellowish, slightly thick-walled basidiospores (up to 4 μm long). Biogeographically, *Polyporus subflexibilis* was collected from Cuba, and *A. roseoalbus* was collected from Africa, thus Parmasto and Hallenberg (2000) separated *P. subflexibilis* from *A. roseoalbus* and proposed the new combination *A. subflexibilis* (Berk. & M.A. Curtis) Parmasto. In the present study, examination of the type specimen showed that the two species cannot be separated based on morphology, so, here, *Polyporus subflexibilis* is treated as a synonym of *A. roseoalbus*, as proposed by Ryvarden (1998). The biogeographic disjunction is interesting, and deserving of further analysis. Unfortunately, good sequences of *A. subflexibilis* were not available for this study. When appropriate sequences become available, the circumscription of *A. subflexibilis* can be re-evaluated.

Key to accepted species of *Abundisporus*

1 Pore surface white when fresh, basidiospores > 6 μm in length *A. quercicola*

1* Pore surface buff to greyish brown when fresh, basidiospores<6 μm in length

2 Basidiocarps soft, skeletal hyphae < 3 μm in width *A. mollissimus*

2* Basidiocarps corky, skeletal hyphae > 3 μm in width

3 Basidiocarps resupinate to effused-reflexed, skeletal hyphae non-dextrinoid *A. pubertatis*

3* Basidiocarps pileate, skeletal hyphae dextrinoid

4 Pores > 7 per mm, skeletal hyphae branched

4* Pores < 7 per mm, skeletal hyphae unbranched

5 Pileal margin acute, basidiospores < 3 μm in length *A. fuscopurpureus*

5* Pileal margin rounded, basidiospores > 3 μm in length *A. sclerosetosus*

6 Pileal surface ochraceous to violet, pores angular, 3–5 per mm *A. violaceus*

6* Pileal surface clay-buff to umber-brown, pores round, 5–7 per mm *A. roseoalbus*

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