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The genus *Phylloporus* (*Boletaceae, Boletales*) from China: morphological and multilocus DNA sequence analyses

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Abstract Species of the genus *Phylloporus* in China were investigated based on morphology and molecular phylogenetic analysis of a three-locus (nrLSU, ITS and *tef-1a*) DNA sequence dataset. Twenty-one phylogenetic species were recognized among the studied collections. Seven of them are described as new: *P. brunneiceps*, *P. imbricatus*, *P. maculatus*, *P. pachycystidiatus*, *P. rubeolus*, *P. rubrosquamosus*, and *P. yunnanensis*. In addition, four of them correspond with the previous morphology-based taxa: *P. bellus*, *P. luxiensis*, *P. parvisporus*, and *P. rufescens*. The remaining ten phylogenetic species were not described due to the paucity of the materials. A key to the Chinese morphologically recognizable taxa was provided. A preliminary biogeographical analysis showed that (1) *Pylloporus* species in East Asia and Southeast Asia are mostly closely related, (2) species pairs or closely related species of *Phylloporus* between East Asia and North/Central America are relatively common, and (3) the biogeographic relationship of *Phylloporus* between East Asia and Europe was supported by only a single species pair. Unexpectedly, no taxa common either to both Europe and East Asia, or to both East Asia and North/Central America, were uncovered. Clades look to have taxa from both sides of the Pacific and Europe/Asia though.

Keywords Biogeography · New taxa · Phylogenetic species · Species diversity · Taxonomy

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Introduction

Species of *Boletaceae* are interesting and important in forestry for their mycorrhizal properties and the edibility of many species (Singer 1986; Li and Song 2002; Wang et al. 2004; Binder and Hibbett 2007; Dai et al. 2010). In that family, *Phylloporus* Quél. encompasses a group with predominantly lamellate instead of poroid hymenophore (Singer 1986; Binder and Bresinsky 2002; Neves and Halling 2010; Neves et al. 2012). Molecular systematic studies, based on analyses of DNA sequence data have confirmed the monophyly of *Phylloporus* (Neves et al. 2012).

Although a large number of taxa have been described in *Phylloporus*, species limits in the genus have only recently been investigated (Neves and Halling 2010; Zeng et al. 2011; Neves et al. 2012). Due to phenotypic plasticity, morphological species recognition (MSR) in the genus might be problematic. It would be interesting to elucidate species diversity of the genus using multilocus DNA sequence data and phylogenetic species recognition based on genealogical concordance and nondiscordance (Taylor et al. 2000; Dettman et al. 2003). Data gained from such a survey would be essential for a deeper understanding of the morphological evolution, genetic diversity, evolutionary relationships and geographic distribution of boletes (Binder and Bresinsky

2002; Binder and Hibbett 2007; Desjardin et al. 2008, 2009; Yang 2011; Feng et al. 2012).

In China, species of *Boletaceae* have received much attention by mycologists, and many species and genera have been discovered across the country (Chiu 1948; Teng 1963; Wen 1985; Zang 1992, 2006; Zang et al. 1999, 2001, 2006; Wang and Liu 2002; Yang et al. 2003; Li 2007; Zhou and Yang 2008; Li et al. 2009, 2011; Li and Yang 2011; Zeng and Yang 2011; Zeng et al. 2011, 2012). To date, 14 taxa of *Phylloporus* have been described from China (Teng 1963; Zang and Zeng 1978; Li et al. 1992; Bi et al. 1993, 1994, 1997; Dai and Li 1994; Zang et al. 1996; Chen et al. 2002; Zeng et al. 2011), and these were solely based on morphological criteria. In recent years, many collections of *Phylloporus* from China were accumulated and are available for molecular phylogenetic analysis.

In this study, a phylogenetic investigation of *Phylloporus* species was conducted using both morphological and molecular data in an effort to elucidate the species diversity of *Phylloporus* in China, and to evaluate the phylogenetic relationships and geographic diversity of species within the genus.

Materials and methods

Morphological studies

Specimens were described and photographed in the field, and deposited in the Herbarium of Cryptogams, Kunming Institute of Botany, Chinese Academy of Sciences (HKAS). Additional collections from Royal Botanic Gardens, Kew (K), and the Fungal Herbarium of Guangdong Institute of Microbiology (GDGM) were also examined. Color codes are from Kornerup and Wanscher (1981). Sections of the pileipellis were cut tangentially and halfway between center and margin of the pileus. Sections of the squamules on the stipe were taken from the middle part along the longitudinal axis of the stipe. Five percent KOH was used as a mounting medium for microscopic studies. Basidiospores of dried specimens were examined with a Hitachi S-4800 scanning electron microscope (SEM) at 10.0 kV (Li et al. 2011). The notations "basidiospores (n/m/p)" indicate that the measurements were made on *n* basidiospores from *m* basidiomata of *p* collections. Dimensions of basidiospores were given using the notation (a)b–c(d), where the range b–c represents a minimum of 90 % of the measured values, and extreme values (a and d), whenever present, were given in parentheses. Q refers to the length/breadth ratio of basidiospores; Q_m refers to the average Q of basidiospores ± sample standard deviation. All line-drawings of microstructures were made from rehydrated material.

Molecular procedures and phylogenetic analyses

DNA extraction, PCR and DNA sequencing

Total genomic DNA was obtained using a modified Cetyltrimethylammonium bromide (CTAB) procedure of Doyle and Doyle (1987) from material dried with silica-gel. A portion of the nuclear ribosomal large subunit (nrLSU) was amplified with the primers LROR and LR5 (Vilgalys and Hester 1990). The internal transcribed spacer (ITS/5.8 S rRNA) was amplified using primers ITS1 and ITS4 (White et al. 1990). The translation elongation factor 1-alpha (*tef-1a*) gene was amplified with the primers EF1-2 F (5′-TGATCACCGGTACTTCTCAGG-3′) and EF1-2R (5′-ACCATGCCAGCCTTGAT-3′) designed by the first author of this paper. PCR was performed in a total volume of 25 μl containing 2.5 μl of PCR reaction buffer, 0.5 μl of dNTP mix (0.2 mM), 1 μl of each primer (5 μM), 1 U of Taq polymerase, and 1 μl of DNA template. PCR reactions were performed with 4 min initial denaturation at 95 °C, followed by 34 cycles of denaturation at 94 °C for 40 s, annealing at 52 °C for 60 s, extention at 72 °C for 80 s, and by a final extension at 72 °C for 7 min. Amplified PCR products were purified using the Bioteke Purification Kit (Bioteke Corporation, Beijing, China). Purified PCR products were sequenced on an ABI 3730 DNA analyzer with an ABI BigDye3.1 terminator cycle sequencing kit (Shanghai, China) with the same primers used for PCR amplifications. DNA sequences were compiled with SeqMan (DNASTAR Lasergene 9) and BioEdit (Hall 1999). Sequences were aligned using MUSCLE v3.6 (Edgar 2004), and manually adjusted where necessary.

Dataset assembly

One hundred and twenty nine sequences (43 nrLSU, 43 ITS, and 43 *tef-1a*) from 45 collections were newly generated for this study (Table 1). For the concatenated multilocus dataset, the nrLSU, ITS and *tef-1a* sequences generated in the study were aligned with selected sequences from previous studies (Chapela et al. 1994; Neves et al. 2012; Zeng et al. 2012), *Xerocomus magniporus* and *X. subtomentosus* were chosen as the outgroup as described by Neves et al. (2012). For 24 previously studied taxa without *tef-1a* sequences, they were also included in this dataset but their *tef-1a* sequences were treated as missing data, as done by Binder et al. (2010) and Li et al. (2011).

Phylogenetic analyses

The combined nuclear dataset (nrLSU + ITS + *tef-1a*) was analyzed using Randomized Accelerated Maximum Likelihood (RAxML), and Bayesian methods, respectively.

Table 1 Species used in molecular phylogenetic analyses, their vouchers, and GenBank accession numbers

Species	Voucher	Locality	GenBank accession numbers		
			nrLSU	ITS	*tef-1a*
Phylloporus alborufus	MAN022	Costa Rica	JQ003678	JQ003624	–
Phylloporus arenicola	JT27954	USA	JQ003704	–	–
Phylloporus bellus	REH8710	eastern USA	JQ003686	JQ003618	–
Phylloporus bellus	MCA559	Japan	AY612817	–	–
Phylloporus bellus	REH7733	Costa Rica	JQ003661	–	–
Phylloporus bellus[a]	HKAS 56763	Yunnan, SW China	JQ967196	JQ967239	JQ967153
Phylloporus bellus[a]	HKAS 42850	Yunnan, SW China	JQ967197	JQ967240	JQ967154
Phylloporus bogoriensis	DED7785	Indonesia	JQ003680	JQ003625	–
Phylloporus brunneiceps[a]	HKAS 56903	Yunnan, SW China	JQ967198	JQ967241	JQ967155
Phylloporus brunneiceps[a]	HKAS 59551	Yunnan, SW China	JQ967199	JQ967242	JQ967156
Phylloporus brunneiceps[a]	HKAS 59726	Chongqing, SW China	JQ967200	JQ967243	JQ967157
Phylloporus brunneiceps[a]	HKAS 59727	Chongqing, SW China	JQ967201	JQ967244	JQ967158
Phylloporus caballeroi	REH7906	Panama	JQ003662	JQ003638	–
Phylloporus castanopsidis	MAN104	Thailand	JQ003689	JQ003642	–
Phylloporus castanopsidis	MAN107	Thailand	JQ003691	JQ003643	–
Phylloporus castanopsidis	MAN118	Thailand	JQ003693	JQ003646	–
Phylloporus centroamericanus	MAN016	Costa Rica	JQ003663	JQ003637	–
Phylloporus centroamericanus	MAN037	Costa Rica	JQ003664	JQ003634	–
Phylloporus cyanescens	REH8681	Australia	JQ003684	JQ003621	–
Phylloporus dimorphus	MAN128	Thailand	JQ003697	JQ003648	–
Phylloporus foliiporus	JLM1677	eastern USA	JQ003687	JQ003641	–
Phylloporus imbricatus[a]	HKAS 54647	Yunnan, SW China	JQ967202	JQ967245	JQ967159
Phylloporus imbricatus[a]	HKAS 54859	Yunnan, SW China	JQ967203	JQ967246	JQ967160
Phylloporus imbricatus[a]	HKAS 54860	Yunnan, SW China	JQ967204	JQ967247	JQ967161
Phylloporus imbricatus[a]	HKAS 54861	Yunnan, SW China	JQ967205	JQ967248	JQ967162
Phylloporus infuscatus	MAN123	Thailand	JQ003695	–	–
Phylloporus leucomycelinus	MB00-043	eastern USA	JQ003677	JQ003628	–
Phylloporus leucomycelinus	MB05-007	eastern USA	JQ003666	JQ003653	–
Phylloporus leucomycelinus	REH4582	eastern USA	JQ003679	–	–
Phylloporus leucomycelinus[a]	HKAS 74678	eastern USA	JQ967206	JQ967249	JQ967163
Phylloporus luxiensis[a]	HKAS 57036	Yunnan, SW China	JQ967207	JQ967250	JQ967164
Phylloporus luxiensis[a]	HKAS 57037	Yunnan, SW China	JQ967208	JQ967251	JQ967165
Phylloporus luxiensis[a]	HKAS 57048	Yunnan, SW China	JQ967209	JQ967252	JQ967166
Phylloporus maculatus[a]	HKAS 56683	Yunnan, SW China	JQ967210	JQ967253	JQ967167
Phylloporus maculatus	HKAS 59730	Yunnan, SW China	JQ678698	JQ678696	JQ967194[a]
Phylloporus orientalis	REH8755	Australia	JQ003701	JQ003651	–
Phylloporus orientalis	REH8756	Australia	JQ003709	JQ003652	–
Phylloporus pachycystidiatus[a]	HKAS 54540	Yunnan, SW China	JQ967211	JQ967254	JQ967168
Phylloporus pachycystidiatus[a]	HKAS 54541	Yunnan, SW China	JQ967212	JQ967255	JQ967169
Phylloporus parvisporus[a]	HKAS 54768	Yunnan SW China	JQ967214	JQ967257	JQ967171
Phylloporus parvisporus[a]	HKAS 59725	Fujian, SE China	JQ967213	JQ967256	JQ967170
Phylloporus pelletieri	Q7199c	Slovakia	JQ003668	JQ003639	–
Phylloporus pelletieri[a]	K 128205	England	JQ967215	JQ967258	–
Phylloporus phaeoxanthus	MAN064	Costa Rica	JQ003670	–	–
Phylloporus phaeoxanthus var. *simplex*	REH7388	Costa Rica	JQ003671	–	–
Phylloporus purpurellus	MAN050	Costa Rica	JQ003672	JQ003630	–
Phylloporus rhodoxanthus	SAR 89.457	eastern USA	U11925	–	–

Table 1 (continued)

Species	Voucher	Locality	GenBank accession numbers		
			nrLSU	ITS	*tef-1a*
Phylloporus rhodoxanthus	MAN075	eastern USA	JQ003674	–	–
Phylloporus rhodoxanthus	REH8714	eastern USA	JQ003675	JQ003629	–
Phylloporus rhodoxanthus	MAN099	eastern USA	JQ003676	–	–
Phylloporus rhodoxanthus	JLM1808	eastern USA	JQ003688	JQ003654	–
Phylloporus rubeolus[a]	HKAS 52573	Yunnan, SW China	JQ967216	JQ967259	JQ967172
Phylloporus rubeolus[a]	HKAS 54543	Yunnan, SW China	JQ967218	JQ967261	JQ967174
Phylloporus rubiginosus	MAN117	Thailand	JQ003692	JQ003645	–
Phylloporus rubiginosus	MAN117	Thailand	JQ003694	JQ003647	–
Phylloporus rubrosquamosus[a]	HKAS 54542	Yunnan, SW China	JQ967217	JQ967260	JQ967173
Phylloporus rubrosquamosus[a]	HKAS 54559	Yunnan, SW China	JQ967219	JQ967262	JQ967175
Phylloporus rufescens[a]	HKAS 59722	Hainan, southern China	JQ967220	JQ967263	JQ967176
Phylloporus rufescens[a]	HKAS 59723	Hainan, southern China	JQ967221	JQ967264	JQ967177
Phylloporus scabripes	REH8531	Belize	JQ003683	JQ003623	–
Phylloporus yunnanensis[a]	HKAS 52225	Yunnan, SW China	JQ967222	JQ967265	JQ967178
Phylloporus yunnanensis[a]	HKAS 52527	Yunnan, SW China	JQ967223	JQ967266	JQ967179
Phylloporus yunnanensis[a]	HKAS 56999	Yunnan, SW China	JQ967224	JQ967267	JQ967180
Phylloporus yunnanensis[a]	HKAS 58673	Yunnan, SW China	JQ967225	JQ967268	JQ967181
Phylloporus yunnanensis[a]	HKAS 59412	Yunnan, SW China	JQ967226	JQ967269	JQ967182
Phylloporus sp.	REH8729	Australia	JQ003699	JQ003650	–
Phylloporus sp.	MAN105	Thailand	JQ003690	–	–
Phylloporus sp.	MAN131	Thailand	JQ003698	JQ003649	–
Phylloporus sp.	48854	China	–	JQ003640	–
Phylloporus sp.1[a]	HKAS 74679	Hunan, central China	JQ967228	JQ967271	JQ967184
Phylloporus sp.2[a]	HKAS 74680	Fujian, SE China	JQ967229	JQ967272	JQ967185
Phylloporus sp.3[a]	HKAS 74681	Hainan, southern China	JQ967227	JQ967270	JQ967183
Phylloporus sp.4[a]	HKAS 74682	Yunnan, SW China	JQ967230	JQ967273	JQ967186
Phylloporus sp.4[a]	HKAS 74683	Yunnan, SW China	JQ967231	JQ967274	JQ967187
Phylloporus sp.5[a]	HKAS 74684	Fujian, SE China	JQ967232	JQ967275	JQ967188
Phylloporus sp.6[a]	HKAS 74687	Yunnan, SW China	JQ967235	JQ967278	JQ967190
Phylloporus sp.7[a]	HKAS 74688	Yunnan, SW China	JQ967236	JQ967279	JQ967191
Phylloporus sp.8[a]	HKAS 74686	Shandong, eastern China	JQ967234	JQ967277	–
Phylloporus sp.9[a]	HKAS 74685	Yunnan, SW China	JQ967233	JQ967276	JQ967189
Phylloporus sp.10[a]	HKAS 74689	Hainan, southern China	JQ967237	JQ967280	JQ967192
Xerocomus magniporus	HKAS 59820	Yunnan, SW China	JQ678699	JQ678697	JQ967195[a]
Xerocomus subtomentosus[a]	K 167686	England	JQ967238	JQ967281	JQ967193

[a] Sequences obtained in this study. AY612817 was from GenBank; U11925 was from Chapela et al. (1994); JQ678696–JQ678699 were from Zeng et al. (2012); the remains were from Neves et al. (2012). *SW* southwestern; *SE* southeastern

Maximum likelihood tree generation and bootstrap analyses were performed with the program RAxML 7.2.6 (Stamatakis 2006) running 500 replicates combined with a ML search. Bayesian analysis with MrBayes 3.1 (Huelsenbeck and Ronquist 2005) implementing the Markov Chain Monto Carlo (MCMC) technique and parameters predetermined with MrModeltest 2.3 (Nylander 2004) was performed. The model of evolution used in the Bayesian analysis was determined with MrModeltest 2.3 (Nylander 2004). For the three-gene combined dataset, the best-fit likelihood models of nrLSU, ITS and *tef-1a* were GTR + I + G, GTR + I + G and K80 + I + G, respectively. Bayesian analyses were repeated for 7 million generations and sampled every 100. Trees sampled from the first 25 % of the generations were discarded as burn-in, and Bayesian posterior probabilities (PP) were then calculated for a majority consensus tree of the retained Bayesian trees.

Species recognition

Three-locus (nrLSU, ITS and *tef-1a*) DNA sequence dataset was used for the phylogenetic species recognition based on genealogical concordance and nondiscordance (Taylor et al. 2000; Dettman et al. 2003). In the absence of the ability to test the monophyly of lineages represented by single collections, these lineages were interpreted as putatively phylogenetically distinct if they were significantly divergent from and not sympatric with their putative sisters (Du et al. 2012). Previous morphology-based taxa or new species with enough collections available were named or described when morphology and/or ecology substantiated this phylogenetic species concept (van de Putte et al. 2010).

Results

Morphological data

One hundred and twenty-nine specimens were examined, including 63 recent collections of *Phylloporus*, 64 materials of *Phylloporus* cited in the previous reports, and 2 samples of *Xerocomus*. Although 14 taxa of the genus were reported from China, our re-examination of the available vouchers confirmed the occurrence of only 5 taxa in China, viz. *P. bellus* (Massee) Corner, *P. luxiensis* M. Zang, *P. orientalis* var. *brevisporus* Corner, *P. orientalis* var. *orientalis* Corner, and *P. parvisporus* Corner. Whether *P. ater* (Beeli) Heinem., *P. borneensis* Corner, *P. depressus* Heinem., *P. foliiporus* (Murrill) Singer, *P. incarnatus* Corner, *P. pinguis* (Hook.) Singer, *P. rhodoxanthus* (Schwein.) Bres. and *P. sulphureus* (Berk.) Singer occur in China remains an open question.

Our morphological observations also revealed that 11 species, including 3 previous records from China (*P. bellus*, *P. luxiensis*, and *P. parvisporus*) and 1 new record from China (*P. rufescens* Corner), plus 7 new species (*P. brunneiceps*, *P. imbricatus*, *P. maculatus*, *P. pachycystidiatus*, *P. rubeolus*, *P. rubrosquamosus*, and *P. yunnanensis*), can be described on the basis of MSR. To date, 13 taxa of *Phylloporus* are recognized by morphology, including the 11 phylogenetic species, and 2 additional taxa, i.e., *P. orientalis* var. *brevisporus* and *P. orientalis* var. *orientalis*. These latter lacked DNA sequences from Chinese specimens. Because 3 of them, *P. luxiensis*, *P. orientalis* var. *brevisporus* and *P. orientalis* var. *orientalis*, were described in detail in the literature (Chen et al. 2002; Bi et al. 1993, 1994, 1997; Zeng et al. 2011), we therefore focused on the remaining 10 species in this study.

Molecular data

The three-locus dataset consisted of 82 taxa and 3979 nucleotide sites, and the alignment was submitted to TreeBase (S12634). The phylogram with branch lengths inferred from the dataset with RAxML including the support values was shown (Fig. 1). Bayesian analysis produced nearly identical estimates of tree topology except for some trivial differences: the clade V and clade VII, clade VI and clade IX were clustered together, respectively, but with low RAxML likelihood bootstrap (BS) and Bayesian posterior probability (PP) support (BS<50 %, PP<0.95).

The monophyly of *Phylloporus* was strongly supported (RAxML BS=100, PP=1) based on the three-locus dataset (Fig. 1), which confirmed Neves et al. (2012). Nine major clades (I–IX) were recovered within *Phylloporus*, but with little support in the backbone, and their relationships are largely unresolved.

Clade I included species from both sides of the Pacific: *P. arenicola* A.H. Smith & Trappe, *P. brunneiceps*, *P. castanopsidis* M.A. Neves & Halling, *P. dimorphus* M.A. Neves & Halling, *P. imbricatus*, *P. luxiensis*, *P. phaeoxanthus* Singer & L.D. Gómez, *P. phaeoxanthus* var. *simplex* Singer & L.D. Gómez, *P. rhodoxanthus*, *P. scabripes* Ortiz & Neves, *P. yunnanensis*, *P.* sp. 1 (HKAS 74679), *P.* sp. 2 (HKAS 74680) and *P.* sp. 3 (HKAS 74681) with 63 % RAxML likelihood bootstrap and 0.96 bayesian PP support; the sister relationship of *P. imbricatus* and *P. yunnanensis* was also relatively highly supported (RAxML BS=76, PP=0.99).

Clade II included *P. pelletieri* (Lév.) Quél., *P.* sp. 4 (HKAS 74682, and 74683), and one collection from Thailand (MAN105) was strongly supported (RAxML BS=92, PP=1). In clade III, *P. infuscatus* M.A. Neves & Halling, *P. parvisporus*, and *P.* sp.5 (HKAS 74684) were clustered together with high statistical support (RAxML BS=100, PP=1), and a sister relationship of *P. infuscatus* and *P. parvisporus* was also recovered (RAxML BS=100, PP=1).

In clade IV, *P. bellus*, *P. centroamericanus* Singer & L.D. Gómez, *P. maculatus*, *P. pachycystidiatus*, and *P. rubrosquamosus* grouped together with high statistical support (RAxML BS=98, PP=1), and the monophyly of *P. centroamericanus* with its sister taxon *P. pachycystidiatus* was also strongly supported (RAxML BS=100, PP=1). In clade V, *P. alborufus* M.A. Neves & Halling, *P. caballeroi* Singer, *P. leucomycelinus* (Singer & M.H. Ivory) Singer, *P.* sp. 6 (HKAS 74687), and *P.* sp. 7 (HKAS 74688) formed a well-supported group (RAxML BS=100, PP=1).

In clade VI, the so-called "*P. bellus*" from North/Central America was clustered with the North American specimens labeled as "*P. leucomycelinus*" and "*P. rhodoxanthus*", *P.* sp. 8 (HKAS 74686), and one collection from Thailand (MAN 131) with strong statistical support (RAxML BS=100, PP=1). Clade VII included *P. rubeolus* and *P.* sp. 9 (HKAS 74685) with high statistical support (RAxML BS=100, PP=1).

In clade VIII, *P. rubiginosus* M.A. Neves & Halling was clustered with *P. foliiporus* with strong statistical support (RAxML BS=100, PP=1). Within clade IX, the monophyly

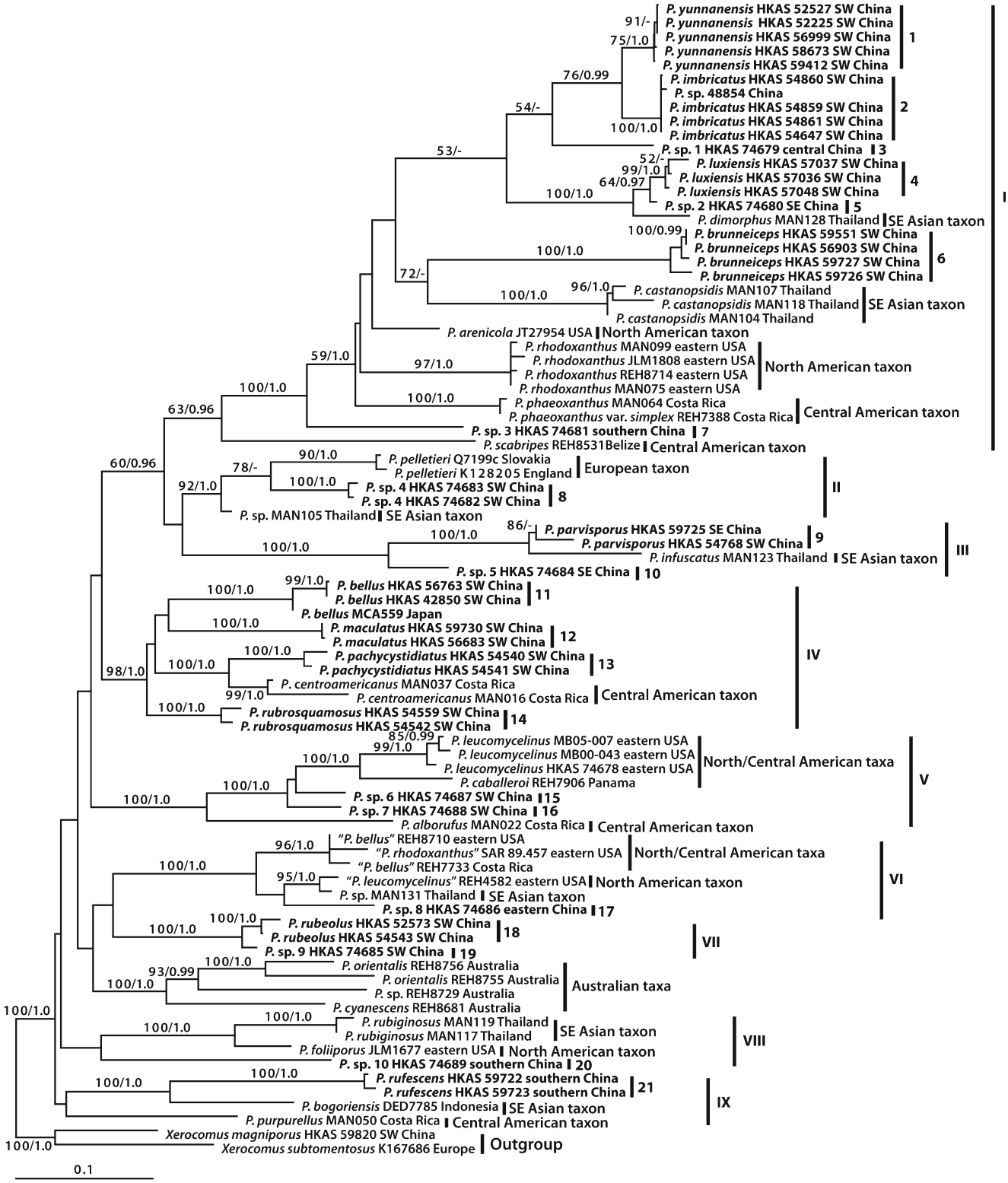

Fig. 1 Phylogram inferred from a multilocus (nrLSU, ITS and *tef-1a*) dataset using RAxML. RAxML likelihood bootstrap (BS>50 %) and Bayesian posterior probabilities (PP >0.95) are indicated above or below the branches as RAxML BS/PP. Lineages numbered 1 through 21 were unrevealed from China. SW=southwestern; SE=southeastern

of *P. bogoriensis* Höhn. and *P. rufescens* was well-supported (RAxML BS=100, PP=1).

The samples collected from China were grouped into 21 lineages (lineages 1–21 of Fig. 1). Four of them corresponded

with the previous morphology-based taxa, 7 of them were described as new, and the remaining 10 species with limited materials available were tentatively named *P.* spp.1–10, respectively.

Taxonomy

1. *Phylloporus bellus* (Massee) Corner, Nova Hedwigia 20 (3–4): 798, 1970 (Figs. 2a–b, 3a and 4)

Flammula bella Massee, Bull. Misc. Inform. Kew: 74, 1914

Basidiomata small to medium-sized. *Pileus* 4–6 cm in diameter, convex, then applanate, finally center slightly depressed; surface dry, densely tomentose, yellowish brown to reddish brown; margin slightly inrolled; context pale yellowish, unchanging in color when injured. *Hymenophore* lamellate, decurrent. *Lamellae* subdistant, up to 0.5 cm in height, commonly anastomosing, primose yellow, changing blue when injured, then back to yellow slowly; lamellulae common, attenuate, concolor with lamellae. *Stipe* central, 3–7×0.5–0.7 cm, subcylindric, solid; surface dry, tomentose, yellowish to pale reddish brown; upper part sometimes ribbed by the decurrent lines of the lamellae; context pale yellowish, unchanging in color when injured; annulus absent. *Basal mycelium* whitish. *Odor* indistinct.

Basidia 38–49×8–10 μm, clavate, thin-walled, 4-spored, colorless to yellowish in KOH; sterigmata 4–5 μm in length. *Basidiospores* [220/12/4] (8–) 9–12 (–13)×4 – 5 (–5.5) μm, Q=(1.78–) 2.00–2.75 (–3.13), Q_m=2.36±0.23, subfusiform to ellipsoid, slightly thick-walled (< 1 μm thick), olive brown to yellowish brown in KOH, smooth under the light microscope, but with bacillate ornamentation under SEM, dextrinoid. *Hymenophoral trama* slightly bilateral, with similar longitudinal hyphae densely arranged; these hyphae 5–15 μm wide, thin- to slightly thick-walled (up to 0.5 μm), colorless to yellowish in KOH. *Cheilocystidia* 40–67×10–17 μm, ventricose, subfusiform or subclavate, thin- to slightly thick-walled (up to 1 μm), hyaline, colorless to yellowish in KOH, no encrustations. *Pleurocystidia* 60–127×11–22 μm, abundant, fusiform, subfusiform or subclavate, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH, no encrustations. *Pileipellis* a trichoderm composed of colorless to yellowish brown, 6–20 μm wide, thin- to slightly thick-walled (up to 1 μm) hyphae; terminal cells 14–50×8–16 μm, clavate or subcylindrical, with obtuse apex. *Pileal trama* composed of 6–17 μm wide, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH, irregular hyphae. *Stipitipellis* a trichoderm-like structure composed of thin- to slightly thick-walled (up to 1 μm) hyphae; terminal cells 30–95×7–21 μm, clavate or subfusiform. *Stipe trama* composed of 5–17 μm wide, cylindrical, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH, parallel hyphae. *Clamp connections* absent in all tissues.

HABITAT: Solitary on the ground in forests mixed with *Lithocarpus* spp. and *Pinus* spp.

KNOWN DISTRIBUTION: Originally described from Singapore (Massee 1914; Corner 1970), then found in Malaysia (Corner 1970), New Guinea (Hongo 1973), Korea (Lee et al. 1982), Japan (Singer and Gómez 1984; Hongo and Izawa 1994), China (Li et al. 1992; Bi et al. 1993, 1994, 1997) and Philippines (Sims et al. 1997).

MATERIALS EXAMINED: *CHINA*. *Yunnan Province*: Yingjiang County, Xima Town, Huanglianhe Village, alt. 1700 m, 17 July 2003, Z.L. Yang 3731 (HKAS 42850); Yingjiang County, Xima Town, Tongbiguan Nature Reserve, alt. 2171 m, 17 July 2009, L.P. Tang 806 (HKAS 56763); Nanjian County, Wuliangshan Nature Reserve, alt. 2229 m, 28 July 2009, L.P. Tang 984 (HKAS 56941). *Guangdong Province*: Zhaoqing County, Dinghushan Nature Reserve, 15 June 1980, Z.S. Bi s. n. (GDGM 4218, as "*P. rhodoxanthus*" in Bi et al. 1993, 1994).

COMMENTS: *Phylloporus bellus* is well characterized by its yellowish brown to reddish brown pileus with a densely tomentose surface, a yellowish to pale reddish brown stipe with a whitish basal mycelium, cyanescent lamellae, and inflated hyphae in the pileipellis.

Phylogenetically, *P. bellus* is closely related to *P. maculatus*, *P. pachycystidiatus*, *P. centromericanus* and *P. rubrosquamosus* (Clade IV of Fig. 1). *Phylloporus maculatus* differs from *P. bellus* in having a brown to dark brown pileus with cinnamon brown spots, and a yellow stipe covered with minute squamules. *Phylloporus pachycystidiatus* and *P. centroamericanus* differ significantly from *P. bellus* by their thick-walled cystidia (Corner 1970; Singer and Gómez 1984; Montoya and Bandala 1991; Neves and Halling 2010). *Phylloporus rubrosquamosus* has a pileus covered with brownish red squamules composed of uninflated hyphae.

In China, *P. bellus* was misidentified as *P. rhodoxanthus* (Bi et al. 1993, 1994), a species described from the USA, but the latter has non-staining lamellae, a yellow stipe with a yellow basal mycelium, and a stipe context staining cinnamon (Neves and Halling 2010).

The name *P. bellus* has been widely applied (Massee 1914; Corner 1970; Hongo 1973; Lee et al. 1982; Singer and Gómez 1984; Li et al. 1992; Hongo and Izawa 1994; Sims et al. 1997; Neves and Halling 2010). However, the collections labeled as "*P. bellus*" from Mexico, Costa Rica and USA can be separated from those of East/SE Asia by the lamellae sometimes turning green when injured, slightly narrower basidiospores, and uninflated hyphae in the pileipellis (Singer and Gómez 1984; Neves and Halling 2010). Phylogenetic analysis indicated that collections of *P. bellus* from East/SE Asia (Clade IV of Fig. 1) and those of "*P.*

Fig. 2 Basidiomata of *Phylloporus* species **a**–**b.** *P. bellus* (HKAS 56763); **c.** *P. brunneiceps* (HKAS 56903, holotype); **d**–**e.** *P. imbricatus* (d from HKAS 54647, holotype; e from HKAS 53307); **f.** *P. maculatus* (HKAS 56683, holotype); **g.** *P. pachycystidiatus* (HKAS 54540, holotype); **h**–**i.** *P. parvisporus* (HKAS 54768); **j.** *P. rubeolus* (HKAS 52573, holotype); **k.** *P. rubrosquamosus* (HKAS 54559, holotype); **l**–**m.** *P. rufescens* (HKAS 59722); **n**–**o.** *P. yunnanensis* (HKAS 56999, holotype)

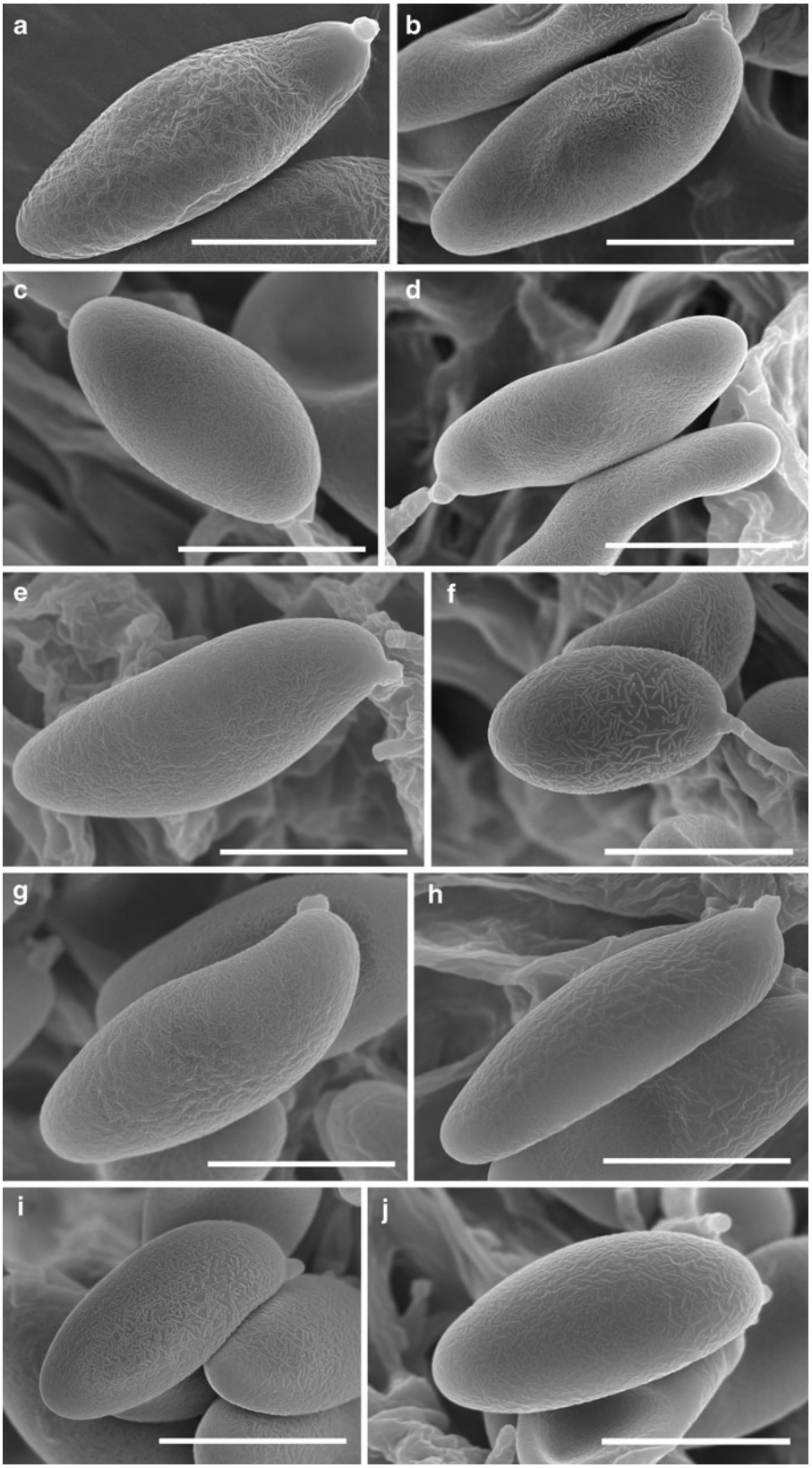

Fig. 3 Basidiospores of *Phylloporus* species from herbarium materials under SEM **a.** *P. bellus* (HKAS 56763); **b.** *P. brunneiceps* (HKAS 56903, holotype); **c.** *P. imbricatus* (HKAS 54647, holotype); **d.** *P. maculatus* (HKAS 56683, holotype); **e.** *P. pachycystidiatus* (HKAS 54540, holotype); **f.** *P. parvisporus* (HKAS 54768); **g.** *P. rubeolus* (HKAS 52573, holotype); **h.** *P. rubrosquamosus* (HKAS 54559, holotype); **i.** *P. rufescens* (HKAS 59722); **j.** *P. yunnanensis* (HKAS 56999, holotype). Note basidiospores with bacillate surface ornamentation. (Bars=5 μm.)

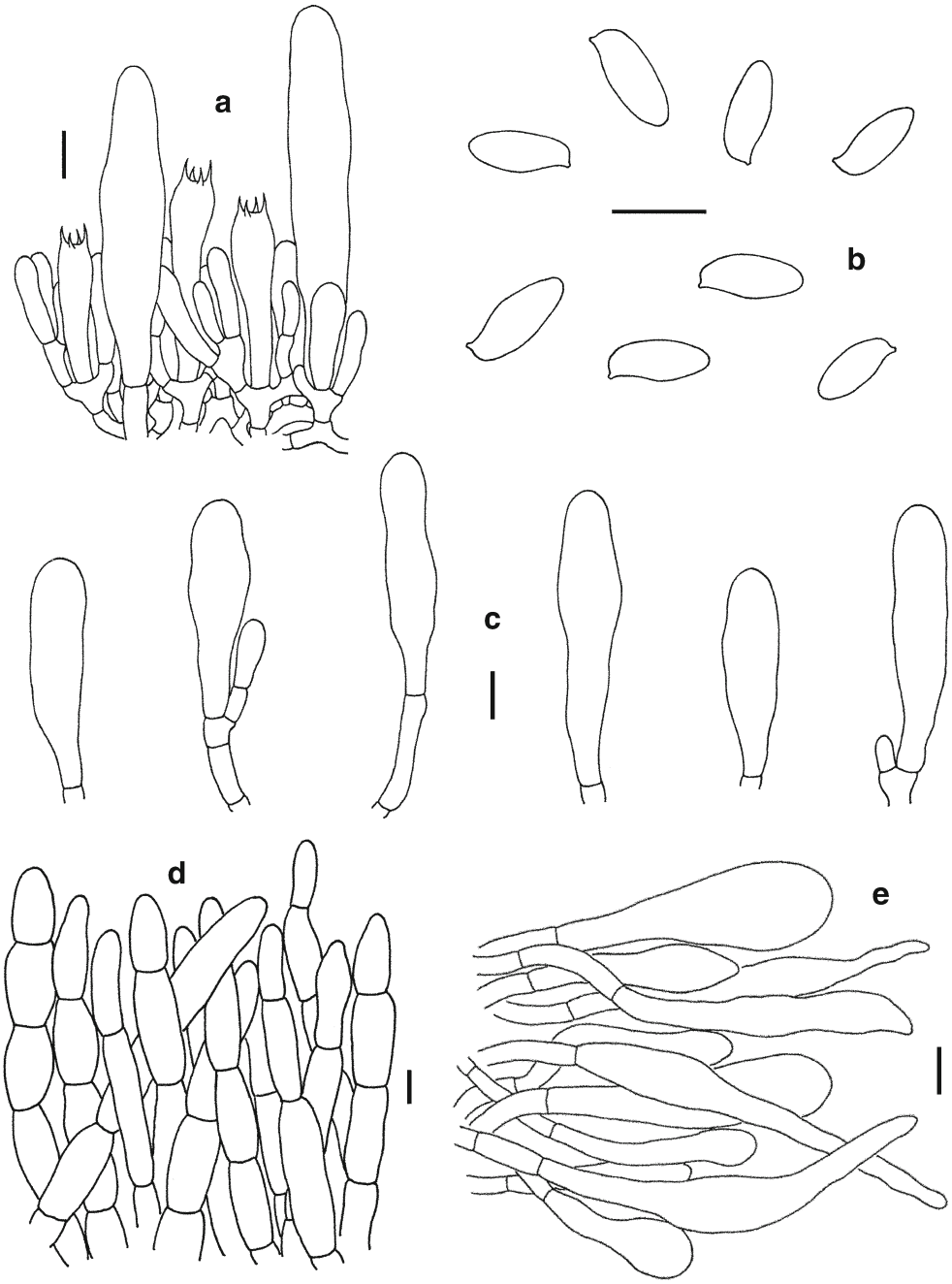

Fig. 4 Microscopic features of *P. bellus* (HKAS 56763) **a.** Basidia and pleurocystidia; **b.** Basidiospores; **c.** Cheilocystidia; **d.** Pileipellis; **e.** Stipitipellis. (Bars=10 μm.)

bellus" from North/Central America (Clade VI of Fig. 1) are not in the same clade.

2. *Phylloporus brunneiceps* N.K. Zeng, Zhu L. Yang & L.P. Tang, **sp. nov.** (Figs. 2c, 3b and 5)

MYCOBANK: MB 800146

ETYMOLOGY: named because of its brown pileus.

Pileus center slightly depressed; surface densely tomentose, then subsquamulose, brown to dark brown. Hymenophore yellow, changing blue when injured. Stipe central, subcylindric; surface tomentose, yellow to yellowish brown. Basal mycelium yellowish. Context cream-colored to yellowish, unchanging in color when injured. Basidiospores (9–)10–12(–14)×4–4.5(–5), subfusiform to ellipsoid, surface smooth under light microscopy but with bacillate ornamentation under SEM. Pleuro- and cheilocystidia present. Pileipellis a trichoderm composed of 4–11(–16) μm wide hyphae. Clamp connections absent.

Basidiomata small to medium-sized. *Pileus* 4–5 cm in diameter, center slightly depressed; surface dry, densely tomentose, then subsquamulose, brown (5 C6) to dark brown (6E6); margin inrolled; context cream-colored to yellowish, unchanging in color when injured. *Hymenophore* lamellate, decurrent. *Lamellae* up to 0.5 cm high, subdistant, commonly anastomosing, yellow (2A7), changing blue

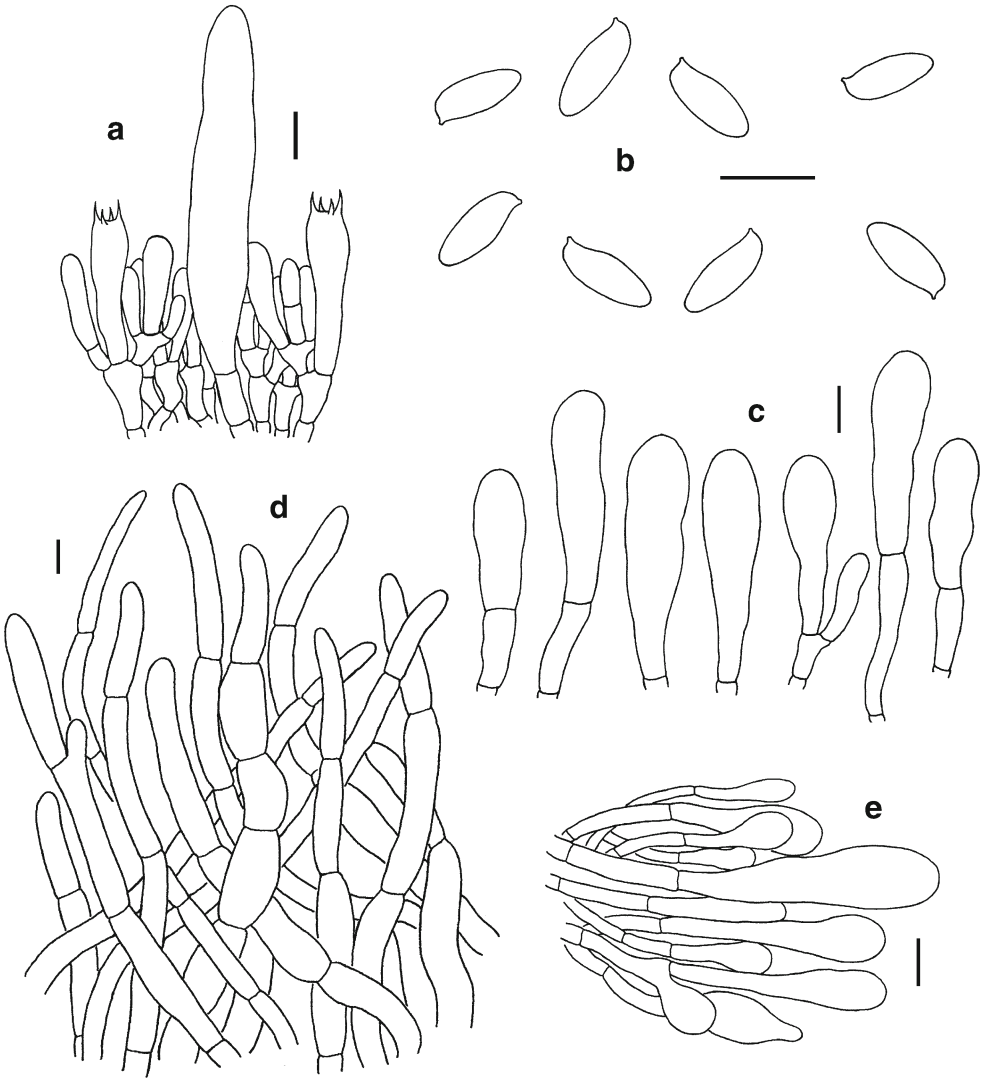

Fig. 5 Microscopic features of *P. brunneiceps* (HKAS 56903, holotype) **a**. Basidia and pleurocystidia. **b**. Basidiospores. **c**. Cheilocystidia. **d**. Pileipellis**.** **e.** Stipitipellis. (Bars=10 μm.)

when injured, then back to yellow slowly; lamellulae common, attenuate, concolor with lamellae. *Stipe* 3–4×0.4–0.7 cm, central, subcylindric, solid; surface dry, tomentose, yellow (2A7) to yellowish brown (4B8); upper half sometimes ribbed by the decurrent lines of the lamellae; context cream-colored to yellowish, unchanging in color when injured; annulus absent. *Basal mycelium* yellowish.

Basidia 32–43×8–10 μm, clavate, thin-walled, 4-spored, colorless to yellowish in KOH; sterigmata 4–5 μm in length. *Basidiospores* [280/14/5] (9–)10–12(–14)×4–4.5(–5) μm, Q=(2.00–)2.22–3.00(–3.50), Q_m=2.54±0.24, subfusiform to ellipsoid, slightly thick-walled (< 1 μm thick), olive brown to yellowish brown in KOH, smooth under the light microscope, but with bacillate ornamentation under SEM, dextrinoid. *Hymenophoral trama* slightly bilateral, with similar longitudinal hyphae densely arranged; these hyphae 4–20 μm wide, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH. *Cheilocystidia* 30–52×10–14 μm, subclavate or clavate, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH, no encrustations. *Pleurocystidia* 66–103×10–17 μm, abundant, fusiform or subfusiform, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH, no encrustations. *Pileipellis* a trichoderm composed of colorless, yellowish to yellowish brown in KOH, occasionally branched, 4–11 (–16) μm wide, thin- to slightly thick-walled (up to 1 μm) hyphae; terminal cells 15–66×4–11 (–14) μm, narrowly clavate or subcylindrical, with obtuse apex. *Pileal trama* made up of hyphae 4–18 μm in diameter, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH. *Stipitipellis* a trichoderm-like structure composed of thin- to slightly thick-walled (up to 1 μm) hyphae; terminal cells 22–57×6–14 μm, clavate. *Stipe trama* composed of 5–16 μm wide, cylindrical, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH, parallel hyphae. *Clamp connections* absent in all tissues.

HABITAT: Solitary on the ground in mixed forests of *Lithocarpus* spp. and *Pinus* spp.

KNOWN DISTRIBUTION: Southwestern China.

MATERIALS EXAMINED: *CHINA*. *Yunnan Province*: Changning County, alt. 2016 m, 25 July 2009, L.P. Tang 946 (HKAS 56903, *holotype*); Changning County, Huitou Village, alt. 2020 m, 25 July 2009, Y.C. Li 1804 (HKAS 59551). *Guizhou Province*: Daozhen County, Yangxi Town, alt. 1200 m, 28 July 2010, X.F. Shi 396 (HKAS 59728). *Chongqing Municipality*: Nanchuan, Mazui, alt. 985 m, 1 July 2009, B. Xiao 7339–7344 (HKAS 59726); Jinfoshan Nature Reserve, alt. 1201 m, 6 July 2009, B. Xiao 7984–7986 (HKAS 59727). *Sichuan Province*: Xichang, Louji Mountain, alt. 2100 m, 9 August 1983, D.C. Zhang 83 (HKAS 11897, as "*P. rhodoxanthus*" in Zang et al. 1996).

COMMENTS: *Phylloporus brunneiceps* is distinguished by its centrally depressed pileus covered with brown to dark brown squamules, cyanescent lamellae, a yellow stipe with a yellow basal mycelium, and uninflated hyphae in the pileipellis.

Phylloporus brunneiceps is similar to *P. sulcatus* (Pat.) E.-J. Gilbert, a species originally described from Vietnam, but the latter appears to differ from the former in its non-staining lamellae, wider basidiospores [10.5–12.5(–13)×(4.5–)5–5.5 (–6) μm] and narrower pleurocystidia (Patouillard 1909; Perreau and Joly 1964; Corner 1970; Zeng et al. 2011). The Chinese *P. luxiensis* also shares some common features with *P. brunneiceps*, but it can be separated from the latter by its stipe surface with reddish tinge, non-staining lamellae, and uninflated hyphae in the pileipellis. In China, *P. brunneiceps* was previously misidentified as *P. rhodoxanthus* (Zang et al. 1996), but the latter has a cinnamon brown pileus, and non-staining lamellae (Neves and Halling 2010).

Phylogenetic analysis demonstrated that *P. brunneiceps* is distinct from *P. luxiensis* and *P. rhodoxanthus* (Clade I of Fig.1). The phylogenetic relationship between *P. brunneiceps* and *P. sulcatus* is unknown due to a lack of the sequences from the latter species.

3. *Phylloporus imbricatus* N.K. Zeng, Zhu L. Yang & L. P. Tang, **sp. nov.** (Figs. 2d–e, 3c and 6)

MYCOBANK: MB 800147

ETYMOLOGY: named because its pileus has imbricate squamules when mature.

Pileus center slightly depressed, surface densely tomentose, then subsquamulose, finally imbricate-squamulose, yellowish brown, brown, dark brown, brownish red. Hymenophore yellow, changing blue when injured. Stipe central, subcylindric; surface tomentose, yellowish brown, brown to brownish red. Basal mycelium yellowish. Context cream-colored to yellowish, unchanging in color when injured. Basidiospores (9–)10–13 (–14.5)×4–5 μm, subfusiform to ellipsoid, surface smooth under light microscopy but with bacillate ornamentation under SEM. Pleuro- and cheilocystidia present. Pileipellis a trichoderm composed of 5–23 μm wide hyphae. Clamp connections absent.

Basidiomata medium to large-sized. *Pileus* 4.5–11 cm in diameter, center slightly depressed, surface dry, densely tomentose, then subsquamulose, finally imbricate-squamulose, yellowish brown (4A6), brown (6B6), dark brown (6E6) to brownish red (7 C7); margin slightly uplifted; context 0.3–0.6 cm in thickness in the halfway to the margin, cream-colored to yellowish, unchanging in color when injured. *Hymenophore* lamellate, decurrent. *Lamellae* up to 1.4 cm in height, subdistant, commonly anastomosing, yellow (2A7), changing blue when injured, then back to yellow slowly; lamellulae common, attenuate, concolor with lamellae. *Stipe* 5–10×0.3–1.5 cm, central, subcylindric, solid; surface dry, tomentose, yellowish brown (4A5), brown (6B6) to brownish red (7 C7); upper part usually ribbed by the decurrent lines of the lamellae; context cream-colored to yellowish, unchanging in color when injured; annulus absent. *Basal mycelium* yellowish.

Basidia 34–52×8–10 μm, clavate, thin-walled, 4-spored, colorless to yellowish in KOH; sterigmata 4–6 μm in length. *Basidiospores* [300/17/17] (9–)10–13 (–14.5)×4–5 μm, Q= (2.00–)2.11–2.90(–3.50), Q_m=2.46±0.26, subfusiform to ellipsoid, slightly thick-walled (< 1 μm thick), olive brown to yellowish brown in KOH, smooth under the light microscope, but with bacillate ornamentation under SEM, dextrinoid. *Hymenophoral trama* slightly bilateral, made up of hyphae 4–20 μm in width, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH. *Cheilocystidia* 27–58×8–16 μm, subclavate, clavate or subfusiform, thin- to slightly thick-walled (up to 1 μm), colorless, yellowish to pale yellowish brown in KOH, no encrustations. *Pleurocystidia* 50–76×9–17 μm, fusiform or subfusiform, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH, no encrustations. *Pileipellis* a trichoderm composed of colorless, pale yellowish brown to yellowish brown in KOH, occasionally branched, 5–23 μm wide, thin- to slightly thick-walled (up to 1 μm) hyphae; terminal cells 18–57×6–10 μm, clavate or subcylindrical, with obtuse apex. *Pileal trama* made up of hyphae 6–14 μm in diameter, thin-walled, colorless to yellowish in KOH. *Stipitipellis* a trichoderm-like structure composed of thin- to slightly thick-walled (up to 1 μm) hyphae; terminal cells 20–57×7–16 μm, subfusiform, narrowly or broadly clavate. *Stipe trama* composed of 4–17 μm wide, cylindrical, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH, parallel hyphae. *Clamp connections* absent in all tissues.

HABITAT: Solitary on the ground in forests of *Abies* and/or *Picea* between 3000 and 4100 m altitude.

KNOWN DISTRIBUTION: Southwestern China.

MATERIALS EXAMINED: *CHINA*. *Yunnan Province*: Yulong County, Laojunshan Nature Reserve, alt 3400 m, 26 July 2001, Z.L. Yang 3091 (HKAS 38268); same location, 2 September 2009, G. Wu 230 (HKAS 57762); Yulong

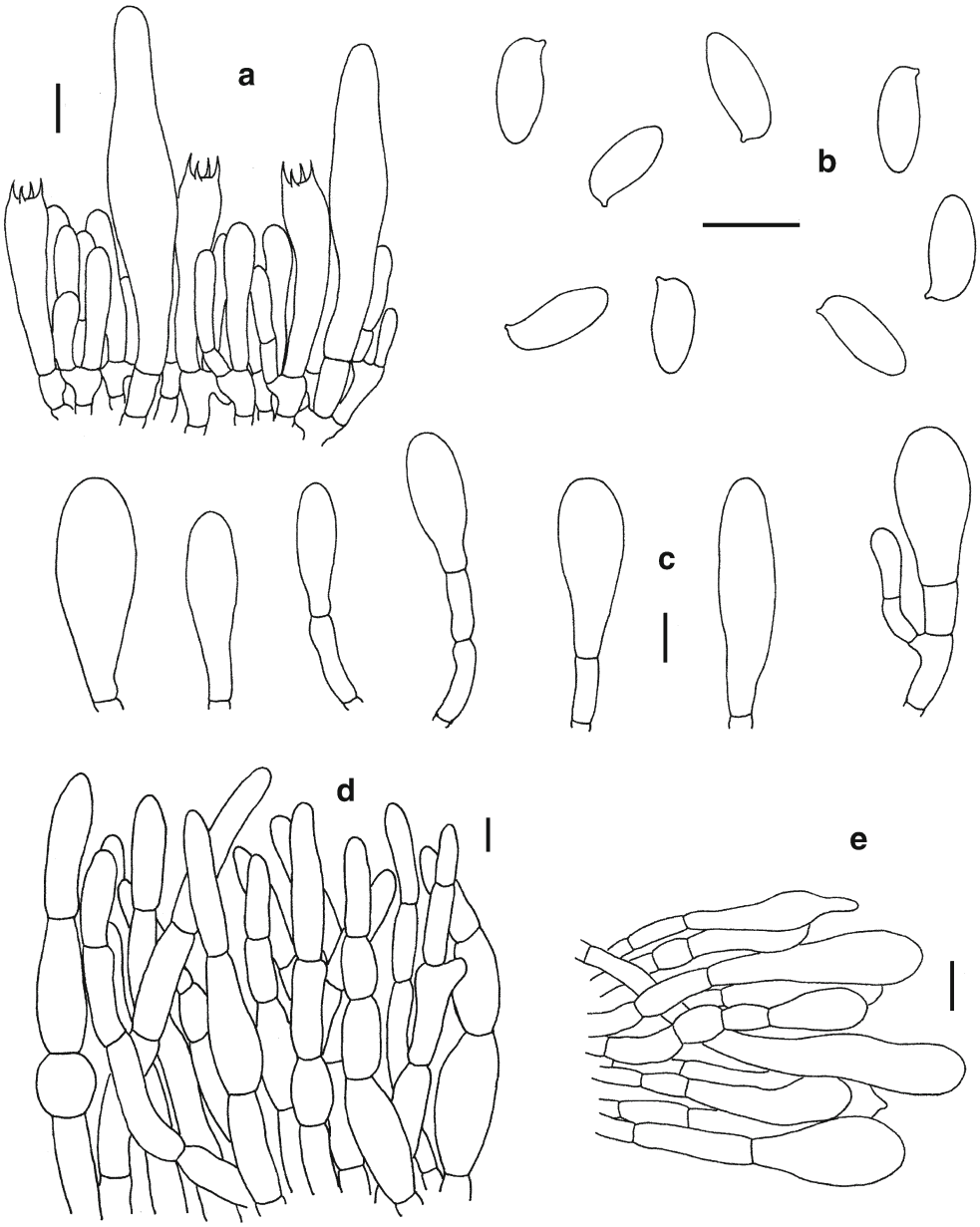

Fig. 6 Microscopic features of *P. imbricatus* (HKAS 54647, holotype) **a.** Basidia and pleurocystidia; **b.** Basidiospores; **c.** Cheilocystidia; **d.** Pileipellis; **e.** Stipitipellis. (Bars=10 μm.)

County, Shitou Town, Liju Village, alt. 3400 m, 23 August 2007, L.P. Tang 264, 266, 267, and 268 (HKAS 53307, 53309, 53310, and 53311 respectively); Yulong County, Tianwentai, alt. 3230 m, 20 July 2008, L.P. Tang 391 (HKAS 54622); Yulong County, Jade-Dragon Snow Mountain, alt. 3200 m, 21 July 2008, L.P. Tang 416 (HKAS 54647, *holotype*); Shangri-La County, Haba Snow Mountain Nature Reserve, alt. 3100 m, 14 August 2008, L.P. Tang 628, 629, and 630 (HKAS 54859, 54860, and 54861, respectively); Shangri-La County, Hongshan, alt. 3700 m, 29 July 1986, M. Zang 10590 (HKAS 17609, as "*P. rhodoxanthus*" in Zang et al. 1996); Lijiang Prefecture, Lijiang Alpine Botanic Garden, 27 August 2009, Q. Cai 151 (HKAS 58816); Yunlong County, alt. 3100 m, 8 September 1986, M. Zang 10846 (HKAS 17896, as "*P. rhodoxanthus*" in Zang et al. 1996). *Sichuang Province*: Xiangcheng County, alt. 4100 m, 3 August 1981, L.S. Wang 937 (HKAS 7866, as "*P. orientalis*" in Zang et al. 1996); Daocheng County, Julong Town, alt. 3600 m, 11 August 1984, M.S. Yuan 944 (HKAS 15323, as "*P. orientalis*" in Zang et al. 1996); Muli County, alt. 3350 m, 27 August 1983, K.K. Chen 861 (HKAS 13963, as "*P. sulphureus*" in Zang et al. 1996).

COMMENTS: *Phylloporus imbricatus* is well characterized by its large, yellowish brown, brown, dark brown to brownish red pileus with a non-staining context and with imbricate squamules when mature, cyanescent lamellae, a yellowish brown, brown to brownish red stipe with a yellowish basal mycelium, inflated hyphae in the pileipellis, and its association with subalpine to alpine trees.

Morphological differences between *P. imbricatus* and *P. yunnanensis* are subtle, the basidiomata of *P. imbricatus* are usually larger and robuster than those of *P. yunnanensis*. The main differences between them are probably their ecological preferences. *Phylloporus imbricatus* usually grows in high altitudes (alt. 3000–4100 m), in southwestern China, and it is associated with subalpine to alpine trees, while *P. yunnanensis* is distributed in southern parts of Yunnan Province under subtropical and tropical host trees. In China, *P. imbricatus* was misidentified as *P. foliiporus* (Dai and Li 1994), *P. orientalis* Corner (Zang et al. 1996), *P. rhodoxanthus* (Zang et al. 1996), and *P. sulphureus* (Zang et al. 1996). However, *P. foliiporus*, originally described from the USA, has a cyanescent context, cystidia with a melleous-colored apex, and clamp connections (Neves and Halling 2010). *Phylloporus orientalis*, a species described from Malaysia, has large-sized basidiomata, a cyanescent context, and larger basidiospores [13–16.5×5–5.5(–6)] (Corner 1970). *Phylloporus rhodoxanthus* has non-staining lamellae, and a yellow stipe with staining cinnamon context (Neves and Halling 2010). *Phylloporus sulphureus*, originally described from India, has a sulphur yellow to orange pileus, very broad and distant lamellae, and narrower basidiospores (9–12.5×3.5–4.5) (Berkeley 1851; Singer 1951; Manjula 1983).

In our phylogenetic analysis, *P. imbricatus* is sister to *P. yunnanensis* with a relatively high statistical support (Clade I of Fig. 1). The phylogenetic relationship between *P. imbricatus* and *P. sulphureus* is unknown due to the absence of DNA sequences of the latter taxon.

The collections of *P. imbricatus* were clustered with "48854 China" (Neves et al. 2012) with strong statistical support (RAxML BS=100, PP=1), indicating that "48854 China" is likely to be *P. imbricatus*.

4. *Phylloporus maculatus* N.K. Zeng, Zhu L. Yang & L.P. Tang, **sp. nov.** (Figs. 2f, 3d and 7)

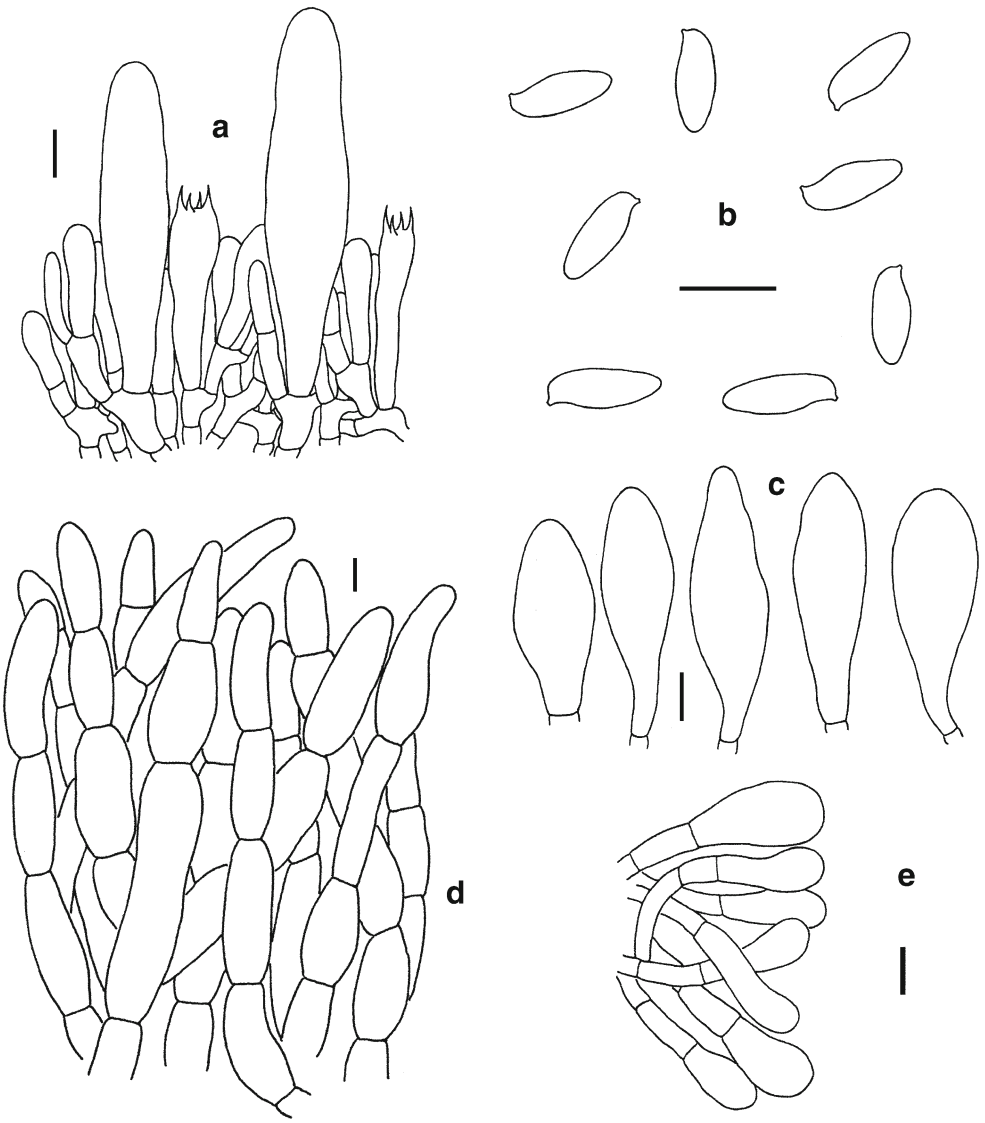

Fig. 7 Microscopic features of *P. maculatus* (HKAS 56683, holotype) **a.** Basidia and pleurocystidia; **b.** Basidiospores; **c.** Cheilocystidia; **d.** Pileipellis; **e.** Stipitipellis. (Bars=10 μm.)

MYCOBANK: MB 800148

ETYMOLOGY: named because of its spotted pileus.

Pileus convex, then applanate, finally center slightly depressed; surface densely subtomentose, brown to dark brown, covered with cinnamon brown spots. Hymenophore primose yellow, changing blue when injured. Stipe central, subcylindric; surface primose yellow to brownish yellow, covered with minute, brown squamules. Basal mycelium whitish. Context cream-colored to yellowish, unchanging in color when injured. Basidiospores (9–)10–12×(3.5–) 4–4.5(–5), subfusiform to ellipsoid, surface smooth under light microscopy but with bacillate ornamentation under SEM. Pleuro- and cheilocystidia present. Pileipellis a trichoderm composed of 8–25 μm wide hyphae. Clamp connections absent.

Basidiomata small-sized. *Pileus* 2–5 cm in diameter, convex, then applanate, finally center slightly depressed; surface dry, densely subtomentose, brown (5 C6) to dark brown (6 C7), covered with cinnamon brown (6D8) spots; margin decurved when young, then slightly uplifted; context cream-colored to yellowish, unchanging in color when injured. *Hymenophore* lamellate, decurrent. *Lamellae* subdistant, commonly anastomosing, primose yellow (2A7), changing blue when injured, then back to yellow slowly; lamellulae common, attenuate, concolor with lamellae. *Stipe* 2.5–4×0.5–0.6 cm, central, subcylindric, solid; surface dry, yellowish, apical part primose yellow (2A7) and basal part brownish yellow (3A8), covered with minute, brown (5B7) squamules; context cream-colored to yellowish, unchanging in color when injured; annulus absent. *Basal mycelium* whitish.

Basidia 41–59×8–11 μm, clavate, thin-walled, 4-spored, colorless to yellowish in KOH; sterigmata 4–6 μm in length. *Basidiospores* [80/4/2] (9–)10–12×(3.5–)4–4.5(–5) μm, Q=(2.38–)2.44–3.00, Q_m=2.66±0.19, subfusiform to ellipsoid, slightly thick-walled (< 1 μm thick), olive brown to yellowish brown in KOH, smooth under the light microscope, but with bacillate ornamentation under SEM, dextrinoid. *Hymenophoral trama* slightly bilateral, made up of hyphae 5–15 μm in width, thin-walled, colorless to yellowish in KOH. *Cheilocystidia* 41–59×12–18 μm, abundant, subfusiform or subclavate, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH, no encrustations. *Pleurocystidia* 52–120×12–20 μm, abundant, fusiform or subfusiform, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH, no encrustations. *Pileipellis* a trichoderm composed of yellowish to yellowish brown in KOH, 8–25 μm wide, thin- to slightly thick-walled (up to 1 μm) hyphae; terminal cells 30–70×11–17 μm, narrowly clavate or subcylindrical, with obtuse apex. *Pileal trama* made up of hyphae 5–16 μm in diameter, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH. *Stipitipellis* a trichoderm-like structure composed of thin- to slightly thick-walled (up to 1 μm) hyphae; terminal cells 18–32×9–16 μm, clavate. *Stipe trama* composed of 4–15 μm wide, cylindrical, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH, parallel hyphae. *Clamp connections* absent in all tissues.

HABITAT: Solitary on the ground in forests of *Lithocarpus* spp.

KNOWN DISTRIBUTION: Southwestern China.

MATERIALS EXAMINED: *CHINA*. *Yunnan Province*: Tengchong County, Qushi Town, Linjiapu Village, alt. 2100 m, 4 July 2009, Z.L. Yang 5260 (HKAS 56683, *holotype*); Yingjiang County, Xima Town, Tongbiguan Nature Reserve, alt. 2171 m, 17 July 2009, Q. Zhao 161 (HKAS 59730).

COMMENTS: *Phylloporus maculatus* is well characterized by its brown to dark brown pileus with cinnamon brown spots, cyanescent lamellae, yellowish stipe covered with minute squamules, whitish basal mycelium, and inflated hyphae in the pileipellis.

Phylloporus maculatus looks like the Vietnamese *P. sulcatus*, both sharing the brown pileus and yellowish stipe, but the latter differs from the former by non-staining lamellae, wider basidiospores [10.5–12.5(–13)×(4.5–)5–5.5(–6) μm] and narrower pleurocystidia (Patouillard 1909; Perreau and Joly 1964; Corner 1970; Zeng et al. 2011).

Phylogenetically, *P. maculatus* is allied with *P. bellus*, *P. pachycystidiatus*, *P. centromericanus* and *P. rubrosquamosus* (Clade IV of Fig. 1). The morphological differences of the five taxa were elucidated under *P. bellus* (above). The phylogenetic relationship between *P. maculatus* and *P. sulcatus* has not been resolved due to the lack of sequences of the latter.

5. *Phylloporus pachycystidiatus* N.K. Zeng, Zhu L. Yang & L.P. Tang, **sp. nov.** (Figs. 2g, 3e and 8)

MYCOBANK: MB 800149

ETYMOLOGY: named because of its thick-walled cystidia.

Pileus convex, then applanate, finally center slightly depressed; surface densely tomentose, then squamulose, yellowish brown to reddish brown. Hymenophore yellow, changing blue when injured. Stipe central, subcylindric; surface tomentose, yellowish brown to reddish brown. Basal mycelium whitish. Context cream-colored to yellowish, unchanging in color when injured. Basidiospores (10–)11–14(–15)×(4–)4.5–5(–5.5) μm, subfusiform to ellipsoid, surface smooth under light microscopy but with bacillate ornamentation under SEM. Pleuro- and cheilocystidia present, thick-walled (2–4 μm). Pileipellis a trichoderm composed of 6–15(–20) μm wide hyphae. Clamp connections absent.

Basidiomata small-sized. *Pileus* 3–5 cm in diameter, convex, then applanate, finally center slightly depressed; surface dry, densely tomentose, then squamulose, yellowish brown (4A5) to reddish brown (6B7); margin inrolled when young, then uplifted; context cream-colored to yellowish, unchanging in color when injured (sometimes changing

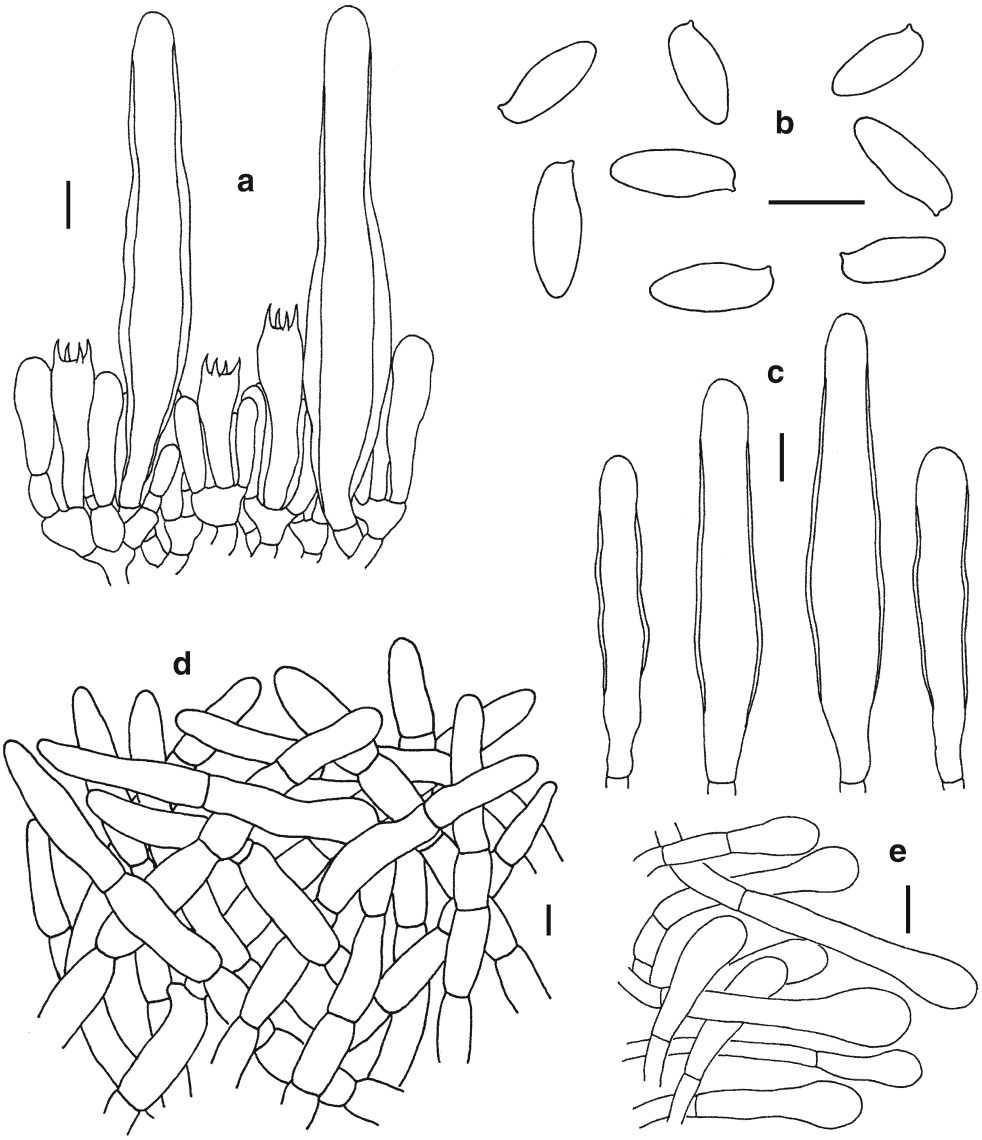

Fig. 8 Microscopic features of *P. pachycystidiatus* (HKAS 54540, holotype) **a.** Basidia and pleurocystidia; **b.** Basidiospores; **c.** Cheilocystidia; **d.** Pileipellis; **e.** Stipitipellis. (Bars=10 μm.)

slightly blue near the hymenophore). *Hymenophore* lamellate, decurrent. *Lamellae* up to 0.6 cm in height, subdistant, commonly anastomosing, yellow (2A7), changing blue (sometimes strongly and quickly) when injured; lamellulae common, crowded, concolor with lamellae. *Stipe* 2–3.5× 0.3–0.6 cm, central, subcylindric, solid; surface dry, tomentose, yellowish brown (4A5) to reddish brown (6B7); context cream-colored to yellowish, unchanging in color when injured, upper part sometimes ribbed by the decurrent lines of the lamellae; annulus absent. *Basal mycelium* whitish.

Basidia 25–44×9–13 μm, clavate, thin-walled, 4-spored, colorless to yellowish in KOH; sterigmata 4–5 μm in length. *Basidiospores* [140/7/5] (10–)11–14(–15)×(4–)4.5–5(–5.5) μm, Q=(2.17–)2.30–2.90(–3.22), Q_m=2.61±0.20, subfusiform to ellipsoid, slightly thick-walled (< 1 μm thick), olive brown to yellowish brown in KOH, smooth under the light microscope, but with bacillate ornamentation under SEM, dextrinoid. *Hymenophoral trama* slightly bilateral, with similar longitudinal hyphae densely arranged; these hyphae 5–15 μm wide, thin-walled, colorless to yellowish in KOH. *Cheilocystidia* 64–102×11–19 μm, abundant, subfusiform, subclavate or clavate, slightly thick-walled (1 μm), colorless to yellowish in KOH, no encrustations. *Pleurocystidia* 109–153×11–20 μm, abundant, subfusiform or fusiform, thick-walled (2–4 μm), colorless to yellowish in KOH, without encrustations. *Pileipellis* a trichoderm composed of compact, occasionally branched hyphae, more or less vertically arranged when young, then slightly interwoven; these 6–15 (–20) μm in diameter, thin- to slightly thick-walled (up to 1 μm), colorless, yellowish to yellowish brown in KOH; terminal cells 30–60×8–15 μm, narrowly clavate or subcylindrical, with obtuse apex. *Pileal trama* made up of hyphae 5–13 μm in diameter, thin-walled, colorless in KOH. *Stipitipellis* a trichoderm-like structure composed of thin- to slightly thick-walled (up to 1 μm) hyphae; terminal cells 18–56×8–13 μm, clavate. *Stipe trama* composed of 4–

18 μm wide, cylindrical, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH, parallel hyphae. *Clamp connections* absent in all tissues.

HABITAT: Solitary to scattered, on the ground in forests dominated by *Lithocarpus* spp.

KNOWN DISTRIBUTION: Southern and southwestern China.

MATERIALS EXAMINED: *CHINA*. *Yunnan Province*: Jingdong County, Ailaoshan Nature Reserve, alt. 2400 m, 14 July 2008, L.P. Tang 309 (HKAS 54540, *holotype*); same location and date, L.P. Tang 310 (HKAS 54541); same location, alt. 2380 m, 15 July 2008, L.P. Tang 327 and 329 (HKAS 54558 and 54560, respectively). *Hainan Province*: Wuzhishan County, Wuzhishan Nature Reserve, alt. 1323 m, 2 August 2009, N.K. Zeng 428 (HKAS 59724).

COMMENTS: *Phylloporus pachycystidiatus* is well characterized by its reddish brown pileus, yellowish brown to reddish brown stipe with a whitish basal mycelium, cyanescent lamellae (sometimes intensively), non-staining or occasionally blue context, thick-walled (2–4 μm in diameter) but nonencrusted pleurocystidia, and uninflated hyphae in the pileipellis.

Phylloporus centroamericanus, *P. rubiginosus* M.A. Neves & Halling, and *P. tunicatus* Corner, originally described from Costa Rica, Thailand, and Malaysia, respectively, also have thick-walled cystidia (Corner 1970; Singer and Gómez 1984; Neves and Halling 2010; Neves et al. 2012). However, *P. centroamericanus* has very small-sized basidiomata, a non-staining or rarely blue-green context, conspicuously encrusted cystidia. *Phylloporus rubiginosus* has a dark red pileus and stipe, a yellow mycelium at the base of the stipe, and cystidia with only 2 μm thickness. *Phylloporus tunicatus* has very small-sized basidiomata with a fuscous brown pileus, a subglobose base of cystidia, and somewhat wider hyphae (up to 30 μm) in the pileipellis (Corner 1970).

In the phylogenetic analyses, *P. pachycystidiatus* is allied with *P. bellus*, *P. centromericanus*, *P. maculatus* and *P. rubrosquamosus*, and form a sister relationship with *P. centroamericanus* (Clade IV of Fig. 1). The morphological differences of the five species have been discussed under *P. bellus* (above). The phylogenetic relationship of *P. pachycystidiatus* to *P. tunicatus* is unknown.

6. *Phylloporus parvisporus* Corner, Nova Hedwigia 20 (3–4): 811, 1970. (Figs. 2h–i, 3f and 9)

Basidiomata small-sized. *Pileus* 2–3 cm in diameter, applanate, then center slightly depressed; surface dry, densely tomentose, brown, dark brown or olivaceous; margin slightly inrolled; context pale brownish fuliginous or pale fuscous, unchanging in color when injured. *Hymenophore* lamellate, slightly decurrent. *Lamellae* subdistant, up to 0.5 cm in height, commonly anastomosing, yellow, unchanging in color when injured; lamellulae common, attenuate, concolor with lamellae. *Stipe* 1–2.5×0.2–0.3 cm, central, subcylindric, solid; surface dry, densely tomentose, yellowish brown, brown, or olivaceous; context pale brownish fuliginous or pale fuscous, unchanging in color when injured; annulus absent. *Basal mycelium* whitish.

Basidia 30–36×8–10 μm, clavate, thin-walled, 4-spored, colorless to yellowish in KOH; sterigmata 4–6 μm in length. *Basidiospores* [100/5/2] 6–7.5(–8)×(4–)4.5–5(–5.5) μm, Q=1.20–1.56(–1.63), Q_m=1.43±0.11, subfusiform to ellipsoid, slightly thick-walled (< 1 μm thick), olive brown to yellowish brown in KOH, smooth under the light microscope, but with bacillate ornamentation under SEM, dextrinoid. *Hymenophoral trama* slightly bilateral, with similar longitudinal hyphae densely arranged; these hyphae 4–15 μm wide, thin-walled, colorless to yellowish in KOH. *Cheilocystidia* 66–104×12–17 μm, abundant, subclavate, subfusiform or fusiform, thin-walled, colorless to yellowish in KOH, no encrustations. *Pleurocystidia* 98–126×15–19 μm, abundant, fusiform or subfusiform, thin-walled, colorless to yellowish in KOH, no encrustations. *Pileipellis* a trichoderm composed of colorless to yellowish in KOH, occasionally branched, 6–17 μm wide, thin- to slightly thick-walled (up to 1 μm) hyphae; terminal cells 29–65×9–14 μm, narrowly clavate or subcylindrical, with obtuse apex. *Pileal trama* made up of hyphae 6–15 μm in diameter, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH. *Stipitipellis* a trichoderm-like structure composed of thin- to slightly thick-walled (up to 1 μm) hyphae; terminal cells 22–40×5–10 μm, clavate. *Stipe trama* composed of 3–14 μm wide, cylindrical, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH, parallel hyphae. *Clamp connections* absent in all tissues.

HABITAT: Solitary or gregarious on the ground in forests of *Lithocarpus* spp.

KNOWN DISTRIBUTION: Singapore (Corner 1970), southeastern and southwestern China.

MATERIALS EXAMINED: *CHINA*. *Yunnan Province*: Jinghong County, Dadugang Town, alt. 1300 m, 31 July 2008, L.P. Tang 537 (HKAS 54768). *Fujian Province*: Zhangping County, Tiantai National Forest Park, alt. 356 m, 28 August 2009, N.K. Zeng 598 (HKAS 59725).

COMMENTS: *Phylloporus parvisporus* is well characterized by its pileus and stipe tinged with olivaceous, pale brownish fuliginous context, non-staining lamellae and context, and small basidiospores.

Phylloporus parvisporus can be confused with *P. infuscatus*, which also has a pileus tinged with an olivaceous color, an unusual context color and small basidiospores (Neves et al. 2012), but the latter has cyanescent lamellae, narrower basidiospores (6.3–7.7×3.5–4.2), and short cystidia (Neves et al. 2012). *Phylloporus cingulatus* Corner and *P. coccineus* Corner, both originally described from Singapore, also have small basidiospores. However, *P. cingulatus* has an obturbinate pileus with a reddish tinge, wide poroid gills, and a stipe with lurid blue-green zone at the apex (Corner 1970). *Phylloporus coccineus* has orange-red

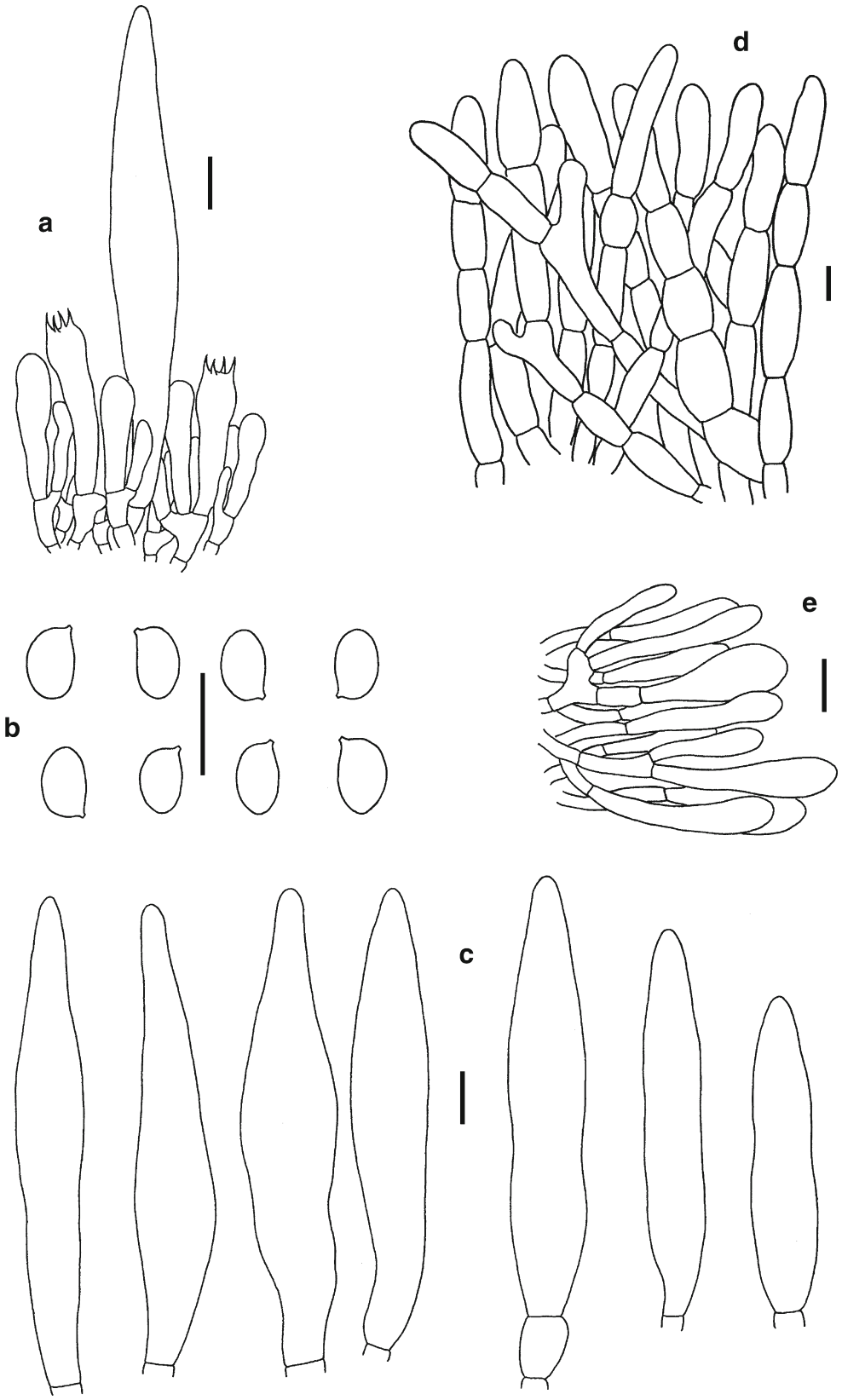

Fig. 9 Microscopic features of *P. parvisporus* (HKAS 54768) **a.** Basidia and pleurocystidia; **b.** Basidiospores; **c.** Cheilocystidia; **d.** Pileipellis; **e.** Stipitipellis. (Bars=10 μm.)

basidiomata, cyanescent lamellae and context, and wider basidiospores [7.5–9(–10)×6.5–7.5(–8)] μm (Corner 1970).

In our phylogenetic analysis, *P. parvisporus* is sister to *P. infuscatus* (Clade III of Fig. 1), but its phylogenetic

relationships to *P. cingulatus* and *P. coccineus* are unknown due to a lack of sequences from the latter two.

7. *Phylloporus rubeolus* N.K. Zeng, Zhu L. Yang & L.P. Tang, **sp. nov.** (Figs. 2j, 3g and 10)

MYCOBANK: MB 800150

ETYMOLOGY: named because of its somewhat reddish pileus.

Pileus convex, then applanate, finally center slightly depressed; surface densely tomentose, somewhat reddish. Hymenophore yellow, changing blue when injured. Stipe central, subcylindric; surface tomentose, brown to brownish red. Basal mycelium whitish. Context cream-colored to yellowish, unchanging in color when injured. Basidiospores (8.5–)9–12×(3.5–)4–5 μm, subfusiform to ellipsoid, surface smooth under light microscopy but with bacillate ornamentation under SEM. Pleuro- and cheilocystidia present. Pileipellis a trichoderm composed of 6–25 μm wide hyphae. Clamp connections absent.

Basidiomata small to medium-sized. *Pileus* 2.4–7 cm in diameter, convex, then applanate, finally center slightly

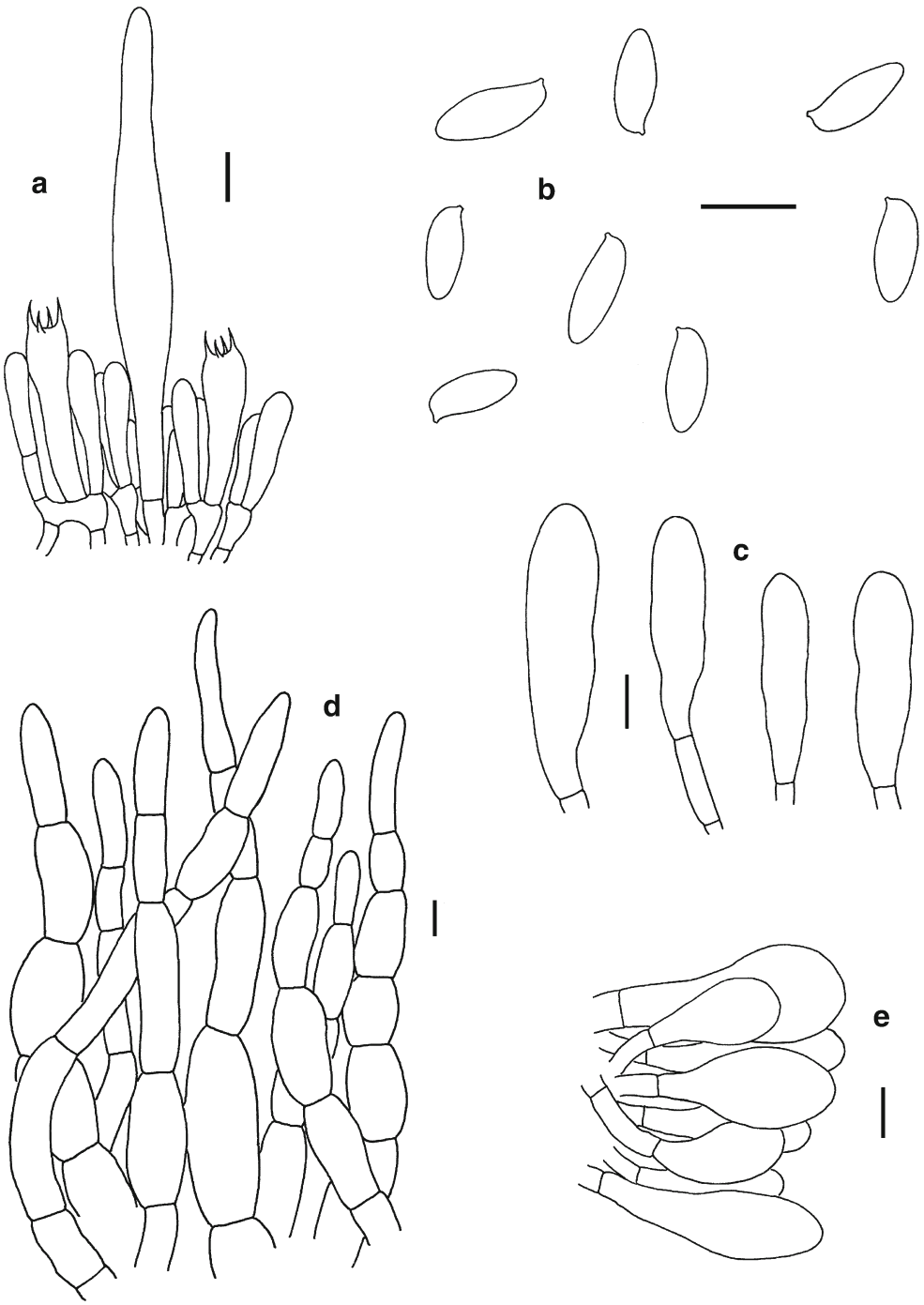

Fig. 10 Microscopic features of *P. rubeolus* (HKAS 52573, holotype) **a.** Basidia and pleurocystidia; **b.** Basidiospores; **c.** Cheilocystidia; **d.** Pileipellis; **e.** Stipitipellis. (Bars=10 μm.)

depressed; surface dry, densely tomentose, somewhat reddish (9B8); margin slightly inrolled; context cream-colored to yellowish, unchanging in color when injured. *Hymenophore* lamellate, decurrent. *Lamellae* up to 0.8 cm high, subdistant, occasionally anastomosing, yellow (2A7), changing blue when injured, then back to yellow slowly; lamellulae common, attenuate, concolor with lamellae. *Stipe* 3–6×0.4–1 cm, central, subcylindric, solid; surface dry, tomentose, brown (7B7) to brownish red (9B8); context cream-colored to yellowish, unchanging in color when injured; annulus absent. *Basal mycelium* whitish.

Basidia 31–42×8–10 μm, clavate, thin-walled, 4-spored, colorless to yellowish in KOH; sterigmata 4–5 μm in length. *Basidiospores* [160/8/4] (8.5–)9–12×(3.5–)4–5 μm, Q=(2.00–)2.11–2.75(–3.43), Q_m=2.48±0.23, subfusiform to ellipsoid, slightly thick-walled (< 1 μm thick), olive brown to yellowish brown in KOH, smooth under the light microscope, but with bacillate ornamentation under SEM, dextrinoid. *Hymenophoral trama* slightly bilateral, with similar longitudinal hyphae densely arranged; these hyphae 8–20 μm wide, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH. *Cheilocystidia* 35–57×9–17 μm, abundant, subfusiform or subclavate, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH, no encrustations. *Pleurocystidia* 52–130×10–15 μm, abundant, fusiform or subfusiform, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH, no encrustations. *Pileipellis* a trichoderm composed of yellowish to yellowish brown in KOH, 6–25 μm wide, thin- to slightly thick-walled (up to 1 μm) hyphae; terminal cells 25–60×7–11 μm, narrowly clavate or subcylindrical, with acute apex. *Pileal trama* made up of hyphae 6–18 μm in diameter, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH. *Stipitipellis* a trichoderm-like structure composed of thin- to slightly thick-walled (up to 1 μm) hyphae; terminal cells 20–55×7–20 μm, clavate. *Stipe trama* composed of 4–18 μm wide, cylindrical, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH, parallel hyphae. *Clamp connections* absent in all tissues.

HABITAT: Solitary on the ground in forests of *Lithocarpus* spp.

KNOWN DISTRIBUTION: Southwestern China.

MATERIALS EXAMINED: *CHINA*. *Yunnan Province*: Jingdong County, Ailaoshan Nature Reserve, alt. 1450 m, 18 July 2009, Y.C. Li 888 (HKAS 52573, *holotype*); same location, alt. 2400 m, 14 July 2008, L.P. Tang 304, 306, and 312 (HKAS 54535, 54537, and 54543, respectively).

COMMENTS: *Phylloporus rubeolus* is well characterized by its yellowish brown to brownish red pileus and stipe, whitish basal mycelium, cyanescent lamellate, basidiospores with bacillate ornamentation under SEM, narrower cystidia, and inflated pileipellis hyphae with acute apex.

Phylloporus alborufus, *P. rubiginosus*, and *P. rubriceps* Corner, originally described from Costa Rica, Thailand, and Malaysia, respectively, also share the same color of basidiomata with *P. rubeolus*. However, *P. alborufus* has slightly narrower basidiospores with smooth to finely rugulose ornamentation under SEM (Neves and Halling 2010). *Phylloporus rubiginosus* has a cyanescent context, yellow basal mycelium, thick-walled (1–2 μm) cystidia, and uninflated pileipellis hyphae (Neves et al. 2012). *Phylloporus rubriceps* has relatively longer basidiospores, somewhat wider cystidia (up to 30 μm), and hyphae in the pileipellis with obtuse apices (Corner 1970).

In the phylogenetic analysis, *P. rubeolus* is clustered with *P.* sp. 9 (Clade VII of Fig. 1). However, the latter species has a pale brown to dark brown pileus, a flesh pink stipe context, and hyphae in the pileipellis with obtuse apex.

8. *Phylloporus rubrosquamosus* N.K. Zeng, Zhu L. Yang & L.P. Tang, **sp. nov.** (Figs. 2k, 3h and 11)

MYCOBANK: MB 800151

ETYMOLOGY: named because of its reddish squamules on the pileus.

Pileus applanate, then center slightly depressed, surface covered with reddish squamules. Hymenophore yellow, changing blue slightly when injured. Stipe central, subcylindric; surface covered with yellowish brown to reddish squamules. Basal mycelium whitish. Context cream-colored to yellowish, unchanging in color when injured. Basidiospores (10–)11–12.5(–13)×4.5–5 μm, subfusiform to ellipsoid, surface smooth under light microscopy but with bacillate ornamentation under SEM. Pleuro- and cheilocystidia present. Pileipellis a trichoderm composed of 4–12 μm wide hyphae. Clamp connections absent.

Basidiomata small to medium-sized. *Pileus* 4.5–6 cm in diameter, convex, then applanate, finally center slightly depressed; surface dry, brownish yellow (3A5), covered with reddish (8A8) squamules; margin inrolled; context cream-colored to yellowish, unchanging in color when injured. *Hymenophore* lamellate, decurrent. *Lamellae* up to 0.8 cm in height, subdistant, commonly anastomosing, yellow (2A7), changing blue slightly when injured; lamellulae common, attenuate, concolor with lamellae. *Stipe* 5–8×0.6–0.7 cm, central, subcylindric, solid; surface dry, brownish yellow (3A5), covered with yellowish brown (4A5) to reddish (8A8) squamules; context cream-colored to yellowish, unchanging in color when injured; annulus absent. *Basal mycelium* whitish.

Basidia 30–50×8–11 μm, clavate, thin-walled, 4-spored, colorless to yellowish in KOH; sterigmata 4–6 μm in length. *Basidiospores* [40/3/3] (10–)11–12.5(–13)×4.5–5 μm, Q=(2.20–)2.30–2.67(–2.78), Q_m=2.48±0.15, subfusiform to ellipsoid, slightly thick-walled (< 1 μm thick), olive brown to yellowish brown in KOH, smooth under the light microscope, but with bacillate ornamentation under SEM, dextrinoid. *Hymenophoral trama* slightly bilateral, with similar longitudinal hyphae densely arranged; these hyphae 4–

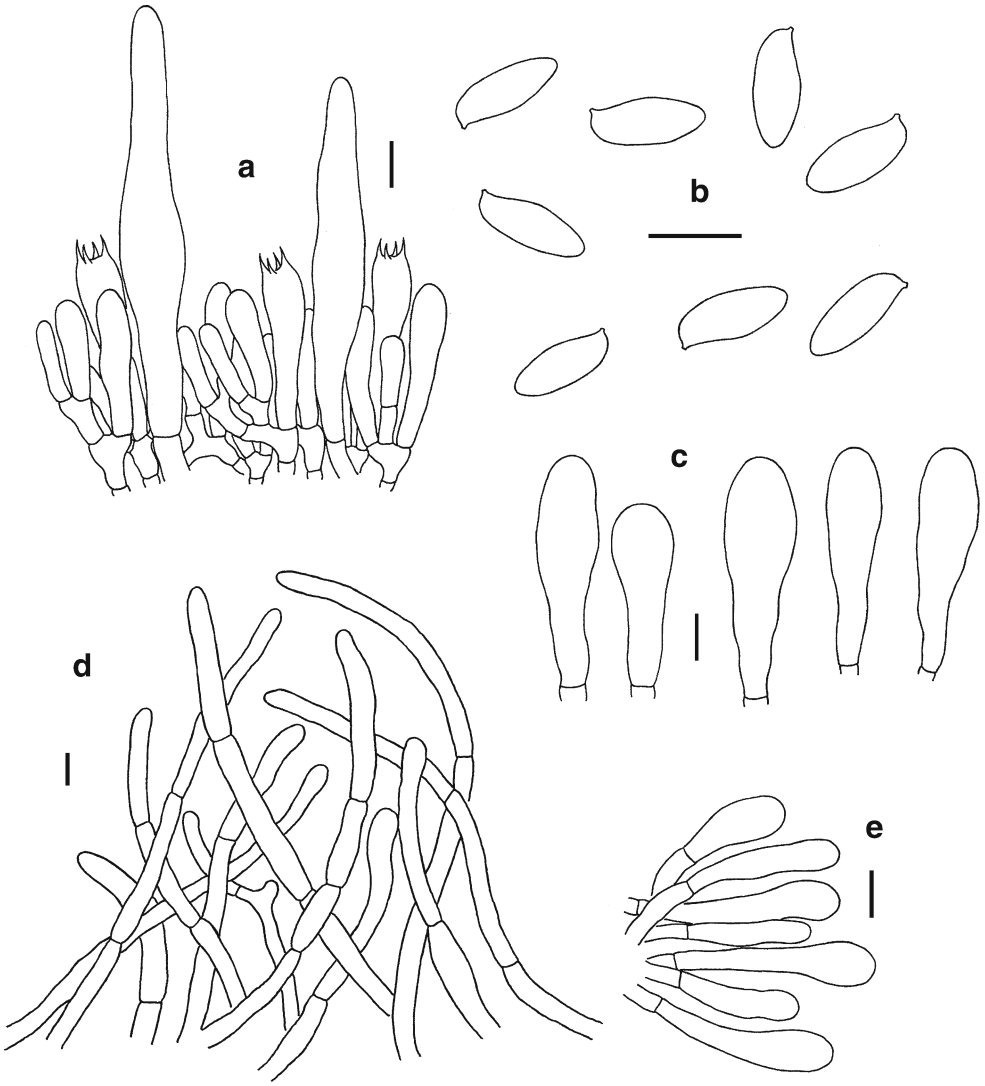

Fig. 11 Microscopic features of *P. rubrosquamosus* (HKAS 54559, holotype) **a.** Basidia and pleurocystidia; **b.** Basidiospores; **c.** Cheilocystidia; **d.** Pileipellis; **e.** Stipitipellis. (Bars=10 μm.)

22 μm wide, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH. *Cheilocystidia* 39–54×13–16 μm, abundant, subclavate or clavate, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH, no encrustations. *Pleurocystidia* 65–103×11–17 μm, abundant, fusiform or subfusiform, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH, no encrustations. *Pileipellis* (*Squamosus*) a trichoderm composed of yellowish to yellowish brown in KOH, 4–12 μm wide, thin-walled hyphae; terminal cells 40–77×4–10 μm, narrowly clavate or subcylindrical, with obtuse apex. *Pileal trama* made up of hyphae 5–22 μm in diameter, thin-walled, colorless to yellowish in KOH. *Stipitipellis* a trichoderm-like structure composed of thin- to slightly thick-walled (up to 1 μm) hyphae; terminal cells 26–43×6–10 μm, clavate. *Stipe trama* composed of 3–24 μm wide, cylindrical, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH, parallel hyphae. *Clamp connections* absent in all tissues.

HABITAT: Solitary on the ground in forests of *Lithocarpus* spp.

KNOWN DISTRIBUTION: Southwestern China.

MATERIALS EXAMINED: *CHINA*. *Yunnan Province*: Jingdong County, Ailaoshan Mountain, alt. 2380 m, 15 July 2008, L.P. Tang 328 (HKAS 54559, *holotype*); same location, alt. 2400 m, 14 July 2008, L.P. Tang 311 (HKAS 54542). *Tibet*: Motuo County, 13 November 1982, Y.G. Su 1212 (HKAS 16020, as "*P. sulphureus*" in Zang et al. 1996).

COMMENTS: *Phylloporus rubrosquamosus* is well characterized by its pileus covered with brownish red squamules composed of uninflated hyphae, cyanescent lamellae, non-staining context, and a yellowish brown to brownish red stipe with a whitish basal mycelium.

Phylloporus brunneiceps, *P. coccineus* Corner, *P. flavidulus* Corner, *P. incarnatus* Corner, *P. luxiensis*, *P. ochraceobrunneus* Corner, *P. orientalis* and *P. phaeosporus* Corner, all originally described from tropical Asia, share the narrow pileipellis hyphae with *P. rubrosquamosus*.

However, *P. brunneiceps* has a brown to dark brown pileus, a stipe without reddish tinge, and a yellow basal mycelium. *Phylloporus coccineus* has orange-red basidiomata, a context turning bluish green when injured, and smaller basidiospores [7.5–9(–10)×6.5–7.5(–8) μm] (Corner 1970). *Phylloporus flavidulus* has pale yellowish basidiomata, narrower cystidia and wider basidiospores (9–11×4.7–5.7 μm) (Corner 1970). *Phylloporus incarnatus* has a pale pink pileus, a pale yellowish stipe and relatively shorter basidiospores [9–11(–12)×4.3–5.3 μm] (Corner 1970). *Phylloporus luxiensis* has a brown, cinnamon-brown to grayish brown pileus, non-staining lamellae, and a yellow basal mycelium (Zang and Zeng 1978; Zeng et al. 2011). *Phylloporus ochraceobrunneus* has non-staining lamellae, longer basidiospores (11–15×4–4.7 μm), and cheilocystidia with narrowly filiform appendage (Corner 1970). *Phylloporus orientalis* has large-sized basidiomata, a cyanescent context, and longer basidiospores [13–16.5×5–5.5(–6) μm] (Corner 1970). *Phylloporus phaeosporus* has a pale pinkish tan pileus, a pale yellow to greenish stipe, and somewhat longer basidiospores (11–14×4.5–5.5 μm) (Corner 1970).

In China, *P. rubrosquamosus* was previously misidentified as *P. sulphureus* (Zang et al. 1996). For the diagnostic morphological characters of the latter species, see the discussion under *P. imbricatus* (above).

In the phylogenetic analyses, *P. rubrosquamosus* is allied with *P. bellus*, *P. centromericanus*, *P. maculatus* and *P. rubrosquamosus* (Clade IV of Fig. 1). The differences of the five taxa in morphology have been discussed under *P. bellus* (above). Phylogenetic relationships to other taxa including *P. coccineus*, *P. flavidulus*, *P. incarnatus*, *P. ochraceobrunneus*, *P. phaeosporus* and *P. sulphureus* are unknown.

9. *Phylloporus rufescens* Corner, Nova Hedwigia 20 (3–4): 814, 1970. (Figs. 2l–m, 3i and 12)

Basidiomata medium- to large-sized. *Pileus* 7–13 cm in diameter, convex, then applanate, finally center slightly depressed; surface dry, densely tomentose, pale brown to reddish-brown; margin decurved when young, then recurved; context 2.9–3.2 cm in thickness in the center of pileus, dirty white, changing blue quickly, then turning red and finally black when injured. *Hymenophore* lamellate,

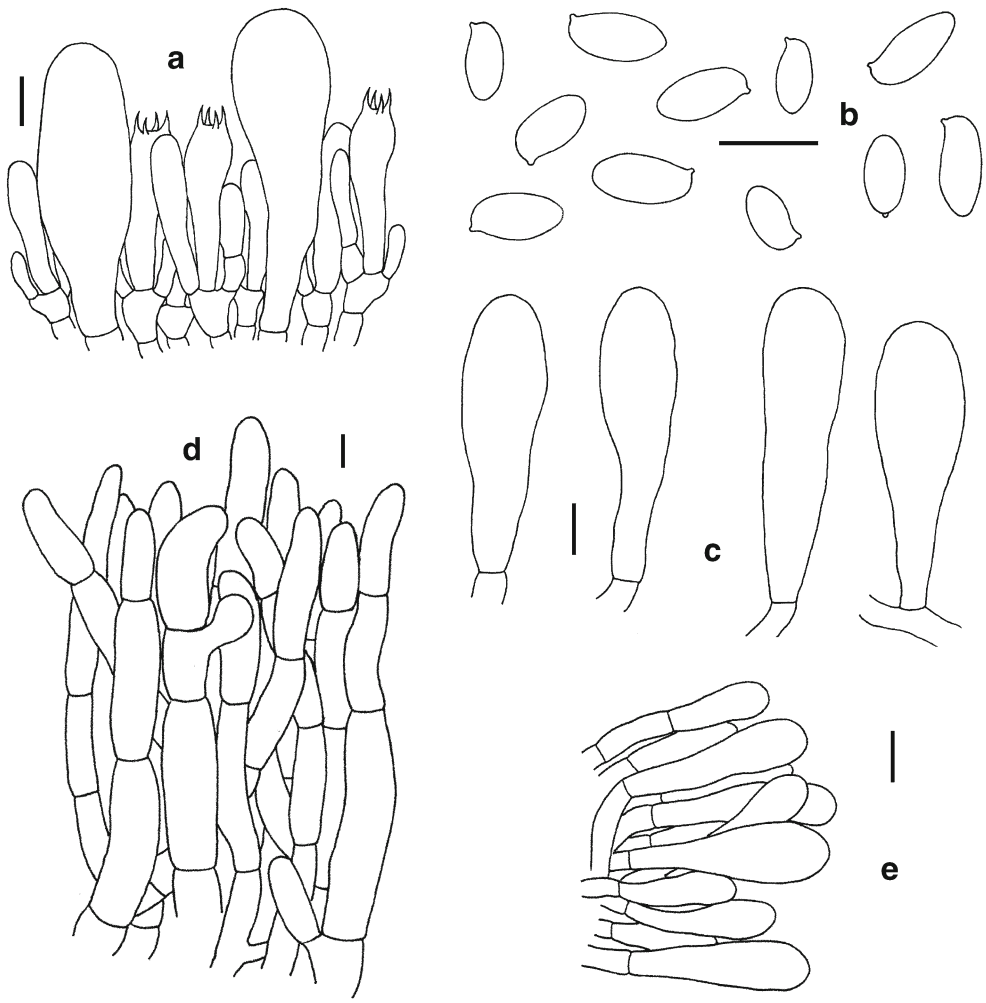

Fig. 12 Microscopic features of *P. rufescens* (HKAS 59722) **a.** Basidia and pleurocystidia; **b.** Basidiospores; **c.** Cheilocystidia; **d.** Pileipellis; **e.** Stipitipellis. (Bars=10 μm.)

decurrent. *Lamellae* up to 1 cm in height, crowded, commonly anastomosing, more or less reticulate at the base, yellow, changing blue quickly when injured; lamellulae common, attenuate, concolor with lamellae. *Stipe* 5–7×1–3 cm, central, subcylindric, slightly attenuate downwards, solid, firm; surface dry, densely tomentose, pale brown to reddish brown; context dirty white, changing blue quickly, then turning red and finally black when injured; annulus absent. *Basal mycelium* whitish. *Taste and odor* not distinctive.

Basidia 30–40×7–9 μm, clavate, thin-walled, 4-spored, colorless to yellowish in KOH; sterigmata 4–5 μm in length. *Basidiospores* [40/2/2] 7–10(–11)×4–5 μm, Q=(1.56–)1.78–2.50, Q_m=2.04±0.24, subfusiform to ellipsoid, slightly thick-walled (< 1 μm thick), olive brown to yellowish brown in KOH, smooth under the light microscope, but with bacillate ornamentation under SEM, dextrinoid. *Hymenophoral trama* slightly bilateral, with similar longitudinal hyphae densely arranged; these hyphae 5–20 μm wide, thin-walled, colorless to yellowish in KOH. *Cheilocystidia* 32–87×11–17 μm, abundant, subfusiform, subclavate or clavate, thin- to slightly thick-walled (up to 1 μm), yellowish brown in KOH, no encrustations. *Pleurocystidia* abundant, similar to cheilocystidia in size, form and color. *Pileipellis* a trichoderm composed of compact, occasionally branched hyphae, more or less vertically arranged when young, then interwoven; these 4–16 μm in diameter, thin-walled, yellowish to yellowish brown in KOH, sometimes with yellowish brown granular encrustations; terminal cells 28–70×7–15 μm, narrowly clavate or subcylindrical, with obtuse apex. *Pileal trama* made up of hyphae 5–13 μm in diameter, thin-walled, colorless to yellowish in KOH. *Stipitipellis* a trichoderm-like structure composed of thin- to slightly thick-walled (up to 1 μm) hyphae; terminal cells 20–40×8–12 μm, clavate or subfusiform. *Stipe trama* composed of 5–15 μm wide, cylindrical, thin- to slightly thick-walled (up to 0.5 μm), colorless to yellowish in KOH, parallel hyphae. *Clamp connections* absent in all tissues.

HABITAT: Solitary or gregarious on the ground in forests of *Lithocarpus* spp.

KNOWN DISTRIBUTION: Singapore (Corner 1970) and southern China (new record to China).

MATERIALS EXAMINED: *CHINA*. *Hainan Province*: Wangning County, Tongtieling Mountain, alt. 258 m, 29 April 2009, N.K. Zeng 67 (HKAS 59722); same location, alt. 267 m, 30 April 2009, N.K. Zeng 79 (HKAS 59723).

COMMENTS: *Phylloporus rufescens* is well characterized by its large-sized basidiomata, pale brown to reddish brown pileus, crowded lamellae, whitish basal mycelium, relatively shorter basidiospores, and blue-red-black color change of context. The Chinese specimens match well with the protologue of *P. rufescens*, except that the cystidia were described as "colorless" by Corner (1970) whereas those of Chinese collections are yellowish brown in KOH.

Phylloporus rufescens looks like *P. rhodoxanthus*, but the latter has non-staining lamellae and context, relatively longer basidiospores, and a yellow basal mycelium (Neves and Halling 2010). *Phylloporus bogoriensis*, *P. brunneolus* Corner and *P. stenosporus* Corner, all described from SE Asia, also possess cyanescent lamellae and rufescent context. However, *P. bogoriensis* has a red-black color change in the context, and slightly longer basidiospores [9–11.5(–12.5)×4–4.7(–5) μm] (Corner 1970). *Phylloporus brunneolus* has small-sized basidiomata, a red color change of context, and somewhat longer basidiospores (10–12×4.5–5 μm) (Corner 1970). *Phylloporus stenosporus* has small-sized basidiomata, a red color change of context, and narrow basidiospores [9.5–11.5(–12.5)×3.7–4.2 μm] (Corner 1974).

Phylogenetically, *P. rufescens* is allied with *P. bogoriensis* (Clade IX of Fig. 1). Its phylogenetic relationships to *P. brunneolus* and *P. stenosporus* are unknown.

10. *Phylloporus yunnanensis* N.K. Zeng, Zhu L. Yang & L.P. Tang, **sp. nov.** (Figs. 2n–o, 3j and 13)

MYCOBANK: MB 800152

ETYMOLOGY: refering to Yunnan, holotype locality.

Pileus center usually depressed; surface densely tomentose, then subsquamulose, finally squamulose, yellowish brown to reddish brown. Hymenophore yellow, changing blue when injured. Stipe central, subcylindric; surface tomentose, yellowish brown to reddish brown. Basal mycelium yellowish. Context cream-colored to yellowish, unchanging in color when injured. Basidiospores (9–)10–12×(3.5–)4–4.5(–5) μm, subfusiform to ellipsoid, surface smooth under light microscopy but with bacillate ornamentation under SEM. Pleuro- and cheilocystidia present. Pileipellis a trichoderm composed of 6–23 μm wide hyphae. Clamp connections absent.

Basidiomata small to medium-sized. *Pileus* 4–6.5 cm in diameter, center usually depressed; surface dry, densely tomentose, then subsquamulose, finally squamulose, yellowish brown (4A5) to reddish brown (6B7); margin inrolled; context cream-colored to yellowish, unchanging in color when injured. *Hymenophore* lamellate, decurrent. *Lamellae* subdistant, occasionally anastomosing, yellow (2A7), changing blue when injured, then back to yellow slowly; lamellulae common, attenuate, concolor with lamellae. *Stipe* 3–7×0.4–0.7 cm, central, subcylindric, solid; surface dry, tomentose, yellowish brown (4A5) to reddish brown (6B7); context cream-colored to yellowish, unchanging in color when injured; annulus absent. *Basal mycelium* yellowish.

Basidia 31–42×8–9 μm, clavate, thin-walled, 4-spored, colorless to yellowish in KOH; sterigmata 5–6 μm in length. *Basidiospores* [400/20/17] (9–)10–12×(3.5–) 4–4.5(–5) μm, Q=(2.38–)2.44–3.00, Q_m=2.66±0.19, subfusiform to ellipsoid, slightly thick-walled (< 1 μm thick), olive brown to yellowish brown in KOH, smooth under the light

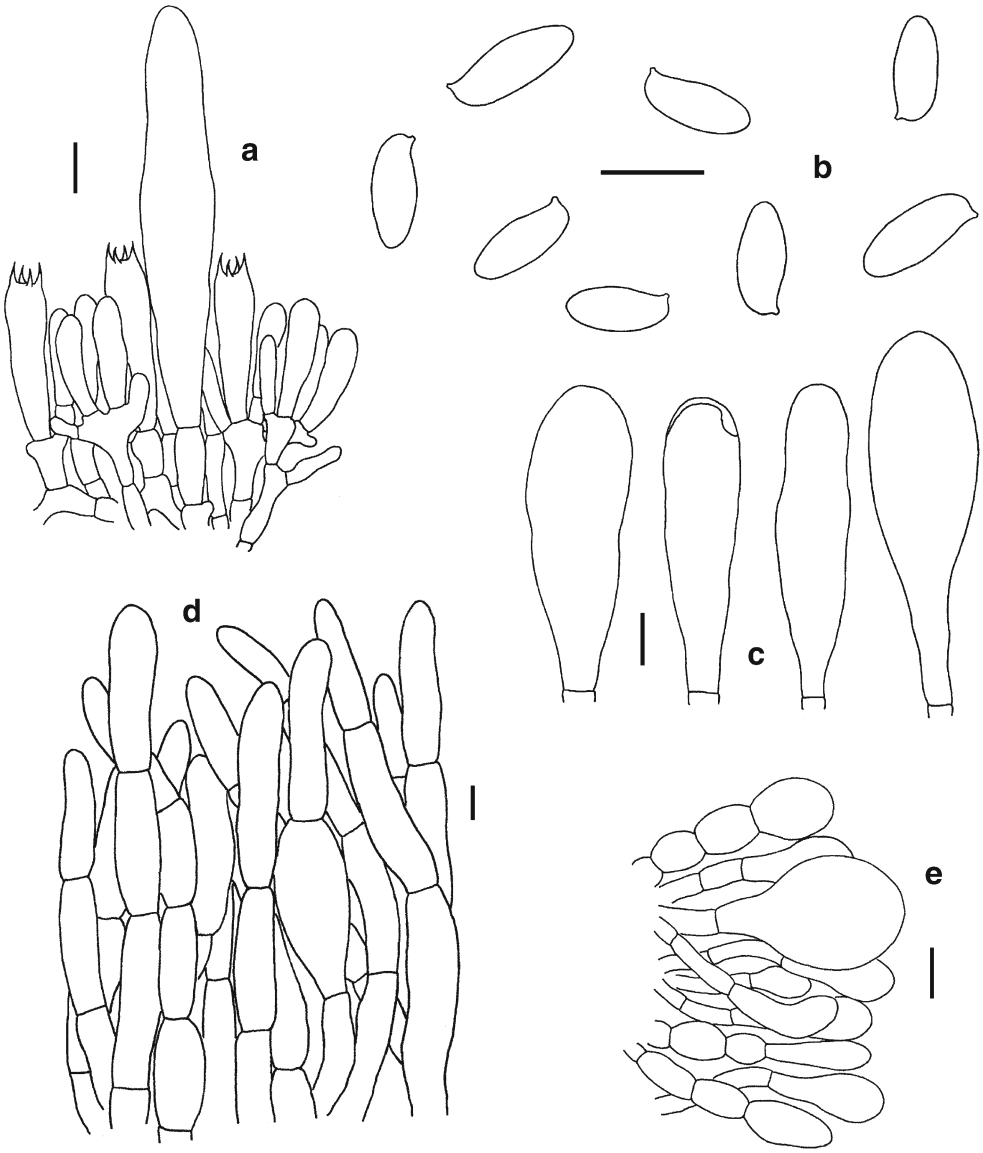

Fig. 13 Microscopic features of *P. yunnanensis* (HKAS 56999, holotype) **a.** Basidia and pleurocystidia; **b.** Basidiospores; **c.** Cheilocystidia; **d.** Pileipellis; **e.** Stipitipellis. (Bars=10 μm.)

microscope, but with bacillate ornamentation under SEM, dextrinoid. *Hymenophoral trama* slightly bilateral, with similar longitudinal hyphae densely arranged; these hyphae 4–15 μm wide, thin-walled, colorless to yellowish in KOH. *Cheilocystidia* 52–76×14–23 μm, subfusiform or subclavate, sometimes strongly thick-walled (up to 8 μm) at the top, colorless, yellowish to yellowish brown in KOH, no encrustations. *Pleurocystidia* 77–107×12–21 μm, abundant, subfusiform, fusiform or subclavate, thin- to slightly thick-walled (up to 1 μm), colorless, yellowish to yellowish brown in KOH, no encrustations. *Pileipellis* a trichoderm composed of colorless, yellowish to yellowish brown in KOH, 6–23 μm wide, thin- to slightly thick-walled (up to 1 μm) hyphae; terminal cells 35–64×7–15 μm, narrowly clavate or subcylindrical, with obtuse apex. *Pileal trama* made up of hyphae 6–18 μm in diameter, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH. *Stipitipellis* a trichoderm-like structure composed of thin- to slightly thick-walled (up to 1 μm) hyphae; terminal cells 14–43×8–27 μm, clavate or occasionally subfusiform. *Stipe trama* composed of 5–20 μm wide, cylindrical, thin- to slightly thick-walled (up to 1 μm), colorless to yellowish in KOH, parallel hyphae. *Clamp connections* absent in all tissues.

HABITAT: Solitary on the ground in forests of *Lithocarpus* spp.

KNOWN DISTRIBUTION: Southwestern China.

MATERIALS EXAMINED: *CHINA*. *Yunnan Province*: Kunming City, near Qiongzhu Temple, 8 August, 2007, Z.L. Yang 4908 (HKAS 52225); Jingdong County, Ailaoshan Nature Reserve, alt. 1450 m, 14 July 2007, Y.C. Li 842 (HKAS 52527); Yingjiang County, Xima Town, alt. 1940 m, 18 July 2009, L.P. Tang 839 (HKAS 56796); Yongping County, alt. 2087 m, 31 July 2009, L.P. Tang 1042 (HKAS 56999,

holotype); Roadside from Tengchong County to Longling County, alt. 2012 m, 19 July 2009, L.P. Tang 845 (HKAS 56802); Yongping county, Longmen Town, Lizishu Village, alt 2344 m, 1 August 2009, L.P. Tang 1067 (HKAS 57024); Changning County, alt. 2016 m, 25 July 2009, Q. Cai 6 (HKAS 58673); Nanhua County, Maan Mountain, 3 August 2009, Q. Zhao 468 (HKAS 58931); Yingjiang County, Xima Town, Tongbiguan Nature Reserve, alt. 2171 m, 17 July 2009, Y.C. Li 1665 (HKAS 59412); Roadside fromYongping County to Baoshan City, 30 July 2009, Y.C. Li 1892 (HKAS 59640); Yongping County, Longmeng Town, Lizishu Village, alt. 2344 m, 1 August 2009, Y.C. Li 1933 (HKAS 59681); Yingjiang County, Xima Town, Tongbiguan Nature Reserve, alt. 2171 m, 17 July 2009, Q. Zhao 157 (HKAS 59729); Changning County, alt. 2016 m, 25 July 2009, Q. Zhao 294 (HKAS 59731); Yongping County, Longmen Town, Lizishu Village, alt. 2344 m, 1 August 2009, Q. Zhao 442 (HKAS 59733); Jingdong County, Ailaoshan Nature Reserve, alt. 2400 m, 14 July, 2008, L.P. Tang 308-2 (HKAS 59734); Dulong River, Long Yuan, alt. 2200 m, 30 August 1982, D.C. Zhang 563 (HKAS 10800, as *P. rhodoxanthus*" in Zang et al. 1996; Yuan and Sun 2007). *Sichuan Province*: Weiyuan County, Xinchang Town, alt. 500 m, 12 July 1985, M.S. Yuan 1033 (HKAS 15861, as "*P. rhodoxanthus*" in Zang et al. 1996; Yuan and Sun 2007).

COMMENTS: *Phylloporus yunnanensis* is a common species in the south of Yunnan Province and is well characterized by its yellowish brown to reddish brown pileus, cyanescent lamellae but non-staining context, yellowish brown to reddish brown stipe with a yellowish basal mycelium, and association with subtropical and tropical trees.

Phylloporus yunnanensis is very similar to *P. bellus* and *P. imbricatus*, and was misidentified as *P. rhodoxanthus* (Zang et al. 1996; Yuan and Sun 2007). For comparison of the four taxa, see discussion under *P. bellus* and *P. imbricatus* (above).

Discussion

Correlation of morphological and phylogenetic species recognition

Morphological species recognition and phylogenetical species delimitation in *Phylloporus* correlate quite well. All Chinese species delimited by multilocus DNA sequences showed their own unique morphological characters or unique combination of features. In the absence of the ability to test the monophyly of lineages represented by single collections (lineages 3, 5, 7, 8, 10, 15, 16, 17, 19, and 20 of Fig. 1), these were interpreted as distinct phylogenetical species because they were morphologically and molecular phylogenetically significantly divergent from and, in most cases, not sympatric with their putative sisters.

In agreement with the previous hypotheses (Neves and Halling 2010; Neves et al. 2012), the pigmentation in the basal mycelium is an important character, and the taxa with yellowish basal mycelium grouped together in clades I, II and VIII (Fig. 1). A careful observation of the color of the basal mycelium in the field is therefore a prerequisite species identification. In addition, the pigmentation in the context, and the staining of the hymenophore and context are also reliable features for discriminating species (Corner 1970; Neves and Halling 2010; Neves et al. 2012).

The color of pileus and stipe supports the delimitation of at least some phylogenetic species in our studies. However, infraspecific variability can be present, or the same pileus and stipe color can be observed in several species. For example, yellowish brown, brown, dark brown and brownish red can be observed in different samples of *P. imbricatus*. *Phylloporus brunneiceps* and *P. maculatus* are both characterized by their brown to dark brown pileus and yellow to yellowish brown stipe. An olivaceous tinged pileus and stipe is characteristic for both *P. parvisporus* and its sister *P. infuscatus*. Yellowish brown to reddish brown colors are observed in *P. bellus*, *P. pachycystidiatus* and *P. yunnanensis*. Therefore, the color of the pileus and the stipe should not be used as a diagnostic character without correlation to other features.

In contrast to macro-morphology, only a limited number of micro-morphological features can be used to discriminate *Phylloporus* species. The morphology of the stipitipellis is, for example, quite variable, and different collections of the same species may have hyphae forming the stipitipellis with different forms and sizes. Whereas, the basidia, hymenophoral trama, pileal trama and stipe trama seem to be rather constant among the different species. However, the form, size, pigmentation and encrustations of cystidia can be used reliably to identify species as done previously (Corner 1970; Neves and Halling 2010; Neves et al. 2012). In addition, we found that the thickness of the cystidial wall is an important delimitation character: although most *Phylloporus* species have thin- to slightly thick-walled ($\leq$ 1 μm) cystidia, some with moderately thick walls (1–2 μm), and others with strongly thick-walled (2–4 μm) cystidia. The configuration of the pileipellis is also an important diagnostic feature: some species have inflated hyphae, while others have uninflated ones. The form, size and ornamentation of basidiospores can be reliable characters for a few unique species. For example, most species possess basidiospores with bacillate ornamentation (Šutara 2008), while a few species have either smooth or rugulose basidiospores (Neves and Halling 2010; Neves et al. 2012).

In regard to ecological preference, most species are associated with *Fagaceae* (Neves and Halling 2010; Neves et al.

2012), whereas *P. imbricatus* and *P. arenicola* are associated with *Pinaceae*. Some species, like *P. foliiporus*, can be associated with both *Pinaceae* and *Fagaceae* (Neves and Halling 2010). Thus, the ecological characters can not be used alone to recognize taxa.

Species diversity of *Phylloporus* in China

The genus *Phylloporus*, which is very diverse in species in tropical regions of the world (Corner 1970, 1974; Singer and Gómez 1984; Halling 1989; Singer et al. 1983, 1990; Montoya and Bandala 1991; Halling et al. 1999; Ortiz-Santana et al. 2007; Watling 2008; Neves and Halling 2010; Neves et al. 2010, 2012), is also rich in China, especially in its southern areas. Our data demonstrated that there are at least 21 phylogenetic species among the studied collections (Fig. 1), and many of them have not been previously distinguished. In the present study, 4 of the phylogenetic species (lineages 4, 9, 11, and 21 of Fig. 1) corresponded with the previous morphology-based species: *P. luxiensis*, *P. parvisporus*, *P. bellus*, and *P. rufescens*, respectively, and 7 new taxa proposed in this study (lineages 1, 2, 6, 12, 13, 14, and 18 of Fig. 1) could be characterized by morphological features. The remaining lineages (3, 5, 7, 8, 10, 15, 16, 17, 19, and 20 of Fig. 1) also showed morphological and/or ecological differences, but no formal descriptions are offered because only limited collections are available.

Phylloporus pachycystidiatus and *P. centroamericanus*, both having the synapomorphy of thick-walled cystida, are sisters (Clade IV of Fig. 1). However, *P. rubiginosus*, a species also with thick-walled cystidia was grouped together with *P. foliiporus*, a species with thin-walled cystidia (Clade VIII of Fig. 1), suggesting that "thick-walled cystidia" have originated more than once.

Phylloporus yunnanensis and *P. imbricatus* are sister taxa based on our three-locus dataset (Clade I of Fig. 1). The 2 taxa share quite similar macro- and micro-features. Field observations showed *P. yunnanensis* is distributed in the south of Yunnan Province between 1400 and 2400 m altitude, and is associated with subtropical and tropical broad-leaved trees, while *P. imbricatus* grows at 3000–4100 m altitude in the Hengduan Mountains, and is associated with subalpine to alpine coniferous trees. The geographical distribution and phylogenetic relationships of the 2 taxa suggest they may have diverged recently from each other, probably in correlation with the uplifts of the Himalaya-Hengduan Mountains (Yang 2005). Such examples might be found in other genera, such as *Boletus* and *Zangia* (Li et al. 2011; Feng et al. 2012).

To date, 13 taxa, including the 10 species described in this work, and 3 other taxa described in detail in the literature, can be summarized in the following key.

Key to the taxa of *Phylloporus* known from China

1. Basal mycelium yellowish…2
1. Basal mycelium whitish…5
2. Pileus brown, without reddish tinge…3
2. Pileus reddish to reddish brown…4
3. Hymenophore unchanging in color when injured…*P. luxiensis*
3. Hymenophore turning blue when injured…*P. brunneiceps*
4. Pileus 4.5–11 cm, stipe 0.3–1.5 cm diam., associated with subalpine to alpine tree hosts…*P. imbricatus*
4. Pileus 4–6.5 cm, stipe 0.4–0.7 cm diam., associated with subtropical or tropical tree hosts…*P. yunnanensis*
5. Cystidia thick-walled (≥ 2 μm)…*P. pachycystidiatus*
5. Cystidia thin-walled (≤ 1 μm)…6
6. Context dark-colored, fuliginous or reddish…7
6. Context light-colored, whitish, cream-colored or yellowish…9
7. Context pale brownish fuliginous or pale fuscous…*P. parvisporus*
7. Context reddish or reddish brown…8
8. Basidiospores 13–16×5–5.5 μm…*P. orientalis* var. *orientalis*
8. Basidiospores 9–13×4.5–5 μm…*P. orientalis* var. *brevisporus*
9. Context turning red when injured…*P. rufescens*
9. Context unchanging in color…10
10. Pileus surface with dark-colored spots…*P. maculatus*
10. Pileus surface without spots…11
11. Uninflated hyphae in the pileipellis…*P. rubrosquamosus*
11. Inflated hyphae in the pileipellis…12
12. Pileus somewhat reddish, pileipellis terminal cells with acute apex…*P. rubeolus*
12. Pileus yellowish brown to reddish brown, pileipellis terminal cells with obtuse apex…*P. bellus*

Phylogenetic relationships and geographic divergence of *Phylloporus*

Recent phylogenetic studies based on a ribosomal two-locus dataset have uncovered some useful information in regard to the phylogeny and geography of *Phylloporus* (Neves et al. 2012). Our molecular data based on three-locus DNA sequences with a large number of additional collections from East Asia provided new insights. In our molecular analyses, 9 major clades (I–IX) are inferred for *Phylloporus*, with usually high statistical support, although there is little or no statistical support in the deeper nodes of the phylogeny. It is clear that there are several clades having taxa from both sides of the Pacific, and species pairs or allied sister

species from East/Southeast Asia and North/Central America are obviously inferred from this dataset (Fig. 1). For example, in clade IV vicariously paired or closely related species (*P. pachycystidiatus*-*P. centroamericanus*) between East Asia and Central America were uncovered. In the five closely related species within clade V, *P.* sp. 6 and sp. 7 occur in East Asia, while *P. leucomycelinus, P. caballeroi* and *P. alborufus* fruit in North and Central America. In the past, *P. bellus*, *P. foliiporus* and *P. rodoxanthus* have been identified as occurring in both in East Asia and North/Central America (Teng 1963; Singer and Gómez 1984; Dai and Li 1994; Neves and Halling 2010). Our study did not identify disjunct populations of the same purported taxon in the two regions (Fig. 1). Similar scenarios have been documented for many other fungi (Redhead 1989; Halling 2001; Mueller et al. 2001; Yang 2005; Petersen and Hughes 2007; Li et al. 2009; Zhang et al. 2010; Feng et al. 2012).

The affinities of *Phylloporus* species between Tropical China and Southeast Asia (Indonesia-Malaya) are evident (Fig. 1), both regions share several common taxa, i.e., *P. bellus*, *P. orientalis* var. *brevisporus*, *P. orientalis* var. *orientalis*, *P. parvisporus* and *P. rufescens*.

Biogeographic connections between East Asia and Europe have been discussed in other fungi such as *Amanita*, *Boletus* and *Chroogomphus* (Zhang et al. 2004; Li et al. 2009; Zhang et al. 2010; Feng et al. 2012). So far, we have not found disjunct populations of the same putative species of *Phylloporus* between the two regions. However, *P. pelletieri*, Chinese *P.* sp. 4 (HKAS 74682, and 74683) and Thai *P.* sp. (MAN105) grouped together with high statistical support (Clade II of Fig. 1), so there would appear to be sister species in this clade also.

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