

Phylogeny and taxonomy of *Spongipellis* (Meripilaceae, Basidiomycota) and its micromorphological similar genera in Cerrenaceae

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Abstract

Phylogenetic and morphological analyses on *Spongipellis* and its micromorphological similar genera, *Irpiciporus*, *Pseudospongipellis* and *Radulodon*, were carried out. Phylogenies on *Spongipellis* are reconstructed with multiple loci DNA sequences including the internal transcribed spacer regions (ITS), the large subunit (nLSU) and the small subunit (nSSU) of nuclear ribosomal RNA gene and the translation elongation factor 1- α gene (*TEF1*). The results demonstrate the polyphyly of *Spongipellis*, including two genera belong to different families, *Pseudospongipellis* gen. nov. is established including three new combinations. Three new species, *Irpiciporus sinuosus*, *Radulodon yunnanensis* and *Spongipellis quercicola* spp. nov., are described and illustrated.

Introduction

The genus *Spongipellis* Pat. (Polyporales, Basidiomycota), typified by *S. spumeus* (Sowerby) Pat., was established by Patouillard (1887). Traditionally it is characterized by annual and pileate basidiomata, broadly attached, semicircular pilei, usually tomentose pileal surface, the heterogeneous context, a monomitic hyphal system, generative hyphae with clamp connections, hyaline, thick-walled cyanophilous basidiospores, and a white rot ecology (Murrill 1905, Torti c 1974, Pi tek et al. 2004, Tom ovsk y 2012, 2016; Westphalen et al. 2016, Szczepkowski and Kowalczyk 2021). *Loweomyces* Kotl. & Pouzar was treated as a subgenus of *Spongipellis* previously, until J lich (1982) based on shorter basidia and tubes than *Spongipellis* in type species *L. fractipes* (Berk. & Curt) J lich, so that considered it as a separate genus. In addition, Miettinen et al. (2012) and Westphalen et al. (2016) also proved *Loweomyces* belongs to Steccherinaceae Parmasto based on molecular evidence, but did not mention the systematic position of *Spongipellis*. Spirin (2001) and Zmitrovich et al. (2006) combined some species of *Spongipellis* viz. *S. delectans* (Peck) Murrill, *S. pachyodon* (Pers.) Kotl. & Pouzar, *S. spumeus* and *S. unicolor* (Fr.) Murrill into *Sarcodontia* Schulzer just based on similar micromorphological characters of a monomitic hyphal system with clamp connections on generative hyphae, ellipsoid to subglobose, thick-walled basidiospores. The above conclusions lack molecular evidence. However, Tom ovsk y (2016) and Nakasone et al. (2021) proved these species do not correspond the phylogeny of *Sarcodontia*.

The systematic position of *Spongipellis pachyodon* seems to have always been inconclusive. It was combined as *Irpiciporus pachyodon* (Pers.) Kotl. & Pouzar (Kotl ba and Pouzar 1957) and *Sarcodontia pachyodon* (Pers.) Spirin (Spirin 2001) based on morphology. However, Nakasone et al. (2021) excluded it from *Sarcodontia*.

Morphologically, *Climacocystis* Kotl. & Pouzar resembles *Spongipellis* by sharing tomentose upper surface, a monomitic hyphal system, generative hyphae with clamp connections and hyaline basidiospores, but the former has cystidia and thin-walled basidiospores (Pi tek et al. 2004). In addition, *Climacocystis* pertains to independent clade in Polyporales (Binder et al. 2013, Justo et al. 2017).

So far, the phylogenetic relationships of species in *Spongipellis* and its micromorphological similar genera are not well analyzed. Based on more samples from Asia phylogenies based on a 2-gene dataset (ITS + nLSU) and a 4-gene dataset (ITS + nLSU + nSSU + *TEF1*) on *Spongipellis* and its micromorphological similar genera are carried out, three new species, *Irpiciporus sinuosus*, *Radulodon yunnanensis* and *Spongipellis quercicola*, are described and illustrated. In addition, a new genus *Pseudospongipellis* belonging to Cerrenaceae Miettinen is established, and it is phylogenetically distant from *Spongipellis* belonging to Meripilaceae J lich, then three new combinations are proposed.

Materials And Methods

Morphological studies

The studied specimens are deposited in the herbaria of the Institute of Microbiology, Beijing Forestry University (BJFC) and the Institute of Applied Ecology, Chinese Academy of Sciences (IFP). Morphological descriptions are based on field notes and herbarium specimens. The microscopic analysis follows Miettinen et al. (2018). Sections were studied at a magnification of up to 1000 \times using a Nikon Eclipse 80i microscope and phase contrast illumination. Microscopic features and measurements were made from slide preparations stained with Cotton Blue and Melzer's reagent. Spores were measured from sections cut from the tubes or spines. To represent variation in the size of spores, 5% of measurements were excluded from each end of the range and are given in parentheses. In the description: KOH = 5% potassium hydroxide, IKI = Melzer's reagent, IKI- = neither amyloid nor dextrinoid, CB = Cotton Blue, CB+ = cyanophilous in Cotton Blue, CB- = acyanophilous in Cotton Blue, L = arithmetic average of spore length, W = arithmetic average of spore width, Q = L/W ratios, and n = number of basidiospores/measured from given number of specimens. Color terms are from Anonymous (1969) and Petersen (1996).

DNA extraction, amplification and sequencing

A CTAB rapid plant genome extraction kit-DN14 (Aidlab Biotechnologies Co., Ltd,

Beijing) was used to obtain DNA from dried specimens, and to perform the polymerase chain reaction (PCR) according to the manufacturer's instructions with some modifications (Shen et al. 2019; Sun et al. 2020). Two DNA gene fragments – internal transcribed spacer (ITS) and large subunit nuclear ribosomal RNA gene (nLSU) – were amplified using the primer pairs ITS5/ITS4 and LR0R/LR7 (White et al. 1990; Hopple and Vilgalys 1999). The nSSU region was amplified with primer pairs NS1 and NS4 (White et al. 1990). Part of *TEF1* was amplified with primer pairs EF1-983F and EF1-1567R (Rehner & Buckley 2005). The PCR procedure for ITS and *TEF1* was as follows: initial denaturation at 95°C for 3 min, followed by 34 cycles at 94°C for 40 s, 54°C for ITS, 54°C for TEF for 45 s and 72°C for 1 min, and a final extension of 72°C for 10 min. The PCR procedure for nLSU and nSSU was as follows: initial denaturation at 94°C for 1 min, followed by 34 cycles of denaturation at 94°C for 30 s, annealing at 50°C for nLSU and 52°C for nSSU for 1 min and extension at 72°C for 1.5 min, and a final extension at 72°C for 10 min. The PCR products were purified and sequenced at the Beijing Genomics Institute (BGI), China, with the same primers. DNA sequencing was performed at Beijing Genomics Institute and the newly-generated sequences were deposited in GenBank (Sayers et al. 2021). All sequences analysed in this study are listed in Table 1. Sequences generated from this study were aligned with additional sequences downloaded from GenBank using BioEdit (Hall 1999) and ClustalX (Thompson et al. 1997). The final ITS and nLSU datasets were subsequently aligned using MAFFT v.7 under the E-INS-i strategy with no cost for opening gaps and equal cost for transformations (command line: mafft –genafpair –maxiterate 1,000) (Kato and Standley 2013) and visualized in BioEdit (Hall 1999).

Table 1
Taxa information and GenBank accession numbers of the sequences used in this study

Species	Sample	Location	GenBank accession No.			
			ITS	nLSU	nSSU	TEF1
<i>Antrodiella trivialis</i>	MCW 497/14	Brazil	MH475304	MH475304	–	–
<i>A. trivialis</i>	MCW 369/12	Brazil	MH475302	MH475302	–	–
<i>Butyrea japonica</i>	MN 1065	Japan	JN710556	JN710556	–	–
<i>B. luteoalba</i>	FP-105786-Sp	USA	KP135320	KP135226	–	–
<i>Cerrena albocinnamomea</i>	Dai 12892	China	KC485522	KC485539	–	–
<i>C. albocinnamomea</i>	Dai 12955	China	KC485521	KC485538	–	–
<i>C. aurantiopora</i>	NIBRFG0000102423	Korea	FJ821532	FJ821521	–	–
<i>C. aurantiopora</i>	SNU-m 03110102	Korea	FJ821531	FJ821520	–	–
<i>C. consors</i>	F20080702KCM29	Korea	FJ821527	FJ821516	–	–
<i>C. consors</i>	F20080208LYW10	Korea	FJ821528	FJ821517	–	–
<i>C. unicolor</i>	KHL-GB	Sweden	JQ031127	JQ031127	–	–
<i>C. unicolor</i>	FD 299	USA	KP135304	KP135209	–	–
<i>C. zonata</i>	Dai 7821	China	KC485529	KC485547	–	–
<i>C. zonata</i>	Dai 7359	China	KC485528	KC485546	–	–
<i>Flaviporus minutus</i>	Dai 16222	China	KY131881	KY131938	–	–
<i>F. minutus</i>	Dai 16240	China	KY131883	KY131940	–	–
<i>Hyphoderma litschaueri</i>	FP-101740-Sp	USA	KP135295	KP135219	–	–
<i>H. medioburiense</i>	FD-335	USA	KP135298	KP135220	–	–
<i>H. mutatum</i>	HHB-15479-Sp	USA	KP135296	KP135221	–	–
<i>H. setigerum</i>	FD-312	USA	KP135297	KP135222	–	–
<i>Irpiciporus pachyodon</i>	PRM 846564	Czechia	HQ728293	HQ729003	–	–
<i>I. pachyodon</i>	SP-Lgt	Italy	AY849307	–	–	–
<i>I. sinuosus</i>	PW17-171	Thailand	MK589288	–	–	–
<i>I. sinuosus</i>	Dai 12234	China	KX161649	KX161658	–	OM982699 ^a
<i>I. xuchilensis</i>	Ryvarden 44669	Ecuador	KX161650	KX161659	–	–
<i>Junghuhnia fimbriatella</i>	Miettinen2091	Russia	JN710555	JN710555	–	–
<i>Loweomyces fractipes</i>	X 1250	USA	JN710568	JN710568	–	–
<i>L. fractipes</i>	X 1253	USA	JN710569	JN710569	–	–
<i>L. spissus</i>	MCW 468/13	Brazil	KX378867	KX378867	–	–
<i>L. spissus</i>	MCW 471/13	Brazil	KX378868	KX378868	–	–
<i>L. tomentosus</i>	MCW 366/12	Brazil	KX378870	KX378870	–	–
<i>L. tomentosus</i>	MCW 382/12	Brazil	KX378871	KX378871	–	–
<i>L. wynneae</i>	X 1215	Denmark	JN710604	JN710604	–	–

^a Newly generated sequences in this study.

Bold = new species and combinations.

Species	Sample	Location	GenBank accession No.			
			ITS	nLSU	nSSU	TEF1
<i>Meripilus giganteus</i>	FP-135344-Sp	UK	KP135307	KP135228	—	—
<i>M. sumstinei</i>	Russell 5913	USA	MN906088	—	—	—
<i>Panus fragilis</i>	HHB-11042-Sp	USA	KP135328	KP135233	—	—
<i>P. rudis</i>	DSH-92-139	—	AF287878	AF026569	—	—
<i>Phlebia radiata</i>	AFTOL-484	—	AY854087	AF287885	—	—
<i>Physisporinus eminens</i>	Dai 11400	China	KY131852	KY131909	OM670035	OM810103
<i>P. pouzarii</i>	Dai 21043	Belarus	MT840124	MT840142	—	—
<i>P. pouzarii</i>	Dai 15005	China	KP420014	KP420017	—	—
<i>P. sanguinolentus</i>	Dai 20995	Belarus	MT309483	—	—	—
<i>P. sanguinolentus</i>	Dai 20976	Belarus	MT840118	MT840136	—	—
<i>Pseudolagarobasidium acaciicola</i>	CBS 115543	South Africa	DQ517883	—	—	—
<i>P. acaciicola</i>	CBS 115544	South Africa	DQ517882	—	—	—
<i>P. baiyunshanense</i>	Han 405	China	MT428549	MT428547	—	—
<i>P. baiyunshanense</i>	Han 406	China	MT428550	MT428548	—	—
<i>P. belizense</i>	VPB 197	Brazil	KJ832058	—	—	—
<i>P. belizense</i>	CFMR: DCL04-31	Belize	JQ070173	—	—	—
<i>Pseudospongipellis delectans</i>	OSM F925	Czechia	HQ728296	HQ729006	—	—
<i>P. delectans</i>	BRNM 686401	Czechia	HQ728295	HQ729005	—	—
<i>P. litschaueri</i>	Dai 14361	China	OM971905 ^a	—	—	—
<i>P. litschaueri</i>	Dai 20900	China	OM971906 ^a	OM971891 ^a	OM971928 ^a	—
<i>P. litschaueri</i>	Dai 3041	China	OM971907 ^a	OM971892 ^a	—	—
<i>P. litschaueri</i>	Dai 20266	China	OM971908 ^a	OM971893 ^a	OM971929 ^a	—
<i>P. litschaueri</i>	Dai 13963	China	OM971909 ^a	OM971894 ^a	OM971930 ^a	—
<i>Pseudospongipellis litschaueri</i>	Cui 11913	China	OM971910 ^a	—	—	—
<i>P. litschaueri</i>	Dai 13845	China	OM971911 ^a	OM971895 ^a	OM971931 ^a	OM982700 ^a
<i>P. litschaueri</i>	Dai 14739	China	OM971912 ^a	—	OM971932 ^a	—
<i>P. litschaueri</i>	Dai 3921	China	OM971913 ^a	—	OM971933 ^a	—
<i>P. litschaueri</i>	Yuan 1099	China	OM971914 ^a	OM971896 ^a	OM971934 ^a	—
<i>P. litschaueri</i>	BRNM 712626	Czechia	HQ728305	HQ729014	—	—
<i>P. litschaueri</i>	BRNM 670693	Czechia	HQ728303	HQ729013	—	—
<i>P. unicolor</i>	CFMRcc FP-59199-T	USA	HQ728310	HQ729012	—	—
<i>P. unicolor</i>	CFMRcc FP-71791-T	USA	HQ728313	HQ729011	—	—
<i>Radulodon americanus</i>	CFMR: HHB11240	USA	JQ070174	—	—	—
<i>R. americanus</i>	RLG 6350	USA	JQ070175	—	—	—
<i>R. casearius</i>	HHB-9567-sp	USA	KY948752	KY948871	—	—

^a Newly generated sequences in this study.

Bold = new species and combinations.

Species	Sample	Location	GenBank accession No.			
			ITS	nLSU	nSSU	TEF1
<i>R. casearius</i>	KRT-Iso-26	USA	MN430944	–	–	–
<i>R. erikssonii</i>	CBS 126044	Sweden	MH864059	MH875514	–	–
<i>R. erikssonii</i>	X 3536	Norway	KY415963	KY415963	–	–
<i>R. yunnanensis</i>	He 6183	China	OM971915 ^a	OM971897 ^a	OM971935 ^a	OM982704 ^a
<i>R. yunnanensis</i>	Dai 12204	China	OM971916 ^a	–	OM971936 ^a	OM982705 ^a
<i>R. yunnanensis</i>	Cui 17979	China	OM971917 ^a	OM971898 ^a	OM971937 ^a	OM982706 ^a
<i>Spongipellis quercicola</i>	Cui 10114	China	OM971918 ^a	–	–	–
<i>S. quercicola</i>	Cui 10009	China	OM971919 ^a	OM971899 ^a	OM971938 ^a	OM982701 ^a
<i>S. quercicola</i>	Dai 20899	China	OM971920 ^a	–	OM971939 ^a	OM982702 ^a
<i>S. sibirica</i>	Dai 1723	China	OM971921 ^a	–	–	–
<i>S. spumeus</i>	BRNM 734877	Czechia	HQ728283	HQ729018	–	–
<i>S. spumeus</i>	BRNM 712630	Czechia	HQ728288	HQ729019	–	–
<i>S. spumeus</i>	PRM 846565	Czechia	HQ728284	–	–	–
<i>S. spumeus</i>	MJ 7/08	Czechia	HQ728285	HQ729017	–	–
<i>S. spumeus</i>	Sample 24	–	AJ006671	–	–	–
<i>S. spumeus</i>	Cui 10100	China	OM971922 ^a	–	–	–
<i>S. spumeus</i>	Cui 11912	China	OM971923 ^a	–	–	–
<i>S. spumeus</i>	He 6736	China	OM971924 ^a	OM971900 ^a	–	–
<i>S. spumeus</i>	Dai 7168	China	OM971925 ^a	–	–	–
<i>S. spumeus</i>	Dai 3770	China	OM971926 ^a	–	–	–
<i>S. spumeus</i>	Dai 20901	China	OM971927 ^a	OM971901 ^a	OM971940 ^a	OM982703 ^a
<i>Steccherinum ochraceum</i>	KHL11902	Sweden	JN710590	JN710590	–	–
<i>S. tenue</i>	KHL 12316	USA	JN710598	JN710598	–	–
^a Newly generated sequences in this study.						
Bold = new species and combinations.						

Table 2
The main morphological differences of *Spongipellis* and its micromorphological similar genera

Genera	Basidiomata	Pileal surface	Hymenophore type	Hymenophore color	Hyphal system	Wall of basidiospores	References
<i>Irpiciporus</i>	effused-reflexed to pileate	white, cream to buff yellow; azonate, glabrous, velutinous to tomentose	poroid or hydroid	white, buff yellow to ochraceous	monomitic	thick-walled	Murrill 1905, this study
<i>Loweomyces</i>	resupinate, pileate to stipitate	cream, saffron yellow to ochraceous; finely sulcate and zonate, glabrous, tomentose to hirsute	poroid	white to cream	monomitic to dimitic	thin-walled	Westphalen et al. 2016
<i>Pseudospongipellis</i>	pileate	white, yellow to pale brownish; azonate, glabrous, tomentose or short hispid	poroid	white, buff yellow to ochraceous	monomitic	thick-walled	this study
<i>Radulodon</i>	resupinate to effused-reflexed	light orange to grayish orange; azonate, glabrous	hydroid	pale yellow, grayish orange to yellowish brown	monomitic to dimitic	thin- to slightly thick-walled	Ryvarden 1972, Nakasone 2001, this study
<i>Sarcodontia</i>	resupinate	—	hydroid to aculeate	cream, sulfur yellow to light brown	monomitic to pseudodimitic	thick-walled	Tomšovský 2016, Nakasone et al. 2021
<i>Spongipellis</i>	pileate	white, cream to cinnamon buff; azonate, glabrous, velutinous to tomentose	poroid	white, pale yellow, clay buff to fawn	monomitic	thick-walled	Tomšovský 2012, this study

Phylogenetic analyses

In this study, two combined matrixes were reconstructed for phylogenetic analyses; a 2-gene dataset (ITS + nLSU) and a 4-gene dataset (ITS + nLSU + nSSU + *TEF1*) were used to determine the phylogenetic position of the new species. The sequences alignments and the retrieved topologies were deposited in TreeBase (<http://www.treebase.org>), under accession ID: 29547

(<http://purl.org/phylo/treebase/phylows/study/TB2:S29547?x-access-code=1ecb1ce914be19185b78751eeafd4ade&format=html>).

Sequences of *Phlebia radiata* Fr., obtained from GenBank, were used as the outgroup. The phylogenetic analyses followed the approach of Han et al. (2016) and Zhu et al. (2019). Maximum Likelihood (ML) and Bayesian Inference (BI) analyses were performed based on the two datasets respectively. The best-fit evolutionary model was selected by Hierarchical likelihood ratio tests (hLRT) and Akaike Information Criterion (AIC) in MrModeltest 2.2 (Nylander 2004) after scoring 24 models of evolution in PAUP* version 4.0b10 (Swofford 2002).

Sequences were analysed using ML with RAxML-HPC2 through the CIPRES Science Gateway (www.phylo.org; Miller et al. 2009). Branch support (BT) for ML analysis was determined by 1000 bootstrap replicates. Bayesian phylogenetic inference and Bayesian Posterior Probabilities (BPP) were computed with MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003). Four Markov chains were run for 2,000,000

generations (2-gene dataset and 4-gene dataset) until the split deviation frequency value was less than 0.01, and trees were sampled every 100 generations. The first 25% of the sampled trees were discarded as burn-in and the remaining ones were used to reconstruct a majority rule consensus and calculate Bayesian Posterior Probabilities (BPP) of the clades. All trees were viewed in FigTree v. 1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree/>). Branches that received bootstrap support for ML ($\geq 75\%$ (ML-BS)), and BPP (≥ 0.95 BPP) were considered as significantly supported. In our study, the ML bootstrap (ML) $\geq 50\%$ and BPP (BPP) ≥ 0.90 were presented on topologies from ML analyses, respectively.

Results

Molecular phylogeny

The combined 2-gene dataset (ITS and nLSU) included sequences from 91 samples representing 44 taxa. The dataset had an aligned length of 2,133 characters, of which 1,408 (66%) characters are constant, 88 (4%) are variable and parsimony-uninformative and 637 (30%) are parsimony informative. The phylogenetic reconstruction performed with Maximum Likelihood (ML) and Bayesian Inference (BI) analyses for two combined datasets showed similar topology and few differences in statistical support. The best model-fit applied in the Bayesian analysis was GTR + I + G, Iset nst = 6, rates = invgamma, and prset statefreqpr = dirichlet (1, 1, 1, 1). Bayesian analysis resulted in a nearly congruent topology with an average standard deviation of split frequencies = 0.003568 to ML analysis, and thus only the ML tree is provided (Fig. 1). The phylogeny (Fig. 1) indicate that the traditional *Spongipellis* is polyphyletic, and *S. spumeus* did not nest with other four species viz. *S. delectans*, *S. litschaueri*, *S. pachyodon*, *S. unicolor*, and formed an independent clade. Our phylogeny re-confirmed the polyphyly nature of *Spongipellis* (Tomšovský 2012, Binder et al. 2013).

The combined 4-gene dataset (ITS + nLSU + nSSU + *TEF1*) included sequences from 67 samples representing 30 taxa. The dataset had an aligned length of 3,639 characters, of which 2,760 (76%) characters are constant, 164 (4%) are variable and parsimony-uninformative and 715 (20%) are parsimony informative. The phylogenetic reconstruction performed with ML and BI analyses for two combined datasets showed similar topology and few differences in statistical support. The best model-fit applied in the Bayesian analysis was GTR + I + G, Iset nst = 6, rates = invgamma, and prset statefreqpr = dirichlet (1, 1, 1, 1). Bayesian analysis resulted in a nearly congruent topology with an average standard deviation of split frequencies = 0.003340 to ML analysis, and thus only the ML tree is provided (Fig. 2). The topotaxy of *Spongipellis* and its micromorphological similar genera both combined 4-gene and 2-gene datasets is almost identical.

Taxonomy

Irpiciporus Murrill, Bull. Torrey bot. Club 32(9): 471. 1905. – MycoBank MB17861

Type species. *Irpiciporus pachyodon* (Pers.) Kotl. & Pouzar, Česká Mykol. 11(3): 156 (1957).

Basidiomata annual, effused-reflexed to pileate, solitary or imbricate, soft when fresh, corky when dry. Pilei broadly attached, flabelliform to dimidiate. Pileal surface white, cream to buff yellow, glabrous, velutinous to tomentose, usually azonate, sometimes finely zonate near the margin. Pore surface white, buff yellow to ochraceous; hymenophore poroid to hydroid. Context indistinctly duplex, white to cream, spongy to corky. Hyphal system monomitic; generative hyphae with clamp connections, hyaline to pale yellow, thin- to thick-walled. Cystidia absent. Basidiospores ellipsoid, broadly ellipsoid to subglobose, hyaline, slightly thick-walled, smooth, often with one large guttule, IKI–, CB+.

Notes – The genus *Irpiciporus*, typified by *I. mollis* (Berk. & M.A. Curtis) Murrill, was established by Murrill (1905). Then, Kotlába and Pouzar (1957) considered *I. mollis* as a synonym of *I. pachyodon*. In our study, three species of *Irpiciporus* are accepted.

Irpiciporus xuchilensis (Murrill) Y.C. Dai & Chao G. Wang, comb. nov. – MycoBank MB843481

Basionym. *Coriolus xuchilensis* Murrill, Bull. New York Bot. Gard. 8: 143 (1912).

≡ *Tyromyces xuchilensis* (Murrill) Ryvarden, Mycotaxon 23: 175 (1985).

Specimen examined. Ecuador. Orellana Province, Yasuni National Park, on dead wood, 12.Ⅹ.2002, Ryvarden 44669 (O, dupl. BJFC012567).

Notes – *Irpiciporus xuchilensis* was originally described from Mexico (Murrill 1912), and was combined in *Tyromyces* (Ryvarden 1985). We studied a specimen Ryvarden 44669 from Ecuador. It is characterized by white pileate basidiomata, poroid to hydroid hymenophore, a monomitic hyphal system, generative hyphae with clamp connection, the absence of cystidia, broadly ellipsoid to globose, thick-walled, cyanophilous basidiospores measuring 4.3–5× 3.9–4.3 μm. These morphological characteristics fit well the definition of *Irpiciporus*. In

addition, our phylogenetic analyses confirm *I. xuchilensis* forms an independent lineage in *Irpiciporus* with strong supports (Figs. 1, 2). Thus, the above combination is proposed.

Irpiciporus sinuosus Y.C. Dai & Chao G. Wang, sp. nov. — MycoBank MB843476; Figs. 3, 4

Etymology. *Sinuosus* (Lat.) Refers to the species having sinuous pores.

Holotype. China. Yunnan Province, Puer, Laiyanghe Forest Park, on fallen angiosperm trunk, 6.Ⅷ.2011, Dai 12234 (BJFC010517).

Basidiomata annual, pileate, solitary, fleshy and soft, without odor or taste when fresh, hard corky when dry. Pilei flabelliform, projecting up to 3 cm, 4.5 cm wide, and 2.5 mm thick at base. Pileal surface cream to buff yellow, glabrous to velutinous, matted, usually azonate or faintly zonate near the margin when dry; margin sharp. Pore surface peach to clay buff when dry; sterile margin cream to buff yellow when dry; pores sinuous to irregular, 4–5 per mm; dissepiments thin, lacerate to dentate. Context pale cream to light brown, soft corky when dry, up to 1.5 mm thick. Tubes concolorous with pore surface, hard corky when dry, up to 1 mm long.

Hyphal system monomitic; generative hyphae with clamp connections, hyaline, smooth, IKI–, CB+; tissues unchanged in KOH. Contextual hyphae in upper part of context thin-walled, unbranched, straight, regularly arranged, 2.8–3.2 μm in diam; contextual hyphae in context close to tubes obviously thick-walled, occasionally branched, slightly flexuous, loosely interwoven, 4–5 μm in diam. Tramal generative hyphae slightly thick-walled, occasionally branched, slightly flexuous, subparallel along the tubes, agglutinated, 3–4 μm in diam. Cystidia absent; cystidioles fusoid, thin-walled, smooth, 20–23 × 3.5–5.5 μm. Basidia clavate, with four sterigmata and a basal clamp connection, 17–23 × 5–6 μm; basidioles of similar shape to basidia but smaller. Basidiospores broadly ellipsoid to subglobose, hyaline, slightly thick-walled, smooth, often with one big or medium guttule, IKI–, CB+, (4.8–)5–6(–6.2) × 4.1–4.9(–5.1) μm, L = 5.31 μm, W = 4.42 μm, Q = 1.20 (n = 30/1).

Notes — *Irpiciporus sinuosus* is characterized by pileate basidiomata, sinuous to irregular pores, homogeneous context, broadly ellipsoid to subglobose, a monomitic hyphal system, generative hyphae with clamp connection, slightly thick-walled, cyanophilous basidiospores measuring 5–6 × 4.1–4.9 μm. It grows on angiosperm wood occurrence in southwest China.

Irpiciporus sinuosus resembles *I. xuchilensis* by pileate basidiomata, sinuous to irregular pores, generative hyphae with clamp connections, absence of cystidia. However, the latter has silky white pileal surface when dry, smaller basidiospores (4.3–5 × 3.9–4.3 μm vs. 5–6 × 4.1–4.9 μm), and it is an American species. Phylogenetically, *Irpiciporus sinuosus* is also closely related to *I. xuchilensis* (Figs. 1, 2), but both form two independent lineages nested in *Irpiciporus* (100% ML, 1.00 BPP, Figs. 1, 2).

One sequence of sample-PW17-171-from Thailand submitted as *Tyromyces xuchilensis* in GenBank (GenBank accession NO. MK589288), is nested in *Irpiciporus sinuosus* in our phylogenies (Figs. 1, 2), we treat it as "*Irpiciporus sinuosus*" as we did not study the sample.

Radulodon Ryvardeen, Can. J. Bot. 50(10): 2073. 1972. — MycoBank MB18441

Type species. *Radulodon americanus* Ryvardeen, Can. J. Bot. 50(10): 2074 (1972).

For a detailed description of *Radulodon* see Ryvardeen (1972) and Nakasone (2001).

Notes — The genus *Radulodon* was established by Ryvardeen (1972) and then redefined and described by Nakasone (2001), now including eight species with resupinate to effused-reflexed basidiomata, hydroid hymenophore, conical, cylindrical or flattened spines, a monomitic or dimitic hyphal system, generative hyphae with clamp connections, sometimes presence of micro-binding hyphae, thin-walled cystidia, ellipsoid, subglobose to globose, hyaline, thin- to slightly thick-walled, more or less cyanophilous basidiospores. It is a cosmopolitan genus growth on angiosperm wood and all species are found in the North Hemisphere.

So far, eight species are included in *Radulodon*, viz. *Radulodon acaciae* G. Kaur et al., *R. americanus*, *R. aneirinus* (Sommerf.) Spirin, *R. casearius* (Morgan) Ryvardeen, *R. cirrhatus* Hjortstam & Spooner, *R. erikssonii* Ryvardeen, *R. indicus* Jyoti & Dhingra and *R. revolubilis* Hjortstam & Ryvardeen, among them three species have molecular sequences.

Radulodon is similar to *Irpiciporus*, but the latter has a monomitic hyphal system and the absence of cystidia (Murrill 1905, Kotlába and Pouzar 1957). *Radulodon* and *Irpiciporus* are also closely related in our phylogenies and nested in the Cerenaceae clade (Figs. 1, 2).

Radulodon yunnanensis Y.C. Dai & Chao G. Wang, sp. nov. — MycoBank MB843483; Figs. 5, 6

Etymology. *Yunnanensis* (Lat.) refers to the species being found in Yunnan Province of China.

Holotype. China. Yunnan Province, Pingbian County, Daweishan Forest Park, on fallen trunk of *Castanea*, 5.VI.2011, Dai 12204 (BJFC010487).

Basidiomata annual, resupinate, inseparable, soft, without odor or taste when fresh, soft corky to fragile when dry, up to 20 cm long, 3 cm wide. Hymenophore hydroid, cream to buff yellow when fresh, buff yellow to cinnamon buff when dry; sterile margin narrow to almost lacking; spines soft when fresh, fragile when dry, up to 2 mm long, subulate, 5–7 per mm at base. Subiculum very thin, white to cream, soft corky when dry, up to 0.5 mm thick.

Hyphal system monomitic; generative hyphae with clamp connections, hyaline, smooth, IKI–, moderately CB+; tissues unchanged in KOH. Subicular hyphae thin- to slightly thick-walled, frequently branched, slightly flexuous, loosely interwoven, 4–4.5 µm in diam. Spine tramal hyphae thin- to slightly thick-walled, rarely branched, straight, subparallel along the spines, agglutinated, 3–4 µm in diam. Cystidia rare, clavate to fusoid, thin-walled, arising from tramal hyphae and completely embedded in trama or projecting from the hymenium, thin-walled, smooth, 33–35 × 7–7.5 µm; cystidioles absent. Basidia clavate, with four sterigmata and a basal clamp connection, usually with several small guttules, 20–26 × 5–6 µm; basidioles of similar shape to basidia but smaller. Basidiospores broadly ellipsoid to subglobose, hyaline, slightly thick-walled, smooth, usually with one large or medium guttule, IKI–, weakly CB+, 5–6 × (4.3–)4.5–5.2(–5.5) µm, L = 5.32 µm, W = 4.79 µm, Q = 1.10 – 1.12 (n = 90/3).

Additional specimens (paratypes) examined – China. Yunnan Province, Dali, Cangshan Park, on fallen trunk of *Pinus*, 4.XI.2019, Cui 17979 (BJFC034838); Pingbian County, Daweishan Forest Park, on fallen angiosperm trunk, 11.XI.2019, He 6183 (BJFC033128).

Notes – *Radulodon yunnanensis* is characterized by resupinate basidiomata, buff yellow to cinnamon buff spines when dry, 5–7 per mm at base, very thin subiculum, broadly ellipsoid to subglobose, lightly thick-walled, slightly cyanophilous basidiospores measuring 5–6 × 4.5–5.2 µm. It grows on both angiosperm and gymnosperm wood occurrence in southwest China.

Radulodon yunnanensis with *R. acacia*, *R. indicus* and *R. cirrhatinus* are Asian species. However, *R. acacia* has the dark grayish hymenophore when dry, while it is buff yellow to cinnamon buff in *R. yunnanensis*; *R. indicus* is different from *R. yunnanensis* by larger basidiospores (6.8–8.5 × 5.2–7.2 µm vs. 5–6 × 4.5–5.2 µm, Jyoti and Dhingra 2014); *R. cirrhatinus* differs from *R. yunnanensis* by the effused-reflexed basidiomata, smaller basidiospores (4.5–5 × 3.5–3.8 µm vs. 5–6 × 4.5–5.2 µm, Hjortstam et al. 1990).

Radulodon yunnanensis, *R. americanus* and *R. erikssonii* are closely related in our phylogenies (Figs. 1, 2), but *R. americanus* and *R. erikssonii* have thicker spines (3–4 per mm in *R. americanus*, 2–4 per mm in *R. erikssonii* vs. 5–7 per mm) and obviously fibrillose or fimbriate sterile margin (Nakasone 2001).

Spongipellis Pat., Hyménomyc. Eur. (Paris): 140. 1887. – MycoBank MB18576

Type species. *Spongipellis spumeus* (Sowerby) Pat., Hyménomyc. Eur. (Paris): 140 (1887).

Basidiomata annual, pileate, soft and watery when fresh, hard corky and shrunken when dry. Pilei broadly attached, semicircular. Pileal surface white, cream to cinnamon buff, glabrous, velutinous to tomentose when dry. Pore surface white to pale yellow when fresh, clay buff to fawn when dry; pores round to angular. Context duplex consistently, white to cream when fresh, cream to buff yellow, spongy to corky when dry. Hyphal system monomitic; generative hyphae with clamp connections, hyaline, thin- to thick-walled. Cystidia and cystidioles absent. Basidiospores broadly ellipsoid to globose, hyaline, thick-walled, often with guttules, IKI–, CB+.

Notes – The duplex context, thick-walled and cyanophilous basidiospores facilitate the identification of *Spongipellis*. Nevertheless, our phylogenetic analyses demonstrate the separation of type species *S. spumeus* from other species (including *S. delectans*, *S. litschaueri*, *S. unicolor*, *S. pachyodon*), even they belong to different families. Here, we consider *Spongipellis* belong to Meripilaceae, while *Pseudospongipellis delectans*, *P. litschaueri*, *P. unicolor* and *Irpiciporus pachyodon* belong to Cerrenaceae.

Spongipellis quercicola Y.C. Dai & Chao G. Wang, sp. nov. – MycoBank MB843485; Figs. 7, 8

Etymology. *Quercicola* (Lat.) Refers to the species growth on *Quercus*.

Holotype. China. Jilin Province, Yanbian, Antu County, Changbaishan Nature Reserve, on fallen trunk of *Quercus*, 8.VIII.2011, Cui 10009 (BJFC010902).

Basidiomata annual, pileate, fleshy and soft, without odor or taste when fresh, corky and shrunken when dry. Pilei semicircular to flabelliform, projecting up to 5.2 cm, 6 cm wide, and 9 mm thick at base. Pileal surface pale cream to straw color, glabrous to velutinous, azonate when dry; margin irregularly lobed to slightly petaloid, obtuse. Pore surface cream to buff yellow when fresh, cinnamon buff to clay

buff or snuff brown when dry; pores angular to irregular, 2–3 per mm; dissepiments thin, entire to slightly lacerate. Context pale cream to buff, spongy to corky when dry, heterogeneous, upper part spongy, up to 1 mm thick; lower part dense and fibrous to corky, up to 4 mm thick. Tubes paler than pore surface, cream to buff yellow when dry, corky, up to 4 mm long.

Hyphal system monomitic; generative hyphae with clamp connections, hyaline, smooth, IKI–, CB–; tissues unchanged in KOH. The upper contextual hyphae thick-walled with a medium lumen, unbranched, slightly flexuous, interwoven, 4.8–6.5 µm in diam; the lower contextual hyphae slightly thick-walled with a wide lumen, unbranched, slightly flexuous, regularly arranged, agglutinated, 5.5–8.5 µm in diam. Tramal hyphae thin- to slightly thick-walled, rarely branched, flexuous, slightly interwoven, 3–5 µm in diam. Cystidia and cystidioles absent. Basidia barrel-shaped, with four sterigmata and a basal clamp connection, with several small guttules, 15–18 × 5.5–7 µm; basidioles of similar shape to basidia but smaller. Basidiospores ellipsoid to subglobose, hyaline, slightly thick-walled, smooth, often with one to a few guttules, IKI–, CB+, (5.1–)5.5–6.5(–7) × (4.3–)4.5–5.4(–5.5) µm, L = 5.95 µm, W = 5.10 µm, Q = 1.17–1.21 (n = 90/3).

Additional specimens (paratypes) examined – China. Jilin Province, Baishan, Fusong County, Lushuihe Forest Farm, on fallen trunk of *Quercus*, 11.VIII.2011, Cui 10114 (BJFC011007); Yanbian, Antu County, Changbaishan Natural Reserve, on living tree of *Quercus*, 2.IX.2019, Dai 20899 (BJFC032557).

Notes – *Spongipellis quercicola* is characterized by cinnamon buff to clay buff or snuff brown pore surface when dry, irregularly lobed pileal margin, round to angular pores 2–3 per mm, and ellipsoid to subglobose basidiospores measuring 5.5–6.5 × 4.5–5.4 µm. It grows on *Quercus* in northeast China.

Spongipellis spumeus resembles *S. quercicola* by duplex context, ellipsoid to subglobose, thick-walled basidiospores. However, the former has even circular pileal margin, round to regular pores, and relatively larger basidiospores (5.8–7 × 4.7–5.5 µm vs. 5.5–6.5 × 4.5–5.4 µm, Tomšovský 2012). *Spongipellis sibirica* (Penzina & Ryvarden) Penzina & Kotir. resembles *S. quercicola* by shrunken basidiomata when dry and thick-walled, cyanophilous basidiospores, but the former has white to cream pore surface when dry, smaller pores (4–5 per mm vs. 2–3 per mm, Kotiranta and Penzina 2001).

Phylogenetically, *Spongipellis quercicola* is also closely related to *S. sibirica* and *S. spumeus*, but it forms an independent lineage nested in *Spongipellis* (98% ML, 0.99 BPP, Fig. 1; 100% ML, 1.00 BPP, Fig. 2).

Pseudospongipellis Y.C. Dai & Chao G. Wang, gen. nov. – MycoBank MB843486

Type species. *Pseudospongipellis litschaueri* (Lohwag) Y.C. Dai & Chao G. Wang

Etymology. *Pseudospongipellis* (Lat.), refers to the genus resembling *Spongipellis*.

Basidiomata annual, pileate, soft when fresh, hard corky when dry. Pilei applanate to dimidiate. Pileal surface white when fresh, yellow to pale brownish when dry, glabrous, tomentose to hispid. Pore surface white when fresh, buff yellow to ochraceous when dry; pores round to angular. Context duplex consistently, white to cream. Hyphal system monomitic; generative hyphae with clamp connections, hyaline, slightly thick- to thick-walled. Cystidia and cystidioles absent. Basidiospores broadly ellipsoid to subglobose, hyaline, thick-walled, IKI–, CB+.

Notes – *Pseudospongipellis* is very similar to *Spongipellis* in morphology, but phylogenetically, the former nested in Cerrenaceae, while the latter in Meripilaceae (Figs. 1, 2).

Combinations. – *Spongipellis delectans*, *S. litschaueri*, *S. unicolor* were accepted in *Spongipellis* (Tomšovský 2012, Westphalen et al. 2016, Szczepkowski and Kowalczyk 2021). In our phylogenies (Figs. 1, 2), these species formed a new clade belonging to Cerrenaceae, so the following new combinations are proposed.

Pseudospongipellis delectans (Murrill) Y.C. Dai & Chao G. Wang, comb. nov. – MycoBank MB843487

Basionym: *Polyporus delectans* Peck, Bull. Torrey bot. Club 11(3): 26 (1884).

≡ *Spongipellis delectans* (Peck) Murrill, N. Amer. Fl. (New York) 9(1): 38 (1907).

Pseudospongipellis litschaueri (Lohwag) Y.C. Dai & Chao G. Wang, comb. nov. – MycoBank MB843488.

Basionym: *Spongipellis litschaueri* Lohwag, Arch. Protistenk. 75: 301 (1931).

≡ *Irpiciporus litschaueri* (Lohwag) Zmitr., Folia Cryptogamica Petropolitana (Sankt-Peterburg) 6: 105 (2018).

Specimens examined: China. Heilongjiang Province, Heihe, Shengshan Nature Reserve, on *Quercus*, 25.VIII.2014, Dai 14361 (BJFC017761), Huma County, Nanwonghe Nature Reserve, on *Quercus*, 27.VIII.2014, Dai 14739 (BJFC017856), Ning'an, Lake Jingpo Forest Park, on *Quercus*, 4.VIII.2014, Dai 13845 (BJFC017575), Xunke County, Xunbielahe Nature Reserve, on *Quercus*, 24.VIII.2014, Dai 13963 (BJFC017693), Yichun, Jiayin County, Maolangou National Forest Park, on *Quercus*, 30.VIII.2014, Cui 11913 (BJFC016925); Hubei Province, Shiyang, Saiwudang Nature Reserve, on living tree of *Quercus*, 6.VIII.2019, Dai 20266 (BJFC031934); Jilin Province, Yanbian, Antu County, Changbaishan Natural Reserve, on fallen trunk of *Quercus*, 2.IX.2019, Dai 20900 (BJFC032558); Liaoning Province, Anshan, Qianshan Forest Park, on *Quercus*, 26.IX.1998, Dai 3041 (BJFC012868); Shanxi Province, Qinshui County, Lishan Nature Reserve, on *Quercus*, 20.X.2004, Yuan 1099 (IFP006612).

Pseudospongipellis unicolor (Murrill) Y.C. Dai & Chao G. Wang, comb. nov. – MycoBank MB843489

Basionym: *Polyporus unicolor* Fr., Epicr. syst. mycol. (Upsaliae): 458 (1838).

≡ *Spongipellis unicolor* (Fr.) Murrill, N. Amer. Fl. (New York) 9(1): 37 (1907).

Discussion

Gilbertson and Ryvarden (1987) and Ryvarden and Gilbertson (1994) accepted four species in *Spongipellis*: *S. delectans*, *S. pachyodon*, *S. spumeus* and *S. unicolor*, and treated *Spongipellis litschaueri* as a synonym of *S. delectans*. Tomšovský (2012) provided phylogenetic analyses on *Spongipellis* based on single gene fragment (ITS or LSU) with specimens from Europe and North America and indicated that *Spongipellis* was polyphyletic. He also demonstrated that *S. litschaueri* and *S. delectans* are two independent species which are accepted by Ryvarden and Melo (2017). Our study re-confirmed polyphyletic of *Spongipellis* (Binder et al. 2013, Justo et al. 2017), and a new genus *Pseudospongipellis* is proposed for including *P. delectans*, *P. litschaueri* and *P. unicolor*. Thus, *Pseudospongipellis* and *Spongipellis* are monophyletic.

Spongipellis quercicola is described in the present paper, and it together with *S. spumeus* and *S. sibirica* form a clade nested in Meripilaceae. *Pseudospongipellis delectans*, *P. litschaueri* and *P. unicolor* form another clade nested in Cerrenaceae. *Pseudospongipellis* is morphologically very similar to *Spongipellis*, and the above separation is mainly based on phylogenetic analysis.

Irpiciporus pachyodon, *I. sinuosus* and *I. xuchilensis* form a clade in Cerrenaceae, and phylogenetically it is close to *Radulodon*. Unlike *Spongipellis* and *Pseudospongipellis*, *Irpiciporus* and *Radulodon* have different morphology: *Irpiciporus* has effused-reflexed to pileate basidiomata, poroid or hydroid hymenophore, a monomitic hyphal system, absence of cystidia, while *Radulodon* has mostly resupinate basidiomata, hydroid hymenophore, a monomitic to dimitic hyphal system, and presence of thin-walled cystidia (Murrill 1905, Ryvarden 1972, Nakasone 2001, Kaur et al. 2014, Jyoti and Dhingra 2014).

Beside the three species of *Spongipellis* in our phylogenies (Figs. 1, 2), another five taxa – *S. africana* Ipulet & Ryvarden, *S. caseosus* (Pat.) Ryvarden, *S. chubutensis* J.E. Wright & J.R. Deschamps, *S. malicola* (Lloyd) Ginns and *S. subcretaceus* (Lloyd) Decock – were included in the genus. However, *Spongipellis africana* has effuse-reflexed basidiomata, hydroid hymenophore, broadly ellipsoid to globose and thick-walled basidiospores. We studied its type specimen (Ipulet 1683, O; dupl. BJFC012592), but unfortunately, we could not obtain DNA from it. We did not study specimens of the remaining four species, and nor DNA data are available. So, we can't comment them for the time being.

Pseudospongipellis litschaueri mostly grows on *Quercus* in China, the Chinese specimens have smaller basidiospores than European specimens ($6-7 \times 4.1-5 \mu\text{m}$ vs. $7-8 \times 5-6 \mu\text{m}$, Tomšovský 2012). Tomšovský (2012) also indicated above conclusion and considered the Asian specimens as *Spongipellis* cf. *unicolor*. However, the Chinese specimens nested in *Pseudospongipellis litschaueri* in our phylogenies (Figs. 1, 2). Thus, we believe the Eurasia samples represent *Pseudospongipellis litschaueri* and the difference in spore dimension is interspecific.

Declarations

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AUTHORS' CONTRIBUTIONS

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

CONFLICT OF INTERESTS

The authors declare no competing interests.

DATA AVAILABILITY

All data generated or analyzed during this study are included in this published article.

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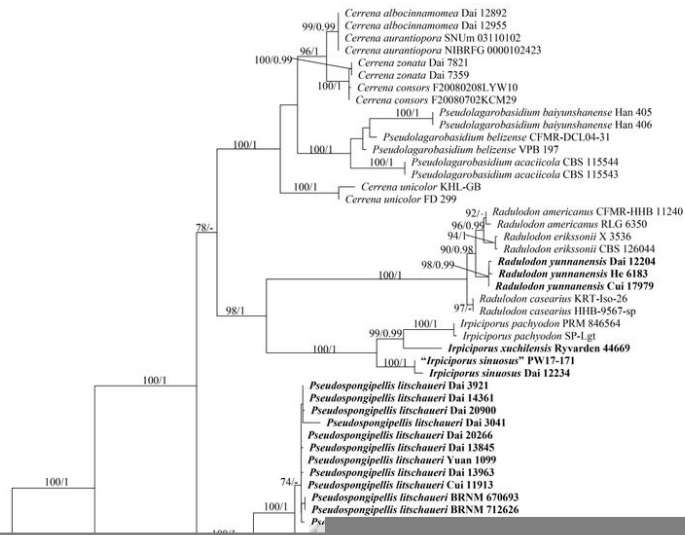


Figure 1

ML analysis of *Spongipellis* and its micromorphological similar genera based on dataset of ITS+nLSU. ML bootstrap values $\geq 50\%$ and Bayesian posterior probabilities values ≥ 0.90 are shown. New taxa are in bold

Figure 2

ML analysis of *Spongipellis* and its micromorphological similar genera based on dataset of ITS+nLSU+nSSU+TEF1. ML bootstrap values $\geq 50\%$ and Bayesian posterior probabilities values ≥ 0.90 are shown. New taxa are in bold



Figure 3

Basidiomata of *Irpiciporus sinuosus* (holotype, Dai 12234). Scale bar: 1 cm

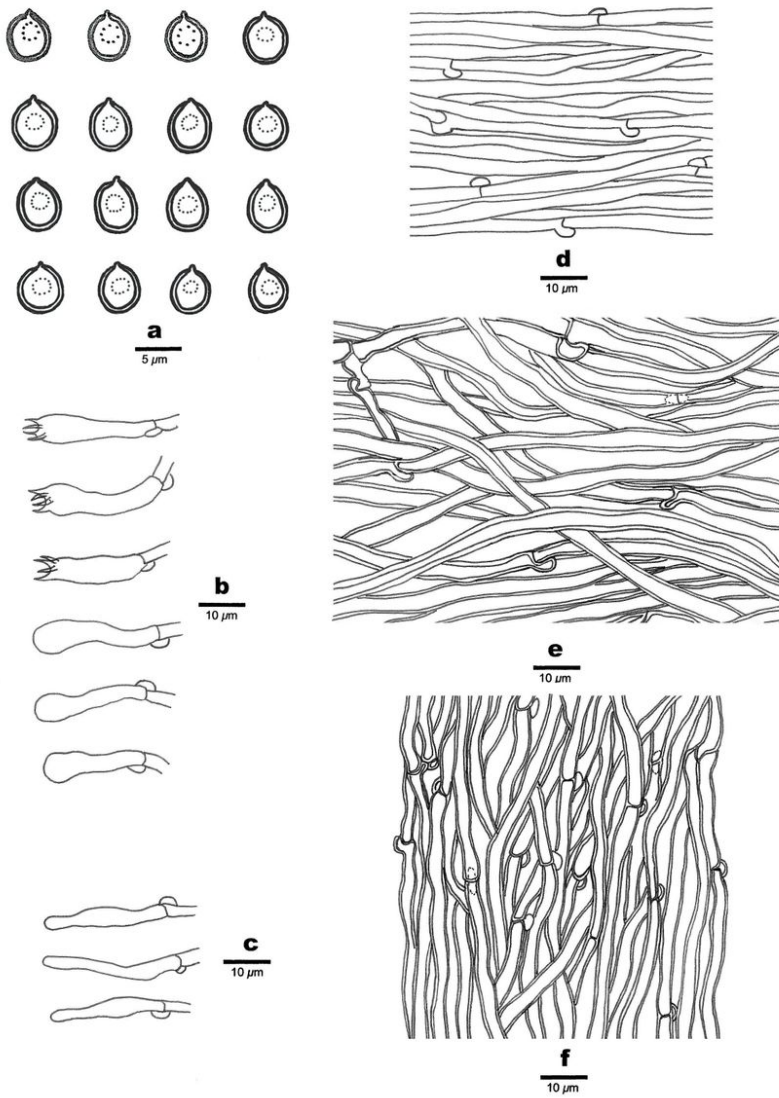


Figure 4

Microscopic structures of *Irpiciporus sinuosus* (drawn from the holotype, Dai 12234). a. Basidiospores. b. Basidia and basidioles. c. Cystidioles. d. Hyphae from upper context. e. Hyphae from context near to tubes. f. Hyphae from trama



Figure 5

Basidiomata of *Radulodon yunnanensis* (paratype, Cui 17979). Scale bar: 1 cm

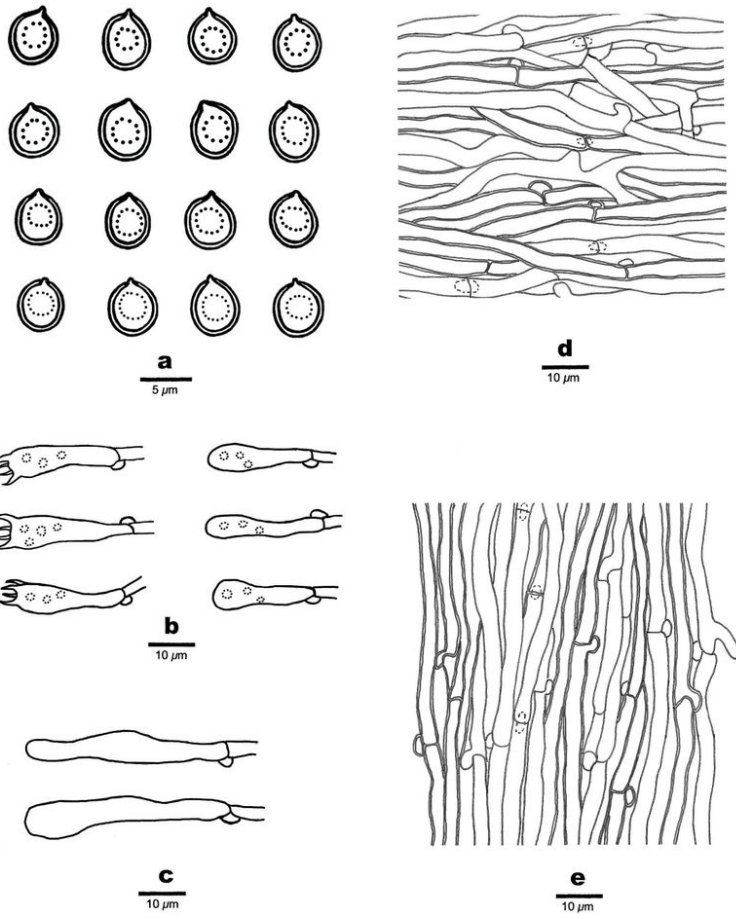


Figure 6

Microscopic structures of *Radulodon yunnanensis* (drawn from the holotype, Dai 12204). a. Basidiospores. b. Basidia and basidioles. c. Cystidia. d. Hyphae from subiculum e. Hyphae from trama

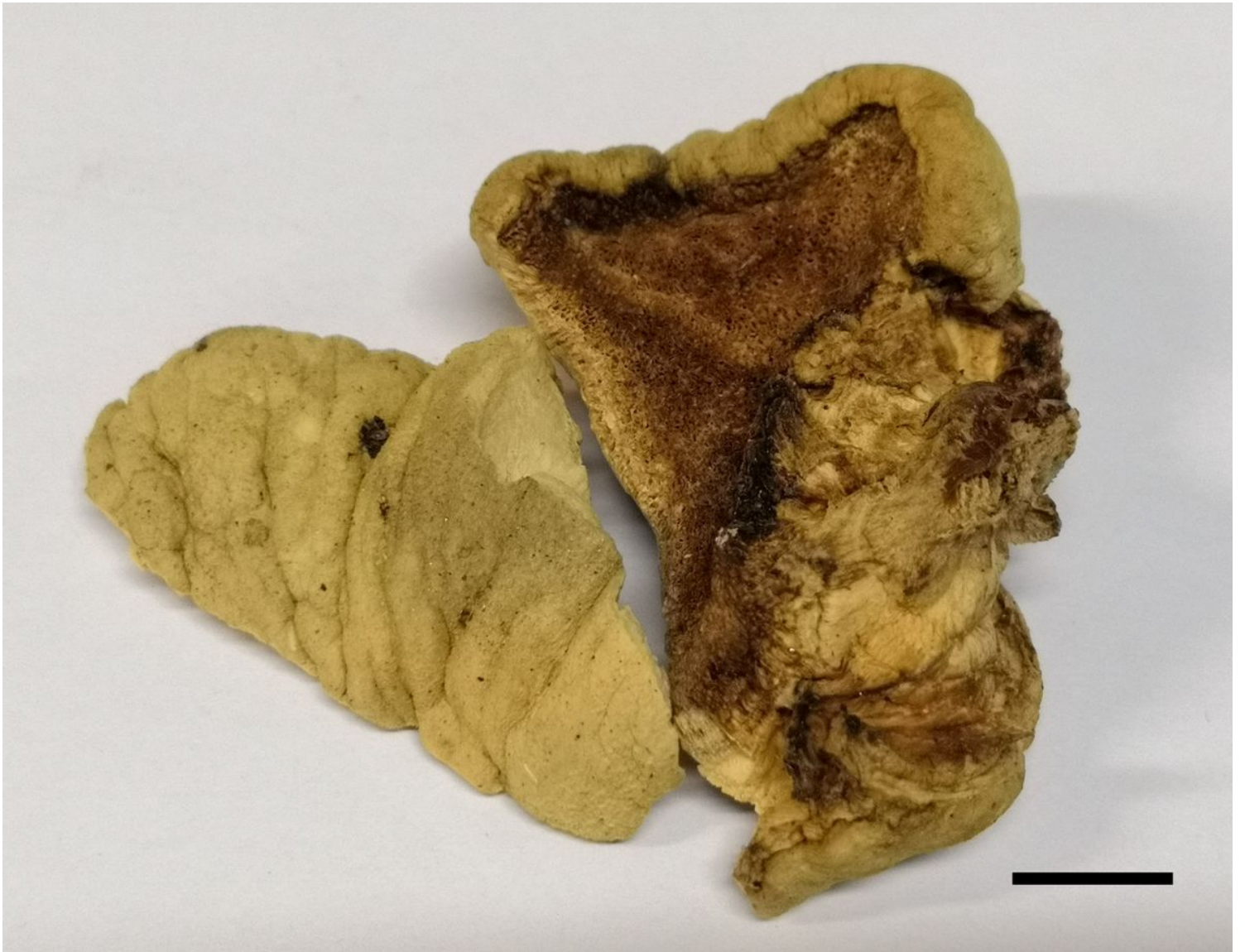


Figure 7

Basidiomata of the *Spongipellis quercicola* (holotype, Cui 10009). Scale bar: 1 cm

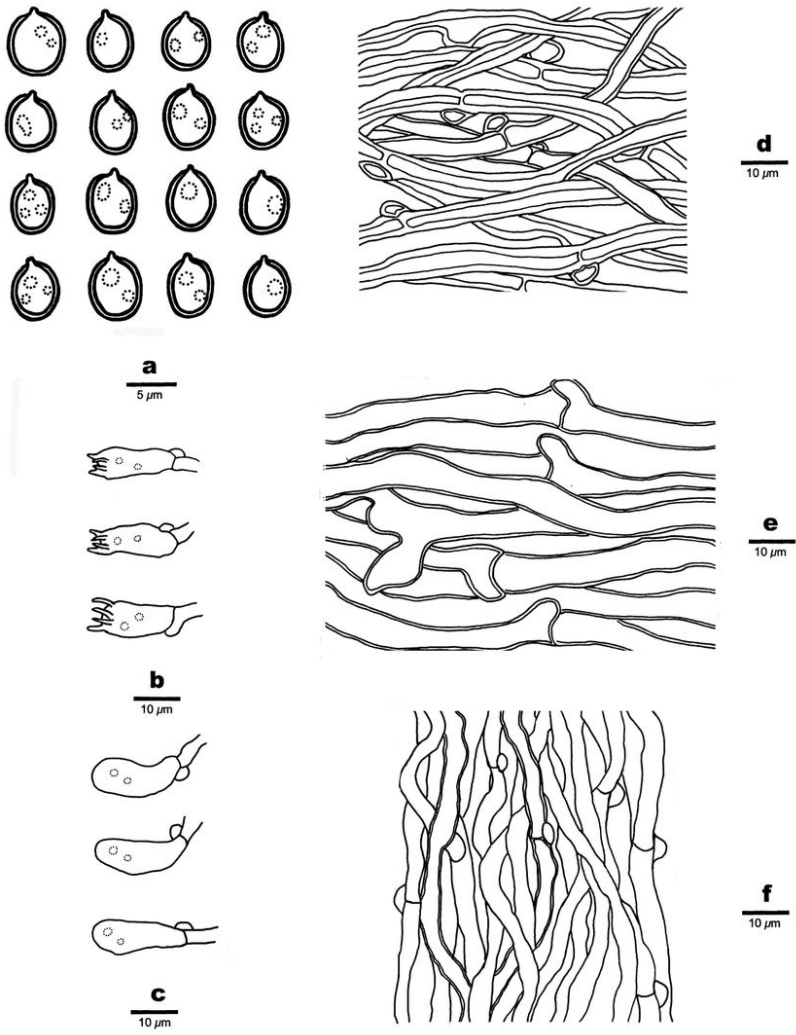


Figure 8

Microscopic structures of *Spongipellis quercicola* (drawn from the holotype, Cui 10009). a. Basidiospores. b. Basidia. c. basidioles. d. Hyphae from upper context. e. Hyphae from lower context. f. Hyphae from trama