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Spirin, Viacheslav

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Estudios en *Spongipellis sensu stricto* (Polyporales, Basidiomycota)

Spirin, Viacheslav*; Josef Vlasák; Tuomo Niemelä; Otto Miettinen

Botany Unit (Mycology), Finnish Museum of Natural History, P.O. Box 7 FI-00014 University of Helsinki, Finland.
* Corresponding author: <viacheslav.spirin@helsinki.fi>

ABSTRACT

Taxonomy of *Spongipellis sensu stricto* is revised based on morphological studies and DNA data. Here, the genus is accepted as a member of Meripilaceae, and it contains five species. Of them, *S. spumea*, the generic type, occurs in Europe, two species, *S. ambiens* (= *Tyromyces sibiricus*) and *S. variispora* sp. nov., are found in East Asia, and *S. profissilis* comb. nov., is reported from Central Europe, Siberia and Far East Asia. The North-American species, *S. occidentalis*, is reinstated as a separate species and redescribed here based on historical material.

Keywords — Phylogeny; residual polyporoid clade; taxonomy.

RESUMEN

Se revisa la taxonomía de *Spongipellis sensu stricto* con base en estudios morfológicos y datos de ADN. Aquí el género se acepta como miembro de Meripilaceae y contiene cinco especies. De ellas, *S. spumea*, el tipo genérico, se encuentra en Europa, dos especies, *S. ambiens* (= *Tyromyces sibiricus*) y *S. variispora* sp. nov., se encuentran en el este de Asia, y *S. profissilis* comb. nov., se reporta en Europa Central, Siberia y el Lejano Oriente de Asia. La especie *S. occidentalis* de Norteamérica se reintegra como una especie independiente y se describe aquí con base en material histórico.

Palabras clave — Clado poliporoide residual; filogenia; taxonomía.

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INTRODUCTION

Spongipellis Pat. is a small genus of polypores currently embracing about ten species. Its modern concept was introduced by Bondartsev & Singer (1941). Ryvarden (1991) emphasized monomitic basidiocarps with duplex context and ellipsoid or subglobose, cyanophilous basidiospores as important morphological characters of the genus. However, recent DNA-based studies showed that *Spongipellis* in the current scope is polyphyletic (Tomšovský, 2012; Dvořák *et al*., 2014; Wang & Dai, 2022). In addition, the study of Tomšovský (2012) indicated that the species limits in *Spongipellis* should be reconsidered.

In this paper, we revise taxonomy of *Spongipellis* based on newly obtained morphological and DNA evidence. For a long time, its position within the *Polyporales* remained unresolved (Binder *et al.*, 2013; Justo *et al.*, 2017). Kotiranta *et al.* (2017) revealed *S. spumea* to be a sister lineage of Meripilaceae. The same result was obtained by Wang & Dai (2022). The latter authors stated that *Spongipellis* should be included in Meripilaceae although no arguments were provided for this reclassification. Here we reconsider the phylogenetic position of *Spongipellis* based on a three-gene dataset. As a monophyletic unit, it encompasses five species only, including the generic type, *S. spumea* (Sowerby) Pat. We provide updated descriptions of the accepted species below.

MATERIAL AND METHODS

Morphological study. Specimens used in the present study are mostly preserved in the mycological herbarium of the Botanical Museum, Finnish Museum of Natural History, University of Helsinki (H). Type specimens as well as some additional collections from herbaria BPI, NY, MJ, O, as well as from private herbarium of Josef Vlasák (JV), were studied.

Morphological routine of this study follows Miettinen *et al.* (2018). In all cases, 20 tramal hyphae and 30 basidiospores per specimen were measured. For presenting measurements of basidiospores, 5% extreme values from both ends of variation are given in parentheses. For hyphal diameter measurements, the 20% tails are put in parentheses. The following abbreviations are used in descriptions below: L – mean spore length, W – mean spore width, Q – L/W ratio, n – number of measurements per specimens.

DNA methods. DNA was extracted as described in Spirin *et al.* (2013) and Kutuzova *et al.* (2017). Primers used in PCR and Sanger sequencing were: ITS5 and ITS4/LR22 for nrDNA ITS, LR0R/CTB6 and LR5/LR7 for partial 28S alias nrDNA LSU (White *et al.*, 1990; Vilgalys & Hester, 1990), 983F and 2218R for partial translation elongation factor 1-alpha (*tef1*; Rehner & Buckley, 2005), bRPB2-6f and bRPB2-7.1R for the second largest subunit of RNA polymerase II (*rpb2*; Matheny, 2005), and gRPB1-Af and fRPB1-Cr for the largest subunit of RNA polymerase II (*rpb1*; Matheny *et al.*, 2002). Sequence reads were produced by Eurofin Genomics and Macrogen European facilities. Reads were assembled with Chromas Pro 2.1.8 (Technelysium Pty Ltd).

One of the samples, the epitype of *Spongipellis spumea*, was sequenced with Illumina NextSeq 500 at the Biomedicum Functional Genomics Unit, University of Helsinki. Read cleaning was done using the FastQC 0.11.7 (https://www.bioinformatics.babraham.ac.uk/projects/fastqc/). Bowtie2 v2.3.4.3 (Langmead & Salzberg, 2012) was used to map the reads to a dataset of target markers; alignment was done using the sensitive option. Following the mapping of the reads the aligned read files were assembled using the MEGAHIT assembler v1.2.9 (Li *et al*., 2015) with Kmer 79,99,119.

Phylogenetic analyses. We produced 41 new sequences for this study and used 97 sequences from GenBank, listed in Table 1. Residual polyporoid clade dataset included 29 species and was partitioned in three (ITS, LSU, *rpb1*). Species were selected based on (Justo *et al*., 2017). *Candelabrochaete africana* and *Ischnoderma benzoinum* were used as an outgroup and forced together in the analysis. Sequences were initially aligned with webPRANK (Löytynoja & Goldman, 2010) and then adjusted manually in PhyDE 0.9971 (Müller *et al*., 2010). After removing unalignable characters, the alignment length was 2697 bp with 630 parsimony informative characters. GTR+G+I models were used for each of the partitions, as advised by AIC of ModelTest-NG 0.2.0 (Darriba *et al*., 2020). MrBayes 3.2.7 was used for phylogeny construction, analyses were run for 4 million generations, temp=0.1, 3 runs of 8 chains each in parallel (Ronquist *et al*., 2012). Runs converged well (average standard deviation of split frequencies <0.01).

Spongipellis ITS dataset (568 bp, 42 parsimony informative sites, 53 variable sites) contained 29 sequences (model GTR+G), *tef1* dataset (547 bp, 33/68 parsimony informative/variable sites) 16 sequences (SYM+I) and *rpb2* dataset (682 bp, 21/36 parsimony informative/variable sites) 10 sequences (GTR+G+I). No characters needed to be removed from these alignments. Phylogenetic analyses were done for each marker separately, but these datasets were also concatenated to a three-marker dataset (1795 bp, 76/160 parsimony informative/variable sites) that included specimens with at least two markers, 16 altogether. All these analyses were run for 1-4 million generations to achieve high convergence.

RESULTS

Our residual polyporoid clade analysis resolves *Spongipellis* sensu stricto as a sister clade to the *Meripilus* clade (Fig. 1). *Spongipellis* should either be given its own family or included in Meripilaceae. We prefer inclusion to Meripilaceae and provide some morphological arguments for this below. A number of species formerly included in *Spongipellis* belong to the Cerrenaceae, including the genus *Irpiciporus* (*S. pachyodon*). The analysis covers most known lineages of the residual polyporoid clade.

Analysis of the *Spongipellis sensu stricto* ITS sequences fall into three clades: *Spongipellis ambiens*, *S. profissilis*, and *S. spumea sensu lato* (Fig. 2). An Asian subclade of *S. spumea* is well supported, but it is nested along the European specimens that do not form a separate clade, and only 1 bp separates the two subclades. However, *rpb2* and *tef1* phylogenies (not shown) and morphology separate the Asian and European

Table 1. DNA sequences used in the present study.
Table 1. Secuencias de ADN usadas en este estudio.

Species	Specimen/ strain	Country of origin	ITS	LSU	*rpb1*	*rpb2*	*tef1*
Abortiporus biennis		United States: Massachusetts	KP135300	KP135195	KP134783		
Antella americana		United States: Tennessee	KP135316	KP135196	KP134885		
Antrodiella semisupina		United States: Massachusetts	KP135314	KP135197	KP134886		
Butyrea luteoalba		United States: Maryland	KP135320	KP135226	KP134887		
Candelabrochaete africana		Puerto Rico	KP135294	KP135199	KP134872		
Caudicicola gracilis		Finland	KY415962	KY415962	KY415972		
Cerrena unicolor		United States: Massachusetts	KP135304	KP135209	KP134874		
Cymatoderma sp.		United States: Florida	KY948826	KY948872	KY948971		
Diplomitoporus crustulinus		United States: Massachusetts	KP135299	KP135211	KP134883		
Etheirodon aff. fimbriatum		United States: Illinois	KY948821	KY948864	KY948950		
Hyphoderma litschaueri		United States: Wisconsin	KP135295	KP135219	KP134868		
Hyphoderma medioburiense		United States: Massachusetts	KP135298	KP135220	KP134869		
Hyphoderma mutatum		United States: Alaska	KP135296	KP135221	KP134870		
Hyphoderma setigerum		United States: Massachusetts	KP135297	KP135222	KP134871		
Hypochnicium cf. sphaerosporum		United States: Arizona	KY948803	KY948861	KY948940		
Hypochnicium punctulatum		United States: New York	KY948827	KY948860	KY948932		
Hypochnicium sp.		United States: Arkansas	KY948804	KY948862	KY948944		
Ischnoderma resinosum		United States: Maryland	KP135303	KP135225	KP134884		
Meripilus giganteus		United Kingdom	KP135307	KP135228	KP134873		
Panus rudis		Puerto Rico	OM337524	OM337524	JACDTX0100003 12.1:73153-74486		
Physisporinus sp.		Indonesia: Nusa Tenggara Barat	KY948732	KY948867	KY948946		
Physisporinus sp.		United States: Minnesota	KY948733	KY948863	KY948947		
Podoscypha parvula	Niemelä 7690	Kenya	**OP099440**	**OP099440**	KY948934		
Pouzaroporia subrufa		Indonesia: Papua Barat	KY948736	KY948896	KY948972		
Radulodon casearius		United States: Florida	KY948752	KY948871	KY948943		
Spongipellis ambiens	Dai 1723	China	KU509500				
Spongipellis ambiens	Niemelä 6407	China: Jilin	**ON979313**	**ON979313**			
Spongipellis ambiens	Penzina 176 (holotype of *S. sibiricus*)	Russia: Buryatia	**ON979314**				
Spongipellis ambiens	Spirin 5389	Russia: Khabarovsk	**ON979322**	**ON979322**			**OP019470**
Spongipellis delectans		United States: Michigan	KP135301	KP135287	KP134876		
Spongipellis pachyodon		United States: Massachusetts	KP135302	KP135288	KP134875		
Spongipellis profissilis	BRA CR 13410	Slovakia	HQ728282				
Spongipellis profissilis	Cui 10009 (holotype of *S. quercicola*)	China: Jilin	OM971919				OM982701
Spongipellis profissilis	Cui 10114	China: Jilin	OM971918				
Spongipellis profissilis	Dai 3934	China: Jilin	**ON979321**	**ON979321**		**OP114174**	**OP019468**
Spongipellis profissilis	Kotiranta 26990	Russia: Tuva	**OP104014**	**OP104014**		**OP114175**	**OP019469**
Spongipellis profissilis	Vlasák (JV2111/1)	Czech Republic	**ON979319**			**OP114176**	**OP019472**
Spongipellis spumea	BRNM712630	Czech Republic	HQ728288				
Spongipellis spumea	BRNM734877	Czech Republic	HQ728283				
Spongipellis spumea	Kotiranta 26889	Finland	**ON979311**	**ON979311**	**OP114177**	**OP114169**	**OP019461**
Spongipellis spumea	Miettinen 24146	Finland	**ON979325**			**OP114168**	**OP019456**
Spongipellis spumea	Miettinen 6716	Finland	**ON979317**				
Spongipellis spumea	MJ41/09	Czech Republic	HQ728289				
Spongipellis spumea	Oksanen 100	Finland	KY415960	KY415960			
Spongipellis spumea	PRM891931	France	HQ728287	HQ729021			
Spongipellis spumea	Spirin 6741	Russia: Nizhny Novgorod	**ON979326**	**ON979326**		**OP114171**	**OP019464**
Spongipellis spumea	Vlasák (JV0110/36)	Czech Republic	**ON979324**				**OP019471**
Spongipellis spumea	Vlasák (JV1511/6)	Czech Republic	**ON979318**	**ON979318**		**OP114172**	**OP019465**
Spongipellis spumea	Vlasák (JV8909/18)	Czech Republic	**ON979323**				
Spongipellis spumea		Czech Republic				LN714711	
Spongipellis variispora	Cui 11912	China	OM971923				
Spongipellis variispora	Dai 20901	China	OM971927				OM982703
Spongipellis variispora	He 6736	China	OM971924				
Spongipellis variispora	Niemelä 6423	China: Jilin	**ON979320**	**ON979320**			**OP019467**
Spongipellis variispora	Spirin 10708	Russia: Khabarovsk	**ON979315**	**ON979315**			**OP019462**
Spongipellis variispora	Spirin 10711	Russia: Khabarovsk	**ON979316**	**ON979316**		**OP114170**	**OP019463**
Spongipellis variispora	Spirin 3737	Russia: Khabarovsk	**ON979312**	**ON979312**		**OP114173**	**OP019466**
Steccherinum nitidum		United States: Maryland	KP135323	KP135227	KP134888		
Xanthoporus syringae		China	AY789078	AY684166	AY788846		

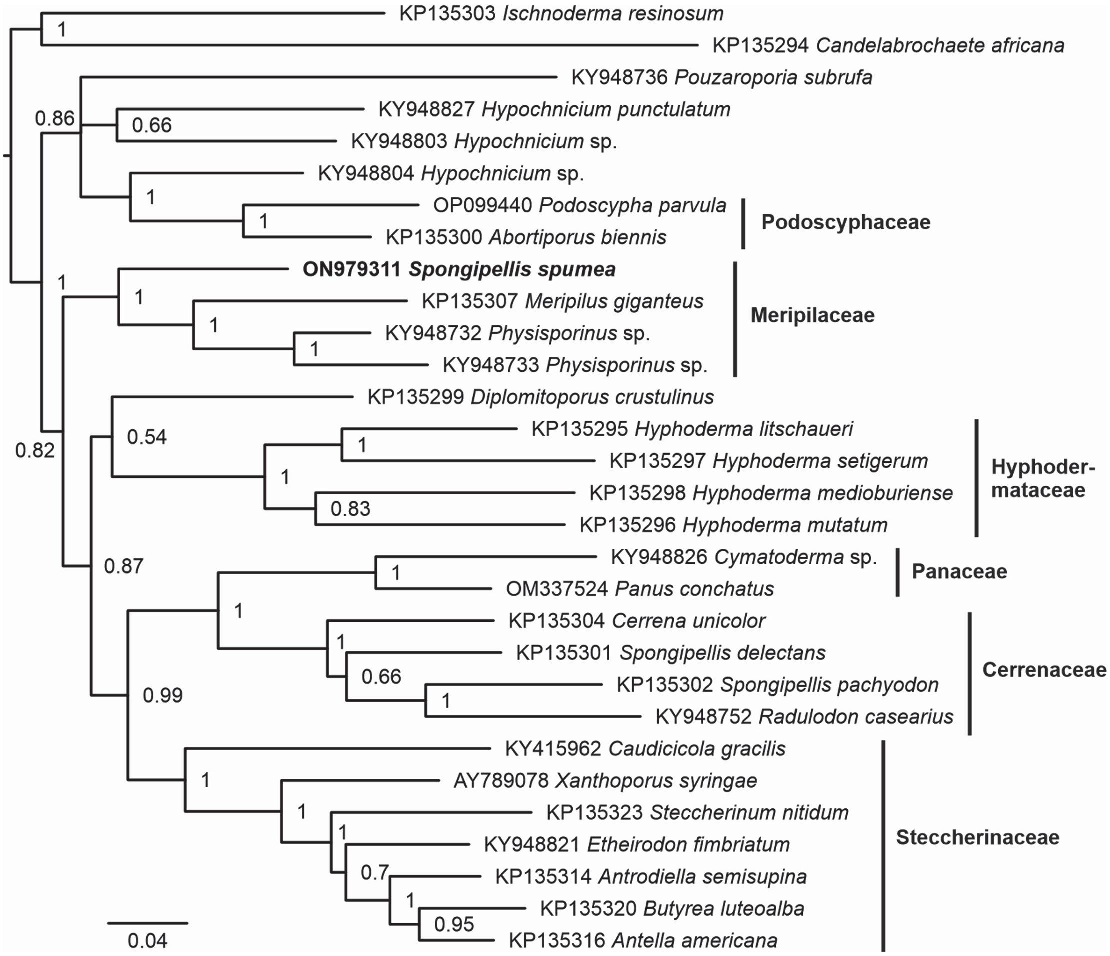

Fig. 1. Bayesian consensus tree of the residual polyporoid clade of the Polyporales, based on nrDNA ITS, LSU and rpb1.

Fig. 1. Árbol de consenso bayesiano del clado poliporoide residual de los Polyporales, basado en ITS, LSU y rpb1.

specimens of this group into well-supported clades. A phylogeny of the concatenated ITS-*rpb2-tef1* dataset (Fig. 3) resolves four species with high support: Asian *S. ambiens*, Eurasian *S. profissilis*, European (true) *S. spumea* and Asian *S. spumea* described here as *S. variispora*.

TAXONOMY

Spongipellis Pat.,
Les Hyménomycètes d'Europe: 140, 1887.

Basidiocarps annual, sessile, light-coloured, juicy in fresh condition, rather tough after drying. Context duplex, with softer upper and more compact lower layers. Pores angular, 3–6 per mm. Hyphal structure monomitic, hyphae clamped and slightly cyanophilous, thin- to slightly thick-walled. Hyphae in the upper context layer loosely interwoven or subparallel and merging in fibrous bundles; hyphae in

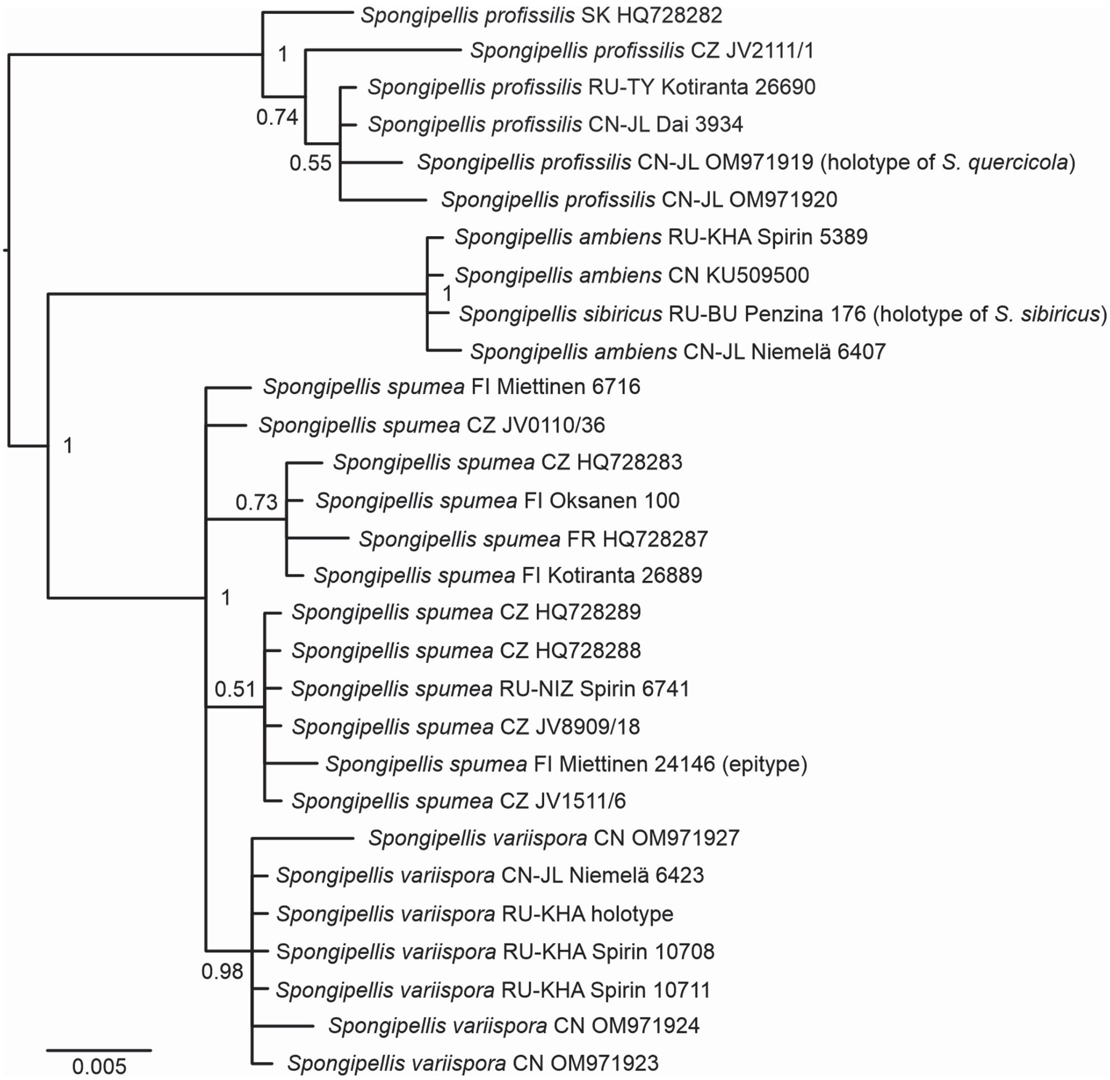

Fig. 2. *Spongipellis sensu stricto* Bayesian consensus tree based on nrDNA ITS. Country and province of origin have been indicated with ISO codes.

Fig. 2. Árbol de consenso bayesiano de *Spongipellis sensu stricto* basado en el marcador ITS. El país y la provincia de origen se han indicado con códigos ISO.

the lower context layer more or less tightly arranged and predominantly subparallel. Subhymenial hyphae thin-walled and often short-celled. Cystidia absent, cystidioles present in some species, tapering. Basidia clavate to broadly clavate, 15–32 × 6–10.5 μm, four-spored, contents often guttulate. Basidiospores broadly ellipsoid or ovoid, more rarely subglobose, slightly thick-walled, with a large central oil-drop and asymmetric apiculus, cyanophilous.

Causes a white rot of living and dead deciduous trees.

Genus type: *Boletus spumeus* Sowerby (selected by Bondartsev & Singer, 1941).

Spongipellis spp. can be separated from other species of Meripilaceae in the genera *Meripilus* P. Karst., *Physisporinus* P. Karst. and *Rigidoporus* Murrill *pro parte* by their clamped hyphae and duplex context of basidiocarps. Otherwise, the representatives of the three genera are quite similar to each other, possessing annual,

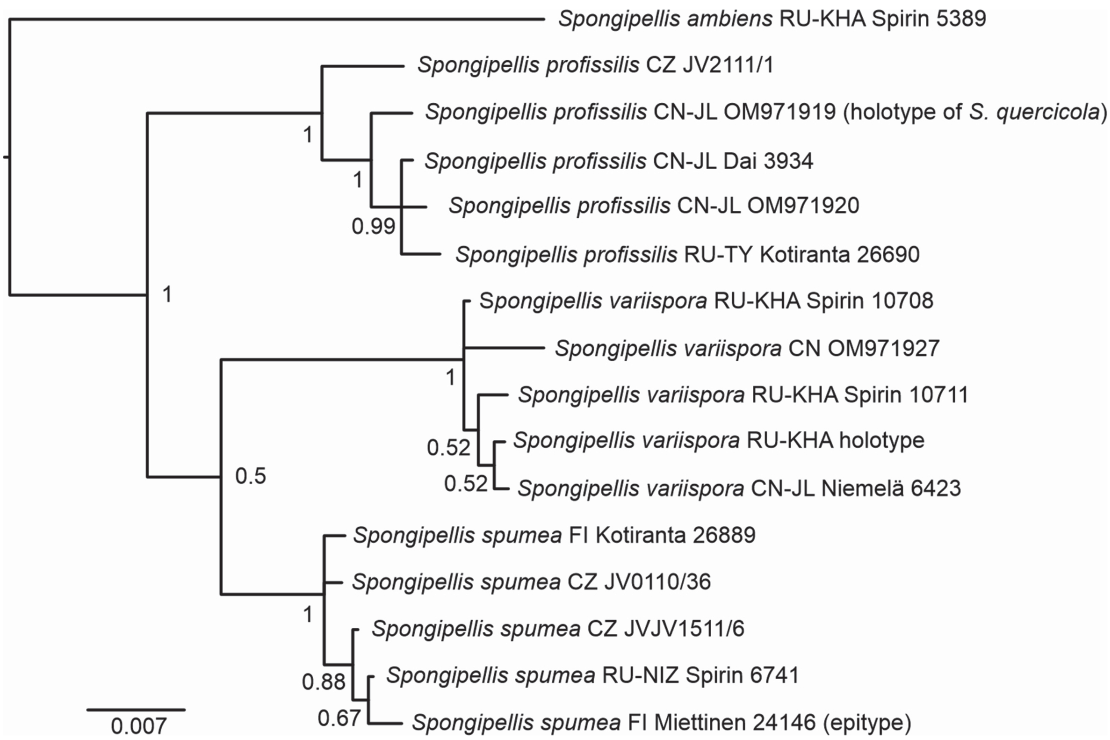

Fig. 3. *Spongipellis* sensu stricto Bayesian consensus tree of three DNA markers, ITS, rpb2 and tef1. Country and province of origin have been indicated with ISO codes.

Fig. 3. Árbol de consenso bayesiano de tres marcadores de ADN, ITS, rpb2 y tef1 de *Spongipellis sensu stricto*. El país y la provincia de origen se han indicado con códigos ISO.

sappy basidiocarps turning reddish or brownish when bruised, monomitic hyphal structure with subparallel, highly visible tramal hyphae, and rather wide basidia with guttulate cytoplasm. Basidiospores in all these genera are often slightly thick-walled, always broadly ellipsoid to subglobose, slightly cyanophilous and usually bear a large central oil drop.

Outside Meripilaceae, *Spongipellis* shares a certain morphological similarity with *Irpiciporus* Kotl. & Pouzar and the *Spongipellis delectans* complex (both belonging to *Cerrenaceae* – Justo *et al*., 2017), as well as with *Aurantiporus fissilis* (Berk. & M.A. Curtis) H. Jahn (*Meruliaceae*). *Irpiciporus* spp. differ from *Spongipellis sensu stricto* in having a hydnoid-irpicoid hymenophore, as well as narrower and on average longer basidia. The members of the *S. delectans* group (= *Pseudospongipellis* Y.C. Dai & Chao G. Wang) have sturdier basidiocarps with larger pores than in *Spongipellis* sensu stricto; their tramal hyphae are distinctly thick-walled, in some species looking almost like skeletal hyphae, and basidia are shorter, not exceeding 20 μm in length. In turn, *A. fissilis* has wider pores and smaller basidiospores than *Spongipellis* spp., and its tissues exude abundant oily matter in microscopic slides. Moreover, the basidiospores of *A. fissilis* are thin-walled and acyanophilous.

Spongipellis ambiens P. Karst.,
Travaux de la Sous-Section de Troïtzkossawsk-Kiakhta, Section du pays d'Amour de la Soc. Imp. Russe de Géographie 8 (1): 61, 1906. Figs. 4, 5.

Neotype. Russia. Krasnoyarsk Reg.: Yeniseisk, deciduous tree, [no collecting date indicated], *Kytmanov* (H 7200356) (selected here, MycoBank MBT10008625).

= *Tyromyces sibiricus* Penzina & Ryvarden,
Folia Crypt. Estonica 33: 109, 1998. Holotype. RUSSIA. Buryatia, Barguzin Dist., Frolikha, *Populus suaveolens*, 04-VIII-1996, *Penzina 176** (O, studied).

Basidiocarps annual, sessile, widely attached to substipitate, contracted at the base, pilei projecting up to 6 cm and up to 2 cm thick at the base. Upper surface hirsute, azonate, first white or cream-coloured, later yellowish to pale ochraceous. Edge of pileus sharp, sterile, concolorous with pileal surface. Hymenial surface flat to more or less concave, first almost white, later yellowish to pale ochraceous; pores angular, 4–6 per mm, dissepiments thin, even to serrate. Section: context cream-coloured to pale ochraceous, watery in fresh condition, compact and distinctly fibrillose when dry, up to 1 cm thick; tube layer tough, concolorous with pore surface, up to 1 cm thick.

Fig. 4. Basidiocarps of *Spongipellis* spp. *in situ*: A) *S. ambiens* (Niemelä 6407). B) *S. spumea* (epitype). C) *S. variispora* (holotype). D) *S. variispora* (Miettinen 10441).

Fig. 4. Basidiocarpos de *Spongipellis* spp. *in situ*: A) *S. ambiens* (Niemelä 6407). B) *S. spumea* (epitipo). C) *S. variispora* (holotipo). D) *S. variispora* (Miettinen 10441).

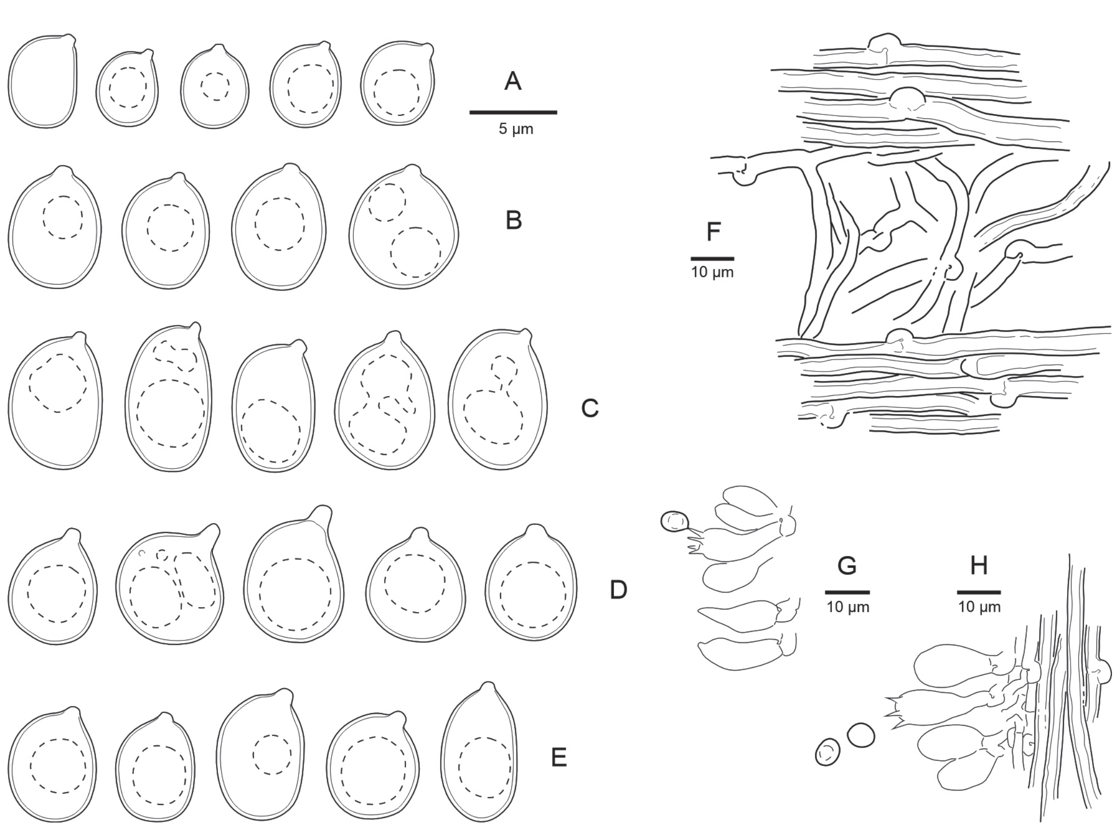

Fig. 5. Microscopic structures of *Spongipellis* spp.: A) Basidiospores of *S. ambiens* (holotype). B) Basidiospores of *S. occidentalis* (holotype). C) Basidiospores of *S. profissilis* (Kotiranta 26690). D) Basidiospores of *S. variispora* (holotype). E) Basidiospores of *S. spumea* (epitype). F) Hyphae of the upper context layer of *S. spumea* (epitype). G) Hymenial cells (basidia and cystidioles) of *S. spumea* (Vampola 200). H) Hymenial cells and tramal hyphae of *S. spumea* (epitype).

Fig. 5. Estructuras microscópicas de *Spongipellis* spp.: A) Basidiosporas de *S. ambiens* (holotipo). B) Basidiosporas de *S. occidentalis* (holotipo). C) Basidiosporas de *S. profissilis* (Kotiranta 26690). D) Basidiosporas de *S. variispora* (holotipo). E) Basidiosporas de *S. spumea* (epitipo). F) Hifas de la capa de contexto superior de *S. spumea* (epitipo). G) Células himeniales (basidios y cistidiolos) de *S. spumea* (Vampola 200). H) Células himeniales e hifas tramales de *S. spumea* (epititipo).

Hyphal structure monomitic; all hyphae with clamp connections. Context: hyphae slightly thick-walled, subparallel, (4.4–) 5.6–7.8 (–7.9) μm in diam. (n = 20/1). Tramal hyphae thin- or slightly thick-walled, subparallel, (3.0–) 3.1–4.7 (–4.9) μm in diam. (n = 20/1). Cystidioles occasionally present, tapering, 11–16 × 4.5–6.5 μm. Basidia clavate to broadly clavate, four-sterigmatic, (12.8–) 13.1–18.1 (–20.2) × (5.9–) 6.1–8.0 (–8.1) μm (n = 40/2). Subhymenial hyphae thin-walled, 3–4.5 μm in diam. Basidiospores slightly thick-walled, broadly ellipsoid to subglobose, (4.4–) 4.5–6.1 (–6.4) × (3.6–) 3.8–4.8 (–5.3) μm (n = 72/2), L = 5.26, W = 4.37, Q = 1.20.

Comments.— *Spongipellis ambiens* was described based on the single collection from Siberia (Karsten, 1906). A few years later Karsten (1911) placed it among the synonyms of *Spongipellis borealis* (now *Climacocystis borealis*). In his type studies of the Karsten species, Lowe (1956) stated that the type of *S. ambiens* was lost. However, Lowe was evidently not aware of Karsten's practice to rename collections in his herbarium in accordance with his changing views. There is one collection from

Siberia, i.e. the specimen of A. Kytmanov from Yeniseisk (H), labelled by Karsten himself as '*Spongipellis borealis*'. Saccardo & Trotter (1912) mentioned another locality as the *locus classicus* of *S. ambiens*, Yamarovka in Chita Reg., and they evidently borrowed this information from Karsten's paper title (1906). In that paper, Karsten did not specify who was the collector of the *S. ambiens* type, however, and its full title, "Fungi in Transbaicalia, *paucis exceptis*, prope fontes minerales Yamarovka aestate ann. 1904 et 1905 a clar. P. Mikhno collecti" [our italics], implies also specimens from other localities or collectors included. In particular, this is a case of *Lenzites sibirica* P. Karst., mentioned in the same paper without any references to the collector or locality. According to Karsten's herbarium, the only collection which could be the source of this indication is the specimen of A. Kytmanov from Yeniseisk (Karsten's herb. # 3113). So, it is highly probable that the presumed type of *S. ambiens* is a part of the same story. Nevertheless, we designate Kytmanov's specimen as the neotype of *S. ambiens*, not as the lectotype, due to the absence of the latter name written by Karsten on the specimen's label. *Tyromyces sibiricus* (= *Spongipellis sibirica*) is conspecific with *S. ambiens*.

The type locality lies in the subarctic climatic zone where no nemoral tree genera like *Acer* or *Ulmus* are present – this alone excludes other species of *Spongipellis*. The type is richly fertile and fits well with the more recent material labelled as *S. sibiricus*.

Spongipellis ambiens is an East Asian species, now reported from boreal to north temperate Northeast China, Siberia and Russian Far East. It inhabits living or recently fallen poplar trees (of the *Populus suaveolens* group), with one record on *Salix arbutifolia* (Kotiranta & Penzina, 2001). Morphologically, it differs from the other four species in having relatively thin basidiocarps with a flat or more often concave hymenial surface and a distinctly contracted base. The upper surface of *S. ambiens* is covered by long hairs arranged radially at the very base of pilei. *Spongipellis ambiens* has the smallest basidiospores in the genus (Table 2) although this character alone is not enough for separating it from another East Asian species, *S. variispora* (see remarks under the latter species).

Specimens examined.— CHINA. Jilin Prov., Antu Co., Changbaishan Nat. Res., *Populus koreana*, 18-IX-1998, *Niemelä 6407** (H). RUSSIA. Buryatia (holotype of *Tyromyces sibiricus*, see above). Khabarovsk Reg., Khabarovsk Dist., Malyi Kukachan, *Populus maximowiczii*, 18-VIII-2012, *Spirin 5389** (H). Krasnoyarsk Reg.: Yeniseisk (neotype, see above).

Spongipellis occidentalis Murrill,
North American Flora 9 (1): 38, 1907. – Fig. 5.

Holotype. USA. New York, Tompkins Co., Ithaca, *Fagus grandifolia*, X-1899 *Wiegand* (NY 00776400, studied).

= *Polyporus whetstonei* Lloyd, Mycological Writings 7: 1146, 1922. Lectotype. USA. Minnesota, [no collecting date indicated], *Whetstone* (Lloyd's herbarium # 26028 – BPI US0307606, studied) (selected by Lowe 1975: 22).

Basidiocarps annual, sessile, widely attached, pilei projecting up to 7 cm and up to 4 cm thick at the base. Upper surface pubescent to hirsute, azonate, first cream-coloured or yellowish, later ochraceous or dirty grey. Edge of pileus blunt, fertile, concolorous with pileal surface. Hymenial surface even to more or less concave, pale ochraceous or brownish; pores angular, 4–6 per mm, dissepiments thin, uneven to serrate. Section: context cream-coloured to pale ochraceous, compact and indistinctly zonate, up to 3 cm thick; tube layer fragile, concolorous with pore surface, up to 2 cm thick.

Hyphal structure monomitic; all hyphae with clamp connections. Context: hyphae slightly thick-walled, interwoven or arranged in subparallel bundles, (4.0–) 4.2–8.1 (–8.2) μm in diam. (n = 40/2). Tramal hyphae thin- to distinctly thick-walled, subparallel, (2.6–) 3.2–6.0 (–6.3) μm in diam. (n = 40/2). Cystidioles not seen. Basidia clavate, four-sterigmatic, 14.2–20.8 × 7.0–8.1 μm (n = 3/1), quickly collapsing. Basidiospores slightly thick-walled, ellipsoid or broadly ellipsoid, rarely subglobose, (5.2–) 5.3–7.1 (–7.8) × 4.2–6.1 (–6.2) μm (n = 60/2), L = 6.24, W = 5.00, Q = 1.25.

Comments.— Lowe (1975) treated *S. occidentalis* as a synonym of *S. spumea*. Here we reinstate *S. occidentalis* as a species on its own and place *P. whetstonei* to its synonymy. Morphologically, *S. occidentalis* is most similar to the East Asian *S. variispora*. The main differences between these species can be found in spore shape and size. The basidiospores of *S. occidentalis* are much less variable in size than in *S. variispora*, and they have a rather small (up to 0.5 μm long), conventionally located apiculus. In *S. variispora*, apiculus is larger, up to 1 μm long, quite often asymmetric and sometimes shifted to the ventral side. Moreover, tramal hyphae of *S. occidentalis* are wider than in *S. variispora*. The European *S. spumea* possesses basidiospores of approximately the same size as in *S. occidentalis* but it has larger pores, 3–4 per mm.

Spongipellis occidentalis is the only member of the genus so far detected in North America. At the moment, no DNA sequences are available for it. Newly collected and sequenced specimens are highly desirable to clarify its phylogenetic position within the genus.

Specimens examined.— USA. Minnesota (lectotype of *P. whetstonei*, see above). New York (holotype of *S. occidentalis*, see above).

Spongipellis profissilis (Lloyd) Spirin & Vlasák, comb. nova. – Fig. 5.

≡ *Polyporus profissilis* Lloyd, Mycol. Writings 5 (56): 810, 1918. Lectotype. JAPAN. Miyagi: Sendai, 16-XI-1917, *Yasuda 493* (BPI, studied) (selected by Ryvarden 1990: 97).

MycoBank MB845181

= *Spongipellis quercicola* Y.C. Dai & Chao G. Wang, Mycological Progress 21 (73): 13, 2022.

Basidiocarps annual, sessile, widely attached, pilei projecting up to 20 cm and up to 7 cm thick at the base. Upper surface pubescent, azonate, first cream-coloured or yellowish, later ochraceous to brownish. Edge of pileus first rather sharp, then blunt, fertile, concolorous with pileal surface. Hymenial surface even to more or less convex, first cream-coloured to yellowish, later ochraceous or reddish brown, often obtaining reddish-brown stains when bruised; pores angular, 3–4 per mm, dissepiments thin, uneven to serrate. Section: context cream-coloured to pale ochraceous, watery in fresh condition, compact and sometimes indistinctly fibrillose when dry, up to 6 cm thick; tube layer fragile, concolorous with pore surface, up to 3 cm thick.

Hyphal structure monomitic; all hyphae with clamp connections. Context: hyphae slightly thick-walled, interwoven or arranged in subparallel bundles, (4.0–) 4.7–6.5 (–7.2) μm in diam. (n = 20/1). Tramal hyphae thin- or slightly thick-walled, subparallel, (3.0–) 3.1–5.2 (–5.4) μm in diam. (n = 100/5). Cystidioles absent. Basidia clavate to broadly clavate, four-sterigmatic, (13.8–) 14.0–31.6 (–34.4) × (6.2–) 6.3–10.3 (–12.2) μm (n = 80/4). Basidiospores slightly thick-walled, ellipsoid to ovoid, (5.6–) 6.0–8.2 (–8.8) × (4.2–) 4.5–6.2 (–6.4) μm (n = 196/6), L = 7.07, W = 5.22, Q = 1.35.

Comments.— *Spongipellis profissilis* was described from Japan (Lloyd, 1918, as *Polyporus profissilis*) based on a single collection by Yasuda. Ryvarden (1990) designated it as a lectotype and synonymized *P. profissilis* with *S. delectans*. Our studies of *P. profissilis* type revealed that it certainly belongs to *Spongipellis* sensu stricto and it is conspecific with recent collections from Europe and Asia used in our DNA analyses.

Macroscopically, *S. profissilis* is most similar to *S. spumea*: both species produce large, sappy basidiocarps with relatively large pores (3–4 per mm) and an obtuse margin. These species can be primarily differentiated due to different spore sizes – *S. profissilis* has clearly longer basidiospores with higher Q values than *S. spumea*. However, a few specimens of *S. profissilis* studied by us have spores smaller than usual, overlapping the uppermost variation limits of basidiospores in *S. spumea*. In these intermediary cases, attention should be paid to hymenial cells: *S. profissilis* has in most cases larger basidia than *S. spumea* and it is devoid of cystidioles (they are rather abundant in hymenium of *S. spumea*). Host tree species may also help in identification: it seems that *S. profissilis* is restricted to *Populus* spp. in Europe and cold temperate Asia while *S. spumea* occurs on other broadleaved trees (*Acer, Aesculus, Tilia, Ulmus* etc.).

Spongipellis profissilis is reported here from Northeast China, Japan, Russian Far East and Siberia. Additionally, it was detected in Central Europe (Austria, Czech Republic and Slovakia). It certainly prefers *Populus* spp., although it has been detected also on *Acer* and *Tilia* in warm-temperate forests of East Asia.

Specimens examined.— AUSTRIA. Tyrol, Innsbruck, *Populus alba*, m. Sept., *Litschauer 3106* (H ex W). CHINA. Jilin, Antu Co., Baihe, angiosperm, 06-IX-1993, *Dai 1112* (H), *Tilia* sp., 10-VIII-1997, *Dai 2346* (H), *Acer* sp., 12-VIII-1997, *Dai 2399* (H), Baoma, *Acer* sp., 24-VII-1993, *Dai 694* (H), 07-IX.1993, *Dai 1142* (H), Changbaishan Nat. Res., *Tilia* sp., 03-IX-1993, *Dai 991* (H), 13-IX-1995, *Dai 2064* (H), *Populus* sp., 21-IX-2002, *Dai 3934** (H), Huinan Co., Hongqi, *Acer* sp., 11-X-1993, *Dai 1532* (H). Qinghai, Huzhu Co., Beishan, fallen log, 31-VIII-2003, *Dai 4939* (H). CZECH REPUBLIC. Jihočeský kraj, České Budějovice, Hluboká nad Vltavou, Podskalska louka, *Populus nigra*, XI-2021, *Vlasák 2111/1** (JV, H). JAPAN. Miyagi (lectotype, see above). RUSSIA. Altai Rep., Ulagan Dist., Uchar, *Populus* sp., 03-VIII-2017, *Schigel 7786* (H). Irkutsk Reg., Irkutsk, Central Park, *Populus* sp., 06-VIII-1995, *Kotiranta 11969* (H). Kamchatka Reg., Bystrinsky Dist., Uksichan, *Salix arbutifolia*, 03-VIII-1997, *Kotiranta 12880* (H), Milkovo, *Populus suaveolens*, 27-VIII-1997, *Kotiranta 30527* (H). Khabarovsk Reg., Solnechnyi Dist., Suluk-Makit, *Populus maximowiczii*, 19-VIII-2011, *Spirin 4236* (H). Tuva, Kyzyl, City Park, *Populus* sp., 25-VIII-2014, *Kotiranta 26838* (H), Malyi Yenissei, *Populus* sp., 05-VIII-2014, *Kotiranta 26520* (H), Serlik, *Populus laurifolia*, 18-VIII-2014, *Kotiranta 26690** (H). Zabaikalie Reg., Chita, *Populus* sp., 23-VIII-2010, *Kotiranta 29578* (H).

Spongipellis spumea (Sowerby) Pat.,
Catalogue Raisonné des Plantes Cellulaires de la Tunisie 7: 48, 1897.
Figs. 4, 5.

≡ *Boletus spumeus* Sowerby,
Coloured Figures of English Fungi 2: 89, pl. 211, 1799.
Lectotype (iconotype): Sowersby's original picture, loc. cit. (selected by Ryvarden 1991: 225). Epitype. FINLAND. Uusimaa, Helsinki, Punavuori, Tehtaanpuisto, 60.15877° 24.94118°, living *Ulmus* (80 cm in diam.) in a park, 25-IX-2020, *Miettinen 24146** (H6200666, selected here, MycoBank MBT10008626).

Basidiocarps annual, sessile, widely attached, pilei projecting up to 12 cm and up to 5 cm thick at the base. Upper surface pubescent to hirsute, azonate, first cream-coloured or yellowish, later ochraceous to brownish, in very old basidiocarps dirty grey. Edge of pileus blunt, fertile, concolorous with pileal surface. Hymenial surface even to more or less convex, first cream-coloured to yellowish, later ochraceous or brownish, sometimes obtaining reddish-brown stains when bruised; pores angular, 3–4 (5) per mm, dissepiments thin, uneven to serrate. Section: context cream-coloured to pale ochraceous, watery in fresh condition, strongly fibrous and sometimes indistinctly zonate when dry, up to 4 cm thick; tube layer fragile, concolorous with pore surface, up to 2 cm thick.

Hyphal structure monomitic; all hyphae with clamp connections. Context: hyphae slightly thick-walled, interwoven or arranged in subparallel bundles, (5.2–) 5.7–8.3 (–9.7) μm in diam. (n = 20/1). Tramal hyphae thin- to distinctly thick-walled, subparallel, (2.8–) 2.9–4.9 (–5.3) μm in diam. (n = 100/5). Cystidioles usually rather abundant, tapering, 12–20 × 4–7 μm. Basidia clavate to broadly clavate, four-sterigmatic, (13.2–) 13.3–22.8 (–27.2) × (5.2–) 5.6–8.8 (–10.1) μm (n = 80/4), senescent basidia slightly thick-walled. Basidiospores slightly thick-walled, ellipsoid-ovoid or broadly ellipsoid, more rarely subglobose, (5.1–) 5.2–7.3 (–8.6) × (4.1–) 4.3–5.8 (–6.2) μm (n = 260/8), L = 6.34, W = 5.06, Q = 1.25.

Comments.— *Spongipellis spumea* is a European species with a southern distribution. In North Europe it occurs mostly in parks and gardens, often attacking living maple trees. Morphologically, it is most similar to *S. profissilis* and *S. variispora* – their differences are discussed under those species. No authentic material of *B. spumeus* has survived, and therefore the species was typified with the original illustration by Sowerby (Ryvarden, 1991). Considering that a mere basidiocarp illustration is not enough for reliable species identification, we supplement this typification by selecting an epitype (see above). The epitype was cultured and we have produced a partial genome of it.

Specimens examined.— CZECH REPUBLIC. Jihočeský kraj, Hluboká nad Vltavou, Vondrov, *Aesculus hippocastanum*, 15-IX-1989, *Vlasák 8909/18C** (JV), Castle Park, 21-XI-2015, *Vlasák 1511/6** (JV). Jihomoravský kraj, Břeclav, Valtice, *Quercus cerris*, X-2001, *Vlasák 0110/36*, 0110/37* (JV). Vysočina, Doupě, *A. hippocastanum*, 12-X-2004, *Vampola 200** (H ex MJ). FINLAND. Uusimaa, Espoo, Träskända, *Acer platanoides*, 27.X.2005, *Oksanen 100** (H), 21-XI-2015, *Kotiranta 26889** (H); Helsinki, Kallio, *A. platanoides*, 23-VIII-1984, *Kotiranta 5965* (H), Punavuori, *Ulmus*, 25-IX-2020, *Miettinen 24146** (H, epitype), Viikki, *Acer platanoides*, 26-IX-2002, *Miettinen 6716** (H). Etelä-Häme, Nokia, Maatiala, *Ulmus laevis*, 15.X.1993, *Syrjänen* (H). NORWAY. Oslo, Blindern, *A. platanoides*, 26-IX-1990, *Niemelä 5426* (H). RUSSIA. Nizhny Novgorod Reg., Lukoyanov Dist., Razino, *Tilia cordata*, 28-IX-2013, *Spirin 6741** (H), *U. laevis*, 08-VIII-2014, *Spirin 7213* (H), Sanki, *Ulmus scabra*, 11-VIII-2016, *Spirin 10651* (H). SWEDEN. Uppland, Stockholm, Stadshuset, *A. hippocastanum*, 23-XI-1981, *Nordin* (H).

Spongipellis variispora Spirin, Miettinen & Vlasák, sp. nova – Figs. 4, 5.

Holotype. RUSSIA. Khabarovsk Reg., Khabarovsk, City Arboretum, 48.4824° 135.082°, base of a living *Ulmus pumila*, 02-VIII-2011, *Spirin 3737** (H7021424).
Etymology. Variisporus (Lat., adj.) – referring to variable size of basidiospores.
MycoBank MB845182

Basidiocarps annual, sessile, widely attached, projecting up to 8 cm, more rarely effused-reflexed and up to 4 cm thick at the base. Upper surface pubescent to hirsute, azonate, first cream-coloured, later yellowish to pale ochraceous, wrinkled after drying. Edge of pileus blunt, fertile, concolorous with pileal surface. Hymenial surface even to concave, first cream-coloured to yellowish, later pale ochraceous to brownish, sometimes obtaining reddish-brown stains when bruised; pores angular, 4–6 per mm, dissepiments thin, uneven to serrate. Section: context cream-coloured to pale ochraceous, watery in fresh condition, spongy and indistinctly zonate when dry, up to 1.5 cm thick; tube layer fragile, concolorous with pore surface, up to 1 cm thick.

Hyphal structure monomitic; all hyphae with clamp connections. Context: hyphae moderately thick-walled (walls up to 1.5 μm), interwoven or arranged in subparallel bundles, (4.2–) 4.4–6.6 (–7.3) μm in diam. (n = 20/1). Tramal hyphae thin- or slightly thick-walled, subparallel, (3.0–) 3.1–4.8 (–5.2) μm in diam. (n = 60/3). Subhymenial hyphae thin-walled, 3–4 μm in diam. Cystidioles present, rather abundant, tapering, 11–20 × 4–6.5 μm. Basidia clavate to broadly clavate, four-sterigmatic, (11.7–) 12.1–20.1 (–23.2) × (5.4–) 5.7–8.8 (–10.1) μm (n = 40/2). Basidiospores thick-walled, broadly ellipsoid to subglobose, (4.8–) 5.1–7.3 (–8.5) ×(4.0–) 4.2–6.2 (–7.2) μm (n = 180/6), L = 6.15, W = 5.19, Q = 1.19, normally with prominent, asymmetric apiculus sometimes shifted to the ventral side; abnormal spores reaching 9 × 7.5 μm excluded from measurements.

Comments.— *Spongipellis variispora* is most similar to *S. profissilis* and *S. spumea*, although it differs from them in having smaller pores and basidiospores with a distinct apiculus occasionally shifted to the ventral side (Fig. 5). *Spongipellis ambiens* is another small-pored species occurring in East Asia. It possesses on average smaller basidiospores than *S. variispora* (Fig. 6). However, juvenile individuals of *S. variispora* may have basidiospores of approximately the same size as in *S. ambiens*. In these cases, macroscopic traits help in the identification of these species. Basidiocarps of *S.*

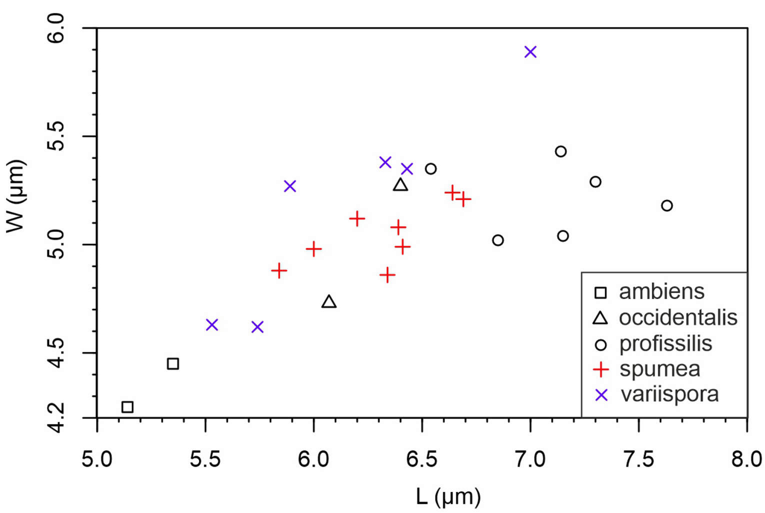

Fig. 6. Average basidiospore size of specimens of *Spongipellis* spp.

Fig. 6. Tamaño promedio de basidiosporas de especímenes de *Spongipellis* spp.

variispora are more or less triangular in section, with obtuse margin, and hairs on its pileal surface (if present) show no signs of regular arrangement. In turn, *S. ambiens* has thinner, flabelliform pilei with a sharp edge; hairs on the upper surface show a tendency to radial arrangement at least at the very base of basidiocarps.

Spongipellis variispora is widely distributed in temperate Russian Far East and adjacent parts of China. Usually, it inhabits old but still growing deciduous trees, in particular *Ulmus* spp.

Specimens examined.— CHINA. Jilin Prov., Antu Co., Baihe, *Tilia* sp., 06-IX-1993, *Dai 1108* (H), Baoma, *Ulmus* sp., 07-IX.1993, *Dai 1126* (H), Changbaishan Nat. Res., angiosperm, 16-VII-1993, *Dai 535* (H), *Acer* sp., 15-VIII-1997, *Dai 2509* (H), 19-IX-1998, *Niemelä 6423** (H), Fushong Co., Shuguang, *Ulmus* sp., 20-VII-1993, *Dai 606* (H). Liaoning, Shenyang, Botanical Garden, *Rhamnus* sp., 21-VIII-2005, *Miettinen 10441* (H). RUSSIA. Khabarovsk Reg., Khabarovsk Dist., Bolshoi Khekhtsir Nat. Res., *Fraxinus mandshurica*, 02-IX-2013, *Spirin 6558* (H); Khabarovsk, City Arboretum (holotype, see above); Komsomolsk-na-Amure, *U. pumila*, 30–31-VIII-2016, *Spirin 10708**, *10711** (H). Primorie Reg., Spassk Dist., Spassk-Dalnii, *Acer* sp., 23-VII-2018, *Kotiranta 28655* (H), Ussuriisk Dist., Ussuri Nat. Park., *Ulmus* sp., 29-VII-2018, *Kotiranta 28743* (H), *Acer* sp., 02-VIII-2018, *Kotiranta 28807* (H). Zabaikalie Reg., Ononsky Dist., Nizhny Zasuzej, *U. pumila*, 04-IX-2010, *Kotiranta 29892* (H).

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BIBLIOGRAPHY

Binder, M., Justo, A., Riley, R., Salamov, A., Lopez-Giraldez, F., Sjökvist, E., Copeland, A., Foster, B., Sun, H., Larsson, E., Larsson, K. H., Townsend, J., Grigoriev, I. V. & Hibbett, D. S. (2013). Phylogenetic and phylogenomic overview of the Polyporales. *Mycologia 105*: 1350-1373.

Bondartsev, A. & Singer, R. (1941). Zur Systematik der Polyporaceae. *Annales Mycologici 39*: 43-65.

Darriba, D., Posada, D., Kozlov, A. M., Stamatakis, A., Morel, B. & Flouri, T. (2020). ModelTest-NG: A New and Scalable Tool for the Selection of DNA and Protein Evolutionary Models. *Molecular Biology & Evolution 37* (1): 291-294. doi:10.1093/molbev/msz189

Dvořák, D., Běťák, J. & Tomšovský, M. (2014). *Aurantiporus alborubescens* (Basidiomycota, Polyporales) – first record in the Carpatians and notes on its systematic position. *Czech Mycology 66*: 71-84.

Justo, A., Miettinen, O., Floudas, D., Ortiz-Santana, B., Sjökvist, E., Lindner, D., Nakasone, K., Niemelä, T., Larsson, K. H., Ryvarden, L. & Hibbett, D. S. (2017).

A revised family-level classification of the Polyporales (Basidiomycota). *Fungal Biology 121* (9): 798-824. doi:10.1016/j.funbio.2017.05.010

Karsten, P. A. (1906). Fungi in Transbaicalia, paucis exceptis, prope fontes minerales Yamarovka aestate ann. 1904 et 1905 a clar. P. Mikhno collecti. Travaux de la Sous-Section de Troïtzkossawsk-Kiakhta, *Section du pays d'Amour de la Société Impériale Russe de Géographie 8* (1): 60-64.

Karsten, P. A. (1911) Fungi in Transbaicalia imprimis prope oppidum Tchita ann. 1908 et 1909 a cl. P. Mikhno collecti. Travaux de la Sous-Section de Troïtzkossawsk-Kiakhta, *Section du pays d'Amour de la Société Impériale Russe de Géographie 12* (1/2): 108-113.

Kotiranta, H., Kulju, M. & Miettinen, O. (2017). *Caudicicola gracilis* (Polyporales, Basidiomycota), a new polypore species and genus from Finland. *Annales Botanici Fennici 54*: 159-167. doi:10.5735/085.054.0325

Kotiranta, H. & Penzina, T. (2001). *Spongipellis sibirica*, comb. nov. (Basidiomycetes), and its affinities to the polypore genera *Tyromyces*, *Aurantioporus* and *Climacocystis*. *Annales Botanici Fennici 38*: 201-209.

Kutuzova, I. A., Kokaeva, L. Y., Pobendinskaya, M. A., Krutyakov, Y., Skolotneva, E., Chudinova, E. & Elansky, S. (2017). Resistance of *Helminthosporium solani* strains to selected fungicides applied for tuber treatment. *Journal of Plant Pathology 99*: 635-642.

Langmead, B. & Salzberg, S. L. (2012). Fast gapped-read alignment with Bowtie 2. *Nature Methods 9* (4): 357-359.

Li, D., Liu, C. M., Luo, R., Sadakane, K. & Lam, T. W. (2015). MEGAHIT: an ultra-fast single-node solution for large and complex metagenomics assembly via succinct de Bruijn graph. *Bioinformatics 31* (10): 1674-1676.

Lloyd, C. G. (1918). Mycological notes 56. *Mycological Writings 5*: 797-812.

Lowe, J. L. (1956). Type studies of the polypores described by Karsten. *Mycologia 48*: 99-125.

Lowe, J. L. (1975). Polyporaceae of North America. The genus *Tyromyces*. *Mycotaxon 2*: 1-82.

Löytynoja, A. & Goldman, N. (2010). webPRANK: a phylogeny-aware multiple sequence aligner with interactive alignment browser. *BMC Bioinformatics 11*: 579. doi:10.1186/1471-2105-11-579

Matheny, P. B. (2005). Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (*Inocybe*; Agaricales). *Molecular Phylogenetics and Evolution 35* (1): 1-20.

Matheny, P. B., Liu, Y. J., Ammirati, J. F. & Hall, B. D. (2002). Using RPB1 sequences to improve phylogenetic inference among mushrooms (*Inocybe*, Agaricales). *American Journal of Botany 89* (4): 688-698.

Miettinen, O., Vlasák, J., Rivoire, B. & Spirin, V. (2018). *Postia caesia* complex (Polyporales, Basidiomycota) in temperate Northern Hemisphere. *Fungal Systematics and Evolution 1*: 101-129.

Müller, J., Müller K. & Quandt, D. (2010). PhyDE – Phylogenetic Data Editor, version 0.997. Retrieved from http://phyde.de

Rehner, S. A. & Buckley, E. (2005). A *Beauveria* phylogeny inferred from nuclear ITS and EF1-á sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs. *Mycologia* 97: 84-98.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M. A. & Huelsenbeck, J. P. (2012). MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology 61* (3): 539-542. doi:10.1093/sysbio/sys029

Ryvarden, L. (1990). Type studies in the Polyporaceae. 22. Species described by C.G. Lloyd in *Polyporus*. *Mycotaxon* 38: 83-102.

Ryvarden, L. (1991). Genera of polypores. *Synopsis Fungorum 5*: 1-363.

Saccardo, P. A. & Trotter, A. (1912). Supplementum universale. Pars VIII. *Sylloge Fungorum 21*: 1-928.

Spirin, V., Vlasák, J., Niemelä, T. & Miettinen, O. (2013). What is *Antrodia* sensu stricto? *Mycologia 15*: 1555-1576.

Tomšovský, M. (2012). Delimitation of an almost forgotten species *Spongipellis litschaueri* (Polyporales, Basidiomycota) and its phylogenetic position within the genus. *Mycological Progress 11*: 415-424.

Vilgalys, R. & Hester, M. (1990). Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology 172* (8): 4238-4246.

Wang, C.G. & Dai, Y.C. (2022). Phylogeny and taxonomy of *Spongipellis* (Polyporales, Basidiomycota) and its micromorphological similar genera. *Mycological Progress* 21 (73): 1-18.

White, T. J., Bruns, T., Lee, S. & Taylor, J. W. (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: M.A. Innis, D.H. Gelfand, J.J. Sinisky & T.J. White (Eds.), PCR protocols, a guide to method and application (pp. 315-322). San Diego: Academic Press.