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Geographic distribution of *Sarcoporia polyspora* and *S. longitubulata* sp. nov.

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ABSTRACT — DNA study of *Sarcoporia polyspora* (= *Parmastomyces transmutans*) revealed only negligible sequence differences between conifer-dwelling specimens with cartilaginous layer in the context from USA, Brazil, Europe, and Far East Asia, but a very different sequence from three resupinate and hardwood-bound collections without such a layer and with slightly narrower and pale brown spores from USA and Madeira Islands. This fungus, found also among historical USA collections of *S. polyspora* in the BPI herbarium, is described here as *Sarcoporia longitubulata*. The phylogenetic position of *Sarcoporia* is discussed.

KEY WORDS — *Basidiomycota*, brown rot fungi, molecular taxonomy, *Parmastomyces kravtzevianus*

Introduction

Sarcoporia polyspora P. Karst. is a very distinct, brown-rot polypore with soft, resupinate to effused-reflexed basidiomes that are white to crème at first but turn reddish-brown after bruising or drying. It can be easily recognized by its ellipsoid and thick-walled, dextrinoid spores, which are quite unique in polypores. The species is rare in Europe but rather common in North America (on *Tsuga* spp. and *Pinus* spp.) and in Asia (Vlasák & Kout 2010, Dai 2012). The fungus was described by Karsten (1894) but Karsten's name was abandoned for years. Based on collections from Estonia and Siberia, it was independently described by Parmasto (1957) as *Tyromyces kravtzevianus* Bondartsev & Parmasto, and a few years later Kotlaba & Pouzar (1964) created the genus *Parmastomyces* for this unique polypore. In the USA, Overholts (1941) described this species (invalidly, without a Latin diagnosis) as "*Polyporus subcartilagineus*." Later he described still another species, *Polyporus*

transmutans Overh., which he distinguished by the more distinctly pileate habit and its growth on *Prunus* (Overholts 1952). Ryvarden & Gilbertson (1984), who found the type of *P. transmutans* identical with "*P. subcartilagineus*" as well as with European specimens of *Parmastomyces kravtzevianus*, coined the name *Parmastomyces transmutans* (Overh.) Ryvarden & Gilb. for all collections with typical spores. Niemelä et al. (2005), however, studied Karsten's type material and re-established the oldest name, *Sarcoporia polyspora*, for this species.

Somewhat aberrant morphology of some recent collections from hardwood hosts and conifers led us to question the identity of Eurasian/American and of hardwood/conifer-inhabiting *Sarcoporia*. We have sampled European, American, and Asian collections from conifers and hardwoods and also studied the type of *Polyporus transmutans* from the BPI herbarium along with several other American BPI collections determined as *P. transmutans* to explore whether or not all these specimens represent the same species.

Materials & methods

Morphological study

The studied specimens are deposited in the US National Fungus collection, Beltsville, USA (BPI), in private herbarium of J. Vlasák (JV), and in mycological herbarium of Finnish Museum of Natural History, University of Helsinki, Finland (H). They were examined from slides prepared in cotton blue (CB) and Melzer's reagent (IKI) with a Leitz Diaplan microscope ($\times 1250$ magnification). Measurements were done in cotton blue using phase contrast illumination and oil immersion (with a subjective accuracy of $0.1 \mu\text{m}$; Miettinen et al. 2006). For presenting the size range of basidiospores, 5% of the measurements were excluded from each end of the range and are given in parentheses. The following abbreviations are used: L' = basidiospore length, L = mean basidiospore length (arithmetical average of all basidiospores), W' = basidiospore width, W = mean basidiospore width (arithmetical average of all basidiospores), $Q = L'/W'$ ratio range, and n = the number of basidiospores measured from given number of specimens. KOH- indicates unchanged in 5% KOH and IKI- indicates unchanged in Melzer's reagent.

Molecular phylogeny

DNA isolation and nrDNA ITS region sequencing methods follow Vlasák & Kout (2011). The sequences were aligned with Clustal X and manually pruned. Evolutionary analyses were conducted in MEGA6 (Tamura et al. 2013) using "all sites" and "uniform rates" options. Other options, such as "complete deletion" and "gamma distributed with invariant sites," and all their combinations provided virtually identical phylogeny.

Results

Phylogenetic analysis

Sarcoporia specimens collected on hardwoods and conifers in the USA, Madeira Island, Czech Republic, and European and Far East Russia were

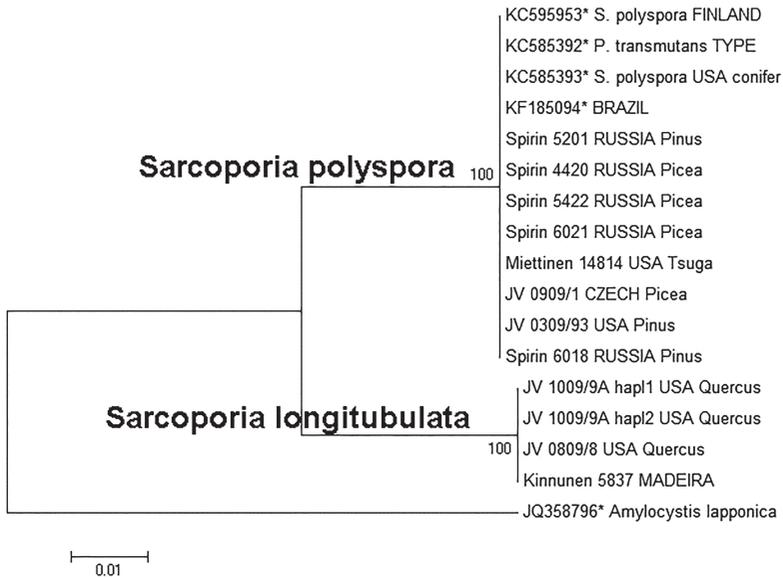


FIGURE 1: Phylogenetic relationships of 15 *Sarcoporia* specimens inferred from ITS rRNA sequences. *Amylocystis lapponica* was used as outgroup. Topology from maximum likelihood (ML) analysis. Support values along branches from ML bootstrap (1000 replicates). Branch lengths are drawn proportional to the number of substitutions per site. GenBank numbers with asterisk indicate sequences retrieved from GenBank; other GenBank numbers in Specimens examined.

sequenced and compared with *Sarcoporia* sequences in GenBank. A total of 14 ITS and 2 nuLSU sequences were newly generated for this study and deposited in GenBank. The ITS dataset comprising 16 sequences resulted in an alignment with 653 characters, of which 81 were variable and 30 parsimony informative. Extremely high sequence conservation could be demonstrated among all conifer-dwelling specimens from different continents, with Eurasian specimens differing from American in only one base insertion in ITS1 and some specimens showing two haplotypes, with and without this insertion (not shown in FIG. 1). On the other hand, most of hardwood-dwelling specimens showed a very different sequence with about 40 mutations in ITS region. Similarly large sequence differences were found with the nuLSU sequence dataset (not shown), using only two sequences from each species. The aberrant hardwood specimens were also characterized by very thick and soft resupinate basidiocarps with long tubes and thin subiculum without cartilaginous layer. They are described below as a new species, *S. longitubulata*.

Taxonomy

Sarcoporia longitubulata Vlasák & Spirin, **sp. nov.**

FIGS 2– 4

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Sarcoporiae polysporae *similis*, *sed tubulis longis et sporis coloratis*.

TYPE: USA, Pennsylvania: Phoenixville, Schuylkill Canal, Ravine Trail, log of *Quercus*, 2 Sep 2008, J. Vlasák JV 0809/8 (Holotype, BPI 892956; isotypes, JV, H; GenBank, KM207860, KM207863).

ETYMOLOGY: *longitubulata* (Lat.), referring to the very long tubes found in most of the collected specimens.

BASIDIOMES annual, resupinate, pulvinaceous, up to 20 cm long, 15 cm wide, and 2 cm thick, strikingly soft to downy, drying brittle; margin whitish to crème, about 1 mm broad, soft and cottony, later indistinct; pore surface at first crème with reddish tints, distinctly reddish-brown after bruising, brown to blackish-brown on drying, the pores circular, with thin dissepiments, 3–5 per mm; context 1–3 mm thick, soft and cottony, persistently crème colored; tube layer very thick, up to 20 mm, extremely brittle and shattering easily when dry, crème at first but deep brown when dry and contrasting with crème subiculum. Spore print brown.

HYPHAL STRUCTURE monomitic; hyphae with clamp connections, KOH–, IKI–. CONTEXT. Hyphae arranged in subparallel bundles, mostly thin-walled, 4–10 µm in diam., some hyphae with thick-walls and refractive, hyaline or pale

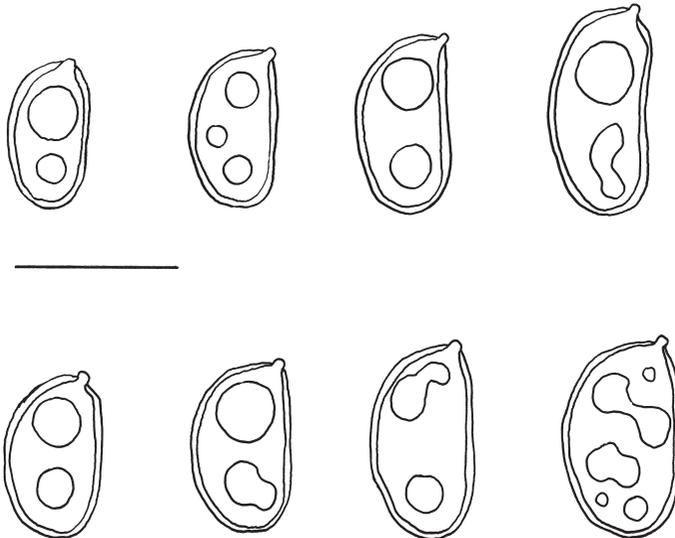


FIGURE 2: *Sarcoporia* basidiospores: above – *S. longitubulata* (holotype); below – *S. polyspora* (lectotype). Scale bar = 5 µm.



FIGURE 3: *Sarcoporia longitubulata* (JV 0809/8, holotype), underside of oak log, photo in situ. Spore deposits below left.

brown, with cyanophilous content, strongly inflated at septa, 7–18(–22) μm in diam., occasionally with double clamps. TUBES. Hyphae subparallel, rather loosely arranged, thin-walled, hyaline, easily collapsing, some with cyanophilous content, (3.5–)4–5(–6) μm in diam. Cystidia absent. BASIDIOSPORES thick-walled, brownish, oblong-ellipsoid, ventral side slightly concave or rarely flat, dextrinoid, a few spores weakly or moderately cyanophilous, (4.3–)4.4–6.2 (–7.2) \times (2.3–)2.5–3.3(–3.5) μm ($n = 150/5$), $L = 5.29$, $W = 2.88$, $Q = 1.78$ –1.93.

DISTRIBUTION & ECOLOGY. On hardwood logs (predominantly *Quercus* spp.) in the US North-East (Michigan, New York, Pennsylvania, Tennessee) and Macaronesia (Madeira Is.); causing a brown rot.

ADDITIONAL SPECIMENS EXAMINED: PORTUGAL. MADEIRA: Madeira Island, 3 km W from Funchal, fallen angiosperm logs, 19 Jan 2011, Kinnunen 5837 (H, GenBank KM207865), 5845, 5848 (H). USA. PENNSYLVANIA: Gettysburg, Big Round Top, *Quercus*, 5 Sep 2010, Vlasák JV 1009/9A (JV, H, GenBank KM207861, KM207862, KM207864). MICHIGAN: Ann Arbor, hardwood, Jul 1958, Wehmeyer (BPI 223824). NEW YORK: Rye, *Quercus*, 30 Oct 1980, Stein (BPI 222859). TENNESSEE: Great Smoky Mt., New Found Gap, *Fagus*, 9 Sep 2005, Vlasák JV 0509/103 (JV, H).

COMMENTS. Macroscopically, *S. longitubulata* is very distinct, so that we felt certain from first glance that it must be a different species (FIGS 3, 4). The brown spore deposits around the basidiocarp, the very long and soft tubes, and the relatively thin subiculum lacking a cartilaginous layer are its most striking morphological features. *Sarcoporia polyspora* produces white spore deposits and more or less pileate basidiocarps with short tubes and a thick subiculum containing a distinct cartilaginous layer. We noted no odor of fresh



FIGURE 4: *Sarcoporia longitubulata* (JV 0809/8, holotype), underside of oak log, photo in situ.

basidiocarps, but on drying, *S. longitubulata* smelled so repugnantly that it was impossible to keep in the same room for more than one week, although it was not contaminated with yeasts. The primary microscopic difference of *S. longitubulata* is the pale brown coloration of the basidiospores, visible in cotton blue even with low resolution; only a few spores are more or less stained (slightly or moderately cyanophilous). In contrast, *S. polyspora* basidiospores are exceptionally strongly cyanophilous (uniformly bright blue), so that their natural color is totally undetectable in cotton blue. Moreover, the *S. longitubulata* spores are a bit narrower than in *S. polyspora* (TABLE 1) and less variable in shape and size, being uniformly oblong-ellipsoid and slightly concave on their ventral side (FIG. 2). The basidiospores of this type occur in *S. polyspora*, too, but only as a rare variation.

Discussion

We have shown that *S. polyspora* is widely distributed from America to Europe and Far East Asia. The slight morphological differences we observed—e.g., longer spores and more pileate habit in USA collections vs. shorter spores in Far East Asian collections—have no support in DNA sequence differences and so should be regarded as regional morphological variation. A tropical distribution remains uncertain, as the sequenced specimens from Brazil were collected from *Pinus* logs probably imported from the USA (Baldoni et al. 2015).

All studied collections were from conifers except for BPI 844703, the type of *Polyporus transmutans* (Overholts 1952), collected on *Prunus serotina* Ehrh. in northwestern USA. This specimen displays strikingly large and tough pilei with

TABLE 1. Spore measurements of two *Sarcoporia* species. (Limit and mean values for each species shown in bold.)

SPECIES / SPECIMEN	L'	L	W'	W	Q	n
<i>S. polyspora</i>	(4.2)4.7–7.2(7.3)	5.53	(2.5)2.6–3.8(4.0)	3.10	1.79	270
Miettinen 14814	(5.0)5.1–6.3(6.7)	5.64	(2.7)2.8–3.6(4.2)	3.14	1.81	30
Spirin 4420	(4.9)5.0–6.3(6.7)	5.51	(2.7)2.8–3.2(3.3)	2.97	1.86	30
Spirin 5201	(4.2)4.7–5.7(5.8)	5.05	(2.6)2.7–3.3	3.02	1.68	30
Spirin 5422	(4.7)4.8–5.7(7.1)	5.22	(2.5)2.6–3.2(3.3)	2.93	1.79	30
Spirin 6021	(4.8)5.2–6.8(7.3)	5.70	(2.6)2.7–3.6(3.7)	3.07	1.86	30
Spirin 6018	(4.8)4.9–6.1(6.2)	5.30	(2.7)2.8–3.4(3.7)	3.11	1.71	30
Vlasák 0908/15	(4.8)5.0–6.2(6.4)	5.56	(2.7)2.8–3.7(3.9)	3.17	1.76	30
Vlasák 0309/93	(5.2)5.3–7.2(7.3)	6.27	(2.8)2.9–3.8(4.0)	3.19	1.97	30
<i>S. longitubulata</i>	(4.3)4.4–6.2(7.2)	5.29	(2.3)2.5–3.3(3.5)	2.88	1.84	150
Vlasák 0809/8	(4.3)4.4–5.8(6.0)	5.03	(2.6)2.7–3.1(3.3)	2.82	1.79	30
Vlasák 1009/9a	(4.6)4.8–6.2(6.3)	5.42	(2.3)2.5–3.2(3.3)	2.82	1.93	30
Vlasák 0509/103	(4.4)4.8–5.8(7.2)	5.30	(2.7)2.8–3.3(3.5)	2.97	1.78	30
BPI 222859	(4.8)4.9–6.2(6.7)	5.39	(2.6)2.7–3.2(3.3)	2.90	1.86	30
BPI 223824	(4.8)4.9–6.0	5.32	(2.5)2.6–3.3(3.4)	2.91	1.83	30

short tubes and thick context in which no distinct gelatinous layer is present but scattered gelatinous streaks are present. This suggests just a very large specimen of *S. polyspora* and our examination revealed no distinct microscopic differences from other *S. polyspora* specimens. Moreover, the ITS sequence of the culture derived from this specimen available in GenBank (KC585392; Ortiz-Santana et al. 2013) is identical with other *S. polyspora* sequences.

When we sought for a possible existing name for *S. longitubulata*, *Tyromyces mollissimus* Maire, described from North Africa (Maire 1945) and presently regarded as a synonym of *S. polyspora*, seemed a reasonable candidate. Unfortunately, the type material is now unavailable (Pouzar 1984, Kotiranta 1998). Nevertheless, the protologue of *T. mollissimus* is very clear and leaves no doubts about its identity: it was described as growing on *Pinus halepensis* Mill. and having pileate or effused-reflexed, very soft basidiocarps with thick contextual layer (see fig. 7b, Maire 1945: 37), and a white spore print. All these features fit well with the current concept of *S. polyspora* and certainly rule out our new species. The recently described *Sarcoporia neotropica* from Costa Rica (Ryvarden 2013) has imbricate soft basidiocarps and hyaline basidiospores, characters that preclude its identity with *S. longitubulata*.

Because of similar spores and some of tissue features, Ryvarden & Melo (2014) speculated about *Sarcoporia*'s position in the *Coniophoraceae*. Molecular phylogeny refutes this hypothesis, however. The sequences of typical

coniophoraceous species such as *Coniophora puteana* (Schumach.) P. Karst. and *Serpula lacrymans* (Wulfen) J. Schröt. differ greatly from *Sarcoporia*, which has already been recognized as a member of “antrodia clade” within the *Polyporaceae*, most closely related to *Amylocystis* and *Auriporia* (Ortiz-Santana et al. 2013). *Amylocystis lapponica* (Romell) Bondartsev & Singer, is in fact quite similar, being soft and turning reddish brown after bruising and drying, causing a brown rot, and with some microstructures staining in Melzer’s reagent. *Bondarceomyces taxi* (Bondartsev) Parmasto, which was once referred to *Parmastomyces* (= *Sarcoporia* in current sense) by Dai & Niemelä (1995), belongs to the *Boletales* (Binder & Hibbett 2006). It does share some characters with *S. longitubulata* (brownish spores, strong pungent odor of drying basidiocarps) although they indicate only superficial similarity.

ADDITIONAL MATERIAL EXAMINED: *Sarcoporia polyspora*. CZECH REPUBLIC. Hluboká, Karluv Hradek, *Picea abies*, 2 Sep 2009 Vlasák JV 0909/1 (JV, GenBank KM207858, KM207859), 11 Aug 2009, Vlasák JV 0908/15 (JV, PRM 915664, H). FINLAND. UUSIMAA: Inkoo, Fagervik, Sept 1893, Hisinger (H) (lectotype of *S. polyspora*; Lowe 1956). RUSSIA. KHABAROVSK REG.: Khabarovsk Dist., Ulika, *Pinus koraiensis*, 13 Aug 2012, Spirin 5201 (H, GenBank KM207856, KM207857), Malyi Kukachan, *Picea ajanensis*, 19 Aug 2012, Spirin 5422 (H, GenBank KM207852); Solnechnyi Dist., Evoron, *Picea obovata*, 27 Aug 2011, Spirin 4420 (H, GenBank KM207853). NIZHNY NOVGOROD REG.: Lukoyanov Dist., Panzelka, *Pinus sylvestris*, 8 Aug 2013, Spirin 6018 (H, GenBank KM207851), *Picea abies*, 8 Aug 2013, Spirin 6021 (H, GenBank KM207854, KM207855). USA. MASSACHUSETTS: Holden, Quinapoxet, *Tsuga canadensis*, 26 Sep 2011, Miettinen 14814.1 (H, GenBank KM207850). PENNSYLVANIA: Wilkes-Barre, Ricketts Glen St. Park, *Pinus*, 11 Sep 2003, Vlasák JV 0309/93 (JV, H, GenBank KM207849); Haycock, Nockamixon St. Park, *Pinus strobus*, 7 Aug 2004, Vlasák Jr. JV 0408/4J (JV); McKean Co., *Prunus serotina*, 10 Sep 1940, Campbell & Davidson 22971 (BPI 844703, holotype of *Polyporus transmutans*, GenBank KC585392). NEW YORK: Adirondack Park, Keene Valley, Johns Brook Trail, conifer, 23 Sep 2005, Vlasák Jr. JV 0509/193J (JV).

Bondarceomyces taxi. RUSSIA. KHABAROVSK REG.: Khabarovsk Dist., Bol’shoi Khekhtsir Nat Res., *Picea ajanensis*, 5 Sep 2013, Spirin 6674 (H, JV); Komsomol’sk Dist., Boktor, *Larix gmelinii*, 18 Aug 2013, Spirin 6141 (H, JV).

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