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Searching for indicator species of old-growth spruce forests: studies in the genus *Jahnoporus* (Polyporales, Basidiomycota)

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Abstract – *Jahnoporus hirtus* is an old-growth forests inhabiting polypore distributed widely in the northern hemisphere. Our morphological, ecological and DNA data confirm that at least three closely related species exist under that name. *Jahnoporus hirtus* in the strict sense is distributed in old mountain forests of Central Europe and North America, and it inhabits many conifer substrates. *Jahnoporus brachiatus* sp. nov. is an East Asian species, found in the secondary lowland forest. Its close relative, the East Asian *J. oreinus* sp. nov. is a strong indicator of pristine spruce forests in highlands.

Forest conservation / polypores / wood-rotting fungi

INTRODUCTION

Diversity and natural dynamics of wood-inhabiting fungi in the old-growth spruce (*Picea* spp.) forests have been a popular subject of ecological research for decades. This forest type has drawn research and conservation attention due to the threat of industrial logging and consequent disappearance of pristine habitats, especially in North Europe, Siberia and East Asia (Penttilä *et al*., 2006; Siitonen, 2010; Baltzer, 2010; Josephson *et al.*, 2013). Peculiar biology of spruce is an important reason for fragility of spruce forests: spruce species possess rather weak ability to regenerate naturally after clearcut logging or wild fires (Kuuluvainen, 1994; Yaroshenko *et al*., 2001; Zielonka & Niklasson, 2001; Krestov, 2003).

Along with lichens and bryophytes, wood-decaying fungi (polypores, in particular) constitute a key component of species diversity in spruce-dominated forests, while the species richness of higher plants is usually comparatively low. Decay fungi form the basis of the saprotrophic wood web, which supports high

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insect species richness. Therefore the strong argument for forest conservation and protection is a presence and (or) abundance of easily detectable species (the so called "indicator species") from the aforementioned groups limited to rare or threatened forest types, such as old-growth forests (Nordén & Appelqvist, 2001; Hottola & Siitonen, 2008; Halme, 2010).

The wood-inhabiting polypore *Jahnoporus hirtus* (Quél. ex Cooke) Nuss was described from Switzerland (Quélet, 1873). It is considered very rare in Europe, so far known only from 7 localities in Czech Republic, France, Germany and Switzerland (Jahn, 1973; Keller, 1977; Antonín *et al*., 1989; Vlásak & Kout, 2010). All European records come from old-growth mountain spruce-dominated forests, with *Abies* and *Picea* as host trees. In addition, *J. hirtus* has been reported from North America (Gilbertson & Ryvarden, 1986) and East Asia (Ljubarsky, 1962; Dai, 2000) but considered a rarity everywhere. Núñez & Ryvarden (2001) emphasized stipitate, fleshy, large-pored basidiocarps with dark-colored hispid upper surface, monomitic hyphal structure and long, spindle-like basidiospores as the most distinctive features of this peculiar polypore.

Starting from 2011, the first and the third authors of this paper have prepared intensive plot studies in spruce-dominated forests of Russian Far East (Khabarovsk and Primorie Regions). The main purpose of these studies is to estimate diversity and abundance of wood-inhabiting fungi and create a list of indicator species. In 2011 and 2013, a polypore tentatively labelled as *J. hirtus* was found in virgin highland spruce forests (alt. 800–1100 m). At the same time, one more specimen of *J. hirtus* sensu lato was collected in the secondary lowland mixed forest (alt. 140 m) dominated by *Quercus mongolica*. The striking difference of these habitats forced us to check morphological characters and DNA sequences of our collections closely and compare them with European and North American specimens of *J. hirtus*. As a result, two new species of *Jahnoporus* are introduced below, and identity of *J. hirtus* in the strict sense is discussed. We propose that one of the new species, *J. oreinus*, is a strong indicator of untouched spruce-dominated forests in East Asia.

MATERIAL AND METHODS

Morphological protocols. Pore measuring and microscopic routine follow Miettinen *et al*. (2012). The following abbreviations are used in the species descriptions: L – mean spore length, W – mean spore width, Q – mean length / width ratio. For presenting a variation of setae and spore size, 5% of measurements have been excluded from each end of the range, and are given in parentheses.

Molecular protocols. DNA extraction and sequencing. An amount of 0.25 g of context tissue was disintegrated for 60 s with an MM301 RETSCH steel ball mixer mill at room temperature. DNA was isolated using the CTAB/NaCl extraction buffer as de-scribed by Murray & Thompson (1980), followed by repeated extraction with chloroform and isopropanol precipitation. Crude DNA was dissolved in 100 µl of sterile water and further purified using Promega Wizard Clean Up kit. The resulting DNA solution (50 µl) was diluted ten times and 1 µl was used as a template for amplification with ITS5 and ITS4 primers (White *et al*., 1990) in 25 µl reaction mixture using an annealing temperature of 55°C. Amplified DNA was sequenced in the Genomics laboratory of the Biology Centre, Academy of Sciences of the Czech Republic, České Budějovice, on an ABI 3730xl DNA analyzer, using a BigDye

Terminator 3.1 kit. We produced nrDNA ITS sequences of six *Jahnoporus* specimens, and in addition used two sequences from GenBank. ITS sequences were aligned manually in PhyDE (Müller *et al*., 2010). Following AIC in Jmodeltest (Darriba *et al*., 2012) we used HKY as the substitution model in the phylogenetic analysis. We constructed the phylogram by using MrBayes 3.2 (Ronquist *et al*., 2012), 2 runs with 8 chains each run for 2 million generations, sampling every 1000 generations, burnin 25%. Convergence between the runs was excellent (average st. dev. of split frequencies < 0.01).

Sampling. Specimens for this study were collected in Russian Far East (VS and BM), Czech Republic (JV) and the US North-West (OM and VS). Specimens studied are kept in mycological herbarium of Finnish Museum of Natural History, University of Helsinki (H), Field Museum of Natural History, Chicago (F), and in private herbarium of the author JV (Czech Republic). In addition, type specimen of *Polyporus hispidellus* from herbarium of New York State (NYS), as well as 2 collections of *J. hirtus* from herbarium of Center for Forest Mycology Research (CFMR), were studied. Sequenced collections are marked by asterisk (*), GenBank accession numbers are given in parentheses.

– *J. brachiatus*. Russia. Khabarovsk Reg.: Komsomolsk Dist., Boktor, on buried wood in mixed forest, 18 August 2013, Spirin 6116* (H, holotype – see below) (X3232, GenBank KU165781).

– *J. hirtus*. Czech Republic. South Bohemia: Hluboká nad Vltavou, Libochovka Nat. Res., *Picea abies*, August 2011, Vlasák 1108/1* (JV, H) (X3231, GenBank KU165782). USA. Arizona: Graham Co., Shannon Campground, *Pseudotsuga menziesii*, 31 August 1973, Lindsey 293 (CFMR). New York: Essex Co., North Elba, buried wood, August 1898, Peck (NYS F1480, holotype of *Polyporus hispidellus*). Washington: Clark Co., Gifford Pinchot Nat. Forest, gymnosperm, 9 October 2014, De Santo (H, F); Jefferson Co., Hoh Rain Forest, gymnosperm, 16 October 1993, Volk 93-183 (CFMR). Lewis Co., Mineral, gymnosperm, 10 October 2014, Raymond* (H, F) (X3239, GenBank KU165783); Pierce Co., Bug Creek Recreational Area, gymnosperm, 10 October 2014, Spinosa* (H, F) (X 3240, GenBank KU165784).

– *J. oreinus*. Russia. Khabarovsk Reg.: Khabarovsk Dist., Bolshoi Khekhtsir Nat. Res., *Picea ajanensis*, 4 September 2013, Spirin 6614, 6617 (H); Solnechnyi Dist., Razlivnaya, *P. ajanensis*, 22 August 2011, Spirin 4264* (H, holotype – see below) (X3241, GenBank KU165785). Primorie Reg.: Krasnoarmeiskii Dist., Valinku, *P. ajanensis*, 25 August 2013, Spirin 6342* (H) (X3243, GenBank KU165786).

Sequences of *J. hirtus* retrieved from GenBank: DQ911605 (USA, Washington), FJ439517 (Canada, Quebec).

RESULTS

Four ITS clades can be distinguished from the data: two in East Asia (*J. brachiatus*, *J. oreinus*), one in Europe and Eastern North America, and one in Western North America (Fig. 1). ITS differences between the clades are small – ranging between 4-14 bp (0.7-2.5%). We found no good morphological differences between European and North American specimens, and consider them conspecific for now (*Jahnoporus hirtus*). ITS difference between European and American west coast specimens is only 4 bp (0.7%). ITS differences between the East Asian clades and *J. hirtus* are larger, and those correspond well with ecological and morphological

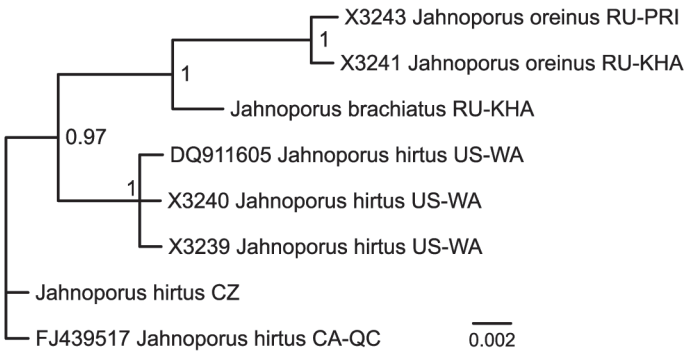

Fig. 1. Phylogeny of *Jahnoporus* spp. based on ITS sequences. Consensus phylogram of the 3002 trees retained in the Bayesian analysis. Numbers represent posterior probabilities.

data. Two East Asian collections from highlands have identical sequences and possess broad basidiospores, so they represent *J. oreinus* sp. nov. The specimen from the lowland area with a different ITS sequence has narrow basidiospores – it is introduced as *J. brachiatus* sp. nov.

Jahnoporus brachiatus Spirin, Vlasák & Miettinen, **spec. nov.** **Figs 2d, 3a**

Holotype. Russia. Khabarovsk Reg.: Komsomolsk Dist., Boktor, on buried wood in mixed forest, 18 August 2013, Spirin 6116* (H) (51.1023 N, 137.4143 E, alt. 141 m).

Mycobank: MB 815064

Etymology: brachiatus (Lat., adj.) – spreading, patulous, referring to the shape of basidiocarp.

Basidiocarps annual, fleshy, laterally stipitate, pilei up to 7 cm wide. **Pileal surface** hispid, covered by densely arranged and partly agglutinated hairs (300-700 μm long), pale grey to pale ochraceous, indistinctly zonate; margin sharp, fertile, even or slightly lobed, incurved after drying. **Pore surface** even, cream-colored in fresh condition, pale ochraceous in herbarium specimens; **pores** angular, 2-3 per mm, partly shrinking upon drying, dissepiments thin, even. **Stipe** up to 5 cm long, 7-10 mm thick, smooth or covered by incomplete pores in the upper part, cream-colored to pale ochraceous, continuing as a root-like appendix into the soil. **Section of pileus:** upper layer 0.1-0.2 mm thick, pale grey, agglutinated, context white or pale cream-colored, 1-1.5 mm thick, tube layer concolorous with pore surface, 1-1.5 mm thick. **Odour** absent, **taste** mild.

Hyphal structure monomitic; hyphae clamped, faintly amyloid (pale grey in IKI), acyanophilous, unchanged in KOH. **Pileal hairs and upper surface** consisting of greyish, parallel hyphae, (3.8-) 4.2-5.9 (-6.2) μm in diam. (n = 20/1). **Hyphae of pileal context** thin-walled, mostly in parallel bundles, (4.1-) 4.6-6.4 (-7.2) μm in diam. (n = 20/1). **Tramal hyphae** thin-walled, parallel, (3.0-) 3.1-5.1 (-5.2) μm in diam. (n = 20/1), often covered by rosette-like crystals 15-20 μm in diam. **Hyphae of stipe tissue** slightly and unevenly thick-walled, tightly and irregularly arranged, (5.8-) 5.9-11.8 (-12.9) μm in diam. (n = 20/1). **Cystidioles** absent. **Basidia** clavate, 4-spored, (24.8-) 25.9-33.3 (-34.0) × (7.2-) 7.4-10.6 (-10.7) μm (n = 20/1), with oily droplets in cytoplasm. **Basidiospores** smooth, thin-walled,

Table. Key ecological and morphological characters of *Jahnoporus* spp.

Species	*Distribution/ habitats*	*Cap*	*Cap surface*	*Diameter of tramal hyphae*	*Basidia*	*Basidiospores*
J. brachiatus	East Asia; lowland mixed forest	up to 7 cm in diam., 2-3 mm thick, margin sharp	pale gray to pale ochraceous, hispid, hairs up to 700 μm long	3.1-5.1 μm	25.9-33.3 × 7.4-10.6 μm	narrowly fusoid, 13.2-17.1 × 4.2-5.2 μm, L = 14.23, W = 4.54, Q = 3.14
J. hirtus	Central Europe, North America; mountain spruce-dominated forests	up to 15 cm in diam., 3-10 mm thick, margin rather blunt	brownish gray to reddish brown, hispid to warted, hairs up to 300 μm long	2.3-4.2 μm	22.4-35.5 × 7.1-10.2 μm	fusoid to navicular, 10.4-15.4 × 4.0-5.8 μm, L = 12.61, W = 4.51, Q = 2.90-3.17
J. oreinus	East Asia; mountain spruce-dominated forests	up to 6 cm in diam., 2-5 mm thick, margin sharp	brownish grey to brown, hispid, hairs up to 400 μm long	2.6-4.2 μm	29.5-53.0 × 8.2-10.6 μm	fusoid to navicular, 13.2-17.3 × 4.6-6.0 μm, L = 15.37, W = 5.08, Q = 2.69-3.04

narrowly fusoid (spindle-like), (13.1-) 13.2-17.1 (-17.3) × (4.1-) 4.2-5.2 (-5.3) μm (n = 40/1), L = 14.23, W = 4.54, Q = 3.14, strongly tapering to the distal end, with oil-rich content, IKI and CB–.

Notes. J. brachiatus was collected in the mixed middle-aged (80-100 years old) forest dominated by *Quercus mongolica*; *Larix gmelinii* and *Acer mono* are present in tree stand as well. The basidiocaprs were found on soil but certainly connected with buried wood remnants, probably, those of oak. So far the species is known from the type locality. Its differences from the closely related species are listed in Table. Dai *et al*. (2009) reported *J. hirtus* as growing on angiosperms in Central China; these records may belong to *J. brachiatus* or another species preferring deciduous trees.

J. pekingensis (J.D. Zhao & L.W. Xu) Y.C. Dai was described from Northeast China as a presumably terrestrial species. It differs from *J. brachiatus* in having wider pilei (up to 18 cm in diam.) and pores (1-1.5 per mm), and its basidiospores are considerably smaller, 9-11.2 × 2.5-3.5 μm (Dai, 2003). Identity of *J. pekingensis* (especially, its generic position) should be studied with DNA methods.

Jahnoporus hirtus (Quél. ex Cooke) Nuss, Hoppea 39: 176, 1980 **Figs 2a, 3b**

J. hirtus is the type species of genus *Jahnoporus* (Nuss 1980). According to DNA data, it is a member of the *Antrodia* clade (as outlined by Ortiz-Santana et al. 2013) within the *Polyporales*. However, phylogenetic relations of *Jahnoporus* and allied taxa of brown-rot polypores should be studied separately.

Differences of *J. hirtus* from two newly described species are summarized in Table. Due to absence of morphological differences and very similar ITS

Fig. 2 Fresh fruiting bodies of *Jahnoporus* spp., **a.** *J. hirtus*, USA, Washington, Rayner s.n.; **b-c.** *J. oreinus*, Russia, Khabarovsk, Spirin 4264 (holotype); **d.** *J. brachiatus*, Russia, Khabarovsk, Spirin 6116 (holotype). Photos OM (a), VS (b-d).

sequences, we consider European and North American collections as belonging to one species. However, further studies may elucidate this problem. *J. hirtus* is a species of old-growth conifer forests although its habitat requirements are seemingly not as strict as in the case of *J. oreinus*. In Europe it is reported from spruce and fir and in North America from other conifer hosts as well (*Pseudotsuga*, *Thuja*, *Tsuga*) (Jahn, 1973; Vlásak & Kout, 2010).

Jahnoporus oreinus Spirin, Vlasák & Miettinen, **spec. nov.** **Figs 2b-c, 3c**

Holotype. Russia. Khabarovsk Reg.: Solnechnyi Dist., Razlivnaya, *Picea ajanensis*, 22 August 2011 *Spirin 4264** (H) (51.0898 N, 135.7165 E, alt. 818 m).

Mycobank: MB 815065

Etymology: oreinos (Greek, adj.) – mountain, referring to ecological requirements of the species.

Basidiocarps annual, fleshy, laterally stipitate, pilei 3-6 cm wide. **Pileal surface** hispid, covered by densely arranged hairs (200-400 µm long), brownish grey to brown, azonate; margin sharp, fertile, even, incurved after drying. **Pore surface** even, cream-colored in fresh condition, pale ochraceous in herbarium specimens; **pores** angular to sinuous, often fusing together, 2-3 per mm, strongly shrinking upon drying, dissepiments thin, even to serrate. **Stipe** up to 5 cm long, 5-7 mm thick, smooth or covered by incomplete pores or scattered hairs, pale ochraceous to pale gray. **Section of pileus:** upper layer up to 0.1mm thick, grey to brownish, agglutinated, context white or pale cream-colored, 1-3 mm thick, tube

layer concolorous with pore surface, 1-2 mm thick. **Odour** faint, mushroom-like, **taste** mild or slightly bitter.

Hyphal structure monomitic; hyphae clamped, faintly amyloid (pale grey in IKI), acyanophilous, unchanging in KOH. **Pileal hairs and upper surface** consisting of brownish, parallel hyphae, (3.8-) 4.0-5.9 (-6.3) μm in diam. (n = 20/1). **Hyphae of pileal context** slightly and unevenly thick-walled, mostly in parallel bundles, (6.2-) 6.7-11.4 (-12.6) μm in diam. (n = 20/1). **Tramal hyphae** thin-walled, parallel, (2.2-) 2.6-4.2 (-4.3) μm in diam. (n = 40/2), crystals absent. **Hyphae of stipe tissue** slightly and unevenly thick-walled, tightly and irregularly arranged, (3.7-) 4.7-8.7 (-10.2) μm in diam. (n = 20/1). **Cystidioles** rare, bottle-shaped, 25-37 × 6-11 μm. **Basidia** clavate, 4-spored, (27.2-) 29.5-53.0 (-55.8) × (7.8-) 8.2-10.6 (-11.4) μm (n = 40/2), with oily droplets in cytoplasm. **Basidiospores** smooth, thin-walled, fusoid to navicular, (13.1-) 13.2-17.3 (-18.3) × (4.2-) 4.6-6.0 (-6.1) μm (n = 60/2), L = 15.37, W = 5.08, Q = 2.90-3.17, strongly tapering to the distal end, with oil-rich content, IKI and CB–.

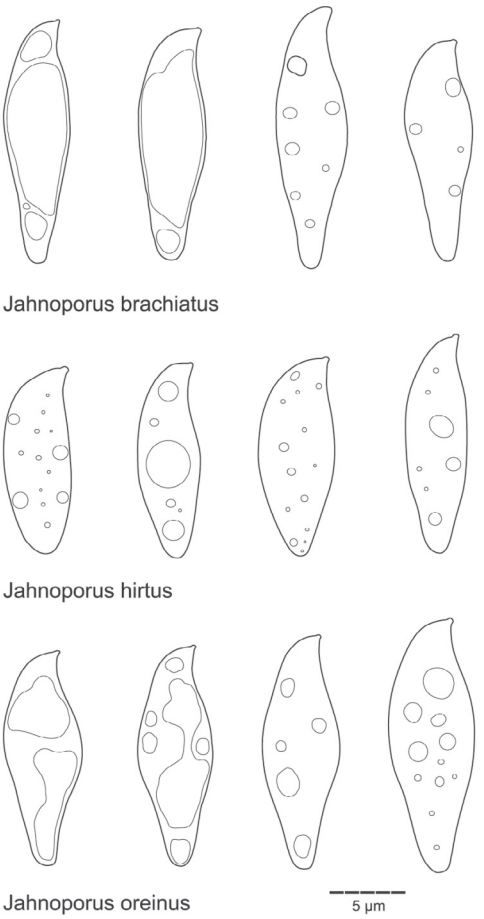

Fig. 3. Basidiospores of *Jahnoporus* spp., **a.** *J. brachiatus* (holotype), **b.** *J. hirtus*, USA, New York (holotype of *Polyporus hispidellus*), **c.** *J. oreinus* (holotype).

Notes. *J. oreinus* was detected in three very distant localities in Khabarovsk Reg. (Badzhal Mts. and Bolshoi Khekhtsir Nat. Reserve) and Primorie (Sikhote-Alin), Russian Far East. Of the 234 plots studied in 2011-2014, they represent the oldest (300 years old and more) virgin forests dominated almost exclusively by spruce. The absence of larch (*Larix gmelinii*) in the tree stand indicates that these forests underwent no catastrophic disturbances (i.e., wild fires) at least several centuries. Basidiocarps of *J. oreinus* were collected from large (up to 50 cm in diam.) standing or fallen logs of *P. ajanensis*, as well as from natural stumps. The type locality, where the species was observed 3 times on different substrates, reveals an unusual diversity and abundance of basidiomycetes, with a repeated occurrence of such a rarities as *Amylocystis lapponica* (Romell) Bondartsev & Singer, *Antrodia sitchensis* (D.V. Baxter) Ryvarden & Gilb. and *Polyozellus multiplex* (Underw.) Murrill. The strict habitat requirements of *J. oreinus* suggest that it is a strong indicator species of the oldest and most valuable spruce forests in Russian Far East. Ljubarsky (1962) published a few records of *J. hirtus* from pristine highland forests of Primorie; they seem to belong to *J. oreinus* as well.

CONCLUSION

Due to easily detectable basidiocarps and growth on wood, polypores remain one of the most important groups of indicators for forest conservation value. A significant proportion of them is threatened by logging-related forest degradation, and therefore included in regional or national Red Lists. However, many species are yet deficiently studied because of sparse sampling and difficult morphological identification.

Recent DNA studies of *Antrodia crassa* (P. Karst.) Ryvarden (Runnel *et al*., 2014), regarded earlier as a rare, conservation-reliant polypore, revealed that its current morphology-based concept covers two closely related species distinguishable mostly by host demands and distribution areas. One of these species is widely distributed in the human-induced ecosystems and therefore does not need any protection, whereas the other is a strict old-growth forest species. The same cases were earlier detected in genera *Antrodiella* (*A. pallescens* (Pilát) Niemelä & Miettinen versus *A. pallasii* Renvall, Johann. & Stenlid – Miettinen *et al*., 2006) and *Skeletocutis* (*S. biguttulata* (Romell) Niemelä versus *S. brevispora* Niemelä – Niemelä, 1998). *J. hirtus* dealt with in this paper represents a similar case. We can expect that a large share of traditional, collective polypore species contain actually several, as yet unidentified, ecologically differentiated species. Further meticulous taxonomic studies combining morphological, ecological/geographical and DNA data offer good opportunities for subsequent applied research, in particular for finding more solid ground for bioindication and habitat conservation.

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