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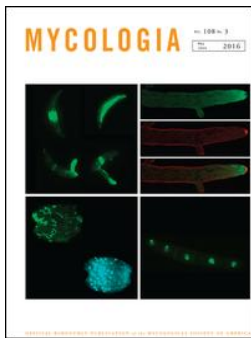
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To cite this article: Fang Wu, Shu-Juan Dai, Josef Vlasák, Viacheslav Spirin & Yu-Cheng Dai (2019): Phylogeny and global diversity of *Porodaedalea*, a genus of gymnosperm pathogens in the Hymenochaetales, *Mycologia*, DOI: [10.1080/00275514.2018.1526618](https://doi.org/10.1080/00275514.2018.1526618)

To link to this article: <https://doi.org/10.1080/00275514.2018.1526618>



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Phylogeny and global diversity of *Porodaedalea*, a genus of gymnosperm pathogens in the Hymenochaetales

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ABSTRACT

Porodaedalea is a polypore genus of the Hymenochaetales that encompasses pathogens of conifer trees. In this study, we conduct a comprehensive study of the phylogeny and diversity of *Porodaedalea* based on collections and isolates from Europe, North America, North Africa, and Asia. Phylogenetic analysis of a two-gene data set, nuc ribosomal DNA internal transcribed spacers (ITS1-5.8S-ITS2 = ITS) and translation elongation factor 1-alpha (*tef1*), shows that 20 terminal clades that correspond to phylogenetic species well supported within *Porodaedalea*. Based on morphological evidence, five new species, *P. alpicola*, *P. indica*, *P. kesiyae*, *P. microsperma*, and *P. yunnanensis*, are described and illustrated. In addition, four still unnamed lineages are detected in North America and East Asia.

ARTICLE HISTORY

Received 6 March 2018
Accepted 18 September 2018

KEYWORDS

Hymenochaetales;
phylogeny; taxonomy;
wood-inhabiting fungi; 5
new taxa

INTRODUCTION

Porodaedalea Murrill is a small poroid genus of the Hymenochaetales (Basidiomycota) first described over 100 y ago (Murrill 1905). Initially, only *P. pini* (Brot.) Murrill (the generic type) was recognized in the genus, and subsequently *P. chrysoloma* (Fr.) Fiasson & Niemelä was separated from *P. pini* by Donk (1974). For a long time, both species were considered members of *Phellinus* Quél. and referred to as the *Phellinus pini* complex (Gilbertson and Ryvarden 1987; Ryvarden and Gilbertson 1994). A more recent circumscription of *Porodaedalea* was made by Fiasson and Niemelä (1984) on morphological and biochemical grounds, supported by DNA data, and it was found to be a monophyletic group (Wagner and Fischer 2002). *Porodaedalea* is distinguished from *Phellinus* by duplex context, generative hyphae bearing crystals at dissepiment edges, long hymenial setae, hyaline to pale yellow and slightly to fairly thick-walled basidiospores, and occurrence on gymnosperm trees.

Porodaedalea is characterized by perennial, effused-reflexed to distinctly pileate to imbricate basidiomes, duplex context of actively growing fructifications, and a dimitic hyphal structure with simple-septate generative and skeletal hyphae. Generative hyphae occasionally produce crystals at dissepiment edges. Setae are abundant, originating mostly from the subhymenium, and

they are rather long and ventricose to subulate. Tramal setae occur in some species, although their presence is not constant and thus of minor taxonomic value. Basidia of *Porodaedalea* are short-clavate, usually distinctly longer than basidioles, and basidiospores are hyaline to pale yellow, slightly to fairly thick-walled, broadly ellipsoid or ovoid to subglobose, and inamyloid but moderately cyanophilous (Murrill 1905; Dai 2010; Tomšovský et al. 2010; Dai et al. 2017). Members of the genus are pathogenic on gymnosperm trees, causing a white pocket rot (Fischer 1994; Dai 2010).

Fourteen species of *Porodaedalea* are known from all forested continents of the northern hemisphere, although they are more common in the boreal-temperate and conifer-dominated forests. Previous studies reported *Porodaedalea* from Europe, North America, North Africa, and Asia (Gilbertson and Ryvarden 1987; Fischer 1994; Ryvarden and Gilbertson 1994; Dai 2010; Tomšovský and Kout 2013). In Europe, four species of *Porodaedalea* are currently recognized: *P. pini*, *P. chrysoloma*, *P. laricis* (Jacz. ex Pilát) Niemelä (= *Phellinus abietis* (P. Karst.) Jahn (Niemelä et al. 2005; Tomšovský et al. 2010; Ryvarden and Melo 2014), and *P. cedrina* Pilát ex Tomšovský & Kout, recently described from the Mediterranean area and occurring on *Cedrus atlantica* (Tomšovský and Kout 2013).

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In North America, five described species of *Porodaedalea*—*Porodaedalea piceina* (Peck) Niemelä (Niemelä 1985), which belongs to the *Porodaedalea* “holarctic group” (Brazeo and Lindner 2013), *P. chrysoloma*, *P. pini* (Gilbertson and Ryvarden 1987), *P. cancriformans* (M.J. Larsen, Lombard & Aho) T. Wagner & M. Fischer (Wagner and Fischer 2002), and *Porodaedalea gilbertsonii* (M.J. Larsen) V. Papp (2018)—and two unnamed taxa have been recorded. In addition, Fischer (1994) reported seven unique taxa of *Porodaedalea* in North America based on mating tests but confirmed only five *Porodaedalea* groups in the region based on DNA methods (Fischer 1996). Using a multilocus phylogenetic analysis, Brazeo and Lindner (2013) indicated that *P. pini* s. str. and *P. chrysoloma* s. str. do not occur in North America. Their results were in accordance with earlier studies by Fischer (1994, 1996), Larsen and Melo (1996), Larsen and Stenlid (1999), and Larsen (2000). Only *P. piceina* and *P. cancriformans* were mentioned in a list of North American polypores (Zhou et al. 2016).

In Asia, *Porodaedalea chrysoloma* and *P. pini* were recognized based on morphology by Núñez and Ryvarden (2000). Dai (2010) recorded five species of *Porodaedalea* in China: *P. chrysoloma*, *P. himalayensis* (Y.C. Dai) Y.C. Dai, *P. laricis*, *P. pini*, and *P. yamanoi* (Imazeki) Y.C. Dai. However, DNA-based taxonomic studies revealed a much more complicated picture. In particular, *P. chinensis* S.J. Dai & F. Wu was described from southwestern China inhabiting living trees of *Pinus yunnanensis* (Dai et al. 2017).

Porodaedalea is taxonomically difficult because of the similar morphology among species. Evolutionary relationships of European taxa of *Porodaedalea* were demonstrated by Tomšovský et al. (2010) using phylogenetic analysis based on nuc rDNA internal transcribed spacer (ITS1-5.8S-ITS2 = ITS) and translation elongation factor 1- α (*tef1*) sequences, and North American taxa were studied by Brazeo and Lindner (2013) with a multilocus phylogeny of four gene regions, including ITS and *tef1*. In Asia, only two species from China were analyzed by molecular data (Tomšovský and Kout 2013; Dai et al. 2017).

In this study, newly collected specimens have been examined by morphological and DNA methods. As a result, five previously unknown species have been detected in Asia. In addition, specimens and sequences of all 20 accepted *Porodaedalea* taxa from the Northern Hemisphere were studied. The aim of this work is to substantiate the current knowledge of phylogeny and species diversity of *Porodaedalea*.

MATERIALS AND METHODS

Morphological studies.—Specimens studied are deposited at BJFC, IFP, H, and in the private herbarium of J. Vlasák (JV), which will be forwarded to PRM. Herbarium abbreviations follow Thiers [continuously updated]. Microscopic procedures follow Dai (2010). At least 30 basidiospores and hymenial setae were measured in each specimen. In presenting basidiospore size data, 5% of the measurements were excluded from each end of the range and shown in parentheses. The following abbreviations are used: IKI = Melzer’s reagent, IKI– = negative in Melzer’s reagent, KOH = 5% potassium hydroxide, CB = cotton blue, CB+ = cyanophilous, L = mean spore length (arithmetic average of all spores), W = mean spore width (arithmetic average of all spores), Q = variation in the L/W ratios, and n = number of spores measured from given number of specimens. Sections were studied at magnifications up to 1000 \times using a Nikon Eclipse 80i microscope (Tokyo, Japan) with phase-contrast illumination. Drawings were made with a drawing tube. Color terms follow Petersen (1996).

DNA extraction, PCR, and sequencing.—DNA was extracted from dried basidiomes. ITS and *tef1* were selected for genetic analyses. ITS was amplified with the primer pair ITS5 and ITS4 (White et al. 1990), and *tef1* sequences were amplified with primers 983F and 2218R (Rehner and Buckley 2005). In some cases, the primer pair 1487F and 2218R was used in nested polymerase chain reaction (PCR) amplifications of *tef1* following Brazeo and Lindner (2013). The following PCR reaction for ITS was used: initial denaturation at 95 C for 3 min, followed by 35 cycles at 94 C for 40 s, 54 C for 45 s, and 72 C for 1 min, and a final extension of 72 C for 10 min. For *tef1*, the PCR protocol used a touchdown regime initiated with a 2-min denaturation at 94 C. The annealing temperature in the first amplification cycle was 60 C, which was subsequently incrementally reduced by 1 C per cycle over the next nine cycles. An additional 35 amplification cycles were then performed, each consisting of a 45-s denaturation at 94 C, a 90-s annealing step at 53 C, and a 2-min extension at 72 C, concluding with a 10-min incubation at 72 C. All newly generated sequences were deposited at GenBank (TABLE 1).

Phylogenetic analyses.—Thirty-four sequences were generated by this study, and 55 related sequences were obtained from GenBank. The ITS and *tef1* data

Table 1. Specimens and GenBank accession numbers of sequences used in this study.

Species	Sample no.	Locality	Substrate	GenBank accession nos.	
				ITS	<i>tef1</i>
<i>Porodaedalea alpicola</i>	Cui 12272 (BJFC)	China, Xizang	<i>Abies</i> sp.	MG585275	MG585294
<i>P. alpicola</i>	Cui 12280 (BJFC)	China, Xizang	<i>Abies</i> sp.	MG585276	MG585295
<i>P. alpicola</i>	Cui 12283 (BJFC)	China, Xizang	<i>Abies</i> sp.	MG585277	MG585296
<i>P. cancriformans</i>	1-Sp (CFMR)	USA, California	<i>Abies concolor</i>	JX110042	JX109998
<i>P. cancriformans</i>	FP133112-R (CFMR)	USA, Oregon	<i>Abies magnifica</i>	JX110043	JX109999
<i>P. cedrina</i>	JK 0908/04-3(JV)	Morocco, Middle Atlas	<i>Cedrus atlantica</i>	JQ772468	JQ772474
<i>P. cedrina</i>	MCF 03/1167 (MCF)	Turkey, Fethiye-Babadağ Mt.	<i>Cedrus libani</i>	JQ772467	JQ772473
<i>P. chinensis</i>	Cui 10252 (BJFC)	China, Yunnan	<i>Pinus yunnanensis</i>	KX673606	MG585301
<i>P. chinensis</i>	Dai 15487 (BJFC)	China, Gansu	Gymnosperm	MG585284	MG585302
<i>P. chinensis</i>	Dai 16864 (BJFC)	China, Yunnan	<i>Pinus yunnanensis</i>	KX852282	MG585303
<i>P. chrysoloma</i>	Dai 12674 (BJFC)	Finland, Helsinki	<i>Picea abies</i>	KY000004	MG585306
<i>P. chrysoloma</i>	JV 1411/13 (JV)	Czech, Hluboka	<i>Picea abies</i>	MG585285	MG585305
<i>P. chrysoloma</i>	JV 1408/40-J (JV)	Czech, Hrensko	<i>Picea abies</i>	KY000006	MG585304
<i>P. gilbertsonii</i>	H7002004 (H)	USA, California	<i>Pseudotsuga menziesii</i>	FJ775560	FJ775594
<i>P. gilbertsonii</i>	NAMA 2012-153 (F)	USA, California	—	MG585290	MG585313
<i>P. gilbertsonii</i>	JV 0709/116-J (JV)	USA, Oregon	<i>Pseudotsuga menziesii</i>	MG585289	MG585312
<i>P. himalayensis</i>	Cui 9320 (BJFC)	China, Xizang	<i>Picea likiangensis</i>	JQ772471	JQ772477
<i>P. himalayensis</i>	Cui 9609 (BJFC)	China, Xizang	<i>Picea likiangensis</i>	MG585286	MG585293
<i>P. himalayensis</i>	Cui 9618 (BJFC)	China, Xizang	<i>Picea likiangensis</i>	KX673604	MG585307
<i>P. himalayensis</i>	Cui 9620 (BJFC)	China, Xizang	<i>Picea likiangensis</i>	KX673605	KX852285
<i>P. indica</i>	Korhonen 1136 (H)	India, Himachal Pradesh	<i>Cedrus deodara</i>	KM011966	—
<i>P. kesiyae</i>	Dai 18417 (BJFC)	Vietnam, Lam Dong	<i>Pinus kesiya</i>	MG585278	MG585297
<i>P. kesiyae</i>	Dai 18427 (BJFC)	Vietnam, Lam Dong	<i>Pinus kesiya</i>	MG585279	MG585298
<i>P. laricis</i>	TFC 1981-38 (TFC)	Russia, Primorsk	<i>Picea ajanensis</i>	FJ775559	FJ775585
<i>P. laricis</i>	H7002007 (H)	Russia, Bashkortostan	<i>Larix</i> sp.	FJ775562	FJ775586
<i>P. microsperma</i>	Cui 12047 (BJFC)	China, Heilongjiang	<i>Larix gmelinii</i>	MG585280	MG585299
<i>P. microsperma</i>	Dai 4926 (BJFC)	China, Inner Mongolia	<i>Picea crassifolia</i>	MG585281	MG585291
<i>P. pini</i>	BRNM 737548 (CFMR)	Turkey, Isparta	<i>Pinus</i> sp.	JQ772470	JQ772476
<i>P. pini</i>	No-6170-T (CFMR)	Portugal, Lisbon	<i>Pinus pinaster</i>	JX110037	JX109993
<i>P. yamanoi</i>	Dai 14795 (BJFC)	China, Jilin	<i>Picea jezoensis</i>	KX673607	MG585309
<i>P. yamanoi</i>	TFC 1971-24 (TFC)	Russia, Sakhalin	<i>Picea jezoensis</i>	FJ775551	FJ775592
<i>P. yamanoi</i>	Dai 8202 (BJFC)	China, Jilin	<i>Picea jezoensis</i>	JQ772469	JQ772475
<i>P. yunnanensis</i>	Dai 3072 (BJFC)	China, Yunnan	<i>Pinus armandii</i>	MG585282	MG585292
<i>P. yunnanensis</i>	Dai 16878 (BJFC)	China, Yunnan	<i>Pinus armandii</i>	MG585283	MG585300
<i>P. sp. 1</i>	FP-103366-T (CFMR)	USA, Georgia	<i>Pinus virginiana</i>	JX110038	JX109994
<i>P. sp. 1</i>	FP-71757 (CFMR)	USA, Virginia	<i>Pinus virginiana</i>	JX110039	JX109995
<i>P. sp. 2</i>	AZ-10-T (CFMR)	USA, Arizona	<i>Pinus strobiformis</i>	JX110040	JX109996
<i>P. sp. 2</i>	AZ-14-T (CFMR)	USA, Arizona	<i>Pinus strobiformis</i>	JX110041	JX109997
<i>P. sp. 3</i>	Miettinen 10543 (H)	China, Jilin	<i>Pinus koraiensis</i>	KM011978	KY024313
<i>P. sp. 3</i>	Spirin 3918 (H)	Russia, Khabarovsk	<i>Larix gmelinii</i>	KM011979	KY024314
<i>P. sp. 4</i>	Spirin 5568-1 (H)	Russia, Khabarovsk	<i>Pinus pumila</i>	KM011968	KY024315
<i>P. sp. 4</i>	Spirin 5567 (H)	Russia, Khabarovsk	<i>Pinus pumila</i>	KM011967	KY024316
<i>P. sp. Holarctic Group 1</i>	FP-135945-T (CFMR)	USA, California	<i>Pseudotsuga menziesii</i>	JX110057	JX110013
<i>P. sp. Holarctic Group 2</i>	FP-97385-T (CFMR)	USA, Colorado	<i>Picea engelmannii</i>	JX110062	JX110018
<i>Onnia leporina</i>	BRNM 712782	Czech, Jihlava	<i>Picea abies</i>	FJ775542	FJ775573

Note. New sequences are in bold.

sets were aligned in BioEdit with Clustal X and edited manually as necessary (Hall 1999). The sequences of *Onnia leporina* (Fr.) H. Jahn were chosen as outgroup following Tomšovský and Kout (2013).

Maximum parsimony (MP) implemented in PAUP* 4.0b10 (Swofford 2003) and Bayesian inference (BI) implemented in MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003) were used in phylogenetic analyses of the individual data sets and the combined data set. Phylogenetic trees were visualized using TreeView. For MP analysis, we used 1000 random sequence additions during a heuristic search, and all characters of the sequences were equally weighted and gaps treated as missing data. MaxTrees was set to 5000, branches of zero length were collapsed, and all parsimonious trees were saved. Branch supports was assessed using a

bootstrap (BT) analysis by performing 1000 replicates data sets with random sequence addition for each bootstrap replicate (Felsenstein 1985). BT values >50% are shown. Descriptive tree statistics, tree length (TL), consistency index (CI), retention index (RI), rescaled consistency index (RC), and homoplasy index (HI) were calculated for each tree generated.

The best-fit evolutionary model was determined by MrModeltest 2.3 (Nylander 2004; Posada and Crandall 1998) for the BI analysis. BI was performed using a general time-reversible (GTR) model of DNA substitution and gamma distributed among-site rate variation (Ronquist and Huelsenbeck 2003). Four Markov chains were executed during two independent runs from random starting trees with 4 million generations, keeping one tree every 1000 generations. The first 25% of the

samples from the posterior distribution were discarded as the burn-in. A majority rule consensus tree of all remaining trees was calculated. MP and BI analyses generated nearly identical topologies for each data set; thus, only the topology from the MP analysis is presented, along with statistical values from the MP and BI algorithms.

RESULTS

The combined data set had an aligned length of 1784 sites, of which 1483 were constant, 166 variable and parsimony-uninformative, and 135 parsimony-informative. MP analysis yielded four equally parsimonious trees (TL = 415, CI = 0.807, HI = 0.193, RI = 0.854, RC = 0.690). The best-fit model for the *tef1* data set for the BI analysis was a GTR+I+G model. The best-fit models for three partitions of the ITS data set were as follows: HKY+G for ITS1, K80+I+G for 5.8S, HKY+I +G for ITS2. Bayesian analysis resulted in a similar topology as the MP analysis, with an average standard deviation of split frequencies reaching >0.01. The MP tree is provided in FIG. 1. BT and Bayesian posterior probability (BPP) values are shown at internodes.

Asian samples form five well-supported lineages (*P. alpicola*: BT = 100%, BPP = 1; *P. indica*: BT = 54%, BPP = 0.89; *P. kesiyae*: BT = 100%, BPP = 1; *P. microsperma*: BT = 98%, BPP = 1; *P. yunnanensis*: BT = 100%, BPP = 1), and they are separate from all other known species of *Porodaedalea* by morphology of basidiomes, the size of hymenial setae, the presence or absence of cystidioles, size and shape of the basidiospores, and preference of plant hosts and distribution. On the basis of the phylogenetic evidence and morphological characters, these species are described below. In addition, four other distinct lineages from North America and boreal East Asia with strong support values were detected: *Porodaedalea* sp. 1, *Porodaedalea* sp. 2, *Porodaedalea* sp. 3 and *Porodaedalea* sp. 4. These remain undescribed due to unavailable or inadequate collection materials gathered to date.

TAXONOMY

Porodaedalea alpicola S.J. Dai, F. Wu & Y.C. Dai, sp. nov. FIGS. 2A, 3
MycoBank MB823674

Typification: CHINA. XIZANG AUTONOMOUS REGION: Linzhi County, Lulang, Sejila Mountain, 29° 34'24"N, 94°29'10"E, 2850 m, on live *Abies*, 23 Sep 2014, Cui 12272 (**holotype** BJFC017186).

Etymology: *alpicola* (Latin), referring to the species dwelling in high mountainous areas.

Basidiomes perennial, pileate, solitary to imbricate, without odor or taste, hard corky when fresh, heavy and woody hard when dry. Pilei projecting up to 5 cm, 5.3 cm wide and 0.6 cm thick at base. Pileal surface brown to dull brown, concentrically sulcate with narrow zones, becoming encrusted with age; margin obtuse. Pore surface cinnamon-buff to honey yellow and slightly shining; pores circular to angular, 4–6 per mm; dissepiments thick, entire. Context cinnamon-brown, woody hard, up to 3 mm thick. Tubes cinnamon-buff, woody corky, up to 0.3 cm long.

Hyphal system dimitic, generative hyphae simple-septate, tissue darkening in KOH.

Context: Generative hyphae hyaline, thin-walled, occasionally branched, frequently simple-septate, 2–3 µm in diam; skeletal hyphae dominant, yellowish brown, thick-walled with a wide lumen, rarely branched, frequently septate, straight, more or less regularly arranged, 3.5–5 µm in diam.

Tubes: Generative hyphae frequent, hyaline, thin-walled, occasionally branched, frequently septate, 1.5–2 µm in diam; skeletal hyphae yellowish brown, thick-walled with a narrow to wide lumen, unbranched, frequently septate, straight, more or less parallel along the tubes, 2.5–3 µm in diam. Hymenial setae frequent, mostly originating from subhymenium, sometimes embedded in trama but not seen at dissepiment edges, subulate, dark brown, thick-walled, encrusted with irregular crystals, (30–)32–46(–47) × 5–9(–11) µm; cystidioles infrequent, fusoid, hyaline, thin-walled; basidia clavate, with four sterigmata and a simple septum at the base, 11–19 × 5–7 µm; basidioles dominating in hymenium, barrel-shaped to pear-shaped, distinctly shorter than basidia.

Basidiospores 4.5–5.5(–)6 × 4–4.5(–)5 µm, L = 5 µm, W = 4.2 µm, Q = 1.19–1.21 (n = 60/2), broadly ellipsoid to subglobose, hyaline, thin- to slightly thick-walled, smooth, without guttule, usually in tetrads, IKI–, moderately CB+.

Ecology and distribution: on live *Abies*, south Asia, Sep.

Other specimens examined: CHINA. XIZANG AUTONOMOUS REGION: Linzhi County, Lulang, Sejila Mountain, 29°34'24"N, 94°29'10"E, 2850 m, on live *Abies smithii*, 23 Sep 2014, Cui 12280 (BJFC017194); same locality and date as previous, Cui 12283 (BJFC017197).

Notes: *Porodaedalea alpicola* is most closely related to *P. himalayensis*; the two species are sister taxa (FIG. 1), which is corroborated by their morphological similarity. However, *P. himalayensis* has an irregularly cracked

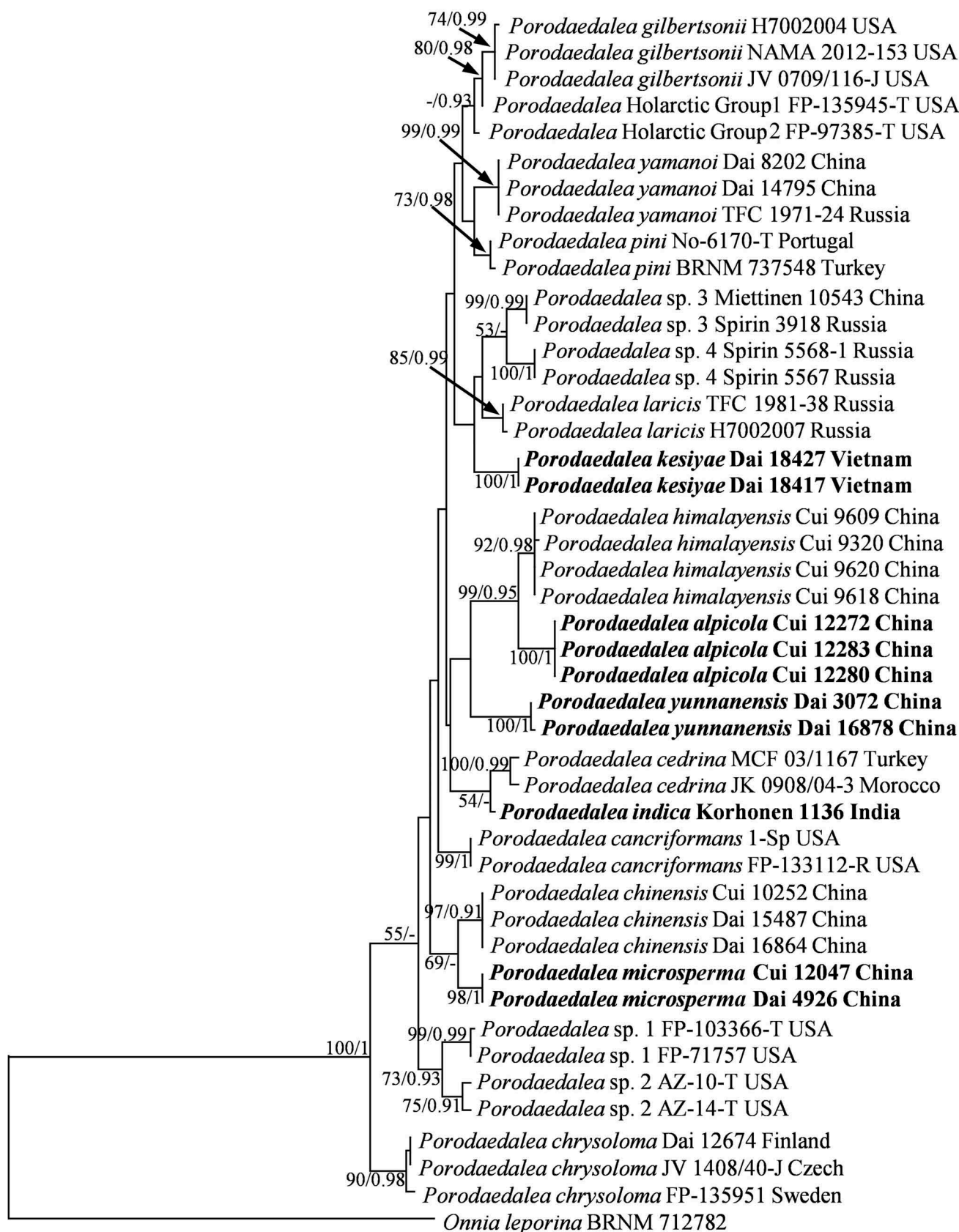


Figure 1. MP phylogeny of *Porodaedalea* inferred from the combined ITS and *tef1* sequences. The newly sequenced specimens are in boldface. The tree shown is a phylogram and represents 1 of 10 equally MP trees. Bootstrap and BPP values are indicated at internodes.

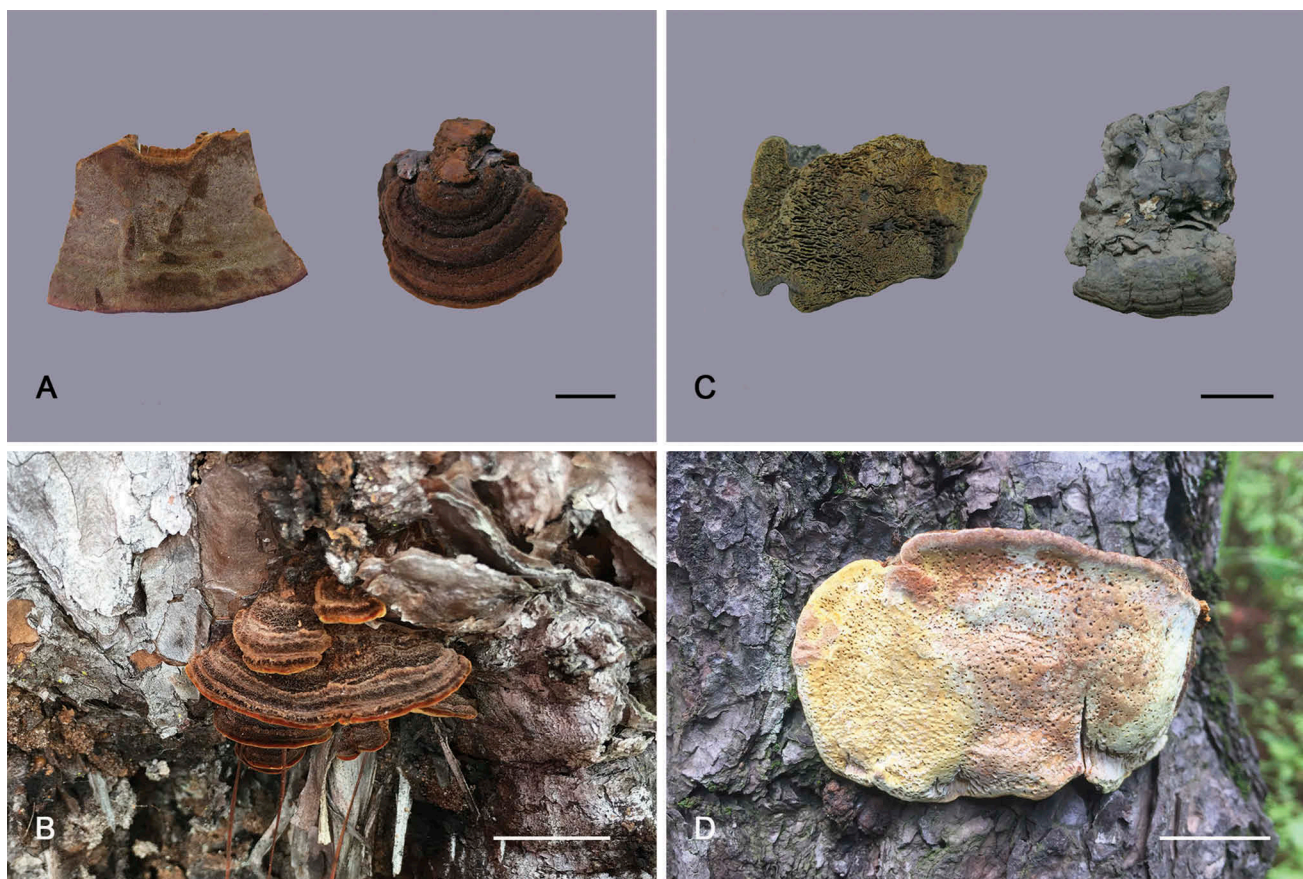


Figure 2. Basidiomes of new *Porodaedalea* species. A. *Porodaedalea alpicola* (holotype, Cui 12272). B. *Porodaedalea kesiyae* (paratype, Dai 18417). C. *Porodaedalea microsperma* (paratype, Dai 4926). D. *Porodaedalea yunnanensis* (holotype, Dai 16878). Bars = 1 cm.

pileal surface, the generative hyphae at dissepiment edges usually bear crystals, and this species occurs on *Picea* (Dai 2010). In contrast, *P. alpicola* has an uncracked pileal surface, smooth generative hyphae at dissepiment edges, and is so far found on *Abies*.

Porodaedalea indica Spirin, Y.C. Dai & Vlasák, sp. nov. FIG. 4

Mycobank MB823675

Typification: INDIA. HIMACHAL PRADESH: Kullu District, Manali, 32°16'12"N, 77°10'12"E, 2000 m, on live *Cedrus deodara*, 20 Jun 1972, Korhonen 1136 (**holotype** H).

Etymology: *indica* (Latin), referring to India, the country of origin.

Basidiomes pileate, dimidiate, conchate, often with decurrent base, projecting part up to 7 cm wide. Pileal surface dark gray to blackish, indistinctly sulcate, often covered by mosses; margin sharp. Pore surface even to slightly notched, ochraceous brown to rusty-colored when dry; pores angular to sinuous, elongated on sloping substrates, (2–)3–4 per mm, shining; dissepiments rather thin, even to wavy. Context rusty brown, woody

hard, indistinctly fibrillose, about 1 mm thick; tubes indistinctly stratified, ochraceous brown (lower layers) to brown (upper parts), up to 60 mm thick.

Hyphal system dimitic, generative hyphae simple-septate, tissue darkening in KOH.

Context: Generative hyphae hyaline, thin-walled, occasionally branched, frequently simple-septate, 2–3.5 μm in diam; skeletal hyphae thick-walled (lumen narrow to capillary), dark brown, regularly arranged, 3.2–4.4 μm in diam.

Tubes: Generative hyphae hyaline, thin-walled to slightly thick-walled, occasionally branched, frequently simple-septate, 2–3 μm in diam; skeletal hyphae brown, with a clear lumen, loosely interwoven, 2.3–3.1 μm in diam. Tramal setae absent. Hymenial setae thick-walled, usually asymmetric, ventricose, some biradicate, mostly with blunt apices, (33–)35–51 \times 10–18(–19) μm ; cystidioles common, fusoid, often with long hyphoid apical outgrowth, hyaline, thin-walled; basidia clavate, with four sterigmata and a simple septum at the base, 11–14 \times 4–5.5 μm ; basidioles dominating in hymenium, barrel-shaped to pear-shaped, distinctly shorter than basidia.

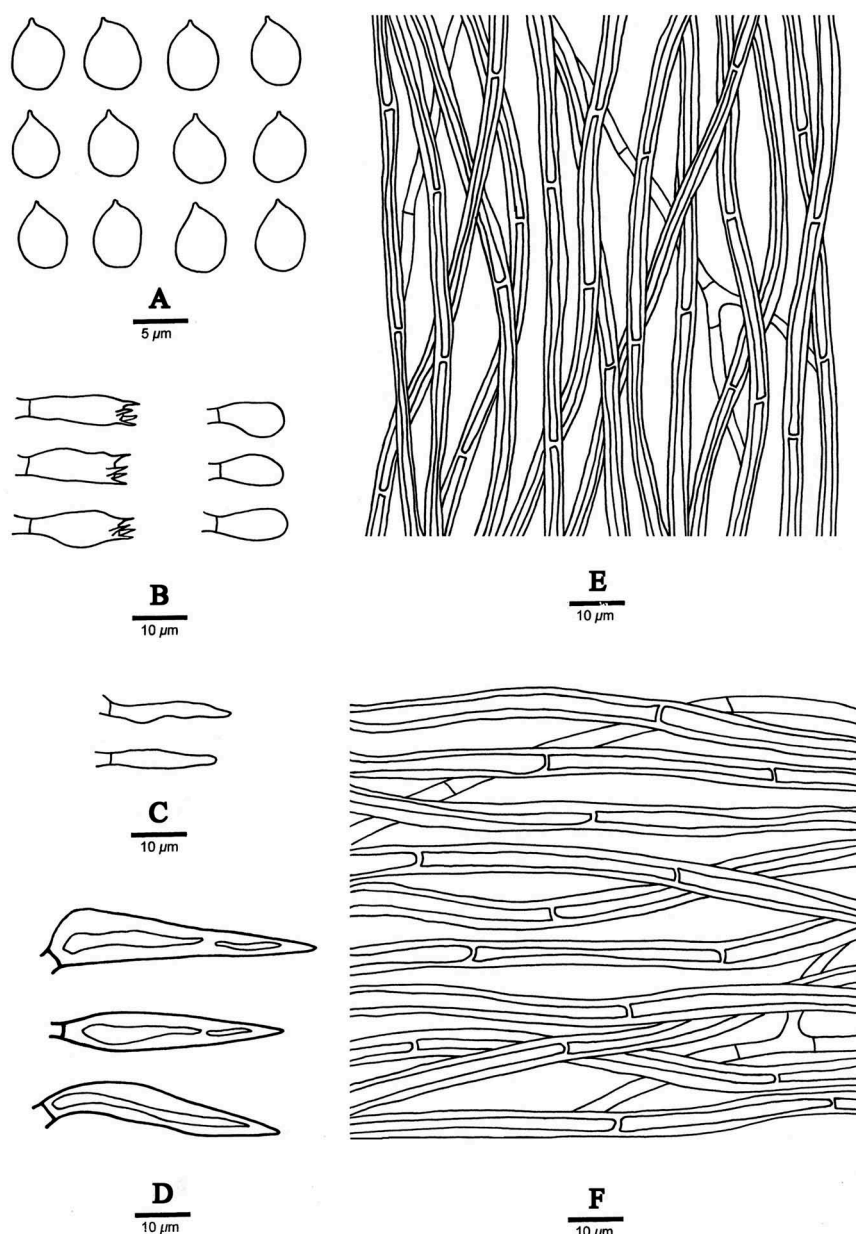


Figure 3. Microscopic structures of *Porodaedalea alpicola* (holotype, Cui 12272). A. Basidiospores. B. Basidia and basidioles. C. Cystidioles. D. Hymenial setae. E. Hyphae from trama. F. Hyphae from context.

Basidiospores $4\text{--}5 \times 4\text{--}4.5 \mu\text{m}$, $L = 4.7$, $W = 4.2$, $Q = 1.12$ ($n = 30/1$), subglobose, hyaline, slightly thick-walled, smooth, without guttule, usually in tetrads, IKI $^-$, moderately CB $^+$.

Ecology and distribution: on live *Cedrus*, south Asia (India), Jun.

Notes: *Porodaedalea indica* is morphologically and phylogenetically close to *P. cedrina* recently described from the Mediterranean (Tomšovský and Kout 2013). Both species occur on living cedar trees, and they share some morphological characters (number of pores per mm, wide, blunt-pointed hymenial setae, rather loose tramal tissue).

However, hymenial setae are longer ($30\text{--}62 \mu\text{m}$) and basidiospores larger ($5\text{--}6 \times 4\text{--}5 \mu\text{m}$) in *P. cedrina* in comparison with those of *P. indica* (TABLE 2). In addition, tramal skeletal hyphae of *P. cedrina* ($3.5\text{--}5 \mu\text{m}$ diam) are wider than in *P. indica* ($2.5\text{--}3 \mu\text{m}$ diam). *Porodaedalea cedrina* was described based on a single specimen on live *Cedrus* in Himachal Pradesh of India, so its pathogenicity and distribution range is not quite known.

Porodaedalea kesiyae S.J. Dai, F. Wu & Y.C. Dai, sp. nov. **FIGS. 2B, 5**

Mycobank MB823677

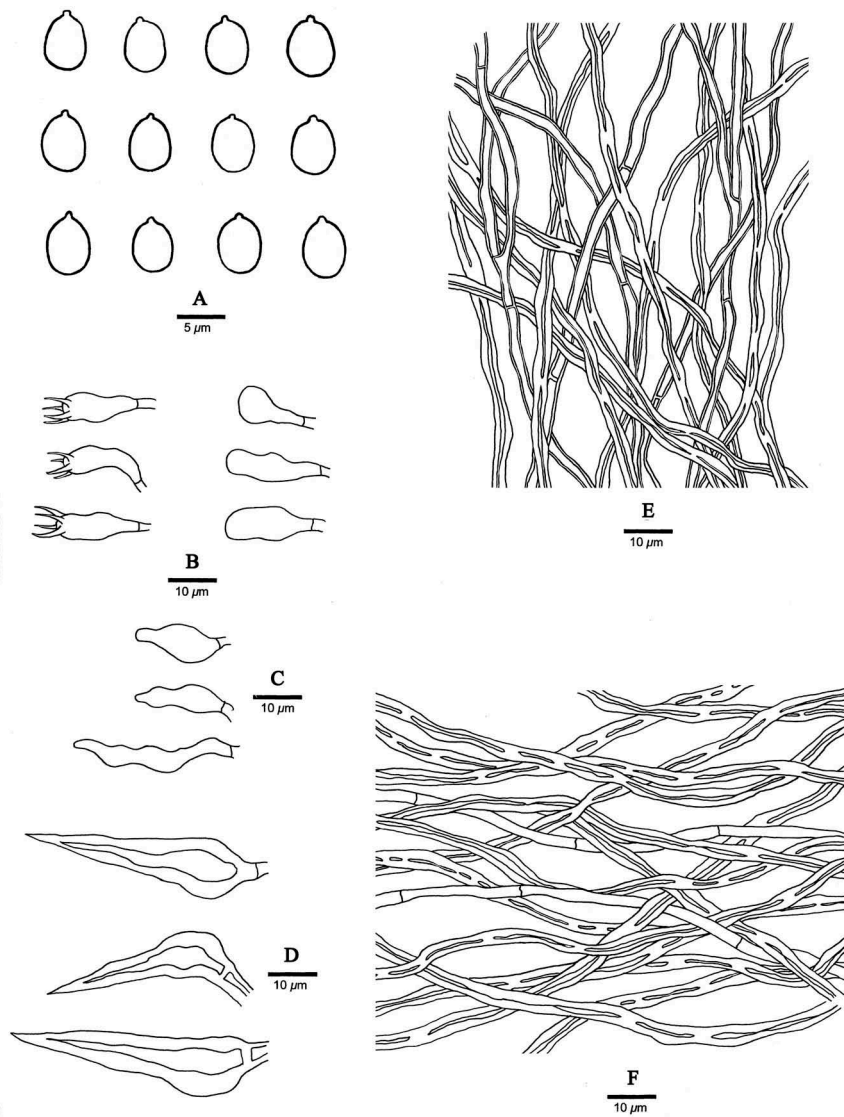


Figure 4. Microscopic structures of *Porodaedalea indica* (holotype, Korhonen 1136). A. Basidiospores. B. Basidia and basidioles. C. Cystidioles. D. Hymenial setae. E. Hyphae from trama. F. Hyphae from context.

Typification: VIETNAM. LAM DONG PROVINCE: Lac Duong District, Bidoup Nui Ba National Park, 12° 07'35"N, 108°33'41"E, 1590 m, on live *Pinus kesiya*, 15 Oct 2017, *Dai 18427* (**holotype** BJFC).

Etymology: *kesiyae* (Latin), referring to occurrence on the host tree *Pinus kesiya*.

Basidiomes perennial, pileate, solitary to imbricate, without odor or taste, hard corky when fresh, heavy and woody hard when dry. Pilei projecting up to 4 cm, 6.5 cm wide and 0.5 cm thick at base. Pileal surface grayish brown to black, concentrically sulcate with narrow zones, irregularly cracked and becoming encrusted with age; margin obtuse. Pore surface honey yellow to cinnamon and slightly shining; pores mostly circular to angular, 3–4 per mm; dissepiments thick, entire. Context

dull brown, woody hard, up to 2 mm thick. Tubes cinnamon-brown, woody corky, up to 0.3 cm long.

Hyphal system dimitic, generative hyphae simple-septate, tissue darkening in KOH.

Context: Generative hyphae hyaline, thin-walled, occasionally branched, frequently simple-septate, 2–3 µm in diam; skeletal hyphae dominant, yellowish brown, thick-walled with a wide lumen, rarely branched, frequently septate, straight, loosely interwoven to more or less regularly arranged, 3–4.5 µm in diam.

Tubes: Generative hyphae frequent, hyaline, thin-walled, occasionally branched, frequently septate, 2–3 µm in diam; skeletal hyphae yellowish brown, thick-walled with a narrow to wide lumen, unbranched, frequently septate, straight, loosely interwoven to more or

Table 2. Morphological and ecological/geographic features of *Porodaedalea* taxa.

Species	Distribution; Substrate	Pores (per mm)	Setae (μm)	Basidiospores (μm)	Cystidioles	Source
<i>P. alpicola</i>	South Asia; <i>Abies</i>	4–6	32–46 \times 5–9, L = 36, W = 7	4.5–5.5 \times 4–4.5, L = 5, W = 4.2, Q = 1.19–1.21	+	This study
<i>P. cancriformans</i>	North America; <i>Abies</i>	3–5	50 \times 13	4.5–5 \times 3.5–4	–	Larsen and Cobb-Pouille (1990)
<i>P. cedrina</i>	North Africa/west Asia; <i>Cedrus</i>	1–2	30–62 \times 6–18	5–6 \times 4–5, L = 5.5, W = 4.6, Q = 1.04–1.38	+	Tomšovský and Kout (2013)
<i>P. chinensis</i>	Asia; <i>Pinus</i>	2–3	35–69 \times 5–14, L = 53, W = 9	4.5–5.5 \times 3.5–4.5, L = 4.9, W = 4, Q = 1.17–1.26	+	This study
<i>P. chrysoloma</i>	Europe; <i>Picea</i>	2–3	30–55 \times 6–11, L = 42, W = 8	4–5.5 \times 3–4.5, L = 5, W = 4.1, Q = 1.24	–	This study
<i>P. gilbertsonii</i>	North America; <i>Pseudotsuga</i>	2–3	30–40 \times 7–9	5–5.5 \times 5	–	Larsen (2000)
<i>P. himalayensis</i>	South Asia; <i>Picea</i>	5–6	24–43 \times 6–10, L = 33, W = 8	4.5–6 \times 3.5–5, L = 4.8, W = 4, Q = 1.21	+	This study
<i>P. indica</i>	South Asia; <i>Cedrus</i>	3–4	35–50 \times 10–18, L = 42, W = 14	4–5 \times 4–4.5, L = 4.7, W = 4.2, Q = 1.12	+	This study
<i>P. kesiyae</i>	Southeast Asia; <i>Pinus</i>	3–4	43–58 \times 8–11, L = 50, W = 10	5–5.5 \times 4.5–5, L = 5.3, W = 4.6, Q = 1.13–1.16	–	This study
<i>P. laricis</i>	North Asia; <i>Larix</i>	2–3	30–58 \times 6–12, L = 45, W = 8	5–5.5 \times 3.5–4, L = 5, W = 3.9, Q = 1.27	+	This study
<i>P. microsperma</i>	Asia; <i>Larix/Picea</i>	1–2	27–46 \times 5–8, L = 35, W = 6	4–5 \times 3–4, L = 4.3, W = 3.6, Q = 1.17–1.21	–	This study
<i>P. pini</i>	Europe; <i>Pinus</i>	1–3	39–67 \times 8–15, L = 51, W = 11	5.5–6 \times 4–5.5, L = 5.9, W = 4.9, Q = 1.2	+	This study
<i>P. yamanoi</i>	Northeast Asia; <i>Picea</i>	3–4	36–65 \times 7–13, L = 48, W = 10	4–6 \times 4–4.5, L = 4.9, W = 4.1, Q = 1.19	+	This study
<i>P. yunnanensis</i>	South Asia; <i>Pinus</i>	2–3	36–56 \times 6–10, L = 49, W = 8	4.5–5.5 \times 4–4.5, L = 5, W = 4.4, Q = 1.13–1.15	+	This study
<i>Porodaedalea</i> sp. 3	East Asia; <i>Pinus/Larix</i>	2–3	33–78 \times 9–17	4.5–5.5 \times 3.5–4.5	–	This study
<i>Porodaedalea</i> sp. 4	East Asia; <i>Pinus</i>	6–7	24–38 \times 8–12	4.5–5 \times 4–4.5	–	This study

less parallel along the tubes, 3–4 μm in diam. Hymenial setae frequent, mostly originating from subhymenium, rarely embedded in trama, not seen at dissepiment edges, subulate, dark brown, thick-walled, (30–)43–58(–70) \times 8–11(–12) μm ; cystidioles absent; basidia clavate, with four sterigmata and a simple septum at the base, 15–22 \times 4.5–5 μm ; basidioles dominating in hymenium, mostly pear-shaped, distinctly shorter than basidia.

Basidiospores 5–5.5(–6) \times (4–)4.5–5 μm , L = 5.3 μm , W = 4.6 μm , Q = 1.13–1.16 (n = 60/2), subglobose, hyaline, thin- to slightly thick-walled, smooth, without guttule, usually glued in tetrads, IKI–, moderately CB+.

Ecology and distribution: On live *Pinus*, southeast Asia, Oct.

Other specimen examined: VIETNAM. LAM DONG PROVINCE: Lac Duong District, Bidoup Nui Ba National Park, 12°07'35"N, 108°33'41"E, 1590 m, on living tree of *Pinus kesiyae*, 15 Oct 2017, *Dai 18417* (BJFC).

Notes: *Porodaedalea kesiyae* is most closely related to *P. laricis* and two unnamed species from boreal east Asia (FIG. 1). However, *P. laricis* and *Porodaedalea* sp. 3 have slightly bigger pores (2–3 per mm) and a boreal distribution, whereas *P. kesiyae* has smaller pores (3–4 per mm) and occurs in tropical pine forests. *Porodaedalea* sp. 4

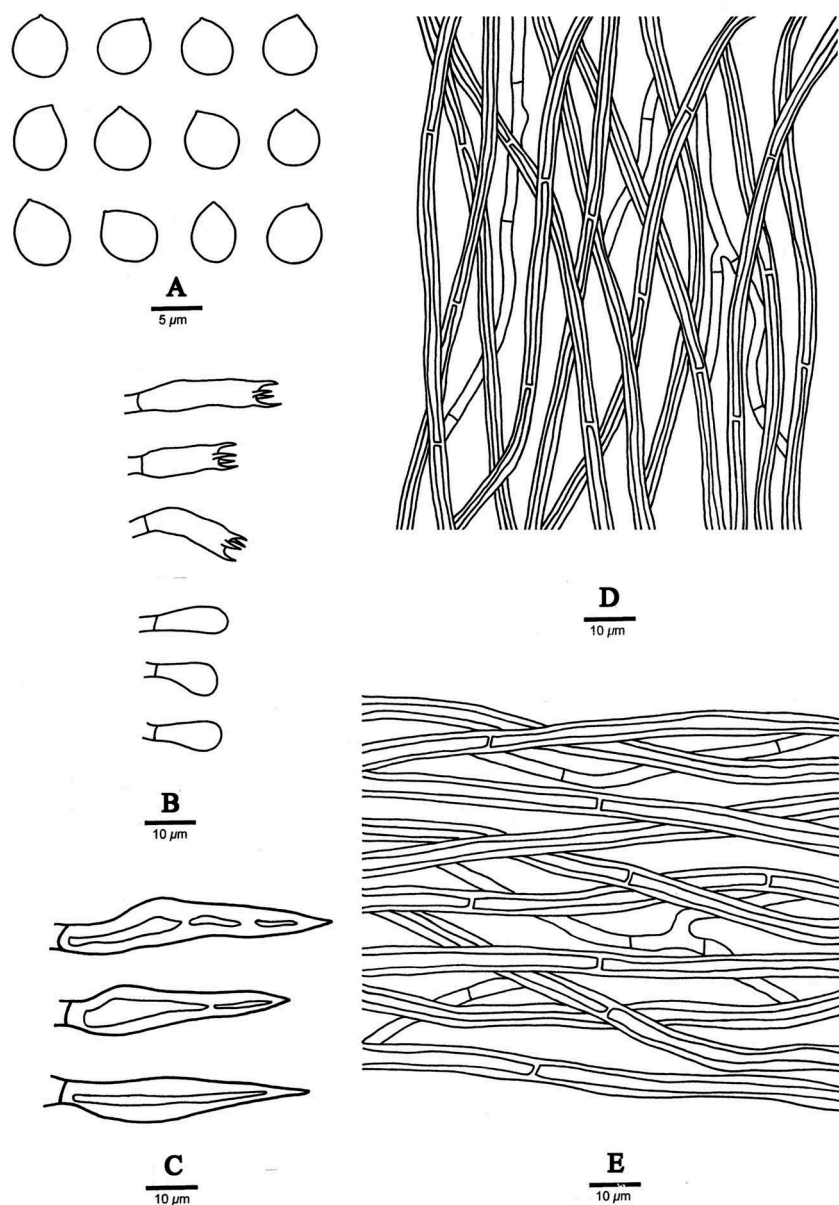


Figure 5. Microscopic structures of *Porodaedalea kesiyae* (holotype, Dai 18427). A. Basidiospores. B. Basidia and basidioles. C. Hymenial setae. D. Hyphae from trama. E. Hyphae from context.

differs from *P. kesiyae* in having smaller pores (6–7 per mm), shorter hymenial setae (24–38 μm), and smaller basidiospores (4.5–5 \times 4–4.5 μm ; TABLE 2). *Porodaedalea yunnanensis* and *P. cedrina* have basidiospores similar to those of *P. kesiyae*, but *P. yunnanensis* differs from *P. kesiyae* in having cystidioles, and *P. cedrina* is distinguished from *P. kesiyae* mainly due to the wider hymenial setae (6–18 μm) and larger pores (1–2 per mm).

Porodaedalea microsperma S.J. Dai, F. Wu & Y.C. Dai, sp. nov. FIGS. 2C, 6

MycoBank MB823678

Typification: CHINA. HEILONGJIANG PROVINCE: Yichun, Xing'an Forest Park, 47°42'23"N, 128°56'41"E, 350 m, on live *Larix gmelinii*, 31 Apr 2014, Cui 12047 (**holotype** BJFC016969).

Etymology: *microsperma* (Greek), referring to the small basidiospores.

Basidiomes perennial, pileate, solitary or imbricate, without odor or taste, hard corky when fresh, heavy and woody hard when dry. Pilei projecting up to 3.8 cm, 5 cm wide and 0.5 cm thick at base. Pileal surface grayish brown to black, concentrically sulcate with narrow zones, irregularly cracked and becoming

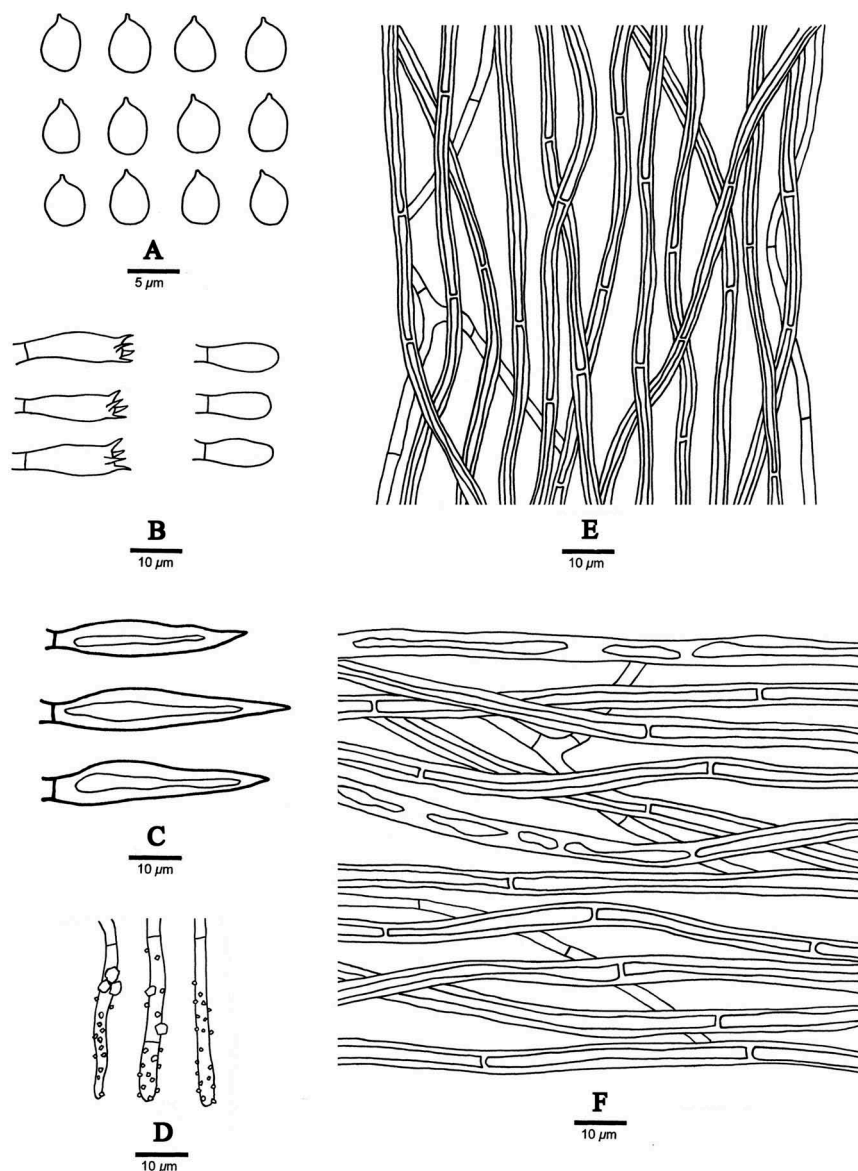


Figure 6. Microscopic structures of *Porodaedalea microsperma* (holotype, Cui 12047). A. Basidiospores. B. Basidia and basidioles. C. Hymenial setae. D. Generative hyphae at dissepiment edge. E. Hyphae from trama. F. Hyphae from context.

encrusted with age; margin obtuse. Pore surface clay-buff to dull brown and slightly glancing; pores mostly daedaleoid, some circular, 1–2 per mm; dissepiments thick, entire. Context dull brown, woody hard, up to 1 mm thick. Tubes cinnamon, woody corky, up to 0.4 cm long.

Hyphal system dimitic, generative hyphae simple-septate, tissue darkening in KOH.

Context: Generative hyphae hyaline, thin-walled, occasionally branched, frequently simple-septate, 2–3 µm in diam; skeletal hyphae dominant, yellowish brown, thick-walled with a wide lumen, rarely branched, frequently septate, straight, more or less regularly arranged, 3–5 µm in diam.

Tubes: Generative hyphae frequent, hyaline, thin-walled, occasionally branched, frequently septate, some bearing crystals at dissepiment edges, 2–2.5 µm in diam; skeletal hyphae yellowish brown, thick-walled with a narrow to wide lumen, unbranched, occasionally septate, straight, more or less parallel along the tubes, 2.5–3 µm in diam. Hymenial setae frequent, mostly originating from subhymenium, not or rarely embedded in trama, not seen at dissepiment edges, subulate, dark brown, thick-walled, encrusted with irregular crystals, (24–)27–46(–50) × 5–8 µm; cystidioles absent; basidia clavate, with four sterigmata and a simple septum at the base, 15–17 × 4–5 µm; basidioles dominating in hymenium, clavate or barrel-shaped, distinctly shorter than basidia.

Basidiospores $4\text{--}5 \times 3\text{--}4 \mu\text{m}$, $L = 4.3 \mu\text{m}$, $W = 3.6 \mu\text{m}$, $Q = 1.17\text{--}1.21$ ($n = 60/2$), ovoid, hyaline, thin- to slightly thick-walled, smooth, without guttule, usually in tetrads, IKI $^-$, moderately CB $^+$.

Ecology and distribution: On live *Larix* and fallen *Picea*, Asia, Apr.

Other specimen examined: CHINA. INNER MONGOLIA AUTONOMOUS REGION: Alashan zuoqi (County), Helanshan Natural Reserve, $38^{\circ}41'22''$ N, $105^{\circ}53'19''$ E, 2150 m on fallen trunk of *Picea*, 29 Apr 2003, Dai 4926 (IFP 004120).

Notes: *Porodaedalea microsperma* is most phenotypically similar to *P. cedrina* described from northern India. However, the latter has longer hymenial setae ($30\text{--}62 \mu\text{m}$) and larger basidiospores ($5\text{--}6 \times 4\text{--}5 \mu\text{m}$) compared with

P. microsperma. *Porodaedalea microsperma*, *P. chrysoloma*, *P. chinensis*, and *P. laricis* have pores of approximately the same size, but *P. chrysoloma* has longer hymenial setae ($30\text{--}55 \mu\text{m}$) and larger basidiospores ($4\text{--}5.5 \times 3\text{--}4.5$; TABLE 2). *Porodaedalea chinensis*, shown as the sister lineage to *P. microsperma*, has longer and wider hymenial setae ($35\text{--}69 \times 5\text{--}14 \mu\text{m}$) and larger basidiospores ($4.5\text{--}5.5 \times 3.5\text{--}4.5 \mu\text{m}$; TABLE 2) compared with *P. microsperma*. *Porodaedalea laricis* differs from *P. microsperma* by the wider hymenial setae ($6\text{--}12 \mu\text{m}$) and larger basidiospores ($5\text{--}5.5 \times 3.5\text{--}4 \mu\text{m}$; TABLE 2).

Porodaedalea yunnanensis S.J. Dai, F. Wu & Y.C. Dai, sp. nov. FIGS. 2D, 7

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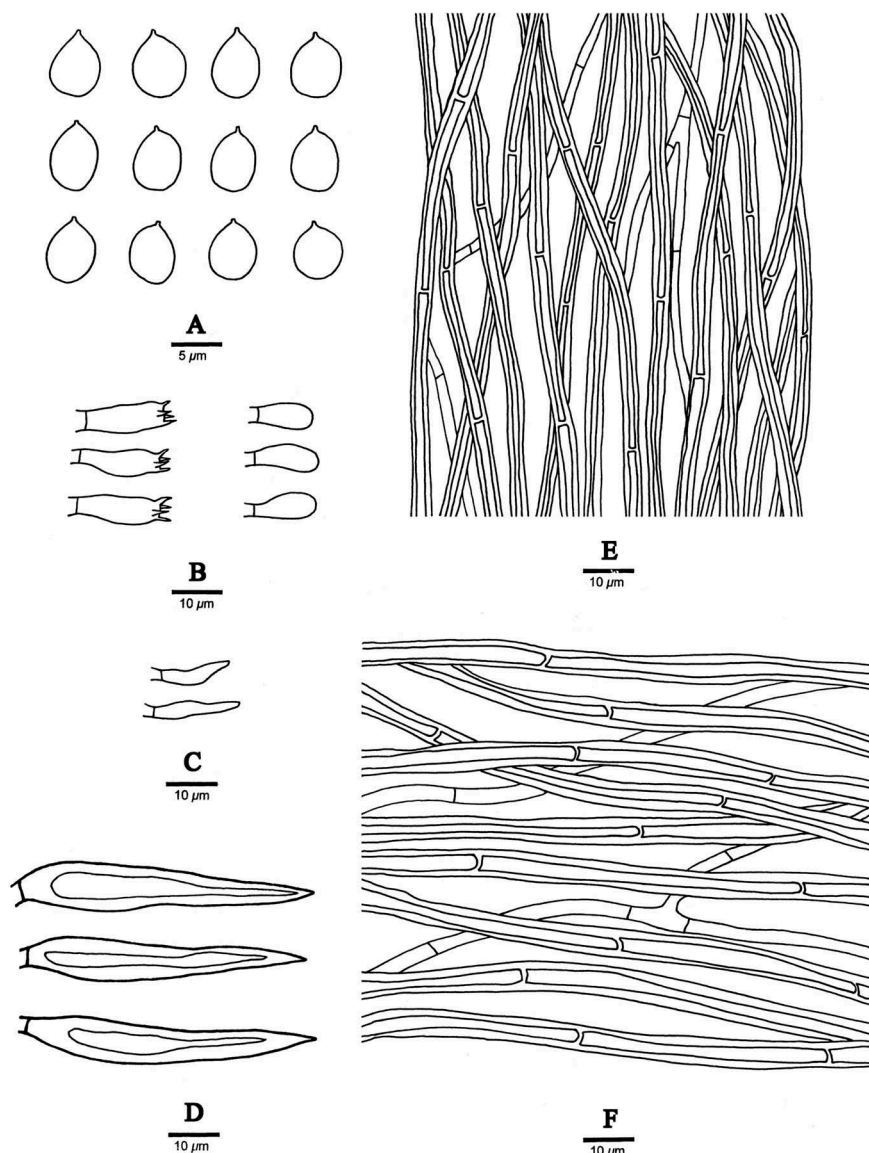


Figure 7. Microscopic structures of *Porodaedalea yunnanensis* (holotype, Dai 16878). A. Basidiospores. B. Basidia and basidioles. C. Cystidioles. D. Hymenial setae. E. Hyphae from trama. F. Hyphae from context.

Typification: CHINA. YUNNAN PROVINCE: Kunming, Heilong Pool, 25°08'34"N, 102°44'52"E, 2460 m, on live *Pinus armandii*, 2 Apr 2016, Dai 16878 (**holotype** BJFC022984).

Etymology: *yunnanensis* (Latin), referring to the locality of the species in Yunnan Province.

Basidiomes perennial, pileate, solitary or imbricate, without odor or taste, hard corky when fresh, heavy and woody hard when dry. Pilei projecting up to 3.3 cm, 5 cm wide and 0.6 cm thick at base. Pileal surface grayish brown to black, concentrically sulcate with narrow zones, irregularly cracked and becoming encrusted with age; margin obtuse. Pore surface buff to cinnamon-buff and slightly glancing; pores circular to angular, 2–3 per mm; dissepiments thick, entire. Context dull brown, woody hard, up to 2 mm thick. Tubes cinnamon, woody corky, up to 0.4 cm long.

Hyphal system dimitic, generative hyphae simple-septate, tissue darkening in KOH.

Context: Generative hyphae hyaline, thin-walled, occasionally branched, frequently simple-septate, 2–3 µm in diam; skeletal hyphae dominant, yellowish brown, thick-walled with a wide lumen, rarely branched, frequently septate, straight, more or less regularly arranged, 3.5–5 µm in diam.

Tubes: Generative hyphae frequent, hyaline, thin-walled, occasionally branched, frequently septate, 1.8–2.5 µm in diam; skeletal hyphae yellowish brown, thick-walled with a narrow to wide lumen, unbranched, occasionally septate, straight, parallel along the tubes, 2–3.5 µm in diam. Hymenial setae frequent, mostly originating from subhymenium, rarely embedded in trama, not seen at dissepiment edges, subulate, dark brown, thick-walled, (33–)36–56(–60) × 6–10(–14) µm; cystidioles present, fusoid; basidia clavate, with four sterigmata and a simple septum at the base, 13–20 × 5–6 µm; basidioles dominating in hymenium, clavate or barrel-shaped, mostly shorter than basidia.

Basidiospores 4.5–5.5 × 4–4.5(–5) µm, L = 5 µm, W = 4.4 µm, Q = 1.13–1.15 (n = 60/2), subglobose, hyaline, thin- to slightly thick-walled, smooth, without guttule, usually in tetrads, IKI–, moderately CB+.

Ecology and distribution: On live *Pinus*, south Asia, Apr and Jun.

Other specimen examined: CHINA. YUNNAN PROVINCE: Lijiang County, Yufengshi, 26°59'39"N, 100°11'46"E, 2960 m, on living tree of *Pinus armandii*, 17 Jun 1999, Dai 3072 (BJFC012865).

Notes: Phylogenetically, *P. yunnanensis* groups with *P. himalayensis* and *P. alpicola* but with poor support (FIG. 1). However, *P. himalayensis* differs from *P. yunnanensis* by smaller pores (5–6 per mm) and shorter hymenial setae (24–43 µm; TABLE 2). In

turn, *P. alpicola* differs from *P. yunnanensis* by smaller pores (4–6 per mm) and occurrence on *Abies*. *Porodaedalea yunnanensis* is morphologically similar to *P. pini*, and both species inhabit *Pinus*, but *P. pini* has wider hymenial setae (8–15 µm), usually larger basidiospores (5.3–6.2 × 4–5.5 µm; TABLE 2), and distribution in Europe.

KEY TO DESCRIBED SPECIES OF *PORODAEDEALEA*

1. Cystidioles present..... 2
- 1'. Cystidioles absent..... 10
2. Pores 4–6 per mm 3
- 2'. Pores 1–4 per mm 4
3. On *Abies*..... *P. alpicola*
- 3'. On *Picea*..... *P. himalayensis*
4. On *Cedrus* 5
- 4'. On other gymnosperm trees rather than *Cedrus* 6
5. Pores 1–2 per mm, basidiospores 5–6 µm long
..... *P. cedrina*
- 5'. Pores 3–4 per mm, basidiospores 4–5 µm long
..... *P. indica*
6. On *Larix*..... *P. laricis*
- 6'. On *Picea* or *Pinus* 7
7. On *Picea*..... *P. yamanoi*
- 7'. On *Pinus* 8
8. Basidiospores 5.5–6 µm long..... *P. pini*
- 8'. Basidiospores 4.5–5.5 µm long..... 9
9. Basidiospores broadly ellipsoid, 3.5–4.5 µm wide
..... *P. chinensis*
- 9'. Basidiospores subglobose, 4–4.5 µm wide
..... *P. yunnanensis*
10. Pores 1–2 per mm..... *P. microsperma*
- 10'. Pores 2–5 per mm 11
11. Pores 3–5 per mm 12
- 11'. Pores 2–3 per mm 13
12. On *Abies*, basidiospores 4.5–5 µm long
..... *P. cancriformans*
- 12'. On *Pinus*, basidiospores 5–5.5 µm long
..... *P. kesiyae*
13. On *Picea*, basidiospores <4.5 µm wide
..... *P. chrysoloma*
- 13'. On *Pseudotsuga*, basidiospores >4.5 µm wide
..... *P. gilbertsonii*

ACKNOWLEDGMENTS

We are grateful to Professor Bao-Kai Cui (BJFC, China) for allowing us to study his specimens and to Dr. Michal Tomšovský (Brno, Czech Republic) for laboratory assistance. The authors thank two anonymous reviewers and an executive editor for comments and suggestions of improvement to an earlier version of the manuscript.

FUNDING

This research was financed by the National Natural Science Foundation of China (project no. 31530002). The research of J. Vlasák was funded by institutional support (RVO 60077344).

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