

FULL PAPER

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## Second report of *Polyporus longiporus* and its phylogenetic position

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**Abstract** *Polyporus longiporus*, belonging to group Polyporellus, is newly reported from Japan in what also constitutes the second report of the species since its original description. This species is characterized by radially elongated pores, smooth and brown to dark brown pileus, and cylindrical and slightly curved basidiospores. Phylogenetic analysis based on the ITS region revealed that *P. longiporus* forms a terminal, strongly supported clade that is closely related to *P. ciliatus*. A description and illustrations of the present species and a key to the species of group Polyporellus are provided.

**Key words** *Lentinus* · Phylogeny · Polyporales · Polypores · Taxonomy

### Introduction

*Polyporus* P. Micheli ex Adams. (Polyporales, Basidiomycota) is characterized by stipitate basidiocarps, a dimitic hyphal system with arboriform skeleto-binding hyphae, cylindrical and smooth basidiospores, and causing a white rot (Gilbertson and Ryvarden 1987; Núñez and Ryvarden 1995a, 2001). Six infrageneric groups are commonly recognized within the genus, mainly based on macromorphology (Núñez and Ryvarden 1995a).

Among these, the group Polyporellus is characterized by medium-sized basidiocarps (up to 10 cm high) with a central stipe commonly lacking black cuticles and inflated skeleto-binding hyphae (Núñez and Ryvarden 1995a). Núñez and

Ryvarden (1995a) included seven species in this group, but since then, some additional species were described (Dai 1996; Boulet 2003; Silveira and Wright 2005). Many species of group Polyporellus are morphologically similar, and some of them had often been confused with each other [ex. *P. brumalis* and *P. ciliatus* (Kreisel 1963)]. However, mating tests and phylogenetic analyses in addition to critical morphological characterization allowed us to better circumscribe the species (Hoffmann and Esser 1978; Núñez and Ryvarden 1995b; Silveira and Wright 2002; Krüger et al. 2004). Phylogenetic studies revealed that species of group Polyporellus form a monophyletic clade more closely related to several species of *Lentinus* Fr. than other *Polyporus* species, however (Hibbett and Donoghue 1995; Hibbett and Thorn 2001; Krüger and Gargas 2004; Sotome et al. 2008).

Recently, a species obviously belonging to group Polyporellus was collected from boreal forest of Japan. This species is morphologically very similar to *Polyporus longiporus* Audet, Boulet & Sirard, a species hitherto known only from restricted areas of Canada (Boulet 2003). Among other features, our collection shares with *P. longiporus* a dark brown pileus and elongated pores.

Our collection was compared to the type of *P. longiporus*, and their phylogenetic relationships were inferred based on parsimony analysis of the nuclear ribosomal internal transcribed spacer (ITS) DNA sequence.

### Materials and methods

#### Morphological observation

The procedure for morphological observation follows Sotome et al. (2007). Color descriptions are given according to the Munsell system (Color Atlas). Herbaria holding specimens are abbreviated according to Holmgren et al. (1990). Cultures examined are deposited in the culture bank of the Microbial Ecology Laboratory, Forestry and Forest Products Research Institute, Tsukuba, Japan. Basidiospore measurements were made from materials mounted in

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**Table 1.** Taxa sequenced in this study

Species	Strain no.	Locality	Culture bank	GeneBank accession no.
<i>Ganoderma lucidum</i>	WD565	Ibaraki, Japan	FFPRI	AB462322
<i>Lentinus polychrous</i>	BCC 29606	Mae La Noi, Thailand	BIOTEC	AB478882
<i>Lentinus squarrosulus</i>	C500W	Kouchi, Japan	FFPRI	AB478883
<i>Lentinus tigrinus</i>	MUCL22821	Belgium	MUCL	AB478881
<i>Perenniporia tephropora</i>	WD1618	Okinawa, Japan	FFPRI	AB462323
<i>Polyporus arcularius</i>	WD2138	Ibaraki, Japan	FFPRI	AB478874
<i>Polyporus arcularius</i>	WD2359	Ibaraki, Japan	FFPRI	AB478875
<i>Polyporus brumalis</i>	WD2371	Miyagi, Japan	FFPRI	AB478876
<i>Polyporus brumalis</i>	WD2372	Miyagi, Japan	FFPRI	AB478877
<i>Polyporus brumalis</i> <sup>a,b</sup>	IFP Dai 2929 <sup>d</sup>	Jilin, China	–	AB478885
<i>Polyporus brumalis</i> <sup>a,b</sup>	IFP Yuan 853 <sup>d</sup>	Shanxi, China	–	AB478886
<i>Polyporus longiporus</i> <sup>a,c</sup>	DAOM 229479 <sup>d</sup>	Ontario, Canada	–	AB478880
<i>Polyporus longiporus</i>	WD2391	Hokkaido, Japan	FFPRI	AB478878
<i>Polyporus longiporus</i>	WD2579	Hokkaido, Japan	FFPRI	AB478879
<i>Polyporus tricholoma</i>	9591	Puerto Rico, USA	TENN	AB478884

<sup>a</sup>Specimens used for the DNA extraction

<sup>b</sup>Originally identified as *Polyporus mongolicus*

<sup>c</sup>Holotype

<sup>d</sup>Specimen number

Melzer's reagent. The following abbreviations are used for basidiospore measurements: L = mean basidiospore length, W = mean basidiospore width, R = the ratio of length/width of a basidiospore,  $r$  = arithmetic mean of R; ( $n = x/y$ ) means  $x$  measurements of basidiospores from  $y$  specimens. Cultural characters were studied on malt agar (Difco) plates at 25°C and described according to Nobles (1965). Mycelial growth rate  $K_r$  at 25°C was calculated as follows:  $R_1 = R_0 + K_r(t_1 - t_0)$ , where  $R_1$  = colony radius at time  $t_1$  and  $R_0$  = colony radius at time  $t_0$ . Extracellular oxidase reactions were tested according to Käärik (1965).

#### Molecular techniques and phylogenetic analyses

DNA was extracted from cultured mycelia or dried specimens using DNeasy Plant Mini Kit (Qiagen, Foster City, CA, USA) or EZNA Fungal DNA Kit (Omega Bio-Tek, Norcross, GA, USA). ITS region was amplified and sequenced with primers ITS4 and ITS5 (White et al. 1990). Polymerase chain reactions (PCR) for ITS was performed in 50 µl reaction mixtures containing 1 µg extracted template DNA, 200 µM dNTPs, 5 µl 10× PCR buffer, 1 unit TaKaRa Ex Taq (Takara Bio, Tokyo, Japan), and 2 pM of each PCR primer. The PCR conditions for ITS were (1) 5 min at 92°C; (2) 35 cycles of 1 min at 92°C, 1 min at 55°C, and 1 min at 72°C; and (3) 5 min at 72°C. All PCR products were purified using a MonoFas DNA Purification Kit (GL Sciences, Tokyo, Japan). DNA sequences were determined using a Big Dye Terminator 3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA) with the ABI 3100 DNA sequencer. Several sequences were downloaded from GenBank for phylogenetic positioning of the present fungus. ITS sequences generated in this study were submitted to GenBank (accession numbers AB462322, AB462323, AB478874-AB478886) and are listed in Table 1.

The ITS sequences were aligned with MAFFT version 6 (Katoh 2008). The alignment of ITS region was deposited

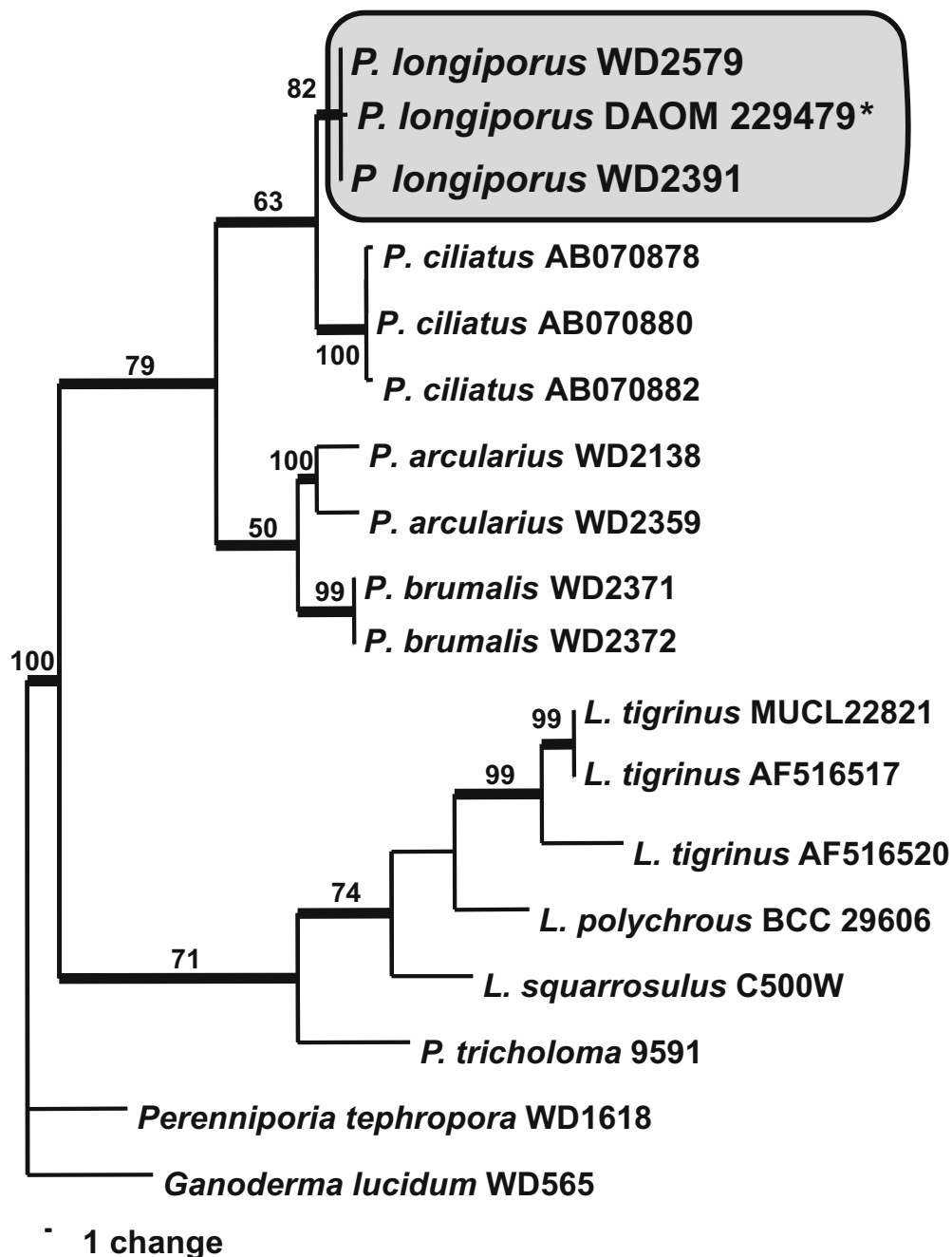
in TreeBase (accession S2389). Maximum parsimony (MP) analysis was performed in PAUP\* 4.0b10 (Swofford 2003) with gaps treated as missing data. The most parsimonious trees were identified using heuristic searches with random addition sequences (1000), maxtree set to auto increase, and tree-bisection-reconnection (TBR) branch swapping was employed. A bootstrap (BS) analysis was performed with 1000 replicates with 10 random taxon sequence additions per replicate and branch swapping set to TBR. *Ganoderma lucidum* (Curtis.) P. Karst. and *Perenniporia tephropora* (Mont.) Ryvarden were used as out-groups because these are close to, but outside of, the clade including group Polyporellus and *Lentinus* species (Sotome et al. 2008).

## Results

### Phylogenetic analysis

The ITS dataset consisted of 518 characters, of which 88 characters were phylogenetically informative for parsimony analysis. Three equally MP trees with 220 steps (CI = 0.77, RI = 0.80) were constructed by the MP analysis. The resulting topology is represented in Fig. 1. In this topology, the two Japanese collections (WD2391 and WD2579) and the holotype of *Polyporus longiporus* form a distinct monophyletic clade with strong bootstrap support (BS, 82%). The sequence of the holotype of *P. longiporus* differed from those of two Japanese collections only in 1 bp, suggesting that they are conspecific. Our phylogenetic tree also showed that *P. longiporus* is distinct from other species of group Polyporellus distributed in cool temperate to boreal areas of the Northern Hemisphere. *Polyporus longiporus* is most closely related to *P. ciliatus*, forming a moderately supported clade (BS, 63%), and not to *P. arcularius*, a species with similarly elongated pores.

**Fig. 1.** One of the three most parsimonious trees obtained from heuristic searches based on ITS region. Bootstrap support values above 50% are indicated at the nodes. Asterisk indicates holotype of *Polyporus* (*P.*) *longiporus*



## Taxonomy

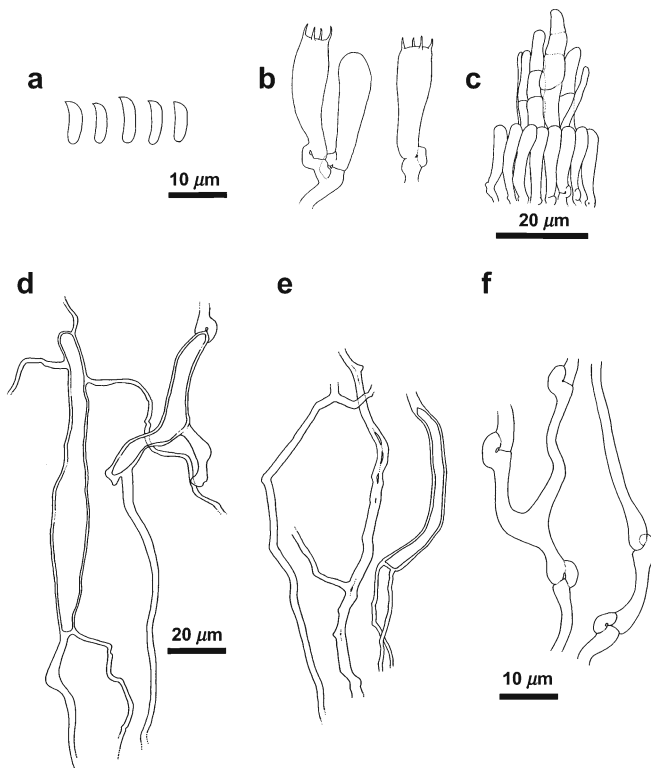
***Polyporus longiporus*** Audet, Boulet & Sirard, in Boulet, Les Champignons des Arbres de l'Est de l'Amérique du Nord: 530, 2003. Figs. 2, 3

Basidiocarps annual, centrally stipitate, solitary. Pileus circular in outline, flat to convex, 1.2–5 cm in diameter, up to 5 mm thick; surface smooth, glabrous, yellowish brown to dark brown (5YR2-4/4, 10YR5/8), azonate; margin flat to incurved, entire. Stipe cylindrical, equal, 1.3–8 cm long, 3–7 mm in diameter. Context fleshy to leathery in fresh condition, drying brittle, up to 5 mm thick, white in fresh

condition. Pore surface pale orange (10YR8-9/4-8), radially elongated, 0.5–2 × 0.1–0.5 mm, dissepiments thin, entire to slightly lacerate. Tubes concolorous with the context, up to 3.5 mm deep. Hyphal system dimitic with generative hyphae and skeleto-binding hyphae. Contextual generative hyphae 3–6.5 μm in diameter, often inflating, then up to 13.8 μm in diameter, thin walled, hyaline, with clamp connections, often composing a barrel-shaped cell, then up to 14 μm in diameter, with many transitions to skeleto-binding hyphae. Contextual skeleto-binding hyphae 1.5–4.5 μm in diameter, subsolid to thick walled, hyaline, non-dextrinoid, partly inflating and composing an elongate skeletal element, then up to 15 μm in diameter, slightly thick walled, with one to three lateral skeletal branches; sparse to almost lacking in



**Fig. 2.** *Polyporus longiporus* (TFM F-23203). Basidiocarps in natural habitat



**Fig. 3.** *Polyporus longiporus* (holotype). **a** Basidiospores. **b** Basidia and unripe basidium. **c** Hyphal peg. **d** Skeleto-binding hyphae from context, comprising elongate skeletal element with several lateral branches. **e** Skeleto-binding hyphae from trama. **f** Generative hyphae from trama

one specimen (TFM F-23203). Hymenophoral trama generative hyphae hyaline, 2–5 µm in diameter, often inflating, then up to 7.5 µm in diameter, thin walled, hyaline; skeleto-binding hyphae 2–3.5 µm in diameter, subsolid to thick walled, hyaline, non-dextrinoid, often consisting of elongate fusoid elements up to 7 µm in diameter, with one to several lateral and tapering branches; sparse to almost lacking in one specimen (TFM F-23203). Basidia clavate, 15–25.5 × 4–6 µm, with four sterigmata. Basidiospores cylindrical,

slightly curved, hyaline, non-dextrinoid, 6.3–8.6 × 1.8–2.3 (–2.7) µm, L = 7.34 µm, W = 2.05 µm, R = 3–4.25, r = 3.63 (n = 269/5). Hyphal pegs sparse, consisting of fascicle of thin-walled hyphae, up to 6 µm in diameter, projecting up to 30 µm above hymenium.

Specimens examined: CANADA: Ontario, Limoges, Forêt Larose, on *Salix* sp., Y. Lamoureux, May 1995 (holotype; DAOM 229479); Manitoba, Winnipeg, S. of Manitoba Agricultural College, on old willows, G.R. Bisby, 24 May 1995 (paratype; DAOM 205049); Ontario, Ottawa, Arboretum of Central Experimental Farm, on ground under *Salix* sp., J.W. Groves, 18 May 1942 (paratype; DAOM 10447). JAPAN: Hokkaido, Ishikari, riverside of Ishikari R., on hardwood, leg. T. Kasuya & S. Takehashi, 27 Apr. 2006 (TFM F-23203); same place, S. Takehashi, 11 May 2006 (TFM F-23202); Hokkaido, Ebetsu, near Satori Pond, M. Nakai, 30 Apr. 2007 (TFM F-23204); Hokkaido, Ishikari, on ground under hardwood, leg. H. Shirayama, 5 May 2007 (TFM F-23205).

Cultural characters: Growth fast, 6.5–8.5 mm/day, plates covered in 1 week. Advancing zone even, appressed, some mycelia submerged in the agar, white. Mat usually white, sometimes brownish grey (5YR7-8/2), aerial mycelium cottony to downy, partly becoming pale orange (10YR8-9/4) with crust. Reverse unchanged. Odor none. Hymenophore development not seen within 6 weeks. Generative hyphae from advancing zone thin walled, hyaline, 2–4 µm in diameter, with clamp connections. Generative hyphae from aerial mycelium thin- to thick walled, hyaline to brown, 2–5.5 µm in diameter, with clamp connections. Fiber hyphae present, frequently branched, hyaline, thick walled to solid, up to 2 µm in diameter. Interlocking hyphae abundantly present.

Extracellular peroxidase activities; 1-naphthol, +; tyrosine, –.

Species code: 2, 3, 5, 8, 11, 17, 32, 34, 36, 38, 41, 54

## Discussion

*Polyporus longiporus* is characterized by the centrally stipitate basidiocarps with flat to convex pileus, smooth, glabrous, and dark brown pileus surface, elongated pores, the dimitic hyphal system with often inflating (up to 13.8 µm) generative hyphae, skeleto-binding hyphae that often comprise elongate fusoid skeletal elements and narrow cylindrical basidiospores. According to our measurement, the spores are larger [6.3–8.6 × 1.8–2.3(–2.7) µm] than those given in the original description [5.3–6.9 × 1.3–1.9(–2.6)] µm (Boulet 2003).

The hyphal system with inflating generative hyphae having abundant clamp connections and inflating skeleto-binding hyphae is characteristic of group Polyporellus. In *Polyporus longiporus*, the skeleto-binding hyphae are abundant to dominant in most specimens examined, but sparse to almost lacking in one specimen. Several species of *Lentinus* also have similar hyphal characters [ex. *L. tigrinus* (Pegler 1983; Núñez and Ryvarden 1995a)]. Group Polypo-

rellus and *Lentinus* also share other morphological characters such as the centrally stipitate and medium-size basidiocarps and a stipe without a black crust (Sotome et al. 2008). Hyphal morphology as indicated above is also phylogenetically significant to define the clade, as suggested by Krüger and Gargas (2004).

Among the species examined here, *P. ciliatus* is the closest relative of *P. longiporus*. Both species share similar middle-sized and centrally stipitate basidiocarps (up to 10 cm in diameter) with grayish and convex pileus, inflating generative hyphae, and skeleto-binding hyphae and cylindrical basidiospores (Núñez and Ryvarde 1995a). However, *P. ciliatus* is distinct from *P. longiporus* by the circular pores and smaller basidiospores ( $5-7 \times 1-2 \mu\text{m}$ ) (Núñez and Ryvarde 1995a; Bernicchia 2005). Furthermore, basidiomata of *P. longiporus* appear in spring in boreal areas of Japan and Canada, whereas in *P. ciliatus*, they appear during summer and the species is distributed in temperate areas of Eurasia (Núñez and Ryvarde 1995a, 2001; Bernicchia 2005).

*Polyporus arcularius* resembles *P. longiporus* in having radially elongated pores and frequent occurrence in spring. However, *P. arcularius* is distinct from *P. longiporus* by the smaller basidiocarps (up to 2.5 cm in diameter), dark brown pileus covered with distinct scales, thin and leathery context, and the distinctly hexagonal pores (Núñez and Ryvarde 1995a). *Polyporus brumalis* is similar to *P. longiporus* in the shape of the basidiocarps but has angular to round pores [ $(1-2-3(-4)/\text{mm}$ ] and smaller basidiospores ( $5.5-7 \times 2-2.5 \mu\text{m}$ ) (Núñez and Ryvarde 1995a; Dai 1996; Bernicchia 2005). *Polyporus longiporus* is phylogenetically distinct from both *P. arcularius* and *P. brumalis*.

A key to the accepted species of group Polyporellus is provided below.

### A key to species of group Polyporellus

1. Growing on roots of living grass (mostly Gramineae) . . . . . 2
1. Growing on dead wood . . . . . 3
2. Basidiospores subcylindrical to subfusiform,  $6-10 \times 2.5-4 \mu\text{m}$ ; pileus light brown to grayish brown, glabrous; pores angular, 2–3/mm (Sotome et al. 2007). Known from Great Plains region of central United States (Overholts 1953; Gilbertson and Ryvarde 1987). . . . . *P. cryptopus*
2. Basidiospores cylindrical to fusiform,  $7-11 \times 2.5-4 \mu\text{m}$ ; pileus grayish orange to grayish brown, wrinkled, glabrous; pores angular,  $(1-2-3)/\text{mm}$  (Sotome et al. 2007). Known from Argentina, China, central Europe, Kazakhstan, and Morocco (Domański et al. 1967; Núñez and Ryvarde 1995a; Zhao 1998; Silveira and Wright 2005). . . . . *P. rhizophilus*
3. Pores more than 4/mm. . . . . 4
3. Pores fewer than 4/mm . . . . . 5
4. Basidiospores ellipsoid to cylindrical,  $6-9 \times (2-3)3-4 \mu\text{m}$ ; pileus pale tan to pale brown, smooth, glabrous, usually

ciliate along the margin; pores round to angular,  $(5-7)7-9/\text{mm}$ . Common in the neotropics and very rare in the paleotropics (Núñez and Ryvarde 1995a). . . . .

- . . . . . *P. tricholoma*
4. Basidiospores cylindrical, slightly curved,  $5-7 \times 1-2 \mu\text{m}$ ; pileus brown, reddish brown to tobacco brown, glabrous or minutely squamulose; pores round, 5–7/mm. Common in the temperate area of Eurasia, usually appear in the summer (Núñez and Ryvarde 1995a; Bernicchia 2005). . . . . *P. ciliatus*
5. Basidiospores ellipsoid,  $7-9 \times 3-4 \mu\text{m}$ ; pileus brown to ochraceous, covered with numerous fine appressed scales; pores radially elongated,  $1(-2)/\text{mm}$ . Known from Mediterranean and Micronesian areas (Núñez and Ryvarde 1995a; Bernicchia 2005). . . . . *P. meridionalis*
5. Basidiospores cylindrical, straight or slightly curved. . . . . 6
6. Pileus white to ochre, glabrous, areolate, with small and darker scales when old; pores hexagonal, radially elongated, 1–2/mm; basidiospores cylindrical and slightly curved  $(6-7)6.5-7.5(-8) \times 2.3-2.8(-3)$ . Known from eastern Mediterranean region (Núñez and Ryvarde 1995a; Bernicchia 2005). . . . . *P. corylinus*
6. Pileus not as above. . . . . 7
7. Pileus reddish brown to dark brown or dark gray; pores regular or elongated but never hexagonal . . . . . 8
7. Pileus ochraceous, yellowish brown, brown. Pores hexagonal. . . . . 9
8. Pores angular to elongated,  $(1-2)2-3(-4)/\text{mm}$ ; pileus reddish brown to dark brown, glabrous, finely tomentose or densely hirsute; basidiospores cylindrical, slightly curved,  $5.5-7 \times 2-2.5 \mu\text{m}$ . Common in the boreal area of Eurasia and North America (Núñez and Ryvarde 1995a; Dai 1996; Bernicchia 2005). . . . . *P. brumalis*
8. Pores radially elongated,  $0.5-2 \times 0.1-0.5 \text{ mm}$ ; pileus dark gray to almost black, smooth, glabrous; basidiospores allantoid to cylindrical,  $6.3-8.6 \times 1.8-2.3(-2.7) \mu\text{m}$ . Known from boreal areas in Canada and Japan . . . . . *P. longiporus*
9. Pileus yellowish brown to brown, frequently with minute scales; pores radially elongated,  $1-2(-3)/\text{mm}$ ; cylindrical, straight or slightly curved,  $6-9 \times 2-3 \mu\text{m}$ . Cosmopolitan species except for the boreal region (Núñez and Ryvarde 1995a) . . . . . *P. arcularius*
9. Pileus pale brown to ochraceous brown, glabrous or downy, wrinkled when dry; pores radially elongated, 1–3/mm; basidiospores cylindrical to subellipsoid  $6-8(-9) \times 2.5-3.5 \mu\text{m}$ . Known from Argentina, Bolivia, Brazil, Martinique, and Paraguay (Silveira and Wright 2005) . . . . . *P. arcularioides*

### Species excluded from the key

*Polyporus mongolicus* (Pilát) Y.C. Dai, Ann. Bot. Fenn. 33: 154, 1996.

This species was originally described as a variety of *P. arcularius* by Pilát (1940). Later, Kreisel (1963) placed it as a

variety of *P. brumalis*, and Dai (1996) accepted it as an independent species characterized by the stipitate basidiocarps, tomentose to densely hirsute and gray to blackish pileus surface, duplex context, and freely arranged pores [(2–)3–4/mm]. Dai (1996) distinguished this species from *P. brumalis* by the narrower generative hyphae and narrow and more abundant skeletal hyphae. However, some specimens of '*P. mongolicus*' indicated below have microscopic characters identical to those of *P. brumalis* and share the same ITS sequences (AB478885 and AB478886) with some isolates of *P. brumalis* (AB478876, AB478877). Consequently, we conclude *P. mongolicus* as a synonym of *P. brumalis*.

Specimens examined: CHINA: Jilin, Antu, on fallen *Betula*, Y.-C. Dai, 15 Sep. 1995 (IFP Dai 2929); Shanxi, Jiacheng, Pangquangou Nature Reserve, on fallen branch of *Betula*, 12 Oct. 2004 (IFP Yuan 831, IFP Yuan 853); same place, on fallen branch of *Betula*, 22 Sep. 2006 (IFP Yuan 2462).

***Polyporus sublignosus*** J.D. Zhao & X.Q. Zhang, Acta Mycol. Sin. 10: 269, 1991.

Dai (1996) included this species in group Polyporellus, but it is now considered as a synonym of *Laccocephalum hartmannii* (Cooke) Núñez & Ryvarden (Núñez and Ryvarden 2001; Dai 2009).

***Polyporus yuananensis*** X.Q. Zhang & J.D. Zhao, Acta Mycol. Sin. Suppl. 1: 275, 1986.

This species has a basidiocarp with a sub-central stipe lacking a black crust (Zhao and Zhang 1992). Dai (2009) concluded that this is a synonym of *Abortiporus biennis* (Bull.) Singer after a type study.

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## References

- Bernicchia A (2005) Polyporaceae s.l. Edizioni Candusso, Alassio
- Boulet B (2003) Les champignons des arbres de l'est de l'Amérique du Nord. Les Publications du Québec, Québec
- Dai Y-C (1996) Changbai wood-rotting fungi 5. Study on *Polyporus mongolicus* and *P. tubaeformis*. Ann Bot Fenn 33:153–163
- Dai Y-C (2009) Type studies on polypores described by J.D. Zhao, either alone or with other mycologists. Ann Bot Fenn (in press)
- Domański S, Orłós H, Skirgiełło A (1967) Fungi. Polyporaceae II (pileatae) Mucronoporaaceae II (pileatae) Ganodermataceae, Bondarzewiaceae, Boletopsidaceae, Fistulinaceae (Grzyby), revised edition. Translated from Polish. Foreign scientific publications department of the National Center for Scientific, Technical, and Economic Information, Warsaw, 1973
- Gilbertson RL, Ryvarden L (1987) North American polypores, vol. 2. Fungiflora, Oslo
- Hibbett DS, Donoghue MJ (1995) Progress toward a phylogenetic classification of the Polyporaceae through parsimony analyses of mitochondrial ribosomal DNA sequences. Can J Bot 73(suppl 1): S853–S861
- Hibbett DS, Thorn RG (2001) Basidiomycota: Homobasidiomycetes. In: McLaughlin FJ, McLaughlin EG, Lemke PA (eds) Systematics and evolution. The Mycota, vol VII. Springer-Verlag, Berlin, 121–168
- Hoffmann P, Esser K (1978) Genetics of speciation in the basidiomycetous genus *Polyporus*. Theor Appl Genet 53:273–282
- Holmgren PK, Holmgren NH, Barnett LC (1990) Index herbariorum. Part 1: The herbaria of the world, 8th edn. New York Botanical Garden, New York
- Käärik A (1965) The identification of the mycelia of wood-decay fungi by their oxidation reactions with phenolic compounds. Bibl Mycol 81:1–151
- Katoh T (2008) Recent developments in the MAFFT multiple sequence alignment program. Brief Bioinform 9:286–298 (preprint)
- Kreisel H (1963) Über *Polyporus brumalis* und verwandte Arten. Feddes Rept 68:129–138
- Krüger D, Gargas A (2004) The basidiomycete genus *Polyporus*: an emendation based on phylogeny and putative secondary structure of ribosomal RNA molecules. Feddes Rept 115:530–546
- Krüger D, Hughes KW, Petersen RH (2004) The tropical *Polyporus tricholoma* (Polyporaceae): taxonomy, phylogeny, and the development of methods to detect cryptic species. Mycol Prog 3:65–80
- Nobles MK (1965) Identification of cultures of wood-inhabiting Hymenomycetes. Can J Bot 43:1097–1139
- Núñez M, Ryvarden L (1995a) *Polyporus* (Basidiomycotina) and related genera. Synopsis Fungorum 10:1–85
- Núñez M, Ryvarden L (1995b) *Polyporus* new to Japan 1. Species of *Polyporus*, with a note on *P. hartmannii*. Mycoscience 36:61–65
- Núñez M, Ryvarden L (2001) East Asian polypores 2. Polyporaceae s. lato. Synopsis Fungorum 14:170–522
- Overholts LO (1953) Polyporaceae of the United States, Alaska and Canada. University of Michigan Press, Ann Arbor
- Pegler DN (1983) The genus *Lentinus*: a world monograph. Kew Bull Addit Ser 10:1–281
- Pilát A (1940) Basidiomycetes chinenses. Ann Mycol 38:61–82
- Silveira RMB, Wright JE (2002) *Polyporus* s. str. in southern South America: mating tests. Mycol Res 106:1323–1330
- Silveira RMB, Wright JE (2005) The taxonomy of *Echinochaete* and *Polyporus* s. str. in South America. Mycotaxon 93:1–59
- Sotome K, Hattori T, Kakishima M (2007) *Polyporus phyllostachydis* sp. nov. with notes on other rhizophilic species of *Polyporus* (Basidiomycota, Polyporaceae). Mycoscience 48:42–46
- Sotome K, Hattori T, Ota Y, To-anun C, Salleh B, Kakishima M (2008) Phylogenetic relationships of *Polyporus* and morphologically allied genera. Mycologia 100:603–615
- Swofford DL (2003) PAUP 4.0b10: phylogenetic analysis using parsimony. Sinauer Associates, Sunderland, MA
- White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds) PCR protocols: a guide to methods and applications. Academic Press, San Diego, pp 315–322
- Zhao J-D (1998) Flora fungorum sinicorum, vol. 3. Polyporaceae. Science Press, Beijing
- Zhao J-D, Zhang X-Q (1992) The polypores of China. Bibl Mycol 145:1–524