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FULL PAPER

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A new species of *Melampsora* on *Populus yunnanensis* from China

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Abstract *Melampsora nujiangensis*, a rust fungus found on *Populus yunnanensis* in China, is described as a new species. Light and scanning electron microscopy with herbarium specimens of the rust fungus show that the shape of its urediniospores differs from that of other known species of *Melampsora*, and its urediniospore walls are thinner than the other species. Furthermore, in phylogenetic trees based on the DNA sequences (28S and ITS) the rust fungus is phylogenetically separated by high bootstrap values. These results indicate that the fungus is an isolated species among the genus *Melampsora*.

Key words *Melampsora nujiangensis* · Molecular phylogeny · *Populus* · rDNA · Rust fungus · Taxonomy · Uredinales

Introduction

Rust fungi in the genus *Melampsora* Castagne (1843) cause premature defoliation of poplars, and most species alternate to conifers and dicotyledonous and monocotyledonous plants. About 90 species of *Melampsora* have been described worldwide (Kirk et al. 2001). *Melampsora* species on Salicaceae are classified mainly based on their morphological characteristics of uredial and telial states and aecial and telial host range (Cummins and Hiratsuka 2003). At present, some 13 species and two hybrids of *Melampsora* on *Populus* are known worldwide (Van Kraayenoord et al. 1974; Bagyanarayana 1998; Cellerino 1999). However, their taxonomic identity and phylogenetic relationships are still poorly defined.

In China, Miyake (1914) first described *Melampsora* species on popular based on specimens collected in northeastern China (Tai 1979), and thereafter some rust species were reported to produce uredinia and telia on *Populus* by some authors (Miura 1928; Huo and Wang 1934; Liou and Wang 1935). Tai (1979) reviewed earlier studies of *Melampsora* spp. on poplars in China and listed five species: *M. larici-populina* Kleb., *M. laricis* R. Hartig, *M. magnusiana* G. Wagner ex Kleb., *M. rostrupii* G. Wagner ex Kleb., and *M. pruinosae* Tranzschel. In the following years, some authors added six more species in China based on morphological examination, i.e., *M. abietis-canadensis* (Farl.) C.A. Ludw., *M. abieti-populi* S. Imai, *M. allii-populina* Kleb., *M. occidentalis* H.S. Jacks., *M. multa* Y.Z. Shang, M.H. Pei et Z.W. Yuan, and *M. populnea* (Pers.: Pers.) P. Karst. (Yuan 1984; Shang et al. 1986a; Guo 1989; Zhuang and Wei 1994; Zhang et al. 1997; Cao and Li 1999). Tian and Kakishima (2005) reviewed the current taxonomic status of *Melampsora* species on poplars in China. In these reports, the rust fungus on *P. yunnanensis* Dode has only been reported as *M. larici-populina* in China. During a monographic study of the genus *Melampsora* in China and Japan (Tian et al. 2004; Tian and Kakishima 2005), the rust fungus on *P. yunnanensis* collected in Yunnan Province was found to be morphologically different from *M. larici-populina.* Therefore, morphological examinations and phylogenetic analysis were carried out to clarify the taxonomic status of this rust fungus.

Materials and methods

Materials examined

The rust specimens on *P. yunnanensis* were collected from Nujiang District, Yunnan Province, China, in September

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1998 and kept in the Mycological Herbarium, Graduate School of Life and Environmental Sciences, University of Tsukuba, Japan (TSH). Several rust specimens on *P. yunnanensis* were borrowed from the following herbaria for comparative examination; the Herbarium of Systematic Mycology and Lichenology Laboratory, Institute of Microbiology, Beijing, China (HMAS) and the Mycological Herbarium of College of Forestry, Northwest Sci-Tech University of Agriculture and Forestry, Xian, China (HMNWFC).

Morphological observations

Urediniospores and teliospores from specimens were mounted in a drop of lactophenol-cotton blue solution for light microscopic examination. About 30–50 spores were randomly chosen from each sample and observed under a BH 100 microscope (Olympus, Tokyo, Japan). Length, width, and wall thickness of urediniospores, distance between spines on the surface of urediniospores, and size of teliospores were measured with a Q-Win Image Analyzer (Leica, Tokyo, Japan). The surface features of urediniospores were observed by scanning electron microscopy (SEM). For SEM, urediniospores were dusted onto specimen holders attached with double-sided adhesive tape and then coated with platinum-palladium with an E-1030 Ion Sputter Coater (Hitachi, Tokyo, Japan). They were examined with a S-4200 SEM (Hitachi) operating at 15 kV.

DNA extraction and PCR amplification

DNA was extracted from about 100–200 urediniospores obtained from a single sorus. Spores were crushed between two sterile glass slides and suspended in 20 µl extraction buffer [10 mM Tris-HCl (pH 8.3), 1.5 mM $MgCl_2$, 50 mM KCl, 0.01% Proteinase K, and 0.01% sodium dodecyl sulfate (SDS)], incubated at 37°C for 60 min, then at 95°C for 10 min (Suyama et al. 1996; Virtudazo et al. 1998). From these crude extracts, a 5-µl aliquot was used directly for polymerase chain reaction (PCR) amplification.

Amplifications were carried out using 40-µl PCRs, each containing 0.2 µM primer, 1 unit TaKaRa Taq DNA polymerase (Takara, Tokyo, Japan), a commercial deoxynucleoside triphosphate (dNTP) mixture (containing 2.5 mM each dNTP), and Taq reaction buffer (containing 2 mM Mg^{2+}). PCR was carried out using a GeneAmp PCR System 9700 (Applied Biosystems, Foster City, CA, USA) under the following conditions: 95°C for 3 min, then 35 cycles of 95°C for 30 s, 55°C for 1 min, 72°C for 1 min, and a final step of 72°C for 10 min. PCR of the D1/D2 region of nuclear large subunit rDNA was accomplished using the primer pair NL1 (5′-GCATATCAATAAGCGGAGGAAAAG) and NL4 (5′-GGTCCGTGTTTCAAGACGG) (O'Donnell 1993). The internal transcribed spacer (ITS) and 5.8S regions of rDNA were amplified with primers ITS1F (5′-CTTGGTCATTTAGAGGAAGTAA) (Gardes and Bruns 1993) and ITS4 (5′- TCCTCCGCTTATTGATATGC) (White et al. 1990). After amplification, 3-µl aliquots of the reaction products were electrophoresed on 1% (w/v) agarose gel containing 0.5 µg/ml ethidium bromide in TAE buffer [40 mM Tris- HCl, 20 mM sodium acetate, 1 mM ethylenediaminetetraacetic acid (EDTA), pH 7.4].

DNA sequencing

PCR products were purified with MicroSpin TM S-400 HR columns (Amersham Pharmacia Biotech, Piscataway, NJ, USA). The purified PCR products were sequenced directly using a Big Dye Terminator ver. 3.1 Cycle Sequencing Ready Reaction Kit (PE Applied Biosystems, Foster City, CA, USA) with the same primers as used for PCR. Cycle sequencing reactions were finally purified using Centri-Sep spin columns CS-901 (Princeton Separations, Adelphia, NJ, USA), and sequence data collected using an ABI Prism 3100 Automated DNA sequencer (Applied Biosystems).

Phylogenetic analysis

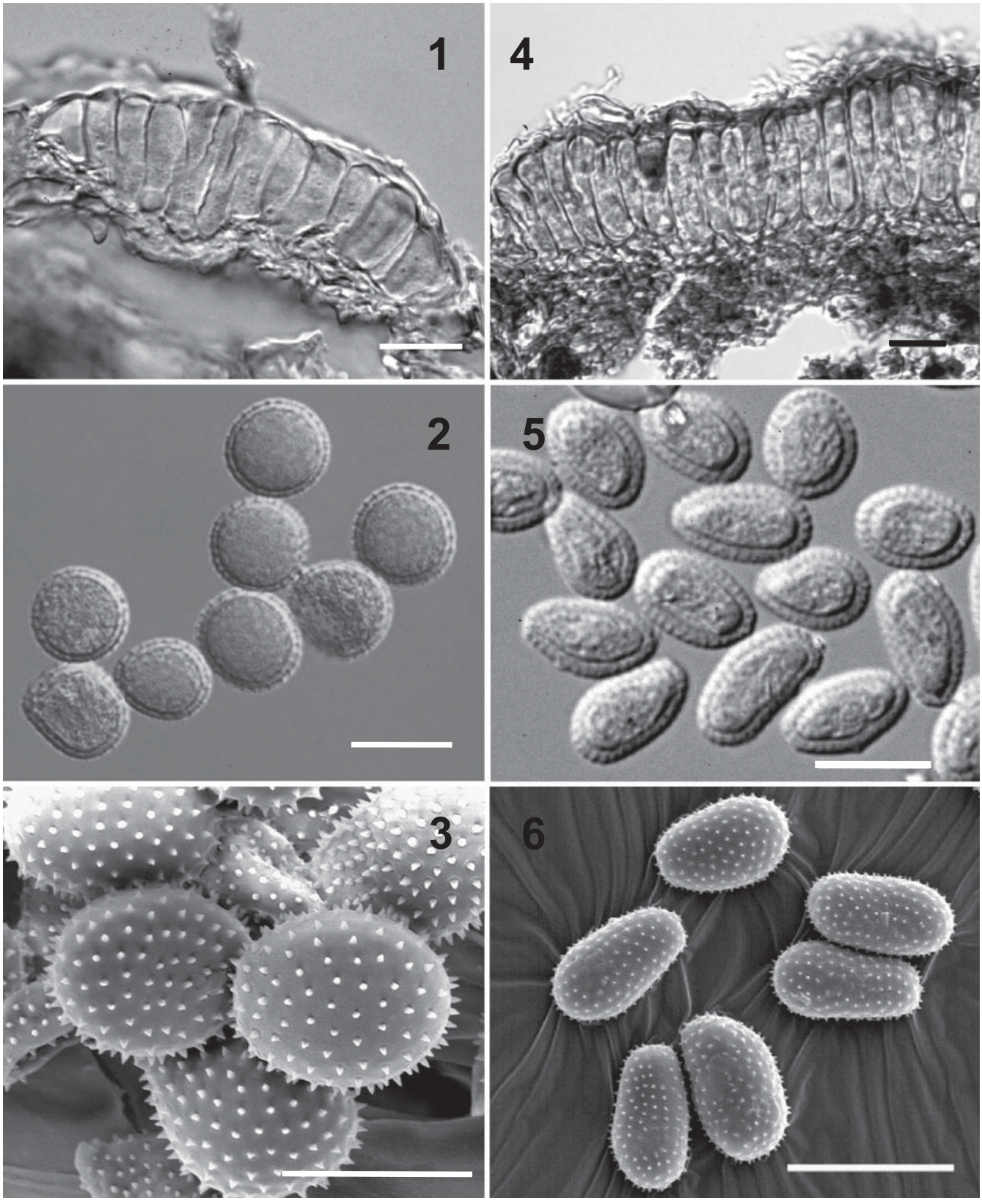
DNA sequences alignment was performed using the Clustal X multiple alignment program, version 1.8 (Thompson et al. 1997). Further manual alignment was done in Se-Al v2.07a (Rambaut 2001). Alignment gaps were treated as a "fifth characters" base in the analysis. Phylogenetic trees were constructed using PAUP version 4.0b10 (Swofford 2002) with the neighbor-joining method (Saitou and Nei 1987) from large subunit (LSU) rDNA and ITS1–5.8S–ITS2 (ITS region) sequences, respectively. Neighbor-joining (NJ) analysis of a distance matrix produced by the Kimura two-parameter model (Kimura 1980) with a transition: transversion rate of 2.0 was applied with the default parameters of the program. Bootstrap analysis was based on 1000 bootstrap replicates using the NJ option for NJ trees (Felsenstein 1985).

Taxonomy

Melampsora nujiangensis Y. M. Liang, C. M. Tian et Kakishima. sp. nov. Figs. 1–3

Spermogoniis et aeciis ignotis; urediniis hypophyllis, subepidermalibus, mox nudis, sparsis vel rarius aggregatis, rotundatis vel ellipsoideis, 0.2–0.8 mm diametro, auratiacis vel luteo-brunneis, aliquantum pulveraceis; urediniosporis globosis vel rarius ovoideis, 17.0–26.8 (21.3) × 18.2–22.8 (19.7) µm, episporio echinulato 0.9–1.9 (1.3) µm crasso; paraphysibus capitatis, 33–56 × 12.1–15.3 µm, episporio 2–6 µm; teliis subepidermalibus, sparsis, minutis, flavo-brunneis, 0.4–0.8 mm diametro; teliosporis prismaticis, 23.1–43.8 (36.3) × 5.4–12.4 (8.8) µm, episporio levigato 1 µm crasso.

Holotypus: In foliis *Populi yunnanensis* Dode (Salicaceae), Pianma, Nujiang Districtus, Yunnan Province, China, Sept. 29, 1998, M. Kakishima, TSH-R20042, in



Figs. 1–6. 1–3 *Melampsora nujiangensis* on *Populus yunnanensis* (TSH-R20042, holotype). **1** Hypophyllous telia and teliospores. **2** Globoid urediniospores with thin walls. **3** Uniformly echinulate urediniospores. **4–6** *M. abieti-populi* on *P. wilsonii* (HMAS-55410). **4** Hypophyllous telia and teliospores. **5** Ellipsoid urediniospores. **6** Uniformly echinulate urediniospores. *Bars* 20 µm

Table 1. *Melampsora* species and their GenBank accession numbers used for phylogenetic analysis

Species	Host plants	Year and collectors	Voucher specimens[a]	GenBank accession no.	
				D1/D2	ITS
M. abieti-populi	*P. wilsonii*	1994, N. Zhang	HMAS55410	AB116799	AB116870
M. abieti-populi	*P. wilsonii*	1996, Z.M. Cao	HMNWFC-TR0009	–	AB116869
M. allii-populina	*P. laurifolia*	1986, J.Y. Zhuang	TSH-R04141 (HMAS52890)	AB116801	AB116875
M. allii-populina	*P. laurifolia*	1986, J.Y. Zhuang	TSH-R04138 (HMAS52892)	AB116803	AB116872
M. allii-populina	*P. talassica*	1981, Z.K. Liu	HMNWFC-T035		AB116871
M. epitea	*Salix* sp.	2004, J.A. Smith et al.	GenBank	–	AY471630
M. helioscopiae	*Euphorbia helioscopia*	2003, W. Maier,et al.	GenBank	AF426197	–
M. laricis	*P. davidiana*	1983, J.Y. Zhuang	TSH-R4149 (HMAS46905)	AB116809	AB116867
M. larici-populina	*P. cathayana*	2000, C.M. Tian	HMNWFC-T003 (TSH-R16927)	AB116769	AB116828
M. larici-populina	*P. maximowiczii* × *P. balsamifera*	2004, L. Innes et al.	GenBank	–	AY429656
M. larici-populina	*P. simonii*	1994, Z.S. Hou	HMNWFC-T017	AB116785	AB116834
M. larici-populina	*P. laurifolia*	1984, Z.K. Liu	HMNWFC-T040	AB116788	AB116835
M. magnusiana	*P. alba* var. *pyramidalis*	1983, C.L. Wang	TSH-R04130 (HMAS58578)		AB116856
M. magnusiana	*P. alba*	1966, Z.K. Liu	TSH-R04125 (HMAS37769)	AB116811	AB116854
M. magnusiana	*P. tomentosa*	2003, C.M. Tian	HMNWFC-T023	AB116780	AB116848
M. magnusiana	*P. tomentosa*	1978, J. Yao	HMNWFC-T025	AB116777	AB116845
M. medusae	*P.* × *P. euramericana*	2003, P. Frey et al.	GenBank	–	AY375273
M. medusae	*P. deltoids*	2000, G. Newcombe et al.	GenBank	–	AF087711
M. occidentalis	*P. trichocarpa*	2000, G. Newcombe et al.	GenBank	–	AF087710
M. pruinosae	*P. euphratica*	1992, Y.Z. Shang	HMNWFC-T036	AB116795	AB116858
M. pruinosae	*P. euphratica*	1992, Y.Z. Shang	HMNWFC-T045	AB116796	AB116860
M. nujiangensis	*P. yunnanensis*	1998, M. Kakishima	TSH-R20046	AB116821	AB116823
M. nujiangensis	*P. yunnanensis*	1998, M. Kakishima	TSH-R20042	AB116820	AB116824

ITS, internal transcribed spacer region; *P.*, *Populus*

[a]HMAS, The Mycological Herbarium of Institute of Microbiology, Chinese Academy of Sciences; HMNWFC, The Mycological Herbarium of College of Forestry, Northwest Sci-Tech University of Agriculture and Forestry, China; TSH, The Mycological Herbarium of Institute of Agriculture and Forestry, University of Tsukuba, Japan

Mycological Herbarium, University of Tsukuba, Japonia (TSH) conservatus.

Spermogonia and aecia unknown. Uredinia hypophyllous, subepidermal, scattered or rarely aggregated in small groups, round or ellipsoid, 0.2–0.8 mm, orange-yellow or pale yellow, initially covered by epidermis, later erumpent, pulverulent; urediniospores mostly globoid or rarely ovoid, 17.0–26.8 × 18.2–22.8 µm (average, 21.3 × 19.7 µm); walls uniformly thick, 0.9–1.9 µm (average, 1.3 µm; Fig. 2), echinulate, distance between spines 1.1–2.0 µm (average, 1.5 µm; Fig. 3), paraphyses capitate, 33–56 × 12–15 µm, walls colorless, smooth, 2–6 µm thick. Telia hypophyllous, subepidermal, scattered, minute, yellow to reddish-brown when fresh, 0.4–0.8 mm; teliospores prismatic, clavate or cylindrical, 23.1–43.8 (36.3) × 5.4–12.4 (8.8) µm, wall 1 µm thick.

Holotype: On *Populus yunnanensis* Dode (Salicaceae), Pianma, Nujiang District, Yunnan Province, China, September 29, 1998, M. Kakishima, TSH-R20042, Mycological Herbarium, Graduate School of Life and Environmental Sciences, University of Tsukuba, Japan.

Results and discussion

This newly described poplar rust fungus was placed in the genus *Melampsora* because of its telial morphology (Wilson and Henderson 1966; Shang et al. 1986a,b; Van Kraayenoord et al. 1974; Bagyanarayana 1998; Cellerino 1999). This species is clearly different from any other known species of *Melampsora* on *Populus* by its globoid urediniospores and thin urediniospore walls. *Melampsora nujiangensis* is somewhat similar to several other rust fungi, such as *M. magnusiana* or *M. rostrupii* and *M. laricis,* in the shape and size of urediniospores. However, the uredinospore walls of these species are thicker (about 2.8 µm in each species) than those of *M. nujiangensis* (average, 1.3 µm). In addition, the distance between the spines of the urediniospores is shorter (average, 1.5 µm) than those of other species (about 2.7 µm in each species). Furthermore, these species are parasitic on *Populus* species in section *Leuce*, but *M. nujiangensis* occurs on section *Tacamahaca.*

Melampsora abieti-populi was also reported to have thin walls (Imai 1942; Ito and Murayama 1943) of urediniospores (average, 1.8 µm). However, the urediniospore walls of *M. nujiangensis* are thinner (average,

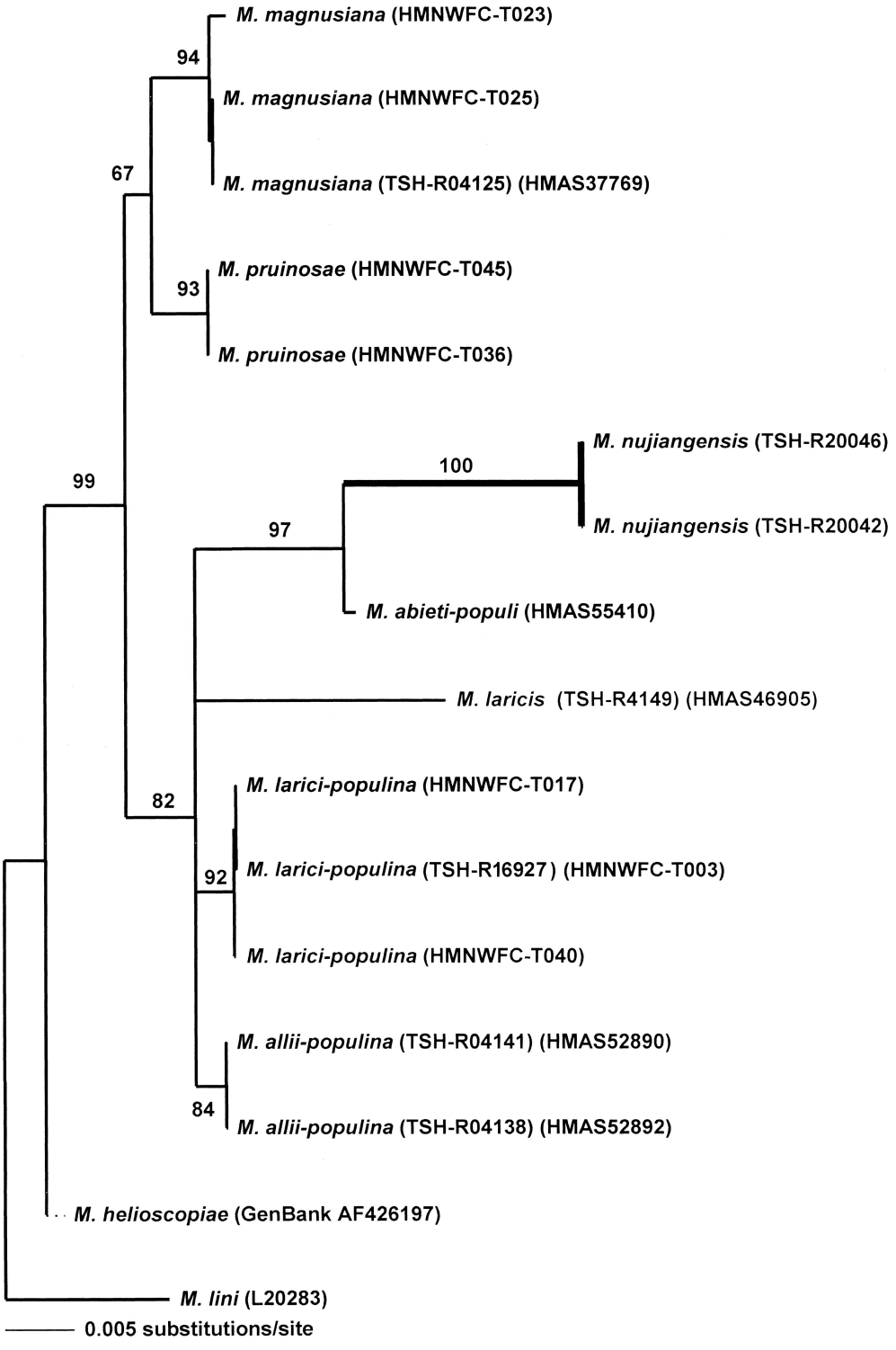


Fig. 7. Neighbor-joining (NJ) tree based on the sequences of 28S rDNA (D1/D2) regions for the species of *Melampsora*. Bootstrap values >50% are shown *above branches*

1.3 µm) than those of *M. abieti-populi*. Moreover, the spore shape of *M. nujiangensis* is globoid, rarely ovoid, whereas those of *M. abieti-populi* are oblong, ellipsoid, or pyriform (Figs. 4–6).

The present fungus is the second *Melampsora* species found on *Populus yunnanensis*. This poplar species is distributed only in Sichuan, Guizhou, and Yunnan provinces of China. The first rust fungi on *P. yunnanensis* have been identified as *M. larici-populina* based on the epiphyllous telia, elongate urediniospores with distinct laterally thickened walls, and paraphyses with apical wall thickened up to 25 µm. This species is widespread in China and is the most common poplar rust in China (Tai 1979; Tian and Kakishima 2005). We examined specimens of *M. larici-populina* on *P. yunnanensis* (HMAS 50167–50170, HMAS 55167, TSH-R20044) collected from Yunnan Province. This

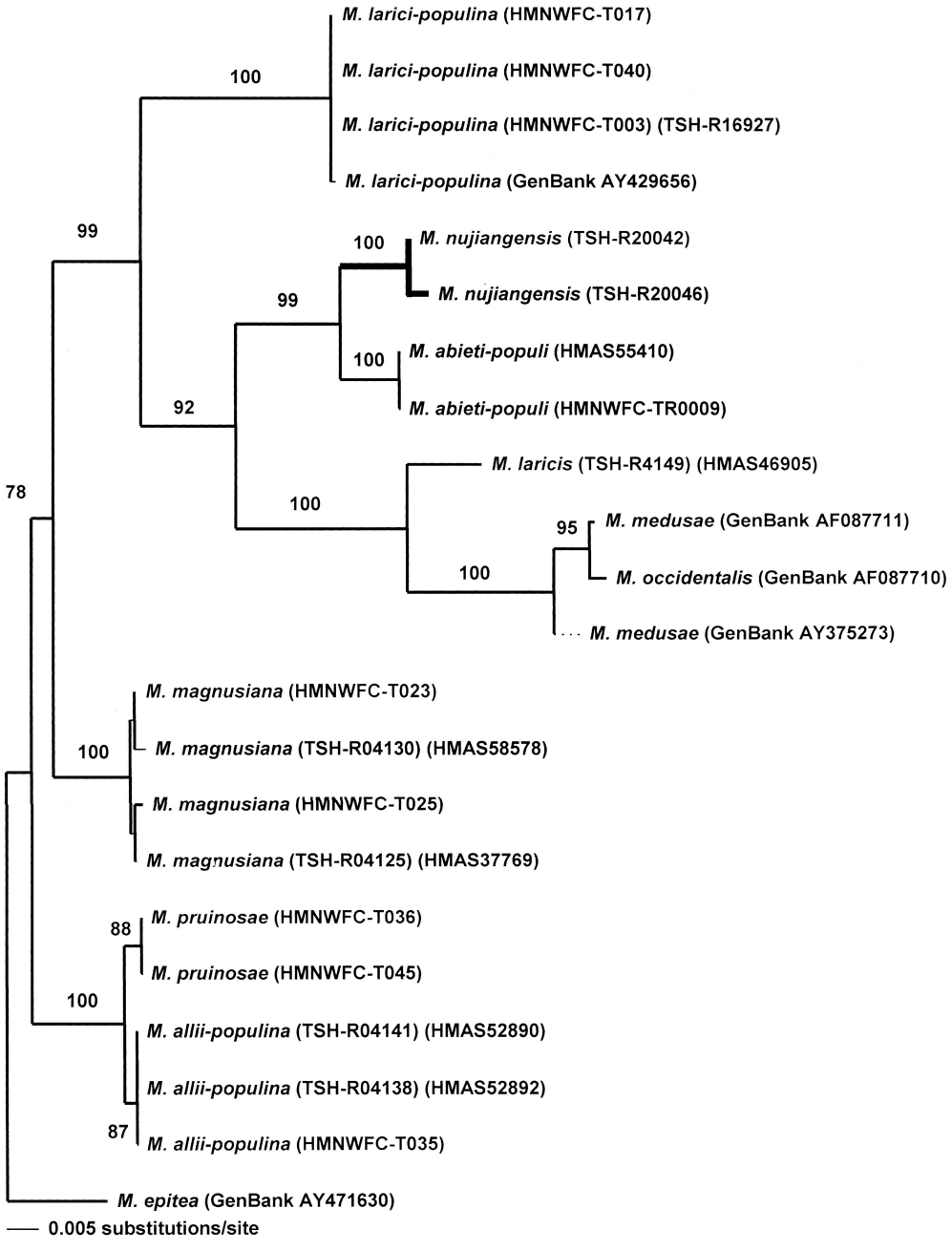


Fig. 8. Neighbor-joining (NJ) tree based on the sequences of the internal transcribed spacer (ITS1)–5.8S–ITS2 region for the species of *Melampsora*. Bootstrap values >50% are shown *above branches*

rust fungus is quite different from *M. nujiangensis* in morphology of uredinia and urediniospores.

To clarify the phylogenetic placement of *M. nujiangensis*, complete nucleotide sequences of the D1/D2 region and the ITS region from 11 taxa covering *Melampsora* were used for the phylogenetic analysis. The data of the rust fungi and their accession numbers are listed in Table 1. *Melampsora* species on *Populus* were separated into several different clades based on the phylogenetic trees using the NJ method when *M. lini* (28S; L20283) for the D1/D2 region and *M. epitea* (ITS, AY471630) for the ITS region were used as the outgroup taxon, respectively (Figs. 7, 8).

By amplifying the D1/D2 and ITS1–5.8S–ITS2 regions, two specimens (TSH-R20042, TSH-R 20046) of *M. nujiangensis* generated a 605-bp fragment from the D1/D2 region and a 661-bp fragment from the ITS region. A blast similarity search of this rust fungus on the consensus sequence of the D1/D2 and ITS regions demonstrated a close relationship with the genus *Melampsora*. A cladogram based on phylogenetic analysis of the D1/D2 region (Fig. 7) shows that *M. nujiangensis* is loosely clustered together with other several species of *Melampsora*. However, this species was clearly separated from these species by a high bootstrap value (97%).

Neighbor-joining analysis of the ITS region produced a tree quite similar (Fig. 8) to that of the D1/D2 region. The result supports that *M. nujiangensis* is a distinct taxon in the *Melampsora*. From these trees, it is also suggested that this

new species is phylogenetically close to *M. abieti-populi*. Five bases are different in the D1/D2 regions (bootstrap values, 97%) and 12 bases in the ITS regions (bootstrap values, 99%) between these two species. However, *M. nujiangensis* is morphologically different, as already described.

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