

Article

A New Species of *Marasmius* Sect. *Globulares* Growing in Grassland from Japan [†]

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[†] MycoBank: <https://www.mycobank.org/page/Name%20details%20page/623835>.

Abstract

Marasmius neooreades sp. nov. from Japan is described. This species produces fleshy, medium-sized basidiomata that are macromorphologically similar to *M. oreades*, with a pileus ranging from wheat-colored to dark brown and a tough stipe covered with brownish tomentose squamules. The gill edges bear cheilocystidia that are clavate to diverticulate. The pileipellis is hymeniform and composed of *Globulares*-type elements containing brown pigments. The species typically occurs gregariously in grasslands and occasionally forms fairy rings. Phylogenetic analyses based on ITS and LSU sequences indicated that *M. neooreades* forms a well-supported, independent clade distinct from previously described species of *Marasmius*. In addition, a combination of morphological characters clearly differentiates this species from all described taxa. An illustrated description and the phylogenetic placement of the new species are provided.

Keywords: Agaricales; Basidiomycota; grassland; Japan; Marasmiaceae; *Marasmius*; mushroom; new species; phylogeny

1. Introduction

Marasmius Fr., typified by *Marasmius rotula* (Scop.) Fr., is the type genus of the family Marasmiaceae Roze ex Kühner [1]. The genus is distributed on all continents except Antarctica and is particularly diverse in tropical regions [2–13]. Approximately 700 species are currently recognized worldwide [14]. Most species are saprotrophic, typically inhabiting woody debris or litter in forested environments, although some also occur on soil in grasslands [12]. Members of the genus are not known to form ectomycorrhizae [3]. Several species, such as *M. oreades* (Bolton) Fr. and *M. heinemannianus* Antonín, are edible and are traded in European and African markets, respectively [15,16]. Notably, *M. oreades* is also recognized as a turfgrass pathogen and is considered economically important [17–19].

Marasmius sect. *Globulares* Kühner is characterized by medium- to large-sized tough basidiomata, often with a hygrophanous and $\pm$ sulcate pileus. The gills are spaced from distant to crowded and lack a collarium. The pileipellis is usually hymeniform, composed of smooth, non-diverticulate elements, although short branches may be present in some species (e.g., in *M. oreades*) [20,21]. Basidiospores produce a white spore print and are smooth and ellipsoid to clavate; the hymenial trama is dextrinoid. Ecologically, species of this section are non-ectomycorrhizal and primarily occur on litter or soil in forested or grassland habitats, although some are known to be plant pathogens [18,19]. Phylogenetic



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studies based on LSU, SSU, ITS, *rpb2*, and *ef1- α* markers have demonstrated that *Marasmius* is a complex and polyphyletic genus [22,23]. Furthermore, morphological and molecular studies of *Marasmius* sect. *Globulares* sensu Singer have revealed that species assigned to this section are intermixed across traditional sectional boundaries, leading to the proposal of further taxonomic subdivisions and further taxonomic subdivisions have since been proposed [6,23–25].

In Japan, seven species of sect. *Globulares* have been reported: *M. aurantioferrugineus* Hongo, *M. brunneospermus* Har. Takah., *M. macrocystidiosus* Kiyashko & E.F. Malysheva, *M. maximus* Hongo, *M. nivicola* Har. Takah., *M. oreades*, and *M. purpureostriatus* Hongo. Except for *M. oreades* and *M. macrocystidiosus*, all were originally described from Japan [8,9,26–29]. While *M. oreades* typically occurs in turf habitats, the remaining Japanese species are mainly associated with forest environments. Nevertheless, several species of this section elsewhere in the world, such as *M. albogriseus* (Peck) Singer, *M. heinemannianus*, *M. oreades*, *M. campestris* N.K. Zeng, Zhi Q. Liang & M.S. Su, *M. collinus* (Scopoli) Singer, and *M. pseudocollinus* (Singer & Digilio ex Singer) Singer, are known to occur in turf habitats.

During surveys conducted in the Honshu region of Japan, we collected specimens of *Marasmius* sect. *Globulares* from turf environments. Detailed morphological examinations and molecular analyses revealed that these collections represent an undescribed taxon, distinguishable from known species by a unique combination of morphological characters and distinct DNA sequences. In this study, we describe this new species based on macro- and micromorphological observations in conjunction with molecular phylogenetic analyses. This study contributes to a better understanding of turf-inhabiting species of *Marasmius* sect. *Globulares* in East Asia.

2. Materials and Methods

Fresh basidiomata were photographed in situ with their surrounding habitat using a compact digital camera (TG-6, Olympus, Tokyo, Japan). Macromorphological features were examined shortly after collection in the laboratory. Color descriptions follow the color standards of Kornerup and Wanscher [30], under ambient room light, using notations such as “orange white (5A2)” and “greyish orange (5B3–4)”. After macroscopic observations, specimens were dried for 48 h at 45 °C using a food dehydrator and preserved as dried vouchers for subsequent microscopic molecular analyses.

Microscopic features were examined from the dried specimens, with particular attention to basidiospore colors and dimensions, the morphology of hymenial cystidia, and the structure of the pileus. All tissues were mounted in 3% aqueous potassium hydroxide (KOH); Cotton Blue or Melzer’s reagent was applied as needed to enhance the visibility of specific structures. Spore measurements are expressed as (Lmin–) L₅–L₉₅% (–Lmax) × (Wmin–) W₅–W₉₅% (–Wmax), where Lmin and Lmax represent the minimum and maximum observed spore lengths and L₅% and L₉₅% indicate the 5th and 95th percentiles, respectively. Width measurements follow the same convention. Mean spore length and width (Lave and Wave) and their standard deviations (Lstd and Wstd) were calculated based on measurements of *n* spores from *c* specimens. The spore length-to-width ratio (*Q*) also is given as (Qmin–) Q₅–Q₉₅% (–Qmax), with Qave and Qstd representing the mean and standard deviation, respectively. Microscopic observations were conducted using a differential interference contrast microscope (BX53, Olympus, Tokyo, Japan). Photographs of the microstructures were taken with a digital microscope camera (TS-2500, J-SCOPE, Kawasaki, Japan) and analyzed using Piximètre software (version 5.10) to measure basidiospores, basidia, and other microscopic structures.

2.1. DNA Extraction

Genomic DNA was extracted from specimens using either a microwave-based rapid extraction method [31] or a modified CTAB extraction method [32]. For the microwave-based method, gill tissues were excised dried basidiomata and cut into approximately 1×1 mm fragments using fine forceps. The tissue fragments were placed in 0.5 mL microcentrifuge tubes containing 100 μ L of $0.1 \times$ Tris-EDTA buffer and heated in a turntable-type microwave oven (RE-TX1-W5, Sharp Corporation, Osaka, Japan) at 600 W for 1 min and 10 s. After standing for 30 s, samples were reheated for an additional 1 min and 10 s and then stored at -30 °C until use.

In the modified CTAB method, tissue fragments prepared in the same manner were placed in 1.5 mL microcentrifuge tubes containing 300 μ L of $2 \times$ CTAB solution. Samples were frozen at -30 °C and thawed at 65 °C; this freeze–thaw cycle was repeated three times. Powdered quartz sand (FUJIFILM Wako Pure Chemical Corporation, Osaka, Japan) was added, and the tissue was ground using a pestle (Thermo Fisher Scientific Inc., Waltham, MA, USA) attached to an electric drill. After grinding, samples were incubated at 65 °C for 30 min. Subsequently, 300 μ L of CIA (chloroform : isoamyl alcohol = 24:1) solution was added, and the mixture was homogenized by vortexing. Samples were centrifuged at 6000 rpm for 15 min, and 150 μ L of the supernatant was transferred to a new tube. An equal volume of isopropanol (FUJIFILM Wako Pure Chemical Corporation) was added, mixed by vortexing, and incubated at room temperature for 10 min. DNA was pelleted by centrifugation at 15,000 rpm for 30 min. The supernatant was discarded, and the pellet was washed with 1 mL of 70% ethanol (FUJIFILM Wako Pure Chemical Corporation), followed by centrifugation at 15,000 rpm for 3 min. After the removal of residual ethanol, the pellet was dried at 65 °C and resuspended in 50 μ L of $0.1 \times$ Tris-EDTA buffer. DNA extracts were stored at -30 °C.

2.2. PCR and Sequencing

Polymerase chain reaction (PCR) was performed using two protocols. In the first protocol, each 25 μ L reaction contained 14.375 μ L of sterile distilled water, 2.5 μ L of PCR buffer (Thermo Fisher Scientific), 2.5 μ L each of forward and reverse primers (5 μ M), 2.5 μ L of dNTP mix (Thermo Fisher Scientific), 0.125 μ L of polymerase (Thermo Fisher Scientific), and 0.5 μ L of template DNA. Alternatively, PCRs were prepared in 0.2 mL tubes using 3.5 μ L of sterile distilled water, 5 μ L of EmeraldAmp MAX PCR Master Mix (TaKaRa, Kusatsu, Japan), 0.25 μ L each of forward and reverse primers (10 μ M), and 1 μ L of template DNA. All reaction mixtures were prepared on ice.

PCR amplification was conducted using either a T100™ Thermal Cycler (BIO-RAD, Hercules, CA, USA) or a Veriti® 96-Well Thermal Cycler (Applied Biosystems Inc., Foster City, CA, USA). The ITS region was amplified using primer pairs ITS5/ITS4 [33] or ITS1F [34]/ITS4, and the LSU region using LROR/LR5 [35]. Thermal cycling conditions consisted of an initial denaturation at 95 °C for 3 min, followed by 35 cycles of denaturation at 94 – 95 °C for 30–35 s, annealing at 51 – 52 °C for 30 s, and extension at 72 °C for 1 min (all primer sets). Final extension was carried out at 72 °C for 5–10 min, depending on the primer pair.

PCR products were confirmed by electrophoresis on 1% agarose gel stained with ethidium bromide and visualized under UV light. Visible DNA bands were either column-purified using a DNA Purification Kit (Qiagen, Hilden, Germany) or cleaned using ExoSAP-IT (Millipore, Molsheim, France). Sequencing was performed either by a commercial sequence service (FASMAC Co., Ltd., Atsugi, Japan) or using a BigDye Terminator Cycle Sequencing Kit on an ABI 3500 Genetic Analyzer (Applied Biosystems Inc., Foster City, CA, USA), following the manufacturer's instructions.

2.3. Phylogenetic Analyses

Raw sequence chromatograms were visually inspected using BioEdit ver. 7.2.5 [36], and consensus sequences were assembled by aligning forward and reverse reads using Clustal W v2.1 [37]. Consensus sequences were compared with those deposited in GenBank using BLAST web server (<https://blast.ncbi.nlm.nih.gov>, accessed on 10 January 2026) to identify closely related taxa, and representative sequences showing high ITS similarity were selected for inclusion in the phylogenetic analyses. The accession numbers of all sequences used are listed in Table 1.

Table 1. Species, specimen/strain numbers, GenBank accession (ITS and LSU) numbers of the specimens.

Species	Specimen/Strain Number *	ITS	LSU	Location
<i>Marasmius albogriseus</i>	FDS-CA-04303	PV263509	—	USA
<i>M. albogriseus</i>	JLF4827	MH090925	—	USA
<i>M. aurantioferrugineus</i>	HCCN 3571	FJ904964	FJ904946	KOREA
<i>M. aurantioferrugineus</i>	VLA M-10513	KJ662667	—	RUSSIA
<i>M. brunneospermus</i>	KPM-NC 0005011 (T)	FJ904969	FJ904951	Kanagawa, JAPAN
<i>M. brunneospermus</i>	BRNM 714568	FJ904966	FJ904948	KOREA
<i>M. campestris</i>	HKAS80857 (T)	KJ126766	KJ126768	CHINA
<i>M. campestris</i>	HKAS80858	KJ126767	KJ126769	CHINA
<i>M. centrocinnamomeus</i>	SFC20180704-02 (T)	OP730947	—	KOREA
<i>M. centrocinnamomeus</i>	SFC20140703-03	OP730948	—	KOREA
<i>M. desjardinii</i>	KD 16-19	MF630621	—	INDIA
<i>M. desjardinii</i>	KD 16-32 (T)	MF630620	—	INDIA
<i>M. macrocystidiosus</i>	TNS F-82701	OR298280	OR298282	Niigata, JAPAN
<i>M. macrocystidiosus</i>	LE295996 (T)	KF774136	KF896246	RUSSIA
<i>M. maximus</i>	NS16081406	MN523279	—	CHINA
" <i>M. maximus</i> "	HTBM2533	PX308931	—	CHINA
" <i>M. maximus</i> "	B6	JX434662	—	CHINA
<i>M. maximus</i>	MHHNU 8461	MK250944	—	CHINA
<i>M. maximus</i>	KG 224	FJ904974	FJ904956	KOREA
<i>M. maximus</i>	BRNM 714571	FJ904977	FJ904959	KOREA
<i>M. nigrodiscus</i>	TENN 049828	KF774140	—	USA
<i>M. nigrodiscus</i>	TENN 59556	KF774139	—	USA
<i>M. nivicola</i>	KPM-NC 0006038 (T)	FJ904973	FJ904955	Kanagawa, JAPAN
<i>M. nivicola</i>	BRNM 714574	FJ904971	FJ904953	KOREA
<i>M. oreades</i>	PBM 2701 (CUW) Massachusetts	DQ490641	—	USA
<i>M. oreades</i>	MW66	PP944579	—	SWEDEN
<i>M. oreades</i>	NN055694	JN943604	JN941144	DENMARK
<i>M. oreades</i>	BUNS12-00735	MK226504	MK238549	SERBIA
<i>M. oreades</i>	WA0000071064	MK028920	—	POLAND
<i>M. oreades</i>	H33	KC686867	—	SWITZERLAND
<i>M. oreades</i>	ZRL2015086	LT716048	KY418864	CHINA
<i>M. oreades</i>	KP-3	HF546217	—	PAKISTAN
<i>M. oreades</i>	ASIS21388	KF668290	—	KOREA
<i>M. neooreades</i>	TNS F-84794	PX091511	—	Chiba, JAPAN
<i>M. neooreades</i>	TNS F-84738	PX091512	—	Ibaraki, JAPAN
<i>M. neooreades</i>	TNS F-84730	PX091513	—	Ibaraki, JAPAN
<i>M. neooreades</i>	TNS F-84759	PX091514	PX090882	Ibaraki, JAPAN
<i>M. neooreades</i>	TNS F-84785	PX091515	—	Ibaraki, JAPAN
<i>M. neooreades</i>	TNS F-84844	PX091516	PX090883	Shiga, JAPAN
<i>M. neooreades</i>	TNS F-84727 (T)	PX091517	PX090884	Tottori, JAPAN
<i>M. neooreades</i>	TNS F-84894	PX091518	PX090885	Tottori, JAPAN
<i>M. neooreades</i>	TNS F-84756	PX091519	PX090886	Tokyo, JAPAN

Table 1. Cont.

Species	Specimen/Strain Number *	ITS	LSU	Location
<i>M. torquescens</i>	BRNM 691427	GU266258	GU266265	KOREA
<i>M. torquescens</i>	LE234906	KF774164	—	RUSSIA
<i>M. vagus</i>	AQ1008080 (T)	MT117839	MT110674	AUSTRALIA
<i>M. vagus</i>	Malka_1	MN764296	—	USA
<i>M. wynneae</i>	DMS-9344190	MT644909	—	DENMARK
<i>M. wynneae</i>	HCCN G86	FJ904979	FJ904961	KOREA
<i>Cryptomarasmius brunneipurpurea</i>	JFK84	FJ167646	OR656945	INDONESIA
<i>C. zonata</i>	VPI3355	AY916692	AY916690	USA
<i>C. birhizomorpha</i>	BRNM 751593	KF380831	KF380835	KOREA

* T: type specimen; bold: sequences obtained in this study.

For concatenated ITS + LSU analyses, individual loci were manually combined in BioEdit, with visual adjustments to ensure alignment accuracy. Multiple sequence alignments of the ITS and ITS + LSU datasets were generated using MUSCLE v3.8 [38], as implemented in MEGA ver. 7.0.26 [39]. Maximum likelihood (ML) analyses were performed using the IQ-TREE web server [40]. The best-fit substitution models were selected automatically. For the ITS dataset, the HKY model with gamma-distributed rate heterogeneity (four rate categories) and empirical state frequencies were applied. For the ITS + LSU dataset, the ITS partition was modeled with gamma-distributed rate heterogeneity, whereas the LSU partition assumed a proportion of invariable sites both partitions used the HKY substitution model with empirical state frequencies.

Branch support was assessed by performing ultrafast bootstrap approximation (UFBoot [41]) with 1000 replicates, the SH-aLRT test with 1000 replicates, and the approximate Bayes (aBayes) test. Species of *Crinipellis* Pat. (JFK84, VPI3355, BRNM 751593) were selected as the outgroup, as this genus forms a sister lineage to *Marasmius* [4].

3. Results

3.1. Phylogeny

The Japanese specimens examined in this study (TNS F-84727, F-84730, F-84738, F-84756, F-84759, F-84785, F-84794, F-84844) formed a well-supported, independent clade in both the ITS and concatenated ITS + LSU phylogenetic trees (Figures 1 and 2). In the ITS tree, two Chinese specimens labeled as “*Marasmius maximus*” (B6 and HTBM2533) were nested within this clade.

The Japanese sequences were phylogenetically closely related to *M. maximus* from China (NS16081406) and Korea (KG 224 and BRNM 714571), *M. wynneae* Berk. & Broome from Korea (HCCN G86) and *M. nivicola* from Japan (KPM-NC 0006038) and Korea (BRNM 714574). Together, these taxa formed a larger assemblage corresponding to Series *Wynneae* J.S. Oliveira & Moncalvo [25].

Branch support values for the clade representing the Japanese specimens were high in both analyses, indicating strong phylogenetic support for their separation from previously described species of *Marasmius*.

Furthermore, following Oliveira et al. (2024) [23], we performed an ITS-based phylogenetic analysis with limited taxon sampling, using the sister taxa of section *Globulares* (*M. nigrobrunneus* (Pat.) Sacc. NW223 and *M. ruforotula* Singer BRNM 714674) as the outgroup. The SH-aLRT support values were slightly lower in this analysis, but the overall tree topology was identical to that obtained when *Crinipellis* was used as the outgroup.

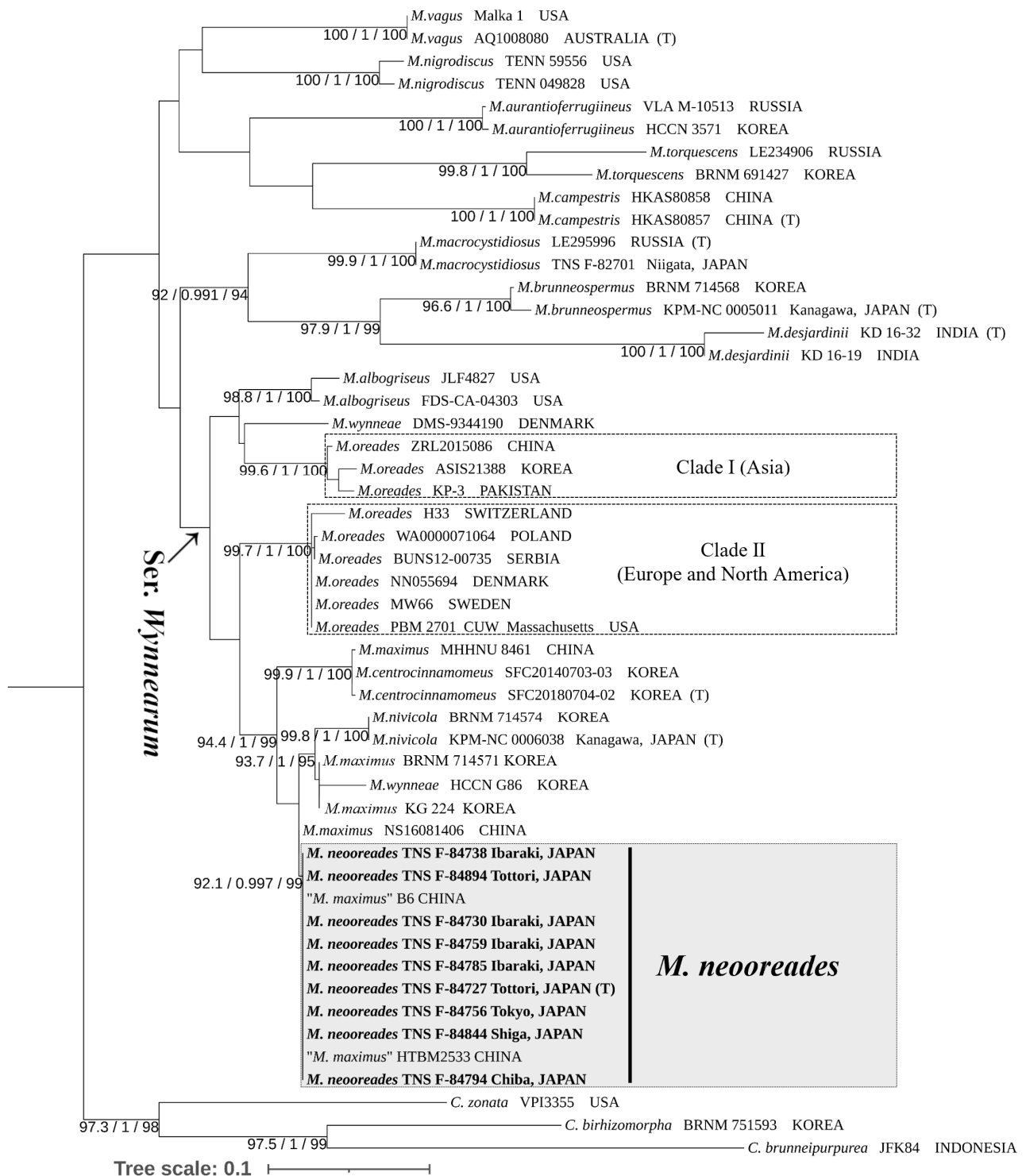


Figure 1. Phylogenetic placement of *Marasmius neooreades* based on the ITS dataset using IQ-TREE. SH-aLRT support ($X \geq 90\%$), aBayes support ($Y \geq 0.95$) and ultrafast bootstrap support ($Z \geq 90\%$) are indicated above or below the branches as X/Y/Z.

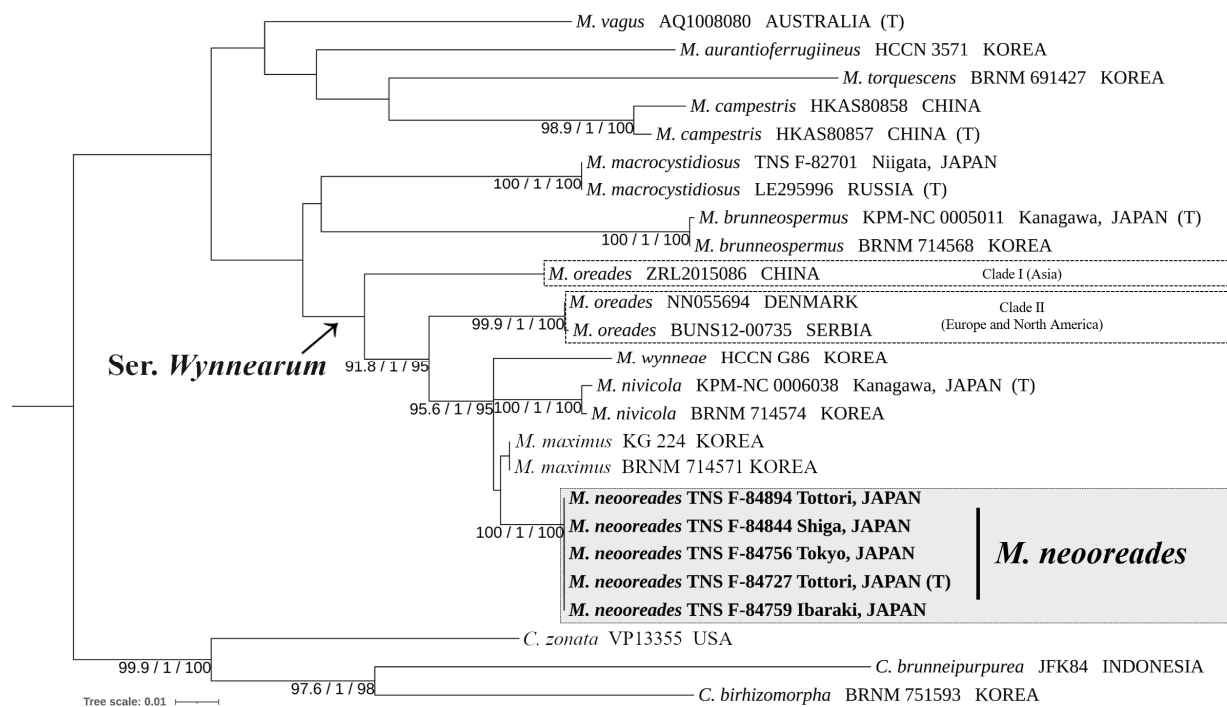


Figure 2. Phylogenetic placement of *Marasmius neooreades* based on the concatenated ITS + LSU dataset using IQ-TREE. SH-aLRT support ($X \geq 90\%$), aBayes support ($Y \geq 0.95$) and ultrafast bootstrap support ($Z \geq 90\%$) are indicated above or below the branches as X/Y/Z.

3.2. Taxonomic Treatment

Marasmius neooreades K. Oguchi & K. Hosaka, sp. nov. (Figures 1–5).



Figure 3. Basidiomata of *Marasmius neooreades*. (A,B) TNS F-84738. (C) holotype TNS F-84727. (D) TNS F-84844. (E) TNS F-84759. Scale bars = 1 cm in (A–C,E); 2 cm in (D).

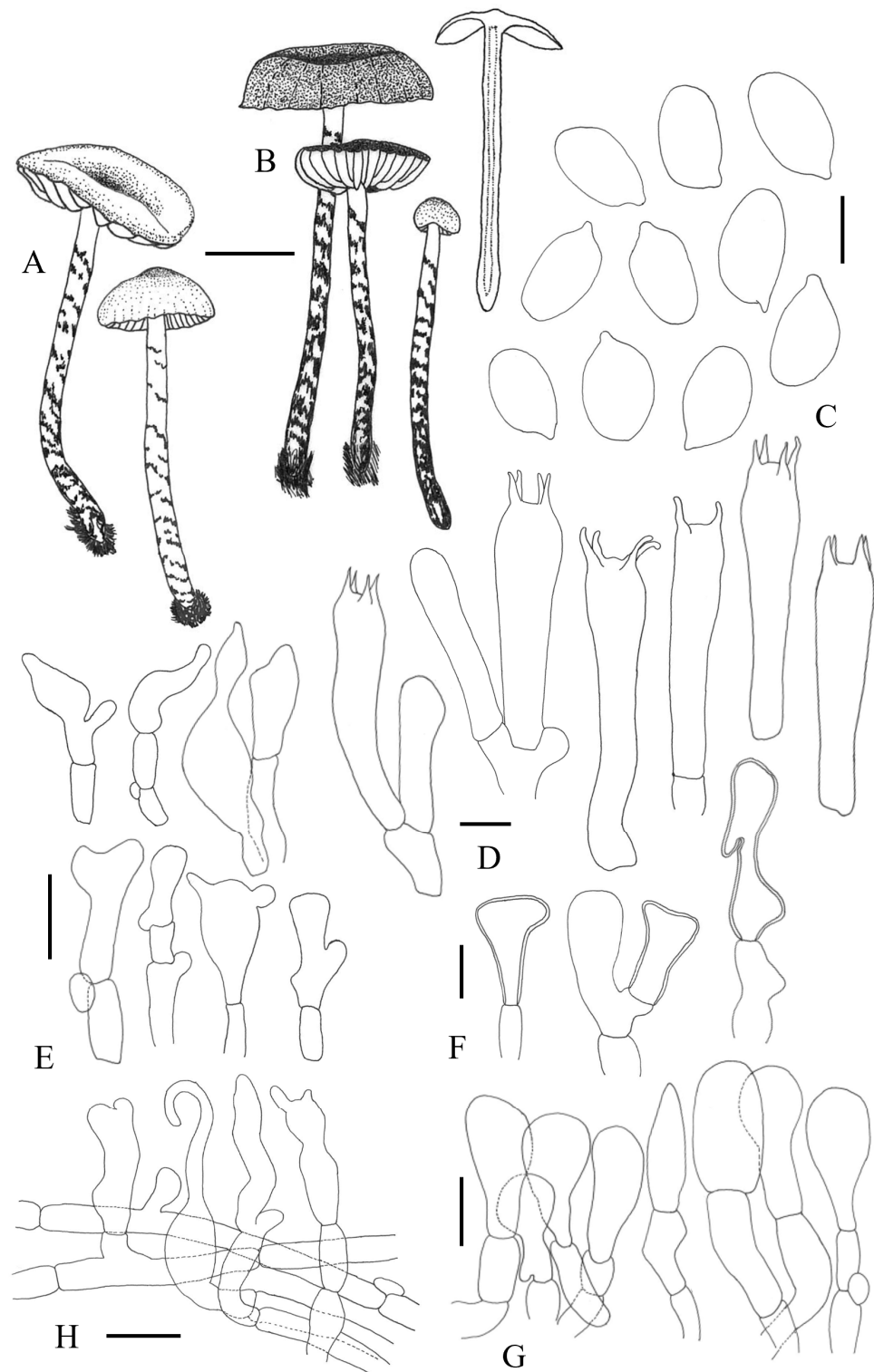


Figure 4. *Marasmius neooreades*. (A) Basidiomata (TNS F-84738). (B) Basidiomata (TNS F-84727, holotype). (C) Basidiospores (TNS F-84727, holotype). (D) Basidia (TNS F-84759). (E) Cheilocystidia (TNS F-84759). (F) *Globulares*-type elements on the pileipellis (F-84727, holotype). (G) Part of pileipellis (TNS F-84756). (H) Caulocystidia (TNS F-84756). Scale bars = 2 cm in (A,B); 5 μ m in (C,D); 10 μ m in (E–H).

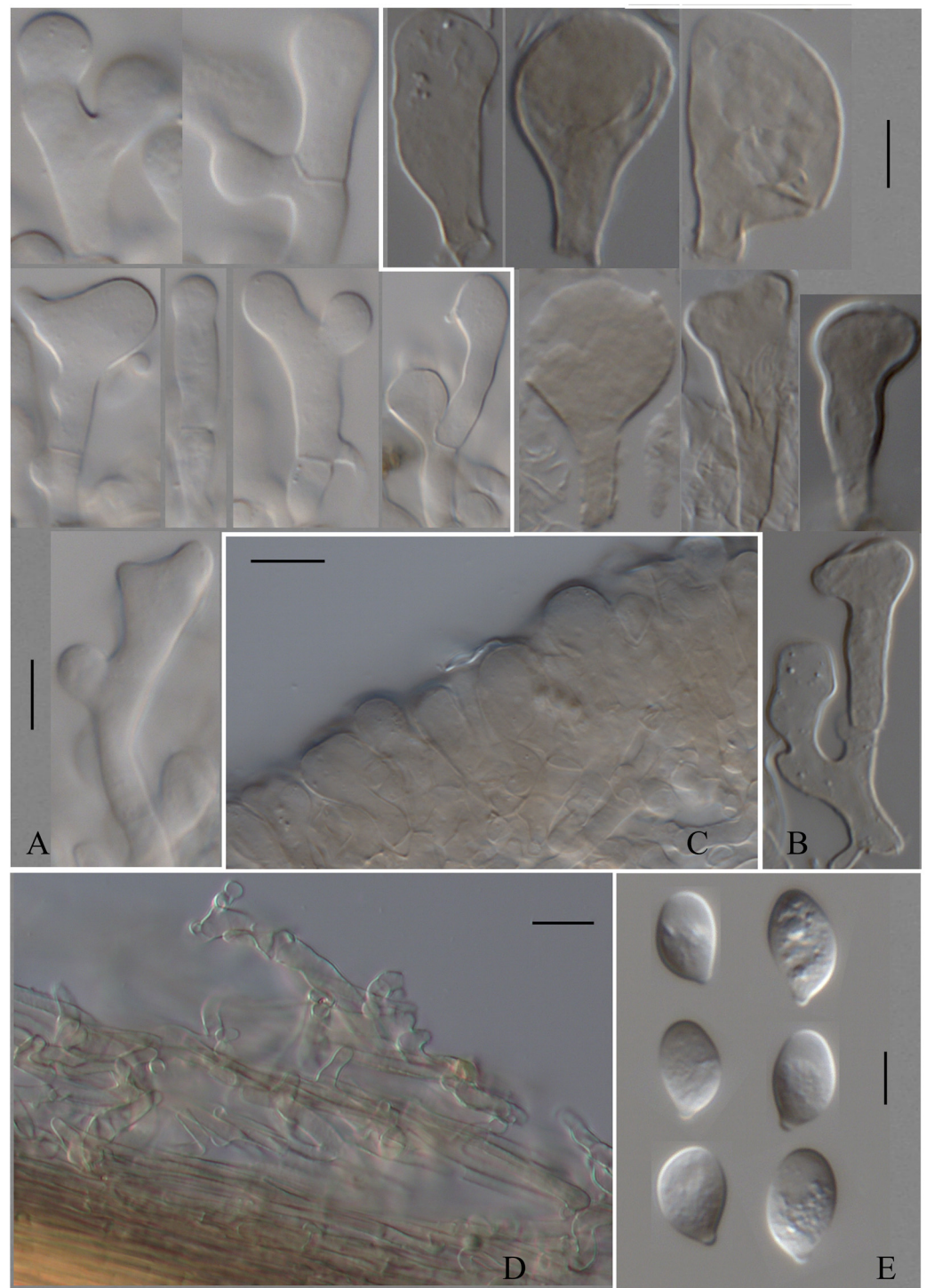


Figure 5. *Marasmius neooreades*. (A) Cheilocystidia (TNS F-84738). (B) Elements on the pileipellis (TNS F-84844). (C) Pileipellis (TNS F-84756). (D) Stipitipellis (TNS F-84756) in Melzer's reagent. (E) Basidiospores (TNS F-84727, holotype). Scale bars = 5 µm in (A,B,E); 10 µm in (C,D).

MycoBank no.: MB862605.

Diagnosis: Differs from *Marasmius oreades* in having more slender basidiomata, the presence of cheilocystidia, and a distinct phylogenetic placement based on nuclear ribosomal DNA regions.

Etymology: The epithet "*neooreades*" refers to the macromorphological resemblance of the basidiomata to *Marasmius oreades* (Bolton) Fr.

HOLOTYPE: JAPAN: Tottori Prefecture, Tottori University, Koyama-chō-minami, Tottori-shi, 29 June 2023, K. Oguchi (TNS F-84727).

Gene sequences ex-holotype: PX091517 (ITS), PX090884 (LSU).

Basidiomata (Figures 3 and 4A,B) medium-sized, marasmious, fleshy and tough. **Pileus** 5–30 mm broad, up to 40 mm diam.; convex to plane, finally flattening to slightly upturned, usually with umbo; surface initially glabrous, becoming sulcate or rugulose toward the margin with age; dry to slightly oily when young; hygrophanous in most conditions, especially in mature basidiomata. When moist, pileus brown (6E7-cognac, 6E8-rust brown), becoming brownish orange (6C4-red hired, 6C5-sahara) to light brown (6D5-sunburn, 6D6-cinnamon, 6D7-raw sienna) when dry; when mature pale yellow (4A3-cream) to orange white (5A2-orange white) to pale orange (5A3-pale orange) to grayish orange (5B3–4) or brown (6E7-cognac, 6E8-rust brown, 7E7, 7E8-agate) at the margin when dry, the center light brown (6D5-sunburn, 6D6-cinnamon, 6D7-raw sienna) or brown (6E7-cognac, 6E8-rust brown) when dry, especially tinged dark brown (6F4-chocolate, 6F5-teak, 6F6-burnt umber, 6F7-dark brown chestnut, 6F8-brownish gray, 7F4–5, 7F6-eye brown, 7F7–8, 8F4–5, 8F6-liver, 8F7-caput mortuum, 8F8) when moist. **Gills** 2–6 mm wide, distant to subdistant, relatively thick; edges smooth, non-marginate, intervenose; color yellowish white (4A2), pale yellow (4A3-cream), orange white (5A2-orange white), pale orange (5A3-pale orange) to grayish orange (5B3); collarium absent. **Stipe** 30–80 mm long, 1.5–3 mm wide, equal or slightly tapering toward the apex or base; surface squamulose, light brown (6D4-camel, 6D5-sunburn, 6D6-cinnamon, 6D7-raw sienna) to brown (6E5, 6E6-cocoa, 6E7-cognac, 6E8-rust brown) except the apex, the apex showing ground color off-white or yellowish white (4A2) to pale yellow (4A3-cream) to orange white (5A2-orange white); context hollow. **Flesh** white and tough. **Taste** and **odor** indistinct. **Spore print** white.

Basidiospores (Figures 4C and 5E) $(7.2\text{--}8.1\text{--}10.7\text{--}(11.3) \times (4.5\text{--}4.9\text{--}6.7\text{--}(7.7)) \mu\text{m}$, mean = $9.6 \pm 0.8 \times 5.7 \pm 0.6 \mu\text{m}$, $Q = (1.3\text{--}1.4\text{--}2\text{--}(2.1))$, $Q_{\text{mean}} = 1.7 \pm 0.2$, (specimens = 6, $n = 30$), ellipsoid, smooth, thin-walled, with a distinct apiculus; oil droplets usually present; hyaline in KOH, inamyloid in Melzer's reagent. **Basidia** (Figure 4D) $34\text{--}54.4 \times 6.3\text{--}9.2 \mu\text{m}$, mean = $43.3 \pm 6.1 \times 7.6 \pm 0.7 \mu\text{m}$, thin-walled, clavate to cylindrical, four-spored or occasionally two-spored, with basal clamp connections, hyaline in KOH, non-amyloid in Melzer's reagent. **Pleurocystidia** absent. **Cheilocystidia** (Figures 4E and 5A) present, very variable, $6\text{--}49 \times 4\text{--}20 \mu\text{m}$, clavate to irregular, sometimes diverticulate; thin-walled, smooth, with clamp connections, hyaline, inamyloid in Melzer's reagent. **Hymenial trama** subparallel to interwoven, composed of hyphae $5\text{--}7 \mu\text{m}$ wide; smooth, with clamp connections, hyaline in KOH, dextrinoid in Melzer's reagent. **Pileipellis** (Figures 4F,G and 5B,C) hymeniform, with clamp connections, composed of irregular, clavate to *Globulares*-type terminal elements, $12\text{--}37 \times 4\text{--}18 \mu\text{m}$; walls thin to moderately thickened; *Globulares*-type elements often with brownish pigment; pileus trama dextrinoid. **Stipitipellis** (Figure 5D) form cutis, composed of cylindrical hyphae $2\text{--}8 \mu\text{m}$ wide, hyaline to brownish, with clamp connections, sometimes make short branches, faintly encrusted; sometimes forming hyphal mass layer $100\text{--}(200) \mu\text{m}$ wide; **caulocystidia** (Figure 4H) present, fusiform and somewhat twisted shape, thin-walled, $24\text{--}42.4\text{--}(63.9) \times 3.9\text{--}7.4 \mu\text{m}$, inamyloid in Melzer's reagent, stipe trama dextrinoid.

3.3. Additional Collections Examined (Paratypes)

JAPAN: Chiba: Shisui sōgō-kōen, Sumi, Shisui-chō, Imba-gun, 1 September 2024, K. Oguchi KO24-218NR (TNS F-84794). Ibaraki: Ami machi sōgō undo-koen, Yoshiwara, Amimachi, Inashiki-gun, 2 July 2024, K. Oguchi KO24-81NR (TNS F-84748). Ayumizaki-kōen, Saka, Kasumigaura-shi, K. Oguchi & K. Fujii KO24-210NR (TNS F-84788). Oshibi, Chikuseishi, 1 June 2024, K. Oguchi KO24-3NR (TNS F-84730). Hanabatake, Tsukuba-shi, 1 July

2024, K. Oguchi KO24-67 (TNS F-84738); the same locality, 15 July 2024, K. Oguchi KO24-111NR (TNS F-84759). In Tsukuba Botanical Garden, Amakubo, Tsukuba-shi, 1 September 2024, K. Oguchi KO24-206NR (TNS F-84785). Kagawa: Sanuki kodomono-kuni, Yusa, Konan-chō, Takamatsu-shi, 5 November 2025, K. Oguchi KO25-379NR (TNS F-110979). Shiga: Karasaki-jinja, Karasaki, Ōtsu-shi, 22 June 2023, K. Oguchi KO23-3AD (TNS F-84844); Nagisa-kōen, Hama-Ōtsu, 2 November 2025, K. Oguchi & Y. Aso KO25-331NR (TNS F-110980). Shibafu-hiroba, Oroshimo-chō, Kusatsu-shi, 24 June 2025, K. Oguchi KO25-123 (TNS F-110975); the same locality, 2 November 2025, K. Oguchi & Y. Aso KO25-327NR (TNS F-110976). Tokushima: Tsukimigaoka-kōen, Yamanote, Toyooka, Matsushige-chō, Itano-gun, 4 November 2025, K. Oguchi KO25-349NR (TNS F-110977). Tokyo: Yakushi-ike-kōen, Machida-ku, Machida-shi, 6 July 2024, K. Oguchi KO24-107NR (TNS F-84756). Tottori: In the campus of Tottori University, Koyama-chō-minami, Tottori-shi, 29 June 2023, K. Oguchi KO23-36AD (TNS F-84727). Tottori deaino-mori, Katsurami, Tottori-shi, 29 June 2019, K. Oguchi 000333 (TNS F-84851); the same locality, 19 June 2020, K. Oguchi KO20-1AD (TNS F-84894). Wakayama: Near Manyō-kan, Wakaura-minami, Wakayama-shi, 26 June 2025, K. Oguchi & Y. Aso KO25-125 (TNS F-110978).

4. Habitat and Distribution

Usually gregarious in rows, often forming rows or incomplete to complete fairy rings. On soil in turf habitats, mainly dominated by *Zoysia* Willd. spp. and other plants represented by *Artemisia princeps* Pamp., *Capsella bursa-pastoris* (L.) Medik., *Cyperus rotundus* L., *Digitaria ciliaris* (Retz.) Koel., *Eleusine indica* (L.) Gaertn., *Equisetum arvense* L., *Euphorbia maculata* (L.) Small, *Glechoma hederacea* subsp. *grandis* (A.Gray) H.Hara, *Hydrocotyle sibthorpioides* Lam. (1789), *Ixeridium dentatum* subsp. *dentatum* (Thunb.) Tzvelev, *Oenothera laciniata* Hill, *Oxalis corniculata* L., *Persicaria capitata* (Buch.-Ham. ex D.Don) H.Gross, *Persicaria longiseta* (Bruijn) Kitag., *Plantago asiatica* L., *Poa annua* L., *Portulaca oleracea* L., *Pseudognaphalium affine* (D.Don) Anderb. (1991), *Sagina japonica* (Sw.) Ohwi, *Setaria viridis* (L.) P. Beauv., *Spiranthes sinensis* var. *amoena* (Pers.) Ames (M.Bieb.) H.Hara, *Taraxacum* spp., *Trifolium pratense* L. (1753), *Trifolium repens* L., *Veronica persica* Poir. and *Vicia sativa* subsp. *nigra* (L.) Ehrh.

JAPAN: Honshu (Chiba, Ibaraki, Shiga, Tokyo, Tottori and Wakayama Prefs.) and Shikoku (Kagawa and Tokushima Prefs.). CHINA: Guangdong Province (labeled as “*M. maximus*”, B6 and HTBM2533 in Figures 1 and 2). Occurring in warm temperate to subtropical regions of East Asia.

5. Remarks

The basidiomata and habitat of *M. neooreades* are superficially similar to those of the European species *M. oreades*. However, *M. oreades* differs from *M. neooreades* by having larger and more robust basidiomata (pileus 13–50 mm and stipe 45–78 mm long × 2.5–6 mm wide) and, critically in lacking cheilocystidia [21]. These diagnostic differences are also evident in descriptions based on the neotype of *Marasmius oreades* (Bolton) F., which was designated based on the material from England [42]. Although DNA sequence data from the neotype specimens are not yet available, its European origin supports the application of the name *M. oreades* sensu stricto to European and North American populations.

Phylogenetically, sequences identified as *M. oreades* are divided into two distinct clades: one comprising European and North American specimens (Clade II in Figures 1 and 2) and another including Asian collections from China, Korea, and Pakistan (Clade I in Figures 1 and 2). Although no material from the type locality (England) was examined in this study, the former clade (Clade II) is interpreted here as *M. oreades* sensu stricto because all sequences from Europe were included in this clade. In contrast, *M. neooreades* is not

nested within either lineage, and forms an independent, well-supported clade, indicating that it represents a distinct species rather than a geographic variant of *M. oreades*.

Several species of *Marasmius* sect. *Globulares* possess fleshy basidiomata and pilei that are off-white to brownish and thus resemble *M. neooreades* macroscopically, but all differ in key morphological, ecological, or phylogenetic characters. *Marasmius albogriseus*, *M. aurantioferrugineus*, *M. brunneospermus*, *M. collinus*, *M. desjardinii* K.Das, Antonín & D.Chakr., *M. heinemannianus*, *M. macrocystidiosus*, *M. maximus*, *M. nigrodiscus* (Peck) Halling, *M. nivicola*, *M. pseudocollinus*, *M. torquecens* Quél., *M. vagus* Guard, M.D. Barrett & Farid and *M. wynneae*.

Marasmius albogriseus is similar in habit and habitat, but differs in its overall grayish coloration and the morphology of caulocystidia [2,21,43–45]. *Marasmius aurantioferrugineus* is distinguished by its larger basidiomata, reddish-brown pileus with radially rugulose surface, and occurrence on litter beneath *Larix* Mill. [28,46]. *Marasmius brunneospermus* differs in having a rugulose-reticulate pileus, strigose mycelium at the stipe base, a white to yellow-orange or brown spore print, and narrower basidiospores, and it occurs in forest habitats [6,11]. *Marasmius collinus*, although similar in basidiomata and grassland habitat, has crowded lamellae, a smooth stipe, a distinctive odor, and lacks cystidia [21,43,47,48].

The Indian species *M. desjardinii* differs from *M. neooreades* in its more slender basidiomata, closer lamellae, non-diverticulate cheilocystidia, forest habitat, and phylogenetic placement [49]. *Marasium heinemannianus*, another grassland species, is readily distinguished by its very large basidiomata, pale yellowish-white spore print, and large, subfusoid basidiospores [16]. *Marasmius macrocystidiosus*, known from Russia and Japan, differs in having a pubescent stipe surface, large clavate cheilocystidia, and a forest habitat, as well as in its phylogenetic position [4,29]. *Marasmius maximus* shares a similar pileus coloration and the presence of brownish squamules on the stipe, but is distinguished by its much larger basidiomata, radially sulcate-striate pileus surface, forest habitat, and smaller basidiospores [27,46].

Additional species can be distinguished from *M. neooreades* as follows: *M. nigrodiscus* possesses pleurocystidia [44]; *M. nivicola* has white basidiomata and occurs in forest habitats [8,21]; *M. pseudocollinus* has smaller basidiospores [43]; *M. torquecens* lacks stipe scales and shows a color transition from brown to black toward the stipe base [21,50]; *M. vagus* has orange to apricot pileus and *Siccus*-type broom elements [51]; and *M. wynneae* is characterized by whitish pileus and dark-colored stipes except at the apex [11]. *Marasmius campestris*, which also inhabits grasslands, differs markedly in its deeply sulcate, striate, purple-tinged pileus and exceptionally large basidiospores [52].

Morphologically and ecologically, *M. neooreades* accords well with the diagnostic features of Series *Wynnearum* [25], including fleshy basidiomata, distant and intervenose lamellae, absence of pleurocystidia, a hymeniform pileipellis composed of *Globulares*-type elements, and a grassland habitat. Its phylogenetic placement within the *Wynnearum* clade further supports this assignment.

In Japan, *M. oreades* has long been reported [26,46,53], but published accounts lack information on cheilocystidia, a critical character for distinguishing species within sect. *Globulares*. Based on the macromorphological descriptions provided by Imai [26] and Imazeki & Hongo [46], Japanese specimens previously identified as *M. oreades* show substantial overlap with *M. neooreades* in pileus size, coloration, lamellar spacing, stipe dimensions, and grassland habitat. Although microscopic features were not documented in those early studies, these similarities suggest that many Japanese records of “*M. oreades*” from temperate regions may in fact represent *M. neooreades*.

To clarify this issue, we re-examined historical specimens identified as *M. oreades* by Imai from Hokkaido (voucher specimens TMI 5745–5747, collected in 1930–1932). These

specimens are approximately a century old and are largely contaminated by molds, precluding DNA extraction and detailed examination of critical characters such as the lamellar edge and stipe surface. Nevertheless, the available morphological features, including basidiospore shape and dimensions and a hymeniform pileipellis composed of *Globulares*-type elements, indicate that these specimens belong to *Marasmius* sect. *Globulares*. At present, it remains unclear whether the Hokkaido material represents *M. oreades*, *M. neooreades*, or a different taxon altogether. Accordingly, the occurrence of *M. oreades* sensu stricto in Japan cannot be excluded, although our results strongly suggest that populations widely distributed in temperate regions of Japan (excluding Hokkaido) and long identified as “*M. oreades*” correspond to *M. neooreades*.

In the phylogenetic analyses, *M. neooreades* formed a clade with two Chinese sequences labeled as *M. maximus* (B6 and HTBM2533). BLAST comparisons of the ITS region revealed high sequence similarity between the ex-holotype of *M. neooreades* (PX091517) and these Chinese sequences (99.84% for HTBM2533 and 98.80% for B6). However, *M. maximus* is morphologically distinct from *M. neooreades*, differing in its much larger basidiomata, forest habitat, felt-like mycelial mat, and smaller, more narrowly ellipsoid basidiospores. Moreover, other sequences identified as *M. maximus* from China and Korea formed a separate clade. These results strongly suggest that the Chinese vouchers B6 and HTBM2533 were misidentified and instead represent *M. neooreades*. Because HTBM2533 was collected from Guangdong Province (approximately 22° N) [54], *M. neooreades* is inferred to have a broad distribution spanning warm temperate to subtropical regions of East Asia. Further sampling from East and Southeast Asia will be necessary to understand its distributional range.

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