



A new and edible species of *Hygrophoropsis* (Boletales, Basidiomycota) from North China

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Abstract: *Hygrophoropsis* is a small genus in Hygrophoropsidaceae of Boletales. A new and edible species, *H. phragmiticola*, is described based on morphological characteristics, molecular evidence, ecology and geographic distribution. The new species is characterized by creamy-whitish to pale-ochraceous pileal surface, white to cream gills, oblong or ellipsoid, thick-walled, weakly dextrinoid basidiospores measuring 6–10×4–5.5 μm, and growing on *Phragmites* species in northern China. Molecular analysis based on ITS and nrLSU sequences demonstrates the phylogenetic position of the new species in *Hygrophoropsis*. The new species and its closely related species are compared and discussed.

Keywords: edible mushroom; *Hygrophoropsis*; *Phragmites*; taxonomy

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中国北方拟蜡伞属一个可食用的新种

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摘要: 拟蜡伞属 *Hygrophoropsis* 是牛肝菌目中的一个小属, 现归属于独立的科——拟蜡伞科。本研究从形态学特征、分子生物学证据、生态学和地理分布等方面描述了一种可食用的新种——芦苇拟蜡伞。该新种的特征为菌盖表面乳白色至淡赭色; 菌褶白到奶油色; 担孢子长圆形至椭圆形, 厚壁, 具轻微糊精反应, 大小为 6–10×4–5.5 μm, 生长在我国北方芦苇上。基于 ITS 和 nrLSU 序列的系统发育分析, 表明该新种在拟蜡伞属的系统发育地位, 并讨论了新种与其近缘种的鉴别特征。

关键词: 食用菌; 拟蜡伞属; 芦苇; 分类学

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Hygrophoropsis (J. Schröt.) Maire ex Martin-Sans (Boletales, Hygrophoropsidaceae), typified by *H. aurantiaca* (Wulfen) Maire, is characterized by lamellate hymenophore; thick, narrow, often forked, strongly decurrent gills; central, often somewhat reduced and tapering stem; hyaline, thick-walled, dextrinoid basidiospores (Knudsen & Vesterholt 2008; Kibby 2012; Holec & Kolařík 2013). *Hygrophoropsis* is related to *Tapinella* E.-J. Gilbert, *Coniophora* DC. and *Leucogyrophana* Pouzar. Unlike most species of Boletales, the species of *Hygrophoropsis* are non-ectomycorrhizal, but saprotrophic and causing brown-rot, shown to be distant from Paxillaceae where the genus formerly addressed in Kibby (2012).

So far, 16 *Hygrophoropsis* species are known in the world (Kirk 2017). *H. aurantiaca*, *H. bicolor* Hongo, *H. coacta* McNabb, *H. flabelliformis* (Berk. & Ravenel) Corner, *H. fuscosquamula* P.D. Orton, *H. kivuensis* Heinem., *H. laevis* Heinem. & Rammeloo, *H. macrospora* (D.A. Reid) Kuyper, *H. mangelotii* Locq., *H. ochraceolutea* Contu & Bon, *H. panamensis* Singer, *H. psammophila* (Cleland) Grgur., *H. purpurascens* (Berk. & M.A. Curtis) Dennis, *H. rufa* (D.A. Reid) Knudsen, *H. rufescens* Singer and *H. tapinia* Singer (Singer 1946; Dennis 1952; Locquin 1954; Heinemann 1963; McNabb 1969; Singer *et al.* 1983; Heinemann & Rammeloo 1985; Contu & Bon 1991; Grgurinovic 1997).

During a study on wild edible mushrooms in northern China, a species growing on *Phragmites* is found, and the species is characterized by decurrent, forked gills and dextrinoid basidiospores. These characteristics show the mushroom reminds of *Hygrophoropsis*. After phylogenetic analysis based on internal transcribed spacer (ITS) and the large subunit nuclear ribosomal RNA gene (nrLSU) sequences the samples of this edible mushroom form a new lineage in *Hygrophoropsis* clade. Therefore, we

describe it as a new species, *H. phragmiticola*.

1 MATERIALS AND METHODS

1.1 Morphological studies

Specimen examined was deposited in the herbarium of the Institute of Microbiology, School of Ecology and Nature Conservation, Beijing Forestry University (BJFC). Macro-morphological descriptions referred to field records and photographs. Sections of basidiocarps were studied microscopically at magnifications 1 000× using a Nikon Eclipse 80i microscope with phase contrast illumination. Microscopic morphology drawing was done by drawing tubes. Microscopic features, measurements, and drawings were made from sections stained with cotton blue and Melzer's reagent. The basidiospores' size range excludes 5% of the measurement extremes and gives the measurement extremes in parentheses to show the variation of basidiospores' size. Abbreviations: IKI=Melzer's reagent, CB=cotton blue, CB=acyanophilous, L=mean basidiospore length (arithmetic average of all basidiospores), W=mean basidiospore width (arithmetic average of all basidiospores) (Thiers 2018), Q=the L/W ratio, and n=number of basidiospores measured from given number of specimens. Terms of special color follow Petersen (1996).

1.2 DNA extraction and sequencing

A CTAB rapid plant genome extraction kit (Aidlab Biotechnologies, Beijing) was used to obtain PCR products from dried specimens. Some modifications were made based on the manufacturer's instructions followed Cao *et al.* (2012) and Zhao & Cui (2013). The primer pair amplified the ITS region ITS5 and ITS4 followed White *et al.* (1990). The primer pair amplified the nrLSU region LR0R and LR7 followed <http://www.biology.duke.edu/fungi/mycolab/primers.htm>. The PCR procedure for ITS was as follows: initial denaturation at 95 °C for 3 min, followed by 34 cycles at 94 °C

for 40 s, 54 °C for 1 min and 72 °C for 1 min, and a final extension of 72 °C for 10 min. The PCR procedure for nrLSU was as follows: initial denaturation at 94 °C for 1 min, followed by 34 cycles at 94 °C for 30 s, 50 °C for 1 min and 72 °C for 1.5 min, and a final extension of 72 °C for 10 min. The PCR products were purified with a gel extraction and PCR purification combo kit (spin-column) in Beijing

Genomics Institute, Beijing, China. The purified products were then sequenced on an ABI-3730-XL DNA analyzer (Applied Biosystems, Foster City, CA, USA) using the same primers as in the original PCR amplifications (Cai *et al.* 2020). The sequence quality was checked followed Nilsson *et al.* (2012). All newly generated sequences were submitted to GenBank and were listed in Table 1.

Table 1 Specimens of *Hygrophoropsis* and related genera used for this study

Taxa	Voucher number	Locality	ITS	nrLSU	Reference
<i>Coniophora arida</i>	CFMR FP-104367	USA	GU187510	GU187573	Binder <i>et al.</i> 2010
<i>Coniophora marmorata</i>	MUCL 31667	Belgium	GU187515	GU187571	Binder <i>et al.</i> 2010
<i>Coniophora puteana</i>	MUCL 1000	Germany	GU187521	GU187578	Binder <i>et al.</i> 2010
<i>Gyrodontium sacchari</i>	MUCL 40589	Thailand	—	GU187579	Binder <i>et al.</i> 2010
<i>Hydnomerulius pinastri</i>	CFMR MD312	USA	GU187523	—	Binder <i>et al.</i> 2010
<i>Hygrophoropsis aurantiaca</i>	AFTOL-ID 714	Germany	AY854067	AY684156	Binder & Hibbett 2006
<i>Hygrophoropsis aurantiaca</i>	EL42 99	Sweden	AY586659	—	Larsson <i>et al.</i> 2004
<i>Hygrophoropsis aurantiaca</i>	MA-Fungi 47694	Spain	AJ419201	—	Martín & Raidl 2002
<i>Hygrophoropsis aurantiaca</i>	UBCF28389	Canada	KP454025	—	Berbee <i>et al.</i> direct submission
<i>Hygrophoropsis aurantiaca</i>	2487	Canada	KM248881	—	Berube <i>et al.</i> direct submission
<i>Hygrophoropsis aurantiaca</i>	AR09732	Mexico	KT875014	—	Garibay-Orijel <i>et al.</i> direct submission
<i>Hygrophoropsis aurantiaca</i>	CB0849	Mexico	KT875013	—	Garibay-Orijel <i>et al.</i> direct submission
<i>Hygrophoropsis aurantiaca</i>	MA-Fungi 47695	Spain	AJ419202	—	Martín & Raidl 2002
" <i>Hygrophoropsis aurantiaca</i> "	12	USA	KM373254	—	Russell direct submission
" <i>Hygrophoropsis aurantiaca</i> "	43	USA	KM373264	—	Russell direct submission
" <i>Hygrophoropsis aurantiaca</i> "	ASIS22496	Korea	KF668314	—	Seok <i>et al.</i> direct submission
" <i>Hygrophoropsis aurantiaca</i> "	S.D. Russell MycoMap #79	USA	MK575241	—	Russell direct submission
<i>Hygrophoropsis</i> cf. <i>aurantiaca</i>	Mushroom Observer 284484	USA	MN204474	—	Clements direct submission
<i>Hygrophoropsis rufa</i>	Montri 209	Switzerland	MK028418	—	Valerie <i>et al.</i> 2019
<i>Hygrophoropsis rufa</i>	PRM899303	Czech	HF951529	—	Holec & Kolařík 2013
<i>Hygrophoropsis phragmiticola</i>	Dai 20901A fruitbody	China	OK380762	OK384507	Present study
<i>Hygrophoropsis phragmiticola</i>	Dai 20901B culture	China	OK380763	OK384508	Present study
<i>Hygrophoropsis</i> sp.	MES 1300	Argentina	KY462457	—	Truong <i>et al.</i> 2017
<i>Leucogyrophana lichenicola</i>	DAOM 194172	Canada	GU187531	GU187583	Binder <i>et al.</i> 2010
<i>Leucogyrophana mollusca</i>	CFMR L-10277	USA	GU187525	GU187584	Binder <i>et al.</i> 2010
<i>Leucogyrophana olivascens</i>	CFMR HHB-11134	USA	GU187532	GU187587	Binder <i>et al.</i> 2010
<i>Leucogyrophana romellii</i>	CFMR T-547	Canada	GU187529	GU187586	Binder <i>et al.</i> 2010
<i>Pseudomerulius curtisii</i>	REH8912	Australia	GU187533	GU187589	Binder <i>et al.</i> 2010
<i>Serpula lacrymans</i>	REG383	—	GU187542	GU187596	Binder <i>et al.</i> 2010

Note: Accession numbers in bold represent newly generated sequences.

1.3 Phylogenetic analysis

For validating the phylogenetic position of our target samples, their ITS sequences were searched in the GenBank by BLAST tool. Consequently, our samples mapped into the genus of *Hygrophoropsis* of the order Boletales. Meanwhile the relative ITS and nrLSU sequences of representative species were downloaded, which belong to the target genus *Hygrophoropsis* and allied genera including *Leucogyrophana*, *Coniophora*, *Pseudomerulius*, *Gyrodontium*, *Hydnomerulius*, *Serpula*. In total, 29 samples from seven genera of Boletales are incorporated in the study. *Serpula lacrymans* (Wulfen) J. Schröt was selected as outgroup following Binder *et al.* (2010). Detailed information of the voucher specimens is listed in Table 1. Sequences of two loci (ITS and nrLSU) were aligned separately with MAFFT 7.402 using the E-INS-i strategy (Katoh & Standley 2013) and were separately trimmed using GBLOCKS 0.91b (Castresana 2000). Single-locus phylogenetic trees were first constructed to assess the potential conflicts in the gene tree topologies. The job of connecting the two DNA fragments was done using PHYUTILITY 2.2 software (Smith & Dunn 2008) if there are no significant conflicts detected among them. The JMODELTEST software (Darriba *et al.* 2012) was implemented to evaluate the best-fitting model of each DNA fragments.

For the ultimate phylogenetic analyses, both maximum likelihood (ML) and Bayesian inference (BI) methods were utilized. In the ML analysis by RAXML 8.2.10 (Stamatakis 2014), all parameters were kept at default settings, except that model was set as GTRGAMMAI which was selected by JMODELTEST, and statistical support was obtained using nonparametric bootstrapping with 1 000 replicates. For the BI analysis implemented in MRBAYES 3.2.7 (Ronquist *et*

al. 2012), individual best-fitting substitution models were assigned to the corresponding DNA fragments. Two runs and four chains for each were processed and run for approximately 2.77 million generations sampling from the posterior distribution every 100 generations to ensure that potential scale reduction factors (PSRF) were reasonably close to 1.0 for all parameters indicative of chain convergence (Ronquist *et al.* 2012; Cai *et al.* 2020; Wu *et al.* 2020). The first 25% sampled trees were discarded as burn-in, while the remaining ones were used to obtain Bayesian posterior probabilities (BPP) of the clades.

2 RESULTS

2.1 Phylogenetic analyses

A total of two ITS and two nrLSU sequences was newly generated from the target samples. In the two single-locus phylogenetic analyses, no strongly supported conflict was observed. The trimmed- concatenated matrix remained 2 111 aligned positions. The best-fitting substitutional models of the two loci were both determined as GTR+I+G. ML and BI analyses results are verified by each other, so only ML topology was presented in Fig. 1.

Based on the multi-locus phylogenetic analysis, the monophyly of the genus *Hygrophoropsis* was validated with high support values (ML=90, BI=1.00). Our target samples (fruiting body and culture) were well clustered within the genus *Hygrophoropsis* and closed to *H. rufa* and *H. aurantiaca*, and formed a distinct lineage with strong support (100% ML, 100% MP, 1.00 BPPs).

2.2 Taxonomy

Hygrophoropsis phragmiticola L.T. Ban & Meng Zhou, **sp. nov.** Figs. 2–3

MycoBank No.: MB 840695

Etymology: *Phragmiticola* (Lat.): referring to the species growing on *Phragmites*.

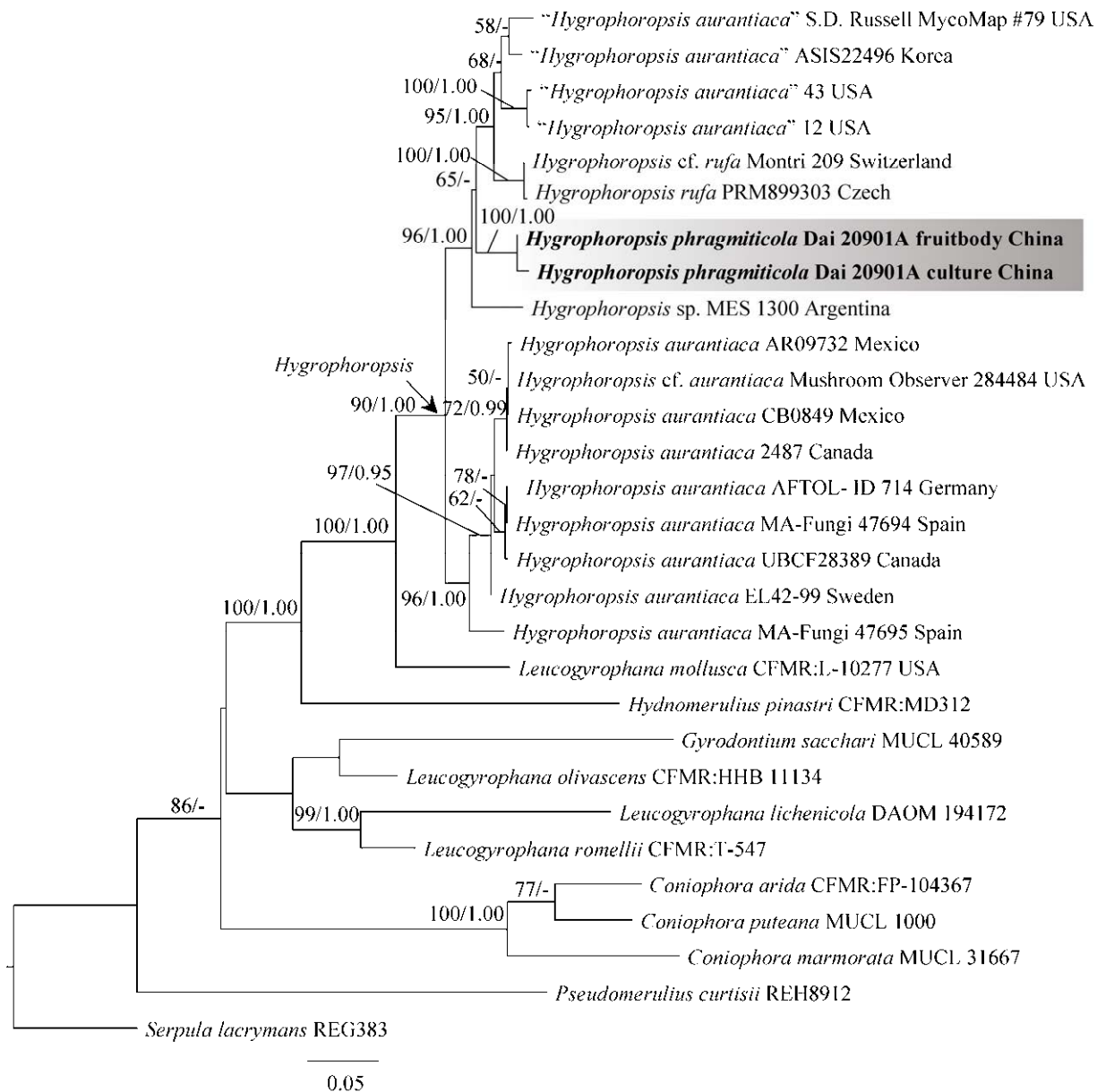


Fig. 1 The molecular phylogenetic tree of the genus *Hygrophoropsis* with allied genera using ML method based on ITS and nrLSU nucleotide sequences. Bootstrap values (≥ 50) and posterior probabilities (≥ 0.90) are shown on supported branches. The new species *H. phragmiticola* is labelled in bold within a grayish box.

Type: China, Tianjin, Ninghe, Beihuaidian, Qilhai Nature Reserve, 2 Sep 2019, Dai 20901A (Holotype, BJFC 032560).

Basidiomata epigeous, stipitate-pileate with lamellate hymenophore. Pilei 15–40 mm in diameter, initially slightly convex, plano-convex to applanate; pileal surface felty, creamy-whitish to pale-ochraceous when fresh, becoming lemon yellow upon drying; center

sometimes umbilicate, glabrous; margin undulate, continuously involute. Gills white to cream when fresh, cream when dry; lamellae moderately dense, regular to subregular, thin, deeply decurrent, about 10–20 mm of them connected with stipe, forked towards the pileus margin, unchanging when bruised. Context 2–4 mm thick in the center of the pilei, soft, white to creamy, usually unchanging when

bruised. Stipe 10–30×5–12 mm, central to eccentric, cylindrical, smooth, white to cream, white tomentose towards the base. Taste and odor mild.



Fig. 2 Basidiocarps of *Hygrophoropsis phragmiticola*. Scale bars=1.0 cm.

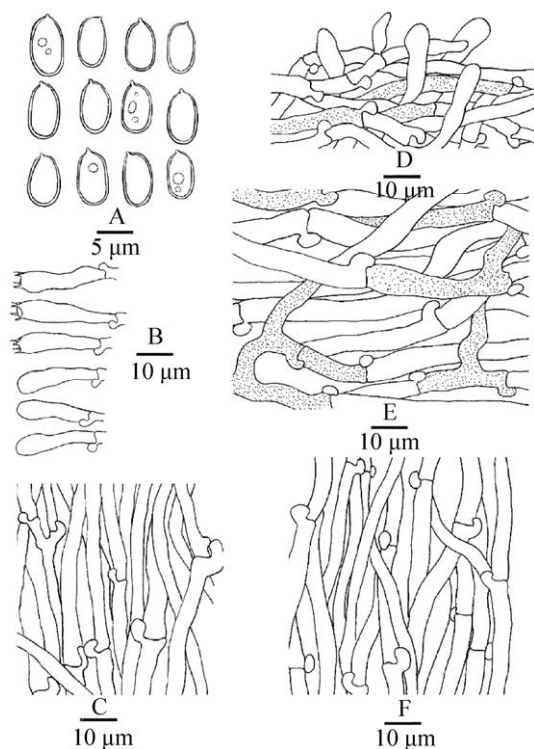


Fig. 3 Microscopic structures of *Hygrophoropsis phragmiticola*. A: Basidiospores; B: Basidia and basidioles; C: Hyphae of the stipe; D: Hyphae of pileipellis; E: Hyphae of pileal trama; F: Hyphae of gills.

Basidiospores oblong-ellipsoid, with a few small guttules, hyaline, slightly thick-walled, smooth, weakly dextrinoid, CB–, 6–10(–10.6)×4–5.5(–6.1) µm, L=7.78 µm, W=4.90 µm, Q=1.59 (n=30/1). Basidia 25–35×6–7.5 µm, cylindrical to narrowly clavate, 4-spored, with a basal clamp connection. Basidioles 17–22×5.5–6.5 µm, narrowly clavate. Cystidia absent.

Pileipellis consisting of loosely arranged, interwoven hyphae, branched, thin-walled, hyaline, gelatinous, 3.5–7 µm diam., cells cylindrical or slightly inflated, terminal cells narrowly clavate to clavate with a low, broad, obtuse umbo, thin-walled; some gloeoplerous hyphae present, as the same size of normal hyphae. Trama of gills consisting of parallel to slightly interwoven hyphae, 3.5–5.5 µm diam., cells cylindrical to slightly fusiform inflated, thin-walled, hyaline, non-dextrinoid; some gloeoplerous hyphae present, as the same size of normal hyphae. Context hyphae loosely arranged, interwoven, branched, thin-walled, hyaline, gelatinous, 5–10 µm diam., cells cylindrical to slightly inflated. Stipe hyphae loosely arranged, hyaline, 3.5–5.5 µm diam., cells cylindrical. Clamp connections frequent in all tissues.

Habitat and distribution: Saprotrophic, on rot roots of living *Phramites*.

3 DISCUSSIONS

Based on the multi-locus phylogenetic analysis, the monophyly of the genus *Hygrophoropsis* is validated with high support values (ML=90, BI=1.00). However, regarding the delimitation of the genus, our phylogeny (Fig. 1) demonstrates that *H. aurantiaca* is a species complex including more taxa. The convinced *H. aurantiaca* from Germany represented by the AFTOL (Assembling the Fungal Tree of Life) nested in the *Hygrophoropsis*, while other taxa outside of

Europe may represent unnamed species although they are named as *H. aurantiaca* or “*H. aurantiaca*”. Our target samples (fruiting body and culture) are well clustered within the genus *Hygrophoropsis* and closely related to *H. rufa* and “*H. aurantiaca*”.

Morphologically, *Hygrophoropsis aurantiaca* differs from *H. phragmiticola* in having smaller basidiospores ($5.5\text{--}7\times3\text{--}4\text{ }\mu\text{m}$ vs. $6\text{--}10\times4\text{--}5\text{ }\mu\text{m}$), brighter orange lamellae, slender and darker orange stipe and white, minute crystals coated mycelial cords in the stipe base (Kibby 2012). *Hygrophoropsis rufa* differs from *H. phragmiticola* by its large orange brown cap (up to 100 mm) and smaller basidiospores ($5\text{--}6.5\times3\text{--}4\text{ }\mu\text{m}$ vs. $6\text{--}10\times4\text{--}5\text{ }\mu\text{m}$, Holec & Kolařík 2013). In addition, *H. rufa* usually grows on or around conifer stumps or on wood chips (Holec & Kolařík 2013).

Hygrophoropsis bicolor Hongo is another species reported in Asia, but it is different from *H. phragmiticola* by its smaller and subcylindrical basidiospores ($4.5\text{--}7\times2.5\text{--}3\text{ }\mu\text{m}$ vs. $6\text{--}10\times4\text{--}5\text{ }\mu\text{m}$) and growing on decaying wood of *Pinus densiflora* (Hongo 1963).

Hygrophoropsis phragmiticola is similar to the pale-colored species of *Hygrophoropsis*, *H. fuscusquamula*, *H. macrospora* and *H. pallida*. However, *H. fuscusquamula* is well distinguished by the dark-brownish hairs on the pileal surface, broader cylindric-clavate end cells $12\text{--}16\text{ }\mu\text{m}$ in diam., at pileipellis and the shorter basidiospores ($6\text{--}8\times3.5\text{--}4.5\text{ }\mu\text{m}$ vs. $6\text{--}10\times4\text{--}5\text{ }\mu\text{m}$, Kibby 2012).

It's worth discussing that the species *Hygrophoropsis macrospora*, used to be treated as *H. aurantiaca* var. *macrospora* D.A. Reid, has been known as synonym of *H. pallida* (Peck) Kreisel (Gyosheva & Stoykov 2017). According to Knudsen & Vesterholt (2008), the *H. pallida* has ovate-ellipsoid basidiospores measuring $6\text{--}10\times4\text{--}5\text{ }\mu\text{m}$ which are different from those of *H. macrospora* ($10\text{--}12\times4.5\text{--}5\text{ }\mu\text{m}$).

However, Kuyper (1996) considered *H. pallida* was invalidly published when he proposed combination *H. macrospora*, and Kibby (2012) did not accept the combination of *H. macrospora* because *H. pallida* included several pale-colored taxa of *Hygrophoropsis* according to Knudsen & Vesterholt (2008). Gyosheva & Stoykov (2017) mentioned that compared with other species of the genus, the length of the spores (up to $13\text{ }\mu\text{m}$) is the main micromorphological character of *H. macrospora*. Therefore, we treat *H. macrospora* and *H. pallida* as two independent species in this study.

Hygrophoropsis macrospora differs from *H. phragmiticola* by its longer basidiospores (up to $13\text{ }\mu\text{m}$), and it is so far reported in Europe only (Krisai-Greilhuber 1999; Krieglsteiner 2001; Kibby 2012; Glejdura 2013; Gyosheva & Stoykov 2017). *Hygrophoropsis pallida* was originally described from USA, and it differs from *H. phragmiticola* by its preference for dry habitat, as previous records. *H. pallida* often found in dried out, but temporarily wet meadows and coastal meadows with sedges and grasses and on extensively used hay-field (Knudsen & Vesterholt 2008), so that *H. phragmiticola* can be distinguished from *H. pallida* by its ecology and distribution.

Hygrophoropsis phragmiticola is an edible mushroom in the local area of Tianjin, and it is now a rare species because of extensive collecting in recent years. Fortunately, Qilihai Nature Reserve was set up a few years ago, and the fungus has good opportunity to grow over there.

Most new species of macro-fungi were found in forests in China (Wu *et al.* 2020; Dai *et al.* 2021), and it is worth mentioning that some new mushrooms, *e.g.*, *Hygrophoropsis phragmiticola*, could be found even in wetlands.

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