



Species diversity of *Hygrophorus* in China and a phylogenetic study of the genus

Wang CQ^{1#}, Zhang M^{1#}, He XL², Liu JW³, Wei TZ⁴, Liu TZ⁵, Wang K⁴, Adamčík S^{6,7}, Li TH^{1*} and Deng WQ^{1*}

¹Guangdong Provincial Key Laboratory of Microbial Culture Collection and Application, State Key Laboratory of Applied Microbiology Southern China, Guangdong Institute of Microbiology, Guangdong Academy of Sciences, Guangzhou 510070, Guangdong, China

²Sichuan Institute of Edible Fungi, Chengdu 610066, Sichuan, China

³The Germplasm Bank of Wild Species, Yunnan Key Laboratory for Fungal Diversity and Green Development, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650201, Yunnan, China

⁴State Key Laboratory of Mycology, Institute of Microbiology, Chinese Academy of Sciences, Beijing 100101, China

⁵College of Chemistry and Life Sciences, Chifeng University, Chifeng 024000, Inner Mongolia, China

⁶Laboratory of Molecular Ecology and Mycology, Institute of Botany, Plant Science and Biodiversity Centre, Dubravska cesta 9, 84523 Bratislava, Slovakia

⁷Department of Botany, Faculty of Natural Sciences, Comenius University in Bratislava, Révová 39, 81102 Bratislava, Slovakia

Wang CQ, Zhang M, He XL, Liu JW, Wei TZ, Liu TZ, Wang K, Adamčík S, Li TH, Deng WQ 2023 – Species diversity of *Hygrophorus* in China and a phylogenetic study of the genus. Mycosphere 14(1), 1742–1834, Doi 10.5943/mycosphere/14/1/21

Abstract

Hygrophorus is among the most species rich and frequent ectomycorrhizal genera of Agaricales, and several species are popular wild edible mushrooms in northern and southwestern China. In the past two decades, there has been an increasing number of taxonomic and phylogenetic studies of the genus, however, the comprehensive studies on the species diversity and phylogenetic relationship of *Hygrophorus* in China were lacking. In this study, an extensive survey on the species diversity of *Hygrophorus* in China was conducted. In total, 62 Chinese *Hygrophorus* taxa were included in this study. Fifty-five of them are described, illustrated and discussed, including 26 new species; in addition, two recently described species (*H. habaensis* and *H. viridiflavus*) and 5 insufficiently known species are listed with notes. A large-scale phylogenetic study of *Hygrophorus* was conducted based on the newly obtained sequences and the available internal transcribed spacer (ITS) sequences in the international public databases; and a multi-gene (ITS-LSU-*rpb2-tef1-α*) phylogeny was also conducted. The species boundaries of *Hygrophorus* delimited by morphological data are broadly congruent with those based on the ITS phylogenetic analysis. In general, the multi-locus dataset could resolve a section-level phylogeny of the genus; and a new section, i.e. sect. *Vividi*, is proposed based on both phylogenetic and morphological evidences. However, the subgenera classified by morphology are not supported well by molecular phylogenetic analysis.

Keywords – Hygrophoraceae – Novel taxa – Phylogeny – Taxonomy – Waxcap

Introduction

The genus *Hygrophorus* Fr. (Fungi, Basidiomycota, Agaricales, Hygrophoraceae) (Kirk et al. 2008) is a well recognized and distinct group of mushroom forming fungi. The hygrophoroid clade represented by *Hygrophorus* was recognised as one of the six major lineages of Agaricales (Matheny et al. 2006) by early phylogenetic study based on six DNA loci. Bon (1990) even proposed the order Hygrophorales with *Hygrophorus* as the type genus. Members of the genus *Hygrophorus* are mainly distributed in the holarctic and temperate zones in northern hemisphere. Worldwide, about 100 *Hygrophorus* species had been described 15 years ago (Kirk et al. 2008), and about 30 new species have been published since then (Indexfungorum, 1 April 2023). In China, 41 species had been reported based on morphology identification 10 years ago (Chen & Li 2013), and at least 19 new species have been added in the last decade (Yu et al. 2007, Huang et al. 2018, 2021a, b, 2022a, b, Wang & Li 2020, Wang et al. 2020, 2021, Zhang et al. 2023).

Morphologically, *Hygrophorus* species have the following characters: often sticky pileus, waxy and thick lamellae, colourless basidiospores, slender basidia, and divergent hymenophoral trama (Lodge et al. 2014). Phylogenetically, *Hygrophorus* is the unique genus in the tribe Hygrophoreae within the family Hygrophoraceae, and is close to the tribe Chrysomphalineae (including genera *Aeruginospora*, *Chrysomphalina* and *Haasiella*) (Lodge et al. 2014). Ecologically, as one of the 15 well known ectomycorrhizal genera within Agaricales (Feng & Yang 2019), the species of *Hygrophorus* mostly form ectomycorrhizal relationships with partner trees mostly of families Betulaceae, Fagaceae and Pinaceae in different forest ecosystems. Economically, several *Hygrophorus* species are popular wild edible mushrooms in southwestern and northern China. For example, *H. annulatus* C.Q. Wang & T.H. Li and *H. deliciosus* C.Q. Wang & T.H. Li are common and high yielding wild edible fungi in Sichuan and Yunnan provinces, China (Wang & Li 2020, Wang et al. 2021); *H. lucorum* Kalchbr. and *H. hedrychii* (Helen.) K. Kult are popular wild edible mushrooms in Inner Mongolia Autonomous Region and Jilin province (Bau & Bao 2016, Wang et al. 2020, Huang et al. 2022a).

The taxonomic delimitation of the genus *Hygrophorus* has been gradually improving to be more congruent with phylogeny and biology of its members. Fries (1836) established the genus *Hygrophorus* with the type species *H. eburneus* (Bull) Fr. Afterwards, some mycotaxonomists, such as Quélet (1888), Hesler & Smith (1963) and Largent (1985), adopted the concept of *Hygrophorus* s.l, that is, related groups such as *Hygrocybe* (Fr.) Kummer were regarded as the members of genus *Hygrophorus*. Other mycotaxonomists, however, have adopted the definition of *Hygrophorus* s.s., for example, Kummer (1871) elevated the three “tribes” to three independent genera, namely *Camarophyllus* (Fr.) Kummer, *Hygrocybe* and *Limacium* (Fr.) Kummer; and Karsten (1879) used the genus name *Hygrophorus* instead of *Limacium*. In recent years, the genus concept of *Hygrophorus* s.s. has been widely accepted (Horak 1990, Young 2005, Bessette et al. 2012, Lodge et al. 2014, Campo 2015, Wang et al. 2018).

Based on morphological characteristics, different infrageneric classifications were proposed. Singer (1986) divided the genus *Hygrophorus* into four sections (sect. *Colorati*, sect. *Discoidei*, sect. *Hygrophorus* and sect. *Pudorini*); and Candusso (1997) proposed six sections (sect. *Discoidei*, sect. *Fulventes*, sect. *Hygrophorus*, sect. *Olivaceoumbrini*, sect. *Pudorini* and sect. *Tephroleuci*). However, those systematic arrangements were often unstable and even contradictory.

In the last two decades, phylogenetic studies based on DNA sequences have been applied in the genus *Hygrophorus*, and some important progresses have been obtained. Moncalvo et al. (2002) applied the nrLSU sequences of *H. bakerensis* A.H. Sm. & Hesler and *H. sordidus* Peck in the phylogeny study of Agaricales. Matheny et al. (2006) constructed a six-gene phylogenetic tree, in which four *Hygrophorus* species formed a monophyletic group. In the study of Lodge et al. (2014), 66 ITS sequences, 13 ITS-nrLSU sequences and nine ITS-nrLSU-SSU-*rpb2* sequences mainly from America and Europe were included in the phylogenetic trees, respectively; and a taxonomic system was proposed, in which the genus is divided into three subgenera (subg. *Hygrophorus*, subg. *Colorati* (Bataille) E. Larss. and subg. *Camarophylli* Fr.), each subgenus is divided into three sections, and some sections are further divided into subsections. Recently, phylogenetic studies

have been used to reveal the species diversity and biogeography of some infrageneric groups of *Hygrophorus*. Section *Olivaceoumbrini* s.l. (Bataille) Konrad & Maubl. was further divided into five sections based on the ITS phylogenetic result of Bellanger et al. (2021). In addition, phylogenetic studies were also carried out in both sect. *Hygrophorus* (Larsson & Jacobsson 2004, Endo et al. 2018, Naseer et al. 2019, Wang et al. 2020) and sect. *Aurei* (Moreau et al. 2018, Huang et al. 2022a). Recently, 13 new species were published based on both morphology and molecular analyses (Larsson et al. 2014, 2018, Larsson & Bendiksen 2020, Bellanger et al. 2021, Wang et al. 2021, Huang et al. 2022a).

The species richness of Chinese *Hygrophorus* is still underestimated. For examples, the Chinese collections of the *H. russula*-like waxcaps were commonly treated as *H. russula* (Schaeff.) Kauffman for several decades based on morphological identification; but recent studies have shown that *H. russula*-complex includes at least 5 species in China, i.e. *H. deliciosus* C.Q. Wang & T.H. Li, *H. orientalis* H.Y. Huang & L.P. Tang, *H. parvirussula* H.Y. Huang & L.P. Tang, *H. qinggangjun* H.Y. Huang & L.P. Tang and *H. yunnanensis* H.Y. Huang & L.P. Tang (Huang et al. 2018, 2021a, Wang & Li 2018). In short, over 2/3 of the species recorded in China based on morphology were identified as the European or North American taxa, but their identity require molecular support and detailed morphological observation. In addition, relevant studies of other genera also indicate that China has a high diversity of macrofungal species (Cui et al. 2018, Luo & Zhao 2022, Hu et al. 2023).

Therefore, further studies are needed to reveal the species diversity of the Chinese *Hygrophorus*; and multi-locus phylogenetic studies with more extensive taxon sampling are needed to more comprehensively understand the infrageneric relationships of the genus *Hygrophorus*. The goals of this study were: 1) to document the Chinese *Hygrophorus* species, especially new species, with descriptions and illustrations using morphological characters, molecular evidence and ecological data; 2) to provide a robust hypothesis for relationships within *Hygrophorus* using the combined multi-gene datasets; 3) to present a deeper insight into the geographical distribution of the species.

Materials & Methods

Sample collection

Samples were mainly collected from southern, southwestern, central, northeastern and northwestern China over the last decade. Fresh samples were usually photographed in situ, recorded, and then dried in a Dörrex dehydrator (Stockli, Switzerland) or other electric driers at about 50 °C until dry. For reference, some North American samples from David Hibbett's lab were also observed. Voucher specimens were deposited in the Mycological Herbarium of Chifeng University (CFSZ), Fungarium of the Guangdong Institute of Microbiology, Guangdong Academy of Sciences, Guangzhou, China (GDGM); the Herbarium of Mycology, Institute of Microbiology, Chinese Academy of Sciences, Beijing, China (HMAS); the Herbarium of Mycology, Jilin Agricultural University, Changchun, Jilin, China (HMJAU); the Herbarium of Cryptogams at the Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, China (KUN-HKAS); the Mycological Herbarium of Soil and Fertilizer Institute, Sichuan Academy of Agricultural Sciences (SAAS). Acronyms of the herbaria follow Thiers (2018). Species names were registered in Indexfungorum (www.indexfungorum.org).

Morphological study

Macromorphological characters of specimens were prepared based on the field notes and photographs. Colour codes and names followed Kornerup & Wanscher (1978). Micromorphological characters of dry specimens were observed using an Olympus BX51 microscope (Olympus Co., Tokyo, Japan) or an AX10 light microscopy (Carl Zeiss Inc., Oberkochen, Germany). To observe colours and/or gelatinous zones, dry pileus and stipe surface and lamellar tissues were rehydrated in distilled water; to measure sizes of basidiospores, basidia,

pileipellis, stipitipellis, and hymenophoral trama, tissues were mounted in 5% KOH solution with or without 1% Congo red. At least 20 basidiospores and 10 basidia were randomly selected and measured for each individual. Q value refers to the length/width ratio of basidiospores and basidia. Range of size and Q value of basidiospores and basidia are presented as (a–)b–c(–d): the range ‘b–c’ represents 90% of the measured values, and ‘a’ and ‘d’ represent extreme values. Qm/Lm/Wm refers to the average of values/length/width \pm standard deviation.

DNA extraction, PCR and sequencing

Total DNA was extracted using the HiPure Fungus DNA Mini Kit (Magen Biotech Co., Ltd., Guangzhou, China) according to the manufacturer’s instructions. The following primer pairs were used for Polymerase Chain Reaction (PCR) amplification and sequencing: 1) ITS1F/ITS1/ITS5 and ITS4 were used for the internal transcribed spacers 1 and 2 with the 5.8S rDNA (ITS) (White et al. 1990, Gardes & Bruns 1993); 2) LR0R and LR5/LR7 (Vilgalys & Hester 1990) for the D1–D3 domains of the nuc 28S rDNA (nrLSU); 3) bRPB2-6F and bRPB2-7.1R (Matheny 2005) for the RNA polymerase II second largest subunit (*rpb2*); 4) EF1-983F and EF1-1967R/EF1-2212R (Rehner & Buckley 2005) for the translation elongation factor 1-a (*tef1-a*). Sanger DNA sequencing for PCR products was performed by Beijing Liuhe Co., Limited (Guangzhou, China) on an ABI 3730 DNA sequencer analyzer (Applied Biosystems, Foster City, CA, USA) usually with the same primer pairs and occasionally with additional primers. Raw forward and reverse sequences were assembled and checked using SeqMan (DNA STAR package; DNAStar Inc., Madison, WI, USA). The generic level preliminary identification was performed via BLAST queries in the NCBI GenBank nucleotide database (<https://www.ncbi.nlm.nih.gov/genbank>). All newly generated sequences in this study were deposited in the GenBank.

Nucleotide alignment and phylogenetic analyses

Apart from the newly generated sequences, additional sequences were retrieved from GenBank and Unite (<https://unite.ut.ee/>). Two sets of alignment were constructed. The first set consisted of the ITS region (ITS1, 5.8S and ITS2) since this region had the highest species coverage, made up of available ITS sequences (longer than 200 bps). To avoid exclusion of regions useful for resolving terminal interspecific relationships, no outgroup sequence was selected and the tree was midpoint rooted. The second set concatenated from the alignment of the ITS, LSU, *rpb2* and *tef1-a*, and outgroups were selected based on phylogenies in Lodge et al. (2014), Wang et al. (2018) and He & Yang (2021); in addition, the ambiguous head and tail were excluded before concatenated. Sequences were initially aligned using the default settings in MAFFT version 7 (<https://mafft.cbrc.jp/alignment/software/>). Maximum likelihood tree analyses were generated in the PhyloSuite platform (Zhang et al. 2020) using the IQ-TREE software (Nguyen et al. 2014). Trees were viewed in FigTree 1.4.4 and processed in Adobe Illustrator CS6.

Table 1 Information of DNA sequences used in multilocus analyses with species names, vouchers, locality and GenBank accession numbers.

Species name	Voucher	Locality	ITS	LSU	<i>rpb2</i>	<i>tef1-a</i>
<i>Chrysomphalina chrysophylla</i>	PBM 684	USA	DQ192180	DQ457656		
<i>C. grossular</i>	OSC 113683	USA	EU644704	EU652373		
<i>Haasiella splendidissima</i>	Roux n. 3666		JN944398	JN944399		
<i>Ha. splendidissima</i>	Roux n. 4044		JN944400	JN944401		
<i>Ha. venustissima</i>	A. Gminder 971488	Italy	KF291092	KF291093		
<i>Ha. venustissima</i>	E.C. 8191	Italy	JN944393	JN944394		
<i>Hygrophorus abieticola</i>	GDGM44322	China: Sichuan	OP547627	OP558617	OR566146	OR575224

Table 1 Continued.

Species name	Voucher	Locality	ITS	LSU	<i>rpb2</i>	<i>tef1-a</i>
<i>H. abieticola</i>	GDGM44324	China: Sichuan	OP547629	OP558619	OR566145	OR575225
<i>H. abieticola</i>	GDGM44334	China: Sichuan	OP547633	OP558623	OR566144	OR575226
<i>H. abieticola</i>	GDGM83191	China: Yunnan	OP547683	OP558675		
<i>H. abieticola</i>	HMAS280807	China	OP547749	OP558733		
<i>H. abieticola</i>	XHW6354 (HKAS 131104)	China	OP547765	OP558751		
<i>H. abieticola</i>	XHW6452 (HKAS 131106)	China	OP547767	OP558753		
<i>H. aff. russula</i>	CLO-4280 (CFMR BZ- 2427)	Belize	KF381523		KF407937	
<i>H. agathosmoides</i>	CFSZ20158	China: Inner Mongolia	OP547738	OP558604		
<i>H. agathosmoides</i>	CFSZ20162	China: Inner Mongolia	OP547739	OP558605		
<i>H. agathosmoides</i>	HMAS 281303	China	MZ605814	ON764316		MZ614633
<i>H. alboflavescens</i>	LAH 35243	Pakistan	MK066236	MK066240		
<i>H. albofloccosus</i>	GDGM70044	USA	OP547639	OP558630		OR575228
<i>H. albofloccosus</i>	GDGM70063	USA	OP547642	OP558633		OR575229
<i>H. albofloccosus</i>	GDGM70150	USA	OP547648	OP558639		OR575230
<i>H. fragilipurpurascens</i>	GDGM43354	China: Sichuan	OP547624	OP558614	OR566143	OR575231
<i>H. fragilipurpurascens</i>	GDGM44331	China: Sichuan	OP547631	OP558621		OR575232
<i>H. fragilipurpurascens</i>	GDGM44332	China: Sichuan	OP547632	OP558622		OR575233
<i>H. alpinus</i>	GDGM79203	China	OP547656	OP558648	OR566142	OR575234
<i>H. alpinus</i>	GDGM84536	China	OP547707	OP558699	OR566140	OR575235
<i>H. alpinus</i>	GDGM84566	China	OP547713	OP558705	OR566139	OR575236
<i>H. alpinus</i>	MHKMU W.H. Zhang 463 1	China: Yunnan	MW762962	MW762752		
<i>H. alpinus</i>	MHKMU W.H. Zhang 463 2	China: Yunnan	MW762963	MW762753		
<i>H. annulatus</i>	GDGM45124	China: Sichuan	MT758324	OQ867282	OR566138	OR575237
<i>H. annulatus</i>	GDGM84413	China: Sichuan	OP547692	OP558684	OR566137	OR575238
<i>H. annulatus</i>	GDGM84591	China	OP547715	OP558707	OR566136	OR575239
<i>H. annulatus</i>	XHW6338 (HKAS 107621)	China: Sichuan	MT758340	OP558750		
<i>H. annulatus</i>	XHW6454 (HKAS 107623)	China: Sichuan	MT758323	OP558754		
<i>H. armeniacus</i>	GDGM82364	China: Yunnan	OP547665	OP558658		
<i>H. armeniacus</i>	GDGM90096	China: Yunnan	OP547733	OP558725		
<i>H. armeniacus</i>	XHW6877 (HKAS 131110)	China	OP547772	OP558759		
<i>H. armeniacus</i>	XHW6886 (HKAS 131111)	China	OP547773	OP558760		
<i>H. atrofuscus</i>	HKAS 54818	China: Yunnan	MZ605836	MZ605793		
<i>H. atrofuscus</i>	HKAS 55483	China: Yunnan	MZ605835	MZ605792		
<i>H. atrofuscus</i>	HKAS56277	China	MZ605834	OP558726		

Table 1 Continued.

Species name	Voucher	Locality	ITS	LSU	<i>rpb2</i>	<i>tef1-a</i>
<i>H. atrofuscus</i>	MHKMU T. Huang 541	China: Yunnan	ON764314	ON764317		
<i>H. aurantioluteus</i>	SAAS191	China: Sichuan	OP547759	OP558743		
<i>H. aurantiosquamosus</i>	GDGM84401	China: Sichuan	OP547690	OP558682	OR566135	OR575240
<i>H. aurantiosquamosus</i>	GDGM84424	China: Sichuan	OP547693	OP558685	OR566134	OR575241
<i>H. aurantiosquamosus</i>	GDGM84517	China: Sichuan	OP547704	OP558696	OR566133	OR575242
<i>H. aurantiosquamosus</i>	LJW2129 (GDGM92368)	China: Yunnan	OP547752	OP558736		
<i>H. aurantiosquamosus</i>	XHW6433 (HKAS 131105)	China	OP547766	OP558752		
<i>H. alboflavescens</i>	GDGM73222	China: Sichuan	OP547651	OP558643		
<i>H. alboflavescens</i>	GDGM79202	China	OP547655	OP558647		
<i>H. alboflavescens</i>	GDGM79205	China	OP547657	OP558649		
<i>H. alboflavescens</i>	GDGM82808	China: Sichuan	OP547675	OP558668	OR566132	OR575227
<i>H. alboflavescens</i>	GDGM85775	China: Sichuan	OP547729	OP558721		
<i>H. alboflavescens</i>	GDGM85777	China: Sichuan	OP547730	OP558722		
<i>H. alboflavescens</i>	GDGM85780	China: Sichuan	OP547731	OP558723		
<i>H. brunneiceps</i>	GDGM84527	China: Sichuan	OP547705	OP558697	OR566131	OR575243
<i>H. brunneiceps</i>	GDGM84530	China: Sichuan	OP547706	OP558698	OR566130	OR575244
<i>H. brunneiceps</i>	GDGM84682	China: Sichuan	OP547725	OP558717	OR566129	OR575245
<i>H. brunneiceps</i>	HKAS 54804	China: Yunnan	MZ605840	MZ605797		
<i>H. brunneiceps</i>	HMAS 254315	China: Tibet	MZ605838	MZ605795		MZ614641
<i>H. brunneodiscus</i>	GDGM76934	China: Hunan	MT093605	MT093621		OR575246
<i>H. brunneodiscus</i>	GDGM79240	China: Yunnan	OP547658	OP558651		
<i>H. brunneodiscus</i>	CFSZ21108	China: Inner Mongolia	OP547741	OP558607		
<i>H. brunneodiscus</i>	GDGM73213	China: Hunan	MN378318	MT093623		
<i>H. brunneodiscus</i>	GDGM75489	China: Hunan	MN378317	MT093622		
<i>H. brunneoloaurantiacus</i>	GDGM82433	China: Yunnan	OP547672	OP558665		
<i>H. brunneoloaurantiacus</i>	GDGM83034	China: Yunnan	OP547677	OP558670		
<i>H. brunneoloaurantiacus</i>	GDGM83080	China: Yunnan	OP547679		OR566128	OR575247
<i>H. brunneoloaurantiacus</i>	GDGM83133	China	OP547681	OP558673		
<i>H. brunneolus</i>	SAAS510	China: Sichuan	OP547761	OP558745		
<i>H. brunneolus</i>	SAAS617	China: Sichuan	OP547762	OP558746		
<i>H. brunnescens</i>	GDGM84456	China: Sichuan	OP547694	OP558686	OR566127	OR575248
<i>H. cf. chrysodon</i>	GDGM70067	USA	OP547645	OP558636		OR575249

Table 1 Continued.

Species name	Voucher	Locality	ITS	LSU	<i>rpb2</i>	<i>tef1-a</i>
<i>H. cf. exiguus</i>	GDGM44612	China: Jilin	OP547635	OP558625		
<i>H. cf. mesotephros</i>	TENN 71861	USA	MG773826	MT237450		
<i>H. cf. purpurascens</i>	JLF8524	USA:	MW019597	MW019598		
		Oregon				
<i>H. cf. purpurascens</i>	JLF8641	USA:	MW015745	MW019590		
		California				
<i>H. cf. pusillus</i>	GDGM70043	USA	OP547638	OP558629		OR575250
<i>H. chrysodon</i>	KUN-HKAS 112569 (QH 135)	China: Tibet	MW762876	MW763001	MW789180	MW773440
<i>H. chuxiongensis</i>	GDGM79225	China: Yunnan		OP558650	OR566126	OR575251
<i>H. chuxiongensis</i>	GDGM83746	China	OP547689	OP558681	OR566125	OR575252
<i>H. chuxiongensis</i>	XHW6689 (HKAS 131108)	China	OP547770	OP558757		
<i>H. brunneololamellatus</i>	GDGM84600	China: Sichuan	OP547716	OP558708	OR566124	OR575253
<i>H. cinnamoneus</i>	GDGM84554	China: Sichuan	OP547711	OP558703	OR566123	OR575254
<i>H. cinnamoneus</i>	GDGM84654	China: Sichuan	OP547721	OP558713	OR566122	OR575255
<i>H. cinnamoneus</i>	GDGM84699	China: Sichuan	OP547726	OP558718	OR566121	OR575256
<i>H. deliciosus</i>	GDGM73208	China: Tibet	MT363821	OP558642	OR566120	OR575257
<i>H. deliciosus</i>	GDGM79208	China: Yunnan	MT363808	OQ867281	OR566119	OR575258
<i>H. deliciosus</i>	GDGM81877	China: Sichuan	OP547660	OP558653	OR566118	OR575259
<i>H. deliciosus</i>	XHW6125 (HKAS 131102)	China: Yunnan	MT363814	OP558748		
<i>H. deliciosus</i>	XHW6916 (HKAS 131112)	China: Yunnan	MT363820	OP558761		
<i>H. erubescens</i>	GDGM84466	China: Sichuan	OP547695	OP558687	OR566117	OR575260
<i>H. erubescens</i>	GDGM84603	China	OP547717	OP558709	OR566116	OR575261
<i>H. erubescens</i>	GDGM84676	China	OP547722	OP558714	OR566115	OR575262
<i>H. erubescens</i>	HMAS280471	China	OP547747	OP558731		
<i>H. erubescens</i>	HMAS280721	China	OP547748	OP558732		
<i>H. esculentus</i>	MHKMU Y.J. Pu 321	China: Yunnan	MW762967	MW762757		
<i>H. esculentus</i>	SAAS4747	China: Sichuan	OQ860085	OQ867283		
<i>H. flavoalbus</i>	XHW7197 (HKAS 131114)	China	OP547775	OP558763		
<i>H. flavoalbus</i>	XHW7264 (HKAS 131115)	China	OP547776	OP558764		
<i>H. flavodiscus</i>	GDGM70070	USA	OP547646	OP558637		
<i>H. flavodiscus</i>	DSH101009.2	USA	HM020691	HM026550		
<i>H. flavodiscus</i>	KUN-HKAS 55043 (ZQ 842)	China: Yunnan	MW616465	MW600484	MW656474	MW656464
<i>H. flavodiscus</i>	KUN-HKAS 68013 (Hao 41)	China: Yunnan	MW616464	MW600483	MW656473	MW656463
<i>H. fuligineus</i>	GDGM70057	USA	OP547641	OP558632		OR575263
<i>H. fuligineus</i>	GDGM70064	USA	OP547643	OP558634		OR575264
<i>H. fuligineus</i>	GDGM70071	USA	OP547647	OP558638		
<i>H. fuligineus</i>	GDGM70153	USA	OP547649	OP558640		
<i>H. fuligineus</i>	DSH101009.3	USA	HM020693	HM026551		
<i>H. fuscodiscus</i>	GDGM84468	China: Sichuan	OP547696	OP558688	OR566114	

Table 1 Continued.

Species name	Voucher	Locality	ITS	LSU	<i>rpb2</i>	<i>tef1-a</i>
<i>H. fuscodiscus</i>	GDGM84543	China: Sichuan	OP547708	OP558700	OR566113	OR575265
<i>H. fuscodiscus</i>	GDGM84677	China: Sichuan	OP547723	OP558715	OR566112	OR575266
<i>H. fuscodiscus</i>	XHW6501 (HKAS 131107)	China	OP547768	OP558755		
<i>H. fuscodiscus</i>	XHW6713 (HKAS 131109)	China	OP547771	OP558758		
<i>H. fuscopapillatus</i>	GDGM44412	China: Sichuan	MN378337	MT093625	OR566111	OR575267
<i>H. fuscopapillatus</i>	GDGM81878	China: Sichuan	OP547661	OP558654	OR566110	OR575268
<i>H. fuscopapillatus</i>	LJW1858	China: Yunnan	MT093606	MT093626		
<i>H. fuscopapillatus</i>	LJW1984 (GDGM92369)	China: Yunnan	OP547751	OP558735		
<i>H. fuscopapillatus</i>	XHW6609	China: Yunnan	MT093607	MT093627		
<i>H. gliocyclus</i>	GDGM84514	China: Sichuan	OP547703	OP558695	OR566109	OR575269
<i>H. gliocyclus</i>	KUN-HKAS 79929 (Liu 228)	China: Tibet	MW616466	MW600485	MW656475	MW656465
<i>H. gliocyclus</i>	LJW1983 (GDGM92370)	China: Yunnan	OP547750	OP558734		
<i>H. gliocyclus</i>	MHKMU H.Y.Huang 877	China: Yunnan	MW762984	MW762772		OK063799
<i>H. gliocyclus</i>	XHW7149 (HKAS 131113)	China	OP547774	OP558762		
<i>H. glutiniceps</i>	FHMU2013	China: Hainan	MN378312	MT093614		
<i>H. glutiniceps</i>	GDGM42140	China: Guangdong	MN378310	MT093619		
<i>H. glutiniceps</i>	GDGM42188	China: Guangdong	MN378313	MT093618		
<i>H. glutiniceps</i>	GDGM42217	China: Guangdong	MN378309	MT093617		
<i>H. glutiniceps</i>	MHKMU H.Y. Huang 797	China: Hainan	OK011526	OK001711		OK063786
<i>H. glutinifer</i>	E00218159	UK: Scotland	MZ605844	MZ605800		
<i>H. griseodiscus</i>	GDGM84572	China: Sichuan	OP547714	OP558706		OR575270
<i>H. griseodiscus</i>	GDGM84644	China: Sichuan	OP547720	OP558712		OR575271
<i>H. griseodiscus</i>	SAAS462	China: Sichuan	MN378338	MT093624		OR575272
<i>H. habaensis</i>	MHKMU W.H. Zhang 513 1	China: Yunnan	MZ605845	MZ605801		MZ614644
<i>H. habaensis</i>	MHKMU W.H. Zhang 513 2	China: Yunnan	MZ605846	MZ605802		
<i>H. hedrychii</i>	GDGM44600	China: Inner Mongolia	OP547634	OP558624	OR566108	OR575273
<i>H. hedrychii</i>	GDGM84408	China: Sichuan	OP547691	OP558683	OR566107	OR575274
<i>H. hedrychii</i>	GDGM84550	China	OP547710	OP558702	OR566106	OR575275
<i>H. hedrychii</i>	CFSZ18269	China: Inner Mongolia	MN378307	MT093630		
<i>H. hedrychii</i>	HMAS 290140	China	OK011527	OK001712		OK063787

Table 1 Continued.

Species name	Voucher	Locality	ITS	LSU	<i>rpb2</i>	<i>tef1-a</i>
<i>H. hypothejus</i>	KUN-HKAS 56550 (Yang 5052)	Germany	MW616467	MW600486	MW656476	
<i>H. pseudohypothejus</i>	XHW7324	China	OP547777	OP558765		
<i>H. lucorum</i>	GDGM42148	Italy	OP547621	OP558611	OR566105	OR575276
<i>H. lucorum</i>	GDGM79101	China: Inner Mongolia	OP547653	OP558645	OR566104	OR575277
<i>H. lucorum</i>	CFSZ20149	China: Inner Mongolia	OP547737	OP558603		
<i>H. lucorum</i>	HKAS 56532	Germany	MW762988	MW762776		OK063801
<i>H. magnisporus</i>	SAAS132	China: Sichuan	OP547756	OP558740		
<i>H. magnisporus</i>	SAAS146	China: Sichuan	OP547757	OP558741		
<i>H. magnisporus</i>	SAAS170	China: Sichuan	OP547758	OP558742		
<i>H. magnisporus</i>	SAAS397	China: Sichuan	OP547760	OP558744		
<i>H. marcocontui</i>	KATO Fungi 3604	Spain	MG888785	MG888786		
<i>H. murinidiscus</i>	GDGM82120	China: Sichuan	OP547662	OP558655	OR566103	OR575278
<i>H. murinidiscus</i>	GDGM82183	China: Sichuan	OP547663	OP558656	OR566102	OR575279
<i>H. murinidiscus</i>	GDGM82186	China: Sichuan	OP547664	OP558657	OR566101	OR575280
<i>H. pallidoaurantiacus</i>	GDGM79190	China	OP547654	OP558646	OR566100	OR575281
<i>H. pallidoaurantiacus</i>	GDGM82410	China: Yunnan	OP547670	OP558663	OR566099	OR575282
<i>H. pallidoaurantiacus</i>	GDGM82424	China: Yunnan	OP547671	OP558664		
<i>H. pallidoaurantiacus</i>	GDGM82435	China: Yunnan	OP547673	OP558666		
<i>H. olivaceoalbus</i>	ectomycorrhiza S15	Germany	AF430253	AF430274		
<i>H. olivaceoalbus</i>	KR6419	Germany	AF430252	AF430271		
<i>H. orientalis</i>	GDGM84641	China: Sichuan	OP547719	OP558711	OR566098	OR575283
<i>H. orientalis</i>	CFSZ20884	China: Inner Mongolia	MW290182	MW928625		MW928556
<i>H. orientalis</i>	HKAS 75586	China: Hubei	MW290176	MW290239		MW928555
<i>H. orientimarzuolus</i>	LJW2439 (GDGM92361)	China: Yunnan	OP547754	OP558738		
<i>H. pallidoflavodiscus</i>	GDGM89619	China: Yunnan	OQ860089	OQ867287	OR566097	
<i>H. pallidofulvus</i>	GDGM84470	China: Sichuan	OP547698	OP558690	OR566096	OR575284
<i>H. pallidofulvus</i>	GDGM84501	China: Sichuan	OP547700	OP558692	OR566095	OR575285
<i>H. pallidofulvus</i>	GDGM84502	China: Sichuan	OP547701	OP558693	OR566094	OR575286
<i>H. pallidofulvus</i>	GDGM84506	China: Sichuan	OP547702	OP558694	OR566093	OR575287
<i>H. orientipurpurascens</i>	GDGM83073	China: Yunnan	OP547678	OP558671	OR566092	OR575288
<i>H. pallidoagathosmus</i>	GDGM84681	China: Sichuan	OP547724	OP558716	OR566091	OR575289
<i>H. pallidoagathosmus</i>	GDGM84702	China: Sichuan	OP547728	OP558720	OR566090	OR575290

Table 1 Continued.

Species name	Voucher	Locality	ITS	LSU	<i>rpb2</i>	<i>tef1-a</i>
<i>H. pallidoagathosmus</i>	CFSZ22807	China: Inner Mongolia	OP547742	OP558608		
<i>H. pallidoagathosmus</i>	CFSZ22828	China: Inner Mongolia	OP547743	OP558609		
<i>H. parvirussula</i>	GDGM45208	China: Tibet	MT363822	OP558627	OR566089	OR575291
<i>H. parvirussula</i>	GDGM83135	China: Yunnan	OP547682	OP558674	OR566088	
<i>H. parvirussula</i>	GDGM85782	China: Sichuan	OP547732	OP558724	OR566087	OR575292
<i>H. parvirussula</i>	HMAS280347	China	MT363824	OP558730		
<i>H. parvirussula</i>	MHKMU N.K. Zeng 2878	China: Yunnan	MH160770	MH160774		
<i>H. penarioides</i>	DB4411	Hungary	MK088122	MK278196		
<i>H. pinophilus</i>	GDGM43348	China: Sichuan	OP547622	OP558612	OR566086	OR575293
<i>H. pinophilus</i>	GDGM43349	China: Sichuan	OP547623	OP558613	OR566085	OR575294
<i>H. pinophilus</i>	MHKMU H.Y. Huang 878	China: Yunnan	MZ605854	MZ605806		MZ614647
<i>H. pinophilus</i>	MHKMU L.P. Tang 3487	China: Yunnan	MZ605858	MZ605810		MZ614649
<i>H. pseudodiscoideus</i>	HMAS277088	China: Sichuan	OP547744	OP558727		
<i>H. pseudodiscoideus</i>	HMAS277234	China: Tibet	OP547745	OP558728		
<i>H. pseudohypothejus</i>	MHKMU T. Huang 477	China: Yunnan	MW762991	MW762779		
<i>H. pseudopurpurascens</i>	GDGM82365	China: Yunnan	OP547666	OP558659	OR566084	OR575295
<i>H. pseudopurpurascens</i>	GDGM83033	China: Yunnan	OP547676	OP558669	OR566083	OR575296
<i>H. pseudopurpurascens</i>	GDGM83197	China: Yunnan	OP547686	OP558678		
<i>H. pseudopurpurascens</i>	XHW6124 (HKAS 131101)	China	OP547763	OP558747		
<i>H. pseudopurpurascens</i>	XHW6336 (HKAS 131103)	China	OP547764	OP558749		
<i>H. pudorinus</i>	GDGM44321	China: Sichuan	OP547626	OP558616	OR566082	OR575297
<i>H. pudorinus</i>	GDGM44323	China: Sichuan	OP547628	OP558618	OR566081	OR575298
<i>H. pudorinus</i>	GDGM44328	China: Sichuan	OP547630	OP558620	OR566080	OR575299
<i>H. pudorinus</i>	GDGM84620	China: Sichuan	OP547718	OP558710	OR566079	OR575300
<i>H. pudorinus</i>	GDGM84701	China: Sichuan	OP547727	OP558719	OR566078	OR575301
<i>H. pudorinus</i>	AFTOL-ID 1723	USA: Colorado	DQ490631	DQ457678	DQ472725	GU187710
<i>H. qinggangjun</i>	GDGM83741	China: Yunnan	OP547688	OP558680	OR566077	OR575302
<i>H. qinggangjun</i>	MHKMU H.Y. Huang 724	China: Yunnan	MW290157	MW290224		MW928548
<i>H. qinggangjun</i>	MHKMU L.P. Tang 1683	China: Yunnan	MW290150	MW290221		
<i>H. qinggangjun</i>	MHKMU M. Mu 464	China: Yunnan	MW290155	MW290222		MW928546
<i>H. qinggangjun</i>	MHKMU S.D. Yang 20	China: Yunnan	MW290149	MW290220		MW928545
<i>H. queletii</i>	CFSZ12607	China	OP547734	OP558600		

Table 1 Continued.

Species name	Voucher	Locality	ITS	LSU	<i>rpb2</i>	<i>tef1-a</i>
<i>H. queletii</i>	CFSZ18527	China: Inner Mongolia	OP547735	OP558601		
<i>H. queletii</i>	CFSZ18958	China: Inner Mongolia	OP547736	OP558602		
<i>H. queletii</i>	CFSZ20283	China: Inner Mongolia	OP547740	OP558606		
<i>H. queletii</i>	HMAS 290046	China: Inner Mongolia	MZ605862	MZ605813		MZ614652
<i>H. roseoviolaceus</i>	SAAS4509	China: Chongqing	OQ860087	OQ867285		
<i>H. russula</i>	GDGM42113	China: Jilin	MT363802	OP558610	OR566076	
<i>H. russula</i>	AH19677	Spain: Torrelodones	MW290205	MW290260		
<i>H. russula</i>	AH37145	Spain: Huesca	MW290206	MW290261		
<i>H. russula</i>	CFMR JP-3	Japan: Shiga Prefecture	KF291216	KF291217	KF291219	
<i>H. rutilans</i>	GDGM89538	China: Yunnan	OQ860086	OQ867284	OR566075	
<i>H. rutilans</i>	XHW6661	China	OP547769	OP558756		
<i>H. rutilans</i>	XHW7521 (HKAS 131117)	China	OP547779	OP558767		
<i>H. scabrellus</i>	LAH 35245	Pakistan	MK066234	MK066238		
<i>H. siccipes</i>	GDGM70041	USA	OP547637	OP558628		OR575303
<i>H. siccipes</i>	GDGM75574	USA	OP547652	OP558644	OR566141	OR575304
<i>H. sichuanensis</i>	GDGM84471	China: Sichuan	OP547699	OP558691	OR566074	OR575305
<i>H. sichuanensis</i>	GDGM84546	China: Sichuan	OP547709	OP558701	OR566073	OR575306
<i>H. sichuanensis</i>	GDGM84557	China: Sichuan	OP547712	OP558704	OR566072	OR575307
<i>H. sordidus</i>	GDGM70065	USA	OP547644	OP558635		OR575308
<i>H. sp. 1</i>	GDGM83568	China: Gansu	OP547687	OP558679	OR566070	OR575311
<i>H. sp. 2</i>	GDGM79241	China: Jilin	OP547659	OP558652	OR566071	OR575310
<i>H. sp. 3</i>	XHW7387 (HKAS 131116)	China	OP547778	OP558766		
<i>H. sp. 4</i>	XML1910693	China	OP547780	OP558768		
<i>H. sp.</i>	GDGM70051	USA	OP547640	OP558631		OR575309
<i>H. sp.</i>	GDGM82406	China	OP547669	OP558662		
<i>H. sp.</i>	GDGM84469	China	OP547697	OP558689		
<i>H. sp.</i>	KUN-HKAS 112566 (QH 126)	China: Yunnan	MW762877	MW763002	MW789181	MW773441
<i>H. sp.</i>	KUN-HKAS 112567	China: Tibet	MW762878	MW763003	MW789182	MW773442
<i>H. sp.</i>	KUN-HKAS 112568 (QH 131)	China: Tibet	MW762879	MW763004	MW789183	MW773443
<i>H. sp.</i>	KUN-HKAS 87261 (Liu 713)	China: Jilin	MW616468	MW600487	MW656477	MW656466
<i>H. sp.</i>	Mushroom Observer 285692	USA: Arizona	MG783389	MG493163		
<i>H. sp.</i>	ZRL20151871	China	LT716040	KY418856	KY419003	KY419059
<i>H. speciosus</i>	HMAS 221453	China: Jilin	MW762992	MW762780		
<i>H. speciosus</i>	HMAS 278060	China	OP547746	OP558729		

Table 1 Continued.

Species name	Voucher	Locality	ITS	LSU	<i>rpb2</i>	<i>tef1-α</i>
<i>H. speciosus</i>	MHKMU H.Y. Huang 1010	China: Jilin	MW762993	MW762781		OK063806
<i>H. subcapreolarius</i>	GDGM43379	China: Sichuan	OP547625	OP558615	OR566069	
<i>H. subcapreolarius</i>	GDGM45123	China: Sichuan	OP547636	OP558626	OR566068	OR575312
<i>H. subcapreolarius</i>	GDGM82403	China: Yunnan	OP547668	OP558661	OR566067	OR575313
<i>H. subcapreolarius</i>	GDGM83194	China: Yunnan	OP547684	OP558676	OR566066	OR575314
<i>H. vividus</i>	GDGM82385	China: Yunnan	OP547667	OP558660	OR566065	OR575315
<i>H. vividus</i>	GDGM82437	China: Yunnan	OP547674	OP558667		
<i>H. vividus</i>	GDGM83100	China: Yunnan	OP547680	OP558672		
<i>H. vividus</i>	GDGM83196	China: Yunnan	OP547685	OP558677		
<i>H. vividus</i>	MHHNU32258	China: Yunnan	OP547755	OP558739		
<i>H. xiangjun</i>	LJW2256 (GDGM92371)	China: Yunnan	OP547753	OP558737		
<i>H. xiangjun</i>	MHKMU H.Y. Huang 817	China: Yunnan	MW762979	MW762768		
<i>H. xiangjun</i>	MHKMU Y.J. Pu 407	China: Yunnan	MW762978	MW762767		
<i>H. yadigaraii</i>	KATO Fungi 3843	Turkey	MF370227	MF370228		
<i>H. yukishiro</i>	SAAS4870	China: Sichuan	OQ860088	OQ867286		
<i>H. yunnanensis</i>	GDGM89522	China: Yunnan	OQ860084			
<i>H. yunnanensis</i>	MHKMU H.Y. Huang 321	China: Yunnan	MW290213	MW290272		MW928563
<i>H. yunnanensis</i>	MHKMU H.Y. Huang 322	China: Yunnan	MW290214	MW290273		MW928564
<i>H. yunnanensis</i>	MHKMU L.P. Tang 2772	China: Yunnan	MW290211	MW290268		MW928561
<i>H. yunnanensis</i>	MHKMU L.P. Tang 2773	China: Yunnan	MW290212	MW290269		MW928562

Results

Phylogenetic analysis

New sequences and alignments

In this study, 516 new sequences were generated: 165 ITS, 175 LSU, 82 *rpb2* and 94 *tef1- α* . The ITS dataset combining new sequences and available ITS sequences retrieved from GenBank and Unite included 1214 sequences and consisted of 1065 nucleotide sites (including gaps) of which 644 are parsimony informative (Fig. 1). And midpoint rooting was used for the ITS phylogenetic tree due to the ITS sequences of related genera could not be aligned with confidence. The multilocus dataset (ITS-nrLSU-*rpb2-tef1- α* dataset) (Table 1) comprised four partially overlapping loci (one sample has not less than two loci), and rooted with sequences of *Chrysomphalina* and *Haasiella* (Fig. 2). The multilocus alignment included 258 samples and consisted of 3272 nucleotide sites (including gaps), including 1539 parsimony informative sites.

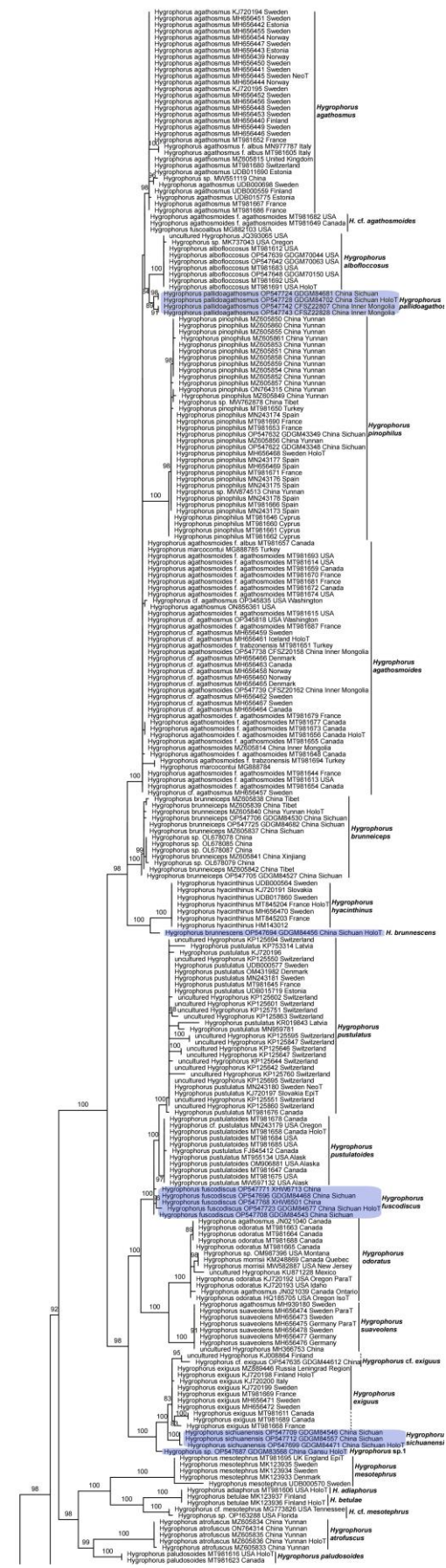


Figure 1 – ITS maximum likelihood (ML) tree of *Hygrophorus* specimens and environmental sequences. ML bootstrap values (MLBS) $\geq 80\%$ are shown around the nodes. Sequences of new species are highlighted in blue colour.

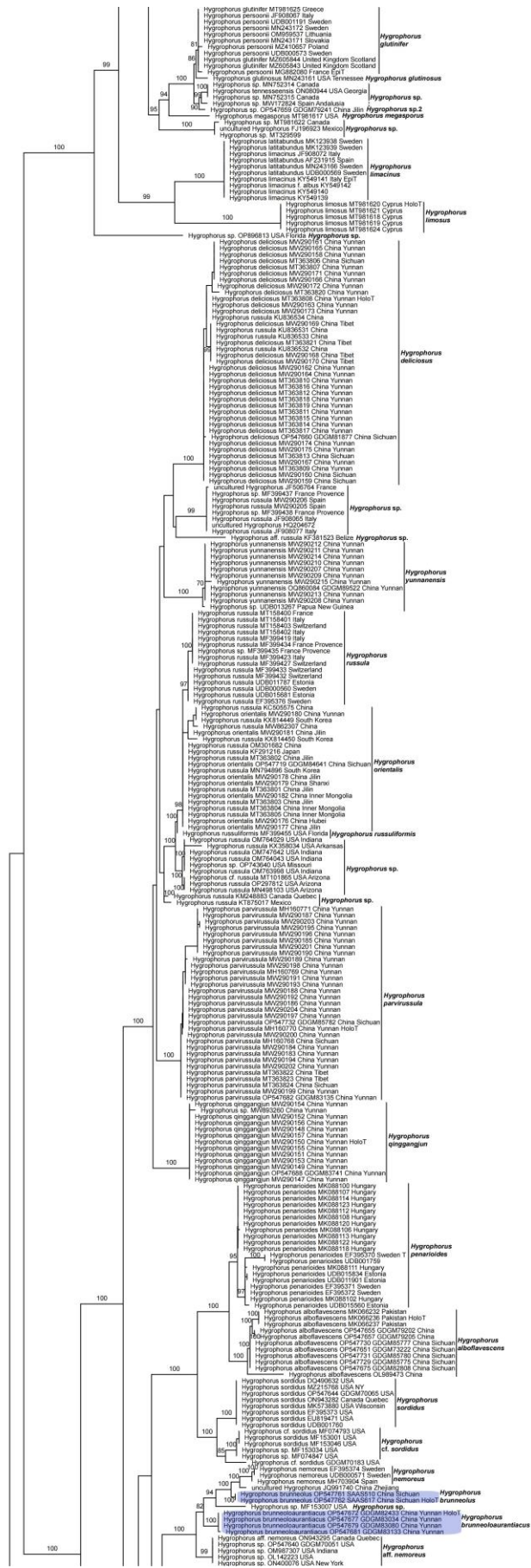


Figure 1 – Continued.

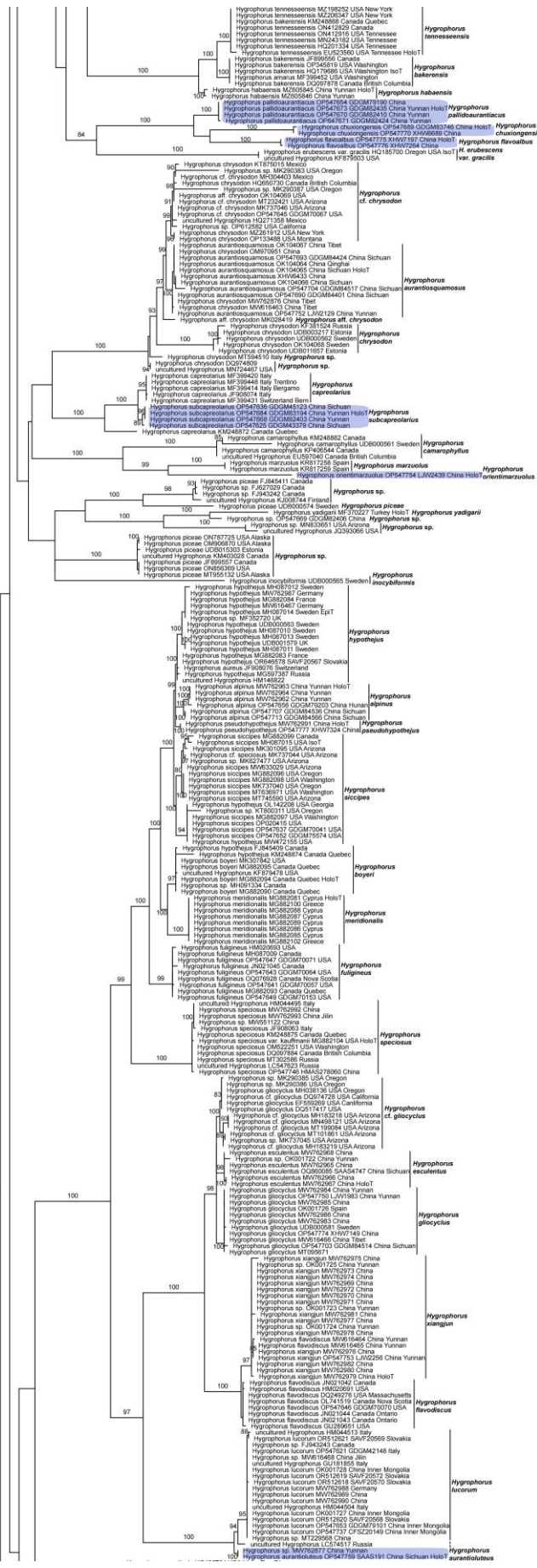


Figure 1 – Continued.

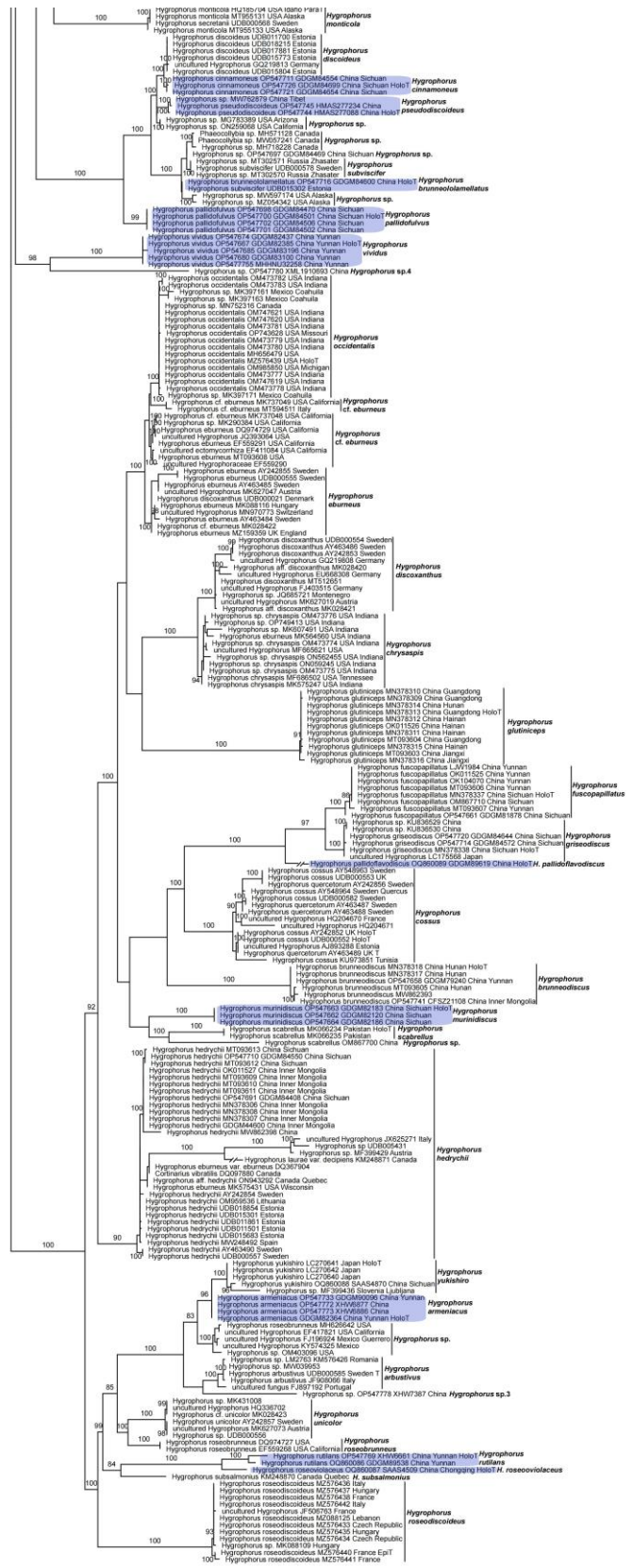


Figure 1 – Continued.

Meta-analysis of ITS rDNA sequences

To make a comprehensive overview of all available *Hygrophorus* ITS sequences, sequences downloaded from GenBank and Unite databases were included and sequences of compromised

quality were excluded. The following species names are labelled on over 20 *Hygrophorus* sequences in databases: 43 sequences labelled as *H. russula*, 42 as *H. annulatus*, 34 as *H. agathosmus*, 34 as *H. deliciosus*, 31 as *H. pinophilus*, 29 as *H. parvirussula*, 25 as *H. olivaceoalbus*, 20 as *H. hedrychii*, and 20 as *H. penarioides* (Fig. 1). While the following species names were used only for a single sequence in public databases (three of them from holotype): *H. adiaphorus* (holotype), *H. goetzei*, *H. griseodiscus* (holotype), *H. inocybiformis*, *H. megasporus*, *H. neoerubescens*, *H. secretanii*, *H. unicolor* and *H. yadigarii* (holotype). Moreover, 65 type (epitype, holotype, isotype, paratype, type) sequences were available for specific or infraspecific taxa. In addition, 4 sequences of *H. lucorum* newly generated from type locality were included.

In total, 1214 *Hygrophorus* ITS were included in the dataset. The full length of holotypes' ITS (ITS1-5.8S-ITS2) sequences ranged from 425 bps (*H. limosus*) to 601 bps (*H. vividus*). Amongst the ingroup sequences, 68 sequences (5.67%) generated from environmental samples (labelled as “uncultured ectomycorrhiza *Hygrophorus*”, “uncultured fungus”, “uncultured Hygrophoraceae” or “uncultured *Hygrophorus*”), the rest from basidiomata.

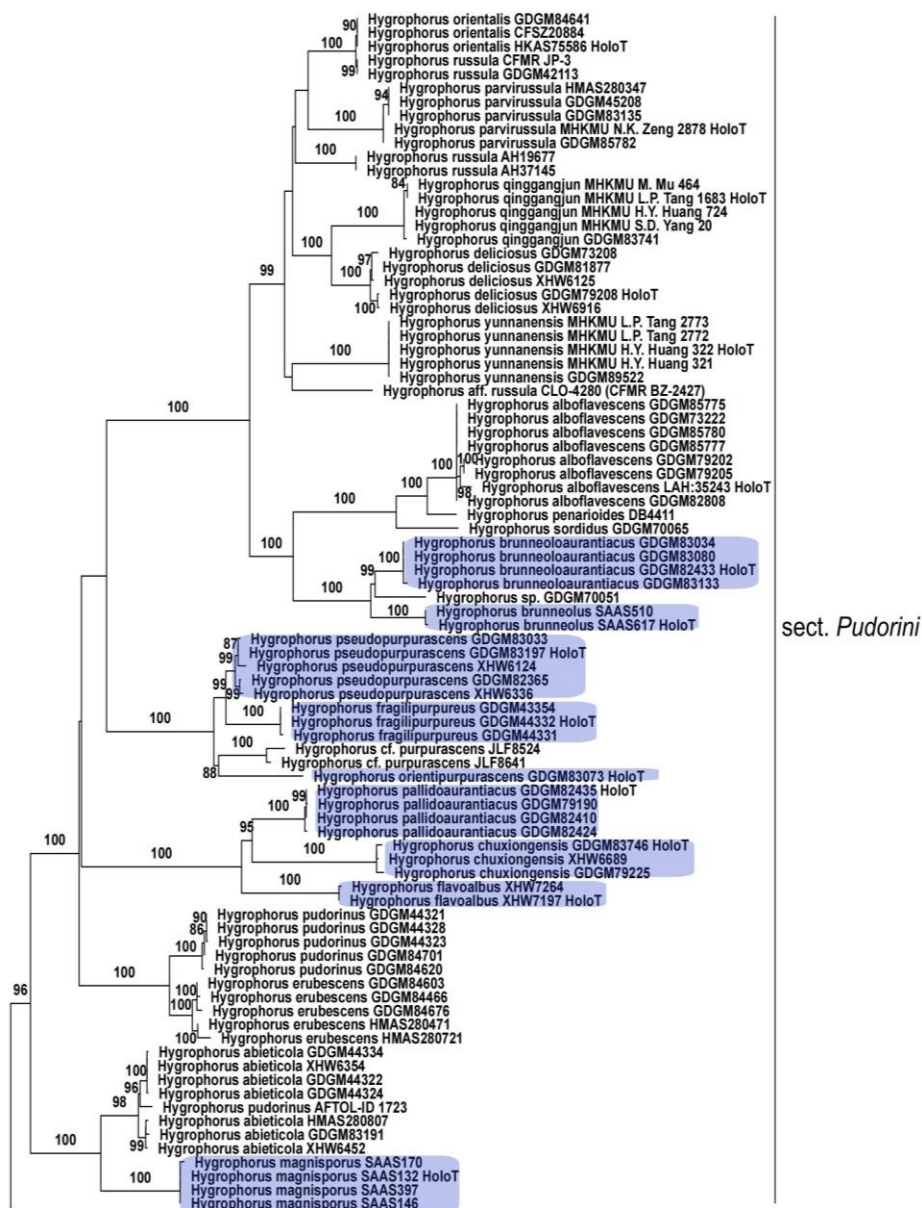


Figure 2 – Phylogeny of *Hygrophorus* inferred from the multilocus dataset (ITS/nrLSU/*rpb2/tefl-a*) using the maximum likelihood (ML) analysis. ML bootstrap values (MLBS) $\geq 70\%$ were showed around the nodes. Sequences of new species are highlighted in blue colour.

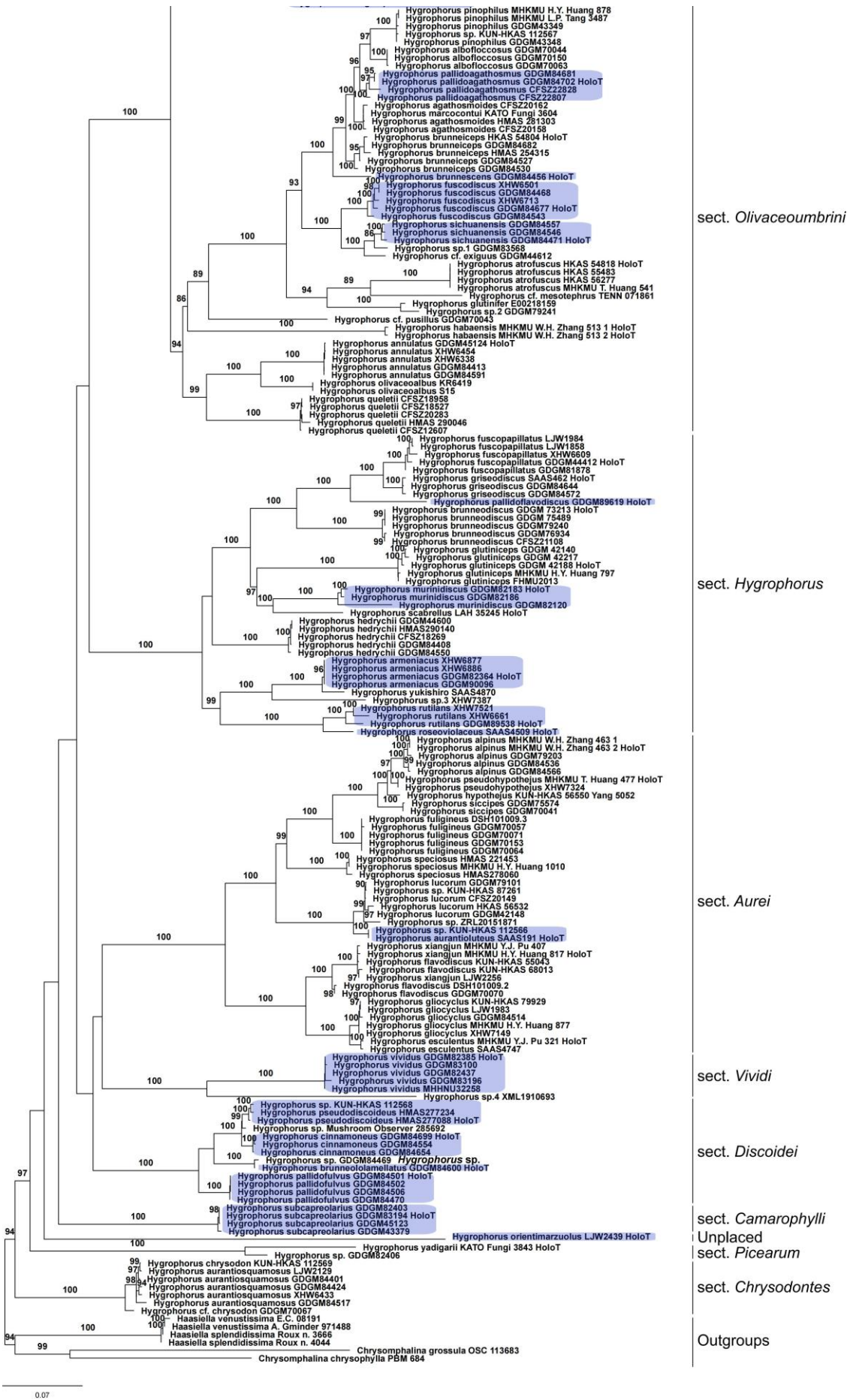


Figure 2 – Continued.

Analysis of multigene sequences

In the multilocus tree, the genus *Hygrophorus* is supported as a monophyletic lineage. There was not a support for three subgenera such as defined by Lodge et al. (2014) and the support received at higher rank nodes better suited to existing classification of the genus into sections. Our phylogeny supported eight of nine sections defined by Lodge et al. (2014): sections *Pudorini*, *Olivaceoumbrini*, *Hygrophorus*, *Aurei*, *Discoidei*, *Camarophylli* P. Karst., *Picearum*, and *Chrysodontes* (Singer) E. Larss. Because of strong support of the lineage that includes *H. vividus* C.Q. Wang, Ming Zhang & T.H. Li, sp. nov. and a single collection XML1910693 and their unresolved position within the tree, we proposed a new section *Vividi* C.Q. Wang, Ming Zhang & T.H. Li, sect. nov. for this species pair. The position of a single sequence of *H. orientimarzuolus* C.Q. Wang, J.W. Liu & T.H. Li, sp. nov. is unresolved and we did not place it in any of recognized sections.

Taxonomy

Below, the Chinese *Hygrophorus* species are described, illustrated and discussed. The descriptions are arranged alphabetically within the sections resolved by multilocus phylogenetic analyses (Fig. 2) in this study.

Hygrophorus sect. *Hygrophorus*

Phylogenetic support: Section *Hygrophorus* is well supported in both the ITS (MLBS = 100%) and multilocus (MLBS = 100%) trees (Figs 1–2).

Studied Chinese species included in this section: *Hygrophorus armeniacus*, *H. brunneodiscus*, *H. fuscopapillatus*, *H. glutiniceps*, *H. griseodiscus*, *H. hedrychii*, *H. murinidiscus*, *H. pallidoflavodiscus*, *H. roseoviolaceus*, *H. rutilans* and *H. yukishiro*.

Hygrophorus armeniacus C.Q. Wang, Ming Zhang, X.H. Wang & T.H. Li, sp. nov. Fig. 3

Index Fungorum Number: IF901126; Facesoffungi number: FoF14926

Etymology – *armeniacus* = apricot coloured, referring the apricot colour of the pileus.

Type – China, Yunnan Province, Diqing Tibetan Autonomous Prefecture, Shangri-la County, Pudacuo National Park, on moss in a subalpine forest dominated by *Quercus* sp., elev. ca. 3720 m, 3 September 2020, M. Zhang & L.Q. Wu (GDGM82364, Holotype).

Pileus 25–80 mm across, convex when young, becoming plano-convex, plane to depressed when mature, viscid when wet, white, yellowish white, light yellow, yellowish grey, greyish yellow, orange grey, greyish orange to brownish orange (4A1–5, 4B2–5, 5B2–4, 5C2–4), or pale apricot-coloured to pale greyish apricot-coloured, unchanging when bruised; margin decurved when young, straight to uplifted when mature, usually entire, sometimes irregularly splitted. *Lamellae* adnate to subdecurrent, subdistant, L = 30–35, l = 1–3, waxy, thick, fragile, white; edge entire and even. *Stipe* 35–65 mm long, 9–11 mm thick, central, cylindrical, equal or thinner upwards, stuffed, white, covered with tiny white dots. Context solid, whitish.

Basidiospores (7.5)8–10(10.5) × (4)4.5–6.5(7.5) μm, Lm = 9.19 ± 0.74, Wm = 5.59 ± 0.69, Q = (1.2)1.5–1.89(2), Qm = 1.66 ± 0.14, broadly ellipsoid, ellipsoid to elongate, smooth, hyaline, thin-walled. *Basidia* 36–65 × 7–10 μm, Q = 3.79–8.13, 4-spored, clavate, sterigmata 4–12 μm long. *Hymenophoral trama* divergent, made up of cylindrical, thin-walled, hyaline hyphae 3.5–23 μm wide. *Pileipellis* an ixotrichoderm, made up of upturned aerial hyphae 2–6.5 μm wide. *Stipitipellis* an ixotrichoderm to ixocutis, made up of repent or upturned cylindrical thin-walled hyphae 2–5.5 μm wide. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Solitary or scattered on the ground in forests dominated by oak trees, basidioma occurring in autumn, so far known from southwestern China.

Additional specimen examined – China, Yunnan Province, Ninglang County, Mianmian Mountain, elev. 3593 m, 27°32'31"N, 100°38'15"E, 26 May 2019, 22 September 2019, X.H. Wang, XHW6877 (HKAS 131110).

Notes – *Hygrophorus armeniacus* is characterized by the pale apricot-coloured to pale greyish apricot-coloured pileus, adnate with a short decurrent tooth and white lamellae, broadly ellipsoid, ellipsoid to elongate basidiospores, and the distribution in high elevation area (over 3500 m so far).

Hygrophorus yukishiro, originally described from Japan, is a sister species to *H. armeniacus* which is distinguished morphologically by the pale reddish-brown pileus surface with indistinct fibrils, the ellipsoid basidiospores measuring $6.5\text{--}10 \times 4.5\text{--}6.5 \mu\text{m}$, and early spring fruiting (Endo et al. 2018). Another similar species, *Hygrophorus arbustivus* differs in its ochraceous brown pileus and smaller basidiospores ($7.5\text{--}9.5 \times 4.5\text{--}5.5 \mu\text{m}$) (Candusso 1997). *Hygrophorus subsalmonius* A.H. Sm. & Hesler, described from North America, is distinguished from *H. armeniacus* by larger basidiomata, madder brown to rufous pileus and smaller basidiospores measuring $6.5\text{--}8 \times 3\text{--}5 \mu\text{m}$ (Hesler & Smith 1963, Bessette et al. 2012).

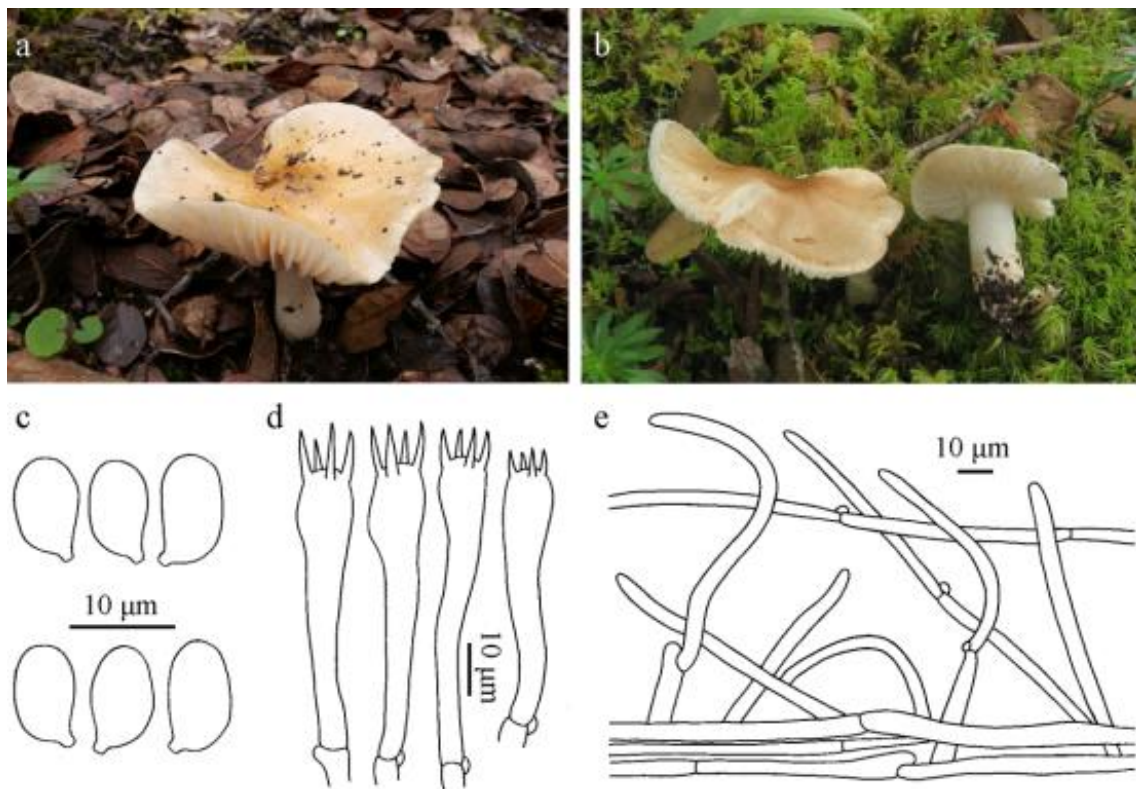


Figure 3 – *Hygrophorus armeniacus*. a Basidiomata (XHW6877, by X.H. Wang). b Basidiomata (GDGM82364). c Basidiospores (GDGM82364). d Basidia (GDGM82364). e Pileipellis (GDGM82364).

Hygrophorus brunneodiscus C.Q. Wang & T.H. Li, MycoKeys 68: 56 (2020)

Fig. 4

Pileus 20–50 mm broad, hemispherical to blunt conical when young, convex when mature, whitish, greyish-yellow, greyish-white, brownish-orange, light brown, yellowish-brown, paler from disc to margin, viscid. *Lamellae* subdecurrent to decurrent, white, waxy, subdistant, $L = 36\text{--}40$, $l = 1\text{--}3$; edge concolorous, entire. *Stipe* 40–90 mm long, 4–7 mm thick, cylindrical, hollow, subequal, pale yellow to greyish-yellow, white to yellowish-white at apex, sometimes white at base, sticky. *Context* thin, white to light brown, with slight fishy odour.

Basidiospores $(6.5)7\text{--}9(9.5) \times 4\text{--}5.5(6) \mu\text{m}$, $Lm = 7.7 \pm 0.69 \mu\text{m}$, $Wm = 4.65 \pm 0.51 \mu\text{m}$, $Q = (1.3)1.4\text{--}2(2.1)$, $Qm = 1.67 \pm 0.18$, ellipsoid to oblong, smooth. *Basidia* $32\text{--}48 \times 6\text{--}8.5 \mu\text{m}$, $Q = 4.1\text{--}6.6$, clavate, thin-walled, 4-spored; sterigmata $5.5\text{--}7(9) \mu\text{m}$ long. *Pileipellis* an ixotrichoderm, composed of septate cylindrical thin-walled hyphae $2.5\text{--}5 \mu\text{m}$ wide. *Hymenophoral trama* divergent, composed of septate, thin-walled and cylindrical hyphae $6\text{--}10 \mu\text{m}$ broad. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Solitary to scattered, on the ground of subtropical broad-leaf forest dominated by *Quercus* sp., so far only known from Hunan Province in South Central China.

Specimens examined – China, Hunan Province, Zhangjiajie City, Zhangjiajie Campus of Jishou University, in a forest dominated by *Quercus fabri* and *Q. serrata*, elev. ca. 220 m, 29°8'24"N, 110°27'42"E, 26 May 2019, W.Q. Qin (GDGM73213, Holotype); ibidem, 26 October 2018, W.Q. Qin (GDGM75489); ibidem, 30 June 2019, W.Q. Qin (GDGM76934).

Notes – *Hygrophorus brunneodiscus* was described from southwestern China by Wang et al. (2020). It is characterized by the brownish pileus centre and its distribution in subtropical forests at low elevation. *Hygrophorus brunneodiscus* is similar to *H. cossus*, *H. discoxanthus*, *H. eburneus* and *H. scabrellus*. However, *H. cossus* has pale ochraceous grey colour at the pileus centre and slender basidia ($48\text{--}60 \times 7\text{--}8.5 \mu\text{m}$) (Larsson & Jacobsson 2004); *H. discoxanthus* has rusty brown discolouration at lamellar edges and its association with *Fagus* (Candusso 1997, Larsson & Jacobsson 2004); *H. eburneus* has a white or ivory pileus and is associated with *Fagus* (Larsson & Jacobsson 2004); *H. griseodiscus* has grey pileus with a dark grey to olive grey disc and emarginate to subdecurrent lamellae (Wang et al. 2020); *H. scabrellus* described from South Western Himalaya in Pakistan has the off-white pileus with dark green and greyish fibrils and smaller basidiospores (in average $6.5 \times 3.84 \mu\text{m}$) (Naseer et al. 2019). For detailed descriptions and comparisons with similar species of *H. brunneodiscus* see Wang et al. (2020).

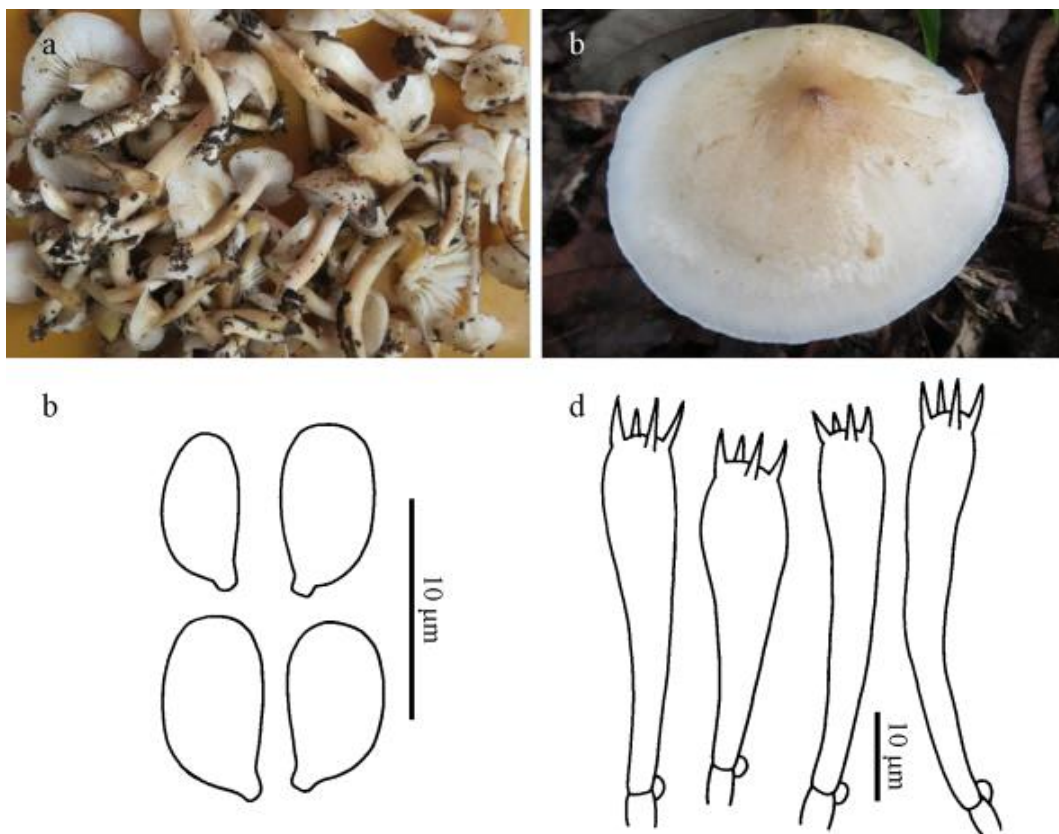


Figure 4 – *Hygrophorus brunneodiscus* (GDGM73213). a–b Basidiomata (by W.Q. Qin). c Basidiospores. d Basidia.

Hygrophorus fuscopapillatus C.Q. Wang & T.H. Li, MycoKeys 68: 58 (2020)

Fig. 5

Pileus 20–30 mm broad, convex or broadly conical to hemispherical when young, appanate to plano-concave when mature, with a papilla or small umbo at centre, white, pale grey, grey, brownish grey to olive brown at papilla, paler from centre to margin, glutinous when wet; margin even, occasionally split, white to pale grey at margin. *Lamellae* adnate to subdecurrent, white, thick, L = 28–36, l = 1–3. *Stipe* 40–60 mm long, 4–5 mm wide, cylindrical, white to yellowish-grey, covered with a glutinous layer, often with white mycelium at base. *Context* thin, whitish.

Basidiospores (6)7–9.5(10) × (4)4.5–5.5(6) μm, Lm = 8.16 ± 0.83 μm, Wm = 4.97 ± 0.45 μm, Q = 1.3–1.9, Qm = 1.65 ± 0.18, broadly ellipsoid, ellipsoid to oblong, smooth, hyaline. *Basidia* (32)35–46(48) × (6)6.5–8.5(9) μm, Q = 4.4–6.8, clavate, thin-walled, 4-spored; sterigmata 5–7.5 μm long. *Pileipellis* an ixotrichoderm, composed of septate and thin-walled cylindrical hyphae 3–5 μm broad. *Hymenophoral trama* divergent, composed of septate, thin-walled and cylindrical hyphae 13–31.5 μm broad. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Solitary, on the ground of Fagaceae dominated forests, so far only known from Sichuan and Yunnan provinces in Southwest China.

Specimens examined – China, Sichuan Province, Panzhihua City, Yanbian County, Gesala Ecotourism Area, elev. ca. 2900 m, 27°08'10"N, 101°11'33"E, 25 August 2013, M. Zhang & C.Q. Wang (GDGM44412, Holotype). Yunnan Province, Yulong County, Lijiang Alpine Botanic Garden, in a forest dominated by *Quercus pannosa*, elev. 3281 m, 27°00'26"N, 100°11'09"E, 13 September 2019, J.W. Liu, LJW1984 (GDGM92369).

Notes – *Hygrophorus fuscopapillatus* was described from China by Wang et al. (2020). It is characterized by the brownish-grey to olive brown papilla in the pileus centre, and the broadly ellipsoid, ellipsoid to oblong basidiospores. *Hygrophorus brunneodiscus* and *H. griseodiscus* are similar to *H. fuscopapillatus*. However, *H. brunneodiscus* has the broader pileus (up to 5 cm in diam.) and the brownish pileus disc; *H. griseodiscus* has the larger pileus (up to 4.5 cm broad), the larger basidiospores measuring (7)8–10(10.5) × (4)4.5–6(6.5) μm in size, and the host association with Pinaceae. For images, line drawings, detailed descriptions, and comparisons with species similar to *H. fuscopapillatus* see Wang et al. (2020).

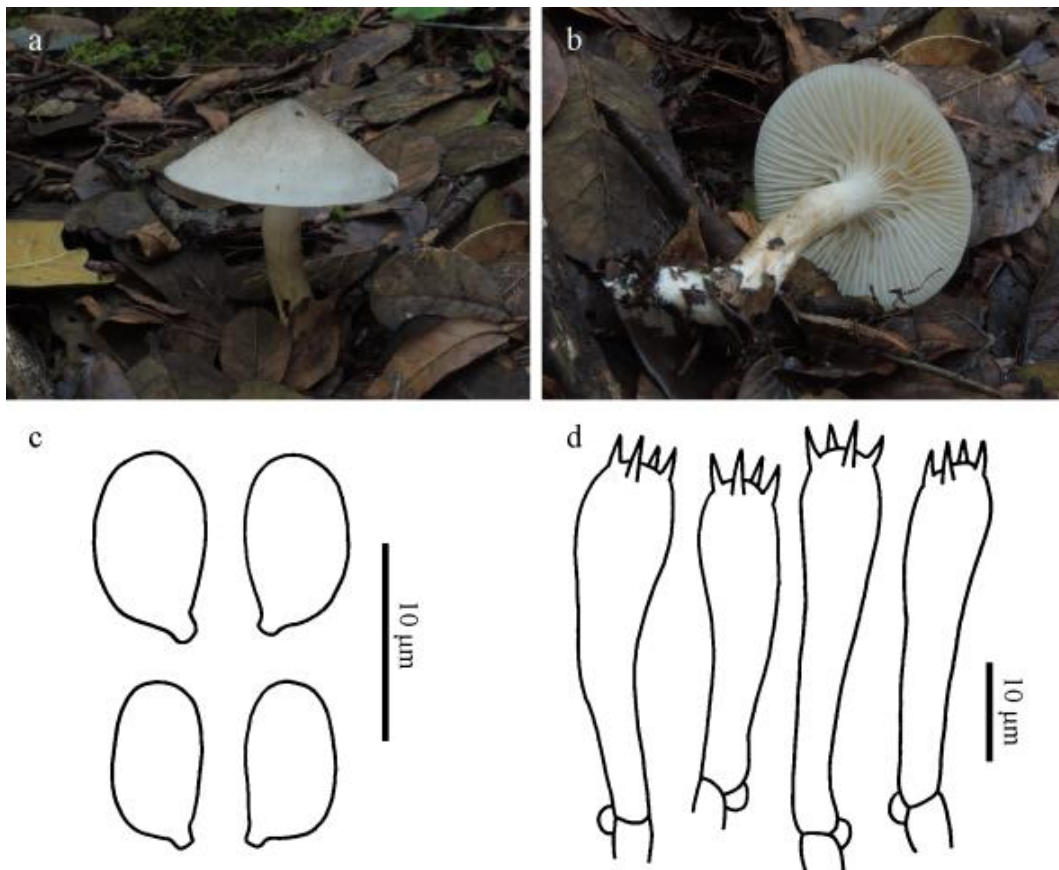


Figure 5 – *Hygrophorus fuscopapillatus* (LJW1984). a–b Basidiomata. c Basidiospores. d Basidia.

Hygrophorus glutiniceps C.Q. Wang & T.H. Li, MycoKeys 68: 60 (2020)

Fig. 6

Pileus 8–40 mm broad, hemispherical to convex at first, broad-convex to depressed at maturity, white with cream or light yellow to orange tint at disc when young, becoming light to yellowish-brown with age, covered with a layer of transparent gluey materials when wet; margin

involute when young, slightly incurved to rarely uplifting when mature. *Lamellae* broadly adnate or with a decurrent tooth when young, subdecurrent when mature, distant to subdistant, $L = 24\text{--}48$, $l = 1\text{--}3$, white when young, then changing to ochraceous or even brown, waxy when wet. *Stipe* 25–60 mm long, 3–6 mm broad, equal but often tapered at base, cylindrical, usually curved, white, occasionally with yellowish tint, covered with transparent glutinous materials when wet. *Context* thin, white when young, changing to brown when old.

Basidiospores $(5)6\text{--}8.5(10) \times (3.5)4\text{--}5.5(6) \mu\text{m}$, $L_m = 7.11 \pm 0.79 \mu\text{m}$, $W_m = 4.7 \pm 0.59 \mu\text{m}$, $Q = (1.2)1.3\text{--}1.77(2)$, $Q_m = 1.52 \pm 0.14$, ellipsoid to oblong, smooth, hyaline. *Basidia* $35\text{--}47 \times 5\text{--}8.5 \mu\text{m}$, $Q = 4.67\text{--}8.2$, 4-spored, clavate, thin-walled, hyaline; sterigmata up to $7.5 \mu\text{m}$ long. *Pileipellis* an ixotrichoderm, composed of septate and thin-walled hyphae $3\text{--}5 \mu\text{m}$ wide, usually covered with a gelatinous layer, with yellowish gluten in KOH. *Stipitipellis* an ixotrichoderm, composed of thin-walled hyphae $3\text{--}5 \mu\text{m}$ wide. *Hymenophoral trama* divergent, composed of septate, thin-walled and cylindrical hyaline hyphae $4\text{--}17 \mu\text{m}$ broad. *Clamp connections* present in all tissues.

Habit, habitat and Distribution – Gregarious to scattered, on the ground of subtropical broad-leaf forest dominated by *Castanopsis* spp., currently only known from subtropical to tropical areas of China (Guangdong, Hainnan, Hunan and Jiangxi provinces).

Specimens examined – China, Guangdong Province, Guangzhou City, Tianluhu Forest Park, in a forest dominated by *Castanopsis* spp., elev. ca. 250 m, $23^\circ 13' 39''\text{N}$, $113^\circ 25' 53''\text{E}$, 6 September 2012, M. Zhang (GDGM42188, GDGM42217); ibidem, 6 September 2012, J. Xu (GDGM42140). Hainan Province, Changjiang County, 3 July 2013, M. Zhang (GDGM45220). Jiangxi Province, Chongyi County, Yangling Forest Park, 31 August 2016, M. Zhang (GDGM53153).

Notes – *Hygrophorus glutiniceps* is characterized by its white and sticky pileus and stipe, whitish lamellae sometimes changing to ochraceous or even brown, the subtropical to tropical distribution in East Asia, and the association with *Castanopsis*. *Hygrophorus cossus* looks similar but has longer basidiospores ($7\text{--}9.5 \mu\text{m}$ long), and is associated with *Quercus* in temperate areas (Candusso 1997). *Hygrophorus eburneus* differs in the sturdier basidiomata, larger basidiospores ($8\text{--}10 \times 4.5\text{--}5.5 \mu\text{m}$), and the association with *Fagus*. For more detailed descriptions, comparisons with similar species, and line drawings of *H. glutiniceps* see Wang et al. (2020).

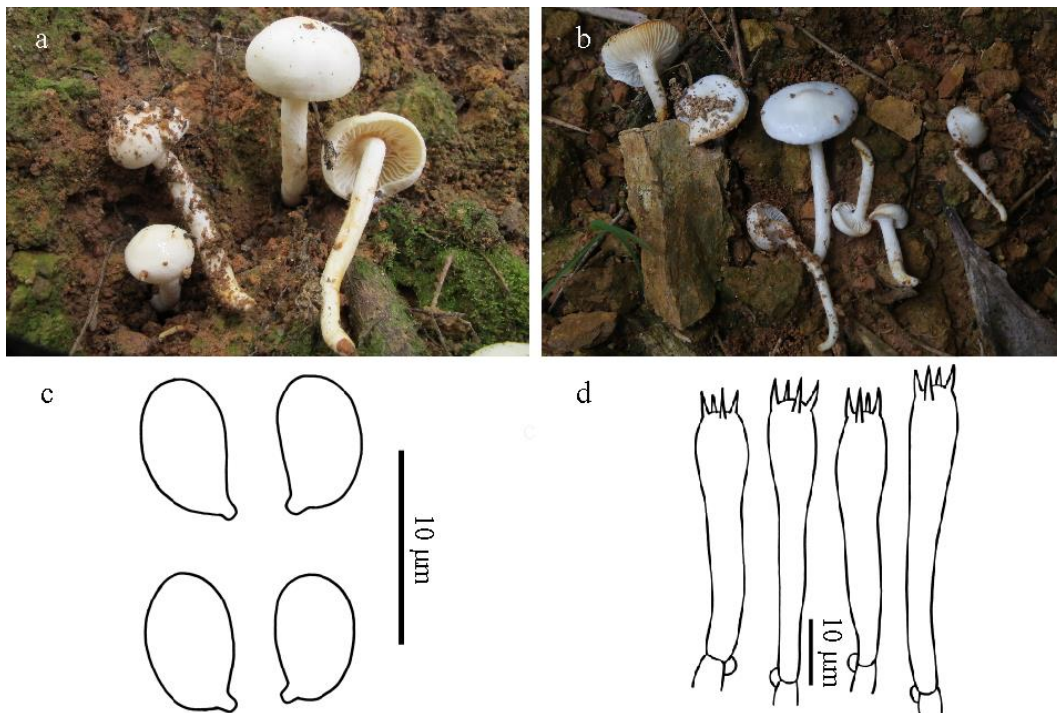


Figure 6 – *Hygrophorus glutiniceps*. a Basidiomata (GDGM42188). b Basidiomata (GDGM53153). c Basidiospores (GDGM42188). d Basidia (GDGM42188).

Hygrophorus griseodiscus C.Q. Wang & T.H. Li, MycoKeys 68: 64 (2020)

Fig. 7

Pileus 20–45 mm broad, convex, with or without an obtuse umbo, grey, light grey, dark grey to olive grey at disc, glutinous when wet; margin even, slightly involuted to extended, white to pale grey. *Lamellae* emarginate with a decurrent tooth or subdecurrent, white, thick, subdistant to close, $L = 32\text{--}40$, $l = 1\text{--}3$. *Stipe* 40–70 mm long, 4–6 mm wide, cylindrical to subcylindrical, white to pale grey, covered with transparent glutinous materials when wet. *Context* slightly thick, white.

Basidiospores $(7)8\text{--}10(10.5) \times (4)4.5\text{--}6(6.5) \mu\text{m}$, $Lm = 9.05 \pm 0.83 \mu\text{m}$, $Wm = 5.14 \pm 0.54 \mu\text{m}$, $Q = 1.4\text{--}2.1$, $Qm = 1.77 \pm 0.19$, ellipsoid, oblong to subcylindrical, smooth, hyaline. *Basidia* $29\text{--}56.5 \times 7\text{--}11 \mu\text{m}$, $Q = 3.05\text{--}6(6.9)$, clavate to cylindrical, thin-walled, 4-spored; sterigmata up to 6 μm long. *Pileipellis* an ixotrichoderm, composed of thin-walled hyphae 2.5–6 μm wide. *Hymenophoral trama* divergent, composed of septate, thin-walled and cylindrical hyphae 5.5–20 μm broad. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Scattered, on the ground of subalpine coniferous forest dominated by *Abies* and *Picea*, often surrounded by mosses, so far only known from Sichuan Province in Southwest China.

Specimens examined – China, Sichuan Province, Jiuzhaigou County, Jiuzhaigou, elev. ca. 3100 m, 11 September 2012, X.L. He (SAAS462, Holotype); same locality, 19 September 2020, M. Zhang (GDGM84644).

Notes – *Hygrophorus griseodiscus* was recently described from southwestern China, it is a relatively rare fungus (Wang et al. 2020). It is characterized by the dark grey to olive grey pileus disc, emarginate to subdecurrent lamellae, and the association with conifer trees. *Hygrophorus brunneodiscus* and *H. cossus* are similar to *H. griseodiscus*. However, *H. brunneodiscus* has the brownish pileus and smaller basidiospores measuring $6.5\text{--}9.5 \times 4\text{--}5 \mu\text{m}$; *H. cossus* has the greyish-white lamellae with a cream yellow tint, and a thicker stipe (6–20 mm wide) (Candusso 1997, Campo 2015). For detailed descriptions, comparisons with similar species, line drawings and images of *H. griseodiscus* see Wang et al. (2020).

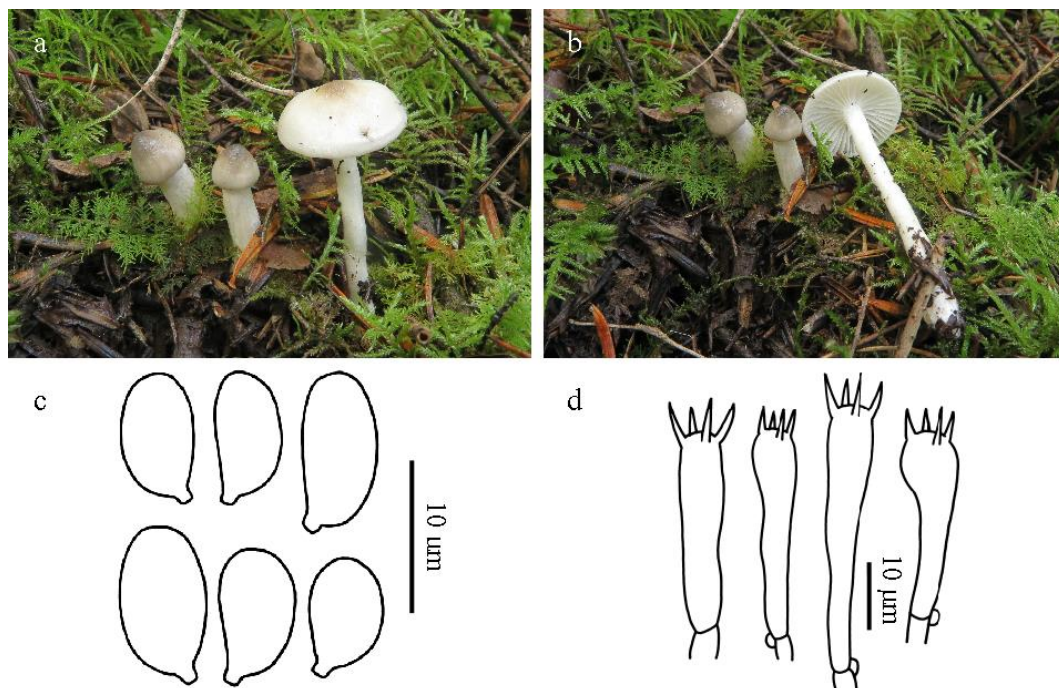


Figure 7 – *Hygrophorus griseodiscus* (GDGM84644). a–b Basidiomata. c Basidiospores. d Basidia.

Hygrophorus hedrychii (Velen.) K. Kult, Česká Mykol. 10(4): 232 (1956)

Fig. 8

Pileus 20–70 mm broad, subglobose when young, hemispherical to convex when mature; margin incurved when young; surface covered with a sticky layer, whitish. *Lamellae* adnate to short

decurrent, white at first, cream, pale yellow to pinkish-white at maturity, waxy, $L = 32\text{--}48$, $l = 1\text{--}3$. *Stipe* 30–130 mm long, 5–13 mm broad, almost cylindrical, whitish. *Context* thick, whitish.

Basidiospores $(6)7\text{--}8(9) \times (3.5)4\text{--}4.5(5) \mu\text{m}$, $Lm = 7.53 \pm 0.69$, $Wm = 4.19 \pm 0.36$, $Q = 1.5\text{--}2(2.3)$, $Qm = 1.81 \pm 0.21$, ellipsoid to subcylindrical, colourless, thin-walled, smooth. *Basidia* $30\text{--}40 \times 6\text{--}9 \mu\text{m}$, $Q = 4.1\text{--}5.7$, clavate, 4-spored; sterigmata 4–5 μm long. *Pileipellis* an ixotrichoderm, composed of septate, thin-walled hyphae 4–5 μm broad. *Stipitipellis* a trichoderm, composed of hyphae 7–10 μm broad. *Hymenophoral trama* divergent, composed of septate, thin-walled and cylindrical hyphae 3–23 μm broad. *Clamp connections* present.

Habit, habitat and distribution – Scattered to gregarious in *Betula* dominated forests, so far known from north-eastern and south-western China (Heilongjiang Province, Inner Mongolia Autonomous Region and Tibet Autonomous Region) and Europe (Larsson & Jacobsson 2004, Campo 2015, Huang 2022, Wang et al. 2020, this study).

Specimens examined – China, Inner Mongolia Autonomous Region, Chifeng City, Hexigten Banner, Jingpeng Town, 15 August 2017, T.Z. Liu & G.L. Yu (CFSZ18269). Sichuan Province, Songpan County, Erdaohai, in a subalpine forest, elev. ca. 3385 m, 23 September 2020, M. Zhang & J.H. Xing (GDGM84408).

Notes – *Hygrophorus hedrychii* was described from Europe and pan-arctic distributed so far. *Hygrophorus hedrychii* appears in the basal clade in the ITS analysis (Fig. 1). For more detailed descriptions and comparisons with similar species of *H. hedrychii* see Wang et al. (2020).

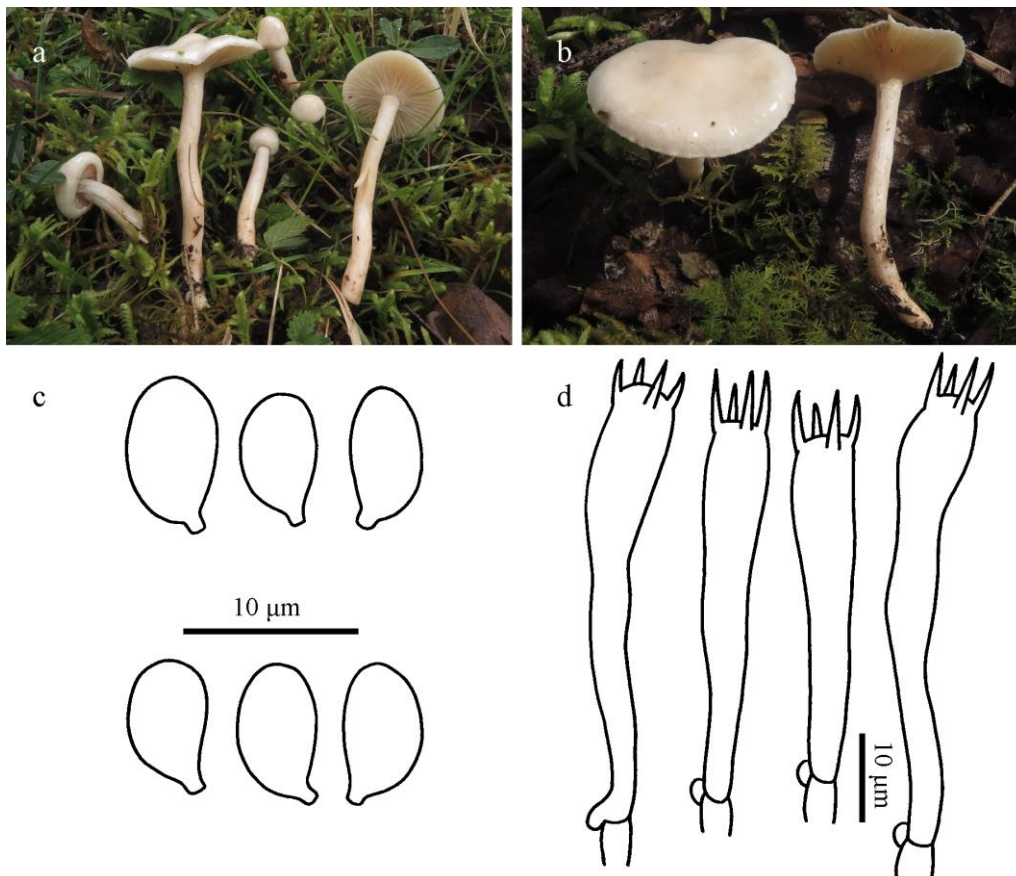


Figure 8 – *Hygrophorus hedrychii* (GDGM84408). a–b Basidiomata. c Basidiospores. d Basidia.

Hygrophorus murinidiscus C.Q. Wang & T.H. Li, sp. nov.

Fig. 9

Index Fungorum Number: IF901127; Facesoffungi number: FoF14927

Etymology – *murinidiscus*, from *murini* = mouse grey, and *discus* = disc, referring to its mouse grey central disc of pileus.

Type – China, Sichuan Province, Xiaojin County, Meiwo Town, in a *Quercus* spp. dominated forest, elev. ca. 3100 m, 3 August 2020, C.Q. Wang (GDGM82183, Holotype).

Pileus 25–65 mm across, conico-convex to convex when young, then expanded to convex to plano-convex, with or without an obtuse umbo, greyish yellow, yellowish grey to olive brown (4C2–5, 4D2–5, 4E3–5) at disc, paler to white, yellowish white, yellowish grey to greyish yellow (4A1–3, 4B2–3) out of the centre, viscid to sticky when wet; margin incurved when young, becoming straight to partially uplifted when mature. *Lamellae* adnexed to adnate at first, then subdecurrent, subdistant, L = 40–52, l = 1–3, thickish, waxy, sometimes translucent, sometimes crisped, white, even at edge. *Stipe* 50–70 mm long, 7–14 mm broad, cylindrical, equal or slightly enlarged in lower middle, often narrower at apex and base, usually curved, white, slightly fibrillose. *Context* white, thin in pileus. Odour pleasant. Spore deposit white.

Basidiospores 7–9.5 × 4–5.5 μm, Lm = 7.82 ± 0.80, Wm = 4.5 ± 0.46, Q = 1.5–2.1, Qm = 1.75 ± 0.18, ellipsoid, elongate, cylindrical, smooth, hyaline, thin walled, inamyloid. *Basidia* 43–52 × 7–8.5 μm, Q = 5.5–6.9, 4-spored, clavate; sterigmata up to 9 μm long. *Hymenophoral trama* divergent, made up of cylindrical or inflated hyaline hyphae, 3.5–18 μm broad. *Pileipellis* an ixotrichoderm, made up of erected and interwoven, gelatinized, often curved hyphae, 3–7 μm wide, usually with brown intracellular pigment. *Stipitipellis* an ixotrichoderm, consisting of cylindrical, thin-walled hyphae 3–6 μm wide, erected or interwoven, often curved, sometimes with intraparietal brown pigment. *Clamp connections* present in all tissues.

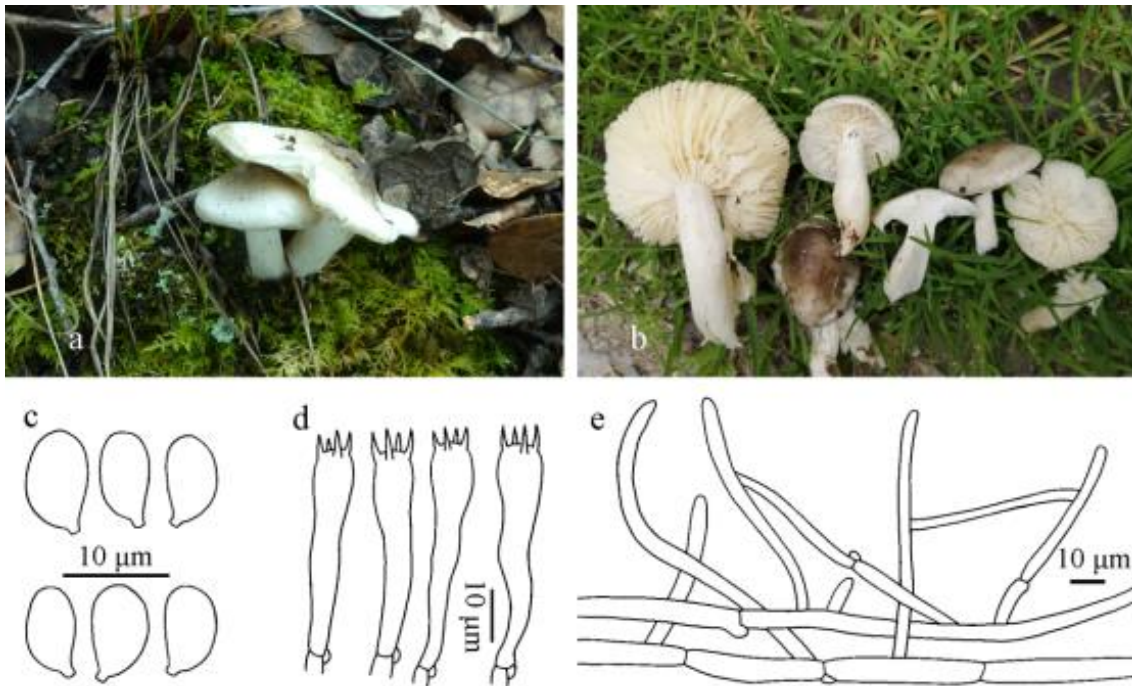


Figure 9 – *Hygrophorus murinidiscus* (GDGM82183). a–b Basidiomata. c Basidiospores. d Basidia. e Pileipellis.

Habit, habitat and distribution – Solitary to scattered on the ground under *Quercus* trees, occurring in summer, so far known from southwestern China (Sichuan Province).

Additional specimens examined – China, Sichuan Province, Xiaojin County, Meiwo Town, in a forest dominated by *Quercus* sp., elev. ca. 3100 m, 1 August 2020, C.Q. Wang (GDGM82120, GDGM82186).

Notes – *Hygrophorus murinidiscus* is characterized by the mouse grey pileus, the diameter of the pileus is similar to the length of the stipe, the adnexed, adnate to subdecurrent lamellae, the association with *Quercus* trees, and the distribution in high elevation areas (over 3000 m so far). In the ITS phylogenetic analysis (Fig. 1), *H. scabrellus* is sister to *H. murinidiscus*, however,

H. scabrellus is different from *H. murinidiscus* by the smaller and off-white with dark green coloured pileus (24–28 mm in diam.), smaller basidiospores (average $6.5 \times 3.84 \mu\text{m}$) (Naseer et al. 2019). *Hygrophorus brunneodiscus* differs from *H. murinidiscus* by its brown tint on pileus disc, and its distribution in subtropical and low elevation areas.

Hygrophorus pallidoflavodiscus C.Q. Wang, X.L. Gao & T.H. Li, sp. nov.

Fig. 10

Index Fungorum Number: IF901128; Facesoffungi number: FoF14928

Etymology – *pallidoflavodiscus*, from *pallido* = pale, *flavo* = yellow, and *discus* = disc, referring to its light-yellow pileus disc.

Type – China, Yunnan Province, Dali Prefecture, Binchuan County, in a mixed broadleaf-conifer forest, elev. ca. 2400 m, 24 August 2022, X.L. Gao (GDGM89619, Holotype).

Pileus 20–40 mm across, conical when young, then expanded to convex, with an umbo, greyish white, yellowish white to white at disc, viscid to sticky when wet; margin incurved when young, expanding to straight when mature. *Lamellae* adnate, subdistant, $L = 40\text{--}52$, $l = 1\text{--}3$, thickish, waxy, whitish, even at edge. *Stipe* 50–80 mm long, 7–9 mm broad, cylindrical, sometimes curved, nearly equal or tapered downward, glutinous, white, with transparent dots at the apex. *Context* white, thin in pileus.

Basidiospores $(7.5)8\text{--}10(10.5) \times (4)4.5\text{--}5.5 \mu\text{m}$, $Lm = 9.33 \pm 0.79$, $Wm = 5.13 \pm 0.39$, $Q = (1.36)1.6\text{--}2(2.38)$, $Qm = 1.83 \pm 0.2$, ellipsoid, elongate to cylindrical, smooth, hyaline, thin walled. *Basidia* $37\text{--}50 \times 6.5\text{--}9 \mu\text{m}$, $Q = 4.4\text{--}6$, 4-spored, clavate; sterigmata up to $5 \mu\text{m}$ long. *Hymenophoral trama* divergent, made up of cylindrical or inflated hyaline hyphae, $4\text{--}20 \mu\text{m}$ broad. *Pileipellis* an ixotrichoderm, made up of repent and erected, gelatinized, sometimes curved hyphae, $3\text{--}7 \mu\text{m}$ wide, usually with brown intracellular pigment. *Stipitipellis* an ixotrichoderm, consisting of repent, erected or interwoven, cylindrical, sometimes curved, thin-walled hyphae $3\text{--}6 \mu\text{m}$ broad, sometimes with brown intracellular pigment. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Scattered to gregarious on the ground in a mixed broadleaf-conifer forest, occurring in autumn, known from Yunnan Province of China.

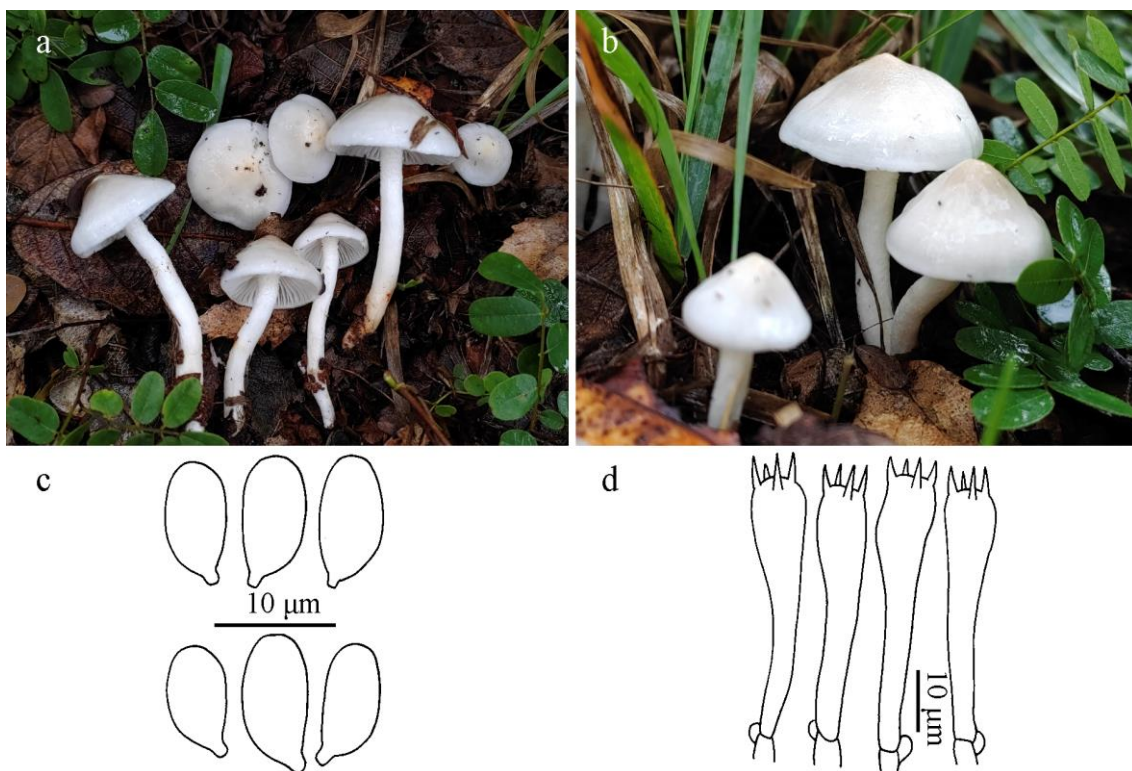


Figure 10 – *Hygrophorus pallidoflavodiscus* (GDGM89619). a–b Basidiomata (by X.L. Gao). c Basidiospores. d Basidia.

Notes – *Hygrophorus pallidoflavodiscus* is distinguished by the yellowish white to white umbo at disc, the ellipsoid, elongate to cylindrical basidiospores measuring $(7.5)8\text{--}10(10.5) \times (4)4.5\text{--}5.5 \mu\text{m}$. Amongst the known members of subsect. *Hygrophorus*, the most similar species is *isglutiniceps*, which also has yellowish tint on pileus disc, but differs by the hemispherical to convex pileus, the darkening lamellae when mature or wounded, the subtropical-tropical distribution, and shorter basidiospores measuring $(5)6\text{--}8.5(10) \times (3.5)4\text{--}5.5(6) \mu\text{m}$ (Wang et al. 2020). *Hygrophorus fuscopapillatus* is also similar by having distinct papilla in the pileus centre, but differs by its brownish-grey to olive brown near pileus centre, solitary habit, and shorter basidiospores measuring $(6)7\text{--}9.5(10) \times (4)4.5\text{--}5.5(6) \mu\text{m}$ (Wang et al. 2020).

Hygrophorus roseoviolaceus C.Q. Wang, Xiao Lan He & T.H. Li, sp. nov.

Fig. 11

Index Fungorum Number: IF901129; Facesoffungi number: FoF14929

Etymology – *roseoviolaceus*, from *roseo* = rose or pink, and *violaceus* = violet, referring to its light rose to light violet pileus.

Type – China, Chongqing City, Chengkou County, Beipin Town, in a mixed broadleaf-conifer forest, 13 October 2022, X.L. He (SAAS4509, Holotype).

Pileus 30–60 mm across, convex when young, broadly convex to plano-convex when mature, with or without an obtuse umbo, dull red, greyish red, greyish brown, violet brown, rose, greyish rose, brownish violet (10B3–5, 10C3–5, 10D3–5, 10E3–5, 11A3–5, 11B3–5, 11C3–5, 11D3–5), with violet brown (10E5–8, 10F5–8, 11E6–8, 11F6–8) disc and margin in exsiccata, viscid when wet; margin always incurved, usually darker than the submarginal area. *Lamellae* subdecurrent to decurrent, subdistant, L = 40–52, l = 1–3, thickish, waxy, sometimes crisped, whitish, yellowish white to yellowish in mature exsiccata, yellowish to brownish in exsiccata, even at edge. *Stipe* 60–100 mm long, 7–10 mm broad, cylindrical, equal or taper downward, white to yellowish white, usually floccose at the apex, usually curved at the lower part. *Context* whitish.

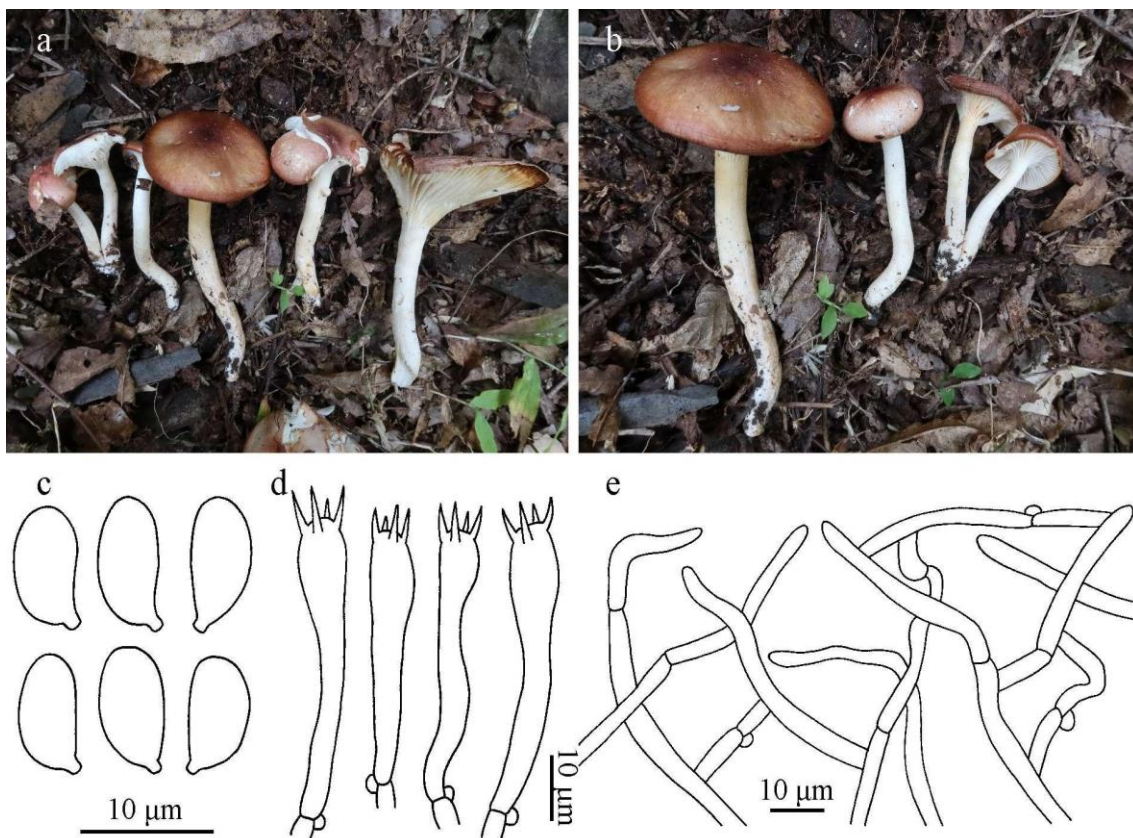


Figure 11 – *Hygrophorus roseoviolaceus* (SAAS4509). a–b Basidiomata. c Basidiospores. d Basidia. e Pileipellis.

Basidiospores (7)7.5–9(9.5) × 4–5 µm, $L_m = 8.23 \pm 0.62$, $W_m = 4.53 \pm 0.34$, $Q = (1.56)1.6–2(2.13)$, $Q_m = 1.82 \pm 0.15$, ellipsoid, elongate, cylindrical, smooth, hyaline, thin walled. *Basidia* 38–46 × 6.5–8.5 µm, $Q = 5.06–6.62$, 4-spored, clavate; sterigmata up to 6 µm long. Hymenophoral trama divergent, made up of cylindrical hyaline hyphae, 5–12 µm broad. *Pileipellis* an ixotrichoderm, made up of erected and interwoven hyphae, 2–6 µm wide. *Stipitipellis* an ixotrichoderm, consisting of usually repent and occasionally erected hyphae 1.5–6.5 µm broad. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Scattered on the ground in a mixed broadleaf-conifer forest, occurring in autumn, so far known from Chongqing City of China.

Notes – *Hygrophorus roseoviolaceus* is easily identified by its rose to violet brown pileus, darker pileus disc and margin, and whitish lamellae changing to yellowish to brownish in young exsiccata. Compare with *H. rutilans*, which has paler pileus surface, and strongly violet brown lamellae in all exsiccata. *Hygrophorus erubescens* is somewhat similar to *H. roseoviolaceus*, while the former is more robust, and mycorrhizal with *Picea abies* (Læssøe & Petersen 2019).

Hygrophorus roseoviolaceus is the first new species of *Hygrophorus* described from Chongqing City of southwestern China. Due to limited macrofungus collection activities, few samples of *Hygrophorus* from Chongqing City were collected and studied. In the future, more attention should be paid to *Hygrophorus* resources in Chongqing City.

Hygrophorus rutilans C.Q. Wang, X.L. Gao, X.H. Wang & T.H. Li, sp. nov.

Fig. 12

Index Fungorum Number: IF901130; Facesoffungi number: FoF14930

Etymology – *rutilans* = being red; *rutilans* is proposed due to its red pileus.

Type – China, Yunnan Province, Chuxiong Yi Autonomous Prefecture, Lufeng County, in a mixed broadleaf-conifer forest, elev. ca. 2400 m, 5 October 2022, X.L. Gao (GDGM89538, Holotype).

Pileus 30–50 mm across, hemispherical when young, becoming convex, broadly convex, flat or undulating when mature, usually depressed at disc, densely covered with pale red, pastel red, dull red, rose, red, greyish rose, brownish violet (10A4–6, 10B4–6, 11A4–6, 11B4–6, 11C4–6, 11D4–6) fibrils or small scales; with pinkish to whitish ground colour beneath showing through; margin incurved when young, expanded later. *Lamellae* adnate, adnate with subdecurrent tooth to subdecurrent, subdistant to dense, $L = 48–68$, $l = 1–3$, waxy, fragile, whitish to yellowish, edge even. *Stipe* 40–90 mm long, 7–13 mm thick, cylindrical to subcylindrical, tapering downward, central, solid, whitish to yellowish. *Context* whitish.

Basidiospores (5.5)6–8 × 3.5–5 µm, $L_m = 7.33 \pm 0.61$, $W_m = 4.28 \pm 0.41$, $Q = 1.5–1.88$, $Q_m = 1.72 \pm 0.12$, ellipsoid to elongate, smooth, hyaline, thin-walled. *Basidia* 32.5–48 × 6.5–9 µm, $Q = 4.33–6.4$, 4-spored, clavate, sterigmata 4.5–6 µm long. *Hymenophoral trama* divergent, yellowish to brownish yellow in 5% KOH solution, made up of cylindrical to inflated hyphae 3–21 µm wide. *Pileipellis* an ixotrichoderm, made up of interwoven hyphae 4–9.5 µm wide. *Stipitipellis* an trichoderm, made up of usually uplifted hyphae 3–7 µm wide; hyphae slightly enlarged near the terminals. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Scattered on the ground in mixed forests, occurring in autumn, so far known from southwestern China (Yunnan Province).

Additional specimens examined – China, Yunnan Province, Dali Bai Autonomous Prefecture, Binchuan County, Jizu Mountain, 25°57'N, 100°21'E, elev. ca. 2630 m, 18 September 2019, X.H. Wang (XHW6661).

Notes – *Hygrophorus rutilans* is easily recognized by the densely packed, pale red to brownish violet fibres and scales on the pileus, and the whitish to yellowish lamellae and stipe. In the ITS phylogenetic analysis (Fig. 1), *H. rutilans* is sister to *H. roseodiscoideus* Bon & Chevassut, however, *H. roseodiscoideus* differs by the larger (up to 120 mm broad) and brownish pileus, and pink lamellae when mature (Candusso 1997, Campo 2015). *Hygrophorus unicolor* is similar to *H. roseodiscoideus*, but the former has brownish pileus with finely radially fibrillose surface (Breitenbach & Kränzlin 1991). *Hygrophorus roseobrunneus* [Misspelling as *H. roseibrunneus* in

Bessette et al. (2012)] is close to the species described here, but it has, as the name indicates, rose brown pileus, and the agglutinated-fibrillose pileus surface.

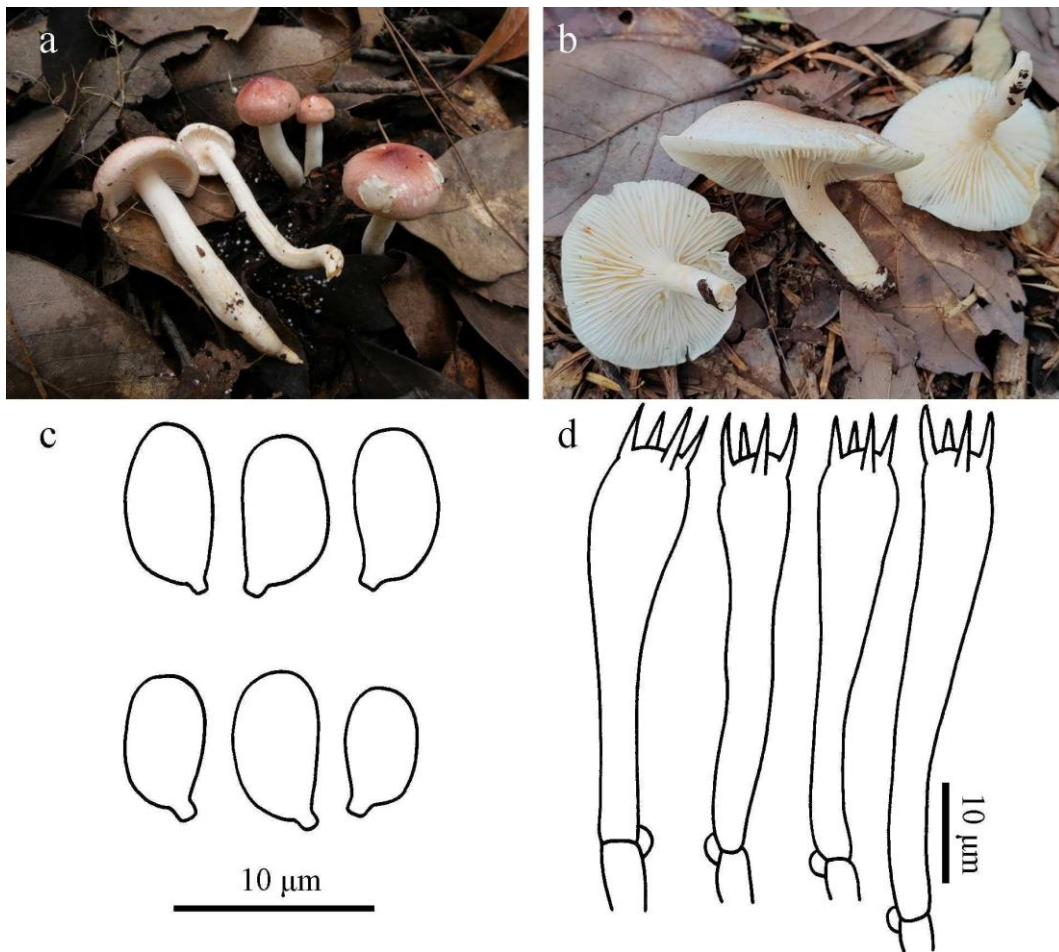


Figure 12 – *Hygrophorus rutilans*. a Basidiomata (XHW6661, by X.H. Wang). b Basidiomata (GDGM89538, by X.L. Gao). c Basidiospores (GDGM89538). d Basidia (GDGM89538).

Hygrophorus yukishiro N. Endo, Tokoo, & A. Yamada, in Endo, Tokoo, Fukuda & Yamada, Mycoscience 59(6): 450 (2018) Fig. 13

Pileus 35–50 mm across, broadly conical to convex when young, convex to plane when mature, smooth, viscid when wet, pale yellow, light yellow, light orange, orange, greyish orange (4A3–5, 5A2–7, 5B4–7), gradually shallower from disc to margin; margin straight when mature. *Lamellae* adnate to subdecurrent, subdistant, L = 32–44, l = 1–3, whitish; edge entire, sometimes serrate. *Stipe* 35–50 mm long, 9–14 mm broad, cylindrical, tapering upward, surface whitish, sometimes dirty white when touched. *Context* whitish.

Basidiospores (6.5)7–8 × 4.5–5(5.5) µm, Lm = 7.43 ± 0.47, Wm = 4.88 ± 0.76, Q = 1.4–1.6(1.78), Qm = 1.52 ± 0.09, ellipsoid to elongate, thin-walled, hyaline. *Basidia* 41–58 × 5.5–9 µm, Q = 5.13–8.9, clavate, 4-spored, thin-walled, hyaline, with sterigmata up to 6 µm long, hyaline. *Hymenophoral trama* divergent, consist of thin-walled hyphae 3.5–18 µm broad. *Pileipellis* ixotrichoderm, consist of thin-walled and hyaline hyphae 3–7 µm broad. *Stipitipellis* cutis to trichoderm, made up of thin-walled, hyaline hyphae 2–6 µm broad. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Solitary to gregarious on the ground in *Quercus* dominated forests, occurring in autumn in Sichuan, China (this study) and spring in Nagano Prefecture, Janpa (Endo et al. 2018), so far known from Japan and China (Anhui Province, Henan Province, Sichuan Province, Zhejiang Province) (Endo et al. 2018, Huang 2022, this study).

Specimen examined – China, Sichuan Province, Guangyuan County, Lizhou District, Tianzhao Mountain, 24 September 2022, D. Wang (SAAS4870).

Notes – *Hygrophorus yukishiro*, is an edible mushroom described from Nagano Prefecture, Japan, and placed in subsect. *Fulventes* (Endo et al. 2018). The ITS sequence from our material is 97.6% similar to the type specimen of *Hygrophorus yukishiro*. Apart from the brighter pileus colour and the accuracy in autumn, the Chinese sample is very similar to the type specimen. Considering the colour variation is common in the genus *Hygrophorus*, the Chinese sample is identified as *H. yukishiro*.

Hygrophorus arbustivus is phylogenetically close to *H. yukishiro*, but the former differs by the slightly darker pileus surface with the brownish fibrils, and slightly narrower basidiospores (Candusso 1997). *Hygrophorus subsalmonius* A.H. Sm. & Hesler differs from *H. yukishiro* by its larger basidiomata and smaller basidiospores measuring $6.5\text{--}8 \times 3\text{--}5 \mu\text{m}$ (Hesler & Smith 1963). *Hygrophorus roseobrunneus* is distinguished from *H. yukishiro* by its bigger basidiomata, fibrillose pileus surface, and ixocutis pileipellis (Hesler & Smith 1963).

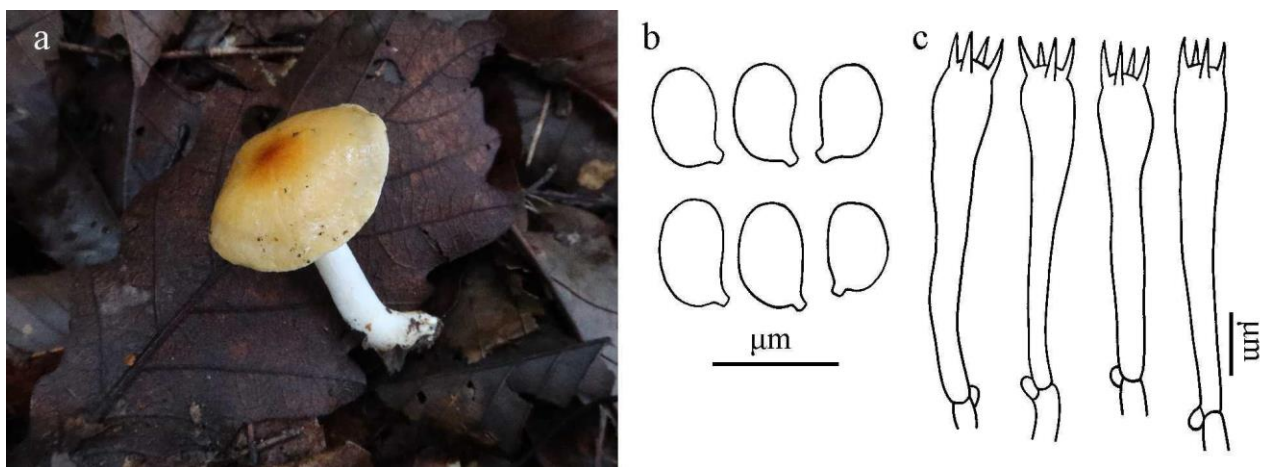


Figure 13 – *Hygrophorus yukishiro*. a Basidiomata (SAAS4870). b Basidiospores (SAAS4870). c Basidia (SAAS4870).

Hygrophorus sect. *Pudorini*

Phylogenetic support: Section *Pudorini* is well supported in the multilocus (MLBS = 96%) trees (Fig. 2), although it is not supported in the ITS tree (Fig. 1).

Studied Chinese species included in this section: *Hygrophorus abieticola*, *H. alboflavescens*, *H. brunneoloaurantiacus*, *H. brunneolus*, *H. chuxiongensis*, *H. deliciosus*, *H. erubescens*, *H. flavoalbus*, *H. fragilipurpurascens*, *H. magnisporus*, *H. orientalis*, *H. orientipurpurascens*, *H. pallidoaurantiacus*, *H. parvirussula*, *H. pseudopurpurascens*, *H. pudorinus*, *H. qinggangjun* and *H. yunnanensis*.

Hygrophorus abieticola Krieglst. ex Gröger & Bresinsky, in Bresinsky, Regensb. Mykol. Schr. 15: 211 (2008) Fig. 14

Pileus 20–70 mm across, hemispherical to convex when young, then expanded to convex to plano-convex, usually with a broad umbo, pale yellow, light yellow, pale orange to orange (4A3–5, 5A3–6), sometimes with brownish tint at disc, rarely squarrose at centre when mature; margin decurved to incurved when young, then expanded to decurved or straight. *Lamellae* adnate to subdecurrent, L = 48–76, l = 1–3, subdistant to dense, thickish, waxy, fragile, orange white to pale orange, usually with a pinkish or orange tint. *Stipe* 60–150 mm long, 7–17 mm thick, cylindrical, equal, usually slight enlarged toward base, often narrower at apex, usually curved, solid, yellowish white, light orange to pale orange brown at centre, often white at apex and near base, occasionally with bright yellow patches on the lower portio, rarely broken, fibrillose to scabrous when young, squarrose at maturity. *Context* yellow to orange, 5–9 mm thick at stipe. Taste mild.

Basidiospores 9–10.5(11.5) × 5.5–6.5(7) μm, Lm = 9.85 ± 0.67, Wm = 6.03 ± 0.41, Q = (1.43)1.46–1.82(1.92), Qm = 1.64 ± 0.14, ellipsoid, broadly ellipsoid, elongate, smooth, hyaline, thin-walled. *Basidia* 50–86 × 8–11 μm, Q = 5.55–8, 4-spored, narrowly clavate; sterigmata up to 7 μm long. *Hymenophoral trama* divergent, made up of cylindrical hyaline hyphae. *Pileipellis* an ixotrichoderm, covered with strongly gelatinised materials, made of slender cylindrical hyphae 2.5–6.5 μm wide, with yellow brown colour intracellular pigment. *Stipitipellis* made of gelatinised slender hyphae 3–10 μm wide. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Scattered to gregarious on the ground under *Abies* trees, occurring in summer and autumn, known from Asia, Europe and North America, distributed from northeastern and southwestern China (Helongjiang Province, Sichuan Province) (Larsson & Jacobsson 2014, Huang 2022, this study).

Specimens examined – China, Sichuan Province, Jiuzhaigou County, in a forest dominated by *Abies* sp., elev. ca. 2100 m, 21 August 2013, C.Q. Wang (GDGM44322, GDGM44324). Yunnan Province, Shangri-la, Bitahai, in a subalpine forest dominated by *Abies georgei* Orr, elev. ca. 3870 m, 4 September 2020, M. Zhang & L.Q. Wu (GDGM83191).

Notes – *Hygrophorus abieticola* was described from Europe (Larsson & Jacobsson 2014). It is characterized by orange tints on pileus, orangish to pinkish lamellae, growing under mosses, and association with *Abies*. In the ITS phylogenetic analysis (Fig. 1), there are three phylogenetic lineages within *H. abieticola*, the Asian lineage is close to the European lineage, and the North American lineage is placed at the basal position. *Hygrophorus pudorinus* var. *fragrans* (Murrill) Hesler & A.H. Sm. is the sister taxon to *H. abieticola* in the ITS tree (Fig. 1). Considering *H. pudorinus* var. *fragrans* is phylogenetically supported as distinct from *H. pudorinus*, it is necessary to elevate it to the species level in futher study. In the multigene phylogeny analysis (Fig. 2), *H. magnisporus* (a new species described below), which is closely related to *H. abieticola*, differs by its white and slender basidioma, and larger basidiospores [(10.5)11.5–15 × (6)6.5–9(9.5) μm].



Figure 14 – *Hygrophorus abieticola*. a Basidiomata (GDGM44322). b–c Basidiomata (GDGM44324). d Basidiospores (GDGM44322). e Basidia (GDGM44322).

Hygrophorus alboflavescens A. Naseer & A.N. Khalid, in Naseer, Khalid, Healy & Smith, MycoKeys 56: 37 (2019) Fig. 15

Pileus 40–120 mm across, hemispherical to convex when young, then expanding to convex to plano-convex, with or without an obtuse umbo, white to yellowish white (4A1–2), yellowish white to pale yellow (4A2–3) at disc, often white with violet tinct at margin, incurved then straight at margin. *Lamellae* adnate to subdecurrent, L = 56–80, l = 1–3, white, waxy, thick, fragile, subdistant to dense, occasionally bifurcated, white to pinkish white or violet white (16A1, 16A2), usually entire at edge, sometimes brownish when bruised. *Stipe* 45–100 × 10–28 mm, cylindrical or sometimes compressed, equal or slightly narrowed toward the base, usually curved, white, sometimes violet white (16A1, 16A2), slightly longitudinally striate, sometimes slightly tomentose or with brownish floccules on lower surface. *Context* white. *Taste* mild.

Basidiospores (5.5)6–7 × 3.5–4.5(5), Q = 1.33–1.86, ellipsoid, oblong, smooth, thick-walled. *Basidia* 34–47 × 5–7 μm, 4-spored, clavate, with sterigmata 3–5.5 μm long. *Hymenophoral trama* divergent, composed of thin-walled hyphae up to 11 μm in diameter. *Pileipellis* an ixotrichoderm, made up of hyphae 2.5–6 μm wide. *Stipitipellis* a cutis, made up of parallel and rarely erect hyphae 2–6 μm with. *Clamp Connections* present in all tissues.



Figure 15 – *Hygrophorus alboflavescens*. a Basidiomata (GDGM82808). b Basidiomata (GDGM43398). d Basidiomata (GDGM85775). e Basidiospores (GDGM82808). f Basidia (GDGM82808). g Pileipellis (GDGM43398).

Specimens examined – China, Sichuan Province, Xiaojin County, in a forest dominated by *Quercus* sp., elev. ca. 3000 m, 1 August 2020, C.Q. Wang (GDGM82808).

Habit, habitat and distribution – Scattered on the ground under *Quercus* trees, occurring in summer and autumn, known from China (Hunan Province, Jilin Province and Sichuan Province) and Pakistan (Naseer et al. 2019, Dong & Bau 2022, this study).

Notes – *Hygrophorus alboflavescens* was described from Pakistan (Naseer 2019). This fungus was recorded in Northeast and Southwest China (He et al. 2021, Dong & Bau 2022). It is a common edible mushroom in local markets in Aba Prefecture of Sichuan Province (He et al. 2021). The Chinese specimens clustered and form a supported clade with the Pakistani specimens in both the ITS and multilocus trees (Figs 1–2), but both trees showed some genetic differences. Considering the limited genetic variation and morphological similarity, we still treat those differences as intraspecific variation.

Hygrophorus brunneoloaurantiacus C.Q. Wang, Ming Zhang & T.H. Li, sp. nov. Fig. 16
Index Fungorum Number: IF901141; Facesoffungi number: FoF14931

Etymology – *brunneoloaurantiacus*, from *brunneolo-* = brownish or pale brown, *aurantiacus* = orange, referring to its brownish orange colour of pileus.

Type – China, Yunnan Province, Diqing Tibetan Autonomous Prefecture, Shangri-la County, Pudacuo National Park, in a subalpine forest dominated by *Quercus* spp., 27°83' N, 99°99' E, elev. ca. 3720 m, 3 September 2020, M. Zhang & L.Q. Wu (GDGM82433, Holotype).

Pileus 20–150 mm across, convex when young, plane to plano-depressed with an obtuse and broad umbo when mature, pale orange, light orange, orange, greyish orange to brownish orange (5A3–7, 5B5–7, 5C5–7), lighter from disc to margin, viscid when wet; margin decurved when young, straight to uplifted when mature. *Lamellae* adnate to subdecurrent, subdistant to close, waxy, fragile, orangish, rarely furcate, L = 50–60, l = 1–3; edge entire, often lacerated when old. *Stipe* 30–60 mm long, 5–15 mm thick, cylindrical, central, solid, usually curved, orangish, slightly tomentose, often with white weak mycelium at base. *Context* white, unchanged when bruised.



Figure 16 – *Hygrophorus brunneoloaurantiacus*. a Basidiomata (GDGM82433). b Basidiomata (GDGM83034). c Basidiospores (GDGM82433). d Basidia (GDGM82433). e Pileipellis (GDGM82433).

Basidiospores 6–7.5(8) × (3.5)4–5 μm, Lm = 6.78 ± 0.60, Wm = 4.40 ± 0.38, Q = 1.33–1.71, Qm = 1.54 ± 0.10, ellipsoid to elongate, smooth, hyaline, thin-walled. *Basidia* 45–64 × 7–10 μm, Q = 5.1–9.07, 4-spored, clavate; sterigmata 5–5.5 μm long. *Hymenophoral trama* divergent, made up of cylindrical, thin-walled, hyaline hyphae 4–32 μm wide. *Pileipellis* an ixocutis, made up of repent or interwoven hyphae 3.5–6.5 μm wide. *Stipitipellis* an ixocutis, made up of cylindrical thin-walled hyphae 3.5–5.5 μm wide. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Scattered on the ground in forests dominated by *Quercus* spp., occurring in autumn, known from southwestern China (Yunnan Province).

Additional specimens examined – China, Yunnan Province, Shangri-la County, Pudacuo National Park, in a subalpine forest dominated by *Quercus* spp., 27°82'N, 99°96'E, elev. ca. 3560 m, 2 September 2020, M. Zhang & L.Q. Wu (GDGM83034, GDGM83080).

Notes – *Hygrophorus brunneolaurantiacus* is characterized by its pale orange to brownish orange pileus, orangish and rarely furcate lamellae. Phylogenetic analyses of the ITS and multilocus datasets (Figs 1–2) supported *H. brunneolaurantiacus* to be a distinct species within the *H. nemoreus* complex. Compared with *H. nemoreus*, *H. brunneolaurantiacus* shows a larger (up to 150 mm in diam.), brighter colored and fragile pileus, a high elevation distribution (over 3500 m so far) in southwestern China. Compared with *H. brunneolus*, *H. brunneolaurantiacus* has bigger basidiomata at maturity, brighter pileus, and bigger basidiospores [6–7.5(8) × (3.5)4–5 μm].

Hygrophorus brunneolus C.Q. Wang, Xiao Lan He & T.H. Li, sp. nov.

Fig. 17

Index Fungorum Number: IF901142; Facesoffungi number: FoF14932

Etymology – *brunneolus* = brown colour, referring to its brownish to light brown pileus.

Type – China, Sichuan Province, Panzhihua City, Yanbian County, Gesala Eco-tourism Area, in a mixed forest dominated by *Abies*, *Quercus* and *Rhododendron* trees, 27°16'N, 101°26'E, elev. ca. 3200 m, 9 July 2013, X.L. He (SAAS617, Holotype).

Pileus 20–70 mm across, convex to plano-convex when young, plane to depressed with an obtuse umbo when mature, light brown to orangish brown (5D4–8, 5E4–8) at centre, becoming lighter from disc to margin, orange white, pale orange to greyish orange (5A2–3, 5B4–5) outside the centre, viscid when wet; margin decurved when young, usually straight when mature. *Lamellae* adnate to subdecurrent, up to 6 mm broad, subdistant, L = 56–68, l = 1–3, thick, waxy, fragile, whitish; edge entire. *Stipe* 35–60 mm long, 6–15 mm thick, central, solid, cylindrical, usually slightly curved, yellowish to slightly brownish, punctate, often weakly longitudinally striate.

Basidiospores 5.5–6.5(7) × 3.5–4.5 μm, Lm = 6.06 ± 0.41, Wm = 3.96 ± 0.33, Q = 1.33–1.86, Qm = 1.54 ± 0.15, ellipsoid to elongate, smooth, hyaline, thin-walled. *Basidia* 35–55 × 6–8 μm, Q = 4.63–7.33, 4-spored, clavate; sterigmata 4–5.5 μm long. *Hymenophoral trama* divergent, made up of cylindrical, thin-walled, hyaline hyphae 3–14 μm wide. *Pileipellis* an ixocutis, made up of repent or interwoven hyphae 1.5–7.5 μm wide. *Stipitipellis* an ixocutis, made up of cylindrical thin-walled hyphae 3–7.5 μm wide. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Scattered on the ground in mixed forests dominated by *Abies*, *Quercus* and *Rhododendron* trees, occurring in summer, so far known from southwestern China (Sichuan Province).

Additional specimens examined – China, Sichuan Province, Panzhihua City, Yanbian County, Gesala Eco-tourism Area, in a mixed forest dominated by *Abies*, *Quercus* and *Rhododendron* trees, 27°16'N, 101°26'E, elev. ca. 3200 m, 9 July 2013, X.L. He (SAAS510).

Notes – *Hygrophorus brunneolus* is characterized by its orange white to orangish brown pileus, adnate to subdecurrent and whitish lamellae, and ellipsoid to elongate basidiospores measuring 5.5–6.5(7) × 3.5–4.5 μm. In the ITS tree (Fig. 1), this fungus is placed close to the European *H. nemoreus* and an ectomycorrhizal root tip sample (JQ991740) from Zhejiang Province of China. In both trees (Figs 1–2), this fungus clustered with members of subsect. *Clitocyboides*. Morphologically, *H. nemoreus* differs from *H. brunneolus* by having a darker pileus, larger basidiospores [6–8(10) × 3.8–5.2 μm], and the occurrence in lower elevations (usually lower than 1100 m) (Candusso 1997, Campo 2015). The European *H. pudorinus* is also similar to this fungus,

however, the former has pale orange pileus, larger basidiospores [(7)8–10.2 × 4.8–5.5(6.5) μm] and is associated with *Abies*. *Hygrophorus penarius* differs from *H. brunneolus* by having rather robust basidiomata, white to light yellow pileus, and its association with *Fagus*.

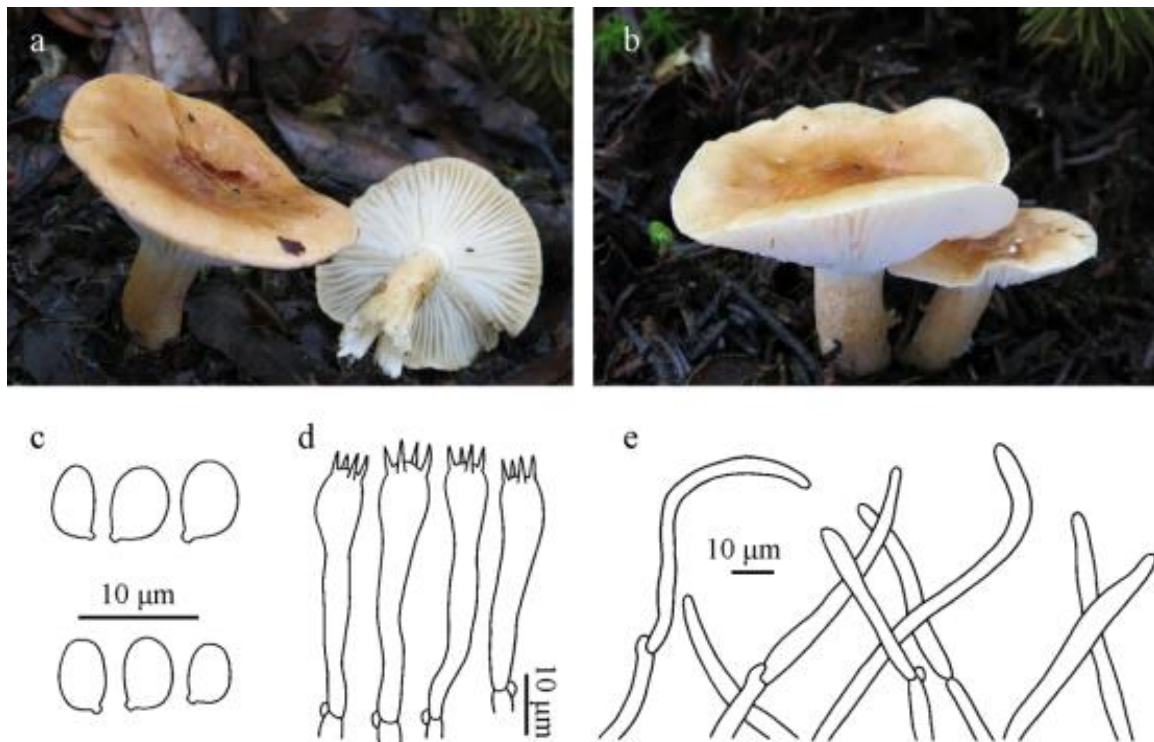


Figure 17 – *Hygrophorus brunneolus*. a Basidiomata (SAAS510). b Basidiomata (SAAS617). c Basidiospores (SAAS617). d Basidia (SAAS617). e Terminal hyphae of pileipellis (SAAS617).

Hygrophorus chuxiongensis C.Q. Wang, X.H. Wang, H. F. Bai & T.H. Li, sp. nov. Fig. 18

Index Fungorum Number: IF901143; Facesoffungi number: FoF14933

Etymology – *chuxiongensis*, referring to its type location in Chuxiong Yi Autonomous Prefecture, Yunnan Province, China.

Type – China, Yunnan Province, Chuxiong Yi Autonomous Prefecture, Wuding County, in a mixed forest dominated by pine and oak trees, 25°38'N, 102°5'E, elev. 2363 m, 6 October 2019, H.F. Bai (GDGM83746, Holotype).

Pileus 35–110 mm across, convex when young, plano-convex to plane when mature, yellowish white, pale yellow to light yellow (4A2–4), or pale orange to light orange (4A2–4), often greyish orange or brownish orange at disc (5B4), gradually lighter from disc to margin, sticky when wet; margin incurved to decurved when young, arched to straight or even uplifted when mature. *Lamellae* adnate to slightly subdecurrent, dense, L = 72–100, l = 1–3, waxy, fragile, whitish to yellowish or orangish; edge entire. *Stipe* 60–90 mm long, 10–20 mm thick, central, solid, cylindrical, ususally curved, sometimes tapered downwards, whitish to yellowish, sometimes partially nearly concolorous with pileus or a little paler, slightly dotted and obviously fibrillose. *Context* white to whitish, 6–11 mm thick at stipe.

Basidiospores (6.5)7–9 × 4–5.5 μm, Lm = 7.75 ± 0.62, Wm = 4.86 ± 0.44, Q = 1.27–2, Qm = 1.61 ± 0.18, broadly ellipsoid, ellipsoid to elongate, smooth, hyaline, thin-walled. *Basidia* 39.5–54.5 × 7–10.5 μm, Q = 4.32–6.5, 4-spored, clavate; sterigmata 4.5–6 μm long. *Hymenophoral trama* divergent, made up of cylindrical, thin-walled, hyaline hyphae 3.5–8 μm wide. *Pileipellis* an ixotrichoderm, made up of repent or interwoven hyphae 3–6.5 μm wide. *Stipitipellis* a trichoderm, made up of cylindrical thin-walled hyphae 3.5–9.5 μm wide. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Scattered to caespitose on the ground in mixed forests dominated by *Pinus* spp. and *Quercus* spp., occurring in autumn, so far only known from southwestern China (Yunnan Province).

Additional specimens examined – China, Yunnan Province, Chuxiong Yi Autonomous Prefecture, Nanhua County, Nanhua Wild Fungus Market, 16 October 2019, C.Q. Wang (GDGM79225); Dali Bai Autonomous prefecture, Binchuan County, Jizu Mountain, 19 September 2019, X.H. Wang, XHW6689 (HKAS 131108).

Notes – *Hygrophorus chuxiongensis* is characterized by its yellowish pileus, mainly adnate to slightly subdecurrent lamellae, and an association with mixed or broadleaved trees in subtropical forests. This fungus is an uncommon edible mushroom at local market.

In the ITS phylogenetic analysis (Fig. 1), *H. chuxiongensis* is sister to *H. pallidoaurantiacus* (described in this study) with high support values, while in the multilocus phylogenetic tree (Fig. 2), *H. chuxiongensis* is sister to the (weakly supported) *H. pallidoaurantiacus*-*H. flavoalbus* clade. All these three species are described from southwestern China in this study, and they form a strongly supported independent clade in both phylogenetic analyses.

Morphologically, *H. pallidoaurantiacus* differs from *H. chuxiongensis* by having larger basidiomata (pileus up to 130 mm in diam.), narrower basidia ($36.5\text{--}53.5 \times 5.0\text{--}7.0 \mu\text{m}$), and distributed in high elevation areas (over 3800 m so far). *Hygrophorus flavoalbus*, also described in this study, differs from *H. chuxiongensis* by having usually depressed pileus centre, narrower lamellae and smaller basidiospores [$(5.5)6\text{--}7.5 \times 3.5\text{--}4.5 \mu\text{m}$].

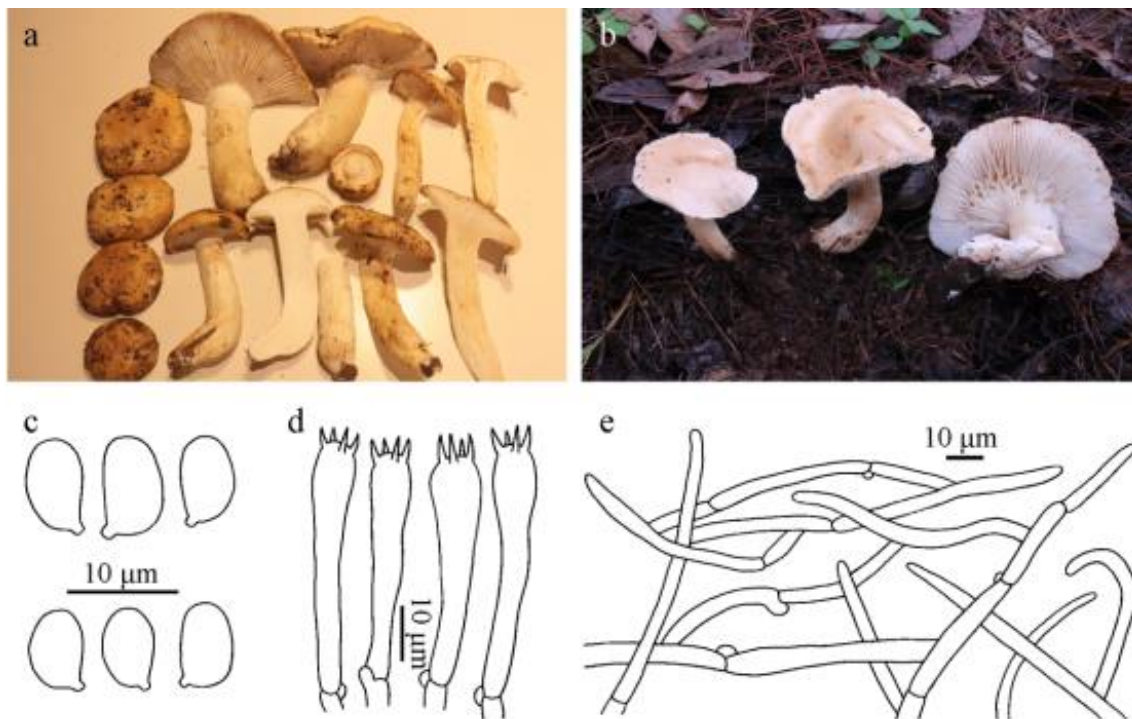


Figure 18 – *Hygrophorus chuxiongensis*. a Basidiomata (GDGM79225). b Basidiomata (GDGM83746, by H.F. Bai). c basidiospores (GDGM83746). d Basidia (GDGM83746). e Terminal hyphae of pileipellis (GDGM83746).

Hygrophorus deliciosus C.Q. Wang & T.H. Li, Phytotaxa 449(3): 235 (2020)

Fig. 19

Pileus 40–140 mm, hemispherical to convex at first, then becoming broadly convex, plane, plano-concave to concave, pinkish white (10A2), pale red (10A3), pastel pink (10A4–5), brownish red (10C7), to violet brown (10E8), paler towards the margin, with brownish red discolouration when bruised, scaly densely at centre and more sparsely towards margin; margin inrolled and entire when young, gradually extended, usually unrolling and often lacerated when old. *Context* up to 24 mm thick at stipe, white to pinkish. *Lamellae* adnate to shortly decurrent or arcuate, up to 10 mm

broad, subdistant, white, pinkish white, waxy, thick, fragile, $L = 82\text{--}100$, $l = 1\text{--}3$; edge usually with pale red even to brownish red discolouration. *Stipe* 40–120 mm long, 10–22 mm thick, central to slightly eccentric, cylindrical, usually equal, white, pinkish white, red to brownish red, longitudinally fibrillose, solid. *Taste* mild. *Odour* indistinctive.

Basidiospores $(6.5)7\text{--}9(10) \times 4.5\text{--}6(6.5) \mu\text{m}$, $Lm = 7.84 \pm 0.8$, $Wm = 5.16 \pm 0.44$, $Q = (1.2)1.3\text{--}1.8(1.9)$, $Qm = 1.52 \pm 0.17$, ellipsoid to oblong, hyaline, smooth, thin-walled. *Basidia* mainly 4-spored, rarely 2-spored, $(49)50\text{--}61(72) \times (5.5)6\text{--}8 \mu\text{m}$, $Q = (6.3)7\text{--}9.4(9.8)$, $Qm = 8.24 \pm 0.87$, slenderly clavate; sterigmata up to 11 μm long. *Lamellar trama* divergent, made up of thin-walled hyphae 4–22 μm in width. *Pileipellis* an ixotrichoderm, made up of thin-walled hyphae 3–5 μm broad. *Stipipellis* a cutis, made up of repent hyphae 3–5 μm broad. *Clamp connections* present.

Habit, habitat and distribution – Scattered to gregarious on soil under *Quercus aquifolioides* trees in broad-leaved forests, occurring in summer and autumn and in the subalpine regions at high elevations (usually above elev. 3000 m), known from southwestern China (Sichuan Province, Tibet Autonomous Region, Yunnan Province).

Specimens examined – China, Tibet Autonomous Region, Nyingchi Prefecture, Milin County, 29°22'N, 94°22'E, elev. ca. 3500 m, 18 August 2019, in a broad-leaved forest dominated by *Q. aquifolioides*, Tamdrin Tsering 159 (GDGM73208). Yunnan Province, Chuxing City, Nanhua County, Nanhua Wild Fungus Market, 16 October 2019, C.Q. Wang 457 (GDGM79208, Holotype). *Notes* – *Hygrophorus deliciosus*, a popular and common wild edible mushroom in southwestern China, was described from China by Wang et al. (2020). In the ITS tree (Fig. 1), *H. deliciosus* is placed close to European “*H. russula*” (common in France, Italy and Spain), but there is a distinct interspecific genetic distance between them. Morphologically, this species is characterized by robust fruitbodies, usually dense pileus scales, pinkish white lamellae with pink to reddish discoloration at lamellar edges when mature, and white context when fresh and dry. The known distribution of *H. deliciosus* is in southwestern China. For detailed descriptions and comparisons with similar species, see Wang et al. (2020).

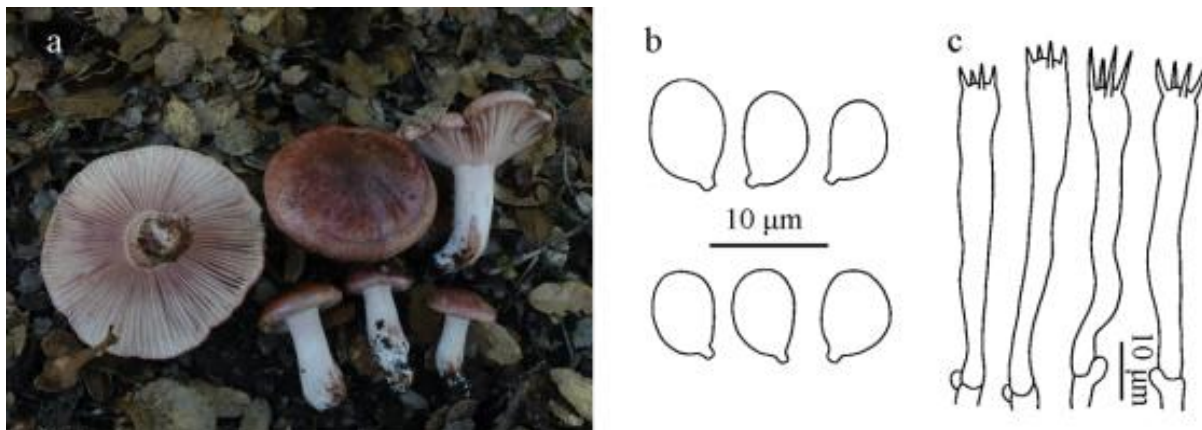


Figure 19 – *Hygrophorus deliciosus*. a Basidiomata (GDGM81877). b Basidiospores (GDGM79208). c Basidia (GDGM79208).

Hygrophorus erubescens (Fr.) Fr., *Epicer. syst. mycol.* (Upsaliae): 322 (1838) [1836–1838]

Fig. 20

Pileus 35–100 mm across, hemispherical to convex when young, convex to plano-convex when mature, pinkish white, pale red, pastel red, dull red to greyish red (9A2–5, 9B3–5), paler at margin, sticky when wet, bald, or finely hairy in places; margin decurved when young, then straight to uplifted. *Lamellae* adnate to subdecurrent, waxy, fragile, whitish to pinkish white when young, pinkish white to pale red with reddish spots, or becoming pinkish overall, subdistant, $L = 52\text{--}64$, $l = 1\text{--}3$; edge entire and smooth when young. *Stipe* 30–80 mm long, 5–9 mm thick, central, solid, more or less cylindrical, whitish to pinkish white at first, presenting pinkish to reddish discolourations when mature, bald or finely hairy. *Context* whitish, thick.

Basidiospores (7.5)8–10 × 4.5–6 μm, Lm = 8.8 ± 0.68, Wm = 5.18 ± 0.42, Q = (1.33)1.42–1.9(2.1), Qm = 1.71 ± 0.16, ellipsoid to elongate, smooth, hyaline, thin-walled. *Basidia* 42–60 × 7.0–9.0 μm, Q = 4.89–7.33, 4-spored, clavate to cylindrical, sterigmata 4.5–8.5 μm long. *Hymenophoral trama* divergent, made up of cylindrical, thin-walled, hyaline hyphae 4–22 μm wide. *Pileipellis* an ixotrichoderm, made up of upturned or interwoven aerial hyphae 2–4.5 μm wide, with a glutinous layer at the surface in KOH. *Stipitipellis* an ixocutis, mainly made up of repent cylindrical thin-walled hyphae 3–9 μm wide, occasionally made up of upturned and clustered hyphae. *Clamp connections* present in all tissues.

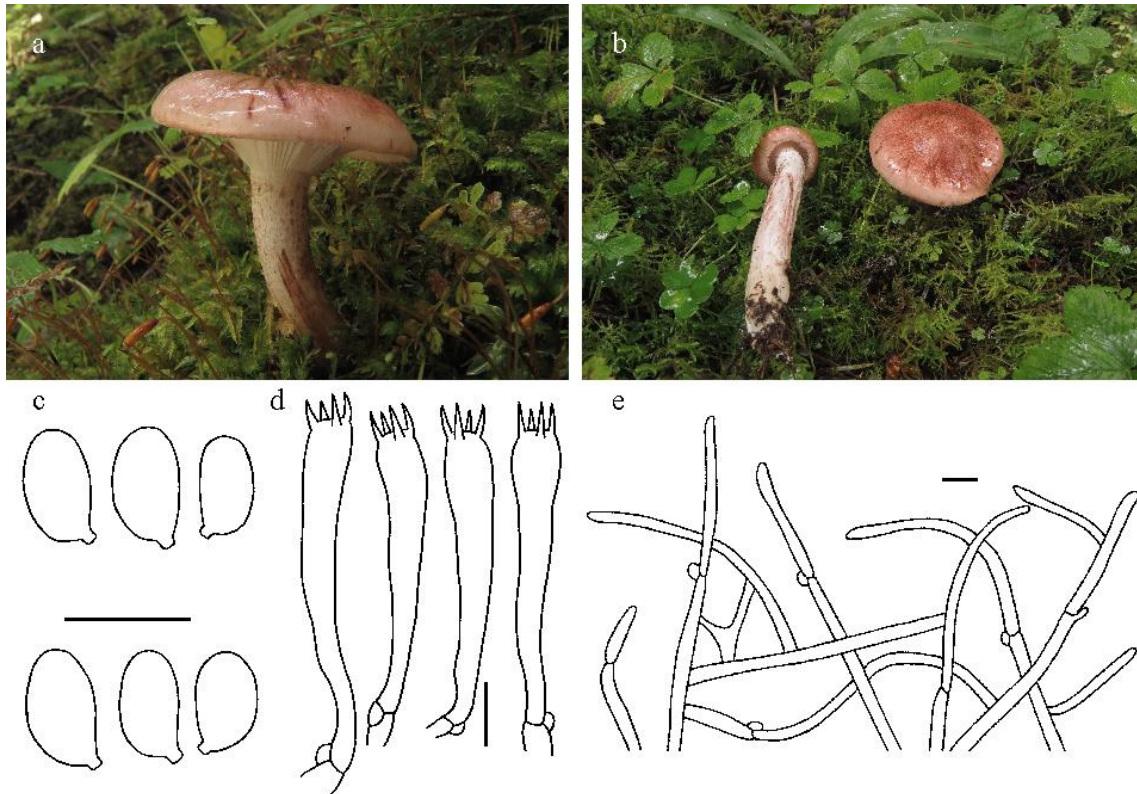


Figure 20 – *Hygrophorus erubescens*. a Basidiomata (GDGM84466). b Basidiomata (GDGM84603). c Basidiospores (GDGM84466). d Basidia (GDGM84466). e Pileipellis (GDGM84466).

Habit, habitat and distribution – Solitary or scattered in subalpine forests; basidioma occurring in autumn; known from Asia, Europe and North America, in China known from southwestern region (Sichuan Province) (This study).

Specimens examined – China, Sichuan Province, Jiuzhaigou County, on the ground of a subalpine forest, elev. ca. 3000 m, 19 September 2020, M. Zhang & J.H. Xing (GDGM84676); Songpan County, Erdaohai, in a subalpine forest, elev. ca. 3300 m, 23 September 2020, M. Zhang & J.H. Xing (GDGM84466, GDGM84603).

Notes – *Hygrophorus erubescens*, commonly known as the blotched woodwax or pink waxcap, was originally described from Europe (Bas 1990). This fungus belongs to subsect. *Pudorini* (Lodge et al. 2014). It is characterized by its pinkish to reddish pileus with darker pink or red marks when bruised, whitish to pinkish lamellae with dark red dots when mature, and ellipsoid to elongate basidiospores measuring (7.5)8–10 × 4.5–6 μm.

According to the ITS phylogenetic analysis (Fig. 1), sequences named as “*H. erubescens*”, “*H. neoerubescens*” and “*H. persicolor*” are clustered in a terminal clade that includes samples from the Northern Hemisphere (Austria, China, Estonia, Italy, and USA) In both ITS and multigene phylogenetic analysis (Figs 1–2), *H. erubescens* is sister to *H. pudorinus*. Although *Hygrophorus erubescens* was widely recorded in Northeastern and Southwestern China (Gansu, Heilongjiang,

Jilin, Shannxi, Sichuan, Yunnan), these records were identified based on morphology identification (Chen & Li 2013). To clarify the real distribution area of *H. erubescens* in China, more investigation and reliable data are needed.

Hygrophorus flavoalbus C.Q. Wang, X.H. Wang, L.Q. Mu & T.H. Li, sp. nov.

Fig. 21

Index Fungorum Number: IF901144; Facesoffungi number: FoF14934

Etymology – *flavoalbus*, from *flavo* = yellow, and *albus* = white, referring to its white to yellowish pileus colour.

Type – China, Yunnan Province, Lanping County, Yunling Nature Reserve, in a forest dominated by pine trees, 26°31'26"N, 99°21'28"E, elev. 2702 m, 26 September 2019, X.H. Wang, XHW7197 (HKAS 131114, Holotype).

Pileus 50–120 mm across, convex with an obtuse umbo when young, plano-convex, plane to depressed with an umbo when mature, white, yellowish white to pale yellow to greyish yellow (4A2–3, 4B2–3), becoming lighter from disc to margin, viscid to glutinous when wet; margin decurved when young, then straight to uplifted, entire, rarely lacerated. *Lamellae* adnate to subdecurrent, waxy, fragile, whitish, dense, L = 85–110, l = 1–3; edge entire. *Stipe* 35–85 mm long, 13–30 mm thick, central, solid, cylindrical, usually tapered upward, whitish, somewhat fibrillose or short flocculose. *Context* whitish, thick.

Basidiospores (5.5)6–7.5 × 3.5–4.5 μm, Lm = 6.53 ± 0.55, Wm = 4.13 ± 0.36, Q = 1.44–1.86, Qm = 1.59 ± 0.11, ellipsoid to elongate, smooth, hyaline, thin-walled. *Basidia* 33–48 × 5.5–7.5 μm, Q = 4.71–8.73, 4-spored, clavate to cylindrical; sterigmata 2.5–5 μm long. *Hymenophoral trama* divergent, made up of cylindrical or inflated, thin-walled, hyaline hyphae 2.5–17 μm wide. *Pileipellis* an ixotrichoderm, made up of upturned or interwoven aerial hyphae 2.5–4 μm wide. *Stipitipellis* as an ixotrichoderm, made up of upturned cylindrical thin-walled hyphae 4–7 μm wide. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Scattered under conifer forests dominated by *Pinus* spp., occurring in autumn, so far known from southwestern China (Yunnan Province).

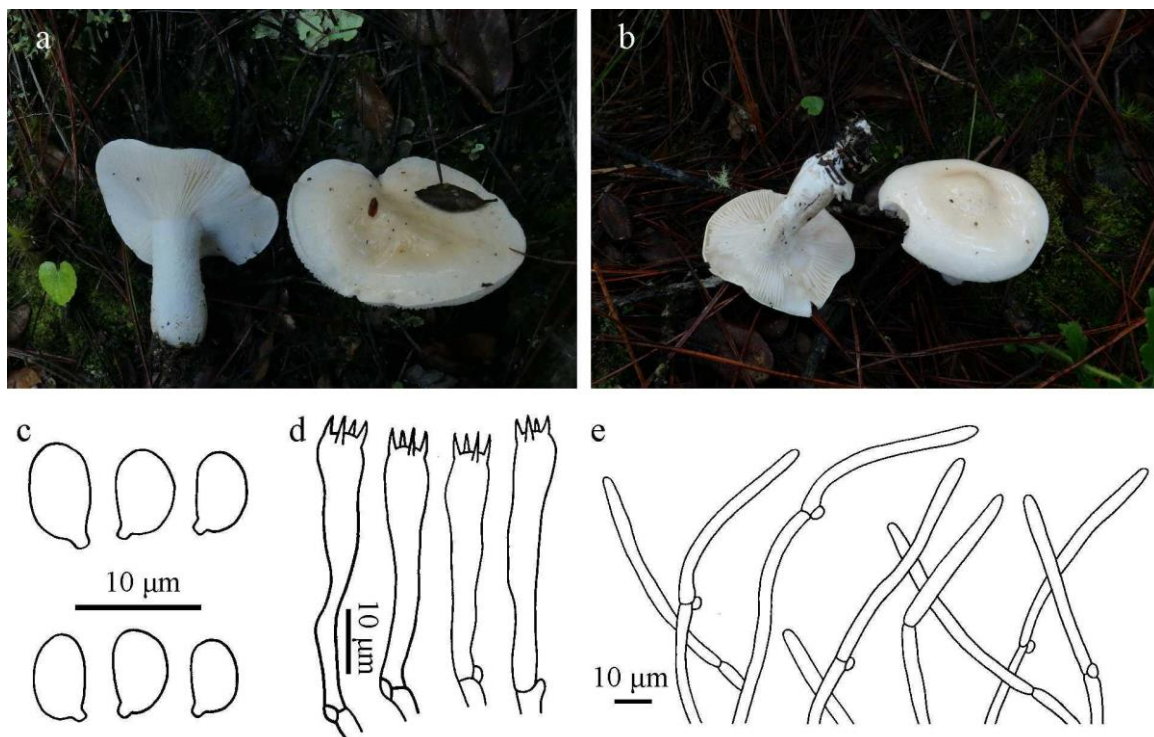


Figure 21 – *Hygrophorus flavoalbus*. a Basidiomata (XHW7197, by X.H. Wang). b Basidiomata (XHW7264, by X.H. Wang). c Basidiospores (XHW7197). d Basidia (XHW7197). e Terminal hyphae of pileipellis (XHW7197).

Additional specimens examined – China, Chuxiong Yi Autonomous Prefecture, Zixi Mountain, in a mixed broadleaf-conifer forest dominated by *Pinus* and *Quercus*, elev. 2148 m, 16 October 2022, L.Q. Mu (GDGM89557); Yunnan Province, Lanping County, Yunling Nature Reserve, in a forest dominated by pine trees, 26°31'26"N, 99°21'29"E, elev. 2686 m, 26 September 2019, X.H. Wang, XHW7264 (HKAS 131115).

Notes – *Hygrophorus flavoalbus* is characterized by a white to yellowish pileus, adnate to subdecurrent, whitish and dense lamellae, and ellipsoid to elongate basidiospores.

The phylogenetic relationship and morphological differences among *H. flavoalbus*, *H. chuxiongensis* and *H. pallidoaurantiacus* are discussed above. The white to yellowish pileus and the white lamellae also reminiscent of *H. cossus* and *H. hedrychii*. However, *H. cossus* differs from *H. flavoalbus* in its obvious typical smell, bigger basidiospores ($7\text{--}9.5 \times 4\text{--}5.5 \mu\text{m}$), and association with *Quercus* (Candusso 1997). *Hygrophorus hedrychii* differs in its cossus-like smell, more distant lamellae, and association with *Betula* (Larsson & Jacobsson 2004).

Hygrophorus fragilipurpurascens C.Q. Wang, Ming Zhang & T.H. Li, sp. nov.

Fig. 22

Index Fungorum Number: IF901145; Facesoffungi number: FoF14935

Etymology – *fragilipurpurascens*, *fragili* = fragile, and *purpurascens* = *Hygrophorus purpurascens*, is proposed for the new species is similar to *H. purpurascens* but it has obvious fragile lamellae.

Type – China, Sichuan Province, Panzhihua City, Yanbian County, Gesala Eco-tourism Area, in a forest dominated by pine trees, 27°16'N, 101°26'E, elev. ca. 3100 m, 9 July 2013, C.Q. Wang & M. Zhang (GDGM44332, Holotype).

Pileus 40–70 mm across, convex when young, convex to plano-convex when mature, pink, greyish pink, greyish pink, greyish ruby (11A3–6, 11B3–6, 12B3–6, 12C3–6), discolouring to pale purplish red when injured, subglabrous to fibrillose; margin decurved when young, arched to straight when mature, whitish to pinkish white. *Lamellae* adnate to subdecurrent, subdistant, waxy, fragile, often cracked at maturity, white, usually with pinkish spots or streaks when mature, partially discolouring to pale purplish red when injured, $L = 56\text{--}72$, $l = 1\text{--}3$; edge even to not entire or lacerated when mature, usually pinkish to purplish discoloured. *Stipe* 40–70 mm long, 8–15 mm thick, cylindrical, central, solid, sometimes curved, usually concolorous with pileus margin, slightly discolouring to pale purplish red where injured.

Basidiospores $(6)6.5\text{--}8.5 \times 4\text{--}5.5(6) \mu\text{m}$, $Lm = 7.28 \pm 0.68$, $Wm = 4.68 \pm 0.54$, $Q = 1.25\text{--}1.78$, $Qm = 1.57 \pm 0.15$, broadly ellipsoid, ellipsoid to elongate, smooth, hyaline, thin-walled. *Basidia* $37\text{--}47 \times 5\text{--}8 \mu\text{m}$, $Q = 5.33\text{--}9$, 4-spored, clavate to narrowly clavate, sterigmata $3\text{--}5.5 \mu\text{m}$ long. *Hymenophoral trama* divergent, made up of cylindrical, thin-walled, hyaline hyphae $7\text{--}14 \mu\text{m}$ wide. *Pileipellis* an ixocutis to ixotrichoderm, made up of repent or interwoven hyphae $2.5\text{--}6 \mu\text{m}$ wide. *Stipitipellis* an ixocutis, made up of usually repent and occasionally uplifted and clustered, cylindrical, thin-walled hyphae $2.5\text{--}6 \mu\text{m}$ wide. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Solitary or scattered on the ground in mixed forests dominated by *Pinus* sp., occurring in autumn, known from southwestern China (Sichuan Province).

Additional specimens examined – China, Sichuan Province, Panzhihua City, Yanbian County, Gesala Eco-tourism Area, in a forest dominated by pine trees, 27°16'N, 101°26'E, elev. ca. 3100 m, 9 July 2013, C.Q. Wang & M. Zhang (GDGM43354, GDGM44331).

Notes – *Hygrophorus fragilipurpurascens* is well distinguished by its rose to greyish ruby pileus, fragile lamellae with usually discolored edge, broadly ellipsoid, ellipsoid to elongate basidiospores [$(6)6.5\text{--}8.5 \times 4\text{--}5.5(6) \mu\text{m}$], and distributions in subalpine forests. In both phylogenetic trees, *H. fragilipurpurascens* is placed in an independent position within the *H. purpurascens* complex. This taxon is phylogenetically sister to the *H. purpurascens* (Alb. & Schwein.) Fr. (UDB000576) from Sweden in the ITS tree (Fig. 1), and to the Chinese *H. pseudopurpurascens* in the multilocus tree (*H. purpurascens* is not represented, Fig. 2). However, *H. purpurascens* has relatively robust basidiomata, duller pileus colour, and paler lamellar

discoloration (Candusso 1997). *Hygrophorus pseudopurpurascens*, described in this study, has usually depressed pileus centre and a partial veil when young.

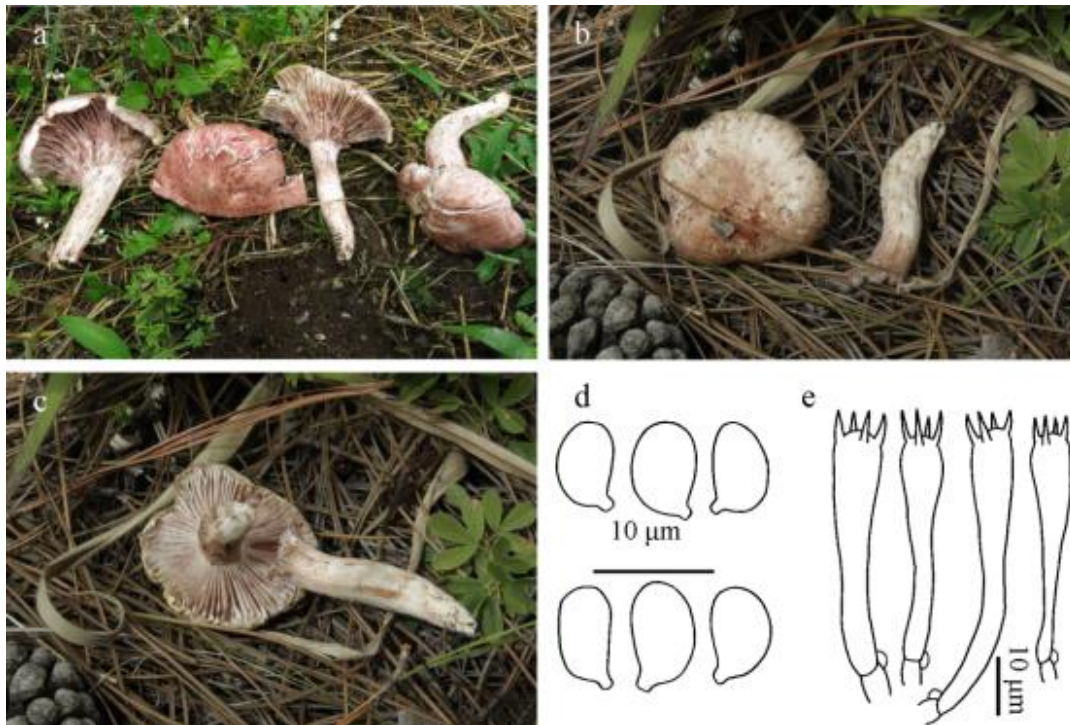


Figure 22 – *Hygrophorus fragilipurpurascens*. a Basidiomata (GDGM43354). b–c Basidiomata (GDGM44331). d Basidiospores (GDGM44332). e Basidia (GDGM44332).

Hygrophorus magnisporus C.Q. Wang, Xiao Lan He & T.H. Li, sp. nov.

Fig. 23

Index Fungorum Number: IF901146; Facesoffungi number: FoF14936

Etymology – *magnisporus*, from *magni* = large, and *sporus* = spore, referring to its large basidiospores.

Type – China, Sichuan Province, Jiuzhaigou County, Jiuzhaigou, in a subalpine forest, elev. ca. 3100 m, 11 September 2012, X.L. He (SAAS132, Holotype).

Pileus 8–40 mm across, hemispherical when young, convex to plano-convex when mature, white to whitish in general, sometimes yellowish white, pale yellow to dull yellow at disc (3A2–3, 4B3), sticky when wet, glabrous; margin slightly decurved to straight when young, straight to uplifted when mature. *Lamellae* adnate, arched with decurrent tooth to subdecurrent, subdistant, waxy, fragile, whitish, distant, L = 24–32, l = 1–3; edge entire and even. *Stipe* 40–100 mm long, 2–6 mm thick, central, solid to soft, more or less cylindrical, usually curved, white, occasionally with yellowish macules, viscid when wet, fibrillose. *Context* white, thin.

Basidiospores (10.5)11.5–15 × (6)6.5–9(9.5) µm, Lm = 12.76 ± 1.05, Wm = 7.68 ± 0.71, Q = (1.38)1.47–2, Qm = 1.67 ± 0.15, ellipsoid to elongate, smooth, hyaline, thin-walled. *Basidia* 51–77 × 10–14 µm, Q = 4.14–3.7, 4-spored, clavate, sterigmata 3.5–8.5 µm long. *Hymenophoral trama* divergent, made up of cylindrical, thin-walled, hyaline hyphae 4–30 µm wide. *Pileipellis* an ixotrichoderm, made up of upturned or interwoven aerial hyphae 2.5–6 µm wide. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Scattered on the ground in subalpine forests, occurring in autumn, so far known from southwestern China (Sichuan Province).

Additional specimens examined – China, Sichuan Province, Garze Tibetan Autonomous Prefecture, Luding County, Hailuoguo National Glacier Forest Park, in a subalpine forest, elev. ca. 3000 m, 20 September 2020, X.L. He (SAAS170); Huanglong County, in a subalpine forest, 14 September 2012, X.L. He (SAAS146, SAAS151); Jiuzhaigou County, Jiuzhaigou, in a subalpine forest, elev. ca. 3100 m, 11 September 2012, X.L. He (SAAS397).

Notes – *Hygrophorus magnisporus* is characterized by its white and slender basidiomata, convex to plano-convex pileus when mature, distant lamellae, and large basidiospores measuring $(10.5)11.5\text{--}15 \times (6)6.5\text{--}9(9.5) \mu\text{m}$. In the ITS phylogenetic analysis (Fig. 1), *H. magnisporus* is sister to an isotype sequence of *H. erubescens* var. *gracilis* A.H. Sm. & Hesler (HQ185700 from Isotype) and probably another sequence of the same taxon from Oregon in the USA (KF879503). The white basidiomata reminds several species within subgen. *Hygrophorus*, sect. *Hygrophorus*, but this fungus is close to *abieticola*, the type species of subgen. *Colorati*, sect. *Pudorini*, subsect. *Salmonicolors* in Lodge et al. (2014). However, *H. abieticola* has a robuster basidiomata and orange pileus and stipe surface (Larsson & Jacobsson 2014, Campo 2015). *Hygrophorus erubescens* var. *gracilis* differs by “Vandyke red” colour on the disc, white or flushed greyish pink lamellae with reddish staining, and smaller basidiospores measuring $8\text{--}11 \times 5.5\text{--}6(7) \mu\text{m}$ (Hesler & Smith 1963).

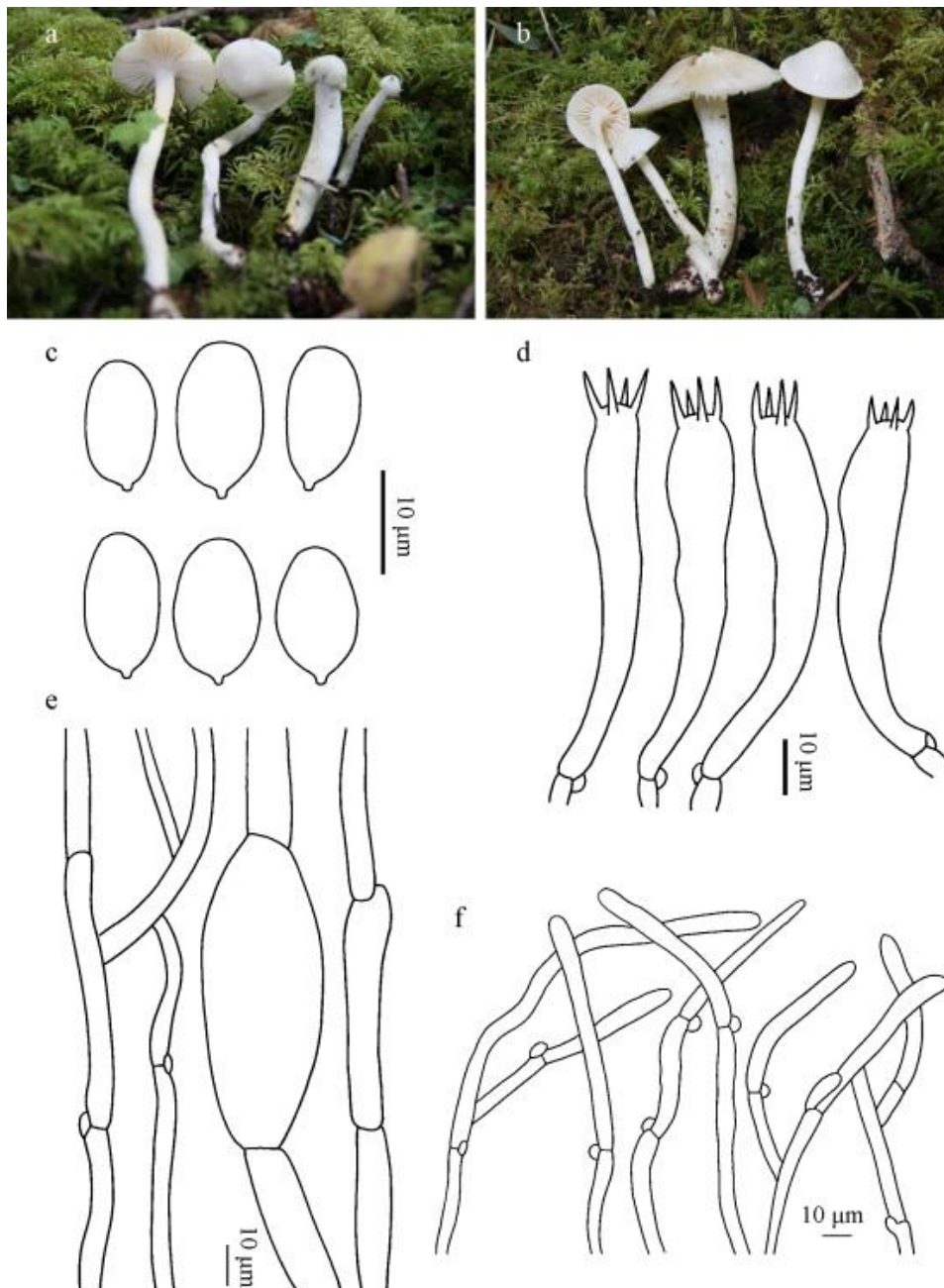


Figure 23 – *Hygrophorus magnisporus*. a Basidiomata (SAAS132). b Basidiomata (SAAS397). c Basidiospores (SAAS132). d Basidia (SAAS132). e Gill trama hyphae (SAAS132). f Pileipellis (SAAS132).

Hygrophorus orientalis H.Y. Huang & L.P. Tang, in Huang, Zhang, Huang, Gabriel, Liu & Tang, Mycol. Progr. 20(9): 1123 (2021) Fig. 24

Pileus 50–150 mm across, convex when young, then expanded to plano-convex or plane, usually with a broad umbo, reddish white to pale white (9A2–3, 10A2–3, 11A2–3), darker or somewhat reddish brown at disc, covered with reddish brown, greyish red, brownish red, brownish violet (9D4–8, 9E4–8, 10C4–8, 11D4–8) dots; margin incurved when very young, then expanded. *Lamellae* adnate to subdecurrent, L = 100–150, l = 1–3, dense, waxy, fragile, whitish at first, with a reddish brown to reddish brown tint when bruised or mature. *Stipe* 50–160 × 10–25 mm, cylindrical, equal to slightly enlarged toward base, solid; surface concolorous with pileus, unsmooth, fibrillose to scaly. *Context* pinkish white, or nearly white with pinkish tint and even with pinkish markings, usually thin near pileus margin, thicker at pileus disc, up to 10 mm or more at stipe. *Taste* mild.

Basidiospores 6–7.5(8) × 3.5–5 μm, Lm = 6.65 ± 0.59, Wm = 4.15 ± 0.46, Q = (1.4)1.44–1.88(2), Qm = 1.61 ± 0.15, ellipsoid to elongate, smooth, hyaline, thin-walled. *Basidia* 4-spored, narrowly clavate, 32–45 × 3.5–6 μm, thin-walled; sterigmata up to 5 μm long. *Hymenophoral trama* divergent, made up of cylindrical hyaline hyphae 3.5–20 μm wide. *Pileipellis* an ixotrichoderm, covered with strongly gelatinised materials, made of slender cylindrical and thin-walled hyphae 2.5–5 μm wide. *Stipitipellis* a cutis, composed of thin-walled hyphae 3–7 μm wide. *Clamp connections* present in all tissues.

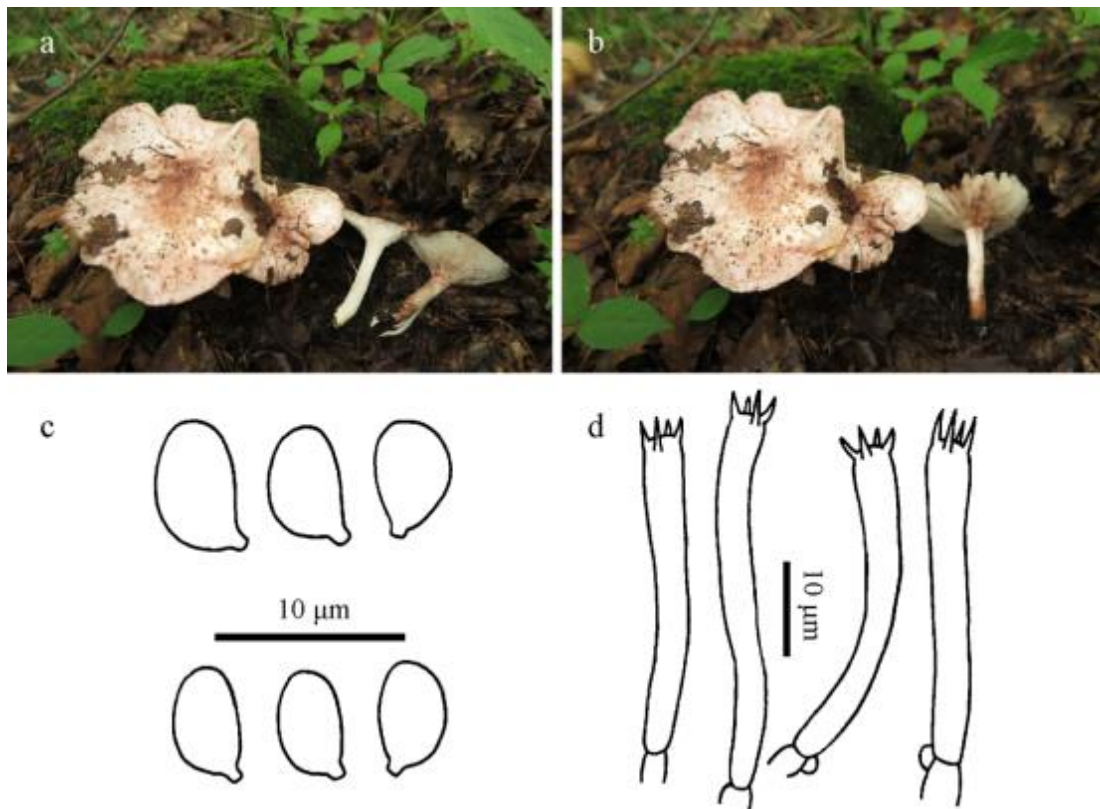


Figure 24 – *Hygrophorus orientalis*. a–b Basidiomata (GDGM41951). c Basidiospores (CFSZ18156). d Basidia (CFSZ18156).

Habit, habitat and distribution – Scattered to gregarious on the ground in broad-leaved forests dominated *Quercus* spp., occurring in summer and autumn, known from China (Hubei Province, Inner Mongolia Autonomous Region, Jilin Province, Shanxi Province, Yunnan Province), Japan and South Korea (Huang et al. 2021, Huang 2022, this study).

Specimens examined – China, Inner Mongolia Autonomous Region, Chifeng City, Harqin Banner, Wangyedian National Forest Park, in a broad-leaved forest dominated by *Q. mongolica*, 8

August 2017, T.Z. Liu, Y.Q. Guan & N. Liu (CFSZ18156). Jilin Province, Antu County, Changbai Mountain, in a broad-leaved forest dominated by *Quercus mongolica*, 21 August 2017, C.Q. Wang & M. Zhang (GDGM41951).

Notes – *Hygrophorus orientalis* was recently described from China by Huang et al. (2021). Previously, this species was treated as *H. russula* in numerous published sources (Chen & Li 2013). It is a common wild edible mushroom, locally called Rousimo or Tangzimo in northeastern China (Bau & Bao 2016, this study). Phylogenetically, *H. orientalis* is close to European *H. russula*. Four basepair positions showed stable difference between the two species. Morphologically, this species is characterized by its large pileus [up to 250 mm diam. according to Huang et al. (2021a)], dense lamellae, and small basidiospores [$5.5\text{--}7 \times 3.5\text{--}4.8 \mu\text{m}$ in Huang et al. (2021a) and $6\text{--}7.5(8) \times 3.5\text{--}5 \mu\text{m}$ in this study]. In China, the known distribution of this species is central, northeastern, and southwestern China, it is much more common in northeastern China than central China. For more images, detailed descriptions and comparisons with similar species, see Huang et al. (2021a) and Huang (2022).

Hygrophorus orientipurpurascens C.Q. Wang, Ming Zhang & T.H. Li, sp. nov. Fig. 25

Index Fungorum Number: IF901148; Facesoffungi number: FoF14938

Etymology – *orientipurpurascens*, from *orientalis* = eastern, and *purpurascens* = *Hygrophorus purpurascens*, is proposed because this new species is close to *H. purpurascens* and its type locality from the eastern country China.

Type – China, Yunnan Province, Diqing Tibetan Autonomous Prefecture, Shangri-la County, in a subalpine forest dominated by *Abies* sp. and *Quercus* sp., $27^{\circ}82'N$, $99^{\circ}96'E$, elev. ca. 3560 m, 2 September 2020, M. Zhang & L.Q. Wu (GDGM83073, Holotype).

Pileus 30–80 mm across, hemispherical to convex when young, becoming convex, plano-convex to appanate when mature, pinkish white, pale red, rose to red (11A2–6), sometimes with reddish to rosy discolouration when bruised, smooth or with minute fibrils when young, with rose to red squamules on the outer zone near margin when mature; margin decurved when young, arched, straight to even uplifted when mature, entire or lacerate when mature. *Lamellae* subdecurrent, decurrent to deeply decurrent, close, waxy, fragile, white, $L = 88\text{--}108$, $l = 1\text{--}3$; edge entire to subeven, usually changing to rose when mature. *Stipe* 40–70 mm long, 10–20 mm thick, cylindrical, robust, central, solid, usually concolorous with pileus, whitish when young with pinkish discolouration when bruised, becoming pinkish to purplish at maturity, with a white to light pinkish evanescent veil at apex when young. *Context* whitish, thick.

Basidiospores $(6)6.5\text{--}7.5 \times 4\text{--}5(5.5) \mu\text{m}$, $Lm = 6.99 \pm 0.37$, $Wm = 4.58 \pm 0.29$, $Q = (1.3)1.4\text{--}1.67$, $Qm = 1.53 \pm 0.09$, ellipsoid to elongate, smooth, hyaline, thin-walled. Basidia $31\text{--}46 \times 5.5\text{--}7 \mu\text{m}$, $Q = 5.64\text{--}7.33$, 4-spored, clavate, sterigmata $4\text{--}7 \mu\text{m}$ long. *Hymenophoral trama* divergent, made up of cylindrical, thin-walled, hyaline hyphae $3\text{--}19 \mu\text{m}$ wide. *Pileipellis* an ixotrichoderm, made up of interwoven hyphae $2.5\text{--}5.5 \mu\text{m}$ wide. *Stipitipellis* an ixocutis to ixotrichoderm, made up of usually repent and uplifted, cylindrical, thin-walled hyphae $3\text{--}6 \mu\text{m}$ wide. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Scattered on the ground in subalpine forests dominated by *Abies* sp. and *Quercus* spp., occurring in autumn, so far known from southwestern China (Yunnan Province).

Notes – *Hygrophorus orientipurpurascens* is characterized by its robust basidiomata, white lamellae with rose edges when mature, and the veil at stipe apex when young. In our phylogenetic analysis (Figs 1–2), *H. orientipurpurascens* is an independent species within the *H. purpurascens* complex. Species morphologically similar to this fungus are *H. purpurascens*, *H. fragilipurpurascens* and *H. pseudopurpurascens*. However, *H. purpurascens* has darker pileus, bigger [$7\text{--}8.5(9) \times 4\text{--}5 \mu\text{m}$] and narrower [$Qm = 1.70\text{--}1.76$] basidiospores and the distribution in Europe (Candusso 1997). *Hygrophorus fragilipurpurascens*, a new species described in this study (see above), differs from this fungus in its slender basidiomata with fragile lamellae. *Hygrophorus pseudopurpurascens* (see below) has slender basidiomata and usually depressed pileus disc.

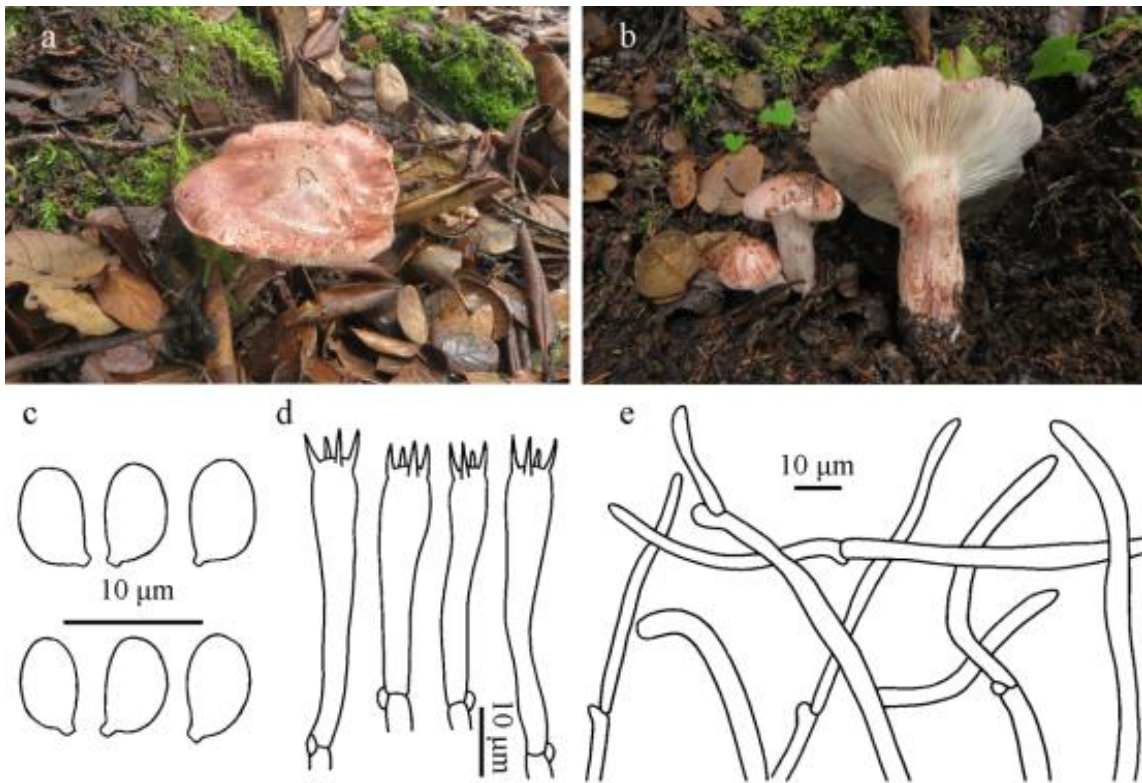


Figure 25 – *Hygrophorus orientipurpurascens* (GDGM83073). a–b Basidiomata. c Basidiospores. d Basidia. e Pileipellis.

Hygrophorus pallidoaurantiacus C.Q. Wang, Ming Zhang & T.H. Li, sp. nov.

Fig. 26

Index Fungorum Number: IF901147; Facesoffungi number: FoF14937

Etymology – *pallidoaurantiacus*, from *pallidus* = *pale*, and *aurantiacus* = orange, referring to its pale orange colour of pileus.

Type – China, Yunnan Province, Zhongdian County, in a subalpine coniferous forest dominated by *Abies* spp., 27°84'N, 99°98'E, elev. ca. 3830 m, 3 September 2020, M. Zhang & L.Q. Wu (GDGM82435, Holotype).

Pileus 50–130 mm across, convex when young, plano-convex, plane to depressed with an umbo when mature, pale yellow, light yellow, orange white, pale orange (4A3–4, 5A2–3), pale ochraceous overall, becoming lighter from disc to margin, viscid when wet, subviscid to non-viscid when dry; subglabrous when young, often fibrillose-squamulose or with exfoliating split pileipellis near margin when mature; margin decurved and entire when young, straight to uplifted and lacerated when mature. **Lamellae** adnate to subdecurrent, close, L = 64–80, l = 1–3, waxy, fragile, concolorous with pileus margin; edge entire and even when young, usually lacerated when mature. **Stipe** 40–120 mm long, 7–25 mm thick, central, solid, cylindrical, usually tapered downward to somewhat short radicate underground, pale yellow to pale orange, often fibrillose- to flocculose-squamulose. **Context** thick, white to orange white, 5–8 mm thick at stipe.

Basidiospores 6.5–7.5 × 4–4.5(5) μm, Lm = 7.15 ± 0.40, Wm = 4.38 ± 0.28, Q = 1.44–1.88, Qm = 1.64 ± 0.11, ellipsoid to elongate, smooth, hyaline, thin-walled. **Basidia** 36.5–53.5 × 5.0–7.0 μm, Q = 5.62–9.20, 4-spored, clavate to cylindrical; sterigmata 5.0–7.5 μm long. **Hymenophoral trama** divergent, made up of cylindrical or inflated, thin-walled, hyaline hyphae 3.5–22 μm wide. **Pileipellis** an ixotrichoderm, made up of upturned or interwoven aerial hyphae 3–5 μm wide, with a glutinous layer on surface in KOH. **Stipitipellis** as a trichoderm, made up of repent or upturned cylindrical thin-walled hyphae 4–6.5 μm wide. **Clamp connections** present in all tissues.

Habit, habitat and distribution – Scattered, gregarious or caespitose on the ground under conifer forests dominated by *Abies* spp., occurring in autumn, known from southwestern China (Yunnan Province).

Additional specimens examined – China, Yunnan Province, Zhongdian County, in a subalpine coniferous forest dominated by *Abies* spp., 27°84'N, 99°98'E, elev. ca. 3830 m, 3 September 2020, M. Zhang & L.Q. Wu (GDGM82424).

Notes – *Hygrophorus pallidoaurantiacus* is characterized by its large (up to 130 mm in diam.) and pale orange to pale ochraceous pileus, densely covered with white fibrills, usually adnate and fragile lamellae when mature, ellipsoid to elongate basidiospores measuring [6.5–7.5 × 4–4.5(5) μm], and the distribution in high elevation areas in southwestern China. In addition, the caespitose habit is not very common within the genus *Hygrophorus*. In the ITS phylogenetic analysis (Fig. 1), *H. pallidoaurantiacus* is sister to *H. flavoalbus* with low support value, while in the multigene phylogenetic analysis (Fig. 2), *H. pallidoaurantiacus* is sister to *chuxiongensis* with strong support value. The combination of abovementioned characters can distinguish *H. pallidoaurantiacus* from *H. chuxiongensis* and *H. flavoalbus*.

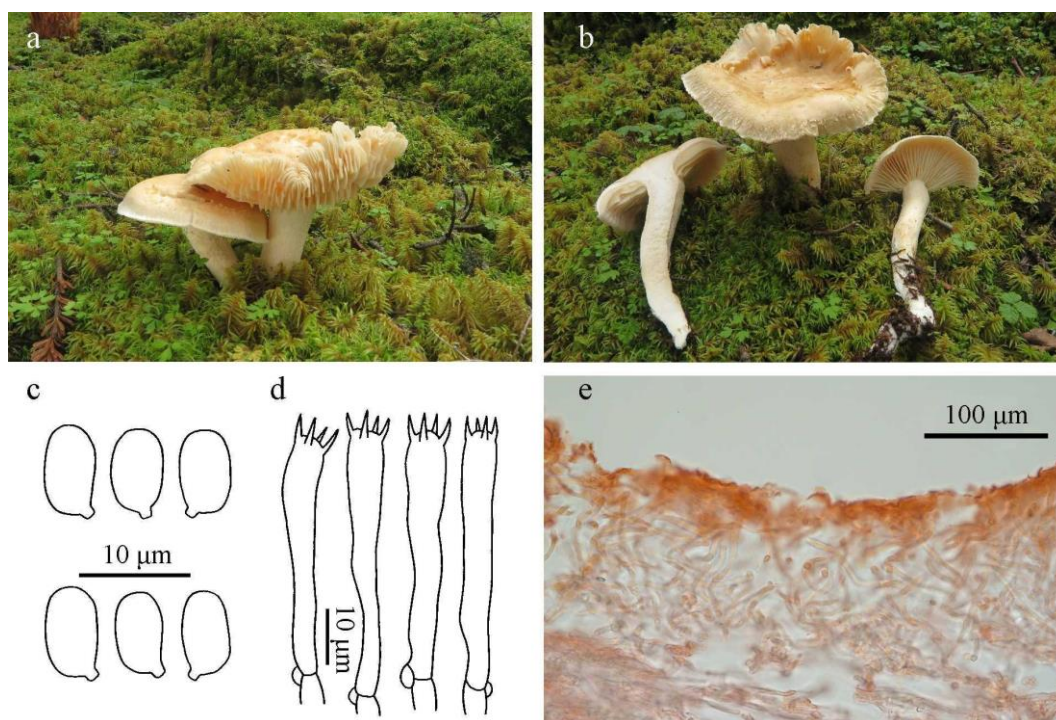


Figure 26 – *Hygrophorus pallidoaurantiacus* (GDGM82435). a–b Basidiomata. c Basidiospores. d Basidia. e Pileipellis.

Hygrophorus parvirussula H.Y. Huang & L.P. Tang, in Huang, Yang, Zeng, Zhang, Hu & Tang, *Phytotaxa* 373(2): 142 (2018) Fig. 27

Pileus 40–80 mm across, hemispheric to convex when young, then expanded to plano-convex, dull red, greyish red, orange red to red (8B3–7, 9B3–7), darker at disc, covered with reddish brown to greyish squamules at centre; margin incurved when young, then expanded. *Lamellae* adnate to subdecurrent, L = 68–84, l = 1–3, subdistant to close, waxy, fragile, whitish when young, pinkish to reddish purple when mature, sometimes with a brownish tint when bruised or mature. *Stipe* 60–120 × 12–25 mm, central to slightly eccentric, cylindrical, solid, equal, often slightly enlarged towards base; surface usually concolorous with lamellae, unsmooth, covered with greyish to reddish brown fine fibrils or scattered scales; basal mycelium white and dense. *Context* whitish to pinkish, usually thin in pileus.

Basidiospores (7)8–10 × 5–6.5(7) μm, Lm = 8.9 ± 0.69, Wm = 5.83 ± 0.5, Q = (1.33)1.36–1.67(1.8), Qm = 1.53 ± 0.12, ellipsoid to elongate, smooth, hyaline, thin-walled. *Basidia* 4-spored, clavate, 30–55 × 6–8 μm, thin-walled; sterigmata up to 6 μm long. *Hymenophoral trama* divergent, made up of cylindrical hyaline hyphae 3–15 μm wide. *Pileipellis* an ixotrichoderm, covered with strongly gelatinised materials, made of slender cylindrical and thin-walled hyphae 3–5 μm wide.

Stipitipellis a cutis, composed of thin-walled hyphae 3–8 μm wide. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Scattered on the ground under *Quercus* trees in broad-leaved forests, occurring in summer and autumn, known only from China (Sichuan Province, Tibet Autonomous Region, and Yunnan Province) (Huang et al. 2021).

Specimens examined – China, Tibet Autonomous Region, Nyingchi City, in a subalpine forest dominated by *Quercus* spp., 13 September 2015, M. Zhang (GDGM45208); Nyingchi City, Milin County, in a mixed subalpine forest with *Quercus aquifolioides*, *Picea* sp., *Betula* sp. 29°01'N, 93°53'E, elev. ca. 3220 m, 14 September 2016, T.Z. Wei, Z.X. Wu, L. Yang, H.D. Zheng, X.C. Wang (HMAS 280756); Nyingchi City, Nyingchi County, Lulang Town, in a subalpine forest dominated by *Q. aquifolioides*, 29°46'N, 94°44'E, elev. ca. 3400 m, 23 September 2016, T.Z. Wei, Z.X. Wu, L. Yang, H.D. Zheng, X.C. Wang (HMAS 280347). Yunnan Province, Diqing Tibetan Autonomous Prefecture, Shangri-la County, Pudacuo National Park, in a subalpine forest dominated by *Quercus* spp., 27°82'N, 99°96'E, elev. ca. 3560 m, 2 September 2020, M. Zhang & L.Q. Wu (GDGM83135).

Notes – *Hygrophorus parvirussula* was described from China by Huang et al. (2018). Phylogenetically, *H. parvirussula* is placed in an independent position within the *H. russula*-complex in both ITS and multilocus trees (Figs 1–2). Morphologically, this species is characterized by its fibrillose squamules at the pileus centre, and pinkish to reddish purple lamellae when mature. The species is only known to be distributed in southwestern China. For detailed descriptions and comparisons with similar species, see Huang et al. (2018).

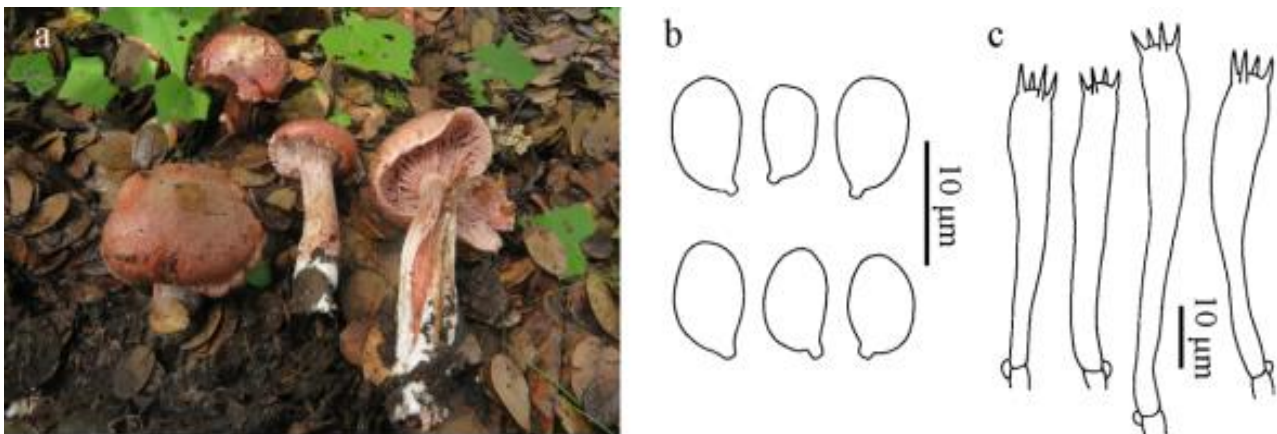


Figure 27 – *Hygrophorus parvirussula*. a Basidiomata (GDGM83135). b Basidiospores (HMAS280347). c Basidia (HMAS280347).

Hygrophorus pseudopurpurascens C.Q. Wang, Ming Zhang & T.H. Li, sp. nov. Fig. 28

Index Fungorum Number: IF901149; Facesoffungi number: FoF14939

Etymology – *pseudopurpurascens*, from *pseudo* = false, and *purpurascens* = *Hygrophorus purpurascens*; is proposed for the new species is similar to *H. purpurascens*.

Type – China, Yunnan Province, Diqing Tibetan Autonomous Prefecture, Shangri-la County, Pudacuo National Park, in a subalpine forest dominated by *Pinus* sp. and *Quercus* sp., 27°84'N, 99°98'E, elev. ca. 3850 m, 4 September 2020, M. Zhang & L.Q. Wu (GDGM83197, Holotype).

Pileus 30–65 mm across, hemispherical to convex when young, becoming convex to plano-convex when mature, usually depressed at disc, pinkish white, pale red, pastel red to red (9A2–6), usually lighter towards margin, subglabrous, slightly fibrillose to scaly, sometimes more or less concentrically scaly, sticky when wet; margin decurved when young, arched to straight when mature, whitish to pinkish white. *Lamellae* adnate to subdecurrent, subdistant to dense, waxy, fragile, white when young, usually spotted or streaked pinkish when mature, L = 55–65, l = 1–3 edge even when young, often slightly denticulate when mature. *Stipe* 35–110 mm long, 10–14 mm

thick, cylindrical, central, solid, ususally curved, usually concolorous with pileus or paler, often discolouring reddish to light reddish brown where injured, sometimes with a white to light pinkish cottony to fibrillose partial veil at apex. *Context* whitish, thick.

Basidiospores $6.5\text{--}7.5(8) \times 4\text{--}5(6.5) \mu\text{m}$, $Lm = 7.12 \pm 0.46$, $Wm = 4.54 \pm 0.48$, $Q = (1.08)1.4\text{--}1.75(1.88)$, $Qm = 1.58 \pm 0.15$, ellipsoid to elongate, smooth, hyaline, thin-walled. *Basidia* $32\text{--}58 \times 6.5\text{--}8 \mu\text{m}$, $Q = 4.53\text{--}7.86$, 4-spored, clavate, sterigmata $4.5\text{--}6 \mu\text{m}$ long. *Hymenophoral trama* divergent, made up of cylindrical, thin-walled, hyaline hyphae $4.5\text{--}6 \mu\text{m}$ wide. *Pileipellis* an ixocutis to ixotrichoderm, made up of repent or interwoven hyphae $2.5\text{--}6 \mu\text{m}$ wide. *Stipitipellis* an ixocutis, made up of usually repent and occasionally uplifted and clustered, cylindrical, thin-walled hyphae $2.5\text{--}6 \mu\text{m}$ wide. *Clamp connections* present in all tissues.

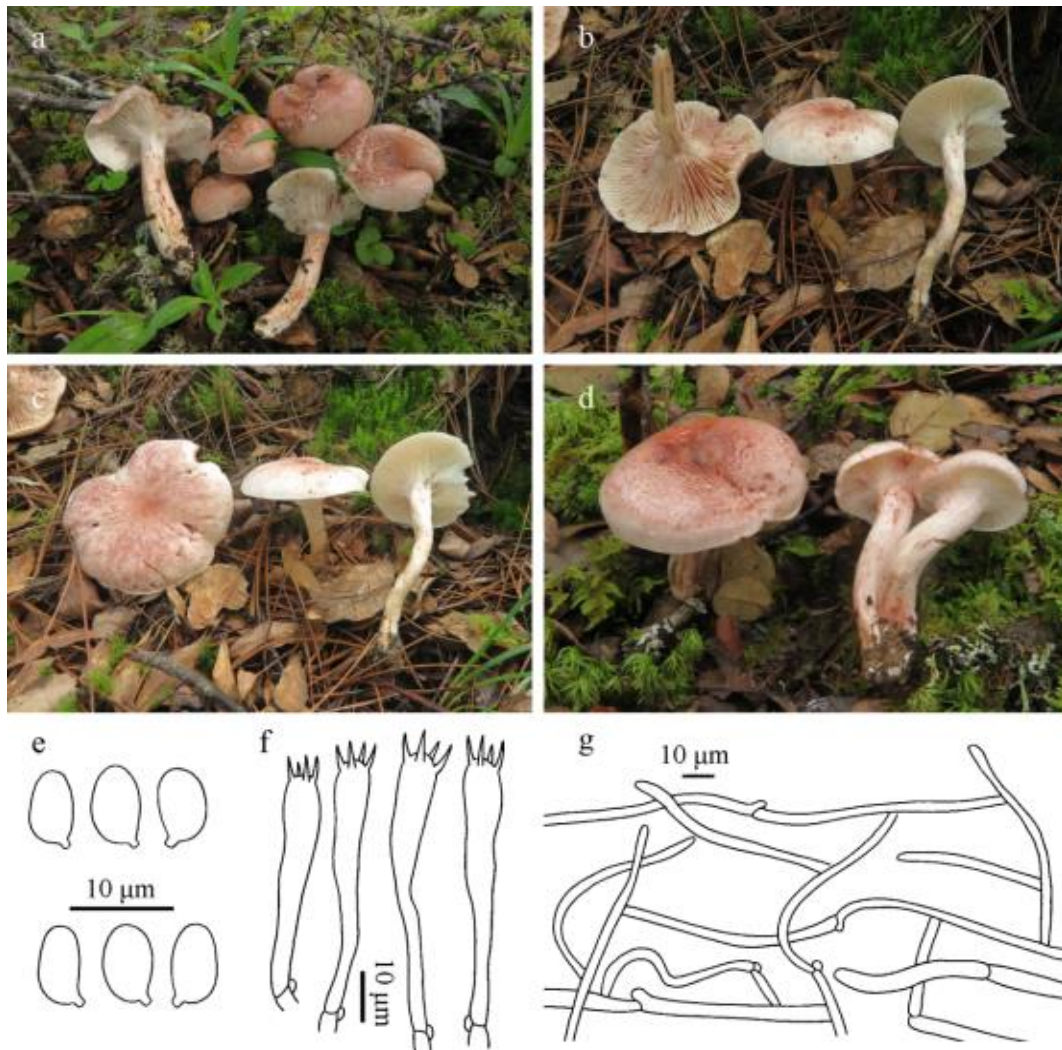


Figure 28 – *Hygrophorus pseudopurpurascens*. a Basidiomata (GDGM82365). b–c Basidiomata (GDGM83033). d Basidiomata (GDGM83197). e Basidiospores (GDGM83197). f Basidia (GDGM83197). g *Pileipellis* (GDGM83197).

Habit, habitat and distribution – Scattered on the ground in mixed forests dominated by *Pinus* spp. and *Quercus* spp., occurring in autumn, so far known from southwestern China (Yunnan Province).

Additional specimens examined – China, Yunnan Province, Diqing Tibetan Autonomous Prefecture, Shangri-la County, Pudacuo National Park, in a subalpine forest dominated by *Pinus* sp. and *Quercus* sp., $27^{\circ}84'N$, $99^{\circ}98'E$, elev. ca. 3850 m, 4 September 2020, M. Zhang & L.Q. Wu (GDGM82365); Shangri-la County, in a subalpine forest dominated by *Pinus* sp. and *Quercus* sp., $27^{\circ}71'N$, $99^{\circ}72'E$, elev. ca. 3330 m, 1 September 2020, M. Zhang & L.Q. Wu (GDGM83033).

Notes – *Hygrophorus pseudopurpurascens* is a slender, pale red tinged species with a squamosa pileus surface and usually depressed pileus disc, growing in a mixed broadleaf-coniferous forest. Phylogenetic analysis of ITS dataset (Fig.1) supported this fungus to be a distinct species related to the European *H. purpurascens*. Compared with *H. purpurascens*, *H. pseudopurpurascens* has slender basidiomata and smaller basidiospores [$6.5\text{--}7.5(8) \times 4\text{--}5(6.5) \mu\text{m}$]. This fungus is similar to species of *H. russula* complex and *H. erubescens* complex, but the cottony to fibrillose partial veil of young fruitbodies make it easy to distinguish this new taxon from those similar species.

Hygrophorus pudorinus (Fr.) Fr., Anteckn. Sver. Ätl. Svamp.: 46 (1836)

Fig. 29

Pileus 40–140 mm across, hemispherical when young, convex, plano-convex to depressed with an obtuse umbo when mature, pinkish white, pale red, pastel red (9A2–5), and pale orange, light orange, greyish orange (5A3–4, 5B3–4) in dry season, sticky when wet, bald; margin decurved when young, then straight to uplifted, usually entire. *Lamellae* adnate, adnate with decurrent tooth, adnexed, subdistant to close, waxy, fragile, pinkish white, usually without obvious discolouration when mature, sometimes with pinkish discolouration when injured, L = 56–80, l = 1–3; edge entire and smooth. *Stipe* 30–180 mm long, 8–15 mm thick, central, solid, more or less cylindrical, pinkish white at first, reddish hairy or dotted when mature, with reddish discolourations when mature. *Context* pinkish white, thick.

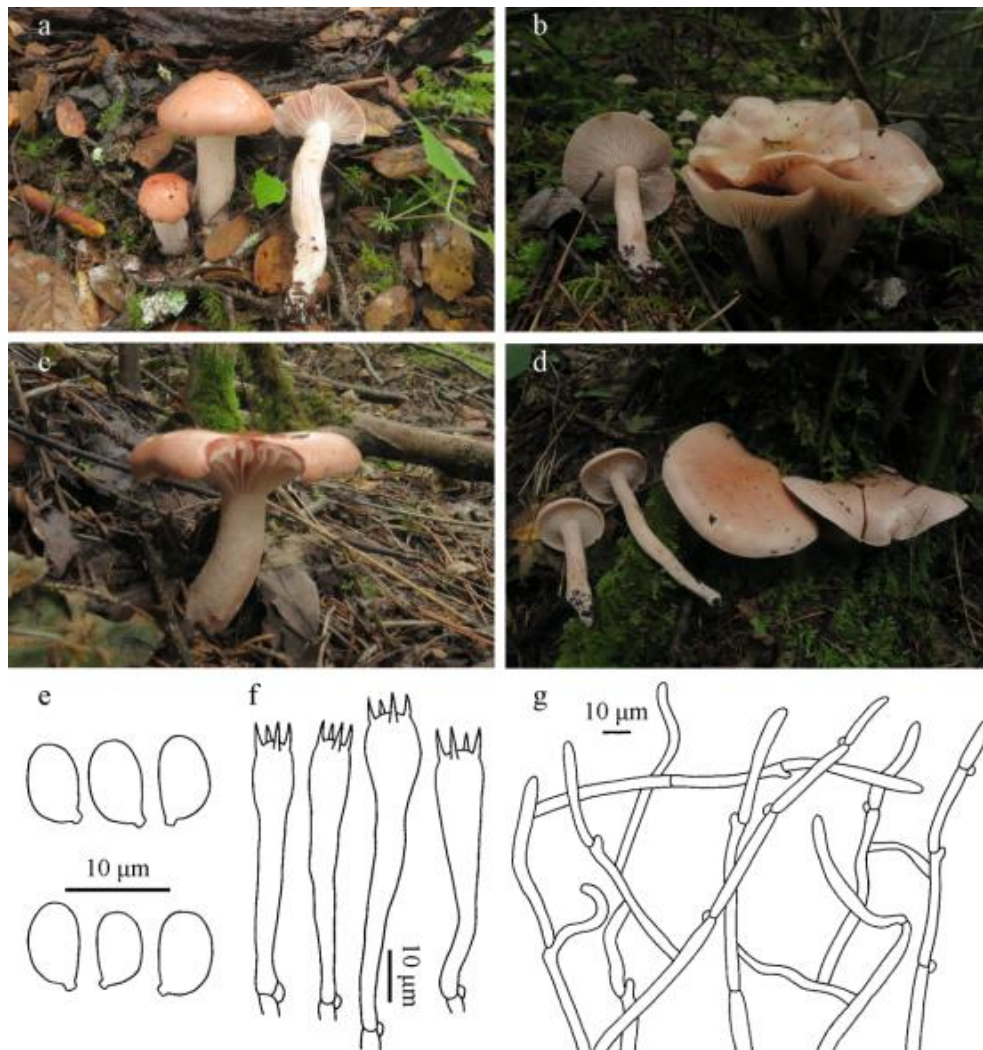


Figure 29 – *Hygrophorus pudorinus*. a Basidiomata (GDGM83072). b Basidiomata (GDGM84620). c–d Basidiomata (GDGM84701). e Basidiospores (GDGM84701). f Basidia (GDGM84701). g Pileipellis (GDGM84701).

Basidiospores 7–9(9.5) × 4.5–5.5 μm, Lm = 7.85 ± 0.63, Wm = 4.73 ± 0.34, Q = 1.56–1.78(1.89), Qm = 1.66 ± 0.08, broadly ellipsoid to elongate, smooth, hyaline, thin-walled. *Basidia* 40–78 × 6–9.5 μm, Q = 4.71–12.91, 4-spored, clavate, sterigmata 5–6 μm long. *Hymenophoral trama* divergent, made up of cylindrical, thin-walled, hyaline hyphae 5–14 μm wide. *Pileipellis* an ixotrichoderm, made up of upturned or interwoven aerial hyphae 2–5.5 μm wide, with a glutinous layer on the surface in KOH. *Stipitipellis* an ixocutis, made up of repent or upturned and clustered cylindrical thin-walled hyphae 3–7 μm wide. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Solitary, scattered or gregarious in subalpine forests; basidioma occurring in autumn; known from Asia, Europe and North America; in China only known from southwestern China (Sichuan Province and Yunnan Province).

Specimens examined – China, Sichuan Province, Jiuzhaigou County, Jiuzhaigou Scenic Spot, in a subalpine forest dominated by *Picea* sp., elev. ca. 3000 m, 19 September 2020, M. Zhang & J.H. Xing (GDGM84620, GDGM84701). Yunnan Province, Shangri-la, in a subalpine forest, 27°82'N, 99°96'E, elev. ca. 3560 m, 2 September 2020, M. Zhang & L.Q. Wu (GDGM83072).

Notes – *Hygrophorus pudorinus* is a tricholoma-like mushroom within the genus *Hygrophorus*. Morphologically, *H. pudorinus* is a very variable fungus, having pinkish white to red and almost smooth pileus in normal condition but pale orange to greyish orange and squamose pileus in a dry condition. This species is described from Europe, and according to sequence data it also occur in Asia and North America. Ecologically, *H. pudorinus* grows with *Picea*. For a long time, specimens associated with *Abies* were indentified as *H. pudorinus*. Recently, *Abies* associated collections were formally described as *H. abieticola* Krieglst. ex Gröger & Bresinsky (Larsson & Jacobsson 2014). In addition, Larsson & Jacobsson (2014) confirmed that *H. persicolor* is a later synonym of *H. pudorinus*.

Hygrophorus qinggangjun H.Y. Huang & L.P. Tang, in Huang, Zhang, Huang, Gabriel, Liu & Tang, Mycol. Progr. 20(9): 1128 (2021) Fig. 30

Pileus 80–120 mm across, hemispherical when young, then expanding to convex, convex, plano-concave to concave, purple, greyish rose, greyish ruby (12B4–7, 12C4–7, 12D4–7, 12E4–7), paler from disc to margin; margin entire, occasionally split, decurved when young, straight to upturned when mature. *Lamellae* adnate to subdecurrent, subdistant, L = 64–88, l = 1–3, waxy, fragile, whitish to pinkish, with scattered pinkish dots; edge usually entire, with light discolouration when bruised or touched. *Stipe* 70–100 × 13–16 mm, central to slightly eccentric, cylindrical, occasionally with 1–2 grooves, subequal, sometimes curved; surface unsmooth, covered with fibrils. *Context* whitish to pinkish white, colour slightly deepening on exposure.

Basidiospores (6)7–8(8.5) × 4.5–5.5 μm, Lm = 7.5 ± 0.54, Wm = 4.93 ± 0.37, Q = 1.33–1.78, Qm = 1.53 ± 0.13, ellipsoid to elongate, thin-walled, hyaline in KOH. *Basidia* 37.0–51.0 × 6.0–7.0 μm, Q = 5.29–7.85, 4-spored, clavate, with sterigmata 3.5–7 μm long. *Hymenophoral trama* divergent, made up of cylindrical or inflated hyaline hyphae 3–12 μm wide. *Pileipellis* an ixotrichoderm, made up of mostly upturned or interwoven, branched or non-branched, gelatinized, often curved hyphae 2–6 μm wide. *Stipitipellis* a cutis, consisting of repent, cylindrical, thin-walled hyphae 2.5–6 μm wide. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Solitary or scattered on the ground under mixed forests dominated by *Pinus* and *Quercus* trees, occurring in summer and autumn, so far known from China (Yunnan Province) (Huang et al. 2021).

Specimens examined – China, Yunnan Province, Wuding County, Wansongshan, in a *Pinus* and *Quercus* trees dominated mixed forest, elev. 2523 m, 5 October 2019, H.F. Bai (GDGM83741).

Notes – *Hygrophorus qinggangjun* was recently described from southwestern China. It is a wild edible mushroom, but less common than *H. deliciosus*, which is called as “Qinggangjun” or “Hongqinggangjun” in Sichuan and “Mitangjun” in Yunnan. Phylogenetically, *H. qinggangjun* formed an independent clade within *H. russula*-complex in the ITS tree (Fig. 1), while it is placed close to *H. deliciosus* in the multilocus tree (Fig. 2). Morphologically, *H. qinggangjun* differs from

H. deliciosus by thinner context, and occurrence in lower elevations (usually 2000–2800 m) in *Quercus serrata* dominated forest. For detailed descriptions, comparisons with similar species and more images see Huang et al. (2021).

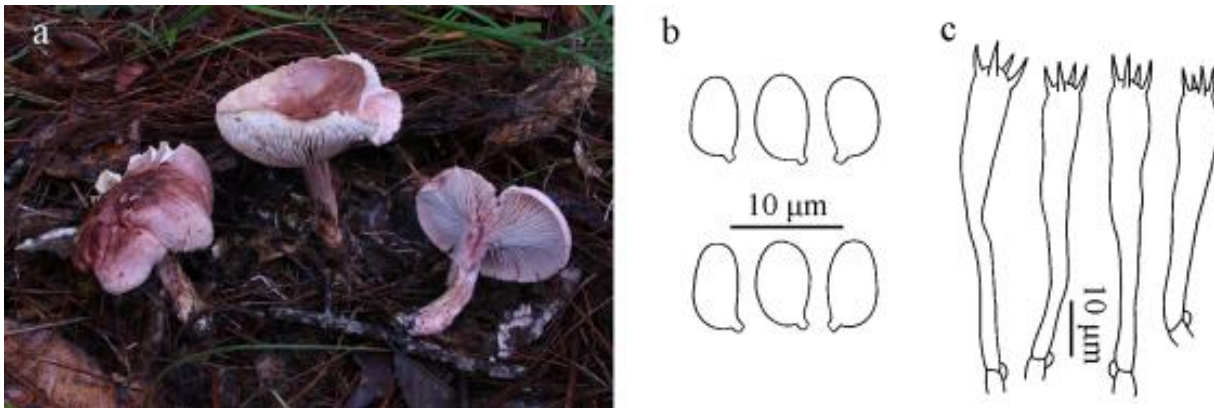


Figure 30 – *Hygrophorus qinggangjun*. a Basidiomata (GDGM83741, by H.F. Bai). b Basidiospores (GDGM83741). c Basidia (GDGM83741).

Hygrophorus yunnanensis H.Y. Huang & L.P. Tang, in Huang, Zhang, Huang, Gabriel, Liu & Tang, Mycol. Progr. 20(9): 1130 (2021) Fig. 31

Pileus 40–80 mm across, conical to hemispherical when young, then expanding to convex to plane, greyish rose, purple, greyish ruby (12B3–5, 12C3–5, 12D3–5, 11E3–5), obviously scaly when dry; margin incurved at first, then decurved to straight. *Lamellae* adnate to subdecurrent, subdistant, L = 76–100, l = 1–3, pinkish, with reddish-purple discolouration when bruised; edge whitish to pinkish. *Context* whitish to pinkish, becoming darker on exposure. *Stipe* 40–100 mm long, 10–20 mm broad, central, cylindrical, tapering downwards, whitish, pinkish to brownish violet.

Basidiospores (5)6–7(7.5) × (3)3.5–5 µm, Lm = 6.57 ± 0.59, Wm = 4.1 ± 0.54, Q = 1.4–1.86(2), Qm = 1.62 ± 0.18, ellipsoid to oblong, smooth, thin-walled, hyaline, non-amyloid. *Basidia* 37–55 × 6–10 µm, 4-spored, clavate, slender, thin-walled; sterigmata 4–9 µm long. *Lamellar trama* divergent, composed of slender and inflated, thin-walled hyphae 3–20 µm broad. *Pileipellis* an ixotrichoderm, consisting of hyphae 3–5 µm broad. *Stipitipellis* a cutis, composed of thin-walled hyphae 3–5 µm broad. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Solitary to scattered on the ground under *Lyonia ovalifolia* or *Ternstroemia gymnanthera* trees in broad-leaved forests, occurring in summer and autumn (Huang et al. 2021), known from China (Yunnan Province).

Specimens examined – China, Yunnan Province, Chuxiong Yi Autonomous Prefecture, Lufeng County, in a mixed broadleaf-conifer forest, elev. ca. 2400 m, 17 September 2022, X.L. Gao (GDGM89522); Kunming City, Miaogao Temple, elev. ca. 2100 m, 6 August 2006, Y.C. Li 688 (HKAS 50442); Yongping Prefecture, National Highway 320, 25°29'N, 99°39'E, elev. ca. 2200 m, 30 July 2009, L.P. Tang 1025 (HKAS 56982).

Notes – *Hygrophorus yunnanensis* was described from Yunnan Province in southwestern China (Huang et al. 2021). According to local people, the fungus is relatively frequent but not tasty, therefore, it is hard to see this fungus on local market. Morphologically, *H. yunnanensis* is distinctive by its ellipsoid to oblong basidiospores [7.5–9.5 × 4–5 µm in Huang et al. (2021a), (5)6–7(7.5) × (3)3.5–5 µm in this study], and occurring at elevations 2100–2600 m. Phylogenetically, this fungus is placed in an independent position within *H. russula*-complex in both ITS and multilocus trees (Figs 1–2). In the ITS tree, a sequence (UDB013267) from Papua New Guinea is clustered with sequences of *H. yunnanensis* from Yunnan, suggesting that this species is not limited to this Chinese Province. For more images, detailed descriptions and comparisons with similar species, see Huang et al. (2021a).

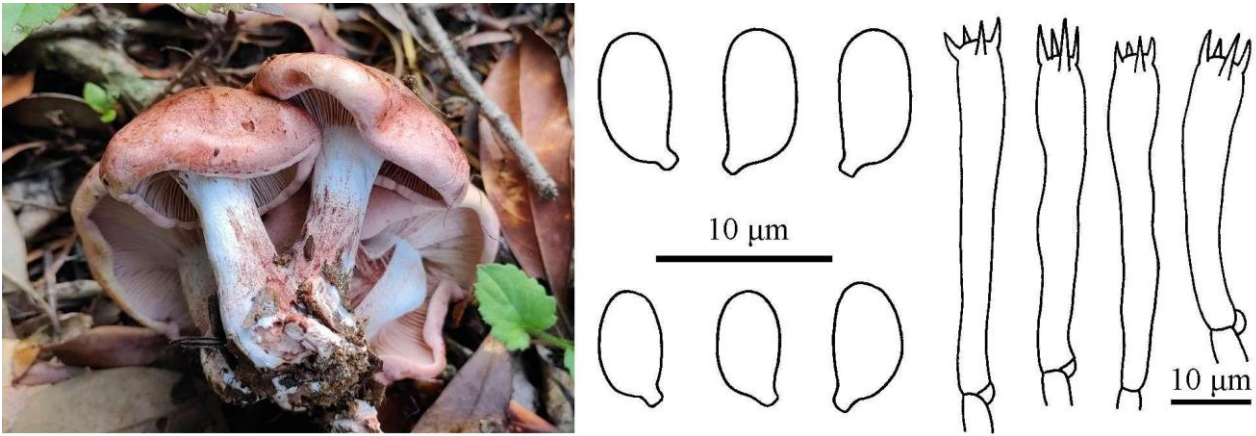


Figure 31 – *Hygrophorus yunnanensis*. a Basidiomata (GDGM89522, by X.L. Gao). b Basidiospores (HKAS 50442). c. Basidia (GDGM89522).

Hygrophorus sect. *Olivaceoumbrini*

Phylogenetic support: Although section *Olivaceoumbrini* s.l. is not a monophyletic group in the ITS analysis (Fig. 1), section *Olivaceoumbrini* s.l. appears as a well-supported (94% MLBS) monophyletic group in the multigene analysis (Fig. 2). Thus, the traditional section *Olivaceoumbrini* is accepted in this study.

Studied Chinese species included in this section: *Hygrophorus agathosmoides*, *H. annulatus*, *H. atrofuscus*, *H. brunneiceps*, *H. fuscodiscus*, *H. habaensis*, *H. pallidoagathosmus*, *H. pinophilus*, *H. queletii*, *H. sichuanensis* and *H. viridiflavus*.

Hygrophorus agathosmoides Lebeuf, E. Larss. & Bellanger, in Bellanger, Lebeuf, Sesli, Loizides, Schwarz, Moreau, Liimatainen & Larsson, *Persoonia* 46: 295 (2021) Fig. 32

Pileus 25–65 mm across, hemispherical to convex when young, then expanding to plano-convex, often with a low obtuse umbo, grey, orange grey to brownish grey (5B1–2, 5C1–2), darker at centre; margin incurved, sometimes undulating when mature. *Lamellae* subdecurrent to decurrent, arcuate, subdistant, waxy, white, L = 44–56, l = 1–3; edge usually even, sometimes irregularly eroded, rarely lacerate. *Stipe* 40–60 × 4–8 mm, cylindrical, often slightly enlarging upwards or downwards, white, whitish to brownish, covered with white to brownish floccules from apex to one half or lower third. *Context* white to greyish white, thick. *Taste* mild.

Basidiospores (7.5)8–9.5(10) × (4.5)5.0–6.0 µm, Q = 1.42–1.8, ellipsoid to elongate, smooth, hyaline, thin-walled, inamyloid. *Basidia* 4-spored, narrowly clavate, 40–67 × 7.5–11.5 µm, with sterigmata 3.5–5 µm long. *Hymenophoral trama* divergent, made up of cylindrical or inflated, thin-walled, hyaline hyphae 2–7.5 µm wide. *Pileipellis* an ixotrichoderm, made up of gelatinized, distant, branched, upturned or interwoven hyphae 1.5–3.5 µm wide. *Stipitipellis* a trichoderm, made up of repent and upturned cylindrical thin-walled hyphae 3–7.5 µm wide. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Scattered in *Picea mongolica* dominated forest; basidiomata occurring in summer and autumn; known from northeastern China (Inner Mongolia Autonomous Region) and Europe (Bellanger et al. 2021, this study).

Specimens examined – China, Inner Mongolia Autonomous Region, Chifeng City, Hexigten Banner, Baiyin Aobao National Nature Reserve, in a *Picea mongolica* dominated forest, elev. ca. 1300 m, 4 September 2018, G.L. Yu & T.Z. Liu (CFSZ20158). Italy, Becetto di Sampeyre, 2 October 2010, T.H. Li (GDGM40324).

Notes – *Hygrophorus agathosmoides* was reported from Canada, France, Norway, Sweden and USA by Bellanger et al. (2021); and subsequently recorded from Yunnan Province of China in Huang et al. (2022b). Phylogenetically, the newly generated Chinese and Italian sequences are clustered with the holotypes of *H. agathosmoides* (MT981656), *H. agathosmoides* f. *albus* E. Larss.

& Lebeuf (MH656461) and *H. agathosmoides* f. *trabzonensis* Sesli (MG888785). Morphologically, the Chinese samples of *H. agathosmoides* has grey to brownish grey pileus [having less orangish tint comparing with holotype collections HRL2823/DAOM984765 from Canada in Bellanger et al. (2021)], and the Italian sample has paler pileus [similar to the collection EL294-13 from Norway in Bellanger et al. (2021)]. In China, the species is only known from Inner Mongolia Autonomous Region, but it may also occur in other temperate continental climate areas in northern China. For images, detailed descriptions and comparisons with similar species of *H. agathosmoides* see Bellanger et al. (2021).



Figure 32 – *Hygrophorus agathosmoides*. a Basidiomata from China (CFSZ20158). b Basidiomata from Italy (GDGM40324). c Basidiospores. d Basidia. e Pileipellis.

Hygrophorus annulatus C.Q. Wang & T.H. Li, in Wang, Li, Wang, Wei, Zhang & He, *Mycoscience* 62(2): 138 (2021) Fig. 33

Pileus 20–100 mm across, hemispherical to convex when young, later becoming subumbilicate, plano-convex or applanate, olive brown, greyish brown, to dark brown (4F3–7, 6E3–4, 6F3–7) at disc, paler from disc to margin, sticky when wet; margin involute when young and inflexed to deflexed when mature, entire to irregularly fissured, even to wavy. *Lamellae* narrowly adnate or subdecurrent, up to 5 mm broad, white, sometimes with pinkish tint, waxy, subdistant, L = 40–60, l = 1–3; edge even, concolorous. *Stipe* 60–150 mm long, 5–20 mm broad, central, subcylindrical, solid, with a brownish annulus or partial veil at upper part of stipe, white above the annulus and greyish to dark brown below the annulus. *Context* thick, white, soft. *odour* mild.

Basidiospores (8.0–)8.5–11.0(–12.0) × 5.0–7.5(–8.0) µm, Lm = 10.0 ± 0.9, Wm = 6.3 ± 0.8, Q = (1.33–)1.36–1.82(–1.83), Qm = 1.60 ± 0.12, ellipsoid to elongate, thin-walled, hyaline in KOH. *Basidia* (37.0–)41.0–65.0(–71.0) × (7.5–)8.0–11.0(12.5) µm, Lm = 51.8 ± 9.2, Wm = 10 ± 1.2, Q = 4.2–6.8, Qm = 5.26 ± 0.82, clavate, 4-spored, thin-walled; sterigmata 4.5–8.5 µm long. *Hymenophoral trama* divergent, consisting of thin-walled, hyaline and septate hyphae 30–85 × 4–12 µm. *Pileipellis* an ixocutis to ixotrichoderm, covering with a gelatinous zone; composed with thin-walled hyphae 3–5 µm wide, with brown intracellular pigment. *Stipitipellis* an ixocutis,

composed of thin-walled, hyphae 3–5 μm wide, with brown intracellular pigment. *Clamp connections* present in all tissues.

Habit, habitat and distribution – solitary to scattered on the ground in subalpine coniferous forests or coniferous and broadleaved mixed forests, under various spruces and/or firs, particularly *A. forrestii*, *A. georgei*, *P. asperata*, *P. likiangensis*.; so far only known from southwestern China (Sichuan Province, Tibet Autonomous Region and Yunnan Province), mostly found at elevations between 3000 m and 4300 m.

Specimens examined – China, Sichuan Province, Jiuzhaigou County, on the way to Shenxianchi Scenic Spot, in a subalpine mixed forest, 21 September 2020, Ming Zhang (GDGM84540, GDGM84591). Songpan County, in a forest of conifer trees, 23 September 2020, Ming Zhang (GDGM84413).

Notes – *Hygrophorus annulatus* was recently described from southwestern China by Wang et al. (2021). This species belongs to the *H. olivaceoalbus* complex in subsect. *Olivaceoumbrini* (Bataille) Singer. This fungus was previously treated as *H. olivaceoalbus* in numerous published sources from China (Chen & Li 2013). It is a common wild edible mushroom called as “Jisijun” or “Lushuijun” in Aba and Garze Prefectures of Sichuan Province (He et al. 2021). For detailed descriptions, comparisons with similar species and images of *H. annulatus* see Wang et al. (2021) and Huang et al. (2022b).

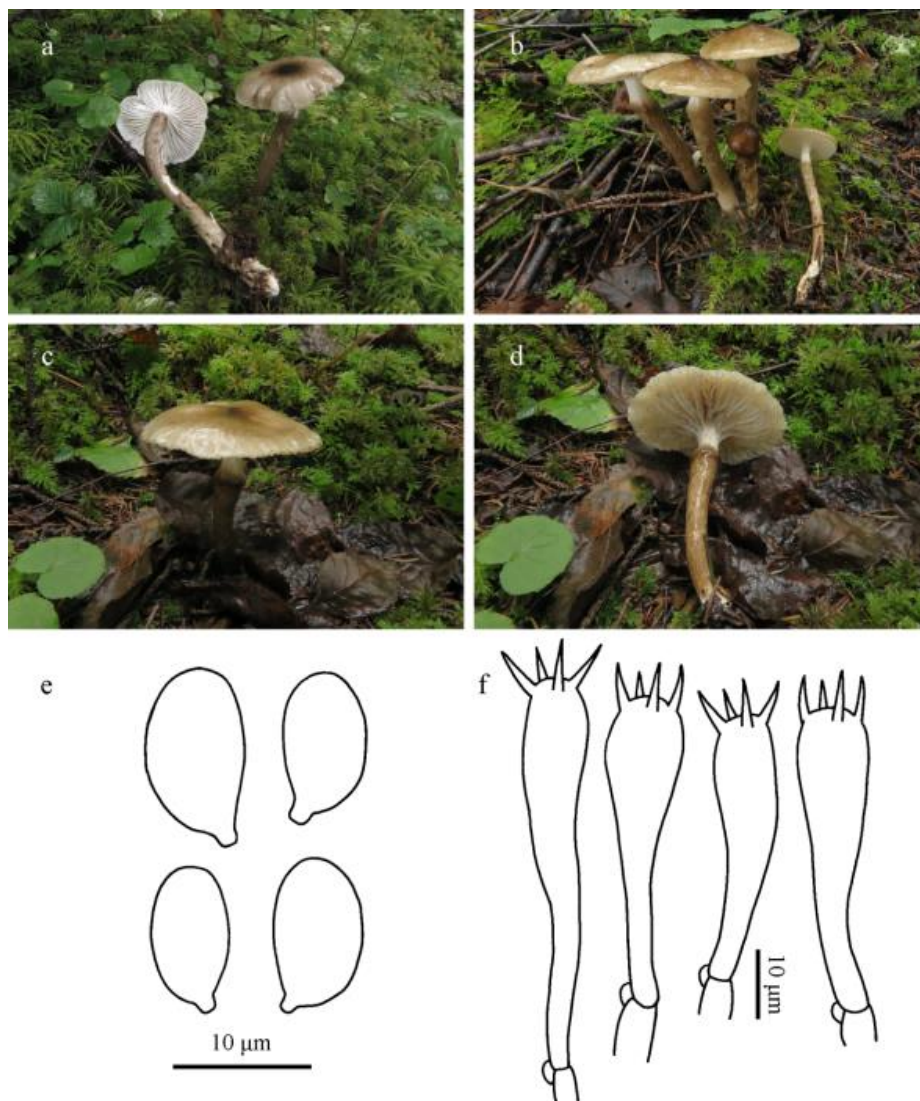


Figure 33 – *Hygrophorus annulatus*. a Basidiomata (GDGM84413). b Basidiomata (GDGM84540). d Basidiomata (GDGM84591). e Basidiospores (GDGM84591). f Basidia (GDGM84591).

Hygrophorus atrofuscus H.Y. Huang & L.P. Tang, in Huang, Zhang, Huang, Jiang, Hao, Mu & Tang, Mycol. Progr. 21(5, no. 51): 10 (2022) Fig. 34

Pileus 40–60 mm diam., convex to plane, grey, brown to dark brown; surface covered with a thick glutinous layer. *Lamellae* adnate, subdistant, L = 52–68, l = 1–3, whitish. *Stipe* 50–150 mm long, 6–20 mm broad, central, cylindrical, with viscid partial veil at apex, white above partial veil, covered with glutinous brown fibrils below partial veil.

Basidiospores (8)8.5–10(11.5) × (5)5.5–7(8) μm, Q = (1.31)1.36–1.73(1.9), Qm = 1.56 ± 0.14, ellipsoid to oblong, thin-walled, hyaline, non-amyloid. *Basidia* (44.5)46–56 × (8)9–14.5(16.5) μm, thin-walled, 4-spored, clavate, slender; sterigmata up to 10 μm in length. *Hymenophoral trama* divergent, composed of cylindrical or inflated, thin-walled and hyaline hyphae. *Pileipellis* an ixotrichoderm, consisted of slender, thin-walled, branched or non-branched hyphae. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Scattered to gregarious in broadleaf or broadleaf-conifer tree forests (elev. over 2000 m), occurring in summer; so far only known from China (Yunnan Province).

Specimens examined – China, Yunnan Province, Chuxiong Yi Autonomous Prefecture, Nanhua County, Wild Mushroom Market, 12 August 2008, Y.C. Li 1437 (HKAS 56277); Yulong Prefecture, Stone Town, in broadleaved tree forests, elev. ca. 2200 m, August 2008, Q. Zhao 8307 (HKAS 55271).

Notes – *Hygrophorus atrofuscus*, is an uncommon edible mushroom in local markets of Yunnan Province. In the ITS phylogenetic tree (Fig. 1), *H. atrofuscus* was sister to the North American *H. paludosoides* Hesler & A.H. Sm. However, *H. paludosoides* has lighter pileus colour (olive brown to pale fuliginous), and smaller basidiospores measuring 7–9 × 5–5.5 μm (Hesler & Smith 1963). For more detailed descriptions and comparisons with similar species, see Huang et al. (2022b).

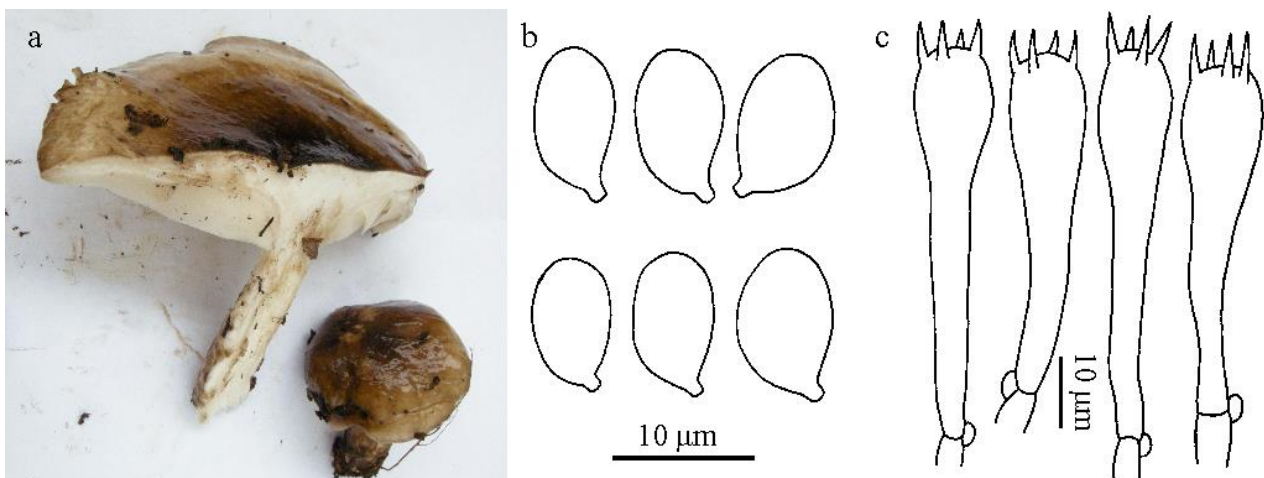


Figure 34 – *Hygrophorus atrofuscus*. a Basidiomata (HKAS 56277, by Y.C. Li). b Basidiospores (HKAS 55271). c Basidia (HKAS 55271).

Hygrophorus brunneiceps H.Y. Huang & L.P. Tang, in Huang, Zhang, Huang, Jiang, Hao, Mu & Tang, Mycol. Progr. 21(5, no. 51): 11 (2022) Fig. 35

Pileus 20–70 mm across, conic to convex with an umbo when young, then plano-convex, applanate, greyish brown, light brown, brown (5D3–4, 5E3–4), usually darker at disc and lighter outwards to margin, sometimes brownish grey to greyish brown (5C2, 5D2–3) at very margin when mature, viscid to sticky when wet; margin arched, straight to uplifted. *Lamellae* adnate to subdecurrent, L = 36–60, l = 1–3, distant to subdistant, thickish, waxy, fragile, white when young, orange grey to brownish grey (5B2, 5C2, 5D2) when mature, even at edge. *Stipe* 40–90 mm long,

4–10 mm broad, cylindrical, often narrower at the apex and base, usually curved, easily broken, with obvious brownish floccules. *Context* white, thin in the pileus.

Spores (7.5) 8.0–10.0(10.5) × 5.0–7.0 μm, Q = 1.21–1.8, broadly ellipsoid, elliptical to elongate, smooth, hyaline, thin walled, inamyloid. *Basidia* 4-spored, clavate, 46–65 × 8.5–12 μm; sterigmata 6–9 μm long. *Hymenophoral trama* divergent, made of cylindrical or inflated, rarely branched, thin-walled subparallel hyaline hyphae 2–13 μm broad. *Pileipellis* an ixotrichoderm, covering with refractive granular material in the gelatinous layer, especially on the outermost part, sometimes made up of repent hyphae and sometimes made up of upturned and interwoven hyphae, hyphae 3–7 μm wide, often curved, thin walled, usually with brown intracellular pigment. *Stipitipellis* an ixocutis, made up of slender, cylindrical, smooth, hyaline and thin-walled, hyphae 2–5 μm wide, with brown intracellular pigment. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Scattered to gregarious on the ground under coniferous trees, occurring in autumn, so far known from northwestern and southwestern China (Gansu Province, Sichuan Province, Tibet Autonomous Region, Yunnan Province and Xinjiang Autonomous Region) (Huang et al. 2022, this study).

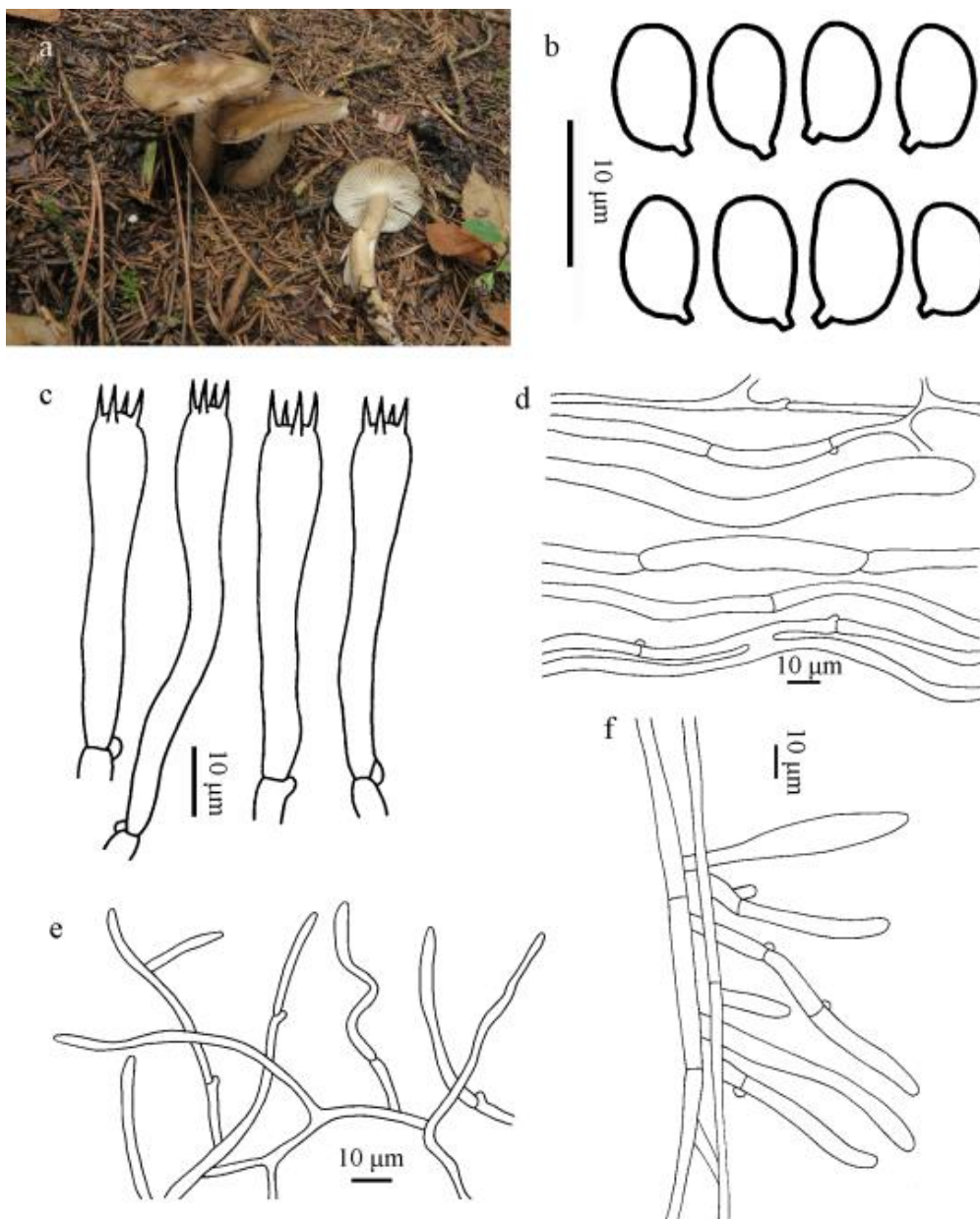


Figure 35 – *Hygrophorus brunneiceps* (GDGM84530). a Basidiomata. b Basidiospores. c Basidia. d Hymenophoral trama hyphae. e Terminal hyphae of pileipellis. f Elements of stipitipellis.

Specimens examined – China, Gansu Province, Sunan Yugur Autonomous County, Sidalong forestry farm, in a forest dominated in *Picea crassifolia*, elev. ca. 2700 m, 38°26'31"N, 99°54'25"E, 8 September 2020, C.Q. Wang (GDGM81654). Sichuan Province, Jiuzhaigou County, Jiuzhaigou, elev. ca. 3100 m, 11 September 2012, X.L. He (SAAS156); Jiuzhaigou, in a forest of conifer trees, elev. ca. 2600 m, 23 September 2020, M. Zhang & J.H. Xing (GDGM84530).

Notes – *Hygrophorus brunneiceps* was described based on material from Sichuan, Tibet, Yunnan and Xinjiang of China by Huang et al. (2022b). It can be distinguished by yellowish-brown to brown pileus, obvious brownish floccules on stipes, and the host association with *Picea* spp. in western China. This is a common species within *H. agathosmus* complex in both northwestern and southwestern China. The known elevation range (2400–3900 m) of *H. brunneiceps* is similar to that of *Picea* spp. in China. For detailed descriptions, comparisons with similar species, and photos of *H. agathosmoides* see Huang et al. (2022b).

Hygrophorus brunnescens C.Q. Wang, Ming Zhang & T.H. Li, sp. nov.

Fig. 36

Index Fungorum Number: IF901150; Facesoffungi number: FoF14940

Etymology – *brunnescens* = discolouring to brown, referring to its browning discolouration of lamellae when mature.

Type – China, Sichuan Province, Songpan County, Erdaohai, in a forest of conifer trees, elev. ca. 3300 m, 23 September 2020, M. Zhang & J.H. Xing (GDGM84456, Holotype).

Pileus 30–70 mm across, depressed, umbilicate to shallowly infundibuliform, greyish brown, light brown, brown (5D3–4, 5E3–4), brownish grey to greyish brown (5C2, 5D2–3) at margin, usually lighter towards the margin, viscid to sticky when wet; margin arched, straight to uplifted. *Lamellae* adnate to subdecurrent, distant to subdistant, L = 36–60, l = 1–3, thickish, waxy, fragile, white when young, orange grey to brownish grey (5B2, 5C2, 5D2) when mature, even at edge. *Stipe* 70–90 mm long, 4–9 mm broad, cylindrical, equal or slightly enlarged in the middle, often narrower at the apex and base, usually curved, brittle, with brownish fibrils. *Context* white, thin. *Basidiospores* (7.5) 8.0–10.0(10.5) × 5.0–7.0 μm, Q = 1.21–1.8, broadly ellipsoid, elliptical to elongate, smooth, hyaline, thin walled, inamyloid. *Basidia* 4-spored, narrowly clavate, 46–65 × 8.5–12 μm; sterigmata 6–9 μm long. *Hymenophoral trama* divergent, made of cylindrical or inflated, rarely branched, thin-walled subparallel hyaline hyphae 2–13 μm broad. *Pileipellis* an ixotrichoderm, covering with refractive granular material in the gelatinous layer, especially on the outermost part, sometimes made up of repent hyphae and sometimes made up of upturned and interwoven hyphae, hyphae 3–7 μm wide, often curved, thin walled, usually with brown intracellular pigment. *Stipitipellis* an ixocutis, made up of slender, cylindrical, smooth, hyaline and thin-walled, hyphae 2–5 μm wide, with brown intracellular pigment. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Solitary to scattered on the ground under coniferous trees, occurring in autumn, so far known from southwestern China (Sichuan Province).

Additional specimen examined – China, Sichuan Province, Jiulong County, Wuxuhai, in a conifer forest dominated by *Abies*, 8 October 2021, X.L. He (SAAS3999).

Notes – *Hygrophorus brunnescens* is an uncommon species within *H. agathosmus* complex. Morphologically, *H. brunnescens* can be separated from the other member of *H. agathosmus* complex by its slender basidiomata, pure white lamellae when young which discolour brown when mature, and its distribution which is restricted so far to southwestern China.

Both the ITS and multigene molecular phylogenetic analyses (Figs 1–2) support the recognition of *H. brunnescens* as an independent and distinct species within sect. *Tephroleuci*. In the ITS phylogenetic analysis, *H. brunnescens* is actually closest to the European *H. hyacinthinus* (neotype from France). However, *H. hyacinthinus* can be separated from *H. brunnescens* by a more greyish tone on the pileus surface, less distinct floccules on the stipe, and the distribution in Europe (Bellanger et al. 2021).

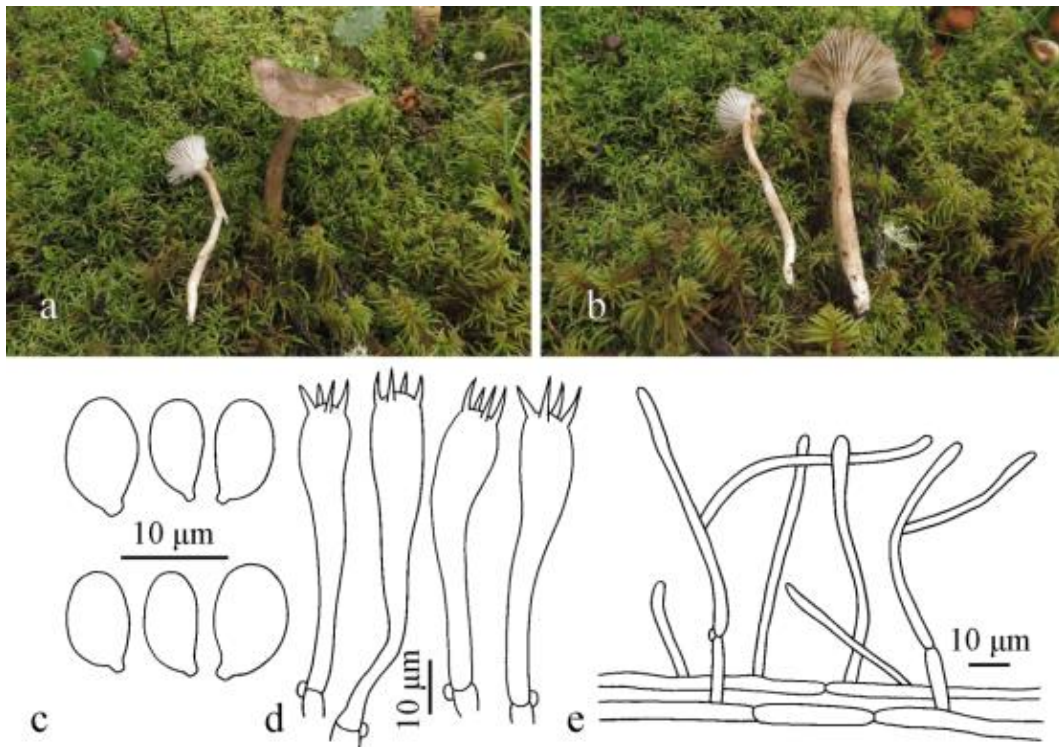


Figure 36 – *Hygrophorus brunnescens* (GDGM84456). a–b Basidiomata. c Basidiospores. d Basidia. e Terminal hyphae of pileipellis.

Hygrophorus fuscodiscus C.Q. Wang, Ming Zhang & T.H. Li, sp. nov.

Fig. 37

Index Fungorum Number: IF901151; Facesoffungi number: FoF14941

Etymology – *fuscodiscus*, from *fusco* = dark brown, and *discus* = disc, referring to its dark brown pileus disc.

Type – China, Sichuan Province, Jiuzhaigou County, in forest dominated by *Abies*, elev. ca. 3000 m, 19 September 2020, M. Zhang & J.H. Xing (GDGM84677, Holotype).

Pileus 20–70 mm across, hemispherical to convex when young, becoming plano-convex, plano-concave to concave, with or without a papilla or small umbo when young, then depressed at centre around the papilla or umbo, viscid to glutinous under wet conditions, dark brown to blackish at the disc, lighter from the umbo to margin. *Lamellae* adnate to adnate with a decurrent tooth, at times short decurrent, L = 40–48, l = 1–3, subdistant, thickish, waxy, almost entire at edge, pure white. *Stipe* 30–60 mm long, 3–9 mm broad, cylindrical, equal or slightly enlarged toward the base, and often broader at very apex, usually curved, greyish white, with white to light brown fibrils. *Context* white, thin.

Basidiospores 8–10.5(11) × 4.5–6 µm, Q = 1.64–2, ellipsoid to oblong, smooth, hyaline, thin-walled. *Basidia* 4-spored, clavate, 31–60 × 7–9.5 µm, with sterigmata up to 6 µm long. *Hymenophoral trama* divergent, made up of cylindrical hyaline hyphae, 5.5–13 µm broad. *Pileipellis* a trichoderm, consisting of cylindrical, thin-walled hyphae 2–3.5 µm wide. *Stipitipellis* a trichoderm, consisting of cylindrical, thin-walled hyphae 4–6 µm wide, often curved. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Scattered on the ground under *Abies* trees, occurring in autumn, so far known from southwestern China (Sichuan Province).

Additional specimen examined – China, Sichuan Province, Jiuzhaigou County, in a mixed forest dominated by *Abies*, elev. ca. 3000 m, 21 September 2020, M. Zhang & J.H. Xing (GDGM84543).

Notes – *Hygrophorus fuscodiscus* is morphologically similar to the other member of the *H. pustulatus* complex. *Hygrophorus pustulatus* differs from it by its less pronounced colour contrast between the disc and the margin of the pileus, less or none squamulose pileus disc, and the

distribution in Europe. *Hygrophorus pustuloides* Lebeuf, E. Larss. & Bellanger, recently described from North American, has lighter pileus disc, broad basidia (8–11 μm broad), and association with *Picea* (Bellanger et al. 2021). In the ITS phylogenetic analysis (Fig. 1), *H. fuscodiscus* is sister to the *H. pustulatus*-*H. pustuloides* clade. Both the morphological evidences and molecular differences support the establishment of this new fungus.

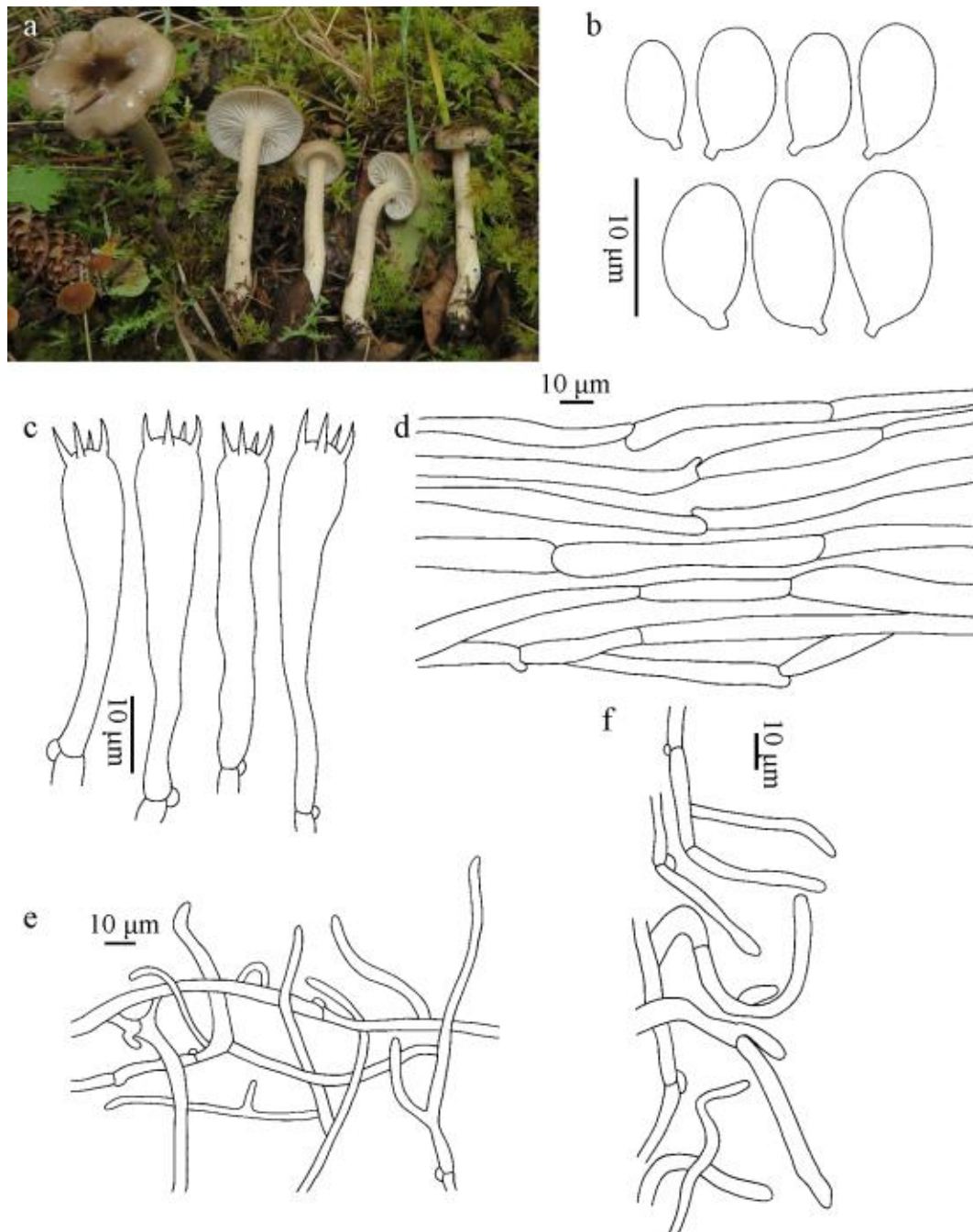


Figure 37 – *Hygrophorus fuscodiscus* (GDGM84677). a Basidiomata. b Basidiospores. c Basidia. d Hymenophoral trama hyphae. e Terminal hyphae of pileipellis. f Terminal hyphae of stipeipellis.

Hygrophorus habaensis H.Y. Huang & L.P. Tang, in Huang, Zhang, Huang, Jiang, Hao, Mu & Tang, Mycol. Progr. 21(5, no. 51): 14 (2022)

Notes – In this study, we did not find any specimens of this species, so no morphological description was given. For detailed morphological descriptions, comparisons with similar species, and illustrations of *H. habaensis* see Huang et al. (2022b). *Hygrophorus habaensis* was recently described from Haba Snow Mountain in Yunnan Province (Huang et al. 2022b). According to

Huang et al. (2022), it is characterized by the fawn-colored, yellowish-brown to brown pileus, ellipsoid to oblong basidiospores measuring $8.5\text{--}10 \times 5.2\text{--}7 \mu\text{m}$, the infrequent occurrence and the distribution in the alpine belt. In our ITS phylogenetic analysis (Fig. 1), *H. habaensis* is related to North American species *H. bakerensis* A.H. Sm. & Hesler and *H. tennesseensis* A.H. Sm. & Hesler; these phylogenetic placement is consistent with Huang et al. (2022b).

Hygrophorus pallidoagathosmus C.Q. Wang, Ming Zhang & T.H. Li, sp. nov. Fig. 38

Index Fungorum Number: IF901152; Facesoffungi number: FoF14942

Etymology – *pallidoagathosmus*, from *pallido* = pale, and *agathosmus* = *Hygrophorus agathosmus*, referring to its basidioma similar but paler than *H. agathosmus*.

Type – China, Sichuan Province, Jiuzhaigou County, Jiuzhaigou, in a conifer forest, elev. ca. 3000 m, 19 September 2020, M. Zhang & J.H. Xing (GDGM84702, Holotype).

Pileus 30 – 65 mm across, hemispherical to convex when young, expanding to convex to plano-convex, yellowish white, pale yellow, yellowish grey, greyish yellow to yellowish brown (4A1 – 3, 4B2 – 4), paler at margin, glabrous to finely fibrillose, viscid to glutinous in wet conditions, sometimes cracked under dry conditions; margin usually entire, rarely split, incurved when young, straight to uplifted when mature, whitish. Lamellae adnate to subdecurrent, distant to subdistant, $L = 32 - 60$, $l = 1 - 3$, pure white to ivory white, sometimes changing to light brown (5D3 – 6) when bruised, thickish, waxy, fragile; edge usually entire to finely eroded, sometimes crenate at pileus margin. Stipe 30 – 75 mm long, 3 – 8 mm wide, cylindrical, sometimes curved, sometimes compressed, equal or slightly enlarged downward the base, white, tomentose to short fibrillose, with dense white granules on upper part. Context white.

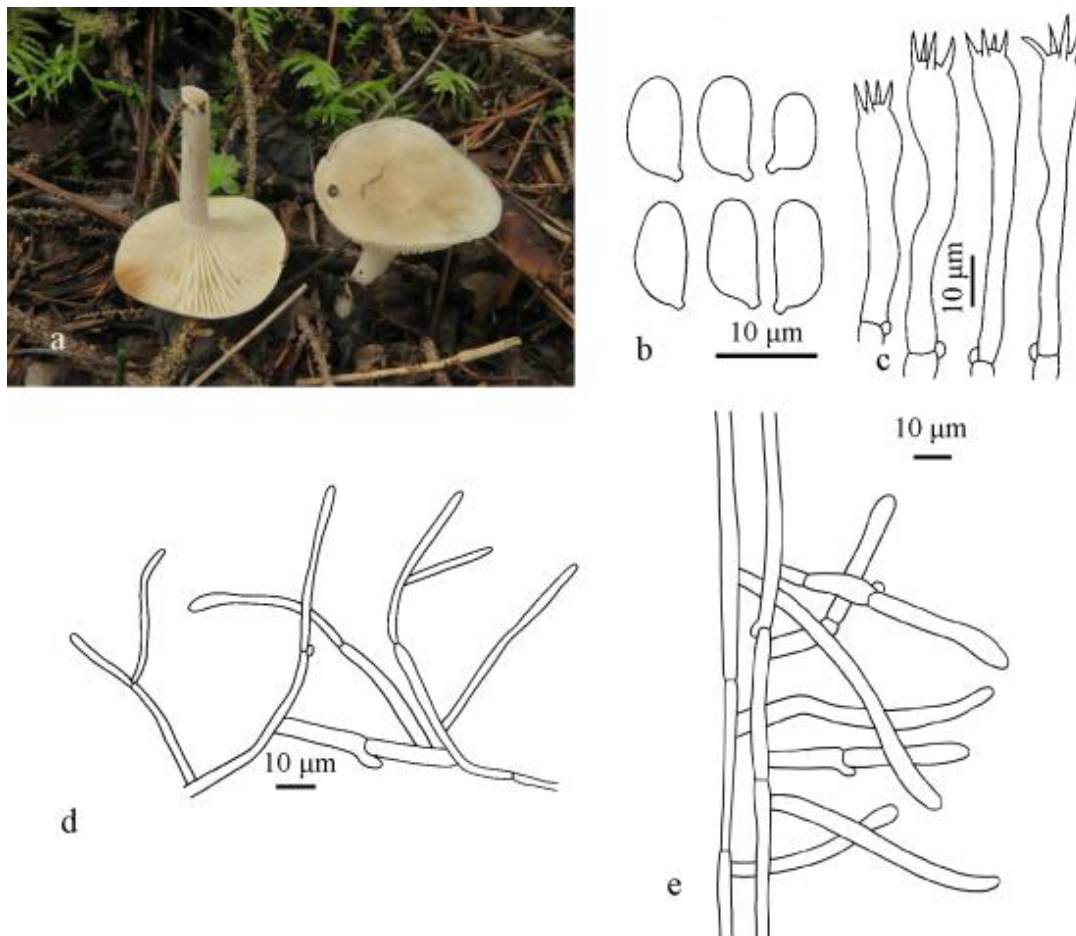


Figure 38 – *Hygrophorus pallidoagathosmus* (GDGM84702). a Basidiomata. b Basidiospores. c Basidia. d Pileipellis. e Stipitipellis.

Basidiospores 7.5–9.5(10) × 4–5.5(6) μm, Lm = 8.23 ± 0.82, Wm = 4.88 ± 0.5, Q = 1.4–2(2.25), Qm = 1.7 ± 0.19, ellipsoid, elongate to cylindrical, smooth, hyaline, thin-walled, hyaline in KOH. *Basidia* 39–65 × 6–11 μm, Q = 3.9–8.7, 4-spored, clavate, with sterigmata 4.5–10.5 μm long. *Hymenophoral trama* divergent, made up of cylindrical or inflated hyaline hyphae 4–32 μm broad. *Pileipellis* an ixotrichoderm, made up of branched, interwoven hyphae 2–6 μm wide. *Stipitipellis* an ixotrichoderm, made of gelatinized slender cylindrical hyphae 2.5–8 μm wide. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Scattered to caespitose on the ground in a mixed forest, occurring in summer and autumn, so far known from northeastern (Inner Mongolia Autonomous Region) and southwestern China (Sichuan Province).

Additional specimens examined – China, Inner Mongolia Autonomous Region, Chifeng City, Hexigten Banner, Huamugou Forest Farm, in a spruce and larch trees dominated forest, 6 August 2020, T.Z. Liu & D.L. Song (CFSZ22828). Sichuan Province, Jiuzhaigou County, Jiuzhaigou, in a conifer forest, elev. ca. 3000 m, 19 September 2020, M. Zhang & J.H. Xing (GDGM84681).

Notes – *Hygrophorus pallidoagathosmus* is characterized by paler basidiomata, the brownish tint on some parts of lamellar, and the ellipsoid, elongate to cylindrical basidiospores measuring 7.5–9.5(10) × 4–5.5(6) μm.

In the ITS phylogenetic analysis (Fig. 1), this novel and well-supported species is placed in the *H. agathosmus* complex sister to *H. albofloccosus*. However, *H. albofloccosus* differs by more robust basidiomata, its host association with *Pseudotsuga menziesii*, and the occurrence along the Pacific Coast of the United States and Canada. *Hygrophorus pallidoagathosmus* is close to *H. agathosmus*, *H. hyacinthinus* and *H. pinophilus*. However, *H. agathosmus* differs from this fungus by grey to greyish brown pileus and larger basidiospores [(8.6)9.4–9.8 (11.0) × (4.9) 5.6–5.9 (6.4) μm in Larsson et al. (2018)]. *Hygrophorus hyacinthinus* differs by white to greyish white pileus and white lamellae; and *H. pinophilus* differs by greyish brown pileus, and the strong odour of almond (Bellanger et al. 2021).

***Hygrophorus pinophilus* E. Larss., Sesli & Loizides**, in Bellanger, Lebeuf, Sesli, Loizides, Schwarz, Moreau, Liimatainen & Larsson, *Persoonia* 46: 300 (2021) Fig. 39

Pileus 30–80 mm across, hemispherical to convex when young, then expanded, with an obtuse umbo, whitish to greyish when young, becoming yellowish grey, brownish grey to greyish yellow (4B2–3, 4C2–3, 4D2–3), darker at disc, usually glabrous, occasionally subsquamulose at centre, dry, incurved at margin. *Lamellae* adnate to arcuate-subdecurrent, up to 5 mm broad, distant to subdistant, L = 36–56, l = 1–3, thick, waxy, fragile, white to yellowish white (4A1–2); edge entire when young, usually denticulate to irregularly lacerated when mature. *Stipe* 30–75 mm long, 7–95 mm broad, cylindrical, sometimes slightly tapering downwards, usually curved, dry, white to greyish brown, with white minute floccules at upper part, with or without greyish brown floccules when mature. *Context* white. *Odour* reminiscent of bitter almonds.

Basidiospores (7)7.5–9(10) × (4)4.5–6(7) μm, Q = 1.4–2, ellipsoid to elongate, smooth, hyaline, thin-walled. *Basidia* 4-spored, narrowly clavate, 32–50 × 7–9 μm, sterigmata 4–8 μm long. *Hymenophoral trama* divergent, made up of cylindrical hyaline hyphae 3.5–10 μm wide. *Pileipellis* an ixotrichoderm, made up of interwoven, gelatinized, often curved hyphae 2–4.5 μm wide. *Stipitipellis* an ixotrichoderm, consisting of cylindrical, thin-walled hyphae 3–5.5 μm wide. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Solitary to scattered on the ground under pine trees, occurring in summer in southwestern China, so far known from southern Europe, Fennoscandia (Sweden and Norway), Turkey and southwestern China (Sichuan Province and Yunnan Province) (Bellanger et al. 2021, Huang et al. 2022, this study).

Specimens examined – China, Sichuan Province, Panzhihua City, Yanbian County, Gesala Eco-tourism Area, in a forest dominated by *Pinus* sp., elev. ca. 3100 m, 25 August 2013, M. Zhang & C.Q. Wang (GDGM43348, GDGM43349).

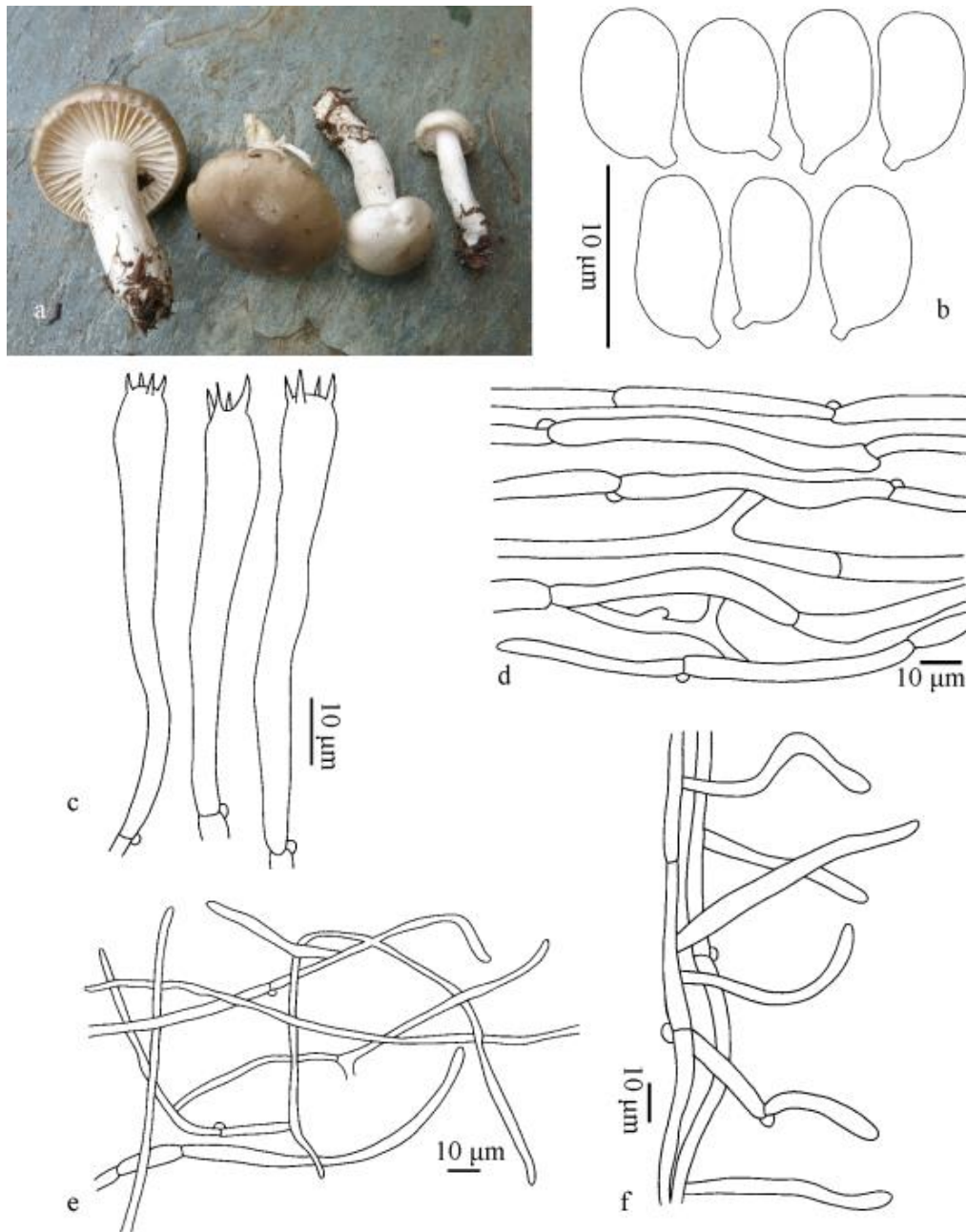


Figure 39 – *Hygrophorus pinophilus* (GDGM43349). a Basidiomata. b Basidiospores. c Basidia. d Hymenophoral trama hyphae. e Terminal hyphae of pileipellis. f Stipitipellis hyphae.

Notes – *Hygrophorus pinophilus* is characterized by its more or less robust basidiomata, a grey to greyish-brown pileus, adnate to arcuate-subdecurrent and usually distant lamellae, obvious bitter almond odour, and association with *Pinus* spp. (Bellanger et al. 2021, this study). It was recently described from Europe (Cyprus, France, Norway, Spain, Sweden, Turkey) by Bellanger et al. (2021), and subsequently recorded in Yunnan Province of China by Huang et al. (2022b) and Sichuan Province of China in this study. Previously, Chinese specimens of this species were incorrectly identified as *H. agathosmus* based on morphology (Chen & Li 2013). However, *H. agathosmus* differs from *H. pinophilus* by dark greyish brown pileus disc, and host association with *Picea abies*, and so far occurrence only known in Europe (Bellanger et al. 2021). *Hygrophorus agathosmoides* differs by more robust basidiomata and usually subdecurrent lamellae, association with *Abies* or *Picea* spp., and so far known distribution in pan-arctic region. For detailed descriptions, comparisons with similar species, and images of *H. pinophilus* see Bellanger et al. (2021) and Huang (2022b).

Hygrophorus queletii Bres., Fung. trident. 1(1): 11 (1881)

Fig. 40

Pileus 25–60 mm across, hemispherical to convex when young, becoming plano-convex to depressed when mature, often with an obtuse umbo, white, greyish white, greyish to pale pinkish grey (1A1, 1B1); margin decurved when young, then expanded. *Lamellae* adnate to subdecurrent when young, decurrent when mature, subdistant, waxy, white at first, often changing to yellow when mature, L = 40–48, l = 1–3; edge entire, even. *Stipe* 35–80 mm long, 5–15 mm thick, cylindrical, mostly equal to subequal, sometimes slightly enlarged downwards, white to whitish, often with a little pinkish tinge, minutely granular at up-most, subglabrous in the middle, with white mycelium at base. *Context* whitish.

Basidiospores 7.0–10.0(10.5) × 4.0–5.5 μm, Lm = 8.53 ± 0.16, Wm = 4.68 ± 0.54, Q = 1.50–2.25, Qm = 1.84 ± 0.23, ellipsoid, elongate to cylindrical, smooth, hyaline, thin-walled. *Basidia* 40.0–72.0 × 7.5–10 μm, Q = 4.5–8.47, 4-spored, clavate to slender clavate; sterigmata 3.0–8.5 μm long. *Hymenophoral trama* divergent, made up of cylindrical, thin-walled, hyaline hyphae 3–15 μm wide. *Clamp connections* not observed.

Habit, habitat and distribution – Scattered to gregarious under mixed broadleaf-conifer forests with pine trees, occurring in autumn., so far known from Europe and northeastern China (Inner Mongolia Autonomous Region).

Specimens examined – China, Inner Mongolia Autonomous Region, Chifeng City, Ningcheng County, in a mixed broadleaf-conifer forest dominated by pine trees, 24 September 2016, T.Z. Liu & Y.Q. Guan (CFSZ12607).

Notes – *Hygrophorus queletii* is characterized by its pinkish tint on pileus disc, yellowish lamellae, and the lack of clamp connections. In both ITS and multilocus phylogenetic analyses (Figs 1–2), *H. queletii* belongs to the *H. olivaceoalbus* complex. *Hygrophorus queletii* is sister to *H. pusillus* in the ITS tree. However, *H. pusillus*, described from North America, differs by its smaller pileus [15–30 mm broad in Siegel & Schwarz (2016) and 10–40(50) mm broad in Hesler & Smith (1963)] and widely spaced lamellae.

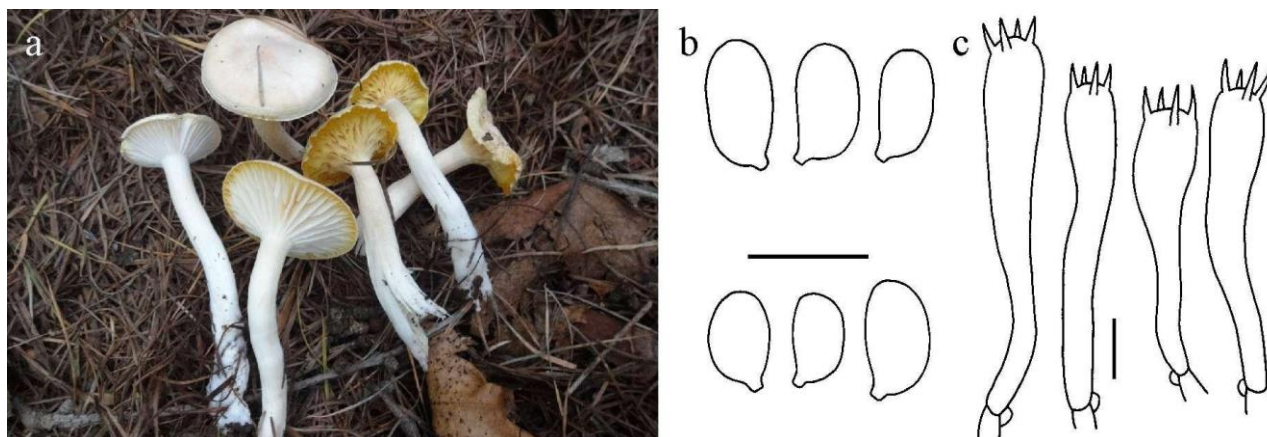


Figure 40 – *Hygrophorus queletii* (CFSZ12607). a Basidiomata. b Basidiospores. c Basidia.

Hygrophorus sichuanensis C.Q. Wang, Ming Zhang & T.H. Li, sp. nov.

Fig. 41

Index Fungorum Number: IF901153; Facesoffungi number: FoF14943

Etymology – *sichuanensis*, referring to the type locality of this species in Sichuan Province.

Type – China, Sichuan Province, Songpan County, Erdaohai, in a coniferous forest, elev. ca. 3300 m, 23 September 2020, M. Zhang & J.H. Xing (GDGM84471, Holotype).

Pileus 25–40 mm across, convex when young, expanded to plano-convex when mature, with an unobvious or low umbo, yellowish white to brownish, darker to pale brown at disc, paler towards margin, viscid when wet; margin incurved when young, then expanded to straight to partially uplifted. *Lamellae* arcuate-subdecurrent to decurrent, L = 32–40, l = 1–3, subdistant, thick, waxy, white to pinkish white, becoming brown when bruised or mature in some areas, even at edge.

Stipe 35–65 × 5–8 mm, cylindrical, equal or slightly enlarged downwards or upwards, usually curved, viscid to sticky when wet, slightly tomentose, fibrillose to minutely flocculose, concolorous with pileus. *Context* white.

Basidiospores 9–12(12.5) × 5–6.5(7) μm, Q = 1.5–2.3, ellipsoid, elongate to cylindrical, smooth, hyaline. *Basidia* 45–70 × 6.5–10, clavate; sterigmata 4–8 μm long. *Hymenophoral trama* divergent, made up of cylindrical hyaline hyphae, 4–8 μm broad. *Pileipellis* an ixotrichoderm, made up of hyphae 2.5–5 μm wide. *Stipipellis* a trichoderm, made up of hyphae 4–6 μm wide. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Solitary on the ground under coniferous trees, occurring in autumn, so far known from southwestern China (Sichuan Province).

Notes – *Hygrophorus sichuanensis* is characterized by the plano-convex pileus when mature, yellowish white to brownish pileus with darker to pale brown disc, white to pinkish white lamellae becoming brown when bruised or mature in some areas, ellipsoid, elongate to cylindrical basidiospores measuring 9–12(12.5) × 5–6.5(7) μm.

Morphologically, *H. sichuanensis* can be distinguished from *H. exiguus* E. Larss., E. Campo & M. Carbone by its bigger basidiomata and discolorous pileus when bruised (Larsson et al. 2014). Phylogenetically, *H. sichuanensis* is related to *H. exiguus*, and it was recognized here as a new member of the *H. exiguus* complex (Fig. 1).

In addition, *H. fuscodiscus*, also described in this study from southwestern China, differs from *H. sichuanensis* by dark brown to blackish and usually depressed pileus disc, and pure white lamellae which are adnate and sometimes with a decurrent tooth. *Hygrophorus odoratus*, originally described from the USA, differs from *H. sichuanensis* by whitish to creamy lamellae unchanging when bruised, and the wider basidiospores measuring 11–14 × 6.5–8 μm (Hesler & Smith 1963). *Hygrophorus suaveolens*, recently described from Sweden, differs from *H. sichuanensis* by smaller basidiomata and darker olive-brown pileus disc (Larsson et al. 2018).

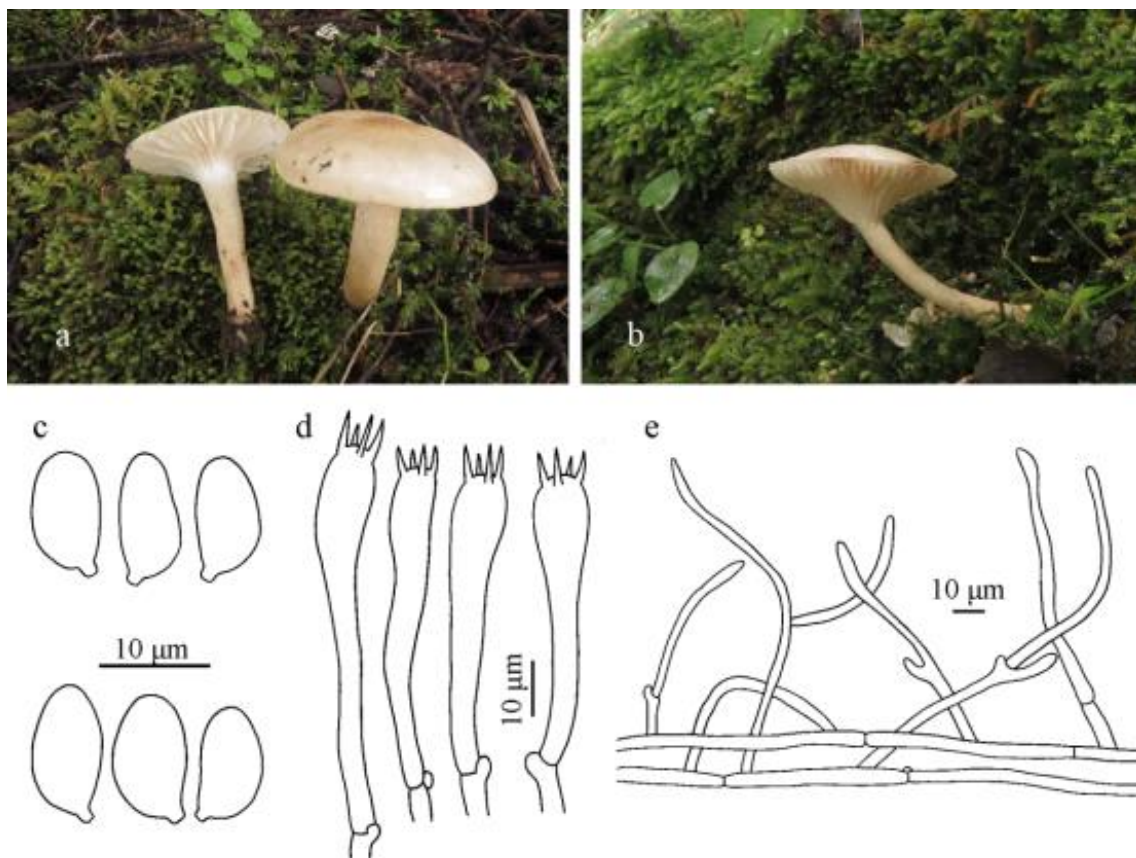


Figure 41 – *Hygrophorus sichuanensis* (GDGM84471). a–b Basidiomata. c Basidiospores. d Basidia. e Pileipellis.

Hygrophorus viridiflavus L. Fan & Y.X. Zhang, in Zhang, Mao & Fan, *Phytotaxa* 579(3): 191 (2023)

Notes – Zhang et al. (2023) reported this species of the sect. *Olivaceoumbrini*, so far restricted to Shanxi Province, China. According to Zhang et al. (2023), *H. viridiflavus* can be distinguished from *H. glutinifer* E. Larss., E. Campo & M. Carbone by its shorter and narrower basidia (35.0–46.5 × 8.0–10.5 μm). In this study, we did not find any collections of this species, thus we did not provide any morphological description. For detailed morphological descriptions, comparisons with similar species, and illustrations of *H. viridiflavus* see Zhang et al. (2023).

Hygrophorus* sect. *Aurei

Phylogenetic support: In the multilocus phylogenetic analysis, this clade is strongly supported as a monophyletic group (MLBS = 100%).

Studied Chinese species included in this section: *Hygrophorus alpinus*, *H. aurantioluteus*, *H. esculentus*, *H. gliocyclus*, *H. lucorum*, *H. pseudohypothejus* and *H. xiangjun*.

Hygrophorus alpinus H.Y. Huang & L.P. Tang, in Huang, Zhang, Huang, Moreno, Pu, Fan, Yang, Liu & Tang, *Mycol. Progr.* 21(9, no. 79): 3 (2022) Fig. 42

Pileus 20–50 mm across, convex with a dark umbo when young, then expanding to plano-convex, yellowish orange, greyish yellow to olive brown (4B6–7, 4C6–7, 4D6–7, 4E6–7, 4F6–7), usually dark grey brown at centre and paler outwards, viscid or glutinous, usually covered with a layer of glutinous materials in wet conditions; margin entire and incurved at first, expanded to straight or slightly uplifted when old. *Lamellae* arcuate, subdecurrent to decurrent, subdistant, L = 42–60, l = 1–3, yellowish white, pale yellow to light yellow (4A2–4), thick, waxy, fragile; edge entire and even when young. *Stipe* 40–50 mm long, 5–7 mm wide, cylindrical, often slightly tapered at base, usually curved, with a transient yellowish veil at upper part of stipe, yellowish white above the veil, viscid to glutinous and yellowish white to yellow below the veil, slightly fibrillose. *Context* yellowish white, thin. *Basidiospores* 6.5–8.0 × 4.0–5.0 μm, Q = 1.40–1.78, elliptical to elongate, smooth, hyaline, thin walled, inamyloid. *Basidia* 32–48 × 6.5–9 μm, 4-spored, clavate; sterigmata 5.5–9 μm long. *Hymenophoral trama* divergent, made up of cylindrical hyaline hyphae 3–13 μm broad. *Pileipellis* an ixotrichoderm, made up of upturned to interwoven slender cylindrical hyphae 2.5–5.5 μm wide, gelatinized, usually with a brown intracellular pigment. *Stipitipellis* consisting of slender cylindrical, thin-walled hyphae 3–5 μm wide, repent or interwoven, often curved, gelatinized, sometimes with brown intraparietal pigment. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Scattered under pine trees, basidioma occurring in autumn, so far known from southwestern China (Sichuan Province and Yunnan Province) (Huang et al. 2022, this study).

Specimens examined – China, Sichuan Province, Jiuzhaigou County, Jiuzhaigou, in forest dominated by pine and birch trees, elev. ca. 2400 m, 21 September 2020, Ming Zhang (GDGM84566); same location, in a forest dominated by pine trees, elev. ca. 2800 m, 20 September 2020, Ming Zhang (GDGM84536).

Notes – *Hygrophorus alpinus* was a cryptic species introduced by Huang et al. (2022a) and previously identified as *H. hypothejus*. After Moreau et al. (2018) designated the epitype of *H. hypothejus*, *H. alpinus* was subsequently described from southwestern China (Huang et al. 2022a). *Hygrophorus alpinus* is characterized by a yellowish orange, greyish yellow to olive brown pileus, elliptical to elongate basidiospores, and the occurrence in coniferous forests with known elevations above 2400 m. *Hygrophorus hypothejus* differs from *H. alpinus* by its occurrence late in the year and the European distribution at low elevations (< 900 m) (Moreau et al. 2018).

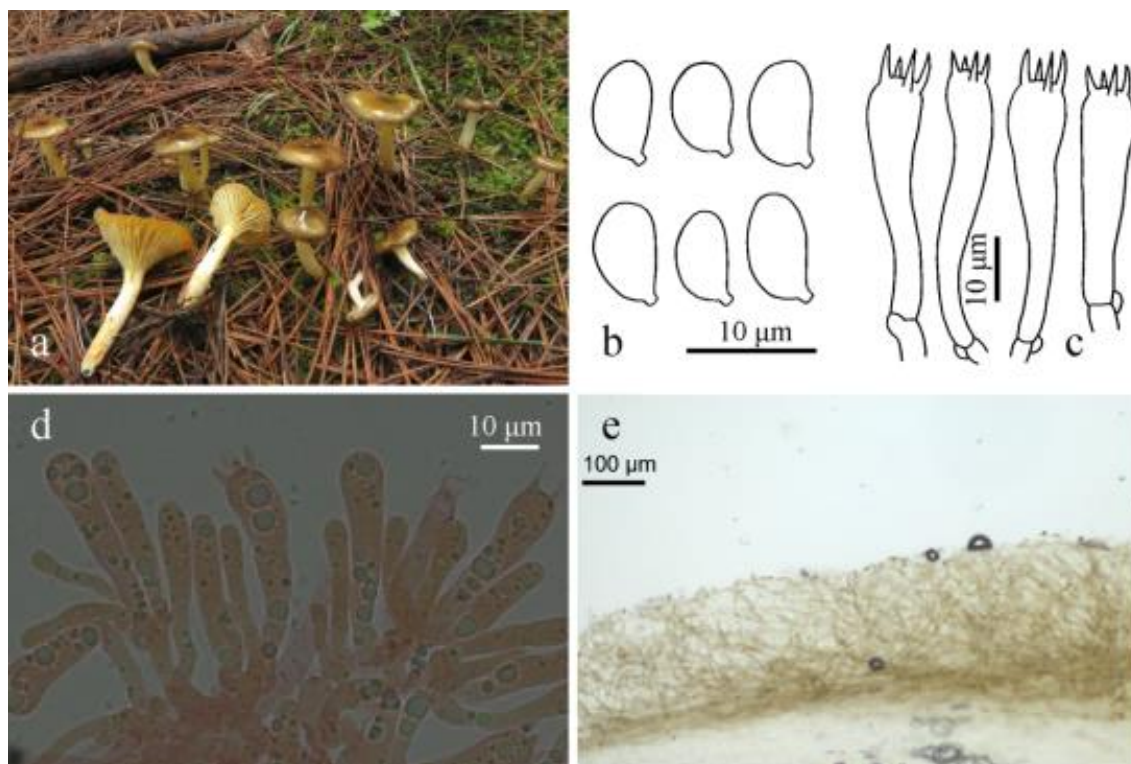


Figure 42 – *Hygrophorus alpinus* (GDGM84566). a Basidiomata. b Basidiospores. c Basidia. d Hymenium. e Pileipellis.

Hygrophorus aurantioluteus C.Q. Wang, Xiao Lan He & T.H. Li, sp. nov. Fig. 43

Index Fungorum Number: IF901154; Facesoffungi number: FoF14944

Etymology – *aurantioluteus*, from *aurantio* = orange, and *luteus* = yellow, referring to its orange to yellow pileus colour.

Type – China, Sichuan Province, Xiaojin County, Siguniang Mountain, in a subalpine forest, 16 September 2012, X.L. He (SAAS191, Holotype).

Pileus 15–60 mm across, convex when young, plano-convex, plane to depressed, yellowish white, pale yellow, pale orange, light orange, orange, pale red, pastel red, reddish orange, orange red (4A2–4, 5A3–5, 6A2–6, 7A2–6), viscid when wet; margin decurved when young, usually straight when mature, usually entire, sometimes with some indistinct white remnants of inner veil. *Lamellae* adnate with a short decurrent tooth, subdistant to close, L = 40–60, l = 1–3, waxy, fragile, white, up to 6 mm broad; edge entire and even. *Stipe* 35–70 mm long, 5–11 mm thick, central, cylindrical, equal or broader towards base, white at apex and base, yellowish to orangish in the rest of stipe surface, fibrillose, with an indistinct fibrillose or cortinoid inner veil at area 3–6 mm from the apex when young, often with a white annular zone of remnants of the inner veil, often with white mycelium at base. *Context* white.

Basidiospores (7)7.5–10.5(11) × (4.5)5–6(6.5) µm, Lm = 9.27 ± 0.82, Wm = 5.47 ± 0.5, Q = (1.27)1.42–2.1(2.2), Qm = 1.71 ± 0.24, ellipsoid, elongate to cylindrical, smooth, hyaline, thin-walled. *Basidia* 42–58 × 8–13 µm, Q = 3.82–6.5, 4-spored, clavate, sterigmata 3–7 µm long. *Hymenophoral trama* divergent, made up of cylindrical, thin-walled, hyaline hyphae 4–15 µm wide. *Pileipellis* an ixotrichoderm, made up of upturned and interwoven aerial hyphae 2–5.5 µm wide. *Stipitipellis* an ixocutis to an ixotrichoderma, made up of repent or upturned cylindrical thin-walled hyphae 3–7 µm wide. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Solitary or scattered on the ground in subalpine forests, occurring in autumn, so far known from southwestern China (Sichuan Province).

Additional specimen examined – China, Sichuan Province, Xiaojin County, Siguniang Mountain, in a subalpine forest, 16 September 2012, X.L. He (SAAS320).

Notes – *Hygrophorus aurantioluteus* is characterized by its a yellowish to orangish pileus, whitish lamellae, whitish stipe at the apex, orangish under the ring zone, and the association with *Larix*. Based on the ITS phylogenetic analysis (Fig. 1), a GenBank deposited sequence (MW762877) from Yunnan of China is representing the same species as the newly generated sequence from SAAS191, and a sequence (LC574517) from an uncultured *Hygrophorus* from Russia might be conspecific to them. Although *H. lucorum* is phylogenetically related to *H. aurantioluteus*, it is easy to distinguish them. *Hygrophorus lucorum* differs by light yellow to lemon yellow pileus with scarce orangish tint and smaller basidiospores [$7.0\text{--}9.0 \times (4)4.5\text{--}5.5 \mu\text{m}$]. Morphologically, *H. speciosus* differs from the *H. aurantioluteus* by umbonate pileus disc and more distant lamellae.

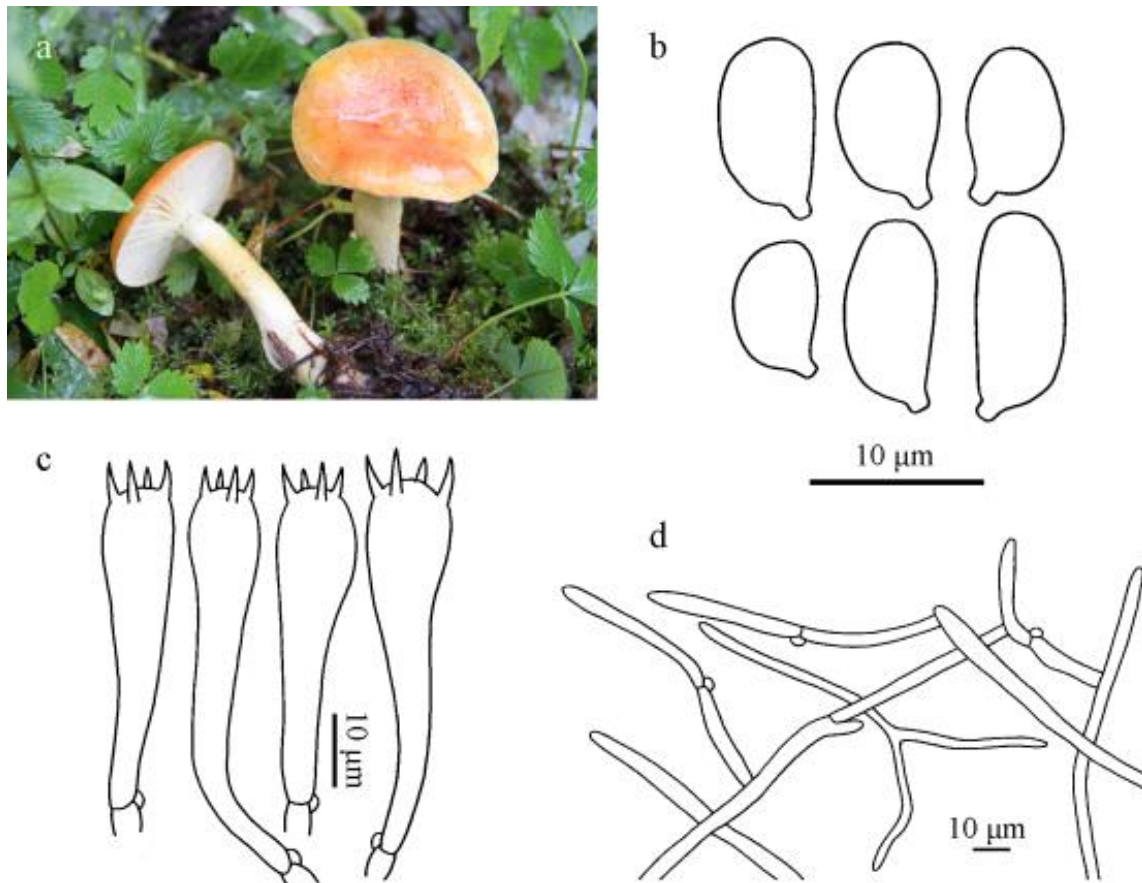


Figure 43 – *Hygrophorus aurantioluteus* (SAAS191). a Basidiomata. b Basidiospores. c Basidia. d Terminal hyphae of pileipellis.

Hygrophorus esculentus H.Y. Huang & L.P. Tang, in Huang, Zhang, Huang, Moreno, Pu, Fan, Yang, Liu & Tang, Mycol. Progr. 21 (9, no. 79): 8 (2022) Fig. 44

Pileus 30–65 mm diam., convex to plane, usually with a small umbo at disc when young, smooth, glabrous, covered with a gelatinous slime layer when wet, light yellow, orange white, pale orange on disc (4A4–5, 5A2–3), cream to white toward the margin; margin incurved when young, expanded when mature. *Lamellae* adnate to subdecurrent, subdistant, L = 32–48, l = 1–3, whitish; edge entire and even. *Stipe* 40–70 mm long, 7–11 mm broad, central, cylindrical, equal or slightly enlarged downward, covered with a gelatinous slime layer when wet, white to cream. *Context* thin, white.

Basidiospores $7.5\text{--}9(10.5) \times 5\text{--}6(6.5) \mu\text{m}$, Lm = 8.33 ± 0.67 , Wm = 5.53 ± 0.44 , Q = (1.33) 1.36–1.7 (1.75), Qm = 1.51 ± 0.13 , ellipsoid to elongate, thin-walled, hyaline. Basidia (40.5) 44–56(58) \times 7–9 μm , Q = 4.5–8.3, clavate, slender, thin-walled, mostly 4-spored; sterigmata usually up to 7 μm long and rarely up to 12 μm in length. *Hymenophoral trama* divergent, made up of

cylindrical or inflated hyphae 4–30 μm broad, thin-walled, hyaline. *Pileipellis* an ixotrichoderm, cover with a gelatinized layer, consisting of interwoven, cylindrical and thin-walled hyphae 3–6 μm broad; hyphae usually containing yellow intracellular pigment. *Stipitipellis* an ixotrichoderm to ixocutis, composed of interwoven or repent, cylindrical and thin-walled hyphae 3–8 μm broad. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Solitary to scattered on the ground in forests dominated by pine trees, occurring in summer and autumn, so far known from southwestern China (Sichuan Province and Yunnan Province) (Huang et al. 2022, this study).

Specimens examined – China, Sichuan Province, Mao County, in a forest dominated by pine trees, 19 October 2022, D. Wang (SAAS4747).

Notes – *Hygrophorus esculentus*, recently described from China, is a member of *H. gliocyclus* complex (Huang et al. 2022a). This taxon is characterized by the light yellow, orange white, pale orange pileus disc, paler pileus margin, ellipsoid to oblong basidiospores, and association with *Pinus*. *Hygrophorus esculentus* is related to *H. gliocyclus* Fr., which differs by yellowish pileus, lower elevation range in China, and the occurrence in mixed broadleaf-conifer forests (Candusso 1997). *Hygrophorus flavodiscus* Frost, described from North America, differs from *H. esculentus* by pinkish lamellae when young, smaller basidiospores (6–8 \times 3.5–5 μm), and the gregarious to subcaespitose habit (Hesler & Smith 1963).

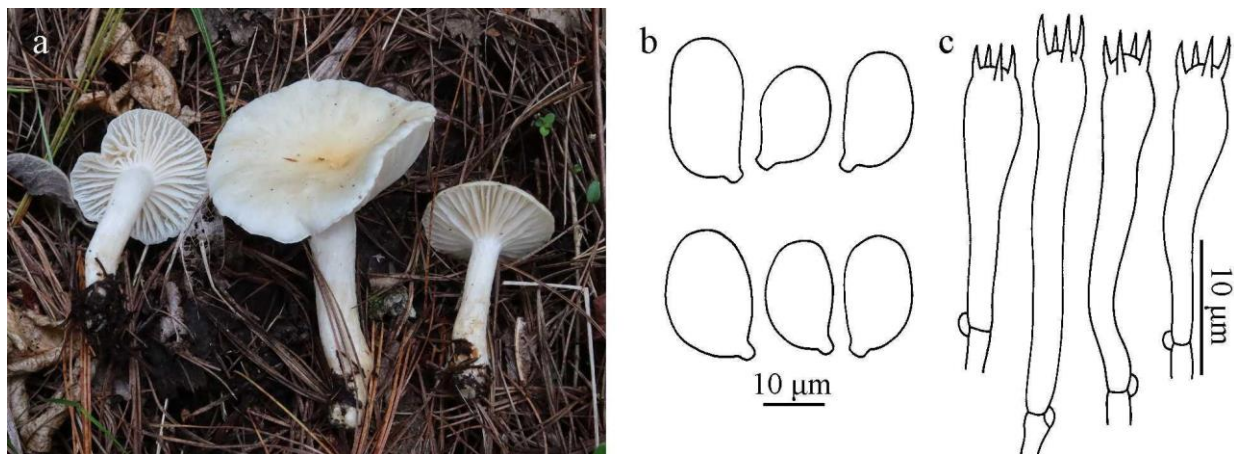


Figure 44 – *Hygrophorus esculentus* (SAAS4747, by D. Wang). a Basidiomata b Basidiospores. c Basidia.

***Hygrophorus gliocyclus* Fr.**, Öfvers. K. Svensk. Vetensk.-Akad. Förhandl. 18(1): 27 (1861) Fig. 45

Pileus 20–70 mm across, hemispherical to convex when young, becoming plano-convex when mature, often with a low obtuse umbo, white, yellowish white, pale yellow to light yellow (5A1–4), darker at disc, glutinous when moist; margin incurved when young, then decurved to plane. *Lamellae* adnate to subdecurrent when young, decurrent when mature, subdistant, L = 52–56, l = 1–3, waxy, white to pinkish white; edge entire, rarely furcate, even. *Stipe* 25–60 mm long, 10–20 mm thick, cylindrical, slightly narrower upwards, whitish, slimy, covered with transparent slime from about 1 cm below the apex to a half or lower third; inner veil present when young, superior, glutinous and cortinoid, evanescent (sometimes remaining in young exsiccata), as a slimy ring on stipe when mature. *Context* whitish, thick.

Basidiospores (6.5)7.0–9.0 \times (4.5)5.0–6.0 μm , Lm = 7.93 \pm 0.65, Wm = 5.43 \pm 0.47, Q = 1.25–1.60, Qm = 1.46 \pm 0.08, ellipsoid to elongate, smooth, hyaline, thin-walled. *Basidia* 38.0–52.0 \times 7.0–9.5 μm , Q = 4.47–6.29, 4-spored, clavate; sterigmata 4.0–7.5 μm long. *Hymenophoral trama* divergent, made up of cylindrical, thin-walled, hyaline hyphae 3–16.5 μm wide. *Pileipellis* an ixotrichoderm, made up of gelatinized, distant, branched, upturned or interwoven hyphae 2.5–4 μm wide. *Stipitipellis* an ixotrichoderm, made up of repent and upturned cylindrical thin-walled hyphae 2.5–7 μm wide. *Clamp connections* present in all tissues.

Habit, habitat and distribution – Scattered under mixed broadleaf-conifer forests with pine trees, occurring in autumn, so far known from Europe and southwestern China (Sichuan Province, Tibet Autonomous Region and Yunnan Province) (He & Yang 2021, Huang et al. 2022a, this study).

Specimens examined – China, Sichuan Province, Jiuzhai County, in a mixed forest dominated by *Betula* sp. and *Pinus* sp. trees, elev. ca. 2600 m, 20 September 2020, M. Zhang (GDGM84514). Yunnan Province, Ninglang County, Hongqiao Town, Mianmian Mountain, in a artificial pure forest near Lugu Lake Airport, elev. 3188 m, 27°32'33"N, 100°44'59"E, 24 September 2019, X.H. Wang, XHW7149 (HKAS 121113).

Notes – *Hygrophorus gliocyclus*, originally described by Fries (1861), was recorded in holarctic area (e.g. Hesler & Smith 1963, Yuan & Sun 1995, Candusso 1997). However, recent studies showed that *H. gliocyclus* s.s. is an Eurasian species, while the “*H. gliocyclus*” from North American is an undescribed cryptic species (Huang et al. 2022a). In our ITS phylogenetic analysis (Fig. 1), the Eurasian *H. gliocyclus* s.s. and the North American “*H. gliocyclus*” are supported as distinct species, and another clade of “*H. esculentus*” group is close to them.

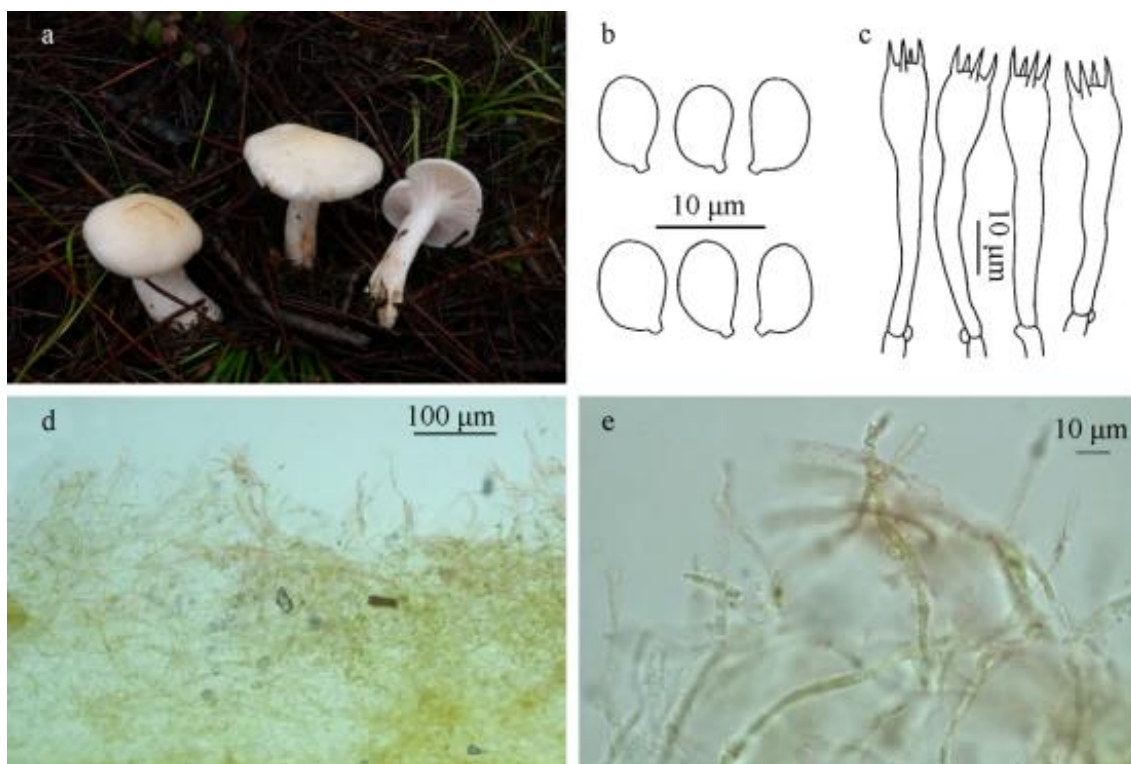


Figure 45 – *Hygrophorus gliocyclus* (XHW7149). a Basidiomata (by X.H. Wang). b Basidiospores. c Basidia. d–e Elements of pileipellis.

Hygrophorus lucorum Kalchbr., Icon. Sel. Hymenomyc. Hung. (Budapest) 2: 35 (1874)

Fig. 46

Pileus 25–45 mm across, hemispherical to broadly conic when young, convex to plano-convex when mature, more or less lemon yellow in general, pale yellow to light yellow (2A3–5) at disc, becoming paler toward the margin, often with greenish tint, viscid when wet; margin incurved when young, then decurved to straight. *Lamellae* subdecurrent to decurrent, subdistant, L = 44–56, l = 1–3, waxy, white to pale yellow; edge entire, even. *Stipe* 35–85 mm long, 5–10 mm thick, cylindrical, sometimes slightly thinner upwards, whitish to yellowish, sometimes with lemon yellow tint, covered with a layer of sticky materials, fibrillose, sometimes cortinoid at apex. *Context* whitish, thick.

Basidiospores 7.0–9.0 × (4)4.5–5.5 µm, Lm = 8.15 ± 0.61, Wm = 5.00 ± 0.41, Q = 1.40–2.00, Qm = 1.63 ± 0.16, ellipsoid to elongate, smooth, hyaline, thin-walled. *Basidia* 44.0–58.0 × 7.0–9.0

μm , $Q = 4.94\text{--}7.86$, 4-spored, clavate; sterigmata $4.0\text{--}7.0\ \mu\text{m}$ long. *Hymenophoral trama* divergent, made up of cylindrical or inflated, thin-walled, hyaline hyphae $3\text{--}26\ \mu\text{m}$ wide. *Pileipellis* an ixotrichoderm, made up of gelatinized, repent or upturned hyphae $2\text{--}5.5\ \mu\text{m}$ wide, with yellow endochrome, and with randomly distributed yellow materials on hyphal surface in KOH. *Stipitipellis* made up of repent and interwoven cylindrical thin-walled hyphae $2.5\text{--}3.5\ \mu\text{m}$ wide. *Clamp connections* present in all tissues.

Habit, habitat and Distribution – Scattered or gregarious under conifer forests dominated by *Larix*, occurring in autumn, so far known from Europe (Candusso 1997, Adamcik et al. 2005) and northeastern China (Inner Mongolia Autonomous Region and Jiling Province) (Huang et al. 2022, this study).

Specimens examined – China, Inner Mongolia Autonomous Region, Arxan City, Donggouli, in a conifer forest dominated by pine trees, elev. ca. 1100 m, 9 September 2019, W. Wang (GDGM79101).

Notes – *Hygrophorus lucorum* (Larch Woodwax), originally described from Slovakia, is a popular wild edible mushroom in Northeastern China (Bau & Bao 2016). Adamčík et al. (2005) selected the lectotype and epitype; and for purpose of this study, new ITS sequences from type collection area were generated (including epitype). *Hygrophorus lucorum* is distinguished by light yellow basidiomata, and association with *Larix* in the temperate region of Eurasia. It is often confused with the *H. speciosus*, however, the latter differs by orange tinted pileus, and distinct sticky veil ring zone on the stipe. *Hygrophorus lucorum* is somewhat similar to *H. chrysodon* (Batsch) Fr., but the latter differs by prominent yellow granules on pileus and stipe.



Figure 46 – *Hygrophorus lucorum* (GDGM79101). a–b Basidiomata (by W. Wang). c Basidiospores. d Basidia. e Pileipellis.

Hygrophorus pseudohypothejus H.Y. Huang & L.P. Tang, in Huang, Zhang, Huang, Moreno, Pu, Fan, Yang, Liu & Tang, Mycol. Progr. 21(9, no. 79): 13 (2022) Fig. 47

Pileus 30–40 mm diam., convex, broadly convex to plane, with an umbo, olivaceous yellow, dark brown to yellowish black, deepening from margin to centre, covered with viscid to gelatinous surface. *Lamellae* subdecurrent, subdistant, $L = 40\text{--}56$, $l = 1\text{--}3$, white to yellowish white, up to 5

mm broad. *Stipe* 65–75 mm long, 6–8 mm broad, central, cylindrical, tapering toward the base, whitish to light yellow, viscid, with glutinous and transparent veil when young. *Context* yellowish white.

Basidiospores (6.5)7–9 × (4)4.5–6(6.5) μm, Q = 1.33–1.88, Qm = 1.58 ± 0.15, Lm = 7.83 ± 0.71, Wm = 5 ± 0.67, ellipsoid to oblong, smooth, thin-walled, hyaline. *Basidia* 29–37 × 5.5–7 μm, clavate, thin-walled, 4-spored, with sterigmata up to 7 μm in length. *Hymenophoral trama* divergent, made up of thin-walled, hyaline, cylindrical to inflated hyphae 3–26 μm broad. *Pileipellis* an ixocutis, covered with a strongly gelatinized layer, consisted of slender, branched or non-branched, thin-walled hyphae 2–6 μm broad, usually with brownish intracellular pigment. *Stipitipellis* an ixocutis, composed of slender, parallel, thin-walled hyphae 3–6 μm broad. *Clamp connections* present in all tissues.

Habit, habitat and Distribution – Solitary under mixed broadleaf-conifer forests dominated by *Pinus* and *Quercus*, occurring in summer, so far known from southwestern China (Yunnan Province) (Huang et al. 2022, this study).

Specimens examined – China, Yunnan Province, in a *Pinus* and *Quercus* dominated conifer forest, 26°27'13"N, 99°18'56"E, elev. 3113 m, 27 September 2019, X.H. Wang (XHW7324).

Notes – *Hygrophorus pseudohypothejus* was recently described from Yunnan Province of China by Huang et al. (2022a). This species is distinctive by dark brown umbo at the pileus centre, solitary habit, and association with pine trees.

In both the ITS and multilocus phylogenetic analysis (Figs 1–2), a new specimen (XHW7324) is clustered with the type specimen of *H. pseudohypothejus*. In addition, *H. pseudohypothejus* is sister to *H. alpinus*. For detailed descriptions, comparisons with related species and more images of *H. pseudohypothejus* see Huang et al. (2022a).

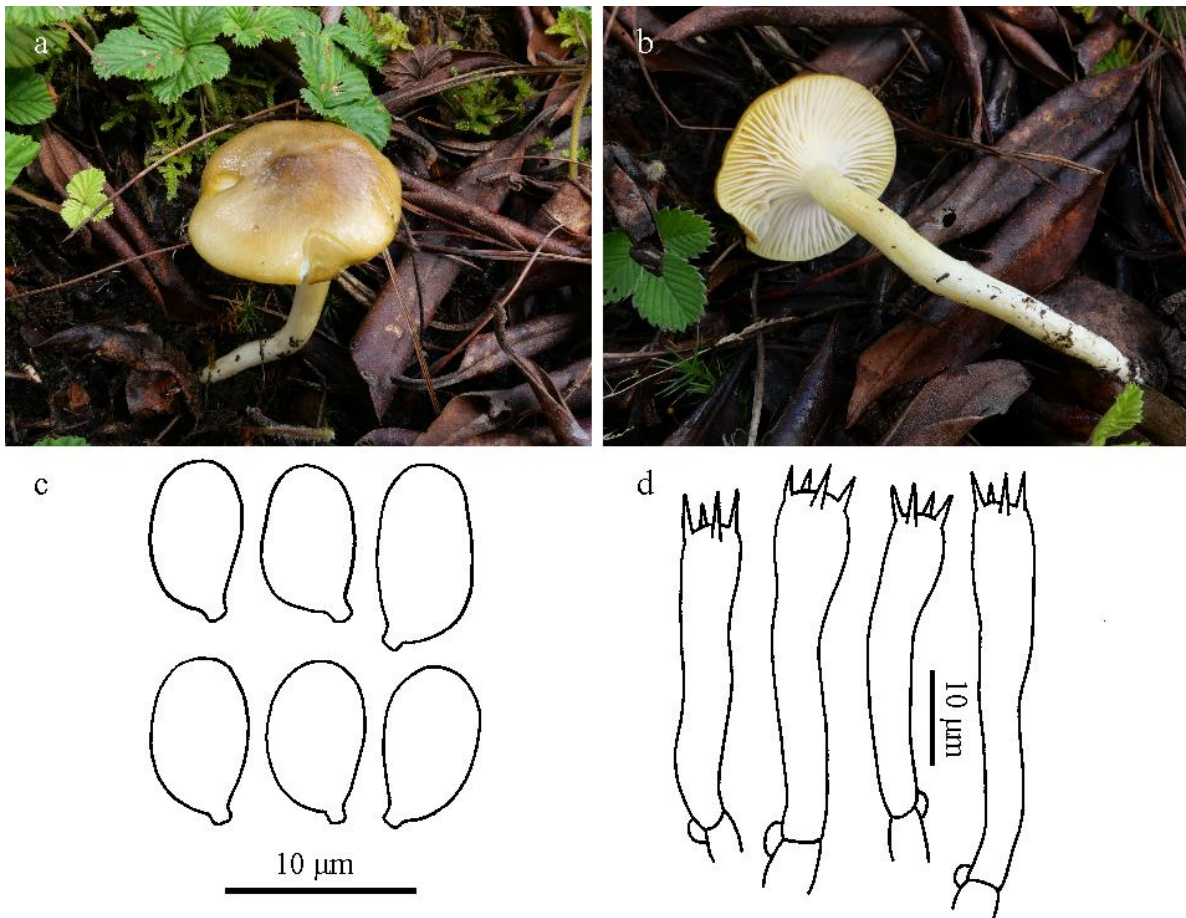


Figure 47 – *Hygrophorus pseudohypothejus* (XHW7324). a–b Basidiomata (by X.H. Wang). c Basidiospores. d Basidia.

Hygrophorus speciosus Peck, Ann. Rep. N.Y. St. Mus. nat. Hist. 29: 43 (1878) [1876]

Fig. 48

Pileus 20–40 mm across, hemispherical when young, becoming convex to plano-convex when mature, brightly coloured, pale yellow, pale yellow, light yellow, golden yellow, greyish yellow, orange white, pale orange, light orange to greyish orange (4A3–6, 4B4–6, 5A2–6, 5B4–6), usually darker at disc, fading with age, glutinous when moist; margin decurved when young, then straight. *Lamellae* adnate to subdecurrent, subdistant, L = 32–44, l = 1–3, waxy, white; edge entire, even. *Stipe* 30–50 mm long, 10–22 mm thick, central, cylindrical to slightly compressed, more or less equal, sometimes tapering at base, with a whitish sheath-like zone of gluten below the apex, white at apex, yellowish to orangish below the sheath. *Context* whitish to yellowish, without discolouration when bruised.

Basidiospores (7.5)8.0–9.0 × (4.5)5.0–6.0 μm, Lm = 8.5 ± 0.49, Wm = 5.48 ± 0.38, Q = 1.45–1.67(1.8), Qm = 1.56 ± 0.09, ellipsoid to elongate, smooth, hyaline, thin-walled. *Basidia* 39.0–55.0 × 7.0–10.0 μm, Q = 4.32–6.67, 4-spored, clavate; sterigmata 6.0–8.5 μm long. *Hymenophoral trama* divergent, made up of cylindrical, thin-walled, hyaline hyphae 5–20 μm wide. *Pileipellis* an ixotrichoderm, made up of gelatinized, distant, branched, upturned or interwoven hyphae 2–5 μm wide. *Clamp connections* present in all tissues.

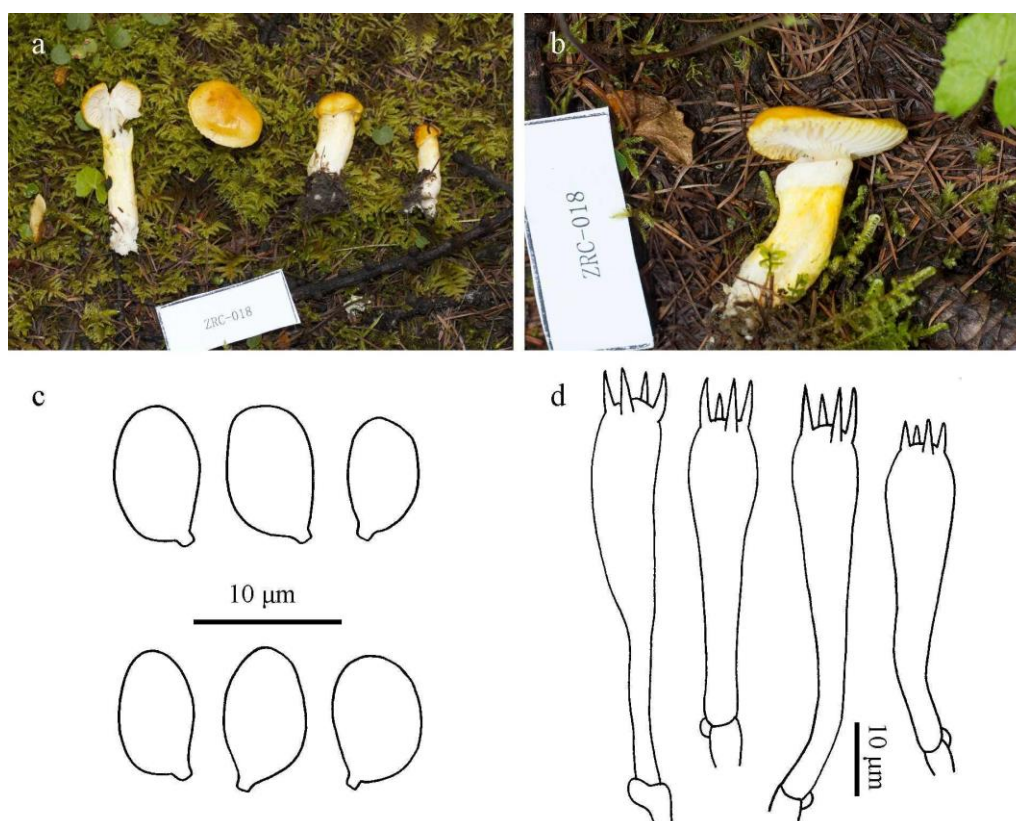


Figure 48 – *Hygrophorus speciosus* (HMAS278060). a–b Basidiomata (by R.C. Zhang). c Basidiospores. d Basidia.

Habit, habitat and Distribution – Scattered under mixed broadleaf-conifer forests, occurring in summer, so far known from Europe, North America and China (Sichuan Province, Jilin Province) (Huang et al. 2022, this study).

Specimen examined – China, Sichuan Province, Xiaojin County, Mountain Siguniang, in a mixed broadleaf-conifer forest, 102°49'E, 31°14'N, elev. 3385 m, 11 August 2016, R.C. Zhang 018 (HMAS 278060).

Notes – *Hygrophorus speciosus*, originally described from New York State, USA, is associated with *Larix* (Peck 1878). It is characterized by its orange to orangish red and sticky pileus,

white stipe under lamellae contrasting to orangish surface below glutinous ring zone. In the ITS phylogenetic analysis, Huang et al. (2022a) confirmed that Chinese sequences were clustered with North American and European sequences of this species. This beautiful species was previously documented as an edible ectomycorrhizal mushroom in China (Wei et al. 2021) and was recorded in many provinces (Fujian, Helongjiang, Jilin and Yunnan) in China based on morphological identification (Chen & Li 2013). However, some Chinese records need additional confirmation.

Hygrophorus xiangjun H.Y. Huang & L.P. Tang, in Huang, Zhang, Huang, Moreno, Pu, Fan, Yang, Liu & Tang, *Mycol. Progr.* 21(9, no. 79): 15 (2022) Fig. 49

Pileus 30–80 mm across, hemispherical to convex when young, convex to broadly convex when mature, pale yellow to light yellow (5A1–4) at disc, gradually lighter from disc to margin, white to yellowish white at margin, glutinous when moist; margin incurved when young, then decurved. *Lamellae* adnate to subdecurrent, subdistant, L = 52–60, l = 1–3, waxy, white to pale pinkish; edge entire, even to minutely denticulate. *Stipe* 35–80 mm long, 7–18 mm thick, cylindrical, usually slightly thinner downwards, whitish, with a weak glutinous and cortinoid ring superiorly, weakly longitudinally striate and slightly fibrillose. *Context* whitish, thick.

Basidiospores (6.5)7.0–8.5(9.0) × 4.5–6.0 μm, Lm = 7.58 ± 0.61, Wm = 4.93 ± 0.41, Q = 1.27–1.78, Qm = 1.54 ± 0.11, broadly ellipsoid, ellipsoid to elongate, smooth, hyaline, thin-walled. *Basidia* 42.0–57.0 × 6.5–8.0 μm, Q = 6–8.14, 4-spored, clavate; sterigmata 3.0–4.5 μm long. *Hymenophoral trama* divergent, made up of cylindrical or inflated, thin-walled, hyaline hyphae 7–21 μm wide. *Pileipellis* an ixotrichoderm, made up of gelatinized, distant, branched, upturned or interwoven hyphae 37–4 μm wide, with bright yellow materials in the surface and randomly distributed under the surface in KOH. *Stipitipellis* made up of repent and upturned cylindrical thin-walled hyphae 3–6 μm wide, with bright yellow materials in KOH. *Clamp connections* present in all tissues.

Habit, habitat and Distribution – Gregarious under conifers, in forests dominated by pine trees, occurring in autumn, so far known from southwestern China (Yunnan Province).

Specimens examined – China, Yunnan Province, Lijiang Alpine Botanical Garden, in a mixed forest dominated by *Pinus yunnanensis* and *Quercus* sp., 100°11'E, 27°0'N, elev. 3282 m, 12 October 2019, J.W. Liu, LJW2256 (GDGM92371).

Notes – *Hygrophorus xiangjun* was recently described from southwestern China (Huang et al. 2022a). It is characterized by a pale yellow to light yellow and depressed pileus disc when mature, whitish pileus margin, usually gregarious habit, and association with pine trees. Previously, some Chinese sequences of *H. xiangjun* were identified as North American *H. flavodiscus* Frost (He & Yang 2021). In our ITS phylogenetic analysis (Fig. 1), *H. xiangjun* is sister to *H. flavodiscus*. However, *H. flavodiscus* differs from *H. xiangjun* by less whitish area on pileus margin, smaller basidiospores (6–8 × 3.5–5 μm), and association with *Pinus strobus*, which is native in eastern North America (Bessette et al. 2012).

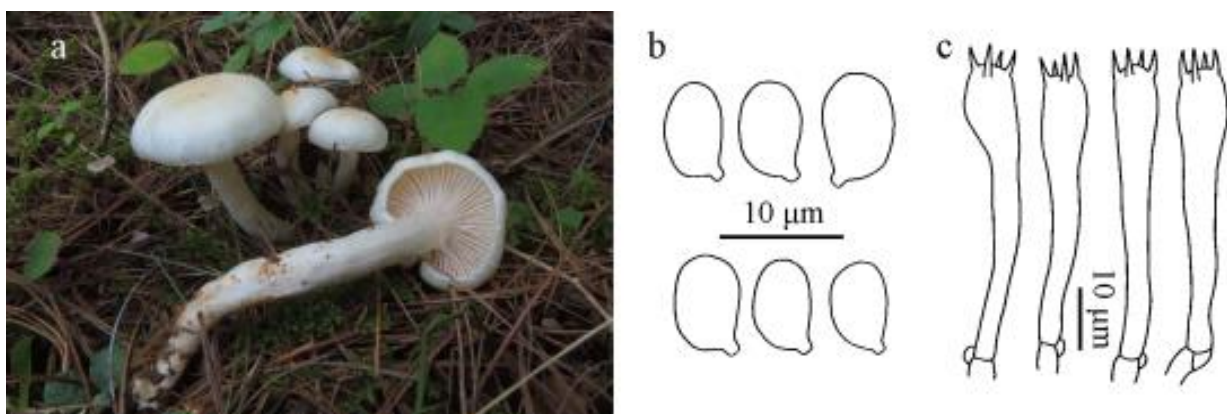


Figure 49 – *Hygrophorus xiangjun* (LJW2256). a Basidiomata. b Basidiospores. c Basidia.

Hygrophorus* sect. *Vividi C.Q. Wang, Ming Zhang & T.H. Li, sect. nov.

Index Fungorum Number: IF901162

Type species: *Hygrophorus vividus*.

Etymology – *vividi*, derived from the name of the type species of the section.

Basidioma small to medium, dry to subviscid. *Pileus* hemispherical to plano-convex, surface almost smooth. *Lamellae* adnate to subdecurrent. *Stipe* almost cylindrical, orange to white. *Context* orange or nearly concolorous with pileus.

Notes – Section *Vividi* is a moderately supported (84% MLBS) monophyletic group in the ITS analysis (Fig. 1). It includes sequences of *H. vividus* and a sample of an undescribed taxon (XML1910693), all originated from China. In the multilocus analysis (Fig. 2), *H. vividus* and the sample (XML1910693) form a monophyletic clade with 100 % MLBS support. Section *Aurei* is the sister lineage to sect. *Vividi* with limited support. Sect. *Vividi* is relatively easy distinguished within *Hygrophorus* by orangish tints of basidiomata and occurrence in high elevations (over 3800 m so far known).

Studied Chinese species included in this section: *Hygrophorus vividus*.

Hygrophorus vividus C.Q. Wang, Ming Zhang & T.H. Li, sp. nov.

Fig. 50

Index Fungorum Number: IF901155; Facesoffungi number: FoF14945

Etymology – *vividus* = vividly coloured, referring the vivid colour of the whole basidioma.

Type – China, Yunnan Province, Diqing Tibetan Autonomous Prefecture, Zhongdian County, Bitahai, in a subalpine forest dominated by *Quercus* sp., elev. ca. 3830 m, 3 September 2020, M. Zhang & L.Q. Wu (GDGM82385, Holotype).

Pileus 30–60 mm across, hemispherical to convex when young, convex to plano-convex when mature, viscid when wet, pale orange, light orange, light orange, orange to reddish orange (5A3–6, 6A4–8, 7A6–8, 8A6–8), and paler at some parts of disc; margin decurved when young, straight when mature, concolorous to often paler. *Lamellae* adnate with a short decurrent tooth to subdecurrent, subdistant to close, L = 40–52, l = 1–4, waxy, thick, fragile, orange; edge entire and even. *Stipe* 30–60 mm long, 9–11 mm thick, central, almost cylindrical, concolorous or lighter than pileus, sometimes with whitish tomentum, hygrophanous. *Context* orange or nearly concolorous with pileus.

Basidiospores (6.5)7–9.5(10.5) × (4)4.5–6 μm, Lm = 8.07 ± 0.87, Wm = 4.98 ± 0.45, Q = (1.3)1.45–1.88(1.91), Qm = 1.63 ± 0.14, ellipsoid to elongate, thin-walled. Basidia 31–60 × 5.5–9.5 μm, Q = 4.13–10.18, 4-spored, clavate, sterigmata 4–8 μm long. *Hymenophoral trama* divergent, made up of cylindrical, thin-walled, hyaline hyphae 3.5–20 μm wide. *Pileipellis* an ixocutis, made up of mainly repent and occasionally upturned hyphae 2–8.5 μm wide. *Stipitipellis* an ixocutis, made up of repent or upturned cylindrical thin-walled hyphae 3–9 μm wide. *Clamp connections* present in all tissues.

Habit, habitat and Distribution – Scattered to gregarious on the ground in forests dominated by oak trees, occurring in autumn, so far known from southwestern China (Yunnan Province).

Additional specimens examined – China, Yunnan Province, Diqing Tibetan Autonomous Prefecture, Zhongdian County, Bitahai, on the ground around mosses in a subalpine forest dominated by *Quercus* sp., 27°84'N, 99°98'E, elev. ca. 3850 m, 4 September 2020, M. Zhang & L.Q. Wu (GDGM83100, GDGM83196).

Notes – *Hygrophorus vividus* is an attractive and abundant waxcap found in subalpine forest in southwestern China. When *H. vividus* was found in the field, it resembled a larger individuals of *Sinohygrocybe tomentosipes* (Wang et al. 2018). But *H. vividus* differs from *S. tomentosipes* by the more orangish tint and less yellowish tint, hymenium with adnate to subdecurrent lamellae rather than cantharellus-like, and the divergent rather than subregular lamellar trama. *Hygrophorus leporinus* Fr. is similar to *H. vividus*, this species is only known from low elevations in Europe and has smaller basidiospores [6–7.5(8.2) × 4–5.2(6) μm] (Candusso 1997). *Hygrophorus nemoreus* is somewhat similar to *H. vividus*, but it differs by paler pileus, whitish lamellae and whitish to light yellowish stipe (Campo 2015).



Figure 50 – *Hygrophorus vividus*. a Basidiomata (GDGM82385). b Basidiomata (GDGM83196). c Basidiospores (GDGM82385). d Basidia (GDGM82385). e Pileipellis (GDGM82385).

Hygrophorus sect. *Discoidei*

Phylogenetic support: Section *Discoidei* is a strongly support (MLSB = 100%) independent group in both ITS and multilocus phylogenetic trees (Figs 1–2).

Studied Chinese species included in this section: *Hygrophorus brunneololamellatus*, *H. cinnamoneus*, *H. pallidofulvus* and *H. pseudodiscoideus*.

Hygrophorus brunneololamellatus C.Q. Wang, Ming Zhang & T.H. Li, sp. nov. Fig. 51

Index Fungorum Number: IF901158; Facesoffungi number: FoF14948

Etymology – *brunneololamellatus*, from *brunneolo* = brownish, and *lamellatus* = *lamellae*, referring the brownish lamellae of the new species.

Type – China, Sichuan Province, Jiuzhaigou County, Fairy pool Scenic Area, in a forest dominated by *Betula* sp., elev. ca. 3000 m, 22 September 2020, M. Zhang & J.H. Xing (GDGM84600, Holotype).

Pileus 30–70 mm across, convex with a low umbo to convex when young, broadly convex when mature, orange grey, greyish orange, greyish brown, light brown, brown (5C2–3, 6D3–5, 6E3–5), viscid when wet; margin decurved when young, then straight to uplifted, usually entire, covered with silver materials when young. *Lamellae* adnate to subdecurrent, subdistant, L = 42–48, l = 1–3, waxy, fragile, greyish orange, brownish orange, greyish orange, brownish orange, light brown (5B3–5, 5C4–5, 6B2–3, 6D3–4, 6E3–4); edge usually entire and even. *Stipe* 25–70 mm long, 5–11 mm thick, central, cylindrical, usually slightly curved, concolorous with pileus, more or less fibrillose, often with white mycelium at base. *Context* yellowish white to white.

Basidiospores 5.5–6.5(7.5) × 3.5–4.5 µm, Lm = 5.98 ± 0.53, Wm = 3.87 ± 0.32, Q = (1.33)1.38–1.71(1.88), Qm = 1.55 ± 0.13, ellipsoid to elongate, smooth, hyaline, thin-walled. *Basidia* 34–45 × 6–8 µm, Q = 4.5–6.77, 4-spored, clavate, sterigmata 4–6 µm long. *Hymenophoral trama* divergent, made up of cylindrical, thin-walled, hyaline hyphae 3–16 µm wide. *Pileipellis* an

ixotrichoderm, made up of repent or upturned aerial hyphae 2.5–5 µm wide. *Clamp connections* present in all tissues.

Habit, habitat and Distribution – Scattered to gregarious on the ground around mosses in broad-leaved forests with *Betula* sp., occurring in autumn, so far known from southwestern China (Sichuan Province).

Notes – *Hygrophorus brunneololamellatus* is characterised by its orange grey to brown pileus, greyish orange to light brown lamellae, and the ellipsoid to elongate basidiospores measuring 5.5–6.5(7.5) × 3.5–4.5 µm. Simila species *H. subviscifer* (P. Karst.) Harmaja is different in its smaller pileus and bigger basidiospores (7–8.5 × 4.2–5 µm) (Karsten 1878, Harmaja 1969).

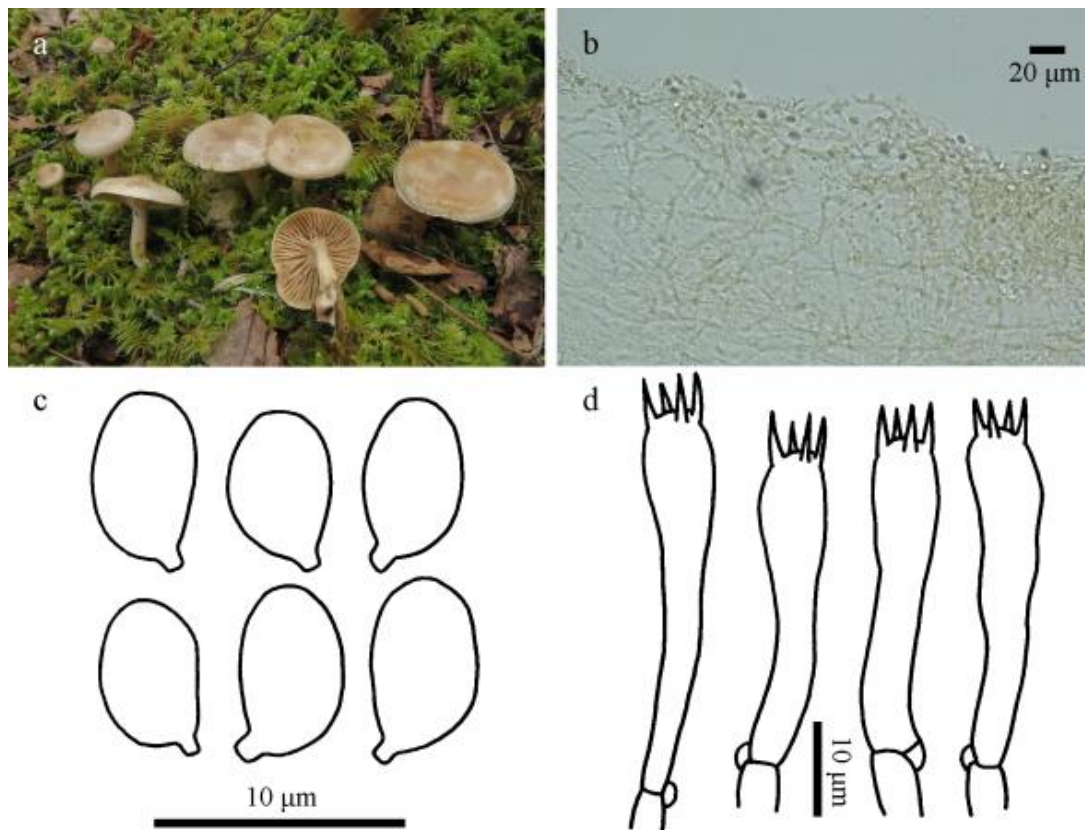


Figure 51 – *Hygrophorus brunneololamellatus* (GDGM84600). a Basidiomata. b Pileipellis. c Basidiospores. d Basidia.

Hygrophorus cinnamoneus C.Q. Wang, Ming Zhang & T.H. Li, sp. nov. Fig. 52

Index Fungorum Number: IF901156; Facesoffungi number: FoF14946

Etymology – *cinnamoneus*, from *cinnamoneus* = cinnamon-coloured, referring to the cinnamon colour of the pileus disc of the new species.

Type – China, Sichuan Province, Jiuzhaigou County, Jiuzhaigou National Park, in a subalpine forest dominated by *Picea* sp., elev. ca. 3000 m, 19 September 2020, M. Zhang (GDGM84699, Holotype).

Pileus 25–60 mm across, hemispherical to convex with an umbo when young, plano-convex to depressed when mature, orange white, pale orange, light brown, brown to dark brown (5A2–3, 6D4–8, 6E4–8, 6F4–6), usually darker or cinnamon-coloured to dark cinnamon-coloured at disc, gradually paler toward margin, sometimes weakly concentrically zonate, viscid when wet; margin incurved to decurved when young, then straight to uplifted, usually entire, sometimes lacerated to splitted. *Lamellae* adnate, adnate with a decurrent tooth, subdistant to close, L = 35–40, l = 1–3, waxy, fragile, orange white to white; edge entire and even. *Stipe* 30–60 mm long, 7–11 mm thick, cylindrical, equal to slightly enlarged downwards, sometimes radicate with a downward tapering

pseudorhiza underground, central, soft when mature, usually curved, white to orange white at first, usually brownish hairy when mature, more or less longitudinally striate. *Context* orange white.

Basidiospores $6-8 \times 3.5-5 \mu\text{m}$, $Lm = 7 \pm 0.61$, $Wm = 4.28 \pm 0.55$, $Q = 1.4-1.86(2)$, $Qm = 1.65 \pm 0.15$, ellipsoid to elongate, smooth, hyaline, thin-walled. *Basidia* $37-49 \times 6-8 \mu\text{m}$, $Q = 4.63-7.08$, 4-spored, clavate, sterigmata $4-6 \mu\text{m}$ long. *Hymenophoral trama* divergent, made up of cylindrical, thin-walled, hyaline hyphae $2-12 \mu\text{m}$ wide. *Pileipellis* an ixotrichoderm, made up of upturned or interwoven aerial hyphae $2.5-9 \mu\text{m}$ wide. *Stipitipellis* an ixocutis, made up of repent cylindrical thin-walled hyphae $3-10 \mu\text{m}$ wide. *Clamp connections* present in all tissues.



Figure 52 – *Hygrophorus cinnamoneus*. a Basidiomata (GDGM84554). b Basidiomata (GDGM84654). c–d Basidiomata (GDGM84699). e Basidiospores (GDGM84699). f Basidia (GDGM84699). g Elements of hymenophoral trama (GDGM84699). h Terminal hyphae of pileipellis (GDGM84554).

Habit, habitat and Distribution – Solitary, scattered or gregarious on the ground in subalpine forests; basidioma occurring in autumn; so far known from southwestern China (Sichuan Province).

Additional specimens examined – China, Sichuan Province, Jiuzhaigou County, Jiuzhaigou National Park, in a subalpine forest dominated by *Picea* sp., elev. ca. 3000 m, 22 September 2020, M. Zhang & J.H. Xing (GDGM84554); same locality, 19 September 2020, M. Zhang & J.H. Xing (GDGM84654, GDGM84649).

Notes – *Hygrophorus cinnamoneus* is characterized by its orangish to brownish pileus, plano-convex to depressed pileus centre, cinnamon-coloured umbo at pileus centre when mature, more or less hollow and fragile stipe, and the association with *Picea*. In our ITS tree (Fig. 1), this new fungus is sister to the European *H. discoideus* (Pers.) Fr., which differs by hemispherical to convex pileus when young, and the darker lamellae (Breitenbach & Kränzlin 1991).

Hygrophorus pallidofulvus C.Q. Wang, Ming Zhang & T.H. Li, sp. nov.

Fig. 53

Index Fungorum Number: IF901159; Facesoffungi number: FoF14949

Etymology – *pallidofulvus*, from *pallido* = pale, and *fulvus* = yellowish brown, referring the pale yellowish-brown pileus of the new species.

Type – China, Sichuan Province, Jiuzhaigou County, Jiuzhaigou, in a forest dominated by *Abies* sp., elev. ca. 2600 m, 20 September 2020, M. Zhang (GDGM84501, Holotype).



Figure 53 – *Hygrophorus pallidofulvus*. a Basidiomata (GDGM84501). b Basidiomata (GDGM84502). c Basidiospores (GDGM84501). d Basidia (GDGM84501). e Terminal hyphae of pileipellis (GDGM84501).

Pileus 15–70 mm across, convex when young, broadly convex, plano-convex to depressed when mature, pale yellow to light yellow (5A2–4, 5B4) when mature, viscid when wet; margin decurved when young, then straight to uplifted, usually entire. *Lamellae* adnate to adnate with a decurrent tooth when young, subdecurrent to obviously decurrent when mature, subdistant, L = 35–50, l = 1–3, waxy, fragile, yellowish white to pale yellow (4A2–3); edge usually entire and even. *Stipe* 20–65 mm long, 5–11 mm thick, cylindrical, central, soft when mature, usually slightly curved, concolorous with lamellae, sometimes with brownish discolouration when bruised, often weakly longitudinally striate, more or less fibrillose when young, glabrescent when mature, often with white mycelium or fibrills at base. *Context* yellowish white to white.

Basidiospores 6.5–7.5(8) × (4)4.5–5 μm, Lm = 6.98 ± 0.38, Wm = 4.53 ± 0.2, Q = (1.4)1.44–1.75(1.77), Qm = 1.54 ± 0.1, ellipsoid to elongate, smooth, hyaline, thin-walled. *Basidia* 34–52 × 7–8 μm, Q = 4.25–7.14, 4-spored, clavate, sterigmata 4–6 μm long. *Hymenophoral trama* divergent, made up of cylindrical, thin-walled, hyaline hyphae 4–12 μm wide. *Pileipellis* an ixotrichoderm, made up of repent or upturned aerial hyphae 2.5–5 μm wide. *Clamp connections* present in all tissues.

Habit, habitat and Distribution – Solitary or scattered on the ground in coniferous or mixed forests with *Abies* sp., occurring in autumn, so far known from southwestern China (Sichuan Province).

Additional specimens examined – China, Sichuan Province, Jiuzhaigou County, Jiuzhaigou, in a forest dominated by *Abies* sp., elev. ca. 2600 m, 20 September 2020, Ming Zhang & Jiahui Xing (GDGM84502).

Notes – *Hygrophorus pallidofulvus* is easily distinguished by its orange white to dark brown pileus, yellowish white to pale yellow, subdistant lamellae, and, association with *Abies*. In our ITS phylogenetic analysis (Fig. 1), *H. pallidofulvus* is related to *H. discoideus* and *H. subviscifer*. However, *H. discoideus* has more obvious colour differences between pileus centre and margin, usually glutinous pileus surface and a ring zone on the stipe (Candusso 1997, Campo 2015, Læssøe & Petersen 2019). *Hygrophorus subviscifer* has whitish pileus margin, and narrower basidiospores measuring 7–8.5 × 4.2–5 μm (Candusso 1997).

Hygrophorus pseudodiscoideus C.Q. Wang, T.Z. Wei & T.H. Li, sp. nov.

Fig. 54

Index Fungorum Number: IF901157; Facesoffungi number: FoF14947

Etymology – *pseudodiscoideus*, from *pseudo* = false, and *discoideus* = *Hygrophorus discoideus*, is proposed because this new species is close to *H. discoideus*.

Type – China, Sichuan Province, Litang County, in a forest dominated by *Abies* sp., *Picea* sp. and Rosaceae, elev. 3937 m, 17 August 2016, T.Z. Wei, L.H. Sun, Z.X. Wu & R.C. Zhang (HMAS277088, Holotype).

Pileus 25–55 mm across, hemispherical to convex when young, broadly convex when mature, orange grey, greyish orange, brownish orange, greyish red, brownish red, brownish orange, greyish brown, light brown (6B2–3, 6C3–5, 6D3–5, 7B2–3, 7C3–5, 7D3–5), viscid when wet; margin decurved at first, then straight to uplifted, whitish, usually entire. *Lamellae* adnate to subdecurrent, distant to subdistant, L = 40–48, l = 1–3, waxy, fragile, whitish to brownish; edge usually entire and even. *Stipe* 30–70 mm long, 5–10 mm thick, central, cylindrical, densely covered with minute, concolorous, snakeskin-shaped squamules. *Context* yellowish white to white.

Basidiospores (5)6.5–8(9) × 3.5–4.5 μm, Lm = 7.14 ± 0.68, Wm = 4.1 ± 0.32, Q = (1.43)1.44–2(2.14), Qm = 1.75 ± 0.18, ellipsoid, elongate to cylindrical, smooth, hyaline, thin-walled. *Basidia* 35–52 × 5.5–7.5 μm, Q = 4.67–8.18, 4-spored, clavate, sterigmata 5–7 μm long. *Hymenophoral trama* divergent, made up of cylindrical or inflated hyphae 3–22 μm wide. *Pileipellis* an ixocutis, made up of repent hyphae 2–5 μm wide. *Clamp connections* present in all tissues.

Habit, habitat and Distribution – Scattered to gregarious on the ground in forests dominated by *Picea* sp., occurring in summer and autumn, so far known from southwestern China (Sichuan Province and Tibet Autonomous Region).

Additional specimens examined – China, Sichuan Province, Garze Tibetan Autonomous Prefecture, Daochengyading, 2 August 2022, D. Wang (SAAS4114). Tibet Autonomous Region, Nyingchi County, in a forest dominated by *Picea* sp., elev. 3133 m, 13 September 2016, T.Z. Wei, Z.X. Wu, L. Yang, H.D. Zheng & X.C. Wang (HMAS 277234).

Notes – *Hygrophorus pseudodiscoideus* is characterized by its small to medium-sized basidioma with brownish orange pileus margin, umbonate and darker pileus centre, snakeskin-shaped squamules on stipes, ellipsoid, elongate to cylindrical basidiospores, and association with *Picea* trees.

Hygrophorus discoideus, *H. roseodiscoideus* and *H. lindtneri* M.M. Moser are similar to *H. pseudodiscoideus*. However, *H. discoideus* differs by its usually glutinous pileus surface and ring zone on the stipe (Candusso 1997, Læssøe & Petersen 2019); *H. roseodiscoideus* has bigger basidiospores [$8\text{--}10(12) \times 5.5\text{--}7 \mu\text{m}$] and is associated with *Quercus* (Candusso 1997); and *H. lindtneri* differs by its slender basidiomata and lighter pileus centre.

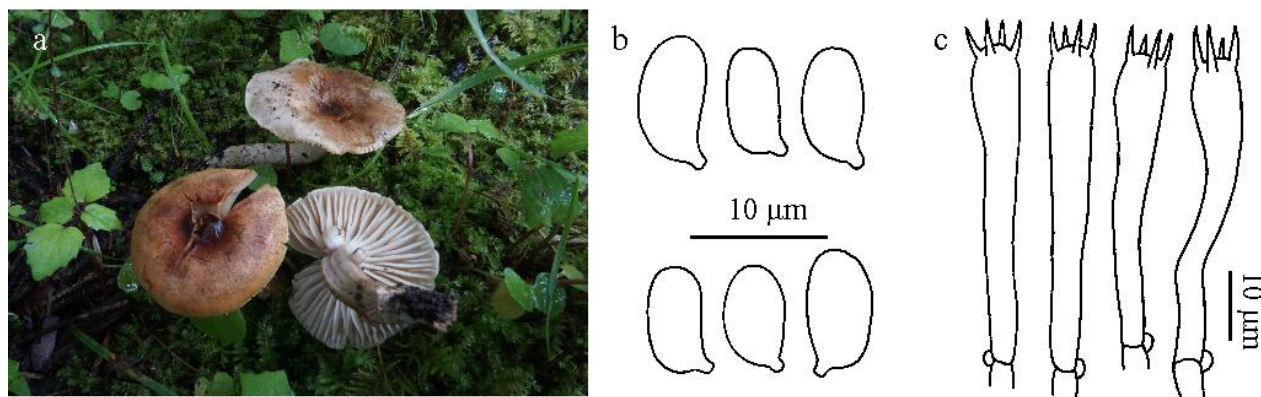


Figure 54 – *Hygrophorus pseudodiscoideus*. a Basidiomata (SAAS4114, by D. Wang). b Basidiospores (HMAS 277088). c Basidia (HMAS 277088).

Hygrophorus sect. *Camarophylli*

Phylogenetic support: In the multilocus analysis (Fig. 2), sect. *Camarophylli* appears as a strongly supported (MLBS = 100%) independent group.

Studied Chinese species included in this section: *Hygrophorus subcapreolarius*.

Hygrophorus subcapreolarius C.Q. Wang, Ming Zhang & T.H. Li, sp. nov.

Fig. 55

Index Fungorum Number: IF901160; Facesoffungi number: FoF14950

Etymology – *subcapreolarius*, from *sub* = close to, and *capreolarius* = *Hygrophorus capreolarius*, referring to the new species similar to *H. capreolarius*.

Type – China, Yunnan Province, Zhongdian County, in a subalpine forest, $27^{\circ}84'N$, $99^{\circ}98'E$, elev. ca. 3850 m, 4 September 2020, M. Zhang & L.Q. Wu (GDGM83194, Holotype).

Pileus 19–50 mm across, convex when young, convex to hemispherical when mature, dull red, greyish red, brownish red, reddish brown to dark brown (9B2–8, 9C3–8, 9D4–8, 9E4–8, 9F5–8), often partially maculate with darker spots or patches, more or less discolouring to reddish brown or darker where injured, slightly sticky when wet, finely granular-scaly; margin incurved when young, then straight to uplifted, entire to irregularly wavy. *Lamellae* adnate to subdecurrent, subdistant to distant, L = 28–36, l = 1–3, waxy, fragile, brownish orange, light brown to brown (6C4–6, 6D4–6, 6E4–6), darkening with age; edge entire and smooth. *Stipe* 40–80 mm long, 5–10 mm thick, central, solid, more or less equal, almost concolorous with pileus, often paler upwards, discolouring to reddish brown or darker where injured, with or without some white mycelium at base, often short radicate. *Context* medium.

Basidiospores $4\text{--}7.5(8.5) \times 4\text{--}5 \mu\text{m}$, Lm = 6.83 ± 0.61 , Wm = 4.6 ± 0.42 , Q = 1.3–1.75, Qm = 1.49 ± 0.12 , ellipsoid to elongate, smooth, hyaline, thin-walled. Basidia $42\text{--}55 \times 5\text{--}9 \mu\text{m}$, Q = 5.6–11, 4-spored, clavate, sterigmata 5–7 μm long. *Hymenophoral trama* divergent, made up of cylindrical, thin-walled, hyaline hyphae 2.5–11 μm wide. *Pileipellis* an ixotrichoderm, made up of upturned or interwoven aerial hyphae 3–5 μm wide. *Stipitipellis* an cutis, made up of repent cylindrical thin-walled hyphae 2.5–5 μm wide. *Clamp connections* present in all tissues.

Habit, habitat and Distribution – Solitary to scattered on the mossy ground in subalpine forests dominated by *Picea* sp., occurring in autumn, so far known from southwestern China (Yunnan Province).

Additional specimen examined – China, Yunnan Province, Shangri-la, Pudacuo National Park, in a subalpine forest, 3 September 2020, M. Zhang & L.Q. Wu (GDGM82403).

Notes – *Hygrophorus subcapreolarius* is characterized by dull red to dark brown pileus often partially covered with darker spots or patches, adnate to subdecurrent and subdistant to distant lamellae, and ellipsoid to elongate basidiospores. Prior to this study, *H. subcapreolarius* was recorded in Hengduan Mountains as *H. capreolarius* (Kalchbr.) Sacc. (Chinese Academy of Sciences Qinghai-Tibet Plateau Comprehensive Scientific Expedition Team 1996). Morphologically, *H. capreolarius* differs from *H. subcapreolarius* by more distinctly fibrilous pileus surface, and more purplish tint on lamellae (Waldvogel et al. 2001). In our ITS phylogenetic analysis (Fig.1), *H. subcapreolarius* is sister to the European *H. capreolarius*, and the North American “*H. capreolarius*” is located at the basal of the *H. subcapreolarius*-*H. capreolarius* clade. Therefore, the North American “*H. capreolarius*” needs an urgent taxonomic revision.

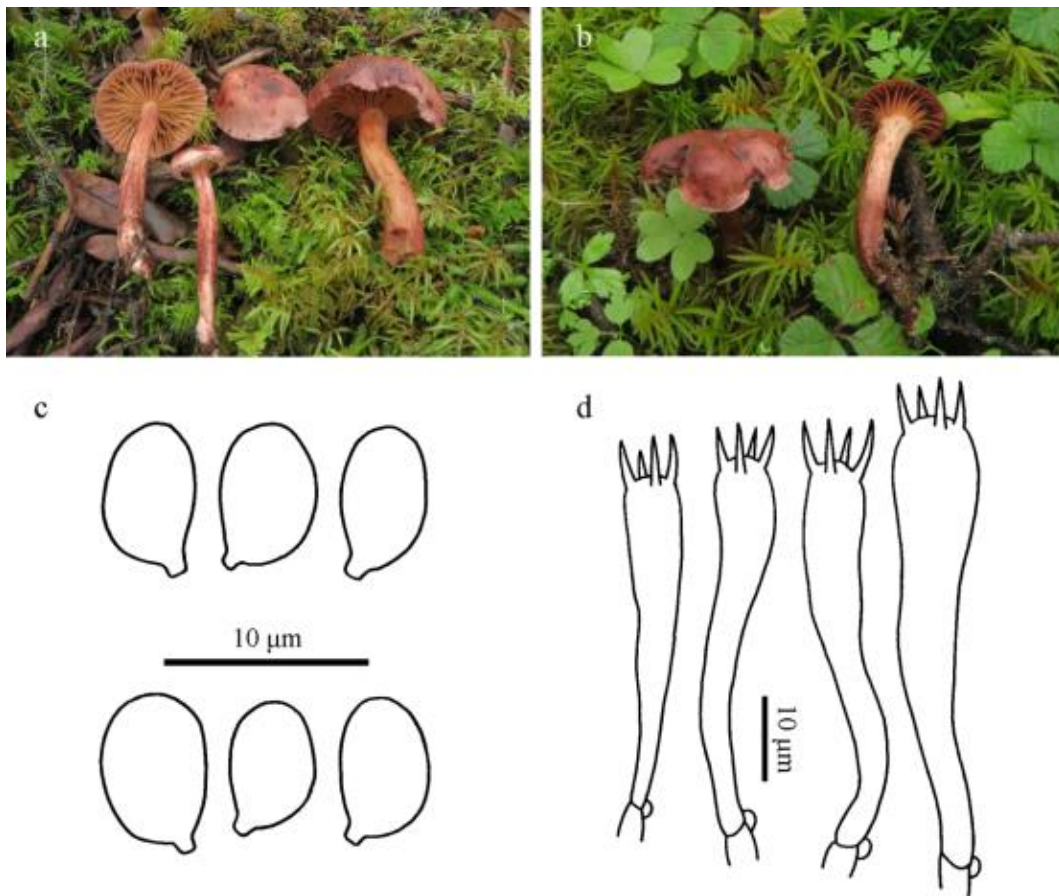


Figure 55 – *Hygrophorus subcapreolarius*. a Basidiomata (GDGM82403). b Basidiomata (GDGM83194). c Basidiospores (GDGM83194). d Basidia (GDGM83194).

Hygrophorus sect. *Chrysodontes*

Phylogenetic support: Section *Chrysodontes* is a strongly supported (100% MLBS) monophyletic clade comprising the *H. chrysodon* species complex in both ITS analysis and multilocus analysis (Figs 1–2).

Studied Chinese species included in this section: *Hygrophorus aurantiosquamosus*.

Hygrophorus aurantiosquamosus H.Y. Huang & L.P. Tang, Phytotaxa 528(5): 282 (2021) Fig. 56

Pileus 25–65 mm broad, conic to broadly conic when young, convex to plane when mature, yellowish white, pale yellow, light yellow to greenish yellow (2A2–7), covered with yellowish floccules and drops, surface viscid when wet; margin decurved at first, then expanded to straight, usually with yellowish fibrils. *Lamellae* decurrent, subdistant, L = 42–68, l = 1–3, whitish; edge

entire and even. *Stipe* 40–80 mm long, 6–15 mm broad, cylindrical to subcylindrical, equal to subequal, concolorous with the pileus, with obvious yellowish floccules and drops on the apex. *Context* white, thin.

Basidiospores (7.5)8.0–11(12) × (3.5)4–5(5.5) μm, $Lm = 9.48 \pm 0.97$, $Wm = 4.39 \pm 0.42$, $Q = (1.80)1.89–2.63(2.86)$, $Qm = 2.17 \pm 0.24$, elongate to cylindrical, smooth, thin-walled, hyaline. *Basidia* 30–53 × 6–9 μm, $Q = 4.47–7.33$, 4-spored, clavate, thin-walled; sterigmata up to 6.5 μm long. *Hymenophoral trama* divergent, made up of cylindrical or inflated hyphae 2.5–21 μm broad, thin-walled, hyaline. *Pileipellis* an ixotrichoderm, made up of repent, interwoven or upturned hyphae 1.5–6.5 μm broad, with yellowish intracellular pigment. *Stipitipellis* a cutis, composed of hyphae 1.5–7 μm broad, made up of erect hyphae with yellowish intracellular pigment at apex. *Clamp connections* present in all tissues.

Habit, habitat and Distribution – Scattered to gregarious on the ground in forests dominated by *Picea* trees, occurring in summer and autumn, so far known from southwestern and northwestern China (Qinghai Province, Sichuan Province, Tibet Autonomous Region, Yunnan Province) and Pakistan (Huang et al. 2021, this study).



Figure 56 – *Hygrophorus aurantiosquamosus*. a–b Basidiomata (GDGM84517). c–d Basidiomata (LJW2129). e Basidiospores (GDGM84517). f Basidia (GDGM84517).

Specimens examined – China, Sichuan Province, Jiuzhaigou County, Jiuzhaigou Scenic Spot, in a subalpine forest dominated by *Picea* sp., elev. ca. 2600 m, 20 September 2020, M. Zhang & J.H. Xing (GDGM84517); Songpan County, Erdaohai, in a subalpine forest dominated by *Picea* sp., elev. ca. 3300 m, 23 September 2020, M. Zhang & J.H. Xing (GDGM84401, GDGM84424). Yunnan Province, Yulong County, Lijiang Alpine Botanical Garden, in a subalpine forest dominated by *Abies* sp., *Picea* sp. and *Rhododendron* sp., elev. 3962 m, 26 September 2020, J.W. Liu, LJW2129 (GDGM92368).

Notes – *Hygrophorus aurantiosquamosus*, recently described from southwestern China by Huang et al. (2021b), is the second species of *H. chrysodon* complex. According to our observation, the squamulae of the pileus are rarely orange but usually gold. *Hygrophorus aurantiosquamosus* is characterized by whitish to yellowish pileus covered with golden yellow squamules, floccose pileus margin and upper stipe, and elongate to cylindrical basidiospores [$9.5\text{--}12 \times 4\text{--}5.5 \mu\text{m}$ in Huang et al. (2021b), $(7.5) 8.0\text{--}11 (12) \times (3.5)4\text{--}5(5.5) \mu\text{m}$ in this study], association with *Picea*, and occurrence in high elevations (above 3000 m so far). Macromorphologically, *H. chrysodon* has similar pileus with yellowish squamules, but it differs micromorphologically by smaller basidiospores ($7\text{--}9 \times 4\text{--}5 \mu\text{m}$) and shorter basidia ($38\text{--}50 \times 6.5\text{--}8 \mu\text{m}$) (Candusso 1997). In our ITS phylogenetic analysis (Fig. 1), *H. aurantiosquamosus* is sister to the “*H. chrysodon*” clade from North America (Canada, Mexico and USA). In addition, a holarctic region distributed “*H. chrysodon*” clade is close to *H. aurantiosquamosus* and the American “*H. chrysodon*” clade. Thus, these two clades could represent two undescribed species.

Unplaced species

Hygrophorus orientimarzuolus C.Q. Wang, J.W. Liu & T.H. Li, sp. nov.

Fig. 57

Index Fungorum Number: IF901161; Facesoffungi number: FoF14951

Etymology – *orientimarzuolus*, from *orienti* = east, and *marzuolus* = *Hygrophorus marzuolus*, referring to its type location in East Asia and it is close to *H. marzuolus*.

Type – China, Yunnan Province, Nanhua County, in a subalpine forest dominated by Fagaceae and *Pinus* sp., $25^{\circ}13'53''\text{N}$, $100^{\circ}59'24''\text{E}$, elev. 2559 m, 9 October 2021, J.W. Liu, LJW2439 (GDGM92361, Holotype). *Pileus* 50–100 mm across, convex to plano-convex when young, depressed to infundibuliform when mature, greyish white, light grey, medium grey to dark grey (1B1, 1C1, 1D1, 1E1, 1F1), subglabrous to finely tomentose in places; margin straight to uplifted when mature. *Lamellae* adnate to adnexed, distant to subdistant, $L = 44\text{--}60$, $l = 1\text{--}3$, waxy, thick, whitish when young, with some light grey discoloration when mature; edge entire and even when young. *Stipe* 60–90 mm long, 15–25 mm thick, central, solid, more or less cylindrical, usually tapered towards the base, concolorous with pileus, light grey to whitish at the base, subglabrous to tomentose in places, slightly with white mycelium at base. *Context* whitish, thick.

Basidiospores $5.5\text{--}6.5(7) \times 4.5\text{--}5.5 \mu\text{m}$, $Lm = 6.25 \pm 0.44$, $Wm = 4.98 \pm 0.34$, $Q = (1.09)1.2\text{--}1.3(1.44)$, $Qm = 1.26 \pm 0.07$, subglobose, broadly ellipsoid to ellipsoid, smooth, hyaline, thin-walled. *Basidia* $34\text{--}52 \times 5\text{--}8 \mu\text{m}$, $Q = 5\text{--}9.2$, 4-spored, slenderly clavate to clavate, sterigmata $4\text{--}6.5 \mu\text{m}$ long. *Hymenophoral trama* divergent, made up of cylindrical, thin-walled, hyaline hyphae $5\text{--}13 \mu\text{m}$ wide. *Pileipellis* an ixocutis, made up of repent hyphae $3.5\text{--}9.5 \mu\text{m}$ wide, with brownish intracellular pigment in KOH. *Stipitipellis* an cutis, mainly made up of repent cylindrical thin-walled hyphae $2\text{--}13 \mu\text{m}$ wide, occasionally made up of upturned hyphae. *Clamp connections* present in all tissues.

Habit, habitat and Distribution – Solitary on the ground in mixed forests with *Pinus* sp., occurring in autumn, so far known from southwestern China (Yunnan Province).

Notes – *Hygrophorus orientimarzuolus* is recognized by dark greyish pileus and stipe, adnate to adnexed and distant to subdistant lamellae, subglobose, broadly ellipsoid to ellipsoid basidiospores, and the habitat in mixed forest.

Hygrophorus atramentosus (Alb. & Schwein.) H. Haas & R. Haller Aar. ex Bon, *H. camarophyllus* (Alb. & Schwein.) Dumée, Grandjean & Maire and *H. marzuolus* (Fr.) Bres. are

similar to *H. orientimarzuolus* in the pileus color. However, *H. atramentosus* differs from *H. orientimarzuolus* by more slimy and always convex pileus, larger basidiospore measuring 8–9×4–5 μm, and association with *Picea* (Læssøe & Petersen 2019). *Hygrophorus camarophyllus* has more orangish tint on pileus, subdecurrent to decurrent lamellae, and is associated with *Picea* (Læssøe & Petersen 2019). *Hygrophorus marzuolus* lacks depressed pileus, has whitish stipe, and grows in spring (Breitenbach & Kränzlin 1991, Candusso 1997).

In the ITS phylogenetic analysis (Fig. 1), the Chinese *H. orientimarzuolus* is sister to the European *H. marzuolus*, and *H. camarophyllus* is close to them. In addition, the European and North American *H. camarophyllus* have significant differences, thus the name of the North American taxon needs to be reconsidered in the future.

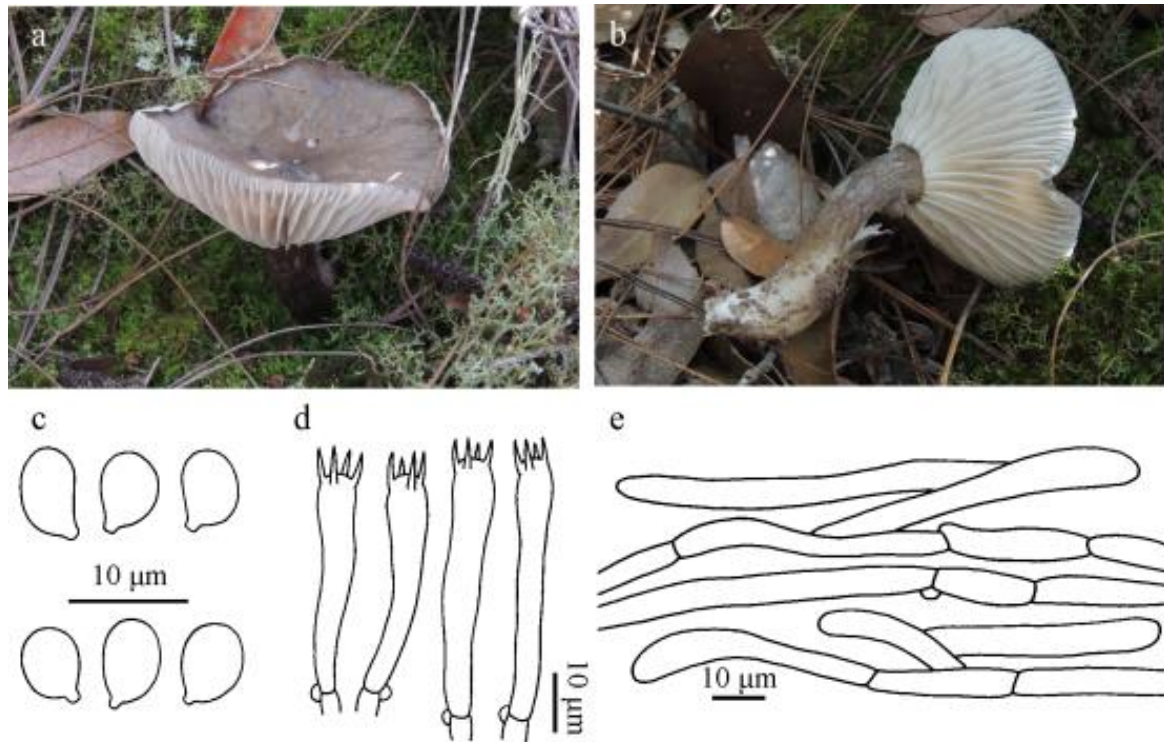


Figure 57 – *Hygrophorus orientimarzuolus* (LJW2439). a–b Basidiomata. c Basidiospores. d Basidia. e Pileipellis.

Insufficiently known taxa from China

Hygrophorus cf. *exiguus*

Notes – *Hygrophorus* cf. *exiguus* represented in our study by a single collection GDGM44612 is a taxon similar to *H. exiguus* E. Larss., E. Campo & M. Carbone. The multilocus analysis (Fig. 2) lack representative sequences of *H. exiguus* and the most closely related to *Hygrophorus* cf. *exiguus* are *H. sichuanensis* and *H. sp.1*. However, additional collections and sequences are essential to prove if *H. cf. exiguus* represents a novel taxon.

Hygrophorus sp. 1

Notes – *Hygrophorus* sp. 1 is represented in our study only by a single collection GDGM83568 which contain a single basidioma insufficient for morphological study. Our ITS phylogenetic analysis (Fig. 1) indicated that the unknown taxon *H. sp. 1* is closely related to two sister species (*H. exiguus* and *H. sichuanensis*); and the multilocus analysis (Fig. 2) place *H. sp. 1* as sister species to *H. sichuanensis*. Therefore, *Hygrophorus* sp. 1 should be classified in the sect. *Olivaceoumbrini*. To allow a formal description of this probably new species, more material and detailed observations are needed.

***Hygrophorus* sp. 2**

Notes – *Hygrophorus* sp.2 is represented in our study by a single collection GDGM79241. Our ITS phylogenetic analysis (Fig. 1) indicated that GDGM79241 belongs to the *H. glutinifer* complex, but shows differences from the known species. In the multilocus analysis (Fig. 2), GDGM79241 is placed close to *H. glutinifer*. Unfortunately, there is no available sufficient material in GDGM for morphological study. To allow a full formal description and correct identification of this taxon, more collections and detailed studies are needed.

***Hygrophorus* sp. 3**

Notes – The collection XHW7387 (HKAS 131116) represents an undescribed species in the sect. *Hygrophorus*. In our ITS phylogenetic analysis (Fig. 1), XHW7387 is placed as sister to *H. arbustivus*. In the multigenetic analysis (Fig. 1), XHW7387 is close to *H. armeniacus* and *H. yukishiro*, but at position showing clear genetic distance from both these species. Unfortunately, XHW7387 contains only a single basidioma. More collections are needed to allow a formal description of this probably new species.

***Hygrophorus* sp. 4**

Notes – The collection XML1910693 represents an undescribed species in the sect. *Vividi*. In both the ITS and multilocus trees (Figs 1–2), XML1910693 is placed as sister to *H. vividus*. Unfortunately, XML1910693 contains only a single basidioma. More material is needed to allow a formal description of this possibly new species.

Discussion

Species diversity of *Hygrophorus* from China

In this study, one new section and 26 new species are described. In total, 62 species (including 5 insufficiently known species) of *Hygrophorus* from China are presented here, which makes 42% of them new to science. Some new taxa have previously been misidentified as other morphologically similar species. For example, *H. subcapreolarius* was recorded as *H. capreolarius* based solely on morphological characters (Chinese Academy of Sciences Qinghai-Tibet Plateau Comprehensive Scientific Expedition Team, 1996). While others recently discovered were morphologically distinct, such as *H. brunneololamellatus*, *H. orientimarzuolus* and *H. vividus*. There are also differences in species numbers among *Hygrophorus* sections. Four sections (*Hygrophorus*, *Pudorini*, *Olivaceoumbrini* and *Aurei*) include 78% of the species of the genus *Hygrophorus* from China. And the species number of the remaining five sections is obviously much lower than those four sections.

Although we have included a lot of Chinese *Hygrophorus* in this study, some taxa still have not been included. In fact, the distribution of some species previously reported in China (Chen & Li 2013) are not confirmed in this study. Some of them may not exist in China, and some may not have been discovered recently. Therefore, it is still necessary to continue in field survey and to document and describe *Hygrophorus* species with both morphological and molecular approaches.

Meta-analysis of ITS rDNA sequences reveals incorrect sequences and unreliable species identification

The ITS region has been adopted as the universal DNA barcode in the genus *Hygrophorus* (Moreau et al. 2018, Huang et al. 2021a, Bellanger et al. 2021, Wang et al. 2022). There are over 1100 ITS sequences labeled as *Hygrophorus* in GenBank and Unite public databases. However, according to the blast search and alignment analysis results, apart from some sequences of low quality or error reads, there are a lot of unreliable sequence identifications in public databases:

(i) Some sequences labeled as *Hygrophorus* do not belong to the genus due to the use of *Hygrophorus* s.l. conception or due to misidentification. For example, sequences with accession

numbers MF061322 and MZ018504 labeled as *Hygrophorus* should belong to *Hygrocybe* and *Suillus*, respectively.

(ii) Few sequences are incorrectly placed into wrong genus, for example, DQ097880 labelled as *Cortinarius vibratilis* is *H. hedrychii* or a related species.

(iii) Some sequences are labeled by names of morphologically similar species, usually because they belong to a complex of closely related and sometimes unrecognized taxa. For example, sequences labeled as *H. russula* represented at least 6 species of *H. russula* complex.

In conclusion, the identification using direct Blast search in the public databases must be taken with caution, but it serves as a simple and powerful tool for preliminary taxonomic placement of the studied samples (Hofstetter et al. 2019). However, sequences come from a wide range of sources and obtained by various sampling and sequencing methods can provide indispensable data about ecology, distribution and even species diversity.

Species for which multiple names are applied

There are some phylogenetic species that are currently described under multiple names with identical ITS sequences.

The ITS sequences from holotype specimens of *H. adiaphorus* and *H. betulae* fall within one strongly supported clade (MLBS = 100%), therefore, *H. betulae* might be a later synonym of *H. adiaphorus*. Considering the morphological differences between them as mentioned in Bellanger et al. (2021), the two species still are preserved. It is worth mentioning that recently diverged taxa could not be distinguished from each other might be the weakness of a single gene (ITS) study of the genus *Hygrophorus*.

Hygrophorus glutinifer-*H. persoonia* and *H. latitabundus*-*H. limacinus* are presented in a phylogenetic clade in both this study and Bellanger et al. (2021). We agree with the opinion of Bellanger et al. (2021) that *H. persoonia* is a later synonym of *H. glutinifer*, and *H. latitabundus* is a later synonym of *H. limacinus*. The */secretanii* clade contains *H. monticola* A.H. Sm. & Hesler and *H. secretanii* in this study and Lodge et al. (2014). Here, we followed the treatment of Lodge et al. (2014) who considered *H. monticola* as a later synonym of *H. secretanii* (Hesler & Smith 1963). In addition, the */ponderatus* clade contains two North American species, i.e. *H. ponderatus* and *H. subalpinus*. If the species identification of the corresponding specimens are correct, then *H. ponderatus* should be treated as the valid name and *H. subalpinus* is its later synonym.

It is also necessary to verify the hypothesis based solely on comparison of identified ITS sequences by analysing sequences and morphological observations originating from type specimens. For this reason, we did not make any nomenclatural proposals based on sequence placement in the ITS tree.

Megaphylogeny in general supports morphologically defined species

The present study includes the most comprehensive phylogenetic analysis of *Hygrophorus* so far, with a focus on Chinese taxa. By combining all the sequences available from GenBank and Unite, and newly generated sequences in this study, we assembled the newest species concepts for the genus *Hygrophorus*. In particular, the availability of multiple sequences per species allowed us to infer intraspecific and interspecific genetic variations. The ITS tree showed a little support on the backbone and should not be taken as a basis for infrageneric taxonomic classification, but seems to be sufficient for reliable estimation of interspecific phylogenetic distances.

In general, congruence was observed between ITS-defined phylogenetic species and morphological species. In most cases, multiple sequences of a single species received support and were distinctive from sister species. For example, three closely related Chinese new species, i.e. *H. chuxiongensis*, *H. flavoalbus*, *H. ochraceus*, are well separated in the ITS phylogenetic tree.

In some cases, long branches were observed within a phylogenetic species and these branches were occasionally longer than distance between two species clades. For example, a sequence (MW874514) downloaded from GenBank formed such a long branch within the

H. pseudopurpuracens clade. These discrepancies may be caused by the poor quality of the sequences, and are unfortunately impossible to verify, since chromatograms of sequences in public databases were not available.

Recent release of a large number of sequences of European and also some North American type specimens allowed the identification of some morphologically similar species, which had long puzzled taxonomists. For example, Larsson & Jacobsson (2004) obtained ITS sequences from 200-year-old type specimens of *H. quercetorum* P.D. Orton, which proved that this species was the later synonym of *H. cossus* (Sowerby) Fr. Thus, obtaining more sequences of the type specimens and correctly identified samples is essential for the species identification of *Hygrophorus*.

Phylogeny and systematic treatment of *Hygrophorus*

Our multilocus phylogenetic analysis indicates that the genus *Hygrophorus* is a well supported monophyletic clade. Neither the ITS nor the multilocus dataset could clarify the delimitation of subgenera within this genus. Similar phenomenon occurred in the genus *Tricholoma*, to clarify the delimitation of subgenera within this genus, a dataset with much more locus was used (Ding et al. 2023).

Our multilocus dataset resolved a section-level phylogeny of the studied genus, and nine sections are supported as monophyletic clades. To promote nomenclatural stability and continuity in the name usage, we followed the comprehensive study of Lodge et al. (2014) and we proposed only a necessary reorganization.

Species distributions of *Hygrophorus* from China

In China, the genus *Hygrophorus* is widely distributed. The highest species richness was observed in temperate zones, especially southwestern China is a hot spot region of this genus. The only species found in tropical region (Hainan Province) of China was *Hygrophorus glutiniceps*.

For the purposes of the discussion, 4 distribution patterns of the Chinese *Hygrophorus* are considered:

(i) Holarctic: uncommon, *H. agathosmoides*, *H. hedrychii*, *H. pudorinus* and *H. speciosus*. Whether this distribution is natural or due to the introduction of tree species needs more research. It is worth mentioning that the intraspecific differences of *H. pudorinus* are associated with the distribution regions.

(ii) China-Europe: *H. abieticola*, *H. brunneololamellatus*, *H. erubescens*, *H. gliocyclus*, *H. pinophilus* and *H. queletii*.

(iii) Asia: *H. griseodiscus*, *H. orientalis* and *H. yukishiro*.

(iv) Endemic to China. At present, the majority of the Chinese *Hygrophorus* species are endemic. As species from East Asia even Asia are discovered, it is possible to find some species that are common distributed species, but we still speculate that China is very rich in endemic species.

To clarify the true distribution pattern of the Chinese *Hygrophorus*, more extensive sampling in and out of China is needed.

Ectomycorrhizal association of *Hygrophorus* from China

In China, the current data show that the most common symbiotic plants of *Hygrophorus* are the following constructive tree species (e.g. Betulaceae, Fagaceae and Pinaceae).

As indicated in previous studies (Larsson & Jacobsson 2004, Jacobsson & Larsson 2007, Larsson et al. 2018), many *Hygrophorus* species has strong host preferences. For example, in both Europe and northeastern China, *H. lucorum* is associated with *Larix*; in Asia, Europe and North America, *H. abieticola* grows under *Abies*. Therefore, the records of host trees can be useful for species identification.

In this study, we found that some closely related species exhibit apparent host switch. For examples, *H. chrysdon* occurs in *Abies* and *Fagus* forests in Europe, while its morphologically and phylogenetically close relative, *H. aurantiosquamosus*, is associated with *Picea* in China (Huang et

al. 2021b). Host switching may be one of the driving forces for the diversity of ectomycorrhizal fungi (Feng & Yang 2019).

Conclusions and future directions

In total, 62 *Hygrophorus* species (57 species plus 5 insufficiently known species) from China are presented in this study. Overall, this study represents a global phylogenetic analysis of the genus *Hygrophorus*. We observed strong congruence between morphological species and ITS/multilocus-defined phylogenetic species. The phylogenetic analyses presented here provide a robust hypothesis for section division within the genus *Hygrophorus*. More extensive sampling and the analyses using more gene sequences may solve the subgenus level relationship within *Hygrophorus*.

Although a large number of correctly identified sequences are released in the past 5 years, sequences of some morphologically defined species are still missing. Therefore, to clarify the species diversity and phylogenetic relationship of global *Hygrophorus*, the shortage of those sequences is a basic issue that needs to be urgently addressed. In addition, we predict that further investigations will help to elucidate the real species diversity of *Hygrophorus* in China.

Acknowledgements

We thank the curators and librarians of CFSZ, GDGM, HKAS, HMAS, MHHNU, SAAS, for loan of *Hygrophorus* collections used in this study. The authors thank Hongfen Bai, Xuelian Gao, Yuqing Guan, Yanchun Li, Nan Liu, Liqin Mu, Weiqiang Qin, Hua Qu, Delin Song, Lihui Sun, Liping Tang, Di Wang, Wei Wang, Xingcun Wang, Liqiang Wu, Zuxun Wu, Jiahui Xing, Jiang Xu, Liu Yang, Guolin Yu, Niankai Zeng, Qi Zhao, Runchao Zhang and Huandi Zheng for kindly providing specimens and photos on some Chinese collections. Thanks are given to Xianghua Wang for providing specimen loan and constructive suggestions. Thanks are given to David Hibbett for given some North American specimens. Xintong Chen, Yiwen Guo, Xiaoqing Huang, Yinyou Huang, Yanzhen Li, Wanqing Xie, Jiawen Zhang, Guorui Zhong and Mengjia Zhu are acknowledged for their help in DNA extraction and sequencing. Funding for this research was provided by the National Natural Science Foundation of China (Nos. 32170010, 32070020, 31970024 and 32000016), the Ministry of Science and Technology of China (No. 2022FY100505), and the National GDAS' Project of Science and Technology Development (2020GDASYL-20200103027). The research of Slavomir Adamčík was funded by by Slovak national projects APVV 20-0257, APVV 20-0284 and VEGA 2/0050/22. Katarína Adamčíková is acknowledged for sequencing of *Hygrophorus lucorum* collections from the type origin area.

References

- Adamčík S, Lizon P, Ripkova S. 2005 – *Hygrophorus* taxa from Slovakia described by Kalchbrenner. *Sydowia* 57, 154–165.
- Bas C. 1990 – Notulae ad floram agaricinam neerlandicam – XVII on tribus names in the family Tricholomataceae sensu lato. *Persoonia* 14, 233–235.
- Bau T, Bao HY. 2016 – Market Mushrooms of Northeastern China. Northeast Forestry University Press, Harbin.
- Bellanger JM, Lebeuf R, Sesli E, Loizides M et al. 2021 – *Hygrophorus* sect. *Olivaceoumbrini*: new boundaries, extended biogeography and unexpected diversity unravelled by transatlantic studies. *Persoonia* 46, 272–312.
- Bessette AE, Roody WC, Sturgeon WE, Bessette AR. 2012 – Waxcap Mushrooms of Eastern North America. Syracuse University Press. Syracuse, New York.
- Bon M. 1990 – Flore Mycologique d'Europe 1. Les Hygrophores. *Documns Mycol Memoire hors série* 1.
- Breitenbach J, Kränzlin F. 1991 – Fungi of Switzerland Vol. 3 Boletes and Agarics 1st Part. Mycological Society of Lucerne, Lucerne.

- Campo E. 2015 – *Hygrophorus*, *Hygrocybe* e *Cuphophyllus* del Friuli Venezia Giulia. Gruppo Micologico Sacilese, Viale Zancanaro, Sacile.
- Candusso M. 1997 – Fungi Europaei 6. *Hygrophorus* s.l. Libreria Basso, Alassio.
- Chen JL, Li Y. 2013 – The checklist of species in Hygrophoraceae from China and their distribution. *Journal of Fungal Research* 11, 3–13, 37. (in Chinese).
- Chinese Academy of Sciences Qinghai-Tibet Plateau Comprehensive Scientific Expedition Team. 1996 – Fungi of Hengduan Mountain. Science Press, Beijing. (in Chinese).
- Cui YY, Cai Q, Tang LP, Liu JW. 2018 – The family Amanitaceae: molecular phylogeny, higher-rank taxonomy and the species in China. *Fungal Diversity* 91, 5–230.
- Ding XX, Xu X, Cui YY, Kost G et al. 2023 – A fifty-locus phylogenetic analysis provides deep insights into the phylogeny of *Tricholoma* (Tricholomataceae, Agaricales). *Persoonia* 50, 1–26.
- Dong QQ, Bau T. 2022 – A New Combination and Two Newly Recorded Species of Hygrophoraceae from China. *Journal of Fungal Research*, online. (in Chinese).
- Endo N, Tokoo R, Fukuda M, Yamada A. 2018 – *Hygrophorus yukishiro* sp. nov., a new vernal edible mushroom from Nagano Prefecture, Japan. *Mycoscience* 59(6), 449–454.
- Feng B, Yang ZL. 2019 – Ectomycorrhizal symbioses: Diversity of mycobionts and molecular mechanisms that entail the development of ectomycorrhizae. *Scientia Sinica Vitae* 49, 436–444. (in Chinese).
- Fries EM. 1836 – *Corpus Florarum provincialium Sueciæ*, Vol. 1: *Floram Scanicam*, Uppsala.
- Gardes M, Bruns TD. 1993 – ITS primers with enhanced specificity for basidiomycetes — application to the identification of mycorrhizae and rusts. *Molecular Ecology* 2, 113–118.
- Harmaja H. 1969 – The genus *Clitocybe* (Agaricales) in Fennoscandia. *Karstenia* 10, 5–168.
- He XL, Peng WH, Wang D. 2021 – *Atlas of Important Wild Edible Fungi in Sichuan*. Science Press, Beijing. (in Chinese).
- He ZM, Yang ZL. 2021 – A new clitocyboid genus *Spodocybe* and a new subfamily Cuphophylloideae in the family Hygrophoraceae (Agaricales). *MycologyKeys* 79, 129–148.
- Hesler LR, Smith AH. 1963 – *North American Species of Hygrophorus*. University of Tennessee Press, Knoxville.
- Hofstetter V, Buyck B, Eyssartier G, Schnee S et al. 2019 – The unbearable lightness of sequenced-based identification. *Fungal Diversity* 96, 243–284.
- Horak E. 1990 – *Monograph of the New Zealand Hygrophoraceae (Agaricales)*. *New Zealand Journal of Botany* 28, 255–309.
- Hu JH, Yu WJ, Deng LS, Fan YG et al. 2023 – The detection of major clades and new species of *Mallocybe* (Inocybaceae, Agaricales) from China with elongate cheilocystidia. *Mycological Progress* 22, 15.
- Huang HY. 2022 – *The Species Resources of Hygrophorus in Parts of China*. PhD Thesis. Kunming Medical University. (in Chinese)
- Huang HY, Yang SD, Zeng NK, Zhang GL et al. 2018 – *Hygrophorus parvirussula* sp. nov., a new edible mushroom from southwestern China. *Phytotaxa* 373, 139–146.
- Huang HY, Zhang WH, Huang T, Gabriel M et al. 2021a – *Hygrophorus russula* complex (Hygrophoraceae, Agaricales) in China. *Mycological Progress* 20, 1115–1134.
- Huang HY, Zhang WH, Huang T, Gabriel M et al. 2022a – Phylogeny and species diversity in *Hygrophorus* section *Aurei* in China. *Mycological Progress* 21, 9.
- Huang HY, Zhang WH, Huang T, Jiang S et al. 2022b – Revising the species diversity of *Hygrophorus* section *Olivaceoumbrini* s.l. (Hygrophoraceae, Agaricales) in China. *Mycological Progress* 21, 51.
- Huang HY, Zhang WH, Huang T, Tang LP. 2021b – *Hygrophorus aurantiosquamosus* (Hygrophoraceae, Agaricales), a new species of *Hygrophorus* section *Chrysodontes* from western China. *Phytotaxa* 528, 279–289.
- Index Fungorum. 2022 – <http://www.indexfungorum.org/names/Names.asp> (Accessed on December 1, 2022).

- Karsten P. 1878 – Symbolae ad mycologiam fennicam. IV. Meddelanden af Societas pro Fauna et Flora Fennica 2, 171–183.
- Karsten PA. 1879 – Rysslands, Finlands och den Skandinaviska halföns Hattsvampar. Första Delen: Skifsvampar. Bidrag till Kännedom av Finlands. Natur och Folk 32, 1–571.
- Kirk PM, Cannon PF, Minter DW, Stalpers JA. 2008 – Dictionary of the Fungi 10th edn. CABI, Wallingford.
- Kornerup A, Wanscher JH. 1978 – Methuen Handbook of Colour (3rd edn). Eyre Methuen, London.
- Kummer P. 1871 – Der Führer in die Pilzkunde. C. Luppe, Zerbst.
- Læssøe T, Petersen JH. 2019 – Fungi of Temperate Europe Volume 1. Princeton University Press, Princeton and Oxford.
- Largent. 1985 – The Agaricales (Gilled Fungi) of California. 5. Hygrophoraceae. Mad River Press, Eureka, California.
- Larsson E, Bendiksen K. 2020 – *Hygrophorus betulae*, a new species described from subalpine birch forest in Finland. Karstenia 58, 1–9.
- Larsson E, Campo E, Carbone M. 2014 – *Hygrophorus exiguus*, a new species in subgenus *Colorati* section *Olivaceoumbrini*, subsection *Tephroleuci*. Karstenia 54 (2), 41–48.
- Larsson E, Jacobsson S. 2004 – Controversy over *Hygrophorus cossus* settled using ITS sequence data from 200-year-old type material. Mycological Research 108, 781–786.
- Larsson E, Jacobsson S. 2014 – Vilken vaxskivling var det som Fries beskrev som *Agaricus pudorinus*. Svensk Mykologisk Tidskrift 35 (2), 5–9.
- Larsson E, Kleine J, Jacobsson S, Krikorev M. 2018 – Diversity within the *Hygrophorus agathosmus* group (Basidiomycota, Agaricales) in northern Europe. Mycological Progress 17 (12), 1293–1304.
- Lodge DJ, Padamsee M, Matheny PB, Aime MC et al. 2014 – Molecular phylogeny, morphology, pigment chemistry and ecology in Hygrophoraceae (Agaricales). Fungal Diversity 64, 1–99.
- Luo KY, Zhao CL. 2022 – Morphology and multigene phylogeny reveal a new order and a new species of wood-inhabiting basidiomycete fungi (Agaricomycetes). Frontiers in Microbiology 13, 970731.
- Matheny PB. 2005 – Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (*Inocybe*, Agaricales). Molecular Phylogenetics and Evolution 35, 1–20.
- Matheny PB, Curtis JM, Hofstetter V, Aime MC et al. 2006 – Major clades of Agaricales: a multilocus phylogenetic overview. Mycologia 98, 982–995.
- Moncalvo JM, Vilgalys R, Redhead SA, Johnson JE et al. 2002 – One hundred and seventeen clades of euagarics. Molecular Phylogenetics and Evolution 23, 357–400.
- Moreau PA, Bellanger JM, Lebeuf R, Athanassiou Z et al. 2018 – Hidden diversity uncovered in *Hygrophorus* sect. *Aurei* (Hygrophoraceae), including the Mediterranean *H. meridionalis* and the North American *H. boyeri*, spp. nov. Fungal Biology 122, 817–836.
- Naseer A, Khalid AN, Healy R, Smith ME. 2019 – Two new species of *Hygrophorus* from temperate Himalayan Oak forests of Pakistan. MycoKeys 56, 33–47.
- Nguyen LT, Schmidt HA, von Haeseler A, Minh BQ. 2014 – IQ-TREE: A Fast and Effective Stochastic Algorithm for Estimating Maximum-Likelihood Phylogenies. Molecular Biology and Evolution 32, 268–274.
- Peck CH. 1878 – Report of the Botanist. New York State Museum Annual Report 29, 29–82.
- Quélet L. 1888 – Flore Mycologique. Octave Dion, Paris.
- Rehner SA, Buckley E. 2005 – A *Beauveria* phylogeny inferred from nuclear ITS and EF1-a sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs. Mycologia 97(1), 84–98.
- Siegel N, Schwarz C. 2016 – Mushrooms of the Redwood Coast. Ten Speed Press, Berkeley.
- Singer R. 1986 – The Agaricales in Modern Taxonomy, 4th edn. Koeltz Scientific Books, Koenigstein.
- Thiers B. 2018 – (And Continuously Updated). Index Herbariorum: A Global Directory of Public Herbaria and Associated Staff. New York Botanical Garden's Virtual Herbarium.

- Vilgalys R, Hester M. 1990 – Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* 172(8), 4238–4246.
- Waldvogel F, Neukom HP, Winkler R. 2001 – Pilze Champignons Fungi Bd.1, Strobilomycetaceae, Boletaceae, Paxillaceae, Gomphidiaceae, Hygrophoraceae, Tricholomataceae. AT Verlag, Aarau, Schweiz.
- Wang CQ, Li TH. 2020 – *Hygrophorus deliciosus* (Hygrophoraceae, Agaricales), a popular edible mushroom of the *H. russula*-complex from southwestern China. *Phytotaxa* 449 (3), 232–242.
- Wang CQ, Li TH, Wang XH, Wei TZ et al. 2021 – *Hygrophorus annulatus*, a new edible member of the *H. olivaceoalbus*-complex from southwestern China. *Mycoscience* 62, 137–142.
- Wang CQ, Li TH, Zhang M, He XL et al. 2020 – *Hygrophorus* subsection *Hygrophorus* (Hygrophoraceae, Agaricales) in China. *MycosKeys* 68, 49–73.
- Wang CQ, Zhang M, Li TH, Liang XS et al. 2018 – Additions to tribe Chromosereae (Basidiomycota, Hygrophoraceae) from China, including *Sinohygrocybe* gen. nov. and a first report of *Gloioxanthomyces nitidus*. *MycosKeys* 38, 59–76.
- Wei J, Gao W, Huang CY. 2021 – A checklist of edible ectomycorrhizal mushrooms in China. *Mycosystema* 40(8), 1938–1957. (in Chinese)
- White TJ, Bruns TD, Lee S, Taylor JW. 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, San Diego, 315–322.
- Young AM. 2005 – *Fungi of Australia: Hygrophoraceae*. CSIRO Publishing, Australian Biological Resources Study, Canberra.
- Yu FQ, Xu GB, Liu PG. 2007 – A new and noteworthy species of *Hygrophorus* from Yunnan, China. *Mycotaxon* 100, 169–175.
- Zhang D, Gao F, Jakovlic I, Zou H et al. 2020 – PhyloSuite: An integrated and scalable desktop platform for streamlined molecular sequence data management and evolutionary phylogenetics studies. *Molecular Ecology Resources* 20, 348–355.
- Zhang YX, Mao N, Fan L. 2023 – *Hygrophorus viridiflavus* sp. nov. (Hygrophoraceae, Agaricales), from North China. *Phytotaxa* 579(3), 187–197.