

Four new species of *Hygrocybe* sect. *Pseudofirmae* (Hygrocybaceae, Agaricales) from the Cristalino basin in the Southern Brazilian Amazon

JULI SIMON CARDOSO^{1,2,7*}, D. JEAN LODGE^{3,8}, JEAN-MARC MONCALVO^{4,5,9}, SIMONA MARGARITESCU^{4,10}, MARIA ALICE NEVES^{2,11} & JADSON J. S. OLIVEIRA^{1,6,12}

¹*Divisão do Curso de Pós-graduação em Botânica, Instituto Nacional de Pesquisas da Amazônia (INPA), Av. André Araújo 2936, 69067-375, Manaus, AM, Brazil*

²*Graduate Program in Biology of Fungi, Algae and Plants, Federal University of Santa Catarina (UFSC), Campus Universitário Reitor João David Ferreira Lima, s/n, 88040-900, Florianópolis, Brazil*

³*Department of Plant Pathology and Odum School of Ecology, University of Georgia, Athens, GA 30602, United States*

⁴*Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks Street, Toronto, ON M5S 3B2, Canada*

⁵*Department of Natural History, Royal Ontario Museum, 100 Queens Park, Toronto, ON M5S 2C6, Canada*

⁶*Laboratório de Patologia da Madeira, Coordenação de Tecnologia e Inovação (COTEI), Instituto Nacional de Pesquisas da Amazônia (INPA), Av. André Araújo 2936, 69067-375, Manaus, AM, Brazil*

⁷  jul3asc@gmail.com;  <https://orcid.org/0000-0003-2795-7067>

⁸  dlodgester@gmail.com;  <https://orcid.org/0000-0003-4807-348X>

⁹  jeanmarcm@gmail.com;  <https://orcid.org/0000-0003-4011-1381>

¹⁰  margaritescu.simona@gmail.com;  <https://orcid.org/0000-0001-5560-8847>

¹¹  maliceneves@gmail.com;  <https://orcid.org/0000-0002-1810-4890>

¹²  oliveira.j.j.s.86@gmail.com;  <https://orcid.org/0000-0001-6643-3421>

*Corresponding author:  jul3asc@gmail.com

Abstract

Hygrocybe subgen. *Hygrocybe* sect. *Pseudofirmae*, includes tropical species with dimorphic basidiospores and basidia, and an often perforated pileus. Field expeditions in the Cristalino basin in the Southern Brazilian Amazon revealed four new species of *Hygrocybe* sect. *Pseudofirmae*: *Hygrocybe cristalinoensis*, forming entirely deep green basidiomes, with a convex-umbilicate, perforated pileus and whitish fringed margin; *H. viridilacerata*, characterized by basidiomes with green, umbonate pileus that is perforated at the centre, whitish lamellae and predominantly 2-spored microbasidia; *H. pegleri*, characterized by a squamulose pileus and a long stipe (> 100 mm); and *H. vinaceosquamulosa*, characterized by a squamulose, purple to pink pileus, pale yellow to pinkish lamellae and oblong to cylindrical macrospores with a middle constriction. These new species are proposed based on combined morphological and ITS sequence data. Phylogenetic analyses revealed the placement and uniqueness of the new species in the sect. *Pseudofirmae* clade, and their relationship with close species of the section. Descriptions, illustrations, and phylogenetic analyses results for the new species are provided. In addition, the new species are compared with closely related taxa.

Key words: Funga, ITS, Mato Grosso, phylogeny, taxonomy

Introduction

Hygrocybe subgen. *Hygrocybe* (Fr.) P. Kumm. (1871: 26) includes species with brightly coloured basidiomes, which can sometimes stain black or grey in age or when bruised, with free to adnexed or uncinat lamellae that have a trama with long parallel elements and basidia usually 3 to 5 times the length of their basidiospores (Lodge *et al.* 2013). Species in subg. *Hygrocybe* can be mono- or dimorphic in their basidia and basidiospores sizes and are classified in five sections: *Hygrocybe* (Fr.) P. Kumm., *Chlorophanae* (Herink) Arnolds ex Candusso, *Microspora* Boertm., *Pseudofirmae* Lodge, Padamsee & S.A. Cantrell, and *Velosae* Lodge, Ovrebo & Padamsee. The dimorphism of basidia and basidiospores was first mentioned by Petch (1917) and was later recognised by various tropical agaricologists (Heinemann 1963, Courtecuisse 1989, Heim 1967, Pegler 1983, Cantrell & Lodge 2001, Lodge *et al.* 2013). These species were classified into a single section within *Hygrocybe*, viz. *Firmae* Heinemann (1963). Recently, in a multi-locus phylogenetic and morphological study, Lodge *et al.* (2013) recognised that the dimorphism had multiple origins,

occurring in two other sections of *Hygrocybe* subg. *Hygrocybe*, viz. *Pseudofirmae* and *Velosae*, while sect. *Firmae* is now classified in subg. *Pseudohygrocybe* Bon.

Section *Pseudofirmae* groups tropical dimorphic species characterized by having an often-perforated pileus that is smooth to tomentose or squamulose, macrobasidia usually broadly clavate or clavate-stipitate, which are conspicuously wider than the microbasidia, a regular lamellar trama with parallel hyphae often mixed with interwoven refractive hyphae, and a pileipellis that can vary from being a cutis to a trichoderm with or without a gelatinous layer (Lodge *et al.* 2013).

The Brazilian Amazon is a vast territory, but very little is known about its Funga. Therefore, unsurprisingly, recent and ongoing field expeditions in the Brazilian Amazon are resulting in the discovery of many new species (e.g., Komura *et al.* 2016, 2020, Oliveira *et al.* 2021, Silva-Filho *et al.* 2020, 2021, 2023, Cardoso *et al.* 2023, Soares *et al.* 2024). With the increase in deforestation—especially in the Southern Amazon, an area known as the “Arc of Deforestation”—species extinction is expected to occur rapidly (Stropp *et al.* 2020), and many undescribed species are at risk of extinction. From August 2018 to July 2019, 1,702 km² of Amazon Forest were deforested in the state of Mato Grosso, representing 16.8% of the total loss of Amazon Forest in the Brazilian territory during this period (INPE 2020).

The Cristalino Private Reserve of Natural Heritage (RPPN) is an important conservation area in this fragile and threatened region. Together with other conservation units such as Cristalino State Park, Juruena National Park, Serra do Cachimbo Springs Biological Reserve, the Indigenous Lands, and the Brazilian Air Force Base, they form a protection layer against the constantly rising deforestation in the region (Fundação Ecológica Cristalino 2025). The Reserve is managed by the NGO Cristalino Ecological Foundation (Fundação Ecológica Cristalino—FEC), and one of its projects is the Cristalino Fungi Project, created in 2015 by the fungal parataxonomist and citizen scientist Susanne Sourell. So far, more than 1,381 fungal collections have been documented in this project and are stored at the FLOR Fungarium (Neves *et al.* 2018). The main goal of the project is to raise awareness about fungal conservation, highlighting the importance of protecting forests, especially in the constantly threatened Southern Amazon.

In this study, we propose four new species of subgen. *Hygrocybe* sect. *Pseudofirmae* from the Cristalino basin Amazon Forest in Mato Grosso state, based on morphology and ITS sequence data, inferring their uniqueness and relationships with close species in phylogenetic analyses. An identification key to the species of *Hygrocybe* subg. *Hygrocybe* sect. *Pseudofirmae* occurring in Brazil, including the newly described species, is provided.

Material and methods

Study area

The specimens were collected in RPPN Cristalino, located along the Cristalino River in the very North of the Mato Grosso state, close to the boundary with the Pará state, between Alta Floresta and Novo Mundo municipalities, in the Southern Amazon (9°35'51" S, 55°55'52" W). The Cristalino River is a tributary of the Teles Pires River, which empties into the Tapajós River, the fifth-largest tributary of the Amazon River (WCS 2025). The area is characterised mostly by clayish soils typical of *terra-firme* (upland) forests (Pires & Prance 1985).

Morphological analysis

Specimens were photographed *in situ*, tagged with collection details (Rathnayaka *et al.* 2025), taken to the laboratory, and morphologically described while still fresh. Specimens were dried at 40°C until no more moisture was left and preserved in zipped plastic bags (Hu *et al.* 2022). Morphological descriptions were conducted following Largent (1986) and Largent *et al.* (1977). Colour codes are from the *Online Auction Color Chart* (Kramer 2004). Micromorphological features were observed in a LEICA DM2500 microscope under magnifications of 1000x from hand-cut sections of different parts of the basidiomes mounted in KOH 3% or 5% and Congo Red 1%, and another section mounted with Melzer's reagent. Thirty macrospores and 30 microspores of each specimen were measured, excluding the hilar appendage. The basidiospore quotient (Q, length/width ratio) and mean values were calculated for each specimen, separately for macro- and microspores. The mean values for basidiospore dimensions and Q are indicated between the measurements in italic font. Specimens were deposited at FLOR Fungarium, and new names were registered in the MycoBank database. A fragment of each specimen was crushed on FTA Cards to preserve DNA for later extraction.

Phylogenetic analyses

Under the registration number A76D0E6 on the platform of the National System for the Management of Genetic Heritage and Associated Traditional Knowledge (SISGen) in accordance with Brazilian Law 13.123/2015, the samples were sent abroad for DNA sequencing. Following the protocols of Dentinger *et al.* (2010), DNA extraction, PCR amplification, purification, and sequencing were conducted at the Molecular Systematics Laboratory of the Royal Ontario Museum (ROM). Genomic DNA was extracted from the samples in the FTA Cards. ITS1F/ITS4 primers were used to amplify the Internal Transcribed Spacer (ITS) (Gardes & Bruns 1993, Lodge *et al.* 2013, White *et al.* 1990) as the ITS is informative for distinguishing and relating closely related *Hygrocybe* species (Lodge *et al.* 2013). Reads were checked for quality, assembled, and edited in Geneious R7 (<https://www.geneious.com>). The sequences were deposited in the GenBank NCBI database (<https://www.ncbi.nlm.nih.gov/genbank/>).

The Dataset 1 strategy for the phylogenetic analysis was to combine ITS+LSU data, where ITS resolves more terminal nodes and LSU, more conservative, resolves deeper nodes, providing a backbone framework. BLAST searches were conducted using the ITS queries and the newly produced sequences against the NCBI GenBank database. Within the first hundred entries deemed the closest in GenBank, identified via BLAST searches of each query, entries of species belonging to *Hygrocybe* subg. *Hygrocybe* representing sect. *Pseudofirmae*, sect. *Hygrocybe* and sect. *Chlorophanae* were selected in particular when the LSU of the corresponding specimens was also available. Representatives of *Hygrocybe* subg. *Pseudohygrocybe* were selected to serve as the outgroup. All ITS and LSU sequences, when corresponding to the same specimen, were downloaded from the GenBank database (Table 1). Non-determined taxa were included in the analyses to fill gaps in diversity within the sampling space.

The ITS and LSU datasets were separately aligned using Muscle v3.8.31 (Edgar 2004). The alignments were edited in Geneious R7 to resolve ambiguous blocks and trim ends. The best-scored nucleotide substitution models for each dataset were selected in ModelTest-NG (Darriba *et al.* 2020) using the AKAIKE Information Criterion (AIC). The best model for both datasets was GTR+I+G. Then, the ITS and LSU datasets were combined using the concat.jar application. For the specimens lacking LSU, missing data were allowed by filling with an unspecified base (N), ensuring that each clade and subclade has representatives including LSU sequences, and aiming for a balanced framework for grouping more terminal branches resolved by ITS data. Based on the resulting tree from the Dataset 1 analyses, a more restricted Dataset 2 of the species clade in which the new species were grouped (sect. *Pseudofirmae* clade) was prepared, using only ITS for a single-locus analysis, with some representatives of sect. *Hygrocybe* as the outgroup.

Maximum Likelihood analyses (ML) were conducted in RAxML 7.0.4 (Stamatakis 2006) using fast-bootstrapping with 1,000 pseudoreplicates, implementing GTRGAMMAI with GAMMA+P-Invar Model parameters estimated up to an accuracy of 0.001 Log Likelihood units for both Dataset 1 and 2. The best-scored ML tree was chosen after full ML optimization. Bayesian analyses (BA) were performed in MrBayes 3.2.1 (Ronquist *et al.* 2012), consisting of MCMCMC using selected models to determine the parameters Nst = 6 for both partitions. The BA implemented two independent runs of: 1) 10,000,000 generations, sampling every 1,000 generations, six independent chains, and two swaps for the Dataset 1; and 2) 1,000,000 generations, sampling every 100 generations, four independent chains, and two swaps for the Dataset 2. The burn-in was set at 10%. Final BA trees were summarized using the 50 % majority-rule consensus method. Branch lengths were summarized from the 95 % highest posterior density trees. The trees generated were visualized in FigTree v1.4.3 (Rambaut 2007) and edited in CorelDraw X7 (Corel Corporation ©).

TABLE 1. Sequences used in the phylogenetic analyses, including taxon name, country, voucher, and GenBank accession numbers for ITS and LSU. Sequences generated in this study are presented in bold type. MD indicates missing data.

Taxon	Country	Voucher	ITS	LSU
<i>Hygrocybe acutoconica</i>	Ukraine	CWU(MYC)8343	OK157454	MD
<i>Hygrocybe acutoconica</i>	Ukraine	CWU(MYC)8339	OK157449	MD
<i>Hygrocybe acutoconica</i>	Canada	ubco39	OP456289	MD
<i>Hygrocybe acutoconica</i>	USA	MICH139910	OM985861	MD
<i>Hygrocybe acutoconica</i> var. <i>microspora</i>	USA	OMDL iNat 164322057	OR987249	MD
<i>Hygrocybe acutoconica</i> var. <i>microspora</i>	USA	PUL:PUL00034569(2)	ON561595	MD

.....continued on the next page

TABLE 1. (Continued)

Taxon	Country	Voucher	ITS	LSU
<i>Hygrocybe acutoconica</i> var. <i>microspora</i>	USA	OMDL iNat 173306097	OR785940	MD
<i>Hygrocybe acutoconica</i> var. <i>microspora</i>	USA	OMDL iNat 176367795	OR824663	MD
<i>Hygrocybe acutoconica</i> var. <i>microspora</i>	USA	OMDL MO 520623	OR783493	MD
<i>Hygrocybe acutoconica</i> var. <i>pallidocarnea</i>	Spain	AH39432	PP965551	PP965546
<i>Hygrocybe acutoconica</i> var. <i>pallidocarnea</i>	Italy	SIENA-5495	PP965547	MD
<i>Hygrocybe acutoconica</i> as <i>H. persistens</i>	USA	TRTC155647	JN021038	MD
<i>Hygrocybe acutoconica</i> as <i>H. persistens</i>	Switzerland	KN_1149	OR194908	KF291169
<i>Hygrocybe acutoconica</i> as <i>H. persistens</i>	Italy	9266	JF908062	MD
<i>Hygrocybe acutoconica</i> as <i>H. persistens</i>	Australia	MEL:2416713	OL771708	MD
<i>Hygrocybe acutoconica</i> as <i>H. persistens</i>	China	G06.seq	OP317307	MD
<i>Hygrocybe chloochlora</i>	Puerto Rico	SAC-PR-9899 (CFMR PR-5350)	KF381522	MD
<i>Hygrocybe</i> aff. <i>chloochlora</i>	Belize	CFMR BZ-3042	EU435147	EU435147
<i>Hygrocybe chlorophana</i>	Denmark	CFMR Boertmann 2002/9	EU435148	EU435148
<i>Hygrocybe chlorophana</i>	Sweden	F282	PQ641308	PQ641308
<i>Hygrocybe citrinovirens</i>	Sweden	F1249	PQ653342	PQ653342
<i>Hygrocybe citrinovirens</i>	Sweden	MV1008	PQ653436	PQ653436
<i>Hygrocybe citrinovirens</i>	United Kingdom	RBG Kew K(M)126565	EU784292	MD
<i>Hygrocybe citrinovirens</i>	Hungary	isolate_H44	FM208889	MD
<i>Hygrocybe citrinovirens</i>	United Kingdom	RBG_Kew_K_M_126105	EU784291	MD
<i>Hygrocybe citrinovirens</i>	Switzerland	13140	OP538820	MD
<i>Hygrocybe citrinovirens</i>	Switzerland	12126	OP538807	MD
<i>Hygrocybe citrinovirens</i>	Hungary	isolate_H2	FM208853	MD
<i>Hygrocybe citrinovirens</i>	United Kingdom	RBG Kew K(M)12694	EU784293	MD
<i>Hygrocybe conica</i>	China	HMJAU61878	ON045774	ON046286
<i>Hygrocybe conica</i>	India	KUBOTKRMK202061	MW449855	MW449854
<i>Hygrocybe conica</i> var. <i>conicoides</i>	China	QHU20235	OM970939	OM942720
<i>Hygrocybe cristalinensis</i>	Brazil	CJL647_FLOR67406	PX675223	MD
<i>Hygrocybe cristalinensis</i>	Brazil	JS556_FLOR67424	PX675224	MD
<i>Hygrocybe cristalinensis</i>	Brazil	CJL652_FLOR67408	PX675225	MD
<i>Hygrocybe</i> sp. as <i>H. flavescens</i>	China	HMJAU61910	ON054950	MD
<i>Hygrocybe chlorophana</i> as <i>H. flavescens</i>	United Kingdom	RBG Kew K(M)61287	EU784301	MD
<i>Hygrocybe helobia</i> as <i>Pseudohygrocybe coccineocrenata</i> var. <i>sphaginophila</i>	Russia	A. Kovalenko 99-9-1 (LE)	KF291182	KF291183
<i>Hygrocybe helobia</i>	Sweden	F2639	PQ652789	PQ652789
<i>Hygrocybe helobia</i>	Italy	14600	JF908056	MD
<i>Hygrocybe konradii</i>	Mexico	ECO-TA-HO 7869	MF156251	MD
<i>Hygrocybe konradii</i>	Malta	SM670 (B436a)	OR567846	MD
<i>Hygrocybe konradii</i> var. <i>konradii</i>	China	QHU20330	OM970947	MD
<i>Hygrocybe macrosiparia</i>	Ecuador	QCAM4359	KY582490	KY582490

.....continued on the next page

TABLE 1. (Continued)

Taxon	Country	Voucher	ITS	LSU
<i>Hygrocybe miniata</i> as <i>Pseudohygrocybe coccineocrenata</i>	Russia	Kovalenko 00-7-209 (LE)	KF291179	KF291180
<i>Hygrocybe miniata</i>	Canada	ubc f16574	FJ627028	FJ627028
<i>Hygrocybe miniata</i>	Slovakia	SNMH250	MW996448	MW996446
<i>Hygrocybe miniata</i>	Canada	UBC F16295	EU486456	EU486456
<i>Hygrocybe miniata</i>	Australia	MEL:2060103	OL771710	MD
<i>Hygrocybe miniata</i> f. <i>longipes</i>	USA	AFTOLID_1891	DQ490630	DQ457677
<i>Hygrocybe mollis</i>	United Kingdom	RBG Kew K(M)139410	EU784329	MD
<i>Hygrocybe mollis</i> var. <i>mollis</i>	United Kingdom	RBG Kew K(M)62585	EU784330	MD
<i>Hygrocybe nigrescens</i>	China	clone_58	MZ919418	MD
<i>Hygrocybe nigrescens</i> var. <i>brevispora</i>	Puerto Rico	SAC-0005 (CFMR PR-5964)	KF291130	KF291131
<i>Hygrocybe occidentalis</i>	French Guiana	RC-Guy-09-073	MK546630	MD
<i>Hygrocybe occidentalis</i>	French Guiana	RC-GUY-12-075	MK546842	MD
<i>Hygrocybe occidentalis</i> var. <i>occidentalis</i>	Puerto Rico	PR-6493	EU435151	EU435151
<i>Hygrocybe</i> cf. <i>occidentalis</i>	Ecuador	RLC_633_iNat_122526305	OQ878423	MD
<i>Hygrocybe pegleri</i>	Brazil	JS561_FLOR67428	PX675227	MD
<i>Hygrocybe</i> aff. <i>pegleri</i>	Brazil	JS593_FLOR67453	PZ577558	MD
<i>Hygrocybe acutoconica</i> as <i>H. persistens</i> var. <i>persistens</i>	Canada	4613HRL_1176	KM248897	MD
<i>Hygrocybe prieta</i>	French Guiana	RC-GUY-12-095	MF038954	MD
<i>Hygrocybe pseudoconica</i>	Italy	5159	JF908060	MD
<i>Hygrocybe rosea</i>	Puerto Rico	DJLPR4_CFMR_PR6526	KF291197	KF291198
<i>Hygrocybe sangayensis</i>	Ecuador	QCAM4254	KY582489	KY582489
<i>Hygrocybe</i> sp.	Sweden	DS2024b_SNMH798	MD	OR614491
<i>Hygrocybe</i> sp.	Spain	JP2024a_AH60277	MD	PP965548
<i>Hygrocybe</i> sp.	Sweden	DS2024b_SNMH798	OR614484	MD
<i>Hygrocybe</i> sp.	Ecuador	RLC_780_iNat_126148798	OQ878431	MD
<i>Hygrocybe</i> sp.	Ecuador	RLC83	OQ211589	MD
<i>Hygrocybe</i> sp.	Thailand	NanCU3	AB453022	MD
<i>Hygrocybe</i> sp.	Spain	JP2024a_AH60277	PP965552	MD
<i>Hygrocybe</i> sp. ‘ <i>poena</i> ’	Ecuador	QCAM4115	MN419324	MN419324
<i>Hygrocybe</i> sp. 1	Australia	GMB2014_MEL_2382719	KP012900	MD
<i>Hygrocybe spadicea</i>	United Kingdom	GriffithHafod 26Oct2006	KF291199	MD
<i>Hygrocybe spadicea</i>	United Kingdom	DJH2003	MT940836	MD
<i>Hygrocybe spadicea</i>	United Kingdom	GriffithWauenfawr 25Oct2006	KF291201	MD
<i>Hygrocybe spadicea</i> var. <i>spadicea</i>	Hungary	H32	FM208879	MD
<i>Hygrocybe sparsifolia</i>	China	GDGM_40080	KJ747391	KJ747393
<i>Hygrocybe vinaceosquamulosa</i>	Brazil	JS543_FLOR67412	PX675228	MD
<i>Hygrocybe viridilacerata</i>	Brazil	JS583_FLOR67446	PX675226	MD
<i>Hygrocybe</i> aff. <i>viridilacerata</i>	Brazil	JS555_FLOR67423	PZ577559	MD
<i>Hygrophoraceae</i> sp.	USA	iNat87025957	ON856353	MD
Uncultured fungus clone	Puerto Rico	GL12217_110_S049	KY687683	KY687683

Results and discussion

Phylogeny

The ML phylogenetic analyses of Dataset 1 resulted in the best-scoring tree depicted in Figure 1, which agrees with the BA tree (not shown) and is largely congruent with the results presented in Lodge *et al.* (2013). The nodes include the bootstrap (BS) and posterior probability (PP) statistical support values resulting from the ML and BA analyses, respectively. Three out of the five sections of subgenus *Hygrocybe* are represented in distinct clades in Figure 1: sect. *Hygrocybe* is sister to sect. *Pseudofirmae* with moderate support (BS 73/ PP 0.95), and sect. *Chlorophanae* is basal (BS 84 / PP 1.0). The four new *Hygrocybe* species presented here branched within a clade representing sect. *Pseudofirmae*, whose monophyly is strongly supported (BS 88 / PP 1.0), which provides phylogenetic evidence for their classification in that section. Likewise, in Dataset 1, the relationship among species in the Dataset 2 tree (Figure 2) is not well-resolved nor supported, even for the analysis restricted to the sect. *Pseudofirmae* using only ITS. Only species-levels or a few branches are supported, indicating that ITS alone cannot resolve relationships (Figure 2) and suggesting no improvement in this strategy.

In the Dataset 1 tree (Figure 1), *H. vinaceosquamulosa* sp. nov. is sister to *H. sangayensis* (BS 90 / PP 0.98); these two species are followed by *H. macrosiparia*, then *H. pegleri* sp. nov., then *H. aff. pegleri*. All these five species form a clade with strong support (BS 87 / PP 0.99). In the Dataset 2 tree (Figure 2), based only on the ITS, however, *H. vinaceosquamulosa* sp. nov. is clustered sister to *H. macrosiparia*, with weak support (BS 70), and these are sister to *H. sangayensis* (BS 87 / 1.0). *Hygrocybe* aff. *pegleri* is morphologically similar to *H. pegleri* sp. nov. and was previously thought to be conspecific, but it diverged as paraphyletic, and these two are genetically very distinct (82.47% E-value 8e-113 based on the ITS). *Hygrocybe cristalinoensis* sp. nov. (BS 100 / 1.0) formed an independent branch, not closely related to any species in the clade, both in the Datasets 1 and 2 trees (Figures 1 and 2). *Hygrocybe viridilacerata* sp. nov. is sister to *H. aff. viridilacerata* (Figures 1 and 2), which was previously considered conspecific based on morphology. However, these are genetically divergent (88% E-value 2e-142 based on the ITS), and the branch support is moderate (BS 74/PP 0.99 in the Dataset 1 tree and BS 78/PP 1.0 in the Dataset 2 tree). This species is also not closely related to other species in the sect. *Pseudofirmae* clade.

Taxonomy

Hygrocybe cristalinoensis J.S. Cardoso, M.A. Neves & J.S. Oliveira, sp. nov. (Figs. 3. a–c, 5)
Mycobank # 861151

Etymology:—*cristalinoensis* refers to the type locality, the Cristalino River Region.

Type:—BRAZIL. Mato Grosso: Alta Floresta, Reserva Particular do Patrimônio Natural Cristalino, Trilha do Francisco, 9°35'52" S, 55°56'12" W, 250 m, 4 January 2019, Santos, C. CJL647 (FLOR67406, holotype!). GenBank: PX675223 (ITS).

Diagnosis:—Basidiomes entirely deep green, pileus convex-umbilicate, perforated, with whitish fringed margin. Differs from *Hygrocybe prieta* Lodge & Pegler (1990: 453) in the lack of purple, red and orange tints in the basidiomes and presence of cheilocystidia.

Description:—*Pileus* 10–36 mm diam., convex when young, then becoming umbilicate, often perforated at the centre, smooth, radially fibrillose, moist to lubricous, intense dark green (oac103) or sometimes leaf green (oac89), with flushes of olive green (oac866) to brownish green (oac831), light green (oac75) to yellowish-green (oac24, oac10) at the centre, translucent-striate towards margin; margin straight to slightly incurved, with a whitish to very pale green (oac51) minutely appendiculate fringe. *Lamellae* decurrent to uncinat, subdistant, narrow to broad, up to 6 mm broad, green (oac82, oac112); edge entire or eroded, very pale green (oac67) to pale yellow (oac858); lamellulae of one or two lengths. *Stipe* (20–) 49–104 × 2–7 mm, central, regular to flexuous, hollow, tapering towards the base, dry to lubricous, silky, fibrillose, vivid green (oac103) at the apex, then fading to lighter hues of green (oac89, oac68, oac77), base yellow (oac5, oac857) to whitish.

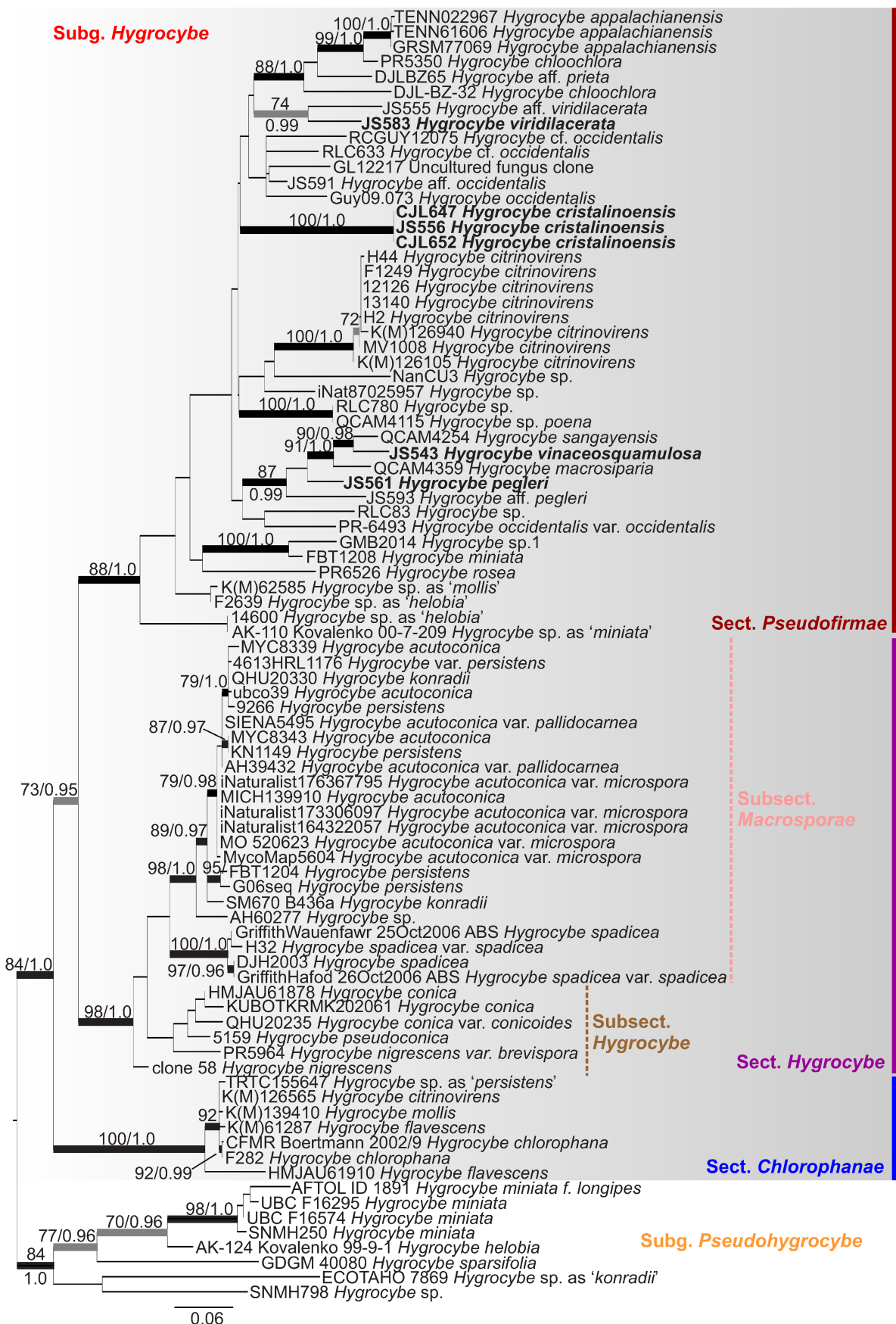


FIGURE 1. ML phylogenetic tree of concatenated ITS and LSU Dataset 1. Branches in black bold are those with pp ≥ 0.97 and bootstrap $\geq 80\%$, branches in grey bold are those with pp 0.95–0.97 and bootstrap 70–80%.

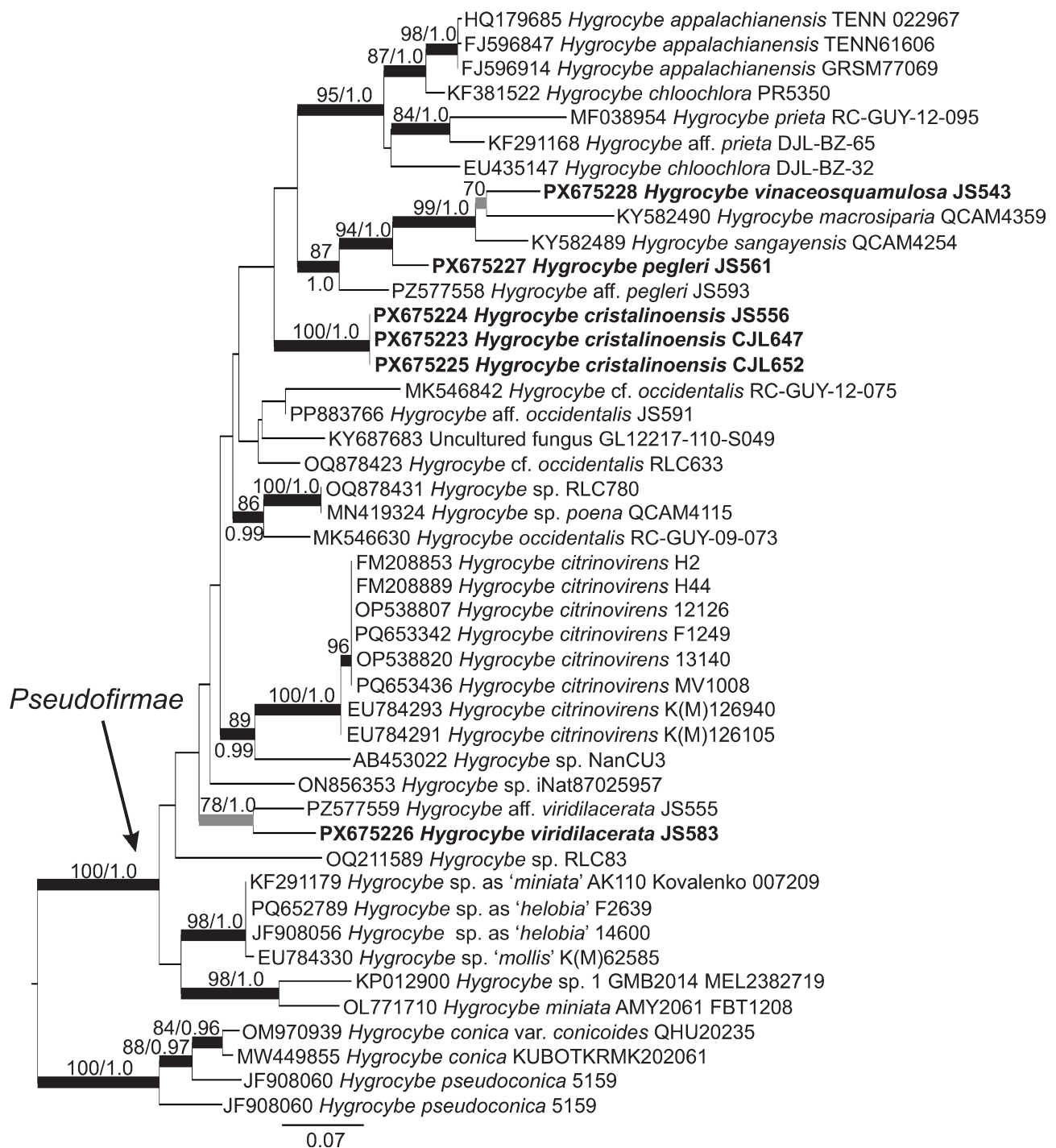


FIGURE 2. ML phylogenetic trees of the ITS Dataset 2 composed of the sect. *Pseudofirmiae* clade. Branches in black bold are those with pp ≥ 0.97 and bootstrap ≥ 80 %, branches in grey bold are those with pp 0.95–0.97 and bootstrap 70–80%.



FIGURE 3. a–c. *Hygrocybe cristalinensis* (JS251). d–h. *Hygrocybe pegleri*. e, f, g, JS561; d, JS268; h, JS551. Scales = 10 mm, except for h, scale = 5 mm. Photos a–c by S. Sourell, d–h by J.S. Cardoso.

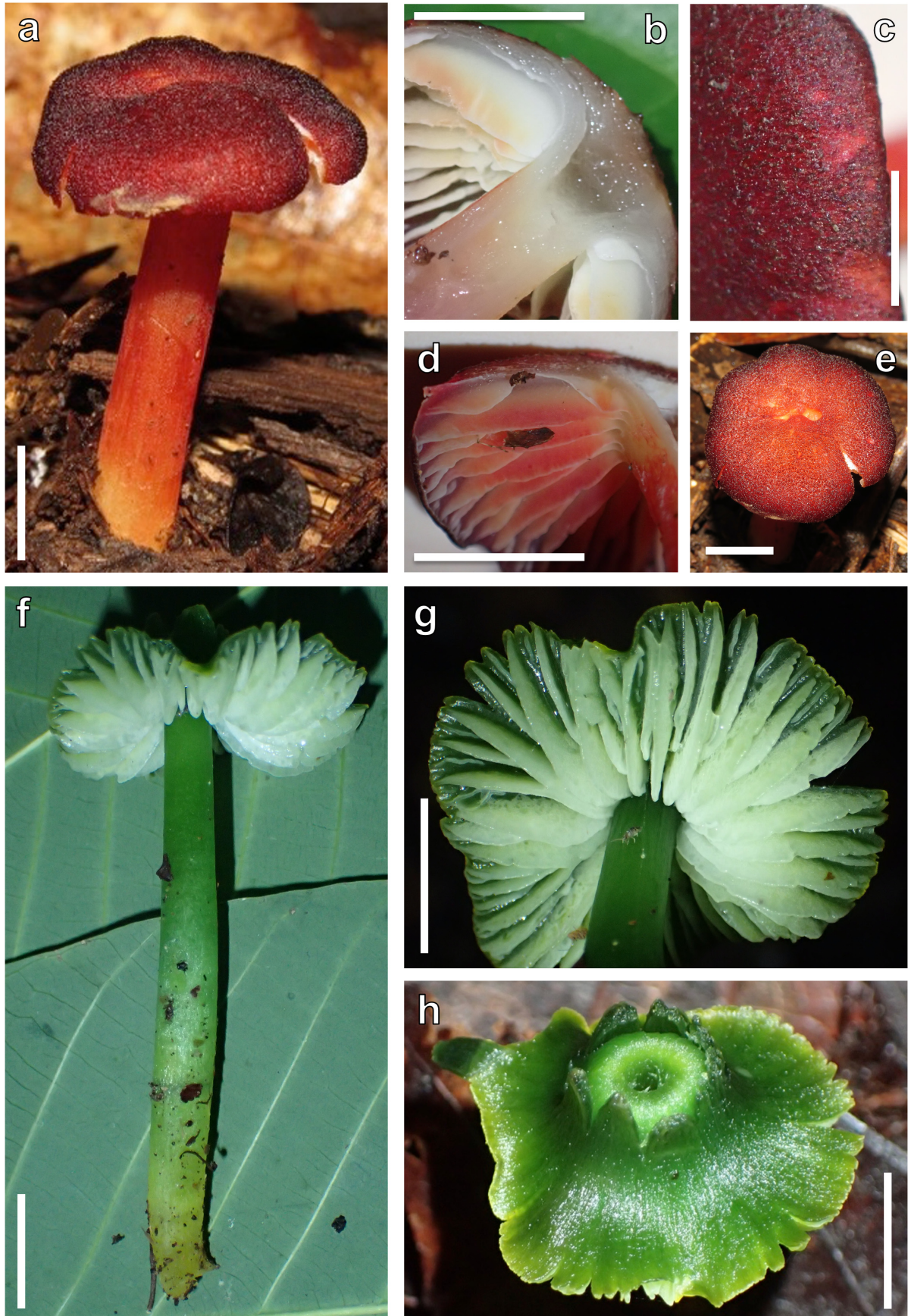


FIGURE 4. a–e. *Hygrocybe vinaceosquamulosa*. a, b, e. JS186; c, d. JS543. f–h. *Hygrocybe viridilacerata* (CJL648). Scales = 10 mm, except for c, scale = 5 mm. Photos a, e by R. C. Hoyer; b–d by J. S. Cardoso; f–h by S. Sourell.

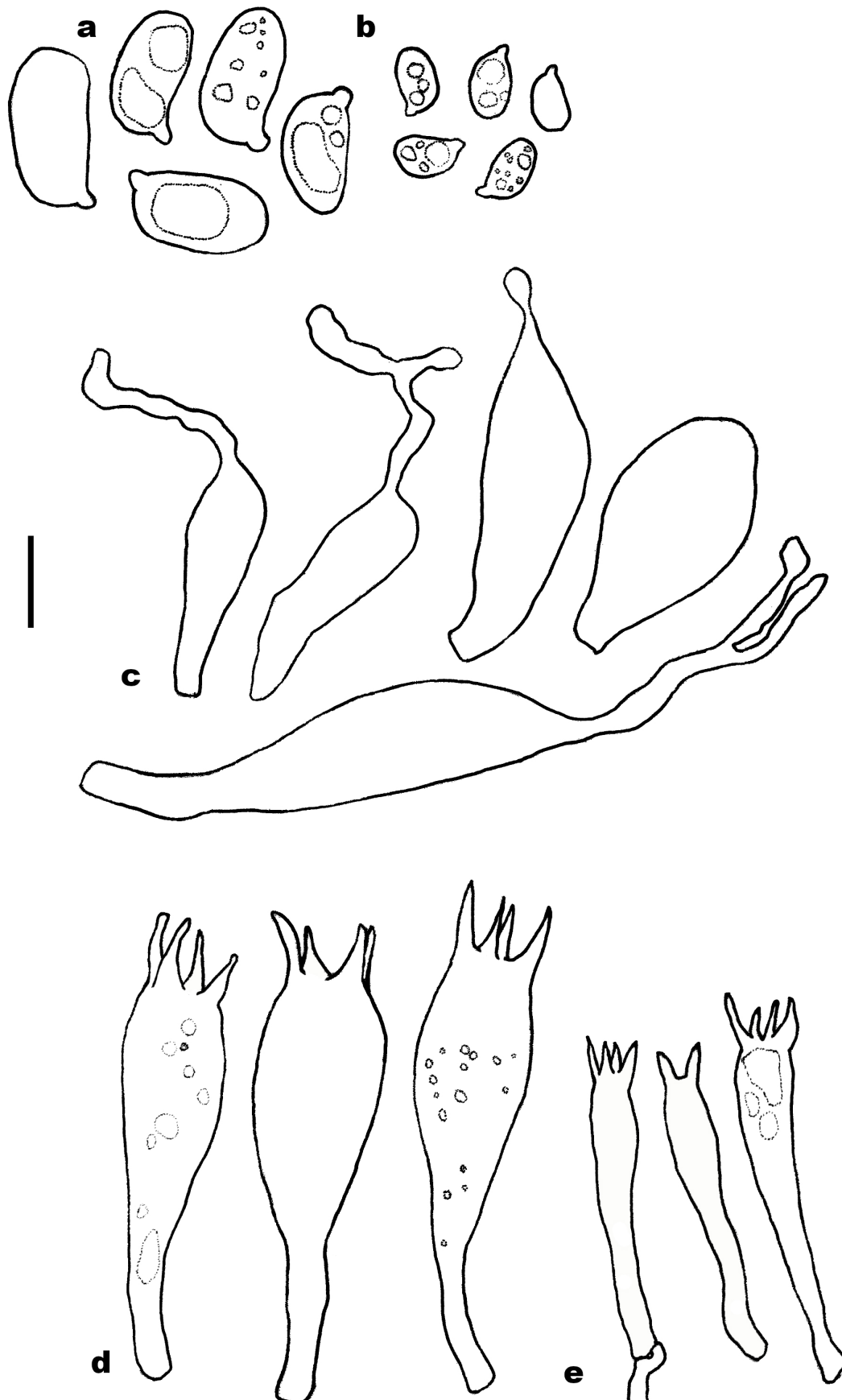


FIGURE 5. *Hygrocybe cristalinoensis* (CJL647). a. macrospores, b. microspores, c. cheilocystidia, d. macrobasidia, e. microbasidia. Scale = 10 μ m.

Basidiospores and *basidia* dimorphic. *Macrospores* 11.1–13.70–15.9 (–17.6) $\times$ 6.2–7.89–9.8 μm , $Q = 1.640\text{--}1.740\text{--}1.839$, oblong, smooth, thin-walled, hyaline, inamyloid, guttulate. *Microspores* 4.8–5.91–7.7 $\times$ 2.8–3.57–4.6 μm , $Q = 1.640\text{--}1.655\text{--}1.671$, oblong, smooth, thin-walled, hyaline, inamyloid, guttulate. *Macrobasidia* 32.8–55.3 $\times$ 10.8–18.4 μm , clavate, thin-walled, hyaline, inamyloid, guttulate, with basal clamp connections, 4-spored, sterigmata up to 9.7 μm . *Microbasidia* 27.7–39.6 $\times$ 4.6–7.9 μm , cylindro-clavate, thin-walled, hyaline, inamyloid, guttulate, with basal clamp connections, 4-spored, sterigmata up to 6.5 μm . *Lamellar edge* fertile. *Cheilocystidia* 20.6–89.7 $\times$ 3.9–13.0 μm , ventricose-rostrate, mucronate, papillate, oval or ogival, frequently with apical hyphoid projections or with a digitiform appendix, thin-walled, hyaline, with basal clamp connections. *Pleurocystidia* and *pseudocystidia* absent. *Lamellar trama* regular, with parallel inflated hyphae, 9.7–15.0 μm diam., clamp connections present. *Pileipellis* a cutis with a thin layer of uplifted hyphae, 69.9–171.7 $\times$ 7.8–9.0 μm , encrusted pigments present but not abundant, clamp connections present. *Stipitipellis* a cutis with clusters of erect interwoven hyphae, terminal hyphae very thin, 2.8–4.9 μm diam., contorted, interlaced, with abundant clamp connections.

Additional specimens examined:—BRAZIL, Mato Grosso, Alta Floresta, Reserva Particular do Patrimônio Natural Cristalino, Trilha do Francisco, 9°35'52"S, 55°56'12"W, 250 m, 4 January 2019, Santos, C. CJL652 (FLOR67408, paratype); 10 January 2019, Cardoso J.S. & Furtado A.N.M. 605 (FLOR67462, paratype); Trilha da Serra Nova, 9°34'26"S, 55°55'18"W, 250 m, 12 January 2018, Ribeiro, R.S. CJL554 (FLOR63512, paratype); Trilha do Dr. Haffer, 9°33'24"S, 55°54'54"W, 250 m, 6 January 2019, Cardoso J.S. & Furtado A.N.M. 556 (FLOR67424, paratype); Trilha do Cajá, 9°35'58"S, 55°55'55"W, 250 m, 7 January 2019, Cardoso J.S. & Furtado A.N.M. 570 (FLOR67438, paratype); Novo Mundo, Reserva Particular do Patrimônio Natural Cristalino, Trilha da Torre 2, 9°35'50"S, 55°55'27"W, 250 m, 24 January 2018, Cardoso, J.S. 249 (FLOR63509, paratype); Cardoso, J.S. 251 (FLOR63511, paratype); Trilha da Castanheira, 9°33'44"S, 55°54'24"W, 250 m, 5 January 2019, Cardoso J.S. & Furtado A.N.M. 545 (FLOR67414, paratype).

Distribution:—Known only from the type locality, in the Southern Amazon.

Habitat:—Growing solitary or in groups in soils of *terra-firme* forests.

Comments:—This is the most common *Hygrocybe* species forming green basidiomes at RPPN Cristalino. There are three green dimorphic *Hygrocybe* species previously described for the neotropics: *Hygrocybe chloochlora* Pegler & Fiard (1978: 303) from Martinique, *H. prieta* from Puerto Rico, and *Hygrocybe viridis* Capelari & Maziero (1988: 192) from Northern Brazil (Lodge & Pegler 1990). The general morphology of the basidiomes of *H. cristalinoensis* is very similar to *H. prieta*, but basidiomes of *H. prieta* have purple, red and orangish colours and conspicuous waxy squamules on the stipe (Lodge & Pegler 1990). In microscopy, *H. cristalinoensis* differs from *H. prieta* in the presence of cheilocystidia and by having microspores that are slightly wider (2.5–3.6 μm , $Q = 1.78\text{--}1.95$ in *H. prieta*), becoming oblong rather than elongate (Lodge & Pegler 1990). The second most closely related taxon, *H. chloochlora*, differs by having lighter green colours on the pileus, lamellae that are white to very pale green and a stipe that is yellowish green (Pegler & Fiard 1978). Microscopically, the macrospores of *H. chloochlora* are bigger (17.5 $\times$ 10.0 μm) and the cheilocystidia are hyphoid to narrowly clavate or cylindrical rather than predominantly ventricose-rostrate with apical projections as found in *H. cristalinoensis* (Lodge & Pegler 1990). The other green dimorphic species, *H. viridis*, was described for the Brazilian Amazon, in Rondônia State (Capelari & Maziero 1988). *Hygrocybe viridis* differs in having an overall green basidiome, with no traces of yellow, much smaller macrospores (8.4–11.0 $\times$ 4.8–6.0 μm), narrower macrobasidia (8.4–9.6 μm) and absence of cheilocystidia (Capelari & Maziero 1988). Finally, *H. cristalinoensis* differs from the other green dimorphic species described in this work by the following: *Hygrocybe viridilacerata* sp. nov. has a conic-convex to umbonate pileus with a star-shaped perforation at the centre, the pileus is vivid green, never dark green, the lamellae are white or pale green and almost free, the microspores are slightly bigger (7.6 $\times$ 4.8 μm), the microbasidia are predominantly 2-spored, and the cheilocystidia are absent.

Hygrocybe pegleri J.S. Cardoso, M.A. Neves & J.S. Oliveira, sp. nov. (Figs. 3 d–h, 6)

Mycobank # 861153

Etymology:—in honour of David N. Pegler, who described and studied many neotropical *Hygrocybe* species.

Type:—BRAZIL. Mato Grosso: Novo Mundo, Reserva Particular do Patrimônio Natural Cristalino, Trilha da Castanheira, 9°33'44"S, 55°54'24"W, 250 m, 6 January 2019, Cardoso, J.S. & Furtado, A.N.M. 561 (FLOR67428, holotype!). GenBank: PX675227 (ITS).

Diagnosis:—Pileus squamulose, stipe > 100mm length, basidiospores and basidia dimorphic. Differs from *Hygrocybe firma* var. *firma* (Berk. & Broome) Singer (1958: 355) by having a smaller pileus, taller stipe, with no colour changes in the basidiomes, fertile lamellar edge and branched hyphae with brown pigments in the pileipellis.

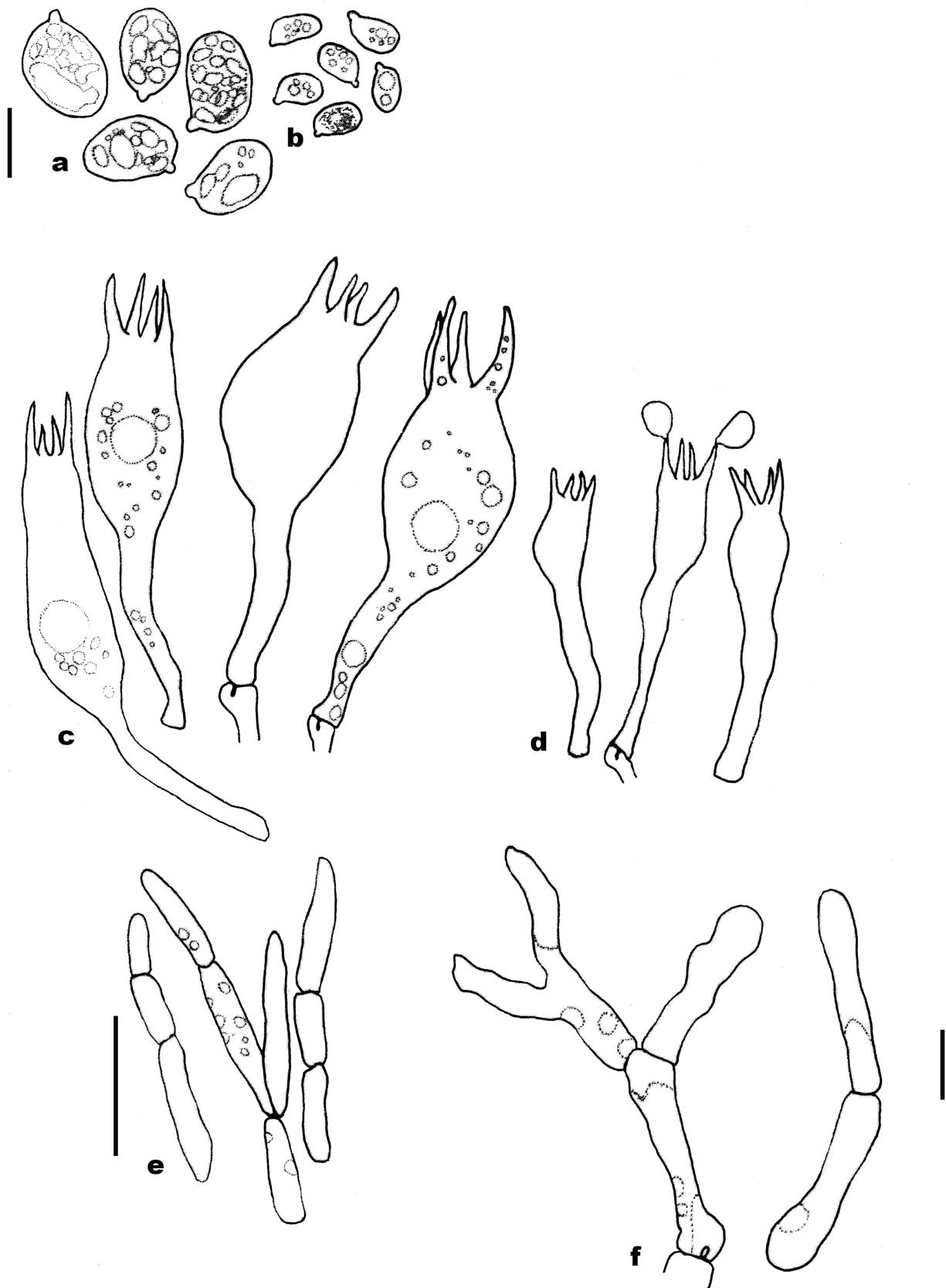


FIGURE 6. *Hygrocybe pegleri* (JS561). a. macrospores, b. microspores, c. macrobasidia, d. microbasidia, e. pileipellis terminal hyphae, f. stipitipellis hyphae. a–d. Scale = 10 μ m. e, f. Scales = 50 μ m.

Description:—*Pileus* 32–47 mm diam., umbilicate, depressed, squamulose, squamules more abundant in the centre and margin, moist to dry, pale yellow (oac899, oac857) to pale orange (oac812, oac810) with brown (oac733, oac734) squamules; margin arched or straight, entire, sometimes splitting, concolorous with the pileus, but with an aspect of being darker due to the concentrated squamules. *Lamellae* decurrent to uncinata, ventricose, up to 10 mm broad, subdistant, pale yellow (oac855) to almost white (oac899), margin eroded, concolorous; lamellulae of 3 lengths. *Stipe* 102–155 × 4–8 mm, central, sometimes eccentric, equal, hollow, usually with longitudinal fissure, tomentose, dry, yellow (oac855, oac857), covered with brown (oac734) microsquamules. Solitary on clay soils.

Basidiospores and *basidia* dimorphic. *Macrospores* 12.4–15.06–20.0 × 7.5–9.67–10.9 (–12.0) µm, Q = 1.487–1.597–1.775, ellipsoid to oblong, smooth, thin-walled, hyaline, inamyloid, multiguttulate. *Microspores* 5.7–7.14–9(–9.5) × 3.4–4.40–5.0(–5.5) µm, Q = 1.533–1.622–1.735, ellipsoid to oblong, smooth, thin-walled, hyaline, inamyloid, multiguttulate. *Macrobasidia* 49.3–70.2 (–82.0) × 11.7–18.9 (–25.0) µm, ventricose-clavate, thin-walled, hyaline, 4-spored, sterigmata up to 14.2 µm, with basal clamp connections. *Microbasidia* 30.8–51.0(–55.0) × 5.6–8.6(–10.0) µm, clavate, thin-walled, hyaline, 4-spored, sterigmata up to 8.6 µm, with basal clamp connections. *Lamellar edge* fertile. *Cystidia* absent. *Lamellar trama* regular, with parallel inflated hyphae, 76.8–282.8 × 12.8–30.7 µm, refractive hyphae present, interwoven, clamp connections present. *Pileipellis* a trichoderm with clusters of brown pigmented terminal hyphae (14–)22–67.7(–81) × 7–17.9(–23) µm, branched, forming a pyramidal structure, clamp connections present. *Stipitipellis* a trichoderm with clusters of interwoven brown hyphae, 14.5–49.4 × 3.3–9.3 µm, clamp connections present.

Additional specimens examined:—BRAZIL. Mato Grosso: Novo Mundo, Reserva Particular do Patrimônio Natural Cristalino, Trilha da Torre 2, 9°35'50"S, 55°55'27"W, 250 m, 5 January 2019, *Cardoso J.S. & Furtado A.N.M.* 551 (FLOR67419, paratype); Alta Floresta, Reserva Particular do Patrimônio Natural Cristalino, Trilha do Francisco, 9°35'52"S, 55°56'12"W, 250 m, 9 January 2018, *Cardoso, J.S.* 268 (FLOR63558, paratype); Santa Catarina: Parque Estadual da Serra do Tabuleiro, Santo Amaro da Imperatriz, Plaza Caldas da Imperatriz, Trilha da Cachoeira, 27°44'24.7"S, 48°48'25.0"W, 10 April 2014, *Magnago, A.C. & Cardoso, J.S.* 1029 (FLOR 57243).

Distribution:—Southern Amazon in the Mato Grosso state.

Habitat:—Growing on soil amongst litter in *terra-firme* forest in the Amazon.

Comments:—This taxon is similar to *Hygrocybe firma* var. *firma* (Berk. & Broome) Singer *sensu* Pegler (1983) based on collections from the Antilles, but it differs significantly in the colour photographs and illustrations provided in previous publications (e.g., from Africa by Heinemann, 1966; from the Lesser Antilles by Pegler & Fiard 1978 and Pegler 1983). *Hygrocybe firma* was originally described from Sri Lanka as *Hygrophorus firmus* Berk. & Broome. In the macromorphology, *H. firma* var. *firma sensu* Pegler differs by having a wider pileus [(20–)40–70 mm vs. 32–47 mm diam. in *H. pegleri*], a shorter stipe (up to 110 mm vs. 155 mm height in *H. pegleri*), and colour changes on bruising or with time.

Microscopically, *H. firma* var. *firma sensu* Pegler differs by having a sterile lamellar edge with basidioles, smaller macrobasidia [50–60 × 14–16 µm vs. 49.3–70.2 (–82.0) × 11.7–18.9 (–25.0) µm in *H. pegleri*] and unbranched hyphae with no pigments in the pileipellis (Pegler 1983). Other closely related taxa with squamulose pileus, dimorphic basidia and basidiospores are *H. brunneosquamosa* Lodge & S.A. Cantrell (2001: 216) and *H. neofirma* Lodge & S.A. Cantrell (2001: 221) (Cantrell & Lodge 2001). *Hygrocybe brunneosquamosa* also has brown pigmented hyphae in the trichodermal pileipellis, but it has an entire brown pileus that lacks yellow or orange pigments, the lamellae are cinnamon brown, and the macrospores are oblong to cylindrical (Cantrell & Lodge 2001). *Hygrocybe neofirma* differs from *H. pegleri* by the presence of staining reactions, by a much shorter stipe, and by the absence of brown pigmented pileipellis hyphae (Cantrell & Lodge 2001).

In the phylogenetic tree (Figure 1), a supported clade is shown with *H. pegleri* and the following taxa: *H. vinaceosquamulosa* sp. nov., *H. sangayensis* Barili, C.W. Barnes, J.A. Flores & Ordoñez in Crous (2017: 335), and *H. macrosiparia* Barili, C.W. Barnes, J.A. Flores & Ordoñez in Crous (2017: 337), along with another specimen morphologically similar to *H. pegleri*, but molecularly divergent, which is displayed in the phylogenetic tree as *H. aff. pegleri* (JS593, Figure 1). They all share similar characteristics, such as a squamulose pileus, dimorphic basidia, and basidiospores. The other new species presented herein, *H. vinaceosquamulosa*, differs from *H. pegleri* by the presence of purple and pink colours in the basidiomes, a shorter stipe (28–55 mm high), and macrospore sizes, which are oblong to cylindrical (Q = 2.014). Both *H. sangayensis* and *H. macrosiparia* are described from high-altitude (1,500m) locations in Ecuador. Besides the different habitat, *H. sangayensis* differs from *H. pegleri* by having a broader pileus (50mm) and shorter stipe (70mm high), and the presence of cheilo- and pleurocystidia in the hymenium; *H. macrosiparia* differs by a shorter stipe (70mm high), and much shorter macrospores (10.5 × 6.5 µm).

A morphologically similar specimen (ACM1029) was collected in 2014 from a hilly area with well-preserved remnants of the Atlantic Rainforest in Southern Brazil, but its identity was not confirmed by molecular analyses.

Hygrocybe vinaceosquamulosa J.S. Cardoso, M.A. Neves & J.S. Oliveira, *sp. nov.* (Figs. 4 a–e, 7)
MycoBank # 861154

Etymology:—From Latin “vinaceus” = purple and “squamulosus” = refers to the squamules on the pileus.

Type:—BRAZIL. Mato Grosso: Novo Mundo, Reserva Particular do Patrimônio Natural Cristalino, Trilha da Castanheira, 9°33'44" S, 55°54'24" W, 250 m, 6 January 2019, *Cardoso, J.S. & Furtado, A.N.M.* 543 (FLOR67412, holotype!). GenBank: PX675228 (ITS).

Diagnosis:—Pileus squamulose, purple to pink, lamellae pale yellow with pink shades, macrospores oblong to cylindrical with a middle constriction. Differs from *Hygrocybe siparia* (Berk.) Singer (1965: 17) by the convex pileus, which is never umbilicate, by the colour of the pileus and the lamellae, by a fibrillose stipe, and by the length of both macro- and microspores.

Description:—*Pileus* 19–38 mm diam., convex, tomentose-squamulose, moist to dry, dark cherry red (oac563, oac600, oac601, oac607), crimson (oac579, oac586), pink (oac617), sometimes with flushes of orange (oac632) covered with dark purple small squamules; margin entire, decurved, slightly incurved, concolorous or paler. *Context* translucent to white, gelatinous. *Lamellae* adnate to slightly sinuate, up to 4 mm broad, pale yellow (oac857, oac898) to orangish (oac812) or beige (oac766, oac 814) with shades of dark pink (oac594), or stained with orangish pink (oac615) towards the edge; edge entire to finely fimbriate, sometimes eroded, concolorous; lamellulae of two lengths. *Stipe* 28–55 × 4–6 mm, central, regular, hollow, fibrillose, moist to dry, yellowish orange (oac789, oac812) with shades of cherry red (oac614), or pink (oac572) stained with pale orange (oac632), base pale yellow (oac858).

Basidiospores and *basidia* dimorphic. *Macrospores* (11.4–) 12.2–14.75–19 (–20.7) × 5.5–7.38–8.7 µm, $Q = 1.728–2.014–2.300$, oblong to cylindrical, often constricted at the middle, smooth, thin-walled, hyaline, inamyloid, multiguttulate. *Microspores* 6.0–7.52–9.5 (–10.9) × 3.2–4.26–5.1 µm, $Q = 1.622–1.762–1.902$, oblong, often constricted at the middle, smooth, thin-walled, hyaline, inamyloid, multiguttulate. *Macrobasidia* 41.7–61.2 × 11.2–16.2 (–17.1) µm, clavate, thin-walled, hyaline, predominantly 4-spored, or 1–2–3-spored also common, sterigmata up to 13.5 µm, with basal clamp connections. *Microbasidia* 29.0–44.3 (–54.3) × 6.0–8.3 (–10.2) µm, cylindro-clavate, thin-walled, hyaline, predominantly 4-spored, 1–2–3-spored also common, 5-spored rare, sterigmata up to 10.0 µm, with basal clamp connections. *Lamellar edge* fertile. *Cystidia* absent. *Lamellar trama* regular to subregular, inflated hyphae with pigments, 4.9–22.1 µm diam., clamp connections present, interlaced with refractive hyphae, 4.2–5.3 µm diam., with clamp connections of the medallion type. *Pileipellis* a trichoderm, with pigmented hyphae forming chains arranged in pyramidal form, therefore creating the squamules, terminal elements 15.9–116.0 × 6.6–12.3 µm, branching, with clamp connections, brown in KOH. *Pileus trama* with abundant interwoven refractive hyphae. *Stipitipellis* a trichoderm of thin hyphae, 2.6–7.1 µm diam., slightly brownish in KOH.

Additional specimens examined:—BRAZIL. Mato Grosso: Novo Mundo, Reserva Particular do Patrimônio Natural Cristalino, Trilha da Castanheira, 9°33'44"S, 55°54'24"W, 250 m, 17 January 2018, *Cardoso, J.S.* 186 (FLOR63504, paratype); 7 January 2019, *Cardoso, J.S. & Furtado, A.N.M.* 566 (FLOR67434, paratype); 1 January 2019, *Santos, C.* CJL624 (FLOR67398, paratype).

Distribution:—Only known from the type locality.

Habitat:—Growing solitary or gregarious on clay soils in *terra-firme* forest.

Comments:—This species is very remarkable due to its cherry colours and dark purple squamules in the pileus. It resembles *Hygrocybe siparia*, which was first described by Berkeley (1856, p. 134) based on a collection from the Upper Rio Negro region, in the Uaupés River in the Amazon; it was later recollected by Singer (1965) in the Northeast of Brazil (Pernambuco state) and also re-examined by Pegler (1997) from collections found in the Southeast of Brazil (São Paulo state). *Hygrocybe siparia* differs in the pileus shape, which is umbilicate, in the lack of pink tints on the lamellae, and in a stipe that is smooth rather than fibrillose. Microscopically, *H. siparia* has ellipsoid macrospores, which are shorter (up to 13 µm, $Q = 1.53$), and the microspores are also shorter and are ellipsoid (up to 6.7 µm, $Q = 1.42$).

Hygrocybe macrosiparia differs in the lack of pink or purple colours on the basidiomes, macrospore sizes (10.5 × 6.5 µm), and the much shorter sterigmata (6.5 µm in macrobasidia and 6.0 µm in microbasidia) (Crous *et al.* 2017). *Hygrocybe sangayensis* also differs in the lack of purple and pink colours in the basidiomes, and by the presence of cheilo- and pleurocystidia in the hymenium (Crous *et al.* 2017). Unfortunately, the species authors (Barili & Barnes) did not provide Q values for the basidiospores, and the pileipellis description (in Crous *et al.* 2017) is not well detailed.

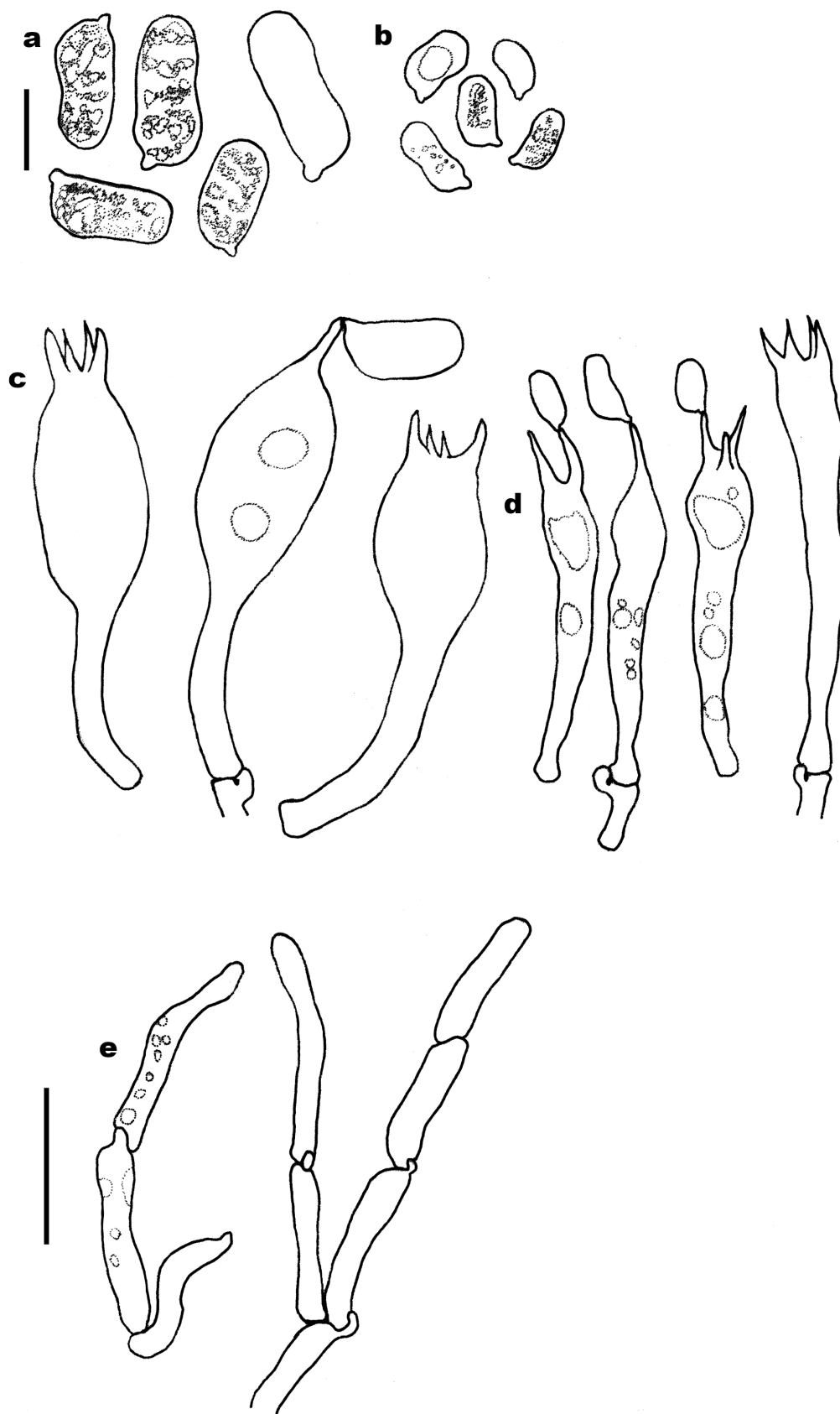


FIGURE 7. *Hygrocybe vinaceosquamulosa* (JS543). a. macrospores, b. microspores, c. macrobasidia, d. microbasidia, e. pileipellis terminal hyphae. a–d. Scale = 10 μ m. e. Scale = 50 μ m.

Hygrocybe viridilacerata J.S. Cardoso, M.A. Neves & J.S. Oliveira, *sp. nov.* (Figs. 4.f–h, 8, 9)
MycoBank # 861152

Etymology:—From the Latin “viridis” = green and “lacerata” = refers to the ragged pileus centre.

Type:—BRAZIL. Mato Grosso: Alta Floresta, Reserva Particular do Patrimônio Natural Cristalino, Trilha do Francisco, 9°35'52"S, 55°56'12"W, 250 m, 8 January 2018, *Cardoso, J.S. & Furtado, A.N.M.* 583 (FLOR67446, holotype!). GenBank: PX675226 (ITS).

Diagnosis:—Pileus umbonate and perforated like a star-shaped rupture at the centre, vivid green; lamellae whitish; stipe green to yellow near the base; microbasidia predominantly 2-spored. Differs from *H. cristalinoensis* in the lack of deep green lamellae and the lack of cheilocystidia.

Description:—*Pileus* 11–37 mm diam., conic to convex when young, umbonate or plane-convex at maturity, ragged like a star-shaped rupture at the centre, smooth, fibrillose, moist to lubricous, translucent-striate towards margin, vivid green (oac110, oac117) to olive green (oac82, oac38) with brownish-green (oac866) to brown (oac719) tints when old; margin straight, decurved or uplifted, translucent-striate, irregular, plicate to eroded, often splitting, light green (oac32) to yellow (oac854, oac896). *Lamellae* adnexed or uncinat, sometimes free, subdistant, broad to ventricose, up to 6 mm broad, white to very pale green (oac30, oac67) with greenish tints (oac50, oac51, oac97, oac90); margin eroded, concolor; lamellulae of two or three lengths. *Stipe* 41–83 × 3–6 mm, central, rarely eccentric, regular to flexuous, hollow, smooth, dry to moist, green (oac47, oac68, oac83) to pale yellow (oac855, oac856) at the base. Solitary to gregarious on clay soils.

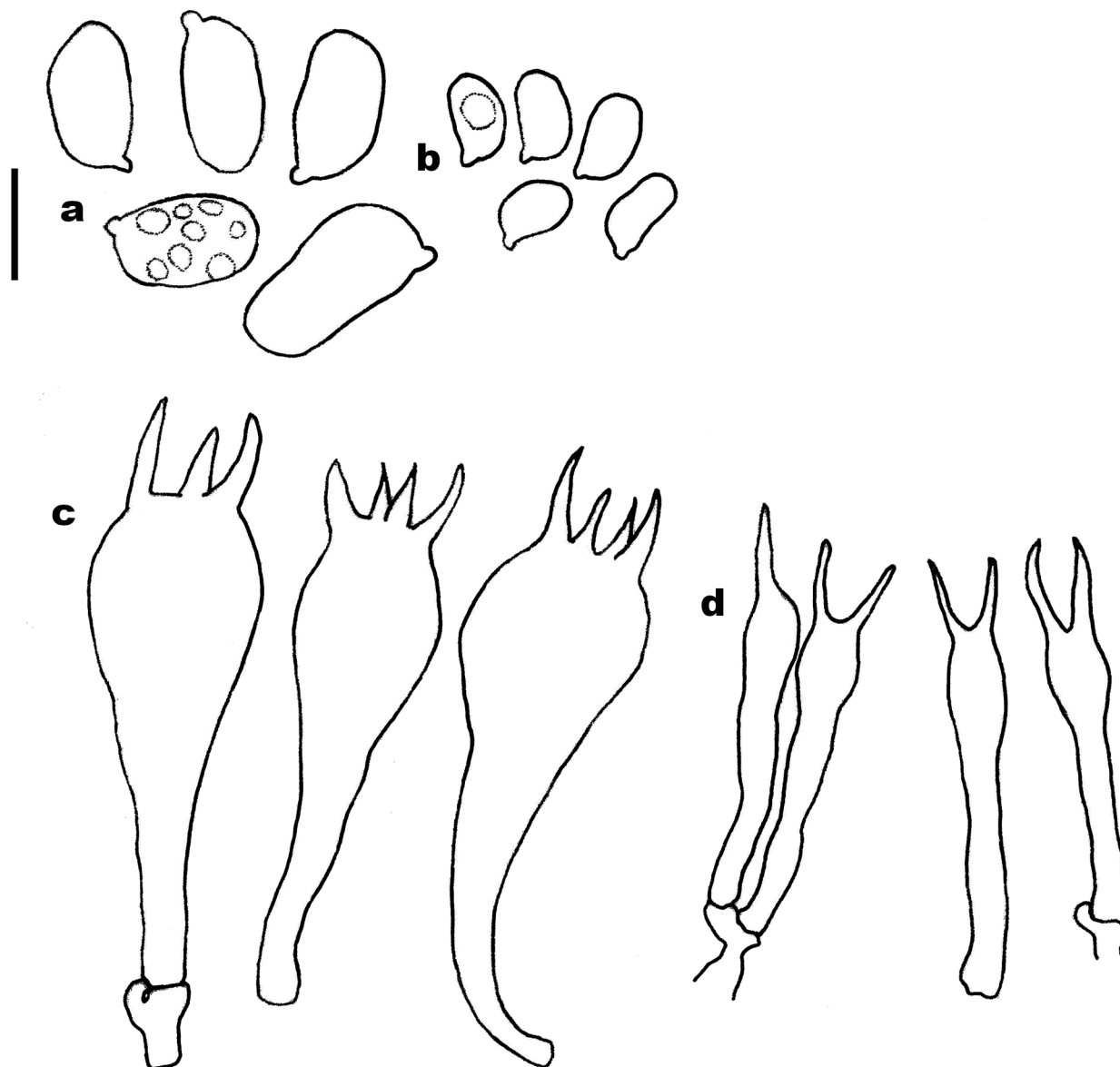


FIGURE 8. *Hygrocybe viridilacerata* (JS583). a. macrospores, b. microspores, c. macrobasidia, d. microbasidia. Scale = 10 μ m.

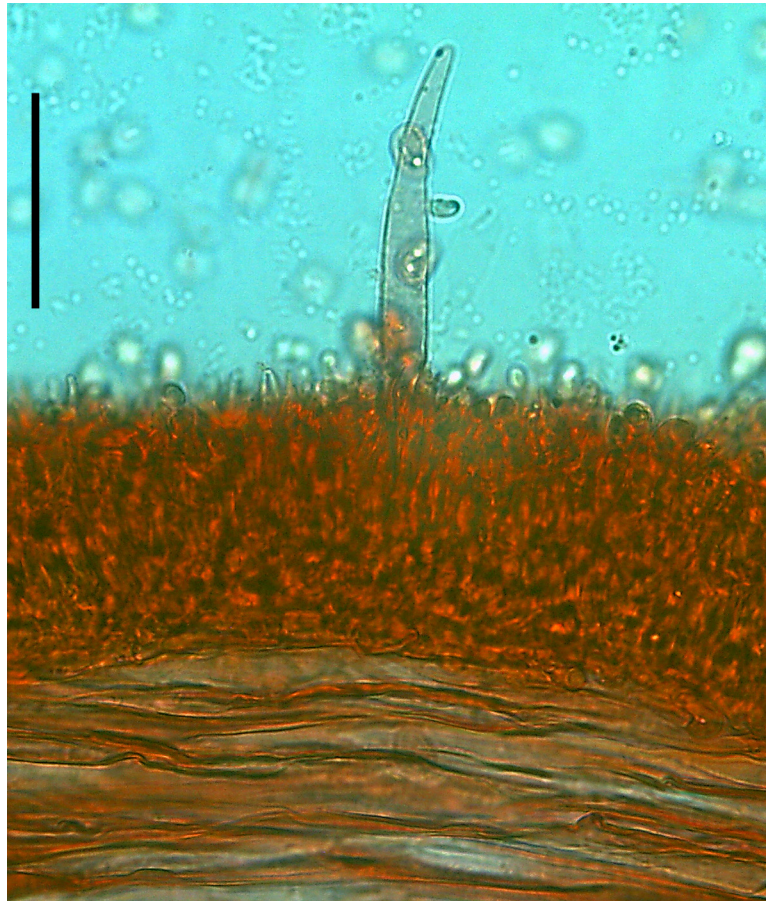


FIGURE 9. *Hygrocybe viridilacerata* (JS583). Detail of the hymenium showing the pseudocystidia emerging from the lamellar trama. Scale = 50 μm .

Basidiospores and *basidia* dimorphic. *Macrospores* (9.7–) 10.6–13.54–17.6 (–18.4) $\times$ 5.8–7.64–9.5 (–10.0) μm , $Q = 1.672\text{--}1.771\text{--}1.853$, oblong, smooth, thin-walled, hyaline, inamyloid, guttulate. *Microspores* 5.6–7.65–9.7 $\times$ 3.7–4.85–6.6 μm , $Q = 1.533\text{--}1.578\text{--}1.635$, ellipsoid to oblong, smooth, thin-walled, hyaline, inamyloid, guttulate. *Macrobasidia* 30.3–47.7 (–51.1) $\times$ 10.4–17.7 (–19.4) μm , broadly clavate, thin-walled, hyaline, predominantly 4-spored, few 1–3-spored, sterigmata up to 9 μm , with basal clamp connections. *Microbasidia* (19.7–) 21.9–34.3 (–39.1) $\times$ 4.4–9.5 (–10.8) μm , clavate, predominantly 2-spored, or 1–3–4-spored, thin-walled, hyaline, sterigmata up to 8.8 μm , with basal clamp connections. *Lamellar edge* fertile, microbasidia more abundant. *Cheilocystidia* and *pleurocystidia* absent, but *pseudocystidia* sometimes present (Figure 7), as hyphae projecting from the lamellar trama up to 80 μm above the hymenium, cylindrical, tapering towards a rounded apex. *Lamellar trama* regular, with inflated parallel elements 19.3–54.7 μm diam., with interwoven refractive hyphae 2.1–4.3 μm diam., clamp connections present. *Pileipellis* a cutis of repent hyphae, 6.5–31.4 μm diam., inflated, sometimes with encrusted pigments, refractive hyphae present, but not abundant, clamp connections present. *Stipitipellis* a cutis, 7.6–19.0 μm diam., inflated hyphae with encrusted pigments, similar to the pileipellis, clamp connections present.

Additional specimens examined:—BRAZIL. Mato Grosso: Alta Floresta, Reserva Particular do Patrimônio Natural Cristalino, Trilha do Francisco, 9°35'52"S, 55°56'12"W, 250 m, 4 January 2019, Santos, C. CJL648 (FLOR67407, paratype); Santos, C. CJL654 (FLOR67378 paratype); Trilha do Dr. Haffer, 9°33'24"S, 55°54'54"W, 25 January 2018, Cardoso, J.S. 273 (FLOR63560, paratype); 30 December 2018, Santos, C. CJL606 (FLOR67388, paratype); 6 January 2019, Cardoso, J.S. & Furtado, A.N.M. 554 (FLOR67422, paratype); Trilha da Torre 1, 9°36'2"S, 55°56'9"W, 250 m, 31 December 2018, Santos, C. CJL613 (FLOR67392, paratype); Trilha do Saleiro Novo, 9°35'52"S, 55°56'2"W, 250 m, 16 January 2019, Cardoso, J.S. & Furtado, A.N.M. 538 (FLOR67409, paratype); Santa Catarina: Lages, Coxilha Rica, 28°00'18.3" S, 50°19'05.3" W, 916 m, 28 February 2016, Santos, B.B. 001.

Distribution: Known from the Southern Brazilian Amazon in Mato Grosso state.

Habitat: Growing in *terra-firme* forest in the Amazon.

Comments:—This species is easily distinguished from the other green dimorphic *Hygrocybe* species due to its pileus shape, which is never umbilicate, but somewhat umbonate to plane-convex at maturity and the umbo seems to tear up forming a star-shaped rupture in the centre of the pileus. The lamellae are whitish and almost free, while the other taxa have broadly attached lamellae that have deep green tints. The microscopy does not show many distinct characteristics, except for the microbasidia that are often predominantly 2-spored, a feature not reported for the closely related taxa, and the presence of pseudocystidia emerging from the hymenium. A morphologically similar specimen (JS555) has been shown to be divergent in the ITS sequence and is named in the phylogenetic tree as *H. aff. viridilacerata* (Figure 1). Another morphologically similar specimen was found in the high plains of Southern Brazil (BBS001), but the identity was not confirmed through molecular analyses.

Identification Key to Sections of *Hygrocybe* subg. *Hygrocybe*

1. Lamellae broadly attached, often decurrent, lamellar trama subregular with short elements, not exceeding 140 µm long, basidia long, cylindro-clavate with a mean ratio of basidiospore to basidia length usually greater than 5..... Subg. *Pseudohygrocybe*
1. Lamellae free, adnexed or with a decurrent tooth, lamellar trama regular or subregular, with long parallel hyphae (> 200 µm) and tapered ends, basidia clavate, mean ratio of basidiospores to basidia length 3 to 5..... Subg. *Hygrocybe*, 2
2. Basidiospores and basidia monomorphic3
2. Basidiospores and basidia dimorphic5
3. Basidiomes stain black or slightly grey on the stipe Sect. *Hygrocybe*
3. Basidiomes without dark staining reactions.....4
4. Pileus conical or conico-campanulate, dry, tomentose, squamulose or fibrillose, basidiospores mostly < 10 µm long, pileipellis a trichoderm..... Sect. *Microspora*
4. Pileus convex-applanate, sometimes umbonate, viscid to glutinous, smooth, basidiospores often > 10 µm long, pileipellis an ixotrichodermSect. *Chlorophanae*
5. Basidiomes entirely glutinous, red or pink, pileus not perforated at the centre, stipe usually with a glutinous annulus, lamellar edge with pseudocystidia, basidiospores globose, subglobose to broadly ellipsoid, macrobasidia clavateSect. *Velosae*
5. Basidiomes not glutinous, but pileus often viscid, usually red, orange, yellow, green or purple, pileus often perforated at the centre, without annulus on the stipe, pseudocystidia sometimes present, basidiospores usually ellipsoid, oblong or cylindrical, macrobasidia broadly clavate or clavate-stipitate.....Sect. *Pseudofirmae*

Identification Key for *Hygrocybe* subg. *Hygrocybe* sect. *Pseudofirmae* occurring in Brazil

1. Basidiomes predominantly green or tinted green on pileus, lamellae or stipe.....2
1. Basidiomes predominantly red, orange, yellow, pink or purple.....6
2. Pileus convex to umbilicate, perforated at the centre, entirely green or with green tints on the pileus, lamellae or stipe.....3
2. Pileus conico-convex, umbonate, umbo surface ruptured and ragged, vivid green*H. viridilacerata*
3. Basidiomes green with yellow, red, orange and/or purple tints4
3. Basidiomes entirely green, without yellow tints*H. viridis*
4. Pileus conspicuously green, with or without a fringed margin, lamellae green without purple tints, stipe mostly green, without squamules5
4. Pileus a mixture of purple, crimson, dark red and green, with a white fringe, lamellae green turning purplish, stipe green to orange-yellow, turning purplish, most with furfuraceous waxy squamules '*H. prieta*' sensu Pegler and *Hygrocybe* spp. aff. *prieta*
5. Pileus deep dark green, with a pale green fringed margin, lamellae deep green, stipe central, equal, cheilocystidia 20.6–89.7 × 3.9–13.0 µm.....*H. cristalinensis*
5. Pileus vivid green, margin eroded, lamellae greyish green, stipe often eccentric, tapering towards the base, cheilocystidia absent, from the Cristalino basin*H. aff. chloochlora* (FLOR63533, FLOR67391, FLOR67418)
6. Pileus glabrous or finely fibrillose7
6. Pileus tomentose to squamulose.....13
7. Basidiomes predominantly yellow8
7. Basidiomes predominantly red, orange or violaceous.....9
8. Basidiomes entirely yellow, pileus convex, glabrous, slightly depressed at the centre, moist to vaguely viscid, macrospores 16.5–22 × 11–14 µm, cheilocystidia 100 × 7–12 µm.....*H. megistospora*
8. Basidiomes predominantly yellow, pileus convex-applanate, finely fibrillose, translucent-striate, perforated at the centre, dry to moist, macrospores (9–)11–15 × 6.3–10(–12) µm, cheilocystidia 37–60 × 5–20 µm *H. occidentalis* var. *occidentalis*
9. Basidiomes entirely red10
9. Basidiomes orange or violaceous carmine12
10. Pileus ≤10 mm diam., convex-umbilicate, red with a yellow margin, lamellae decurrent, macrospores 10–13 × 6–7.5 µm.....*H. trinitensis*
10. Pileus >10 mm diam., pileus convex-depressed, lamellae adnexed, sinuate or adnate with a decurrent tooth, macrospores usually wider11
11. Pileus translucent-striate, finely fibrillose, perforated at the centre, lamellae sinuate or adnate with a decurrent tooth, macrospores (9–)11–15 × 6.3–10(–12) µm, cheilocystidia 37–60 × 5–20 µm, basidiomes growing in soil*H. occidentalis* var. *scarletina*
11. Pileus glabrous, smooth, not perforated, lamellae adnexed, macrospores 11.5–15 × 7.3–11.5 µm, cheilocystidia 19 × 3.5 µm, basidiomes found on well-decayed pieces of wood in white sand forests*H. campinaranae*

12. Pileus 9–10 mm diam., orange, margin yellow, lamellae orange with yellow margin, stipe orange, macrospores $16.5\text{--}18.5 \times 10\text{--}12 \mu\text{m}$, from Brazilian Amazon *H. amazoniensis*
12. Pileus 10–15 mm diam., violaceous carmine, lamellae pinkish vinaceous, stipe yellow with pinkish vinaceous apex, macrospores $10\text{--}14 \times 6.5\text{--}8 \mu\text{m}$, from Trinidad *H. naranjana*
13. Pileus yellow to orange with brown to black squamules 14
13. Pileus red to crimson or violaceous, tomentose to squamulose 15
14. Pileus not perforated, yellow with brown small squamules, basidiomes without staining reactions, stipe 102–155 mm tall, tomentose, macrospores $12.4\text{--}20 \times 7.5\text{--}10.9\text{--}(12) \mu\text{m}$, pileipellis a trichoderm with brown pigmented hyphae *H. pegleri*
14. Pileus with a star-shaped perforation at the centre, yellow-orange with blackish-brown staining squamules, lamellae and stipe staining, stipe up to 22 mm long, fibrillose, macrospores $12.8\text{--}17.6 \times 8\text{--}10.4 \mu\text{m}$, pileipellis a trichoderm without pigmented hyphae *H. neofirma*
15. Pileus convex-umbilicate, red to crimson, tomentose to furfuraceous, lamellae pale yellow, stipe glabrous, macrospores $10\text{--}13 \times 6\text{--}8.5 \mu\text{m}$, pileipellis a disrupted trichoderm without pigmented hyphae *H. siparia*
15. Pileus convex, crimson with dark purple squamules, lamellae pale yellow with pink tints, stipe fibrillose, macrospores $(11.4\text{--}) 12.2\text{--}19\text{--}(20.7) \times 5.5\text{--}8.7 \mu\text{m}$, pileipellis a trichoderm with brown pigmented hyphae *H. vinaceosquamulosa*

Acknowledgements

The first author thanks the *Conselho Nacional de Desenvolvimento Científico e Tecnológico* (CNPq) for a Masters' scholarship (2018–2020), the *Programa de Pós-graduação em Ciências Biológicas (Botânica)*—PPG-BOT, INPA, and the *Programa de Pós-graduação em Biologia de Fungos, Algas e Plantas*—PPGFAP, UFSC. J.J.S. de Oliveira thanks the *Coordenação de Aperfeiçoamento de Pessoal de Nível Superior* (CAPES) for the *Programa Nacional de Pós-doutorado* (PNPD) scholarship (2016–2021) and PPG-BOT. The first author thanks the Cristalino Ecological Foundation (FEC), Susanne Sourell and all the Cristalino Lodge crew for the field support at RPPN Cristalino. Financial support for J.-M. Moncalvo was provided by the ROM Governors and the Natural Sciences and Engineering Research Council of Canada, Discovery Program. The authors acknowledge the editor and the anonymous reviewers for their valuable contributions to this work.

References

- Berkeley, M.J. (1856) Decades of fungi. Decades LXI–LXII. Rio Negro fungi. *Hooker's Journal of Botany and Kew Garden Miscellany* 8: 272–280.
- Cantrell, S.A. & Lodge, D.J. (2001) Hygrophoraceae (Agaricales) of the Greater Antilles: *Hygrocybe* subgenus *Pseudohygrocybe* section *Firmae*. *Mycological Research* 105 (2): 215–224.
<https://doi.org/10.1017/S0953756200003397>
- Capelari, M. & Maziero, R. (1988) Two new species of Agaricales from Brazil. *Mycotaxon* 33: 191–196.
<https://doi.org/10.5962/p.416662>
- Cardoso, J.S., Moncalvo, J.-M., Lodge, D.J., Margaritescu, S., Neves, M.A. & Oliveira, J.J.S. (2023) Studies in *Hygrocybe* s.l. (Hygrocyboideae, Hygrophoraceae) in Brazil: New species of *Humidicutis* and *Neohygrocybe*. *Phytotaxa* 607 (1): 057–071.
<https://doi.org/10.11646/phytotaxa.607.1.5>
- Courtecuisse, R. (1989) Éléments pour un inventaire mycologique des environs du Saut Pararé (Arataye) et de l'inselberg de Norages (Guyane Française). I. Introduction. II. Hygrophoraceae. *Crypto-Mycologie* 10: 181–216.
<https://doi.org/10.5962/p.354297>
- Crous, P.W., Wingfield, M.J., Burgess, T.I., Hardy, G.E.ST.J., Barber, P.A., Alvarado, P., Barnes, C.W., Buchanan, P.K., Heykoop, M., Moreno, G., Thangavel, R., Van der spuy, S., Barili, A., Barrett, S., Cacciola, S.O., Cano-Lira, J.F., Crane, C., Decock, C., Gibertoni, T.B., Guarro, J., Guevara-Suarez, M., Hubka, V., Kolarik, M., Lira, C.R.S., Ordoñez, M.E., Padamsee, M., Ryvarden, L., Soares, A.M., Stchigel, A.M., Sutton, D.A., Vizzini, A., Weir, B.S., Acharya, K., Aloï, F., Baseia, I.G., Blanchette, R.A., Bordallo, J.J., Bratek, Z., Butler, T., Cano-Canals, J., Carlavilla, J.R., Chander, J., Cheewangkoon, R., Cruz, R.H.S.F., Da Silva, M., Dutta, A.K., Ercole, E., Escobio, V., Esteve-Raventós, F., Flores, J.A., Gené, J., Góis, J.S., Haines, L., Held, B.W., Horta jung, M., Hosaka, K., Jung, T., Jurjević, Z., Kautman, V., Kautmanova, I., Kiyashko, A.A., Kozanek, M., Kubátová, A., Lafourcade, M., La spada, F., Latha, K.P.D., Madrid, H., Malysheva, E.F., Manimohan, P., Manjón, J.L., Martín, M.P., Mata, M., Merényi, Z., Morte, A., Nagy, I., Normand, A.-C., Paloi, S., Pattison, N., Pawłowska, J., Pereira, O.L., Petterson, M.E., Picillo, B., Raj, K.N.A., Roberts, A., Rodríguez, A., Rodríguez-Campo, F.J., Romański, M., Ruszkiewicz-Michalska, M., Scanu, B., Schena, L., Semelbauer, M., Sharma, R., Shouche, Y.S., Silva, V., Staniaszek-Kik, M., Stielow, J.B., Tapia, C., Taylor, P.W.J., Toome-Heller, M., Vabeikhokhei, J.M.C.,

- van Diepeningen, A.D., Van-Hoa, N., Van-Tri, M., Wiederhold, N.P., Wrzosek, M., Zothanzama, J. & Groenewald, J.Z. (2017) Fungal Planet description sheets: 558–624. *Persoonia* 38: 240–384.
<https://doi.org/10.3767/003158517X698941>
- Darriba, D., Posada, D., Kozlov, A.M., Stamatakis, A., Morel, B. & Flouri, T. (2020) ModelTest-NG: a new and scalable tool for the selection of DNA and protein evolutionary models. *Molecular Biology and Evolution* 37 (1): 291–294.
<https://doi.org/10.1093/molbev/msz189>
- Dentinger, B.T.M., Margaritescu, S. & Moncalvo, J.M. (2010) Rapid and reliable high-throughput methods of DNA extraction for use in barcoding and molecular systematics of mushrooms. *Molecular Ecology Resources* 10 (4): 628–633.
<https://doi.org/10.1111/j.1755-0998.2009.02825.x>
- Edgar, R.C. (2004) MUSCLE: a multiple sequence alignment method with reduced time and space complexity. *BMC Bioinformatics* 5: 113.
<https://doi.org/10.1186/1471-2105-5-113>
- Fundação Ecológica Cristalino—FEC (2025) Reservas Naturais Cristalino. Available from: <http://www.fundacaocristalino.org.br/> (accessed 15 October 2025)
- Gardes, M. & Bruns, T.D. (1993) ITS primers with enhanced specificity for basidiomycetes—application to the identification of mycorrhizae and rusts. *Molecular Ecology* 2: 113–118.
<https://doi.org/10.1111/j.1365-294X.1993.tb00005.x>
- Heim, R. (1967) Hygrophores tropicaux recueillis par Roger Heim 1: Espèces de Guyan française et de Nouvelle-Guinée australienne. *Revue de Mycologie* 32: 16–27.
- Heinemann, P. (1963) Champignons récoltés au Congo par Madame M. Goossens-Fontana, V. Hygrophoraceae. *Bulletin du Jardin Botanique de l'État, Bruxelles* 33: 421–458, figs. 1–41.
<https://doi.org/10.2307/3667377>
- Heinemann, P. (1966) Flore Iconographique des Champignons du Congo, Fasc. 15: Hygrophoraceae, Laccaria et Boletineae II (Compl.). *Bulletin du Jardin Botanique de l'État, Bruxelles*. [279–308, pl. 47–49]
- Hu, Y., Karunarathna, S.C., Li, H., Galappaththi, M.C., Zhao, C.L., Kakumyan, P. & Mortimer, P.E. (2022) The impact of drying temperature on basidiospore size. *Diversity* 14 (4): 239.
<https://doi.org/10.3390/d14040239>
- Instituto Nacional de Pesquisas Espaciais—INPE (2020) A taxa consolidada de desmatamento por corte raso para os nove estados da Amazônia Legal (AC, AM, AP, MA, MT, PA, RO, RR e TO) em 2019 é de 10.129 km², Brazilian Federal Government. Available from: <http://www.obt.inpe.br/OBT/noticias-obt-inpe/a-taxa-consolidada-de-desmatamento-por-corte-raso-para-os-nove-estados-da-amazonia-legal-ac-am-ap-ma-mt-pa-ro-rr-e-to-em-2019-e-de-10-129-km2> (accessed 15 October 2025)
<https://doi.org/10.18472/SustDeb.v9n1.2018.7143>
- Komura, D.L., De Olivera, J.J.S., Moncalvo, J.M., Margaritescu, S. & Zartman, C.E. (2016) *Marasmius calvocystidiatus* sp. nov. and *M. horridulus* (Marasmiaceae): characterization of two unusual species from central Amazonia. *Phytotaxa* 280: 222–240.
<https://doi.org/10.11646/phytotaxa.280.3.2>
- Komura, D.L., Oliveira, J.J.S., Moncalvo, J.M., Margaritescu, S. & Zartman, C.E. (2020) Six new species of *Tetrapyrgos* (Basidiomycota, Agaricales, Marasmiaceae) from the Brazilian Amazon. *Phytotaxa* 440: 193–214.
<https://doi.org/10.11646/phytotaxa.440.3.2>
- Kramer, L.A. (2004) *The Online Auction Color Chart*. Stanford, Online Auction Color Chart Company, USA, 6 pp.
- Kummer, P. (1871) *Der Führer in die Pilzkunde*. C. Luppe, Zerbst, Germany, 146 pp.
- Largent, D.L. (1986) *How to Identify Mushrooms to Genus I: Macroscopic features*. 3ed, Mad River Press Inc., Eureka, CA, USA, 166 pp.
- Largent, D.L., Johnson, D. & Watling, R. (1977) *How to Identify Mushrooms to Genus III: Microscopic features*. 3ed, Mad River Press Inc., Eureka, CA, USA, 148 pp.
- Lodge, D.J. & Pegler, D.N. (1990) Hygrophoraceae of the Luquillo Mountains of Puerto Rico. *Mycological Research* 94 (4): 443–456.
[https://doi.org/10.1016/S0953-7562\(10\)80002-4](https://doi.org/10.1016/S0953-7562(10)80002-4)
- Lodge, D.J., Padamsee, M., Matheny, P.B., Aime, M.C., Cantrell, S.A., Boertmann, D., Kovalenko, A., Vizzini, A., Dentinger, B.T.M., Kirk, P.M., Ainsworth, A.M., Moncalvo, J.-M., Vilgalys, R., Larsson, E., Lucking, R., Griffith, G.W., Smith, M.E., Norvell, L.L., Desjardin, D.E., Redhead, S.A., Ovrebo, C.L., Lickey, E.B., Ercole, E., Hughes, K.W., Courtecuisse, R., Young, A., Binder, M., Minnis, A.M., Lindner, D.L., Ortiz-Santana, B., Haight, J., Laessoe, T., Baroni, T.J., Geml, J. & Hattori, T. (2013) Molecular phylogeny, morphology, pigment chemistry and ecology in Hygrophoraceae (Agaricales). *Fungal Diversity* 64: 1–99.
<https://doi.org/10.1007/s13225-013-0259-0>
- Neves, M.A., Sourell, S., Lodge, D.J., Cardoso, J.S., Silva, D.F., Cardoso, S.M.C., Ribeiro, R.S. & Araújo-Silva, L.E. (2018) *Amazonian fungi: knowledge as a key to conservation—the Cristalino Fungi Project*. [Conference paper, State of the World's Fungi Symposium.

London, England]

- Oliveira, J.J.S., Vargas-Isla, R., Cabral, T.S., Cardoso, J.S., Andriolli, F.S., Rodrigues, D.P., Ikeda, T., Clement, C.R. & Ishikawa, N.K. (2021) The Amazonian luminescent *Mycena cristinae* sp. nov. from Brazil. *Mycoscience* 62 (6): 395–405.
<https://doi.org/10.47371/mycosci.2021.05.004>
- Pegler, D.N. (1983) *Agaric flora of the Lesser Antilles*. Kew Bulletin Additional Series 9, HMSO, London, 668 pp.
- Pegler, D.N. (1997) *The Agarics of São Paulo: An account of the agaricoid fungi (Holobasidiomycetes) of São Paulo State, Brasil*. Royal Botanic Gardens, Kew, UK, 68 pp.
- Pegler, D.N. & Fiard, J.P. (1978) *Hygrocybe* sect. *Firmae* (Agaricales) in Tropical America. *Kew Bulletin* 32 (2): 297–312.
<https://doi.org/10.2307/4117101>
- Petch, T. (1917) Revision of Ceylon fungi (Part V). *Annals of the Royal Botanic Gardens Peradeniya* 6: 307–355.
- Pires, J.M. & Prance, G.T. (1985) The Vegetation Types of the Brazilian Amazon. In: Prance, G.T. & Lovejoy, T.E. (Eds.) *Key environments: Amazonia*. Pergamon Press, Oxford.
- Rambaut, A. (2007) FigTree v1.4.3. Institute of Evolutionary Biology, University of Edinburgh, Edinburgh. Available from: <http://tree.bio.ed.ac.uk/software/figtree/> (accessed 17 November 2025)
- Rathnayaka, A.R., Tennakoon, D.S., Jones, G.E., Wanasinghe, D.N., Bhat, D.J., Priyashantha, A.H., Stephenson, S.L., Tibpromma, S. & Karunarathna, S.C. (2025) Significance of precise documentation of hosts and geospatial data of fungal collections, with an emphasis on plant-associated fungi. *New Zealand Journal of Botany* 63 (2–3): 462–489.
<https://doi.org/10.1080/0028825X.2024.2381734>
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542.
<https://doi.org/10.1093/sysbio/sys029>
- Silva-Filho, A.G.S., Sa, M.C.A., Komura, D.L., Moncalvo, J.M., Margaritescu, S., Roy, M. & Wartchow, F. (2020) Two novel species of *Lactifluus* subg. *Pseudogymnocarpi* (Russulaceae) from Brazil. *Phytotaxa* 436: 222–236.
<https://doi.org/10.11646/phytotaxa.436.3.2>
- Silva-Filho, A.G.S., Sa, M.C.A., Komura, D.L., Baseia, I.G., Marinho, P., Moncalvo, J.M., Roy, M. & Wartchow, F. (2021) Novelities in *Lactifluus* subg. *Gymnocarpi* (Russulales, Basidiomycota) from Brazilian tropical forests. *Mycological Progress* 20: 549–565.
<https://doi.org/10.1007/s11557-021-01693-w>
- Silva-Filho, A.G.S., Sa, M.C.A., Komura, D.L., Braga-Neto, R., Baseia, I.G., Marinho, P., Moncalvo, J.M., Roy, M. & Wartchow, F. (2023) *Lactifluus* subg. *Lactariopsis* (Russulales/Basidiomycota) from Brazilian tropical forests. *Botany* 101: 570–581.
<https://doi.org/10.1139/cjb-2023-0077>
- Singer, R. (1958) Fungi Mexicani, series Prima, Agaricales. *Sydowia* 11: 354–374.
- Singer, R. (1965) Interesting and new Agaricales from Brazil. *Atas do Instituto de Micologia* 2: 15–59.
- Soares, C.C., Cabral, T.S., Vargas-Isla, R., Cardoso, J.S., Rodrigues, D.P., Ishikawa, N.K. & Oliveira, J.J. (2024) *Mycena lamprocephala*, a new luminescent species from the Brazilian Amazon. *Phytotaxa* 634 (3): 187–203.
<https://doi.org/10.11646/phytotaxa.634.3.1>
- Stamatakis, S. (2006) RAXML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690.
<https://doi.org/10.1093/bioinformatics/btl446>
- Stropp, J., Umbelino, B., Correia, R.A., Campos-Silva, J.V., Ladle, R.J. & Malhado, A.C.M. (2020) The ghosts of forests past and future: deforestation and botanical sampling in the Brazilian Amazon. *Ecography* 43: 979–989.
<https://doi.org/10.1111/ecog.05026>
- White, T.J., Bruns, T., Lee, S. & Taylor, J.W. (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis, M.A., Gelfand, D.H., Sninsky, J.J. & White, T.J. (Eds.) *PCR protocols: a guide to methods and applications*. Academic Press, New York, pp. 315–322.
<https://doi.org/10.1016/B978-0-12-372180-8.50042-1>
- Wildlife Conservation Society—WCS (2025) Aliança Águas Amazônicas. Bacias Principais: Tapajós. Available from: <https://pt.aguasamazonicas.org/bacia/bacias-principais/tapajos/> (accessed 15 October 2025)