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Mythicomycetaceae fam. nov. (*Agaricineae*, *Agaricales*) for accommodating the genera *Mythicomyces* and *Stagnicola*, and *Simocybe parvispora* reconsidered

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Abstract: The analysis of a combined dataset including 5.8S (ITS) rDNA, 18S rDNA, 28S rDNA, and *rpb2* data from species of the *Agaricineae* (Agaricoid clade) supports a shared monophyletic origin of the monotypic genera *Mythicomyces* and *Stagnicola*. The new family *Mythicomycetaceae*, sister to *Psathyrellaceae*, is here proposed to name this clade, which is characterised, within the dark-spored agarics, by basidiomata with a mycenoid to phaeocollybioid habit, absence of veils, a cartilaginous-horny, often tapering stipe, which discolours dark brown towards the base, a greyish brown, pale hazel brown spore deposit, smooth or minutely punctate-verruculose spores without a germ pore, cheilocystidia always present, as metuloids (thick-walled inocybe-like elements) or as thin-walled elements, pleurocystidia, when present, as metuloids, pileipellis as a thin ixocutis without cystidioid elements, clamp-connections present everywhere, and growth on wood debris in wet habitats of boreal, subalpine to montane coniferous forests. *Simocybe parvispora* from Spain (two collections, including the holotype), which clusters with all the sequenced collections of *Stagnicola perplexa* from Canada, USA, France and Sweden, must be regarded as a later synonym of the latter.

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INTRODUCTION

The *Agaricineae emend*. Aime *et al.* represents one of the seven suborders recently recognised in the *Agaricales* by Dentinger *et al.* (2016) using a phylogenomic approach. This corresponds to a previously recognised "Agaricoid" clade, which has been consistently recovered as monophyletic in recent studies (Matheny *et al*. 2006, 2015, Garnica *et al*. 2007, Binder *et al*. 2010, Kohler *et al.* 2015). Many species in this suborder show pigmented and thick-walled spores (Matheny *et al*. 2006, 2015, Garnica *et al*. 2007). Although species producing dark-pigmented spores (dark-pigmented agarics) are present in a few other lineages (e.g. *Melanomphalia,* Aime *et al*. 2005 or *Ripartites*, Walther *et al.* 2005, Garnica *et al*. 2007), the overwhelming majority of these have evolved within *Agaricineae*. The presence of spores with a thickened, dark-pigmented wall is perhaps indicative of adaptations to specialised environments (e.g. dung, burnt sites) (Garnica *et al*. 2007, Halbwachs *et al*. 2015).

Within the dark (brown)-spored agarics, the monotypic genera *Mythicomyces* and *Stagnicola* were established by Redhead & Smith (1986) based on the two morphologically similar species *Agaricus corneipes* and *Phaeocollybia perplexa*, respectively. The two taxa occupy a rather isolated position within the brown-spored agarics and share a complex of characters that make it difficult to place them at the family level: a mycenoid to phaeocollybia-like appearance (i.e. a widely acute umbonate pileus and a dark brown, cartilaginous-horny, tapering stipe with a tawny strigosity at base), a pallid spore deposit, greyish brown, pale hazel brown to milk coffee brown with light purple tones, spores without a germ-pore and almost hyaline or faintly brownish under light microscope, a pileipellis as a thin ixocutis, growth on wood debris, presence of clamp-connections. *Mythicomyces* differs from *Stagnicola* mainly by minutely verrucose spores, thick-walled hymenial cystidia and a spore deposit with purple hues. Redhead & Smith (1986) tentatively placed the two genera in the *Strophariaceae s.* Kuhner (1984) and the *Cortinariaceae s.l.*, respectively, mainly based on spore-print colour. In subsequent years, such family placements were debated and questioned. On morphological basis only, Watling & Gregory (1993) suggested *S. perplexa* to be probably better placed in *Inocybeae* within *Cortinariaceae*. Horak (2005) recognised both in *Cortinariaceae* and Gulden (2008a, b) in *Crepidotaceae* (family which includes also *Inocybaceae* according to the author). Extensive phylogenetic studies based on large datasets by Moncalvo *et al*. (2002), Matheny *et al*. (2006, 2015), Padamsee *et al.* (2008), Nagy *et al*. (2011) and Zhao *et al*. (2017) resolved either one or both of these genera in a clade sister to the *Psathyrellaceae* (*Agaricineae*, formerly Agaricoid clade *s.* Matheny *et al*. 2006, 2015, Garnica *et al*. 2007, Binder *et al.* 2010). The molecular work by Matheny & Griffith (2010) based on a dataset limited to *Squamanita* and allied taxa, indicated *M. corneipes* as sister (with low support) to a superclade formed by *Psathyrellaceae*, *Cystodermateae* and *Nidulariaceae*. In the phylogenetic analysis by Gulden *et al*. (2005) based on a dataset

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of only brown-spored agarics, *Stagnicola* occupied an *incertae sedis* position, while *Mythicomyces* clustered in *Strophariaceae s. l.* In Broussal & Dumesny (2015), *Mythicomyces* and *Stagnicola* were sister to each other (with low support) and were part of a superclade, consisting of *Cortinariaceae*, *Bolbitiaceae*, *Tubariaceae*, *Strophariaceae* and *Hymenogastraceae*, which was sister to *Psathyrellaceae*.

However, in molecular studies where both *Mythicomyces* and *Stagnicola* were taken into account at the same time, they were represented at most by two collections each with only 28S rDNA sequences (Moncalvo *et al.* 2002, Gulden *et al*. 2005, Padamsee *et al.* 2008, Broussal & Dumesny 2015).

In accordance with all these molecular studies indicating a sisterhood relationship of the two genera to *Psathyrellaceae*, *Mythicomyces* and *Stagnicola* have recently been classified within the *Psathyrellaceae* by Gulden (2012a, b), Strittmatter & Obenauer (2013) and Prydiuk (2015, 2018). Inexplicably, and probably because they were unaware of the results of the previous molecular studies, the two most frequently used online registries, *Index Fungorum* (http://www.indexfungorum.org), Mycobank (http://www.mycobank.org/), and Begerow *et al*. (2018) assigned the two genera to two different families, namely *Mythicomyces* to the *Psathyrellaceae* and *Stagnicola* to the *Strophariaceae*.

Currently, whereas at least one collection of *Mythicomyces corneipes* (AFTOL-ID 972) is represented by multiple markers in GenBank (https://www.ncbi.nlm.nih.gov/genbank/), only a few collections of *Stagnicola perplexa* are present and only with ribosomal (ITS and 28S) sequences. The aim of the present paper was to provide *Stagnicola* with a sound phylogenetic placement within the *Agaricineae* by increasing its taxon sampling and the number of molecular markers. The study of the type collections of *Simocybe parvispora*, which is part of a research project in progress on the European species of the genus *Simocybe*, has revealed its conspecificity with *Stagnicola perplexa*. Morphological and molecular data of these collections were also included because they are central to the main focus of the present work.

MATERIALS AND METHODS

Morphological examination

The microscopic structures were examined from dried material, in different mountants: water, L4 [7.2 g KOH, 160 mL glycerine, 840 mL dH_2O, 7.6 g NaCl and 5 mL Invadin (Ciba-Geigy), Clémençon 1972], Melzer's reagent, ammoniacal Congo red, Phloxine, Cresyl blue and Cotton blue. Cresyl blue and Cotton blue were utilised to highlight the ortho-/metachromatic reactions in the spores. Dried fragments were rehydrated in water and mounted in L4. All microscopic measurements were carried out under oil immersion at ×1 000 with Nikon Eclipse 80i microscope.

Spore measurements were made by photographing all the spores (taken from lamellar squashes of exsiccate material of mature specimens) occurring in the visual field of the microscope using the Mycomètre software (Fannechère 2011). Spore dimensions do not include the hilar appendix, and are reported as follows: average minus standard deviation – average plus standard deviation of length × average minus standard deviation – average plus standard deviation of width; Q = average minus standard deviation – average plus standard deviation of ratio length/width; Q_m = average ± standard deviation of ratio length/width; V = average minus standard deviation – average plus standard deviation of the volume [μm^3]; V_m = average ± standard deviation of the volume [μm^3]. The approximate spore volume was calculated as that of an ellipsoid (Gross 1972, Meerts 1999). The notation "n/m/p" indicates that measurements were made on "n" randomly selected spores from "m" basidiomes of "p" collections. The width of the basidia was measured at the widest part, and the length was measured from the apex (sterigmata excluded) to the basal septum. Microscopic pictures were taken using a Nikon DS 5M digital connected to a Nikon Eclipse 80i microscope with both brightfield and interferential contrast optics.

DNA extraction, amplification and sequencing

Total DNA was extracted from eight dry specimens (Table 1) employing a modified protocol based on Murray & Thompson (1980). PCR amplification was performed with the primers ITS1F and ITS4 (White *et al*. 1990, Gardes & Bruns 1993) for the ITS rDNA region, while LR0R and LR5 (Vilgalys & Hester 1990, Cubeta *et al.* 1991) were used to amplify the 28S (LSU) rDNA region, NS19b and NS41 for the 18S (SSU) rDNA ribosomal region (Hibbett 1996), and bRPB2-6F and bRPB2-7R2 for the RNA polymerase II second largest subunit (*rpb2*) gene (Liu *et al.* 1999, Matheny *et al*. 2007a). PCR reactions were performed under a program consisting of a hot start at 95 °C for 5 min, followed by 35 cycles at 94 °C, 54 °C and 72 °C (45, 30 and 45 s respectively) and a final 72 °C step for 10 min. PCR products were checked in 1 % agarose gels, and positive reactions were sequenced with one or both PCR primers. Chromatograms were checked searching for putative reading errors, and these were corrected. The sequences were submitted to GenBank (http://www.ncbi.nlm.nih.gov/genbank/) and their accession numbers are reported in Table 1.

Phylogenetic analysis

BLAST (Altschul *et al.* 1997) was used to select the most closely related sequences from INSD public databases (www.insd.org). Two distinct alignments were built. 1) A multigenic alignment including 5.8S rDNA, 28S (LSU) rDNA, 18S (SSU) rDNA and *rpb2* sequences from representative species of the major lineages in the *Agaricineae* based mainly on Matheny *et al.* (2015). Two species of *Tricholoma* (*T. myomyces*, *T. palustre*) (*Tricholomatineae*), were used as outgroups to root the tree, because of their phylogenetic position external to the *Agaricineae* (Matheny *et al.* 2015, Dentinger *et al.* 2016). 2) A ITS rDNA data alignment of *Mythicomyces* and *Stagnicola* sequences, using *Psathyrella candolleana* as outgroup taxon. Sequences were aligned in MEGA v. 6.0 (Tamura *et al.* 2013) software with its Muscle application and then corrected manually. GTR+G models were chosen for both the alignments. The datasets were analysed using Bayesian inference (BI) and Maximum likelihood (ML) criteria. The Bayesian analysis was performed through the CIPRES Science Gateway platform (Miller *et al*. 2010) by using the MrBayes v. 3.2.6 algorithm with 28S rDNA-18S rDNA-5.8S rDNA-*rpb2* data partitioned, two simultaneous runs, four chains, temperature fixed at 0.2 and sampling every 1 000 generations until reaching the convergence parameters (standard deviation less than 0.01) after about 5 M generations. The first 25 % trees were discarded

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Table 1. Samples used for the present phylogenetic studies. Newly sequenced collections are in **bold**.

Taxon	Voucher	Country	GenBank acc. numbers			
			ITS	28S	18S	*rpb2*
Agaricaceae sp.	RC_Mart06_016	Martinique	HQ839742	HQ839743	HQ839744	HQ839745
Agaricus aff. *campestris*	PBM 2580	Massachusetts, USA	DQ486682	DQ110871	DQ113914	—
Agaricus bisporus	AFTOL-ID 448/strain OMF	Denmark/USA	DQ404388	AY635775	AY787216	AF107785
Agaricus sylvaticus	JFM-AS	Taiwan	—	AJ244523	AJ012405	—
Agrocybe pediades	AFTOL-ID 1493	California, USA	DQ484057	DQ110872	DQ113915	—
Agrocybe praecox	AFTOL-ID 728	Washington, USA	AY818348	AY646101	AY705956	DQ385876
Agrocybe rivulosa	strain CCB160	Tennessee, USA	KF830098	KF830090	KF830078	KF830069
Agrocybe smithii	AFTOL-ID 1494	Washington, USA	DQ484058	DQ110873	DQ115779	—
Bogbodia uda (*"Nematoloma longisporum"*)	AFTOL-ID 1893	Massachusetts, USA	DQ490634	DQ457681	DQ444863	—
Bolbitius viscosus	PBM 3032	Tennessee, USA	HQ840656	HQ840657	KJ137269	HQ840658
Bolbitius vitellinus	AFTOL-ID 1730	Washington, USA	DQ200920	AY691807	AY705955	DQ385878
Chlorophyllum agaricoides	AFTOL-ID 440	Greece	DQ200928	AY700187	AY657010	—
Conocybe lactea	PBM 2706	Massachusetts, USA	DQ486693	DQ457660	DQ437683	DQ470834
Conocybe smithii	CCB 185	Oregon, USA	KF830097	KF830088	—	KF830068
Coprinellus disseminatus	SFSU MRK18/strain 24.3/ strain C345.1	Various	AY461838	AF056456	—	DQ056143
Coprinopsis atramentaria	PBM 992	Washington, USA	DQ486694	DQ457661	DQ115781	—
Coprinopsis cinerea	KACC49356/C13/okayama 7#130	Various	AF345819	AF041494	M92991	XM_001829088
Coprinus comatus	AFTOL-ID 626	California, USA	AY854066	AY635772	AY665772	AY780934
Cortinarius aurilicis	TSJ1998-101	France	DQ083772	AY684152	AY705957	DQ083880
Cortinarius bolaris	IB19990199 /strain REG MB 96-086/	Germany	AF389169	AY293173	AY293125	—
Cortinarius iodes	IB19850061/AFTOL-ID 285	Massachusetts, USA	AF389133	AY702013	AY771605	AY536285
Cortinarius sodagnitus	TF2001-094/AFTOL-ID 811	Denmark	DQ083812	AY684151	AY752975	DQ083920
Cortinarius violaceus	MTS 4854/AFTOL-ID 814	Washington, USA	DQ486695	DQ457662	AY705950	DQ470835
Crassisporium funariophylum (*"Pachylepyrium carbonicola"*)	TENN 028784/AHS44809	Idaho, USA	HQ222013	HQ832460	HQ832427	—
	TENN 028785/AHS65056	Idaho, USA	HQ222014	HQ222015	HQ832428	—
	PBM 2293/PBM1411	Washington, USA	—	DQ986294	—	HQ832438
	strain Moser 49/22	Austria	KF830095	KF830085	—	—
	strain Moser 49/8	Austria	KF830096	KF830086	—	—
Crepidotus cf. *applanatus*	PBM717 (WTU)	Washington, USA	DQ202273	AY380406	AY705951	AY333311
Crepidotus sp.	PBM3463	Western Australia, AU	HQ728537	HQ728538	HQ728539	HQ728540
Crepidotus variabilis	REG JE 5.3	Unknown	—	AY293174	AY293126	—
Crucibulum laeve	REG Crul1/DSH 96-02	Unknown	DQ486696	AF336246	AF026624	DQ470836
Cyathus striatus	DSH 96-028/Cyst1/DSH 96-001	Unknown	DQ486697	AF336247	AF026617	DQ472711
Cystoderma amianthinum	TENN063549/AFTOL-ID 1553	Wales, UK	GU296098	DQ154108	GU296097	—
Descolea maculata	AFTOL-ID 1521	Western Australia, AU	DQ192181	DQ457664	DQ440633	—
Descolea phlebophora	TENN 063626/PBM 3108	New Zealand	HQ728543	HQ728544	KJ137258	HQ728545
Descolea recedens	TENN 063870/PBM 3211	Tasmania, AU	HQ728546	HQ827174	—	HQ827175
Descolea tenuipes	TENN 063871/PBM 3212	Tasmania, AU	HQ832453	HQ832466	HQ832432	HQ832443
Flammula alnicola	PBM 2608/AFTOL-ID 1501	Tennessee, USA	DQ486703	DQ457666	DQ113916	DQ472714
Flammulaster sp.	PBM 1871	Washington, USA	—	AY380408	—	AY333315
	PBM 3449	Tasmania, AU	HQ827176	HQ827177	HQ827178	—
Galerina atkinsoniana	PBM 2719/AFTOL-ID 1760	Colorado, USA	DQ486705	DQ457668	DQ440634	—

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Table 1. (Continued).

Taxon	Voucher	Country	GenBank acc. numbers			
			ITS	28S	18S	*rpb2*
Galerina clavus	Contu_15122007	Italy	—	HQ832461	HQ832429	—
Galerina marginata	AFTOL-ID 465	Massachusetts, USA	DQ192182	DQ457669	DQ440635	—
Galerina semilanceata	PBM 1398/AFTOL-ID 1497	Washington, USA	DQ486706	AY038309	DQ440639	AY337357
Galerina sp.	PR 6574	USA, Puerto Rico	HQ827182	HQ827183	HQ827184	HQ839737
Hebeloma affine	NI 270904	Ontario, Canada	FJ436320	EF561632	HQ832422	FJ436321
Hebeloma angustilamellatum (*"Anamika angustilamellata"*)	AFTOL-ID 543	China	AY575919	AY575919	DQ092918	—
Hebeloma olympianum	BK 21-Nov-98-20	Washington, USA	—	AY038310	—	AY337359
Hebeloma velutipes	AFTOL-ID 980 PBM2277	California, USA	AY818351	AY745703	AY752972	DQ472718
Hydnangium carneum	TENN 063868/PBM 3209	Tasmania, AU	HQ832445	HQ832455	HQ832423	HQ832433
Hymenagaricus taiwanensis	AFTOL-ID 1383	Taiwan	DQ490633	DQ457680	DQ089016	—
Hypholoma australianum (*"Hypholoma australe"*)	PBM 3481	Western Australia, AU	HQ832446	HQ832456	KJ137259	HQ832434
Hypholoma fasciculare	PBM 1844	Washington, USA	—	AY380409	—	AY337413
Hypholoma sublateritium	AFTOL-ID 597	Massachusetts, USA	AY818349	AY635774	AY787215	—
Hypholoma subviride	TENN 062712/TJB10226	Tennessee, USA/Belize	HQ222020	HQ832457	HQ832424	HQ832435
Inocybe aff. *asterospora*	PBM 2014/PBM 2453	New York, USA	DQ404390	AY702015	AY654889	—
Inocybe mutata	PBM 2953/PBM 2542/ AFTOL-ID 1632	Tennesse/ Massachusetts, USA	JQ801410	AY732212	DQ457623	DQ472729
Inocybe myriadophylla	AFTOL-ID 482	Finland	DQ221106	AY700196	AY657016	AY803751
Inocybe pallidicremea	PBM2448 /PBM2039	Washington, USA	HQ201357	AY380385	—	AY337388
Inocybe rimosoides	AFTOL-ID 520	New York, USA	DQ404391	AY702014	AY752967	DQ385884
Inocybe unicolor	PBM 2589/ PBM1841/DUKE RV7/4	Tennessee/Missouri, USA	EU523554	AY380403	AF287836	AY337409
Laccaria amethystina	DSH s.n.	Unknown	—	AF393062	AF287837	—
Laccaria bicolor	TWO 752 (MONT)/Cham3/ S238N-H82	Montana, USA/France	DQ149869	AF042588	—	XM_001873347
Laccaria ochropurpurea	AFTOL-ID 1477	France/New York, USA	AF006598	AY700200	AY654886	DQ472731
Laccaria pumila	DSH s.n.	Unknown	—	AF287869	AF287838	—
Lacrymaria velutina	AFTOL-ID 478	Massachusetts, USA	DQ490639	AY700198	AY654885	DQ472733
Langermannia gigantea	DSH96-032	Unknown	—	AF518603	AF026622	—
Lepiota cristata	ECV2449/AFTOL-ID 1625	Michigan, USA	AF391041	DQ457685	DQ457627	—
Lepiota maculans	JMB 080509_18	Tennessee, USA	HM222939	HQ832458	HQ832425	HQ832436
Leucoagaricus barssii	AFTOL-ID 1899	California, USA	DQ911600	DQ911601	GU187658	DQ911602
Lycoperdon pyriforme	AFTOL-ID 480/DSH96-054	Unknown	AY854075	AF287873	AF026619	AY218495
Macrolepiota dolichaula	AFTOL-ID 481/AFTOL-ID 529	China	DQ221111	DQ411537	AY771602	DQ385886
Macrolepiota procera	18-X-1990, R.P.J. de Kok/ DSH 96-038	Netherlands	AY243589	AF518628	—	—
Mycocalia denudata	AFTOL-ID 2018/CBS 494.85	Canada	DQ911596	DQ911597	DQ911598	KJ137274
Mythicomyces corneipes	AFTOL-ID 972	Washington, USA	DQ404393	AY745707	DQ092917	DQ408110
	DAOM 178138	Canada	—	AF261381	—	—
	strain KB51	Pakistan	KY648897	—	—	—
	ES11.10.2.A	Germany	KC964108	—	—	—
Naucoria escharioides	PAM03/99/PBM 1719	France/Washington, USA	AY900086	AY380405	—	AY337411
Nidula niveotomentosa	AFTOL-ID 1945/CBS250.84	Canada	DQ917654	DQ986295	GU296099	KJ137275
Phaeocollybia festiva	AFTOL-ID 1489/PBM 2366	Norway	DQ494682	AY509119	DQ462516	AY509118
Phaeomarasmius fulvidulus	Okada 170163	Argentina	KF830092	KF830087	—	—
	T 1495	Argentina	KF830091	KF830080	KF830072	KF830063

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Table 1. (Continued).

Taxon	Voucher	Country	GenBank acc. numbers			
			ITS	28S	18S	*rpb2*
Phaeomarasmius proximans	AFTOL-ID 979/PBM1936 (WTU)	Vermont, USA	DQ404381	AY380410	AY752970	AY333314
Phaeomyces dubiosus	strain PAM06110301	France	KF830099	KF830089	KF830077	KF830070
Pholiota aff. *astragalina*	PBM 2975	Tennessee, USA	HQ832448	HQ832462	KJ137263/ KJ137264	HQ832439
Pholiota multicingulata	TENN 063875	New Zealand	HQ832449	HQ832463	HQ832430	HQ832440
Pholiota nubigena (*"Nivatogastrium nubigenum"*)	AFTOL-ID 1500	California, USA	DQ494679	DQ470815	DQ459373	—
Pholiota squarrosa	AFTOL-ID 1627	Colorado, USA	DQ494683	DQ470818	DQ465337	—
Pholiotina filaris	AFTOL-ID 1498	Massachusetts, USA	DQ494684	DQ470819	DQ465338	—
Pleuroflammula flammea	AFTOL-ID 1381/MCA 339	Unknown	DQ494685	AF367962	DQ089021	DQ474124
Pleuroflammula praestans	PBM3461	Western Australia, AU	HQ832450	HQ832464	HQ832431	HQ832441
Pleuroflammula tuberculosa	PAM 02072903	France	HQ832452	HQ832465	KJ137265	HQ832442
Psathyloma catervatim	PBM 3420	Tasmania, AU	HQ840663	HQ840664	HQ840665	HQ840666
Psathyloma leucocarpum	PBM 3116	New Zealand	HQ840659	HQ840660	HQ840661	HQ840662
Psathyrella candolleana	AFTOL-ID 1507	Massachusetts, USA	DQ494689	DQ110874	DQ465339	—
Psathyrella gracilis	J 130	Unknown	—	AF041533	DQ851582	—
Psathyrella rhodospora	AFTOL-ID 723 MP133 (MIN)	Minnesota, USA	DQ267129	AY645058	DQ089018	—
Psathyrella spadicea	AFTOL-ID 1628	Colorado, USA	DQ494690	DQ470822	DQ465340	—
Psilocybe caerulipes	T SAT09-216-06	Tennessee, USA	KC669282	KF830084	KF830075	KF830067
Psilocybe cubensis	strain DNA2052	Unknown	KF830094	KF830083	KF830074	KF830066
Psilocybe cyanescens	PSMICSY-200	Unknown	KJ137276	KJ137277	KJ137266	KJ137278
Psilocybe sp. (*"Pachylepyrium funariophilum"*)	strain TENN 6030	Washington, USA	—	AF261513	—	—
Psilocybe stuntzii	VT1263	Unknown	—	AF042567	DQ851584	—
Psilocybe subaeruginosa	PBM 3218 TENN065481	Tasmania, AU	KC669278	KF830079	KF830071	KF830062
Romagnesiella clavus	**AMB 15091**	**Italy**	—	**MK353795**	**MK353799**	**MK359092**
Romagnesiella clavus (*"Tubaria minima"*)	PAM 06090110	France	EF051060	EF051055	—	—
Simocybe serrulata	AFTOL-ID 970	Massachusetts, USA	DQ494696	AY745706	DQ465343	DQ484053
Simocybe sp.	PBM 3031	Tennessee, USA	GQ893023	GQ892979	KJ137267	HQ832444
Squamanita paradoxa	TENN 063549/GG_BM05B	Wales, UK	GU296096	EF535266	GU296095	—
Stagnicola perplexa	DAOM 191293	British Columbia, Canada	—	AF261509	—	—
Stagnicola perplexa	**Broussal 20160928_909MB**	**France**	**MK351604**	**MK353788**	**MK353797**	**MK359087**
	DAOM 191292	**British Columbia, Canada**	**MK351605**	**MK353789**	—	**MK359088**
	DAOM 191296	**Newfoundland Labrador, Canada**	**MK351606**	**MK353790**	—	**MK359089**
	DAOM 191295	**British Columbia, Canada**	**MK351607**	**MK353791**	—	—
	SFSU F-032462	**California, USA**	**MK351608**	**MK353792**	**MK353798**	**MK359090**
***Stagnicola perplexa* (*"Simocybe parvispora"*)**	**AH 25260 holotype**	**Spain**	**MK351609**	**MK353793**	—	**MK359091**
	AH 25282 paratype	**Spain**	**MK351610**	**MK353794**	—	—
	KS-BR126	Sweden	MK045203	—	—	—
Stropharia ambigua	AFTOL-ID 726	Washington, USA	AY818350	AY646102	DQ092924	DQ484054
Stropharia rugosoannulata	Hopple D258	Unknown	DQ494697	AF518654	AF026635	—
Tricholoma myomyces	KMS 589	Unknown	DQ825428	U76459	DQ367422	DQ367436
Tricholoma palustre	AFTOL-ID 1497	Massachusetts, USA	DQ494699	AY700197	AY757267	DQ484055

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Table 1. (Continued).

Taxon	Voucher	Country	GenBank acc. numbers			
			ITS	28S	18S	*rpb2*
Tubaria confragosa	AFTOL-ID 498	Washington, USA	DQ267126	AY700190	AY665776	DQ408113
Tubaria furfuracea	MCA 391	California, USA	—	AF205710	DQ851587	—
Tubaria serrulata	AFTOL-ID 1528	Western Australia, AU	DQ182507	DQ156128	DQ462517	—
Tubaria sp.	PBM 3355	Tasmania, AU	HQ839739	HQ839740	HQ839741	—
	BM378_17	Washington, USA	HQ832454	HQ832467	KJ137268	HQ839738
Tubaria vinicolor	AFTOL-ID 499	Washington, USA	DQ536417	DQ536415	DQ536416	DQ536418
Tulostoma macrocephala	strain Long 10111	Unknown	—	AF518663	AF026625	—
Verrucospora flavofusca	AFTOL-ID 655	China	DQ241779	DQ470825	AY665783	—

as burn-in. Finally, a full search for the best-scoring Maximum Likelihood tree was performed in RAxML v.7.0.4 (Stamatakis 2006) using the standard search algorithm (data partitioned, GTRMIX model, 2 000 bootstrap replications). Significance threshold was set above 0.95 for posterior probability (BPP) and 70 % for bootstrap proportions (MLBP).

RESULTS

Phylogenetic analyses

The final multigenic alignment is composed of 129 OTU and contained 4 100 total sites: 1 443 sites from 28S, 1 800 sites from 18S, 158 sites from 5.8S and 699 sites from *rpb2*. The ITS alignment consisted of 12 collections and contained 664 sites.

As both Bayesian and Maximum likelihood analyses produced similar topologies, only the Bayesian trees with both BPP and MBP values are shown (Figs 1, 2). The concatenated analysis (Fig. 1) supported the existence of at least 14 major lineages (families) within the *Agaricineae*. Nine of these (*Agaricaceae*, *Bolbitiaceae*, *Cortinariaceae*, *Crassisporiaceae*, *Hydnangiaceae*, *Inocybaceae*, *Mythicomycetaceae*, *Psathyrellaceae* and *Tubariaceae*) received strong statistical support (BPP ≥ 0.95 and MLBP ≥ 70 %); *Crepidotaceae*, *Nidulariaceae*, *Squamanitaceae* and *Strophariaceae* showed high BPP values (≥ 0.95) but only poor maximum likelyhood bootstrap support (< 70 %). For the first time a significant sister relationship (BPP = 0.96) was obtained between *Crassisporiaceae* and *Cortinariaceae* based on Bayesian inference. *Mythicomyces* and *Stagnicola* clustered as sister (BPP = 100 and MLBP = 100 %) in a strongly supported clade (BPP = 100 and MLBP = 100 %), the *Mythicomycetaceae*. The family is sister with strong statistical support (BPP = 100 and MLBP = 100 %) to the *Psathyrellaceae*.

The ITS analysis (Fig. 2) highlighted the presence of three subclades in *Stagnicola perplexa* which would seem to be quite related to a different geographic origin (North America vs. Europe, but see below the notes about the species).

Taxonomy

Mythicomycetaceae Vizzini, Consiglio & M. Marchetti, ***fam. nov.*** MycoBank MB829479.

Habit mycenoid to phaeocollybioid (phaeocollybia-like). *Veils* absent (gymnocarpic development). *Pileus* 5–30 mm, hemispherical-conical, obtusely to acutely conical, bell-shaped, umbonate or papillate. *Lamellae* adnexed to narrowly adnate. *Stipe* 15–70 × 0.5–2 mm, cylindrical, often tapering towards the base (but without pseudorhiza), typically cartilagineous-elastic, tough, corneus (horny) (marasmius cohaerens-like), shiny, gradually darkening (reddish-brown to blackish) from base upwards, with tawny basal strigosity. *Spore deposit* greyish-brown, pale hazel brown to milky coffee brown with light purple hues. *Spores* ovoid to ellipsoid, often somewhat inequilateral, smooth or minutely punctate-verruculose, without a germ pore, thin- to thick-walled, almost hyaline or faintly brownish under light microscope, binucleate, walls cyanophilous, inamyloid or dextrinoid. *Basidia* clavate, usually 4-spored. *Cheilocystidia* present, thick-walled, inocybe-like, often with hyaline crystals at apex and slightly amyloid at apex, or thin-walled and inamyloid. *Pleurocystidia* absent, if present then only as thick-walled elements. *Hymenophoral trama* regular, consisting of parallel hyphae. *Pileipellis* a thin ixocutis with parietal pigment. *Clamp-connections* present.

Type genus: *Mythicomyces* Redhead & A.H. Sm., *Canad. J. Bot*. **64**: 643. 1986.

Habit: Saprotrophic on wood debris, Northern Hemisphere, mostly temperate to boreal.

Genera included: *Mythicomyces* and *Stagnicola*.

Notes: The genus *Mythicomyces* and not the genus *Stagnicola* was chosen as type of the family because *Stagnicola* Jeffreys (1830) is also a genus of snails (aquatic pulmonate gastropod mollusks) and there is a larger body of literature on *Stagnicola* Jeffreys (e.g. searches in GenBank®, Scopus®, Biosis®) than there is on *Stagnicola* Redhead & Smith, which can cause confusion.

Fig. 1. Phylogeny of the *Agaricineae* based on Bayesian Inference and Maximum Likelihood analysis of a dataset of four nuclear gene regions (5.8S-rDNA, 28S-rDNA, 18S-rDNA and *rpb2*). *Tricholoma myomyces* and *T. palustre* were used as outgroup taxa. Only BPP ≥ 0.95 and ≥ MLBP 70 % are indicated above branches. The newly sequenced collections are in **bold**. Clade nomenclature follows mainly Matheny *et al.* (2015).

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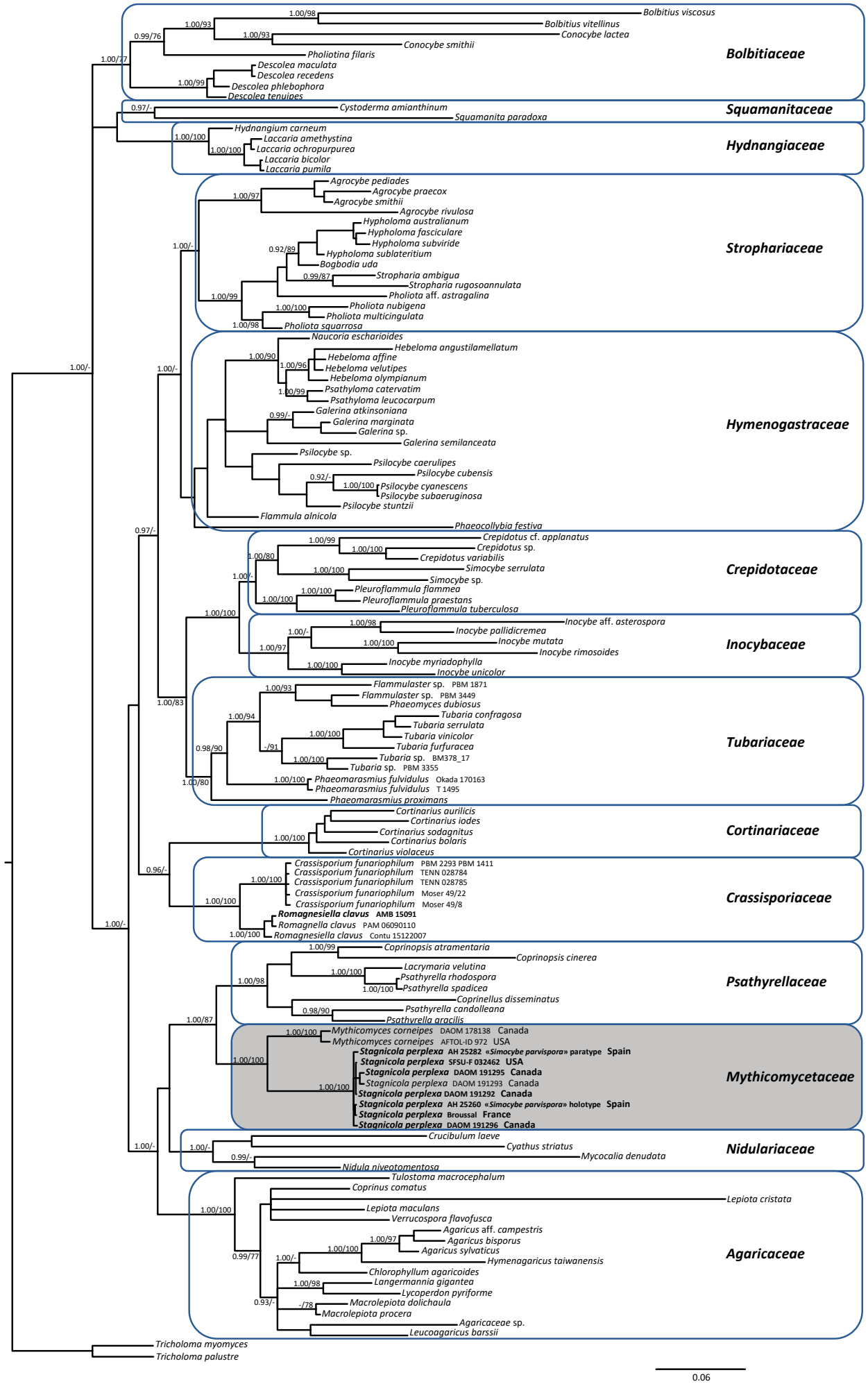
Bolbitiaceae
Bolbitius viscosus
Bolbitius vitellinus
Conocybe lactea
Conocybe smithii
Pholiotina filaris
Descolea maculata
Descolea recedens
Descolea phlebophora
Descolea tenuipes
Squamanitaceae
Cystoderma amianthinum
Squamanita paradoxa
Hydnangiaceae
Hydnangium carneum
Laccaria amethystina
Laccaria ochropurpurea
Laccaria bicolor
Laccaria pumila
Strophariaceae
Agrocybe pediades
Agrocybe praecox
Agrocybe smithii
Agrocybe rivulosa
Hypholoma australianum
Hypholoma fasciculare
Hypholoma subviride
Hypholoma sublateritium
Bogbodia uda
Stropharia ambigua
Stropharia rugosoannulata
Pholiota aff. astragalina
Pholiota nubigena
Pholiota multicingulata
Pholiota squarrosa
Hymenogastraceae
Naucoria escharioides
Hebeloma angustilamellatum
Hebeloma affine
Hebeloma velutipes
Hebeloma olympianum
Psathyloma catervatim
Psathyloma leucocarpum
Galerina atkinsoniana
Galerina marginata
Galerina sp.
Galerina semilanceata
Psilocybe sp.
Psilocybe caerulipes
Psilocybe cubensis
Psilocybe cyanescens
Psilocybe subaeruginosa
Psilocybe stuntzii
Flammula alnicola
Phaeocollybia festiva
Crepidotaceae
Crepidotus cf. applanatus
Crepidotus sp.
Crepidotus variabilis
Simocybe serrulata
Simocybe sp.
Pleuroflammula flammea
Pleuroflammula praestans
Pleuroflammula tuberculosa
Inocybaceae
Inocybe aff. asterospora
Inocybe pallidicremea
Inocybe mutata
Inocybe rimosoides
Inocybe myriadophylla
Inocybe unicolor
Tubariaceae
Flammulaster sp. PBM 1871
Flammulaster sp. PBM 3449
Phaeomyces dubiosus
Tubaria confragosa
Tubaria serrulata
Tubaria vinicolor
Tubaria furfuracea
Tubaria sp. BM378_17
Tubaria sp. PBM 3355
Phaeomarasmius fulvidulus Okada 170163
Phaeomarasmius fulvidulus T 1495
Phaeomarasmius proximans
Cortinariaceae
Cortinarius aurilicis
Cortinarius iodes
Cortinarius sodagnitus
Cortinarius bolaris
Cortinarius violaceus
Crassisporiaceae
Crassisporium funariophilum PBM 2293 PBM 1411
Crassisporium funariophilum TENN 028784
Crassisporium funariophilum TENN 028785
Crassisporium funariophilum Moser 49/22
Crassisporium funariophilum Moser 49/8
Romagnesiella clavus AMB 15091
Romagnella clavus PAM 06090110
Romagnesiella clavus Contu 15122007
Psathyrellaceae
Coprinopsis atramentaria
Coprinopsis cinerea
Lacrymaria velutina
Psathyrella rhodospora
Psathyrella spadicea
Coprinellus disseminatus
Psathyrella candolleana
Psathyrella gracilis
Mythicomycetaceae
Mythicomyces corneipes DAOM 178138 Canada
Mythicomyces corneipes AFTOL-ID 972 USA
Stagnicola perplexa AH 25282 «Simocybe parvispora» paratype Spain
Stagnicola perplexa SFSU-F 032462 USA
Stagnicola perplexa DAOM 191295 Canada
Stagnicola perplexa DAOM 191293 Canada
Stagnicola perplexa DAOM 191292 Canada
Stagnicola perplexa AH 25260 «Simocybe parvispora» holotype Spain
Stagnicola perplexa Broussal France
Stagnicola perplexa DAOM 191296 Canada
Nidulariaceae
Crucibulum laeve
Cyathus striatus
Mycocalia denudata
Nidula niveotomentosa
Agaricaceae
Tulostoma macrocephalum
Coprinus comatus
Lepiota cristata
Lepiota maculans
Verrucospora flavofusca
Agaricus aff. campestris
Agaricus bisporus
Agaricus sylvaticus
Hymenagaricus taiwanensis
Chlorophyllum agaricoides
Langermannia gigantea
Lycoperdon pyriforme
Macrolepiota dolichaula
Macrolepiota procera
Agaricaceae sp.
Leucoagaricus barssii
Tricholoma myomyces
Tricholoma palustre
0.06

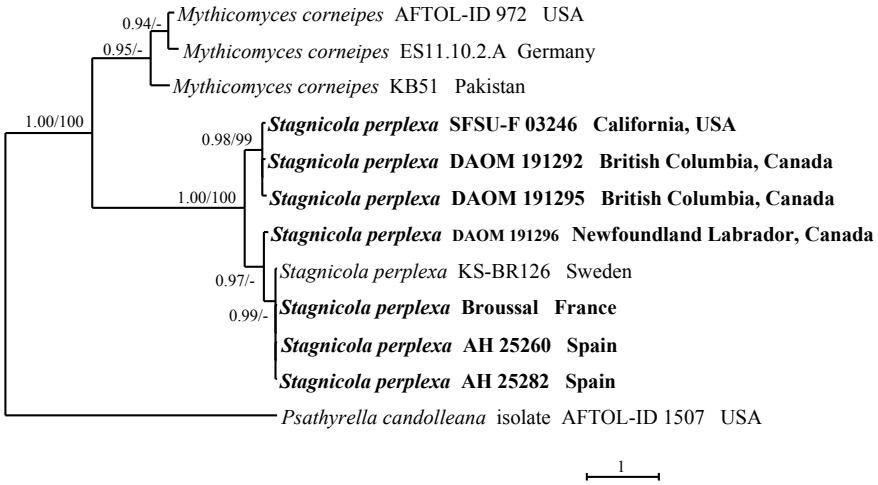

Fig. 2. Phylogeny of the *Mythicomycetaceae* based on Bayesian Inference and Maximum likelihood analysis of ITS rDNA sequences with *Psathyrella candolleana* as outgroup taxon. Only BPP ≥ 0.95 and ≥ MLBP 70 % are indicated above branches. The newly sequenced collections are in **bold**.

Mythicomyces Redhead & A.H. Sm., *Canad. J. Bot*. **64**: 643. 1986.

Etymology: from Greek mythikòs = mythical and mykes = fungus.

Development gymnocarpic. *Habit* mycenoid/collybioid to phaeocollybia-like. *Pileus* obtusely conical later convex, with a broad umbo, up to 4/5-striate, hygrophanous, greasy-shiny, slightly viscid, smooth, reddish brown, orange brown, at margin yellowish brown. *Lamellae* adnate to narrowly adnate, crowded, straw yellow, then cinnamon to greyish-brown. *Stipe* central, smooth, cartilaginous, rigid, glossy, shiny, flexuous, red brown at apex, darker and discolouring brown to blackish towards the base, with a tawny basal mycelial tomentum. Smell indistinct, taste indistinct or slightly bitterish. *Spore print* greyish brown to yellowish brown, pale purplish brown. *Spores* ovoid to ellipsoid, often somewhat inequilateral, minutely roughened, punctate-verruculose, with a small plage, lacking a germ-pore, thick-walled; pale greyish to yellowish brown in water (practically hyaline) under the microscope, cyanophilous, dextrinoid, inamyloid, slightly metachromatic in Cresyl blue, binucleate. *Basidia* usually 4-spored. *Cheilocystidia* and *Pleurocystidia* metuloid (thick-walled), thin-walled at the pedicel, abundant, ventricose, utriform to lageniform or fusiform, someones with hyaline crystals at apex, moderately amyloid in the apical part. *Pileipellis* a thin ixocutis. *Caulocystidia* present. *Clamp-connections* present. *Tissues* non-sarcodimitic.

Type species: *Mythicomyces corneipes* (Fr.) Redhead & A.H. Sm.

Ecology and distribution: Saprotrophic on plant debris, mainly wood, in wet, mossy areas, usually hemiboreal to boreal, Europe, North America and Asia.

Mythicomyces corneipes (Fr.) Redhead & A.H. Sm., *Mycotaxon* **118**: 456. 2011.
Basionym: *Agaricus corneipes* Fr., *Öfvers. K. Vetensk Akad. Förh*. **18**: 25. 1861.
Synonyms: *Psilocybe corneipes* (Fr.) P. Karst., *Bidr. Känn. Finl. Nat. Folk* **32**: 504. 1879.
Geophila corneipes (Fr.) Quél., *Enchiridion Fungorum in Europa media et praesertim in Gallia Vigentium*: 114. 1886.
Mythicomyces corneipes (Fr.) Redhead & A.H. Sm., *Canad. J. Bot*. **64**: 643. 1986 (*Nom. inval*., Art. 33.5, 33.7, 33.8).

Gruber P-88 (neotype, MICH).

Selected descriptions: Smith (1938: 26, fig. 2b, d, f, as *Psilocybe corneipes*); (Smith (1949: 518–520, as *Psilocybe corneipes*); Redhead & Smith (1986: 643–645); Moser & Jülich (1987: III *Mythicomyces* 1); Huhtinen & Vauras (1992: 7–10); Stålberg (1991: 64–67); Ludwig (2001a: 397–398, 2001b: plate 107, 51.1); Strittmatter & Obenhauer (2013: 338–340); Prydiuk (2015: 56–58).

Ecology and distribution: Rare. Gregarious, in autumn, saprotrophic on plant debris, among mosses in moist habitats, such as edges of bogs, brook ravines, or under conifers or birch in soil wet from spring flooding. Found throughout the Northern Hemisphere, Europe (mainly northern part), North America (most common in the Pacific Northwest region) and Asia (Pakistan). So far known from Finland, Norway, Sweden (Fries 1861, Stålberg 1991, Huhtinen & Vauras 1992, Gulden 2008a, 2012a), Estonia (see locked ITS sequence UDB024379 in UNITE, https://unite.ut.ee, specimen TU109530, 11.09.2015, Valga maakond, Otepää vald, *leg*. I. Kytövuori), Spain (*Mythicomyces* sp. environmental 18S sequence DQ304712T4B-S13. L. Laiz *et al.*), Germany (Gminder & Saar 2012, Strittmatter & Obenhauer 2013), Russia (Palamarchuk 2009), Ukraine (Prydiuk 2015, 2018), USA, Canada (Morgan 1917, Smith 1938, 1975, Redhead & Smith 1986, Castellano *et al*. 2003), and Pakistan (ITS sequence KY648897, strain KB51, 06.09.2013, *leg.* A.N. Khalid & K. Bakht).

Notes: The species was originally named *Agaricus corneipes* by Fries (1861), who described it from collections made in a fir forest near Alsike, Sweden, as mainly characterised by a glossy, shiny, very rigid horny stipe darkening towards the base and similar to that of *Agaricus cohaerens*. The species was placed in *Psilocybe* by Karsten (1879) and in *Geophila* by Quélet (1886). It was subsequently recorded in North America (northwestern USA) by Morgan (1907, as *Psilocybe corneipes*), who again underlined its resemblance to *Marasmius cohaerens* and by Smith (1938, 1975, as *Psilocybe corneipes*), who also provided photos. These last two authors described the spores as smooth and with a hyaline germ-pore.

Subsequently, in his monographic treatment of the genus *Psilocybe* worldwide, Guzmán (1983), after examining Smith's collections, excluded the taxon from *Psilocybe*, because of its roughened spores lacking a germ pore, presence of metuloids, a pale spore print, stipe texture, and the tawny basal mycelium. Guzmán suggested that probably the best placement for the species would be in *Galerina*.

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Redhead & Smith (1986) pointed out that some of the features of the species did not fully fit *Galerina*, in particular the colour of the spore in mass (not ochre to rusty brown), the spores lacking a plage, presence of metuloids, stipe texture and tawny basal mycelium, and established *Mythicomyces* for accommodate this puzzling species.

Redhead & Smith (1986) proposed the genus *Mythicomyces* citing as type "*Mythicomyces corneipes* (Fries) comb. nov." and listing Fries (1863) (and not the earlier Fries 1861) for the basionym *Agaricus corneipes*. They listed also as obligate synonym the validly published name *Psilocybe corneipes* (Fr.) P. Karst. (Karsten 1879: 504). While the indication of the type fulfilled the requirements for a valid publication of the generic name (Art. 37.2), the incorrect citation of the basionym did not meet the requirements for a valid publication of the binomial. Therefore, they published the correct, valid combination later (Redhead *et al.* 2010).

Redhead & Smith (1986) placed the genus provisionally in the *Strophariaceae*, mainly because the habit of the basidiomes and spore print colour fit the broad concept of that family as circumscribed by Kühner (1980, 1984), which included all the non-ectomycorrhizal taxa with a cinnamon-brown, rusty-brown to lilac-brown spore deposit. They noted, however, that the genus did not fit a more restricted concept of *Strophariaceae* (Singer 1986) due to the lack of a germ-pore and the roughened spore wall.

Later, Huhtinen & Vauras 1992, after studying several collections from Fennoscandia, Canada and USA, discovered features never reported by previous authors. In particular, an amyloid reaction in cystidial walls, the dextrinoid reaction of the spores and the presence of a small plage (visible in light microscopy). The latter spore character, detected by scanning electron microscopy also by Prydiuk (2015) in Ukrainian collections, is typical of most *Galerina* species (Smith 1964, Bon 1992, Wood 2001, Gulden *et al*. 2005, Haan & Walleyn 2009, Gulden 2012c). Subsequent molecular works demonstrated, however, that *Galerina* is phylogenetically unrelated to *Mythicomyces* and had to be placed in the family *Hymenogastraceae* (Matheny *et al*. 2006, 2015).

Stagnicola Redhead & A.H. Sm., *Canad. J. Bot*. **64**: 645. 1986.

Development gymnocarpic. *Habit* mycenoid/collybioid to phaeocollybia-like. *Pileus* conical to convex, umbonate, hygrophanous, smooth, lubricous-viscid to greasy, striate, tawny, fulvous to sienna, orange yellowish at margin. *Lamellae* adnexed-ventricose, crowded with olivaceous tints and concolorous edge. *Stipe* central, smooth, bay or purplish reddish, dark brown to blackish towards the base, horny, cartilaginous, shiny, often deeply tapering towards base, marasmius cohaerens-like, xeromphalina-like (but without forming a true pseudorhiza), with a saffron to ochre basal mycelial tomentum. *Smell* and *taste* indistinct or astringent, bitterish. *Spore print* deep olive buff to pale hazel brown. *Spores* ellipsoid to amygdaliform-reniform, smooth, without a germ-pore, pale hazel, yellowish brown in water (practically hyaline) under the microscope, non-dextrinoid, inamyloid, cyanophilous, non-metachromatic, binucleate. *Basidia* usually 4-spored, rarely 1–2-spored. *Cheilocystidia* thin-walled, cylindrical to fusiform. *Pleurocystidia* absent. *Hymenophoral trama* regular, consisting of parallel hyphae. *Pileipellis* a thin ixocutis of encrusted hyphae with yellow brown parietal pigment. *Caulocystidia* present. *Clamp-connections* present. *Tissues* non-sarcodimitic.

Habit: Saprotrophic, usually on rotten plant debris (buried needles, leaves, twigs), in damp places, in moist to wet sites, coniferous forests, acid soils, often among *Sphagnum*, montane-boreal, Europe and North America.

Type species: *Stagnicola perplexa* (P.D. Orton) Redhead & A.H. Sm.

Stagnicola perplexa (P.D. Orton) Redhead & A.H. Sm., *Canad. J. Bot*. **64**: 645. 1986.
Basionym: *Phaeocollybia perplexa* P.D. Orton, *Kew Bull*. **31**: 713. 1977.
Synonyms: *Agaricus cidaris* var. *minor* Fr., *Icon. select. Hymenomyc. t*. **123**: 2. 1878.
Naucoria cidaris var. *minor* (Fr.) Sacc., *Syll. Fung*. **5**: 831. 1887.
Simocybe parvispora Bandala *et al.*, *Sydowia* **60**: 183. 2008.

Selected descriptions: Orton (1977: 713, as *Phaeocollybia perplexa*); Redhead & Smith (1986: 645, 646); Laber & Marklund (1992: 54–56); Watling & Gregory (1993: 93–95; figs 136–138, p. 128, 129); Ludwig (2001a: 659, 660, 2001b: plate 173, 82.1); Bandala *et al.* (2008: 183–185, fig. 1 p. 188, fig. 2 p. 189; as *Simocybe parvispora*); Broussal & Dumesny (2015: 238–240).

Microscopy (based mainly on Broussal 20160928_909MB, SFSU-F-032462 and DAOM 191295). Fig. 3.

Spores 5.1–6.1 × 3.0–3.5 µm (145/3/3) (on average 5.6 × 3.3 µm), Q = 1.57–1.85 (Q_m 1.71), V = 24.3–38.8 µm^3 (V_m = 31.5 µm^3), subellipsoid with a flat to depressed adaxial side in lateral view, mainly ellipsoid in front view, hilar appendix visible, smooth, wall up to 0.3–0.5 µm thick, pale yellowish in water, slightly darker at wall level, often mono- to multiguttulate, cyanophilic, inamyloid, non-dextrinoid, non-metachromatic in Cresyl blue. *Basidia* 18–28 × 5–8 µm, mainly tetra-spored, subcylindrical to clavate, even subcapitate, with up to 6 µm long sterigmata, content mostly smooth, at times guttulate. *Hymenophoral trama* regular, consisting of thin-walled, hyaline to yellowish cylindrical hyphae, 4–8 µm wide, having a parallel arrangement. Occasionally, it was observed the occurrence of crystalline particles either free or sticking to the hyphal walls. *Subhymenium* hardly differentiated. *Cheilocystidia* 25–40(–45) × 4.5–7(–8) µm, thin-walled, sub-cylindrical, at times flexuous or slightly ventricose or clavate, with a rounded, occasionally subogival or lobate apex, other times with a tapered base; edge heteromorphous. *Pleurocystidia* not found. *Pileipellis* a regular thin ixocutis, consisting of cylindrical, yellowish, thin-walled hyphae, 3–8(–10) µm wide, smooth but with occasional crystalline deposits, at times with clavate terminal elements; subcutis well differentiated, composed of short articles, l6–12(–15) µm wide, subvesicular or allantoid. *Pileocystidia* not found. *Stipe hyphae* 2–8(–10) µm wide, mostly cylindraceous, at times fusiform, parallel, often short-celled, hyaline to yellowish, thin-walled, occasionally it can be noted the presence of polymorphous, refractive, small-sized crystalline deposits. *Caulocystidia* present in the apical portion of the stipe, similar to the hymenial ones but more irregular in shape. *Clamp-connections* common everywhere. *Tissues* non-sarcodimitic.

Specimens examined: **France**: *Haute-Auvergne*: Condat, Cantal, Maubert et Gaulis forest, alt. 872 m, coniferous forest (*Picea abies*, *Abies alba*), on debris in mossy area, 28 Sep. 2016, *H. Dumesny* [*det. M. Broussal*] (Broussal 20160928_909MB). **Canada**: *British*

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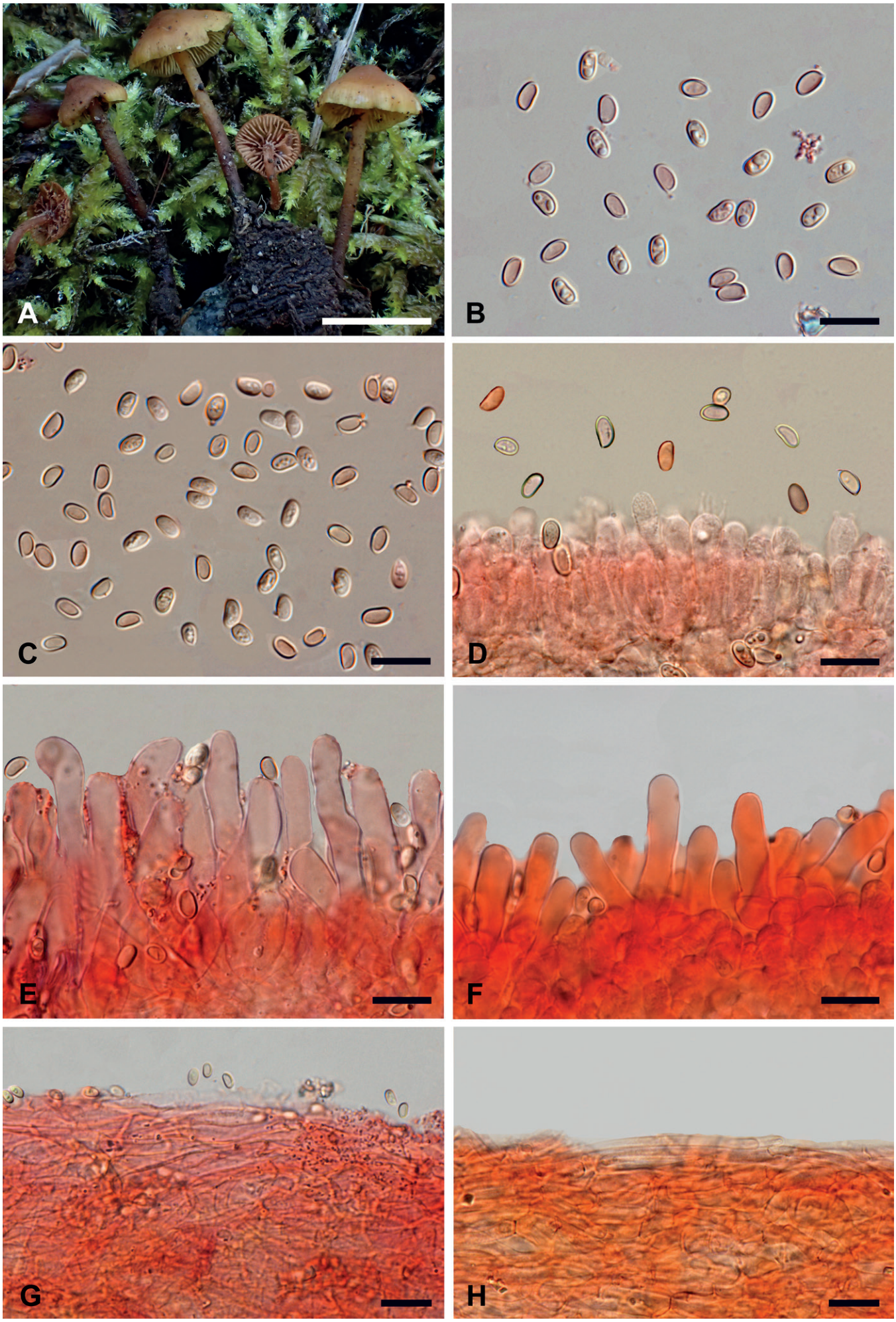

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Columbia: Queen Charlotte Is., Graham I., Kliki Damen Cr. mouth, in a drying temporary pool amongst *Carex*, 16 Sep. 1982, *S.A. Redhead* (DAOM 191292); Queen Charlotte Is., Graham I., Yakoun R. near Port Clements, on reed bed, along river, 15 Sep. 1982, *S.A. Redhead* (DAOM 191295). *Newfoundland-Labrador*: Gros Morne Natl. Park, on debris in wet depression by alders, Bakers Brook Pond trail, !9 Sep. 1983, *S.A. Redhead* (DAOM 191296). **USA**: *California*: Siskiyou County, Shasta-Trinity National Forest, alt. 485 m, *Abies magnifica* litter with an understory of *Symphoricarpos* sp., 8 Nov. 2012, *C. Schwarz* [*det. S. Davison*] (SFSU-F-032462).

Microscopy (based on *Simocybe parvispora* AH 25282 (paratype). Fig. 4.

Spores 5.2–6 × 3–3.5 µm (44/1/1) (av. 5.6 × 3.2 µm), Q = 1.57–1.90 (Q_m 1,74), V = 25.2–36.6 µm^3 (V_m = 30.9 µm^3), ellipsoid in side-view, often with an almost flat adaxial side, occasionally with central constriction, mostly ellipsoid in front-view, smooth. Lacking a germ pore, wall up to 0.3–0.5 µm thick, hilar appendix visible, pale yellowish in water, often mono- or multi-guttulate, cyanophilic, iodine-negative, non-metachromatic in Cresyl blue. *Basidia* 18–28 × 5–7 µm, tetrasporic, sterigmata up to 6 µm long, often even monosporic with a sterigm up to 10 µm long, subcylindrical to clavate or even subcapitate, content mostly smooth, at times guttulate. *Hymenophoral trama* regular, made up by cylindrical, hyaline to yellowish, thin-walled hyphae, 4–8 µm wide, occasionally it is possible to observe minute crystalline formations. *Subhymeniun* hardly differentiated. *Cheilocystidia* 25–55(–60) × 4.5–7(–8) µm, thin-walled, hyaline, subcylindrical, often flexuous or slightly ventricose or clavate, with rounded or ogival apex, plentiful to scarce, at times completely absent. *Pleurocistidia* not found. *Pileipellis* a regular thin ixocutis, with long to short hyphae, at times with clavate terminal elements, 3–7 µm wide, thin-walled, yellowish, with occasional crystalline deposits; subcutis and underlying layer well differentiated, consisting of short hyphae, 8–20 µm wide, subvesicular or allantoid. *Pileocystidia* not found. *Stipe hyphae* 2–8(–10) µm wide, mostly cylindrical, at times fusiform, parallel, often short-celled, with yellowish content, thin-walled, refractive polymorphous crystalline deposits present. *Caulocystidia* numerous in the apical portion, tufted, at times multi-septate, subcylindrical-clavate or utricular, even lageniform, 20–40 × 3–8 µm. *Clamp-connections* common everywhere. *Tissues* non-sarcodimitic.

Ecology and distribution: Rare. Gregarious, in autumn, saprotrophic on plant debris, in moist to wet areas, usually in acid coniferous forests among mosses. Found throughout the Northern Hemisphere (Europe and North America) and so far known from Sweden and Finland (Fries 1878 as *Agaricus cidaris* var. *minor*, Stridvall & Stridvall 1996, Gulden 2008b, 2012b), Great Britain (Scotland, Orton 1977 as *Phaeocollybia perplexa*; Watling & Gregory 1993), Germany (Laber & Marklund 1992), France (Broussal & Dumesny 2015, Spain (Bandala *et al*. 2008 as *Simocybe parvispora*), Moldova (Manic 2015), USA and Canada (Smith 1937, Redhead & Smith 1986). In Index Fungorum and MycoBank, *Panaeolus sphinctrinus* var. *minor*, described by Singer (1960, 1969) based on Mexican and Argentine collections, is (mistakenly) considered as a posterior synonym of *A. corneipes* and consequently Niveiro & Albertó (2012), Coimbra (2015) and Begerow *et al*. (2018) reported in their checklists *S. perplexa* (= *P. sphinctrinus* var. *minor*) as present in Argentine. In comparison with *M. corneipes*, however, *P. sphinctrinus* var. *minor* has a non-corneous stipe, lacks a tawny mycelial tomentum at stipe base and its spores are darker, hexagonal to citriform in shape, have a with germ-pore and measure 12–13.3 × 9–9.3 µm (Singer 1960, Guzmán & Pérez-Patraca 1972, Gerhardt 1996).

Specimens examined: **Spain**: *Castilla-La Mancha*: Guadalajara, road from Aldeanueva de Atienza to Condemios de Arriba, river Pelagallinas, on decaying branches of *Pinus sylvestris*, alt. 1380 m, 2 Oct. 1999, *Villarreal et coll.* (AH 25282-paratype/topotype).

Notes: The species was clearly first reported from Sweden by Fries (1878) as *Agaricus* (*Naucoria*) *cidaris* var. *minor* (plate 123, fig. 2). Fries differentiated the variety from the type (to date considered a true *Phaeocollybia*), mainly on the lack of a rooting stipe. Saccardo (1887) then combined this variety in *Naucoria*. Smith (1937) signalled it from North America, providing also a photo (plate 23, fig. c). When the species was collected for the first time by Orton (1977), the English mycologist, unaware of Fries's taxon, was not able, at first, to place it in a known genus (hence the specific epithet of "*perplexa*", i.e. puzzled). Subsequently, after additional collections, in spite of the smooth, pale-coloured spores and the pileus not strongly viscid, he became convinced that the new taxon had to be placed in the genus *Phaeocollybia* [traditionally included in *Cortinariaceae* due to the presence of a viscid pileus surface, a pseudorhiza, rusty-brown, ornamented spores, and the absence of a veil (Heim 1931, Horak 1977, Laber 1982, 1991)]. It was accommodated near *P. jennyae*, since other features such as the conical umbonate pileus, horny cartilaginous rooting stipe, absence of veils, absence of pleurocystidia, bitter astringent taste and yellowish olive lamellae fitted neatly into the genus. Horak (1977) considered the inclusion of the species in *Phaeocollybia* doubtful and questionable. Redhead & Smith (1986) removed *P. perplexa* from *Phaeocollybia* mainly because of its pale smooth spores, a not truly rooting stipe and presence of a tawny tomentum at stipe base, transferring it to the monotypic genus *Stagnicola*. Subsequent accurate morpho-ecological works by Redhead & Malloch (1986), Norvell (1998a, b, 2000, 2004) and Norvell & Exeter (2008) allowed a better circumscription of *Phaeocollybia*, which, when additional distinguishing features were discovered, led to a better delimitation of *P. stagnicola* and the other brown-spored agarics. Noteworthy among the new features are the (pileo)stipitocarpic-monovelangiocarpic development revealed by the presence of a thin pellicular veil (primordial envelope sheath) sheathing the subterranean primordium, but tearing during basidiome elongation and easily overlooked in mature basidiomes (where velar remnants are only observable as fibrillose patches on the aerial stipe); the presence of a rhizomorphic pseudorhiza (a pseudorhiza forming several thread-like myceliar cords that

Fig. 3. Macro- and micromorphological features of *Stagnicola perplexa*. **A.** Basidiomata in the field (Broussal 20160928_909MB). **B.** Spores (Broussal 20160928_909MB). **C.** Spores (DAOM 191295). **D.** Spores and hymenium (SFSU-F-032462). **E.** Cheilocystidia (DAOM 191295). **F.** Cheilocystidia (SFSU-F-032462). **G.** Pileipellis (DAOM 191295). **H.** Pileipellis (SFSU-F-032462). B–H in ammoniacal Congo red. Scale bars: A = 10 mm; B–H = 10 µm. Photographs: A, Hélène Dumesny; B–H, Mauro Marchetti.

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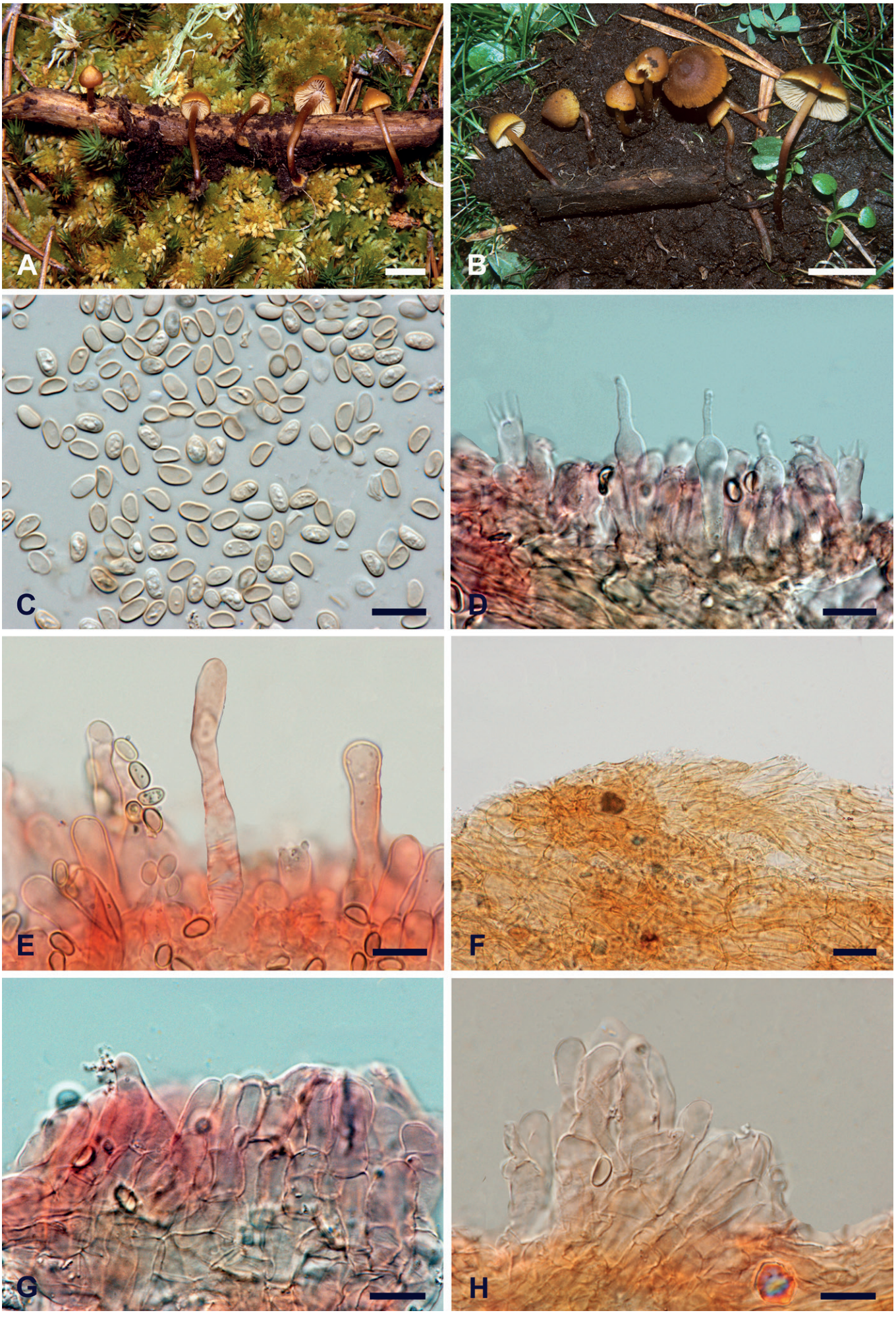

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make contact with the plant root tips); tibiiform diverticula on the hyphae of the mycelium, a pellicular veil and sarcodimitic pseudotissues in the pseudorhizal trama, often present also in the stipititrama, pileitrama, and hymenophoral trama. Last but not least, evidence that *Phaeocollybia* is an ectomycorrhizal genus (trophic lifestyle confirmed also by the stable isotopes analysis by Trudell *et al.* 2004), even though some species are possibly parasitic. Molecular phylogeny placed *Phaeocollybia* in *Hymenogastraceae* (Matheny *et al*. 2006, 2015).

As first suggested by Redhead & Smith (1985), species of the genus *Tubaria* (*Tubariaceae*) may resemble *S. perplexa*, but they possess a non-umbonate pileus, veils, broadly attached, adnate to subdecurrent lamellae, a non-tapering stipe which is fibrous and fleshy and with white basal mycelium, and thin-walled easily collapsing spores (Singer 1986, Bon 1992, Volders 2002, Matheny *et al.* 2007b).

Stagnicola perplexa could be confused with the central-stemmed species of *Simocybe* (e.g. *S. centunculus*, *S. sumptuosa*) (*Crepidotaceae*), but the latter differ in having olivaceous tinges on pileus surface, more pigmented, distinctly ovoid-reniform spores and a trichodermic-hymenidermic pileipellis with well-developed pileocystidia (Romagnesi 1962, Senn-Irlet 1995, Aime *et al.* 2005, Horak & Ronikier 2011). The morphological affinities between *Stagnicola* and *Simocybe* are such that, according to our phylogenetic analyses (Figs 1, 2), the recently described *Simocybe parvispora* from Spain (Bandala *et al*. 2008) is to be regarded as identical to *S. perplexa.* Moreover, also the morphological study of the two sequenced *Simocybe parvispora* collections (holotype and paratype) showed characters that, based on the descriptions in the literature (Orton 1977, Redhead & Smith 1986, Laber & Marklund 1992, Watling & Gregory 1993, Broussal & Dumesny 2015) and our personal observations, match perfectly those of *S. perplexa*.

Finally, also the two recently described sister genera *Crassisporium* and *Romagnesiella* (*Crassisporiaceae*) have some characters in common with *Stagnicola*. In particular, they share a collybioid habit, a filamentous pileipellis, pale-coloured, smooth spores and presence of clamp-connections. Nonetheless, they differ in the non-umbonate pileus, fleshy, non-rooting stipe, which does not progressively darken towards the base and lacks a tawny basal tomentum and the non-dextrinoid spores with walls becoming rusty brown to reddish brown or reddish cinnamon in KOH. Additionally, *Crassisporium*, typified by *Pholiotina funariophila*, a taxon traditionally placed in the polyphyletic genus *Pachylepirium* (Matheny *et al.* 2015), is distinguished by a fugacious veil on pileus and stipe surface, thick-walled spores (> 0.5 µm thick) with a broad and conspicuous germ pore (often > 0.5 µm wide) and carbonicolous habitat (Matheny *et al*. 2015), while *Romagnesiella*, typified by *Galerina clavus*, may be differentiated by a dry, non-hygrophanous pileus (Matheny *et al.* 2015).

The phylogenetic analysis based on ITS sequences (Fig. 2) showed that *Stagnicola perplexa* collections from Europe and from North America form slightly different subclades, but, in the multigene analysis (Fig. 1), these small differences are no longer perceptible.

DISCUSSION

In the field, *Mythicomyces corneipes* and *Stagnicola perplexa* can be easily confused due to a series of shared characters such as a similar habit, absence of veils, pale-coloured lamellae, pale spore deposit, a tapering corneus-rigid stipe, gradually blackening from base upward and with a tawny basal mycelium and occurrence in the same habitats. Microscopically, however, *Mythicomyces* can be easily distinguished by the minutely roughened, verrucose spores and the presence of thick-walled, encrusted hymenial cystidia.

The presence in both *Agaricus corneipes* and *Phaeocollybia perplexa* of this unusual combination of characters, which is anomalous in dark-spored agarics, caused uncertainty as to their intergeneric relationships and family placement, which remained controversial and debated (Redhead & Smith 1986, Huhtinen & Vauras 1992) until the application of molecular techniques. However, while the molecular works provided a definitive answer regarding both the validity and independence of these two genera within the dark-spored agarics (Gulden *et al*. 2005) and their sister relationships (Moncalvo *et al*. 2002, Padamsee *et al*. 2008, Broussal & Dumesny 2015), the data on their definitive family placement have remained inconclusive, because of the poor taxon sampling and the few sequences available for these two taxa, for *S. perplexa* in particular.

Our analysis, which includes seven new *Stagnicola* collections with four molecular markers, clearly indicates that, in agreement with previous works (Moncalvo *et al*. 2002, Padamsee *et al*. 2008, Broussal & Dumesny 2015), the two genera are sister (with high support, BPP = 1, MLBP = 87%) to the *Psathyrellaceae*. The family *Psathyrellaceae* includes all the taxa formerly treated under the name *Coprinaceae*, but with the exclusion of *Coprinus comatus* (type of the genus) and allied species, which were found to be more closely related to *Agaricaceae* (Redhead *et al*. 2001). They have a saprotrophic nutritional mode or, rarely, parasite other agarics (e.g. *Psathyrella epimyces*) and are characterized by a dark brown, purplish brown to black spore deposit, non-cyanophilous thick-walled spores, usually with a distinct germ-pore and, in the psathyrelloid taxa, with pigment in the walls bleaching in concentrated sulfuric acid, without iodine reactions, hymenial cystidia often present, sterile pseudoparaphyses surrounding the basidia present in the coprinoid taxa, a non-radicating, fleshy, fibrous, non-corneous stipe, lamellae deliquescing in the coprinoid genera [ability to digest themselves by means of autodigestive chitinases (Kües 2000)], pileipellis a cutis or more commonly an ephitelium/hymeniderm, often covered with velar structures (Singer 1986, as *Coprinaceae*, Redhead *et al*. 2001, Noordeloos 2005, as *Coprinaceae partim*; Knudsen & Vesterholt 2012).

There is an evident morphological hiatus between *Mythicomyces*/*Stagnicola* with their pale- coloured spores without germ-pore, corneous, tapering stipe and absence of veils, pileipellis as a thin ixocutis, and the members of the *Psathyrellaceae*. No genus within the coprinoid taxa *Coprinellus*, *Coprinopsis*, *Parasola* (Redhead *et al*. 2001, Nagy *et al*. 2009, 2010, 2011, 2012, 2013a, b) as well as in the polyphyletic

Fig. 4. Macro- and micromorphological features of *Simocybe parvispora*. **A.** Basidiomata in the field (AH 25260, holotype). **B.** Basidiomata in the field (AH 25282, paratype). **C.** Spores (AH 25282). **D.** Mono- and tetrasporic basidia (AH 25282). **E.** Cheilocystidia (AH 25282). **F.** Pileipellis (AH 25282). **G.** Caulocystidia (AH 25282). **H.** Caulocystidia (AH 25282). C–H in ammoniacal Congo red. Scale bars: A, B = 10 mm; C–H = 10 µm. Photographs: A, B, Fernando Esteve-Raventós; C–H, Mauro Marchetti.

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Psathyrella s.l. (Kits van Waveren 1985), including the recently segregated genera *Homophron*, *Kauffmania*, *Typhrasa* (Örstadius & Knudsen 2012, Örstadius *et al*. 2015), shows clear morphological affinities with *Mythicomyces* and *Stagnicola*.

It stands to reason that forcing the two genera into *Psathyrellaceae s.l.,* as proposed by Gulden 2012a, b, Strittmatter & Obenauer 2013, Prydiuk 2015, 2018), makes this family heterogeneous and non-natural, hence the necessity to establish the new family, *Mythicomycetaceae* proposed in this paper.

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REFERENCES

Aime MC, Vilgalys R, Miller OK (2005). The *Crepidotaceae* (*Basidiomycota*, *Agaricales*): phylogeny and taxonomy of the genera and revision of the family based on molecular evidence. *American Journal of Botany* **92**: 74–82.

Altschul SF, Gish W, Miller W, *et al.* (1990). Basic local alignment search tool. *Journal of Molecular Biology* **215**: 403–410.

Bandala VM, Esteve-Raventós F, Montoya L (2008). Two remarkable brown-spored agarics from Spain: *Simocybe parvispora sp. nov.* and *Crepidotus ibericus comb. nov. Sydowia* **60**: 181–196.

Begerow D, McTaggart A, Agerer R (2018). *Syllabus of Plant Families. Part 1/3. Basidiomycota and Entorrhizomycota*. Borntraeger Science Publishers, Stuttgart, Germany.

Binder M, Larsson KH, Matheny PB, *et al*. (2010). *Amylocorticiales* ord. nov. and *Jaapiales ord. nov.*: early diverging clades of agaricomycetidae dominated by corticioid forms. *Mycologia* **201**: 865–888.

Bon M (1992). Clé monographique des espèces galéro-naucorioides. *Documents Mycologiques* **21**: 1–89.

Broussal M, Dumesny E (2015). Une récolte française de *Stagnicola perplexa*. *Bulletin de la Société Mycologique de France* **131**: 237–243.

Castellano MA, Cázares E, Fondrick B, *et al*. (2003). *Handbook to Additional Fungal Species of Special Concern in the Northwest Forest Plan. General Technical Report PNW-GTR-572. Part 7: Species Gyromitra montana* to *Phaeocollybia fallax* (PDF) (Report). United States Department of Agriculture, Forest Service: S3–81.

Clémençon H (1972). Zwei verbesserte Präparierlösungen für die microskopische Untersuchung von Pilze. *Zeitschrift für Pilzkunde* **38**: 49–53.

Coimbra VRM (2015). Checklist of Central and South American *Agaricales* (*Basidiomycota*) II: *Strophariaceae*. *Mycosphere* **6**: 441–458.

Cubeta MA, Echandi E, Abernethy T, *et al.* (1991). Characterization of anastomosis groups of binucleate *Rhizoctonia* species using restriction analysis of an amplified ribosomal RNA gene. *Phytopathology* **81**: 1395–1400.

de Haan A, Walleyn R (2009). Studies in *Galerina*. *Galerinae Flandriae* (3). *Fungi non Delineati* **46**: 1–84.

Dentinger BTM, Gaya E, O'Brien H, *et al.* (2016). Tales from the crypt: genome mining from fungarium specimens improves resolution of the mushroom tree of life. *Biological Journal of the Linnean Society* **117**: 11–32.

Fannechére G (2011). *Mycomètre, logiciel d'aide à la mesure et de traitement statistique*. http://mycolim.free.fr/DOC_SML/mycm202/Charg_Mycm202.htm

Fries EM (1861). Hymenomycetes novi vel minus cogniti, in Suecia 1852–1860 observati. *Öfversigt af Kongliga Vetenskaps-Akademiens förhandlingar* **18**: 19–34.

Fries EM (1863). *Monographia Hymenomycetum Sueciae* 2: [147]–355. CA Leffler, Uppsala, Sweden.

Fries EM (1878). *Icones selectae Hymenomycetum nondum delineatorum / sub auspiciis Regiae Academiae Scientiarum Holmiensis editae ab Elia Fries; Volumen secundum, Fasc. II-III.* Typographia centralis & Ed. Berling, Holmiae et Upsaliae, Sweden.

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.

Garnica S, Weiss M, Walther G, *et al.* (2007). Reconstructing the evolution of agarics from nuclear gene sequences and basidiospore ultrastructure. *Mycological Research* **9**: 1019–1029.

Gerhardt E (1996). Taxonomische revision der Gattungen *Panaeolus* und *Panaeolina* (*Fungi*, *Agaricales*, *Coprinaceae). Bibliotheca Botanica* **147**: 1–150.

Gminder A, Saar G (2012). Ergänzungen zur Großpilzflora von Baden-Württemberg. *Andrias* **19**: 185–223.

Gross G (1972). Kernzahl und sporenvolumen bei einigen Hymenogasterarten. *Zeitschrift für Pilzkunde* **38**: 109–158.

Gulden G, Stensrud O, Shalchian-Tabrizi K, *et al.* (2005). *Galerina* Earle: A polyphyletic genus in the consortium of dark-spored agarics. *Mycologia* **97**(4): 823–837.

Gulden G (2008a). *Mythicomyces* Redhead & A.H. Sm. In: *Funga Nordica. Agaricoid, boletoid and cyphelloid genera* (Knudsen H, Vesterholt J, eds). Nordsvamp, Copenhagen, Denmark: 907.

Gulden G (2008b). *Stagnicola* Redhead & A.H. Sm. In: *Funga Nordica. Agaricoid, boletoid and cyphelloid genera* (Knudsen H, Vesterholt J, eds). Nordsvamp, Copenhagen, Denmark: 910.

Gulden G (2012a). *Mythicomyces* Redhead & A.H. Sm. In: *Funga Nordica. Agaricoid, boletoid, clavarioid, cyphelloid and gastroid genera* (Knudsen H, Vesterholt J, eds). 2nd edn. Nordsvamp, Copenhagen, Denmark: 688.

Gulden G (2012b). *Stagnicola* Redhead & A.H. Sm. In: *Funga Nordica. Agaricoid, boletoid, clavarioid, cyphelloid and gastroid genera* (Knudsen H, Vesterholt J, eds). 2nd edn. Nordsvamp, Copenhagen, Denmark: 728.

Gulden G (2012c). *Galerina* Earle. In: *Funga Nordica. Agaricoid, boletoid, clavarioid, cyphelloid and gastroid genera* (Knudsen H, Vesterholt J, eds). 2nd edn. Nordsvamp, Copenhagen, Denmark: 886–903.

Guzmán G, Pérez-Patraca AM (1972). Las especies conocidas del género *Panaeolus* en México. *Boletín de la Sociedad Mexicana de Micologia* **6**: 17–53.

Guzmán G (1983). The genus *Psilocybe*. A systematic revision of the known species including the history, distribution and chemistry of the hallucinogenic species. *Beihefte Nova Hedwigia* **74**: 1–439.

Jeffreys JG (1830). A synopsis on the testaceous pneumonobranchous Mollusca of Great Britain. *Transactions of the Linnean Society of London* **16**: 323–392.

Halbwachs H, Brandl R, Bässler C (2015). Spore wall traits of ectomycorrhizal and saprotrophic agarics may mirror their distinct lifestyles. *Fungal Ecology* **17**: 197–204.

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Heim R (1931). *Le genre Inocybe: Précédé d'une introduction générale à l'étude des agarics ochrosporés*. Paul Lechevalier & Fils, Paris, France.

Hibbett DS (1996). Phylogenetic evidence for horizontal transmission of group I introns in the nuclear ribosomal DNA of mushroom-forming fungi. *Molecular Biology and Evolution* **13**: 903–917.

Horak E (1977). Further additions towards a monograph of *Phaeocollybia*. *Sydowia* **29**: 28–70.

Horak E (2005). *Röhrlinge und Blätterpilze in Europa*. Elsevier GmbH, Spectrum Akademischer Verlag, München, Germany.

Horak E, Ronikier A (2011). *Simocybe montana* (*Crepidotaceae*, *Agaricales*), a new species from the alpine belt in the Swiss Alps and the Romanian Carpathians. *Mycological Progress* **10**: 439–443.

Huhtinen S, Vauras J (1992). *Mythicomyces corneipes*, a rare agaric, in Fennoscandia. *Karstenia* **32**: 7–12.

Karsten PA (1879). Rysslands, Finlands och den Skandinaviska halföns Hattsvampar. Förra Delen: Skifsvampar. *Bidrag till Kännedom av Finlands Natur och Folk* **32**: 1–571.

Kits van Waveren E (1985). The Dutch, French and British species of *Psathyrella*. *Persoonia* Suppl. **2**: 1–300.

Knudsen H, Vesterholt J (eds) (2012). *Psathyrellaceae* Redhead, Vilgalys & Hopple. In: *Funga Nordica. Agaricoid, boletoid, clavarioid, cyphelloid and gastroid genera*. 2nd edn. Nordsvamp, Copenhagen, Denmark: 661–728.

Kohler A, Kuo A, Nagy LG, *et al.* (2015). Convergent losses of decay mechanisms and rapid turnover of symbiosis genes in mycorrhizal mutualists. *Nature Genetics* **47**: 410–415.

Kües U (2000). Life history and developmental processes in the basidiomycete *Coprinus cinereus*. *Microbiology and Molecular Biology Reviews* **64**: 316–353.

Kühner R (1980). Les Hyménomycètes agaricoïdes (*Agaricales*, *Tricholomatales*, *Pluteales*, *Russulales*). Etude générale et classification. *Bulletin mensuel de la Société linnéenne de Lyon* **49** Numero special: 1–1027.

Kühner R (1984). Some mainlines of classification in the gill fungi. *Mycologia* **76**: 1059–1074.

Laber D (1982). Die europäischen Arten der Gattung *Phaeocollybia* (Wurzelschnitzlinge) und ihr Vorkommen in südliches Schwarzwald. *Zeitschrift für Mykologie* **48**: 89–98.

Laber D (1991). Erganzung zu 'Die europäischen Arten der Gattung *Phaeocollybia* und ihr Vorkommen in südliches Schwarzwald.' *Zeitschrift für Mykologie* **57**: 109–116.

Laber D, Marklund H (1992). *Stagnicola perplexa* (Orton) Redhead & Smith = *Agaricus cidaris* var. *minor* Fries, eine sehr seltene Art in Europa? *Zeitschrift für Mykologie* **58**: 53–56.

Liu YJ, Whelen S, Hall BD (1999). Phylogenetic relationships among *Ascomycetes*: evidence from an RNA Polymerase II Subunit. *Molecular Biology and Evolution* **16**: 1799–1808.

Ludwig E (2001a). *Pilzkompendium Band 1: Beschreibungen*. IHW Verlag, Eching, Germany.

Ludwig E (2001b). *Pilzkompendium Band 1: Abbildulgen*. IHW Verlag, Eching, Germany.

Manic S (2015). *Macromicetele din ecosistemele Republicii Moldova (taxonomie, bioecologie, corologie)*. PhD Dissertation, Biological Sciences, Academia de Ştiinţe a Moldovei Grădina Botanică (Institut), Chişinău, Moldova.

Matheny PB, Curtis JM, Hofstetter V, *et al.* (2006). Major clades of *Agaricales*: a multilocus phylogenetic overview. *Mycologia* **98**: 982–995.

Matheny PB, Griffith JW (2010). Mycoparasitism between *Squamanita paradoxa* and *Cystoderma amianthinum* (*Cystodermateae*, *Agaricales*). *Mycoscience* **51**: 456–461.

Matheny PB, Wang Z, Binder M, *et al*. (2007a). Contributions of rpb2 and tef1 to the phylogeny of mushrooms and allies (*Basidiomycota*, Fungi). *Molecular Phylogenetics and Evolution* **43**: 430–451.

Matheny P B, Vellinga EC, Bougher N, *et al*. (2007b). Taxonomy of displaced species of *Tubaria*. *Mycologia* **99**: 569–585.

Matheny PB, Moreau PA, Vizzini A, *et al.* (2015). *Crassisporium* and *Romagnesiella*: two new genera of dark-spored *Agaricales*. *Systematics and Biodiversity* **13**: 28–41.

Meerts P (1999). The evolution of spores in agarics: do big mushrooms have big spores? *Journal of Evolutionary Biology* **12**: 161–165.

Miller MA, Pfeiffer W, Schwartz T (2010). Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 November 2010, New Orleans, LA: 1–8.

Moncalvo JM, Vilgalys R, Redhead SA, *et al.* (2002). One hundred and seventeen clades of euagarics. *Molecular Phylogenetics and Evolution* **23**: 357–400.

Morgan AP (1907). North American species of *Agaricaceae*. *The Journal of Mycology* **13**: 246–255.

Moser M, Jülich W (1987). *Farbatlas der Basidiomyceten. 3*. Gustav Fischer, Stuttgart, Germany.

Murray HG, Thompson WF (1980). Rapid isolation of high molecular weight DNA. *Nucleic Acids Research* **8**: 4321–4325.

Nagy LG, Kocsubé S, Papp T, *et al*. (2009). Phylogeny and character evolution of the coprinoid mushroom genus *Parasola* as inferred from LSU and ITS nrDNA sequence data. *Persoonia* **22**: 28–37.

Nagy GL, Urban A, Örstadius L, *et al*. (2010). The evolution of autodigestion in the mushroom family *Psathyrellaceae* (*Agaricales*) inferred from Maximum Likelihood and Bayesian methods. *Molecular Phylogenetics and Evolution* **57**: 1037–1048.

Nagy GL, Walther G, Házi J, *et al*. (2011). Understanding the evolutionary processes of fungal fruiting bodies: correlated evolution and divergence times in the *Psathyrellaceae*. *Systematic Biology* **60**: 303–331.

Nagy LG, Házi J, Vágvölgyi C, *et al*. (2012). Phylogeny and species delimitation in the genus *Coprinellus* with special emphasis on the haired species. *Mycologia* **104**: 254–275.

Nagy LG, Desjardin ED, Vágvölgyi C, *et al*. (2013a). Phylogenetic analyses of *Coprinopsis* section *Lanatuli* and *Atramentarii* identify multiple species within morphologically defined taxa. *Mycologia* **105**: 112–114.

Nagy LG, Vágvölgyi C, Papp T (2013b). Morphological characterization of clades of the *Psathyrellaceae* (*Agaricales*) inferred from a multigene phylogeny. *Mycological Progress* **12**: 505–517.

Niveiro N, Albertó EO (2012). Checklist of the Argentine *Agaricales* 2. *Coprinaceae* and *Strophariaceae*. *Mycotaxon* **120**: 505, http://dx.doi.org/10.5248/119.505.

Noordeloos ME (2005). *Coprinaceae* Overeem. In: *Flora Agaricina Neerlandica 6* (Noordeloos ME, Kuyper THW, Vellinga EC, eds). CRC Press, Taylor & Francis Group, Boca Raton, USA: 21.

Norvell LL (1998a). *The biology and taxonomy of Pacific Northwest species of Phaeocollybia Heim* (*Agaricales*, *Cortinariaceae*). Ph.D. dissertation (Dept. Botany), University of Washington, Seattle, USA.

Norvell LL (1998b). Observations on development, morphology and biology in *Phaeocollybia*. *Mycological Research* **102**: 615–630.

Norvell LL (2000). *Phaeocollybia* in Western North America 1: The *Phaeocollybia kauffmanii* complex. *Canadian Journal of Botany* **78**: 1055–1076.

Norvell LL (2004). *Phaeocollybia* in western North America 4: Two new species with tibiiform cheilocystidia and section *Versicolores* reconsidered. *Mycotaxon* **90**: 241–260.

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Norvell LL, Exeter RL (2008). *Phaeocollybia of Pacific Northwest North America*. United States Department of Interior Bureau of Land Management Salem District, Salem, USA.

Örstadius L, Knudsen H (2012). *Psathyrella* (Fr.) Quél. In: *Funga Nordica. Agaricoid, boletoid, cyphelloid and gasteroid genera* (Knudsen H, Vesterholt J, eds). 2nd edn. Nordsvamp, Copenhagen, Denmark: 692–728.

Örstadius L, Ryberg M, Larsson E (2015). Molecular phylogenetics and taxonomy in *Psathyrellaceae* (*Agaricales*) with focus on psathyrelloid species: introduction of three new genera and 18 new species. *Mycological Progress* **14**: 25.

Orton PD (1977). Notes on British Agarics: V. *Kew Bulletin* **31**: 709–721.

Padamsee M, Matheny PB, Dentinger BT, *et al.* (2008). The mushroom family *Psathyrellaceae*: evidence for large-scale polyphyly of the genus *Psathyrella*. *Molecular Phylogenetics and Evolution* **46**: 415–429.

Palamarchuk MA (2009). The xylotrophic agaricoid *Basidiomycetes* of Pechoro-Ilych reserve (North Urals). *Conifers of the Boreal Area* **26**: 67–72. (in Russian)

Prydiuk MP (2015). *Mythicomyces* (*Psathyrellaceae*), a new for Ukraine genus of mushrooms. *Ukrainian Botanical Journal* **72**: 55–60.

Prydiuk MP (2018). *Mushrooms of the families Bolbitiaceae and Psathyrellaceae of Ukraine: species composition, distribution, evolution*. Ph.D. dissertation for Doctor of Science degree in Biology (Dr. Sci. Biol.), specialty 03.00.21 – Mycology. M.G. Kholodny Institute of Botany of National Academy of Sciences of Ukraine, Kyiv, Ukraine.

Quélet L (1886). *Enchiridion fungorum in Europa media et prasertim in Gallia vigentium*. O. Doin, Paris, France.

Redhead SA, Malloch DW (1986). The genus *Phaeocollybia* (*Agaricales*) in eastern Canada and its biological status. *Canadian Journal of Botany* **64**: 1249–1254.

Redhead SA, Smith AH (1986). Two new genera of agarics based on *Psilocybe comeipes* and *Phaeocollybia perplexa*. *Canadian Journal of Botany* **64**: 643–647.

Redhead SA, Vilgalys R, Moncalvo JM, *et al.* (2001). *Coprinus* Persoon and the disposition of *Coprinus* species *sensu lato*. *Taxon* **50**: 203–241.

Redhead SA, Ammirati JF, Norvell LL, *et al.* (2011). Validation of combinations with basionyms published by Fries in 1861. *Mycotaxon* **118**: 455–458.

Romagnesi H (1962). Les *Naucoria* du groupe *Centunculus* (*Ramicola* Velen.). *Bulletin Trimestriel de la Société Mycologique de France* **78**: 337–358.

Saccardo PA (1887). *Sylloge Hymenomycetum*, Vol. I. *Agaricineae*. *Sylloge Fungorum* **5**: 1–1146.

Senn-Irlet B (1995). Die Gattung *Simocybe* Karsten in Europa. *Mycologia Helvetica* **7**: 27–61.

Singer R (1960). Sobre algunas especies de hongos presumiblemente psicotropicos. *Lilloa* **30**: 117–127.

Singer R (1969). Mycoflora australis. *Beihefte zur Nova Hedwigia* **29**: 1–405.

Singer R (1986). *The Agaricales in modern taxonomy*, 4th ed. Koeltz Scientific Books, Koenigstein, Germany.

Smith AH (1937). Unusual agarics from Michigan. IV. *Papers from the Michigan Academy of Science, Arts and Letters* **22**: 215–223.

Smith AH (1938). New and unusual Agarics from North America: I. *Mycologia* **30**: 20–41.

Smith AH (1949). *Mushrooms in their natural habitats*. Sawyer's Inc, Portland, USA.

Smith AH (1975). *A field guide to Western Mushrooms*. Univ. Mich. Press, Ann Arbor, USA.

Smith AH, Singer R (1964). *A Monograph of the Genus Galerina Earle*. Hafner Publishing, New York, USA.

Stålberg J (1991). *Mythicomyces corneipes* (Fr.) Redhead & Smith. Mystisk skivling identifierad. *Jordstjärnan* **12**: 64–67.

Stamatakis A (2006). RAxML-VI-HPC: maximum likelihood based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **22**: 2688–2690.

Stridvall A, Stridvall L (1996). Fynd av två för Sverige nya skivlingar *Russula rutila* Romagn. och *Stagnicola perplexa* (Orton) Redhead & Smith. *Jordstjärnan* **17**: 11–16.

Strittmatter E, Obenauer H (2013). Ein Fund des Hornstieligen Scheinschwefelkopfes *Mythicomyces corneipes* (Fr.) Redhead & A. H. Sm. in Südwestdeutschland. *Zeitschrift für Mykologie* **79**: 337–349.

Tamura K, Stecher G, Peterson D, *et al.* (2013). MEGA6: Molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution* **30**: 2725–2729.

Trudell SA, Rygiewicz PT, Edmonds RL (2004). Patterns of nitrogen and carbon stable isotope ratios in macrofungi, plants and soils in two old-growth conifer forests. *New Phytologist* **164**: 317–335.

Vilgalys R, Hester M (1990). Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* **172**: 4238–4246.

Volders J (2002). Het genus *Tubaria* in Vlaanderen en het Brussels Gewest. *Sterbeeckia* **21–22**: 3–28.

Watling R, Gregory NM (1993). *British Fungus Flora 7. Cortinariaceae pp*. Royal Botanic Garden, Edinburgh, UK.

Walther G, Garnica S, Weiss M (2005). The systematic relevance of conidiogenesis modes in the gilled *Agaricales*. *Mycological Research* **109**: 525–544.

White TJ, Bruns TD, Lee S, *et al.* (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: *PCR protocols: a guide to methods and applications* (Innis MA, Gelfand DH, Sninsky J, White TJ, eds). Academic Press, San Diego, USA: 315–322.

Wood AE (2001). Studies in the genus *Galerina* (*Agaricales*) in Australia. *Australian Systematic Botany* **14**: 615–676.

Zhao R-L, Li G-J, Sánchez-Ramírez S, *et al.* (2017). A six-gene phylogenetic overview of *Basidiomycota* and allied phyla with estimated divergence times of higher taxa and a phyloproteomics perspective. *Fungal Diversity* **84**: 43–74.

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