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Family matters inside the order *Agaricales*: systematic reorganization and classification of *incertae sedis* clitocyboid, pleurotoid and tricholomatoid taxa based on an updated 6-gene phylogeny

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Abstract: The phylogenetic position of several clitocyboid/pleurotoid/tricholomatoid genera previously considered *incertae sedis* is here resolved using an updated 6-gene dataset of *Agaricales* including newly sequenced lineages and more complete data from those already analyzed before. Results allowed to infer new phylogenetic relationships, and propose taxonomic novelties to accommodate them, including up to ten new families and a new suborder. *Giacomia* (for which a new species from China is here described) forms a monophyletic clade with *Melanoleuca* (*Melanoleucaceae*) nested inside suborder *Pluteineae*, together with the families *Pluteaceae*, *Amanitaceae* (including *Leucocortinarius*), *Limnoperdaceae* and *Volvariellaceae*. The recently described family *Asproinocybaceae* is shown to be a later synonym of *Lyophyllaceae* (which includes also *Omphaliaster* and *Trichocybe*) within suborder *Tricholomatineae*. The families *Biannulariaceae*, *Callistosporiaceae*, *Clitocybaceae*, *Fayodiaceae*, *Macrocystidiaceae* (which includes *Pseudoclitopilus*), *Entolomataceae*, *Pseudoclitocybaceae* (which includes *Aspropaxillus*), *Omphalinaceae* (*Infundibulicybe* and *Omphalina*) and the new families *Paralepistaceae* and *Pseudoomphalinaceae* belong also to *Tricholomatineae*. The delimitation of the suborder *Pleurotineae* (= *Schizophyllineae*) is discussed and revised, accepting five distinct families within it, *viz. Pleurotaceae*, *Cyphellopsidaceae*, *Fistulinaceae*, *Resupinataceae* and *Schizophyllaceae*. The recently proposed suborder *Phyllotopsidineae* (= *Sarcomyxineae*) is found to encompass the families *Aphroditeolaceae*, *Pterulaceae*, *Phyllotopsidaceae*, *Radulomycetaceae*, *Sarcomyxaceae* (which includes *Tectella*), and *Stephanosporaceae*, all of them unrelated to *Pleurotaceae* (suborder *Pleurotineae*) or *Typhulaceae* (suborder *Typhulineae*). The new family *Xeromphalinaceae*, encompassing the genera *Xeromphalina* and *Heimiomyces*, is proposed within *Marasmiineae*. The suborder *Hygrophorineae* is here reorganized into the families *Hygrophoraceae*, *Cantharellulaceae*, *Cuphophyllaceae*, *Hygrocybaceae* and *Lichenomphaliaceae*, to homogenize the taxonomic rank of the main clades inside all suborders of *Agaricales*. Finally, the genus *Hygrophorocybe* is shown to represent a distinct clade inside *Cuphophyllaceae*, and the new combination *H. carolinensis* is proposed.

Key words: *Agaricales*, *Agaricanae*, *incertae sedis* taxa, multi-locus, new taxa, phylogeny, taxonomy.

Taxonomic novelties: New suborder: *Typhulineae* Vizzini, Consiglio & P. Alvarado. **New families:** *Aphroditeolaceae* Vizzini, Consiglio & P. Alvarado, *Melanoleucaceae* Locq. *ex* Vizzini, Consiglio & P. Alvarado, *Paralepistaceae* Vizzini, Consiglio & P. Alvarado, *Pseudoomphalinaceae* Vizzini, Consiglio & P. Alvarado, *Volvariellaceae* Vizzini, Consiglio & P. Alvarado, *Xeromphalinaceae* Vizzini, Consiglio & P. Alvarado. **New species:** *Giacomia sinensis* J.Z. Xu. ***Stat. nov.*****:** *Cantharellulaceae* (Lodge, Redhead, Norvell & Desjardin) Vizzini, Consiglio & P. Alvarado, *Cuphophyllaceae* (Z.M. He & Zhu L. Yang) Vizzini, Consiglio & P. Alvarado, *Hygrocybaceae* (Padamsee & Lodge) Vizzini, Consiglio & P. Alvarado, *Lichenomphaliaceae* (Lücking & Redhead) Vizzini, Consiglio & P. Alvarado. **New combination:** *Hygrophorocybe carolinensis* (H.E. Bigelow & Hesler) Vizzini, Consiglio & P. Alvarado. **New synonyms:** *Sarcomyxineae* Zhu L. Yang & G.S. Wang, *Schizophyllineae* Aime, Dentinger & Gaya, *Asproinocybaceae* T. Bau & G.F. Mou. ***Incertae sedis* taxa placed at family level:** *Aphroditeola* Redhead & Manfr. Binder, *Giacomia* Vizzini & Contu, *Hygrophorocybe* Vizzini & Contu, *Leucocortinarius* (J.E. Lange) Singer, *Omphaliaster* Lamoure, *Pseudoclitopilus* Vizzini & Contu, *Resupinatus* Nees ex Gray, *Tectella* Earle, *Trichocybe* Vizzini. ***New delimitations of taxa*****:** *Hygrophorineae* Aime, Dentinger & Gaya, *Phyllotopsidineae* Zhu L. Yang & G.S. Wang, *Pleurotineae* Aime, Dentinger & Gaya, *Pluteineae* Aime, Dentinger & Gaya, *Tricholomatineae* Aime, Dentinger & Gaya. ***Resurrected taxa*****:** *Fayodiaceae* Jülich, *Resupinataceae* Jülich.

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INTRODUCTION

Tricholomatineae is one of the suborders in which order *Agaricales* is currently divided. It names a lineage whose monophyletic status is significantly supported by phylogenomic and multilocus phylogenetic analyses (Dentinger *et al*. 2016, Zhao *et al*. 2017, Varga *et al*. 2019, Ke *et al*. 2020, Olariaga *et al*. 2020, Sánchez-García *et al*. 2020, Wang *et al*. 2023b). This suborder corresponds to the Tricholomatoid clade as delimited by Binder *et al*. (2010), which was also detected before them by other authors (Moncalvo *et al*. 2002, Matheny *et al*. 2006, Garnica *et al*. 2007). It currently contains about thirty genera, including ectomycorrhizal and non-ectomycorrhizal groups (Sánchez-García *et al*. 2014, Sánchez-García 2016). In addition to the *Tricholomataceae* (Sánchez-García *et al*. 2014), it currently encompasses another 10 families: *Asproinocybaceae* (Bau & Mou 2021), *Biannulariaceae* (Vizzini *et al*. 2020a), *Callistosporiaceae* (Vizzini *et al*. 2020a), *Clitocybaceae* (Alvarado *et al*. 2015, Vizzini *et al*. 2020b), *Entolomataceae* (Kluting *et al*. 2014), *Fayodiaceae* (Moncalvo *et al*. 2002), *Lyophyllaceae*

(Hofstetter *et al*. 2014, Bellanger *et al*. 2015), *Macrocystidiaceae* (Dentinger *et al*. 2016), *Omphalinaceae* (Vizzini *et al*. 2020b), and *Pseudoclitocybaceae* (Alvarado *et al*. 2018a).

Still, many white-spored clitocyboid and tricholomatoid-looking genera cannot be easily classified within any of these families, and even their position inside suborder *Tricholomatineae* cannot be confirmed with phylogenetic analyses because of the incomplete data available from some of them (mostly ribosomal DNA sequences). For example, the classification of *Asproinocybe*, *Aspropaxillus*, *Dendrocollybia*, *Giacomia*, *Hertzogia*, *Hygrophorocybe*, *Infundibulicybe*, *Lepistella*, *Leucocortinarius*, *Notholepista*, *Omphaliaster*, *Omphalina*, *Paralepista*, *Paralepistopsis*, *Pseudoclitopilus*, *Pseudoomphalina*, *Resupinatus*, *Rimbachia*, *Ripartites*, *Trichocybe* or *Tricholosporum* is not fully clear (Vizzini *et al*. 2010, 2012a, b, 2020, Hofstetter *et al*. 2014, Sánchez-García *et al*. 2014, 2016, 2017, Vizzini 2014a, Angelini *et al*. 2017, Alvarado *et al*. 2018a, b, He *et al*. 2019, Raj *et al*. 2019, Varga *et al*. 2019, Kalichman *et al*. 2020, Olariaga *et al*. 2020, He & Yang 2022, Wiest 2022).

The classification of these *incertae sedis* lineages requires the reconstruction of the phylogeny of the entire order *Agaricales*. DNA-based studies of the evolutionary history and taxonomy of *Agaricales* can be classified in different stages, depending on the scope and the sources of information employed:

Early works: the first sequence-based phylogenetic analyses of fungi were not specifically focused on the internal structure of *Agaricales*, but instead addressed fungal classification at higher ranks and/or investigated the origin of specific morphological types (Swann & Taylor 1993, 1995a, b, Gargas *et al*. 1995, Hibbett *et al*. 1997, Bruns *et al*. 1998, Pine *et al*. 1999, Thorn *et al*. 2000, Hibbett & Donoghue 2001, Hibbett & Thorn 2001, Binder & Hibbett 2002, Hibbett & Binder 2002). These works were based on too scarce information, often coming from a single ribosomal DNA (rDNA) gene region obtained from distant and highly diverse groups.

Mainly LSU-based works: the internal structure of order *Agaricales* was specifically addressed at first employing sequences of nuclear rDNA, typically the 28S or large subunit (LSU). These works (Moncalvo *et al*. 2000, 2002, Bodensteiner *et al*. 2004, Binder *et al*. 2005, 2006, Walther *et al*. 2005) successfully obtained significant support for multiple clades inside *Agaricales*, helping to delimit the phylogenetic concept of classical families. However, the relationships between these families were rarely resolved with this approach, and sometimes results varied if different datasets were employed.

Multigene works: the addition of more information coming from protein-coding genes greatly improved the outcome of phylogenetic analyses of *Agaricales*. A relationship between the amount of information and the significance of results seems plausible. For example, the use of LSU, SSU (the 18S nrDNA or small subunit), *RPB1* (DNA-directed RNA polymerase II, largest subunit) and *RPB2* (DNA-directed RNA polymerase II, second largest subunit) (Matheny *et al*. 2006) allowed to produce a seminal reconstruction of the structure of *Agaricales*, obtaining statistical support for multiple major clades (now suborders). However, a more limited analysis using only LSU and *RPB1* (Garnica *et al*. 2007) led to good support values for most suborders, excepting *Tricholomatineae* and *Marasmiineae*, while *Hygrophorineae* could not be separated from the pteruloid lineages. The analysis of additional information, coming from LSU, SSU, *RPB1*, *RPB2* and *TEF1* (translation elongation factor 1-alpha) sequences (Matheny *et al*. 2007) suggested some changes to the previous results (*i.e.*, in the position of *Pluteus* and *Amanita*) but the new dataset also contained a different selection of taxa. A too diverse dataset could be the cause behind the lack of support of most suborders of *Agaricales* in the analysis of Binder *et al*. (2010), a work focused on the closely related order *Amylocorticiales* which included also sequences of *Boletales*, *Atheliales* and *Jaapiales*, as well as other orders as outgroups. The phylogenies in Zhao *et al*. (2017) and He *et al*. (2019) used even larger datasets containing all lineages of *Basidiomycotina* and some *Ascomycotina*, and both failed to obtain significant support for most suborders and families of *Agaricales*. On the other hand, Olariaga *et al*. (2020) employed a dataset filling an important gap in the diversity of this order, that of typhuloid fungi, obtaining good support for most suborders, but missed important lineages from some of them (*i.e.*, *Giacomia*, *Hohenbuehelia*, *Limacella*, *Mycena*, *Resupinatus*, *Volvariella*). The most recent study of *Agaricales* following the multigene phylogenetic approach is that of Sheikh *et al*. (2022), which analyzed a large dataset of LSU, SSU, *RPB1* and *RPB2* sequences of multiple species of *Ascomycotina*, *Basidiomycotina* and *Mucoromycotina*. While support values cannot be directly checked in the published figures, the position of several clades does not fit with that in previous works, *i.e.*, *Amanitaceae* (nested in *Agaricineae*), *Hypsizygus* (nested in *Pluteineae*), *Cantharocybe* and *Tricholomopsis* (nested in *Pleurotineae*), *Sarcomyxaceae* (sister to *Hygrophorineae*), or *Typhulaceae* and *Phyllotopsidineae* (related and sister to *Marasmiineae*).

Phylogenomic works: Next generation sequencing (NGS) of entire genomes provides a much larger amount of information than Sanger sequencing of individual target regions. The first attempts to build a genome database of fungi (Grigoriev *et al*. 2014) were followed by the first phylogenomic analysis of *Agaricales* (Dentinger *et al*. 2016), that employed 208 different loci. The result was the proposal of a new taxonomic arrangement dividing *Agaricales* into seven distinct suborders, which matched more or less the clades found in previous phylogenetic studies based on 5–6 loci. Later, Ke *et al*. (2020) incorporated additional information from genomes produced by multiple researchers, as well as those of five bioluminiscent species of *Mycenaceae* obtained by them. After the analysis of 360 loci, they produced a phylogeny consistent with that of Dentinger *et al*. (2016), but unfortunately important clades were not included (*i.e.*, *Hygrophorineae*, *Clavariineae*, *Phyllotopsidineae*, *Tricholomatineae*). Li *et al*. (2021) built a phylogeny of the kingdom *Fungi* based on sequences of 290 loci obtained from genomic data of 1 679 taxa (89 *Agaricales*), obtaining significant support for the suborders *Agaricineae*, *Pluteineae* and *Tricholomatineae*, but apparently merging *Hygrophorineae* and the family *Clavariaceae*, as well as *Pleurotineae* and *Pterulaceae*. Recently, Wang *et al*. (2023b) further improved the resolution of phylogenomic studies by sequencing 38 new genomes, from which 555 genes were compared with those of the other sequenced *Agaricales*. As a result, ten suborders were recognized (after separating *Phyllotopsidineae* and *Sarcomyxineae* from *Pleurotineae*), but some families did not nest inside any of them (*i.e.*, *Mycenaceae* and *Typhulaceae*).

In the present study, new sequences from some of the aforementioned *incertae sedis* taxa (Tables 1–3, S1, Figs 6–8) were produced in order to resolve their most probable phylogenetic position after the analysis of an updated 6-gene dataset of *Agaricales*. Additional sequences from other clades were produced as well to create a representative background for phylogenetic analysis. Results are compared with those published in previous works and different taxonomic decisions are taken accordingly.

Table 1. Taxa, vouchers, and GenBank accessions numbers of the DNA sequences used in the *Agaricales*-wide phylogenetic analysis inferred from a six-gene dataset (5.8S, LSU, SSU, *RPB1*, *RPB2* and *TEF1*). Sequences in bold were generated in this study.

Group	Species	Voucher	LSU	*RPB2*	SSU	*TEF1*	ITS	*RPB1*
Agaricineae	*Agaricus bisporus*	AFTOL-ID 448, RWK1885	AY635775	genome	AY787216	GU187673	DQ404388	—
	Apioperdon pyriforme	AFTOL-ID 480, DSH 96-054	AF287873	AY218495	AF026619	AY883426	AY854075	AY860523
	Bolbitius vitellinus	AFTOL-ID 730, MTS5020	AY691807	—	AY705955	DQ408148	DQ200920	DQ435802
	Conocybe lactea	AFTOL-ID 1675, CUW:PBM2706 + NL1012	DQ457660	DQ470834	DQ437683	JX968427	DQ486693	DQ447893
	Coprinopsis cinereus	A43mut B43mut pab1-1 #326	AF041494	genome	genome	genome	genome	genome
	Coprinus comatus	AFTOL-ID 626, ECV3198	AY635772	AY780934	AY665772	AY881026	AY854066	AY857983
	Cortinarius iodes	AFTOL-ID 285, PBM2426	AY702013	AY536285	AY771605	AY881027	AF389133	AY857984
	Crepidotus cf. *applanatus*	WTU:PBM717	AY380406	AY333311	AY705951	DQ028581	DQ202273	AY333303
	Crucibulum laeve	CBS:166.37	MH867376	genome	genome	genome	genome	genome
	Cyathus striatus	NPCB87405	genome	genome	genome	genome	genome	genome
	Cystoderma amianthinum	HKAS:107327 + AFTOL-ID 1553	MW258914	MW289806	DQ440632	MW324496	MW258862	MW289817
	Echinoderma flavidoasperum	KUN-HKAS:87905	MN810098	MN820969	—	MN820903	MN810147	—
	Floccularia luteovirens	FLZJUC10	genome	genome	genome	genome	genome	genome
	Hebeloma velutipes	AFTOL-ID 980, PBM2277	AY745703	DQ472718	AY752972	GU187707	AY818351	DQ447904
	Hydnangium carneum	Trappe31123	KU685892	KU686038	—	KU686144	KU685741	—
	Inocybe myriadophylla	AFTOL-ID 482, V19652F	AY700196	AY803751	AY657016	DQ435791	DQ221106	DQ447916
	Laccaria bicolor	S238N-H82	genome	XM001873347	genome	XM001873179	JX312964	XM001881359
	Macrolepiota dolichaula	AFTOL-ID 481, HKAS:38718	DQ411537	DQ385886	AY771602	DQ435785	DQ221111	DQ447920
	Mythicomyces corneipes	AFTOL-ID 972, PBM1210	AY745707	DQ408110	DQ092917	DQ029197	DQ404393	DQ447929
	Parasola conopilea	ZRL20151990 + LO186-02	DQ389725	KY419025	KY418946	KJ732832	LT716064	—
	Pholiota gummosa	TENN:074768, HMJAU:37426, ET34-ET8	MN251152	MN329726	—	MN311973	MN209769	—
	Romagnesiella clavus	AMB:15091, ALV16952 + LIP:PAM06090110	MK353795	MK359092	MK353799	—	EF051060	—
	Squamanita schreieri	ZT:Myc2185	MW258904	MW289801	MW258882, MW258931	MW324510	MW258852	—
	Tubaria confragosa	AFTOL-ID 498, PBM2105	AY700190	DQ408113	AY665776	—	DQ267126	DQ447944
Clavariineae	*Camarophyllopsis hymenocephala*	AFTOL-ID 1892, DJL98-081505	DQ457679	DQ472726	DQ444862	—	DQ484066	DQ516070
	Ceratellopsis acuminata	CBS:146691 + S.Huhtinen 15/07 - EPITYPE	NG_075348	MT242330	NG_070864	MT242352	MT232347	MT242316
	Clavaria inaequalis	AFTOL-ID 984, CUW:MB04-016	AY745693	DQ385880	DQ437680	DQ029198	DQ202267	DQ447890

Table 1. (Continued).

Group	Species	Voucher	LSU	*RPB2*	SSU	*TEF1*	ITS	*RPB1*
	Clavaria zollingeri	AFTOL-ID 563, TENN:58652	AY639882	AY780940	AY657008	AY881024	AY854071	AH014578
	Ramariopsis kunzei	GG141104	EF561638	GU187807	GU187647	GU187745	GU187552	GU187479
Hygrophorineae	*Ampulloclitocybe clavipes*	AFTOL-ID 542, PBM2474	AY639881	AY780937	AY771612	AY881022	AY789080	AY788848
	Cantharocybe gruberi	AFTOL-ID 1017	DQ234540	DQ385879	DQ234546	DQ059045	DQ200927	—
	Chromosera cyanophylla	AFTOL-ID 1684, WTU:PBM1577	DQ457655	KF381509	DQ435813	—	DQ486688	—
	Chrysomphalina grossula	OSC:113683	EU652373	DQ470832	AY752969	—	EU644704	DQ516072
	Cuphophyllus aurantius	CFMR:PR6601	KF291100	KF291102	KF291101	—	KF291099	—
	Cuphophyllus sp.	KUN-HKAS:105671, JSP346	MW763000	MW789179	—	—	MW762875	MW789163
	Gloioxanthomyces nitidus	GDGM:41710	MG712282	MG711911	—	—	MG712283	—
	Hygroaster albellus	AFTOL-ID 1997	EF551314	KF381510	KF381532	—	KF381521	—
	Hygrocybe coccinea	AFTOL-ID 1715, WTU:PBM915	DQ457676	DQ472723	—	GU187705	DQ490629	DQ447910
	Hygrophorocybe nivea	**LPA:SMGC2020121621**	**OR863514**	**OR828267**	**OR863576**	**OR828325**	**OR863446**	**—**
	Hygrophorus aurantiosquamosus	KUN-HKAS:112569	MW763001	MW789180	—	MW773440	MW762876	MW789164
	Hygrophorus pudorinus	AFTOL-ID 1723, CUW:PBM2721	DQ457678	DQ472725	DQ444861	GU187710	DQ490631	DQ447912
	Lichenomphalia umbellifera	CFMR:J.Geml2 + GAL9547	GU811045	KF381515	KF381538	GU811010	GU810969	—
	Neohygrocybe ingrata	TENN:DJL05TN62	KF381558	KF381516	KF381539	—	KF381525	—
	Neohygrocybe ovina	Rhosisaf ABS + K:M187568, GEDC0877	KF291234	KF291236	KF291230	—	KF291233	—
	Porpolomopsis aff. *calyptriformis*	TENN:DJL05TN80	KF291247	KF291249	KF291248	—	KF291246	—
	Porpolomopsis lewelliniae	CORT:TJB10034	KF291239	KF291241	KF291240	—	KF291238	—
	Pseudoarmillariella ectypoides	AFTOL-ID 1557, PBM1588	DQ154111	DQ474127	DQ465341	GU187733	DQ192175	DQ516076
	Spodocybe rugosiceps	KUN-HKAS:112563 - TYPE	MW763013	MW789192	—	MW789160	MW762888	MW789176
Marasmiineae	*Anthracophyllum archeri*	AFTOL-ID 973, PBM2201	AY745709	DQ385877	DQ092915	DQ028586	DQ404387	DQ435799
	Armillaria mellea	AFTOL-ID 449, PBM2470	AY700194	AY780938	AY787217	AY881023	AY789081	AY788849
	Baeospora myosura	AFTOL-ID 1799, CUW:PBM2748	DQ457648	—	DQ435796	GU187762	DQ484063	DQ435801
	Cheimonophyllum candidissimum	AFTOL-ID 1765, WTU:PBM2411	DQ457654	DQ470831	DQ435812	GU187760	DQ486687	DQ447888
	Dictyopanus pusillus	LMB36	genome	genome	genome	genome	genome	genome
	Favolaschia claudopus	**BBC-V 001 23/10/2022**	**OR863498**	**OR828255**	**OR863564**	**OR828316**	**OR863428**	—
	Flammulina velutipes	AFTOL-ID 558, TENN:52002	AY639883	AY786055	AY665781	AY883423	AY854073	AY858966
	Gymnopus contrarius	AFTOL-ID 1758, CUW:PBM2711	DQ457670	DQ472716	DQ440643	GU187700	DQ486708	DQ447902
	Heimiomyces* aff. *tenuipes	**McAdoo725**	**OR863508**	**OR828263**	**OR863572**	**OR828321**	**OR863439**	—
	Hemimycena lactea	**OULU:GAJ15636**	**OR863509**	**OR828264**	**OR863573**	**OR828322**	**OR863440**	—

Table 1. (Continued).

Group	Species	Voucher	LSU	*RPB2*	SSU	*TEF1*	ITS	*RPB1*
	Megacollybia platyphylla	AFTOL-ID 560, TENN:59432	AY635778	DQ385887	AY786053	DQ435786	DQ249275	DQ447923
	Mycena chlorophos	110903 Hualien Pintung	genome	genome	genome	genome	genome	genome
	Mycena citricolor	CBS:193.57	MH869233	genome	genome	genome	genome	genome
	Mycena galopus	ATCC:62051	genome	genome	genome	genome	genome	genome
	Mycena indigotica	171206 Taipei	genome	genome	genome	genome	genome	genome
	Mycena kentingensis	111111 Pintung	genome	genome	genome	genome	genome	genome
	Mycena sanguinolenta	160909 Yilan	genome	genome	genome	genome	genome	genome
	Mycetinis alliaceus	AFTOL-ID 556, TENN:55620	AY635776	AY786060	AY787214	AY883431	AY854076	—
	Panellus luminescens	KLU:M1278, ACL205	KJ206955	KJ406362	—	—	KJ206979	—
	Panellus stypticus	CORT:11CA052	KR869943	KC816996	—	KC816902	—	—
	Phloeomana gracilis	AFTOL-ID 1732, CUW:PBM2715	DQ457671	DQ472719	DQ440644	GU187709	DQ490623	DQ447905
	Porotheleum fimbriatum	AFTOL-ID 1725, CBS:788.86	DQ457673	DQ472721	DQ444854	—	DQ490626	DQ447907
	Rhodocollybia maculata	AFTOL-ID 540, PBM2481	AY639880	AY787220	AY752966	DQ061279	DQ404383	DQ447936
	Roridomyces sp.	KLU:M1292, ACL273	KJ206958	KJ406372	—	—	—	—
	Xeromphalina campanella	TENN:F069178 + GLM 46039	KM011910	KP835655	—	—	KP835678	DQ067940
	Xerula radicata	AFTOL-ID 561, TENN:59235	AY645051	AY786067	AY654884	DQ029194	DQ241780	DQ447946
Outgroup	*Amylocorticium cebennense*	CFMR:HHB-2808	GU187561	GU187770	GU187612	GU187675	GU187505	GU187439
	Ceraceomyces borealis	CFMR:L-8014	GU187570	GU187782	GU187624	GU187686	GU187512	—
	Suillus pictus	AFTOL-ID 717, MB 03-002	AY684154	AY786066	AY662659	AY883429	AY854069	AY858965
Phyllotopsidineae	*Aphanobasidium pseudotsugae*	CFMR:HHB-822	GU187567	GU187781	GU187620	GU187695	GU187509	GU187455
	***Aphroditeola* sp.**	**HRL1230**	**OR863490**	**OR828247**	**OR863558**	**OR828309**	**OR863420**	—
	***Aphroditeola* sp.**	**TRgmb00556**	**OR863491**	**OR828248**	**OR863559**	**OR828310**	**OR863421**	—
	***Aphroditeola* sp.**	**TRgmb00561**	**OR863492**	**OR828249**	**OR863560**	—	**OR863422**	—
	Cristinia sp.	CFMR:FP100305	GU187585	—	GU187637	GU187718	GU187526	GU187470
	Lindtneria flava	K:M143556	KM086909	—	—	KM087001	KM086815	—
	Macrotyphula fistulosa	S:IO.14.214, UPS:IO.14.214 + IO.15.123	KY224088	MT242336	MT232495	MT242354	MT232352	MT242317
	Macrotyphula juncea	IO.14.177	MT232306	MT242337	—	MT242355	MT232353	—
	Macrotyphula phacorrhiza	S:IO.14.200	MT232314	—	MT232505	MT242366	MT232363	—
	Phyllotopsis sp.	AFTOL-ID 773, MB35	AY684161	AY786061	AY707090	DQ059047	DQ404382	DQ447933
	Pleurocybella porrigens	UPS:F611822 + AFTOL-ID 2001, JFA12544 + TUB:012154	EF537894	MT242339	GU187660	GU187740	MT232355	DQ067994
	Pterula echo	AFTOL-ID 711, DJM302S58	AY458123	GU187805	DQ092911	GU187743	DQ494693	—

Table 1. (Continued).

Group	Species	Voucher	LSU	*RPB2*	SSU	*TEF1*	ITS	*RPB1*
	Pterula echo	ZRL20151311	KY418881	KY419026	KY418947	KY419076	LT716065	KY418979
	Pterula gracilis	S:IO.14.142	MT232310	—	MT232498	—	MT232356	—
	Radulomyces molaris	ARAN:Fungi2003	MT232311	MT242340	MT232499	MT242359	—	MT242320
	Sarcomyxa edulis	HMJAU:7066	GQ219739	genome	genome	genome	genome	genome
	Sarcomyxa serotina	AFTOL-ID 536, PBM2519	AY691887	DQ859892	U59088	GU187754	DQ494695	DQ447938
	Stephanospora caroticolor	IOC-137/97 + TUB:019072	AF518652	—	AF518591	GU187747	AJ419224	KF211335
	Tectella patellaris	**McAdoo991**	**OR863548**	**OR828299**	**OR863602**	**OR828350**	**OR863481**	—
	Tricholomopsis decora	AFTOL-ID 537, PBM2482	AY691888	DQ408112	DQ092914	DQ029195	DQ404384	DQ447943
	Tricholomopsis osiliensis	ZRL20151760	KY418884	KY419029	KY418949	KY419079	—	—
Pleurotineae	*Auriculariopsis ampla*	NL-1724	OL957174	genome	genome	genome	OL957174	—
	Fistulina antarctica	AFTOL-ID 1335, CBS:701.85	AY293181	DQ472713	AY293131	GU187698	DQ486702	—
	Flagelloscypha sp.	PMI 526	genome	genome	genome	genome	genome	genome
	Hohenbuehelia atrocoerulea	AMB:18080	KU355389	KU355418	—	KU355439	KU355304	—
	Hohenbuehelia faerberioides	Mertens	MG553645	MW240980	—	MW240984	MG553638	—
	Hohenbuehelia grisea	MCVE:27293	KU355394	—	—	KU355447	KU355329	—
	Hohenbuehelia tremula	AFTOL-ID 1503, PBM2301	—	—	DQ440645	—	DQ182504	—
	Hohenbuehelia tremula	**DAOM:180808**	KU355405	KU355434	—	KU355465	KU355357	**OR828361**
	Hohenbuehelia unguicularis	Z+ZT:1112	KU355408	—	—	KU355467	KU355361	—
	Lachnella villosa	CBS:609.87, AFTOL-ID 525 + CCJ1547	DQ097347	—	AY705959	GU187721	DQ097362	DQ068007
	Pleurotus citrinopileatus	HfpriPC051Y1-BHFW01000088	genome	genome	genome	genome	genome	genome
	Pleurotus dryinus	**AMB:18868**	**OR863538**	**OR828286**	**OR863593**	**OR828338**	**OR863471**	**OR828363**
	Pleurotus fuscosquamulosus	**A. Baglivo 13-07-2014**	—	**OR828287**	—	**OR828339**	**OR863472**	—
	Pleurotus ostreatus	AFTOL-ID 564, TENN:53662	AY645052	AY786062	AY657015	AY883432	AY854077	AY862186
	Pleurotus salmoneostramineus	NBRC-31859	genome	genome	genome	genome	genome	genome
	Pleurotus tuber-regium	ACCC:50657-18	genome	genome	genome	genome	genome	genome
	Porodisculus orientalis	G0896 + SNU-m 030828-101	MK278522	EU423191	—	—	EU423186	—
	Resupinatus applicatus	**AMB:18098**	MH430596	—	—	MH449588	MH137821	—
	Resupinatus europaeus	AMB:18078	KU355409	—	—	KU355468	KU355368	—
	Resupinatus griseopallidus	**AMB:18277**	MH165881	—	—	—	MH137823	—
	Resupinatus kavinae	**AMB:19612**	**OR863543**	**OR828293**	—	**OR828344**	**OR863477**	—
	Resupinatus niger	AMB:18095	KU355413	—	—	KU355470	KU355371	—

Table 1. (Continued).

Group	Species	Voucher	LSU	*RPB2*	SSU	*TEF1*	ITS	*RPB1*
	Resupinatus rouxii	Z+ZT:971	MH190787	—	—	MH449590	MH137828	—
	Resupinatus striatulus	**JA:Cussta8634**	MH430597	—	—	MH449591	MH137829	—
	Resupinatus vetlinianus	TENN:F69285, TFB14587	KP987309	—	—	—	KP026243	—
	Schizophyllum radiatum	AFTOL-ID 516, CBS:301.32	MH866782	DQ484052	AY705952	—	MH855328	DQ447939
Pluteineae	*Amanita brunnescens*	AFTOL-ID 673, PBM2429	AY631902	AY780936	AY707096	AY881021	AY789079	AY788847
	Amanita phalloides	HKAS:75773 + TUB:011556	JX998060	KJ466612	—	JX998000	JX998031	DQ067953
	Amanita subglobosa	HKAS:58837	JN941152	JQ031121	JN941126	KJ482004	JN943177	JN994123
	Catatrama costaricensis	DAOM:211663	KT833804	KT833819	—	KT833834	—	—
	Giacomia mirabilis	**AMB:19297**	JQ639154	**OR828261**	**OR863570**	—	JQ639153	—
	Giacomia mirabilis	**ANGE1598**	**OR863505**	**OR828262**	**OR863571**	**OR828320**	**OR863436**	**OR828360**
	Giacomia sinensis	**HMJU:265 - TYPE**	**MZ435884**	**MZ441372**	**MZ435869**	**MZ441376**	**MZ435888**	MZ441380
	Giacomia sinensis	**HMJU:268**	**MZ435885**	**MZ441373**	**MZ435870**	**MZ441377**	**MZ435889**	MZ441381
	Leucocortinarius bulbiger	**AMB:19593**	**OR864301**	**OR828271**	**OR863581**	**OR828326**	—	—
	Leucocortinarius bulbiger	TUB:011568	DQ071745	—	—	—	—	DQ068019
	Limacella glioderma	HKAS:90169 + ZLYD 72	KT833808	KT833823	—	KT833836	MH508658	DQ067952
	Limacellopsis asiatica	HKAS:101436	MH486964	MH486357	—	MH509184	—	—
	Limacellopsis guttata	MB100157	KT833813	KT833828	—	KT833841	—	—
	Limnoperdon incarnatum	IFO:30398	AF426958	—	AF426952	—	DQ097363	—
	***Limnoperdon* sp.**	**CBS:160.95**	**OR863524**	**OR828272**	**OR863582**	**OR828327**	**OR863457**	—
	Melanoleuca* aff. *graminicola	**AMB:19613**	**OR863528**	**OR828276**	**OR863586**	**OR828331**	**OR863461**	—
	Melanoleuca communis	ZRL20151882	KY418885	KY419030	KY418950	KY419080	LT716069	—
	Melanoleuca exscissa	**AMB:19614**	**OR863530**	**OR828278**	**OR863588**	**OR828332**	**OR863463**	—
	Melanoleuca exscissa	BRNM:781061 + LAS97-019	—	LT594191	—	LT594175	LT594122	JX429104
	Melanoleuca friesii	**AMB:18865**	**OR863531**	**OR828279**	**OR863589**	**OR828333**	**OR863464**	—
	Melanoleuca microcephala	HMJAS:00138 + BRNM:817787	MK660045	MW488179	—	MW488164	MW491334	—
	Melanoleuca rasilis	BRNM:751967, G0924	MK278374	LT594187	—	LT594171	LT594154	—
	Melanoleuca tristis	**AMB:18866**	**OR863532**	**OR828280**	**OR863590**	**OR828334**	**OR863465**	**OR828362**
	Melanoleuca verrucipes	WTU:PBM2289, AFTOL-ID 818	DQ457687	DQ474119	DQ457645	GU187726	DQ490642	DQ447924
	Pluteus cervinus	**AMB:18870**	**OR863539**	**OR828288**	**OR863594**	**OR828340**	**OR863473**	**OR828364**
	Pluteus hongoi	ZRL20151600	KY418878	KY419023	—	KY419074	LT716062	—
	Pluteus multiformis	PL40, AC4249, AH:40107 - TYPE	MK278503	LR697101	—	LR697100	HM562201	—

Table 1. (Continued).

Group	Species	Voucher	LSU	*RPB2*	SSU	*TEF1*	ITS	*RPB1*
	Pluteus romellii	AFTOL-ID 625, ECV3201	AY634279	AY786063	AY657014	AY883433	AY854065	AY862187
	Pluteus romellii	**AMB:18871**	**OR863540**	**OR828289**	**OR863595**	**OR828341**	**OR863474**	—
	Pluteus variabilicolor	**AMB:18872**	**OR863541**	**OR828290**	**OR863596**	**OR828342**	**OR863475**	**OR828365**
	Pluteus variabilicolor	**AMB:18873**	**OR863542**	**OR828291**	**OR863597**	**OR828343**	**OR863476**	**OR828366**
	Saproamanita thiersii	SKay4041	HQ593114	genome	genome	genome	HQ625010	genome
	Volvariella aff. _nigrovolvacea_	**AMB:18775**	**OR863550**	**OR828301**	**OR863604**	**OR828352**	**OR863483**	**OR828367**
	Volvariella aff. _pusilla_	**AMB:19290**	**OR863552**	**OR828303**	**OR863606**	**OR828354**	**OR863485**	**OR828368**
	Volvariella aff. _pusilla_	**K:M145618**	**OR863551**	**OR828302**	**OR863605**	**OR828353**	**OR863484**	—
	Volvariella bombycina	**AMB:19312**	**OR863553**	**OR828304**	**OR863607**	**OR828355**	**OR863486**	—
	Volvariella caesiotincta	**AMB:19319**	**OR863554**	**OR828305**	—	**OR828356**	**OR863487**	—
	Volvariella volvacea	PDD:96362, JAC12235	MN738572	genome	genome	genome	genome	genome
	Volvopluteus earlei	**AGMT-71**	**OR863556**	**OR828307**	**OR863609**	**OR828358**	MK204989	—
	Volvopluteus gloiocephalus	AFTOL-ID 890	AY745710	—	DQ089020	—	DQ494701	DQ447945
	Volvopluteus gloiocephalus	**NTNU:27884555**	**OR863557**	**OR828308**	**OR863610**	**OR828359**	**OR863489**	—
	Zhuliangomyces illinitus	HKAS:90168	KT833814	KT833829	—	KT833842	MH508659	—
Tricholomatineae	*Asproinocybe sinensis*	HMJAU:59026	OK377051	OK625401	OK377040	OK625331	OK377048	OK625398
	Aspropaxillus giganteus	**AMB:18857**	**OR863493**	**OR828250**	**OR863561**	**OR828311**	**OR863423**	—
	Atractosporocybe inornata	HKAS:105578 + TO:AV201012d	MZ714592	MZ681898	KJ681075	MZ681877	MZ714587	MZ681888
	Bonomyces sinopicus	KATO:Fungi-3689	MG696627	MG702595	MG696623	MG702592	MG696619	—
	Callistosporium graminicolor	AFTOL-ID 978, WTU:PBM2341	AY745702	—	AY752974	GU187761	DQ484065	GU187493
	Catathelasma ventricosum	DAOM:225247	MN017477	MN018851	MN017585	MN026906	MN017537	KP255480
	Clitocella fallax	CBS:129.63	AF223166	EF421018	—	EF421089	AF357017	EF421051
	Clitocybe dealbata	IE-BSG HC95.cp3	AF223175	DQ825407	DQ825431	EF421080	AF357061	DQ825414
	Clitocybe ditopa	**AMB:19311**	**OR863496**	**OR828253**	**OR863563**	**OR828314**	**OR863426**	—
	Clitocybe nebularis	AFTOL-ID 1495, WTU:PBM2259 + CBS:362.65	DQ457658	EF421011	DQ437681	EF421081	AF357063	DQ825415
	Clitocybe subditopoda	AFTOL-ID 533, PBM2489	AY691889	AY780942	AY771608	DQ408150	DQ202269	DQ447892
	Clitolyophyllum akcaabatense	**P. Alvarado 5836**	**OR863497**	**OR828254**	—	**OR828315**	**OR863427**	—
	Clitopaxillus alexandri	TO:AV45634	MG321393	MG334546	MG321329	MG334537	MG321345	—
	Clitopilopsis hirneola	CORT:TB8490 + CORT:REH8490	GU384611	GU384646	—	KC816820	—	—
	Clitopilus pallidogriseus	MENoordeloos2004032 + CORT:E652	GQ289216	GQ289283	—	KC816875	—	—

Table 1. (Continued).

Group	Species	Voucher	LSU	*RPB2*	SSU	*TEF1*	ITS	*RPB1*
	Collybia tuberosa	AFTOL-ID 557, TENN:53540	AY639884	AY787219	AY771606	AY881025	AY854072	AY857982
	Entoloma prunuloides	AFTOL-ID 523, TJB4765	AY700180	DQ385883	AY665784	DQ457633	DQ206983	DQ447898
	Entoloma undatum	HKAS:115925	MZ853561	MZ852824	—	—	MZ855875	MZ852812
	Fayodia bisphaerigera	**OW241-19**	**OR863499**	**OR828256**	—	**OR828317**	**OR863429**	—
	***Gamundia* sp.**	**YM18172**	**OR863500**	**OR828257**	**OR863565**	**OR828318**	**OR863430**	—
	Gamundia striatula	**JL45-18**	**OR863501**	**OR828258**	**OR863566**	**OR828319**	**OR863431**	—
	Harmajaea harperi	LIP:0401361	MG321399	MG334549	MG321333	MG334541	MG321366	—
	Hertzogia martiorum	**AMB:18863**	**OR863510**	**OR828265**	**OR863574**	**OR828323**	**OR863441**	—
	Hypsizygus ulmarius	DUKE:JM/HW	AF042584	EF420996	—	EF421062	EF421105	EF421030
	Infundibulicybe geotropa	**AMB:18861**	**OR863518**	**OR828268**	**OR863577**	—	**OR863450**	—
	Infundibulicybe gibba	AFTOL-ID 1508, CUW:JCS0704B	DQ457682	DQ472727	DQ115780	GU187759	DQ490635	DQ447913
	Lepista glaucocana	**AMB:18862**	**OR863520**	—	**OR863579**	—	**OR863452**	—
	Lepista irina	AFTOL-ID 815, WTU:PBM2291	DQ234538	DQ385885	AY705948	DQ028591	DQ221109	DQ447919
	Lepista ricekii	**AMB:18864**	**OR863521**	**OR828270**	**OR863580**	—	**OR863453**	—
	Lepista saeva	TENN:066100, ADW0097	KJ417193	KJ424376	KJ417159	—	KJ137270	—
	Leucocybe candicans	AFTOL-ID 541, PBM2476	AY645055	DQ385881	AY771609	DQ408149	DQ202268	DQ447891
	Lyophyllum semitale	HC85/13	AF042581	EF421002	—	EF421068	AF357049	EF421036
	Lyophyllum turcicum	**GB:0065321**	**OR863525**	**OR828273**	**OR863583**	**OR828328**	**OR863458**	—
	Macrocystidia cucumis	**JX.1294733#45**	**OR863527**	**OR828275**	**OR863585**	**OR828330**	**OR863460**	—
	***Macrocystidia* sp.**	**Kekki3956**	**OR863526**	**OR828274**	**OR863584**	**OR828329**	**OR863459**	—
	Musumecia bettlachensis	TO:HG2284	JF926521	KJ681060	KJ681069	KJ681082	JF926520	—
	Nolanea sericea	VHAs03/02	DQ367423	DQ367435	DQ367421	DQ367428	DQ367430	DQ825424
	Notholepista fistulosa	HKAS:115934	OK104059	OK105137	—	OK105127	OK104077	OK105132
	Notholepista fistulosa	**HMJU:288**	**MZ435886**	**MZ441374**	**MZ435871**	**MZ441378**	**MZ435890**	MZ441382
	Notholepista fistulosa	**HMJU:592**	**MZ435887**	**MZ441375**	**MZ435872**	**MZ441379**	**MZ435891**	MZ441383
	Notholepista subzonalis	GB:0087013	KJ417208	KJ424385	KJ417167	—	KP453695	—
	Omphaliaster borealis	**TROM:43**	**OR863533**	**OR828281**	—	**OR828335**	**OR863466**	—
	Omphalina pyxidata	**AMB:19294**	**OR863534**	**OR828282**	**OR863591**	—	**OR863467**	—
	Omphalina pyxidata	**AMB:19295**	**OR863535**	**OR828283**	**OR863592**	—	**OR863468**	—
	Paralepista flaccida	KUN-HKAS:115937	MZ853571	MZ681894	—	MZ857193	MZ855885	MZ857194
	Paralepista flaccida	**TO:AV20140410**	**OR863536**	**OR828284**	—	**OR828336**	**OR863469**	—

Table 1. (Continued).

Group	Species	Voucher	LSU	*RPB2*	SSU	*TEF1*	ITS	*RPB1*
	Paralepistopsis amoenolens	**AMB:18867**	**OR863537**	**OR828285**	—	**OR828337**	**OR863470**	—
	Pogonoloma spinulosum	K:M107286	KJ417238	KJ424401	KU058571	—	KP453705	KU139037
	Pseudoclitocybe cyathiformis	AFTOL-ID 1998, WTU:JFA12811 + GLM46020	EF551313	GU187815	GU187659	GU187742	GU187553	DQ067939
	Pseudoclitopilus rhodoleucus	GB:0110967, TK03/203	KJ417218	KJ424393	KU058577	—	KP453696	KU139046
	Pseudoclitopilus rhodoleucus	KUN-HKAS:105563	MZ714594	MZ681899	—	MZ681878	MZ714588	MZ681889
	Pseudolaccaria pachyphylla	GB:0066637, LAS07/012	KU058542	KU139006	KU058579	—	KU058504	KU139048
	Pseudoomphalina kalchbrenneri	GB:0066625, LAS06/037	KU058541	KU139005	KU058578	—	KU058503	KU139047
	Pseudoomphalina umbrinopurpurascens	**LSS20181215-2**	MK424271	**OR828292**	**OR863598**	—	MK424270	—
	Pseudotricholoma metapodium	AH22102006-K	KJ417219	KJ424394	KJ417171	—	KJ417308	KU139049
	Rhizocybe alba	KUN-HKAS:55110	MZ675571	MZ681893	—	MZ681871	MZ675560	MZ681882
	Rhodophana stangliana	KUN-HKAS:115926	MZ853562	MZ852825	—	MZ852801	MZ855876	MZ852813
	Ripartites odorus	**F. Di Rita 08-12-2018**	MN595290	**OR828295**	**OR863599**	**OR828346**	MN595290	—
	Ripartites odorus	**T. Clements 248705**	**OR863544**	**OR828294**	—	**OR828345**	MK559718	—
	***Ripartites* sp.**	**Kekki2112**	**OR863545**	**OR828296**	**OR863600**	**OR828347**	**OR863478**	—
	Ripartites tricholoma	**Kekki1910**	**OR863546**	**OR828297**	**OR863601**	**OR828348**	**OR863479**	—
	Ripartites tricholoma	KUN-HKAS:77956	MZ675573	—	—	MZ681873	MZ675562	MZ681884
	Singerocybe umbilicata	KUN-HKAS:105572	MZ714591	MZ681896	—	MZ681875	MZ714585	MZ681886
	Trichocybe puberula	**Ferisin11.3.2016-03**	**OR863549**	**OR828300**	**OR863603**	**OR828351**	**OR863482**	—
	Tricholoma viridiolivaceum	TENN:063670, PDD:97890, PBM3093	JF706317	JF706319	JF706318	—	JF706316	KU139072
	Tricholomella constricta	HC84/75	AF223188	DQ825412	DQ825434		AF357036	DQ825422
	Tricholosporum goniospermum	AR122, TUR:A209107	MW367864	KU559863	KU559865	—	KU559848	—
	Tricholosporum guangxiense	HMJAU:59028	OK377056	OK625403	OK377043	OK625333	OK377047	—
Typhulineae	*Typhula erythropus*	S:IO.14.123, UPS:IO.14.123	KY224096	MT242343	—	MT242362	MT232359	—
	Typhula gyrans	S:IO.14.103, UPS:IO.14.103	KY224097	MT242344	—	MT242363	MT232360	MT242323
	Typhula incarnata	S:IO.14.92, UPS:IO.14.92 + CBS:359.79	MT232313	MT242346	MT232504	MT242365	MT232362	MT242325
	Typhula sclerotioides	S:IO.14.22	MT232317	MT242349	MT232507	MT242369	MT232365	MT242327

Table 2. Taxa, vouchers, and GenBank accessions numbers of the DNA sequences used in the *Hygrophorineae*-wide phylogenetic analysis inferred from a three-gene dataset (LSU, *RPB2* and *TEF1*). Sequences in bold were generated in this study.

Species	Herbarium	LSU	*RPB2*	*TEF1*
Acantholichen campestris	CGMS:Gumboski1043b, Spielmann10243b - TYPE	NG_070392	KT429818	–
Acantholichen galapagoensis	GMUF:DalForno1204	KT429799	KT429811	–
Acantholichen pannarioides	GMUF:DalForno1752, MDF352	KT429807	KT429817	–
Ampulloclitocybe clavipes	KUN-HKAS:54426	MW600481	MW656471	MW656461
	TENN:DJL06TN40	KF381542	KF407938	–
	WTU:PBM2474, AFTOL-ID 542	AY639881	AY780937	AY881022
Amylocorticium cebennense	CFMR:HHB-2808	GU187561	GU187770	GU187675
Cantharellula umbonata	CBS:398.79	MH872990	–	–
Cantharocybe brunneovelutina	CFMR:DJL-BZ-1883 - TYPE	NG_068731	–	–
Cantharocybe gruberi	AH:24539	JN006420	–	–
	WTU:PBM510, AFTOL-ID 1017	DQ234540	DQ385879	DQ059045
Cantharocybe virosa	HKAS:79012	KF303143	–	–
	TENN:063483	JX101471	–	–
Ceraceomyces borealis	CFMR:L-8014	GU187570	GU187782	GU187686
Chromosera ambigua	GE18008-1	MK645587	MK645593	–
Chromosera cyanophylla	WTU:PBM1577, AFTOL-ID 1684	DQ457655	KF381509	–
Chromosera lilacina	GE18035	MK645591	MK645597	–
Chromosera xanthochroa	GE18033	MK645590	MK645596	–
Chrysomphalina chrysophylla	WTU:PBM684, AFTOL-ID 1523	DQ457656	–	–
Chrysomphalina grossula	OSC:113683	EU652373	–	–
Cora aspera	F:Lücking 29128, DIC110	KF443257	KF443267	–
Cora pavonia	F:Lücking s/n, DIC215	KF443261	KF443275	–
Cora reticulifera	F:Lücking 26201, DIC119	KF443262	KF443269	–
Cora squamiformis	KRAM:Wilk7577 - TYPE + Wilk7562	NG_060405	KF443273	–
Corella brasiliensis	GMUF:DalForno1271, MDF017	KF443255	KF443276	–
Corella sp.	GMUF:Eliasaro5006, MDF200	KY861725	–	–
Cuphophyllus acutoides var. *pallidus*	CFMR:TN-257	KF291097	–	–
Cuphophyllus aff. *pratensis*	WTU:PBM2752, AFTOL-ID 1682	DQ457650	–	–
Cuphophyllus aurantius	CFMR:PR6601	KF291100	KF291102	–
Cuphophyllus cinerellus	GB:0156961, EL30-16	MN430913	MN556847	–
Cuphophyllus esteriae	TU:117603	MN430911	MN556855	–
Cuphophyllus flavipes	TUR:A-199692, Campo131027	MN430919	MN556851	–
Cuphophyllus fornicatus	CFMR:D. Boertmann 2009/94	KF291124*	–	–
Cuphophyllus hygrocyboides	GB:0156992, EL177-13	MN430917	MN534321	–
Cuphophyllus lamarum	TU:117564	MN430915	MN556853	–
Cuphophyllus pratensis	CFMR:DJL-Scot-8	KF291058	–	–
	Lueck7	KP965789	–	–
Cuphophyllus sp.	KUN-HKAS:105671	MW763000	MW789179	–
Cyphellostereum galapagoense	CDS:41163 - TYPE	NG_068806	–	–
Cyphellostereum imperfectum	F:Lücking25588, DIC115a	KF443243	KF443277	–
Dictyonema interruptum	BR:Ertz10475, DIC065	EU825967	KF443282	–
Dictyonema schenckianum	F:Lücking30062, DIC113	KF443251	KF443285	–
Eonema pyriforme	G1063, DK1524	MK278075	–	–
Gliophorus aff. *laetus*	CFMR:PR-5408, SAC-PR-9901	KF291070	–	–
Gliophorus graminicolor	CORT:TJB-10048	KF381545	KF407936	–
Gliophorus psittacinus	CFMR:D. Boertman 2002/10, DEN25	KF291076	KF291078	–
Gloioxanthomyces nitidus	GDGM:41710	MG712282	MG711911	–
Haasiella splendidissima	Roux4044	JN944401	–	–

Table 2. (Continued).

Species	**Herbarium**	**LSU**	***RPB2***	***TEF1***
Haasiella venustissima	STU: A.Gminder971488	KF291093	–	–
Humidicutis auratocephala	CUW:JCS071105E, AFTOL-ID 1727	DQ457672	DQ472720	–
Humidicutis dictiocephala	QCAM:6000 - TYPE	NG_066384	–	–
Humidicutis marginata	JM96/33	AF042580	–	–
Humidicutis sp.	CFMR:BZ3923, D.J.Lodge DJL-BZ-3	KF291111	–	–
Hygroaster albellus	CFMR:PR-6377, AFTOL-ID 1997	EF551314	–	–
Hygroaster nodulisporus	CFMR:PR-6378, AFTOL-ID 2020	EF561625	–	–
Hygrocybe aff. *conica*	WTU:PBM918, AFTOL-ID 729	AY684167	AY803747	–
Hygrocybe cf. *acutoconica*	CFMR:NC-256, DJL04NC2	KF291118	KF291120	–
Hygrocybe coccinea	WTU:PBM915, AFTOL-ID 1715	DQ457676	DQ472723	GU187705
Hygrocybe conica	FO:46714	DQ071739	–	–
Hygrophorocybe* aff. *carolinensis	**UCSC:F0690**	**OR863511**	**OR828266**	**OR828324**
Hygrophorocybe nivea	**AMB:19292**	**OR863512**	–	–
	AMB:19293	**OR863513**	–	–
	LPA:SMGC2020121621	**OR863514**	**OR828267**	**OR828325**
	TO:AV20100811	**OR863516**	–	–
	TO:AV20112411	**OR863517**	–	–
Hygrophorus aurantiosquamosus	KUN-HKAS:112569	MW763001	MW789180	MW773440
	KUN-HKAS:82501	MW600482	MW656472	MW656462
Hygrophorus eburneus	US97/138	AF430279	–	–
Hygrophorus gliocyclus	KUN-HKAS:79929	MW600485	MW656475	MW656465
Hygrophorus hypothejus	KUN-HKAS:56550	MW762775	MW656476	–
Hygrophorus pinophilus	KUN-HKAS:112567	MW763003	MW789182	MW773442
Hygrophorus pudorinus	CUW:PBM2721, AFTOL-ID 1723	DQ457678	DQ472725	GU187710
Hygrophorus sp.	KUN-HKAS:112566	MW763002	MW789181	MW773441
	KUN-HKAS:112568	MW763004	MW789183	MW773443
	KUN-HKAS:87261	MW600487	MW656477	MW656466
Hygrophorus xiangjun	KUN-HKAS:55043	MW600484	MW656474	MW656464
	KUN-HKAS:68013	MW600483	MW656473	MW656463
Lichenomphalia hudsoniana	GAL18249	JQ065875	–	–
Lichenomphalia meridionalis	S-270-FB1, Hiroshi Masumoto 270	LC428307	–	–
Neohygrocybe griseonigra	GDGM:44492 - TYPE	NG_067810	–	–
Neohygrocybe ingrata	TENN:DJL05TN62	KF381558	KF381516	–
Neohygrocybe ovina	ABS:Rhosisaf	KF291234	KF291236	–
Neohygrocybe subovina	GRSM:77065, DJL04TN16	KF291141	–	–
Porpolomopsis aff. *calyptriformis*	TENN:DJL05TN80	KF291247	KF291249	–
Porpolomopsis calyptriformis	CFMR:EB-ENG-3	KF291243	KF291245	–
Porpolomopsis lewelliniae	CORT:TJB-10034	KF291239	KF291241	–
Pseudoarmillariella bacillaris	HKAS:76377	KC222316	–	–
Pseudoarmillariella ectypoides	WTU:PBM1588, AFTOL-ID 1557	DQ154111	DQ474127	GU187733
Sinohygrocybe tomentosipes	GDGM:43351 - TYPE	NG_064497	MG696905	–
	GDGM:50075	MG696902	MG696906	–
Spodocybe bispora	KUN-HKAS:112564	MW763007	MW789186	MW773446
	KUN-HKAS:73310 - TYPE	MW763005	MW789184	MW773444
Spodocybe cf. *trulliformis*	G0460, DB1302	MK277728	–	–
Spodocybe collina	**AMB:19296**	**OR863547**	**OR828298**	**OR828349**
	WU:0018453	MK277717	–	–
Spodocybe herbarum	G0171, NL-2261	MK277719	–	–
Spodocybe rugosiceps	KUN-HKAS:112563 - TYPE	MW763013	MW789192	MW789160

Table 2. (Continued).

Species	Herbarium	LSU	*RPB2*	*TEF1*
Spodocybe sp.	KUN-HKAS:71071	MW763011	MW789190	MW773449
	KUN-HKAS:112560	MW763014	MW789193	MW789161
	KUN-HKAS:112565	MW763015	MW789194	MW789162

Table 3. Taxa, vouchers, and GenBank/Unite accessions numbers of the DNA sequences used in the *Cuphophylloideae*-wide phylogenetic analysis inferred from a four-gene dataset (ITS, LSU, *RPB2* and *TEF1*). Sequences in bold were generated in this study.

Species	Herbarium	ITS	LSU	*RPB2*	*TEF1*
Ampulloclitocybe clavipes	KUN-HKAS:54426	MW616462	MW600481	MW656471	MW656461
	TENN:DJL06TN40	FJ596912	KF381542	KF407938	—
	WTU:PBM2474, AFTOL-ID 542	AY789080	AY639881	AY780937	AY881022
Amylocorticium cebennense	CFMR:HHB-2808	GU187505	GU187561	GU187770	GU187675
Cantharocybe brunneovelutina	CFMR:DJLBZ1883 - TYPE	NR_160458	NG_068731	—	—
Cantharocybe gruberi	AH:24539	JN006422	JN006420	—	—
	WTU:PBM510, AFTOL-ID 1017	DQ200927	DQ234540	DQ385879	DQ059045
Cantharocybe virosa	HKAS:79012	—	KF303143	—	—
	TENN:063483	KX452405	JX101471	—	—
Ceraceomyces borealis	CFMR:L-8014	—	GU187570	GU187782	GU187686
Cuphophyllus acutoides var. *pallidus*	CFMR:TN-257	KF291096	KF291097	—	—
Cuphophyllus aff. *pratensis*	WTU:PBM2752, AFTOL-ID 1682	DQ486683	DQ457650	—	—
Cuphophyllus aurantius	CFMR:PR-6601	KF291099	KF291100	KF291102	—
Cuphophyllus cinerellus	GB:0156961, EL30-16	MK573935	MN430913	MN556847	—
Cuphophyllus esteriae	TU:117603	MK547063	MN430911	MN556855	—
Cuphophyllus flavipes	TUR:A-199692, Campo131027	MN453872	MN430919	MN556851	—
Cuphophyllus fornicatus	CFMR:D.Boertmann 2009/94	KF291123	KF291124	—	—
Cuphophyllus hygrocyboides	GB:0156992, EL177-13	MK573937	MN430917	MN534321	—
Cuphophyllus lamarum	TU:117564	MK547062	MN430915	MN556853	—
Cuphophyllus pratensis	CFMR:DJL-Scot-8	KF291057	KF291058	—	—
	Lueck7	—	KP965789	—	—
Cuphophyllus sp.	KUN-HKAS:105671	MW762875	MW763000	MW789179	—
Hygrophorocybe* aff. *carolinensis	UCSC:F0690	**OR863442**	**OR863511**	**OR828266**	**OR828324**
Hygrophorocybe aff. *carolinensis* (as *Clitocybe carolinensis*)	TENN:021888 - TYPE	NR_119886	—	—	—
Hygrophorocybe nivea	AMB:19292	**OR863444**	**OR863512**	—	—
	AMB:19293	**OR863445**	**OR863513**	—	—
	LPA:SMGC2020121621	**OR863446**	**OR863514**	**OR828267**	**OR828325**
	TO:AV20100811	**OR863448**	**OR863516**	—	—
	TO:AV20112411	**OR863449**	**OR863517**	—	—
Hygrophorocybe nivea (as *Clitocybe alni-glutinosae*)	IB:19960896 - TYPE	UDB023989	—	—	—
Hygrophorocybe nivea (as *Clitocybe hypotheja*)	MCVE:530 - TYPE	**OR863443**	—	—	—
Spodocybe bispora	KUN-HKAS:112564	MW762882	MW763007	MW789186	MW773446
	KUN-HKAS:73310 - TYPE	MW762880	MW763005	MW789184	MW773444
Spodocybe cf. *trulliformis* (as *Clitocybe* cf. *trulliformis*)	G0460, DB1302	—	MK277728	—	—
Spodocybe collina	AMB:19296	**OR863480**	**OR863547**	**OR828298**	**OR828349**
	WU:0018453, G0342	—	MK277717	—	—
Spodocybe herbarum (as *Clitocybe herbarum*)	G0171, NL-2261	—	MK277719	—	—
Spodocybe rugosiceps	KUN-HKAS:112563 - TYPE	MW762888	MW763013	MW789192	MW789160
Spodocybe sp.	KUN-HKAS:71071	MW762886	MW763011	MW789190	MW773449
	KUN-HKAS:112560	MW762889	MW763014	MW789193	MW789161
	KUN-HKAS:112565	MW762890	MW763015	MW789194	MW789162

MATERIALS AND METHODS

Morphological studies

Macroscopic morphological features were studied in fresh specimens. Colour codes follow Kornerup & Wanscher (1978). The following abbreviations are employed: L = number of lamellae reaching the stipe, l = number of lamellulae between each pair of lamellae. Microscopic structures were examined in dried material using different mounting media: water, L4 (Clémençon 1972), Melzer's reagent, ammoniacal Congo red, phloxine, Cresyl blue and Cotton blue. Dried pieces of the samples were rehydrated in water and mounted in L4. All microscopic measurements were carried out with a Nikon Eclipse 80i microscope, using immersion oil at ×1 000. Spore measurements were taken by capturing images of a single visual field with multiple spores (obtained from lamellar squashes of exsiccate material of mature specimens) which were then measured using the DS-L1 Nikon camera control unit. Spore dimensions do not include the hilar appendix, and are reported as follows: (minimum–) average minus standard deviation of length–*average of length*–average plus standard deviation of length (–maximum) × (minimum–) average minus standard deviation of width–*average of width*–average plus standard deviation of width (–maximum); Q (ratio length/width) = (minimum–) average minus standard deviation–*average*–average plus standard deviation (–maximum); V (volume, μm^3) = (minimum–) average minus standard deviation–*average*–average plus standard deviation (–maximum). 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. Microscopy images were taken using a Nikon DS 5M digital connected to the microscope with both bright field and interferential contrast optics. Macro- and microchemical testing of pigments were performed using basic solutions (5 % KOH and 10 % ammonia, separately). In some cases, basidiospores were observed under the scanning electron microscope (SEM), using the following procedure: lamellae were attached to specimen holders by carbon tape, coated with platinum-palladium using a Hitachi MC 1000 Ion Sputter Coater and examined with a FEI Quanta 200 FE-SEM operated at 5–10 kV as in Xu *et al*. (2019). For nomenclatural matters, reference was made to the Shenzhen Code (Turland *et al*. 2018).

DNA extraction, amplification, and sequencing

Total DNA was extracted from dry specimens (Table 1) employing a modified protocol based on Murray & Thompson (1980). Amplification reactions (Mullis & Faloona 1987) included 35 cycles with an annealing temperature of 54 ºC. The primers ITS1F and ITS4 (White *et al*. 1990, Gardes & Bruns 1993) were employed to amplify the internal transcribed spacer region 1, 5.8S rDNA and internal transcribed spacer region 2 (ITS), LR0R and LR5 (Vilgalys & Hester 1990, Cubeta *et al*. 1991) were used for the 28S rDNA region (LSU), NS19b and NS41 (Hibbett 1996) for the 18S rDNA (SSU), EF1-728F, EF1-983F, EF1-1567R and EF1- 2218R (Carbone & Kohn 1999, Rehner & Buckley 2005) for the translation elongation factor-1a (*TEF1*) gene, bRPB2-6F2 (reverse of bRPB2-6R2), and bRPB2-7R2 for the DNA-directed RNA polymerase II second largest subunit (*RPB2*) gene (Matheny *et al*. 2007), as well as RPB1-Af (Stiller & Hall 1997) and RPB1-Cr (Matheny *et al*. 2002) for DNA-directed RNA polymerase II largest subunit (*RPB1*) gene. The PCR products were checked in 1 % agarose gels, and amplicons were sequenced with one or both PCR primers. Sequences were corrected to remove reading errors in chromatograms using MEGA v. 6.0 (Tamura *et al*. 2013).

Phylogenetic analyses

Three different datasets were built from sequences produced in the present work and others downloaded from public databases (Tables 1–3). Dataset 1 (*Agaricales*) aimed to resolve the phylogenetic relationships of the *incertae sedis* lineages studied with the different suborders of *Agaricales*. It included sequences of six different loci (5.8S, LSU, SSU, *RPB1*-exons, *RPB2*-exons, *TEF1*-exons) from the main lineages analyzed by Matheny *et al*. (2006), Varga *et al*. (2019), Ke *et al*. (2020), Olariaga *et al*. (2020) and Sánchez-García *et al*. (2020). Sequences of *Amylocorticium cebennense* and *Ceraceomyces borealis* (*Amylocorticiales*, Binder *et al*. 2010, Hodkinson *et al*. 2014, Zhao *et al*. 2017), as well as *Suillus pictus* (*Boletales*, Hodkinson *et al*. 2014, He *et al*. 2019) were employed as outgroup taxa. Dataset 2 (*Hygrophorineae*) aimed to provide a more accurate view of the major clades within suborder *Hygrophorineae*. This dataset included sequences of LSU, *RPB2*-exons (from which a small region of up to 57 bp with multiple insertions/deletions of codons was removed), and *TEF1*-exons from all specimens of *Hygrophorineae* in Dataset 1 (as well as *A. cebennense* and *C. borealis* as outgroups) plus additional lineages known to belong in this suborder (Lodge *et al*. 2014, He & Yang 2021). Finally, Dataset 3 (*Cuphophylloideae*) aimed to focus on species included in this subfamily, and employed sequences of ITS, LSU, *RPB2*-exons, and *TEF1*-exons (using *A. cebennense* and *C. borealis* again as outgroup taxa). Another two datasets of *Agaricales* including taxa of suborder *Clavariineae* (Dataset 4) or the family *Cyphellopsidaceae* (Dataset 5) were built too (same loci as Dataset 1), but they failed to produce significant support for several major clades of *Agaricales*, probably due to the insufficient information available from the linages included or missing lineages in the diversity analyzed. As a result, the phylogenetic trees obtained from them are provided as Supplementary Figs S1, S2 and their sequences are included in Table 1. Alignments of Datasets 1–5 are available online (https://figshare.com/; Dataset 1 – *Agaricales*: 10.6084/m9.figshare.24999359, Dataset 2 – *Hygrophorineae*: 10.6084/m9.figshare.24999371, Dataset 3 – *Cuphophylloideae*: 10.6084/m9.figshare.24999362, Dataset 4 – *Clavariineae*: 10.6084/m9.figshare.24999365, Dataset 5 – *Cyphellopsidaceae*: 10.6084/m9.figshare.24999368. Sequences newly generated in this study and their GenBank (http://www.ncbi.nlm.nih.gov) accession numbers are shown in Tables 1–3 and Supplementary Table S1.

BLASTn (Altschul *et al*. 1990) was used to select related homologous sequences from the International Nucleotide Sequence Database Collaboration public database (INSDC, Arita *et al*. 2021) and UNITE (Nilsson *et al*. 2018). All sequences employed are listed in Table 1. Sequences were first aligned in MEGA v. 6.0 with its ClustalW application and then realigned manually as needed to establish positional homology. Dataset 1 (*Agaricales*) included the following partitions (variable sites/total sites/sequences): 53/158/209 (5.8S), 489/864/221 (LSU), 413/1 683/166 (SSU), 440/654/112 (*RPB1*), 629/999/203 (*RPB2*), and 548/960/183 (*TEF1*). Dataset 2 (*Hygrophorineae*) included the following partitions (variable sites/total sites/sequences): 416/792/100 (LSU), 344/660/63 (*RPB2*), and 171/472/26 (*TEF1*). Dataset 3 (*Cuphophylloideae*) included the following partitions (variable sites/total sites/sequences):

677/1 101/35 (ITS), 292/792/38 (LSU), 277/660/22 (*RPB2*), and 155/472/14 (*TEF1*). Aligned loci also were subjected to MrModeltest v. 2.3 (Nylander 2004) in PAUP v. 4.0b10 (Swofford 2003). Model GTR+G+I was selected and implemented in all partitions in MrBayes v. 3.2.6 (Ronquist *et al*. 2012), where a Bayesian analysis was performed (each locus analyzed in a different partition, two simultaneous runs, four chains, temperature set to 0.2, sampling every 1 000th generation) until the average split frequencies between the simultaneous runs fell below 0.01 after 16.39 M (*Agaricales*), 2.01 M (*Hygrophorineae*) and 0.25 M (*Cuphophylloideae*) generations, respectively. Finally, a full search for the best-scoring maximum likelihood tree was performed in RAxML v. 8.2.12 (Stamatakis 2014) using the standard search algorithm (same partitions, GTRCAT model, 2 000 bootstrap replications). All the analyses were run through the CIPRES Science Gateway platform (Miller *et al*. 2010). The significance threshold was set above 0.95 for posterior probability (PP) and 70 % bootstrap proportions (BP).

RESULTS

DNA phylogeny

Bayesian analysis of Dataset 1, order *Agaricales* (Figs 1–3), significantly supported the following hypotheses: 1) family *Typhulaceae* has a basal position to the remaining suborders analyzed; 2) seven main clades with a significant monophyletic origin were found, matching suborders *Agaricineae*, *Pleurotineae* (including *Schizophyllineae*), *Pluteineae*, *Hygrophorineae*, *Marasmiineae*, *Phyllotopsidineae* (including *Aphroditeola* and *Sarcomyxineae*) and *Tricholomatineae*; 3) suborder *Pleurotineae* also encompasses the families *Fistulinaceae* and *Schizophyllaceae*, and so it could be considered a synonym of *Schizophyllineae*; 4) suborder *Pluteineae* includes *Amanitaceae* and *Leucocortinarius* (PP 0.99), as well as the families *Pluteaceae*, *Limnoperdaceae*, a strongly supported clade (1.00 PP, 98 % BP) consisting of *Melanoleuca* and *Giacomia*, and another including *Volvariella*; 5) suborder *Tricholomatineae* has at least twelve families: *Macrocystidiaceae* (type *Macrocystidia*, probably related to *Pseudoclitopilus*); *Omphalinaceae* (including *Infundibulicybe* and *Omphalina*), *Pseudoclitocybaceae* (including *Aspropaxillus*), *Fayodiaceae* (here including *Fayodia* and *Gamundia*, but probably also *Caulorhiza*, *Conchomyces* and *Myxomphalia* according to Moncalvo *et al*. 2002); *Biannulariaceae*, *Callistosporiaceae*, *Tricholomataceae*, *Clitocybaceae*, *Lyophyllaceae sensu lato*, *Entolomataceae*, as well as the unclassified lineages of *Neohygrocybe*/*Pseudoomphalina*, *Paralepistopsis*, *Hertzogia* and the clade formed by *Notholepista*, *Ripartites*, and *Paralepista*; 6) family *Clitocybaceae* includes the genera *Clitocybe sensu stricto*, *Lepista*, *Singerocybe*, *Collybia sensu lato* (He et al. 2023), and the lineage of *C. ditopa*; 7) family *Lyophyllaceae sensu lato* is integrated by *Lyophyllaceae sensu stricto* as well as the so-called hemilyophylloid lineages (Binder *et al*. 2010, Hofstetter *et al*. 2014), including the genera *Asproinocybe*/*Tricholosporum* (family *Asproinocybaceae*), *Atractosporocybe*, *Clitolyophyllum*, *Leucocybe*, *Omphaliaster*, *Rhizocybe*, *Trichocybe*, and several species whose generic status needs to be reviewed; 8) family *Mycenaceae* is part of the suborder *Marasmiineae*, where it is sister to the significant clade formed by *Xeromphalina* and *Heimiomyces*; 9) the previous concepts of the genera *Mycena* and *Hemimycena* are polyphyletic; 10) genus *Hygrophorocybe* is nested inside suborder *Hygrophorineae*.

The Bayesian analysis of Dataset 2, the extended dataset of suborder *Hygrophorineae* (Fig. 4), supported the following five major monophyletic clades: 1) subfamily *Lichenomphalioideae*; 2) subfamily *Hygrocyboideae*, 3) tribe *Cantharelluleae*, 4) subfamily *Hygrophoroideae*, and 5) subfamily *Cuphophylloideae*, which includes the genera *Ampulloclitocybe*, *Cantharocybe*, *Cuphophyllus*, *Hygrophorocybe* (including *Clitocybe* aff. *carolinensis*) and *Spodocybe*.

The Bayesian analysis of Dataset 3, the extended dataset of subfamily *Cuphophylloideae* (Fig. 5), supported the same hypotheses as Fig. 4. The analysis of ITS rDNA allowed also to infer that the holotype collections of *Clitocybe alni-glutinosae* and *C. hypotheja* are identical to that of *Hygrophorocybe nivea* and confirmed that the holotype of *C. carolinensis* belongs to another clade of *Hygrophorocybe*.

The taxo nomy of all these lineages is updated below in accordance with the results obtained from phylogenetic analysis.

Taxonomy

Agaricales Underw., Moulds, mildews, and mushrooms: 97. 1899.
Synonyms: Agarics, Euagarics, Euagarics clade, Euagaricoid clade *sensu* Hibbett *et al*. (1997), Pine *et al*. (1999), Moncalvo (2000, 2002), Hibbett & Binder (2001), Hibbett & Thorn (2001), Redhead *et al*. (2002a, b), Bodensteiner *et al*. (2004), Larsson *et al*. (2004), Binder *et al*. (2005), Walther *et al*. (2005), Wilson & Desjardin (2005), Garnica *et al*. (2007).

Type: *Agaricus* L., Species Plantarum 2: 1171. 1753.

Representative suborders: *Agaricineae*, *Clavariineae*, *Hygrophorineae*, *Marasmiineae*, *Phyllotopsidineae*, *Pluteineae*, *Pleurotineae*, *Tricholomatineae*, and *Typhulineae*.

Notes: There is no known morphological synapomorphy that unites the order *Agaricales*. This lineage evolved into several basidiome types, from resupinate (corticioid) to conchate, cyphelloid, stereoid, clavarioid, agaricoid (pileostipitate, with open or enclosed hymenophore), and gasteroid/sequestrate (epigeous or hypogeous). Pileostipitate forms with protective veils (universal and partial) and lamellate hymenophore are the most frequent, but hymenophores can also be smooth, wrinkled, odontoid or poroid. The sequestrate forms show locules, and a columella (vestigial structure of the stipe) can be present, reduced, or absent. The hyphal system is mainly monomitic, with or without clamp connections, rarely dimitic or sarcodimitic. Basidia are holobasidiate, chiastic, usually sterigmate, ballistosporic (when the hymenophore is very early exposed to air) or statismosporic (in gasteroid/sequestrate epigeous to hypogeous forms). Basidiospores are extremely diverse with regards to their shape, wall thickness, colour in mass (white, pink, brown, purple-brown, black), ornamentation, and reactivity, sometimes being dextrinoid/amyloid (Melzer’s reagent), metachromatic (Cresyl blue), or cyanophilous (Cotton blue). Cystidia, pseudocystidia, setae and other sterile elements (acanthocytes, stephanocytes) may be present in the hymenium, pileus and stipe surface and basal mycelium. An asexual morph phase is sometimes present, conidiogenesis mainly thallic, rarely blastic. Dolipores are usually provided with perforate parenthesomes. For a delimitation of *Agaricales* see Matheny *et al*. (2006), Dentinger *et al*. (2016), (Agerer 2018), He *et al*. (2019), and Olariaga *et al*. (2020). *Agaricales* species are mostly ectomycorrhizal (mainly associated with the roots of conifers and dicotyledons), saprotrophic

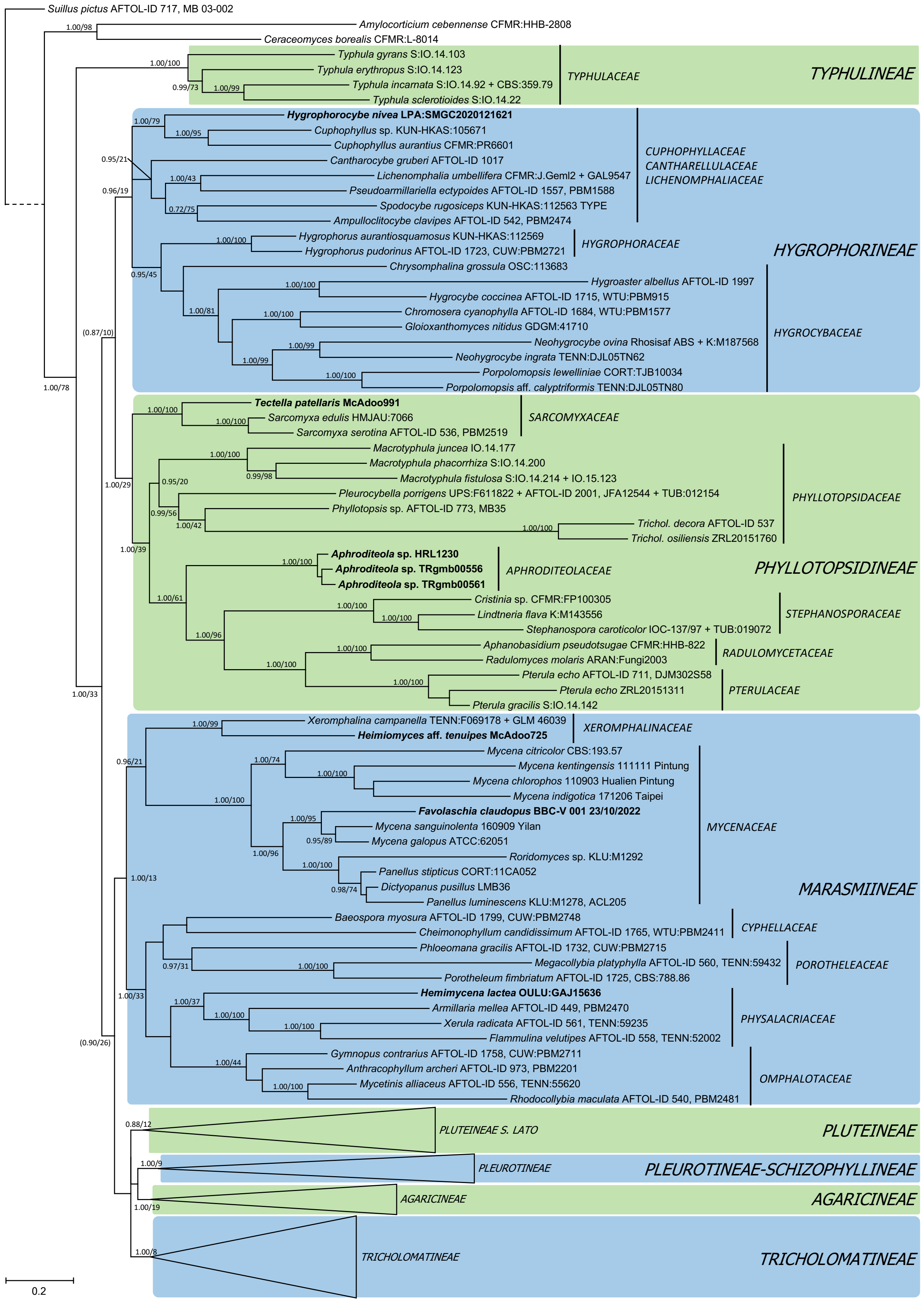

Fig. 1. Bayesian inference phylogram built with nucleotide sequence data of six loci (5.8S, LSU, SSU, *RPB1*-exons, *RPB2*-exons and *TEF1*-exons) of the main lineages inside order *Agaricales* (focused on suborders *Hygrophorineae*, *Marasmiineae* and *Phyllotopsidineae*), rooted with *Suillus pictus* (*Boletales*), *Amylocorticium cebennense* and *Ceraceomyces borealis* (*Amylocorticiales*) as outgroups. The main suborders are shown in color boxes, while family names are shown next to vertical bars. Nodes were annotated with Bayesian PP (left) and ML BP (right) values, with the significance threshold considered as Bayesian PP >0.95 and/or ML BP >70 %. Subsignificant support values were annotated in parentheses. Boldface names represent samples sequenced for this study. The dashed branch was shortened for graphic presentation.

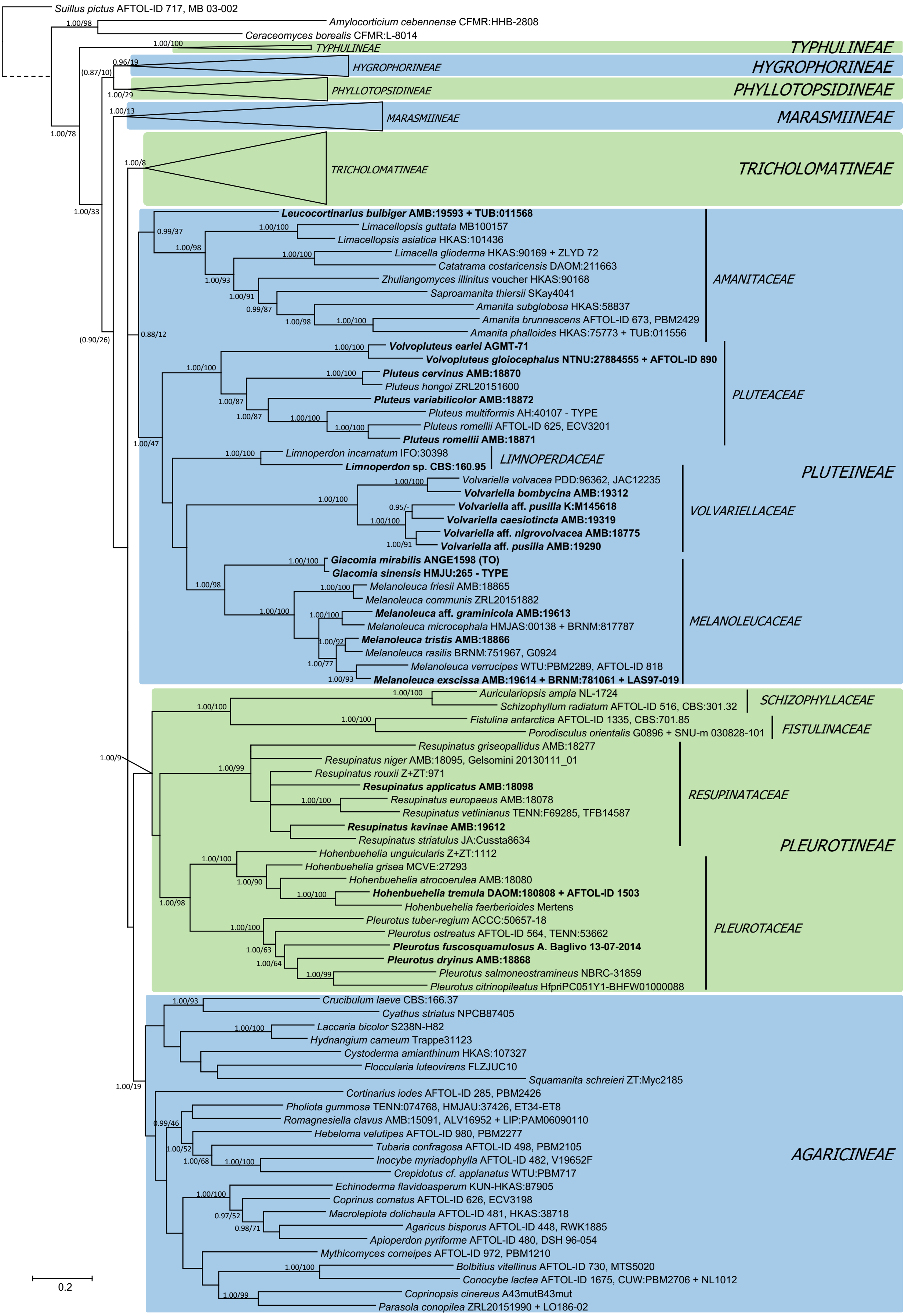

Fig. 2. Bayesian inference phylogram built with nucleotide sequence data of six loci (5.8S, LSU, SSU, *RPB1*-exons, *RPB2*-exons and *TEF1*-exons) of the main lineages inside order *Agaricales* (focused on suborders *Agaricineae, Pleurotineae* and *Pluteineae*), rooted with *Suillus pictus* (*Boletales*), *Amylocorticium cebennense* and *Ceraceomyces borealis* (*Amylocorticiales*) as outgroups. The main suborders are shown in color boxes, while family names are shown next to vertical bars. Nodes were annotated with Bayesian PP (left) and ML BP (right) values, with the significance threshold considered as Bayesian PP >0.95 and/or ML BP >70 %. Subsignificant support values were annotated in parentheses. Boldface names represent samples sequenced for this study. The dashed branch was shortened for graphic presentation.

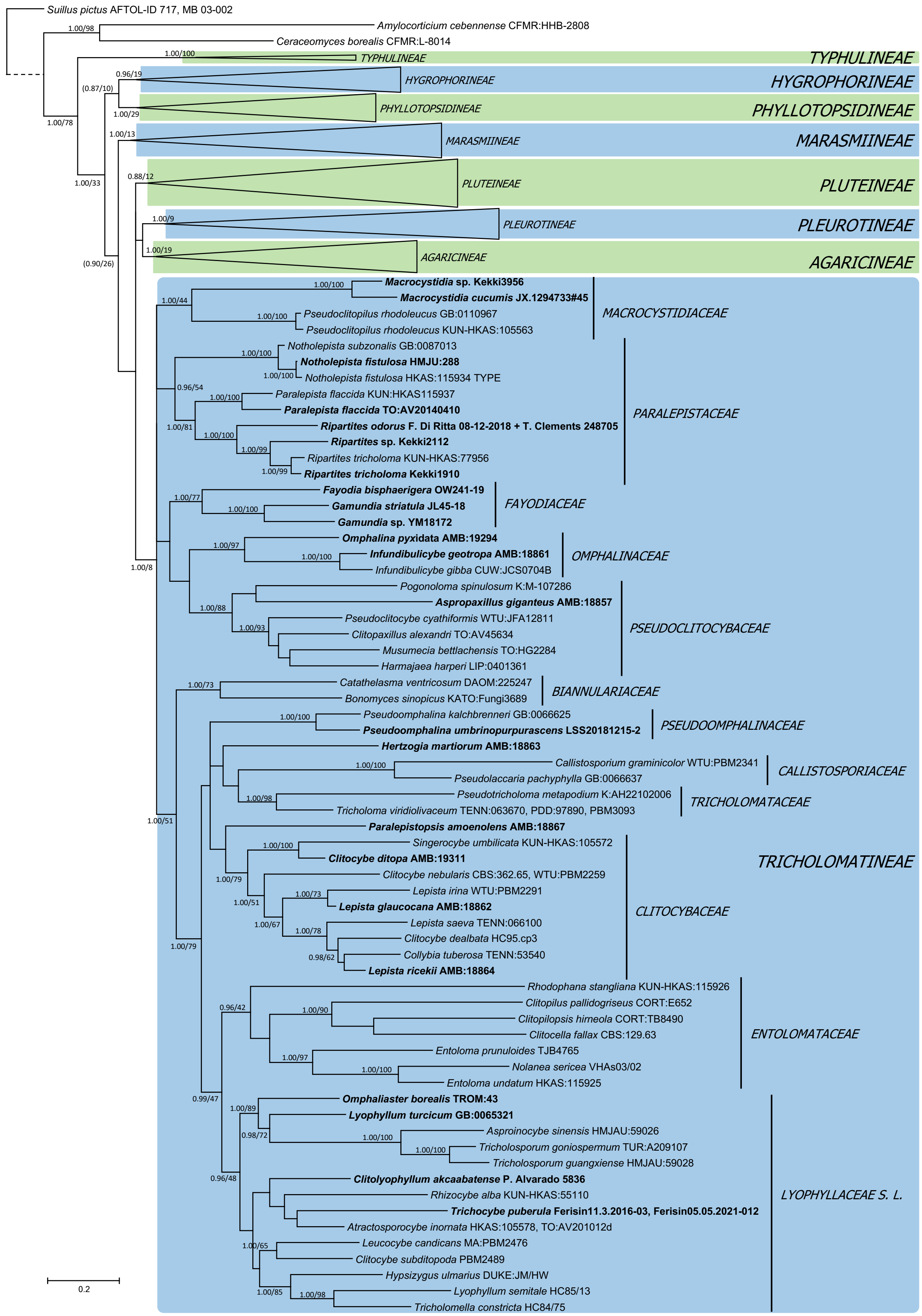

Fig. 3. Bayesian inference phylogram built with nucleotide sequence data of six loci (5.8S, LSU, SSU, *RPB1*-exons, *RPB2*-exons and *TEF1*-exons) of the main lineages inside order *Agaricales* (focused on suborder *Tricholomatineae*), rooted with *Suillus pictus* (*Boletales*), *Amylocorticium cebennense* and *Ceraceomyces borealis* (*Amylocorticiales*) as outgroups. The main suborders are shown in color boxes, while family names are shown next to vertical bars. Nodes were annotated with Bayesian PP (left) and ML BP (right) values, with the significance threshold considered as Bayesian PP >0.95 and/or ML BP >70 %. Subsignificant support values were annotated in parentheses. Boldface names represent samples sequenced for this study. The dashed branch was shortened for graphic presentation.

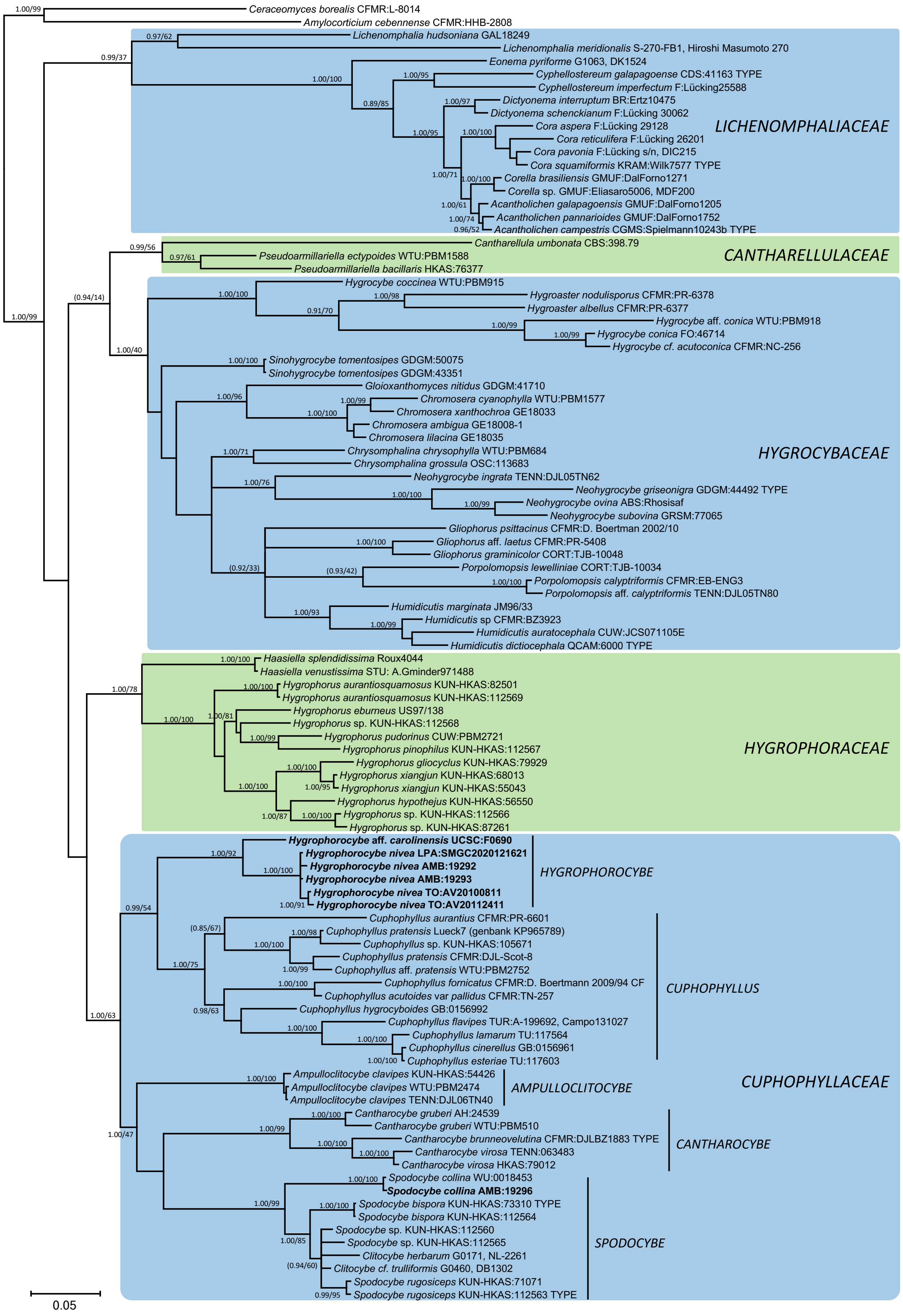

Fig. 4. Bayesian inference phylogram built with nucleotide sequence data of three loci (LSU, *RPB2*-exons and *TEF1*-exons) of the main lineages inside suborder *Hygrophorineae* rooted with *Amylocorticium cebennense* and *Ceraceomyces borealis* (*Amylocorticiales*) as outgroups. The main families are shown in color boxes, while generic names are shown next to vertical bars. Nodes were annotated with Bayesian PP (left) and ML BP (right) values, with the significance threshold considered as Bayesian PP >0.95 and/or ML BP >70 %. Subsignificant support values were annotated in parentheses. Boldface names represent samples sequenced for this study.

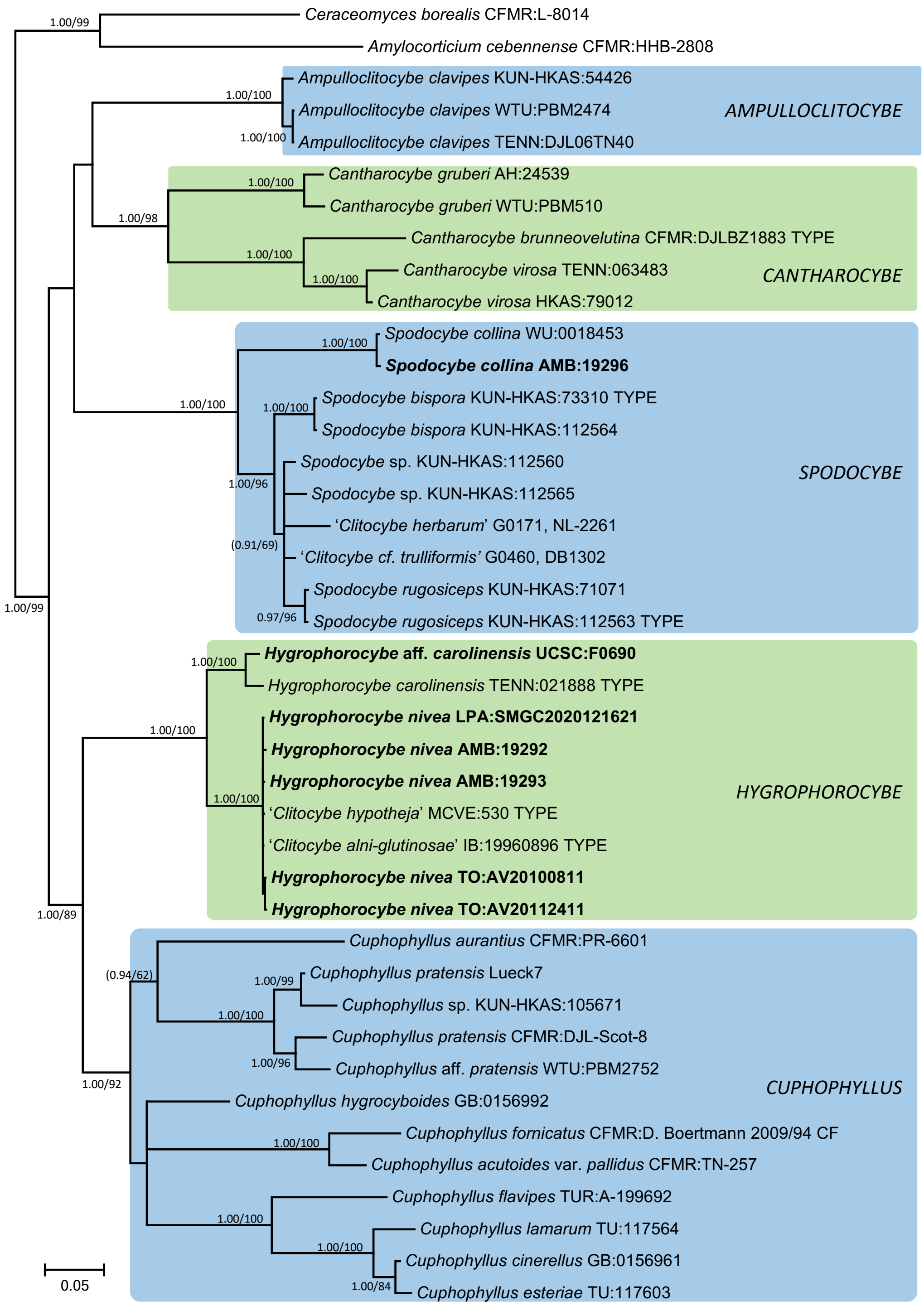

Fig. 5. Bayesian inference phylogram built with nucleotide sequence data of four loci (ITS, LSU, *RPB2*-exons and *TEF1*-exons) of the main lineages inside family *Cuphophyllaceae* rooted with *Amylocorticium cebennense* and *Ceraceomyces borealis* (*Amylocorticiales*) as outgroups. The main genera are shown in color boxes. Nodes were annotated with Bayesian PP (left) and ML BP (right) values, with the significance threshold considered as Bayesian PP >0.95 and/or ML BP >70 %. Subsignificant support values were annotated in parentheses. Boldface names represent samples sequenced for this study.

(decaying leaf litter, plant debris, and decaying wood, and include coprophilous, humicolous, and lignicolous species), or parasitic (red algae, plants, including some important phytopathogens), while endophytic and lichenized lifestyles are less frequent (Hibbett & Thorn 2001, Oberwinkler 2012, Agerer 2018). A few species are nematode-trapping or form mutualistic symbiosis with ants and termites (Money 2016, Agerer 2018, Kalichman *et al*. 2020). The vast majority of *Agaricales* is terrestrial, found in almost any habitat, from woods and grasslands to deserts and dunes (Kusuma *et al*. 2021), only a few taxa are known for freshwater (Desjardin *et al*. 1995, Frank *et al*. 2010, Abdel-Aziz 2016) or marine environments (Hibbett & Binder 2001, Binder *et al*. 2006, Jones *et al*. 2015, 2019, Abdel-Wahab *et al*. 2019). Lignicolous *Agaricales* are mainly associated with white rot (Worrall *et al*. 1997). Brown rot is a rare feeding strategy in *Agaricales*, associated with small genera such as *Hypsizygus* and *Ossicaulis* (Redhead & Ginns 1985). An unusual intermediate wood decomposition type was recently detected in the polyporoid *Fistulina* and corticioid *Cylindrobasidium* (Floudas *et al*. 2015). Enzymes secreted by *Agaricales* fungi responsible for wood rot are highly relevant to carbon and nutrient cycling in nature play important roles in maintaining environmental balance (Yang *et al*. 2017, Ruiz-Dueñas *et al*. 2020, Floudas *et al*. 2020, Sánchez-Ruiz *et al*. 2021). Toxic secondary metabolites as amatoxins, psilocybin, muscarine and oxazole compounds which can lead to poisoning in humans are produced mainly by taxa in *Agaricineae*, *Pluteineae* and *Tricholomatineae* (Enjalbert *et al*. 2002, Sgambelluri *et al*. 2014, Lee *et al*. 2018, Luo *et al*. 2018, Reynolds *et al*. 2018, Lüli *et al*. 2019, Sarawi *et al*. 2022, He *et al*. 2023). By now, about 25 400 species have been ascribed to the order *Agaricales* (Bánki *et al*. 2023), which contains 684 genera, including at least nine extinct (fossil) taxa (Hibbett *et al*. 2003, Poinar 2016, Cai *et al*. 2017, Heads *et al*. 2017), clustered in 45 families (Catalogue of Life, https://www.catalogueoflife.org/).

Agaricales is sister to *Amylocorticiales* (Binder *et al*. 2010, Hodkinson *et al*. 2014, Dentinger *et al*. 2016, Zhao *et al*. 2017, He *et al*. 2019, Sánchez-García *et al*. 2020, Li *et al*. 2021, Liu *et al*. 2023) together forming the superorder *Agaricanae* (Agerer 2018). *Amylocorticiales* consists mainly of lignicolous saprotrophic fungi with predominantly resupinate, rarely effuse-reflexed, cupulate or flabellate basidiomes with smooth, wrinkled to tuberculate, rarely tubulose hymenophore (Binder *et al*. 2010, Garnica *et al*. 2021). *Agaricanae* and “Boletanae *ad int*.” (composed of *Boletales* and *Atheliales*; Agerer 2018) form the subclass *Agaricomycetidae* of the class *Agaricomycetes*. *Jaapiales* was proposed in *Agaricomycetidae* based on multigene data (Binder *et al*. 2010), but later placed outside it by Li *et al*. (2021) based on genomic data.

Agaricineae Fr. [as ‘Agaricini’], Syst. orb. veg. (Lundae) 1: 65 (1825) *emend*. Aime *et al*., Biol. J. Linn. Soc. 117: 27. 2016.

Representative families: *Agaricaceae* (including *Coprinaceae*, *Lycoperdaceae*, *Podaxaceae* and *Tulostomataceae*), *Bolbitiaceae*, *Cortinariaceae*, *Crassisporiaceae*, *Crepidotaceae*, *Galeropsidaceae*, *Hydnangiaceae*, *Hymenogastraceae* (including *Chromocyphellaceae*), *Inocybaceae*, *Mythicomycetaceae*, *Nidulariaceae*, *Psathyrellaceae*, *Squamanitaceae*, *Strophariaceae*, and *Tubariaceae*.

Notes: Saprotrophic (Singer 1986), some associated with rodent latrines (ammonia-fungi or post-putrefaction fungi, *Hymenogastraceae*, *Psathyrellaceae*, Sagara 1975, 1995, Sagara *et al*. 2000, Suzuki 2009), ECM (ectomycorrhizal) forming (*Cortinariaceae*, *Hydnangiaceae*, *Hymenogastraceae* and *Inocybaceae*; Rinaldi *et al*. 2008, Tedersoo *et al*. 2010, Tedersoo & Smith 2013, Soop *et al*. 2016), arbutoid mycorrhizas forming (Smith & Read 2008, Kühdorf *et al*. 2016), leaf cutting ants associated (*Leucoagaricus*, Fisher *et al*. 1994, Araújo *et al*. 2022, Urrea-Valencia *et al*. 2023), nematode hunters (nematophagy, Vizzini 2008) or mycoparasitic (*Squamanita*, *Dissoderma*, *Psathyrella epimyces*; Redhead *et al*. 1994, Liu *et al*. 2021, Saar *et al*. 2022). A previously unknown ectomycorrhizal relationship between poplar roots and *Bovista limosa* (*Agaricaceae*) was recently described by Xiao *et al*. (2023a). The *Agaricineae* emend. Aime *et al*. represents one of the seven suborders of *Agaricales* identified by Dentinger *et al*. (2016) using a phylogenomic approach and later confirmed in different works, *i.e.*, Varga *et al*. (2019), Olariaga *et al*. (2020), Li *et al*. (2021), Wang *et al*. (2023b). This suborder corresponds to the “Agaricoid” clade found in previous works (Matheny *et al*. 2006, 2015, Garnica *et al*. 2007, Binder *et al*. 2010, Kohler *et al*. 2015). The present results agree with recent studies focusing on relationships at the family level within *Agaricineae*, *i.e.*, Matheny *et al*. (2015), Vizzini *et al*. (2019a) or Liu *et al*. (2021). Many species in *Agaricineae* show pigmented and/or thick-walled spores (Matheny *et al*. 2006, 2015, Garnica *et al*. 2007, Vizzini *et al*. 2019a). Although species producing dark-pigmented spores (dark-pigmented agarics) are present in a few other lineages (*e.g.*, *Melanomphalia*, *Hygrophorineae*, *Lichenomphaliaceae*, Aime *et al*. 2005 or *Ripartites*, *Tricholomatineae*, *Paralepistaceae*, see below), the overwhelming majority of these have evolved within *Agaricineae*. The presence of basidiospores with a thickened, dark-pigmented wall, and occasionally also germ pores, is probably indicative of adaptations to survive harsh conditions in specialised environments (*e.g.*, dung, burnt sites) (Watling 1988, Garnica *et al*. 2007, Halbwachs *et al*. 2015, Halbwachs & Bässler 2021). As pigmentation and thick walls are necessary, for example, to the basidiospores of coprophilous species to survive harsh conditions in digestive systems of animals but reduce their germination capability, the germ pore is suggested facilitating germination providing a preferential thin-walled spot where the germ tube can force its way through the tough spore wall (Watling 1988, Halbwachs*et al*. 2015, Halbwachs & Bässler 2021). In the taxa with asexual morphs, thallic conidiogenesis is the most frequent (Watling 1979, Pantidou *et al*. 1983, Buchalo 1988, Walther *et al*. 2005, Walther & Weiß 2006).

Clavariineae Olariaga *et al*., Stud. Mycol. 96: 171. 2020.

Type: *Clavaria* Vaill. ex L., Species Plantarum 2: 1182. 1753.

Representative family: *Clavariaceae*.

Notes: Suborder *Clavariineae* is characterized by clavarioid basidiomes (*Ceratellopsis*, *Clavaria*, *Clavicorona*, *Clavulinopsis*, *Hirticlavula*, *Holocoryne*, *Ramariopsis*), more rarely agaricoid, gymnocarpic with waxy hygrophoroid decurrent lamellae (*Camarophyllopsis*, *Hodophilus*, *Lamelloclavaria*), hydnoid (*Mucronella*) or corticioid (*Hyphodontiella*). Hyphal system monomitic, or more rarely dimitic. Basidiospores colourless, usually thin-walled, smooth or ornamented, usually with multiguttulate contents, sometimes with amyloid or dextrinoid reactions. Basidia claviform, with up to four sterigmata, occasionally sometimes with a loop-like (medallion) basal clamp (*Clavaria* subgen. *Holocoryne*). Cystidia usually absent. Pileipellis either a hymeniderm or a trichoderm with rounded terminal elements in genera with pileostipitate basidiomes. Clamp connections present or absent, sometimes restricted to basidia. Saprotrophic on dead wood, herbaceous plants, or leaves, or biotrophic with grasses and bryophyte gametophytes (Birkebak 2015, Birkebak *et al*. 2013, 2016). The presence of *TEF1* intron 21 (numbering according to Matheny *et al*. 2007), absent in the rest of the *Agaricales* (Matheny *et al*. 2007), seems so far restricted to some genera of *Clavariaceae* (*Camarophyllopsis, Clavaria*, *Clavulinopsis*; absent in *Ceratellopsis*).

The traditional concept of the family *Clavariaceae* as circumscribed by Corner (1950, 1970), Thind (1961), Parmasto (1965), Jülich (1984), and Petersen (1988) was later expanded upon by several authors based on the results of DNA-based phylogenetic analyses. The family *Clavariaceae* was first shown to have affinities with the *Agaricales* by Pine *et al*. (1999) using nuclear and mitochondrial rDNA loci. *Clavaria fusiformis* (now *Clavulinopsis*) was apparently near to the /tricholomopsis clade and sister to the /hemimycena clade in Moncalvo *et al*. (2002). *Clavaria*, *Clavulinopsis*, *Mucronella* and *Ramariopsis* were found to be monophyletic by Larsson *et al*. (2004) and Dentinger & McLaughlin

(2006). Matheny *et al*. (2006) demonstrated that the gilled pileate-stipitate genus *Camarophyllopsis* belongs in the *Clavariaceae*, and not inside the *Hygrophoraceae* as suggested by Hesler & Smith (1963), Arnolds (1974a, b, 1986), Kühner 1980, Singer (1986), Kovalenko (1989), Young (1999, 2005), and Boertmann (2002). The resupinate wood-inhabiting genus *Hyphodontiella* was shown to belong in the *Clavariaceae* too by Larsson (2007). Kautmanová *et al*. (2012a) included in their phylogenetic analysis of *Clavariaceae* the type of *Clavaria* (*C. fragilis*), confirming the previous assumptions. The genera *Hodophilus* (gilled) and *Clavicorona* (clavarioid) were also shown to be members of the *Clavariaceae* by Birkebak *et al*. (2013); and so was the clavarioid *Hirticlavula* by Petersen *et al*. (2014), the clavarioid *Holocoryne*, the gilled *Lamelloclavaria* by Birkebak *et al*. (2016), and the clavarioid *Ceratellopsis* emended by Olariaga *et al*. (2020).

As regards the phylogenetic placement of the family, members of *Clavariaceae* were considered *incertae sedis* for a long time by Pine *et al*. (1999), Moncalvo *et al*. (2002), Larsson *et al*. (2004), Larsson (2007), and in Lodge *et al*. (2014). In subsequent analyses, *Clavariaceae* was found to be an early diverging basal clade of *Agaricales*, either showing an isolated position (*e.g*., Binder *et al*. 2010, Sánchez-García *et al*. 2020, Olariaga *et al*. 2020) or related to *Atheliaceae p.p*. (Plicaturopsidoid clade, Matheny *et al*. 2006), or *Hygrophoraceae* (Ryberg & Matheny 2011, Dentinger *et al*. 2016, Varga *et al*. 2019). Based on a more diverse dataset, Olariaga *et al*. (2020) established suborder *Clavariineae* inside the order *Agaricales*, although most species were represented only by ribosomal DNA (LSU) sequences. Suborder *Clavariineae* was removed from the present analysis to avoid adding too much phylogenetic noise from a clade already shown to be basal to the remaining ones (Olariaga *et al*. 2020, Wang *et al*. 2023b), and because of the incomplete information available in databases (*i.e*., multigene data of *Hirticlavula* or *Hyphodontiella* are not available). However, additional analyses (Supplementary Fig. S1) agree to place *Clavariineae* in an early branching (basal) clade not related to any other in the dataset employed.

Hygrophorineae Aime *et al*., Biol. J. Linn. Soc. 117: 26. 2016.
Synonyms: *Hygrophorales* Bon, Flore mycologique d'Europe 1: 87. 1990.
Hygrophorales Locq., Mycol. Gén. Struct. (Paris): 98. 1984, *nom. inval.*, Art. 39.1 (Shenzhen).

Type: *Hygrophorus* Fr., Fl. Scan.: 339. 1836. [1835].

Representative families: *Cantharellulaceae*, *Cuphophyllaceae*, *Hygrocybaceae*, *Hygrophoraceae*, and *Lichenomphaliaceae*.

Notes: *Hygrophorineae* is characterized by basidiomes primarily agaricoid, hymenophore predominantly lamellate, occasionally smooth, wrinkled or forked, often pigmented with L-DOPA betalains or carotenoids, and waxy; spore deposit white or rarely lightly pigmented (ochraceous, salmon, green); hyphae monomitic, usually with clamp connections; cystidia normally absent; basidia normally 2–4-sporic, mean ratio of basidia to basidiospore length 3–7; basidiospores colourless, predominantly inamyloid; terricolous, lignicolous, bryicolous, pteridicolous, saprotrophic, rarely parasitic on mosses, or symbiotic and then lichen-forming with cyanobacteria and/or green algae or ectomycorrhizal.

To treat the major monophyletic clades within *Hygrophorineae* (Fig. 4) at the same level as those of the other suborders, the main clades (four subfamilies and one tribe) recovered by Lodge *et al*. (2014) and He & Yang (2021) within *Hygrophoraceae* are here upgraded to the rank of independent families. As a result, five families are recognized in the present work inside *Hygrophorineae* (see below).

Hygrophoraceae Lotsy, Vortr. Bot. Stammesgesch. 1: 705. 1907.
Perhaps based on Hygrophorées Roze, Bull. Soc. Bot. France 23: 110. 1876, *nom. inval.*, Art. 32.1(b); see Art. 18.4 (Shenzhen).

Representative genera: *Haasiella* and *Hygrophorus*.

Notes: *Hygrophoraceae* is characterized by gymnocarpous or secondarily mixangiocarpous basidiomes; lamellae subdecurrent to deeply decurrent; trama inamyloid; hymenophoral trama divergent (hyphae diverging from a central strand), or bidirectional (horizontal hyphae that are parallel to the lamellar edge present, sometimes woven through vertically oriented, regular or subregular generative hyphae that are confined or not to a central strand) and a pachypodial structure below the active hymenium; basidiospores thin- or thick-walled, inamyloid, metachromatic or not, colorless or lightly pigmented (ochraceous, salmon, green); pigments muscaflavin (betalain) or carotenoids; habit terricolous (ectomycorrhizal, *Hygrophorus*) or xylophagous (saprotrophic, *Haasiella*) (Tedersoo *et al*. 2010, Seitzman *et al*. 2011, Lodge *et al*. 2014, Feng & Yang 2019). The phylogenetic affinities of *Haasiella* with *Hygrophorus* (Fig. 4) had already been previously highlighted by Vizzini *et al*. (2012b), Lodge *et al*. (2014), He & Yang (2021) and Wang *et al*. (2023a). The genus *Aeruginospora* (typified with *A. singularis*) is probably closely related to *Haasiella* based on their morphology: a similar basidiome form, bidirectional hymenophoral trama, a thickening hymenium forming a pachypodial structure, and spores that are thick-walled, pigmented, and with a red metachromatic endosporium (Lodge *et al*. 2014).

Hygrocybaceae (Padamsee & Lodge) Vizzini, Consiglio & P. Alvarado, ***stat. nov. & comb. nov.*** MycoBank MB 851141.
Synonym: *Hygrophoraceae* subfamily *Hygrocyboideae* Padamsee & Lodge, Fungal Diversity 64: 19. 2013. [2014].

Type: *Hygrocybe* (Fr.) P. Kumm., Führ. Pilzk. (Zwickau): 111. 1871.
Synonym: *Hygrophorus* subg. *Hygrocybe* Fr., Summa veg. Scand., Section Post. (Stockholm): 308. 1849.

Representative genera: *Chromosera*, *Chrysomphalina*, *Gliophorus*, *Gloioxanthomyces*, *Humidicutis*, *Hygrocybe* (*Hygroaster* included), *Neohygrocybe*, *Porpolomopsis*, and *Sinohygrocybe*.

Notes: The circumscription of the family *Hygrocybaceae* is similar to those outlined by Lodge *et al* (2014), Wang *et al*. (2018) and He & Yang (2021) for *Hygrophoraceae* subfamily *Hygrocyboideae* except for the position of *Chrysomphalina* (typified with *C. chrysophylla*), which was included in *Hygrophoraceae* subfamily *Hygrophoroideae* by these latter authors and recently by Wang *et al*. (2023a). Our analysis (Fig. 4) indicated *Chrysomphalina* as part of *Hygrocybaceae*. Prior to the first sequencing and phylogenetic analyses of *Haasiella*, Redhead *et al*. (2002a) postulated a close relationship between this genus and *Chrysomphalina* based on pigments and micromorphology, although Kost (1986) disagreed based on the micromorphology. Clémençon (1982) combined *Chrysomphalina grossula* into *Camarophyllus* (subg. *Aeruginospora*) owing to the similar structure of their hymenophoral trama. Romagnesi (1996) included *Haasiella* and *Phyllotopsis* along with the type, *Chrysomphalina*, in his tribe *Chrysomphalineae* (invalidly published before that as tribe *Paracantharelleae*, Romagnesi 1995) due to the presence of carotenoid pigments in all of them. *Hygrocybaceae* is characterized by basidiomes with colors usually bright, rarely dull; lamellae, usually thick, yielding a waxy substance when crushed, rarely absent; true veils lacking, rarely with false peronate veils formed by fusion of the gelatinous ixocutis of the pileus and stipe, and fibrillose partial veils formed by hyphae emanating from the lamellar edge and stipe apex; basidiospores thin-walled, guttulate, colourless (though species with black staining basidiomes may have fuscous inclusions), smooth or ornamented by conical spines, inamyloid, usually acyanophilous; basidia guttulate, mono- or dimorphic; pleurocystidia absent; pseudocystidia sometimes present; true cheilocystidia usually absent but cystidia-like hyphoid elements emanating from the lamellar context or cylindric or strangulated ixo-cheilocystidia embedded in a gelatinous matrix sometimes present; hymenophoral trama inamyloid, regular or subregular but not highly interwoven, divergent or pachypodial; comprised of long or short hyphal segments with oblique or perpendicular cross walls, often constricted at the septations, usually thin-walled but hyphae of the central mediostratum sometimes slightly thickened. Pileipellis structure a cutis, disrupted cutis, ixocutis, ixotrichodermium or trichodermium, but never hymeniform; pigments muscaflavin or carotenoids; clamp connections present or absent; habit terrestrial, rarely on wood or arboreal, often associated with mosses, growing in grasslands or forests; possibly biotrophic (Seitzman *et al*. 2011) but not known to form ectomycorrhizae with woody plants.

Lichenomphaliaceae (Lücking & Redhead) Vizzini, Consiglio & P. Alvarado, ***stat. nov. & comb. nov.*** MycoBank MB851143.
Synonyms: *Hygrophoraceae* subfamily *Lichenomphalioideae* Lücking & Redhead, Fungal Diversity 64: 68. 2013. [2014].
Arrheniaceae Locq., Mycol. Gén. Struct. (Paris): 109. 1984, *nom. inval.*, Art. 39.1 (Shenzhen).

Type: *Lichenomphalia* Redhead *et al*., Mycotaxon 83: 38. 2002.

Representative genera: *Acantholichen*, *Arrhenia*, *Cora*, *Corella*, *Cyphellostereum*, *Dictyonema*, *Eonema*, and *Lichenomphalia*.

Notes: The present work does not include collections of *Arrhenia*, but other studies suggest that this genus belongs in *Lichenomphaliaceae* (Lodge *et al* 2014, Wang *et al*. 2018, He & Yang 2021). The delimitation of this family corresponds quite well to subfamily *Lichenomphalioideae* (in Lodge *et al*. 2014) except for its tribe *Cantharelluleae* which is here raised to family rank. *Lichenomphaliaceae* is characterized by basidiomes omphalinoid, pleurotoid, stereoid-corticioid or lentoid-cyphelloid, rarely absent, usually fuscous, green or colourless, rarely orange or yellow; hymenium lamellate, cantharelloid, merulioid (wrinkled) or smooth; basidiospores inamyloid; basidia elongated or not; clamp connections present or absent; L-DOPA betalains and apparently also carotenoid pigments absent; habit primarily bryophilous or phycophilous, often lichenized, rarely parasitic, or saprobic. The basidiolichens are mainly distributed in five orders of *Agaricomycetes*, *viz. Agaricales*, *Atheliales*, *Lepidostromatales*, *Cantharellales* and *Corticiales* (Oberwinkler 2012, Hodkinson *et al*. 2014, Lücking *et al*. 2017, Masumoto & Degawa 2020, Zhang *et al*. 2022). Among the *Agaricales*, virtually all lichenized species are accommodated within the *Lichenomphaliaceae* with the only striking exception of *Omphalina licheniformis* which belongs to *Omphalinaceae* (*Tricholomatineae*, Zhang *et al*. 2022). Some species of *Collybiopsis* (*Omphalotaceae*, *Marasmiineae*) are associated to the green alga *Coccomyxa* and suspected to be lichenized (Lepp 2011a, b, Cooper & Leonard 2013).

Cantharellulaceae (Lodge *et al.*) Vizzini, Consiglio & P. Alvarado, ***stat. nov. & comb. nov.*** MycoBank MB851144.
Synonym: *Hygrophoraceae* subfamily *Lichenomphalioideae*, tribe *Cantharelluleae* Lodge *et al.*, Fungal Diversity 64: 74. 2013. [2014].

Type: *Cantharellula* Singer, Rev. Mycol. (Paris) 1: 281. 1936.

Representative genera: *Cantharellula* and *Pseudoarmillariella*.

Notes: *Cantharellulaceae* is characterized by basidiomes clitocyboid or omphalinoid; pileus convex, depressed or infundibuliform; lamellae decurrent, repeatedly forked, sometimes staining reddish brown; stipe central or eccentric; basidiospores smooth, with a length usually at least twice the diameter, colourless, distinctly amyloid, acyanophilous; basidia with basal clamp connections, about 4 times the length of the basidiospores; cheilocystidia and pleurocystidia absent; pileipellis hyphae with cytoplasmatic pigments, with or without encrusting pigments; hymenophoral trama partly gelatinized at the lamellar edge, tridirectional, with a subregular or regular central strand, lateral strands with frequent hyphae parallel to the lamellar edge woven through a few vertically oriented hyphae, and abundant generative hyphae arranged predominantly in parallel to the basidia and giving rise to the subhymenial cells, but obliquely angled (divergent) at the lamellar edge; subhymenium subramose or pachypodial, composed of short- or long-celled hyphal segments predominantly parallel and oriented in the same direction as the basidia, but a few highly curved and intertwined; forming a weak hymenial palisade via proliferation of basidia from subhymenial cells (thickening hymenium); L-DOPA betalains and apparently also carotenoid pigments absent; bryophilous or lignicolous. The forked lamellae, long, smooth, amyloid spores, thickening hymenium and subhymenium, and tridirectional hymenophoral trama is a unique combination of characters within *Hygrophorineae* shared by *Cantharellula* and *Pseudoarmillariella* (Singer 1956, 1986, Norvell *et al*. 1994, Redhead *et al*. 2002a, Yang *et al*. 2013, Lodge *et al*. 2014). Singer (1936) established the genus *Cantharellula* to accommodate *Merulius umbonatus* where then he transferred *Agaricus ectypoides* (Singer 1942a). Later, he classified both species in *Cantharellula* subg. *Pseudoarmillariella* (Singer 1948), and finally raised *Cantharellula* subg. *Pseudoarmillariella* to genus rank around *P. ectypoides* (Singer 1956). Two species were recognized within *Cantharellula* by Lodge *et al*. (2014), *viz*. the type *C. umbonata* (with a wide distribution) and *C. infundibuliformis*, another species from Argentina by now lacking sequence data. Several species of *Cantharellula* were recently moved to other genera: *Cantharellula foetida* to *Pseudoclitocybe* by Cooper (2014); *C. humicola* to *Corneriella* and *C. umbrosa* to *Pseudotricholoma* by Sánchez-García *et al*. (2014); and *C. intermedia* to *Pseudoomphalina* by Voitk *et al*. (2020a). Regarding *Pseudoarmillariella*, three are the species known, *viz*. the type *P. ectypoides* (present in North and Central America, Singer 1986, Norvell *et al*. 1994, Lodge *et al*. 2014), *P. fistulosa* (New Zealand, Stevenson 1964, Horak 1971), and *P. bacillaris* (China, Yuan & Sun 2007, as *Cantharellus melanoxeros*; Yang *et al*. 2013). DNA sequences of *P. ectypoides* and *P. bacillaris* are present in public databases (Yang *et al*. 2013, Lodge *et al*. 2014). *Pseudoarmillariella* differs from *Cantharellula* in the presence of encrusting pigments on the pileipellis hyphae, presence of bright ochraceous pigments in the hymenophore (Norvell *et al*. 1994, Singer 1986, Lodge *et al*. 2014), and in growing on fallen rotting gymnospermous wood (Stevenson 1964, Singer 1986, Yang *et al*. 2013) (while *C. umbonata* is associated with mosses; Lawrey *et al*. 2009, Lodge *et al*. 2014).

The systematic position of these two genera has been debated for a long time, being unclear until recently. Singer (1942, 1948, 1986) recognized the close relationship between *C. umbonata* and *P. ectypoides* and placed them together with other amyloid spored genera in the *Tricholomataceae*, tribe *Leucopaxilleae*. Moncalvo *et al*. (2002) were the first to provide molecular evidence of the sister relation between the lineages of *Cantharellula* and *Pseudoarmillariella*, a clade apparently close to the *Arrhenia* group on the basis of nrLSU sequences. Lodge *et al*. (2006) were the first to obtain a significant support for the Cantharelluleae clade using an extended four-gene dataset, while Matheny *et al*. (2006) and Lawrey *et al*. (2009) obtained significant evidence for the placement of *P. ectypoides* and *Lichenomphalia umbellifera* inside the family *Hygrophoraceae*. Lodge *et al*. (2014), employing an extended multigene dataset, placed *Cantharellula* and *Pseudoarmillariella* in a new tribe, *Cantharelluleae*, within subfamily *Lichenomphalioideae*. Because of the peculiar morphological traits of this tribe and the taxonomic treatment of the other clades of suborder *Hygrophorineae*, it is here raised to the family rank (see above).

Cuphophyllaceae (Z.M. He & Zhu L. Yang) Vizzini, Consiglio & P. Alvarado, ***stat. nov. & comb. nov.*** MycoBank MB 851145.
Synonym: *Hygrophoraceae* subfamily *Cuphophylloideae* Z.M. He & Zhu L. Yang, MycoKeys 79: 138. 2021.

Type: *Cuphophyllus* (Donk) Bon, Doc. Mycol. 14(no. 56): 10. 1985. [1984].
Synonym: *Hygrocybe* subgen. *Cuphophyllus* Donk, Beih. Nova Hedwigia 5: 45. 1962.

Representative genera: *Ampulloclitocybe*, *Cantharocybe*, *Cuphophyllus*, *Hygrophorocybe*, and *Spodocybe* (Fig. 8E).

Notes: The family corresponds well to the Cuphophylloid grade in Lodge *et al*. (2014) and Wang *et al*. (2018), and to *Hygrophoraceae* subfamily *Cuphophylloideae* (He & Yang 2021) plus *Hygrophorocybe*. *Cuphophyllaceae* is characterized by basidiomes mostly clitocyboid, rarely omphalinoid or mycenoid, pileus convex, applanate to funnel-shaped; surface usually dry, smooth, lubricous or rarely viscid; lamellae decurrent to long decurrent; veils absent; basidiospores ellipsoid, oblong or subglobose, thin-walled, smooth (light microscopy), cyanophilous or not and inamyloid; pileipellis usually a cutis, sometimes ixocutis or trichoderm; hymenophoral trama regular, subregular, interwoven or bidirectional; clamp connections usually present; L-DOPA betalains and apparently also carotenoid pigments absent; terricolous, rarely on wood, widespread in temperate and tropical regions. Most species are presumably saprotrophic (Lodge *et al*. 2014, He & Yang 2021). *Ampulloclitocybe clavipes* (Merlini *et al*. 2000), and *C. virgineus* (Farrell *et al*. 1977), have been successfully cultured on agar media – a trait shared, for example, with saprotrophic species of the related suborder *Phyllotopsidineae* (see below) such as *Aphroditeola* (Redhead 2013), *Phyllotopsis nidulans* (Jayasinghe & Parkinson 2008), *Sarcomyxa serotina* (Kim *et al*. 2012), *Tricholomopsis rutilans* (Murphy & Mitchell 2001), and *Macrotyphula* spp. (Dentinger & McLaughlin 2006). Some species of *Cuphophyllus* have a biotrophic mode of nutrition, but the nature of the fungus-plant association is largely unknown (Griffith *et al*. 2002, Seitzman *et al*. 2011, Halbwachs *et al*. 2018). *Cuphophyllus virgineus* was shown to be a root endophyte of *Plantago lanceolata* and vertically transmitted via seeds (Tello *et al*. 2014).

The genus *Cuphophyllus* is characterized by lamellae mostly arcuate-decurrent, subdecurrent or decurrent, rarely sinuate, usually thick near the pileus, often forked or veined, usually distant, usually brittle, often acquiring a chalky opaque appearance, basidiospores frequently broadly ellipsoid, subglobose or globose, sometimes ellipsoid or oblong, smooth also under SEM, acyanophilous, basidia long typically 7−8 (rarely 5−6) times the length of the basidiospores, hymenophoral trama usually highly interwoven (rarely subregular), with or without a regular or subregular central strand; cystidia absent; hyphae predominantly or partly interwoven, usually with dissolved pigments, sometimes with intraparietal and encrusting pigments (Lodge *et al*. 2014, Voitk *et al*. 2020b). *Ampulloclitocybe* (= *Clavicybe*) differs from *Cuphophyllus* in having not forked, thin and close lamellae, basidia less than 5 times the length of the basidiospores, a bidirectional hymenophoral trama, subparallel rather than interwoven pileipellis hyphae, and basidiospores appearing smooth with light microscopy but minutely roughened-rugose when viewed under SEM (scanning electron microscope) (Pegler & Young 1971, Bon 1997, Redhead *et al*. 2002a, Harmaja 2002, Lodge *et al*. 2014). It is known to produce a coprine-like (antabuse-like) aldehyde dehydrogenase inhibitor (Cochran & Cochran 1978, Yamaura *et al*. 1986) as well as a tyrosine kinase inhibitor named clavilactone (Cassinelli *et al*. 2000). *Cantharocybe* differs in having a regular hymenophoral trama, basidia to basidiospore length less than 5 and presence of cheilo- and caulocystidia (Bigelow & Smith 1973, Ovrebo *et al*. 2011, Kumar & Manimohan 2013, Lodge *et al*. 2014, Hosen *et al*. 2016, Kumla *et al*. 2018, Parnmen *et al*. 2020, Hussain *et al.* 2021). *Spodocybe* (Fig. 8E) is characterized by a rugose to felty-squamulose grey-brown pileus depressed (funnel-shaped) at maturity, usually with farinaceous odours, the ratio of basidia to basidiospore length less than 5, and subregular hymenophoral trama (Bon 1997, as *Clitocybe*, He & Yang 2021, Xiao *et al*. 2023b, Xu *et al*. 2023). Finally, *Hygrophorocybe* has thin lamellae, cyanophilous basidiospores, and a subregular hymenophoral trama (Romagnesi 1974, Bellú 1996, Bon 1997, as *Clitocybe*, Vizzini 2014a, and see below).

Hygrophorocybe Vizzini & Contu, Index Fungorum 161: 1. 2014.

Type: *Hygrophorocybe nivea* (Velen.) Vizzini & Contu, in Vizzini, Index Fungorum 161: 1. 2014.

Representative species: *Hygrophorocybe nivea*, *H. carolinensis*.

Notes: Bon (1997) included *H. nivea* in *Clitocybe* subgenus *Hygroclitocybe* (typified with *C. clavipes*, therefore a synonym of *Ampulloclitocybe*) because of the hygrophoroid long basidia, hymenophoral trama not strictly regular, and vacuolar pigment. This extremely artificial subgenus also included species of the unrelated genus *Infundibulicybe* (Harmaja 2003, *Omphalinaceae*, *Tricholomatineae*), so Vizzini (2014b) proposed a new genus, *Hygrophorocybe*, to accommodate *C. nivea* based on its morphology and unpublished rDNA data. Its position was considered uncertain by He *et al*. (2019), as DNA sequences were not yet available in public databases. In the present work, phylogenetic analyses based on sequences of rDNA and protein-coding genes suggest that *Hygrophorocybe* belongs in suborder *Hygrophorineae* (family *Hygrophoraceae* in Lodge *et al*. 2014) (Fig.

1), family *Cuphophyllaceae* (Figs 4, 5), being a sister lineage of *Cuphophyllus*. *Cuphophyllus* differs from *Hygrophorocybe* in its thick lamellae, acyanophilous basidiospores, interwoven (rarely almost subregular) hymenophoral trama, with or without a regular or subregular central strand, and very long basidia relative to spore length (usually 7–8, rarely 5–6 times spore length) (Bon 1985, 1990a, Lodge *et al*. 2014, Voitk *et al*. 2020b). Based on the original description by Maire (1928), *Clitocybe chudacae*, a species first collected in Algeria, should be considered a later synonym of *C. nivea*. Due to their white basidiomes with hygrophoroid habit, long basidia and large spores, two species from North America, *Clitocybe hygrophoroides* (Bigelow 1965, 1982) and *C. variabilis* (Murrill 1913, Smith 1944, Bigelow 1982, Gregory 2007) are here thought to be putative members of *Hygrophorocybe* too.

Hygrophorocybe nivea (Velen.) Vizzini & Contu, in Vizzini, Index Fungorum 161: 1. 2014. Figs 6L, 9.
Basionym: *Clitocybe nivea* Velen., České Houby (Praze) 2: 255. 1920.
Synonyms: *Clitocybe hypotheja* Bellù, Rivista Micol. 39(2): 106. 1996.
Clitocybe alni-glutinosae Contu & Ruggero, in Contu, Rivista Micol. 41(4): 349. 1999 [1998].
? *Clitocybe chudacae* Maire, Bull. Trimestriel Soc. Mycol. France 42: 38. 1928.

Description: *Habit* clitocyboid/hygrophoroid. *Pileus* 10–80(–120) mm diam, broadly convex at first then expanding, becoming plane or obtusely umbonate, rarely infundibuliform when old; margin incurved and inrolled at first, minutely ribbed (as in *Tricholoma stiparophyllum*); surface dry, smooth, glabrous, pruinose to velutinous, non-hygrophanous, sometimes rivulose to cracked, whitish, sometimes with light ochre-yellow (3A6-8, 4A7-8) tinges at centre. *Lamellae* decurrent to long decurrent, subdistant to distant, L = 35–45, l = 1–2(–3), narrow, 2–3(–4) mm broad, often forked or anastomosing, pinkish-cream (5A4-6) to yellowish (4A5-6) at maturity (yellowish in dried basidiomes), easily separable from the pileus context. *Stipe* (20)–30–60(–80) × 5–8(–12) mm, central, equal, or tapered upward, curved at times; interior solid, stuffed, finally hollow; surface smooth, with thin fibrillose coating, glabrescent; concolorous with the pileus. *Context* thick and firm at pileus centre (up to 15 mm thick), white. *Odour* none or very faintly fragrant; *taste* mild. *Spore deposit* whitish to light pinkish cream. *Basidiospores* (5.3–)6.4–*7.2*–7.9(–9.9) × (3.2–)3.9–*4.2*–4.6(–5.1) µm [208/6/6], Q= (1.34–)1.53–*1.71*–1.88(–2.19), V= (33.0–)51.7–*68.3*–84.8(–121) µm^3, ovoid to ellipsoid, sometimes nearly oblong-cylindrical, smooth, wall thin or somewhat thickened, inamyloid, cyanophilous. *Basidia* hygrophoroid, 30–45(–50) × 6.5–8.5 µm, 4–5(–6) times spore length, mostly 4-sporic, but sometimes 1- and 2-sporic, subclavate or narrowly clavate; sterigmata up to 6 µm long, sometimes delimited by secondary septa, clamped; sclerobasidia (crassobasidia) occasionally present; basidioles sometimes irregular in shape, clamped. *Subhymenium* consisting of short to elongated intertwined elements. *Hymenial cystidia* not observed. *Hymenophoral trama* subregular, unidirectional of subparallel hyphae; hyphae 1.5–8 µm diam, mostly cylindrical, some inflated, smooth, pale yellow in KOH, clamped. *Pileipellis* a cutis, loosely woven; hyphae 3–10 µm diam, cylindrical, some pileocystidioid, most smooth, with rare and short diverticula, some finely encrusted, yellow in KOH, clamped. *Subpellis* consisting of cylindrical or inflated, 4–15 µm wide hyphae, smooth, refractive, yellow in KOH, clamped. *Stipitipellis* arranged as a cutis of parallel, cylindrical (2–)2.5–4(–5) µm wide hyphae. *Caulocystidia* present often in tufts, mostly at stipe apex, 15–40(–50) × (2–)3–4(–5) µm, thin-walled, cylindrical, sinuous, with rounded apex, often trapping mature basidiospores fallen from the overlying hymenium. *Stipititrama* non-sarcodimitic, composed of colourless 4–7(–8) µm wide cylindrical hyphae (wall up to 0.5 µm thick). *Thromboplerous hyphae* present. *Clamp connections* present, very common in the pileipellis and stipitipellis. *Hyphal system* monomitic.

Habitat and distribution: Scattered or gregarious, in soil or needle litter, usually under coniferous trees, *Picea*, *Pinus* spp., *Pseudotsuga menziesii*, *Cryptomeria japonica*, *Chamaecyparis lawsoniana*, *Cedrus atlantica* (Cavet & Martin 1998) but also in mixed forest of broad-leaved trees; alpine and Mediterranean areas; autumn.

Materials examined: **Italy**, Emilia-Romagna, Ronchi (Monterenzio, BO), in a mixed forest of *Quercus pubescens* and *Q. cerris*, 5 Nov. 1992 and 1 Nov. 1994, G. Consiglio & G. Spisni (AMB:19314 and AMB:19293); Tudiano (Grizzana Morandi, BO), in a mixed forest of broad-leaved trees, 9 Oct. 1998, G. Consiglio & G. Spisni (AMB:19315); Puzzola (Grizzana Morandi, BO), in a mixed forest of broad-leaved trees, 13 Nov. 1999, G. Consiglio, G. Perdisa & G. Spisni (AMB:19316); Eremo di Zena (S. Lazzaro di Savena, BO), in a mixed forest of broad-leaved trees, 8 Dec. 1999, G. Consiglio & G. Bordoni (AMB:19317); Val Serena (San Benedetto Val Di Sambro, BO), under *Picea abies*, 30 Oct. 2001, G. Consiglio & E. Franceschini (AMB:19292); Lombardia, Brallo di Pregola (PV), Cima Colletta, 1493 m a.s.l., among litter in an artificial planting of *Pseudotsuga menziesii*, 15 Oct. 2022, M. Carbone (TUR-A 216591); Piemonte, Torino, Parco Leopardi, on *Chamaecyparis lawsoniana* litter, 8 Nov. 2010, A. Vizzini (TO:AV20100811); Torino, Parco della Rimembranza (Parco della Maddalena), on *Cryptomeria japonica* litter, 24 Nov. 2011, A. Vizzini (TO:AV20112411). **Spain**, Canary Islands, El Hierro, under *Myrica faya* and *Erica arborea*, 16 Dec. 2020, V. Escobio García (LPA:SMGC2020121621).

Notes: *Clitocybe nivea* was briefly described for the first time from specimens collected in some areas of the Czech Republic (Velenovský 1920) as a large and fleshy species with a pileus 3–10 cm diam, convex, white, felted-cottony at the margin; lamellae at first white then with pinkish hues; large ellipsoid spores, 6–9 µm; and growing gregarious in coniferous (spruce) litter. After the original description, the species fell into oblivion until Romagnesi (1974) resurrected the name for collections found under *Picea* in southern France. The species was later found again in France (*e.g.*, Bon 1997, Cavet & Martin 1998, Eyssartier & Roux 2011), Italy (*e.g.*, Bellú 1996, Consiglio 1997, Contu 1998, Migliozzi & Camboni 1999, Mua & Sanna 2006), Spain (*e.g.*, Tabarés 1996, Bañares & Beltrán 2009), Cyprus (under *Pinus brutia*; Loizides 2021), and Turkey (Oğuzhan Kaygusuz, pers. comm.). Its white hygrophoroid basidiomes (pileus convex and long decurrent subdistant lamellae), lamellae with pinkish cream to yellowish tones when mature and large basidiospores (on average over 7 µm in length) have a useful diagnostic value. *Clitocybe hypotheja* (1996) is probably a later synonym of *H. nivea*, at least based on the ITS rDNA sequence available from the holotype (Fig. 5). *Clitocybe alni-glutinosae*, described also from Sardinia (Italy) (Contu 1998), was thought to differ from *H. nivea* because of its small-sized basidiomes (pileus 10–30 mm diam, stipe 15–25 × 2–5 mm), faint odour, less spaced, narrower and less decurrent lamellae, slightly smaller basidia (30–37.5 × 6–7.5 µm), absence of pileocystidioid elements, and growth under *Alnus glutinosa*. The ITS rDNA sequence (UDB023989) available from the holotype of *C. alni-glutinosae* (IB19960896) suggests that this species is also conspecific with *H. nivea* (Fig. 5).

Fig. 6. Basidiomes of taxa within *Agaricales* sequenced in the present work. **A.** *Aphroditeola olida* (HRL1230). **B.** *Aspropaxillus giganteus* (AMB:18858). **C.** *Clitocybe ditopa* (AMB:19311). **D.** *Favolaschia claudopus* (B. Child-Villiers 23-10-22). **E.** *Fayodia bisphaerigera* (OW241-19). **F.** *Gamundia* sp. (YM18172). **G.** *Giacomia mirabilis* [ANGE1598 (TO)]. **H.** *Giacomia sinensis* (HMJU:265 holotype). **I.** *Heimiomyces* aff. *tenuipes* (McAdoo 725). **J.** *Hemimycena lactea* (OULU:GAJ15636). **K.** *Hertzogia martiorum* (AMB:18863). **L.** *Hygrophorocybe nivea* (AMB:19292). **M.** *Hygrophorocybe* aff. *carolinensis* (UCSC:F0690). **N.** *Infundibulicybe gibba* (AMB:19313). **O.** *Lepista glaucocana* (AMB:18862). Photographs A by R. Lebeuf, B, C, K, L, N, O by G. Consiglio, D by B. Child-Villiers, E by Ø. Weholt, F by Y. Mourgues, G by C. Angelini, H by J. Xu, I by W. McAdoo, J by S. Huhmarniemi, M by C. Schwarz.

Hygrophorocybe carolinensis (H.E. Bigelow & Hesler) Vizzini, Consiglio & P. Alvarado, ***comb. nov.*** MycoBank MB 851148. Fig. 6M.
Basionym: *Clitocybe carolinensis* H.E. Bigelow & Hesler, J. Elisha Mitchell Sci. Soc. 76: 156. 1960.

Notes: The ITS rDNA sequence (NR_119886) obtained by Schoch *et al*. (2014) from the holotype of *C. carolinensis* (TENN:021888; North Carolina, Bigelow & Hesler 1960, Bigelow 1982) is very similar (97.47 %) to that of a recently collected specimen (UCSC:F-0690, USA: Santa Cruz County, CA, mixed evergreen forest dominated by Coast Redwood, leg. Christian Schwarz, Fig. 5) sequenced in the present work, which nests inside *Hygrophorocybe* based on

Fig. 7. Basidiomes of taxa within *Agaricales* sequenced in the present work. **A.** *Lepista ricekii* (AMB:18864). **B.** *Leucocortinarius bulbiger* (AMB:19593). **C.** *Lyophyllum turcicum* (GB:0065321). **D.** *Macrocystidia cucumis* (JX.1294733#45). **E.** *Macrocystidia* sp. (Kekki3956). **F.** *Melanoleuca friesii* (AMB:18865). **G.** *Melanoleuca tristis* (AMB:18866). **H.** *Notholepista fistulosa* (HMJU:288). **I.** *Omphalina pyxidata* (AMB:19295). **J.** *Paralepista flaccida* (TO:AV20140410). **K.** *Paralepistopsis amoenolens* (AMB:18867). **L.** *Pleurotus dryinus* (AMB:18868). **M.** *Pleurotus fuscosquamulosus* (A. Baglivo 13-07-2014). **N.** *Pluteus romellii* (AMB:18871). **O.** *Pluteus variabilicolor* (AMB:18872). Photographs A, B, F, G, I, K, L, N, O by G. Consiglio, C by L. Stridvall, D by T. Vuorinen, E by Tapio Kekki, H by J. Xu, J by A. Vizzini, M by A. Baglivo.

multigene data (Figs 4, 5). While both collections could belong to distinct species, the results support the combination of *C. carolinensis* into *Hygrophorocybe*. *Hygrophorocybe carolinensis*, a species originally described from pine woods in USA (North Carolina), is characterized by a grey pileus surface, close and narrow lamellae, smaller basidiospores, 5–7 × 2.5–4 µm, and shorter basidia, 19–35 × 4–7 µm (Bigelow & Hesler 1960, Bigelow 1982).

Marasmiineae Aime *et al*., Biol. J. Linn. Soc. 117: 26. 2016.

Type: *Marasmius* Fr., Fl. Scan.: 339. 1836 [1835].

Representative families: *Cyphellaceae*, *Cystostereaceae*, *Marasmiaceae*, *Mycenaceae*, *Omphalotaceae*, *Physalacriaceae*, *Porotheleaceae*, and *Xeromphalinaceae*.

Fig. 8. Basidiomes of taxa within *Agaricales* sequenced in the present work. **A.** *Pseudoomphalina umbrinopurpurascens* (LSS20181215-2). **B.** *Resupinatus applicatus* (AMB:18098). **C.** *Ripartites odorus* (F. Di Rita 08-12-2018). **D.** *Ripartites tricholoma* (Kekki1910). **E.** *Spodocybe collina* (AMB:19296). **F.** *Tectella patellaris* (McAdoo991). **G.** *Trichocybe puberula* (Ferisin11.3.2016-03). **H.** *Volvariella bombycina* (AMB:19312). **I.** *Volvariella* aff. *nigrovolvacea* (AMB:18775). **J.** *Volvariella* aff. *pusilla* (AMB:19290). **K.** *Volvopluteus earlei* (AGMT-71). **L.** *Volvopluteus gloiocephalus* (NTNU:27884555). Photographs A by L. Sánchez, B, E, H–J by G. Consiglio, C by M. Atzeni, D by T. Kekki, F by W. McAdoo, G by G. Ferisin, K by F. Giannoni, L by P.G. Larssen.

Notes: In the present phylogeny (Fig. 1), suborder *Marasmiineae sensu lato* (including *Mycenaceae*, *Xeromphalina* and *Heimiomyces*) received high support in the Bayesian analysis (1.0 PP). To ascertain the limits of the *Marasmiaceae* (not included in the present analysis) multigene data from additional genera other than *Marasmius* are necessary. Species of *Marasmiineae* are characterized by basidiomes mostly gymnocarpic, agaricoid (pileistipitate with central stipe), pleurotoid, rarely corticioid, gasteroid or cyphelloid, often gracile, slender in stature; hymenophore smooth, wrinkled, lamellate to rarely poroid; lamellae or tubes, when present, not free; hyphal system monomitic to sarcodimitic; basidiospores are colourless, usually smooth, without a germ pore, amyloid or not; basidia mostly 4-sporic, usually ballistosporic; cystidia often present; pileipellis very diverse, ranging from a cutis to a hymeniderm; clamp connections present or absent. Most species are litter saprobes, with some rare pathogenic species of economically important plants, *e.g.*, *Moniliophthora perniciosa*, *Paramarasmius palmivorus* (Sena *et al.* 2014, Antonín *et al.* 2022). Some species of *Collybiopsis* (= *Marasmiellus*) are presumably lichenized (Singer 1970, 1973a, Kantvilas & May 1995, Kantvilas & Jarman 2006, Lepp 2011a, b, Oberwinkler 2012, Cooper & Leonard 2013, Lücking *et al.* 2017, Hubregtse 2019). Extensive research has shown that several *Mycena* species are essential for stimulating germination and the early stages of protocorm development in the myco-heterotrophic *Gastrodia elata* and other orchids (Park & Lee 2013, Liu *et al.* 2022). Harder *et al.* (2023) argued that *Mycena* species, usually considered saprotrophic fungi, can be opportunist-generalist plant root invaders. A few species of *Marasmiineae* are known to reproduce predominantly by conidia, *e.g.*, blastic conidiogenesis in *Baeospora* spp. (Walther *et al.* 2005, Hutchison *et al.* 2012) and *Hemimycena conidiogena* (Moreau *et al.* 2005), as well as rhexolytic thallic conidiation in *Flammulina*, *Marasmius puerariae*, *Mycena citricolor*, *Moniliophthora roreri*, *M. perniciosa* (Delgado & Cook 1976, Ingold 1980, Petersen 1995, Petersen *et al.* 1999, Redhead *et al.* 2000a, Kirschner *et al.* 2013,

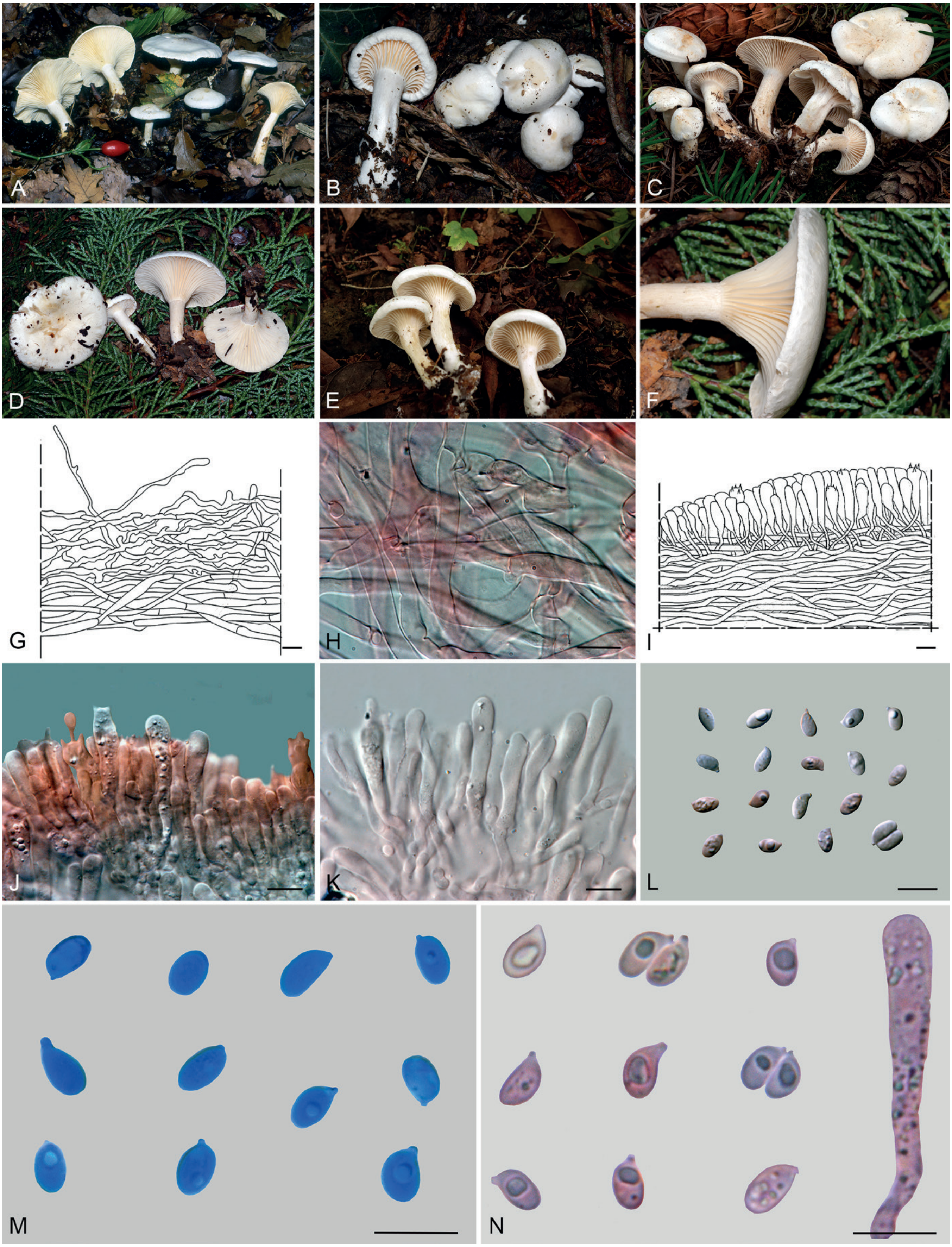

Fig. 9. *Hygrophorocybe nivea*. **A–F.** Basidiomes (A. AMB:19293; B. TO:AV20100811; C. TUR-A 216591; D, F. TO:AV20112411; E. LPA SMGC2020121621). **G.** Pileipellis (TO: AV20112411). **H.** Elements of the pileipellis (AMB:19293). **I.** Hymenium and hymenophoral trama (TO:AV20112411). **J, K.** Hymenium (J. AMB:19293; K. AMB:19292). **L, M.** Basidiospores (AMB:19293). **N.** Basidiospores and young basidium (AMB:19292). Mounting media were Congo Red in ammonia (J–L, N), and Cotton Blue (M). Scale bars: G–N = 10 µm. Photographs A by G. Consiglio, B, D, F by A. Vizzini, C by M. Carbone, E by V.J. Escobio García, H, J–N by M. Marchetti; drawings by L. Panno.

Díaz-Valderrama & Aime 2016). Other taxa reproduce by means of vegetative rhizomorphs, *e.g.*, *Armillaria* spp., *Brunneocorticium* spp., *Crinipellis* spp., *Gymnopus* spp., *Marasmius* spp., *Rhizomarasmius* spp. (Yafetto 2018). Rhizomorphs of *Marasmiineae* are not always restricted to a subterranean habit; in moist tropical rainforests, they are also found in the tree canopy or subcanopy as a dense tangle of black and brown wiry webs. These aerial rhizomorphs trap falling leaf litter for subsequent nutrient exploitation (Hedger 1990) and, interestingly, they are used by birds as construction material in nests (Aubrecht *et al*. 2013, César *et al*. 2018, 2020, Koch *et al*. 2018, 2020, Elliott *et al*. 2019, Bach *et al*. 2022).

The evolution of reduced astipitate and cyphelloid forms has occurred multiple times in *Agaricales* (Bodensteiner *et al*. 2004, Agerer 2018, Consiglio *et al*. 2021, Vizzini *et al*. 2022) and they are striking cases of parallel evolutionary reduction of complex fungal morphology. Most of them are present in *Marasmiineae*.

All the bioluminescent fungi known so far are *Basidiomycota*, with the remarkable exception of a *Xylaria hypoxylon* collection and undetermined species of *Xylariaceae* (*Ascomycota*, *Sordariomycetes*, *Xylariales*; Foerster *et al*. 1965, Seas-Carvajal & Avalos 2013). Within *Basidiomycota*, all the bioluminescent taxa (with the possible exception of the recently described cyphelloid genus *Eoscyphella* included in *Cyphellopsidaceae* by Silva-Filho *et al*. 2023, a family considered affiliated to *Pleurotineae* in the present analysis, Supplementary Fig. S2, see below) belong to suborder *Marasmiineae*, occurring in four major lineages: the Omphalotus lineage (*Omphalotaceae*), Armillaria lineage (*Physalacriaceae*), Lucentipes lineage (*Porotheleaceae*), and the mycenoid lineages (mostly *Mycenaceae*) (Desjardin *et al*. 2008, Oliveira *et al*. 2012, Chew *et al*. 2015, Kotlobay *et al*. 2018, Antonín *et al*. 2019, Cortés-Pérez *et al*. 2023). Ke *et al*. (2020) showed that bioluminescence in *Marasmiineae* evolved from a common ancestor 160 M years ago.

Xeromphalinaceae Vizzini, Consiglio & P. Alvarado, ***fam. nov.*** MycoBank MB 851150.

Diagnosis: It is characterized by basidiomes omphalinoid, marasmioid to collybioid, gymnocarpic, pileus usually brightly coloured, lamellae broadly adnate to decurrent, never purely white; stipe usually central, rarely eccentric, dry, with yellowish-brownish basal tomentum and rhizomorphs usually present. Taste mild to bitter. Spore deposit white. Basidiospores ellipsoid, broadly ellipsoid, oblong, cylindrical, or slightly allantoid, colourless, thin-walled, smooth, amyloid, acyanophilous; cheilocystidia always present; pleurocystidia absent or present; pileocystidia present, often of two types i) thin-walled and unbranched, ii) thin- to slightly thick-walled and often branched or coralloid (circumcystidia). Hyphae neither amyloid nor dextrinoid. Stipe context sarcodimitic. Clamp connections present. Saprotrophic, on conifers, less frequently also on broadleaved wood, sometimes in *Sphagnum* bogs or in forest litter. Known from temperate zones of both hemispheres and alpine zones of tropical regions.

Type: *Xeromphalina* Kühner & Maire, in Konrad & Maublanc, Icon. Select. Fung. 6: 236. (1934) [as '*Xeromphalia*', orth. cons.]; see also Kühner & Maire, Bull. Trimestriel Soc. Mycol. France 50: 18. 1934.

Synonyms: *Valentinia* Velen., Novitates Mycologicae Novissimae: 38. 1939. (fide Kühner 1979b).

Omphalopsis Earle, Bull. New York Bot. Gard. 5: 425. 1909, [*nom. illegit.*, non *Omphalopsis* Grev. 1863 (Algae)].

Representative genera: *Heimiomyces* (Fig. 6I) and *Xeromphalina*.

Notes: *Xeromphalinaceae* differs from its sister family *Mycenaceae* by an omphalinoid or collybioid to marasmioid habit, basidiomes with bright yellow-brown, rusty-yellow to rusty-brown tinges, a yellowish-brown tomentum at stipe base with radiating hairs, abundant encrusting epiparietal pigment on pileipellis elements, non-dextrinoid trama hyphae, sarcodimitic structure of stipe trama and common presence of highly structured armillaria-like rhizomorphs (Miller 1968, Klán 1984, Singer 1986, Redhead 1987, 1988, Rizzo *et al*. 1990, Watling & Turnbull 1998, Antonín & Noordeloos 2004, Aldrovandi *et al*. 2015). *Xeromphalina*, typified by *X. campanella*, was segregated from the heterogeneous *Marasmius* and *Omphalia* to accommodate omphaloid species with a stipe always (yellow) rusty-brown, hispidulo-tomentose at the base, a golden-coloured basal mycelium, and amyloid basidiospores (Kühner & Maire in Konrad & Maublanc 1934, Kühner & Maire 1934). Other differential characteristics highlighted by subsequent authors are the presence of rhizomorphs in many species, incrusting extracellular yellow-brown pigment in the pileipellis elements, abundant caulocystidia, cheilocystidia more or less fusoid, thin-walled, usually without prolongations, and clamp connections in all tissues (Miller OK 1968, Singer 1965, 1986, Horak 1979a, Klán 1984, Redhead 1988, Maas Geesteranus & Horak 1995, Moreno & Heykoop 1996, Watling & Turnbull 1998, Antonín 2000a, b, Antonín & Noordeloos 2004, Noordeloos 2008, 2012, Esteve-Raventós *et al*. 2010, Aldovrandi *et al*. 2015, Liu & Bau 2018). *Xeromphalina* species form exocarpic, apertopileate and amphiblemate basidiomes (Clémençon 2005). Mating systems are tetrapolar in all 12 species studied (Johnson & Petersen 1997). In spite of the few known taxa (about 32 species, Agerer 2018), *Xeromphalina* is a rather well-studied genus in Europe, where it has been the object of several monographic works at a local and continental scale (Klán 1984, Gulden 1992, Moreno & Heykoop 1996, Watling & Turnbull 1998, Bon 1999, Antonín 2000a, b, Ludwig 2001a, b, Antonín & Noordeloos 2004, Noordeloos 2008, 2012, Esteve-Raventós *et al*. 2010). Monographic studies on North American species have been made by Smith (1953), Miller (1968), Redhead (1988) and Aldovrandi *et al*. (2015), who dealt also with the northern Eurasian taxa. Additional works studied species of *Xeromphalina* in South America (Singer 1965, Redhead & Halling 1987), Papua New Guinea and New Caledonia (Maas Geesteranus & Horak 1995), and Asia (Horak 1979a, Liu & Bau 2018).

Outdated classifications based on morphological characters placed *Xeromphalina* in various families. Kühner (1980) included it in the tribe *Marasmieae* of the *Marasmiaceae*; Jülich (1981) in the *Mycenaceae*; Klán (1984) in the *Tricholomataceae*; Singer (1986) in the tribe *Myceneae* of the *Tricholomataceae*; and Redhead (1987, 1988) in the *Xerulaceae*. Antonín & Noordeloos (2004), Noordeloos (2008, 2012) and Agerer (2018) agreed to classify *Xeromphalina* close to mycenoid fungi, while Kühner's point of view was followed by Bon (1999). The rDNA phylogeny in Moncalvo *et al*. (2002) contains a significantly distinct xeromphalinoid clade consisting of *Xeromphalina* and *Heimiomyces*, among the core of the white-spored euagarics. *Xeromphalina campanella*, type of the genus, was found to be nested inside the Hygrophoroid clade by Matheny *et al*. (2006), close to the gilled genera *Sarcomyxa* and *Phyllotopsis*, as well as the morphologically distinct members of the families *Pterulaceae* and *Typhulaceae*. Not much later, Garnica *et al*. (2007) found that *Xeromphalina* was sub-significantly related to a clade containing *Lachnella villosa*, *Fistulina hepatica* and *Schizophyllum commune*. In the phylogeny obtained by Binder *et* *al*. (2010), *Xeromphalina* appears (without support) near *Mycena galericulata* and *M. plumbea*, all of them considered members of a broad Hygrophoroid clade, and therefore it was considered an *incertae sedis* lineage at the base of the Hygrophoroid clade by Ovrebo *et al*. (2011) and Lodge *et al*. (2014). Finally, Olariaga *et al*. (2020) found that *Xeromphalina* was significantly related to a clade including *Marasmiineae* and *Schizophyllineae*, apparently representing an early diverging lineage of this group; it is considered as *incertae sedis* in Sánchez-García *et al*. (2020).

Singer (1942) segregated *Heimiomyces* (type *H. rheicolor*) from *Xeromphalina*, but later Smith (1953), Singer (1962, 1965, 1986), Miller (1968), Redhead (1988) and Ramírez *et al*. (2013) considered it a subgenus or section of *Xeromphalina*. On the other hand, Horak (1968, 1979) recognized *Heimiomyces* as an independent genus, and his point of view was followed by Klán (1984), Maas Geesteranus & Horak (1995), Corner (1996) and Desjardin & Perry (2017). The independent status of *Heimiomyces* seems molecularly supported in Moncalvo *et al*. (2002), Esteve-Raventós *et al*. (2010) and Sánchez-García *et al*. (2020). It seems that species of *Heimiomyces* differ from those of *Xeromphalina* by their collybioid/marasmioid habit, *viz*. adnate to adnexed or broadly emarginate lamellae and not depressed pileus (papillate, umbonate), stipe entirely pruinose-velvety, a duplex pileus trama (the upper half gelatinized and the lower half of thick-walled glassy hyphae), and cheilocystidia with numerous rod-like projections. *Heimiomyces* species are common pantropical taxa (Singer 1965) that had also been recorded in North America (Smith 1953, Singer 1965, Miller 1968, Horak 1979a, Redhead 1988, Maas Geesteranus & Horak 1995, Corner 1996, Ramírez *et al*. 2013, Desjardin & Perry 2017).

Phyllotopsidineae Zhu L. Yang & G.S. Wang, Mycology, 2023 DOI: 10.1080/21501203.2023.2263031, ***hic emend.***
Synonym: *Sarcomyxineae* Zhu L. Yang & G.S. Wang, Mycology, 2023 DOI: 10.1080/21501203.2023.2263031

Type: *Phyllotopsis* E.-J. Gilbert & Donk ex Singer 1936.

Emended circumscription of the family: Basidiomes are very variable, primarily clavarioid to pleurotoid/tricholomatoid (*Pterulaceae*, *Sarcomyxaceae*, *Phylloporopsis*, *Pleurocybella*, *Tricholomopsis*), polyporoid (*Radulotubus*), corticioid/resupinate (*Radulomycetaceae* partim, *Stephanosporaceae* partim), pustulose (*Bulbillomyces*), sequestrate-hypogeous (*Stephanosporaceae* partim), rarely agaricoid (*Aphroditeola*) or maybe cyphelloid (*Cyphelloporia* and *Rectipilus*, unverified), often tough textured; hyphal system often dimitic, hyphae colourless, non-amyloid; basidia clavate, 2–4 sporic; basidiospores colourless, inamyloid or amyloid, clamp connections often present. They show a diverse spectrum of trophic strategies ranging from saprotrophism (on ground or wood), parasitism (as plant pathogens, *e.g.*, *Pterulicium xylogenum*, Acharya 2010), symbiotic lifestyle (ant mutualisms, *Myrmecopterula velohortorum*, *M. nudihortorum*, Dentinger *et al*. 2009, Leal-Dutra *et al*. 2020).

Representative families: *Aphroditeolaceae*, *Phyllotopsidaceae* (including *Tricholomopsis*), *Pterulaceae*, *Radulomycetaceae*, *Sarcomyxaceae* (including *Tectella*), and *Stephanosporaceae*.

Notes: The suborder *Phyllotopsidineae* is here emended to include also *Sarcomyxaceae*, in accordance with the phylogenetic results obtained. Six families are recognized within suborder *Phyllotopsidineae*: *Aphroditeolaceae fam. nov.*, *Phyllotopsidaceae*, *Pterulaceae*, *Radulomycetaceae*, *Sarcomyxaceae* and *Stephanosporaceae* (Larsson 2007a, Lebel *et al*. 2015, Liu *et al*. 2016, Zhao C-L *et al*. 2016, Leal-Dutra *et al*. 2020, Karasiński *et al*. 2023). Basidiome shape is very diverse and there are no obvious synapomorphic traits shared by all *Phyllotopsidineae*. The group is mostly delimited on a molecular basis, roughly corresponding to the 'lower' Hygrophoroid clade identified by Lodge *et al*. (2014), and most lineages of the *Pleurotineae sensu* Olariaga *et al*. (2020) excepting *Pleurotus* and *Typhulaceae*. Wang *et al*. (2023b) separated *Phyllotopsidineae* from *Pleurotineae* after their phylogenomic study showed that both clades were not related, a result found also in the present work with a multigene phylogeny including an extended dataset with important lineages of *Phyllotopsidineae* and *Pleurotineae* not present in the previous works. *Pterulaceae* and *Radulomycetaceae* are recently split sister families (Leal-Dutra *et al*. 2020) constituted by a complex of taxa with clavarioid, corticioid or polyporoid basidiome types. All species of *Pterulaceae* and *Radulomycetaceae* show a distinct phenolic or naphthalene odour when fresh, as described for *Pterula multifida* (Corner 1950, 1970). It was suggested by Olariaga *et al*. (2020) that such an odour, produced by an unidentified volatile metabolite, may be a synapomorphic character of these two families. In the present work, the family *Aphroditeolaceae* is introduced, and the family *Sarcomyxaceae* (suborder *Sarcomyxineae* in Wang *et al*. 2023b) is significantly linked to *Phyllotopsidineae* for the first time. The addition of sequences of *Aphroditeola* and *Tectella* (and other lineages in the remaining suborders) might be the cause of the different result, suggesting that gaps in the diversity analyzed could affect the phylogenetic (and phylogenomic) results. Karasiński *et al*. (2023), recovered a significant relationship between *Phyllotopsidaceae* and a clade formed by the cyphelloid genera *Cyphelloporia* and *Rectipilus*, but the correct classification of these genera needs to be further explored analyzing multigene data in the context of the entire suborder *Phyllotopsidineae*. A new family name might be necessary to accommodate them.

Sarcomyxaceae Olariaga *et al.*, Stud. Mycol. 96: 177. 2020.
Synonym: *Tectellaceae* Locq., Mycologie générale et structurale: 109. 1984, *nom. inval.*, Art. 36.1 (Shenzhen).

Type: *Sarcomyxa* P. Karst., Meddn Soc. Fauna Flora fenn. 18: 62. 1891.

Representative genera: *Sarcomyxa* and *Tectella* (Fig. 8F).

Notes: The family is here characterized by basidiomes pleurotoid, with a gelatinous layer in the pileus, lamellae slightly decurrent, crowded, usually forked. Stipe lateral to reduced. Partial veil present or absent. Spore deposit white. Basidiospores cylindrical to allantoid, amyloid. Basidia (2–)4-sporic, clamped. Cheilo- and pleurocystidia fusiform to clavate, more or less thick-walled. Thick-walled hyphae present in almost all tissues of basidiomes. Pileipellis and part of trama gelatinised. Clamp connections present. Saprotrophic, lignicolous. The family was originally established by Olariaga *et al*. (2020), who classified it within *Pleurotineae*, to accommodate *Sarcomyxa*, a genus containing only two cryptic species (*S. serotina* and *S. edulis*, once considered to belong to the genus *Panellus*) with pleurotoid basidiome, gelatinised pileipellis, fusiform to clavate cheilo- and pleurocystidia, thick-walled hyphae in the context, and amyloid basidiospores (Horak 1968, Jin *et al*. 2001, Dai *et al*. 2003, Knudsen & Vesterholt 2012, Kunze *et al*.

2012, Saito *et al*. 2014, Læssøe & Petersen 2019, Olariaga *et al*. 2020, Tian *et al*. 2021, Cai *et al*. 2023). Two new species, *S. baishanzuensis* and *S. ochracea*, have been recently described from China (Cai *et al*. 2023).

The present analysis (Fig. 1) suggests that the genus *Tectella* (represented by ITS, LSU, SSU, *RPB2* and *TEF1* sequences obtained from a Northamerican collection of *T. patellaris*) is part of the family *Sarcomyxaceae*. *Tectella*, typified by *T. operculata* (= *T. patellaris*) was considered an *incertae sedis* genus based on rDNA alone (Aime 2001, Jin *et al*. 2001, Moncalvo *et al*. 2002, Cifuentes *et al*. 2003). Bodensteiner *et al*. (2004) found that *T. patellaris* is subsignificantly related to *Panellus serotinus* (51 BP) within *Agaricales* (Euagarics), but not close to the type of the morphologically similar genus *Panellus*, *P. stipticus*, which is nested within *Mycenaceae* (*Marasmiineae*) (Moncalvo *et al*. 2002, Bodensteiner *et al*. 2004, Binder *et al*. 2005, Saito *et al*. 2014, Ke *et al*. 2020, Tian *et al*. 2021, Zhang & Dai 2021, Zhang *et al*. 2022, present work Fig. 1). Matheny *et al*. (2006) found that *Sarcomyxa*, *Xeromphalina*, *Pterulaceae* (*Pterula* and *Phyllotopsis*) and *Typhulaceae* formed a significantly monophyletic group nested inside the Hygrophoroid clade, but this result could be due to an incomplete dataset lacking representative lineages and/or sufficient DNA data from them.

Tectella patellaris (Fig. 8F) mainly differs from *Sarcomyxa* because of its pseudostipitate basidiome which displays a partial veil at least in young stages (*e.g*., Earle 1909, Pilát 1935, Horak 1968, Miller 1970, Candoussau *et al*. 1974, Perrin 1979, Reijnders 1983, Singer 1986, Cavet & Moreau 1994, Cucchi 1997, Elborne & Læssøe 2008, 2012, Schmitt & Heseler 2009a, b, Seok *et al*. 2011, Trnkoczy 2011, Jančovičová *et al*. 2012, Læssøe & Petersen 2019). *Tectella patellaris* occurs in Europe (Elborne & Læssøe 2012), Asia (Seok *et al*. 2011) and North America (Miller 1970). The species was classified into various genera such as *Panellus* (Subgen. *Mitellus*, Burdsall & Miller 1975), *Panus* (where it was originally described, Fries 1838, Kühner 1980), *Pleurotus* and *Pocillaria* (Pilát 1935, Kirk 2012), *Velopanus* (Singer 1936b, *nom. prov.*), as well as in the families *Favolaschiaceae* (Elborne & Læssøe 2008, 2012), *Mycenaceae* (Elborne & Læssøe 2012), *Pleurotaceae* (*e.g.*, Kühner 1980, Roux 1997, 2006) or *Tricholomataceae sensu lato* (*e.g*., Moser 1978, Singer 1986, Hansen & Knudsen 1992). The status of other species of *Tectella* proposed on the basis of morphology, such as *T. luteohinnulea* (Stevenson 1964) from New Zealand and *T. phellodendri* (Singer 1942b) from Asia (Khabarovsk, Russian Far East), needs to be checked with molecular tools.

Phyllotopsidaceae Locquin ex Olariaga *et al.*, Stud. Mycol. 96: 175. 2020.

Type: *Phyllotopsis* E.-J. Gilbert & Donk ex Singer, Beih. Bot. Centralbl., Abt. 2 56: 143. 1936.

Representative genera: *Conoloma*, *Macrotyphula*, *Phyllotopsis*, *Pleurocybella*, *Tricholomopsis* and maybe also *Bulbillomyces*, *Cyphelloporia* and *Rectipilus*.

Notes: The family is characterized here by basidiomes pleurotoid, tricholomatoid, clavarioid (typhuloid) and sometimes arising from a sclerotium, corticioid, or cyphelloid (*Cyphelloporia*, *Rectipilus*, unverified). Spore deposit white to salmon pink, pale ochre. Hyphal system monomitic. Basidiospores colourless, cylindrical, allantoid or subglobose, smooth, without iodine reactions. Cheilocystidia sometimes present in pleurotoid genera. Clamp connections present, rarely absent. Saprotrophic, usually lignicolous. *Macrotyphula*, *Phyllotopsis* and *Pleurocybella* were first found to be closely related by Dentinger & McLaughlin (2006), and later Olariaga *et al*. (2020) established the new family *Phyllotopsidaceae* for this monophyletic group. Wang *et al*. (2023b) added a new monospecific genus, *Conoloma*, which differs from the allied *Tricholomopsis* mainly by its pileus with a mucronate umbo, a fibrillose annuliform zone on the stipe apex, and smaller cheilocystidia. No obvious synapomorphic characters could be identified between the typhuloid *Macrotyphula* and the pleurotoid *Phyllotopsis* and *Pleurocybella* (Moncalvo *et al*. 2002). All three genera contain saprotrophic species, mostly lignicolous, and possess clamp connections (Singer 1986, Watling & Gregory 1989, Knudsen 2008a, 2012a, Vesterholt 2008b, 2012b, Knudsen & Shiryaev 2012). A corticioid sample identified as *Bulbillomyces farinosus* seems related to *Macrotyphula* in some works (Karasiński *et al*. 2023), but another candidate lineage for this name exists in the *Polyporales* (Larsson 2007b, Justo *et al*. 2017). The classification of the monospecific genus *Bulbillomyces* needs to be confirmed by selecting an epitype, and so its position inside *Phyllotopsidaceae* is by now doubtful.

The present analysis (Fig. 1) also supports that the genus *Tricholomopsis* could be part of the family *Phyllotopsidaceae*, sister to a clade formed by the gilled genera *Pleurocybella* and *Phyllotopsis*, as previously suggested by other works, some of them including the type species *T. rutilans* (Garnica *et al*. 2007, Binder *et al*. 2010, Lodge *et al*. 2014, Sánchez-García *et al*. 2020). In the molecular phylogeny produced by Moncalvo *et al*. (2002), *Tricholomopsis*, represented by the LSU nrDNA sequences of *T. rutilans* and *Collybia aurea* (later combined in *Tricholomopsis* by Desjardin & Perry 2017), was placed in one phylogenetic clade together with *Clavaria fusiformis* and *Marasmius rhyssophyllus*. In a multigene analysis (*RPB1*, *RPB2*, ncRNA) another representative species, *T. decora*, nested inside the Pluteoid clade, outside of any conventional families, close to *Amanitaceae* (Matheny *et al*. 2006). In Garnica *et al*. (2007), *T. rutilans* formed a clade with *Macrotyphula fistulosa*, *Pleurocybella porrigens*, *Phyllotopsis nidulans*, sister to *Hygrophorus chrysodon*, *Lentaria albovinacea* and *Sarcomyxa serotina*. In Binder *et al*. (2010) *T. decora* is placed in the Hygrophoroid clade (minus *Pterulaceae*) together with *Phyllotopsis* sp., *Pleurocybella porrigens*, *Macrotyphula fistulosa*, *Typhula phacorrhiza*, and *Sarcomyxa serotina*). He *et al*. (2019) considered *Tricholomopsis* an *incertae sedis* genus inside *Agaricales*. Wang *et al*. (2023b) found also that *Tricholomopsis* is nested inside *Phyllotopsidaceae* after analyzing genome data of multiple species in this genus.

The genus *Tricholomopsis* includes lignicolous species that cause white rot of conifers (Singer 1986, Smith, 1960, Murphy & Mitchell 2001, Vauras 2009, Razaq *et al*. 2012, Wang *et al*. 2023b), as well as very few species reported to be bambusicolus, *Pteridium*-associated or terrestrial (Dennis 1951, Hongo 1959, 1960, Olariaga *et al*. 2015). Species of *Tricholomopsis* have tricholomatoid, brightly colored (mostly yellow) basidiomes, a tomentose or finely fibrillose-squamulose pileus (but basidiome collybioid, pileus smooth, hygrophanous and shallowly depressed or umbilicate in age in the pantropical *T. aurea*, Desjardin & Perry 2017), adnate-sinuate lamellae, whitish spore deposit, smooth, inamyloid and broadly ellipsoid basidiospores, large cheilocystidia, absent or sparse pleurocystidia, a trichoderm to cutis type pileipellis, and clamp connections (Smith 1960, Bon 1984, Singer 1986, Boekhout & Noordeloos 1999, Vesterholt 2008c, Holec 2009, 2012a, b, Vauras 2009, Holec & Kolařík 2011, 2012, Vauras *et al*. 2012, Cooper & Park 2016, Olariaga *et al*. 2015, Agerer 2018, Holec *et al*. 2019, Hosen *et al*. 2020, Mao *et al*. 2021, Jayawardena *et al*. 2022, Wang *et al*. 2023b). The genus was traditionally considered a member of the *Tricholomataceae* (*e.g.*, Kühner 1980, Bon 1984, 1991, Singer 1986, Boekhout & Noordeloos 1999, Holec 2012a, Agerer 2018). *Phyllotopsis nidulans*, type of *Phyllotopsis*, shows the same yellow lamellae (due to carotenoids in *Phyllotopsis*, Fiasson 1969, Arpin & Fiasson 1971, Kost 1986, but yet undetermined in *Tricholomopsis*, Gill & Steglich 1987), squamulose-hirsute pileus and growth on dead wood, as most *Tricholomopsis* species, but its basidiomes are conchate, shell to kidney-shaped and sessile, its basidiospores are reniform, allantoid, cheilocystidia absent or acicular-filiform and spore deposit yellowish-pink to pale ochre (Pilát 1935, Domański 1969, Singer 1986, Hrouda 2001, Knudsen 2008a, 2012a, Agerer 2018).

Aphroditeolaceae Vizzini, Consiglio & P. Alvarado, ***fam. nov.*** MycoBank MB 851151.

Diagnosis: Basidiomes pileostipitate, pileus depressed to infundibuliform, hymenophore folded with folds dichotomously forked, cystidia absent, basidiospores colourless, faintly amyloid and indextrinoid, clamp connections present, terricolous, in forests.

Type: *Aphroditeola* Redhead & Manfr. Binder, Index Fungorum 15: 1. 2013.

Representative genus: *Aphroditeola.*

Notes: The genus *Aphroditeola* was established in a brief note in Index Fungorum (Redhead 2013) to accommodate *Cantharellus olidus*. This species is traditionally characterized by small and pink cantharelloid to omphalinoid basidiomes with fruity-sweetish to floral fragrant odour (described as candy-like, *Hebeloma sacchariolens*-like, cinnamony or pink bubble gum-like), dichotomously forked hymenophoral folds, smooth, colourless inamyloid and indextrinoid basidiospores, absence of hymenial cystidia, presence of clamp connections, *in vitro* pinkish to reddish-orange mycelium, and growing on coniferous litter (Smith 1944, Petersen 1976, Fries 1979, Kuyper 1995a, Knudsen & Taylor 2008, 2012 as *Hygrophoropsis*, Redhead 2013). Basidiospores are reported as non-amyloid by nearly all authors except Petersen (1976) who found a faint amyloidity in the holotype. All the collections examined in the present work showed weakly amyloid basidiospores (see below). Recently, *Aphroditeola* was found to be associated to the white females of the cereal cyst nematode (CCN, *Heterodera avenae*) in China (Hu *et al*. 2020). Traditionally, *Cantharellus olidus* was classified in *Hygrophoropsis* (Métrod 1949, Kuyper 1995a, Knudsen & Taylor 2008, 2012, Kibby 2012) as part of the family *Hygrophoropsidaceae*, a lineage shown to be nested within the order *Boletales* (Moncalvo *et al*. 2002, Binder & Hibbett 2006). However, *Hygrophoropsis* produces saprotrophic lignicolous and brown-rotting basidiomes with strongly dextrinoid spores (*e.g.*, Kuyper 1995a, Gminder 2001, Watling & Hills 2005, Knudsen & Taylor 2008, 2012, Kibby 2012, Sesli 2014). Bigelow (in Bigelow & Barr 1962) examined type material of *Cantharellus morganii*, concluding that it was conspecific with *C. olidus* and *C. rosellus*. Phylogenetically, *Aphroditeola* was previously thought to be close to the family *Hygrophoraceae*, inside the Hygrophoroid clade (= *Hygrophorineae sensu* Dentinger *et al*. 2016) (Lodge *et al*. 2014, Lavorato *et al*. 2015, He & Yang 2021). However, Sánchez-García *et al*. (2017) found that *Aphroditeola* is related to *Stephanosporaceae*, *Radulomycetaceae* and *Pterulaceae*. According to the present analysis (Fig. 1) *Aphroditeola* represents an independent evolutionary line inside suborder *Phyllotopsidineae*, sister to a clade formed by *Stephanosporaceae*, *Radulomycetaceae* and *Pterulaceae*. This clade is, in turn, sister to *Phyllotopsidaceae*.

Aphroditeola olida (Quél.) Redhead & Manfr. Binder, Index Fungorum 15: 1 (2013). Figs 6A, 10.

Basionym: *Cantharellus olidus* Quél., in Cooke & Quélet, Clavis syn. Hymen. Europ. (London): 148. 1878.

Synonyms: *Merulius olidus* (Quél.) Kuntze, Revis. gen. pl. (Leipzig) 2: 862. 1891.
Clitocybe olida (Quél.) Konrad, Bull. Trimestriel Soc. Mycol. France 45: 60. 1929.
Hygrophoropsis olida (Quél.) Métrod, Schweiz. Z. Pilzk. 14(3): 15. 1949.
Cantharellus morganii Peck [as 'morgani'], Bot. Gaz. 7(4): 43. 1882.
Merulius morganii (Peck) Kuntze, Revis. gen. pl. (Leipzig) 2: 862. 1891.
Clitocybe morganii (Peck) H.E. Bigelow, Rhodora 64: 129. 1962.
Hygrophoropsis morganii (Peck) H.E. Bigelow, Beih. Nova Hedwigia 51: 66. 1975.
Cantharellus rosellus Peck, Rep. (Annual) New York State Mus. Nat. Hist. 42: 120. 1889.
Merulius rosellus (Peck) Kuntze, Revis. gen. pl. (Leipzig) 3(3): 494. 1898.

Description: *Pileus* 10–40 mm, convex when young, then plane with a depressed centre, finally funnel-shaped, margin typically incurved, irregularly undulating, lobate to subcrenulate, not hygrophanous, not translucently striate, surface smooth to finely tomentose, flesh-pinkish (7A5-6) to ochre-orange (5A7-8, 6A7-8) or pale buff (7A7-8) (like *Hydnum rufescens*), paler at margin. *Lamellae* crowded, L = 35–50, l = 1–2, very narrow (thin), long-decurrent, repeatedly forked, intervenose in age, sometimes foldlike, whitish to pale pinkish buff (7A3-4), with an obtuse, entire, concolorous edge. *Stipe* 15–35 × 2–5 mm, slightly eccentric, solid, somewhat broadened at apex (up to 8 mm), conic, attenuated towards the base, very finely pruinose-fibrillose then polished, concolorous with the pileus or paler. *Context* thin, whitish to very pale pinkish buff (7A2-3) at stipe base. *Odour* evident, strong, fragrant, sweetish, of cinnamom candy, as in *Entoloma ameides*, *Hebeloma sacchariolens*; *taste* sharp but soon mild, hard to distinguish because of the odour. *Spore deposit* whitish. *Basidiospores* (3.34–)3.53–*3.78*–4.03(–4.37) × (2.62–)2.75–*2.93*–3.11(–3.55) µm [90/2/1], Q = (1.11–)1.19–*1.29*–1.40(–1.57), V= (12–)14.56–*17.07*–19.58(–26.5) µm^3, ellipsoid to broadly ellipsoid, thin-walled, smooth, colourless, often mono- to multiguttulate, apiculus prominent, up to 1 µm long, abrupt, wall cyanophilous, weakly amyloid, non- to very weakly dextrinoid. *Basidia* (18–)20–35 × 5–7(–7.2) µm, clavate, 4-sporic, rarely 2-sporic, sterigmata up to 4 µm long, minutely guttulate, often with basal clamp connection. *Subhymenium* thickening, formed by short, intertwined, 2–4 µm wide elements. *Hymenial cystidia* absent. *Hymenophoral trama* irregular of subcylindrical, tightly interwoven hyphae, 3–8 µm wide, thin- to moderately thick-walled (and then wall up to 1(–1.5) µm thick), colourless to pale yellowish (pigment parietal and intracellular), dextrinoid. *Pileipellis* an ixocutis of repent, subparallel to subintricate hyphae with several single or agglutinated ascending elements, cylindrical to claviform, 5–8(–10) µm wide, with pale yellowish intracellular pigment. *Subpellis* (pileitrama) formed by cylindrical to claviform 4–8(–10) µm wide, colourless or pale yellowish hyphae. *Stipitipellis* made up of loose, sub-intertwined, 4–8 µm wide cylindrical colourless hyphae, with abundant clamp connections, with reclining or emerging terminal elements together with up to 60–80 µm long cystidioid hyphae aggregating dense deposits of basidiospores; present at the base of the cystidioid elements also subglobose to claviform cells. *Stipititrama* regular to subirregular made up of cylindrical, 3–8(–12)

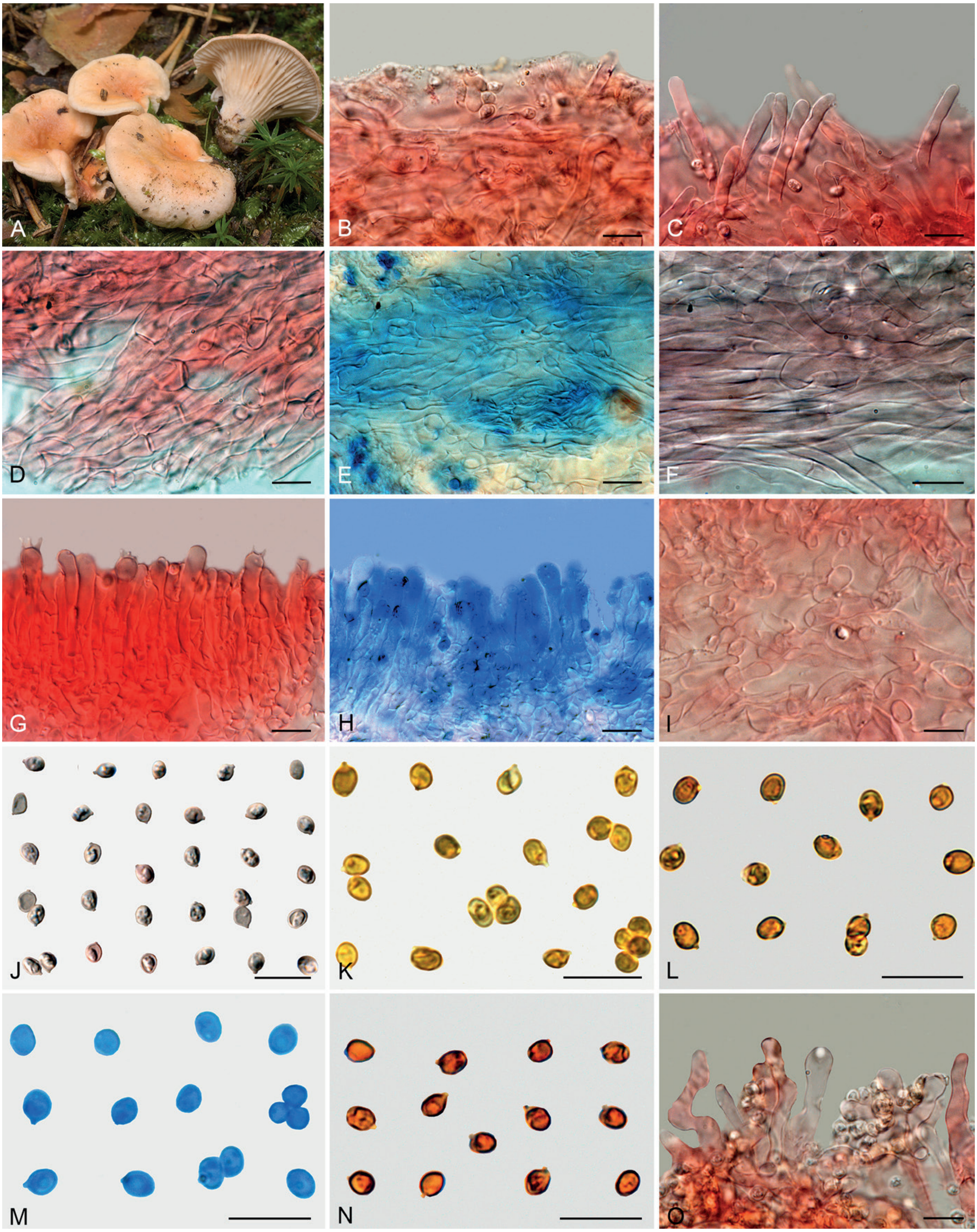

Fig. 10. *Aphroditeola olida*. **A.** Basidiomes (TRgmb00561). **B, C.** Pileipellis (B. TRgmb00561; C. TRgmb00556). **D.** Subpellis (pileitrama) (TRgmb00561). **E, F.** Hymenophoral trama (E. TRgmb00561; F. TRgmb00556). **G, H.** Hymenium (G. TRgmb00556; H. TRgmb00561). **I.** Subhymenium (TRgmb00561). **J–N.** Basidiospores (J–M. TRgmb00561; N. TRgmb00556). **O.** Caulocystidia (TRgmb00561). Mounting media were Melzer's reagent (K, L, N), Congo Red in ammonia (B–D, F, G, I, O), and Cotton Blue (E, H, M). Scale bars: B–O = 10 µm. Photographs A by M. Floriani, B–O by M. Marchetti.

µm wide hyphae, sometimes enlarged at the septa, colourless to slightly yellow, with wall up to 1 µm thick. *Thromboplerous hyphae* not observed. *Clamp connections* present in all tissues.

Habitat and distribution: Scattered or gregarious, in soil or needle litter, usually under coniferous trees. Europe, Asia and North America.

Materials examined: **Canada**, Quebec, MRC Lac-Saint-Jean-Est, Alma, on fir's litter, coniferous forest, 11 Sep. 2012, R. Lebeuf, HRL1230. **Italy**, Trentino-Alto Adige, Loc. Brusoladi (Valfloriana, TN), 1 160 m asl, Lat.: 46,2512° N - Long.: 11,3609° E, mixed coniferous forest with a prevalence of *Picea abies* and *Pinus sylvestris*, 7 Aug. 2011, M. Floriani & L. Eccher (TRgmb00561); Loc. Castelìr (Predazzo, TN), 1 550 m asl, Lat.: 46,31428° N - Long.: 11,69167° E, subalpine coniferous forest with a prevalence of *Picea abies*, 24 Aug. 2004, M. Floriani, M. Donini *et al*. (TR gmb00556).

Notes: According to the present results (and additional unpublished data), genus *Aphroditeola* is probably composed of at least three distinct species with a phylogenetic similarity between them ranging from 94 % to 96.5 % in ITS rDNA (and an intraspecific variability between 0 % and 1.5 %). Two of these lineages are present in North America and Europe, while the only known sample of the third one comes from Europe. No diagnostic traits have been identified to discriminate these clades from one another, so by now they are considered cryptic species. Whether the holotypes of *Cantharellus olidus*, *C. morganii* and *C. rosellus* belong in the same or different clades should be further investigated to take the appropriate taxonomic decisions at species level.

Pleurotineae Aime *et al*., Biol. J. Linn. Soc. 117(1): 26. 2016, ***hic emend.***
Synonyms: *Schizophyllineae* Aime *et al*., Biol. J. Linn. Soc. 117(1): 26. 2016.
Schizophyllales Nuss., Hoppea 39: 179. 1980.

Type: *Pleurotus* (Fr.) P. Kumm., Führ. Pilzk. (Zerbst): 24. 1871.

Emended circumscription of the family: Basidiomes pileate, conchate, spathulate, tongue-shaped, resupinate to cyphelloid/cupulate; dry or viscid; pileus convex to plane-depressed, urniform to reniform, bell-shaped, cupulate solitary or forming a pore-like compound structure on a subiculum or disc; stipe present (lateral to eccentric, rarely central), rudimentary or absent; hymenophore lamellate, smooth, tubular (tubes separate but closely packed or coherent), merulioid, or folded (pseudolamellate), lamellae usually decurrent or attenuating towards the centre; veils usually absent, rarely present; spore deposit white to cream, pale ochre; hymenophoral trama irregular to subregular, immersed or not in a gelatinous matrix; hyphal system monomitic or dimitic, hyphae colourless, inamyloid, non-dextrinoid, with or without clamp connections; acantophyses sometimes present (*Porodisculus*, *Pseudofistulina*, *Resupinatus*); context gelatinous or with a distinct gelatinous layer or non-gelatinous; basidiospores colourless, or occasionally yellow-brown, smooth, thin-walled, inamyloid, non-dextrinoid, acyanophilous; basidia clavate or subclavate, 4- or 2-sporic holobasidia; hymenial cystidia and pileocystidia absent or present; pileipellis a cutis or a trichoderm of smooth or irregularly ramified and with gnarled outgrowing hyphae; asexual morph phase usually present in *Hohenbuehelia* (*Nematoctonus*), *Fistulina* (*Confistulina*), rarely in *Pleurotus* (*Antromycopsis* in *Pleurotus* subgenus *Coremiopleurotus*). Lignicolous, herbicolous, saprotrophic, or parasitic on angiosperms and gymnosperms, producing a white rot or showing an intermediate behaviour between white-rot and brown-rot fungi (*Fistulinaceae* and *Schizophyllaceae*); nematode trapping via toxin droplets (*Pleurotus*) or adhesive knobs (*Hohenbuehelia*).

Representative families: *Fistulinaceae*, *Pleurotaceae*, *Resupinataceae*, *Schizophyllaceae*, and presumably *Cyphellopsidaceae* Jülich.

Notes: The first phylogenomic study focused on *Agaricales* (Dentinger *et al*. 2016) found a close relationship between *Pleurotus ostreatus* (*Pleurotaceae*) and *Pterula multifida* (*Pterulaceae*), coining the suborder *Pleurotineae* for them. *Pleurotus* appeared related to *Pterula* too in the phylogenomic analysis by Varga *et al*. (2019). It appeared as an *incertae sedis* lineage basal to the rest of *Agaricales* in the phylogenomic study by Ke *et al*. (2020), but *Pterula* was absent from this analysis. In the multigene analysis by Olariaga *et al*. (2020), *Pleurotineae sensu* Dentinger *et al*. (2016) was emended to include also *Phyllotopsidaceae*, *Sarcomyxaceae*, *Radulomycetaceae*, *Stephanosporaceae* and *Typhulaceae*. In the phylogenomic work by Li *et al*. (2021), *Pleurotus* and *Pterula* are again close to each other, but their monophyletic origin lacks significant support. In contrast with the previous phylogenetic and phylogenomic works, Wang *et al*. (2023b) found that *Phyllotopsidineae* and *Pleurotineae* were not directly related after analyzing more information (555 genes) from a more diverse dataset of *Agaricales*. The present analysis (Fig. 2), based on multigene sequence data from several species of *Pleurotus*, *Hohenbuehelia* and *Resupinatus*, confirms this result, but it also suggests a monophyletic origin of *Pleurotineae* and *Schizophyllineae* (*Auriculariopsis*, *Fistulina*, *Porodisculus*, *Schizophyllum*). Wang *et al*. (2023b) did not find a direct relation between *Pleurotineae* and *Schizophyllineae*, but this could be due to the lack of important lineages in their analysis (*i.e.*, basal species of *Pleurotus*, *Hohenbuehelia*, *Resupinatus*).

The family *Cyphellopsidaceae* Jülich 1982 [= *Digitatisporaceae* Jülich 1982, *nom. inval.*, Art. 36.1; *Niaceae* Jülich 1982, *nom. inval.*, Art. 36.1; *Lachnellaceae* Boud. 1907, as 'Lachnellacées', *nom. inval.*, Art. 32.1(c), see Art. 18.4 (Shenzhen)] encompasses the genera *Calathella*, *Dendrothele*, *Digitatispora*, *Eoscyphella*, *Flagelloscypha*, *Halocyphina*, *Lachnella*, *Merismodes* (including also *Cyphellopsis* and *Maireina*, Silva-Filho *et al*. 2023), *Nia*, *Peyronelina*, and *Woldmaria* (Binder *et al*. 2001, 2066, Bodensteiner et. 2004, Matheny *et al*. 2006, Yamaguchi *et al*. 2009, Henkel *et al*. 2010, Læssøe *et al*. 2016, Azevedo *et al*. 2018, Abdel-Wahab *et al*. 2019, Silva-Filho *et al*. 2023). It seemed related to *Schizophyllaceae* (but often lacking statistical support) in Binder *et al*. (2001, 2005, 2010), Matheny *et al*. (2006, significant support, inside the Marasmioid clade), Garnica *et al*. (2007, subsignificant support), Yamaguchi *et al*. (2009), and Henkel *et al*. (2010). However, in other works, *i.e.*, Bodensteiner *et al*. (2004) and Olariaga *et al*. (2020), this clade seems to be far from the Schizophylloid clade (/*Schizophyllineae*). Wang *et al*. (2023b) found a significant relation between *Cyphellopsidaceae* (as *Niaceae*) and *Schizophyllaceae* and *Fistulinaceae* (as *Schizophyllineae*) with a phylogenomic approach, although they only included a single species of this family (*Flagelloscypha* sp.). Additional analyses conducted in the present work (Dataset 5: 10.6084/m9.figshare.24999368) seem to confirm that the family *Cyphellopsidaceae* is closely related to *Schizophyllaceae* and *Fistulinaceae* inside suborder *Pleurotineae* (Supplementary Fig. S2), but the resulting phylogeny lost support for other major nodes, maybe because the species analyzed do not represent properly the biodiversity in these lineages and/or the DNA markers employed contain incomplete or insufficient information. The clade of *Henningsomyces sensu stricto* (Bodensteiner 2004) has been recently found to be apparently related to the family *Cyphellopsidaceae* too (Karasiński *et al*. 2023), but its status needs to be confirmed analyzing multigene or genomic data. Regardless of its actual classification, this clade will probably need its own family name to reflect the great genetic distance from the other families of *Agaricales*.

Pleurotaceae Kühner, Bull. Mens. Soc. Linn. Lyon 49: 784. 1980.

Type: *Pleurotus* (Fr.) P. Kumm., Führ. Pilzk. (Zerbst): 24. 1871.

Representative genera: *Hohenbuehelia* and *Pleurotus* (Fig. 7L, M).

Notes: The family *Pleurotaceae* is characterized by its basidiomes pileate, conchate, spathulate; dry or viscid; pileus convex to plane-depressed, urniform to reniform; stipe present (lateral to eccentric, rarely central), rudimentary or absent; hymenophore lamellate, lamellae usually decurrent or attenuating towards the centre; veils absent, rarely present; spore deposit white to cream; hymenophoral trama irregular to subregular, immersed or not in a gelatinous matrix; hyphal system monomitic or dimitic, hyphae colourless, inamyloid, non-dextrinoid, with clamp connections; context gelatinous or with a distinct gelatinous layer or non-gelatinous; basidiospores colourless, smooth, thin-walled, inamyloid, non-dextrinoid, acyanophilous; basidia clavate or subclavate, 2- or 4-sporic holobasidia; hymenial cystidia and pileocystidia absent or present; pileipellis a cutis or a trichoderm of smooth hyphae; asexual morph phase usually present in *Hohenbuehelia* (*Nematoctonus*), rarely in *Pleurotus* (*Antromycopsis* in *Pleurotus* subgenus *Coremiopleurotus*). Lignicolous, herbicolous, saprotrophic, or parasitic on angiosperms and gymnosperms, producing a white rot; nematode trapping via toxin droplets (*Pleurotus*) or adhesive knobs (*Hohenbuehelia*). The family was established by Kühner (1980) with very broad limits, for all subcoriaceous, white-spored taxa with a pleurotoid habit (*viz*. *Pleurotus*, *Lentinus*, *Panus*, *Phyllotopsis*, *Sarcomyxa*). However, Singer (1986) did not recognize *Pleurotaceae* and placed *Pleurotus* in tribe *Lentineae* of *Polyporaceae* and *Hohenbuehelia* within tribe *Resupinateae* of *Tricholomataceae*. *Pleurotaceae* (including *Pleurotus* and *Hohenbuehelia*) was early recognized as a monophyletic lineage by Moncalvo *et al*. (2000, 2002) and Thorn *et al*. (2000, 2005) based on rDNA data, a conclusion confirmed later by multigene analyses (Binder *et al*. 2005, Matheny *et al*. 2006, McDonald 2015, Petersen *et al*. 2015, Varga *et al*. 2019, Olariaga *et al*. 2020, Sánchez-García *et al*. 2020). Members of *Hohenbuehelia* possess a thick gelatinous zone, metuloid cystidia, a nematoctonus-like asexual morph, and capture nematodes predominantly by means of adhesive knobs (Thorn & Barron 1986, Thorn *et al*. 2000, Consiglio & Setti 2018, Consiglio *et al*. 2018). Species of *Pleurotus* lack a gelatinous zone (although some species have a gelatinized pileipellis), metuloid cystidia and a nematoctonus-like asexual morph, and they capture nematodes by non-adhesive droplets containing the biotoxic volatile ketone, 3-octanone, named toxocysts by Clémençon (2004) (Hilber 1982, Barron & Thorn 1987, Thorn *et al*. 2000, Satou *et al*. 2008, Marlin *et al*. 2019, Lee *et al*. 2023). Nematophagous fungi can be found also in suborder *Agaricineae*, *i.e*., *Crepidotus* (*Crepidotaceae*, Senn-Irlet 1994, Senn-Irlet & Scheidegger 1994), *Stropharia* (*Strophariaceae*, Luo *et al*. 2006), and *Coprinus comatus* (*Agaricaceae*, Luo *et al*. 2004, 2007). Unlike *Pleurotus*, the *Conocybe lactea* mycelium does not locate and colonize immobilized nematodes and (or) consume them as a nutrient source. Toxin droplets exuded by its hyphae probably act only as antifeedant compounds, by repelling or killing fungus-feeding nematodes (Hutchison *et al*. 1996, Hallen *et al*. 2003).

Resupinataceae Jülich, Biblioth. Mycol. 85: 388. 1982. [1981].
Synonym: *Tricholomataceae* tribe *Resupinateae* Singer, Sydowia 2: 30. 1948.

Type: *Resupinatus* Nees *ex* Gray, Nat. Arr. Brit. Pl. (London) 1: 617. 1821. (Fig. 8B).

Synonyms: *Phyllotus* P. Karst., Bidr. Känn. Finl. Nat. Folk 32: XIV. 1879.
Stigmatolemma Kalchbr., Grevillea 10(no. 55): 104. 1882.
Asterotus Singer, Mycologia 35: 161. 1943.
Rhodocyphella W.B. Cooke, Beih. Sydowia 4: 105. 1961.
Lignomyces R.H. Petersen & Zmitr., Mycologia 107: 1046. 2015.

Notes: Traditionally, the genus *Resupinatus*, typified with *R. applicatus* (Fig. 8B), has always been considered closely related to *Hohenbuehelia* (Singer 1948, 1975, 1986, Kühner 1980) from which it differs because it lacks metuloid cystidia (except *R. niger*), the *Nematoctonus* asexual morph, nematophagy, the presence of ramified hyphae in the pileipellis (*Rameales* type), which in some species is repeatedly dichotomously branched (asterostromelloid), and diverticulate coralloid cheilocystidia (Singer 1986, Consiglio & Setti 2017, 2018). In addition, *Resupinatus* has been shown to possess a peculiar hymenophore development: while in most other species of the *Agaricales* lamellae production is usually completed within the mushroom primordium, and lamellae only become larger (either wider, longer, or both) during development, in *Resupinatus* they increase in number during the maturation of the basidiome (Reijnders 1948, 1963, Moore 1987). The similarities between the two genera were so striking as to induce Kühner (1980) to consider *Hohenbuehelia* a subgenus of *Resupinatus*. Singer (1948) established the tribe *Resupinateae* of *Tricholomataceae* to include *Resupinatus* and *Hohenbuehelia* because they share a gelatinous layer in their pileus context and colourless inamyloid spores. Later, Singer (1962) included in the tribe also the reduced genera *Asterotus* and *Stigmatolemma* based on micromorphological characters, but *Asterotus* was later considered a posterior synonym of *Resupinatus*, and reduced to a subgenus of *Resupinatus* (Singer 1973b, 1975). Kühner (1980) included only *Resupinatus* (with *Hohenbuehelia* as a subgenus) inside the tribe *Resupinatae* of *Pleurotaceae*. Jülich (1981) established the family *Resupinataceae* for *Resupinatus*. Finally, Singer (1986) widened the concept of his tribe *Resupinateae* (*Tricholomataceae*) to include the lamellate genera *Agaricochaete*, *Hohenbuehelia* and *Resupinatus*, and the cyphelloid genera *Aphyllotus*, *Stigmatolemma*, and *Stromatocyphella*.

With the aid of molecular phylogenetic studies, *Asterotus*, *Lignomyces*, *Rhodocyphella*, *Stigmatolemma*, and *Stromatocyphella* were shown to be later synonyms of *Resupinatus* (Thorn *et al*. 2000, 2005, McDonald 2015, Consiglio & Setti 2018, McDonald & Thorn 2019), while *Aphyllotus* was moved to *Marasmiaceae* (McDonald 2015, based only on morphology). However, the classification of *Resupinatus* (tribe *Resupinateae sensu stricto*) has always been very uncertain. Most works failed to obtain significant support for any phylogenetic relationship of *Resupinatus*, *i.e*., Moncalvo *et al*. (2000) placed *Resupinatus* near *Phyllotopsis* and *Pleurocybella* within the euagarics clade; Thorn *et al*. (2000) near the *Tricholomataceae sensu lato* (*Tricholomatineae*); Moncalvo *et al*. (2002) close to *Marasmiaceae*; Bodensteiner *et al*. (2004) as part, together with *Stigmatolemma*, of the /resupinatus clade in the euagarics clade; Binder *et al*. (2005) as sister to *Arrhenia* in the core euagarics clade; Thorn *et al*. (2005) placed it close to the /hemimycena clade and the /phyllotopsis clade; Matheny *et al*. (2006) as part of the *Pleurotaceae* (together with *Cantharocybe gruberi*) within the Pluteoid clade; McDonald (2015) close to the *Pleurotaceae*, *Entolomataceae*, and *Tricholomataceae*; Petersen *et al*. (2015) as *incertae sedis* within *Agaricales* (sister with no support to *Phyllotopsis*); Liu *et al*. (2016) as sister to *Mycena* spp. in *Tricholomataceae sensu lato* in the ITS analysis and sister to *Arthromyces* in the LSU analysis; Consiglio & Setti (2017), as sister to *Pleurotaceae*; Varga *et al*. (2019), within

Marasmiineae; Sánchez-García *et al.* (2020), within *Marasmiineae*, close to *Phloeomana* and *Hemimycena* (*Cyphellaceae*, *Marasmiineae*, see Vizzini *et al*. 2022); Karasiński *et al*. (2023) as *incertae sedis* in *Cyphellaceae*, *Marasmiineae* (LSU-based analysis). The present analysis (Fig. 2) suggests that *Resupinatus* is an independent clade within *Pleurotineae*. The important morphological differences with the family *Pleurotaceae*, and the lack of a significant support for their monophyletic origin excluding the family *Schizophyllaceae*, are the basis to propose restoring the family name *Resupinataceae* to accommodate this clade.

Schizophyllaceae Quél., Fl. Mycol. France (Paris): 365. 1888.
Synonyms: *Auriculariopsidaceae* Jülich, Biblioth. Mycol. 85: 355. 1982. [1981].
Schizophyllaceae Roze [as ‘Schizophyllées’], Bull. Soc. Bot. France 23: 108 (1876), *nom. inval.*, Art. 32.1(c), 32.1(b); see Art. 18.4 (Shenzhen); see Donk (1964).

Type: *Schizophyllum* Fr. [as ‘Schizophyllus’, *orth. cons.*], Observ. Mycol. (Havniae) 1: 103. 1815.

Representative genera: *Auriculariopsis* and *Schizophyllum*.

Notes: The family *Schizophyllaceae* is characterized by its basidiomes typically astipitate, gymnocarpic, resupinate to cyphelloid/cupulate. Hymenophore smooth or folded (pseudolamellate). Hyphal system monomitic to dimitic, hyphae usually presenting clamp connections, non-amyloid, and often immersed in a gelatinous matrix. Basidia usually 4-sporic and basidiospores colourless or occasionally yellow-brown, non-dextrinoid, inamyloid. Cystidia usually absent. In culture, *Schizophyllum commune* and *Auriculariopsis ampla* are characterized by clamped hyphae with spines (Essig 1922, Nobles 1948, Watling & Sweeney 1971, Nuss 1980, Stalpers 1988, Nakasone 1996). Lignicolous, often bark-specialized, pioneer colonizers of dead plant debris, intermediate behaviour between white-rot and brown-rot fungi (see below), with a suggested weak phytopathogenic potential in *Schizophyllum* (Takemoto *et al*. 2010, Rezgui *et al*. 2018). *Schizophyllum commune* is also known to be an opportunistic pathogen in humans due to its peculiar wood-degrading enzymes and toxic metabolites (Viswanathan *et al*. 2019, Tam *et al*. 2022).

The first to find a significant phylogenetic relationship between *Fistulina* and *Schizophyllum* were Hibbett *et al*. (1997), a result confirmed later by Moncalvo *et al*. (2002), Bodensteiner *et al*. (2004) and Henkel *et al*. (2010), suggesting that the families *Schizophyllaceae* and *Fistulinaceae* have a monophyletic origin. Taxa belonging to *Schizophyllaceae* and *Fistulinaceae* clustered together within or as a basal clade of the Marasmioid clade (*Marasmiineae*) in several works (Matheny *et al*. 2006, Maynard *et al*. 2019, Olariaga *et al*. 2020, Ke *et al*. 2020, Li *et al*. 2021, Wang *et al*. 2023b), or else as a distinct *incertae sedis* clade (Yamaguchi *et al*. 2009, Binder *et al*. 2010, Floudas *et al*. 2015, Dentinger *et al*. 2016, Almási *et al*. 2019, Varga *et al*. 2019, Sánchez-García *et al*. 2020). In the phylogenomic work by Dentinger *et al*. (2016) the new suborder *Schizophyllineae* was established for the clade containing *Schizophyllum commune* and *Fistulina hepatica*. Wang *et al*. (2023b) showed that this clade contains at least the families *Schizophyllaceae*, *Fistulinaceae* and *Cyphellopsidaceae* (as *Niaceae*). In the present analysis (Fig. 2) suborder *Schizophyllineae* seems to have a monophyletic origin with the families *Pleurotaceae* and *Resupinataceae*, and consequently *Schizophyllineae* and *Pleurotineae* are here considered synonyms. Since both were proposed in the same work (Dentinger *et al*. 2016), priority is given here to *Pleurotineae*. Comparative genomic and transcriptomic analyses of *Schizophyllaceae* (*Auriculariopsis ampla* and *Schizophyllum commune*) and *Fistulinaceae* (*Fistulina hepatica*) suggest that these fungi have peculiar plant cell wall-degrading enzymes transitional between those of white rot species and less efficient wood-degraders such as brown rot or mycorrhizal fungi (Floudas *et al*. 2015, Almási *et al*. 2019, Veloz Villavicencio *et al*. 2020).

Fistulinaceae Lotsy, Vortr. Bot. Stammesgesch. 1: 695, 704. 1907.
Synonym: *Fistulinaceae* Maire, Bull. Soc. Mycol. France 18 (Suppl.): 111. 1902, *nom. inval.*, Art. 32.1(b); see Art. 18.4 (Shenzhen).

Type: *Fistulina* Bull., Hist. Champ. Fr. (Paris) 1(2): 313. 1791.
Synonyms: *Agarico-carnis* Paulet, Traité champ. (Paris) 2: 97. 1793.
Buglossus Wahlenb., Fl. Upsal.: 459. 1820.
Hypodrys Pers., Mycol. Eur. (Erlanga) 2: 148. 1825.
Confistulina Stalpers, Canad. J. Bot. 61: 1660. 1983.

Representative genera: *Fistulina*, *Porodisculus*, and *Pseudofistulina*.

Notes: The family *Fistulinaceae* is characterized by its basidiomes gymnocarpic, large (20–300 mm wide), pileate, non-stipitate, or pileate-stipitate, pileus circular, tongue- or kidney-shaped, base often attenuate, or flabelliform, lobate or tiny (1–4 mm), pendant, soft or resinous hard when dried, horny, very dense, surface velutinous or tufted by hairs to pruinose, reddish or brownish; stipe absent or present, solitary to confluent, lateral or eccentric, sometimes rooting, minutely velutinous; hymenophore tubular, tubes independent, separate but closely packed or coherent, fused (polyporoid), whitish to yellowish or reddish brown, particularly after bruising. Hyphal system monomitic, pileipellis a trichoderm or an interwowen cutis. Hyphae simple or as acanthophyses, thin- to thick-walled, colourless, inamyloid, non-dextrinoid. Clamp connections present or absent. Cystidia absent or rarely present as pileocystidia-like hyphal ends or as hymenial elements. Basidia clavate or suburniform, sterigmata 4-sporic. Basidiospores subglobose or ellipsoid, cylindrical to allantoid, smooth, colourless to pale cream, thin- or thick-walled, inamyloid, non-dextrinoid. Pileipellis and stipitipellis sometimes with coralloid brown hyphae. Lignicolous, terricolous, saprotrophic, or parasitic on wood or roots. Asexual morph phase sometimes present (*Confistulina*). Inducing wood decay in living trees (*Fistulina* and *Pseudofistulina*; Gilbertson & Ryvarden 1986, Guzmán 1987, Schwarze *et al*. 2000, González *et al*. 2021).

Phylogenetically, *Fistulina*, with its pileate basidiomes, tongue- or kidney-shaped gelatinous soft pileus and separate tubes (Song *et al*. 2015, Sun *et al*. 2019, González *et al*. 2021, Zhou *et al*. 2022), is closely related to *Porodisculus* (Bodensteiner *et al*. 2004, Binder *et al*. 2005, Henkel *et al*. 2010, Song *et al*. 2015, Sun *et al*. 2019, González *et al*. 2021, Zhou *et al*. 2022) and *Pseudofistulina* (González *et al*. 2021, Zhou *et al*. 2022). *Porodisculus* is characterized by tiny and pendant basidiomes, resinous hard when dried, coherent tubes, and coralloid brown hyphae (acanthophyses) in pileipellis and stipitipellis (Gilbertson & Ryvarden 1987, Ginns 1997, Lee & Jung 2008, Chuzho & Dkhar 2020). *Pseudofistulina* has pileate-stipitate basidiomes, fleshy coriaceus, soft, stipe solitary to somewhat confluent, lateral or eccentric, often rooting, separate tubes, and slightly amyloid acanthophyses in pileipellis and hymenium (Wright 1961, Fidalgo & Fidalgo 1962, Burdsall 1971, Gilbertson & Ryvarden 1986, Guzmán 1987).

Pluteineae Aime *et al.*, Biol. J. Linn. Soc. 117: 27. 2016.
Synonym: *Pluteales* Kühner, Bull. Mens. Soc. Linn. Lyon 49(Num. Spéc.): 357. 1980.

Type: *Pluteus* Fr., Fl. Scan.: 338. 1836.

Representative families: *Amanitaceae*, *Limnoperdaceae*, *Melanoleucaceae*, *Pluteaceae*, and *Volvariellaceae*.

Notes: Five families are here recognized within suborder *Pluteineae*: *Amanitaceae* (including *Leucocortinarius*), *Limnoperdaceae*, *Melanoleucaceae*, *Pluteaceae*, and *Volvariellaceae*. There is no obvious morphological synapomorphy that unites the *Pluteineae*. Basidiomes are pileostipitate (agaricoid) (with open or enclosed hymenophore) or gasteroid/sequestrate (angiocarpic development, epigeous or hypogeous), mostly fleshy, heterogeneous (context of the pileus not continuous with the context of the stipe and consequently pileus and stipe separable from each other) and with free lamellae (homogeneous with adnate to subdecurrent lamellae in *Leucocortinarius* and *Melanoleucaceae*). Hyphae monomitic; clamp connections present or absent; non-amyloid, sometimes slightly metachromatic. Basidia ballistosporic or statismosporic. Basidiospores colourless or with pink/red tinges, smooth or verrucose, without a germ pore, amyloid or inamyloid, cyanophilous (Cotton blue) or not, slightly metachromatic (Cresyl blue) in *Leucocortinarius*. Hymenial cystidia often present. Hymenophoral tramal regular, bilateral, or inverse. Pileipellis typically a cutis or a trichoderm except for the hymenodermic/cellulodermic structure found in some species of *Pluteus*. Protective veils are often present (monovelangiocarpic to bivelangiocarpic development). Most *Amanitaceae* are ectomycorrhizal, except species of *Saproamanita*, and the remaining families include mostly terricolous or lignicolous saprotrophic taxa, rarely mycoparasitic (*i.e.*, *Volvariella surrecta*). In the present analysis, the family *Amanitaceae* is only subsignificantly related to the remaining families of *Pluteineae* (0.88 PP), but this seems to be caused by insufficient data from some lineages (*i.e.*, *Leucocortinarius*), as their exclusion from the analyses resulted in full support for a monophyletic origin of *Amanitaceae* and the remaining *Pluteineae* (*i.e.*, Supplementary Fig. S1).

Amanitaceae E.-J. Gilbert, Iconogr. Mycol., Suppl. I (Milan) 27: 63. 1940.
Synonym: *Torrendiaceae* Jülich, Biblioth. Mycol. 85: 392. 1982. [1981].

Type: *Amanita* Pers., Tent. disp. meth. fung. (Lipsiae): 65. 1797.

Representative genera: *Amanita*, *Catatrama*, *Leucocortinarius*, *Limacella*, *Limacellopsis*, *Saproamanita* and *Zhuliangomyces* (= *Myxoderma* Kühner 1926 *sensu* Cui *et al*. 2018 and Yang *et al*. 2018; *nom. illegit.*, *non Myxoderma* Schmidle 1901, *Cyanophyta*).

Notes: For general features of the family and generic delimitation see Redhead *et al*. (2016), Cui *et al*. (2018), and Yang *et al*. (2018). Basidiomes are predominantly agaricoid (but *Amanita* also includes angiocarpic/sequestrate species formerly classified in *Torrendia* and *Amarrendia*, see Justo *et al*. 2010), mono- to bivelangiocarpic, with or without a schizohymenial development of the hymenophore (Reijnders 1963, Bas 1969), pileus convex to applanate with margin smooth or radially sulcate, dry or greasy, sometimes glutinous, covered or not with remnants of the universal veil; lamellae usually free, rarely subfree or adnate (*Leucocortinarius*); stipe, when present, cylindrical, with or without a basal inflation or a bulb, with or without a partial veil as an annulus, dry or slimy, base with or without remnants of the universal veil which can form a saccate volva; spore deposit white, greenish to light pink; basidiospores globose to ellipsoid or cylindrical, colourless, mostly thin-walled, predominantly smooth, rarely echinulate-verrucose, amyloid or not, dextrinoid or not, cyanophilous or not, metachromatic in *Leucocortinarius*, usually binucleate; basidia usually 4-sporic, ballistosporic or statismosporic; hymenophoral trama bilateral or irregular to regular (*Leucocortinarius*); hymenial cystidia usually absent but spheropeduncolate elements present on the lamella edge in *Amanita*, resembling cheilocystidia, rare cheilocystidia in *Leucocortinarius*; pileipellis a cutis, ixocutis, ixotrichoderm or ixopalisadoderm; stipe trama longitudinally acrophysalidic (heteromerous) or not; clamp connections present or absent. Species are terricolous, mainly symbiotic mutualists forming ectomycorrhizas with angiospermous and gymnospermous trees (Trappe 1962, Singer 1986, Cuvelier 1990, Mleczko 2004, Daniele *et al*. 2005, Agerer 2006, Rinaldi *et al*. 2008, Bai *et al*. 2009, Niazi *et al*. 2009, Tedersoo *et al*. 2010) and/or arbutoid mycorrhizas with *Ericaceae* (Molina & Trappe 1982, Smith & Read 2008), or saprotrophic (*Saproamanita*, *Limacella sensu lato* and *Catatrama*, Wolfe *et al* 2012, Hess & Pringle 2014, Redhead *et al*. 2016, Li *et al*. 2020).

Leucocortinarius (J.E. Lange) Singer, Lloydia 8(3): 141. 1945.
Synonym: *Cortinarius* subgen. *Leucocortinarius* J.E. Lange, Dansk Bot. Ark. 8(no. 7): 6. 1935.

Type: *Leucocortinarius bulbiger* (Alb. & Schwein.) Singer, Lloydia 8: 141. 1945. Figs 7B, 11.
Basionym: *Agaricus bulbiger* Alb. & Schwein., Consp. fung. (Leipzig): 150. 1805.
Synonyms: *Armillaria bulbigera* (Alb. & Schwein.) P. Kumm., Führ. Pilzk. (Zerbst): 135. 1871.
Gyrophila bulbigera (Alb. & Schwein.) Quél., Enchir. fung. (Paris): 9. 1886.
Mastoleucomyces bulbiger (Alb. & Schwein.) Kuntze, Revis. gen. pl. (Leipzig) 2: 861. 1891.
Cortinellus bulbiger (Alb. & Schwein.) Pat., Essai Tax. Hyménomyc. (Lons-le-Saunier): 161. 1900.
Tricholoma bulbigerum (Alb. & Schwein.) Ricken, Die Blätterpilze: 331. 1914.
Cortinarius bulbiger (Alb. & Schwein.) J.E. Lange, Dansk Bot. Ark. 8(no. 7): 13. 1935.
Agaricus malleipes Lasch, Linnaea 4: 519. 1829.
Agaricus cupreus Secr., Mycographie Suisse 1: 70. 1833 (*nom. inval.*), Art. 34.1 (Shenzhen).

Description: *Habit* cortinarioid (phlegmacioid), bivelangiocarpic, basidiome homogeneous non-schizohymenial. *Pileus* 30–120(–150) mm diam, convex, with incurved margin when young, later plane, smooth, slightly gelatinous, orange brown to reddish brown (6A5-8), vinaceous brown (7A7-8), cracking as it ages; when young covered with white veil remnants (mainly as patches). *Lamellae* moderately crowded, adnate-emarginate to subfree, white, becoming cream (4A4-6) with age. *Stipe* 30–90 × 6–20 mm, usually tapering towards the apex, base swollen and usually abruptly bulbous with a rounded to

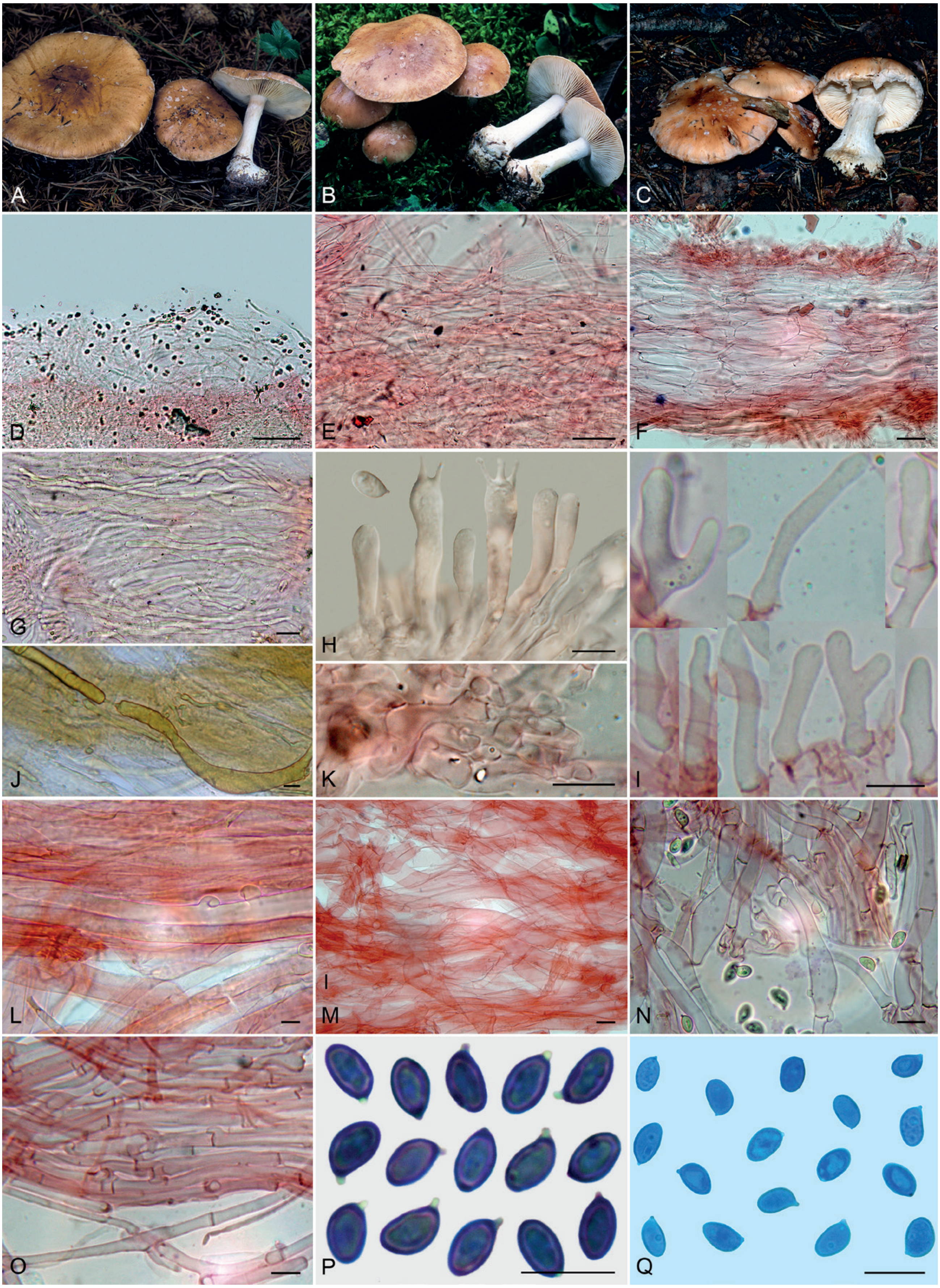

Fig. 11. *Leucocortinarius bulbiger*. **A–C.** Basidiomes (A. JV13908F TUR-A; B, JV25486F TUR-A; C, AMB:19592). **D.** Pileipellis (AMB:19593). **E.** Subpellis (AMB:19593). **F.** Hymenophoral trama (JV13908F). **G.** Thromboplerous hyphae of the hymenophoral trama (GC96078). **H.** Hymenium (basidia) (AMB:19593). **I.** Cheilocystidioid elements (JV13908F TUR-A). **J.** Thromboplerous hypha of the stipitipellis (B JV25486F TUR-A). **K.** Subhymenium (GC96078). **L.** Stipititrama (JV13908F TUR-A). **M.** Bulb trama (JV13908F TUR-A). **N.** Elements of the universal veil (JV13908F TUR-A). **O.** Elements of the partial veil (JV13908F TUR-A). **P, Q.** Basidiospores (P. JV13908F TUR-A; Q. AMB:19593). Mounting media were Melzer's reagent (J), Congo Red in ammonia (D–I, K–O), Cotton Blue (Q), and Cresyl Blue (P). Scale bars: D, E = 30 µm; F–Q = 10 µm. Photographs A, B by J. Vauras, C by G. Consiglio, D, E, G, H, K, Q by M. Marchetti, F, I, J, L–P by E. Campo.

flattened marginate 20–40 mm wide bulb, white, staining somewhat brownish (5B5-7) when mature; partial veil present, coarsely fibrillose (not cobweb-like as in *Cortinarius sensu lato*), forming both a fragile cottony- ring-like zone at stipe apex and abundant remnants on pileus margin; universal veil white, on pileus disk and bulb rim (margin). *Context* white, *odour* agreable, *taste* mild. *Spore deposit* white to pale cream. *Basidiospores* (5.6–)6.6–*7.1*–7.7(–9.4) × (3.4–) 4.2–*4.6*–4.9(–5.3) µm [166/4/4], Q = (1.29–)1.44–*1.57*–1.70(–2.06), V = (41.5–)63.4–*78.1*–92.8(–119) µm^3, ellipsoid to broadly ellipsoid (rounded apex) or subamygdaliform (slightly tapered apex), smooth, thick-walled and with weak suprahilar depression and prominent apiculus, containing numerous greenish guttulae or a single large central guttula, wall slightly congophilous, cyanophilous in Cotton blue and weakly metachromatic in Cresyl blue (Fig. 11P), inamyloid and indextrinoid. *Basidia* 30–45(–50) × 7–9(–10.5) µm, long claviform, most 4-sporic, rarely 2-sporic, sterigmata up to 4–5 µm long, with minute greenish internal droplets. *Cheilocystidioid elements* present in some collections, (18–)20–27(–32) × (4–)4.2–5(–5.5) µm, colourless, thin-walled, cylindrical to fusoid, sometimes bifid, with basal clamp connection. *Hymenophoral trama* regular, consisting of subparallel, colourless to light yellow, weakly metachromatic, thin-walled hyphae, often slightly constricted at septa, in the medium stratum voluminous, (5–)6–14(–25) µm wide, in the lateral stratum 3–7 µm wide; thromboplerous hyphae abundant, 4–10 µm wide, with grey yellowish to greenish content. *Subhymenium* thin, of 3–6 µm wide, short and often intertwined hyphal elements. *Partial veil* formed by parallel-oriented, thin-walled and clamped cylindrical hyphae, 2–5 µm wide, with a faint yellowish parietal pigment and slightly metachromatic. *Universal veil* constituted by a network of 3–6 µm wide clamped hyphae, cylindrical, sometimes spindle-shaped, enlarged in the median part up to 13 µm, faintly coloured by a yellowish parietal pigment and weakly metachromatic; rare 3–8 µm wide thromboplerous hyphae are present. *Pileipellis* an ixotrichocutis (transition between cutis and trichoderm) of congophobic, 2–4(–5) µm wide, loose, and sinuous ascending clamped hyphae with spaced septa, often forming tufts, some with a gold yellow vacuolar pigment, immersed in a gelatinized matrix and arising from deeper layers of horizontal 3–7 µm wide congophilous hyphae, some with minute brownish granular epiparietal pigments. *Subpellis* of subparallel, up to 10 µm wide colourless hyphae; nodulose 4–10 µm wide thromboplerous hyphae present. *Stipitipellis* consisting of a cutis of thin-walled, 4–10 µm wide colourless hyphae, slightly metachromatic, with long, just emerging terminal elements with obtuse apex and clamp connections on each septum; 5–15 µm wide thromboplerous hyphae abundant. *Stipititrama* (both the cylindrical portion and the bulb) not acrophysalidic, characterized by 5–25(–30) µm wide colourless and slightly metachromatic clamped hyphae, subparallel oriented in the cylindrical portion, somewhat intertwined in the bulb; abundant nodulose, 5–25 µm wide thromboplerous hyphae. *Clamp connections* and *thromboplerous hyphae* frequent in all parts of the basidiome. *Trama hyphae* neither amyloid nor dextrinoid but weakly metachromatic.

Habitat and distribution: Terricolous, usually associated with coniferous trees, especially *Picea*, *Abies*, and *Pinus sylvestris*, usually on calcareous soil, Europe, Asia, and North America. Late summer to autumn. It is ectomycorrhizal (Singer & Morello 1960, Trappe 1962, Newton & Haigh 1998, Bai *et al*. 2009, Zheng *et al*. 2016).

Materials examined: **Finland**, Etelä-Häme, Hattula commune, Retulansaari, S side of the road, pastured meadows with abundant *Juniperus communis* and scattered *Pinus sylvestris*, under *P. sylvestris*, 12 Aug. 1998, J. Vauras, 13908F (TUR-A); Etelä-Häme, Tammela, Mustiala, Syrjänharju, near and S of Toivonsilta, fairly rich forest with mainly *Picea abies*, by walking trail, 19 Sep. 2007, J. Vauras, 25486F (TUR-A). **Italy**, Castel Lamberto (BZ), under *Picea abies*, 5 Sep. 1996, G. Consiglio (AMB:19592); Laghestel, Baselga di Piné (TN) under *Picea abies*, 28 Sep. 2005, G. Consiglio (AMB:19593).

Notes: By now, the genus *Leucocortinarius* is presumably monospecific. The only other species described in *Leucocortinarius* is *L. castulifer* (≡ *Armillariella castulifera*), a very rare taxon (there are three samples at PC from the 1970s and 1980s) no longer found by other authors after its description. According to the original reports (Romagnesi 1978, 1980) it seems to differ from *L. bulbiger* only in a more consistent and striated ring. *Agaricus bulbiger* was described as characterized by an orange cinnamomeus reddish pileus with white veil remnants, white emarginate-adnexed lamellae, stipe with a marginate depressed bulb and a white annulus at apex, white spore deposit, and occurring in deciduous thorn-thickets among leaves and mosses, everywhere solitary or somewhat gregarious (Albertini & Schweinitz 1805). It was later transferred into numerous genera until Lange (1935) established *Cortinarius* subg. *Leucocortinarius* for it. This subgenus was later raised to the rank of genus by Singer (1945). The taxon has been considered to be either akin to pale-spored genera of *Tricholomataceae sensu lato* (*Armillaria*, *Tricholoma*; *e.g.*, Kummer 1871, Quélet 1886, Kuntze 1891, Ricken 1914, Singer 1945, Kühner & Romagnesi 1953, Romagnesi 1978, 1980, Bon 1987a, 2004, Courtecuisse & Duhem 1994, Consiglio & Papetti 2001, Ludwig 2001a, b, Boccardo *et al*. 2008, Frøslev 2012, Agerer 2018, Læssøe & Petersen 2019, Kalichman *et al*. 2020, Kibby 2020) or to ochre-spored *Cortinarius* and allied taxa (*e.g.*, Patouillard 1900, Lange 1935, Konrad & Maublanc 1952, Singer 1951, 1962, 1975, 1986, Singer & Morello 1960, Horak 1968, 2005, Moser 1978, Kühner 1980, Jülich 1981, Reijnders & Stalpers 1992, Watling & Gregory 1994, Bas & Kuyper 1995, Eyssartier & Roux 2011).

Leucortinarius shares with most tricholomataceous fungi the white spore deposit, non-free lamellae, smooth basidiospores, green reaction of basidiomes surfaces with TL-4 (Romagnesi 1978, 1980) and with some species of *Cortinarius sensu lato* the bivelangiocarpic development (Reijnders 1979), the presence of a marginate bulb and of binucleate basidiospores (Kühner 1945, 1980, Singer 1951, 1986). Macromorphologically, *Leucocortinarius* bears a superficial resemblance to some bulbous-based webcaps (*Cortinarius* sect. *Scauri* species) but its spore deposit is white rather than rusty brown; more specifically it resembles a pale-spored form of *Cortinarius multiformis* (now included in *Thaxterogaster* emend. Niskanen & Liimat. subgen. *Multiformes*, Liimatainen *et al*. 2022).

Molecular phylogenetic analyses based only on one or a few markers (mainly ribosomal DNA) and/or a limited taxon sampling did not provide a satisfactory answer about the classification of this taxon within the *Agaricales* (He *et al*. 2019 considered it as *incertae sedis*) *i.e*., Garnica *et al*. (2007), Varga *et al*. (2019) and Kalichman *et al*. (2020) placed it in *Tricholomataceae sensu lato*; Saar *et al*. (2009) as close (wihout support) to *Hygrocybe coccinea*; Zheng *et al*. (2016) as sister to *Hebeloma cylindrosporum* and Sánchez-García *et al*. (2020) as sister to *Amanitaceae*, the latter a conclusion supported also by the present analysis (Fig. 2).

Limnoperdaceae G.A. Escobar, Mycologia 68: 878. 1976.

Type: *Limnoperdon* G.A. Escobar, Mycologia 68: 875. 1976.

Representative genus: *Limnoperdon*.

Notes: This monogeneric and by now monospecific family (type *L. incarnatum*) is characterized by a reduced minute basidiome (0.3–1.5 mm diam) at first cupulate (cyphelloid) then sequestrate (enclosed), puffball-like, with a 1-loculate gleba lined up by a hymenium, at maturity opening by a pore through which a spore-containing drop extrudes, statismosporic (gasteroid) basidia, basidiospores symmetrical, thin- to thick walled, in mass pink/red-coloured, inamyloid, thin-walled hyphae with clamp connections, absence of hymenial cystidia, and growing on plant material (leaves, twigs) exposed to estuarian or fresh water (Escobar *et al*. 1976, Escobar & McCabe 1979, McCabe 1979, Webster & Descals 1981, Michaelides & Kendrick 1982, Nakagiri & Ito 1991, Webster *et al*. 1993, Voglmayr 1994, Abdel-Aziz 2016). It has been reported from Japan, Austria, Canada, USA, Egypt, South Africa, and Argentina (Webster *et al*. 1993, Voglmayr 1994, Donoghue & Alverson 2000, Hibbett & Binder 2001, Bärlocher *et al*. 2008, Abdel-Aziz 2016, Agerer 2018). Hibbett & Binder 2001 placed *Limnoperdon* in the core Euagaricoid clade; Bodensteiner *et al*. (2004) as sister (without support) of a clade with *Melanoleuca* and *Pluteus*; Binder *et al*. (2005) as basal to core euagarics and close to *Pluteus* and *Entoloma*; Matheny *et al*. (2006) as sister to *Pluteaceae* in the Pluteoid clade; Justo *et al*. 2011 as part of the Pluteoid clade (consisting also of *Pluteus*, *Volvariella gloiocephala*-group = *Volvopluteus*, *Amanitaceae*, *Melanoleuca*, and *Macrocystidia*) with moderate to high statistical support in all the analyses; and Sánchez-García *et al*. (2020, suppl. mat.) as sister to a clade encompassing *Melanoleuca*, *Pluteus*, and *Volvopluteus*. The present analysis includes for the first-time sequences of protein-coding genes of *Limnoperdon* sp. (aff. *incarnatum*) (voucher CBS:160.95, WU 12660, Austria, studied in Voglmayr 1994), suggesting an ancient origin of this evolutive lineage and its treatment at the rank of family within *Pluteineae*. The closest ITS sequence to that obtained from CBS:160.95 is that of the ex-type strain of *L. incarnatum*, DSM1832 (UDB034350), but both are only 90 % similar, while their LSU is 99.3 % identical. Such a great distance between their ITS sequences seems to point to the existence of a reproductive barrier between these samples, but a larger sampling is necessary to draw reliable conclusions. Other sequences identified as *Limnoperdon* spp. in public databases seem to represent at least two other distinct species. Unfortunately, many of these sequences were obtained from environmental samples, so their taxonomic status cannot be resolved yet.

Melanoleucaceae Locq. *ex* Vizzini, Consiglio & P. Alvarado, ***fam. nov.*** MycoBank MB 851152.
Synonym: *Melanoleucaceae* Locq. Mycol. gén. struct. (Paris): 145. 1984, *nom. inval.*, Art. 39.1 (Shenzhen).

Diagnosis: Basidiomes pileostipitate, large collybioid to tricholomatoid, homogeneous (context of the pileus continuous with the context of the stipe and consequently pileus and stipe not separable from each other), lamellae adnexed to subdecurrent, partial veil absent or present. Spore deposit white to pale cream. Hyphal system monomitic. Hymenophoral trama subregular. Basidiospores colourless, subglobose to ellipsoid, decorated with rounded to acute-blunt amyloid verrucae, cyanophilous or not. Basidia sometimes containing micro-type siderophilous granules (*Melanoleuca*). Cheilocystidia usually present. Pleurocystidia usually absent or rare. Pileipellis typically a cutis or a trichoderm. Clamp connections present or absent. Terricolous, probably saprotrophic, although *Giacomia mirabilis* cannot be easily cultured *in vitro* (Moser 1963), suggesting an ectomycorrhizal lifestyle.

Type: *Melanoleuca* Pat., Cat. Rais. Pl. Cellul. Tunisie (Paris) (7): 22. 1897.

Representative genera: *Giacomia* (Figs 6G, 12–14) and *Melanoleuca* (7F–G).

Notes: The present analysis supports for the first time that *Giacomia* and *Melanoleuca* have a monophyletic origin inside suborder *Pluteineae* (Fig. 2), a result not found in previous studies based only on ribosomal DNA data of *Giacomia*, which placed this genus in an uncertain position within the *Tricholomatineae* (Vizzini *et al*. 2012a, Sánchez-García *et al*. 2014, Sánchez-García 2016, Angelini *et al*. 2017, He *et al*. 2019). However, Varga *et al*. (2019) suggested that *Giacomia* is not related to suborder *Tricholomatineae*. On the other hand, the phylogenetic proximity of *Melanoleuca*, *Pluteus* and allied taxa had already been highlighted by Moncalvo *et al*. (2002), Matheny *et al*. (2006), Garnica *et al*. (2007), Justo *et al*. (2011), and Sánchez-García *et al*. (2020, suppl. mat.). *Melanoleuca* is a cosmopolitan genus with more than 440 species epithets (Index Fungorum, https://www.indexfungorum.org/names/Names.asp) corresponding to *ca*. 60 confirmed species (Agerer 2018, He *et al*. 2019). Morphologically, *Melanoleuca* is characterized by collybioid to tricholomatoid gymnocarpic basidiomes, convex to slightly depressed pileus often with a low central umbo, emarginate, adnate, or shortly decurrent (with tooth) lamellae, pileipellis in the form of cutis to trichoderm, cyanophilous, amyloid ornamented basidiospores, basidiospores with a well-delimited suprahilar plage (Singer 1986, Bon 1991), basidia with siderophilous granules of the micro type, the frequent presence of long, thin- to thick-walled and often muricate cheilocystidia (macrocystidia), pleurocystidia (if present) similar to cheilocystidia, and the absence of clamp connections (Singer 1972, Clémençon 1978, 2004, Kühner 1978, Singer 1986, Boekhout 1988, 1999a, Bon 1991, Watling & Turnbull 1998, Garnica *et al*. 2007, Vesterholt 2008a, 2012a, Vizzini *et al*. 2011a, Xu *et al*. 2019, Antonín *et al*. 2022).

Giacomia Vizzini & Contu, Mycosphere 3: 84. 2012.

Type: *Giacomia mirabilis* (Bres.) Vizzini & Contu

Notes: *Giacomia* differs from *Melanoleuca* because of the presence of clamp connections, basidia without inner siderophilous granules, evanescent veil at stipe apex, not well differentiated and not muricate hymenial cystidia, and basidiospores without a well-delimited suprahilar plage (Vizzini *et al*. 2011a and see below). Until the present work, *Giacomia* was considered a monospecific genus. Hereafter, a second species is formally described and a full description of the very rare *G. mirabilis* is provided.

Giacomia mirabilis (Bres.) Vizzini & Contu, Mycosphere 3: 84. 2012. Figs 6G, 12–13.
Basionym: *Tricholoma mirabile* Bres., Fungi Tridentini 1(2): 16. 1881.
Synonyms: *Melanoleuca mirabilis* (Bres.) Singer, Lloydia 5: 121. 1942.
Leucopaxillus mirabilis (Bres.) Konrad & Maubl., Encyclop. Mycol. 20: 191. 1952.
Tricholoma mirabile Bres. var. *nigrescens* Bres., Icon. Mycol. 2: 92. 1927.

Fig. 12. *Giacomia mirabilis*. **A–F.** Basidiomes (A. TUR-A 209709; B. AMB:18860; C. TUR-A 195638; D. AMB:19594; E. *G. f. nigrescens* AMB:19297; F. TO:AV20231010). **G.** Pileus margin (TUR-A 209709). **H, I.** Stipe apex (H. AMB:19595; I. TUR-A 195638). Photographs A, C, G, I by E. Campo; B, E by G. Consiglio; D by C. Feltrin; F by J. Ferrari; H by E. Zanella.

Melanoleuca nigrescens (Bres.) Bon, Doc. Mycol. 9: 47. 1978.
Leucopaxillus mirabilis var. *nigrescens* (Bres.) Fontenla & Para, Rivista Micol. 50: 233. 2007.
Giacomia mirabilis f. *nigrescens* (Bres.) Vizzini & Contu, Mycosphere 3: 84. 2012.
Leucopaxillus amarus f. *phaeopus* J. Favre & Poluzzi, Vita Helvetica 71: 74. 1949.
Leucopaxillus phaeopus (J. Favre & Poluzzi) Bon, Bull. Trimestriel Féd. Mycol. Dauphiné-Savoie 27: 29. 1987.
Leucopaxillus mirabilis var. paxilloides M.M. Moser *ex* Bon, Doc. Mycol. 9(no. 33): 22. 1978, *nom. inval.*, Art. 39.1 (Shenzhen).

Description: *Habit* tricholomatoid to leucopaxilloid. *Pileus* (30–)40–100(–120) mm diam, at first convex, then expanded and depressed at centre, sometimes with an obtuse flat umbo; surface dry, not or slightly hygrophanous, minutely tomentose to fibrillose, dark brown (4E6-8), grey brown (7D3-5), reddish brown (5B6-8), blackish brown (4F2-8, 5F3-6), but also ochre-brown (6C5-8) or yellowish-cream (4A6-8, 4B7-8), sometimes paler at centre; margin paler, initially inrolled and often wavy when old, sometimes costate to furrowed, typically minutely hairy with white hairs up to 8 mm long (Fig. 12G), single or in tufts (it looks like *Pogonoloma spinulosum*). *Lamellae* arcuate, decurrent to adnexed with tooth, crowded (L = 45–70), with lamellulae [l = (1–)2–5], white then cream, sometimes brownish at the edge and face level near the stipe (as in *Lactarius lignyotus*), with an entire edge. *Stipe* (30–)40–60(–70) × (6–)8–12(–15) mm, cylindric, terete, sometimes attenuated towards the base, dry, fibrillose-squamulose, ochre-brown, reddish-brown, blackish-brown, white to cream toward the base. The stipe apex can appear in two ways: concolorous with the rest of the stipe and exhibiting brown reticulating lines which appear to be extensions of the lamellae (Fig. 12H), or with an evident white belt (band) delimited by a hoary ring-like zone (Fig. 12I). *Context* whitish, ochre-brownish under the cortical parts. *Odour* subfarinaceous, sometimes subspermatic, herbaceous. *Taste* mild, sometimes slightly bitterish after a long time of mastication. *Spore deposit* whitish to pale cream. *Basidiospores* (5.39–)6.11–*6.68*–7.25(–8.73) × (3.8–)4.52–*5.0*–5.48(–5.96) µm [99/3/3], Q = (1.1–)1.21–*1.33*–1.45(–1.75), V = (50.4–)68.3–*90.2*–112.0(–139.7) µm^3, broadly ellipsoid to ellipsoid, sometimes in profile adaxially flattened, colourless, thin-walled, pluriguttulate, with a well-developed hilar appendix, warty, amyloid, cyanophilous, with irregularly distributed, rounded to acute-blunt verrucae, without a suprahilar plage. *Basidia* (25.0–)29.13–34.87(–37.0) × (5.52–)6.42–8.38(–9.64) µm, Q = (3.14–)3.83–4.91(–5.43), 4-sporic, rarely 2-sporic, clavate, with up to 6 µm long sterigmata, not siderophilous, with numerous inner refractive droplets. *Hymenophoral trama* regular to subregular, consisting of parallel cylindrical hyphae, (3.0–)5.0–15.0(–20.0) µm wide, colourless, thin-walled, sometimes with extracellular refractive crystalline deposits. *Subhymenium* 20–30 µm thick, of 2–4 µm wide, short and often intertwined hyphal elements. *Cheilocystidia* 20–40 × (2–)3.5–7 µm, sometimes very rare, versiform, polymorphic, cylindrical, lageniform, sinuous, diverticulate, forked, subcapitate, colourless, thin-walled, without inner content. *Pleurocystidia* absent. *Pileipellis* a cutis of parallel to intertwined cylindrical hyphae, 2–8 µm wide, terminal elements slightly gelatinized and sometimes ascendant and with enlarged apex, thin-walled; pigment yellowish, intracellular and parietal; grey-yellowish thromboplerous hyphae

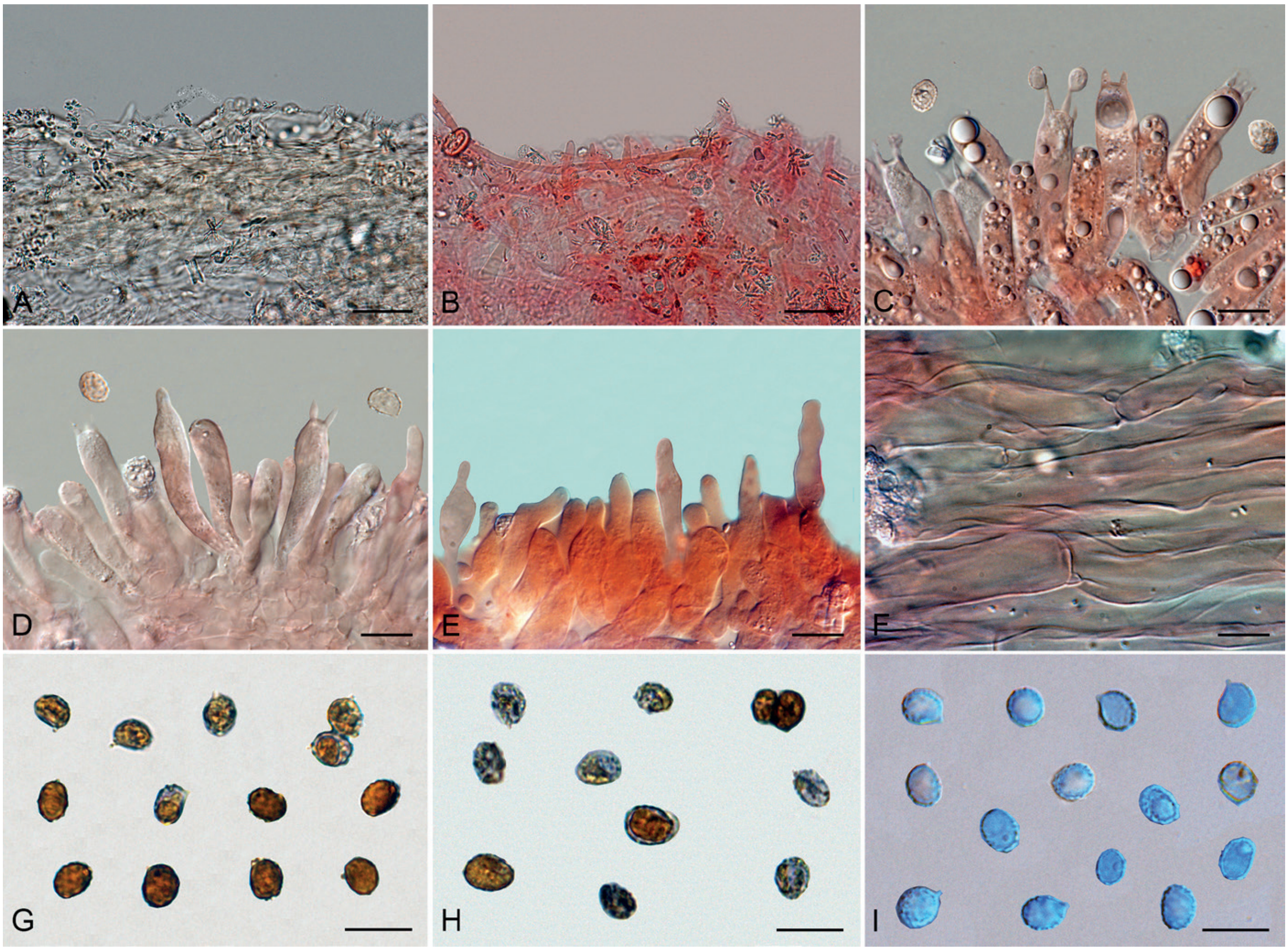

Fig. 13. *Giacomia mirabilis*. **A, B.** Pileipellis (A. AMB:18860; B. AMB:19297). **C.** Basidia and basidiospores (AMB:18860). **D.** Hymenium (AMB:19297). **E.** Cheilocystidia (AMB:18860). **F.** Elements of the hymenophoral trama (AMB:19297). **G–I.** Basidiospores (G, I. AMB:18860; H. AMB:19297). Mounting media were water (A), Melzer's reagent (G, H), Congo Red in ammonia (B–F), and Cotton Blue (I). Scale bars: A, B = 30 µm; C–I = 10 µm. Photographs M. Marchetti.

(oleiferous hyphae *sensu* Clémençon 2004) common; polymorphic, extracellular refractive crystalline deposits present on superficial hyphae. *Subcutis* consisting of cylindrical, 4–10 µm wide thin-walled hyphae. *Stipitipellis* of yellow-brown cylindrical hyphae 2–6 µm wide, thin- to thick-walled, intertwined, irregular-nodose, some terminal elements ascendant (emerging, repent), with abundant refractive crystalline deposits. *Stipititrama* of colourless, parallel, thin-walled, cylindrical, 5–10 µm wide hyphae. *Clamp connections* abundant in all tissues.

Habitat and distribution: Gregarious, growing with coniferous trees, often with *Picea abies* (spruce), *Pinus sylvestris* (Scots pine) or *Abies cephalonica* (Pantidou 1973, 1990, Zervakis *et al.* 1998). Restricted to alpine habitats with calcareous soils. So far known from northeast Italy, France, Germany, Switzerland, Austria, Spain, and Greece (Bresadola 1927, Moser 1963, Kühner 1977, Bon 1991, Breitenbach & Kränzlin 1991, Moser & Jülich 1993, Ballarà 1997, Zervakis *et al.* 1998, Consiglio & Contu 2000, Karasch & Hahn 2009).

Materials examined: *Giacomia mirabilis* var. *mirabilis*. **Italy**, Friuli-Venezia Giulia, Prato Carnico (UD), Località Pradibosco, 1 200 m asl, forest of *Fagus sylvatica*, *Picea abies* and *Abies alba*, among the *Petasites*, at the edge of a ski run, 5 Sep. 2020, C. Angelini, ANGE1598 (TO); Udine, Villa Santina, Invillino, among grass at the border of a path, near *Corylus avellana* and *Pinus sylvestris*, 2 Nov. 2011, E. Campo (TUR-A 195638); Auronzo di Cadore (BL), Ponte Malon, under *Picea abies*, 5 Sep. 2020, E. Campo (TUR-A 209709); Trentino-Alto Adige, Bolzano, San Vigilio di Marebbe, Villa Romantica, in a grassy meadow, among apple and plum trees, 5 Sep. 2017, C. Feltrin (AMB:19594); Trento, Predaia, Sette Larici, forest of *Pinus pinaster*, 28 Sep. 2018, A. Marangon (AMB: 19595); Trento, Terzolas, Le Tovare, mixed forest with *Abies alba* and *Fagus sylvatica*, 6 Sep. 2007, G. Consiglio (AMB:18860); Braies (BZ), Braies Vecchia, 1 200 m asl, on the edge of a forest of *Picea abies* and *Pinus sylvetris*, 10 Oct. 2022, R.J. Ferrari (TO:AV20231010). *Giacomia mirabilis f. nigrescens*. **Italy**, Trentino-Alto Adige, Trento, Brez, Traversara, forest of *Picea abies*, 18 Oct. 1987, M. Donini (AMB:19596); Trento, Sarnonico, Regole di Malosco, forest of *Picea abies*, 17 Sep. 1994, G. Consiglio (AMB:19297).

Notes: *Giacomia mirabilis* was originally described as *Tricholoma mirabile* (Bresadola 1881), then combined in *Melanoleuca* (Singer 1942a) and *Leucopaxillus* (Konrad & Maublanc 1952), and finally separated from *Leucopaxillus sensu lato* in the monotypic genus *Giacomia* on the basis of molecular studies (Vizzini *et al*. 2012a). It is a rare striking European taxon that can be easily recognized in the field due to its dark brown pileus and stipe, a hairy pileus margin, a wrinkled stipe apex with a thin ring formed by an araneous partial veil, abundant polymorphic cheilocystidia, and basidiospores varying in size, shape and ornaments (Moser 1963, Kühner 1950, 1977, Bon 1978, 1987, 1991, Marchand 1986, Breitenbach & Kränzlin 1991, Moser & Jülich 1993, Consiglio & Contu 2000, Ludwig 2001a, b). When present, basidiospore ornaments consist in isolated hemispherical warts, like those of *Melanoleuca cognata* (Pegler & Young 1973). *Giacomia mirabilis* cannot be easily cultured *in vitro* (Moser 1963), suggesting an ectomycorrhizal lifestyle. Due to its peculiar features, Bon (1991) classified this species in the monospecific subsection *Mirabilini* (characterized by the presence of a stipe with an areaneous ring-like veil) of sect. *Mirabiles* (characterized by the presence of cheilocystidia) of *Leucopaxillus*. *Leucopaxillus mirabilis* var. *nigrescens* differs only in having a darker pileus (Bresadola 1927, Bon 1991, Fontenla & Para 2007). The ITS sequences obtained in the present work from samples of *L. mirabilis* var. *mirabilis* [ANGE1598 (TO), AMB:18860, AMB:19297, AMB:19595, TO:AV20231010, TUR-A 195638, TUR-A 209709] and *L. mirabilis* var. *nigrescens* (AMB: 19297, AMB:19596) (Supplementary Table S1) are 99.9 % identical, supporting the infraspecific rank of this taxon, which is here considered as a colour form. Phylogenetic results (Fig. 2) suggest that *Giacomia mirabilis* is not closely related to *Leucopaxillus* (*Tricholomataceae*, *Tricholomatineae*), but to the genus *Melanoleuca* (*Pluteineae*), forming a monophyletic clade with it. The great genetic distance and the important morphological differences between these genera discourage to merge them, and so the current taxonomical arrangement is not changed.

Giacomia mirabilis is a morphologically variable species: colours range from almost whitish to blackish brown; spores can be smooth to coarsely warty, globose to ellipsoid; cheilocystidia are also polymorphic, sometimes scarce or even completely absent. It displays a hoary belt at the apex of the stipe. The taste is mild or sometimes slightly bitterish after some time. It grows in calcareous soils under alpine conifers, especially *Picea* sp. and *Pinus sylvestris*. After checking multiple collections, the remnants of a cortiniform veil reported previously in the upper part of the stipe (Kühner 1977, Bon 1991, Vizzini *et al*. 2012a) were occasionally observed, and some specimens present a distinctly delimited 5–10 mm broad, white, and almost smooth zone (like that observed in *Tricholoma ustaloides*, Christensen & Heilmann-Clausen 2013, Halama *et al*. 2016). *Leucopaxillus phaeopus* (= *L. amarus f. phaeopus*) is said to differ from *G. mirabilis* because of its parietal and incrusting pigments (intracellular in *Giacomia mirabilis*), and the absence of a pseudoanular zone at the apex of the stipe (Bon 1987b, Ballarà 1997, Consiglio & Contu 2000, Lavorato & Contu 2001). Based on the original description and colour illustration (Favre & Poluzzi 1949), and the fact that all collections studied present both intracellular and parietal pigmentation, we agree with Ludwig (2001a) who considered *L. phaeopus* a synonym of *G. mirabilis*.

Giacomia sinensis J.Z. Xu, ***sp. nov.*** MycoBank MB 851153. Figs 6H, 14.

Etymology: *sinensis* (Latin) meaning 'from China', the country where the holotype collection was found.

Diagnosis: *Giacomia sinensis* differs from *G. mirabilis* by its brownish orange and creamy white pileus, a white stipe, a trichodermal pileipellis, and absence of cheilocystidia.

Type: **China**, Qinghai Prov., Haixi Mongolian and Tibetan Autonomous Prefecture, Halihatu National Forest Park, 37°2'9" N, 98°39'39" E, on the ground covered with moss under *Picea crassifolia*, 7 Aug. 2018, J.Z. Xu (**holotype** designated here HMJU:265).

Description: *Pileus* 26–32 mm diam, almost applanate, brownish orange (6C6) in the centre, sometimes slightly pinkish-shaded become paler towards the margin, margin light beige to creamy white (6A2, 5A2, 5A3), surface smooth, dry, with brownish orange (6C6) spots, margin involute, tomentose. *Lamellae* adnate with decurrent tooth, 0.15–0.25 mm wide, moderately crowded, white, with 1–2 tiers of lamellulae intercalated, edges entire, even. *Stipe* 36–44 × 5–6 mm wide, central, cylindrical, surface white, slightly fibrillose, with residual arachnoid cortina. *Context* white, *odour* and *taste* not distinct. *Spore deposit* white. *Basidiospores* (6.3–)6.9–*7.3*–7.7(–8.2) × (5.1–)5.4–*5.7*–6.1(–6.4) µm [40/2/2], Q = (1.14–)1.21–*1.28*–1.34(–1.41), V = (86.7–)107–*127*–147(–172) µm^3, ellipsoid, surface verruculose, warts hemispherical, up to 0.2 µm high, amyloid, not or slightly cyanophilous. *Basidia* (25.5–)25.9–38.9(–44.1) × (4.4–)6.7–11.1(–11.3) µm, clavate, 4-sporic, sterigmata up to 2–5 µm long. *Hymenial cystidia* not observed. *Hymenophoral trama* subregular, parallel, colourless, hyphae cylindrical, 2–11 µm wide, thin-walled. *Pileipellis* an intricate trichoderm, composed of cylindrical hyphae, hyphae 2–12 µm wide, thin-walled. *Stipitipellis* a cutis, composed of parallel, cylindrical, repent, colourless hyphae, 2–13 µm wide, thin-walled. *Clamp connections* present.

Habitat and distribution: Single on the ground covered with mosses under *Picea crassifolia*. So far only known from China.

Additional materials examined: **China**, Gansu Prov., Zhangye City, Sunan Yugu Autonomous County, on soil or moss in mixed forests, 9 Aug. 2018, J.Z. Xu (HMJU:268).

Notes: *Giacomia sinensis* is a distinctive species found on the ground covered with mosses under *Picea crassifolia* (endemic tree species in China). It is mainly characterized by its tricholomatoid basidiomes with a brownish orange pileus with a light beige to creamy white margin, a white stipe with a residual arachnoid cortina, verruculose spores and pileipellis of an intricate trichoderm. *Giacomia sinensis* is phylogenetically related to *G. mirabilis*, which also presents a hairy pileus margin and basidiospores ornamented with hemispherical warts, but *G. mirabilis* has a larger pileus, abundant cheilocystidia and pileipellis as a cutis, while *G. sinensis* lacks cheilocystidia and has a pileipellis as an intricate trichoderm. Additionally, *G. mirabilis* produces a dark brown stipe, but the stipe of *G. sinensis* is white (see above).

Pluteaceae Kotl. & Pouzar, Česká Mykol. 26(4): 218. 1972.

Type: *Pluteus* Fr., Fl. Scan.: 338. 1836.

Representative genera: *Pluteus* (including *Chamaeota*) (Fig. 7N–O) and *Volvopluteus* (Fig. 8K–L).

Notes: Based on the present phylogenetic analysis (Fig. 2), this family is restricted here to the genera *Pluteus* and *Volvopluteus*. *Pluteus* also includes species with partial veil traditionally classified in the genus *Chamaeota* (Minnis *et al*. 2006, Justo *et al*. 2011a, b, Vizzini & Ercole 2011). The family is characterized by basidiomes pileostipitate, heterogeneous, pileus dry or viscid, lamellae free, stipe central, partial veil absent or present and forming an annulus, universal veil absent or present and then forming a persistent volva at stipe base; spore deposit pinkish to pinkish brown or reddish; basidiospores subglobose to ovoid, or ellipsoid, exceptionally triangular, smooth, colourless, usually exceeding 11 µm in length in the taxa with saccate volva

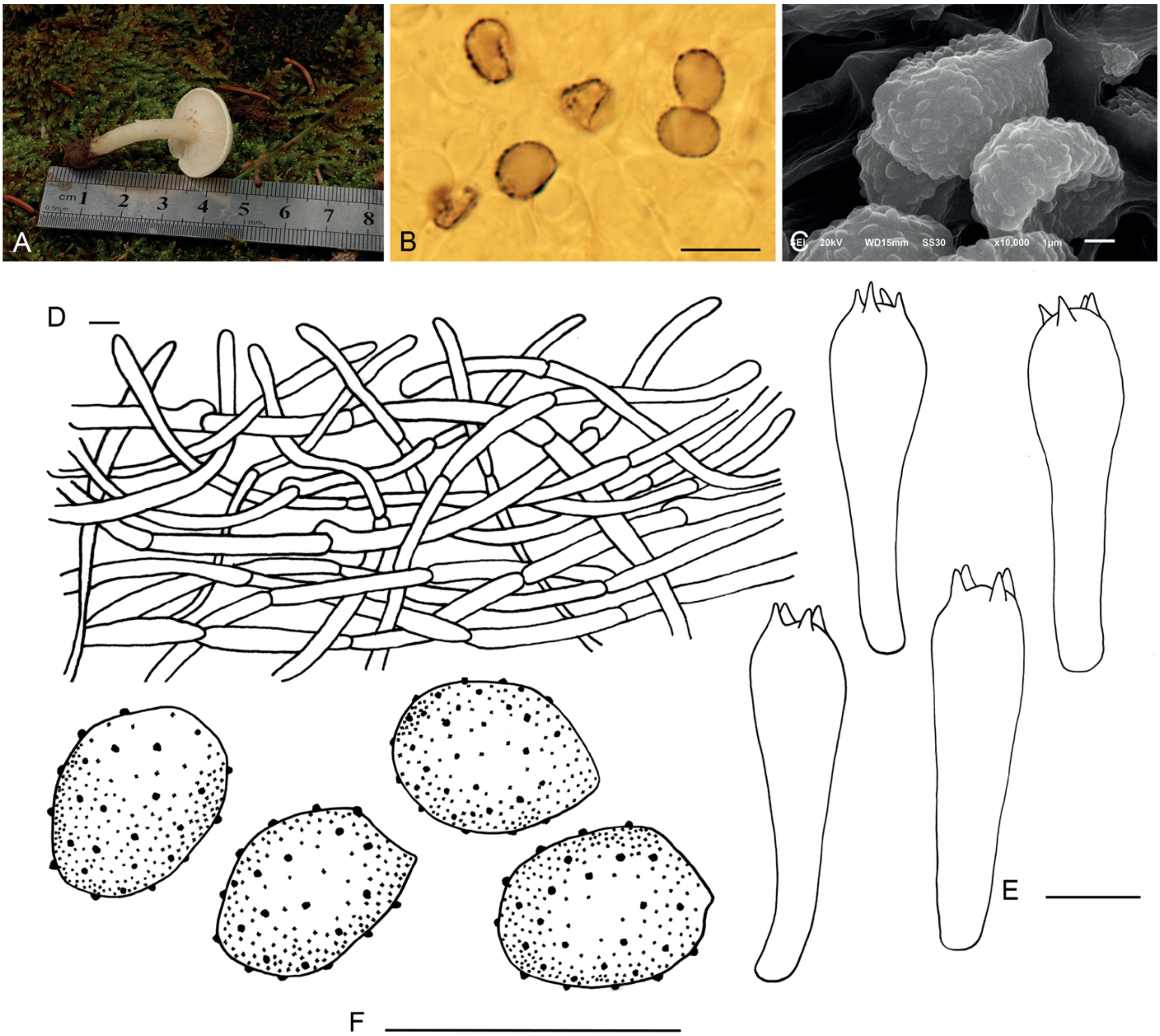

Fig. 14. *Giacomia sinensis* (HMJU:265 holotype). **A.** Basidiome. **B.** Basidiospores (Melzer's reagent). **C.** Basidiospores (SEM). **D.** Pileipellis. **E.** Basidia. **F.** Basidiospores. Scale bars: B, D–F = 10 µm. Photographs and drawings by J. Xu.

(*Volvopluteus*), inamyloid, non-dextrinoid or slightly dextrinoid; hymenial cystidia normally present as cheilo- and pleurocystidia, apex sometimes digitate or with hooks; hymenophoral trama inverse; pileipellis an (ixo)cutis or (ixo)trichoderm, trichopalisade or hymeniderm; clamp connections predominantly absent, rarely present. *Pluteus* and *Volvopluteus* species grow mostly on wood or other decaying plant material (sawdust, straw, wood chips). *Volvopluteus* (type *V. gloiocephalus*) shows a unique combination of characters that separate it from *Pluteus* and *Volvariella sensu stricto* (*Volvariellaceae*), such as an average basidiospore length >11 µm, a pileipellis arranged as an ixocutis, composed of relatively thin hyphae (on average <15 µm wide), embedded in a very thick gelatinous matrix (Justo *et al*. 2011a, b, Giannoni *et al*. 2018, Montoya *et al*. 2021). The presence of a volva can be used as an additional character to separate *Volvopluteus* and *Pluteus*, although inconspicuous (but constant) 'volva-like' remnants have been described also for *P. stephanobasis*, a species of *Pluteus* sect. *Pluteus* (Singer 1958).

Volvariellaceae Vizzini, Consiglio & P. Alvarado, ***fam. nov.*** MycoBank MB 851154.

Diagnosis: Basidiomes pileostipitate, heterogeneous, pluteoid (lamellae free, context of the pileus discontinuous with the context of the stipe, stipe usually longer than pileus diameter), with a saccate universal veil (volva) at the stipe base, and a pink to pinkish brown spore deposit. Basidiospores usually < 11 µm in length, non-amyloid, non-dextrinoid, cyanophilous. Hymenial cystidia present in most species. Hymenophoral trama inverse. Pileipellis usually not strongly gelatinized. Species of *Volvariella* grow as soil or litter saprotrophs, directly on wood, or more rarely as parasites on basidiomes of other mushrooms, *e.g*., *V. surrecta* on basidiomes of *Clitocybe nebularis*.

Type: *Volvariella* Speg., Anales Mus. Nac. Hist. Nat. Buenos Aires 6: 119. 1898. [1899].

Representative genus: *Volvariella* (Fig. 8H–J).

Notes: *Volvariella* (typified with *V*. *argentina* = *V*. *pusilla* following Shaffer 1962) was traditionally considered a member of the *Pluteaceae* due to its heterogeneous basidiomes (the pileus separates easily from the stipe) with lamellae that are free from the stipe; pink or pinkish brown spore deposit; basidiospores smooth, inamyloid, non-dextrinoid, cyanophilous; and inverse hymenophoral trama (Kotlaba & Pouzar 1972, Singer 1986, Justo *et al*. 2011a), differing from the other genera of the family by the presence of a sac-like volva. The genus *Volvariella* includes about 50–57 species worldwide (Agerer 2018, He *et al*. 2019). Taxonomic reviews of *Volvariella* that include molecular data have been published for different areas of Eurasia (*e.g*., Vizzini *et al*. 2011b, Senthilarasu *et al*. 2012, Li *et al*. 2009, Xu *et al*. 2015, Malysheva *et al*. 2019, 2022, 2023, Kaygusuz *et al*. 2020, Niego *et al*. 2021, Kumla *et al*. 2022, Malysheva & Popov 2022, Haqnawaz *et al*. 2023), Africa (Daniëls *et al*. 2015), and South America (Menolli & Capelari 2008, with molecular data in Justo *et al*. 2011a). Apparently, the genus *Volvariopsis* (type *V. volvacea*) is phylogenetically distinct from *Volvariella sensu stricto*, but putatively intermediate lineages between them (Malysheva *et al*. 2019, Chattopadhyay *et al*. 2022, Kumla *et al*. 2022) need to be analyzed to confirm its most suitable taxonomic status. The volvariella-like habit and inverse hymenophoral trama seem to have arisen at least twice independently within the *Pluteineae*, *viz.* in *Volvopluteus* and *Volvariella*.

Tricholomatineae Aime *et al*., Biol. J. Linn. Soc. 117(1): 27. 2016.
Synonym: *Tricholomatales* Kühner, Bull. Mens. Soc. Linn. Lyon 49(Num. Spéc.): 677. 1980.

Type: *Tricholoma* (Fr.) Staude, Schwämme Mitteldeutschl. 1: xxviii, 125. 1857, *nom. cons*., see Art. 14 (Shenzhen).

Representative families: *Biannulariaceae*, *Callistosporiaceae*, *Clitocybaceae*, *Entolomataceae*, *Fayodiaceae*, *Lyophyllaceae* (including *Asproinocybaceae*), *Macrocystidiaceae*, *Omphalinaceae*, *Paralepistaceae*, *Pseudoclitocybaceae*, *Pseudoomphalinaceae*, and *Tricholomataceae*.

Orphaned genera: *Hertzogia*, *Paralepistopsis*.

Notes: Suborder *Tricholomatineae* is characterized by basidiomes predominantly agaricoid (pileostipitate), mostly fleshy, homogeneous (context of the pileus continuous with the context of the stipe), mostly with adnate, subdecurrent or decurrent lamellae. Hyphal system monomitic or rarely sarcodimitic; clamp connections present or absent; pigments often encrusting. Basidiospores colourless or with pink tinges and then often angular in at least one plane or longitudinally striate, smooth, or verrucose, without a germ pore, thin-walled, immediately or latently amyloid or inamyloid, cyanophilous or acyanophilous. Basidia mostly 4-sporic, usually ballistosporic, with or without siderophilic granulations. Pileipellis usually a cutis or trichoderm (rarely hymenidermic in a few *Entolomataceae* and *Lyophyllaceae*). Protective veils rarely present (monovelangiocarpic development with partial veil). *Tricholomatineae* contains mushrooms with a wide spectrum of trophic roles ranging from ectomycorrhizal symbionts (Sánchez-García & Matheny 2017), wood and soil saprobes, necrotrophism (*Collybia*), mycoparasites (some *Entolomataceae*), and obligate insect-associated species (*Termitomyces* and allied genera of the termitomycetoid clade; van de Peppel *et al*. 2021, 2022). Asexual morph sometimes present on basidiome surface (some *Lyophyllaceae* and *Dendrocollybia*) This suborder corresponds well to the Tricholomatoid clade of Matheny *et al*. (2006), except for the exclusion of *Mycenaceae* and inclusion of *Infundibulicybe*, as well as to the Tricholomatoid clade of Binder *et al*. (2010). *Tricholomatineae* was established by Dentinger *et al*. (2016) (69 % BP) and a well-supported clade corresponding to the *Tricholomatineae* was recovered by Varga *et al*. (2019) (99 % BP), Olariaga *et al*. (2020) (1 PP, 54 % BP), Li *et al*. (2021) (98 % BP) and in the present work (1 PP).

Biannulariaceae Jülich, Biblioth. Mycol. 85: 356. 1982. [1981].
Synonyms: *Tricholomataceae* tribe *Biannularieae* Singer *ex* Bas, Persoonia 14: 235. 1990.
Catathelasmataceae Wasser, Agarikovye griby SSSR (Kiev): 29. 1985.

Type: *Catathelasma* Lovejoy, Bot. Gaz. 50: 383. 1910.

Representative genera: *Bonomyces*, *Catathelasma* and *Cleistocybe*.

Notes: The molecular circumscription of the limits of the family was first carried out by Vizzini *et al*. (2020a). It is characterized by basidiomes with tricholomatoid, clitocyboid or pleurotoid habit; lamellae adnate, adnexed, sinuate, emarginate to decurrent; partial veil present (simple or double) or inconsistent and reduced to a granular, pseudoanular zone at the apex of the stipe; odour usually farinaceous; spore deposit white; basidiospores ellipsoid to fusoid, cylindrical, colourless, smooth, inamyloid or amyloid, acyanophilous or cyanophilous; basidia lacking siderophilous inner bodies; cheilocystidia present or absent, pleurocystidia absent or if present then only as pseudocystidia; hymenophoral trama regular to bilateral becoming regular, pileipellis a cutis, an ixocutis or a cutis becoming a trichoderm, context (pileitrama and stipititrama) formed by densely arranged slender hyphae which give rise to a dry and fibrous consistency, clamp connections present. Specimens grow on soil or rotten wood, saprotrophic or ectomycorrhizal in conifer forests. They can be found in Europe, Asia, North and Central America. *Bonomyces* was recently monographed by Alvarado *et al*. (2018b), *Cleistocybe* by Ammirati *et al*. (2007) and Wu *et al*. (2018), and *Catathelasma* by Vizzini *et al*. (2020a). Recently, the newly discovered species *Bonomyces squamulosus*, *B*. *pseudoarnoldii* and *Cleistocybe vernaloides* have been described from China (Wu *et al*. 2018, He & Yang 2022, Mao *et al*. 2022).

Callistosporiaceae Vizzini *et al*., Fungal Diversity 101: 223. 2020.

Type: *Callistosporium* Singer, Mycologia 36: 363. 1944.

Representative genera: *Anupama*, *Callistosporium* (including *Pleurocollybia*), *Guyanagarika*, *Macrocybe*, *Pseudolaccaria*, and *Xerophorus*.

Notes: The molecular circumscription of the limits of the family was first carried out by Vizzini *et al*. (2020a). It is distinguished by basidiomes with tricholomatoid, collybioid or pleurotoid habit, veils absent; lamellae adnate, adnexed, sinuate, emarginate to decurrent; spore deposit white, basidiospores ellipsoid, colourless, smooth, inamyloid or amyloid (*Pseudolaccaria*), cyanophilous or acyanophilous; basidia lacking siderophilous inner bodies; cheilocystidia present or absent, pleurocystidia absent or if present then only as pseudocystidia; hymenophoral trama regular to slightly bilateral becoming regular, pileipellis a cutis, ixocutis or cutis becoming a trichoderm, clamp connections usually absent, very rarely present (in *Xerophorus*, partim; in *Callistosporium imbricatum* at the base of basidia). Specimens are found growing on soil or rotten wood, saprotrophic or ectomycorrhizal (Sánchez-García *et al*. 2016, Raj *et al*. 2019, Vizzini *et al*. 2020a).

Clitocybaceae Vizzini *et al*., Index Fungorum 462: 1. 2020.
Synonyms: Agaricinées tribe *Clitocybeae* Fayod *ex* Lotsy, Vorträge Bot. St. Gesch. 1: 711. 1907.
Tricholomataceae subfamily *Clitocyboideae* (Fayod) M. Bon, Doc. Mycol. 78: 37. 1990.
Clitocybaceae Roze [as 'Clitocybées'], Bull. Soc. Bot. France, Act. Bot. 23: 112. 1876 [*nom. inval.*, Art. 32.1l, see Art. 18.4 (Shenzhen)], van Overeem, Bull. Jard. Bot. Buitenzorg, ser. 3, 9: 21. 1927 [correctly spelled but *nom. inval.*, Art. 32.1(c)].
Lepistaceae Locq., Mycol. Gén. Struct. (Paris): 139. 1984, *nom. inval.*, Art. 39.1 (Shenzhen).
Lepistamycetidae Locq., Mycol. Gén. Struct. (Paris): 97. 1984, *nom. inval.*, Art. 39.1 (Shenzhen).

Type: *Clitocybe* (Fr.) Staude, Schwämme Mitteldeutschl.: xxviii, 122. 1857.

Representative genera: *Clitocybe* (Fig. 6C), *Collybia*, *Lepista* (= *Rhodopaxillus*) (Figs 6O, 7A), *Singerocybe*, *Dendrocollybia* (this latter according to Mou & Bau 2021, He & Yang 2022 and He *et al*. 2023 on multigene analyses; Sánchez-García & Matheny 2017 and Sánchez-García *et al*. 2020 on ribosomal DNA markers), and *Pseudolyophyllum* (He *et al.* 2023). *Leucocalocybe* was first considered an independent genus inside *Clitocybaceae* (Yu *et al*. 2011, Sánchez-García *et al*. 2020), but recently downgraded to a subgenus of *Collybia sensu lato* (He *et al*. 2023). Based only on ribosomal DNA markers, *Lepistella* (Varga *et al*. 2019), and *Paralepistopsis* (Varga 2019, Sánchez-García *et al*. 2020 but see below) might belong here.

Notes: The family *Clitocybaceae* was first referred to as the "Clitocybées" by Roze (1876), including 24 species of the genus *Clitocybe*; however, this name was not validly published since it contains a French termination instead of a Latin termination (Shenzhen, 2018: Art. 18.4). In 1927, Van Overeem (1927) published the name "Clitocybaceae" as a *nomen nudum* (Art. 38.1). This name was informally used for this clade in some works (Cooper 2016, Kalichman *et al*. 2020, Kibby 2020), but it was only recently validly published by Vizzini *et al*. (2020b). It corresponds to "Agaricinés" tribe *Clitocybeae* (Fayod 1889, originally including *Clitocybe*, *Lepista*, *Nyctalis* and *Laccaria*) and to *Tricholomataceae* subfamily *Clitocyboideae* (Bon 1990b, 1997, including *Clitocybe* and *Armillaria*). It can be loosely circumscribed because of the clitocyboid, lepistoid or collybioid habit, veils absent (gymnocarpic development), lamellae adnexed, sinuate, emarginate to decurrent, removable (separable) or not from the pileus context, spore deposit white, cream to pale pink or pinkish buff, basidiospores colourless, smooth to warty, verrucose (verruculose to spiny) inamyloid, cyanophilous or acyanophilous, basidia clavate, usually 4-sporic, not hygrophoroid, lacking siderophilous inner bodies, hymenophoral trama regular to subregular composed of parallel cylindrical hyphae, cheilocystidia absent or present, thin-walled, pleurocystidia absent, pileipellis a cutis or trichoderm, with (*Singerocybe*) or without swollen elements (vesicles), clamp connections present or absent. Stipe sometimes with conidiogenous branches (*i.e.*, *Tilachlidiopsis* asexual morph in *Dendrocollybia*). Presence of muscarine (most species of *Collybia sensu lato*, He *et al*. 2023). Habitat on soil, litter, or associated with dead wood (*Lepistella*) or with basidiomes of other species (mycosaprobic) and then usually forming small sclerotia (*Collybia*, *Dendrocollybia*); saprotrophic or mycosaprobic/mycoparasitic.

Entolomataceae Kotl. & Pouzar, Česká Mykol. 26(4): 218. 1972.

Type: *Entoloma* (Fr.) P. Kumm., Führ. Pilzk. (Zerbst): 23. 1871.

Representative genera: *Calliderma*, *Clitocella*, *Clitopiloides*, *Clitopilopsis*, *Clitopilus*, *Entocybe*, *Entoloma* (including *Richoniella* and *Rhodocybella*), *Fibropilus*, *Lulesia*, *Rhodocybe*, and *Rhodophana*.

Notes: The molecular circumscription of the limits of the family and intergeneric relationships were studied by Co-David *et al*. (2009), Baroni *et al*. (2011, 2020), Baroni & Matheny (2011), Kinoshita *et al*. (2012), and Kluting *et al*. (2014). Basidiomes are pileostipitate with a very diverse habit: mycenoid, clitocyboid, collybioid, omphalinoid, tricholomatoid, or rarely secotioid; lamellae adnate, adnexed, emarginate, occasionally almost free, subdecurrent, decurrent; stipe usually central and well-developed, reduced or absent; veils absent; spore deposit pinkish or rarely greyish; basidiospores angular, rhomboid, ribbed with longitudinal ribs, with pustules, bumps or verrucae, rarely reticulate, thin- to thick-walled, inamyloid, non-dextrinoid, usually cyanophilous, colourless on light microscopy, typically binucleate; basidia not siderophilous or with micro type siderophilic granules; hymenial cystidia absent, or as cheilocystidia, occasionally as pleurocystidia or pseudocystidia; hymenophoral trama regular to subregular, pileipellis a cutis or a trichoderm, sometimes a hymeniderm, colourless or with wall, encrusting or cytoplasmatic pigment, clamp connections absent or present. The family encompasses mainly saprotrophic species; mycoparasites are present in *Clitopilus*, *Entoloma*, and *Rhodophana* (Noordeloos 1988, 1993, Czederpiltz *et al*. 2001, Koch & Herr 2021); the ECM taxa are restricted to the Rhodopolioid clade of *Entoloma* (Sánchez-García & Matheny 2017, Brandrud *et al*. 2018) and often associate with *Quercus*, *Salix*, *Alnus*, *Populus*, and exceptionally with *Pyrus*, usually with an incomplete Hartig net (Linkins & Antibus 1982, Loree *et al*. 1989, Læssøe & Rosendahl 1994, Agerer 1997, 1998, Smith *et al*. 2007, Shishikura *et al*. 2021).

The genera recognized in *Entolomataceae* by Kluting *et al*. (2014) and Baroni *et al*. (2020) were recently supplemented with *Lulesia* by Varga *et al*. (2019) based on a single LSU sequence. This genus, typified with *L. densifolia* was placed by Singer (1970, 1986) in subtribe *Omphalineae* (tribe *Clitocybeae*, family *Tricholomataceae*). *Lulesia* is apparently different from the rest of the genera of the *Entolomataceae* due to its withish to cream lamellae without pink tinges when mature, and whitish spore deposit, but at least two of the three known species have basidiospores appearing slightly angular and nodulose on light microscopy (Singer 1970, 1986, Lechner *et al*. 2006). *Macrocystidia* and *Rhodotus* had been classified within or close to *Entolomataceae* on account of their pink spores (*e.g.*, Kühner 1980, Romagnesi 1992), but molecular phylogenetic studies place them outside this family (Moncalvo *et al*. 2000, 2002, Walther *et al*. 2005, Matheny *et al*. 2006, Garnica *et al*. 2007, Petersen & Hughes 2010, Varga *et al*. 2019, Sánchez-García *et al*. 2020).

Fayodiaceae Jülich, Biblioth. Mycol. 85: 367. 1982. [1981].
Synonyms: *Marasmiaceae* Tribu *Fayodieae* Kühner, Bull. Mens. Soc. linn. Lyon 49(3): 770. 1980.
Tricholomataceae, Subfamily *Clitocyboideae*, tribe *Omphalineae*, subtribe *Heterosporulae* Bon, Doc. Mycol. 26 (102): 19. 1996.
Fayodiamycetidae Locq., Mycol. Gén. Struct. (Paris): 96. 1984, *nom. inval.*, Art. 39.1 (Shenzhen).
Fayodiales Locq., Mycol. Gén. Struct. (Paris): 126. 1984, *nom. inval.*, Art. 39.1 (Shenzhen).

Type: *Fayodia* Kühner, Bull. Soc. linn. Lyon 9: 68. 1930.

Representative genera: *Caulorhiza*, *Conchomyces*, *Fayodia* (Fig. 6E), *Gamundia* (Fig. 6F), *Myxomphalia*.

Notes: The family *Fayodiaceae* was established by Jülich (1981) based on morphological features: omphalinoid basidiomes (rarely collybioid or mycenoid); basidiospores colourless, globose or ellipsoid, thin-walled, and smooth, or somewhat thick-walled and with a complex wall structure consisting of a spiny endosporium overlain by a smooth episporium, amyloid in most taxa; 2–4-sporic basidia, thin-walled hymenial cystidia; hymenophoral trama regular, pileipellis of smooth repent, rarely diverticulate hyphae, clamp connections present; terricolous, saprotrophic. Jülich recognized only *Fayodia* and *Myxomphalia* within the family and suggested (following previous indications by Smith & Reid 1962) a possible affinity with the *Cribbeaceae*, where the same spore wall structure is present. *Cribbea* species were found to belong to the family *Physalacriaceae* (*Marasmiineae*) with affinities to *Xerula* and *Oudemansiella* by Lebel & Catcheside (2009). Before the publication of the family *Fayodiaceae*, Kühner (1980) had placed *Fayodia* and allied genera in tribu *Fayodieae* of *Marasmiaceae* together with *Delicatula*, *Clitocybula*, *Hydropus* and *Megacollybia*, with affinity to *Collybia*. Other authors considered *Fayodiaceae* a synonym of *Tricholomataceae sensu lato* (Pouzar 1985, Korf 1988), a synonym of tribe *Myceneae* of the *Tricholomataceae* (Kuyper 1995b, c, Singer 1986), or an independent tribe *Fayodieae* of subfamily *Clitocyboideae* inside *Tricholomataceae* (Bon 1997). The first pioneering molecular works focusing on the *Agaricales* (mainly based on nrLSU sequences alone, *i.e.*, Moncalvo *et al*. 2002), found an *incertae sedis* /fayodioid clade consisting of *Gamundia leucophylla*, *Caulorhiza hygrophoroides*, *Conchomyces bursaeformis*, *Myxomphalia maura*, and *Fayodia gracilipes*. In a combined analysis of LSU and *RPB1* sequences of a smaller dataset of *Agaricales*, Garnica *et al*. (2007) found a relationship between *F. gracilipes*, *Leucocortinarius bulbiger* and *Infundibulicybe geotropa*. In the present analysis (Fig. 3) *Fayodia bisphaerigera* and *Gamundia striatula* formed an independent clade within suborder *Tricholomatineae*. Accordingly, the family name *Fayodiaceae* is here applied for this clade.

The genera *Fayodia*, *Myxomphalia* and *Gamundia* (= *Heterosporula*; = *Stachyomphalina*) were sometimes considered subgenera of a single genus *Fayodia sensu lato* (*e.g.*, Singer 1986) but important authors as Bigelow (1979), Kühner (1980), Bon (1997), Kuyper (1995b, c), or Antonín & Noordeloos (2004) separated them. *Fayodia* (typified by *F. bisphaerigera*) is characterized by a very distinct, two-layered basidiospore wall consisting of a non-amyloid, echinulate-verruculose epispore and a smooth amyloid perispore, 2-sporic basidia, and a dry, non-gelatinized pilei- and stipitipellis (Kühner 1930, 1938a, 1973, 1980, Besson 1969, Pegler & Young 1971, Bigelow 1979, 1983, Emmett 1993, Kuyper 1995b, Antonín 2004, Antonín & Noordeloos 2004, Clémençon 2004). *Gamundia* (typified by *G. pseudoclusilis* = *G. striatula*) is distinguished by its verruculose-echinulate, thin-walled, non-amyloid basidiospores and gelatinized pileipellis (Bigelow 1979, 1983, Kuyper 1995c, Antonín 2004, Antonín & Noordeloos 2004, Musumeci *et al*. 2010). Bon (1996) accommodated *Gamundia* in the subtribe *Heterosporulae* of tribe *Omphalineae* within subfamily *Clitocyboideae*, *Tricholomataceae*. Finally, *Myxomphalia* (typified by *M. maura*) has thick-walled, smooth to minutely verruculose (when observed under SEM) amyloid spores and gelatinized pilei- and stipitipellis (Bigelow 1979, Weholt 1988, Antonín 1999, Antonín & Noordeloos 2004).

Lyophyllaceae Jülich, Biblioth. Mycol. 85: 378. 1982. [1981].
Synonyms: *Tricholomataceae* Tribe *Lyophylleae* Kühner, Bull. Mens. Soc. Linn. Lyon 7(7): 209. 1938.
Tricholomataceae subfamily *Lyophylloideae* Kühner ex Bon, Doc. Mycol. 3(12): 7. 1974.
Asproinocybaceae T. Bau & G.F. Mou, J. Fungi 7(12, no. 1086): 7. 2021.

Type: *Lyophyllum* P. Karst., Acta Soc. Fauna Flora fenn. 2(no. 1): 29. 1881. [1881-1885].

Representative genera: *Arthromyces*, *Asproinocybe*, *Asterophora*, *Atractosporocybe*, *Australocybe*, *Blastosporella*, *Calocybe* (including *Rugosomyces*), *Calocybella*, *Clitolyophyllum*, *Fibulochlamys*, *Gerhardtia*, *Hypsizygus*, *Leucocybe*, *Lyophyllopsis*, *Lyophyllum* (Fig. 7C), *Myochromella*, *Nigrocarnea*, *Omphaliaster*, *Ossicaulis*, *Phaeotephrocybe*, *Praearthromyces*, *Sagaranella*, *Sphagnurus*, *Termitomyces*, *Tephrocybe*, *Tephrocybella*, *Tephroderma*, *Trichocybe* (Fig. 8G), *Tricholomella*, *Tricholosporum*, and *Tricholyophyllum*.

Notes: The family *Lyophyllaceae* is characterized by basidiomes with an extremely diverse habit: mycenoid, collybioid, clitocyboid or tricholomatoid; hymenophore lamellate, lamellae attached, adnate, emarginate or exceptionally almost free; partial veil absent or rarely present, general veil exceptionally present; stipe central to eccentric, cylindrical to distinctly rooting (pseudorhiza, termitomycetoid clade *sensu* van de Peppel *et al*. 2021, 2022); spore deposit white to pale cream; hyphal system monomitic, hyphae with or without clamp connections; basidia usually with siderophilous granules (macro- and oligo-type, Clémençon 1978, 1986a, b, 2004) or without them; basidiospores colourless, with distinct apiculus, predominantly smooth, but also verrucose, warty, undulate, echinulate, tuberculate to stellate (*Asproinocybe*), or cruciform to stauriform (*Tricholosporum*), thin- to slightly thick-walled, neither amyloid nor dextrinoid, cyanophilous or not; no other part of the basidiome is amyloid, dextrinoid or cyanophilous; cystidia absent or present as cheilocystidia, rarely as pleurocystidia; hymenophoral trama regular to subregular; pileipellis ranging from a cutis, trichoderm, celluloderm, sometimes a conioderm of chlamydospores (*Asterophora*) or arthroconidia (*Arthromyces*, *Blastosporella*, *Nigrocarnea*, *Praearthromyces*). *Lyophyllaceae* display broad ecological strategies with frequent transitions between them, ranging from terricolous saprotrophs (most of the species), plant decayers (*Hypsizygus*, *Ossicaulis*), parasite species (*Asterophora*, *Sphagnurus*), symbiotic species of insects (termitomycetoid clade, *Termitomyces*, insect-associated mutualistic genus, or *Arthromyces* and *Blastosporella*, insect-faecal associated genera) to ectomycorrhizal species with angiospermous and gymnospermous trees (*Lyophyllum decastes* species complex, *Lyophyllum shimeji* and *L. decastes*) (Singer 1986, Agerer &

Beenken 1998, Yamada *et al*. 2001a, b, Tedersoo *et al*. 2010, Larsson & Sundberg, 2011, Hofstetter *et al*. 2014, van de Peppel 2021, 2022). The presence of an asexual morph phase seems to be quite common in the family *Lyophyllaceae*. The genera *Calocybe*, *Fibulochlamys*, *Gerhardtia*, *Hypsizygus*, *Ossicaulis*, *Sagaranella*, *Sphagnurus*, and *Termitomyces* have asexual morph life cycles at the vegetative mycelium stage, *viz.* arthroconidia production on hyphal strands at the stipe base, and mycelium with both schizolytic and rhexolytic secession (Clémençon 1968, Brunner & Miller 1988, Nagasawa & Arita 1988, Walther *et al*. 2005, Madrid *et al*. 2010, Endo *et al*. 2019, 2022). In addition, *Asterophora*, *Arthromyces*, *Blastosporella*, *Nigrocarnea* and *Praearthromyces* produce arthroconidia or chlamydospores on the basidiomes (Thompson 1936, Corner 1966, Singer 1986, Redhead & Seifert 2001, Baroni *et al*. 2007, van de Peppel 2021, 2022).

Historically, the tribe *Lyophylleae* was circumscribed by Kühner (1938b) based on the shared synapomorphic character of basidia with inner siderophilous (carminophilous) granules upon acetate carmine staining. He included in the tribe the genera *Calocybe*, *Lyophyllum* (type), *Nyctalis* (current name *Asterophora*) and *Tephrophana* (now *Tephrocybe*). Later, Bon (1974) upgraded the tribe to subfamily rank as *Lyophylloideae*, and finally Jülich (1981) established the new family *Lyophyllaceae*. Molecular phylogenetic studies provided support to the monophyletic status of the traditional concept of *Lyophyllaceae* (*e.g*., Hofstetter *et al*. 2002, Moncalvo *et al*. 2002 as *Lyophylleae* group; Matheny *et al*. 2006, Baroni *et al*. 2011, Sánchez-García *et al*. 2014).

In the present analysis (Fig. 3), *Aspropaxillaceae* is part of the *Lyophyllaceae*, and a sister relationship (0.99 PP, 47 % BP) between *Lyophyllaceae sensu lato* and *Entolomataceae* was found, as previously highlighted by Hofstetter *et al*. (2002), Matheny *et al*. (2006), Sánchez-García *et al*. (2016, 2020), Sánchez-García & Matheny (2017), Raj *et al*. (2019), and He & Yang (2022). Whereas Baroni *et al*. (2011) recovered a sister relationship of *Lyophyllaceae* with *Entoloma sensu lato* and a paraphyletic *Entolomataceae*, Sánchez-García *et al*. (2014) found that *Lyophyllaceae* was basal to *Tricholomataceae sensu stricto* and *Entolomataceae*, and Hofstetter *et al*. (2014) retrieved *Entolomataceae* at the base of a clade formed by *Lyophyllaceae* and *Tricholomataceae.* Morphological affinities between the families *Lyophyllaceae* and *Entolomataceae* were already pointed out by Kühner & Romagnesi (1953) and Clémençon (1978). They share the same diverse habit and pileipellis structure of the basidiomes, the non-free lamellae, the regular to subregular hymenophoral trama, often cyanophylous basidiospores, and basidia often containing siderophilous granules (macro-type in *Lyophyllaceae*, micro- and crypto-type in *Entolomataceae*; Clémençon 1978, 2004). Species with collybioid habit and basidiospores ± angular in polar view are present both in *Lyophyllaceae* (*Calocybella* and *Gerhardtia*, white-spored) and *Entolomataceae* (*Rhodocybe sensu lato*, pink-spored) (Kluting *et al*. 2014, Vizzini *et al*. 2017, Endo *et al*. 2019, 2022). The macro-type of siderophilous granulation seems to be restricted to *Lyophyllaceae sensu stricto* (= *sensu* Matheny *et al*. 2006, excluding the hemilyophylloid clade). It was found in three closely related species of *Rhodocybe* (*Entolomataceae*) and this lead Clémençon (1968) to combine two of them into *Lyophyllum* (*L. suburens* and *L. leucopaxilloides*), a proposal first rejected by Singer (1975) and only partially accepted later by him (Singer 1986), placing them in *Lyophyllum* subg. *Lyophyllopsis* Gerhardt with great uncertainty. The two species were finally transferred to the genus *Gerhardtia* by Contu & Consiglio (2004).

Macrocystidiaceae Kühner, Bull. Mens. Soc. Linn. Lyon 48(3): 172. 1979.

Type: *Macrocystidia* Joss., Bull. Trimestriel Soc. Mycol. France 49: 373, 376. 1934 [1933].
Synonym: *Macrocystis* R. Heim, Encyclop. Mycol., 1 Le Genre *Inocybe* (Paris): 71 .1931., *nom. illegit.*, Art. 53.1, non *Macrocystis* C. Agardh 1820 (Algae)].

Representative genera: *Macrocystidia* (Fig. 7D, E) and *Pseudoclitopilus*.

Notes: *Macrocystidia*, typified by *M. cucumis*, is characterized by gymnocarpic mycenoid to collybioid basidiomes, almost free lamellae, a usually strong rancid-farinaceous to fish-like odour, brownish pink spore deposit, regular to subregular hymenophoral trama, presence of lageniform to fusiform, thin-walled cystidia (as hymenial cystidia, pileo- and caulocystidia), basidiospores ellipsoid, thick-walled (multilayered), cyanophilous, inamyloid and mononucleate, pileipellis arranged as a cutis, presence of clamp connections; presence of conidiogenous hyphae in the mycelium, mostly fragmenting into up to eight conidia; terricolous, saprotrophic (Heim 1931, Josserand 1933, Capellano 1976, Kühner 1979a, 1980, Noordeloos 1995a, Walther *et al*. 2005, Knudsen 2012, Læssøe & Petersen 2019).

The present analysis (Fig. 3) supports that *Macrocystidiaceae* belongs to an independent evolutive lineage within *Tricholomatineae*, where it is significantly related to *Pseudoclitopilus* (1.00 BPP). *Pseudoclitopilus*, typified by *P. rhodoleucus*, is a genus recently segregated from *Leucopaxillus sensu lato* (Vizzini *et al*. 2012a), characterized by its agaricoid basidiomes resembling *Clitopilus prunulus* or *Hygrophorus karstenii* due to their strongly decurrent lamellae with pinkish tinges (especially in young stages), and a white, somewhat hygrophanous pileus, veils absent, white spore deposit, basidiospores with amyloid warts, cystidia and pseudocystidia absent, pileipellis a cutis of repent to interwoven, cylindrical hyphae, clamp connections present, and no sarcodimitic texture in any part of the basidioma. Specimens of *Pseudoclitopilus* occur on the ground, never on wood (Szemere 1966, Pegler & Young 1973, Trimbach 1978, Verde & Calonge 1980, Fanelli 1984, Bon 1991, Watling & Turnbull 1998, Winterhoff 1998, Consiglio & Contu 2000, Anon. 2001, Markones 2003, Christensen 2008, 2012, Vizzini *et al*. 2012a). Two species are known so far, *P. rhodoleucus* and *P. salmonifolius*, both very rare. *Pseudoclitopilus salmonifolius* differs mainly in having shorter basidiospores (4.5–6 µm *vs*. 6–8 µm in *P. rhodoleucus*) (Moser 1979, Bidaud 1993). All previous molecular works placed *Pseudoclitopilus* in an uncertain position (Sánchez-García *et al*. 2014, 2016, 2020, Sánchez-García & Matheny 2017, Alvarado *et al*. 2018a, b, He *et al*. 2019, 2023, Raj *et al*. 2019, Vizzini *et al*. 2020a, He & Yang 2022). While *Macrocystidia* and *Pseudoclitopilus* share a gymnocarpic agaricoid basidiome, a cutis-like pileipellis, presence of clamp connections, and a terricolous growth, no other synapomorphic trait could be found. As a result, the inclusion of *Pseudoclitopilus* in *Macrocystidiaceae* needs to be confirmed with additional data from other species.

Omphalinaceae Vizzini *et al.*, Index Fungorum 462: 1. 2020. Fig. 15.
Synonyms: *Tricholomataceae* tribe *Clitocybeae*, subtribe *Omphalininae* Singer, Fl. Neotrop. Monogr. 3: 5. 1970. [as ‘*Omphalinae*’]

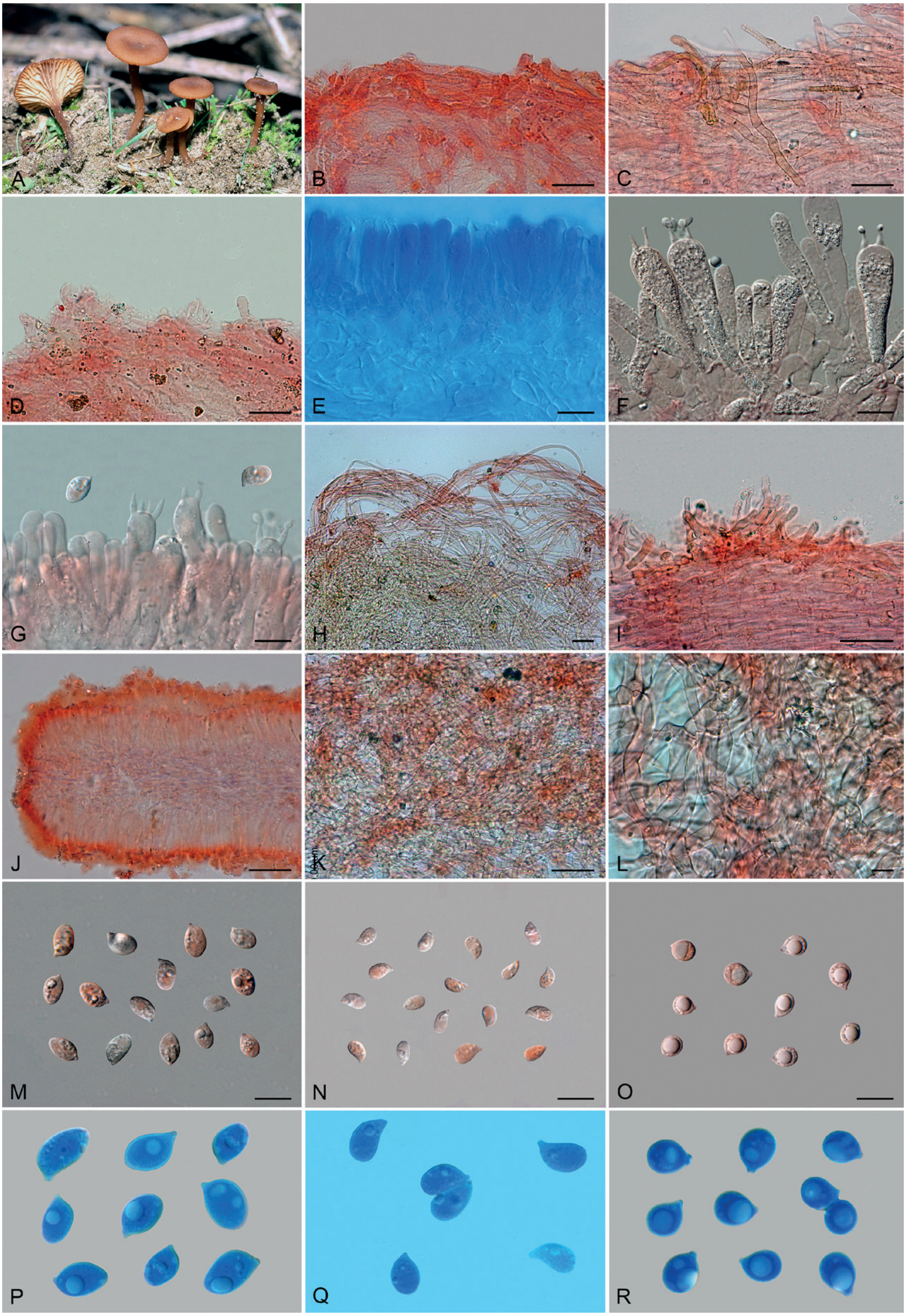

Fig. 15. *Omphalinaceae*. **A.** *Omphalina pyxidata* basidiomes (AMB:19294). **B–D.** Pileipellis (B. *Infundibulicybe gibba* AMB:19313; C. *I. geotropa* AMB:18861; D. *O. pyxidata* AMB:19295). **E.** Hymenium and subhymenium (*I. gibba* AMB:19313). **F, G.** Hymenium (F. *I. geotropa* AMB:18861; G. *O. pyxidata* AMB:19295). **H.** Stipitipellis (*I. geotropa* AMB:18861). **I.** Stipitipellis and caulocystidia (*O. pyxidata* AMB:19295). **J, K.** Hymenophoral trama (J. *O. pyxidata* AMB:19295; K. *I. gibba* AMB:19313). **L.** Elements of the hymenophoral trama (*I. gibba* AMB:19313). **M–R.** Basidiospores (M, P. *O. pyxidata* AMB:19295; N, Q. *I. gibba* AMB:19313; O, R. *I. geotropa* AMB:18861). Mounting media were Congo Red in ammonia (B–D, F–O), and Cotton Blue (E, P–R). Scale bars: B–D, H–K = 30 µm, E–G, L–R = 10 µm. Photographs A by G. Consiglio, B–R by M. Marchetti.

Tricholomataceae tribe *Omphalineae* (Singer) Bon, Doc. Mycol. 24(93): 40. 1995.

Type: *Omphalina* Quél., Enchir. Fung.: 42. 1886.

Representative genera: *Infundibulicybe* (Figs 6N, 15B, C, E, F, H, K, L, N, O, Q, R) and *Omphalina* (Figs 7I, 15A, D, G, I, J, M, P).

Notes: *Omphalinaceae* is characterized by basidiomes with an omphalinoid or clitocyboid habit, veils absent (gymnocarpic development), pileus usually depressed at centre, dry, often with ochre, reddish brown, rusty, vinaceous brown or orangish brown tinges; lamellae decurrent; spore deposit white to cream; basidiospores colourless, smooth-walled (except *I. trachyspora*), inamyloid, acyanophilous (cyanophobic wall but cyanophilic cytoplasm); basidia clavate, usually 4-sporic, not hygrophoroid, lacking siderophilous inner bodies; hymenophoral trama subregular or irregular of intertwined, interwoven hyphae; hymenial cystidia usually absent, rarely present, thin-walled; pileipellis arranged as a cutis to a trichoderm; pigments intracellular and wall encrusting; clamp connections present; habitat on soil, litter, or associated with bryophites (bryophilous); usually saprotrophic but, recently, Zhang *et al*. (2022) described *O. licheniformis* from China, the first example of a lichenized omphalinoid fungus outside genus *Lichenomphalia* (*Lichenomphaliaceae*, *Hygrophorineae*); Northern Hemisphere, mostly temperate to boreal.

The family is currently thought to include the type genus *Omphalina*, as well as *Infundibulicybe* (Vizzini *et al*. 2020b, Zhang *et al*. 2022). *Infundibulicybe* differs from *Omphalina* mainly because of its larger basidiomes (pileus 20–200 mm diam, stipe 5–20 mm wide), thicker context, pileus non-hygrophanous, not translucently striate, hymenophoral trama regular in young stages, subirregular to irregular only in aged basidiomes (Harmaja 2003, Vizzini *et al*. 2011c), and not strictly moss-associated (non-bryophilous). Historically, Singer (1943) and Bigelow (1974, 1985) were the first to recognize morphological affinities between *Clitocybe* sect. *Pyxidatae* and sect. *Infundibuliformes*. They believed sect. *Pyxidatae* derived from section *Infundibuliformes* due to the shared presence of abundant brownish encrusting pigment. Phylogenetic evidence of a shared monophyletic origin between *Infundibulicybe* and *Omphalina* was first obtained by Moncalvo *et al*. (2000, 2002), and then confirmed by Vizzini *et al*. (2011a, 2012a, b), Vizzini & Ercole 2012, Lodge *et al*. 2014, Varga *et al*. (2019), and Sánchez-García *et al*. (2016, 2017, 2020). The lineage was then formally accommodated in the family *Omphalinaceae* by Vizzini *et al*. (2020b), and recent phylogenetic analyses by He & Yang (2022) and Zhang *et al*. (2022) also support this decision.

Omphalina Quél., Enchir. fung. (Paris): 42. 1886.
Synonyms: *Agaricus* ** *Pyxidatae* Fr., Epicr. syst. mycol. (Upsaliae): 122. 1838. [1836–1838].
Clitocybe subg. *Infundibuliformes* (Fr.) Bigelow, sect. *Pyxidatae* (Fr.) Bigelow, Bull. Soc. Linn Lyon (Num. Spéc.): 39. 1974.
Omphalina sect. *Pyxidatae* (Fr.) Bon, Doc. Mycol. 22(86): 40. 1992.
Omphalia (Fr.) Gray, Nat. Arr. Brit. Pl. (London) 1: 611. 1821 [*nom. illegit.*, Art. 53.2; *non Omphalea* L. 1759, *nom. cons.* (*Euphorbiaceae*)]

Type: *O. pyxidata* (Bull.) Quél. [lectotype, proposed by Redhead (1993), recommended by Gams (1995), accepted, and published in Greuter *et al*. (2000)].

Notes: *Omphalina* was originally upgraded to genus by Quélet (1886) from a previous undetermined rank in Fries (1838), although no type was indicated. Redhead (1993) proposed the lectotype *O. pyxidata* (accepted in Greuter *et al*. 2000, p. 192). Recent molecular analyses showed that the classical concept of *Omphalina*, mainly based on morphology (Bigelow 1970, Lamoure 1974, 1975, Clémençon 1982, Norvell *et al*. 1994, Kuyper 1995d, Bon 1997) includes both non-lichenized and lichenized omphalinoid genera phylogenetically nested inside different clades of the order *Agaricales* (Moncalvo *et al*. 2002, Redhead *et al*. 2002a, Matheny *et al*. 2006, Lawrey *et al*. 2009, Lodge *et al*. 2014, Varga *et al*. 2019, Chalange & Moreau 2023), as well as *Hymenochaetales* (Redhead et *al*. 2002b, Larsson *et al*. 2006, Korotkin *et al*. 2018, Olariaga *et al*. 2020). The non-lichenized omphalinoid bryophilous species of *Omphalina* with a greyish, blackish, bluish, brown-grey or whitish pileus and stipe, as well as concolorous hymenia were transferred to an emended genus *Arrhenia* inside suborder *Hygrophorineae* (Redhead *et al*. 2002a, Barrasa & Rico 2003, Barrasa *et al*. 2003, Lodge *et al*. 2014, Blanco-Dios 2019). *Omphalina* was restricted to the usually bryophilous species phylogenetically related to *O. pyxidata* (the conserved lectotype of *Omphalina*, Redhead 1993, Moncalvo *et al*. 2000, 2002, Redhead *et al*. 2002a), which nest inside suborder *Tricholomatineae*. Species in this lineage typically display reddish brown, rusty, vinaceous brown or orange brown tinges on the pileus and stipe, a paler, non-concolorous hymenophore, and no hymenial cystidia (Redhead *et al*. 2002a). This reduced concept of *Omphalina* contains more or less the same species as the *Omphalina* complex/stirp as delimited by Lamoure (1974, 1982), *Clitocybe* sect. *Pyxidatae* by Bigelow (1974, 1985), as well as *Omphalina* sect. *Pyxidatae* by Bon (1997). Lamoure (1974) recognized six different taxa based on morphological data and compatibility tests. Micromorphological features, such as non-amyloid spores, subregular to irregular hymenophoral trama and pileipellis with incrusting pigment, are shared by all members of the genus. Vizzini *et al*. (2012b) described a molecularly confirmed collection of *O. pyxidata* with well-developed hymenial cystidia as well as pileo-, and caulocystidia.

Infundibulicybe Harmaja, Ann. Bot. Fenn., 40(3): 215. 2003.

Type: *I. gibba* (Pers.) Harmaja, Ann. Bot. Fenn., 40(3): 217. 2003.

Notes: *Infundibulicybe* is one of the multiple genera proposed to accommodate deviant lineages originally classified within *Clitocybe sensu lato*, now limited to the species phylogenetically related to the currently accepted lectotype, *C. nebularis* (Redhead *et al*. 2002a, b, Harmaja 2003, Vizzini *et al*. 2010, Vizzini & Ercole 2012, Musumeci & Contu 2014, Vizzini 2014a, b, Sesli *et al*. 2016, Alvarado *et al*. 2015, 2018a, b, He *et al*. 2023). The genus corresponds to *Clitocybe* sect. *Infundibuliformes sensu* Harmaja (1969), and to *Clitocybe* subg. *Infundibuliformes*, sect. *Infundibuliformes*, subsect. *Infundibuliformes* (Bigelow 1985), and sect. *Clitocybe sensu* Bon 1997, but not sect. *Infundibuliformes sensu* Bigelow (1968), whose concept is too broad and includes multiple unrelated taxa. *Infundibulicybe* is characterized by: (i) basidiospores smooth (except for *Infundibulicybe trachyspora* which exhibits minutely warted basidiospores on both light and SEM microscopy) that do not adhere to form tetrads (ii) all or most of the basidiospores have lacrymoid appearance, confluent base and a cyanophobic spore wall, and (iii) mycelia unable to reduce nitrates (Schwöbel 1984, Harmaja 2003, Vizzini *et al*. 2011c, Zhao *et al*. 2016, He & Yang 2023). The independence of *Infundibulicybe* from *Clitocybe* has been confirmed by phylogenetic analyses based on DNA sequences and shown to belong in suborder *Tricholomatineae* (*e.g*., Binder *et al*. 2010, Sánchez-García *et al*. 2016, 2017, 2020, Alvarado *et al*. 2018a, b, Varga *et al*. 2019, Vizzini *et al*. 2020a, He & Yang 2022). Twenty-two species of *Infundibulicybe* were recognized worldwide by He *et al*. (2019) but multiple new taxa have been described afterwards from Asia (Ishaq *et al*. 2019, Ali *et al*. 2020, Xu *et al*. 2022). Species of *Infundibulicybe* are distributed mainly in temperate, boreal, and alpine regions of the Northern Hemisphere (Harmaja 2003, Kirk *et al* 2008, Vizzini *et al*. 2011c, Zhao *et al*. 2016, Ishaq *et al*. 2019, Ali *et al*. 2020, Xu *et al*. 2022, He & Yang 2023).

Paralepistaceae Vizzini, Consiglio & P. Alvarado, ***fam. nov.*** MycoBank MB 851155.

Diagnosis: Basidiomes clitocyboid, spore deposit white, cream, or sordid ochre, basidiospores subglobose to broadly ellipsoid with pustulose-aculeate, inamyloid or amyloid, cyanophilous or acyanophilous ornamentation, hymenial cystidia usually absent, hymenophoral trama regular, clamp connections present, terricolous, among litter, presumably saprotrophic.

Type: *Paralepista* Raithelh., Die Gattung *Clitocybe* (Stuttgart) 1: 17. 1981.

Representative genera: *Notholepista* (Figs 7H, 16), *Paralepista* (Fig. 7J), and *Ripartites* (Figs 8C, D).

Notes: The three genera inside *Paralepistaceae* (*Notholepista*, *Paralepista* and *Ripartites*) share a group of morphological features, namely, small to medium-sized basidiomes, clitocyboid habit (centrally depressed pileus and sub-decurrent to long decurrent lamellae), usually detachable lamellae, a regular hymenophoral trama, presence of clamp connections, and subglobose to broadly ellipsoid mononucleate basidiospores with pustulose-aculeate ornamentation (Huijsman 1960, Pegler & Young 1974, Kühner 1976, 1980, Breitenbach & Kränzlin 1991, Noordeloos 1995b, Vizzini & Ercole 2012, Vizzini *et al*. 2012a, Bau *et al*. 2013, Læssøe & Petersen 2019, He & Yang 2022). However, the spores of *Notholepista* are amyloid and warted while those of *Paralepista* and *Ripartites* are inamyloid and spiny (Pegler & Young 1974, Vizzini & Ercole 2012, Vizzini *et al*. 2012a, Bau *et al*. 2013, Læssøe & Petersen 2019). *Ripartites* shows a sordid brown spore deposit (Huijsman 1960, Singer 1986, Noordeloos 1995b, Bon 1997, Antonini *et al*. 1998, Bau *et al*. 2013) while that of *Notholepista* and *Paralepista* is white or whitish with cream-ochre hues, respectively (Bon 1991, 1997, Raithelhuber 2004, Vizzini & Ercole 2012, Vizzini *et al*. 2012a, He & Yang 2022). The presence in the same family of genera with amyloid and non-amyloid basidiospores has been already reported in suborder *Tricholomatineae*, *i.e*., *Biannulariaceae*, *Callistosporiaceae*, *Pseudoclitocybaceae*, and *Tricholomataceae* (Sánchez-García *et al*. 2014, 2017, Alvarado *et al*. 2018a, Vizzini *et al*. 2020a, c), and in *Tricholoma* most species have been found to be latently amyloid (Vizzini *et al*. 2020c). The presence, within the same genus, of species with amyloid and non-amyloid basidiospores is also well known, *e.g*., *Dermoloma* (*Tricholomataceae*, Sánchez-García *et al*. 2021), or *Amanita* (*Amanitaceae*, *Pluteineae*, Neville & Poumarat 2004, Cui *et al*. 2018). Similarly, pale-spored and dark-spored species can be found within the same family in suborders *Agaricineae* (*Agaricaceae*, *Agaricus*, *Coprinus*, Matheny *et al*. 2006, Dentinger *et al*. 2016) and *Hygrophorineae* (*Lichenomphaliaceae*, *Melanomphalia*, Aime *et al*. 2005).

On a morphological basis, affinities between members of these three genera had already been recognized previously. Historically, *Ripartites* was first thought by some authors to be close to the ochre-spored *Galera*, *Conocybe* and *Hebeloma* (Heim 1969), or to belong to *Crepidotaceae* (Singer 1951), or *Paxillaceae* (*Boletales*) (*e.g*., Fries 1821, Quélet 1886, Machol & Singer 1971, Jülich 1981, Singer 1986) due to its spore deposit colour. Other authors classified it very generically in the *Agaricales* (Reijnders & Stalpers 1992) or inside *Tricholomataceae sensu lato*, close to *Lepista* (Kühner & Romagnesi 1953, Harmaja 1974a, Pegler & Young 1974, Kühner 1976, 1980, Noordeloos 1995b, Bon 1997), where Kühner (1976) even established a separate tribe *Lepisteae* for both genera. Besson (1970), Harmaja (1974a), Kühner (1976, 1980) and Pegler & Young (1969, 1971, 1974) recognized strong affinities between *Ripartites* and the *L. inversa* species complex (*Lepista* sect. *Gilva* = sect. *Inversae*) because of their basidiospores showing the same electron microscopy ultrastructure, with a strong cyanophilous perispore.

Notholepista Vizzini & Contu, Mycosphere 3: 84. 2012.

Type: *Notholepista subzonalis* (Peck) Vizzini & Contu, Mycosphere 3: 85. 2012.

Notes: The type species, *N. subzonalis*, resembles *Paralepista gilva* macroscopically, developing clitocyboid basidiomes with a yellow to orange pileus with distinct drop-like blotches (Bon 1978, 1997, Læssøe & Petersen 2019). In addition, basidiospores of *Notholepista* under SEM (Fig. 16A, B) are very similar to those of *Paralepista* and *Ripartites* species presented in literature (*e.g*, Pegler & Young 1969, 1971, 1974, Besson 1970, Kühner 1980, Bigelow 1981). A full description of new records of the recently described species *Notholepista fistulosa* is provided below. ITS sequences in public databases (KP453712, MF686504) obtained from specimens identified as *Leucopaxillus pulcherrimus* (FH:00301901 and TENN:070768, respectively) seem to be closely related to those of *N. subzonalis* and *N. fistulosa*, suggesting that this species should be transferred to *Notholepista* as well.

Notholepista fistulosa Z.M. He & Zhu L. Yang, Mycol. Progr. 21(2, no. 26): 9. 2022. Figs 7H, 16.

Description: *Pileus* 20–36 mm diam, centre depressed, slightly infundibuliform, dark orange (6A7, 6A8), sometimes chrome yellow (5A6, 5A8) at margin, surface hygrophanous, smooth, margin slightly involute. *Lamellae* decurrent, almost crowded, 0.7–1 mm wide, white, with 2–3 tiers of lamellulae intercalated, edges entire, even. *Stipe* 24–38 × 3–4 mm wide, central, cylindrical, concolorous with pileus or a little paler (6A7, 6A8), surface smooth, sometimes tomentose at the base, solid. *Context* dark orange (6A7, 6A8), *odour* and *taste* not distinct. *Basidiospores* (4.2–)4.7–*5.0*–5.4(–5.8) × (3.1–)3.4–*3.7*–4.1(–4.8) µm [40/2/2], Q= (1.15–)1.26–*1.36*–1.46(–1.60), V= (20.7–)28.0–*37.6*–47.1(–69.3) µm^3 broadly ellipsoid to ellipsoid, surface verruculose, warts hemispherical, up to 0.5 µm high, amyloid, cyanophobic. *Basidia* (26.7–)28.4–38.1(–39.1) × (5.9–)6.0–9.0(–9.2) µm, clavate, sometimes cylindrical, 4-sporic, sterigmata up to 0.5 µm long. *Cystidia* not observed. *Hymenophoral trama* regular, parallel, colourless, hyphae cylindrical, 2–17 µm wide, thin-walled. *Pileipellis* an intricate trichoderm, composed of dense cylindrical

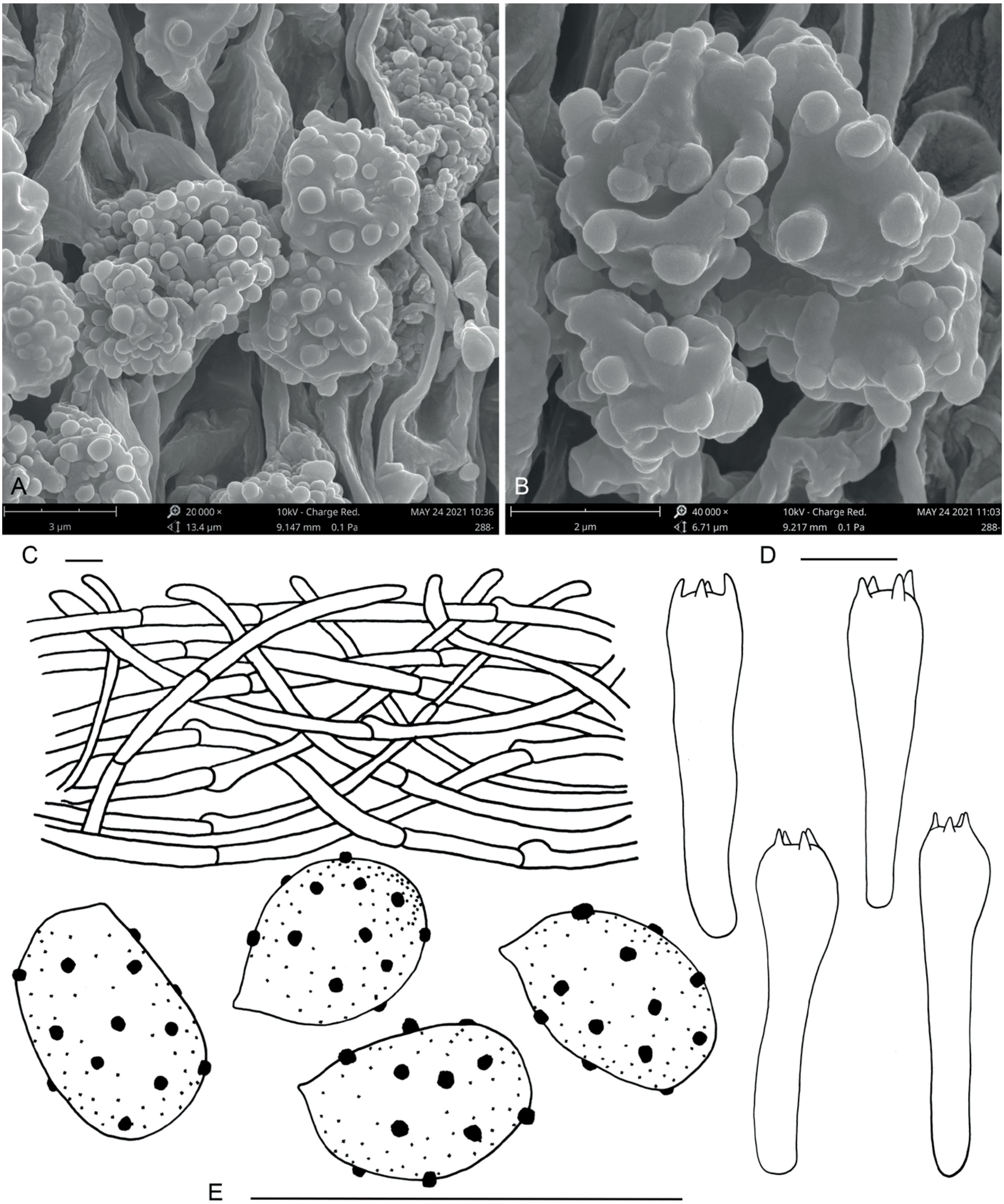

Fig. 16. *Notholepista fistulosa* (HMJU:288). **A, B.** Basidiospores (SEM). **C.** Pileipellis. **D.** Basidia. **E.** Basidiospores. Scale bars: C–E = 10 µm. Photographs and drawings by J. Xu.

hyphae, hyphae 3–14 µm wide, thin-walled. *Stipitipellis* a cutis, composed of parallel, cylindrical, repent, colourless hyphae, 3–18 µm wide. *Clamp connections* present.

Habitat and distribution: Scattered on soil in mixed forests dominated by *Pinus koraiensis*. So far only known from China.

Materials examined: **China**, Heilongjiang Prov., Yichun City, Liangshui National Nature Reserve, 47°10'50" N, 128°53'20" E, on soil under mixed forests dominated by *Pinus koraiensis*, 10 Sep. 2017, J.Z. Xu (HMJU:288, HMJU:592).

Notes: *Notholepista fistulosa* is a conspicuous species found on the ground in mixed forests. It is characterized by its small, entirely dark orange basidiomes, slightly infundibuliform pileus, decurrent lamellae, verruculose spores and pileipellis arranged as a cutis. The type species of genus *Notholepista*, *N. subzonalis*, resembles *N. fistulosa* because of their similar infundibuliform pileus with hygrophanous surface, solid stipe, verruculose amyloid spores and lack of cystidia. However, they differ in some features: basidiomes of *N. fistulosa* (pileus 20–36 mm diam, stipe 24–38 × 3–4 mm) are smaller than those of *N. subzonalis* (pileus 50–100 mm diam, stipe 20–50 × 10–20 mm); the pileus margin of *N. fistulosa* is almost entire, while that of *N. subzonalis* is frequently incised or wavy; and finally, *N. fistulosa* has a pileipellis arranged as an intricate trichoderm, while *N. subzonalis* has it arranged as a cutis (Singer & Smith 1943, 1947 as *L. pulcherrimus*; Bigelow 1965, 1985).

Pseudoclitocybaceae Vizzini *et al.*, Fungal Diversity 90: 112. 2018.

Type: *Pseudoclitocybe* (Singer) Singer, Mycologia 48: 725. 1956.

Representative genera: *Aspropaxillus*, *Clitopaxillus*, *Harmajaea*, *Musumecia*, *Pogonoloma*, and *Pseudoclitocybe*.

Notes: The family *Pseudoclitocybaceae* shares several morphological traits with *Tricholomataceae* and *Clitocybaceae*, being loosely characterized by often large- to medium-sized basidiomes (50–150 mm), clitocyboid or tricholomatoid, decurrent to subdecurrent or uncinate lamellae; a tendency of most species to turn yellowish to dirty brown when drying; basidia small (mostly < 35 × 8 µm), without siderophilic granulations, hymenial cystidia usually absent; spores usually smooth, acyanophilous, often amyloid, with broad, truncate and prominent apiculus; context homomorphous with cylindrical hyphae >4 µm wide (sarcodimitic in *Pogonoloma*), mixed or not with thromboplerous hyphae, hymenophoral trama regular to subregular with usually long, parallel or subparallel hyphae, loop-like (medallion) clamp connections usually present at least in mycelium, and pileipellis as a dry or weakly gelatinized cutis or a trichocutis. They are presumably saprotrophic species (uncertain for *Pogonoloma*), occurring worldwide, mostly in temperate to boreal regions (Alvarado *et al*. 2018a).

Aspropaxillus Kühner & Maire, Bull. Soc. Mycol. France 50: 13. 1934.
Synonyms: *Leucopaxillus* sect. *Aspropaxilli* (Kühner & Maire) Singer & A.H. Sm., Pap. Michigan Acad. Sci. 28: 96. 1943. [1942].
Clitocybe subgen. *Aspropaxillus* (Kühner & Maire) Konr. & Maubl., Rév. Hymén. France: 339. 1936.
Clitocybe sect. *Clitocybe* subsect. *Aspropaxillus* (Kühner & Maire) H.E. Bigelow, Beih. Nova Hedwigia 72: 55. 1982.
Leucopaxillus subgen. *Aspropaxillus* (Kühner & Maire) Bon, Doc. Mycol. 20(79): 57. 1990.

Type: *Aspropaxillus giganteus* (Sowerby) Kühner & Maire, Bull. Soc. Mycol. France 50: 13. 1934.

Notes: The genus *Aspropaxillus* was established to accommodate the large clitocyboid species morphologically similar to *Leucopaxillus* but producing smooth amyloid spores (Kühner & Maire 1934). Morphologically, *Aspropaxillus* is close to *Pogonoloma sensu stricto* (Kühner 1980, Singer 1986, Bon 1991, Sánchez-García *et al*. 2014, Alvarado *et al*. 2018a), which differs mainly in a tricholomatoid habit (convex pilus and non-decurrent lamellae), lamellae not easily separable from the context, and sarcodimitic context. Known species of *Aspropaxillus* are characterized by large basidiomes with pale coloured pileus, decurrent lamellae, smooth amyloid basidiospores, presence of clamp connections, absence of hymenial cystidia (Vizzini *et al*. 2012a) (Kühner & Maire 1934, Singer & Smith 1943, Singer 1989, Bon 1991, Dhancholia *et al*. 1991, Noordeloos 1995c, Consiglio & Contu 2000, Riva 2001, Christensen 2008, 2012, Vizzini *et al*. 2012a). They are all terricolous and presumably saprotrophic.

Aspropaxillus giganteus (Sowerby) Kühner & Maire, Bull. Soc. Mycol. France 50: 13. 1934. Figs 6B, 17.
Basionym: *Agaricus giganteus* Sowerby, Col. fig. Engl. Fung. Mushr. (London) 3(no. 19): tab. 244 1803.
Synonyms: *Clitocybe gigantea* (Sowerby) Quél., Mém. Soc. Émul. Montbéliard, Sér. 2 5: 88. 1872.
Paxillus giganteus (Sowerby) Fr., Hymenomyc. eur. (Upsaliae): 401. 1874.
Omphalia geotropa var. *gigantea* (Sowerby) Quél., Enchir. fung. (Paris): 23. 1886.
Leucopaxillus giganteus (Sowerby) Singer, Schweiz. Z. Pilzk. 17: 14. 1939.
Clitocybe candida Bres., Fung. trident. 1(2): 16. 1882.
Leucopaxillus candidus (Bres.) Singer, Rev. Mycol. (Paris) 4: 68. 1939.
Aspropaxillus candidus (Bres.) M.M. Moser, Kl. Krypt.-Fl. Mitteleuropa - Die Blätter- und Bauchpilze (Agaricales und Gastromycetes) (Stuttgart) 2: 66. 1953.
Leucopaxillus septentrionalis Singer & A.H. Sm., Mycologia 39(6): 726. 1948. [1947].
Clitocybe septentrionalis (Singer & A.H. Sm.) H.E. Bigelow, Canad. J. Bot. 37(5): 772. 1959.
Aspropaxillus septentrionalis (Singer & A.H. Sm.) Vizzini, Mycosphere 3(1): 83. 2012.

Description: *Pileus* 80–250(–450) mm; at first convex, then flat, eventually developing a central depression and becoming somewhat funnel-shaped to subinfundibuliform; dry, not hygrophanous, smooth, subtomentose, velutinous at centre; the margin inrolled at first, later wavy and sometimes obscurely lined/ribbed; fragile in age; whitish at first, buff to tan (4A2-5, 5A2-4) at maturity. *Lamellae* running down the stipe, deeply arcuate decurrent; very crowded; easily detachable from the context, whitish or buff (5A2-3), becoming light brown (5A5) in age; some forking, with entire, concolorous edge. *Stipe* 40–80(–100) × 20–45(–60) mm, more or less equal; dry; whitish, with tiny fibers that darken in age; base with abundant white mycelium. *Context* whitish; rather thick, turning brownish in places in old basidiomes, proportionally thin in age. *Odour* and *taste*: taste pleasant, foul or mealy; odor similar. *Spore deposit* white. *Basidiospores* (5.6–) 6.2–*7.0*–7.7(–9.1) × (3.6–)4.1–*4.7*–5.3(–6.2) µm [113/3/3], Q= (1.24–)1.36–*1.49*–1.63(–1.85), V= (43.6–)54.1–*83.6*–113(–182) µm^3, broadly ellipsoid to ellipsoid, smooth, colourless, thin-walled, congophilous, acyanophilous, amyloid, with prominent apiculus, mono-pluriguttulate. *Basidia* 25–35(–40) × 6.5–8.5(–9) µm, clavate to slightly suburniform, sometimes with median constriction or with a long curved basal portion, 4-sporic, rarely 2-sporic, sterigmata 3–4(–5) µm long, with basal clamp connection, with numerous inner refractive droplets. *Hymenophoral trama* regular, consisting of parallely oriented cylindrical hyphae, septa very close together, thin-walled, colourless, 5–10(–15) µm wide, with extracellular refractive and polymorphic crystalline deposits and thromboplerous hyphae. *Subhymenium* textura intricata type, elements short and 2–4 µm wide. *Hymenial cystidia* absent. *Pileipellis* a transition between a cutis and a trichoderm (or trichocutis), formed of subparallel to

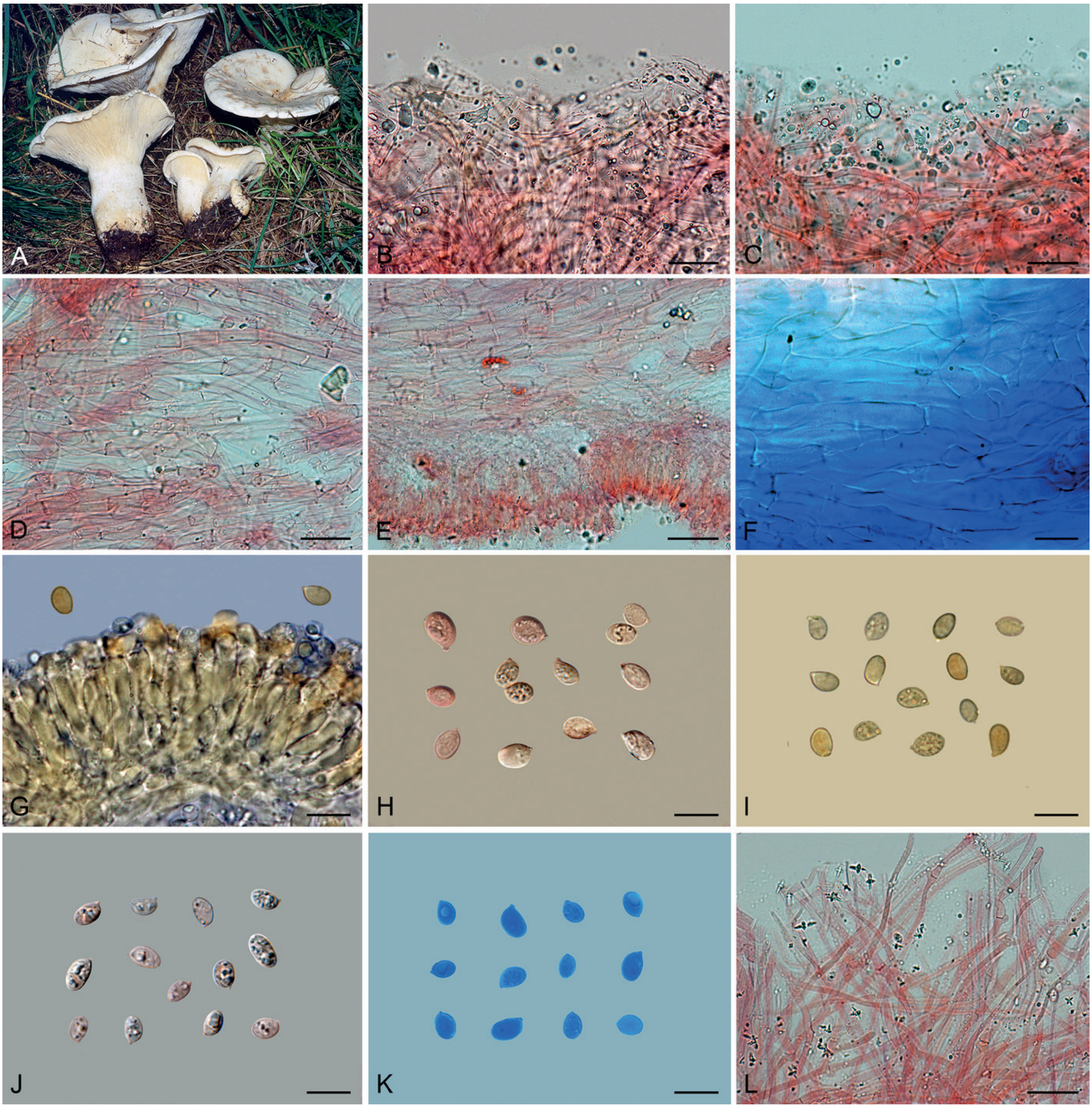

Fig. 17. *Aspropaxillus giganteus*. **A.** Basidiomes (AMB:18857). **B, C.** Pileipellis (B. AMB:19305; C. AMB:18858). **D.** Subpellis (AMB:18857). **E, F.** Hymenophoral trama (AMB:18858). **G.** Hymenium (AMB:18858). **H–K.** Basidiospores (H, I, K. AMB:18858; J. AMB:19305). **L.** Stipitipellis (AMB:18857). Mounting media were Melzer's reagent (G, I), Congo Red in ammonia (B–E, H, J, L), and Cotton Blue (F, K). Scale bars: B–E, L = 30 µm; F–K = 10 µm. Photographs A by G. Consiglio, B–L by M. Marchetti.

intertwined cylindrical hyphae, 2–6 µm wide, slightly immersed in a gelatinous matrix, colourless to pale yellowish, extracellular refractive and polymorphic crystalline deposits abundant; *subpellis* composed of colourless, cylindrical, 5–12 µm wide hyphae, sometimes enlarged at septa. *Stipitipellis* composed of tufts of hyphae in gelled matrix with long, straight to intertwined (tangled) articles, 3–7 µm wide, often with a wall up to 0.8(–1.0) µm thick, yellowish-cream, with copious presence of extracellular polymorphic crystalline deposits. *Stipititrama* composed of subirregular up to intertwined, cylindrical, 6–12(–14) µm wide hyphae, with up to 0.8(–1.0) µm thick, slightly yellowish wall. *Clamp connections* present in all parts of the basidiome, voluminous, some of the medallion (loop-like) type.

Habitat and distribution: Gregarious, terricolous, saprotrophic, often forming large fairy rings, in grasslands, rarely in open forests. Found in Europe, Asia, and North America.

Materials examined: **Italy**, Trentino-Alto Adige, Regole di Fondo (TN), under *Picea abies*, 17 Sep. 1994, G. Consiglio (AMB:18857); Bellamonte (TN), under *Picea abies*, 26 Aug. 2015, G. Consiglio (AMB:19305); Abruzzo, Rocca di mezzo (AQ), under *Picea abies*, 18 Sep. 1998, G. Consiglio (AMB:18858).

Notes: Currently, six species of *Aspropaxillus* have been described (Agerer 2018, He *et al*. 2019), distributed in the northern Hemisphere (Europe, Asia, and North America, Vizzini *et al*.

2012a) but *A*. *candidus* from Europe and *A*. *septentrionalis* from USA would appear to be later synonyms of *A*. *giganteus* according to the phylogenetic analyses by Angelini *et al*. (2017) and Harada *et al*. (2021). *Aspropaxillus giganteus* usually produces fairy rings in acid grasslands, its mycelium is easily cultured *in vitro*, and is considered as surely non-mycorrhizal (Kaiser 1998, Kohzu 1999, Yamada *et al*. 2001a, b, Barros *et al*. 2006, Harada *et al*. 2021).

Pseudoomphalinaceae Vizzini, Consiglio & P. Alvarado, ***fam. nov.*** MycoBank MB 851156.

Diagnosis: Basidiomes omphalinoid or rarely clitocyboid, spore deposit white, basidiospores smooth, amyloid, hymenial cystidia usually absent, rarely as very slender, cylindrical to filiform (hyphal) pseudoparaphysoid-like sterile elements, hymenophoral trama irregular to interwoven, pileipellis a cutis with encrusting pigment, clamp connections present and abundant, terricolous, saprotrophic.

Type: *Pseudoomphalina* (Singer) Singer, Mycologia 48(5): 725. 1956 (Fig. 8A).

Representative genus: *Pseudoomphalina* (including *Neohygrophorus*)

Notes: *Pseudoomphalina*, typified with *P. kalchbrenneri*, is mainly characterized by its clitocyboid/omphalinoid habit, presence of clamp connections, interwoven hymenophoral trama, and amyloid spores (Singer 1986, Consiglio *et al*. 2006, Contu 2010, Lavorato *et al*. 2015, Voitk *et al*. 2020a). Originally proposed as a subgenus of *Cantharellula* (Singer 1948), it was later upgraded to genus (Singer 1956). However, Kühner (1980) included *Pseudoomphalina* as part of *Aspropaxillus* inside tribe *Clitocybeae* of *Tricholomataceae*, and Bon (1997) considered it a member of tribe *Fayodiae* inside subfamily *Clitocybeae* of *Tricholomataceae* together with *Clitocybula*, *Fayodia*, *Myxomphalia*, and *Pseudoclitocybe*. Based on rDNA data, Lavorato *et al*. (2015) found *Pseudoomphalina kalchbrenneri* and allied species (Pseudoomphalina clade) in an uncertain position within the Tricholomatoid clade (suborder *Tricholomatineae*) and treated the genus *Neohygrophorus* as a later synonym of *Pseudoomphalina*. *Neohygrophorus* (typified with *N. angelesianus*) and *Pseudoomphalina* share the clitocyboid/omphalinoid habit, hyphae with clamp connections, interwoven hymenophoral trama and amyloid spores but *Neohygrophorus* differs in the grey-violaceous pigments turning red in alkali solutions and in the absence of filiform, hyphal sterile elements in hymenium and stipitipellis (Singer 1986, Redhead *et al*. 2000b, Consiglio *et al*. 2006, Contu 2010, Lavorato *et al*. 2015, Voitk *et al*. 2020a). *Pseudoomphalina umbrinopurpurascens* seems to fill the morphological gap between these two genera, as it has the peculiar violaceous pigments of *Neohygrophorus* (even though they are not reddening in alkaline solutions) and the filiform cystidia of *Pseudoomphalina* (Contu 2010, Lavorato *et al*. 2015 , Rubio & Sánchez 2019). Lavorato *et al*. (2015) also introduced the new genus *Pseudolaccaria* to accommodate the phylogenetically distant *Pseudoomphalina pachyphylla* which is nested inside the Callistosporioid clade (now *Callistosporiaceae*, Vizzini *et al*. 2020a). The analyses by Sánchez-García *et al*. (2016, 2017, 2020), Alvarado *et al*. (2018a, b), Vizzini *et al*. (2020a) and He & Yang (2022) confirmed the affiliation of *Pseudoomphalina* to the *Tricholomatineae* but without showing significant phylogenetic affinities with other clades. The present analysis (Fig. 3) supports that the clade of *Pseudoomphalina* represents a distinct evolutionary lineage within suborder *Tricholomatineae* and, hence, a new family for it is proposed here.

Tricholomataceae R. Heim ex Pouzar, Česká Mykol. 37(3): 175. 1983, *nom. cons.*, see Art. 14.
Synonyms: *Tricholomataceae* subfamily *Tricholomatoideae* see Bon, Doc. Mycol. 3(12): 5. 1974.
Leucopaxillaceae Jülich, Biblioth. Mycol. 85: 376. 1982. [1981].
Tricholomataceae Roze [as 'Tricholomées'], Bull. Soc. Bot. France, Act. Bot. 23: 112. 1876, *nom. inval.*, Art. 32.1(c), see Art. 18.4 (Shenzhen).
Agaricinès Tribe Tricholomées (as Tricholomés) Fayod, Ann. Sci. Nat., Bot., Série 7, 9: 346. 1889, *nom. inval.*, Art. 32.1(c), see Art. 18.4 (Shenzhen).
Dermolomataceae Bon, Bull. Fed. Hist. Nat. Mycol. 1: 10. 1979 [*nom. inval.*, Art. 33.2; *nom. rejic.*, Art. 14 (Shenzhen)].

Type: *Tricholoma* (Fr.) Staude, Schwämme Mitteldeutschl. 1: xxviii, 125. 1857, *nom. cons.*, see Art. 14 (Shenzhen).

Representative genera: *Albomagister*, *Dennisiomyces*, *Dermoloma*, *Corneriella*, *Leucopaxillus*, *Porpoloma sensu stricto*, *Pseudobaeospora*, *Pseudotricholoma*, and *Tricholoma*.

Notes: A major clade, named *Tricholomataceae sensu stricto*, which encompasses seven monophyletic subclades corresponding to the genera *Leucopaxillus*, *Tricholoma*, *Pseudotricholoma*, *Porpoloma sensu stricto*, *Dennisiomyces*, *Corneriella*, and *Albomagister*, was first recovered by Sánchez-García *et al*. (2014) based on a multigene analysis. A similar phylogeny was reconstructed by Corriol & Jargeat (2019) who reported the first collection of *Dennisiomyces* in Europe. Later, *Pseudobaeospora* and *Dermoloma* were also placed in *Tricholomataceae sensu stricto* (Desjardin *et al*. 2014, Sánchez-García & Matheny 2017, Sánchez-García *et al*. 2021, He & Yang 2022). Only *Porpoloma sensu stricto* and *Tricholoma* are considered ECM-forming genera without doubt (Kühner 1980, Garrido 1988, Tedersoo *et al*. 2010, Sánchez-García *et al*. 2014, Sánchez-García & Matheny 2017). The family *Tricholomataceae* is characterized by a tricholomatoid or rarely tricholomatoid-collybioid habit; pileus conical, convex, plano-convex to applanate, smooth, tomentose, or scaly, dry or viscid, rarely hygrophanous; lamellae adnate, adnexed, sinuate-emarginate to decurrent; spore deposit pure white, rarely pale cream; basidiospores subglobose, ellipsoid or ellipsoid-oblong, colourless, thin-walled, without a germ pore, smooth or verrucose, positive reacting to Melzer's reagent (immediately amyloid, latently amyloid or dextrinoid, Vizzini *et al*. 2020c); basidia without siderophilous granulation; hymenial cystidia present or absent as cheilocystidia, pleurocystidia present in some groups; hymenophoral trama regular; pileipellis a cutis, ixocutis or trichoderm; clamp connections present or absent; ectomycorrhizal or saprotrophic on soil, humus and debris in forests and grass-lands; mainly found in temperate regions of the northern and southern hemispheres, but also in the tropics.

Orphaned *incertae sedis* genera inside *Tricholomatineae*

Paralepistopsis Vizzini, Mycotaxon 120: 257. 2012.

Type: *Paralepistopsis amoenolens* (Malençon) Vizzini, Mycotaxon 120: 257. 2012. (Fig. 7K).
Basionym: *Clitocybe amoenolens* Malençon, Trav. Inst. Sci. Chérifien, Sér. Bot. Biol. Veg. 33: 141. 1975.

Notes: The two species of *Paralepistopsis* known so far, *P. acromelalga* and *P. amoenolens* are characterized by clitocyboid habit (decurrent and crowded lamellae), confluent pileus and stipe and pileus colours (ochre-orange tinges) reminiscent of *Paralepista* or *Infundibulicybe*; lamellae easily separating from the pileus context; whitish to cream spore deposit; smooth cyanophilous broadly ellipsoid basidiospores often arranged in tetrads in dried specimens and rarely exceeding 5(–6) µm in length; basidia reaching 35–40 µm in length; (rare) shortly diverticulate hyphae in the pileipellis, thromboplerous hyphae rare to abundant; presence of toxic compounds, acromelic acids, *viz.* powerful neurotoxic aminoacids responsible for erythromelalgic poisoning (Nakamura *et al.* 1987, Saviuc *et al.* 2001, 2002, Leonardi *et al.* 2002, Marinetti & Recchia 2005) and structurally homologous with kainic acid (a strong agonist of non-*N*-methyl-*D*-aspartate glutamate receptor subtypes) and domoic acid; and saprotrophic growth on soil (Moreau *et al.* 2001, Vizzini & Ercole 2012). *Paralepista* differs in having conspicuously ornamented basidiospores (Raithelhuber 1995, 2004, Consiglio & Contu 2003, Vizzini & Ercole 2012); *Infundibulicybe* is distinguished by its smooth lacrymoid spores with confluent bases and not arranged in tetrads, and cyanophobic spore walls (Harmaja 2003). Other morphologically look alike genera as *Cleistocybe* and *Catathelasma* are distinguished from *Paralepistopsis* mainly by the presence of a partial veil, divergent to interwoven hymenophoral trama, and larger cyanophobic basidiospores (Ammirati *et al*. 2007, Vizzini *et al*. 2020a); additionally, *Catathelasma* basidiospores are amyloid (Singer 1986, Vizzini *et al*. 2020a).

Paralepistopsis amoenolens was first described employing specimens found in Morocco (Malençon & Bertault 1975), but it was later found also in southern and southwestern Europe (mainly France, Italy, and Spain). This species is delimited by a unique combination of macro-/micromorphological and chemical features, such as a convex pileus with orange tinges, a strong aromatic, floral odour reminiscent of *Tricholoma caligatum*, *Inocybe corydalina*, *Lepista irina*, and *Entoloma ameides* [caused by volatile metabolites as methyl-(E)-cinnamate, methylbenzoate, (E)-nerolidol, and methylanthranilate, Fons *et al.* (2006)], basidiospores (3.8–)4.0–5.4(–5.6) × (2.3–)3.2–4.0(–4.3) µm, thromboplerous hyphae very common, and the presence of the toxic metabolite acromelic acid A (Bon 1987c, Poumarat & Neville 1993, Moreau *et al*. 2001, Leonardi *et al*. 2002, Bessard *et al*. 2004, Martínez *et al*. 2010, Vizzini & Ercole 2012, Vizzini 2014c). The Asiatic species *Paralepistopsis acromelalga* differs from *P. amoenolens* in a darker pileus and stipe, a pileus that soon becomes depressed, a different odour, thromboplerous hyphae occurring only rarely, smaller basidiospores (Ichimura 1918, Romagnesi 1989, Guez 1990, Miyauchi 1998, Moreau *et al*. 2001), and a more complex metabolite pattern (presence of acromelic acids A–E with 19 other toxins among which clitidine; Konno *et al*. 1983, 1988, Fushiya *et al*. 1990, 1992, Saviuc & Danel 2006, Wurita *et al*. 2019). In accordance with these differences, *P. acromelalga* was shown to be related but phylogenetically distinct from *P. amoenolens* with rDNA sequences, both species clustering together near *Cleistocybe* (Vizzini & Ercole 2012). However, based on the same rDNA information, Sánchez-García & Matheny (2017), Varga *et al*. (2019) and Sánchez-García *et al*. (2020) found that *P. amoenolens* is sister or embedded inside *Clitocybaceae*. In the present multigene analysis (Fig. 3) *P. amoenolens* seems to be sister (with no significant support) to *Clitocybaceae*.

Since Singer (1986) transferred *P. acromelalga* to the heterogeneous genus *Neoclitocybe* based on the presence of rare diverticulate hyphae in the pileipellis, the status of this genus should be addressed too after studying authentic material of the type species, *N. byssiseda*, to check for a putative synonymy with *Paralepistopsis*. Based on their small basidiospores and the *Paralepista*-like habit, *Clitocybe gilvaoides* and *C. gracilis* (part of *Clitocybe* sect. *Gilvaoideae*) from the coniferous forests of North America and Scandinavia (Harmaja 1969, Bigelow 1985) may also belong to *Paralepistopsis*, but modern specimens are needed to perform molecular and biochemical studies to test it.

Hertzogia R. Wiest, Bull. Soc. Mycol. Strasbourg 121: 33. 2022.

Type: *Hertzogia martiorum* (J. Favre) R. Wiest, Bull. Soc. Mycol. Strasbourg 121: 33. 2022. (Fig. 6K).
Basionym: *Clitocybe martiorum* J. Favre, Schweiz. Z. Pilzk. 34(11): 169. 1956.
Synonym: *Lepista martiorum* (J. Favre) Bon, Doc. Mycol. 22(no. 88): 46. 1993.

Notes: Wiest (2022) proposed the new monospecific genus *Hertzogia* to accommodate *Clitocybe martiorum*, a species with an uncertain position within *Tricholomatineae* in the present work (Fig. 3). It is characterized by pileostipitate clitocyboid basidiomes with convex pileus, lamellae adnate to subdecurrent, more or less separable from the pileus context; spore deposit pinkish; basidiospores small (less than 6 µm in length), appearing smooth on light microscopy, cyanophilous, inamyloid, hymenial cystidia absent, clamp connections present, terricolous, presumably saprotrophic. Favre (1956) already reported that the classification of *C. martiorum* seemed uncertain due to its pinkish spore deposit, presence of clamp connections, and its lamellae easily separable from pileus context. He observed that it resembles *Rhodopaxillus* (= *Lepista*) but its smooth basidiospores led him to classify it inside *Clitocybe*. The species is not covered in Harmaja's milestone monograph (1969). Later, Clémençon (1984) placed *C. martiorum* within *Clitocybe* sect. *Roseospora*, and finally Bon (1993, 1997), after discussing the subtle boundaries between *Clitocybe* and *Lepista*, proposed to include it in *Lepista* because of the lamellae detachable from the pileus and strongly cyanophilous basidiospores with minute ornamentations under SEM. Raithelhuber (2004) reported it as *Clitocybe* (*Lepista*?) *martiorum*.

Typhulineae Vizzini, Consiglio & P. Alvarado, ***subord. nov.*** MycoBank MB 851161.

Type: *Typhula* (Pers.: Fr.) Fr. Obs. Mycol. 2: 296. 1818: Fr., Syst. Mycol. 1: 494. 1821, *nom. cons. prop.*, see Olariaga *et al*. (2022) and Stalpers *et al*. (2021).
Basionym: *Clavaria* [unranked] *Typhula* Pers.: Fr., Syn. Meth. Fung. 1: XVIII. 1801.
Synonyms: *Pistillaria* Fr., Syst. Mycol. (Lundae) 1: 464, 496. 1821.
Phacorhiza Pers., Mycol. Eur. 1: 192. 1822.
Cnazonaria Corda in J. Sturm, Deutschl. Fl., Pilze 2: 55. 1829.
Scleromitra Corda in Sturm, Deutschl. Fl., 3 Abt., 2: 59. 1829.
Pistillina Quél., Compt. Rend. Assoc. Franç. Avancem. Sci. 9: 671. 1881. ["1880"].
Sphaerula Pat., Tab. Anal. Fung. 1: 27. 1883.
Phaeotyphula Henn., Bot. Jahrb. Syst. 28(3): 320. 1900.
Gliocoryne Maire, Bull. Soc. Bot. France 55: 121. 1909.
Dacryopsella Höhn., Anz. Kaiserl. Akad. Wiss. Wien, Math. - Naturwiss. Kl., Abt. 1, 124: 50. 1915.
Sclerotiomyces Woron., Ann. Mycol. 24(3/4): 233 (1926)
Tygervalleyomyces Crous, Persoonia 39: 387. 2017.

Representative family: *Typhulaceae* Jülich, Biblioth. Mycol. 85: 393. 1982. ["1981"].

Representative genus: *Typhula*. The monospecific genus *Lutypha* (Khurana *et al*. 1977), morphologically assignable to this suborder, has not yet been sequenced.

Diagnosis: Basidiomes clavarioid, simple or branched, solitary or densely gregarious, usually erect, exceptionally prostrate, cylindrical to slightly flattened or apically with an inflated clavate, cylindrical or subglobose head, stipe (when differentiated) filiform and sterile, usually arising from a sclerotium. Hymenium not thickening, covering the inflated portion completely or leaving the lower or upper portion free. Spore deposit white. Hyphal system monomitic. Cystidia occasionally present as caulocystidia. Basidia 2–4-sporic, basidiospores colourless, smooth, thin-walled, amyloid or inamyloid, non-dextrinoid. Clamp connections present or absent. Dolipores with continuous parenthosomes. Lignicolous, herbicolous, saprotrophic, or parasitic.

Notes: Two genera, *Typhula* and *Macrotyphula*, were traditionally accepted in *Typhulaceae* (*e.g*., Berthier 1976, Jülich 1984, Petersen 1988, Knudsen & Shiryaev 2012). *Typhula* [type *T. incarnata* Lasch, in Fries, Epicr. syst. mycol. (Upsaliae): 585 (1838) [1836–1838], *typ. cons. prop.*, see Olariaga *et al*. (2022)] includes phytopathogenic species with small basidiomes (usually under 10 mm long) that often arise from sclerotia and have amyloid spores (Berthier 1976, Jülich 1984). Additionally, an asexual morph forming cylindrical conidia with a truncate base may be present in some species of *Typhula* (*Tygervalleyomyces*, Berthier 1976, Crous *et al*. 2017, Olariaga *et al*. 2020). The genus *Typhula* comprises about 90 currently accepted species (Olariaga *et al*. 2022), including several important cold-adapted plant-pathogenic fungi, with *T. incarnata* and *T. ishikariensis* complex, *T. variabilis* and *T. japonica* of special economic importance (Vergara *et al*. 2004, Hoshino *et al*. 2022, 2023). These species are causal agents of "grey snow mould", also called "Typhula blight", producing considerable damage to turf grass and cereal crops (*e.g*., Matsumoto 1992, 2009, Hsiang & Wu 2000, Hoshino *et al*. 2009, 2023, Ikeda *et al*. 2015, 2016). The clade of *Typhula sensu stricto* was shown to be independent from all other suborders of *Agaricales* by Olariaga *et al*. (2020), and later confirmed by the phylogenomic analysis of Wang *et al*. (2023b). The analyses conducted in the present work using a more diverse dataset (Fig. 1, Suppl. Figs S1, S2), agree with the previous results, and so the lineage of *Typhula* is here accommodated in its own suborder, *Typhulineae*.

DISCUSSION

In the present work, the phylogenetic affinities of several *incertae sedis* genera are resolved using an extended dataset with newly sequenced lineages of *Agaricales* and more complete data than those analyzed in previous works. Sequences of *TEF1*, *RPB1* and *RPB2* genes were obtained from multiple genera previously represented mainly by ribosomal DNA markers (*i.e*., *Aphroditeola*, *Aspropaxillus*, *Clitolyophyllum*, *Fayodia*, *Gamundia*, *Heimiomyces*, *Hemimycena*, *Hertzogia*, *Leucocortinarius*, *Limnoperdon*, *Melanoleuca*, *Omphaliaster*, *Omphalina sensu stricto*, *Paralepistopsis*, *Pseudoomphalina*, *Resupinatus*, *Ripartites*, *Tectella*, *Trichocybe*, *Volvopluteus*), as well as lineages not present before in public databases (*Giacomia*, *Hygrophorocybe*), increasing the number and representativeness of informative positions in the analyses (Frøslev *et al*. 2005, Matheny *et al*. 2006, Schoch *et al*. 2009). Incomplete information coming from a limited number of species and/or genes could be the cause of some of the differences between the present results and previous multigene studies (*i.e*., Olariaga *et al*. 2020). The present phylogeny is based on less information from each species compared with phylogenomic approaches (*i.e*., Dentinger *et al*. 2016, Ke *et al*. 2020, Wang *et al*. 2023b), but adds important lineages not present in these works, which could help to resolve ancient nodes. The diversity analyzed could play an important role on the results, maybe like that of the amount of information analyzed from each lineage, at least at the scale of the present study. Philippe *et al*. (2011) discussed that ancient evolutionary events are difficult to be resolved by phylogenetic studies, even with extensive genomic data, producing erroneous (but statistically supported) inferences in case the diversity analyzed does not represent the evolutionary history of the ingroups properly. This could be a problem also in studies using a phylogenomic backbone constraint for deep nodes (*i.e*., Varga *et al*. 2019). The analysis of a more representative dataset filling diversity gaps should help to reduce the phylogenetic noise produced by the accumulation of multiple mutations and other sources of homoplasies.

During the preliminary analyses made for the present work, Bayesian results were greatly influenced too by the identity of the taxa analyzed, leading to the complete failure to reach convergence in a reasonable timeframe, or important changes in the resulting topology and statistical support of several major nodes occurring when some lineages were excluded from the analyses or represented by too few species. The information available from each lineage seemed to affect results critically too, producing artifactual support values between lineages with incomplete information (*i.e*., those represented by ribosomal DNA data alone) and unrelated clades. These problems could be caused by the Markov chains falling into suboptimal states that cannot be overcome without restarting the analysis from another random state. In turn, the maximum likelihood analysis (ML) was found to be more conservative than Bayesian inference, producing low support values for many deep nodes of the present phylogeny. This probably indicates that the information contained in the 6-gene dataset is barely enough to represent the evolutionary history of the lineages studied, probably due to the great amount of phylogenetic 'noise' introduced by homoplasies. Genome sequencing projects (*i.e*., Li *et al*. 2018, Ruiz-Dueñas *et al*. 2020, Wang *et al*. 2023b), greatly increase the amount of information available, but still some important phylogenetic gaps need to be filled to analyze truly representative information. Genomic studies including lineages that apparently fill such gaps in the present work would be necessary to test if the present phylogenetic backbone is right or not.

Based on the phylogenetic results obtained in the present work (Figs 1–3, Suppl. Figs S1, S2), it is here hypothesized that the order *Agaricales* contains at least nine suborders: *Agaricineae*, *Clavariineae*, *Hygrophorineae*, *Marasmiineae*, *Phyllotopsidineae* (= *Sarcomyxineae*), *Pleurotineae* (= *Schizophyllineae*), *Pluteineae*, *Tricholomatineae* and *Typhulineae*. Many clitocyboid/pleurotoid/tricholomatoid *incertae sedis* genera analyzed nest inside *Tricholomatineae*, but results led to the creation of ten new families throughout the entire order *Agaricales*. The main results are discussed below.

HYGROPHORINEAE

Matheny *et al*. (2006) identified the Hygrophoroid clade as the one formed by the families *Hygrophoraceae*, *Pterulaceae* and *Typhulaceae*, as well as the genera *Sarcomyxa* and *Xeromphalina*. A similar relation was also found between some of these lineages by Garnica *et al*. (2007) analyzing LSU and *RPB1* sequences. However, in Matheny *et al*. (2007), *Pterulaceae* and *Tricholomopsis* were found to be independent from the family *Hygrophoraceae*, and Binder *et al*. (2010) did not find either a significant similarity between *Hygrophoraceae* and these clades using an extended dataset. Lodge *et al*. (2014) reviewed the entire group (as family *Hygrophoraceae*), which they divided into three subfamilies (*Hygrophoroideae*, *Hygrocyboideae* and *Lichenomphalioideae*), as well as a basal '*Cuphophylloid*' grade. Later, He & Yang (2021) found significative support for a subfamily *Cuphophylloid*eae. These subfamilies, as well as the tribe *Cantharelluleae* of *Lichenomphalioideae* (first recognized by Lodge *et al*. 2014), are upgraded to the rank of independent families in the present work. This decision was taken on the basis of a 3-gene dataset including a quite diverse, but still not complete, subset of genera of *Hygrophorineae*. Additional lineages need to be sequenced to get a more accurate phylogeny of this suborder, and ultimately, a phylogenomic analysis should be conducted to confirm the present decisions. The genera *Macrotyphula*, *Phyllotopsis*, *Pleurocybella*, *Sarcomyxa*, *Tricholomopsis* and *Typhula* were also considered basal to the Hygrophoroid group (but without a significant support) by Lodge *et al*. (2014), but they were accommodated (except for *Typhula*) in the suborder *Phyllotopsidineae* by Wang *et al*. (2023b), a result confirmed in the present work. A subsignificant relationship between *Hygrophorineae* and *Phyllotopsidineae* (PP 0.87) was found (Fig. 1), suggesting that both suborders could have a monophyletic origin, a result already observed by Wang *et al*. (2023b). The genome-based phylogenies by Dentinger *et al*. (2016) and Li *et al*. (2021), placed *Hygrophoraceae* and *Clavariaceae* in a monophyletic group, named *Hygrophorineae* by Dentinger *et al*. (2016), but Olariaga *et al*. (2020) found no significant similarities between an extended dataset of *Clavariaceae* (*Ceratellopsis acuminata*, *Clavaria zollingeri*, *Clavulinopsis laeticolor*, *Hodophilus hymenocephalus*, *Mucronella calva*, and *Ramariopsis kunzei*) and *Hygrophoraceae* (*Ampulloclitocybe clavipes*, *Cantharocybe gruberi, Hygrocybe coccinea*, *Hygrophorus pudorinus*, and *Pseudoarmillariella ectypoides*), and therefore, they proposed the new suborder *Clavariineae* to accommodate *Clavariaceae*, a result confirmed by Wang *et al*. (2023b) with an extended phylogenomic dataset, and the present work (Suppl. Fig. S1).

MARASMIINEAE

Suborder *Marasmiineae* was formally proposed by Dentinger *et al*. (2016) for the clade containing families *Cyphellaceae*, *Marasmiaceae*, *Omphalotaceae*, *Physalacriaceae* and the hydropoid clade (now *Porotheleaceae*, Antonín *et al*. 2019, Vizzini *et al*. 2019b, 2022, Matheny *et al*. 2020a, Consiglio *et al*. 2021), as well as the *Mycenaceae* (with a lower statistical support). This decision was later confirmed by Varga *et al*. (2019), Ke *et al*. (2020) and Olariaga *et al*. (2020). In some studies, *Marasmiineae* (or the Marasmioid clade) included also *Schizophyllineae*, either nested inside (Thorn *et al*. 2005, Matheny *et al*. 2006, Varga *et al*. 2019, Olariaga *et al*. 2020, Sánchez-García *et al*. 2020, Li *et al*. 2021), or sister to (Ke *et al*. 2020, Wang *et al*. 2023b) the core lineage of *Marasmiineae*. Regarding the family *Mycenaceae*, it was found to be unrelated to *Marasmiineae* in Moncalvo *et al*. (2002) and Thorn *et al*. (2005); nested in the Tricholomatoid clade in Matheny *et al*. (2006) and Sánchez-García *et al*. (2020); nested in the Marasmioid clade / *Marasmiineae* but without support in Binder *et al*. (2010) and Dentinger *et al*. (2016); and finally significantly related to *Marasmiineae* (*Mycena luteopallens*, Varga *et al*. 2019, Ke *et al*. 2020, Li *et al*. 2021, Wang *et al*. 2023b). Interestingly, some phylogenomic studies found a significant monophyletic origin between *Mycenaceae* and the remaining families of *Marasmiineae* (Ke *et al*. 2020), while others found a monophyletic origin between *Mycenaceae* and *Schizophyllineae* instead (Li *et al*. 2021, Wang *et al*. 2023b), a difference maybe caused by the representativeness of the diversity analyzed.

The present results (Fig. 1) suggest that the sister families *Mycenaceae* and *Xeromphalinaceae* are significantly related to *Marasmiineae*. A phylogenomic analysis including *Xeromphalina* and *Heimiomyces* would be useful to confirm this hypothesis. The family *Mycenaceae* includes the genera *Mycena* (apparently polyphyletic), *Favolaschia* (Fig. 6D), *Panellus* (including *Dictyopanus*) and *Roridomyces*. The analysis of a specimen identified as *Hemimycena lactea* (type of the genus) (OULU:GAJ15636, Fig. 6J) suggested that this species is not related to *H. gracilis*, but this problem should be addressed separately to take reliable taxonomic decisions. The polyphyletic status of *Hemimycena* had already been suggested by the molecular works of Dima (in Lehmann & Lüderitz 2018), Bau *et al*. (2021) and Vizzini *et al*. (2022). In these works, most species clustered together with *Phloeomana* (type *P. speirea*, *Cyphellaceae*) (Lehmann & Lüderitz 2018, Vizzini *et al*. 2022), a genus corresponding to species in *Mycena*, section *Hiemales* (Maas Geesteranus 1992, Ronikier & Aronsen 2007, Redhead 2013, Aronsen & Læssøe 2016, Robich 2016, Holec & Kolařík 2017, Lehmann & Lüderitz 2018), characterized by greyish brownish mycenoid to omphalinoid basidiomes, non-amyloid spores, cheilocystidia of shape slightly different from that of basidia, hyphae of pileipellis with ramified digitations, usually smooth stipe hyphae with scattered caulocystidia, growing on bark and dead wood. However, the core clade of *Hemimycena* (= *Hemimycena sensu stricto*, where the type, *H. lactea* is included) occupied an isolated position and is distantly related to *Cyphellaceae* (Lehmann & Lüderitz 2018). To better understand the status of *Hemimycena* versus *Phloemana*, additional species should be analyzed, and other markers (protein-coding genes) sequenced.

PLEUROTINEAE AND *PHYLLOTOPSIDINEAE*

Dentinger *et al*. (2016) found that *Pleurotus ostreatus* and *Pterula multifida* formed a significantly supported clade, which they called suborder *Pleurotineae* (type *Pleurotaceae*). Later, Olariaga *et al*. (2020) defended a monophyletic origin between two species of *Pleurotus* (one of them represented only by 18S and 5.8S rDNA sequences), and the families *Phyllotopsidaceae*, *Pterulaceae*, *Radulomycetaceae*, *Sarcomyxaceae*, *Stephanosporaceae*, and *Typhulaceae*. Wang *et al*. (2023b) produced genomic data of these families and concluded that they are not directly related to *Pleurotineae* (represented only by two species of *Pleurotus*), accommodating them in the suborder *Phyllotopsidineae*. This result is confirmed in the present work using a more diverse dataset of *Pleurotineae* including 19 species of the genera *Pleurotus*, *Hohenbuehelia* and *Resupinatus*. These pleurotoid genera were sometimes merged in different ways (Pilát 1935, Coker, 1944, Kühner

1980) or at least classified together inside the family *Pleurotaceae* (Singer 1962a, 1975, 1986, Barron 1986). In the present work, two distinct families are recognized: *Pleurotaceae* (*Pleurotus* and *Hohenbuehelia*) and *Resupinataceae* (*Resupinatus*), on account of the multiple differences between both clades (*i.e*., habit, pileipellis structure, nematophagy) and the lack of a significant support for their monophyletic origin. The genera *Auriculariopsis*, *Fistulina*, *Porodisculus* and *Schizophyllum* were considered by Dentinger *et al*. (2016), Olariaga *et al*. (2020) and Wang *et al*. (2023b) as part of the *Schizophyllineae*, but this suborder is apparently related to *Pleurotineae* in the present work (Figs 1, 2, Suppl. Fig. S2). As a result, both suborders are considered synonyms here, giving priority to *Pleurotineae*. A phylogenomic analysis including representatives of the genera *Hohenbuehelia* and *Resupinatus* would be useful to confirm this hypothesis.

PLUTEINEAE

The lineage of *Pluteineae* was first found to be independent from all others in Moncalvo *et al*. (2000) as clade G (*Amanita*, *Limacella* and *Pluteus*) and Moncalvo *et al*. (2002) (/pluteus, /melanoleuca plus Amanitaceae group including *Amanita*, *Limacella* and *Catatrama*) but without a formal clade designation. A broad non-significant Pluteoid clade containing *Pleurotaceae*, *Pluteaceae*, *Amanitaceae*, *Lymnoperdaceae*, *Melanoleuca* and *Tricholomopsis* was reported by Matheny *et al*. (2006) and Binder *et al*. (2010) with *Pluteus*, *Volvopluteus*, *Melanoleuca* and *Amanita*. Other studies failed to obtain significant similarities between *Amanitaceae* and *Pluteaceae* (Bodensteiner *et al*. 2004, Sheikh *et al*. 2022) or *Volvariella* and *Pluteaceae* (Moncalvo *et al*. 2002, Justo *et al*. 2011). Pioneer phylogenomic analyses at Mycocosm (Grigoriev *et al*. 2014) suggested a close relation of *V*. *volvacea* with *Pluteus cervinus* and various species of *Amanita*. Based on genomic data, Dentinger *et al*. (2016) established *Pluteineae* for the clade consisting of *Amanita muscaria*, *Aspidella thiersii* (*Saproamanita*) and *Volvariella volvacea*, a result reproduced later by Ke *et al*. (2020). Employing a phylogenomic backbone, Varga *et al*. (2019) found a nearly significant support for the same clade including also *Pluteus cervinus*. In the six-gene analysis by Olariaga *et al*. (2020) a monophyletic clade formed by *Amanita brunnescens*, *Pluteus romellii* and *Lachnella villosa* was found (0.98 PP). In the phylogeny by Sánchez-García *et al*. (2020, suppl. mat.), a clade including a collection named "*Volvariella media*", *Pluteus* species, *Volvopluteus gloiocephalus*, *Melanoleuca* species and *Limnoperdon incarnatum* was recovered, but *Volvariella* species (*V. perciliata*, *V. bombycina*, *V. volvacea*, *V. surrecta*, *V. hypopithys*, *V. taylorii* and *V. caesiocincta*) were found sister to *Lachnellaceae*. In the phylogenomic analysis by Li *et al*. (2021), eight species of *Amanita sensu lato* (six *Amanita* and two *Saproamanita*) were found to be sister (98 % BP) to *V*. *volvacea* and *P*. *cervinus*. The phylogenomic analysis performed by Wang *et al*. (2023b) found that *Amanita*, *Pluteus* and *Volvariella* have a monophyletic origin. In the present analysis (Fig. 2) *Pluteineae* consisted in two major clades: the family *Amanitaceae* plus *Leucocortinarius* (0.99 PP) and a clade formed by *Limnoperdaceae*, *Melanoleucaceae*, *Pluteaceae* and *Volvariellaceae* (1 PP). While the Bayesian support for the entire suborder (0.88 PP) is subsignificant, this is probably due to the existence of gaps in the diversity analyzed and/or a low ratio signal/noise in the sequences included in the analysis. Analyses lacking *Leucocortinarius* produced a significant support for the rest of *Pluteineae* (*i.e*., Supplementary Fig. S1). Genomic studies of *Leucocortinarius* are necessary to confirm it truly belongs to the family *Amanitaceae*.

Amanitaceae

The widening of the limits of the *Amanitaceae* to accommodate *Leucocortinarius* is supported by several shared morphological features. *Leucortinarius* and most species of *Amanitaceae* have a bivelangiocarpic development, a bulbous stipe base, white spore deposit, binucleate basidiospores, and an ectomycorrhizal trophic status (Bas 1969, Reijnders 1979, Kühner 1980, Singer 1986, Neville & Poumarat 2004, Cui *et al*. 2018). A non-schizohymenial development of the hymenophore and non-acrophysalidic stipititrama are also known in other genera of *Amanitaceae* (*Limacella sensu lato*, *Catatrama*, Franco-Molano 1991, Vrinda *et al*. 2000, Wartchow *et al*. 2007). Non-free lamellae might also be present in some species of *Amanita* and *Limacella* (Neville & Poumarat 2004, Hahn & Lohmeyer 2010, Cui *et al*. 2018). Furthermore, genera with free lamellae and others with attached to subfree lamellae (homogeneous versus heterogeneous basidiome texture) do coexist in the same family or different families of the suborders *Pluteineae* and *Agaricineae* (Singer 1986, Moncalvo *et al*. 2002, Matheny *et al*. 2006, 2015). In *Leucocortinarius*, only the presence of a regular hymenophoral trama (vs. an inverse one) and metachromatic basidiospores constitute truly new characters for the family. Sporal metachromacy, highlighted in *Leucocortinarius* for the first time in the present work, is not shared either by any other member of the *Pluteineae*. The character is sparingly present in other gilled agaricoid genera, being so far known only in the Tribe *Leucocoprineae* (*Macrolepiota*, *Leucoagaricus*, *Leucocoprinus*, *Chlorophyllum*, Singer 1986) of the *Agaricaceae* in the *Agaricineae* (Matheny *et al*. 2006, Vellinga 2004, Vellinga *et al*. 2011), in *Haasiella* and *Aeruginospora* of the *Hygrophoraceae* in the *Hygrophorineae* (Lodge *et al*. 2014, Vizzini *et al*. 2012b) and in *Tricholoma cookeanum* (Bon 1984, Bon 1991) of the *Tricholomataceae sensu stricto* in the *Tricholomatineae* (Matheny *et al*. 2006, Sánchez-García *et al*. 2014, Sánchez-García 2016, Sánchez-García & Matheny 2017).

Melanoleucaceae

The phylogenetic position of *Giacomia*, a name resulting from the fragmentation of the classical concept of *Leucopaxillus*/*Porpoloma* (Vizzini *et al*. 2012a, 2016, Sánchez-García *et al*. 2014), has always been uncertain (He *et al*. 2019, Kalichman *et al*. 2020). According to previous studies based on ribosomal DNA data (Sánchez-García *et al*. 2014, Sánchez-García 2016, Angelini *et al*. 2017), *Giacomia* does not belong to the families *Tricholomataceae*, *Entolomataceae* or *Lyophyllaceae*, while others (Varga *et al*. 2019) suggest that it is not even related to suborder *Tricholomatineae*. In the preliminary analyses of the present work (data not shown), *Giacomia* and *Melanoleuca* appeared significantly related to *Limnoperdon* (represented only by rDNA sequences of the ex-type strain in public databases), but the addition of newly obtained sequences of protein-coding genes (*RPB2*, *TEF1*) did not support that hypothesis anymore. As a result, *Melanoleuca* and *Giacomia* are here accommodated in a new family, *Melanoleucaceae* (not "*Melanoleucaceae*" Locq., Loquin 1984, invalid Art. 39), which is related to *Limnoperdaceae* (Escobar *et al*. 1976), *Pluteaceae* and *Volvariellaceae*, as well as *Amanitaceae* inside suborder *Pluteineae*. Both *Melanoleuca* and *Limnoperdon* were already found to be related to genus *Pluteus* (Moncalvo *et al*. 2002, Bodensteiner *et al*. 2004, Matheny *et al*. 2006, Garnica *et al*. 2007, Binder *et al*. 2010, Zhao *et al*. 2017). In addition, genus *Volvariella* was found to be related to *Pluteus* in most previous phylogenies of order *Agaricales*, forming the so-called Pluteoid clade, loosely characterized by the presence of hymenial cystidia and salmon pink to reddish brown spores with complex spore walls (Matheny *et al*. 2006). Suborder *Pluteineae* (type *Pluteaceae*) was created by Dentinger *et al*. (2016) for the families *Pluteaceae* and *Amanitaceae* after observing a significant similarity between 208 genes of one species of *Volvariella* and two *Amanitaceae*.

TRICHOLOMATINEAE

Clitocybaceae

Matheny *et al*. (2006), Binder *et al*. (2010), Vizzini *et al*. (2011d), Vizzini & Ercole (2012), Raj *et al*. (2019), and Olariaga *et al*. (2020) recovered significant support for a monophyletic origin of *Clitocybe*, *Collybia sensu stricto* and *Lepista*, and Alvarado *et al*. (2015, 2018a, b), Sánchez-García *et al*. (2016), Sesli *et al*. (2016), Sánchez-García & Matheny (2017), Vizzini *et al*. (2020a), Mou & Bau (2021), He & Yang (2022) and He *et al*. (2023) found also that genus *Singerocybe* is nested inside it. Similar results were obtained for *Leucocalocybe* (Yu *et al*. 2011, Sánchez-García *et al*. 2020), *Dendrocollybia* (Sánchez-García & Matheny 2017, Sánchez-García *et al*. 2020, Mou & Bau 2021, He & Yang 2022, He *et al*. 2023), as well as *Lepistella* and *Paralepistopsis* (Varga *et al*. 2019). In the present analyses, *Paralepistopsis* was not significantly similar to the other genera of *Clitocybaceae*, but its phylogenetic position should be confirmed with data from additional species other than the type and/or genomic data. While *Clitocybe sensu stricto* (type *C. nebularis*), *Lepista* and *Singerocybe* seem to represent independent clades within *Clitocybaceae*, the relationships between the other genera need to be re-examined with a more complete dataset. Unlike most other genera in *Clitocybaceae*, *Singerocybe* has a distinct epicutis presenting vesicles (Harmaja 1974b, Qin *et al*. 2014), evidencing that this feature can vary among the different lineages of the family (*i.e.*, *textura epidermoidea* in *Dendrocollybia*, Hughes *et al*. 2001). The position of *Clitocybe ditopa* in the present phylogeny suggests that this species could belong to a different genus too, in accordance with its own deviant morphological traits (subglobose spores < 4 µm long), but this issue will be treated in a different work. The phylogenetic placement of *Clitocybe sensu stricto* is also debatable, because the currently accepted lectotype species, *C. nebularis*, is not related to the bulk of muscarine-producing species, which are closer to *Collybia sensu stricto* (He *et al*. 2023). The status of other putatively related genera, *i.e.*, *Lepistella*, *Leucocalocybe*, *Pseudolyophyllum*, or *Rubeolarius*, needs to be specifically addressed too in order to propose an integral taxonomic solution for the family.

Lyophyllaceae

Binder *et al*. (2010) found multiple clitocyboid lineages sister to the main core clade of *Lyophyllaceae*, and Hofstetter *et al*. (2014) named them the “hemilyophylloid” clade, which included *Clitocybe candicans*, *C. connata*, *C. subditopoda*, and *Hypsizygus ulmarius*. *Hypsizygus ulmarius* and *C. connata* (as *Lyophyllum connatum*) are two species traditionally classified in tribe *Lyophylleae* (*e.g.*, Kühner & Romagnesi 1953, Moser 1978, Singer 1986) or family *Lyophyllaceae* (Bon 1999, Consiglio & Contu 2002, Kalamees 2004, Horak 2005) because they show siderophilous granulation in their basidia. However, these two species exhibit granules of the oligo-type (Clémençon 1978, 1986a, b, 2004) compared to those of the *Lyophyllaceae sensu stricto* which are of the macro-type. In *Ossicaulis*, which is part of the core *Lyophyllaceae* in several molecular analyses (*e.g.*, Hofstetter *et al*. 2014, Bellanger *et al*. 2015, Sánchez-García *et al*. 2020), granulation was reported to be absent by Singer (1947) but found by Hofstetter *et al*. (2014) as very small granules seen in phase contrast that can easily escape attention when observed in bright field microscopy. However, granules are absent from the basidia of other ‘hemilyophylloids’, such as *C. candicans* and *C. cf. subditopoda* (Hofstetter *et al*. 2014). Alvarado *et al*. (2015) proposed three new generic names for clitocyboid lineages inside the ‘hemilyophylloid’ clade: *Leucocybe* for *C. connata* and *C. candicans*, *Atractosporocybe* for *C. inornata*, and *Rhizocybe* for *C. vermicularis* and related taxa. Subsequently, other clitocyboid taxa lacking siderophilous basidia were shown to nest within this clade, namely *Tephroderma* (Musumeci & Contu 2014), and *Clitolyophyllum* (Sesli *et al*. 2016). Consequently, it must be accepted that *Lyophyllaceae sensu lato* includes both species with siderophilic granules (macro-type and oligo-type) and without them.

In the present work, two *incertae sedis* genera were confirmed to belong inside *Lyophyllaceae sensu lato* (but outside *Lyophyllaceae sensu stricto*, therefore ‘hemilyophylloids’), *Omphaliaster* and *Trichocybe*, after the analysis of rDNA and protein-coding genes. *Omphaliaster borealis* (type of the genus) is a species with a troubled systematic history. Originally described as *Omphalia asterospora* (Lange 1930), it was then combined in *Clitocybe* (Moser 1953), *Hygroaster* (Singer 1962b), *Rhodocybe* (Lange & Sivertsen 1966), *Omphaliaster* (Lamoure 1971), *Omphalina* (Kühner 1980), and *Austroclitocybe* (Raithelhuber 1983). *Omphaliaster borealis* was found to form, together with *Dendrocollybia racemosa*, a clade sister to a clade consisting of *Collybia*-*Clitocybe* group and *Lyophylleae* group by Moncalvo *et al*. (2002). Yu *et al*. (2011) recovered it as *incertae sedis* in *Tricholomatineae* and Sánchez-García *et al*. (2020) as part of a clade including also *Clitocybe subditopoda*, *Hypsizygus*, *Tephroderma*, *Clitolyophyllum*, *Clitocybe* sp. and *Leucocybe*. The genus *Omphaliaster*, which contains six species so far (Agerer 2018), is characterized by basidiomes omphalinoid, no clamp connections, pileipellis a cutis with encrusting pigments, no hymenial cystidia, basidia non-siderophilic, basidiospores subglobose, warty, or with a few conical projections (bumped), inamyloid, acyanophilous, colourless, spore deposit white, terricolous, saprotrophic (Lamoure 1971, Einhellinger 1977, Kuyper 1995e, Bon 1997, Bresinsky 2008, Vašutová *et al*. 2013). Because of its ornamented but non-amyloid basidiospores *Omphaliaster* was included together with *Gamundia* within *Tricholomataceae*, subfamily *Clitocyboideae*, tribe *Omphalineae*, subtribe *Heterosporulae* by Bon (1997). The monospecific genus *Trichocybe* was erected by Vizzini *et al*. (2010) to include the peculiar species *Clitocybe puberula* (type of *Clitocybe* sect. *Puberulae*). It is distinguished by habit clitocyboid, pileipellis a plagiotrichoderm, basidiospores inamyloid, acyanophilous, basidia non-siderophilic, clamp connections present, hymenial cystidia present, lignicolous, saprotrophic, and growth in spring (Kuyper 1983, Vizzini *et al*. 2010, Ferisin *et al*. 2021). Considered as an *incertae sedis* genus (Vizzini *et al*. 2010, Qin *et al*. 2014, He *et al*. 2019, Kalichman *et al*. 2020), the present analysis indicated it as part of the hemilyophylloid clade (Fig. 3). Finally, multigene data obtained from specimen GB:0065321 of *Lyophyllum turcicum* suggest that this species is not related to *Lyophyllaceae sensu stricto*, but to *Asproinocybe*, *Tricholosporum* and *Omphaliaster*, and might need to be combined into a different genus. On the other hand, specimen GB:0065321 was originally identified as *Lyophyllum putidum* (= *Tephrocybe putida*) by the collectors, so a putative synonymy between both epithets should be explored too.

Asproinocybaceae

The family *Asproinocybaceae* was established by Mou & Bau (2021) to accommodate the genera *Asproinocybe* (typified with *A. lactifera*) and *Tricholosporum* (typified with *T. goniospermum*). *Asproinocybe* has irregularly turberculate to stellate spores and laticiferous hyphae, while *Tricholosporum* has cruciform to stauriform spores and lacks laticiferous hyphae (Singer 1986, Guzmán *et al*. 1990, 2004, Roux *et al*. 2000, Angelini *et al*. 2014, Lebel *et al*. 2020). Both genera have tricholomatoid basidiomes with distinctive purplish, violaceous, or lilac-vinaceous tinges, and non siderophilous basidia (Angelini *et al*. 2014). *Asproinocybe* was recently reported to be an ectomycorrhizal genus (Kumar & Atri 2021). Historically, Singer (1986) placed *Asproinocybe* as an independent genus in tribe *Tricholomateae* of *Tricholomataceae* (a decision later followed by Guzmán *et al*. 1990, 2004, Angelini *et al*. 2014, Xu *et al*. 2018, Lebel *et al*. 2020), but considered *Tricholosporum* a later synonym of *Tricholoma*, placing *T. goniospermum* and allied species in *Tricholoma* section *Iorigida*. This view was followed by some authors such as Bohus (1982, 1985), Bon (1984, 1991), Alessio (1986), Hongo (1988), and Bon & Braiotta (1989), but more recently other authors considered *Tricholosporum* an independent genus (Baroni 1982, Halling & Franco Molano 1996, Reid *et al*. 1998, Bohus *et al*. 1999, Contu & Mua 2000, Boisselet & Moreau 2008, Riva 2008, Fernandez Vicente *et al*. 2010, Christensen & Heilmann-Clausen 2013, Angelini *et al*. 2014, Lebel *et al*. 2020).

The classification of *Tricholosporum* and *Asproinocybe* seemed doubtful after independent analyses using ITS and LSU data linked these genera to different families of *Tricholomatineae* (Heaton & Kropp 2013, Liu *et al*. 2016, Sánchez-García & Matheny 2017, Lebel *et al*. 2020, Ralaiveloarisoa *et al*. 2020, Sánchez-García *et al*. 2020). Using information from ITS, LSU, SSU and *RPB2*, *T. goniospermum* appeared loosely related to several families of the Tricholomatoid clade (Angelini *et al*. 2017). Mou & Bau (2021) conducted an analysis using sequences of ITS, LSU, SSU, *RPB1*, *RPB2* and *TEF1*, and concluded that *Asproinocybe* and *Tricholosporum* formed an independent clade sister to *Callistosporiaceae*, for which they established the new family *Asproinocybaceae*. A similar result was later obtained by He & Yang (2022) and He *et al.* (2023). However, these works did not include a truly representative sample of the biodiversity of *Lyophyllaceae sensu lato*, missing many lineages of the Hemilyophylloid group. In the present analysis multigene sequences of two such species, '*Lyophyllum*' *turcicum* and *Omphaliaster borealis*, were added, showing that *Asproinocybaceae* is not significantly different from *Lyophyllaceae*. These two species were selected among many others in the Hemilyophylloid clade sequenced by the present authors (unpublished data) to clarify the position of *Asproinocybaceae*.

Asproinocybe and *Tricholosporum* share many features with the rest of *Lyophyllaceae*, such as a tricholomatoid habit, veils absent; lamellae adnate, adnexed, sinuate, emarginate to decurrent; spore deposit white, spores thin-walled, cyanophilous or acyanophilous; hymenophoral trama regular; and pileipellis arranged as a cutis. All species of *Asproinocybe* and *Tricholosporum* present purplish, violaceous, or lilac-vinaceous tinges, a coloration present also in some species of *Calocybe* (*e.g.*, *C. onychina*, *C. favrei* or *C. hypoxantha*). Also, most species in the Hemilyophylloid clade have non siderophilic basidia, similar to those of *Asproinocybaceae* (Lamoure 1971, Vašutová *et al*. 2013). Finally, inequilateral (asymmetrically rhomboidal, triangular…), goniosporous, or bumped basidiospores similar to those of *Asproinocybe* and *Tricholosporum* are also present in several species of *Calocybella*, *Gerhardtia*, *Lyophyllum*, and *Sagaranella* (Hongo & Clémençon 1983, Clémençon 1986b, Hofstetter *et al*. 2002, 2014, Mešić & Tkalčec 2009, Vizzini *et al*. 2015, 2017, Li *et al*. 2017, Endo *et al*. 2019, 2022, Latha *et al*. 2020, Mu *et al*. 2021, Wei *et al*. 2023). Other families containing both genera with inequilateral or bumped basidiospores and genera with smooth and regular spores are known in *Agaricales*, *e.g.*, *Tetrapyrgos* in *Marasmiaceae* (Horak 1983, Honan *et al*. 2015, Desjardin *et al*. 2017, Komura *et al*. 2020), *Rhodotus* in *Physalacriaceae* (Moncalvo *et al*. 2000, 2002, Tang *et al*. 2014), *Mycenella* in *Cyphellaceae* (Boekhout 1985, 1999b, Komorowska 2005, Malysheva & Morozova 2005, Vizzini *et al*. 2022), *Inocybe sensu stricto* in *Crepidotaceae*-*Inocybaceae* (Horak 1979b, 1987, Matheny *et al*. 2020b), *Clavaria* in *Clavariaceae* (Petersen 1988, Geesink & Bas 1992, Kautmanová *et al*. 2012a, b, Olariaga *et al*. 2015, Franchi & Marchetti 2021), and *Catatrama* in *Amanitaceae* (Franco-Molano 1991, Cui *et al*. 2018, Yang *et al*. 2018). Historically, Kühner & Romagnesi (1953) had already underlined morphological affinities between *Tricholoma goniospermum* and *Lyophyllum sensu lato*, and invalidly transferred *Tricholoma cossonianum* to *Lyophyllum* (*nom. inval.*, Art. 41.5, Shenzhen), a species described from Algeria with lilac lamellae and subtriangular basidiospores (Maire 1926), based on a doubtful presence of siderophilic granules inside the basidia. Later, Moreau & Contu (2007), after studying the type and recent collections of *Tricholoma cossonianum*, and finding them devoid of siderophilic basidia, combined it in *Tricholosporum*. The rDNA sequences (ITS: MW367842, MW367843; LSU: MW367863) of two *Tricholoma cossonianum* collections from Sardinia and Tuscany recently deposited in GenBank (Puddu *et al*., unpubl. data) seem to confirm this decision.

Macrocystidiaceae

Since its creation, the classification of the genus *Macrocystidia* has long been debated. Singer (1951, 1962, 1964) first placed *Macrocystidia* in the family *Tricholomataceae*, tribe *Marasmieae*, subtribe *Macrocystidiinae*, close to *Flammulina*, but he later moved it to *Tricholomataceae* tribe *Clitocybeae* (Singer 1975) or *Tricholomataceae* tribe *Tricholomateae*, subtribe *Omphalineae*, close to *Lactocollybia* (Singer 1970, 1986). Kühner (1979a) established the independent family *Macrocystidiaceae* because of the peculiar features of the genus, and later, due to the pink spore deposit, included it within his concept of order *Pluteales* (corresponding to the '*Hyporhodiales*' in Romagnesi 1992), representing an evolutionary link between the *Pluteaceae* and *Rhodophyllaceae* (now *Entolomataceae*), because of the similar spore structure as in *Pluteus* and same hymenophoral trama as in the *Rhodophyllaceae* (Kühner 1980, 1984). Kühner (1980, 1984) predicted also a closer phylogenetic relationship between *Macrocystidiaceae* and *Pluteaceae* based on their similar features (almost free lamellae, pinkish spore deposit and smooth complex cyanophilous spore walls) but distinguished the former by the non-inverse hymenophoral trama. While some authors accepted the status of *Macrocystidiaceae* (*i.e.*, Jülich 1981, Knudsen 2008b, 2012b), Bas (1988a, b) highlighted the similarities in pileipellis structure and cystidia between *Macrocystidia* and *Flammulina*, suggesting that *Macrocystidia* belongs in *Tricholomataceae*, and more specifically inside *Tricholomataceae* tribe *Macrocystidieae* (Bas 1990, Noordeloos 1995a). Finally, other authors (Agerer 2018) included *Macrocystidia* inside *Marasmiaceae*. Most molecular works including *Macrocystidia* were not able to resolve its phylogenetic position within *Agaricales* (Moncalvo *et al*. 2002, Matheny *et al*. 2006), probably due to the lack of sequences from protein-coding genes. Walther *et al*. (2005) found a significant relationship with *Ripartites*, and more recently, Sánchez-García *et al*. (2020) found *Macrocystidia* nested in a clade consisting of *Ripartites* and *Paralepista*. In the phylogenomic works by Dentinger *et al*. (2016), Varga *et al*. (2019) and Wang *et al*. (2023b), *Macrocystidia* was found to be related to the remaining families of *Tricholomatineae*. In the present work, this hypothesis is supported, and *Pseudoclitopilus* is accepted as a member of *Macrocystidiaceae*, although additional information probably needs to be analyzed to confirm this conclusion.

Omphalinaceae

The genus *Infundibulicybe* was proposed by Harmaja (2003) for *Clitocybe gibba* and allied species because of their morphological differences with genus *Clitocybe sensu stricto*. *Infundibulicybe* did not show significant phylogenetic similarities with any lineage of the order *Agaricales* analyzed in the phylogeny of Matheny *et al*. (2006), but later Binder *et al*. (2010) provided the first evidence supporting that *Infundibulicybe* belongs in the Tricholomatoid clade (suborder *Tricholomatineae*), where it sometimes clustered with *Pseudoclitocybe* and/or *Omphalina sensu stricto* (Lutzoni 1997, Lutzoni & Pagel 1997, Moncalvo *et al*. 2000, 2002, Binder *et al*. 2010, Vizzini *et al*. 2010, 2011a, 2012a, Yu *et al*. 2011, Vizzini & Ercole 2012, Vizzini *et al*. 2012c, Sánchez-García *et al*. 2016, Sánchez-García & Matheny 2017, Olariaga *et al*. 2020, He & Yang 2022), as well as some species of *Rimbachia* (Varga *et al*. 2019, Sánchez-García *et al*. 2020), and *Macrocystidia* (Dentinger *et al*. 2016). The present analysis supports a close relationship between *Infundibulicybe* and *Omphalina sensu stricto*, suggesting that *Infundibulicybe* should be classified inside the family *Omphalinaceae*. Both *Infundibulicybe* and *Omphalina* display cream-reddish brown tinges in their pileus and stipe, and develop long-decurrent lamellae, lacrymoid spores, a similar hymenophoral trama (first subregular, then irregular to interwoven), and strongly encrusting pigment (Harmaja 2003, Elborne 2008, 2012, Vesterholt 2008d, 2012c, Vizzini *et al*. 2011c, 2012c). *Omphalinaceae* probably also contains some species of *Rimbachia* (*i.e*., *R. bryophila*, Sánchez-García *et al*. 2020; *R. arachnoidea*, Gaya *et al*. unpubl. pers. comm.), a hypothesis apparently confirmed by unpublished results of the present authors. However, the taxonomic status of *Rimbachia sensu stricto* needs to be addressed before drawing conclusions, as other species of this genus seem related to *Hygrophorineae* (*i.e*., *R. neckerae*, Varga *et al*. 2019). DNA sequences from the type, *R. paradoxa*, would be necessary to this end.

Paralepistaceae

The traditional concept of genus *Lepista*, *viz*. clitocyboid fungi with lamellae usually detachable from the context, a white to pinkish yellow spore deposit, and inamyloid cyanophilous ornamented (verruculose to spiny) basidiospores (Singer 1986, Bon 1997, Consiglio & Contu 2003) was first shown to be polyphyletic by Vizzini & Ercole (2012). Species of *Lepista* subg. *Paralepista* (= *Lepista* sect. *Gilva*, = *Lepista* sect. *Inversae*), a group typified with *L. inversa*, were found to be unrelated to *Lepista sensu stricto* (lectotype *Lepista densifolia*) and all other taxa in the *Tricholomatineae* by Vizzini & Ercole (2012), and consequently, the genus name *Paralepista* (Raithelhuber 1981) was accepted for *Lepista flaccida*, *L. gilva* and allies. These species show very crowded decurrent lamellae and whitish spore deposit with subglobose to largely ellipsoidal spores (Bigelow 1985, Bon 1997, Raithelhuber 2004). Later, Sánchez-García *et al*. (2016, 2020) indicated a close relationship (without significant statistical support) between *Paralepista* and *Ripartites*. The enigmatic genus *Ripartites*, typified with *R. tricholoma*, had also an uncertain systematic placement until the molecular works of Walther *et al*. (2005), where it seemed significantly related to the ochre-reddish spored species *Macrocystidia cucumis*, and Garnica *et al*. (2007) where it nested in a clade consisting of the white-spored *Catathelasma* and *Pseudoclitocybe*, as well as *Infundibulicybe*, *Fayodia* and *Leucocortinarius*. Later, a significant similarity between sequences of *Paralepista*, *Ripartites* and *Notholepista* was found by Sánchez-García & Matheny (2017) and He & Yang (2022). Sánchez-García *et al*. (2020) recovered a significant clade composed of *Ripartites*, *Macrocystidia* and *Paralepista*. The classification of *Notholepista* (typified with *N. subzonalis*), a genus resulting from the fragmentation of *Leucopaxillus sensu lato*, has been unclear since its creation (Vizzini *et al*. 2012a, Sánchez-García *et al*. 2014, 2016, Angelini *et al*. 2017, Alvarado *et al*. 2018a, b, Mou *et al*. 2021). In the present work, significant support was obtained in the Bayesian analysis (0.96 PP) (and subsignificant in the ML analysis, 54 % BP) for a clade consisting of *Notholepista*, *Paralepista* and *Ripartites*.

Pseudoclitocybaceae

In the present work, *Aspropaxillus* is classified in the family *Pseudoclitocybaceae* based on results from a phylogenetic analysis of rDNA and protein-coding genes (Fig. 3). This result agrees with the phylogeny inferred from rDNA data alone published by He & Yang (2022). The classification of *Aspropaxillus* has been uncertain since its creation by Kühner & Maire (1934). Singer & Smith (1943) reduced it to a section of *Leucopaxillus*, while Kühner (1979b, 1980) considered *Aspropaxillus* (including also *Pseudoclitocybe* and *Pseudoomphalina*) a subgenus of *Clitocybe*, as previously proposed by Konrad & Maublanc (1936). Bigelow (1982) made it a subsection within his very broad concept of genus *Clitocybe*, and finally Bon (1990c, 1991) combined *Aspropaxillus* again as a subgenus of *Leucopaxillus*. However, based on its deviant ITS and LSU rDNA sequences, *Aspropaxillus* was resurrected by Vizzini *et al*. (2012a) as an independent *incertae sedis* genus within the Tricholomatoid clade (suborder *Tricholomatineae*). In the ITS analysis published by these latter authors, *Aspropaxillus* was sister (PP = 0.95; BP = 67 %) to *Pogonoloma*, and both genera were related to a clade formed by *Pseudoclitocybe* and *Musumecia*. This decision was later confirmed by Sánchez-García *et al*. (2014) and Angelini *et al*. (2017). The multigene analyses by Sánchez-García *et al*. (2016, 2020), Sánchez-García & Matheny (2017), Raj *et al*. (2019) and He & Yang (2022) also retrieved a significant relationship between *Aspropaxillus*, *Pogonoloma* and *Pseudoclitocybe* (the type of family *Pseudoclitocybaceae*, Alvarado *et al*. 2018a). The present analyses confirm these results with additional data coming from non-ribosomal genes.

TYPHULINEAE

The first phylogenetic inferences on *Typhulaceae* made by Dentinger & McLaughlin (2006), Matheny *et al*. (2006), Binder *et al*. (2010), and Lodge *et al*. (2014) were mainly based on *Typhula phacorrhiza* which is now considered a species of *Macrotyphula* (family *Phyllotopsidaceae*, Olariaga *et al*. 2020). *Macrotyphula* (type *M. fistulosa*) differs from *Typhula* (type *Typhula incarnata*, Olariaga *et al*. 2020, 2022) in having large, yellow-brown long clavarioid basidiomata (30–300 mm) that never arise from sclerotia, and non-amyloid spores (Petersen 1972, 1988, Berthier 1976, Jülich 1984). Olariaga & Salcedo (2012) first reduced *Macrotyphula* to a later synonym of *Typhula* based on morphological data, but it was later shown (Olariaga *et al*. 2020) to represent an independent lineage nested inside the family *Phyllotopsidaceae*, which the authors classified inside the suborder *Pleurotineae*. However, Wang *et al*. (2023b) showed that they are not related and erected the suborder *Phyllotopsidineae* for the former. In the present work, this result is confirmed including additional lineages of *Pleurotineae* (*Hohenbuehelia*, *Resupinatus*) and *Phyllotopsidineae* (*Aphroditeolaceae*), and a more complete sampling of the other suborders of *Agaricales*. The family *Typhulaceae* consistently formed an independent clade, apparently basal to all other suborders (except *Clavariineae*), that is here accommodated in the new suborder *Typhulineae*.

CONCLUDING REMARKS

The taxonomic decisions taken in the present work are mainly the result of Bayesian analysis of an updated dataset built to fill important gaps in the diversity of *Agaricales* observed in previous works. The new arrangement at suborder level differs in some ways from those based on phylogenomic studies of this group, and, ultimately, genomic data of the newly sequenced lineages would be necessary to test the present hypotheses. The status of some important missing lineages (*i.e*., the clades of *Henningsomyces* and *Rectipilus*) still needs to be addressed, as they might represent new families or even new suborders. Also, some lineages of clitocyboid and tricholomatoid fungi inside *Tricholomatineae* are still considered *incertae sedis* (*i.e*., *Hertzogia*, *Paralepistopsis*), and therefore need more research to be satisfactorily classified.

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DECLARATION ON CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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Fig. S1. Bayesian inference phylogram built with nucleotide sequence data of six loci (5.8S, LSU, SSU, *RPB1*, *RPB2* and *TEF1*) of the main lineages inside order *Agaricales* (including taxa of the suborder *Clavariineae*), rooted with *Suillus pictus* (*Boletales*), *Amylocorticium cebennense* and *Ceraceomyces borealis* (*Amylocorticiales*) as outgroups. The main suborders are shown in color boxes, while family names are shown next to vertical bars. Nodes were annotated with Bayesian PP (left) and ML BP (right) values, with the significance threshold considered as Bayesian PP >0.95 and/or ML BP >70 %. Subsignificant support values were annotated in parentheses. Boldface names represent samples sequenced for this study. The dashed branch was shortened for graphic presentation.

Fig. S2. Bayesian inference phylogram built with nucleotide sequence data of six loci (5.8S, LSU, SSU, *RPB1*, *RPB2* and *TEF1*) of the main lineages inside order *Agaricales* (including taxa of *Cyphellopsidaceae*), rooted with *Suillus pictus* (*Boletales*), *Amylocorticium cebennense* and *Ceraceomyces borealis* (*Amylocorticiales*) as outgroups. The main suborders are shown in color boxes, while family names are shown next to vertical bars. Nodes were annotated with Bayesian PP (left) and ML BP (right) values, with the significance threshold considered as Bayesian PP >0.95 and/or ML BP >70 %. Subsignificant support values were annotated in parentheses. Boldface names represent samples sequenced for this study. The dashed branch was shortened for graphic presentation.

Table S1. Data of the collections used for phylogenetic analyses and/or morphological studies with details of their host, location, collector, and GenBank accessions numbers.