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Taxonomic revision and examination of ecological transitions of the Lyophyllaceae (Basidiomycota, Agaricales) based on a multigene phylogeny

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Abstract – We explored evolutionary relationships within the Lyophyllaceae by combining sequence data from six loci. The most likely phylogram led us to reconsider the Lyophyllaceae classification with the recognition of two new genera (*Myochromella* and *Sagaranella*) based on ecological and/or morphological distinctiveness. Lyophyllaceae are ecologically highly diversified and our phylogeny suggests that four to five ecological transitions from free-living to parasitic or mutualistic lifestyles have occurred within the family. Due to moderate phylogenetic support recovered for several relationships within that clade and due to the uncertainty about the ecological strategy adopted by five of the sampled species, three out of these transitions could be unequivocally reconstructed suggesting that saprotrophy is plesiomorphic for Lyophyllaceae. Significant differences in rates of molecular evolution were detected among taxa. These differences are not associated with ecological transitions throughout the Lyophyllaceae, however, within each of the major clades identified in the family, taxa of different ecological strategies show an overall tendency to evolve at different speeds at the molecular level.

Bayesian / maximum likelihood / molecular clock / molecular systematics / multigene (ITS / nucLSU / mitSSU / *RPB*1 / *RPB*2 / *TEF1-α*) / relative rate tests

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# Equal contribution

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INTRODUCTION

The family Lyophyllaceae Jülich (Agaricales, Basidiomycota), or the tribe Lyophylleae Kühner, is part of the Tricholomatoid clade *sensu* Matheny *et al.* (2006), the latter being a group assembling white to cream and pink-spored agarics. The Lyophyllaceae include species commonly referred to the following genera: *Asterophora* Ditmar ex Link (= *Nyctalis* Fr.), *Calocybe* Kühner ex Donk, *Hypsizygus* Singer, *Lyophyllum* P. Karst., *Podabrella* Singer, *Tephrocybe* Donk, *Ossicaulis* Redhead and Ginns, *Gerhardtia* M. Bon (= subgenus *Lyophyllopsis* Gerhardt), *Clitocybe* p. p. and *Termitomyces* R. Heim (Hofstetter *et al.,* 2002; Moncalvo *et al.,* 2002; Matheny *et al.,* 2006; Sánchez-García *et al.,* 2014). All of these genera, with the exception of *Ossicaulis* and most of *Clitocybe,* have been characterized by the presence of siderophilous granule-filled basidia (Clémençon 1974, 1978, 1984, 1986, 1997; Kühner 1938; Singer 1986; Hofstetter *et al.*, 2002).

Clémençon (1986) defined various types of siderophilous granulation within Agaricales. The macro-type of siderophilous granulation is restricted to Lyophyllaceae *sensu* Matheny *et al.* (2006). However, some species classified in this family exhibit an oligo-type of granulation: *Hypsizygus ulmarius* (Bull.: Fr.) Redhead (= *Lyophyllum ulmarium* [Bull.: Fr.] Kühner) and *Clitocybe connata* variously treated in the literature as *C. connata* (Schum.: Fr.) Gillet or *Lyophyllum* (*L. connatum* (Schum.: Fr.) Singer) and recently segregated as *Leucocybe* (Alvarado *et al*., in press). Some doubts were raised as to the monophyly of the Lyophylleae *sensu* Singer (1986), in which were included *Hypsizygus* and *Clitocybe connata*, as was the monophyly of the residual Lyophyllaceae if the Termitomycetaceae were to be excluded. Moncalvo *et al.* (2002) built a single locus (nucLSU) phylogeny for Agaricales with representatives of Lyophyllaceae. Using multiple genes (nLSU, mtSSU and ITS), Hofstetter *et al.*, (2002) analyzed species that were representative of all genera in the Lyophylleae, including some members of the closely related families Tricholomataceae and Entolomataceae along with several outgroups. The combined results of both studies shed new light on the taxonomic relationships in and around the Lyophyllaceae *sensu auct*. However, the weak phylogenetic support recovered in both studies for basal relationships prevented the authors from proposing a new classification for Lyophyllaceae. Three more recent phylogenetic studies added support to the monophyly of Lyophyllaceae (Baroni *et al.*, 2011; Matheny *et al.*, 2006; Sánchez-García *et al.*, 2014). However, Matheny *et al.* (2006) recovered a sister relationship between Lyophyllaceae and Entolomataceae, whereas Baroni *et al.* (2011) recovered a sister relationship of Lyophyllaceae with *Entoloma s.l.* and a paraphyletic Entolomataceae. Recently, Sánchez-García *et al.* (2014) recovered the Lyophyllaceae basal to Tricholomataceae *sensu stricto* and Entolomataceae. Yet, none of these three studies recovered significant support for these basal relationships. Consequently relationships between Lyophyllaceae, Tricholomataceae and Entolomataceae remain unclear.

The use of some morphological characters to define the different sections of the genus *Lyophyllum* is now debated because of the discovery of new species (*i.e.* Colucci and Galli, 2010; Contu *et al.*, 2011; Dähncke *et al.*, 2010; Dähncke *et al.*, 2011; Vizzini and Contu, 2010). As shown by Hofstetter *et al.* (2002), the original generic type of *Lyophyllum*, *L. leucophaeatum* (P. Karst.) P. Karst., was more closely related to *Calocybe sensu lato* (incl. the generic type, *C. gambosa* (Fr.: Fr.) Donk), than to other "*Lyophyllum*". The generic name, *Lyophyllum* was consequently maintained with a conserved type, *L. semitale* (Redhead *et al.,* 2006)

whereas *L. leucophaeatum* was placed in *Calocybe* as *Calocybe gangraenosa* (Fr.) Hofstetter, Moncalvo, Redhead and Vilgalys (Redhead, 2012).

The Lyophyllaceae are ecologically highly diversified. This family contains the ectomycorrhizal species *L. shimeji* (Kawam.) Hongo and *L. decastes* (Fr.) Singer, which are part of the *Lyophyllum decastes* species complex (Agerer and Beenken, 1998; De Roman *et al.*, 2005; Larsson and Sundberg, 2011; Moncalvo, 1991; Moncalvo *et al.*, 1993; Ohta, 1994a,b; Pera and Alvarez 1995; Saito and Tanaka, 1999; Visnovsky *et al.*, 2014; Yamada *et al.*, 2001a,b). *Hypsizygus* and *Ossicaulis* decay wood on living trees (Singer, 1986; Holec and Kolarík, 2013; Redhead and Ginns, 1985) and might be considered either saprotrophs or parasites since it is not clearly assessed if they decompose wood that is already dead or not. *Tephrocybe palustris* is a necroparasite on *Sphagnum* (Limpens *et al.*, 2003; Redhead, 1981; Untiedt and Mueller, 1985) that causes host protoplast degeneration (Davey and Currah, 2006; Limpens *et al.*, 2003; Redhead, 1981; Untiedt and Mueller, 1985). *Asterophora* is parasitic on other mushrooms (Redhead and Seifert, 2001; Singer, 1986). The family also includes several nitrophilic species such as *Tephrocybe tylicolor*, *T. gibberosa* and *Tricholomella constricta* (Hofstetter *et al.*, 2002). The genus *Termitomyces*, which is nested within the Lyophyllaceae (Hofstetter *et al.*, 2002; Moncalvo *et al.*, 2002; Matheny *et al.,* 2006; Sánchez-García *et al.*, 2014), is a group of insect-associated fungi cultivated by termites (Aanen *et al.*, 2002; Guldberg-Frøslev *et al.*, 2003; Heim, 1977; Rouland-Lefèvre *et al.*, 2002, Wei *et al.*, 2006). The other species of Lyophyllaceae are all saprotrophic according to Singer (1986).

The high frequency of fungal symbioses in nature such as mycorrhizal associations with plants roots (Hibbett *et al.*, 2002; Matheny *et al.*, 2006, Moncalvo *et al.*, 2002; Pirozynski and Malloch, 1975; Redecker *et al.*, 2000; Tedersoo *et al.*, 2010) or mutualistic relationships with algae and cyanobactaeria resulting in lichenization (Miadlikovska *et al.*, 2006; Lutzoni *et al.*, 2001; Schoch *et al.*, 2009; Spatafora *et al.*, 2006) suggest that mutualism is a successful evolutionary mechanism (Hawksworth, 2001; James *et al.*, 2006). The clustering of mushroom-forming fungi with similar ecological strategies in specific taxonomic groups strongly indicates that ecological traits are evolutionary relatively stable, and are often better indicators of natural relationships than morphology (Moncalvo *et al.*, 2002, Matheny *et al.*, 2006). However, with few exceptions (*e.g.* Heim, 1977; Hughes *et al.*, 2001; Redhead and Ginns, 1985; Redhead *et al.*, 1994, 2002a,b; Thorn *et al.*, 2000), little attention has been given to the ecology for the classification of fungi in general (Peay, 2014) except for its descriptive aspects (Ahmadjian, 1993; Hale, 1983; Hawksworth, 1984; Kühner, 1980; Singer, 1986). Part of the inherent difficulty in studying ecological shifts in fungi lays in the lack of direct empirical investigation of the transitional processes from saprotrophy to parasitism or mutualism and reversals. To date, such investigations have mainly focused on high systematic ranks (James *et al.*, 2006; Hibbett *et al*., 2000; Lutzoni *et al.*, 2001; Matheny *et al.*, 2006; Miadlikovska *et al.*, 2006; Schoch *et al.*, 2009). Wolfe *et al*. (2012) investigated the transition from saprotrophy to ectomycorrhiza in the family Amanitaceae (recognized as two genera by some, *Amanita sensu stricto* [ectomycorrhizal] versus *Aspidella* E.-J. Gilbert [saprotrophic], Vizzini *et al.*, 2012) and suggested that such transition was accompanied by partial or complete loss of the ability to degrade cellulose and therefore likely to be irreversible. Including four of the major ecological types found in the Basidiomycota (ectomycorrhizae, insect-associated mutualists, parasites and saprobes), the Lyophyllaceae-Tricholomataceae-Entolomataceae clade provides therefore a good model to study transitions between major ecological strategies adopted by more terminal ranks in the Basidiomycota.

This study revises the systematics of the Lyophyllaceae Jülich 1981 (Agaricales, Basidiomycota), or Lyophylleae *sensu* Singer (1986), and of the genus *Lyophyllum* P. Karst. using a molecular approach. Here we combine sequence data produced by Hofstetter *et al.* (2002) and Matheny *et al.* (2006, 2007), while expanding the taxonomic coverage of Lyophyllaceae with newly produced sequences. We generated sequences from six loci: parts of two subunits of the RNA polymerase II (largest subunit [*RPB*1] and second largest subunit [*RPB*2]), part of the transcription elongation factor 1-alpha (*TEF1-α*), part of the nuclear large subunit [nucLSU], part of the mitochondrial small subunit [mitSSU], and the internal transcribed spacers plus 5.8S [ITS]). The recovered phylogeny was used to infer the relationships within the Lyophyllaceae and to determine how many ecological transitions did occur during the evolution of this family. We also tested for molecular clock and for equality of evolutionary rates to determine which lifestyles, if any, were associated with a change in evolutionary speed at the molecular level (Lutzoni and Pagel, 1997).

MATERIAL AND METHODS

Taxon sampling and molecular data – We sampled 51 species in the "Tricholomatoid" clade *sensu* Matheny *et al.* (2006) (Table 1) including 30 Lyophyllaceae that covered all of the segregate genera, subgenera and sections of this family (Jülich, 1981; Bon, 1999; Courtecuisse and Duhem, 1995; Kühner and Romagnesi, 1978; Moser, 1978; Singer, 1986) and *Ossicaulis lachnopus* (*Ossicaulis lignatilis* was nested in the "lyophylloid" clade in Moncalvo *et al.* (2002) and in the Lyophyllaceae in Sánchez-García *et al.* (2014), eight species of Tricholomataceae, *Clitocybe candicans* and *C. subditipoda* resolved at the base of the Entolomataceae-Lyophyllaceae clade, *Dendrocollybia racemosa* resolved at the base of the Tricholomataceae-Entolomataceae-Lyophyllaceae clade, and seven species of Entolomataceae. We sampled three outgroup species from the "*Catathelasma* clade" according to Matheny *et al.* (2006) being aware that this clade is not basal to Lyophyllaceae in Sánchez-García *et al.* (2014). We made this choice because the basal position of the "*Catathelasma* clade" toward the Lyophyllaceae-Entolomataceae-Tricholomataceae clade is supported in Matheny *et al.* (2006) while none of the basal relationships between these families are supported in Sánchez-García *et al.* (2014).

Nucleotide sequences of six loci (ITS, mitSSU, nucLSU, *RPB1*, *RPB2* and *TEF1-α*) for the 51 selected taxa were sampled from previous studies (Hofstetter *et al.*, 2002; Matheny *et al.*, 2006; Matheny *et al.*, 2007) or newly produced for this study. DNA was isolated from fresh or dried fruit bodies. New rDNA data were produced as described in Hofstetter *et al.* (2002). Parts of *RPB1* and *RPB2* genes were produced as described in Matheny *et al.* (2002) and Liu and Hall (2004). Primers and amplification of *TEF1-α* gene followed Morehouse *et al.* (2003). When amplification generated residual bands, PCR products were cloned using pSTBlue-1 AccepTor Vector™ Kit (Novagen). Sequencing used primers of the corresponding vector, reagents and conditions of the *BibDye®Terminator v3.1 Cycle sequencing Kit* and an automated capillary sequencer ABI 3700 DNA analyzer (Perkin Elmer, Applied Biosystems, Foster City, CA, USA). Sequences were assembled and edited using the software package Sequencher 3.0 (Gene Codes Corp., USA).

Table 1. Voucher table listing taxa with authorities, collection numbers, type of material used and corresponding sequence data with GenBank accession Numbers

Taxon[a]	*Coll. Nr.*[b]	*Coll. and DNA sources*[c]	*GenBank Accession Nos.*[d]					
			nucLSU	*mitSSU*	*ITSs*	*RPB1*	*RPB2*	*TEF1-α*
Family Lyophyllaceaeae								
Genus *Asterophora*								
A. lycoperdoides (Bull.) Ditmar 1809	CBS170.86	MAA	AF223190	AF357109	AF357037	EF421021	DQ367431	DQ367424
A. parasitica (Bull. ex Pers.) Singer 1951	CBS683.82	MAA	AF223191	AF357110	AF357038	EF421022	EF420988	EF421054
Genus *Calocybe*								
C. carnea (Bull.) Donk 1962	CBS552.50	CHA	AF223178	AF357097	AF357028	DQ825423	DQ367432	DQ367425
C. fallax (Sacc.) Redhead & Singer 1978	IE-BSG-HC80/103	CHA	AF223180	AF357099	AF357030	EF421023	EF420989	EF421055
C. favrei (R. Haller Aar. & R. Haller Suhr) Bon	IE-BSG-HC96cp4	Cpph	AF223184	AF357104	EF421102	EF421024	EF420990	EF421056
C. gangraenosa (Fr.) Hofstetter, Moncalvo, Redhead & Vilgalys 2012	IE-BSG-HAe251.97	Cpph	AF223202	AF357101	AF357032	DQ825419	DQ367434	DQ367427
C. ionides (Bull.) Donk 1962	IE-BSG-HC77/133	CHA	AF223179	AF357098	AF357029	EF421025	EF420991	EF421057
C. obscurissima (A. Pearson) M.M. Moser 1967	IE-BSG-HC79/181	CHA	AF223181	AF357100	AF357031	EF421026	EF420992	EF421058
C. persicolor (Fr.) Singer 1962	IE-BSG-HC80/99	CHA	AF223176	AF357095	AF357026	EF421027	EF420993	EF421059
Genus *Gerhardtia*								
Gerhardtia sp.	HC01/025	Cpph	EF421091	EF421093	EF421103	EF421028	EF420994	EF421060
Genus *Hypsizygus*								
H. ulmarius (Bull.) Redhead 1984	DUKE-JM/HW	DNA	AF042584	AF357140	EF421105	EF421030	EF420996	EF421062
Genus *Lyophyllum* *(Lyophyllum and Tephrocybe pro parte)*								
L. ambustum (Fr.) Singer 1953	CBS452.87	MAA	AF223216	AF357133	AF357057	EF421031	EF420997	EF421063
L. anthracophilum (Lasch) M. Lange & Sivertse n 1966	IE-BSG-HC79/132	MAA	AF223212	AF357132	AF357055	EF421032	EF420998	EF421064
L. atratum (Fr.) Singer 1953	CBS709.87	MAA	AF223210	AF357129	AF357053	EF421033	EF420999	EF421065
L. caerulescens Clémençon 1982	IE-BSG-HC80/140	MAA	AF223209	AF357128	AF357052	EF421034	EF421000	EF421066
L. decastes (Fr.) Singer 1951	IE-BSG-JM87/16	MAA	AF042583	AF357136	AF357059	DQ825418	DQ367433	DQ367426
L. semitale (Fr.) Kühner, 1978	IE-BSG-HC85/13	MAA	AF042581	AF357125	AF357049	EF421036	EF421002	EF421068
L. shimeji (Kawam.) Hongo 1915	JM-Hon/k	MAA	AF357078	AF357137	AF357060	EF421035	EF421001	EF421067
L. sykosporum Hongo & Clémençon 1983	IFO30978	MAA	AF223208	AF357126	AF357050	EF421037	EF421003	EF421069
Genus *Myochromella gen. nov.*								
M. inolens comb. nov. *= Tephrocybe boudieri Kühner & Romagn.) Derbsch 1977*	IE-BSG-BSI96/84	CHA	AF223204	AF357122	AF357047	DQ825421	DQ825411	EF421070
M. inolens comb. nov. *= Tephrocybe inolens (Fr.) M.M. Moser 1967*	CBS330.85	CHA	AF223201	AF357120	AF357045	EF421038	EF421004	EF421071
Genus *Ossicaulis*								
O. lachnopus(Fr.) Contu 2007	DUKE-D604(VT)	DNA	AF261397	EF421094	DQ825426	DQ825420	DQ825410	EF421072

Table 1. Voucher table listing taxa with authorities, collection numbers, type of material used and corresponding sequence data with GenBank accession Numbers *(continued)*

Taxon[a]	*Coll. Nr.*[b]	*Coll. and DNA sources*[c]	*GenBank Accession Nos.*[d]					
			nucLSU	*mitSSU*	*ITSs*	*RPB1*	*RPB2*	*TEF*1-α
Genus *Sagaranella gen. nov.*								
S. gibberosa comb. nov. = *Tephrocybe gibberosa (Jul. Schäff.) P.D. Orton 1969*	CBS328.50	MAA	AF223197	AF357115	AF357041	EF421039	EF421005	EF421073
S. tylicolor comb. nov. = *Tephrocybe tylicolor (Fr.) M.M. Moser 1978*	IE-BSG-BSI92/245	MAA	AF223195	AF357112	AF357040	EF421040	EF421006	EF421074
Genus *Sphagnurus*								
S. paluster (Peck) Redhead & Hofstetter 2014	CBS717.87	CHA	AF223200	AF357119	AF357044	EF421041	EF421007	EF421075
Genus *Tephrocybe*								
T. rancida (Fr.) Donk 1962	CBS204.47	CHA	AF223203	AF357094	AF357025	EF421042	EF421008	EF421076
Genus *Termitomyces*								
T. microcarpus (Berk. & Broome) R. Heim 1942	DUKE-PRU3900	Cpph	AF042578	AF357092	AF357023	EF421043	EF421009	EF421077
T. sp.	IE-BSG-BSIsp.1	MAA	AF223174	AF357093	AF357024	EF421044	EF421010	EF421078
Genus *Tricholomella*[e]								
T. constricta (Fr.) Zerova ex Kalamees 1992	IE-BSG-HC84/75	MAA	AF223188	AF357105	AF357036	DQ825422	DQ825412	EF421079
Family Tricholomataceae								
Genus *Clitocybe*								
C. candicans (Pers.) P. Kumm. 1871	AFTOL-ID 541	Unknown	AY645055	–	DQ202268	DQ447891	DQ385881	DQ408149
C. connata (Schumach.) Gillet 1874	DUKE-JM 90 c	DNA	AF042590	AF357139	EF421104	EF421029	EF420995	EF421061
C. dealbata (Sowerby) P. Kumm. 1871	IE-BSG-HC95.cp3	Cpph	AF223175	AF357138	AF357061	DQ825414	DQ825407	EF421080
C. nebularis (Batsch) P. Kumm. 1871	CBS362.65	MAA	AF223217	AF357142	AF357063	DQ825415	EF421011	EF421081
C. subditopoda Peck 1889	AFTOL-ID 533	Unknown	AY691889	–	DQ202269	DQ447892	AY780942	DQ408150
Genus *Collybia*								
C. tuberosa (Bull.) P. Kumm. 1871	DUKE- DAOM191061	DNA	AF261385	KP255470	AF274376	KP255479	KP255481	KP255474
Genus *Corneriella* Sánchez-García								
Corneriella sp.	DUKE-PR3995	DNA	AF261395	EF421095	EF421106	EF421046	EF421013	EF421083
Genus *Lepista*								
L. nuda (Bull.) Cooke 1871	DUKE-RV84/1	DNA	AF042624	AF357141	AF357062	EF421045	EF421012	EF421082
Genus *Tricholoma*								
T. myomyces (Pers.) J.E. Lange 1933	DUKE- KMS589	DNA	U76459	EF421096	DQ825428	DQ842013	DQ367436	DQ367429
T. portentosum (Fr.) Quél. 1873	DUKE- KMS591	DNA	U76464	AF357081	AF357015	EF421047	EF421014	EF421084
T. subaureum Ovrebo 1986	DUKE- KMS590	DNA	U76466	AF357082	AF357016	EF421048	EF421015	EF421085
Genus *Callistosporium*								
C. luteoolivaceum (Berk. & M.A. Curtis) Singer 1946	DUKE-JM99124	Cpph	AF261405	KP255473	AF325666	DQ825413	DQ825406	KP255477

Table 1. Voucher table listing taxa with authorities, collection numbers, type of material used and corresponding sequence data with GenBank accession Numbers *(continued)*

Taxon[a]	*Coll. Nr.*[b]	*Coll. and DNA sources*[c]	*GenBank Accession Nos.*[d]					
			nucLSU	*mitSSU*	*ITSs*	*RPB1*	*RPB2*	*TEF*1-α
Tricholomataceae of *incertae sedis*								
Genus *Catathelasma*								
C. imperiale (Quél.) Singer 1940	DUKE-DAOM225247	DNA	AF261402	KP255471	KP255468	KP255480	–	KP255475
C. ventricosum (Peck) Singer 1940	DUKE-DAOM221514	DNA	AF261401	–	KP255469	–	KP255482	–
Genus *Dendrocollybia*								
D. racemosa (Pers.) R.H. Petersen & Redhead 2001	DUKE-DEB5575	DNA	AF042598	KP255472	DQ825425	DQ825417	DQ825409	KP255476
Family Entolomataceae								
Genus *Clitopilus*								
C. prunulus (Scop.) P. Kumm. 1871	VHAs07/02	Cpph	EF421092	EF421097	EF421107	DQ825416	DQ825408	EF421086
Genus *Entoloma*								
E. undatum (Gillet) M.M. Moser 1978	TB7144	DNA	AF261315	EF421098	EF421108	EF421049	EF421016	EF421087
E. sericeum Quél. 1872	VHAs03/02	Cpph	DQ367423	EF421099	DQ367430	DQ825424	DQ367435	DQ367428
Genus *Nolanea*								
N. strictior (Peck) Pomerl 1980	DUKE-JM96/10	DNA	AF042620	EF421100	EF421109	EF421050	EF421017	EF421088
Genus *Rhodocybe*								
R. fallax (Quél.) Singer 1946	CBS129.63	CHA	AF223166	AF357083	AF357017	EF421051	EF421018	EF421089
R. truncata (Schaeff.) Singer 1946	CBS482/50	CHA	AF223167	AF357086	EF421110	EF421052	EF421019	KP255478
Genus *Trichopilus*								
T. porphyrophaeus (Fr.) P.D. Orton 1991	VHAs09/02/TB6957	Cpph	AF261290	EF421101	EF421111	EF421053	EF421020	EF421090

[a]We report the generic names currently in use (names authorities found in Mycobank http://www.mycobank.org/Biolomics.aspx?Table=Mycobank&Page=200&ViewMode=Basic)

[b]Collections sources: AFTOL: "Assembling the Fungal Tree of Life" consortium; CBS = Centraalbureau foor Schimmelcultures, Netherlands; DUKE = Duke; IE-BSG = Institut d'Ecologie-Botanique Systématique et Geobotanique, University of Lausanne, Switzerland; NY = New York Botanical Garden, USA; VHAs = collected in Asheville (NC) by Valérie Hofstetter; TB = collected by Tim Baroni.

[c]DNA source: Cpph = carpophores; MAA = mycelia grown on malt-asparagine-agar; CHA = mycelia grown on cherry-agar; DNA = aliquots of DNA stored at Duke University, NC, USA.

[d]Regions sequenced : nucLSU = nuclear ribosomal large subunit; mitSSU = mitochondrial ribosomal small subunit; ITS = internal transcribed spacers 1 and 2 and nuclear ribosomal 5.8S; RPB1 = subunit B220 of the DNA polymerase II, region A-C; RPB2 = subunit B150 of the DNA polymerase II, region 5-7; TEF1-*a* = transcription elongation factor 1-alpha.

Phylogenetic analyses – The 6-locus 51 taxa DNA sequence alignment was performed by eye using the editor of MacClade v.4.06 (Maddison and Maddison, 2003) and is accessible at the Treebase website (no 16735).

Topological incongruence was examined based on 500 bootstrap replicates conducted in RAxML-VI-HPC (RAxML-bs; Stamatakis, 2006) implementing a GTRMIX model with gamma distribution, approximated with four categories. RAxML bootstrap analyses were conducted on each locus separately. To screen for putative conflict we used the program compat.py (available at www.lutzonilab.net), which compares maximum likelihood (ML) bootstrap values (ML-BS) between analyses of the different loci. Topological conflict among phylogenetic trees was considered significant when conflicting branches had bootstrap proportions ≥ 75% (Mason-Gamer and Kellog, 1996).

The search for the most likely tree used 500 RAxML runs and the same settings as described for bootstrapping. Searches were implemented with two different partitions of the data: with 15 partitions (nucLSU, mitSSU, 5.8S, ITS1, ITS2, *RPB*1 [intron, 1st, 2nd, 3rd position] and *RPB*2 and *TEF*1-α [1st, 2nd, and 3rd position] or with 10 partitions (nucLSU, mitSSU, 5.8S, ITS1+ITS2, *RPB*1, *RPB*2 and *TEF*1-α (1st + 2nd, and 3rd position). Branch robustness was estimated based on 500 bootstrap replicates of RAxML implemented as described for combinability tests. Bayesian Metropolis coupled Markov chain Monte Carlo analyses (B-MCMCMC) as implemented in MrBayes V3.2.01 (Huelsenbeck and Ronquist, 2001) consisted of three independent runs to ensure stationary and convergence toward the same log-likelihood level. We sampled one of 500 trees during 20,000,000 generations and the last 20,000 trees sampled from each run were used to build the majority-rule consensus tree. Branch support was considered significant only if posterior probabilities (PP) were ≥ 0.95.

Ancestral state reconstruction (Pagel, 1999) was conducted on post burn-in trees sampled from the Bayesian analysis, using maximum likelihood or parsimony and the option Trace Character Over Trees in Mesquite version 1.0 (Maddison and Maddison, 2003). We considered four ecological character states: saprotrophic (= 0), ectomycorrhizal (= 1), insect-related (= 2) and parasitic (= 3). To assign ecological character states to the taxa we used as primary references De Roman *et al.* (2005), Hutchison (1992), Kalamees (2004), Larsson and Sundberg (2011), Redhead (1981) and Singer (1986) for Lyophyllaceae, Hutchison (1992) for *Catathelasma*, Kobayashi *et al.* (2003, 2005), Co-David *et al.* (2009) and Noordeloos (2004) for Entolomataceae. Finally we followed Hughes *et al.* (2001), Matheny *et al.* (2006), and Sánchez-García *et al.* (2014) for *Tricholomataceae*. Only character states unequivocally reconstructed on more than 95% of the sampled credible trees were considered. An ancestral state at a given node was considered significant if its likelihood value was higher by at least two log units than the likelihood value of the other ancestral state (likelihood threshold values set to two by default in Mesquite as suggested by Pagel at http:// sapc34. rdg.ac.uk/meade/Mark/files/ DiscreteManual.pdf).

Molecular clock and relative rate tests – Likelihood ratio tests (LTRs; $-2 \log L = 2[\log L_0 - \log L_1]$) for molecular clock behavior (Hasegawa *et al.*, 1985) was performed on the 6-locus 51 taxa dataset using the program PAUP v4.0b10 (Swofford, 2002). The most likely tree was scored under the null hypothesis (L_0: molecular clock) and alternative hypothesis (L_1: branches allowed to vary independently) implementing a GTR model, gamma distributed rate variation with 4 rate categories, and with all parameters estimated during searches. The significance of that test was approximated using a chi-square distribution with 2 degrees of freedom.

The program HyPhy (Kosakovsky and Muse, 2000) was used to test for equality of evolutionary rates in applying LRTs to all possible pair wise comparisons of the ingroup taxa under general reversible model and gamma shape parameter = 4. Rate heterogeneity has been shown to vary within and between genes (Bevan *et al.*, 2007). Also, when applied to short sequences, relative rate tests are very sensitive to type II error, and more reliable results are obtained from a combination of several loci (Bromham *et al.*, 2000; Rambaut and Bromham, 1998). We therefore tested for equality of evolutionary rates for each possible pair of species of the ingroup taxa using our sequence data in combination.

RESULTS AND DISCUSSION

Molecular data, combinability tests and phylogenetic analyses

Genbank accession numbers of the sequences are listed in Table 1. After removal of ambiguously aligned regions (2149 characters), the 6-locus 51 taxa alignment included 4317 characters. Combinability tests detected a single significant conflict within the 15 possible pairwise comparisons of topologies reconstructed from single loci. This conflict was for terminal relationships (the monophyly of *Rhococybe truncata* and *R. fallax* is inferred by ITS and *RPB*1 [with respectively ML-BS = 78 and 81%] while *R. fallax* clusters with *Clitopilus* sp. [ML-BS = 98%] based on *RPB*2). Despite this conflict both species of *Rhodocybe* are recovered as monophyletic with strong support in the combined analyses.

The most likely tree (Fig. 1) recovered for the 6-locus 51 taxa data set (-ln = 64660.4834) used the 10 partitions model that was slightly better than the model using 15 partitions to support part of the internodes. Only nodes that received ML-BS ≥ 70% and Bayesian posterior probabilities (PP ≥ 0.95) were considered significant (Alfaro *et al.*, 2003). Using *Callistosporium luteoolivaceum* as outgroup, the Entolomataceae (ML-BS: 94%; PP: –) are basal and sister to a monophyletic Tricholomataceae-Lyophyllaceae clade but without significant support. Based on Bayesian inference a different topology is recovered (not shown), with the Tricholomataceae as the most basal group and *D. racemosa* monophyletic with the Entolomataceae-Lyophyllaceae clade (ML-BS: –; PP: 0.95). Within the Tricholomataceae *sensu* Matheny *et al.* (2006), the Clitocybeae (ML-BS: 84%; PP: 1.0) and the Tricholomateae (ML-BS: 100%; PP: 1.0) are sister groups with *Corneriella* sister to *Tricholoma* (ML-BS: 100%; PP: 1.0). *Dendrocollybia racemosa* is resolved at the base of the Tricholomataceae but without support. The monophyly of the Lyophyllaceae *sensu* Matheny *et al.* (2006) and Sánchez-García *et al.* (2014) is significantly supported (ML-BS: 96%; PP: 1.0). Sister to the Lyophyllaceae is a weakly supported "hemilyophylloid" clade (ML-BS: 63%, PP: –) including part of *Clitocybe* (*C. candicans*, *C. subditipoda* and *C. connata*; ML-BS: 84%; PP: 1.0) that clusters without significant support with *Hypsizygus ulmarius*.

Within Lyophyllaceae *sensu* Matheny *et al.* (2006) four major clades are recovered and the genus *Tephrocybe* is shown to be paraphyletic. The four clades are:

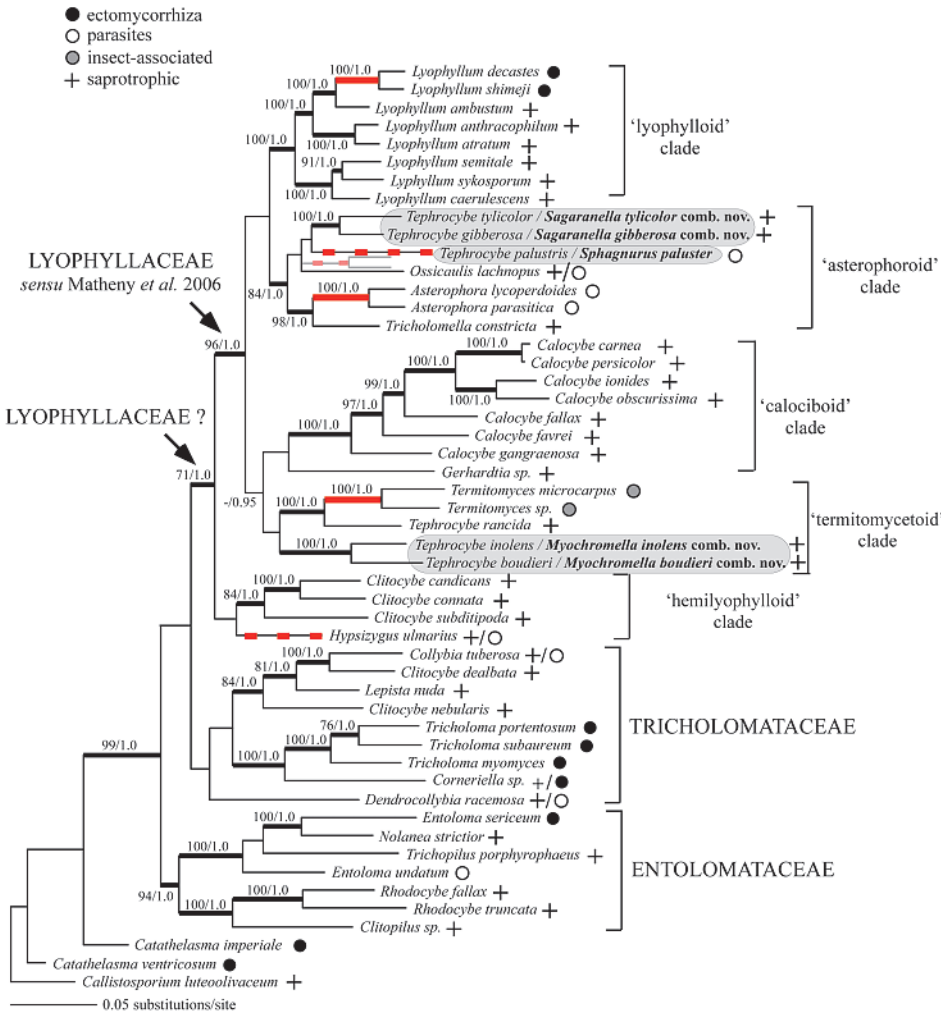

Fig. 1. Maximum likelihood tree produced by using ITSs, nLSU, mtSSU, *RPB1*, *RPB2* and *TEF1-α* sequence data in combination. Bold black branches are significantly supported (ML bootstrap values greater than 70%/Bayesian posterior probabilities (PP) ≥ 0.95 are indicated along the branches). Pale branches indicate a relationship that was only recovered by Bayesian inference. Internodes highlighted in red are ecological transitions (dash traits indicate transitions that could not be reconstructed).

(1) A "termitomycetoid" clade including a new genus *Myochromella* represented by *Tephrocybe inolens* and *T. boudieri*, together with *Tephrocybe rancida* (type species of the genus *Tephrocybe*) and *Termitomyces*. This clade is not significantly supported but shows high support for more terminal relationships (*Myochromella* [ML-BS: 100%; PP: 1.0]; *Termitomyces* [ML-BS: 100%; PP: 1.0]; and *Termitomyces* + *T. rancida* [ML-BS: 100%; PP: 1.0]). *Tephrocybe* is here restricted to the type species.

(2) A "calocyboid" clade with *Gerhardtia* resolved but not significantly supported to be the most basal taxon in that clade. Maximal support is recovered for the monophyly of *Calocybe* (ML-BS: 100%; PP: 1.0).

(3) A strongly supported "asterophoroid" clade (ML-BS: 84%; PP: 1.0) composed of the parasitic taxa (*Asterophora*, *Sphagnurus*† [currently monospecific including only *S. paluster* (Peck) Redhead & V. Hofstetter] and *Ossicaulis lachnopus*) and ruderal species (in a new genus *Sagaranella* represented by *Tephrocybe tylicolor* and *T. gibberosa*, and *Tricholomella constricta*). Within this clade only terminal relationships are well supported (*Asterophora* [ML-BS100%; PP: 1.0]; *Asterophora* + *Tricholomella* [ML-BS: 98%; PP: 1.0]; *Sagaranella* [ML-BS: 100%; PP: 1.0]). The two species, *O. lachnopus* (primarily saprotrophic) and *Sphagnurus paluster* (a necroparasite), remain unresolved within that clade.

(4) A strongly supported "lyophylloid" clade (ML-BS: 100%; PP: 1.0) that includes *Lyophyllum sensu* Redhead *et al.* (2006), with its conserved type.

Finally the monophyly of the "termitomycetoid" and "calocyboid" clades (ML-BS = –; PP: 0.95) is weakly supported.

Delimitation of the Lyophyllaceae in the "Tricholomatoid" clade sensu Matheny *et al.* (2006)

The present phylogeny (Fig. 1) suggests, however without significant support, a sister relationship between the Lyophyllaceae sensu Matheny *et al.* (2006) and the Tricholomataceae. This topology is inferred only by ML analysis of our 6-locus 51 taxa dataset. When using Bayesian inference, Entolomataceae are resolved and supported (PP = 0.95) as sister to Lyophyllaceae with Tricholomataceae occupying a more basal position (not shown). This last topology was also inferred by Matheny *et al.* (2006) but with *C. candicans* and *C. subditipoda* supported as basal to a monophyletic Entolomataceae-Lyophyllaceae clade based on maximum parsimony bootstrap value. Sánchez-García *et al.* (2014) retreived the Lyophyllaceae basal to Entolomataceae and Tricholomataceae *sensu strictus.* Their topoplogy suggests, however without support, the monophyly of part of *Clitocybe*, including *C. candicans* and *C. subditipoda,* with *Lepista, Collybia* and Lyophyllaceae. The present study (Fig. 1) also resolves *C. candicans* and *C. subditipoda* at the base of Lyophyllaceae but infer their monophyly with two species that have been previously classified in Lyophyllaceae *sensu auct.*: *Clitocybe connata* (Schum.: Fr.) Gillet (= *Lyophyllum connatum* (Schum.: Fr.) Singer) and *Hypsizygus ulmarius* (Bull.: Fr.) Redhead (= *Lyophyllum ulmarium* [Bull.: Fr.] Kühner). The monophyly of *Clitocybe connata* and *C. candicans* has also been inferred in a very recent study (Alvarado *et al.*, in press) and led the authors to propose genus *Leucocybe* Vizzini, P. Alvarado, G. Moreno & Consiglio for these two species.

Three other recent publications have examined elements of the "Tricholomatoid" clade (Vizzini, Musumeci and Murat, 2010; Vizzini and Ercole, 2012; Yu, Deng and Yao, 2011). These studies inferred a sister relationship between *Hypsizygus* and *Ossicaulis* with significant support. The placement of *Hypsizygus* appears therefore incongruent between previous studies and the phylogeny depicted here (Fig. 1). However, these previous studies only sampled *Hypsizygus tessulatus*, type species of this genus, while the present study only

† The etymology for the name *Sphagnurus*, which was coined by our esteemed colleague and mentor, Heinz Clémençon, was based on its host, *Sphagnum* and "*-urus*" (Latin meaning "tail") hence *Sphagnum*-tail.

sampled *H. ulmarius*. On the other hand, Holec and Kolarík (2013) found *H. ulmarius* to be monophyletic with maximum support with *H. marmoreus*. To check for the phylogenetic placement of *H. tessulatus*, we introduced the sequence data available in GenBank for this taxon in our dataset (AFTOL-ID 1898; *RPB*1: DQ917665, nucLSU: DQ917664, ITS: DQ917653) and ran maximum parsimony (MP) analyses. The best MP topology (a single MP tree: length = 12793 steps, CI = 0.228, HI = 0.772, RC = 0.1025; tree not shown) places *H. tessulatus* sister to *Ossicaulis lachnopus* with significant support (MP-BS: 98%). Consequently the genus *Hypsizygus,* as presently delimited, appears to be polyphyletic but the identities of the source materials should be confirmed.

The "hemilyophylloid" clade (Fig. 1) includes two species traditionally classified in Lyophyllaceae (*Hypsizygus ulmarius* and *Clitocybe connata* (= *Lyophyllum connatum* (Schum.: Fr.) Singer), which questions the delimitation of Lyophyllaceae sensu Matheny *et al.* (2006). These two species have both been included in tribe Lyophylleae (Kühner 1953, Moser 1978, Singer 1986) or family Lyophyllaceae (Bon, 1999) because they exhibit granulation in their basidia, a key character for that tribe or family. However these two species exhibit a granulation of the oligo-type (Clémençon, 1978) compared to the typical Lyophyllaceae, which all exhibit a macro-type granulation except for *Ossicaulis* in which granulation is absent according to Singer (1947). As *Clitocybe candicans* and *C. subditipoda* cluster in the same clade as *C. connata*, we therefore checked for the presence or absence of granulation in the basidia of these two species and in the basidia of *Ossicaulis* sp.*, O. lignatilis.* Staining the basidia of *Clitocybe candicans* and *C. subditopoda* with iron-acetocarmine (Clémençon, 1978), granules are absent from the basidia of these two species. Performing the same coloration on basidia of *O. lignatilis*, a few, very small granules are seen in phase contrast that can easily escape attention when observed in bright field microscopy (Fig. 2).

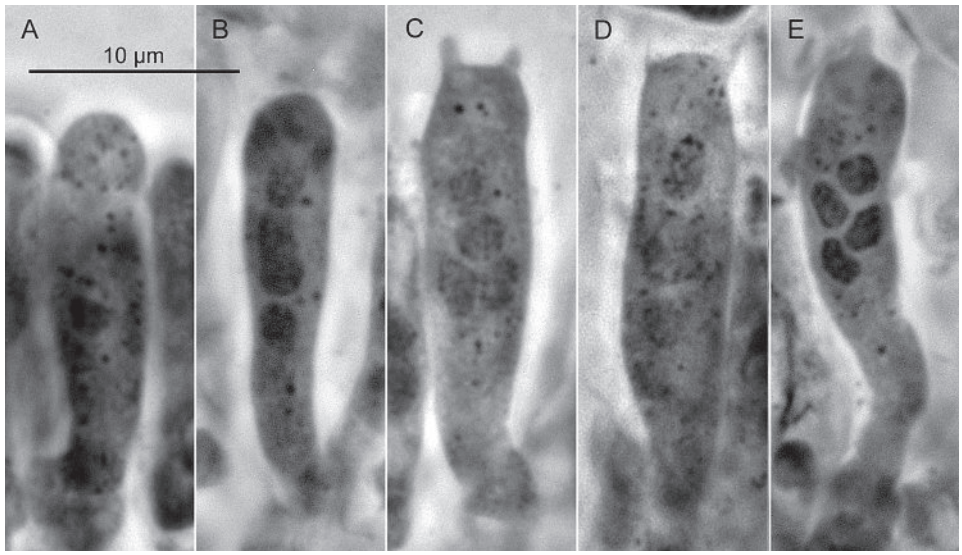

Fig. 2. **A-E:** Siderophilous granulation during maturation of basidia from *Ossicaulis lignatilis* stained with iron-acetocarmine. **A.** Mature basidium (2N), **B.** Basidium after first nuclear division. **C., D.** and **E.** Basidia after second nuclear division (phase contrast microscopy, photo: Heinz Clémençon).

Two possible systematic solutions can be considered: a first solution would be to keep the delimitation of Lyophyllaceae as recovered in Matheny *et al.* (2006) and Sánchez-García *et al.* (2014), which would leave the clade including *H. ulmarius* and part of *Clitocybe* including *C. connata* unnamed. This solution would be systematically advantageous if Lyophyllaceae *sensu* Matheny *et al.* (2006) only included taxa exhibiting granulation of the macro-type, character largely viewed as the key taxonomic feature for this family. However, Lyophyllaceae as delimited by Matheny *et al.* (2006) includes *Ossicaulis* with granulation of the oligo-type (Fig. 2) and *Hypsizygus tessulatus* (analyses not shown) lacking granulation (Singer, 1947). Also the "hemilyophylloid" clade is clearly separated from the Tricholomataceae and supported to be monophyletic with the Lyophyllaceae (ML-BS: 71%; PP: 1.0). We refrain from proposing a new genus(era) for species of this clade considering our poor sampling of genera *Clitocybe* and *Hypsisygus*, the apparent polyphyly of genus *Hypsizygus*, and the current lack of characters to predict delimitation of the "hemilyophylloid" clade. More extensive taxon and gene sampling for the Lyophyllaceae-Tricholomataceae-Entolomataceae clade are needed to clarify the delimitation of Lyophyllaceae and its relationship with closely related families.

Introducing two new genera: Myochromella and *Sagaranella* with notes on *Sphagnurus*

Previous studies (Hofstetter *et al.* 2002; Redhead *et al.*, 2006) resulted in maintaining the name *Lyophyllum* with a conserved type, *L. semitale*, and to place *Lyophyllum leucophaeatum* in *Calocybe* as *C. gangraenosa* (Redhead *et al.*, 2012). *Lyophyllum sensu stricto*, once segregated from *Lyophyllum sensu lato*, forms a monophyletic lineage, the "lyophylloid clade" (Fig. 1), composed only of staining species and more or less characterized by brown or dusky pigments and presence of siderophilous lysosomes of the macro-type (Clémençon, 1978). However *Lyophyllum s.s.* includes some species from section *Tephrophana* (Fr.) Singer (now frequently classified in *Tephrocybe: i.e. Lyophyllum ambustum, L. anthracophilum and L. atratum;* Fig. 1). *Tephrocybe*, as defined by Donk (1962), was composed of small, more or less hygrophanous, collybioid taxa, several of which have since been transferred back into *Lyophyllum*. One taxonomic and nomenclatural solution to resolve the conflict between named taxa and results from inferred phylogenies would be to follow Singer (1986) and to lump all Lyophyllaceae species, except the ones that are part of the "hemilyophylloid" clade, under a single generic name. However, a single genus *Lyophyllum* would not be a reasonable choice based on the following considerations.

(1) Several biologically well-characterized taxa are recognized phylogenetically in the complex of siderophilous granule producing agarics (Hofstetter *et al.,* 2002; Moncalvo *et al.*, 2002), the most well-known, conspicuous genus being *Termitomyces* (Clémençon, 1984). *Termitomyces* is the famous agaric genus assiduously cultivated by termites, about which considerable literature has been written (Aanen *et al.*, 2002; Aanen and Eggleton, 2005; Heim, 1977; Johnson *et al.* 1981; Nobre and Aanen, 2010; Nobre *et al.*, 2010). The type for the generic name *Podabrella*, *T. microcarpus* (Berk and Broome) R. Heim, is nested by molecular phylogenetic analysis within the greater *Termitomyces* lineage (Frøslev *et al.*, 2003), and therefore we follow Heim (1977) and Pegler (1977) who do not recognize *Podabrella* as a distinct genus (Table 1). The closest ally to the *Termitomyces* clade is *Tephrocybe rancida* (Fr.) Donk (Fig. 1), type species

of *Tephrocybe*. This species, which occurs in soil in coniferous forests, is characterized by a long pseudorrhiza and virtually free lamellae (as in *Termitomyces*), but unlike *Termitomyces* has clamp connections. We restrict *Termitomyces* to clampless taxa with conspicuous hymenial cystidia and mutualistic association with termites. *Tephrocybe* is a clamp forming sister taxon to the clampless genus *Termitomyces* and is not associated with termites. Two recently described conidia-producing genera *Arthromyces* Baroni & Lodge (clampless) [*non* "*Arthromyces*" Amano *nom. invalid*.] and *Blastosporella* Baroni & Franco-Molano (clamp connections present on hyphae of pileipellis and stipitipellis) are probably part of this "termitomycetoid" clade but their relationships toward the other genera that are part of this clade remain unknown (Baroni *et al.*, 2006).

(2) Two additional taxa previously placed in either *Tephrocybe* or *Lyophyllum*, *i.e. T. bouderi* and *T. inolens*, like *Tephrocybe rancida* and *Termitomyces* species, have nearly free lamellae, and are neither obvious parasites, nitrophiles, nor are they cultivated by insects. Together they form another monophyletic group, possibly with affinities to *Tephrocybe* and *Termitomyces* (Fig. 1). Unlike *T. rancida*, their basidiomata do not originate from a pseudorrhizae deep in the ground. It could reasonably be argued that *T. rancida* and the *T. boudieri-inolens* lineage represent together the ancestral group from which *Termitomyces* originated. Therefore both *T. boudieri* (Kühner and Romagn.) Derbsch and *T. inolens* (Fr.) M.M. Moser ought to be retained in *Tephrocybe*, thus possibly making the genus paraphyletic. However, given an obvious morphological feature (radicating pseudorrhiza) that might be linked to a biological function for *T. rancida* (unknown hypogeous food source?) shared by *T. rancida* and *Termitomyces*, but absent in their sister taxa (*Myochromella* gen. nov.) we opt to recognize a separate monotypic small genus, *Mycochromella* (Fig. 1). This leaves *Tephrocybe (T. rancida*) as a monotypic genus for now.

(3) The traditionally recognized and well-characterized mycoparasitic genus *Asterophora* (Buller 1924, Corner 1966, Clémençon 1997, Redhead and Seifert 2001) forms silvery to dusky colored basidiomata and possesses siderophilous macrogranules in its basidia (Clémençon 1978). In our phylogeny the two *Asterophora* species form a strongly supported monophyletic group (Fig. 1). The nomenclatural type for *Tricholomella* Kalamees, *T. constricta* (Fr.) Kalamees (Kalamees 1992, Bon 1999), shows affinity to *Asterophora* (Fig. 1) but differs markedly in morphology and habitat. Hence we recognize both *Asterophora* and *Tricholomella* as distinct genera. The lignicolous *Ossicaulis lachnopus* also appears to be the closest relative of *Hypsizygus tessulatus* (not shown) and thus to typically siderophilous granule-producing taxa. We recognize both *Ossicaulis* and *Hypsizygus* as valid genera. Also included in the "asterophoroid" clade (Fig. 1) is another unusual species, alternatively called *Lyophyllum palustre* (Peck) Singer or *Tephrocybe palustris* (Peck) Donk. This species is a known parasite of *Sphagnum* (Redhead, 1981; Untiedt and Mueller 1985; Simon 1987). In our phylogenetic analyses it occupies a somewhat isolated position. Given its uniqueness, both biologically and phylogenetically, we choose to recognize a distinct genus, *Sphagnurus* (Redhead 2014) that was also recently named *Bryophyllum* Vizzini (2014) nom. illeg. [non *Bryophyllum* Salisb. 1805] without any explanation.

(4) Two other species previously placed in *Tephrocybe*, namely *T. tylicolor* (Fr.) M.M. Moser and *T. gibberosa* (J. Schaeff.) P.D. Orton, represent yet another lineage (Fig. 1) of nitrophilous fungi associated in nature with decomposing corpses, non-herbivore faeces, decomposed fungi, or urine or urea

treated soils (Sagara 1975, Redhead 1984). Ecologically these could be considered "ammonia fungi" (Sagara 1973, 1975), but remain clearly differentiated from the pyrophilous taxa, now in *Lyophyllum*. We considered placing *T. tylicolor* and *T. gibberosa* into two nitrophilous genera based additionally upon spore morphology, but for now we prefer to retain them in a new genus *Sagaranella* Hofstetter, Clémençon, Moncalvo & Redhead. *Sagaranella gibberosa* comb. nov. forms unique basidiospores within Lyophyllaceae resembling those of nodulose-spored *Inocybe* species and forms clamps in its basidiomata although some isolates may lack clamp connections (another unusual feature, but one also characterizing some species in *Termitomyces* for example). This species also forms blackish sclerotia in nature (Lange and Siverstsen 1966) as well as masses of arthroconidia in culture (Moncalvo, 1991). *Sagaranella tylicolor* comb. nov does not form sclerotia and is representative of a small group of species, incl. *Tephrocybe erosa* (Fr.) Bon and *T. tesquorum* (Fr.) M.M. Moser with spinose (not gibbose) basidiospores.

Ancestral state reconstruction: systematics versus ecological transitions within Lyophyllaceae

Five species could not be clearly assigned to one or the other ecological strategies (see also Fig. 3 for the two different coding matrices of the ecology of the following taxa [the two last columns]): *Corneriella* sp. (saprophytes or ectomycorrhizal?), and *Collybia tuberosa*, *Dendrocollybia racemosa, Ossicaulis lachnopus* and *Hypsizygus ulmarius* (saprophytes or parasites?). As defined by Singer (1986), genus *Porpoloma* included both ectomycorrhizal and saprotrophic species. Very recently Sánchez-García *et al.* (2014) proposed the genus *Corneriella* Sánchez-García for the clade in which the previously named *Porpoloma* sp. collection, also used in the present study, was nested. After these last authors *Corneriella* spp. grow on soil and humus and are putatively saprotrophic but confirmation is still required. *Collybia tuberosa* and *Dendrocollybia racemosa* are considered by some as mycoparasites of other mushrooms that essentially feed on mummified basidiomes (*Collybia s. str.*) or by rapid digestion of the host for *D. racemosa.* Others consider that these species normally fruit on decayed fruitbodies, therefore suggesting saprotrophy (Hughes *et al.*, 2001; Redhead *et al.,* 1994). Finally *O. lachnopus* and *Hypsizygus ulmarius* can be decay agents on living trees but it remains unclear if the latter two species are parasites or saprobes (see the introduction section). We therefore ran two different ancestral state reconstructions considering these species as ectomycorrhizal or not for *Corneriella* sp., and as parasitic or not for *C. tuberosa*, *D. racemosa*, *H. ulmarius* and *O. lachnopus*. In our analyses we followed Pera and Alavarez (1995) and Visnovsky *et al.* (2014) respectively to score *L. decastes* and *L. shimeji* as ectomycorrhizal. However, *L. decastes* represents a species complex of which several members can be found in absence of ectotrophic plants in their vicinity (Moncalvo, 1991; Kuo, 2010). Also, these ectomycorrhizal species, unlike other well established ectomycorrhizal genera such as for instance *Cortinarius*, *Russula* and *Cantharellus*, grow well *in vitro* (Moncalvo, 1991) and strains of *L. shimeji* were shown to be capable to grow saprobically and to fruit on artificial substrates (Yamaka, 2008). Otha (1994a) reported *L. shimeji* as a facultative ectomycorrhizal taxon. This may also be the case of other species of the *L. descastes* species complex that have shown the ability to form ectomycorrhizal association with root tips.

We only reconstructed ancestral character states within Lyophyllaceae because our sampling was very poor for the other families and because support was lacking to unequivocally reconstruct ancestral character states outside Lyophyllaceae. Only nodes significantly supported by Bayesian analysis were considered. Our Bayesian topology (not shown but see Fig. 1) suggested that five ecological transitions might have occurred during the evolution of Lyophyllaceae. Out of these five transitions, four were not restricted to a single taxon and could be considered for ancestral state reconstruction: (1) two transitions from saprotrophy toward parasitism: one on the internode leading to *Asterophora* spp. and one on the internode leading to *S. paluster*/*O. lachnopus* but only when considering *O. lachnopus* as a parasite. This last transition could not be reconstructed because it was not significantly supported by Bayesian phylogenetic analysis (and not even inferred by ML analyses [Fig 1]); (2) one transition from saprotrophy to an ectomycorrhizal lifestyle on the internode leading to the *L. decastes* species complex; (3) one transition from saprotrophy toward insect-related lifestyles on the internode leading to *Termitomyces*. We were also interested to determine which ancestral state, if any, could be unequivocally assigned by ancestral state reconstruction to the ancestor of Lyophyllaceae *sensu stricto* (*sensu* Matheny *et al.*, 2006) and to the ancestor of the Lyophyllaceae *sensu lato* (including the "hemilyophylloid" clade, see Fig. 1).

Coding the terminal state of the five species of uncertain ecology as saprotrophic, the three transitions mentioned above were all unequivocally reconstructed (in 100% of the 7500 credible trees sampled from Baysian analysis) by both ML and by parsimony reconstruction methods. These two analyses also reconstructed the ancestor of Lyophyllaceae *s. str.* and of the Lyophyllaceae *s.l.* as saprotrophic (again in 100% of the 7500 credible trees sampled).

Coding the same five species as not saprotrophic (the *Corneriella* sp. as ectomycorrhizal and *C. tuberosa*, *D. racemosa, O. lachnopus* and *H. ulmarius* as parasitic), these same three transitions were unequivocally reconstructed (in 100% of the credible trees) and again by both ML and parsimony reconstruction methods. But while parsimony reconstructed unequivocally the ancestor of Lyophyllaceae *s. str.* and the ancestor of Lyophyllaceae *s.l.* as saprotrophic (respectively with 136 and 129 trees with equivocal reconstruction; *i.e.* saprotrophy reconstructed in 98,2% and 98,3% of the credible trees), ML did not reconstruct unequivocally the ancestor of Lyophyllaceae *s. str.* and Lyophillaceae *s.l.* as saprobes (respectively with 410 and 1021 trees with equivocal reconstruction; *i.e.* saprotrophy reconstructed in 94.5% and 86.4% of the credible trees sampled).

Overall the results of ancestral state reconstructions suggest that at least three ecological transitions happened during the evolution of Tricholomataceae-Entolomataceae-Lyophyllaceae clade. These transitions took place in Lyophyllaceae *s. str.*: a transition from saprotrophy to parasitism (for *Asterophora*), a transition from saprotrophy to ectomycorrhizal (*L. decastes* species complex) and a transition from saprotrophy to an insect-associated lifestyle (for *Termitomyces*). As ancestral states of Lyophyllaceae *s. str.* and *s.l.* were unequivocally reconstructed as saprotrophic in three out of the four different ancestral state reconstructions conducted here (by parsimony despite the coding of the ecology of taxa of uncertain ecology and by ML but only maximizing the number of saprotrophic taxa) parasitism, ectomycorrhiza and insect-association appear to be derived states in the evolution of Lyophyllaceae. Previous studies have shown that many ecological transitions to parasitism (James *et al.*, 2006) or to the ectomycorrhizal mode of nutrition (James *et al.*, 2006; Matheny *et al.*, 2006;

Moncalvo *et al.*, 2002) have occurred during the evolution of euagarics. Some of these studies, e.g. Hibbett *et al.* (2000), also suggested that mycorrhizae were unstable associations that evolved repeatedly from saprotrophic ancestors but with multiple reversals to saprotrophy. This view has since been questioned repeatedly (e.g. Tedersoo *et al.*, 2010). In particular, Wolfe *et al.* (2012) have shown that for *Amanita* such transition is accompanied by the loss of cellulase genes and consequently by the loss of the capacity to live as saprobes, which suggests that transitions from saprotrophy to an ectomycorrhizal mode of nutrition are likely to be irreversible contrary to the premature report by Hibbett *et al.* (2000). Our phylogeny and ancestral state reconstructions are in accordance with Tedersoo *et al.* (2010) in retrieving no evidence for reversals. Results of ancestral state reconstruction also suggest that the facultative ectomycorrhizal species in the *L. decastes* species complex are still undergoing their transition toward an ectomycorrhizal lifestyle. This species complex appears to be a very promising fungal group for the study of transitional processes from saprotrophy to mutualism.

Our study also underlines the necessity for unambiguous experimental data concerning the ecological strategies adopted by the various species of fungi, which is too often neglected in species descriptions. As pointed out by Bruns and Shefferson (2004), determining whether mutualism and parasitism are ancestral or derived stages in the evolution of euagarics, and whether transitions are labile or not, will not only necessitate a good taxon sampling and a well resolved and supported phylogeny (Heath *et al.*, 2008) but also an unambiguous knowledge about the ecology of all the sampled taxa. Studies dealing with large environmental fungal sequence data will also benefit from ecology assessment of individual fungal species in providing essential tools to understand the precise role of fungi in ecosystems (Peay, 2014).

Testing for molecular clock and for equality of evolutionary rates in the Tricholomatoid clade

Even though our phylogeny was based on six loci and used a relatively small taxon sampling (51 taxa), basal relationships between Lyophyllaceae, Tricholomataceae and Entolomataceae as well as some relationships within Lyophyllaceae still lacked significant support. Some of the major causes for weak phylogenetic support are rate heterogeneity (Moreira and Philippe, 2000, Bevan *et al.*, 2007) and taxon sampling (Heath *et al.*, 2008). Also previous studies that had used a different taxon sampling and several loci to solve relationships within the "Tricholomatoid" clade also failed to recover significant support for basal relationships within the Lyophyllaceae-Entolomataceae-Tricholomataceae clade (Matheny *et al.*, 2006; Sánchez-García *et al.,* 2014; Baroni *et al.*, 2011)

We consequently tested our phylogeny for molecular clock-like behavior. Under the null hypothesis, with a rooted phylogeny and branch lengths constrained so that all of the tips can be drawn in a single time plane, the best likelihood score for the 6-locus 51 taxa phylogeny is $-\log L_0 = 53260.72931$. Under the alternative hypothesis, where each branch is allowed to vary independently, $-\log L_1 = 52810.64878$. Statistics for the likelihood ratio test result in $-2 \log L = 2 \times (53260.72931 - 52810.64878) = 900.16106$. When comparing this value with a Chi-square statistics value for 49 (number of taxa minus two) degrees of freedom (critical value = 85.351; $P < 0.001$), the hypothesis of a molecular clock is rejected.

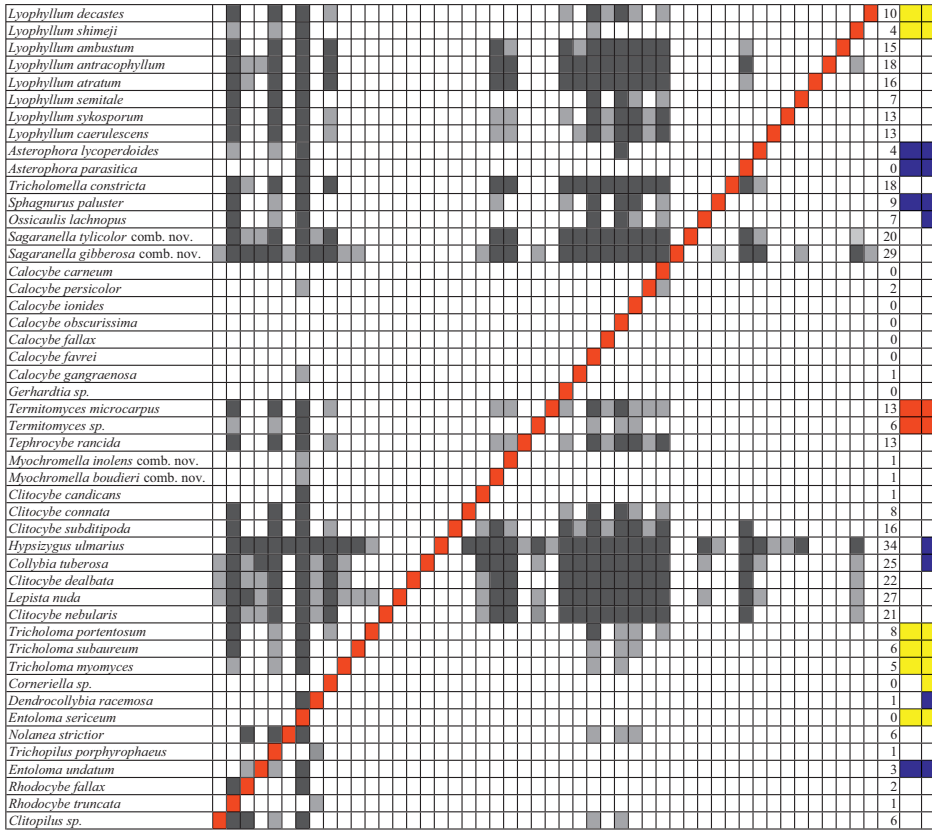

Fig. 3. ML ratio test for equality of evolutionary rates in the 6-locus 51 taxa dataset. Columns report pair wise comparisons between a given species (red box) and the other 50 species sampled (non red box). A white box indicates that the evolutionary rates of the two compared species are not significantly different. Grey and black boxes indicate that the considered species is significantly slower (respectively with $P > 0.05$ and $P > 0.01$) than the compared species (red box which is in the same column). The column with numbers reports the number of comparisons in which a given species was found to evolve significantly slower at the molecular level than the compared taxon (= total number of PCESS for a species) and the two last columns report the ecological strategy of the taxa as used for the two ancestral state reconstructions (white: saprobe, yellow: ectomycorrhiza, blue: parasite, red: insect-associated).

Therefore we also conducted relative rate tests to determine in which clades and for which taxa significant differences in evolutionary rate were observed and if these differences were coupled or not with transitions in the ecological strategy of these taxa. Tests for equality of substitution rates used *C. luteoolivaceum* as outgroup. Results of these tests are reported (Fig. 3) as proposed by Lutzoni and Pagel (1997), *i.e.* as descriptive only and with uncorrected values (Nakagawa, 2004). Significant differences in evolutionary rates between species (*i.e.* taxa totalizing the highest number of pairwise comparisons in which they evolve significantly slower [PCESS] than the compared taxon) are found in five out of the seven major clades identified by phylogenetic analyses

(Figs 1 and 3): in the Tricholomataceae (Clitocybeae: 21-25 PCESS), in the "hemilyophylloid" clade (*"H." ulmarius*: 34 PCESS; *Clitocybe subditopoda*: 16 PCESS), in the "termitomycetoid" clade (*Termitomyces microcarpus* and *Tephrocybe rancida*: both 13 PCESS), in the "asterophoroid" clade (*Tricholomella constricta* and *Sagaranella* spp.: 18-29 PCESS), and in the "lyophylloid" clade (up to 18 PCESS for *L. anthracophilum*). Relatively fast evolving species (*i.e.* totalizing the least PCESS) are also found in these same clades: in the Tricholomataceae (*Corneriella sp.*: 0 PCESS; *Dendrocollybia racemosa*: 1 PCESS; and to a lesser extent *Tricholoma*: 5-8 PCESS), in the "hemilyophylloid" clade (*Clitocybe connata* and *C. candicans*: both 1 PCESS), in the "asterophoroid" clade (*Asterophora* spp., *Sphagnurus paluster,* and *Ossicaulis lachnopus*: respectively 1-4, 9 and 7 PCESS), in the "termitomycetoid" clade (*Myochromella* spp.: 1 PCESS; *Termitomyces sp.*: 6 PCESS), and in the "lyophylloid" clade (*L. shimeji*: 4 PCESS and *L. semitale*: 7 PCESS). Finally the "calocyboid" clade and the Entolomataceae are only composed of relatively "fast" evolving species ("calocyboid" clade, saprobes: 0-2 PCESS; Entolomataceae, saprobes [except *E. undatum*: ectomycorrhizal and *E. sericeum*: parasite]: 0-6 PCESS). The simultaneous presence of relatively fast as well as slow evolving taxa in the majority of the clades identified within the Tricholomatoid clade might therefore be responsible for the low phylogenetic support retrieved here and in previous studies (Matheny *et al.*, 2006; Sánchez-García *et al.*, 2014; Vizzini *et al.*, 2010; Vizzini and Ercole, 2012; Yu *et al.*, 2011).

Parasitic (see *Asterophora* spp. [1-4 PCESS] versus *Hypsizygus ulmarius* [34 PCESS]), insect-related spp. (see *Termitomyces* sp. [6 PCESS] versus *T. microcarpus* [13 PCESS]) and saprotrophic species (see *Sagaranella* spp. [20-29 PCESS] versus *Myochromella* spp. [1 PCESS] can be either relatively "fast" or, on the contrary, "slow" evolving species. Differences in evolutionary rates are consequently not related to any particular ecological strategy. Nevertheless, within clades including taxa with different ecological strategies, mutualistic and parasitic taxa show a tendency to totalize different numbers of PCESS than saprotrophic species. In the "asterophoroid" clade, saprotrophic species are found to evolve significantly slower than *Asterophora* spp. (fungal parasites) and, to a lesser extent, also slower than *S. paluster* (moss parasite; significantly faster only than *T. gibberosa*). In theory, parasites are expected to evolve rapidly so as to disproportionately infect the most common genotype and thereby drive it down in frequency (Clarke, 1976; Hutson and Law, 1981). *Asterophora* exhibits low sexual reproduction (lamellae and production of basidiospores reduced) and propagates essentially by asexual chlamydospores that are produced by transformation of hyphal segments (De Bary, 1859). These features fit theoretical predictions that parasites with asexual reproduction accumulate more mutations than sexually reproducing taxa because they do not benefit from the recombination mechanism of genome repair (Law and Lewis, 1983). Within the Tricholomataceae, *Clitocybeae* spp. (saprobes: 21-27 PCESS) appear relatively slower evolving than the species of the sister clade (*Tricholoma spp., Corneriella sp.* and *D. racemosa*: 0-8 PCESS), which is partially composed of ectomycorrhizal species. Also *L. nuda* evolves significantly slower than all the species of its sister clade and *Clitocybe dealbata*, *C. nebularis* (saprobes) and *Collybia tuberosa* (possibly parasitic) are also slower evolving than *D. racemosa* (possibly parasitic) and *Corneriella* sp. (possibly ectomycorrizal) but not slower than part or all of the *Tricholoma* spp. (ectomycorrizal). In the "hemilyophylloid" clade, *H. ulmarius* (34 PCESS) is found to evolve relatively slower than the saprotrophic species of its clade (*Clitocybe* spp.: 1-16 PCESS). This decay agent of

heartwood, possibly parasitic, evolves significantly slower than at least *C. connata* and *C. candicans* (saprobes). Finally, in the "lyophylloid" and in the "termitomycetoid" clades, the subclades containing mutualistic taxa also totalized different numbers of PCESS than the subclades including only saprobes. Ectomycorrhizal species within the "lyophylloid" clade (*L. shimeji* and *L. decastes*: 4 and 10 PCESS respectively) are overall faster evolving than all the other species of *Lyophyllum* (13-18 PCESS) but with the exception of *L. semitale* (7 PCESS). The subclade including insect-associated species (*Termitomyces* spp.: 6 and 13 PCESS) and a saprobe (*T. rancida:* 13 PCESS) appears to evolve slower than its sister saprotrophic subclade (*Myochromella* spp.: 1 PCESS). However, even if a tendency is observed at the molecular level that parasitic and mutualistic taxa evolve at different speeds than saprobes, the factors that could account for an increase of mutation rates in part of the species in the "Tricholomatoid" clade are difficult to discuss, apart from a reduction of sexual reproduction for *Asterophora* spp. Virtually nothing is known about generation time (Andreasen and Baldwin, 2001; Laroche and Bousquet, 1999) and DNA repair systems (Britten, 1986) of Fungi. Neither is there any reason to suspect the presence of free radicals in any of the fast evolving species in our sampling (Droge, 2002; Lutzoni and Pagel, 1997; Wei and Lee, 2002). A better knowledge of the ecology and of biochemical pathways of fungi will be essential to understand why ecological transitions appear so common in the fungal kingdom (Harrier, 2001). Sequencing of fungal genomes is therefore a really promising field to achieve this goal.

NEW TAXA

Myochromella V. Hofstetter, Clémençon, Moncalvo & Redhead, gen. nov. (MB810938)

Basidiomata smallish, solitary, gregarious or occasionally paired (not caespitose); pileus striate and hygrophanous and lamellae broad and free or nearly free; stipes relatively narrow and somewhat cartilaginous; not staining; basidiospores smooth, nonamyloid, hyaline, white in mass. Basidia containing abundant, conspicuous macro-siderophilous granules. Clamp connections present.

Holotype: ***Myochromella inolens*** (Fr.) V. Hofstetter, Clémençon, Moncalvo & Redhead, **comb. nov.** (MB810939)

Basionym: *Agaricus inolens* Fr., *Epicr. Syst Mycol. (Upsaliae)*: 96. 1838 [1836-1838].

Etymology: Latin Myo- (mouse), -chrom- (color), -ella (small), hence "little mouse color"

Additional taxa:

Myochromella boudieri (Kühner & Romagn.) V. Hofstetter, Clémençon, Moncalvo & Redhead, **comb. nov.** (MB810940)

Basionym: *Lyophyllum boudieri* Kühner and Romagn., *Bull. Soc. Nat. Oyonnax* 8: 75. 1954.

Sagaranella V. Hofstetter, Clémençon, Moncalvo & Redhead, **gen. nov.** (MB810942)

Basidiome gray, brown, mycenoid, not staining; stipe without a pseudorhiza. No visible veil. Nitrophilous. Basidiospores echinulate, finely warty

or gibbose, hyaline, nonamyloid. Clamp connections present. Basidia containing abundant, conspicuous macro-siderophilous granules.

Holotype: ***Sagaranella tylicolor*** (Fr.) V. Hofstetter, Clémençon, Moncalvo & Redhead, **comb. nov.** (MB810943)

Basionym: *Agaricus tylicolor* Fr., *Observ. mycol. (Havniae)* 2: 128 (1818)

Etymology: In honour of Prof. Dr. Noahiko Sagara, now retired from Kyoto University, for his fruitful research on the ecology and physiology of the ammonia fungi which include the type species of this new genus.

Additional taxa:

Sagaranella gibberosa (Jul. Schäff.) V. Hofstetter, Clémençon, Moncalvo & Redhead, **comb. nov.** (MB810944)

Basionym: *Collybia gibberosa* Jul. Schäff., *Ann. Mycol. (Berlin)* 40 (1-2): 150. 1942.

Sagaranella erosa (Fr.) V. Hofstetter, Clémençon, Moncalvo & Redhead, **comb. nov.** (MB810945)

Basionym: *Agaricus erosus* Fr., *Syst. Mycol.* 1: 145. 1821.

Sagaranella tesquorum (Fr.) V. Hofstetter, Clémençon, Moncalvo & Redhead, **comb. nov.** (MB810946)

Basionym: *Agaricus tesquorum* Fr., *Öfvers. Kongl. Svensk. Vet.-Akad. Förh.* 18(1): 22. 1861.

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