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***Cibaomyces* and *Cyptotrama*, two new genera for Europe, and an emendation of *Rhizomarasmius* (Basidiomycota, Physalacriaceae)**

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Abstract

A new species, *Cyptotrama fagiphila*, sp. nov., and a noteworthy species recently described from China, *Cibaomyces glutinis*, are reported from Europe. Their systematic position was confirmed by DNA sequence analyses of the ITS and partial 28S regions of the nuclear rDNA cistron. Based on these data, an emendation of *Rhizomarasmius* is also proposed to encompass the alpine species *Oudemansiella oreina* and the marasmioid species *Marasmius setosus*, and the appropriate combinations *Rhizomarasmius oreinus* comb. nov. and *R. setosus* comb. nov. are introduced. The position of *Laccariopsis* (*Oudemansiella*) *mediterranea* is also discussed. Unpublished data on the holotypes of the extra-European species *Cyptotrama hygrocycoides*, *C. platensis*, and *C. songolarum* are provided along with sequence data that indicate *C. songolarum* belongs in the genus *Termitomyces* (Lyophyllaceae).

Keywords

Agaricales *Dactylosporina* *Termitomyces* *Xerula* Xerulaceae Taxonomy Phylogeny

Introduction

Systematic classification of the white-spored agarics grouped by Fries (1821) in section *Collybia* of the old genus *Agaricus*, has evolved throughout the last century as new data from pileipellis structures (Singer 1951, 1986), cystidia, and spore ultrastructure (Kühner 1980; Pegler and Young 1987; Petersen 2008) were compiled and analyzed. Jülich (1981) introduced the family Xerulaceae Jülich for collybioid species with large basidia and thick-walled spores, originally including the genera *Oudemansiella* Speg., *Xerula* Maire, and *Lampteromyces* Singer.

The Xerulaceae sensu Jülich grew in size as additional noteworthy micromorphological characters, such as sarcodimitic tissue (Redhead 1987) and a three-layered spore wall with a cyanophilic inner layer (Kühner 1980; Petersen 2000), were evaluated. After decades of morphological explorations leading to either splitting (Singer 1964, 1986) or lumping genera (from Kühner 1980, to Yang et al. 2009), a new and fundamental understanding was achieved due to DNA-based phylogenetic analyses (Moncalvo et al. 2002; Bodensteiner et al. 2004; Wilson and Desjardin 2005; Matheny et al. 2006; Binder et al. 2006; Mata et al. 2007; Lebel and Catcheside 2009; Henkel et al. 2010; Hao et al. 2014; Qin et al. 2013). All these studies confirmed monophyly of this family (with the exclusion of *Lampteromyces*, now a synonym of *Omphalotus* Fayod, Kirchmair et al. 2004, and *Mycenella* (J.E. Lange) Singer, included by Singer 1986), but also added new genera with less typical characters such as *Armillaria* (Fr.: Fr.) Staude as well as "reduced" or secotioid genera including non-gilled taxa such as *Cribbea* A.H. Sm. & D.A. Reid, *Gloiocephala* Masee, *Mycaureola* Maire & Chemin, and *Physalacria* Peck. Because the name Physalacriaceae Corner (1970), based on *Physalacria*, is older than Xerulaceae, the principle of priority dictates that the name Physalacriaceae be used for this primarily agaricoid lineage.

Petersen and Hughes (2010) recently proposed a partial revision of Physalacriaceae based on morphology and ITS and 28S phylogenetic reconstructions, which resulted in an increase in the number of genera in the family. Thus, at present the family currently includes 21 genera ranging from agaricoid [*Armillaria*, *Cibaomyces* Zhu L. Yang et al., *Cyptotrampa* Singer, *Flammulina* P. Karst., *Hymenopellis* R.H. Petersen, *Laccariopsis* Vizzini, *Mucidula* Pat., *Oudemansiella*, *Paraxerula* R.H. Petersen, *Ponticulomyces* R.H. Petersen, *Protoxerula* R.H. Petersen, *Pseudohiatula* (Singer) Singer, *Rhizomarasmius* R.H. Petersen, *Rhodotus* Maire, *Strobilurus* Singer, *Xerula*], cantharelloid (*Gloiocephala*), clavarioid (*Physalacria*), secotioid (*Cribbea*, *Guyanagaster* T.W. Henkel, M.E. Sm. & Aime), and corticioid (*Cylindrobasidium* Jülich) genera, in addition to marasmiod fungi such as *Cryptomarasmius* T.S. Jenkinson & Desjardin (Jenkinson et al. 2014), and the "*Marasmius*" *epiphyllus* group (Antonín et al. 2010) and other reduced species requiring generic reassignment. Recently some European species placed in genera outside the Physalacriaceae were revealed to be confamilial with *Rhizomarasmius*, such as "*Marasmius*" *epidryas* Kühner ex A. Ronikier (formally recombined by Ronikier and Ronikier 2011) and "*Hydropus*" *mediterraneus* Pacioni and Lalli, suggested by Petersen (2000) and Antonín and Noordeloos (2010) to be related to *Rhizomarasmius*, and for which Vizzini et al. (2012) created a new genus, *Laccariopsis*.

Over the past few years we have become familiar with two European species for which no names were available, despite a unique suite of macro- and microscopic characters. These characters were so unlike any described European taxa (Bon 1999; Horak 2005) that their generic placement remained unresolved for years. In the present study, phylogenetic analyses of two ribosomal DNA loci are used to support placement of these species in the Physalacriaceae. One of them is referable to the genus *Cyptotrampa*, in its original sense, and is proposed as *Cyptotrampa fagiphila*, sp. nov. The second, very recently published by Hao et al. (2014) as *Cibaomyces glutinis* Zhu L. Yang, Y.J. Hao & J. Qin, is an unusual species with spectacular stellate spores analogous to those of *Dactylosporina steffenii* or "*Xerula*" *kuehneri* (see Locquin 1943; Petersen and Hughes 2010). The comparisons with related species in *Cyptotrampa* and *Rhizomarasmius* based on DNA sequences available in public databases and the authors' personal data, as well as on unpublished microscopic

observations made by E. Horak of various type collections worldwide, are presented. Furthermore, our analyses of various marasmioid species revealed that “*Marasmius*” *setosus* (Sow.) Noordel. and “*Oudemansiella*” *oreina* Pacioni and Lalli also belong to the *Rhizomarasmius* clade. An emendation of the genus *Rhizomarasmius* is thus proposed to accommodate these additional taxa.

Material and methods

Herbarium material

Basidiomata were studied from herbarium material preserved in herbaria AQUI, BRNM, LIP, and SEST, as well as material from the authors’ personal herbaria. Macroscopic descriptions are adapted from the collectors’ notes. Colors are coded following Kornup and Wanscher (1978). Microscopic observations were made in 5 % KOH (aqueous solution), Melzer’s reagent (0.5 g I, 1.5 g IK, 20 g chloral hydrate, 20 cl H₂O), and sulfobenzaldehyde (SBA: 80 % SO₄H₂, benzaldehyde, 50/50 vol., extemporaneous mix). Spore dimensions are estimated from a natural deposit on the stipe surface and from pictures taken on a digital camera Moticam1000 connected to a microscope Nachet Andromede 0181.

DNA extraction, amplification, and sequencing

DNA extraction from dried tissue and PCR amplification were carried out with the REDEExtract-N-Amp[™] Plant PCR Kit (Sigma-Aldrich, St. Louis, MO, USA), following the manufacturer’s instructions. The internal transcribed spacer region (ITS) and the first ca. 1000 bp of the nuclear ribosomal large subunit 28S rDNA of the ribosomal DNA were amplified and sequenced with ITS-1 F/ITS-4 (Gardes and Bruns 1993) and LR0R/LR7 (O’Donnell et al. 1997), respectively. Repeated attempts to obtain 28S sequences from the holotype of *Gloiocephala resinopunctata* failed.

Phylogenetic analyses

Based on preliminary BLASTn searches, a set of select Physalacriaceae sequences (ITS and 28S) were downloaded from the GenBank (<http://www.ncbi.nlm.nih.gov/genbank/>) database to include in analyses, as well as additional sequences generated by us for this study. The origin of sequences generated for this study is provided in Table 1.

Table 1

Species	Origin	Leg	Herbarium n°	ITS	28S
<i>Cibaomyces glutinis</i>	France	P.-A. Moreau	PAM99082601 (LIP)	KM588673	
<i>Cyptotrama asprata</i>	France, Martinique	C. Lécuro	CL/Mart03.156 (LIP)	KM588682	
<i>Cyptotrama fagiphila</i>	Spain	J.L. Pérez-Butrón	SEST06071604 (BRNM 751955, holotype)	KM588686	KM588686
<i>Cyptotrama fagiphila</i>	Spain	J.L. Pérez-Butrón	SEST09081503	KM588687	KM588687

Species	Origin	Leg	Herbarium n°	ITS	28S
<i>Cryptotrama songolarum</i>	Congo Brazzaville	Songola people	Y. Ankei A3 (LIP, holotype)	KM588685	
<i>Laccariopsis mediterranea</i>	Italy	G. Turrini	TO AV230467	KM588671	KM588691
<i>Laccariopsis mediterranea</i>	Italy	A. Pierotti	AP2011111204 (TO AVP378)	KM588680	
<i>Laccariopsis mediterranea</i>	Italy	A. Vizzini	TO AV230471	KM588681	
<i>Rhizomarasmius oreinus</i>	Italy	G. Pacioni and G. Lalli	AQUI 6763 (holotype)	KM588676	
<i>Rhizomarasmius oreinus</i>	Italy		AQUI 6116	KM588678	
<i>Rhizomarasmius oreinus</i>	Italy		AQUI 4558	KM588677	
<i>Rhizomarasmius oreinus</i>	Italy		AQUI 6115	KM588679	
<i>Rhizomarasmius oreinus</i>	Italy	A. Alpago- Novello	VA10.453 (BRNM 751553)	KM588669	KM588689
<i>Rhizomarasmius oreinus</i>	Italy	A. Alpago- Novello	VA10.489 (BRNM 751554)	KM588670	KM588690
<i>Rhizomarasmius pyrrocephalus</i>	Canada, Québec	R. Lebeuf and A. Paul	PAMCan13.86 (LIP)	KM588675	
<i>Rhizomarasmius setosus</i>	Italy	V. Antonín	VA10-459 (BRNM 736121)	KM588674	KM588688
<i>Rhizomarasmius undatus</i>	France	C. Hannoire	PAM07092201 (LIP)	KM588672	

Datasets were aligned with Clustal W (Higgins et al. [1994](#)). Alignments were carefully refined by eye with the editor in Mega 4.0 (Tamura et al. [2007](#)). Bayesian analyses were conducted in Mr Bayes v3.1 (Ronquist and Huelsenbeck [2003](#)). According to the Bayesian Information Criterion (BIC) score, K80 + G (K2P) was chosen as the optimal substitution model defined by TOPALi v2.5 (Milne et al. [2004](#)) for both the ITS and 28S datasets. Bayesian analyses were conducted using four Metropolis-coupled Markov chain Monte Carlo (MCMC) with one tree sampled per 100th. The first 5,000 trees were excluded of from our analyses. Bayesian Posterior Probabilities (Bayesian PP) for each node were obtained with majority rules with all compatible partitions. Gaps were scored as missing data.

Taxonomy

Cibaomyces glutinis Zhu L. Yang, Y.J. Hao & J. Qin in Hao et al., Phytotaxa 162(4): 203. 2014. (Figs. [1a-c](#) and [2a](#))



Fig. 1

Basidiomata. **a–c** *Cibaomyces glutinis*. A, C: PAM96082601. B: unpublished drawing by René Maire (MPU). **d** *Rhizomarasmius setosus* PAM95091202. **e** *Rhizomarasmius oreinus*, AQUI 6763 (HOLOTYPE), **f–h**: *Cyptotrama fagiphila*. F: SEST-09081503. G: BRNM 751955 (HOLOTYPE). H: JVG 1060708. Credits: A,C, E: P.-A. Moreau; B: V. Bourgade/MPU; E: G. Lalli; F-H : J.-L. Pérez-Butrón

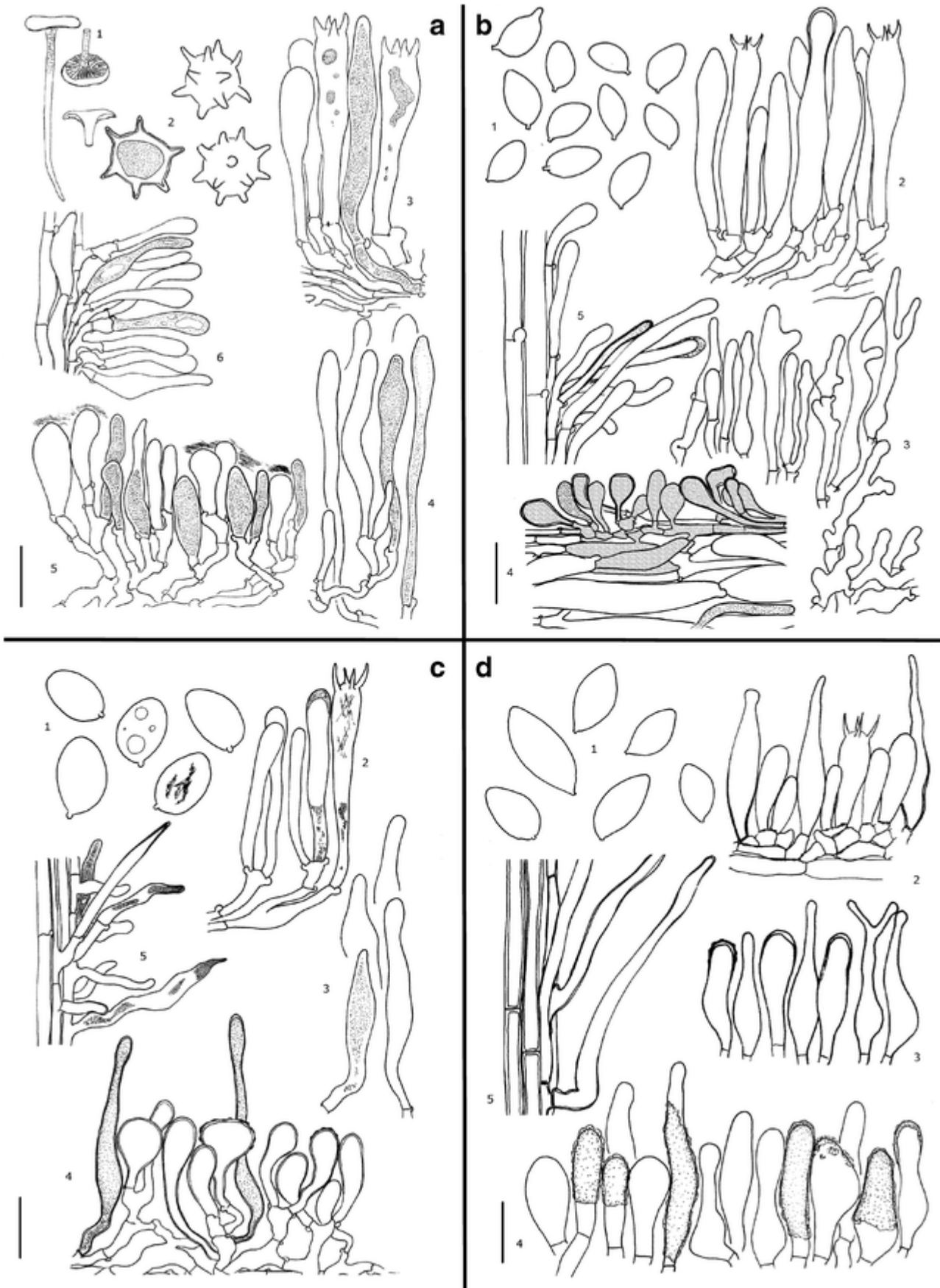
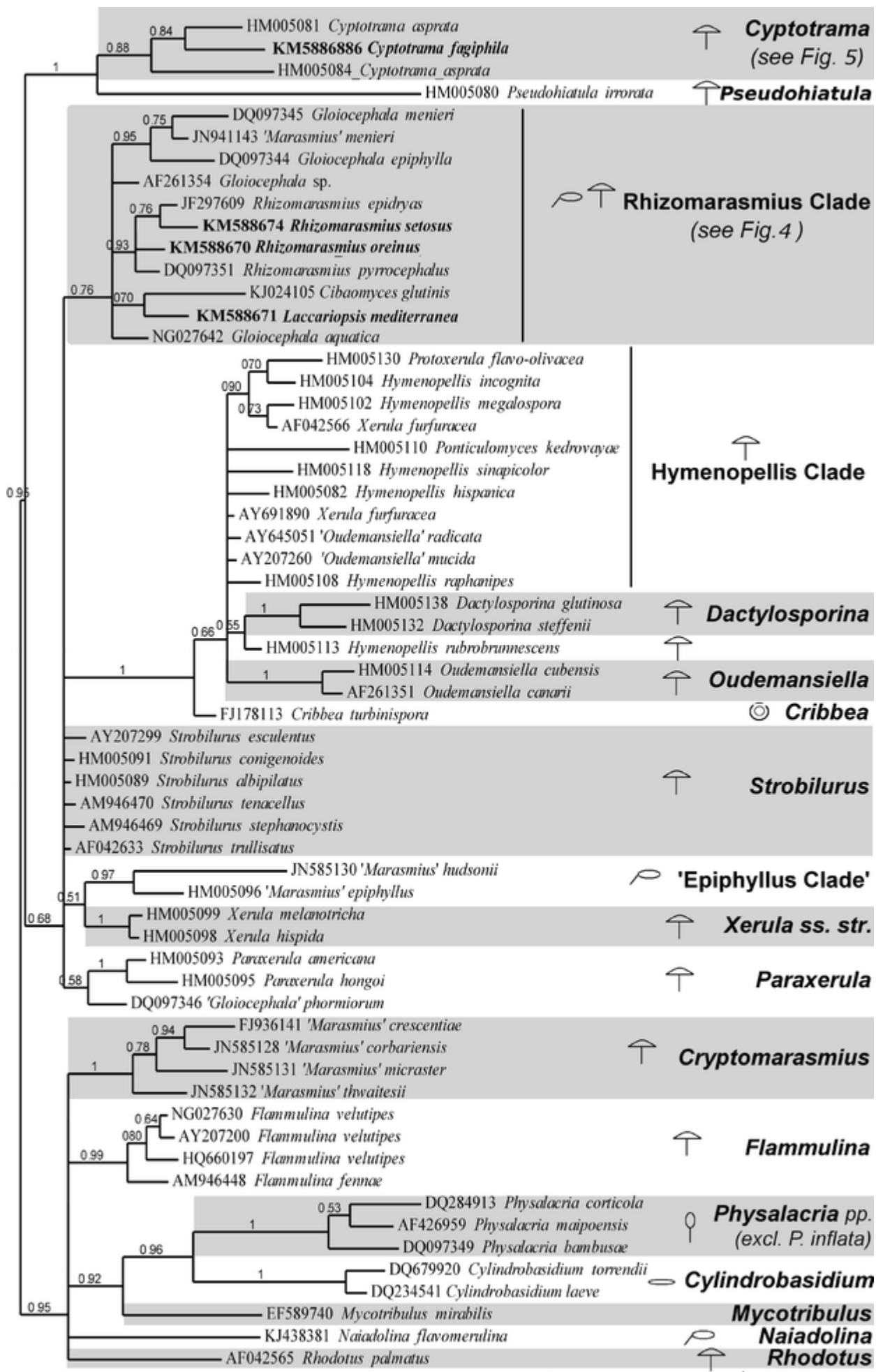


Fig. 2

Microscopic features. **a** *Cibaomyces glutinis*. 1: Basidiomata (facsimile of unpublished drawings by René Maire, MPU). 2: spores. 3: hymenium and subhymenium, cross-section, with basidia and one

gloeocystidium. 4: cheilocystidia. 5: pileipellis, cross-section. 6: stipitipellis, cross-section (PAM99082803). **b** *Cyptotrampa fagiphila* (JVG1060708A). 1: spores. 2: hymenium and subhymenium, cross-section, with basidia and one pleurocystidium. 3: cheilocystidia. 4: pileipellis, cross-section. 5: stipitipellis, cross-section. **c** *Rhizomarasmius oreinus* (AQUI 4558). 1: spores. 2: hymenium and subhymenium, cross-section, with basidia and one pleurocystidium. 3: cheilocystidia. pileipellis, cross-section. 4: pileipellis, cross-section. 5: stipitipellis with one hair and a portion of another, cross-section. **d** *Rhizomarasmius setosus* (PAM95091202, spores from M. Bon 24 Oct 1987, LIP). 1: spores. 2: hymenium and subhymenium, cross-section, with basidia and one pleurocystidium. 3: cheilocystidia. pileipellis, cross-section. 4: pileipellis, cross-section. 5: stipitipellis with one hair and a portion of another, cross-section. Scale bar = 1 cm (basidiomata), 10 µm (spores), 20 µm (basidia, cystidia), 40 µm (pileipellis and stipitipellis). Drawings by P.-A. Moreau

Illustrations. Moreau ([1997](#):146, as “*Hygrophoraceae* sp.”), Hao et al. ([2014](#):204).



0.3

↑ agaricoid
○ corticioid

⤴ cantharellloid (veined hymenophore)
○ sequesterate

⤴ Physalacrioid

Fig. 3

Phylogenetic reconstruction of Physalacriaceae (Rhizomarasmius-clade) based on ITS rDNA sequences. Species of *Xerula* were selected as outgroups

Description. Pileus 8–15–(20) mm, convex-hemispherical then flattened to slightly depressed, smooth, adherent-viscidulous, not striate, at first pure white then pale yellowish on disk, turning reddish brown with age; margin smooth, slightly incurved. Lamellae distant (16–20 reaching stipe, one lamellulae per lamella), slightly to distinctly decurrent, thick, white; edge white, gelatinized, secreting reddish droplets also present on sides; spore print not obtained, presumably white. Stipe 30–40–(60) × 2 mm, progressively thickened at base to slightly rooting, pale yellowish covered by a minute greyish pruina, then punctuate by reddish exudation dots on upper part, turning brownish from base with age, fistulose with enlarged cavity at base. Context hyaline in stipe cortex and hymenopodium, well-distinct from pileus context which is pure white and soft. Smell weakly fungoid when cut, taste none.

Spores 9.5–12 µm diam. (without excrescences), not amyloid, not cyanophilous, before maturity spherical to slightly angular, when mature with 20–30 spine-like excrescences up to 3 µm long; apiculus protruding, up to 5 µm long; content with a large oily drop, brownish in KOH when mature, blackening in sulfobenzaldehyde (SBA). Basidia 50–80 × 12–15 µm, 4-spored, broadly clavate, base often tapering, sterigmata up to 9 µm long, clamped. Subhymenium pseudoparenchymatous, not gelatinized. Lamella edge sterile, gelatinized; cheilocystidia (gloeocystidia) protruding in clusters, 50–80 × 8–10 µm, cylindrical to lageniform, filled by numerous oily droplets, blackening in SBA. Pleurocystidia (gloeocystidia) sparse, fusiform to cylindrical, 45–70 × 7–10 µm, mostly with 1–3 oily droplets, blackening in SBA. Hymenophoral trama subregular with weak bilateral tendency, homomorphous. Pileipellis a pileocystidiate ixohymenoderm; elements cylindrical to clavate or sphero-pedunculate, colourless, forming a subregular hymenoderm, mixed with numerous gloeocystidia 30–45 × 5–8 µm, cylindrical to slightly clavate, with brownish content in KOH and blackening in SBA, more abundant at disc; subpellis thin, compact, made of slender hyphae 2–2.5 µm wide. Pileus trama gelatinized, made of slender hyphae 2–3 µm wide, mixed with large, thin-walled physalohyphae up to 25 µm wide. Stipitipellis an ixohymenoderm with cylindrical to clavate elements, mixed with numerous worm-shaped gloeocystidia measuring 50–70 × 5–7 µm, with yellow content not darkening in KOH, all with numerous oily inclusions. Resinoid secretions on hymenium and stipe reddish, not soluble in water and KOH but in alcohol (R. Maire, unpublished notes), blackening in SBA. No pigment seen, but yellowish content of gloeocystidia. Clamps present at all septa.

Collections examined. **FRANCE:** Haute-Marne, Marac, plateau de Langres, along a rivulet under *Crataegus*, on very wet muddy soil, not far from *Betula* and *Quercus*, 8 Oct 1984, F. Fourot and J.-P. Maurice, M. Bon 84-254 (LIP; duplicate in herb. E. Horak); Savoie, Landry, domanial forest, 45°33'56.96" N, 6°44'54.84" E, on clay soil along a rivulet in a ravine forest, under *Corylus avellana*, *Picea abies* and *Juglans regia*, linked to buried twigs of *Corylus*, 940 m, 26 Aug 1996, P.-A. Moreau, PAM 96082601 (herb. E. Horak); *ibidem*, P.-A. Moreau, PAM 99082803 (LIP). **GERMANY:** Thüringen, near the village Ballstädt, Northern side of the Fahnersche Höhe, 350 m, under frondose trees (*Quercus*, *Tilia*, *Betula*, possibly *Corylus*) with some planted conifers (*Picea* ?), 8 Sept 1996, F. Gröger (herb. E. Horak ZT6144).

Other documented report: **FRANCE:** Haute-Marne, Vignory, « talus du chemin creux de Ribévaux », mixed broadleaved forest (beech, oak with dominant *Corylus* thicket), on bare soil, one basidiome (lost), 18 Sept 1934, R. Maire (MPU, personal notes of R. Maire, material lost).

Observations: This notable species is only known to us from four collections from France (the first, of R. Maire in 1934, probably lost) and one from Germany. The first collection made by P.-A. M. was described, without name (and erroneously placed in the Hygrophoraceae; Moreau [1997](#)), with a color picture. In reaction to this article, two collections came to our knowledge: the late F. Fourot (comm. pers.) directed us to a collection he submitted to M. Bon 1984, who named it “*Oudemansiella cf. kuehneri*” and kindly sent to us a specimen and corresponding notes; E. Ludwig (comm. pers.) directed us to F. Gröger in Germany, who already sent his own collection to E. Horak. Finally a new specimen was found after careful search at the Savoy locality (annual visits on the site between 1996 and 2011 only provided three basidiomata, the last observed in 1999).

An additional, carefully detailed record of this fungus was discovered within René Maire’s numerous unclassified notes preserved at MPU under a provisional name “*Omphalia haemastigma*”. The locality, now known as “combe de Ribévaux”, is only 70 km (43 miles) from F. Fourot’s collection site at Marac. As far as we could trace Maire never published this collection, and unfortunately, the corresponding specimen, preserved by Maire in 80 % alcohol, has been likely lost with many other liquid collections before Maire’s herbarium reached MPU.

It was another surprise to read the description of *Cibaomyces glutinis* by Hao et al. ([2014](#)) from two collections from Yunnan (China) and Japan a few days before the planned submission of the present study. Comparisons between the published microscopic description and our taxon left no doubt about the conspecificity of our European collections with *C. glutinis*, a conclusion that was confirmed by the sequences kindly sent to us by their authors (Fig. [3](#)). The macroscopic description given by Hao et al. ([2014](#)) concerns developed specimens reaching 4.5 cm in diameter in pileus, 9.5 cm in height in stipe (twice larger than the European specimens), and with a broader range of spore size, reaching 14(–15) µm in diameter. In addition to the extension of the geographical distribution range of this species to Eurasia, we add to the knowledge of this species our observation of orange exudates and of the black reaction of oily content of spores and gloeohyphae with sulfoaldehydic reagents, not observed by the original authors.

Three ITS sequences are available for *C. glutinis* (Fig. [3](#)), from China (KJ0024101), Japan (KJ024100), and France (KM588673), respectively, with some significant differences. Pairwise alignments under BioEdit provide the following similarity (total length of the alignment: 735 bp): China/Japan: 98.2 % (five subst, six ins/del); China/France: 95.9 % (20 subst, four ins/del); Japan/France: 95.1 % (21 subst, eight ins/del). Phylogenetic analyses (Fig. [3](#)) do not reflect these differences which are interpreted here as intraspecific variability between fragmented populations, in correlation with geographical distances.

Cibaomyces glutinis was observed in the Savoy locality on a deep soil rich in buried branches and roots of *Corylus avellana* (hazelnut tree) and a contact could be found with a dead twig of this tree. Hao et al. ([2014](#)) reported it on buried wood of Fagaceae, suggesting this species to be purely saprobic. The presence of *Corylus* on wet, clay soil seems to be a common point to most European reports of this species.

Ludwig ([1997](#)) mentioned Moreau’s collection (as “*Hygroaster* sp.”) in comparison with other gibbose-spored species while describing his *Hygroaster lacteus* E. Ludw. and Ryberg (Ludwig [1997](#)). No other taxon cited by Ludwig as *Hygroaster* spp. is likely to have affinities with the Physalacriaceae.

Cyptotrama fagiphila Vila, Pérez-Butrón and P.-A. Moreau, sp. nov. (Figs. [1f-h](#) and [2b](#))

Mycobank MB810294

Etymology from Latin, *fagi-*, *Fagus*, *i*, m. (beech), and *philus*, *a*, *um* (loving), derived from Greek *φίλος*.

Diagnosis:

Pileus up to 60 mm diam, convex then flattened with depressed center, striate-sulcate at margin, cream white to greyish, fuliginous grey at center, sometimes with greenish tinges. Lamellae distant, adnate to subdecurrent, whitish to cream-yellow. Stipe white to whitish with brownish fibrils. Spores 8–11 × 5–6.5 μm, elliptical to amygdaliform, hyaline, smooth, not amyloid. Cheilocystidia inconspicuous, 31–57 × 6–9.5 μm, clavate to subfusiform, thin-walled. Pileipellis an hymeniderm of clavate cells 20–60 × 8–30 μm, with vacuolar pigment. Clamps present. On decaying branches of *Fagus sylvatica*.

Holotype: Spain, Burgos, Castrobaroto, 16-7-2006, leg. J.L. Pérez-Butrón (BRNM 751955), isotypes: pers. herb. J. Vila JVG 1060716A and BRNM 751956.

Description. Pileus up to 60 mm diam., elastic, young convex, later plano-convex, usually centrally depressed, sometimes umbonate, margin regular to undulate-lobate at maturity; pileipellis not separable, smooth, silky, somewhat greasy when young, later dry, minutely cracked under lens, sulcate-caniculate near the margin; creamy white to cream-greyish, with faint greenish tint in some basidiomata, paler along margin, disc fuliginous grey; not hygrophorous. Lamellae distant, thick, not fragile, adnate to shortly decurrent (sinuate), up to 7 mm broad, ventricose, intervenose and anastomosing in sinuses, sometimes furcate, white to yellowish cream. Stipe up to 60 × 7 mm, cylindrical, sometimes compressed or canaliculate, fistulose, broader in the upper part, curved, attenuate or bulbous at base, white with brown fibrils, elastic, fibrose; basal mycelium white. Context white, elastic, reviviscent. Smell fungoid, not remarkable.

Spores (7)–8–11–(12) × (4.2)–5–6–(7) μm, on average 9.2 × 5.6 μm, Qm = 1.6, ellipsoidal to amygdaliform, with a conical apex, becoming umbonate before germination, and a prominent apiculus, hyaline, smooth, not amyloid, faintly cyanophilous, guttulate, with a thickened wall. Basidia 40–55 × 7–9 μm, 4-spored, narrowly claviform to subcylindric, scarcely clamped. Edge sterile, covered by very polymorphic cheilocystidia, on old parts locally replaced by proliferating tramal ends (Fig. 2b3, right bottom). No true pleurocystidia or pseudocystidia seen, but occasionally weakly differentiated basidioles with thickened wall at apex. Hymenophoral trama not amyloid nor dextrinoid, with a narrow mediostratum of subregular sarcodimitic structure, with fusiform elements reaching 165 × 5–27 μm and cylindrical, sometimes moniliform hyphae, usually elongated, hyaline, septate; subhymenium ramose, thick (30–40 μm) and well-differentiated, of distinctly bilateral orientation, made of slender hyphae 3–4.5 μm diam., short and often ramose. Pileipellis a regular slightly gelatinized hymenoderm, made of claviform to subglobose, sometimes pyriform cells, thick-walled (up to 1.5 μm), with diffuse greyish vacuolar pigment, interconnected by hyaline, cylindric hyphae 4–18 μm in diam., septate. Caulocystidia from the apical part of the stipe, 24–55 × 5–12 μm, lageniform, claviform, fusiform, thick-walled, clamped. Caulocystidia from the basal part of the stipe 26–70–(87) × 6–13–(15) μm, claviform, fusiform, sinuose. Near stipe base, hyphae diverticulate mixed with hyaline setae, thick-walled, filiform, acute, broadened near the base, reaching 120–250 × 3–10 μm. Hyphae in stipe context hyaline, not dextrinoid. Clamps present at all septa.

Ecology and distribution. Lignicolous, growing single to gregarious, on old dead trunks covered by mosses and dead branches of *Fagus sylvatica*, in a calcicolous beech forest, 900 m, May to August. Only known from Eastern Pyrenees (Spain).

Collections examined. **SPAIN:** Burgos, Castrobarro, *Fagus* forest of Sorrebalenco, UTM 30 T VN6869, 900 m, on decaying and mossy branches of *Fagus sylvatica*, 30 May 2004, J.L. Pérez-Butrón (SEST-04053001); *ibidem*, 8 Jul 2006, J.L. Pérez-Butrón (SEST-06070805; BRNM 751956, JVG 1060708A); *ibidem*, 16 Jul 2006, J.L. Pérez-Butrón (BRNM 751955, holotype; JVG 1060716A isotype); *ibidem*, 22 Jul 2006, J.L. Pérez-Butrón (SEST-06072203); *ibidem*, 19 Aug 2006, J.L. Pérez-Butrón (SEST-06081905); *ibidem*, 26 Aug 2006, J.L. Pérez-Butrón (SEST-06082601); *ibidem*, 15 Aug 2009, J.L. Pérez-Butrón (SEST-09081503).

Observations. This species shows an unusual combination, within European Agaricales, of systematically important macro- and microscopic features: bilateral trama, regular acystidiate hymeniderm, presence of cheilocystidia, and collybioid-xeruloid habit (fibrous-rigid stipe, reviviscence, white distant lamellae). The genus *Hydropus* Kühner ex Singer was envisaged, but the absence of lactiferous hyphae and the regular hymeniform pileipellis, as well as the tough consistency made us reject a relationship with this genus and other mycenoid genera. The relatively large basidia and pileipellis structure are found in various genera of Physalacriaceae (Petersen and Hughes 2010) and the hypothesis was retained, leading by default to the genus *Cyptotrama* (Singer 1986) because of the bilateral trama. This placement was confirmed by DNA analyses (Figs. 4 and 5). The closest species is the type of the genus, *C. macrobasidium* Singer (*see* Discussion), described from South America and so far only known from the type collection. Unfortunately, the material kept at MICH was too scanty to be authorized for DNA analyses (P. Rogers, pers. comm.); comparisons could be made thanks to E. Horak's examination of this material (Fig. 6a and b; *see also* Horak 1968). *C. macrobasidium* differs mainly from *C. fagiphila* by the following features:

- remarkable wall thickening of elements of pileipellis in *C. macrobasidiatum* (as well as hymenial cystidia), only moderately thickened elements in *C. fagiphila*;
- presence of abundant pleurocystidia in *C. macrobasidium*, rare and only poorly differentiated pleurocystidia with thickened apex in *C. fagiphila*;
- presence of true, thick-walled cheilocystidia in *C. macrobasidium*, only slender polymorphic hair-like cystidia in *C. fagiphila*.

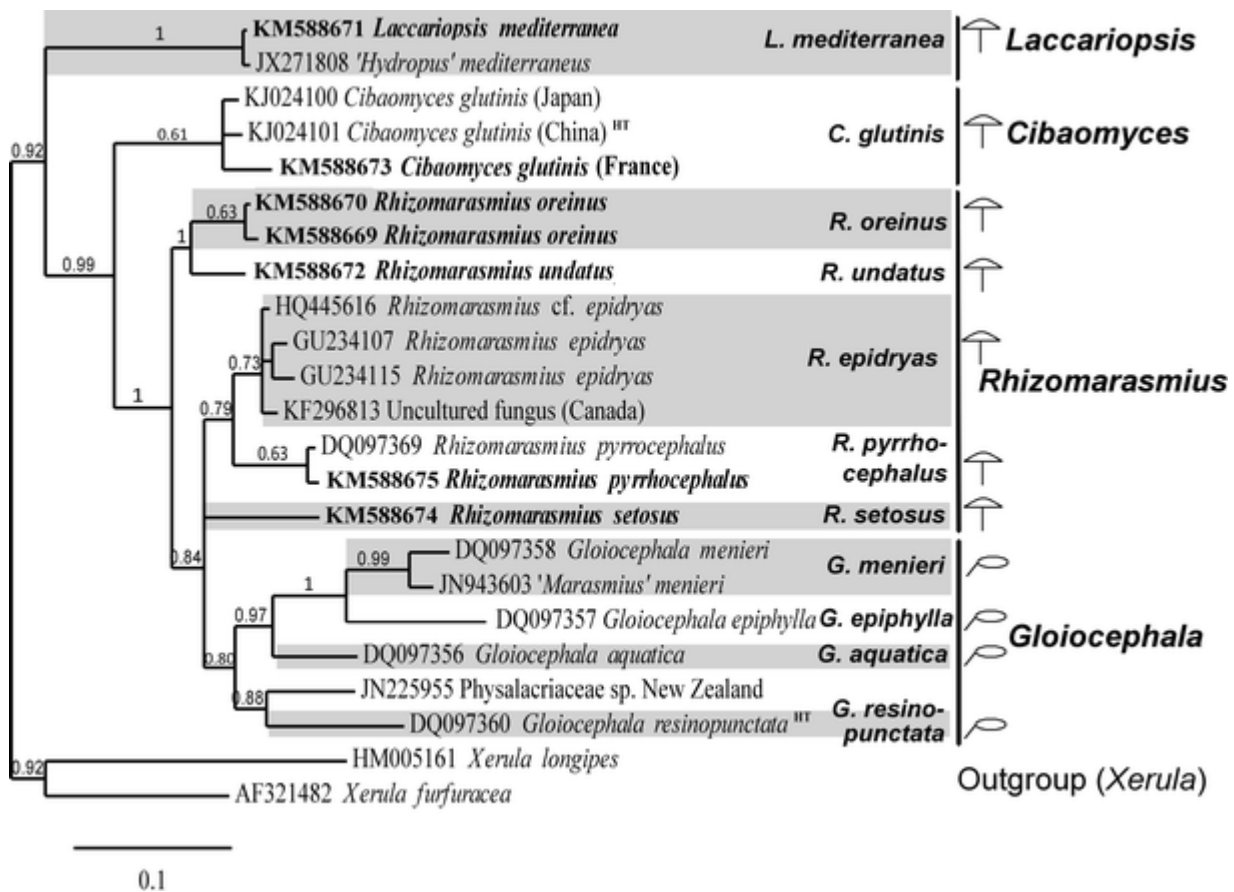


Fig. 4

Phylogenetic reconstruction of Physalacriaceae based on LSU rDNA sequences from Bayesian analysis. The cladogram is mid-rooted

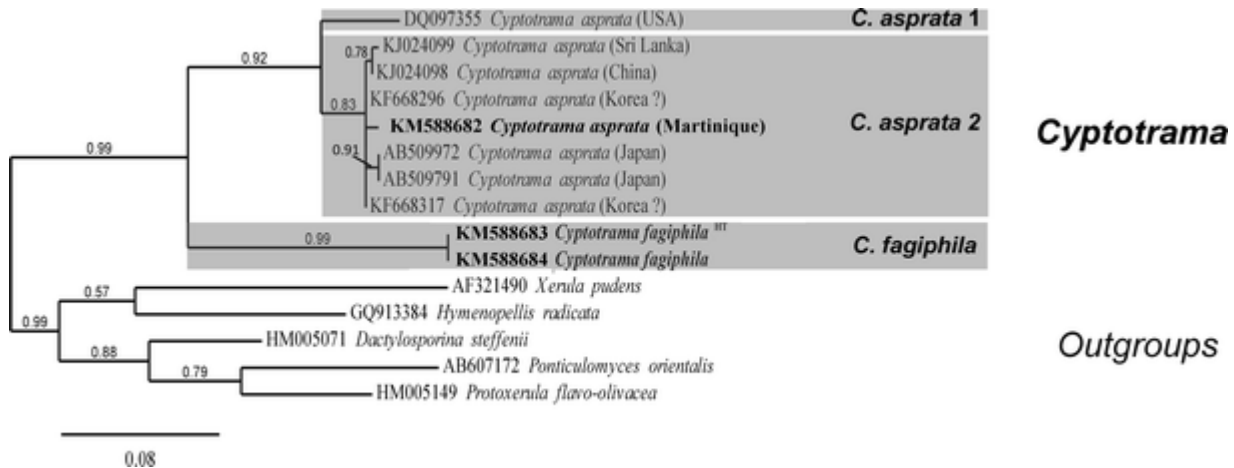


Fig. 5

Phylogenetic reconstruction of Physalacriaceae (Cyptotrama-clade) based on ITS rDNA sequences from Bayesian analysis. Species of *Xerula*, *Hymenopellis*, *Dactylosporina*, *Ponticulomyces* and *Protoxerula* were selected as outgroups

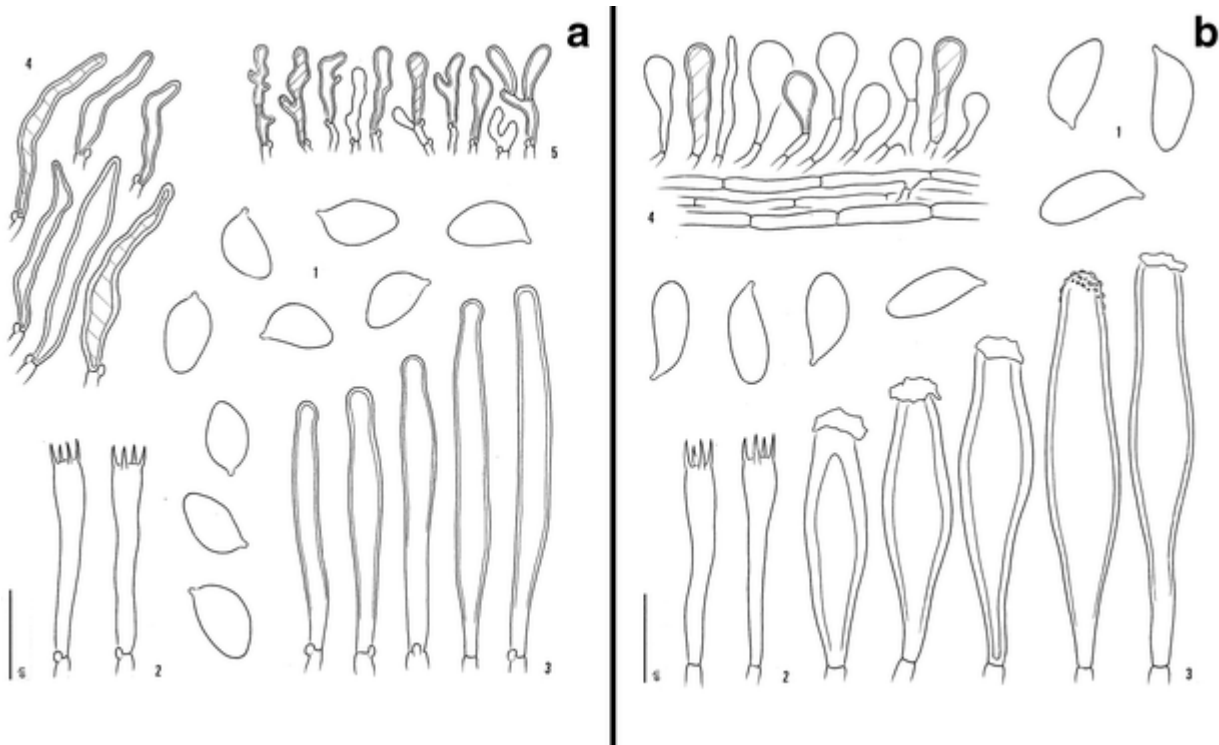


Fig. 6

Microscopical features **a** *Cyptotrama hygrocyboides* (holotype, SGO). 1: spores. 2: basidia. 3: cheilocystidia. 4: pileipellis, cross-section. **b** *Cyptotrama platensis* (holotype, F). 1: spores. 2: basidia. 3: cheilocystidia. 4: pileipellis, cross-section. 5: caulocystidia. Scale bar = 10 μm (spores), 20 μm (basidia and cystidia), 40 μm (pileipellis and stipitipellis). Drawings by E. Horak

No European or north-temperate species is comparable to *C. fagiphila* with such a combination of features. This is the first report of the genus for Europe.

Rhizomarasmius R.H. Petersen, *emend.*

Emended definition. Basidiomata slender, small to moderately large. Pileus convex to hemispherical, smooth, but not glabrous, occasionally sticky, usually radially undulate, small in relation to stipe length. Lamellae subsinuate to arcuate, relatively thick, not crowded, white to off-white. Stipe long in relation to pileus diameter, apically pale, darkening from base to fuscous or black, pruinose, minutely velutinous or with small hairs, insititious or with a pseudorrhiza; when pseudorrhiza present then prolonged, not inflated, black, often with branched mycelium in humus substrate, attached to rotten, buried, small woody twigs, roots or other plant material. Smell indistinct.

Pileipellis a hymeniform layer of clavate to sphaerope-dunculate hyphal tips, possibly gelatinized, with lageniform, lecithiform or elongate pileocystidia. Hymenium comprising basidia and hymenial cystidia; hymenial cystidia tapered upwards to obtusely rostrate or subcapitate apex, sometimes with apical droplets, protruding or not at lamella sides. Lamella edge sterile to substerile. Caulocystidia abundant, elongate-fusiform to tapered with rounded apex. Stipe context monomitic, not sarcodimitic; hyphae not dextrinoid or only in stipititrama and stipitipellis at apex, clamped. Basidiospores white in print, thin- to slightly thick-walled, not amyloid, not cyanophilic, unornamented, ellipsoid, almond- to lemon-shaped.

Type species: *Marasmius pyrrocephalus* Berk. (Petersen [2000](#))

Currently recognized species: *R. epidryas* (Kühner ex A. Ronikier) A. Ronikier and M. Ronikier, *R. oreinus* (Pacioni and Lalli) comb. nov., *R. pyrrocephalus* (Berk.) R.H. Petersen, *R. setosus* (Sowerby) comb. nov., *R. undatus* (Berk.) R.H. Petersen.

Rhizomarasmius oreinus (Pacioni and Lalli) Vizzini, Antonín and A. Urb., comb. nov. (Figs. [1e](#) and [2c](#))

MycoBank MB810295

Basionym : *Oudemansiella oreina* Pacioni and Lalli, *Micol. Veg. Medit.* 4(2): 31 ([1989](#)).

Taxonomic synonym : *Xerula oreina* (Pacioni and Lalli) Contu in Signorello and Contu, *Micol. Veget. Medit.* 13(1): 61 (Pacioni and Lalli [1989](#)).

Description.

Basidioma single. Pileus 9–20 mm diam., almost hemispherical when young, then (plano) convex, obtuse or with a small papilla, then applanate to slightly depressed at centre, involute then inflexed at margin, hygrophanous, never translucently striate or only slightly at margin, dry or slightly sticky, smooth, glabrous, watery (dark) red-brown (paler than 7C–D6–7; Kornup and Wanscher [1978](#)), drying-out to pale orange-brown to (yellow) ochraceous (orangish). Lamellae distant, L = 15–18, l = 1–2, emarginate and ± broadly attached to slightly decurrent with tooth, cream to cream yellowish, with concolorous, finely pubescent edge. Stipe long and slender, up to 80 × 1.5–2.5 mm, rooting, cylindrical, slightly broadened at apex, entirely tomentose pubescent, concolorous with lamellae at apex, brown (7E–F6–7) towards base. Context brownish in stipe base, otherwise whitish, without any distinct smell or with slightly fungoid smell, taste mild.

Spores (10.5)–11.5–13.5–(14) × (7.5)–8.5–9.5–(10) µm, average 12.5 × 8.8 µm, Qm = 1.42–1.45, ellipsoid, broadly ellipsoid, ellipsoid-fusoid, thin-walled, non-dextrinoid, with one large guttula. Basidia 45–60 × 12–15 µm, 4-spored, clavate. Basidioles up to 55 × 6–14 µm, clavate, fusoid or cylindrical. Cheilocystidia numerous, 35–95 × (7)–9–15 µm, fusoid, subcylindrical, often capitate, sometimes rostrate, thin-walled, clamped. Pleurocystidia scattered, 47–88 × 6–12 µm, fusoid, clavate, subcylindrical, sometimes capitate, sometimes irregular, thin-walled. Pileipellis a hymeniderm covered with a gelatinous layer, composed of cells 20–47 × 10.5–17 µm, clavate, subutriform, smooth, thin-walled, clamped. Pileocystidia scattered, c. 40–42 × 5–8 µm, fusoid, rostrate, sometimes capitate, thin-walled, clamped. Stipitipellis a cutis of cylindrical, parallel, slightly thick-walled, clamped, non-dextrinoid, up to 5 (–7) µm wide hyphae. Caulocystidia 35–76 × 4–10 µm, adpressed to erect, cylindrical, fusoid, (sub)lageniform, obtuse, thin- to often slightly thick-walled, sometimes covered with a granular matter.

Collections examined. Italy: Capistrello (AQ), Piano della Renga, on a meadow, 12 Nov 1987, G. Pacioni and G. Lalli (AQUI 6763, HOLOTYPE); Aragno (AQ), L'Inforatura, on a meadow, 25 Oct 2002 (AQUI 6116); Votigno (RE), on a meadow, 7 Oct 2005 (AQUI 4558); Monti Sibillini, Castelluccio, Piano di Castelluccio, on soil, in grass on a meadow, in connection with *Consolida regalis*, 21 Oct 2010, A. Alpago Novello (Antonín 10.453, BRNM 751553); *ibidem.* (different place), in connection with *Erodium cicutarium*, 23 Oct 2010, A. Alpago Novello (Antonín 10.489, BRNM 751554).

Observations. As pointed out by Pacioni and Lalli ([1989](#)) and Contu ([2000](#)) *Rhizomarasmius oreinus* is very similar to *Laccariopsis mediterranea*, which especially differs in having more robust basidiomata (pileus 15–32 mm broad, stipe 2–4 mm wide), subdecurrent to decurrent, thick

lamellae, and by growing in Mediterranean coastal dunes (Antonín and Noordeloos [2010](#); Vizzini et al. [2012](#)). *Rhizomarasmius oreinus* presents a regular ixohymenoderm like all species known in the genus, when *L. mediterranea* has a proliferant, early destructured pileipellis reminiscent of the continuous pileipellis evolution of *Flammulina* (as “cuticula pseudohymeniformis” by Pacioni and Lalli [1985](#)).

Rhizomarasmius setosus (Sowerby) Antonín and A. Urb., comb. nov.

MycoBank MB810296

Basionym: *Agaricus setosus* Sowerby, Col. Fig. Engl. Fungi 3: 25, pl. 302 (1803)

Homotypic synonyms: *Mycena setosa* (Sowerby) Gillet, Hymenomyc. Fr.: 289 (1876); *Pseudomyцена setosa* (Sowerby) Cejp, Publ. Fac. Sci. Charles 98: 140 (1930); *Marasmius setosus* (Sowerby) Noordel., Persoonia 13: 241 (1987).

Taxonomic synonyms: *Marasmius recubans* Quéf., Mém. Soc. Emul. Montbéliard, sér. II, 5: 355 (1873); *Androsaceus eufoliatu*s Kühner, Bull. trimest. Soc. Mycol. France 43: 111 ([1927](#)); *Marasmius eufoliatu*s (Kühner) Kühner, Botaniste 25: 94 ([1933](#)).

Selected descriptions: Kühner ([1927](#): 111–112, 1933: 94–95, as *Marasmius eufoliatu*s); Breitenbach and Kränzlin ([1991](#), as *Marasmius recubans*); Bon ([1999](#), as *Marasmius setosus*); Antonín and Noordeloos ([2010](#): 125–128, as *Marasmius setosus*).

Collections examined. **FRANCE:** massif de l'Escandorgue (Hérault), on petioles of decaying leaves, 24 Oct 1987, *P. Bertéa* (coll. M. Bon, LIP); Poigny-la-Forêt (Yvelines), réserve biologique du Marais du Cerisaie, on petioles of decaying leaves of *Betula pendula*, 12 Sep 1995, *P.-A. Moreau* (PAM95091202, LIP); Wissant (Pas-de-Calais), Sentier du Fartz, on petioles of decaying leaves of *Salix caprea*, 30 Aug 2014, *M. Anquez* and *P.-A. Moreau* (PAM14083002, LIP).

Observations. The inclusion of *M. setosus* in the genus *Rhizomarasmius* was for us unpredictable considering the typical “marasmioid” habitus of this species, habitat on leaf petioles, absence of a pseudorrhiza, dextrinoidity of stipe context, and elongate spores. However, DNA analyses based on three distinct collections reveal that *M. setosus* incontestably belongs to the *Rhizomarasmius*-clade, and the 28S phylogeny (Fig. [4](#)) places it close to *R. epidryas*. Retrospectively this position is justified by the presence of pleurocystidia, large basidia and cystidiate hymenoderm pileipellis, comparable to the other species of the genus. The abundance of coarsely incrustated pileocystidia was noted on the three French collections studied for building the microscopic plate (Fig. [2d](#)); such elements were also observed by Kühner ([1933](#):95), but not mentioned in subsequent descriptions (Breitenbach and Kränzlin [1991](#)), or as inconstant (Antonín and Noordeloos [2010](#)), but are reminiscent of the incrustations described by Singer ([1960b](#)) on most Neotropical species of *Gloiocephala*. The absence of clamps, mentioned by Antonín and Noordeloos ([2010](#)), is noteworthy in the *Rhizomarasmius* Clade, but possibly inconstant; none of the studied collections for the purpose of this paper showed any clamp on hyphae or basidia. It is not excluded that the placement of *M. setosus* in *Rhizomarasmius* will need a reevaluation when more extra-European taxa are sampled and added to the analyses.

The petiolicolous ecology can be compared to that of the closely related *Gloiocephala*-clade, and whether this species is an early-colonizing saprobe or has biotrophic relations with living leaves before leaf fall is unresolved. *Marasmius saccharinus* (Bastch: Fr.) Fr. probably also belongs here. However, the recent detailed description is based on only one known collection, by P.D. Orton from

England (Antonín and Noordeloos 2010). Therefore, in the absence of molecular data for *M. saccharinus* we refrain from formally proposing a new combination at this time.

Results and discussion

Phylogenetic analysis in the Physalacriaceae

The two nuclear rDNA loci analyzed by Petersen and Hughes (2010), i.e., the ITS and partial 28S regions, provide congruent, but still incomplete phylogenetic hypotheses for the Physalacriaceae. The basal position of *Armillaria* in the family was suggested by Binder et al. (2006), Matheny et al. (2006), and confirmed with ITS + 28S sequences by Hao et al. (2014, Fig. 4). However, when included in the 28S analyses (not shown), *Armillaria* spp. appear nested within the *Rhizomarasmius* clade, a position not confirmed by ITS sequences which are too different between *Armillaria* and the others to be even aligned. When *Armillaria* was selected as an outgroup, the *Physalacria* pp.-*Cylindrobasidium* clade appeared in a derived position. The elimination of *Armillaria* from the dataset improved the alignment and the topology of the LSU tree obtained by mid-point rooting (Fig. 4) and supports the generic treatment of Petersen and Hughes (2010) based on ITS sequences. In this figure the *Physalacria* pp.-*Cylindrobasidium* clade appears well-supported in a basal position, a result congruent with the recent multigene analyses of Henkel et al. (2010). However, the type of the genus *Physalacria*, the north-temperate *P. inflata* (Peck 1882; Corner 1950), is documented by a 28S sequence (GenBank AY293265) which is not easily aligned with the dataset analyzed here, and was finally discarded from the analysis presented in Fig. 4. A new generic placement might be envisaged for *P. bambusae* and related tropical species.

ITS sequences are too diverse within the Physalacriaceae, as already pointed out by Petersen and Hughes (2010), to be aligned at the family or even subfamily levels. As revealed by the LSU analysis (Fig. 4), the *Cyptotrama*-clade is monophyletic and strongly supported, and encompasses the pantropical species *C. asprata* sensu lat. and the new species *C. fagiphila* (Fig. 5).

All *Rhizomarasmius* (*R. pyrrocephalus*, *R. undatus* and *R. epidryas*) and some species of *Gloiocephala* (*G. aquatica*, *G. menieri*, *G. resinopunctata*, and the type species *G. epiphylla*) form a well-supported clade in the ITS as well as 28S analyses (with the exclusion of *Armillaria*), identified as “*Rhizomarasmius* Clade” in Fig. 4. The monophyly of *Gloiocephala* could not be established either in ITS or 28S analyses, nor in those of Hao et al. (2014): the gilled genus *Rhizomarasmius* remains monophyletic with the inclusion of *R. oreinus* and *R. setosus*, when the “reduced forms” (*Gloiocephala* spp.) form distinct paraphyletic lineages (Fig. 4). In the restricted ITS phylogeny presented here *Gloiocephala* is nested within *Rhizomarasmius* and the two European species *R. oreinus* and *R. undatus* form a basal clade (Fig. 3). Thus, no conclusion can be drawn concerning the relationships between *Rhizomarasmius* and *Gloiocephala* with the data currently available.

Cibaomyces glutinis has an ambiguous position, either nested as a basal lineage of the *Rhizomarasmius* Clade (ITS, Fig. 5) or as a sister clade of *Laccariopsis mediterranea* within the same clade (28S, Fig. 4). The combined analysis ITS + 28S presented by Hao et al. (2014) does not robustly support the relationships suggested between *Laccariopsis*, *Cibaomyces* and *Rhizomarasmius*.

The genus *Cyptotrama*, an incomplete puzzle

The placement of the new species described here, *Cyptotrama fagiphila*, in this genus may appear audacious, since this genus has never been reported from Europe. However, prior to DNA analyses of this Pyrenean species the keys to genera by Singer (1986) as well as Horak (1968) conspectus of genera led us to retain *Cyptotrama* as the most likely genus for our species. Indeed, the current concept of *Cyptotrama*, which centers in modern literature around the well-known *C. asprata* (Berk.) Redhead and Ginns (formerly a *Xerulina*), has been considerably enlarged by Singer (1973) and Redhead and Ginns (1980). Originally Singer (1960a) circumscribed the genus for a single species, *C. macrobasidium* Singer, with a dry, regular hymenopellis, thus far the type species is known only from its original collection in South America (Singer 1960a; Horak 1968). *Cyptotrama* was defined by possessing the character of a bilateral hymenophoral trama - an uncommon character in the Physalacriaceae, but also present in the monomitic genera *Pseudohiatula* and *Xerulina* (Singer 1964, also report a bilateral trama for *Flammulina*, contested by Kühner 1980: 768), and in the sarcodimitic species *Xerula setulosa* (Murrill) R.H. Petersen and T.J. Baroni (Petersen and Hughes 2010). Singer (1973, 1986) later broadened his view of *Cyptotrama*, including *Xerulina*, on the basis of the bilateral trama. The current concept of *Cyptotrama*, based on its last emendation by Singer (1986), includes species with more or less gelatinized spiny excrescences such as *C. asprata*, a widespread and well-known species which has fixed this genus in many mycologists' minds (see Petersen and Hughes 2010). Unfortunately, species with hymeniform pileipellis seem to be much rarer, and none is documented with DNA sequences so far.

Cyptotrama sect. *Cyptotrama* encompasses species with clamped hyphae and regular hymeniderm (Singer 1986: 439). The four species cited by Singer (*loc. cit.*), and the more recently described *C. songolarum* Courtec. (Courtecuisse 1995), all known from type collections only, form a rather heterogeneous group. *Cyptotrama macrobasidium* is morphologically very similar to *C. fagiphila*, but differs by strongly thick-walled elements of pileipellis, presence of cheilocystidia similar to pleurocystidia and also thick-walled, and broader spores ($7\text{--}8.5(9) \times 6\text{--}7 \mu\text{m}$ according to Horak 1968: 202).

Cyptotrama hygrocyboides Singer (Fig. 6a) is described from Chile as a bright orange-red species, including the stipe (Singer 1969: 90). Its microscopic features are similar to *C. macrobasidium*, with less thickened cystidia and pileipellis, and might illustrate a link between the apparently very distinct dull-colored species (*C. fagiphila*, *C. macrobasidium*) with white stipe, and the bright yellow or orange species of sect. *Xerulina*. The absence of clamps (Singer 1986: 438) and the metuloid cystidia are illustrated from E. Horak's observations on the holotype (Fig. 6a).

Cyptotrama platensis Singer (Fig. 6b), described from Argentina, is microscopically much more similar to *Xerulina* species. Singer himself (1969: 92) described the pileipellis as an irregular hymeniderm with cystidia and erected elements embedded in a resinaceous matter, macroscopically evoking a small *Xerulina* with only small, floccose scales instead of well-developed spines. This structure is confirmed by E. Horak's observations on the holotype (Fig. 6b); characters of spores and cystidia are very comparable with those of *C. fagiphila* (Fig. 2b).

Cyptotrama dennisii Singer is a neotropical species described from Mexico (Veracruz), with dark brown obtuse to subumbonate pileus, long cylindrical spores ($10\text{--}16 \times 3.5\text{--}6 \mu\text{m}$) and hymenial gloeocystidia instead of thick-walled cystidia. Albeit placed in sect. *Cyptotrama* (Singer 1986), it was originally described with a thick trichoderm of long chains of hyphae. Singer (1973) compared it to several species of *Hydropus* (*H. sabalis* Singer, *H. lipocystis* Singer, and *H. bolivianus* Singer). It is unclear in the non-commented description of Singer (1973) why he attributed this species to *Cyptotrama* rather than to *Hydropus*, in fact, where it would find a more natural place than within

the Physalacriaceae. The type collection (M 8763, F) was not available to us for DNA sequencing, due to its scarceness.

Cyptotrama niveum, cited as provisional name by Singer (1986) in sect. *Cyptotrama*, was validated later (1989) without illustrations from a single collection from Amazonas (Brazil). The description presents a small, marasmioid foliicolous species, pure white, with rather thick subdecurrent lamellae, and gloeocystidia on all surfaces. The bilateral trama and all other features are compatible with the Physalacriaceae, but the absence of true cystidia makes its placement in *Cyptotrama* doubtful. It might have affinities with *Gloiocephala* and *Rhizomarasmius* species. The type material was too scarce to be sequenced.

Cyptotrama songolarum Courtec. was described from Eastern Africa as an unusually large fungus, traditionally eaten by the Songola people, with microscopic characters compatible with sect. *Cyptotrama* (hymeniderm, bilateral trama and thick-walled cheilo- and pleurocystidia). An ITS sequence was generated from the holotype (Y. Ankei A3, LIP), which shares 100 % identity with a sequence accessible in GenBank (AF321366) identified as *Termitomyces eurhizus* (Berk.) R. Heim from Congo Brazzaville (Rouland-Lefevre et al. 2002). All 100 first BLASTn results in GenBank return sequences of *Termitomyces* spp. (results not shown). Morphological revision of the specimen lead to the conclusion that *C. songolarum* belongs to the *Termitomyces striatus*-complex. Because Frøslev et al. (2003) showed a strict continentalism in *Termitomyces* species, a misidentification of the African sample AF321366 sequenced as *T. eurhizus* (Berk.) R. Heim (an Asian species) is suspected. Considering the complexity of taxonomy in the *T. striatus*-complex (Heim 1958; Mossebo et al. 2002), no new combination is proposed for *C. songolarum* at this time.

Phylogenetic analyses based on 28S (Fig. 4) suggest that *C. fagiphila* represents a sister lineage of sect. *Xerulina*, supporting Singer's (1986) and Redhead's (1987) enlarged concepts of the genus, while the ITS analysis (Fig. 5) shows *C. fagiphila* to be nested within various collections of *C. asprata* (Berk.) Redhead & Ginns s. lat. Because of the absence of molecular data on other hymeniderm-forming species of *Cyptotrama*, especially the type species *C. macrobasidium*, we can only conclude that *C. fagiphila* is somewhat distant from *C. asprata*, but we are not able to resolve completely its phylogenetic position relative to other sections of this very polymorphic genus, nor discuss further the pertinence of Singer's (1986:439) infrageneric classification based on the pileus structure and the presence/absence of clamps. The analyses of ITS and 28S sequences registered as "*Cyptotrama asprata*" in GenBank suggest that at least two molecularly distinct species, one east-Asian and Caribbean (*C. asprata* s. str.) and one North American (*C. chrysopepla* (Berk. & M.A. Curtis) Singer), are confused under this name (Fig. 5).

Interestingly, the inclusion of a sequence of *Pseudohiatula irrorata* (Pat.) Singer in our 28S analysis (Fig. 4) confirms Singer's (1986: 439) hypothesis of close relationships between the genera *Cyptotrama* and *Pseudohiatula*, segregated by him in a tribe *Pseudohiatula* and here shown to form a monophyletic clade in the Physalacriaceae.

The *Rhizomarasmius*-clade

Petersen (2000) showed the North American species *Marasmius pyrrhocephalus* Berk. to represent a new clade in the Physalacriaceae, which he named *Rhizomarasmius*. He emphasized the absence of sarcodimitic structure, the presence of a long, rooting stipe in relation with buried plant debris, the presence of pleurocystidia, and a cystidiate hymeniform pileipellis as characteristics of this genus; his conclusions were also supported by studies on mating systems. Based on micromorphology Petersen (2000) also placed "*Marasmius*" *undatus* in his new genus, which has not thus far been confirmed by molecular analyses. Recently another species formerly classified in

Marasmius sect. *Chordales*: *M. epidryas* Kühner ex A. Ronikier, associated with roots of *Dryas* spp., was transferred in *Rhizomarasmius* (Ronikier and Ronikier [2011](#)).

Petersen and Hughes ([2010](#)) and Ronikier and Ronikier ([2011](#)) previously demonstrated that the ITS region of ribosomal DNA was appropriate for delimiting genera in the Physalacriaceae, with a strong inter- and infrageneric variability in both the ITS1 and ITS2 regions. The ITS phylogenetic analysis illustrated in Fig. [3](#) conform to Petersen ([2000](#)), Petersen and Hughes ([2010](#)) and Ronikier and Ronikier ([2011](#)), shows *Rhizomarasmius* to form a well-supported clade, but the relationships with *Gloiocephala* are less distinct here with the addition of new sequences. *Cibaomyces glutinis*, because of its striking stellate spores and red droplets exuded on the lamellae, was indeed thought to represent a new genus. However its ITS1-5.8S-ITS2 sequences were easily aligned with those of *Rhizomarasmius undatus* (82.9 % of similarity), *R. epidryas* (69.3 %) and *R. pyrrocephalus* (84.4 %), but also of *Laccariopsis mediterranea* (80.0 %) which currently is not supported within the *Rhizomarasmius*-clade, but not strongly distant, according to both 28S and ITS analyses (Figs. [4](#) and [3](#)).

One of the most spectacular features of *C. glutinis*, the production of red resinaceous droplets, is also found in “*Gloiocephala resinopunctata* (Manimohan and Thomas [1998](#)). Therefore, only the echinate spores become fundamentally distinctive between *C. glutinis* and the abovementioned taxa. In fact, spore shape in *Physalacriaceae* is quite variable, but star-like spores, similar to those of *C. glutinis*, are so far only known in the neotropical *Dactylosporina steffenii* and related species (Petersen and Hughes [2010](#)), and in the European species *Xerula kuehneri*. This character was emphasized by Petersen and Hughes ([2010](#)) who placed *X. kuehneri* in the genus *Dactylosporina*. Since no relationship is supported between *Dactylosporina* spp. and *C. glutinis* in our study, such a spore feature cannot be retained as a synapomorphic character, as it occurred independently at least twice in the Xerulaceae. This de-emphasis on spore shape as a synapomorphic character would also make acceptable the inclusion of *C. glutinis* in an enlarged concept of *Rhizomarasmius* or *Gloiocephala*. As suggested by Hao et al. ([2014](#)), it must also indicate the necessity of revising the position of *X. kuehneri* in which the surface structures are distinct from *Dactylosporina* (Dörfelt [1985](#)), but composed of non-sarcodimitic tissues (Petersen and Hughes [2010](#)) which excludes a close relationship with dry-covered *Xerula* species as proposed by Boekhout and Bas ([1986](#)) and Boekhout ([1999](#)).

The inclusion of the typically marasmioid species “*Marasmius setosus*”, growing insititious on petioles of temperate broadleaved trees, in this clade was equally surprising. The spores of this species are narrowly almond-shaped, and in this context it illustrates an advanced evolution of spores from sublimoniform-subglobose to elongate. Its affinities with species of *Gloiocephala* could be suspected from the shared folicolous ecology and presence of erect hairs on the stipe, but *R. setosus* differs in the absence of sclerocystidia on pileus and absence of clamps (included in the definition of *Gloiocephala* by Pegler [1983](#):194). However, Singer ([1960b](#)) expanded the genus *Gloiocephala* to species with well-formed lamellae and without sclerocystidia (or setae), such as the Neotropical species *G. confusa* Singer, which is comparable to *R. setosus*, but clamped and with narrow “aciculate” spores.

The emendation of *Rhizomarasmius* as proposed here on the bases of phylogenetic analyses makes this genus especially difficult to circumscribe based on morphological characters at present. This proposal is presented as a step towards a phylogenetic revision of the whole *Rhizomarasmius* clade, which is limited here by the lack of available data on tropical species of *Gloiocephala*. If only one genus was considered, *Gloiocephala* would have priority over *Rhizomarasmius* and the appropriate combinations would be required; this does not sound desirable at this time, considering the few data

available for *G. epiphylla* (type of the genus) and the still poorly known related species (Singer [1960b](#), [1973](#)).

The ecology of *Rhizomarasmius* species remains enigmatic, but most of the European species of the genus are narrowly specific on their respective host plants. Ronikier and Ronikier (2012) retain a saprobic behavior for *R. epidryas* on *Dryas* spp. (Rosaceae), when *R. undatus* is apparently parasitic on rhizomes mostly of *Pteridium aquilinum* (eagle fern, Pteridaceae) and *R. oreinus* on roots of herbaceous alpine Angiosperms (Pacioni and Lalli [1989](#)). Filippi ([1991](#)) reported a close association between the pseudorrhizae of *L. mediterranea* and dead roots of *Juniperus macrocarpa* and *J. phoenicea*; Guinberteau and Courtecuisse ([1993](#)) suggested that *Laccariopsis mediterranea* is parasitic on deep rhizomes of *Ammophila arenaria*. An endophytic habit may also be involved, since all these species, including the foliicolous species *R. setosus* and *Gloiocephala* spp., appear fruiting from recently dead plant tissues, and the host plant itself does not present any symptoms of necrotrophic parasitism. *Cibaomyces glutinis* would be a saproxylic exception, as it seems to grow in relation with dead buried wood.

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