

# Article



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## Cibaomyces, a new genus of Physalacriaceae from East Asia

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#### **Abstract**

A new genus in Physalacriaceae, Cibaomyces, typified by C. glutinis, is described using morphological and molecular evidence. Cibaomyces is morphologically characterized by the combination of the following characters: basidioma small to medium-sized, collybioid to tricholomatoid; pileus viscid; hymenophore sinuate to subdecurrent, relatively distant, with brown lamellar edge; stipe sticky and densely covered with felted squamules; basidiospores thin-walled, ornamented with finger-like projections; cystidia nearly cylindrical, thin-walled, often heavily incrusted. Molecular phylogenetic analyses using DNA nucleotide sequences of the internal transcribed spacer region and the large subunit nuclear ribosomal RNA loci indicated that Cibaomyces was related to Gloiocephala, Laccariopsis and Rhizomarasmius. A description, line drawings, phylogenetic placement and comparison with allied taxa are presented.

Key words: Basidiomycetes·distribution·new taxa·taxonomy

#### Introduction

During our study of the fungi in the Physalacriaceae in East Asia (Wang et al. 2008; Yang et al. 2009; Qin et al. 2014; Tang et al. 2014), we have found collections with echinate basidiospores, which are very similar to the species of Oudemansiella sect. Dactylosporina (Clémençon 1979: 77) Pegler & T.W.K. Young (1987: 598) (Yang et al. 2009; Qin et al. 2014), a group of fungi mostly distributed in South and Central America and often treated as a separate genus, namely, Dactylosporina (Clémençon) Dörfelt (1985: 236) (Petersen & Hughes 2010), or as a subgenus of Oudemansiella (Clémençon 1979). Although the European Mycenella kuehneri Romagnesi (1941: 63) [= Oudemansiella kuehneri (Romagn.) Singer (1962: 59)] was also treated as in the genus Dactylosporina by Petersen & Hughes (2010), the molecular phylogenetic evidence for the inclusion of the European or additional Northern Hemispheric species is still unavailable.

In this study, we used morphological data together with DNA nucleotide sequence analysis of the internal transcribed spacer (ITS) region and the large subunit nuclear ribosomal RNA (nrLSU) to assess the phylogenetic position of the East Asian collections with echinate basidiospores, because both morphological and molecular evidence is important for the understanding of the evolutionary relationship of agarics (Moncalvo et al. 2002; Binder et al. 2006; Matheny et al. 2007; Yang 2011). Our analysis indicated that the samples are not close to the species of section Dactylosporina. Rather, they represent a discrete lineage, closely related to the genera Gloiocephala Massee (1892: 33), Laccariopsis Vizzini (2012: 396) and Rhizomarasmius R.H. Petersen (2000: 333). Our results are reported herein.

## Materials and methods

#### Sampling

Materials were collected by the authors from both China and Japan during 2011–2013 in forests dominated by

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Fagaceae. Specimens examined are deposited in the Herbarium of Cryptogams, Kunming Institute of Botany of the Chinese Academy of Sciences, China (HKAS).

#### Morphological studies

The macro-morphological characters were described based on field notes made from fresh materials, and documented by photographs. Color codes are according to Kornerup & Wanscher (1981). Microscopic structures were revived and observed in 5% KOH. Sections of the pileipellis and the surface of the stipe were made halfway across the pileus radius and at the stipe midsection, respectively. All microscopic features were drawn free hand. In the descriptions of the lamellae and basidiospores, the abbreviation L = number of entire lamellae; l = number of lamellulae between each pair of entire lamellae; the notations '(n/m/p)' indicate that the measurements were made on 'n' basidiospores from 'm' basidiomata of 'p' collections. Dimensions of basidiospores were measured without spines and presented in the following form (a) b-c (d); in which 'b-c' contains a minimum value of 90% and extreme values 'a' and 'd' are kept in parentheses. Q is used to mean length/width ratio derived from each basidiospore measured; Qm means average Q of all basidiospores ± sample standard deviation. For the observation of basidiospores under a scanning electron microscope (SEM), tiny pieces of hymenophoral fragments from dried specimens were mounted on aluminum SEM stubs with double-sided tape. The samples were then coated with gold palladium (thickness 10 nm) and a 8600 nA current flow at 10s was applied to make the test sample conductive. After coating a sample, it was placed into the SEM (HITACHI S-4800 or JEOL JSM-6510) for observation and obtaining the image. To get a clear SEM image, the working distance (7700 µm) and the accelerating voltage 10.0kV were maintained.

#### Molecular studies

DNA extraction and PCR amplification

Protocols for DNA extraction, PCR, and sequencing followed those in Qin *et al.* 2014, Li *et al.* 2009 and references therein. The products that failed to be sequenced directly were cloned using PMD18-T vector (Takara, Japan) and then sequenced with primer M13F (5'-GTAAAACGACGCCAGTGAA-3').

DNA sequence alignments and phylogenetic analysis

The ITS nucleotide sequences from our samples were compared with those deposited in the GenBank database and only 81% to 89% match with the ITS sequence of *Gloiocephala*, *Laccariopsis* and *Rhizomarasmius*. To understand the relationship of our samples with the remaining genera in Physalacriaceae (Moncalvo *et al.* 2000, 2002; Bodensteiner *et al.* 2004; Wilson & Desjardin 2005; Binder *et al.* 2006; Dentinger & McLaughlin 2006; Matheny *et al.* 2007; Rungjindamai *et al.* 2008; Lebel & Catcheside 2009; Henkel *et al.* 2010; Petersen & Hughes 2010; Ronikier & Ronikier 2011; Vizzini *et al.* 2012; Redhead 2013; Jenkinson *et al.* 2014), both ITS and nrLSU sequences of the representative genera of the family available in GenBank were retrieved and combined with our own sequences (Table 1). Two datasets, ITS sequences and nrLSU sequences, were aligned with MAFFT v6.8 (Katoh *et al.* 2005) and manually optimized on BioEdit v7.0.9 (Hall 1999) or 4SALE v1.5 (Seibel *et al.* 2006). To investigate the potential conflict between ITS and nrLSU, the partition homogeneity (PH) or incongruence length difference (ILD) test was performed with 1000 randomized replicates, using heuristic searches with simple addition of sequences in PAUP\* 4.0b10 (Swofford 2002). Since the result showed that the two different gene fragments were not in conflict (P<0.5), the two datasets were concatenated using Phyutility v2.2 for further analysis (Smith & Dunn 2008).

Chaetocalathus liliputianus (Mont. 1854: 99) Singer (1942: 527), Atheniella aurantiidisca (Murrill 1916: 336) Redhead (2012: 1), Marasmius rotula (Scop. 1772: 456) Fries (1838: 385) and Marasmius palmivorus Sharples (1928: 323) were selected as outgroups according to recent phylogenetic studies (Wilson & Desjardin 2005; Ronikier & Ronikier 2011). Bayesian Inference (BI) and Maximum Likelihood (ML) were employed by using MrBayes v3.1.2 (Ronquist & Huelsenbeck 2003) and RAxML v7.2.6 (Stamatakis 2006), respectively, based on the combined dataset (ITS-nrLSU). Substitution models suitable for each partition in the database were determined by using the Akaike Information Criterion (AIC) implemented in MrModeltest V2.3 (Nylander 2004). The models chosen as the best models for ITS and nrLSU were GTR+I+G and HKY+I+G, respectively. All parameters in the ML analysis used the default setting, and statistical support values were obtained using the nonparametric bootstrapping with 1000 replicates. BI analyses using selected models and 4 chains were conducted and stopped

when the standard deviation of the split frequencies fell below 0.01 and ESS values >200. Tracer v1.5 (http://tree.bio.ed.ac.uk/software/tracer/) was used to monitor the chain convergence. Trees were sampled every 100 generations. Subsequently, trees were summarized and statistic supports were obtained by using the sumt command complemented in MrBayes by discarding the first 25% generations as burn-ins.

Considering the morphological similarity, we tested the putative monophyly of *Cibaomyces* and *Oudemansiella* sect. *Dactylosporina*. A constraint tree enforcing monophyly of *Cibaomyces* and sect. *Dactylosporina* was constructed in PAUP\* 4.0b10. Shimodaira—Hasegawa (SH) test (Shimodaira & Hasegawa 1999) was applied to determine whether the data rejected the topology. The SH test was conducted by PAUP\* 4.0b10 using 1000 bootstrap replicates and full parameter optimization of the model.

**TABLE 1.** Fungal taxa analyzed and GenBank accession numbers for sequences used in this study. GenBank accession numbers for sequences generated in this study are in boldface.

Taxon	Voucher	GenBank Accession		D.C.	
		ITS	nrLSU	- References	
Armillaria mellea	PBM2470	AY789081	AY700194	Binder et al. 2006	
Armillaria tabescens	Unknown	AY213590	AF042593	Kim et al. 2006	
Atheniella aurantiidisca	PBM1282	DQ490646	DQ470811	Matheny et al. unpublished	
Cibaomyces glutinis	HKAS71038	KJ024100	KJ024105	this study	
Cibaomyces glutinis	HKAS80855	KJ024101	KJ024106	this study	
Chaetocalathus liliputianus	C61867	AY571032	AY570996	Bodensteiner et al. 2004	
"Cribbea gloriosa"	MEL21710	FJ178110	FJ178111	Lebel & Catcheside 2009	
"Cribbea turbinispora"	PIF27162	FJ178112	FJ178113	Lebel & Catcheside 2009	
"Cryptomarasmius corbariensis"	Ngyuen111209	JN601433	JN585128	Jenkinson et al. 2014	
"Cryptomarasmius crescentiae"	BRNM718790	JN003840	JN003845	Jenkinson et al. 2014	
Cylindrobasidium laeve	ННВ8633-Т	DQ205682	DQ234541	Matheny et al. 2007	
Cyptotrama asprata	HKAS76282	KJ024099	KJ024104	this study	
Cyptotrama asprata	HKAS60303	KJ024098	KJ024103	this study	
"Dactylosporina glutinosa"	MCA1775	HM005074	HM005138	Petersen & Hughes 2010	
"Dactylosporina steffenii"	TENN5878	HM005071	HM005132	Petersen & Hughes 2010	
Flammulina rossica	HKAS57924	KC179735	KC179743	Tang et al. 2014	
Flammulina velutipes	TENN56073	AF030877	HM005085	Hughes et al. unpublished	
Gloiocephala aquatica	CIEFAP50	DQ097356	DQ097343	Binder et al. 2006	
Gloiocephala epiphylla	DED5971	DQ097357	DQ097344	Binder et al. 2006	
Gloiocephala amphibia	DAOM170087	DQ097358	DQ097345	Binder et al. 2006	
"Gloiocephala phormiorum"	Horak9310	DQ097359	DQ097346	Binder et al. 2006	
"Gloiocephala resinopunctata"	M703c (SFSU)	DQ097360	_	Binder et al. 2006	
"Guyanagaster necrorhiza"	TH8989	HM131826	HM131826	Henkel et al. 2010	
"Guyanagaster necrorhiza"	TH9065	HM131823	HM131822	Henkel et al. 2010	
"Hymenopellis furfuracea"	TENN61678	GQ913364	HM005124	Petersen & Hughes 2010	
"Hymenopellis radicata"	TENN62837	GQ913375	HM005125	Petersen & Hughes 2010	
Laccariopsis mediterranea	MCVE23445	JX271808	JX271809	Vizzini et al.2012	
"Marasmius epiphyllus"	BRNM695733	FN293008	FN293008	Antonin et al. unpublished	
"Marasmius epiphyllus"	BRNM714560	FN293015	FN293015	Antonin et al. unpublished	
"Marasmius hudsonii"	BRNM658229	_	JN585130	Jenkinson et al. 2014	
Marasmius palmivorus	Unknown	JQ653445	JQ654232	Al-Maliky et al. unpublished	

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TABLE 1 (continued)

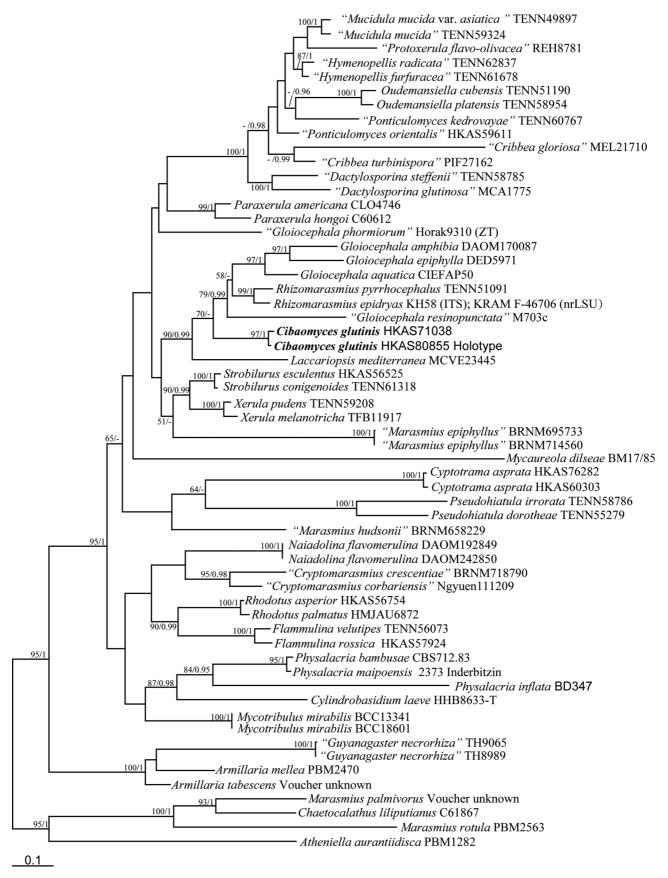
Taxon	Voucher	GenBank Accession		D. C	
		ITS	nrLSU	- References	
Marasmius rotula	PBM2563	DQ182506	DQ457686	Matheny et al. unpublished	
"Mucidula mucida"	TENN59324	GQ844235	HM005127	Petersen & Hughes 2010	
"Mucidula mucida var. asiatica"	TENN49897	GQ844238	HM005100	Petersen & Hughes 2010	
Mycaureola dilseae	BM17/85	DQ097364	DQ097348	Binder et al. 2006	
Mycotribulus mirabilis	BCC13341	_	EF589740	Rungjindamai et al. 2008	
Mycotribulus mirabilis	BCC18601	_	EF589741	Rungjindamai et al. 2008	
Naiadolina flavomerulina	DAOM192849	_	KJ438380	Redhead 2013	
Naiadolina flavomerulina	DAOM242850	_	KJ438381	Redhead 2013	
Oudemansiella cubensis	TENN51190	GQ892794	HM005114	Petersen & Hughes 2010	
Oudemansiella platensis	TENN58954	GQ892789	KJ024108	Petersen & Hughes 2010/this study	
Paraxerula americana	CLO4746	HM005142	HM005094	Petersen & Hughes 2010	
Paraxerula hongoi	C60612	HM005144	HM005095	Petersen & Hughes 2010	
Physalacria bambusae	CBS712.83	DQ097367	DQ097349	Binder et al. 2006	
Physalacria inflata	BD347	_	DQ284915	Dentinger & McLaughlin 2006	
Physalacria maipoensis	2373Inderbitzin	DQ097368	AF426959	Binder et al. 2006	
Ponticulomyces kedrovayae	TENN60767	HM005146	HM005110	Petersen & Hughes 2010	
"Ponticulomyces orientalis"	HKAS59611	KJ024102	KJ024107	this study	
"Protoxerula flavo-olivacea"	NY REH8781	HM005152	HM005111	Petersen & Hughes 2010	
Pseudohiatula dorotheae	TENN55279	_	HM005078	Petersen & Hughes 2010	
Pseudohiatula irrorata	TENN58786	_	HM005080	Petersen & Hughes 2010	
Rhizomarasmius epidryas	KH58 (ITS)/ KRAMF- 46706 (nrLSU)	GU234107	JF297608	Geml <i>et al.</i> 2012/ Ronikier & Ronikier 2011	
Rhizomarasmius pyrrhocephalus	TENN51091	DQ097369	DQ097351	Petersen & Hughes 2010	
Rhodotus asperior	HKAS56754	KC179737	KC179745	Tang et al. 2014	
Rhodotus palmatus	HMJAU6872	KC179742	KC179752	Tang et al. 2014	
Strobilurus conigenoides	TENN61318	GQ892821	HM005091	Petersen & Hughes 2010	
Strobilurus esculentus	HKAS56525	KF530549	KF530564	Petersen & Hughes 2010	
Xerula melanotricha	TFB11917	HM005160	HM005099	Petersen & Hughes 2010	
Xerula pudens	TENN59208	HM005154	HM005097	Petersen & Hughes 2010	

## **Results**

## Molecular studies

In the alignment of the combined dataset, 960 characters were constant, while 1027 characters were variable, of which 832 were parsimony informative. The topology of phylogenetic trees based on the combined dataset generated from ML and BI analyses were almost identical, while statistical supports showed slight differences. Our results showed that *Cibaomyces* was nested within the family Physalacriaceae and clustered with *Gloiocephala*, *Laccariopsis* and *Rhizomarasmius* with relatively high statistical supports (Fig. 1).

The topology resulting from the constraint analysis enforcing the monophyly of Cibaomyces and Oudemansiella sect. Dactylosporina was significantly rejected (P < 0.05) based on the result of the S-H test (Table 2), indicating that Cibaomyces should be treated as a distinct genus despite the morphological similarity of its basidiospores to those of Oudemansiella sect. Dactylosporina.



**FIGURE 1.** Phylogenetic tree generated from combined ITS and nrLSU dataset using ML method. Bootstrap values ( $\geq 50\%$ ) derived from ML analyses and posterior probabilities from Bayesian inference ( $\geq 0.95$ ) are shown above or beneath the branches at nodes. *Cibaomyces* is highlighted in boldface.

**TABLE 2.** Shimodaira-Hasegawa likelihood test values of topologies resulting from unconstrained and constrained analyses of ITS plus nrLSU dataset.

Topology	$-\ln L$	Diff. –ln <i>L</i>	P
Unconstrained maximum likelihood analysis (Fig. 1)	24885.40570	(best)	_
Constrained topology of monophyly Cibaomyces + Oudemansiella sect. Dactylosporina	25297.04948	411.64378	0.000*

<sup>\*</sup> P < 0.001

Species of *Dactylosporina* (Clémençon) Dörfelt, *Hymenopellis* Petersen (2010: 80), *Mucidula* Patouillard (1887: 95), *Ponticulomyces* Petersen (2010: 311), *Protoxerula* Petersen (2010: 318), *Cribbea* Smith & Reid (1962: 98) and *Oudemansiella* form a monophyletic clade (Yang *et al.* 2009; Vellinga 2010; Qin *et al.* 2014). Species of *Gloiocephala* are polyphyletic and were clustered in at least three different lineages (Binder *et al.* 2006). *Marasmius epiphyllus* (Pers. 1801: 468) Fries (1838: 386) and *M. hudsonii* (Pers. 1801: 390) Fries (1838: 386) represent new generic taxa (Jenkinson *et al.* in press.). *Guyanagaster necrorhiza* Henkel *et al.* (2010: 1477) was clustered within *Armillaria* (Fr. 1821: 9) Staude (1857: 130) (Fig. 1).

The genera *Cribbea*, *Dactylosporina*, *Hymenopellis*, *Mucidula*, *Ponticulomyces*, and *Protoxerula* were treated in *Oudemansiella* s.l. as in Qin *et al.* (2014) and thus, quotation marks were placed around the names in the cladogram and the table. Additionally, if the monophyly of the species with the same generic name is questionable, or if a name is not yet validly published, quotation marks were also put around the names. Due to the paraphyly of *Armillaria* with *Guyanagaster*, the names of *Guyanagaster* were cited with quotation marks.

## **Taxonomy**

*Cibaomyces* Zhu L. Yang, Y.J. Hao & J. Qin, **gen. nov**. MycoBank MB 807466

Etymology: Cibao means echinate spores from the Chinese; "Cibaomyces" refers to the fungus with echinate basidiospores.

Basidioma stipitate-pileate with lamellar hymenophore. Pileus glutinous. Lamellae adnate to sinuate to subdecurrent, white to cream-colored, thick; lamellar edge brown to brownish at maturity. Stipe central, densely covered with felted squamules, sticky; pseudorhiza present. Context pallid to cream-colored, unchanging when cut. Basidiospores colorless and hyaline, occasionally with brown to dark brown contents, non-amyloid, non-dextrinoid, subglobose to broadly ellipsoid, thin- to slightly thick-walled, echinate. Cheilocystidia subcylindrical to narrowly clavate, heavily incrusted. Pleurocystidia absent. Pileipellis an ixohymeniderm, intermixed with subcylindrical to narrowly clavate, heavily incrusted pileocystidia. Caulocystidia evenly distributed. Chlamydospores not observed. Clamp connections common.

Typus generis: Cibaomyces glutinis Zhu L. Yang, Y.J. Hao & J. Qin

Cibaomyces glutinis Zhu L. Yang, Y.J. Hao & J. Qin, sp. nov.

Figs. 2-4

MycoBank: MB 807467

Etymology: glutinis refers to the glutinous pileus and stipe.

Type:— CHINA. Yunnan Province: Jizu Mountain, Binchuan County, 25°57'39"N,100°23'31"E, elev. 2200 m, 3 August 2013, *Jiao Qin* 725 (HKAS80855, holotype!).

Basidiomata (Fig. 2a–b) small to medium-sized. *Pileus* 3–4.5 cm, convex to applanate, strongly glutinous, dirty white to brownish to grayish (5B2–5B3, 5C2–5C3), finely rugose, often with brownish irregularly-shaped dots; center slightly darker. *Lamellae* adnate to sinuate or slightly decurrent, subdistant, with lamellulae, L = 20–25, l = 1–3, thick, dirty white to cream, sometimes with reddish to brownish spots, transversely veined, with lamellae frequently anastomosing; lamellar edge rusty brown to brownish. *Context* 2–3 mm thick, dirty white to brownish, unchanging in color when cut. *Stipe* 6–9.5 × 0.3–0.8 cm, subcylindrical, enlarged at ground line, surface dirt white to grayish, sticky, densely covered with brownish felted squamules but nearly white at apex; pseudorhiza dirty white. *Taste* mild; *odor* indistinct.

Lamellar trama  $\pm$  regular, composed of branching, nearly colorless and hyaline, slightly thick-walled ( $\le 1 \mu m$  thick), filamentous to inflated hyphae 3–20  $\mu m$  wide. Subhymenium composed of 3–5  $\mu m$  wide frequently branching

hyphal segments. Basidia (Fig. 3d) 50–70 × 13–15 µm, 4-spored, thin-walled, colorless hyaline, sometimes with yellowish brown contents; sterigmata up to 10 μm in length; basidioles clavate to subfusiform with subacute apex. Spores (Fig. 3b) [55/2/2] (9) 10.5-14 (15) × (8.5) 9-11.5 (12.5)  $\mu$ m, Q = (1.0) 1.05-1.24 (1.30), Qm =  $1.14 \pm 0.07$ , subglobose to broadly ellipsoid, thin-walled, colorless and hyaline, sometimes with brownish to brown contents, non-amyloid, non-dextrinoid, cyanophilous, non-metachromatic, with ca. 25 spines conspicuous, 2–4(5) μm high and 1.5–2 µm broad at base, hollow, conical to subcylindrical spines with obtuse apex. Lamellar edge sterile, composed of crowded cheilocystidia; cheilocystidia (Fig. 3c) 50-130 × 4-8 μm, numerous, narrowly clavate, subcylindrical to cylindrical, often with a round to subcapitate apex, with brownish, brown to chocolate brown intracellular pigment, often incrusted brown substances. Pleurocystidia absent. Pileipellis (Fig. 3a) an ixohymeniderm 40-60 µm thick, composed of clavate, broadly clavate to sphaeropedunculate, brownish to brown intracellularly pigmented cells (20–50 × 10–30 μm) embedded in a gelatinized matrix with brown to dark brown crystalline material. Pileocystidia (Fig. 3a) abundant, subcylindrical to narrowly clavate, occasionally narrowly fusiform to lageniform, 40–80 × 4–8 μm, thin-walled, nearly colorless or with brownish to brown intracellular pigment, with apical parts often incrusted with brown, yellow-brown to ochraceous substances which are slowly soluble in KOH; apex narrowly rounded, rarely acute. Stipitipellis composed of vertically arranged, branching, nearly colorless and hyaline, slightly thick-walled (ca. 0.5 μm thick), filamentous hyphae 3–15 μm broad. Caulocystidia (Fig. 3e) 50–100 × 3–8 μm, numerous and crowded, evenly distributed, narrowly clavate to subcylindrical, thin- to slightly thick-walled (ca. 0.5 µm thick), often with a round apex, with dark brown to yellow-brown intracellular pigment, occasionally nearly colorless and hyaline, often incrusted with brown to yellow-brown substances. *Chlamydospores* not observed. *Clamp connections* abundant in every part of basidioma. Habitat and known distribution: fruiting in broad-leaved forests dominated by Fagaceae, on buried rotten wood; in summer at elev. 1000-2200 m in southwestern China and northern Japan.

Additional specimen examined: JAPAN. Tomakomai: Hokkaido, elev. 1000 m, on buried rotten wood, 13 September 2011, Zhu Liang Yang 5553 (HKAS71038!).

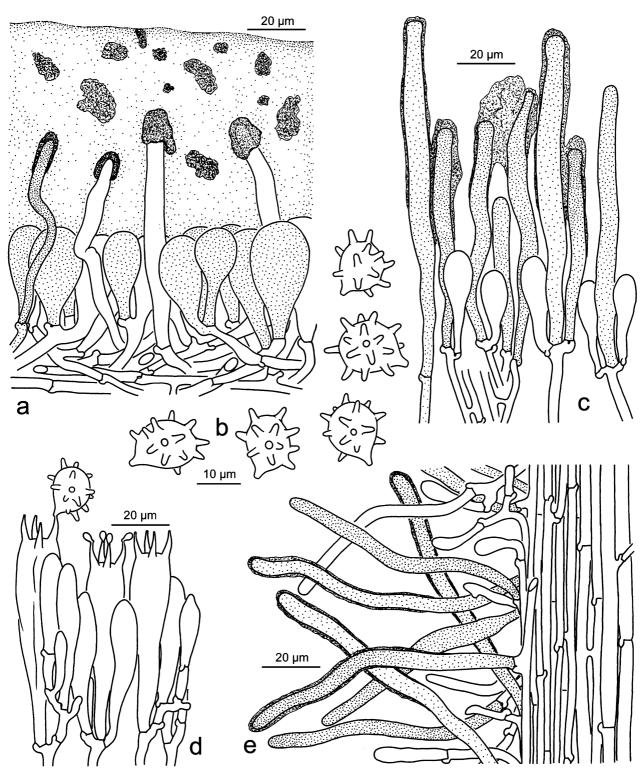


**FIGURE 2.** Basidoma of *Cibaomyces glutinis* in its natural habitat. **a**. showing the pileus and the stipe. **b**. showing the lamellae and the stipe with a pseudorhiza (all from the holotype).

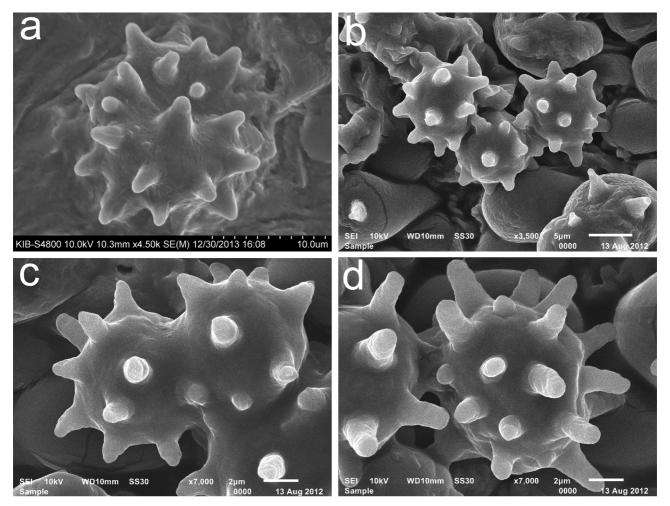
### **Discussion**

Our phylogenetic analyses implied that the novel genus Cibaomyces was clustered with Gloiocephala, Laccariopsis, Rhizomarasmius, and "Gloiocephala resinopunctata" Manim. & K. A. Thomas (1998: 87), the

gloiocephala clade (Vizzini *et al.* 2012), with 90% ML and PP=0.99 (Fig. 1). Members of these three previously known genera and "*Gloiocephala resinopunctata*" all have smooth basidiospores without any coarsely warty or spiny ornamentations (Massee 1892; Bas 1961; Manimohan & Thomas 1998; Petersen 2000; Antonín 2007; Antonín & Noordeloos 2010; Ronikier & Ronikier 2011; Vizzini *et al.* 2012).



**FIGURE 3.** Microscopic features of *Cibaomyces glutinis* **a**. Radial-vertical section of pileipellis. **b**. Basidiospores. **c**. Cheilocystidia. **d**. Basidia and basidioles. **e**. Surface of stipe in longitudinal section showing caulocystidia (all from the holotype).



**FIGURE 4.** SEM of basidiospores is from dried specimens of *Cibaomyces glutinis*. **a.** from the holotype HKAS80855; **b–d.** from HKAS71038.

In addition, the genus *Gloiocephala*, typified by *G epiphylla* Massee (1892: 34), differs in having basidiomata with a slender marasmioid habit, a dry to subviscid pileus, a instititious to pseudoinsititious non-rooting stipe that is usually entirely pruinose, a lamellate to reduced-smooth hymenophore, subfusiform to pip-shaped basidiospores, usually subcapitate to capitate cystidia and growth on herbaceous plant or wood leaves, stems, and debris, usually in wet places (Massee 1892; Singer 1960; Bas 1961; Redhead 1981; Singer 1976, 1986; Horak & Desjardin 1994; Desjardin & Horak 1997; Antonín 2007; Antonín & Noordeloos 2010). Molecular data indicated that *Gloiocephala* sensu Singer (1976, 1986) is probably polyphyletic (Moncalvo *et al.* 2002; Binder *et al.* 2006; Vizzini *et al.* 2012; Fig. 1).

The genus *Rhizomarasmius*, typified by *R. pyrrhocephalus* (Berk. 1847: 316) R.H. Petersen (2000: 334), comprises species characterized by marasmioid basidioma with a dry pileus, a long, rigid, rooting, minutely velutinous dry stipe, a ramified pseudorhiza, smaller basidia and basidiospores, a pileipellis with elongate pileocystidia, as well as the presence of cheilo-, pleuro- and caulocystidia that are often distinctly thick-walled and subcapitate or capitate (Petersen 2000; Antonín & Noordeloos 2010; Ronikier & Ronikier 2011), while *Cibaomyces glutinis* has no pleurocystidia, and its cheilocystidia are usually thin-walled, and not capitate.

Laccariopsis is currently a monotypic genus established for *Hydropus mediterraneus* Pacioni & Lalli (1985: 5). It is featured by a *Laccaria*-like habit, a viscid pileus and upper stipe, glabrous stipe with a long pseudorhiza, a pileipellis consisting of a loose ixohymeniderm with slender pileocystidia, large and thin- to thick-walled spores and basidia, thin- to slightly thick-walled hymenial cystidia and caulocystidia (Pacioni & Lalli 1985, 1989; Bas & Robich 1988; Horak 1988; Vizzini *et al.* 2012).

The basidiospores of *Cibaomyces* are very similar to those of *Oudemansiella* sect. *Dactylosporina*. However, *Cibaomyces* differs from *Oudemansiella* sect. *Dactylosporina* in the common presence of pileocystidia, cylindrical

shape of cheilocystidia, the absence of pleurocystida, and basidiospores with loosely arranged spines (Pegler & Young 1987; Singer 1964, 1986; Petersen & Hughes 2010; Wartchow et al. 2010). In addition, the pileus and stipe of Cibaomyces are usually sticky with brown to dark brown substances exuded from the upper part of the cystidia. The caulocystidia of Oudemansiella sect. Dactylosporina are usually arranged in fascicles, while those of Cibaomyces are evenly distributed on the surface of the stipe. Furthermore, our molecular analysis indicated that Cibaomyces has no close evolutionary relationship with Oudemansiella sect. Dactylosporina (Fig. 1; Table 2). Geographically, the known distribution range of sect. Dactylosporina is restricted to Central and South America (Singer 1964, 1986; Pegler & Young 1987; Halling & Mueller 1999; Wartchow et al. 2010). Although Petersen and Hughes (2010) included a European taxon, Mycenella kuehneri, in Dactylosporina, its systematic position was not elucidated by molecular-phylogenetic data.

The large echinate basidiospores of *Mycenella kuehneri* are comparable to those of *Cibaomyces*. However, it differs phenotypically from *Cibaomyces glutinis* by the very small mycenoid basidioma with a dry pileus 1.2–1.4 cm in diameter, the clavate, fusiform to lageniform hymenial cystidia without any incrustations, and basidiospores with more numerous and more densely arranged spines (Boekhout & Bas 1986; Pegler & Young 1987; Petersen & Hughes 2010). Whether *Mycenella kuehneri* belongs to *Cibaomyces* is an open question.

In the Physalacriaceae, the basidiospores of the genus *Rhodotus* Maire are also similar to those of *Oudemansiella* sect. *Dactylopsorina* (Petersen & Hughes 2010; Tang *et al.* 2014). However, *Rhodotus* has, among other features, basidioma growing on exposed rotten wood and producing chlamydospores and distinctly smaller basidiospores measuring  $5-7 \times 4.5-6.5 \mu m$  with obtuse warts  $0.5-1.5 \mu m$  in height and  $0.5-1 \mu m$  in width (Horak 1968; Pegler & Young 1975; Krieglsteiner 1979; Kühner & Romagnesi 1984; Noordeloos 1995; Sundberg *et al.* 1997; Tang *et al.* 2014). Molecular phylogenetic analysis indicated that *Rhodotus* is distinct from *Cibaomyces*, and clustered in different major groups (Fig. 1; Petersen & Hughes 2010).

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