Morphological and Phylogenetic Reevaluation of the Genera *Mycobonia* and *Pseudofavolus* (Polyporaceae)

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Abstract

Mycobonia and *Pseudofavolus* (Polyporales, Basidiomycota) are polyporoid genera with tropical and subtropical distribution. Both genera are morphologically similar in presenting flabelliform to conchate subsessile basidiomata, with a dimitic hyphal system, consisting of clamped generative hyphae and skeleto-binding hyphae that produce large basidiospores with smooth, thin walls. However, while *Pseudofavolus* species present a poroid hymenophore, in *Mycobonia* it is stereoid with hyphal pegs that resemble thin teeth. *Mycobonia* and *Pseudofavolus* have a controversial taxonomy, and the phylogenetic relationships between their species have yet to be assessed. For this reason, we performed molecular phylogenetic analyses on specimens of *Mycobonia* and *Pseudofavolus* from both the Neotropics and Asia, using internal transcribed spacers (ITS), the large subunit of nuclear rDNA (nc LSU rDNA), and also the genes encoding the second largest subunit of RNA polymerase II (*RPB2*). Furthermore, in order to develop an evolutionary analysis of the hymenophore configuration, we performed stochastic character mapping of ancestral states for the hymenophore type presented in *Polyporus s.l.* Our study revealed that *Pseudofavolus* is an artificial group and its species actually nest in a clade within *Mycobonia*. Therefore, in order to establish a monophyletic group, based upon priority of publication, we re-circunscribed *Mycobonia* to encompass both stereoid and poroid hymenophore species. Two new combinations are presented from the Neotropics: *Mycobonia cucullata* and *M. miquelii*. A new species from tropical Asia, *M. yuchengii*, is also described. We presente a summary of stochastic mapping of ancestral states estimates of hymenophore type in *Polyporus s.l*. The ancestral state for *Mycobonia* clade is estimated to have angular pores.

Introduction

Mycobonia Pat. and *Pseudofavolus* Pat. are genera of wood-decaying Basidiomycota belonging to the family Polyporaceae with tropical to subtropical distribution. Both genera are morphologically similar in presenting flabelliform to conchate subsessile basidiomata, a dimitic hyphal system with clamped generative hyphae, skeleto-binding hyphae and large, smooth basidiospores with thin and smooth walls (Corner 1984).

Macroscopically, the shape, color and consistency of the basidiomata are very similar in both genera; however, while *Pseudofavolus* includes species with poroid hymenophore, *Mycobonia* presents stereoid hymenophore with hyphal pegs (Corner 1984; Julich 1976).

Currently, two species are recognized in *Mycobonia*, *M. brunneoleuca* and *M. flava* (type species), and are distributed throughout the Americas in tropical and subtropical areas, though they differ in their basidiospores differ in shape, size and altitudinal occurrence (Julich 1976; Gerlach and Loguercio-Leite 2011). Currently nine species are accepted in the *Pseudofavolus* genus, with tropical and subtropical worldwide distribution (Ryvarden and Johansen 1981; Ryvarden 2016). Specifically, four of them were originally described from the Neotropics: *P. cucullatus* (Mont.) Pat., *P. miquelii* (Mont.) Pat. (type species), *P. nigrus* Ryvarden, and *P. orinocensis* (Pat. and Gaillard) Ryvarden. Additionally, *P. cucullatus*, which was

originally described from Cuba, has subsequently been recorded from several areas of subtropical and tropical Asia (Dai 2007, 2012; Dai et al. 2011; Cui et al. 2019; Wu et al. 2020).

The taxonomy of *Mycobonia* and *Pseudofavolus* is controversial. Due to the stereoid hymenophore, *Mycobonia* has been included in several families, such as Corticiaceae, Mycoboniaceae, Stereaceae and Thelephoraceae (Corner 1984; Krueger 2002). However, in several studies, the affinities of *Mycobonia* and *Pseudofavolus* with *Polyporus s.l.* were described and discussed based on morphological characteristics (Singer 1951, 1986; Corner 1984). These similarities were subsequently corroborated by phylogenetic studies (Kruguer 2002; Krueger and Gargas 2004, Motato-Vásquez et al. 2018). *Mycobonia* and *Pseudofavolus* have also been treated as synonyms of *Polyporus* (Silveira and Wright 2005; Nakasone 2015). Nevertheless, phylogenetic studies have placed *Mycobonia* next to *Pseudofavolus*, and in distant relation to *Polyporus s.s*. (Krüger and Gargas 2004; Motato-Vasquez et al. 2018), thus representing different genera in the core polyporoid clade. In the present study, we aim to investigate the relationships between *Mycobonia* and *Pseudofavlus* based on morphological and molecular evidence. In addition, we compare the Asian specimens of *P. cucullatus* to neotropical samples in order to determine if they are in fact conspecific. Finally, considering the traditional taxonomic value of hymenophore differentiation, we reconstruct the ancestral state for the hymenophore configuration of *Polyporus s.l*.

Material And Methods

Specimens and morphological studies

The studied specimens are deposited in ICN, BJFC, and SP herbaria. Herbarium acronyms follow Thiers (continuously updated, http://sweetgum.nybg.org/science/ih/). Freehand cross sections of dried materials were mounted on slides and observed under the microscope in Melzer's reagent, 5% KOH and/or 1% phloxine, cresyl blue and/or cotton blue (CB). To observe hyphal systems, small pieces of basidiomata were kept in 3% NaOH solution at 45 ºC for about 2 h; then, pieces were dissected under a stereomicroscope (Decock et al. 2013). Basidiospores were measured (n = 40) in Melzer's reagent. The following abbreviations were also used: IKI– = inamyloid and non-dextrinoid, CB+/– = cyanophilous/acyanophilous, m = arithmetic mean and Q = the ratio of length/width of basidiospores. We followed Stalpers (1996) and the Stalpers database (http://www.cbs.knaw. nl/russulales/) for basidiospore shape terminology.

DNA extraction and sequencing

Following the manufacturer's protocols, DNA was extracted from dried specimens using CTAB rapid plant genome extraction kit-DN14 (Aidlab Biotechnologies Co., Ltd., Beijing, China) and FH plant DNA kit II (Demeter Biotech Co., Ltd., Beijing, China). Primer pairs ITS4/ITS5 (White et al. 1990), LR0R/LR7 (Vilgalys and Hester 1990) and fRPB2-5F/bRPB2-7.1R (Matheny 2005; Frøslev et al. 2005) were used to amplify the ITS, nc LSU rDNA and *RPB2* regions, respectively, by a qualitative simplex Polymerase Chain Reaction (PCR). The parameters of the PCR for each region were followed as described by Dentinger et al. (2010),

Vilgalys and Hester (1990), Frøslev et al. (2005) and Matheny (2005), respectively. The PCR products were purified and sequenced with the same primers at Beijing Genomics Institute in China.

Phylogenetic analyses

Chromatograms were assembled and manually edited using Geneious v. 7.1.9 (http://www.geneious.com). The newly generated ITS, nc LSU rDNA and *RPB2* sequences were deposited in GenBank and were later combined with additional sequences retrieved from GenBank to compose the entire dataset (Table 1). The ITS, nc LSU rDNA and *RPB2* matrices were individually aligned using MAFFT v.7 (Katoh and Standley 2013) under the Auto strategy, then inspected and edited using Aliview (Larsson 2014). We used PartitionFinder v.2 (Lanfear et al. 2017) to estimate the best-fit partitioning strategy and the best-fit model of nucleotide evolution with the following settings: branch lengths = linked, models = mr bayes, model selection = AICc and search = greedy. Two distinct analyses were performed: Bayesian Inference (BI) and Maximum Likelihood (ML). Bayesian Inference analysis was conducted using MrBayes 3.2 (Ronquist et al., 2012) with two independent runs, each one with four chains and starting from random trees. The runs performed 20 million generations, and trees were sampled every 1,000th generation. Of the sampled trees, 25% were discarded as burn-in, while the remainder were used for calculating a consensus tree and Bayesian Posterior Probabilities (BPP).

Table 1
List of species, collections, geographic origin and GenBank accession numbers for the ITS, nc LSU rDNA, mtSSU and RPB2 sequences used in the phylogenetic analyses in this study. New sequences generated from this study are marked in bold.

Taxon	Voucher	Country	GenBank accession number		
			ITS	nc LSU rDNA	*RPB2*
Atroporus diabolicus	DS1266	Brazil	KY631757	KY631768	—
Atroporus rufoatratus	DS816	Brazil	KY631759	KY631770	KY744947
Bresadolia craterella	TENN59383	Ecuador		AJ487944	—
Bresadolia paradoxa	MV23	Brazil	KY777230	KY777235	—
Bresadolia paradoxa	Robledo1958	Argentina	KY777233	KY777237	—
Cerioporus squamosus	AFTOLID704		DQ267123	AY629320	DQ408120
Datronia mollis	RLG6304sp	USA	JN165002	JN164791	JN164872
Datronia stereoides	Holonen	Finland	KC415179	KC415196	KC415202
Datroniella mellanocarpa	Cui10646	China	KC415186	KC415194	KC415201
Datroniella scutellata	RLG9584T	USA	JN165004	JN164792	JN164873
Dichomitus campestris	O103769	Norway	—	AJ487512	—
Dichomitus sp.	IFP14643	China	KX832053	KX832062	—
Echinochaete brachypora	TFMF24996	Japan	AB462321	AB462309	—
Echinochaete russiceps	TFMF15716	Japan	AB462310	AB368065	AB368123
Echinochaete sp.	MN272	Ecuador	AF518754		
Favolus brasiliensis	Kellermann s.n.	Brazil	MN648682	MN648708	—
Favolus emerici	WD2379	Japan	AB587628	AB587619	AB368147
Favolus roseus	PEN33	Malaysia	AB735975	AB368099	AB368156
Favolus rugulosus	MP191	Brazil	MN648684	MN648712	
Favolus yanomami	ACM1295	Brazil	MN648686	MN648714	—
Lentinus bertieri	TENN59773	Dominican Republic	GU207303	AY615984	—

Taxon	Voucher	Country	GenBank accession number		
			ITS	nc LSU rDNA	*RPB2*
Lentinus crinitus	DSH9243C	Costa Rica	KP283495	KP283523	—
Lentinus tigrinus	MUCL22821	Belgium	AB478881	AB368072	AB368130
Megasporoporia cavernulosa	Wu9508328	China	—	AY333800	—
Mycobonia brunneoleuca	GAS625	Brazil	**MZ997324**	**MZ996883**	**OK032602**
Mycobonia brunneoleuca	TENN57579	Costa Rica	AY513570	AJ487934	—
Mycobonia cucullata	MP204	Brazil	**MZ997329**	**MZ996888**	
Mycobonia cucullata	TENN58910	Argentina	AF516600	AJ488124	—
Mycobonia flava	MP207	Brazil	**MZ997326**	**MZ996885**	—
Mycobonia flava	MP213	Brazil	**MZ997325**	**MZ996884**	—
Mycobonia flava	TENN59088	Argentina	AY513571	AJ487933	—
Mycobonia miquelii	GAS1122	Brazil	**MZ997327**	**MZ996886**	—
Mycobonia miquelii	VOG213	Brazil	**MZ997328**	**MZ996887**	**OK032603**
Mycobonia orientalis	Cui8707	China	KX880623	KX880662	—
Mycobonia orientalis	Dai13584	China	KX900071	KX900185	—
Mycobonia orientalis	WD2157	Japan	AB587637	AB368114	AB368170
Neodatronia gaoligongensis	Cui8055	China	JX559269	JX559286	JX559317
Neodatronia sinensis	Dai11921	China	JX559272	JX559283	JX559320
Neodictyopus atlanticae	DS1286	Brazil	KY631763	KY631774	KY744950
Neodictyopus dictyopus	GAS272	Brazil	KY631766	KY631777	KY744952
Neofavolus alveolaris	WD2340	Japan	AB735970	AB368077	AB368135
Neofavolus cremealbidus	TUMH 50009	Japan	AB735980	AB735957	—
Neofavolus mikawae	TFMF-27417	Japan	AB735963	AB735943	—

Taxon	Voucher	Country	GenBank accession number		
			ITS	nc LSU rDNA	*RPB2*
Neofavolus suavissimus	ADD7	USA	KP283501	KP283527	—
Neofavolus subpurpurascens	CG6242	Brazil	MH544277	MH544275	—
Picipes austroandinus	MR10701	Argentina	AF516569	—	—
Picipes badius	WD2341	Japan	AB587625	AB368083	AB368140
Picipes tubaerformis	WD1839	Japan	AB587634	AB368101	AB368158
Polyporellus arcularius	RGT830522	Canada	AF516523	AB368081	AB368138
Polyporellus brumalis	TENN61760	USA	FJ596883	AB368084	AB368141
Polyporellus ciliatus	TENN57698	Denmark	AB070882	AJ487943	—
Polyporus tricholoma	TENN56503	Puerto Rico	AF516555	AB368100	AB368157
Polyporus tuberaster	DAOM7997B	USA	AY218420	AF261544	—
Polyporus tuberaster	WD2382	Japan	AB474086	AB368104b	AB368161
Polyporus varius	WD619	Japan	AB587635	AB368110	AB368167
Trametes hirsuta	RLG5133T	USA	JN164941	JN164801	JN164854
Trametes versicolor	FP135156	USA	JN164919	JN164809	JN164850

ML analysis was performed on the CIPRES SCIENCE GATEWAY 3.1 (Miller et al. 2010) using RAxML 8.1.4 (Stamatakis 2014). The analysis first involved 100 ML searches, each starting from one randomized stepwise-addition parsimony tree, under a GTRGAMMA model, with all other parameters estimated by the software. We provided a partition file with the defined partitions to force RAxML to search for a separate evolution model for each partition. Bootstrap support values (BS) were obtained under the same models and partitioning schemes allowing the program to automatically halt bootstrapping by using the autoMRE option. A node was considered to be strongly supported if it showed BPP ≥ 0.95 and/or BS ≥ 80%. *Trametes hirsuta* (Wulfen) Pilát and *T. versicolor* (L.) Lloyd were used as the outgroup based on Motato-Vásquez et al. (2018).

Ancestral character state reconstruction of hymenophore configuration

In order to reconstruct hymenophore evolution of the phylogeny of *Polyporus s.l.* we evaluated two models of character state evolution: Equal Rates (ER) and All Rates Different (ARD) using the fitDiscrete function of the R package Geiger 2.0 (Harmon et al., 2008). We selected the best model based on the

corrected Akaike Information Criterion (AIC) and used this for the reconstruction. The evolutionary analysis of the hymenophore was performed by stochastic character mapping (Huelsenbeck et al. 2003; Bollback 2006) implemented in the R package Phytools (Revell 2012), using the make.simmap and describe.simmap functions (Revell 2012). A total of 1000 stochastic maps were generated. Results were subsequently summarized and plotted on the phylogeny using the R package Ape 5.3 (Paradis et al. 2004). Hymenophore types were assigned as: circular pores = 0, angular pores = 1, subporoid lamellae = 2, lamellate = 3, stereoid = 4 (Supp Table).

Results

Phylogenetic analyses

Phylogenetic analyses included 57 terminals representing 48 putative species. The final alignment consisted of 2481 characters, of which 1389 were conserved and 908 were parsimony-informative. Best partitioning scheme was six subsets: ITS1-ITS2, 5.8S, nc LSU rDNA, *RPB2* 1st codon position, 2nd codon position and 3rd codon position. The evolutionary model selected were GTR + I + G (ITS1 and ITS2), SYM + I + G (5.8S), GTR + I + G (nc LSU rDNA), GTR + G (*RPB2* 1st codon position), HKY + I + G (*RPB2* 2nd codon position) and GTR + I + G (*RPB2* 3rd codon position). The final alignment was deposited at TreeBASE (28731).

Our phylogenetic analyses showed that *Pseudofavolus* and *Mycobonia* represent artificial groups according to current circumscriptions, as *Pseudofavolus* species actually nest in a clade together with *Mycobonia* species, which are phylogenetically distant from *Polyporus s.s.* (Fig. 1). Therefore, in order to accommodate these species in a natural group based upon priority of publication, we propose to transfer *Pseudofavolus* species into the genus *Mycobonia* (see Taxonomy section). Results from phylogenetic analyses recovered five strongly supported linages within the *Mycobonia* clade, representing five species that can also be recognized by morphological and ecological differences: *M. brunneoleuca* (PP = 1.0, BS = 99), *M. cucullata* (PP = 1.0, BS = 96), *M. flava* (PP = 1.0, BS = 91), *M. miquelii* (PP = 1.0, BS = 96) and the new species *M. yuchengii* (PP = 1.0, BS = 100). *Mycobonia yuchengii* clade is composed by Asian specimens previously identified as "*P. cucullatus"*, which will be treated below in the Taxonomy section. Phylogenetic relationships between *Mycobonia* species are not well resolved and ITS, nc LSU rDNA and *RPB2* sequences are highly conserved in *Mycobonia* clade species, with only 100 variable sites of the 2481 in final alignment. Additionally, the following were recovered as monophyletic: *Atroporus* (PP = 1.0, BS = 100), *Bresadolia* (PP = 1.0, BS = 100), *Datronia* (PP = 1.0, BS = 97), *Datroniella* (PP = 1.0, BS = 100), *Dichomitus* (PP = 1.0, BS = 100), *Echinochaete* (PP = 1.0, BS = 100), *Favolus* (PP = 1.0, BS = 100), *Lentinus*/ *Polyporellus* clade (PP = 1.0, BS = 100), *Neodictyopus* (PP = 1.0, BS = 100), *Neofavolus* (PP = 1.0, BS = 82), and *Picipes* (PP = 1.0, BS = 100).

Ancestral character state reconstruction of hymenophore configuration

The best fitting model for hymenophore configuration evolution was estimated to be the ER (AIC = 93.25), compared with ARD (AIC = 107.55). In the supplemental figures, we present estimates of the hymenophore type in *Polyporus s.l.* based on stochastic mapping of ancestral states. Probabilities are also showed in (Supplementary Fig. 1). The stochastic mapping of this hymenophore transition presented high probabilities of internal nodes, but low probabilities of back-bone nodes. Furthermore, the mapping indicated that the ancestral state for *Mycobonia* clade is estimated to have had angular pores (0.92), as well as for *Neofavolus* (1), as previously shown by Seelan et al. (2015). For the *Lentinus*/ *Polyporellus* clade we found that the probability for circular pores was low, only 0.22, though in contrast Seelan et al. (2015) did estimate them to be circular. *Polyporus s. l.* likely had angular pores (0.72). The number of transitions from circular to angular pores was estimated to be four, while the number from angular to circular was three, and there was a single transition from angular to stereoid which was placed in the *Mycobonia* clade.

Taxonomy

Mycobonia Pat., Bull. Soc. mycol. Fr. 10(2): 76 (1894), emend. Palacio & Westphalen.

= *Pseudofavolus* Pat., Essai Tax. Hyménomyc. (Lons-le-Saunier): 80 (1900)

Type species: *Mycobonia flava* (Sw.) Pat.

Basidiomata annual, solitary to imbricate, pileate, flabelliform, cucullate, conchate-flabelliform, subsessile with a very short lateral stipe to sessile; flexible to hard when fresh, hard and boney consistency when dry; pilear surface glabrous, smooth to tessellate (when poroid), pale ochraceous to brownish ochraceous; context thin up to 3 mm, homogeneous, beige. Hymenophore surface poroid or stereoid with hyphal pegs; when poroid pores large angular to circular, 0.2–3 mm wide, dissepiments entire to lacerated; tubes short up to 4 mm long; when stereoid with sterile prominent hyphal pegs up to 180 µm long. Stipe reduced to subdiscoid, attached to substrate by a basal disc, concolorous with the pilear surface, to absent (Fig. 2).

Hyphal system dimitic; generative hyphae 2–5 µm wide, with clamp connections, hyaline, thin-walled, scanty, CB–, IKI–; skeletal-binding hyphae 2–6 µm wide, densely interwoven, thick-walled, flexuous, densely branched and interwoven dominating throughout the basidiomata, CB – to CB+, IKI – to slightly dextrinoid in mass. Pileipellis not well differentiated. Cystidia not seen. Dendrohypidia present in the dissepiments. Basidia clavate, with four sterigmata. Basidiospores large, up to 25 × 11 µm, ellipsoid to cylindrical, thin-walled, smooth, hyaline, IKI–, CB– (Fig. 3).

Ecology and distribution: growing on fallen branches of unidentified angiosperms, causing white-rot; known from tropical to subtropical areas.

Comments: *Mycobonia* is characterized by the pileate, cucullate and boney consistency of the basidiomata with the hymenophore being stereoid with hyphal pegs or poroid with shallow tubes pores (Fig. 2), and large basidiospores (Fig. 3).

Mycobonia cucullata (Mont.) Palacio & R.M. Silveira, comb. nov.

MycoBank: MB841083

≡ *Favolus cucullatus* Mont., Annls Sci. Nat., Bot., sér. 2 17: 125 (1842)

≡ *Pseudofavolus cucullatus* (Mont.) Pat., Essai Tax. Hyménomyc. (Lons-le-Saunier): 81 (1900)

≡ *Hexagonia cucullata* (Mont.) Murrill, Bull. Torrey bot. Club 31(6): 332 (1904)

≡ *Polyporus miquelii* var. *cucullatus* (Mont.) Corner, Beih. Nova Hedwigia 78: 90 (1984)

= *Favolus curtipes* Berk. & M.A. Curtis, Hooker's J. Bot. Kew Gard. Misc. 1: 234 (1849)

= *Polyporus curtipes* (Berk. & M.A. Curtis) Ryvarden, Syn. Fung. (Oslo) 5: 213 (1991)

Description: Basidiomata annual, solitary to imbricate, laterally short stipitate, dimidiate to subsessile. Pileus 15–40 mm from the base to margin of the pileus, 30–60 mm wide, and 2 mm thick; dimidiate to flabelliform, conchate-flabelliform when dry, flexible when fresh, very tough when dry; surface glabrous, smooth or slightly tessellate, not zoned, beige to pale ochraceous, slightly reddish brown towards the margin when dry; margin entire to fimbriate, involute when dry, pale ochraceous; context of the pileus up to 2 mm wide, homogeneous, beige. Hymenophore surface poroid, light brown, pores 2–3 per mm, angular to circular; dissepiments entire to lacerated; tubes up to 1 mm long. Stipe reduce subdiscoid up to 2 mm long, concolorous with pilear surface, or practically non-existent and attached to the substrate by a basal disc up to 10 mm in diam.

Hyphal system dimitic; generative hyphae 2–4 µm wide, with clamp connections, hyaline, thin-walled, scanty, CB−, IKI−; skeletal-binding hyphae 2–6 µm wide, densely interwoven, thick-walled, flexuous, branched 4–6 times, branches tapering to filiform tips 0.5 µm wide, dominating throughout the basidiomata, CB−, IKI − to slightly dextrinoid in mass in the dissepiments. Hyphal pegs absent. Pileipellis not well differentiated. Cystidia not seen; hymenium with some final tips of skeletal-binding hyphae among the basidia. Basidia 25–36 × 7–14 µm, mostly clavate, with four sterigmata. Basidiospores 14–20 × 5–7 µm (m = 17.5 × 5.7 µm) Q = 2.3–4 (m = 3; n = 100/5), narrowly cylindrical to sub-cylindrical, thin-walled, smooth, hyaline, IKI−, CB−.

Ecology and distribution: growing on fallen branches of unidentified angiosperms; known from Argentina (Robledo and Rajchenberg 2007 as *Polyporus curtipes*), Brazil (Baltazar and Gibertoni 2009 as *Pseudofavolus cucullatus*), Costa Rica (Velázquez and Ruíz-Boyer 2005 as *Pseudofavolus cucullatus*), Cuba (type locality), and Mexico (Nava-Mora and Valenzuela (1997) as *Polyporus curtipes*).

Specimens examined: Brazil, Paraná, Foz do Iguaçu, Parque Nacional do Iguaçu, 25°37'21.1"S, 54°28'11.0"W, 22 Jan 2017, leg. M. Palacio 204, (ICN197323). — Cuba, leg. Ramón de la Sagra & C. Wright (PC) (holotype of *Pseudofavolus cucullatus*).

Comments: *Mycobonia cucullata* can be distinguished by the hexagonal pores 2–3 per mm, short tubes up to 0.7 mm long, thinner context up to 0.2 mm wide, and by the narrowly cylindrical basidiospores. This species has been recorded in South America under the name *Favolus curtipes* Berk. & M.A. Curtis (Silveira and Wright 2005). However, according to the protologue of *F. curtipes*, this species can be differentiated from *M. cucullata* by the smaller and less rigid pores, fleshier context and darker pilear surface (Hooker 1849).

Mycobonia miquelii (Mont.) Palacio & Westphalen, comb. nov.

MycoBank: MB841084

≡ *Polyporus miquelii* Mont., Annls Sci. Nat., Bot., sér. 3 4: 357 (1845)

≡ *Hexagonia miquelii* (Mont.) Sacc., Syll. fung. (Abellini) 6: 361 (1888)

≡ *Scenidium miquelii* (Mont.) Kuntze, Revis. gen. pl. (Leipzig) 3(3): 516 (1898)

≡ *Pseudofavolus miquelii* (Mont.) Pat., Essai Tax. Hyménomyc. (Lons-le-Saunier): 81 (1900)

= *Favolus induratus* Berk., Ann. Mag. nat. Hist., Ser. 2 9: 197 (1852)

= *Hexagonia indurata* (Berk.) Murrill, Bull. Torrey bot. Club 31(6): 332 (1904)

= *Favolus daedaleoides* Speg., Revista Argent. Hist. Nat. 1(2): 108 (1891)

Description: Basidiomata annual, solitary, laterally short stipitate to subsessile. Pileus 20–40 mm from the base to margin of the pileus, 20–60 mm wide, and 2–4 mm thick; flexible when fresh, very tough and convex when dry, flabelliform, conchate-flabelliform; surface glabrous, tessellate bullate-reticulate, not zoned, pale ochraceous to brownish ochraceous with reddish-brown spots mainly towards the margin; margin entire to lacerate, wavy, incurved when dry, reddish-brown; context of the pileus 2–3 mm wide, homogeneous, beige. Hymenophore surface poroid, pale ochraceous to brownish ochraceous, pores 1–1.5 per mm, circular to angular; dissepiments entire to lacerated; tubes up to 4 mm long. Stipe reduce subdiscoid up to 2 mm long, concolorous with pilear surface, or practically non-existant and attached to substrate by a basal disc up to 7 mm in diam.

Hyphal system dimitic; generative hyphae 2–5 µm wide, with clamp connections, hyaline, thin-walled, scanty, CB−, IKI−; skeletal-binding hyphae 2–6 µm wide, densely interwoven, thick-walled, flexuous, branched 4–7 times, branches tapering to filiform tips − 1 µm wide, dominating throughout the basidiomata, CB−, IKI−. Hyphal pegs absent. Pileipellis not well differentiated. Cystidia not seen; hymenium with some final tips of skeleto-binding hyphae between the basidia. Basidia 20–35 × 9–15 µm, mostly clavate, with four sterigmata. Basidiospores 11–17 × 5.5–8.5 µm (m = 14 × 6.5 µm) Q = 2.3–2.8 (m = 2.4; n = 100/5), sub-cylindrical, thin-walled, smooth, hyaline, IKI−, CB−.

Ecology and distribution: growing on fallen branches of unidentified angiosperms; common species originally described from Surinam and also registered from Argentina, Brazil (Capelari and Maziero 1988), Costa Rica (Velázquez and Ruíz-Boyer 2005), and the Dominican Republic.

Specimens examined: Brazil, Espírito Santo, Santa Tereza, Rebio Augusto Ruschi, Trilha da Cachoeira, 13 Dez 2016, leg. A. Magnago 1305 (ICN197324); Rio Grande do Sul, Viamão, Parque Estadual de Itapuã, 21 Apr 2017, leg. G. Alves-Silva 1120 (ICN197320); ibid, leg. G. Alves-Silva 1121 (ICN197321); ibid, leg. G. Alves-Silva 1122, (ICN197322); Guaiba, Fazenda Maximiniano, 11 Nov 2017, leg. V. Oliveira-Garcia 213 (ICN197423); Porto Alegre, Morro Santana, 14 Dez 2007, leg. M. Westphalen 85/07 (ICN134137); Santa Catarina, Florianópolis, Parque Ecológico Córrego Grande, 27°35'55"S, 48°30'36"W, 10 May 2018, leg. M. Monteiro 160 (FLOR); São Paulo, Cananéia, Parque Estadual da Ilha do Cardoso, Trilha do Poço da Anta, 7 Jan 2019, leg. M.P. Drewinski 463, (SP499085); ibid., Parque Estadual das fontes do Ipiranga, 23°38'36.1"S, 46°37'21.6"W, 28 Mar 2019, leg. M.P. Drewinski 459 (SP499083).

Comments: Large and angular pores, 1–1.5 per mm, and a tessellate pilear surface with a reddish-brown margin, which differentiates *M. miquelii* from other *Mycobonia.*

Mycobonia yuchengii Yuan Yuan & Palacio, sp. nov. Figure 4.

MycoBank: MB841082

Type. — China, Hainan Province, Lingshui County, Diaoluoshan Forest Park, on fallen angiosperm trunk, 13 Jun 2014, leg. Dai 13584A (BJFC017323).

Etymology: — Yuchengii (Lat.): in honor of the Chinese mycologist, Prof. Yu Cheng Dai.

Description: Basidiomata annual, pileate, attached to substrate with a short laterally stipe-like base, leathery when fresh, becoming hard or rigid upon drying. Pileus dimidiate to flabelliform, projecting up to 3.5 cm, 4 cm wide, 1.5 mm thick at the center. Pilear surface cream to pale yellow-brown, glabrous, azonate, sometimes radiate-striate; margin acute, wavy when dry. Pore surface yellow-brown to umber; pores irregular, sometimes hexagonal, 1–3 per mm; dissepiments thin, entire to slightly lacerate. Context pale yellow-brown, hard corky, thin, less than 0.5 mm thick. Tube layer concolorous with the poroid surface, up to 2 mm long. Stipe short, concolorous with the pileal surface, up to 0.5 cm long, often forming a small disc at the base.

Hyphal system dimitic; generative hyphae bearing clamp connections; skeletal-binding hyphae dominant, thick-walled, frequently branched, slightly dextrinoid, especially at dissepimental edge, CB+, tissue unchanged in KOH. Contextual generative hyphae infrequent, hyaline, thin-walled, rarely branched, 2.5–3.5 µm in diam; contextual skeletal-binding hyphae dominant, hyaline, thick-walled with a wide to narrow lumen, some of them sub-solid, flexuous, frequently branched, tightly interwoven, 2.5–4 µm in diam. Tramal generative hyphae scanty, hyaline, thin-walled, rarely branched, 2–3.5 µm in diam,; tramal skeletal-binding hyphae thick-walled to almost solid, frequently branched, tightly interwoven, 2–4.5 µm in diam. Cystidia and cystidioles absent. Dendrohyphidia present along the hymenium, especially abundant in the

dissepiments. Basidia broadly clavate, with four sterigmata and a basal clamp connection, 20–35 × 12–15 µm; basidioles in shape similar to basidia, but slightly smaller. Basidiospores ellipsoid to mango-shaped, hyaline, thin-walled, smooth, sometimes with one or two guttule, IKI–, CB–, (11)13–17(18) × (5.5)5.8–8.5(8.8) µm, L = 14.8 µm, W = 7.1 µm, Q = 2.08–2.25 (n = 60/2).

Ecology and distribution: When Wu et al. (2020) made a systematic study on the polypores from subtropical and tropical China, *M. yuchengii* was found as a common species in South China, usually grows on angiosperm trunks or branches and occurring in open areas of the forest.

Specimens examined: China, Hainan Province, Wuzhishan County, Wuzhishan Forest

Park, on fallen angiosperm trunk, 10 Jun 2016 Dai 16493 (BJFC022610); Hunan

Province, Wulingyuan District, on fallen angiosperm trunk, 17 Ago 2010, leg. Dai 11682

(BJFC008806); Guangdong Province, Shixing County, Chebaling Nature Reserve, on fallen angiosperm branch, 23 Jun 2010, Cui 8707 (BJFC007647); ibid., 23 Jun 2010, leg. Cui 8747 (BJFC007687); Yunnan Province, Mengla County, Xishuangbanna Botanical Garden, on fallen angiosperm branch, 23 Jul 2014, leg. Dai 13893 (BJFC017623); ibid., leg. Dai 13894 (BJFC017624); Green Stone Forest Park, on fallen angiosperm branch, 4 Ago 2005, leg. Dai 6678 (IFP015327); Puer County, Laiyanghe Forest Park, on fallen angiosperm trunk, 6 Jun 2011, leg. Dai 12207 (BJFC010490).

Comments: *Mycobonia yuchengii* was previously identified as "*P. cucullatus*" (Dai 2007). *Mycobonia yuchengii* basidiomata have shallow pores, so macroscopically it resembles species of *Grammothele* Berk. & M.A. Curtis. In addition, species in both genera have dendrohyphidia along the hymenia, and their skeletal hyphae are dextrinoid (Zhou and Dai 2012). However, *Grammothele* lacks both stipe and binding hyphae.

Mycobonia brunneoleuca (Berk. & M.A. Curtis) Pat., Enum. Champ. Guadeloupe (Lons-le-Saunier): 23 (1903).

≡ *Hydnum brunneoleucum* Berk. & M.A. Curtis, Trans. Linn. Soc. London

22: 129. 1857, non *Polyporus brunneoleucus* Berk. 1846.

≡ *Polyporus polyacanthophorus* Nakasone, Mycotaxon 130(2): 383. 2015.

Description: see Nakasone (2015).

Ecology and distribution: growing on fallen branches of unidentified angiosperms, in cloud forest at 700–2700 m.a.s.l. in Brazil (Gerlach and Loguercio-Leite 2011), Colombia, Costa Rica, Honduras (Nakasone 2015), Martinique (Burt 1919), Panamá (Martin 1939), Paraguay, Puerto Rico (Nakasone 2015), and Venezuela (type locality).

Specimens examined: Brazil, Rio Grande do Sul, São Francisco de Paula, Floresta Nacional de São Francisco de Paula, 25 May 2019, leg. M. Palacio 438 (ICN202959); Santa Catarina, Joaçaba, Parque Ecológico Municipal Rio do Peixe, leg. G. Alves-Silva 625, (FLOR60335).

Comments: *Mycobonia brunneoleuca* is principally characterized by the large basidiospores 15–24(25) × (6)7–11 µm, narrowly ellipsoid, thin walled and hyaline. Macroscopically is characterized by the concave and shell-like basidiomata with stereoid hymenophore projecting sterile hyphal pegs, which is almost identical to *M. flava*. *Mycobonia brunneoleuca* and *M. flava;* can be differentiated by the basidiospores, which are sub-cylindrical and smaller (up to 5–7 µm wide) in *M. flava*, and also by the ecological niches that these two species occupy (Gerlach and Loguercio-Leite 2011). *Mycobonia brunneoleuca* occurs in cloud forests of the Caribbean, and throughout Central and South America between 700 and 2,700 m asl., while *M. flava* occurs at elevations up to 700 m asl. from North America to Argentina. In addition to these morphological and ecological differences, our phylogenetic analysis showed that *M. brunneoleuca* and *M. flava* represent two different linages (Fig. 1).

Mycobonia flava (Sw.) Pat., Bull. Soc. mycol. Fr. 10(2): 77. 1894.

≡ *Peziza flava* Sw.: Fr., Prod.: 150. 1788.

≡ *Hydnum flavum* (Sw.: Fr.) Berk., Ann. Mag. Nat. Hist., 10: 380. 1843 [“1842”].

≡ *Bonia flava* (Sw.: Fr.) Henn., Hedwigia 36: 192. 1897.

≡ *Auricularia flava* (Sw.: Fr.) Farl., Bibl. Index N. Amer. Fung.: 307. 1905.

≡ *Grandinioides flava* (Sw.: Fr.) Banker, Mem. Torrey Bot. Club 12: 179. 1906.

≡ *Polyporus curtipes* subsp. *flavus* (Sw.: Fr.) D. Krüger, Cryptog. Mycol. 31: 399. 2010.

≡ *Polyporus epitheloides* Nakasone, Mycotaxon 130(2): 383. 2015.

Description: see Julich (1976).

Ecology and distribution: growing on fallen branches of unidentified angiosperms, in Argentina, Colombia (Jülich 1975), Cuba (Burt 1919), Jamaica (Swartz 1788) (type locality), North America (Burt 1919), Brazil (Jülich 1975; Baltazar and Gibertoni 2009) and Venezuela (Corner 1984).

Specimens examined: Brazil, Amazonas, Novo Aripuanã, BR-230, 23 Apr 1985, leg. K.F. Rodrigues 325 (INPA136956); Paraná, Foz do Iguaçu, Parque Nacional do Iguaçu, 25°37'21.1"S, 54°28'11.0"W, 23 Jan 2017, leg. M. Palacio 207 (ICN197318); ibid., leg. M. Palacio 213, (ICN197319); Rio Do Janeiro, Rio de Janeiro, Parque Nacional da Tijuca, 8 Feb 2017, leg. F.T.F. Linhares 228 (ICN197346); São Paulo, São Paulo, Parque Estadual da Cantareira, Trilha da cachoeira, 25 Mar 2019, leg. M.P. Drewinski 449, (SP499082).

Comments: Microscopically *M. flava* is very similar to *M. miquelii*, especially by the sub-cylindrical basidiospores, however *M. flava* can be differentiated by the hymenophore being stereoid with hyphal pegs, while in *M. miquelii* it is poroid.

Other species possibly included in the genus Mycobonia:

Favolus curtipes Berk. & M.A. Curtis, Hooker's J. Bot. Kew Gard. Misc. 1: 234 (1849)

Favolus tenuis Fr., Syst. orb. veg. (Lundae) 1: 76 (1825)

Hexagonia bipindiensis Henn., Bot. Jb. 38(1): 122 (1905) [1907]

Hexagonia pulchella Lév., Annls Sci. Nat., Bot., sér. 3 2: 200 (1844)

Polyporus orinocensis Pat. & Gaillard, Bull. Soc. mycol. Fr. 4(2): 31 (1888)

Polyporus polygrammus Mont., Annls Sci. Nat., Bot., sér. 2 8: 365 (1837)

Pseudofavolus nigrus Ryvarden, Mycotaxon 28(2): 537 (1987)

KEY TO MYCOBONIA **NEOTROPICAL SPECIES**

1 Hymenophoral surface poroid 2

1* Hymenophoral surface stereoid with hyphal pegs 5

2 Pores 1–1.5 per mm; pilear surface tessellate, bullate-reticulate, pale ochraceous to brownish ochraceous with reddish-brown spots mainly towards the margin .....*M. miquelii*

2* Pores 2–3 per mm; pilear surface smooth to slightly tessellate, or radially wrinkled, beige to pale ochraceous, to chesnut to black 3

3 Pores 0.2–0.5 per mm; pilear surface smooth or slightly tessellate, beige to pale ochraceous, slightly reddish brown towards the margin when dry; known from Mexico to Argentina

M. cucullata

3* Pores 4–5 per mm; pilear surface smooth darker, only known from Venezuela. 4

4 Pilear surface pale chestnut to reddish-brown *M. yuchenguii*

4* Pilear surface black *P. nigrus*

5 Basidiospores narrowly ellipsoid 15–24(25) × (6)7–11 µm; growing in cloud forests of the Caribbean and Central and South America between 700 and 2,700 m asl.

*M. brunneoleuc*a

5* Basidiospores sub-cylindrical 12–18 × 5–7 µm; growing at elevations up to 700 m asl. from North America to Argentina *M. flava*

Discussion

Mycobonia and *Pseudofavolus* in their traditional circumscriptions are paraphyletic groups. The differences between ITS, nc LSU rDNA and *RPB2* sequences within *Mycobonia* species are significantly small, with just 100 variable sites from 2481 characters, thus showing that the phylogenetic separation between both genera is artificial. Following the guidelines to define fungi genera formulated by Vellinga et al. (2015), we consider *Pseudofavolus* a synonym of *Mycobonia* (older name with priority). Therefore, we emended *Mycobonia* to encompass stereoid and also poroid species. We combined *M. cucullata* and *M. miquelii* since we could assess phyllogenetic data of those species through molecular analysis. Regarding other *Pseudofavolus* species, such as *P. nigrus* and *P. orinocensis*, we preferred to avoid nomenclatural changes until sequences of those species become available and their phylogenetic position can be confirmed, especially in a group with several genera with similar morphology.

Phylogenetic relationships within *Mycobonia* clade are still not well resolved, especially due to the similarity in the sequences among the different species. More molecular data including other DNA regions could help clarify that in the future. However, *Mycobonia* species can be differentiated and recognized by ecologically through distribution patterns and elevation, while morphologically through the basidiospore shape and size, as well as the hymenophore type.

Hymenophoral transitions within genera have often been documented in other groups of Polyporales, as *Antrodia* (Runnel et al. 2019), *Steccherinum* (Westphalen et al. 2018; Miettinen et al. 2012), *Metuloidea* (Miettinen and Ryvarden 2016), and also within the core polyporoid clade in *Neofavolus*, *Lentinus*/ *Polyporellus* (Seelan et al. 2015). Additionally, Seelan et al. (2015) estimated the ancestral hymenophoral configuration for *Neofavolus* and *Lentinus*/ *Polyporellus*. However, ancestral character state reconstruction including both stereoid and poroid hymenophore had not been estimated previously in the core polyporoid clade. Our results suggest a transition from angular pores to stereoid hymenophore in *Mycobonia* clade, and that the plesiomorphic condition for *Polyporus s.l.* is to have angular pores.

Other groups in the core polyporoid clade can also present stereoid hymenophore with hyphal pegs, as *Dichomitus*, *Ephitele*, and *Gramothele* (Nakasone 2015). However, these groups present resupinate basidiomata, while the basidiomata in *Mycobonia* are pileate. Specifically, hyphal pegs are also present in other clades of Polyporaceae, as *Favolus*, *Lentinus*, and *Neofavolus*, which are different in presenting basidiomata with lamellate hymenophore. The presence of hyphal pegs could represent an anatomical advantage, considering it has been suggested that there exists a possible relation with moisture retention and also protection from insect invasion (Pegler 1983). However, the function of the hyphal pegs is still unknown (Pegler and Young 1983), and it is not a homologous character (Hibbett and Vilgalys 1993).

Mycobonia shares with *Polyporus s.l.* a dimitic hyphal system with skeletal-binding hyphae, hyaline, and thin-walled basidiospores, and caising white-rot, which appear to be a conserved characteristic across all

Polyporus s.l. species. However, relationships between genera, like *Mycobonia* in *Polyporus s.l.* are yet to be solved.

Declarations

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Conflicts of interest/Competing interests: Not applicable

Availability of data and material: the manuscript data are deposited in world-reference repositories (GenBank, TreeBase) and the fungal collections are deposited in herbaria recognized by the Index Herberiorum.

Code availability: Not applicable

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Figures

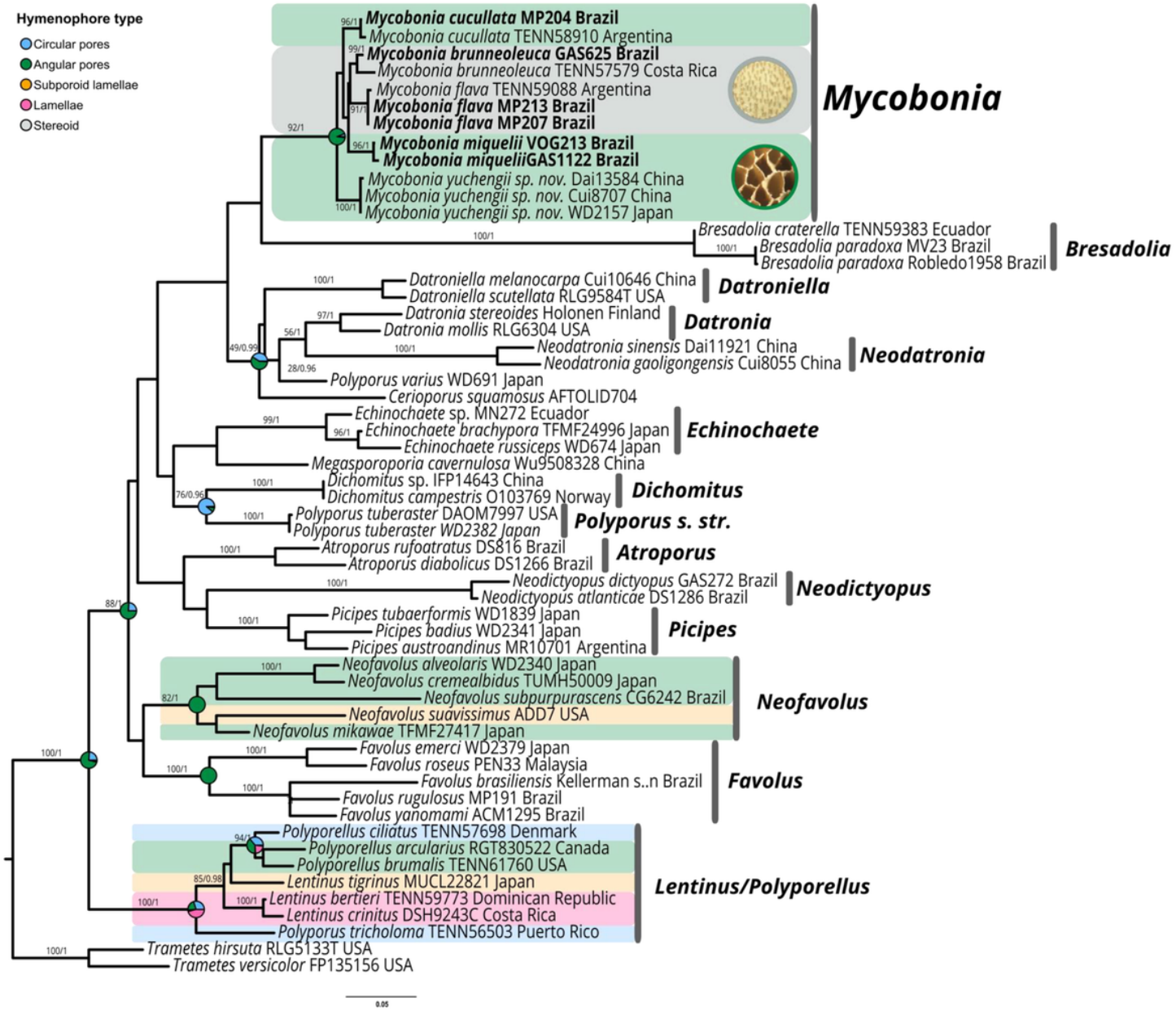

Figure 1

Phylogenetic relationships in Polyporus s.l. from ITS, nc LSU rDNA and RPB2 sequences. Topology from ML analysis. Bayesian posterior probability above 0.95 and bootstrap values above 80% are shown. Pies at nodes represent probability of each state from the summary of stochastic mapping of ancestral state estimates of hymenophore configuration across Polyporus s.l. (blue = circular pores, green = angular pores, orange = subporoid lamellae, pink = lamellae, grey = stereoid).

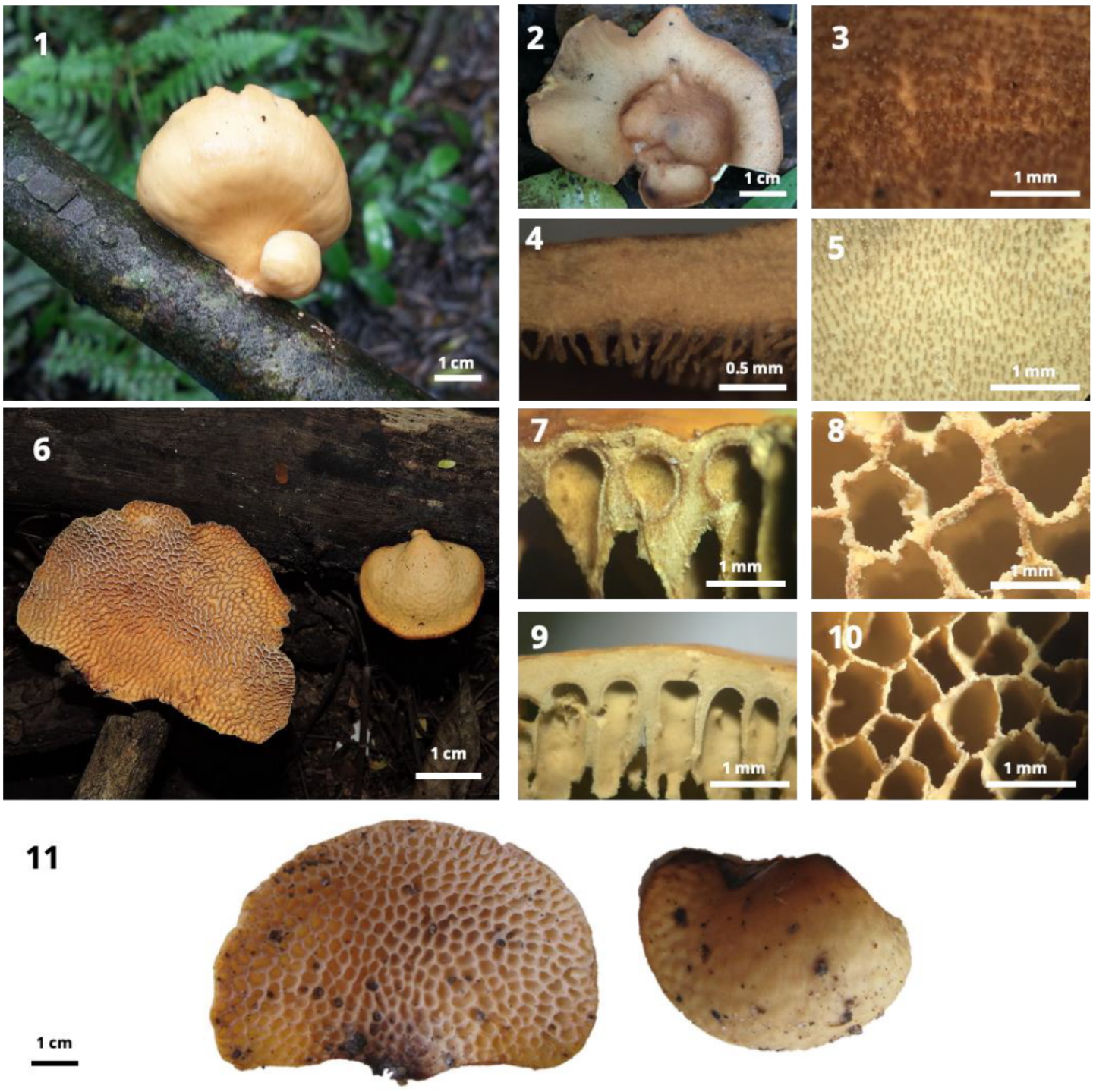

Figure 2

Basidiomata and hymenophore detail of Mycobonia species. A–D. Mycobonia brunneoleuca (GAS625). E. Mycobonia flava (MP207). F–H. M. miquelii (Monteiro 160; GAS 1122). I–J. M. cucullata. K. M. yuchengii (type Dai 13584A). Photo A. by G. Alves-Silva and F. by Felipe Bittencourt.

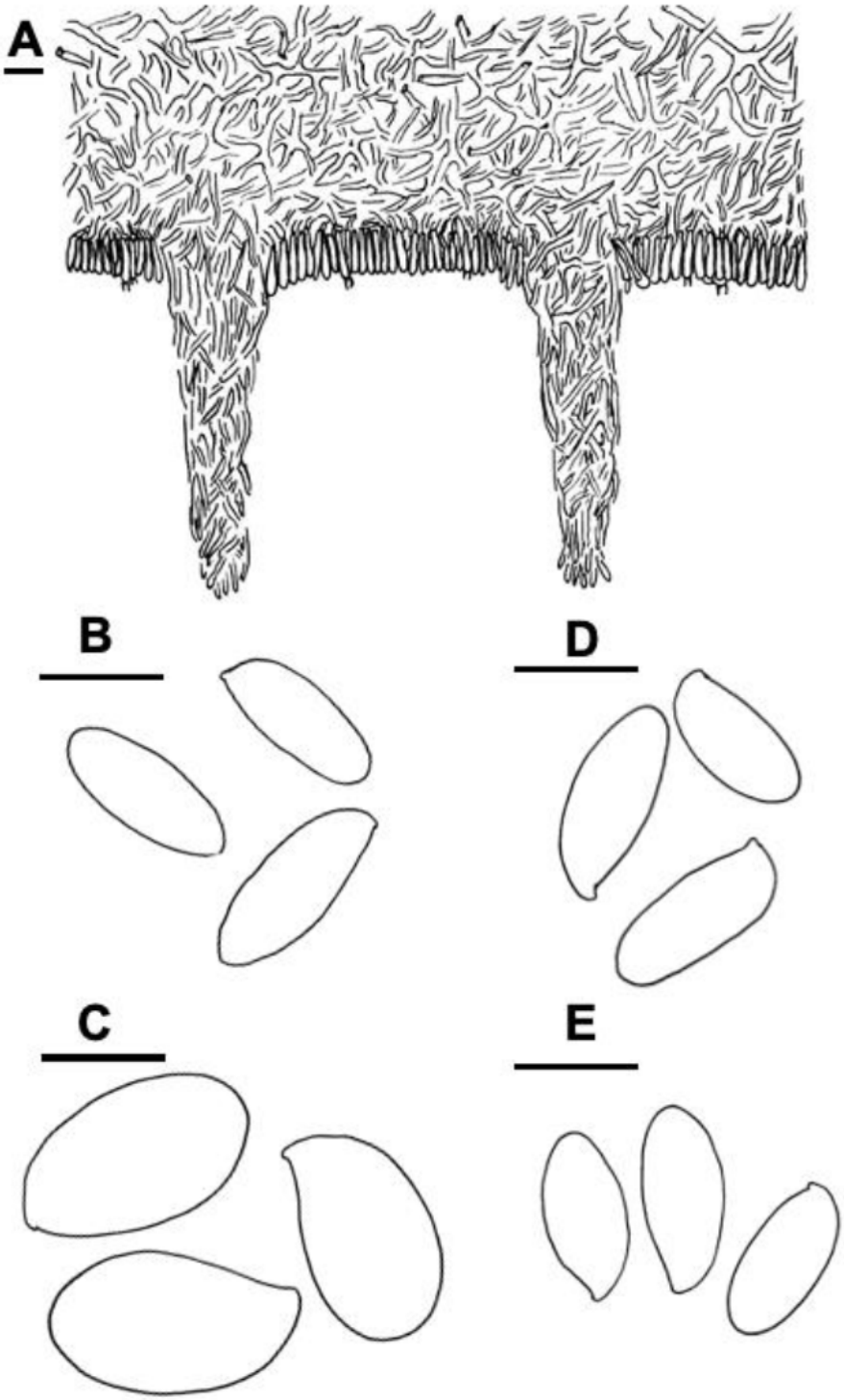

Figure 3

Microscopic features of Mycobonia species. A. Hymenium, tramal hyphae and sterile hyphal pegs in M. flava (MP207). B–E. Basidiospores. B. M. flava. C. M. brunneoleuca. D. M. cucullata. E. M. miquelii.

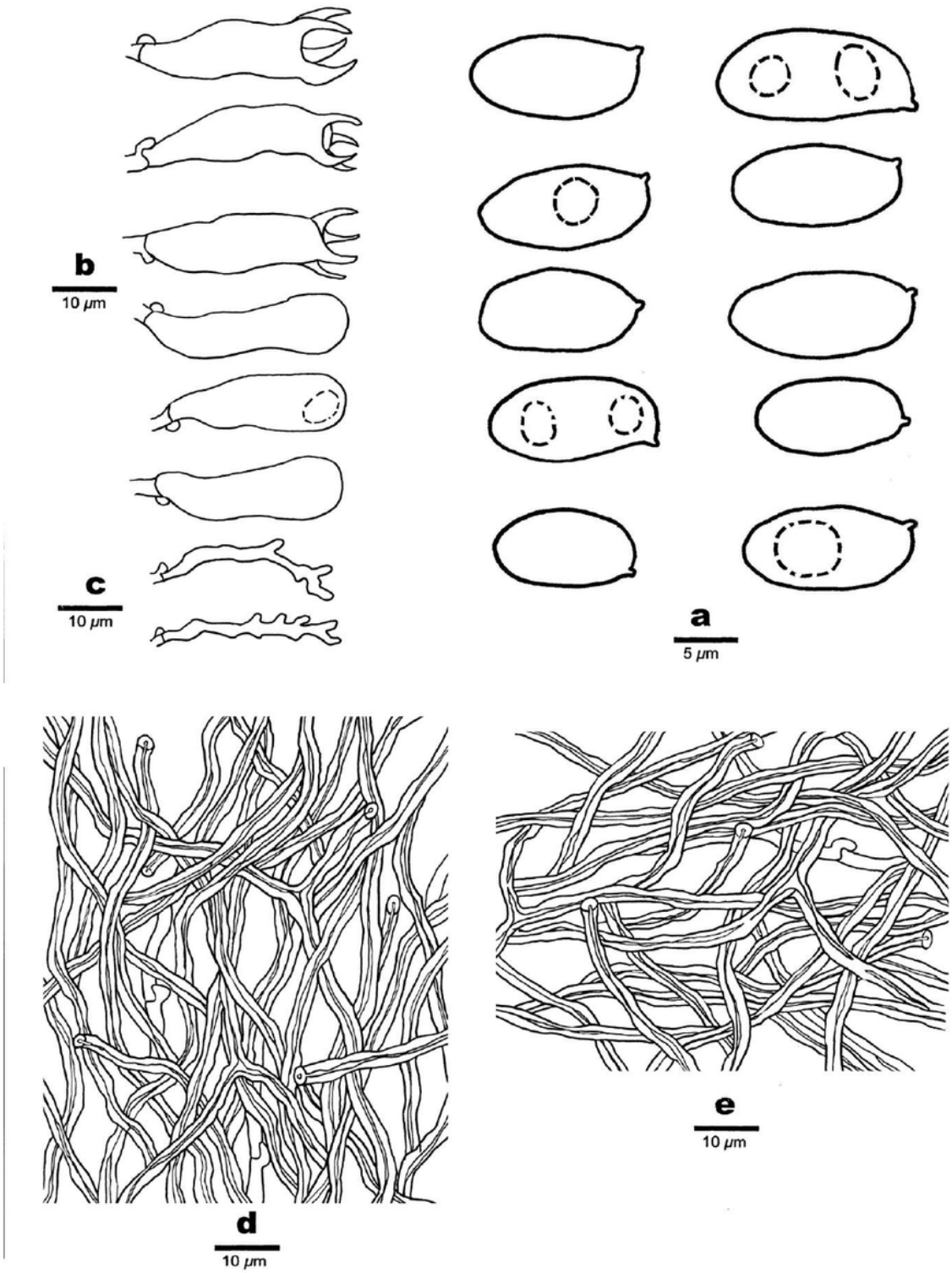

Figure 4

Microscopic features of Mycobonia yuchengii from type Dai 13584A (BJFC017323). A. Basidiospores. B. Basidia. C. Dendrohypidia. D. Hyphae from the trama. E. Hyphae from the context.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SuppFig1.png