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Disentangling cryptic species in the
Marasmius haematocephalus (Mont.) Fr.
and *M. siccus* (Schwein.) Fr. species complexes
(Agaricales, Basidiomycota)

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Disentangling cryptic species in the *Marasmius haematocephalus* (Mont.) Fr. and *M. siccus* (Schwein.) Fr. species complexes (Agaricales, Basidiomycota)

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ABSTRACT

Marasmius haematocephalus (Mont.) Fr. and *M. siccus* (Schwein.) Fr. (ser. *Haematocephali*) were respectively described from Southeastern Brazil and from Eastern United States, and subsequently reported as pantropical and pantemperate. Recent phylogenetic studies indicate that these two species are closely related in their broad concepts and at least *M. haematocephalus* is suggested to be a species complex. We evaluated herein whether *M. haematocephalus* is or is not pantropical and whether *M. siccus* is or is not pantemperate. Combined nrITS + nrLSU and nrITS + *rpb2* + *efl-α* phylogenies were reconstructed using Maximum Likelihood and Bayesian analyses and integrated with detailed morphological data. Results indicated that *M. haematocephalus* 'sensu stricto' (s. str.) is at most Neotropical, with closely related species in Tropical Africa and Indo-Malayan region. Similarly, *M. siccus* s. str. is at most Nearctic, with closely related species in the temperate Palearctic. For the time being, one can recognize about 23 species in the *M. haematocephalus* and *M. siccus* complexes, of which four are described as new herein.

KEY WORDS

Phylogenetics,
pantropical,
pantemperate,
cryptic species,
Marasmiaceae,
epitypification,
new status,
new species.

RÉSUMÉ

Démêler les espèces cryptiques dans les complexes d'espèces Marasmius haematocephalus (Mont.) Fr. et M. siccus (Schwein.) Fr. (Agaricales, Basidiomycota).

Marasmius haematocephalus (Mont.) Fr. et *M. siccus* (Schwein.) Fr. (ser. *Haematocephali*) ont été respectivement décrits du sud-est du Brésil et de l'est des États-Unis, signalés par la suite comme pantropicaux et pantempérés. Dans des études phylogénétiques récentes, ils semblent étroitement liés dans leurs concepts généraux et au moins *M. haematocephalus* est suggéré comme un complexe d'espèces. Nous avons cherché à déterminer ici si *M. haematocephalus* est ou non pantropical et si *M. siccus* est ou non pantempéré. Les phylogénies combinées nrITS + nrLSU et nrITS + *rpb2* + *efl-α* ont été reconstruites dans les analyses de vraisemblance maximale et bayésiennes et intégrées avec des données morphologiques détaillées. Les résultats ont indiqué que *M. haematocephalus* 'sensu stricto' (s. str.) n'est pas pantropical mais tout au plus néotropical, avec des espèces proches en Afrique tropicale et en Indo-Malaisie. De façon similaire, *M. siccus* s. str. est tout au plus néarctique, avec des espèces proches dans le paléarctique tempéré. Pour l'instant, on peut reconnaître environ 23 espèces dans les complexes *M. haematocephalus* et *M. siccus*, dont quatre sont décrites ici comme nouvelles.

MOTS CLÉS
Phylogénétique,
pantropical,
pantempéré,
espèces cryptiques,
Marasmiaceae,
épitypification,
statut nouveau,
espèces nouvelles.

INTRODUCTION

Marasmius Fr. (*Marasmiaceae*, *Agaricales*) groups mostly saprotrophic mushroom-forming species on plant debris (Singer 1976, 1986; Desjardin 1989; Antonín & Noordeloos 2010). It is distributed worldwide, more diverse in tropical and subtropical forests (Singer 1976; Desjardin 1989; Antonín & Noordeloos 2010). Basidiomata vary from small to large, thin to robust, with a mostly dull, dry and generally membranous pileus, whitish lamellae, and a filiform to cylindrical, chitinous to cartilaginous stipe that may be insititious or with basal mycelium; the basidiospores are hyaline, smooth and inamyloid and the pileipellis is hymeniform composed of smooth or broom cells (Singer 1976, 1986; Desjardin 1989; Wilson & Desjardin 2005; Antonín 2007; Antonín & Noordeloos 2010). The Index Fungorum database lists 1993 *Marasmius* names, of which 558 are now classified in other marasmioïd and gymnopoid genera mostly in *Omphalotaceae* Bresinsky and *Physalacriaceae* Corner (Moncalvo et al. 2002; Wilson & Desjardin 2005; Jenkinson et al. 2014).

Based on morphology, *Marasmius* sect. *Sicci* Singer (Singer 1976, 1986) was divided into four series: *Atrorubentes* (Desjardin & Horak 1997), *Haematocephali* (Singer 1976), *Leonini* (Singer 1976) and *Spinulosi* (Antonín & Noordeloos 1993). Antonín & Noordeloos (2010) merged sect. *Sicci* in sect. *Globulares* based on Tan et al. (2009) and Wannathes et al. (2009). In Oliveira et al. (2020), multiple groups of closely related species were grouped into 16 series within at least three subsections in *Globulares* Kühner emend. Antonín & Noordeloos. Series *Haematocephali*, the group evaluated in this study, includes *M. haematocephalus* (Mont.) Fr., and *M. siccus* (Schwein.) Fr.

Marasmius haematocephalus was described as *Agaricus haematocephalus* Mont., based on a collection of Auguste de Saint Hilaire in the Rio de Janeiro State, Southeastern Brazil (Montagne 1837). Later, this species was reported from tropical forests in America, Africa, Asia, and Oceania (Petch 1948;

Dennis 1951, 1970; Singer 1964, 1965, 1976; Pegler 1983; Desjardin 1989; Desjardin & Horak 1997; Desjardin et al. 2000; Antonín 2007; Tan et al. 2009; Wannathes et al. 2009; Shay et al. 2017; Appendix: Figs S1; S3). *Marasmius siccus* was described as *Agaricus siccus* Schwein., based on his own collection in Salem (North Carolina) or Bethlehem (Pennsylvania), in the United States of America, between 1812 and 1821 (Schweinitz 1822; Desjardin 1989). *Marasmius siccus* has been reported as widespread in the subarctic, boreal and temperate zone of the northern hemisphere (Gilliam 1976; Noordeloos 1987; Desjardin 1989; Antonín & Noordeloos 2010; Antonín et al. 2012; Kiyashko et al. 2014; Appendix: Figs S1; S2). Based on Singer (1976) and Desjardin (1989), these two species mainly differ from each other in the pileus pigmentation: purple red to reddish purple in *M. haematocephalus* and pale brownish orange with a darker center for *M. siccus*.

So far, the morphological species recognition (MSR) has led to an understanding of pantropical or pantemperate distribution while at least *M. haematocephalus* seems a species complex. Collections throughout the Earth continue to be determined as *M. haematocephalus* and *M. siccus* following this view. Recent studies reported these species from various localities providing morphological description along with nrITS data. Wannathes et al. (2009) detected six forms (nom. prov.) of *M. haematocephalus* from Thailand. Tan et al. (2009) and Shay et al. (2017) have reported *M. haematocephalus* from Malaysia and Madagascar, respectively. *Marasmius siccus* was reported from South Korea (Antonín et al. 2012) and Russia (Kiyashko et al. 2014).

Is *M. haematocephalus* pantropical? Is *M. siccus* pantemperate? Or are these names harboring cryptic species hidden in two MSR? If so, how many species may be hidden in these names? As a first effort to engage these questions, we used nrITS and nrLSU data available in the GenBank database (NCBI) along with sequences newly produced in this study to evaluate whether specimens of various geographic origins determined as *M. haematocephalus* and *M. siccus* form

monophyletic groups, respectively. Phylogenetic Species Recognition (PSR; species as lineage) was integrated with MSR (species as class) to tentatively circumscribe the taxa in the complexes. “Class” in this text is not the taxonomic rank Class, but the nature of the grouping concepts (lineage or class) according to Taylor *et al.* (2000, 2006). Many specimens of the *M. haematocephalus* complex from South-eastern Brazil (type locality) were included in this analysis along with detailed morphological evaluation. Multilocus (nrITS + *rpb2* + *efl-α*) analyses were conducted to resolve one of the species clusters in which data from nrITS + nrLSU was insufficient to resolve. Our approach combined and evaluated applied theoretical and/or operational species concepts including Morphological Species Recognition (MSR) derived from Morphological Species Concept (MSC) and Phylogenetic Species Recognition (PSR) derived from Phylogenetic Species Concept (PSC) (Mayden 1997; Taylor *et al.* 2000, 2006).

MATERIAL AND METHODS

SITES OF THE COLLECTIONS NEWLY EXAMINED

Specimens newly examined were collected from four areas of the Atlantic Rainforest in Southeastern Brazil between January 2010 and March 2013: 1) Reserva Biológica de Paranapiacaba, Santo André City, SP, Brazil, 23°46'31.10"S, 46°18'48.90"W, consists of 336 ha of preserved Ombrophilous Dense Forest in predominantly mountainous landscape (Domingos *et al.* 2000; Xavier *et al.* 2008); 2) Parque Estadual da Cantareira, Núcleo Engordador, situated north of São Paulo City, 23°24'11.89"S, 46°35'12.29"W, an area of Seasonal Semideciduous Forest of humid mesothermal climate (Ventura *et al.* 1966; Secretaria do Meio Ambiente 2000; Xavier *et al.* 2008); 3) Parque Estadual das Fontes do Ipiranga, center-south of São Paulo City, 23°38'23.78"S, 46°37'7.78"W, an urban park consisting of 543 ha of preserved Seasonal Semideciduous Forest (Fernandes *et al.* 2002; Pivello & Peccinini 2002; Santos & Funari 2002; Xavier *et al.* 2008); and 4) Parque Estadual Turístico do Alto Ribeira, 24°16'40" to 24°38'30"S and 48°27'20" to 48°44'00"W, consists of 35 884.28 ha spanning parts of the Iporanga, Apiaí and Guapiara districts in the State of São Paulo, predominantly composed of Ombrophilous Forest (Köppen 1948; Lepsch *et al.* 1990; Secretaria do Meio Ambiente 2000; Ivanauskas *et al.* 2012). This park represents one of the most conserved remnants of Atlantic Rainforest in the State of São Paulo and is part of the Paranapiacaba ecological continuum (Ivanauskas *et al.* 2012). Within this park, only the unit “Núcleo Santana” (24°32'00"S, 48°40'19"W) and the Betary Private Reserve (24°35'16.58"S, 48°37'41.95"O) were sampled.

MORPHOLOGICAL DESCRIPTIONS

Fresh basidiomata were photographed and macroscopically described with color codes (Küppers 2002) and dried at 30–40°C for herbarium preservation. Lamellae spacing were

determined by L , the number of lamellae; and l , the series of lamellulae. Basidiospores size included the range min.-max. of the length × width (x_{rm} = min.-max. of the means of length × width; x_{mm} = the mean of the means of length [$\pm$ standard deviation, SD] × width [$\pm$ SD]; Q_{rm} = min.-max. of the quotient of length/width; Q_{mm} = the mean of means of Q values [$\pm$ SD]; n/s = number of measured spores per specimen examined/number of specimens [different collections] analyzed for each species). When a single specimen was analyzed for a taxon, the basidiospores size included min.-max. of the length × width (x_{m} = the mean of length [$\pm$ SD] × width [$\pm$ SD]; Q_{m} = the mean of Q values [$\pm$ SD]; n/s = number of unities per number of distinct collections analyzed). Measurements were standardized to 30 basidiospores, 15 cystidia and 10 hyphae diameters, spanning all the variation observed. Collections were deposited in the Maria Eneyda P. K. Fidalgo Herbarium (SP), of Instituto de Botânica, São Paulo.

The original type specimen of *M. haematocephalus* was assumed to be lost (Singer 1976; Desjardin 1989; Antonín 2007; Wannathes *et al.* 2009; Robert *et al.* 2013; Shay *et al.* 2017). However, Dr V. Antonín (pers. comm.) is convinced he found the authentic type material in the PC herbarium, which is currently on a loan in his lab. A topotype (Singer C 3172) collected in the Botanical Garden, Guanabara, Rio de Janeiro (Singer 1976) seems to be housed in BAFC herbarium, but no reply was received for the specimen loan request. Another collection from French Guiana, *M. Leprieur* n° 990 (PC), determined by Montagne as *M. haematocephalus* and regarded as authentic, was already fully revised by Desjardin (1989). Also, the original type of *M. siccus*, “Salem-Beth.”, Schweinitz, no date (PH[PH00062046]), was already fully revised by Desjardin (1989: 671–674) and no additional morphological revision is needed.

SOURCES OF DNA SEQUENCES DATA

DNA extraction, PCR amplification, sequencing, and editing of newly produced sequences were as described in Oliveira *et al.* (2020) and Sánchez-Ramírez *et al.* (2014). Newly produced sequences were deposited in the GenBank database (NCBI). BLAST searches in GenBank were conducted to retrieve similar sequences (95–100% identity and e-value of 0.0). Sequences that were deemed taxonomically relevant and of good quality were downloaded for analyses. A list of the specimens/sequences included in this study is provided in the Appendix (Table S1).

PHYLOGENETIC ANALYSES

Five sequence datasets were constructed. DATASET 1 combined our newly produced nrITS and nrLSU data with relevant sequences downloaded from Genbank, including members of *Marasmius* sect. *Marasmius* subsect. *Sicciformes* as the outgroup (Appendix: Table S1). Based on the tree resulting from the phylogenetic analyses of DATASET 1 (Fig. 1), newly aligned sequences of strains in clade *siccus*_cp1 plus closer taxa formed nrITS + nrLSU DATASET 2 while newly aligned sequences of *haemat*_cp1 formed nrITS + nrLSU DATASET 3, both

using *M. gardneri* Singer as the outgroup. With only haemat_cp2a (Fig. 3) into a newly aligned nrITS + nrLSU matrix, DATASET 4 included *M. roseus* J.S. Oliveira, sp. nov. and *M. castanocephalus* J.S. Oliveira, sp. nov. as the outgroup. DATASET 5 combined nrITS + *rpb2* + *efl-α* (Appendix: Table S2) to fully resolve DATASET 4 tree, with *M. castanocephalus* J.S. Oliveira, sp. nov. as the outgroup. DATASET 5 included analyses with and without ‘MC 4554 *M. auranti-capitatus* J.S. Oliveira, sp. nov.’ (holotype) from which neither *rpb2* nor *efl-α* could be obtained. Sequences’ datasets were aligned in MUSCLE v3.8.31 (Edgar 2004) and edited in Geneious R7 (Kearse *et al.* 2012). Since species involved in the analyses are very close, sequences were not too divergent and badly aligned site were few in DATASET 1, and even fewer in DATASETS 2–5 where data loss were progressively minimized. In the careful inspection of the alignments, base duplication or missing data by sequencing artifacts were removed or filled with “N”, and ambiguously aligned sites were deleted from the alignments as well as flanking residual strands of adjacent regions were trimmed at the alignment extremities. Gaps deemed as indels were preserved. Models selected via MrModeltest 2.3. (Nylander 2004) are shown in the Appendix.

Maximum Likelihood (ML) analyses, all partitioned based on the specified genes, were conducted in RAxML 7.0.4 (Stamatakis 2006), implementing the GTR + G + I model and fast-bootstrapping, with CAT approximations (only for DATASET 1), for 1000 pseudoreplicates and a full ML optimization for the final tree. For DATASETS 2–5, GTR-GAMMAI was implemented with GAMMA + P-Invar Model parameters estimated up to an accuracy of 0.001 Log Likelihood units. MC3 Bayesian analyses (BA) was carried out in MrBayes 3.2.1 (Ronquist *et al.* 2012), using default settings with Nst = 6 for the independent partitions of DATASETS 1–4. The BA for DATASET 5 (with and without MC4554) were partitioned into three: Nst = 2 for the nrITS partition, Nst = 6 for the *rpb2* partition, and Nst = 6 for the *efl-α* partition. The BA of DATASETS 1, 3 and 4 consisted of two independent runs of 5 000 000 generations, sampling frequency every 500 generations, six chains (four chains in DATASET 4) and two swaps (for DATASETS 1 and 4) or of DATASETS 2 and 5 of 1 000 000 generations, sampling frequency every 100 generations, four chains (six chains in DATASET 2) and two swaps. The burn-in reached 10%. Final trees were summarized using the 50% majority-rule consensus method. Branch lengths were summarized across the 95% highest posterior density trees.

The geographic origins of the strains included in the analyses were assigned to the seven biogeographic realms of the world of Dasmann (1974) and Udvardy (1975) as accepted in Olson *et al.* (2001) and Olson & Dinerstein (2002): Afrotropical, Antarctic, Australasia, Indo-Malayan, Neotropical, Nearctic, Oceania, and Palearctic. Globe map (Appendix: Fig. S1) of forested areas based on Olson & Dinerstein (2002) pinpointed with geographic distribution of reports of *M. haematocephalus* (red circles) and *M. siccus* (blue circles) provides the support for the putative range of

distribution of the pantropical *M. haematocephalus* (red area) and the pantemperate *M. siccus* (blue area) in Figure 1. These are based on strains included in this analysis and/or reported in the literature as *M. haematocephalus* and *M. siccus*. Clades regarded as species complexes are named including “cp” (complex) + number of the layer (1 – outmost or 2 – innermost) (Fig. 1), that is followed by a latter per lineage in layer 2 (Figs 2; 3). Strains depicted with blue rectangles means that the basidiomata look like *M. siccus* s.l. (Fig. 2) and those in red rectangles look like *M. haematocephalus* s.l. (Fig. 3).

RESULTS

In the BA tree of DATASET 1 (Fig. 1), the clade haemat_cp1 (PP 1.0/BS 100, red stems and branches) includes *M. haematocephalus* species complex collected across the Tropical zone. The clade siccus_cp1 (PP 1.0/BS 92, blue stems and branches) includes *M. siccus* species complex sampled across the Temperate zone. Between these two groups, a small clade named Ferrugineus (BS 84) groups *M. gardneri* and *M. ferrugineus* Berk. & M.A.Curtis, sensu Antonín *et al.* (2012) + other Asian strains, sister to haemat_cp1 without support. A lineage of strains named as *M. siccus* (India) and *M. aff. pallescens* Murrill, (Thailand) is sister to siccus_cp1 (PP 0.98/BS 74). ‘TFB12243 *M. haematocephalus* – United States, Tennessee’ and ‘ANT202 QFB28665 *M. siccus* – Canada, Quebec’ branched independent from the complexes. The clade Pulcherripes (PP 1.0/ BS 100) including strains of *M. pulcherripes* Peck from United States and South Korea plus additional species branched separated from haemat_cp1 and siccus_cp1, but sister without support to a clade (PP 1.0/ BS 95) bearing *M. anomalus* Lasch, sensu Oliveira *et al.* (2020), *M. hypophaeus* Berk. & M.A.Curtis, sensu Wannathes *et al.* (2009), *M. hinnuleus* Berk. & M.A.Curtis, sensu Shay *et al.* (2017) and *M. grandisetulosus* Singer (Grace *et al.* 2019).

The ML tree of DATASET 2 (Fig. 2) reveals at least five or six lineages named after *M. siccus* indicating different species. *Marasmius siccus* complex is based on the clade indicated by a black arrow and split into the basal *M. siccus* s. str. (BS 98/PP 1.0), and siccus_cp2a (BS 76/PP 0.99) and siccus_cp2b (unsupported), sister each other without support. The taxon named as *M. siccus* from India (AKD 301/2015 and AKD 300/2015) rather branched again conspecificly with *M. aff. pallescens* from Thailand. The ML tree of DATASET 3 formed five subclades (Fig. 3), providing statistical support for the resolution in haemat_cp1 (Fig. 1). With strong support (BS 63/PP 1.0), ‘haemat_cp2a’ is sister to haemat_cp2b. This group is sister to haemat_cp2c with strong support (BS 84/PP 1.0) and then to haemat_cp2d with moderate support (BS 66/PP 0.98); haemat_cp2e is basal. Most of the terminal nodes were highly supported and the support of deep to intermediate nodes are clearly improved by analysing DATASET 3 singly, but not such improvement was observed by analysing DATASET 2 singly. Blue (Fig. 2) and red (Fig. 3) arrows indicate geographic origin of the strains.

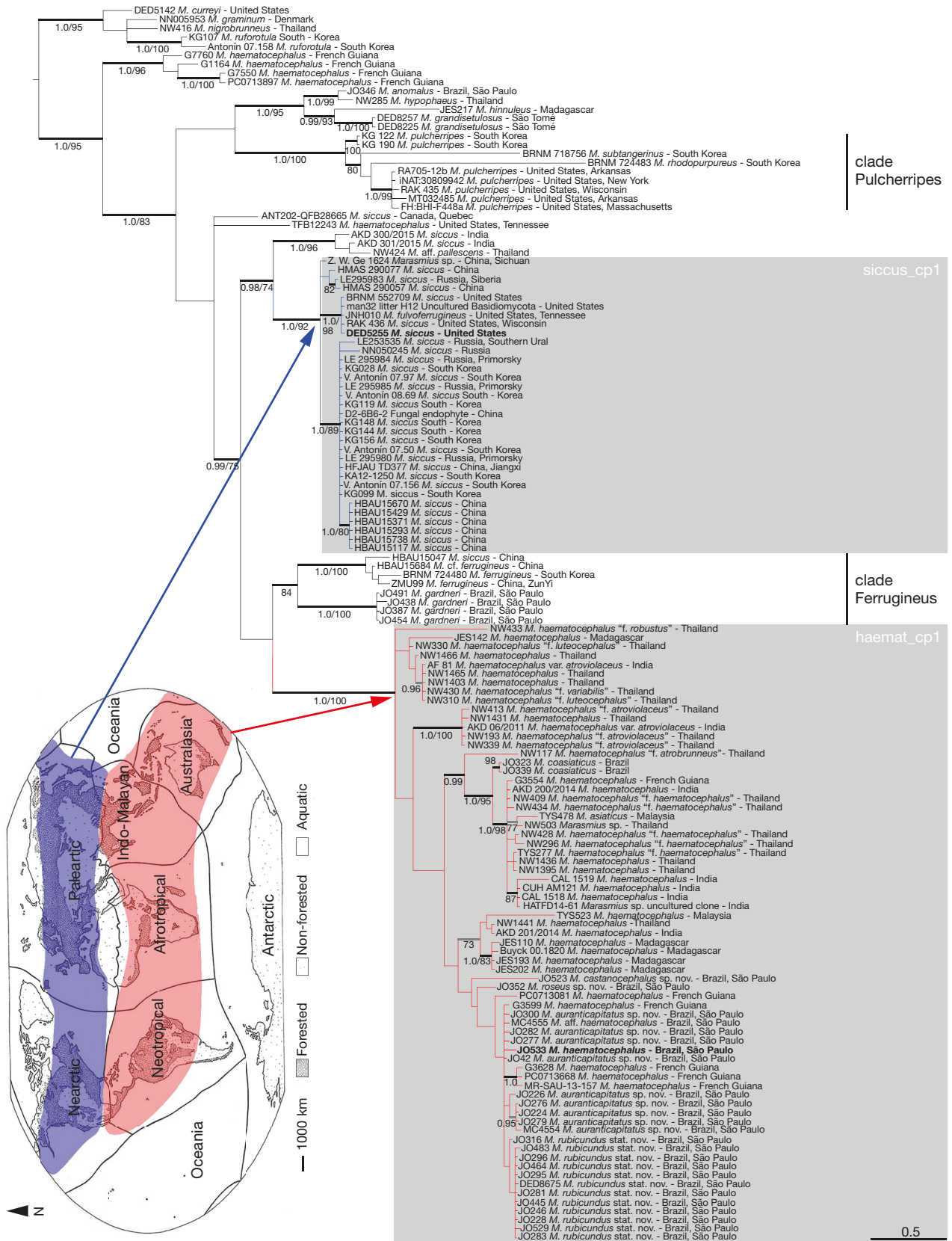


Fig. 1. — 50% majority-rule consensus tree (tree length = TL = 27.160273) of Bayesian analysis reconstructed from multilocus (nrITS and nrLSU) analysis of DATA-SET 1 (*M. haematocephalus* (Mont.) Fr., *M. siccus* (Schwein.) Fr. and close species). Support values are PP (0.95 to 1.0) and BS (70 to 100%). **Black, thick stems** indicate high support and **gray, thick stems** indicate weak to moderate support. Global map is based on Olson & Dinerstein (2002) with depicted forested areas in their biogeographic realms. The **red area** on the map is the putative distribution coverage of haemat_cp1 (in gray shade) on continental and insular terrestrial areas; the **blue area** represents the putative distribution coverage of siccus_cp1 (in gray shade) based on Fig. S1 in the Appendix, with branches colored accordingly.

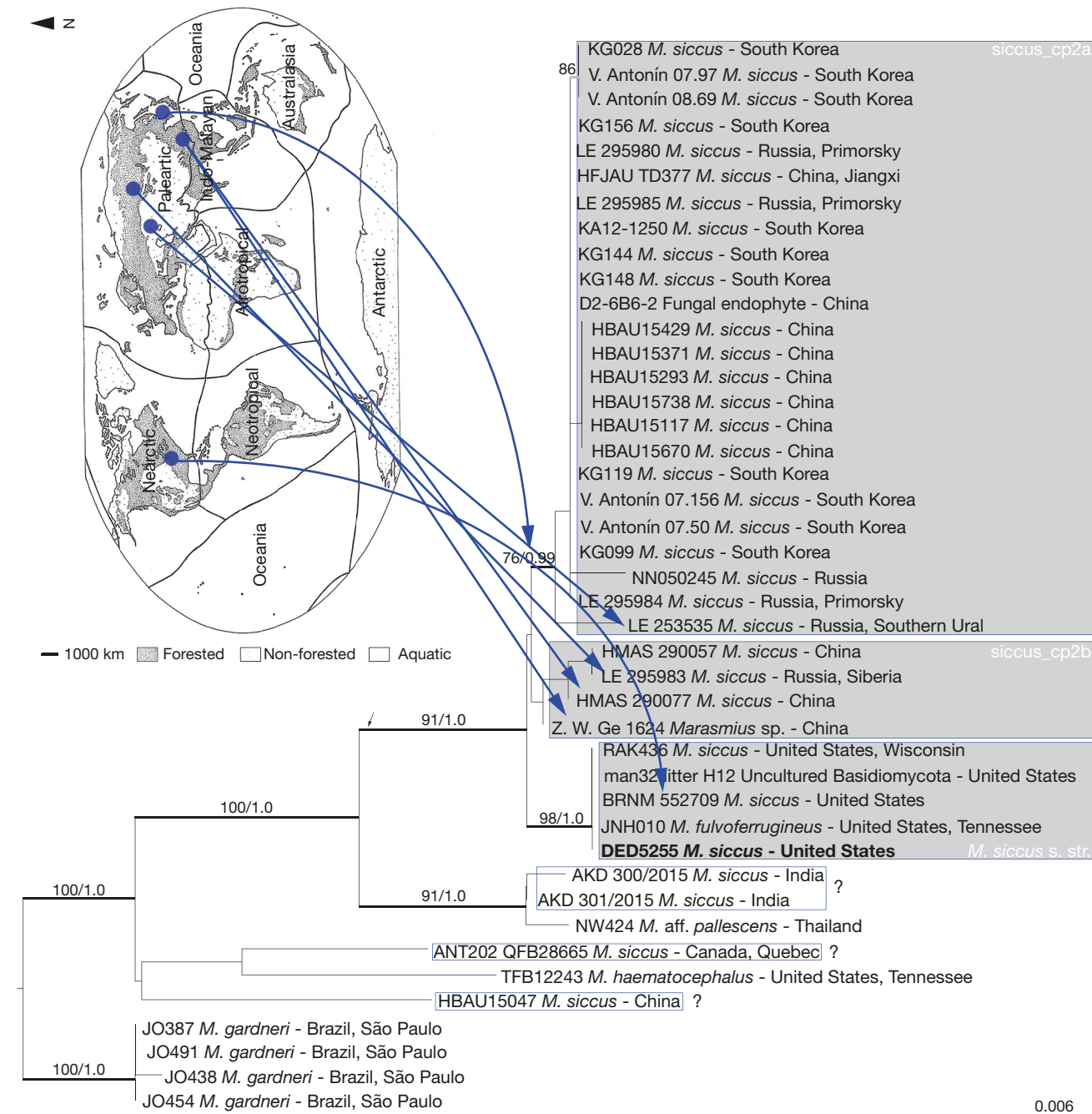


FIG. 2. — Best-scored Maximum Likelihood Tree (TL = 0.164547) built from multilocus (nrITS and nrLSU) analysis based on siccus_cp1 in Fig. 1 (DATASET 2a). Support values are BS (70 to 100 %) and PP (0.95 to 1.0). **Black, thick stems** indicate high support and **gray, thick stems** indicate weak to moderate support. **The gray shades** highlight siccus_cp2a, siccus_cp2b, and *M. siccus* s. str. **Blue arrows** indicate the geographic origin of the strains. Global map is based on Olson & Dinerstein (2002) with forested areas depicted in their biogeographic realms.

ML and BA multilocus analyses of DATASET 4 (nrLSU + nrITS) and DATASET 5 (nrITS + *rpb2* + *efl-α*) provided the trees displayed in the Figures 4 and 5, respectively. In the Figure 4, the tree on the left side (ML) and the one on the right side (BA) resolved *M. haematocephalus* s. str. as sister to ‘*M. auranticapitatus* J.S. Oliveira, sp. nov. + *M. rubicundus* (Singer) J.S. Oliveira, stat. nov.’ within the haemat_cp2a. In the Figure 5, the ML trees on the left side are of DATASET 4 with MC4554 (top) and without MC4554 (bottom) while the BA trees on the right

side are of DATASET 4 with MC4554 (top) and without MC4554 (bottom). These trees resolved *M. auranticapitatus* J.S. Oliveira, sp. nov. and *M. rubicundus* (Singer) J.S. Oliveira, stat. nov. as sister with strong support.

TAXONOMY AND SYSTEMATICS

Family MARASMIACEAE Roze ex Kühner
Genus *Marasmius* Fr.



CRYPTOGAMIE, MYCOLOGIE • 2022 • 43 (5)

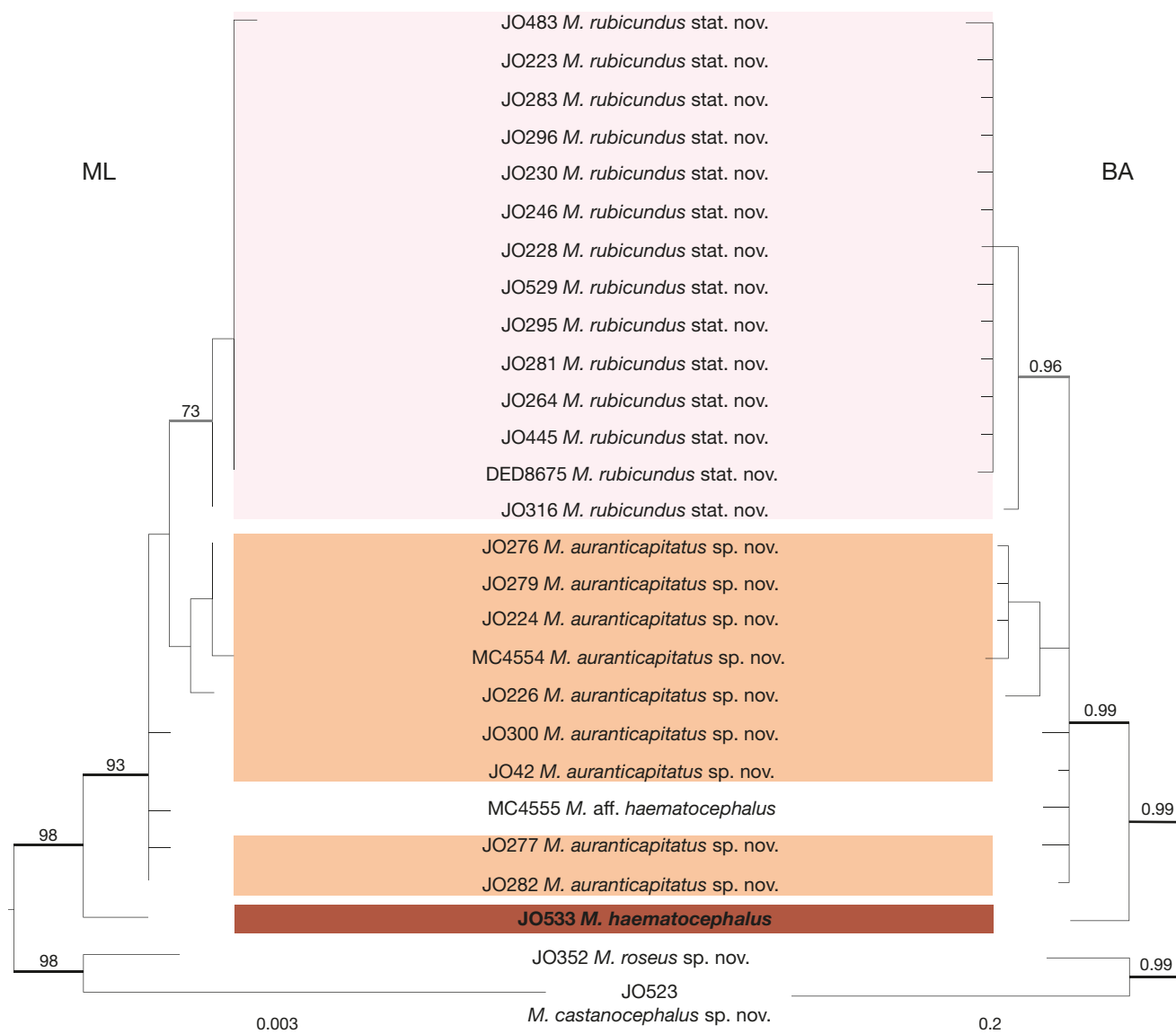


FIG. 4. — Best-scored Maximum Likelihood tree (left side, TL = 0.054576) and 50% majority-rule consensus tree (right side, TL = 4.954404) of Bayesian analyses built from multilocus (nrLSU and nrITS) analyses (DATASET 3) of the haemat_cp2a (Fig. 3). **Black, thick stems** indicate high support and **gray, thick stems** indicate weak to moderate support. **Dark red shade** indicates *M. haematocephalus* (Mont.) Fr., the **orange shade** indicates *M. auranticapitatus* J.S. Oliveira, sp. nov. and the **pink shade** indicates *M. rubicundus* (Singer) J.S. Oliveira, stat. nov.

Marasmius sect. *Globulares* Kühner emend. Antonín & Noordel.

Series *Haematocephali* Singer emend.
J.S. Oliveira & Moncalvo

Persoonia 44: 274 (Oliveira *et al.* 2020).

Basidiomata marasmiod (umbrella-like), thin, small- to medium sized. Pileus membranous, sulcate. Lamellae distant to subdistant, free to adnate. Stipe mostly filiform with a scanty, tomentose basal mycelium. Basidiospores elongate, clavate to subfusoid (11–25 µm long, $x_m = 17.5$ –22 µm, $Q_m = 4.3$ –5.9). Pleurocystidia present, well-developed, elongate, refractive. Pileipellis composed of *Siccus*-type broom cells only. Habit preference for leafy and/or woody substrate.

TYPE SPECIES. — *Marasmius haematocephalus* (Mont.) Fr.

NOTES

In Oliveira *et al.* (2020), this series included stirpes *Ferrugineus*, *Haematocephalus* and *Siccus* of Singer (1976). These informal supraspecific groups are presented below with morphologically described species (except stirps *Siccus*) included in the phylogenetic analyses in this study.

Stirps *Ferrugineus*

Singer (1976: 217) grouped *M. ferrugineus* and its variety (elevated herein to species), and *M. anomalus*, *M. bambusinus* Fr., *M. guzmanianus* Singer, *M. hypophaeus*, *M. montagneanus* Singer, *M. nogalesii* Singer, *M. phaeocystis* Singer, and *M. tenuisetulosus* (Singer) Singer in this stirps. The clade *Ferrugineus* (Fig. 1) seems consistent with stirps *Ferrugineus* as it includes

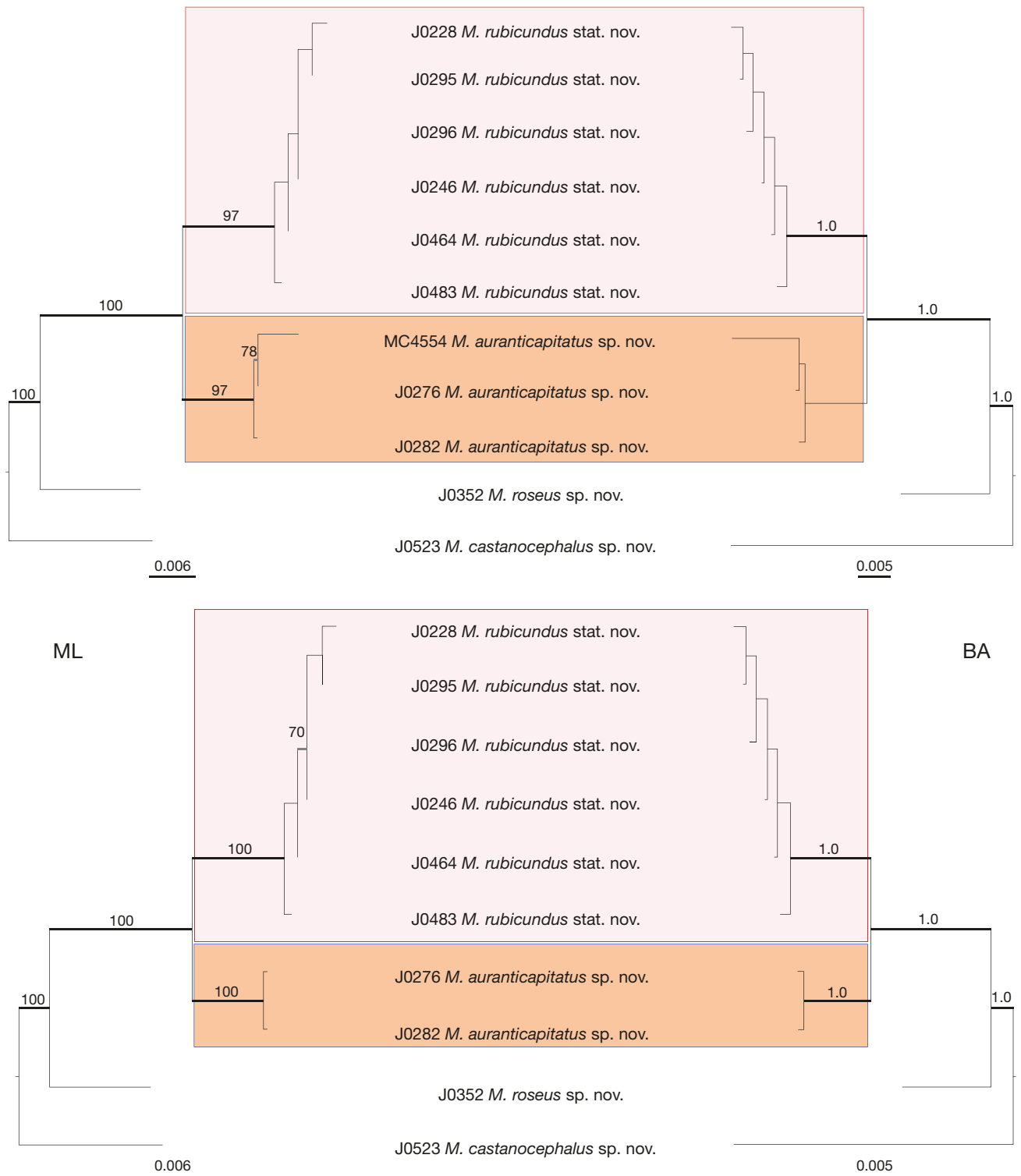


FIG. 5. — Best-scored Maximum Likelihood trees (left side, TL = 0.111755; 0.135069) and 50 % majority-rule consensus trees (right side, TL = 0.106492; 0.120539) of Bayesian analyses built from multilocus (nrITS + *rpb2* + *ef1-α*) analyses (DATASET 4) of the haemat_cp2a (Fig. 3). **Black, thick stems** indicate high support and **gray, thick stems** indicate weak to moderate support. **Orange shade** indicates *M. auranticapitatus* J.S. Oliveira, sp. nov. and the **pink shade** indicates *M. rubicundus* (Singer) J.S. Oliveira, stat. nov. Trees on the top includes MC4554 (holotype of *M. auranticapitatus* J.S. Oliveira, sp. nov.).

M. ferrugineus sensu Antonín *et al.* (2012) from South Korea with additional strains from China and *M. gardneri* from Brazil. Data including *M. ferrugineus* topotypic collections along with other species are needed to further elucidate this group.

Based on morphology, *M. bambusinus* described below seems to belong to this group but sequencing failed in this study. On the other hand, *M. anomalus* grouped with *M. hinnuleus* sensu Grace *et al.* (2019), *M. grandisetulosus* (very similar to

M. tenuisetulosus) and *M. hypophaeus* sensu Wannathes *et al.* (2009) forming a monophyletic group distant from clade Ferrugineus. The authentic *M. hypophaeus* should branch in clade Ferrugineus though.

***Marasmius bambusinus* (Fr.) Fr.**
(Figs 6A; 7)

Epicrisis Systematis Mycologici, seu Synopsis Hymenomycetum: 385 (Fries 1838). — Type: **Brazil**. Not located in Singer (1976), whereabouts unknown, *Beyrich*.

Agaricus bambusinus Fr., *Linnaea* 5: 507 (Fries 1830).

Chamaeceras bambusinus (Fr.) Kuntze, *Revisio generum plantarum* (Leipzig) 3 (3): 455 (Kuntze 1898).

EXAMINED MATERIAL. — **Brazil**. São Paulo State, São Paulo City, Parque Estadual das Fontes do Ipiranga, 3.III.2011, J.J.S. Oliveira & F. Karstedt JO343 (SP[SP 445503]!).

HABIT AND SUBSTRATE. — Marasmioid (Fig. 6A), gregarious, on a mix of dead sticks, small twigs, tendril and leaves of eudicotyledonous plant or petioles and culm-like sticks in the forest litter.

DISTRIBUTION. — *Marasmius bambusinus* was originally described from Brazil as *Agaricus bambusinus* Fr. (Fries 1830), later combined in *Marasmius* (Fries 1838). It was reported again from Brazil (Pernambuco State) and also from Bolivia, Colombia and Venezuela (Singer 1976). This is the first record from the São Paulo State.

DESCRIPTION

Pileus (Figs 6A; 7A)

2–13 mm diam., mostly hemispheric to convex, or campanulate, shallowly or deeply sulcate, center flat or slightly depressed, margin decurved, edge entire or slightly crenate, with rare lacerations; brightly orange to fulvous ($N_{20}Y_{80-99}M_{50-60}$), also pallescent orange ($N_{00}Y_{40-60}M_{20-30}$), center deep orange to brownish, ferrugineous orange ($N_{50}Y_{99}M_{60}$); membranous, context thin (< 1 mm); glabrous, semi humid to dry, dull, subvelutinous, non-hygrophanous.

Lamellae (Figs 6A; 7A)

Free to mainly adnexed, distant, $L = 8-9$, equal, simple, $l = 0$, opaque, smooth, pale cream ($N_{00}Y_{10}M_{10}$), edge even, non-marginate, interlamellar hymenium concolorous with the lamellae faces or partly with the pileus.

Stipe (Figs 6A; 7A)

7–22 × 0.2–0.4 mm, central, often curved, filiform, thin, equal, with circular caliber, chitinous, flexible, hollow; apex concolorous with the lamellae faces, then becoming pale ochraceous ($N_{40}Y_{99}M_{50}$ to $N_{50}Y_{99}M_{50}$) to dark brown downwards, glabrous, smooth, with a silky bright; with a scanty, off-white, tomentose basal mycelium.

Odor

Not distinctive.

Basidiospores (Fig. 7B)

16–21 × 3.5–4 μm ($x_m = 17.8 [± 1.3] × 3.8 [± 0.1] μm$, $Q_m = 4.7 [± 0.3]$, $n/s = 30/1$), oblong, clavate to rarely subfusoid, smooth, hyaline, thin-walled, inamyloid.

Basidia (Fig. 7C)

23–34.4 × 7.3–8.4 μm, clavate, smooth, hyaline, 4-sterigmate, thin-walled, inamyloid.

Basidioles (Fig. 7D)

20–25 × 5.3–8 μm, similar to the basidia.

Pleurocystidia (Fig. 7E)

43.8–56.3(–70) × 10–16 μm, conspicuous, sometimes with base deepened in the subhymenium, clavate, some slightly capitate or solely with shallow constriction near the apex, smooth, semi translucent or fuscous, refractive, inamyloid, thin-walled at the apex, many times moderately thick-walled elsewhere.

Cheilocystidia (Fig. 7F)

Similar to the Siccus-type broom cells of the pileipellis; main body 11.3–21.3 × 5–8.8 μm, clavate to slightly turbinate, thin-walled, hyaline; setulae or diverticula apical, erect, short to somewhat long, 1.3–4.4 × 0.8–1 μm, digitiform, cylindrical or verruciform, hyaline, simple, abundant, solid, pale yellow, apex obtuse to slightly acute.

Lamellar trama

Dextrinoid, irregular, interwoven, hyphae cylindrical, 2–8.8 μm diam., regular in outline, branched, hyaline, smooth, thin-walled.

Pileus trama

Dextrinoid, irregular, very narrow, similar to the lamellar trama, hyphae 1.3–5 μm diam.

Pileipellis

Hymeniform, composed of Siccus-type broom cells (Fig. 7G), pale yellow when grouped, easily bleaching in KOH solution, becoming hyaline when isolated, abundant; main body 10–20 × 6–11.3 μm, clavate to slightly turbinate, hyaline, thin-walled; setulae apical, erect, frequently short to moderately long, 2–5.6 × 0.5–1 μm, digitiform or cylindrical, simple, solid and regular in outline, initially pale yellow, then hyaline, apex acute to almost obtuse.

Stipe trama

Dextrinoid, cortical hyphae parallel, cylindrical, 3.4–7.5 μm diam., regular in outline, smooth, thick-walled, brown to yellowish brown in KOH solution; internal hyphae 1.6–8.8 μm diam., thin-walled, some disorganized, other parallel, smooth, branched.

Clamp connections

Present in almost all tissues, except in the cortical trama of the stipe.



FIG. 6. — Pictures of fresh basidiomata: **A**, *Marasmius bambusinus* (Fr.) Fr. (JO343); **B**, *M. gardneri* Singer (JO491). Scale bars: 10 mm.

REMARKS

Desjardin *et al.* (2000) considered *M. bambusinus* a synonym of either *M. hypophaeus* or *M. ferrugineus*. These three species

have many overlapping morphological characteristics and there is variation of species concepts in Desjardin *et al.* (2000) and Singer (1976). Basidiospores in these species are quite

compatible, but the pigmented lamellar edge (marginate) and the chestnut yellow to fulvous pileus was considered typical and distinctive for *M. hypophaeus* (Singer 1976). *Marasmius bambusinus* differs from *M. ferrugineus* (lignicolous) by a supposed substrate preference on monocotyledonous plant (originally on bamboo leaves), by thin- to thick-walled pleurocystidia, and by a bright orange(-rufescent) pileus (Singer 1976). The holotype of *M. bambusinus* has been reported as lost (Singer 1976; Desjardin 1989). The examined material brings emphasis for the bright orange (rufescent) pileus (Fig. 6A) and the more distant, few (*paucis*) lamellae (8-9), both consistent with the protologue of *M. bambusinus*.

Agaricus (Marasmius) ferrugineus Berk. (synonym of *Marasmius ferrugineus*) was described having a yellow, ferruginous (croceo-ferrugineo) pileus and few lamellae (Berkeley 1843). In Singer (1976), *M. ferrugineus* has 9-13 lamellae. If *M. bambusinus* (not well-known) is synonym of *M. ferrugineus* (more well known), then the former has nomenclatural priority. Based on Singer (1976), the examined material can be either *M. bambusinus* or *M. ferrugineus*, unless we consider strong enough the fine pileus color deviation and the paucity of the lamellae. Antonín *et al.* (2012) revised the type of *M. ferrugineus* and found only slightly larger (overlapping) basidiospores ($18-22 \times 4.5-6.0 \mu\text{m}$) but compatible pleurocystidia ($[28-]35-50[-66] \times 11-17 \mu\text{m}$). Desjardin (1989) studied one of Singer's *M. bambusinus* collections (Singer B 6345) from Colombia. It is similar to JO343 but differs in having reddish lamellar edges (typical for *M. hypophaeus*), by growing on gramineous leaves, by having smaller basidiospores ($15.2-18.4 \times 3.6-4.6 \mu\text{m}$), and by having thin-walled, slightly smaller pleurocystidia ($30-45 \times 6.5-9 \mu\text{m}$). These spores and pleurocystidia are compatible to *M. gardneri* though (next taxon).

Antonín *et al.* (2012) studied the holotype of *M. ferrugineus* to support the identification of the foliicolous specimen (BRNM 724480) from South Korea as *M. ferrugineus*. If so, there is no preference for woody substrate in *M. ferrugineus*. The lamellae edge concolorous with the brownish orange to reddish brown pileus is rather more consistent with *M. hypophaeus* (Singer 1976). Without sequences from JO343, *M. bambusinus* could not be analyzed along with *M. ferrugineus* from South Korea (Antonín *et al.* 2012). Pegler (1988) mentioned *M. ferrugineus* as a common Neotropical and pantropical species. More should be done to elucidate between *M. bambusinus* and *M. ferrugineus*, especially in sequencing collections from the Neotropics (particularly Brazil) matching the morphology and substrate. The species are then regarded as distinct herein.

Marasmius pseudobambusinus Desjardin is similar to *M. bambusinus*, but differs in having indistinctly sulcate pileus, smaller basidiospores ($13.6-19.2 \times 3.6-5.2 \mu\text{m}$) and apically constricted pleurocystidia (Desjardin 1991).

***Marasmius gardneri* Singer**
(Figs 6B; 8)

Sydowia 12 (1-6): 114 (Singer 1958). — Type: **Brazil**. Minas Gerais State, Gardner (Hooker Herbarium set at K), holotype.

Marasmius ferrugineus var. *gardneri* Singer, *Flora Neotropica* 17: 223 (Singer 1976).

EPITYPE. — **Brazil**. São Paulo State, São Paulo City, Parque Estadual da Cantareira, Núcleo Engordador, 16.II.2012, J.J.S. Oliveira & M. Capelari JO491 (epi-, designated here, SP[SP 445564]!).

ADDITIONAL EXAMINED MATERIAL. — **Brazil**. São Paulo State, São Paulo City, Parque Estadual da Cantareira, Núcleo Engordador, 31.X.2011, J.J.S. Oliveira & M. Capelari JO387 (SP[SP 445521]!); 19.XII.2011, J.J.S. Oliveira & M. Capelari JO438 (SP[SP 445532]!); J.J.S. Oliveira & M. Capelari JO454 (SP[SP 445542]!).

HABIT AND SUBSTRATE. — Marasmioid (Figs 6B; 8A1), gregarious, on eudicotyledonous dried leaves and twigs in the forest litter.

DISTRIBUTION. — This species was established with a *nomen novum* in Singer (1958) based on the type material of *M. ferrugineus* originally from Minas Gerais State (Brazil) collected by Gardner. This type consisted of a mix of two close species, later split into two sets where the "Hooker Herbarium set" of basidiomata is the type of this species. Additional collections listed by Singer (1958, 1976) are from the Amazonas and Rio de Janeiro States (Brazil).

DESCRIPTION

Pileus (Figs 6B; 8A1)

Up to 2 mm diam. when immature, then 3-18 mm diam., conical to campanulate (because of a broad umbo), or hemispheric, becoming convex, sometimes applanate, smooth when young, often becoming slightly sulcate, or strongly sulcate when fully developed, center umbonate, later tending to flat and sometimes wrinkled, margin decurved to straight, edge mostly entire, or slightly crenate; center dark reddish brown ($N_{70-90}Y_{90-99}M_{80-90}$) to dark orangish brown ($N_{60}Y_{99}M_{70}$), then becoming more pale chestnut red or fulvous "tawny" ($N_{60}Y_{60}M_{60}$) or dark brown ($N_{60}Y_{70-80}M_{90-99}$) especially when young, or rarely pale orange ($N_{10}Y_{99}M_{30}$) or pale pinkish brown ($N_{60}Y_{80}M_{70}$), many times with darker sulci, some strongly ferruginous ($N_{80}Y_{99}M_{70}$), orangish brown to fulvous-ferruginous ($N_{40-50}Y_{99}M_{60}$ to $N_{40-50}Y_{99}M_{70}$) toward the margin, and orange to ferruginous brown when dried ($N_{80}Y_{99}M_{50-70}$); membranous, context white, thin ($< 1 \text{ mm}$); glabrous, dry, dull, subvelutinous, non-hygrophanous.

Lamellae (Figs 6B; 8A2)

Free to subfree, subdistant, $L = 12-16$, equal, mostly simple, or very slightly intervenose in very mature basidiomata, $l = 0(-1)$, straight to slightly ventricose, opaque, smooth, white, or pale cream to whitish pink ($N_{00}Y_{10}M_{00-10}$), edges even, non-marginate, concolorous with the lamellae faces as well as the interlamellar hymenium.

Stipe (Figs 6B; 8A1)

$15-44 \times 0.3-1 \text{ mm}$, central, filiform, or thicker, almost cylindrical thin, equal, with circular to slightly compressed caliber, simple, chitinous, hollow, apex whitish ($N_{20}Y_{10}M_{30}$) or pale brown ($N_{30}Y_{40}M_{30}$), becoming brown ($N_{90}Y_{90}M_{50-60}$), reaching dark brown ($N_{99}Y_{99}M_{80}$) at the base, glabrous, smooth, with a silky bright; with a more abundant, whitish, tomentose or cotton-like basal mycelium, also developing a mat on the substrate.

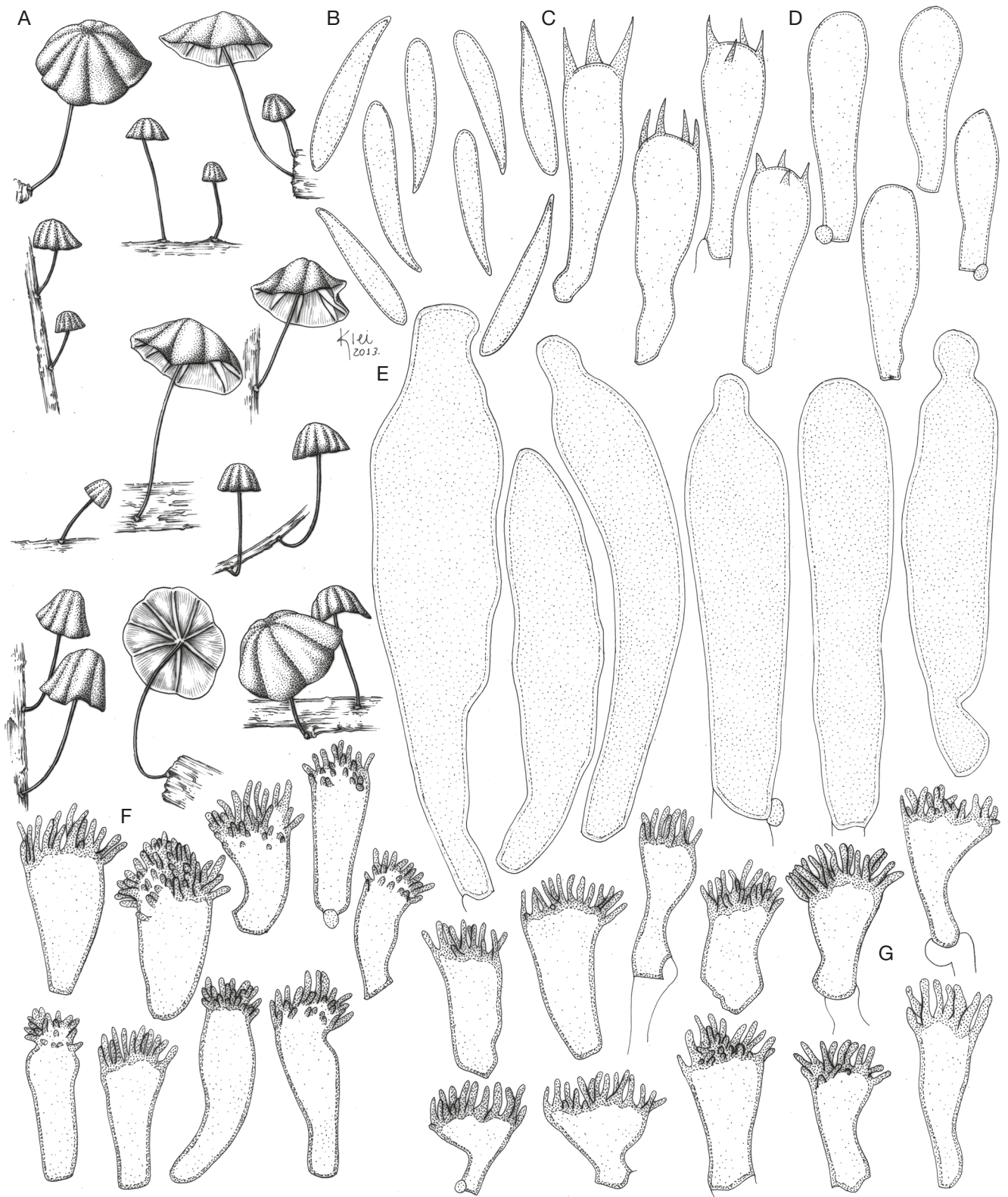


FIG. 7. — *Marasmius bambusinus* (Fr.) Fr. (JO343): **A**, basidiomata; **B**, basidiospores; **C**, basidia; **D**, basidioles; **E**, pleurocystidia; **F**, cheilocystidia; **G**, Siccus-type broom cells of the pileipellis. Scale bar: A, 10.3 mm; B–G, 10 μ m.

Odor

Not distinctive.

Basidiospores (Fig. 8B)

(14.6-)15-19 × 3-5 µm ($x_{rm} = 16.6-17.6 \times 3.9-4.1$ µm; $x_{mm} = 16.7 [\pm 0.6] \times 3.9 [\pm 0.1]$ µm; $Q_{mr} = 4.1-4.6$, $Q_{mm} = 4.3 [\pm 0.3]$; $n/s = 30/3$), oblong, clavate to fusoid, smooth, hyaline, thin-walled, inamyloid.

Basidia

Not observed.

Basidioles (Fig. 8C)

21.3-33 × 5-6.3 µm, clavate, smooth, hyaline, thin-walled, inamyloid.

Pleurocystidia (Fig. 8D)

32.5-62.5 × 4-7.5 µm, conspicuous, well-projecting above the basidioles, clavate to cylindrical, apex obtuse or sometimes fusoid to acuminate, or capitate, with a small apical vesicle, or mucronate, smooth, refractive, inamyloid, few fuscous, thin-walled.

Cheilocystidia (Fig. 8E)

Similar to the Siccus-type broom cells of the pileipellis, but non-pigmented; main body 12.5-23.8 × 5.6-8.8(-10) µm, clavate to somewhat turbinate, or ventricose, regular in outline, thin-walled; setulae apical, erect, generally elongate, 2.5-10.4 × 0.6-1.3 µm, cylindrical, filiform, rarely digitiform, regular in outline, simple, pale yellow, solid, apex obtuse to acute.

Lamellar trama

Dextrinoid, irregular, interwoven, hyphae cylindrical, 2-8.8 µm diam., regular in outline, branched, smooth, hyaline, thin-walled.

Pileus trama

Similar to the lamellar trama, hyphae 1.5-8.8 µm diam.

Pileipellis

Hymeniform, dextrinoid, composed of Siccus-type broom cells (Fig. 8F), abundant, pale orangish brown when grouped, hyaline when isolated; main body (8.8-)12.5-18.8 × 5-9.4 µm, clavate to turbinate, sometimes cylindrical, or branched, or somewhat irregular in outline, thin- to thick-walled, weakly dextrinoid; setulae apical, erect, 3-8.8 × 0.5-1.3 µm, cylindrical, filiform, thin, needle-like, simple, rarely branched, pale brown, apex acute or slightly obtuse.

Stipe trama

Dextrinoid, cortical hyphae parallel, cylindrical, 3.8-9.4 µm diam., regular in outline, pale brown, hyaline at the stipe apex, dark brown near the base, smooth, thick-walled; internal hyphae more hyaline, thin-walled, 2-16.3 µm diam.

Clamp connections

Present in almost all tissues, except in the cortical hyphae of the stipe.

REMARKS

The historical account for this species is not straightforward and it begins with *Agaricus (Marasmius) ferrugineus* (Berkeley 1843). Due to competing prior homonym, it was later combined by Berkeley & Curtis (1869) in *Marasmius ferrugineus*. Singer (1958), by arguing that this name was illegitimate in the basionym, proposed the *nomen novum* *Marasmius gardneri* in replacement, based on the type material of *M. ferrugineus* along with two additional collections: 1) 'part' of *Spruce 139* (from Amazonas State, Brazil) segregated (mixed collection) from the type of *M. poecilus* Berk.; and 2) *Singer B 437* (from Angra dos Reis, Rio de Janeiro State). However, *M. ferrugineus* is deemed legitimate in Berkeley & Curtis (1869) and, therefore, *M. gardneri* became a nom. illegit. by the art. 52.1 of the International Code of Nomenclature for Algae, Fungi and Plants. According to Singer (1976), the type collection of *M. ferrugineus* was potentially a mix of two different species as the Gardner collection existed split into two sets (Singer 1958), both collected at Minas Gerais and kept at K. The first set, kept in the Berkeley Herbarium, was indicated as the holotype of *M. ferrugineus*, and has relatively larger and narrower spores (15-21 × 2.8-4.3 m). The second set, kept in the Hooker Herbarium, has shorter and broader spores (13.5-18.3 × 3.2-5 m), and Singer (1976) named this collection *M. ferrugineus* var. *gardneri* Singer. This variety also differs from the type variety in the pileus often becoming somewhat darker ("cocoa") on drying and in growing on small woody sticks, leaf petioles and veins (Singer 1976).

The examined specimens fit best as *M. ferrugineus* var. *gardneri*. The dimensions of the pileus (3-18 mm diam.) and of the stipe (15-44 × 0.3-1 mm) are larger than those typically found in *M. ferrugineus* var. *ferrugineus* (3-11 mm diam. of the pileus and 11-30 × 0.3 mm of the stipe). Singer (1976) did not mention the dimensions of the pileus and stipe as distinctive for the specimens of var. *gardneri*, which implies that both varieties match relatively the macroscopic proportions. The protologue of *Agaricus (Marasmius) ferrugineus* (synonym of *M. ferrugineus*) emphasizes the tiny proportion of the basidiomata with "pileus 1½-3 lines broad" (3.18-6.35 mm diam.) and stipe "½-¾ of an inch high, ¼ of a line thick" (12.7-19.05 mm long and 0.265 mm thick). The basidiomata of the examined material are evidently larger and more robust (as in *M. hypophaeus*) than a typical *M. ferrugineus* and, in combination with the shorter and broader basidiospores and by growing more on dried leaves or small twigs, should represent a different species. According to Singer (1958, 1976), Dennis also knew very well *M. ferrugineus*, especially the Berkeley Herbarium set which, agreeing with Singer, defended it should be the type of *M. ferrugineus*. With collections from Venezuela, Dennis (1961) found two spore's dimension for "*M. ferrugineus*": *Dennis 1021* (19-21 × 3-4 µm) and *Dennis 1021A* (14-18 × 3-3.5 µm, this should be *M. gardneri*). Revising the type specimen of *M. ferrugineus* (Brazil, Minas Gerais, K [M] 92652), Antonín *et al.* (2012) found even longer and broader basidiospores 18-22 × 4.5-

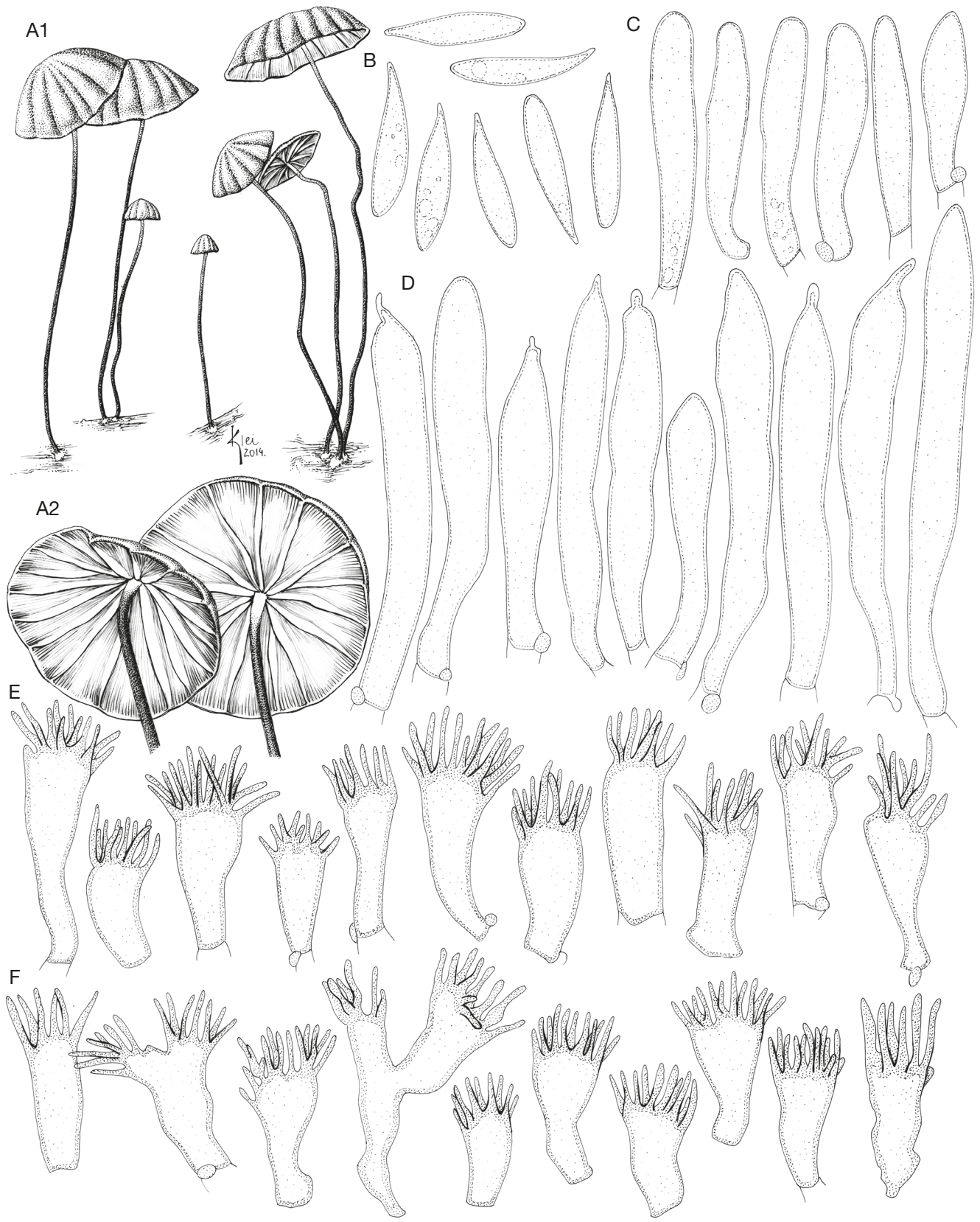


FIG. 8. — *Marasmius gardneri* Singer (JO491): **A1, A2**, basidiomata; **B**, basidiospores; **C**, basidioles; **D**, pleurocystidia; **E**, cheilocystidia; **F**, Siccus-type broom cells of the pileipellis. Scale bar: A1, 10.8 mm; A2, 5.9 mm; B–F, 10 μ m.

6.0 µm and broader pleurocystidia (11–17 µm) which are not consistent with the specimens herein determined as *M. gardneri*. This is sister to *M. ferrugineus* from South Korea and China (Fig. 1).

Based on the combined divergences found between the two sets of Gardner collection together with the examined collections agreeing with the Hooker Herbarium set, we conclude that *M. ferrugineus* var. *gardneri* should be elevated to species level, legitimating the name *M. gardneri* typified on the 'Hooker Herbarium set'. Moreover, if *M. ferrugineus* becomes a synonym of *M. bambusinus* (previous taxon), then we are quite sure we have two different species. Both Singer (1958) and Dennis (1951) considered *M. paucifolius* Murrill, a synonym of *M. ferrugineus*. Singer (1976) rather placed it in *M. ferrugineus* var. *gardneri* and, therefore, should claim its legitimacy for being prior than *M. gardneri*. However, we have scarce evidence to support *M. paucifolius* as synonym of *M. ferrugineus* var. *gardneri* and should be considered an independent species until more collections and analyses become available. If conspecific, the species would also occur in Puerto Rico.

Marasmius hypophaeus is very similar to *M. gardneri* but differs mainly in having distinctly marginate lamellae (rust brown) and larger basidiospores ([12–]14.5–21.5 × 3–5.5 µm), broader pleurocystidia (6–13 µm) and larger setulae (1–14[–20] × 0.7–2.2 µm) on the broom cells of the pileipellis (Singer 1976). Singer (1976) argued that Dennis (1951) described and illustrated a specimen named after *M. ferrugineus* orangish brown in both pileus and lamellar edge, then he suspected that *M. ferrugineus* sensu Dennis (1951) would be rather *M. hypophaeus*. Singer concluded that the pileus pigmentation of *M. hypophaeus* when fresh would be orangish brown (old bronze) rather than red (rufous blood red) as described in the protologue (Berkeley & Curtis 1869) that possibly led Murrill (1915) to suppose it would be a synonym of *M. haematocephalus*. Next, Singer defended that *M. hypophaeus* is closer to *M. ferrugineus* than *M. haematocephalus* but differing from the former by the distinctly ferruginous brown lamellae edge instead of concolorous with the lamellae face.

Marasmius tenuisetulosus (Singer) Singer is similar to *M. gardneri* in many features, especially the basidiospores size (14.5–19 × 3–4 µm). However, the former differs by having larger (up to 28 mm diam.), orangish brown pileus which is radially striped, by having series of lamellulae, and by having thick-walled pleurocystidia (Singer 1964, 1976). These pleurocystidia are long-acuminate and ventricose, tapered from the middle to the apex (Singer 1964). *Marasmius radiatus* Desjardin is similar to *M. gardneri* especially in the orange or brownish orange pileus, in the basidiospores size (15.7–19.2 × 3.8–5.1 µm) and in the general aspects of the pleurocystidia. However, *M. radiatus* differs only in having a ferruginous pileus with pale radial stripes over the lamellae line when dried, and in having dimorphic, hyaline cheilocystidia: 1) Siccus-type broom cells; and 2) non-setulose cystidia similar to the pleurocystidia (Desjardin et al. 1992).

Stirps *Haematocephalus*

Singer (1976: 208) included *M. haematocephalus* and all its varieties, plus *M. pallescens* and *M. panerythrus* Singer in this group. In this paper, stirps *Haematocephalus* is monophyletic in haemat_cp1, now represented by the *M. haematocephalus* complex with pantropical distribution (Fig. 1). Even though similar to *M. haematocephalus* in the pileus color, both *M. pallescens* and *M. panerythrus* seem rather morphologically closer to *M. pulcherripes* (ser. *Pulcherripes*) by the shorter basidiospores.

Marasmius auranticapitatus J.S. Oliveira, sp. nov. (Figs 9A; 10)

Differs from *M. haematocephalus* by having pale orange pileus and slightly larger basidiospores ($x_{mm} = 21.1 [\pm 0.7] \times 3.8 [\pm 0.3] \mu m$, $Q_{mm} = 5.7 [\pm 0.5]$ vs $x_{mm} = 20.5 [\pm 0.3] \times 3.9 [\pm 0.2] \mu m$, $Q_{mm} = 5.2 [\pm 0.1]$); and more distinctly larger than those of the rose or pale red pilated *M. rubicundus* ($x_{mm} = 21.1 [\pm 0.7] \times 3.8 [\pm 0.3] \mu m$, $Q_{mm} = 5.7 [\pm 0.5]$ vs $x_{mm} = 18.9 [\pm 0.5] \times 3.8 [\pm 0.1] \mu m$, $Q_{mm} = 5 [\pm 0.2]$).

HOLOTYPE. — **Brazil**. São Paulo State, Santo André City, Reserva Biológica de Paranapiacaba, 2.XII.2009, *M. Capelari & L.A.S. Ramos 4554* (holo-, SP[SP 445584]!).

ADDITIONAL EXAMINED MATERIAL. — **Brazil**. São Paulo State, Santo André City, Reserva Biológica de Paranapiacaba, 16.III.2010, *J.J.S. Oliveira JO42* (SP[SP 445408]!); 15.X.2010, *J.J.S. Oliveira & C.L.A. Pires JO224* (SP[SP 445445]!); 16.X.2010, *J.J.S. Oliveira & C.L.A. Pires JO226* (SP[SP 445446]!); 7.XI.2010, *J.J.S. Oliveira & A.V. Costa JO276* (SP[SP 445460]!); *J.J.S. Oliveira & A.V. Costa JO277* (SP[SP 445461]!); *J.J.S. Oliveira & A.V. Costa JO279* (SP[SP 445463]!); 7.XII.2010, *J.J.S. Oliveira, A.V. Costa & P.O. Ventura JO282* (SP[SP 445465]!); *J.J.S. Oliveira & P.O. Ventura JO300* (SP[SP 445479]!).

ETYMOLOGY. — Based on the orange pileus.

MYCOBANK. — MB 842535.

HABIT AND SUBSTRATE. — Marasmioid (Figs 9A; 10A), dispersed to gregarious on dead eudicotyledonous leaves in the forest litter.

DESCRIPTION

Pileus

2.4–19 mm diam. (Figs 9A; 10A), initially conical, then campanulate or hemispherical, sulcate, sometimes deeply sulcate, center flat or slightly umbonate, wrinkled when dried, margin decurved, edge entire; when young deep reddish orange ($N_{10}Y_{80}M_{30}$ to $N_{10}Y_{99}M_{60}$, $N_{40}Y_{70}M_{70}$), with center dark orange ($N_{10}Y_{99}M_{70}$), becoming yellowish orange or pale orange ($N_{00}Y_{80}M_{30}$, $N_{10}Y_{99}M_{50}$ to $N_{20}Y_{60}M_{50}$) when mature, sometimes with beige hue ($N_{00}Y_{40-60}M_{20-40}$ to $N_{10}Y_{50}M_{50-60}$) or ferruginous orange ($N_{20}Y_{99}M_{60}$) to reddish brown ($N_{20}Y_{50}M_{50}$) when dried, keeping the same pigmentation at the center or becoming chestnut orange ($N_{30}Y_{99}M_{50-70}$, $N_{40}Y_{99}M_{80}$ or $N_{50}Y_{99}M_{70}$); membranous, context thin (< 1 mm); glabrous, dry, dull, subvelutinous, non-hygrophanous.

Lamellae (Fig. 9A)

Free, subfree to narrowly adnate, subdistant to distant, $L = 9$ –14, equal, simple, rarely biforked or intervenose, $l = 0$, smooth, pale cream ($N_{00}Y_{10}M_{00}$), edge even, non-marginate, interlamellar hymenium concolorous with the lamellae faces.



FIG. 9. — Pictures of fresh basidiomata: **A**, *Marasmius auranticapitatus* J.S. Oliveira, sp. nov. (*M. Capelari* & L.A.S. Ramos 4554); **B**, *M. castanocephalus* J.S. Oliveira, sp. nov. (JO523); **C**, *M. coasiaticus* J.S. Oliveira, sp. nov. (JO323). Scale bars: 10 mm.

Stipe (Figs 9A; 10A)

9–56 × 0.3–0.8 mm, central, filiform, thin, equal, regular, with circular caliber, chitinous, flexible, hollow, apex whitish pink (N₀₀Y_{10–40}M_{20–60}) to pale orange, becoming orange or amber brown (N₄₀Y₆₀M₅₀) to brown or dark brown (N₇₀Y₉₉M₆₀) toward the base, glabrous, smooth, with a silky bright; with a scarce, cream, tomentose basal mycelium.

Odor

Not distinctive.

Basidiospores (Fig. 10B)

17.1–24.8 × 2.8–5 µm ($x_{rm} = 19.4\text{--}22.3 \times 3.5\text{--}4.2$ µm; $x_{mm} = 21.1 [\pm 0.7] \times 3.8 [\pm 0.3]$ µm; $Q_{rm} = 5.1\text{--}6.3$; $Q_{mm} = 5.7 [\pm 0.5]$, $n/s = 30/8$), exceptional spore size of JO226 with 17–21.9 × 3–4.2(–5) µm ($x_m = 19.4 [\pm 1.0] \times 3.6 [\pm 0.4]$ µm; $Q_m = 5.4 [\pm 0.7]$; $n/s = 30$, $s = 1$), oblong, subclavate to fusoid, smooth, hyaline, thin-walled, inamyloid.

Basidia

Observed in JO279, 20.1–30.4 × 6–7.6 µm, clavate, hyaline, thin-walled, inamyloid, 4-sterigmate, sterigmata coarse or broad, with obtuse apex.

Basidioles (Fig. 10C)

21.3–28.8 × 6–8.8 µm, clavate, hyaline, thin-walled, inamyloid.

Pleurocystidia (Fig. 10D)

(15.1–)22.3–74.3 × 5.2–12.1 µm, clavate, with tapered apex, subacuminate, vesiculose, capitate or papillate, sublageniform, hyaline, thin-walled, refractive.

Cheilocystidia (Fig. 10E)

Similar to the Siccus-type broom cells of the pileipellis; main body (10–)15–18.8 × 5.6–11.3 µm, clavate to turbinate, hyaline, thin-walled; setulae apical, erect, 2.5–7.5 × 0.8–1.8 µm, cylindrical, regular in outline, solid, apex acute.

Lamellar trama

Dextrinoid, irregular, interwoven, hyphae cylindrical, 1.6–10 µm diam., regular in outline, branched, smooth, hyaline, thin-walled.

Pileus trama

Similar to the lamellar trama, hyphae 2–6.3 µm diam.

Pileipellis

Hymeniform, composed of Siccus-type broom cells (Fig. 10F), abundant, pale yellow when grouped; main body 9.4–18.8 × 7–10.6 µm, clavate to frequently turbinate, sometimes inflated, or irregular in outline, hyaline, thin-walled, weakly dextrinoid; setulae apical, erect, 3.8–7.5 × 0.6–1.3 µm, filiform, thin, regular in outline, sometimes branched, solid, hyaline, apex acute.

Stipe trama

Dextrinoid, cortical hyphae parallel, 3–13.8 µm diam., cylindrical, regular in outline, rarely branched, smooth, pale brown,

thick-walled; internal hyphae 2.5–7.5 µm diam., hyaline, thin-walled.

Clamp connections

Present in all tissues.

REMARKS

Marasmius auranticapitatus J.S. Oliveira, sp. nov. is very similar to *M. haematocephalus* (blood red pileus) but has more pale yellowish orange pileus (reddish when young) and slightly longer basidiospores ($x_{mm} = 21.1 [\pm 0.7] \times 3.8 [\pm 0.3]$ µm, $Q_{mm} = 5.7 [\pm 0.5]$ vs $x_{mm} = 20.4 [\pm 0.3] \times 3.9 [\pm 0.1]$ µm, $Q_{mm} = 5.3 [\pm 0.1]$). Yet, the ranges of the basidiospores sizes are largely overlapping. *Marasmius auranticapitatus* J.S. Oliveira, sp. nov. is 0.2–1 % dissimilar to *M. haematocephalus* based on the nrITS and 0.6–1 % dissimilar on the nrLSU. However, *M. auranticapitatus* J.S. Oliveira, sp. nov. is closer and sister to *M. rubicundus* (Singer) J.S. Oliveira, stat. nov. (Figs 4; 5). Based on the nrITS data, *M. auranticapitatus* J.S. Oliveira, sp. nov. is 0.7–1.7 % dissimilar to *M. rubicundus* (Singer) J.S. Oliveira, stat. nov., 0.2–0.6 % dissimilar in the nrLSU, 4.7–5.2 % dissimilar in the *rpb2* and 1.4–1.9 dissimilar in the *efl-α*. *Marasmius auranticapitatus* J.S. Oliveira, sp. nov. differs from *M. rubicundus* (Singer) J.S. Oliveira, stat. nov. in the pale yellowish orange pileus (vs rose, pink or pale red) and longer basidiospores ($x_{mm} = 21.1 [\pm 0.7] \times 3.8 [\pm 0.3]$ µm, $Q_{mm} = 5.7 [\pm 0.5]$ vs $x_{mm} = 18.9 [\pm 0.5] \times 3.8 [\pm 0.1]$ µm, $Q_{mm} = 5 [\pm 0.2]$). With a transitional/intermediate pattern and possibly a hybrid, the exceptional spore sizes of JO226 (more compatible with *M. rubicundus* (Singer) J.S. Oliveira, stat. nov.) strengthens the plausibility of the most recent common ancestry between *M. auranticapitatus* J.S. Oliveira, sp. nov. and *M. rubicundus* (Singer) J.S. Oliveira, stat. nov., a bridge of intercompatibility and gene flow or an ancestry trace. Quoting Taylor *et al.* (2000): “Even when BSR (Biological Species Recognition) can be applied to fungi, there is evidence that the criterion of reproduction lumps together groups of fungi that are genetically isolated in nature, but that retain the ancestral character of interbreeding”.

Marasmius auranticapitatus J.S. Oliveira, sp. nov. is similar to *M. siccus* in the pileus pigmentation. However, based on the holotype, *M. siccus* has smaller basidiospores 15.2–20 × 3.2–4.6 µm (Desjardin 1989). Also, *M. siccus* s.l. has more robust basidiomata (Gilliam 1976; Noordeloos 1987; Antonín & Noordeloos 2010; Antonín *et al.* 2012;) and temperate distribution. In the phylogenetic trees (Fig. 1), *M. auranticapitatus* J.S. Oliveira, sp. nov. is close to *M. haematocephalus* (embedded in haemat_cp1) and distant from *M. siccus*. *Marasmius auranticapitatus* J.S. Oliveira, sp. nov. is part of the haemat_cp2a (Fig. 3), only fully resolved in Figure 5. *Marasmius haematocephalus* var. *anomaloide* Desjardin originally described from the Tennessee, United States, also has orange pileus but differs from *M. auranticapitatus* J.S. Oliveira, sp. nov. in having much shorter basidiospores (14.4–19.2 × 3.4–4.6 µm) (Desjardin 1991). The new species is neither similar to any of the varieties of *M. haematocephalus* in Singer (1976) nor to any of the heterotypic synonyms once listed under *M. haematocephalus* (Appendix).

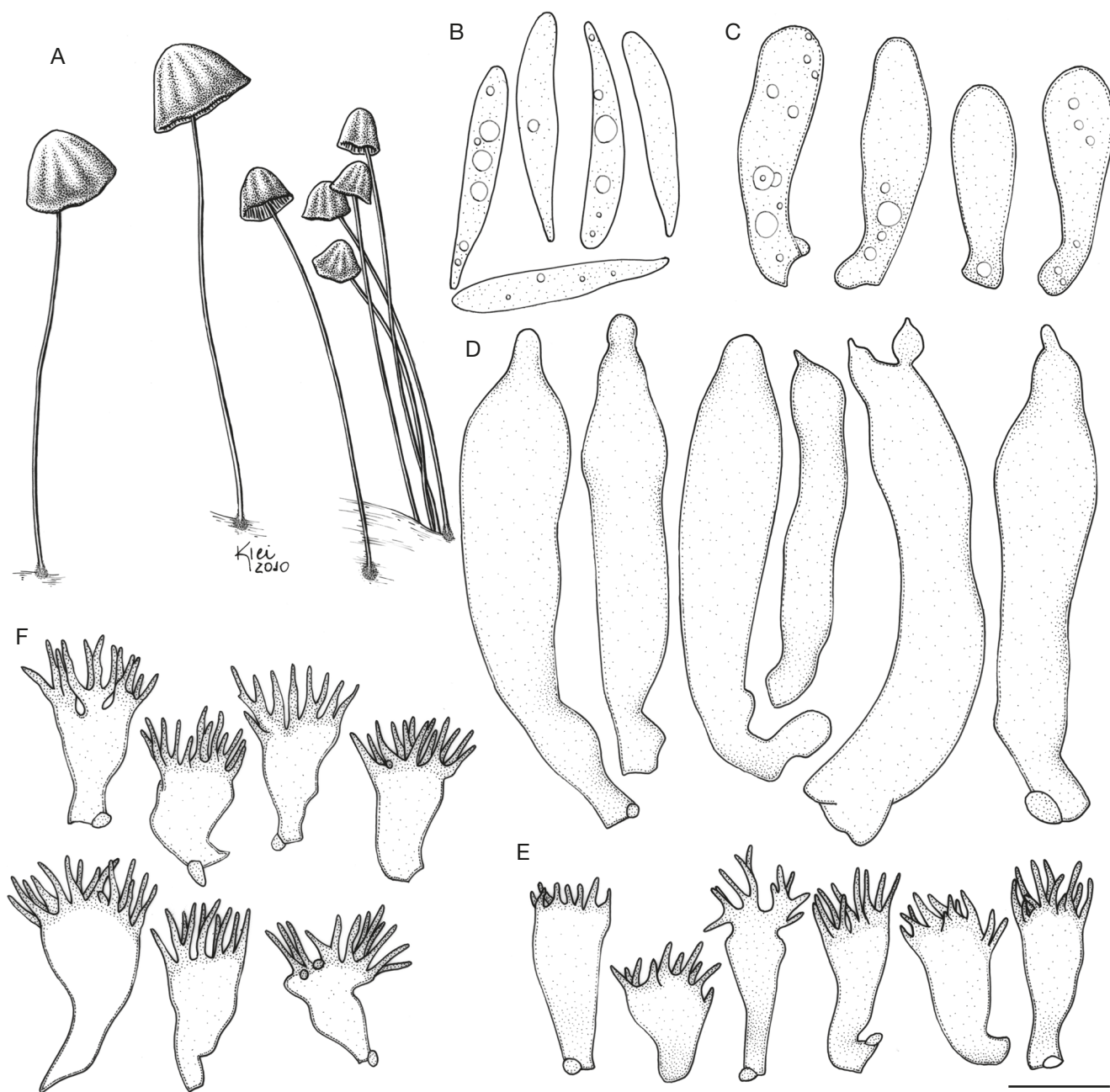


FIG. 10. — *Marasmius auranticapitatus* J.S. Oliveira, sp. nov. (*M. Capelari* & L.A.S. Ramos 4554): **A**, basidiomata; **B**, basidiospores; **C**, basidioles; **D**, pleurocystidia; **E**, cheilocystidia; **F**, Siccus-type broom cells of the pileipellis. Scale bar: A, 10 mm; B-F, 10 μ m.

Marasmius castanocephalus J.S. Oliveira, sp. nov.
(Figs 9B; 11)

Differs from *Marasmius davidii* Antonín in having non-marginate lamellae, slightly smaller basidiospores ($20\text{--}26 \times 3\text{--}4 \mu\text{m}$ vs $20\text{--}27 \times 4\text{--}6 \mu\text{m}$), in having yellowish pleurocystidia, and in growing on dried leaves.

HOLOTYPE. — **Brazil.** São Paulo State, Iporanga City, Parque Estadual Turístico do Alto Ribeira, 29.II.2012, *J.S. Oliveira & D.E. Desjardin* JO523 (holo-, SP[SP 445573]!).

ETYMOLOGY. — From Greek *καστανός* (*kastanos*) and *κεφάλι* (*kephali*), based on the brownish pileus.

MYCOBANK. — MB 842536.

HABIT AND SUBSTRATE. — Marasmioid (Figs 9B; 11A1), close, on dried eudicotyledonous leaves in the forest litter.

DESCRIPTION

Pileus (Figs 9B; 11A1)

7.5–15.7 mm diam., hemispheric to conical-campanulate, sulcate, center flat or slightly umbonate, margin decurved, edge entire to crenate; center to mid disc light chestnut to buff brown ($N_{50}Y_{60\text{--}80}M_{30\text{--}40}$), margin pale sepia brown ($N_{40}Y_{40}M_{30}$) to pale buff brown or brownish beige ($N_{20}Y_{30}M_{20}$ to $N_{10}Y_{30}$).

$_{40}M_{10}$); membranous, context white, thin (< 1 mm); glabrous, dry, dull, papyraceous to subvelutinous, non-hygrophanous.

Lamellae (Fig. 11A2)

Free to adnexed, subclose to subdistant, $L = 11-12$, equal, narrow to slightly broad, simple, $l = 0$, opaque, smooth, pale cream ($N_{00}Y_{10}M_{00}$), edge even, non-marginate, interlamellar hymenium concolorous with the lamellae faces.

Stipe (Figs 9B; 11A1)

61–80 × 0.5–0.8 mm, central, filiform, thin, equal, with circular caliber, chitinous, tough, hollow, apex concolorous with the lamellae, amber ($N_{60}Y_{50}M_{30}$) to dark brown ($N_{90}Y_{70-99}M_{50}$), or almost black downwards, glabrous, smooth, with a silky bright; with a scarce, cream, tomentose basal mycelium.

Odor

Not distinctive.

Basidiospores (Fig. 11B)

20–26 × 3–4 μm ($x_m = 22.6 [\pm 1.2] \times 3.7 [\pm 0.3] \mu\text{m}$, $Q_m = 6.1 [\pm 0.5]$, $n/s = 32/1$), oblong, clavate to subfusoid, smooth, hyaline, thin-walled, inamyloid.

Basidia

Not observed.

Basidioles (Fig. 11C)

(16.3–)20–25 × 5–8 μm , clavate, rarely tending to acuminate, smooth, hyaline, thin-walled, inamyloid.

Pleurocystidia (Fig. 11D)

33–50 × 9.8–13.8 μm , abundant, broadly clavate, sometimes tapered towards the apex, some capitate, or with a small apical vesicle, or mucronate, smooth, refractive, with faint content, somewhat fuscous, yellowish, thin-walled, inamyloid.

Cheilocystidia (Fig. 11E)

Similar to the Siccus-type broom cells in the pileipellis, pale brown when grouped, main body 8–22.5 × 5–15 μm , clavate to slightly turbinate, or pyriform to almost globose, sometimes ventricose, thin-walled; setulae apical, erect, short to generally elongate, 2.5–8.8 × 0.6–1 μm , cylindrical, filiform, thin, rarely digitiform, regular in outline, simple, pale yellow to hyaline, solid, apex somewhat obtuse or more frequently acute.

Lamellar trama

Dextrinoid, irregular, interwoven, hyphae cylindrical, 2.5–17.5 μm diam., regular or irregular in outline, branched, hyaline, smooth, thin-walled.

Pileus trama

Dextrinoid, irregular, hyphae interwoven, cylindrical, 1.3–8 μm diam., similar to the lamellar trama, but with some inflated hyphal segments.

Pileipellis

Hymeniform, composed of Siccus-type broom cells (Fig. 11F), abundant, yellowish to pale chestnut when grouped; main body 8.8–18.8 × 5.6–14 μm , clavate to turbinate, rarely globose or branched, hyaline, thin-walled; setulae apical, erect, 2–7.5 × 0.5–1.3 μm , cylindrical, thin, filiform, simple, regular in outline or contorted, yellowish, solid, apex acute or slightly obtuse.

Stipe trama

Dextrinoid, cortical hyphae parallel, cylindrical, 1.8–8.8 μm diam., regular in outline, branched, brownish, smooth, thick-walled; internal hyphae hyaline, thin-walled, 2.5–8 μm diam.

Clamp connections

Present in all tissues, except in the cortical hyphae of the stipe.

REMARKS

Marasmius castanocephalus J.S. Oliveira, sp. nov. is mainly characterized by the buff brown to brownish beige pileus, the large basidiospores (20–26 × 3–4 μm) and somewhat fuscous to yellowish pleurocystidia (33–50 × 9.8–13.8 μm). It seems a member of stirps *Helvolus* (Singer 1976) in ser. *Haematocephali* (sensu Singer 1976) because of the brown pileus as in *M. helvolus* Berk.

Marasmius castanocephalus J.S. Oliveira, sp. nov. is closer to *M. davidii* from Sri Lanka (Indo-Malayan realm), initially described as *M. helvolus* var. *brunneolus* Berk. & Broome (Berkeley & Broome 1873). Pegler (1986) elevated this variety to *M. brunneolus* (Berk. & Broome) Pegler. *Marasmius helvolus* has much smaller basidiospores (11–15 × 2.8–4 μm) and not projecting, inconstant, smaller (19–25 × 5–10.2 μm), opaque and thick-walled pleurocystidia (Singer 1976). Due to the homonym with *M. brunneolus* (Beeli) Singer, in sect. *Globulares* (traditional sense) (Singer 1964), Antonín (2003) replaced *M. brunneolus* (Berk. & Broome) Pegler with *M. davidii*. This species differs from *M. castanocephalus* J.S. Oliveira, sp. nov. mainly in having very distant, marginate lamellae (brown edge), slightly larger basidiospores (20–27 × 4–6 μm), only hyaline pleurocystidia and brownish cheilocystidia (setulae), and basidiomata found on dead sticks (Pegler 1986). *Marasmius brunneolus* var. *fuliginosus* Desjardin & E. Horak was described having dark brown to fuliginous pileus (Desjardin & Horak 1997). *Marasmius castanocephalus* J.S. Oliveira, sp. nov. is close to *M. haematocephalus* var. *leucophyllus* Singer, and to *M. musicola* Murrill, *M. allocystis* Singer, and *M. oleiger* Singer (stirps *Oleiger*) because of the brownish pigmentation of the pileus within ser. *Haematocephali* sensu Singer (Singer 1976). All these taxa, however, have much shorter basidiospores (up to 20.5 μm) and the last three have distinct pleurocystidia with oil-like content. No other formally published variety under *M. haematocephalus* seems close. *Marasmius semipellucidus* Berk. & Broome is discarded as conspecific with *M. castanocephalus* J.S. Oliveira, sp. nov. (Appendix) by the translucent stipe and geography of the original collection.

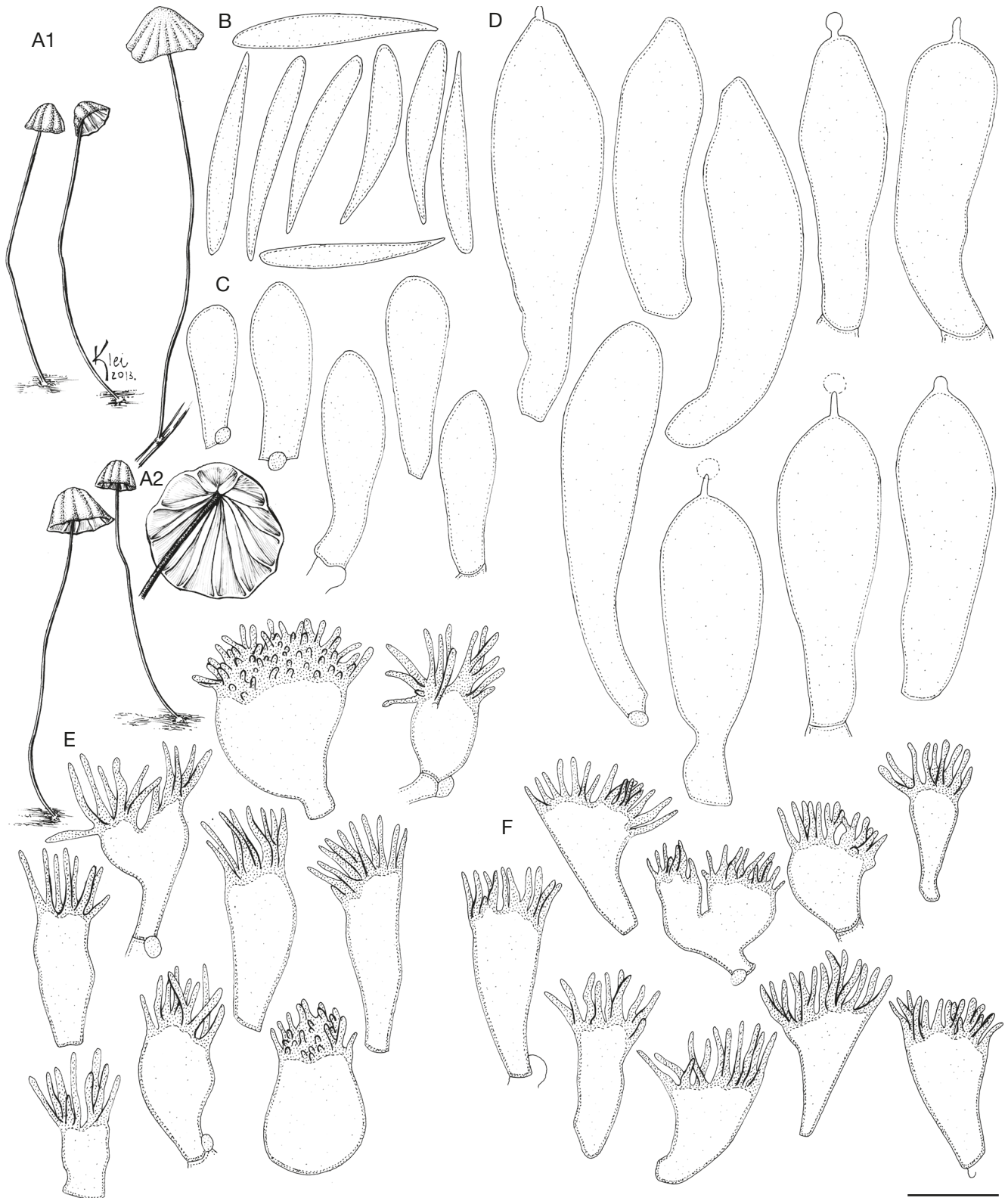


FIG. 11. — *Marasmius castanocephalus* J.S. Oliveira, sp. nov. (JO523): **A1, A2**, basidiomata; **B**, basidiospores; **C**, basidioles; **D**, pleurocystidia; **E**, cheilocystidia; **F**, Siccus-type broom cells of the pileipellis. Scale bar: A1, 18 mm; A2, 10 mm; B–F, 10 μ m.

In the phylogenetic trees (Figs 1; 3), *M. castanocephalus* J.S. Oliveira, sp. nov. appears close to *M. roseus* J.S. Oliveira, sp. nov., but with unsupported resolution. Both species branched in haemat_cp1.

Marasmius castanocephalus J.S. Oliveira, sp. nov. is close to *M. haematocephalus* but is 4.4% dissimilar in nrITS and 2.6% in nrLSU and differs by the pale brown pileus and larger basidiospores.

Marasmius coasiaticus J.S. Oliveira, sp. nov.
(Figs 9C; 12)

Differs from *Marasmius asiaticus* Mesic & Tkalec (synonym: *M. distantifolius* Y.S. Tan & Desjardin) in not having violet or ruby nor bright pink pileus which is rather larger (3.5–17 mm diam. vs 2–8 mm diam.), in having more numerous (10–12) non-marginate lamellae, in having smaller basidiospores ($13.8\text{--}20 \times 3.3\text{--}4.4 \mu\text{m}$ vs $18.5\text{--}23\text{--}[25] \times 3.5\text{--}5\text{--}[6] \mu\text{m}$), in having shorter and especially broader pleurocystidia ($35\text{--}51.3 \times 12\text{--}18.8 \mu\text{m}$ vs $37\text{--}42 \times 9\text{--}12 \mu\text{m}$), and in having non-mottled pileipellis.

HOLOTYPE. — **Brazil.** São Paulo State, Santo André City, Reserva Biológica de Paranapiacaba, 9.XII.2010, J.J.S. Oliveira, P.O. Ventura & A.V. Costa JO323 (holo-, SP[SP 445491]!).

ADDITIONAL MATERIAL EXAMINED. — **Brazil.** São Paulo State, São Paulo City, Parque Estadual das Fontes do Ipiranga, 1.III.2011, J.J.S. Oliveira & F. Karsedt JO339 (SP[SP 445502]!).

ETYMOLOGY. — Due to its close relationship as sister to *M. asiaticus*, in the Tropical Asia.

MYCOBANK. — MB 842537.

HABIT AND SUBSTRATE. — Marasmioid (Figs 9C; 12A), gregarious, on dried eudicotyledonous leaves and twigs in the forest litter.

DESCRIPTION

Pileus (Figs 9C; 12A)

3.5–17 mm diam., hemispheric to convex, becoming plane, slightly sulcate, center flat or with a shallow depression, margin decurved to straight, edge entire to slightly crenate; mostly brownish red ($N_{60}Y_{70}M_{90}$), sometimes brownish pink ($N_{40}Y_{60}M_{60\text{--}70}$) or orangish red ($N_{50}Y_{80}M_{70}$), with dark reddish brown center ($N_{80}Y_{99}M_{80}$); membranous, context thin (< 1 mm); glabrous, dry, dull, subvelutinous, non-hygrophanous.

Lamellae (Figs 9C; 12A)

Adnate, subdistant to distant, $L = 10\text{--}12$, equal, simple or slightly intervenose, $l = 0$, opaque, cream ($N_{00}Y_{10}M_{00}$), edge even, non-marginate, interlamellar hymenium concolorous with the pileus.

Stipe (Figs 9C; 12A)

$9\text{--}20 \times 0.3\text{--}0.5$ mm, central, generally short, curved, filiform, thin, equal, with circular caliber, chitinous, hollow, apex concolorous with the lamellae, becoming black elsewhere, glabrous, smooth, glossy; with a scarce, white to cream, tomentose basal mycelium.

Odor

Not distinctive.

Basidiospores (Fig. 12B)

$13.8\text{--}20\text{--}(20.6) \times 3.3\text{--}4.4 \mu\text{m}$ ($x_{mr} = 17\text{--}18.2 \times 3.8\text{--}3.9 \mu\text{m}$; $x_{mm} = 17.6 [\pm 0.8] \times 3.9 [\pm 0.1] \mu\text{m}$; $Q_{rm} = 4.4\text{--}4.8$; $Q_{mm} = 4.6 [\pm 0.3]$; $n/s = 30/2$), oblong, clavate to subfusoid, smooth, hyaline, thin-walled, inamyloid.

Basidia (Fig. 12C)

$19.4\text{--}25 \times 6.6\text{--}9 \mu\text{m}$, broadly clavate, smooth, hyaline, 2–4-sterigmate, inamyloid, thin-walled.

Basidioles (Fig. 12D)

$17.3\text{--}22.5 \times 7\text{--}9.8 \mu\text{m}$, broadly clavate, smooth, hyaline, thin-walled, inamyloid.

Pleurocystidia (Fig. 12E)

$(16.3\text{--})35\text{--}51.3 \times 12\text{--}18.8 \mu\text{m}$, abundant, broadly clavate to inflated, bacilliform, almost oval, smooth, slightly fuscous, yellowish, sometimes hyaline, thin-walled, refractive, inamyloid.

Cheilocystidia (Fig. 12F)

In form of Siccus-type broom cells, hyaline, walls thinner than those of the pileipellis; main body $10\text{--}16.3 \times 5.6\text{--}11.3 \mu\text{m}$, cylindrical to clavate, sometimes pyriform to turbinate, thin-walled, hyaline; setulae apical, sometimes slightly divergent, erect, generally short, $1.3\text{--}3.8\text{--}(5) \times 0.6\text{--}1 \mu\text{m}$, filiform, cylindrical, digitiform, or conical to verruciform, simple or rarely branched, solid, hyaline, regular to slightly irregular in outline, apex obtuse to somewhat acute.

Lamellar trama

Dextrinoid, irregular, interwoven, hyphae cylindrical, $2\text{--}6.3 \mu\text{m}$ diam., regular or irregular in outline, smooth, hyaline, branched and strongly connected, thin-walled.

Pileus trama

Similar to the lamellar trama, hyphae $2\text{--}7.5 \mu\text{m}$ diam.

Pileipellis

Hymeniform, composed of Siccus-type broom cells (Fig. 12G), abundant, brownish when in group; main body $11.3\text{--}18.8 \times 6.3\text{--}16.3 \mu\text{m}$, clavate to turbinate, sometimes flattened, or branched, or irregular in outline, hyaline, thin- to somewhat thick-walled; setulae or diverticula apical, sometimes slightly divergent, erect, $0.6\text{--}3.8\text{--}(5) \times 0.5\text{--}1.1 \mu\text{m}$, cylindrical, digitiform, or verruciform to vesiculose, simple to branched, regular to irregular in outline, almost moniloid, solid, hyaline, or melleus to pale brown, apex obtuse to slightly acute.

Stipe trama

Slightly dextrinoid, cortical hyphae parallel, cylindrical, regular in outline, $2.5\text{--}8.8 \mu\text{m}$ diam., branched, smooth, dark brown, yellowish brown when separated, thick-walled; internal hyphae hyaline, $1.3\text{--}11.3 \mu\text{m}$ diam., thin-walled.

Clamp connections

Present, except in the cortical hyphae of the stipe.

REMARKS

Marasmius coasiaticus J.S. Oliveira, sp. nov. is morphologically very close to *M. haematocephalus*, but produces smaller, thinner and more delicate basidiomata, having often short and curved stipe. The basidiospores are shorter in average ($17\text{--}18.2 \mu\text{m}$ vs $20.1\text{--}21 \mu\text{m}$) and the pleurocystidia are pale yellow, distinctly broadly clavate or bacilliform inflated ($12\text{--}18.8 \mu\text{m}$ vs $7\text{--}9.9 \mu\text{m}$ in width). Finally, the apical setulae of the Siccus-type broom cells are many times shorter and verruciform. *Marasmius coasiaticus* J.S. Oliveira, sp. nov.

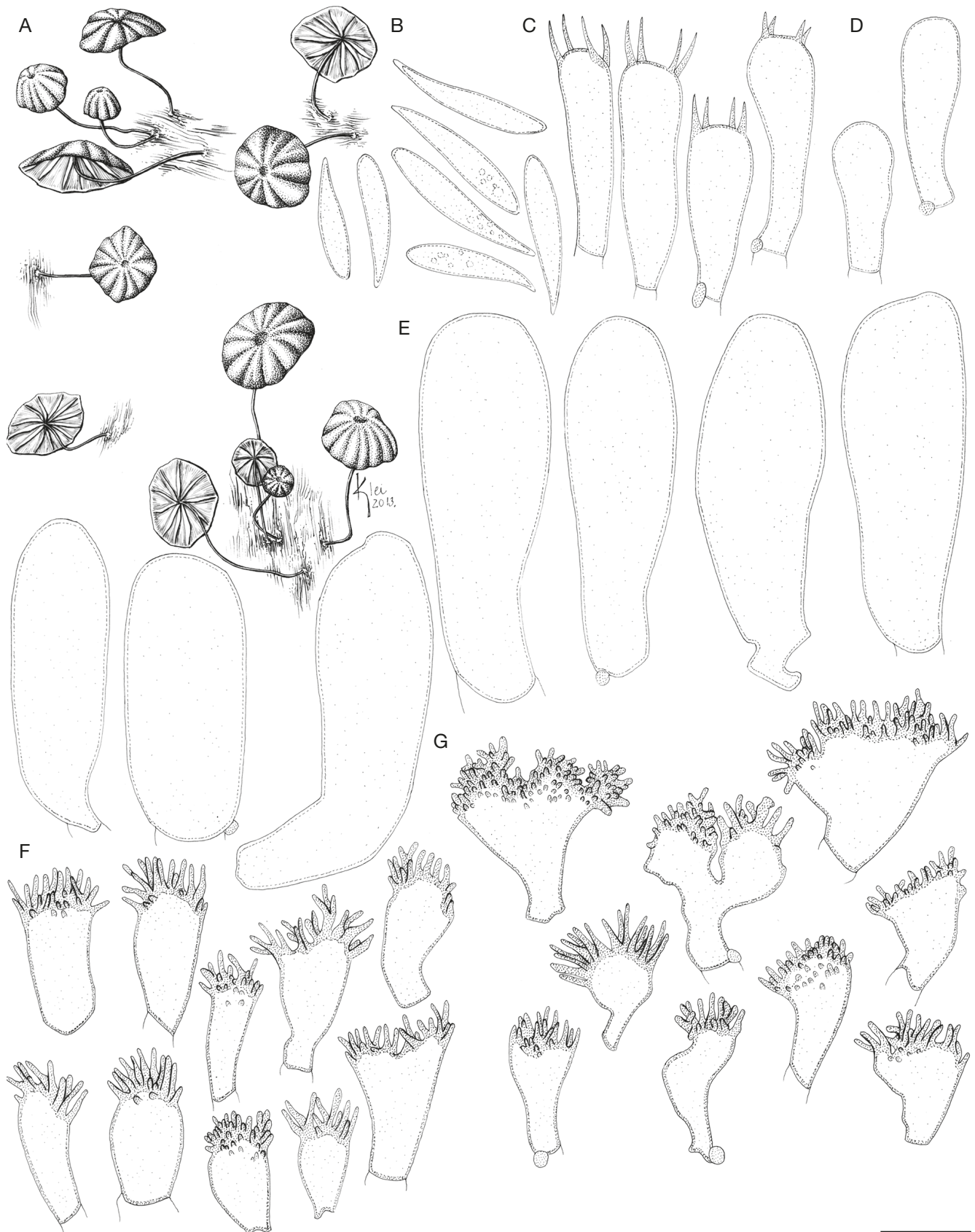


FIG. 12. — *Marasmius coasiaticus* J.S. Oliveira, sp. nov. (JO323): **A**, basidiomata; **B**, basidiospores; **C**, basidia; **D**, basidioles; **E**, pleurocystidia; **F**, cheilocystidia; **G**, Siccus-type broom cells of the pileipellis. Scale bar: A, 12.8 mm; B–G, 10 μ m.

is 1.8% dissimilar to *M. haematocephalus* in nrITS. The evident broader pleurocystidia combined with the shorter basidiospores in *M. coasiaticus* J.S. Oliveira, sp. nov. easily separate it from all varieties under *M. haematocephalus* (Singer 1976). *Marasmius sanguineus* Cooke & Massee may be similar, but differs in the adnexed, ventricose, marginate lamellae and longer stipe (up to 40 mm vs up to 20 mm) with lower pileus/stipe length proportion (Cooke 1889; Appendix).

Marasmius coasiaticus J.S. Oliveira, sp. nov. from Brazil is rather sister to *M. asiaticus* from Malaysia and additional collections from India and Thailand (Figs 1; 3) and, therefore, distant from *M. auranticapitatus* J.S. Oliveira, sp. nov., *M. castanocephalus* J.S. Oliveira, sp. nov., *M. haematocephalus*, *M. roseus* J.S. Oliveira, sp. nov. and *M. rubicundus* (Singer) J.S. Oliveira, stat. nov. from Brazil. *Marasmius asiaticus* was originally named *M. distantifolius* but, due to competing homonymy with *Marasmius distantifolius* (Murrill) Murrill, was renamed in Mesic & Tkalec (2010). *Marasmius asiaticus* (synonym: *M. distantifolius*) differs from *M. coasiaticus* J.S. Oliveira, sp. nov. by having ruby to pinkish hues in the brownish red to brownish violet pileus, marginate, 7–8 lamellae, larger basidiospores ($18.5\text{--}23\text{--}[25] \times 3.5\text{--}5\text{--}[6] \mu\text{m}$), smaller pleurocystidia ($37\text{--}42 \times 9\text{--}12 \mu\text{m}$), and mottled pileipellis (Tan *et al.* 2009).

Marasmius haematocephalus (Mont.) Fr.
(Figs 13; 14)

Epicrisis Systematis Mycologici, seu Synopsis Hymenomycetum: 382 (Fries 1838). — Type: **Brazil**. Rio de Janeiro State, Rio de Janeiro City, Auguste de Saint Hilaire, holotype not found (Singer 1976), or none located (Desjardin 1989), or not extant (Robert *et al.* 2013), or supposedly found in the PC herbarium (V. Antonín, pers. comm.).

Agaricus haematocephalus Mont., *Annales des Sciences naturelles, Botanique*, séries 2, 8: 369 (Montagne 1837).

Androsaceus haematocephalus (Mont.) Pat., *Journal de Botanique* (Morot) 3 (20): 336 (Patouillard 1889).

Chamaeceras haematocephalus (Mont.) Kuntze, *Revisio generum plantarum* (Leipzig) 3 (3): 456 (Kuntze 1898).

EPITYPE. — **Brazil**. São Paulo State, Iporanga City, Parque Estadual Turístico do Alto Ribeira, Núcleo Santana, 02.III.2012, J.J.S. Oliveira & D.E. Desjardin JO533 (epi-, designated here, SP[SP 445580]!), nrITS (ON502673) and nrLSU (ON502729).

ADDITIONAL EXAMINED MATERIAL. — **Brazil**. São Paulo State, São Paulo City, Parque Estadual da Cantareira, Núcleo Engorador, 16.II.2012, J.J.S. Oliveira & M. Capelari JO507 (SP[SP 446044]!); Iporanga City, Parque Estadual Turístico do Alto Ribeira, Núcleo Santana, 04.XII.2011, J.J.S. Oliveira JO435 (SP[SP 446079]!); 29.II.2012, J.J.S. Oliveira & D.E. Desjardin JO527 (SP[SP 446068]!); Amazonas State, Novo Airão City, Urubiquara, Rio Unini, 24.X.2019, J.J.S. Oliveira & Francisco JO1363 (INPA[INPA289980]!).

HABIT AND SUBSTRATE. — Marasmioid (Figs 13; 14A1), close, on dried eudicotyledonous petioles in the forest litter.

DISTRIBUTION. — The species was originally described from Rio de Janeiro, Brazil. Based on the present study, it is only confirmed

in the Neotropics. In Brazil, it was reported from Amazonas State (Berkeley 1856; Berkeley & Cooke 1876; Hennings 1904; this present study), Paraná State (de Meijer 2001), Pernambuco State (Kimbrough *et al.* 1995), Rio de Janeiro State (Singer 1976), Rondônia State (Capelari & Maziero 1988) and São Paulo State (Spegazzini 1889; Grandi *et al.* 1984; Pegler 1997; Puccinelli & Capelari 2009). However, these collections need to be revised, especially from the other states far from Southeastern Brazil. Based on the traditional view, the species is pantropical, occurring in tropical forests of South America, Africa, Tropical Asia and Oceania.

DESCRIPTION

Pileus (Figs 13; 14A1)

2.5–16 mm diam., conical, hemispherical to convex, or campanulate, deeply sulcate, center flat, or wrinkled, margin decurved, edge entire to slightly crenate; dark purplish red ($N_{90}Y_{00\text{--}40}M_{99}$) when young, then deep to dark blood red ($N_{70}Y_{50\text{--}90}M_{99}$) or deep purplish red ($N_{80}Y_{10\text{--}50}M_{99}$), dark pinkish red almost purple ($N_{60}Y_{50}M_{80}$); membranous, context thin (< 1 mm); glabrous, dry, dull, subvelutinous, non-hygrophanous.

Lamellae (Figs 13; 14A2)

Free to narrowly adnate, distant, $L = 7\text{--}10$, equal, narrow, subcultriform, simple, $l = 0$, opaque, smooth, white to cream ($N_{00}Y_{10}M_{00}$), or whitish pink ($N_{00}Y_{10}M_{10}$ or $N_{00}Y_{40}M_{10\text{--}20}$), edges even, non-marginate, interlamellar hymenium concolorous with the lamellae faces or partly concolorous with the pileus (especially near the pileus edge).

Stipe (Figs 13; 14A1)

$22.4\text{--}62 \times 0.2\text{--}0.5$ mm, central, filiform, thin, equal, sometimes with slightly broader base, with circular caliber, chitinous, hollow; apex concolorous with the lamellae, becoming bronze brown ($N_{40}Y_{60}M_{50}$ to $N_{80}Y_{70}M_{40}$) to dark brown ($N_{90}Y_{99}M_{80}$), or almost black at the base, glabrous, smooth, with a silky bright; with a scarce (subinsititious), white, tomentose basal mycelium.

Odor

Not distinctive.

Basidiospores (Fig. 14B)

$(18\text{--})18.3\text{--}22.6\text{--}(23) \times 3\text{--}4.9 \mu\text{m}$ ($x_{rm} = 20.1\text{--}21 \times 3.8\text{--}4.2 \mu\text{m}$; $x_{mm} = 20.5 [\pm 0.3] \times 3.9 [\pm 0.2] \mu\text{m}$; $Q_{rm} = 5\text{--}5.4$; $Q_{mm} = 5.2 [\pm 0.1]$; $n/s = 30/5$), oblong, clavate, subfusoid to fusoid, smooth, hyaline, thin-walled, inamyloid.

Basidia (Fig. 14C)

$19\text{--}26.8 \times (5.6\text{--})6.2\text{--}7.9 \mu\text{m}$, clavate, smooth, hyaline to slightly fuscous, thin-walled, with four short and conical obtuse sterigmata, inamyloid.

Basidioles (Fig. 14D)

$(15\text{--})18.5\text{--}25.9 \times (3.3\text{--})4.8\text{--}7.1 \mu\text{m}$, cylindrical clavate, clavate, sometimes wavy or with tapered apex, smooth, hyaline to slightly fuscous, inamyloid.

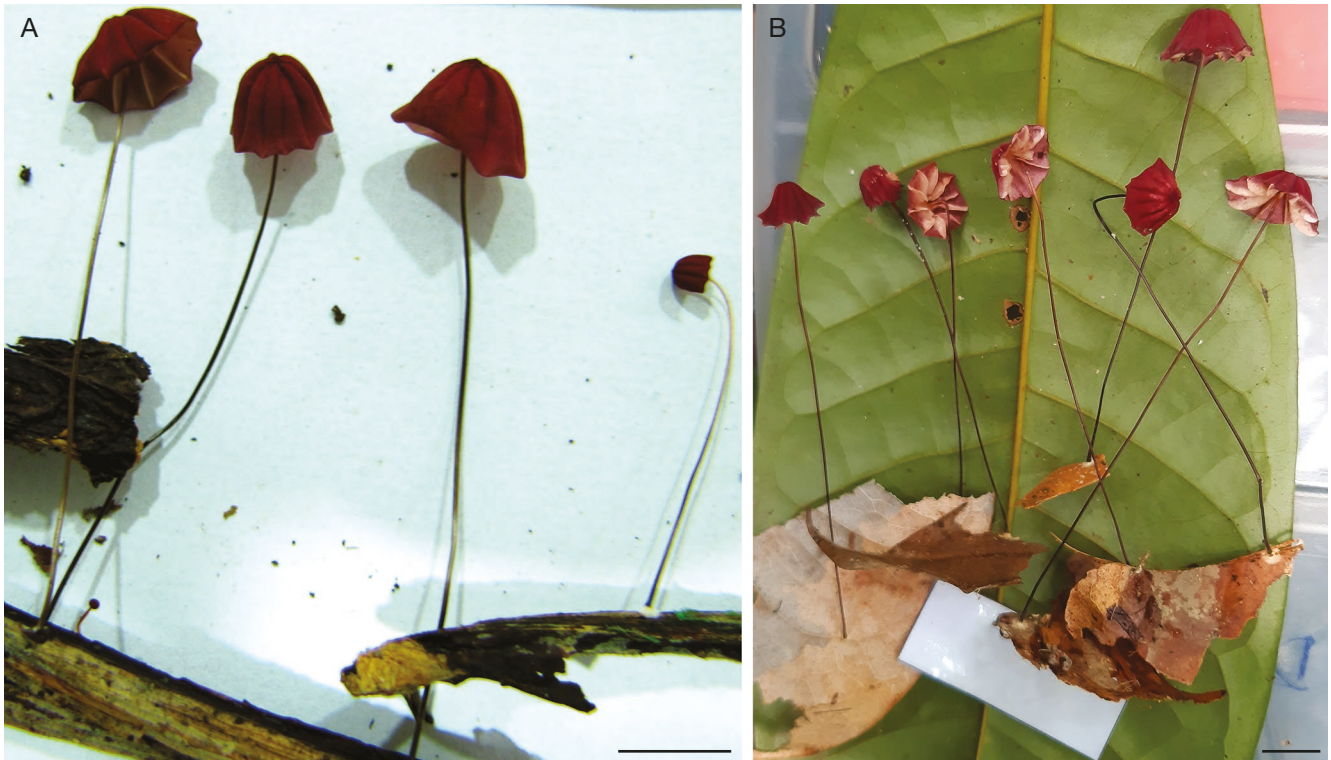


FIG. 13. — Pictures of fresh basidiomata of *Marasmius haematocephalus* (Mont.) Fr.: **A**, JO533 from Atlantic Rainforest (epitype); **B**, JO1363 from Amazon Forest. Scale bars: 10 mm.

Pleurocystidia (Fig. 14E)

30.1–76.2 × 7–13.9(–15.5) µm, clavate or cylindrical clavate, lageniform, some capitate, papillate or rarely mucronate, occasionally wavy with apical and shallow constrictions, smooth, fuscous, thin-walled, refractive, inamyloid, abundant although sparse.

Cheilocystidia (Fig. 14F)

Similar to the *Siccus*-type broom cells of the pileipellis, but hyaline and with thinner walls; main body 10.3–19.3 × 5.5–10.6 µm, clavate to slightly turbinate, sometimes flat, seldom branched; setulae apical, erect, 2.1–5.2 × 0.5–1 µm, cylindrical or filiform, needle-like, rarely digitiform, regular in outline, simple or rarely branched, solid, hyaline to fuscous, apex acute.

Lamellar trama

Strongly dextrinoid, irregular, interwoven, hyphae cylindrical, 1.8–5.4 µm diam., regular in outline, branched, hyaline, thin-walled, smooth to slightly rough.

Pileus trama

Strongly dextrinoid, similar to the lamellar trama, hyphae 1.8–6.2 µm diam.

Pileipellis

Hymeniform, composed of *Siccus*-type broom cells (Fig. 14G), pale brown or chestnut brown, bleaching in KOH solution; main body 7.2–20.4 × 5.5–12.1 µm, clavate, turbinate, sometimes branched, ventricose, or flat, hyaline, thin-walled to

slightly thick-walled (particularly at the apex), inamyloid; setulae apical, erect, 2.8–6.2 × 0.6–1.3 µm, cylindrical or filiform, needle-like, rarely digitiform, simple, regular in outline, solid, mostly pale brown, apex tapered, obtuse to slightly acute.

Stipe trama

Dextrinoid, especially the internal hyphae and those of the stipe apex, cortical hyphae parallel, packed, cylindrical, regular in outline, 2.7–7.7 µm diam., or slightly inflated, sometimes branched, smooth, dark chestnut brown, yellowish brown when separate, thick-walled; internal hyphae regular in outline, 1.8–8.1 µm diam., hyaline, parallel or interwoven, sometimes with short segments.

Clamp connections

Present in all tissues, except in the cortical hyphae of the stipe.

REMARKS

Marasmius haematocephalus is the type species of *Marasmius* sect. *Sicci* subsect. *Siccini* ser. *Haematocephali* sensu Singer (1976) which is characterized by the presence of pleurocystidia, otherwise compatible with ser. *Leonini* (Singer 1976). The species epithet means blood red head, (from Greek αἷματος [haimatos] and κεφάλι [kephali]), “*rubro-sanguineo*” pileus in the protologue. According to a broad concept, this species seems to produce basidiomata with a high variability of characteristics, especially in the pileus pigmentation, length and shape of both spores and pleurocystidia, and substrate preference. Based on Singer (1958), *M. haematocephalus* is

typically, as the description in the protologue indicates, uniformly blood red, purple, deep purple (not violet) pileated. In Singer (1965, 1976), the sulcate pilei have a large color range of variation from pink, red to purple, even brownish, and with shapes from campanulate, hemispherical, convex to plane. Even obeying a reasonable morphological species spectrum, the cryptic nature of taxa in species complex and/or a non-fine species characterization has made *M. haematocephalus* a receptacle of many misdetermined specimens with an allegedly pantropical distribution.

After matching Montagne (1837) and Fries (1838) concepts, the topotypical examined material also agrees with Singer (1958, 1965, 1976) in nearly all aspects. We intended to examine “*R. Singer C 3172*” and confirm compatible spores’ dimension. We contacted BAFC herbarium to search for Singer’s topotype collection, but without reply during this pandemic time. Antonín (2007) and Shay *et al.* (2017) mentioned the collection as neotype but did not examine it. Vladimír Antonín (pers. comm.) informed he has a specimen on loan from PC herbarium named as *M. haematocephalus* collected by Auguste de Saint Hilaire from Brazil that is possibly the authentic type. He shared pictures of the dried specimen that seems macromorphologically quite similar to our specimens. The examined material herein also agrees with “French Guyana, Ann. 1850, *M. Leprieur n° 990* (PC)”, determined by Montagne as *M. haematocephalus*, and fully revised by Desjardin (1989), but the basidiospores in the Leprieur’s collection seems smaller ($16\text{--}21.6 \times 4.4\text{--}5.6\ \mu\text{m}$, $x_m = 19.1 [\pm 1.3] \times 4.7 [\pm 0.4]\ \mu\text{m}$, $Q = 3.5\text{--}4.6$, $Q_m = 4.1 [\pm 0.3]$, $n = 18$).

There was a probable confusion in Dennis (1951); where *M. tageticolor* Berk., should be *M. haematocephalus* from Trinidad (fresh collection), Dominique (type of *M. sanguineus* Cooke & Masee) and Bahamas (type of *M. atropurpureus* Murrill), compatible with our collections except for the distinctly marginate lamellae of these two later. In fact, Singer (1976) considered *M. sanguineus* and *M. atropurpureus* synonyms under *M. haematocephalus*. However, would the ventricose (broad), distinctly marginate lamellae (edge concolorous with the pileus) be compatible with the protologue of *M. haematocephalus*? In Singer (1976), the lamellar edges are not concolorous with the pileus in mature basidiomata except “sometimes” near the pileus margin. It is possible that Singer’s concept was broadened to include the synonyms. *Marasmius haematocephalus* in Desjardin (1989), of collections from North America forests in the United States (Florida, North Carolina and Tennessee) along with collections from British Honduras, Cuba and Guyana, differs from the examined material only in having more numerous (10–15), broad (up to 2.5 mm), and marginate (pinkish red, deep reddish or violet red) lamellae (sometimes non-marginate) and a wider spore range ($16\text{--}22 \times [3.6\text{--}]4\text{--}5.6\ \mu\text{m}$). If the broad, marginate lamellae is a strong diagnostic characteristic in separating species, then there are *M. haematocephalus* with non-marginate lamellae vs *M. sanguineus* (synonym: *M. atropurpureus*) with marginate lamellae. Thus, the collections with marginate lamellae from North America examined in Desjardin (1989) may be *M. sanguineus* (or *M. atropurpureus*) instead of

M. haematocephalus. Pegler (1983) should have had a broad (mix) concept on examined collections from Martinique, Trinidad, Dominique (including the type of *M. sanguineus*) and Sri Lanka (type of *M. semipellucidus*). The spore range was shorter ($16\text{--}20 \times 3\text{--}4.5\ \mu\text{m}$) than those of collections from São Paulo ($18\text{--}22 \times 3.7\text{--}4.5\ \mu\text{m}$) in Pegler (1997), this later more compatible (the purplish red pileus) with our collection as well as in Dennis (1970) from Venezuela (bright purple pileus with $19\text{--}21 \times 3\text{--}4\ \mu\text{m}$ basidiospores). With the fine-tuned concept of *M. haematocephalus* (s. str.) in this study, its various heterotypic synonyms listed in Singer (1976) and other need to be carefully reevaluated in future studies. By revising their protologues (Appendix), none of them seems morphologically compatible with *M. haematocephalus* s. str. except for the illegitimate *M. vinosus* Beeli from Africa.

In Brazil, according to the *speciesLink* – Virtual Herbarium of the Centro de Referência em Informação Ambiental, CRIA (splink.org.br, accessed in November 17th, 2019), 241 collections determined as *M. haematocephalus* are currently deposited in 23 Brazilian herbaria, collected from the states of Amazonas, Bahia, Espírito Santo, Maranhão, Minas Gerais, Pará, Paraíba, Pernambuco, Piauí, Rio de Janeiro, Rio Grande do Norte, Rio Grande do Sul, Rondônia, Roraima, Santa Catarina and São Paulo (Brazil). A review of these material is due in another paper considering the *M. haematocephalus* (s. str.) or *M. rubicundus* system. Singer (1976) recognized nine varieties in *M. haematocephalus* based on subtle distinctions and overlapping morphological characteristics: 1) *atroviolaceus* Singer; 2) *haematocephalus*; 3) *leucophyllus* Singer; 4) *macrocephalus* Singer; 5) *oenechinus* Singer; 6) *pseudotageticolor* Singer (partly marginate lamellae, red); 7) *purpureomarginatus* Singer (marginate lamellae, garnet red); 8) *rubicundus* Singer; and 9) *transiens* Singer. All these varieties are from the Neotropical realm, mostly from forests of South America. Except for the 8th, these taxa need to be reevaluated with fresh collections. The sixth and seventh may be morphologically compatible with those in Desjardin (1989) with marginate lamellae. In Pegler (1987), the supposed (seems not formalized) additional *M. haematocephalus* var. *obscurior* Berk. & Curtis from Cuba has pileus browner than the typical form and with marginate lamellae, more compatible with *M. hypophaeus*. Desjardin (1991) proposed *M. haematocephalus* var. *anomaloideus* Desjardin, of collections from Tennessee, United States.

According to the current broad morphological concept, *M. haematocephalus* has been reported from various localities in South and Central America including some Caribbean islands (Neotropics), and less frequently from southern continental and insular North America (Nearctic) (Singer 1965, 1976; Dennis 1970; Pegler 1983, 1997; Desjardin 1989), Tropical Africa including Madagascar (Singer 1964; Pegler 1977; Antonín 2007; Shay *et al.* 2017), Tropical Asia (Petch 1948; Pegler 1986; Desjardin *et al.* 2000; Tan *et al.* 2009; Wannathes *et al.* 2009) and Oceania (Desjardin & Horak 1997). These collections need to be reevaluated given these new data and analyses, and a better understanding of the species complex.

Marasmius haematocephalus may be confused with *M. asiaticus*, *M. pallescentis*, *M. panerythrus* Singer, *M. pulcherripes*,

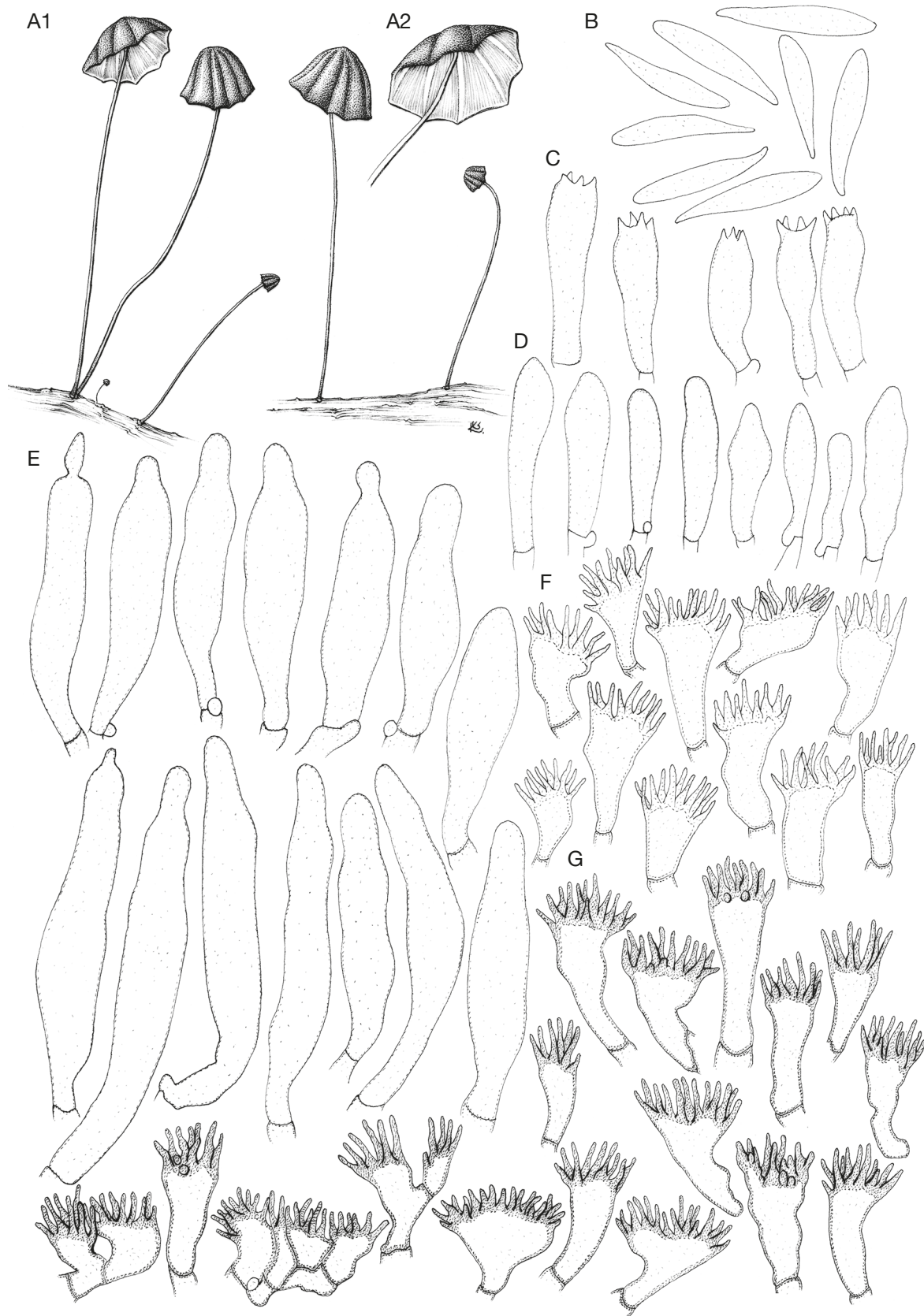


FIG. 14. — *Marasmius haematocephalus* (Mont.) Fr. (JO533): **A1, A2**, basidiomata; **B**, basidiospores; **C**, basidioles; **D**, basidia; **E**, pleurocystidia; **F**, cheilocystidia; **G**, Siccus-type broom cells of the pileipellis. Scale bar: A1, 8.9 mm; A2, 5.9 mm; B–G, 10 μ m.

and *M. rhodopurpureus* Antonín, R.Ryoo & H.D.Shin. *Marasmius asiaticus* differs by having “less violet” pileus, less numerous lamellae (7–8), slightly larger basidiospores ($18.5\text{--}23\text{--}[25] \times 3.5\text{--}5\text{--}[6] \mu\text{m}$) and a mottled pileipellis (Tan *et al.* 2009; as *M. distantifolius*). *Marasmius pallescens* differs by having a pale red pileus, shorter basidiospores (11–17 μm in length) and mottled pileus (Singer 1976). *Marasmius panerythus* and *M. pulcherripes* diverges by having shorter basidiospores (13–14 μm in length [Singer 1976] and [11–]12–15[–16] μm [Desjardin 1989; Antonín *et al.* 2012], respectively); and *M. rhodopurpureus* also has shorter basidiospores (12–15[–16] μm) and shorter (35–42 μm), non-refractive, clavate pleurocystidia (Antonín *et al.* 2012).

In the phylogenetics trees (Figs 1; 3), various strains named after *M. haematocephalus* in previous studies forming a pantropical distribution branched in multiple lineages (para- or polyphyletic), indicating them to be not a single but close, cryptic species in haemat_cp1. Based on combined nrLSU + nrITS data, *M. haematocephalus* s. str. (JO533) branched in a distinct phylogenetic position as sister to *M. auranticapitatus* J.S. Oliveira, sp. nov. + *M. rubicundus* (Singer) J.S. Oliveira, stat. nov. (Fig. 4).

***Marasmius roseus* J.S. Oliveira, sp. nov.**
(Figs 15A; 16; 17)

Differs from *M. pallescens* in having longer basidiospores (12–20 μm vs 11–17 μm) and pleurocystidia (37.5–75.5 μm vs 32–43 μm); from *M. pulcherripes* also in the longer basidiospores (12–20 μm vs 11–15 μm), shorter setulae on the pileipellis broom cells (up to 4 μm vs up to 10 μm) and is devoid of the peculiar red stipe apex and inner extremities of the lamellae; from *M. rubicundus* (Singer) J.S. Oliveira, stat. nov. mainly in having smaller basidiospores, $12\text{--}20 \times 3\text{--}4 \mu\text{m}$ ($x_m = 16.3 [\pm 2.4] \times 3.6 [\pm 0.3] \mu\text{m}$) vs $(15.4\text{--})16.2\text{--}21.7\text{--}(22) \times 2.7\text{--}4.7\text{--}(5) \mu\text{m}$ ($x_{mm} = 19 [\pm 0.5] \times 3.8 [\pm 0.2] \mu\text{m}$); differs from all in the peculiar dimorphic Siccus-type broom cells in the pileipellis: 1) thick-walled, with pale chestnut lilac lumen, setulae apical, short, often coarse; 2) in transition to Rotalis-type broom cells, thin-walled.

HOLOTYPE. — **Brazil.** São Paulo State, São Paulo City, Parque Estadual das Fontes do Ipiranga, 3.III.2011, J.J.S. Oliveira & F. Karstedt JO352 (holo-, SP[SP 445510]!).

ETYMOLOGY. — Based on the rose pileus.

MYCOBANK. — MB 842538.

HABIT AND SUBSTRATE. — Marasmiod (Figs 15B; 16A), gregarious, on dead eudicotyledonous sticks in the forest litter.

DESCRIPTION

***Pileus* (Figs 15B; 16A)**

2–21 mm diam., convex, orbicular, sulcate to deeply sulcate, center flat, somewhat wrinkled when mature, margin decurved to plane, edge entire to slightly crenate; grayish pink to lilac ($N_{40}Y_{10}M_{60}$), becoming pale pink or rose ($N_{40}Y_{20}M_{50}$), center purple or dark pink ($N_{90}Y_{00}M_{80}$); membranous, context thin (< 1 mm); glabrous, dry, dull to semi translucent, subvelutinous, non-hygrophanous.

***Lamellae* (Figs 15B; 16A)**

Free to adnate, distant, $L = 12$, equal, simple, $l = 0(-1)$, opaque, smooth, whitish pink ($N_{00}Y_{20}M_{20}$), edge even, non-marginate, interlamellar hymenium concolorous with the pileus.

***Stipe* (Figs 15B; 16A)**

8–40 $\times$ 0.3–0.7 mm, central, filiform, thin, equal, with circular caliber, chitinous, hollow; apex concolorous with the lamellae, becoming dark brown to almost black elsewhere, glabrous, smooth, with a silky bright; with a scarce, cream, tomentose basal mycelium.

Odor

Not distinctive.

***Basidiospores* (Fig. 16B)**

$12\text{--}20 \times 3\text{--}4 \mu\text{m}$ ($x_m = 16.3 [\pm 2.4] \times 3.6 [\pm 0.3] \mu\text{m}$, $Q_m = 4.5 [\pm 0.6]$, $n/s = 32/1$), oblong, widely variable in length, clavate to subfusoid, smooth, hyaline, thin-walled, inamyloid.

Basidia

Not observed.

***Basidioles* (Fig. 16C)**

$17.5\text{--}26.3 \times 5.4\text{--}8.8 \mu\text{m}$, cylindrical to clavate, sometimes tapering toward the apex, smooth, hyaline, thin-walled, inamyloid.

***Pleurocystidia* (Fig. 16D)**

$37.5\text{--}75.5 \times 6.3\text{--}10.6 \mu\text{m}$, abundant, conspicuously projecting, cylindrical, clavate, sometimes ventricose, generally with tapered apex, or capitate, some worm-like to irregular in outline, apex easily breakable, smooth, slightly fuscous, yellowish, thin-walled, refractive, inamyloid.

***Cheilocystidia* (Fig. 16E)**

In form of Siccus-type broom cells, some apparently in transition to Rotalis-type similar to the broom cells of the kind 2 in the pileipellis; main body $11.3\text{--}17.5 \times 6.3\text{--}10 \mu\text{m}$, clavate to pyriform, rarely cylindrical to ventricose, thin-walled, hyaline; setulae apical to little divergent to the laterals, erect, generally short, $0.6\text{--}3.8 \times 0.5\text{--}1 \mu\text{m}$, digitiform or verruciform, simple or branched, solid, pale brown, regular to somewhat irregular in outline, apex obtuse to slightly acute.

Lamellar trama

Dextrinoid, irregular, interwoven, hyphae cylindrical, 1.3–7.5 μm diam., regular or irregular in outline, branched, smooth, hyaline, thin-walled.

Pileus trama

Similar to the lamellar trama, hyphae 2–7 μm diam.

Pileipellis

Hymeniform, mottled, composed of Siccus-type broom cells, of two kinds: 1) abundant at the pileus center and abruptly less frequent from the mid disc to the marginal zone (Fig. 17A); main body $5\text{--}17.5 \times 7.5\text{--}11.3 \mu\text{m}$, pyriform, turbinate to sub-



FIG. 15. — Pictures of fresh basidiomata: **A**, *Marasmius roseus* J.S. Oliveira, sp. nov. (JO352); **B**, *M. rubicundus* (Singer) J.S. Oliveira, stat. nov. (JO464); **C**, *M. cf. pallenscens* Murrill (JO426). Scale bars: 10 mm.

clavate, sometimes apically flattened, thick-walled especially at the apex, with pale chestnut lilac lumen; setulae apical, erect, short, $1.3\text{--}4 \times 0.8\text{--}1.3\ \mu\text{m}$, digitiform to verruciform, or vesiculose, sometimes branched, often coarse, regular to irregular in outline, solid, hyaline to pale brown, apex obtuse; and 2) more numerous at the mid disc and predominant at the marginal zone (Fig. 17B), some apparently in transition to Rotalis-type broom cells, rarely almost devoid of apical diverticula; main body $8.8\text{--}20 \times 5.6\text{--}12.5\ \mu\text{m}$, clavate, turbinate, ventricose to subpyriform, walls very thin, completely hyaline, difficult to be

individualized; setulae apical and frequently divergent to the laterals, erect, generally short, $0.3\text{--}2.5(-4) \times (0.2\text{--})0.5\text{--}1\ \mu\text{m}$, vesiculose, verruciform to digitiform, solid, pale brown, apex obtuse and rounded, or irregular.

Stipe trama

Dextrinoid, especially in the internal hyphae, cortical hyphae parallel, cylindrical, regular in outline, $2.5\text{--}8.8\ \mu\text{m}$ diam., wrinkled, dark brown, walls not clearly thick, or thin-walled; internal hyphae hyaline, $2.5\text{--}10\ \mu\text{m}$ diam., thin-walled.

Clamp connections

Present in all tissues, except in the cortical hyphae of the stipe.

REMARKS

Marasmius roseus J.S. Oliveira, sp. nov. differs from *M. haematocephalus* mainly by having pale purplish pink to pale lilac pileus center, then pink or rose from the mid disc to the margin, by having widely variable length of basidiospores (12–20 µm), and by having a mottled pileipellis with two kinds of Siccus-type broom cells (one apparently in transition to Rotalis-type). It is 2.2 % and 0.5 % dissimilar to *M. haematocephalus* s. str. (JO533) in the nrITS and nrLSU, respectively.

Marasmius roseus is morphologically somewhat similar to *M. pallescens* sensu Singer (1976), especially in the light lilac pileus form (Dennis 1961). Singer (1976) also observed a mottled pileipellis in *M. pallescens* due to some broom cells with darker melleous apical setulae among paler broom cells. However, *M. pallescens* has shorter basidiospores (11–17 µm) and smaller pleurocystidia (32–43 × 10–15.2 µm). *Marasmius roseus* J.S. Oliveira, sp. nov. is also very close to *M. rubicundus* (Singer) J.S. Oliveira, stat. nov. (next taxon) in the pileus pigmentation, but this later varies more widely from pale red to rose, ruby pink, even purplish pileus while has basidiospores less variable in length and larger in average ($x_{mm} = 18.8 [\pm 1.3] \times 3.8 [\pm 0.2] \mu m$), and non-mottled pileipellis composed of regular Siccus-type broom cells.

Marasmius pulcherripes is similar especially by having similar pileus pigmentation and mottled pileipellis due to thick-walled, purplish broom cells among more regular ones in the pileipellis (Gilliam 1976; Antonín *et al.* 2012). However, it differs from *M. roseus* J.S. Oliveira, sp. nov. mainly by having shorter basidiospores (11–15 µm) and longer apical setulae (up to 10 µm) on the broom cells of the pileipellis beside the typical stipe pigmentation. None of the heterotypic synonyms under *M. haematocephalus* listed in Singer (1976) nor their varieties seem conspecific with *M. roseus* J.S. Oliveira, sp. nov. *Marasmius haematocephalus* var. *transiens* Singer also has basidiospores largely variable in size ([12.5–]13–22 × 3.5–4.5 µm), but the pileus (3–12 mm diam.) color is completely different with no similar cells in the pileipellis (Singer 1965, 1976).

Marasmius rubicundus (Singer) J.S. Oliveira, stat. nov.
(Figs 15B; 18)

Marasmius haematocephalus var. *rubicundus* Singer, *Sydowia* 18: 337 (Singer 1965). — Type: **Bolivia**. La Paz, Nor-Yungas, Charobamba, 1300 m a.s.l., 30.I.1956, *Singer B 743* (LIL), holotype; *Singer B 737* (LIL); Coroico, 1700 m a.s.l., 7.II.1956, *Singer B 945* (LIL); Beni, Vaca Diez, Guayaranerin, 4.III.1956, *Singer B 1963* (LIL); *Singer B 1755* (LIL).

EPITYPE. — **Brazil**. São Paulo State, São Paulo City, Parque Estadual da Cantareira, Núcleo Engordador, 30.I.2012, *J.J.S. Oliveira & V. Motato-Vásquez JO464* (epi-, designated here, SP[SP 445549]!), nrITS (ON502658) and nrLSU (ON502728).

ADDITIONAL EXAMINED MATERIAL. — **Brazil**. São Paulo State, Santo André City, Reserva Biológica de Paranapiacaba, 16.XII.2009,

M. Capelari & L.A.S. Ramos 4567 (SP[SP 445931]!); *M. Capelari & L.A.S. Ramos 4570* (SP[SP 446073]!); 14.I.2010, *J.J.S. Oliveira & M. Capelari JO1* (SP[SP 446075]!); 16.III.2010, *J.J.S. Oliveira JO43* (SP[SP 446069]!); 15.X.2010, *J.J.S. Oliveira & C.L.A. Pires JO223* (SP[SP 446074]!); 16.X.2010, *J.J.S. Oliveira & C.L.A. Pires JO228* (SP[SP 445448]!); *J.J.S. Oliveira & C.L.A. Pires JO230* (SP[SP 446076]!); 17.X.2010, *J.J.S. Oliveira & C.L.A. Pires JO245* (SP[SP 446046]!); *J.J.S. Oliveira & C.L.A. Pires JO246* (SP[SP 445454]!); 5.XI.2010, *J.J.S. Oliveira JO261* (SP[SP 446051]!); 7.XI.2010, *J.J.S. Oliveira & A.V. Costa JO275* (SP[SP 446059]!); 7.XII.2010, *J.J.S. Oliveira, P.O. Ventura & A.V. Costa JO281* (SP[SP 445464]!); *J.J.S. Oliveira, P.O. Ventura & A.V. Costa JO283* (SP[SP 446061]!); *J.J.S. Oliveira, P.O. Ventura & A.V. Costa JO295* (SP[SP 446063]!); *J.J.S. Oliveira, P.O. Ventura & A.V. Costa JO296* (SP[SP 445476]!); 9.XII.2010, *J.J.S. Oliveira, P.O. Ventura & A.V. Costa JO316* (SP[SP 445488]!); *J.J.S. Oliveira, P.O. Ventura & A.V. Costa JO318* (SP[SP 446048]!); *J.J.S. Oliveira, P.O. Ventura & A.V. Costa JO319* (SP[SP 446047]!); São Paulo City, Parque Estadual das Fontes do Ipiranga, 1.III.2011, *J.J.S. Oliveira & F. Karstedt JO330* (SP[SP 446065]!); *J.J.S. Oliveira & F. Karstedt JO335* (SP[SP 446067]!); *J.J.S. Oliveira & F. Karstedt JO338* (SP[SP 446066]!); 18.X.2011, *J.J.S. Oliveira & P.O. Ventura JO380* (SP[SP 446064]!); São Paulo City, Parque Estadual da Cantareira, Núcleo Engordador, 19.XII.2011, *J.J.S. Oliveira & M. Capelari JO445* (SP[SP 445537]!); *J.J.S. Oliveira & M. Capelari JO446* (SP[SP 446054]!); *J.J.S. Oliveira & M. Capelari JO447* (SP[SP 446053]!); 9.II.2012, *J.J.S. Oliveira & M. Capelari JO481* (SP[SP 446043]!); *J.J.S. Oliveira & M. Capelari JO482* (SP[SP 446055]!); *J.J.S. Oliveira & M. Capelari JO483* (SP[SP 445560]!); 16.II.2012, *J.J.S. Oliveira & M. Capelari JO492* (SP[SP 446045]!); *J.J.S. Oliveira & M. Capelari JO514* (SP[SP 446071]!); *J.J.S. Oliveira & M. Capelari JO516* (SP[SP 446057]!); Iporanga City, Parque Estadual Turístico do Alto Ribeira, Núcleo Santana, 29.II.2012, *J.J.S. Oliveira & D.E. Desjardin JO529* (SP[SP 445577]!); *D.E. Desjardin DED8675* (SP[SP 445665]!); Lageado, 29.II.2012, *J.J.S. Oliveira & D.E. Desjardin JO534* (SP[SP 446077]!).

MYCOBANK. — MB 842539.

HABIT AND SUBSTRATE. — Marasmioid (Figs 15A; 18A), solitary to gregarious, on dried eudicotyledonous leaves and sticks in the forest litter.

DISTRIBUTION. — Originally from La Paz and Beni, Bolivia, as *M. haematocephalus* var. *rubicundus* (Singer 1965, 1976), it is now known from Southeastern Brazil.

DESCRIPTION

Pileus (Figs 15A; 18A)

2.5–20.5 mm diam., conical, hemispherical to convex, sulcate, center flat to umbonate, smooth or somewhat wrinkled, margin decurved to almost straight, edge entire to crenate; sometimes pale pinkish beige or salmon color (N₁₀Y₂₀M₄₀ to N₁₀Y₃₀M₅₀), often “Canna” pink or rose (N₂₀Y_{00–20}M_{40–60}), tending to very pale pinkish lilac (N₂₀Y₂₀M₆₀), then vibrant or ruby pink (N₄₀Y₅₀M₈₀), pinkish red (N₂₀Y₅₀M₇₀, N₂₀Y₆₀M₇₀ to N₂₀Y₇₀M₇₀), or pinkish brown “Egyptian red” (N₄₀Y_{50–60}M₆₀), sometimes pink with a slight hue of yellow (N₃₀Y₅₀M₅₀), or many times pale red or “Carnelian” (N₆₀Y_{40–60}M_{90–99}), light reddish brown (N_{50–60}Y_{90–99}M₉₀), with center darker red (N₇₀Y₆₀M₉₉) or pinkish brown (N₅₀Y₇₀M₇₀), or dark lilac (N₇₀Y₀₀M₉₉) or dark pink (N₇₀Y₄₀M₉₀); membranous, context thin (< 1 mm); glabrous, dry, dull, papyraceous to subvelutinous, non-hygrophanous.

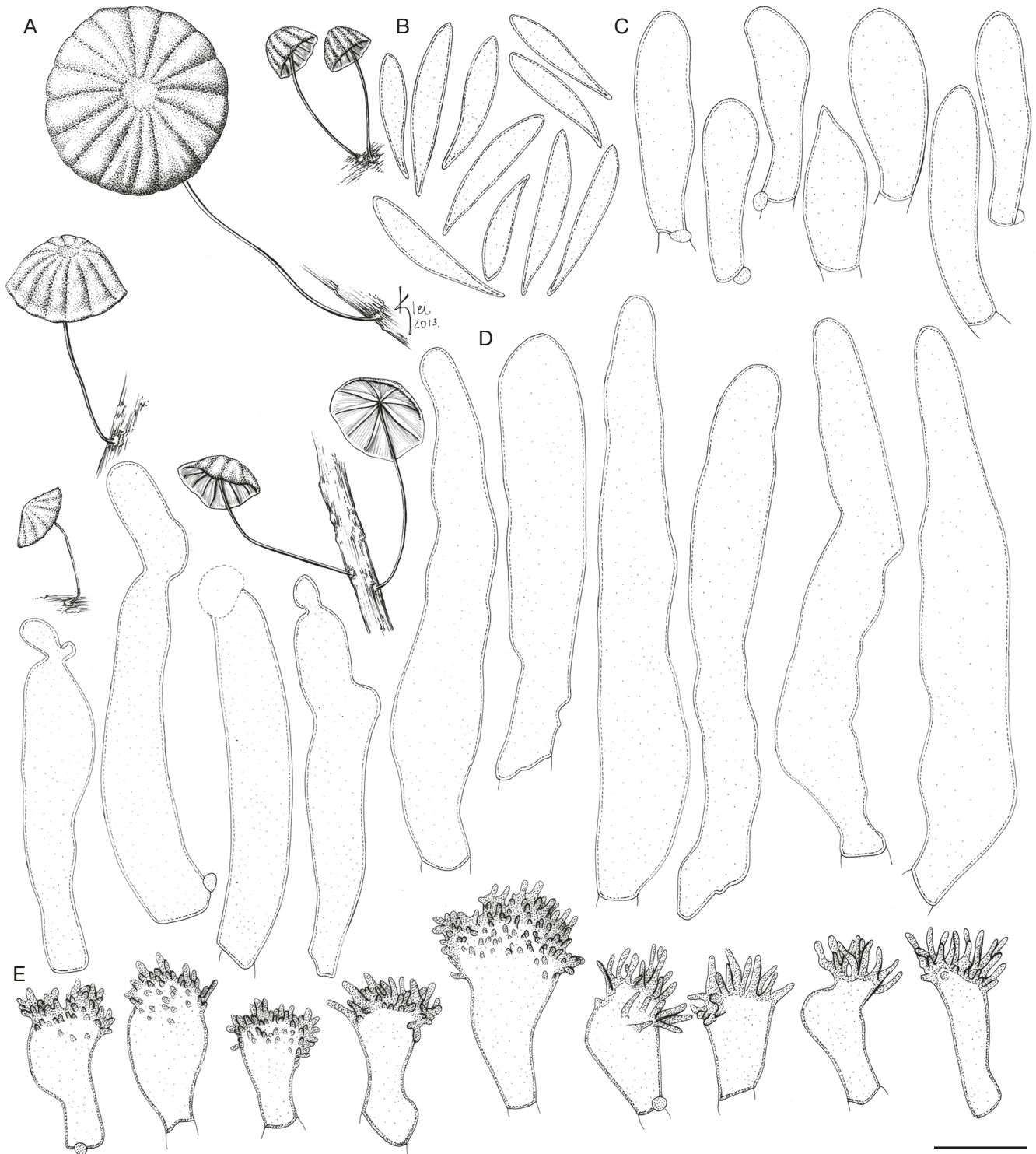


FIG. 16. — *Marasmius roseus* J.S. Oliveira, sp. nov. (JO352): **A**, basidiomata; **B**, basidiospores; **C**, basidioles; **D**, pleurocystidia; **E**, cheilocystidia. Scale bar: A, 10.5 mm; B-E, 10 μ m.

Lamellae (Figs 15A; 18A)

Free, adnexed, or sinuate to narrowly adnate, distant to subdistant, $L = 7-12$, equal, narrow to broad, straight, cultriform to ventricose, simple, $l = 0$ (-1), dull, smooth, white to cream ($N_{00}Y_{10}M_{00}$), or whitish pink ($N_{00}Y_{10}M_{10}$ or $N_{00}Y_{40}M_{10-20}$), edges even, non-marginate, interlamellar hymenium con-

colorous with the lamellae faces or partly concolorous with the pileus.

Stipe (Figs 15A; 18A)

8-63 $\times$ 0.3-0.8 mm, central, filiform, thin, equal, sometimes with broader base, with circular caliber, compressed when dried,

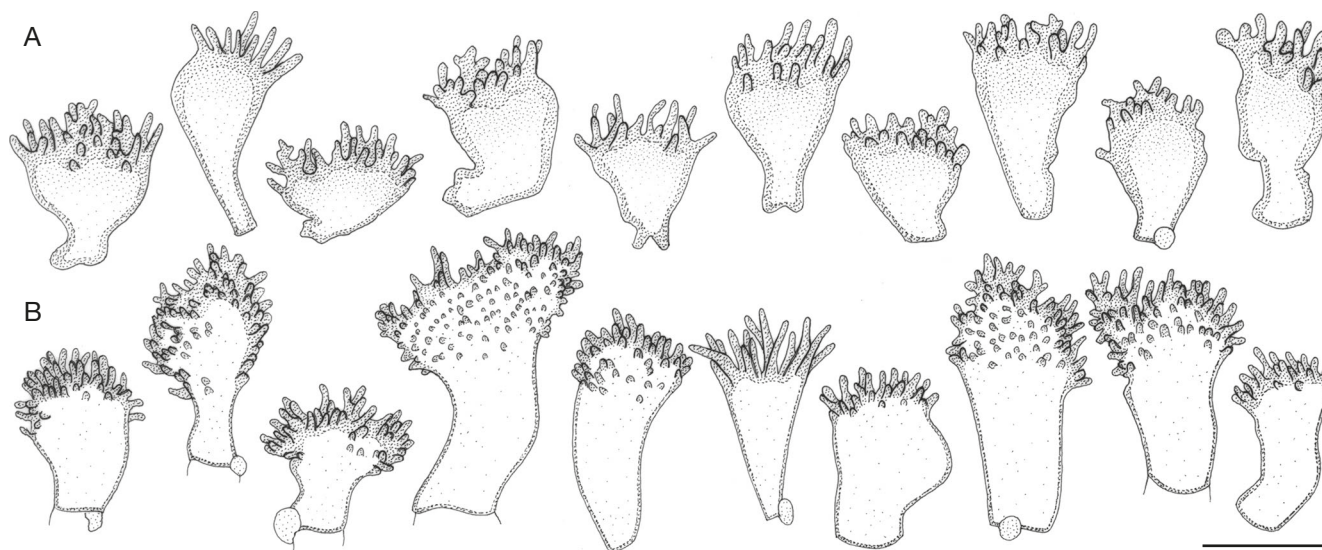


FIG. 17. — *Marasmius roseus* J.S. Oliveira, sp. nov. (JO352): **A**, Siccus-type broom cells of the pileipellis (type 1); **B**, Siccus- to Rotalis-type broom cells (type 2). Scale bar: 10 μ m.

chitinous, hollow; apex pale pink ($N_{00}Y_{10}M_{10}$ or $N_{30}Y_{50}M_{80}$) becoming bronze brown ($N_{40}Y_{60}M_{50}$ to $N_{80}Y_{70}M_{40}$) to dark brown ($N_{80}Y_{99}M_{30}$), or almost black at the base, glabrous, smooth, with a silky bright; with a scarce, white, tomentose basal mycelium.

Odor

Not distinctive.

Basidiospores (Fig. 18B)

(15.4–)16.2–21.7(–22) $\times$ 2.7–4.7(–5) μ m ($x_{rm} = 18$ –19.7 $\times$ 3.5–4 μ m; $x_{mm} = 19 [\pm 0.5] \times 3.8 [\pm 0.2] \mu$ m; $Q_{rm} = 4.6$ –5.5; $Q_{mm} = 5 [\pm 0.3]$; $n/s = 30/28$), exceptional spore size of JO316 with 18.3–23.9 $\times$ 3.1–4.8 μ m ($x_m = 21.3 [\pm 1.3] \times 3.9 [\pm 0.4] \mu$ m; $Q_m = 5.4 [\pm 0.6]$; $n/s = 30/1$), oblong, clavate to subfusoid, smooth, hyaline, thin-walled, inamyloid.

Basidia (Fig. 18C)

21.3–36.3 $\times$ 6–7.5 μ m, clavate, smooth, hyaline to slightly fuscous, thin-walled, 4-sterigmate, inamyloid.

Basidioles (Fig. 18D)

22–28.8 $\times$ 5.6–8.8 μ m, clavate, sometimes as cystidioles, smooth, hyaline to slightly fuscous, inamyloid.

Pleurocystidia (Fig. 18E)

(19.5–)25.6–71.7 $\times$ 5–12.3 μ m, broadly clavate, capitate, almost mucronate or acuminate, with a conical apex, or ampullaceous, or occasionally with apical, serial, slight constrictions, ending with a capitate, smooth, slightly fuscous, thin-walled, refractive, inamyloid, abundant.

Cheilocystidia (Fig. 18F)

Similar to the Siccus-type broom cells of the pileipellis; main body 11.3–20 $\times$ 5.6–10.6 μ m, clavate to slightly turbinate, wall

somewhat thick, hyaline; setulae more strictly apical, rarely somewhat divergent, erect, 2–7.5 $\times$ 0.5–1 μ m, cylindrical, digitiform or needle-like, simple, solid, hyaline to pale brown, regular in outline, apex obtuse to slightly acute.

Lamellar trama

Dextrinoid, irregular, interwoven, hyphae cylindrical, 1.5–10 μ m diam., regular in outline, branched, hyaline, thin-walled, smooth.

Pileus trama

Dextrinoid, similar to the lamellar trama, hyphae 2–10 μ m diam.

Pileipellis

Hymeniform, composed of Siccus-type broom cells (Fig. 18G), abundant, brown when grouped, bleaching in KOH solution; main body 7.5–20 $\times$ 6.3–11.3 μ m, clavate, turbinate, sometimes branched, ventricose to irregular in outline, hyaline, thin-walled to slightly thick-walled, weakly dextrinoid; setulae apical, erect, 2–7.5 $\times$ 0.6–1 μ m, cylindrical, digitiform or needle-like, simple, regular in outline, or slightly contorted, solid, hyaline to pale brown, apex obtuse to slightly acute.

Stipe trama

Dextrinoid especially the internal hyphae and those of the stipe apex, cortical hyphae parallel, cylindrical, regular in outline, 3.8–8 μ m diam., smooth, dark chestnut brown, yellowish brown when separated, thick-walled; internal hyphae regular in outline, 2.5–6.5 μ m diam., parallel.

Clamp connections

Present in all tissues, except in the cortical hyphae of the stipe.

REMARKS

The type collections were not examined in the present study as we had no reply from LIL herbarium in this pandemic

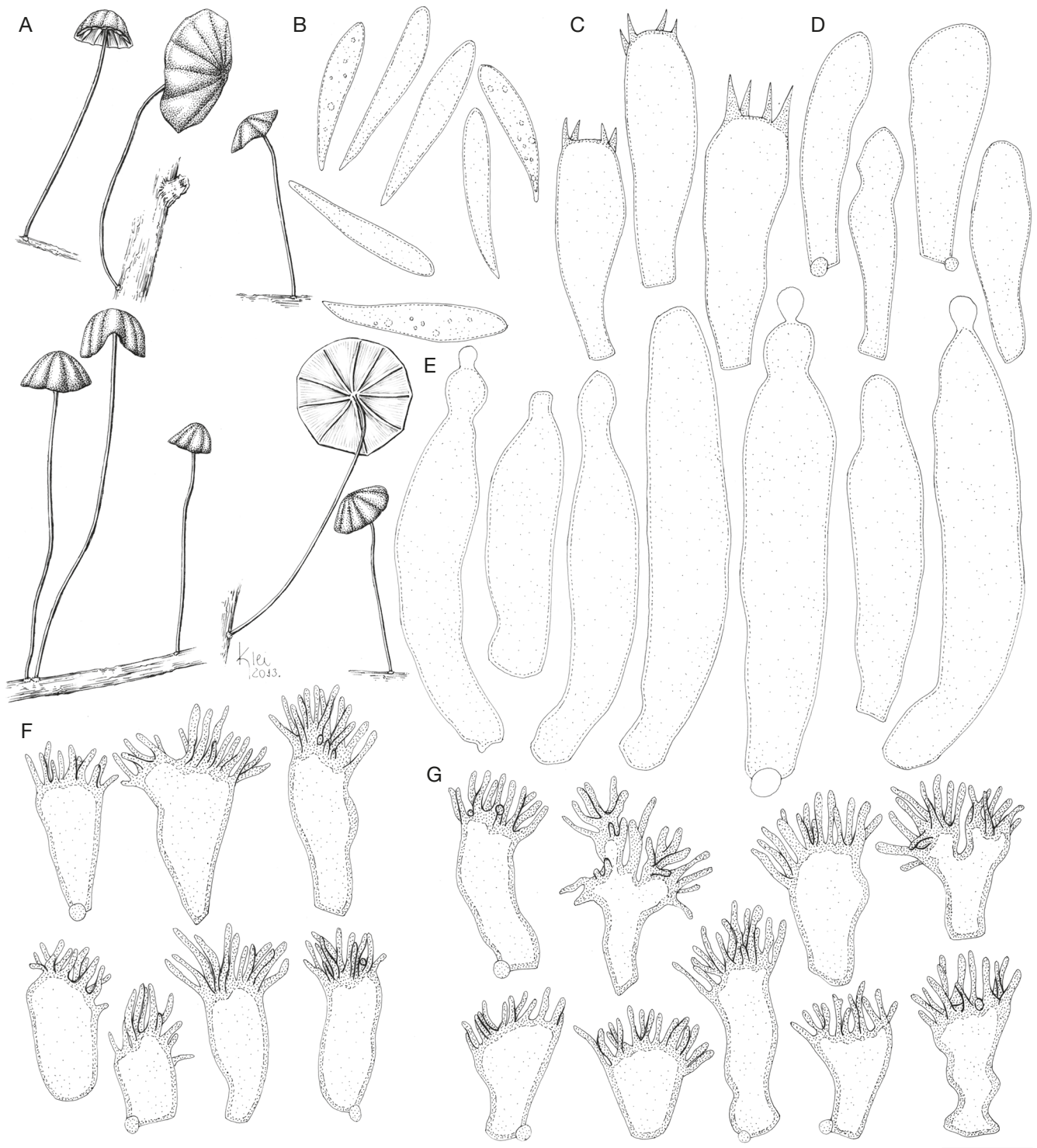


FIG. 18. — *Marasmius rubicundus* (Singer) J.S. Oliveira, stat. nov. (JO464): **A**, basidiomata; **B**, basidiospores; **C**, basidia; **D**, basidioles; **E**, pleurocystidia; **F**, cheilocystidia; **G**, Siccus-type broom cells of the pileipellis. Scale bar: A, 19.2 mm; B–G, 10 μ m.

time. However, Singer (1965, 1976) provided enough morphological data to unambiguously determine the examined specimens from São Paulo as authentic representatives of *M. haematocephalus* var. *rubicundus*. The pigmentation and size of the pileus, the number of lamellae, and the size of the basidiospores ($15\text{--}21 \times 4\text{--}4.8 \mu\text{m}$ in Singer [1976])

match the examined material. *Marasmius rubicundus* is 0.7–0.9% (nrITS) and 0.5–0.7% (nrLSU) dissimilar to *M. haematocephalus*, but cladogenesis reveals vicariance in sympatry. In the phylogenetic trees (Figs 1; 3) of nrITS, *M. rubicundus* (Singer) J.S. Oliveira, stat. nov., *M. aurantipitatus* J.S. Oliveira, sp. nov., and *M. haematocephalus*

are embedded within haemat_cp2a. In multilocus analyses, nrITS + nrLSU (Fig. 4) and nrITS + *rpb2* + *ef1-α* (Fig. 5), three species were resolved within this complex: *M. rubicundus* (Singer) J.S. Oliveira, stat. nov. sister to *M. auranticapitatus* J.S. Oliveira, sp. nov. with high support, and paraphyletic to *M. haematocephalus*.

Morphologically, *M. rubicundus* (Singer) J.S. Oliveira, stat. nov. is very similar to *M. haematocephalus*, only more conspicuously distinct by having a lighter pileus pigmentation and slightly smaller basidiospores ($x_{mm} = 18.9 [\pm 0.5] \times 3.8 [\pm 0.1] \mu m$, $Q_{mm} = 5 [\pm 0.2]$ vs $x_{mm} = 20.5 [\pm 0.3] \times 3.9 [\pm 0.2] \mu m$, $Q_{mm} = 5.2 [\pm 0.1]$). *Marasmius haematocephalus* s. str. regards the “*rubro-sanguineo*” of its protologue as deep or dark blood red or vinaceous (Singer 1958). In fact, the separation of *M. rubicundus* (Singer) J.S. Oliveira, stat. nov. and *M. haematocephalus* is very narrow in a broad sense, as they are nearly identical in other morphological characteristics. The species divergence is only evident in multilocus phylogenetic analyses where *M. rubicundus* (Singer) J.S. Oliveira, stat. nov. is rather closer to *M. auranticapitatus* J.S. Oliveira, sp. nov. (Figs 4; 5). The exceptional spore sizes of *JO316*, possibly a hybrid, strenghtens the plausibility of the most recent common ancestor between them. Although speciation is demonstrated, this ancestry trace or possible partial intercompatibility and gene flow are elements of a recent divergence. The strain *JO316* seems in a transitional/intermediate position (Fig. 4) along with other strains of *M. rubicundus* (Singer) J.S. Oliveira, stat. nov., but the basidiospores are more compatible with *M. auranticapitatus* J.S. Oliveira, sp. nov.. *JO316* and *JO226* highlights the powerful phylogenetic signal of spore sizes, an evident correlation between this characteristic and the genotype behind the species concepts.

The pale red pileus in *M. rubicundus* (Singer) J.S. Oliveira, stat. nov. is consistent with *M. pallescens*, but this later has shorter (11–17 μm) basidiospores (Singer 1976). For more color pictures showing variation of pileus pigmentation of *M. rubicundus* (Singer) J.S. Oliveira, stat. nov., see Appendix (Figs S7–S11). It is not similar to any of the heterotypic synonyms of *M. haematocephalus* listed in Singer (1976) but *M. rhodocephalus* Fr. (Fries 1851; Appendix) with type presumed lost but connection is not sharp.

Stirps *Siccus*

Based on Singer (1976), stirps *Siccus* includes *M. wilsonii* Murrill and *M. dennisii* Singer. In this paper, it seems consistent with *siccus_cp1* (Figs 1; 2) that includes *M. siccus* s. str. (Fig. 2), species that names the stirps. *Marasmius siccus* sensu Antonín *et al.* (2012) from South Korea, and the other lineages assigned to this species are included in *siccus_cp1*, then members of the stirps. This group seems to be strictly pantemperate and should also become a series in future studies with new data, more described specimens and the addition of more species that can be proposed based on *siccus_cp2a* and *siccus_cp2b* (Fig. 2).

Marasmius siccus (Schwein.) Fr.

Epicrisis Systematis Mycologici, seu Synopsis Hymenomycetum: 382 (Fries 1838). — Type: United States. North Carolina (Salem) or Pennsylvania (Bethlehem): “Salem-Beth.”, Schweinitz, no date (holo-, PH[PH00062046]) (based on Desjardin [1989]).

Agaricus siccus Schwein., *Schriften der Naturforschenden Gesellschaft zu Leipzig* 1: 84 (Schweinitz 1822).

Chamaeceras siccus (Schwein.) Kuntze, *Revisio generum plantarum* (Leipzig) 3 (3): 457 (Kuntze 1898).

REFERENCE STRAINS. — United States. Tennessee, 19.VII.1991, D.E. Desjardin DED5255 (SFSU[SFSU-F-029078]; GenBank: FJ431272); J.N. Hill JNH010 (TENN[TENN-F-070783]; GenBank: MF686511) as *Marasmius fulvoferrugineus*; V. Antonín (BRNM[BRNM 552709]; GenBank: HQ607384), published in Antonín *et al.* (2012).

REMARKS

Marasmius siccus s. str. regards DED5255, a topotype specimen collected and determined by Dr Dennis E. Desjardin, as the most authentic for the species in the phylogenetic trees (Figs 1; 2). The species is known by the umbrella-like basidiomata (the orange pinwheel) that are somewhat larger and more robust than *M. haematocephalus*, with a membranous, radially sulcate, yellow-orange-brown pileus (2.5–27 mm diam.) with darker center, a filiform to cylindrical, glabrous, brown stipe ([17–]23–62[–85] $\times$ 0.2–1.25 mm) with a floccose basal mycelium, and distant, whitish (15–22) lamellae (lamellulae often absent or 1–2) (Gilliam 1976; Desjardin 1989). Desjardin (1989: 671–674) revised the holotype that singly had oblong, 15.2–20.4 $\times$ 3.4–4 μm ($n = 13$) basidiospores, refractive, well-developed, 32–56 $\times$ 5.5–8 μm pleurocystidia, and a pileipellis composed of orangish to brownish *Siccus*-type broom cells. His review of the type specimen (Desjardin 1989: 671–674) as well as the description based on fresh collections (Desjardin 1989: 246–249) agreed with Gilliam (1976), especially in the dimensions of basidiospores (15.2–20.8 $\times$ 3.2–4.6 μm vs [13.3–]16–21[–23] $\times$ 2.8–4.2[–5] μm , respectively) and of pleurocystidia (32–60 $\times$ 5–9 μm vs 23–67[–81] $\times$ 3–14 μm , respectively). Besides the holotype, examined collections from the United States included in Desjardin (1989) were from Connecticut, Delaware, Idaho, Illinois, Indiana, Kansas, Maryland, Michigan, Minnesota, Nebraska, New Hampshire, New York, North Carolina, Ohio, Pennsylvania, Rhode Island, Tennessee, Vermont, Virginia, West Virginia, Wisconsin, along with one collection from Japan. Gilliam (1976) also included to the list of states in United States collections from the District of Columbia, Massachusetts and Missouri, besides collections from Ontario (Canada) and Japan. So, the North American collections are the preferred starting point to delimit *M. siccus*. The pantemperate species concept recognizes the taxon as widespread across the subarctic, boreal and temperate zone of the northern hemisphere with circumpolar distribution (Noordeloos 1987; Antonín & Noordeloos 2010) based on collections from Canada, Finland, Norway, Republic of Korea, Russia, Sweden, and United States. This pantemperate *M. siccus* would cover specimens

with larger spores ($15\text{--}23 \times 4\text{--}5 \mu\text{m}$ in Noordeloos [1987] and $15\text{--}23.5 \times [2.5\text{--}]3\text{--}4.5\text{--}[5] \mu\text{m}$ in Antonín & Noordeloos [2010]) and larger pleurocystidia ($25\text{--}70 \times 5\text{--}10 \mu\text{m}$ Noordeloos [1987] and $25\text{--}80 \times 5\text{--}21.5 \mu\text{m}$ in Antonín & Noordeloos [2010]) than those predominantly from North America (Gilliam 1976; Desjardin 1989). Noordeloos (1987) and Antonín & Noordeloos (2010) also included collections from North America that should be *M. siccus* s. str. This species has been referred as a very variable species, or with a broad concept, or one of the most misapplied binomials of *Marasmius* (Gilliam 1976; Desjardin 1989; Antonín & Noordeloos 2010), usually confused with *M. bellipes* Morgan, *M. borealis* Gilliam, *M. glabellus* Peck, *M. ferrugineus*, *M. fulvoferrugineus* Gilliam, *M. pulcherripes* and *M. robinianus* Gilliam.

Based on nrITS, the Nearctic *M. siccus* s. str. (DED5255) is 1.6–3.5 dissimilar to the Palearctic *M. siccus* lineages. Strains of *M. siccus* s. str. without preserved basidiomata collection, solely based on the GenBank accessions are: GU328526 (United States, Michigan, $44^{\circ}48'N$, $85^{\circ}48'W$, date unshown, environmental sample “man22_litter_H12” in Edwards & Zak [2010]). Dedicated to the *M. siccus* complex, a review study of the involved collections in the phylogenetic analyses herein and/or fresh collections should be carried out considering *M. siccus* s. str. and the other close/cryptic species across the temperate zone based on *siccus_cp1* (Figs 1; 2).

Series *Pulcherripes* J.S. Oliveira & Moncalvo

Persoonia 44: 274 (Oliveira *et al.* 2020).

Basidiomata marasmiod (umbrella-like), small- to medium-sized. Pileus membranous, campanulate to convex, smooth to shallowly sulcate, papillate ($1.4\text{--}33 \text{ mm}$ diam). Lamellae distant to subdistant. Stipe thin-cylindrical, dark-coloured, with a scarce basal mycelium. Basidiospores medium-sized, oblong ($11\text{--}17 \mu\text{m}$ long, $x_m = 12.5\text{--}15.3 \mu\text{m}$, $Q_m = 3.1\text{--}4.2$). Pleurocystidia present (not clear in some cases), small- to medium-sized (up to $65 \mu\text{m}$ long). Pileipellis composed of *Siccus*-type broom cells. Habit solitary to gregarious, on dead, eudicotyledonous leaves and twigs.

TYPE SPECIES. — *Marasmius pulcherripes*.

REMARKS

Marasmius pulcherripes was originally described from United States. Some strains determined after this species from Northwest Arkansas (MT032485) and Boston Harbor Islands (MF161270; Haelewaters *et al.* 2018), United States, branched in clade *Pulcherripes* (Fig. 1). This placement indicates the plausibility of the series.

Marasmius cf. *pallenscens* Murrill (Figs 15C; 19)

North American Flora 9 (4): 261 (Murrill 1915). — Type: **Puerto Rico**. Rio Piedras, 18.VIII.1912, *J. R. Johnston* 556 (NY[NY774585]).

EXAMINED MATERIAL. — **Brazil**. São Paulo State, Iporanga City, Parque Estadual Turístico do Alto Ribeira, Reserva Betary, 05.XII.2011,

J.J.S. Oliveira JO426 (SP[SP 446078]!); 28.II.2012, *D.E. Desjardin* & *C. Stevani* DED8673 (SP[SP 445666]!).

HABIT AND SUBSTRATE. — Marasmiod (Figs 15C; 19A1), gregarious, close, scattered to solitary on dried eudicotyledonous leaves and sticks in the forest litter.

DISTRIBUTION. — Originally described from Puerto Rico (Murrill 1915), it is also reported from Venezuela (Dennis 1961; Singer 1965, 1976; Pegler 1983) and Martinique (Pegler 1983). If the identity of this “ruby pink form” is confirmed as conspecific, this would be the first record from Brazil.

DESCRIPTION

Pileus (Figs 15C; 19A1, A2)

$5\text{--}15\text{--}(20) \text{ mm}$ diam., obtusely conical to broadly convex, or plano-convex, sulcate, center flat or slightly umbonate, shallowly depressed when fully matured, margin decurved to applanate, edge entire to slightly crenate; at first ruby overall (12E7–8), then remaining ruby pink ($N_{30}Y_{30\text{--}50}M_{99}$) to pinkish red ($N_{30}Y_{70\text{--}90}M_{90}$), or fainting to greyish ruby (12D6–7), with a dark purplish red ($N_{70}Y_{40\text{--}60}M_{99}$) or ruby (12E7–8) center; membranous, context thin ($< 1 \text{ mm}$); glabrous, dry, dull, subvelutinous, non-hygrophanous.

Lamellae (Figs 15C; 19A1, A2)

Free to adnexed, few toothed seceding, distant, $L = 6\text{--}16$, equal, broad (up to 1.5 mm), slightly ventricose, simple, $l = 0\text{--}(1)$, opaque, smooth, white, edges even, non-marginate, interlamellar hymenium paler than the pileus or ruby.

Stipe (Figs 15C; 19A1)

$19\text{--}55 \times 0.3\text{--}0.8 \text{ mm}$, central, thick filiform, equal, or broadening toward apex, with circular caliber, chitinous, hollow; apex whitish pink ($N_{10}Y_{20\text{--}40}M_{20}$), abruptly becoming reddish brown ($N_{80}Y_{99}M_{60\text{--}80}$) to dark brown ($N_{90}Y_{99}M_{80\text{--}99}$), or almost black at the base, glabrous, smooth, with a silky bright; subinsititious or with a scarce, white, tomentose to strigose basal mycelium.

Odor

Not distinctive.

Basidiospores (Fig. 19B)

$(11.1\text{--})12.3\text{--}17.3 \times (3.2)3.7\text{--}5 \mu\text{m}$ ($x_{rm} = 14.7\text{--}15 \times 4.2 \mu\text{m}$; $x_{mm} = 14.9 [\pm 0.2] \times 4.2 \mu\text{m}$; $Q_{rm} = 3.6$; $Q_{mm} = 3.6$; $n/s = 30/2$), oblong, clavate, subfusoid to fusoid, smooth, hyaline, thin-walled, inamyloid.

Basidia (Fig. 19D)

$20\text{--}26.7 \times 4.8\text{--}7.4 \mu\text{m}$, clavate, smooth, hyaline, thin-walled, with four short, verruciform sterigmata, inamyloid.

Basidioles (Fig. 19C)

$(15.2\text{--})18.7\text{--}28 \times (3.8\text{--})4.5\text{--}6.9\text{--}(7.5) \mu\text{m}$, clavate, smooth, hyaline, inamyloid.

Pleurocystidia (Fig. 19E)

$31.4\text{--}47 \times 7.2\text{--}10.6 \mu\text{m}$, mostly clavate, or broadly clavate, some slightly lageniform or ventricose, sometimes apically

capitate, papillate or mucronate, or with digitiform projection, occasionally wavy with shallow constrictions, smooth, hyaline to somewhat fuscous, thin-walled, refractive, inamyloid.

Cheilocystidia (Fig. 19F)

Similar to the Siccus-type broom cells of the pileipellis, but hyaline and with thinner walls; main body $7.6\text{--}19.8 \times 5.2\text{--}9.9 \mu\text{m}$, clavate to slightly turbinate, seldom branched or lobulate, thin-walled, inamyloid; setulae apical, erect, $3.5\text{--}7.1 \times 0.5\text{--}1.1 \mu\text{m}$, cylindrical or filiform, needle-like, regular in outline, simple, solid, hyaline, apex acute.

Lamellar trama

Strongly dextrinoid, irregular, interwoven, hyphae cylindrical, $1.2\text{--}6.1 \mu\text{m}$ diam., regular in outline, hyaline, smooth, thin-walled.

Pileus trama

Dextrinoid, similar to the lamellar trama, hyphae $2.8\text{--}6.9\text{--}8.7 \mu\text{m}$ diam., branched.

Pileipellis

Hymeniform, composed of Siccus-type broom cells (Fig. 19G), pale brown, but with rare more deeply pigmented cells, bleaching in KOH solution; main body $9\text{--}18.6 \times 4.1\text{--}9.5\text{--}(15) \mu\text{m}$, cylindrical thin, clavate, turbinate, sometimes almost pedicellate, pale brown, later hyaline, thin-walled to slightly thick-walled (firm-walled), inamyloid or weakly dextrinoid; setulae apical, erect, $2.5\text{--}7.7 \times 0.7\text{--}1.5 \mu\text{m}$, cylindrical or filiform, needle-like, rarely digitiform, simple, regular in outline, solid, pale brown, apex tapered, obtuse to mostly acute.

Stipe trama

Dextrinoid, some strands apparently inamyloid, stipitipellis and cortical hyphae parallel, packed, cylindrical, regular in outline, $2.6\text{--}9 \mu\text{m}$ diam., sometimes branched, smooth, those of the superficial layer highly melanized, dark chestnut brown, brown at the cortex, thick-walled; internal hyphae regular in outline, $2.6\text{--}6.8 \mu\text{m}$ diam., hyaline, thin-walled.

Clamp connections

Present in all tissues.

REMARKS

Murrill (1915) would have named *Marasmius pallescens* based on the pale-red pileus (5–8 mm broad), fading to isabelline on drying. Dennis (1961) reported the species from Venezuela with lilac pileus (7 mm diam.). Singer (1965, 1976) studied both the type from Puerto Rico (18 August 1912, *J. R. Johnston* 556) and the collection from Venezuela (20 June 1958, *Dennis* 117) and reported a pale red or light lilac (5–8 mm broad.) pileus when fresh (Murrill 1915; Dennis 1961), but reddish brown when dried. Pegler (1983) examined the same collections, adding a third from Dominique, and reported a “Pale Flesh Colour” pileus (5–15 mm diam.), sometimes paling to buff but retaining a slightly darker disc. All of them agreed for the campanulate sulcate pileus and distant, white,

about 10 lamellae (10–14 in Pegler 1983) in the protologue. These collections from Brazil agree in nearly all characteristics but differs in the ruby pink to pinkish red (Fig. 15C), larger pileus (11–15 mm diam.). The size of the basidiospores perfectly agree with Singer (1976) and Pegler (1983), but those in Dennis (1961) are shorter ($11\text{--}14 \times 3.5 \mu\text{m}$); the shape and size of pleurocystidia are nicely compatible. The size of basidia and basidioles is slightly larger in our collections. Despite the distinctions mentioned above, the examined collections match the morphological concept of the species.

Singer (1976) commented that “at first sight one might be inclined to consider this species one of the numerous color variants of *Marasmius haematocephalus*”. Indeed, *M. pallescens* seems very similar to *M. haematocephalus*, especially considering these possible collections from Brazil. However, both basidiospores and pleurocystidia are clearly shorter and the lamellae are broader and ventricose in *M. pallescens*. This species is also similar to *M. panerythrurus* Singer, but this later differs by having more deeply pigmented pileus (purple red with paler “copper leaf” margin), by having marginate, pinkish lamellae, by having smaller basidiospores ($13\text{--}14.7 \times 3.5\text{--}4.2 \mu\text{m}$), and by having larger pleurocystidia ($20\text{--}62 \times 6.8\text{--}9.8 \mu\text{m}$) (Singer 1976).

Marasmius cf. *pallescens* is similar to *M. pulcherripes* “the pinkish-red form” (Desjardin 1989), and originally described from Nearctic (New York, United States). *Marasmius pulcherripes*, however, has more numerous lamellae (15–16), more colorful stipe, slightly smaller basidiospores ($[10.4\text{--}]12\text{--}16 \times 3.2\text{--}4.6 \mu\text{m}$), and regular lamellar trama. Antonín *et al.* (2012) reported *M. pulcherripes* from South Korea with marginate lamellae and larger pleurocystidia ($37\text{--}65 \times 7.0\text{--}12 \mu\text{m}$), and this branched as a distinct lineage closer to *M. siccus* species complex (siccus_cp1) than to *M. haematocephalus* species complex (haemat_cp1) in Fig. 1. Unfortunately, no DNA sequences were obtained from the examined collections here as *M. cf. pallescens*. Because of the morphological similarity, one may predict it would branch closely related to *M. pulcherripes* sensu Antonín *et al.* (2012). Based on morphology, *M. cf. pallescens* is classified in ser. *Pulcherripes* (Oliveira *et al.* 2020) along with *M. pallescens*, *M. panerythrurus* and *M. rhodopurpureus*.

DISCUSSION

PANTROPICAL AND PANTEMPERATE SPECIES?

Morphology (MSR, Taylor *et al.* 2006) has led taxonomists to accept a pantropical *M. haematocephalus* and a pantemperate *M. siccus*. Would molecular phylogeny (PSR, Taylor *et al.* 2006) support this understanding?

According to the resulting trees (Figs 1–3), the pantropical and pantemperate species concepts are inadequate for the species level and do not represent properly the species diversity *tempo* of the involved lineages in their evolutionary history. The “pantropical *M. haematocephalus*” and “pantemperate *M. siccus*” are groups harboring very morphologically close or cryptic species. Quoting Taylor *et al.* (2006), “if the rate of

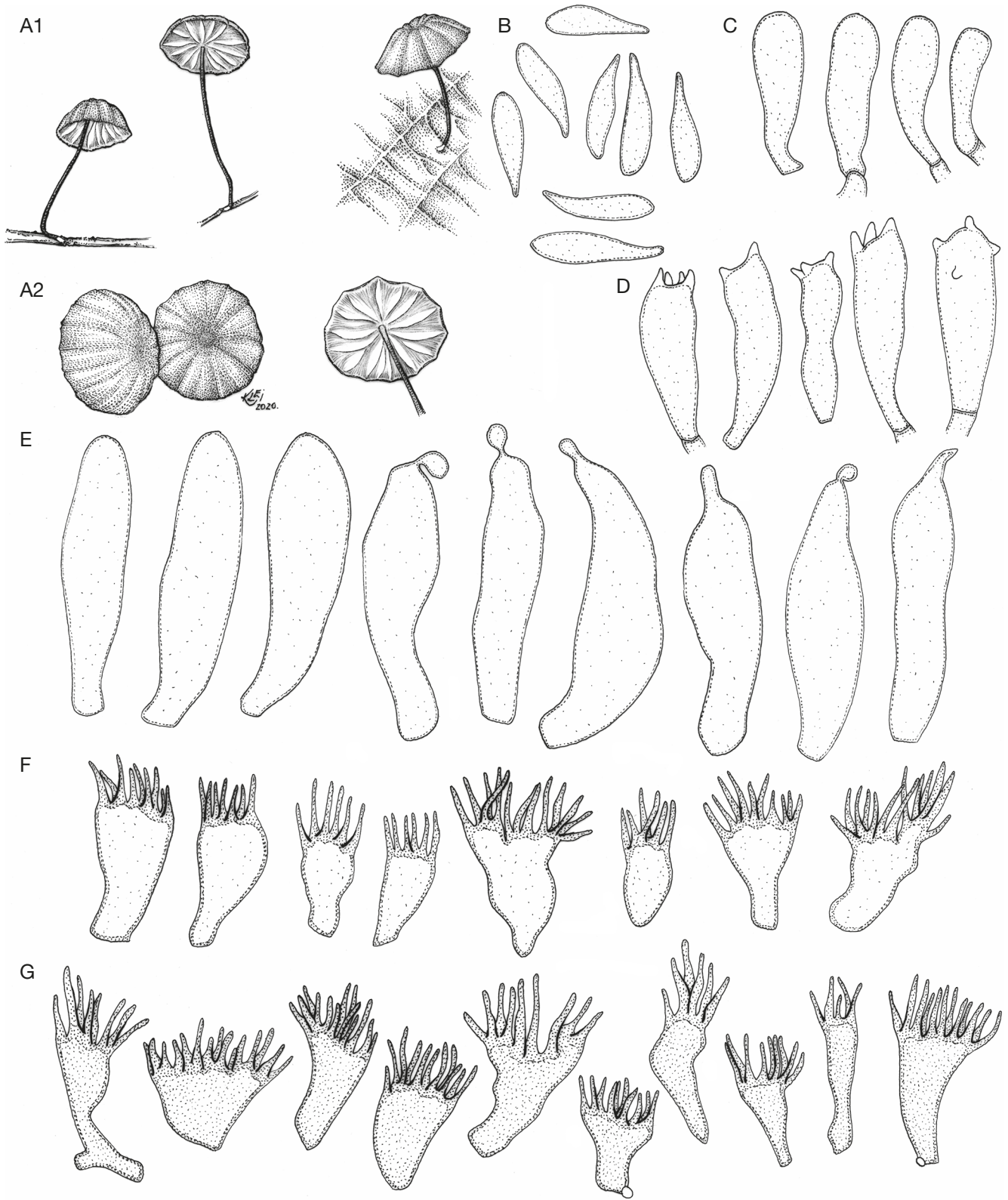


FIG. 19. — *Marasmius cf. pallescens* Murrill (JO426): **A1, A2**, basidiomata; **B**, basidiospores; **C**, basidioles; **D**, basidia; **E**, pleurocystidia; **F**, cheilocystidia; **G**, Siccus-type broom cells of the pileipellis. Scale bar: A1, 12.5 mm; A2, 10.5 mm; B-G, 10 µm.

change of morphological characters is slow when compared with genetic or reproductive isolation, fewer species will be recognized by morphology and their ranges will appear to be

larger”, even more for microbial eukaryotes such as Fungi. The trees indicate at least 23 species hidden in the *M. haematocephalus* and *M. siccus* complexes. With few exceptions

KEY TO THE *MARASMIUS* SPP. INVOLVED IN THIS STUDY

1. Basidiospores up to 18 µm long, cheilocystidia never dimorphic 2
 — Basidiospores longer than 18 µm and/or cheilocystidia dimorphic 5
2. Pileus red pink to red-purple 3
 — Pileus more light or greyish orange or brown 4
3. Lamellae marginate, basidiospores (11-)12-15(-16) × 3-4.5(-5) µm *M. pulcherripes* Peck^a
 — Lamellae non-marginate, basidiospores 12.3-17.3 × 3.7-5 µm *M. cf. pallescens* Murrill
4. Pileus 4-15 mm diam., lamellae non-marginate, basidiospores (16-)17-18(-19) × 4-5 µm, pleurocystidia 46-53 × 10-15 µm *M. aff. pallescens*^b
 — Pileus 13-25 mm diam., lamellae marginate, basidiospores 14.5-17.5(-18) × 3.5-4.02(-4.5) µm, pleurocystidia (50-)55-68(-72) × (7-)8-9(-9.5) µm *M. siccus* (Schwein.) Fr.^c
5. Pileus deep bright orange, fulvous-ferruginous, brownish orange to reddish brown or fulvous “tawny” 6
 — Pileus with different pigmentation 9
6. Pileus bright orange to fulvous, pleurocystidia somewhat thick-walled *M. bambusinus* (Fr.) Fr.
 — Pileus brownish orange to reddish brown, pleurocystidia thin-walled 7
7. Pileus up to 18 mm diam., stipe more robust (0.3-1 mm diam.), lamellae free to almost adnexed, basidiospores 15-19 × 3-5 µm *M. gardneri* Singer
 — Pileus about 10 mm diam., stipe thinner (about 0.3 mm diam.), lamellae free to adnate, basidiospores larger 8
8. Lamellae free to emarginate with a small tooth, marginate, basidiospores 14-20 × 4.0-5.5 µm, on dead leaves, from temperate Asia *M. ferrugineus* Berk. & M.A.Curtis^d
 — Lamellae free to adnate, non-marginate, basidiospores 15-21 × 2.8-4.3 µm (18-22 × 4.5-6.0 µm), on woody substrate, Tropical South America *M. ferrugineus*^e
9. Pileus strictly pale yellowish to brownish orange and from temperate forests (pantemperate) 10
 — Pileus with various pigmentations and strictly from tropical forests (pantropical) 11
10. From the Nearctic, basidiospores 16-20.4 × 3.4-4 µm, pleurocystidia 32-56 × 5.5-8 µm *M. siccus*^f
 — From the Palearctic, basidiospores (15-)18-25 × 3.5-5 µm, pleurocystidia 38-72(-80) × 5.0-12(-15) µm *M. siccus*^g
11. Cheilocystidia monomorphic 12
 — Cheilocystidia dimorphic 20
12. Pileus pale brown, basidiospores up to 26 µm in length *M. castanocephalus* J.S. Oliveira, sp. nov.
 — Pileus differently pigmented, basidiospores up to 24 µm in length 13
13. Pileus dark purple to dark violet (blackish) *M. haematocephalus* (Mont.) Fr.^h
 — Pileus with paler pigmentation 14
14. Pileus pale to yellowish orange, basidiospores 20.5-24 µm in length
 *M. auranticapitatus* J.S. Oliveira, sp. nov.
 — Pileus never orange but red-pink-lilac-purple, basidiospores shorter, up to 22 µm in length 15
15. Pleurocystidia very elongate, up to 75 µm in length, pileipellis with two kinds of broom cells
 *M. roseus* J.S. Oliveira, sp. nov.
 — Pleurocystidia shorter, up to 60 µm, pileipellis with uniform broom cells 16
16. Pleurocystidia short (37-42 µm), basidiospores 18.5-23(-25) × 3.5-5(-6) µm .. *M. asiaticus* Mesic & Tkalcecⁱ
 — Pleurocystidia longer than 42 µm, basidiospores shorter (up to 22 µm) 17
17. Stipe short, 9-20 mm in length, curved, pleurocystidia inflated up to 18.8 µm broad, basidiospores up to 20 µm in length *M. coasiaticus* J.S. Oliveira, sp. nov.
 — Stipe elongate, up to 60 mm in length, erect, pleurocystidia up to 11 µm broad, basidiospores reaching 21-22 µm long 18
18. Lamellar trama regular, pileipellis mottled *M. haematocephalus*^j
 — Lamellar trama irregular, pileipellis uniform 19

19. Pileus deep blood red, basidiospores $x_{mm} = 20.4 (\pm 0.3) \times 3.9 (\pm 0.1) \mu m$, $Q_{mm} = 5.3 (\pm 0.1)$ *M. haematocephalus*
 — Pileus more pale red, Canna pink or rose, or vibrant ruby pink, basidiospores $x_{mm} = 18.9 (\pm 0.5) \times 3.8 (\pm 0.1) \mu m$, $Q_{mm} = 5 (\pm 0.2)$ *M. rubicundus* (Singer) J.S. Oliveira, stat. nov.
20. Pileus yellowish orange or with a pale brownish yellow disc and nearly white margin *M. haematocephalus* “f. *luteocephalus*”^k
 — Pileus with red, violet, olive, greyish blue or brown pigments 21
21. Pileus 1-5 mm diam., dark brown all over *M. haematocephalus* “f. *atrobrunneus*”^l
 — Pileus larger than 5 mm diam., with red, violet, purple, olive, or greyish blue hues 22
22. Pileus olive to greyish blue all over when young, disc often with red, orange or reddish purple tints in age *M. haematocephalus* “f. *variabilis*”^m
 — Pileus lacking olive and greyish blue tints 23
23. Pileus typically 10-20(-30) mm diam., margin and mid disc lilac and center deep lilac *M. haematocephalus* “f. *robustus*”ⁿ
 — Pileus typically smaller than 10 mm diam., deep reddish brown to maroon or deep violet-purple 24
24. Pileus deep reddish brown to maroon color; basidiomata often on eudicot leaves *M. haematocephalus* “f. *haematocephalus*”^o
 — Pileus magenta, deep violet-purple or dark purple; basidiomata often on bamboo leaves 25
25. Basidiospores $13-14.5(-15) \times (2.5-)3.5-4(-5) \mu m$ *M. haematocephalus* f. 1^p
 — Basidiospores $(18-)18.5-22 \times 3.5-4.2(-4.7) \mu m$ *M. haematocephalus* “f. *atroviolaceus*”^q

^a, *Marasmius pucherriipes* Peck based on collections from South Korea (Antonin et al. 2012); ^b, *Marasmius* aff. *pallescentis* Murrill based on *N. Wannathes* 424 from Thailand (Wannathes et al. 2009); ^c, *Marasmius siccus* (Schwein.) Fr. based on AKD 300/2015 and AKD 301/2015 from India (Dutta 2017); ^d, *Marasmius ferrugineus* Berk. & M.A. Curtis based on collections from South Korea (Antonin et al. 2012); ^e, *Marasmius ferrugineus* based on the type material from Brazil (Gardner, Berkeley Herbarium set, K) in Singer (1976); ^f, *Marasmius siccus* based on Desjardin (1989); ^g, *Marasmius siccus* based on V. Antonin 07.97 & R. Ryoo and collections from South Korea (Antonin et al. 2012); ^h, *Marasmius haematocephalus* (Mont.) Fr. based on Yee-Shin Tan TYS 523 from Malaysia (Tan et al. 2009); ⁱ, *Marasmius asiaticus* Mesic & Tkalec based on the type collection (TYS 478) from Malaysia (Tan et al. 2009); ^j, *Marasmius haematocephalus* based on J.E. Shay 202 and additional collections from Madagascar (Shay et al. 2017); ^k, *Marasmius haematocephalus* “f. *luteocephalus*” based on *N. Wannathes* 310 from Thailand (Wannathes et al. 2009); ^l, *Marasmius haematocephalus* “f. *atrobrunneus*” based on *N. Wannathes* 117 and additional collections from Thailand (Wannathes et al. 2009); ^m, *Marasmius haematocephalus* “f. *variabilis*” based on *N. Wannathes* 430 and additional collections from Thailand (Wannathes et al. 2009); ⁿ, *Marasmius haematocephalus* “f. *robustus*” based on *N. Wannathes* 433 and additional collections from Thailand (Wannathes et al. 2009); ^o, *Marasmius haematocephalus* “f. *haematocephalus*” based on CAL 1518 and additional collections from India (Dutta 2017), and based on *N. Wannathes* 428 and additional collections from Thailand (Wannathes et al. 2009); ^p, *Marasmius haematocephalus* f. 1 based on AKD 201/2014 from India (Dutta 2017); ^q, *Marasmius haematocephalus* “f. *atroviolaceus*” based on AKD 06/2011 from India (Dutta 2017), and based on *N. Wannathes* 413 from Thailand (Wannathes et al. 2009).

discussed below, all taxa included in the *M. haematocephalus* MSR formed a monophyletic group based on tropical strains (haemat_cp1) and taxa included in the *M. siccus* MRS based on all temperate strains grouped in monophyly (siccus_cp1). *Marasmius haematocephalus* complex (haemat_cp1) seems strictly pantropical while *M. siccus* complex (siccus_cp1) seems strictly pantemperate (Fig. 1), respectively represented by the red and blue areas, their putative range of distribution across forested terrestrial areas based on their reports (Appendix: Fig. S1). This hypothesis also predicts two possible main connecting interfaces between haemat_cp1 and siccus_cp1: 1) Florida-Caribbean; and 2) China.

Marasmius siccus complex (siccus_cp1) consists of at least five or six close or cryptic species (Figs 1; 2). The strain DED5255 (Tan et al. 2009), a topotypical specimen (D.E. Desjardin, pers. comm.), is considered the authentic *M. siccus* (s. str.) along with other four strains from United States (Nearctic) forming the highly supported branch (Fig. 2). The other four or five taxa are from temperate Asia (Palearctic) into siccus_cp2a and siccus_cp2b. The strains of siccus_cp2a were sampled from China, Russian Far East (excepting LE253535 from Southern Ural that may represent a distinct species and NN050245 with

uninformed specific site) and South Korea and strains from this last country are morphologically described in Antonin et al. (2012). No morphological data was found for the other strains. The strains of the unsupported siccus_cp2b are from China and Russia (Siberia). At this point, based on the species concept accepted in this study, *M. siccus* is confirmed only in the Nearctic.

There are at least 18 different but close or cryptic species within the *M. haematocephalus* complex (haemat_cp1) (Figs 1; 3). Four, *M. auranticapitatus* J.S. Oliveira, sp. nov., *M. castanoccephalus* J.S. Oliveira, sp. nov., *M. coasiaticus* J.S. Oliveira, sp. nov. and *M. roseus* J.S. Oliveira, sp. nov. are from Brazil (Neotropical realm). *Marasmius rubicundus* (Singer) J.S. Oliveira, stat. nov. is elevated from *M. haematocephalus* var. *rubicundus*. A sixth species is *M. asiaticus* (synonym: *M. distantifolius*) from Malaysia. Twelve other species are named after *M. haematocephalus* (Fig. 3): one from Brazil, one from Malaysia (Tan et al. 2009), two from Madagascar (Shay et al. 2017), six others consist of informal “forms” of *M. haematocephalus* from Thailand (Wannathes et al. 2009), and two from India (Dutta 2017). The most authentic *M. haematocephalus* (s. str.) is represented by the strain JO533 (Fig. 13A) depicted

by a black arrow in the DATASET 2b tree (Fig. 3), collected from the same region of the holotype and the Singer's topology. Yet, *M. haematocephalus* s. str. is part of a deeper species complex along with *M. auranticapitatus* J.S. Oliveira, sp. nov. and *M. rubicundus* (Singer) J.S. Oliveira, stat. nov. within haemat_cp2a (Fig. 3). *Marasmius haematocephalus* s. str., *M. rubicundus* (Singer) J.S. Oliveira, stat. nov. and *M. auranticapitatus* J.S. Oliveira, sp. nov. are only fully resolved within haemat_cp2a integrating the multilocus 'nrLSU + nrITS' and 'nrITS + *rpb2* + *ef1-α* (introns included)' analyses of DATASETS 3 and 4 (Figs 4; 5), respectively. *Marasmius rubicundus* (Singer) J.S. Oliveira, stat. nov. and *M. auranticapitatus* J.S. Oliveira, sp. nov. are sister, then sister to *M. haematocephalus*. At this point, *M. haematocephalus* s. str. is confirmed only in the Neotropical realm as well as haemat_cp2a (Fig. 3).

Sister to subclade haemat_cp2a, haemat_cp2b is part Afro-tropical and part Indo-Malayan. Within haemat_cp2b, there are possibly three species named as *M. haematocephalus* from India, Madagascar, and Malaysia. The Indian (Dutta 2017) and Malaysian (Tan *et al.* 2009) lineages are very similar in pileus pigmentation (greyish magenta to deep magenta or dark purple overall vs dark purple to dark violet) and other features, but the former (as "*M. haematocephalus* f. 1") has shorter basidiospores ($13\text{--}14\text{--}14.5\text{--}15 \times 2.5\text{--}3.5\text{--}4.0\text{--}5.0 \mu\text{m}$ vs $15\text{--}17\text{--}20\text{--}23 \times 3.5\text{--}4.5 \mu\text{m}$) and dimorphic cheilocystidia. The Madagascan lineage (Shay *et al.* 2017), however, has a paler pileus (buff with pale orangish pink hue, or pinkish purple to dull reddish purple), larger basidiospores ($13.6\text{--}16\text{--}22 \times 3.2\text{--}4.8 \mu\text{m}$), larger pleurocystidia ($20.8\text{--}68 \times 7.2\text{--}15.2 \mu\text{m}$) and monomorphic cheilocystidia, and is morphologically more compatible to *M. haematocephalus* sensu Antonín (2007).

Marasmius coasiaticus J.S. Oliveira, sp. nov. from Brazil is interestingly sister to *M. asiaticus* from Malaysia (TYS 478, holotype) in haemat_cp2c, almost entirely Indo-Malayan. This subclade is sister, with strong support, to the clade bearing haemat_cp2a and haemat_cp2b. Also, haemat_cp2c is a species cluster with possibly five species, only three fully resolved in this analysis. *Marasmius asiaticus* is entangled with *M. haematocephalus* "f. *haematocephalus*" from Thailand (Wannathes *et al.* 2009) and from India (Dutta 2017). *Marasmius asiaticus* differs from *M. haematocephalus* "f. *haematocephalus*" from Thailand mostly by having more distant and less numerous (7–8 vs 9–14), marginate lamellae, shorter stipe (11–22 mm vs 10–40 mm), slightly larger basidiospores ($18.5\text{--}23\text{--}25 \times 3.5\text{--}5\text{--}6 \mu\text{m}$ vs $15\text{--}17\text{--}20\text{--}25 \times 3\text{--}4\text{--}5 \mu\text{m}$), cheilocystidia only as Siccus-type broom cells (vs. dimorphic cheilocystidia, one type similar to the pleurocystidia), and smaller pleurocystidia ($37\text{--}42 \times 9\text{--}12 \mu\text{m}$ vs $32\text{--}54 \times 6\text{--}12\text{--}15 \mu\text{m}$). *Marasmius haematocephalus* "f. *haematocephalus*" from India (Dutta 2017) and *Marasmius* sp. (HATFD14-61) also from India are a slightly more divergent lineage in haemat_cp2c, but unsupported. *Marasmius haematocephalus* "f. *haematocephalus*" from India has compatible pileus color (light red to brownish red when young, on maturity disc dark brown, margin red or reddish brown to violet brown) and dimorphic cheilocystidia like those in f. *haematocephalus* from Thailand,

but has more pigmented lamellae (greyish red to reddish brown, mostly concolorous, often with slightly paler edge), smaller basidiospores ($15\text{--}17.03\text{--}19 \times 3.5\text{--}4\text{--}5 \mu\text{m}$) and larger pleurocystidia ($32\text{--}54 \times 6\text{--}12\text{--}15 \mu\text{m}$). *Marasmius haematocephalus* "f. *atrobrunneus*" has a dark brown pileus, intermediate basidiospores dimension ($17\text{--}19 \times 4\text{--}5 \mu\text{m}$), and shorter pleurocystidia ($34\text{--}48 \times 7\text{--}9 \mu\text{m}$) with many apical constrictions.

The lineage haemat_cp2d is a single species from Thailand (Wannathes *et al.* 2009) to India (Dutta 2017), but the basidiospores in the collection from India is much smaller than those in the collections from Thailand ($18\text{--}18.5\text{--}19.5\text{--}21 \times 3.5\text{--}3.9\text{--}4.04\text{--}4.7 \mu\text{m}$ vs $19\text{--}20\text{--}24\text{--}25 \times 3.5\text{--}5 \mu\text{m}$) beside the smaller pleurocystidia ($42\text{--}47\text{--}54 \times 5.5\text{--}7\text{--}8\text{--}9 \mu\text{m}$ vs $38\text{--}73 \times 7\text{--}13 \mu\text{m}$). Basal in haemat_cp1, there is more morphological diversity in haemat_cp2e than it looks in the tree (Fig. 3), especially in the pileus color. Most of the strains are from Indo-Malayan realm, excepting the strain 'JES142 *M. haematocephalus*' from Madagascar, but haemat_cp2e is unsupported.

Marasmius ferrugineus (temperate strains) and *M. gardneri* (tropical strains) are sister, forming the clade Ferrugineus with support (Fig. 1), both with brownish orange or reddish-brown pileus. It is intermediate between *M. siccus* complex and *M. haematocephalus* complex. *Marasmius ferrugineus* was described from Brazil (Neotropical realm) while the representatives in the tree (BRNM 724480) is from South Korea (Palearctic), foliicolous, with marginate lamellae (Antonín *et al.* 2012). Additional strains from China (Palearctic/Indo-Malayan realms interface) are named as *M. ferrugineus* too.

Marasmius siccus sensu Dutta (2017) from India (AKD 300/2015 and AKD 301/2015) is a different species, possibly conspecific with 'NW424 *Marasmius* aff. *pallescentis*' from Thailand (Figs 1; 2), sister with strong support to the temperate siccus_cp1 but as divergent as Ferrugineus is to haemat_cp1. AKD 300/2015 and AKD 301/2015 have greyish orange to light orange pileus with brown center recalling *M. siccus* but differs in having marginate lamellae (light orange) and smaller basidiospores ($14.5\text{--}17.5\text{--}18 \times 3.5\text{--}4.02\text{--}4.5 \mu\text{m}$) (Dutta 2017). This basidiospores dimension is closer to those in *M. aff. pallescens* (NW424, $16\text{--}17\text{--}18\text{--}19 \times 4\text{--}5 \mu\text{m}$) that has light brown to pale greyish brown pileus when young, grey to greyish orange in age, but the lamellae are non-marginate (Wannathes *et al.* 2009). *Marasmius* aff. *pallescentis* is different from *M. pallescens* as described in Murrill (1915), Dennis (1961), Singer (1965, 1976), or Pegler (1983) who examined collections with pale pinkish lilac pilei from Martinique, Venezuela and Puerto Rico (the type). Singer (1976) considered *M. pallescens* quite similar to *M. haematocephalus* (see *M. cf. pallescens* above), possibly being confused with one of its numerous color variants, but the spores are clearly shorter ($11\text{--}17 \times 3.2\text{--}4.5 \mu\text{m}$). Based on morphology, *M. pallescens* seems closer to *M. pulcherripes* the "pinkish-red form" (Desjardin 1989) and considered herein a member of ser. *Pulcherripes* (clade *Pulcherripes* in Fig. 1).

Marasmius pulcherripes was originally described from the United States (Nearctic) in Peck (1872) having a soft maroon or

vinous red pileus. The species is common throughout Eastern North America (Desjardin 1989), also reported from California (Desjardin 1987), and Japan (Imazeki & Hongo 1987; Desjardin 1989) in “pinkish red form” and “brownish orange form” (Desjardin 1989). The strains from South Korea (Antonín *et al.* 2012) in the tree (Fig. 1) agree with the “pinkish red form” (Desjardin 1989), differing only in having larger ($37\text{--}65 \times 7.0\text{--}12\text{ }\mu\text{m}$) and refractive, more conspicuous pleurocystidia. In the tree (Fig. 1), strains named *M. pulcherripes* from United States were also placed in clade Pulcherripes. By considering the strains from United States more authentic for the species, those from South Korea is a distinct species in the series.

Oliveira *et al.* (2020) systematised *Marasmius* sect. *Globulares* sensu Antonín & Noordeloos (2010) in subsections and series, and ser. *Haematocephali* is currently *incertae sedis*. Based on this study, this series herein splits into at least four groups: 1) *M. haematocephalus* complex (haemat_cp1) that is stirps *Haematocephalus*; 2) clade Ferrugineus that bears the stirps’ name; 3) *M. siccus* complex (siccus_cp1) that is stirps *Siccus*; and 4) the lineage sister to siccus_cp1.

CRYPTIC SPECIES

According to Bickford *et al.* (2007), cryptic species are two or more distinct species erroneously classified (and hidden) under one species name because they are at least superficially morphologically indistinguishable. However, as explained by the authors, this concept is not straightforward and is, therefore, subject of debate (Appendix).

Although taxonomists would accept a pantropical *M. haematocephalus*, most of them agree it harbors a species complex: either subspecies, varieties or forms (Singer 1976; Desjardin 1989; Wannathes *et al.* 2009), or also possibly quite similar or even cryptic species embedded within the MSR. In the first case, the species may present a range of very subtle differences that can be the result of variation among populations set by differential gene flow or phenotypic plasticity within a species. Or, close or cryptic independent species resulted from recent divergence, parallelism, convergence, or morphostasis hidden in one name, leading taxonomists to misdetermine specimens from various tropical areas across the World.

The most authentic *M. haematocephalus* (Montagne 1837; Fries 1838; Singer 1958, 1976, this paper) is confirmed only in the Neotropical realm (Brazilian Atlantic Rainforest) and the pantropical concept represents a supraspecific taxa (phylogeny in this paper). Intercontinental divergence among strains was already reported for presumed cosmopolitan, pantemperate or pantropical macrofungi species: *Schizophyllum commune* Fr. (James *et al.* 1999, 2001), *Lentinula* spp. (Hibbett 2001), *Suillus spraguei* (Berk. & M.A. Curtis) Kuntze (Mueller *et al.* 2001), *Amanita muscaria* (L.) Lam. (Geml *et al.* 2008), *Tricholoma sculpturatum* (Fr.) Quél. (Jargeat *et al.* 2010), *Gastrum triplex* Jungh. (Kasuya *et al.* 2012), *Auricularia auricula-judae* (Bull.) Quél. (Wu *et al.* 2015), *Sparassis crispa* (Wulfen) Fr. and *S. spathulata* (Schwein.) Fr. – *S. brevipes* Krombh. complexes (Hughes *et al.* 2014; Petersen *et al.* 2015), *Gymnopus confluens* (Pers.) Antonín, Halling & Noordel. (Hughes & Petersen 2015) now in *Collybiopsis* (J. Schröt.) Earle (Petersen &

Hughes 2021), *Myriostoma coliforme* (Dicks.) Corda (Sousa *et al.* 2017), and *Phallus indusiatus* Vent. (Cabral *et al.* 2019).

Based on haemat_cp1, stirps *Haematocephalus* is monophyletic and seems to have a pantropical distribution (Fig. 1). Species radiation encompasses allopatric speciation driving divergence of a remote, widely distributed common ancestor into multiple lineages following continental drift, or long-distance dispersal. Diverged species are maintained by early extrinsic (Taylor *et al.* 2006) and possibly intrinsic barriers. If the pileus pigmentation is set aside due to its subjectiveness, all this species group (Fig. 3) would be cryptic in the view of Bickford *et al.* (2007), hidden in *M. haematocephalus*. If pileus pigmentation is considered determinant, only the strains in the red rectangles (Fig. 3) are considered truly cryptic, morphologically indistinguishable from *M. haematocephalus* s. str. These six cryptic species are polyphyletic, originating from: 1) Brazil (Neotropical realm); 2) Madagascar, Insular Africa (Afrotropical realm); and 3) India, Malaysia, and Thailand (Indo-Malayan realm). As observed in the morphological analyses, the pileus color is fundamental in combination with the other characteristics. In terms of evolutionary process, these first outermost layers of crypticity may be the result of parallelism, convergence, or even morphostasis (Struck *et al.* 2018). Layers of crypticity was previously reported in other groups of organisms (Korshunova *et al.* 2019). Interestingly, stirps *Haematocephalus* is suggested to form a biogeographic structure from the Neotropical (most recent), Afrotropical (intermediate) to Indo-Malayan (more remote) realms that seems more plausibly explained by the vicariance hypothesis. *Marasmius coasiaticus* J.S. Oliveira, sp. nov. and ‘JES142 *M. haematocephalus*’ break this pattern (Fig. 3), seemingly more compatible with a long dispersal hypothesis.

The pantemperate *M. siccus* is also a species complex, stirps *Siccus*, with a pantemperate distribution (Fig. 1) in recent radiation, with the most authentic *M. siccus* strains in the Nearctic (Fig. 2). *Marasmius siccus* sensu Antonín *et al.* (2012) from South Korea is very similar to *M. siccus* s. str. as described in Desjardin (1989) mostly from North America (United States) with overlapping basidiospores dimension ($[15\text{--}]18\text{--}25 \times 3.5\text{--}5.0\text{ }\mu\text{m}$ vs $15.2\text{--}20.8 \times 3.2\text{--}4.6\text{ }\mu\text{m}$ [only the holotype], respectively) and pleurocystidia ($38\text{--}72[80] \times 5.0\text{--}12[15]\text{ }\mu\text{m}$ vs $32\text{--}60 \times 5\text{--}9\text{ }\mu\text{m}$ [only the holotype], respectively). Collections named as *M. siccus* in Antonín & Noordeloos (2010) from Europe and Asia should also include cryptic species. With smaller and less evenly distributed sampling, siccus_cp1 does not show biogeographic pattern similar to haemat_cp1. On the other hand, the five putative species in siccus_cp1 present consistency of local/regional distribution, reason why *M. siccus* s. str. is given to be strictly Nearctic while *M. siccus* ‘sensu Antonín *et al.* (2012)’ appears to be concentrated in the Far East Coast of Asia.

The cryptic species within the two species complexes also include a deeper, innermost layer of crypticity: siccus_cp2a and siccus_cp2b (Fig. 2), haemat_cp2a, haemat_cp2b, haemat_cp2c, haemat_cp2d and haemat_cp2e (Fig. 3). These species groups have very recently radiated in sym-, peri- or parapatric speciation (Natvig & May 1996) with insufficient time to accumulate more significant genetic divergence. Speciation has been prompted by intrinsic barriers (Taylor *et al.* 2006). Partial intercompatibil-

TABLE 1. — Overlapping basidiospores dimensions of *Marasmius rubicundus* (Singer) J.S. Oliveira, stat. nov. < *M. haematocephalus* (Mont.) Fr. < *M. auranticapitatus* J.S. Oliveira, sp. nov. Abbreviations: **s**, number of specimens evaluated; **x**, min.-max. range of length × width; **x_{rm}**, min.-max. range of means of length × width; **x_{mm}**, mean of means of length (± stan. dev.) × width (± stan. dev.); **Q_{rm}**, min.-max. range of Qm (mean of the quotient length/width); **Q_{mm}**, mean of means of Qm (± stan. dev.).

Species	s	x	x _{rm}	x _{mm}	Q _{rm}	Q _{mm}
<i>M. rubicundus</i> stat. nov.	28	(15.4-)16.2-21.7(-22) × 2.7-4.7(-5) µm	18-19.7 × 3.5-4 µm	19 (± 0.5) × 3.8 (± 0.2) µm	4.6-5.5	5 (± 0.3)
<i>M. haematocephalus</i>	5	(18-)18.3-22.6(-23) × 3-4.9 µm	20.1-21 × 3.8-4.2 µm	20.5 (± 0.3) × 3.9 (± 0.2) µm	5-5.4	5.2 (± 0.1)
<i>M. auranticapitatus</i> sp. nov.	8	17.1-24.8 × 2.8-5 µm	19.4-22.3 × 3.5-4.2 µm	21.1 (± 0.7) × 3.8 (± 0.3) µm	5.1-6.3	5.7 (± 0.5)

TABLE 2. — Overlapping pleurocystidia dimensions of *Marasmius rubicundus* (Singer) J.S. Oliveira, stat. nov.; *M. haematocephalus* (Mont.) Fr.: *M. auranticapitatus* J.S. Oliveira, sp. nov.

Species	Pleurocystidia
<i>M. rubicundus</i> stat. nov.	(19.5-)25.6-71.7 × 5-12.3 µm
<i>M. haematocephalus</i>	30.1-76.2 × 7-13.9(-15.5) µm
<i>M. auranticapitatus</i> sp. nov.	(15.1-)22.3-74.3 × 5.2-12.1 µm

ity at several degrees or viable hybrids may occur within these clusters (see *JO226* in *M. auranticapitatus* J.S. Oliveira, sp. nov. and *JO316* in *M. rubicundus* (Singer) J.S. Oliveira, stat. nov.), merging back the lineages with divergence in progress (Natvig & May 1996; Taylor *et al.* 2000). Meanwhile true interspecies hybridization can move genes between species and blur species boundaries, ancestral polymorphism may play a part (Natvig & May 1996). The trends of the process, however, seem to push the disruption forward until reticulation is fully ceased. This is supported by the vast majority of the other examined strains to be fully dichotomized. This layer of very recent divergence forms species complexes of cryptic taxa in morphology and even for the nrITS. This usually polymorphic DNA region is not powerful enough to resolve the phylogenetic relationships with support, and some studies have already reported its limitation in taxa discrimination within species complexes (Nilsson *et al.* 2008; Schoch *et al.* 2012; Vu *et al.* 2019). Multilocus analyses combining markers with greater PI (Balasundaram *et al.* 2015) were necessary to dissect these groups. For *haemat_cp2a*, the multilocus analyses combining nrITS + nrLSU including only *haemat_cp2a* (Fig. 4) and nrITS + *rpb2* + *efl-α* (Fig. 5) were able to resolve *M. auranticapitatus* J.S. Oliveira, sp. nov., *M. haematocephalus* s. str. and *M. rubicundus* (Singer) J.S. Oliveira, stat. nov. The multilocus analyses evoke gene coalescence integrated with morphology in Genealogical Concordance Concept to avoid subjectivity in PSR (Mayden 1997; Taylor *et al.* 2000). Besides pileus pigmentation, the basidiospores size, although overlapping in min.-max. ranges, has a fine trace of phylogenetic signal (Table 1), but pleurocystidia dimension are nearly indistinguishable (Table 2). These three are sibling species (Bickford *et al.* 2007).

CONCLUSION

Based on the available data and the present analyses, a pantropical *M. haematocephalus* and a pantemperate *M. siccus* concepts

are unsupported. But these two concepts seem represented by two monophyletic, supraspecific groups determined as stirps *Haematocephalus* and stirps *Siccus*, respectively. Seven species complexes were detected in a deeper, innermost layer of crypticity. Overall, four new species were proposed, all within stirps *Haematocephalus*. At least 15 lineages would need names different from *M. haematocephalus* and *M. siccus*. By clearing more about these species' complexes, next studies may add more data and further elucidate about these species groups.

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APPENDIX

APPENDIX. — Supplementary material. https://doi.org/10.5852/cryptogamie-mycologie2022v43a5_s1