Biodiversity and phylogeny of *Marasmius* (Agaricales, Basidiomycota) from Madagascar

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Abstract

Prior to this monographic treatment, limited research on the genus *Marasmius* (Basidiomycota, Agaricales) had been conducted in Madagascar. Based on field work in January 2013 and January–February 2014, which generated 45 specimens of *Marasmius sensu stricto*, supplemented by herbarium exsiccate and published literature, 35 species of *Marasmius* are documented from Madagascar. Of these, 5 species are recognized herein as new to science, viz., *Marasmius madagascariensis*, *M. rubrobrunneus*, *M. dendrosetosus*, *M. sokola* and *M. tanaensis*; an additional 11 species represent new distribution records for Madagascar. Species delimitations are based on comprehensive morphological descriptions and molecular sequences (ITS) data. Line drawings of salient micromorphological features, color photographs of basidiomes, comparisons with allied taxa, a key to aid in identification, and phylogenetic inferences are provided.

Keywords: endemism, internal transcribed spacer, marasmioid fungi, saprotrophic, taxonomy

Introduction

Members of the mushroom genus *Marasmius* (Marasmiaceae) Fries (1836:339) play key roles in the decomposition of wood and leaf litter, nutrient cycling, and soil genesis. *Marasmius* diversity has been found to strongly correlate with plant host diversity, especially in tropical habitats (Lodge *et al.* 1995). There has been recent interest in understanding the global biodiversity and evolution of *Marasmius* (Antonín, 2003, 2004a, b, 2007, 2013; Antonín & Buyck 2006; Antonín & Noordeloos 2010; Desjardin 1990, Desjardin & Horak 1997, Desjardin & Ovrebo 2006, Desjardin *et al.* 2000, Tan *et al.* 2007, 2009; Wannathes *et al.* 2007, 2009a, b; Wilson & Desjardin 2005), although only limited attention has been paid to the *Marasmius* of Madagascar. The island of Madagascar is a model tropical system that has evolved in isolation, characterized by high levels of endemism and species diversification (Vences *et al.*, 2009).

The earliest records of *Marasmius* from Madagascar were reported by Hennings (1893) based on collections made by J. Braun in 1891 of *Marasmius foetidus* (Sowerby) Fries (1838:380) [= *Gymnopus foetidus* (Sowerby) P.M. Kirk (2014:120)] from Ankoraka, and *M. oreades* (Bolton) Fries (1836:510). from a meadow at “Champ de Meclas”. Hennings (1908) reported *Marasmius rotula* (Scop.) Fries (1838:385) and *M. rhodocephalus* Fries (1851:31) [= *M. haematocephalus* (Mont.) Fries (1838:382)], both from SW Madagascar near Andranohinany. George Métrod, who documented many fungi from Madagascar, studied Decary’s specimens, but his observations...
were never published. The Decary specimens were kept in formol or alcohol and subsequently dried out in later years, making them unsuitable for any descriptive purposes, particularly for describing new taxa.

In a preliminary investigation of *Marasmius* from the region, Antonín & Buyck (2006) reported 19 species of *Marasmius* from Madagascar, Mauritius and Réunion, and noted that approximately one fourth of the Malagasy fungal taxa appeared to be endemic. They documented the macro- and micromorphological characteristics for these taxa, and provided a key to aid in identification. They did not provide molecular sequence data for any specimens. In 2007, Antonín published the first part of a monograph representing marasmioid genera from tropical Africa. This study documented 110 taxa of *Marasmius*, however it was estimated that there might be 2–3 times more taxa. The geographic region encompassed the continent of Africa between the Tropics of Capricorn and Cancer, but excluded the island of Madagascar. Antonín (2013) followed with a supplement to the African *Marasmius* monograph in which he reported an additional 40 taxa.

Fieldwork was conducted in Madagascar January–February 2014 by J.E. Shay and D.S. Newman, and in January 2013 by Taylor Lockwood. These excursions yielded 83 specimens of *Marasmius sensu lato*, of which 45 specimens represented *Marasmius sensu stricto* treated herein. Analyses of the latter material resulted in the recognition of five new species, 11 new distribution records for Madagascar, and recollection of five of the species reported by Antonín & Buyck (2006). Species reported herein are delineated using morphological characteristics and DNA sequence data from the nuclear ribosomal internal transcribed spacer region (ITS), the universal DNA barcode marker for Fungi (Schoch et al. 2012). Comprehensive descriptions of macro- and micromorphological features, illustrations, photographs, a dichotomous key to aid in identification, comparisons with similar taxa, and phylogenetic inferences are provided.

**Materials and Methods**

**Sampling protocols**

A variety of eastern rainforests in Madagascar were surveyed, chosen for their diversity of plants, habitats types, and accessibility. Sites sampled include Ranomafana National Park, the forests near Andasibe, the littoral forests of the east coast near Brickaville, and the Ambohitantily Reserve on the northern central plateau. All specimens matching the morphotype of *Marasmius sensu lato* were collected, totaling 83 by the end of the expedition.

**Morphological protocols**

Data on substrate-type, GPS coordinates of collection site, and photographs of fresh material were documented in the field at the time of collection. Soon after collection, macromorphological features of the basidiomes were recorded. Portions of basidiomes were subjected to 3% potassium hydroxide (KOH) and Melzer’s reagent and observed staining reactions were recorded. Colors terms and notations are from Kornerup & Wanscher (1978). Photographic images were made with a Canon Rebel T3i EF–S 60MM F/2.8 Macro USM lens. Specimens were dried overnight using a food dehydrator and packaged promptly in plastic bags to avoid condensation and subsequent mold contamination. Micromorphological features were analyzed at SFSU by hand-sectioning dried material, rehydrating in 95% ethanol followed by 3% KOH or Melzer’s reagent, and observed with an Olympus CH-30 or Nikon Optiphot-2 compound microscope. Line drawings were made with the aid of a drawing tube. The term “inamyloid” refers to a negative reaction in Melzer’s reagent (neither amyloid nor dextrinoid). Spore statistics include: $\mu$, the arithmetic mean of the spore length by spore width (± standard deviation) for n spores measured in a single specimen; $\mu_l$, the range of $\mu$ values and $\mu_w$, the mean of $\mu$ values where more than one specimen is available; $Q$, the quotient of spore length by spore width, indicated as a range in variation in n spores measured; $Q_{\mu}$, the mean of $Q$ values (± standard deviation) in a single specimen; $Q_{\mu_l}$, the range of $Q_{\mu}$ values and $Q_{\mu_w}$, the mean of $Q_{\mu}$ values where more than one specimen is available; n, the number of spores measured per specimen; s, the number of specimens involved. The micromorphological analyses indicated that only 45 of the 83 specimens of *Marasmius sensu lato* represented *Marasmius sensu stricto* and are included in this monographic treatment. The remaining 38 specimens represent members of the *Gymnopus/ Marasmiellus* lineage and will be treated in the future.

Herbarium specimens of Madagascar material previously collected by Antonín and Buyck (2006) were borrowed from the Moravian Museum (BR–Brno, Czech Republic) and the Muséum National D’Histoire Naturelle (PC–Paris, France), examined, sequenced, and compared with material collected during our expedition.
Molecular protocols

Genomic DNA was extracted from dried herbarium specimens using the E.Z.N.A. Forensic DNA Extraction Kit (Omega Bio-tek Inc., Norcross, GA) following provided protocol. PCR was performed with AccuPower® HotStart PCR PreMix (Bioneer, Daejeon, Korea) following the methods outlined in Cubero et al. (1999). The internal transcribed spacer (ITS) regions 1 and 2, as well as 5.8s rDNA, were amplified using primers ITS1-F and ITS4 (Gardes & Bruns 1993; White et al. 1990). DNA fragments were amplified on an MJ Research PTC-200 Peltier Thermal Cycler (GMI, Ramsey, Minnesota, USA). The thermocycling profile was as follows: an initial denature at 94°C for five minutes, 39 cycles of denaturing at 94°C for 30 seconds, annealing at 57°C for 30 seconds, and extension at 72°C for 45 seconds. The final extension was at 72°C for seven minutes. PCR products were purified using ExoSAPIT (USB Corporation, Cleveland, OH, USA). Cycle sequencing was performed with ITS1-F and ITS4 primers using BigDye® Terminator v3.1 (Thermo Fisher Scientific Inc., Life Technologies Corporation, Grand Island, NY, USA) and visualized on an ABI PRISM® 3100 Genetic Analyzer (PE Biosystems and Hitachi, Ltd., Life Technologies, Carlsbad, CA, USA). Sequence editing was performed with Geneious v.7 software (Kearse et al. 2012; Biomatters, Auckland 1010, New Zealand).

Maximum likelihood analysis (Felsenstein 1981) was conducted using RAxML 8.1.11 (Stamatakis 2014) under the GTRGAMMA model using default parameters and run on the CIPRES Science Gateway (Miller et al. 2010), with node support estimated via 1000 RAxML rapid bootstrap (BS) replicates. Bayesian analyses were performed using Metropolis Coupled MCMC methods as implemented in MrBayes 3.2.6 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003; Ronquist et al. 2012) under a GTR+I+G model of sequence evolution as determined under the Akaie Information Criterion in PAUP* (Swofford 2002). Analyses consisted of two parallel searches, run for 25 million generations on the CIPRES Science Gateway (Miller et al. 2010), and initiated with random starting trees. Eight chains (temp = 0.3) were sampled every 2500 generations for a total of 10,001 trees each, sampled from the posterior distribution. Those topologies sampled prior to the runs reaching a split deviation frequency of 0.1 were discarded, while the remaining topologies were used to calculate the posterior probabilities (PP) of the individual clades. The default settings were used in MrBayes to set unconstrained branch lengths and uninformative topology priors. All ITS sequences generated as part of this study are deposited in GenBank (Table 1; accessions KX148977–KX149019). The aligned ITS dataset and associated tree files are deposited in TreeBase (submission ID 19993).

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Results

Phylogenetic Analysis

Phylogenetic analyses were performed on 135 taxa of Marasmius sensu stricto representing a global sampling of the genus, and including representatives of all infrageneric groups. Of the 222 ITS sequences included in the dataset, 154 were downloaded from GenBank, and 68 were generated for this study, including 43 sequences of Marasmius from Madagascar (Table 1). Crinipellis malesiana Kerekes, Desjardin & Vikineswary (2009:125) was chosen as the outgroup based on the results of previous research (Tan et al. 2009, Wannathes et al. 2009a). A total of 343 ambiguously aligned nucleotides were removed prior to all analyses, resulting in a final dataset of 687 nucleotide characters.
FIGURE 1a. Maximum likelihood phylogeny based on ITS sequence data. Marasmius from Madagascar are indicated in bold type. Values separated by / refer to nonparametric ML bootstrap proportions and Bayesian posterior probabilities, respectively. Values greater than 70/0.70 are shown (- designates a value below 70% or below 0.70). Nodes receiving support values greater than 90/0.95 are represented by bold branches. 

FIGURE 1b. Maximum likelihood phylogeny based on ITS sequence data. *Marasmius* from Madagascar are indicated in bold type. Values separated by / refer to nonparametric ML bootstrap proportions and Bayesian posterior probabilities, respectively. Values greater than 70/0.70 are shown (- designates a value below 70% or below 0.70). Nodes receiving support values greater than 90/0.95 are represented by bold branches. G—sect. *Globulares*; SA—sect. *Sicci* s. *Atrorubentes*; SL—sect. *Sicci* s. *Leonini*; SS—sect. *Sicci* s. *Spinulosi*; SH—sect. *Sicci* s. *Haematocephali*.

G—sect. *Globulares*

SA—sect. *Sicci* s. *Atrorubentes*

SL—sect. *Sicci* s. *Leonini*

SS—sect. *Sicci* s. *Spinulosi*

SH—sect. *Sicci* s. *Haematocephali*

The RAxML tree with best ML score is presented in Fig. 1 (-lnL = -13820.463). In general, statistical support for the deep nodes distinguishing major lineages was low, indicating that the ITS gene region is too variable to delimit infrageneric clades in *Marasmius*. Only sect. *Marasmius* subsect. *Marasmius*, including the type species of the genus *Marasmius* (*M. rotula*) (Fig. 1c), was monophyletic (98% BS, 1.0 PP). All members of this group form lamellae attached to a collarium, have an insititious stipe and *Rotalis*-type broom cells in the pileipellis. Members of sect. *Marasmius* subsect. *Sicciformes*, which also form a collarium and an insititious stipe, but have *Siccus*-type broom...
cells, formed a grade basal to subsect. *Marasmius* (Fig. 1c), and included a few members of sects. *Globulares + Sicci*. There was low support for these relationships. The historically recognized sects. *Globulares + Sicci* (lamellae lacking a collarium, with a non-insitious stipe, *Globulares*-type or *Siccius*-type boom cells) formed a clade with low support (Figs. 1a, 1b) and included most members traditionally placed there, except for a few species that appear to be more closely related to members of sect. *Marasmius* subsect. *Sicciformes* (Fig. 1c), as noted above.

Members of sect. *Neosessiles* occur in two distinct parts of the tree. The recently described *M. griseoroseus* (Montagne) Singer (1976:256) and *M. conchiformis* de Oliveira & Capelari (2014:5), plus *M. elaeocephalus* Singer (1964:384) (a member of sect. *Sicci* ser. *Haematocephali*) align with members of sect. *Globulares + Sicci* (Fig. 1a), whereas *M. tenuissimus* (Jungh.) Singer (1976:258) and *M. neosessiliformis* Antonin & Buyck (2006:34) are sister to *Leveilleani* and together are sister to one clade of sect. *Marasmius* subsect. *Sicciformes* (Fig. 1c). *Marasmius nodulocystis* Pegler (1977:200) (sect. *Sicci* ser. *Leonini*) is morphologically nearly indistinguishable from *M. leveilleanus* (Berk.) Saccardo (1925:149) (type species of sect. *Leveilleani*) and the ITS sequences of three specimens of *M. nodulocystis* are sister to a sequence of *M. leveilleanus* from Thailand.

None of the historically recognized infrageneric groups within sect. *Sicci*, viz., ser. *Atrorubentes* (SA), *Haematocephali* (SH), *Leonini* (SL), and *Spinulosi* (SS) are monophyletic in the ITS phylogeny (Figs. 1a, 1b), although small groups of species within each of these infrageneric groups do form clades but with limited support. For the most part, members of these series are scattered throughout a clade containing most of sects. *Globulares (G) + Sicci*.


Concerning Madagascar taxa in Fig. 1b: The new species *M. dendorosetosus* (SS) is sister to *M. longisetosus* (SS) de Oliveira & Capelari (2014:19) with 99% BS and 1.0 PP support, in a clade with other members of ser. *Spinulosi*. A sequence of *Marasmius nummularius* (SS) Berkeley & Broome (1873:33) from Madagascar forms a well-supported clade with two sequences from Thailand (90% BS, 1.0 PP), in a clade with other members of ser. *Spinulosi*. Five sequences of *M. haematocephalus* (SH) align with several sequences from Thailand with 99% BS support, and are sister to *M. pulcherripes* (SH) Peck (1872:77) but with low support. *Marasmius bekolacongoli* (G) Beeli (1928:157) forms an unresolved trichotomy with other members of sect. *Globulares* plus *M. coarctatus* (SS) Wannathes, Desjardin & Lumyong (2009:251). The new species *M. sokola* (SL) is on a long branch sister to *M. imitarius* (SL) Wannathes, Desjardin & Lumyong (2009:279) with low support.

Concerning Madagascar taxa in Fig. 1c: Three sequences of *M. somalomoensis* (MM) Antonin (2003:66) are unresolved in a clade containing other members of sect. *Marasmius*. *Marasmius* with low support. Three sequences of Madagascar *M. rotalis* (MM) Berkeley and Broome (1873:40) form a well-supported clade (98% BS, 1.0 PP) sister to a GenBank sequence of *M. rotalis* plus other members of subsect. *Marasmius*. Two sequences of Madagascar *M. apatelius* (MM) Singer (1964:332) form a grade with other *M. apatelius* sequences from Thailand and Principe and *M. andasibensis* var. obscurostipitatus (MM) Antonin & Buyck (2006:23) from Madagascar, but with low support. Three sequences of *M. cf. subfurorotula* (MS) Singer (1964:339) form a well-supported clade (99% BS, 1.0 PP) and are sister to several sequences of *M. subfurorotula* (MS) from Principe with 100% BS and 1.0 PP support. The new species *M. rubrobrunneus* (MS) is on a long branch sister to *M. purpureobrunneolus* (MS) Hennings (1899:151) with 81% BS and 1.0 PP support. A sequence of *Marasmius curreyi* (MS) Berkeley & Broome (1879:209) from Madagascar (KX148980) forms an unresolved clade with a sequence of *M. curreyi* from North Carolina (FJ431237) plus *M. graminum* (MS) Berkeley (1860:22) with low support. This clade is sister to a well-supported clade (98% BS, 1.0 PP) clade containing a Madagascar sequence of *M. aff. curreyi* (MS) plus a Korean sequence of *M. curreyi* (FJ936152). Eight sequences of *M. brunneopulchellus* (MS) Antonin & Buyck (2006:24) form a well-supported clade (100% BS, 1.0 PP) sister to other members of subsect. *Sicciformes*. *Marasmius neosessiliformis* (N) forms an unresolved clade with Malaysian and Thailand sequences of *M. tenuissimus* (N) plus a Malaysian sequence of *M. leveilleanus* (L) with low support. The new species *M. madagascariensis* (MS) is on a long branch sister to a clade containing Malaysian sequences of *M. guyanensis* (MS) Montagne (1854:114) and *M. crinisequi* (MS) with 0.97 PP support.
Tests of Sectional Monophyly

Two maximum likelihood analyses were conducted in RAxML: 1) an unconstrained analysis; and 2) an analysis that constrained the tree into two monophyletic groups representing the major division of the genus Marasmius into section Globulares and section Marasmius. The resulting constrained and unconstrained topologies were compared using the Shimodaira-Hasegawa (SH) test (Simodaira & Hasegawa 1999) as implemented in PAUP* (Swofford 2002) using 1000 RELL bootstrap replicates. Results of the SH test indicate no statistically significant difference between these topologies, and we are therefore unable to reject the monophyly of these sections given the data presented.

Artificial Key to Marasmius of Madagascar

1. Lamellae attached to a distinct collarium; stipe insitious (sect. Marasmius). ................................................................. 2
   - Lamellae attached directly to the stipe or free and collarium absent; stipe not insitious ........................................... 17
2. Pileipellis composed of Rotalis-type broom cells (subsect. Marasmius) .................................................................................. 3
   - Pileipellis composed of Siccus-type broom cells (subsect. Sicciformes) ................................................................. 7
3. Pileus white, pale grey, or buff ................................................................. 1. M. rotales
   - Pileus greyish orange, tan, or pale brown ....................................................................................................................... 4
4. Pileus tan to pale brown; lamellae subdistant (11–14) ............................................... 2. M. somalomoensis
   - Pileus greyish orange to buff; lamellae distant (9–12) ........................................................................................................ 5
5. Pileus with a dark brown papilla ........................................................................ 3. M. apatelius
   - Papilla absent or concolorous with pileus surface ........................................................................................................... 6
6. Papilla absent; stipe pale brown ........................................................................ 4. M. andasibensis var. andasibensis
   - Papilla present, concolorous with pileus surface; stipe brown-black .......................................................... 5. M. andasibensis var. obscurostipitatus
7. Pileus brownish black or black ........................................................................ 8
   - Pileus differently colored (reddish brown, brown, greyish orange, tan or cream) .......................................................... 9
8. Basidiospores 8.5–10.5 × 4–5 µm; cheilocystidia 10–25 × 7–12 µm; pileus bicolored black and grey .............. 6. M. nigrogriseus
   - Basidiospores 9–12 × 4.5–6.5 µm; cheilocystidia 10–14 × 5–8 µm; pileus brownish black ....................... 7. M. nigrobrunneus
9. Pileus reddish brown, or white, cream, tan to light brown ........................................ 10
   - Pileus greyish orange to brownish orange ..................................................................................................................... 15
10. Pileus white to cream with prominent, dark brown conical papilla ............................... 8. M. conicopapillatus
    - Pileus more deeply pigmented ................................................................................................................................. 11
11. Pileus reddish brown with pinkish tinge at center and paler yellow-brown towards margin, or tan to light brown .......... 12
    - Pileus dark reddish brown ........................................................................................................................................... 14
    - Pileus reddish brown with or without pink tones ..................................................................................................... 13
13. Basidiospores 8.5–10.5 × 4.5–5.5 µm; cheilocystidia of one type ........................................ 9. M. curreyi
    - Basidiospores 10–12.5 × 4.5–6 µm; cheilocystidia of two types ...................................................................................... 11. M. curreyi var. bicystidiatus
14. Basidiospores mean range 14.9–16.5 × 3.2 µm; lamellae distant (11–12) ............... 12. M. rubrobrunneus
    - Basidiospores mean range 8.8–9.5 × 4.1–4.6 µm; lamellae subdistant (12–16) ......................................................... 13. M. brunneoaurentiacus
15. Basidiomes arising directly from black rhizomorphs; pileus 1–2 mm diam; lamellae distant (6); stipe 2–4 mm long ............. 14. M. crinisequi
    - Basidiomes not arising directly from black rhizomorphs; pileus 1–7 mm diam; lamellae subdistant (9–12); stipe 6–40 mm long .......................................................... 16
16. Basidiospores mean range 8–8.4 × 3.8–3.9 µm; lamellae white to buff ......................... 15. M. cf. subruforotula
    - Basidiospores mean range 11.3–11.6 × 4.8–5 µm; lamellae light orange to cream .......................... 16. M. madagascariensis
17. Stipe absent or very short and lateral to strongly eccentric (sect. Neosessiles) ................................. 18
    - Stipe well-developed and central (sect. Globulares + Siccii) ..................................................................................... 19
18. Pileus 1–4 mm diam, reddish brown; basidiospores 10–11 × 5–6 µm, ellipsoid; pleurocystidia absent ................................................................. 17. M. neosessiliformis
- Pileus 5–8 mm diam, orangish brown to yellowish brown or pink; basidiospores 14.5–17 × 6.5–8 µm, lacrimoid or clavate-fusoid; pleurocystidia present .................................................. 18. *M. cecripiformis*

19. Pileipellis composed of smooth, broadly clavate, non-setulose cells (sect. *Globulares*) .................................................. 20

- Pileipellis composed of *Siccus*-type broom cells (sect. *Sicii*) ................................................................................. 21

20. Pileus 100–120 mm diam, pale mouse grey overall; pleurocystidia present .................................................. 19. *M. sulcatipes*

- Pileus up to 85 mm diam, striped, brown to violaceous brown with pinkish-violaceous sulcae and cream ridges; pleurocystidia absent .................................................. 20. *M. bekolacongoli*

21. Stipe pruinose to hispid, ornamented with simple smooth cystidia or setae .................................................. 22

- Stipe glabrous, simple cystidia and setae absent .................................................................................. 25

22. Setae present on pileus, lamellae and/or stipe (ser. *Spinulosi*) .................................................. 23

- Setae absent, stipe with simple smooth cystidia (ser. *Atrorubentes*) ............................................................................. 24

23. Pileosetae branched, common, up to 300 µm long; pleurocystidia absent; basidiospores mean range 8.2–9.1 × 3.9 µm; caulocystidia absent, *Siccus*-type broom cells ........................................... 21. *M. dendrosetosus*

- Pileosetae unbranched, rare; pleurocystidia present; basidiospores mean range 12.4–12.7 × 4.3–4.8 µm; caulocystidia abundant ............... 22. *M. nummularius*

24. Basidiospore mean 9.0 × 4.0 µm; caulocystidia dextrinoid, of one type (non-setulose cells) .................. 23. *M. corrugatiformis*

- Basidiospores mean 7.8 × 4.0 µm; caulocystidia inamyloid, of two types (non-setulose cells and *Siccus*-type broom cells) .................................................................................. 24. *M. katangensis*

25. Pleurocystidia absent (ser. *Leonini*) .................................................................................. 26

- Pleurocystidia present (ser. *Haematocephali*) .................................................................................. 29

26. Pileus 20 mm diam, dark brown .................................................................................. 25. *M. sokola*

- Pileus 4–9 mm diam, orangish ochraceous, reddish orange to orange or pale violet brown with reddish grey sulcae .................. 27

27. Stipe 3–4 mm long; pileus pale orangish ochraceous .................................................................................. 26. *M. rammlooi*

- Stipe 25–115 mm long; pileus reddish orange to orange, or pale violet brown with reddish grey sulcae .................................................. 28

28. Pileus 6.5–9 mm diam, violet brown with reddish grey sulcae; stipe 104–115 mm long; basidiospore mean 32 × 2.5 µm ............... 27. *M. megistus*

- Pileus 4–5 mm diam, reddish orange to orange; stipe 25–30 mm long; basidiospore mean 16.4 × 3.5 µm .......... 28. *M. bumbuniformis*

29. Basidiospores 12–22 µm long, with mean length 13.4–21 µm .................................................................................. 30

- Basidiospores 8–12.8 µm long, with mean length 10–12 µm .................................................................................. 33

30. Pileus pale orangish pink, pinkish purple, dull reddish pink or red; basidiospores 16–22 µm long .......... 29. *M. haematocephalus*

- Pileus orangish pink, dark brown, light brown or reddish brown; basidiospore 11.2–18 µm long .................................................. 31

31. Pileus orangish pink, 1–3 mm diam; stipe up to 22 mm long; pleurocystidia 6–9.5 µm diam .................. 30. *M. tanaensis*

- Pileus brown to reddish brown, 3–15 mm diam; stipe up to 40 mm long; pleurocystidia 8–15 µm diam .................................................. 32

32. Pileus 5–15 mm diam, dark brown at center, light brown towards the margin; basidiospores 15–18 × 4–5 µm; pleurocystidia 38–65 × 9–15 µm, subfusoid, often rostrate; pileipellis cells with 8–20 projections up to 6 µm long ........ 31. *M. cf. grandisetosus*

- Pileus 3–5 mm diam, brown to reddish brown; basidiospores 13.5–16 × 3.5–5 µm; pleurocystidia 30–50 × 8–14 µm, clavate to subfusoid, sometimes rostrate; pileipellis cells with up to 40 projections up to 10 µm long .......................................................... 32. *M. eysartieri*

33. Pileus up to 3 mm diam; *Siccus*-type broom cells present on stipe apex .................. 33. *M. cf. confractus var. parvisporus*

- Pileus 6–9 mm diam; *Siccus*-type broom cells absent on stipe apex .................................................. 34

34. Pileus orange to reddish orange; lamellae close (17–20); pleurocystidia 5–7.2 µm diam .................. 34. *M. ferruginoides*

- Pileus brownish orange to reddish brown; lamellae distant (15–17); pleurocystidia 7–10 µm diam .................. 35. *M. hinnuleus*

**Taxonomy**

I. Sect. *Marasmius*


= *Marasmius* B. Rotulalae Qüel., Enchir.: 145. 1886.
= Marasmius, I. Rotaria J. Schröt. in Cohn, Kryptogr.-Fl. Schles. 3(1): 556. 1889.
– Type species: Marasmius rotula (Scop.) Fr.

Ia. Subsect. Marasmius
– Type species: Marasmius rotula (Scop.) Fr.

1. Marasmius rotalis Berk. & Broome, J. Linn. Soc., Bot. 14: 40. 1873 (1875). (Fig. 2, Plate 1)

Type:—SRI LANKA. Peradeniya, Thwaites 810 (K!)

Description:—Pileus 1–5 mm diam, campanulate to umbilicate, shallowly depressed; margin plicate to sulcate, crenate; surface dry, glabrous; white to buff or pale gray (5B2–3). Context thin, concolorous. Lamellae adnate to a collarium, distant (8–11), no lamellulae, non-intervenose, broad (0.5–0.8 mm), white, non-marginate. Stipe 8–54 × 0.2 mm, central, cylindrical, hollow, wiry, insititious; surface glabrous; dark brown to black overall. Odor and taste not distinctive.

FIGURE 2. Marasmius rotalis (JES 141, JES 145, JES 150B) a) basidiospores; b) basidioles; c) cheilocystidia; d) pileipellis cells. Scale bar = 10 µm. Illustrated by J.E. Shay.

Basidiospores (6.4–) 7.2–10.4 (–11.2) × 3.2–4.8 (–5) µm [x_μ = 8.4–8.9 × 3.7–4.2 µm; x_μμ = 8.7 ± 0.3 × 4.0 ± 0.3 µm; Q = 1.5–3.3; Q_μ = 2.09–2.28; Q_μμ = 2.19 ± 0.1, n = 24–25, s = 3], ellipsoid, smooth, hyaline, inamyloid, thin-walled. Basidia not observed. Basidioles 13.6–23.2 × 4–8 µm, clavate to fusoid, some utriform, hyaline, inamyloid, thin-walled. Cheilocystidia numerous, of Rotalis-type broom cells; main body 6.8–20 × 8–22.4 µm, clavate to broadly clavate, globose, subglobose or obpyriform, hyaline, inamyloid, thin-walled; divergent setulae 0.5–2.4 × 0.5–2.4 µm, cylindrical to conical, obtuse, hyaline, inamyloid, thin-walled. Pleurocystidia absent. Pileipellis not mottled, a hymeniform layer of Rotalis-type broom cells; main body 8–34 × 8–28 µm, clavate to broadly clavate, subglobose or globose, pale yellowish brown to hyaline, inamyloid, thin-walled; divergent setulae 0.5–3 × 0.2–1.6 µm, numerous, cylindrical to conical, pale yellowish brown to hyaline, inamyloid, thin-walled. Pileus trama interwoven; hyphae 1.6–4.8 µm diam, cylindrical, smooth, hyaline, inamyloid, thin-walled. Lamellar trama regular; hyphae 1.6–9.6 µm diam, cylindrical to slightly inflated, smooth, hyaline, inamyloid, thin-walled. Stipe tissue monomitic; cortical hyphae 3–4
µm diam, parallel, cylindrical, smooth, yellowish brown to brown, dextrinoid, thick-walled; medullary hyphae 1.6–6 µm diam, parallel, cylindrical, smooth, hyaline, inamylloid, thin-walled. Caulocystidia absent. Clamp connections present.

Habit, habitat, and known distribution:—Solitary or gregarious on leaves of Cephalostachium vigueri (bamboo), Cynodon dactylon (Poaceae), and various unknown dicotyledonous leaves and stems. Africa (Benin, Cameroon, DR Congo, Kenya, Malawi, Nigeria, Tanzania, Uganda), Indonesia (Java), Madagascar, Papua New Guinea, South America (Colombia), Sri Lanka.


Notes:—Marasmius rotalis forms small (1–5 mm diam), white to pale grayish pilei, distant (8–11), collariate lamellae, dark brown, wiry insititious stipe, basidiospores in the range 7.2–10.4 × 3.2–5 µm, Rotalis-type broom cells, and growth on dicotyledonous leaves, bamboo or various grasses. A quick comparison with M. apatelius indicates that they differ primarily in pileus color, paler and whitish in M. rotalis and more brownish in M. apatelius. ITS sequences of the Madagascar specimens of M. rotalis (KX148999, KX149000, KX149001) align with GenBank sequences of M. rotalis and M. rotula, in a clade with other members of sect. Marasmius. (Fig. 1c).

2. Marasmius somalomoensis Antonín, Mycotaxon 88: 66. 2003. (Fig. 3, Plate 1)

Type:—CAMEROON. Sud Province, Somalomo, Dja Biosphere Reserve, 8 April 2001, V. Antonín Cm 01.42 (BRNM 666108).

Description:—Pileus 2–9 mm diam, plano-convex to campanulate, umbilicate, with a brown papilla; margin plicate to sulcate; surface dry, glabrous; tan to pale brown (4–5A3). Context thin (<1 mm), white. Lamellae adnate to a collarium, distant to subdistant (11–14), no lamellulae, broad, buff (4A2), non-marginate. Stipe 13–32 × <0.5 mm, central, narrow, wiry, twisted, insititious; surface glabrous; dark brown (6F8). Odor and taste not distinctive.

![FIGURE 3. Marasmius somalomoensis (JES 129, JES 165, JES 181) a) basidiospores; b) basidioles; c) basidia; d) cheilocystidia; e) pileipellis cells. Scale bar = 10 µm. Illustrated by J.E. Shay.](image)

Basidiospores (6.4–) 7.2–10.4 × 3.2–4.8 µm [x̄ = 7.9–9.3 × 3.6–3.9 µm; x̄ = 8.53 ± 0.70 × 3.79 ± 0.10; Q = 1.5–2.8; Q = 2.18–2.44; Q = 2.27 ± 0.10, n = 25, s = 3], ellipsoid to narrowly ellipsoid, smooth, hyaline, inamylloid, thin-walled. Basidia 16.8–22.4 × 6.4–7.2 µm, cylindrical to subclavate, 4-spored, hyaline, inamylloid, thin-walled; sterigmata 3.2–4.8 × 0.8 µm. Basidioles 18.4–24 × 5.6–8 µm, clavate to fusoid, hyaline, inamylloid, thin-walled.
Cheilocystidia few, of Rotalis-type broom cells; main body 7.2–28.8 × 6.4–21.6 μm, cylindrical to clavate, subglobose or irregular, hyaline, inamyloid, thin-walled; divergent setulae 0.3–1.6 × 0.8 μm, dense, cylindrical, hyaline, inamyloid, thin-walled. Pleurocystidia absent. Pileipellis mottled, a hymeniform layer of Rotalis-type broom cells; main body 12–31.2 × 8.8–24 μm, globose to subglobose, broadly clavate or irregular, hyaline, inamyloid, thin-walled; divergent setulae 0.5–1.6 × 0.5–1.6 μm, dense, cylindrical, hyaline to brown, inamyloid, thin-walled. Pileus trama interwoven; hyphae 1.6–12 μm diam, cylindrical to inflated, smooth, hyaline, inamyloid, thin-walled. Lamellar trama regular; hyphae 1.6–14.4 μm diam, cylindrical to inflated, smooth, inamyloid, thin-walled. Stipe tissue monomitic; cortical hyphae 2–8.8 μm diam, parallel, cylindrical, dark brown, dextrinoid, thick-walled; medullary hyphae 1.6–8 μm diam, parallel, cylindrical to inflated, hyaline, inamyloid, thin-walled. Caulocystidia absent. Clamp connections present.

Habit, habitat and known distribution:—Solitary or in small gregarious clusters on *Uapaca densifolia* (dicot, Phyllanthaceae). Africa (Cameroon, DR Congo), Madagascar.


Notes:—Described originally from Cameroon, *Marasmius somalomoensis* is characterized by a tan to pale brown pileus, subdistant (11–14), collariate, non-marginate lamellae, a brown stipe with cortical hyphae that do not turn olive in KOH, basidiospores in the range 7.2–10.4 × 3.2–4.8 µm with mean 8.5 × 3.8 µm, *Rotalis*-type broom cells, and growth on dicotyledonous leaves. It is nearly indistinguishable from *M. colorimarginatus*, which differs in forming a darker brown pileus, greyish brown lamellae with brown margins, and stipe cortical hyphae that are olive in KOH.

ITS sequences of the Madagascar material of *M. somalomoensis* (KX149002, KX149003, KX149004) are more than 3% different from the single available sequence of *M. somalomoensis* (EU935559) derived from a specimen from Thailand (NW 232), but it should be noted that the Thai material is reported as forming pilei with more reddish brown tones and more lamellae (12–18) with brown edges. It is possible that the Thai material represents a species different from the African *M. somalomoensis*. (Fig. 1c).

3. *Marasmius apatelius* Singer, Bull. Jard. Bot. État Brux. 34: 332. 1964. (Fig. 4, Plate 1)

Type:—DR CONGO, Kisantu, 20 March 1907, *H. Vanderyst* s.n. (BR 11377–28, as *M. friesianus*).

Description:—*Pileus* 2–5 mm diam, campanulate to umbilicate, with a dark brown (5F4) papilla; margin sulcate to plicate; surface dry, glabrous; greyish orange (5B4–5, 6A–C2) to buff, dries dark brown. *Context* thin, buff. *Lamellae* adnate to a collarium, distant (9–12), broad (2–3 mm), white to orange-white (5A2), non-marginate. *Stipe* 18–54 × <0.5 mm, central, hollow, thin, wiry, insitious; surface glabrous, dark brown (6F8). *Odor and taste* not distinctive.

**FIGURE 4. Marasmius apatelius (JES 150, JES 203) a) basidiospores; b) basidia; c) basidioles; d) cheilocystidia; e) pileipellis cells. Scale bar = 10 µm. Illustrated by J.E. Shay.**

*Basidiospores* (7.2–) 8–10.4 (–11.2) × 3.2–4.8 (–5) µm [x<sub>av</sub> = 8.9–9.0 × 4.0–4.1 µm; x<sub>4sp</sub> = 8.94 ± 0.02 × 4.02 ± 0.03; Q = 1.8–2.8; Q<sub>av</sub> = 2.23–2.25; Q<sub>4sp</sub> = 2.24 ± 0.02, n = 25, s =2], ellipsoid, smooth, hyaline, inamyloid, thin-walled. *Basidia* 23.2–24.8 × 6.4–8 µm, clavate, 4-spored, hyaline, inamyloid, thin-walled. *Basidioles* 12–22.4 × 4–8 µm, clavate to fusoid or cylindrical, hyaline, inamyloid, thin-walled. *Cheilocystidia* abundant, of *Rotalis*-type broom cells; main body 7.6–23.2 × 8–14.4 µm, globose to subglobose or broadly clavate, hyaline, inamyloid, thin-walled; divergent setulae 0.5–3.2 × 0.5–2 µm, cylindrical to conical, hyaline, inamyloid, thin-walled. *Pleurocystidia* absent.
Pileipellis not mottled, a hymeniform layer of \textit{Rotalis}-type broom cells; main body 12–27.2 × 8–27.2 μm, globose to broadly clavate, hyaline, inamyloid, thin-walled; divergent setulae 0.5–2 × 0.5–2 μm, numerous, cylindrical, hyaline to brown, dextrinoid, thin-walled. \textit{Pileus trama} interwoven; hyphae 1.6–12.8 μm diam, cylindrical to inflated, smooth, hyaline, inamyloid, thin-walled. \textit{Lamellar trama} regular; hyphae 1.6–8 μm diam, cylindrical to inflated, smooth, hyaline, inamyloid, thin-walled. \textit{Stipe tissue} monomitic; cortical hyphae 2.4–4 μm diam, parallel, cylindrical, yellow, dextrinoid, thick-walled; medullary hyphae 3.2–6 μm diam, parallel, cylindrical, hyaline, inamyloid, thin-walled. \textit{Caulocystidia} absent. Clamp connections present.

Habit, habitat and known distribution:—In gregarious clusters on \textit{Uapaca littoralis} (dicot, Phyllanthaceae). Africa (DR Congo, Tanzania, Uganda), Madagascar, Thailand.

Material examined:—MADAGASCAR. Region Atsinanana, District Brickaville, Commune Andevoranto, Andavakimanen Forest, elev.-1 m, GPS: 18° 53.231' S, 49° 07.490' E, 28 January 2014, \textit{J.E. Shay} 203 (SFSU); Region Vatovavy-Fitovinany, District Ifanadiana, Commune Randomafana, Ranomafana National Park, Piste B, elev. 1004 m, GPS: 21° 15.413' S, 47° 25.253' E, 22 January 2014, \textit{J.E. Shay} 150 (SFSU).

Notes:—\textit{Marasmius apatelius} is characterized by small (2–5 mm diam), greyish orange to buff pileus, distant (9–12) collariate lamellae, a dark brown, wiry insitious stipe, basidiospores in the range 8–10.4 × 3.2–5 μm with mean 8.9 × 4.0 μm, \textit{Rotalis}-type broom cells, and growth on dicotyledonous leaves. Described originally from the DR Congo, the Madagascar material matches nicely the African specimens reported by Antonín (2007) and Thai material reported by \textit{Wannathes} et al. (2009a). An ITS sequence of the holotype of \textit{M. andasibensis} var. \textit{obscurostipitatus} Antonín & Buyck (KX149005) places the taxon in a clade with \textit{M. apatelius} (Fig. 1c), and differs primarily in several 21–25 base pair insertions. For a comparison with numerous other members of \textit{Marasmius} sect. \textit{Marasmius} subsect. \textit{Marasmius}, refer to Antonín (2007).


Type:—MADAGASCAR. Andasibe, 23 February 2000, \textit{B. Buyck} 00.1704 (PC!).

For a description and illustrations of Madagascar material, refer to Antonín and Buyck (2006). Repeated attempts to sequence material from collection \textit{Buyck} 00.1704 (PC) were unsuccessful.


Type:—MADAGASCAR. Andasibe, 21 February 1997, \textit{B. Buyck} 00.1699b (PC!).

For a description and illustrations of Madagascar material, refer to Antonín & Buyck (2006). The holotype collection \textit{Buyck} 00.1699b (PC) was sequenced (KX149005) and falls in a clade with \textit{M. apatelius} but with low support.

\textbf{Ib. Subsect. \textit{Sicciformes} Antonín}


– Type species: \textit{Marasmius curreyi} Berk. & Broome.


Type:—MADAGASCAR. Andasibe, 22 February 1997, \textit{B. Buyck} 97.011 (PC!).

For a description and illustrations of Madagascar material, refer to Antonín & Buyck (2006). Repeated attempts to sequence material from collection \textit{Buyck} 97.011 (PC) were unsuccessful.


Type:—VIETNAM. Hanoi, Keso, 31 May 1890, \textit{Bon} 4397 (FH).

For a description and illustrations of Madagascar material, refer to Antonín & Buyck (2006). Repeated attempts to sequence material from collection \textit{Buyck} 97.156 (PC) were unsuccessful.
8. *Marasmius conicopapillatus* Henn., Bot. Jb. 22: 100. 1895. (Fig. 5, Plate 2)

Type:—CAMEROON. Ekundu–Liongo, 20 May 1892, *P.* Dusén 41 (UPS).

Description:—*Pileus* 1–4 mm diam, convex to plano-convex, umbilicate, with prominent dark brown conical papilla; margin sulcate; surface dull, dry, glabrous; white at margins becoming tan to cream towards disk. *Context* thin (<1 mm), buff. *Lamellae* adnate to a collarium, distant (11–12), no lamellulae, ventricose, buff to cream (5A2), non-marginate. *Stipe* 2–9 × <0.5 mm, central, wiry, pliant, hollow; surface glabrous; initially white darkening to light brown or brown (6E8) at the base. *Odor and taste* not distinctive.

![Figure 5](https://example.com/figure5.png)

**FIGURE 5. Marasmius conicopapillatus (JES 180)** a) basidiospores; b) basidia; c) basidioles; d) cheilocystidia; e) pileipellis cells. Scale bar = 10 µm. Illustrated by J.E. Shay.

*Basidiospores* (7.2–) 8–9.6 × (3.8–) 4–4.4 µm \[x_{m} = 8.50 \pm 8.4 \times 4.02 \pm 0.12 \mu m; Q = 1.36–2.40; Q_{m} = 2.11 \pm 0.18, n = 25, s = 1\], ellipsoid, smooth, hyaline, inamylloid, thin-walled. *Basidia* 19.2–28 × 4.8–6.4 µm, clavate, 4-spored, hyaline, inamylloid, thin-walled; sterigmata 3.2–4.8 × 1.6 µm. *Basidioles* 12–29.6 × 3.3–5.6 µm, clavate, hyaline, inamylloid, thin-walled. *Cheilocystidia* of *Siccus*-type broom cells; main body 9.6–16 × 7.2–8 µm, clavate to subglobose or irregular, seldom lobed, hyaline, inamylloid, thin-walled; apical setulae 0.8–2.4 × 0.8 µm, cylindrical, hyaline, inamylloid, thin-walled. *Pleurocystidia* absent. *Pileipellis* not mottled, a hymeniform layer of *Siccus*-type broom cells; main body 7.2–20 × 4.8–10.4 µm, clavate to subglobose, seldom lobed, hyaline, inamylloid, thick-walled; apical setulae 0.8–3.2 × 0.8 µm, cylindrical, hyaline, inamylloid, thick-walled. *Pileus trama* interwoven; hyphae 3.2–14.4 µm diam, cylindrical to inflated, smooth, hyaline, inamylloid, thin-walled. *Lamellar trama* regular; hyphae 2.4–6.4 µm diam, cylindrical, hyaline, inamylloid, thin-walled. *Stipe tissue* monomitic; cortical hyphae 3.2–8.8 µm diam, cylindrical to slightly inflated, smooth, hyaline, dextrinoid, thick-walled; medullary hyphae 0.8–22.4 µm diam, cylindrical to inflated, smooth, hyaline, inamylloid, thin-walled. *Caulocystidia* absent. *Clamp connections* present.

Habit, habitat and known distribution:—Gregarious, in clusters on leaves of *Eugenia* (dicot, Myrtaceae). Africa (Burundi, DR Congo, Cameroon, Ghana, Ivory Coast, Nigeria, Uganda, Sierra Leone), Indonesia (Java), Madagascar.


Notes:—*Marasmius conicopapillatus* is distinguished by small (1–4 mm diam), sulcate, umbilicate pileus with a prominent dark brown conical papilla and initially white margin that develops tan to cream tones in age, distant (11–12) non-marginate collariate lamellae, a short stipe initially white to cream and becoming brown in age, basidiospores with mean 8.5 × 4 µm, *Siccus*-type cheilocystidia and pileipellis broom cells, and growth on dicotyledonous leaves. The Madagascar specimen (*JES 180*) matches nicely the description of African material by Antonín (2007). Unfortunately, repeated attempts to obtain an ITS sequence were unsuccessful.

Type:—UNITED KINGDOM. Fineshade, 1859, M.J. Berkeley (K).

For a description and illustrations of Madagascar material, refer to Antonín & Buyck (2006). An ITS sequence from the Madagascar collection *Buyck* 97.374 (PC) (KX148980) formed a weakly supported trichotomy with a Malaysian sequence of *M. curreyi* (FJ431237) and *M. graminum* (JN943595) from Denmark.
10. *Marasmius aff. curreyi* (Fig. 6, Plate 2)

Description:—*Pileus* 2–7 mm diam, campanulate, umbilicate, with a dark brown papilla; margin plicate to sulcate; surface dry, glabrous; tan to light brown with greyish tones (6D6) or cream (5A2) becoming paler at the margin. *Context* thin, white. *Lamellae* adnate to a collarium, distant (10–11), no lamellulae, narrow (0.3–0.5), white to cream, non-marginate. *Stipe* 5–30 × <0.5 mm, central, cylindrical, hollow, wiry, insititious; surface glabrous; dark brown. *Odor and taste* not distinctive.

**FIGURE 6.** *Marasmius aff. curreyi* (JES 135) a) basidiospores; b) basidioles; c) pileipellis cells. Scale bar = 10 μm. Illustrated by J.E. Shay.

*Basidiospores* (7.2–) 8–9.6 × 4–4.8 μm [x̄ = 9.02 ± 0.71 × 4.29 ± 0.37 μm; Q = 1.80–2.40; Qm = 2.11 ± 0.20, n = 25, s = 1], ellipsoid, smooth, hyaline, inamyloid, thin-walled. *Basidia* 4–14.4 μm, clavate to cylindrical, 4-spored, hyaline, inamyloid, thin-walled; sterigmata 0.8 × 0.2 μm. *Basidioles* 12–20 × 4.8–8 μm, clavate to cylindrical, hyaline, inamyloid, thin-walled. *Cheilocystidia* not observed. *Pleurocystidia* absent. *Cheilocystidia* not observed. *Pileipellis* mottled, a hymeniform layer of *Siccus*-type broom cells; main body 8–16 × 6.4–8.8 μm, clavate, hyaline, inamyloid, thin-walled; apical setulae 0.8–2.4 × 0.8–2.4 × 0.8–1.6 μm, cylindrical to conical, brown to hyaline, inamyloid, thin-walled. *Pileus trama* interwoven; hyphae 2.4–8.8 μm diam, cylindrical to inflated, smooth, hyaline, inamyloid, thin-walled. *Lamellar trama* regular; hyphae 2.4–12 μm diam, cylindrical, smooth, dextrinoid, thin-walled. *Stipe tissue* monomitic; cortical hyphae 2–8 μm diam, parallel, cylindrical, smooth, dark brown to brownish yellow, sometimes dextrinoid, thin-walled; medullary hyphae 2–6 μm diam, parallel, cylindrical, smooth, hyaline, weakly dextrinoid, thin-walled. *Caulocystidia* absent. *Clamp connections* present.

Habit, habitat, and known distribution:—Solitary to gregarious on stems of *Justicia* (Acanthaceae). Madagascar.


Notes:—Distinctive features of Madagascar populations of *Marasmius aff. curreyi* are a rather small (2–7 mm diam) tan to light brown pileus with yellowish brown tones that soon fades to tan, distant (10–11) collariate non-marginate lamellae, a relatively short (<30 mm) stipe, basidiospores in the range 8–9.6 × 4–4.8 μm, and growth on dead stems. An ITS sequence of material from Madagascar (KX148980) identified as *M. curreyi* by Antonín & Buyck (2006) was only 96.3% similar to *JES 135* (KX149008). The latter Madagascar sequence, however, was nearly indistinguishable from material determined as *M. curreyi* from Korea (FJ936152) (Fig. 1c). Although the morphology of the Madagascar material is similar to that of *M. curreyi*, this species was described originally from England and no sequences of U.K. or European material determined as *M. curreyi* are available for comparison. Accordingly, we recognize our material as *M. aff. curreyi*.


Type:—MAURITIUS. Rivière du Rempart, Grand Baie, Bougain Villas, 4 March 1993, leg. Hausknecht MA04a (WU 14896).

For a description and illustrations of Madagascar material, refer to Antonín & Buyck (2006). Material from collection *A. Hausknecht MA04a* (WU 14896) was unavailable for sequencing.
12. *Marasmius rubrobrunneus* J.E. Shay & Desjardin, sp. nov. (Fig. 7, Plate 2)

MycoBank no.: MB818617


Etymology:— *rubro*—reddish, *brunneus*—brown, referring to the dark reddish brown pileus.

Description:— *Pileus* 4–9 mm diam, campanulate, umbilicate, with a dark brown papilla; margin sulcate; surface glabrous; dark reddish brown (7–8E–F5–8). *Context* thin, dark reddish brown. *Lamellae* adnate to a collarium, distant (11–12), broad, no lamellulae; white to buff (4A2) with reddish brown edges. *Stipe* 16–26 × <0.5 mm, central, hollow, twisted, wiry, insititious; surface glabrous; dark brown. *Odor and taste* not distinctive.

**FIGURE 7. Marasmius rubrobrunneus (JES 183, JES 191) a) basidiospores; b) basidioles; c) cheilocystidia; d) pileipellis cells. Scale bar = 10 µm. Illustrated by J.E. Shay.**

*Basidiospores* (12–) 13.6–19.2 × 2.4–4 µm [x<sub>av</sub> = 14.9–16.5 × 3.2 µm; x<sub>num</sub> = 15.71 ± 1.13 × 3.2 ± 0.06; Q = 2.8–6.7; Q<sub>av</sub> = 4.6–5.18; Q<sub>num</sub> = 4.89 ± 0.41, n = 25, s = 2], narrowly fusoid, smooth, hyaline, inamyloid, thin-walled. *Basidia* not observed. *Basidioles* 17.6–26.4 × 4.8–7.2 µm, clavate to fusoid, hyaline, inamyloid, thin-walled. *Cheilocystidia* abundant, of *Siccus*-type broom cells; main body 12–20 × 6.4–8 µm, clavate to cylindrical or subglobose, seldom bilobed, light brown, inamyloid, thick-walled; apical setulae 0.8–4.8 × 0.8–2.4 µm, cylindrical to conical, sometimes branched, light brown, inamyloid, thick-walled. *Pleurocystidia* absent. *Pileipellis* mottled, a hymeniform layer of *Siccus*-type broom cells; main body 9.6–19.2 × 6.4–12 µm, clavate to cylindrical or subglobose, brown to hyaline, inamyloid, thick-walled; apical setulae 0.8–6.4 × 0.8–2.4 µm, cylindrical to conical, obtuse, seldom branched, brown to hyaline, inamyloid, thick-walled. *Pileus trama* interwoven; hyphae 3.2–8.8 µm diam, smooth, hyaline, inamyloid, thin-walled. *Stipe tissue* monomitic; cortical hyphae 2.4–8 µm diam, parallel, cylindrical, smooth, light brown to brown, dextrinoid, thick-walled; medullary hyphae 4–10.4 µm diam, parallel, cylindrical, smooth, light yellow to hyaline, inamyloid, thin-walled. *Caulocystidia* absent. *Clamp connections* present.

Habit, habitat and known distribution:—Solitary or in small gregarious clusters on a variety of leaf litter and stems of *Uapaca densifolia* (Phyllanthaceae), *Canarium boivinii* (Burseraceae), *Pandanus*, *Contium* and other unknown dicots. Madagascar.


Notes:—Features of *Marasmius rubrobrunneus* include a small (4–9 mm diam), sulcate, dark reddish brown pileus, distant collariate lamellae with reddish brown edges, a black wiry insititious stipe, basidiospores with mean 15.7 × 3.2 µm (Q<sub>av</sub> = 4.9), *Siccus*-type broom cells, and growth on dicotyledonous leaves and twigs. Morphologically,
the new species is nearly indistinguishable from *M. purpureobrunneolus* Henn., described originally from Java. The latter species has been redescribed several times (Desjardin et al. 2000, Tan et al. 2009, Wannathes et al. 2009a) from material collected in southeast Asia, and is distinguished by a dark purplish brown pileus and basidiospores in the range 12–17 (–19) × 2.5–5 µm, with means in the range 14.0–14.8 × 3.2–4.1µm (Q_{mr} = 3.6–4.5). In comparison, *Marasmius rubrobrunneus* has a dark reddish brown pileus lacking purple tones, and basidiospores with means in the range 14.9–16.5 × 3.2 µm, i.e., slightly longer and narrower than in *M. purpureobrunneolus*. Although this variability may seem trivial, a comparison of the ITS sequence of the Madagascar holotype specimen (KX148989) with two specimens of *M. purpureobrunneolus* from Thailand (EU935556, EU935557) show only 85% similarity. In the ITS phylogenetic analysis (Fig. 1c), *M. rubrobrunneus* is sister to *M. purpureobrunneolus* with good support (81% BS; 1.0 PP).

13. *Marasmius brunneoaurantiacus* Antonín & Buyck, Fungal Diversity 23: 24. 2006. (Fig. 8, Plate 3)

Type:—MADAGASCAR. Ranomafana National Park, 4 February 1999, leg. B. Buyck & G. Eyssartier, Buyck 99.450 (PC!).

Description:—*Pileus* 5–20 mm diam, campanulate to hemispherical, umbilicate, with a dark brown papilla; margin sulcate to plicate; surface dry, glabrous; reddish brown (7C–E7–8, 8D8, 6D6). *Context* thin (<1 mm), white to cream (4A3). *Lamellae* adnate to a collarium, subdistant (12–16), broad (0.5–1mm), cream, non-marginate or with brown edges. *Stipe* 16–67 × 0.2–0.4 mm, central, cylindrical, wiry, pliant, insititious; surface glabrous, light brown at apex to dark brown (7E6) towards the base. *Odor and taste* not distinctive.

**FIGURE 8.** *Marasmius brunneoaurantiacus* (*JES 113, JES 137, JES 166, JES 218*) a) basidiospores; b) basidia; c) basidioles; d) cheilocystidia; e) pileipellis cells. Scale bar = 10 µm. Illustrated by J.E. Shay.

**Basidiospores** (6.2–) 8–10.4 (–11.2) × (3.2–) 4–4.8 (–5.6) µm [x_{mr} = 8.8–9.5 × 4.1–4.6 µm; x_{mm} = 9.03 ± 0.3 × 4.28 ± 0.2; Q = 1.3–3.0; Q_{mr} = 2.0–2.3; Q_{mm} = 2.14 ± 0.1, n = 25, s = 6], ellipsoid, smooth, hyaline, inamyloid, thin-walled. **Basidia** 16.8–27.2 × 5.6–6.4 µm, clavate, 4-spored, hyaline, inamyloid, thin-walled; sterigmata 3.2–4 × 1.6 µm. **Basidioles** 14.4–30.4 × 3.2–8 µm, clavate to fusoid, hyaline, inamyloid, thin-walled. **Cheilocystidia** few to abundant, of *Siccus*-type broom cells; main body 12–29.6 × 4.8–14.4 µm, cylindrical to clavate, subglobose or irregular, often 2–3-lobed, hyaline, inamyloid, thin-walled; apical setulae dense, 0.8–5.6 × 0.8–2.4 µm, cylindrical to conical, hyaline, inamyloid, thick-walled. **Pleurocystidia** absent. **Pileipellis** mottled, a hymeniform layer of *Siccus*-type broom cells; main body 8.8–20 × 6.4–8.8 µm, clavate to subglobose or irregular, seldom 2–4-lobed, hyaline, inamyloid, thin-walled; apical setulae 0.8–7.2 × 0.8–2.4 µm, cylindrical to conical, seldom branched, hyaline to dark
brown, inamyloid, thick-walled. *Pileus trama* interwoven; hyphae 1.6–16 µm diam, cylindrical to inflated, smooth, hyaline, inamyloid, thin-walled. *Lamellar trama* regular; hyphae 2.4–14.4 µm diam, cylindrical to inflated, smooth, hyaline, inamyloid, thin-walled. *Stipe tissue* monomitic; cortical hyphae 3.2–10.4 µm diam, parallel, cylindrical to inflated, smooth, brown, dextrinoid, thick-walled; medullary hyphae 3.2–27 µm diam, parallel, cylindrical to inflated, smooth, hyaline, dextrinoid, thick-walled. *Caulocystidia* absent. *Clamp connections* present.

Habit, habitat and known distribution:—Solitary or gregarious on leaves and stems of *Uapaca* (Phyllanthaceae), *Cryptocarya* (Lauraceae), *Maesa* (Primulaceae), *Volina madagascariensis* (bamboo) and *Cephalostachium vigueri* (bamboo). Madagascar.


Notes:—*Marasmius brunneoaurantiacus* is characterized by a rather large (5–20 mm diam), light brown to brown or reddish brown pileus, subdistant (12–16), collariate, non-marginate or brown-marginate lamellae, a relatively long stipe (up to 67 mm), basidiospores in the range 8.8–10.4 (−11) × 4–4.8 µm, *Siccus*-type borough cells, and growth mainly on bamboo leaves, occasionally on dicot leaves.

Antonín & Buyck (2006) described the species as having brown-marginate lamellae, basidiospores in the range 9.5–11 × 4.5–6 µm, and growth on dead leaves of *Uapaca ferruginea* (Buyck 99.439). The holotype specimen (Buyck 99.450), however, is undoubtedly growing on bamboo leaves. Our material of *M. brunneoaurantiacus* occurs mainly on bamboo leaves, (although several specimens are on both grasses and dicot leaves (*JES 115, JES 133*)), has basidiomes with brown-marginate or non-marginate lamellae, and the basidiospores are in the shorter end of the range. In other features, our material is indistinguishable from the holotype. An ITS sequence of the holotype specimen (KX148978) shows 99.1–99.6% similarity to seven additional specimens from Madagascar (KX149009–KX149014, KX149016), forming a clade with 100% BS and 1.0 PP support (Fig. 1c).

14. *Marasmius crinisequi* F. Muell. ex Kalchbr., in Kalchbrenner, Grevillea 8(48): 153. 1880. (Fig. 9, Plate 3)

= *Androsaceus crinisequi* (F. Muell. ex Berk.) Overeem, De nuttige planten van Nederlandsch Indië 1: 69. 1927.

Type:—AUSTRALIA. North Queensland, Rockingham Bay, *F. von Mueller s.n.* (K(M) 99658, lectotype).

Description:—*Pileus* 1–2 mm diam, convex to campanulate, umbilicate, with a dark brown papilla; margin plicate to sulcate; surface dull, dry, glabrous; light brownish orange (5B–6). *Context* thin, buff. *Lamellae* adnate to a collarium, distant (6), no lamellulæ, broad, buff (5A3), non-marginate. *Stipe* 2–4 × <0.5 mm, central, wiry, plant, arising directly from coarse black rhizomorphs; surface glabrous; dark brown. *Odor and taste* not distinctive.

*Basidiospores* (8.8–) 9.6–13.6 × 4–5.6 µm [x m = 10.14 ± 1.24 × 4.54 ± 0.50 µm; Q = 1.57–3.40; Q m = 2.27 ± 0.18, n = 25, s = 1], ellipsoid, smooth, hyaline, inamyloid, thin-walled. *Basidiation* 18.4–28 × 8.8–9.6 µm, clavate to broadly clavate, 4-spored, hyaline, inamyloid, thin-walled; sterigmata 4.4–8 × 1.6 µm. *Basidioles* 16.8–24 × 5.6–7.2 µm, clavate to fusoid, hyaline, inamyloid, thin-walled. *Cheilocystidia* of *Siccus*-type borough cells; main body 8.8–15.2 × 6.4–10.4 µm, clavate to broadly clavate, seldom 2–3-lobed, hyaline, inamyloid, thin-walled; apical setulae 0.8–4.8 × 0.8–1.6 µm, cylindrical, obtuse, sometimes branched, hyaline, inamyloid. *Pleurocystidia* absent. *Pileipellis* not mottled, a hymeniform layer of *Siccus*-type borough cells; main body 10.4–16 × 6.4–10.4 µm, cylindrical to clavate or broadly clavate, seldom 2–3-lobed, hyaline, inamyloid, thin-walled; apical setulae 0.8–5.6 × 0.8–1.6 µm, cylindrical, seldom branched, pale brown, inamyloid, thin-walled. *Pileus trama* interwoven; hyphae 2.4–6.4 µm diam, cylindrical, smooth, hyaline, inamyloid, thin-walled. *Lamellar trama* regular; hyphae 1.6–7.2 µm diam, cylindrical, smooth, hyaline,
inamyloid, thin-walled. Stipe tissue monomitic; cortical hyphae 3.2–4.8 μm diam, cylindrical, smooth, dark brown, inamyloid, thick-walled; medullary hyphae 2.4–9.6 μm diam, cylindrical to inflated, smooth, hyaline, dextrinoid, thin-walled. Caulocystidia absent. Clamp connections present.

FIGURE 9. *Marasmius crinisequi* (JES 176) a) basidiospores; b) basidia; c) basidioles; d) cheilocystidia; e) pileipellis cells. Scale bar = 10 μm. Illustrated by J.E. Shay.

Habit, habitat and known distribution:—Solitary arising directly from rhizomorphs, attached to debris of *Uapaca densifolia, Anthocleista madagascarensis, Omphalea oppositifolia, and Noronhia*. Pantropical, common in Africa (Burundi, Cameroon, DR Congo, Ghana, Ivory Coast, Kenya, Nigeria, Sierra Leone), Asia, Australia, Caribbean region, Madagascar.


Notes:—*Marasmius crinisequi*, commonly called the horsehair fungus, forms basidiomes that arise directly from coarse black rhizomorphs. The species is often arboreal, with the rhizomorphs forming a net-like structure that captures falling leaves. The orange to light brown pileus is less than 2 mm diam, sulcate, with a small dark papilla in the umbilicus, distant (6) lamellae, a short (2–4 mm), dark brown stipe, basidiospores with mean 10.1 × 4.5 μm, and *Siccus*-type cheilocystidia and pileipellis broom cells. It represents a pantropical species or complex of species in need of more phylogenetic analyses with multiple genes. Repeated attempts to obtain ITS sequences from the Madagascar material were unsuccessful.

15. *Marasmius cf. subruforotula* Singer, Bull. Jard. Bot. État Brux. 34: 339. 1964. (Fig. 10, Plate 3)

Type:—DR CONGO. Equateur Province, Eala, July 1907, L. Pynaert 1608 (BR 11515–69).

Description:—Pileus 2–7 mm diam, campanulate to convex, umbilicate, with a dark brown (6F8) conical papilla; margin plicate to sulcate; surface dry, glabrous; greyish orange to brownish orange or light brown (5–6B–D4–8). Context thin, white. Lamellae adnate to a collarium, distant (9–12), no lamellulae, broad, white to buff (4A2), non-marginate. Stipe 6–40 × <0.5 mm, central, cylindrical, wiry, hollow, insititious; surface glabrous; dark brown to black. Odor and taste not distinctive.

Basidiospores 7.2–9.6 (–10.4) × 3.2–4 μm \[x_m = 8.8 ± 0.2 × 3.8 ± 0.1 \mu m; Q = 1.8–2.6; Q_m = 2.06–2.19; Q_m = 2.14 ± 0.1, n = 24–25, s = 3\], ellipsoid, smooth, hyaline, inamyloid, thin-walled. Basidia 19.2–32 × 4–8 μm, clavate 4-spored, hyaline, inamyloid, thin-walled; sterigmata 1.6–4.8 × 0.8–1.6 μm. Basidioles 16.8–26.4 × 4–7.2 μm, clavate, hyaline, inamyloid, thin-walled. Cheilocystidia numerous, of *Siccus*-type broom cells; main body 8.8–18.4 × 5.6–10.4 μm, clavate to cylindrical or subglobose, hyaline, inamyloid, thin-walled; apical
setulae 0.5–5.6 × 0.8–1.6 μm, conical to cylindrical, hyaline, inamyloid, thin-walled. Pleurocystidia absent. Pileipellis mottled, a hymeniform layer of Siccus-type broom cells; main body 11.2–20 × 5.6–12.8 μm, clavate to cylindrical, subglobose or irregular, hyaline, inamyloid, thick-walled; apical setulae 0.8–5.6 × 0.8–1.6 μm, cylindrical to conical, sometimes branching, hyaline to yellow or brown, inamyloid, thin-walled. Pileus trama interwoven; hyphae 1.6–11.2 μm diam, cylindrical to inflated, smooth, hyaline, inamyloid, thin-walled. Lamellar trama regular; hyphae 1.6–9.6 μm diam, cylindrical to inflated, smooth, hyaline, inamyloid, thin-walled. Stipe tissue monomitic; cortical hyphae 3–5.6 μm diam, parallel, cylindrical, smooth, light brown to brown, dextrinoid, thick-walled; medullary hyphae 1.6–9.6 μm diam, parallel, cylindrical to inflated, smooth, hyaline, inamyloid, thin-walled. Caulocystidia absent. Clamp connections present.


Habit, habitat and known distribution:—Solitary or gregarious on a variety of monocotyledonous and dicotyledonous leaves including, but not limited to Mallotus (Euphorbiaceae), Pandanus (Pandanaceae), Vernonia (Asteraceae), Noronhia (Oleaceae), Blotia (Euphorbiaceae), Coffea mangoroensis (Rubiaceae), Alafia (Apocynaceae), Uapaca thouarai, Uapaca densifolia (Phyllanthaceae), Ambavia (Annonaceae), Psychotria (Rubiaceae) and Carallia brachiata (Rhizophoraceae). Africa (Cameroon, DR Congo, Nigeria, Tanzania, Uganda), Madagascar, Thailand.

Notes:—The material from Madagascar shows closest phenetic similarity to *Marasmius subruforotula*. The Madagascar taxon is distinguished by a small (2–7 mm diam), brownish orange pileus with a distinct dark brown papilla, distant (9–12), collariate, non-marginate lamellae, dark brown insititious stipe, basidiospores in the range 7.2–10.4 × 3.2–4 µm, *Siccus*-type broom cells, and growth on dicotyledonous leaves and twigs. *Marasmius subruforotula*, described from the DR Congo, has reddish brown pilei, reddish brown-marginate lamellae and broader basidiospores (4–5 µm wide). Our material matches that reported from Madagascar by Antonín & Buyck (2006) as *M. cf. subruforotula*. Pegler (1977) and Antonín (2007) report *M. subruforotula* from throughout Africa with morphology that overlaps that reported here; however, ITS sequences of material from Príncipe (Grace et al., unpubl.) are quite different from those reported here from Madagascar specimens, although they are sister to each other (100% BS, 1.0 PP support; Fig. 1c), suggesting that they represent different species. Until additional materials representing a wide distribution of specimens from the African continent are compared, we tentatively recognize the Madagascar taxon as *Marasmius cf. subruforotula*.

16. *Marasmius madagascariensis* J.E. Shay & Desjardin, sp. nov. (Fig. 11, Plate 4)

MycoBank no.: MB 818620


Etymology:—*madagascariensis*—occurring in Madagascar.

Description:—Pileus 2–6 mm diam, convex to campanulate, umbilicate, with a reddish brown papilla; margin sulcate; surface dry, glabrous; orangish brown (6C–D7, 5B6–7). Context thin (<1 mm), concolorous with pileus. Lamellae adnate to a collarium, subdistant (9–11), broad (0.5–1 mm), light orange (5A4) to cream, non-marginate. Stipe 10–23 × 0.1–1 mm, central, hollow, wiry, insitious; surface glabrous; black; rhizomorphs present. Odor and taste not distinctive.

Basidiospores 8.8–12.8 × 4–5.6 (~7.2) µm [x_{nr} = 11.3–11.6 × 4.8–5.0 µm; x_{mm} = 11.46 ± 0.17 × 4.90 ± 0.09 µm; Q = 1.8–3.2; Q_{nr} = 2.36–2.38; Q_{mm} = 2.37 ± 0.02, n = 21–22, s = 2], ellipsoid, smooth, hyaline, inamyloid, thin-
walled. Basidia 18.4–26.4 × 9.6–11.2 µm, clavate, 4-spored, hyaline, inamyloid. Basidioles 13.6–24.8 × 4.8–8.5 µm, clavate to cylindrical, hyaline, inamyloid, thin-walled. Cheilocystidia of Siccus-type broom cells; main body 8–19.2 × 6.4–11.2 µm, clavate to cylindrical, seldom lobed, hyaline, inamyloid, thin-walled; apical setulae 0.8–6.4 × 0.5–2 µm, cylindrical to conical, often branched, hyaline, inamyloid, thin-walled. Pleurocystidia absent. Pileipellis mottled, a hymeniform layer of Siccus-type broom cells; main body 8–16 × 6.4–16 µm, clavate or irregular, 2–3-lobed, hyaline, inamyloid, thin-walled; apical setulae 1.6–5.6 × 0.5–2 µm, cylindrical to conical, sometimes branched, yellowish brown to hyaline, inamyloid, thin-walled. Pileus trama interwoven; hyphae 2.4–4.8 µm diam, cylindrical, smooth, hyaline, inamyloid, thin-walled. Lamellar trama regular; hyphae 1.6–12 µm diam, cylindrical to inflated, smooth, hyaline, inamyloid, thin-walled. Stipe tissue monomitic; cortical hyphae 2–4 µm diam, parallel, cylindrical, smooth, brown, dextrinoid, thick-walled; medullary hyphae 2.4–8 µm diam, parallel, cylindrical, smooth, hyaline, weakly dextrinoid, thin-walled. Caulocystidia absent. Clamp connections present.

FIGURE 11. Marasmius madagascariensis (JES 139, JES 225) a) basidiospores; b) basidia; c) basidioles; d) cheilocystidia; e) pileipellis cells. Scale bar = 10 µm. Illustrated by J.E. Shay.

Habit, habitat and known distribution:—Solitary or gregarious on stems of Cyathea (tree fern, Cyatheaceae) and on debris of an unknown grass (Poaceae). Madagascar.


Notes:—Marasmius madagascariensis is characterized by small (2–6 mm diam), orangish brown pileus with a reddish brown central papilla, distant (9–11), collariate, non-marginate lamellae, a wiry stipe <23 mm long, abundant rhizomorphs, basidiospores with mean 11.5 × 4.9 µm, Siccus-type broom cells, and growth on grass leaves and tree fern stems. Morphologically it is similar to M. guyanensis Mont., a species described originally from French Guiana (South America), and subsequently reported from the Caribbean region, Indonesia, Singapore, Malaysia, Thailand and Africa. Morphologically, the Madagascar specimens are most similar to Thailand M. guyanensis where basidiomes are formed on dicot leaves and have basidiospores with mean width 3.8 µm. In comparison, the Madagascar specimens differ in growing on grass leaves and tree fern stems and have basidiospores with mean width 4.9 µm. ITS sequences of Madagascar material of M. madagascariensis (KX149015, KX149006) are on a long branch embedded in a clade with two Malaysian specimens determined as M. guyanensis (FJ431246, FJ431247; Tan et al. 2009), two specimens of M. crinisequi, and two Thai specimens of M. guyanensis (EU935552, EU935553; Wannathes et al. 2009a). In addition, the Madagascar specimens are morphologically similar to M. aff. guyanensis reported from the island of Principe (DED 8285, Grace et al., unpubl.), but the latter has longer and narrower basidiospores (12.5–15 × 3.5–4.5 µm), and
an insertion of 38 base pairs (between 593–630) in the ITS region. Because of its distribution in Madagascar, subtle differences in basidiospore size and substrate, and ITS sequence differences, we recognize the Madagascar material as a distinct species.

II. Sect. Neosessiles Singer

– Type species: Marasmius neosessilis Singer


For a description and illustrations of Madagascar material of this provisionally described species, refer to Antonin & Buyck (2006). An ITS sequence of collection Buyck 97.615 (KX149007) formed an unresolved clade with sequences of M. tenuissimus and M. leveilleanus.


Type:—FRANCE. La Réunion, Forêt de Belouve, ca. 140 m elev., 13 March 1996, leg. A. Hausknecht RE 59/96 and G. Wölfel (WU 25700).

For a description and illustrations of Madagascar material, refer to Antonin & Buyck (2006). Material from collection A. Hausknecht RE 59/96 and G. Wölfel (WU 25700) was unavailable for sequencing.

III. Sect. Globulares Kühner

– Type species: Marasmius globularis (Weinm.) Fr. (= M. wynneae Berk. & Broome)

IIIa. ser. Globulares


Type:—MADAGASCAR. Massif de l’Ankaizniana, on old stump of tree in a humid mountain forest at 1500 m alt., leg. M. Decary (PC).

For a description and illustrations of Madagascar material, refer to Antonin & Buyck (2006). Material from collection M. Decary (PC) was unavailable for sequencing. It should be noted that M. sulcatipes Pat. (1924) is an illegitimate name, a later homonym of Marasmius sulcatipes Murrill [N.Amer. Fl. (New York) 9(4): 259. 1915], a species described from Cuba now recognized as belonging to the genus Gymnopus.

20. Marasmius bekolacongoli Beeli, Bull. Soc. R. Bot. Belg. 60(2): 157. 1928. (Fig. 12, Plate 4)

Type:—DR CONGO. Equateur Province, Eala, October 1923, M. Goossens–Fontana 204 (BR 11406–57).

Description:—Macromorphological features derived from a photograph and dried material. Pileus 85 mm diam, obtusely conical; disc rugulose; margin sulcate; surface dry, glabrous; striped, disc brown to violaceous brown, sulcae pinkish-violaceous brown, ridges pale cream to buff. Context thin. Lamellae adnexed, distant (15), cream, non-marginate. Stipe about 120 × 10 mm, central, cylindrical; surface longitudinally ridged; cream to tan or pale brown. Odor and taste not distinctive.

Basidiospores (21.6–) 24–29.4 × (3.2–) 4–6.4 μm [x̄ = 26.05 ± 2.19 × 5.17 ± 0.98 μm; Q = 3.5–7.5; Qm = 5.24 ± 1.41, n=25, s = 1], clavate, smooth, hyaline, inamyloid, thin-walled. Basidia not observed. Basidioles 35–42.4 × 8–11.2 μm, clavate, hyaline, inamyloid, thin-walled. Cheilocystidia few, 18.4–26.4 × 8–12 μm, clavate to broadly clavate or cylindrical, smooth, hyaline, inamyloid, thin-walled. Pleurocystidia absent. Pileipellis not mottled, a hymeniform layer of Globulares-type cells; main body 14.4–28 × 9.6–16 μm, clavate to broadly clavate, pyriform or subglobose, smooth, hyaline, inamyloid, thin-walled. Pileus trama interwoven; hyphae 3.2–16 μm diam, cylindrical to inflated, smooth, hyaline to pale light brown, dextrinoid, thin-walled. Lamellar trama regular; hyphae 3.2–16 μm diam, cylindrical to
inflated, smooth, hyaline, dextrinoid, thin-walled. *Stipe tissue* monomitic; cortical hyphae 3.2–8.8 μm diam, parallel, cylindrical, yellowish brown, dextrinoid, thick-walled; medullary hyphae 2.4–10.4 μm diam, parallel, cylindrical, pale yellowish, inamyloid, thick-walled. *Caulocystidia* absent. *Clamp connections* present.

**FIGURE 12.** *Marasmius bekolacongoli* (Lockwood 2131638) a) basidiospores; b) basidioles; c) cheilocystidia; d) pileipellis cells. Scale bar = 10 μm. Illustrated by J.E. Shay.

Habit, habitat and known distribution:—Solitary on undetermined dicotyledonous debris. Africa (Burundi, Cameroon, DR Congo, Kenya, Malawi, Nigeria, Tanzania, Uganda, Zimbabwe), Madagascar.

Material examined:—MADAGASCAR. Region Vatovavy-Fitovinany, District Ifanadiana, Commune Ranomafana, February 2013, T. Lockwood 2131638 (SFSU).

Notes:—The single specimen from Madagascar (Lockwood 2131638) matches nicely the descriptions of African material (Singer 1965, Pegler 1977, Antonín 2007), although the basidiospores are slightly longer. Our specimen has a violaceous brown and cream striped pileus 85 mm diam, a large (40–70 × 4–6 mm) cream longitudinally ridged stipe, basidiospores in the range 24–29.6 × 4–6.4 µm, no pleurocystidia, clavate cheilocystidia, Globulares-type pileipellis cells, no caulocystidia, and growth in leafy debris. African M. bekolacongoli are reported to have basidiospores 17.5–26 × 3.8–5.4 µm (Antonín 2007), otherwise the morphology is indistinguishable from Lockwood 2131638. Because of the basidiospore size, the Madagascar specimen would key to M. camerunensis Antonín & Mossebo, but the latter has a smaller, non-striped pileus lacking violaceous tones, and a smaller stipe (40–70 × 4–6 mm) and grows on woody debris (Antonín 2007). Only a single basidiome of M. bekolacongoli was collected and photographed by Taylor Lockwood. An ITS sequence of this specimen (KX148982) formed a weakly supported clade with other members of sect. Globulares plus M. coarctatus (sect. Sicci, ser. Spinulosi) (Fig. 1b).

The following four series were formally described within Sect. Sicci Singer, but because they represent non-monophyletic lineages (see Results above) they are herein informally placed in Sect. Globulares for pragmatic reasons; no formal transfers are implied.

IIIb. ser. Spinulosi

– Type species: Marasmius cohaerens (Pers.) Cooke & Quél.

21. Marasmius dendrosetosus J.E. Shay & Desjardin, sp. nov. (Fig. 13, Plate 5)

MycoBank no.: MB 818619
Holotype:—MADAGASCAR. Region Atsinanana, District Brickaville, Commune Andevoranto, Andavakimena Forest, elev. 0–8 m, GPS: 18˚ 53.231’ S, 49˚ 07.490’ E, 28 January 2014, J.E. Shay 203 (SFSU).
Etymology:—dendro-setosus—referring to the branched, tree-shaped pileosetae.

Description:—Pileus 2–9 mm diam, convex to plano-convex; disc rugulose; margin smooth; surface dry, glabrous; cream to orangish white (4A2–3, 5A2–3) or greyish orange (5B3), lighter towards the margin. Context thin (<1 mm), concolorous. Lamellae adnate, distant (8–12) with 3–6 series of lamellulae, narrow, buff to cream (4A2–3, 5A2–3), non-marginate. Stipe 3–11 × 0.5–0.8 mm, central, cylindrical, hollow, non-insitious; surface pruinose; apex buff (4A3, 5A3), centrally light brown (6D5), base dark brown (6F5–7). Odor and taste not distinctive.

Basidiospores 7.2–9.6 (–10.4) × 3.2–4 (–4.8) µm [x_\text{av} = 8.2–9.1 × 3.9 µm; x_\text{min} = 8.66 ± 0.68 × 3.88 ± 0.02 µm; Q = 1.6–2.8; Q_\text{av} = 2.12–2.36; Q_\text{min} = 2.24 ± 0.17, n = 7–25; s = 2], ellipsoid, smooth, hyaline, inamylloid, thin-walled. Basidia 20–24 × 6.4–8 µm, clavate, 4-spored, hyaline, inamylloid, thin-walled. Basidioles 16–21.6 × 5.6–7.2 µm, clavate to fusoid, hyaline, inamylloid, thin-walled. Chelocystidia abundant, of Siccus-type broom cells; main body 14.4–18.4 × 5.6–7.2 µm, clavate to cylindrical or irregular, seldom 2–3-lobed, hyaline, inamylloid, thin-walled; apical setulae dense, 0.8–1.6 × 0.8–1.6 µm, cylindrical or irregular, sometimes branched, hyaline, inamylloid, thin-walled. Pleurocystidia absent. Pileipellis mottled, a hymeniform layer of three types of cells: 1) thin-walled Siccus-type broom cells with main body 6–20 × 5.6–8.8 µm, clavate or irregular, seldom 2–3-lobed, hyaline, inamylloid; apical setulae 0.8–8 × 0.8–1.6 µm, cylindrical to conical or irregular, hyaline, inamylloid, thin-walled, branched; 2) thick-walled Siccus-type broom cells with main body 16.8–21.6 × 5.6–8 µm, clavate, lobed, hyaline, inamylloid; apical setulae 0.8–8 × 0.8–3.2 µm, cylindrical to conical, hyaline, inamylloid, thick-walled; 3) pileosetae 40–300 × 1.6–8 µm, cylindrical to antler-like, often highly branched, clustered, hyaline, inamylloid, thick-walled. Pileus trama interwoven; hyphae 2.4–7.2 µm diam, smooth, hyaline, dextrinoid, thin-walled. Lamellae trama regular; hyphae 2.4–7.2 µm diam, cylindrical, smooth, hyaline, inamylloid, thin-walled. Striae tissue monomitic; cortical hyphae 2.4–7.2 µm diam, parallel, cylindrical, smooth, light brown to pale yellow, dextrinoid, thick-walled; medullary hyphae 2.4–8 µm diam, parallel, cylindrical, hyaline, dextrinoid, thin-walled. Chelocystidia of Siccus-type broom cells emerging directly from hyphae; main body...
3.2–4 × 1.6–5.6 μm, clavate or irregular, frequently lobed, hyaline, inamyloid, thin-walled; apical setulae cylindrical or irregular, branched, hyaline, inamyloid, thin-walled. **Clamp connections** present.

**FIGURE 13.** *Marasmius dendrosetosus* (*JES 205, JES 211*) a) basidiospores; b) basidia; c) basidioles; d) cheilocystidia; e) thick-walled pileipellis cells; f) thin-walled pileipellis cells; g) pileosetae and stipe surface broom cells (bottom center). Scale bar = 10 μm. Illustrated by J.E. Shay.
Habit, habitat and known distribution:—Solitary or in gregarious clusters on stems and leaves of *Uapaca littoralis* and *Pandanus*. Madagascar.


Notes:—*Marasmius dendrosetosus* is characterized by a small (<10 mm) smooth cream to orangish white pileus, subdistant non-marginate lamellae, a minutely pruinose stipe, basidiospores in the range 7.2–10.4 × 3.2–4.8 µm, *Siccus*-type cheilocystidia and caulocystidia, a pileipellis composed of *Siccus*-type broom cells and scattered hyaline branched pileosetae up to 300 µm long, and growth on dicotyledonous leaves and sticks. Morphology and molecular data indicate that this new species is allied with *M. longisetosus* J.S. Oliveira & Capelari, describe recently from Brazil (Oliveira et al. 2014). *Marasmius longisetosus* differs in forming a more deeply pigmented pileus (yellowish orange to pure orange), slightly longer basidiospores (mean 10.5 µm), and shorter, unbranched pileosetae. ITS sequences of *M. dendrosetosus* (KX148995, KX148996) are only 95% similar to the holotype specimen of *M. longisetosus* (JX424040), and align sister to the latter in the ITS phylogenetic analysis (99% BS, 1.0 PP; Fig. 1b). *Marasmius jalapensis* Murrill, reported from tropical Africa, is also similar, but forms more crowded lamellae, a longer stipe (40–60 mm), has hymenial setae, shorter and broader pileosetae, and numerous caulosetae (Antonín 2007).

22. Marasmius nummularius Berk. & Broome, J. Linn. Soc., Bot. 14 (73): 33. 1873 (1875). (Fig. 14, Plate 5)

Type:—SRI LANKA. Kandy District, Peradeniya, Thwaites 102 cum icone (K!).

Description:—Pileus 2–7 mm diam, convex to plano-convex; margin striate; surface glabrous; orangish brown to ochraceous (5B8). Context thin. Lamellae adnexed, subdistant (14–16) with 3–4 series of lamellulae, white with brown to orangish brown edges. Stipe 20–48 × 1 mm, central, tough, non-insititious; surface dull, hispid; apex white, base light brown to orange-brown (6D6). Odor and taste not distinctive.

Basidiospores (10.4–) 11.2–14.4 × 3.2–5.6 μm [xₘr = 12.4–12.7 × 4.3–4.8 μm; xₘm = 12.56 ± 0.21 × 4.56 ± 0.39 μm; Q = 1.9–3.6; Qₘr = 2.69–2.92; Qₘm = 2.80 ± 0.16, n = 25, s = 2], ellipsoid, smooth, hyaline, inamyloid, thin-walled. Basidia 17.6–25.6 × 6.4–8 μm, clavate to broadly clavate or cylindrical, 4-spored, hyaline, inamyloid, thin-walled. Basidioles 16.8–25.6 × 5.6–8.8 μm, clavate to broadly clavate, cylindrical or fusoid, hyaline, inamyloid, thin-walled. Cheilocystidia of Siccus-type broom cells; main body 6–20 × 6–9.6 μm, broadly clavate, hyaline to pale yellow brown, dextrinoid, thick-walled; apical setulae 0.8–10.4 × 0.8–2.4 μm, numerous, cylindrical to conical, subacute, hyaline, inamyloid, thick-walled. Pleurocystidia scattered, not conspicuous, 22–28 × 6.5–7.5 μm, fusoid, hyaline, refractive, inamyloid, thin-walled. Pileipellis mottled, a hymeniform layer of Siccus-type broom cells; main body 9.6–20 × 6.4–8.8 μm, cylindrical to clavate or subglobose, hyaline to light brown, dextrinoid, thick-walled; apical setulae 1.6–12.8 × 0.5–2.4 μm, cylindrical to conical, hyaline, inamyloid, thick-walled. Pileus trama interwoven; hyphae 3.2–7.2 μm diam, cylindrical, smooth, hyaline, dextrinoid, thin-walled. Lamellar trama regular; hyphae 3.2–5.6 μm diam, cylindrical, smooth, hyaline, weakly dextrinoid, thin-walled. Stipe tissue monomitic; cortical hyphae 2.4–4 μm diam,
parallel, cylindrical, hyaline to pale yellow, dextrinoid, thick-walled; medullary hyphae 3.2–9.6 μm diam, parallel, cylindrical to inflated, hyaline, inamyloid, thick-walled. Caulocystidia 28–109 × 7.2–36 μm, conical to cylindrical, fusoid or lageniform, hyaline, inamyloid, thick-walled. Clamp connections present.

Habit, habitat and known distribution:—Solitary on leaves of Dalberjia (Fabaceae) and bark of unknown trees. Indonesia (Java), Madagascar, Sri Lanka, Thailand.

Material examined:—MADAGASCAR.Commune Ranomafana, District Ifanadiana, Region Vatovavy-Fitovinany, Ranomafana National Park, Talatakely Trail, elev. 937–973 m, GPS: 21° 15.237’ S, 47° 25.183’ E, 20 January 2014, J.E. Shay 121 (SFSU); same location and date, J.E. Shay 124 (SFSU).

Notes:—The Madagascar material is characterized by small (2–7 mm diam) orangish brown to ochraceous pileus, subdistant orangish brown-marginate lamellae, a hispid orangish brown to brown non-insititious stipe, basidiospores with mean 12.4–12.7 × 4.3–4.8 μm, Siccus-type cheilocystidia and pileipellis cells with setulae up to 12 mm long, small fusoid pleurocystidia, rare pileosepta, conspicuous caulocystidia, and growth on woody debris. Populations of M. nummularius in Thailand (Wannathes et al. 2009a) and Indonesia (Desjardin et al. 2000) differ in lacking the small pleurocystidia, and often have more reddish brown tones to the pileus. An ITS sequence of Madagascar material (KX148979) shows 98% similarity to two Thai sequences (EU935492, EU935493) forming a well-supported clade (90% BS, 1.0 PP) (Fig. 1b). The African species M. castaneovelutinus Henne. and M. fulvovelutinus Beeli differ in forming larger (4–35 mm diam), chestnut brown to reddish brown pilei, non-marginate lamellae, larger basidiospores (14–18 × 4–6 μm), and more conspicuous pleurocystidia (Antonín 2007).

IIIc. ser. Atrorubentes


– Type species: Marasmius atrorubens (Berk.) Mont.

23. Marasmius corrugatiformis Singer, Bull. Jard. Bot. État Brux. 34: 374. 1964. (Fig. 15, Plate 6)

Type:—DR CONGO. Near Yambao, 21 June 1939, J. Louis 15275 (BR 11426–77).

Description:—Pileus 12–17 mm diam, convex to plano-convex; disc and margin smooth to rugulose; surface, dry, glabrous; orangish red or orange. Context thin, buff. Lamellae subfree, close, narrow, white to buff (5A4–5), non-marginate. Stipe 30–49 × 1 mm, central, cylindrical, hollow; surface pruinose; apex cream to yellow, becoming orange (7C–E7–8) towards the base. Odor and taste not distinctive.

Basidiospores (6.4–) 8–11.2 × 3.2–4.8 μm [x̄ = 9.08 ± 1.08 × 4.04 ± 0.33 μm; Q = 1.67–2.80; Qₘ = 2.26 ± 0.14, n = 25, s = 1], ellipsoid, smooth, hyaline, inamyloid, thin-walled. Basidia 16.8–17.6 × 7.2 μm, clavate, 4-spored, hyaline, inamyloid, thin-walled. Basidioles 8–15.2 × 3.2–6.4 μm, clavate to fusoid, hyaline, inamyloid, thin-walled. Cheilocystidia of two types of cells: 1) Siccus-type broom cells with main body 8–17.6 × 6–12 μm, clavate to cylindrical or irregular, hyaline, inamyloid, apically thick-walled; apical setulae 0.8–10.4 × 0.8–1.6 μm, cylindrical to conical, hyaline to golden brown, inamyloid, thick-walled; 2) interspersed non-setulose cells, clavate, smooth, hyaline, inamyloid, thin-walled. Pleurocystidia absent. Pileipellis a hymeniform layer of Siccus-type broom cells; main body 8–20.8 × 3.2–9.6 μm, clavate to broadly clavate, cylindrical or irregular, seldom 2–3-lobed, smooth, hyaline to brown, inamyloid, apically thick-walled; apical setulae 0.8–12.8 × 0.8–1.6 μm, cylindrical to conical, seldom branched, erect, obtuse, pale brown to hyaline, inamyloid, thick-walled. Pileus trama interwoven; hyphae 1.6–12 μm diam, cylindrical, smooth, hyaline, dextrinoid, thin-walled. Lamellar trama regular; hyphae 3.2–19.2 μm diam, cylindrical to inflated, smooth, pale yellowish brown to hyaline, weakly dextrinoid, thin-walled. Stipe tissue monomitic; cortical hyphae 2.4–12 μm diam, parallel, cylindrical to inflated, smooth, pale yellowish brown to hyaline, dextrinoid, thick-walled; medullary hyphae 2.4–9.6 μm diam, parallel, cylindrical to inflated, smooth, hyaline, dextrinoid, thin-walled. Caulocystidia 11.2–24 × 5.6–7.2 μm, versiform, clavate to lageniform or irregular, seldom lobed, smooth, hyaline, dextrinoid, thin-walled. Clamp connections present.

Habit, habitat and known distribution:—Solitary on leaves of Cryptocarya (Lauraceae). Africa (Cameroon, DR Congo, Ghana, Ivory coast, Uganda), Madagascar.

FIGURE 15. Marasmius corrugatiformis (JES 164, Lockwood 2132268W250) a) basidiospores; b) basidia; c) basidioles; d) cheilocystidia; e) pileipellis cells; f) caulocystidia. Scale bar = 10 µm. Illustrated by J.E. Shay.

Notes:—Marasmius corrugatiformis is characterized by a relatively small (12–17 mm), rugulose, reddish orange to orange pileus, close, non-marginate lamellae, a pruinose stipe with cream-yellow apex and brownish orange base, basidiospores with mean 9 × 4 µm, Siccus-type cheilocystidia plus a few smooth, clavate cells interspersed, simple, broadly rounded, cylindrical to clavate caulocystidia, and a lack of Siccus-type broom cells on the stipe. It is similar to M. katangensis Singer, but the latter has only one type of cheilocystidia (Siccus-type), and two types of caulocystidia (broom cells and simple cylindrical cells). Repeated attempts to generate ITS sequences from JES 164 were unsuccessful; however, an ITS sequence of Madagascar material determined as M. corrugatiformis (Buyck 97.425, KX148981) formed a clade with several sequences of M. corrugatiformis from São Tomé (KX953756, KX953757) but with low support (Fig. 1b).

24. Marasmius katangensis Singer, Bull. Jard. Bot. État Brux. 34: 375. 1964. (Fig. 16, Plate 6)

Type:—DR CONGO. Shaba Province, Kipopo, 10 January 1961, M.C. Schmitz–Levecq 315 (BR 11476–30).

Description:—Pileus 6–16 mm diam, plano-convex to umbonate, with a dark brown papilla; margin striate; surface dry, glabrous; dark orangish brown to orange (6B–D6–8). Context thin, light brown (6B3). Lamellae adnate, close with 6 series of lamellulae, narrow (0.7–1.5 mm), cream (5A2), non-marginate. Stipe 16–50 × 1–2 mm diam, central, cylindrical, hollow; surface pruinose; apex orangish white (5A3–4), centrally yellow (5B6), base orangish brown to brown (6D6–8). Odor and taste not distinctive.

Basidiospores 7.2–8.8 × 3.2–4.8 µm [x̄ = 7.79 ± 0.48 × 3.99 ± 0.38 µm; Q = 1.67–2.50; Q̄ = 1.97 ± 0.21, n = 25, s = 1], ellipsoid, smooth, hyaline, inamylloid, thin-walled. Basidia 16–23.2 × 7.2 µm, clavate, 4-spored, hyaline, inamylloid, thin-walled; sterigmata 2.4–4.8 × 0.8–1.6 µm. Basidioles 13.6–24.8 × 4–5.6 µm, clavate, hyaline, inamylloid, thin-walled. Cheilocystidia abundant, of Siccus-type broom cells; main body 9.6–23.2 × 4.8–7.2 µm, clavate or irregular, seldom 2-lobed, hyaline, inamylloid, apically thick-walled; apical setulae 3.2–8.8 × 0.8–1.6 µm, cylindrical to conical, seldom branched, light yellowish brown, inamylloid, thick-walled. Pleurocystidia absent. Pileipellis mottled, a hymeniform layer of Siccus-type broom cells; main body 8–15.2 × 7.2–8 µm, clavate or irregular,
seldom 2-lobed, hyaline, inamyloid, thin-walled; apical setulae 2.4–20 × 0.8–1.6 µm, 7–9 setulae per cell, cylindrical to conical, light yellowish brown, inamyloid, thick-walled. Pileus trama interwoven; hyphae 1.6–12.8 µm diam, cylindrical to inflated, smooth, hyaline, strongly dextrinoid, thin-walled. Lamellar trama regular; hyphae 3.2–6.4 µm diam, cylindrical to inflated, smooth, hyaline, strongly dextrinoid, thin-walled. Stipe tissue monomitic; cortical hyphae 4–9.6 µm diam, parallel, cylindrical, smooth, hyaline, dextrinoid, thick-walled; medullary hyphae 3.2–14.4 µm diam, parallel, cylindrical to inflated, smooth, hyaline, dextrinoid, thin-walled. Caulocystidia of two types; 1) scattered Siccus-type broom cells; main body 10.4–20 × 5.6–7.2 µm, clavate or irregular, seldom lobed, hyaline, inamyloid, thin-walled; apical setulae 0.8–14.4 × 0.8–2.4 µm, cylindrical to conical, seldom branched, hyaline, inamyloid, thick-walled; 2) smooth non-setulose cystidia with main body 20.8–48 × 7.2–11.2 µm, clavate to cylindrical or irregular, smooth, hyaline, inamyloid, thick-walled. Clamp connections present.

Habit, habitat and known distribution:—Solitary or in small clusters on wood and leaf litter of undetermined trees. Africa (Benin, DR Congo, Kenya, Malawi, Nigeria, Tanzania, Uganda), Madagascar.

Material examined:—MADAGASCAR. Region Analamanga, District Ankazobe, Commune Ambatoharanama, Ambohitantely Forest Reserve, Sentier Botanique, elev. 1574 m, GPS: 18˚ 11.504’ S, 47˚ 17.074’ E, 6 February 2014, J.E. Shay 227 (SFSU).

Notes:—Marasmius katangensis has a centrally rugulose, dark orangish brown pileus with orange margin, close lamellae, a pruinose stipe with two types of caulocystidia, relatively small basidiospores with mean 7.8 × 4.0 µm, no pleurocystidia, and no setae. Morphologically, the species is similar to M. corrugatiformis, but the latter has cheilocystidia of two types, and caulocystidia of only one type (non-setulose, cylindrical to clavate). JES 227, determined here as M. katangensis, is easily confused with Madagascar material determined by Antonín & Buyck (2006) as M. occultatiformis, but ITS sequences clearly distinguish the two (Fig. 1a).

Based solely on ITS data, JES 227 (KX148991) is basal to a clade containing M. occultatiformis Antonín, Ryoo & H.D. Shin, described from Korea on detritus of Acer and Juglans. Morphologically, JES 227 is very similar to M. occultatiformis, differing primarily in the latter species having a glabrous stipe lacking caulocystidia; other features are indistinguishable.

FIGURE 16. Marasmius katangensis (JES 227) a) basidiospores; b) basidia; c) basidioles; d) cheilocystidia; e) pileipellis cells; f) Siccus-type caulocystidia; g) non-setulose caulocystidia. Scale bar = 10 µm. Illustrated by J.E. Shay.
IIId. ser. **Leonini**


–Type species: *Marasmius leoninus* Berk.

25. **Marasmius sokola** J.E. Shay & Desjardin, sp. nov. (Fig. 17)

MycoBank no.: MB 818621

Holotype:—MADAGASCAR. Commune Ranomafana, District Ifanadiana, Region Vatovavy-Fitovinany, Ranomafana National Park, 22 Jan. 2014, J.E. Shay 154 (SFSU).

Etymology:—**sokola**–Malagasy for chocolate, referring the dark chocolate brown colored basidiomes.

Description:—*Pileus* 20 mm diam, campanulate; disc rugulose; margin sulcate; surface dull, glabrous; dark brown (5E7). *Context* thin.

*Pileus* subfree, distant (11), no lamellulae, broad (4 mm), light grey (5C3), with brown edges. *Stipe* 45 × 1 mm, central, cylindrical, hollow, pliant; surface glabrous; dark greyish brown (6F4). *Odor and taste* not distinctive.

*Basidiospores* (16.8–) 18.4–23.2 (–26.4) × 4–4.8 μm [x̄m = 21.93 ± 2.36 × 4.40 ± 0.40 μm; Q = 3.50–6.40; Qm = 5.03 ± 1.20, n = 25, s =1], subcylindrical to subfusoid, smooth, hyaline, inamylloid, thin-walled. *Basidia* 32.8–46.4 × 6.4–8 μm, clavate, 4-spored, hyaline, inamylloid, thin-walled. *Basidioles* 29.6–42.4 × 7.2–8.8 μm, clavate, hyaline, inamylloid, thin-walled. *Cheilocystidia* abundant, of *Siccus*-type broom cells; main body 14.4–22.4 × 6.4–8.8 μm, clavate to subglobose or irregular, seldom 2–3-lobed, hyaline, inamylloid, thin-walled; apical setulae 0.8–13.6 × 0.8–1.6 μm, cylindrical to conical, often branched, brown, inamylloid, thick-walled. *Pileipellis* mottled, a hymeniform layer of *Siccus*-type broom cells; main body 8.8–22.4 × 5.6–10.4 μm, cylindrical to clavate or irregular, seldom 2–3-lobed, hyaline, inamylloid, thick-walled; apical setulae 0.8–9.6 × 0.8–1.6 μm, cylindrical to conical, seldom branched, hyaline to brown, inamylloid, thick-walled. *Pileus trama* interwoven; hyphae 2.4–17.6 μm diam, cylindrical to inflated, rough, hyaline, dextrinoid, thick-walled. *Lamellar trama* regular; hyphae 3.2–8.8 μm diam, cylindrical, smooth, hyaline, dextrinoid, thin-walled. *Stipe tissue* mononitic; cortical hyphae 3.2–11.2 μm diam, cylindrical, smooth, pale greenish brown, dextrinoid, thick-walled; medullary hyphae 2.4–12.8 μm diam, cylindrical to inflated, smooth, hyaline to pale brown, inamylloid, thin-walled. *Caulocystidia* absent. *Clamp connections* present.

Habit, habitat and known distribution:—Solitary on woody sticks of *Weinmannia* (Cunoniaceae). Madagascar.

Notes:—*Marasmius sokola* is characterized by a dark brown, smooth to rugulose pileus 20 mm diam, distant (11), broad (4 mm), brown-marginate lamellae, a glabrous, dark brown stipe 45 mm long, basidiospores with mean 21.9 × 4.4 µm (Q = 5.0), basidia 32–46 µm long, *Siccus*-type cheilocystidia and pileipellis cells with brown setulae up to 12 µm long, no pleurocystidia or caulocystidia, and growth on woody dicotyledonous debris. The new species shows closest phenetic similarity to *M. carcharus* Singer, *M. selangorensis* Y.S. Tan & Desjardin, and *M. mazatecus* Singer. *Marasmius carcharus*, described from the DR Congo, differs in a pinkish brown pileus, broader (6–7 mm), non-marginate lamellae, cheilocystidia with shorter apical setulae (up to 8 µm), and growth on dicotyledonous leaves (Antonín 2007). *Marasmius selangorensis*, described from Malaysia, differs in a paler brown pileus with pink tones, narrower and more numerous (12–18) lamellae, and growth on dead dicotyledonous leaves (Tan et al. 2009); its micromorphology is indistinguishable from *M. sokola*. ITS sequences of two specimens of *M. selangorensis* from Malaysia (Fig. 1a), however, show only 70% similarity to *JES 154* (KX148994) (Fig. 1b) and are distant in the ITS phylogeny. *Marasmius mazatecus*, described from Mexico, differs in an orange-ferruginous pileus, fewer (9) and narrower (2 mm) lamellae with orange-ferruginous edges, a shorter (20 mm) stipe, and slightly shorter basidiospores (17–21 µm) (Singer 1976). *Marasmius sokola* is on a long branch in the ITS phylogeny, sister to *M. imitarius* Wannathes, Desjardin & Lumyong, a species described from Thailand.


Type:—MAURITIUS. Trou d’eau douce, 10 June 1990, leg. J. Rammelo 9251 (BR 6902-15).

For descriptions and illustrations of Madagascar material, refer to Antonín (2004a) and Antonín & Buyck (2006). Material was not available for sequencing.
27. *Marasmius megistus* Singer, Bull. Jard. Bot. État Brux. 34: 356. 1964. (Fig. 18, Plate 7)

Type:—DR CONGO. Binga, 7 May 1928, M. Goossens–Fontana 733 (BR 11492–46).

Description:—*Pileus* 6.5–15 mm diam, campanulate; margin deeply sulcate; surface dry, glabrous; disc yellowish grey (4B2), sulcae pale violet brown (10E4) to reddish grey (10B2), ridges and margin buff (4A2) to cream (4A3). *Context* thin. *Lamellae* subfree, distant (14) broad (1–2 mm wide), buff (4A2), non-marginate. *Stipe* 104–115 × 1–2 mm, central, cylindrical, hollow; surface glabrous; brownish grey (10D2) to brownish red (10E6). *Odor and taste* not distinctive.

**FIGURE 18.** *Marasmius megistus* (JES 163, Lockwood 2132155) a) basidiospores; b) basidioles; c) cheilocystidia; d) pileipellis cells. Scale bar = 10 µm. Illustrated by J.E. Shay.

*Basidiospores* (26.4–) 29.6–32.8 (–40) × 4.8–7.2 µm \[x_{\text{mr}} = 30.7–34.2 \times 5.8–6.7 \mu m; x_{\text{mm}} = 32.44 \pm 2.49 \times 6.23 \pm 0.66 \mu m; Q = 2.8–6.8; Q_{\text{mr}} = 5.09–5.33; Q_{\text{mm}} = 5.21 \pm 0.17, n = 2–27, s = 2\], narrowly ellipsoid to clavate, smooth, hyaline, inamylloid, thin-walled. *Basidia* not observed. *Basidioles* 18.4–57 × 5.6–10.4 µm, clavate to fusoid, hyaline, inamylloid, thin-walled. *Cheilocystidia* evenly distributed, of *Siccus*-type broom cells; main body 16–25.6 × 4.8–9.6 µm, clavate or irregular, 2–3-lobed, hyaline, inamylloid, thin-walled; apical setulae 0.8–8 × 0.8–1.6 µm, cylindrical to conical, sometimes branched, hyaline, inamylloid, thin-walled. *Pileus* 6.5–15 mm diam, campanulate; margin deeply sulcate; surface dry, glabrous; disc yellowish grey (4B2), sulcae pale violet brown (10E4) to reddish grey (10B2), ridges and margin buff (4A2) to cream (4A3). *Context* thin. *Lamellae* subfree, distant (14) broad (1–2 mm wide), buff (4A2), non-marginate. *Stipe* 104–115 × 1–2 mm, central, cylindrical, hollow; surface glabrous; brownish grey (10D2) to brownish red (10E6). *Odor and taste* not distinctive.

Habit, habitat and known distribution:—Solitary on dicotyledonous leaves. Africa (Burundi, Cameroon, DR Congo, Tanzania, Uganda), Madagascar.

163 (TAN); Region Vatovavy-Fitovinany, District Ifanadiana, Commune Ranomafana, February 2013, T. Lockwood 2132155 (SFSU).

Notes:—Marasmius megistus forms some of the largest basidiospores in the genus. The Madagascan material is distinguished by a relatively small (up to 15 mm diam) sulcate striped pileus with violet-brown sulcae and cream ridges, distant non-marginate lamellae, a very long (up to 115 mm) glabrous stipe, basidiospores in the range 29.6–40 × 4.8–7.2 µm, no pleurocystidia, Siccus-type broom cells with few setulae, and growth singly on dicotyledonous leaves. Antonín (2007) reports the species as forming a larger pileus (26–50 mm diam) but in all other respects the specimens from Madagascar match those reported from tropical Africa. ITS sequences of two Madagascan specimens (KX148992, KX148993) are sister to a specimen from São Tomé (KX953750) with strong support (100% BS, 1.0 PP; Fig. 1a).

28. Marasmius bambusiniformis Singer, Fl. Neotrop. Monogr. 17: 167. 1976. (Fig. 19, Plate 7)

Type:—ECUADOR. Napo, Lago Agrio, 16 May 1973, Singer B7480 (F!)

Description:—Pileus 4–5 mm diam, convex to campanulate; margin smooth to sulcate; surface dull, dry, glabrous; reddish orange becoming more orange towards the margin (6C–E8). Context thin, white. Lamellae adnate, distant (12–17), no lamellulae, not intervenose, narrow; white with reddish brown edges. Stipe 25–30 × 0.5–1 mm, central, cylindrical, hollow, wiry; surface glabrous, apex white (3A3), grading to brownish orange (6C–E5–8) at the base. Odor and taste not distinctive.

FIGURE 19. Marasmius bambusiniformis (JES 199) a) basidiospores; b) basidioles; c) cheilocystidia; d) pileipellis cells. Scale bar = 10 µm. Illustrated by J.E. Shay.

Basidiospores (14.4–) 16–18.4 × 3.2–4 µm [x̄ = 16.35 ± 1.44 × 3.46 ± 0.36 µm; Q = 4–5.75; Qm = 4.76 ± 0.57, n = 25, s = 1], narrowly ellipsoid, smooth, hyaline, inamyloid, thin-walled. Basidia not observed. Basidioles 19.2–24 × 5.6–7.2 µm, clavate to fusoid, hyaline, inamyloid, thin-walled. Cheilocystidia numerous, of Siccus-type broom cells; main body 9.6–14.4 × 5.6–10.4 µm, clavate to broadly clavate, seldom 2–3-lobed, hyaline, inamyloid, apically thick-walled; apical setulae 1.6–7.2 × 0.8 µm, dense, cylindrical to conical, seldom branched, hyaline, inamyloid, thick-walled. Pleurocystidia absent. Pileipellis mottled, a hymeniform layer of Siccus-type broom cells; main body 10.4–17.6 × 6.4–8 µm, clavate to broadly clavate, seldom 2–3-lobed, hyaline, inamyloid, apically thick-walled; apical setulae 1.6–4.8 × 0.8 µm, dense, cylindrical to conical, pale yellowish brown, inamyloid, thick-walled. Pileus trama interwoven; hyphae 1.6–16.8 µm diam, cylindrical, smooth, hyaline, inamyloid, thin-walled. Lamellar trama regular; hyphae 1.6–8 µm diam, cylindrical to inflated, smooth, hyaline, dextrinoid, thick-walled. Stipe tissue monomitic; cortical hyphae 1.6–4 µm diam, parallel, cylindrical, smooth, dark brown, dextrinoid, thick-walled; medullary hyphae 2.4–8 µm diam, parallel, cylindrical to inflated, hyaline, dextrinoid, thin-walled. Caulocystidia absent. Clamp connections present.
Habit, habitat, and known distribution:—Solitary on stems of *Uapaca* (Phyllanthaceae). Malaysia, Madagascar, Papua New Guinea, South America (Brazil, Ecuador), Thailand, United States (Florida).


Notes:—*Marasmius bambusiniformis* was described originally from Ecuador (Singer 1976), and subsequently reported from Papua New Guinea (Desjardin & Horak 1997), Malaysia (Tan et al. 2009) and Thailand (Wannathes et al. 2009a). Distinctive features include a small (3–10 mm diam), obtusely conical, striate, reddish orange pileus, distant (12–17) lamellae with reddish orange edges, a glabrous, non-insititious stipe lacking caulocystidia, no pleurocystidia, Siccus-type broom cells, and growth on dicotyledonous leaves and twigs. The material from Madagascar (JES 199) matches nicely that reported from Southeast Asia and Papua New Guinea, and ITS sequences support this determination.

*Marasmius conicoparvus* Antonin, C. Sharp & Stubbe is quite similar, differing primarily in forming non-marginate lamellae and slightly shorter basidiospores (13–16 μm); this may represent the same taxon as what we report from Madagascar, but until more material becomes available for comparison and sequencing, we prefer to recognize the Madagascan taxon as *M. bambusiniformis. Marasmius berteroi* (Lév.) Murr. described from Puerto Rico, and reported from Indonesia (Desjardin et al. 2000), is similar but has non-marginate lamellae and shorter basidiospores (12–16 μm).
µm). An ITS sequence of *JES199* (KX148990) is sister to a Thai specimen of *M. bambusiniformis* (EU935521) and together are sister to *M. berteroi* (FJ917632) (Fig. 1a)

**IIe. ser. Haematocephali**


–Type species: *Marasmius haematocephalus* (Mont.) Fr.

29. *Marasmius haematocephalus* (Mont.) Fr., Epicr. Syst. Mycol. (Upsaliæ): 382. 1838 (1836–1838). (Fig. 20, Plate 8)


Description:—*Pileus* 2–12 mm diam, convex to campanulate, umbilicate with age, with or without a papilla; margin sulcate to plicate; surface dry, glabrous; buff (5A2) with pale orangish pink tones (6–7A3–4), or pinkish purple (11C–D5–6) to dull reddish purple (9D–E5–8). *Context* thin, cream to buff. *Lamellae* subfree to adnexed, distant (10–13), narrow; buff to pale beige with pink tones, non-marginate. *Stipe* 12–25 × 0.1–0.2 mm, central, cylindrical or wiry, hollow; surface glabrous; apex white to light orange (5B5), base brownish orange (6C6) to light brown or dark brown (9F8). *Odor and taste* not distinctive.

![FIGURE 20. Marasmius haematocephalus (JES 147, JES 202, JES 193) a) basidiospores; b) basidioles; c) cheilocystidia; d) pleurocystidia; e) pileipellis cells. Scale bar = 10 µm. Illustrated by J.E. Shay.](image)

Basidiospores (13.6–) 16–22 × 3.2–4.8 µm [x_{mr} = 17.1–20.9 × 3.6–4.1 µm; x_{mm} = 18.71 ± 1.7 × 3.84 ± 0.3 µm; Q = 3.7–7.0; Q_{mr} = 4.80–5.08; Q_{mm} = 4.93 ± 0.1, n = 9–25, s = 4], narrowly fusiform to elongate-ellipsoid, smooth, hyaline, inamyloid, thin-walled. *Basidia* not observed. *Basidioles* 16–30.4 × 5.6–8.8 µm, clavate, hyaline,
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inamyloid, thin-walled. Cheilocystidia abundant, of Siccus-type broom cells; main body 6.4–24 × 4.8–8.8 µm, clavate to subglobose, cylindrical or irregular, seldom lobed, hyaline, inamyloid, thin-walled; apical setulae 0.8–7.2 × 0.8–1.6 µm, conical to cylindrical, obtuse, hyaline, inamyloid, thin-walled. Pleurocystidia 20.8–68 × 7.2–15.2 µm, clavate to fusoid, lecythiform or lageniform, some strangulate, rarely apically bilobed, hyaline, inamyloid, thin-walled. Pileipellis mottled, a hymeniform layer of Siccus-type broom cells; main body 6.4–24 × 4.8–9.6 µm, clavate to subglobose, cylindrical or irregular, seldom lobed, hyaline to light brown, inamyloid, thin-walled or apically thick-walled; apical setulae 0.5–8 × 0.5–2.4 µm, conical to cylindrical, obtuse, hyaline to light brown, inamyloid, thick-walled. Pileus trama interwoven; hyphae 2.4–9.6 µm diam, cylindrical, smooth, hyaline, dextrinoid, thin-walled. Lamellar trama regular; hyphae 2.4–8.8 µm diam, cylindrical to inflated, smooth, hyaline, weakly dextrinoid, thin-walled. Sippe tissue monomitic; cortical hyphae 2.4–9.6 µm diam, parallel, cylindrical to inflated, smooth, hyaline to light yellow brown, dextrinoid, thin-walled; medullary hyphae 2.4–15.2 µm diam, parallel, cylindrical to inflated, smooth, hyaline, dextrinoid, thin-walled. Caulocystidia absent. Clamp connections present.

Habit, habitat, and known distribution:—Solitary, scattered on leaves of Aframomum angustifolium (Zingiberaceae), Psorospermum (Clusiaceae), Uapacca densifolia (Phyllanthaceae), Mammea (Calophyllaceae) and Garcinia (Clusiaceae). Pantropical: Africa (Cameroon, DR Congo, Gabon, Ghana, Ivory Coast, Kenya, Nigeria, Sierra Leone, Tanzania, Uganda, Zimbabwe), Caribbean region, Indonesia (Java), Madagascar, Malaysia, Papua New Guinea, South America (Brazil, Argentina), Sri Lanka, Thailand.

Material examined:—MADAGASCAR. Region Alaotra-Mangoro, District Moramanga, Commune Andasibe, Vohimana Forest, Piste 5, elev. 844 m, GPS: 18° 55.422° S, 48° 30.201° E, 27 January 2014, J.E. Shay 193 (SFSU); Region Vatovavy-Fitovinany, District Ifanadiana, Commune Ranomafana, City of Ranomafana near riverbed next to Forest Service Station, elev. ~900 m, 20 January 2014, J.E. Shay 110 (SFSU), same region Ranomafana National Park, Circuit Vohipara, elev. 1062 m, GPS: 21° 14.255° S, 47° 23.409° E, 21 January 2014, J.E. Shay 142 (SFSU); Region Atsinanana, District Brickaville, Commune Andevoranto, Andavakimena Forest, elev. 1 m, GPS 18° 53.231° S, 49° 7.490° E, 28 January 2014, J.E. Shay 202 (SFSU); Melville oil palm plantation, near Tamatave, 24 February 2000, B. Buyck 00.1820 (PC).

Notes:—Marasmius haematocephalus has been reported from tropical habitats around the world and probably represents a complex of species. Wannathes et al. (2009a) reported multicolored forms from Thailand, with pilei ranging from yellowish white to olive, red, violet, greyish blue and brown, or a combination of many of these pigments, all of which grouped in a well-supported clade with 1.0 PP and 99% BS support. The typical form of the species, described originally from southern Brazil, has a reddish purple to blood red pileus, clavate basidiospores in the range 14–20 × 3.5–5 µm, conspicuous pleurocystidia, and grows on leaves and twigs (Singer 1976). Our material from Madagascar forms sulcate, pink to pinkish purple pilei, distant (10–12), non-marginate lamellae, a glabrous, non-dextrinoid, thin-walled; apical setulae 0.8–7.2 × 0.8–1.6 µm, conical to cylindrical, obtuse, hyaline, inamyloid, thin-walled. Caulocystidia absent. Clamp connections present.

30. Marasmius tanaensis J.E. Shay & Desjardin sp. nov. (Fig. 21, Plate 8)

MycoBank no.: MB 818618

Holotype:—MADAGASCAR. Region Analamanga, City of Antananarivo, Parc Botanique de Zoologique (P.B.Z.T.), near the garden of Crops Wild and Relatives (CWR), elev. 1270 m, GPS: 18° 55.530° S, 47° 31.350° E, 8 Feb. 2014, J.E. Shay 220 (SFSU). Etymology:—tanaensis—occurring in “tana”, the local name for Antananarivo where the holotype specimen was collected.

Description:—Pileus 1–3 mm diam, convex to hemispherical; margin smooth to striate; surface dull, dry, glabrous; light orange (6A4) to orange (6B6). Context thin, pale orangish pink to light orange (6A3–4). Lamellae adnexed, subdistant (14–15), no lamellulae, narrow (<0.3 mm); white, non-marginate. Stipe 1–22 × 0.1–0.5 mm, central, cylindrical, wiry, hollow; surface glabrous; white at apex, becoming brownish orange (6B–C4–6) to brown (6E7) at the base. Odor and taste not distinct.
FIGURE 21. Marasmius tanaensis (JES 220) a) basidiospores; b) basidia; c) basidioles; d) cheilocystidia; e) pleurocystidia; f) pileipellis cells. Scale bar = 10 µm. Illustrated by J.E. Shay.

Basidiospores 11.2–16 × (3.2–) 4–4.8 (–5.6) µm \[x_m = 13.37 \pm 1.41 \times 4.26 \pm 0.49 \mu m; Q = 2.43–5.0; Q_m = 3.19 \pm 0.26, n = 31, s =1\], broadly ellipsoid, smooth, hyaline, inamyloid, thin-walled. Basidia 22.4 × 5.6–6.4 µm clavate, 4-spored, hyaline, inamyloid, thin-walled; sterigmata 2.4–3.2 × 0.8 µm. Basidioles 8.8–28.8 × 4.8–7.2 µm, clavate to fusoid, hyaline, inamyloid, thin-walled. Cheilocystidia abundant, of Siccus-type broom cells; main body 16–29.6 × 4–8 µm, clavate to broadly clavate, seldom 2–3 lobed, hyaline, inamyloid, thin-walled; apical setulae 0.8–4 × 0.8, cylindrical to conical, seldom branched, hyaline to light brown, inamyloid, thick-walled. Pleurocystidia 22–48 × 6–9.5 µm, utriform to fusiform, mucronate, hyaline, inamyloid, thin-walled. Pileipellis mottled, a hymeniform layer of Siccus-type broom cells; main body 12–16.8 × 4.8–9.6 µm, clavate to broadly clavate, seldom 2–3 lobed, hyaline, inamyloid, thin-walled; apical setulae 0.8–5.6 × 0.8–1.6 µm, clustered, cylindrical to conical, seldom branching, light brown, inamyloid, thick-walled. Pileus trama interwoven; hyphae 2.4–12 µm diam, cylindrical to inflated, smooth, hyaline, dextrinoid, thin-walled. Lamellar trama regular; hyphae 3.2–8.8 µm diam, cylindrical to inflated, smooth, hyaline, dextrinoid, thick-walled. Stipe tissue monomitic; cortical hyphae 2.4–6.4 µm diam, parallel, cylindrical, smooth, pale light brown, dextrinoid, thick-walled; medullary hyphae 3.2–8.8 µm diam, parallel, cylindrical to inflated, smooth, hyaline, dextrinoid, thin-walled. Caulocystidia absent. Clamp connections present.

Habit, habitat and known distribution:—Clustered on bamboo debris. Madagascar.

Material examined:—MADAGASCAR. Region Analamanga, City of Antananarivo, Parc Botanique de Zoologique (P.B.Z.T.), near the garden of Crops Wild and Relatives (CWR), elev. 1270 m, GPS: 18˚ 55.530’ S, 47˚ 31.350’ E, 8 February 2014, J.E. Shay 220 (SFSU).

Notes:—Marasmius tanaensis forms tiny (1–3 mm diam), smooth to striate, orange pilei, subdistant (14–15), non-marginate lamellae, a short (up to 22 mm), glabrous, white (upper half) to brown (base) stipe that grows on bamboo debris, basidiospores with mean 13.4 × 4.3 µm, narrow (6–9.5 µm), mucronate pleurocystidia, Siccus-type cheilocystidia and pileipellis cells, and no caulocystidia. The small orange pilei and growth on bamboo debris is similar to M. bambusinus (Fr.) Fr., described from Brazil, but the latter forms fewer lamellae (6–13), longer basidiospores (13.8–22 µm), and broader pleurocystidia (8–12.5 µm diam) (Singer 1976). We were unable to obtain a quality ITS sequence from the holotype specimen.

Type:—DR CONGO. Kivu, Panzi, November 1948, *M. Goossens-Fontana* 5076 (BR 11460–14).

For a description and illustrations of Madagascan material, refer to Antonín & Buyck (2006). Repeated attempts to sequence material from collection *Buyck 97.004* (PC) were unsuccessful.


For a description and illustrations of Madagascan material, refer to Antonín & Buyck (2006). Repeated attempts to sequence material from collection *Buyck 99.375* (PC) were unsuccessful.


Type:—KENYA. Central Province, Nairobi District, Thika Fall, 16 March 1968, *D.N. Pegler* K101 (K(M) 8833).

For a description and illustrations of Madagascan material, refer to Antonín & Buyck (2006). Repeated attempts to sequence material from collection *Buyck 99.424* (PC) were unsuccessful.

34. *Marasmius ferruginoides* Antonín Mycotaxon 89(2): 399–422. 2004. (Fig. 22, Plate 8)

Type:—DR CONGO. Tshopo Province, Kisangani, forest near Zoo, 2 May 1984, *B. Buyck 1615* (BR 11731–91).

Description:—
Pileus 7–9 mm diam, campanulate, umbilicate; margin smooth to rugulose; surface dry, glabrous; orange to reddish orange (8C7). Context thin, orangish red. Lamellae adnexed, close (17–20) with 3 series of lamellulae, narrow; yellowish white (3A3), non-marginate. Stipe 29–50 × 0.5–1 mm, central, cylindrical, wiry, hollow; surface glabrous; apex buff to cream (3A3), centrally light brown (5B6), base dark brown (6C4, 6F8). Odor and taste not distinctive.

Basidiospores 10.4–12.8 × 4–4.8 μm \(x_m = 11.52 \pm 1.07 \times 4.48 \pm 0.44 \mu m; Q = 2.17–3.20; Q_m = 2.61 \pm 0.48, n=5, s =1\], narrowly ellipsoid to oblong, smooth, hyaline, inamyloid, thin-walled. Basidia not observed. Basidioles 17.6–29.6 × 5.6–7.2 μm, clavate to fusoid, hyaline, inamyloid, thin-walled. Cheilocystidia scattered, of Siccus-type broom cells; main body 17.6–24.8 × 5.6–7.2 μm, clavate to cylindrical, 2–3 lobed, hyaline, inamyloid, thin-walled; apical setulae 0.8–8.8 × 0.8–1.6 μm, cylindrical to conical, seldom branched, hyaline, inamyloid, thin-walled. Pleurocystidia few, 26.4–38.4 × 4.8–7.2 μm, subfusoid to subcylindrical, seldom lobed, often mucronate or capitulate, hyaline, inamyloid, thin-walled. Pileipellis mottled, a hymeniform layer of Siccus-type broom cells; main body 15.2–20 × 5.6–7.2 μm, clavate to broadly clavate or irregular, light brown, inamyloid, thick-walled; apical setulae 1.6–5.6 × 0.8–1.6 μm, conical, strict, often forked, hyaline, inamyloid, thick-walled. Pileus trama interwoven; hyphae 3.2–10.4 μm diam, cylindrical to inflated, smooth, hyaline, dextrinoid, thick-walled. Lamellar trama regular; hyphae 2.4–6.4 μm diam, cylindrical, smooth, hyaline, inamyloid, thick-walled. Stipe tissue monomitic; cortical hyphae 3.2–5.6 μm diam, parallel, cylindrical, smooth, brown, dextrinoid, thick-walled; medullary hyphae 1.6–10.4 μm diam, parallel, cylindrical, smooth, hyaline, inamyloid, thin-walled. Caulocystidia absent. Clamp connections present.

Habit, habitat and known distribution:—Solitary or in gregarious clusters on leaves of *Intsia bijuga* (Fabaceae). Africa (Cameroon, DR Congo, Ghana, Kenya, Nigeria), Madagascar.

Material examined:—MADAGASCAR. Region Atsinanana, District Brickaville, Commune Andevoranto, Andavakimena Forest, elev. 8 m, GPS: 18˚ 53.082' S, 49˚ 07.559' E, 30 January 2014, *J.E. Shay 209* (SFSU).

Notes:—*Marasmius ferruginoides* is characterized by a relatively small (7–9 mm diam), campanulate, smooth to wrinkled, orange to reddish orange pileus, close (17–20), non-collariate, non-marginate lamellae, a glabrous stipe lacking caulocystidia, narrow (4.8–7.2 μm), mucronate pleurocystidia, Siccus-type broom cells, and growth on dicotyledonous leaves. Antonín (2004) established *M. ferruginoides* for African material determined by Pegler (1977) as *M. gardneri* Singer (= *M. ferrugineus* (Berk.) Berk. & M.A. Curtis, a different species from Brazil), and subsequently reported the species from Cameroon, DR Congo, Ghana, Kenya, and Nigeria (Antonín 2007). The Madagascan specimen (*JES 209*) reported here differs from continental specimens in forming a more reddish orange pileus (rather than yellowish
orange). Antonín and Buyck (2006) reported *M. confertus* var. *parvisporus* from Madagascar, and our material of *M. ferruginoides* would key there, but the former has smaller pilei (up to 3 mm diam), fewer lamellae (15), and shorter basidiospores (8.5–12 µm long). An ITS sequence of *JES 209* (KX148983) places *M. ferruginoides* in an isolated position in the ITS phylogeny (Fig. 1a).

**FIGURE 22.** *Marasmius ferruginoides* (*JES 209*) a) basidiospores; b) basidioles; c) cheilocystidia; d) pleurocystidia; e) pileipellis cells. Scale bar = 10 µm. Illustrated by J.E. Shay.

35. *Marasmius hinnuleus* Berk. & M.A. Curtis, J. Linn. Soc., Bot. 10(45): 297. 1868 (1869). (Fig. 23, Plate 8)

*Type:*—CUBA. On dead leaves, October, *Wright 155* (K).

*Description:*—*Pileus* 6–8 mm diam, campanulate to hemispherical, some with a small umbo; margin sulcate; surface dry, rugulose around disc, glabrous along margin; disc dark brown (6E6), ferruginous to brownish orange or reddish brown (6E7–D6–7) elsewhere. *Context* thin (<1 mm), white. *Lamellae* adnate, distant (15–17), no lamellulae, broad, not intervenose; cream to buff (4A2–3), edges ferruginous or non-marginate. *Stipe* 33–52 × 0.5 mm, central, cylindrical, wiry, hollow; surface glabrous; apex light brown (5D5), base dark brown (6F8). *Odor and taste* not distinctive.

*Basidiospores* 10.4–13.6 × 2.4–4 µm \( x_n = 12.13 \pm 0.94 \times 3.24 \pm 0.49 \) µm; \( Q = 3–5; Q_m = 3.82 \pm 0.45, n = 25, s =1 \], fusoid to oblong or narrowly ellipsoid, smooth, hyaline, inamylloid, thin-walled. *Basidia* not observed. *Basidioles* 22.4–25.6 × 5.6–8 µm, clavate to fusoid, hyaline, inamylloid, thin-walled. *Cheilocystidia* of *Siccus*-type broom cells; main body 12–23.2 × 4.8–7.2 µm, clavate to cylindrical, hyaline, inamylloid, apically thick-walled; apical setulae 0.8–7.2 × 0.8–1.6 µm, cylindrical to conical or irregular, seldom branched, hyaline, inamylloid, thick-walled. *Pleurocystidia* 36–47.2 × 7–10 µm, common, subcylindrical to fusoid, some mucronate, hyaline, inamylloid, refractive, thin-walled. *Pileipellis* mottled, a hymeniform layer of *Siccus*-type broom cells; main body 8–16.8 × 4–7.2 µm, clavate, seldom 2–3 lobed, hyaline, inamylloid, thick-walled; apical setulae 0.8–4.8 × 0.8–1.6, cylindrical to conical, light brown to brown, inamylloid, thick-walled. *Pileus trama* interwoven; hyphae, 2.4–8 µm diam, cylindrical, smooth, hyaline, dextrinoid, thin-walled. *Lamellar trama* regular; hyphae 2.4–8.8 µm diam, cylindrical to inflated, hyaline, dextrinoid, thin-walled. *Pleurocystidia* monomitic; cortical hyphae 4.8–7.2 µm diam, parallel, cylindrical, hyaline, dextrinoid, thin-walled; medullary hyphae 4–7.2 µm, cylindrical, parallel, hyaline, dextrinoid, thin-walled. *Caulocystidia* absent. *Clamp connections* present.

Habit, habitat, and known distribution:—Solitary or in small clusters on bamboo debris in groomed park. Cuba, Guadeloupe, Madagascar.
Material examined:—MADAGASCAR. Region Analamanga, City of Antananarivo, Parc Botanique de Zoologique (P.B.Z.T.), near the garden of Crops Wild and Relatives (CWR), elev. 1270 m, GPS: 18˚ 55.530’ S, 47˚ 31.350’ E, 8 February 2014, J.E. Shay 217 (TAN).

Notes:—Marasmius hinnuleus, described originally from Cuba, is characterized by a small (<10 mm diam), sulcate, brownish orange to reddish brown pileus, distant (15–17), non-marginate lamellae, a non-insititious, glabrous stipe lacking caulocystidia, refractive, often mucronate pleurocystidia 7–10 µm diam, Siccus-type broom cells, and growth on dead leaves. The Madagascan specimen matches quite closely material reported from the Caribbean (Singer 1976, Pegler 1983). The species shows similarities to Marasmius hypophaeus Berk. & M.A. Curtis, Marasmius confertus Berk. & Broome, Marasmius suthepensis, and Marasmius ferrugineus (Berk.) Berk. & M.A. Curtis. Marasmius hypophaeus forms fewer lamellae (11–13) with brownish orange edges, a smaller stipe (23–35 mm long), larger basidiospores (x = 17.2 × 4.0 µm) and strangulate pleurocystidia (Desjardin et al. 2000, Wannathes et al. 2009a). Marasmius confertus and Marasmius suthepensis have nearly smooth pilei and more numerous lamellae with multiple series of lamellulae (Antonín 2007, Wannathes et al. 2009a). Marasmius ferrugineus forms a paler pileus, has fewer lamellae (8–10) and larger basidiospores (x = 17.0 × 4.0 µm) (Singer 1976, Desjardin et al. 2000). An ITS sequence of JES 217 (KX148988) places M. hinnuleus in a clade with M. hypophaeus and M. grandisetulosus with 89% BS and 1.0 PP support (Fig. 1a).
FIGURE 23. *Marasmius hinnuleus* (JES 217) a) basidiospores; b) basidioles; c) cheilocystidia; d) pleurocystidia; e) pileipellis cells. Scale bar = 10 µm. Illustrated by J.E. Shay.

**Discussion**

As of 2006, only 19 species of *Marasmius sensu stricto* were known from Madagascar. Our fieldwork in 2014 revealed another 16 species for the region, of which 11 are new distribution reports and 5 represent new species. A nearly doubling of the number of *Marasmius* species from only a month of fieldwork in 2014 suggests that continued explorations would undoubtedly yield numerous more species. Documenting the biodiversity of *Marasmius* and allied litter-decomposing species from Madagascar is in its infancy and much more work is needed.

Over 1700 epithets have been published to date in *Marasmius*, representing over 600 distinct species. As this project highlights, there are numerous species awaiting discovery through intensive sampling of underexplored habitats. Circumscribing species of *Marasmius* requires a combination of morphological, ecological and molecular characters. Historically, morphology alone was used to develop infrageneric groups. All species with collariate lamellae and insititious stipes were recognized as belonging to sect. *Marasmius*, and within this group, those with *Rotalis*-type broom cells were grouped in subsect. *Marasmius*, while those with *Siccus*-type broom cells belonged to subsect. *Sicciformes*. If a species lacked a collarium but the stipe was insititious, the species was accepted in sect. *Leveilleani*. All species lacking a stipe or with a very rudimentary lateral stipe were placed in sect. *Neosessiles*. By far the most diverse group of *Marasmius* are those species with non-collariate lamellae and non-insititious stipes, historically placed in sections *Globulares* (with smooth *Globulares*-type cells in the pileipellis) and *Sicci* (with *Siccus*-type broom cells in the pileipellis). Recent molecular studies by Tan *et al.* (2009) and Wannathes *et al.* (2009a) have shown that these two sections are not monophyletic, and the current trend is to accept members of the two groups in a single section, sect. *Globulares* (Antonín & Noordeloos 2010). Within this lineage, historical infrageneric classifications have distinguished groups based on the presence or absence of setae, pleurocystidia, and simple cylindrical caulocystidia. For example, species with setae on the pileus, hymenium and/or stipe surface were grouped in ser. *Spinulosi*; those with simple cylindrical caulocystidia were placed in ser. *Atrorubentes*; those lacking setae and simple cylindrical caulocystidia but with distinct pleurocystidia were accepted in ser. *Haematocephali*, while those lacking setae, caulocystidia and pleurocystidia were recognized in ser. *Leonini*.

In most historically recognized infrageneric groups of *Marasmius*, species may be nearly indistinguishable in morphology but very different molecularly. This is particularly true in sect. *Marasmius*, where most species are small,
have plicate pilei, distant collariate lamellae lacking lamellulae, black, wiry glabrous stipes, basidiospores in a limited size range, lack pleurocystidia and caulocystidia, and are generally character-poor. For these taxa, molecular sequences are invaluable in delimiting species. As in previous studies based on ITS sequences (Tan et al. 2009, Wannathes et al. 2009a), the phylogenetic analyses presented here indicate that the historical infrageneric classification based on morphology does not represent monophyletic lineages. The ITS phylogeny (Fig. 1) clearly indicates that setae (ser. Spinulosi) have evolved independently numerous times, as have pleurocystidia (ser. Haematocephali), simple cylindrical caulocystidia (ser. Atrorubentes), pileipelli with smooth Globulares-type cells (sect. Globulares), and collariate species with Siccus-type broom cells (subsect. Sicciformes). Morphology alone does not indicate phylogenetic relationships. Molecular datasets are needed to better understand relationships in this diverse and widespread genus.

The genus Marasmius is over 90 million years old, worldwide in distribution, and megadiverse. With such a long evolutionary history, a quickly evolving gene region such as the ITS region shows extensive variability amongst species. This creates problems in accurately aligning sequences for phylogenetic analyses, especially among species from geographically distant populations, and provides low resolution at the deeper nodes. Sequences from additional gene regions, particularly RPB2 and EF1-α, need to be analyzed to develop an infrageneric classification that better reflects the phylogeny of Marasmius.

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