

BIODIVERSITY AND PHYLOGENY OF *MARASMIUS* FROM MADAGASCAR

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Master of Science
In
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by

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CERTIFICATION OF APPROVAL

I certify that I have read *Marasmius of Madagascar: A Monograph* by Jacqueline Elizabeth Shay, and that in my opinion this work meets the criteria for approving a thesis submitted in partial fulfillment of the requirements for the degree: Master of Science in Biology: Ecology, Evolution, and Conservation Biology at San Francisco State University.



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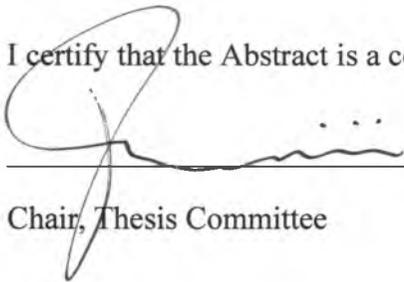
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San Francisco, California
2016

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 exsiccatae 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. dendrosetae*, *M. sokola* and *M. tanaensis*; an additional 11 species represent new distribution records for Madagascar. Comprehensive descriptions based on morphological and molecular sequences (ITS) data, illustrations and color photographs, comparisons with allied taxa, a key to aid in identification, and phylogenetic inferences are provided.

I certify that the Abstract is a correct representation of the content of this thesis.



Chair, Thesis Committee

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Introduction

Members of the mushroom genus *Marasmius* play key roles in the decomposition of leaf litter, nutrient cycling, and soil genesis (Tan et al, 2007). *Marasmius* diversity has been found to strongly correlate with the diversity of local flora, especially in tropical habitats (Lodge et al, 1995). The island of Madagascar is a model tropical system that has evolved in isolation, and is characterized by patterns of endemism and species diversification (Vences et al, 2009). There has been recent interest in understanding the global biodiversity and evolution of *Marasmius* (Antonín, 2003, 2004a, b; Wannathes et al., 2004; Antonín et al., 2005; Antonín & Buyck 2006; Desjardin and Ovrebo, 2006, Antonín 2007, Tan et al. 2009, Wannathes et al. 2009). However, only limited attention has been paid to the *Marasmius* of Madagascar. In this work, I document 35 species from Madagascar. Species of *Marasmius* previously reported from Madagascar (Antonín and Buyck 2006), are confirmed using morphological and molecular characteristics.

The earliest records of *Marasmius* from Madagascar were reported by Patouillard (1924, 1928), based on collections made by J. Braun in 1891 of *Marasmius foetidus* (Sowerby: Fr.) Fr. (= *Gymnopus foetidus* (Sowerby) P.M. Kirk) from Ankoraka and *M. oreades* (Bolton) Fr. from a meadow at “Champ de Meclas”. Hennings (1908) reported *Marasmius rotula* (Scop.) Fr. and *M. rhodocephalus* Fr., both from SW Madagascar near Andranohinaly.

Collections of *Marasmius* and *Androsaceus* made by Raymond Decary in 1923 and 1924 and sent to the Natural History Museum in Paris were studied by Patouillard (1928). These collections were made on the central plateau of the island towards Antananarivo and Maromandia, and included the European *Marasmius candidus* Fr. (= *Marasmiellus candidus* (Fr.) Singer) and *M. ramealis* (Bull.) Fr. (= *Marasmiellus*

ramealis (Bull.) Singer), and tropical *M. aureotomentosus* Kalchbr., *M. aculeatus* Pat. and *M. sulcatipes* Pat. (nom. illeg., non *M. sulcatipes* Murrill 1915). In addition, Patouillard (1928) reported four taxa of *Androsaceus*, viz., *A. rhodocephalus* (Fr.) Pat. (= *Marasmius haematocephalus* (Mont.) Fr.), *A. haematocephalus* (Mont.) Pat. (= *Marasmius haematocephalus* (Mont.) Fr.), *A. polyadelphus* (Lasch) Pat. (= *Mycena polyadelpa* (Lasch) Kühner) and introduced a new variety “*substipitatus*” for *A. sessilis* Pat. (= *Marasmius sessilis* (Pat.) Sacc. & Sydow). Decary's specimens were studied later by George Métrod, who documented many fungi from Madagascar, but his observations were never published. These 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 and Buyck (2006) reported 19 taxa 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; however, 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, except for the island of Madagascar. Antonín (2013) followed with a supplement to the African *Marasmius* monograph in which he reported an additional 40 taxa.

Fieldwork in Madagascar in January–February 2014 by Jackie Shay and Danny Newman, and in January 2013 by Taylor Lockwood yielded 83 specimens of *Marasmius*

sensu lato, of which 45 specimens represented *Marasmius sensu stricto*. From the 19 species reported from Madagascar by Antonín and Buyck (2006), 5 were recollected, an additional 11 species are reported as new distribution records, and 5 species represent new species. In total, 35 taxa of *Marasmius* are documented from Madagascar in this treatment. Species are delineated using morphological characteristics and DNA sequence data. Comprehensive descriptions of macromorphological and micromorphological features, illustrations, photographs, a dichotomous key to aid in identification, comparisons with similar taxa, and phylogenetic inferences are provided. This represents the first treatment of *Marasmius* from Madagascar that incorporates molecular data in circumscribing and distinguishing species, as well as investigate phylogenetic relationships.

Materials and Methods

Sampling protocols

Rainforests are an ideal location for sampling tropical biotas. Additionally, Madagascar is a model site for sampling litter-decomposing fungi. The country serves as a natural lab for understanding evolutionary diversification and biodiversity patterns (Vences, 2009). For this project, a variety of eastern rainforests in Madagascar were surveyed, including Ranomafana National Park, the forests near Andasibe, the littoral forests of the east coast near Brickavile, and the Ambohitantily Reserve on the northern central plateau (Fig. 24). Using the characteristics of known *Marasmius* morphotypes (pliant pileus; attached white lamellae; wiry stipe; white spores; growing from leaf litter or wood) all specimens of *Marasmius sensu lato* were collected, totaling 83 by the end of the expedition. Notes were taken on morphological features and substrate, and GPS coordinates were recorded for each sample. Collections were dried overnight using a food dehydrator and packaged promptly to avoid condensation, and subsequent mold.

Previously collected material from Antonín and Buyck was borrowed from Moravian Museum (BR), Dept. of Botany, Brno, Czech Republic and the Muséum National D'Histoire Naturelle (PC), Dépt. Systématique et Evolution, Paris, France respectively. Their macro- and micromorphological features were compared to newly collected material during our analyses.

Morphological protocols

Macromorphological data were documented in the field at time of collection. Features noted include cap diameter and depth, color and surface features; number and width of lamellae, color and attachment to stipe; length and width of stipe, color and surface features, attachment to the substrate; presence or absence of rhizomorphs; odor and taste. Colors noted are from Kornerup and Wanscher (1978). Other macroscopic data include plant host species names, habitat, GPS coordinates, altitude and specificity to hosts. Material was subjected to 3% potassium hydroxide (KOH) and Melzer's reagent and any staining reactions were recorded. Photographic images of all specimens were made with a Canon Rebel T3i EF-S 60MM F/2.8 Macro USM lens. Specimens were then dried, packaged in plastic bags, and shipped to SFSU.

Micromorphological features were observed at SFSU by sectioning dried material, soaking it in 95% ethanol followed by 3% KOH or Melzer's reagent, and reactions were recorded. The term "inamyloid" refers to a non-reaction in Melzer's reagent (neither amyloid nor dextrinoid). All microscopic features were documented and include shape, size, and ornamentation of basidiospores, basidia, basidioles, cystidia or setae, stipe cortical and medullary hyphae, lamellar tissue, and pileus tissue. Spore statistics include \bar{x}_m , the arithmetic mean of the spore length by spore width (\pm standard deviation) for n spores measured in a single specimen; \bar{x}_{mm} , the mean of spore means (\pm standard deviation) when more than one specimen is available; Q, the quotient of spore length by spore width by spore, indicated as a range in variation in n spores measured;

Q_m , the mean of Q values (\pm standard deviation) in a single specimen; Q_{mr} , the range of Q_m values and Q_{mm} , the means of Q_m values where more than one specimen is available; n , the number of spores measured per specimen; s , the number of specimens involved. Results of the micromorphological analyses indicated that only 45 of the 83 specimens of *Marasmius sensu lato* represented *Marasmius sensu stricto* and were included in this monographic treatment. The remaining 38 specimens represented species of *Gymnopus* or *Marasmiellus*.

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 4AccuPower® HotStart PCR PreMix (Bioneer, Daejeon, Korea) instructions or methods for PCR amplification outlined in Cubero et al. (1997). The internal transcribed spacer (ITS) regions 1 and 2, as well as 5.8S rDNA, were amplified using primers ITS1-F and ITS-4 (Gardes and 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 separated through 1.8% agarose gel electrophoresis, and purified using ExoSAPIT Kit (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 software (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. The ITS sequences of *Marasmius* have been deposited in GenBank with submission ID #1912023. For GenBank submission numbers for individual collections, refer to Table 1.

Results

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*. These resulting constrained and unconstrained topologies were compared using the Shimodaira-Hasegawa (SH) test (Simodaira and Hasegawa, 1999) as implemented in PAUP* (Swofford 2003) using 1000 RELL bootstrap replicates. Results of the SH test indicate no statistically significant difference between these topologies, and I am therefore unable to reject the monophyly of these sections given the data presented.

Phylogenetic Analysis

Phylogenetic analyses were performed on 222 ITS sequences of *Marasmius* representing a global sampling of the genus, and included 43 sequences of *Marasmius* from Madagascar. *Crinipellis malesiana* was chosen as the outgroup based on the results of previous research (Tan et al. 2009, Wannathes et al. 2009). A total of 343 ambiguously aligned nucleotides were removed prior to all analyses, resulting in final data set of 687 nucleotide characters (Table 1).

Table 1: List of *Marasmius* specimens sequenced (ITS1–5.8S–ITS2) for this study, itemized by infrageneric group.

Species	Section/Series	Collection No.	GenBank No.
<i>M. bekolacongoli</i>	<i>Globulares</i>	Lockwood 2131638	KX148982
<i>M. apatelius</i>	<i>Marasmius/Marasmius</i>	JES150	KX148997
<i>M. apatelius</i>	<i>Marasmius/Marasmius</i>	JES203	KX148998
<i>M. rotalis</i>	<i>Marasmius/Marasmius</i>	JES141	KX148999
<i>M. rotalis</i>	<i>Marasmius/Marasmius</i>	JES145	KX149000
<i>M. rotalis</i>	<i>Marasmius/Marasmius</i>	JES150B	KX149001
<i>M. somalomoensis</i>	<i>Marasmius/Marasmius</i>	JES129	KX149002
<i>M. somalomoensis</i>	<i>Marasmius/Marasmius</i>	JES165	KX149003
<i>M. somalomoensis</i>	<i>Marasmius/Marasmius</i>	JES181	KX149004
<i>M. andasibensis</i> var. <i>obsurostipitatus</i>	<i>Marasmius/Marasmius</i>	Buyck 00.1699b	KX149005
<i>M. aff. curreyi</i>	<i>Marasmius/Sicciformes</i>	JES135	KX149008
<i>M. brunneoaurantiacus</i>	<i>Marasmius/Sicciformes</i>	JES113	KX148980
<i>M. brunneoaurantiacus</i>	<i>Marasmius/Sicciformes</i>	JES125	KX149010
<i>M. brunneoaurantiacus</i>	<i>Marasmius/Sicciformes</i>	JES115	KX149011
<i>M. brunneoaurantiacus</i>	<i>Marasmius/Sicciformes</i>	JES137	KX149012
<i>M. brunneoaurantiacus</i>	<i>Marasmius/Sicciformes</i>	JES166	KX149013
<i>M. brunneoaurantiacus</i>	<i>Marasmius/Sicciformes</i>	JES218	KX149014
<i>M. cf. subruforotula</i>	<i>Marasmius/Sicciformes</i>	JES186	KX149017
<i>M. cf. subruforotula</i>	<i>Marasmius/Sicciformes</i>	JES192	KX149018
<i>M. cf. subruforotula</i>	<i>Marasmius/Sicciformes</i>	JES190	KX149019
<i>M. madagascariensis</i>	<i>Marasmius/Sicciformes</i>	JES139	KX149015
<i>M. madagascariensis</i>	<i>Marasmius/Sicciformes</i>	JES225	KX149006
<i>M. rubrobrunneus</i>	<i>Marasmius/Sicciformes</i>	JES191	KX148989
<i>M. curreyi</i>	<i>Marasmius/Sicciformes</i>	Buyck97.374	KX148980
<i>M. brunneoaurantiacus</i>	<i>Marasmius/Sicciformes</i>	JES133	KX149016
<i>M. corrugatiformis</i>	<i>Sicci/Atrorubentes</i>	Buyck97.425	KX148981
<i>M. katangensis</i>	<i>Sicci/Atrorubentes</i>	JES227	KX148991
<i>M. ferruginoides</i>	<i>Sicci/Haematocephali</i>	JES209	KX148983
<i>M. haematocephalus</i>	<i>Sicci/Haematocephali</i>	JES110	KX148984
<i>M. haematocephalus</i>	<i>Sicci/Haematocephali</i>	JES193	KX148985

Table 1 continued: List of *Marasmius* specimens sequenced (ITS1–5.8S–ITS2) for this study, itemized by infrageneric group.

<i>M. haematocephalus</i>	<i>Sicci/Haematocephali</i>	JES202	KX148986
<i>M. haematocephalus</i>	<i>Sicci/Haematocephali</i>	JES142	KX148987
<i>M. hinnuleus</i>	<i>Sicci/Haematocephali</i>	JES217	KX148988
<i>M. haematocephalus</i>	<i>Sicci/Haematocephalus</i>	Buyck 00.1820	KX148977
<i>M. bambusiniformis</i>	<i>Sicci/Leonini</i>	JES199	KX148990
<i>M. megistus</i>	<i>Sicci/Leonini</i>	JES163	KX148992
<i>M. megistus</i>	<i>Sicci/Leonini</i>	Lockwood 2132155	KX148993
<i>M. sokola</i>	<i>Sicci/Leonini</i>	JES154	KX148994
<i>M. brunneoaurantiacus</i>	<i>Sicci/Leonini</i>	Buyck 99.450	KX148978
<i>M. neosessiliformis</i>	<i>Sicci/Neosessiles</i>	Buyck97.615	KX149007
<i>M. dendrosetae</i>	<i>Sicci/Spinulosi</i>	JES205	KX148995
<i>M. dendrosetae</i>	<i>Sicci/Spinulosi</i>	JES211	KX148996
<i>M. nummularius</i>	<i>Sicci/Spinulosi</i>	JES121	KX148979

The accepted RAxML tree is represented here as an ITS phylogeny of *Marasmius* (Fig. 1: $-\ln L = -13820.463$). In general, statistical support for the deep nodes 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). All members of this group form lamellae attached to a collarium, 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-insititious stipe, *Globulares*-type or *Siccus*-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* occurs in two distinct parts of the tree. The recently described *M. griseoroseus* and *M. conchiformis*, plus *M. elaeocephalus* (a member of sect. *Sicci* ser. *Haematocephali*) align with members of Sect. *Globulares* + *Sicci* (Fig. 1a), whereas *M. tenuissimus* and *M. neosessiliformis* are sister to sect. *Leveilleani* and together are sister to one clade of sect. *Marasmius* subsect. *Sicciformes* (Fig.1c). *Marasmius nodulocystis* (sect. *Sicci* ser. *Leonini*) is morphologically nearly indistinguishable from *M. leveilleanus* (type species of sect. *Leveilleani*) and 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. 1a: *Marasmius katangensis* (SA) is sister to a clade containing *M. occultatiformis* (SL), *M. cf. cladophyllus* (SL) and *M. aurantioferrugineus* (G) with low support. *Marasmius corrugatiformis* (SA) is sister to *M. subarborescens* (SA) with low support. *Marasmius bambusiniiformis* (SL) is sister to *M. berteroi* (SL) with 100% BS support. *Marasmius ferruginoides* (SH) holds an isolated position basal to numerous members of sects. *Globulares* + *Sicci*, in a grade with other members of ser. *Haematocephali*. *Marasmius hinnuleus* (SH) is on a long branch sister to *M. grandisetulosus* (SH) with low support. Two sequences of *Marasmius megistus* (SL) from Madagascar form a well-supported clade with a sequence from São Tomé (100% BS) and are on a long branch sister to members of ser. *Haematocephali*.

Concerning Madagascar taxa in Fig. 1b: The new species *M. dendrosetae* (SS) is sister to *M. longisetosus* (SS) with 99% BS support, in a clade with other members of ser. *Spinulosi*. A sequence of *Marasmius nummularius* (SS) from Madagascar forms a well-supported clade with two sequences from Thailand (90% BS), 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) but with low support. *Marasmius bekolacongoli* (G) forms an unresolved trichotomy with other members of sect. *Globulares* plus *M. coarctatus* (SS). The new species *M. sokola* (SL) is on a long branch sister to *M. imitarius* (SL) with low support.

Concerning Madagascar taxa in Fig. 1c: Three sequences of *M. somalomoensis* (MM) are unresolved in a clade containing other members of sect. *Marasmius* subsect.

Marasmius with low support. Three sequences of Madagascar *M. rotalis* (MM) form a well-supported clade (98% BS) sister to a GenBank sequence of *M. rotalis* plus other members of subsect. *Marasmius*. Two sequences of Madagascar *M. apatelius* (MM) form a grade with other *M. apatelius* sequences from Thailand and Príncipe and *M. andasibensis* var. *obscurostipitatus* (MM) from Madagascar, but with low support. Three sequences of *M. cf. subruforotula* (MS) form a well-supported clade (99% BS) and are sister to several sequences of *M. subruforotula* (MS) from Príncipe with 100% BS support. The new species *M. rubrobrunneus* (MS) is on a long branch sister to *M. purpureobrunneolus* (MS) with 81% BS support. A sequence of *Marasmius curreyi* (MS) from Madagascar (KX148980) forms an unresolved clade with a sequence of *M. curreyi* from North Carolina (FJ431237) plus *M. graminum* (MS) with low support. This clade is sister to a well-supported clade (98% BS) clade containing a Madagascar sequence of *M. aff. curreyi* (MS) plus a Korean sequence of *M. curreyi* (FJ936152). Eight sequences of *M. brunneoaurantiacus* (MS) form a well-supported clade (100% BS) 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. leveillianus* (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) and *M. crinisequi* (MS) with low support.

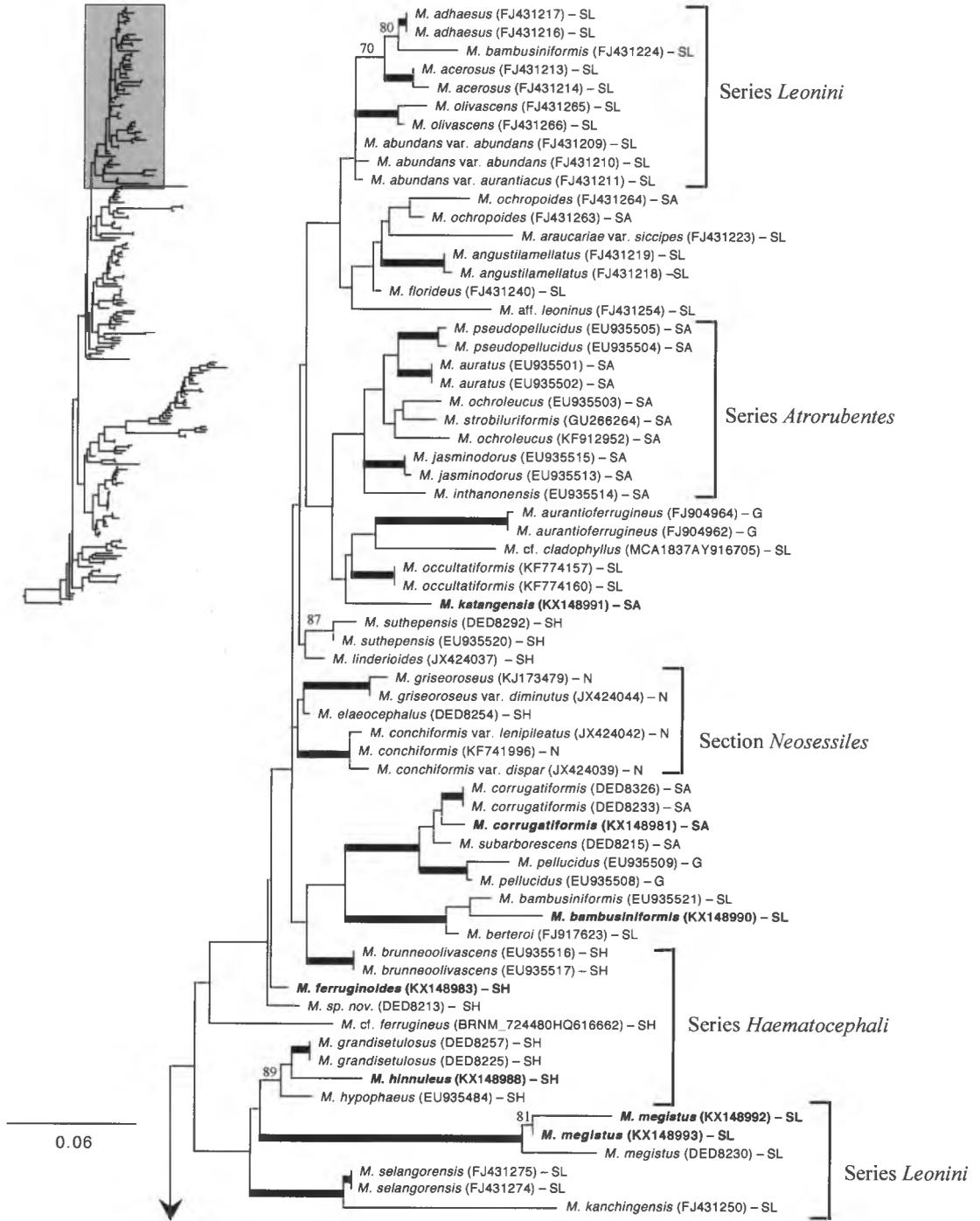


Figure 1a: Maximum likelihood phylogeny based on ITS sequence data. *Marasmius* from Madagascar are indicated in bold type. Values separated refer to nonparametric ML bootstrap proportions. Only values greater than 70 are shown. Nodes receiving support values greater than 90 are highlighted in bold. G – sect. *Globulares*. N – sect. *Neosessiles*. SA – sect. *Sicci* ser. *Atrorubentes*; SL – sect. *Sicci* ser. *Leonini*; SH – sect. *Sicci* ser. *Haematocephali*.

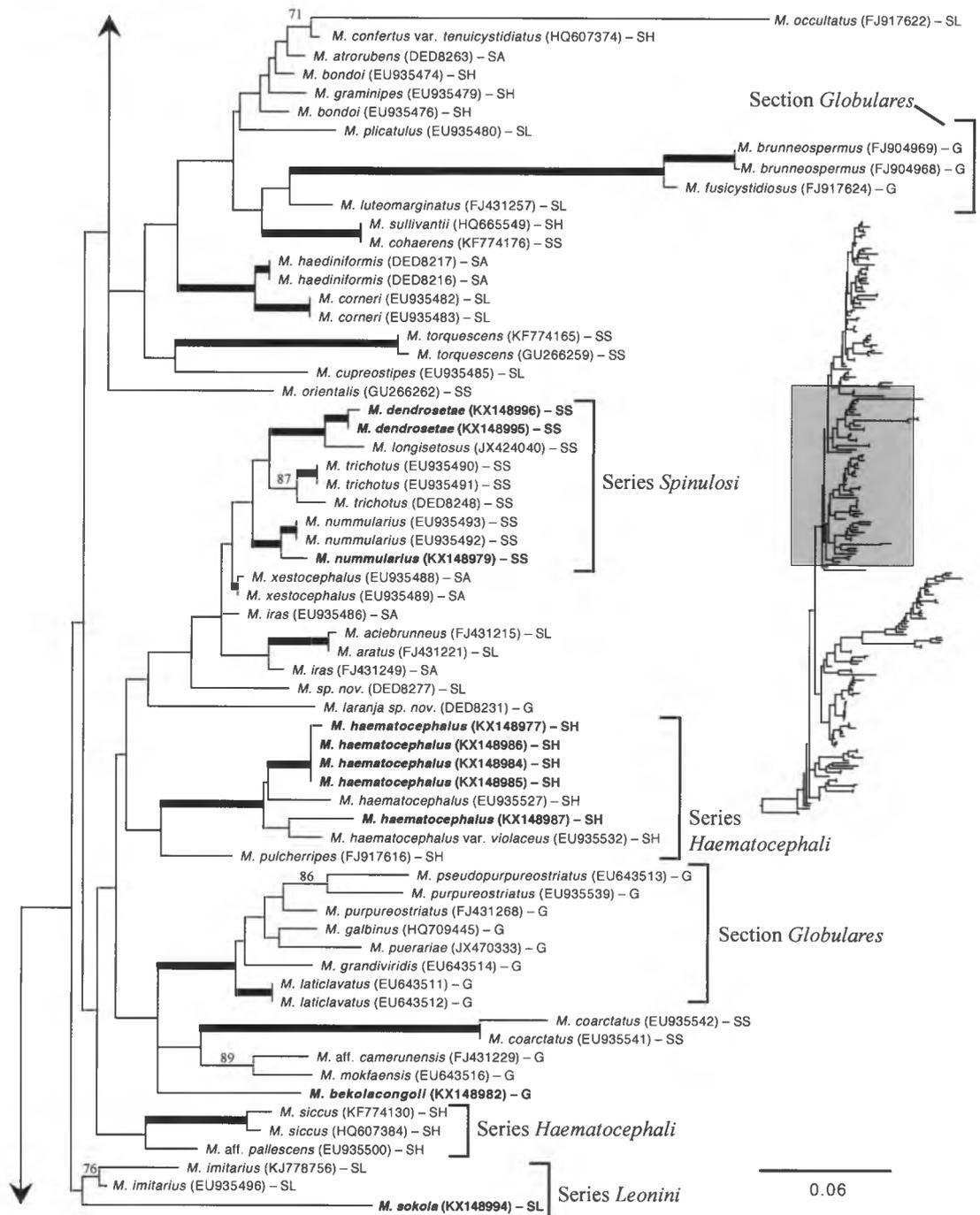


Figure 1b: Maximum likelihood phylogeny based on ITS sequence data. *Marasmius* from Madagascar are indicated in bold type. Values refer to nonparametric ML bootstrap proportions. Only values greater than 70 are shown. Nodes receiving support values greater than 90 are highlighted in bold. G – sect. *Globulares*. SA – sect. *Sicci* ser. *Atrorubentes*; SL – sect. *Sicci* ser. *Leonini*; SS – sect. *Sicci* ser. *Spinulosi*; SH – sect. *Sicci* ser. *Haematocephali*.

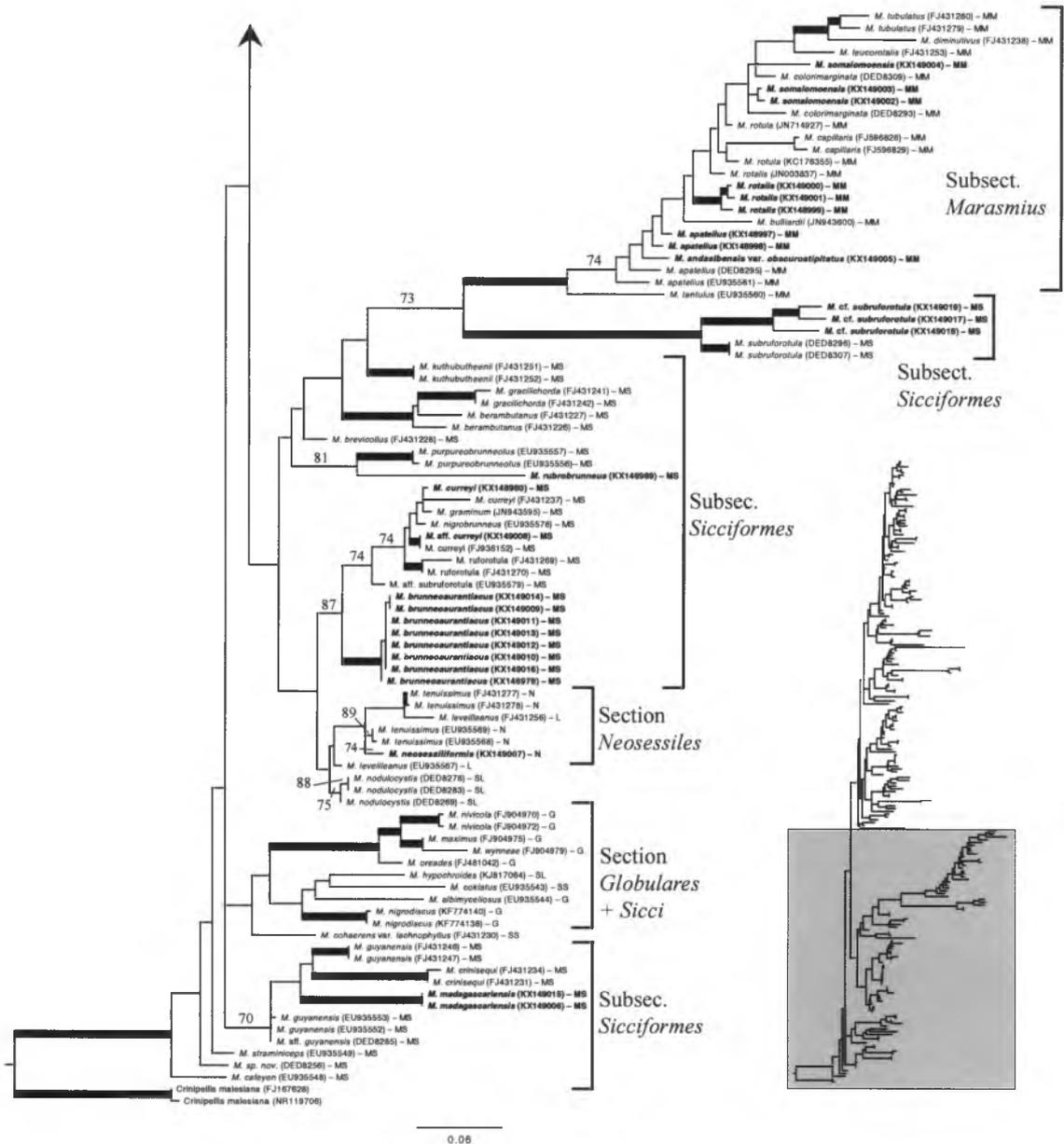


Figure 1c: Maximum likelihood phylogeny based on ITS sequence data. *Marasmius* from Madagascar are indicated in bold type. Values refer to nonparametric ML bootstrap proportions. Only values greater than 70 are shown. Nodes receiving support values greater than 90 are highlighted in bold. G – sect. *Globulares*. N – sect. *Neosessiles*. L – sect. *Leveilleani*. MM – sect. *Marasmius* subject. *Marasmius*; MS – sect. *Marasmius* subject. *Sicciformes*. SA – sect. *Sicii* ser. *Atrorubentes*; SL – sect. *Sicii* ser. *Leonini*; SS – sect. *Sicii* ser. *Spinulosi*; SH – sect. *Sicii* ser. *Haematocephali*.

Key for identification of *Marasmius* from Madagascar

1. Lamellae attached to a distinct collarium; stipe insititious (sect. *Marasmius*)2
 1'. Lamellae attached directly to the stipe or free and collarium absent; stipe not insititious17
2. Pileipellis composed of *Rotalis*-type broom cells (subsect. *Marasmius*)3
 2'. Pileipellis composed of *Siccus*-type broom cells (subsect. *Sicciformes*)7
3. Pileus white, pale grey, or buff **1. *M. rotalis***
 3'. Pileus greyish orange, tan, or pale brown4
4. Pileus tan to pale brown; lamellae subdistant (11–14) **2. *M. somalomoensis***
 4'. Pileus greyish orange to buff; lamellae distant (9–12)5
5. Pileus with a dark brown papilla **3. *M. apatelius***
 5'. Papilla absent or concolorous with pileus surface6
6. Papilla absent; stipe pale brown **4. *M. andasibensis* var. *andasibensis***
 6'. Papilla present, concolorous with pileus surface; stipe brown-black
 **5. *M. andasibensis* var. *obscurostipitatus***
7. Pileus brownish black or black8
 7'. Pileus differently coloured (reddish brown, brown, greyish orange, tan or cream)9
8. Basidiospores $8.5\text{--}10.5 \times 4\text{--}5 \mu\text{m}$; cheilocystidia $10\text{--}25 \times 7\text{--}12 \mu\text{m}$; pileus bicolored black and grey **6. *M. nigrogriseus***
 8'. Basidiospores $9\text{--}12 \times 4.5\text{--}6.5 \mu\text{m}$; cheilocystidia $10\text{--}14 \times 5\text{--}8 \mu\text{m}$; pileus brownish black **7. *M. nigrobrunneus***

9. Pileus reddish brown, or white, cream, tan to light brown	10
9'. Pileus greyish orange to brownish orange	15
10. Pileus white to cream with prominent, dark brown conical papilla	8. <i>M. conicopapillatus</i>
10'. 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
11'. Pileus dark reddish brown	14
12. Pileus tan to light brown	10. <i>M. aff. curreyi</i>
12'. 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. <i>M. curreyi</i>
13'. Basidiospores 10–12.5 × 4.5–6 μm; cheilocystidia of two types	11. <i>M. curreyi</i> var. <i>bicystidiatus</i>
14. Basidiospores mean range 14.9–16.5 × 3.2 μm; lamellae distant (11–12)	12. <i>M. rubrobrunneus</i>
14'. Basidiospores mean range 8.8–9.5 × 4.1–4.6 μm; lamellae subdistant (12–16)	13. <i>M. brunneoaurantiacus</i>
15. Basidiomes arising directly from black rhizomorphs; pileus 1–2 mm diam; lamellae distant (6); stipe 2–4 mm long	14. <i>M. crinisequi</i>
15'. 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. subrufotula***
- 16'. 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
- 17'. Stipe well-developed and central (sect. *Globulares* + *Sicci*)19
18. Pileus 1–4 mm diam, reddish brown; basidiospores 10–11 × 5–6 μm, ellipsoid; pleurocystidia absent..... **17. *M. neosessiliformis***
- 18'. 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. cecropiformis***
19. Pileipellis composed of smooth, broadly clavate, non-setulose cells (sect. *Globulares*)20
- 19'. Pileipellis composed of *Siccus*-type broom cells (sect. *Sicci*).....21
20. Pileus 100–120 mm diam, pale mouse grey overall; pleurocystidia present **19. *M. sulcatipes***
- 20'. 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
- 21'. Stipe glabrous, simple cystidia and setae absent 25
22. Setae present on pileus, lamellae and/or stipe (ser. *Spinulosi*) 23
- 22'. 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 \times 3.9 μm ; caulosetae absent, caulocystidia of *Siccus*-type broom cells **21. *M. dendrosetae***
- 23'. Pileosetae unbranched, rare; pleurocystidia present; basidiospores mean range 12.4–12.7 \times 4.3–4.8 μm ; caulosetae abundant **22. *M. nummularius***
24. Basidiospore mean 9.0 \times 4.0 μm ; caulocystidia dextrinoid, of one type (non-setulose cells) **23. *M. corrugatiformis***
- 24'. Basidiospores mean 7.8 \times 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
- 25'. Pleurocystidia present (ser. *Haematocephali*) 29
26. Pileus 20 mm diam, dark brown **25. *M. sokola***
- 26'. 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. rammelooi***
- 27'. 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 \times 2.5 μm **27. *M. megistus***
- 28'. Pileus 4–5 mm diam, reddish orange to orange; stipe 25–30 mm long; basidiospore mean 16.4 \times 3.5 μm **28. *M. bambusiniformis***
29. Basidiospores 12–22 μm long, with mean length 13.4–21 μm 30
- 29'. 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***
- 30'. 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***
- 31'. 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 \times 4–5 μm ; pleurocystidia 38–65 \times 9–15 μm , subfusoid, often rostrate; pileipellis cells with 8–20 projections up to 6 μm long.....**31. *M. cf. grandisetulosus***
- 32'. Pileus 3–5 mm diam, brown to reddish brown; basidiospores 13.5–16 \times 3.5–5 μm ; pleurocystidia 30–50 \times 8–14 μm , clavate to subfusoid, sometimes rostrate; pileipellis cells with up to 40 projections up to 10 μm long **32. *M. eyssartieri***
33. Pileus up to 3 mm diam; *Siccus*-type broom cells present on stipe apex.....
.....**33. *M. cf. confertus* var. *parvisporus***
- 33'. 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***
- 34'. Pileus brownish orange to reddish brown; lamellae distant (15–17); pleurocystidia 7–10 μm diam **35. *M. hinnuleus***

Enumeration of *Marasmius* Taxa from Madagascar

I. Sect. *Marasmius*

Marasmius, II. *Mycena*, 2. *Rotulae* Fr., Epicr.: 384. 1838.

= *Marasmius* B. *Rotulae* Quél., Enchir.: 145. 1886.

= *Marasmius* sect. *Rotulae* Kühner, Botaniste 25: 98. 1933.

= *Marasmius*, I. *Rotularia* J. Schröt. in Cohn, Kryptog.-Fl. Schles. 3(1): 556. 1889.

= *Marasmius*, "sect." *Setipedes*, α *Collariati* Bataille, Marasmes Eur.: 26. 1919.

= *Marasmius* sect. *Pararotulae* Singer, Sydowia 18: 140. 1965.

– *Type species*: *Marasmius rotula* (Scop.) Fr.

Ia. Subsect. *Marasmius*

= *Marasmius* sect. *Pararotulae* Singer, Sydowia 18: 336. 1965.

= *Marasmius* sect. *Marasmius*, subsect. *Pararotulae* (Singer) Singer, Fl. Neotrop. Monogr. 17: 92. 1976.

– *Type species*: *Marasmius rotula* (Scop.) Fr.

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

– *Type*: Sri Lanka, Peradeniya, Thwaites 810 (K!)

(Figure 2, Plate 1)

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.

Basidiospores (6.4–) 7.2–10.4 (–11.2) × 3.2–4.8 (–5) μm [$x_{mr} = 8.4\text{--}8.9 \times 3.7\text{--}4.2$ μm; $x_{mm} = 8.7 \pm 0.3 \times 4.0 \pm 0.3$ μm; $Q = 1.5\text{--}3.3$; $Q_{mr} = 2.09\text{--}2.28$; $Q_{mm} = 2.19 \pm 0.1$, n =

24–25, $s = 3$], ellipsoid, smooth, hyaline, inamyloid, thin-walled. *Basidia* not observed. *Basidioles* $13.6\text{--}23.2 \times 4\text{--}8 \mu\text{m}$, clavate to fusoid, some utriform, hyaline, inamyloid, thin-walled. *Cheilocystidia* numerous, of *Rotalis*-type broom cells; main body $6.8\text{--}20 \times 8\text{--}22.4 \mu\text{m}$, clavate to broadly clavate, globose, subglobose or obpyriform, hyaline, inamyloid, thin-walled; divergent setulae $0.5\text{--}2.4 \times 0.5\text{--}2.4 \mu\text{m}$, cylindrical to conical, obtuse, hyaline, inamyloid, thin-walled. *Pleurocystidia* absent. *Pileipellis* not mottled, a hymeniform layer of *Rotalis*-type broom cells; main body $8\text{--}34 \times 8\text{--}28 \mu\text{m}$, clavate to broadly clavate, subglobose or globose, pale yellowish brown to hyaline, inamyloid, thin-walled; divergent setulae $0.5\text{--}3 \times 0.2\text{--}1.6 \mu\text{m}$, numerous, cylindrical to conical, pale yellowish brown to hyaline, inamyloid, thin-walled. *Pileus trama* interwoven; hyphae $1.6\text{--}4.8 \mu\text{m}$ diam, cylindrical, smooth, hyaline, inamyloid, thin-walled. *Lamellar trama* regular; hyphae $1.6\text{--}9.6 \mu\text{m}$ diam, cylindrical to slightly inflated, smooth, hyaline, inamyloid, thin-walled. *Stipe tissue* monomitic; cortical hyphae $3\text{--}4 \mu\text{m}$ diam, parallel, cylindrical, smooth, yellowish brown to brown, dextrinoid, thick-walled; medullary hyphae $1.6\text{--}6 \mu\text{m}$ diam, parallel, cylindrical, smooth, hyaline, inamyloid, 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.

Material examined: Madagascar. Commune Ranomafana, District Ifanadiana, Region Vatovavy-Fitovinany, Ranomafana National Park, Circuit Vohiparara, elevation 1062 m, GPS: $-21\ 14.255\ \text{S}, 47\ 23.409\ \text{E}$, 21 Jan. 2014, J.E. Shay 141 (SFSU) & J.E. Shay 145 (SFSU); Piste B, elevation 1004 m, GPS: $-21\ 15.413\ \text{S}, 47\ 25.253\ \text{E}$, 22 Jan. 2014, J.E. Shay 150B (SFSU).

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 $7.2\text{--}10.4 \times 3.2\text{--}5 \mu\text{m}$, *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 (KX148999, KX149000, KX149001) align with GenBank sequences of *M. rotalis* and *M. rotula*, in a clade with other members of sect. *Marasmius* subsect. *Marasmius*. (Fig. 1c).

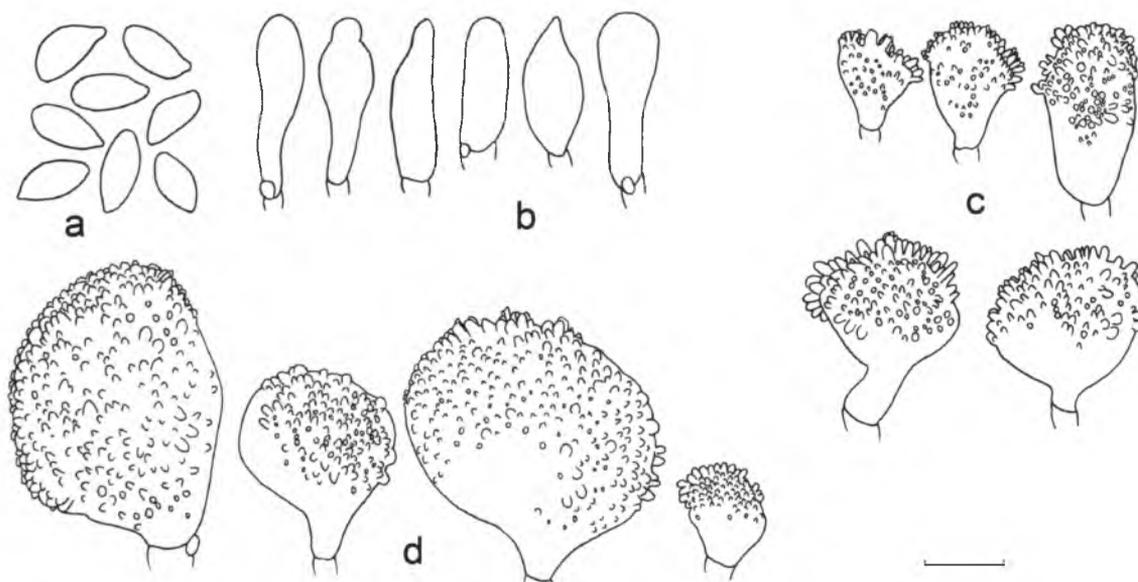


Figure 2: *Marasmius rotalis* (JES 141, JES 145 and JES 150B). a) basidiospores; b) basidioles; c) cheilocystidia; d) pileipellis cells. Scale bar = 10 μm .

2. *Marasmius somalomoensis* Antonín, Mycotaxon 88: 66. 2003.

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

(Figure 3, Plate 1)

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 \times <0.5 mm, central,

narrow, wiry, twisted, insititious; surface glabrous; dark brown (6F8). *Odor and taste* not distinctive.

Basidiospores (6.4–) 7.2–10.4 × 3.2–4.8 μm [$x_{mr} = 7.9\text{--}9.3 \times 3.6\text{--}3.9 \mu\text{m}$; $x_{mm} = 8.53 \pm 0.70 \times 3.79 \pm 0.10$; $Q = 1.5\text{--}2.8$; $Q_{mr} = 2.18\text{--}2.44$; $Q_{mm} = 2.27 \pm 0.10$, $n = 25$, $s = 3$], ellipsoid to narrowly ellipsoid, smooth, hyaline, inamyloid, thin-walled. *Basidia* 16.8–22.4 × 6.4–7.2 μm, cylindrical to subclavate, 4-spored, hyaline, inamyloid, thin-walled; sterigmata 3.2–4.8 × 0.8 μm. *Basidioles* 18.4–24 × 5.6–8 μm, clavate to fusoid, hyaline, inamyloid, 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* monomitric; 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.

Material examined: Madagascar. Commune Ranomafana, District Ifanadiana, Region Vatovavy-Fitovinany, Ranomafana National Park, Talatahely Trail, elevation 973 m, GPS: -21 15.44 S, 47 25.116 E, 20 Jan. 2014, J.E. Shay 129 (SFSU); Ranomafana National Park, Piste B, elevation 1004 m, GPS -21 15.413 S, 47 25.253 E, 22 Jan. 2014, J.E. Shay 165 (SFSU); District Moramanga, Region Alaotra-Mangoro, Commune

Andasibe, Vohimana forest, Piste 5, elevation 844 m, GPS -18 55.422 S, 48 30.201 E, 27 Jan. 2014, J.E. Shay 181 (SFSU).

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 $7.2\text{--}10.4 \times 3.2\text{--}4.8 \mu\text{m}$ with mean $8.5 \times 3.8 \mu\text{m}$, *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-marginate lamellae, 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 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).

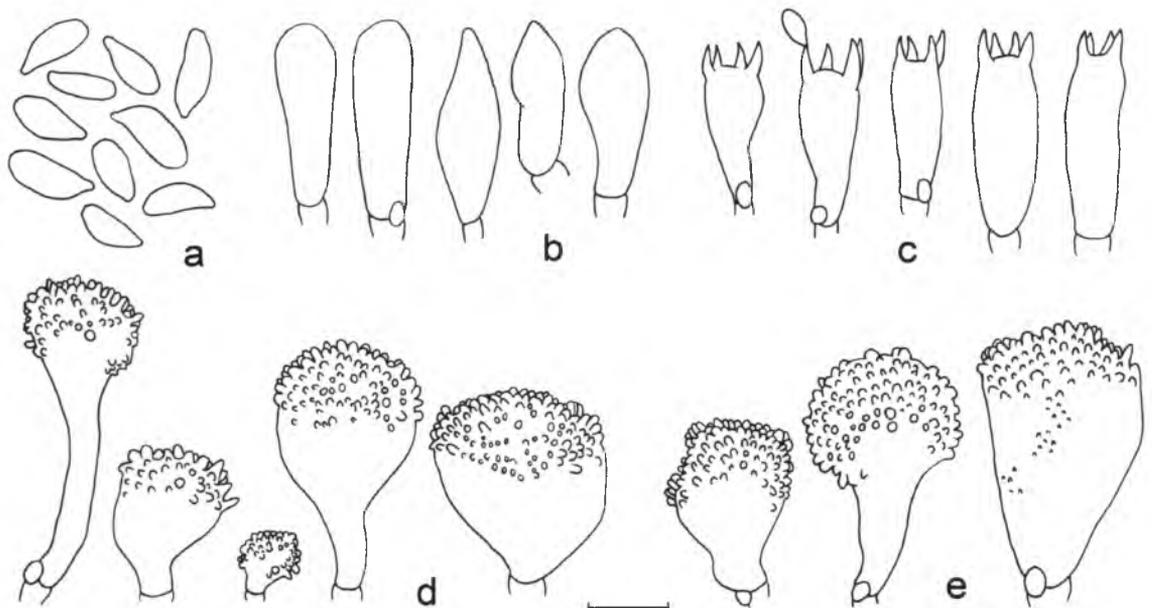


Figure 3: *Marasmius somalomoensis* (JES 129, JES 165 and JES 181). a) basidiospores; b) basidioles; c) basidia; d) cheilocystidia; e) pileipellis cells. Scale bar = 10 μm .

3. *Marasmius apatelius* Singer, Bull. Jard. Bot. État Brux. 34: 332. 1964.

– *Type*: Democratic Republic of Congo, Kisantu, 20 March 1907, *H. Vanderyst* s.n. (BR 11377–28, as *M. friesianus*).

(Figure 4, Plate 1)

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, insititious; surface glabrous, dark brown (6F8). *Odor and taste* not distinctive.

Basidiospores (7.2–) 8–10.4 (–11.2) × 3.2–4.8 (–5) μm [$x_{mr} = 8.9–9.0 \times 4.0–4.1$ μm; $x_{mm} = 8.94 \pm 0.02 \times 4.02 \pm 0.03$; $Q = 1.8–2.8$; $Q_{mr} = 2.23–2.25$; $Q_{mm} = 2.24 \pm 0.02$, $n = 25$, $s = 2$], 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 *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. *Pileus trama* interwoven; hyphae 1.6–12.8 μm diam, cylindrical to inflated, smooth, hyaline, inamyloid, thin-walled. *Lamellar trama* regular; hyphae 1.6–8 μm diam, cylindrical to inflated, smooth, hyaline, inamyloid, thin-walled. *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. *Caulocystidia* absent. *Clamp connections* present.

Habit, habitat and known distribution: growing in gregarious clusters on *Uapaca littoralis* (dicot, Phyllanthaceae). Africa (DR Congo, Tanzania, Uganda), Madagascar, Thailand.

Material examined: Madagascar. Region Atsinanana, District Brickaville, Commune Andevoranto, Andavakimena Forest, elevation -1 m, GPS: -18 53. 231 S, 49 07.490 E, 28 Jan. 2014, J.E. Shay 203 (SFSU); Region Vatovavy-Fitovinany, District Ifanadiana, Commune Randomafana, Ranomafana National Park, Piste B, elevation 1004 m, GPS: -21 15.413 S, 47 25.253 E, 22 Jan. 2014, J.E. Shay 150 (SFSU).

Notes – Marasmius apatelius is characterized by small (2–5 mm diam), greyish orange to buff pileus, distant (9–12), collariate lamellae, dark brown, wiry insititious stipe, basidiospores in the range $8\text{--}10.4 \times 3.2\text{--}5 \mu\text{m}$ with mean $8.9 \times 4.0 \mu\text{m}$, *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 Wannathes et al. (2009). An ITS sequence of the holotype of *M. andasibensis* var. *obscurostipitatus* Antonín & Buyck (KX149005) places the taxon in a clade with *M. apatelius*, and differs primarily in several 21–25 base pair insertions (Fig. 1c). For a comparison with numerous other members of *Marasmius* sect. *Marasmius* subsect. *Marasmius*, refer to Antonín (2007).

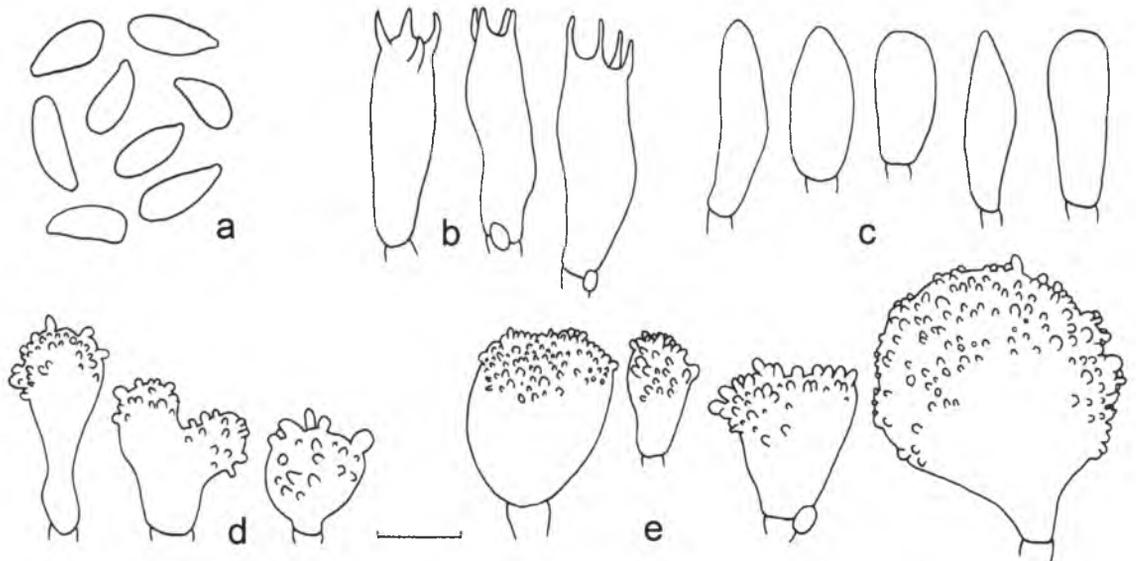


Figure 4: *Marasmius apatelius* (JES 150 and JES 203). a) basidiospores; b) basidia; c) basidioles; d) cheilocystidia; e) pileipellis cells. Scale bar = 10 μ m.

4. *Marasmius andasibensis* var. *andasibensis* Antonín & Buyck, Fungal Diversity 23: 21. 2006.

– *Type*: Madagascar, Andasibe, 23 Feb. 2000, 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 Buyck00.1704 (PC) were unsuccessful.

5. *Marasmius andasibensis* var. *obscurostipitatus* Antonín & Buyck, Fungal Diversity 23: 23. 2006.

– *Type*: Madagascar, Andasibe, 21 Feb. 1997, B. Buyck 00.1699b (PC).

For a description and illustrations of Madagascar material, refer to Antonín and Buyck (2006). The holotype collection Buyck00.1699b (PC) was sequenced (GenBank reference number KX149005) and falls in a clade with *M. apatelius* but with low support.

Ib. Subsect. *Sicciformes* Antonín

Marasmius sect. *Marasmius*, subsect. *Sicciformes* Antonín, Acta Mus. Moraviae, Sci. Nat., 76: 145. 1991.

= subsect. *Penicillati* Singer sensu Singer, Fl. Neotrop. Monogr. 17: 121. 1976.

– *Type species*: *Marasmius curreyi* Berk. & Broome

6. *Marasmius nigrogriseus* Antonín & Buyck, Fungal Diversity 23: 29. 2006.

– *Type*: Madagascar, Andasibe, 22 Feb. 1997, B. Buyck 97.011 (PC).

For a description and illustrations of Madagascar material, refer to Antonín and Buyck (2006). Repeated attempts to sequence material from collection Buyck97.011 (PC) were unsuccessful.

7. *Marasmius nigrobrunneus* (Pat.) Sacc., Syll. Fung. (Abellini) 11: 37. 1895.

– *Type*: Vietnam, Hanoi, Keso, 31 May 1890, Bon 4397 (FH).

For a description and illustrations of Madagascar material, refer to Antonín and Buyck (2006). Repeated attempts to sequence material from collection Buyck97.156 (PC) were unsuccessful.

8. *Marasmius conicopapillatus* Henn., Bot. Jb. 22: 100. 1895.

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

(Figure 5, Plate 2)

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.

Basidiospores (7.2–) 8–9.6 × (3.8–) 4–4.4 μm [$x_m = 8.50 \pm 8.4 \times 4.02 \pm 0.12$ μm; Q = 1.36–2.40; $Q_m = 2.11 \pm 0.18$, n = 25, s = 1], ellipsoid, smooth, hyaline, inamyloid, thin-walled. *Basidia* 19.2–28 × 4.8–6.4 μm, clavate, 4-spored, hyaline, inamyloid, thin-walled; sterigmata 3.2–4.8 × 1.6 μm. *Basidioles* 12–29.6 × 3.3–5.6 μm, clavate, hyaline, inamyloid, 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, inamyloid, thin-walled; apical setulae 0.8–2.4 × 0.8 μm, cylindrical, hyaline, inamyloid, 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, inamyloid, thick-walled; apical setulae 0.8–3.2 × 0.8 μm, cylindrical, hyaline, inamyloid, thick-walled. *Pileus trama* interwoven; hyphae 3.2–14.4 μm diam, cylindrical to inflated, smooth, hyaline, inamyloid, thin-walled. *Lamellar trama* regular; hyphae 2.4–6.4 μm diam, cylindrical, hyaline, inamyloid, 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, inamyloid, 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.

Material examined: Madagascar, Region Alaotra-Mangora, District Moramanga, Commune Andasibe, Vohimana Forest, Piste 5, elevation 820–860 m, GPS: -18 55.422 S, 48 30.201 E, 26 Jan. 2014, J.E. Shay 180 (SFSU).

Notes – Maramius 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.

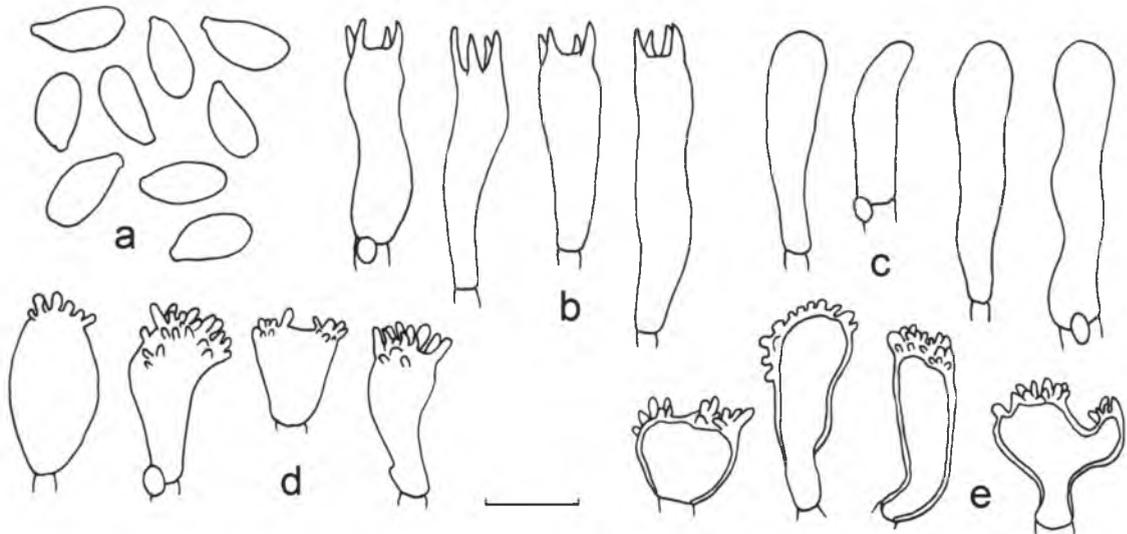


Figure 5: *Marasmius conicopapillatus* (JES 180). a) basidiospores; b) basidia; c) basidioles; d) cheilocystidia; e) pileipellis cells. Scale bar = 10 μ m.

9. *Marasmius curreyi* Berk. & Broome, Ann. Mag. Nat. Hist., Ser. 5, 3: 209. 1879.

– *Type*: United Kingdom, Fineshade, 1859, M.J. Berkeley (K).

For a description and illustrations of Madagascar material, refer to Antonín and Buyck (2006). An ITS sequence from Madagascar collection Buyck 97.374 (PC) (GenBank reference number KX148980) formed a weakly supported trichotomy with a Malaysian sequence of *M. curreyi* and *M. graminum*.

10. *Marasmius* aff. *curreyi*

(Figure 6, Plate 2)

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.

Basidiospores (7.2–) 8–9.6 × 4–4.8 μm [$x_m = 9.02 \pm 0.71 \times 4.29 \pm 0.37$ μm; $Q = 1.80$ –2.40; $Q_m = 2.11 \pm 0.20$, $n = 25$, $s = 1$], 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. *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 × 0.8–1.6 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, hyaline, 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.

Material examined: Madagascar. Region Vatovavy-Fitovinany, District Ifanadiana, Commune Ranomafana, Ranomafana National Park, Circuit Vohiparara, elevation 1062 m, GPS: -21 14.255 S, 47 23.409 E, 21 Jan. 2014, J.E. Shay 135 (SFSU).

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 and Buyck (2006) was only 96.3% similar to JES 135 (KX149008), and both were distant from GenBank sequences determined as *M. curreyi* based on

specimens from Korea (FJ936152) and Malaysia (FJ431237) (Fig. 1c). Although the morphology of 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 matching *M. curreyi* are available for comparison. Accordingly, we recognize our material as *M. aff. curreyi*.

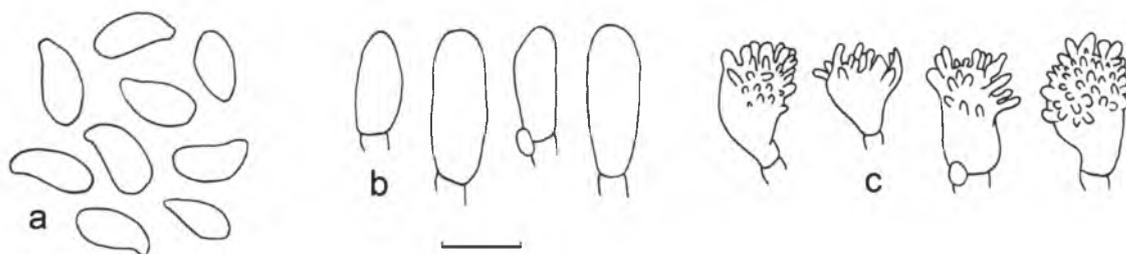


Figure 6: *Marasmius aff. curreyi* (JES 135). a) basidiospores; b) basidioles; c) pileipellis cells. Scale bar = 10 μ m.

11. *Marasmius curreyi* var. *bicystidiatus* Antonín & Hauskn., Fungal Diversity 23: 26. 2006.

– *Type*: Mauritius, Rivière du Rempart, Grand Baie, Bougain Villas, 4 Mar. 1993, leg. Hausknecht MA04a (WU 14896).

For a description and illustrations of Madagascar material, refer to Antonín and Buyck (2006). Material from collection A. Hausknecht MA04a (WU 14896) was unavailable for sequencing.

12. *Marasmius rubrobrunneus* J.E. Shay & Desjardin, *sp. nov.*

Holotype: Madagascar, District Moramanga, Region Alaotra-Mangoro, Commune Andasibe, Vohimana Forest, Piste 5, elevation 844 m, GPS: -18 55.422 S, 48 30.201 E, 27 Jan. 2014, J.E. Shay 191 (SFSU).

(Figure 7, Plate 2)

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.

Basidiospores (12–) 13.6–19.2 × 2.4–4 μm [$x_{mr} = 14.9–16.5 \times 3.2 \mu\text{m}$; $x_{mm} = 15.71 \pm 1.13 \times 3.2 \pm 0.06$; $Q = 2.8–6.7$; $Q_{mr} = 4.6–5.18$; $Q_{mm} = 4.89 \pm 0.41$, $n = 25$, $s = 2$], 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. *Lamellar trama* regular; hyphae 2.4–16 μm diam, cylindrical, 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.

Material examined: Madagascar. District Moramanga, Region Alaotra-Mangoro, Commune Andasibe, Vohimana Forest, Piste 5, elevation 844 m, GPS: -18 55.422 S, 48 30.201 E, 27 Jan. 2014, J.E. Shay 191 (SFSU) & J.E. Shay 183 (SFSU).

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 $15.7 \times 3.2 \mu\text{m}$ ($Q_m = 4.9$), *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. 2009) from material collected in Southeast Asia, and is distinguished by a dark purplish brown pileus and basidiospores in the range $12\text{--}17$ ($\text{--}19$) $\times 2.5\text{--}5 \mu\text{m}$, with means in the range $14.0\text{--}14.8 \times 3.2\text{--}4.1 \mu\text{m}$ ($Q_{mr} = 3.6\text{--}4.5$). In comparison, *Marasmius rubrobrunneus* has a dark reddish brown pileus, lacking purple tones, and basidiospores with means in the range $14.9\text{--}16.5 \times 3.2 \mu\text{m}$, 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 from Thailand (EU935556, EU935557) show only 85% similarity. In the ITS phylogenetic analysis (Fig. 1c), *M. rubrobrunneus* is sister to *M. purpureobrunneolus* with 81% BS support.

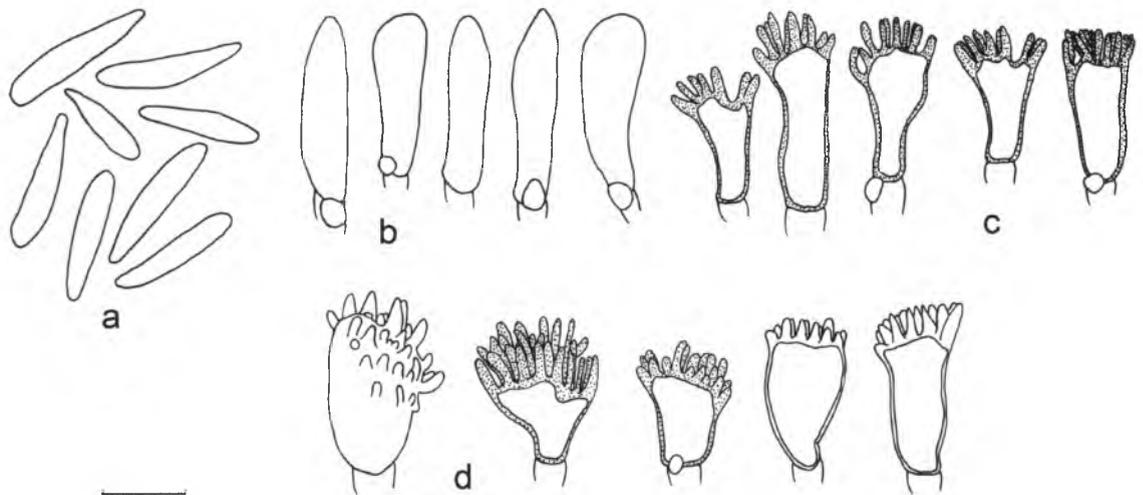


Figure 7: *Marasmius rubrobrunneus* (JES 183 and JES 191). a) basidiospores; b) basidioles; c) cheilocystidia; d) pileipellis cells. Scale bar = 10 μm .

13. *Marasmius brunneoaurantiacus* Antonín & Buyck, Fungal Diversity 23: 24. 2006.

– *Type*: Madagascar, Ranomafana National Park, 4 Feb. 1999, leg. B. Buyck & G. Eyssartier, Buyck 99.450 (PC).

(Figure 8, Plate 3)

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 (0.5–1 mm), 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.

Basidiospores (6.2–) 8–10.4 (–11.2) × (3.2–) 4–4.8 (–5.6) μm [$x_{mr} = 8.8–9.5 \times 4.1–4.6$ μm; $x_{mm} = 9.03 \pm 0.3 \times 4.28 \pm 0.2$; $Q = 1.3–3.0$; $Q_{mr} = 2.0–2.3$; $Q_{mm} = 2.14 \pm 0.1$, $n = 25$, $s = 6$], 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.

Material examined: Madagascar. Commune Ranomafana, District Ifanadiana, Region Vatovavy-Fitovinany, Ranomafana National Park, Talatakely Trail, elevation 937-973 m, GPS: -21 15.237 S, 47 25.183 E, 20 Jan. 2014, J.E. Shay 113 (SFSU), J.E. Shay 115 (SFSU), J.E. Shay 125 (SFSU) & J.E. Shay 131 (SFSU); Ranomafana National Park, Circuit Vohiparara, elevation 1062 m, GPS: -21 14.255 S, 47 23.409 E, 21 Jan. 2014, J.E. Shay 133 (SFSU) & J. E. Shay 137 (SFSU); Ranomafana National Park, Piste B, elevation 1004 m, GPS: -21 15.413 S, 47 25.253 E, 22 Jan. 2014, J.E. Shay 166 (TAN); Region Analamanga, City of Antananarivo, Parc Botanique de Zoologique (P.B.Z.T.), near the garden of Crops Wild and Relatives (CWR), elevation 1270 m, GPS: -18 55.53 S, 47 31.35 E, J.E. Shay 218 (SFSU).

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 8–10.4 (–11) \times 4–4.8 μm , *Siccus*-type broom cells, and growth mainly on bamboo leaves, occasionally on dicot leaves.

Antonín and Buyck (2006) described the species as having brown-marginate lamellae, basidiospores in the range 9.5–11 \times 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 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 (KX148980, KX149010–KX149014, KX149016), forming a clade with 100% BS support (Fig. 1c).

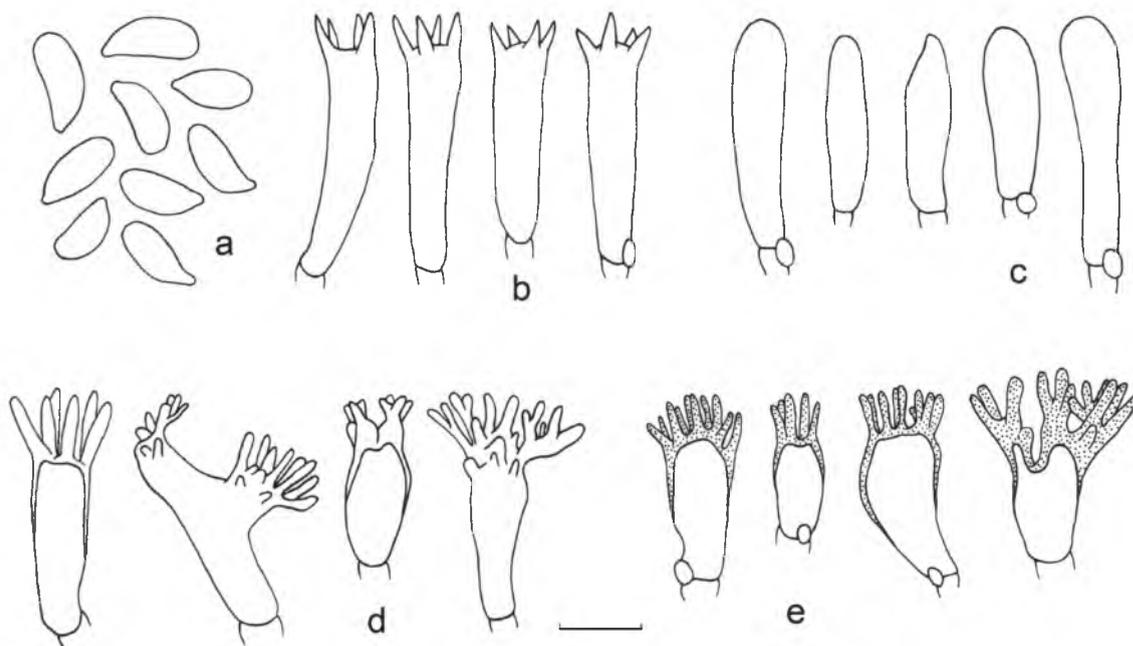


Figure 8: *Marasmius brunneoaurantiacus* (JES 113, JES 137, JES 166 and JES 218). a) basidiospores; b) basidia; c) basidioles; d) cheilocystidia; e) pileipellis cells. Scale bar = 10 μ m.

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

= *Marasmius equicrinis* F. Muell. ex Berk., *J. Linn. Soc. Bot.* 18: 383. 1881.

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

= *Marasmius graminum* var. *equicrinis* (F. Muell. ex Berk.) Dennis, *Trans. Brit. Mycol. Soc.* 34: 416. 1951.

= *Marasmius repens* Henn., *Bot. Jb.* 23: 548. 1897 (nom. illeg., non *Marasmius repens* (Bull.) Quél. 1886).

= *Marasmius ramentaceus* (Pat.) Sacc. & Traverso, Syll. Fung. (Abellini) 20: 21. 1911.

= *Androsaceus ramentaceus* Pat., Ann. Jard. Bot. Buitenzorg, Suppl. 1: 107. 1897.

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

(Figure 9, Plate 3)

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 (5B5–6). *Context* thin, buff. *Lamellae* adnate to a collarium, distant (6), no lamellulae, broad, buff (5A3), non-marginate. *Stipe* 2–4 × <0.5 mm, central, wiry, pliant, 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 [$x_m = 10.14 \pm 1.24 \times 4.54 \pm 0.50$ μm; $Q = 1.57\text{--}3.40$; $Q_m = 2.27 \pm 0.18$, $n = 25$, $s = 1$], ellipsoid, smooth, hyaline, inamyloid, thin-walled. *Basidia* 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 broom 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 broom 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.

Habit, habitat and known distribution: solitary on 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.

Material examined: Madagascar. Region Alaotra-Mangora, District Moramanga, Commune Andasibe, Vohimana Forest, Piste 2, elevation 820–860 m, GPS: -18 55.422 S, 48 30.201 E, 26 Jan. 2014, J.E. Shay 176 (SFSU).

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 $10.1 \times 4.5 \mu\text{m}$, 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 at obtaining ITS sequences from the Madagascar material were unsuccessful.

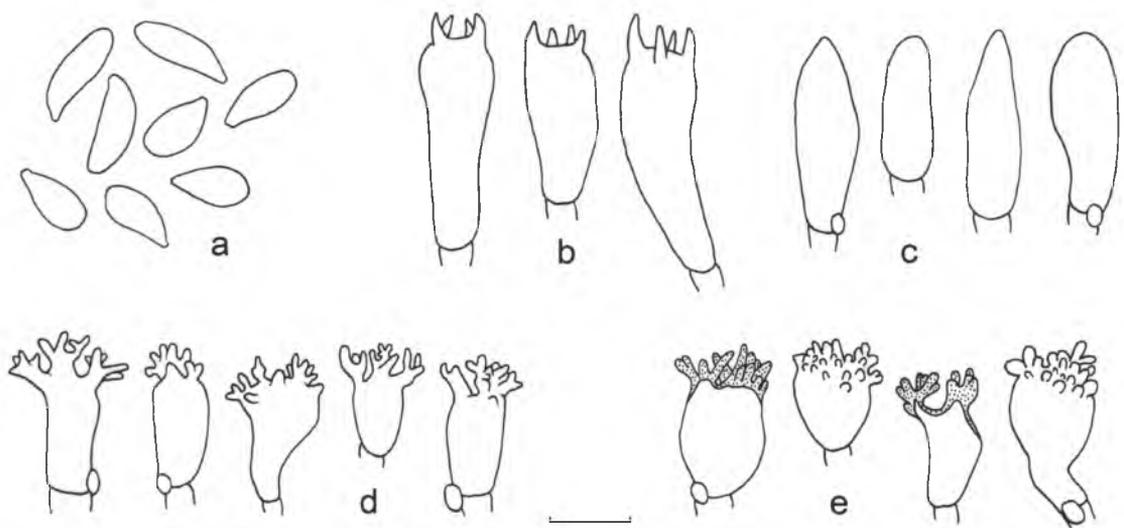


Figure 9: *Marasmius crinisequi* (JES 176). a) basidiospores; b) basidia; c) basidioles; d) cheilocystidia; e) pileipellis cells. Scale bar = 10 μm .

15. *Marasmius cf. subruforotula* Singer, Bull. Jard. Bot. État Brux. 34: 339. 1964.

– *Type*: Democratic Republic of Congo, Equateur Province, Eala, July 1907, L. Pynaert 1608 (BR 11515–69).

(Figure 10, Plate 3)

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 [$x_{mr} = 8–8.4 \times 3.8–3.9 \mu\text{m}$; $x_{mm} = 8.23 \pm 0.2 \times 3.87 \pm 0.1 \mu\text{m}$; $Q = 1.8–2.6$; $Q_{mr} = 2.06–2.19$; $Q_{mm} = 2.14 \pm 0.1$, $n = 24–25$, $s = 3$], 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.

Material examined: Madagascar. District Moramanga, Region Alaotra-Mangoro, Commune Andasibe, Vohimana forest, Piste 5, elevation 844 m, GPS: -18 55.422 S, 48 3.0201E, 27 Jan. 2014, J.E. Shay 186 (SFSU), J.E. Shay 190 (SFSU) & J.E. Shay 192 (SFSU).

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 $7.2\text{--}10.4 \times 3.2\text{--}4 \mu\text{m}$, *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 and Buyck (2006) as *M. cf. subruforotula*. Pegler (1977) and Antonin (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 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*.

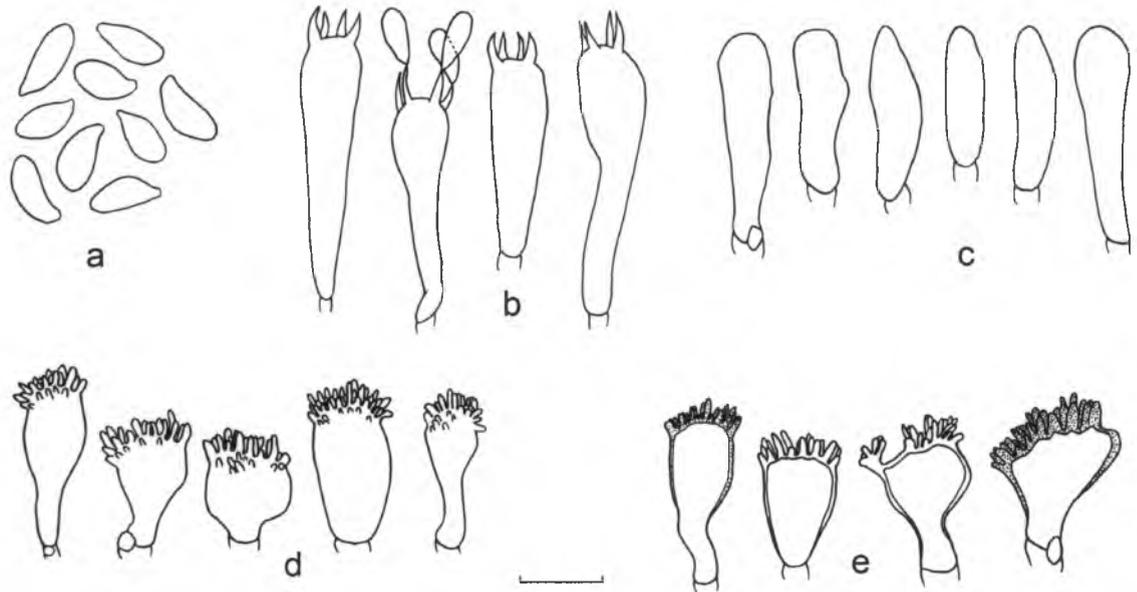


Figure 10: *Marasmius cf. subruforotula* (JES 186, JES 190 and JES 192). a) basidiospores; b) basidia; c) basidioles; d) cheilocystidia; e) pileipellis cells. Scale bar = 10 μ m.

16. *Marasmius madagascariensis* J.E. Shay & Desjardin, *sp. nov.*

Holotype: Madagascar, Region Vatovavy-Fitovinany, District Ifanadiana, Commune Ranomafana, Ranomafana National Park, Circuit Vohiparara, elevation 1062 m, GPS: -21 14.255 S, 47 23.409 E, 21 Jan. 2014, J.E. Shay 139 (SFSU).

(Figure 11, Plate 4)

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 \times 0.1–1 mm, central, hollow, wiry, insititious; surface glabrous; black; rhizomorphs present. *Odor and taste* not distinctive.

Basidiospores 8.8–12.8 × 4–5.6 (–7.2) μm [$x_{mr} = 11.3–11.6 \times 4.8–5.0 \mu\text{m}$; $x_{mm} = 11.46 \pm 0.17 \times 4.90 \pm 0.09 \mu\text{m}$; $Q = 1.8–3.2$; $Q_{mr} = 2.36–2.38$; $Q_{mm} = 2.37 \pm 0.02$, $n = 21–22$, $s = 2$], 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.

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

Material examined: Madagascar. Region Vatovavy-Fitovinany, District Ifanadiana, Commune Ranomafana, Ranomafana National Park, Circuit Vohiparara, elevation 1062 m, GPS: -21 14.255 S, 47 23.409 E, 21 Jan. 2014, J.E. Shay 139 (SFSU); Region Analamanga, District Ankazobe, Commune Ambatoharanama, Ambohitantely Forest Reserve Sentier Botanique, 1574 m, GPS: -18 11.504 S, 47 17.074 E, 8 Feb. 2014, J.E. Shay 225 (SFSU).

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 $11.5 \times 4.9 \mu\text{m}$, *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 Guyana (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 $3.8 \mu\text{m}$. In comparison, the Madagascar specimens differ in growing on grass leaves and tree fern stems and have basidiospores with mean width $4.9 \mu\text{m}$. 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. 2009). In addition, the Madagascar specimens are morphologically similar to *M. aff. guyanensis* reported from the island of Príncipe (DED 8285, Grace et al., unpubl.), but the latter has longer and narrower basidiospores ($12.5\text{--}15 \times 3.5\text{--}4.5 \mu\text{m}$), 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.

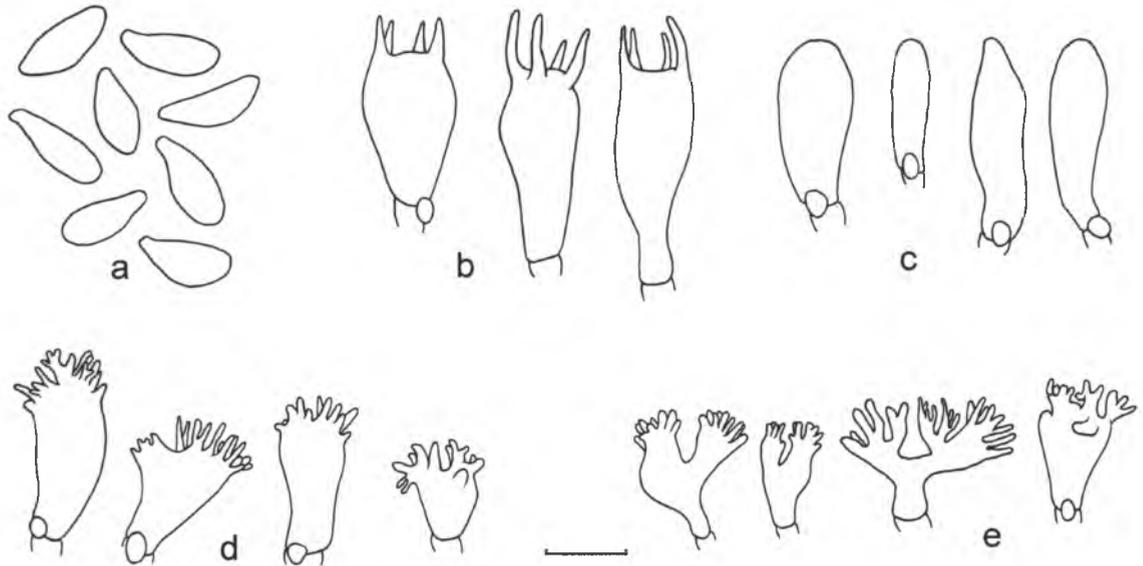


Figure 11: *Marasmius madagascariensis* (JES 139 and JES 225). a) basidiospores; b) basidia; c) basidioles; d) cheilocystidia; e) pileipellis cells. Scale bar = 10 μ m.

II. Sect. *Neosessiles* Singer

Marasmius sect. *Neosessiles* Singer, Mycologia 50: 104 (1958).

– Type species: *Marasmius neosessilis* Singer

17. *Marasmius neosessiliformis* Antonín & Buyck *nom. prov.*, Fungal Diversity 23: 34. 2006.

For a description and illustrations of Madagascar material of this provisionally described species, refer to Antonín and Buyck (2006). An ITS sequence of collection Buyck97.615 (GenBank reference number KX149007) formed an unresolved clade with sequences of *M. tenuissimus* and *M. leveillanus*.

18. *Marasmius cecropiformis* Antonín & Hauskn., Fungal Diversity 23: 33. 2006.

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

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

III. Sect. *Globulares* Kühner

Marasmius sect. *Globulares* Kühner, Botaniste 25: 100. 1933 (ut *Globularinae*).

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

IIIa. ser. *Globulares* Kühner

Marasmius sect. *Globulares* Kühner, Botaniste 25: 100. 1933 (ut *Globularinae*).

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

19. *Marasmius sulcatipes* Pat., Bull. Mus. Nat. Hist. Natur. 13: 526. 1924.

– *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 descriptions and illustrations of Madagascar material, refer to Antonín and Buyck (2006). Material from collection M. Decary (PC) was unavailable for sequencing. It should be noted that *M. sulcatipes* Pat. 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.

– *Type*: Democratic Republic of Congo, Equateur Province, Eala, Oct. 1923, M. Goossens–Fontana 204 (BR 11406–57).

(Figure 12, Plate 4)

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 [$x_m = 26.05 \pm 2.19 \times 5.17 \pm 0.98$ μm; $Q = 3.5–7.5$; $Q_m = 5.24 \pm 1.41$, $n = 25$, $s = 1$], 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* monomitotic; 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.

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, Feb. 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 (120 × 10 mm), cream, longitudinally ridged

stipe, basidiospores in the range $24\text{--}29.6 \times 4\text{--}6.4 \mu\text{m}$, no pleurocystidia, clavate cheilocystidia, *Globulares*-type pileipellis cells, no caulocystidia, and growth in leafy debris. African *M. bekolacongoli* are reported to have basidiospores $17.5\text{--}26 \times 3.8\text{--}5.4 \mu\text{m}$ (Antonín 2007), otherwise the morphology is indistinguishable. Because of 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 ($40\text{--}70 \times 4\text{--}6 \text{mm}$) that 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).

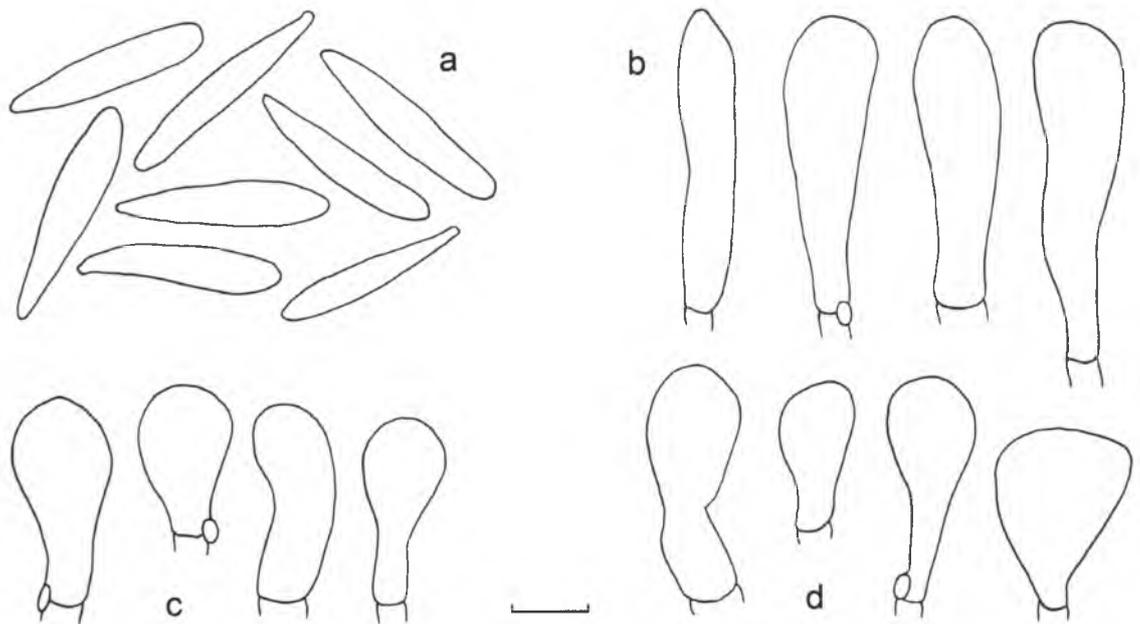


Figure 12: *Marasmius bekolacongoli* (Lockwood 2131638) a) basidiospores; b) basidioles; c) cheilocystidia; d) pileipellis cells. Scale bar = $10 \mu\text{m}$.

IIIb. ser. *Spinulosi*

Subsect. *Siccini* Singer, ser. *Spinulosi* (Clémençon) Desjardin in Antonín & Noordeloos, *Liberi. Bot.* 8: 179. 1993.

= Subsect. *Spinulosi* Clémençon, *Z. Mykol.* 48: 15. 1982.

= Ser. *Actinopodes* Singer *pro parte*, *Fl. Neotrop. Monogr.* 17: 236. 1976.

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

21. *Marasmius dendrosetae* J.E. Shay & Desjardin, *sp. nov.*

Holotype: Madagascar, Region Atsinanana, District Brickaville, Commune Andevoranto, Andavakimena Forest, elevation -1–8 m, GPS: -18 53.231 S, 49 07.490 E, 28 Jan. 2014, J.E. Shay 205 (SFSU).

(Figure 13, Plate 5)

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-insititious; 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 [$x_{mr} = 8.2–9.1 \times 3.9 \mu\text{m}$; $x_{mm} = 8.66 \pm 0.68 \times 3.88 \pm 0.02 \mu\text{m}$; $Q = 1.6–2.8$; $Q_{mr} = 2.12–2.36$; $Q_{mm} = 2.24 \pm 0.17$, $n = 7–25$; $s = 2$], ellipsoid, smooth, hyaline, inamyloid, thin-walled. *Basidia* 20–24 × 6.4–8 μm, clavate, 4-spored, hyaline, inamyloid, thin-walled. *Basidioles* 16–21.6 × 5.6–7.2 μm, clavate to fusoid, hyaline, inamyloid, thin-walled. *Cheilocystidia* 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, inamyloid, thin-walled; apical setulae dense, 0.8–1.6 × 0.8–1.6 μm, cylindrical or irregular, sometimes branched, hyaline, inamyloid, thin-walled. *Pleurocystidia* absent. *Pileipellis* mottled, a hymeniform layer of three types of cells: 1)

thin-walled *Siccus*-type broom cells with main body $6\text{--}20 \times 5.6\text{--}8.8 \mu\text{m}$, clavate or irregular, seldom 2–3-lobed, hyaline, inamyloid; apical setulae $0.8\text{--}8 \times 0.8\text{--}1.6 \mu\text{m}$, cylindrical to conical or irregular, hyaline, inamyloid, thin-walled, branched; 2) thick-walled *Siccus*-type broom cells with main body $16.8\text{--}21.6 \times 5.6\text{--}8 \mu\text{m}$, clavate, lobed, hyaline, inamyloid; apical setulae $0.8\text{--}8 \times 0.8\text{--}3.2 \mu\text{m}$, cylindrical to conical, hyaline, inamyloid, thick-walled; 3) pileosetae $40\text{--}300 \times 1.6\text{--}8 \mu\text{m}$, cylindrical to antler-like, often highly branched, clustered, hyaline, inamyloid, thick-walled. *Pileus trama* interwoven; hyphae $2.4\text{--}7.2 \mu\text{m}$ diam, smooth, hyaline, dextrinoid, thin-walled. *Lamellar trama* regular; hyphae $2.4\text{--}7.2 \mu\text{m}$ diam, cylindrical, smooth, hyaline, inamyloid, thin-walled. *Stipe tissue* monomitic; cortical hyphae $2.4\text{--}7.2 \mu\text{m}$ diam, parallel, cylindrical, smooth, light brown to pale yellow, dextrinoid, thick-walled; medullary hyphae $2.4\text{--}8 \mu\text{m}$ diam, parallel, cylindrical, hyaline, dextrinoid, thin-walled. *Caulocystidia* of *Siccus*-type broom cells emerging directly from hyphae; main body $3.2\text{--}4 \times 1.6\text{--}5.6 \mu\text{m}$, clavate or irregular, frequently lobed, hyaline, inamyloid, thin-walled; apical setulae cylindrical or irregular, branched, hyaline, inamyloid, thin-walled. *Clamp connections* present.

Habit, habitat and known distribution: solitary or in gregarious clusters on stems and leaves of *Uapaca littoralis* and *Pandanus*. Madagascar.

Material examined: Madagascar. Region Atsinanana, District Brickaville, Commune Andevoranto, Andavakimena Forest, elevation $-1\text{--}8 \text{ m}$, GPS: $-18 \ 53.231 \text{ S}$, $49 \ 07.490 \text{ E}$, 28 Jan. 2014, J.E. Shay 205 (SFSU); same location, GPS: $-18 \ 53.082 \text{ S}$, $49 \ 07.559 \text{ E}$, 30 Jan. 2014, J.E. Shay 211 (SFSU).

Notes – Marasmius dendrosetae is characterized by a small ($<10 \text{ mm}$), smooth, cream to orangish white pileus, subdistant, non-marginate lamellae, a minutely pruinose stipe, basidiospores in the range $7.2\text{--}10.4 \times 3.2\text{--}4.8 \mu\text{m}$, *Siccus*-type cheilocystidia and caulocystidia, a pileipellis composed of *Siccus*-type broom cells and scattered, hyaline, branched pileosetae up to $300 \mu\text{m}$ 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. dendrosetae* (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; 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).



Figure 13: *Marasmius dendrosetae* (JES 205 and 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 (at bottom center) . Scale bar = 10 μ m.

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

– *Type*: Sri Lanka, Kandy District, Peradeniya, Thwaites 102 cum icone (K!).

(Figure 14, Plate 5)

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 [$x_{mr} = 12.4–12.7 \times 4.3–4.8 \mu\text{m}$; $x_{mm} = 12.56 \pm 0.21 \times 4.56 \pm 0.39 \mu\text{m}$; $Q = 1.9–3.6$; $Q_{mr} = 2.69–2.92$; $Q_{mm} = 2.80 \pm 0.16$, $n = 25$, $s = 2$], 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. *Cauloetae* 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 to gregarious on leaf litter of *Dalbergia* (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, elevation 937–973 m, GPS: -21 15.237 S, 47 25.183 E, 20 Jan. 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 pileosetae, conspicuous cauloetae, and growth on woody debris. Populations of *M. nummularius* in Thailand (Wannathes et al. 2009) 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) (Fig. 1b). The African species *M. castaneovelutinus* Henn. 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).

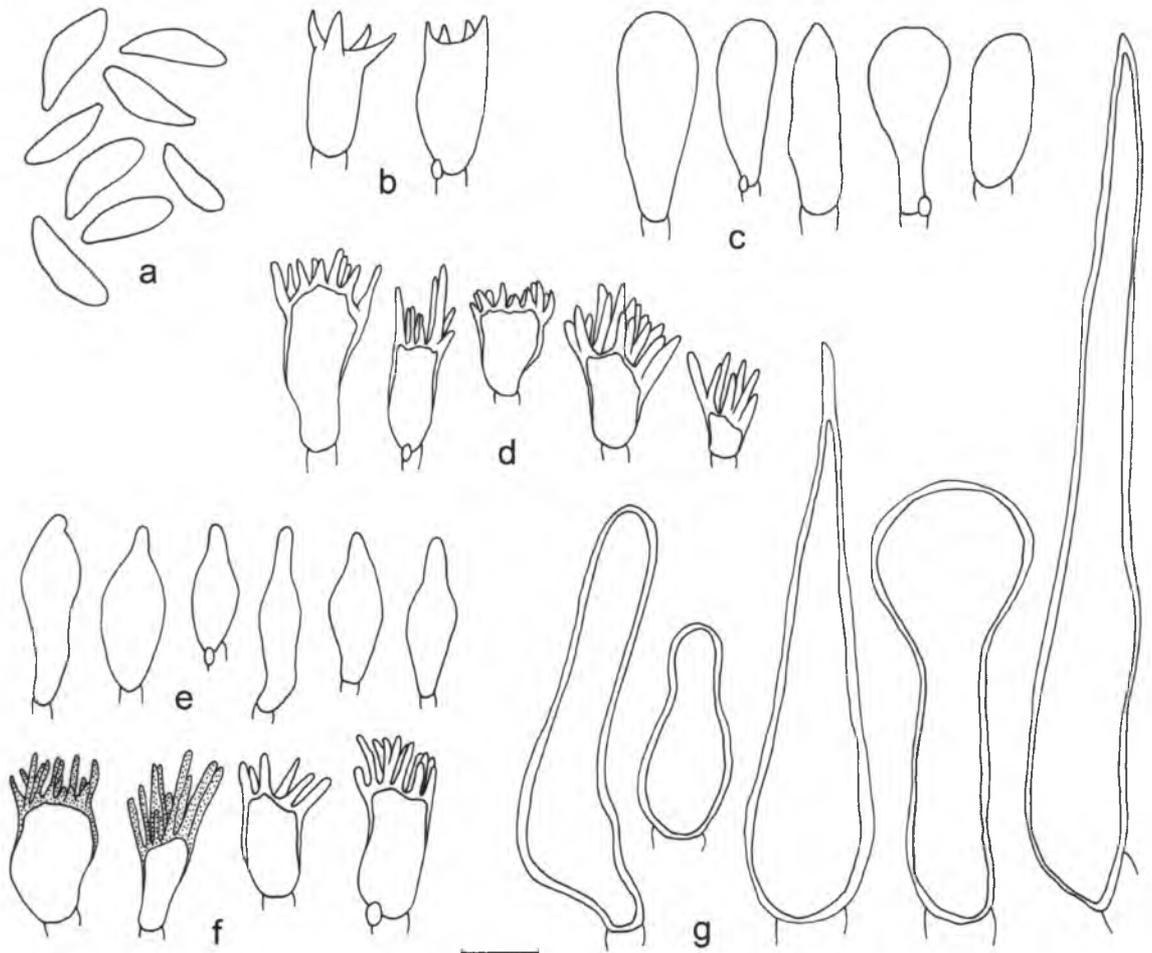


Figure 14: *Marasmius nummularius* (JES 121 and JES 124). a) basidiospores; b) basidia; c) basidioles; d) cheilocystidia; e) pleurocystidia; f) pileipellis cells; g) cauloetae. Scale bar = 10 μ m.

IIIc. ser. *Atrorubentes* Desjardin & E. Horak

Ser. *Atrorubentes* Desjardin & E. Horak, *Bibl. Mycol.* 168: 27. 1997.

= Ser. *Actinopodes* Singer pro parte, *Fl. Neotrop. Monogr.* 17: 236. 1976.

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

23. *Marasmius corrugatiformis* Singer, Bull. Jard. Bot. État Brux. 34: 374. 1964.

– *Type*: Democratic Republic of Congo, near Yambao, 21 June 1939, J. Louis 15275 (BR 11426–77).

(Figure 15, Plate 6)

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) to brown (6D7) towards the base. *Odor and taste* not distinctive.

Basidiospores (6.4–) 8–11.2 × 3.2–4.8 μm [$x_m = 9.08 \pm 1.08 \times 4.04 \pm 0.33$ μm; $Q = 1.67–2.80$; $Q_m = 2.26 \pm 0.14$, $n = 25$, $s = 1$], 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* mottled, 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.

Material examined: Madagascar. Region Vatovavy-Fitovinany, District Ifanadiana, Commune Ranomafana, Ranomafana National Park, Piste B, elevation 1004 m, GPS: -21 15.413 S, 47 25.253 E, 22 Jan. 2014, J.E. Shay 164 (SFSU). Madagascar, unknown location, Jan. 2013, Lockwood 2132268W250 (SFSU).

Notes – Maramius 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* (Buyck97.425, KX148981) formed a clade with several sequences of *M. corrugatiformis* from São Tomé (DED8326, DED8233) but with low support (Fig. 1b).

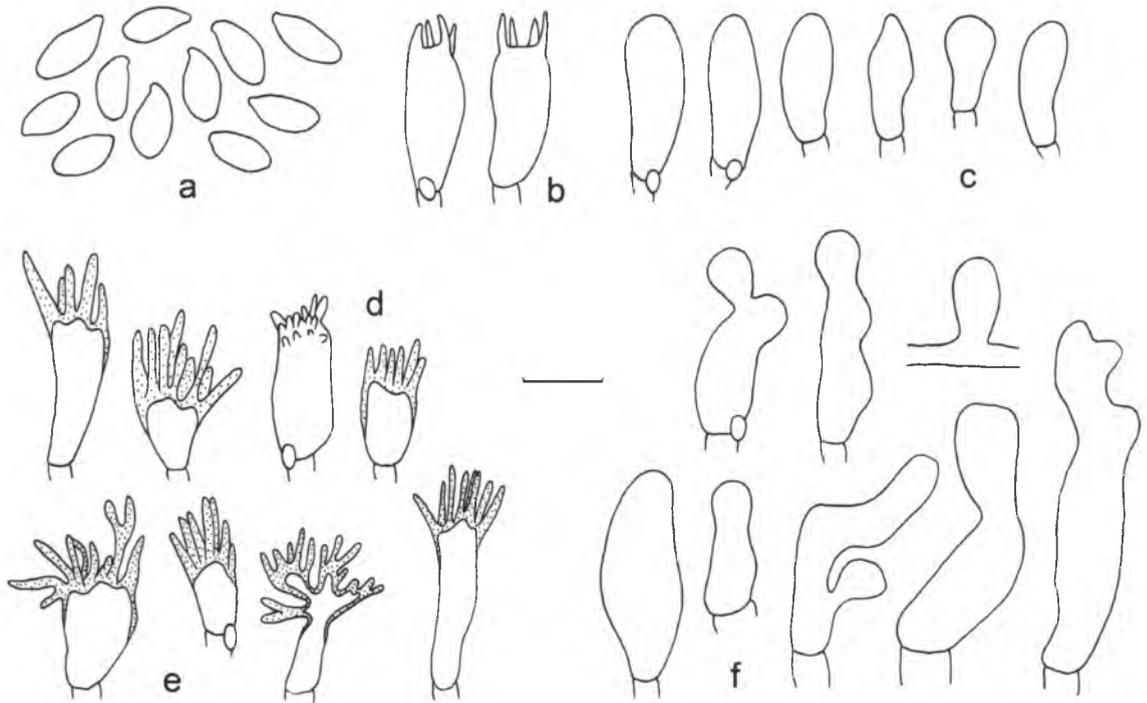


Figure 15: *Marasmius corrugatiformis* (JES 164 and Lockwood 2132268W250). a) basidiospores; b) basidia; c) basidioles; d) cheilocystidia; e) pileipellis cells; f) caulocystidia. Scale bar = 10 μm .

24. *Marasmius katangensis* Singer, Bull. Jard. Bot. État Brux. 34: 375. 1964.

– *Type*: Democratic Republic of Congo, Shaba Province, Kipopo, 10 Jan. 1961, M.C. Schmitz–Levecq 315 (BR 11476–30).

(Figure 16, Plate 6)

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 \times 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 \times 3.2–4.8 μm [$x_m = 7.79 \pm 0.48 \times 3.99 \pm 0.38 \mu\text{m}$; $Q = 1.67\text{--}2.50$; $Q_m = 1.97 \pm 0.21$, $n = 25$, $s = 1$], ellipsoid, smooth, hyaline, inamyloid, thin-

walled. *Basidia* 16–23.2 × 7.2 µm, clavate, 4-spored, hyaline, inamyloid, thin-walled; sterigmata 2.4–4.8 × 0.8–1.6 µm. *Basidioles* 13.6–24.8 × 4–5.6 µm, clavate, hyaline, inamyloid, 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, inamyloid, apically thick-walled; apical setulae 3.2–8.8 × 0.8–1.6 µm, cylindrical to conical, seldom branched, light yellowish brown, inamyloid, 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, elevation 1574 m, GPS: -18 11.504 S, 47 17.074 E, 6 Feb. 2014, J.E. Shay 227 (SFSU).

Notes – *Maramius 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 $7.8 \times 4.0 \mu\text{m}$, 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 and Buyck (2006) as *M. corrugatiformis* (KX148981), 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.

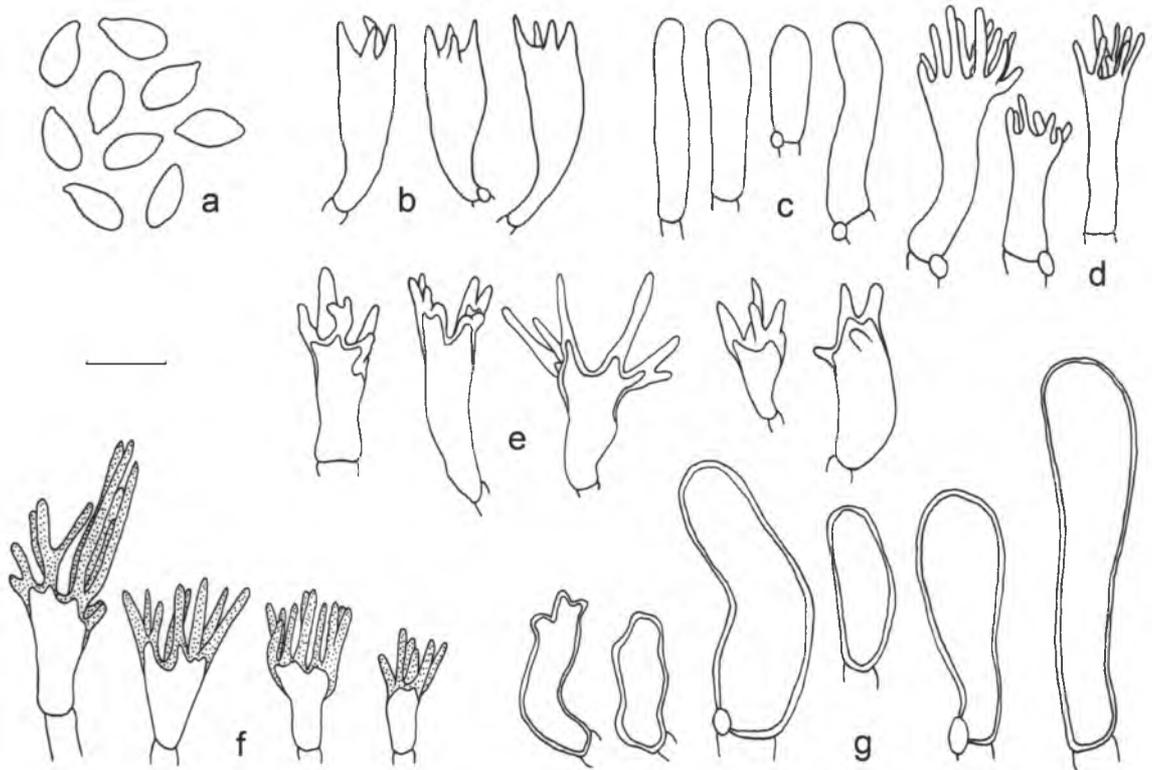


Figure 16: *Marasmius katangensis* (JES 227). a) basidiospores; b) basidia; c) basidioles; d) cheilocystidia; e) pileipellis cells; f) *Siccus*-type caulocystidia; g) non-setulose caulocystidia. Scale bar = 10 μ m.

III d. ser. *Leonini* Singer

Subsect. *Siccini* Singer, ser. *Leonini* Singer, Fl. Neotrop. Monogr. 17: 160. 1976.

– *Type species*: *Marasmius leoninus* Berk.

25. *Marasmius sokola* J.E. Shay & Desjardin, *sp. nov.*

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

(Figure 17)

Pileus 20 mm diam, campanulate; disc rugulose; margin sulcate; surface dull, glabrous; dark brown (5E7). *Context* thin. *Lamellae* 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 [$x_m = 21.93 \pm 2.36 \times 4.40 \pm 0.40$ μm; $Q = 3.50–6.40$; $Q_m = 5.03 \pm 1.20$, $n = 25$, $s = 1$], subcylindrical to subfusoid, smooth, hyaline, inamyloid, thin-walled. *Basidia* 32.8–46.4 × 6.4–8 μm, clavate, 4-spored, hyaline, inamyloid, thin-walled. *Basidioles* 29.6–42.4 × 7.2–8.8 μm, clavate, hyaline, inamyloid, 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, inamyloid, thin-walled; apical setulae 0.8–13.6 × 0.8–1.6 μm, cylindrical to conical, often branched, brown, inamyloid, thick-walled. *Pleurocystidia* absent. *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, inamyloid, thick-walled; apical setulae 0.8–9.6 × 0.8–1.6 μm, cylindrical to conical, seldom branched, hyaline to brown, inamyloid, 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* monomitic; 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, inamyloid, thin-walled. *Caulocystidia* absent. *Clamp connections* present.

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

Material examined: Madagascar. Commune Ranomafana, District Ifanadiana, Region Vatovavy-Fitovinany, Ranomafana National Park, Piste B, elevation 1004 m, GPS: -21 15.413 S, 47 25.253 E, 22 Jan. 2014, J.E. Shay 154 (SFSU).

Etymology. *sokola* – Malagasy for chocolate, referring the dark chocolate brown pigmented basidiomes.

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 $21.9 \times 4.4 \mu\text{m}$ ($Q = 5.0$), 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.

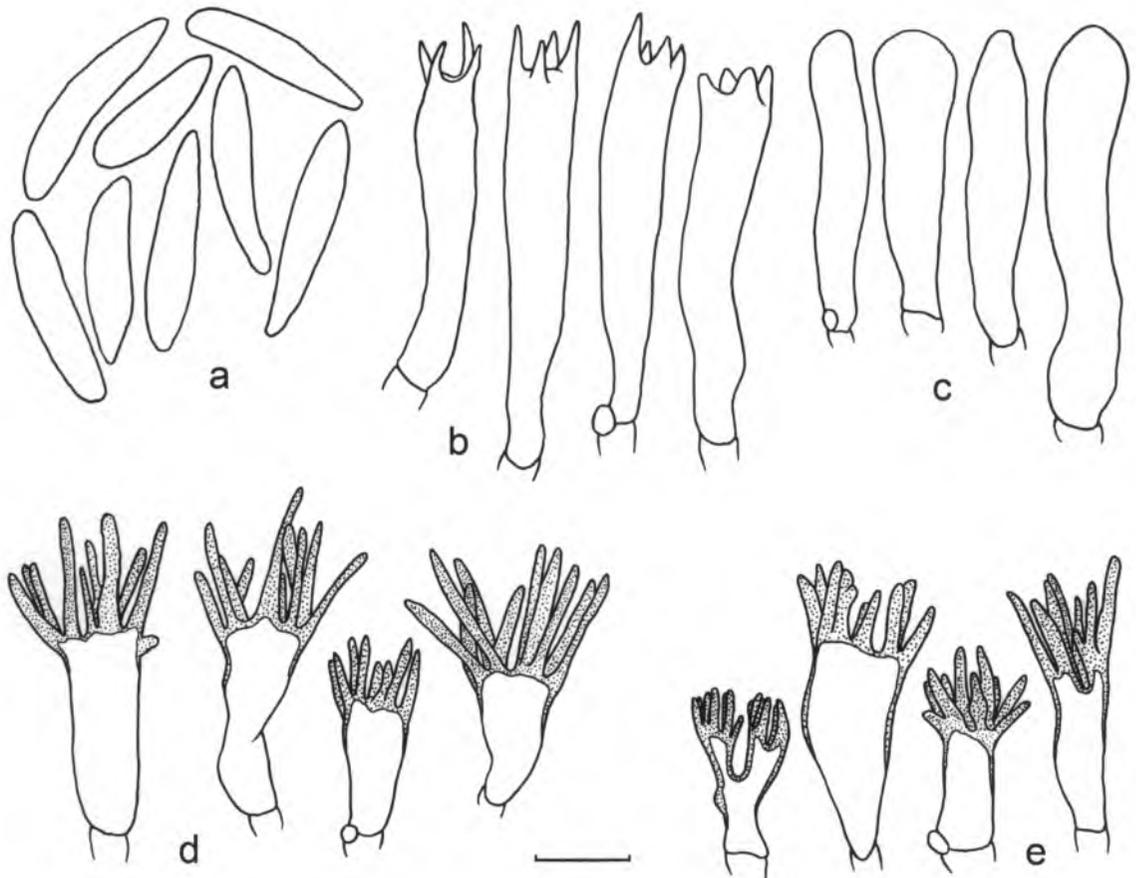


Figure 17: *Marasmius sokola* (JES 154). a) basidiospores; b) basidia; c) basidioles; d) cheilocystidia; e) pileipellis cells. Scale bar = 10 μ m.

26. *Marasmius rammelooi* Antonín, Mycotaxon 89(2): 410. 2004.

– Type: Mauritius, Trou d' eau douce, 10 June 1990, leg. J. Rammeloo 9251 (BR 6902-15).

For descriptions and illustrations of Madagascar material, refer to Antonín (2004a) and Antonín and Buyck (2006). Material not available for sequencing.

27. *Marasmius megistus* Singer, Bull. Jard. Bot. État Brux. 34: 356. 1964.

– *Type*: Democratic Republic of Congo, Binga, 7 May 1928, M. Goossens–Fontana 733 (BR 11492–46).

(Figure 18, Plate 7)

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.

Basidiospores (26.4–) 29.6–32.8 (–40) × 4.8–7.2 μm [$x_{mr} = 30.7–34.2 \times 5.8–6.7$ μm; $x_{mm} = 32.44 \pm 2.49 \times 6.23 \pm 0.66$ μm; $Q = 2.8–6.8$; $Q_{mr} = 5.09–5.33$; $Q_{mm} = 5.21 \pm 0.17$, $n = 2–27$, $s = 2$], narrowly ellipsoid to clavate, smooth, hyaline, inamyloid, thin-walled. *Basidia* not observed. *Basidioles* 18.4–57 × 5.6–10.4 μm, clavate to fusoid, hyaline, inamyloid, 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, inamyloid, thin-walled; apical setulae 0.8–8 × 0.8–1.6 μm, cylindrical to conical, sometimes branched, hyaline, inamyloid, thin-walled. *Pleurocystidia* absent. *Pileipellis* not mottled, a hymeniform layer of *Siccus*-type broom cells; main body 16–32 × 6.4–10.4 μm, clavate or irregular, hyaline, inamyloid, thin-walled; apical setulae 2.4–8 × 0.8–3.2 μm, few per cell, broadly conical to cylindrical or utriform, seldom branched, hyaline, inamyloid, thin-walled. *Pileus trama* interwoven; hyphae 1.6–8 μm diam, cylindrical smooth, hyaline, dextrinoid, thick-walled. *Lamellar trama* regular; hyphae 2–7.2 μm diam, cylindrical to inflated, smooth, hyaline to pale yellow, dextrinoid, thin-walled. *Stipe tissue* monomitic; cortical hyphae 1.6–8 μm diam, parallel, cylindrical, smooth, pale yellow, green brown, dextrinoid, thick-walled; medullary hyphae 1.6–9.6 μm diam, parallel, cylindrical to inflated, smooth, hyaline, dextrinoid, thin-walled. *Caulocystidia* absent. *Clamp connections* present.

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

Material examined: Madagascar. Region Vatovavy-Fitovinany, District Ifanadiana, Commune Ranomafana, Ranomafana National Park, Piste B, elevation 1004 m, GPS: -21 15.413 S, 47 25.253 E, 22 Jan. 2014, J.E. Shay 163 (TAN). Madagascar, unknown location, Feb. 2013, T. Lockwood 2132155 (SFSU).

Notes – *Marasmius megistus* forms some of the largest basidiospores in the genus. The Madagascar 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 $29.6\text{--}40 \times 4.8\text{--}7.2 \mu\text{m}$, 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 Madagascar specimens (KX148992, KX148993) are sister to a specimen from São Tomé with 100% BS support (Fig. 1a).

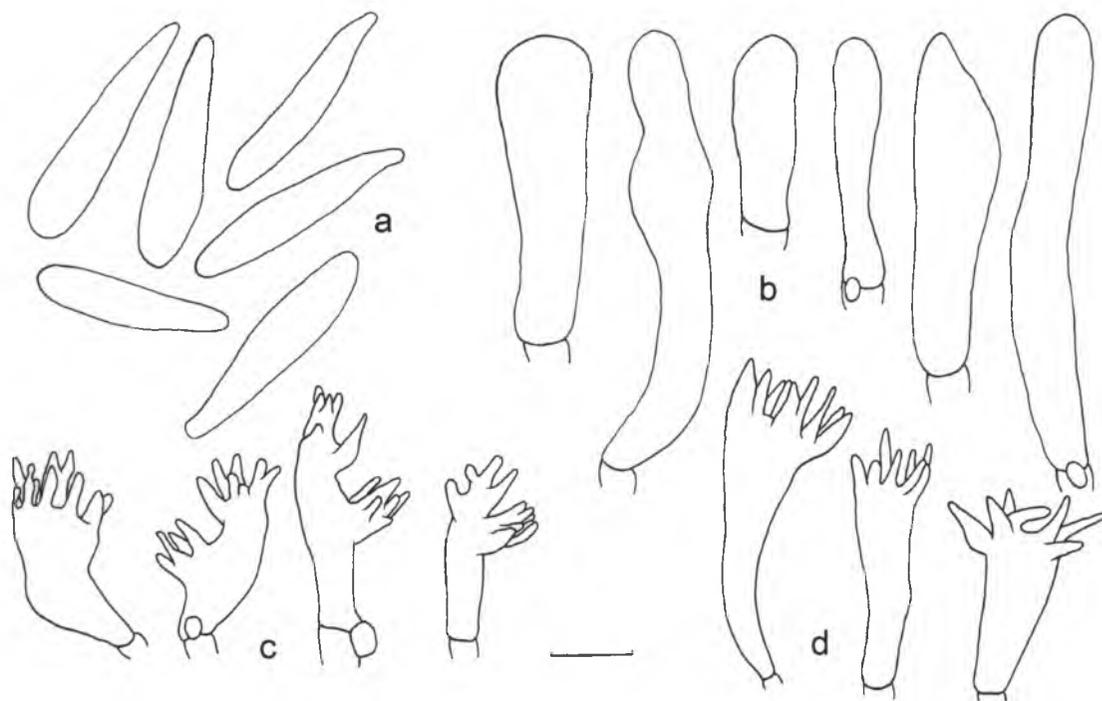


Figure 18: *Marasmius megistus* (JES 163 and Lockwood 2132155). a) basidiospores; b) basidioles; c) cheilocystidia; d) pileipellis cells. Scale bar = 10 μ m.

28. *Marasmius bambusiniformis* Singer, Fl. Neotrop. Monogr. 17: 167. 1976.

– *Type*: Ecuador, Napo, Lago Agrio, 16 May 1973, Singer B7480 (F!)

(Figure 19, Plate 7)

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 \times 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.

Basidiospores (14.4–) 16–18.4 \times 3.2–4 μ m [$x_m = 16.35 \pm 1.44 \times 3.46 \pm 0.36 \mu$ m; $Q = 4–5.75$; $Q_m = 4.76 \pm 0.57$, $n = 25$, $s = 1$], narrowly ellipsoid, smooth, hyaline, inamyloid, thin-walled. *Basidia* not observed. *Basidioles* 19.2–24 \times 5.6–7.2 μ m, clavate

to fusoid, hyaline, inamyloid, thin-walled. *Cheilocystidia* numerous, of *Siccus*-type broom cells; main body $9.6\text{--}14.4 \times 5.6\text{--}10.4 \mu\text{m}$, clavate to broadly clavate, seldom 2–3-lobed, hyaline, inamyloid, apically thick-walled; apical setulae $1.6\text{--}7.2 \times 0.8 \mu\text{m}$, dense, cylindrical to conical, seldom branched, hyaline, inamyloid, thick-walled. *Pleurocystidia* absent. *Pileipellis* mottled, a hymeniform layer of *Siccus*-type broom cells; main body $10.4\text{--}17.6 \times 6.4\text{--}8 \mu\text{m}$, clavate to broadly clavate, seldom 2–3-lobed, hyaline, inamyloid, apically thick-walled; apical setulae $1.6\text{--}4.8 \times 0.8 \mu\text{m}$, dense, cylindrical to conical, pale yellowish brown, inamyloid, thick-walled. *Pileus trama* interwoven; hyphae $1.6\text{--}16.8 \mu\text{m}$ diam, cylindrical, smooth, hyaline, inamyloid, thin-walled. *Lamellar trama* regular; hyphae $1.6\text{--}8 \mu\text{m}$ diam, cylindrical to inflated, smooth, hyaline, dextrinoid, thick-walled. *Stipe tissue* monomitic; cortical hyphae $1.6\text{--}4 \mu\text{m}$ diam, parallel, cylindrical, smooth, dark brown, dextrinoid, thick-walled; medullary hyphae $2.4\text{--}8 \mu\text{m}$ 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).

Material examined: Madagascar. Region Alaotra-Mangoro, District Moramanga, Commune Andasibe, Vohimana Forest, Piste 5, elevation 844 m, GPS: -18 55.422 S, 48 30.201 E, 27 Jan. 2014, J.E. Shay 199 (TAN).

Notes – *Marasmius bambusiniiformis* 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. 2009). 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.

Antonín (2007) provided a description of a provisional taxon, *Marasmius conicoparvus* Antonín & C. Sharp ad int., that 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 Madagascar taxon as *M. bambusiformis*. *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). An ITS sequence of JES199 (KX148990) is sister to Thai specimen of *M. bambusiformis* (EU935521) and within the same clade as *M. berteroi* (FJ917632) (Fig. 1a)

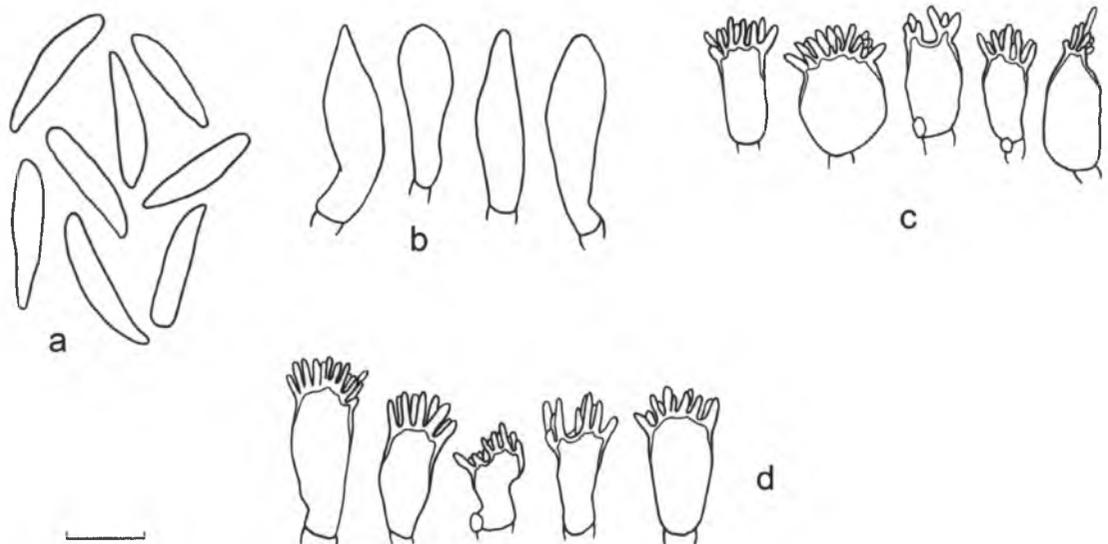


Figure 19: *Marasmius bambusiformis* (JES 199). a) basidiospores; b) basidioles; c) cheilocystidia; d) pileipellis cells. Scale bar = 10 μm .

IIIe. ser. *Haematocephali* Singer

Subsect. *Siccini* Singer, ser. *Haematocephali* Singer, Fl. Neotrop. Monogr. 17: 201. 1976.

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

29. *Marasmius haematocephalus* (Mont.) Fr. Epicr. Syst. Mycol. (Upsaliae): 382. 1838 (1836–1838).

– *Type*: Brazil, not preserved. Neotype: Guanabara, Jardim Botânico, 28 Jan. 1961, *R. Singer* C 3172 (BAFC).

(Figure 20, Plate 8)

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.

Basidiospores (13.6–) 16–22 × 3.2–4.8 μm [$x_{mr} = 17.1–20.9 \times 3.6–4.1 \mu\text{m}$; $x_{mm} = 18.71 \pm 1.7 \times 3.84 \pm 0.3 \mu\text{m}$; $Q = 3.7–7.0$; $Q_{mr} = 4.80–5.08$; $Q_{mm} = 4.93 \pm 0.1$, $n = 9–25$, $s = 4$], narrowly fusiform to elongate-ellipsoid, smooth, hyaline, inamyloid, thin-walled. *Basidia* not observed. *Basidioles* 16–30.4 × 5.6–8.8 μm, clavate, hyaline, 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 $0.5\text{--}8 \times 0.5\text{--}2.4 \mu\text{m}$, conical to cylindrical, obtuse, hyaline to light brown, inamyloid, thick-walled. *Pileus trama* interwoven; hyphae $2.4\text{--}9.6 \mu\text{m}$ diam, cylindrical, smooth, hyaline, dextrinoid, thin-walled. *Lamellar trama* regular; hyphae $2.4\text{--}8.8 \mu\text{m}$ diam, cylindrical to inflated, smooth, hyaline, weakly dextrinoid, thin-walled. *Stipe tissue* monomitic; cortical hyphae $2.4\text{--}9.6 \mu\text{m}$ diam, parallel, cylindrical to inflated, smooth, hyaline to light yellow brown, dextrinoid, thin-walled; medullary hyphae $2.4\text{--}15.2 \mu\text{m}$ 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 *Aframomium 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, elevation 844 m, GPS: -18 55.422 S, 48 30.201 E, 27 Jan. 2014, J.E. Shay 193 (SFSU); Region Vatovavy-Fitovinany, District Ifanadiana, Commune Ranomafana, City of Ranomafana near riverbed next to Forest Service Station, elevation ~900 m, 20 Jan. 2014, J.E. Shay 110 (SFSU), same region Ranomafana National Park, Circuit Vohipara, elevation 1062 m, GPS: -21 14.255 S, 47 23.409 E, 21 Jan. 2014, J.E. Shay 142 (SFSU); Region Atsinanana, District Brickaville, Commune Andevoranto, Andavakimena Forest, elevation -1 m, GPS -18 53.231 S, 49 7.490 E, 28 Jan. 2014, J.E. Shay 202 (SFSU).

Notes – *Marasmius haematocephalus* has been reported from tropical habitats around the world and probably represents a complex of species. Wannathes et al. (2009) 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 $14\text{--}20 \times 3.5\text{--}5 \mu\text{m}$, 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-insititious stipe, basidiospores with mean range $17.1\text{--}20.9 \times 3.6\text{--}4.1 \mu\text{m}$, stangulate pleurocystidia, and growth on dicotyledonous leaves. It matches well with the material reported from Madagascar by Antonín and Buyck (2006), and ITS sequences of KX148977, KX148984, KX148985, KX148986 and KX148987 form a well-supported clade (99% BS; Fig. 1b) with several sequences of *M. haematocephalus* from Thailand (EU935527, EU935532).

Specimen JES 142 (KX148987) shows some differences with the other Madagascar specimens in forming slightly longer basidiospores with mean $20.8 \times 4.1 \mu\text{m}$, faintly reddish purple lamellar edges near the pileus margin, and an ITS sequence that is only 94% similar to other specimens in the well-supported *M. haematocephalus* clade. JES 142 consists of only a single basidiome with reddish purple pileus, and until additional material becomes available, it is accepted as belonging to the *M. haematocephalus* complex.

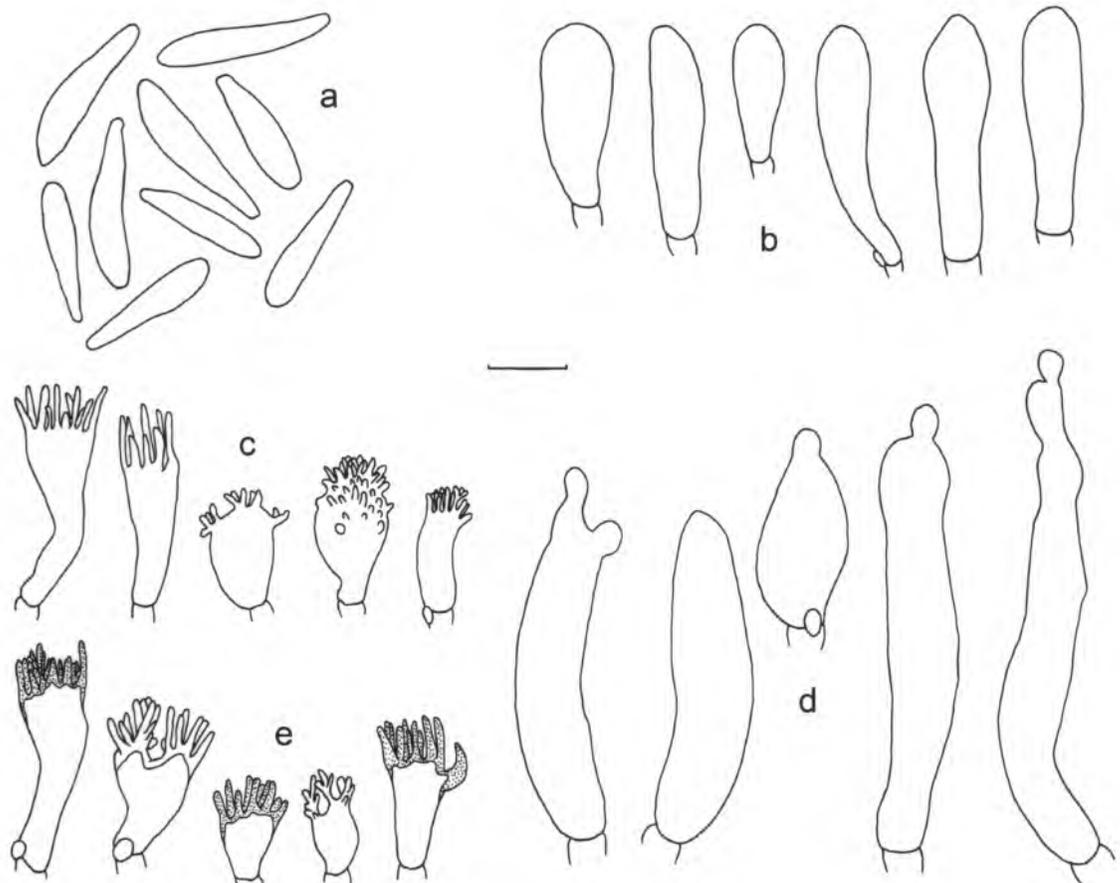


Figure 20: *Marasmius haematocephalus* (JES 147, JES 202 and JES 193). a) basidiospores; b) basidioles; c) cheilocystidia; d) pleurocystidia; e) pileipellis cells. Scale bar = 10 μ m.

30. *Marasmius tanaensis* J.E. Shay & Desjardin *sp. nov.*

Holotype: Madagascar, Region Analamanga, City of Antananarivo, Parc Botanique de Zoologique (P.B.Z.T.), near the garden of Crops Wild and Relatives (CWR), elevation 1270 m, GPS: -18 55.530 S, 47 31.350 E, 8 Feb. 2014, J.E. Shay 220 (SFSU).

(Figure 21, Plate 8)

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.

Basidiospores 11.2–16 × (3.2–) 4–4.8 (–5.6) μm [$x_m = 13.37 \pm 1.41 \times 4.26 \pm 0.49$ μm; $Q = 2.43–5.0$; $Q_m = 3.19 \pm 0.26$, $n = 31$, $s = 1$], 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), elevation 1270 m, GPS: -18 55.530 S, 47 31.350 E, 8 Feb. 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 $13.4 \times 4.3 \mu\text{m}$, 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.

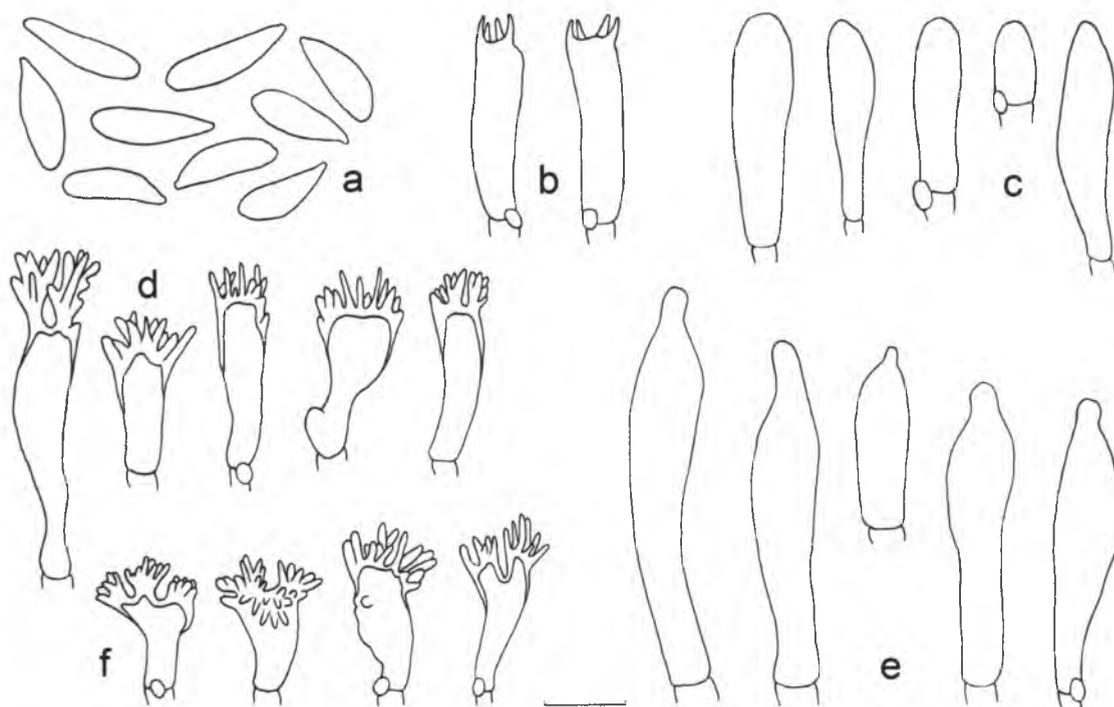


Figure 21: *Marasmius tanaensis* (JES 220). a) basidiospores; b) basidia; c) basidioles; d) cheilocystidia; e) pleurocystidia; f) pileipellis cells. Scale bar = 10 μm .

31. *Marasmius* (cf.) *grandisetulosus* Singer, Bull. Jard. Bot. État Brux. 34: 379. 1964.
– *Type*: Democratic republic of Congo, Kivu, Panzi, Nov. 1948, M. Goossens-Fontana 5076 (BR 11460–14).

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

32. *Marasmius eyssartieri* Antonín & Buyck, Fungal Diversity 23: 42. 2006.

– *Type*: Madagascar, Sainte Lucie, near Fort Dauphin, 27 Jan. 1999, leg. B. Buyck & G. Eyssartier, Buyck 99.375 (PC).

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

33. *Marasmius cf. confertus var. parvisporus* Antonín. Mycotaxon 89: 401. 2004.

– *Type*: Kenya, Central Province, Nairobi District, Thika Fall, 16 Mar. 1968, D.N. Pegler K101 (K(M) 8833).

For a description and illustrations of Madagascar material, refer to Antonín and 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.

– *Type*: Democratic Republic of Congo, Tshopo Province, Kisangani, forest near Zoo, 2 May 1984, B. Buyck 1615 (BR 11731–91).

(Figure 22, Plate 8)

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 [$x_m = 11.52 \pm 1.07 \times 4.48 \pm 0.44$ μm; 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 capitate, 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, apically 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, elevation 8 m, GPS: -18 53.082 S, 49 07.559 E, 30 Jan. 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 Madagascar 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).

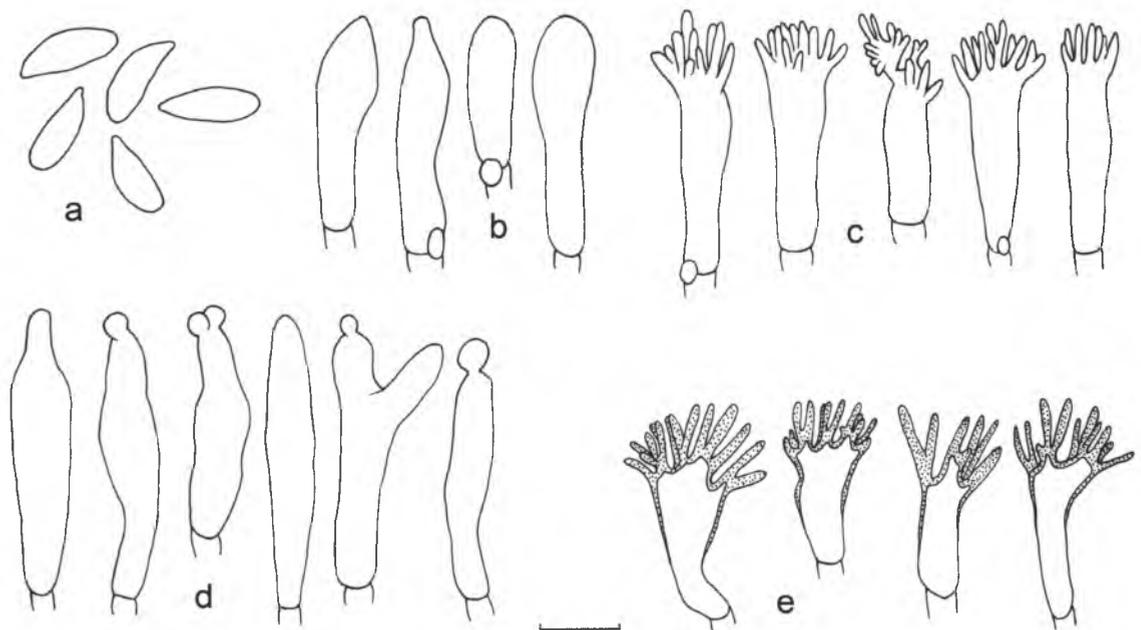


Figure 22: *Marasmius ferruginoides* (JES 209). a) basidiospores; b) basidioles; c) cheilocystidia; d) pleurocystidia; e) pileipellis cells. Scale bar = 10 μm .

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

– *Type*: Cuba, on dead leaves, Oct., Wright 155 (K).

(Figure 23, Plate 8)

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 [$x_m = 12.13 \pm 0.94 \times 3.24 \pm 0.49$ μm; Q = 3–5; $Q_m = 3.82 \pm 0.45$, n = 25, s = 1], fusoid to oblong or narrowly ellipsoid, smooth, hyaline, inamyloid, thin-walled. *Basidia* not observed. *Basidioles* 22.4–25.6 × 5.6–8 μm, clavate to fusoid, hyaline, inamyloid, thin-walled. *Cheilocystidia* of *Siccus*-type broom cells; main body 12–23.2 × 4.8–7.2 μm, clavate to cylindrical, hyaline, inamyloid, apically thick-walled; apical setulae 0.8–7.2 × 0.8–1.6 μm, cylindrical to conical or irregular, seldom branched, hyaline, inamyloid, thick-walled. *Pleurocystidia* 36–47.2 × 7–10 μm, common, subcylindrical to fusoid, some mucronate, hyaline, inamyloid, 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, inamyloid, thick-walled; apical setulae 0.8–4.8 × 0.8–1.6, cylindrical to conical, light brown to brown, inamyloid, 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. *Stipe tissue* 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), elevation 1270 m, GPS: -18 55.530 S, 47 31.350 E, 8 Feb. 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 Madagascar specimen matches quite closely material reported from the Caribbean (Singer 1976, Pegler 1983). The species shows similarities to *M. hypophaeus* Berk. & M.A. Curtis, *M. confertus* Berk. & Broome, *M. suthepensis*, and *M. 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 ($x = 17.2 \times 4.0 \mu\text{m}$) and strangulate pleurocystidia (Desjardin et al. 2000, Wannathes et al. 2009). *Marasmius confertus* and *M. suthepensis* have nearly smooth pilei and more numerous lamellae with multiple series of lamellulae (Antonín 2007, Wannathes et al. 2009). *Marasmius ferrugineus* forms a paler pileus, has fewer lamellae (8–10) and larger basidiospores ($x = 17.0 \times 4.0 \mu\text{m}$) (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 support (Fig. 1a).

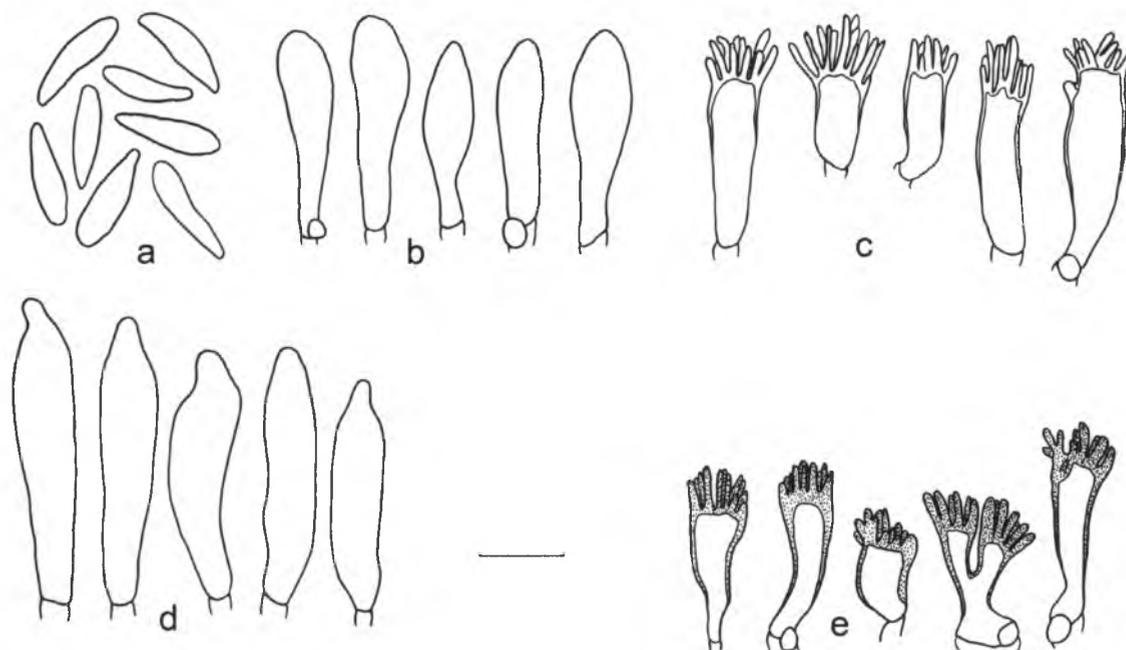


Figure 23: *Marasmius hinnuleus* (JES 217) a) basidiospores; b) basidioles; c) cheilocystidia; d) pleurocystidia; e) pileipellis cells. Scale bar = 10 μ m.

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 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. (2009) 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 groups of *Marasmius*, closely related 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. 2009), 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 tremendous 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*.



Figure 24: Map of collection sites for 2006 (Antonín and Buyck) and 2014 (Shay and Newman).

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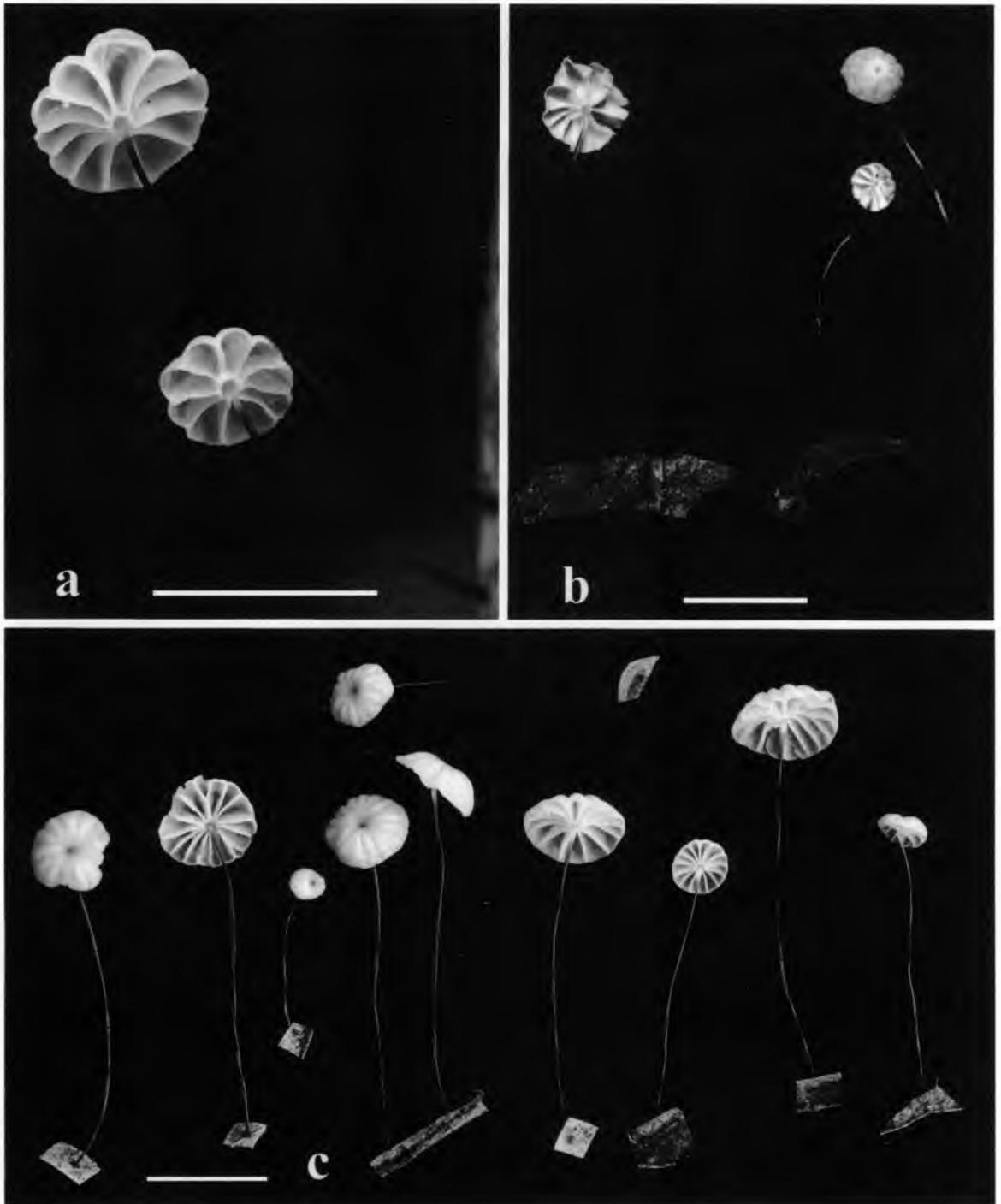


Plate 1: Basidiocarps representing sect. *Marasmius* subsect. *Marasmius* – a) *Marasmius rotalis* (JES 154). – b) *Marasmius apatelius* (JES 203). – c) *Marasmius somalomoensis* (JES 129). Scale bar = 5 mm (a); = 10 mm (b, c).

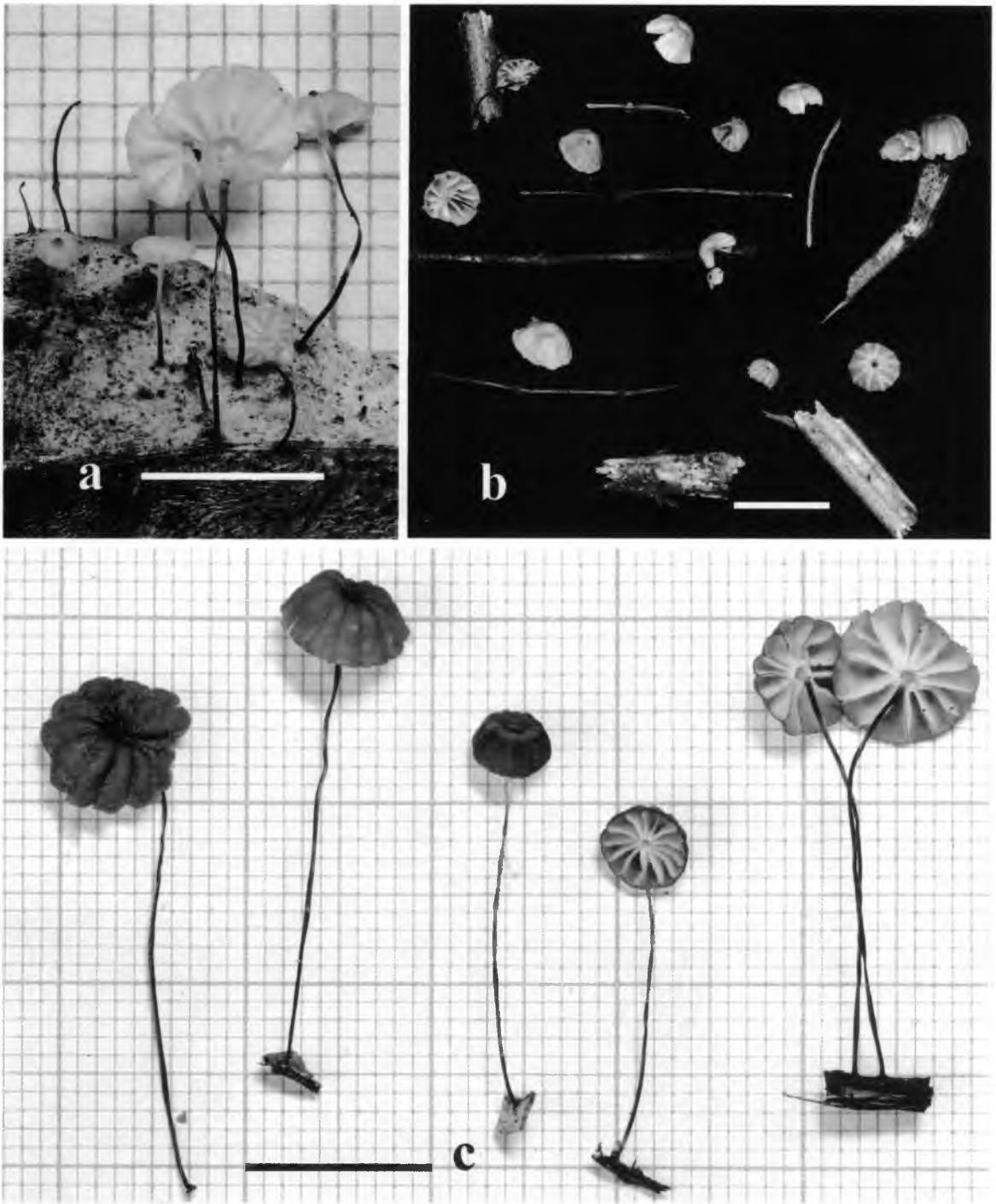


Plate 2: Basidiocarps representing sect. *Marasmius* subsect. *Sicciformes*
 – a) *Marasmius conicopapillatus* (JES 180). – b) *Marasmius* aff. *curreyi* (JES 135).
 – c) *Marasmius rubrobrunneus* (JES 183). Scale bar = 5 mm (a); = 10 mm (b, c).

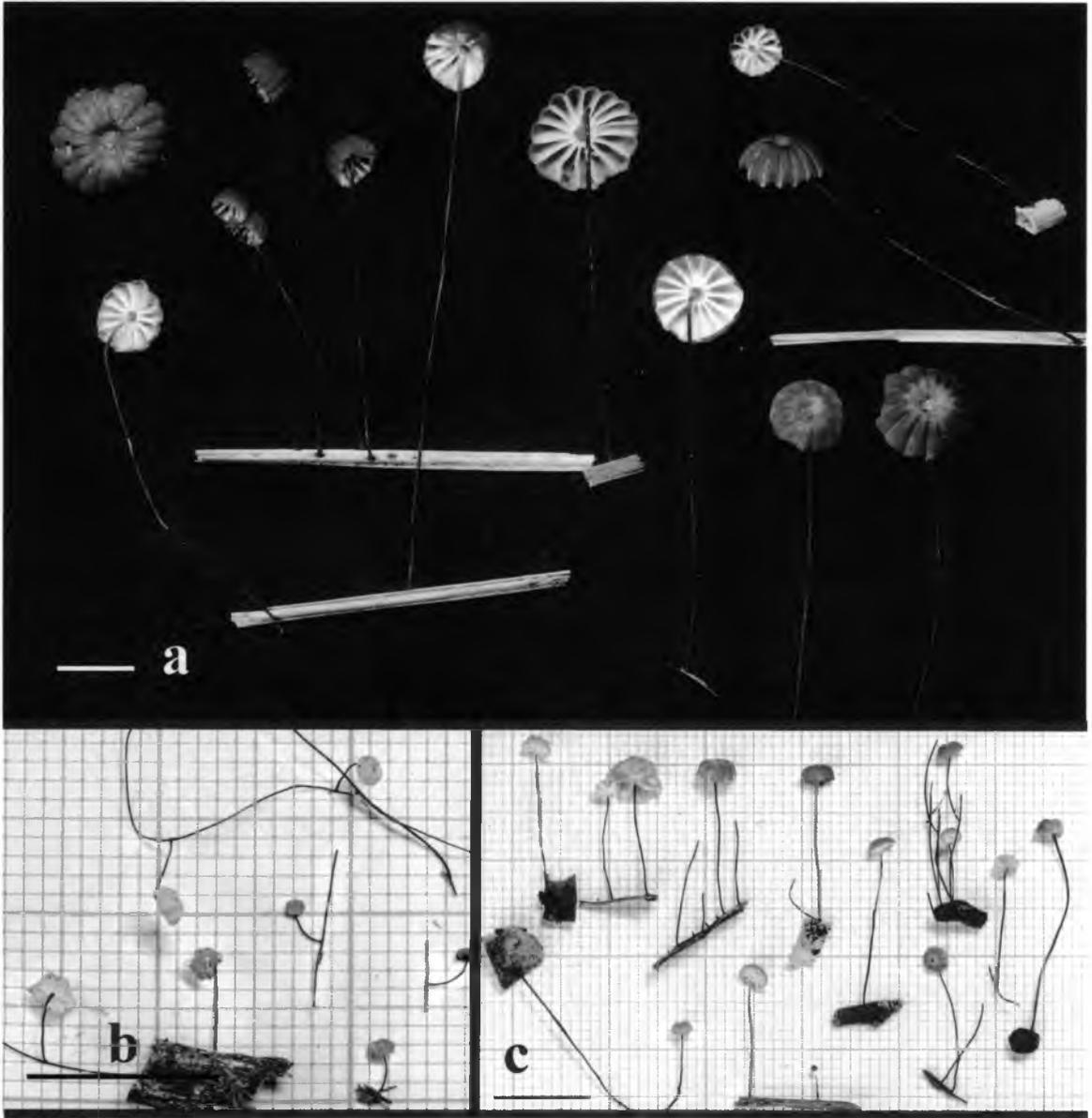


Plate 3: Basidiocarps representing sect. *Marasmius* subsect. *Sicciformes*
 – a) *Marasmius brunneoaurantiacus* (JES 113). – b) *Marasmius crinisequi* (JES 176).
 – c) *Marasmius* cf. *subruforotula* (JES 186). Scale bar = 10 mm.



Plate 4: Basidiocarps representing sect. *Marasmius* subsect. *Sicciformes* – a) *Marasmius madagascariensis* (JES 225); sect. *Globulares* – b) *Marasmius bekolacongoli* (Lockwood 2131638), photo generously donated by Taylor Lockwood. Scale bar = 10 mm (a); = 20 mm (b).

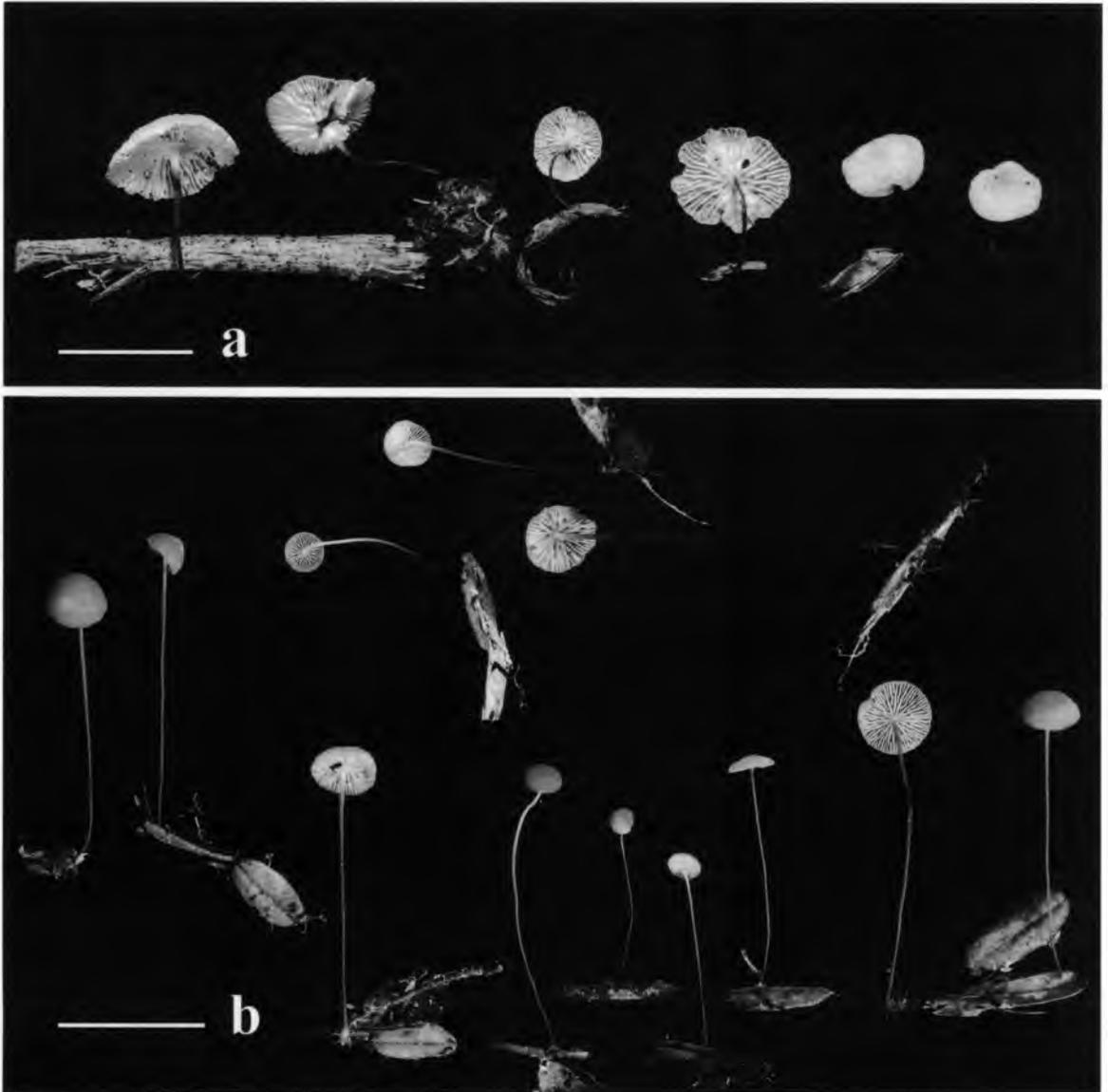


Plate 5: Basidiocarps representing sect. *Sicci* ser. *Spinulosi* – a) *Marasmius dendrosetae* (JES 205) – b) *Marasmius nummularius* (JES 124). Scale bar = 10 mm.

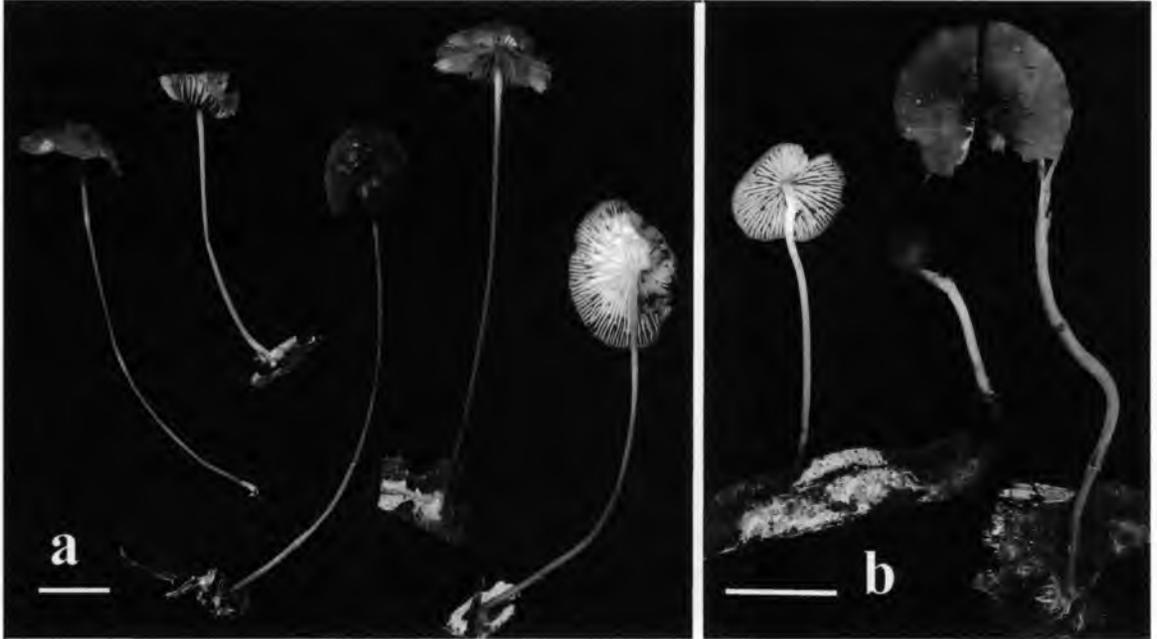


Plate 6: Basidiocarps representing sect. *Sicci* ser. *Atrorubentes*— a) *Marasmius corrugatiformis* (JES 164) — b) *Marasmius katangensis* (JES 227). Scale bar = 10 mm.

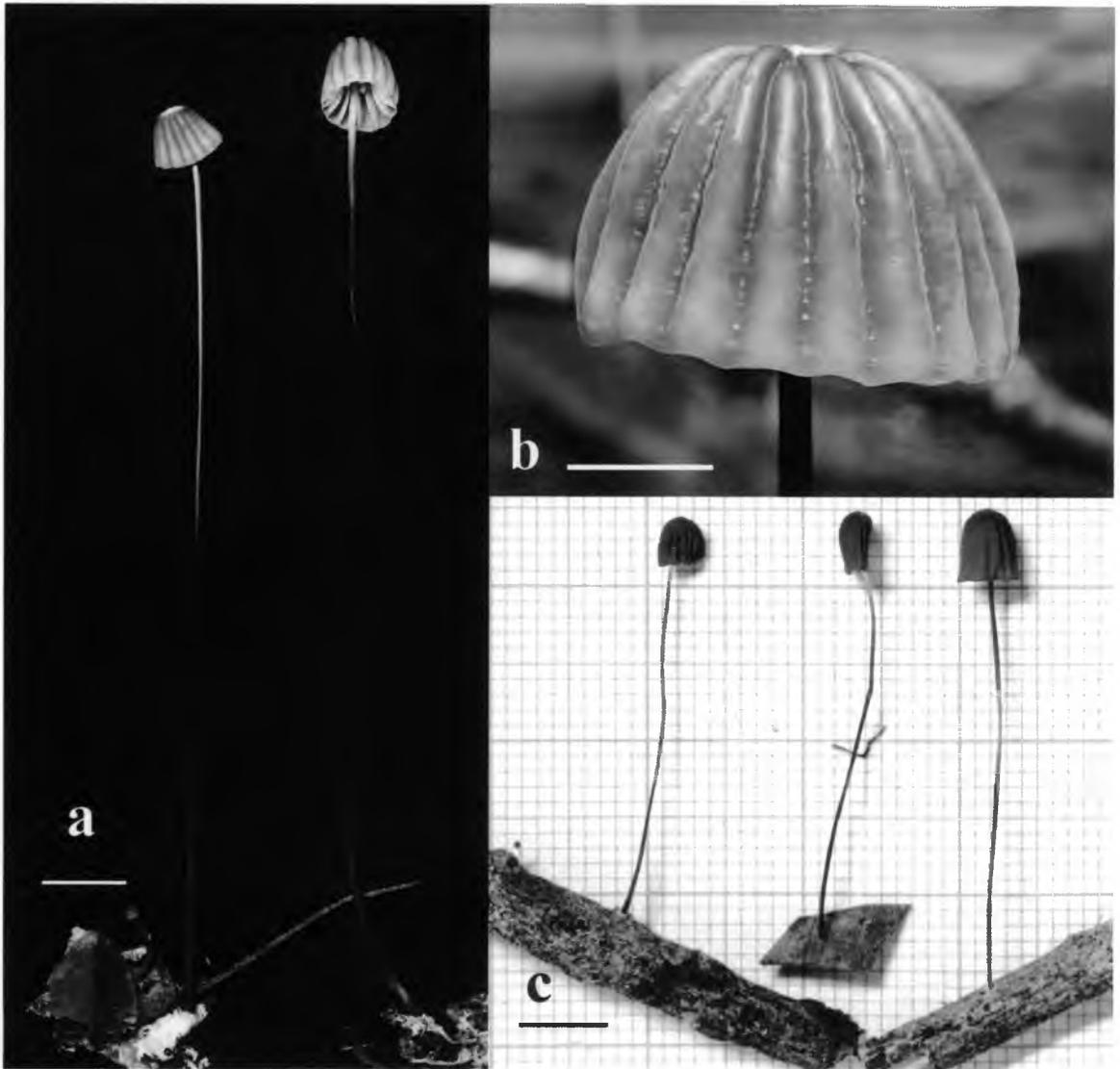


Plate 7: Basidiocarps representing sect. *Sicci* ser. *Leonini* a) *Marasmius megistus* (JES 163), b) *Marasmius megistus* (Lockwood 2132155), photo generously donated by Taylor Lockwood. – c) *Marasmius bambusiniiformis* (JES 199). Scale bar = 10 mm (a, c); = 5 mm (b).

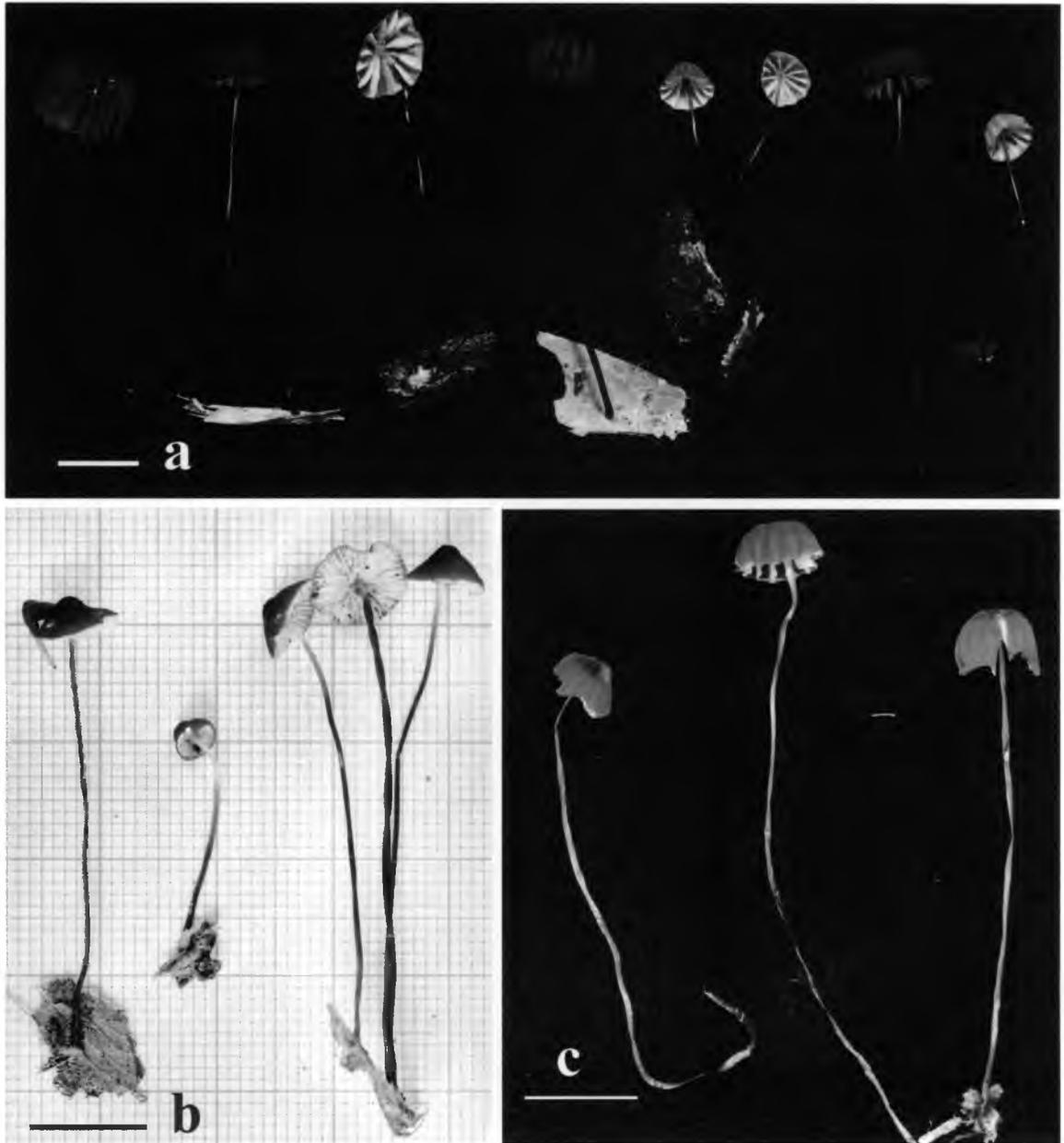


Plate 8: Basidiocarps representing sect. *Sicci* ser. *Haematocephali* a) *Marasmius haematocephalus* (JES 202) – b) *Marasmius ferruginoides* (JES 209) – c) *Marasmius hinnuleus* (JES 217). Scale bar = 10 mm.