

PRELIMINARY MONOGRAPH OF *MARASMIUS* FROM SÃO TOMÉ AND
PRÍNCIPE

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A Thesis submitted to the faculty of
San Francisco State University
In partial fulfillment of
the requirements for
the Degree

Master of Science

In

Biology: Ecology, Evolution, and Conservation Biology

by

Christopher Lee Grace

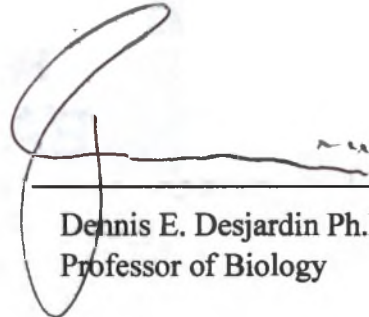
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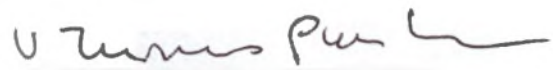
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CERTIFICATION OF APPROVAL

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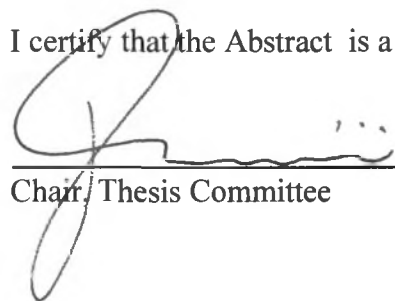
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PRELIMINARY MONOGRAPH OF *MARASMIUS* FROM SÃO TOMÉ AND
PRÍNCIPE

Christopher Lee Grace
San Francisco, California
2019

This treatise serves as a preliminary monograph and phylogenetic treatment of *Marasmius* from the African island nation of São Tomé and Príncipe (ST&P), based on data generated from 30 specimens collected in 2008. Twenty-one species are described, five of which represent species new to science (*Marasmius albisubiculosus*, *M. elaeocephaliformis*, *M. laranja*, *M. segregatus*, *M. leptcephalus*), and all represent new distribution records for ST&P. Species are delimited based on comprehensive morphological characters and DNA sequence data. Prior to the collection of these specimens, only one *Marasmius* species had been documented from these islands. Phylogenetic hypotheses generated from analyses of DNA sequences of the Internal Transcribed Spacer regions (ITS1+5.8S+ITS2) are proposed to explore the evolutionary relationships amongst ST&P *Marasmius* and global *Marasmius* diversity. A dichotomous key to aid in identification, illustrations of pertinent micromorphological features, color photographs of basidiomes, comprehensive descriptions and commentaries are provided.

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



Chair, Thesis Committee

2/19/2019

Date

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Introduction

The island nation of São Tomé and Príncipe (ST&P) is located in the Gulf of Guinea, south of Nigeria and Cameroon and west of Equatorial Guinea and Gabon. The islands were colonized by the Portuguese in the 15th century, before which they were reported to be uninhabited, and operated as a center and waypoint for the African slave trade throughout the 16th century. Controlled by Portugal for over 400 years, ST&P achieved independence in 1975. The islands are volcanic in origin, arising from a submerged hot spot near 0° latitude and 0° longitude. They have never been connected to the continental mainland of Africa and support rich multi-kingdom biodiversity. Many organisms that live on ST&P have not yet been found elsewhere and may be endemic to these islands.

São Tomé and Príncipe, the two major islands composing the nation, are characterized by steep mountains and flat lowlands. The lowlands, the result of erosion, serve as the major population and agricultural centers. Much of the original forests and biodiversity of the islands is restricted to the mountains and their steep slopes, usually above 800 m. The lowland vegetation consists primarily of agricultural land including sugarcane fields, cacao plantations, coconut groves, and stands of bamboo. Areas of second generation forest occur in areas where agriculture and settlement have been abandoned.

Expeditions to São Tomé and Príncipe were conducted in 2006 and 2008 by Dr. Dennis E. Desjardin, joined in 2008 by Dr. Brian A. Perry, as a part of the California Academy of Sciences' Biodiversity Description Mission lead by Dr. Robert Drewes (CAS). These researchers focused on documenting the biodiversity of fleshy fungi, macromycetes belonging to the Basidiomycota and Ascomycota. Hundreds of specimens were collected, of which a subset of 30 specimens represent species belonging to the genus *Marasmius sensu stricto*. The *Marasmius* specimens serve as the source material for this preliminary monograph of *Marasmius* from São Tomé and Príncipe.

The genus *Marasmius* (Agaricales, Basidiomycota) is worldwide in distribution, and is composed of over 1000 species of white-rot, litter and wood decomposers. Prior to the fieldwork of Desjardin and Perry, only one species currently accepted in *Marasmius*, *M. collinus* (reported as *Collybia collina*), was reported from São Tomé or Príncipe (Bresadola & Roumeguère, 1890). *Marasmius amadelphus* and *M. splachnoides* were also reported (Bresadola & Roumeguère, 1890), but these taxa were transferred subsequently to the genera *Marasmiellus* and *Gymnopus*, respectively. Only limited research has been conducted on *Marasmius* from Africa and adjacent regions. Pegler (1977) reported a number of *Marasmius* species from East Africa in his treatment of Agaricales from the region. A monograph of tropical mainland African species of *Marasmius* was published by Antonín (2007) in which he provided type studies and descriptions of all known species from tropical habitats on the continent; 110 species of *Marasmius* were documented with comprehensive descriptions. Antonín (2013) followed with a supplement to the African *Marasmius* monograph that included an additional 40 taxa. Additionally, Antonín & Buyck (2006) provided an accounting of *Marasmius* from Madagascar and the Mascarenes based on very limited collecting; 19 species were reported. Recently, Shay et al. (2017) provided an updated monograph of Madagascar *Marasmius* in which 35 species were documented from the region. No comprehensive accounting of *Marasmius* from ST&P has been published. This research will serve as a preliminary monograph of *Marasmius* for these islands, based on analyses of morphology and molecular sequences data (ITS) generated from 30 specimens collected in 2008. For this work, *Marasmius sensu stricto* is accepted as circumscribed by Wilson and Desjardin (2005), Tan et al. (2009), Wannathes et al. (2009), Antonín and Noordeloos (2010), Jenkinson et al. (2014) and Shay et al. (2017).

Materials & Methods

Taxon Sampling

Six weeks were spent in the field on São Tomé and Príncipe collecting and documenting fleshy basidiomycetous fungi during the rainy month of April 2006 and April 2008. Specimens were collected from a diverse range of habitats present on the islands including native primary and secondary forests, coastal cacao and banana groves, coastal secondary forests, and coastal xerophytic habitats. These locations varied in their level of anthropogenic impact and modification. Each day over the six weeks, 6–8 hours were spent collecting all marasmiod agarics encountered, followed by 6–8 hours focused on documenting morphological features, photographing specimens, drying and preparing material for transport. Only 30 specimens of *Marasmius sensu stricto* were encountered during these expeditions, and all specimens are treated herein.

Morphological descriptions

Macromorphological data and photographs from fresh material were recorded by Desjardin and Perry at the time of the collection, following the protocols of Largent (1986). Color terms are those of Kornerup and Wanscher (1978). Habitat data reported for each species refers to that of the material from ST&P, not all known habitats for the species. The terms used to describe lamellae spacing refer to the number of lamellae that reach from the stipe to the pileus margin and do not include the lamellulae, whose spacing is indicated by the number of series present. The term "marginate" refers to a colored lamellar edge, while "non-marginate" means a lamellar edge the same color as the lamellar sides. Collections were dried in a Nesco® food dehydrator, packed in airtight Ziplock® bags, stored in boxes for transport back the USA, and are deposited in the Harry D. Thiers Herbarium at San Francisco State University (SFSU).

Micromorphological data were derived from each of the dried specimens using an

Olympus CH30 compound microscope and Leica Zoom 2000 dissecting scope. Relevant hand-made tissue sections were revived with 100% ethanol then mounted in 3% potassium hydroxide (KOH), Melzer's reagent, or a combination of Congo Red and 3% KOH. All pertinent cell-types (Cl  men  on 2004) were illustrated at a minimum of 1000  with the aid of a drawing tube. 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; x_{mr} , the range of spore means, and \bar{x}_{mm} , the mean of spore means (\pm SD) when more than one specimen is available; Q , the quotient of spore length by spore width in any one spore, indicated as a range of variation in n spores measured; \bar{Q}_m , the mean of Q -values in a single specimen; Q_{mr} , the range of Q_m values and \bar{Q}_{mm} , the mean 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.

Molecular Protocols

Genomic DNA was extracted from dried herbarium specimens using the E.Z.N.A. Forensic DNA Kit (Omega Bio-Tek Inc., Doraville, Georgia) following the manufacturer's protocol, with the exception of using the first 50 μ l elution flow-through for the second elution in an effort to maximize DNA yield. For all specimens, the nuclear ribosomal internal transcribed spacer region (ITS1+5.8S+ITS2) was amplified using primers ITS1-F and ITS4 (Gardes and Bruns 1993, White et al. 1990). DNA amplification was performed using AccuPower  PCR PreMix tubes (BIONEER, Daejeon, Republic of Korea) with the addition of 1-3 μ l genomic DNA, 19-22 μ l PCR water, and 1 μ l of each 10 μ M primer. The ITS amplification protocol consisted of an initial denaturation time of 4 min at 95 C, followed by 39 cycles at 94 C for 30 sec, 54 C for 30 sec, and 72 C for 45 sec, with a final extension temperature of 5 min. at 72 C. PCR products were cleaned using ExoSAP-IT (Affymetrix, Cleveland, Ohio, USA) following the manufacturer's instructions, except for first diluting it 1:5 with ultrapure water. Cleaned PCR products were sent to Elim Biopharmaceuticals (Hayward, CA) for

sequencing. Resulting sequences were edited, assembled and aligned using Geneious v. 7.1 (<http://www.geneious.com>, Kearse et al., 2012).

Phylogenetic Analyses

Maximum likelihood analyses were run in RAxML 8.1.1 (Stamatakis 2014) under a GTRGAMMA model and consisted of 100 alternative runs using the default parameters, with node support estimated by 1000 RAxML rapid bootstrap replicates. Bayesian analyses were performed using Metropolis Coupled MCMC methods as implemented in MrBayes 3.2.6 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003) under a GTR+I+G model of sequence evolution as determined under the Akaike Information Criterion in PAUP* (Swofford 2002). Analyses consisted of two parallel searches, run for 25 million generations initiated with random starting trees. Eight chains (temp = 0.3) were sampled every 2500 generations for a total of 10,001 trees each, sampled from the posterior distribution. Those topologies sampled prior the runs reaching a split deviation frequency of 0.1 were discarded, while the remaining topologies were used to calculate the posterior probabilities of the individual clades. The default settings were used in MrBayes to set unconstrained branch lengths and uninformative topology priors. All maximum likelihood and Bayesian analyses were run on the CIPRES Science Gateway (Miller et al. 2010).

Pairwise Sequence Comparisons

Pairwise sequence similarity between aligned, overlapping regions was calculated using Geneious v.7.1 (<http://www.geneious.com>, Kearse et al., 2012). Specimens are recognized as conspecific if their respective sequences show 97% ITS sequence similarity ($\leq 3\%$ sequence divergence) and are morphologically indistinguishable in features considered taxonomically significant at the species rank. If specimens show 97–98% ITS sequence similarity (2–3% sequence divergence) but have 2 or more distinctly

different morphological features of the type considered taxonomically significant (e.g., presence/absence of cystidia, setae, stipes or rhizomorphs; non-overlapping basidiospore size ranges; setulose/non-setulose cystidia; dextrinoid/non-dextrinoid tissues; distant/crowded lamellae; monocot/dicot substrate), these are recognized as distinct species.

Results

Our phylogenetic analyses compared the ITS gene region of 135 taxa of *Marasmius sensu stricto* representing a global distribution of the genus and including members of all infrageneric groups. The dataset of 222 ITS sequences, includes 154 sequences that were acquired from GenBank, 43 sequences that were added from a monograph of Madagascar *Marasmius* (Shay *et al.* 2017), and 25 sequences from ST&P generated for this preliminary monograph. The ITS dataset used and analyses performed are the same as those previously published in Shay *et al.* 2017 which included the species from ST&P described in this study. *Crinipellis malesiana* Kerekes, Desjardin & Vikinesw. was included as an outgroup to *Marasmius* based on the findings of previous phylogenetic analyses (Tan *et al.* 2009, Wannathes *et al.* 2009). The dataset used for all analyses included 687 informative nucleotide characters. Prior to all analyses 343 ambiguously aligned nucleotides were excluded from the dataset.

Figure 1 depicts the RAxML tree with the best statistical support, represented by an ML score of $-\ln L = 13820.463$. Statistical support for the deep nodes distinguishing major lineages was low, reaffirming that the ITS gene region is too variable to delimit infrageneric clades in *Marasmius* (Tan *et al.* 2009, Wannathes *et al.* 2009). Of the historically recognized infrageneric groups of *Marasmius*, only *Marasmius* subsect. *Marasmius* (MM) forms a monophyletic clade (98% BS, 1.0 PP) (Fig. 1c). The clade includes the type species of the genus *Marasmius* (*M. rotula* (Scop.) Fr.). Members of subsect. *Marasmius* are characterized by a morphology including the following traits:

lamellae attached to a collarium, forming an insititious stipe, and a pileipellis containing *Rotalis*-type broom cells. Taxa belonging to *Marasmius* subsect. *Sicciformes* (MS) formed a grade basal to subsect. *Marasmius* (Fig. 1c) that also includes a small number of species of sects. *Neosessiles* (N), *Leveilleani* (L) and *Globulares* (G). Members of subsect. *Sicciformes* are characterized by a morphology including the following traits: lamellae attached to a collarium, forming a insititious stipe, and a pileipellis with *Siccus*-type broom cells. Most taxa of the historically recognized sects. *Globulares* + *Sicci* formed a clade with low support (Figs. 1a, 1b). Members of sects. *Globulares* + *Sicci* are characterized by a morphology including the following traits: lamellae without a collarium, forming a non-insititious stipe, and a pileipellis with either *Globulares*-type or *Siccus*-type broom cells. None of the series level infrageneric groups historically recognized within *Sicci*, viz., ser. *Atrorubentes* (SA), *Haematocephali* (SH), *Leonini* (SL), and *Spinulosi* (SS) formed monophyletic clades in this ITS phylogeny (Figs. 1a, 1b), though small groups of species representing each respective series are present with varied levels of support.

Concerning ST&P taxa in Fig.1a: *Marasmius suthepensis* (SH) is sister to *M. linderoides* (SH) with low support. *Marasmius elaeocephalus* (SH) is sister to the pleurotoid *M. griseoroseus* (N) with low support. *Marasmius corrugatiformis* (SA) is sister to *M. subarborescens* (SA) in a well-supported clade (100% BS, 1.0 PP) with *M. pellucidus* (G). *Marasmius elaeocephaliformis* (SH) holds an isolated position near *M. ferruginoides* (SH), while *Marasmius grandisetulosus* (SH) belongs in a clade with *M. hinnuleus* (SH) and *M. hypophaeus* (SH). *Marasmius megistus* (SL) forms a well-supported clade (100% BS, 1.0 PP) with two other sequences determined as *M. megistus*, on a long branch embedded in a clade with members of ser. *Leonini* and *Haematocephali*.

Concerning ST&P taxa in Fig.1b: *Marasmius atrorubens sensu* Antonín of ser. *Spinulosi* is embedded in a clade with members of ser. *Leonini* and *Haematocephali*. *Marasmius haediniformis* (SL) is sister to *M. corneri* (SL) with strong support (100% BS, 1.0 PP). *Marasmius trichotus* (SS) belongs in a low-supported clade with two other

members of ser. *Spinulosi*, while *M. albisubiculosus* (SL) and *M. laranja* (G) on long branches hold isolated positions.

Concerning ST&P taxa in Fig.1c: *Marasmius colorimarginatus* is embedded in a grade with sequences determined as *M. somalomoensis*, as is *M. aff. apatelius* with sequences determined as *M. apatelius*, all belonging to a well-supported clade of sect. *Marasmius* subsect. *Marasmius* (98% BS, 1.0 PP). *Marasmius subruforotula* is sister to *M. cf. subruforotula* from Madagascar in a well-supported subsect. *Sicciformes* clade (100% BS, 1.0 PP), on a long branch sister to subsect. *Marasmius*. *Marasmius nodulocystis* (SL) is sister to a clade containing *M. leveilleanus* (L), *M. tenuissimus* (N) and *M. neosessiliformis* (N). *Marasmius aff. guyanensis* belongs in a clade (70% BS, 0.97 PP) with other members of subsect. *Sicciformes* (MS) including *M. guyanensis*, *M. crinisequi* and *M. madagascariensis*. *Marasmius segregatus* (MS) holds an isolated position near the base of the well-supported (100% BS, 1.0 PP) genus *Marasmius* clade.

TABLE 1. List of *Marasmius* species sequenced (ITS1–5.8S-ITS2) for this study.

Species	Section/Subsection or Section/Series	Collection No.	GenBank No.
<i>M. albisubiculosus</i>	<i>Sicci/Leonini</i>	DED 8277	KX953752
<i>M. aff. apatelius</i>	<i>Marasmius/Marasmius</i>	DED 8295	KX953762
<i>M. atrorubens</i>	<i>Sicci/Spinulosi</i>	DED 8263	KX953751
<i>M. colorimarginatus</i>	<i>Marasmius/Marasmius</i>	DED 8293	KX953746
<i>M. colorimarginatus</i>	<i>Marasmius/Marasmius</i>	DED 8309	KX953745
<i>M. corrugatiformis</i>	<i>Sicci/Atrorubentes</i>	DED 8233	KX953757
<i>M. corrugatiformis</i>	<i>Sicci/Atrorubentes</i>	DED 8326	KX953756
<i>M. elaeocephaliformis</i>	<i>Sicci/Haematocephali</i>	DED 8213	KX953758
<i>M. elaeocephalus</i>	<i>Sicci/Haematocephali</i>	DED 8254	KX953754
<i>M. grandisetulosus</i>	<i>Sicci/Haematocephali</i>	DED 8225	KX953743
<i>M. grandisetulosus</i>	<i>Sicci/Haematocephali</i>	DED 8257	KX953744
<i>M. aff. guyanensis</i>	<i>Marasmius/Sicciformes</i>	DED 8285	KX953747
<i>M. haediniformis</i>	<i>Sicci/Leonini</i>	DED 8216	KX953759
<i>M. haediniformis</i>	<i>Sicci/Leonini</i>	DED 8217	KX953760
<i>M. laranja</i>	<i>Globulares/Globulares</i>	DED 8231	KX953748
<i>M. megistus</i>	<i>Sicci/Leonini</i>	DED 8230	KX953750
<i>M. nodulocystis</i>	<i>Sicci/Leonini</i>	DED 8269	KX953740
<i>M. nodulocystis</i>	<i>Sicci/Leonini</i>	DED 8278	KX953741
<i>M. nodulocystis</i>	<i>Sicci/Leonini</i>	DED 8283	KX953742
<i>M. segregatus</i>	<i>Marasmius/Sicciformes</i>	DED 8256	KX953761
<i>M. subarborescens</i>	<i>Sicci/Atrorubentes</i>	DED 8215	KX953755
<i>M. subruforotula</i>	<i>Marasmius/Sicciformes</i>	DED 8296	KX953739
<i>M. subruforotula</i>	<i>Marasmius/Sicciformes</i>	DED 8307	KX953738
<i>M. suthepensis</i>	<i>Sicci/Haematocephali</i>	DED 8292	KX953753
<i>M. trichotus</i>	<i>Sicci/Spinulosi</i>	DED 8248	KX953749

Key to *Marasmius* from São Tomé and Príncipe

1. Lamellae attached to a collarium (sect. *Marasmius*) 2
1. Lamellae attached directly to the stipe, collarium absent (sect. *Globulares*) 7
2. Pileipellis composed of *Rotalis*-type broom cells (subsect. *Marasmius*) 3
2. Pileipellis composed of *Siccus*-type broom cells (subsect. *Sicciformes*) 5
3. Pileus off-white to cream with a darker central spot or papilla; lamellae 9–14 ...
..... 1. *M. rotalis*
3. Pileus tan-beige, pale grayish orange, light brown or brown, lacking a darker central spot, lacking a papilla; lamellae 13–18 4
4. Pileus 2–5 mm, tan-beige to pale grayish orange 2. *M. aff. apatelius*
4. Pileus 4–12 mm, light brown to brown 3. *M. colorimarginatus*
5. Basidiospores >12.5 µm long; lamellae 7–8, non-marginate 4. *M. aff. guyanensis*
5. Basidiospores typically < 12.5 µm long; lamellae 9–14, with brownish orange to reddish orange or reddish brown edges 6
6. Pileus reddish brown with a distinct black papilla; basidiospores 8.2–9.6 × 4.2–5.6 µm; on leaves 5. *M. subruforotula*
6. Pileus brownish orange, lacking a distinct papilla; basidiospores 8.5–12.5 × 5–7 µm; on woody debris 6. *M. segregatus*

7. Pileipellis composed of smooth, clavate cells lacking apical setulae 7. *M. laranja*
7. Pileipellis composed of *Siccus*-type broom cells 8
8. Stipe pruinose, covered with setae or non-setulose caulocystidia 9
8. Stipe glabrous, lacking setae and non-setulose caulocystidia (if pruinose, then covered with arachnoid cells) 12
9. Pileosetae and caulosetae present (ser. *Spinulosi*) 10
9. Pileosetae and caulosetae absent; caulocystidia of smooth, clavate cells (ser. *Atrorubentes*) 11
10. Pileus 15–24 mm diam; lamellae crowded (24–35); basidiospores $13.5\text{--}15.2 \times 4.2\text{--}4.8 \mu\text{m}$; pleurocystidia present 8. *M. atrorubens*
10. Pileus 5–10 mm diam; lamellae subdistant (12–16); basidiospores $10.4\text{--}12.6 \times 3.7\text{--}4.4 \mu\text{m}$; pleurocystidia absent 9. *M. trichotus*
11. Pileus reddish brown to brownish orange 10. *M. corrugatiformis*
11. Pileus creamy white to white 11. *M. subarborescens*
12. Pleurocystidia absent (ser. *Leonini*) 13
12. Pleurocystidia present (ser. *Haematocephali*) 18
13. Basidiospores $> 30 \mu\text{m}$ long 12. *M. megistus*
13. Basidiospores $< 30 \mu\text{m}$ long 14

14. Pileus white, orangish white, cream or light yellow 15
14. Pileus more deeply pigmented—brownish orange, reddish brown, maroon 17
15. Basidiospores $> 12 \mu\text{m}$ long; lamellae 13–18 13. *M. haediniformis*
15. Basidiospores $< 12 \mu\text{m}$ long; lamellae 10–13 16
16. Pileus 2–3 mm broad; stipe pruinose, covered with Siccus-type broom cells and broccoli-like intercalary outgrowths; pileipellis with scattered arachnoid cells; basidiospores $8\text{--}9.5 \times 3.2\text{--}3.8 \mu\text{m}$ 14. *M. albisubiculosus*
16. Pileus 8–13 mm broad; stipe glabrous, caulocystidia absent; arachnoid cells absent; basidiospores $10.5\text{--}12 \times 3.5\text{--}5 \mu\text{m}$ 15. *M. leptcephalus*
17. Pileus disc brownish orange, margin fading in age to orangish white or white; basidiospores $> 12 \mu\text{m}$ long 13. *M. haediniformis*
17. Pileus reddish brown to dark reddish brown, margin fading in age to brownish orange or cream-striped; basidiospores $< 12 \mu\text{m}$ long 16. *M. nodulocystis*
18. Pileus smooth to rugulose or weakly rugulose-striate; lamellae narrow (1–2 mm), with 2–3 series of lamellulae; basidiospores $< 14.5 \mu\text{m}$ long 19
18. Pileus distinctly sulcate to plicate; lamellae broad (2–4 mm), with 0–1 series of lamellulae; basidiospores $> 14.5 \mu\text{m}$ long 21
19. Pileus orange 17. *M. suthepensis*
19. Pileus olive, brown, orangish brown, or yellowish olive-brown 20

20. Lamellae close (18–30), non-marginate 18. *M. elaeocephalus*

20. Lamellae distant (11–14), often pale brown-marginate 19. *M. elaeocephaliformis*

21. Basidiospores $19\text{--}23 \times 4.4\text{--}5.6 \mu\text{m}$; pileus dark reddish brown to brown

..... 20. *M. grandisetulosus*

21. Basidiospores $14.5\text{--}18 \times 3.6\text{--}4.5 \mu\text{m}$; pileus brownish orange to ferruginous

..... 21. *M. tenuisetulosus*

Taxonomy

Molecular data generated in the past decade (Wannathes et al. 2009, Tan et al. 2009, Jenkinson et al. 2014, Shay et al. 2017) have indicated that the infrageneric classification adopted by Singer (1976), Desjardin and Horak (1997), Desjardin et al. (2000), Antonín (2007) and others does not entirely reflect monophyletic groups. Two major clades are supported as monophyletic, the collariate species with insititious stipe in what can be recognized as sect. *Marasmius*, and the non-collariate species with non-insititious stipe in sect. *Globulares*.

Section *Marasmius* includes a well-supported clade currently recognized as subsect. *Marasmius* (with the type species of genus *Marasmius*, *M. rotula*), that is embedded in a paraphyletic clade historically recognized as subsect. *Sicciformes*.

Section *Globulares* includes species historically recognized as belonging to both sect. *Globulares* and sect. *Sicci*. The infrageneric series within sect. *Sicci* that were established to accommodate species with setae (ser. *Spinulosi*), simple clavate caulocystidia (ser. *Atrorubentes*), and species with glabrous stipes that have pleurocystidia (ser. *Haematocephali*) or lack pleurocystidia (ser. *Leonini*), have been shown to be non-monophyletic. To date, no formal rearrangement of species or establishment of new monophyletic infrageneric taxa supported with molecular data has been published. Until such new classification is developed, the species of *Marasmius* from São Tomé and Príncipe are herein organized in the traditional, artificial infrageneric classification to aid in identification.

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.

Description:—*Pileus* 4–7 mm diam, broadly convex, umbilicate, striate to sulcate; surface dull, dry, glabrous, pale cream (<4A3) to off-white overall with a concolorous or grayish brown (7E3–4) umbilicus. *Lamellae*, collariate, horizontal, distant (9–14) with no

lamellulae, broad (1–1.5 mm), white. *Stipe* 15–18 × 0.2 mm, central, wiry, insititious; surface dull to shiny, dry, glabrous, dark brown to black.

Basidiospores 7.2–9 × 3.5–4.0 µm [\bar{x} = 8.0 ± 0.6 × 3.8 ± 0.2 µm, Q = 2.0–2.3, Q_m = 2.11 ± 0.12, n = 10, s = 1], amygdaliform, smooth, hyaline, inamyloid, thin-walled.

Basidia 17–21 × 5.7–6.5 µm, clavate, 4-spored. *Basidioles* clavate to fusoid.

Cheilocystidia scattered, of *Rotalis*-type broom cells; main body 11.5–16 × 7–9.5 µm, broadly clavate, hyaline, inamyloid; setulae 1.5–2.5 × 0.5–1.0 µm, cylindrical, obtuse, hyaline, inamyloid, thin-walled. *Pleurocystidia* absent. *Pileipellis* not mottled, a hymeniform layer of *Rotalis*-type broom cells; main body 14–24 × 10–22.5 µm, broadly clavate to vesiculose, hyaline, inamyloid, thin-walled; setulae 1–2 × 0.5–1 µm, cylindrical, obtuse, hyaline, inamyloid, thin- to thick-walled. *Pileus trama* interwoven; hyphae 2–5 µm diam, cylindrical, hyaline, weakly dextrinoid, thin-walled. *Lamellar trama* regular; hyphae 2–5 µm diam, cylindrical, hyaline, inamyloid, thin-walled. *Stipe cortical hyphae* parallel, 3–4.5 µm diam, cylindrical, smooth, golden brown, weakly dextrinoid, thick-walled; *medullary hyphae* 3–7 µm diam, cylindrical, hyaline, inamyloid to weakly dextrinoid, thin-walled. *Caulocystidia* absent. *Clamp connections* present.

Habit, habitat and known distribution:—Solitary on undetermined dicot leaves in primary forest. Africa (Benin, Cameroon, DR Congo, Kenya, Malawi, Nigeria, São Tomé, Tanzania, Uganda), Indonesia (Java), Malaysia, Papua New Guinea, Sri Lanka, South America (Colombia).

Material examined:—AFRICA. São Tomé, Parque Nacional Obo, on trail to Lagoa Amelia, between N00°17.112', E06°35.967 and N00°16.922', E06°36.062', 14 April 2008, collected by D.E. Desjardin, DED 8246 (SFSU).

Commentary:—*Marasmius rotalis* is distinctive because of the small, sulcate, cream to off-white pileus often with a darker central spot or papilla, subdistant, collariate, non-marginate lamellae, a black insititious stipe, relatively small basidiospores, *Rotalis*-type cheilocystidia and pileipellis broom cells, and growth on dicotyledonous leaves. The

material from São Tomé matches quite closely the description of African material reported by Antonín (2007), and material from the type locality (Sri Lanka) described by Pegler (1986). São Tomé specimen DED 8246 did not yield a usable ITS sequence. Four sequences of *M. rotalis* downloaded from Genbank did not form a monophyletic group, although they did align with other members of sect. *Marasmius* subsect. *Marasmius*.

2. *Marasmius apatellus* Singer, Bull. Jard. Bot. Etat Brux. 34: 332. 1964.

Description:—*Pileus* 2–5 mm diam, broadly convex, umbilicate, with a shallow broad umbo in the umbilicus, plicate, not papillate and lacking a dark central spot; surface dull, dry, glabrous to minutely granulose, evenly pigmented tan-beige to pale grayish orange (5B3). *Lamellae* collariate, horizontal, subdistant (14–17) with no lamellulae, narrow (<1 mm), white to off-white, non-marginate. *Stipe* 7–13 × 0.1 mm, central, wiry, insititious; surface shiny, dry, glabrous, dark brown (6F7–8) to black; rhizomorphs absent.

Basidiospores 7.5–8.2 × (3.5–) 3.8–4.2 µm [$x = 7.8 \pm 0.3 \times 3.9 \pm 0.2$ µm, $Q = 1.9$ –2.1, $Q_m = 2 \pm 0.06$, $n = 7$, $s = 1$], ellipsoidal, smooth, hyaline, inamyloid, thin-walled. *Basidia* not observed. *Basidioles* 17.5–23 × 5.5–7.8 µm, cylindrical or uticate or rarely rostrate, hyaline, inamyloid, thin-walled. *Cheilocystidia* of *Rotalis*-type broom cells; abundant on gill edge, main body 11.3–28.1 × 10.5–15.6 µm, broadly clavate or inflated, hyaline or yellow, inamyloid, thin-walled; apical setulae crowded to sparse, 0.5–2.8 × 0.5–1.3 µm, cylindrical, apex obtuse to subacute, hyaline or pale yellow, thin-walled. *Pleurocystidia* absent. *Pileipellis* a hymeniform layer of *Rotalis*-type broom cells; abundant, main body 11.5–20 (–30) × 6–17.5 (–20) µm, clavate to broadly clavate, inflated, or rarely cylindrical, hyaline, inamyloid, thin-walled; apical setulae crowded to sparse, 1.7–4.5 × 0.5–1.6 µm, cylindrical, apex subacute, hyaline or pale yellow, inamyloid, thin-walled; rare inflated cells with no setulae, other characters of these cells the same. *Pileus trama* interwoven; hyphae 2.5–6.5 µm diam, cylindrical, hyaline, inamyloid, thin-walled. *Lamellar trama* interwoven; hyphae 2–6 µm diam, cylindrical,

hyaline, inamyloid, thin-walled. *Stipe cortical hyphae* 2.8–5.3 μm diam, cylindrical, parallel, brown to yellowish brown, dextrinoid, thick-walled; *medullary hyphae* 3.8–6.1 μm diam, cylindrical, parallel, hyaline, inamyloid, thin-walled. *Caulocystidia* absent. *Clamp connections* present.

Habit, habitat and known distribution:—Gregarious on undetermined dicot leaves in secondary forest. Africa (DR Congo, Príncipe, Tanzania, Uganda), Thailand.

Material examined:—AFRICA. Príncipe, Roça Pico Papagaio, N01°37.182', E07°23.474', 21 April 2008, collected by B.A. Perry, DED 8295 (SFSU; KX953762).

Commentary:—*Marasmius apatelius* is characterized by small, umbilicate, plicate, beige-brown pilei often lacking a papilla, subdistant to distant, collariate lamellae, a short, wiry, insititious stipe, relatively small basidiospores, *Rotalis*-type cheilocystidia and pileipellis broom cells, and growth on dicotyledonous leaves. The Príncipe specimen matches material reported from Thailand (Wannathes et al. 2009) and Madagascar (Shay et al. 2017) and differs from other African specimens by forming more lamellae (14–17 v.s. 9–12) (Antonín 2007). The Príncipe specimen (KX953762) belongs in a grade with other *M. apatelius* specimens at the base of sect *Marasmius* subsect. *Marasmius*.

3. *Marasmius colorimarginatus* Antonín, Mycotaxon 88: 57. 2003.

Description:—*Pileus* 4–12 mm diam, broadly convex to plano-convex, umbilicate, with or without a low, broad umbo in the umbilicus, not papillate, sulcate to plicate; surface dull, dry, glabrous, evenly pigmented light brown (6–7D4) to brown (7D–E5–6) or with a slightly darker umbo. *Odor* indistinct. *Lamellae* collariate, horizontal, distant (13–18)

with no lamellulae, moderately broad (1–2 mm), white to dingy tan, beige or cream-buff, non-marginate or with brown edges. *Stipe* 15–32 × 0.5–0.1 mm, central, cylindrical, wiry, insititious; surface shiny, dry, glabrous, dark brown (6F6–8) to black overall; rhizomorphs absent.

Basidiospores (7.6–) 8.5–9 (–10.2) × 4.3–5.1 µm [$x_{mr} = 8.5\text{--}9.4 \times 4.5\text{--}4.7$ µm, $x_{mm} = 9 \pm 0.7 \times 4.6 \pm 0.1$ µm, $Q_{mr} = 1.8\text{--}2.1$, $Q_{mm} = 1.94 \pm 0.2$, $n = 28$, $s = 2$], narrowly ellipsoid to broadly ellipsoid, smooth, hyaline, inamyloid, thin-walled. *Basidia* not observed. *Basidioles* cylindrical, hyaline, inamyloid, thin-walled. *Cheilocystidia* of *Rotalis*-type broom cells; diffuse, main body 6.4–27.2 × 7.8–22 µm, cylindrical to broadly cylindrical, inflated, or clavate to broadly clavate, yellow or yellowish brown, inamyloid, thin-walled or occasionally thick-walled; apical setulae crowded, small, 0.5–2.4 × 0.5–1.2 µm, cylindrical, apex subobtuse to obtuse, yellow to yellowish brown, inamyloid, thin-walled. *Pleurocystidia* absent. *Pileipellis* a hymeniform layer of *Rotalis*-type broom cells; main body 8–15 × 8–23 µm, clavate to broadly clavate, inflated, or prostrate-cylindrical with setulae arising laterally, rarely lobed, hyaline or yellowish brown to olive, inamyloid, thin-walled; setulae crowded, small, 0.5–3.2 × 0.8–2 µm, cylindrical, apex obtuse; hyaline or yellowish brown to olive, inamyloid, thin-walled. *Pileus trama* interwoven; hyphae 1.5–7.2 µm diam, cylindrical to subinflated, hyaline, inamyloid, thick-walled. *Lamellar trama* interwoven; hyphae 2.4–20 µm diam, cylindrical to subinflated, hyaline, inamyloid, thin-walled. *Stipe cortical hyphae* 3.2–5.6 µm diam, cylindrical, parallel, hyaline or yellow, dull greenish yellow to olive, dextrinoid, thick-walled; *medullary hyphae* 4.5–13 µm diam, cylindrical, parallel, hyaline, inamyloid or dextrinoid, thin-walled. *Caulocystidia* absent. *Clamp connections* present.

Habit, habitat and known distribution:—Gregarious on undetermined dicotyledonous leaves or woody twigs in secondary or primary forests. Africa (Cameroon, Príncipe).

Material examined:—AFRICA. Príncipe, Roça Pico Papagaio, N01°37.182', E07°23.474', 21 April 2008, collected by B.A. Perry, DED 8293 (SFSU; KX953746). Príncipe, south side of island at Rio São Tomé, N01°33'40.54", E07°21'15.51", 22 April 2008, collected by B.A. Perry, DED 8309 (SFSU; KX953745).

Commentary:—*Marasmius colorimarginatus* is characterized by small, brown, plicate pilei lacking a central papilla, distant (13–18), collariate lamellae usually with brown edges, a dark brown, wiry, insititious stipe with cortical hyphae greenish yellow to olive in KOH, basidiospores in the range $8\text{--}10 \times 4.5\text{--}5 \mu\text{m}$, *Rotalis*-type cheilocystidia and pileipellis broom cells, and growth on dicot leaves and twigs. Antonín (2003b, 2007) described the lamellae as intervenose, which is observed in dried basidiomes of DED8309 but not in DED8293 nor in fresh material of either. Otherwise, the Príncipe material is indistinguishable from the protologue. ITS sequences of the Príncipe specimens (KX953745, KX953746) fall into a clade with other members of sect. *Marasmius* subsect. *Marasmius*.

Ib. subsect. *Sicciformes*

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

4. *Marasmius* aff. *guyanensis* Mont., Ann. Sci. Nat. Bot., sér. 4, 1: 114. 1854.

Description:—*Pileus* 3–4 mm diam, convex, umbilicate, sulcate, papilla absent; surface dull, dry, subvelutinous, deep reddish orange to brownish orange (7B–C6–8) overall, fading in age to brownish orange (6C6–8) with a brown central dot. *Lamellae* collariate, distant (7–8) with no lamellulae, moderately broad (–1 mm), creamy white, non-marginate. *Stipe* 18–25 × 0.1 mm, central, wiry, insititious; surface shiny, dry, glabrous, black; rhizomorphs scattered.

Basidiospores 12.5–15 × 3.5–4.5 µm [$x = 13.8 \pm 0.8 \times 4.0 \pm 0.3$ µm, $Q = 3.0$ –3.9, $Q_m = 3.45 \pm 0.3$, $n = 21$, $s = 1$], narrowly lacrimoid (subcylindrical with suprahilar depression), smooth, hyaline, inamyloid, thin-walled. *Basidia* not observed. *Basidioles* cylindrical, apex obtuse, truncate, or subacute. *Cheilocystidia* abundant, *Siccus*-type broom cells; main body 5.6–19.2 × 4.8–11.2 µm, cylindrical or clavate, rarely lobed, pale yellow or yellow brown to light brown, inamyloid, thin-walled, some thick-walled with darker pigmentation; apical setulae 0.4–4.8 × 0.4–2 µm, cylindrical or broad knobs, apex obtuse or subacute, pale yellow or yellow brown to light brown, inamyloid, thin-walled or thick-walled. *Pleurocystidia* absent. *Pileipellis* very diffusely mottled, composed of a hymeniform layer of *Siccus*-type broom cells; main body 8–20 × 5.6–9.6 µm, cylindrical or clavate to broadly clavate, sometimes inflated, often lobed, hyaline to yellowish brown, inamyloid, thin-walled or thick-walled; apical setulae 0.4–2.6 × 0.4–1.6 µm, rarely forked, cylindrical or knobby, apex obtuse to acute, yellowish brown, inamyloid to very weakly dextrinoid, thick-walled. *Pileus trama* interwoven, hyphae 3.2–7.5 µm diam., cylindrical, hyaline, inamyloid to very weakly dextrinoid, thin-walled. *Lamellar trama* interwoven, hyphae 2.8–5 µm diam., cylindrical, hyaline, weakly dextrinoid, thin-walled. *Stipe cortical hyphae* 2.4–7 µm diam., parallel, cylindrical, smooth, light brown to golden brown or brownish yellow, strongly dextrinoid, thick-walled; *medullary hyphae* 4.4–9.6 µm diam., parallel, cylindrical, smooth, hyaline, inamyloid, thin-walled. *Caulocystidia* absent. *Clamp connections* present.

Habit, habitat and known distribution:—Densely gregarious on leaves of undetermined dicots, in secondary forest. Africa (Benin, Cameroon, Democratic Republic

of the Congo, Nigeria, Príncipe, Sierra Leone, Togo), Indonesia (Java), Malaysia (Selangor), South America (Brazil, Bolivia, French Guyana, Trinidad, Venezuela), Thailand.

Material examined:—AFRICA. Príncipe, along road to Roça Pico Papagaio, N01°38.600', E07°23.827', 21 April 2008, collected by B.A. Perry and D. E. Desjardin, DED 8285 (SFSU; KX953747).

Commentary:—*Marasmius* aff. *guyanensis* is distinguished by a reddish orange, brownish orange or yellowish orange pileus with or without a dark central spot or small papilla; distant (6–10), collariate, non-marginate lamellae; a black, glabrous, insititious stipe associate with scattered rhizomorphs; moderately long basidiospores in the range $12.5\text{--}15 \times 3.5\text{--}4.5 \mu\text{m}$; *Siccus*-type cheilocystidia and pileipellis broom cells; no pleurocystidia or caulocystidia; and growth in dense troops on dead leaves. The specimen from Príncipe differs from *M. guyanensis* reported from Southeast Asia (Tan et al 2009; Wannathes et al 2009) in forming more deeply pigmented pilei and slightly longer basidiospores, but compares nicely with other African specimens reported by Antonín (2007) and Indonesian populations (Desjardin et al 2000). An ITS sequence of DED 8285 (KX953747) places the taxon in a clade with ITS sequences of *M. guyanensis* derived from material collected in Thailand (EU935552, EU935553), but distinct from sequences of *M. guyanensis* from Malaysia (FJ431246, FJ431247). Until more material becomes available for study, and compared with material from Guyana (type locality), we will refer to the African taxon as *M. aff. guyanensis*.

5. *Marasmius subruforotula* Singer, Bull. Jard. Bot. Etat Brux. 34: 339. 1964.

Description:—*Pileus* 3–6 mm diam, convex to plano-convex, umbilicate, with a tiny acute papilla, sulcate to plicate; surface dull, dry, subvelutinous, deep reddish brown (9–

10D–E8) to reddish brown (9D7–8) overall with a dark reddish brown to black papilla. Lamellae collariate, horizontal, distant (9–12) with no lamellulae, broad (1–1.5 mm), white with reddish orange (8B7–8) to deep red (9C–D7–8) edges. Stipe 18–40 × 0.1–0.2 mm, central, wiry, insititious; surface shiny, dry, glabrous, dark brown (6F8) to black; associated with a few, thin (≤ 0.1 mm), dark brown to black rhizomorphs, but not arising from them.

Basidiospores 8.2–9 (–9.6) × (4.2–) 4.6–5.2 (–5.6) μm [$x_{\text{mr}} = 8.8\text{--}9 \times 4.8\text{--}5 \mu\text{m}$, $x_{\text{mm}} = 8.9 \pm 1.4 \times 4.9 \pm 0.1 \mu\text{m}$, $Q_{\text{mr}} = 1.8\text{--}1.9$, $Q_{\text{mm}} = 1.83 \pm 0.07$, $n = 41$, $s = 2$], ellipsoid or limoniform, smooth, hyaline, inamyloid, thin-walled. *Basidia* not observed. *Basidioles* cylindrical, apex obtuse. *Cheilocystidia* abundant, of *Siccus*-type broom cells; main body 8.8–28 × 4.4–13 μm , cylindrical, clavate to broadly clavate, or inflated, rarely lobed, hyaline or pale yellow to brownish yellow, inamyloid, thin-walled; apical setulae crowded, 0.5–9.6 × 0.5–1.6 μm , rarely forked, cylindrical, apex obtuse to subacute, pale yellow or yellow to brownish yellow, inamyloid, thin-walled. *Pleurocystidia* absent. *Pileipellis* a hymeniform layer of *Siccus*-type broom cells with scattered smooth or knobby thick-walled cells; main body 8–24 × 4–12 μm , cylindrical or clavate to broadly clavate, often lobed, hyaline or yellow to dull yellowish brown, inamyloid, thin-walled; apical setulae crowded, 0.5–8.8 × 0.5–2.6 μm , cylindrical, apex obtuse to subacute, yellow to dull yellowish brown, inamyloid, mostly thin-walled; smooth or knobby cells with or without a few knob-like or partially formed setulae, forming apically or laterally from cell, yellowish brown, weakly dextrinoid, thick-walled (–1.2 μm). *Pileus trama* interwoven, hyphae 3–8.2 μm diam., cylindrical, hyaline, inamyloid, thin-walled. *Lamellar trama* interwoven, hyphae 1.6–16 μm diam, cylindrical, hyaline, inamyloid, thin-walled. *Stipe cortical hyphae* 2.2–5.6 μm diam, cylindrical, parallel, yellow to golden brown, strongly dextrinoid, thick-walled; *medullary hyphae* 3.8–8.8 μm diam, cylindrical, parallel, hyaline, dextrinoid, thin-walled. *Caulocystidia* absent. *Clamp connections* present.

Habit, habitat and known distribution:—Solitary on undetermined dicot leaves in

native primary or secondary forests. Africa (Benin, Cameroon, DR Congo, Nigeria, Príncipe, Tanzania, Uganda), Madagascar, Thailand.

Material examined:—AFRICA. Príncipe, Roça Pico Papagaio, N01°37.182', E07°23.474', 21 April 2008, collected by D.E. Desjardin, DED 8296 (SFSU; KX953739); Príncipe, south side of island at Rio São Tomé, N01°33'40.54", E07°21'15.51", 22 April 2008, collected by B.A. Perry, DED 8307 (SFSU; KX953738).

Commentary:—*Marasmius subruforotula*, described from the Democratic Republic of the Congo, has a small pileus with chestnut brown to deep reddish brown center, reddish orange to reddish brown margin and a distinct conical papilla; distant (8–14), reddish orange-marginate lamellae; a relatively long, black, glabrous, insititious stipe associated with dark brown rhizomorphs; small basidiospores in the range $8.2\text{--}9.6 \times 4.2\text{--}5.6 \mu\text{m}$; *Siccus*-type cheilocystidia and pileipellis broom cells with a few scattered coralloid cells; and growth on dicotyledonous leaves. The Príncipe specimens differ only subtly from material reported throughout Africa (Antonín 2007) in having more deeply pigmented reddish brown pilei. ITS sequences of the Príncipe specimens (KX953737, KX953738) are sister to three sequences of *M. cf. subruforotula* (KX149017–KX149019) reported from Madagascar (Shay et al. 2017) with 100% BS and 1.0 PP support.

6. *Marasmius segregatus* C.L. Grace, Desjardin & B.A. Perry *sp. nov.*

MycoBank no.: MB 829075

Holotype:—AFRICA. São Tomé, along main road (EN-1) on north side of island at 18.25 km marker, Shipwreck Cove, N00°23.687', E06°36.302', 17 April 2008,

collected by D.E. Desjardin, DED 8256 (SFSU).

Etymology:—*segregatus*—set apart, isolated, referring to the isolated position of the species in the phylogenetic tree and its isolation on the island of São Tomé.

Description:—*Pileus* 5–8 mm diam, convex to broadly convex, umbilicate, papilla absent, sulcate to plicate; surface dull, dry, granulose to subvelutinous, ferruginous (7C7) to brownish orange (6C7–8), reddish brown (8D6–8) or maroon to ruby (11–12E7–8). *Context* <0.5 mm thick, white. *Odor* and *taste* indistinct. *Lamellae* collariate, horizontal, distant (9–14) with no lamellulae or rarely one lamellula, broad (–2 mm), white to creamy white, seldom with a hint of pink, with brownish orange to reddish brown edges. *Stipe* 20–40 × 0.2 mm, central, wiry, tough, insititious; surface dull to shiny, dry, glabrous, dark brown to black; rhizomorphs not observed.

Basidiospores 8.5–12 (–12.5) × 5.2–6.5 (–7) μm [$x_{\text{mr}} = 10.4\text{--}10.9 \times 5.7\text{--}6.1 \mu\text{m}$, $x_{\text{mm}} = 10.7 \pm 0.9 \times 5.9 \pm 0.3 \mu\text{m}$, $Q_{\text{mr}} = 1.77\text{--}1.83$, $Q_{\text{mm}} = 1.80 \pm 0.05$, $n = 41$, $s = 2$], broadly ellipsoid, smooth, hyaline, inamyloid, thin-walled. *Basidia* 19–25 × 7–8.5 μm , clavate, 4-spored. *Basidioles* clavate. *Cheilocystidia* abundant, lamellar edge mostly sterile, of *Siccus*-type broom cells; main body 11.2–21 × 6.2–12 μm , subcylindrical to clavate, seldom lobed, hyaline, inamyloid, thin-walled; apical setulae 2–6 × 1–2.5 μm , subconical, knobby, broadly obtuse, hyaline to pale yellow or golden brown, inamyloid, thick-walled. *Pleurocystidia* absent. *Pileipellis* slightly mottled, a hymeniform layer of *Siccus*-type broom cells; main body 6–21 × 6–12 μm , clavate to irregular in outline, seldom lobed, hyaline to pale yellowish brown or pale orange, inamyloid, thin-walled to apically thick-walled; apical setulae 2–5 × 1.2–2 μm , obtusely conical, often forked yellowish brown, inamyloid, thick-walled; with a few, scattered, thicker-walled cells with fewer setulae or completely smooth and thick-walled. *Pileus trama* interwoven; hyphae 2.5–7 μm diam, cylindrical to irregular, hyaline, weakly dextrinoid, thin-walled.

Lamellar trama regular, 3–6.6 μm diam, interwoven, cylindrical, hyaline, weakly dextrinoid, thin-walled. *Stipitipellis* composed of parallel *cortical hyphae* 2.5–5 μm diam, cylindrical, smooth, brown, dextrinoid, thick-walled; geniculate terminal cells on some cortical hyphae; *medullary hyphae* 3–7 μm diam, cylindrical, hyaline, dextrinoid. *Caulocystidia* absent. *Clamp connections* present in all tissues.

Habit, habitat and known distribution:—Solitary to densely gregarious on woody debris in coastal secondary forest. São Tomé.

Material examined:—AFRICA. São Tomé, along main road (EN-1) on north side of island at 18.25 km marker, Shipwreck Cove, N00°23.687', E06°36.302', 17 April 2008, collected by D.E. Desjardin, DED 8255 (SFSU) and DED 8256 (Holotype, SFSU; KX953761).

Commentary:—*Marasmius segregatus* is characterized by a small, brownish orange to reddish brown pileus with or without a central brown spot but lacking a distinct papilla; distant (9–14), brownish orange-marginate lamellae; a black, glabrous, insititious stipe not associated with rhizomorphs; basidiospores in the range $8.5\text{--}12.5 \times 5.2\text{--}6.5 \mu\text{m}$ (mean $10.7 \times 5.9 \mu\text{m}$); *Siccus*-type cheilocystidia $11.2\text{--}21 \times 6.2\text{--}12 \mu\text{m}$; similar pileipellis broom cells with scattered thick-walled coralloid cells; no pleurocystidia or caulocystidia; and growth on dead wood. This new species shows morphological similarities to the difficult *Marasmius ruforotula/subruforotula* species complex, although ITS data place the taxon in an isolated position adjacent to *M. straminiceps* Wannathes, Desjardin & Lumyong and *M. cafeyen* Wannathes, Desjardin & Lumyong but with low support.

Marasmius subruforotula Singer, described from the Democratic Republic of the Congo and reported here from Príncipe is similar, but differs in a pileus with grey to chestnut brown or deep reddish brown center, reddish orange to orange margin and a distinct conical papilla, slightly smaller basidiospores ($8.2\text{--}9.6 \times 4.2\text{--}5.6 \mu\text{m}$), and

growth on dead leaves. ITS sequences of *Marasmius segregatus* (KX953761) and *M. subruforotula* from Príncipe are only 89.44% similar.

Marasmius ruforotula Singer differs in forming paler pilei with a distinct acute papilla, lacks smooth, thick-walled pileipellis cells, and grows on dead leaves (Tan et al 2009; Wannathes et al 2009). ITS sequence comparisons between *Marasmius segregatus* and specimens of *M. ruforotula* from Thailand (FJ431269, FJ431270) are 95.2–96.4% similar.

Marasmius lovedalensis Antonín & Verbeken, known from Zimbabwe, grows on woody debris, but differs in forming a smaller (2–5 mm), orange pileus, non-marginate lamellae, and larger basidiospores $11\text{--}14.5 \times 4.5\text{--}6 \mu\text{m}$ (Antonín 2007). No sequences are available for comparison.

The New World *Marasmius praecox* Singer, described from Argentina, shows many phenetic similarities to *Marasmius segregatus*, but it has black rhizomorphs associated with the basidiomes and slightly smaller basidiospores ($7\text{--}9.5 \times 4.7\text{--}5.3 \mu\text{m}$) (Singer 1976). No sequences are available for comparison.

II. sect. *Globulares*

Marasmius sect. *Globulares* Kühner, Botaniste 25: 100. 1933.

= *Marasmius* sect. *Sicci* Singer, Mycologia 50: 106. 1958. – Type species:

Marasmius siccus (Schwein.) Fr.

– Type species: *Marasmius globularis* Fr. (= *Marasmius wynnei* Berk. & Broome)

A. Species with non-setulose *Globulares*-type pileipellis cells:

IIa. ser. *Globulares*

7. *Marasmius laranja* C.L. Grace, Desjardin & B.A. Perry *sp. nov.*

MycoBank no.: **xxxxxx**

Holotype:—AFRICA. São Tomé, Parque Nacional Obo, on trail to Lagoa Amelia, approx. 1300 m elev., between N00°17.112', E06°35.967 and N00°16.922', E06°36.062', 14 April 2008, collected by D.E. Desjardin, DED 8231 (SFSU).

Etymology:—*laranja*—orange in Portuguese, referring to the color of the pileus and lamellae.

Description:—*Pileus* 10–35 mm diam, convex to plano-convex, sulcate to plicate to the depressed, rugulose disc, margin crenate in age; surface dull, moist to dry, glabrous, hygrophanous, at first deep orange (5A6–8) overall, in age disc brownish orange (6C5–8), margin orange to yellowish brown (5E4–5), fading to pale orangish white (5A2–3) or cream (4A3) with moisture loss. *Context* <1 mm thick. *Odor* indistinct. *Lamellae* horizontal, adnexed, distant (14–17) with 2 series of lamellulae, broad (3–5 mm), deep orange (6A–C7–8), non-marginate. *Stipe* 55–75 × 1–2 mm, central, cylindrical, tough, hollow, non-insititious with cream-buff (4A3) to brownish orange (6C5–6) basal mycelium; surface dull, dry, appressed-pubescent overall, apex pale brownish gray (6C3) to grayish brown (6D3), base brown (7D4).

Basidiospores 24–26 × 4.8–5.5 µm [$x = 24.8 \pm 1.0 \times 5.0 \pm 0.24$ µm, $Q = 4.2$ –5.0, $Q_m = 4.87 \pm 0.37$, $n = 8$, $s = 1$], clavate, slightly curved, hyaline, inamyloid, thin-walled.

Basidia not observed. *Basidioles* $34\text{--}48 \times 8\text{--}9.5 \mu\text{m}$, clavate to subclavate or subfusoid. *Cheilocystidia* abundant, lamellar edge sterile, $17\text{--}32 \times 7\text{--}18 \mu\text{m}$, broadly clavate to nearly sphaeropedunculate (never nodulose, lobate or subcoralloid), hyaline, inamyloid, thin-walled. *Pleurocystidia* absent. *Pileipellis* a hymeniform layer of broadly clavate cells, $16\text{--}28 \times 8\text{--}19 \mu\text{m}$, hyaline, inamyloid, thin-walled. *Pileus trama* composed of interwoven hyphae $3\text{--}10 \mu\text{m}$ diam, cylindrical, smooth, hyaline, strongly dextrinoid. *Lamellar trama* regular, hyphae as in pileus trama. *Stipitipellis* composed of a loose layer of hyphae $3\text{--}10 \mu\text{m}$ diam, cylindrical, smooth or roughened-incrusted, hyaline, giving rise to numerous terminal caulocystidia; *caulocystidia* $30\text{--}65 \times 7\text{--}15 \mu\text{m}$, cylindrical to clavate, hyaline, inamyloid, thin-walled or slightly thick-walled. *Stipe cortical hyphae* $3\text{--}10 \mu\text{m}$ diam, cylindrical, parallel, smooth or roughened, hyaline to pale brown, dextrinoid, thin- to thick-walled; *medullary hyphae* $3\text{--}13 \mu\text{m}$ diam, strongly dextrinoid. *Clamp connections* present in all tissues.

Habit, habitat and known distribution:—Solitary on woody debris in primary forest. São Tomé.

Material examined:—AFRICA. São Tomé, Parque Nacional Obo, on trail to Lagoa Amelia, approx. 1300 m elev., between N00°17.112', E06°35.967 and N00°16.922', E06°36.062', 14 April 2008, collected by D.E. Desjardin, DED 8231 (Holotype, SFSU; KX953748).

Commentary:—*Marasmius laranja* is characterized by the following features: a moderately large, sulcate, deep orange, hygrophamous pileus; distant, broad, non-collariate, non-intervenose, deep orange lamellae; a relatively slender, pubescent, grayish brown stipe; large basidiospores with mean $24.8 \times 5.0 \mu\text{m}$; long basidioles (up to $48 \mu\text{m}$); no pleurocystidia; small, broadly clavate cheilocystidia; a typical *Globulares*-type pileipellis; abundant cylindrical to clavate caulocystidia; and growth on woody debris in primary forests.

The most similar species that shares an orange pileus and deep orange lamellae is *Marasmius portentosus* Antonín & DeKesel, described recently from Benin (Antonín 2013). The latter species differs, however, in forming a smaller pileus (only up to 10 mm broad), more lamellae (17–19), a yellowish orange to greenish yellow stipe, smaller basidiospores (mean $18.2 \times 4.3 \mu\text{m}$), and mostly irregular cheilocystidia (lobate, subcoralloid or with a few projections). Two additional species described from the Democratic Republic of the Congo are also similar. *Marasmius tshopoensis* Antonín differs in a yellowish ochraceous, striped pileus, yellowish white, strongly intervenose lamellae, irregular cheilocystidia and lacks conspicuous caulocystidia (Antonín 2003a, 2007). *Marasmius missangoensis* Pat. differs in a rufous-colored pileus, putatively pallid lamellae, a more robust ($120 \times 5\text{--}6 \text{ mm}$), brownish black stipe, and broader basidiospores ($5.5\text{--}7 \mu\text{m}$) (Antonín 2007). An ITS of *M. laranja* (KX953748) holds an isolated position at the base of a clade composed of species with *Siccus*-type pileipellis cells.

B. Species with setulose *Siccus*-type pileipellis cells:

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

Ilb.** ser. *Spinulosi***

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

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

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

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

8. *Marasmius atrorubens* (Berk.) Mont., Ann. Sci. Nat. Bot., sér 4, 1: 118. 1854.

sensu Antonín, Fung. Fl. Trop. Africa 1: 85. 2007.

Description:—*Pileus* 15–24 mm diam, campanulate to broadly convex, expanding to plano-convex, margin smooth (not striate); surface dull, dry, subvelutinous, canescent with a white bloom, disc light brown (6D6–8) to brown (7E7–8), margin brownish orange (6C5–6), mottled with pallid spots. *Context* 0.5 mm thick, white. *Odor* indistinct. *Lamellae* horizontal, adnexed to shallowly adnate, crowded (24–35) with 4–5 series of lamellulae, narrow (1–1.5 mm), off-white to pale cream (<4A3), non-marginate. *Stipe* 30–38 × 1 mm, central, cylindrical, tough, hollow, non-insititious with orangish white (5A3) basal tomentum; surface dull, dry, reddish brown-pruinose, apex yellowish white (4A2) to brownish orange (6C6), base reddish brown (8E6–8).

Basidiospores (13.6) 14–15.2 × 4.2–4.8 µm [$x = 14.2 \pm 0.6 \times 4.5 \pm 0.3$ µm, $Q = 2.8$ –3.4, $Q_m = 3.15 \pm 0.15$, $n = 12$, $s = 1$], lacrimoid, widest closer to base, smooth, hyaline, inamyloid, thin-walled. *Basidia* not observed. *Basidioles* clavate to subfusoid, apex obtuse. *Cheilocystidia* of *Siccus*-type broom cells; main body 4–13.6 × 3–7.2 µm, cylindrical, hyaline or yellow, inamyloid or weakly dextrinoid, thin-walled; apical setulae non-crowded, 2–9.6 × 0.4–2.4 µm, cylindrical, apex subacute, hyaline or yellow, inamyloid to weakly dextrinoid, thin-walled. *Pleurocystidia* common, reflective, cylindrical to substrangulate, hyaline, 33–40 × 5.5–9 µm. *Pileipellis* mottled, a hymeniform layer of *Siccus*-type broom cells; main body 4.8–28 × 4–15.2 µm, cylindrical to clavate, often lobed, mostly hyaline thin-walled broom cells interspersed with larger yellow to brownish yellow larger thick-walled broom cells, inamyloid or

weakly dextrinoid; apical setulae sparse to crowded, $1.8\text{--}11.2 \times 0.6\text{--}4.8\text{ }\mu\text{m}$, cylindrical to conical, small thin-walled setulae on small broom cells, sometimes forked, hyaline, weakly dextrinoid; large thick-walled setulae on large darker pigmented broom cells, inamyloid. *Pileosetae* $25.5\text{--}51 \times 4.8\text{--}15.2\text{ }\mu\text{m}$, cylindrical to broadly cylindrical base tapering to a cylindrical or conical tip, apex subacute to acute, yellow to brownish yellow, inamyloid, thick-walled $1.2\text{--}1.6\text{ }\mu\text{m}$. *Pileus trama* interwoven; hyphae $2.2\text{--}14.4\text{ }\mu\text{m}$ diam, cylindrical, hyaline, dextrinoid, thin-walled. *Lamellar trama* interwoven; hyphae $2.6\text{--}12.8\text{ }\mu\text{m}$, cylindrical, hyaline, dextrinoid, thin-walled. *Stipitipellis* giving rise to numerous *Siccus*-type broom cells; *cortical hyphae* $2.8\text{--}8.8\text{ }\mu\text{m}$ diam, cylindrical, parallel, yellow or greenish yellow, weakly dextrinoid, thick-walled; *medullary hyphae* cylindrical, parallel, hyaline, strongly dextrinoid, thin-walled. *Caulocystidia* scattered, $10.4\text{--}20 \times 4.4\text{--}9.6\text{ }\mu\text{m}$, cylindrical or forming setulae from prostrate hyphae, hyaline or yellow to brownish yellow, inamyloid, thin-walled or thick-walled; *setulae* cylindrical, $1.4\text{--}29.6 \times 1.2\text{--}3.6\text{ }\mu\text{m}$, hyaline or yellow to brownish yellow, inamyloid, thin-walled or thick-walled. *Caulosetae* $12\text{--}60 \times 5.8\text{--}8.2\text{ }\mu\text{m}$, cylindrical to irregularly cylindrical base, often forming lobes and forking, upper portion cylindrical or irregularly cylindrical, $3.6\text{--}4 \times 2\text{--}4.4\text{ }\mu\text{m}$, apex subacute to acute, yellow to brownish yellow, inamyloid, thick-walled $2\text{ }\mu\text{m}$.

Habit, habitat and known distribution:—Solitary on woody debris in coastal cacao and banana grove. Africa (Benin, Burundi, Cameroon, DR Congo, Niger, São Tomé, Tanzania, Uganda).

Material examined:—AFRICA. São Tomé, along main road (EN-1) on west side of island at 33 km marker, N00°19.607', E06°30.666', 18 April 2008, collected by B.A. Perry and D.E. Desjardin, DED 8263 (SFSU; KX953751).

Commentary:—Distinctive features of *M. atrorubens* sensu Antonín include a brown to brownish orange, mostly non-striate pileus, close, narrow, non-marginate lamellae, a pruinose, reddish brown, non-insititious stipe, moderately long basidiospores,

refractive pleurocystidia, and a pileipellis and stipitipellis with *Siccus*-type broom cells, setae, and cells transitional between broom cells and setae.

Many features of DED 8263 match those reported for *M. nummularius* Berk. & Broome from Thailand (Wannathes et al. 2009), Madagascar (Shay et al. 2017), and Indonesia (Desjardin et al. 2000), but the latter forms basidiomes with fewer lamellae (12–18), lacks pleurocystidia, has longer pileosetae and caulosetae (up to 100+ μm), and grows on dicotyledonous leaves. Basidiospore size, non-marginate lamellae and stipitipellis morphologies are otherwise similar. An ITS sequence of DED 8263 (KX953751) is quite distant from several sequences of *M. nummularius* from Thailand (EU935492, EU935493) and Madagascar (KX148979).

Antonín's (2007) description of *M. atrorubens* is most phenetically similar to the São Tomé specimen, differing only in fewer lamellae (14–20), slightly shorter basidiospores (11–14 (–18) μm), and growth on dicotyledonous leaves. Because of the proximity of São Tomé to mainland tropical Africa and the widespread occurrence of *M. atrorubens* sensu Antonín in Africa, we tentatively identify our material as *M. atrorubens*.

It should be noted that *M. atrorubens* was described from Surinam (South America; Montagne 1854), and a type study by Desjardin (unpubl.) shows a species different from that reported from Africa—viz., with a pileipellis lacking pileosetae, and a stipe lacking branched caulosetae and *Siccus*-type broom cells. Indeed, Desjardin and Horak (1997) established ser. *Atrorubentes*, based on *M. atrorubens*, as an assemblage of species that lack pileosetae and caulosetae, and have cylindrical to clavate or acuminate caulocystidia, lacking *Siccus*-type broom cells on the stipe. Until material from the vicinity of Surinam is sequenced and compared with African material reported as *M. atrorubens*, the identity of African material will remain problematical. We suspect that the São Tomé specimen and other specimens reported from Africa as *M. atrorubens* represent a species distinct from the South American taxon, and are more morphologically similar to members of ser. *Spinulosi* than to those of ser. *Atrorubentes*.

An ITS sequence of DED 8263 places *M. atrorubens* sensu Antonín as sister to *M. confertus* var. *tenuicystidiatus* Antonín and *M. occultatus* Har. Takah. but with low support.

9. *Marasmius trichotus* Corner, Beih. Nova Hedwigia 111: 102. 1996.

Description:—*Pileus* 5–10 mm diam, obtusely conical to convex, expanding to plano-convex, seldom shallowly depressed, disc smooth to rugulose, margin smooth to weakly striatulate; surface dull, dry, subvelutinous, orange (6A–B7–8) overall when young, in age disc brownish orange (7C6–7), margin pale brownish orange (6C5–7) to golden yellow (5B6–7), orange (5A6) or pale orange (5A3–4). *Context* <0.5 mm thick, white. *Odor* indistinct. *Lamellae* horizontal, adnexed, subdistant to close (12–16) with 2 series of lamellulae, moderately broad (–1 mm), white, non-marginate. *Stipe* 15–30 × 0.75–1.25 mm, central, cylindrical, tough, non-insititious with radiating-stigose cream-orange (4–5A3) basal mycelium; surface dull, dry, hispidulous to hispid overall, apex white to pale orangish white (5A2), centrally orangish white (5A2–3), base orangish white to pale brownish orange (6C4–6).

Basidiospores 10.4–12 (–12.6) × 3.7–4.4 (–4.6) μm [$x = 11.3 \pm 0.7 \times 4.1 \pm 0.2$ μm , $Q = 2.4\text{--}3.2$, $Q_m = 2.76 \pm 0.24$, $n = 38$, $s = 1$], elongate-lacrimoid, smooth, hyaline, inamyloid, thin-walled. *Basidia* not observed. *Basidioles* cylindrical, some rostrate, apex subacute, hyaline, inamyloid, thin-walled. *Cheilocystidia* abundant, of *Siccus*-type broom cells; main body 12.8–20 × 4.8–8.5 μm , cylindrical or clavate, some lobed, hyaline, inamyloid, thin-walled; apical setulae crowded, 2.4–8.8 × 0.5–1.4 μm , cylindrical, rarely forked, apex subacute to acute, greenish yellow or grayish yellow, inamyloid, thin-walled. *Pleurocystidia* absent. *Pileipellis* very weakly mottled, a hymeniform layer of

Siccus-type broom cells; main body $8.8\text{--}20 \times 3.2\text{--}10.4 \mu\text{m}$, cylindrical to broadly cylindrical or narrowly clavate to broadly clavate, some lobed, pale yellow or cream, inamyloid or weakly dextrinoid, thin-walled or rarely thick-walled; apical setulae crowded, $0.5\text{--}8.4 \times 0.5\text{--}2.6 \mu\text{m}$, cylindrical or irregularly cylindrical, rarely forked, apex obtuse to subacute, pale yellow or cream, inamyloid or weakly dextrinoid, thin-walled or rarely thick-walled. *Pileosetae* $57\text{--}125 \times 9.6\text{--}12 \mu\text{m}$, cylindrical at base, lanceolate above, apex subacute to acute, yellow, inamyloid, thick-walled ($\sim 1.8 \mu\text{m}$). *Pileus trama* interwoven; hyphae $2.4\text{--}8 \mu\text{m}$ diam, cylindrical, hyaline, dextrinoid, thin-walled. *Lamellar trama* interwoven with extensive branching; hyphae $2\text{--}6.4 \mu\text{m}$ diam, cylindrical, hyaline, dextrinoid, thin-walled. *Stipe cortical hyphae* $2\text{--}8 \mu\text{m}$ diam, cylindrical, parallel, yellow, dextrinoid, thick-walled; *medullary hyphae* $2.5\text{--}8.2 \mu\text{m}$ diam, cylindrical, parallel, hyaline, dextrinoid, thick-walled. *Caulocystidia* rare, of *Siccus*-type broom cells; main body $14.5\text{--}20.5 \times 6.4\text{--}12 \mu\text{m}$, cylindrical to broadly cylindrical, clavate, or subinflated to inflated, rarely lobed, dull yellowish brown or pale yellow, inamyloid, thin-walled or thick-walled; apical setulae uncrowded, $0.8\text{--}6.4 \times 1.4\text{--}1.6 \mu\text{m}$, cylindrical, rarely forked, apex obtuse or rarely subacute, golden yellow, inamyloid, thin-walled or thick-walled. *Caulosetae* $32\text{--}170 \times 10.5\text{--}14 \mu\text{m}$, secondarily septate, cylindrical to irregularly cylindrical or conical, apex subacute to acute, some forming lobes or forking, yellow to golden yellow, inamyloid, thick-walled ($1.6\text{--}3 \mu\text{m}$). *Clamp connections* present.

Habit, habitat and known distribution:—Gregarious on woody debris under baobab trees in coastal xerophytic habitat. Africa (São Tomé), Singapore, Thailand.

Material examined:—AFRICA. São Tomé, along main road (EN-1) on north side of island at 16.5 km marker, N00°24.374', E06°37.092', 17 April 2008, collected by D.E. Desjardin, DED 8248 (SFSU; KX953749).

Commentary:—*Marasmius trichotus* is characterized by a small, orange to brownish orange, weakly striatulate pileus, close, white, non-collariate, non-marginate lamellae, an orangish white, hispidulous, non-insititious stipe, moderately long

basidiospores, abundant pileosetae and caulosetae, no pleurocystidia, and *Siccus*-type cheilocystidia and pileipellis broom cells.

The specimen from São Tomé matches quite closely the descriptions of material from Singapore (holotype; Corner 1996) and Thailand (Wannathes et al. 2009), differing only in growing on woody debris rather than on dicotyledonous leaves. The ITS sequence similarity between DED 8248 (KX953749) from São Tomé and two specimens of *M. trichotus* from Thailand (EU935492, EU935493) is 96.9–97.1%, which we accept as conspecific because of the overall morphological similarities between these disjunct populations of this character-rich species. Together, the three sequences form a well-supported clade (87% BS, 1.0 PP) sister to a clade containing *M. longisetosus* J.S. Oliveira & Capelari and *M. dendrosetosus* J.E. Shay & Desjardin, several species with pileosetae and caulosetae.

IIC. ser. *Atrorubentes*

Sect. *Sicci* Singer, 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.

10. *Marasmius corrugatiformis* Singer, Bull. Jard. Bot. Etat Brux. 34: 374. 1964.

Description:—*Pileus* 10–35 (–55) mm diam, obtusely conical to convex or campanulate, expanding to plano-convex; disc with a small umbo, flattened or shallowly depressed in age, smooth to radially rugulose-venose or nearly reticulate; margin smooth to finely

striatulate or radially rugulose, wavy at maturity; surface dull, moist to dry, glabrous, subhygrophanous, reddish brown (8E6–8) overall when young, in age disc reddish brown (8D7–8), surrounded by a zone of brownish orange (6–7C5–7), margin yellowish white to cream (4A2–3). *Context* <0.5 mm thick, off-white to pale yellowish white (4A2). *Odor* mild. *Lamellae* horizontal, subfree to shallowly adnexed, sometimes with a narrow smooth zone around stipe apex, crowded with 4–6 series of lamellulae, narrow (1 mm), pale yellowish white (4A2), non-marginate. *Stipe* 25–65 × 1–2 (–3) mm, central, cylindrical, equal, tough, pliant, hollow, non-insititious with pale yellowish white (4A2) basal mycelium and pink coarse rhizomorphs; surface dull, dry, minutely pruinose, apex pale yellowish white (4A2), centrally brownish orange (6C6–8), base brown (7D–E6–8) to reddish brown (8D–E5–8) or darker.

Basidiospores (5.7–) 6–7.9 × (2.5–) 2.8–3.6 μm [$x_{\text{mr}} = 6.7\text{--}7.2 \times 3.1\text{--}3.2 \mu\text{m}$, $x_{\text{mm}} = 7 \pm 0.3 \times 3.2 \pm 0.03 \mu\text{m}$, $Q_{\text{mr}} = 2.13\text{--}2.29$, $Q_{\text{mm}} = 2.21 \pm 0.12$, $n = 39$, $s = 2$], ellipsoid, smooth, hyaline, inamyloid, thin-walled. *Basidia* 20–23 × 6–7.5 μm , cylindrical to narrowly clavate. *Basidioles* cylindrical to clavate or rarely subrostrate. *Cheilocystidia* abundant, 12–17.6 × 6.8–8.8 μm , irregularly cylindrical with knobby protuberances or coralloid, often branching, hyaline, weakly dextrinoid, thin-walled. *Pleurocystidia* absent. *Pileipellis* very weakly mottled, composed of a hymeniform layer of *Siccus*-type broom cells; main body 6–30 × 6.5–10 μm , cylindrical to broadly cylindrical or clavate to broadly clavate or rarely inflated, seldom lobed, hyaline or pale orange to orange, weakly dextrinoid to dextrinoid, thin-walled or thick-walled from middle to apex; apical setulae 2.8–8.8 × 0.6–1.8 μm , crowded to diffuse, non-forked, cylindrical or knobby, apex obtuse, hyaline to orange, weakly dextrinoid, thin-walled. *Pileus trama* interwoven, hyphae 3–11.2 μm diam., cylindrical, hyaline, strongly dextrinoid, thin-walled. *Lamellar trama* interwoven, hyphae 3.2–10.4 μm diam, cylindrical, hyaline, strongly dextrinoid, thin-walled. *Stipitipellis* giving rise to large irregularly geniculate cells (caulocystidia) and rare setulae arising laterally from hyphae, seldom in small clusters; *cortical trama* 2–8.8 μm diam., parallel, cylindrical, smooth, hyaline, strongly dextrinoid, thin-walled;

medullary hyphae is similar in characteristics. *Caulocystidia* abundant, $10\text{--}64 \times 4.5\text{--}8$ μm , irregularly cylindrical with knobby protuberances, often forked at septa, hyaline, weakly dextrinoid, thin-walled. *Clamp connections* present.

Habit, habitat and known distribution:—Solitary or in small clusters on leaf mulch and woody debris in primary forest. Africa (Benin, Cameroon, DR Congo, Gabon, Ghana, Ivory Coast, São Tomé, Uganda), Madagascar.

Material examined:—AFRICA. São Tomé, Parque Nacional Obo, on trail to Lagoa Amelia, approx. 1170–1300 m elev., between N00°17.112', E06°35.967 and N00°16.922', E06°36.062', 14 April 2008, collected by B.A. Perry and D.E. Desjardin, DED 8233 (SFSU; KX953757); Macambrara, radio antenna area, 1300 m elev., N00°16.557', E06°36.326', 25 April 2008, collected by D.E. Desjardin, DED 8326 (SFSU; KX953756).

Commentary:—Distinctive features of *Marasmius corrugatiformis* include a rugulose-venose pileus with a reddish brown to orangish brown disc and yellowish white margin; crowded and narrow lamellae; a pruinose stipe with yellowish white apex and brownish orange to reddish brown base; small basidiospores; no pleurocystidia; irregularly cylindrical cheilocystidia and caulocystidia; and growth in clusters on leaf mulch and woody debris.

The macro- and micromorphology of São Tomé specimens match quite closely the details reported by Antonín (2007), Pegler (1977), Singer (1964, 1965) and Shay et al. (2017), except for the cheilocystidia shape. The São Tomé populations have irregularly cylindrical to knobby or forked cheilocystidia, whereas material from elsewhere in tropical Africa has typical *Siccus*-type broom cells or smooth cells with or without a few knobby projections. Without molecular data from specimens from the Democratic Republic of the Congo (the type locality) for comparison, we accept the São Tomé material as a form of *M. corrugatiformis*. ITS sequences of the São Tomé specimens

form a clade with a sequence of *M. corrugatiformis* from Madagascar (KX148981), and together are sister to *M. subarborescens* Singer but with low support.

11. *Marasmius subarborescens* Singer, Bull. Jard. Bot. Etat Brux. 34: 364. 1964.

Description:—*Basidiomata* immature. *Pileus* 5–8 mm diam, obtusely conical to flattened-convex, radially rugulose to nearly smooth, not striate; surface dull, hygrophanous, creamy white (4A2) overall, fading to white. *Context* <1 mm thick, soft, white. *Odor* indistinct. *Lamellae* narrowly adnexed to adnate, extremely crowded with 3–4 series of lamellulae, very narrow (<1 mm), white, non-marginate. *Stipe* 20–30 × 1–1.5 mm, central, cylindrical, tough, hollow, non-insititious; surface dull, dry, pruinose overall, creamy white overall, base developing pale brownish orange (6C4) tones in age.

Basidiospores and *basidia* not observed; material immature. *Basidioles* 16–21 × 4–5 µm, cylindrical to subclavate, clamped. *Cheilocystidia* common, lamellar edge sterile, of unusual *Siccus*-type broom cells; main body 11–20 × 4–7 µm, irregularly cylindrical, hyaline, inamyloid, thin-walled; apical setulae few (3–6), 2.5–13 × 1.2–2.5 µm, conical, often forked, hyaline, thin-walled. *Pleurocystidia* absent. *Pileipellis* a hymeniform layer of *Siccus*-type broom cells; main body 11–18 × 5.5–9.5 µm, clavate, rarely lobed, hyaline, inamyloid, thin-walled; apical setulae 3–8 × 1–2.5 µm, irregularly cylindrical to conical, often wavy, hyaline, inamyloid, thin-walled to firm-walled; with a few scattered smooth cells interspersed. *Pileus trama* interwoven; hyphae 1.5–8 µm diam, cylindrical to slightly inflated, hyaline, strongly dextrinoid, thin-walled. *Lamellar trama* regular; hyphae 2–6 µm diam, cylindrical, hyaline, dextrinoid. *Stipitipellis* composed of erect to repent caulocystidia; cortical hyphae 2.5–5 µm diam, parallel, cylindrical, smooth, hyaline, dextrinoid, thin- to thick-walled; medullary hyphae 3–8 µm

diam, cylindrical, hyaline, strongly dextrinoid. *Caulocystidia* abundant, $10\text{--}38 \times 5\text{--}8 \mu\text{m}$, cylindrical to subclavate or seldom narrowly ventricose, apex obtuse, hyaline, inamyloid, thin- to firm-walled (up to $0.6 \mu\text{m}$); with rare cells like the cheilocystidia interspersed. *Clamp connections* present in all tissues.

Habit, habitat and known distribution:—Subcespitate on rotten woody debris in coastal cacao-banana grove. Africa (Angola, Cameroon, DR Congo, Ghana, Ivory Coast, São Tomé, Uganda).

Material examined:—AFRICA. São Tomé, along main road (EN-1) on north side of island near Conde, N00°22.802', E06°39.334', 12 April 2008, collected by B.A. Perry, DED 8215 (SFSU; KX953755).

Commentary:—Distinctive features of *Marasmius subarborescens* include: a smooth to rugulose, white, hygrophanous pileus; extremely crowded, narrow, non-marginate, white lamellae; a pruinose, apically white, basally brownish orange stipe covered with simple, cylindrical caulocystidia; no pleurocystidia; *Siccus*-type cheilocystidia and pileipellis broom cells; and subcespitate growth on woody debris. Unfortunately, the specimen from São Tomé was immature and did not have mature basidia or basidiospores, hence this diagnosis is tentative. The white, lignicolous, subcespitate basidiomes with crowded, narrow lamellae and cylindrical-clavate caulocystidia match nicely the data reported for *M. subarborescens* by Antonín (2007). The cheilocystidia of the São Tomé specimen with a few, long setulae were unusual and different from those noted by Antonín (2007) and Pegler (1977). An ITS sequence of DED 8215 (KX953755) places *M. subarborescens* sister to *M. corrugatiformis* with low support.

Ild. ser. Leonini

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

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

12. *Marasmius megistus* Singer, Bull. Jard. Bot. Etat Brux. 34: 356. 1964.

Description:—*Pileus* 20 mm diam, convex, plicate, disc rugulose; surface dull, dry, nearly translucent, disc brown (6E5–6), margin brownish gray (6C3) to cream-brown or paler, slightly striped. *Lamellae* horizontal, adnexed, distant (14) with no lamellulae, broad (3 mm), pale grayish orangish white (<6B2), non-marginate. *Stipe* 120 × 1–1.25 mm, central, cylindrical, tough, hollow, non-insititious; surface dull, dry, glabrous, dark brown (7F6–8) overall.

Basidiospores (33.5–) 34.2–36 (–38) × 4.8–5.7 (–6) μm [$x = 35.2 \pm 1.5 \times 5.3 \pm 0.4 \mu\text{m}$, $Q = 6\text{--}7.7$, $Q_m = 6.69 \pm 0.41$, $n = 19$, $s = 1$], clavate and often curved (musinoid), smooth, hyaline, inamyloid, thin-walled. *Basidia* not observed. *Basidioles* 54–65 × 7.5–13.5 μm , cylindrical to clavate, apex obtuse, hyaline, inamyloid, thin-walled.

Cheilocystidia of *Siccus*-type broom cells; main body 12–25.5 × 5.6–10.5 μm , clavate to broadly clavate, often lobed, hyaline, inamyloid, thin-walled; apical setulae 3.2–17.5 × 1.8–3 μm , cylindrical or narrowly conical, apex obtuse to subacute, hyaline, thin-walled.

Pleurocystidia absent. *Pileipellis* a hymeniform layer of *Siccus*-type broom cells; main body 10.5–17.8 × 3.2–10.5 μm , cylindrical or narrowly clavate to clavate, often lobed, hyaline, inamyloid, thick-walled; apical setulae 3.2–12.8 × 1.2–2.5 μm , cylindrical to narrowly conical, often forked, apex subacute to acute, hyaline, inamyloid, thick-walled.

Pileus trama interwoven; hyphae 2.2–4.8 μm diam, cylindrical, hyaline, strongly

dextrinoid, slightly thick-walled. *Lamellar trama* interwoven; hyphae 1.8–9.6 μm diam, cylindrical, hyaline, strongly dextrinoid, thin-walled. *Stipe cortical hyphae* 3.4–8.2 μm diam, cylindrical, parallel, light green to yellowish green, strongly dextrinoid, staining vibrant green with long exposure (30 min) to KOH, thick-walled; *medullary hyphae* 4.4–12 μm diam, cylindrical, parallel, hyaline, dextrinoid to dextrinoid, thin-walled. *Caulocystidia* absent. *Clamp connections* present.

Habit, habitat and known distribution:—Solitary on woody debris in primary forest. Africa (Burundi, Cameroon, DR Congo, São Tomé, Tanzania, Uganda).

Material examined:—AFRICA. São Tomé, Parque Nacional Obo, on trail to Lagoa Amelia, between N00°17.112', E06°35.967 and N00°16.922', E06°36.062', 14 April 2008, collected by D. E. Desjardin, DED 8230 (SFSU; KX953750).

Commentary:—Distinctive features of *Maramius megistus* are a moderately large, plicate, brown to cream-brown pileus that is often striped, distant, broad, non-collariate, non-marginate lamellae, a long, glabrous, non-insititious stipe lacking caulocystidia, very large basidiospores $33.5\text{--}38 \times 4.8\text{--}6 \mu\text{m}$, no pleurocystidia, *Siccus*-type cheilocystidia and pileipellis broom cells with long setulae, and growth on dicotyledonous leaves and twigs. The single São Tomé basidiome lacks purple or violaceous colors in the pileus and stipe, otherwise it matches nicely the descriptions provided by Singer (1964), Pegler (1977), Antonín (2007) and Shay et al. (2017). An ITS sequence of DED 8230 (KX953750) is sister to two sequences of *M. megistus* from Madagascar (KX148992, KX148993) with strong support (100% BS, 1.0 PP).

13. *Marasmius haediniformis* Singer, Bull. Jard. Bot. Etat Brux. 34: 363. 1964.

Description:—*Pileus* 8–20 mm diam, convex to obtusely conical, expanding to nearly plano-conical, striate to sulcate; surface dull, glabrous, subhygrophanous, disc brownish orange (6–7C4–5) to pale orangish white (5A3), grading through pale orangish white (5–6A2–3) to nearly white on the margin. *Context* <1 mm thick, white. *Odor* mild. *Lamellae* horizontal, narrowly adnate, subdistant to distant (13–18) with 2 series of lamellulae, forked and weakly intervenose at maturity, narrow (1–2 mm), white, non-marginate. *Stipe* 20–55 × 1 mm, central, cylindrical, tough, hollow, non-insititious with yellowish white basal mycelium; surface dull, dry, glabrous, apex white or lemon yellow (2A5–7), centrally brownish orange (6C5–6) to light brown (6D4–5), base reddish brown to brown or dark brown (7–8E–F6–8).

Basidiospores (13–) 13.6–16.8 (–19.2) × (3–) 3.2–4.4 μm [$x_{\text{mr}} = 15.1\text{--}15.3 \times 3.5\text{--}4.0 \mu\text{m}$, $x_{\text{mm}} = 15.1 \pm 0.05 \times 3.7 \pm 0.3 \mu\text{m}$, $Q_{\text{mr}} = 3.9\text{--}4.3$, $Q_{\text{mm}} = 4.09 \pm 0.3$, $n = 42$, $s = 2$], clavate, smooth, hyaline, inamyloid, thin-walled. *Basidia* 36–40 × 6.4–7.0 μm , cylindrical, hyaline, thin-walled. *Basidioles* cylindrical, hyaline, inamyloid, thin-walled. *Cheilocystidia* abundant, of *Siccus*-type broom cells; main body 15–21.6 × 5–10 μm , cylindrical or clavate to broadly clavate, hyaline, inamyloid, thin-walled; apical setulae crowded, 0.4–6.4 × 0.4–2.4 μm , cylindrical or irregularly cylindrical, some coralloid or knob-like, apex subobtuse, hyaline, inamyloid, thin-walled. *Pleurocystidia* absent. *Pileipellis* weakly mottled, a hymeniform layer of *Siccus*-type broom cells; main body 5.6–16 × 3.6–11.2 μm , cylindrical to clavate or subinflated, often lobed, hyaline to pale yellow or yellowish green, inamyloid, thin-walled; apical setulae crowded, 3–7 × 0.5–1.5 μm , some forked, cylindrical to narrowly conical, apex obtuse to subacute; hyaline or pale yellow to yellowish green, inamyloid to weakly dextrinoid, thin-walled; occasional broom cells with much larger setulae, 35–40 × 5.5–8 μm , irregularly cylindrical to coralloid or nodulose, thick-walled. *Pileus trama* interwoven; hyphae 3.2–8.8 μm diam, cylindrical to subinflated, hyaline, dextrinoid, thin-walled. *Lamellar trama* interwoven;

hyphae 3.2–12.8 μm , cylindrical, hyaline, strongly dextrinoid, thin-walled. *Stipe cortical hyphae* 2.8–8.8 μm diam, cylindrical, parallel, hyaline, inamyloid, thin-walled; *medullary hyphae* 2.8–16.4 μm diam, cylindrical, parallel, hyaline, dextrinoid, thin-walled.

Caulocystidia absent. *Clamp connections* present.

Habit, habitat and known distribution:—Scattered on rotten woody debris or banana debris in coastal cacao-banana grove. Africa (Benin, Cameroon, DR Congo, Ghana, Malawi, Nigeria, São Tomé, Sierra Leone, Uganda, Zimbabwe), South America (Ecuador).

Material examined:—AFRICA. São Tomé, along main road (EN-1) on north side of island near Conde, N00°22.802', E06°39.334', 12 April 2008, collected by B.A. Perry, DED 8216 (SFSU; KX953759); São Tomé, along main road (EN-1) on north side of island, off dirt road near Muquiqui, N00°22.653', E06°38.676', 12 April 2008, collected by B.A. Perry, DED 8217 (SFSU; KX953760).

Commentary:—Features of the São Tomé specimens are a mix of those reported for *Marasmius luteostipitatus* Mossebo & Antonín and *M. haediniformis* (Antonín 2007). DED 8217 has a bright lemon yellow stipe apex, some pileipellis cells approaching coralloid, and cheilocystidia 15–20 μm long—features identical to *M. luteostipitatus*. However, the basidiospores of DED 8217 are 13.6–16.8 μm long (with only a few reaching 19.2 μm), and the cheilocystidia are up to 10 μm broad—features matching *M. haediniformis*. In comparison, DED 8216 has a white stipe apex, pileipellis cells all of which are shorter and not coralloid, and spores 13.8–16.8 μm long—features of *M. haediniformis*, but with narrow cheilocystidia more like those of *M. luteostipitatus*. The ITS sequences of DED 8216 (KX953759) and DED 8217 (KX953760) are identical, indicating that the two specimens represent the same taxon. We choose to recognize the São Tomé specimens as *M. haediniformis*, originally described from the Democratic Republic of the Congo, with the caveat that *M. luteostipitatus* (described from Cameroon) with its lemon yellow stipe apex may represent a synonym. The ITS data suggest that *M. haediniformis* is closely related to *M. corneri* Wannathes, Desjardin & Lumyong,

forming a clade with 100% BS and 1.0 PP support. *Marasmius corneri*, a species originally described as *M. incarnatus* Corner (nom. illegit.) from Singapore and subsequently reported from Northern Thailand (Wannathes *et al.* 2007), differs from *M. haediniformis* in forming longer basidiospores (mean $19 \times 4.5 \mu\text{m}$; Wannathes *et al.* 2007, 2009).

14. *Marasmius albisubiculosus* C.L. Grace, Desjardin and B.A. Perry *sp. nov.*

MycoBank no.: MB 829077

Holotype:—AFRICA. Príncipe, Bom Bom resort, N01°41.559', E07°24.171', 20 April 2008, collected by D. E. Desjardin, DED 8277 (SFSU).

Etymology:—*albi* – white, *subiculosus* – subiculum, referring to a white subiculum from which the basidiomes arise.

Description:—*Pileus* 2–3 mm diam, convex to plano-convex, rugulo-venose overall, striatulate in age; surface dull, dry, glabrous, cream (4A4) to light yellow (4A4) overall. *Lamellae* horizontal, adnate, distant (10–12) with 2 series of lamellulae, narrow (<0.5 mm), pale yellowish white to cream (4A2–3), non-marginate. *Stipe* 6–8 \times 0.2 mm, central, cylindrical, solid; surface dull, dry, minutely pruinose overall, non-insititious with buff basal mycelium; apex pale yellowish white (4A2), base brown (7E4–5); growing from a whitish buff subiculum with white rhizomorphs.

Basidiospores 8–9 (–9.6) \times 3.2–3.8 μm [$x = 8.5 \pm 0.6 \times 3.5 \pm 0.3 \mu\text{m}$, $Q = 2.1$ – 2.7 , $Q_m = 2.46 \pm 0.16$, $n = 10$, $s = 1$], elongate-ellipsoid, smooth, hyaline, inamyloid, thin-walled. *Basidia* not observed. *Basidioles* 18–21 \times 4.8–6.5 μm , clavate to subfusoid. *Cheilocystidia* of *Siccus*-type broom cells; main body 11–21 \times 6.5–10 μm , clavate, seldom lobed, hyaline, inamyloid, thin-walled; apical setulae numerous, 1–2.5 \times 0.5–1 μm , irregularly cylindrical, nodulose, hyaline to pale yellow, inamyloid, thick-walled. *Pleurocystidia* absent. *Pileipellis* a hymeniform layer of *Siccus*-type broom cells with scattered arachnoid cells; main body 11–15 \times 5.5–11 μm , broadly clavate to vesiculose, hyaline, inamyloid, thin-walled; apical setulae crowded, small, 1–2.5 \times 0.5–1 μm , irregularly cylindrical, often nodulose, hyaline to yellow, inamyloid, thick-walled; arachnoid cells with 7–20 filiform setulae 4–12 \times 1–1.5 μm arising from a small basal body, yellow, dextrinoid, thick-walled. *Pileus trama* interwoven; hyphae 2.5–6.5 μm diam, cylindrical, hyaline, dextrinoid. *Lamellar trama* regular, hyphae similar. *Stipitipellis* giving rise to numerous *Siccus*-type broom cells and broccoli-like intercalary outgrowths; *cortical hyphae* 2–4.5 μm diam, cylindrical, parallel, hyaline, strongly dextrinoid, thin-walled; *medullary hyphae* 3–6.5 μm diam, otherwise similar. *Caulocystidia* similar to the cheilocystidia, or composed of small, reduced broom cells arising as intercalary setulose outgrowths. *Clamp connections* present in all tissues.

Habit, habitat and known distribution:—Scattered on herbaceous stems in secondary forest, Príncipe.

Material examined:—AFRICA. Príncipe, Bom Bom resort, N01°41.559', E07°24.171', 20 April 2008, collected by D. E. Desjardin, DED 8277 (Holotype, SFSU; KX953752).

Commentary:—*Marasmius albisubiculosus* is characterized by a tiny, cream to light yellow, rugulose-venose pileus; distant, non-collariate, yellowish white lamellae; a tiny, pruinose, non-insititious stipe with yellowish white apex and brown base, covered with broom cells and setulose outgrowths; basidiospores with mean $8.5 \times 3.5 \mu\text{m}$; no

pleurocystidia; rather broad *Siccus*-type cheilocystidia and pileipellis broom cells; arachnoid cells scattered in the pileipellis; and basidiomes arising from a white subiculum growing over herbaceous stems and associated with white rhizomorphs.

Three species of *Marasmius* in sect. *Sicci* form tiny, pallid basidiomes associated with white rhizomorphs. *Marasmius pseudoarachnoideus* Dennis, described from Trinidad and accepted by many as *Amyloflagellula pseudoarachnoidea* (Dennis) Singer, differs in forming fewer lamellae (4–6), a shorter (1–3 mm), glabrous stipe, much longer basidiospores (14–20 µm), no cheilocystidia, and a pileipellis formed entirely of arachnoid broom cells (Dennis 1951, Singer 1976). *Marasmius pometiae* Corner, described from Singapore, differs in forming sulcate, depressed pilei, a glabrous stipe lacking caulocystidia, larger basidiospores (15–18 × 4–5 µm), lacks arachnoid pileipellis cells, and grows on the bark of living *Pometia* (Sapindaceae) trees (Corner 1996). *Marasmius pusio* Berk. & M.A. Curtis, described from South Carolina (USA) and reported from New Zealand, differs in larger (4–10 mm diam), apricot to pale brownish orange pilei, a longer (7–18 mm) stipe, *Siccus*-type broom cells with longer setulae (up to 6 µm), and lacks arachnoid pileipellis cells (Desjardin & Horak 1997).

Marasmius subconiatius Petch, from Sri Lanka and Indonesia, differs in a larger (4–7 mm diam), sulcate pileus, a glabrous, dark brown to black stipe lacking caulocystidia, *Siccus*-type broom cells with longer setulae (up to 6 µm), lacks arachnoid cells, and grows on bamboo leaves (Desjardin et al. 2000). From Africa, the only species in sect. *Sicci*, ser. *Leonini* that is similar in size is *M. leptus* Singer, but it has a red (puniceous) pileus, a longer (18–24 mm), glabrous stipe lacking caulocystidia, longer basidiospores (10.5–12.5 µm), much narrower broom cells (5–7 µm), and lacks arachnoid cells (Singer 1964, Antonín 2007).

ITS data place *Marasmius albisubiculosus* in an isolated position amongst other members of sect. *Globulares* with *Siccus*-type pileipellis cells and otherwise disparate micromorphology.

15. *Marasmius leptocephalus* C.L. Grace, Desjardin & B.A. Perry *sp. nov.*

MycoBank # MB 829078

Holotype:—AFRICA. São Tomé, along main road (EN-1) on north side of island at 18.25 km marker, Shipwreck Cove, N00°23.687', E06°36.302', 17 April 2008, collected by D.E. Desjardin, DED 8253 (SFSU).

Etymology:—*tenui* – thin, *cep* – head, referring to the very thin, translucent tissue of the pileus.

Description:—*Pileus* 8–13 mm diam, convex, depressed in age, sulcate; surface dull, dry, glabrous, subtranslucent, disc pale orangish white (5A2), margin white. *Context* <0.2 mm thick. *Lamellae* horizontal, pseudocollariate, adnate, distant (10–13) with no lamellulae, sometimes forked, narrow (–1.5 mm), white, non-marginate. *Stipe* 18–25 × 0.5 mm, central, wiry, tough, hollow, non-insititious with cream (4A3) basal mycelium; surface dull, dry, glabrous, apex white, base dark brown (6–7F5–8).

Basidiospores (10.5–) 11.2–12 (–12.2) × (3.5–) 4–4.5 (–5) μm [$x = 11.2 \pm 0.5 \times 4.3 \pm 0.6 \mu\text{m}$, $Q = 1.7\text{--}3.4$, $Q_m = 2.66 \pm 0.07$, $n = 18$, $s = 1$], elongate-lacrimoid, smooth, hyaline, inamyloid, thin-walled. *Basidia* not observed. *Basidioles* 20–30 × 6.4–7.2 μm , clavate to subfusoid. *Cheilocystidia* of *Siccus*-type broom cells; main body 9.6–16 × 4.8–7.6 μm , cylindrical to clavate, hyaline, inamyloid, thin-walled; apical setulae crowded, 0.4–2 × 0.4–1 μm , cylindrical, apex obtuse, hyaline, inamyloid, thin-walled.

Pleurocystidia absent. *Pileipellis* a hymeniform layer of *Siccus*-type broom cells with scattered thick-walled smooth cells; main body $3.2\text{--}12 \times 3.2\text{--}8.8\text{ }\mu\text{m}$, cylindrical to clavate, hyaline to pale yellow or brownish yellow, inamyloid, thin-walled or thick-walled; apical setulae crowded, $0.4\text{--}2.4 \times 0.4\text{--}1\text{ }\mu\text{m}$, cylindrical, apex obtuse to acute, pale yellow to yellowish brown, inamyloid, thin-walled or thick-walled. *Pileus trama* interwoven; hyphae $2.0\text{--}6.4\text{ }\mu\text{m}$ diam, cylindrical, hyaline, dextrinoid, thin-walled. *Lamellar trama* interwoven; hyphae $2.3\text{--}9.6$, cylindrical, hyaline, dextrinoid. *Stipe cortical hyphae* $3.2\text{--}7.2\text{ }\mu\text{m}$ diam, cylindrical, parallel, yellowish brown, or greenish brown when exposed to 3% KOH for at least one hour, strongly dextrinoid, thick-walled; *medullary hyphae* $3.4\text{--}25.6\text{ }\mu\text{m}$ diam, cylindrical, parallel, hyaline, weakly dextrinoid, thin-walled. *Caulocystidia* absent. *Clamp connections* present in all tissues.

Habit, habitat and known distribution:—Solitary on woody debris of undetermined dicot trees in coastal secondary forest. São Tomé.

Material examined:—AFRICA. São Tomé, along main road (EN-1) on north side of island at 18.25 km marker, Shipwreck Cove, N00°23.687', E06°36.302', 17 April 2008, collected by D.E. Desjardin, DED 8253 (Holotype, SFSU).

Commentary:—*Marasmius leptocephalus* is characterized by the following features: a small, sulcate, depressed, white pileus with orangish white disc; narrow, distant (10–13) and sometimes forked, pseudocollariate, non-marginate lamellae; a glabrous, non-insititious, dark brown stipe; basidiospores in the range $10.5\text{--}12 \times 3.5\text{--}5\text{ }\mu\text{m}$; no pleurocystidia or caulocystidia; *Siccus*-type cheilocystidia; *Siccus*-type broom cells with numerous and tiny setulae and interspersed thicker, darker pigmented cells with fewer setulae; and growth on woody debris.

It is similar to *M. haediniformis*, but the latter has more lamellae (13–18), a thicker, brownish orange to reddish brown stipe, and longer basidiospores ($13.5\text{--}16.8\text{ }\mu\text{m}$). *Marasmius subarborescens* Singer, from Africa, has similar pileus and stipe coloration, but differs in very close lamellae, smaller basidiospores ($6\text{--}8 \times 2.7\text{--}3.2\text{ }\mu\text{m}$),

numerous clavate to fusoid caulocystidia, and growth in dense clusters (Antonín 2007). *Marasmius cremeus* Wannathes, Desjardin & Lumyong, described from northern Thailand, has a more consistently smaller and conical-umbonate pileus (not depressed), longer basidiospores (12–14 µm), and larger broom cells (Wannathes et al. 2009). *Marasmius halimunensis* Desjardin, Retnowati & E. Horak, described from Java, differs in pileus context up to 2 mm thick, closer (15–18), adnate to subdecurrent lamellae, minutely pruinose stipe with numerous cylindrical to clavate caulocystidia, and *Siccus*-type cheilocystidia and pileipellis broom cells with fewer and larger setulae (Desjardin et al. 2000). Repeated attempts to obtain quality ITS and RPB2 sequences from *Marasmius leptcephalus* were unsuccessful.

16. *Marasmius nodulocystis* Pegler, Kew Bull. Addit. Ser. 6: 200. 1977.

Description:—*Pileus* (6–) 14–25 (–35) mm diam, campanulate to convex or broadly convex-depressed, expanding to plano-umbonate with a depression surrounding the umbo, coarsely rugulose-venose on umbo, plicate to sulcate elsewhere; surface dull, dry, minutely subvelutinous or granulose, at first deep dark reddish brown (9–10E8) to deep reddish brown (8–9E6–8) overall, disc remaining deep reddish brown, margin fading to reddish brown (8–9D6–8) or brownish orange (7C5–6), in age sometimes striped with ridges reddish brown and grooves cream-buff (4A3). *Context* <1 mm thick, white. *Odor* indistinct. *Lamellae* horizontal, narrowly adnate to free, subdistant (18–26) with 0–1 series of lamellulae, broad (2–4 mm), off-white to pale yellowish white (4A2) with reddish brown edges. *Stipe* 30–90 × 1–1.5 mm, central, cylindrical, tough, pliant, hollow, insititious or subinsititious with buff scant basal mycelium; surface dull, dry, glabrous, when young apex yellowish white (4A2), in age dark brown (7–8F5–8) overall; with scattered erect, dark brown rhizomorphs.

Basidiospores (8–) $8.5\text{--}10.5$ (-10.8) \times $4.0\text{--}4.8$ μm [$x_{mr} = 8.9\text{--}9.6 \times 4.1\text{--}4.4$ μm , $x_{mm} = 9.2 \pm 0.3 \times 4.3 \pm 0.2$ μm , $Q_{mr} = 2.1\text{--}2.3$, $Q_{mm} = 2.18 \pm 0.1$, $n = 67$, $s = 3$ specimens], narrowly ellipsoid or lacrimoid, smooth, hyaline, inamyloid, thin-walled. *Basidia* clavate, 4-spored. *Basidioles* cylindrical, subobtuse to obtuse. *Cheilocystidia* abundant, of *Siccus*-type broom cells; main body $16.8\text{--}26.4 \times 5\text{--}10.4$ μm , cylindrical to clavate, rarely lobed, hyaline, inamyloid, thin-walled or thick-walled; apical setulae $2.4\text{--}8.2 \times 1.2\text{--}4$ μm , cylindrical to broadly cylindrical, obtuse or rarely truncate, hyaline to yellowish brown, inamyloid to weakly dextrinoid, thick-walled. *Pleurocystidia* absent. *Pileipellis* mottled, composed of a hymeniform layer of *Siccus*-type broom cells; main body $12\text{--}21.6 \times 6\text{--}13.2$ μm , cylindrical to broadly cylindrical or clavate to broadly clavate, sometimes lobed, hyaline to yellowish brown or pale yellow, weakly dextrinoid, thick-walled; with a few scattered thick-walled and smooth cells; apical setulae $3.1\text{--}7 \times 2.4\text{--}4$ μm , often forked, cylindrical or knob-like, apex obtuse, hyaline to yellowish brown or pale yellow, dextrinoid, thick-walled. *Pileus trama* interwoven; hyphae $3\text{--}11.2$ μm diam., cylindrical, hyaline to orangish white, weakly dextrinoid or dextrinoid, thin-walled. *Lamellar trama* interwoven; hyphae $4\text{--}12$ μm diam, cylindrical, hyaline, inamyloid to weakly dextrinoid, thin-walled. *Stipe cortical hyphae* $3\text{--}10.5$ μm diam, parallel, cylindrical, smooth, orange to brown, dextrinoid, thick-walled; *medullary hyphae* $5.5\text{--}10.5$ μm diam, cylindrical, hyaline, dextrinoid, thin-walled. *Caulocystidia* absent. *Clamp connections* present.

Habit, habitat and known distribution:—Solitary on woody debris in coastal cacao and banana grove or secondary forests. Africa (Cameroon, DR Congo, Gabon, Nigeria, Príncipe, São Tomé, Tanzania, Uganda).

Material examined:—AFRICA. São Tomé, along main road (EN-1) on west side of island at 33 km marker, N00°19.607', E06°30.666', 18 April 2008, collected by B.A. Perry and D.E. Desjardin, DED 8269 (SFSU; KX953740). Príncipe, Bom Bom resort, N01°41.559', E07°24.171', 20 April 2008, collected by D. E. Desjardin, DED 8278

(SFSU; KX953741); Roça Pico Papagaio, N01°37.182', E07°23.474', 21 April 2008, collected by D. E. Desjardin, DED 8283 (SFSU; KX953742).

Commentary:—*Marasmius nodulocystis*, described from Uganda and known throughout tropical Africa, is distinguished by a deep reddish brown, sulcate pileus that fades marginally or in the sulcae to pale reddish cream or cream; non-collariate, distant lamellae with no or few lamellulae and concolorous or reddish brown edges; a dark brown, glabrous, insititious or subinsititious stipe sometimes associated with rhizomorphs; basidiospores in the range 8–10.5 x 4.0–4.8 µm; no pleurocystidia or caulocystidia; *Siccus*-type cheilocystidia with short, coarse setulae; similar pileipellis broom cells with scattered thick-walled smooth or coarsely knobby cells; and growth on woody debris. The lamellar and pileus tramal tissues are weakly dextrinoid. ITS sequence data place *M. nodulocystis* close to *M. leveilleanus* (Berk.) Pat., a nearly macromorphologically indistinguishable species described from Sri Lanka, with insititious stipe, rhizomorphs, non-marginate lamellae and non-dextrinoid tissues. Published descriptions of *M. nodulocystis* differ from *M. leveilleanus* only in the former having a non-insititious stipe, no rhizomorphs and dextrinoid tissues. Another very similar species, *M. ferruginacies* Antonín differs from the latter two species only in forming broader basidiospores (5–6 µm), reddish brown-marginate lamellae, and a pileipellis supposedly lacking smooth cells.

The São Tomé and Príncipe specimens show a range of variability overlapping features reported for *M. nodulocystis*, *M. leveilleanus* and *M. ferruginacies*. DED 8283 has an insititious stipe with rhizomorphs, whereas DED 8278 and DED 8269 have subinsititious stipes without rhizomorphs. All three specimens have reddish brown-marginate lamellae, dextrinoid tissues, pileipelli with some smooth, thick-walled cells, and nearly identical ITS sequences.

Due to the similar spore size, pileipellis anatomy, dextrinoid tissues and African distribution, we accept the São Tomé and Príncipe specimens as representing *M. nodulocystis*, but showing 97.1% ITS sequence similarity with a specimen (EU935567)

reported from Thailand (Wannathes et al. 2009) as *M. leveilleanus*. ITS sequences of the three specimens of *M. nodulocystis* from São Tomé and Príncipe (KX953740–KX953742) form a well-supported clade (75% BS, 1.0 PP) sister to a clade containing *M. leveilleanus* and *M. tenuissimus* (Jungh.) Singer.

Ile. ser. *Haematocephali*

Sect. *Sicci* Singer, Subsect. *Siccini* Singer, ser. *Haematocephali* Singer, Fl. Neotrop.

Monogr. 17: 201. 1976.

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

17. *Marasmius suthepensis* Wannathes, Desjardin & Lumyong, Fungal Diversity 37: 288. 2009.

Description:—*Pileus* 12–25 (–33) mm diam, conical to broadly conical, smooth becoming rugulose-striate in age; surface dull, subvelutinous, hygrophanous, disc orange (6B5–7), margin pale orange (5–6A3–4), darkening in age. *Context* thin, white. *Odor* mild. *Lamellae* ascending, adnate, distant (14–16) with 2–3 series of lamellulae, narrow (1–2 mm), white, non-marginate. *Stipe* 25–50 × 1 mm, central, cylindrical, tough, pliant, hollow, non-insititious with pale orange basal mycelium; surface subshiny, dry, glabrous, apex orange to reddish brown (8E6–8), base reddish brown to dark reddish brown (8E–F6–8).

Basidiospores (12–) 12.6–13.6 (–14) × 4–4.6 µm [$x = 13.2 \pm 0.7 \times 4.3 \pm 0.3$ µm, $Q = 2.7–3.4$, $Q_m = 3.09 \pm 0.16$, $n = 18$, $s = 1$], elongate-lacrimoid, smooth, hyaline,

inamyloid, thin-walled. *Basidia* 10–18 × 5 µm, clavate, hyaline. *Basidioles* cylindrical. *Cheilocystidia* of *Siccus*-type broom cells; main body 11–21 × 6.5–10 µm, cylindrical to clavate, seldom lobed, hyaline, inamyloid, thin-walled; apical setulae numerous, 1.2–4.4 × 0.8–1.2 µm, cylindrical, seldom forking, hyaline to very pale yellow, inamyloid, thin-walled. *Pleurocystidia* 24–36 × 6.5–8.8 µm, cylindrical to clavate, apex subacute or capitate, hyaline, inamyloid, thin-walled. *Pileipellis* not mottled, a hymeniform layer of *Siccus*-type broom cells; main body 8.8–23 × 4–9.6 µm, narrowly clavate to broadly clavate or cylindrical, hyaline or light gold to yellow, inamyloid, thin-walled or thick-walled; apical setulae mostly crowded, 2–9.2 × 0.4–1.4 µm, irregularly cylindrical, gold-yellow or yellow, inamyloid, thick-walled; some brooms cells with fewer, longer and thicker-walled setulae. *Pileus trama* interwoven; hyphae 2.4–14.4 µm diam, cylindrical, hyaline, dextrinoid, thin-walled. *Lamellar trama* interwoven; hyphae 3.2–12 µm diam, cylindrical, hyaline, strongly dextrinoid, thin-walled. *Stipe cortical hyphae* 1.6–5.6 µm diam, parallel, cylindrical, hyaline or yellow, inamyloid, thick-walled; *medullary hyphae* 3.2–12.4 µm diam, parallel, cylindrical, hyaline, strongly dextrinoid, thin-walled. *Caulocystidia* absent. *Clamp connections* present in all tissues.

Habit, habitat and known distribution:—Scattered on dicot leaves and small twigs in secondary forest. Príncipe, Thailand.

Material examined:—AFRICA. Príncipe, Roça Pico Papagaio, N01°37.182', E07°23.474', 21 April 2008, collected by B.A. Perry and D. E. Desjardin, DED 8292 (SFSU; KX953753).

Commentary:—Distinctive features of *Marasmius suthepensis* include a broadly conical, smooth to striate, orange pileus, distant, non-marginate lamellae, a glabrous, non-insititious stipe lacking caulocystidia, basidiospores in the range 12–14 × 4–4.6 µm, narrow pleurocystidia, *Siccus*-type cheilocystidia and pileipellis broom cells, and growth on dicotyledonous leaves and twigs. The ITS sequence of the Príncipe specimen (KX953753) matches 98.6% that of the holotype specimen of *M. suthepensis*

(EU935520) from northern Thailand (Wannathes *et al.* 2009), and shows 97.1% similarity with the holotype of *M. linderioides* J.S. Oliveira & Capelari (JX424037), described recently from Brazil (Oliveira & Capelari 2014). *Marasmius linderioides*, although micromorphologically indistinguishable from *M. suthepensis*, shows few macromorphological similarities; indeed, *M. linderioides* forms a stipe only 1–3 mm long that arises from a cream to pink subiculum.

Based on overall morphology, *Marasmius suthepensis* is nearly indistinguishable from *M. confertus* var. *tenuicystidiatus* Antonín, described from Cameroon (Antonín 2004) and reported from Burundi and the DR Congo (Antonín 2007). An ITS sequence of *M. confertus* var. *tenuicystidiatus* from Korea, downloaded from Genbank (HQ607374), is far distant in our ITS phylogeny from *M. suthepensis*, indicating that either these two taxa are quite distinct, or that the Korean specimen does not represent the African taxon *M. confertus* var. *tenuicystidiatus*.

18. *Marasmius elaeocephalus* Singer, Bull. Jard. Bot. Etat Brux. 34: 384. 1964.

Description:—*Pileus* 7–27 mm diam, obtusely conical to campanulate, expanding to plane-depressed or plano-umbonate, disc coarsely rugulose-venose, margin smooth to weakly rugulose; surface dull, dry, glabrous to subvelutinous, subhygrophanous, brown (6–7E6–8) overall when young, disc remaining brown or becoming light brown (6D6–8) to brownish orange (6C6–8), seldom with a hint of olive, margin golden yellow (5B6–8) to grayish orange (5B5) or brownish yellow (5C6–8), darkening to brown as dried *in situ*. *Context* –1 mm thick, white. *Odor* and *taste* indistinct. *Lamellae* horizontal or ascending, adnexed, close (18–30) with 2–3 series of lamellulae, moderately broad (1.5–2 mm), pale yellowish white (4A2), non-marginate. *Stipe* 20–50 × 1–2 mm, central, ±cylindrical,

terete or flattened-cleft, tough, hollow, non-insititious with cream (4A3) to pale orangish white (<5A2) basal mycelium; surface dull, dry, glabrous, apex white to yellowish white (4A2) or pale orange (5A3), base brownish orange (6C4–8) to brown (6E5–6) or dark brown (7F6–8).

Basidiospores (10–) 10.4–12 (–12.8) \times (3.2–) 3.6–4.4 (–4.6) μm [$x_{\text{mr}} = 10.9\text{--}11.2 \times 3.6\text{--}4.1 \mu\text{m}$, $x_{\text{mm}} = 11.1 \pm 0.2 \times 3.9 \pm 0.3 \mu\text{m}$, $Q_{\text{mr}} = 2.7\text{--}3.1$, $Q_{\text{mm}} = 2.88 \pm 0.3$, $n = 42$, $s = 2$], elongate-lacrimoid to clavate, smooth, hyaline, inamyloid, thin-walled. *Basidia* not observed. *Basidioles* 20–25 \times 5–7.5 μm , cylindrical to acuminate, apex obtuse to subacute, hyaline, inamyloid, thin-walled. *Cheilocystidia* abundant, of *Siccus*-type broom cells; main body 12–17 \times 3.5–8 μm , cylindrical or clavate to broadly clavate, hyaline to yellowish white, inamyloid, thin-walled; apical setulae crowded, 1.5–5.5 \times 0.5–0.8 μm , cylindrical or conical, apex obtuse to subacute, hyaline to yellowish white, thin-walled. *Pleurocystidia* common, 20–45 \times 5–9 μm , cylindrical, apex obtuse or mucronate, refractive, hyaline, inamyloid. *Pileipellis* very weakly mottled, a hymeniform layer of *Siccus*-type broom cells; main body 11–17.6 \times 4–10.5 μm , cylindrical to clavate, some lobed, hyaline, inamyloid, thin-walled; apical setulae crowded, 2.2–6.5 \times 0.6–1 μm , cylindrical to narrowly conical, some forked, apex subacute to acute, hyaline or pale yellow, inamyloid, thin-walled. *Pileus trama* interwoven; hyphae 3.2–15 μm diam, cylindrical to inflated, hyaline, strongly dextrinoid, thin-walled. *Lamellar trama* interwoven; hyphae 3.2–15.2 μm diam, cylindrical to inflated, hyaline, strongly dextrinoid, thin-walled. *Stipe cortical hyphae* 3.4–10 μm diam, cylindrical, parallel, greenish yellow to brown, dextrinoid, thick-walled; *medullary hyphae* 3.9–8 μm diam, cylindrical, parallel, hyaline, weakly dextrinoid to dextrinoid, thin-walled. *Caulocystidia* absent. *Clamp connections* present.

Habit, habitat and known distribution:—Solitary on woody debris of undetermined dicot trees in coastal secondary forest or cacao/banana groves. Africa (Cameroon, DR Congo, Nigeria, São Tomé, Uganda).

Material examined:—AFRICA. São Tomé, along main road (EN-1) on north side of island at 18.25 km marker, Shipwreck Cove, N00°23.687', E06°36.302', 17 April 2008, collected by D.E. Desjardin, DED 8254 (SFSU; KX953754); São Tomé, along main road (EN-1) on west side of island at 33 km marker, N00°19.607', E06°30.666', 18 April 2008, collected by D.E. Desjardin, DED 8264 (SFSU).

Commentary:—Distinctive features of the São Tomé material of *M. elaeocephalus* include a conical to campanulate, smooth to rugulose-striate pileus with olive, brown, yellowish brown and orangish brown tones; close (18–30), non-marginate lamellae; a glabrous, non-insititious, brown to dark brown stipe with yellowish white to pale orange apex; basidiospores in the range 10.4–12.8 µm long; narrow pleurocystidia (5–9 µm); no caulocystidia; and growth on woody debris in coastal forests. Antonín (2007) reports the species with a more coarsely striate-sulcate pileus (although the color plate #17.96 does not show this feature), more distant lamellae (14–19), and growth in close clusters or cespitose. All other morphological features of the São Tomé specimens match those reported by Antonín (2007). ITS data suggest that *M. elaeocephalus* is closely related to *M. griseoroseus* (Mont.) Singer, a tiny pleurotoid species from South America with white to pale orange pileus <6 mm broad, distant, forked lamellae, and no stipe.

19. *Marasmius elaeocephaliformis* C.L. Grace, Desjardin & B.A. Perry *sp. nov.*

MycoBank no.: MB 829079

Holotype:—AFRICA. São Tomé, Macambrara, radio antenna area, 1300 m elev.,

N00°16.557', E06°36.326', 11 April 2008, collected by B.A. Perry, DED 8213

(SFSU).

Etymology:—*elaeocephaliformis* – similar in morphology to *M. elaeocephalus*.

Description:—*Pileus* 6–18 mm diam, obtusely conical, broadly conical or plano-convex in age, not striate, smooth to weakly rugulose overall; surface dull, dry, subvelutinous, dark yellowish olive-brown (5F5–8) overall when young, in age disc dark brown (6F6–8) to yellowish olive-brown (5F5–8), margin yellowish brown (5E4–5) with olive tones.

Odor indistinct. *Lamellae* ascending, adnexed, distant (11–14) with 2 series of lamellulae, broad (–2 mm), white to pale yellowish white (<4A2), edges white or brown. *Stipe* 30–35 × 1 mm, central, cylindrical, tough, non-insititious with strigose, white basal mycelium; surface dull, dry, glabrous, apex white, base brownish orange (6C6–7) to brown (6D6–8) or dark brown (6F6–8).

Basidiospores 10.4–14.8 × 3.6–4.4 (–4.6) μm [\bar{x} = 12.5 ± 1.4 × 4.0 ± 0.4 μm, $Q = 2.7$ –3.8, $Q_m = 3.11 \pm 0.34$, $n = 24$, $s = 1$], narrowly fusiform to elongate-lacrimoid, smooth, hyaline, inamyloid, thin-walled. *Basidia* 20–24 × 7.5–9.0 μm, cylindrical to narrowly clavate, 4-spored. *Basidioles* cylindrical, obtuse. *Cheilocystidia* abundant, of *Siccus*-type broom cells; main body 11.2–18.4 × 6.2–12 μm, cylindrical or clavate to broadly clavate or inflated, rarely lobed, hyaline to yellow or gold, inamyloid to weakly dextrinoid, wall thickness; apical setulae crowded, 2.6–5.9 × 1–2.4 μm, occasionally forked, cylindrical to subconical or knob-like, subacute to obtuse, hyaline to yellow or golden brown, inamyloid to weakly dextrinoid, thin-walled to thick-walled.

Pleurocystidia scattered, 32–40 × 6.5–8 μm, clavate-mucronate to fusiform, hyaline, inamyloid, not or weakly refractive. *Pileipellis* mottled, composed of a hymeniform layer of *Siccus*-type broom cells; main body 6–10.8 × 6–20.8 μm cylindrical to broadly clavate, often lobed, hyaline to brown or pale orange, inamyloid to dextrinoid apex, entirely thin-walled or thick-walled from middle to apex; occasional cells smooth and thick-walled, brown, dextrinoid; apical setulae crowded, 3.6–7.2 μm, cylindrical to obtusely conical or

knob-like, often forked, apex subacute to obtuse, yellowish brown to orangish brown, inamyloid to dextrinoid, thin-walled or thick-walled. *Pileus trama* interwoven; hyphae 3–7 μm diam, cylindrical, hyaline, inamyloid, thin-walled. *Lamellar trama* interwoven; hyphae 3–6.6 μm diam, cylindrical, hyaline, inamyloid to weakly dextrinoid, thin-walled. *Stipe cortical hyphae* 3.9–6.4 μm diam, parallel, cylindrical, smooth, brown, dextrinoid, thick-walled; *medullary hyphae* 3.2–8 μm diam, parallel, cylindrical, smooth, hyaline, weakly dextrinoid, thin-walled. *Caulocystidia* absent. *Clamp connections* present.

Habit, habitat and known distribution:—Solitary on woody twigs in primary forest. São Tomé.

Material examined:—AFRICA. São Tomé, Macambrara, radio antenna area, 1300 m elev., N00°16.557', E06°36.326', 11 April 2008, collected by B.A. Perry, DED 8213 (Holotype, SFSU; KX953758).

Commentary:—*Marasmius elaeocephaliformis* is characterized by a smooth to weakly rugulose-striate, dark yellowish olive brown pileus; distant (11–14), faintly brown-marginate lamellae; a glabrous, non-insititious, brown stipe with white apex; basidiospores in the range 10.4–14.8 x 3.4–4.4 μm ; scattered pleurocystidia; no caulocystidia; and growth on woody twigs in high elevation primary forest.

Marasmius elaeocephaliformis is most phenetically similar to *M. elaeocephalus* Singer, described from the Democratic Republic of the Congo, sharing olive-toned pileus, similar pleurocystidia and absence of caulocystidia. *Marasmius elaeocephalus* differs, however, in forming a paler pileus, more lamellae (18–30) lacking discolored edges, and on São Tomé growing in coastal disturbed forests. *Marasmius elaeocephaliformis* holds an isolated position in the ITS phylogeny, closest to *M. ferruginoides* Antonín, and distant from *M. elaeocephalus*.

20. *Marasmius grandisetulosus* Singer, Bull. Jard. Bot. Etat Brux. 34: 379. 1964.

Description:—*Pileus* (6–)10–25 mm diam, conical to convex, expanding to broadly conical or broadly convex with a small umbo, sometimes umbilicate, with or without a rounded-flattened umbo in the umbilicus, plicate; surface dull, dry, subvelutinous, dark reddish brown (8F6–8) or brown (7E7–8) overall when young, in age margin reddish brown (8D–E6–8) or light brown (7D6–8), with or without paler stripes; distinctly striped when dried. *Context* <1 mm thick, white, *Odor* indistinct. *Lamellae* horizontal to ascending, adnexed to adnate, distant (13–18) with no lamellulae, broad (2–4 mm), white to pale yellowish white (4A2), non-marginate; sometimes lamellae ends do not reach pileus margin. *Stipe* 25–55 × 1–1.5 mm, central, cylindrical, tough, hollow, non-insititious with white basal mycelium; surface dull, dry, glabrous, apex white to yellowish white (4A2), base reddish brown to dark brown (7–8E–F5–8).

Basidiospores 19–23 × 4.4–5.6 µm [$x_{mr} = 20.4\text{--}21.3 \times 4.6\text{--}4.7 \mu\text{m}$, $x_{mm} = 20.9 \pm 0.7 \times 4.7 \pm 0.03 \mu\text{m}$, $Q_{mr} = 4.4\text{--}4.4$, $Q_{mm} = 4.52 \pm 0.17$, $n = 48$, $s = 2$], clavate, smooth, hyaline, inamyloid, thin-walled. *Basidia* none observed. *Basidioles* cylindrical, obtuse. *Cheilocystidia* abundant, of *Siccus*-type broom cells; main body 10.4–19.6 × 7–9.5 µm, cylindrical to clavate, some lobed, hyaline, inamyloid, thin-walled; apical setulae 1.6–7.2 × 0.8–1.8 µm, cylindrical to conical, apex obtuse to subacute, pale yellow, inamyloid, thin-walled. *Pleurocystidia* 44.8–80 × 10.5–16 (–24) µm, fusoid to ventricose, apex obtuse to subacute or rostrate, hyaline, inamyloid. *Pileipellis* mottled, composed of a hymeniform layer of *Siccus*-type broom cells; main body 12–20 × 6–15 µm, cylindrical to clavate, often lobed, hyaline to yellow or yellowish brown, thick-walled (0.6–2.8 µm); with scattered thick-walled and smooth cells, yellowish-brown, dextrinoid; apical setulae 1–12 × 0.5–2.0 µm, rarely forked, cylindrical, apex obtuse to subacute, hyaline or

browning yellow or yellow, inamyloid, thin-walled or thick-walled. *Pileosetae* absent. *Pileus trama* interwoven; hyphae 2.6–8.8 μm diam, cylindrical, hyaline, weakly dextrinoid, thin-walled. *Lamellar trama* interwoven; hyphae 1.6–10.4 μm diam, cylindrical, hyaline, strongly dextrinoid, thin-walled. *Stipe* cortical hyphae 1.6–6.8 μm diam, parallel, cylindrical, smooth, golden brown or yellow brown, dextrinoid, slightly thick-walled; *medullary hyphae* 6.4–10.4 μm diam, parallel, cylindrical, smooth, hyaline, inamyloid or weakly dextrinoid, thin-walled. *Caulocystidia* absent. *Clamp connections* present.

Habit, habitat and known distribution:—Solitary to gregarious on undetermined dicotyledenous woody debris and leaves in coastal secondary forests. Africa (Cameroon, DR Congo, Ghana, Ivory Coast, Nigeria, São Tomé, Tanzania, Zambia).

Material examined:—AFRICA. São Tomé, along main road (EN-2) on south side of island near 38 km marker, N00°08.500', E06°39.560', 13 April 2008, collected by D.E. Desjardin, DED 8225 (SFSU; KX953743); São Tomé, along main road (EN-1) on north side of island at 18.25 km marker, Shipwreck Cove, N00°23.687', E06°36.302', 17 April 2008, collected by B.A. Perry, DED 8257 (SFSU; KX953744).

Commentary:—Diagnostic features of *Marasmius grandisetulosus* include: a moderately large, plicate, dark reddish brown to brown pileus that may have paler striae; distant (13–18), non-collariate, non-marginate, broad lamellae; a glabrous, dark brown stipe that lacks caulocystidia; large basidiospores in the range $19\text{--}23 \times 4.4\text{--}5.6 \mu\text{m}$; large clavate to fusoid pleurocystidia (up to $80 \times 24 \mu\text{m}$); *Siccus*-type cheilocystidia and pileipellis broom cells with thick-walled setulae often up to 12 μm long; and growth on woody debris. Although Antonín (2007) and Singer (1964) report a distinctly striped pileus, the photograph of fresh material provided by Antonín (2007–pl. 16, fig. 90b) shows an evenly pigmented pileus. The specimens from São Tomé have a mostly evenly pigmented pileus with a few paler striae, although dried material is distinctly striped. In addition, the basidiospores are at the long end of the range; otherwise the morphological features match nicely those reported from other African material (Antonín 2007).

Marasmius bingaensis Singer is nearly indistinguishable, differing only in lacking a striped pileus (compare descriptions in Antonín 2007). *Marasmius tenuisetulosus* differs primarily in having slightly smaller basidiospores and shorter setulae on pileipellis broom cells. ITS data place *M. grandisetulosus* is a well-supported clade (89% BS, 1.0 PP) with *M. hypophaeus* Berk. & M.A. Curtis (EU935484) and *M. hinnuleus* Berk. & M.A. Curtis (KX148988). *Marasmius hypophaeus* is a species with ferruginous pileus, brownish orange-marginate lamellae, smaller basidiospores ($16\text{--}18 \times 4\text{--}5 \mu\text{m}$), narrower pleurocystidia ($7\text{--}13 \mu\text{m}$) and less prominent broom cell setulae (Singer 1976, Wannathes *et al.* 2009). *Marasmius hinnuleus* also forms smaller basidiospores ($10.4\text{--}13.6 \times 2.4\text{--}4 \mu\text{m}$), narrower pleurocystidia ($7\text{--}10 \mu\text{m}$) and less prominent broom cell setulae (Shay *et al.* 2017).

21. *Marasmius tenuisetulosus* (Singer) Singer, Fl. Neotropica Monogr. 17: 220. 1976.

Basionym: *Marasmius grandisetulosus* var. *tenuisetulosus* Singer, Bull. Jard. Bot. Etat Brux. 34: 379. 1964.

Description:—*Pileus* 10–25 (–35) mm diam, obtusely conical to campanulate, disc rugulose, plicate; surface dull, dry, subvelutinous, subhygrophanous, disc brown (7E6–8), elsewhere light brown (7D6–8) to brownish orange (6C5–8) or brownish yellow (5C5–8). *Context* <1 mm thick, white. *Odor* indistinct. *Lamellae* ascending, adnexed, distant (15–18) with 0–1 series of lamellulae, broad (2–4 mm), white to dingy yellowish white (<4A2), non-marginate. *Stipe* 25–45 \times 1–1.5 mm, central, cylindrical, tough, hollow, non-insititious with orangish white (5A2) basal mycelium; surface shiny, dry, glabrous, apex white when young, in age light brown (7D6–8) to reddish brown (7D–E6–8) overall.

Basidiospores 14.4–17.6 (–18) \times 3.6–4.5 μm [$x = 16.4 \pm 1.3 \times 4.11 \pm 0.4 \mu\text{m}$, $Q = 3.2$ –4.8, $Q_m = 4.02 \pm 0.47$, $n = 26$, $s = 1$], clavate, smooth, hyaline, inamyloid, thin-walled. *Basidia* not observed. *Basidioles* cylindrical, obtuse, hyaline. *Cheilocystidia* of *Siccus*-type broom cells; main body 10–19.2 \times 4–9.8 μm , cylindrical or broadly clavate, some lobed, hyaline, inamyloid, thin-walled or rarely thick-walled; apical setulae crowded, 2.8–10 \times 0.6–1.7 μm , cylindrical or narrowly conical, apex obtuse to subacute, yellow, thick-walled. *Pleurocystidia* 28.5–46 \times 6–11.5 μm , cylindrical to fusoid, seldom broadly rostrate, obtuse, refractive, hyaline, inamyloid. *Pileipellis* mottled, a hymeniform layer of *Siccus*-type broom cells; main body 7.2–16 \times 4.5–9.5 μm , cylindrical or broadly clavate, often lobed, dull golden brown, inamyloid, thick-walled; apical setulae crowded, 2.4–9 \times 0.6–1.8 μm , cylindrical to narrowly conical, rarely forked, apex subacute to acute, golden brown to light brown, inamyloid or weakly dextrinoid, thick-walled. *Pileus trama* interwoven; hyphae 2.8–8 μm diam, cylindrical, hyaline, strongly dextrinoid, thin-walled. *Lamellar trama* interwoven; hyphae 2.6–8.8 μm diam, cylindrical, hyaline, dextrinoid, thin-walled. *Stipe cortical hyphae* 3.4–7.4 μm diam, cylindrical, parallel, golden brown to golden yellow, inamyloid, slightly thick-walled; *medullary hyphae* 4.8–13.6 μm diam, cylindrical, parallel, hyaline, strongly dextrinoid, thin-walled. *Caulocystidia* absent. *Clamp connections* present.

Habit, habitat and known distribution:—Solitary to scattered on woody debris in coastal cacao and banana grove. Africa (DR Congo, Ghana, São Tomé).

Material examined:—AFRICA. São Tomé, along main road (EN-1) on west side of island at 33 km marker, N00°19.607', E06°30.666', 18 April 2008, collected by B.A. Perry and D.E. Desjardin, DED 8267 (SFSU).

Commentary:—*Marasmius tenuisetulosus*, described originally from the Democratic Republic of the Congo, is characterized by a campanulate, plicate, brownish orange to ferruginous pileus often with paler radial stripes, distant (15–18), non-collariate, non-marginate lamellae, a glabrous, reddish brown stipe, long basidiospores,

refractive pleurocystidia, no caulocystidia, *Siccus*-type cheilocystidia and pileipellis broom cells, and growth on woody debris.

The São Tomé specimen shows features nearly indistinguishable from those reported for *M. tenuisetulosus* by Antonín (2007), differing only in forming more lamellae (15–18 versus 13–16, respectively). *Marasmius grandisetulosus* Singer is similar, but tends to form yellowish brown-lamellar edges and cheilocystidia, has longer basidiospores (18–23 µm long), and longer setulae (up to 12 µm) on the pileipellis broom cells (hence the epithet). Repeated attempts to obtain quality ITS and RPB2 sequences from DED 8267 were unsuccessful.

Discussion

The California Academy of Sciences' Biodiversity Description Mission and this subsequent preliminary monograph have greatly increased the known biodiversity of *Marasmius sensu stricto* from ST&P. Previous to this study, only one species currently accepted in *Marasmius* (Bresadola & Roumeguère, 1890) had been documented from ST&P. Our examination adds 21 described species to the known *Marasmius* biodiversity on these islands. All described species represent new geographic distribution records for ST&P including 5 that were previously undescribed. The rich biodiversity of ST&P and the discovery of previously undocumented species suggests there would be a benefit to future expeditions to further study these island's fungal biodiversity. The impact of increasing anthropogenic development could also make further investigation time sensitive.

Our results reflect previous findings that while phylogenetic analyses of the ITS gene region is informative for distinguishing between species in *Marasmius*, it is too variable to provide sufficient statistical support to delimit infrageneric clades (Tan *et al.*

2009, Wannathes *et al.* 2009). *Marasmius* subsect. *Marasmius* is the only historically recognized infrageneric group in the ITS phylogeny that formed a monophyletic clade with strong statistical support. The lack of support for deep nodes suggests that different genetic loci need to be examined for a better understanding of the genus. Analyses including multiple loci, or loci that are more conserved than ITS, may provide finer resolution and support for delimiting additional infrageneric groupings in *Marasmius*. RPB2 and EF1- α are two promising genes, in terms of phylogenetic signal, that could prove informative as additional markers and should be further examined for their potential.

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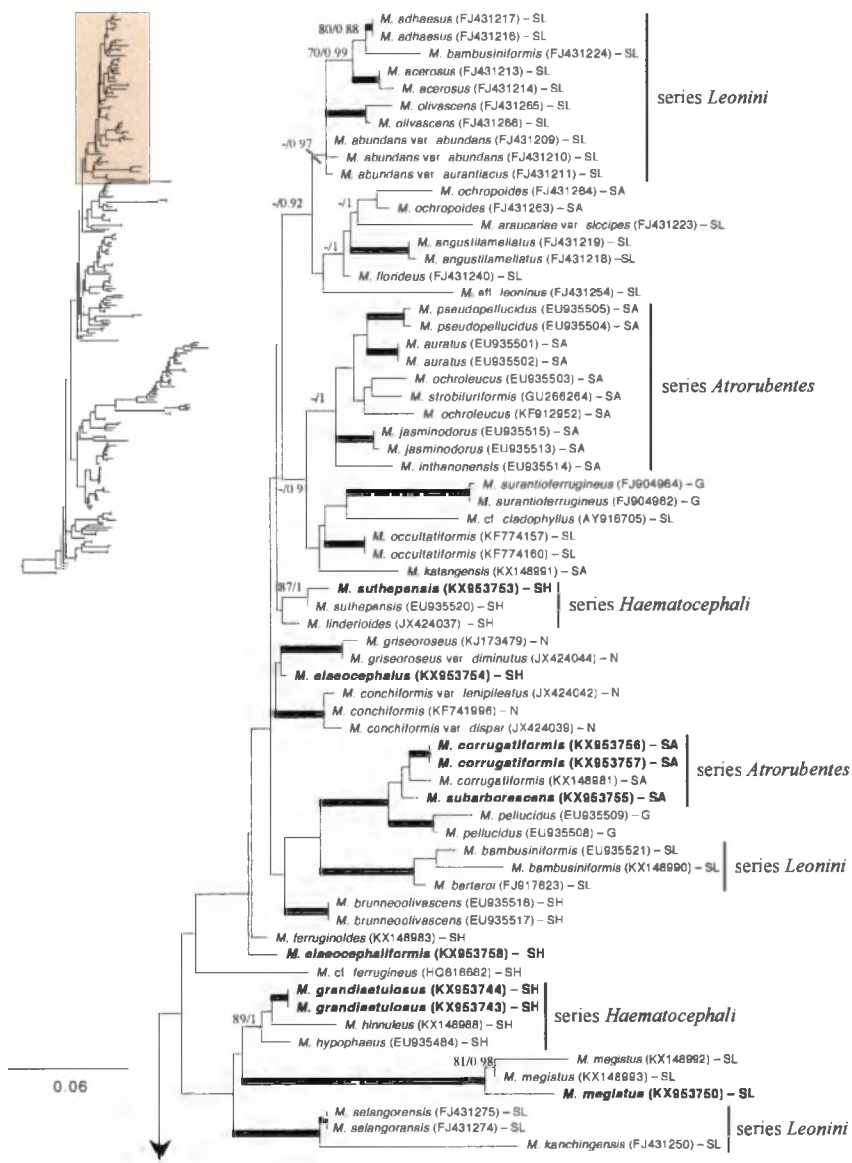


FIGURE 1a. Maximum likelihood phylogeny based on ITS sequence data. *Marasmius* from São Tomé and Príncipe are indicated in bold type. Values separated by / refer to nonparametric ML bootstrap proportions and Bayesian posterior probabilities, respectively. Values greater than 70/0.70 are shown (- designates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

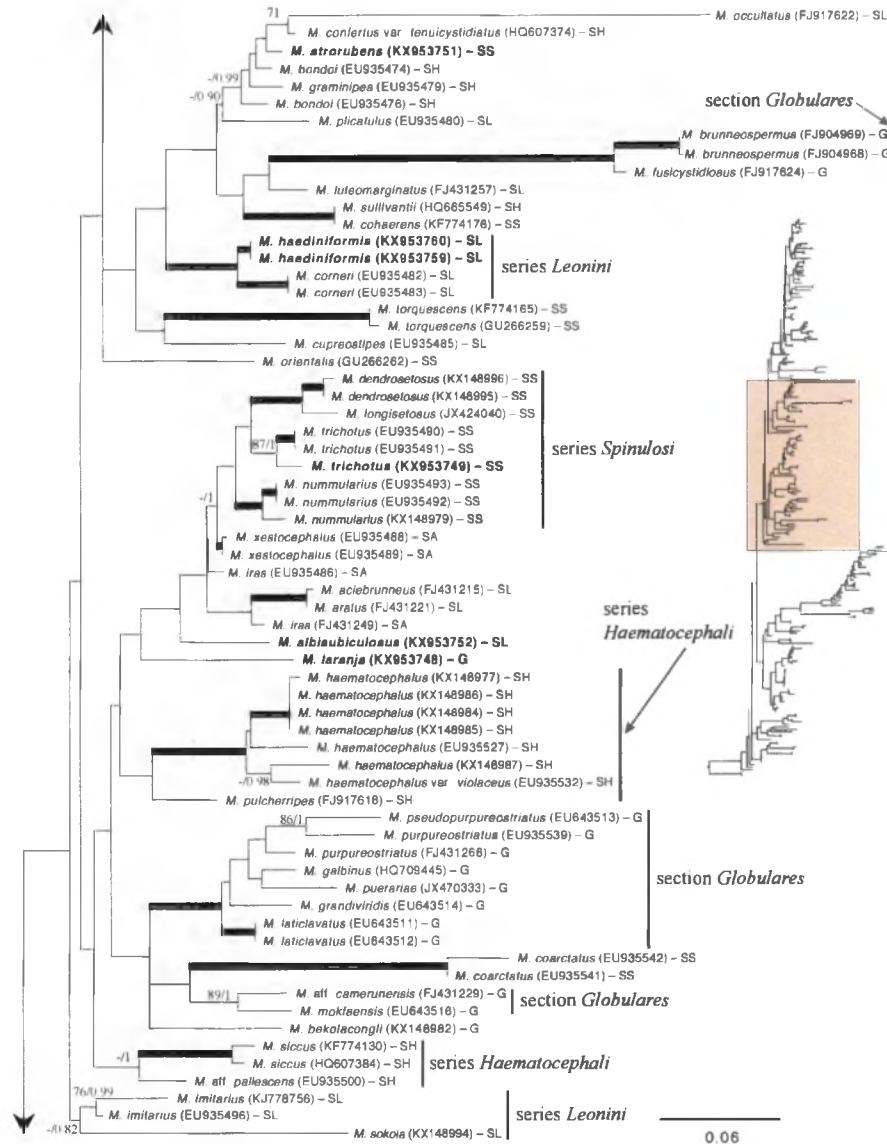


FIGURE 1b. Maximum likelihood phylogeny based on ITS sequence data. *Marasmius* from São Tomé and Príncipe are indicated in bold type. Values separated by / refer to nonparametric ML bootstrap proportions and Bayesian posterior probabilities, respectively. Values greater than 70/0.70 are shown (- designates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

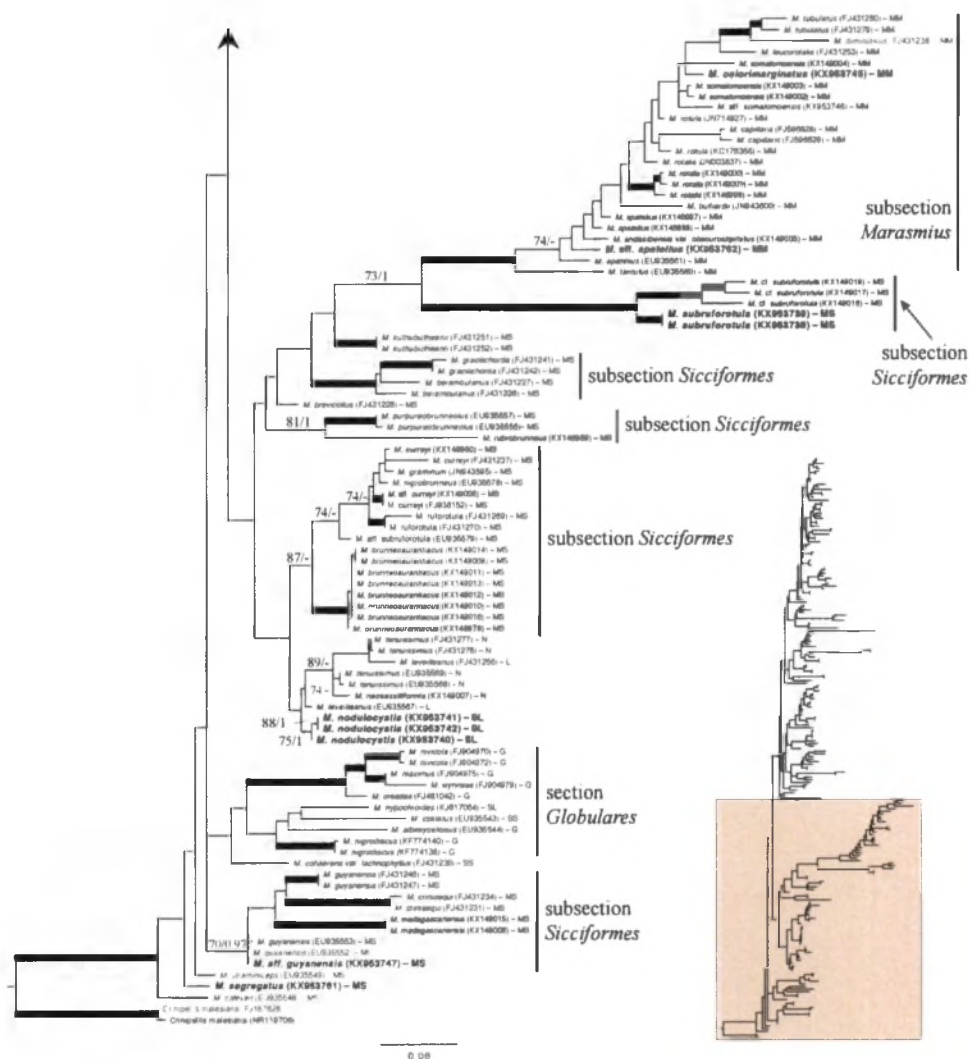


FIGURE 1c. Maximum likelihood phylogeny based on ITS sequence data. *Marasmius* from São Tomé and Príncipe are indicated in bold type. Values separated by / refer to nonparametric ML bootstrap proportions and Bayesian posterior probabilities, respectively. Values greater than 70/0.70 are shown (- designates a value below 70% or below 0.70). Nodes receiving support values greater than 90/0.95 are represented by bold branches. G – sect. *Globulares*; N – sect. *Neosessiles*; L – sect. *Leveilleani*; MM – sect. *Marasmius* subsect. *Marasmius*; MS – sect. *Marasmius* subsect. *Sicciformes*; SA – sect. *Sicci* ser. *Atrorubentes*; SL – sect. *Sicci* ser. *Leonini*; SS – sect. *Sicci* ser. *Spinulosi*; SH – sect. *Sicci* ser. *Haematocephali*

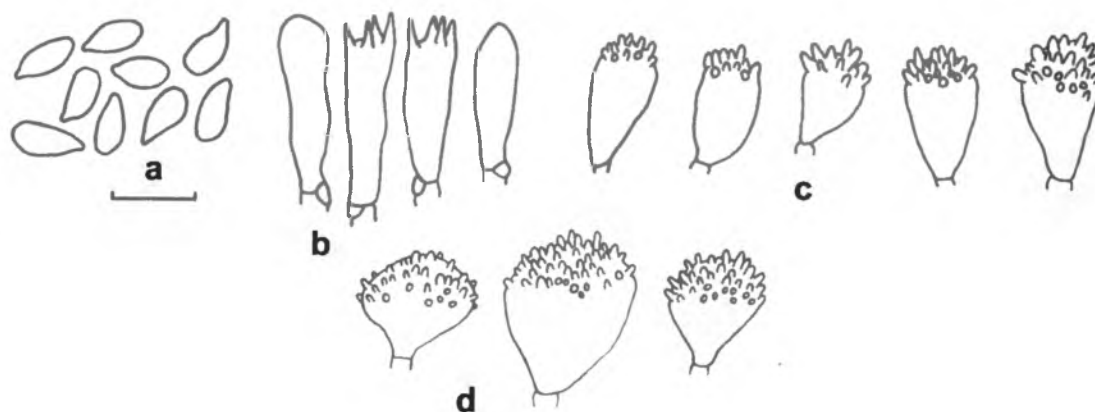


FIGURE 2. *Marasmius rotalis* (DED 8246). a. Basidiospores. b. Basidia and basidioles. c. Cheilocystidia. d. Pileipellis broom cells. Scale bar = 10 μ m. Illustrated by C.L. Grace.

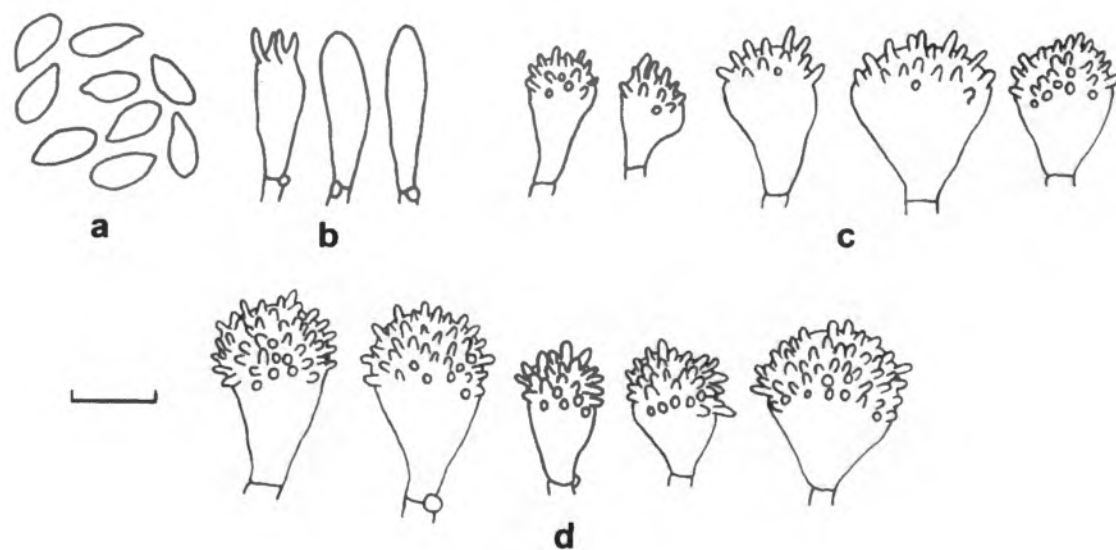


FIGURE 3. *Marasmius apatelius* (DED 8295). a. Basidiospores. b. Basidium and basidioles. c. Cheilocystidia. d. Pileipellis broom cells. Scale bar = 10 μ m. Illustrated by C.L. Grace.

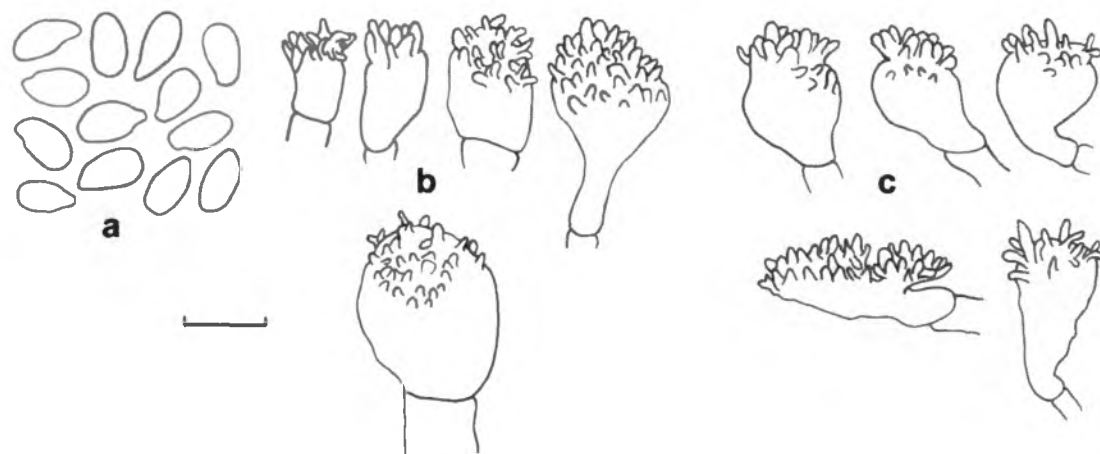


FIGURE 4. *Marasmius colorimarginatus* (DED 8309). a. Basidiospores. b. Cheilocystidia. c. Pileipellis broom cells. Scale bar = 10 μ m. Illustrated by C.L. Grace.

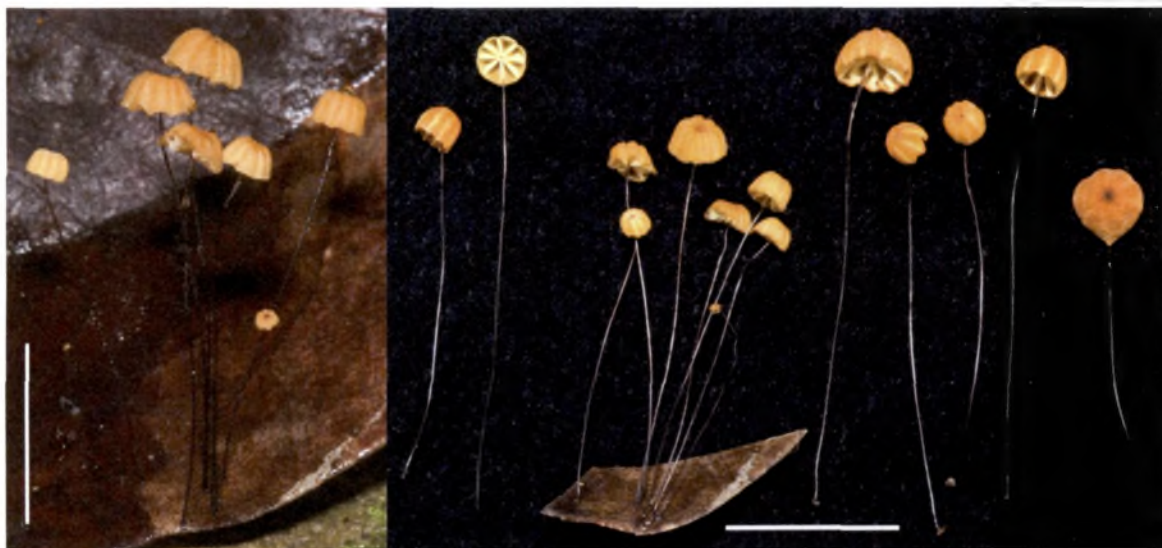


FIGURE 5. Basidiomata of *Marasmius* aff. *guyanensis* (DED 8285). Scale bar = 10 mm. Photography by B.A. Perry.

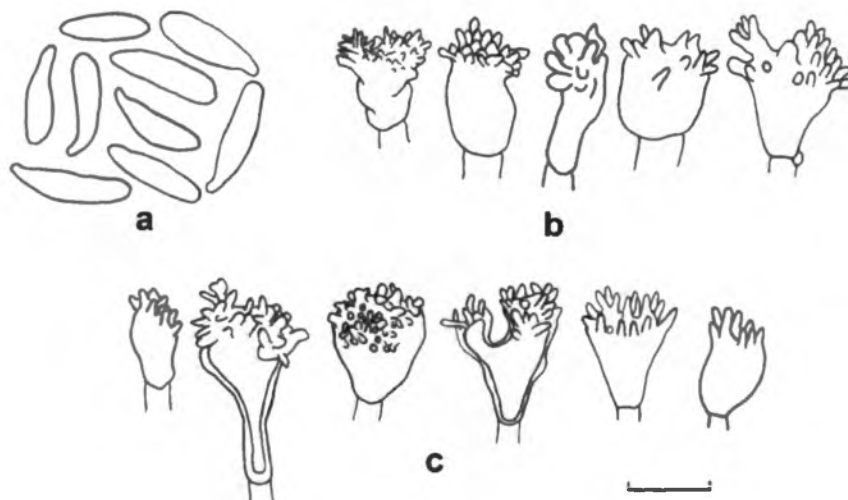


FIGURE 6. *Marasmius* aff. *guyanensis* (DED 8285). a. Basidiospores. b. Cheilocystidia. c. Pileipellis broom cells. Scale bar = 10 μ m. Illustrated by C.L. Grace.

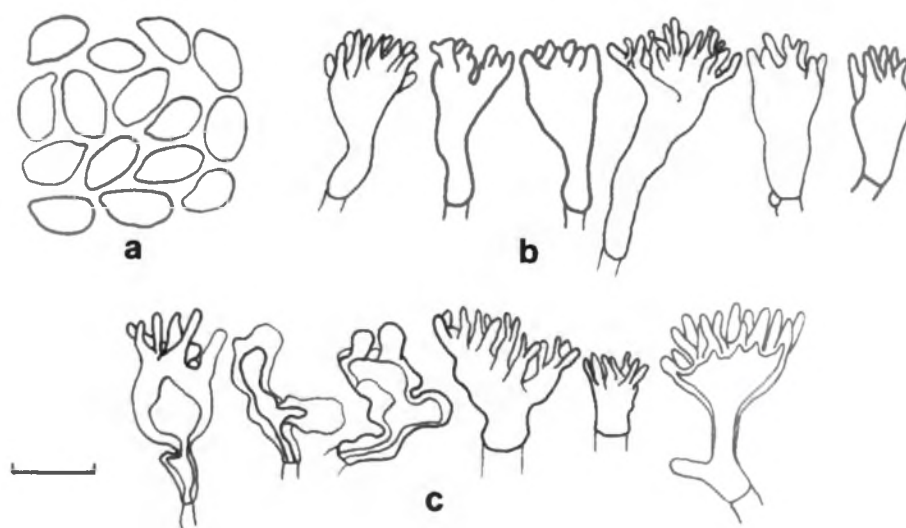


FIGURE 7. *Marasmius subruforotula* (DED 8296). a. Basidiospores. b. Cheilocystidia. c. Pileipellis broom cells. Scale bar = 10 μ m. Illustrated by C.L. Grace.



FIGURE 8. Basidiomata of *Marasmius segregatus* (DED 8256, Holotype). Scale bar = 10 mm. Photography by B.A. Perry.

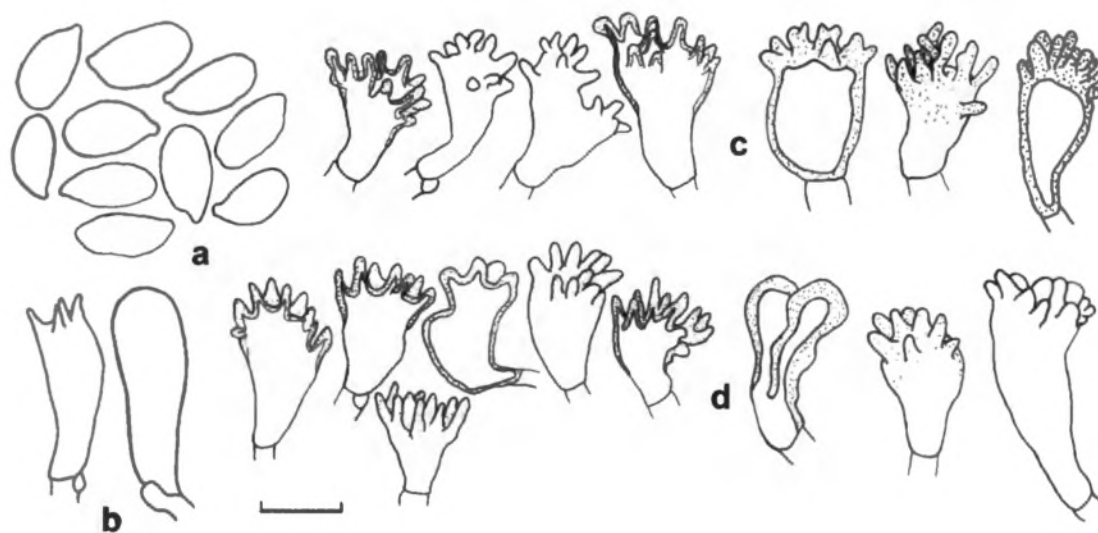


FIGURE 9. *Marasmius segregatus*. a. Basidiospores b. Basidium and basidiole c. Cheilocystidia. d. Pileipellis broom cells. a, b, c-right, d-right (DED 8256, Holotype). c-left, d-left (DED 8255). Scale bar = 10 μ m. Illustrated by C.L. Grace.



FIGURE 10. Basidiomata of *Marasmius laranja* (DED 8231, Holotype). Scale bar = 10 mm. Photography by B.A. Perry.

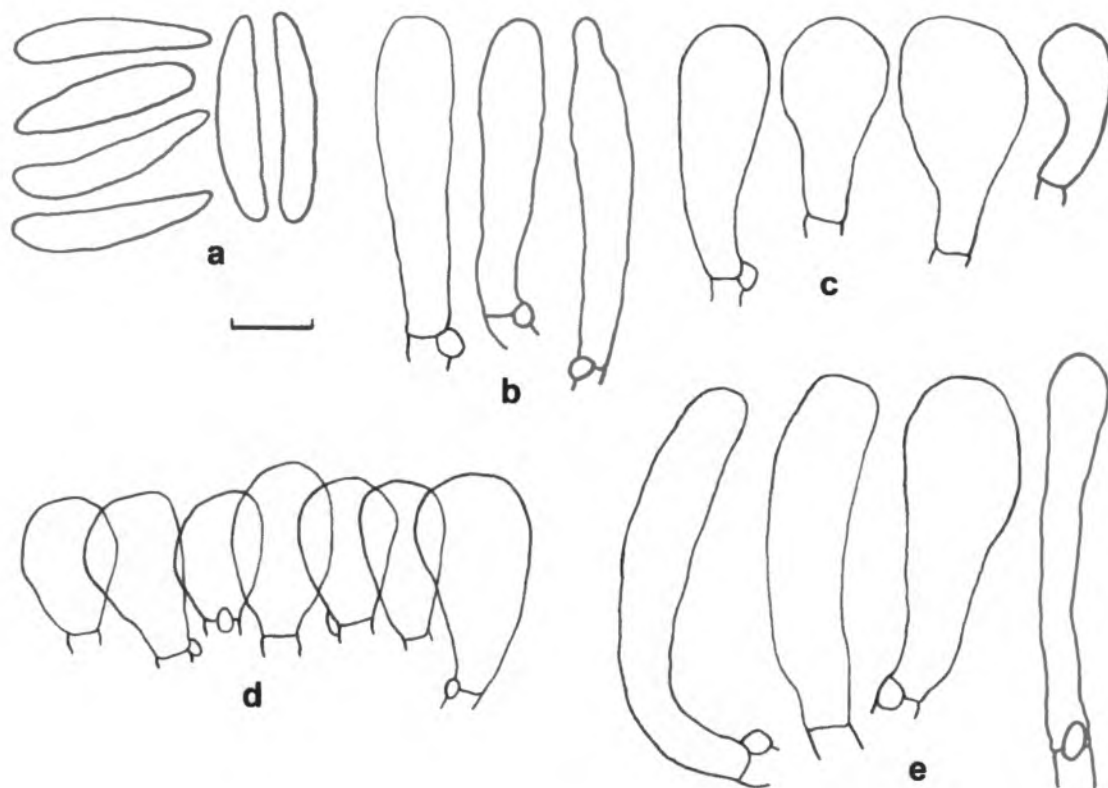


FIGURE 11. *Marasmius laranja* (DED 8231, Holotype). A. Basidiospores. b. Basidioles. c. Cheilocystidia. d. Pileipellis cells. e. Caulocystidia. Scale bar = 10 μ m. Illustrated by C.L. Grace.



FIGURE 12. Basidiomata of *Marasmius atrorubens* sensu Antonín (DED 8263). Scale bar = 10 mm. Photography by B.A. Perry.

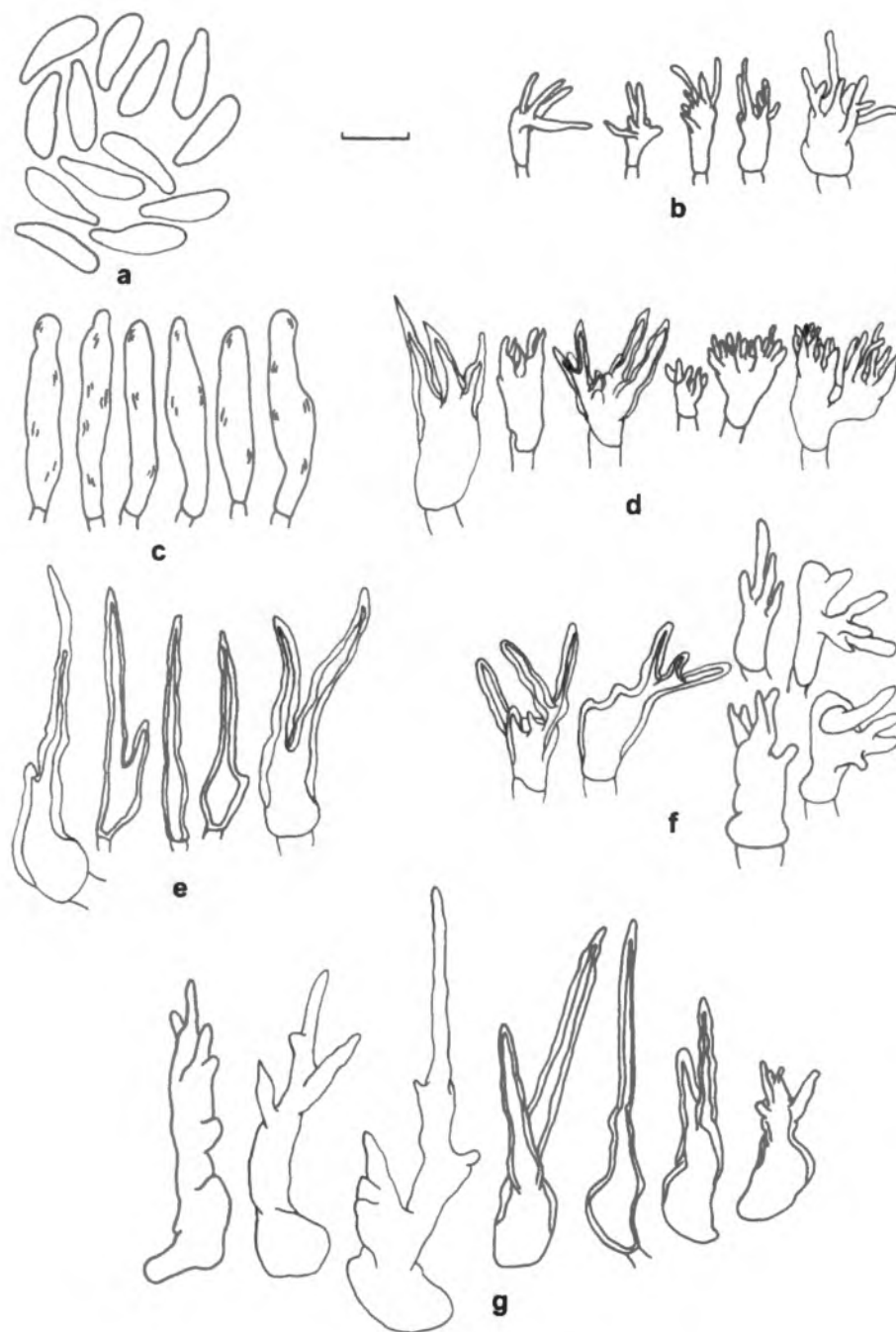


FIGURE 13. *Marasmius atrorubens* sensu Antonín (DED 8263). a. Basidiospores. b. Cheilocystidia. c. Pleurocystidia. d. Pileipellis broom cells. e. Pileosetae. f. Caulocystidia. g. Setoid caulocystidia and caulosetae. Scale bar = 10 μ m. Illustrated by C.L. Grace.



FIGURE 14. Basidiomata of *Marasmius trichotus* (DED 8248). Scale bar = 10 mm.
Photography by B.A. Perry.

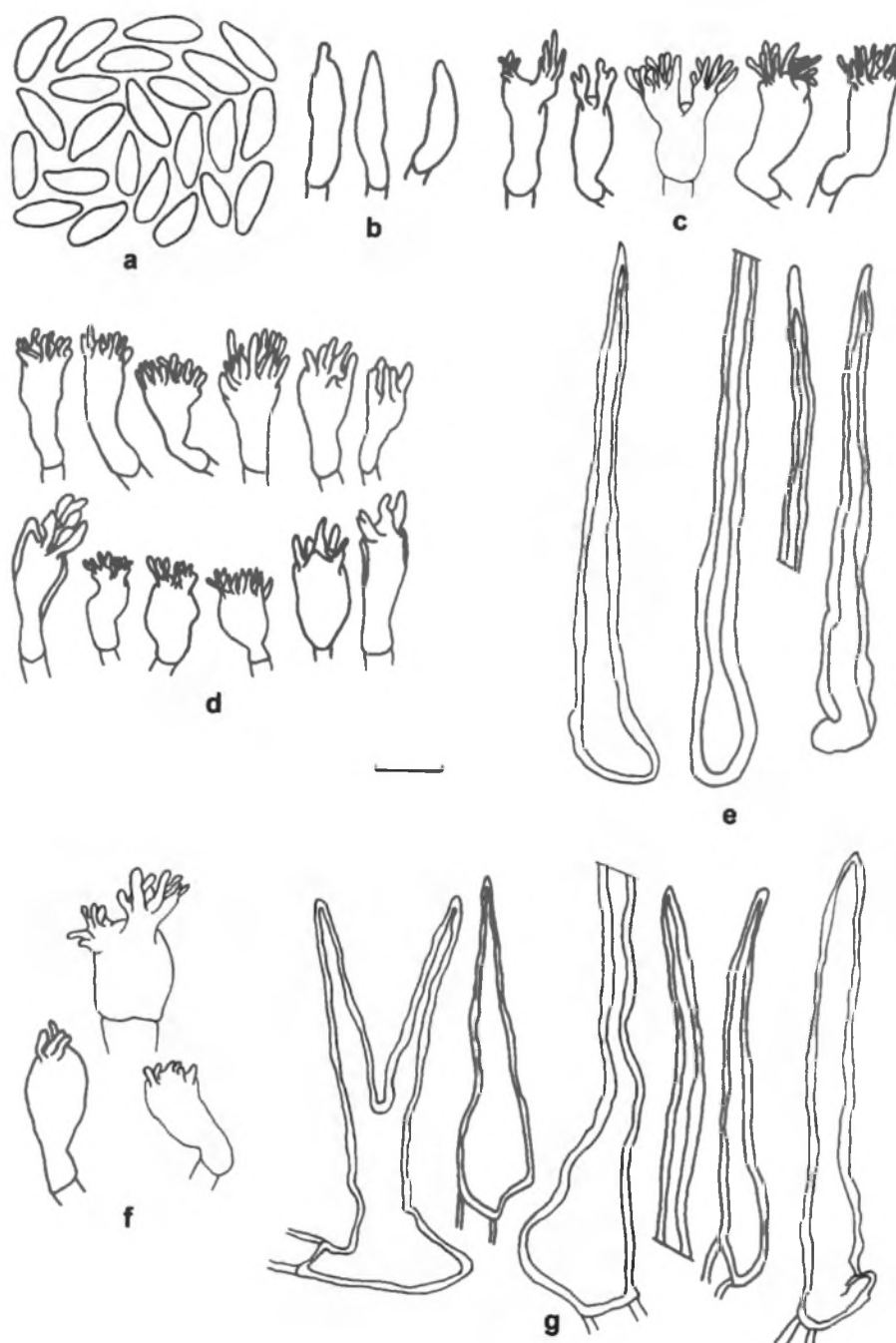


FIGURE 15. *Marasmius trichotus* (DED 8248). a. Basidiospores. b. Basidioles. c. Cheilocystidia. d. Pileipellis broom cells. e. Pileosetae. f. Caulocystidia. g. Caulosetae. Scale bar = 10 μ m. Illustrated by C.L. Grace.



FIGURE 16. Basidiomata of *Marasmius corrugatiformis* (DED 8233). Scale bar = 10 mm. Photography by B.A. Perry.

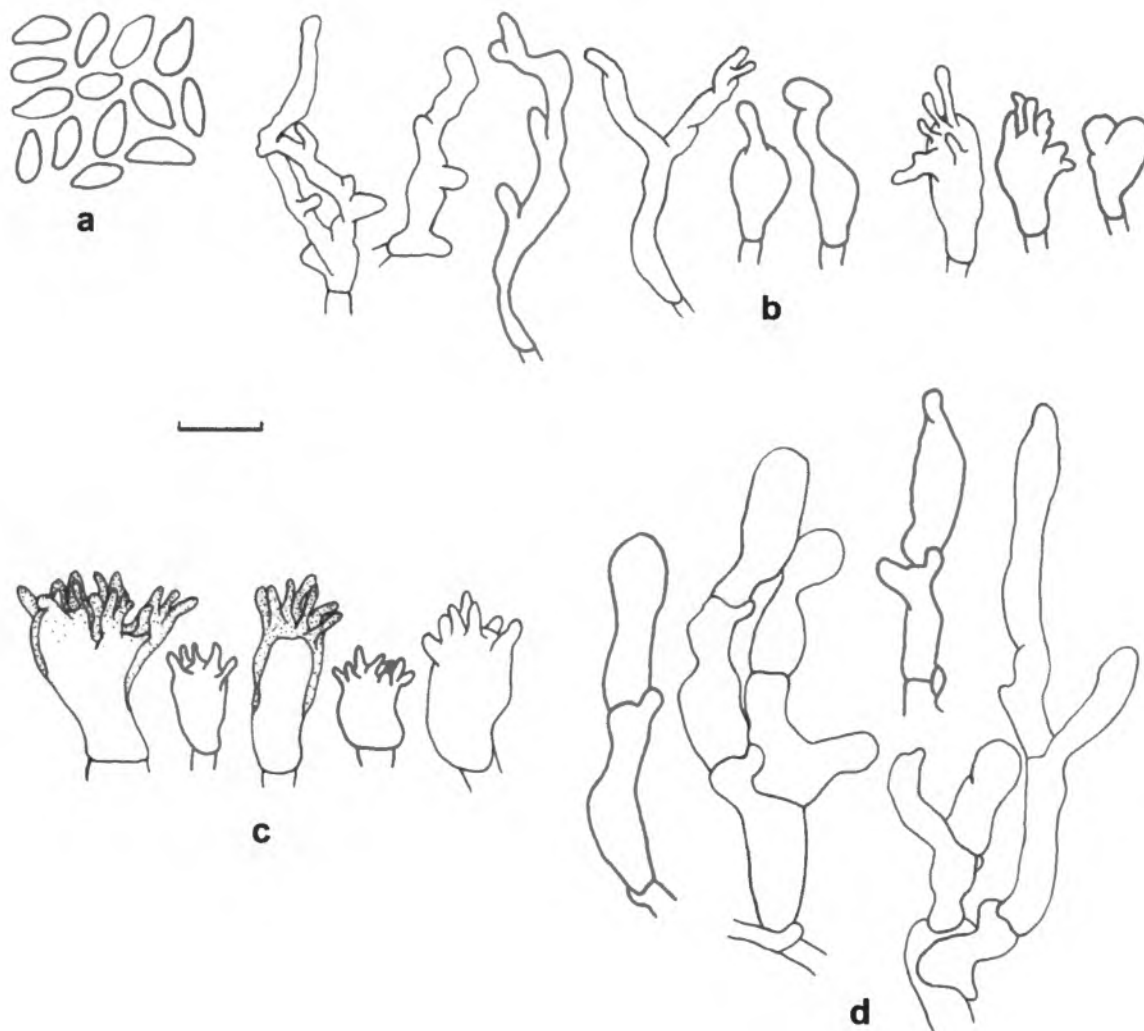


FIGURE 17. *Marasmius corrugatiformis* (DED 8233). a. Basidiospores. b. Cheilocystidia. c. Pileipellis broom cells. d. Caulocystidia. Scale bar = 10 μm . Illustrated by C.L. Grace.



FIGURE 18. Basidiomata of *Marasmius subarborescens* (DED 8215). Scale bar = 10 mm. Photography by B.A. Perry.

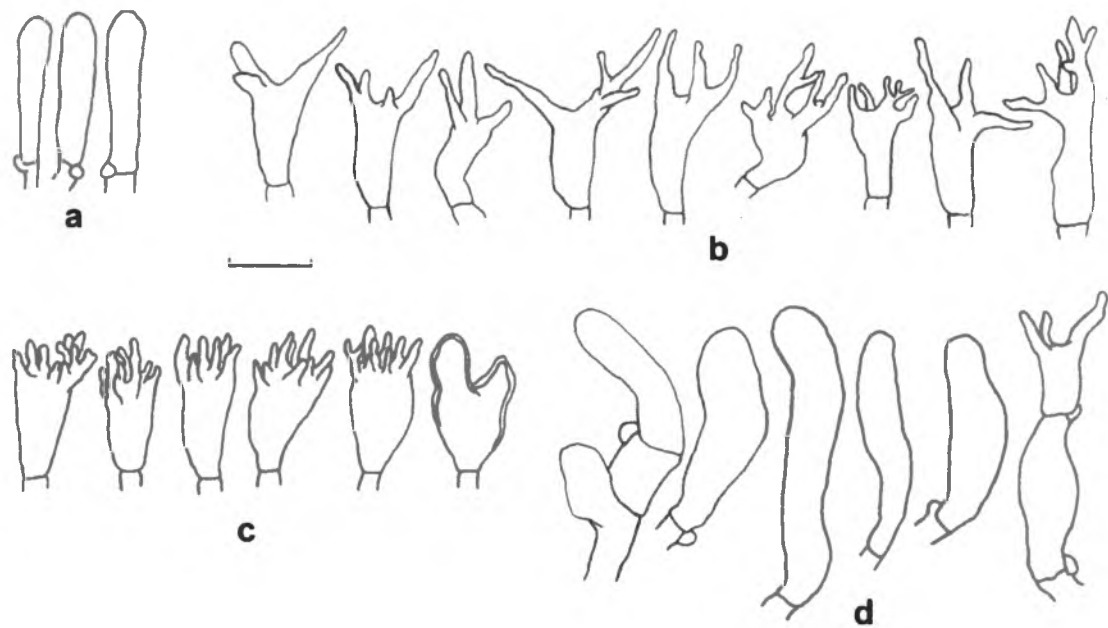


FIGURE 19. *Marasmius subarborescens* (DED 8215). a. Basidioles. b. Cheilocystidia. c. Pileipellis broom cells. d. Caulocystidia. Scale bar = 10 μ m. Illustrated by C.L. Grace.



FIGURE 20. Basidiomata of *Marasmius megistus* (DED 8230). Scale bar = 10 mm. Photography by B.A. Perry.

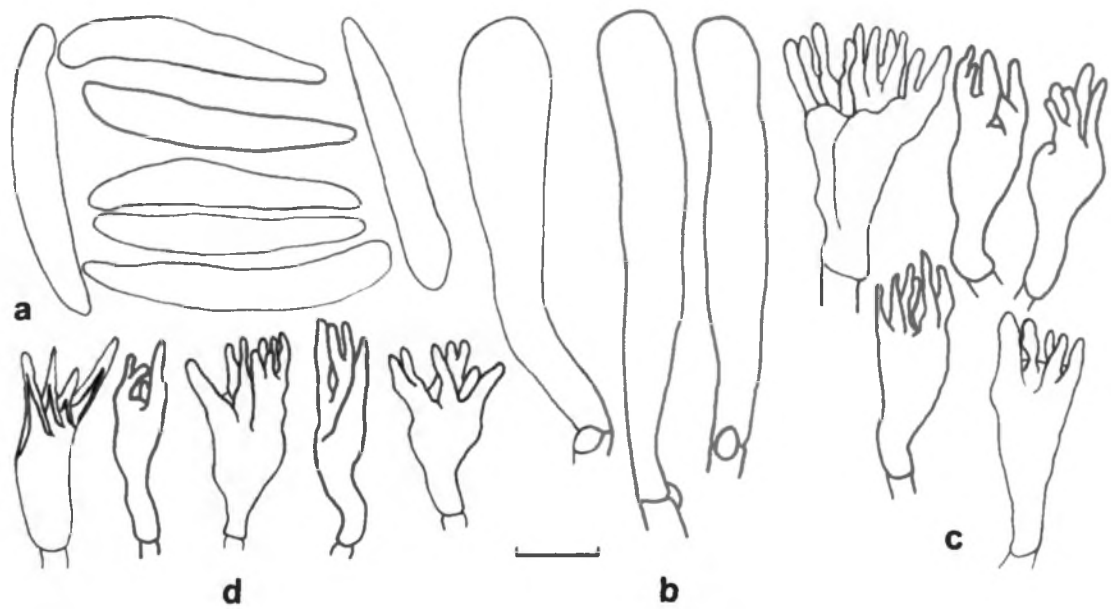


FIGURE 21. *Marasmius megistus* (DED 8230). a. Basidiospores. b. Basidioles. c. Cheilocystidia. d. Pileipellis broom cells. Scale bar = 10 μ m. Illustrated by C.L. Grace.



FIGURE 22. Basidiomata of *Marasmius haediniformis* (DED 8217). Scale bar = 10 mm. Photography by B.A. Perry.

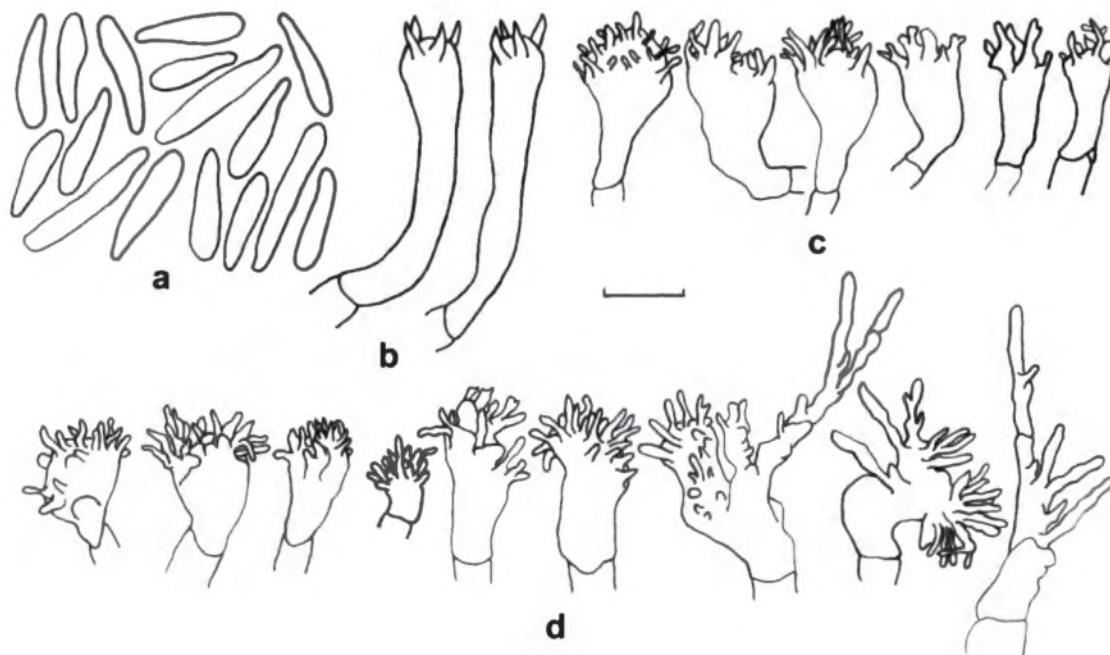


FIGURE 23. *Marasmius haediniformis* (DED 8217). a. Basidiospores. b. Basidia. c. Cheilocystidia. d. Pileipellis broom cells. Scale bar = 10 μ m. Illustrated by C.L. Grace.

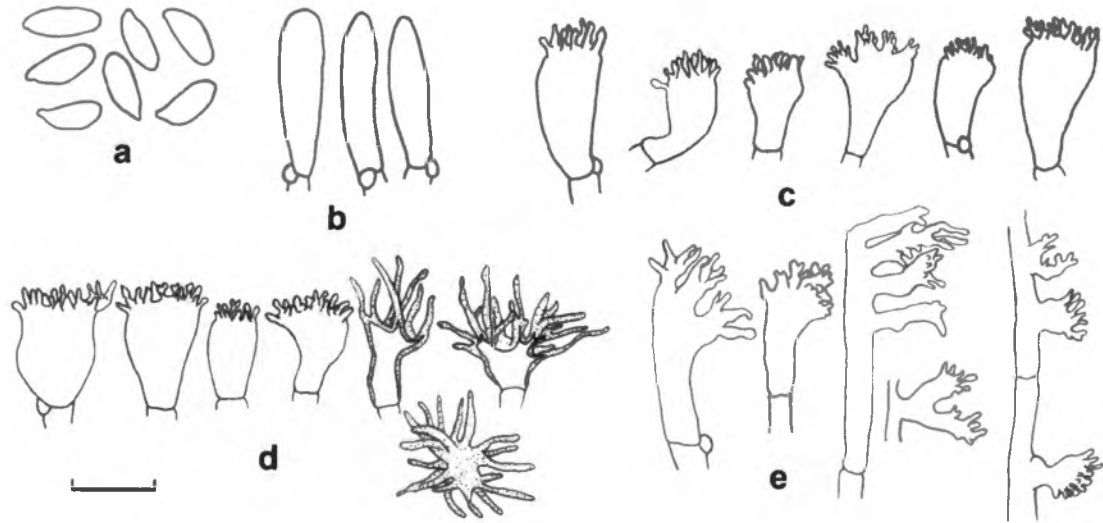


FIGURE 24. *Marasmius albisubiculosus* (DED 8277, Holotype). a. Basidiospores. b. Basidioles. c. Cheilocystidia. d. Pileipellis broom cells. e. Caulocystidia. Scale bar = 10 μm . Illustrated by C.L. Grace.



FIGURE 25. Basidiomata of *Marasmius leptcephalus* (DED 8253, Holotype). Scale bar = 10 mm. Photography by B.A. Perry.

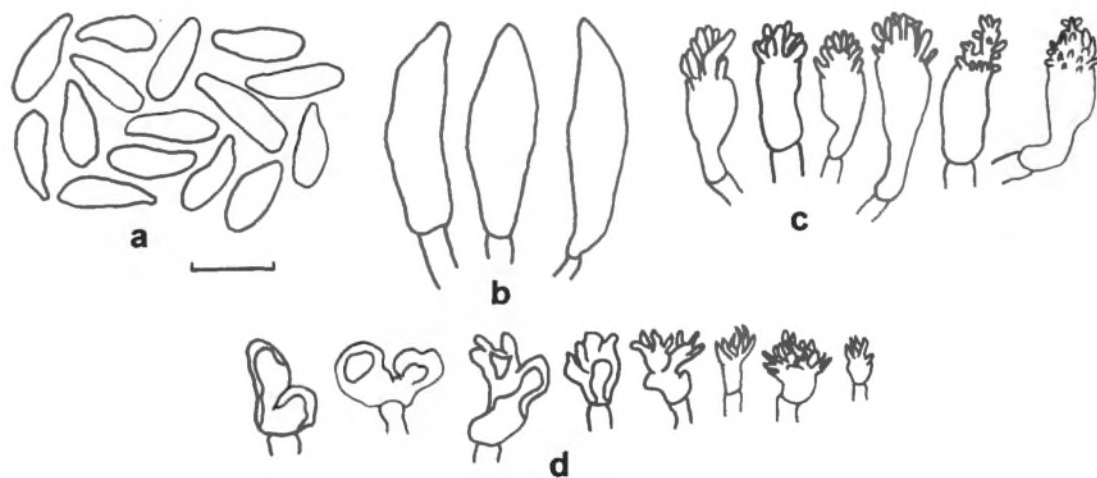


FIGURE 26. *Marasmius leptocephalus* (DED 8253, Holotype). a. Basidiospores. b. Basidioles. c. Cheilocystidia. d. Pileipellis broom cells. e. Caulocystidia. Scale bar = 10 μ m. Illustrated by C.L. Grace.



FIGURE 27. Basidiomata of *Marasmius nodulocystis* (DED 8283). Scale bar = 10 mm. Photography by B.A. Perry.

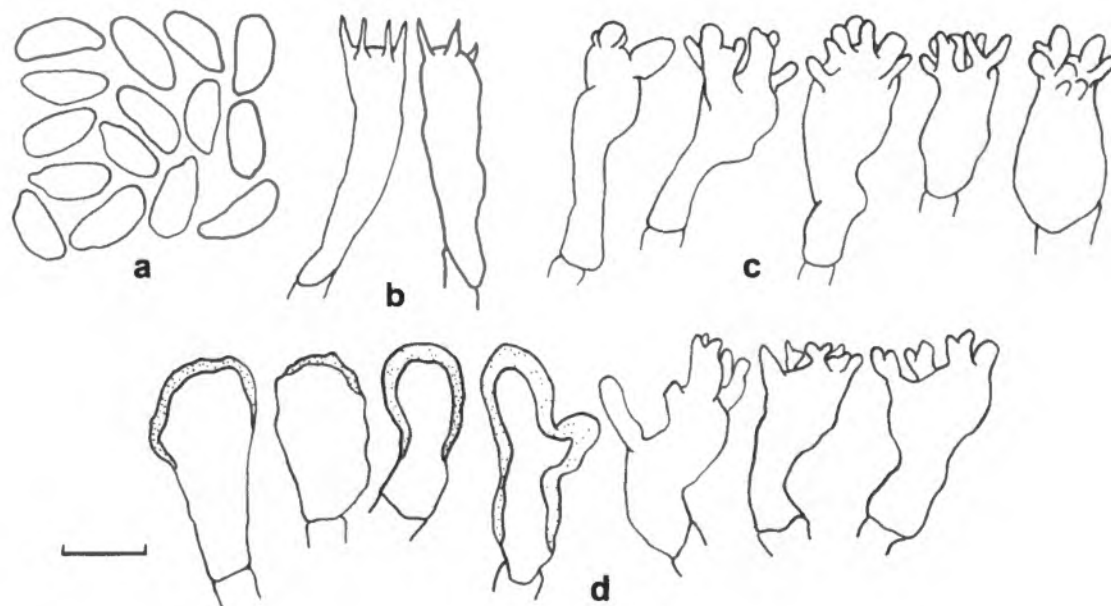


FIGURE 28. *Marasmius nodulocystis* (DED 8269). a. Basidiospores. b. Basidia. c. Cheilocystidia. d. Pileipellis cells. Scale bar = 10 μ m. Illustrated by C.L. Grace.

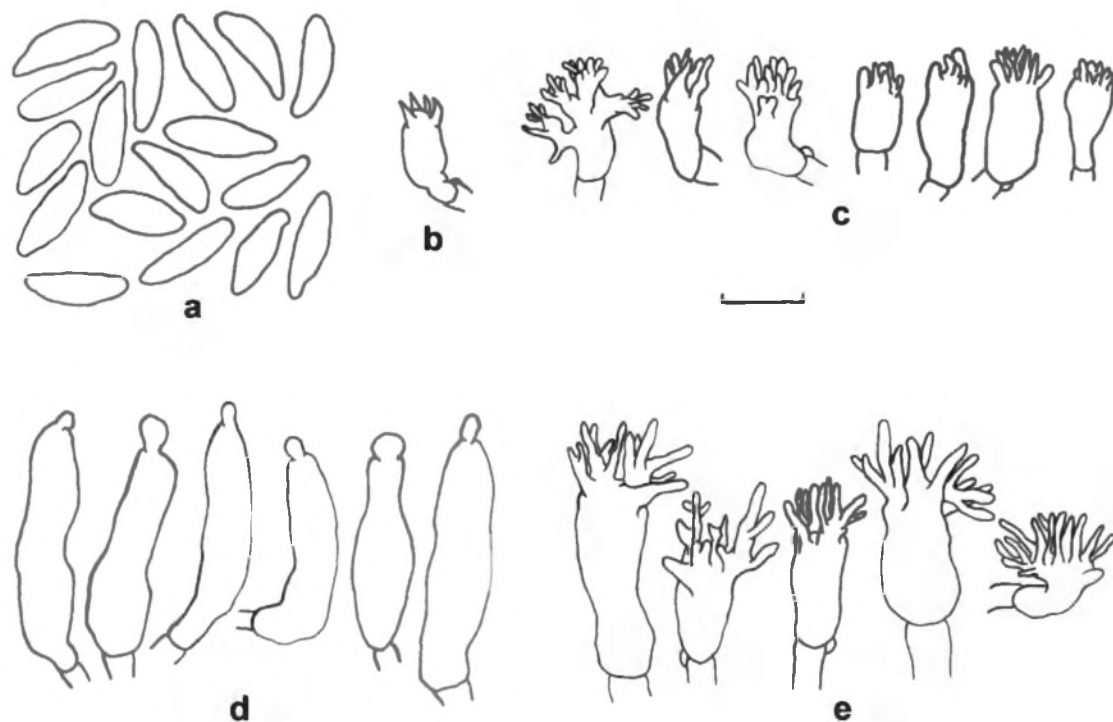


FIGURE 29. *Marasmius suthepensis* (DED 8292). a. Basidiospores. b. Basidium. c. Cheilocystidia. d. Pleurocystidia. e. Pileipellis broom cells. Scale bar = 10 μ m. Illustrated by C.L. Grace.



FIGURE 30. Basidiomata of *Marasmius elaeocephalus* (DED 8254). Scale bar = 10 mm. Photography by B.A. Perry.

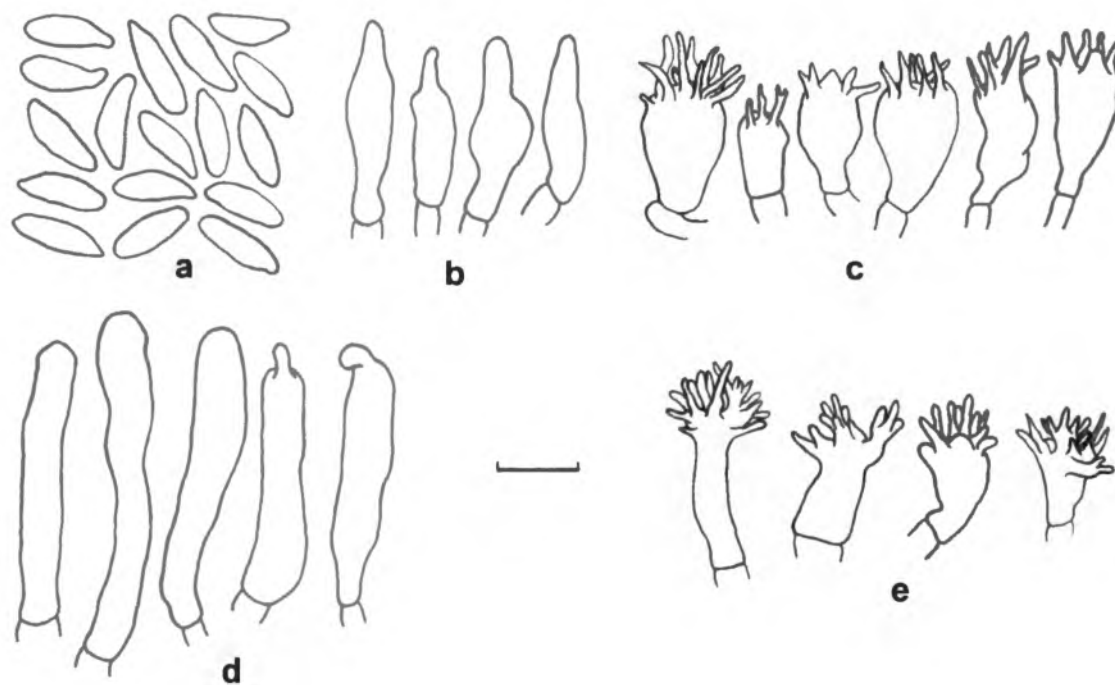


FIGURE 31. *Marasmius elaeocephalus* (DED 8254). a. Basidiospores. b. Basidioles. c. Cheilocystidia. d. Pleurocystidia. e. Pileipellis broom cells. Scale bar = 10 μm . Illustrated by C.L. Grace.



FIGURE 32. Basidiomata of *Marasmius elaeocephaliformis* (DED 8213, Holotype). Scale bar = 10 mm. Photography by B.A. Perry.

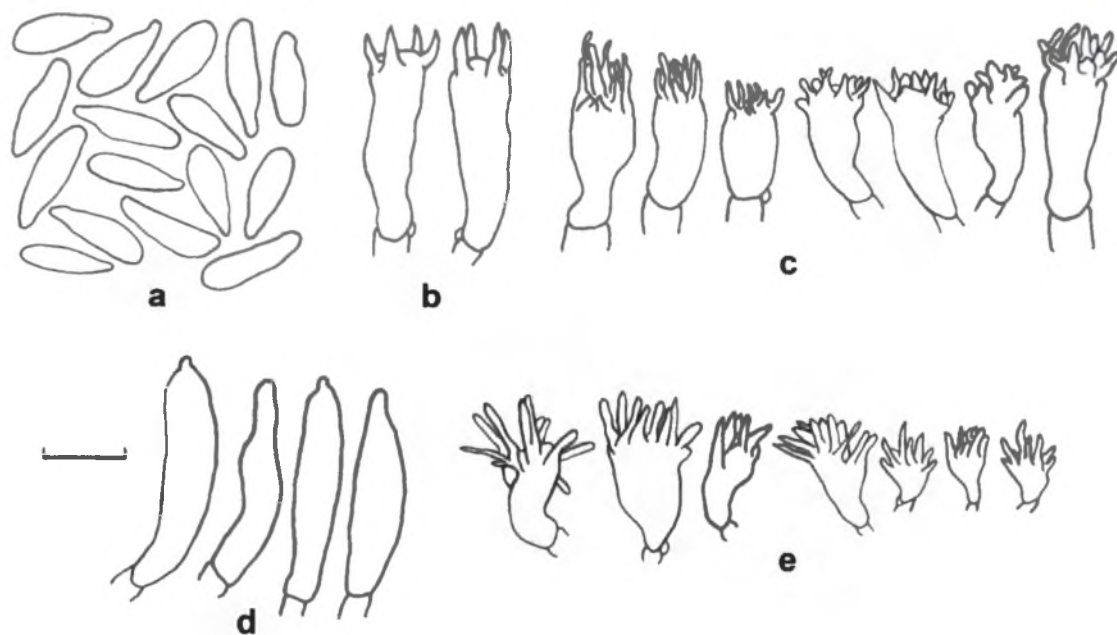


FIGURE 33. *Marasmius elaeocephaliformis* (DED 8213, Holotype). a. Basidiospores. b. Basidia. c. Cheilocystidia. d. Pleurocystidia. e. Pileipellis broom cells. Scale bar = 10 μ m. Illustrated by C.L. Grace.



FIGURE 34. Basidiomata of *Marasmius grandisetulosus* (left-DED 8225, right-DED 8257). Scale bar = 10 mm. Photography by B.A. Perry.

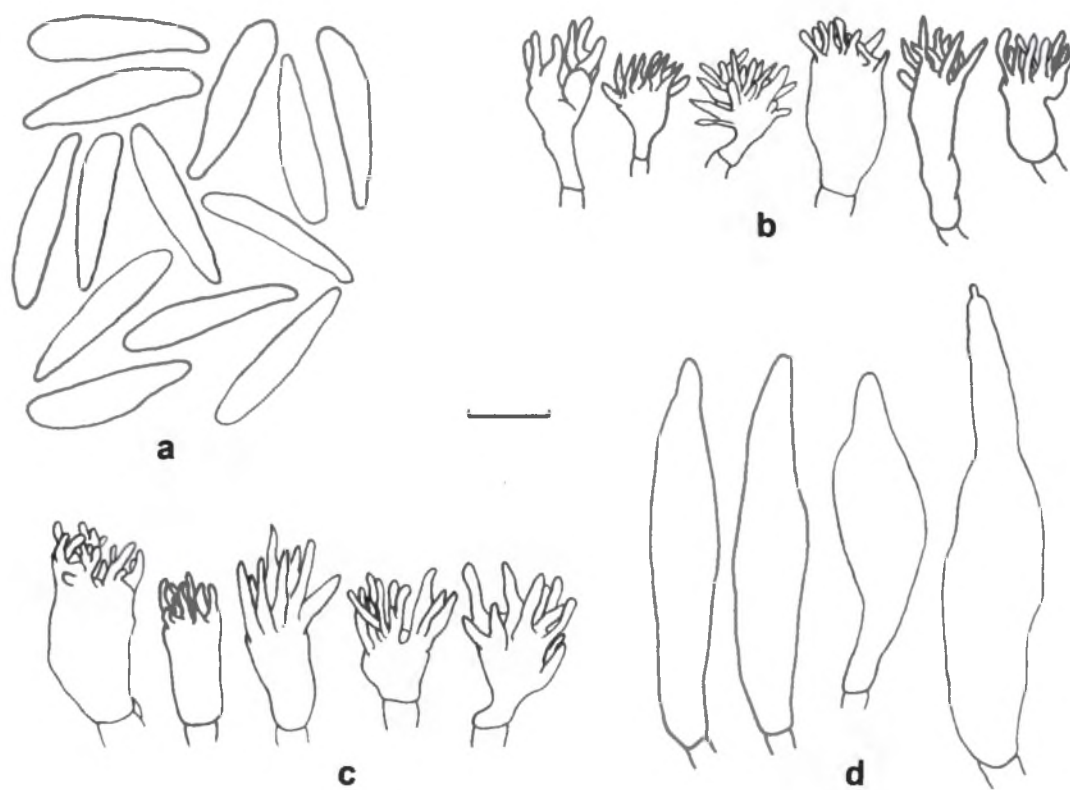


FIGURE 35. *Marasmius grandisetulosus* (DED 8257). a. Basidiospores. b. Cheilocystidia. c. Pileipellis broom cells. d. Pleurocystidia. Scale bar = 10 μm . Illustrated by C.L. Grace.



FIGURE 36. Basidiomata of *Marasmius tenuisetulosus* (DED 8267). Scale bar = 10 mm. Photography by B.A. Perry.

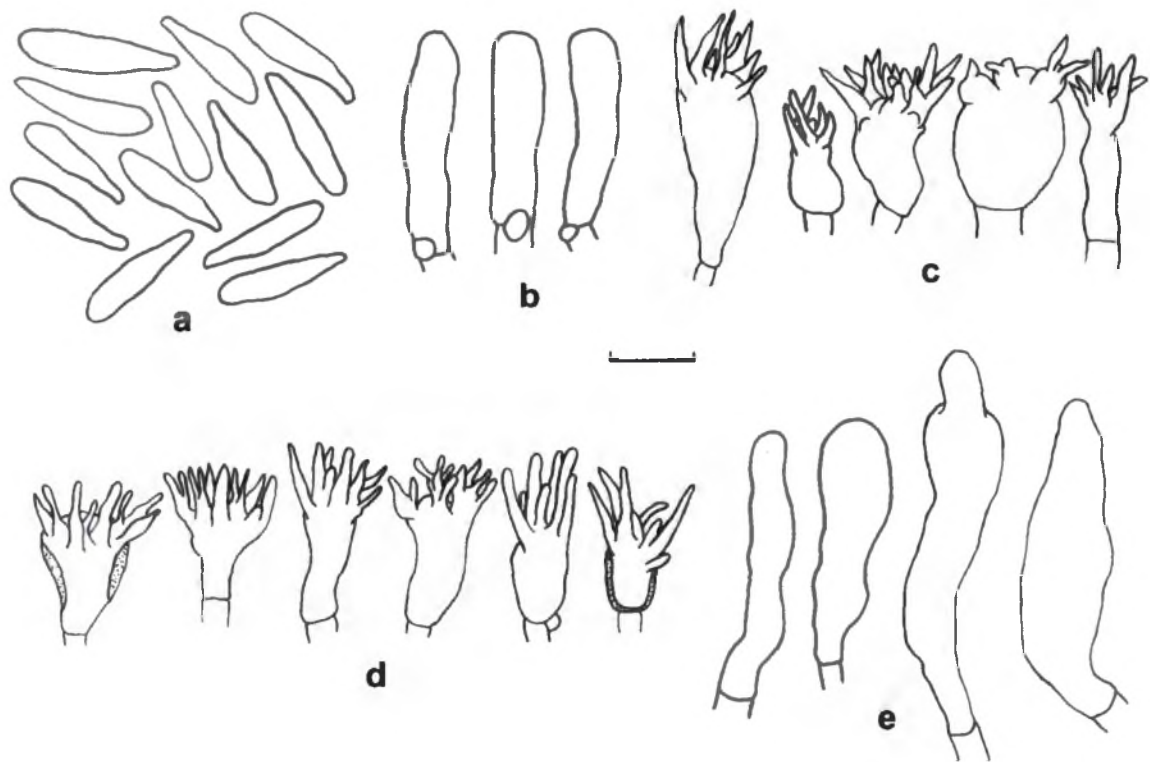


FIGURE 37. *Marasmius tenuisetulosus* (DED 8267). a. Basidiospores. b. Basidioles. c. Cheilocystidia. d. Pileipellis broom cells. e. Pleurocystidia. Scale bar = 10 μ m. Illustrated by C.L. Grace.