



# A morphological and phylogenetic evaluation of *Marasmius* sect. *Globulares* (Globulares-Sicci complex) with nine new taxa from the Neotropical Atlantic Forest

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## Key words

Agaricales  
Marasmiaceae  
Neotropics  
phylogenetics  
stirpes  
systematics  
taxonomy

**Abstract** The largest and most recently emended *Marasmius* sect. *Globulares* (Globulares-Sicci complex) has increased in number of species annually while its infrasectional organization remains inconclusive. During forays in remnants of the Atlantic Rainforest in Brazil, 24 taxa of *Marasmius* belonging to sect. *Globulares* were collected from which nine are herein proposed as new: *Marasmius altoribeirensis*, *M. ambicellularis*, *M. hobbitii*, *M. luteoolivaceus*, *M. neotropicalis*, *M. pallidibrunneus*, *M. pseudoniveoaffinis*, *M. rhabarbarinoides* and *M. venatifolius*. We took this opportunity to evaluate sect. *Globulares sensu* Antonín & Noordel. in particular, combining morphological examination and both single and multilocus phylogenetic analyses using LSU and ITS data, including Neotropical samples to a broader and more globally distributed sampling of over 200 strains. Three different approaches were developed in order to better use the genetic information via Bayesian and Maximum Likelihood analyses. The implementation of these approaches resulted in: i) the phylogenetic placement of the new and known taxa herein studied among the other taxa of a wide sampling of the section; ii) the reconstruction of improved phylogenetic trees presenting more strongly supported resolution especially from intermediate to deep nodes; iii) clearer evidence indicating that the series within sect. *Sicci* and sect. *Globulares* in the traditional concept are non-monophyletic by this more stringent evaluation; and iv) the existence of several monophyletic supraspecific groups equivalent to the stirpes of Singer – clusters of morphologically similar species. These two latter points corroborate with findings of previous studies implementing analyses with the entire genus. Based on these results, we proposed a new infrasectional classification elevating Singer's concept of stirpes to series. Thirteen new series, the emendation of three extant series and three subsections gathering these series based on the major clades are proposed.

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## INTRODUCTION

The genus *Marasmius* (*Marasmiaceae*, *Agaricales*) is mostly composed of saprotrophic mushroom-forming fungi that are commonly found on leaves and wood debris in forest litter worldwide. It is overwhelmingly diverse morphologically and genetically, and thus is taxonomically challenging. Out of 1973 *Marasmius* records in Index Fungorum (<http://www.indexfungorum.org/>, accessed on 20 Apr. 2018), 1415 are valid species, varieties, or synonyms in *Marasmius*, and 558 are names currently classified and combined in different genera (55): *Gymnopus* (91), *Marasmiellus* (58), *Collybia* (23), *Cryptomarasmius* (20), *Mycetinis* (20), *Strobilurus* (15), *Crinipellis* (13), *Mycena* (8), and the rest distributed into 47 genera of various families in *Agaricales*. In addition, the infrageneric classification of *Marasmius sensu stricto* (s.str.) is still unclear (Antonín & Noordeloos 2010).

Wannathes et al. (2009) and Tan et al. (2009) were the first published studies to carry out phylogenetic analyses of a large sampling of *Marasmius* s.str. They evaluated similar datasets of regional sampling to tentatively verify the phylogeny of the whole *Marasmius* s.str. using ITS data only, which resulted in poor reconstruction of trees with most of the intermediate and

deeper nodes unsupported, plus discrepancies in some relationships. Wannathes et al. (2009) recovered a monophyletic clade composed of representatives of sect. *Globulares sensu* Singer and sect. *Sicci* (Globulares-Sicci complex) with strong statistical support while Tan et al. (2009) showed no support for such clade. However, both studies reached very important conclusions regarding the ITS data, based on their analyses of the entire genus: a) ITS data supported recognition of morphospecies useful for taxonomic delimitation at the species level; b) this marker is of limited value in clarifying infrageneric groups due to the lack of statistical support for deeper nodes in the tree; c) none of the series of sect. *Sicci* or sect. *Globulares sensu* Singer are monophyletic in their analyses; d) ITS can be used to define small clades of species sharing some morphological characteristics; e) morphological features once traditionally used to delimitate sections and series in the genus may have different taxonomic relevance at various ranks.

Singer (1986) recognized 12 sections, of which sect. *Globulares* is composed of species having a hymeniform pileipellis exclusively composed of *Globulares*-type smooth cells while sect. *Sicci* groups species having *Siccus*-type broom cells in the pileipellis, as well as few species presenting both cell types. Based on the phylogenetic results of the Globulares-Sicci complex discussed in Tan et al. (2009) and Wannathes et al. (2009), Antonín & Noordeloos (2010) proposed to merge sections *Globulares* and *Sicci* into a single section, *Globulares* Kühner emend. Antonín & Noordel. However, in spite of forming a single monophyletic group, members of both sect. *Globulares sensu* Singer and *Sicci* were mixed with the existence of multiple

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scattered subclades, suggesting that the infrasectional groups (subsections or series) are non-monophyletic not only within this clade, but throughout other evaluated sections as well (Tan et al. 2009, Wannathes et al. 2009). Based on that, Antonín & Noordeloos (2010) did not propose infrasectional organization and the old morphological concepts of sect. *Globulares* and sect. *Sicci* (including series *Atrorubentes*, *Haematocephali*, *Leonini* and *Spinulosi*) were preserved as morphogroups (Singer 1958, 1976, Antonín & Noordeloos 1993, Desjardin & Horak 1997).

The problem with ITS data is that while it is very helpful for species-level investigations in fungi, it is a fast-evolving gene region that can present serious sequence alignment problems (especially for large and diverse sampling) at higher ranks such as sectional level (Nilsson et al. 2008, Schoch et al. 2012). We examined the ITS data matrix (M4240 in [www.treebase.org](http://www.treebase.org)) of Tan et al. (2009) and observed misaligned sites and ambiguities caused by the presence of very divergent groups of species in the same dataset, and also many regions with gaps. We were unable to examine the matrix used in Wannathes et al. (2009) since it is not publicly available. Both studies pointed out the need for broader and global sampling, including the use of additional genetic markers.

In the present study, we aimed to evaluate *Marasmius* sect. *Globulares sensu* Antonín & Noordeloos (2010) (sections *Globulares* and *Sicci sensu* Singer) in particular, combining morphological data and phylogenetic analyses on a broader and more globally distributed sampling, including one additional, more conserved marker: LSU. This study comprises the first attempt of multilocus analysis in *Marasmius* combining LSU and ITS matrices, but solely including members of sect. *Globulares* and sect. *Sicci* as the ingroup.

Recent forays in remnants of the Atlantic Rainforest in South-eastern Brazil yielded 24 taxa of *Marasmius* belonging to sect. *Globulares* and *Sicci*. *Marasmius altoribeirensis*, *M. ambicellularis*, *M. hobbitii*, *M. luteoolivaceus*, *M. neotropicalis*, *M. pallidibrunneus*, *M. pseudoniveoaffinis*, *M. rhabarbarinoides* and *M. venatifolius* are described here as new species. All the 24 taxa were morphologically examined and arranged according to the informal subsectional groups as outlined by Antonín & Noordeloos (2010) to assist the taxonomic discussion. However, a new infrasectional classification is proposed at the end of this paper. Detailed macro- and micromorphological descriptions, line-drawing illustrations, and taxonomic comments are herein provided. Furthermore, ITS and LSU data were obtained from the specimens of this Neotropical sampling.

These neotropical taxa were included in a broad sampling of species of the *Globulares-Sicci* complex from different geographic areas of the World in order to carry out phylogenetic analyses using combined evidence from ITS and LSU sequence data. We developed three approaches (detailed in Material and Methods) to enhance the use of the available genetic data in producing datasets for the analyses. Our goals were to: i) observe the phylogenetic placement of the new and known taxa studied herein among the other taxa of this wider sampling (in number of taxa, geographic distribution and morphological diversity); ii) produce better reconstructed phylogenetic trees presenting more strongly supported relationships especially from intermediate to deep nodes; iii) verify if the series in sect. *Sicci* and sect. *Globulares sensu* Singer are non-monophyletic by this more stringent evaluation; and iv) tentatively find monophyletic groups, correlating the molecular phylogeny with morphological data. We also addressed some taxonomic issues about morphological characteristics traditionally used to delimit sections or series in particularly sect. *Globulares* Kühner emend. Antonín & Noordel.

## MATERIAL AND METHODS

### Areas sampled

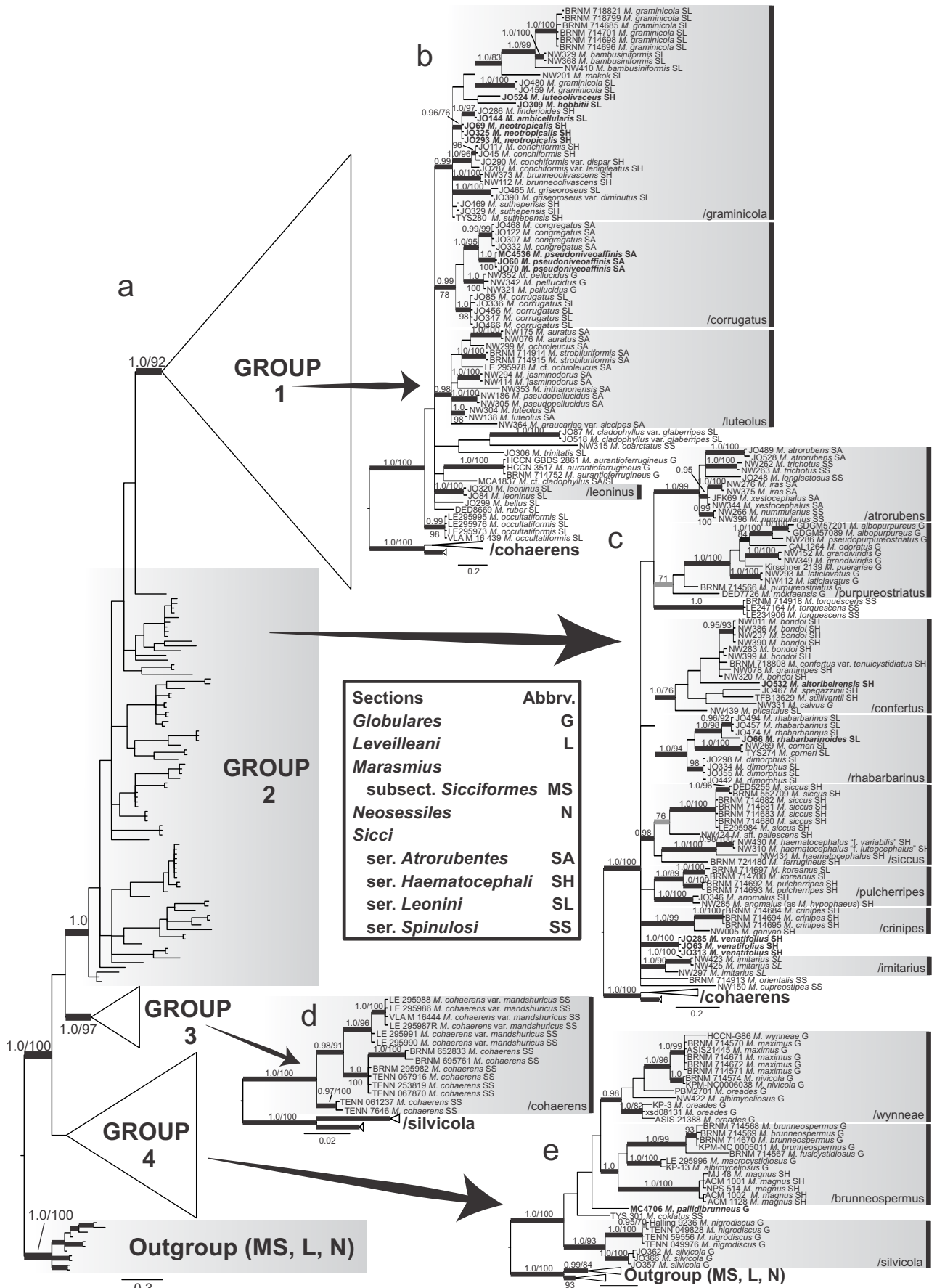
Collections were obtained from four areas: 1) Reserva Biológica de Paranapiacaba (S23°46'00"–S23°47'10" and W46°18'20"–W46°18'40"), a predominantly mountainous area, close to the coast, covered by Ombrophilous Dense Forest up to 891 m in altitude (Domingos et al. 2000, Xavier et al. 2008), with mean annual rainfall of 3381 mm and mean temperature around 17.9 °C (Domingos et al. 2000); 2) Parque Estadual da Cantareira, Núcleo Engordador (S23°24'11.89" and W46°35'12.29"), an area covered by Seasonal Semideciduous Forest of humid mesothermal climate up to 1215 m in altitude (Xavier et al. 2008), mean annual rainfall 1545 mm (Ventura et al. 1966) and temperatures 14.3–18.2 °C (Secretaria do Meio Ambiente 2000); 3) Parque Estadual das Fontes do Ipiranga (S23°38'08"–S23°40'18" and W46°36'48"–W46°38'00"), an urban park of preserved Seasonal Semideciduous Forest (Pivello & Peccinini 2002) reaching 798 m in altitude on the Atlantic plateau (Xavier et al. 2008), mean annual rainfall 1368 mm and mean annual temperature 23.9 °C (Santos & Funari 2002); 4) Parque Estadual Turístico do Alto Ribeira (S24°16'40"–S24°38'30" and W48°27'20"–W48°44'00") with a karst mountainous residual landscape (Godoy 2001) predominantly covered by Ombrophilous Forest (Ivanauskas et al. 2012), and a humid Cfb-Subtropical climate (Köppen 1948), with mean temperatures from 18–22 °C (Secretaria do Meio Ambiente 2000), and annual rainfall from 1500–2000 mm (Lepsch et al. 1990).

### Morphological examination

Colour codes from fresh material followed Kornerup & Wanscher (1978) (only for *Marasmius ruber*) and Küppers (2002). Colour plates of the species in this study can be found in Fig. S8–S10. Specimens were dried at 30–40 °C for subsequent herbarium preservation and microscopic examination. Sections of dried material were treated with 70 % ethanol and mounted in 5 % KOH or Melzer's reagent. In specific cases, sections were mounted in Cresyl blue or 5 % NH<sub>4</sub>OH. In species represented by a single collection, basidiospore dimensions were measured as the following: the range of length × width;  $x_m$ , the arithmetic mean of length (± standard deviation, SD) × width (± SD);  $Q_m$ , the mean of the range of length/width of basidiospores (± SD); and  $n$ , the number of spores measured. For replicated collections, we calculated:  $x_{mm}$ , the range of spore means of length × width;  $x_{mm}$ , the mean of spore means of length (± SD) × width (± SD);  $Q_{mm}$ , the range of  $Q_m$  values;  $Q_{mm}$ , the mean of  $Q_m$  values (± SD);  $n/s$ , number of spores measured per specimen; and  $s$ , number of specimens analysed of a taxon. For lamellae spacing: ' $L$ ' is the number of lamellae that range from the stipe apex to the pileus margin, and ' $I$ ' is the number of series of lamellulae among the lamellae. The collections were deposited in the SP herbarium.

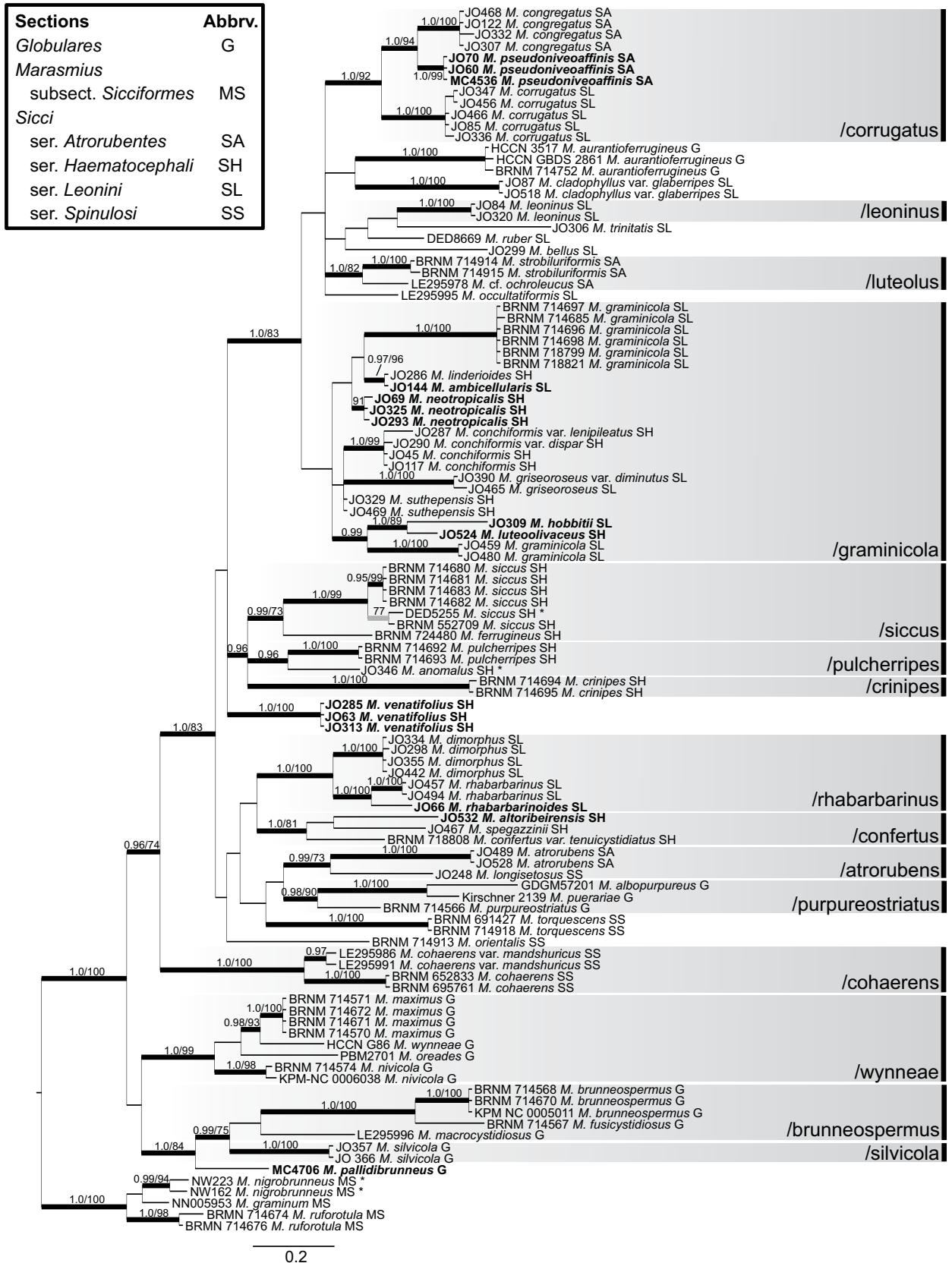
### DNA extraction, amplification and sequencing

Mycelium tissues and lyophilised basidiome fragments were obtained according to Oliveira et al. (2014) and were used for DNA extraction following various protocols (Zolan & Pukkila 1986, Dentinger et al. 2010, Justo et al. 2011). PCR reagents were mixed as specified in Oliveira et al. (2014) and Sánchez-Ramírez et al. (2014). Primers used were ITS1-F (Gardes & Bruns 1993) and ITS4 (White et al. 1990) for the ITS rDNA and LR0R and LR5 (Vilgalys & Hester 1990) for the LSU. PCR was performed according to Oliveira et al. (2014); other alternatives of PCR programs were: for ITS, 95 °C (2 min), 5 × (95 °C (30 s), 60–56 °C (45 s) and 72 °C (45 s)), 30 × (95 °C (45 s), 55 °C (45 s) and 72 °C (45 s)) and 72 °C (10 min); and for LSU, 94 °C (2 min); 5 × (94 °C (45 s), 60–56 °C (50 s)



**Fig. 1** Bayesian 50% majority-rule trees from different ITS datasets. a. Dataset 1 tree (Tree Length (mean of 2 runs) – TL: 38.332837; -lnL (mean): -6103.95). b. Dataset 2.1 tree (TL: 13.374592; -lnL: -3654.65) based on Group 1. c. Dataset 2.2 tree (TL: 11.660204; -lnL: -4033.93) based on Group 2. d. Dataset 2.3 tree (TL: 0.248540; -lnL: -1509.58) based on Group 3. e. Dataset 2.4 (TL: 2.755805; -lnL: -2512.77) based on Group 4. Support values at the nodes consist of PP ≥ 0.95 and BS ≥ 70; unsupported nodes under PP 0.5 are collapsed. Thicker stems in black represent highly supported nodes, and those in grey moderately supported nodes. Taxa omitted in the Outgroup (MS, L, N) in 'a' and 'e' are those members of sect. *Marasmius* subsect. *Sicciformes*, sect. *Leveilleani* and sect. *Neosessiles*, and also FJ524299 in Fig. S1–S7. The sections and series indication are according to the traditional classification (Singer 1986, Antonín 1991, Antonín & Noordeloos 1993, Desjardin & Horak 1997).





**Fig. 2** Bayesian 50% majority-rule Dataset 3 tree of multilocus LSU + ITS matrices (TL: 17.399771; -lnL: -7435.56). Support values at the nodes consist of PP  $\geq$  0.95 and BS  $\geq$  70; unsupported nodes under PP 0.5 are collapsed. Thicker stems in black represent highly supported nodes, and those in grey moderately supported nodes. Taxa followed by an asterisk (\*) are represented by ITS only. The sections and series indication are according to the traditional classification (Singer 1986, Antonín 1991, Antonín & Noordeloos 1993, Desjardin & Horak 1997).

and 72 °C (80 s)), 30× (95 °C (45 s), 55 °C (50 s) and 72 °C (80 s)), and 72 °C (10 min). Sequencing procedures followed Oliveira et al. (2014) and Sánchez-Ramírez et al. (2014). Assembled and edited sequences were deposited in GenBank (Table S4). Sequenced samples from Brazil are registered in SISGen (Sistema Nacional de Gestão do Patrimônio Genético e do Conhecimento Tradicional Associado) number AEFD754.

### Phylogenetic analyses

Sequences of species belonging to the Globulares-Sicci complex were downloaded from GenBank database (NCBI) through BLAST searches (<http://blast.ncbi.nlm.nih.gov/>), with ITS sequences showing high similarity (90–100 % identity and e-value of 0.0) and deemed to be reliable both qualitatively and taxonomically. LSU dataset was composed of all sequences from GenBank of species of *Marasmius* of the Globulares-Sicci complex that also had ITS corresponding to the same strain for the concatenated LSU+ITS analyses. Based on certain data similarity with taxa of the ingroup observed during BLAST searches, alignment and further phylogenetic test analyses including the whole genus (not shown), we selected species of sect. *Marasmius* subsect. *Sicciformes*, *Marasmius leveilleanus* (sect. *Leveilleani*) and *M. tenuissimus* (sect. *Neosessiles*) to form the outgroups. All data used in this study are listed in Table S4. The alignments were conducted using MUSCLE (Edgar 2004; <http://www.ebi.ac.uk/Tools/msa/muscle/>) with default parameters. Ambiguously aligned regions were manually excluded from all nucleotide matrices by visual inspection in Geneious R7 (Kearse et al. 2012). The nucleotide substitution models were selected with jModeltest 2.1.3 (Darriba et al. 2012) or MrModeltest 2.3. (Nylander 2004).

Different datasets were prepared based on three different approaches: Dataset 1, a large ITS dataset of the most comprehensive sampling spanning the whole Globulares-Sicci complex; 2) Datasets 2.1, 2.2, 2.3 and 2.4 which are small ITS datasets derived from Dataset 1, corresponding respectively to Group 1, Group 2, Group 3 and Group 4 depicted in Fig. 1a in order to gather the sequences of close species for more congruent alignments; 3) Dataset 3, which is the concatenation of the LSU and ITS datasets (same strain per taxon) to produce a tree with combined *loci*. The purpose of the first two approaches was to minimize the loss of information due to the high variability in the ITS and misaligned blocks in ITS matrices. This loss is greater inasmuch as a larger number of *Marasmius* ITS sequences of highly diverse species are included in a single dataset, generating many ambiguous blocks within the alignment. In Dataset 3, the LSU data was useful when combined with ITS data where intermediate and deep nodes were favoured. Unfortunately, the scanty LSU sequences of *Marasmius* available in GenBank prevented the accomplishment of very thorough analyses with a sampling equivalent to Dataset 1, which is why we also performed the first two approaches instead of only Dataset 3. Furthermore, we allowed for missing LSU data of few exceptional taxa having only ITS sequences (taxa with asterisk in Fig. 2). All dataset and alignments can be found in TreeBASE ID 21680. The model selected per dataset were: GTR+I+G for Datasets 1, 2.1, 2.2, 2.4 and 3 (LSU matrix), HKY+I for Dataset 2.3 and HKY+I+G for Dataset 3 (ITS matrix).

For Maximum Likelihood analyses (ML), the trees (Fig. S2–S7) were reconstructed using the GTR+I+I model in RAxML 7.0.4 (Stamatakis 2006) and fast-bootstrapping implementing CAT approximations (only for Datasets 1, 2.1, 2.2 and 3) for 1 000 pseudoreplicates and a full ML optimization for the final tree (Fig. S2–S7). For Datasets 2.3 and 2.4, GTRGAMMAI was implemented with GAMMA+P-Invar Model parameters estimated up to an accuracy of 0.001 Log Likelihood units. We

performed MC<sup>3</sup> Bayesian analyses (BA) with MrBayes 3.2.1 (Ronquist et al. 2012), using default settings with exception of the specifications from the models (Nst = 6 for Datasets 1, 2.1, 2.2, 2.4, 3 (LSU partition) and Nst = 2 for Datasets 2.3 and 3 (ITS partition)). The BA consisted of two independent runs of: a) 10 000 000 generations, sampling frequency every 1 000 generations, 8 independent chains and 2 swaps for Dataset 1; b) 5 000 000 generations, sampling frequency every 500 generations, 6 chains and 2 swaps for Dataset 2.1 and 2.2; c) 1 000 000 of generations and sampling frequency every 100 generations, 4 independent chains and 2 swap for Datasets 2.3 and 2.4; and d) the same of the settings in letter 'a', but implementing only 6 chains for Dataset 3 (LSU and ITS concatenated). All burnin was set at 10 %. Final trees were summarized using the 50 % majority-rule consensus method. Branch lengths were summarized across the 95 % highest posterior density trees. In addition, some matrices of distance by pairwise comparisons of ITS sequences were provided for evaluation within species complex, using the total extension of the aligned ITS region (Table S1–S3).

## RESULTS

### Morphological analyses and taxonomy

Key for the 24 taxa of *Marasmius* sect. *Globulares sensu* Antonín & Noordeloos (the Globulares-Sicci complex) from the Brazilian Atlantic Forest

1. Pileipellis composed strictly of smooth cells . . . . . 2
1. Pileipellis consisting mainly of *Siccus*-type broom cells . . 3
2. Pileus yellowish orange, becoming cream with a ochraceous disc, 45–81 mm diam, pleurocystidia 55–118 µm long. . . . . *M. silvicola*
2. Pileus pale brown, 7–37 mm diam, pleurocystidia 43–87 µm long . . . . . *M. pallidibrunneus*
3. Stipitipellis bearing cylindrical clavate to setoid caulocystidia . . . . . 4
3. Stipitipellis without smooth, clavate to cylindrical caulocystidia, but broom cells may be present . . . . . 6
4. Pileus orange, up to 11 mm diam, basidiospores 13.8–18 µm long, caulocystidia setoid, elongate, up to 415 µm long, pileipellis made up only by *Siccus*-type broom cells . . . . . *M. atrorubens*
4. Pileus mainly white to cream, up to 66 mm diam, basidiospores up to 10 µm long, caulocystidia shorter and non-setoid, pileipellis formed either by smooth cells or by *Siccus*-type broom cells . . . . . 5
5. Pileus pale cream, cheilocystidia of two types, both smooth and broom cells, caulocystidia rare and short near the stipe base, up to 21.3 µm long, basidiospores up to 9 µm long. . . . . *M. congregatus*
5. Pileus mainly pure white, cheilocystidia hyphoid, caulocystidia numerous covering the whole stipe surface, up to 62 mm long, basidiospores up to 10.4(–11) µm long. . . . . *M. pseudoniveoaffinis*
6. Pleurocystidia present . . . . . 7
6. Pleurocystidia absent . . . . . 13
7. Lamellae intervenose or veined . . . . . *M. venatifolius*
7. Lamellae simple . . . . . 8
8. Pileus olivaceous . . . . . 9
8. Pileus not olivaceous, varying between yellow and orange . . . . . 10
9. Pileus up to 23 mm diam, olivaceous-brown, basidiospores 6.3–10 µm long . . . . . *M. altoribeirensis*
9. Pileus up to 12 mm diam, yellowish olive, basidiospores 9.3–12.5 µm long. . . . . *M. luteoolivaceus*

- 10. Pileus 21–45 mm diam, brownish orange, basidiospores 7.5–11.3 µm long . . . . . *M. spagazzinii*
- 10. Pileus up to 20 mm diam, yellow to orange, basidiospores > 11 µm long . . . . . 11
- 11. Pileus up to 12 mm diam, lamellae marginate, orange, basidiospores 12.5–17.5 µm long . . . . . *M. anomalus*
- 11. Pileus reaching 20 mm diam, lamellae non-marginate, basidiospores up to 14 µm long . . . . . 12
- 12. Pileus yellow with a slight orangish tint, setulae of broom cells of the pileipellis no more than 7.5 µm long; more frequently on leaves . . . . . *M. suthpensis*
- 12. Pileus bright orange, setulae of broom cells of the pileipellis reaching 14.3(–17.5) µm long; often on wood . . . . . *M. neotropicalis*
- 13. Lamellae strongly reticulate to meruloid-anastomosed . . . . . *M. cladophyllus* var. *glaberripes*
- 13. Lamellae non-reticulate or meruloid-anatomosed . . . . . 14
- 14. Pileus cream-coloured . . . . . *M. bellus*
- 14. Pileus strongly pigmented . . . . . 15
- 15. Pileus olivaceous grey, basidiospores 10–13.3 µm long . . . . . *M. trinitatis*
- 15. Pileus not olivaceous, basidiospores with different dimensions . . . . . 16
- 16. Basidiospores > 11 µm long . . . . . 19
- 16. Basidiospores < 11 µm long . . . . . 17
- 17. Pileus bright orange to dark reddish orange (fulvous), stipe trama with dimorphic hyphae (few vermiform conspicuous hyphae in a matrix of regular hyphae) . . . . . *M. ruber*
- 17. Pileus yellowish orange or pale orange (not fulvous), stipe trama without dimorphic hyphae (only regular hyphae) . . . . . 18
- 18. Pileus trama heteromorphic, hyphae thin- to thick-walled, pileipellis not mottled, broom cells with regular apical setulae, 2–6.3 µm long . . . . . *M. leoninus*
- 18. Pileus trama not heteromorphic, hyphae only thin-walled, pileipellis mottled, some broom cells with thick walls and very elongate setulae . . . . . *M. corrugatus*
- 19. Pileus < 10 mm diam, pileipellis not mottled . . . . . 20
- 19. Pileus > 10 mm diam, pileipellis mottled . . . . . 22
- 20. Pileus up to 7.5 mm diam, stipe 33–60 mm long, basidiospores 10–14.4 µm long . . . . . *M. graminicola*
- 20. Pileus up to 4 mm diam, stipe shorter, up to 15 mm long, basidiospores longer . . . . . 21
- 21. Pileus 1.8–4 mm diam, stipe 13–15 mm long, basidiospores 14–19 × 5.4–8 µm . . . . . *M. hobbitii*
- 21. Pileus 1–3 mm diam, stipe 1–2.5 mm long, basidiospores 12.3–17 × 3.8–5 µm . . . . . *M. ambicellularis*
- 22. Pileus beige to pale brown, basidiospores 12.8–16 × 3.5–4 µm . . . . . *M. dimorphus*
- 22. Pileus dark orange, basidiospores longer . . . . . 23
- 23. Basidiospores 20–25.4 µm long . . . . . *M. rhabarbarinoides*
- 23. Basidiospores (12–)14.4–21.5 µm long . . . . . *M. rhabarbarinus*

1 — *Marasmius* sect. *Globulares* Kühner emend. Antonín & Noordel. group *Globulares*  
[Sect. *Globulares* sensu Singer (1986)]

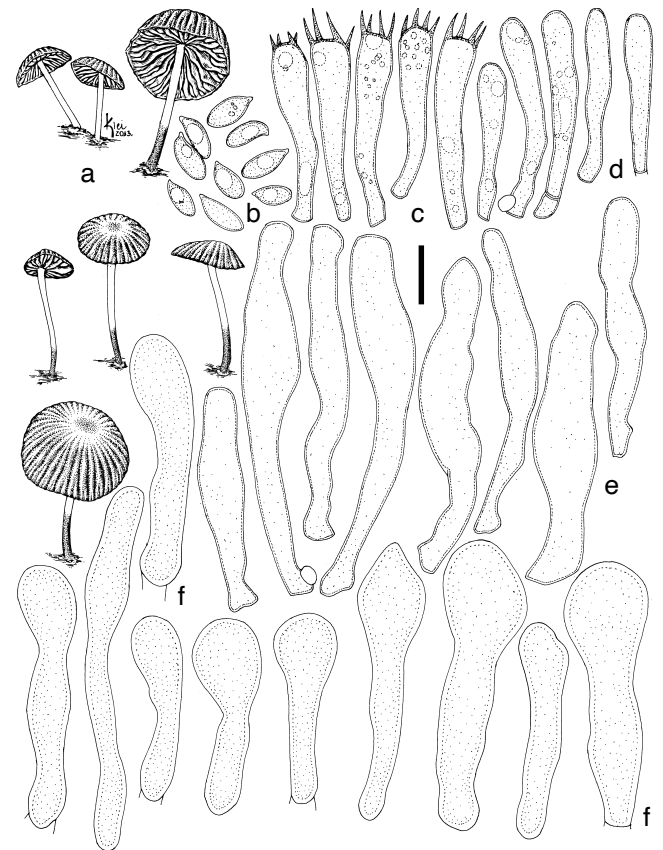
***Marasmius pallidibrunneus*** J.S. Oliveira, *sp. nov.* — MycoBank MB811130; Fig. 3, 4

*Holotype.* BRAZIL, São Paulo State, São Paulo City, Parque Estadual das Fontes do Ipiranga, on rotten debris of dicotyledonous tree, 3 Apr. 2013, *M. Capelari* 4706 (SP 445668!).

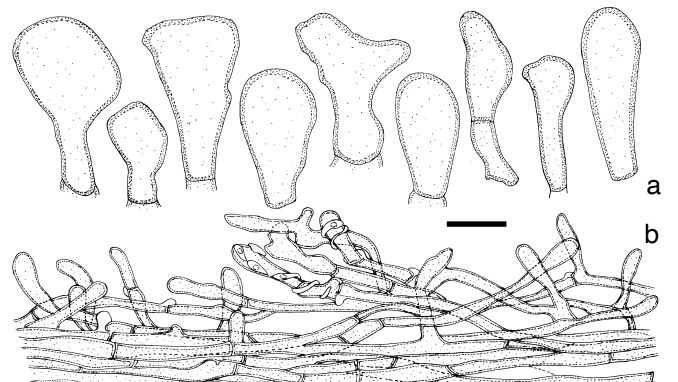
*Etymology.* Referring to the pileus with pale brown pigmentation.

*Pileus* 7–37 mm diam, shallowly sulcate, pale brown or buff brown. *Lamellae* adnate to adnexed, subdistant (18–21). *Stipe* 18–50 × 2–4 mm, cylindrical, entirely white, except dark brown at the base and with a white basal pad. *Basidiospores* 6.3–9 × 3–4.4 µm, lacrimoid to clavate. *Pleurocystidia* 43–87.5 × 6.3–11.3 µm, cylindrical, clavate, ampullaceous, ventricose to vermiform. *Cheilocystidia* 34–65 × 8–15 µm, ampullaceous to often bulboid-pedicellate, yellow to pale ochraceous. *Pileipellis* hymeniform, composed of dextrinoid *Globulares*-type smooth cells, 16.3–43.8 × 7.8–21.3 µm.

*Pileus* 7–37 mm diam, hemispheric to convex, sometimes tending to plane, shallowly to deeply sulcate, centre flat, margin incurved, decurved to straight, edge regular; whitish brown to pale brown (N<sub>40</sub>Y<sub>30</sub>M<sub>20</sub>), or light brown (N<sub>30–40</sub>Y<sub>30</sub>M<sub>20</sub>), darkening to ochraceous brown (N<sub>60</sub>Y<sub>50</sub>M<sub>40</sub>) or dark rust brown (N<sub>90</sub>Y<sub>80</sub>M<sub>50</sub>) with humidity change, with a central, rounded spot, which is ochraceous brown (N<sub>60</sub>Y<sub>50</sub>M<sub>40</sub>) to dark rust brown (N<sub>90</sub>Y<sub>80</sub>M<sub>50</sub>); thin-fleshy or thin-cartilaginous to almost membranous at the margin, context white (≤ 1.5 mm); surface glabrous, dry, dull,



**Fig. 3** *Marasmius pallidibrunneus* (*M. Capelari* 4607). a. Basidiomata; b. basidiospores; c. basidia; d. basidioles; e. pleurocystidia; f. cheilocystidia. — Scale bars: a = 21 mm, b–f = 10 µm.



**Fig. 4** *Marasmius pallidibrunneus* (*M. Capelari* 4607). a. *Globulares*-type smooth cells of the pileipellis; b. stiptipellis. — Scale bars: 10 µm.

papyraceous, darkening after collected, non- or partly hygrophanous. *Lamellae* adnate to adnexed, subdistant, ventricose (4 mm broad),  $L = 18–21$ , equal,  $l = 1–2$ , opaque, smooth, cream ( $N_{10}Y_{20}M_{10}$ ) to greyish beige ( $N_{20}Y_{30}M_{20}$ ), or pale brown ( $N_{30}Y_{30}M_{20}$ ), edge even, concolorous. *Stipe* 18–50 × 2–4 mm, central, cylindrical, slightly compressed at the middle, equal, cartilaginous, hollow; white or greyish white all over because of a fine mycelial vestiture on the surface, changing to brownish grey (near  $N_{30}Y_{20}M_{10}$ ) when mature, and dark brown ( $N_{80}Y_{99}M_{50}$ ) to fuliginous brown ( $N_{80}Y_{20}M_{20}$ ) at the base; surface with mycelial covering or a fine tomentum, stamped with finger print, but with thin pubescence at the stipe base, sometimes fibrillose; with a white, cottony basal mycelial pad, and forming a subiculum over the substrate.

*Basidiospores* 6.3–9 × 3–4.4  $\mu\text{m}$  ( $x_m = 7.9 (\pm 0.8) \times 3.9 (\pm 0.3) \mu\text{m}$ ;  $Q_m = 2.1 (\pm 0.2)$ ;  $n = 30$ ), oblong, tear-shaped to short clavate, hyaline, smooth, thin-walled, inamyloid. *Basidia* 27–36.3 × 6.3–7.5  $\mu\text{m}$ , cylindrical to clavate, smooth, hyaline, 4 sterigmata, thin-walled, inamyloid. *Basidioles* 27.5–36.3 × 4.4–6.3  $\mu\text{m}$ , cylindrical to clavate, smooth, hyaline, thin-walled, inamyloid. *Pleurocystidia* 43–87.5 × 6.3–11.3  $\mu\text{m}$ , cylindrical, clavate, ampullaceous, ventricose to vermiform, smooth, hyaline, base a little deepened in the subhymenium, apex at the same height or a little more projected above the basidia or basidioles apex, solely conspicuous when individualized, thin-walled. *Cheilocystidia* 34–65 × 8–15  $\mu\text{m}$ , abundant, conspicuous, erect to frequently repent, clavate, hyphoid, ampullaceous to frequently spheropedunculate, with the apical portion generally vesiculose or inflated, few hyaline, generally opaque, yellow to pale ochraceous, thin- or thick-walled, sometimes seeming solid likely due to contents. *Lamellar trama* dextrinoid, irregular, composed of strongly interwoven, cylindrical hyphae, 1.3–7.5  $\mu\text{m}$  diam, regular in outline, branched, smooth, thin-walled, hyaline. *Pileus trama* dextrinoid, irregular, composed of hyphae similar to those of the lamellar trama, 3–15  $\mu\text{m}$  diam, some inflated. *Pileipellis* hymeniform, composed of *Globulares*-type smooth cells, 16.3–43.8 × 7.8–21.3  $\mu\text{m}$ , vesiculose, clavate to pyriform, pedicellate, some flattened at the apex, others tending to be lobed, sometimes septate, hyaline, dextrinoid, thin- to slightly thick-walled. *Stipe trama* strongly dextrinoid, cortical hyphae parallel, cylindrical, 3.8–12.5  $\mu\text{m}$  diam, regular in outline, branched, smooth, pale brownish yellow, with walls moderately thick, septate; internal hyphae hyaline, thin-walled. *Stiptipellis* with a tomentum-like covering of loose hyphae on the cortical layer (the cause of the pale pigmentation of the stipe), with many basidiospores adhered to the hyphae of this vestiture, some of them germinating, tomentum formed by filamentous extensions of cylindrical hyphal endings, clavate to broadly clavate, or irregular in outline, septate, hyaline, thin-walled, inamyloid; caulocystidia (if present) in form of terminal hyphae growing from this layer, but definitely not obvious. *Clamp connections* present in almost all tissues, not seen at the base of the cheilocystidia or smooth cells of the pileipellis.

**Habit & Substrate** — Gymnoid, gregarious, on rotten debris of dicotyledonous tree (leaves, branches and twigs), debris connected by a white to cream-coloured subiculum.

**DNA barcode** — GenBank KP635186 (ITS1-5.8S-ITS2) and KP635141 (LSU).

**Notes** — This species is similar to *M. cibarius* (Singer 1976), which also has pileus darkening to fuliginous brown, lamellae tending to be sordid grey, and the stipe is pale and slightly fibrillose. However, *M. cibarius* strongly differs in having smaller basidiospores (5.5–6.5 × 2.8–3.8  $\mu\text{m}$ ) and lacking pleurocystidia. *Marasmius pallidibrunneus* also resembles *M. heliomyces* (Singer 1976) in the colour and size of the pileus, the pale stipe and basidiospores dimensions (6–8.8 × 2.8–3.8  $\mu\text{m}$ ), but the latter species differs by the absence of pleurocystidia.

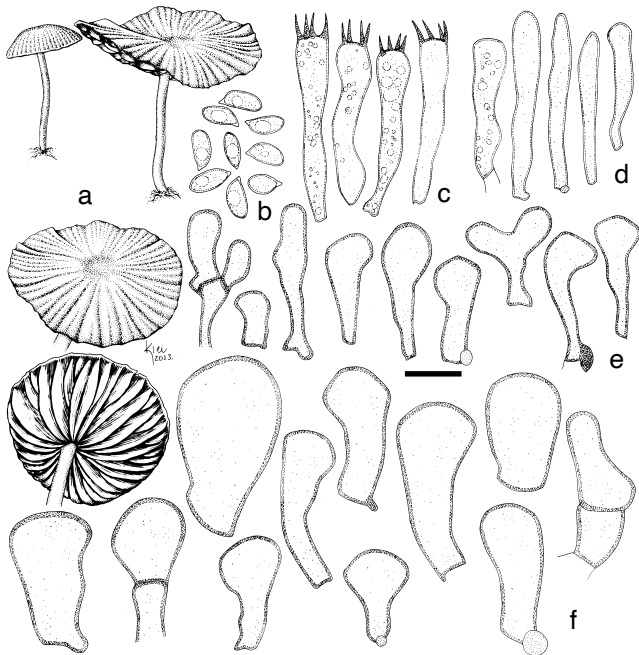
Some resemblances between *M. pallidibrunneus* and *M. brunneospermus* are the white pruinose stipe surface (at least sometimes in the latter), the presence of long pleurocystidia (50–95  $\mu\text{m}$  long in the latter), the slightly pigmented cheilocystidia (pale melleous in the latter) of somewhat similar shape, the smooth cells of the pileipellis, size and shape of the basidiospores, and the lamellae tinted brown. However, both species are different according to the macroscopic features of the pileus (colour, texture and surface aspects) and in the number of lamellae (Takahashi 1999), and the lamellae are not intervenose in the new species. Moreover, the basidiospores or spore print of *M. pallidibrunneus* are not brownish. The presence of fusoid pleurocystidia and well-developed cheilocystidia also differentiate *M. brunneospermus* from *M. pallidibrunneus*.

In the Dataset 2.4 tree (Fig. 1e), *M. pallidibrunneus* was basal to the subclades /wynneae and /brunneospermus without support. On the other hand, in the Dataset 3 tree (Fig. 2), *M. pallidibrunneus* is sister to the branch bearing *M. silvicola*, *M. macrocystidiosus*, *M. fuscicystidiosus* and *M. brunneospermus*, with significant support.

**Marasmius silvicola** Singer in Singer & Digilio, Lilloa 25: 199. 1952 — Fig. 5, 6

*Pileus* 45–81 mm diam, convex, tending to plane, orbicular, striate, corrugated or slightly sulcate, centre flat or with a shallow depression, sometimes slightly umbonate, margin incurved to straight, or tending to revolute, edge regular, crenate to lacerate; brownish yellow to orangish ( $N_{30}Y_{90}M_{40}$ ), fading to yellow or beige ( $N_{20}Y_{60}M_{30}$ ) to almost cream ( $N_{10}Y_{60}M_{20}$ ) at the margin, centre ochraceous ( $N_{10}Y_{99}M_{50}$ ) to dark yellowish brown (darker than  $N_{40}Y_{99}M_{50}$ ); membranous to thin-fleshy, context moderately thick ( $\pm 1.5$  mm); surface glabrous, semi-humid to moist, sometimes dry, dull at the central disc, usually pellucid at the margin, smooth to papyraceous, hygrophanous. *Lamellae* adnate, adnexed to sinuate, sometimes descending from the stipe, somewhat close to subdistant,  $L = 18–20$ , broad (17 mm), regular, some weakly intervenose,  $l = 3–5$ , opaque, smooth, greyish yellow to sordid cream ( $N_{00}Y_{20}M_{00}$ ), edge even, sometimes eroded or irregularly toothed, concolorous with the lamellar faces (darkening after losing water or when completely dried) and with the hymenium between lamellae. *Stipe* 75–87 × 3–5 mm, central or somewhat eccentric, cylindrical, equal or with a flared apex, sometimes compressed, with scarce, white, tomentose basal mycelium, forming a subiculum; cartilaginous, hollow; apex and middle cream ( $N_{00}Y_{10}M_{80}$ ) or becoming brownish ( $N_{20}Y_{40}M_{30}$  to  $N_{40}Y_{50}M_{40}$ ) when touched, and dark greyish brown ( $N_{50}Y_{50}M_{30}$ ) downward to the base; surface glabrous or with very scanty, white pubescence, smooth, opaque, fibrillose. *Odour* not distinguished.

*Basidiospores* 5.6–9 × 3–4.8  $\mu\text{m}$  ( $x_m = 6.7–7.6 \times 3.4–3.8 \mu\text{m}$ ,  $x_{mm} = 6.9 (\pm 0.5) \times 3.6 (\pm 0.2) \mu\text{m}$ ,  $Q_m = 2$ ,  $n/s = 30$ ,  $s = 3$ ), obovoid, rarely ellipsoid, generally subellipsoid, lacrimoid or amygdaliform, smooth, hyaline, thin-walled, inamyloid. *Basidia* 27.5–38.8 × 5–6.3  $\mu\text{m}$ , clavate, elongate, smooth, hyaline, thin-walled, with 2–4 sterigmata, inamyloid. *Basidioles* (17.5–) 22.5–35 × 3.8–6.3  $\mu\text{m}$ , cylindrical to clavate, short to elongate, slender, smooth, hyaline, thin-walled, inamyloid. *Pleurocystidia* generally very elongate, 55–118 × 8.8–13.8  $\mu\text{m}$ , clavate or frequently fusoid, tapering upward to an obtuse or acute apex, base elongate and very narrow, deepened in the subhymenium, some opaque (either when in 5 % KOH or in 5 %  $\text{NH}_4\text{OH}$  or  $\text{NH}_3$ ), yellowish to very pale melleous, or hyaline, present either on the faces or at lamellae edges (repent at the edge), smooth, thin-walled, metachromatic, inamyloid. *Cheilocystidia* in form of smooth cells, subclavate, pyriform, sometimes bilobed, or pedicellate, (8.8–)12.5–27.5 × 5.6–8.8(–14.5)  $\mu\text{m}$ , hyaline, with thinner walls, inamyloid. *Lamellar trama* dextrinoid, irregular,



**Fig. 5** *Marasmius silvicola* (JO357). a. Basidiomata; b. basidiospores; c. basidia; d. basidioles; e. cheilocystidia; f. *Globulares*-type smooth cells of the pileipellis. — Scale bars: a = 17 mm, b–f = 10  $\mu$ m.

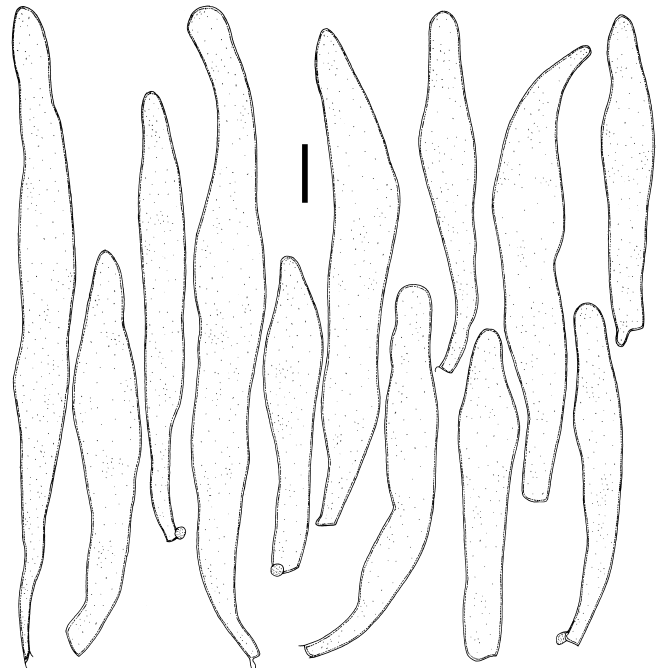
tending to regular at the trama core, hyphae interwoven, cylindrical or inflated, 2.5–12.5  $\mu$ m diam, broad, smooth, hyaline, thin-walled. *Pileus trama* dextrinoid, irregular, with a loose core, subcutis and subhymenium more compact, hyphae interwoven, 2.5–20  $\mu$ m diam, cylindrical or inflated, broad, smooth, hyaline, thin-walled. *Pileipellis* hymeniform, composed of *Globulares*-type smooth cells, clavate to pyriform, sometimes slightly pedicellate, or with variable shape, sometimes like segments of hyphal endings, 16–33  $\times$  (8.8–)10.4–18.8  $\mu$ m, smooth, hyaline when isolated, brownish yellow when grouped (pigmented walls), inamyloid, thin-walled. *Stipe trama* dextrinoid, especially the inner hyphae; cortical hyphae parallel, cylindrical, 2.5–17.5  $\mu$ m diam, regular in outline, melleous or pale yellow, smooth, walls thin to moderately thick; internal hyphae similar to those of the cortex, but disorganised. *Stipitipellis* without differentiated cells. *Clamp connections* present in most tissues, mostly inconspicuous, not observed in the stipe trama or on the pileipellis elements.

**Habit & Substrate** — Gymnoid, gregarious, scattered or solitary, on trunks or rotten vegetal humus of dicotyledonous trees.

**Distribution** — The species was originally described from Argentina (Singer & Digilio 1952), later collected from Rio Grande do Sul State in Brazil, Ecuador, Bolivia (Singer 1976), and more recently from Indonesia (Desjardin et al. 2000). This is the first record from São Paulo State in Brazil.

**Specimens examined.** BRAZIL, São Paulo State, São Paulo City, Parque Estadual das Fontes do Ipiranga, 23 Mar. 2011, J.J.S. Oliveira & P.O. Ventura JO357 (SP 445514!), J.J.S. Oliveira & P.O. Ventura JO362 (SP 445517!), 4 May 2011, J.J.S. Oliveira & P.O. Ventura JO366 (SP 445519!).

**Notes** — The examined samples correspond to the species as described by Singer (1976), differing only by having slightly larger basidiospores, reaching 9  $\mu$ m long, though the longer spores may have come from 2-spored basidia. The cheilocystidia ((8.8–)12.5–27.5  $\times$  5.6–8.8(–14.5)  $\mu$ m) resemble the smooth cells of the pileipellis rather than the pleurocystidia, and this is consistent with the second pattern found by Singer (1976): “or else more inconspicuous, vesiculose hyaline, smooth, 11–28  $\times$  6–10  $\mu$ m”. As the pleurocystidia also occur at the lamellar edge, they may be confused with the cheilocystidia.



**Fig. 6** *Marasmius silvicola* (JO357). Pleurocystidia. — Scale bars: 10  $\mu$ m.

No other significant differences are found. Desjardin et al. (2000) recorded this species as having very large basidiomata, with pileus ranging from 50–90(–200) mm diam and stipe with 80–140  $\times$  5–10 mm.

*Marasmius silvicola* is also comparable to *M. goossensiae*, *M. nigrodiscus*, *M. notandus*, *M. ochraceus*, *M. phlebodiscus* and *M. trogioides*, differing from all by having much larger pleurocystidia. Furthermore, *M. goossensiae* has smaller basidiospores, reaching 7.5  $\mu$ m long and pleurocystidia only up to 72  $\mu$ m long (Singer 1964, Pegler 1977); *M. notandus* has dry, smooth, some weakly striate pileus, larger basidiospores (reaching 11  $\mu$ m long), and completely unpigmented and shorter pleurocystidia, up to 70  $\mu$ m (Corner 1996); *M. ochraceus* has completely smooth pileus, smaller basidiospores (5.5–7.2  $\times$  2.5–4.2  $\mu$ m) and pleurocystidia with strongly greenish yellow content (Pegler 1986); *M. phlebodiscus* has a pileus with a reticulated central disc by wrinkles in the form of a web, shorter basidiospores (up to 6.5  $\mu$ m long) and cheilocystidia with tapered apex (Desjardin & Horak 1997); and *M. trogioides* has a smooth to rugulose-reticulate, or to rivulose-rugulose pileus, stipe with dilated base, longer basidiospores (9–11.5  $\mu$ m), pleurocystidia reaching 70  $\mu$ m long and very elongate cheilocystidia, up to 80  $\mu$ m long (Corner 1996).

Based on the Dataset 2.4 tree (Fig. 1e), *M. silvicola* is sister to *M. nigrodiscus* with high support forming the subclade / *silvicola*. In the Dataset 3 tree (Fig. 2), *M. silvicola* has a stable phylogenetic position basal to the ‘*M. brunneuspermus* + *M. fuscicystidiosus* + *M. macrocystidiosus*’ branch, three species that similarly have elongate and apically tapered pleurocystidia.

2 — *Marasmius* sect. *Globulares* Kühner emend. Antonín & Noordel. group *Sicci* Singer ser. *Atrorubentes* Desjardin & E. Horak  
[Sect. *Sicci sensu* Singer (1986)]

***Marasmius atrorubens*** (Berk.) Sacc., Syll. Fung. (Abellini) 5: 560. 1887 — Fig. 7

≡ *Agaricus atrorubens* Berk., London J. Bot. 1(3): 138. 1842.

≡ *Androsaceus atrorubens* (Berk.) Pat., J. Bot., Paris 11: 338. 1897.



*Pileus* 1.4–3 mm diam when immature, reaching 2.6–11 mm diam, hemispheric to slightly conical when young, remaining conical, conical-campanulate or even convex to plano-convex when mature, smooth, striate or very slightly sulcate at the margin, centre shallowly umbonate, margin incurved to rarely straight, edge regular to slightly crenate; dark ferruginous or orangish brown (darker than  $N_{60}Y_{99}M_{80}$ ) and centre with an orangish brown papilla ( $N_{40}Y_{99}M_{70}$  to  $N_{60}Y_{99}M_{70}$ ) when immature, becoming orange to bright orange ( $N_{20}Y_{99}M_{50-60}$ ), some paler orange ( $N_{30}Y_{99}M_{50}$ ) when mature at the margin, fulvous orange ( $N_{40}Y_{99}M_{60-70}$ ) at the centre, usually becoming ochraceous brown ( $N_{60}Y_{80}M_{50}$ ) when dried; membranous, context pale cream, thin (< 1 mm); surface glabrous, dry, dull, papyraceous to subvelutinous, non-hygrophanous. *Lamellae* sinuate, adnexed or subfree, substipitate to subclose,  $L = 12-22$ , equal or unequal, regular,  $l = 2-4(-5)$ , opaque, smooth, pale cream ( $N_{00}Y_{10}M_{00}$ ), edge even, finely concolorous with the pileus, hymenium between the lamellae partly concolorous with the pileus. *Stipe* 4.3–73 × 0.3–1 mm, central, cylindrical, equal; semichitinous to semicartilaginous, hollow; apex concolorous with the lamellae or pale orange ( $N_{10}Y_{70}M_{30}$ ) to pale yellow ( $N_{00}Y_{50}M_{10}$ ), becoming ochraceous brown ( $N_{50}Y_{99}M_{50}$ ), orangish brown ( $N_{40}Y_{80-90}M_{70}$ ), reaching somewhat reddish brown ( $N_{70}Y_{99}M_{70}$ ) near the base; surface opaque, pubescent, with fuliginous brown pubescences; strigose basal mycelium long-filamentous, cream to orange, sometimes scarce.

*Basidiospores* 12.5–18 × 3–4.6 µm ( $x_m = 14.5-15.9 \times 3.5-3.6$  µm;  $x_{mm} = 14.8 (\pm 0.7) \times 3.6 (\pm 0.1)$  µm;  $Q_m = 4-4.4$ ;  $Q_{mm} = 4.3 (\pm 0.2)$ ;  $n/s = 30$ ;  $s = 3$ ), oblong, clavate to very slightly fusoid, smooth, hyaline, thin-walled, inamyloid. *Basidia* not observed. *Basidioles* 17.5–28 × 5.8–7.5 µm, clavate, hyaline, thin-walled, inamyloid; cystidioles, 21.3–30 × 3.8–6.5 µm, fusoid to subfusoid, with apex generally tapered and acute, rarely almost mucronate, some with a broadened apical portion, projecting 8 µm beyond the basidia and basidioles, smooth, hyaline,

thin-walled. *Cheilocystidia* concentrated at the lamellar edge, but also dispersed toward the middle of the lamellar face, in form of *Siccus*-type broom cells, abundant, ochraceous or pale brownish orange, similar to those of the pileipellis, main body 8.8–22.5 × 6.3–7.8 (–10) µm, clavate to slightly turbinate, rarely truncate or ventricose, or branched, regular in outline, hyaline when isolated, walls relatively thin; setulae apical, erect, short to slightly elongate, 1.6–7.8 × 0.5–1 µm, simple, cylindrical to filiform, or setoid, regular in outline, hyaline to pale yellow, apex acute to somewhat obtuse. *Lamellar trama* strongly dextrinoid, irregular, composed of interwoven hyphae, cylindrical, 1.5–10 µm diam, regular in outline, branched, hyaline, thin-walled. *Pileus trama* strongly dextrinoid, irregular, interwoven hyphae, cylindrical, 2–10 µm diam, regular or sometimes irregular in outline. *Pileipellis* hymeniform, composed of *Siccus*-type broom cells, abundant, pale brownish orange when grouped, hyaline with apex and setulae hyaline to light yellow when isolated, main body 10–25 × 5–9.4 µm, clavate to turbinate, sometimes ventricose, regular in outline, hyaline, with walls somewhat thick; setulae apical, erect, 1.5–6.3 × 0.6–1 µm, cylindrical, digitiform to spinule-shaped, regular in outline, simple, solid, hyaline to light yellow, apex obtuse to more frequently acute. *Stipe trama* strongly dextrinoid, cortical hyphae parallel, cylindrical, 2.5–7.5 µm diam, regular in outline, smooth, ochraceous brown or pale hazel, thick-walled; internal hyphae hyaline, 2.5–9 µm diam, thin-walled. *Caulocystidia* (or *Caulosetae*) short to very elongate, 35–415 × 4.5–17.5 µm, setoid, cylindrical, tapering at the apex, sometimes forming an inflated spherical portion at the apex or in the middle of the cystidia, apex acute, not branched, pale brown to brown, thick-walled. *Clamp connections* present in almost all tissues, except for the cortical hyphae of the stipe.

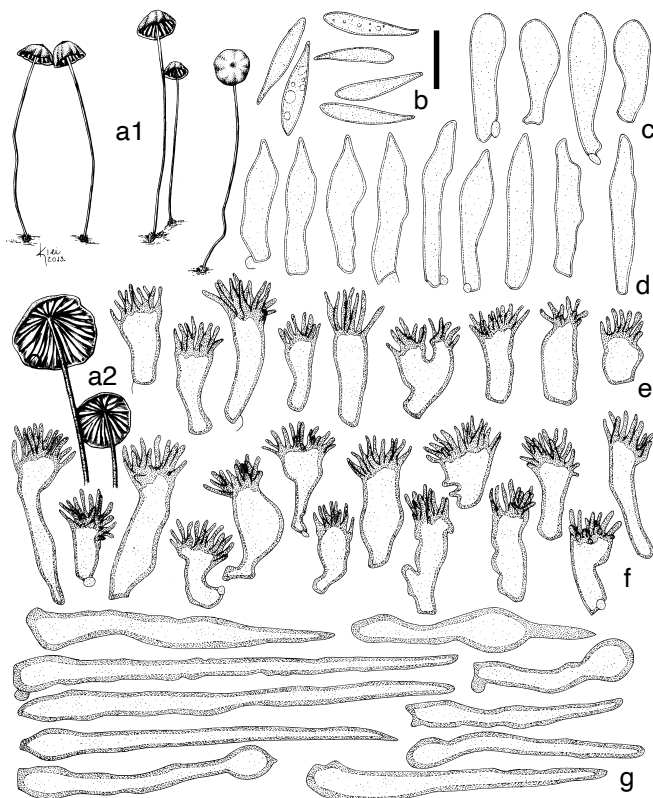
**Habit & Substrate** — Marasmioid, scattered or gregarious, growing on dried dicotyledonous leaves on the forest litter.

**Distribution** — Originally described from Suriname, it has also been recorded from Guadalupe, Venezuela, Ecuador (Singer 1976), Tanzania, Uganda (Pegler 1977), Martinique, Trinidad (Pegler 1983), Puerto Rico (Lodge 2003, Cantrell et al. 2006) and Brazil (Pegler 1997).

**Specimens examined.** BRAZIL, São Paulo State, São Paulo City, Parque Estadual das Fontes do Ipiranga, 1 Mar. 2011, J.J.S. Oliveira & F. Karstedt JO337 (SP 445501!); Parque Estadual da Cantareira, Núcleo Engordador, 30 Jan. 2012, J.J.S. Oliveira & V. Motato-Vásquez JO455 (SP 445906!); ibid., 16 Feb. 2012, J.J.S. Oliveira & M. Capelari JO489 (SP 445563!); Iporanga, Parque Estadual Turístico do Alto Ribeira, Núcleo Santana, 29 Feb. 2012, J.J.S. Oliveira & D.E. Desjardin JO528 (SP 445576!); ibid., D.E. Desjardin DED8684 (SP 445663!).

**Notes** — *Marasmius atrorubens* is the type species of the ser. *Atrorubentes* according to the traditional view. Singer (1976) described *M. atrorubens* var. *cystidifer* based on specimens with abundant, ventricose to tapered 'fusoid' cystidioles, 22–27 µm long, with a conical or mucronate apex, slightly granular surface or covered with hyaline incrustations, all hyaline or having a distinct yellowish and opaque content, thick-walled and refractive. The specimens examined also have ventricose to tapered ('fusoid apex') cystidioles, 21.3–30 µm long, with a conical-subacute to mucronate apex, but differ by being hyaline, thin-walled, smooth, and non-refractive. These cystidioles are mostly concordant with the description of the species by Puccinelli & Capelari (2009). Sequencing more collections across this range of variation should clarify the relevance of these characteristics in the species.

Pegler (1977), based on material from Africa, mentioned the presence of ventricose and fusoid cystidioles (22–26 µm long). However, in Pegler (1983), cystidia or cystidioles were apparently absent in specimens from Martinique and Trinidad, but with only fusoid basidioles instead, and the basidiospores were much smaller (10–15 µm long), so this identification is



**Fig. 7** *Marasmius atrorubens* (JO489). a1, a2. Basidiomata; b. basidiospores; c. basidioles; d. cystidioles; e. cheilocystidia; f. *Siccus*-type broom cells of the pileipellis; g. setoid caulocystidia. — Scale bars: a1 = 15 mm, a2 = 7 mm, b–g = 10 µm.

dubious. Later, Pegler (1997) observed basidiospores ranging from 13–18 µm long in material from São Paulo and this agrees with the basidiospore dimension originally described for *M. atrorubens*.

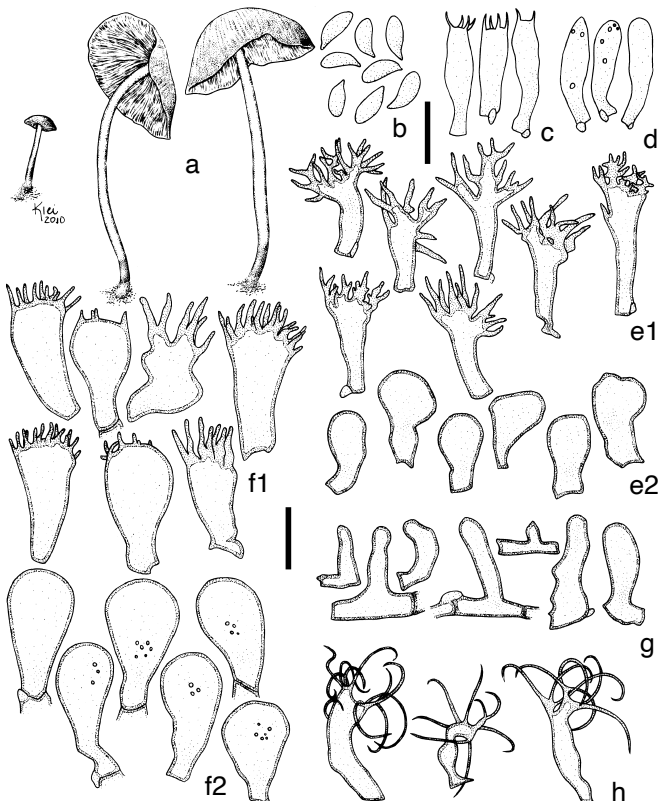
*Marasmius atrorubens* var. *dumontii* (Singer 1976) differs from the other varieties by not bearing cystidia/cystidioles in the hymenium, but elongate, hair-like, thick-walled structures in the pileipellis. This latter characteristic points to a strong resemblance between this variety and *M. trichotus*, which has long pileosetae and shorter basidiospores, ranging from 11–14 µm (Corner 1996).

In the subtree of the Group 2 (Fig. 1c), *M. atrorubens* grouped with *M. trichotus*, *M. longisetosus*, *M. iras*, *M. xestocephalus* and *M. nummularius*, forming the subclade 'atorubens'. *Marasmius atrorubens* appears close to *M. trichotus* but, despite the considerable morphological similarity, the subtending branch is unsupported (Fig. 1c). Nevertheless, both branches of *M. atrorubens* and *M. trichotus* are strongly supported, indicating that the presence of pileosetae in *M. trichotus* represents a strong delimitation and that they represent distinct taxa.

***Marasmius congregatus* Mont., Ann. Sci. Nat., Bot., ser. 4, 1: 113. 1854 — Fig. 8**

≡ *Chamaeceras congregatus* (Mont.) Kuntze, Revis. Gen. Pl. (Leipzig) 3: 455. 1898.

*Pileus* 5–66 mm diam, hemispheric to almost globose when young, hemispheric to convex when mature, smooth, translucent-striate, slightly sulcate at the margin, centre flat to somewhat depressed, sometimes umbonate, margin incurved to plane, sometimes revolute, edge regular to crenate, frequently lacerate; light orange ( $N_{00}Y_{80}M_{30}$ ) to brownish orange ( $N_{20}Y_{90}M_{50}$ ) when immature, becoming paler, whitish cream ( $N_{00}Y_{10}M_{00}$  to  $N_{00}Y_{00}M_{10-20}$ ) or pale yellow ( $N_{00}Y_{30-50}M_{00-10}$  to  $N_{10}Y_{70}M_{20}$ ), with



**Fig. 8** *Marasmius congregatus* (J061). a. Basidiomata; b. basidiospores; c. basidia; d. basidioles; e. cheilocystidia: e1. *Siccus*-type broom cells, e2. smooth cells; f. pileipellis: f1. *Siccus*-type broom cells, f2. smooth cells; g–h. stipitipellis: g. caulocystidia, h. *Amyloflagellula*-type broom cells. — Scale bars: a = 8.6 mm, b–h = 10 µm.

light brownish yellow sulci and centre ( $N_{00}Y_{50}M_{10}$  to  $N_{20}Y_{60}M_{40}$ ), or completely light orange ( $N_{00}Y_{50}M_{10-20}$ ); membranous, fragile, context thin (< 1 mm); surface glabrous, humid to moist, semi-translucent or pellucid, especially near the margin, dull at the central disc, papyraceous, hygrophanous. *Lamellae* free to subfree when mature, adnate to adnexed when very young, subclose to seemingly close because of several lamellulae,  $L = 16–20$ , unequal, regular, rarely intervenose, or forked,  $l = 4$ , very narrow, smooth, translucent to opaque, white to whitish cream ( $N_{00}Y_{10}M_{00}$ ), edge even, concolorous with the lamellar faces as well as the hymenium between them. *Stipe* 15–85 × 1–4 mm, central, cylindrical, generally expanded above and below, or entirely equal, regular; cartilaginous with a harder, chitinous base, hollow; apex and middle concolorous with the lamellae, fading to yellow or orangish ( $N_{10}Y_{99}M_{10-20}$ ) or brownish orange ( $N_{20}Y_{70}M_{40-50}$ ), reaching orangish brown ( $N_{50}Y_{99}M_{70}$ ) or dark reddish brown ( $N_{70-80}Y_{90-99}M_{70-80}$ ) at the base; surface glabrous, but almost imperceptibly pubescent at the base, smooth, with a bright silky sheen; basal mycelium abundant, white to yellow, strigose to almost tomentose.

*Basidiospores* 5–9 × 2.5–4 µm ( $x_{\text{m}} = 7–7.7 \times 2.5–4 \mu\text{m}$ ;  $x_{\text{nm}} = 7 (\pm 0.4) \times 3.4 (\pm 0.2) \mu\text{m}$ ;  $Q_{\text{m}} = 2.1–2.5$ ,  $Q_{\text{nm}} = 2.1 (\pm 0.3)$ ;  $n/s = 30$ ,  $s = 3$ ), somewhat oblong, clavate, subfusoid, or lacrimoid, smooth, hyaline, thin-walled, inamyloid. *Basidia* 17.3–26.8 × 4–5.6 µm, clavate or cylindrical, slender, hyaline, thin-walled, inamyloid, 2–4 sterigmata. *Basidioles* 14–24 × 3.5–5.4 µm, cylindrical, clavate or apically tapered, hyaline, inamyloid, thin-walled. *Pleurocystidia* absent. *Cheilocystidia* similar to the elements of the pileipellis, consisting of two cellular types: 1) *Siccus*-type broom cells, main body 13.8–23.8 × 4.4–8.8 µm, clavate to turbinate, cylindrical or irregular in outline, hyaline, with thin to moderately thick walls; setulae erect, apical, short to elongate, 3.8–8 × 0.9–1.3 µm, cylindrical, somewhat dendriform, regular to irregular in outline, simple or branched, solid, with an acute to obtuse apex; 2) *Globulares*-type smooth cells, 12.5–20 × 7–11.3 µm, pyriform to vesiculose, hyaline, thin-walled, inamyloid. *Lamellar trama* dextrinoid, irregular, formed by interwoven hyphae, cylindrical, 2.3–10 µm diam, regular, branched, hyaline, thin-walled, smooth. *Pileus trama* strongly dextrinoid, irregular, interwoven hyphae, cylindrical, 1.8–10.8 µm diam, some segments inflated, branched, very hyaline, thin-walled. *Pileipellis* hymeniform, composed of two cellular types: 1) *Siccus*-type broom cells, main body 14.0–25.7 × 6–14.4 µm, clavate to vesiculose, turbinate to pyriform, thin-walled at the base and thick-walled at the apex, hyaline; setulae erect, apical, very short to moderately elongate, 2.2–9 × 0.8–1.5 µm, rare to abundant, cylindrical or conical, regular to irregular in outline, rarely branched, solid, with an acute to obtuse apex, some vesiculose; 2) *Globulares*-type smooth cells, 14.7–26.7 × 7.6–13 µm, pyriform to vesiculose or balloon-shaped, hyaline, thin-walled. *Stipe trama* dextrinoid, cortical hyphae parallel, cylindrical, somewhat broad, 5–15.2 µm diam, regular in outline, branched, very pale yellowish in KOH, but the hyphae of the stipe base are yellowish brown, with moderately thick walls, septate; internal hyphae very similar to those of the cortex, but narrower, more hyaline, and thin-walled. *Stipitipellis* with rare caulocystidia, inamyloid, small, 5–21.3 × 2.8–6.3 µm, cylindrical, clavate or with a tapered and acute apex, or even inflated like a vesicle, hyaline, with walls moderately thick, rising from the cortical hyphae. *Amyloflagellula*-type broom cells also present, even more rare than the caulocystidia, with main body 6.3–20 × 2.5–5 µm, cylindrical to clavate, hyaline, thin-walled; setulae filiform, thin, elongate, flagellum-like, 7.5–11.3 × 0.5–0.6 µm, solid, regular, flexible, curved, some branched. *Clamp connections* present in all tissues.

**Habit & Substrate** — Gymnoid, scattered, or frequently gregarious or caespitose, on dried leaves and barks of twigs, or rotten wood of dicotyledonous plants.

**Distribution** — The species was originally described from French Guiana and it was previously recorded from São Paulo, Brazil (Puccinelli & Capelari 2009).

**Specimens examined.** BRAZIL, São Paulo State, Santo André City, Reserva Biológica de Paranapiacaba, 18 Mar. 2010, J.J.S. Oliveira JO61 (SP 445415!); *ibid.*, J.J.S. Oliveira JO62 (SP 445416!); *ibid.*, 21 Apr. 2010, J.J.S. Oliveira & J.F. Santos JO100 (SP 445426!); *ibid.*, 25 Apr. 2010, J.J.S. Oliveira & J.F. Santos JO122 (SP 445433!); *ibid.*, 9 Dec. 2010, J.J.S. Oliveira & P.O. Ventura JO307 (SP 445482!); São Paulo City, Parque Estadual das Fontes do Ipiranga, 1 Mar. 2011, J.J.S. Oliveira & F. Karstedt JO328 (SP 445495!); *ibid.*, J.J.S. Oliveira & F. Karstedt JO332 (SP 445498!); *ibid.*, 3 Mar. 2011, J.J.S. Oliveira & F. Karstedt JO349 (SP 445779!); *ibid.*, J.J.S. Oliveira & F. Karstedt JO354 (SP 445771!); *ibid.*, 2 Feb. 2012, J.J.S. Oliveira JO468 (SP 445553!); *ibid.*, 16 Dec. 2014, J.J.S. Oliveira & G.F. Silva JO556 (SP 466008!); Parque Estadual da Cantareira, Núcleo Engordador, 30 Jan. 2012, J.J.S. Oliveira & V. Motato-Vásquez JO463 (SP 445498!); *ibid.*, J.J.S. Oliveira & M. Capelari JO478 (SP 446040!); *ibid.*, J.J.S. Oliveira & M. Capelari JO511 (SP 446039!); *ibid.*, 16 Feb. 2012, J.J.S. Oliveira & M. Capelari JO512 (SP 446038!); *ibid.*, J.J.S. Oliveira & M. Capelari JO513 (SP 446037!); Iporanga City, Parque Estadual Turístico do Alto Ribeira, Lageado, 2 Mar. 2012, J.J.S. Oliveira & D.E. Desjardin JO531 (SP 446036!).

**Notes** — *Marasmius congregatus* was described by Montagne (1854) from French Guiana. It was later recorded in Sri Lanka by Petch (1948) who considered *Cantharellus elegans* as a synonym of the species. However, in a review of *Marasmius pellucidus*, Wannathes et al. (2004) noted that what was previously determined as *M. congregatus* by Petch (1948) actually corresponded to *M. pellucidus* and, consequently, synonymized *C. elegans* under *M. pellucidus*. In the same study, Wannathes et al. (2004) analyzed the holotype of *M. congregatus* and provided a modern but limited description (for instance, no basidiospores were found in the holotype), recognizing the taxon as an independent species in *Marasmius* sect. *Sicci* subsect. *Siccini* ser. *Leonini*. Wannathes et al. (2004) also commented that, perhaps, *M. congregatus* may have been ignored by Dennis (1951b, c) and Singer (1965, 1976) in their studies in South America, and might have considered *M. congregatus* as a *nomen dubio*. Based on a type study by Wannathes et al. (2004), however, *M. congregatus* is a singular species based on the type material labelled 'Leprieur # 1081 (PC)' from French Guiana.

Puccinelli & Capelari (2009) identified some specimens of *M. congregatus* from São Paulo based on the description provided by Wannathes et al. (2004). However, the specimens from São Paulo have short caulocystidia (16–36 mm long) on the stipe base, which were not observed in the holotype (Wannathes et al. 2004). The collections herein examined, also from São Paulo, agree with those studied by Puccinelli & Capelari (2009), especially by having rare and short caulocystidia on the stipe base, but with shorter basidiospores (up to 9 vs 10 µm). The presence or absence of caulocystidia is not conclusive in the holotype, probably because its stipe base is damaged (D.E. Desjardin, pers. comm. *apud* Puccinelli & Capelari 2009), and, perhaps, because of the short size of these cystidia. Also concerning the stipitipellis, the *Amyloflagellula*-type broom cells found are similar to those found in *M. sullivantii* (f. 30 in Gilliam (1976)) and we have interpreted it as an occasional characteristic.

*Marasmius pseudoniveoaffinis* (Singer 1976) is a closely related species, mostly differing by having a distinctly sulcate, pure white pileus; remarkably pubescent-pruinose stipe; larger basidiospores up to 10.3 µm long; and abundant, conspicuous and larger caulocystidia, ranging from 20–60(–100) µm long. The phylogenetic placement of *M. congregatus* in this study is consistent in the Datasets 2.1 and 3 trees (Fig. 1b, 2), appearing as sister to *M. pseudoniveoaffinis*, within the subclade */corrugatus*, with strong support. This relationship is further supported by the similar morphology of these two species.

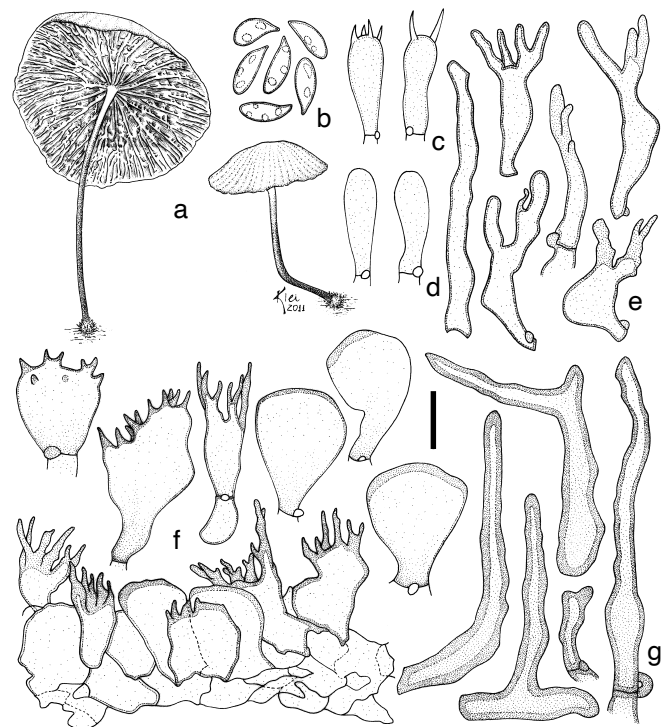
***Marasmius pseudoniveoaffinis* J.S. Oliveira, sp. nov.** — MycoBank MB811131; Fig. 9

**Holotype.** BRAZIL, São Paulo State, Santo André City, Reserva Biológica de Paranapiacaba, on twigs and dried branches of dicotyledonous tree, 2 July 2009, M. Capelari & L.A.S. Ramos 4536 (SP 445583!).

**Etymology.** Refers to the affinity with *Marasmius pseudoniveus* in morphology.

**Pileus** up to 65 mm diam, convex to plane, sulcate-striate or irregularly sulcate, often pure white. **Lamellae** adnate to free, distant (9–16), with lamellulae inserted (3), regular or interveined-anastomosed. **Stipe** 8–70 × 1–3 mm, cylindrical, brown, with a strigose basal mycelium. **Basidiospores** 7–10.4 × 3–4 µm. **Cheilocystidia** hyphoid, elongate, irregularly cylindrical, clavate, often forked or ramoso. **Pileipellis** hymeniform, made up by both *Siccus*-type and *Globulares*-type cells. **Caulocystidia** cylindrical to setoid. On decaying twigs or branches of dicotyledonous trees.

**Pileus** 4.5–65 mm diam, convex tending to plane, sulcate-striate or slightly and irregularly sulcate, centre flat or shallowly depressed, margin incurved tending to straight, edge regular, sometimes lacerate; most often completely pure white, but sometimes cream ( $N_{00}Y_{10}M_{00}$ ), centre sometimes yellowish brown ( $N_{20}Y_{50-60}M_{20-40}$ ); membranous, context thin (< 1 mm); surface glabrous, dry, a little translucent to opaque, papyraceous to subvelutinous, non-hygrophanous. **Lamellae** adnate to sinuate, sometimes free, distant,  $L = 9-16$ , equal or unequal,  $l = 3$ , regular or interveined-anastomosed, forked or almost reticulate, faces and edges concolorous with the pileus. **Stipe** 8–70 × 1–3 mm, central, cylindrical, sometimes a little broader upward to the apex, tough, cartilaginous to horny or chitinous downwards from the middle to the base, hollow; apex white to cream, grading from yellowish or orange brown ( $N_{20}Y_{70}M_{50}$  to  $Y_{90}M_{50}C_{20}$ ) to dark chestnut brown ( $N_{80}Y_{99}M_{70}$  or  $Y_{90}M_{99}C_{80}$ ) at the base; surface pruinose to pubescent at the base, opaque; with a well-developed, strigose, cream to whitish brown basal mycelium. **Basidiospores** (6.3–)7–10.4(–11.3) × (2.5–)3–4 µm ( $x_{mm} = 8.3-9.1 \times 3.2-3.8 \mu\text{m}$ ;  $x_{mm} = 8.7 (\pm 0.3) \times 3.5 (\pm 0.3) \mu\text{m}$ ;  $Q_{mm} = 2.3-2.7$ ,  $Q_{mm} = 2.5 (\pm 0.2)$ ;  $n/s = 30$ ,  $s = 4$ ), subellipsoid, lacrimoid to subclavate, hyaline, thin-walled, inamyloid. **Basidia**



**Fig. 9** *Marasmius pseudoniveoaffinis* (M. Capelari & L.A.S. Ramos 4536). a. Basidiomata; b. basidiospores; c. basidia; d. basidioles; e. cheilocystidia; f. pileipellis: *Siccus*-type broom cells and smooth cells; g. caulocystidia. — Scale bars: a = 10 mm, b–g = 10 µm.

18–22.5(–25) × 6.3–7.5 µm, clavate, hyaline, 2–4 sterigmata. *Basidioles* 18.8–22.5 × 5–7(–8.8) µm, clavate, hyaline, thin-walled. *Pleurocystidia* absent. *Cheilocystidia* inconspicuous, hyphoid, elongate, irregularly cylindrical to clavate, without diverticula, sometimes mucronate, but more often forked, rarely ramose; main body 12.5–52.5 × 3.8–9 µm, hyaline, inamyloid, thin-walled; some with appendices or apical, broad branches with lumen, 3.8–17.3 × 1.8–3.3 µm. *Lamellar trama* strongly dextrinoid, irregular, hyphae interwoven, cylindrical, 1.3–8.8 µm diam, smooth and regular in outline, some branched, hyaline, thin-walled. *Pileus trama* strongly dextrinoid, irregular, hyphae interwoven, cylindrical, 2–17.5 µm diam, abundantly septate, similar to those in the lamellar trama in the other aspects. *Pileipellis* hymeniform, composed of two cellular types: 1) *Siccus*-type broom cells, main body 10–30.6 × 7.5–16.3(–18) µm, pyriform to cylindrical-clavate, hyaline, thin-walled; setulae apical, erect, elongate to very short, 2–18 × 1–2.5 µm, cylindrical, digitiform or verruciform, regular or irregular in outline, abundant or scarce, solid or with lumen, apex acute to obtuse; 2) *Globulares*-type smooth cells, more numerous than the first type at the mature basidiomata, 16.3–26.3 × 12.5–17.5 µm, pyriform or balloon-shaped, vesiculose to clavate, or irregular in outline, hyaline, apical portion with thicker walls, dextrinoid. *Stipe trama* strongly dextrinoid, cortical hyphae parallel, cylindrical, 2.5–17.5 µm diam, regular in outline, yellowish, thick-walled; internal hyphae and those of the stipe apex completely hyaline, thin- to thick-walled, smooth. *Stipitipellis* containing caulocystidia cylindrical to setoid, some irregular in outline, short to moderately elongate, 16.3–62.5 × 3.8–8.8 µm, some branched, with a rounded apex, hyaline, more numerous and longer than those of the stipe apex, dextrinoid solely in the base, otherwise inamyloid, thick-walled. *Clamp connections* present in almost all tissues, inconspicuous to conspicuous, not observed in the cortical stipe trama.

**Habit & Substrate** — Gymnoid, scattered, on twigs and dried branches of dicotyledonous tree.

**DNA barcode** — GenBank KP635189 (ITS1-5.8S-ITS2) and KP635144 (LSU).

**Distribution** — This new species is known from Brazil and Costa Rica (Ovrebø 1996).

**Additional specimens (paratypes) examined.** BRAZIL, São Paulo State, Santo André City, Reserva Biológica de Paranapiacaba, 18 Mar. 2010, J.J.S. Oliveira JO60 (SP 445414!); *ibid.*, 21 Mar. 2010, J.J.S. Oliveira JO70 (SP 445421!); *ibid.*, 8 Dec. 2010, J.J.S. Oliveira & P.O. Ventura JO321 (SP 445917!). — COSTA RICA, Heredia Province, La Selva Biological Reserve, Camino Experimental Sul, as *Marasmius pseudoniveus* var. *pseudoniveus* Singer, 17 Mar. 1991, Ovrebø 3090 (CSU!).

**Notes** — *Marasmius pseudoniveoaffinis* is similar to *Marasmius pseudoniveus* (Singer 1965, 1976), especially in the colour of the pileus, macro features of the stipe, size of basidiospores, composition of the pileipellis and the elements of the stipitipellis. However, *M. pseudoniveus* differs by having a hygrophanous pileus (22–45 mm diam), subclose to almost crowded, regular lamellae instead of distant, often interveined-anastomosed lamellae, and by the cheilocystidia in form of the typical *Siccus*-type broom cells rather than irregular, elongate, clavate or filamentous, to often forked or ramose cheilocystidia.

*Marasmius pseudoniveus* var. *amylocystis* (Singer 1976) is also similar to *M. pseudoniveoaffinis* mainly by the similar elements at the lamellar edge. However, *M. pseudoniveus* var. *amylocystis* differs especially by having shorter basidiospores (7.7–8.7 µm long), by having dextrinoid cheilocystidia, also present at the lamellar faces like pleurocystidia; and by having dermatocystidia in the pileipellis similar to those of the hymenium. *Marasmius pseudoniveoaffinis* is also similar to *M. cohortalis* in the pileus pigmentation and by having intervenose-anastomosed lamellae, but differs in having somewhat longer basidiospores (7–10.4

vs 7–8.3 µm, respectively), the presence of peculiar hyphoid cheilocystidia and the pileipellis composed of both *Siccus*-type broom cells and *Globulares*-type smooth cells.

The collection from Costa Rica (Ovrebø 3090) identified as *M. pseudoniveus* var. *pseudoniveus* by Ovrebø (1996) was also examined and this material has the morphological characteristics completely in concordance with *M. pseudoniveoaffinis*, especially regarding the cheilocystidia, and is re-determined as conspecific herein. This information shows that this species presents a wide distribution in the Neotropics, at least throughout the zone covered by Atlantic and Amazon forest and their connections between them and with tropical forest in Central America.

3 — *Marasmius* sect. *Globulares* Kühner emend. Antonín & Noordel. group *Sicci* Singer ser. *Haematocephali* Singer [Sect. *Sicci sensu* Singer (1986)]

***Marasmius altoribeirensis*** J.S. Oliveira, *sp. nov.* — MycoBank MB811132; Fig. 10, 11

**Holotype.** BRAZIL, São Paulo States, Iporanga City, Parque Estadual Turístico do Alto Ribeira, on rotten dicotyledonous debris, 2 Mar. 2012, J.J.S. Oliveira JO532 (SP 445579!).

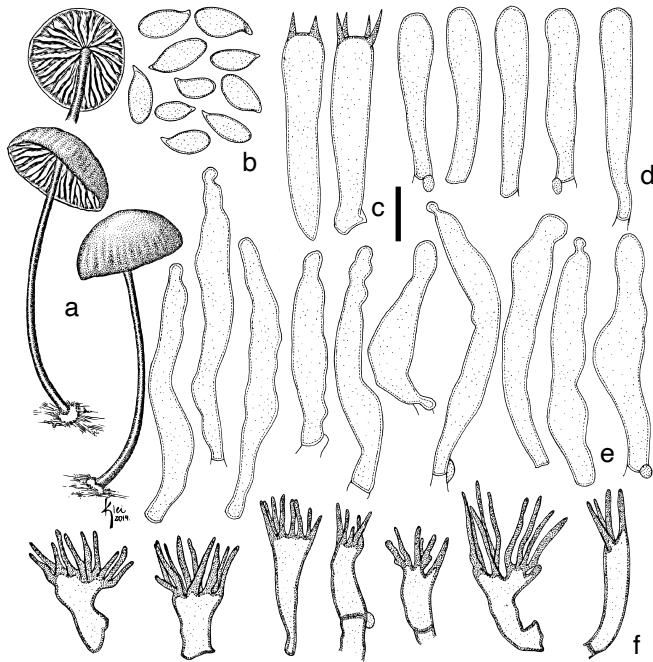
**Etymology.** The epithet refers to Alto Ribeira (São Paulo, Brazil), the name of the area where the holotype was collected.

*Pileus* 23 mm diam, convex, smooth, slightly sulcate-striate, olive brown. *Lamellae* free, subdistant (11), with lamellulae (3), pale cream. *Stipe* 58 × 2 mm, cylindrical, ochraceous brown, with a tomentose basal mycelium. *Basidiospores* 6.3–10 × 3.4–5.6 µm, ellipsoid to tear-shaped. *Pleurocystidia* 30–55 × 4.4–8.8 µm, not projecting, vermiform, ventricose, moniloid or capitate. *Pileipellis* hymeniform, with brownish *Siccus*-type broom cells bearing apical, elongate setulae. *Stipitipellis* containing *Siccus*-type broom cells.

*Pileus* 23 mm diam, convex, smooth, or very slightly sulcate-striate, centre flat or somewhat umbonate, margin incurved, edge regular; centre dark-brown ( $N_{90}Y_{90}M_{60}$ ), becoming olivaceous brown ( $N_{60}Y_{99}M_{50}$ ); membranous, context cream, thin ( $\leq 1$  mm); surface glabrous, somewhat micaceous, dry, dull, subvelutinous, non-hygrophanous. *Lamellae* free, subdistant,  $L = 11$ , unequal, regular,  $l = 3$ , opaque, cream ( $N_{00}Y_{10}M_{00}$ ); edge even, concolorous as well as the hymenium between the lamellae. *Stipe* 58 × 2 mm, central, cylindrical, equal, semi-cartilaginous to cartilaginous, hollow; apex concolorous with the lamellae, becoming ochraceous brown ( $N_{60}Y_{99}M_{50}$ ); surface glabrous or slightly pruinose at the apex, smooth, with a silky shine; basal mycelium white, tomentose.

*Basidiospores* 6.3–10 × 3.4–5.6 µm ( $x_m = 8 (\pm 2) \times 4.5 (\pm 0.6)$  µm,  $Q_m = 1.8 (\pm 0.2)$ ,  $n = 32$ ), obovoid to suboblong, ellipsoid or lacrimoid, smooth, hyaline, thin-walled, inamyloid. *Basidia* 30.6–35 × 6.3–7.5 µm, clavate, noticeably elongate, hyaline, thin-walled, inamyloid, few observed. *Basidioles* 27.5–38.8 × 5–8(–10.3) µm, clavate, noticeably elongate, smooth, hyaline, inamyloid, thin-walled. *Pleurocystidia* 30–55 × 4.4–8.8 µm, more frequent near the lamellar edge, inconspicuous, deeply rooted in the subhymenium, not projecting much beyond the basidia/basidioles, generally irregular in outline, worm-shaped, sometimes ventricose, moniloid near the apex, or capitate, smooth, somewhat opaque, inamyloid. *Cheilocystidia* similar to the *Siccus*-type broom cells in the pileipellis, or completely hyaline, rare, main body 10–21.3 × 3.8–8.8 µm, cylindrical to clavate, turbinate, thin- or thick-walled; setulae apical, erect, generally elongate, 6.3–17.5 × 0.8–1.3 µm, cylindrical, filiform, setoid, regular in outline, simple, pale, solid. *Lamellar trama* dextrinoid, irregular, hyphae interwoven, cylindrical to inflated, 5–16.3 µm diam, regular or irregular in outline, branched, hyaline, smooth, thin-walled. *Pileus trama* dextrinoid, irregular, hyphae interwoven, cylindrical to inflated, 2.5–17 µm diam, similar





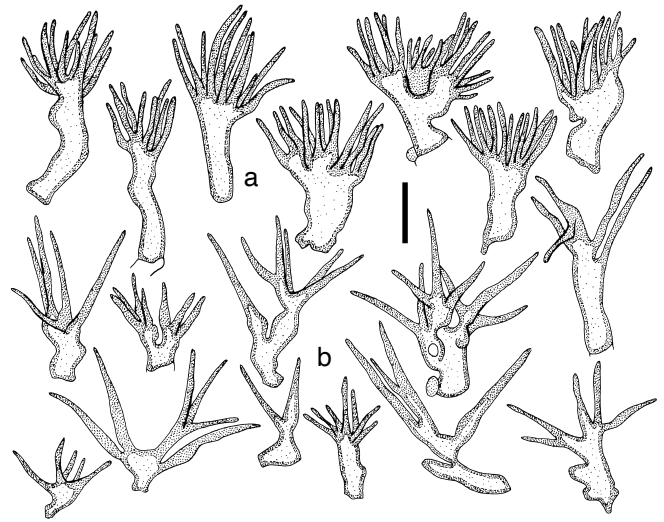
**Fig. 10** *Marasmius altoribeirensis* (JO532). a. Basidiomata; b. basidiospores; c. basidia; d. basidioles; e. pleurocystidia; f. cheilocystidia. — Scale bars: a = 12.8 mm, b–f = 10 µm.

to those of the lamellar trama. *Pileipellis* hymeniform, composed of *Siccus*-type broom cells, appearing brown in mass, some hyaline when isolated, main body 12.5–25 × 3.8–13.8 µm, cylindrical, clavate, frequently turbinate, sometimes branched, walls slightly thick at the apex, but becoming thinner toward the base; setulae apical, erect, generally very elongate, 6.3–18.3 × 0.6–2 µm, cylindrical, thin, filiform, setoid, simple, brown, apex acute or slightly obtuse. *Stipe trama* dextrinoid, cortical hyphae parallel, cylindrical, 4.4–12.5 µm diam, regular in outline, melleous or brown, smooth, walls slightly thick; internal hyphae hyaline, thin-walled, 2.5–13.8 µm diam. *Stipitipellis* with *Siccus*-type broom cells, more often present at the apical portion of the stipe, main body generally reduced, 5–13.8(–18.8) × 2.5–12.5 µm, many times irregular in outline, thick-walled, hyaline to pale brown; setulae very elongate, 3.8–23.8 × 0.9–2.5 µm, cylindrical, filiform to thick setoid, appearing tough, solid or with lumen, regular in outline, simple. *Clamp connections* present in all tissues.

**Habit & Substrate** — Gymnoid, solitary, on rotten dicotyledonous debris.

**DNA barcode** — GenBank KP635204 (ITS1-5.8S-ITS2) and KP635158 (LSU).

**Notes** — *Marasmius altoribeirensis* is one of the few species of *Marasmius* combining olivaceous pileus and pleurocystidia. It also has broom cells of the pileipellis and stipitipellis with very long apical setulae. Few species with olivaceous pileus are known in *Marasmius* (Antonín 2007). One example is *M. brunneoolivacens*, which strongly differs from the new species by the much more elongate basidiospores (12–14 µm) and by the presence of two types of pleurocystidia, one in form of *Siccus*-type broom cells and the other in form of cylindrical to clavate cells, sometimes with lobes or constrictions, but not diverticulate (Wannathes et al. 2009). *Marasmius elaeocephalus sensu* Antonín (2007) is another species with olive-brown pileus very similar to *M. altoribeirensis*, but differs by having thinner basidiomata, smaller pileus (6–14 mm diam), slender stipe, larger basidiospores (10.8–13.8 µm long), refractive, slightly shorter pleurocystidia (19–47 µm long), and not so elongate setulae at the apex of the broom cells.

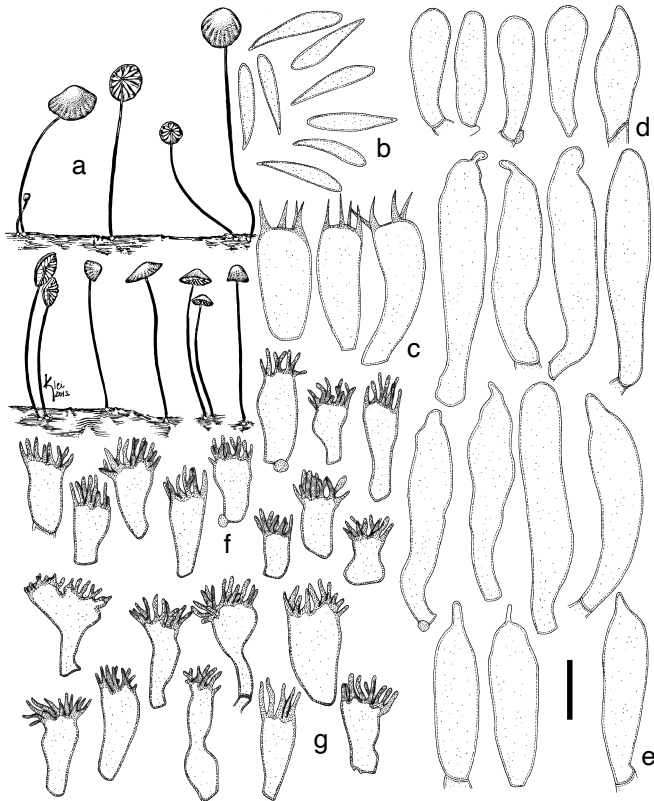


**Fig. 11** *Marasmius altoribeirensis* (JO532). a. *Siccus*-type broom cells of the pileipellis; b. broom cells of the stipitipellis. — Scale bars: 10 µm.

In the trees recovered, *M. altoribeirensis* showed an unsupported relationship with *M. spegazzinii* (Fig. 2), within the strongly supported /confertus clade. These two species share characteristics such as a firm (not thin-membranous) pileus and the presence of medium-sized pleurocystidia.

***Marasmius anomalus*** Lasch ex Rabenh., Klotzsch. Herb. Vivum. N° 1806, pl. 17, f. 97. 1854. (non *Marasmius anomalus* Peck 1872) — Fig. 12

*Pileus* 1.4–11.7 mm diam, conical to campanulate, or hemispheric, later convex to plane, centre smooth, flat or somewhat umbonate, smooth in the youngest basidiomata, becoming radially striate or slightly sulcate and sometimes rugulose with age; margin incurved to decurved, edge entire or crenate; centre brownish orange ( $N_{40}Y_{90}M_{60}$ ), dark orange or almost ochraceous ( $N_{40}Y_{99}M_{60}$ ), remaining the same or becoming orange ( $N_{10}Y_{80-90}M_{40}$ ), or paler orange ( $N_{10}Y_{60}M_{30}$ ) toward the margin with age; membranous, context thin (< 1 mm); surface glabrous, dry, dull, subvelutinous, non-hygrophanous. *Lamellae* free, subfree to adnexed, subdistant to distant,  $L = 12-14$ , equal, regular,  $l = 0$ , opaque, smooth, white to cream ( $N_{00}Y_{10}M_{00}$ ), edge even, cream to finely concolorous with the pileus as well as with the hymenium between the lamellae. *Stipe* 9–38 × 0.2–0.7 mm, central, cylindrical, thin or filiform, equal, simple; tough, cartilaginous to chitinous, hollow; apex concolorous with the lamellar faces, grading to yellowish brown ( $N_{50}Y_{99}M_{40}$ ), then dark reddish brown ( $N_{80-90}Y_{99}M_{50-60}$ ) or black at the base; surface glabrous, smooth, with a silky shine; strigose basal mycelium white to cream, scarce (visible only under good lens), or stipe subsinistitious. *Basidiospores* (11.6–)12.5–17.5 × 3–4.5(–5) µm ( $x_{m10} = 15.3-15.7 \times 3.6-3.8 \mu\text{m}$ ;  $x_{m11} = 15.3 (\pm 0.4) \times 3.7 (\pm 0.1) \mu\text{m}$ ;  $Q_{m11} = 4-4.2$ ;  $Q_{m12} = 4.2 (\pm 0.1)$ ;  $n/s = 30$ ,  $s = 3$ ), oblong, clavate, smooth, hyaline, thin-walled, inamyloid. *Basidia* 18.8–26.3 × 8.4–12 µm, clavate, smooth, hyaline, 3–4 sterigmata, thin-walled, inamyloid. *Basidioles* 18.8–27.5 × 5.6–10 µm, broadly clavate in general, some tapering upward to the apex, tending to have a acute apex, smooth, hyaline, thin-walled, inamyloid. *Pleurocystidia* 31.3–46.3 × 7.5–9.4 µm, inconspicuous in the hymenial layer, slightly projecting above the basidia, conspicuous when isolated, poorly developed, clavate, frequently capitate, with a small apical vesicle, or mucronate, with slight to strong constrictions upward to the apex, sometimes with a tapered apex, smooth, somewhat opaque, thin-walled, inamyloid. *Cheilocystidia* very similar to the *Siccus*-type broom cells in the pileipellis, with the same colour, abundant, main body



**Fig. 12** *Marasmius anomalus* (JO346). a. Basidiomata; b. basidiospores; c. basidia; d. basidioles; e. pleurocystidia; f. cheilocystidia; g. *Siccus*-type broom cells of the pileipellis. — Scale bars: a = 10.8 mm, b–g = 10 µm.

8.8–17.5 × 5.6–7.5 µm, clavate to slightly turbinate, sometimes ventricose, thin-walled, hyaline; setulae apical, erect, 1.3–6.3 × 0.6–1 µm, cylindrical, filiform, thin, digitiform, regular in outline, pale orange, simple, solid, apex slightly obtuse or frequently acute. *Lamellar trama* dextrinoid, irregular, hyphae interwoven, cylindrical, 2–9.4 (–20) µm diam, regular or irregular in outline, with some inflated segments, branched, smooth, hyaline, thin-walled. *Pileus trama* dextrinoid, irregular, hyphae interwoven, cylindrical, 2.3–12.5 µm diam, similar to those of the lamellar trama. *Pileipellis* hymeniform, composed of abundant *Siccus*-type broom cells, orangish to melleous when in group, main body 12.5–20 × 4.4–13.8 µm, clavate, turbinate, ventricose, thin-walled, hyaline; setulae apical, erect, 1.5–5 (–7.5) × 0.5–1 µm, cylindrical, thin, finger-like, simple, regular in outline, yellowish, solid, apex slightly obtuse or almost acute. *Stipe trama* dextrinoid, cortical hyphae parallel, cylindrical, 2–8.8 µm diam, regular in outline, melleous, yellowish to pale brown, smooth, thick-walled; internal hyphae hyaline, thin-walled, 2.5–8.8 µm diam. *Clamp connections* present in almost all tissues, but absent in the cortical stipe trama.

**Habit & Substrate** — Marasmioid, gregarious or scattered, on rotten twigs of dicotyledonous tree.

**Distribution** — The species was described from Driesen, Germany, and recorded from Austria, Czech Republic, French, Italy, Netherlands, Romania, Slovakia and Spain in Europe (Antonín & Noordeloos 2010); Algeria, Morocco (Antonín & Noordeloos 2010) and Cameroon in Africa (Douanla-Meli & Langer 2008); and from Argentina and Chile in South America (Singer 1976). In Brazil, *M. anomalus* has previously been recorded from Paraná State (De Meijer 2001) and this is the first record from São Paulo State.

**Specimens examined.** BRAZIL, São Paulo State, São Paulo City, Parque Estadual das Fontes do Ipiranga, 1 Mar. 2011, J.J.S. Oliveira & F. Karstedt JO340 (SP 4457771); *ibid.*, 3 Mar. 2011, J.J.S. Oliveira & F. Karstedt JO346 (SP 4455061); *ibid.*, 23 Mar. 2011, J.J.S. Oliveira & P.O. Ventura JO361 (SP 4457741).

**Notes** — Singer (1976) studied the holotype (*Lasch - FH*) from Driesen and confirmed it to be conspecific with collections from Tucumán and Córdoba in Argentina and Santiago in Chile. Antonín & Noordeloos (2010) examined collections from Austria, Czech Republic, French, Germany, Italy, the Netherlands, Romania, Slovakia and Spain, and provided a description of the species with much larger basidiospores ((12–)16–22(–24) × (3–)4–5(–6) µm), very elongate basidia and basidioles (up to 42 µm long), shorter pleurocystidia (36–60 µm long) and some inflated hyphal segments in the lamellar and pileus trama. Their description differed from that published by Singer (1976) and the collections examined by us and may be due to a mixture of collections of different species. Antonín & Noordeloos (2010) also listed other inconsistencies in the literature such as larger pileus reaching 20 mm diam (Battetta 1934, Cléménçon 1982), more numerous lamellae ranging from 10–20 (Noordeloos 1987, Singer 1965, 1976), smaller basidia measuring from 28–30 µm (Battetta 1934, Singer 1976).

The material herein examined are concordant in most morphological aspects with those collections studied by Singer (1976), in others with collections studied by Antonín & Noordeloos (2010), or with both. The dimensions of the basidiospores and almost all other characteristics are consistent with those of Singer (1976) and with the protologue, especially regarding basidiospore dimensions, and differs only by the smaller number of lamellae (12–14 vs 10–20) and by shorter pleurocystidia (31.3–46.3 vs 30–83 µm). On the other hand, the number of lamellae and the size of pleurocystidia are in agreement with Antonín & Noordeloos (2010). However, according to these latter authors, the basidia/basidioles as well as the basidiospores are more elongate. Nonetheless, the specimens from São Paulo fit into the species in a 'broad concept', considering a large range in the basidiospores size. Furthermore, colour pictures of a specimen provided by Antonín & Noordeloos (2010) show that the material examined by them resembles ours. The collection from Paraná has no morphological description in published papers, and only has been cited (in tables) in a survey of macrofungi in the state of Paraná (De Meijer 2001). Unfortunately, the material could not be examined in this study.

Desjardin (1989) established the lectotype of *M. anomalus* on the isotype 'Germany, Driesen, Lasch n° 1806 (FH)', providing a full morphological description which is mostly concordant with this present description, supporting this identification. The only distinction is that the lectotype presents non-marginate lamellae. Nonetheless, it is still not completely certain if the specimens from South America (here we include those specimens examined in Singer (1976)) are actually *M. anomalus* described from Germany and widely distributed across Europe and, thus, a molecular comparison should be done. Currently, the species seems to be globally distributed in a most general morphological sense, with the obvious exception of arctic, subarctic, arid and subarid areas. Singer (1976) argued that this is not a typical Neotropical species, but has entered the American subtropics at least in the Southern Hemisphere.

Unfortunately, only ITS sequence could be obtained from JO346 *M. anomalus* while DMC 011 *M. anomalus*, a specimen collected from Cameroon (Africa), has only nLSU sequence (EF160086) deposited in GenBank, and thus the two strains could not be compared. No sequence from European collections (especially from Germany) representing the species is available for comparison so far. However, JO346 herein representing the singerian concept of a 'neotropical *M. anomalus*' is shown in Fig. 1c as potentially conspecific with NW285 *M. hypophaeus* (Wannathes et al. 2009). Both JO346 and NW285 specimens are morphologically conspecific, with exception of the broom cells also present on the lamellar faces along with non-setulose, medium-sized pleurocystidia (41–48 µm) found in NW285.

Moreover, the collection NW285 seems to correspond to the description of *M. anomalus* in Singer (1976) and Desjardin (1989), despite sharing some similarities with *M. hypophaeus*.

***Marasmius luteoolivaceus*** J.S. Oliveira, *sp. nov.* — MycoBank MB811133; Fig. 13

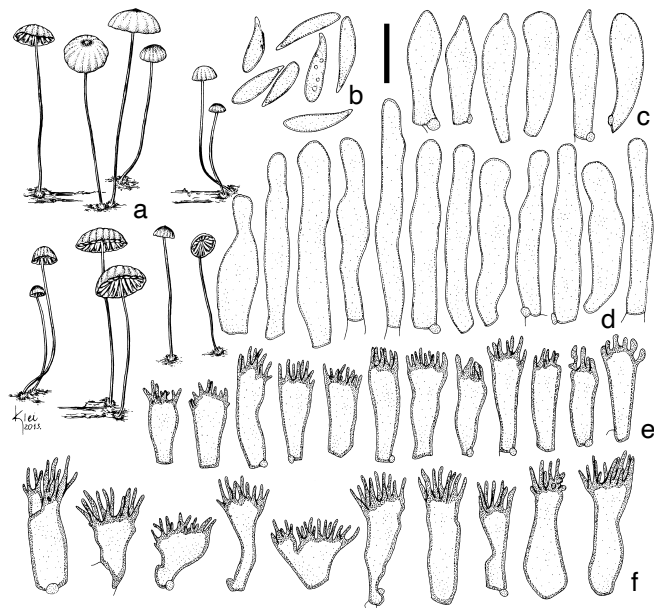
*Holotype.* BRAZIL, São Paulo State, Iporanga City, Parque Estadual Turístico do Alto Ribeira, Núcleo Santana, on dried leaves of dicotyledonous tree, 29 Feb. 2012, J.J.S. Oliveira & D.E. Desjardin JO524 (SP 445574!).

*Etymology.* From the Latin *luteo* = yellow; *olivaceus* = olivaceous, referring to the pileus colour.

*Pileus* 1.5–12 mm diam, hemispherical to convex, shallowly sulcate, umbonate, yellowish olive to greyish yellow. *Lamellae* free, subdistant (16–18). *Stipe* 8.5–38.5 × 0.5–1 mm, reddish brown, with a strigose basal mycelium. *Basidiospores* 9.3–12.5 × 3–3.8 µm, clavate to subfusoid. *Pleurocystidia* 23.8–40 × 3.8–6.5 µm, clavate, slightly ampullaceous, hyaline. *Lamellae* and pileus trama dextrinoid, irregular. *Pileipellis* hymeniform, composed of brownish *Siccus*-type broom cells.

*Pileus* 1.5–12 mm diam, hemispheric to convex, slightly sulcate, centre shallowly to strongly umbonate, margin decurved, edge regular to wavy; pure grey to olivaceous grey ( $N_{80}Y_{40-50}M_{10-20}$ ) when young, then pale olivaceous brown ( $N_{70}Y_{90-99}M_{100-20}$ ), yellowish olive ( $N_{50}Y_{90-99}M_{10-20}$ ) or greyish yellow ( $N_{40}Y_{40-60}M_{10}$ ) when mature, fading to pale brownish yellow ( $N_{50}Y_{80}M_{40}$ ) toward the margin, with a dark olive centre ( $N_{80}Y_{90}M_{100}$ ) or dark olivaceous brown ( $N_{70}Y_{99}M_{10}$ ); membranous, context cream, thin (< 1 mm); surface glabrous, dry, dull, papyraceous to subvelutinous, non-hygrophanous. *Lamellae* free, subclose to subdistant,  $L = 16-18$ , equal, regular,  $l = 0$ , opaque, smooth, pale cream ( $N_{100}Y_{10}M_{100}$ ), edge even, concolorous with the lamellar face or finely concolorous with the pileus, as well as with the hymenium between lamellae. *Stipe* 8.5–38.5 × 0.5–1 mm, central, cylindrical or filiform, equal, semicartilaginous to chitinous, hollow; apex concolorous with the lamellar face, becoming yellowish brown ( $N_{40}Y_{70}M_{40}$ ) or orange ( $N_{60}Y_{90}M_{30}$ ) and reddish brown ( $N_{80}Y_{99}M_{70}$ ) toward the base; surface glabrous, smooth, shiny; with a yellowish, strigose basal mycelium.

*Basidiospores* 9.3–12.5 × 3–3.8 µm ( $x_m = 11.2 (\pm 0.9) \times 3.3 (\pm 0.3) \mu m$ ,  $Q_m = 3.4 (\pm 0.4)$ ,  $n = 30$ ), oblong, clavate to subfusoid, smooth, hyaline, thin-walled, inamyloid. *Basidia* not observed. *Basidiales* 17.5–25 × 4–7 µm, clavate to tapered at the apex, smooth, hyaline, thin-walled, inamyloid. *Pleurocystidia* 23.8–40 × 3.8–6.5 µm, generally cylindrical-clavate, clavate, sometimes tending to ampullaceous, or with constrictions at the apical regions, with a somewhat more inflated apex or a more ventricose base, smooth, hyaline, thin-walled, inamyloid. *Cheilocystidia* forming a sterile, pale yellow lamellar edge, in form of *Siccus*-type broom cells, hyaline when isolated, main body 11.3–18.8 × 4.8–6.5 µm, cylindrical-clavate to clavate, sometimes turbinate to ventricose, thin-walled; setulae apical, erect, short to somewhat elongate, 0.8–4.6 × 0.6–1.3 µm, cylindrical, digitiform to verruciform, rarely globose or broadened, regular to irregular in outline, hyaline, solid, simple, apex acute to obtuse. *Lamellar trama* dextrinoid, irregular, hyphae interwoven, cylindrical, 1.3–10 µm diam, regular in outline, branched, smooth, thin-walled. *Pileus trama* dextrinoid, irregular, hyphae similar to those of the lamellar trama, 1.3–8.8 µm diam. *Pileipellis* hymeniform, composed of *Siccus*-type broom cells, brownish ochre when in group, main body 8.8–20 × 5–8.8(–12.5) µm, clavate, turbinate to ventricose, rarely forked, hyaline, thin- to slightly thick-walled; setulae apical, erect 1.3–7 × 0.5–1 µm, filiform, setiform, cylindrical, thin, simple, regular in outline, generally elongate, sometimes short and verruciform, simple, hyaline to pale yellow, apex acute. *Stipe trama* dextrinoid, cortical hyphae parallel, cylindrical, regular in outline, 2.5–6 µm diam, smooth, yellowish or chestnut brown to olivaceous in KOH, walls somewhat thick; internal hyphae 1.3–5.6 µm



**Fig. 13** *Marasmius luteoolivaceus* (JO524). a. Basidiomata; b. basidiospores; c. basidiales; d. pleurocystidia; e. cheilocystidia; f. *Siccus*-type broom cells of the pileipellis. — Scale bars: a = 13.4 mm, b–f = 10 µm.

diam, hyaline, smooth, thin-walled. *Clamp connections* present in almost all tissues, sometimes inconspicuous, not observed in the cortical stipe trama.

*Habit & Substrate* — Marasmioid, gregarious, on dried leaves of dicotyledonous tree.

*DNA Barcode* — GenBank KP635182 (ITS1-5.8S-ITS2) and KP635137 (LSU).

*Notes* — This new species resembles *M. elaeocephalus* (Singer 1964, Antonín 2007) in the pileus pigmentation and in many other characteristics. However, *M. elaeocephalus* differs by having many series of lamellulae (2–4), larger basidiospores (10.8–13.8(–14.5) × 3.8–5.8 µm) and the pleurocystidia are often subfusoid or rostrate, and somewhat refractive (Antonín 2007).

Based on the Dataset 3 tree (Fig. 2), *M. luteoolivaceus* is strongly supported as sister to *M. hobbitii* within subclade /graminicola.

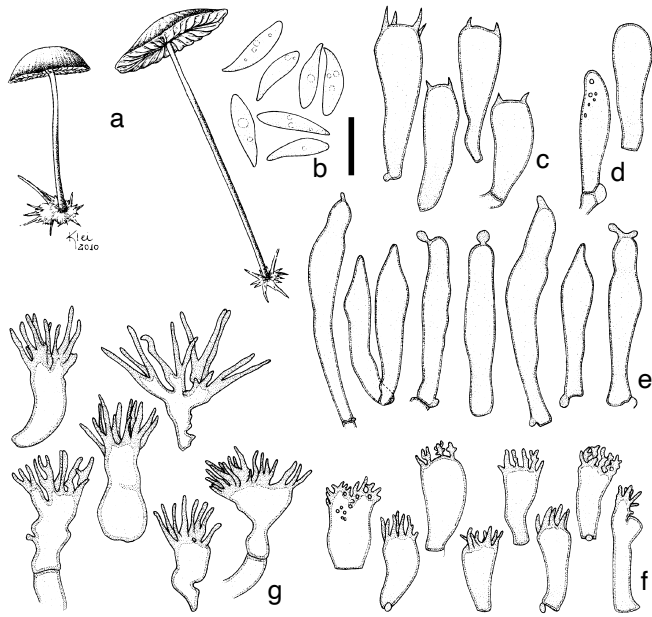
***Marasmius neotropicalis*** J.S. Oliveira, *sp. nov.* — MycoBank MB817805; Fig. 14

*Holotype.* BRAZIL, São Paulo State, Santo André City, Reserva Biológica de Paranapiacaba, on dried twigs of dicotyledonous tree, 21 Mar. 2010, J.J.S. Oliveira JO69 (SP 445420!).

*Etymology.* The epithet refers to 'Neotropical'.

*Pileus* 5–20 mm diam, convex to plano-convex, smooth or shallowly sulcate, often bright orange. *Lamellae* free, subdistant (12–16), with 2–3 series of lamellulae. *Stipe* 16–34 × 0.8–1.3 mm, brownish orange, with a strigose basal mycelium. *Basidiospores* 7.5–13.5 × 2.8–4 µm, clavate to subfusoid. *Pleurocystidia* 27.5–44.5 × 5–7.5 µm, cylindrical, lageniform, clavate, submoniliform, acuminate or capitate. *Cheilocystidia* in form of broom cells with short nodulose setulae. *Trama* dextrinoid. *Pileipellis* hymeniform, composed of *Siccus*-type broom cells, having setulae (2.5–)4.8–14.3(–17.5) × 0.5–1.6 µm. On dried branches and thin twigs of dicots.

*Pileus* 5–20 mm diam, convex to plano-convex, smooth or more often sulcate-striate at least on the margin, centre flat or umbonate, margin incurved to decurved, tending to plane, edge regular or slightly undulate; pale brownish orange ( $N_{20}Y_{60}M_{50}$ ), pale orange, bright orange to frequently darker orange ( $N_{10}Y_{50-80}M_{10-50}$ ;  $N_{10}Y_{50}M_{40}$  to  $N_{10}Y_{60}M_{50}$ ), sometimes pale yellow ( $N_{100}Y_{30}M_{100}$ ), centre yellowish brown ( $N_{20}Y_{60}M_{40}$ ) to orangish brown ( $N_{40}Y_{99}M_{60}$ );



**Fig. 14** *Marasmius neotropicalis* (JO69). a. Basidiomata; b. basidiospores; c. basidia; d. basidioles; e. pleurocystidia; f. cheilocystidia; g. *Siccus*-type broom cells in the pileipellis. — Scale bars: a = 9.2 mm, b–g = 10  $\mu$ m.

membranous, context thin (< 1 mm); surface glabrous, dry, sometimes a little translucent, usually dull, subvelutinous, non-hygrophanous. *Lamellae* free, subdistant,  $L = 12–16$ , equal,  $l = 2–3$ , rarely forked or slightly reticulate, faces and edges white to pale cream ( $N_{00}Y_{20}M_{00}$ ). *Stipe* 16–34  $\times$  0.8–1.3 mm, central, cylindrical, equal, semicartilaginous to slightly chitinous downwards, tough, hollow; apex concolorous with the lamellae or pale yellow ( $N_{00}Y_{50}M_{10}$ ), becoming yellowish brown ( $N_{30}Y_{80}M_{60}$ ) or orangish brown ( $N_{20}Y_{60}M_{60}$ ) in the middle, reaching dark brown ( $N_{40}Y_{99}M_{80}$  to  $N_{90}Y_{99}M_{70}$ ) near the base; surface glabrous, smooth, opaque or with a somewhat silky shine; basal mycelium strigose, abundant, long-filamentose, cream to yellowish. *Basidiospores* 7.5–13.5  $\times$  2.8–4  $\mu$ m ( $x_{rm} = 9.6–11.7 \times 3.5–3.6 \mu$ m;  $x_{mm} = 10 (\pm 1.1) \times 3.6 (\pm 0.1) \mu$ m;  $Q_{m1} = 2.7–3.2$ ;  $Q_{m2} = 2.7 (\pm 0.3)$ ;  $n/s = 30$ ,  $s = 3$ ), oblong, clavate to subfusoid, smooth, hyaline, thin-walled, inamyloid. *Basidia* 18.8–29  $\times$  6–9  $\mu$ m, clavate to vesiculose, generally with an inflated apex, hyaline, thin-walled, inamyloid, 2–4 sterigmata. *Basidioles* 18.5–28  $\times$  5.6–9.3  $\mu$ m, clavate or tapering towards the apex, hyaline, inamyloid. *Pleurocystidia* 27.5–44.5  $\times$  (3.4–)5–7.5  $\mu$ m, sparse, inconspicuous, not prominently projecting beyond the basidia, some with the basal portion more deeply rooted in the subhymenium, cylindrical, lageniform, clavate to submoniliform, apex acuminate, sometimes capitate or with an apical, vesicle or mucro-shaped capitule, smooth, hyaline, thin-walled, inamyloid, some simply as cystidioles with a fusoid apex. *Cheilocystidia* numerous, somewhat different from the *Siccus*-type broom cells of the pileipellis, main body 10.6–20  $\times$  4.5–8  $\mu$ m, clavate to vesiculose, sometimes lobed, hyaline, thin-walled; setulae apical, erect, short, 1–3.8(–5)  $\times$  0.5–1.3  $\mu$ m, many nodulose or irregularly finger-like to conical, others submoniloid, many branched and vesiculose, coralloid, irregular in outline, hyaline, solid, abundant to scarce, apex acute or mostly obtuse and rounded. *Lamellar trama* strongly dextrinoid, irregular, hyphae interwoven, cylindrical, 2–11  $\mu$ m diam, regular in outline, branched, hyaline, thin-walled, smooth. *Pileus trama* strongly dextrinoid, irregular, hyphae similar to those of the lamellar trama, 2.3–12.5  $\mu$ m diam. *Pileipellis* hymeniform, composed of *Siccus*-type broom cells, abundant, pale orange in mass, main body 10–18(–22.5)  $\times$  4.6–12.5  $\mu$ m, clavate to turbinate, somewhat vesiculose, sometimes irregular in outline, forked or branched, hyaline, thin- to slightly thick-walled at the apex;

setulae apical, erect, with a moderate length to frequently elongate, (2.5–)4.8–14.3(–17.5)  $\times$  0.5–1.6  $\mu$ m, cylindrical, regular in outline, simple or branched, solid, abundant, hyaline to pale yellow, apex acute to slightly obtuse. *Stipe trama* strongly dextrinoid, cortical hyphae parallel, 3.5–8  $\mu$ m diam, cylindrical, regular in outline, branched, smooth, yellowish brown, walls moderately thick, septate; internal hyphae similar to those of the cortex, but hyaline, disorganized, 2–9.4  $\mu$ m diam, thin- to moderately thick-walled. *Clamp connections* present in all tissues.

**Habit & Substrate** — Gymnoid to almost marasmioid, scattered, on dried branches and thin twigs of dicotyledonous tree.

**DNA Barcode** — GenBank KP635183 (ITS1-5.8S-ITS2) and KP635138 (LSU).

**Additional specimens (paratypes) examined.** BRAZIL, São Paulo State, Santo André City, Reserva Biológica de Paranapiacaba, 16 Dec. 2009, M. Capelari & L.A. Ramos 4568 (SP 445908!); *ibid.*, 10 Feb. 2010, J.J.S. Oliveira & A.V. Costa JO29 (SP 445909!); *ibid.*, 23 Mar. 2010, J.J.S. Oliveira JO82 (SP 445910!); *ibid.*, 21 Apr. 2010, J.J.S. Oliveira & J.F. Santos JO99 (SP 445912!); *ibid.*, 25 Apr. 2010, J.J.S. Oliveira & J.F. Santos JO118 (SP 445431!); *ibid.*, J.J.S. Oliveira & J.F. Santos JO119 (SP 445913!); *ibid.*, J.J.S. Oliveira & J.F. Santos JO121 (SP 445914!); *ibid.*, 7 Dec. 2010, J.J.S. Oliveira & P.O. Ventura JO293 (SP 445473!); *ibid.*, 9 Dec. 2010, J.J.S. Oliveira & P.O. Ventura JO325 (SP 445493!).

**Notes** — Morphologically, *M. neotropicalis* is very similar to *M. suthepensis* (Wannathes et al. 2009), differing by having a generally brighter orange pileus; by the nodulose and short setulae at the apex of the completely hyaline *Siccus*-type broom cells on the lamellar edge, while those in the pileipellis have much more elongate setulae ((2.5–)4.8–14.3(–17.5) vs 3–8  $\mu$ m); and by the noticeable substrate preference for wood or twigs of dicotyledonous tree instead of leaves.

However, in the Datasets 2.1 and 3 trees recovered (Fig. 1b, 2), *M. neotropicalis* appears very close to the *M. linderioides* complex, within the /graminicola clade. This latter species (type variety) differs by the pileus pigmentation tending to beige, by the very short stipe (1–3 mm vs 16–34 mm long), by the larger basidiospores (10–15  $\times$  3.4–5  $\mu$ m), by having cheilocystidia with more elongate and regular setulae, and broom cells of the pileipellis having shorter setulae (1.5–4  $\mu$ m). A pairwise comparison matrix (Table S1) of ITS sequences including *M. linderioides*, *M. neotropicalis* and *M. suthepensis* reveals they are very close, showing a dissimilarity of c. 2–3 % between *M. linderioides* and *M. neotropicalis*, and c. 2–3 % between *M. neotropicalis* and *M. suthepensis*. The canonical 3 % criterion seems to fail for ITS (Nilsson et al. 2008) to resolve this species complex. This may be due to incomplete data as some sequences are shorter than the expected (due to sequencing artifacts), but also likely shows limitation of the ITS to delimit these species. These three taxa may have recently diverged to form different species and thus there are too few genetic differences found among the taxa of this species group. Interestingly, almost all collections are sympatric where speciation processes are still occurring. The differences in the substrate preferences may also reflect this divergence and serve as a diagnostic character.

***Marasmius spegazzinii*** Sacc. & P. Syd., Syll. Fung. (Abellini) 14: 117. 1899 — Fig. 15

= *Marasmius balansae* Speg., Revista Argentina de Historia Natural 1 (2): 102 (1891).

*Pileus* 21–45 mm diam, convex to more often becoming plane, tending to revolute, smooth, somewhat sulcate-striate, centre flat or shallowly umbonate, margin straight or somewhat up-lifted, edge regular, with some lacerations; centre dark brown ( $N_{90}Y_{99}M_{70}$ ) or paler ( $N_{80}Y_{99}M_{60}$ ) or fulvous brown ( $N_{50}Y_{99}M_{80}$ ),



becoming brownish orange or ochre ( $N_{40}Y_{80}M_{50}$ ) toward the margin; membranous, context cream, thin ( $< 1$  mm); surface glabrous, dry, dull, subvelutinous to velutinous, non-hygrophanous. *Lamellae* free to subfree, subclose to subdistant,  $L = 18–26$ , broad (up to 4 mm), unequal, regular, forked or rarely anastomosed,  $l = 5$  or more, opaque, smooth, whitish cream ( $N_{00}Y_{10}M_{00}$ ) to more yellowish, edge even, concolorous with the lamellar faces as well as with the hymenium between the lamellae. *Stipe* 46–85 × 1.5–4 mm, central, cylindrical, sometimes compressed, equal, tough, semicartilaginous to chitinous, hollow; apex concolorous with the lamellar faces, becoming brownish orange ( $N_{50}Y_{99}M_{50}$ ), dark reddish brown ( $N_{90}Y_{99}M_{70}$ ) downwards; surface glabrous, smooth, with a silky bright; basal mycelium tinted yellow, strigose.

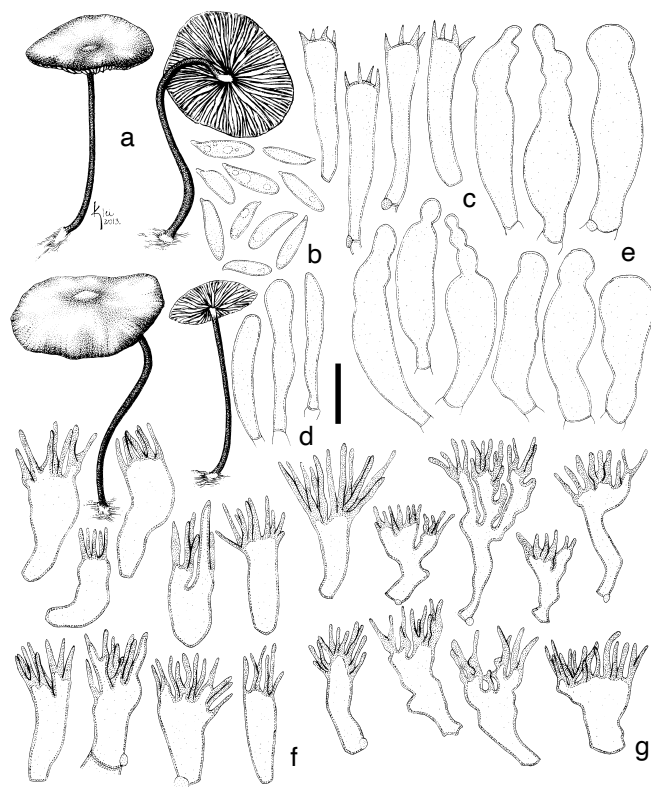
*Basidiospores* 7.5–11.3 × 2.5–3.5  $\mu\text{m}$  ( $x_m = 9.2 (\pm 1) \times 2.9 (\pm 0.3) \mu\text{m}$ ,  $Q_m = 3.2 (\pm 0.3)$ ,  $n = 30$ ), generally oblong, cylindrical, clavate to subfusoid, sometimes subellipsoid, smooth, hyaline, thin-walled, inamyloid. *Basidia* 22.8–31.3 × 4.6–6.3  $\mu\text{m}$ , cylindrical to clavate, smooth, hyaline, 4 sterigmata, thin-walled, inamyloid. *Basidioles* (17.5–)20–28.8 × 3.8–7.2  $\mu\text{m}$ , cylindrical to clavate, smooth, hyaline, thin-walled, inamyloid. *Pleurocystidia* 21.3–40 × 6.3–10  $\mu\text{m}$ , abundant, present not only on the lamellar faces, but also at the edge, almost indistinguishable in the hymenial layer, not prominently projecting above the basidia, versiform, frequently clavate to pyriform, some more elongate, ventricose or with 1–3 constrictions near the apex, which is narrower and somewhat moniloid, or only capitate, completely smooth, hyaline, thin-walled. *Cheilocystidia* in form of *Siccus*-type broom cells similar to those of the pileipellis, but overall hyaline, rare, main body 11.3–22.5 × 6.3–10  $\mu\text{m}$ , clavate to slightly turbinate, thin-walled; setulae apical, erect, 3.4–13 × 0.6–2  $\mu\text{m}$ , cylindrical to digitiform, regular in outline, simple to branched, hyaline, solid or with lumen, apex frequently acute. *Lamellar trama* strongly dextrinoid, irregular, hyphae interwoven, cylindrical, 2–10  $\mu\text{m}$  diam, regular in outline, sometimes inflated, branched, smooth, thin-walled. *Pileus trama* strongly dextrinoid, irregular, or subregular, hyphae resembling those of the lamellar trama, 2.5–16.3  $\mu\text{m}$  diam. *Pileipellis* hymeniform, composed of *Siccus*-type broom cells, abundant, pale ochre in mass, main body 10–20 × 5–13  $\mu\text{m}$ , more often turbinate, sometimes clavate, lobed or irregular in outline, hyaline, thin- to moderately thick-walled, thinner toward the base; setulae apical, erect, 2.5–11.3 × 0.6–1.5  $\mu\text{m}$ , cylindrical, filiform or setiform, simple to forked, regular in outline, hyaline to pale yellow, apex generally acute. *Stipe trama* dextrinoid, cortical hyphae parallel, cylindrical, regular in outline, 2.5–12.5  $\mu\text{m}$  diam, smooth or somewhat rough, pale brown to ochre, thick-walled; internal hyphae, 2–15  $\mu\text{m}$  diam, hyaline, smooth, thin-walled. *Clamp connections* present in almost all tissues, except the cortical stipe trama.

**Habit & Substrate** — Gymnoid, scattered, on rotten leaves of dicotyledonous trees.

**Distribution** — The species was described originally from Guarapí (Paraguay) and subsequently reported from Costa Rica, Peru, Bolivia, Argentina, the United States of America and Tanzania (Singer 1976, Pegler 1977). This is the first record of the species from Brazil.

**Specimen examined.** BRAZIL, São Paulo State, São Paulo City, Parque Estadual das Fontes do Ipiranga, 2 Feb. 2012, J.J.S. Oliveira JO467 (SP 445552!).

**Notes** — The specimen analysed matches consistently the description of *M. spegazzinii* as described by Singer (1976), differing only by the slightly shorter pleurocystidia (21.3–40  $\mu\text{m}$  vs 27.5–52  $\mu\text{m}$ ) and less elongate setulae on the broom cells in the pileipellis. In Pegler (1977), the only relevant difference found was the woody substrate (twigs on the ground) instead of leaves.



**Fig. 15** *Marasmius spegazzinii* (JO467). a. Basidiomata; b. basidiospores; c. basidia; d. basidioles; e. pleurocystidia; f. cheilocystidia; g. *Siccus*-type broom cells of the pileipellis. — Scale bars: a = 20 mm, b–g = 10  $\mu\text{m}$ .

The specimen examined is very close to *Marasmius spadiceus* based on descriptions found in Gilliam (1975, 1976). However, Desjardin (1991) established *M. spadiceus* as synonym of *M. floridanus*, the latter previously considered a synonym of *M. spegazzinii* by Singer (1976). Desjardin (1991) stated that he had not the chance to study the holotype of *M. spegazzinii* (*Balansa* 4284, nom. nov. for *M. balansae* (Spegazzini 1891) non *M. balansae* (Patouillard 1890)), since it was no longer deposited in the LPS herbarium, and was apparently lost. Therefore, the conspecificity of *M. spegazzinii* and *M. floridanus sensu* Singer (1976) was not accepted by Desjardin (1991) until new specimens from Paraguay corresponding to the protologue of *M. spegazzinii* (*Balansa* 4284) could be collected.

However, Singer (1976) examined the holotype (*Balansa* 4284) and a syntype from Guarapí (Paraguay), along with other collections of *M. spegazzinii* from Costa Rica, Peru, Bolivia and Argentina, and the holotype of *M. floridanus* deposited in FLAS, Florida, and concluded that the latter species should be a synonym of *M. spegazzinii*.

The name *Marasmius spegazzinii* Sacc. & P. Syd. (replacing *M. balansae* Speg., for it is a competing homonym with the older name *M. balansae* Pat.) is currently illegitimate (*nomen superfluum*) in MycoBank, whereas the legitimate name is assigned to *Chamaeceras spegazzinii* (Kuntze 1898), a *nomen novum* also for *M. balansae* Speg. However, *Chamaeceras* Rebert. ex Kuntze is illegitimate as a synonym of *Marasmius* Fr. If the priority is for *Chamaeceras spegazzinii* Kuntze against *Marasmius spegazzinii* Sacc. & P. Syd., a new combination may be needed based on *Chamaeceras spegazzinii* Kuntze.

Based on the Dataset 3 tree (Fig. 2), *M. spegazzinii* appears as an unsupported sister to *M. altoribeirensis* within the subclade /confertus.

***Marasmius suthepensis*** Wannathes, Desjardin & Lumyong,  
Fungal Diversity 37: 288. 2009 — Fig. 16

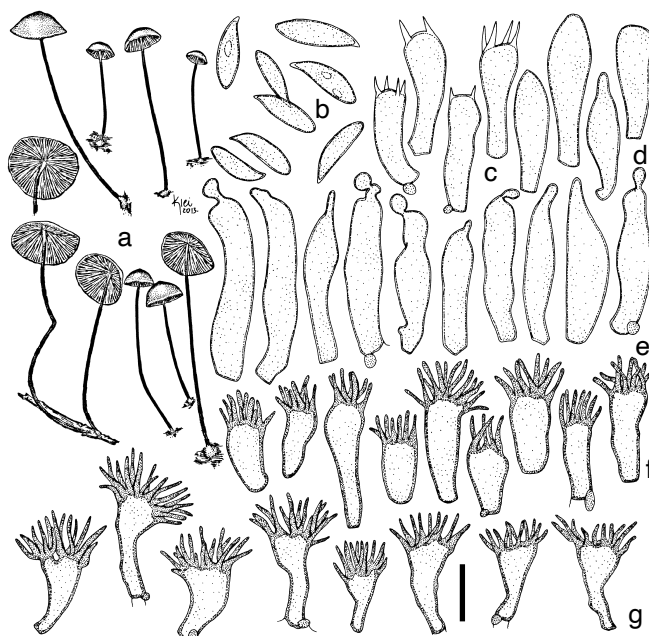
*Pileus* 2 mm diam in youngest stages, later 6.8–19 mm diam, convex, hemispheric to campanulate, smooth or striate, centre slightly umbonate with a small umbo, margin incurved to decurved, edge regular; yellowish brown with faint olivaceous hues ( $N_{60}Y_{70}M_{40}$ ) when immature, becoming yellow ( $N_{10}Y_{90}M_{20}$ ) to orange yellow ( $N_{10}Y_{90}M_{40}$ ) or light orange ( $N_{20}Y_{90}M_{50}$ ) when mature, with centre ochraceous brown ( $N_{40}Y_{70-80}M_{30}$ ) to brown ( $N_{50}Y_{90}M_{50}$ ); membranous, context thin (< 1 mm); surface glabrous, dry, dull, smooth, non-hygrophanous. *Lamellae* free to adnexed, close, abundant considering the lamellulae,  $L = 13-23$ , unequal, regular,  $l = 3-4$ , opaque, smooth, whitish cream ( $N_{00}Y_{10}M_{00}$ ), edge even, concolorous with the lamellar faces, but the hymenium between lamellae is concolorous with the pileus. *Stipe* 10–68 × 0.6–1 mm, central, cylindrical, equal or sometimes with a broadened apex; tough, semicartilaginous to chitinous, hollow; apex greyish yellow ( $N_{10}Y_{50}M_{20}$ ) or even concolorous with the lamellae, becoming ochraceous brown or orange ( $N_{30}Y_{70}M_{40}$  to  $N_{40}Y_{60}M_{50}$ ), reaching dark brown ( $N_{60}Y_{80}M_{70}$ ) to almost black ( $N_{90}Y_{99}M_{60}$ ) downward to the base; surface glabrous, smooth, with a silky shine; basal mycelium strigose, scarce to abundant, tinted yellow.

*Basidiospores* 8.8–14 × 3–5 (–5.4)  $\mu\text{m}$  ( $x_{\text{m}} = 11.3-11.7 \times 3.4-4 \mu\text{m}$ ,  $x_{\text{mm}} = 11.4 (\pm 0.2) \times 3.9 (\pm 0.1) \mu\text{m}$ ,  $Q_{\text{m}} = 2.8-3.1$ ,  $Q_{\text{mm}} = 3 (\pm 0.1)$ ,  $n/s = 30$ ,  $s = 5$ ), oblong, clavate to subfusoid, smooth, hyaline, thin-walled, inamyloid. *Basidia* 20–26.5 × 6–7.5  $\mu\text{m}$ , clavate, hyaline, thin-walled, 2–4 sterigmata, inamyloid. *Basidioles* 18.8–28.3 × 6.3–7.5  $\mu\text{m}$ , clavate to subacuminate, smooth, hyaline, thin-walled, inamyloid. *Pleurocystidia* 21.3–36.3 × 5–7.5  $\mu\text{m}$ , inconspicuous, poorly developed, smooth, subacuminate, mucronate to capitate, with an evident, vesiculose appendage, or apically capitate, hyaline, inamyloid. *Cheilocystidia* abundant, mostly limited to the lamellar edge, but some also dispersed across the face, in form of *Siccus*-type broom cells, main body 11.3–23.8 × 5–7.8  $\mu\text{m}$ , clavate to turbinate, very similar to those of the pileipellis, thin-walled, hyaline; setulae apical, erect, moderately elongate to rarely short, 2.5–7 × 0.5–1  $\mu\text{m}$ , cylindrical, filiform, hyaline, simple, apex acute. *Lamellar trama* strongly dextrinoid, irregular, hyphae cylindrical to rarely inflated, 1.5–12.5  $\mu\text{m}$  diam, smooth, branched, hyaline, thin-walled. *Pileus trama* strongly dextrinoid, irregular, tending to regular near the pileipellis, hyphae cylindrical to inflated, 2–12.5  $\mu\text{m}$  diam, smooth, hyaline, thin-walled. *Pileipellis* hymeniform, composed of *Siccus*-type broom cells, abundant, pale orange, hyaline when isolated, main body 10–18.8 × 6.3–10  $\mu\text{m}$ , clavate to turbinate, thin-walled, dextrinoid; setulae apical, erect, elongate, 2.3–7.5 × 0.6–1  $\mu\text{m}$ , filiform to cylindrical, very thin, solid, simple, apex acute. *Stipe trama* strongly dextrinoid, cortical hyphae parallel, cylindrical, 3–10.6  $\mu\text{m}$  diam, regular in outline, smooth, thick-walled, yellowish brown, septate; internal hyphae hyaline, 2.5–11.3  $\mu\text{m}$  diam, thin-walled, branched. *Clamp connections* present in almost all tissues, but absent in the cortical stipe trama.

**Habit & Substrate** — Gymnoid, scattered or gregarious, on petioles of leaves and dried twigs of dicotyledonous tree.

**Distribution** — Originally described from Thailand (Wannathes et al. 2009) and also found in Príncipe (Grace et al. 2019), it is herein recorded for the first time from Brazil.

**Specimens examined.** BRAZIL, São Paulo State, Santo André City, Reserva Biológica de Paranapiacaba, 2 Dec. 2009, *M. Capelari* & L.A.S. Ramos 4556 (SP 446013!); *ibid.*, 14 Jan. 2010, *J.J.S. Oliveira* & *M. Capelari* JO3 (SP 446115!); *ibid.*, 23 Mar. 2010, *J.J.S. Oliveira* JO83 (SP 445911!); São Paulo City, Parque Estadual das Fontes do Ipiranga, 1 Mar. 2011, *J.J.S. Oliveira* & *F. Karstedt* JO329 (SP 445496!); *ibid.*, 23 Mar. 2011, *J.J.S. Oliveira* & *P.O. Ventura* JO360 (SP 446016!); *ibid.*, 2 Feb. 2012, *J.J.S. Oliveira* JO469 (SP 445554!); *ibid.*, 18 Jan. 2013, *N. Menoll-Jr.* NMJ214 (SP 446032!); *ibid.*, 14 Mar. 2014, *M. Capelari* (SP 446017!).



**Fig. 16** *Marasmius suthepensis* (JO469). a. Basidiomata; b. basidiospores; c. basidia; d. basidioles; e. pleurocystidia; f. cheilocystidia; g. *Siccus*-type broom cells of the pileipellis. — Scale bars: a = 15.2 mm, b–g = 10  $\mu\text{m}$ .

**Notes** — The material examined herein matches perfectly the description of the holotype (Wannathes et al. 2009). The record of *M. suthepensis* in both Thailand and Brazil may seem surprising, given the geographic distance and the presumed barriers to dispersal. However, a simple pairwise comparison of ITS sequences between the holotype from Thailand and the collections from Brazil showed almost no divergence (< 1 %) for this marker (Table S1), supporting the identification of the examined material.

It is possible that *M. suthepensis* have been introduced in South America from regions of Tropical Asia (or *vice versa*), supposing that the basidiospores or mycelium fragments were brought along with plants of economic interest historically exchanged between Asian and South American countries by merchant ships. Another hypothesis is the airborne spores and formation of spore clouds (Money 2016) that amplifies the power of spore discharge to cover long continental distances and transoceanic air trips. As fungal spores are constantly released to the air by many mushroom species, and although the vast majority are deposited in the surroundings, part of the discharged spores can be taken up by wind currents. However, spores of *Marasmius* are typically hyaline and thin-walled (Singer 1986, Desjardin 1989), highly susceptible to desiccation and UV radiation, and probably will not be viable after long aerial journeys (D.J. Lodge, pers. comm.).

Nonetheless, a thorough and specific biogeographic evaluation of pantropical distributions is necessary for many species exhibiting this supposedly wide distribution. As for *M. suthepensis*, other cases in *Marasmius* presenting supposedly wide distribution (showing molecular conspecificity) may suggest that the mycota of the Neotropics and Tropical Asia, which was connected in the remote past, still looks genetically linked. Many studies in Indo-Malaysian, Australasian, Oceanian and Afrotropical areas have already recorded species originally described in the Neotropics (Singer 1976, Corner 1996, Desjardin & Horak 1997, Desjardin et al. 2000, Antonín 2007, Tan et al. 2009, Wannathes et al. 2009, Antonín et al. 2012, Deng et al. 2012), but molecular comparison between strains indicating same morphological species is still in the beginning. We cannot discard the possibility that ITS is limited to solve species complex in allopatry,

indicating that the samples represent very recently diverged taxa with little variation in particularly this marker.

*Marasmius suthepensis* is very close to *M. neotropicalis* in both morphology and genes herein studied. Moreover, *M. suthepensis* closely resembles *M. ferruginoides* (Antonín 2004), a species originally described from Tshopo Province (Democratic Republic of Congo) and also recorded from Cameroon, Ghana, Kenya, Nigeria (Antonín 2004, 2007). The examined material morphologically corresponds to *M. ferruginoides* according to Antonín (2004, 2007), diverging only by having slightly shorter pleurocystidia (21.3–36.3 vs 27–42 µm) while the holotype of *M. suthepensis* has pleurocystidia (27–47 µm) strongly concordant to those recovered from basidiomata of *M. ferruginoides*. The only difference is the number of lamellae: 12–18 with 3–4 lengths of lamellulae in *M. suthepensis* (holotype) vs 18–21 with 2–3 lengths of lamellulae in *M. ferruginoides* (holotype). The collections of *M. suthepensis* from Brazil show a wide variation in the number of lamellae (13–23), that overlaps both ranges above. Based on Shay et al. (2017), *M. ferruginoides* (by collection from Madagascar) seems an independent species.

On the other hand, *M. ferruginoides* and *M. suthepensis* are micro-morphologically very similar to *M. hinnuleus*. Wannathes et al. (2009) argued that *M. hinnuleus*, described from Cuba, differs by having a sulcate to plicate, pale reddish brown to rufous cinnamon, smaller pileus (4–12 mm vs 10–27 mm) and longer basidiospores (mean  $14 \times 3.8$  µm based on descriptions found in Singer (1976) and Pegler (1983)). Singer (1976) mentioned smaller basidiospores ( $7.7$ – $9.7$ – $13.5 \times 3.3$ – $4.5$  µm (generally  $9.7$ – $10.3 \times 3.3$ – $4.5$  µm). The largest basidiospore length was given by Pegler (1983),  $11$ – $15.5 \times 3.5$ – $4.5$  µm. The basidiospore dimensions in Singer and Pegler do not agree. Regarding the pileus colour, the protologue used the term ‘helvolus’, which is a variation of pale red to yellowish (Riddle 1870) and this pigmentation might have been observed in dried material but not in fresh material. Based on Shay et al. (2017), *M. hinnuleus* (by collection from Madagascar) is an independent species.

TYS280 *M. suthepensis* (holotype) grouped along a basal tri- or polytomy with JO329 and JO469 in the /grammicola clade in all trees recovered. These three strains form a weakly supported branch because *M. suthepensis* seems to be part of a species complex that encompasses *M. brunneoolivascens*, *M. conchiformis*, *M. griseoroseus*, *M. hobbitii*, *M. linderioides*, *M. luteoolivaceus* and *M. neotropicalis* (Fig. 1b). Therefore, ITS alone is not sufficient to provide resolution for the clade, especially for *M. suthepensis* which is shown to be the earlier diverging lineage of the complex (see more in ‘Discussion’ section ‘Molecular phylogeny’).

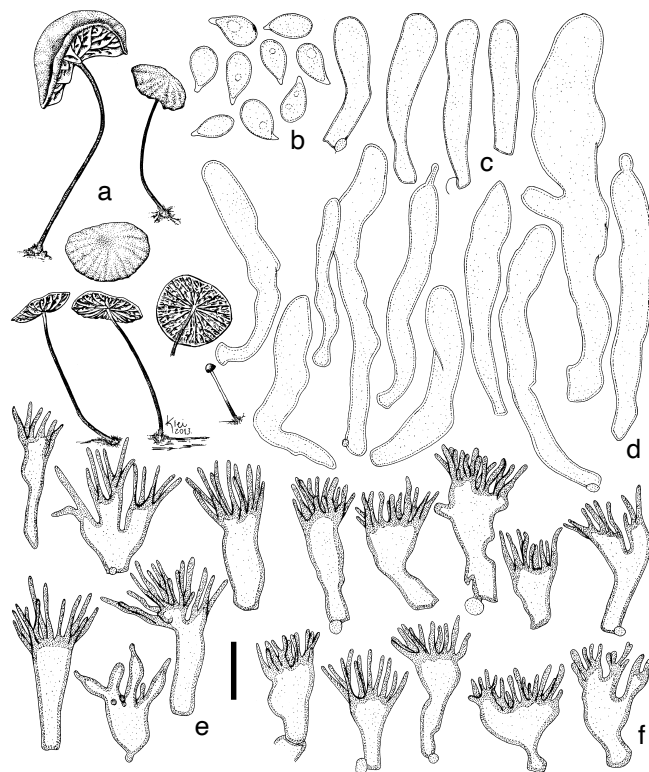
***Marasmius venatifolius* J.S. Oliveira, sp. nov.** — MycoBank MB811134; Fig. 17, 18

**Holotype.** BRAZIL, São Paulo State, Santo André City, Reserva Biológica de Paranapiacaba, on rotten leaves and small twigs of dicotyledonous trees, 9 Oct. 2010, J.J.S. Oliveira & P.O. Ventura JO313 (SP 445485!).

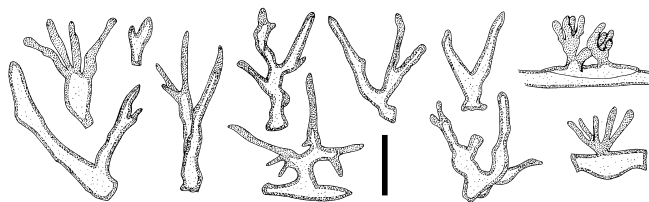
**Etymology.** From the Latin *venatis* = veined and *folius* = lamellae, referring to the veined lamellae.

**Pileus** 17.8–32 mm diam, sulcate-striate or irregularly sulcate, rufous orange or bright orange. **Lamellae** free or subfree, regular to intervenose. **Stipe** central, cylindrical, with a strigose basal mycelium. **Basidiospores** 6–9 × 3.5–5.3 µm, ellipsoid to subellipsoid. **Pleurocystidia** 27–69 × 5–12 µm, elongate, versiform, deeply immersed in the trama. **Hyphae trama** dextrinoid. **Pileipellis** hymeniform, with *Siccus*-type broom cells. **Stipitipellis** covered with forked to multibranched segments.

**Pileus** 17.8–32 mm diam, often convex-applanate, sometimes campanulate, sulcate-striate or slightly sulcate or even slightly



**Fig. 17** *Marasmius venatifolius* (JO313). a. Basidiomata; b. basidiospores; c. basidioles; d. pleurocystidia; e. cheilocystidia; f. *Siccus*-type broom cells of the pileipellis. — Scale bars: a = 16.4 mm, b–f = 10 µm.



**Fig. 18** *Marasmius venatifolius* (JO313). Branched structures or broom cells of the stipitipellis. — Scale bars: 10 µm.

tessellated, centre flat, shallowly depressed or slightly umbonate, margin decurved, plane to uplifted, edge regular, wavy or lacerate; centre dark orangish brown ( $N_{99}M_{60}C_{40}$ ) to purplish brown ( $N_{70}Y_{70}M_{70}$ ) or almost black, becoming ochraceous to rufous orange ( $Y_{99}M_{60}C_{30}$ ,  $N_{30}Y_{99}M_{60}$  or  $N_{40}Y_{99}M_{70}$ ), or bright orange ( $Y_{99}M_{60}C_{20}$ ), to paler orange ( $Y_{99}M_{50}C_{30}$ ) at the margin; membranous, context thin (< 1 mm); surface glabrous, barely pruinose, dry, dull, subvelutinous, non-hygrophanous. **Lamellae** free or subfree, subdistant to distant,  $L = 10$ – $15$ , unequal, regular (only in JO285, but this clearly has some slightly veined lamellae) or mostly strongly interveined or veined,  $l = 1$ – $2$ , opaque, smooth, pale cream ( $N_{00}Y_{10}M_{00}$ ), edge even, partially or finely concolorous with the pileus as well as with the hymenium between the lamellae. **Stipe** 19–72 × 0.7–1.7 mm, central, cylindrical, equal, with a cream to orangish, strigose basal mycelium; tough, semicartilaginous to chitinous; apex concolorous with the lamellar faces, varying from yellowish brown ( $N_{30}Y_{10}M_{30}$ ), to orangish brown ( $N_{40}Y_{60}M_{50}$  to  $N_{60}Y_{99}M_{70}$ ), reaching dark brown or black at the base; surface glabrous, finely pruinose near the base, smooth, opaque or silky bright. **Basidiospores** (5.3–)6–9(–10) × 3.5–5.3(–7) µm ( $x_{mm} = 7$ – $8 \times 4.3$ – $4.5$  µm,  $x_{mm} = 7.6 (\pm 0.7) \times 4.4 (\pm 0.1)$  µm,  $Q_{mm} = 1.7$ – $1.8$ ,  $Q_{mm} = 1.8 (\pm 0.1)$ ,  $n/s = 30$ ,  $s = 2$ ), obovoid, ellipsoid to subellipsoid, lacrimoid, smooth, hyaline, thin-walled, inamyloid. **Basidia** not observed. **Basidioles** 23–36 × 4–8 µm, clavate, rarely

tapering to the apex or somewhat mucronate, some apparently having a granular coating on the apex, hyaline, thin-walled, inamyloid. *Pleurocystidia* 27–69 × (3.4–)5–12 µm, elongate, versiform, clavate, vermiform, filamentous, some capitate or mucronate, generally opaque, often deeply rooted in the lamellar trama, projecting a little above the basidia and basidioles, smooth, inamyloid, sometimes inconspicuous. *Cheilocystidia* similar to the *Siccus*-type broom cells of the pileipellis, pale orange when grouped, main body 10–18.8 × 5.3–8.8(–13.4) µm, clavate to turbinate, sometimes forked, walls somewhat thinner; setulae apical, erect, generally elongate, 4.6–10.6 × 0.6–1.3(–2) µm, filiform, very thin to broad, regular in outline, solid, apex acute or needle-like. *Lamellar trama* dextrinoid, especially in the inner layer, irregular, hyphae interwoven, cylindrical, 2–14.4 µm diam, regular in outline, branched, smooth, hyaline, thin-walled. *Pileus trama* dextrinoid, especially in the subhymenium, irregular, hyphae interwoven, cylindrical, 2–10 µm diam, regular in outline, branched, smooth, hyaline, thin-walled. *Pileipellis* hymeniform, composed of *Siccus*-type broom cells, abundant, pale orange when grouped, hyaline when isolated, main body (8.8–)11.3–25 × 6.3–11.3(–14.3) µm, clavate to often turbinate, sometimes branched, rarely irregular in outline, thick-walled at the apex, narrowed downward to the base; setulae apical, erect, short to elongate, 2.5–8.3 × 0.6–1.3 µm, cylindrical, filiform, very thin, needle-like, simple, pale yellow, apex acute. *Stipe trama* dextrinoid, cortical hyphae parallel, cylindrical, 3–15 µm diam, regular in outline, yellowish brown or pale golden brown, smooth, thick-walled; internal hyphae hyaline, thin-walled, 2–10 µm diam. *Stipitipellis* covered by forked or multibranching segments, dendroid, present especially at the basal region of the stipe, irregular in outline, sometimes as a different type of broom cells, ramifications clavate or similar to digitiform diverticula, horn-shaped, cylindrical, rising from segments or hyphal endings, thick-walled, relatively short, 8–28.8 × 2.5–8.8 µm, tending to disappear or diminish upward to the stipe apex. *Clamp connections* present in almost all tissues, some small and inconspicuous, but not seen in the cortical stipe trama.

**Habit & Substrate** — Gymnoid, scattered or gregarious, on rotten leaves or small twigs of dicotyledonous trees.

**DNA Barcode** — GenBank KP635203 (ITS1-5.8S-ITS2) and KP635157 (LSU).

**Additional specimens (paratypes) examined.** BRAZIL, São Paulo State, Santo André City, Reserva Biológica de Paranapiacaba, 18 Mar. 2010, J.J.S. Oliveira JO63 (SP 445417!); *ibid.*, 7 Dec. 2010, J.J.S. Oliveira & P.O. Ventura JO285 (SP 445467!).

**Notes** — *Marasmius venatifolius* shares some morphological similarities with *M. spissus* (Desjardin 1989), especially the pruinose stipe, abundant basal mycelium, the shape and length of basidiospores (5.6–8 µm), inconspicuous pleurocystidia, and the dendroid elements in the stipitipellis. Otherwise, they are very distinct species. *Marasmius sullivantii* is somewhat similar to the new species, especially in the dimension and pigmentation of the pileus, in the general aspect of the stipe, the shape and length of the basidiospores and the presence of broom cells in the stipitipellis (Desjardin 1989). However, *M. venatifolius* has a brighter orange, not 'soredia-like' spotted pileus, which is slightly tessellated due to the presence of intervenose lamellae; broader basidiospores (3.5–5.3(–7) µm vs 3.2–4 µm); differently shaped, deeper 'rooted' pleurocystidia; and more irregular broom cells bearing more elongate setulae, not accompanied by smooth cells. *Marasmius venatifolius* is a distinct species, arising as a well-supported branch of a polytomy in the Dataset 2.2 tree (Fig. 1c) and in the supported branch with an unresolved placement in the Dataset 3 tree (Fig. 2).

4 — *Marasmius* sect. *Globulares* Kühner emend. Antonín & Noordel. group *Sicci* Singer ser. *Leonini* Singer

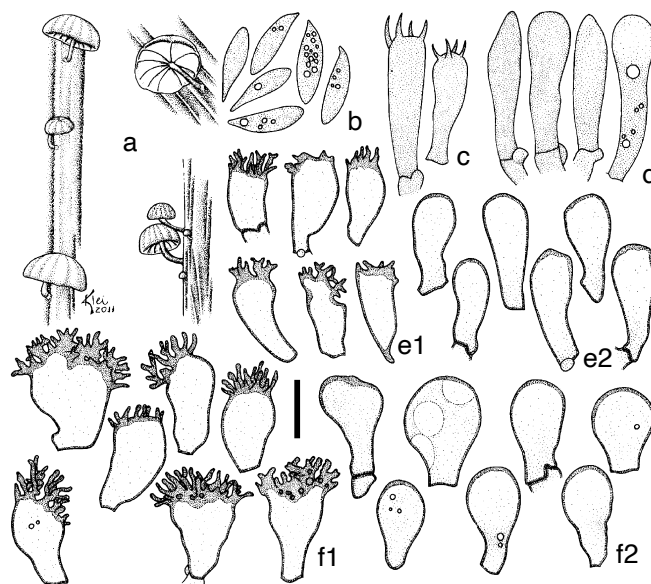
***Marasmius ambicellularis*** J.S. Oliveira, *sp. nov.* — MycoBank MB800886; Fig. 19

**Holotype.** BRAZIL, São Paulo State, Santo André City, Reserva Biológica de Paranapiacaba, on hanging dead palm leaves, 23 May 2010, J.J.S. Oliveira & C.L.A. Pires JO144 (SP 417465!).

**Etymology.** Based on the two types of cells in the pileipellis.

Differs from *Marasmius linderioides* by the absence of pleurocystidia, the presence of both smooth and *Siccus*-type broom cells in the pileipellis and the substrate type which is on hanging dead palm leaves.

**Pileus** 1–3 mm diam, convex, shallowly sulcate, centre plane, margin incurved to decurved, edge regular; pale orange (N<sub>00</sub>Y<sub>50</sub>M<sub>20</sub>), with centre brownish orange (N<sub>10</sub>Y<sub>50</sub>M<sub>60</sub>); membranous, context thin (< 1 mm); surface glabrous, dry, dull, non-hygrophanous. **Lamellae** adnate, distant, L = 8–10, equal, l = 1, faces and edges pale cream (N<sub>00</sub>Y<sub>10</sub>M<sub>00</sub>). **Stipe** 1–2.5 × 0.3–0.5 mm, eccentric or central, reduced, curved, cylindrical, thin, chitinous, hollow; apex concolorous with the lamellae, middle orangish brown (N<sub>20</sub>Y<sub>80</sub>M<sub>60</sub>), with a darker base; surface glabrous, smooth, opaque; basal mycelium scarce, cream, strigose. **Basidiospores** 12.3–17 × 3.8–5 µm (x<sub>m</sub> = 14.2 (± 1.2) × 4 (± 0.3) µm; Q<sub>m</sub> = 3.5 (± 0.4), n = 30), suboblong, lacrimoid or subfusoid, smooth, hyaline, thin-walled, inamyloid. **Basidia** 18.8–31 × 7.3–8.8 µm, clavate, hyaline, thin-walled, 4 sterigmata, inamyloid. **Basidioles** 21.3–31.3 × 6–8 µm, clavate or acuminate, hyaline, thin-walled, inamyloid. **Pleurocystidia** absent. **Cheilocystidia** inconspicuous, similar to the elements of the pileipellis, dimorphic: 1) *Siccus*-type broom cells, main body 11.3–18 × 6.3–8 µm, clavate to vesiculose, or even irregular in outline, hyaline, thin-walled, inamyloid; setulae apical, erect, generally short, 0.9–4.6 × 0.6–1.6 µm, cylindrical or conical, sometimes rare, regular in outline or a little moniloid, hyaline, simple or branched, solid, apex obtuse and rounded; 2) *Globulares*-type smooth cells, 16.3–24 × 6.5–9 µm, very similar to the cells of the pileipellis. **Lamellar trama** dextrinoid, irregular, composed of cylindrical hyphae, 1.6–9.4 µm diam, regular in outline, smooth, hyaline, thin-walled, branched. **Pileus trama** similar to the lamellar trama, hyphae 1.6–10 µm



**Fig. 19** *Marasmius ambicellularis* (JO144). a. Basidiomata; b. basidiospores; c. basidia; d. basidioles; e. cheilocystidia: e1. *Siccus*-type broom cells, e2. smooth cells; f. pileipellis: f1. *Siccus*-type broom cells, f2. smooth cells. — Scale bars: a = 2.8 mm, b–f = 10 µm.



diam. *Pileipellis* hymeniform, composed of dimorphic elements: 1) *Siccus*-type broom cells, abundant, main body  $9.4\text{--}20 \times 6.6\text{--}15 \mu\text{m}$ , clavate, vesiculose or turbinate, occasionally bilobed or irregular in outline, hyaline, thin- to moderately thick-walled, inamyloid; setulae apical, erect, short to a little elongate,  $1.3\text{--}6.5 \times 0.9\text{--}1.6 \mu\text{m}$ , cylindrical or conical, regular in outline to almost moniliform, branched, pale yellow to brown, solid, apex obtuse and rounded; 2) *Globulares*-type smooth cells,  $15\text{--}24 \times 8.5\text{--}14.3 \mu\text{m}$ , pyriform, less numerous, hyaline, thin- to moderately thick-walled. *Stipe trama* dextrinoid, cortical hyphae parallel, cylindrical,  $3\text{--}7.5 \mu\text{m}$  diam, smooth, regular in outline, branched, melleous, thick-walled; internal hyphae similar to the cortical hyphae, but more slender,  $1.5\text{--}6 \mu\text{m}$  diam, irregular, hyaline, thin-walled. *Clamp connections* present in all tissues.

**Habit & Substrate** — Marasmioid, gregarious, on hanging dead palm leaves.

**DNA Barcode** — GenBank KP635181 (ITS1-5.8S-ITS2) and KP635136 (LSU).

**Notes** — *Marasmius ambicellularis* is a distinct species by not having morphological resemblance to any currently known species, except for *M. linderioides* (Oliveira et al. 2014). However, *M. linderioides* differs by having larger pileus (up to 8 mm diam); by more numerous lamellae (12–15) and 2–3 series of lamellulae; by shorter basidiospores (10–15  $\mu\text{m}$  long); by the presence of well-developed pleurocystidia; and by having only *Siccus*-type broom cells in the pileipellis; with basidiomata generally found on substrate on the ground. Additionally, *M. ambicellularis* was collected in the end of the rainy season equivalent to late fall while *M. linderioides* was found in early summer (the beginning of the rainy season) suggesting they might differ seasonally. Also distinguishing, *M. linderioides* was found producing more gregarious and abundant basidiomata on the substrate, suggesting somewhat different spore dispersal strategy. On the other hand, both species are sympatric, collected near each other in the same area and occupying similar niches, decomposing dried palm debris.

No significant phylogenetic distinction was found between the collections of *M. ambicellularis* and *M. linderioides* in all phylogenetic trees (Fig. 1b, 2). A divergence of 0.2 % between ITS sequences of the respective collections may reveal that ITS is perhaps not sufficiently distinct to grant genetic differentiation of these two species. New data (more collections and more genetic markers) regarding this species complex are needed to clarify the molecular systematics of these taxa.

***Marasmius bellus* Berk., Hooker's J. Bot. Kew Gard. Misc. 8: 139. 1856 — Fig. 20**

≡ *Chamaeceras bellus* (Berk.) Kuntze, Revis. Gen. Pl. (Leipzig) 3: 455. 1898.

**Pileus** 16–28 mm diam, convex to applanate, striate or slightly to strongly sulcate-striate, centre flat, margin decurved to straight, edge crenate to wavy; whitish cream to yellowish cream ( $N_{00}Y_{10-30}M_{00}$ ), with a pale brown ( $N_{10}Y_{60}M_{30}$ ) small spot at the centre; membranous, context thin ( $< 1 \text{ mm}$ ); surface glabrous, dry, dull, papery, non-hygrophanous. **Lamellae** free to adnexed, subslose to subdistant,  $L = 14\text{--}18$ , equal, regular or rarely with few veins,  $l = 3$ , opaque, smooth, cream ( $N_{00}Y_{10}M_{00}$ ), edge even, concolorous with the lamellar faces. **Stipe** 25–44  $\times$  0.8–1.2 mm, central, cylindrical to almost filiform, equal, tough, chitinous, hollow; apex concolorous with the lamellar faces, latter orangish brown ( $N_{40}Y_{70}M_{60}$ ) at the middle of the stipe, becoming black toward the base; surface glabrous, smooth, opaque; basal mycelium abundant, pale cream, strigose.

**Basidiospores** 8–13.3  $\times$  3.3–4.5  $\mu\text{m}$  ( $x_m = 9.8 (\pm 0.8) \times 3.8 (\pm 0.3) \mu\text{m}$ ,  $Q_m = 2.6 (\pm 0.3)$ ,  $n = 30$ ), oblong, clavate, subfusoid to lacrimoid, smooth, hyaline, thin-walled, inamyloid. **Basidia** not

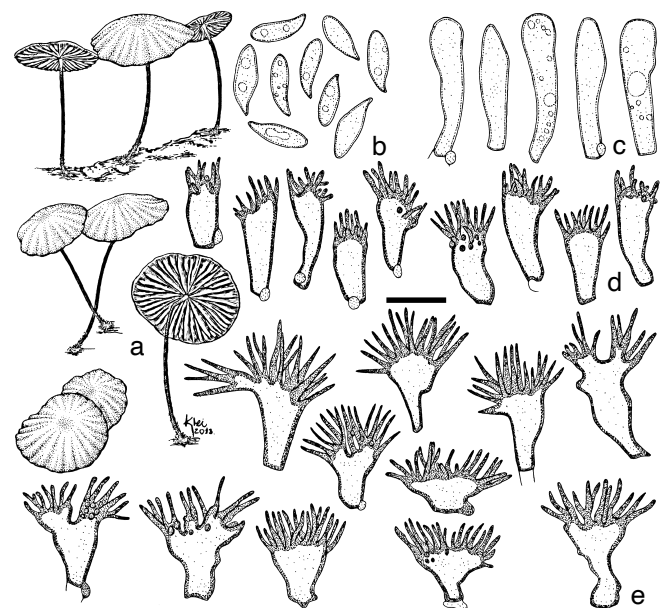
observed. **Basidioles** 20–27  $\times$  4.8–7  $\mu\text{m}$ , clavate to rarely subacute at the apex, hyaline, thin-walled, inamyloid. **Pleurocystidia** absent. **Cheilocystidia** present on the sterile lamellar edge, hyaline, *Siccus*-type broom cells, hyaline to pale yellow, main body 11.3–19  $\times$  5–8(–12.5)  $\mu\text{m}$ , clavate to slightly turbinate, hyaline, thin-walled; setulae apical, erect, generally elongate, sometimes short, 2–7  $\times$  0.5–1  $\mu\text{m}$ , cylindrical, filiform, needle-like, solid, simple, hyaline, apex acute or rarely obtuse. **Lamellar trama** dextrinoid, irregular, hyphae interwoven, cylindrical, 1.6–12  $\mu\text{m}$  diam, regular in outline, branched, smooth, hyaline, thin-walled. **Pileus trama** dextrinoid, irregular, hyphae similar to those of the lamellar trama, 2–12.5  $\mu\text{m}$  diam. **Pileipellis** hymeniform, dextrinoid, *Siccus*-type broom cells, abundant, orange or ochraceous in mass, completely hyaline when isolated, difficult to separate, delicate, easily breakable at the base, main body (6.3–)10–18  $\times$  6.3–14.4  $\mu\text{m}$ , clavate or more often turbinate, sometimes flattened, rarely branched, hyaline, thin-walled; setulae apical, erect, short to elongate, 2–10.3  $\times$  0.4–1.3  $\mu\text{m}$ , filiform, setiform or needle-like, thin, regular in outline, solid, sometimes with lumen, simple, hyaline to pale yellow, apex acute. **Stipe trama** dextrinoid, cortical hyphae parallel, cylindrical, 2.5–11.3  $\mu\text{m}$  diam, regular in outline, smooth, melleous, darkening to olivaceous yellow or almost black, thick-walled; internal hyphae hyaline, cylindrical, 2.5–9.4  $\mu\text{m}$  diam, smooth, thin-walled. **Clamp connections** present in almost all tissues except the cortical stipe trama.

**Habit & Substrate** — Gymnoid to marasmioid, gregarious, on all sorts of debris of dicotyledonous tree.

**Distribution** — The species was originally described from Amazonas State (Brazil), and it has also been recorded from Pernambuco (Singer 1976) and São Paulo (Pegler 1997) States. Other records of the species are from Bolivia (Singer 1976), Venezuela (Dennis 1961), Trinidad, Martinique, Dominique (Pegler 1983) and Puerto Rico (Lodge 2003, Cantrell et al. 2006).

**Specimen examined.** BRAZIL, São Paulo State, Santo André City, Reserva Biológica de Paranapiacaba, 8 Dec. 2010, J.J.S. Oliveira & P.O. Ventura JO299 (SP 445478!).

**Notes** — This is the second record of *M. bellus* from Reserva Biológica de Paranapiacaba. The material herein examined is concordant with descriptions provided by Dennis (1951a), Singer (1976) and Pegler (1983, 1997). The description in Singer



**Fig. 20** *Marasmius bellus* (JO299). a. Basidiomata; b. basidiospores; c. basidioles; d. cheilocystidia; e. *Siccus*-type broom cells of the pileipellis. — Scale bars: a = 22.2 mm, b–e = 10  $\mu\text{m}$ .

(1976) was based on the holotype (also in Singer 1958, 1965), accompanied by specimens more recently collected from Brazil and Bolivia. However, Singer (1976) described the specimens as having a little larger pileus (13–35 mm diam), adnate lamellae (in some cases), and presence of dissimilar basidioles. Dennis (1951a) provided a revised description of the type and reported adnate and slightly interconnected lamellae. He also identified specimens from Venezuela (Dennis 1961) as *M. bellus*, reporting the presence of poorly developed pleurocystidia and apparently shorter setulae on broom cells of the pileipellis. The presence of pleurocystidia is, though, conflicting with all descriptions found in Singer and Pegler studies, and even in the revision of the holotype accomplished by Dennis (1951a).

Pegler (1983) mentioned neither pleurocystidia nor basidioles and described the lamellae as being adnexed to adnate, moderately sized pileus (35 mm diam), and basidiospores ranging from 11–14  $\mu$ m long. Finally, the characteristics mentioned by Pegler (1997) from the material collected from Campinas City and Santo André City (São Paulo State) agree with the material herein examined. *Marasmius cremeus* (which is almost identical to *M. similis*) is a similar species, but differs by the more delicate and smaller pileus (3–14 mm diam), thinner stipe (0.2–0.5 mm) and by the presence of larger basidiospores ((11–)12–14(–16)  $\mu$ m) (Wannathes et al. 2009).

In the Dataset 3 trees (Fig. 2), *M. bellus* has an unsupported relationship with *M. leoninus*, *M. ruber* and *M. trinitatis*. *Marasmius bellus* could be confused with pale pigmented specimens of *M. leoninus*, but does not have a distinctive taste whereas *M. leoninus* tastes very disagreeable (D.J. Lodge, pers. comm).

***Marasmius cladophyllus* var. *glaberripes*** Singer, Fl. Neotrop. Monogr. 17: 214. 1976 — Fig. 21

*Pileus* 9–55 mm diam, globose when young, becoming hemispheric, convex to plane at maturity, sometimes becoming revolute, generally smooth, sometimes slightly tessellated (reticulate-striate), faintly rugose at the centre or with margin slightly sulcate-striate, centre flat to slightly depressed, margin incurved to straight, or somewhat uplifted, edge regular; dark orange when young ( $N_{20}Y_{99}M_{30}$ ), becoming orange ( $N_{00}Y_{99}M_{40}$ ), yellowish orange ( $N_{10}Y_{99}M_{60}$ ) to darker orange ( $N_{10}Y_{99}M_{90}$ ) or reddish orange ( $N_{40}Y_{99}M_{60}$ ), centre dark ochraceous ( $N_{20}Y_{99}M_{50}$ ) to even darker (near  $N_{40}Y_{99}M_{60}$ ); membranous, context white to brownish cream, thin to thickish ( $\leq 1$  mm); surface glabrous, dry, dull, subvelutinous, non-hygrophanous. *Lamellae* sinuate to adnate, close to subdistant,  $L = 12$ –14, unequal, strongly reticulate to merulioid-anastomosed, becoming intervenose near the pileus edge,  $l = 3$ –4, opaque, smooth, pale cream ( $N_{00}Y_{10}M_{00}$ ), pale yellow ( $N_{00}Y_{30}M_{00}$ ) to pale beige ( $N_{00}Y_{20}M_{10}$ ), edge even, concolorous or finely discolorous with the lamellar faces (with a thin orange line), hymenium between lamellae cream. *Stipe* 38–72  $\times$  1–3 mm, central, cylindrical, equal or with a little flared apex, sometimes compressed; tough, chitinous to more semicartilaginous, hollow; apex concolorous with the lamellar faces, sometimes cream 2/3 over the basal 1/3 of the stipe, becoming orange or ochraceous ( $N_{60}Y_{99}M_{70}$ ) or brown ( $N_{20}Y_{90}M_{60}$ ), reaching dark reddish brown ( $N_{60-80}Y_{90-99}M_{70-80}$ ) downward to the base; surface glabrous, slightly pruinose at the base, smooth, opaque or silky bright; basal mycelium strigose, abundant, white to sordid yellow.

*Basidiospores* 8.8–11.3  $\times$  2.5–3.8  $\mu$ m ( $x_m = 10 (\pm 0.8) \times 3 (\pm 0.3)$   $\mu$ m;  $Q_m = 3.2 (\pm 0.4)$ ,  $n = 30$ ), oblong, clavate to subfusoid, hyaline, thin-walled, smooth, inamyloid. *Basidia* not observed. *Basidioles* 17.5–28.8  $\times$  4–7  $\mu$ m, clavate, sometimes with apex tending to acuminate, hyaline, thin-walled. *Pleurocystidia* absent. *Cheilocystidia* abundant and conspicuous, in form

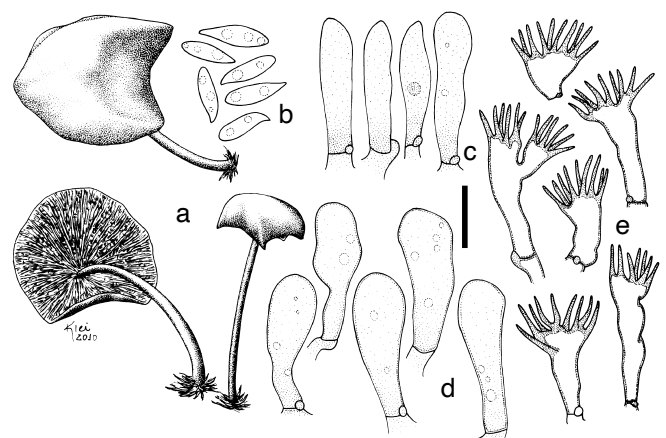
of *Globulares*-type smooth cells, 22.5–32  $\times$  8–10  $\mu$ m, pyriform or vesiculose, hyaline, thin-walled. *Lamellar trama* dextrinoid, irregular, hyphae interwoven, cylindrical, 2–7.5  $\mu$ m diam, smooth, hyaline, thin-walled, septate. *Pileus trama* hyphae similar to those of the lamellar trama, hyphae cylindrical, 2.3–11.3  $\mu$ m diam. *Pileipellis* hymeniform, composed of *Siccus*-type broom cells, abundant, pale orange when in group, main body 7.5–23.8  $\times$  5–8.8  $\mu$ m, broadly cylindrical, clavate to turbinate, almost pedicellate, rarely lobed or branched, hyaline, thin-walled; setulae apical, erect, 3.8–10  $\times$  0.6–1.3  $\mu$ m, cylindrical, filiform, thin, regular in outline, simple, pale orange, abundant, apex acute. *Stipe trama* dextrinoid, cortical hyphae parallel, 7–15  $\mu$ m diam, regular in outline, cylindrical, smooth, pale yellow to pale brown, thick-walled, septate; internal hyphae hyaline, 3.8–6.3  $\mu$ m diam, thin-walled, slender. *Clamp connections* present in all tissues.

**Habit & Substrate** — Gymnoid, gregarious or scattered, on leaves and branches of dicotyledonous trees.

**Distribution** — This variety of *M. cladophyllus* was originally described from Tungurahua, Ecuador (Singer 1976). This is the first record from Brazil.

**Specimens examined.** BRAZIL, São Paulo State, Santo André City, Reserva Biológica de Paranapiacaba, 16 Dec. 2009, *M. Capelari* & L.A.S. Ramos 4562 (SP 445784!); *ibid.*, L.A.S. Ramos & *M. Capelari* 86 (SP 445424!); *ibid.*, 24 Mar. 2010, J.J.S. Oliveira JO87 (SP 445424!); Iporanga City, Parque Estadual Turístico do Alto Ribeira, Núcleo Santana, 29 Feb. 2012, J.J.S. Oliveira & D.E. Desjardin JO518 (SP 445587!); *ibid.*, D.E. Desjardin DED8681 (SP 445664!).

**Notes** — *Marasmius cladophyllus* is easily recognized in the field due to its typical merulioid-anastomosed lamellae or almost favoloid hymenophore. The species currently contains four varieties: *cladophyllus*, *glaberripes*, *intermedius* and *tjibodensis*. *Marasmius cladophyllus* var. *glaberripes* differs from var. *cladophyllus* by having completely glabrous stipe and, therefore, by the absence of caulocystidia, also by having shorter basidiospores (barely reaching 10  $\mu$ m long) and cheilocystidia in form of dextrinoid hyphal ends that are conspicuously contorted and often forked (Singer 1976). Besides the presence of hyaline, thin-walled, versiform or contorted, often cylindrical or ventricose, some diverticulate, hair-like caulocystidia (35–50  $\times$  4–9.8  $\mu$ m) accompanied by ventricose cells with or without a mucro, var. *cladophyllus* also presents, in contrast to var. *glaberripes*, somewhat longer basidiospores (up to 12.7  $\mu$ m) and intermittent clusters of regular broom cells interspersed with versiform or hyphal ends at the lamellar edge (Singer 1976). Mainly because of the glabrescent stipe, the collections examined are determined as belonging to var. *glaberripes*, in



**Fig. 21** *Marasmius cladophyllus* var. *glaberripes* (JO87). a. Basidiomata; b. basidiospores; c. basidioles; d. cheilocystidia; e. *Siccus*-type broom cells of the pileipellis. — Scale bars: a = 16.6 mm, b–e = 10  $\mu$ m.

spite of having a little longer basidiospores and cheilocystidia only in the form of *Globulares*-type cells.

On the other hand, *M. cladophyllus* var. *intermedius* (Singer 1976) has a subglabrous stipe, beset by minute hyphoid excrescences that are occasionally similar to hyaline setulae and few broader elements like those found in the type variety. Additionally, it has cheilocystidia of two types: a) fusoid and long beaked ( $23\text{--}26 \times 5\text{--}6 \mu\text{m}$ ); and b) vesiculose, often mucronate, hyaline, broadened ( $12\text{--}27 \times 6\text{--}18 \mu\text{m}$ ) and inamyloid; and dimorphic trama: a) strongly dextrinoid, with thick-walled hyphae; or b) inamyloid to weakly dextrinoid, with thin-walled hyphae. *Marasmius cladophyllus* var. *tjibodensis*, a fourth variety, was described by Desjardin et al. (2000) and it is similar to var. *glaberripes* in the type of cheilocystidia. But var. *tjibodensis* is distinguished by having a pruinose and fibrillose stipe and, thus, it has caulocystidia as well as longer basidiospores (up to  $13.5 \mu\text{m}$ ).

The presence of elongate caulocystidia suggests that *M. cladophyllus* var. *cladophyllus* is a member of series *Atrorubentes* in the traditional view. Singer (1976) formally classified the species within ser. *Actinopodes*, later separated into ser. *Atrorubentes* and ser. *Spinulosi* (currently morphological concepts). But Singer's decision remained inconclusive since he stated that, because of the varieties *glaberripes* and *intermedius*, the species would belong to series *Leonini* (Singer 1976). This morphological incongruence is problematic since var. *glaberripes* cannot be classified in ser. *Atrorubentes* at all, but would be properly placed in ser. *Leonini*.

In the trees (Fig. 1b, 2), *M. cladophyllus* var. *glaberripes* is an independent basal branch of a polytomy, near but poorly related to other taxa including *M. leoninus*, thus supporting Singer's (1976) alternative suggested placement of *M. cladophyllus* in ser. *Leonini*. Moreover, MCA1837 *M. cf. cladophyllus*, also included in the analyses of Group 1, is a genetically distinct species. ITS sequences retrieved from GenBank and identified as *M. cladophyllus* were not included in the analyses because of their poor quality (JF767003, KF241549, HQ248212, AY216475, HQ248211).

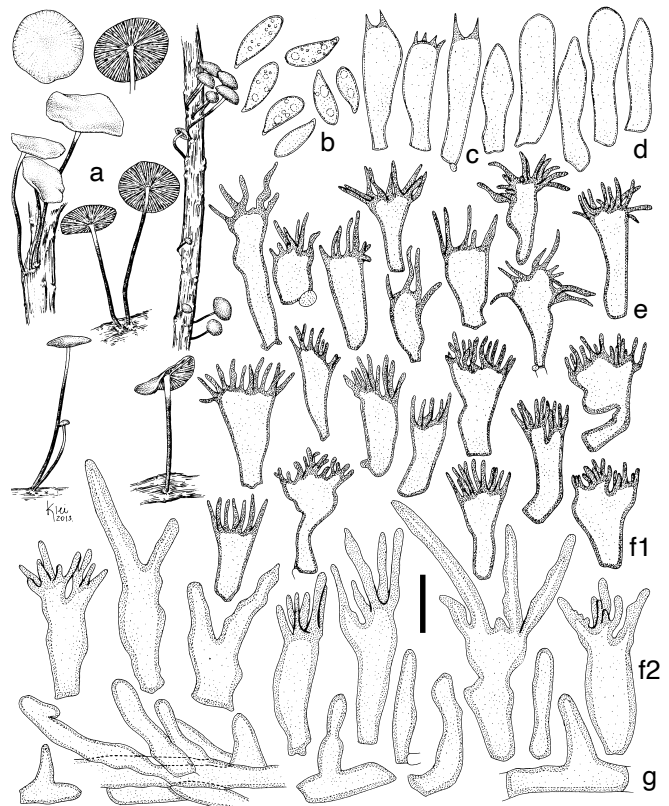
***Marasmius corrugatus* (Pat.) Sacc., Syll. Fung. (Abellini) 16: 54. 1902 — Fig. 22**

≡ *Androsaceus corrugatus* Pat., Bull. Soc. Mycol. France 16: 175. 1900.

≡ *Marasmius corrugatus* (Pat.) P. Syd., Just's Bot. Jahresber. 28: 132. 1902.

*Pileus* 3.2–28 mm diam, hemispheric when young, convex to more often plane, sometimes revolute, orbicular or sometimes almost lobed, centre flat or slightly depressed, sometimes shallowly umbonate, smooth or radially corrugated, margin non-striate or slightly sulcate-striate, decurved, plane or slightly uplifted, edge regular or sometimes lacerate; brownish orange ( $N_{50}Y_{99}M_{50}$ ) when young, becoming yellowish brown or pale orangish brown ( $N_{30}Y_{80}M_{40}$ ), yellowish orange ( $N_{20}Y_{70}M_{40}$ ) or pale orange ( $N_{30}Y_{60}M_{30}$ ) to orange ( $N_{20}Y_{80}M_{50}$ ), centre ochraceous or orangish brown ( $N_{30}Y_{90}M_{50}$  to  $N_{40}Y_{99}M_{50-60}$ ), sometimes almost cream ( $N_{00}Y_{50}M_{10}$  to  $N_{10}Y_{50}M_{20}$ ) toward the margin; membranous, context cream, thin (< 1 mm); surface glabrous, dry, sometimes a little humid, dull, subvelutinous, rarely micaceous, non-hygrophanous. *Lamellae* free, adnexed or adnate, close to subdistant, abundant,  $L = 28\text{--}36$ , unequal, regular, some forked,  $l = 4\text{--}6$ , opaque, smooth, whitish cream ( $N_{00}Y_{10}M_{00}$ ) to pale yellow ( $N_{20}Y_{70}M_{40}$ ), edge even, concolorous with the lamellar faces. *Stipe* 6–55  $\times$  0.5–3 mm, central, cylindrical, equal or slightly broader at the apex or base, sometimes compressed, tough, semicartilaginous to chitinous, hollow; apex concolorous with the lamellae, becoming pale brownish orange ( $N_{20-30}Y_{70}M_{40}$ ) or even darker ( $N_{40}Y_{80-99}M_{50}$  to  $N_{50}Y_{90}M_{70}$ ) at the middle, reach-

ing to dark reddish brown ( $N_{80}Y_{99}M_{70}$  to  $N_{90}Y_{99}M_{70}$ ) or black at the base; surface glabrous, smooth, shiny with a silky sheen; basal mycelium whitish cream to orangish, strigose or tomentose. *Basidiospores* 6.3–11.3(–12.5)  $\times$  3–5.3(–6)  $\mu\text{m}$  ( $x_{\text{m}} = 8.3\text{--}9.5 \times 3.7\text{--}4.6 \mu\text{m}$ ;  $x_{\text{mm}} = 8.8 (\pm 0.4) \times 4 (\pm 0.4) \mu\text{m}$ ,  $Q_{\text{m}} = 1.8\text{--}2.6$ ,  $Q_{\text{mm}} = 2.2 (\pm 0.3)$ ;  $n/s = 30$ ,  $s = 5$ ), obovoid to more often sub-oblong, lacrimoid, subellipsoid, clavate to subfusoid, smooth, hyaline, thin-walled, inamyloid. *Basidia* 17.5–26.3  $\times$  4.4–7.5  $\mu\text{m}$ , clavate, smooth, hyaline, 2–4 sterigmata, thin-walled, inamyloid. *Basidioles* 16.6–23.8  $\times$  4.4–7.5  $\mu\text{m}$ , clavate to subfusoid, smooth, hyaline, thin-walled. *Pleurocystidia* absent. *Cheilocystidia* in form of *Siccus*-type broom cells, completely hyaline, inconspicuous and delicate in some specimens, otherwise conspicuous, but not numerous; main body 10–25  $\times$  4.8–9.4  $\mu\text{m}$ , cylindrical-clavate, clavate to slightly turbinate, some forked, hyaline, thin- to slightly thick-walled, inamyloid; setulae apical, erect, short to elongate, 3.8–15  $\times$  0.8–2  $\mu\text{m}$ , cylindrical, filiform or flagellum-like, simple, sometimes contorted, solid, hyaline, apex acute. *Lamellar trama* strongly dextrinoid becoming vinaceous to ferruginous in Melzer's reagent, some with an inner trama more strongly dextrinoid, completely disorganized or irregular, hyphae interwoven, cylindrical, 2.5–12.5  $\mu\text{m}$  diam, regular in outline, some segments inflated, smooth, branched, hyaline, thin-walled. *Pileus trama* strongly dextrinoid, tending to have a regular arrangement (parallel), slightly interwoven in some places, trama completely irregular in some specimens, hyphae cylindrical, 2–12.5  $\mu\text{m}$  diam, regular in outline, some segments a little inflated. *Pileipellis* hymeniform, orange or ochraceous, mottled, composed of *Siccus*-type broom cells in two types: 1) abundant, smaller in proportion, pale orange or brownish ochre when in group, main body 12.5–17.5(–20)  $\times$  5.6–12  $\mu\text{m}$ , cylindrical-clavate, clavate to turbinate, rarely forked, thin-walled, hyaline, dextrinoid; setulae apical, erect, short to elongate, 1.3–16.3  $\times$  0.5–2.5  $\mu\text{m}$ , cylindrical, filiform,



**Fig. 22** *Marasmius corrugatus* (JO466). a. Basidiomata; b. basidiospores; c. basidia; d. basidioles; e. cheilocystidia; f. pileipellis: f1. small, more numerous, thin-walled *Siccus*-type broom cells; f2. larger, less numerous, thick-walled *Siccus*-type broom cells; g. structures of the stiptipellis. — Scale bars: a = 19.7 mm, b–g = 10  $\mu\text{m}$ .

needle-like, or digitiform, regular in outline, simple to rarely branched, hyaline to pale orange, solid or with lumen, apex acute to slightly obtuse; 2) larger broom cells, less numerous in proportion, but regularly distributed, more irregular in outline, main body 12–26.5 × 5.6–12.5 µm, clavate to slightly turbinate, thick-walled, melleous, apex pale orange, hyaline at the base; setulae apical, erect, short and often very elongate, 3.8–35 × 1.3–5 µm, cylindrical, digitiform, needle-like, simple to branched, solid or with lumen, melleous or pale orange, apex obtuse or acute. *Stipe trama* dextrinoid, cortical hyphae parallel, dark brown to black, becoming olivaceous green, orange or even melleous yellow when isolated, cylindrical, regular in outline, 2.5–13.8 µm diam, smooth, thick-walled; internal hyphae cylindrical, 1.3–11.3 µm diam, disorganized, hyaline, thin-walled, with numerous septa. *Stipitipellis* without broom cells, but with short structures, 10–23.8 × 2–7 µm, clavate to conical, thick-walled, seemingly hyphal endings, or lateral sprouts from cortical hyphae, apex slightly acuminate, but generally obtuse. *Clamp connections* present in almost all tissues, but not seen at the base of the second broom cells type of the pileipellis.

**Habit & Substrate** — Gymnoid, gregarious, sometimes almost caespitose, growing on twigs and leaves of dicotyledonous trees.

**Distribution** — Originally described from Guadeloupe, it is also known from Venezuela, Bolivia, Argentina (Singer 1976), Martinique, Dominique (Pegler 1983), Puerto Rico (Lodge 2003, Cantrell et al. 2006) and Brazil (Pegler 1997).

**Specimens examined.** BRAZIL, São Paulo City, Santo André City, Reserva Biológica de Paranapiacaba, 24 Mar. 2010, J.J.S. Oliveira JO85 (SP 445423!); São Paulo City, Parque Estadual das Fontes do Ipiranga, 1 Mar. 2011, J.J.S. Oliveira & F. Karstedt JO336 (SP 445500!); *ibid.*, 3 Mar. 2011, J.J.S. Oliveira & F. Karstedt JO347 (SP 445507!); *ibid.*, 2 Feb. 2012, J.J.S. Oliveira JO466 (SP 445551!); Parque Estadual da Cantareira, Núcleo Engordador, 30 Jan. 2012, J.J.S. Oliveira & V. Motato-Vásquez JO456 (SP 445543!).

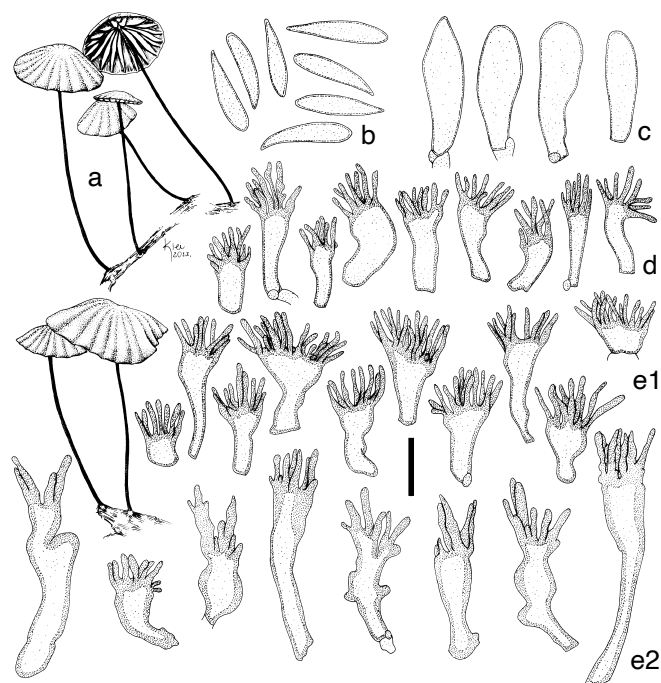
**Notes** — In addition to the type variety of *M. corrugatus*, three other varieties were established by Singer (1976): a) var. *aurantiacus* which differs by forming smaller basidiomata, more orangish pileus, narrower basidiospores (3–3.7 µm broad) and by having well-developed broom cells in the stipitipellis; b) var. *lacustris*, similar in pileus pigmentation to var. *aurantiacus*, but diverging from all by forming much larger pileus (up to 57 mm diam) and by having dimorphic cystidia in the stipitipellis; and c) var. *portonovensis* which differs from the type variety by having more smooth cells than broom cells in the pileipellis and on the lamellar edge, by having strongly dimorphic lamellar trama and shorter basidiospores (6.2–7.5 µm). Desjardin & Horak (1997) established *M. corrugatus* var. *olivaceobrunneus* from New Guinea, which differs by having olivaceous brown pileus and pruinose stipe, covered by caulocystidia in form of broom cells.

The specimens analysed correspond to the type variety as described by Singer (1976), differing only by the smaller pileus (up to 28 mm diam) and by the absence of smooth cells in the pileipellis. The presence of smooth cells mixed with broom cells, in some species, may be considered an occasional characteristic, since it can be present or absent depending on the population or on the stage of development of the basidiomata. The mottled aspect of the pileipellis is due to a gradual pattern of broom cells from small, less pigmented and thin-walled to large, more pigmented and thick-walled. Pegler (1983) also studied the holotype along with collections from Martinique and Dominique, finding larger basidiospores (9–13 × 2.7–4 µm). *Marasmius maculosus* (Takahashi 2002) is very similar to *M. corrugatus*, differing only by the reddish brown pileus and stipitipellis with clusters of thin hyphae.

*Marasmius corrugatus* grouped within a strongly supported, well-defined subclade (Fig. 1b, 2) named /*corrugatus*, which also includes *M. congregatus* and *M. pseudoniveoaffinis*.

***Marasmius dimorphus*** C. Puccin. & Capelari, Mycotaxon 95: 298. 2006 — Fig. 23

**Pileus** 4–37 mm diam, hemispheric, conical or campanulate, but generally convex, especially when mature, sulcate, centre flat or slightly umbonate, margin decurved, edge regular to crenate; light cinnamon (N<sub>30</sub>Y<sub>50–60</sub>M<sub>30</sub>) to ochraceous brown (N<sub>40</sub>Y<sub>60</sub>M<sub>40</sub> to N<sub>50</sub>Y<sub>70</sub>M<sub>40</sub>) or pale pinkish brown or almost beige (N<sub>20</sub>Y<sub>40–50</sub>M<sub>30</sub>), generally light brown (N<sub>30</sub>Y<sub>40</sub>M<sub>20</sub>), some pale hazel brown (N<sub>60</sub>Y<sub>70–80</sub>M<sub>50</sub>) or cocoa (N<sub>70</sub>Y<sub>50–60</sub>M<sub>40</sub>), becoming darker greyish brown (N<sub>60</sub>Y<sub>40</sub>M<sub>30</sub>) when dried, with a dark brown centre (N<sub>90</sub>Y<sub>99</sub>M<sub>60–80</sub>, N<sub>99</sub>Y<sub>99</sub>M<sub>70</sub> or Y<sub>99</sub>M<sub>60</sub>C<sub>50</sub>) or paler (N<sub>90</sub>Y<sub>99</sub>M<sub>60</sub>); membranous, context thin (< 1 mm); surface glabrous, dry, dull, subvelutinous, non-hygrophanous. **Lamellae** free to adnexed, subclose to distant, L = 14–18, equal, regular, rarely forked, thin, l = 0–1, opaque, smooth, cream (N<sub>00</sub>Y<sub>10</sub>M<sub>00</sub>) to pale beige (N<sub>00</sub>Y<sub>30</sub>M<sub>10</sub>), edge even, concolorous with the lamellar faces, hymenium between the lamellae partially concolorous with the pileus. **Stipe** 18–80 × 0.4–1 mm, central, cylindrical, sometimes thin, equal, tough, hardly chitinous, hollow; apex concolorous with the lamellae, becoming brownish beige (N<sub>10</sub>Y<sub>40</sub>M<sub>20</sub>) or golden brown (N<sub>40</sub>Y<sub>50</sub>M<sub>40</sub>), reaching to dark brown (N<sub>90</sub>Y<sub>99</sub>M<sub>50–60</sub>) or to black toward the base; surface glabrous, smooth, glossy; basal mycelium abundant, light cream, strigose or tomentose. **Basidiospores** 11.3–17.5 (–18.8) × 3–5 µm (x<sub>mm</sub> = 13.9–15.4 × 3.8–4.5 µm; x<sub>mm</sub> = 14.7 (± 0.6) × 4.2 (± 0.3) µm, Q<sub>mm</sub> = 3.7–4.5, Q<sub>mm</sub> = 4.1 (± 0.4); n/s = 30, s = 4), oblong, clavate to subfusoid, smooth, hyaline, thin-walled, inamyloid. **Basidia** not observed. **Basidioles** 18.8–27.5 × 5–8 µm, clavate, hyaline, thin-walled, inamyloid. **Pleurocystidia** absent. **Cheilocystidia** in form of *Siccus*-type broom cells, faintly brown to hyaline in mass, main body 8.8–15 × 3.8–7.5 µm, clavate to slightly turbinate, regular in outline, apex with thick walls, but thin-walled at the base, breaking easily under gentle pressure on the coverslip, hyaline, inamyloid; setulae apical, erect, 3–8 × 0.8–1 µm, digitiform



**Fig. 23** *Marasmius dimorphus* (JO298). a. Basidiomata; b. basidiospores; c. basidioles; d. cheilocystidia; e. pileipellis: e1. regular *Siccus*-type broom cells, e2. irregular, thick-walled *Siccus*-type broom cells. — Scale bars: a = 17.6 mm, b–e = 10 µm.

or cylindrical, regular or somewhat irregular in outline, with ramifications, pale brown to hyaline, solid, apex obtuse to acute. *Lamellar trama* dextrinoid, irregular, hyphae interwoven, cylindrical, 2.5–11.3 µm diam, regular in outline, smooth, hyaline, some segments slightly inflated, thin-walled. *Pileus trama* dextrinoid, irregular, hyphae interwoven, cylindrical, 2.5–11.3 µm diam, similar to those of the lamellar trama. *Pileipellis* hymeniform, mottled, composed of *Siccus*-type broom cells in two types: 1) abundant, brownish when in group, main body 5–18.8 × 5–8 (–11.3) µm, clavate to turbinate, sometimes flattened, or with an elongate base, brown, apex with thick wall, but thinning toward the base; setulae apical, erect, 4.4–7.5 × 0.8–1.3 µm, digitiform to cylindrical, filiform, regular in outline, pale brown, simple, solid, apex obtuse to acute; 2) irregular in outline, rare, completely brown or dark melleous, main body 12.5–38.8 × 5–9.8 µm, irregular in outline, tending to clavate, with thicker walls; setulae apical, erect, 5–10 × 1.3–2.5 µm, more elongate and broader compared with type 1, solid, apex obtuse. *Stipitipellis* dextrinoid, cortical hyphae parallel, cylindrical, 3–13.8 µm diam, regular in outline, smooth, light brown to melleous, walls moderately thick, septa numerous and close; internal hyphae hyaline, 2–11.3 µm diam, thin-walled, smooth. *Clamp connections* present in almost all tissues, inconspicuous in the pileus trama and not seen in the lamellar trama.

**Habit & Substrate** — Marasmioid, gregarious, on twigs, thin branches and dried leaves of dicotyledonous trees.

**Distribution** — The species is known only from São Paulo State (Puccinelli & Capelari 2006).

**Specimens examined.** BRAZIL, São Paulo State, Santo André City, Reserva Biológica de Paranapiacaba, 8 Dec. 2010, J.J.S. Oliveira & P.O. Ventura JO298 (SP 445477!); São Paulo City, Parque Estadual das Fontes do Ipiranga, 1 Mar. 2011, J.J.S. Oliveira & F. Karstedt JO334 (SP 445499!); *ibid.*, 3 Mar. 2011, J.J.S. Oliveira & F. Karstedt JO355 (SP 445513!); Parque Estadual da Cantareira, Núcleo Engordador, 19 Dec. 2011, J.J.S. Oliveira & M. Capelari JO442 (SP 445535!); *ibid.*, 30 Jan. 2012, J.J.S. Oliveira & V. Motato-Vásquez JO462 (SP 445548!).

**Notes** — *Marasmius dimorphus* was described from Parque Estadual das Fontes do Ipiranga, and it also occurs in Reserva Biológica de Paranapiacaba and Parque Estadual da Cantareira, areas that are currently devoid of forest connections. The material examined is completely compatible with the original description in Puccinelli & Capelari (2006).

*Marasmius helveloides* (Singer 1976) is a similar species with a pale brown pileus and lacking pleurocystidia, but differs by having more robust stipe (1–2 mm thick) that is indistinctly pruinose due to the presence of broom cells in the stipitipellis; by the absence of dimorphic broom cells in the pileipellis; and by the presence of rare cystidioles.

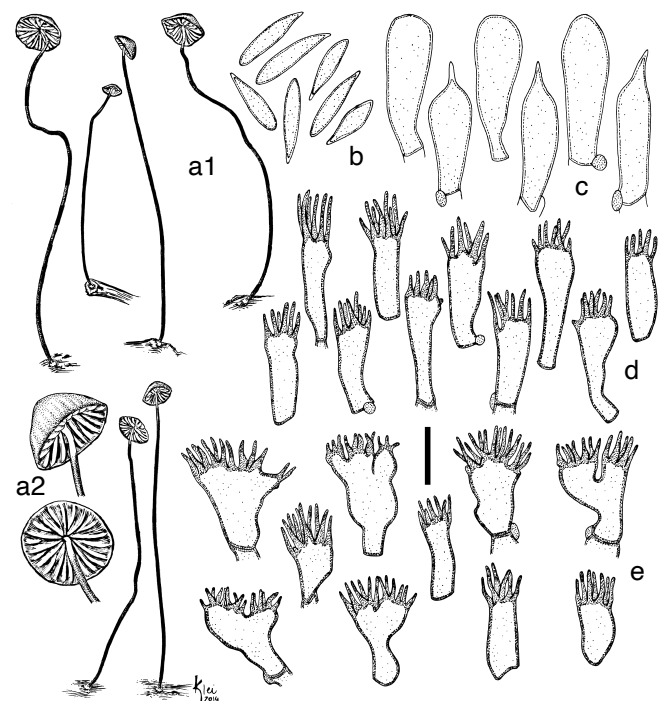
*Marasmius dimorphus* grouped within the strongly supported subclade *rhabarbarinus*, along with *M. coneri*, *M. rhabarbarinoides* and *M. rhabarbarinus* (Fig. 1c). These species are also morphologically close and may represent a species complex (Greenwood 1974). The phylogenetic position is kept in the Dataset 3 tree (Fig. 2), with even higher support because *M. coneri* is absent.

***Marasmius graminicola*** Speg., Anales Mus. Nac. Hist. Nat. Buenos Aires 6: 111. 1899 — Fig. 24

*Pileus* 3–7.5 mm diam, conical-campanulate to parabolic-convex, smooth to striate or shallowly sulcate-striate, more strongly sulcate-striate when mature or dried, centre slightly to strongly umbonate, margin decurved, edge regular; pale orange ( $N_{00}Y_{50}M_{20}$ ) to pale ochraceous ( $N_{10}Y_{70}M_{30}$ ), orange ( $N_{10}Y_{90}M_{40}$ ) to brownish orange ( $N_{30}Y_{99}M_{50}$ ), with centre intensely orange ( $N_{40}Y_{99}M_{60}$ ) to dark brownish orange ( $N_{50}Y_{99}M_{60}$ ) or concolorous with the margin; membranous, context cream, thin (< 1 mm);

surface glabrous, dry, dull, papyraceous to subvelutinous, non-hygrophanous. *Lamellae* free to subfree, or almost adnexed, subclose to subdistant,  $L = 13–16(–20)$ , equal, regular,  $l = 1–2$ , opaque, smooth, whitish cream ( $N_{00}Y_{10}M_{00}$ ), edge even, faintly marginate and finely brownish orange or not marginate and concolorous with the lamellar face, as well as with the hymenium between the lamellae. *Stipe* 33–60 × 0.2–1 mm, central, cylindrical, sometimes filiform, equal, semi cartilaginous to chitinous, hollow; apex pale yellow, becoming brownish orange ( $N_{50}Y_{90}M_{50}$ ), reaching dark amber brown ( $N_{50}Y_{99}M_{50}$ ) or dark brown ( $N_{80}Y_{90–99}M_{50}$ ) below; surface glabrous, smooth, with a silky sheen; basal mycelium yellowish, strigose.

*Basidiospores* 10–14.4 × 3–4.4 µm ( $x_{mm} = 11.8–12.6 \times 3.6–4 \mu\text{m}$ ;  $x_{mm} = 12.2 (\pm 0.6) \times 3.8 (\pm 0.3) \mu\text{m}$ ,  $Q_{mm} = 3–3.5$ ,  $Q_{mm} = 3.3 (\pm 0.4)$ ;  $n/s = 30$ ,  $s = 2$ ), oblong, clavate to subfusoid, smooth, hyaline, thin-walled, inamyloid. *Basidia* not observed. *Basidioles* 22.5–28.8 × 5–7.5 µm, cylindrical, clavate to often fusoid, often with an acute apex, smooth, hyaline, thin-walled, inamyloid. *Pleurocystidia* absent. *Cheilocystidia* in form of *Siccus*-type broom cells similar to those of the pileipellis, cinnamon in mass, abundant, main body 10–22.5 × (3.8–)5–7.5 µm, cylindrical to clavate, sometimes a little turbinate, thin-walled; setulae apical, erect, 3–7.5 × 0.8–1.3 µm, conspicuous, cylindrical or digitiform, some very elongate, setoid, regular in outline, simple, pale yellow, solid, apex acute. *Lamellar trama* dextrinoid, irregular, hyphae interwoven, cylindrical, 1.6–12.5 µm diam, regular or irregular in outline, sometimes inflated, branched, smooth, thin-walled. *Pileus trama* similar to the lamellar trama, hyphae cylindrical, 2–15 µm diam. *Pileipellis* hymeniform, composed of *Siccus*-type broom cells, pale yellow when in group, main body 8.8–22 × 5.6–15 µm, clavate or more frequently turbinate, sometimes ventricose or bilobed, hyaline, thin-walled; setulae apical, erect, 2.5–8 × 0.6–1 µm, filiform, setiform, cylindrical, or digitiform, simple, regular in outline, hyaline, apex generally acute. *Stipe trama* dextrinoid, cortical hyphae parallel, cylindrical, regular in outline, 2.5–7.5 µm diam, smooth, yellowish melleous in KOH, thick-walled; internal hyphae with similar dimensions, also parallel, hyaline, smooth, thin-walled. *Clamp connections* present in almost all tissues, absent in the cortical stipe trama.



**Fig. 24** *Marasmius graminicola* (JO459). a1, a2. Basidiomata; b. basidiospores; c. basidioles; d. cheilocystidia; e. *Siccus*-type broom cells of the pileipellis. — Scale bars: a1 = 10 mm, a2 = 5 mm, b–e = 10 µm.



**Habit & Substrate** — Marasmioid, gregarious, on leaf petioles and dried twigs of dicotyledonous trees.

**Distribution** — The species was originally described from Buenos Aires, Argentina, and it was also reported from Mexico (Singer 1976) and Republic of South Korea (Antonín et al. 2012). This is the first record of the species from Brazil.

**Specimens examined.** BRAZIL, São Paulo State, São Paulo City, Parque Estadual da Cantareira, Núcleo Engordador, 30 Jan. 2012, J.J.S. Oliveira & V. Motato-Vásquez JO459 (SP 445546!); *ibid.*, 9 Feb. 2012, J.J.S. Oliveira & M. Capelari JO480 (SP 445559!); Parque Estadual das Fontes do Ipiranga, 2 Feb. 2012, J.J.S. Oliveira JO473 (SP 445916!).

**Notes** — The collections examined diverge from the description of the species provided by Singer (1976) by having a more elongate stipe (up to 60 vs up to 40 mm) and lamellae more numerous (13–16 vs 8–9), also presenting lamellulae, which are typically absent. Moreover, no dark orange or reddish brown pileus was observed in the examined material and the lamellar edge tends to be only faintly marginate. Singer (1976) also noted that the species was always associated with monocotyledonous plants, mostly *Gramineae*, but spreading to other nearby material.

Antonín et al. (2012) recorded the species from South Korea, describing the collections with stipes much longer (20–100 mm), basidiospores more elongate (12–15(–17.5)  $\mu\text{m}$ ), lamellae more numerous ((10–)16–18(–24)) and growing only on dicotyledonous leaves. *Marasmius bambusiniiformis* is another similar species, but differs by having larger basidiospores ranging from 15–18.5  $\times$  3.7–5  $\mu\text{m}$  (Singer 1976, Desjardin & Horak 1997, Tan et al. 2009, Wannathes et al. 2009).

A pairwise comparison of the ITS region (Table S2), including sequences of *M. graminicola* obtained by Antonín et al. (2012), *M. bambusiniiformis* obtained by Wannathes et al. (2009), and sequences generated from the examined material revealed that the samples of *M. graminicola* collected from São Paulo are not conspecific with the samples of *M. graminicola* in Antonín et al. (2012), so reports from Korea are likely a misapplied name. Sequences by Antonín et al. (2012) of *M. 'graminicola'* from Korea were nearly identical with those of *M. bambusiniiformis* in Wannathes et al. (2009). *Marasmius graminicola* grouped within /graminicola subclade (Fig. 2) as sister to '*M. luteoolivaceus* + *M. hobbitii*' branch with a high support (PP 0.99).

***Marasmius hobbitii*** J.S. Oliveira, *sp. nov.* — MycoBank MB811135; Fig. 25

**Holotype.** BRAZIL, São Paulo State, Santo André City, Reserva Biológica de Paranapiacaba, on fallen palm leaves, 9 Dec. 2010, J.J.S. Oliveira & P.O. Ventura JO309 (SP 445484!).

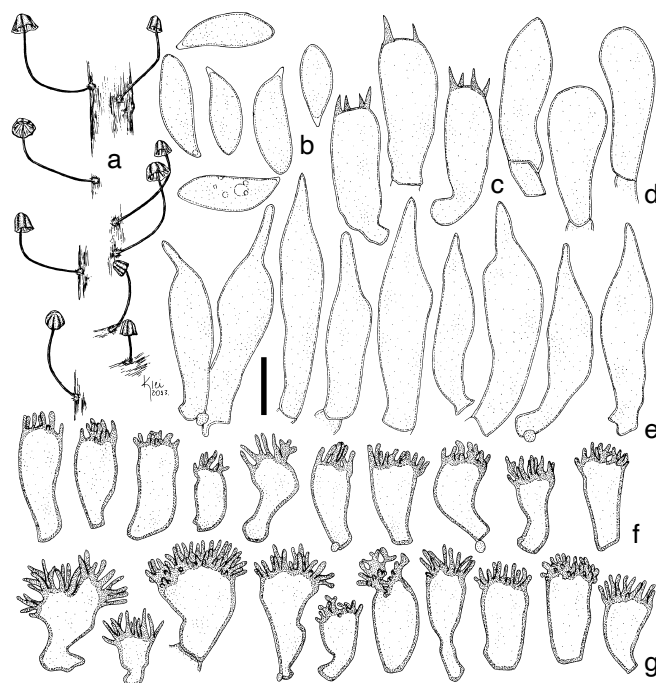
**Etymology.** This species is named after the Hobbits, from the book 'The Hobbit' by J.R.R. Tolkien, a race of usually mycophile, very tiny people (c. 60–120 cm tall), passing unseen by common human eyes and with hairy feet. The small size and hairy feet of the hobbits connect them to the reduced size of the basidiomata and the strigose mycelium (hair) at the base (foot) of the stipes found in *M. hobbitii*.

**Pileus** 1.8–4 mm diam, campanulate, slightly sulcate, orange. **Lamellae** free, subdistant (7), equal, non-marginate. **Stipe** 13–15  $\times$  0.3–0.5 mm, central, curved, filiform, with a strigose basal mycelium. **Basidiospores** 13.8–19(–20)  $\times$  5–9  $\mu\text{m}$ , fusoid-ventricose, rhomboid. **Basidioles** clavate, along with acuminate cystidioles. **Pleurocystidia** absent. **Pileipellis** made up by *Siccus*-type boom cells, with apical setulae 1.5–4.6  $\times$  0.5–1  $\mu\text{m}$ .

**Pileus** 1.8–4 mm diam, campanulate, sometimes hemispheric, shallowly sulcate, centre flat, margin decurved, edge regular or crenate; orange ( $N_{20}Y_{99}M_{50}$ ) to paler orange ( $N_{10}Y_{99}M_{40}$ ) toward the margin, centre somewhat darker orange or rufous ( $N_{30}Y_{90}M_{60}$ ); membranous, context thin (< 1 mm); surface glabrous, dry, dull, subvelutinous, non-hygrophanous. **Lamellae** free, subdistant,  $L = 7$ , equal, regular,  $I = 0$ , opaque, smooth,

pale cream ( $N_{00}Y_{10}M_{00}$ ), edge even, concolorous with the lamellar faces as well as with the interlamellar hymenium. **Stipe** 13–15  $\times$  0.3–0.5 mm, central, curved or oblique, thin, filiform, equal; pliant, chitinous, hollow; apex concolorous with the lamellar face, otherwise dark brown all over; surface glabrous, smooth, opaque; basal mycelium cream-coloured, strigose.

**Basidiospores** 13.8–19(–20)  $\times$  5–9  $\mu\text{m}$  ( $x_{\text{m}} = 17\text{--}18 \times 6.6\text{--}7.3 \mu\text{m}$ ;  $x_{\text{mm}} = 17.5 (\pm 0.7) \times 7 (\pm 0.5) \mu\text{m}$ ,  $Q_{\text{m}} = 2.5\text{--}2.6$ ,  $Q_{\text{mm}} = 2.6 (\pm 0.1)$ ;  $n/s = 30$ ,  $s = 2$ ), oblong, fusoid-ventricose, rhomboid, distinctly broad, smooth, hyaline, thin-walled, inamyloid. **Basidia** 25–36.3  $\times$  8.8–12  $\mu\text{m}$ , clavate, smooth, hyaline, thin-walled, 2–4 sterigmata, inamyloid. **Basidioles** 25–35  $\times$  5.6–12  $\mu\text{m}$ , clavate or broadly clavate, along with acuminate cystidioles, with a tapered, or even with a rostrate and acute apex, orthochromatic in Crezil blue like the basidia and basidioles, hyaline, thin-walled, inamyloid. **Pleurocystidia** absent. **Cheilocystidia** in form of *Siccus*-type broom cells, very similar to those in the pileipellis, abundant, also occasionally found dispersed throughout the lamellar faces, hyaline, main body 11.3–21.3  $\times$  5.5–10  $\mu\text{m}$ , clavate to slightly turbinate, thin-walled; setulae apical, erect, short, 1–3.8  $\times$  0.8–1  $\mu\text{m}$ , digitiform to verruciform, solid, simple, hyaline, apex obtuse to slightly acute. **Lamellar trama** dextrinoid, irregular, hyphae interwoven, cylindrical, 2–8.8  $\mu\text{m}$  diam, regular in outline, branched, smooth, hyaline, thin-walled. **Pileus trama** similar to the lamellar trama, hyphae 2.5–12.5  $\mu\text{m}$  diam. **Pileipellis** hymeniform, composed of *Siccus*-type broom cells, abundant, orange or pale ochraceous in mass, hyaline when isolated, main body 10–20  $\times$  7–13.8  $\mu\text{m}$ , clavate to slightly turbinate, rarely ventricose, sometimes branched, hyaline, thin-walled, dextrinoid; setulae apical, erect, generally short, some a little more elongate, 1.5–4.6  $\times$  0.5–1  $\mu\text{m}$ , verruciform to digitiform, simple or branched, hyaline, solid, apex acute to slightly obtuse. **Stipe trama** weakly dextrinoid, but the reaction is noticeable only in the internal hyphae, cortical hyphae parallel, cylindrical, 2.5–7.5  $\mu\text{m}$  diam, regular in outline, smooth, septate, melleous or brown in KOH, thick-walled; internal hyphae parallel or disorganized, 1.3–6.3  $\mu\text{m}$  diam, thin-walled. **Clamp connections** present in almost all tissues, inconspicuous, not observed in the cortical stipe trama.



**Fig. 25** *Marasmius hobbitii* (JO309). a. Basidiomata; b. basidiospores; c. basidia, d. basidioles; e. cystidioles; f. cheilocystidia; g. broom cells of the pileipellis. — Scale bars: a = 11.7 mm, b–g = 10  $\mu\text{m}$ .

**Habit & Substrate** — Marasmioid, gregarious on fallen palm leaves.

**DNA Barcode** — GenBank KP635180 (ITS1-5.8S-ITS2) and KP635135 (LSU).

**Additional specimen (paratypes) examined.** BRAZIL, São Paulo State, Santo André City, Reserva Biológica de Paranapiacaba, 8 Jan. 1991, L.K. Okino & M. Capelari 10 (SP 4457611).

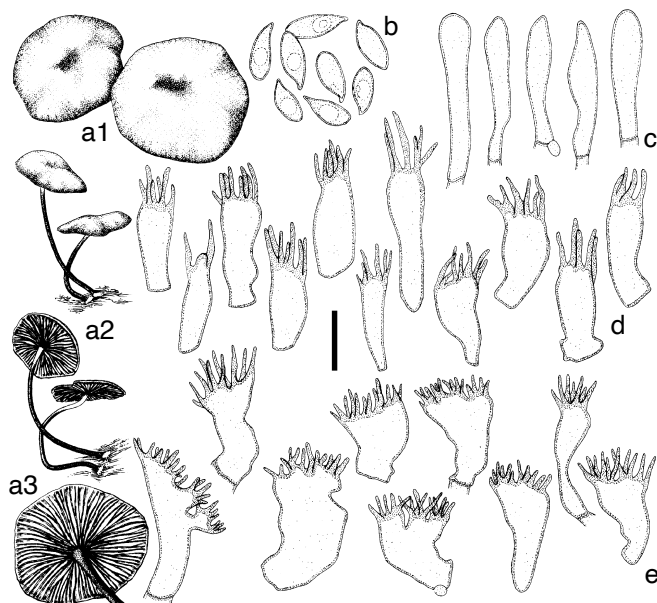
**Notes** — *Marasmius hobbitii* is characterized by small basidiomata with an orange, often campanulate pileus, by thin, short stipes, by broad basidiospores, 5–9 µm in width, and by the presence of very acuminate cystidioles. It is a little difficult to define whether the cystidioles may or may not be considered pleurocystidia in KOH, which would put the species in sect. *Siccis* ser. *Haematocephali* according to Singer (1976). When the lamellae sections are mounted in Cresyl Blue, all cells present in the hymenial layers are orthochromatic (non-reactive or blue), indicating that the longer, acuminate cells should be cystidioles indeed. *Marasmius hobbitii* shows close relationship (PP 1.0/BS 89) with *M. luteoolivaceus* in the Dataset 3 tree (Fig. 2), within the /graminicola subclade.

*Marasmius persicus* (Desjardin et al. 2000) is morphologically similar, differing by having a much paler pileus, more numerous lamellae (10–12), slender basidiospores (3–4 µm in width), and by the absence of acuminate cystidioles. *Marasmius hobbitii* is also comparable with *M. bambusiniiformis* (Singer 1976) and *M. pusio* (Singer 1976). However, *M. bambusiniiformis*, while also occurring on monocotyledonous plants, has a more ferruginous, larger pileus (4.5–7 mm diam), a more thickened stipe, a pubescent stipe base, and narrower basidiospores (3.7–5 µm). Based on Singer (1976), *M. pusio* differs by having more numerous lamellae (8–12) which may be regularly didymous or tridymous (forked twice or three times respectively), by the pallid or paler stipe, by the differently shaped, smaller basidiospores (6–10.3 × 2.5–4.5(–5.5) µm), by the pileipellis with branching *Ramaria*-like broom cells (illustrated and defined in Singer (1965, 1976)), many of them pedicellate, and by the stipitipellis containing broom cells. Despite the differences noted above, both *M. bambusiniiformis* and *M. pusio* have hymenial cystidioles resembling those in *M. hobbitii*.

***Marasmius leoninus* Berk., Hooker's J. Bot. Kew Gard. Misc. 8: 135. 1856 — Fig. 26**

**Pileus** 9–22 mm diam, convex to plane, or almost revolute, tending to form lobes, smooth or slightly sulcate-striate at the margin, centre slightly depressed, margin decurved to straight, edge regular or slightly wavy; orange ( $N_{30}Y_{90}M_{50}$ ) to pale orange ( $N_{00}Y_{70}M_{50}$  to  $N_{20}Y_{60}M_{40}$ ), brownish orange ( $N_{50}Y_{99}M_{70}$ ) or sometimes with diffuse, brownish ( $N_{30}Y_{80}M_{60}$ ) spots or shades at the centre; membranous, but sometimes apparently cartilaginous or coriaceous, context white, thin (< 1 mm); surface glabrous, dry, dull, subvelutinous, non-hygrophanous. **Lamellae** free to adnexed, subclose,  $L = 20$ –22, equal,  $I = 2$ –3, some forked, opaque, smooth, pale cream ( $N_{00}Y_{30}M_{00}$ ), edge even, concolorous with the lamellar faces or finely concolorous with the pileus. **Stipe** 40–57 × 1–1.5 mm, central, cylindrical, sometimes compressed, slightly flared at the apex, contorted; cartilaginous to chitinous, tough, hollow; apex concolorous with lamellar faces, becoming brownish orange ( $N_{40}Y_{90}M_{50}$ ) or brown ( $N_{30}Y_{90}M_{70}$ ), reaching to dark reddish brown ( $N_{80-90}Y_{99}M_{70}$ ) or almost black at the base; surface glabrous, but finely pruinose under lens, opaque; basal mycelium densely strigose, with yellow or orange tints.

**Basidiospores** 7–10(–11.3) × 2.5–4.6 µm ( $x_{\text{m}} = 8.7$ –9.3 × 3.6–4.1 µm;  $x_{\text{mm}} = 9$  (± 0.4) × 3.9 (± 0.4) µm,  $Q_{\text{m}} = 2.1$ –2.7,  $Q_{\text{mm}} = 2.4$  (± 0.4);  $n/s = 30$  from JO84 and 20 from JO320,  $s = 2$ ), obovate to suboblong, ellipsoid, lacrimoid or subclavate,



**Fig. 26** *Marasmius leoninus* (JO84). a. Basidiomata: a1. top view of the pileus, a2. whole basidiomata, a3. hymenophore view; b. basidiospores; c. basidioles; d. cheilocystidia; e. *Siccus*-type broom cells of the pileipellis. — Scale bars: a1, a3 = 9.3 mm, a2 = 16.7 mm, b–e = 10 µm.

smooth, hyaline, thin-walled, inamyloid. **Basidia** not observed. **Basidioles** 21.3–32 × 3.8–6.3 µm, cylindrical, clavate, some subacuminate, smooth, hyaline, thin-walled, inamyloid. **Pleurocystidia** absent. **Cheilocystidia** in form of *Siccus*-type broom cells, somewhat similar to those of the pileipellis, completely hyaline, main body 13.3–22.5 × 5–8.8 µm, clavate to slightly ventricose, thin- to thick-walled; setulae apical, erect, longer and broader than those on the pileipellis broom cells, 2.5–12.5 × 0.6–1.5 µm, cylindrical, filiform, setoid, regular in outline, hyaline, solid, simple, apex acute. **Lamellar trama** dextrinoid, irregular, hyphae interwoven, cylindrical, 2.5–13.8 µm diam, regular or irregular in outline, some inflated, branched, smooth, thin- to thick-walled. **Pileus trama** strongly dextrinoid, irregular, hyphae interwoven, cylindrical, 1.6–15 µm diam, often irregular in outline, inflated, branched, heteromorphic, some thick- and other thin-walled, smooth. **Pileipellis** hymeniform, composed of *Siccus*-type broom cells, abundant, pale orange in mass, becoming hyaline when isolated, main body 12.5–25 × 5.6–17.5 µm, clavate to turbinate, sometimes ventricose, or subglobose, hyaline; setulae apical, erect, 2–6.3 × 0.5–1.3 µm, abundant, cylindrical, filiform, digitiform or setiform, orange, simple, regular in outline, hyaline or pale yellow, solid, apex acute. **Stipe trama** dextrinoid, cortical hyphae parallel, cylindrical, regular in outline, 2.5–11.3 µm diam, smooth, sometimes branched, brown, thick-walled; internal hyphae hyaline, 3–7.5 µm diam, thin-walled. **Stipitipellis** with structures that resemble *Siccus*-type broom cells, with setulae digitiform to cylindrical. **Clamp connections** present in all tissues.

**Habit & Substrate** — Gymnoid, gregarious, on rotten twigs of dicotyledonous trees.

**Distribution** — The species was originally described from Amazonas State, Brazil, and it has also been recorded from the United States, Venezuela, Ecuador, Bolivia, Argentina (Singer 1965, 1976), Martinique, Dominique, Guadalupe, Trinidad (Pegler 1983) and Puerto Rico (Lodge 2003, Cantrell et al. 2006). In Brazil, the species is also known from Rio Grande do Sul (Singer 1976) and São Paulo States (Pegler 1997).

**Specimens examined.** BRAZIL, São Paulo State, Santo André City, Reserva Biológica de Paranapiacaba, 24 Mar. 2010, J.J.S. Oliveira JO84 (SP 4454221); ibid., 9 Dec. 2010, J.J.S. Oliveira, P.O. Ventura & A.V. Costa JO320 (SP 4454891).

Notes — *Marasmius leoninus* has a wide range of variation in morphology. For example, according to Singer (1976), the species varies in pruinosity of the stipe, arrangement of the pileus trama and in the presence or absence of cheilocystidia, and in many other characteristics such as colour, shape, size and texture of the pileus, and the pattern of lamellae attachment to the apex of stipe. D.J. Lodge (pers. comm.) has consistently observed strongly disagreeable taste in all her collections of *M. leoninus*.

The examined material fits within Singer's (1965, 1976) concept in almost all characteristics, only differing by having somewhat smooth to slightly sulcate-striate pileus margin instead of distinctly sulcate and by having more numerous lamellae. The pruinosity of the stipe surface due to the presence of broom cells and the dimorphic pileus trama make *JO84* and *JO320* very compatible with the species. However, neither of these are very strong characteristics for separation of taxa (D.J. Lodge, pers. comm.).

*Marasmius leoninus* var. *aberrans* differs from the material examined by having a foliicolous habit, completely glabrous stipe and slightly shorter basidiospores (up to 9.5 µm). Singer (1976) synonymized *M. orinocensis* ( $\equiv$  *Androsaceus orinocensis*) under *M. leoninus*, but he noticed that it might be considered a variety (*M. leoninus* var. *orinocensis ad interim*) combining the presence of dimorphic pileus trama (thin-walled and thick-walled hyphae) and growth on wood (lignicolous) in contrast to monomorphic trama (thin-walled hyphae) and foliicolous (growing on leaves) in var. *leoninus*. According to the above-mentioned characteristics, the specimens herein examined would fit within the var. *orinocensis* concept. However, the formal separation into var. *leoninus* and var. *orinocensis* was not accomplished. Except for a possible substrate preference, this distinction based on the characteristics of the pileus trama seems very inconclusive.

Pegler (1983) recorded specimens of *M. leoninus* having apricot yellow to cinnamon, glabrous, radially sulcate-striate pileus (10–30 mm diam), glabrous and glossy stipe, subfusoid basidiospores (8–10 µm long), presence of cheilocystidia and absence of broom cells in the stipitipellis, growing on leaves. He also reported the slightly thickened wall for the hyphae of the context (pileus trama). Pegler (1983) also supported the identification of the species by arguing that the number of lamellae is a variable feature in *M. leoninus* and corresponds to the protologue (Berkeley 1856).

*Marasmius leoninus* seems to be closer to *M. bellus* and *M. ruber*, but without a defined resolution or significant support values on the phylogenetic trees of Datasets 2.1 and 3 (Fig. 1b, 2).

***Marasmius rhabarbarinoides* J.S. Oliveira, sp. nov.** — MycoBank MB811136; Fig. 27

*Holotype.* BRAZIL, São Paulo State, Santo André City, Reserva Biológica de Paranapiacaba, on dead leaves of dicotyledonous trees, 20 Mar. 2010, J.J.S. Oliveira *JO66* (SP 445418!).

*Etymology.* The name refers to *Marasmius rhabarbarinus*, based on the resemblance to that species.

*Pileus* 23 mm diam, hemispheric, shallowly sulcate, centre dark brown or orange brown, then ochraceous or carrot orange. *Lamellae* free, subdistant (15), pale cream. *Stipe* 63 × 1 mm, central, cylindrical, dark brown, with a scarce, tomentose basal mycelium. *Basidiospores* 20–25.4 × 3.3–4(–4.8) µm, subclavate or fusoid. *Pleurocystidia* absent. *Hyphal trama* strongly dextrinoid. *Pileipellis* hymeniform, mottled, composed of thin- or thick-walled *Siccus*-type broom cells.

*Pileus* 23 mm diam, convex or almost hemispheric, shallowly sulcate, centre wrinkled, slightly umbonate, margin incurved, edge regular; orangish brown ( $N_{20}Y_{99}M_{60}$ ), reaching to bright

'carrot' orange ( $N_{10}Y_{99}M_{70}$ ) with a dark brown centre ( $N_{60}Y_{99}M_{80}$ ); membranous, context thin (< 1 mm); surface glabrous, dry, dull, somewhat micaceous, velutinous, non-hygrophanous. *Lamellae* free, subdistant,  $L = 15$ , equal,  $l = 0$ , smooth, pale cream ( $N_{00}Y_{20}M_{00}$ ), edge partially concolorous with the pileus, but also with the lamellar faces. *Stipe* 63 × 1 mm, central, cylindrical, equal, tough, chitinous, hollow; apex concolorous with the lamellar face, going to dark brown or black elsewhere down to the base; surface glabrous, smooth, glossy; basal mycelium scarce, cream-coloured, tomentose.

*Basidiospores* 20–25.4 × 3.3–4(–4.8) µm ( $x_m = 22.7 (\pm 1.3) \times 3.8 (\pm 0.3)$  µm;  $Q_m = 6 (\pm 0.5)$ ,  $n = 30$ ), oblong, subclavate or often fusoid, smooth, hyaline, thin-walled, inamyloid. *Basidia* not observed. *Basidioles* 23–34.8 × 5–8.3 µm, cylindrical to clavate, some with a tapered apex, hyaline, thin-walled, inamyloid. *Pleurocystidia* absent. *Cheilocystidia* similar to type 1 of the *Siccus*-type broom cells of the pileipellis, but main body proportionally smaller, abundant, cream when in group, 13.5–21.3(–25) × 6–8.8(–10.3) µm, clavate to turbinate, sometimes ventricose, hyaline, thin-walled; setulae apical, erect, abundant, 3–6 × 0.8–1.5 µm, cylindrical, regular or irregular in outline, solid or with lumen, apex acute or slightly obtuse. *Lamellar trama* strongly dextrinoid, irregular or disorganized, hyphae interwoven, cylindrical, 1.8–12.5 µm diam, regular in outline, branched, hyaline, thin-walled. *Pileus trama* similar to the lamellar trama, hyphae cylindrical, 2.3–17 µm diam. *Pileipellis* hymeniform, mottled, composed of *Siccus*-type broom cells, abundant, consisting of two types: 1) less numerous and more conspicuous, main body more elongate, (13.8–)17.5–30 × 5.3–8.8(–11) µm, subcylindrical, clavate, a little turbinate, sometimes irregular in outline, thin-walled at the base, but strongly thick-walled at the middle toward the apex, golden yellow to orangish yellow, colourless at the base; setulae apical, erect, 4.3–10 × 0.8–1.6 µm, digitiform to cylindrical, regular in outline, some branched, solid, pale golden yellow, apex acute or somewhat obtuse; 2) more numerous and less conspicuous, yellowish when in group, main body smaller, 8.8–17.5 × 5.3–13.8 µm, clavate to turbinate, sometimes bilobed, or irregular in outline, thin-walled, hyaline; setulae apical, erect, 2.8–9 × 0.8–1.3 µm,

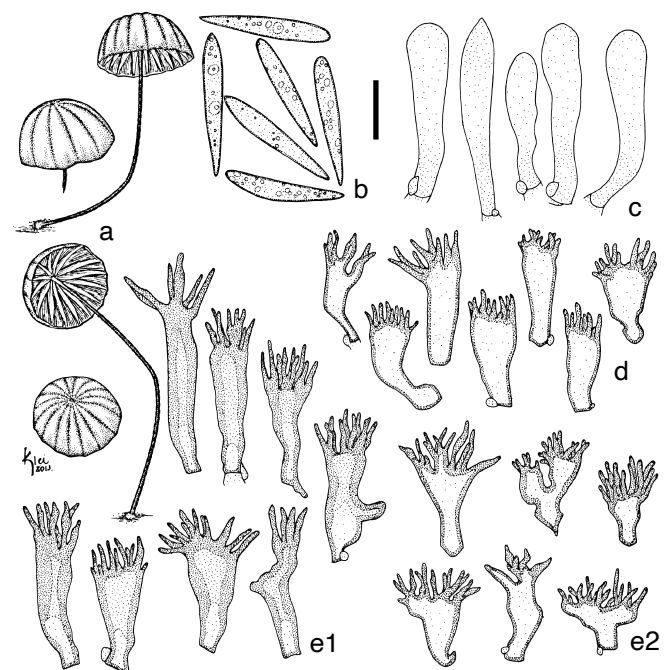


Fig. 27 *Marasmius rhabarbarinoides* (*JO66*). a. Basidiomata; b. basidiospores; c. basidioles; d. cheilocystidia; e. pileipellis: e1. irregular *Siccus*-type broom cells, e2. ordinary *Siccus*-type broom cells. — Scale bars: a = 14.6 mm, b–e = 10 µm.

digitiform to cylindrical, thin, simple or branched, regular in outline, solid, sometimes with lumen, tapering upwards, apex acute or somewhat obtuse. *Stipe trama* strongly dextrinoid at least at the apex, cortical and internal hyphae similar, cylindrical, 2–18.8 µm diam, regular in outline, branched, smooth, light chestnut brown, walls not very thick or almost thin, septa numerous. *Clamp connections* present in all tissues.

Habit & Substrate — Marasmioid, solitary, on dead leaves of dicotyledonous trees.

DNA Barcode — GenBank KP635190 (ITS1-5.8S-ITS2) and KP635145 (LSU).

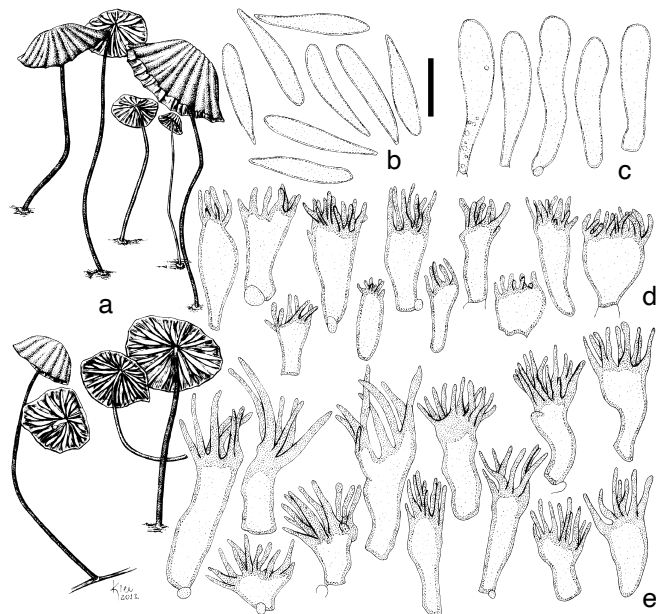
Notes — *Marasmius rhabarbarinoides* differs from *M. rhabarbarinus* mainly by having longer basidiospores (20–25.4 vs 14.4–21.5 µm). Although morphologically similar, *M. rhabarbarinoides* is 4.9–5.9 % divergent from representatives of *M. rhabarbarinus* based on data ITS (Table S3), supporting the establishment of the new species. In all phylogenetic trees (Fig. 1, 2), *M. rhabarbarinoides* is sister to *M. rhabarbarinus*, with a high support within the subclade *rhabarbarinus*.

***Marasmius rhabarbarinus* Berk., Hooker's J. Bot. Kew Gard. Misc. 8: 135. 1856 — Fig. 28**

≡ *Chamaeceras rhabarberinus* (Berk.) Kuntze, Revis. Gen. Pl. (Leipzig) 3: 457. 1898.

*Pileus* 1.3–45 mm diam, hemispheric or slightly conical, tending to campanulate, orbicular, shallowly to deeply sulcate, centre flat to slightly umbonate, margin incurved to decurved, edge regular to crenate; ochraceous (N<sub>30</sub>Y<sub>99</sub>M<sub>50</sub>), ferruginous orange (N<sub>20</sub>Y<sub>99</sub>M<sub>70</sub>), 'carrot' orange or 'rhubarb' fulvous orange (N<sub>40</sub>Y<sub>90</sub>M<sub>60</sub> to N<sub>40</sub>Y<sub>99</sub>M<sub>60</sub>), or brownish orange (N<sub>50</sub>Y<sub>99</sub>M<sub>60</sub>), with a dark orangish brown or brown centre (N<sub>60–90</sub>Y<sub>99</sub>M<sub>70</sub> to N<sub>90</sub>Y<sub>99</sub>M<sub>70–80</sub>); membranous, context pale cream, thin (< 1 mm); surface glabrous, dry, dull, rarely discretely semitranslucent, papyraceous to subvelutinous, non-hygrophanous. *Lamellae* free, subclose to distant, L = 12–20, equal, regular, seldom slightly intervenose, l = 1–3, opaque, smooth, pale cream (N<sub>00</sub>Y<sub>10</sub>M<sub>00</sub>) to pale yellow (Y<sub>40</sub>M<sub>10</sub>C<sub>00</sub>), edge even, concolorous with the lamellar face or very finely brownish orange, hymenium between lamellae partially concolorous with the pileus. *Stipe* 35–98 × 1–3 mm, central, cylindrical, sometimes compressed, base slightly broader, tough, semicartilaginous to chitinous, hollow; apex concolorous with the lamellar faces or a little bit more yellowish (N<sub>10</sub>Y<sub>60–70</sub>M<sub>20</sub>, N<sub>00</sub>Y<sub>80</sub>M<sub>20</sub>), reaching to pale brown (N<sub>40</sub>Y<sub>70</sub>M<sub>40</sub>) or darker brown (N<sub>60</sub>Y<sub>99</sub>M<sub>60</sub>) and blackish brown (N<sub>90</sub>Y<sub>99</sub>M<sub>60–70</sub>) to black toward the base; surface glabrous, smooth, having a silky shine, with a slightly pubescent region restricted to the base; basal mycelium greyish cream, tomentose.

*Basidiospores* (12–)14.4–21.5 × 3–4.8(–6.8) µm (x<sub>mm</sub> = 18–20 × 3.8–4 µm, x<sub>mm</sub> = 18.5 (± 0.7) × 3.9 (± 0.1) µm, Q<sub>mm</sub> = 4.7–5, Q<sub>mm</sub> = 4.9 (± 0.1), n/s = 30, s = 5), oblong, clavate to subfusoid, smooth, hyaline, thin-walled, inamyloid. *Basidia* not observed. *Basidioles* 20–28 × 5–7.3 µm, clavate, smooth, hyaline, thin-walled, inamyloid. *Pleurocystidia* absent. *Cheilocystidia* in form of *Siccus*-type broom cells, hyaline, inconspicuous, main body 8.8–20 × 4.4–9.5(–11.3) µm, clavate, subcylindrical, turbinate, rarely pyriform, hyaline, thin-walled; setulae apical, erect, short to elongate, 1–7.5 × 0.6–1 µm, cylindrical, digitiform or filiform, hyaline, solid, simple, apex obtuse or acute. *Lamellar trama* distinctly dextrinoid, but inamyloid in the subhymenium, irregular, hyphae interwoven, cylindrical, 1.3–14.4 µm diam, regular in outline, some segments inflated, smooth, hyaline, thin-walled. *Pileus trama* dextrinoid, irregular to regular, or organized over the subhymenium, hyphae cylindrical, 2.5–13.8 µm diam, other characteristics similar to those of the lamellar trama. *Pileipellis* hymeniform, mottled, composed of *Siccus*-type broom cells, abundant, pale yellowish orange when in group, especially



**Fig. 28** *Marasmius rhabarbarinus* (JO494). a. Basidiomata; b. basidiospores; c. basidioles; d. cheilocystidia; e. *Siccus*-type broom cells of the pileipellis. — Scale bars: a = 21.4 mm, b–e = 10 µm.

due to the setulae; main body (7–)10–25.6 × 5.3–11.3 µm, clavate to pyriform, sometimes flattened, short to elongate, generally regular in outline: 1) apex solid with a densely thick wall, golden yellow or yellowish, wall thinner toward the base; 2) hyaline and thin-walled all over; setulae apical, erect, short to very elongate, 4.6–15 × 0.6–1.6(–2) µm, regular in outline, cylindrical, digitiform to filiform, some conical, melleous or yellowish, hyaline and thinner on those entirely thin-walled, apex obtuse or acute. *Stipe trama* dextrinoid, cortical hyphae parallel, cylindrical, 5–12.5 µm diam, regular in outline, smooth, not branched, ochre or orangish brown, some segments paler and somewhat olivaceous, or very pale to completely hyaline at the stipe apex, moderately thick-walled; internal hyphae hyaline, 3.8–12.5 µm diam, parallel. *Clamp connections* present in almost all tissues, absent in the cortical stipe trama.

Habit & Substrate — Marasmioid, gregarious, scattered or solitary, more frequently on the lamina or on the petioles of dead leaves, rarely on twigs of dicotyledonous trees.

Distribution — The species was originally described from Amazonas State (Brazil) and it is also known from São Paulo State (Singer 1976, Pegler 1997) and from Argentina (Singer 1976).

*Specimens examined.* BRAZIL, São Paulo State, São Paulo City, Parque Estadual da Cantareira, Núcleo Engordador, 5 Jan. 2012, *M. Capelari* & *P.O. Ventura* 4637 (SP 445783!); *ibid.*, 30 Jan. 2012, *J.J.S. Oliveira* & *V. Motato-Vásquez* JO457 (SP 445544!); *ibid.*, 9 Feb. 2012, *J.J.S. Oliveira* & *M. Capelari* JO474 (SP 445558!); *ibid.*, *J.J.S. Oliveira* & *M. Capelari* JO475 (SP 445918!); *ibid.*, *J.J.S. Oliveira* & *M. Capelari* JO476 (SP 445919!); *ibid.*, 16 Feb. 2012, *J.J.S. Oliveira* & *M. Capelari* JO494 (SP 445565!).

Notes — The collections examined are not only concordant with the morphological description of the species by Singer (1976), but also add more information. The species has previously only been reported on dead leaves. *Marasmius berteroi* is similar, but has shorter spores (11–17 µm) and grows on mixtures of fallen leaves and wood (Singer 1976). *Marasmius rhabarbarinus* is also very close to *M. rhabarbarinoides* (previous taxon) and to *M. dimorphus*, this later differing by having pale brown to cocoa brown pileus, by having 0–1 series of lamellulae, and by having shorter basidiospores (11.3–17.5 (–18.8) µm). Moreover, *M. rhabarbarinus* is also difficult to distinguish from *M. corneri* when comparing their respective morphological descriptions. The unique (but not strictly) dis-

tinguishing characteristic is the absence of a mottled pileipellis in *M. corneri*, but the authors have mentioned the presence of thin- to thick-walled broom cells and setulae pale yellow to tawny, which may produce a mottle aspect (Wannathes et al. 2009). However, the pairwise comparison of ITS sequences (Table S3) confirms that these taxa are different species (c. 10 % divergence). This could be considered an example of cryptic species (Bickford et al. 2007), geographically and genetically separated, but morphologically similar.

*Marasmius rhabarbarinus*, along with *M. rhabarbarinoides*, *M. corneri* and *M. dimorphus*, comprise the highly supported subclade /*rhabarbarinus* (Fig. 1c, 2).

### *Marasmius ruber* Singer, Sydowia 18: 342. 1965 — Fig. 29

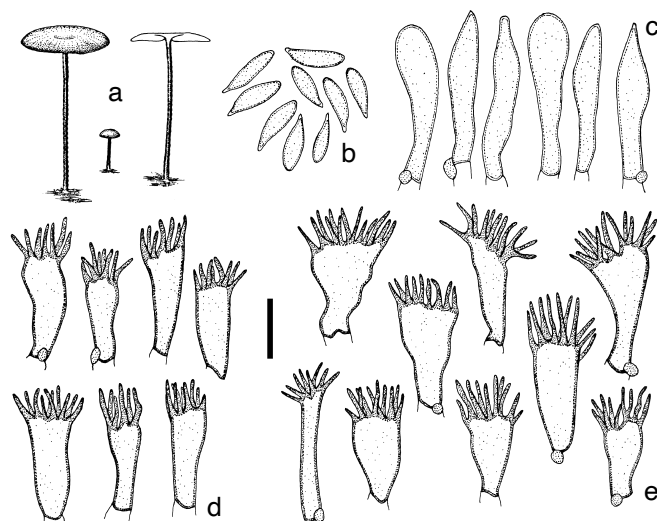
*Pileus* 20 mm diam, convex to plano-convex or plane with a shallow central depression, striate, glabrous or subvelutinous, dull, dry, bright orange (6A7–8). *Lamellae* shallowly adnexed, subdistant with 3–4 series of lamellulae, narrow (< 2 mm), bright orange (6A7–8) with strongly reddish orange (7B8) edge. *Stipe* 35 × 1 mm, cylindrical, equal, fistulose, glabrous, when young light yellow (4A5–6) overall, in age apex light yellow, base brownish orange (6C5–6) to light brown (6D5–6); non-insititious, basal mycelium tawny strigose (macromorphological description and drawing (Fig. 29a) found in a small sheet along with the collection (unpublished), by Dennis E. Desjardin, 2012). *Basidiospores* (6.3–)7.5–10.5 × 2–3.4 µm ( $x_m = 8.8 (\pm 1.1) \times 3 (\pm 0.3) \mu\text{m}$ ,  $Q_m = 3 (\pm 0.4)$ ,  $n = 30$ ), oblong, slender, subfusoid or clavate, smooth, hyaline, thin-walled, inamyloid. *Basidia* not observed. *Basidioles* 20–28 × 4.8–7 µm, narrowly cylindrical, clavate or acuminate, some with a pointed apex, smooth, hyaline, thin-walled, inamyloid. *Pleurocystidia* absent. *Cheilocystidia* in form of *Siccus*-type broom cells similar to those of the pileipellis, losing the reddish pigmentation in KOH, abundant, main body 15–18.8 × 5.6–8 µm, clavate to slightly turbinate, thin-walled; setulae apical, erect, 2–7.5 × 0.6–1 µm, cylindrical, filiform, regular in outline, hyaline, solid, simple, apex acute. *Lamellar trama* dextrinoid, irregular, hyphae interwoven, cylindrical, 2–7.5 µm diam, regular in outline, branched, smooth, thin-walled. *Pileus trama* dextrinoid, similar to the lamellar trama, hyphae 2–7.5 µm diam. *Pileipellis* hymeniform, composed of *Siccus*-type broom cells, abundant, distinctly orange to reddish when grouped, depigmenting in KOH, becoming hyaline, main body 12.5–22.5 × 3–12.5 µm, cylindrical, clavate to often turbinate, hyaline, thin-walled; setulae apical, erect, 2.5–7.5 × 0.5–1.3 µm, abundant, cylindrical, filiform, simple, regular in outline, solid, hyaline, apex acute. *Stipe trama* dextrinoid, cortical hyphae parallel, cylindrical, regular in outline, 3–15 µm diam, smooth, orangish, pale brown or melleous when depigmented in KOH, thick-walled; or a second type of worm-like hyphae present, rough or with shallow or small protuberances, or slightly incrustated, opaque, 2.3–8 µm diam, sometimes vein-like, conspicuous, with strongly thick walls, almost solid, aseptate, resembling skeletal hyphae, distinct within the trama; internal hyphae indistinguishable. *Clamp connections* present in almost all tissues, absent in the second type of hyphae in the cortical stipe trama.

**Habit & Substrate** — Gymnoid, solitary, on dead twigs.

**Distribution** — Originally described from Beni (Bolivia), also known from Trinidad (Singer 1965, 1976) and from São Paulo State, Brazil (Grandi et al. 1984).

**Specimen examined.** BRAZIL, São Paulo, Iporanga City, Parque Estadual Turístico do Alto Ribeira, 28 Feb. 2012, leg. D.E. Desjardin DED8669 (SP 445657!).

**Notes** — The examined material corresponds to the description of the species by Singer (1965, 1976). An important observation is the presence of conspicuous, thick-walled hyphae,



**Fig. 29** *Marasmius ruber* (DED8669). a. Basidiomata; b. basidiospores; c. basidioles; d. cheilocystidia; e. *Siccus*-type broom cells of the pileipellis. — Scale bars: a = 13.6 mm, b–e = 10 µm.

mixed within the stipe trama, which could correspond to the non-septate hyphae mentioned by Corner (1996) as skeletal in the stipe of *M. dimiticus*. *Marasmius ruber* appears in Group 1 (Fig. 1), and in an unsupported grouping formed by *M. bellus*, *M. trinitatis* and the /*leoninus* clade (Fig. 2) and its placement was not strongly supported in the trees recovered.

### *Marasmius trinitatis* Dennis, Trans. Brit. Mycol. Soc. 34: 425. 1951 — Fig. 30

*Pileus* 6–34 mm diam, convex, tending to plane, smooth or slightly sulcate-striate, centre flat, margin incurved to plane, sometimes uplifted, edge regular or wavy; centre dark grey ( $N_{80}Y_{30}M_{10}$ ) and margin paler grey ( $N_{60}Y_{20}M_{10}$ ) when young, becoming olivaceous cinnamon ( $N_{60}Y_{50}M_{20}$ ) or yellowish grey ( $N_{50}Y_{70}M_{20}$ ) or brownish yellow ( $N_{30}Y_{50}M_{20}$ ), with a greenish grey or brownish olive centre ( $N_{70}Y_{50}M_{20}$ ) when mature; membranous, context thin (< 1 mm); surface glabrous, dry, dull to semitranslucent, subvelutinous, non-hygrophanous. *Lamellae* adnexed, adnate to sinuate, subdistant,  $L = 8–10$ , unequal,  $l = 3$ , opaque, smooth, light cream ( $N_{00}Y_{10}M_{00}$ ), edge even, partially concolorous with the pileus, later becoming concolorous with the lamellar faces as well as with the hymenium between the lamellae. *Stipe* 8–40 × 0.9–1.5 mm, central, cylindrical, equal or a little broader at the apex, semicartilaginous to chitinous downwards, hollow; apex concolorous with the lamellar faces, becoming orangish brown ( $N_{30}Y_{80}M_{50-60}$ ) at the middle, reaching dark brown ( $N_{80}Y_{99}M_{60}$ ) at the base; surface glabrous, smooth, opaque; basal mycelium abundant, orangish yellow, strigose. *Basidiospores* 10–13.3 × 3.4–4 µm ( $x_m = 11.7 (\pm 0.9) \times 3.7 (\pm 0.2) \mu\text{m}$ ;  $Q_m = 3.2 (\pm 0.3)$ ,  $n = 30$ ), oblong, clavate, smooth, hyaline, thin-walled, inamyloid. *Basidia* not observed. *Basidioles* 23.8–30.6 × 4.5–7.5 µm, clavate, smooth, hyaline, thin-walled, inamyloid. *Pleurocystidia* absent. *Cheilocystidia* similar to the *Siccus*-type broom cell of the pileipellis, abundant, melleous in mass, main body 11.3–21.3 × 5–8.3 µm, cylindrical to clavate or turbinate, wall relatively thin, but thicker at the apex, hyaline; setulae apical, erect, short to elongate, 2.5–8 × 0.5–1.3 µm, cylindrical, filiform, needle-like, simple, solid, melleous to pale yellow, or hyaline, regular in outline, apex acute. *Lamellar trama* strongly dextrinoid, irregular, hyphae interwoven, cylindrical to inflated, slender to broad, 2.5–16.3 µm diam, branched, smooth, hyaline, thin-walled. *Pileus trama* strongly dextrinoid, irregular, hyphae interwoven, with some loose regions, cylindrical to inflated, 3.5–18.8 µm diam, like those of the lamellar trama.





**Fig. 30** *Marasmius trinitatis* (JO306). a. Basidiomata; b. basidiospores; c. basidioles; d. cheilocystidia; e. *Siccus*-type broom cells of the pileipellis; f. *Siccus*-type broom cells of the stipitipellis. — Scale bars: a = 14.4 mm, b–f = 10 µm.

*Pileipellis* hymeniform, composed of *Siccus*-type broom cells, abundant, golden yellow to pale brown in mass, main body 9.4–19.4 × 5.6–10.6 µm, cylindrical to clavate or turbinate, walls relatively thin, but thicker above, melleous, or hyaline; setulae apical, erect, short to elongate, 1.5–7.5 × 0.4–1 µm, cylindrical, filiform, needle-like, simple, solid, melleous to pale yellow, or hyaline, regular in outline, apex acute. *Stipe trama* dextrinoid, cortical hyphae parallel, cylindrical, 3.5–11.3 µm diam, regular in outline, branched, smooth, dark melleous or brownish yellow, thick-walled; internal hyphae 2.5–20 µm diam, thin- to thick-walled, smooth. *Stipitipellis* containing *Siccus*- or *Amiloflagellula*-type broom cells, more frequent at the upper part of the stipe where the hyphae are more hyaline, other broom cells concolorous with the cortical hyphae of the median and basal part of the stipe, very variable in shape, setulae elongate in both types, apex acute. *Clamp connections* present in all tissues.

**Habit & Substrate** — Gymnoid, gregarious, on rotten wood of dicotyledonous trees.

**Distribution** — Originally described from Trinidad (Dennis 1951c, Pegler 1983), it is also known from the United States, Mexico, Brazil, Bolivia (Singer 1965, 1976), Puerto Rico (Lodge 2003, Cantrell et al. 2006) and Papua New Guinea (Desjardin & Horak 1997). This is the first record of the species from São Paulo State.

**Specimen examined.** BRAZIL, São Paulo State, Santo André City, Reserva Biológica de Paranapiacaba, 9 Dec. 2010, J.J.S. Oliveira & P.O. Ventura JO306 (SP 445481!).

**Notes** — The examined material corresponds to *M. trinitatis* as described by Singer (1976), differing only by the occasional presence of pale melleous cheilocystidia, and the presence of broom cells in the stipitipellis. The latter characteristic is found in *M. trinitatis* var. *immarginatus*, but this variety does not possess cheilocystidia (Singer 1976). Perhaps the presence of broom

cells in the stipitipellis is an occasional characteristic in this species and/or the absence of cheilocystidia in var. *immarginatus* might have been due to the condition of the material examined by Singer (1976). Because of this conflict between the presence of cheilocystidia and the main distinguishing characteristic of var. *immarginatus* (absence of cheilocystidia), the specimen is herein determined as the type variety. Regarding the pigmentation of the cheilocystidia, it was observed that the lamellar edge is concolorous with the pileus in the young basidiomata, but fading at the maturity, when the cheilocystidia become hyaline.

*Marasmius trinitatis* is basal to *M. coarctatus* and *M. cladophyllus* in the group 1 tree of Dataset 2.1 (Fig. 1b), but with weak statistical support. In the Dataset 3 tree (Fig. 2), *M. trinitatis* is basal to *M. leoninus* in *leoninus*, but with weak support. In both analyses, the clade with *M. trinitatis* is placed in a polytomy.

### Phylogenetic analyses

The 50% majority-rule consensus trees from Bayesian analyses depicted in Fig. 1, 2 agree with those produced by ML analyses (Fig. S2–S7). In the Dataset 1 tree (Fig. 1a), four groups were identified that formed Datasets 2.1, 2.2, 2.3 and 2.4, respectively corresponding to Groups 1, 2, 3 and 4 in the Fig. 1a. Group 1 and Group 3 are highly supported monophyletic groups (PP 1.0 / BS 92 and PP 1.0 / BS 97) while Group 4 forms a distinct clade but without significant support and Group 2 consists of a set of several small clades of species in polytomy but all closer to Group 1 with high support (PP 1.0). In spite of not forming a distinct clade, Group 2 was interpreted as containing close groups of species. Within the ingroup (PP 1.0 / BS 100), many of the intermediate and deep nodes were statistically unsupported. Moreover, the lack of resolution within all Groups resulted in many polytomies (complete ITS tree of Dataset 1 in the Fig. S1, S2). Various subclades of taxa, many of them highly supported, do represent important information. Group 4, which is a clade bearing the majority of species of sect. *Globulares* (*sensu* Singer) included in the analyses, also contains few taxa of sect. *Sicci* (*sensu* Singer) embedded in the clade. Three smaller branches within Groups 1 and 2 make sect. *Globulares* (*sensu* Singer) polyphyletic which is also true for sect. *Sicci* (*sensu* Singer) and its series, a result that agrees with Wannathes et al. (2009) and Tan et al. (2009). Datasets 2.1, 2.2, 2.3 and 2.4 produced more congruent alignments with less misaligned blocks. Many of the subclades found in Fig. 1a remained in the subtrees (Fig. 1b–e), with higher support values where some taxa were finally placed in resolved clades forming more intermediate nodes, but few other subclades were dissolved by removing undetermined taxa. The subclades have been labelled after representative taxa in Fig. 1b–e. Furthermore, many of the newly described taxa grouped within some of these subclades and contributed to support the conclusions.

The consensus tree (Fig. 2) resulted from the analysis of Dataset 3 is similar to the Dataset 1 tree (Fig. 1a) relative to the large and diverse sampling of taxa. However, many of the taxa present in the Dataset 1 tree are absent in the Dataset 3 tree because only taxa having both LSU and ITS from the same strain in GenBank and those produced in this study were included, with few missing data exceptions. Some of the subgroups found in the subtrees (Fig. 1b–e) were kept in the Dataset 3 tree (LSU + ITS concatenated) with high support (Fig. 2), but not all, mostly due to the removal of many taxa. The Dataset 3 tree is complementary to the Dataset 1 tree, providing more resolution and increasing statistical support of the nodes previously revealed. Moreover, some of the subclades are only found in Fig. 2. Group 4 remained unsupported in the Dataset 3 tree (Fig. 2), but formed two fully resolved and highly supported subclades.

## DISCUSSION

### **Morphology and infrasectional inconsistencies**

In the traditional view, sect. *Sicci sensu* Singer is composed of species having the pileipellis composed of *Siccus*-type broom cells, in rare cases mixed with *Globulares*-type smooth cells. Within sect. *Sicci* Singer, series *Atrorubentes* is defined by the presence of caulocystidia and the absence of setae (Desjardin & Horak 1997), series *Spinulosi* is composed of species with setae in the pileus, lamellae and/or stipe (Antonín & Noordeloos 1993), species in series *Haematocephali* share the presence of pleurocystidia and absence of setae and caulocystidia (but may have broom cells in the stipitipellis) (Singer 1976), and series *Leonini* is characterized by the absence of all those features mentioned above, with the exception of broom cells in the stipitipellis (Singer 1976). Section *Globulares sensu* Singer is composed of species having the pileipellis solely composed of *Globulares*-type smooth cells. However, some special cases of known species or new morphological data recovered from recently described species bring inconsistencies in those concepts, especially from tropical areas where diversity of species and morphology is high and still mostly unknown.

The presence of elongate caulocystidia as determinant for sect. *Sicci* ser. *Atrorubentes* may be remarkable in some species (i.e., *M. atrorubens*), but inexpressive in others (i.e., *M. congregatus*). Regarding the inexpressive forms of caulocystidia, it is also hard to handle with the reduced structures in the stipitipellis in *M. corrugatus*, classified within sect. *Sicci* ser. *Leonini*. Another example is the case of *M. cladophyllus* var. *glaberripes* (with a completely glabrous stipe) belonging to sect. *Sicci* ser. *Leonini* while *M. cladophyllus* (type variety) has very distinct caulocystidia, being referred amongst species of sect. *Sicci* ser. *Atrorubentes*. It is also uncertain whether the presence of broom cells in the stipitipellis may or may not be considered also one form of caulocystidium.

Additionally, setae like those found in the pileipellis of *M. longisetosus*, or like those in *M. cohaerens*, may also be found in lamellae and/or stipe in other species of sect. *Sicci* ser. *Spinulosi*. Cléménçon (2012) explained that the term 'setae' has received a widened concept to accommodate setoid elements without the xanthocroic reaction, or having basal clamp connection, or with partly or completely hyaline wall, and to admit similar but richly branched cells, or similar, hair-like cells on the stipe and pileus of some agarics. In *Marasmius*, these elements were tentatively termed 'spinulae' by Cléménçon (1982), but the term 'setae' was conserved (Antonín & Noordeloos 1993), only being categorized according to topography. Considering the setae in sect. *Sicci* ser. *Spinulosi*, it is difficult to disregard the fact that the long, setoid elements (at least, the majority) in *M. atrorubens* (also var. *dumontii* with elongate, hair-like structures in the pileipellis), called as caulocystidia (Fig. 7), can be considered setae.

The third case is the presence of pleurocystidia. There is certain difficulty to define true pleurocystidia among a) those sometimes called 'gloeocystidia' which are long and refractive cells, often with constrictions (i.e., *M. ferrugineus*, *M. haematocephalus*, *M. hypophaeus*, *M. siccus*); b) the non-refractive, reduced, but conspicuous elements (i.e., *M. azectus*, *M. helvolus*, *M. hinnuleus*, *M. luteoolivaceus*, *M. spegazzinii*, *M. suthepensis*); c) the inconspicuous elements or cystidioles in some species in ser. *Leonini* studied by Singer (1976) (such as *M. bambusinus*, *M. bellus*, *M. berteroi*, *M. corrugatus*, *M. cuatrecasasii*, *M. helvoloides*, *M. pusio* and *M. neglectus* and in *M. hobbitii* (in this study)); and d) broom cells in the face of the lamellae (i.e., *M. setulosifolius* and *M. pleurocanthus*). According to D.J. Lodge (pers. comm.), the case of letter 'c' can be solved by testing the structures with Cresyl Blue and, if they are metachromatic unlike the basidia

and basidioles, should be considered pleurocystidia. In this study, it was observed that the wide pleurocystidia concept (Singer 1958, 1976) is not informative to group species with these structures (whatever the form) in a single group based on phylogenetic analyses using ITS and LSU. Cases such as *M. ambicellularis* and *M. linderioides* and also the close relationship between *M. hobbitii* and *M. luteoolivaceus* (all discussed in the taxonomic section) also point to phylogenetic inconsistency regarding the presence/absence of pleurocystidia.

The pileipellis composed exclusively of smooth cells was traditionally considered diagnostic to form a section (sect. *Globulares sensu* Singer) likewise those species having *Siccus*-type broom cells in the pileipellis for sect. *Sicci*. However, classification based on the type of pileipellis cells is not supported by phylogenetic analyses (Tan et al. 2009, Wannathes et al. 2009, this study). Pileipellis made up by only smooth cells, or only *Siccus*-type broom cells, or with both are only useful for separating species, or at most, to group closely related species forming a stirps. Smooth cells mixed with broom cells in the pileipellis may denote an intermediate pattern between the species of sect. *Sicci* and the species of sect. *Globulares sensu* Singer (1986). However, there is no phylogenetic evidence that supports this conclusion. The evidence suggests multiple emergence of the different types of cells in the pileipellis within the single large group (sect. *Globulares*). Sometimes both types of cells occurring in the pileipellis may be interpreted as occasional when a minority of smooth cells are inconspicuously found among abundant broom cells, also representing broom cells not fully formed. But in species such as *M. congregatus*, *M. corrugatus* (as described by Singer (1976)), *M. nexus*, *M. pseudoniveus* (all varieties), *M. pseudoniveoaffinis* and *M. ambicellularis*, both type of dermatocystidia appear to be equally distributed or smooth cells are even dominant over the broom cells, possibly indicating that this pattern may also be useful for delimitation of species and varieties.

### **Molecular phylogeny**

Dataset 1 had limited information, preventing full resolution in the phylogeny, particularly for sect. *Globulares sensu* Antonín & Noordeloos (2010), as found previously when including the whole genus in a single dataset (Tan et al. 2009, Wannathes et al. 2009). However, the purpose of this broad analysis was fulfilled as we obtained better resolution and increased statistical support for the nodes compared to the results in the Dataset 1 tree (Fig. 1a) and to previously published trees. Moreover, this first large tree served to find subgroups gathering close taxa (Groups 1, 2, 3 and 4) to produce Datasets 2.1, 2.2, 2.3 and 2.4. This systematic reduction into smaller datasets helped to provide even better resolution and higher statistical support for intermediate to terminal nodes within the Groups 1, 2, 3 and 4 (Fig. 1a) improving topologies in the subtrees (Fig. 1b–e). Despite this fact, Datasets 2.3 tree was the only fully resolved subtree, and Datasets 2.1, 2.2 and 2.4 trees (Fig. 1b–c, e) remained partly resolved. Compared with Dataset 1 and Datasets 2.1, 2.2, 2.3 and 2.4, the tree of the Dataset 3 (LSU + ITS dataset) was more efficient in defining more intermediate and deeper nodes with strong support in a tree representing the whole section. This is the first attempt to use multilocus analyses to resolve phylogeny in *Marasmius*, particularly in sect. *Globulares sensu* Antonín & Noordeloos (2010). Yet, some intermediate and deep nodes had no significant statistical support and there was lack of resolution within some clades.

Studies by Wannathes et al. (2009) and Tan et al. (2009) were the first to demonstrate that both sect. *Globulares sensu* Singer and sect. *Sicci* (and its series) are non-monophyletic groups. By including more data of new species and other known taxa from Neotropical areas in a more global sampling and also LSU

in a multilocus analysis of only sect. *Globulares sensu* Antonín & Noordeloos (2010), the results also support the conclusion that sect. *Globulares sensu* Singer and the series of sect. *Sicci* in traditional view are polyphyletic groups in agreement with Wannathes et al. (2009) and Tan et al. (2009). Therefore, there are herein additional evidence for the deconstruction of the series within sect. *Sicci sensu* Singer and it corroborates with the discussion in the previous section. In the case of sect. *Globulares sensu* Singer, its members grouped into various unrelated lineages in all trees, including the Dataset 3 tree (Fig. 1b–c, e, 2), showing multiple emergence considering the traditional sectional pattern (only *Globulares*-type cells in the pileipellis) across the entire section that is also in agreement with previous studies (Tan et al. 2009, Wannathes et al. 2009). Unfortunately, the data published by Shay et al. (2017) and Grace et al. (2019) were not included in this analysis.

The trees recovered also provide evidence for the recognition of many subgroups based on subclades (Fig. 1b–e, 2), as previously found by Wannathes et al. (2009) and Tan et al. (2009). These subgroups form the basis for a supraspecific classification when correlated with the morphology and some ecological traits such as occupying the same niche, basidiomata production strategy (size, number and habit on the substrate), etc. We observed that these subgroups correspond to the ‘stirpes’ concept used by Singer (1976), outlining small groups of close species based on morphological characteristics. Thus, the characteristics once used to separate the traditional series in sect. *Sicci* and sect. *Globulares* (*sensu* Singer) are actually informative for the recognition of more stringent groups corresponding to the stirpes used by Singer (1976). However, these characteristics still have limited taxonomic signal and their occurrence or expression may vary in particular cases within the groups (see more about it in the characterization of each group below). In this study, we add twelve to the sixteen existent Singerian stirpes in *Marasmius* supporting their plausibility as immediate supraspecific taxa, at least within sect. *Globulares*. Since the traditional series have been proved artificial groups, we propose to establish series based on the subclades recovered (Fig. 1, 2) as we elevate the Singer’s stirpes concept up to series level. Therefore, thirteen new series are proposed (*Brunneospermi*, *Coherentes*, *Conferti*, *Corrugati*, *Crinipes*, *Graminicolae*, *Imitarii*, *Luteoli*, *Pulcherripes*, *Purpureostriati*, *Rhabarbarini*, *Silvicolae*, *Wynnearum*) and three are emendation on extant ones (*Atrorubentes*, *Haematocephali*, *Leonini*).

Additionally, we observed that the major clades formed in the trees recovered can represent groups gathering the series. Examining the Dataset 1 tree (Fig. 1a), three major clades are distinct: Group 1, Group 3 and Group 4. Group 2 is not a single clade, but a set of multiple unrelated subclades (Fig. 1a, c). Based on Group 1, Group 3 and Group 4, we propose the new subsections *Leonini*, *Spinulosi* and *Globulares*, respectively, referring to the series each one bears. From these subsections, only *Globulares* is based on a major clade (Group 4) without statistical support, though it is very distinct and earlier diverging within the ingroup. Particularly within Group 4 clade, the subclade bearing /*brunneospermus* + /*silvicola* is sister to the subclade /*wynneae* without significant support values. Two lineages in subsect. *Globulares* can be detected (Fig. 2) considering the morphology: i) basidiomata without pleurocystidia; and ii) basidiomata with pleurocystidia. In addition, by visual inspection of the alignments in Datasets 1 and 3 (ITS matrix), conspicuous regions of deletion can be detected in the ITS2 region (site 497 to 529 of the final edited alignment) for the members of this major clade (Group 4) in comparison to the rest of the ingroup. Moreover, by examining the Dataset 3 tree (Fig. 2), we can observe two (one supported

and one unsupported) major clades plus the distinct lineage *M. venatifolius* tending to relate the remaining series of Group 2 in at least three more subsections, but these relationships are not conclusive yet. The subsections and series of this new classification are further discussed below:

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

**1 – Subsection *Leonini* J.S. Oliveira & Moncalvo, subsect. nov.** — MycoBank MB823091

Type species: *Marasmius leoninus* Berk.

*Basidiomata* marasmioid, or pleurotoid/crepidotoid, or gymnopoid, small- to large-sized, thin to robust. *Pileus* smooth, striate to shallowly sulcate. *Lamellae* close to distant, simple to reticulate. *Stipe* central to lateral, or absent. *Basidiospores* obovoid to moderately oblong. *Pleurocystidia* absent or present, short- to medium-sized, non-refractive, sometimes as *Siccus*-type broom cells. *Pileipellis* composed of *Siccus*-type or *Globulares*-type cells, or both mixed, or rarely with *Amyloflagellula*-type cells or *Rotalis*-type cells (*M. griseoroseus*). *Caulocystidia* present or absent.

Notes — Based on species within Group 1 (Fig. 1a).

**Series *Graminicolae* J.S. Oliveira & Moncalvo, ser. nov.** — MycoBank MB823099

Type species: *Marasmius graminicola* Speg.

*Basidiomata* mostly marasmioid, or sessile with a pleurotoid/crepidotoid habit (sect. *Neosessiles* in traditional sense) in some taxa, somewhat small and thin. *Pileus* white, cream, yellow, orangish to ferruginous, barely reaching 9 mm diam. *Lamellae* simple, rarely reticulate, subdistant. *Stipe* central or lateral. *Basidiospores* short-oblong to medium-sized oblong, subfusoid to clavate (7–19  $\mu\text{m}$  long,  $x_m = 10\text{--}17.5 \mu\text{m}$ ,  $Q_m = 2.6\text{--}4.4$ ). *Pleurocystidia* present or absent. *Pileipellis* composed of *Siccus*- or rarely *Rotalis*-type (*M. griseoroseus*) broom cells or, in rare cases, *Globulares*-type smooth cells or *Amyloflagellula*-type cells may be also present. *Habit* gregarious, on several kinds of substrates.

Notes — This group is based on the subclade /*graminicola* depicted in the Dataset 2.1 and 3 trees (Fig. 1b, 2). Such subclade may actually be split into two or more subclades with the inclusion of more related taxa and, hence, can form two or more series. The cases where *Globulares*-type smooth cells or *Amyloflagellula*-type cells are present together with regular *Siccus*- or *Rotalis*-type broom cells are *M. ambicellulares* and *M. griseoroseus* var. *diminutus*, respectively.

**Series *Corrugati* J.S. Oliveira & Moncalvo, ser. nov.** — MycoBank MB823101

Type species: *Marasmius corrugatus* (Pat.) Sacc.

*Basidiomata* more gymnopoid, medium-sized. *Pileus* yellowish or orangish to white, typically corrugated, medium- to large-sized (up to 65 mm diam). *Lamellae* distant-reticulate to crowded. *Stipe* cylindrical, orangish to reddish brown. *Basidiospores* short, almost ellipsoid (5–10.4  $\mu\text{m}$  long,  $x_m = 7\text{--}8.8 \mu\text{m}$ ,  $Q_m = 2.1\text{--}2.5$ ). *Pleurocystidia* absent. *Pileipellis* consists of either only *Siccus*-type broom cells, or only *Globulares*-type smooth cells, or both types. *Stipitipellis* contains poorly to well-developed, cylindrical to clavate caulocystidia. *Habit* gregarious to caespitose inhabiting both leafy or woody substrate.

Notes — It is based on the highly supported subclade /corrugatus depicted in the Dataset 2.1 and 3 trees (Fig. 1b, 2). In this group, the ratio broom cells/smooth cells seems to define how pellucid or dull a membranous pileus is, which implicates in the capacity of water retention in the surface, resulting in different strategies that grant the basidiomata to play their role in mesophytic environments.

**Series *Luteoli*** J.S. Oliveira & Moncalvo, *ser. nov.* — MycoBank MB823109

Type species: *Marasmius luteolus* Berk. & M.A. Curtis.

*Basidiomata* small to medium-sized. *Pileus* smooth to striate, or very shallowly sulcate (4–42 mm diam). *Lamellae* unequal, close to subdistant with 2–4 series of lamellulae. *Stipe* pruinose, pubescent to hispidulous. *Basidiospores* medium-sized or short-oblong, lacrimoid to shortly clavate (8–14 µm long,  $x_m = 9.7\text{--}12.2$  µm,  $Q_m = 2\text{--}3$ ). *Pleurocystidia*, if present, in form of *Siccus*-type broom cells. *Caulocystidia* present, clavate to irregular. *Habit* scattered to gregarious (*M. pseudopellucidus* often caespitose), on dicotyledonous or monocotyledonous leaves, less frequent on wood.

Notes — It is represented by the highly supported subclade /luleolus in the Dataset 2.1 and 3 trees (Fig. 1b, 2). It groups species previously classified in sect. *Sicci* ser. *Atrorubentes*. The only case of presence of pleurocystidia, which is in form of *Siccus*-type broom cells, is found in *M. luteolus*.

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

Type species: *Marasmius leoninus* Berk.

*Basidiomata* medium- to large-sized. *Pileus* smooth to shallowly sulcate (up to 70 diam). *Lamellae* subdistant to close, simple. *Stipe* cylindrical, cartilaginous to fibrous, glabrous to finely pruinose. *Basidiospores* short-oblong, subellipsoid, fusoid to sublacrimoid (up to c. 12 µm long). *Pleurocystidia* absent. *Pileipellis* having very hyaline, thin-walled *Siccus*-type broom cells with thin, needle-shaped setulae. *Habit* on leafy and woody substrates.

Notes — This series is based on *M. leoninus* in the phylogenetic trees (Fig. 1b, 2). However, a subclade bearing *M. bellus*, *M. leoninus*, *M. ruber* and *M. trinitatis* has high support in further tests (data not shown) and the morphology of these taxa fit this series concept.

## 2 – Incertae sedis

**Series *Atrorubentes*** Desjardin & E. Horak emend. J.S. Oliveira & Moncalvo

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

*Basidiomata* gymnopoid thin to marasmiod, small- to medium-sized. *Pileus* small- to medium-sized (2.6–23 mm diam), orangish to ochraceous. *Lamellae* unequal, mostly close (11–22), with many series (2–4) of lamellulae. *Stipe* pubescent, velutinous to hispid, cylindrical thin. *Basidiospores* medium-sized to more elongate (8.6–18 µm long,  $x_m = 10.5\text{--}14.8$  µm,  $Q_m = 2.5\text{--}4.3$ ). *Pleurocystidia* absent, unless in form of *Siccus*-type broom cells (*M. nummularius*). *Pileipellis* composed of *Siccus*-type broom cells. *Caulocystidia* present, long-setoid elements (setae), which may also be present in the pileus (pileosetae) (excepting *M. iras* and *M. xestocephalus* which do not present setoid cystidia, even in the stipitipellis). *Habit* consistently found on dicotyledonous leaves.

Notes — The highly supported subclade /atrurubens in the Dataset 2.2 and 3 trees (Fig. 1c, 2) represents this group that consists of some species of ser. *Atrorubentes* and ser. *Spinulosi* in the traditional view.

**Series *Purpureostriati*** J.S. Oliveira & Moncalvo, *ser. nov.* — MycoBank MB823110

Type species: *Marasmius purpureostriatus* Hongo.

*Basidiomata* gymnopoid to marasmiod, small- to large-sized. *Pileus* markedly sulcate (6–110 mm diam), mostly striped in the pigmentation at least in certain stage of development. *Lamellae* distant. *Basidiospores* very elongate, clavate to subfusoid (20–35 µm long,  $x_m = 22.3\text{--}30.4$ ,  $Q_m = 4.1\text{--}6.1$ ). *Pleurocystidia* absent. *Pileipellis* consisting only of *Globulares*-type smooth cells. *Stipitipellis* devoid of caulocystidia. *Habit* mostly found on dicotyledonous leaves, some species also on bamboo leaves.

Notes — It is based on the supported (BS 71) subclade /purpureostriatus in the Dataset 2.2 and 3 trees (Fig. 1c, 2).

**Series *Conferti*** J.S. Oliveira & Moncalvo, *ser. nov.* — MycoBank MB823111

Type species: *Marasmius confertus* Berk. & Broome.

*Basidiomata* gymnopoid, medium- to large-sized. *Pileus* smooth to slightly sulcate, orange to ochraceous, or olivaceous (20–60 mm in the maximum diam). *Lamellae* always with many lamellulae (2–5 series or more). *Stipe* generally very elongate. *Basidiospores* very variable in length. *Pleurocystidia* present, versiform (except *M. plicatulus*). *Pileipellis* consisting of *Siccus*-type broom cells (except *Marasmius calvus*). *Habit* scattered to gregarious, mostly on dicotyledonous leaves, sometimes on wood.

Notes — Represented by the highly supported subclade /confertus in the Dataset 2.2 and 3 trees (Fig. 1c, 2), it contains species sharing typical characteristics of *M. confertus*, and corresponds to the stirps *Confertus sensu* Singer (1976). The size of the basidiospores seems to be inconsistent as two patterns are observed: ellipsoid to short-oblong (6–11.3 µm of total length range,  $x_m = 7\text{--}9.6$  µm,  $Q_m = 1.8\text{--}3.2$ ) and medium- to long-sized, oblong basidiospores (13–21 µm of total length range,  $x_m = 16.4\text{--}19.3$  µm,  $Q_m = 4.2\text{--}4.8$ ). *Marasmius plicatulus* EU935480 (Wannathes et al. 2009) is an outlier in this clade for it lacks pleurocystidia. The corresponding ITS sequence came from a not morphologically described specimen (NW439), which prevents further considerations. *Marasmius calvus* is the only representative of the clade with the pileipellis composed of only smooth cells in the present study.

**Series *Rhabbarbarini*** J.S. Oliveira & Moncalvo, *ser. nov.* — MycoBank MB823113

Type species: *Marasmius rhabbarbarinus* Berk.

*Basidiomata* marasmiod to gymnopoid, medium- to large-sized. *Pileus* convex, sulcate, membranous (1.3–45 mm diam). *Lamellae* free to adnexed, subdistant to distant, simple. *Stipe* cylindrical, fibrous, glabrous. *Basidiospores* oblong (11.3–25.4 µm long,  $x_m = 14.7\text{--}22.7$ ,  $Q_m = 4.1\text{--}6$ ). *Pleurocystidia* absent. *Pileipellis* frequently mottled due to the presence of thick-walled, strongly pigmented *Siccus*-type broom cells besides others that are smaller, more hyaline, thin-walled. *Habit* growing in groups or solitary on leafy and woody substrate.

Notes — Based on the highly supported subclade /rhabbarbarinus in the Dataset 2.2 and 3 trees (Fig. 1c, 2), it contains

species macromorphologically similar to those in the subclade /siccus (next series).

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

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

*Basidiomata* marasmioid (umbrella-like), thin, small- to medium-sized. *Pileus* membranous, sulcate. *Lamellae* distant to subdistant, free. *Stipe* mostly filiform with a scanty, tomentose basal mycelium. *Basidiospores* elongate, clavate to subfusoid (11–25  $\mu\text{m}$  long,  $x_m = 17.5\text{--}22\ \mu\text{m}$ ,  $Q_m = 4.3\text{--}5.9$ ). *Pleurocystidia* present, well-developed, elongate, refractive. *Pileipellis* composed of *Siccus*-type broom cells only. *Habit* an apparent preference for leafy substrate considering the strains included in the analysis, but more collections should be evaluated since the taxa cited are known as generalist (on wood and/or leaves).

Notes — Based on the well-defined, highly supported subclade /siccus in the Dataset 2.2 and 3 trees (Fig. 1c, 2), the series combines the concept of stirpes *Ferrugineus*, *Haematocephalus* and *Siccus* of Singer (1976). To avoid using *Sicci* as the name for this series or establishing a new name, we propose an emendation of ser. *Haematocephali*.

**Series *Pulcherripes*** J.S. Oliveira & Moncalvo, ser. nov. — MycoBank MB823115

Type species: *Marasmius pulcherripes* Peck.

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

Notes — It is based on the clade /pulcherripes, only well-defined in the Dataset 3 tree (Fig. 2) grouping *M. anomalus* and *M. pulcherripes* with high support. In the Dataset 2.2 tree (Fig. 1c), *M. hypopheus* (sister to or conspecific with *M. anomalus*) is considered a misdetermined specimen (see discussion in the comments for *M. anomalus*) and *M. pulcherripes* is sister to *M. koreanus*, a species devoid of pleurocystidia. However, in Antonín et al. (2012), *M. koreanus* has basidioles reaching 10–30  $\mu\text{m}$  long which can be subcylindrical, clavate or fusoid. Some of these basidioles might be considered very reduced pleurocystidia likewise those found in *M. anomalus*.

**Series *Crinipes*** J.S. Oliveira & Moncalvo, ser. nov. — MycoBank MB823116

Type species: *Marasmius crinipes* Antonín, Ryoo & H.D. Shin.

*Basidiomata* marasmioid, thin. *Pileus* conical or parabolic, relatively small (2–10 mm diam) compared to the stipe length. *Lamellae* distant. *Stipe* very elongate, filiform (40–200  $\times$  0.5–0.75 mm). *Basidiospores* fusoid-clavate, very large (20–32  $\mu\text{m}$  long,  $x_m = 22.8\text{--}28.2$ ,  $Q_m = 5.5\text{--}6.6$ ). *Basidia* and *basidioles* equivalent to the basidiospores size. *Pleurocystidia* present, elongate, fusoid to clavate. *Pileipellis* composed of only *Siccus*-type broom cells. *Habit* gregarious, often on dead leaves.

Notes — It is represented by the highly supported subclade /crinipes in the Dataset 2.2 and 3 trees (Fig. 1c, 2). Based on

Wannathes et al. (2009) and Antonín et al. (2012), there is an apparent preference for dead leaves (mono- or dicotyledonous plants), but *M. crinipes* was also found on living branches of *Lonicera chrysantha* according to Antonín et al. (2012).

**Series *Imitarii*** J.S. Oliveira & Moncalvo, ser. nov. — MycoBank MB823117

Type species: *Marasmius imitarius* Wannathes, Desjardin & Lumyong.

*Basidiomata* marasmioid, relatively small and thin. *Pileus* membranous, sulcate (2–15 mm diam). *Lamellae* distant. *Stipe* filiform. *Basidiospores* oblong, clavate (17–20  $\mu\text{m}$  long,  $x_m = 18.6\ \mu\text{m}$ ,  $Q_m = 4.4$ ). *Pleurocystidia* absent. *Pileipellis* composed of *Siccus*-type broom cells. *Habit* scattered to gregarious, on dicotyledonous leaves or on wood.

Notes — The strongly supported subclade /imitarius in the Dataset 2.2 tree (Fig. 1c) is due to an unexpected divergence observed among samples of *M. imitarius* included in the analyses. The specimens sampled can represent two different, but cryptic species (Bickford et al. 2007). The epithet *imitarius* also reflects the difficulty to distinguish this species from others such as *M. kanchingensis*, *M. mazatecus*, *M. sierraleonis* and *M. striapileus* considering the micromorphology, and it can be considered a species complex.

**3 – Subsection *Spinulosi*** J.S. Oliveira & Moncalvo, subsect. nov. — MycoBank MB823093

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

*Basidiomata* gymnopoid. *Pileus* thin-fleshy, often pruinose, velvety. *Lamellae* broad. *Stipe* cylindrical, robust. *Basidiospores* obovoid, ellipsoid. *Pileipellis* composed of thick-walled *Siccus*-type broom cells, some in transition to setae. *Setae* present in the hymenium and/or in the pileipellis and/or in the stipitipellis, pigmented, robust, dextrinoid, thick-walled.

Notes — Based on species within Group 3 (Fig. 1a).

**Series *Cohaerentes*** J.S. Oliveira & Moncalvo, ser. nov. — MycoBank MB823118

≡ ser. *Spinulosi* (Cléménçon) Desjardin, in Antonín & Noordeloos, *Libri Botanici* 8: 179. 1993.

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

*Basidiomata* gymnopoid, medium-sized. *Pileus* orangish to reddish brown, smooth to rugulose (7–45(–65) mm diam). *Lamellae* seldom intervenose, moderately broad. *Stipe* cylindrical, robust, 25–80  $\times$  1–3 mm. *Basidiospores* obovoid, ellipsoid to broadly lacrimoid (7.1–10.4  $\mu\text{m}$  long,  $x_m = 8.3\text{--}8.4\ \mu\text{m}$ ,  $Q_m = 1.7\text{--}1.8$ ). *Pleurocystidia* absent (unless, the setae). *Pileipellis* composed of *Siccus*-type broom cells. *Setae* present in the hymenium, or also in the pileipellis, lanceolate, fusoid or ventricose-acuminate, thick-walled, pigmented. *Habit* solitary to gregarious, sometimes subcaespitose, on leafy or woody debris.

Notes — It is based on a very distinct and strongly supported subclade /cohaerens in the Dataset 2.3 and 3 trees (Fig. 1d, 2). The subclade is formed by a species complex or a set of at least five closely related species, one should represent *M. cohaerens* and the others have been probably misdetermined and may also represent cryptic species (Bickford et al. 2007) with allopatric occurrences and encompasses a variety of niches.

**4 – Subsection *Globulares*** J.S. Oliveira & Moncalvo, subsect. nov. — MycoBank MB823095

Type species: *Marasmius wynneae* Berk. & Broome.



*Basidiomata* gymnopoid, medium- to large-sized, thin to robust. *Pileus* small to large, thin-fleshy, often hygrophanous. *Lamellae* often broad, simple or forked. *Stipe* cylindrical, robust, fibrous. *Basidiospores* obovoid, ellipsoid or lacrimoid. *Pleurocystidia* absent or present. *Pileipellis* solely composed of *Globulares*-type smooth cells (except *M. magnus*).

Notes — Based on species within Group 4 (Fig. 1a).

**Series *Wynnearum*** J.S. Oliveira & Moncalvo, *ser. nov.* — MycoBank MB823439

Type species: *Marasmius wynneae* Berk. & Broome.

*Basidiomata* gymnopoid, medium- to large-sized, tending more to thin (*M. wynneae*), sometimes fleshy (*M. oreades*). *Pileus* small to large, 5–65 mm diam. *Lamellae* less numerous and more distant, frequently intervenose to reticulate, or anastomosed. *Stipe* cylindrical, some very robust, 40–110 × 1–6 mm. *Basidiospores* obovoid, ellipsoid (6–10.3 µm long,  $x_m = 7.2$ –8.7 µm,  $Q_m = 1.7$ –1.8). *Pleurocystidia* absent. *Pileipellis* composed of only *Globulares*-type smooth cells. *Habit* solitary to gregarious, sometimes caespitose, on dicotyledonous leaves, or lawns in open meadows.

Notes — Represented by the strongly supported subclade /wynneae in Fig. 1e and 2, it consists only of species of sect. *Globulares sensu* Singer. Some species in this series are found on meadows or grass lands and are, therefore, very resistant to desiccation on open field: *M. oreades* and *M. maximus*. Their ability to resist desiccation may be expressed by the production of large and fleshy basidiomata, with a possible high concentration of trehalose (Barros et al. 2008).

**Series *Brunneospermi*** J.S. Oliveira & Moncalvo, *ser. nov.* — MycoBank MB823440

Type species: *Marasmius brunneospermus* Har. Takah.

*Basidiomata* gymnopoid, large, robust. *Pileus* generally hygrophanous, mostly smooth, rugose to shallowly sulcate in rare cases, non-pellucid, homogeneously pigmented (20–122 mm diam). *Lamellae* broad, with edge mostly uneven. *Stipe* cylindrical, robust, fibrous, surface frequently fibrillose, with abundant, white basal tomentum. *Basidiospores* mostly ellipsoid to phaeoform, 6–8(–10) µm long. *Pleurocystidia* present, elongate. *Pileipellis* mostly composed of *Globulares*-type smooth cells, rarely composed of *Siccus*-type broom cells (*M. magnus*). *Habit* solitary to gregarious, on dicotyledonous leaves or detritus.

Notes — It is based on a very distinct and strongly supported subclade /brunneospermus in the Dataset 2.4 tree (Fig. 1e). In the Dataset 3 tree (Fig. 2), /brunneospermus is unsupported and it is clearly due to the absence of *M. magnus* in this analysis, as *M. macrocystidiosus* has also unsupported relationship with the '*M. brunneospermus* + *M. fuscicystidiosus*' subclade in Fig. 1e. The strain determined after *M. albomyceliosus* (KP-13) is likely misidentified and should be actually *M. macrocystidiosus* or allied. In addition, with the exception of *M. magnus* (Magnago et al. 2016), all species in /brunneospermus are morphologically consistent regarding the pileipellis dermatocystida (sect. *Globulares sensu* Singer (1986)).

**Series *Silvicolae*** J.S. Oliveira & Moncalvo, *ser. nov.* — MycoBank MB823441

Type species: *Marasmius silvicola* Singer.

*Basidiomata* gymnopoid, large. *Pileus* hygrophanous to subhygrophanous, sometimes umbrinate, sulcate-striate, with a darkened disc, somewhat pellucid at the margin, fading to a

paler pigmentation at the margin (25–100 mm diam). *Lamellae* adnate to adnexed, seceding in age, close to subdistant, broad to very broad (up to 17 mm), with many series of lamellulae. *Stipe* cylindrical, robust, fibrous, surface fibrillose, sometimes pubescent. *Basidiospores* ellipsoid or lacrimoid (5–9 µm long). *Pleurocystidia* present, very elongate. *Pileipellis* composed of *Globulares*-type smooth cells. *Habit* solitary to gregarious, sometimes caespitose, on soil, humus, rotten trunks or leaf debris.

Notes — It is based on the very distinct and strongly supported subclade /silvicola in the Dataset 2.4 tree (Fig. 1e). In this tree, the species having pleurocystidia are split into two distinct, strongly supported subclades: /brunneospermus and /silvicola. Moreover, *M. pallidibrunneus* and *M. coklatus* grouped in unsupported phylogenetic positions between the subclades. However, these two subclades do form one single, monophyletic, highly supported subclade with *M. pallidibrunneus* in a stable position in the Dataset 3 tree (Fig. 2). Series *Brunneospermi* and ser. *Silvicolae* are very difficult to distinguish one from the other in the morphology for there is not a very striking distinction.

## CONCLUSIONS

Since Singer (1959, 1965, 1976), stirpes have been considered informal taxa. Singer (1986) seemed to leave behind this concept, holding only the sections, subsections and series in *Marasmius*. In fact, even now including phylogenetics with molecular data, determining small groups of closely related species at this level of grouping is not a simple task considering the infinitude of possible stirpes, the existence of species complexes (some representing cryptic species), potential subjectivity when interpreting subclades, and the high possibility of proposing superfluous names. Moreover, due to the incomplete resolution of this supraspecific level for all taxa in the phylogenetic trees (mostly because the absence of taxa to be related to), many taxa cannot be classified in stirpes currently and/or subgroups such as the one represented by the subclade /graminicola may represent more than one stirpes. On the other hand, the stirpes are appointed as factual natural groups within the section. The formalization of the stirpes as series is viable based on evidence shown in the phylogenetic trees correlated with observations on morphological and ecological traits. Thus, we are proposing a more stringent view of series in *Marasmius* sect. *Globulares* (*sensu* Antonín & Noordeloos 2010) to correspond to the stirpes concept once used by Singer. Thirteen new series are herein proposed and three traditional series are emended in a more stringent circumscription. Also based on the consistent formation of major clades within the ingroup, we propose three new subsections that include many of the series: *Leonini*, *Spinulosi* and *Globulares*. Based on Fig. 2, there should be at least three more subsections related to series now considered *Incertae Sedis*, and subsection *Leonini* may be divided in two in future studies.

This study also highlights the importance of detailed data about ecology and geographic distribution to be added to genetic and morphological data. These data combined are fundamental for species delimitation and for outlining supraspecific groups. This study also led us to reinterpret the morphological characteristics once used to determine the traditional sect. *Globulares* and sect. *Sicci* (ser. *Atrorubentes*, ser. *Haematocephali*, ser. *Leonini* and ser. *Spinulosi*) in order to support the new subsectional classification. The phylogenetic trees also strongly suggest the occurrence of misdetermined strains named after *M. albomyceliosus*, *M. bambusiformis*, *M. bondoi*, *M. graminicola*, *M. imitarius* and *M. oreades* and such specimens should be accurately revised. Finally, nine new species are herein proposed in sect. *Globulares*.

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### Supplementary material

**Fig. S1** Complete Dataset 1 tree from BA. The full information can be found in the legend of the Fig. 1a in the manuscript.

**Fig. S2** Complete Dataset 1 tree from ML analyses (Optimization Likelihood – OL = -5747.517007; Tree Length –TL = 4.238861).

**Fig. S3** Dataset 2.1 tree from ML analyses (OL = -3428.768140; TL = 1.109381).

**Fig. S4** Dataset 2.2 tree from ML analyses (OL = -3842.658675; TL = 1.593492).

**Fig. S5** Dataset 2.3 tree from ML analyses (OL = -1482.096414; TL = 0.433845).

**Fig. S6** Dataset 2.4 tree from ML analyses (OL = -2445.466127; TL = 1.015247).

**Fig. S7** Dataset 3 tree from ML analyses (OL = -7301.155870; TL = 1.420229).

**Fig. S8** Macroscopic features. a. *Marasmius pallidibrunneus* (*M. Capelari* 4607); b. *M. silvicola* (JO357); c. *Marasmius puberistipitatus* (JO308); d. *M. atrotubens* (JO489); e. *M. congregatus* (JO61); f. *M. pseudoniveoaffinis* (*M. Capelari* & L.A.S. Ramos 4536); g. *M. altoribeirensis* (JO532); h. *M. anomalus* (JO346); i. *M. suthepensis* (JO469). Scale bars = 10 mm.

**Fig. S9** Macroscopic features. a. *Marasmius neotropicalis* (JO69); b. *M. luteoolivaceus* (JO524); c. *M. spegazzinii* (JO467); d. *M. venatifolius* (JO313); e. *M. bellus* (JO299); f. *M. hobbitii* (JO309); g. *M. cladophyllus* var. *glaberripes* (JO518); h. *M. corrugatus* (JO466); i. *M. corrugatus* (JO347); j. *M. dimorphus* (JO298). Scale bars = 10 mm.

**Fig. S10** Macroscopic features. a. *Marasmius graminicola* (JO459); b. *M. leoninus* (JO84); c. *M. ambicellularis* (JO144); d. *M. rhabarbarinoides* (JO66); e. *M. rhabarbarinus* (JO494); f. *M. trinitatis* (JO306). Scale bars = 10 mm.

**Table S1** Identity matrix for pair-wise comparison of distance of ITS sequences of *M. lindierioides*, *M. neotropicalis* and *M. suthepensis*.

**Table S2** Identity matrix of distance by pairwise comparison of the ITS sequences of *M. graminicola* and *M. bambusiformis* available in GenBank with materials determined as *M. graminicola* in the present study.

**Table S3** Identity matrix of distance by pairwise comparison of ITS sequences of *M. comeri*, *M. rhabarbarinoides* and *M. rhabarbarinus*.

**Table S4** Sampling of *Marasmius* included in the phylogenetic analyses with accession numbers of the LSU and ITS sequences, itemized by infrageneric traditional groups. The 14 sections and series indication are according to the traditional sense (Singer 1986, Antonín 1991, Antonín & Noordeloos 1993, Desjardin & Horak 1997).

**References** publications referred to in supplementary material.