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Two new setose species of *Marasmius* from the Paraná riparian forest in Argentina

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Abstract – The aim of this article is to describe two new setoid species of *Marasmius*: *M. chrysoblepharioides* and *M. neotrichotus* from the riparian forest of the Paraná river in Northeastern Argentina. *Marasmius chrysoblepharioides* is characterized by a sulcate-striate, yellowish orange pileus, an entirely pilose, orange brown stipe; caulosetae with a tapering and thick-walled apex, and its bacilliform to fusiform basidiospores. *Marasmius neotrichotus* differs from *M. trichotus* and *M. ciliatus* by its longer caulosetae and spores, respectively. The phylogenetic analyses based on molecular data from ITS sequences indicated that both new species are distinct from closely related species.

Agaricales / Basidiomycota / diversity / Marasmiaceae / *M. chrysoblepharis* / *M. trichotus* / *Sicci* / *Spinulosi* / taxonomy

INTRODUCTION

Marasmius Fr. (Marasmiaceae, Agaricales) comprises ca. 500 species worldwide (Kirk *et al.*, 2008) and more than 1900 epithets recorded in the Index Fungorum website (http://www.indexfungorum.org/Names/Names.asp?pg=1). Due

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to its important diversity and abundance, the genus plays an essential role in litter decomposition, particularly in tropical and subtropical forests (Braga-Neto *et al.*, 2008; López-Quintero *et al.*, 2012). *Marasmius* species are characterized by their generally small to medium-size basidiomata, membranaceous consistency, narrow, cartilaginous stipe, and reviviscent habit (Singer, 1976). This last feature allows them to tolerate seasonal drought or high temperatures (Singer, 1986). Microscopically, the basic character is a hymeniform pileipellis (e.g. Antonín & Noordeloos, 2010).

Marasmius comprises many infrageneric divisions which are based mainly on characters such as the type of broom cells forming the pileipellis, presence or absence of a collarium, the stipe attachment to the substrate (insititious or non-insititious), and the pseudoamyloid (= dextrinoid) or non-amyloid (= non-dextrinoid) trama (Singer, 1976, 1986). However, Wannathes *et al.* (2009a) and Oliveira *et al.* (2014) have recently tested the monophyly of the sections traditionally proposed by Singer (1958, 1976), and confirm that they are highly homoplasic.

A small group of species of *Marasmius* is characterized by having very thick-walled and acuminate cystidia (setae) on the hymenophore, pileus and stipe surface together with a hymeniform pileipellis of broom cells of the Siccus-type (e.g. *M. actinopus, M. jalapensis, M. coharens*). Singer (1958) grouped setose species of *Marasmius* in the series *Actinopodes* Singer, within section *Sicci* Singer; while Desjardin (1989) distributed them into two different series: *Spinulosi* (Clémençon) Desjardin (species with setae) and *Atrorubentes* Desjardin & E. Horak (species with conspicuous caulocystidia, which do not form setae with thickened walls).

The species of *Marasmius* with setae are not common, being better known from southeastern Asia (Pegler, 1986; Desjardin *et al.*, 2000; Tan *et al.*, 2009; Wannanthes *et al.*, 2009a; Antonín *et al.*, 2010; Ryoo *et al.*, 2013) and the Neotropical region (Singer, 1976; Pegler, 1983; Desjardin & Ovrebo, 2006; Puccineli & Capelari, 2006). In the north of Argentina, about 90 species of *Marasmius* are known, many of them described by Spegazzini and Singer (Niveiro & Albertó, 2013), and some species were recently described by Lechner & Papinutti (2011) and Papinutti & Lechner (2011).

The aim of this article is to describe two new setose species of *Marasmius* from the riparian forest of Paraná river, in northeastern Argentina.

MATERIAL AND METHODS

Collections

The specimens studied here were collected in the floodplain on the western bank of Paraná river from Chaco province in northern Argentina, and deposited in CTES Herbarium. These specimens were macroscopically described according to Largent (1986). Colour names are in accordance with Kornerup & Wanscher (1978). For the microscopic characters, a light microscopy (LM) Leica model CME was used. All LM images were made with a Leica EC3 incorporated camera of material mounted in 5% KOH and Phloxine (1%), or Melzer's reagent. The measurements were made directly in the LM or through the photographs taken using the software ImageJ (Schneider *et al.*, 2012). Microstructures (length and width of basidiospores, basidia, hyphae, pileipellis) were measured in LM. The following notations were

used for the basidiospores' measurement: x = arithmetic mean of the basidiospore length and width; Q = quotient of length and width indicated as a range of variation; Q_x = mean of Q values; n = number of basidiospores measured, N = number of analysed basidiomata. All GPS readings were taken on a Garmin eTrex 10, hand held unit using WGS84 standard. Herbarium abbreviations follow Index Herbariorum (Thiers, 2017) and the authors' abbreviations follow Kirk & Ansell (1992).

The specimens analysed were identified using different generic dichotomous keys (Moser, 1983; Raithelhuber, 2004; Antonín & Noordeloos 2010; Niveiro *et al.*, 2014), *Marasmius* specific dichotomous keys (Singer, 1965, 1976; Desjardin *et al.*, 2000; Tan *et al.*, 2009; Wannathes *et al.*, 2009a; Shay *et al.*, 2017), and descriptions found in the specific literature (Singer, 1989; Antonín *et al.*, 2010).

DNA extraction, amplification, and sequencing

Genomic DNA of the two new species was isolated from dried basidiomata tissue following standard protocols of the Canadian Centre for DNA barcoding (CCDB) for fungi (Ivanova *et al.*, 2006, 2016; Fazekas *et al.*, 2012). Approximately 20 ng of DNA were used for polymerase chain reaction (PCR) amplifications of the nuclear ribosomal internal transcribed spacer (ITS) region of the DNA, with primers ITS1-F and ITS4-B (Gardes & Bruns, 1993),which was suggested as the universal DNA barcode marker for fungi (Ivanova *et al.*, 2008; Schoch *et al.*, 2012). Forward and reverse strands were purified and sequenced by Macrogen Inc. (Seoul, South Korea). The ITS sequences retrieved in this study were deposited into GenBank database. Collection data and GenBank accession numbers of the specimens used in this study are detailed in Table 1.

Phylogenetic analysis

The resulting sequences were assembled and manually edited using Geneious v. 6.1.8 (Kearse *et al.*, 2012). These sequences were aligned together with 40 sequences retrieved from GenBank (NCBI) (Table 1), mainly of representatives of ser. *Spinulosi/Atrorubentes*, which were treated by Wannathes *et al.* (2009a, b), Oliveira *et al.* (2014), and Shay *et al.* (2017). *Crinipellis malesiana* Kerekes, Desjardin & Vikinesw. was used as outgroup for phylogenetic inferences (Wannathes *et al.*, 2009a).

The sequences alignment was initially perform with MAFFTv.7 (under the Q–INS–i criteria) (Katoh & Standley, 2013) and manually edited using MEGA6 (Tamura *et al.*, 2011). The final ITS dataset included 44 specimens, and was subdivided into three data partitions: ITS1, 5.8S, and ITS2. The best fit model of nucleotide evolution to the dataset was selected using AIC (Akaike Information Criterion) as implemented in jModelTest2 v.1.6 (Guindon & Gascuel, 2003; Darriba *et al.*, 2012).

The dataset was analysed with Maximum Likelihood (ML) and Bayesian Inference (BI) approaches. ML searches were conducted with RaxML-HPC v.8 (Stamatakis, 2014), searching for the best scored trees with GTRGAMMA model for the entire dataset with all the default parameters estimated by the software. The analysis first involved 100ML independent searches each one starting from one randomized stepwise addition parsimony tree. Only the best scored ML tree was kept, and the confidence of nodes was accessed through non-parametric bootstrapping (BS) replicates under the same model, allowing the program to stop bootstrapping

TABLE 1: ITS dataset of *Marasmius* used in the phylogenetic analyses, itemized by infrageneric group.

Species	*Section / Serie*	*Collection No.*	*ITS GenBank Accession No.*
M. galbinus[b]	*Globulares*	GDGM 27251	HQ709445
M. laticlavatus[i]	*Globulares*	NW 412	EU643511
M. laticlavatus[i]	*Globulares*	NW 293	EU643512
M. auratus[h]	*Sicci/ Atrorubentes*	NW 076	EU935501
M. auratus[h]	*Sicci/ Atrorubentes*	NW 175	EU935502
M. corrugatiformis[f]	*Sicci/ Atrorubentes*	Buyck 97425	KX148981
M. inthanonensis[h]	*Sicci/ Atrorubentes*	NW 414	EU935514
M. iras[h]	*Sicci/ Atrorubentes*	NW 276	EU935486
M. iras[h]	*Sicci/ Atrorubentes*	NW 375	EU935487
M. jasminodorus[h]	*Sicci/ Atrorubentes*	NW 294	EU935515
M. jasminodorus[h]	*Sicci/ Atrorubentes*	NW 353	EU935514
M. katangensis[f]	*Sicci/ Atrorubentes*	JES 227	KX148991
M. luteolus[h]	*Sicci/ Atrorubentes*	NW 138	EU935506
M. luteolus[h]	*Sicci/ Atrorubentes*	NW 304	EU935507
M. ochroleucus[h]	*Sicci/ Atrorubentes*	NW 299	EU935503
M. ochroleucus[d]	*Sicci/ Atrorubentes*	LE 295978	KF912952
M. pseudopellucidus[h]	*Sicci/ Atrorubentes*	NW 186	EU935504
M. pseudopellucidus[h]	*Sicci/ Atrorubentes*	NW 305	EU935505
M. strobiluriformis[a]	*Sicci / Atrorubentes*	BRNM 714914	GU266263
M. strobiluriformis[a]	*Sicci / Atrorubentes*	BRNM 714915	GU266264
M. xestocephalus[h]	*Sicci/ Atrorubentes*	JFK 69	EU935488
M. xestocephalus[h]	*Sicci/ Atrorubentes*	NW 344	EU935489
M. siccus[h]	*Sicci / Haematocephali*	BRNM 552709	HQ607384
M. siccus[d]	*Sicci / Haematocephali*	LE 295980	KF774130
M. acerosus[g]	*Sicci / Leonini*	TYS 427	FJ431214
M. acerosus[g]	*Sicci / Leonini*	TYS 458	FJ431213
M. adhaesus[g]	*Sicci / Leonini*	TYS 467	FJ431216
M. adhaesus[g]	*Sicci / Leonini*	TYS 464	FJ431217

M. olivascens[c]	*Sicci / Leonini*	TYS 424	FJ431266
M. olivascens[c]	*Sicci / Leonini*	TYS 426	FJ431265
M. chrysoblepharioides	*Sicci / Spinulosi*	CTES 0568164	**MF683956**
M. chrysoblepharioides	*Sicci / Spinulosi*	CTES 0568166	**MF683957**
M. dendrosetosus[f]	*Sicci / Spinulosi*	JES 205	KX148995
M. dendrosetosus[f]	*Sicci / Spinulosi*	JES 211	KX148996
M. jalapensis	*Sicci / Spinulosi*	CTES 0568170	**MF683959**
M. longisetosus[e]	*Sicci / Spinulosi*	JO 248	JX424040
M. neotrichotus	*Sicci / Spinulosi*	CTES 0568167	**MF683958**
M. nummularius[h]	*Sicci / Spinulosi*	NW 266	EU935492
M. nummularius[h]	*Sicci / Spinulosi*	NW 396	EU935493
M. nummularius[h]	*Sicci / Spinulosi*	JES 121	KX148979
M. trichotus[h]	*Sicci / Spinulosi*	NW 262	EU935490
M. trichotus[h]	*Sicci / Spinulosi*	NW 263	EU935491
Crinipellis malesiana[g]	–	TYS 346	FJ167628
Crinipellis malesiana[c]	–	BO_AR 491	NR119706

Published sequences are found in: a- Antonín *et al.* (2012), b- Deng & Li (2011), c- Kerekes & Desjardin (2009), d- Kiyashko *et al.* (2014), e- Oliveira *et al.* (2014), f- Shay *et al.* (2017), g- Tan *et al.* (2009), h- Wannathes *et al.* (2009a), i- Wannathes *et al.* (2009b).

automatically by the autoMRE option. An additional alignment partition file to force RAxML software to search for a separate evolution model for each partition was used. BI analyses were carried out with Mr.Bayes 3.2.6 (Ronquist & Huelsenbeck, 2003), and implemented with two independent runs, each one beginning from random trees with four simultaneous independent chains. A total of 2×10^7 generations were carried out, sampling one tree every 1×10^3 generation. The initial 25% of the sampled trees was discarded as burn-in and checked by the convergence criterion (frequencies of average standard deviation of split <0.01) in Tracer v.1.6 (Rambaut *et al.*, 2014), while the remaining ones were used to reconstruct a 50% majority-rule consensus tree and to estimate Bayesian posterior probabilities (BPP) of the branches. J Model Test2 v.1.6, Mr Bayes 3.1.2 and RaxML-HPC v. 8.2.3 were used in CIPRES science gateway (Miller *et al.*, 2010; http://www.phylo.org/). A node was considered to be strongly supported if it showed a BPP ≥ 0.95 and/or BS ≥ 90%, while moderate support was considered BPP ≥ 0.9 and/or BS ≥ 70%.

Only the topology from the best ML tree is shown, indicating support values (BPP/BS) of each node. The alignment was deposited in TreeBASE (http://www.treebase.org/treebase/index.html), under accession number 21518.

RESULTS

Molecular phylogeny

The dataset includes 44 sequences belonging to 2 species of the series *Spinulosi, Atrorubentes, Leonini* and *Haematocephali* of the sect. *Sicci,* one of the sect. *Globulares*, and four newly generated sequences, resulting in an alignment with 637 characters, of which 427 are constant sites, 210 variable and 163 parsimony informative. The best evolutionary model estimated for each dataset were TPM2uf+G, K80 and TPM1uf+G, for ITS1, 5.8S and ITS2, respectively. In the phylogenetic inferences from nITS dataset (Fig 1), the sect. *Sicci* and ser. *Atrorubentes* were recovered as polyphyletic, in comparison to the traditional classification of Singer (1976). A major monophyletic clade was recovered, including the species of the sect. *Globulares* and ser. *Haematocephali*, *Spinulosi* and *Atrorubentes* of the sect. *Sicci* (BS=88/BPP=1); and having as sister clade an assemblage composed of species of ser. *Leonini*, but unsupported. The others species of ser. *Atrorubentes* (named here as Atrorubentes p.p.) of sect. *Sicci* did not form a monophyletic group. The Spinulosi + Atrorubentes p.p. clade is a strongly supported group (BS=98/BPP=1) and appears as the sister to some specimens of *Marasmius* sect. *Globulares* (BS=98/BPP=0.99) and together are sister to *Marasmius siccus* (ser. *Haematocephali*) with strong support (BS=88/BPP=1). The newly described *M. chrysoblepharioides* (MF683956,

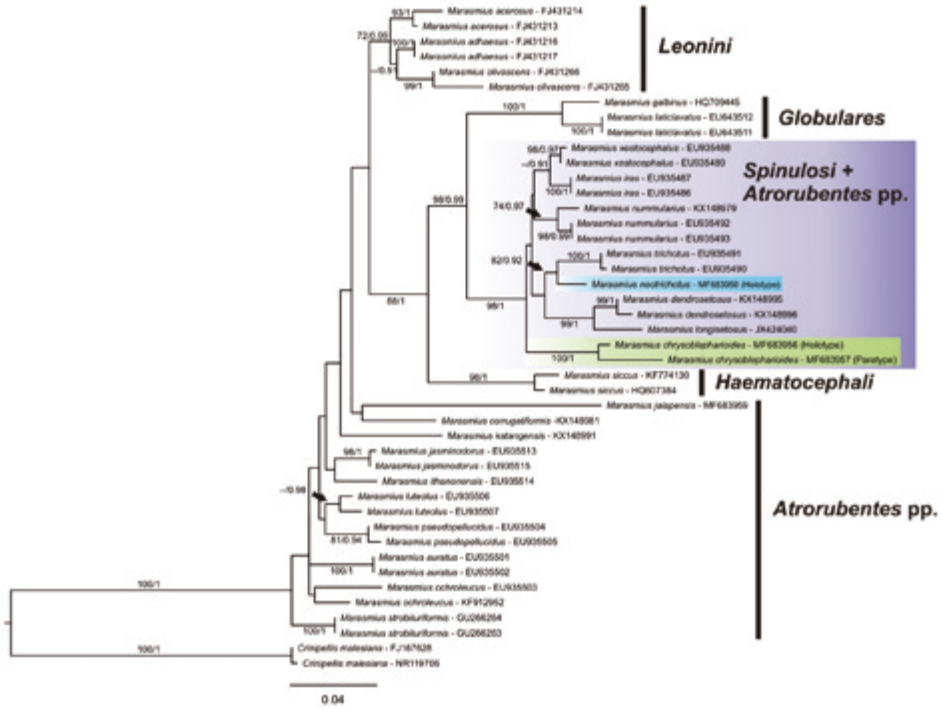


Fig 1. Maximum likelihood (ML) tree of *Marasmius* based on dataset of ITS sequences. Bayesian posterior probability above 0.9 and Bootstrap values above 70 % are shown. (T = Type).

MF683957) and *M. neotrichotus* (MF683958) are included within Spinulosi + Atrorubentes p.p. *Marasmius neotrichotus* (MF683958) was sister to *M. trichotus* E.J.H. Corner in a well-supported clade (BS=82/BPP=0.92). The two sequences of *M. chrysoblepharioides* formed a monophyletic group (BS=100/BPP=1), basal to the other members of the clade Spinulosi + Atrorubentes p.p. Although in the phylogenetic tree a longer branch length is observed for MF683957, we consider both sequences belong to the same species as they are 95% similar. This genetic distance is probably due to the non-optimal quality of the obtained sequence, which included 10 ambiguous sites. In this paper, we introduce two new species following the recommendation of Jeewon & Hyde (2016) for describing new taxon based on molecular data.

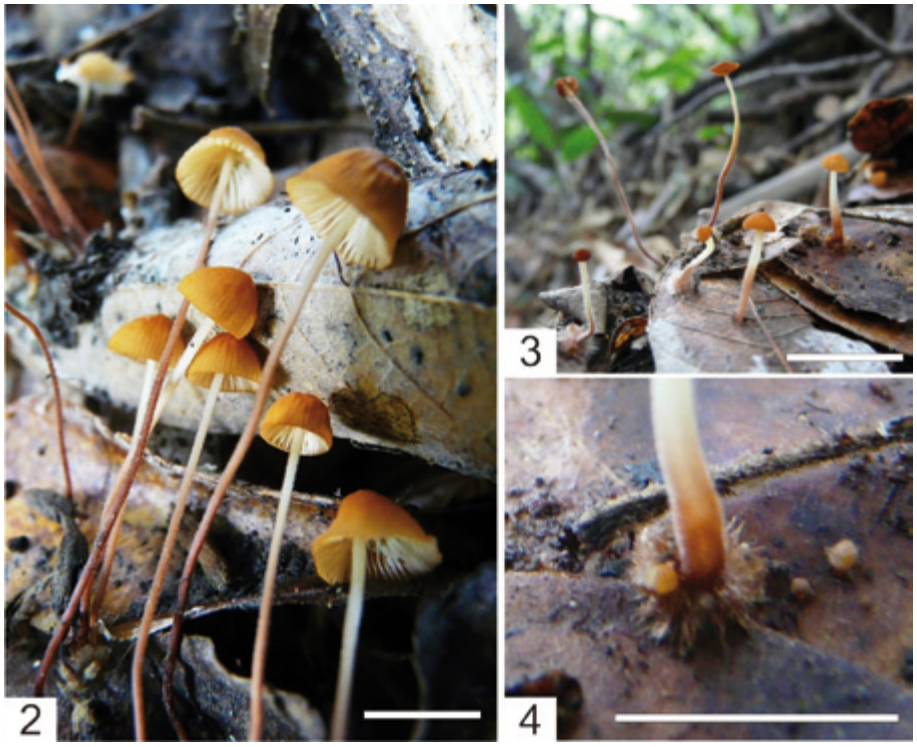
Taxonomy

Marasmius chrysoblepharioides Niveiro & Ramírez, **sp. nov.**, **Figs 2–13**

Mycobank: MB 823883

Genbank: MF683956 (ITS, holotype), MF683957 (ITS, paratype)

Holotype: ARGENTINA, Chaco, 1º de Mayo, floodplain forest, on the margin of the Parana river, 27°25´43.11´´S, 058°51´58.73´´W, 52 m a.s.l., on leaf litter, 07 January 2014, N. Niveiro SI 15-24 (CTES 0568164).



Figs 2–4. *M. chrysoblepharioides* general aspect. **2.** Mature basidiomata. **3.** Young basidiomata. **4.** Base of the stipe in a young basidiomata. Scale bar: 2 = 20 mm; 3–4 = 10 mm.

Diagnosis. Marasmius chrysoblepharioides is characterized by a sulcate-striate, yellowish orange pileus; entirely pilose, orange brown stipe; caulosetae 28.5–23.5 × 6–13.8 µm, with a tapering and thick-walled apex, and its bacilliform to fusiform basidiospores measuring 15–19 × 3.5–4.5 µm.

Etymology. The epithet refers to the similarity with *M. chrysoblepharis.*

Basidiomata reviviscent. *Pileus* up to 25 mm broad, convex-hemispheric to broadly paraboloid, golden yellow (5B7) to pale orange (5A3) or light orange (5A4) at the margin when fresh, orange (5A7) to golden yellow (5B7) at the centre (Figs 2–4), ferrugineous (7A7-7C7) when dried; surface dry, glabrous, margin sulcate (Figs 5–8). *Context* very thin, white (5A1) to cream (5A2), membranaceous. Odor and taste indistinct. *Lamellae* subdistant, L= 11–14, with three series of lamellulae,

Figs 5–8. *M. chrysoblepharioides* dehydrated type specimen. **5.** General aspect. **6.** Detail of the pileus surface. **7.** Detail of the stipe surface. **8.** Detail of the lamellae. Scale bar: 5 = 10 mm; 6–8 = 1 mm.

adnexed to adnate, cream (5A1-5A2); edge entire, concolorous with the side of the lamellae, or in some parts concolorous with the pileus surface; not intervenose (Figs 2, 8). *Stipe* 20–40 × 0.3–1 mm, central, terete, equal, hollow, cartilaginous, dark brown (7E7-7F8) to reddish brown (7C8-7B7), the apex orange-pallid (6B3-6B4); surface entirely hispid, dry, non-insititious; arising from an abundant greyish orange (6B5) to pale orange (6A3) basal mycelium (Figs 2–4, 7). *Spore print* whitish (6A1).

Basidiospores 15–19 × 3.5–4.5 µm, x = 17.2 × 4 µm, Q = 3.7–4.9, Q_x = 4.2, n = 50, N = 3; bacilliform, fusiform to subfusiform, thin-walled, smooth, hyaline, inamyloid (Fig 9). *Basidia* 22–27 × 6–7 µm, clavate, 4-spored, thin-walled (Fig 10). *Basidioles* 29–39 × 5–8 µm, fusiform with a mucronate apex, thin-walled, hyaline (Fig 11). *Pleurocystidia* absent. *Cheilocystidia* like the pileipellis broom cells, but with longer setulae; main body 19–29.5 × 4.7–7.5 µm, clavate, thin-walled, hyaline; apical setulae up to 7 µm long, conical to cylindrical with obtuse to subacute apex, hyaline to yellowish-hyaline or to golden yellow wall (Fig 12). *Hymenophoral trama* regular; hyphae 2.5–4.5 µm diam., hyaline, dextrinoid. *Pileipellis* hymeniform, composed of *Siccus*-type broom cells, 12.5–18.5 × 4.0–6.5 µm, cylindrical, clavate or irregular in outline, thin-walled, with setulae up to 4 µm long. *Pileocystidia* absent. *Stipitipellis* hyphae 3–6 µm diam., cylindrical, subparallel, smooth, yellowish, dextrinoid, thick-walled (up to 1 µm), non-gelatinous, with abundant caulosetae. *Caulosetae* 28.5–235 × 6–13.8 µm, simple, widened at base, with a tapering apex; with walls up to 2 µm thick, ochraceous, inamyloid (Fig 13). *Clamp connections* present in all tissues.

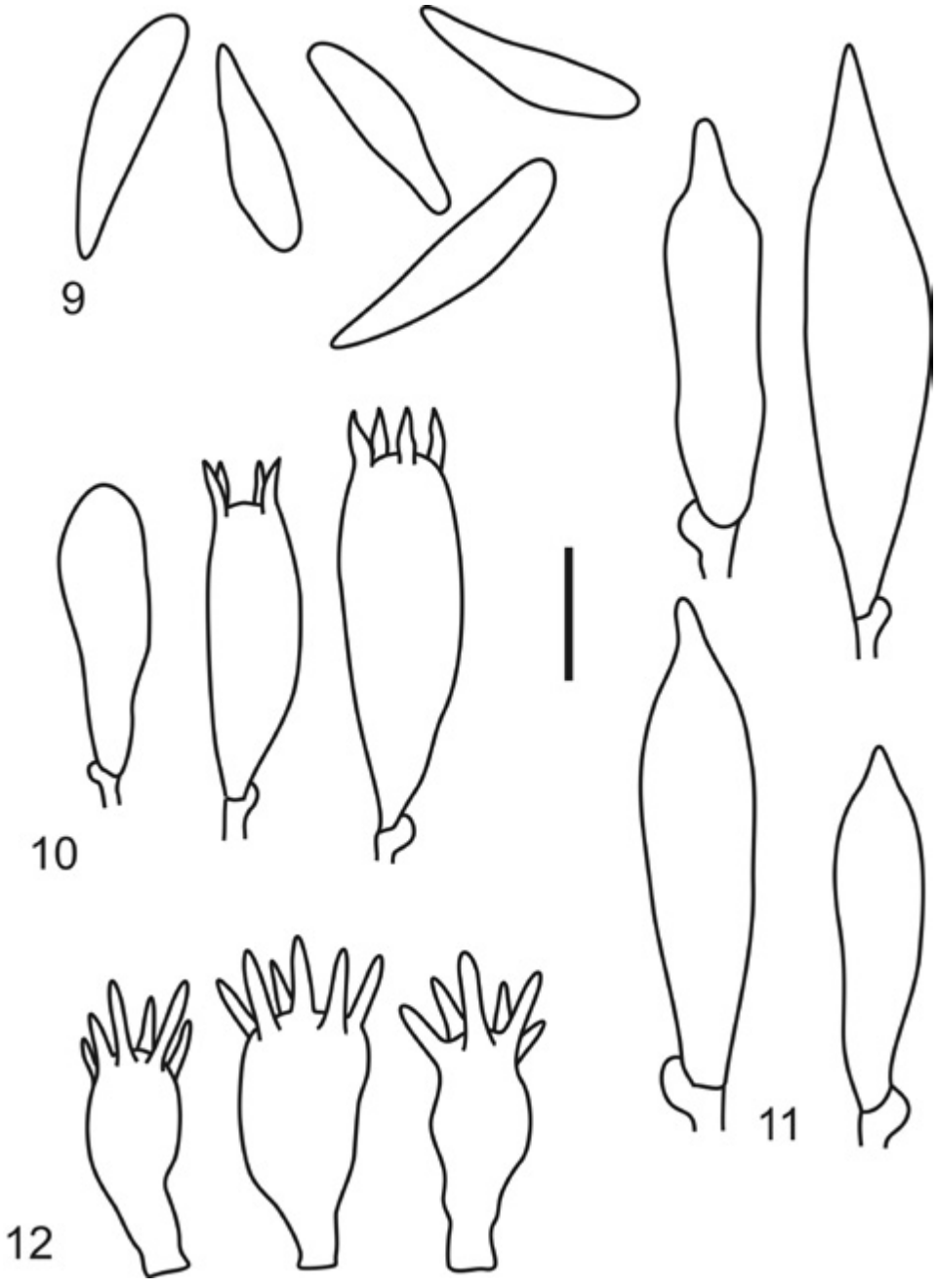
Habit and habitat: mycenoid, gregarious, on leaf-litter.

Specimens studied: ARGENTINA, Chaco, 1º de Mayo, in floodplain forest, on the margin of the Parana river, 27°25´43.11´´S, 058°51´58.73´´W, 52 m a.s.l., 11 November 2013, N. Ramírez & N. Niveiro SI 5-12 (CTES 0568166, paratype); *Ibid.,* 07 January 2014, N. Niveiro SI 15-25 (CTES 0568165).

Additional specimens and species examined: *Marasmius chrysoblepharis* Singer: MEXICO, Veracruz, Tlilapan, banks of Rio Aserradero, 24 June 1969, Singer M8201 (holotype, F). *Marasmius flammans* Berk.: BRAZIL, Panuré, on dead leaves, R. Spruce 97 [holotype, K(M) 200554].

Observations: Marasmius chrysoblepharioides is characterized by its yellowish orange pileus with a sulcate-striate margin, an orange brown, entirely pilose stipe, larger basidiospores and caulocystidia than those in closely allied species, and by lacking cystidia on both pileus surface (pileocystidia) and hymenophore (pleurocystidia). Macroscopically, *M. chrysoblepharis* Singer is the most similar species, however, it differs by smaller basidiospores (9.3–13 × 3.3–3.7 µm) and smaller caulocystidia (up to 120 µm long) (Singer, 1976). In our morphological analysis of *M. chrysoblepharis* type material [Singer M8201(F)!], we found bacilliform to fusiform basidiospores (9.4–10.7 × 3.2–4.0 µm) and setiform caulocystidia (34–95 × 4.5–5.0 µm), thick-walled (walls up to 1 µm thick) and with a rounded-obtuse apex or an acute papilla (Fig 14–17), which corroborates that both species have this distinctive character.

Other morphologically similar species that resemble *M. chrysoblepharioides* are *M. nummularius* Berk. & Broome and *M. nummularioides* Desjardin & Y.S. Tan. The former is widely distributed from southeastern Asia (Pegler, 1986; Desjardin *et al.*, 2000; Wannathes *et al.*, 2009a) and to Madagascar (Shay *et al.*, 2017). *Marasmius nummularius* differs in forming smaller basidiospores that do not exceed 15 µm in length (10–15 × 3–5.5 µm), shorter caulocystidia (20–150 × 6–36 µm) and a darker coloured pileus surface (dark reddish brown to dark brownish orange) (Desjardin *et al.*, 2000; Shay *et al.*, 2017). The second species, *M. nummularioides*, has a more



Figs 9–12. *M. chrysoblepharioides* microscopic characters. **9.** Basidiospores. **10.** Basidia. **11.** Basidioles. **12.** Cheilocystidia. Scale bar = 10 μm.

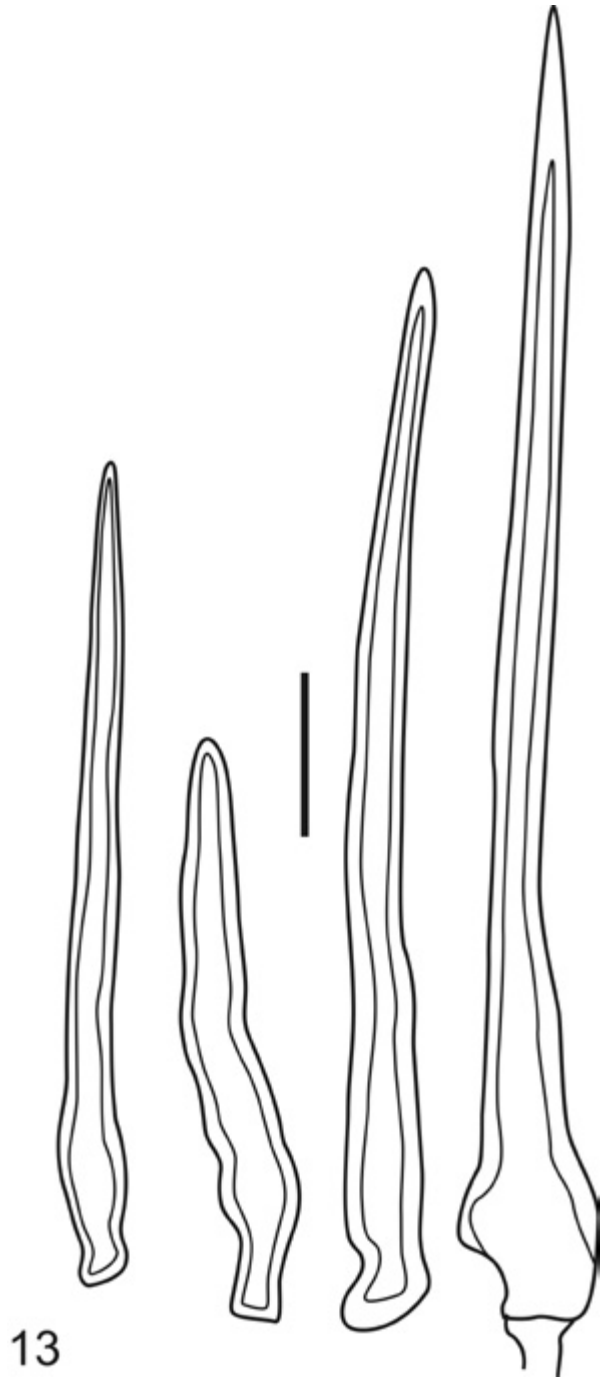
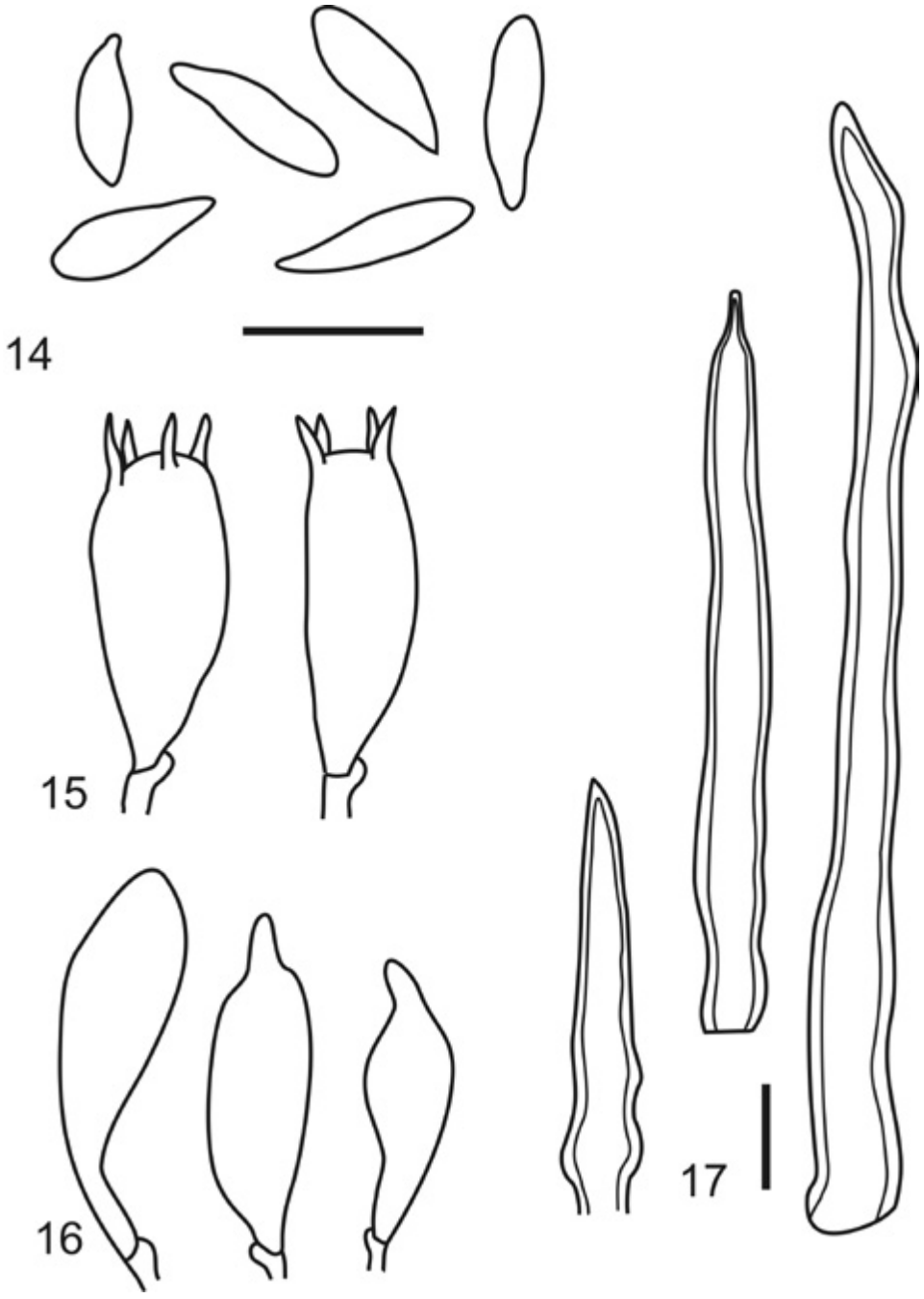


Fig 13. *M. chrysoblepharioides* microscopic characters. Caulocystidia. Scale bar = 20 μm.



Figs 14–17. *M. chrysoblepharis* microscopic characters. **14.** Basidiospores. **15.** Basidia. **16.** Basidioles. **17.** Caulocystidia. Scale bar = 10 μm.

restricted distribution to the Malaysian Peninsular, however, it is distinguished by its non-striate pileus margin, a reddish brown pileus surface, darker than in *M. chrysoblepharioides*, and *Siccus*-type caulocystidia together with setiform structures in the stipitipellis (Tan *et al.*, 2007, 2009).

Marasmius longisetosus J.S. Oliveira & Capelari, described from Brazil (Oliveira *et al.*, 2014) and *M. dendrosetosus* Shay & Desjardin, recently described from Madagascar (Shay *et al.*, 2017), are two phylogenetically closely related species. The former clearly differs in having a smaller, reduced and curved stipe, elongated pileosetae in the pileipellis, the stipitipellis bearing caulocystidia of the *Siccus*-type broom cells without setiform caulocystidia, and smaller basidiospores (up to 12 µm long., Oliveira *et al.*, 2014). *Marasmius dendrosetosus,* has a cream to orangish-white pileus surface, antler-like pileosetae and caulocystidia of the *Siccus*-type (Shay *et al.*, 2017).

There are other, less known South American species of *Marasmius* that resemble *M. chrysoblepharioides* that deserve to be mentioned for some morphological and ecological similarites. *Marasmius flammans* was described from Brazil, and is known only from the type specimen. It is similar to *M. chrysoblepharioides* by its basidiomata size and colouration. However in a redescription of this species, Dennis (1951) and Singer (1958, 1976) showed that *M. flammans* [R. Spruce 97 - K(M) 200554!] has a glabrous stipe, numerous setiform hymenial cystidia, and well-developed pileosetae, which are not present in *M. chrysoblepharioides*. More recently, Singer (1989) described several *Marasmius* species from the Brazilian Amazon, many of them in flooded river margins, a similar environment where *M. chrysoblepharioides* was found. Among them, two species belonging to sect. *Sicci* have a pilose or velutinous stipe surface: *M. asemiformis* Singer and *M. asemus* Singer. Both species differ from *M. chrysoblepharioides* in their shorter caulocystidia (10–50 × 3–9 µm in *M. asemiformis* and 20–30 × 3.5–6.5 µm in *M. asemus*) without thickened walls, characters that would include them to ser. *Atrorubentes*. Another distinctive character is that both species have smaller basidiospores: 7–11 × 2.5–3.7 µm in *M. asemiformis*, and 9–11.5 × 3.5–4.5 µm in *M. asemus* (Singer, 1989).

Other related species without pileosetae and pleurocystidia, *M. opulentus* Har. Takah. described from Japan, has a deep orange to orange pileus, smaller basidiospores, 8–10 × 3.5–4 µm, and two types of caulocystidia, (1) irregularly cylindrical to fusoid, thick-walled cells, and (2) *Siccus*-type cells with long setulae (Takahashi, 2000). *Marasmius atrocastaneus* G. Stev., known from New Zealand, has a deep brown, chestnut brown, orangish brown or reddish brown pileus, smaller basidiospores [(9–)10–12 × 4.5–5.5 µm], and smaller caulosetae, 30–80 × 4–8 µm (Desjardin & Horak, 1997).

Marasmius neotrichotus Niveiro, Ramírez & Antonín, **sp. nov.**, **Figs 18–33**

Mycobank: MB 823884

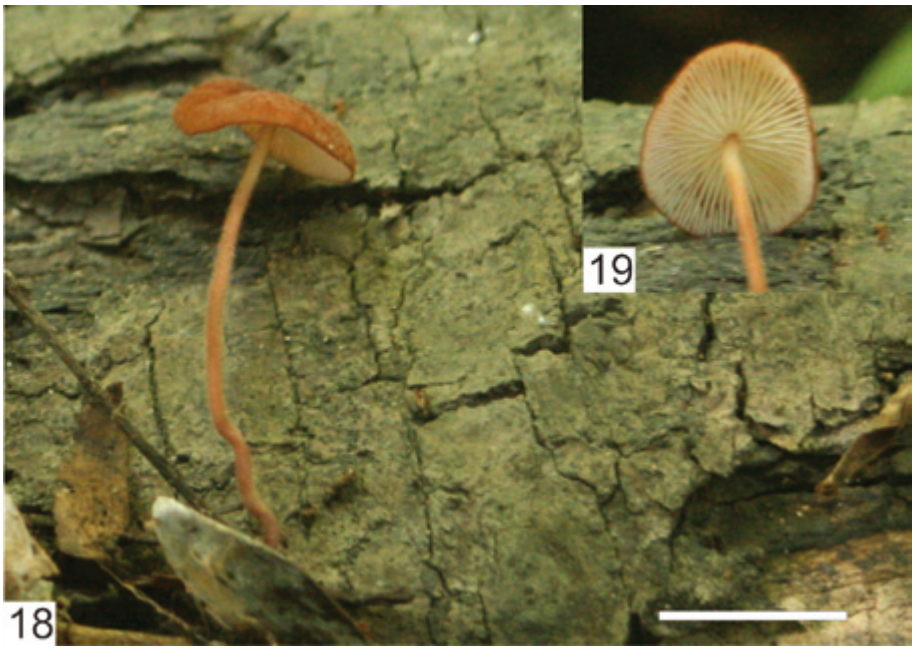
Genbank: MF683958 (ITS, holotype)

Holotype: ARGENTINA, Chaco, 1º de Mayo, in floodplain forest, on the margin of the Parana river, 27°25´43.11´´S, 058°51´58.73´´W, 52 m a.s.l., 25 November 2013, N. Ramírez & N. Niveiro SI 7-13 (CTES 0568167).

Diagnosis. Marasmius neotrichotus differs from *M. trichotus* by having longer caulosetae and from *M. ciliatus* by its larger spores.

Etymology. The epithet refers to the similarity with *M. trichotus* and its Neotropical distribution.

Basidiomata reviviscent. *Pileus* up to 20 mm broad, convex to plano-convex, with a shallow central depression, brownish orange (6C6–6C8) with darker



Figs 18–19. *M. neotrichotus* general aspect. Scale bar = 20 mm.

centre with blackish stains, light brown (6D6–6D7), reddish brown to dark brown (8E6–8F6) when dried; surface dry, velutinous to velvety, margin smooth to slightly striate when fresh (Figs 18, 21). *Context* thin, whitish (4A1–4B1), membranaceous. Odor and taste indistinct. *Lamellae* close, L = 20–24, with three series of lamellulae, adnexed to free, white (4A1) to cream (4A2); edge entire, concolorous with the lamellae sides; not intervenose (Fig 22). *Stipe* 18–40 × 0.5–1.2 mm, central, terete, straight, equal, hollow, cartilaginous, brownish orange (6C5–6C7) to reddish brown (7A4–7A5), pallid toward the apex, light orange (6A4) to pale orange (6A3); surface densely hispid, dry; arising from a basal mycelium, whitish (4A2) to cream (4C3) (Figs 20, 23). *Spore print* whitish (4A1–4A2).

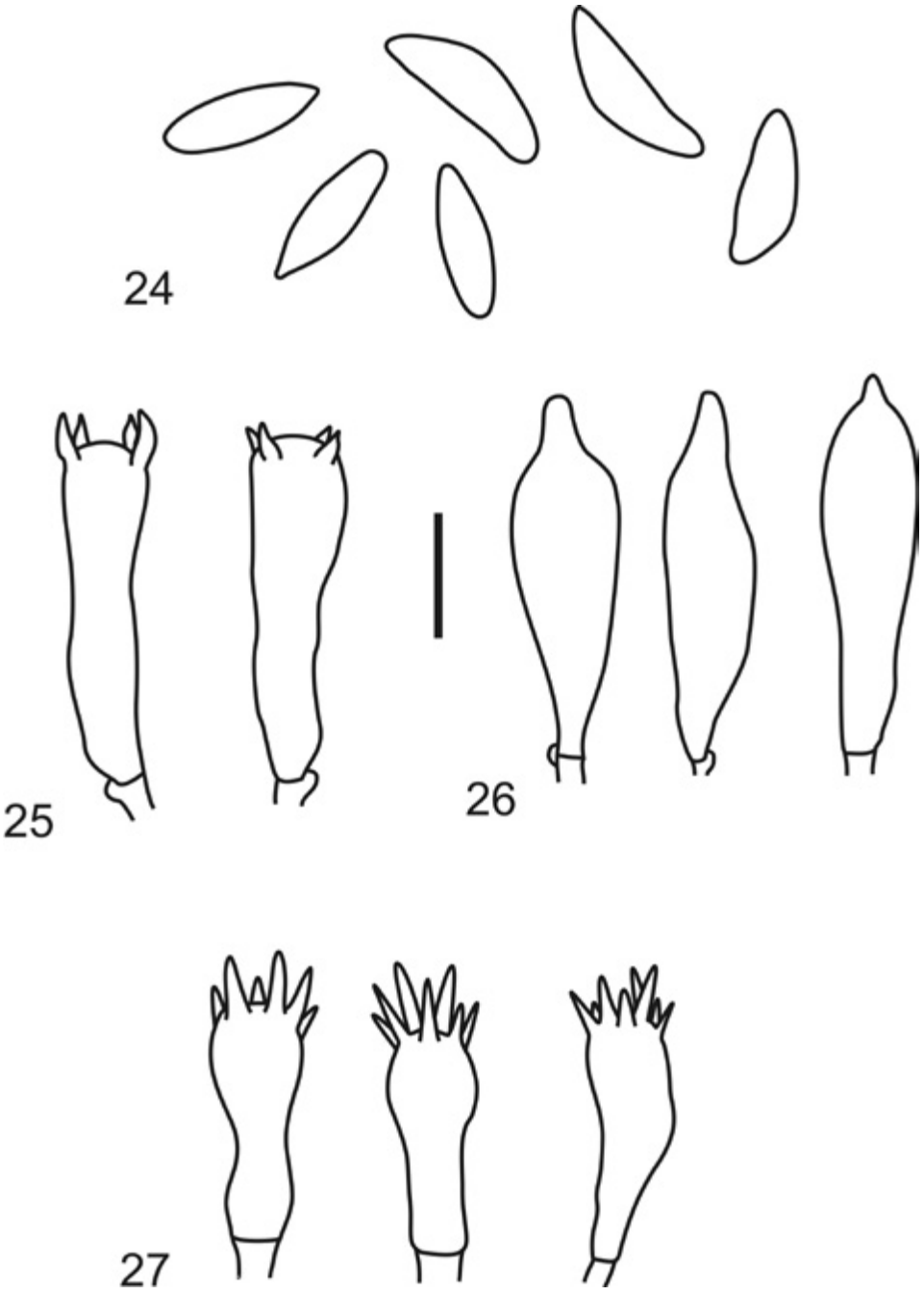
Basidiospores 9–15 × 3.5–5 µm, x = 12.2 × 4.2 µm, Q = 2–3.2, Q_x = 2.8, n = 40, N = 2; cylindrical, fusiform to bacilliform, thin-walled, smooth, hyaline, inamyloid (Fig 24). *Basidia* 20–24 × 6–8 µm, clavate, 4-spored, thin-walled (Fig 25). *Basidioles* 22–28 × 6–7.5 µm, fusiform with a mucronate apex, thin-walled, hyaline (Fig 26). *Pleurocystidia* absent. *Cheilocystidia* abundant, composed of *Siccus*-type broom cells; main body 19–24 × 4.5–6.5 µm, clavate, thin-walled, hyaline; apical setulae up to 5 µm long, conical to cylindrical with obtuse to subacute apex, hyaline to yellowish-hyaline or to golden yellow wall (Fig 27). *Hymenophoral trama* regular, consisting of hyaline hyphae, 1.5–5 µm diam, dextrinoid. *Pileipellis* hymeniform, composed of *Siccus*-type broom cells, 18–22.5 × 6.5–7.5 µm, cylindrical, clavate or irregular in outline, thin- to slightly thick-walled, with spines up to 4 µm long. *Pileosetae* 80–370 × 5–9 µm, needle-shaped, thick-walled, walls 1.5–3 µm wide, brown, abundant, scattered among pileipellis cells (Fig 28–29). *Stipitipellis* hyphae 3–5 µm diam., cylindrical, subparallel, smooth, yellowish to brownish, inamyloid, thick-walled (up to 1 µm), non-gelatinous, with abundant

Figs 20–23. *M. neotrichotus* dehydrated type specimen. **20.** General aspect. **21.** Detail of the pileus surface. **22.** Detail of the lamellae. **23.** Detail of the stipe surface. Scale bar: 20 = 10 mm, 21–23 = 1 mm.

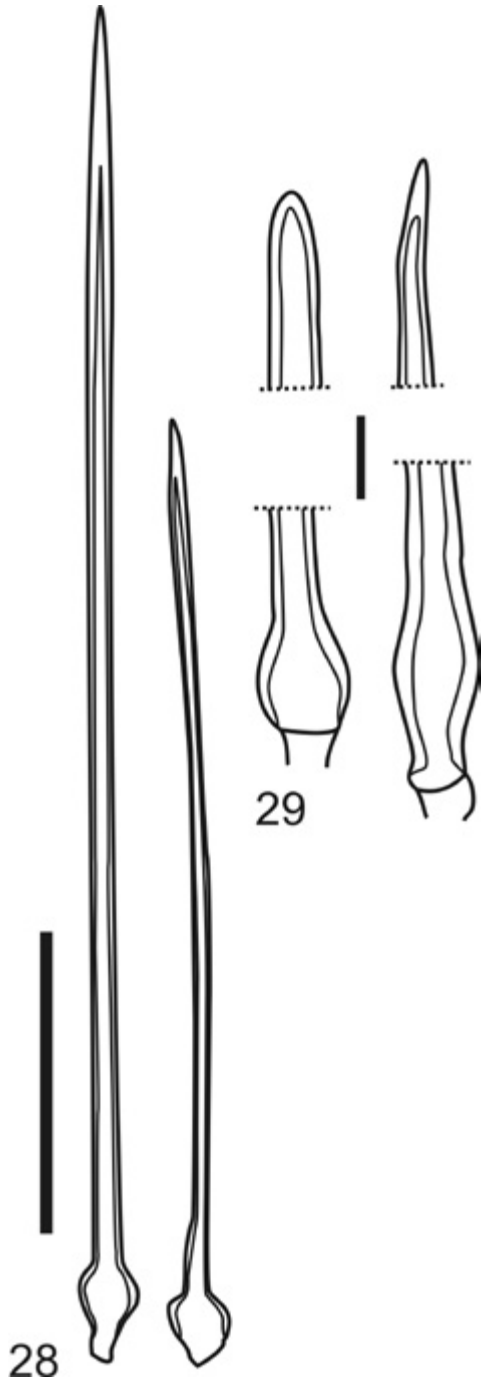
caulocystidia. *Caulocystidia* of two types, a) caulosetae, 40–480 × 5–15 µm, with a tapering apex, thick-walled, walls 0.8–2 µm wide, brown, very abundant, some with few spine-like branches (Figs 30–32); and b) transitional irregular elements between *Siccus*-type broom cells and setae, thin-walled, some formed by a main body 8–13 × 4–9 µm in size, with 3 to 6 apical setulae, up to 40 µm long similar to *Siccus*-type broom cells, others formed by an unique small erect setae, up to 70 × 10 µm, with 3 to 5 branches like as lateral spines, the spines up to 40 µm long, scarce and rare (Fig 33). *Clamp connections* present.

Habit and habitat: collybioid, gregarious, on fallen leaves.

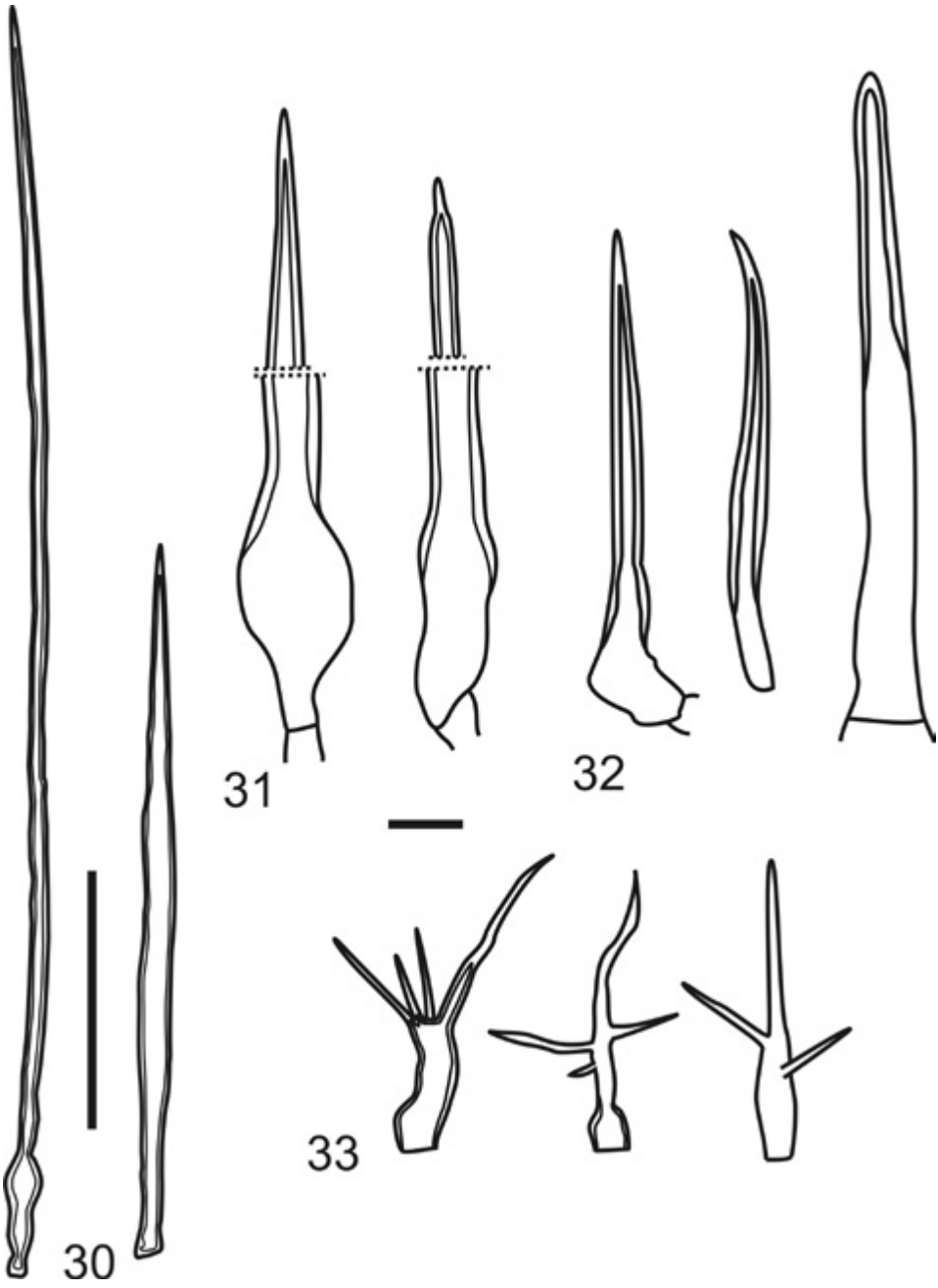
Specimens studied: ARGENTINA, Chaco, 1º de Mayo, in floodplain forest, on the margin of the Parana river, 27°25´43.11´´S, 058°51´58.73´´ W, 52 m a.s.l., 25 November 2013, N. Ramírez & N. Niveiro SI 7-14 (CTES 0568183), 24 March 2014, N. Ramírez & N. Niveiro SI 22-5 (CTES 0568184).



Figs 24–27. *M. neotrichotus* microscopic characters. **24.** Basidiospores. **25.** Basidia. **26.** Basidioles. **27.** Cheilocystidia. Scale bar = 10 μm.



Figs 28–29. *M. neotrichotus* microscopic characters. **28.** General aspect of the pileocystidia. **29.** Detail of the base and apex of the pileocystidia. Scale bar: 28 = 100 μm, 29 = 10 μm.



Figs 30–33. *M. neotrichotus* microscopic characters. **30.** General aspect of the setiform caulocystidia. **31.** Detail of the base and apex of the setiform caulocystidia. **32.** Short setiform caulocystidia. **33.** Transitional caulocystidia. Scale bar: 30 = 100 µm; 31–33 = 10 µm.

Additional specimens and species examined: *Marasmius ciliatus* Pegler: MARTINIQUE, Vallee inferior de la Rivere Lorrain, on dead rotting leaves of *Swietenia sp*., 30 September 1977, D.N. Pegler 2906 [holotype, K(M) 200556]. Precheur, anse couleuvre superieur, 23 September 1977, D.N. Pegler 2840 [K(M) 200555]. – *Marasmius spiculosus* Singer: BOLIVIA, La Paz, Nor Yungas, Rio Yariza, 1450 m a.s.l., on rotting wood, 16 February 1956, R. Singer B1206 (holotype, LIL). – *Marasmius trichotus* E.J.H. Corner: SINGAPORE, Gardens Jungle, 18 March 1943, E.J.H. Corner s/n (holotype, E, liquid collection, as "Crinipellis 5").

Observations: Marasmius neotrichotus is characterized by its long pileosetae and caulosetae, the presence of irregular elements transitional between the *Siccus*-type broom cells and setae as the second type of caulocystidia, the non-striated pileus margin and close white lamellae. These characters make it very similar to *M. trichotus*, described form southeastern Asia and *M. ciliatus*, described from the Lesser Antilles. All together constitutes a species complex that shares small basidiomata, covered by extraordinarily long setiform cystidia (hairs). In the original description, Corner (1996) described *M. trichotus* with a pileus "4–6 mm wide, fawn brown, wholly pilose with short erect ochraceous hairs" and a "wholly puberulous scurfy" stipe. Microscopically, he described the pileipellis with numerous hairs up to 300 µm long, with a ventricose base with thickened pale brown walls, and tapering in an acute apex. However, he did not describe the hairs of stipe surface. In the holotype [Corner s/n, E!], we observed 80–210 µm long setiform cystidia on the pileus surface and caulocystidia in the form of modified broom cells, composed of a basal body, with 2-6 setiform projections of 45–70 µm long, thick-walled (Figs 34–38), differing clearly from those observed in *M. neotrichotus*. Wannathes *et al.* (2009a) described abundant fusoid to lanceolate setiform cystidia on the pileus (60–300 µm long) and stipe surface (22–213 µm long) for *M. trichotus* from Thailand, explaining also that those populations differ from those in Singapore (type locality) in the slightly paler and larger pileus, characters that resemble the species here described.

Marasmius ciliatus differs in its smaller basidiomata, pileus not exceeding 10 mm diam., and the shorter basidiospores, 7.5–10.5 × 4–5 µm in size. The type specimen [Pegler 2906 - K(M) 200556!] consists of one complete basidioma and three stipes without any remnants of pileus. Due to the scarcity of material, only a small portion of stipe and lamellae was analysed. We observed numerous fusiform basidioles, 19–24 × 6–8 µm, with mucronate, occasionally rostrate apex, and cheilocystidia in the form of the *Siccus*-type broom cells with main body 15–19 × 5–7 µm in size, and setulae up to 6 µm long and 1 µm diam., thin-walled and hyaline. On the stipe surface, we observed very long setiform hairs, up to 500 µm long and 7–13 µm diam. in the base, with thickened brown walls, up to 2 µm wide, with acute apex and broadened base, coinciding with the description of Pegler (1983). Unfortunately, mature basidia and basidiospores were not observed.

Marasmius neotrichotus has many similarities with other tropical and subtropical South American species: *M. spiculosus*, *M. echinatulus* Singer and *M. araucariae* Singer. *Marasmius spiculosus* (R. Singer B1206 - LIL!). differs in its subcrowded lamellae, gloeocystidioid pleurocystidia and also by the *Siccus*-type broom cells on the stipe surface (Singer, 1976; Pegler, 1983). *Marasmius echinatulus*, known from Brazil, Colombia and Argentina, differs in having shorter basidiospores (6.5–9.7 × 2.3–4.5 µm) and metuloid cheilocystidia (more numerous in mature individuals) intermixed with the *Siccus*-type broom cells (Singer, 1976). *Marasmius araucariae* is a species described from a adjacent region where these two new species were found. However *M. araucariae* differs in the thin-walled caulocystidia,

Figs 34–38. *M. trichotus* microscopic characters. **34.** Basidiospores. **35.** Basidioles. **36.** Cheilocystidia. **37.** Pileosetae. **38.** Caulosetae. Scale bar = 10 μm.

with a rounded apex and shorter than those observed in *M. neotrichotus* (e.g. 50 × 5.5 µm), which leads to be included to stirp *Cladophyllus*, together with *M. cladophyllus* Berk., as an intermediate species between series *Leonini* Singer and *Actinopodes* by Singer (1976).

Marasmius nummularius and *Marasmius coklatus* Desjardin, Retn. & E. Horak are other two species of sect. *Spinulosi* from southern Asia similar to *M. neotrichotus*. However, both have a different stipitipellis, consisting of the *Siccus*-type cells intermixed with setiform caulocystidia, not exceeding 110 µm long (Wannathes *et al.*, 2009a); Shay *et al.* (2017) described only shorter setiform caulocystidia (28–109 × 7.2–36 µm) in the material from Madagascar. In addition, *M. coklatus* has a larger pileus (up to 60 mm diam.) and well-developed hymenial setae (Desjardin *et al.*, 2000). *Marasmius jalapensis* Murrill, described from Mexico, differs in having a paler, cream to pale cinnamon brown pileus, crowded lamellae, smaller basidiospores [(6.9–)7.7–10(–10.5) × (3.0–)3.5–4.7(–5.2) µm], well-developed hymenial seate, shorter pileosetae (35–112 × 9.2–15 µm) and caulosetae (20–110 × (5.0–)11–13 µm; Antonín, 2007).

Marasmius cohaerens (Pers.) Cooke & Quél. distributed in northern hemisphere, macroscopically resembles *M. neotrichotus*, however, it clearly differs by its yellowish lamellae, glabrous stipe, and smaller basidiospores (Noordeloos, 1995).

DISCUSSION

The phylogenetic analyses based on molecular data from ITS sequences from the holotype of the two new species here proposed, *M. chrysoblepharioides* and *M. neotrichotus*, confirmed that they are clearly different from other *Marasmius* species for which ITS data are available. Unfortunately, there are no available sequences for *M. chrysoblepharis* and *M. nummularioides*, the most phenotypically similar species to *M. chrysoblepharioides,* nor for *M. ciliatus*, the other similar species that together with *M. trichotus* and *M. neotrichotus* would constitute a species complex. However, for these species morphological data allowed to establish that they are different taxa. Both new species belong to the traditional sect. *Sicci* of Singer (1976), or the current concept of the sect. *Globulares* (Antonín & Noordeloos, 2010), which include the artificial traditional sect. *Sicci* and *Globulares* sensu Singer. Shay *et al.* (2017) noted already that small groups of species within each infrageneric group of the sect. *Sicci* (*Haematocephali, Leonini, Spinulosi* and *Atrorubentes*) form clades but with limited support. We observed this in our analyses, especially in the ser. *Spinulosi* and *Atrorubentes*, which are the best represented series in this study (Fig 1). The two new species are related to other species of the ser. *Spinulosi* forming a monophyletic group with low support, in which two species of the ser. *Atrorubentes* (*M. xestocephalus* and *M. iras*) are included. *Marasmius chrysoblepharioides* is phylogenetically related to the remaining species into clade Spinulosi + Atrorubentes p.p. (Fig 1).

Our phylogenetic analyses detected a genetic distance between the sequences of the holotype and paratype of *M. chrysoblepharioides*. As both sequences are almost identical, this distance could probably be a result of the non-optimal quality of the sequence MF683957. In addition, both specimens are morphologically identical, clearly belonging to the same species.

Marasmius neotrichotus is phylogenetically closely related to *M. trichotus*, the most phenotypically similar species (Fig 1).

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