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Spider Fungi: New species of *Marasmius* and *Pusillomyces* in the aerial rhizomorph web-maker guild in Amazonia

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Abstract: Rhizomorphs are hair- or wire-like melanized structures with structural differentiation analogous to plant roots that help fungi spread over an area and find food resources. Some species of multiple groups of the *Ascomycota* and the *Basidiomycota* produce different types of rhizomorphs. In the *Agaricales*, the structures are largely found in *Marasmiineae*, particularly in the *Omphalotaceae*, *Marasmiaceae*, and *Physalacriaceae*. Many rhizomorph-forming species spread over the forest floor (ground level), while others form aerial litter-trapping rhizomorph systems that hang on living branches of the forest understorey. Here, we describe three new species that form aerial systems, two in *Marasmius* and one in *Pusillomyces*, all of which inhabit areas of the Amazon rainforest in Amazonas State, Brazil. Support for these new species is based on evidence derived from morphological and molecular phylogenetic analyses using nuclear ribosomal internal transcribed spacer region (nrITS) and nuclear ribosomal large subunit (nrLSU) markers. *Marasmius foliaiceps* sp. nov., with a pileipellis made up of *Rotalis*-type broom cells, is different from all other species described to date and branched along with species of the monophyletic *Marasmius* sect. *Marasmius* subsect. *Marasmius*, being conspecific with specimens from Guyana. Also different from all other described *Marasmius* species, *Marasmius arachnotropus* sp. nov. has a pileipellis mostly composed of *Siccus*-type but in transition to *Rotalis*-type broom cells and branched along with species of the *Marasmius crinis-equi* species complex. *Pusillomyces cuieirasensis* is morphologically very similar to *Pusillomyces manuripioides* to which it is sister, but it has a non-umbonate pileus and smaller basidiospores. They all form aerial litter-trapping rhizomorph systems that mimic spider webs, particularly those hanging on the understorey. Whether made of mycelia or silk, such webs serve to capture food. The aerial rhizomorph-forming ‘spider fungi’ make up a guild with hidden species diversity in tropical systems.

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INTRODUCTION

According to the concept established in Rayner *et al.* (1985), recently discussed in a review by Yaffeto (2018) and accepted in this study, rhizomorphs are black (or dark brown), wire- or hair-like macrostructures produced by some macrofungi that show remarkable tissue differentiation. These structures have apically dominant and organized growing tips and seem to function in a manner analogous to plant roots (Rayner *et al.* 1985, Yaffeto 2018). Rhizomorphs are resistant to tensile stress and have a

waterproof surface and melanized rind that shields the inner trama layer, cortex, and medulla. The medulla may be solid or hollow, rendering cavities that function as conductive pipes for water and dissolved nutrients (Freymann 2008, Yaffeto 2018). Singer (1986) rather recognized two types of true rhizomorphs in the *Agaricales sensu lato*: 1) the black type and 2) the white type. The black rhizomorph matches the concept established by Rayner *et al.* (1985) and further developed by Yaffeto (2018).

The white rhizomorphs of Singer are, however, mycelial cords or strands which are tender, whitish, and have simple hyphal trama that form macroscopic filaments without sophisticated tissue differentiation and with diffuse mycelia aggregates at the tips (Rayner et al. 1985, Yaffeto 2018).

Many rhizomorph-forming fungi occur in the litter on the forest floor (ground species), while other species make aerial rhizomorph networks (epiphytic species). Hedger (1990) and Hedger et al. (1993) described these as litter-trapping fungi in moist tropical forests. They produce suspended nets of rhizomorphs entangled in and between living plant branches and capture falling leaves, sticks, and twigs from the canopy as food. Lodge & Cantrell (1995) cited these networks as important components of the fungal decomposer communities in wet tropical forests. These communities are found at different heights in the canopy down to the forest floor. Based on Snaddon et al. (2012), the litter-trapping rhizomorph zone may reach up to 20 m in height in a lowland mixed dipterocarp forest in Danum Valley Conservation Area, Sabah, Malaysia. Their results also suggested that the abundance and richness of arthropod (including *Araneae*) communities are proportionally related to and dependent on such litter-trapping rhizomorph systems, which provide both habitats and food resources.

Some aerial rhizomorph-forming fungal species may also affect living plant tissues. *Marasmius crinis-equi*, with its profuse rhizomorphs, may cause defoliation of healthy branches by “strangulation”, with the dead leaves ultimately being decomposed by the rhizomorphs. Su et al. (2011) demonstrated that *M. crinis-equi* rhizomorphs induce defoliation of tea twigs by releasing volatile substances. They identified three volatile constituents from the rhizomorphs: 3-oxo- β -ionol; 2,4,6-tri-*tert*-butyl-4-methyl-cyclohexadien-2,5-one; and 2-phenyl-3,4,5,6-tetramethylpyridine. Therefore, defoliation may occur as a result of chemical as well as mechanical mechanisms. *Pusillomyces manuripioides* was found to cause necrosis on living leaves at the line of the attachment of its rhizomorphs (Oliveira et al. 2019).

In forest communities, animals utilize rhizomorphs such as some species of birds that use them along with plant debris to build nests (Sick 1957, Foster 1976, Singer 1986, McFurland & Rimmer 1996, Elliott et al. 2019, Koch et al. 2020, Rana et al. 2021, Bach et al. 2022). In Koch et al. (2020), of 25 unique fungi species whose rhizomorphs were used to build nests (50 in Cameroon, 22 in Guyana, one in Ecuador, and one in Costa Rica), 17 were *Marasmius*, three were *Crinipellis*, and five were possibly *Collybiopsis*. In addition, 40 nests contained rhizomorphs of a single species, while 13 contained those of two species and one nest contained three species. Of the 17 *Marasmius* species, only one grouped among species of sect. *Globulares*, *Marasmius nidus-avis*, while the other 16 were related to species of sect. *Marasmius*. Of the full 25 rhizomorph-forming species documented, seven formed aerial litter-trapping systems hanging above the ground. Two new species were described, *Marasmius nidus-avis* and *M. neocrinis-equi*. Other species was reported as *Marasmius chrysocephalus*, other was referred as *M. aff. leveilleanus* and other as a close species of *M. neosessiliformis* nom. prov. However, 11 possible new *Marasmius* species remained to be named (*Marasmius* sp. 1–11). Su et al. (2011), Koch et al. (2020) and Bach et al. (2022) suggested that the rhizomorphs of these fungi may also confer protection against pathogenic bacteria by secreting antibiotic compounds into birds’ nests. Moreover, rhizomorphs identified

as *Marasmius brevipes* (syn. *Gymnopus neobrevipes*) were also found to be used for nest construction by flying squirrels (*Glaucomys volans*) (Prange & Nelson 2006).

Rhizomorphs evolved multiple times in the *Ascomycota* and the *Basidiomycota*, in several unrelated macrofungal groups (Webster & Weber 2000, 2007). Within the suborder *Marasmiineae*, this structure is shared by some genera in the *Marasmiaceae* (i.e., *Marasmius* and *Crinipellis*), *Omphalotaceae* (i.e., *Collybiopsis*, *Gymnopus*, *Paramycetinis*, *Pseudomarasmius*, and *Pusillomyces*) and *Physalacriaceae* (i.e., *Armillaria*, *Cryptomarasmius*, and *Gloiocephala*) (Singer 1976, 1986, 1989, McFurland & Rimmer 1996, Yaffeto et al. 2009, Yaffeto 2018, César et al. 2018, Koch et al. 2020).

Marasmius is a very diverse genus in terms of both the number of species (~700 species; Bhunjun et al. 2022) and morphological structures, and is a major driver of litter decomposition in forests worldwide (Singer 1986, Desjardin 1989, Antonín & Noordeloos 2010). The species are currently organized into a few accepted sections in *Marasmius sensu stricto*, with most of the species belonging to sects. *Marasmius* and *Globulares* (Tan et al. 2009, Wannathes et al. 2009, Antonín & Noordeloos 2010, Antonín et al. 2012, 2014a, Shay et al. 2017, Grace et al. 2019, Oliveira et al. 2020a, b, 2022). *Marasmius* sect. *Marasmius* includes most rhizomorph-forming species within the genus, nearly all of which produce small and thin marasmioid basidiomata (Singer 1976, 1986, Koch et al. 2020, Oliveira et al. 2020a). The best-known species is *M. crinis-equi*, which is also the most common causal agent of horse hair blight (HHB) (Seaver 1944, Singer 1986, Skaria et al. 2000, Dassanayake et al. 2009, Amoako-Attah et al. 2020). *Marasmius yanomami* is a good example of the rhizomorph-forming fungi described in detail in the literature (Yanomami et al. 2019). Like other *Marasmius* species, the rhizomorphs of *M. yanomami* are mostly hollow but include bundles of hyphae that are loosely arranged as an aerated tissue. The surface of the cavity is composed of thin-walled, hyaline hyphae that gradually become pigmented, changing from orange brown in the cortex to highly melanized (dark-brown or blackish) in the outer layer; they have a rind of parallel, tightly compact, very thick-walled hyphae (Yanomami et al. 2019). The growing tip is specialized as this is more tender and whitish reflecting to be active to grow, with a hard, root-like cap at the summit. Rhizomorphs of some *Marasmius* species are used in human handicrafts. Yanomami women use those of *M. yanomami*, which they call “përisti” to ornament their baskets made of liana plant fibre. Singer (1986) described the probable use of rhizomorphs of *M. crinis-equi* by the peoples of East India, Indonesia, and the Republic of Congo in making jewellery.

Pusillomyces was recently established to include a few species of *Gymnopus* sect. *Androsacei* that form a distinct unrelated clade along with one “manuripioid” (similar to *Manuripia*) species within the *Omphalotaceae* (Oliveira et al. 2019). *Pusillomyces manuripioides*, the type species, is a rhizomorph-forming fungus that weaves litter-trap web-like systems that hang on branches of the understorey. They facilitate the decomposition of fallen leaves and/or twigs from the canopy that get caught in them. Three other species from the genus (*Pusillomyces asetosus*, *Pusillomyces funalis*, and *Pusillomyces spinulosus*) are only saprotrophic on dead leaves and twigs on the forest floor (Antonín et al. 2014b, Oliveira et al. 2019, César et al. 2020). These three species produce thin, small, marasmioid basidiomata that grow directly from the substrate; they do not form aerial litter-trapping systems.



Fig. 1. *Marasmius arachnotropus* aerial rhizomorph network (JO1150, RBC). **A, B.** Trapped dried leaves being decomposed by the rhizomorphs. **C.** Rhizomorph loop bearing basidiomata. **D.** Rhizomorph network hanging on a living branch of a plant of the understorey. **E, F.** HHB symptoms in a host plant.



Fig. 2. Macroscopy of *Marasmius arachnotropus*: **A.** General view of rhizomorphs attached to sticks and twigs (JO1150, RBC). **B, C.** Basidiomata rising from the rhizomorphs (JO1150, RBC). **D.** View of the lamellar hymenophore (JO1150, RBC). **E.** Lateral view of some basidiomata (JO1150, RBC). **F.** Close-up of the pileus of two basidiomata (JO1155, RBC). **G.** Basidiomata and rhizomorphs (JO1374, PNJ). Scale bars = 10 mm.

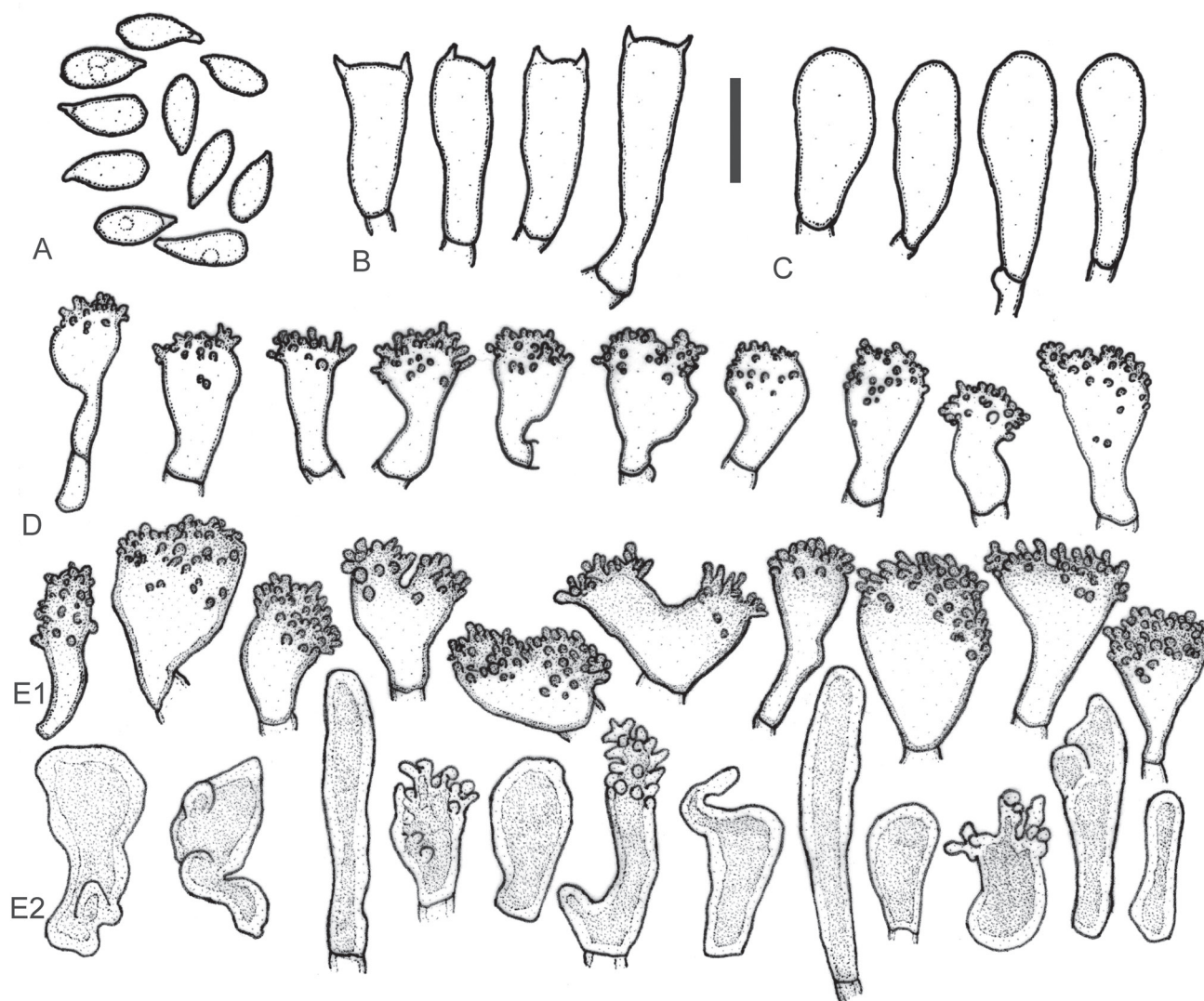


Fig. 3. Microscopy of *Marasmius arachnotropus* (JO1150, RBC). **A.** Basidiospores. **B.** Basidia. **C.** Basidioles. **D.** Cheilocystidia. **E1.** Thin-walled *Siccus-Rotalis*-type broom cells of the pileipellis. **E2.** Thick-walled elements of the pileipellis. Scale bar = 10 µm.

In this study, three rhizomorph-forming species that produce aerial litter-trapping systems in some areas of the Amazon rainforest are described as new to science based on morphological characters and genetic data included in phylogenetic analyses using nuclear ribosomal internal transcribed spacer region (nrITS) and nuclear ribosomal large subunit (nrLSU) markers. Two belong to *Marasmius* and one to *Pusillomyces*. We also discuss the modes of growth and nutrition, and argue why these and other species in this guild can be called “spider fungi”.

MATERIALS AND METHODS

Areas sampled

The *Reserva Biológica do Rio Cuieiras* (RBC) – Biological Reserve of the Cuieiras River (reference point: 2°32′11.05″S, 60°16′9.37″W) – covers 22 735 ha in the lower Negro River basin, and is located 60 km northwest of Manaus City, Amazonas State, Brazil (Marques Filho *et al.* 2005). The reserve includes a Large-Scale Biosphere-Atmosphere Experiment in Amazonia (LBA) research base. The regional vegetation is typically primary forest with trees reaching 30–40 m in height (Jardim & Hosokawa 1987). The RBC is a mosaic of terra-firme (upland) (Prance 1978), campinarana (white sand) (Adeney *et al.* 2016), and

igapó (seasonally flooded black water swamp) (Junk *et al.* 2011) forests. The climate is “Am” in the Köppen classification (Radam 1978), with a mean temperature of 26.7 °C and high rainfall, with monthly precipitation of ~150 mm on average during the rainy season (between October and June) and lower rainfall from July to September (< 99 mm/mo), typical of the Central Amazon (Marques Filho *et al.* 2005). The soils in the terra-firme are principally Alic Yellow Oxisols, acidic, and poor in nutrients (Ranzani 1980).

The *Parque Nacional do Jaú* (PNJ) – Jaú National Park (reference point: 2°15′12.53″S and 62°39′3.47″W) – is a Federal Conservation Unity covering 2 272 000 ha, also in the lower Negro River basin, encompassing the municipalities of Novo Airão and Barcelos, Amazonas State, Brazil. The PNJ encompasses both Jaú and Unini river basins and tributaries of the right margin of the Rio Negro (Ferreira 2000). It has a tropical humid climate with mean annual temperature close to 26.7 °C, mean annual rainfall of about 2 300 mm, with the rainy season from December to May and dry season from June to September (Ferreira 2000). The area is also a mosaic of terra-firme, campinarana, and igapó forest types. The park includes a permanent plot of the *Programa de Pesquisas Ecológicas de Longa Duração Mauá* – PELD MAUA (Long-Term Ecological Research Program) of the Ecology, Monitoring, and Sustainable use of Wetlands group (Quaresma *et al.* 2020).

Sampling and morphological examination

Aerial litter-trapping rhizomorph systems were found in the field by active searches, recognized by the concentration of fallen plant debris held above ground on branches of the understorey. When the presence of such a web-like system was verified, examination of fresh basidiomata rising from the rhizomorphs was performed using a hand lens. The rhizomorphs and their basidiomata were photographed in the field when fresh using a digital camera and in the laboratory when dried using a stereoscopic microscope (Leica M205 C) with a camera (Leica MC 190 HD). The specimens were described macroscopically based on observations and photographs. Colour coding followed Küppers (2002). Specimens were dried at 40 °C, while a small portion of fresh rhizomorphs was used to obtain mycelial cultures by inoculation onto PDA medium. For microscopic examination, thin hand-cut sections of the specimens were rehydrated in 70 % ethanol and mounted in 5 % KOH or Melzer's reagent and analysed through an optical microscope (Leica DM 2500). The following microstructures were measured: 30 basidiospores; 15 basidia, basidioles, and cystidia; and ten hyphae (diameters). The dimensions of basidiospores are presented as the min–max range of length \times the min–max range of width, followed by: x_{rm} , range of the arithmetic means of length \times range of the arithmetic means of width; x_{mm} , mean of the arithmetic means of length (\pm standard deviation [SD]) \times mean of the arithmetic means of length width (\pm SD); Q_{rm} , range of the means of length/width; Q_{mm} , mean of the means of length/width (\pm SD); n , number of spores measured; and s , number of specimens examined per species. When applicable, lamellar spacing was determined by L , the number of full-length lamellae. Microstructures were also photographed using a camera (Leica EC3) coupled with the optical microscope, and LAS EZ software. Line drawings of the microstructures were made with a drawing tube and edited in CorelDRAW v. X7. The specimens were deposited at the INPA Herbarium (Thiers 2023).

DNA sequencing

Genomic DNA was extracted directly from cultured mycelia obtained from the specimens using a DNeasy Plant Mini Kit (Qiagen). The nrITS and nrLSU regions were amplified using the primer pairs ITS5/ITS4 (White *et al.* 1990) and LR0R/LR5 (Vilgalys & Hester 1990, Vilgalys & Sun 1994), respectively. We mixed 3 mM of each dNTP (Promega Corporation), 2 μ M of each primer, and 1 μ L DNA at 25 ng/ μ L in a final volume of 25 μ L containing 1 U Platinum® *Taq* DNA Polymerase, 1 \times PCR buffer, and 1.5 mM MgCl₂ (Invitrogen). For the nrITS and nrLSU amplifications, the PCR profile included an initial denaturation step of 2 min at 95 °C, followed by 35 cycles of 94 °C for 30 s, 55 °C for 30 s, 72 °C for 1 min, and a final extension at 72 °C for 10 min. Amplification products were verified via electrophoresis on 1.5 % agarose gels stained with GelRed™ (Biotium) under ultraviolet light. The products were purified using ExoSAP-IT™ (Thermo Fisher Scientific) and then sequenced using a BigDye™ Terminator v. 3.1 Cycle Sequencing kit (Thermo Fisher Scientific). The quality of the electropherograms was verified using Geneious v. R7 (Biomatters Ltd.).

Data processing and phylogenetic analyses

Forward and reverse reads were assembled into consensus sequences in Geneious v. R7. Based on Oliveira *et al.* (2020a) combined with Koch *et al.* (2020), the ingroup of Dataset 1 included species belonging to *Marasmius* sect. *Marasmius* (Singer 1976, 1986, Desjardin 1989, Antonín 2007, Tan *et al.* 2009, Wannathes *et al.* 2009, Antonín & Noordeloos 2010) with nrITS sequences produced in this study along with nrITS sequences from previous studies available in the NCBI GenBank database (Supplementary Table S1). The outgroup of Dataset 1 was composed of the same few species of *Marasmius* sect. *Globulares* chosen in Oliveira *et al.* (2020a). Dataset 2, combining nrITS + nrLSU, included species of *Pusillomyces* with sequences from GenBank provided by previous studies and newly generated nrITS and nrLSU sequences from the *Pusillomyces* specimen analysed in the present study (Supplementary Table S2). We also included *Setulipes afibulatus* with the nrITS sequences of a specimen from São Tomé provided by Desjardin & Perry (2017) in Dataset 2, since this species branched as sister to *Connopus* in their analysis and, therefore, is possibly *Pusillomyces*. The outgroup in Dataset 2 is *Connopus acervatus*. Sequences in GenBank (NCBI) were downloaded, checked for quality, and used in the respective dataset. Alignments were conducted using MUSCLE software (Edgar 2004). Ambiguously aligned regions were excluded from the nucleotide matrices by visual inspection in Geneious v. R7 (Kearse *et al.* 2012). The nucleotide substitution models were inferred with MrModeltest v. 2.3 (Nylander 2004) for each DNA region.

Parameters were set according to the selected models. The MC³ Bayesian analyses (BA) in MrBayes v. 3.2.1 (Ronquist *et al.* 2012) consisted of two independent runs: 5 000 000 generations, with sampling every 500 generations, six independent chains, and two swaps for Dataset 1; and 1 000 000 generations, with sampling every 100 generations, four independent chains, and two swaps for Dataset 2 with nrLSU and nrITS partitioned analysis. Burn-in was set at 10 % in all cases. Based on the 50 % majority-rule consensus method, final trees were generated with branch lengths and went across the 95 % highest posterior density trees. For maximum likelihood (ML) analyses, trees were reconstructed using the GTR+ Γ +I model with fast bootstrapping implementing CAT approximations for Dataset 1 and GTR+GAMMA+I model for Dataset 2 with GAMMA+P-Invar Model parameters estimated to an accuracy of 0.001 log likelihood units, both in RAxML v. 7.0.4 (Stamatakis 2006). The ML analyses implemented 1 000 pseudoreplicates and full ML optimization for the final tree. The phylogenetic trees were visualized in FigTree v. 1.3.1 and edited in CorelDRAW v. X7. The alignments and phylogenetic trees derived from this study were uploaded to figshare (doi: 10.6084/m9.figshare.25107023). All the species/specimens in the trees have been revised in the literatures about rhizomorphs production. All terminals in bold indicate they produce rhizomorphs (aerial or on the ground, scanty to abundant) in the concept accepted in this paper (Rayner *et al.* 1985, Yaffeto 2018); the ones indicated by a spider illustration are aerial.



Fig. 4. *Marasmius foliaiceps* aerial rhizomorph network. **A, B.** Dried leaves of multiple eudicotyledonous trees trapped by the aerial rhizomorph network (JO1146, RBC). **C.** Dried leaves trapped by the aerial rhizomorph network and some leaves showing HHB symptoms (JO1375, PNJ). **D.** A small shoot with dead leaves and sticks colonized rhizomorphs that fell on a living palm leaf of the understory (JO1375, PNJ).

RESULTS

Morphology and taxonomy

Marasmius arachnotropus J.S. Oliveira, *sp. nov.* MycoBank MB 850818. Figs 1–3.

Etymology: From the Greek: ‘Aráchni’ (Αράχνη) = spider; ‘trópos’ (τρόπος) = mode, way, form; for acting like a spider in building an aerial rhizomorph web to trap food (falling litter).

Typus: **Brazil**, Amazonas State, Manaus City, Biological Reserve of the Cuieiras River, ZF-2 LBA, trail 2, dead leaves and sticks of eudicotyledonous plant, 26 Nov. 2018, J.J.S. Oliveira JO1150 (**holotype** INPA 290678!).

Diagnosis: Pileus dark fuliginous brown with cream sulci, lamellae 7–9, basidiospores $6\text{--}9 \times 2.7\text{--}4.5 \mu\text{m}$, pileipellis composed of *Siccus*-type in transition to *Rotalis*-type broom cells intermixed with conspicuous, bronze brown, thick-walled smooth cells.

Pileus 0.6–4.2 mm diam, convex to plano-convex, umbilicate, with a central dot or a broad and low papilla, sulcate, margin decurved to straight, edge entire to wavy, glabrous, dry, dull, papyraceous, non-hygrophanous, pale ($N_{40}Y_{40}M_{20}$) to dark fuliginous brown ($N_{90}Y_{50}M_{30}$) or blackish brown ($N_{99}Y_{99}M_{40}$), often striped with yellow or cream ($N_{10}Y_{30}M_{10}$) sulci or around the central fuliginous brown dot, becoming dark chestnut brown to blackish when dried; membranous, thin ($< 1 \text{ mm}$). **Lamellae** collariate, distant, 7–9, straight, equal, whitish cream ($N_{00}Y_{10}M_{00}$), edge even, non-marginate. **Stipe** 1.7–7.7 \times 0.2–0.3 mm, central, sometimes slightly eccentric, short, often curved, filiform, circular, insititious directly from the rhizomorph forming inconspicuous, ring-like nodes around the base, chitinous, hollow, black, glabrous, smooth, slightly shiny. **Rhizomorphs** long-filiform, abundant, 0.1–2.6 mm thick, loose or attached to hanging substrate, branching, black, mostly glabrous, forming a litter-trapping epiphytic web on branches of the understorey, eventually with basidiomata. **Basidiospores** $(5.2\text{--}6\text{--}9\text{--}9.7) \times 2.7\text{--}4.5 \mu\text{m}$ [$x_{\text{rm}} = 7.3\text{--}7.6 \times 3.5\text{--}3.8 \mu\text{m}$, $x_{\text{mm}} = 7.4 (\pm 0.2) \times 3.7 (\pm 0.2) \mu\text{m}$, $Q_{\text{rm}} = 1.9\text{--}2.2$, $Q_{\text{mm}} = 2 (\pm 0.2)$, $n = 30$, $s = 3$], obovoid to shortly oblong, subellipsoid to lacrymoid, smooth, hyaline, thin-walled, inamyloid. **Basidia** $16\text{--}26.4 \times 6.6\text{--}7.4 \mu\text{m}$, mostly clavate, hyaline, thin-walled, 2-sterigmate, inamyloid. **Basidioles** $16.2\text{--}25 \times 4.3\text{--}8.3 \mu\text{m}$, clavate to broadly clavate, hyaline, thin-walled, inamyloid. **Pleurocystidia** absent. **Cheilocystidia** in form of *Siccus*-type in transition to *Rotalis*-type broom cells, hyaline, inamyloid, main body $12.5\text{--}17.7 \times 5.2\text{--}8.4 \mu\text{m}$, clavate to pyriform, rarely pedunculate, thin-walled, diverticula apical to often divergent to the laterals, short, $0.4\text{--}1.6 \times 0.6\text{--}0.9 \mu\text{m}$, verruciform, sometimes digitiform, solid, simple, colourless, with obtuse, rounded apex. **Lamellar trama** inamyloid, irregular, hyphae interwoven, cylindrical, $1.5\text{--}5.6 \mu\text{m}$ diam, regular in outline, with some segments slightly broad, hyaline, smooth, thin-walled, clamp connections present. **Pileus trama** inamyloid, irregular, hyphae interwoven, cylindrical, $1.9\text{--}5.2 \mu\text{m}$ diam, regular in outline, branched, hyaline, smooth, thin-walled, clamp connections present. **Pileipellis** hymeniform, mottled, composed of a matrix of 1) *Siccus*-type in transition to *Rotalis*-type broom cells, predominant, brown, inamyloid, main body $9.5\text{--}18.3 \times 7.4\text{--}12\text{--}20.4 \mu\text{m}$, cylindrical to clavate, mostly pyriform, some turbinate, often branched,

few flat, moderately thick-walled, apically pigmented fading to hyaline downwards, diverticula apical to divergent to the laterals, short, $0.9\text{--}1.9 \times 0.6\text{--}1 \mu\text{m}$, mostly verruciform or knob-like, some digitiform, solid, pigmented, simple, with obtuse, rounded apex; and intermixed with more scanty 2) smooth cells, seldom diverticulate, $13\text{--}36 \times 3.6\text{--}10.6 \mu\text{m}$, conspicuous, more deeply pigmented, bronze brown, thick-walled (more thick walls), cylindrical clavate, or pyriform, rarely branched into buds, diverticula apical, broadened, simple or branched, solid, with obtuse, rounded apex. **Stipe trama** composed of highly melanized hyphae layer in the stipitipellis and cortex, dark brown when isolated, cylindrical, $2.7\text{--}8 \mu\text{m}$ diam, slightly irregular, superficially more rough, thick-walled, middle to internal layer abruptly depigmented, apparently dextrinoid, hyaline, pale yellow or brown, cortical hyphae in parallel and non-branched, interwoven and branched, cylindrical, $3.2\text{--}9.7 \mu\text{m}$ diam, more regular in outline, more translucent, pale brownish yellow, thick-walled, with no visible clamp connections, the most internal hyphae inamyloid, cylindrical, $1.3\text{--}7.1 \mu\text{m}$ diam, some inflate or wavy, smooth, thinner walls, with clamp connections.

Habit and substrate: Marasmioid, HHB on branches of the understorey, forming a web of rhizomorphs to trap fallen leaves and sticks.

Additional specimens examined: **Brazil**, Amazonas State, Manaus City, Biological Reserve of the Cuieiras River, ZF-2 LBA, trail 2, dead leaves and sticks of eudicotyledonous plant, 26 Nov. 2018, J.J.S. Oliveira JO1155 (INPA 290679!); Novo Airão City, Jaú National Park, terra-firme forest at the Unini River, dead leaves and sticks of eudicotyledonous plant, 24 Oct 2019, J.J.S. Oliveira & Francisco JO1374 (INPA 290680!).

DNA sequences: JO1150 (ITS: PP118109); JO1155 (ITS: PP118108).

Notes: *Marasmius arachnotropus* is a singular species in *Marasmius* sect. *Marasmius* subsect. *Sicciformes*. The pileus is mostly fuliginous brown with pallid sulci and zone around the central papilla. The pileipellis is composed of brown *Siccus*- (mostly) to *Rotalis*-type broom cells intermixed with fewer, many non-diverticulate, thick-walled, brown cells. The new species is similar to a group of species in the *Marasmius crinis-equi* species complex. In the protologue (Kalchbrenner 1880), *M. crinis-equi* has a whitish yellow or orange pileus. *Marasmius crinis-equi sensu* Wannathes et al. (2009) differs in the reddish brown to orange brown pileus, and longer basidiospores [$(8\text{--})10\text{--}12 \times 4\text{--}4.5 \mu\text{m}$] while *M. crinis-equi sensu* Tan et al. (2009) differs in the brownish orange to greyish orange pileus, longer basidiospores [$(7\text{--})9\text{--}13.5 \times 3\text{--}4 \mu\text{m}$] and in the regular, dextrinoid lamellar trama. *Marasmius* aff. *crinis-equi sensu* Wannathes et al. (2009) differs in having a light orange pileus, with some having marginate lamellae, and in having larger basidiospores ($8\text{--}10 \times 4\text{--}6 \mu\text{m}$). *Marasmius neocrinis-equi* is geographically the closest species with very similar morphology but differs mainly in having a paler pileus, larger basidiospores [$(7.8\text{--})8.1\text{--}11\text{--}12.1 \times (4.1\text{--})4.5\text{--}5.7 \mu\text{m}$], regular lamellar trama, and pileipellis composed only of more typical *Siccus*-type broom cells (Koch et al. 2020).

Marasmius populiformis (Dennis 1951, Singer 1976) has fuscous or dark brown, minute pileus ($< 1 \text{ mm}$ diam), with distant lamellae (5–6), and the stipe also arises from the rhizomorph. However, the lamellae are marginate, both stipe and rhizomorph

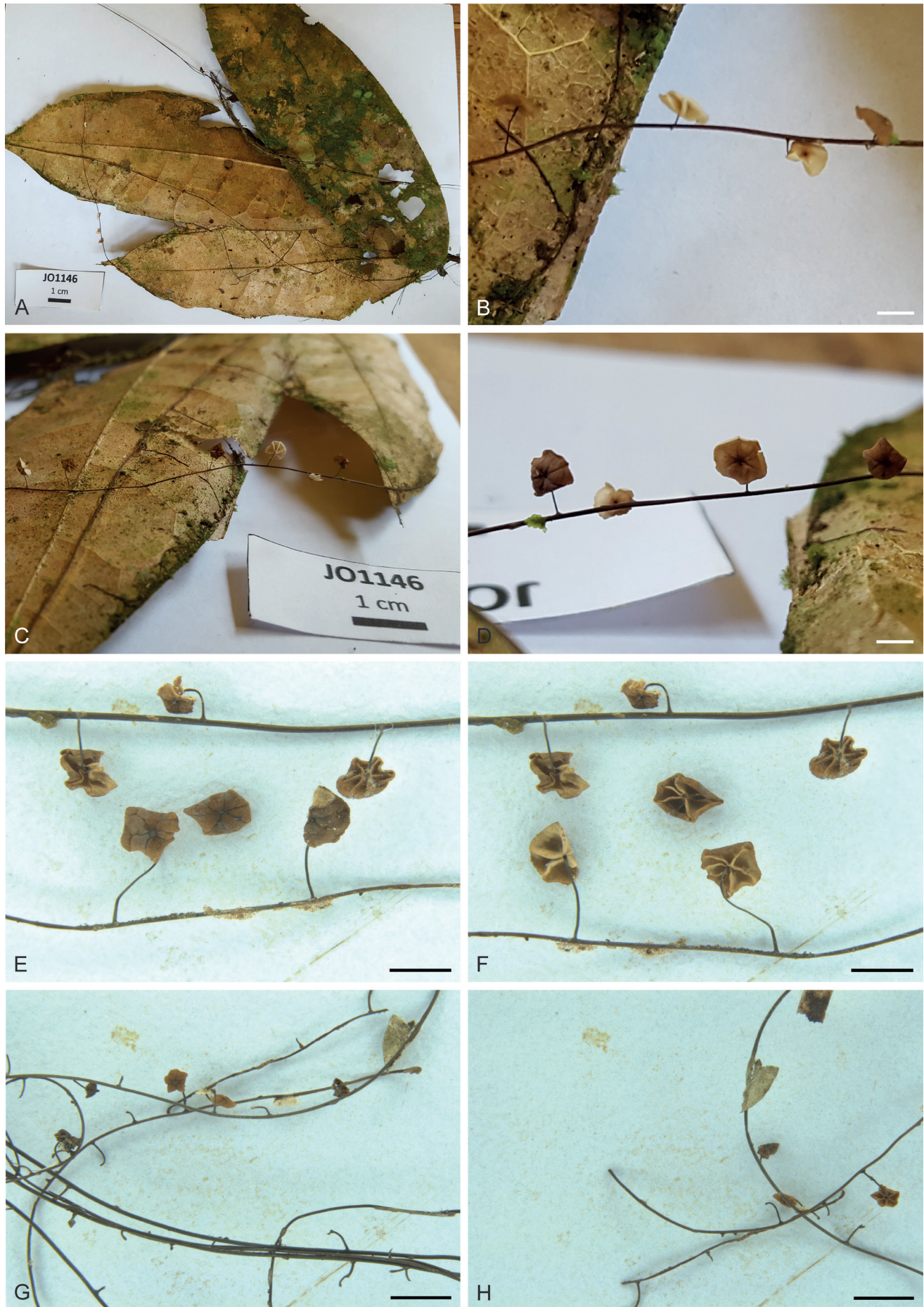


Fig. 5. Macroscopy of *Marasmius foliaiceps* (JO1146, RBC). **A.** Rhizomorphs attached to dead leaves all along the contact with the substrata. **B–D.** Fresh basidiomata rising from the rhizomorphs. **E, F.** Detailed view of dried basidiomata. **G, H.** Dried basidiomata rising from rhizomorphs and stipes without pileus. Scale bars = 2 mm.

(central and standing, with many stipes rising from it) are yellow or golden yellow, and the basidiospores are narrower (about 3 μm). The pileipellis is composed of apparently *Rotalis*-type broom cells only and the species is not reported to be epiphytic.

Marasmius foliaiceps J.S. Oliveira, *sp. nov.* MycoBank MB 850819. Figs 4–6.

Etymology: From the Latin: ‘folia’ = leaves, and ‘auceps’ = trapper; for trapping falling dried leaves in the aerial rhizomorph system.

Typus: Brazil, Amazonas State, Manaus City, Biological Reserve of the Cuieiras River, ZF-2 LBA, trail 2, 26 Nov. 2018, J.J.S. Oliveira JO1146 (holotype INPA 290676!).

Diagnosis: Pileus whitish cream to pale brown, lamellae 5–6, basidiospores 5.2–8.8 \times 3.2–5.4 μm , pileipellis predominantly composed of *Rotalis*-type broom cells.

Pileus 2.3–3.5 mm diam, convex to plano-convex, umbilicate, with a central dot or low papilla, shallowly sulcate, margin decurved to straight, edge entire to wavy, glabrous, dry, dull, papyraceous, non-hygrophanous, whitish cream ($N_{00}Y_{10}M_{00}$) to brown ($N_{30}Y_{50}M_{30}$) or chestnut brown ($N_{60}Y_{50}M_{30}$) with a central, small, black dot, remaining chestnut brown ($N_{60}Y_{60}M_{30}$) when dried; membranous, thin (< 1 mm). **Lamellae** subcollariate (small collarium), distant, 5–6, straight to slightly ventricose, equal, seldom forked, whitish cream ($N_{00}Y_{10}M_{00}$), edge even, non-marginate. **Stipe** 1.8–3 \times 0.05–0.1 mm, central, short, often

curved, filiform, circular, insititious directly from the rhizomorph forming inconspicuous, ring-like nodes around the base, chitinous, hollow, dark brown ($N_{80}Y_{99}M_{50}$), glabrous, smooth, slightly shining. **Rhizomorphs** long-filiform, abundant, 0.1–0.3 mm thick, loose, or attached to hanging substrate, branching, concolourous with the stipe, mostly glabrous, forming a litter-trapping epiphytic web on branches of the understorey, eventually with basidiomata. **Basidiospores** (4.7–)5.2–8.8(–9.9) \times 3.2–5.4(–5.9) μm [$x_{rm} = 6.8\text{--}7.3 \times 4\text{--}4.6 \mu\text{m}$, $x_{mm} = 7.1 (\pm 0.2) \times 4.3 (\pm 0.2) \mu\text{m}$, $Q_{rm} = 1.6\text{--}1.7$, $Q_{mm} = 1.7 (\pm 0.1)$, $n = 30$ (JO1131, $n = 16$), $s = 4$], obovoid, ellipsoid to subellipsoid, amygdaliform, smooth, hyaline, thin-walled, inamyloid. **Basidia** (19–)20.8–26.6(–28.5) \times 4–6.8 μm , cylindrical clavate, hyaline, thin-walled, 2–4-sterigamata, inamyloid. **Basidioles** 18.7–28.2 \times 4.2–7.3(–8.1) μm , clavate to fusoid, some with acuminate apex, hyaline, thin-walled, inamyloid. **Pleurocystidia** absent. **Cheilocystidia** in form of *Rotalis*-type broom cells similar to those of the pileipellis, inconspicuous, main body elliptical to obovoid, pyriform to spheropedunculate, hyaline, rarely pale yellowish brown, inamyloid, thin-walled, diverticula apical divergent to the laterals, short, verruciform or knob-like, rarely digitiform, simple, solid, hyaline, obtuse. **Lamellar trama** inamyloid, irregular, hyphae interwoven, cylindrical to irregular in outline, 1.7–9.5 μm diam, with short segments, strongly branched, hyaline, smooth, thin-walled, clamp connections present. **Pileus trama** inamyloid, irregular, hyphae interwoven, cylindrical to irregular in outline, 1.3–6.3 μm diam, branched, smooth, hyaline, thin-walled, clamp connections present. **Pileipellis** hymeniform, inamyloid, non-mottled or slightly mottled, predominantly composed of *Rotalis*-type broom cells,

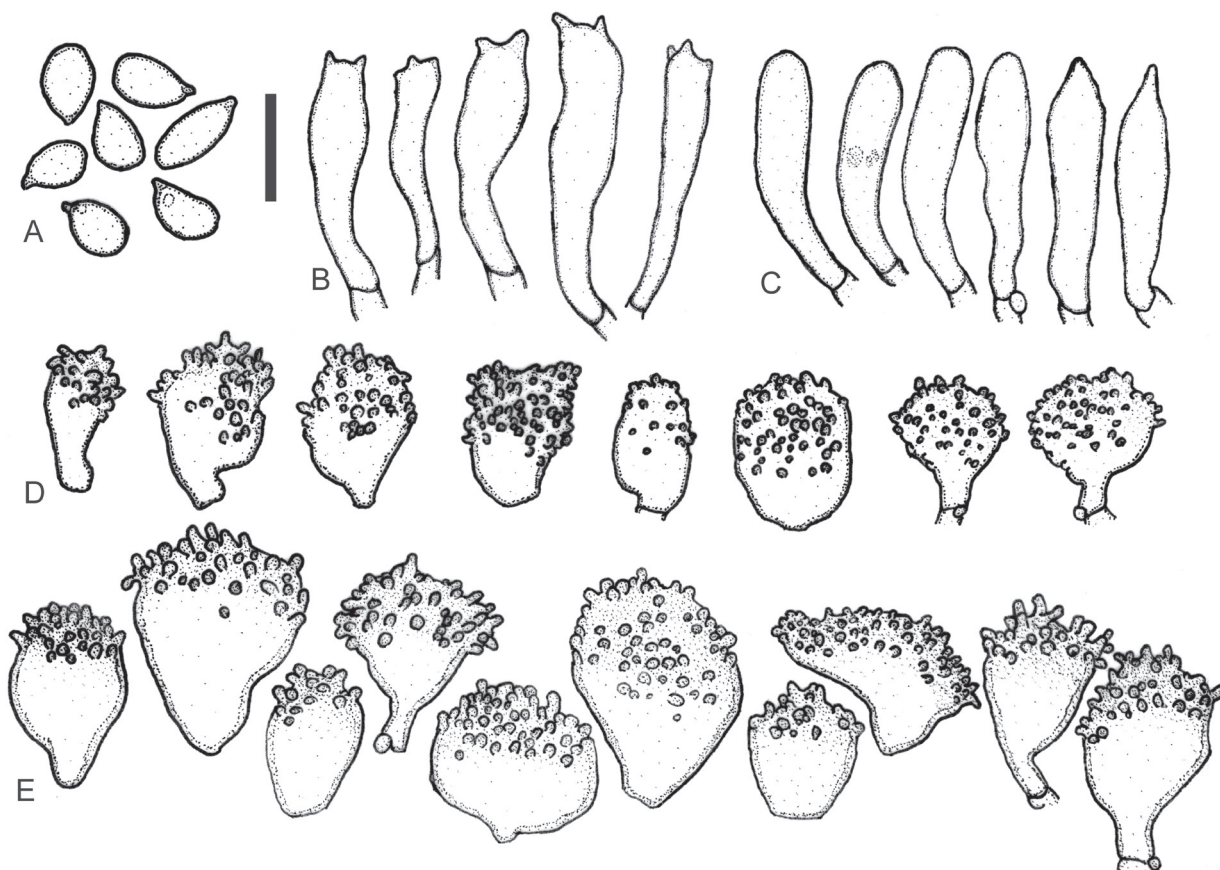


Fig. 6. Microscopy of *Marasmius foliaiceps* (JO1146, RBC). **A.** Basidiospores. **B.** Basidia. **C.** Basidioles. **D.** Cheilocystidia. **E.** *Rotalis*-type broom cells of the pileipellis. Scale bar = 10 μm .

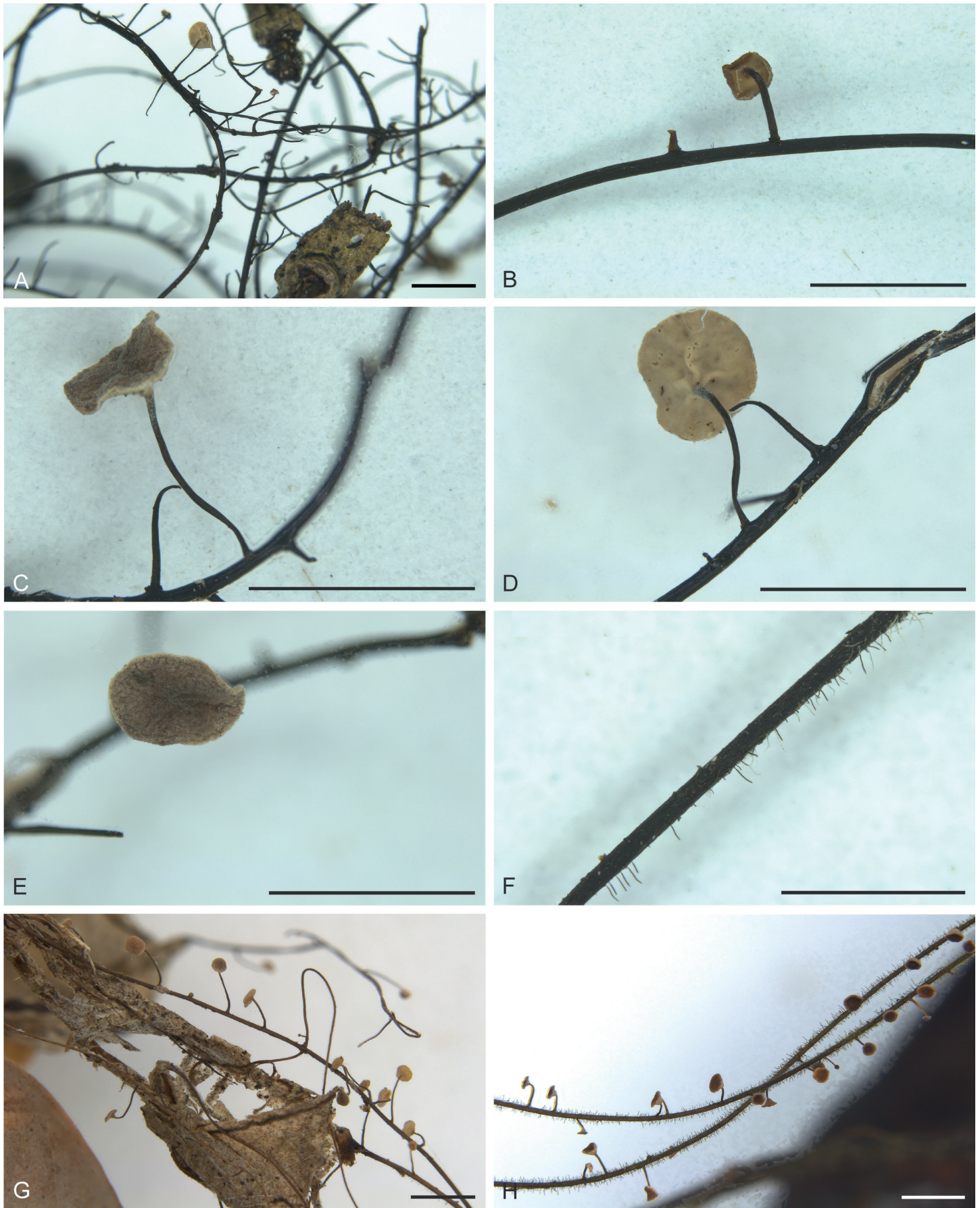


Fig. 7. Macroscopy of *Pusillomyces cuieirasensis* (JO1006, RBC). **A.** Dried rhizomorphs with few entire basidiomata and many stipes without pileus. **B.** Dried younger basidiome rising from the rhizomorph and the base of a broken stipe. **C.** Fully developed basidiome (dried). **D.** Dried basidiome showing the hymenophore. **E.** Pileus surface. **F.** Rhizomorph with setae-like conidiophores. **G, H.** *Pusillomyces manuripioides* (JO674, close to RBC). Scale bars: A–D, G, H = 2 mm; E, F = 1 mm.

rarely in transition to *Siccus*-type broom cells, bronze brown to yellowish brown in mass, pale yellowish brown when isolated, translucent, main body $12\text{--}19.2 \times 9\text{--}18.4\text{--}(20.9) \mu\text{m}$, globose, ellipsoid, pyriform, to slightly spheropedunculate, rarely turbinate or flat, wall slightly thick, with clamp connections, diverticula divergent to the laterals, short, $0.8\text{--}1.5 \times 0.7\text{--}1\text{--}(1.3) \mu\text{m}$, verruciform, or broad digitiform, few conical, solid, simple to branched, pale brown, obtuse. *Stipe trama* inamyloid in the internal hyaline hyphae (if dextrinoid, the reaction may occur on those strongly pigmented), stipitipellis and hyphae of the cortex parallel, cylindrical, $2.7\text{--}8 \mu\text{m}$ diam, regular in outline, strongly pigmented, bronze brown, often non-branched, smooth, thick-walled; internal hyphae hyaline, $1.3\text{--}4.8 \mu\text{m}$ diam, thin-walled.

Habit and substrate: Marasmioid, HHB on branches of the understorey forming a rhizomorph-made web to trap fallen leaves and sticks.

Additional specimens examined: **Brazil**, Amazonas State, Manaus City, Biological Reserve of the Cuieiras River, ZF-2 LBA, trail 1, 25 Nov. 2018, J.J.S. Oliveira & N.K. Ishikawa JO1131 (INPA 290675!); *ibid.*, J.J.S. Oliveira JO1147 (INPA 290677!); Novo Airão City, Jaú National Park, terra-firme forest at the Unini River, 24 Oct 2019, J.J.S. Oliveira & Francisco JO1375 (INPA 290681!).

DNA sequences: JO1146 (ITS: PP118111); JO1147 (ITS: PP118110).

Notes: *Marasmius foliaiceps* is a unique species of sect. *Marasmius* subsect. *Marasmius* with the same habit as *M. crinis-equi* and similar to others in sect. *Marasmius* subsect. *Sicciformes*. The pileus is initially whitish, then becomes pale chestnut brown. The pileipellis is mostly composed of typical *Rotalis*-type broom cells consistent with its placement in subsect. *Marasmius*, but some rare cells are slightly transitional to the *Siccus*-type. No known species are morphologically close to *M. foliaiceps*.

Pusillomyces cuieirasensis J.S. Oliveira, *sp. nov.* MycoBank MB 850820. Figs 7, 8.

Etymology: The epithet refers to the Cuieiras River that also names the RBC, Manaus, Amazonas State, type locality.

Typus: **Brazil**, Amazonas State, Manaus City, Reserva do Cuieiras, 13 Mar. 2018, J.J.S. Oliveira & N.K. Ishikawa JO1006 (**holotype** INPA 280708!).

Diagnosis: Differs from *Pusillomyces manuripioides* in the flat, homogeneously pigmented, slightly wrinkled pileus and slightly smaller basidiospores [$x_{\text{mm}} = 6.2 (\pm 0.3) \times 3 \mu\text{m}$ vs. $x_{\text{mm}} = 7.3 (\pm 0.3) \times 3 (\pm 0.4) \mu\text{m}$]. No evidence of necrosis on living leaves was found.

Pileus $0.7\text{--}1.4 \text{ mm}$ diam, orbicular, plano-convex to plane, centre umbonate to flat, disc and margin smooth, margin incurved to decurved when young, straight to occasionally somewhat uplifted when fully matured, wrinkled all over when dried, edge entire; surface dry, dull, subvelutinous; membranous or coriaceous, context thin ($< 1 \text{ mm}$), white to whitish cream; pale ($N_{50}Y_{70}M_{30}$) to sepia brown ($N_{70}Y_{90}M_{40}$). *Hymenophore* smooth, occasionally

pleated around the stipe apex, pale cream ($N_{00}Y_{10}M_{00}$), papyraceous, dull, dry. *Stipe* $1\text{--}2 \times 0.06\text{--}0.1 \text{ mm}$, central, filiform to cylindrical thin, equal, insititious from apertures along the rhizomorphs, chitinous, hollow, glabrous, smooth, opaque, dark brown ($N_{99}Y_{99}M_{50}$) to black. *Rhizomorphs* thicker, $0.2\text{--}0.3 \text{ mm}$, abundant, elongate, hair-like, part glabrous, part densely pubescent, concolourous with the stipes (dark brown to black pubescence), chitinous, hollow, flexible, branching, irregular networks. *Basidiospores* $4.5\text{--}7.8\text{--}(8) \times 2.4\text{--}3.9 \mu\text{m}$ [$x_{\text{rm}} = 6\text{--}6.4 \times 3 \mu\text{m}$, $x_{\text{mm}} = 6.2 (\pm 0.3) \times 3 \mu\text{m}$, $Q_{\text{rm}} = 1.9\text{--}2.1$, $Q_{\text{mm}} = 2 (\pm 0.1)$, $n = 30$, $s = 2$], obovoid to shortly oblong, ellipsoid to subellipsoid, or amygdaliform, lacrymoid to subclavate, smooth, thin-walled, hyaline, inamyloid. *Basidia* $15.7\text{--}22.5 \times (4\text{--})4.8\text{--}6.4 \mu\text{m}$, clavate to cylindrical clavate, smooth, hyaline, thin-walled, inamyloid, 4 sterigmata. *Basidioles* $11.5\text{--}23.6 \times (2.4\text{--})3.2\text{--}6.3 \mu\text{m}$, clavate to cylindrical clavate, some fusoid or with tapered apex, smooth, hyaline to fuscous, thin-walled, inamyloid. *Hymenial cystidia* absent. *Pileus trama* inamyloid, irregular, non-gelatinized, loose, spongy, more packed near the hymenium, forming a gradient from pale brownish near the pileipellis to more hyaline near the hymenial layer, hyphae interwoven, cylindrical to slightly inflated, $2\text{--}6.5 \mu\text{m}$ diam, regular in outline, branched and anastomosed, smooth, or strongly incrustated (irregular incrustations) towards the pileipellis, thin- to more thick-walled next to the pileipellis. *Pileipellis* non-hymeniform, non-gelatinized, formed by a layer of disorganized elements, abundant and dominant hyphal endings similar to *Rameales*-structures, rarely cystidioid or cellular, filamentous or cylindrical, $2.3\text{--}6.5 \mu\text{m}$ diam (main terminal segment), often lobed or irregular in outline, usually branched like those of the trama, partly smooth and partly incrustated directly associated with incrustated hyphae of the upper pileus trama, pale chestnut brown in mass (5 % KOH), few hyaline when isolated, moderately thick-walled, strongly diverticulate; diverticula apical (terminal), uni- or bilateral, or all around (ramose), generally short, $0.6\text{--}2.7 \times 0.6\text{--}1.5 \mu\text{m}$, rough granular, vesiculose, verruciform to shortly digitiform, often lobed or branched, fuscous or brownish, solid, with obtuse and rounded apex. *Stipe trama* inamyloid or cortical hyphae apparently dextrinoid, or only orangish brown in Melzer's reagent due to pigmentation, parallel, packed, cylindrical, $2.8\text{--}7.5 \mu\text{m}$ diam, regular in outline, septate, grey to greyish brown, losing pigmentation inward, thick-walled, smooth, or sometimes incrustated; internal hyphae $2.2\text{--}8 \mu\text{m}$ diam, hyaline, smooth, thin-walled. *Stipitipellis* without elements or vestiture on the glabrous parts. *Rhizomorphs* corresponding to the stipe trama for the glabrous segments; pubescent segments populated by elongate, cylindrical to fusoid (tapered at the apex) conidiophores immersed in the rhizomorph trama; erect bodies $50.5\text{--}190 \times 5.9\text{--}9.5 \mu\text{m}$ diam, with numerous septa, each short segment (various lengths) slightly inflated, thick-walled (including septa), dark brown, non-fragmentary, but breaking at the septa when firmly compressed, perpendicularly rising from connecting, thinner, irregular, sometimes branched, prostrate bodies, reaction in Melzer's reagent not discernible due to the dark pigmentation. *Clamp connections* usually absent in all tissues, but some inconspicuous at the base of basidia.

Habit and substrate: Manuripioid, tiny, gregarious, epiphytic, forming rhizomorphs hanging on living leaves, twigs, and limbs of branches of several different eudicotyledonous species in terra-firme forest, Amazon.

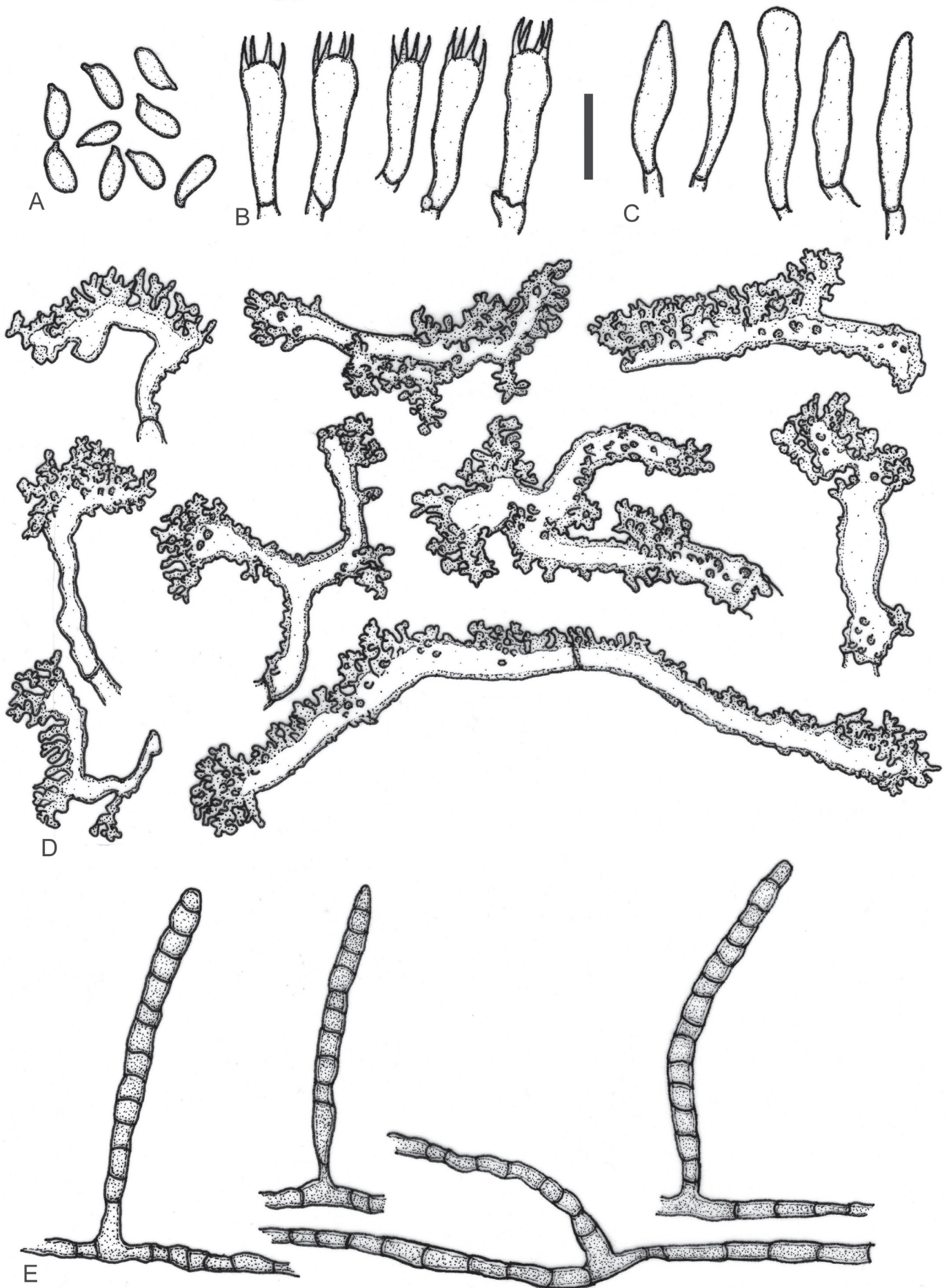


Fig. 8. Microscopy of *Pusillomyces cuieirasensis* (JO1006, RBC). **A.** Basidiospores. **B.** Basidia. **C.** Basidioles. **D.** Diverticulate and incrusting *Rameales*-like structures of the pileipellis. **E.** Melanized and septate conidiophores that colonizes the rhizomorphs. Scale bar A–D = 10 μ m, E = 20 μ m .

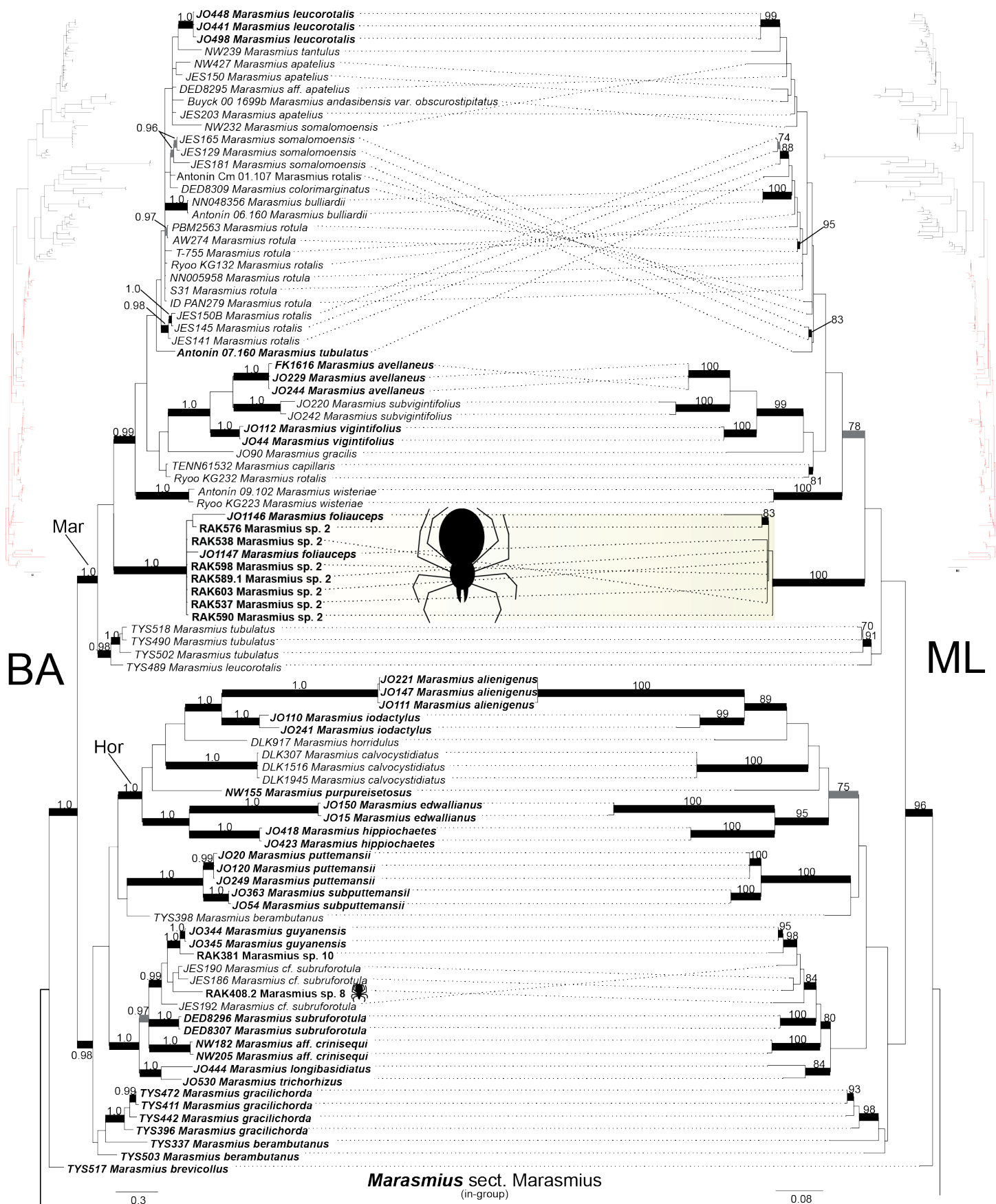


Fig. 9. Bayesian 50 % majority-rule tree (BA) and the best-scored maximum likelihood tree (ML) from the single locus (nrITS) analysis of Dataset 1. Support values at the nodes consist of PP \geq 0.95 and BS \geq 70 %; unsupported nodes under PP 0.5 are collapsed in the BA tree. Thicker branches in black represent highly supported nodes, and those in grey are moderately to weakly supported nodes. The species that produce any rhizomorph are in bold font while those that make an aerial litter trapping rhizomorph system are indicated with a spider. The net lines connect the same specimens from the BA to the ML tree.

Additional specimens examined: **Brazil**, Amazonas State, Manaus City, Reserva do Cuieiras, 4 Jul. 2018, J.S. Cardoso & F.S. Andriolli JS350 (INPA 290673!); *ibid.*, 27 May 2019, J.S. Cardoso & F.S. Andriolli JS772 (INPA 290674!).

DNA sequences: JO1006 (ITS: OR775125; LSU: OR778280).

Notes: The species is very similar to *Pusillomyces manuripioides* in morphology and ecology. In morphology, *P. manuripioides* differs only in having a mostly umbonate pileus, with a central brown spot and slightly larger basidiospores [$x_{nm} = 7.3 (\pm 0.3) \times 3.3 (\pm 0.4) \mu m$]. In ecology, the new species seems to be only saprotrophic, epiphytic on branches of the understorey, trapping falling litter. Both species are “host” of elongate, septate, dark brown, undetermined conidia/conidiophores along their rhizomorphs. These conidiophores are interpreted as exogenous structures both in Oliveira et al. (2019) and the present study. It remains to be investigated whether these are or are not conspecific with those in *P. manuripioides* or are parasitic. Neither HHB symptoms nor necrosis was observed on living leaves of branches entangled with *P. cuieirasensis*.

Phylogenetic analyses

The coupled BA (right) and ML (left) trees of Dataset 1 (Fig. 9) show multiple branches of *Marasmius* sect. *Marasmius* taxa included in the analyses. The whole ingroup was strongly supported, with the upper part (Fig. 9 part 1) well defined

into a clade with better relationship resolution among several strongly supported branches. The lower part (Fig. 9 part 2) mainly represents polytomy of several small strongly supported branches without resolution among them. *Marasmius arachnotropus* and *M. foliaiceps* are represented by highly supported branches depicted in dark brown and in whitish yellowish brown, respectively. The first is part of a strongly supported clade including *Marasmius* sp. 1, *Marasmius* sp. 9, *M. crinis-equi sensu* Koch et al. (2020), *Marasmius* sp. 6, *M. neocrinis-equi*, *M. madagascariensis*, and *M. crinis-equi sensu* Tan et al. (2009) in the lower part of the trees (Fig. 9 part 2). Within this clade, a strongly supported subclade (BA 1.0; ML 92) grouped more closely: *M. arachnotropus*, *Marasmius* sp. 1, *Marasmius* sp. 9, *Marasmius* sp. 6, and *M. crinis-equi sensu* Koch et al. (2020). *Marasmius foliaiceps* branched as conspecific with *Marasmius* sp. 2 of Koch et al. (2020) in the clade Mar (Fig. 9 part 1). This highly supported branch (BA 1.0; ML 100 %) was placed immediately above the basal *M. tubulatus* and *M. leucorotalis sensu* Tan et al. (2009) branch in the clade at the top. The names in bold indicate rhizomorph-forming species and a spider beside the lineages indicate those that form aerial litter-trapping rhizomorph networks (Fig. 9).

The coupled BA (right) and ML (left) trees of Dataset 2 (Fig. 10) show the phylogenetic placement of *P. cuieirasensis* as sister to *P. manuripioides* with high statistical support. The whole ingroup, *Pusillomyces*, is strongly supported, sister to the basal *Setulipes afibulatus* with high statistical support. The tree is rooted with *Connopus acervatus*.

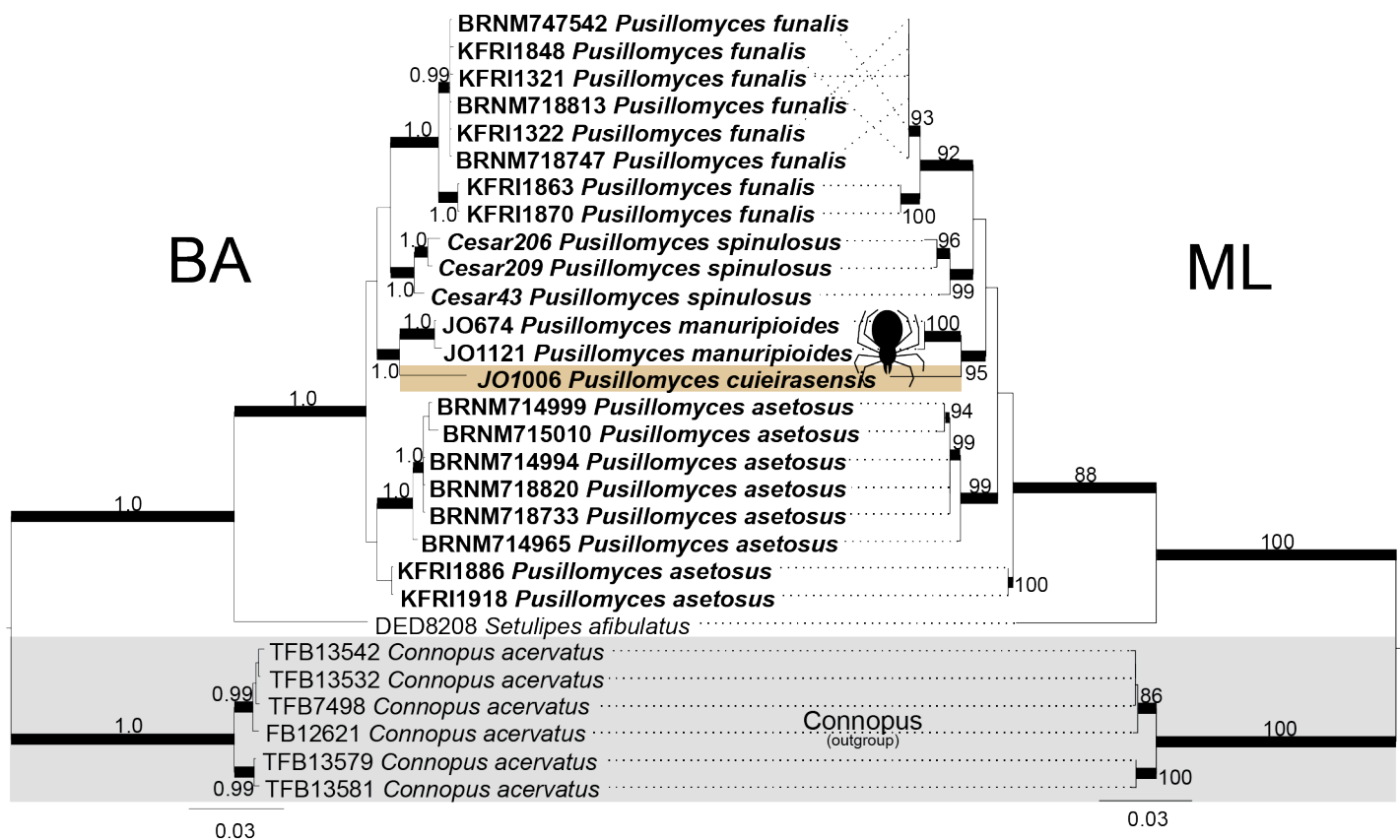


Fig. 10. Bayesian 50 % majority-rule tree (BA) and the best-scored maximum likelihood tree (ML) from the multilocus (nrITS and nrLSU) analysis of Dataset 2. Support values at the nodes consist of PP ≥ 0.95 and BS ≥ 70 %; unsupported nodes under PP 0.5 are collapsed in the BA tree. Thicker branches in black represent highly supported nodes, and those in grey are moderately to weakly supported nodes. The species that produce any rhizomorph are in bold font while those that make an aerial litter-trapping rhizomorph system are indicated with a spider. The net lines connect the same specimens from the BA to the ML tree.

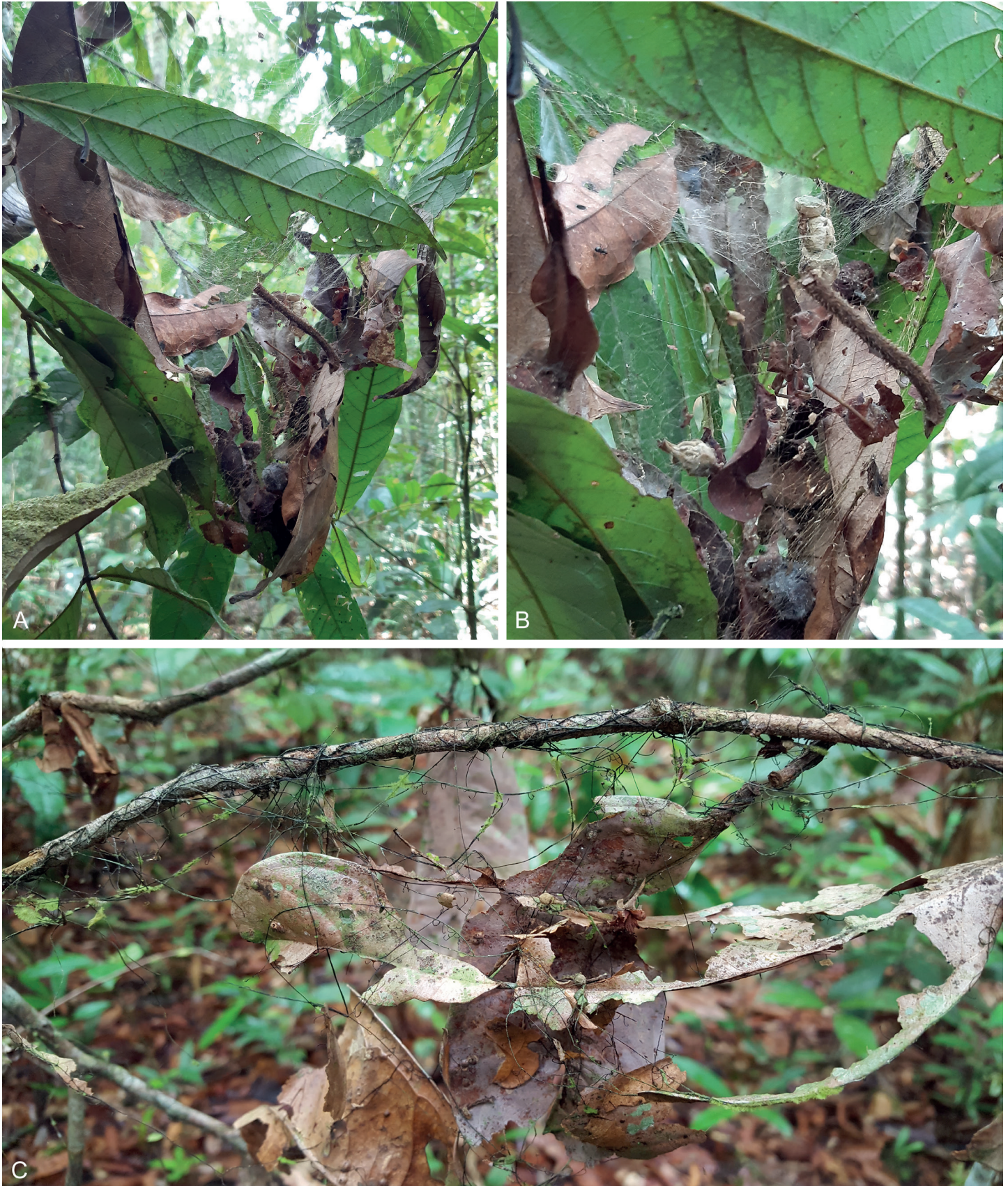


Fig. 11. Epiphytic webs in the Amazon Forest. **A, B.** A spider web with many trapped plant debris. **C.** An aerial litter-trapping rhizomorph system with trapped leaves in advanced decay stage.

DISCUSSION

Phylogenetic relationships

Consistent with their morphology compared to species in the genus, the two *Marasmius* species are classified in sect. *Marasmius*, in the *Marasmiaceae*. In the phylogenetic analyses (Fig. 9), *M. foliaiceps* was resolved to the same clade as species of *Marasmius* sect. *Marasmius* subsect. *Marasmius* (Fig. 9 part 1). In contrast to subsect. *Sicciformes*, this traditional subsection was monophyletic in all previous studies. The most important and informative synapomorphy in the group is the pileipellis composed of *Rotalis*-type broom cells, a character shared with *M. foliaiceps*. The clade Mar, which includes only species of sect. *Marasmius* subsect. *Marasmius* included in this analysis, was strongly supported in BA analyses (Fig. 9 part 1). *Marasmius foliaiceps* is conspecific with *Marasmius* sp. 2, one of the undetermined species that also forms rhizomorphs found entangling birds' nests in Guyana (Koch et al. 2020). Therefore, *M. foliaiceps* ranges from Guyana down to the centre of the Amazonas State in Brazil. As the specimens from Brazil form aerial rhizomorph litter-trapping systems, this does indicate that the specimens from Guyana should also implement the same growth habit. Koch et al. (2020) found *Marasmius* sp. 2 (= *M. foliaiceps*) with basidiomata fruiting from rhizomorphs only in birds' nests.

On the other hand, *M. arachnotropus* was resolved to a clade containing species of the *M. crinis-equi* species complex, which are members of the paraphyletic sect. *Marasmius* subsect. *Sicciformes*. This subsection contains species that produce basidiomata with the pileipellis composed of *Siccus*-type broom cells. *Marasmius crinis-equi* is the best-known species to produce profuse rhizomorph networks, often epiphytic, with minute basidiomata (Kalchbrenner 1880, Seaver 1944, Tan et al. 2009, Wannathes et al. 2009) similar to *M. arachnotropus* rising from wire-like structures. As many para- or polyphyletic lineages are named *M. crinis-equi*, it does represent a species complex or the name harbours cryptic species essentially linked by the shared growth habit and mode of nutrition. The species require an authentic token proxy with topotypical collections for precise evaluation and taxonomy. In this analysis, *M. crinis-equi* from Thailand [NW348 in Wannathes et al. (2009)] and from Malaysia [TYS412 in Tan et al. (2009)], *M. madagascariensis* from Madagascar (Shay et al. 2017), *M. neocrinis-equi* from Guyana (Koch et al. 2020), and the undetermined species *Marasmius* sp. 1, *Marasmius* sp. 6, and *Marasmius* sp. 9 from Cameroon (Koch et al. 2020) are the closest species to *M. arachnotropus* from the Amazon rainforest in Brazil (Fig. 9 part 2). This lineage of species that produces profuse rhizomorph networks with minute basidiomata represents a pantropical species complex. From this group, only *M. madagascariensis* does not exhibit the same growth mode; although it forms some rhizomorphs, its basidiomata grow directly from stems of *Cyathea* and on grass debris on the ground (Shay et al. 2017). Other *Marasmius* species depicted with a spider drawing, in multiple unrelated placements in sect. *Marasmius*, present rhizomorph-forming network growth indicating that this character is not shared by a single monophyletic group, as shown previously by Koch et al. (2020).

In the *Omphalotaceae*, another newly described *Pusillomyces* species exhibits the same strategy as in *M. arachnotropus* and *M. foliaiceps* in the *Marasmiaceae*. With strong support in

the *Pusillomyces* phylogeny (Fig. 10), *P. cuieirasensis* is sister to *P. manuripioides* which has similar basidiomata morphology and growth habit. These are the only two species in the genus reported to date to form hanging litter-trapping systems in the understorey (depicted by a spider drawing in Fig. 10). Either "*M. arachnotropus* and *M. foliaiceps*" or "*P. cuieirasensis* and *P. manuripioides*" can be considered sympatric, as collections were made in the same area, whether in RBC or PNJ, for the *Marasmius* species or in very close proximity for the *Pusillomyces* species. Therefore, the pairs of species may be easily confounded with each other. In terms of genetics, the similarity in morphology and growth habit between *P. cuieirasensis* and *P. manuripioides* suggest common ancestry and close relations based on nrITS sequences.

Spider fungi

There have been reports of fungi that are pathogenic on spider species, but not about fungi that operates analogous to a spider (in this case, web creation). Aerial litter-trapping systems, as produced by *M. arachnotropus*, *M. foliaiceps*, *P. cuieirasensis* (Figs 1, 4), and *P. manuripioides* (Oliveira et al. 2019), are composed of complex rhizomorph networks that hang from branches of single or multiple trees in the forest understorey (Hedger 1990, Hedger et al. 1993) in many height strata (Snaddon et al. 2012). These efficiently catch leaves and small woody debris (sticks and twigs) that fall from the canopy above. The trapped plant material serves as food for these saprotrophic fungi that digest them with secreted lignocellulosic enzymes and ultimately absorb the assimilable resources in their aboveground parts. This nutritional mode mimics spider species that weave webs in the forest, particularly those in the understorey, to catch insects or other prey (Fig. 11A, B). Thus, we refer to these fungi as "spider fungi".

Hedger (1990) described how the rhizomorph firmly attaches to a substrate by mycelial patches named adhesion zones, and bind plant materials together (Fig. 11C). When a leaf falls from the canopy above and lands on the litter-trapping system, rhizomorphs rapidly form adhesive mycelial patches on the surface of the substrate before it can fall loose. Similar adhesion occurs in *M. arachnotropus*, *M. foliaiceps*, *P. cuieirasensis*, and *P. manuripioides* but not in small zones. Adhesion occurs all along the region of contact of the rhizomorph with the substrate. In *P. manuripioides*, the contact of the rhizomorphs induces necrosis in green, living leaves as adhesion progresses (Oliveira et al. 2019). The number of necrotic spots increases until the leaf dies and is ultimately decomposed by the fungus.

Horse hair blight due to aerial rhizomorph networks causes major economic losses in tea plantations, particularly in Asia and Oceania (Pegler 1983, Hu 1984, Dassanayake et al. 2009, Su et al. 2011). This blight also affects cacao trees, having been reported in Ghana (Africa) by Amoako-Attah et al. (2020) when considering the black thread blight (morphotype A). Defoliation caused by this blight produces a typical pattern of killed single-specimen leaves hanging by their petioles in series near the detachment points from their twigs (Fig. 1B, F). This symptom is provoked by the rhizomorphs of *M. arachnotropus* and *M. foliaiceps* on the hosts, but was not clearly observed for *P. cuieirasensis*. The large diversity of epiphyte rhizomorph-forming fungi reported by Koch et al. (2020) in addition to those reported by Tan et al. (2009), Wannathes et al. (2009), Oliveira et al. (2019), Amoako-Attah et al. (2020), and in this study,

indicates that HHB may not be caused by a single species (*i.e.*, *M. crinis-equi*) but rather by multiple species. Although different species, even from different families, the three new species reported here share the same growth habit and occupy the same niche in tropical forests. This is the same niche as occupied by *P. manuripioides*, *M. chrysocephalus sensu* Koch *et al.* (2020), *M. crinis-equi*, *M. cupressiformis* Berk., *M. neocrinis-equi*, and at least four (*Marasmius* sp. 2 was the only proven aerial litter-trapping system maker in the present study) undetermined *Marasmius* species in Koch *et al.* (2020). All these species that produce litter-trapping rhizomorph webs are spider fungi (Fig. 9). Interestingly, litter-trapping rhizomorph systems also function as shelter for some spider species (Snaddon *et al.* 2012).

CONCLUSIONS

Three new fungal species were discovered and described in the Amazon rainforest, all of which share the formation of aerial litter-trapping rhizomorph systems as the mode of growth and for obtaining food. Without basidiomata, *M. arachnotropus* and *M. foliaiceps* could be easily confounded as a single species based on morphology, which would be named *M. crinis-equi*. *Pusillomyces cuieirasensis* would be even more easily confounded with *P. manuripioides* without fine taxonomy. These four species could have passed for a single species. As indicated in previous studies, considerable numbers of species are able to form epiphyte rhizomorph networks hanging on branches of the understorey. Our study highlights the hidden diversity of species of this fungal guild and strengthens the importance of surveying such fungi with fine taxonomy integrating morphological and phylogenetic analyses. These species are referred to here as “spider fungi” because their aerial litter-trapping rhizomorph systems are like spider webs that enhance effectiveness to capture food (trapped in the web) and because fungi and spiders implement analogous extracorporeal digestion by releasing enzymes in their food and absorb the fluid. This growth habit is an important component of the tropical forest ecosystem, increasing the decomposition rate of plant debris and recycling nutrients in the trophic cycle. Spider fungi also provide habitats and food resources for many arthropods, including *Araneae*, within the litter-trapping rhizomorph systems. Rhizomorphs from these epiphyte systems (also from the ground species) are used by several bird species and even flying squirrels to build their nests. This descriptive study may fuel further ecological research by identifying more species of the aerial litter-trapping rhizomorph web-maker guild. These spider fungi are not only of interest for the functioning of tropical forests and for conservation of biodiversity, but also for agriculture. Horse hair blight (HHB) is caused by spider fungi, and this study along with previous research indicate that the blight may not be caused by a single species (*i.e.*, *M. crinis-equi*) but rather by multiple species. Fungal rhizomorphs, therefore, present a wide range of ecological interactions.

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Supplementary Material: <http://fuse-journal.org/>

Table S1. *Marasmius* sampling with nrITS sequences included in the analyzed Dataset 1.

Table S2. *Pusillomyces* sampling with nrITS and nrLSU sequences included in the analyzed Dataset 2.