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Purple Pinwheel and more: The *Marasmius haematocephalus* complex (*Marasmiaceae*) in Australia

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Abstract: *Marasmius haematocephalus* forms a distinctive pan-tropical species complex. While it has been confirmed that *M. haematocephalus* s. s. occurs only in the neotropics, morphologically similar taxa across the world continue to be attributed to this species. Phylogenies utilising nrITS, nrLSU and *TEF1*, were constructed to identify relationships within the complex, and morphological data used to document and explore the taxa endemic to Australia and those which co-occur in Asia, Madagascar and the USA. Seven new species found in Australia are described and illustrated — *M. campaniformis sp. nov.*, *M. pervagatus sp. nov.*, *M. porphyrocephalus sp. nov.*, *M. purpureospadiceus sp. nov.*, *M. vinaceus sp. nov.*, *M. wianwian sp. nov.* and *M. wunga sp. nov.* A key to Australian species of the *M. haematocephalus* complex is provided. Historic records and observational data (iNaturalist and Atlas of Living Australia) were used to indicate potential distributions of all species within the complex that occur in Australia and explore biogeographic relationships more broadly.

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INTRODUCTION

Marasmius is the type genus for the family *Marasmiaceae* (Kühner 1980). Recently both genus and family have been extensively revised by Oliveira *et al.* (2024b), using morphological and multigene phylogenetic data. The genus *Marasmius* contains approximately 700 species worldwide (Bhunjun *et al.* 2022). While the majority of species are forest floor leaf litter saprotrophs, some form aerial leaf litter traps (Guard *et al.* 2024, Oliveira *et al.* 2024a) and a few occur in grasslands (Antonin & Noordeloos 2010, Crous *et al.* 2020). Rarely they are plant pathogens and possible endophytes (Amoako-Attah *et al.* 2020, Huamán-Pilco *et al.* 2023). As in many diverse basidiomycete lineages, while there are unique morphologically distinctive taxa, there are also many species complexes. Historical separation of species and varieties based on morphological variations (*e.g.* colour morphs), cultural or functional roles is not always maintained when data from new geographic regions is incorporated or molecular data investigated.

The purple pinwheel, *Marasmius haematocephalus* is a distinctive species in the genus *Marasmius.* Its blood red basidiome was first described from Brazil by Montagne in 1837 as *Agaricus haematocephalus* and placed in *Marasmius* by Fries (1838). It was considered pan-tropical and sub-tropical by subsequent mycologists examining the species in tropical Africa, East Africa, Cameroon, Papua New Guinea, Madagascar, Indonesia, Central America and southern Asia (Singer 1976, Pegler 1977, Pegler 1986, Desjardin & Horak 1997, Desjardin *et al.* 2000, Mossebo & Antonin 2004, Antonín & Buyck 2006, Antonin 2007, Tan *et al.* 2009, Wannathes *et al.* 2009). Even though colour and size variations, and spore and cystidia differences suggested that all collections were possibly not one species, these morphological variations were considered to be varieties (Singer 1976), forms (Wannathes *et al.* 2009) or of little taxonomic significance (Desjardin & Horak 1997). Singer (1976) listed nine varieties of *M. haematocephalus* in the neotropics, mainly on colour differences, of which only one, *M. rubicundus*, has been recognised at species level (Oliveira *et al.* 2022). Subsequently, Wannathes *et al.* (2009) reported six forms of *M. haematocephalus* based on variations in colour, pileal dimensions, spore size and substrate, in their study of Thai *Marasmius*. The characters of some Thai forms were similar to those of Singer's varieties, e.g. f. "*violaceus*" appeared to be the same as var. *atroviolaceus*, f. "*luteocephalus"* bore some resemblance to var. *leucophyllus* and f. "*robustus*" shared characters with var. *macrocephalus,* though the substrates differed. Wannathes *et al.* (2009) were unwilling to equate these forms with Singer's varieties, given their vast geographic separation and the lack of molecular data from the neotropical populations.

The addition of molecular data (nrITS only) revealed that all the forms of *M. haematocephalus* in the Thai study grouped in a well-supported clade, and some of them clustered in subclades with good support, while others were unresolved (Wannathes *et al.* 2009). Shay *et al.* (2017) in a study of *Marasmius* in Madagascar simply noted that it "probably represents a complex of species". Oliveira *et al.* (2022) completed the essential critical evaluation of type material of many Brazilian species, epitypified *M. haematocephalus*, and described four new cryptic species in the *M. haematocephalus* complex. That study concluded that *M. haematocephalus* s. s. is a neotropical species, restricted at most to Central and South America. However, it forms a well-supported monophyletic clade with closely related species in tropical Africa and Indo-Malaysia. The sequences from the Thai (Wannathes *et al.* 2009), Malaysian (Tan *et al.* 2009) and Madagascan (Shay *et al.* 2017) specimens were included in the analysis and appeared to resolve into several distinct species level clades. The recent revision of the genus *Marasmius* by Oliveira *et al.* (2024b) has placed the species complex in the newly created subgen. *Globulares*, sect. *Sicci*, emend. J.S. Oliveira & Moncalvo, series *Haematocephali*, emend. J.S. Oliveira & Moncalvo. This revision divides the awkwardly combined *Globulares* - '*globulares/sicci*' section (Antonin & Noordeloos 2010) into two separate sections (*Globulares* and *Sicci*) within the upgraded *Globulares* subgenus. Section *Sicci* forms a monophyletic divergent lineage including the characters of small, parasol-like, sulcate, marasmioid basidiomata, with filiform stipes and scant basal mycelium, well-developed pleurocystidia and elongate basidiospores (Oliveira *et al.* 2024b). No Australian sequences or collections were available at the time for inclusion in the analysis of the *M. haematocephalus* complex (Oliveira *et al.* 2022) and few in the broader revision of the genus *Marasmius* (Oliveira *et al.* 2024b).

Eastern Australian tropical and subtropical habitats are rich in species that appear to be part of the broader *Marasmius haematocephalus* complex. Specimens identified as *M. haematocephalus* have been collected in Australia from as early as 1887, though some were misidentifications. The majority of records in the Atlas of Living Australia are from after 2010, when observational records were included. As little was known about the *M. haematocephalus* complex in Australia, collections in Australian fungaria were listed under this name rather than using Singer's (1976) nine varieties or Wannathes' (2009) six 'forms'. Few collections are held in the southern Australian fungaria [MEL (2), CANB (1), AD (0), NSW (0)], which is logical given the subtropical to tropical distribution of all known species in the complex. Only 6 of the 50 collections in the Queensland herbarium (BRI) were made prior to this study.

Collection of substantial new material of *Marasmius* from tropical and subtropical eastern Australia in the last four years, enabled us to document and explore phylogenetic and biogeographic relationships of Australian endemic taxa, and distinguish and describe seven new species in the *M. haematocephalus* complex. The question of colour as a distinguishing character for species was also investigated.

MATERIALS AND METHODS

Collections and observational records

Fresh collections examined in this study were principally made from 2014 to 2024 in the wet season (December to May) on regular surveys within Dilkusha Nature Refuge in southeast Queensland (SEQ), far north Queensland (FNQ) (Feb. 2021 and Feb. 2023) and northern New South Wales (NSW) (Feb. 2022). These were supplemented by collections from the Queensland Mycological Society (QMS) field trips to Linda Garrett National Park (NP), Mt Cordeaux section of Main Range NP, Springbrook NP, Murrumba Downs Reserve and Bornhoffen Campsite in Numinbah Valley. All collections identified as *Marasmius haematocephalus* and held in the Queensland Herbarium (BRI) were examined. The Atlas of Living Australia records were examined for distributional data and records of historic collections in other Australian Herbaria. The iNaturalist citizen science database of observational records was also examined.

All collections in Queensland were made under the Permits Nos. WITK18734918-1 to 2021 and P-PTUKI-100021825 to 2023 (FNQ) and WITK18760918 and WIF418760818 to 2021 and P-PTUKI-100091861-1 to 2024 (SEQ) and with permission from private landowners. The surveys and collections in NSW were made with permission of the relevant local National Parks Rangers.

Fresh collections were photographed in situ, described and samples taken for DNA analysis (desiccated in silica gel in 1.5 mL tubes). Collections were then dried in an *Ezidri* Snackmaker FD500 (Hydraflow Industries Ltd, Upper Hutt, NZ) food dehydrator at lowest setting for at least 12 h before packeting and storing for submission to BRI fungarium.

Morphology

Basidiomata characters were described from fresh material where possible. These included *pileus* diameter range in millimetres, colour using the Flora of British Fungi Colour Identification Chart (Royal Botanic Garden Edinburgh 1969), shape from juvenile to mature; *lamellae* (L) number range for up to 10 basidiomata, *lamellulae* (l) number of tiers where present, colour and whether marginate, attachment to stipe; *stipe* length and diameter range in millimetres, colour from base to apex, surface texture and insertion into substrate. *Substrate, habitat* and number of basidiomata were also noted. *Spore prints* were obtained whenever possible.

Dried specimens were examined microscopically using a Leica dissecting microscope for hand-cutting sections, and a Prism Optical (Model EX-30T) compound microscope with Tucsen GT12 camera (Tucsen Photonics Co., China) with a 100× objective, for examination of hand cut sections, rehydrated in 5 % potassium hydroxide. Microscopic details were recorded with Mosaic v. 2.0 software (http:// www.tucsen.com). Ammoniacal Congo Red stain and Melzer's reagent were used respectively for recording and measuring details of the pileipellis, cheilocystidia, pleurocystidia, stipe, lamellar and pileal trama and spore length and width and for the amyloid/dextrinoid reaction. Spore measurements were made from fresh spore prints within 12–24 h, or from dried spore prints or herbarium material for a minimum of 10 basidiospores per specimen, and up to 50 basidiospores from each of 2–11 basidiomata for new taxa, where possible, obtaining range of length × width in micrometres, mean length [± standard deviation SD], × width [± SD], with Q (Quotient of length/width) measurements for mean (Qm) [± SD], minimum and maximum; N = number of basidiospores measured.

Molecular sampling and analysis

Samples were first ground with two 3-mm-diam. tungsten carbide balls at high speed for 20 s, twice in a bead mill (Fast Prep-24™ 5G, MP Biomedicals, CA, USA). The DNA extraction was performed using the Omega Bio-tek Inc. Norcross, GA, USA, EZNA Forensic Kit following the prescribed protocols for hair, nails & feathers, apart from substituting 0.8 µL b-mercaptoethanol for 20 µL 1 M DTT and using 50 µL elution buffer twice instead of 100 µL, for a more concentrated extract. The internal transcribed spacer region (ITS1-5.8S-ITS2; nrITS) rDNA, was amplified using primers ITS1-F (Gardes & Bruns 1993) and ITS4 (White *et al.* 1990) and the large subunit (nrLSU) with primers LR7 & LROR (Vilgalys & Hester 1990) in a reaction mixture of 1 µL of each primer, 12.5 µL MyTaq Red Mix (Bioline, NSW, Australia), 0.8 µL 10 % bovine serum albumin (BSA) and 7.7 µL sterile water. The thermal cycling conditions included 35 cycles of 95 °C for 60 s, 51 °C for 60 s and 72 °C for 60 s, with a final extension step of 72 °C for 10 min for the nrITS, and 95 °C for 60 s, 48 °C for 60 s, 72 °C for 60 s, with a final extension step of 72 °C for 10 min for nrLSU. In addition, the translation elongation factor (*TEF1*) region, using primers EF1-983F and EF1-1567R (Rehner & Buckley 2005), was amplified from representatives of each group in the complex. The thermocycling conditions used were an initial denaturation for 15 min at 95 °C, followed by 10 cycles of 94 °C for 30 s, 65 °C for 60 s (decreasing by 1 °C per cycle) and 72 °C for 90 s; then 30 cycles of 94 °C for 45 s, 55 °C for 60 s, 72 °C for 70 s (extending 1 s per cycle); with a final elongation step of 72 °C for 5 min. Samples were sent to Macrogen, Seoul, Korea, for purification and Sanger sequencing.

Sequences generated for this project were manually edited using Geneious Prime 3 v. 2023.2.1. (https://www.geneious.com). BLAST searches were conducted in the GenBank NCBI database (http://www.ncbi.nlm.nih.gov/) to recover sequences of conspecific or close species. Initial alignments of nrITS, nrLSU and *TEF1* were constructed using MAFFT (Katoh & Standley 2013). All sequences in GenBank labelled *Marasmius haematocephalus* or aff. *haematocephalus* were also downloaded and included in an initial phylogenetic tree for the nrITS gene region. Subsequent alignments included only those sequences that were good quality and relevant for this study. i.e. exemplars from sect. *Sicci*, ser. *Haematocephali*. Following Oliveira *et al.* (2024b), *Marasmius recreigardneri* in the closely related ser. *Ferruginei*, was used as the outgroup. Table S1 (Supplementary material) lists all sequences used in the phylogenetic analyses of this study, with newly generated sequences in **bold** and those from the holotypes in red. Names of species from sequences downloaded from GenBank are as they appear in GenBank.

Phylogenetic analyses were conducted for each gene region separately using Bayesian and Maximum Likelihood. Maximum likelihood (ML) analyses were conducted using RAxML v. 8.2.11 (Stamatakis 2014) with the GTR+GAMMA+I model using default parameters for 1500 rapid bootstrap (BS) replicates. Bayesian analysis was performed with MrBayes v. 3.2.6 (Huelsenbeck & Ronquist 2001) using the substitution model GTR and Metropolis Coupled (MCMCMC) settings, for 1 M iterations. Here we present the Bayesian phylogenetic tree of the nrITS data with maximum likelihood values shown (BS/PP) at nodes with support =/> 70/0.9 (Fig. 1), and the *TEF1* tree (Fig. 2) in the same way. The nrLSU and concatenated nrITS+nrLSU+*TEF1* alignments are included in Supplementary material (Figs S1, S2). Newly generated sequences were registered with GenBank and new taxa with MycoBank.

RESULTS

DNA sequencing

Approximately 60 fresh collections, supplemented by herbarium specimens, were examined in this study and 52 of them successfully sequenced with nrITS and nrLSU primers. The translation-elongation factor 1-alpha (*TEF1*) region was also sequenced for 31 collections. The Bayesian and Maximum likelihood analyses of all three gene regions gave congruent results in supporting broader clades and grouping of species. While *TEF1* was a much reduced dataset, it was useful in disentangling relationships within some apparent species complexes not clearly resolved by the nrITS alone. The final nrITS alignment included a total of 33 sequences generated for Australian taxa and 50 of several geographic origins from GenBank representing the *M. haematocephalus* complex. The final *TEF1* alignment includes 42 sequences.

A monophyletic clade of the broader *haematocephali* complex (ser. *Haematocephali)* is strongly supported (ITS 100/1), and most species also have strong support with lower support for some relationships between taxa (Fig. 1). Within the complex are four major clades and several geographic subclades, annotated on the nrITS phylogeny as *e.g.* 3A, 3B, etc.

Marasmius wianwian sp. nov. (clade 1A), one of the red-pileate species, is strongly supported (100/1) across all gene regions, as a distinct taxon, sister to all other species in the complex (Figs 1, 2). It appears to be an Australian endemic species with a highly restricted distribution in northern New South Wales and southeast Queensland.

The remainder of the complex then divides into two clades. Clade 2A contains three closely related Australian endemic species (*M. vinaceus*, *M. purpureospadiceus* and *M. campaniformis),* and a single sequence representing a species from Hainan, China. This clade has moderately high support for both nrITS (79/0.99) and *TEF1* (100/1). The sequences are up to 98.2 % identical for the nrITS across the four species in this clade but for the *TEF1* region, they are only 93 to 95.4 % identical between the four species. The Chinese sequence is most similar to that of *M. vinaceus sp. nov.*, with 98.2 % similarity for the nrITS. No morphological information was accessible for the Chinese collection. Morphological differences among the three new Australian species also support their delineation as distinct taxa — *M. vinaceus sp. nov.*, *M. purpureospadiceus sp. nov*. and *M. campaniformis sp. nov.* Interestingly, *M. campaniformis* basidiomata are trimorphic, with the colour variants — cinnamon, lilac and pink showing no significant molecular variation in all three gene regions (99.3 to 100 % identical).

Clade 2B includes all other currently known members of the *M. haematocephalus* complex worldwide with strong support for the nrITS (96/1) (Fig. 1) and moderate to strong support for the *TEF1* (78/0.98) (Fig. 2), in three distinct

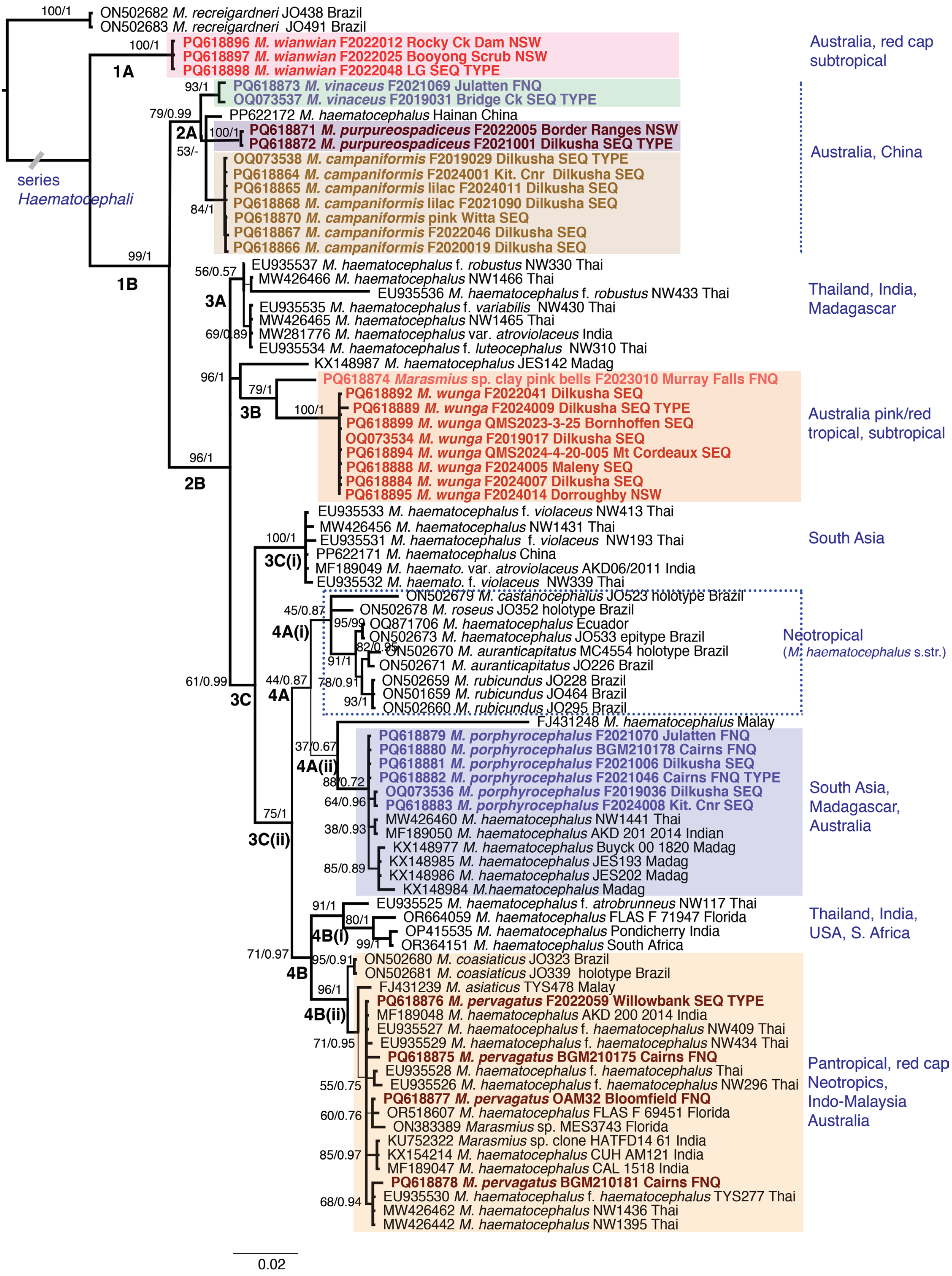

Fig. 1. Phylogenetic analysis of the *Haematocephali* complex in sect. *Sicci*, ser. *Haematocephali* inferred from Bayesian and Maximum Likelihood analysis of the nrITS region with *M. recreigardneri*, subsect. *Ferruginei*, as outgroup, showing the geographic distribution of the complex, with coloured blocks indicating species that occur in Australia. All coloured sequences have been produced in this study.

groupings. With weak support for the nrITS (56/0.57), subclade 3A consists of taxa from Thailand-India-Madagascar and includes four of the six Thai colour variants noted by Wannathes *et al.* (2009) (*M. haematocephalus* f. *robustus*, var. *atroviolaceus*, f. *luteocephalus* and f. *variabilis*) and a single sequence from Madagascar (JES142). JES142 was also noted to be on a long branch from other Madagascan ‘*haematocephalus’* sequences by Shay *et al.* (2017). With the addition of more sequences from Brazil, the Indian subcontinent and Australia, it remains on a separate branch, distant from the other Madagascan *M. ‘haematocephalus’* complex species*.* This whole subclade requires analysis of other gene regions for further clarification of the status of these taxa.

The moderately to strongly supported (nrITS 79/1) subclade 3B consists of two Australian species, *Marasmius* sp. ‘buff pink bells’ represented by a single specimen from north Queensland and *Marasmius wunga sp. nov.* (100/1), which has a limited distribution in south-east Queensland and northern New South Wales. *Marasmius wunga sp. nov*. is the second red-pileate species in Australia. Subclade 3C is weakly to strongly supported (61/0.99) and contains a diverse mix of species, including *M. haematocephalus* s. s. from Brazil, and more Australian, southeast Asian, Madagascan and pan-tropical subclades. The support for this subclade with the *TEF1* region is strong (98/1). Subclade 3C(i) appears to equate with *M. haematocephalus* f. *violaceus,* sensu Wannathes *et al.* (2009). A sequence labelled as *M. haematocephalus* var. *atroviolaceus* from India (AKD06/2011) is 99.4 % similar to the Thai sequences. The recent addition of a sequence from the tropical Chinese island of Hainan, makes this a south Asian species clade.

The moderately well supported subclade 3C(ii) (75/1.0) contains the poorly supported subclade 4A (44/0.87) with a

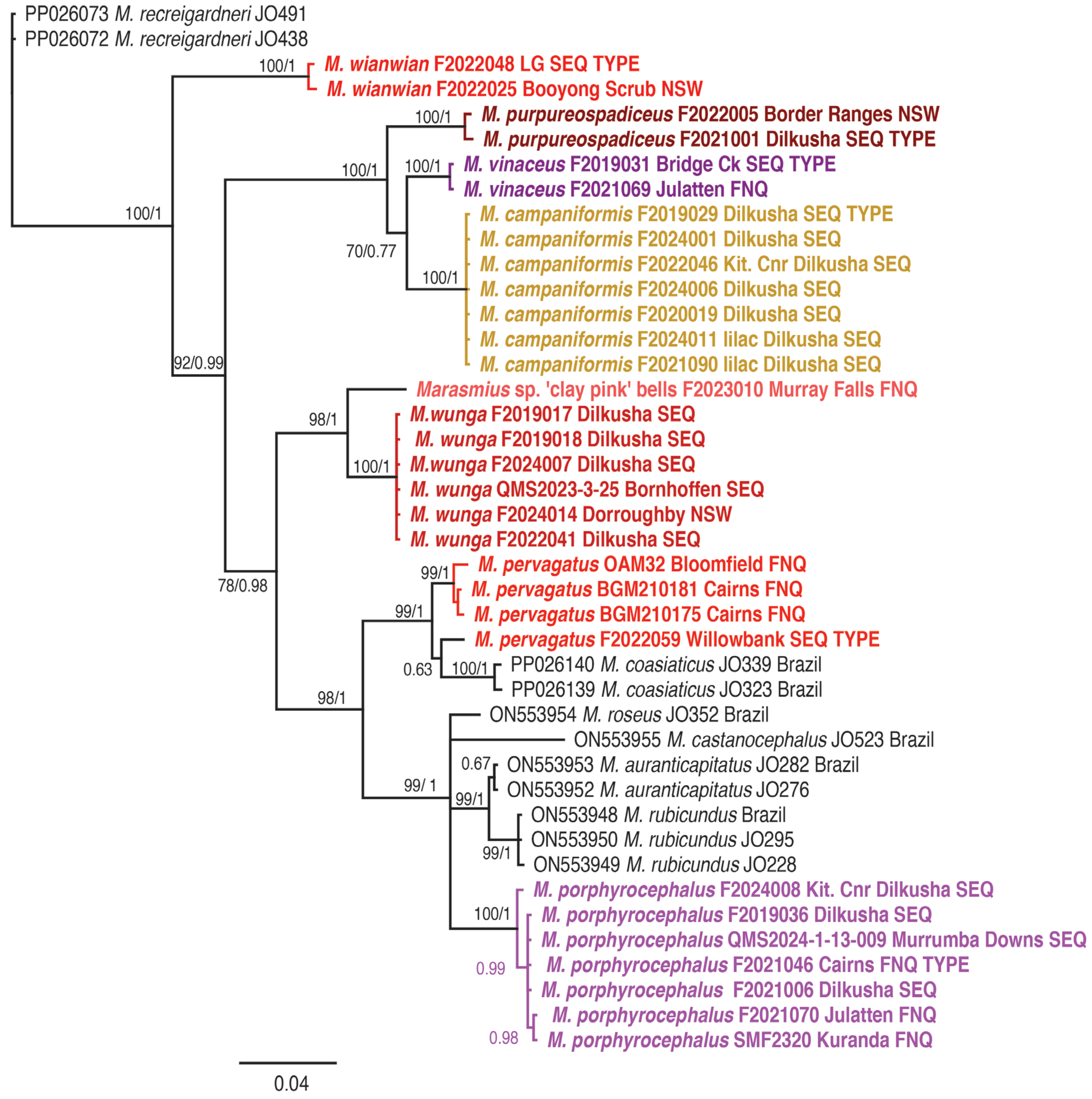

Fig. 2. *TEF1* analysis with Bayesian & RAxML; BS/PP and bolded lines for well-supported nodes. All coloured sequences have been produced in this study.

neotropical group of species 4A(i), and a mixed Australian, Madagascan and south Asian group of species 4A(ii). The neotropical endemic clade from Brazil and surrounds includes *M. haematocephalus* s. s., several recently described species from Brazil — *M. roseus*, *M. castanocephalus*, *M. auranticapitatus* and *M. rubicundus* (was var. *rubicundus* Singer) (Oliveira *et al.* 2022). The clade has low support (45/0.87) with the nrITS. Oliveira *et al.* (2022) used other gene regions (*TEF1* and *RPB2*), together with morphological differences, to separate the closely related, cryptic species in this clade (Fig. 2).

Subclade 4A(ii) includes the Malaysian TYS523 '*M. haematocephalus*' (sequence FJ431248) as sister species on a long branch to the moderately supported (88/0.72) *M. porphyrocephalus sp. nov.*, which includes sequences from Thailand, India and Madagascar. The Australian sequences are 99.1–99.9 % identical for the nrITS, with slightly less support for the Thai-Indian pair (MW426460 and MF189050) and the Madagascan sequences. However, as with the neotropical Brazilian clade 4A(i), further analysis of other gene regions (*TEF1* and *RPB2*) and morphological data are needed to confirm whether non-Australian material represent additional cryptic species.

The final subclade 4B, with moderate to strong support (71/0.97), includes specimens from across the world including Thailand, India, South Africa, Brazil, Malaysia, Queensland (Australia) and Florida (USA). Subclade 4B(i) with strong support (91/1.0), contains a single specimen each from Thailand (f. *atrobrunneus* Wannathes *et al.* 2009), USA (Florida), India and South Africa. More data are required to elucidate this group.

The strongly supported (96/1.0) subclade 4B(ii) includes *Marasmius coasiaticus* from Brazil and *M. asiaticus* from Malaysia. *Marasmius asiaticus* is moderately to strongly supported (71/0.95) as sister species to the final pantropical species, *M. pervagatus sp. nov.*, which shows some molecular (nrITS) and geographic variation. Four Australian specimens (F2022059, OAM32, BGM210175 & BGM210181), and multiple Indian, Thai and USA (Florida) specimens are included in this complex clade. Most of the Thai sequences are from the *M. haematocephalus* form *'haematocephalus'* sensu Wannathes *et al.* (2009). Morphologically they closely resemble *M. pervagatus sp. nov.* Analysis of the *TEF1* data groups three of the Australian sequences (OAM32, BGM210175 & BGM210181) in a clade with strong support (99/1.0) and F2022059 remains on a separate branch with low support (Fig. 2), distinct from *M. coasiaticus*. At this point we prefer not to describe multiple single collection taxa within this complex, even though *TEF1* does suggest that F2022059 is likely a different species. Instead, we describe a single species, *M. pervagatus* to provide a point of reference for international researchers to utilise. Further work is needed on this group, with more collections, morphological data and using more gene regions to resolve these potentially cryptic taxa.

Taxonomy

Marasmius campaniformis F.E. Guard, T. Lebel, Dearnaley, ***sp. nov.*** MB 857168. Figs 3, 4.

Etymology: The epithet is from the Latin '*campaniformis*' meaning bell-shaped, referring to the shape of mature caps of this species.

Typus: **Australia**, Queensland, Balmoral Ridge, Dilkusha Nature Refuge, Kitchen Corner, S26°44'19.9", E152°53'39.9", 335 m.a.s.l., on road verge in *Allocasuarina* needles and regenerating subtropical rainforest leaf litter, 26 Apr. 2019, *F.E. Guard*, F2019029 (cinnamon form) (**holotype** BRI AQ1007372, **isotype** MEL2469586); GenBank numbers nrITS OQ073538, nrLSU OQ073543, *TEF1* PV151757.

Description: *Basidiomata* small marasmioid. *Pileus* 10–20 mm diam., three colour forms: (i) common, sienna (11) to cinnamon (10), smooth central disc with buff (52) outer

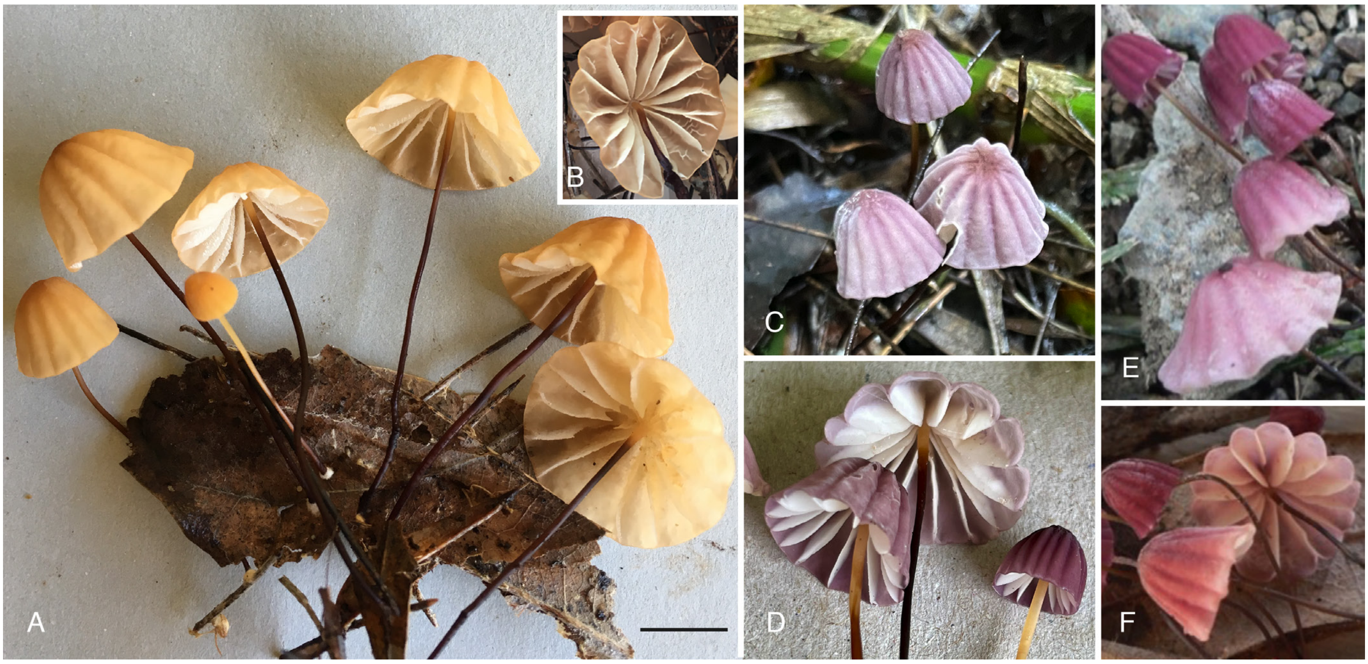

Fig. 3. *Marasmius campaniformis.* **A.** Cinnamon colour variant. **B.** Inset showing lamellae attachment. **C, D.** Lilac to vinaceous-grey. **E, F.** Pink con-specific forms. Scale bar = 10 mm. Images by F.E. Guard.

two-thirds, (ii) uncommon lilac (79) central disc with pale lilac to lavender (81) outer two-thirds, juveniles vinaceous grey (80) and (iii) rare dusty rose (39) with paler margin and maroon juveniles; deeply sulcate-striate, broadly parabolic to campanulate, surface dry. *Lamellae* free, distant, 12–16, cream-buff to pale pink, non-marginate, with low inter-venations or uncommon bifurcations in mature pilei. *Lamellulae* rare to absent. *Stipe* 30–45(–60) × 0.5–1 mm, filiform, central, base black, mid-shaft dark brown to chestnut (23), apex buff, juvenile stipes more reddish with pale pink apex, smooth, glossy, twisted, hollow, non-insititious insertion with small off-white basal mycelial pad. *Spore print* white. *Basidiospores* (14–)17.5–21 × 4–4.5 µm, mean 19 [± 1.09 SD] × 4 [± 0.21 SD] µm, *Q* = 4.43–5.36, *Qm* = 4.73 [± 0.28 SD], N = 20, narrow, clavate, slightly curved, thin-walled, smooth, inamyloid. *Basidia* not found, *Basidioles* clavate, fusoid 19–28 × 5.5–7.5 µm. *Cheilocystidia* of two types in equal proportions – (i) *Siccus*-type cells, narrow to broadly clavate, cylindrical, sub-globose, main body 9–16 × 6.5–13 µm, with crowded to sparse apical setulae 2–5 × 0.5–1 µm and (ii) smooth cells similar to the pleurocystidia, capitate, utriform, lageniform, lecythiform, 21–43 × 6.5–9.5 µm. *Pleurocystidia* common, mostly capitate, occasionally strangulate, fusoid, lageniform, rarely bifid, 31–50 × (6–)7–11 µm. *Lamellar trama* mildly dextrinoid, hyphae thin-walled 6.5–7.5 µm diam. *Pileal trama* hyphae 5.5–8 µm diam. *Pileipellis* a hymeniderm of *Siccus*-type cells, main body clavate, cylindrical, sub-globose 6–16 × 5.5–10 µm, with usually crowded (rarely sparse) thick-walled apical setulae, 3–5 × 0.5–1 µm. *Stipe* hyphae parallel, those in cortex 5–6 µm diam., those in medulla 4–7 µm diam., inamyloid. *Caulocystidia* absent. *Clamp connections* present in all tissues.

Other collections examined: **Australia,** Queensland, Balmoral Ridge, Dilkusha Nature Refuge, road verge Elsie's Grove, in *Allocasuarina* needles and twigs (cinnamon form), 29 Jan. 2020, *F.E. Guard*, F2020019 (BRI AQ1017487; GenBank numbers nrITS PQ618866, nrLSU PQ618826, *TEF1* PV151733); Kitchen Corner in *Allocasuarina* litter (cinnamon form), 5 Mar. 2022, *F.E. Guard*, F2022046, (BRI AQ1041084; GenBank numbers nrITS PQ618867, nrLSU PQ618867, *TEF1* PV151744); towards Kitchen Corner in leaf litter under regenerating subtropical rainforest (cinnamon form), 5 Jan. 2024, *F.E. Guard*, F2024001 (BRI AQ1045954; GenBank numbers nrITS PQ618864, nrLSU PQ618840, *TEF1* PV151749); Hilary's Corner, in road verge litter under regenerating subtropical rainforest (cinnamon form), 9 Jan. 2024, *F.E. Guard*, F2024006 (BRI AQ1045958; GenBank numbers nrITS PQ618869, nrLSU PQ618869, *TEF1* PV151750); above Lot 3, in road verge litter, (lilac form), 19 Mar. 2021, *F.E. Guard*, F2021090 (BRI AQ1034086; GenBank numbers nrITS PQ618868, nrLSU PQ618827, *TEF1* PV151731); above Lot 1 in road verge litter (lilac form), 19 Jan. 2024, *F.E. Guard*, F2024011 (BRI AQ1045963; GenBank numbers nrITS PQ618865, nrLSU PQ618841, *TEF1* PV151753); Witta, Schultz Rd, private garden leaf litter (pink form), 4 Feb. 2009, *F.E. Guard*, FG0036 (BRI AQ1004887; GenBank number nrITS PQ618870).

Habit, habitat and distribution: *Marasmius campaniformis sp. nov.* occurs regularly in scattered groups among leaf litter from *Allocasuarina* needles and pioneer species of regenerating subtropical rainforest, on damp roadside verges in Dilkusha Nature Refuge, Blackall Range, SEQ. Regular observation of fungi in the Refuge, has shown *M. campaniformis* to produce basidiomata in wet seasons from January to April. No basidiomata were produced in the drought year of 2023. On one occasion (2009) the pink form was collected from mulch under regenerating rainforest on private land in Witta, approximately 12 km from Dilkusha.

Notes: Dilkusha Nature Refuge was originally covered by subtropical rainforest, but was cleared in the 1940s and used as a dairy farm until the early 1980s. It has been actively revegetated with native plants since 1990 and was gazetted a Nature Refuge in 1993. In 30 years (1990–2020), the rainforest has become well established, though it will be decades before 'old growth' status is achieved. This transitional phase, as pioneer tree species are gradually replaced by climax species, appears to suit many saprotrophic fungal species, including *M. campaniformis*, which are not found in neighbouring reserves of old growth rainforest. Apart from their colour, the cinnamon, lilac and pink forms are identical morphologically and molecularly. *Marasmius campaniformis* differs from *M. haematocephalus* s. s. in its colour (all forms), pileal size (10–20 mm c.f. 2.5–16 mm), number of lamellae (12–16 c.f. 7–10) and shorter, sturdier stipe (30–40 × 0.5–1 mm c.f. 22–62 × 0.2–0.5 mm) and also the dimorphic cheilocystidia (Oliveira *et al.* 2022). *Marasmius campaniformis* (Fig. 3) in its lilac form resembles the Thai *M. haematocephalus* f. '*robustus*' with its pileal colour and robust stature, though the basidiospores are slightly shorter (mean 19 c.f. 20 µm) and lamellae more numerous (12–16 c.f. 9–15); both have similar dimorphic cheilocystidia (Wannathes *et al.* 2009). However, molecular analysis places them in two widely separated and distinct clades (Fig. 1). *Marasmius campaniformis* in its cinnamon

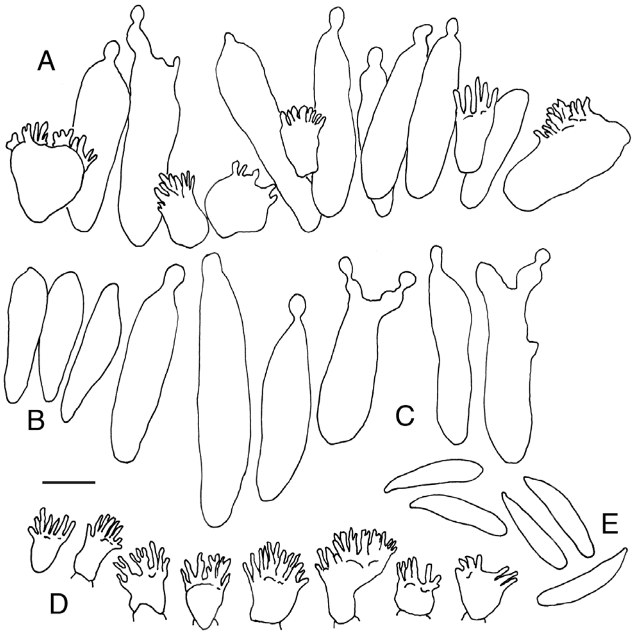

Fig. 4. *Marasmius campaniformis* (F2024001). **A.** Cheilocystidia *Siccus*-type cells and pleurocystidia-type cells. **B.** Basidioles. **C.** Pleurocystidia. **D.** Pileipellis *Siccus*-type cells. **E.** Basidiospores. Scale bar = 10 µm. Illustrated by F.E. Guard.

form resembles *M. lebeliae* (Crous *et al.* 2019) which occurs in the same habitat. However, *M. lebeliae* is more brownish, has smaller pilei (5–12 c.f. 10–20 mm), fewer lamellae (7–11 c.f. 12–16), longer stipes (35–60 c.f. 30–40 mm) and much larger basidiospores (mean 32 × 5 µm). *Marasmius lebeliae* is in the recently established sect. *Globulares*, subsect. *Atrorubentes* (Oliveira *et al.* 2024), ser. *Crinipes* (Oliveira *et al.* 2020). *Marasmius vinaceus sp. nov.* is difficult to distinguish macroscopically from the lilac form (though slightly more pinkish in colour and with smaller pilei on longer stipes), but microscopically the basidiospores are shorter (mean 17.5 c.f. 19 µm); the pleurocystidia are mostly longer and simpler in form and the cheilocystidia are monomorphic, *Siccus*-type cells only, while *M. campaniformis* has both *Siccus*-type and pleurocystidia-type cheilocystidia cells. *Marasmius purpureospadiceus sp. nov.* is similar in colour and pileal size, but has more lamellae (16–18 c.f. 12–16) and longer, more robust stipes (45–60 × 1 mm c.f. 30–40 × 0.5–1 mm). All three species form a strongly supported clade Fig. 1 (79/0.99), Fig. 2 (100/1) with their sister species from China (GenBank nrITS PP622172) in the nrITS tree.

Marasmius pervagatus F.E. Guard, T. Lebel, J. Dearnaley, ***sp. nov.*** MB 857172. Figs 5, 6.

Etymology: The epithet *pervagatus* is Latin for widespread and common, and refers to its pan-tropical distribution.

Typus: **Australia**, Queensland, Brisbane, Willowbank, Champions Way, S 27°41’31.31”, E152°39’55.13”, 56 m.a.s.l., in leaf litter on urban road verge with *Eucalyptus*, *Acacia* and *Alphitonia* sp. trees, 6 Jun. 2022, *N.A. Fechner*, F2022059 (**holotype** BRI AQ1043697); GenBank numbers nrITS PQ618876, nrLSU PQ618876, *TEF1* PV151737.

Description: *Basidiomata* small, marasmioid. *Pileus* 5–10 mm diam., blood red (41), red (42) or coral (44), broadly convex, parabolic to campanulate, sulcate-striate, central disc smooth, dry glabrous. Figure 5 illustrates the colour variations of this species. *Lamellae* distant, 8–13, occasionally bifurcate, free, pale pink (39) with margin concolourous with the pileus. *Lamellulae* sparse, 1–2 tiers. *Stipe* 15–50 × 0.1–0.5 mm, central, filiform, smooth, hollow, dark brown base grading to buff apex, non-insititious, with small off-white basal mycelial disc. *Basidiospores* (15–)16–19.5 × 4–5 µm, mean 17.5 [±0.82 SD] × 4 [± 0.26 SD] µm, Q = 3.78–5.57, Qm = 4.51 [± 0.35 SD], N = 50 from type collection, narrow, clavate, slightly curved, thin-walled, smooth, inamyloid. *Basidia* 4-spored. *Basidioles* fusoid to clavate, 19–25 × 6–7 µm. *Cheilocystidia* dimorphic with (i) common *Siccus*-type cells, cylindrical, clavate, sub-globose, main body 9–20 × 6.5–9 µm, apical setulae thick-walled, refractile, occasionally in bunches, (2–)3–6 × 1–1.5 µm and (ii) less common smooth cells similar to the *pleurocystidia* 29–38 × 7–11.5 µm. *Pleurocystidia* large smooth cells, thin-walled, inamyloid, capitate, with 1–3

Fig. 5. *Marasmius pervagatus* basidiomata. **A–C.** Holotype collection BRI AQ1043697 (images by F.E. Guard). **D, E.** BGM210175 & BGM210181 (images by B.G. Muir). **F.** OAM32 (image by O. Albert-Mitchell). Scale bars = 10 mm.

constrictions, occasionally branched, lageniform, hyphoid or utriform, 24–49 × 5.5–14 µm. *Lamellar trama* dextrinoid, hyphae 3.5–5 µm diam. *Pileipellis* mottled, consisting of a hymeniderm of *Siccus*-type cells, clavate, broadly clavate, sub-globose, pyriform, sometimes bifid, main body 6–22 × 6–10 µm, usually thin-walled, occasionally thick-walled, with multiple thick-walled refractile apical setulae, occasionally bifid, 2–5 × 0.5–1(–2) µm. *Pileal trama* weakly dextrinoid, hyphae 4–6 µm diam. *Stipe* hyphae parallel, cortex 3.5–5.5 µm diam., medulla 5–6 µm diam., inamyloid. *Caulocystidia* absent. *Clamp connections* present in all tissues.

Other collections examined: **Australia**, Queensland, Bloomfield, in wet tropical rainforest, on leaf litter, 10 Jan. 2020, *O. Albert-Mitchell*, OAM32 (envt; GenBank numbers nrITS PQ618877, nrLSU PQ618863, *TEF1* PV151713); Cairns, Flecker Botanic Gardens, in mulched garden bed, 19 Jan. 2021, *B.G. Muir*, BGM210175 (BRI AQ1034090; GenBank numbers nrITS PQ618875, nrLSU PQ618831, *TEF1* PV151728) and BGM210181 (BRI AQ1041070; GenBank numbers nrITS PQ618878, nrLSU PQ618832, *TEF1* PV151738).

Habit, habitat and distribution: Basidiomata of *Marasmius pervagatus* are gregarious, often with 20–30 basidiomata in a group. It has been found in north Queensland (FNQ) and also in Brisbane (SEQ). Basidiomata production may occur from summer through to winter. The habitat is often disturbed vegetation, e.g. mulched garden beds, but may also be undisturbed rainforest.

Notes: *Marasmius pervagatus sp. nov.* is one of the blood red species of the *M. haematocephalus* complex found in Australia. It differs from *M. haematocephalus* s. s. in having overlapping but usually more lamellae (8–13 c.f. 7–10), shorter basidiospores (mean 17.5 µm c.f. 20 µm) and two types of cheilocystidia, both *Siccus*-type cells and pleurocystidia-type cells c.f. *Siccus*-type only. It is morphologically very similar to *M. wianwian sp. nov.,* though the cheilocystidia of *M. wianwian* are mono-morphic; also *M. wunga sp. nov.* which has more lamellae (12–16 c.f. 8–13), larger basidiospores (mean 21 × 4.5 µm) and longer stipes (30–60 mm c.f. 15–50 mm).

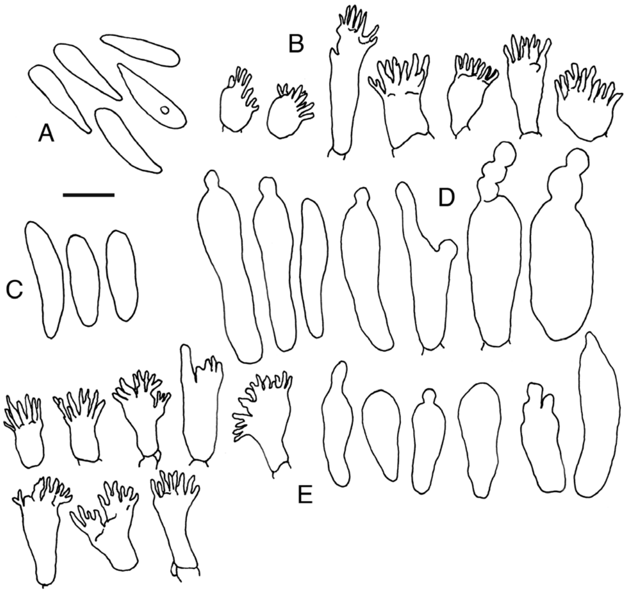

Fig. 6. *Marasmius pervagatus* (BRI AQ1043697). **A.** Basidiospores. **B.** Pileipellis *Siccus*-type cells. **C.** Basidioles. **D.** Pleurocystidia. **E.** Cheilocystidia *Siccus*-type cells and smooth cells. Scale bar = 10 µm. Illustrated by F.E. Guard.

Phylogenetic analysis resulted in the three red-pileate species of the complex occurring in Australia placed in widely separated clades. *Marasmius pervagatus sp. nov.* is closely related to both *M. asiaticus* described from Malaysia (Tan *et al.* 2009) and *M. coasiaticus* described from Brazil (Oliveira *et al.* 2022). It differs in the pileus size, being bigger than that in *M. asiaticus* (5–10 mm pileal diam. c.f. 2–8 mm), with more lamellae (8–13 c.f. 7–8) and longer stipe (15–50 mm c.f. 11–22 mm). The basidiospores are smaller on average (18.5 × 4 µm c.f. 21.5 × 4 µm) and the cheilocystidia are dimorphic, whereas in *M. asiaticus* they are *Siccus*-type cells only. *Marasmius coasiaticus* differs in colour being brownish red to brownish pink, with lamellae that are adnate, cream, non-marginate and no lamellulae, whereas *M. pervagatus sp. nov.* produces purple to blood red pilei, with free to adnexed, pink, marginate lamellae and 1–2 tiers of sparse lamellulae.

Morphologically the Australian specimens are variable in pileal diameter and colour, stipe dimensions and substrate. Specimen OAM32 is at the smaller end of the range for all macro-morphological parameters. However, based on the nrITS (Fig. 1), they form a single clade with low to moderate support (55/0.75) and the *TEF1* tree (Fig. 2) has the three north Queensland collections in a well-supported clade (99/1.0) and the south-east Queensland collection on a separate branch with low support (Fig. 2). No nrLSU or *TEF1* sequences of the Thai collections are available for comparison. In Thailand this species has been called *M. haematocephalus* f. '*haematocephalus*', one of the six morphological forms described by Wannathes *et al.* (2009). Macro- and micro-morphology of these collections match *M. pervagatus sp. nov.*, except for the non-marginate lamellae in the Thai forms. The Indian and Florida, USA specimens are almost identical in the nrITS data, but these collections have not been compared morphologically or using other gene regions.

Although *M. pervagatus sp. nov*. has been found in widely separated locations in Queensland, it does not appear to be as common as *M. porphyrocephalus* and more search effort is required to determine its full distribution and whether there are cryptic species hidden in this clade.

Marasmius porphyrocephalus F.E. Guard, T. Lebel, Dearnaley, ***sp. nov.*** MB 857173. Figs 7, 8.

Etymology: The epithet is from the Greek '*porphyro*' meaning purple, referring to the colour of the pileus of this species and '*cephalus*' is Greek for head.

Typus: **Australia**, Queensland, Cairns Botanical Gardens, S16°53'58.4", E145°44'51.2", in garden mulch, 11 Feb. 2021, *F.E. Guard* & *T. Lebel,* F2021046 (**holotype** BRI AQ1034084); GenBank numbers nrITS PQ618882, nrLSU PQ618852, *TEF1* PV151740.

Description: *Basidiomata* small, marasmioid. *Pileus* (3–)5–14(–20) mm diam., colours varying from candy pink, pinkish-purple (40) to vinaceous (76), with blood red (41) to livid vinaceous (77) central disc and radiating sulci, colour fading with age, broadly parabolic to almost applanate with wavy margins at maturity, and a slightly depressed darker central disc, surface dry, glabrous. *Lamellae* free to adnexed, distant, 12–16, with occasional irregular lamellulae and bifurcations, pale rose (39) to pale vinaceous (76), ± margin faintly concolourous with pileus. *Stipe* (15–)30–45(–60) × 0.2–0.5 mm, blackish-brown base, purplish chestnut (21) trunk, rose pink (39) to purple (40) apex, glabrous, hollow, filiform, non-insititious with tiny basal disc of off-white mycelium. *Spore print* white. *Basidiospores* (15.5–)16.5–19.5(–23) × 4–4.5 µm, mean 17.5 [± 0.99 SD] × 4 [± 0.20 SD] µm, Q = 3.56–4.76, Qm = 4.13 [± 0.32 SD], N = 20, narrow, elongate, clavate, thin-walled, smooth, inamyloid. *Basidia* 4-spored, 20–24 × 7–8.5 µm. *Basidioles* 20–23 × 6–8.5 µm, fusoid to clavate. *Cheilocystidia* (i) *Siccus*-type cells forming a sterile edge, cylindrical, broadly clavate, sub-globose, occasionally bifid, main body 10–22 × 7.5–10 µm with multiple apical thick-walled setulae 2–5 × 1–1.5 µm; (ii) rare smooth, irregular, clavate to bifid cells 12–38 × 10–17 µm. *Pleurocystidia* moderately common 22–54 × 5–13 µm, simple cylindrical with obtuse apex, lageniform, capitate occasionally strangulate, thin-walled, hyaline. *Lamellar trama* hyphae 3.5–5 µm diam. *Pileal trama* dextrinoid, hyphae thin-walled, 5–5.5 µm diam. *Pileipellis* a hymeniderm of *Siccus*-type cells, similar to cheilocystidia type (i), cylindrical, clavate, spathulate, sub-globose, main body 7.5–14.5 × 5.5–9 µm with multiple thick-walled refractile apical setulae 2–6 × 1–2 µm. Stipe hyphae parallel, cortex with hyphae 5–6 µm diam., slightly dextrinoid, medullary hyphae 5–7 µm diam., slightly dextrinoid. *Caulocystidia* absent. *Clamp connections* present in all tissues.

Other collections examined: **Australia**, Queensland, Balmoral Ridge, Dilkusha Nature Refuge, road verge near creek, in subtropical rainforest understorey, 1 May 2019, *F.E. Guard*, F2019036 (BRI AQ1007378; GenBank numbers nrITS OQ073536, nrLSU OQ073539, *TEF1* PV151763); on road verge in leaf litter, 29 Jan. 2020, *F.E. Guard*, F2020021 (BRI AQ1017489; GenBank number nrLSU PQ618834); in subtropical riparian rainforest, on mossy bark, 20 Jan. 2021, *F.E. Guard*, F2021006 (BRI AQ1021681; GenBank numbers nrITS PQ618881, nrLSU PQ618853, *TEF1* PV151741); and on road verge among *Allocasuarina* sp. needles, 9 Jan. 2024, *F.E. Guard*, F2024008 (BRI AQ1045960; GenBank numbers nrITS PQ618883, nrLSU PQ618851, *TEF1* PV151752); Cairns, Edge Hill, Flecker Botanic Gardens, Collins Avenue, in garden bed mulch, 19 Jan. 2021, *B.G. Muir*, BGM210178 (BRI AQ1041069; GenBank numbers nrITS PQ618880, nrLSU PQ618838); Eudlo, 56 Eudlo School Rd, in garden mulch, 14 Feb. 2024, *J. Rodwell*, JR001 (BRI AQ1052603; GenBank number nrLSU PQ618835); Julatten, Clacherty Road, on road verge in leaf litter, 17 Feb. 2021, *F.E. Guard*, F2021070 (BRI AQ1034085; GenBank numbers nrITS PQ618879, nrLSU PQ618833, *TEF1* PV151730); Kuranda, Russett Park, Jeffrey Rd, 300 m from Barron River bridge, in rainforest litter, 22 Jan. 2006, *S.J.M. McMullan-Fisher*, SMF2320 (MEL2297133; GenBank number *TEF1* PV151759); Murrumba Downs, John Oxley Reserve, in wet sclerophyll forest among leaf litter, 13 Jan. 2024, *W.G. Boatwright*, QMS2024-01-13-009 (BRI AQ1045965; GenBank numbers nrLSU PQ618837, *TEF1* PV151754).

Habit, habitat & distribution: This species occurs in leaf litter in natural and disturbed areas, including mulched garden beds and road verges in tropical and subtropical areas of Queensland and northern NSW. The litter is usually thick, consisting of *Allocasuarina* needles, regenerating rainforest tree leaves or artificially mulched garden beds with native or exotic species. At times it occurs on the bark of living trees in a vertical position. It is gregarious and may produce basidiomata in abundance (hundreds).

Fig. 7. *Marasmius porphyrocephalus* holotype collection BRI AQ1034084 and other collections to illustrate variations in colour and form **A.** Campanulate pilei. **B, C.** Applanate pilei. **D.** Lamellae. **E.** Dusty vinaceous (76) colour form. Scale bar = 10 mm. Images by F.E. Guard.

Notes: *Marasmius porphyrocephalus sp. nov.* is a morphologically distinct species. Its candy pink pilei with blood red central disc and radiating striations, habit of opening to almost applanate, the pale pink lamellae — not or only faintly marginate, with short bifurcations and irregular lamellulae make it usually recognisable macroscopically and different from other rust red, blood red and wine red members of the complex in Australia. *Marasmius porphyrocephalus sp. nov.* is by far the most widespread and common with over 150 observational records in the Atlas of Living Australia to 23 May 2024, from Cape York Peninsula, QLD to northern NSW with a few from the Northern Territory. Molecular analysis of the nrITS gene region shows that it forms a well-supported (88/0.72) clade with close relatives from Thailand, India and Madagascar, but is not closely related to other (probably endemic) members of the complex in Australia (Fig. 1).

It differs macroscopically from *M. haematocephalus* s. s. in pileal colour, being more pinkish-purple; with more lamellae (12–16 c.f. 7–10) that are pinkish coloured; in having generally shorter stipes (30–45 c.f. 22.5–62 mm); and in having basidiospores shorter than *M. haematocephalus*, mean 17.5 × 4 µm c.f. 20.5 × 4 µm (Oliveira *et al.* 2022). '*Marasmius haematocephalus'* sensu Desjardin & Horak (1997) from Papua New Guinea is a very good match morphologically, but molecular study is required to confirm. '*Marasmius haematocephalus' sensu* Desjardin, Retnowati & Horak (2000) from Java & Bali has a more reddish-brown pileus, fewer lamellae (9–12), longer basidiospores (mean 20.5 × 4 µm) and more common and larger pleurocystidia with more apical constrictions (no molecular data available). '*Marasmius haematocephalus*' sensu Tan *et al.* (2009) from Malaysia is also similar, but has smaller pilei (2–7 mm diam.) which are darker violet, and also has shorter thicker stipes (8–23 × 0.5–1 mm) and marginally longer basidiospores (mean 18.2 µm c.f. 17.5 µm). Molecular study of the nrITS region suggests this is sister to *M. porphyrocephalus*, with low support [subclade 4A(ii)]. *Marasmius asiaticus* (Mešić & Tkalčec 2010), described by Tan *et al.* (2009) as *M. distantifolius* (nom. illeg.) is more similar in colour, but has fewer lamellae (7–8), no lamellulae, short stipe (11–22 × 0.1–0.2 mm) and longer basidiospores (mean 21.5 × 4 µm). Molecularly this species is distant from *M. porphyrocephalus sp. nov.* and is closer to the neotropical *M. coasiaticus* and *M. pervagatus sp. nov*. Of the six forms of '*M. haematocephalus' sensu* Wannathes *et al.* (2009) in Thailand, form '*violaceous*' is the closest in colour to *M. porphyrocephalus,* but the basidiospores are longer (21.5 µm c.f. 17.5 µm). Phylogenetic analysis shows most specimens of *M. haematocephalus* f. 'violaceous', together with var. *atroviolaceus* (India) and a specimen of '*M. haematocephalus'* (China) form a distinct and separate southern Asian clade not close to *M. porphyrocephalus* [subclade 3C(i) in Fig. 1]. '*Marasmius haematocephalus* f.1' (AKD 201 2014) *sensu* Dutta from India (2017) is morphologically quite distinct with its small pileal size (5–6 mm), non-marginate cream lamellae with no lamellulae, short stipe (11–18 mm) and very small basidiospores (14–15 × 3.5–5 µm). However, phylogenetic analysis of the nrITS region shows it to be 100 % similar to a specimen of '*M. haematocephalus'* from Thailand (GenBank nrITS MW426460, voucher NW1441) and both are within the *M. porphyrocephalus* clade. Pairwise analysis of the nrITS region of *'M. haematocephalus' sensu* Shay *et al.* (2017) from Madagascar shows the Madagascan species to be 99.3 to 99.7 % identical with *M. porphyrocephalus.* It is morphologically similar but differs in the shape of mature pilei (convex to campanulate and umbilicate with age), fewer lamellae (10–12), no lamellulae, shorter stipe (12–25 mm) and wider range of basidiospore lengths (13.5–22 µm). As well, one conspecific collection from Madagascar has cream coloured pilei (JES193, image on iNaturalist7000636). Further collections and analysis of other gene regions are necessary to confirm the morphological distinction of these species. The neotropical species *M. rubicundus* in its ruby pink form is similar, but has fewer lamellae (7–12). With current data, *M. porphyrocephalus* appears to be a widespread and variable species. However, examination of further gene regions may help to resolve taxon boundaries in this group.

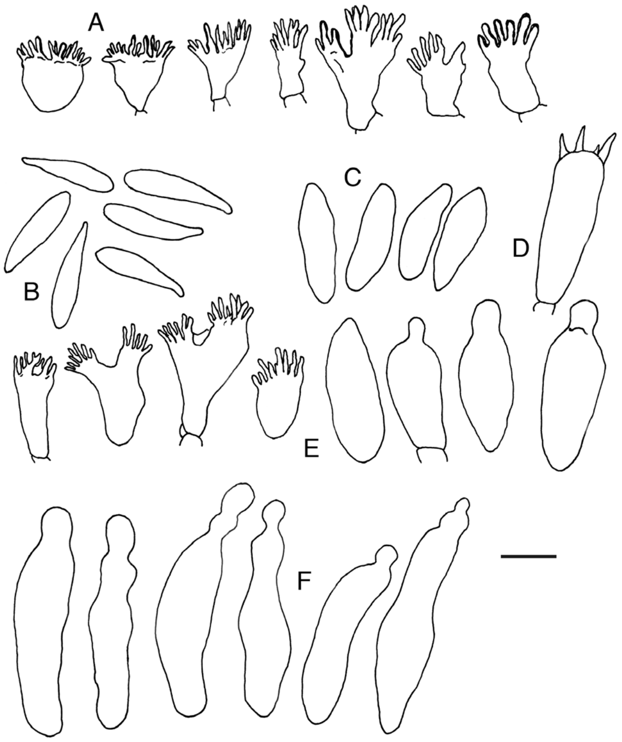

Fig. 8. *Marasmius porphyrocephalus* (F2024008). **A.** Pileipellis *Siccus*-type cells. **B.** Basidiospores. **C.** Basidioles. **D.** Basidium. **E.** Cheilocystidia *Siccus*-type cells and smooth cells. **F.** Pleurocystidia. Scale bar = 10 µm. Illustration by F.E. Guard.

Marasmius purpureospadiceus F.E. Guard, T. Lebel, Dearnaley, ***sp. nov.*** MB 857174. Figs 9, 10.

Etymology: The epithet is a combination of the Latin words "*purpureo*" meaning purplish and "*spadiceus*" meaning date-coloured to describe the purple-brown colour of the pileus.

Typus: **Australia**, Queensland, Balmoral Ridge, Dilkusha Nature Refuge, road verge above Lot 3, in leaf litter, S26°44'24.5", E152°53'36.4", 374 m.a.s.l., 10 Jan. 2021, *F.E. Guard*, F2021001 (**holotype** BRI AQ1021678); GenBank numbers nrITS PQ618872, nrLSU PQ6188622, *TEF1* PV151739.

Basidiomata small to medium-sized, marasmioid. *Pileus* 10–20 mm diam., juvenile: purplish chestnut (21) with paler margins, mature: very distinct, slightly raised, purplish date

(22) central disc, then fawn (29), grading to clay pink (23) outer half with fawn sulci, parabolic to broadly convex, surface dry. *Lamellae* moderately close, 16–18, with occasional lamellulae, free, pale clay pink (23), ± faintly darker margin. *Stipe* 45–60 × 1 mm, central, filiform, blackish base, purplish chestnut (21) upper trunk and clay pink (30) apex, smooth, hollow, non-insititious basal attachment with small buff mycelial pad and moderate cream mycelial mat on surrounding substrate. *Spore print* white. *Basidiospores* 16.5–19.5 × 3.5–4.5 µm, mean 18.0 [± 0.75 SD] × 4.0 [± 0.21 SD] µm, Q = 4.12–4.68, Qm = 4.42 [± 0.17 SD], N = 20, elongate, clavate, with blunt narrow ends, thin-walled, inamyloid. *Basidia* only one seen, 2-spored, 29 × 6.5 µm. *Basidioles* bluntly fusoid, clavate, oblong 19–27 × 5–9 µm. *Cheilocystidia Siccus*-type cells forming a sterile edge variable in shape, clavate, sub-globose, bifid, at times irregular, main body 8–22 × 5–8 µm, with thick-walled, refractile setulae 2.5–5 × 0.5–1.5 µm. *Pleurocystidia* in moderate numbers, smooth walled, utriform, lageniform, occasionally capitate, 30–42 × 6–8 µm. *Lamellar trama* faintly dextrinoid, hyphae 3–4 µm diam. *Pileal trama* dextrinoid, hyphae 4–5 µm diam. *Pileipellis* a hymeniderm of *Siccus*-type cells, narrow to broadly clavate, cylindrical, sub-globose, main body 5–16 × 5–8 µm, setulae, thick-walled, refractile 2–6 × 0.5–1 µm. *Stipe* consists of parallel hyphae 5–5.5 µm diam., cortex dextrinoid. *Caulocystidia* absent. *Clamp connections* present in all tissues.

Other collection examined: **Australia**, NSW, Border Ranges National Park, Helmholtzia Loop, S 28°22′40.5″, E153°04′07.7″, 839 m.a.s.l., 18 Feb. 2022, *F.E. Guard*, F2022005 (BRI AQ1034087; GenBank numbers nrITS PQ618871, nrLSU PQ618839, *TEF1* PV151720).

Habit, habitat and distribution: *Marasmius purpureospadiceus* has only been collected twice, with sparse basidiomata, once in disturbed road verge habitat and once in old growth subtropical rainforest. Its distribution currently appears restricted to SE QLD and northern NSW.

Notes: The medium-sized basidiomata of *Marasmius purpureospadiceus sp. nov.* with purplish-brown pilei and sturdy filiform, non-insititious stipes make it morphologically similar to *M. brunneolorobustus* (Tan *et al.* 2022) which occurs in similar habitat and locations. However, basidiomata of the latter have more lamellae (20–30 c.f. 16–18) and have no pleurocystidia. Molecularly, *M. brunneolorobustus* is in sect. *Globulares,* possibly subsect. *Fusicystides* (Oliveira *et al.* 2024) though this is not yet confirmed, and therefore is not closely related to *M. purpureospadiceus sp. nov. Marasmius haematocephalus* f. *robustus* from Thailand (Wannathes *et al.* 2009) is similar in size and colour, but has fewer lamellae (9–15) and longer basidiospores (mean 20 µm c.f. 18 µm). *Marasmius vinaceus sp. nov.* is also similar, but is generally

Fig. 9. *Marasmius purpureospadiceus* holotype collection BRI AQ1021678. **A.** Lamellae detail. **B.** Basidiomata in situ. **C.** Pilei purplish chestnut (21) central discs. **D.** Stipes. Scale bar = 10 mm. Images by F.E. Guard.

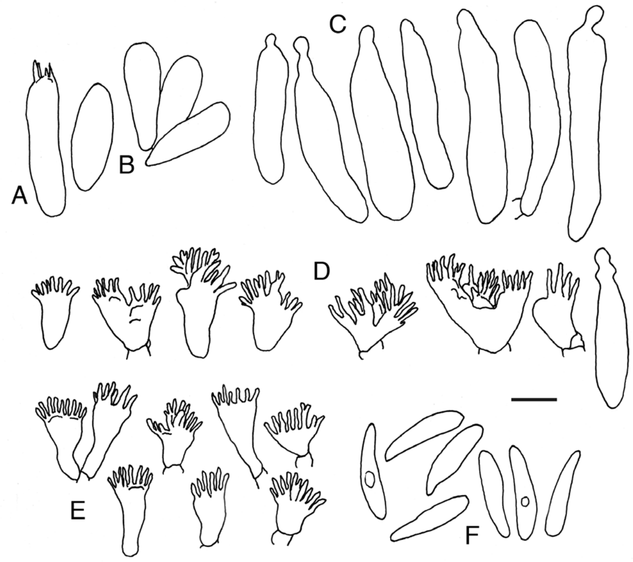

Fig. 10. *Marasmius purpureospadiceus.* **A.** Basidium. **B.** Basidioles. **C.** Pleurocystidia. **D.** Cheilocystidia *Siccus*-type cells and smooth cell. **E.** Pileipellis *Siccus*-type cells. **F.** Basidiospores. Scale bar = 10 µm. Illustrated by F.E. Guard.

less robust and differs in colour (more pinkish grey), in pileal size (6–15 mm diam.) and in fewer lamellae (13–16 c.f. 16–18). They are closely related molecularly being 97.6 to 98.1 % identical on the nrITS, though only 93.6 to 94.2 % identical on *TEF1* pairwise analysis. The lilac colour variant of *M. campaniformis sp. nov.* has a more deeply sulcate, bell-shaped pileus, more purplish colour and fewer lamellae (12–16). *Marasmius purpureospadiceus sp. nov.*, *M. campaniformis sp. nov.* and *M. vinaceus sp. nov*. together with '*M. haematocephalus*' from Hainan, China (GenBank nrITS PP622172) form a monophyletic group based on phylogenetic analysis of the nrITS (Fig. 1). The analysis of the *TEF1* region also supports these three new species in a strongly supported clade wherein *M. purpureospadiceus* is rather sister to *M. vinaceus* (Fig. 2).

Marasmius vinaceus F.E. Guard, T. Lebel, Dearnaley, ***sp. nov.*** MB 857175. Figs 11, 12.

Etymology: The epithet is the Latin word for vinaceous (wine-coloured) or greyish-pink and applies to the pileus colour, as illustrated in Flora of British Fungi Colour Identification Chart.

Typus: **Australia**, Queensland, Maleny, Bridge Creek, Wells Rd S26°43′46.7″, E152°50′51.5″, 333 m.a.s.l., in regenerating wet sclerophyll forest understorey, 27 Apr. 2019, *F.E. Guard*, F2019031 (**holotype** BRI AQ1007374, **isotype** MEL2469588); GenBank numbers nrITS OQ073537, nrLSU OQ073542, *TEF1* PV151757.

Description: *Basidiomata* small, marasmioid. *Pileus* 6–15 mm diam., livid vinaceous (77) central disc, vinaceous (76) remainder of the pileus with a paler margin, sulci darker especially in juveniles, convex to broadly conical, deeply sulcate-striate producing a scalloped margin, surface dry, glabrous. *Lamellae* free, distant, 13–16, with only occasional lamellulae, pale pinkish-cream, non-marginate. *Stipe* 35–70 × 0.5–1 mm, purplish-chestnut (21) base, reddish-brown mid-shaft and buff (52) to pale pink upper end, juveniles reddish-

Fig. 11. *Marasmius vinaceus* holotype collection BRI AQ1007374. **A.** Central disc detail. **B.** Basidiomata collection. **C.** Lamellae detail. **D.** Basal mycelial disc details. Scale bar = 10 mm. Images by F.E. Guard.

brown throughout the length, central, smooth, hollow, non-insititious with small basal off-white mycelial pad. *Spore print* white. *Basidiospores* 16.5–19.5 × 4–5.5 µm, mean 17.5 [± 0.63 SD] × 4.5 [± 0.35 SD] µm, Q = 3.51–4.62, Qm = 3.97 [± 0.27 SD], N = 20, narrow, elongate, clavate, thin-walled, inamyloid. *Basidia* 3- to 4-spored, 10–25 × 7–8 µm. *Basidioles* 20–26 × 6–9 µm, fusoid to clavate. *Cheilocystidia* common, forming sterile edge, *Siccus*-type cells, cylindrical, clavate, sub-globose, main body thin-walled 6–18 × 5.5–8.5 µm, setulae thin to thick-walled and refractile 3–5 × 1–1.5 µm. *Pleurocystidia* common, capitate, utriform, occasionally strangulate 36–52 × 7–12(–14) µm. *Lamellar trama* dextrinoid, hyphae 3–4 µm diam., occasionally inflated hyphae to 12 µm diam. *Pileal trama* dextrinoid, hyphae 3.5–8 µm diam. *Pileipellis* a hymeniderm of *Siccus*-type cells, main body cylindrical, clavate, sub-globose, 6–17 × 4.5–9 µm with multiple apical setulae, thick-walled and refractile 2–6 × 0.5–1 µm. *Stipe* hyphae parallel, those of the cortex 4–5 µm diam., inamyloid, those of the medulla 5–8 µm diam., inamyloid. *Caulocystidia* absent. *Clamp connections* present in all tissues.

Other collections examined: **Australia**, Queensland, Julatten, Clacherty Road, 16 Feb. 2021, *T. Lebel & J. Dearnaley*, F2021069 (BRI AQ1034085; GenBank numbers nrITS PQ618873, nrLSU PQ618829, *TEF1* PV151729) and Mapleton, Linda Garrett National Park, among leaf litter in wet sclerophyll forest, 13 Mar. 2016, *F.E. Guard & QMS members*, QMS LG55 (envt.).

Habit, habitat and distribution: *Marasmius vinaceus sp. nov.* forms gregarious basidiomata, but has only been collected three times, in widely separated locations in subtropical SEQ and tropical FNQ. All collections were made in disturbed habitat among leaf litter by road verges in subtropical or tropical rainforest and wet sclerophyll forest.

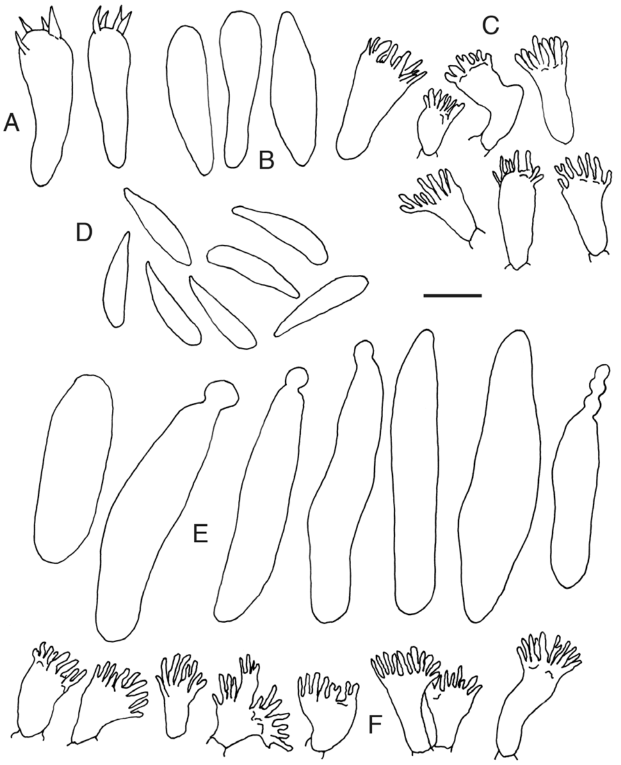

Fig. 12. *Marasmius vinaceus* (BRI AQ1007374). **A.** Basidia. **B.** Basidioles. **C.** Pileipellis *Siccus*-type cells. **D.** Basidiospores. **E.** Pleurocystidia. **F.** Cheilocystidia *Siccus*-type cells. Scale bar = 10 µm. Illustrated by F.E. Guard.

Notes: *Marasmius vinaceus sp. nov.* is very similar to the lilac form of *M. campaniformis sp. nov*., but basidiospores are slightly shorter (17.5 µm c.f. 19 µm), the stipe is often longer (35–70 mm c.f. 30–45 mm), and the pileal size while overlapping is generally smaller (6–15 mm c.f. 10–20 mm). It is also to be noted that, while the basidiospores of the holotype and the Linda Garrett specimen (not sequenced) were identical in size, the Julatten specimen had a greater range in spore size (17–21 × 4–5 µm, mean 19 [± 1.13 SD] × 4.5 [± 0.29 SD] µm, Q = 3.82–5.04, Qm = 4.35 [± 0.31 SD], N = 20). Phylogenetic analyses of the nrITS and *TEF1* regions place *M. vinaceus* as sister with strong support (79/0.99) and (100/1.0) respectively to *M. purpureospadiceus* and *M. campaniformis.* (Figs 1, 2).

Marasmius wianwian F.E. Guard, T. Lebel, Dearnaley, ***sp. nov.*** MB 857176. Figs 13, 14.

Etymology: The epithet *wianwian* (pronounced *"wee-un-wee-un"*) is derived from the local first nation's name for a special place, in the area known by Europeans as The Big Scrub in northern NSW, where the species was first identified. It is a noun in apposition.

Typus: **Australia**, Queensland, Linda Garrett National Park, S26°37'07.35", E152°51'02.6", in leaf litter, 5 Mar. 2022, *W.G. Boatwright*, QMS2022-03-05-013 (**holotype** BRI AQ1041081); GenBank numbers nrITS PQ618898, nrLSU PQ618857, *TEF1* PV151742.

Description: *Basidiomata* small, marasmioid. *Pileus* 4–9 mm diam., colours between blood red (41), rust (13) and dark brick (20), convex to parabolic, sulcate-striate with darker smooth central disc, surface dry, glabrous. *Lamellae* free to adnexed, distant, 11–14, off-white to pale pink with margins concolorous with pileus, *lamellulae* occasional, short. *Stipe* 25–40 × 0.2–0.3 mm, central, filiform, black base, brown mid-stipe, pale apex, glabrous, hollow, non-insititious, with tiny off-white basal mycelial disc. *Spore print* white. *Basidiospores* 16–18 × 3.5–4 µm, mean 17 [± 0.49 SD] × 4 [± 0.19 SD] µm, Q = 3.94–4.79, Qm = 4.46 [± 0.25 SD], N = 20, narrow, clavate, thin-walled, smooth, inamyloid. *Basidia* 4-spored, 19–25 × 7–9 µm, with occasional larger 2-spored basidia. *Basidioles* clavate to fusoid, 22–25 × 5.5–10 µm. *Cheilocystidia Siccus*-type cells, cylindrical, clavate, occasionally bifid or branched, main body 12–26 × 6–10 µm, multiple apical setulae, thick-walled, refractile 3–6(–9) × 0.5–1 µm. *Pleurocystidia* moderately common, smooth cells, 30–50(–62) × 8–11 µm, usually capitate, utriform, thin-walled, hyaline. *Lamellar trama* weakly dextrinoid, hyphae 4.5–7.5 µm diam. *Pileal trama* dextrinoid, hyphae 3–6 µm diam. *Pileipellis* a hymeniderm of *Siccus*-type cells similar to cheilocystidia, cylindrical, clavate, occasionally bifid or elongate, main body 9–24 × 5.5–8 µm with multiple thick-walled, refractile apical setulae 3–6 × 0.5–1 µm. *Stipe* hyphae parallel, those of the cortex 3.5–6 µm diam., weakly dextrinoid, medullary hyphae 6–8 µm, inamyloid. *Caulocystidia* absent. *Clamp connections* present in all tissues.

Fig. 13. *Marasmius wianwian.* **A.** Holotype collection BRI AQ1041081. **B.** Lamellae detail. **C–G.** Collections showing colour variations. C–E. F2022025. F, G. F2022012. Scale bars: A–F = 10 mm; G = 5 mm. Images by F.E. Guard.

Other collections examined: **Australia**, New South Wales, Booyong Scrub Reserve, on fallen leaves in subtropical rainforest, 21 Feb. 2022, *F.E. Guard*, F2022025 (BRI AQ1034089; GenBank numbers nrITS PQ618897, nrLSU PQ618860, *TEF1* PV151732); Rocky Creek Dam, Big Scrub Loop, on leaf litter in subtropical rainforest, 20 Feb. 2022, *F.E. Guard*, F2022012 (BRI AQ1034088; GenBank numbers nrITS PQ618896, nrLSU PQ618859).

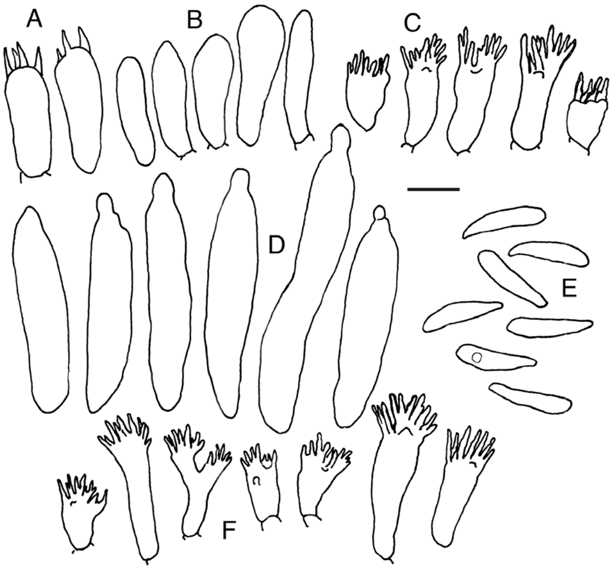

Fig. 14. *Marasmius wianwian* (BRI AQ1041081). **A.** Basidia. **B.** Basidioles. **C.** Cheilocystidia *Siccus*-type cells. **D.** Pleurocystidia. **E.** Basidiospores. **F.** Pileipellis *Siccus*-type cells. Scale bar = 10 µm. Illustrated by F.E. Guard.

Habit, habitat and distribution: Basidiomata of this Australian endemic, *Marasmius wianwian sp. nov.,* occur in small groups, on deep leaf litter, and have to date been found in moderately undisturbed subtropical old growth rainforest, or mixed wet sclerophyll and palm forest. It has been collected from three locations — two remnants of the 'Big Scrub' in northern New South Wales and one National Park in the Sunshine Coast hinterland, Queensland.

Notes: *Marasmius wianwian sp. nov.* is not easily distinguished in the field from the other blood, brick or rust species of the complex in Australia, *M. wunga sp. nov.* and *M. pervagatus sp. nov.* All three species show colour variations. Microscopically, it has shorter basidiospores than *M. wunga* (17 µm c.f. 21 µm) and marginally shorter than *M. pervagatus* (17 µm c.f. 17.5 µm). The smooth pleurocystidia in *M. wianwian sp. nov.* are simpler in form than *M. pervagatus* and smaller in size than *M. wunga. Marasmius haematocephalus* s. s. is similar, but may be bigger in pileal diam. (2.5–16 mm c.f. 4–9 mm), with longer stipes (to 62 mm c.f. 45 mm), fewer lamellae (7–10, non-marginate c.f. 11–14, marginate) and basidiospores that are longer (mean 20 µm c.f. 17 µm). Phylogenetic analysis of the nrITS region shows this well supported (100/1.0) clade to be quite distant from and basal to all others in the broad *haematocephalus* clade, including the epitype from Brazil in the neotropics (Figs 1, 2). Closest to *Marasmius wianwian sp. nov.* molecularly is a well-supported clade of four species, three of which appear to be restricted in distribution to Australia, with a fourth from tropical China (Hainan).

Marasmius wunga F.E. Guard, T. Lebel, Dearnaley, ***sp. nov.*** MB 857177. Figs 15, 16.

Etymology: The epithet ‘*wunga*’ is the name for a fungus in the Dungidau dialect of the Yinibara people on whose land it was first identified. The term ‘*wunga*’ is a noun in apposition.

Typus: **Australia**, Queensland, Balmoral Ridge, Dilkusha Nature Refuge, above Lot 3, S26°44’24.5”, E152°53’36.4”, 374 m.a.s.l., on road verge in leaf litter in regenerating subtropical rainforest, 13 Jan. 2024, *F.E. Guard*, F2024009 (**holotype** BRI AQ1045961); GenBank numbers nrITS PQ618889, nrLSU PQ618848.

Description: *Basidiomata* small, marasmioid. *Pileus* (3–)5–9(–13) mm diam., from scarlet (43) to coral (44), red (42) to blood red (41), occasionally purple (40) with darker, smooth central disc, sulcate-striate, parabolic to campanulate with everted margins, surface dry, glabrous. *Lamellae* usually free, distant, 12–16, with occasional *lamellulae* and rare bifurcations, pale pink to pale salmon (45), margins usually concolorous with the pileus, occasionally non-marginate. *Stipe* 30–60(–80) × 0.2–0.5 mm, central, filiform, black to purplish-chestnut (21) base, bay (19) to blood red (41) mid-stipe, pink to salmon (45) apex, glabrous, hollow, non-insititious with small off-white basal mycelial disc. *Spore print* white. *Basidiospores* 18.5–22.5(–24) × 4–5 µm, mean 21 [± 0.98 SD] × 4.5 [± 0.24 SD] µm, Q = 4.17–5.14, Qm = 4.78 [± 0.25 SD], N = 20, narrow, clavate, slightly curved, thin-walled, smooth, inamyloid. *Basidia* 4-spored, rare, 30–42 × 8.5–10 µm, sterigmata up to 5 µm long. *Basidioles* clavate to fusoid, 22–28 × 6.5–9.5 µm. *Cheilocystidia* (i) common *Siccus*-type cells, forming a sterile edge, main body sub-globose, clavate, narrow clavate, cylindrical, occasionally bifid, or irregular, 9–20(–25) × 5.5–9 µm, with multiple thick-walled, apical setulae 2.5–5 × 0.5–1(–2.5) µm, (ii) uncommon irregular smooth cells 17–20(–28) × 6–12 µm and (iii) rare intermediate cells, bifid with one branch

Fig. 15. *Marasmius wunga* holotype collection BRI AQ1045961. **A–C.** Basidiomata in situ, showing pilei, lamellae and substrate detail. **D–H.** Collections showing colour variations. D. F2024004. E. F2024005. F. 2024007. G. F2020047. H. F2014148. Scale bar = 10 mm. Images by F.E. Guard.

smooth and one branch digitate. *Pleurocystidia* common, (35–)42–76 × 7.5–12 µm, thin-walled, simple cylindrical, lageniform, capitate, occasionally strangulate. *Lamellar trama* weakly dextrinoid, hyphae 7–9 µm diam. *Pileal trama* dextrinoid, hyphae 4–6 µm diam. *Pileipellis* a hymeniderm of *Siccus*-type cells, cylindrical, spathulate, narrow to broadly clavate, occasionally branched, main body 9–16 × 6–10 µm, with multiple apical, thick-walled, refractile setulae 3–6 × 0.5–1.5 µm. *Stipe* hyphae parallel, cortex dextrinoid, hyphae 5–6 µm diam., medulla inamyloid, hyphae 5–9 µm diam. *Caulocystidia* absent. *Clamp connections* present in all tissues.

Other collections examined: **Australia**, Queensland, Balmoral Ridge, Dilkusha Nature Refuge, in regenerating rainforest, near creek, on well-rotted wood, 12 Dec. 2014, *F.E. Guard*, F2014148 (BRI AQ1001910; GenBank number nrITS PQ618887); road verge near entry, in leaf litter under regenerating subtropical rainforest, 22 Apr. 2019, *F.E. Guard*, F2019017 (BRI AQ1007367, MEL2469581; GenBank numbers nrITS OQ073534, nrLSU OQ073540, *TEF1* PV151760); Wren Gully, in leaf litter under regenerating subtropical rainforest, 22 Apr. 2019, *F.E. Guard*, F2019018 (BRI AQ1007368, MEL2469582; GenBank numbers nrITS OQ073535, nrLSU OQ073541, *TEF1* PV151762); road verge leaf litter, 19 Mar. 2021, *F.E. Guard*, F2021091 (envt, GenBank numbers nrITS PQ61889, nrLSU PQ618842); road verge above Lot 3 in leaf litter, 4 Mar. 2022, *F.E. Guard*, F2022041 (BRI AQ1041091; GenBank numbers nrITS PQ618892, nrLSU PQ618861, *TEF1* PV151745); road verge near bunya tree above Lot 3, 8 Jan. 2024, *F.E. Guard*, F2024004 (BRI AQ1045956; GenBank numbers nrITS PQ618893, nrLSU PQ618844); road verge needle-litter under *Allocasuarina* sp., 9 Jan. 2024, *F.E. Guard*, F2024007 (BRI AQ1045959; GenBank numbers nrITS PQ618884, nrLSU PQ618843, *TEF1* PV151751); Maleny, Maleny Precinct, in leaf litter under mixed native and exotic trees, 8 Jan. 2024, *W. Nash* & *F.E. Guard*, F2024005 (BRI AQ1045957; GenBank numbers nrITS PQ618888, nrLSU PQ618850); Mount Cordeaux, Main Range National Park, wet sclerophyll forest in leaf litter, 20 Apr. 2024, *W.G. Boatwright*, QMS2024-4-20-005 (BRI AQ104807; GenBank numbers nrITS PQ618894, nrLSU PQ618846); Numinbah Valley, Bornhoffen Camp, in leaf litter under lantana shrubs, 25 Mar. 2023, *F.E. Guard*, QMS2023-3-25 (BRI AQ1040807; GenBank numbers nrITS PQ618899, nrLSU PQ618849, *TEF1* PV151755); Springbrook, Best of All Lookouts, on leaf litter in roadside grass, 12 Feb. 2015, *J.C. Peuchmarin*, Peuchmarin#1 (BRI AQ1019380; GenBank number nrITS PV016896); New South Wales: Dorroughby, road verge in leaf litter, 15 Jan. 2024, *C. Marciniak*, F2024014, iNaturalist200315251 (BRI AQ1046796; GenBank numbers nrITS PQ618895, nrLSU PQ618845, *TEF1* PV151756).

Habit, habitat and distribution: This species produces gregarious basidiomata that often occur in large numbers, most commonly in disturbed areas including road verges and mulched gardens in subtropical vegetation, growing in deep leaf litter. However, it appears to be a species endemic to Australia, with the current distribution restricted to south east Queensland and northern New South Wales.

Notes: *Marasmius wunga sp. nov.* is one of three red-pileate Australian species (*M. pervagatus sp. nov.*, *M. wianwian sp. nov.* and *M. wunga sp. nov.*) in the broader *M. haematocephalus* complex. *M. wunga* occurs in numerous shades of red and occasionally it is purplish, but usually lacks the pinkish-purple tones of *M. porphyrocephalus*. The red-pileate species can be difficult to differentiate in the field. All three occur in southeast QLD, but only *M. pervagatus sp. nov.* in FNQ. Microscopically, *M. wunga sp. nov.* has the biggest basidiospores (mean 21 × 4.5 µm, c.f. 17.5 × 4 µm in *M. pervagatus* and 17 × 4 µm in *M. wianwian*). Cheilocystidia vary from monomorphic (*M. wianwian*), to dimorphic (*M. pervagatus*) and trimorphic (*M. wunga*), and *M. wunga* has the largest pleurocystidia. These three red-pileate species fall into distantly related clades in analyses of the nrITS and *TEF1* trees (Figs 1, 2).

It differs from *M. haematocephalus* s. s. in its generally smaller pileus (5–9 mm, c.f. 2.5–16 mm), with more

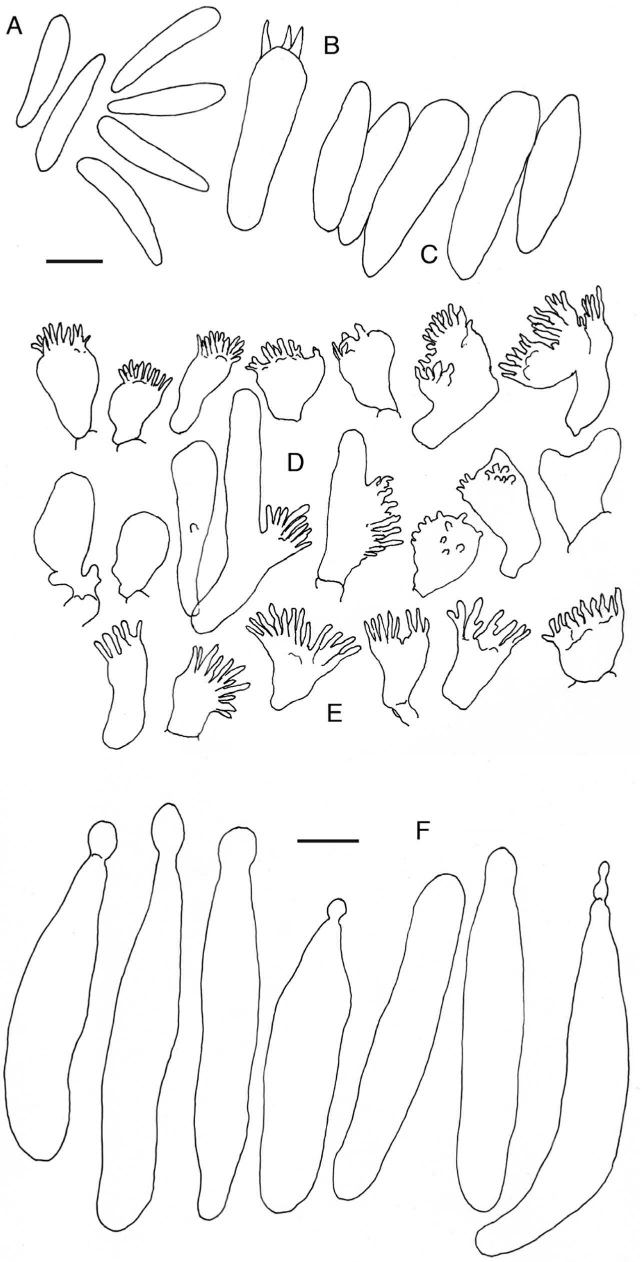

Fig. 16. *Marasmius wunga* (BRI AQ1045961). **A.** Basidiospores. **B.** Basidium. **C.** Basidioles. **D.** Cheilocystidia *Siccus*-type cells, intermediate cells and smooth cells. **E.** Pileipellis *Siccus*-type cells. **F.** Pleurocystidia. Scale bars = 10 µm. Illustrated by F.E. Guard.

numerous (12–16 c.f. 7–10) and marginate lamellae and slightly larger basidiospores (mean 21 × 4.5 µm, c.f. 20 × 4 µm). Despite the morphological similarities, it is molecularly only distantly related to *M. haematocephalus* s. s. (Fig. 1). Its sister species with strong support (79/1.0) is an unnamed Australian taxon, *Marasmius* sp. 'clay-pink bells', from FNQ (F2023010), for which there is only one collection to date.

Key to the species of the *Marasmius haematocephalus* complex occurring in Australia

(The following key was prepared for field mycologists. See list below the key for definition of colours used.)

1a. Pileus **cinnamon** 2
1b. Pileus another colour 3

2a. Basidiospores mean 32 × 5 µm, monomorphic cheilocystidia .... *M. lebeliae*
2b. Basidiospores mean 19 × 4 µm, dimorphic cheilocystidia .... *M. campaniformis* (cinnamon form)

3a. Pileus **lilac to vinaceous grey** 4
3b. Pileus another colour 5

4a. Basidiospores mean 19 × 4 µm, dimorphic cheilocystidia .... *M. campaniformis* (lilac form)
4b. Basidiospores mean 17.5 × 4.5 µm, monomorphic cheilocystidia .... *M. vinaceus*

5a. Pileus **purplish-date** .... *M. purpureospadiceus*
5b. Pileus another colour 6

6a. Pileus **pale pink** 7
6b. Pileus another colour 8

7a. Pileus **pale rose pink**, basidiospores mean 19 × 4 µm, dimorphic cheilocystidia .... *M. campaniformis* (pink form)
7b. Pileus **clay pink**, basidiospores mean 21 × 3.5 µm, monomorphic cheilocystidia .... *Marasmius* sp. "clay-pink"

8a. Pileus **candy pink** with **darker red** disc and sulci .... *M. porphyrocephalus*
8b. Pileus another colour 9

9. Pileus **red – (dark brick, rust red, blood red, wine red, scarlet, coral**) 10

10a. Basidiospores mean 17 × 4 µm, monomorphic cheilocystidia .... *M. wianwian*
10b. Basidiospores mean 17.5 × 4 µm, dimorphic cheilocystidia .... *M. pervagatus*
10c. Basidiospores mean 21 × 4.5 µm, trimorphic cheilocystidia .... *M. wunga*

Colours from Flora of British Fungi Colour Identification Chart, Royal Botanic Garden, Edinburgh 1969 where possible.

"blood red" = blood red (41)
"candy pink" = strong pink with purple tones, not illustrated (Google)
"cinnamon" = cinnamon (10) to 'ochre' (9H)
"clay pink" = clay pink (30)
"coral" = coral (44) which has apricot tones
"dark brick red" = close to dark brick (20) with brownish tones
"lilac" = lilac (79), matures to vinaceous grey (80)
"pink" = rose (39)
"purplish date" = purplish date (22) has brown tones
"rust red" = close to rust (13)
"scarlet" = scarlet (43) red with orange tones
"vinaceous grey" = vinaceous grey (80) has violet tones
"wine red" not illustrated, darker than blood red. (Google)

DISCUSSION

Colour is often used to aid field-identification and in naming of fungal species. The name *"haematocephalus"* means 'blood-red head'. Curiously, the common name for *M. haematocephalus* is 'purple pinwheel', yet the etymology suggests it should be 'blood red pinwheel'. Other species in the complex have been named to emphasise specific colours (e.g. *rubicundus*, *roseus*, *auranticapitatus* and *castanocephalus* in Oliveira *et al.* (2022) and *porphyrocephalus*, *vinaceus* and *purpureospadiceus* (in this study). When *M. haematocephalus* sensu lato was considered to be a single species, Singer (1976) described nine variants in the neotropics based mainly on the colour of the pileus. Wannathes *et al.* (2009) described six forms in Thailand based on the pileal colour and size, two of which, f. *haematocephalus* and f. *violaceus*, did form separate subclades with strong support, and f. *luteocephalus* (with cream pileus) and f. *variabilis* (with greyish-brown pileus) fell in the same subclade. However, none of the forms correlated fully to Singer's varieties. With the larger dataset available for this current study, f. *violaceus* (with its pinkish-purple pileus very similar to *M. porphyrocephalus sp. nov.*) remains in a well-supported clade distant from *M. porphyrocephalus*; f. *haematocephalus* (with its brick red pileus) appears conspecific with *M. pervagatus*; and the cream f. *luteocephalus*, vinaceous f. *robustus* and grey-brown f. *variabilis* remain together in another poorly supported clade.

Madagascan collections studied by Shay *et al.* (2017) show that three collections (JES110, JES202, Buyck_00_1820) have purple pilei and one collection (JES193) has a cream pileus (images on iNaturalist7000636). They are con-specific, not closely related to the f. *luteocephalus* from Thailand, but are part of the *M. porphyrocephalus sp. nov.* clade [4A(ii), Fig. 1]. Oliveira *et al.* (2022) in their study of *M. haematocephalus* s. s. and related cryptic species from Brazil illustrated the colour variations in *M. rubicundus* (from pale pink to purple and salmon peach). In this study, *M. campaniformis* occurs in three colour forms — cinnamon (common), lilac (uncommon) and pink (rare). Morphologically, apart from the pileus colour, they are identical and molecularly they are con-specific across nrITS, nrLSU and *TEF1*. Red-pileate species are difficult to differentiate morphologically and there are three distinct subclades of these in Australia, two endemic and one globally widespread. Colour photography has enhanced our ability to identify species, but has its own biases. Red is a particularly difficult colour to render accurately (pers. comm. Steven Axford, Fungal Photographer). Ambient light, background colours and the camera settings used can all influence the colour outcomes. Our conclusion is that while colour is an important character for identifying species of *Marasmius*, it has limited value for separating some of the species in ser.

Fig. 17. Atlas of Living Australia data: 164 observational records with historic collections from Victoria & southern NSW 1887 (misidentified), Solomon Islands 1972 & Norfolk Is 1995 (within the complex). Of those with images, over 90 % are pinkish-purple and appear to be *Marasmius porphyrocephalus.* Image from *Atlas of Living Australia* accessed 18 Nov. 2024.

Haematocephali and must be used in conjunction with other characters and with caution.

Distribution and phenology

All of the Australian collections investigated have been identified as seven unique species within the broader *M. haematocephalus* clade. They are all tropical or subtropical in origin. No herbarium material studied from locations in temperate Australia appear to be members of the *M. haematocephalus* complex and there are no iNaturalist observational records from the southern Australian states, while there are 225 from QLD, 12 from NSW (Sydney being the most southerly) and 4 from NT (see Fig. 17 and ALA records below). While the type species appears to have a restricted distribution in the neotropics — Brazil and Ecuador (Oliveira *et al.* 2022) and (GenBank nrITS OQ871706), further molecular data from GenBank and analyses in this study have expanded the complex and show there to be at least one taxon that is probably pan tropical (*M. pervagatus sp. nov.*) potentially including cryptic species and another to be Afrotropical, Indo-Malaysian and Australasian (*M. porphyrocephalus sp. nov.*). As well, there are centres of high diversity in the sub-tropical forests of southeast Queensland and northern New South Wales, where morphologically similar species can be separated by multilocus phylogenetic analysis.

Examination of Atlas of Living Australia (ALA) data (accessed on 18 Nov. 2024) records of *Marasmius ‘haematocephalus’* in Australia show the species complex to be a tropical/subtropical group, with few outliers (Fig. 17). The ALA contains 164 observational records of the *M. haematocephalus* complex and 43 preserved specimens held in various herbaria. Three records are likely to be misidentifications, but the remainder appear to be within the complex. Of the records with images, over 90 % appear to be *Marasmius porphyrocephalus sp. nov.* The concentration of records in the wet tropics (centred on Cairns) and the subtropics of southeast QLD and northern NSW (centred on Brisbane) may reveal biodiversity hotspots, or perhaps population centres with concentrations of search effort. The citizen science observations on iNaturalist of this eye-catching group of species support the suggestion of biodiversity hotspots, with additional sporadic occurrences in other, generally drier parts of QLD. All species in the *haematocephalus* complex produce basidiomata after rain, usually in the summer through autumn months (December to May). If significant rain occurs early or late, they may rarely appear in November or June (one record of each on ALA). The year 2022 was a year of record rainfall in SEQ and observations were made of *M. porphyrocephalus* basidiomata in unusual numbers and in unusual places. The central QLD occurrences were in normally dry habitats which had received unusually high rainfall. They are 450–700 km from the nearest areas of regular occurrence. Its usual habitat is variable, ranging from rainforest, wet sclerophyll forest to parks, gardens and road verges under native or exotic trees. The substrate is deep leaf litter and twigs, garden mulch and occasionally mossy bark on living trees (four ALA records). *Marasmius porphyrocephalus* is widespread and is probably present throughout tropical-subtropical Australasia (including Papua New Guinea), south Asia and at least as far as Madagascar. It is not currently threatened. Of the remaining ALA records with images, ca 8 % (15) are red-pileate species, which cannot be further identified. Two other records from north QLD appear to be *Marasmius vinaceus sp. nov*. (Reinhold 2022; iNaturalist 109522131 and 109594364).

The distribution of fresh collections of taxa (2014–2024) in the *M. haematocephalus* complex, with concentrations in the wet tropics and the subtropics, is shown in Fig. 18. The FNQ and NSW collections were from short, targeted forays in the wet season of three consecutive years (2021 FNQ, 2022 NSW and 2023 FNQ). Additionally, a long-term study of *Marasmius* at Dilkusha Nature Refuge SEQ, over more than ten years of daily observations, collections, records of changing habitat and rainfall, has contributed significantly to our knowledge of species diversity and phenology, including five of the new species in this study [*M. campaniformis* (two of the three colour forms), *M. porphyrocephalus*, *M. purpureospadiceus*, *M. vinaceus* and *M. wunga*]. Stallman *et al.* (2024) have analysed the value of long-term studies of fungi in Guyana over and beyond short sporadic forays, in previously understudied tropical areas, for their important contribution to capturing the extent of species diversity. Straatsma, Ayer & Egli (2001) in a weekly survey during the fungal fruiting season in Switzerland over 21 yr came to the same conclusion. Our study has shown the same importance in subtropical areas of Australia.

Of the red-pileate species, *Marasmius wianwian sp. nov*. is endemic to remnant rainforest of the formerly large subtropical lowland rainforest (termed ‘Big Scrub’) of

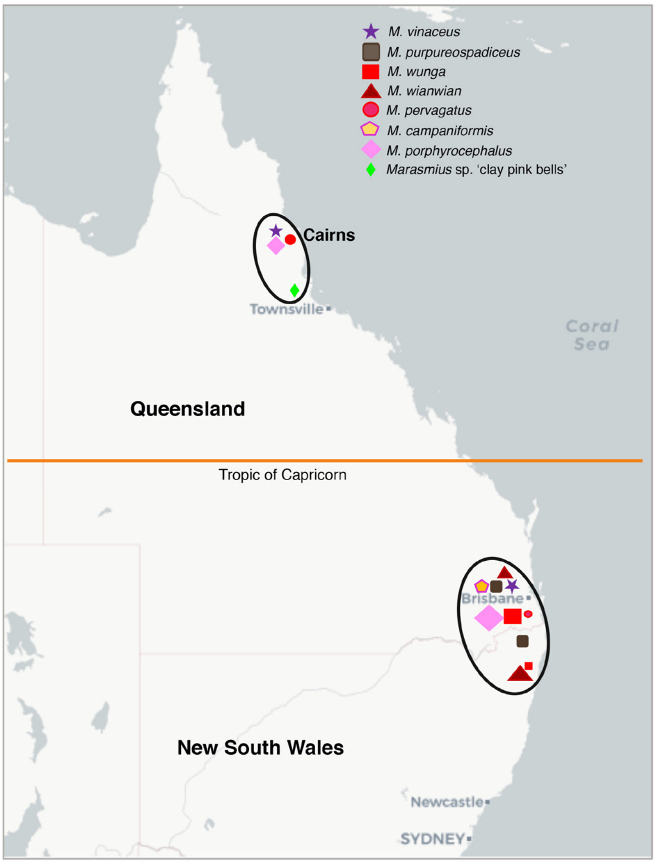

Fig. 18. Map of Queensland and New South Wales illustrating the distribution of the 40 fresh specimens collected and sequenced for this study. Biodiversity hotspots appear to be centred in the wet tropics and in the subtropics of SEQ and northern NSW shown by black ovals.

northern NSW and one small national park in SEQ. Only 1 % of the original 75 000 ha of Big Scrub remains, in fragmented patches of rainforest. *Marasmius wianwian* has only been found three times, always in rainforest habitat, on leaf litter, in February and March of the extremely wet year 2022. Given its limited distribution, in natural forest habitat, areas which are under threat from weed incursion, human activities, drought and fire due to climate change, this species may be threatened and should be considered for conservation protection.

The second red-pileate species, *Marasmius wunga sp. nov.,* is also endemic to southeast QLD and northern NSW. It has been collected in eight sites with multiple collections over ten years (2014–2024) in the months of December to April, with a peak of collections in January. It is much less particular in its habitat requirements than *M. wianwian*. The most common habitat is in leaf litter on road verges and walking tracks in regenerating subtropical rainforest mixed with exotic weeds such as *Lantana camara.* This species occurs with large numbers of basidiomata at times. There is one collection from northern NSW, made on a road verge. Despite its small geographic distribution to date, *M. wunga* does not currently appear to be threatened.

The third red-pileate species, *Marasmius pervagatus sp. nov.*, is not endemic and has been found in Brisbane, Cairns Botanic Gardens (twice) and Bloomfield on Cape York Peninsula. The habitat is garden beds, road verge and disturbed areas, growing on mulch and twigs with native and exotic vegetation. On the nrITS tree (Fig. 1), it forms a clade together with sequences from Thailand, India and Florida. The Bloomfield and Florida sequences have high similarity (99.1–99.5 % identical for the nrITS). Examination of more specimens using other gene regions may help to resolve any cryptic geographically delimited species in this group, and perhaps determine whether the Floridian cluster of specimens are an indication of an exotic introduction to Queensland or vice versa.

CONCLUSION

Marasmius haematocephalus, commonly known in Australia as the 'purple pin-wheel', has been shown in our study to be a much broader complex of taxa, that includes pileal colours ranging from pink to purple, scarlet to coral, blood red to wine red and cinnamon to lavender with many variations in form. The addition of eight novel species adds significantly to our understanding of the global diversity, distribution and relationships of the species complex. Certainly there are more species awaiting discovery, including the undescribed species in this study. Six of the species found in Australia appear to be endemic to highly restricted areas and habitats, which has serious implications for conservation. The two more widespread taxa have more variability both morphologically and molecularly and are probably hiding a number of cryptic species. The nrITS gene region is useful for delimiting most of the species, but the use of *TEF1* gene region together with detailed morphological examination has been important in separating some of the more cryptic species complexes. Further investigation of both *M. porphyrocephalus* and *M. pervagatus* would be useful in studying potential geographic variants and possible dispersal of the species to and from Australia. While this study raises more questions particularly in regard to the relationships between Australian and Asian species, it also contributes significantly to our understanding of the complex across the world.

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REFERENCES

Amoako-Attah I, Akrofi AY, Hakeem R, *et al.* (2016). White thread blight disease caused by *Marasmiellus scandens* (Massee) Dennis & Reid on cocoa and its control in Ghana. *African Journal of Agricultural Research* **11**: 5064–5070. https://doi.org/10.5897/AJAR2016.11681

Antonín V, Buyck B (2006). *Marasmius* (*Basidiomycota*, *Marasmiaceae*) in Madagascar and the Mascarenes. *Fungal Diversity* **23**: 17–50. https://www.fungaldiversity.org/fdp/sfdp/23-2.pdf

Antonin V (2007). Monograph of *Marasmius*, *Gloiocephala*, *Palaeocephala* and *Setulipes* in Tropical Africa. *Fungus Flora of Tropical Africa* **1**: 1–200. https://www.ffta-online.org/ffta1/

Antonin V, Noordeloos M (2010). *A monograph of marasmioid and collybioid fungi in Europe* IHW-Verlag, Eching, Germany.

Bhunjun CS, Niskanen T, Suwannarach N *et al.* (2022). The numbers of fungi: are the most speciose genera truly diverse? *Fungal Diversity* **114**(1): 387–462. https://doi.org/10.1007/s13225-022-00501-4

Crous PW, Carnegie A, Wingfield M, *et al.* (2019). Fungal Planet description sheets: 868–950. *Persoonia* **42**: 291–473. https://doi.org/10.3767/persoonia.2019.42.11

Crous PW, Wingfield M, Chooi Y-H, *et al.* (2020). Fungal Planet description sheets: 1042–1111. *Persoonia* **44**: 301–459. https://doi.org/10.3767/persoonia.2020.44.11

Desjardin D, Retnowati A, Horak E (2000). *Agaricales* of Indonesia. 2. A preliminary monograph of *Marasmius* from Java and Bali. *Sydow* **52**(2): 92–193.

Desjardin DE, Horak E (1997). *Marasmius and Gloiocephala in the south Pacific region: Papua New Guinea, New Caledonia and New Zealand* **Vol 2**. Cramer J, Berlin.

Dutta AK (2017). *Taxonomic study on marasmioid and gymnopoid fungi of West Bengal based on morphological and molecular features.* Thesis submitted for the degree of Doctor of Philosophy (Science) in Botany, University of Calcutta, India.

Fries EM (1836–1838). *Epicrisis systematis mycologici seu synopsis Hymenomycetum* Upsaliae.

Gardes M, Bruns T (1993). ITS primers with enhanced specificity for basidiomycetes - application to the identification of mycorrhizae and rusts. *Molecular Ecology* **2**(2): 113–118. https://doi.org/10.1111/j.1365-294X.1993.tb00005.x

Guard FE, Dearnaley J, May TW *et al.* (2024). Untangling horsehair fungi in Australia: *Marasmius crinis-equi* (*Marasmiaceae*) and related taxa. *Mycological Progress* **23**: 1–27. https://doi.org/10.1007/s11557-024-01995-9

Huamán-Pilco AF, Ramos-Carrasco TA, Franco MEE *et al.* (2023). Morphological, phylogenetic and genomic evidence reveals the causal agent of thread blight disease of cacao in Peru is a new species of *Marasmius* in the section *Neosessiles*, *Marasmius infestans sp. nov*. *F1000Research* **12**: 1327. https://doi.org/10.12688/f1000research.140405.2

Huelsenbeck JP, Ronquist F (2001). MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* **17**(8): 754–755. https://doi.org/10.1093/bioinformatics/17.8.754

Katoh K, Standley DM (2013). MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability. *Molecular Biology and Evolution* **30**(4): 772–780. https://doi.org/10.1093/molbev/mst010

Kühner R (1980). Les Hyménomycètes agaricoides (*Agaricales*, *Tricholomatales*, *Pluteales*, *Russulales*). Étude générale et classification. Numéro spécial *Bulletin de la Société Linnéenne de Lyon* **49**: 76–184.

Mešić A, Tkalčec Z (2010). New names in the genus *Marasmius*. *Mycotaxon* **113**(1): 283. https://doi.org/10.5248/113.283

Mossebo DC, Antonin V (2004). *Marasmius* species (*Tricholomataceae*) found in man-influenced habitats in the vicinity of Yaoundé, Cameroon. *Czech Mycology* **56** (1/2): 85–112. https://czechmycology.org/article/56107

Oliveira JJS, Moncalvo JM, Margaritescu S *et al.* (2020). A morphological and phylogenetic evaluation of *Marasmius* sect. *Globulares* (*Globulares-Sicci* complex) with nine new taxa from the Neotropical Atlantic Forest. *Persoonia* **44**: 240–277. https://doi.org/10.3767/persoonia.2020.44.09

Oliveira JJ, Capelari M, Margaritescu S (2022). Disentangling cryptic species in the *Marasmius haematocephalus* (Mont.) Fr. and *M. siccus* (Schwein.) Fr. species complexes (*Agaricales*, *Basidiomycota*). *Cryptogamie, Mycologie* **43**(5): 91–137. https://doi.org/10.5252/cryptogamie-mycologie2022v43a5

Oliveira JJS, Vargas-Isla R, Cabral TS *et al.* (2024a). Spider fungi: new species of *Marasmius* and *Pusillomyces* in the aerial rhizomorph web-making guild in Amazonia. *Fungal Systematics and Evolution* **14**: 35–55. https://doi.org/10.3114/fuse.2024.14.03

Oliveira J, Desjardin D, Jenkinson T, *et al.* (2024b). Taxonomic revision of *Marasmius* Fr. and *Marasmiaceae* Roze *ex* Kühner based on multigene phylogenetics and morphological evidence. *Fungal Diversity* **127**: 1–54. https://doi.org/10.1007/s13225-024-00534-x

Pegler DN (1977). A preliminary agaric flora of East Africa. *Kew Bull Addit Ser* **6**:1–615.

Pegler D (1986). Agaric flora of Sri Lanka. *Kew Bull Addit Ser* **12**: 1–519.

Rehner SA, Buckley E (2005). A *Beauveria* phylogeny inferred from nuclear ITS and *EF1-α* sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs. *Mycologia* **97**(1): 84–98. https://doi.org/10.3852/mycologia.97.1.84

Reinhold L (2022). iNaturalist: https://www.inaturalist.org/observations/109522131 Accessed on 25 Oct. 2024.

Royal Botanic Garden Edinburgh (1969). *Flora of British fungi Colour Identification Chart*. Her Majesty's Stationery Office, Edinburgh.

Shay JE, Desjardin DE, Perry BA, *et al.* (2017). Biodiversity and phylogeny of *Marasmius* (*Agaricales*, *Basidiomycota*) from Madagascar. *Phytotaxa* **292**: 101–149. https://doi.org/10.11646/phytotaxa.292.2.1

Singer R (1976). Marasmieae (*Basidiomycetes-Tricholomataceae*). *Flora Neotropica* **17**: 1–347.

Stallman JK, Haelewaters D, *et al.* (2024). The contribution of tropical long-term studies to mycology. *IMA Fungus* **15**: 1–18. https://doi.org/10.1186/s43008-024-00166-5

Stamatakis A (2014). RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* **30**(9): 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Straatsma G, Ayer F, Egli S (2001). Species richness, abundance and phenology of fungal fruit bodies over 21 years in a Swiss forest plot. *Mycological Research* **105**(5): 515–523. https://doi.org10.1017/S0953756201004154

Tan Y-P, Bishop-Hurley SL, Shivas RG, *et al* (2022). Fungal planet description sheets: 1436–1477. *Persoonia* **49**: 261–350. https://doi.org/10.3767/persoonia.2022.49.08

Tan Y-S, Desjardin D, Perry B, *et al.* (2009). *Marasmius* sensu stricto in peninsular Malaysia. *Fungal Diversity* **37**: 9–100.

Vilgalys R, Hester M (1990). Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* **172**(8): 4238–4246. https://doi.org/10.1128/jb.172.8.4238-4246.1990

Wannathes N, Desjardin D, Hyde K, *et al.* (2009). A monograph of *Marasmius* (*Basidiomycota*) from northern Thailand based on morphological and molecular (ITS sequences) data. *Fungal Diversity* **37**: 209–306.

White TJ, Bruns T, Lee S, *et al.* (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: *PCR protocols: a guide to methods and applications* (Innis MA, Gelfand DH, Sninsky JJ, *et al.*, eds). *Academic Press, Inc.*, New York, USA: 315–322. https://doi.org/10.1016/B978-0-12-372180-8.50042-1

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

Fig. S1. Phylogenetic analysis of the *Haematocephali* complex in sect. *Sicci*, ser. *Haematocephali* inferred from Bayesian and Maximum Likelihood analysis of the nrLSU region with *M. recreigardneri,* subsect. *Ferruginei,* as outgroup. BS/PP and bolded lines for well supported nodes. All coloured sequences have been produced in this study, except the epitype, *M. haematocephalus* (blue).

Fig. S2. *Marasmius haematocephalus* complex phylogenetic tree using concatenated nrITS, nrLSU and *TEF1* sequences with Bayesian analysis. All coloured sequences have been produced in this study, except the type sequences of *M. haematocephalus* in blue (only the neotropical and Australian sequences have all three gene regions.)

Table S1. Table of all sequences used in this study of the *Marasmius haematocephalus* complex, including GenBank numbers for nrITS, nrLSU and *TEF1* and Herbarium numbers of the Australian collections. Species in **bold** are new collections and /or sequences produced in this study and those in red are holotypes. Not determined = n/d.