

The velvet parachute - *Marasmius elegans* complex (*Marasmius* subgen. *Globulares*, sect. *Globulares*, subsect. *Leonini*, ser. *Luteoli*) in Australasia

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Abstract: *Marasmius elegans* is a large colourful Australasian species in subsect. *Leonini*, ser. *Luteoli*, of the widespread saprotrophic genus *Marasmius*. *Marasmius elegans* has been recorded in all states of Australia and in Aotearoa New Zealand but varies in size and pileal colour across its distribution. Using morphological and molecular data we discovered both: (i) a widespread variable species that showed increasing size of the pileus with distance from the equator; and (ii) three new species, namely *M. dikhusha*, *M. leppii* and *M. durifagus*, to which the name *M. elegans* has been incorrectly applied, and a new variety, *M. elegans* var. *occidentalis*, is described from Western Australia. *Marasmius pseudoelegans*, another *M. elegans* look-alike, is now confirmed as a member of ser. *Luteoli*. *Marasmius atrocastaneus* from New Zealand is redescribed and is also confirmed within ser. *Luteoli*. We establish a new series, *Multicystidiati*, to include *M. multicystidiatus* and *M. sullivantii*. Several other novel taxa await further collections and descriptions.

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INTRODUCTION

Marasmius elegans is a well-known Australasian species that is easily recognisable in the field by its large orange-brown velvety pileus and bi-colour cartilaginous stipe. It was described from South Australia (SA) as *Collybia elegans* by John Cleland (1933), but correctly assigned to the genus *Marasmius* by Cheryl Grgurinovic (1997) in her revision of Cleland's work. The species is said to be widespread, though not common in that state. It has been recorded in a wide variety of habitats, including temperate wet sclerophyll (eucalypt) forest litter, also fern gullies, temperate rainforests and *Allocasuarina* forests across southern Australia, including Western Australia (WA), Victoria (VIC), Tasmania (TAS) and New South Wales (NSW) (Bougher & Syme 1998, Grey & Grey 2005, Young 2005, Moore & O'Sullivan 2013), subalpine eucalypt forest of the Australian Capital Territory (ACT), wet sclerophyll forest and subtropical rainforest in southeast Queensland (SEQ), and in introduced pine forests in VIC (Fuhrer 2005). *Marasmius elegans* also occurs in Aotearoa New Zealand (NZ), where the habitat is Kānuka (*Kunzea ericoides*) scrub, Southern Beech forest (*Nothofagaceae* spp.) and Mānuka (*Leptospermum scoparium*) scrub.

While *M. elegans* is found in all states of Australia, it is less common in Queensland (QLD) and probably restricted to the southeast region, extending west to the Bunya Mts, and north to K'gari (Fraser Is.) and possibly Blackdown Tableland,

though there are no Fungarium collections or observational records in the Atlas of Living Australia (ALA) from that area. Observational records further north (noted in the ALA) have yet to be confirmed. Some represent mistaken identifications of *M. vagus* (Crous *et al.* 2020) and *M. australotrichotus* (Guard *et al.* 2023) (Fig. 1).

Marasmius elegans, as currently recorded, is morphologically variable across its widespread distribution and could represent more than one taxon (Fig. 2). It varies in stature - both pileal diameter and stipe dimensions, the lamellar margins may or may not be concolorous with pileus, and pileal colour varies from pale or deep orange to bay brown.

Size of pileus and overall stature of basidiomata may be highly influenced by environmental factors such as rainfall, temperature and resource availability (Bässler *et al.* 2021). While saprotrophic species can utilise different substrates, i.e. leaf litter versus woody debris, *M. elegans* occurs on both substrates in a wide variety of habitats, from subtropical to cool temperate, including rainforest, palm, wet sclerophyll, *Allocasuarina* forests to New Zealand podocarp and broadleaf forest, *Nothofagaceae* and *Kunzea/Leptospermum* scrub.

To test whether this is a single widespread, morphologically variable species or multiple taxa, collections identified as *M. elegans* from across its putative range were examined and compared macroscopically and microscopically. Molecular analyses (nrITS, nrLSU and *TEF1*) were undertaken on

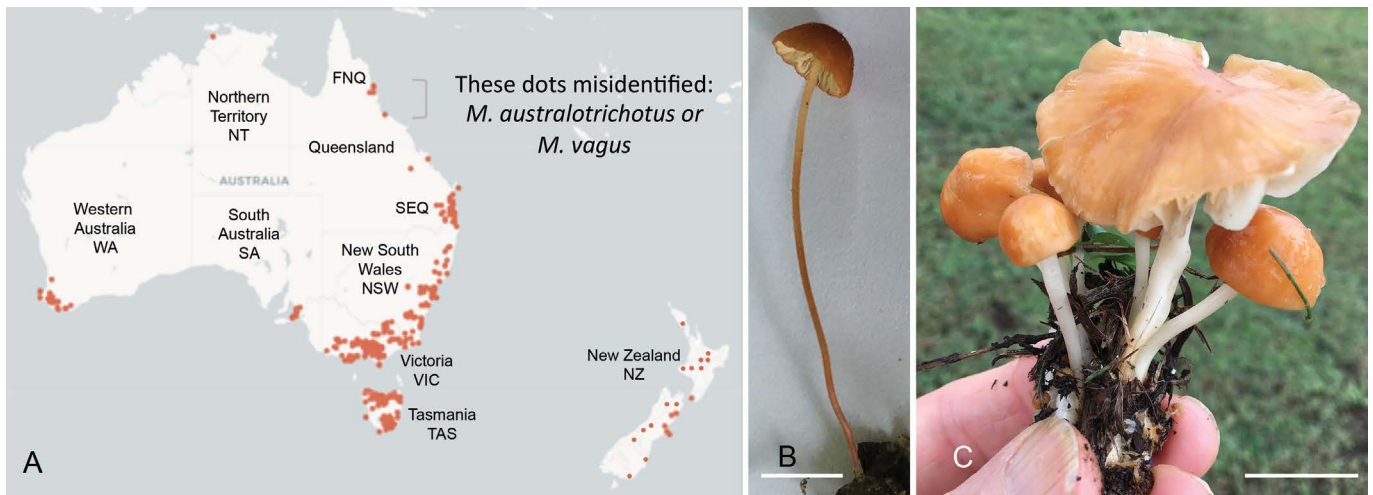


Fig. 1. A. Distribution of 2080 records of *Marasmius elegans*, including collections and observations from the Atlas of Living Australia (NZ records are taken from GBIF data). Records in NT and FNQ are misidentifications of (B) *Marasmius australotrichotus* and (C) *Marasmius vagus*. Scale bars = 10 mm. Images by F.E. Guard.



Fig. 2. A–D. *Marasmius elegans* variations in mature pileal size, colour and lamellar margins. E. *M. elegans* juvenile basidiomata. F. *Marasmius pseudoelegans* juvenile basidiomata. G. *M. pseudoelegans* mature basidiomata. Scale bars = 10 mm. Images by Kathy Warburton NZ (A), J.A. Cooper NZ (B), W.G. Boatwright QLD (C, F & G), ALA cc VIC (D) and R. & E. Kearney NSW (E).

representatives of all morphological variants. Potential reasons for the variations of significant characters including evolutionary change, ecological (climate, habitat) differences and geographic isolation are considered.

We provide an updated description of *Marasmius elegans* including molecular data and morphological variations across its distribution, and the new variety, *M. elegans* var. *occidentalis* var. *nov.* from WA is described. An updated description of *M. atrocaneus* from New Zealand with supporting molecular data is also included. In addition, four new species with morphological similarities to *M. elegans*, namely *M. dikhusha*, *M. durifagus*, *M. leppii* and *M. multicystidiatus*, are described. Placement of several taxa in ser. *Luteoli* is confirmed, and a new series, *Multicystidiati* is established for *M. multicystidiatus* and *M. sullivantii*.

MATERIALS AND METHODS

Sampling

Specimens of the *Marasmius elegans* complex were collected opportunistically on general macrofungal surveys in SEQ. Members of the Queensland Mycological Society (QMS) collected specimens in Linda Garrett, Mapleton Falls and Mt Cordeaux National Parks (N.P.) and Maroochy Bushland Botanic Gardens (wet sclerophyll habitat); also Dikhusha Nature Refuge in regenerating subtropical rainforest, over several years from 2015 to 2023. Further fresh collections were made in NSW from Dorrigo N.P., Hampton State Forest (S.F.) Royal N.P. and Wyong region in central coastal NSW. All herbarium specimens from the QLD Herbarium (BRI), labelled as *Marasmius elegans* or *M. aff. elegans* were examined. These included collections from Bunya Mts N.P. (eucalypt forest), Mt Glorious N.P. (wet sclerophyll and rainforest), Lamington and Springbrook N.P.s [beech-coachwood forest, complex notophyll vine forest (CNVF) and Antarctic beech (*Nothofagus moorei*) forest] and Yarraman hoop pine (*Araucaria cunninghamii*) forest. A total of 38 collections, either already in BRI or freshly collected, were examined macroscopically and microscopically (Table 1).

Additional collections of the *M. elegans* complex from the National Herbarium of Victoria (MEL), including seven specimens from Tasmania, 14 from Victoria, two from Queensland, and two from Northern Territory were examined. A further seven specimens from the New Zealand Fungarium (PDD); eight from the South Australian Herbarium (SA); five from the Western Australia Herbarium (PERTH); and eight from the Australian National Herbarium (CANB) were also included in the study.

Morphological protocols

Fresh collections were photographed, described and a sample placed in silica gel prior to DNA analysis. The basidiomata were then dried using an Ezidri Snackmaker FD500 (Hydraflow Industries Ltd, Upper Hutt, NZ) food dehydrator at the lowest setting for at least 12 h. Spore prints were made where possible. Macroscopic features including details of pileus, lamellae, stipe, substrate and habit were recorded from the fresh material. Pilei were considered small to medium where the diameter was < 25

mm and robust > 25 mm. Robustness of the basidiomata was measured using maximum pileus diameter and this measurement was plotted against latitude on a scatterplot using R (R Development Core Team, 2024) to test the hypothesis of increasing size with higher latitude. Colours were recorded according to the Flora of British Fungi Colour Identification Chart (Royal Botanic Garden Edinburgh 1969).

Microscopic characters of hand-sectioned dried material were examined using a Prism Optical (Model EX-30T) compound microscope with Tucsen GT12 camera (Tucsen Photonics Co., China) with a 100× objective. Sections were rehydrated and examined in Congo Red in water, in 5 % potassium hydroxide (KOH) or Melzer's Reagent. Microscopic details were recorded with Mosaic v. 2.0 software (<http://www.tucsen.com>). For spore measurement, the abbreviation Q refers to the length/width ratio, Q_m the mean of Q values. Values in square brackets are standard deviation [SD] for mean measurements of length, width and Q_m values. N = number of spores measured per specimen. Microscopic examination of the pileus of selected specimens from Herbaria (BRI, MEL, AD, PERTH, CANB and PDD) was performed. Stipe caulocystidia were examined from all *M. elegans* and *M. aff. elegans* collections to assess variability across the geographic range. Caulocystidia were designated short (< 25 µm), medium (26–50 µm) or long (> 51 µm); their density assessed as sparse (< 10 cystidia / field × 40 magnification), moderately dense (11–20), or dense (> 21); presence or absence of clumping and shape of cystidia was noted. A small number of specimens were assessed to see whether caulocystidia varied significantly across the stipe length of individual basidiomata as well as between specimens.

Molecular protocols

Thirty-four collections, representing morphological variants across the broader distribution, were sequenced for nrITS, 25 for nrLSU and 11 for *TEF1* DNA barcoding regions for this study. Protocols for DNA extraction, PCR amplification and sequencing were the same as previously described in Guard *et al.* (2024).

Sequence editing was done within Geneious Prime v. 2023.2.1. (<https://www.geneious.com>) and the initial alignment was performed using MAFFT (Katoh & Standley 2013). Sequences were trimmed, then edited manually. A BLAST search against the National Centre for Biotechnology Information (NCBI) database (<http://www.ncbi.nlm.nih.gov/>) was used to determine closest sequence matches. The final nrITS and nrITS+*TEF1* alignments included sequences generated in other labs (Lebel and Holmes MEL; and Cooper Landcare Res.), and sequences from taxa in sect. *Globulares*, subsect. *Leonini* (Oliveira *et al.* 2024) from GenBank. Newly generated sequences (in **bold**) used in the construction of the phylogenetic tree are shown in Table 1.

Maximum likelihood phylogenetic analysis was conducted using RAxML v. 8.2.11 (Stamatakis 2014) with the GTR+GAMMA+I model using four partitions as recommended by Partition Finder and 1500 rapid bootstrap (BS) replicates. Bayesian analysis was performed with Mr Bayes v. 3.2.6 (Huelsenbeck & Ronquist 2001) using the substitution model GTR and Metropolis Coupled (MCMCMC) settings, for 1 M

Table 1. Table of all sequences used in this study of the *Marasmius elegans* complex and related members of ser. *Luteoli*, including GenBank numbers for nrITS, nrLSU and *TEF1* and Herbarium numbers of the Australian and New Zealand collections. Species in **bold** are new collections and /or sequences produced in this study. HT after the fungarium number indicate holotypes. Sequences from GenBank are named as listed; — = not determined, n/dep = not yet deposited.

Species	Collection #	GenBank #nrITS	GenBank #nrLSU	GenBank #TEF1	Location	Fungarium #
<i>M. abundans</i> var. <i>abundans</i>	TYS513	FJ431209	—	—	Malaysia	—
	TYS460	FJ431210	—	—	Malaysia	—
<i>M. acerosus</i>	TYS458	FJ431213	—	—	Malaysia	—
<i>M. adhaesus</i>	TYS464	FJ431217	—	—	Malaysia	—
<i>M. angustilamellatus</i>	TYS528	FJ431220	—	—	Malaysia	—
	TYS437	FJ431218	—	—	Malaysia	—
<i>M. araucaria</i> var. <i>siccipes</i>	NW364	EU935511	—	—	Thailand	—
	MY38	FJ431263	—	—	Malaysia	—
	TYS529	FJ431222	—	—	Malaysia	—
<i>M. atrocastaneus</i>	NS4027/JAC16292	OQ282820	OQ282771	—	New Zealand	PDD113436
<i>M. aurantioferrugineus</i>	KG254	FJ904962	—	—	Republic of Korea	—
	VLA M-10513	KJ662667	—	—	Far East Russia	—
<i>M. auratus</i>	NW076	EU935501	—	—	Thailand	—
	NW175	EU935502	—	—	Thailand	—
<i>M. bellus</i>	JO299	KP635208	—	—	Brazil	—
<i>M. benghalensis</i>	SOU MITRA205	MF189043	—	—	India	—
	SOU MITRA240	MF189044	—	—	India	—
<i>M. cf. cladophyllus</i>	MCA1837	AY916705	—	—	Guyana	—
<i>M. corrugatiformis</i>	DED8326	KX953756	—	—	Sao Tome	—
<i>M. cystidiatus</i>	CAL1669	MH216191	—	—	India	—
	SI19	OR178481	—	—	Malaysia	—
<i>M. dilkusha</i>	F2020014	PP389603	PP389605	PV151715	Australia: SEQ	BRI AQ1017482 (HT)
	iNat261303016	PV870569	PV870574	—	Australia: NSW	ENV T
<i>M. durifagus</i>	JAC12814	OQ282796	OQ282752	—	New Zealand	PDD96918 (HT)
	JAC13822	OQ282756	OQ282802	—	New Zealand	PDD106027
<i>M. elegans</i> (lectotype)	JBCleland	—	—	—	Australia: SA	AD3788 (HT)
<i>M. elegans</i> (syntype)	JBCleland	—	—	—	Australia: SA	AD3786
<i>M. elegans</i>	PSC2836	PP354953	PP354915	—	Australia: SA	AD-C58058
	PSC4271	PP354951	PP354926	—	Australia: SA	AD-C58967
	PSC1172	PP354952	PP354914	—	Australia: SA	AD-C51208
	s.n.	PP354954	PP354921	—	Australia: VIC	MEL2053823
	FNCV37	PP354948	PP354920	—	Australia: VIC	MEL2047709
	WP100	PP354965	PP354935	—	Australia: VIC	MEL2320395
	TWM1766	PP354947	PP354922	—	Australia: VIC	MEL2329551
	KRT2747	PP354958	PP354912	—	Australia: VIC	MEL2151403
	TL957	—	PP354934	—	Australia: VIC	MEL2220689
	s.n.	PP354959	PP354919	—	Australia: VIC	MEL2053824
	F2022055	PP354946	PP354932	PV151727	Australia: VIC	ENV T
	RS169	PP354963	PP354918	—	Australia: TAS	MEL2403133
	SMF2210	PP354949	PP354917	—	Australia: TAS	MEL2300714
	REH8670	PP354950	PP354916	—	Australia: TAS	MEL2264994
	Ratk223	PP354941	PP354913	—	Australia: TAS	MEL2252667
	Ratk228	PP354962	PP354936	—	Australia: TAS	MEL2252658
	F2022052	PP354961	—	PV151722	Australia: NSW	ENV T
	F2022056	PP354960	PP354930	PV151726	Australia: NSW	BRI AQ1041098
	F2020059	PP354945	PP354928	PV151712	Australia: NSW	ENV T
	F2021087	PP354956	—	—	Australia: NSW	BRI AQ1033128
	QMS025LG19	PP354957	PP354929	PV151735	Australia: QLD	BRI AQ1008147
	QMS20200222031	PP354940	PP354927	—	Australia: QLD	ENV T
	QMS20210313011	PP354955	—	PV151721	Australia: QLD	BRI AQ1033130

Table 1. (Continued)

	QMS2024420010	PV016898	PV012147	—	Australia: QLD	BRI AQ1048075
	F2013068	PP354942	PP354925	—	Australia: QLD	BRI AQ799930
	LNP598	PP354943	PP354923	—	Australia: QLD	BRI AQ808612
	LNP776	PP354944	PP354924	—	Australia: QLD	BRI AQ808614
	JAC9376	OQ282777	—	—	New Zealand	PDD80809
	JAC15582	PP407533	—	—	New Zealand	PDD112731
	JAC11770	PP407531	—	—	New Zealand	PDD96172
	JAC14731	PP407532	—	—	New Zealand	PDD106608
	JAC15582	PP407533	—	—	New Zealand	PDD112731
	JAC11381	PP407530	—	—	New Zealand	PDD95805
	JAC13253	OQ282799	OQ282754	—	New Zealand	PDD105509
	JAC10928	OQ282785	OQ282743	—	New Zealand	PDD95386
<i>M. elegans</i> var. <i>occidentalis</i>	KS3269	PV016900	PV870573	PV151758	Australia: WA	BRI AQ1052601 (HT)
	KS3268	PV016899	—	—	Australia: WA	BRI AQ1052599
	KS3174	PP354966	PP354937	PV151734	Australia: WA	BRI AQ1041082
	FC1594	PV870568	—	—	Australia: WA	PERTH08163278
<i>M. aff. elegans</i> 'tiny'	iNaturalist263822395	PV870570	PV870575	—	Australia: NSW	BRI AQ1054443
<i>M. graminicola</i>	JO459	KP635178	—	—	Brazil	—
	JO480	KP635179	—	—	Brazil	—
<i>M. indojasminodorus</i>	AKD139/2015	KY785171	—	—	India	—
	AKD135/2016	KY785172	—	—	India	—
<i>M. inthanonensis</i>	NW353	EU935514	—	—	Thailand	—
<i>M. jasminodorus</i>	GCMCC17072	MK656317	—	—	Thailand	—
	NW414	EU935515	—	—	Thailand	—
<i>M. katangensis</i>	JES227	KX148991	—	—	Madagascar	—
<i>M. leoninus</i>	JO320	KP635162	—	—	Brazil	—
	JO84	KP635209	—	—	Brazil	—
<i>M. leppii</i>	HL416	PV016897	—	—	Australia: NSW	CANB574279 (HT)
<i>M. luteolus</i>	NW138	EU935506	—	—	Thailand	—
	NW304	EU935507	—	—	Thailand	—
<i>M. midnapurensis</i>	CUH AMT002	KY785179	—	—	India	—
	CAL1523	MF189041	—	—	India	—
<i>M. multicystidiatus</i>	F2015002	PP354939	PP354931	—	Australia: QLD	BRI AQ1019024 (HT)
<i>M. ochroleucus</i>	LE295978	KF912952	—	—	Russia	—
	HMJAU63586	OR364586	—	—	China	—
	NW299	EU935503	—	—	Thailand	—
<i>M. ochropoides</i>	TYS384	FJ431263	—	—	Malaysia	—
	KLU-M89	NR154150	—	—	Malaysia	—
<i>M. occultatiformis</i>	LE295995	KF774155	—	—	Far East Russia	—
	LE295995	KF774157	—	—	Far East Russia	—
	HMJAU63583	OR364585	—	—	China	—
	MHHNU30835	MK388150	—	—	China	—
<i>M. olivascens</i>	KLU-M90/TYS426	NR154151	—	—	Malaysia	—
<i>M. pellucidus</i>	SL1230	OQ147044	—	—	Singapore	—
<i>M. pseudopellucidus</i>	NW186	EU935504	—	—	Thailand	—
	NW305	EU935505	—	—	Thailand	—
<i>M. pseudoelegans</i>	QMS20220305012	PP354971	PP354911	—	Australia: QLD	BRI AQ1033133 (HT)
	WGB523	PP354969	PP354933	—	Australia: QLD	MEL2458237
	Puechmarin#2	PP354968	PP354938	PV151736	Australia: QLD	BRI AQ1019379
	LNP957	PP354967	—	—	Australia: QLD	BRI AQ794523
	QMS20250222036	—	—	—	Australia: QLD	BRI AQ1054053
<i>M. ruber</i>	DED8669	KP635193	—	—	Brazil	—
<i>M. strobiluriformis</i>	BRNM714914	GU266263	—	—	Republic of Korea	—
	BRNM714915	GU266264	—	—	Republic of Korea	—
<i>M. subarborescens</i>	DED8215	KX953755	—	—	Sao Tome	SFSU
<i>M. sullivantii</i>	SD Russell	MK564568	—	—	USA: Indiana	—
	Mycomap6672	—	—	—	—	—

Table 1. (Continued)

	SD Russell Mycomap9564	ON245222	—	—	USA: Indiana	—
	SD Russell Mycomap9753	ON245223	—	—	USA: Indiana	—
	SD Russell Mushroom Observer 209665	ON245228	—	—	USA: Indiana	—
	iNat180138632	PP156330	—	—	USA: Ohio	—
<i>M. suthepensis</i>	JO329	KP635198	—	—	Brazil	—
	JO469	KP635199	—	—	Brazil	—
<i>M. aff suthepensis</i>	F2021002	PP354973	PP354909	PV151723	Australia: QLD	BRI AQ1021679
	F2021084	PP354972	PP354910	PV151724	Australia: QLD	BRI AQ1041095
	F2024003	PQ618899	PQ618856	—	Australia: QLD	BRI AQ1045955
<i>M. thailandicus</i>	NW541	KJ588397	—	—	Thailand	—
	NW740	MH187572	—	—	Thailand	—
<i>Marasmius</i> sp.1 (koae)	GMB2014	KP013014	—	—	Australia: NT	MEL2382678
	GMB2014	KP012802	—	—	Australia: NT	MEL2382938
<i>Marasmius</i> sp.	RAK586	MN930558	—	—	Guyana	—
	RAK595	MN930559	—	—	Guyana	—
<i>Marasmius</i> sp. "orange"	MDB2022012	n/dep	n/dep	—	Australia: QLD	BRI AQ
<i>Hymenogloea papyracea</i>	DED4742	OR636632	—	—	Colombia	—
	NVE228	KF937332	—	—	Colombia	—

iterations. New sequences were registered with GenBank and names of novel taxa with MycoBank.

RESULTS

Morphological analysis

Specimens of the *Marasmius elegans* complex and those labelled as *M. elegans* or aff. *elegans* examined in this study were determined to be from nine distinct taxa. These included 67 *M. elegans* s. str., confirmed by either microscopy, sequencing or both, four *M. elegans* var. *occidentalis* var. nov., seven *M. pseudoelegans* (Crous et al. 2024), one *M. vagus* (Crous et al. 2020), two *M. australotrichotus* (Guard et al. 2023), one *M. atrocastaneus* (Stevenson 1964, Desjardin & Horak 1997), two *M. durifagus* sp. nov., one *M. multicystidiatus* sp. nov., two *M. dilkusha* sp. nov. and one *Marasmius leppii* sp. nov. *Marasmius vagus* (similar in colour, with robust stature, but an all-white stipe and inter-venation of lamellae) (Crous et al. 2020) and *M. australotrichotus* (a smaller species with slender pruinose stipe and microscopic setae on pileus and stipe) (Guard et al. 2023) are readily distinguished morphologically (Fig. 1) and are molecularly distant and not included in the present phylogeny.

Marasmius elegans s. str. is morphologically very variable. Figure 2 (A–E) illustrates the differences in colour, which range from velvety brown to bright orange; lamellae with or without coloured margins; and size from under 10 mm up to 50 mm diam. of pileus with slender to robust stipes. The hypothesis that Queensland specimens were smaller, less robust than the more southerly specimens and could represent another species, was tested and had two outcomes. Firstly, a second species, *M. pseudoelegans*, was discovered, which in its juvenile stage is macroscopically

indistinguishable from the Queensland form of *M. elegans* (Fig. 2E, F). With maturity (Fig. 2G), it remains very similar to the QLD form of *M. elegans*, but on closer examination shows distinctive features of bifurcating lamellae and elongate, at times geniculate *Siccus*-type caulocystidia (see Fig. 15H for illustration). Molecularly it is a distinct species. Secondly, maximum pileus diameter was used as a measure of robustness for 71 collections across the full distribution range of *M. elegans* (Fig. 3). A scatterplot was created comparing maximum pileus diameter (mm) against latitude (degrees S), and the data tested for normality using the Shapiro-Wilks test and for correlation using Spearman's test, in the statistical package of R v. 4.4.2 (R Development Core Team 2024). A weak positive (significant at $p < 0.05$) correlation between maximum pileus diameter (hence robustness) and increasing latitude was found, i.e. pileus diameter does increase the further south the species occurs. A regression line was calculated in ggplot2 (Wickham 2016).

However, the most variable features of the species are the caulocystidia. All herbarium and fresh collections were examined (71 total). Caulocystidia were absent in 8 of the 71, but present in the rest, with varying lengths and densities as shown in Table 2 and illustrated in Figs 4, 5. The specimens with no caulocystidia were limited to three southern states (WA, SA, VIC). Specimens from QLD and NSW showed more variation in length, density and shape than the southern states, but NZ showed the most variety of shapes (Fig. 5).

It is not clear from any published descriptions whether caulocystidia vary in different parts of the stipe. Grgurinovic (1997), in her study of South Australian fungi, including the holotype, noted that there were broom cells toward the apex, and did not mention smooth cylindrical caulocystidia. Desjardin & Horak (1997) commented that *M. elegans* was similar to *M. croceus*, described from New Zealand, but the stipe had 'irregularly cylindrical, thick-walled caulocystidia,

Table 2. *Marasmius elegans* caulocystidia showing Australian states: Western Australia (WA), South Australia (SA), Victoria (VIC, Tasmania (TAS), New South Wales (NSW), Queensland (QLD), and New Zealand (NZ), with number of collections in brackets, in columns across the Table. Caulocystidia presence, length, density and other forms are measured as per *Morphological protocols*. n/p = no other forms present.

Caulocystidia	WA (7)	SA (8)	VIC (17)	TAS (7)	NSW (12)	QLD (16)	NZ (4)
Absent	2	5	1	0	0	0	0
Short/sparse	3	3	11	3	3	2	3
Short/ mod. dense	2	0	0	4	8	10	0
Short-long /mod. dense	0	0	5	0	0	4	1
other	n/p	n/p	Occas. branched	Occas. branched	Rare stellate / broom	Occas. broom / branched / narrow tip	Narrow tip / stellate / strangulate

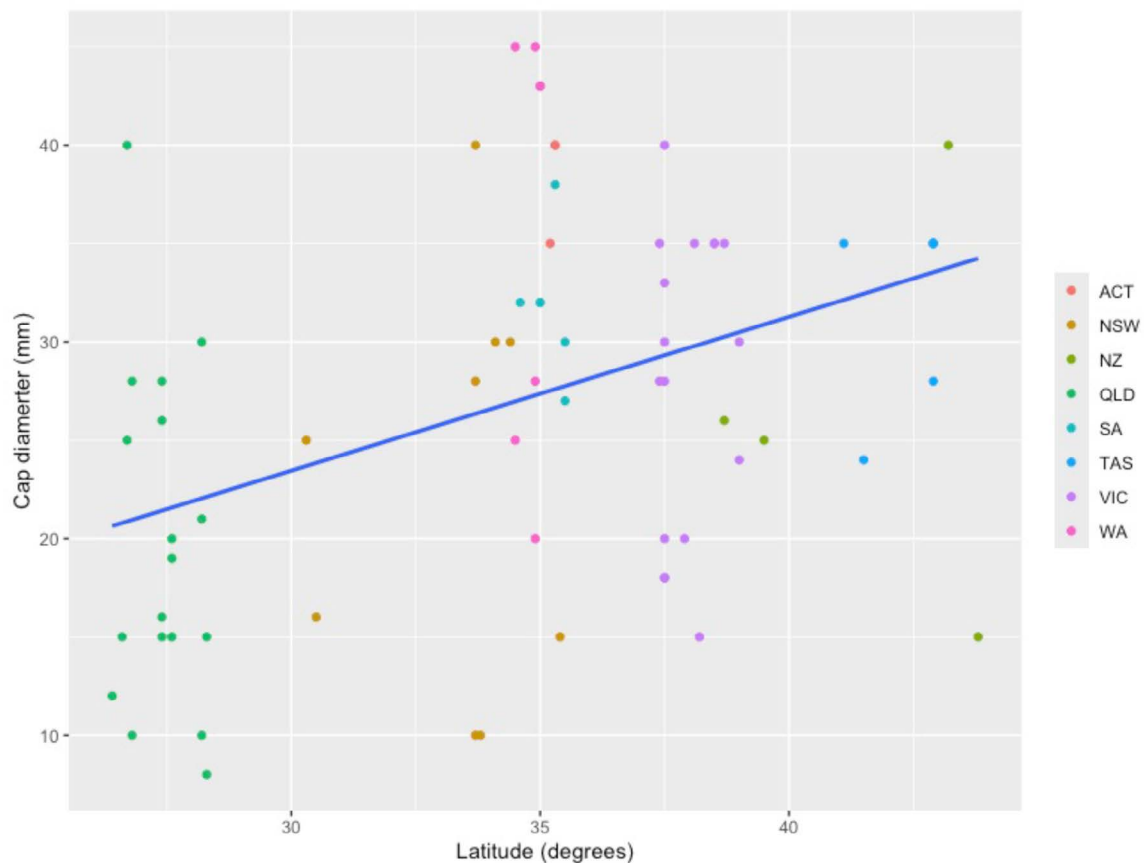


Fig. 3. *Marasmius elegans* scatterplot for 71 collections comparing maximum pileal diameter (mm) as an estimate of robustness against latitude (degrees south). The data was tested for normality using the Shapiro-Wilks test and for correlation using Spearman's test, both from the stats package in R, and showed it was significant ($p < 0.05$) with a weak positive correlation ($\rho = 0.355$). The regression line (blue) was calculated in ggplot2.

whereas *M. croceus* had *Siccus*-type broom cells. Bougher & Syme (1998) focussed on Western Australian and southern Australian fungi, and did not mention caulocystidia in the collections they examined of *M. elegans*. No other published descriptions of the species include microscopic detail (Fuhrer 2005, Grey & Grey 2005, Young 2005, Moore & O'Sullivan 2013, Gates 2016). In the current study *Siccus*-type cells were found only three times in 71 stipes of *M. elegans* examined, and specifically none in South Australian specimens. Five specimens of *M. elegans*, two from Queensland and three from Western Australia, were examined more intensively, looking at cystidia in upper, middle and lower thirds of stipes. No *Siccus*-type cells were found; stipe vestiture was similar in upper, middle and lower thirds in WA samples; however, the lower third of QLD samples contained increasing numbers and lengths of cystidia even though the basal tuft of mycelial

hairs was deliberately excluded. It is recommended as a minimum, that position of sampling of stipe vestiture should be stated when describing taxa, to aid in distinguishing morphologically similar members of the complex.

Molecular analysis

The dataset used for phylogenetic analysis includes the collections of this study and a broad sampling of members of ser. *Luteoli* and ser. *Leonini* retrieved from GenBank, with ser. *Graminicolae* as outgroup. The phylogeny is inferred from Bayesian and Maximum Likelihood (ML) analyses of the barcode nrITS region (Fig. 6). A smaller dataset was used to analyse the *TEF1* gene region, and a concatenated alignment of nrITS and *TEF1* (some missing data) was created and a phylogeny inferred from Bayesian and Maximum Likelihood

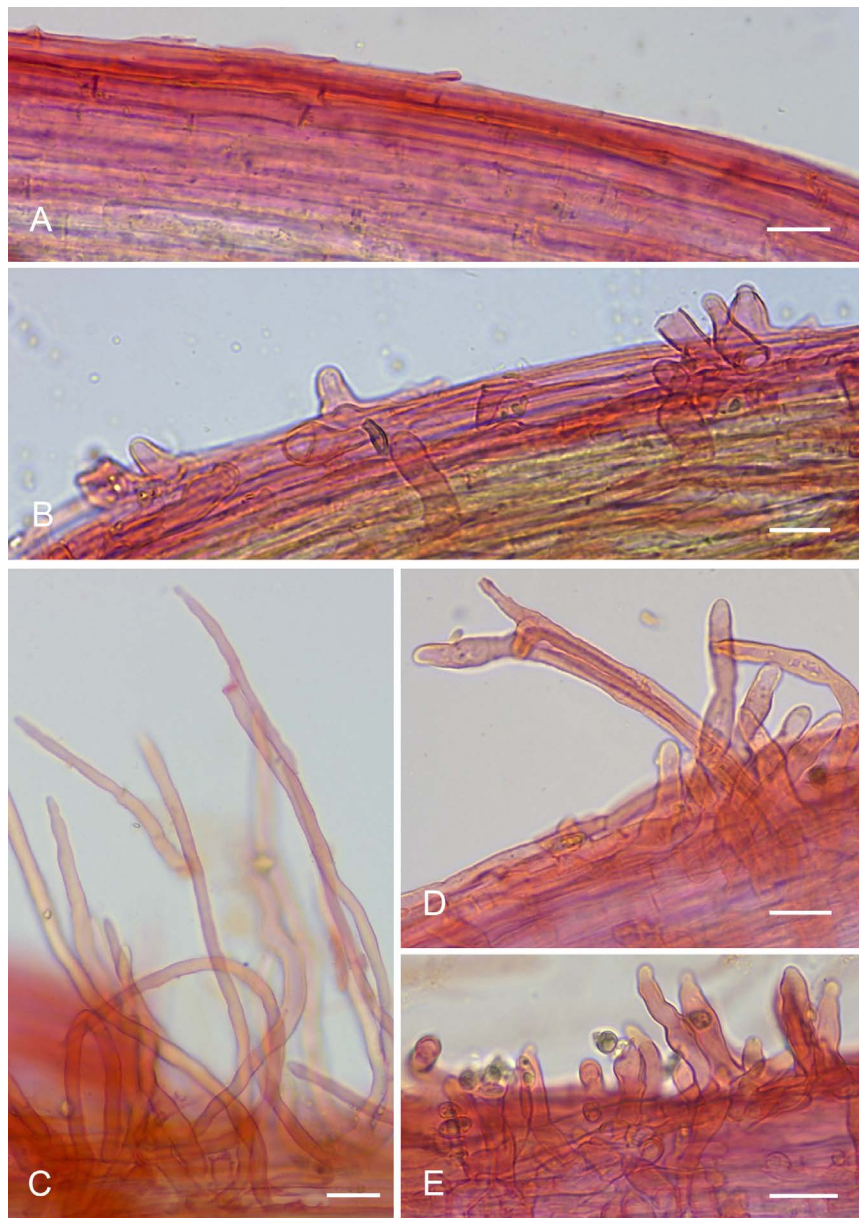


Fig. 4. *Marasmius elegans* variations of stipe caulocystidia across Australian range. **A.** Absent. **B.** Sparse, short. **C.** Dense, long. **D.** Medium length, branched, clustered. **E.** Dense short. Scale bars = 10 μ m. Images by F.E. Guard.

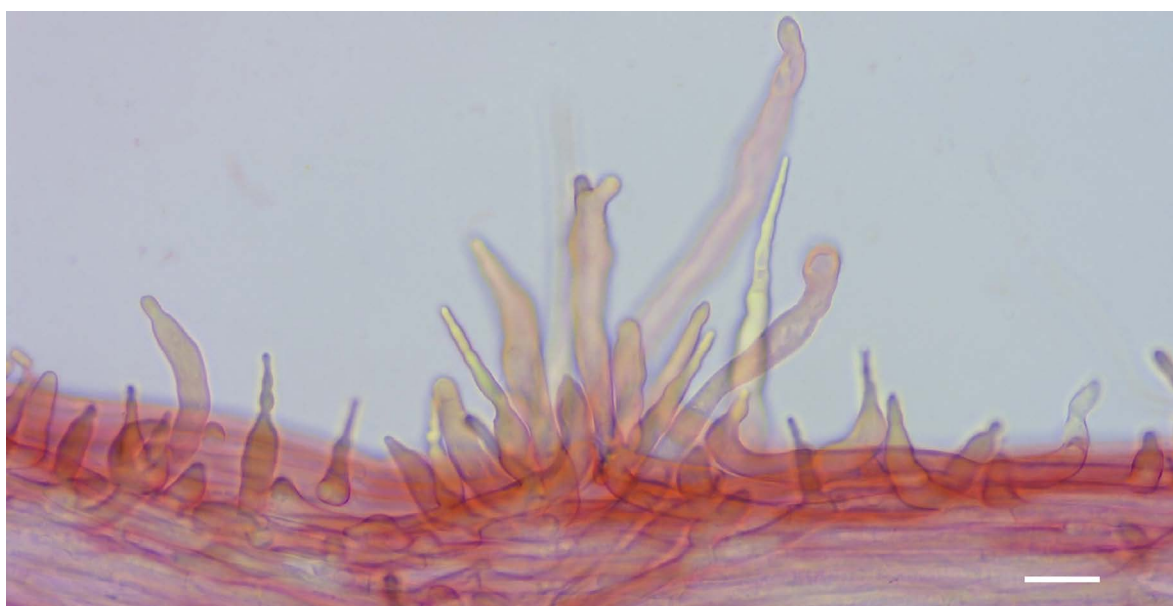


Fig. 5. *Marasmius elegans* stipe caulocystidia New Zealand (PDD80809). Scale bar = 10 μ m. Image by F.E. Guard.



Fig. 6. *Marasmius elegans* and other members of subsect. *Leonini*, ser. *Luteoli*, *Leonini*, *Multicystidiati* (with *M. suthepensis*, ser. *Graminicolae* as outgroup) nrITS in Bayesian analysis for 1 M iterations. Shortened branch ($\times 2$) for FJ431222 (*M. araucaria* var. *siccipes*). Branches with strong support show maximum likelihood bootstrap (BS) and posterior probability (PP), e.g. BS 100/PP 1.



Fig. 7. Concatenated nrITS and *TEF1* Bayesian analysis of *M. elegans* and related species with maximum likelihood bootstrap (BS) and posterior probability (PP) noted for well supported nodes (BS/PP), using sequences generated in this study and others obtained from GenBank.

analyses (Fig. 7).

Marasmius elegans, despite its morphologic variability, is shown to form a discrete monophyletic clade with moderate to strong support – (BS 60/PP 1.0) in ITS and (BS 99/PP 1.0) in the concatenated nrITS and *TEF1* trees. However, the four WA sequences are on a separate branch with strong support (BS 99/PP 1.0) with nrITS and (BS 97/PP 1.0) with concatenated nrITS and *TEF1*, and are at most 97.4 % identical with other members of the clade using nrITS only or the concatenated analysis. Given their geographic distance and isolation from other members of the species, their generally robust pilei and sparse, short, simple or absent caulocystidia, we consider this to be a distinct taxon and here describe it as *Marasmius elegans* var. *occidentalis* var. nov. The sister species of *M. elegans* is *Marasmius* sp. “tiny Wyong” from NSW with moderate to strong support (BS 77/PP 1.0). This species awaits further collections before publishing. The new species from NZ, *Marasmius durifagus*, is close to *M. atrocastaneus*. The Australian species, *Marasmius pseudoelegans*, forms another distant monophyletic clade with strong support (BS 100/PP 1.0). It groups with other species that have been assigned to ser. *Luteoli* (*M. pseudopellucidus*, *M. auratus*, *M. luteolus*, *M. strobiluriformis*, *M. jasminodorus*, *M. ochroleucus*, *M. inthanonensis* and *M. araucariae* var. *siccipes* from Thailand, *M. indojasminodorus*, *M. benghalensis*, *M. cystidiatus* and *M. midnapurensis* from India, *M. araucariae* var. *siccipes*, *M. abundans* var. *abundans*, *M. ochropoides* and *M. angustilamellatus* from Malaysia, *M. strobiluriformis* and *M. ochroleucus* from Republic of Korea and Far East Russia respectively, and *M. ochroleucus* and *M. occultatiformis* from China) as well as *M. elegans* and the newly described species, *M. dikhusha* and *M. leppii* but with low support. *Marasmius multicystidiatus* sp. nov. and its strongly supported sister species, *M. sullivantii* (USA) (BS 93/PP 1.0) are more distant in an unresolved group on long branches with ser. *Leonini*. However, both *M. multicystidiatus* and *M. sullivantii* have pleurocystidia, a character not expected in ser. *Leonini*, and caulocystidia of several varieties, including *Amyloflagellula*-type cells. We establish ser. *Multicystidiati* for these two species in the taxonomy section below.

Taxonomy

Marasmius* subg. *Globulares* sect. *Globulares* subsect. *Leonini* ser. *Luteoli

Marasmius atrocastaneus G. Stev., *Kew Bull.* **19**: 41. 1964. Fig. 8.

Typus: New Zealand, North Island, Wellington Province, Butterfly, on litter of *Nothofagus solandri*, 10 Jul. 1949, G. Stevenson, Stev.715 (**holotype** K-M819354).

Re-description based on PDD 113436: *Basidiomata* medium, collybioid. *Pileus* 13–29 mm diam., broadly convex to applanate with low central umbo, faintly striate towards margins, margins incurved when young, dark brick (20) to purplish chestnut (21) central disc and inner two-thirds of pileus, margin rusty tawny (14), dull dry surface; flesh thin, cream. *Lamellae* moderately crowded, 26–30, adnexed,

off-white to cream, margins orange, 3–4 tiers *lamellulae*. *Stipe* central, cartilaginous, cylindric, 25–40 × 2–4 mm, finely pruinose especially lower one-third, dark brick (20) base, through rust (13), gradually becoming paler towards apex, cream at upper end and base covered with cream strigose hairs; juvenile stipes generally paler. *Spore print* not obtained. *Basidiospores* 9.5–11.5 × 4.5–5.5 µm, $Q = 1.85–2.33$, mean 10.5 [± 0.47 SD] × 5 [± 0.25 SD] µm, $Q_m = 2.06$ [± 0.12 SD], $N = 20$ from one collection, broadly ellipsoid, thin-walled, smooth, inamyloid. *Basidia* not found. *Basidioles* sparse, cylindrical, blunt-ended, 14.6–23.7 × 4.6–6 µm. *Cheilocystidia* (i) very common *Siccus*-type cells, cylindric, bulbous, with thick-walled terminal setulae, main body 13–28 × 4–7.5 µm, setulae sparse and elongate 10–22 × 2 µm and (ii) rare setoid cells 59 × 5 µm, forming a sterile lamellar edge. *Pleurocystidia* absent. *Pileipellis* a hymeniderm of *Siccus*-type cells, cylindric, elongate, occasionally irregular, main body thick or thin-walled 18–32 (–59) × 5–9 µm, setulae terminal, sometimes thick-walled, refractile, sparse 9–21 × 1.5–2 µm. *Stipe* hyphae parallel, cortex thick-walled 3–4 µm diam., medulla inamyloid, 3–5 µm diam. *Cauloetae* (mid-stipe) numerous, sometimes in bunches, thick-walled, lanceolate, rarely branched, cells with acute apices 40–60 × 4–7 µm. *Clamp connections* present in all tissues.

Collection examined: New Zealand, North Island, Prov. Wellington, York Bay, Kaitawa road trail, 7 May 2019, N. Siegal, NS4027 (PDD113436; GenBank sequences nrITS OQ282820 and nrLSU OQ282771).

Additional collections examined by Desjardin & Horak (1997): New Zealand, South Island, Nelson Prov., Whanganui Inlet, 16 May 1968, E. Horak, Horak 68-463 (ZT); Fjordland Prov., Milford Sound, solitary at end of paved road on leaf litter of *Nothofagus menziesii* and *Dacrydium cupressinum*, 1 Apr. 1969, E. Horak, Horak 69-200, (SFSU-F-024643; ZT).

Habit, habitat and distribution: This species has been found on leaf litter in beech (*Nothofagus*) forest in both north and south islands of New Zealand (Stevenson 1964, Desjardin & Horak 1997). It may be solitary or gregarious.

Notes: This collection fits very closely with the descriptions of *Marasmius atrocastaneus* as provided by Stevenson (1964) and Desjardin & Horak (1997) based on the collection Horak 68-463 (ZT). Stevenson used the Singer’s (1958) classification to place *Marasmius atrocastaneus* in sect. *Globulares*, sect. *Sicci*. Desjardin & Horak (1997) examined material from both north and south islands of New Zealand, including the holotype (Stevenson 715). Their further classification of the section placed *M. atrocastaneus* in ser. *Atrorubentes* (Desjardin & Horak 1997), raised for species with cystidiiform elements on the stipe, which it clearly has. However, with the addition of molecular data, ser. *Atrorubentes* was shown to be not monophyletic (Wannathes *et al.* 2009, Shay *et al.* 2017). The most recent reclassification of the genus *Marasmius* (Oliveira *et al.* 2024) places *M. atrocastaneus* in a large, moderately supported clade, grouping species formerly in ser. *Atrorubentes*, now in sect. *Globulares*, subsect. *Leonini*, ser. *Luteoli*. *Marasmius atrocastaneus* is macro-morphologically similar to the brown form of *M. elegans*, but has distinctive microscopy

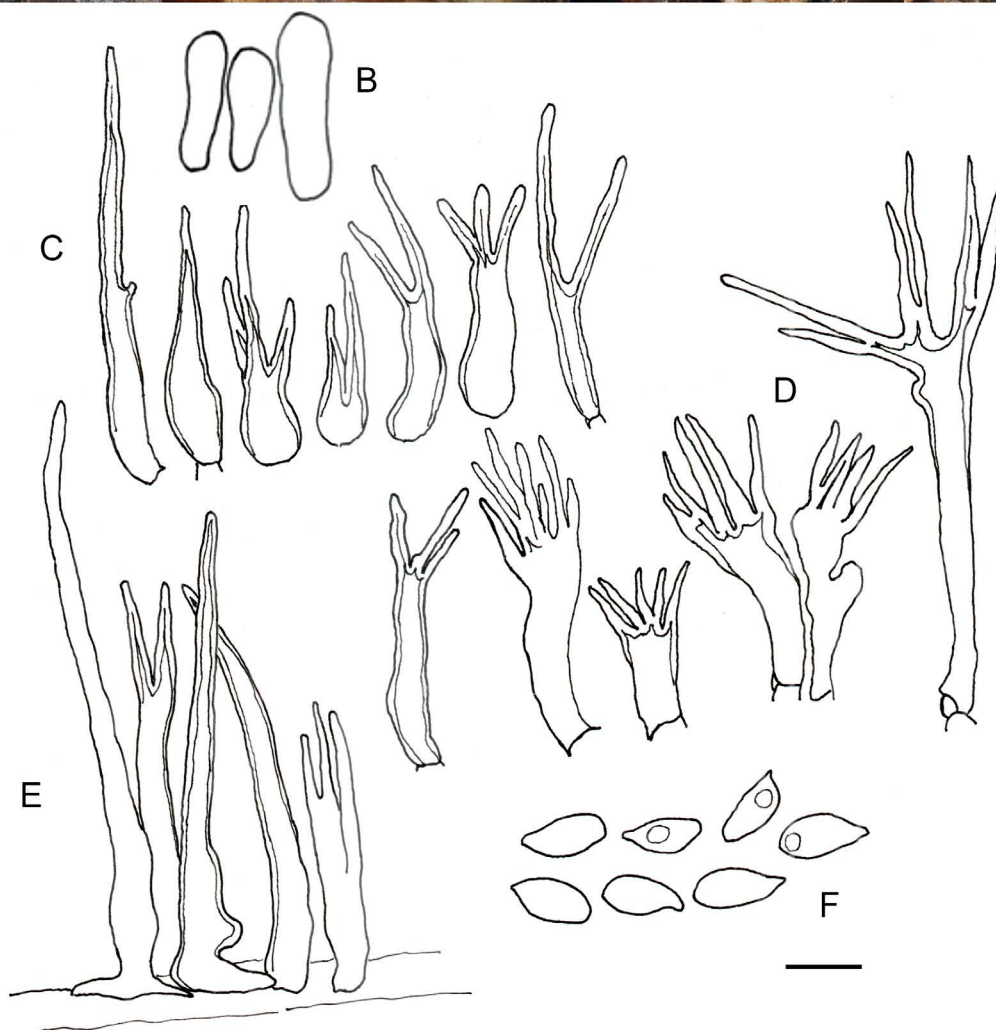


Fig. 8. *Marasmius atrocastaneus* (NH4027). **A.** In situ in *Nothofagus* forest, NZ. **B.** Basidioles. **C.** Cheilocystidia. **D.** Pileipellis *Siccus*-type cells. **E.** Caulocystidia. **F.** Basidiospores. Scale bars = 10 μ m. Image by Noah Siegel (A), illustrations by F.E. Guard (B–F).

with its long, acute setulae on cheilocystidia and pileipellis *Siccus*-type cells, and its cauloseetae. Its sister species with low support are the Australasian *M. elegans*, *M. elegans* var. *occidentalis*, *M. durifagus* and an undescribed species from eastern Australia (iNat263822395).

Marasmius dilkusha F.E. Guard, T. Lebel & Dearnaley, *sp. nov.* MB 860158. Fig. 9.

Etymology: This species epithet is for Dilkusha Nature Refuge where the species was first collected. It is a noun in apposition.

Typus: **Australia**, Queensland, Dilkusha Nature Refuge, S26°44'13.7", E152°53'20.0" on well-rotted bark in remnant subtropical Piccabeen palm (*Archontophoenix cunninghamiana*) forest, 26 Jan. 2020, F.E. Guard, F2020014 (**holotype** BRI AQ 1017482), GenBank sequences nrITS PP389603, nrLSU PP389605, *TEF1* PV151715.

Description: *Basidiomata* small to medium, collybioid. *Pileus* 8–15 mm diam., convex, broadly parabolic to applanate with low central umbo, pale sienna (11) with darker centre, to pale saffron (49) when mature, hygrophanous, surface smooth. *Lamellae* sub-distant, 16–18, free to adnexed,



Fig. 9. *Marasmius dilkusha* (F2020014). **A.** Basidiomata in situ with mycelial mat and inset (**B**) to show lamellae and stipe apex. **C.** Basidiospores. **D.** Basidium. **E.** Basidioles. **F.** Pileipellis *Siccus*-type cells. **G.** Cheilocystidia *Siccus*-type cells. **H.** Caulocystidia and stipe hyphae. Scale bars: A, B = 10 mm; C–H = 10 µm. Images and illustration by F.E. Guard.

off-white, cream, non-marginate, *lamellulae* 3–4 tiers. *Stipe* central, cartilaginous, cylindric, 40–50 × 1.0 mm, very finely pruinose (requires hand lens), rusty-tawny (14) base becoming fulvous (12) in upper quarter, with off-white apex; and off-white strigose base on a thin, yellowish-buff mycelial mat, 50 mm diam., on shed bark; juvenile *stipe* paler. *Spore print* not obtained. *Basidiospores* (6.7–)7.2–8.6 × 3–4 µm, $Q = 2.03\text{--}2.63$, mean $7.7 [\pm 0.51 \text{ SD}] \times 3.4 [\pm 0.22 \text{ SD}] \mu\text{m}$, $Q_m = 2.25 [\pm 0.15 \text{ SD}]$, $N = 30 (10 + 20)$ from 2 collections. *Basidia* 4-spored 18–21 × 6–6.5 µm. *Basidioles* clavate to cylindrical, hyaline, thin-walled 20–23 × 4.6–6 µm. *Cheilocystidia* *Siccus*-type cells ovoid, cylindric, clavate, main body thin-walled 7–17.5 × 5–9 µm, terminal setulae thin or thick-walled, crowded 3–7 × 1–1.5 µm. *Pleurocystidia* absent. *Lamellar trama* dextrinoid, hyphae 7–9 µm diam. *Pileipellis* a hymeniderm of *Siccus*-type cells, narrow cylindric to clavate, main body 10–20 × 7–10 µm, terminal setulae thin-walled, rarely thick-walled, 3–9 × 1–1.5 µm. *Pileal trama* dextrinoid, hyphae 5–8 µm diam. *Stipitipellis* parallel hyphae inamyloid. *Caulocystidia* (mid-stipe) sparse to moderately dense mixture of (i) fairly common simple, short, smooth, obtuse ended cells, occasionally branched once, 8–14 × 4 µm; (ii) occasional *Siccus*-type cells, with sparse, thick-walled long setulae, often branched and usually lying almost parallel to stipe cortex, main body (11.5–) 15–30 × 4–7 µm, setulae irregular 3–8 × 1–2 µm; and (iii) sparse simple, smooth, long cystidia with short knobby lateral branches 35 × 4.5 µm. *Clamp connections* present in all tissues.

Additional collection examined: **Australia**, New South Wales, Wyong Shire, Yarramalong, private land, in native and exotic woody and leafy debris in flood zone of feeder creek for Wyong River, 11 Feb. 2025, *M. Drake*, iNat261303016 (ENVT, GenBank sequences nrITS PV870569, nrLSU PV870574).

Habit, habitat and distribution: *Marasmius dilkusha* is solitary or gregarious, growing on well-rotted bark or wood, in a remnant piccabeen palm (*Archontophoenix cunninghamiana*) forest among dead palm fronds, or mixed debris in riparian flood zones. The large cream-coloured mycelial mat stands out very clearly against the dark shed bark and is a distinctive feature.

Notes: *Marasmius dilkusha* is currently known from two collections, the type in southeast Queensland and another from central coast NSW. It is in subsect. *Leonini*, ser. *Luteoli* and is another species resembling *M. elegans*, though smaller, paler, more brownish and with a proportionally longer stem. Its spores are shorter than *M. elegans* (mean 7.5 µm c.f. 10 µm). Its sister species with no support are *M. inthanonensis* (Wannathes et al. 2009) from Thailand and a well-supported clade of various species from Malaysia.

Marasmius durifagus J.A. Cooper & F.E. Guard, *sp. nov.* MB 860159 Fig. 10.

Etymology: From the Latin meaning associated with the leaves of Hard Beech (*Nothofagus truncata*).

Typus: **New Zealand**, Wellington, Upper Hutt, Keith George Memorial Park, S41°8'19.5", E174°59'55.3", on decaying leaves of Hard Beech (*Nothofagus truncata*), 19 May 2013,

J.A. Cooper, JAC12814 (**holotype** PDD 96918), GenBank sequences nrITS OQ282796, nrLSU OQ282752.

Description: *Basidiomata* small to medium, collybioid. *Pileus* 5–15 mm diam., plano-convex, slightly centrally depressed, perimeter pale orange to salmon (45) becoming pale cinnamon (10) with a darker disk, peach (46) becoming snuff brown (17). Flesh white, solid. *Lamellae* close, 26–32, off-white, narrowly adnate, non-marginate, *lamellulae* 2–4 tiers. *Stipe* central, cartilaginous, cylindric, 20–40 × 1.0 mm at the base, expanding at the apex to 2.5mm, finely pruinose along the entire length, dark brick (20) at the base, becoming rust (13) centrally, and cream (8G) in the upper quarter; non-insititious, attached by a cream strigose mycelial mat on dead leaves. *Spore print* not obtained. *Basidiospores* 7.4–10 × 3.1–4.9 µm, $Q = 1.89\text{--}2.75$, mean $8.5 [\pm 0.7 \text{ SD}] \times 3.8 [\pm 0.49 \text{ SD}] \mu\text{m}$, $Q_m = 2.24 [\pm 0.21 \text{ SD}]$, $N = 25 (20 + 5)$ from 2 collections, broadly ellipsoid, thin-walled, smooth, inamyloid. *Basidia* 4-spored, some very elongate, 23–36.5 × 6–6.5 µm. *Basidioles* cylindrical, obtuse-ended to clavate, narrow to broad, 17–31 × 4–8 µm. *Cheilocystidia* *Siccus*-type cells, cylindric, clavate, with thick-walled terminal setulae, main body 11–17 × 5–8.5 µm, setulae sparse and short to moderately crowded and occasionally very long, 2–6(–10) × 1–1.5 µm. *Pleurocystidia* absent. *Pileal trama* 3.5–8 µm diam., weakly dextrinoid. *Pileipellis* a hymeniderm of *Siccus*-type cells, clavate, occasionally bifid or three-branched, irregular, main body 9–23(–30) × (4.5–)6–8.5 µm, setulae terminal, sometimes thick-walled, sparse to moderately common, 4–8 × 1 µm. *Stipe* hyphae parallel, cortex slightly dextrinoid, thick-walled, 4–5 µm diam., medulla inamyloid, 3–5 µm diam. *Caulocystidia* (mid-stipe) numerous, solitary to bunched, thick-walled *Siccus*-type cells with sparse, very elongate setulae, main body 12–37 × 4–8.5 µm, setulae 12–33 × 1.2–2.5 µm and rare smooth, cylindric, obtuse-ended cells 12–28 × 4–6.5 µm. *Clamp connections* present in all tissues.

Additional collection examined: **New Zealand**, Wellington, Lower Hutt, Butterfly Creek, S41°18'17.2", E174°54' 0.7", on decaying leaves of Hard Beech (*Nothofagus truncata*), 16 May 2015, J.A. Cooper, JAC13822 (PDD 106027, GenBank sequences nrITS OQ282756 and nrLSU OQ282802).

Habit, habitat and distribution: The two available collections are from the lower North Island and both are associated with leaf litter of hard beech, which has a scattered distribution. *M. durifagus* is expected to be present in the north-west of South Island where hard beech is common.

Notes: *Marasmius durifagus* is morphologically similar to *M. elegans*. Molecularly, it is in a poorly supported [BS 33/PP 0.55] clade with *M. atrocastaneus* from New Zealand, *Marasmius* sp. "tiny Wyong" from New South Wales and *M. elegans* from Australasia (Figs 6, 7). *Marasmius atrocastaneus* has larger, darker brown basidiomata and more elongate *cheilocystidia* and setoid *caulocystidia*. *Marasmius* sp. "tiny Wyong" is very small with pileus 3–8 mm diam., basidiospore size range 6.5–8 × 3–3.5 µm and *caulocystidia* a mix of smooth cylindrical, branching, irregular and *Siccus*-type cells. *Marasmius elegans* is usually more robust, pilei more orange-brown and *caulocystidia*,

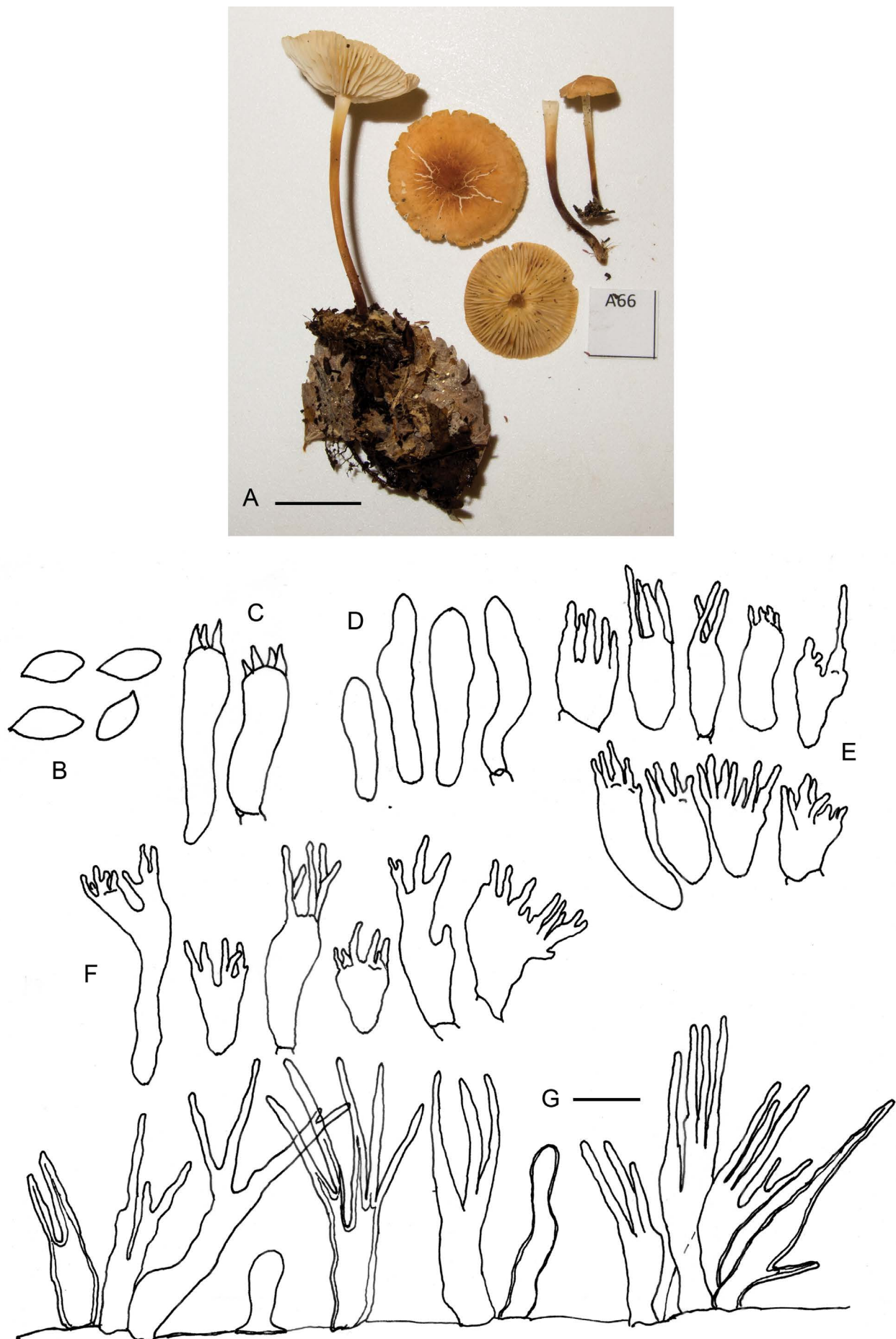


Fig. 10. *Marasmius durifagus* (PDD96918). **A.** Basidiomata and substrate. **B.** Basidiospores. **C.** Basidia. **D.** Basidioles. **E.** Cheilocystidia *Siccus*-type cells. **F.** Pileipellis *Siccus*-type cells. **G.** Caulocystidia. Scale bars: A = 10 mm; B–G = 10 μm. Image by J.A. Cooper (A), illustrations by F.E. Guard (B–G).

though variable, are more likely to be cylindrical cells with or without tapering tips. *Marasmius durifagus* is in ser. *Luteoli* of subsect. *Leonini*. (Oliveira et al. 2024).

Marasmius elegans (Cleland) Grgur., *Larger Fungi of South Australia*: 250. 1997. Fig. 11.

Basionym: *Collybia elegans* Cleland, *Trans. & Proc. Roy. Soc. S. Australia* 57: 187. 1933.

Lectotype: **South Australia**, Mt. Lofty, 21 Jun. 1924, J.B. Cleland, AD3788.

Expanded description from Queensland material with comparisons to other collections: *Basidiomata* small to medium, collybioid. (See results above and Fig. 4 regarding size across geographic range.) *Queensland* specimen QMS20200222031: *Pileus* 8–20 mm diam., [32 mm mean diam. in South Australia where the holotype was described (Grgurinovic 1997), to 50 mm in Victorian collections (Grey & Grey 2005)], apricot (47) (Flora of British Fungi Colour Identification Chart), saffron-orange (49–48) to sienna (11) outer pileus, rust (13) centre, [bay-dark brick (19–20) to chestnut (23) in some New Zealand collections], dry, smooth



Fig. 11. *Marasmius elegans* basidiomata in situ. **A.** Pileus. **B.** Pruinoso stipes and strigose base. **C.** Lamellae. **D–I.** BRI AQ808614. **D.** Basidioles. **E.** Basidium. **F.** Cheilocystidia *Siccus*-type cells. **G.** Basidiospores. **H.** Pileipellis *Siccus*-type cells. **I.** Caulocystidia. Scale bars: A–C = 10 mm; D–I = 10 μ m. Images by W.G. Boatwright (A–C), illustrations by F.E. Guard (D–I).

to minutely velvety surface becoming rugose with age, broadly convex to almost applanate. *Lamellae* close, ca 20, free to adnexed, cream (4D), non-marginate [NZ margins at times concolorous with pileus]. *Lamellulae* 3–4 tiers, with narrow cross-venation and occasional bifurcations. *Stipe* central, cylindric, cartilaginous, hollow, 20–60 × 1–3 mm, [up to 5–6 mm diam. in southerly collections], grading from a dark reddish-brown (20) base through rust (13) in central section to pale cream to white upper section (3C); juvenile stipes have more pale colouration, and may be almost entirely white with only the base orange (48); prominent white to orange strigose base and extensive cream mycelial mat; stipe surface pruinose [but “smooth, polished” (Grgurinovic 1997, Grey & Grey 2005), “smooth, shiny” (Bougher & Syme 1998) in southerly collections]. *Spore print* white. *Basidiospores* 9.5–11.5 × 4–5 µm, mean 10 [± 0.33 SD] × 4.2 [± 0.15 SD] µm, $Q = 2.16$ – 2.69 , $Q_m = 2.38$ [± 0.12 SD], $N = 30$ (20 + 10) from 2 collections, smooth, ellipsoid, thin-walled, inamyloid. [Other measurements in Grgurinovic (1997) and Bougher & Syme (1998) from SA and WA have a range of 10.1–10.3 × 4.9–5.2 µm.] *Basidia* 2- to 4-spored, 23–28 × 7–9 µm. *Basidioles* clavate, 24–28 × 5–8 µm. *Cheilocystidia* common elongate *Siccus*-type broom cells, cylindric to clavate, occasionally branched, main body 14–25 (–33) × 5.5–9 µm, with sparse to multiple apical setulae 3–10 × 0.5–2 µm, thin to thick-walled [Grgurinovic stated that *cystidia* were absent. However, two collections examined from SA (AD-C58058 and AD-C58967) had common *cheilocystidia* of similar dimensions to the QLD collection.] *Lamellar trama* composed of thin-walled hyphae, 3.5–6.5 µm diam., with some inflated hyphae to 16 µm diam., dextrinoid. *Pileal trama* hyphae 5.5–7.0 (–13) µm diam., dextrinoid. *Pleurocystidia* absent. *Pileipellis* consists of a hymeniderm of *Siccus*-type broom cells, cylindrical, clavate, main body 20–31 × 5–8 µm, with apical setulae 4–8 × 1–2 µm; occasionally short – subglobose, pyriform, main body 8–10 × 6–8 µm, multiple apical setulae 3–7 × 1 µm. *Stipe* parallel hyphae, 4–7 µm diam., cortex dextrinoid. *Caulocystidia* (Table 2) usually common, smooth, cylindrical, thin-walled, obtuse-ended simple cells, short to long (10–100 × 4.5–9 µm), occasionally with narrowed tips or bifid apices, rarely stellate, occurring singly or in clusters along full length of stipe; very rarely elongate *Siccus*-type cells found (Figs 4, 5, 11). [*Caulocystidia* are absent in almost 50 % (7/15) of South Australian and Western Australian collections. When present they are more likely to be sparse and short, or at most moderately dense and short to medium length. Only one collection from Victoria (1/17) had no *caulocystidia*; Victorian and Tasmanian collections had mostly sparse, short cylindric cells. The *caulocystidia* of New South Wales collections were similar to Queensland specimens, including rare stellate and *Siccus*-type cells. One NZ collection had more tapering and strangulate *caulocystidia* Fig. 5.]. *Clamp connections* present in all tissues.

Additional collections examined: **Australia**, New South Wales, Dorrigo NP, 22 Feb. 2021, S. Webster, F2021087 (BRI AQ1033128, GenBank sequence nrITS PP354956); Hampton SF, 9 Apr. 2022, K. Millichamp, F2022056 (BRI AQ1041098, GenBank sequences nrITS PP354960, nrLSU PP354930 and *TEF1* PV151726); Queensland, Lamington NP, Nothofagus Spur, 10 Apr. 2002, A. Young, LNP598 (BRI AQ808612, GenBank sequences nrITS PP354943 and nrLSU PP354923);

Main Range NP, Mt Cordeaux, 20 Apr. 2024, W.G. Boatwright, QMS2024-4-20-010 (BRI AQ1048075, GenBank sequences nrITS PV016898 and nrLSU PV012147); South Australia, Belair NP, 4 Jul. 1925, J.B. Cleland, AD3786 syntype; Cape Jervis, Deep Creek Con. Park, 10 Jun. 2008, P.S. Catcheside, PSC2836 (AD58058, GenBank sequences nrITS PP354953 and nrLSU PP354915); Tasmania, Hobart, Waterworks Res., 20 Feb. 1996, D. Ratkowsky, Ratk228 (MEL2252658 GenBank sequences nrITS PP354962 and nrLSU PP354936); Northwest Midlands, Sheffield Shire, Gowrie Park, 30 Apr. 2005, R.E. Halling, REH8670 (MEL2264994, GenBank sequences nrITS PP354950 and nrLSU PP354916); Victoria, Wilsons Prom. NP, 23 May 1998, *Field Naturalist Club Victoria*, FNCV-WP37 (MEL2047709, GenBank sequences nrITS PP354948 and nrLSU PP354920); Eastern Highlands, Dom Dom Saddle, 13 May 2009, T.W. May & H. Rommelaar, TWM1766 (MEL2329551, GenBank sequences nrITS PP354947 and nrLSU PP354922). **New Zealand**, South Island, Christchurch, Port Hills, Ahuriri Res, grassland, 16 Mar. 2014, J.A. Cooper, JAC13253 (PDD105509, GenBank sequences nrITS OQ282799 and nrLSU OQ282754); North Island, Taupo, Ohakune, broad leaf forest, 5 Apr. 2005, J.A. Cooper, JAC 9376 (PDD 80809, GenBank sequence nrITS OQ282777). See Table 1 for full list.

Habit, habitat and distribution: *Marasmius elegans* is widespread, usually occurring in twos or threes, though occasionally in larger groups and rarely, caespitose. The habitat includes wet sclerophyll, hoop pine and palm forests, temperate and subtropical rainforest in Australia, and kanuka, manuka and southern beech forests in New Zealand. The distribution includes SA, VIC, TAS, NSW and QLD, both N & S islands of NZ. The population in SW WA is here described as a distinct variety, var. *occidentalis* var. nov.

Notes: While well-known and usually easily identified in the field, *Marasmius elegans* is morphologically variable. Its stature is at times robust and at other times small and slender-stemmed. Of the specimens examined, 85 % of southern Australian collections were robust, while only 15 % of QLD specimens were robust. However, size is not consistent, with small specimens occurring in at least 22 % of South Australian, Victorian and Tasmanian specimens. In Queensland and New South Wales over 85 % are small. The scatterplot of the maximum diameters (mm) of pilei plotted against latitude (degrees south) shown in Fig. 3. demonstrates the wide range of basidiomata sizes across the full geographic distribution of the species, including the new variety, *M. elegans* var. *occidentalis*, but confirms the clustering of smaller basidiomata in Queensland, and the trend to larger, more robust basidiomata in the southern states and New Zealand.

Caulocystidia are even more variable across the full distribution range. Overall they are absent in 12 %, sparse in 40 % and dense in 48 %. However, in QLD all specimens had *caulocystidia*, being sparse in 12.5 % and dense in 87.5 %. Dense *caulocystidia* present macroscopically as pruinose stipes, making a useful field identification character. However, smooth cell *caulocystidia* and *Siccus*-type cells both cause stipes to appear pruinose, and cannot be differentiated in the field. Despite all the morphological variations, DNA analysis of the nrITS gene region shows little variation between New Zealand, southern states and



Fig. 12. A, B. *Marasmius elegans* var. *occidentalis* basidiomata showing colour variation. Scale bars = 10 mm. Images by Katrina Syme.

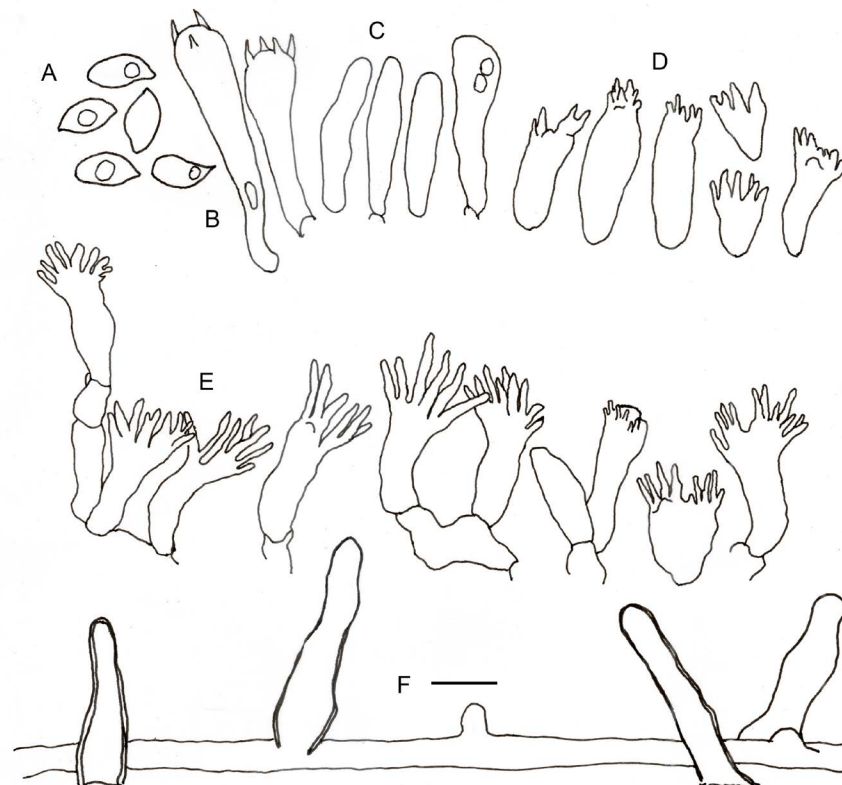


Fig. 13. *Marasmius elegans* var. *occidentalis* (KS3269). A. Basidiospores. B. Basidia. C. Basidioles. D. Cheilocystidia *Siccus*-type cells. E. Pileipellis *Siccus*-type cells. F. Caulocystidia. Scale bar = 10 μ m. Illustrated by F.E. Guard.

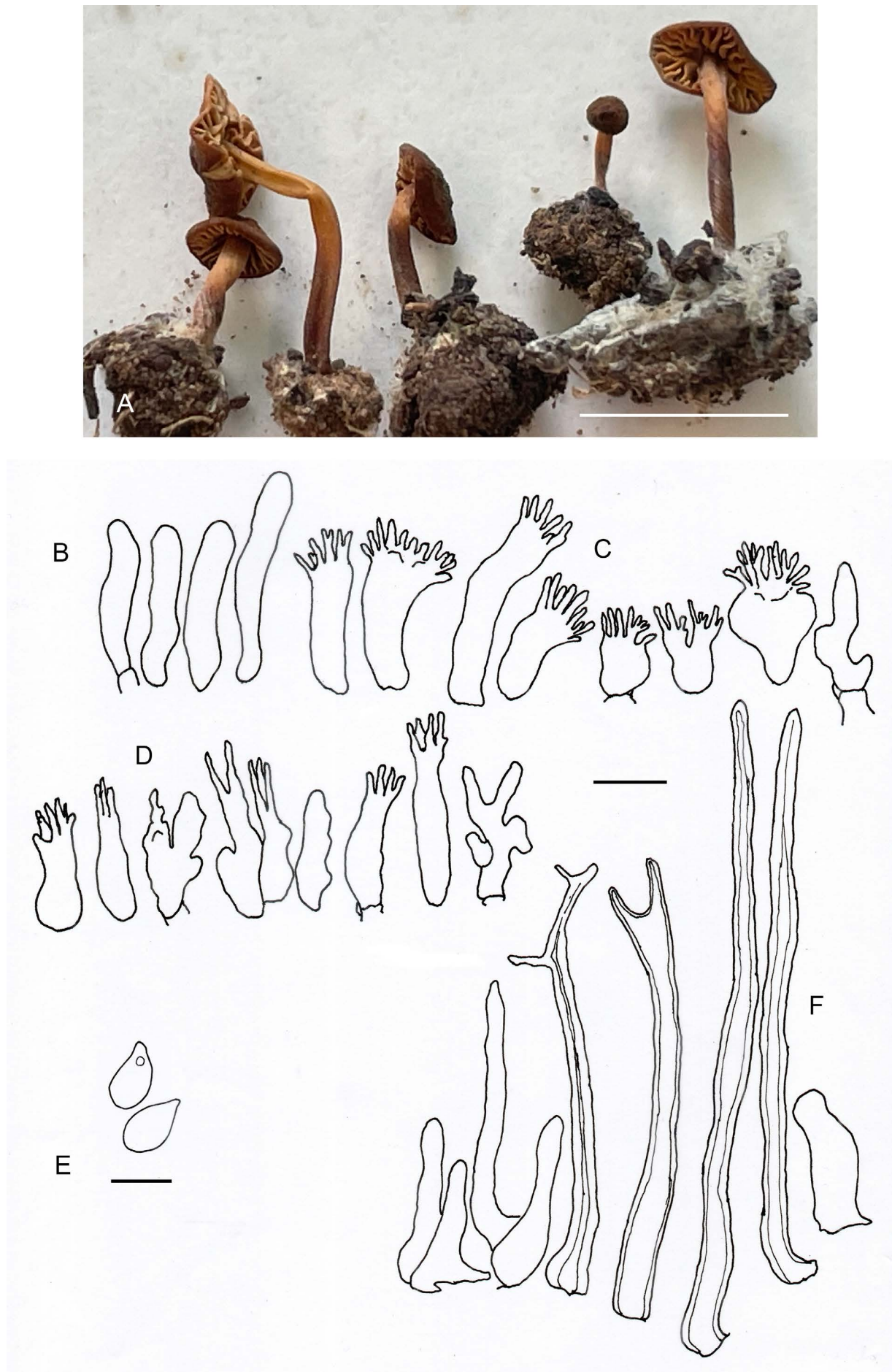


Fig. 14. *Marasmius leppii* (HL416). **A.** Basidiomata (lab shot). **B.** Basidioles. **C.** Pileipellis *Siccus*-type cells. **D.** Cheilocystidia mixed smooth, irregular and *Siccus*-type cells. **E.** Basidiospores. **F.** Caulocystidia. Scale bars: A = 10 mm; B–E = 5 µm; F = 10 µm. Images and illustration by F.E. Guard.

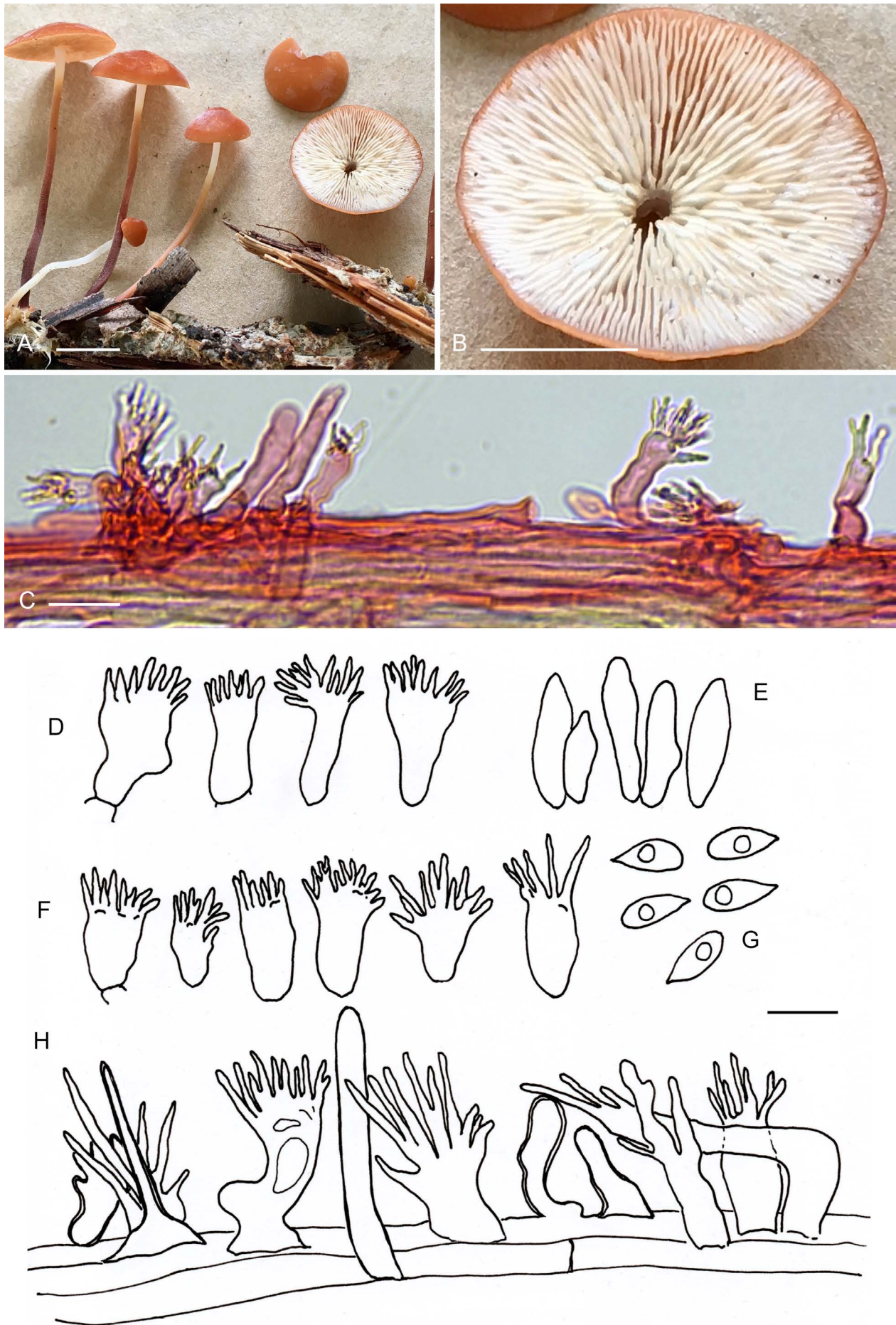


Fig. 15. *Marasmius pseudoelegans*. **A, B.** Basidiomata. **C.** Stipe vestiture microscopy. **D.** Pileipellis *Siccus*-type cells. **E.** Basidioles. **F.** Cheilocystidia *Siccus*-type cells. **G.** Basidiospores. **H.** Caulocystidia smooth and *Siccus*-type cells on stipe. Scale bars: A, B = 10 mm; C–H = 10 μ m. Images and illustration by F.E. Guard.

Queensland collections. However, DNA analysis of the Western Australian collections groups them together on a branch separate from all other *M. elegans*. The recently published *M. pseudoelegans* (Crous *et al.* 2024) introduces further complexity to the identification of the species. The formation of multiple bifurcating lamellulae in *M. pseudoelegans* (Fig. 15) is a helpful character, but not absolute. Microscopic features of the caulocystidia and molecular differences are necessary to separate the two species. Other species macroscopically similar to *M. elegans* include *M. sullivantii* from USA. However, geographically they are very distant and *M. sullivantii* has pleurocystidia. Molecular analysis places them in different series.

Molecular analysis places *Marasmius elegans* in the newly created ser. *Luteoli* (Oliveira *et al.* 2020), within sect. *Globulares*, subsect. *Leonini* (Oliveira *et al.* 2020). Its sister species, with moderate to strong support [BS 77/PP 1.0], is an unnamed taxon from New South Wales with nrITS (Fig. 6). One of the features of ser. *Luteoli* is the presence of caulocystidia. However, this character has been lost in at least 12 % of *M. elegans* examined. It was noted in the Oliveira *et al.* (2024) revision of the genus *Marasmius* that ser. *Luteoli* was almost entirely Indo-Malayan. Other taxa in the series have been found in China, Republic of Korea and Far Eastern Russia. This study has extended that distribution to Australia and New Zealand to include *M. elegans* and other related Australasian species.

Marasmius elegans* var. *occidentalis F.E. Guard, **var. nov.** MB 860160. Figs 12, 13.

Etymology: The epithet *occidentalis* is Latin for western and refers to the location of this variety in Western Australia.

Typus: **Australia**, Western Australia, Walpole, Walpole-Nornalup NP., Bibbulman Track east of Gulley Rd, site 3, S34°58'56.84", E116°47'33.151", 29 Jun. 2024, K. Syme & C. Williams, KS3269 (**holotype** BRI AQ1052601), GenBank sequences nrITS PV016900, nrLSU PV870573, *TEF1* PV151758.

Description: *Basidiomata* small to large, collybioid. *Pileus* 15–45 mm diam., dark brick (20) to bright apricot (47) centre, with outer pileus to sienna (11), dry, smooth to finely felted surface, dull, broadly convex to almost applanate, margin incurved becoming straight, smooth and entire, pileus wrinkling with age. Flesh white, firm, solid to 4 mm thick at centre. *Lamellae* close, adnexed to narrowly adnate, white, relatively smooth margin, occasional bifurcations near pileus margin. *Lamellulae* 2–4 tiers. *Stipe* central, cylindric, cartilaginous, hollow, 25–70 × 2–4 mm, purplish chestnut (21) lower end, rusty-tawny (14) trunk becoming orange, then white at apex, juvenile stipes paler and may be almost entirely white with only the base orange (48); stipe surface smooth, silky; prominent white strigose hairy base and off-white mycelial mat incorporating rotting leaf litter. *Spore print* white. *Basidiospores* 8.7–10.8 × 4.1–5.4 µm, mean 9.7 [± 0.45 SD] × 4.6 [± 0.38 SD] µm, Q = 1.71–2.39, Q_m = 2.13 [± 0.18 SD], N = 30 spores (2 collections), smooth, ellipsoid, thin-walled, inamyloid. *Basidia* 4-spored, 20–35 × 7.5–8.5 µm. *Basidioles* cylindric to narrowly clavate, 28–32 × 6–8 µm. *Cheilocystidia* very sparse, inconspicuous *Siccus-*

type broom cells, cylindric to clavate, irregular, occasionally branched, main body 8.5–20 × 4.5–8 µm, with sparse to multiple apical setulae 2–4.5 × 0.5–2 µm, thin- to thick-walled. *Lamellar trama* composed of thin-walled hyphae 3–4 µm diam., dextrinoid. *Pileal trama* 4–6 µm diam., with some inflated hyphae to 11 µm diam., dextrinoid. *Pleurocystidia* absent. *Pileipellis* consists of a hymeniderm of *Siccus-type* broom cells, cylindrical, long narrowly clavate, main body 14–27 × 5–8 µm, with thin to thick-walled apical setulae 4–9 × 1–2 µm; occasionally subglobose, main body 11 × 5–9 µm, multiple apical setulae 4–8 × 0.5–1 µm; rarely smooth cells 15–22 × 5.5–7 µm. *Stipe* parallel hyphae, 4–7 µm diam. *Caulocystidia* (full length of stipe) uncommon, smooth, cylindrical, thin-walled, obtuse-ended simple cells, short to medium (10–50 × 4–8 µm). *Clamp connections* present in all tissues.

Additional collections examined: **Australia**, Western Australia, Walpole, Walpole-Nornalup NP, Bibbulman track, in thick needles under *Allocasuarina decussata* in long unburnt eucalyptus forest, site 1, 1 Jun. 2022, K. Syme & P. Anderson, KS3174 (BRI AQ1041082 GenBank sequences nrITS PP354966, nrLSU PP354937, *TEF1* PV151734); site 2, 29 Jun. 2024, K. Syme, KS3268 (BRI AQ1052599, GenBank sequence nrITS PV016899); Dwellingup, Holyoake forest block, under tall *Banksia* and *Allocasuarina fraseriana* with *Eucalyptus marginata* regrowth, 16 Jun. 2010, R. Robinson, FC1594 (PERTH08163278, GenBank sequences nrITS PV870568).

Habit, habitat and distribution: Usually gregarious in thick *Allocasuarina* needles under *Allocasuarina decussata*, in tall long unburnt red tingle (*Eucalyptus jacksonii*) and karri (*E. diversicolor*) forest of southwest Western Australia. This variety is restricted to the south-west corner of WA, which has a more Mediterranean, wetter climate than the arid Nullarbor Plain separating it from other members of *M. elegans* to the east.

Notes: The medium to large basidiomata, orange to sometimes dark brownish pilei; absent to sparse, smooth, cylindrical caulocystidia; the very sparse often irregular cheilocystidia, together with geographic isolation and consistently distant molecular placement with both nrITS and concatenated nrITS and *TEF1* phylogenies, have led to our decision to name this a variety, *M. elegans* var. *occidentalis*. Morphologically it is most similar to the New Zealand *M. elegans* in colour and size, but the cheilocystidia and caulocystidia are different.

Marasmius leppii F.E. Guard, T. Lebel & Dearnaley, **sp. nov.** MB 860161. Fig. 14.

Etymology: This species is named for the mycologist, Heino Lepp, for his extensive contribution to mycology at the Australian National Botanic Gardens, Canberra, and for collecting this fungus.

Typus: **Australia**, NSW, Jimberoo State Forest, 11 km NNE of Rankin Springs, S33°45', E146°19', 340 m.a.s.l., in leaf litter in *Callitris* sp. forest, 12 Jun. 1990, H. Lepp, HL416 (**holotype** CANB574279), GenBank nrITS PV016897.

Description: *Basidiomata* very small, collybioid. *Pileus* 2–5

mm diam., conical, broadly convex to almost applanate with slight central umbo, orange-red, surface dry, smooth. *Flesh* very thin, white. *Lamellae* sub-distant, 14–16, with 2–3 tiers *lamellulae*, free, yellowish, non-marginate. *Stipe* central, 5–10 × 0.5–1 mm, orange-red lower two-thirds, off-white upper part, finely pruinose in lower half, with white strigose, basal mycelial pad binding the substrate. *Spore print* not obtained. *Basidiospores* 5.5–6 × 3–4 µm, N = 3, broadly ellipsoid, smooth, inamyloid. *Basidia* not found. *Basidioles* cylindric to narrowly fusoid, 23–28 × 4.5–5.5 µm. *Cheilocystidia* cylindrical, narrow clavate, sub-globose, sparsely to densely digitate, occasionally bifid and some with irregular smooth shapes, main body 10–24 × 3–8 µm, setulae thin to thick-walled, 3–6 × 1–1.5 µm. *Pleurocystidia* absent. *Lamellar trama* hyphae 2–3.5 µm diam. *Pileipellis* a hymeniderm of (i) common *Siccus*-type cells, clavate, cylindric, sub-globose, occasionally bifid, main body 11–20.5 × 5.5–13 µm, setulae thick walled, refractile, 3–8 × 1–1.5 µm and (ii) rare irregular smooth cells 19 × 4.5 µm. *Pileal trama* not examined. *Stipe* parallel hyphae, cortex hyphae 3–4 µm diam., medullary hyphae dextrinoid, 4–5.5 µm diam. *Caulocystidia* (mid-stipe) present in the form of smooth, dextrinoid, cylindric cells, mostly obtuse-ended, rarely bifid, thin- to very thick-walled, 20–100 × 3.5–6 µm. *Clamp connections* present in all tissues.

Habit, habitat and distribution: Gregarious in well-decomposed litter and soil of open forest dominated by *Callitris* (Australian cypress) species on a rocky ridge. *Marasmius leppii* sp. nov. has only been found once in southern inland NSW.

Notes: Normally we would not consider publishing a new species based on a single collection, however the abundant, tiny basidiomata, and unique habitat and geographic location, morphology and molecular placement make this a clear taxonomic novelty worthy of publication. Few basidiospores were found and it was important not to destroy more of the tiny basidiomata in searching. *Marasmius leppii* appears macroscopically to be a member of ser. *Luteoli* and related to *M. elegans*, although its habitat is much drier, more open forest dominated by the Australian cypress pine (*Callitris* sp.), a gymnosperm. While both morphologically and molecularly it is in ser. *Luteoli*, it does not appear to be very close to any other taxa in the series. (Figs 6, 7).

Marasmius pseudoelegans F.E. Guard et al., *Fungal Syst. Evol.* **13**: 290. MB 852546. Fig. 15.

Typus: Australia, Queensland, Linda Garrett National Park, S26°37'24.9", E152°50'51.4" on well-rotted twigs and litter in mixed wet sclerophyll and subtropical rainforest, 5 Mar. 2022, W.G. Boatwright, QMS2022-03-05 012 (F2022047) (**holotype** BRI AQ 1033133), GenBank sequences nrITS PP354971 and nrLSU PP354911.

Description: *Basidiomata* small, collybioid. *Pileus* 5–18(–25) mm, juvenile bluntly conical to hemispheric, mature basidiomata broadly convex to almost applanate, apricot (47), rust (13), rusty tawny (14) to sienna (11), smooth to velvety surface, margin entire, slightly in-rolled. *Flesh* thin,

white. *Lamellae* cream (2B–4D), non-marginate, free to adnexed, narrow, moderately crowded, 26–34 with 4–5 tiers of bifurcations and occasional short lamellulae. *Stipe* central, cartilaginous, 30–45 × 0.75–1.5 mm, cylindric, hollow, deep purplish chestnut (21) at the base, bay (19) mid- and upper shaft, pale cream (4D) only at the apex, with cream to buff basal tuft of mycelium; glossy to pruinose surface. Juvenile stipe paler with brown restricted to base or lower shaft. *Spore print* white. *Basidiospores* 9.4–11.5 × 3.5–4.3 µm, mean 10.3 [± 0.47 SD] × 3.9 [± 0.19 SD] µm, Q = 2.3–3.0, Q_m = 2.61 [± 0.16 SD], N = 50 from 1 collection. *Basidia* not seen. *Basidioles* clavate, fusiform 17–23 × 3.5–6 µm. *Cheilocystidia* *Siccus*-type cells forming a sterile edge, main body 14–21 × 5–10 µm, with slightly thick-walled erect setulae 2.5–6 × 0.5–1 µm. *Pleurocystidia* absent. *Pileipellis* a hymeniderm of *Siccus*-type cells, main body 14–21 × 4–8 µm, with erect setulae 2.5–8 × 0.5–1 µm. *Pileal trama* dextrinoid, hyphae 4–5 µm diam. *Caulocystidia* i) common elongate *Siccus*-type cells, main body 8.5–24 × 6–8 µm, cylindric, branched or broadly clavate with 2–8 apical setulae to 15 × 1–3 µm and ii) uncommon smooth, cylindrical, obtuse cells 12–45 × 4–5 µm. *Clamp connections* present in all tissues.

Habit, habitat and distribution: Usually gregarious, in leaf litter or well-rotted wood, an uncommon saprotroph of subtropical rainforest, palm forest and margins of wet sclerophyll forest. To date it has only been found in southeast Queensland in Lamington and Springbrook NPs on Qld-NSW border, Linda Garrett & Mapleton Falls NPs and Maroochy Bushland Botanical Gardens in the Sunshine Coast hinterland.

Additional material examined: Australia, Queensland, Linda Garrett NP, 22 Feb. 2025, W.G. Boatwright, QMS2025-2-22-036 (BRI AQ 1054053).

Notes: A short description is provided here to enable comparison with other taxa (see Crous et al. 2024 for full description). *Marasmius pseudoelegans* is characterised by its small to medium, orange-rusty smooth pileus, close lamellae, with forking of lamellae and lamellulae and brown stipe with pale apex. Macro-morphologically *M. pseudoelegans* is very similar to *M. elegans*. The distribution of the two species coincides in southeast Queensland, where they occupy similar habitat. They are macroscopically indistinguishable as juveniles, but show some different characters as mature basidiomata, with common bifurcation of lamellulae and dark stipe almost to apex in *M. pseudoelegans*, while these features are uncommon in *M. elegans*. The caulocystidia are the strongest distinguishing features, with *M. elegans* having mostly smooth cells and *M. pseudoelegans* mostly elongate *Siccus*-type cells. (Fig. 18). Classification morphologically and molecularly places *M. elegans* and *M. pseudoelegans* in the same series, though they are not sister clades. To date *M. pseudoelegans* has no close sister species within ser. *Luteoli*.

***Marasmius* subg. *Globulares* sect. *Globulares* Kühner subsect. *Leonini* J.S. Oliveira & Moncalvo (2020).**

Series *Multicystidiati* F.E. Guard, J. Dearnaley & T. Lebel, **ser. nov.** MB 860163.

Basidiomata collybioid, small to medium (8–25 mm diam). *Pileus* smooth. *Lamellae* sub-distant to close (16–20), with numerous lamellulae. *Stipe* central, cartilaginous, pruinose, darker base to pale apex. *Basidiospores* short, narrow to broadly ellipsoid to ca 9.5 µm long. *Pleurocystidia* present, small, barely protruding, narrowly clavate, fusiform, mucronate. *Pileipellis* *Siccus*-type cells. *Caulocystidia* present, including smooth branched cells, *Siccus*-type and *Amyloflagellula*-type cells. *Habit* gregarious, rarely caespitose, on leaves or rotting wood.

Type species: *Marasmius multicystidiatus* F.E. Guard, Dearnaley & T. Lebel

This series is based on *M. multicystidiatus* and *M. sullivantii* which has small pleurocystidia and caulocystidia with both *Amyloflagellula*-type and *Siccus*-type cells. It is represented by a highly supported subclade /multicystidiatus [90/1.0] with nrITS alone and [93/1.0] concatenated nrITS and *TEF1*, augmented by *Marasmius sullivantii* Mont. 1856 (Type no longer available - Indiana, Gilliam 938, Gilliam 1976). (Figs 6, 7)

It fits into the broader subsect. *Leonini* and differs from ser. *Luteoli* by having smooth pleurocystidia and *Amyloflagellula*-type cells in the caulocystidia; and ser. *Leonini*, *Corrugati* and *Bambusiniformis* which have no pleurocystidia (Oliveira *et al.* 2020). It differs from ser. *Graminicolae* which are mostly marasmioid or sessile with pleurotoid habit, smaller, thinner pilei and subdistant lamellae. *Pleurocystidia* may or may not be present. Series *Graminicolae* may have *Amyloflagellula*-type cells in the pileipellis, but not on the stipe.

Note: The distribution of this series is very wide and it is to be expected that more species will be found.

Marasmius multicystidiatus F.E. Guard, T. Lebel & Dearnaley, *sp. nov.* MB 860162. Figs 16–18.

Etymology: The epithet *multicystidiatus* refers to the multiple forms of caulocystidia found in this species.

Typus: **Australia**, Queensland, Dilkusha Nature Refuge, S26°44'21.1", E152°53'31.0" on well-rotted log in remnant subtropical rainforest, 2 Jan. 2015, F.E. Guard, F2015002 (**holotype** BRI AQ 1019024), GenBank sequences nrITS PP354939, nrLSU PP354931.

Description: *Basidiomata* small to medium, collybioid. *Pileus* 8–15 mm diam., convex, broadly parabolic to applanate with low central umbo and upturned wavy margins, apricot (47) to sienna (11) central disc, merging to saffron (49) with cream outer margin, smooth dry surface; flesh thin, white. *Lamellae* moderately close, 16–18, free to adnexed, off-white, cream, non-marginate, *lamellulae* 4–5 tiers, occasional low cross-venations. *Stipe* central, cartilaginous, cylindric, 25–35 × 1.5 mm, finely pruinose especially lower one-third, cinnamon (10) base becoming paler towards apex, cream at upper end and off-white strigose mycelial mat at base; juvenile stipes cream for full length. *Spore print* white. *Basidiospores* 8–9 × 3.5–4 µm, $Q = 1.89–2.29$, mean 8.5 [± 0.48 SD] × 4 [± 0.16 SD] µm, $Q_m = 2.12$ [± 0.14 SD], $N = 20$, ellipsoid, inamyloid, smooth, thin-walled. *Basidia* not seen. *Basidioles* cylindric to clavate 18–21 (–23) × 5.5–7 µm. *Cheilocystidia* *Siccus*-type cells, cylindric to clavate and rarely branched, main body thin-walled, 7.5–20 × 5–10 µm, terminal setulae thin-walled, occasionally thick-walled, long, sparse to crowded, 4–11 × 1–2 µm. *Pleurocystidia* uncommon, small, smooth, thin-walled, mucronate, rarely double-headed, 24–28 × 5.5–6.5 µm. Similar cells were found occasionally on lamellar edge; *lamellar trama* hyphae 3–5 µm diam., dextrinoid. *Pileipellis* a hymeniderm of *Siccus*-type cells, narrow cylindric to clavate, main body thin-walled, 10–19 × 5.5–9 µm, setulae thin to thick-walled, crowded, 1–6 × 0.5–1 µm; *pileal trama* hyphae 3–5 µm diam., dextrinoid. *Stipitipellis* parallel hyphae, inamyloid, 3.5–7.5 µm diam. *Caulocystidia* varied significantly

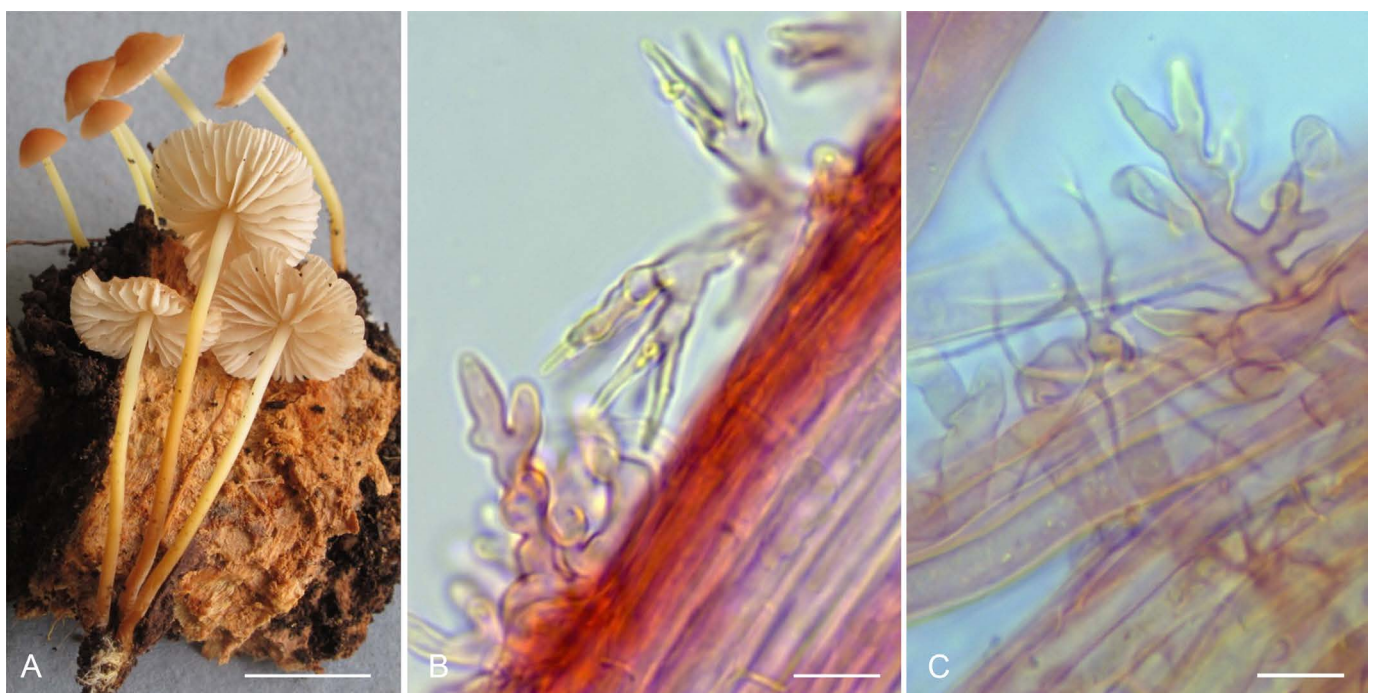


Fig. 16. *Marasmius multicystidiatus*. **A.** Basidiomata and substrate. **B, C.** Microscopy mid-stipe, illustrating variety of caulocystidia – smooth-branched, *Siccus*-type and *Amyloflagellula*-type. Scale bars: A = 10 mm; B, C = 10 µm. Images by F.E. Guard.

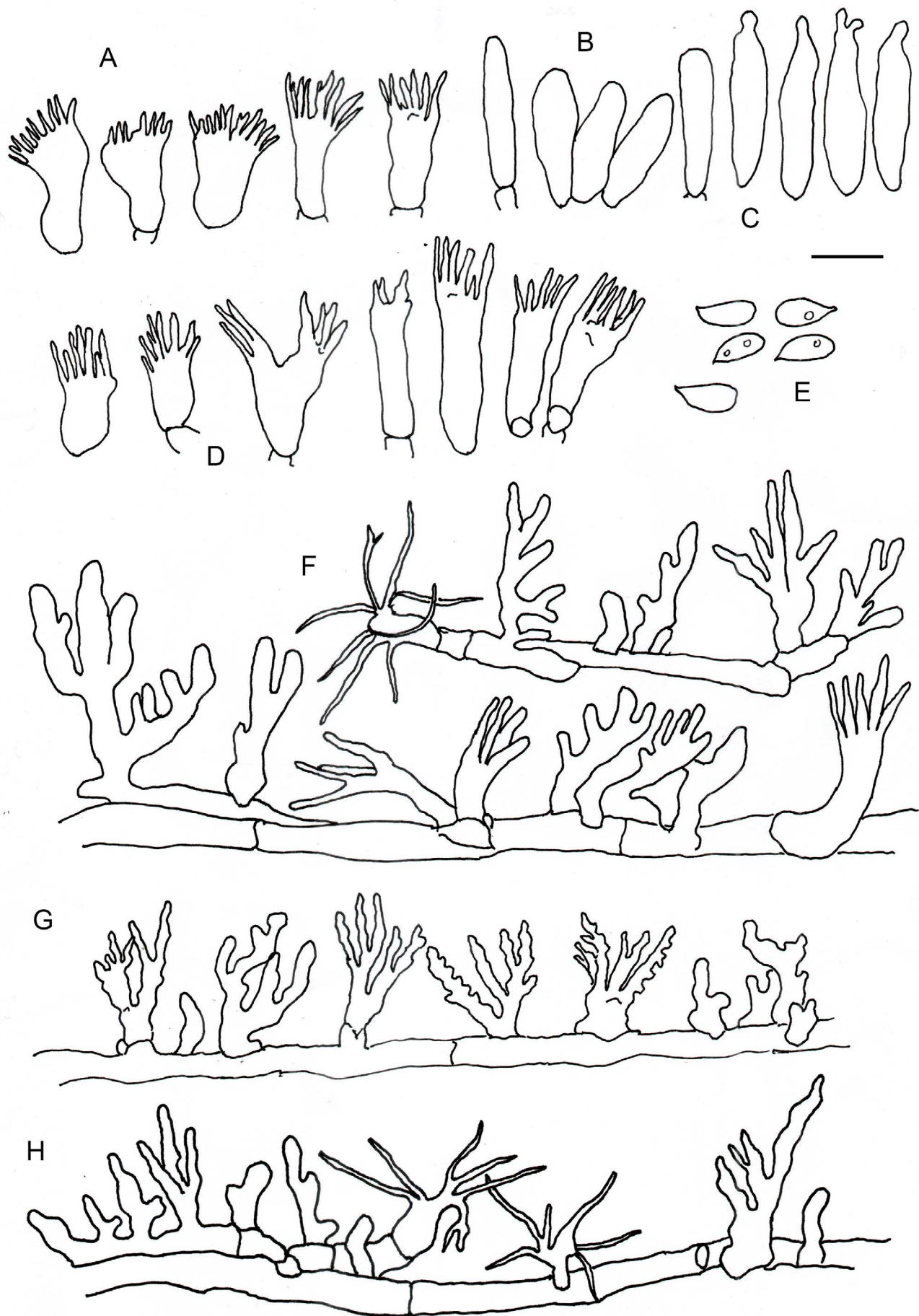


Fig. 17. *Marasmius multicystidiatus* (F2015002). **A.** Pileipellis *Siccus*-type cells. **B.** Basidioles. **C.** Pleurocystidia. **D.** Cheilocystidia *Siccus*-type cells. **E.** Basidiospores. **F.** Mid-stipe caulocystidia. **G.** Upper stipe caulocystidia. **H.** Lower stipe caulocystidia including *Amyloflagellula*-type and smooth branching cells. Scale bar = 10 μ m. Image by F.E. Guard.

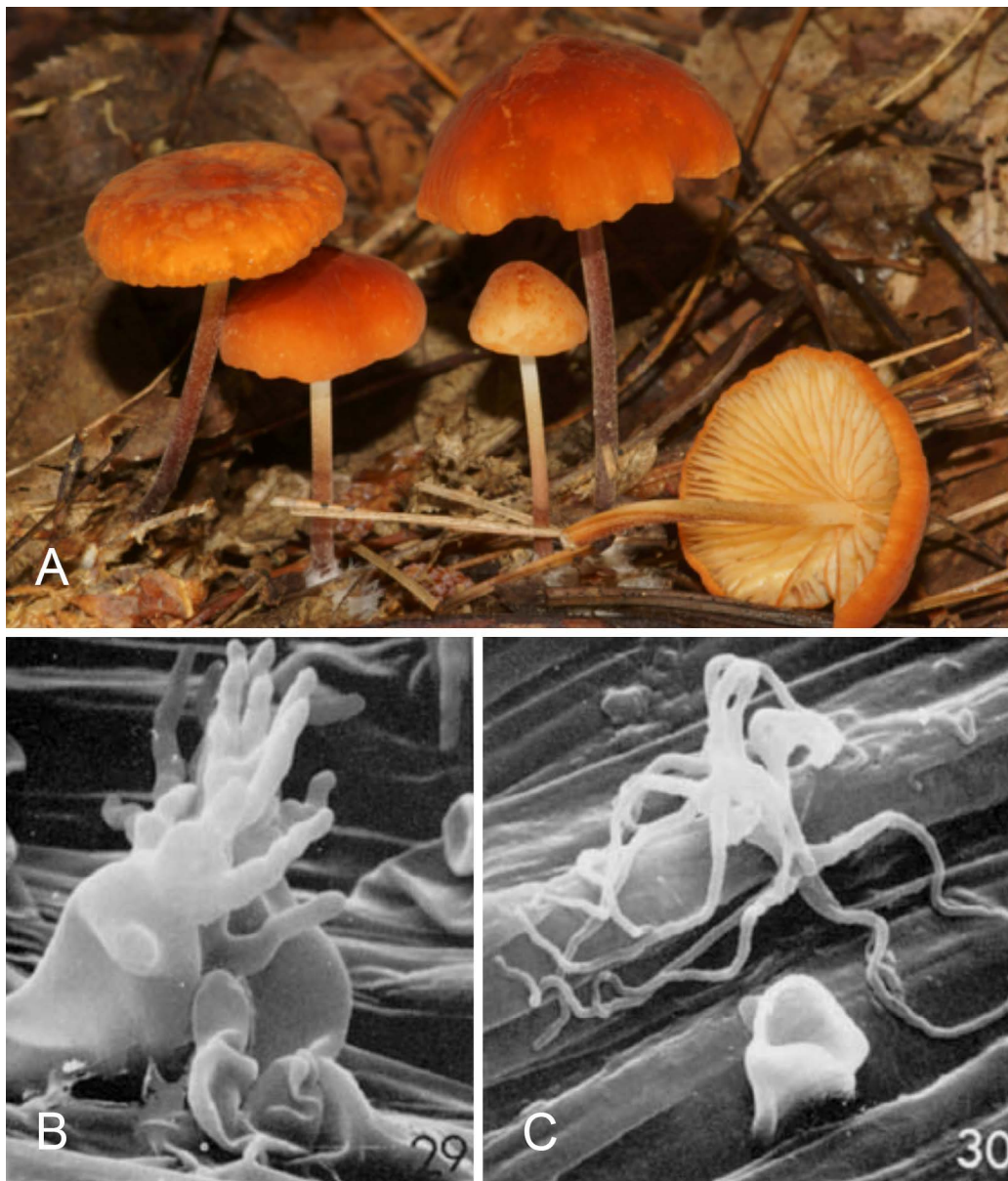


Fig. 18. *Marasmius sullivantii*. **A.** Basidiomata. **B, C.** 4000 $\times$ SEM images of two types of caulocystidia. Images by J. Plischke (A) and by L. Allard from figs 29 & 30 in *Mycotaxon* 4(1): 74. 1976 (B, C). All images used with permission.

between upper, middle and lower stipe. The upper stipe consisted of common, smooth, branching, obtuse ended cells 8–31 μm long; mid-stipe similar branching cells with occasional *Amyloflagellula*-type cells with small, thin-walled bodies, 5–10 $\times$ 3–6 μm and long, narrow, tapering setulae 12–18 $\times$ 0.5 μm and rare *Siccus*-type cells with sparse, thick-walled long setulae, main body 15 $\times$ 5 μm , setulae 10 $\times$ 2 μm ; lower stipe branching smooth cells up to 50 μm long and more common *Amyloflagellula*-type cells similar to mid-stipe. *Clamp connections* present in all tissues.

Habit, habitat and distribution: *Marasmius multicystidiatus* is gregarious, growing on well-rotted wood, at times caespitose. To date it has been found in one location only, in SEQ in remnant subtropical riparian rainforest on a log where the mycoheterotrophic orchid, *Pseudovanilla foliata* was also growing. Any mycorrhizal association between the fungus and orchid has not been demonstrated, although members of *Marasmiaceae* family have been shown to partner with other obligate mycoheterotrophic orchids (Dearnaley & Bougoure 2010).

Notes: *Marasmius multicystidiatus* is morphologically similar to *M. elegans*, though at the smaller end of the pileal diameter and stipe measurements, with paler colour of pileus and stipe. Basidiospores are significantly smaller (mean 8.5 $\times$ 4 μm c.f. 10 $\times$ 4.2 μm) and pleurocystidia are present. The caulocystidia include *Siccus*-type, *Amyloflagellula*-type and multiple branching cells, which are rare in *M. elegans*. *Marasmius sullivantii* from north America is the molecular sister to *M. multicystidiatus* with strong support, [BS 100/PP 1.0] nrITS only; [BS 93/PP 1.0] nrITS + *TEF1*. *Marasmius sullivantii* (Gilliam 1976) is similar macro-morphologically to *M. elegans*, and is larger, brighter orange-brown and thicker fleshed than *M. multicystidiatus*. Microscopically *M. sullivantii* and *M. multicystidiatus* have pleurocystidia, and also caulocystidia of both *Siccus*- and *Amyloflagellula*-types (fig. 21 from Gilliam 1976 and J. Plischke, iNaturalist10632459). Molecular analysis of nrITS and *TEF1* gene regions places *M. multicystidiatus* and *M. sullivantii* close to ser. *Leonini* emend. (Oliveira *et al.* 2020), and not in ser. *Luteoli* despite its morphological similarity to *M. elegans*. Currently *M. sullivantii* is in a group of species

that do not fall clearly within a named series (incertae sedis), even with multigene analyses (Oliveira *et al.* 2024). With the addition of *M. multicystidiatus*, we believe there are sufficient molecular support and morphological characters to distinguish a new series.

DISCUSSION

Systematic placement

Species in the *M. elegans* complex have small to large basidiomata, smooth pilei, lamellae close with 2–4 series of lamellulae, stipe usually pruinose, basidiospores small to medium size (5.5–)7–12 µm length, pleurocystidia absent, caulocystidia usually present, cylindric to irregular, habit scattered to gregarious on leaf litter or occasionally wood. They would traditionally have been placed in sect. *Globulares* emend. Antonín & Noordeloos (2010), ser. *Atrorubentes* (Desjardin & Horak 1997), due to the presence of caulocystidia and the absence of setae. *Marasmius atrocastaneus* is a typical example of this classification. Formerly classified in ser. *Atrorubentes*, it now sits comfortably in ser. *Luteoli*, with other members of the *M. elegans* complex. However, the specimens where caulocystidia are absent could also be placed in ser. *Leonini*. According to Singer (1976) ser. *Leonini* may have broom cells in the stipitipellis, so *M. pseudoelegans* could also be in either ser. *Leonini* or ser. *Atrorubentes*. This problem of presence or absence of caulocystidia was discussed in Oliveira *et al.* (2020) in relation to *M. cladophyllus* (type variety in ser. *Atrorubentes*) and *M. cladophyllus* var. *glaberripes* (in ser. *Leonini*.) In order to make better sense of the morphological characters and using multilocus analysis of nrITS and nrLSU regions of a broader dataset, Oliveira *et al.* (2020) proposed some major changes to the classification of sect. *Globulares* sensu Antonín & Noordeloos (2010). They emended subsect. *Leonini* to include taxa previously included in ser. *Atrorubentes*. In a larger global study Oliveira *et al.* (2024) further revised the taxonomy of the whole genus *Marasmius* and confirmed the series *Luteoli* and *Leonini* within subsect. *Leonini*. However, even with multigene phylogenetic analysis and morphologic evidence the relationships of some taxa remained unresolved in the section *Globulares*, subsect. *Leonini*. According to their proposal, most taxa examined in this study would fall into sect. *Globulares*, subsect. *Leonini*, ser. *Luteoli*. Some, however, are poorly supported and remain incertae sedis. We believe that one pair of those species can now be placed in a new series, *Multicystidiati*, while discovery of more species may help to further resolve issues around placement within specific series.

Distribution

Series *Luteoli* was noted to be almost entirely an Indo-Malayan group in the Oliveira *et al.* (2024) study. However, with additional material available to this study, that distribution has now extended to include China and Australasia. Geographically *Marasmius elegans* and *M. elegans* var. *occidentalis* occur across thousands of kilometres – in locations separated by ocean and extensive desert. In terms of habitat, the range is equally broad, from subtropical

complex notophyll vine forest, palm forest, wet sclerophyll forest to cool temperate forest. The Tasman Sea separates the Australian and Aotearoa New Zealand populations of *M. elegans* by over 2000 km, yet they remain remarkably close genetically, with minor morphological variation in colour and stipe vestiture. New Zealand mycologist, Peter Johnston (2010) examined the origins of New Zealand fungi and concluded there were three main sources of diversity. The first appear to be a few truly ancient lineages which may have arisen before separation of NZ from the Australian landmass in the breakup of Gondwana, where NZ became an isolated landmass in the late Cretaceous period, ca 80 Mya (Hill 1994). Johnston (2010) maintained that species in geographically isolated populations, with vicariate origins, are unlikely to remain morphologically and genetically identical over this length of time. Thus, this source is unlikely for *Marasmius elegans*. Landis *et al.* (2008) suggested that ancient Gondwanan lineages surviving the separation of New Zealand from Australia were unlikely to persist as the Zealandia subcontinent was largely or entirely submerged during the middle Cenozoic era, Oligocene epoch (ca 33 to 23 Mya) and all early flora, fauna and presumably fungi would have become extinct. They argue that modern terrestrial biota would have arrived in New Zealand in the last 22 million years. Other more recent research points to the possibility of refugia during the Oligocene epoch where biota persisted and developed into unique locally endemic species (Jones *et al.* 2009, Mitchell *et al.* 2016, Buckley *et al.* 2020). The second source is through long distance, trans-oceanic dispersal, which has occurred in more recent geological time frames, i.e. divergent origins. While *Marasmius elegans* was not cited in Johnston's paper, other saprotrophic fungi were. Other records of presumed long distance, trans-oceanic, wind-dispersed saprotrophic and pathogenic fungi are noted in Shepherd & Cooper (2018), and ectomycorrhizal fungi (*Pisolithus* spp.) in Moyersoen *et al.* (2003). It is postulated that the maintenance of genetic identity without subsequent evolution of local endemics is through repeated arrivals of fresh genetic material from the source of origin. This hypothesis would explain the presence of *M. elegans* in NZ with its almost identical genetic signature to the Australian population. The third source is through accidental or deliberate human activity and while common worldwide, is unlikely to be relevant to the dispersal of *M. elegans* which is found in widespread natural habitats, and not urban centres or disturbed habitats.

Within Australia the southern populations of *M. elegans* in Victoria, Tasmania and South Australia have probably been separated from the Western Australian population since flora and fungi were isolated by drying of the continent. This may have occurred anywhere from 20 Mya to 5 Mya when major cooling events caused aridification of southern Western Australia (Groom & Lamont 2015). Given that long distance dispersal of fungal spores by air currents would favour west to east transportation (prevailing winds), it is unlikely that gene flow would occur from SA/VIC to WA (i.e. east to west) once a zone of aridity was established between the two populations. *Marasmius elegans* var. *occidentalis* forms a distinct strongly supported clade, which may be in the process of becoming a separate species. This is supported by both nrITS and concatenated nrITS / *TEF1* analyses (Figs 6, 7). However, it could also be due to a single dispersal and

rapid accumulation of apomorphic substitutions in a small founding population. The morphological distinctions are small when compared with other southerly specimens, but significant when compared with QLD specimens. It has been recognised that genetic isolation precedes recognisable morphological change (Taylor *et al.* 2006). Therefore, we have made the more conservative choice of naming a new variety, *M. elegans* var. *occidentalis*.

CONCLUSION

This study expands the range and diversity of *Marasmius*, subsect. *Leonini*, series *Luteoli* from Asia to include Australasia. Many taxa bearing some resemblance to the well-known Australasian species, *Marasmius elegans*, have been examined and sequenced. The study confirms our hypotheses that there are several distinct taxa in Queensland and New South Wales, that have been misidentified as *M. elegans* and that there is a small but significant increase in size of basidiomata of *M. elegans* s. str. with increasing latitude. Our study also demonstrates that *M. elegans* is morphologically variable across its geographic range, with stipe ornamentation showing the most variation. We have nominated a new series, *Multicystidiati*, to accommodate two of the taxa studied, and have separated a new variety of *M. elegans* in Western Australia, var. *occidentalis*.

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