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RESEARCH ARTICLE

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Untangling the *Lactifluus clarkeae* - *Lf. flocktoniae* (*Russulaceae*) species complex in Australasia

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Key words

cryptic species
integrated taxonomy
lactarioid
morphology
new taxa
section *Tomentosi*

Abstract The *Lactifluus clarkeae* complex is a commonly observed, generally brightly coloured, group of mushrooms that are usually associated with *Nothofagus* or Myrtaceous hosts in Australia and New Zealand. For this study collections labelled as '*Lactarius clarkeae*', '*Russula flocktoniae*' and '*Lactarius subclarkeae*' were examined morphologically and molecularly. Analyses of molecular data showed a high cryptic diversity, with sequences scattered across 11 clades in three subgenera within *Lactifluus*, and a single collection in *Russula*. We select epitypes to anchor the currently accepted concepts of *Lf. clarkeae* s.str. and *Lf. flocktoniae* s.str. The name *Lf. subclarkeae* could not be applied to any of the collections examined, as none had a lamprotrichoderm pileipellis. *Lactifluus clarkeae* var. *aurantioruber* is raised to species level, and six new species are described, three in subg. *Lactifluus*: *Lf. jetiae*, *Lf. pagodicystidiatus*, and *Lf. rugulostipitatus*, and three in subg. *Gymnocarpi: Lf. albens*, *Lf. psammophilus*, and *Lf. pseudoflocktoniae*. A new collection of *Lf. russulisporus* provides a significant range extension for the species. Untangling this complex will enable better identification of species and increase understanding of diversity and specific habitat associations of macrofungi.

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INTRODUCTION

The genus *Lactifluus* was separated from *Lactarius* based on multigene phylogenies of *Russulaceae*, which showed that *Lactarius* comprised two distinct clades and neither *Russula* nor *Lactarius* was monophyletic (Buyck et al. 2008, 2010, Verbeken & Nuytinck 2013). While *Lactifluus* is not easily distinguished from *Lactarius* by macroscopic morphology, its species tend to have thicker-walled terminal elements in the pileipellis and stipitipellis, as well as abundant sphaerocytes in hymenophoral, pileus and stipe trama tissues (Verbeken & Nuytinck 2013). Almost all pleurotoid basidiocarps in *Russulaceae* are only known in *Lactifluus* (De Crop et al. 2018) (exception is *Russula pleurogena* (Buyck & Horak 1999)), while sequestrate forms have only thus far been described in *Lactarius* (Wang et al. 2012, Verbeken et al. 2014, Beenken et al. 2016, De Crop et al. 2017) and *Russula* (Lebel 2002, 2003a, b, Lebel & Tonkin 2007, Elliott & Trappe 2019, Vidal et al. 2019). Unlike *Lactarius*, *Lactifluus* has its main distribution in the tropics of the southern hemisphere, with high diversity known from tropical Africa, south-east Asia, and South America (Henkel et al. 2000, Stubbe et al. 2010, 2012, Van de Putte et al. 2010, Verbeken & Walleyn 2010, Smith et al. 2011, Sá & Wartchow 2013, Sá et al. 2013, Wang et al 2015, Lee et al. 2018). De Crop et al. (2017) showed that *Lactifluus* is characterised by high genetic diversity, with subgroups in several distinct clades, resulting in a new infrageneric framework supported by a multigene phylogeny. However, little work has been done on Australasian species apart from a type study by Verbeken et al. (2010), which showed that at least two species originally described in *Lactarius* would be better placed in *Lactifluus* sect. *Tomentosi* (section proposed by McNabb 1971), and the investigation of sect. *Gerardii* by Stubbe et al. (2010), which showed that more species await description.

The Australasian species *Lf. clarkeae*, *Lf. flocktoniae* and *Lf. subclarkeae* s.lat. are geographically widespread, easily detected mushrooms with generally robust, dry, smooth to tomentose orange-yellow to reddish orange caps, with white or orange flesh that in some specimens becomes brownish on exposure to air, and variable latex production and taste. However, the species boundaries are poorly delimited, the phylogenetic relationships unclear, the type material old and in poor condition, and type descriptions lacking in detail (Cleland & Cheel 1919, Cleland 1927, Grgurinovic 1997). While Cleland (1927) selected a type from amongst the material he had collected for '*Lactarius clarkeae*', this was not the case for '*Russula flocktoniae*' (Cleland & Cheel 1919). McNabb (1971) examined Clelands collections, and stated that the original type material of '*L. clarkeae'* (South

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Australia, Mt Lofty, June 1927) could not be traced in Cleland's herbarium and that the paratypes represented different species, one with warty and one with reticulate spores. McNabb (1971) selected AD 15299, a collection with warty spores, as a lectotype for '*L. clarkeae'*, and Grgurinovic (1997) later selected a reticulate spored collection, AD 9800, as lectotype for *L. mea* (which according to Verbeken et al. (2010) belongs to *Lactarius* subg. *Russularia*). Grgurinovic (1997) also selected one of Clelands other '*L. clarkeae*' collections, AD 9807, as the holotype of '*L. subclarkeae'*, distinguishing it from '*L. clarkeae*' on the basis of smaller spores with an incomplete reticulum with few or no isolated elements. Verbeken et al. (2010) suggested that this species was more typical of *Lf.* subg. *Lactariopsis* than sect. *Tomentosi* on the basis of the lamprotrichoderm rather than palisade pileipellis, lack of true cystidia and type of spore ornamentation. For '*Russula flocktoniae*' Grgurinovic (1997) selected one of the five syntypes, AD 9871, cited by Cleland & Cheel (1919), as a lectotype. More detailed examination of types and new material provided further clarification (Grgurinovic 1997, Bougher & Syme 1998, Verbeken et al. 2010), and set the species concepts to: '*Lactarius clarkeae*' (NZ and AU) varying tones of orange cap, stipe concolorous or not, lamellae cream tinged orange, latex white, abundant or scant; '*Russula flocktoniae*' (AU) varying tones of bright orange cap, stipe concolorous or not, lamellae white, latex absent; '*Lactarius subclarkeae*' (AU) pileus yellowish buff to pale salmon, stipe and lamellae slightly paler, latex production variable, and lacking true cystidia. While McNabb (1971) described sect. *Tomentosi* to accommodate '*Lactarius clarkeae*' based on the distinctive cuticular structure, molecular based support for placement of this taxon, '*Russula flocktoniae*' and '*Lactarius subclarkeae*' as distinct species in *Lactifluus* was only established fairly recently (Verbeken et al. 2012, De Crop et al. 2017).

As latex production can be ephemeral under dry conditions, and macro-morphological characters appear variable, mixed collections of these three taxa are to be found in most Australasian herbaria. In this paper we investigated herbarium material labelled as taxa in the *Lactifluus clarkeae - Lf. flocktoniae* complex. Using molecular and morphological characters we describe six new species from Australia and New Zealand, and provide expanded descriptions of four published taxa, designating epitypes as necessary. A further nine provisional species are indicated but not described, across three subgenera of *Lactifluus*.

MATERIALS AND METHODS

Morphology

Macroscopic characters are described and measured from fresh material, field notes, or dried herbarium collections. Measurements taken using dried herbarium material are listed as such and are estimated to be approximately 30 % smaller than measurements taken from fresh specimens. Colours are described in general terms from field observations in daylight conditions. Habitat, associated plant communities, fruiting season, presence and nature of latex, fresh odour, and taste are based on field notes. 'L' and 'l' refer to lamellae and lamellulae, respectively. The L + l/cm measurement is a quantitative measure of lamellae distance recorded on dried mature basidiocarps, counting the total number of lamellae and lamellulae per centimetre half the radius between the margin and the stipe. Estimation of lamellae density was based on the number of lamellae per half pileus relative to the size of the mushroom (Fig. 1).

Microscopic characters are described from examination of dried herbarium material. Hand-cut sections were rehydrated in 5 % KOH solution, then mounted in congo red to observe the hymenium, trama, and pellis tissues. Spore size, shape, ornamentation and amyloidity were observed in lamellae tissue mounted in Melzer's reagent. Measurements of microscopic characters were taken on an Olympus BX-52 microscope at ×400 or ×1000 using either a calibrated ocular micrometre or an Olympus DP-73 camera attachment and measurement tools using Olympus cellSens standard (v. 1.16). Microscopic measurements are given as a raw range of length × width with mean ± standard deviation (SD) of *n* measurements in parentheses. The length/width quotient (Q) of individual spores is presented as the raw range of Q values with mean ± standard deviation (SD) of *n* measurements in parentheses. Basidia, basidioles, and cystidia measurements are given as length (not including sterigmata) × width at widest point, and width at base or apex. Pseudocystidia, laticiferous hyphae, and hyaline hyphae measurements are given as a raw range of diameters.

Scanning electron microscopy (SEM) of gold-sputtered basidiospores mounted on carbon tape was performed using a Thermo Fisher Scientific XL30 FEG microscope (Waltham, USA) at the University of Melbourne Biosciences Microscopy Unit.

All illustrations and photographs are based on the type collection unless otherwise stated. Names of herbaria are abbreviated according to Thiers (http://sweetgum.nybg.org/ih/ continuously updated); all specimens examined labelled with 'AQ' numbers are curated at the Queensland Herbarium (BRI).

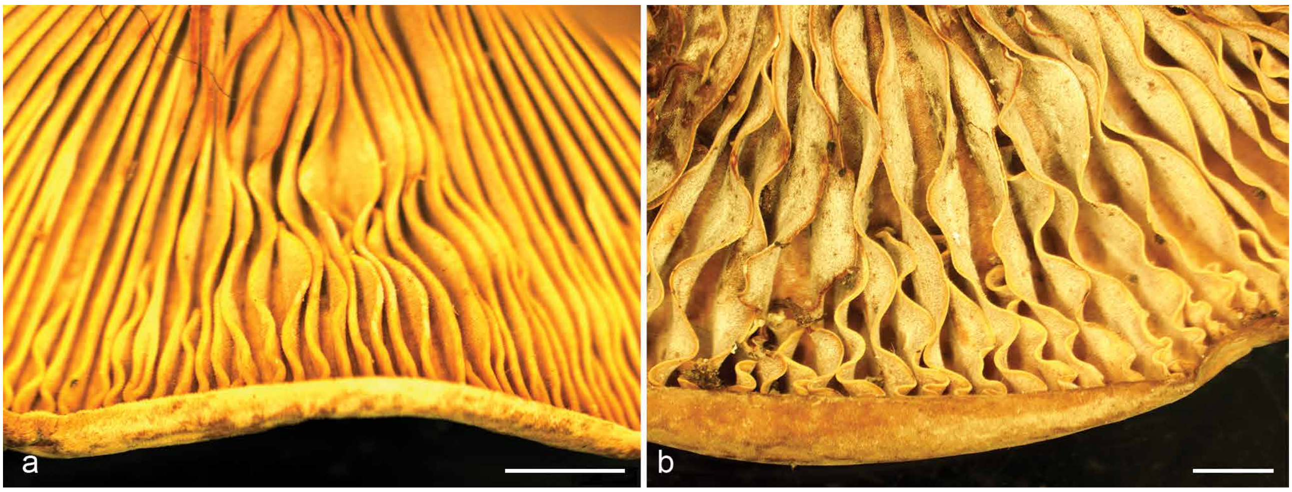

Fig. 1 Estimation of lamellae density was based on the number of lamellae per half pileus relative to the size of the mushroom; a. close (MEL2150077), b. distant (MEL2329677).

Table 1 Specimens used in the phylogenetic analysis, including infrageneric taxon, original identification (as originally identified in the field or as labelled in GenBank), revised identification after this study, fungarium numbers, country of origin, and ITS / LSU GenBank accession numbers. New sequences generated for this study are indicated in **bold**.

(Infrageneric) taxon	Original identification	Revised identification	Herbarium number and type information	Country	GenBank acession number	
					ITS	LSU
Lactarius	*Lactarius azonites*	*Lactarius azonites*	DS08-517 GENT	Belgium	JQ446099	JQ446172
	Lactarius baliophaeus	*Lactarius baliophaeus*	AV05-155 GENT	Malawi	GU258277	GU265576
	Lactarius chrysorrheus	*Lactarius chrysorrheus*	UE04.10.2002-8 UPS	Italy	KF133261	KF133293
	Lactarius deliciosus	*Lactarius deliciosus*	JN2001-046 GENT	Slovakia	KF133272	KF133305
	Lactarius falcatus	*Lactarius falcatus*	KVP08-038 GENT	Thailand	KF133274	KF133307
	Lactarius lignyotus	*Lactarius lignyotus*	2069-QFB-25815	Canada	KJ705223	–
	Lactarius peckii	*Lactarius peckii*	JN2004-020 GENT	USA	KF133277	KF133310
	Lactarius pomiolens	*Lactarius pomiolens*	AV07-159 GENT	Sri Lanka	KF133282	–
	Lactarius psammicola	*Lactarius psammicola*	BPL869	USA	KY848507	–
	Lactarius quietus	*Lactarius quietus*	UE16.09.2004 UPS	Sweden	KF133264	KF133296
	Lactarius subdulcis	*Lactarius subdulcis*	JV2006-024 GENT	Belgium	KF133279	KF133312
	Lactarius torminosus	*Lactarius torminosus*	RW3183 GENT	Czech Republic	KF133281	KF133314
Multifurca	*Multifurca aurantiophylla*	*Multifurca aurantiophylla*	BB644	–	–	KU237581
	Multifurca furcata	*Multifurca furcata*	RH	–	–	DQ421995
	Multifurca ochricompacta	*Multifurca ochricompacta*	BB02107	–	DQ421984	DQ421984
	***Multifurca* sp.**	***Multifurca* sp.**	**MEL238568**	–	**MW134734**	**MW128106**
	Multifurca stenophylla	*Multifurca stenophylla*	CWD584	AU	JX266628	JX266633
	Multifurca zonaria	*Multifurca zonaria*	FH12-009	Thailand	KR364083	KR364212
Russula	*Russula acrolamellata*	*Russula acrolamellata*	FUNNZ2017_879 PDD	NZ	MF461612	–
	Russula aeruginea	*Russula aeruginea*	AT2003017	France	DQ421999	DQ421999
	Russula albonigra	*Russula albonigra*	AT2002064 UPS	–	DQ422029	DQ422029
	Russula brunneonigra	*Russula brunneonigra*	H5813	AU	EU019945	–
	Russula camarophylla	*Russula camarophylla*	PAM01081108	–	DQ421982	DQ421982
	Russula aff. *compacta*	*Russula* aff. *compacta*	JET1103	–	–	JX266639
	Russula foetens	*Russula foetens*	FH12-277	USA	KT934016	KT933877
	Russula fragrantissima	*Russula fragrantissima*	voucher 108	Italy	KJ834596	–
	Russula ingwa	***Russula ingwa***	**MEL2238392**	**AU_VIC**	–	**MW128107**
	Russula neerimea	*Russula neerimea*	MEL2101871	AU	EU019915	EU019915
	Russula nigricans	*Russula nigricans*	UE20.09.2004-07 UPS	–	DQ422010	DQ422010
	Uncultured fungal clone	*Russula* sp.	environmental sample RFLP13	AU	DQ388820	–
	Uncultured fungal clone	*Russula* sp.	environmental sample RFLP7	AU	DQ388814	–
	Lactarius clarkeae	***Russula* sp.**	**MEL2089726**	**AU_WA**	**MW134735**	–
	Russula subfoetens	*Russula subfoetens*	HKAS 78367	China	KF002757	–
subg. *Gymnocarpi*	*Lactarius brunellus*	*Lactifluus brunellus*	TH9130	Guyana	JN168728	–
	Lactifluus sp.	*Lactifluus* sp.	G3185	French Guiana	KJ786694	KJ786603
	Lactifluus sp.	*Lactifluus* sp.	Guad08042 LIP	Guadeloupe	KP691414	KP691423
	Lactarius panuoides	*Lactifluus* sp.	G4360	Guyana	–	KJ786637
	Lactifluus distantifolius	*Lactifluus* sp.	G4257	Guyana	KJ786714	–
	Lactarius panuoides	*Lactifluus* sp.	Clone 395LA	–	–	AF218561
	Lactarius panuoides	*Lactifluus* sp.	TH6843ECM	–	–	AF218566
subg. *Gymnocarpi* sect. *Gymnocarpi*	*Lactifluus* sp.	*Lactifluus albomembranaceus*	355B	Burkina Faso	LN651269	–
	Lactifluus albomembranaceus	*Lactifluus albomembranaceus*	EDC12-46 GENT holotype	Cameroon	KR364193	–
	Lactifluus albomembranaceus	*Lactifluus albomembranaceus*	ADK4284	Togo	KX306941	–
	Lactifluus foetens	*Lactifluus foetens*	ADK3688 BR	Benin	KR364022	KR364149
	Lactifluus sp.	*Lactifluus foetens*	C1819	Togo	LM999910	–
	Lactifluus foetens	*Lactifluus foetens*	C1822_MD359	Togo	LK392603	–
	Lactifluus gymnocarpus	*Lactifluus gymnocarpus*	EDC12-047 GENT	Cameroon	KR364065	KR364194
	Lactifluus flammans	*Lactifluus* sp.	JD941 BR	DR Congo	KR364078	KR364207
	Lactifluus tanzanicus	*Lactifluus tanzanicus*	TS1277	Tanzania	KR364037	–
	Lactifluus cf. *tanzanicus*	*Lactifluus tanzanicus*	AV11-017 GENT	Tanzania	KR364053	–
	Lactifluus albocinctus	*Lactifluus tanzanicus*	AV99-2111 GENT type of Lf. albocinctus	Zimbabwe	KR364117	KR364249

Table 1 (cont.)

(Infrageneric) taxon	Original identification	Revised identification	Herbarium number and type information	Country	GenBank acession number	
					ITS	LSU
subg. *Gymnocarpi* sect. *Luteoli*	*Lactifluus brunneoviolascens*	*Lactifluus brunneoviolascens*	AV13-038 GENT	Italy	KR364123	KR364246
	Lactifluus luteolus	*Lactifluus brunneoviolascens*	Hal_BP_26	Italy	KU885434	–
	Lactifluus brunneoviolascens	*Lactifluus brunneoviolascens*	PDGregorio1493	Spain	MH125231	–
	Lactarius cf. *piperatus*	*Lactifluus caliendrifer*	CUB_Microbiology KHS6	Thailand	AB459515	–
	Uncultured Lactarius	*Lactifluus caliendrifer*		Thailand	AB854675	–
	Lactifluus sp.	*Lactifluus caliendrifer*	KW392 GENT	Thailand	KR364091	–
	Lactifluus sp.	*Lactifluus caliendrifer*	KW378 GENT holotype	Thailand	MK517655	–
	Lactifluus longivelutinus	*Lactifluus longivelutinus*	XHW 1565 holotype	China	KR364114	–
	Lactifluus luteolus	*Lactifluus luteolus*	AV05-253 GENT	USA	KR364016	KR364142
	Lactifluus luteolus	*Lactifluus luteolus*	NAMA2015-216	USA	MH910537	–
	Lactifluus nonpiscis	*Lactifluus nonpiscis*	AV11-137 GENT	Togo	KR364058	KR364185
	Lactifluus nonpiscis	*Lactifluus nonpiscis*	BB3171	Zambia	KR364030	KR364157
	Lactifluus rubrobrunnescens	*Lactifluus rubrobrunnescens*	EH7194 holotype	Indonesia	KR364115	–
	Lactifluus sp.	*Lactifluus russulisporus*	REH9398 NY holotype	AU	KR364097	KR364229
	Lactifluus sp.	*Lactifluus russulisporus*	REH9674	AU	MK517654	–
	Lactarius subclarkeae	***Lactifluus russulisporus***	**MEL2336075**	**AU_NSW**	**MW134736**	**MW128108**
	Lactifluus cf. *luteolus*	*Lactifluus* sp.	KUN_F73547	China	KC154098	KC154124
	Lactifluus cf. *luteolus*	*Lactifluus* sp.	KUN_F73536	South Korea	KC154099	KC154125
	Uncultured fungus	*Lactifluus* sp.	environmental sample	South Korea	AB587755	–
	Lactarius hygrophoroides	*Lactifluus* sp.	KA12-1358	South Korea	KR673574	–
	Lactifluus luteolus	*Lactifluus* sp.	FLAS-F-61152	USA	MH211771	–
	Lactifluus hygrophoroides	*Lactifluus* sp.	MHHNU31250	–	MK430041	–
subg. *Gymnocarpi* sect. *Nebulosi*	*Lactarius chiapanensis*	*Lactifluus chiapanensis*	V.M.Bandala 4374A GENT	Mexico	GU258297	GU265580
	Lactarius cf. *nebulosus*	*Lactifluus guadeloupensis*	RC_Guad11-023 LIP holotype	Guadeloupe	KP691412	KP691421
	Lactarius cf. *castaneibadius*	*Lactifluus murinipes*	CL_Mart06-019 LIP	Martinique	KP691417	KP691426
	Lactarius cf. *murinipes*	*Lactifluus murinipes*	F.1890 LIP	Martinique	KP691418	–
	Lactifluus cf. *caribaeus*	*Lactifluus nebulosus*	PAM_Mart12-90 LIP	Martinique	KP691415	KP691424
	Lactifluus cf. *putidus*	*Lactifluus putidus*	Mart1113 LIP	Martinique	KP691413	KP691422
subg. *Gymnocarpi* sect. *Panuoidei*	*Lactarius panuoides*	*Lactifluus panuoides*	G128	Guyana	KJ786647	KJ786551
	Lactifluus sp.	*Lactifluus* sp.	MVL71	Brazil	KY769855	–
	Lactarius panuoides	*Lactifluus* sp.	TH7460	Guyana	KT339233	KT339233
	Uncultured fungus	*Lactifluus* sp.	environmental sample Clone 59MS_5f	Guyana	KT289975	–
subg. *Gymnocarpi* sect. *Phlebonemi*	*Lactifluus brunnescens*	*Lactifluus brunnescens*	AV05-83 GENT	Malawi	KR364019	–
	Lactifluus aff. *phlebonemus*	*Lactifluus* aff. *phlebonemus*	EDC12-023 GENT	Cameroon	KR364062	KR364191
	Uncultured fungus	*Lactifluus* sp.	environmental sample DB184	DR Congo	KT461403	–
	Uncultured ectomycorrhizal fungus	*Lactifluus* sp.	environmental sample L6595_Russ_Gab19	Gabon	FR731894	–
	Uncultured fungus	*Lactifluus* sp.	environmental sample L6612_Russ_STP3	Sao Tome and Principe	FR731950	–
subg. *Gymnocarpi* sect. *Tomentosi*	***Lactarius* sp.**	***Lactifluus albens* sp. nov.**	**MEL2238278**	**AU_VIC**	**MW134737**	**MW128109**
	Lactarius subclarkeae	***Lactifluus albens* sp. nov.**	**MEL2297067**	**AU_VIC**	**MW134738**	**MW128110**
	Russula flocktonae	***Lactifluus albens* sp. nov.**	**MEL2322071**	**AU_VIC**	**MW134739**	**MW128111**
	***Lactarius* sp.**	***Lactifluus albens* sp. nov.**	**MEL2231695 type**	**AU_WA**	**MW134740**	**MW128112**
	Lactarius clarkeae	***Lactifluus albens* sp. nov.**	**MEL2036515**	**AU_WA**	**MW134741**	**MW128113**
	***Lactifluus* sp.**	***Lactifluus albens* sp. nov.**	**PLWA245**	**AU_WA**	**MW134742**	**MW128114**
	Russula flocktonae	***Lactifluus aurantioruber* stat. nov.**	**MEL2359409**	**AU_TAS**	**MW134743**	–
	Russula flocktonae	***Lactifluus aurantioruber* stat. nov.**	**MEL2036360**	**AU_NSW**	**MW134744**	–
	Lactarius clarkeae	***Lactifluus aurantioruber* stat. nov.**	**MEL2257827**	**AU_TAS**	**MW134745**	**MW128115**
	Lactarius clarkeae	*Lactifluus aurantioruber* stat. nov.	N2004122	AU_TAS	HQ318284	HQ318207
	Lactarius clarkeae	***Lactifluus aurantioruber* stat. nov.**	**MEL2381530**	**AU_TAS**	**MW134746**	–
	Russula flocktonae	***Lactifluus aurantioruber* stat. nov.**	**MEL2036366**	**AU_TAS**	**MW134747**	–
	Lactarius clarkeae	***Lactifluus aurantioruber* stat. nov.**	**MEL2238211**	**AU_VIC**	**MW134748**	**MW128116**
	Lactifluus aurantioruber	***Lactifluus aurantioruber* stat. nov.**	**JAC9351**	**NZ**	**MW134749**	**MW128117**
	Lactifluus aurantioruber	***Lactifluus aurantioruber* stat. nov.**	**PDD104363 PL23209**	**NZ**	**MW134750**	–
	Lactifluus aurantioruber	***Lactifluus aurantioruber* stat. nov.**	**PDD101410 PL380211**	**NZ**	**MW134751**	–

Table 1 (cont.)

(Infrageneric) taxon	Original identification	Revised identification	Herbarium number and type information	Country	GenBank acession number	
					ITS	LSU
subg. *Gymnocarpi* sect. *Tomentosi* (cont.)	*Lactarius clarkeae*	*Lactifluus aurantioruber* stat. nov.	PDD88985	NZ	GU222280	–
	Lactarius clarkeae	***Lactifluus clarkeae* s.str.**	**AQ0808473**	**AU_QLD**	**MW134752**	**MW128118**
	Lactarius subclarkeae	*Lactifluus clarkeae* s.str.	AQ0794333	AU_QLD_FrIsland	KR364095	KR364227
	Lactarius clarkeae	***Lactifluus clarkeae* s.str.**	**MEL2332064**	**AU_QLD_FrIsland**	**MW134753**	**MW128119**
	Lactarius subclarkeae	***Lactifluus clarkeae* s.str.**	**MEL2101947 epitype**	**AU_SA**	**MW134754**	**MW128120**
	Lactarius subclarkeae	***Lactifluus clarkeae* s.str.**	**MEL2024762**	**AU_SA**	**MW134755**	–
	Lactarius clarkeae	***Lactifluus clarkeae* s.str.**	**MEL2257826**	**AU_TAS**	**MW134756**	**MW128121**
	Lactarius clarkeae	***Lactifluus clarkeae* s.str.**	**MEL2238268**	**AU_VIC**	**MW134757**	–
	Russula flocktonae	***Lactifluus clarkeae* s.str.**	**MEL2320759**	**AU_VIC**	**MW134758**	**MW128122**
	Lactarius clarkeae	***Lactifluus clarkeae* s.str.**	**PERTH07680007**	**AU_WA**	**MW134759**	**MW128123**
	Lactarius clarkeae	***Lactifluus clarkeae* s.str.**	**PERTH07676042**	**AU_WA**	**MW134760**	**MW128124**
	Lactarius clarkeae	***Lactifluus clarkeae* s.str.**	**PERTH07670400**	**AU_WA**	**MW134761**	**MW128125**
	Lactarius clarkeae	***Lactifluus clarkeae* s.str.**	**PERTH07676026**	**AU_WA**	**MW134762**	**MW128126**
	Lactarius clarkeae	***Lactifluus clarkeae* s.str.**	**PERTH07574428**	**AU_WA**	**MW134763**	**MW128127**
	Lactarius clarkeae	***Lactifluus clarkeae* s.str.**	**PERTH08318271**	**AU_WA**	**MW134764**	**MW128128**
	Lactarius clarkeae	***Lactifluus clarkeae* s.str.**	**PERTH08019274**	**AU_WA**	**MW134765**	**MW128129**
	Lactarius clarkeae	***Lactifluus clarkeae* s.str.**	**PERTH07665385**	**AU_WA**	**MW134766**	–
	Lactarius clarkeae	***Lactifluus clarkeae* s.str.**	**PERTH05485568**	**AU_WA**	**MW134767**	–
	Lactarius clarkeae	***Lactifluus clarkeae* s.str.**	**PERTH07569041**	**AU_WA**	**MW134768**	–
	Lactarius subclarkeae	***Lactifluus clarkeae* s.str.**	**MEL2101938**	**AU_WA**	**MW134769**	–
	Lactifluus clarkeae	***Lactifluus clarkeae* s.str.**	**PDD102596**	**NZ**	**MW134770**	**MW128130**
	Lactifllus clarkeae	***Lactifluus clarkeae* s.str.**	**JAC11696; PDD96000**	**NZ**	**MW134771**	**MW128131**
	Lactifluus clarkeae	***Lactifluus clarkeae* s.str.**	**JAC11742; PDD96149**	**NZ**	**MW134772**	–
	Lactifluus clarkeae	***Lactifluus clarkeae* s.str.**	**PL25509; PDD95561**	**NZ**	**MW134773**	–
	Lactifluus clarkeae	***Lactifluus clarkeae* s.str.**	**PL5102; PDD76085**	**NZ**	**MW134774**	–
	Lactifluus clarkeae	***Lactifluus clarkeae* s.str.**	**JAC14568; PDD106449**	**NZ**	**MW134775**	–
	Russula erumpens	*Lactifluus flocktoniae* s.str.	MEL2239381	AU_VIC	JX266622	–
	Russula flocktonae	*Lactifluus flocktoniae* s.str.	MEL2238290 epitype	AU_VIC	JX266621	JX266637
	Russula flocktonae	***Lactifluus flocktoniae* s.str.**	**MEL2218977**	**AU_NSW**	**MW134776**	**MW128132**
	Lactarius clarkeae	***Lactifluus flocktoniae* s.str.**	**MEL2298098**	**AU_VIC**	**MW134777**	–
	Russula flocktonae	***Lactifluus flocktoniae* s.str.**	**MEL2322022**	**AU_VIC**	**MW134778**	**MW128133**
	Russula flocktonae	***Lactifluus flocktoniae* s.str.**	**PERTH07650795**	**AU_WA**	**MW134779**	**MW128134**
	Lactarius clarkeae	***Lactifluus flocktoniae* s.str.**	**PERTH07581726**	**AU_WA**	**MW134780**	**MW128135**
	Lactarius clarkeae	***Lactifluus flocktoniae* s.str.**	**PERTH07599102**	**AU_WA**	**MW134781**	**MW128136**
	Russula flocktonae	***Lactifluus flocktoniae* s.str.**	**PERTH07673396**	**AU_WA**	**MW134782**	**MW128137**
	Russula flocktonae	***Lactifluus flocktoniae* s.str.**	**PERTH07675917**	**AU_WA**	**MW134783**	**MW128138**
	Lactifluus flocktonae	***Lactifluus flocktoniae* s.str.**	**PERTH08072728**	**AU_WA**	**MW134784**	**MW128139**
	Russula flocktonae	***Lactifluus flocktoniae* s.str.**	**PERTH07681011**	**AU_WA**	**MW134785**	**MW128140**
	Russula flocktonae	***Lactifluus flocktoniae* s.str.**	**PERTH07676204**	**AU_WA**	**MW134786**	**MW128141**
	Russula flocktonae	***Lactifluus flocktoniae* s.str.**	**PERTH07650469**	**AU_WA**	**MW134787**	–
	Russula flocktonae	***Lactifluus flocktoniae* s.str.**	**PERTH07587643**	**AU_WA**	**MW134788**	–
	Russula flocktonae	***Lactifluus flocktoniae* s.str.**	**MEL2101939**	**AU_WA**	**MW134789**	**MW128142**
	Russula flocktonae	***Lactifluus flocktoniae* s.str.**	**MEL2101940**	**AU_WA**	**MW134790**	**MW128143**
	Russula flocktonae	***Lactifluus psammophilus* sp. nov.**	**MEL2238407 type**	**AU_VIC**	**MW134791**	**MW128144**
	Lactarius clarkeae	*Lactifluus psammophilus* sp. nov.	MEL2238274	AU_VIC	EU019924	EU019924
	Russula flocktonae	***Lactifluus psammophilus* sp. nov.**	**MEL2322029**	**AU_VIC**	**MW134792**	**MW128145**
	Russula flocktonae	***Lactifluus psammophilus* sp. nov.**	**MEL2297068**	**AU_VIC**	**MW134793**	**MW128146**
	Russula flocktonae	***Lactifluus psammophilus* sp. nov.**	**MEL2298102**	**AU_VIC**	**MW134794**	**MW128147**
	Russula flocktonae	***Lactifluus psammophilus* sp. nov.**	**MEL2238406**	**AU_VIC**	**MW134795**	**MW128148**
	Russula flocktonae	***Lactifluus psammophilus* sp. nov.**	**MEL2322070**	**AU_VIC**	**MW134796**	–
	Russula flocktonae	***Lactifluus psammophilus* sp. nov.**	**MEL2036361**	**AU_VIC**	**MW134797**	–
	Lactarius clarkeae	***Lactifluus pseudoflocktoniae* sp. nov.**	**MEL2371747**	**AU_TAS**	**MW134798**	–
	Lactarius clarkeae	*Lactifluus pseudoflocktoniae* sp. nov.	N2004018	AU_TAS	HQ318283	HQ318206
	Lactarius clarkeae	*Lactifluus pseudoflocktoniae* sp. nov.	N2001002	AU_TAS	HQ318282	HQ318205

Table 1 (cont.)

(Infrageneric) taxon	Original identification	Revised identification	Herbarium number and type information	Country	GenBank acession number	
					ITS	LSU
subg. *Gymnocarpi* sect. *Tomentosi* (cont.)	***Lactarius clarkeae***	***Lactifluus pseudoflocktoniae* sp. nov.**	**MEL2036362**	**AU_TAS**	**MW134799**	**MW128149**
	Lactarius clarkeae	***Lactifluus pseudoflocktoniae* sp. nov.**	**MEL2257830**	**AU_TAS**	**MW134800**	**MW128150**
	Lactarius clarkeae	***Lactifluus pseudoflocktoniae* sp. nov.**	**MEL2238269 holotype**	**AU_VIC**	**MW134801**	**MW128151**
	Lactarius clarkeae	***Lactifluus pseudoflocktoniae* sp. nov.**	**MEL2030448**	**AU_VIC**	**MW134802**	**MW128152**
	Lactarius clarkeae	***Lactifluus pseudoflocktoniae* sp. nov.**	**MEL2121981**	**AU_VIC**	**MW134803**	–
	Lactifluus sp.	*Lactifluus* sp. 1	environmental sample CMMy30M1	New Caledonia	KY774240	–
	Lactarius clarkeae	***Lactifluus* sp. 2**	**MEL2364071**	**AU_NSW**	**MW134804**	**MW128153**
	Lactarius clarkeae	***Lactifluus* sp. 3**	**AQ0797938**	**AU_QLD_FrIsland**	**MW134805**	**MW128154**
	Lactarius clarkeae	***Lactifluus* sp. 4**	**AQ0796523**	**AU_QLD**	**MW134806**	**MW128155**
	Lactarius clarkeae	***Lactifluus* sp. 4**	**AQ0808472**	**AU_QLD**	**MW134807**	**MW128156**
	Lactifluus clarkeae	*Lactifluus* sp. 5	PGK13-130 Nothofagus	New Caledonia	KP691436	KR605507
	Uncultured fungus	*Lactifluus* sp. 6	environmental sample KT-26 Tristaniopsis	New Caledonia	LC271308	–
	Uncultured fungus	*Lactifluus* sp. 6	environmental sample KT-47 Tristaniopsis	New Caledonia	LC271325	–
subg. *Lactariopsis*	*Lactarius emergens*	*Lactifluus emergens*	AV99-005 GENT	Zimbabwe	AY606979	KF133290
	Lactifluus leoninus	*Lactifluus leoninus*	EH 72-524 holotype	Papua New Guinea	KR364116	–
	Lactifluus melleus	*Lactifluus melleus*	MD157	Togo	LK392597	–
	Lactifluus sp.	*Lactifluus melleus*	MD108	Togo	LK392598	–
	Lactarius leoninus	*Lactifluus* sp.	DS07-454 GENT	Thailand	KF220055	JN388989
	Lactifluus sp.	*Lactifluus* sp.	C2157	Togo	HG426466	–
subg. *Lactariopsis* sect. *Albati*	*Lactifluus* sp.	*Lactifluus deceptivus*	AV05-275 GENT	USA	MK931336	–
	Lactarius deceptivus	*Lactifluus* sp.	AV04-181 GENT	USA	MK931328	DQ422020
	Lactarius vellereus	*Lactifluus vellereus*	UE20.09.2004-22 UPS	–	DQ422034	DQ422034
subg. *Lactariopsis* sect. *Edules*	*Lactifluus aureifolius*	*Lactifluus aureifolius*	AV11-074 GENT	Tanzania	KR364056	KR364183
	Lactifluus edulis	*Lactifluus edulis*	FN05-628 GENT	Malawi	KR364020	KR364147
	Lactifluus edulis	*Lactifluus edulis*	AV99-041 GENT	Zimbabwe	–	DQ421977
	Lactarius nodosicystidiosus	*Lactifluus nodocystidiosus*	BB97-072 PC	Madagascar	–	DQ421976
	Lactarius phlebophyllus	*Lactifluus phlebophyllus*	BB00-1388 PC	Madagascar	–	DQ421979
subg. *Lactariopsis* sect. *Lactariopsis*	*Lactarius annulatoangustifolius*	*Lactifluus annulatoangustifolius*	BB00-1518 PC	Madagascar	AY606981	KR364253
	Lactifluus annulatoangustifolius	*Lactifluus annulatoangustifolius*	MD145	Togo	HG426475	–
	Lactifluus sp.	*Lactifluus* sp.	C2349	Togo	HG426478	–
	Lactifluus sp.	*Lactifluus* sp.	MD123	Togo	HG426470	–
	Lactarius velutissimus	*Lactifluus* sp.	AV99-185 GENT	–	AY606982	DQ421973
	Lactifluus velutissimus	*Lactifluus velutissimus*	JD886	Congo	KR364075	KR364204
subg. *Lactariopsis* sect. *Neotropicus*	*Lactarius* cf. *venezuelanus*	*Lactifluus venezuelanus*	RC_Gaud11-017 LIP	Guadeloupe	KP691411	KP691420
subg. *Lactifluus* sect. *Allardii*	*Lactifluus allardii*	*Lactifluus allardii*	JN2004-008 GENT	USA	KF220016	KF220125
	Lactifluus allardii	*Lactifluus allardii*	AV05-286 GENT	USA	KF220015	KF220124
subg. *Lactifluus* sect. *Ambicystidiati*	*Lactifluus ambicystidiatus*	*Lactifluus ambicystidiatus*	KUN_F88179	China	KR908670	KR908672
	Lactifluus ambicystidiatus	*Lactifluus ambicystidiatus*	KUNF57008 holotype	China	KC154096	–
subg. *Lactifluus* sect. *Gerardii*	*Lactifluus* sp.	*Lactifluus auriculiformis*	AV12-050 GENT holotype	Thailand	KR364086	KR364216
	Lactifluus sp.	*Lactifluus bhandaryi*	TENN 051830 holotype	Nepal	KR364111	–
	Lactarius conchatulus	*Lactifluus conchatulus*	LTH457 GENT isotype	Thailand	GU258296	GU265659
	Lactarius coniculus	*Lactifluus coniculus*	DS07-496 GENT holotype	Sri Lanka	GU258236	GU265594
	Lactarius coniculus	*Lactifluus coniculus*	DS07-497 GENT	Sri Lanka	GU258237	GU265595
	Lactarius fuscomarginatus	*Lactifluus fuscomarginatus*	GO2010-144	Mexico	KC152157	–
	Lactarius genevievae	*Lactifluus genevievae*	G.Gates_D.Ratkowsky 17-2-2005	AU	GU258294	GU265657
	Lactifluus sp.	*Lactifluus gerardiellus*	KW386 GENT holotype	Thailand	KX889845	KX889844
	Lactarius cf. *gerardii*	*Lactifluus gerardii*	AV05-375 GENT	USA	GU258254	GU265616
	Lactarius cf. *atroolivaceus*	*Lactifluus gerardii*	Desjardin3630	USA	GU258220	–
	Lactifluus igniculus	*Lactifluus igniculus*	LE262983 type	Vietnam	JX442759	–
	Lactifluus indicus	*Lactifluus indicus*	CAL 1282 holotype	India	KU145119	KU145121
	Lactarius leae	*Lactifluus leae*	AV-RW04-90 GENT	Thailand	GU258244	–
	Lactifluus leae	*Lactifluus leae*	FH12-13 GENT	Thailand	KF432957	–

Table 1 (cont.)

(Infrageneric) taxon	Original identification	Revised identification	Herbarium number and type information	Country	GenBank acession number ITS	GenBank acession number LSU
subg. *Lactifluus* sect. *Gerardii* (cont.)	*Lactarius leonardii*	*Lactifluus leonardii*	P.Leonard 35607	AU	GU258295	GU265658
	Lactarius leonardii	*Lactifluus leonardii*	G.Gates 29-1-2002	AU	GU258304	GU265664
	Lactarius limbatus	*Lactifluus limbatus*	DS06-230 GENT	Malaysia	GU258222	GU265578
	Lactarius limbatus	*Lactifluus limbatus*	DS06-247 GENT	Malaysia	GU258223	GU265579
	Lactifluus midnapurensis	*Lactifluus midnapurensis*	CAL 1516 holotype	India	KY785175	KY785177
	Lactarius ochrogalactus	*Lactifluus ochrogalactus*	E.Nagasawa 80-102 TMI type	Japan	GU258280	–
	Lactarius parvigerardii	*Lactifluus parvigerardii*	KUN_F61367 holotype	China	JF975641	JF975642
	Lactarius petersenii	*Lactifluus petersenii*	AV05-267 GENT	USA	GU258282	GU265643
	Lactifluus sp.	*Lactifluus pulchrellus*	KW304_FH12-037 GENT holotype	Thailand	KR364092	KR364223
	Lactifluus sp.	*Lactifluus raspei*	EDC14-517 holotype	Thailand	KX889849	–
	Lactarius reticulatovenosus	*Lactifluus reticulatovenosus*	Horak 6472 GENT holotype	Indonesia	GU258286	GU265649
	Lactifluus tropicosinicus	*Lactifluus robustus*	K16053113	China	KY353803	KY353806
	Lactifluus tropicosinicus	*Lactifluus robustus*	K15052822	China	KY353802	KY353805
	Lactarius cf. *wirrabara*	*Lactifluus sepiaceus*	MEL2300727	AU	GU258293	GU265656
	***Lactarius* sp.**	***Lactifluus sepiaceus***	**MEL1054958**	**AU_VIC**	**MW134808**	–
	Lactarius cf. *wirrabara*	*Lactifluus sepiaceus*	P.Leonard 40509	NZ	GU258287	GU265650
	Lactifluus sp.	*Lactifluus sinensis*	K15060710 holotype	China	KT900208	–
	Lactifluus sp.	*Lactifluus sinensis*	K15070203	China	KT900209	–
	Uncultured fungus	*Lactifluus sinensis*	environmental sample HIB12	China	JX457047	–
	Lactarius atrovelutinus	*Lactifluus* sp.	DS06-003 GENT	Malaysia	GU258231	GU265588
	Lactifluus cf. *uyedae*	*Lactifluus* sp.	AV12-70 GENT	Thailand	KR364090	–
	Lactarius cf. *gerardii* var. *subrubescens*	*Lactifluus* sp.	Desjardin5275	USA	GU258276	–
	Lactarius cf. *gerardii*	*Lactifluus* sp.	AV05-283 GENT	USA	GU258259	–
	Lactarius cf. *gerardii*	*Lactifluus* sp.	DPLewis6983	USA	GU258272	–
	Lactifluus aff. *igniculus*	*Lactifluus* sp.	LE253908	Vietnam	JX442760	–
	Lactarius cf. *gerardii* var. *fagicola*	*Lactifluus* sp.	Desjardin3564	–	GU258273	–
	Lactarius cf. *wirrabara*	*Lactifluus* sp. 10	P.Leonard 10409	AU	JF731001	JF731003
	***Lactarius* sp.**	***Lactifluus* sp. 10**	**MEL2305122**	**AU_QLD**	**MW134809**	–
	Lactarius sepiaceus	***Lactifluus* sp. 10**	**MEL2332066**	**AU_QLD**	**MW134810**	–
	Lactarius mea	***Lactifluus* sp. 11**	**PL26078**	**AU_QLD**	–	**MW128157**
	Lactarius cf. *wirrabara*	*Lactifluus* sp. 12	R.E.Halling 6800	AU	JF731000	JF731002
	Uncultured fungus	*Lactifluus* sp. 13	environmental sample RFLP61	AU	DQ388868	–
	Uncultured fungus	*Lactifluus* sp. 14	environmental sample Toosoil16	AU	KC222796	–
	Uncultured fungus	*Lactifluus* sp. 15	environmental sample Toosoil56	AU	KC222836	–
	Lactarius subgerardii	*Lactifluus subgerardii*	AV05-285 GENT	USA	GU258267	–
	Lactarius subgerardii	*Lactifluus subgerardii*	AV05-389 GENT	USA	GU258271	–
	Lactarius cf. *wirrabara*	*Lactifluus wirrabara*	G.Gates_D.Ratkowsky 12-07-2003	AU	GU258306	GU265666
	Lactarius cf. *wirrabara*	*Lactifluus wirrabara*	G.Gates_D.Ratkowsky 17-01-2002	AU	GU258305	GU265665
	Lactarius cf. *wirrabara*	*Lactifluus wirrabara*	G.Gates_D.Ratkowsky 24-01-2004	AU	GU258307	–
	Lactarius cf. *wirrabara*	*Lactifluus wirrabara*	JET943 MEL	AU	GU258291	–
subg. *Lactifluus* sect. *Lactifluus*	*Lactarius acicularis*	*Lactifluus acicularis*	LTH265 GENT	Thailand	HQ318277	HQ318196
	Lactarius acicularis	*Lactifluus acicularis*	DS07-456 GENT	Thailand	HQ318224	HQ318125
	Lactarius acicularis	*Lactifluus acicularis*	KVP08-033 GENT	Thailand	HQ318242	HQ318150
	Lactarius cf. *corrugis*	*Lactifluus corrugis*	AV05-290 GENT	USA	JN388976	JN388997
	Lactarius cf. *corrugis*	*Lactifluus corrugis*	JN2004-015 GENT	USA	JQ753820	JQ348262
	Lactifluus cf. *corrugis*	*Lactifluus corrugis*	AV05-291 GENT	USA	JQ753823	JQ348266
	Lactarius crocatus	*Lactifluus crocatus*	LTH268 GENT	Thailand	HQ318266	HQ318181
	Lactarius crocatus	*Lactifluus crocatus*	LTH245 GENT	Thailand	HQ318234	HQ318142
	Lactarius crocatus	*Lactifluus crocatus*	LTH202 GENT	Thailand	HQ318248	HQ318157
	Lactifluus dissitus	*Lactifluus dissitus*	AV-KD-KVP09-082 GENT	India	–	JN389035
	Lactarius distantifolius	*Lactifluus distantifolius*	DS07-461 GENT isotype	Thailand	HQ318223	HQ318124
	Lactarius distantifolius	*Lactifluus distantifolius*	LTH288 GENT	Thailand	HQ318274	HQ318193
	Lactarius clarkeae	***Lactifluus jetiae* sp. nov.**	**MEL2238281 holotype**	**AU_VIC**	**MW134811**	**MW128158**
	Russula flocktonae	***Lactifluus jetiae* sp. nov.**	**MEL2238286**	**AU_VIC**	**MW134812**	**MW128159**

Table 1 (cont.)

(Infrageneric) taxon	Original identification	Revised identification	Herbarium number and type information	Country	GenBank acession number	
					ITS	LSU
subg. *Lactifluus* sect. *Lactifluus* (cont.)	***Lactarius clarkeae***	***Lactifluus jetiae* sp. nov.**	**MEL2341759**	**AU_VIC**	**MW134813**	–
	Lactifluus lamprocystidiatus	*Lactifluus lamprocystidiatus*	EH 72-195 holotype	Papua New Guinea	KR364015	–
	Lactifluus leptomerus	*Lactifluus leptomerus*	AV-KD-KVP09-084 GENT	India	JN388974	JN389037
	Lactifluus leptomerus	*Lactifluus leptomerus*	AV-KD-KVP09-130 GENT	India	JN388971	JN389022
	Lactifluus leptomerus	*Lactifluus leptomerus*	AV-KD-KVP09-131 GENT holotype	India	JN388972	JN389023
	Lactarius longipilus	*Lactifluus longipilus*	LTH206 GENT	Thailand	HQ318258	HQ318171
	Lactarius longipilus	*Lactifluus longipilus*	LTH273 GENT	Thailand	HQ318276	HQ318195
	Lactarius longipilus	*Lactifluus longipilus*	LTH168 GENT	Thailand	HQ318235	HQ318143
	Lactifluus maenamensis	*Lactifluus maenamensis*	KD 16-008	India	MF928075	–
	Lactifluus mexicanus	*Lactifluus mexicanus*	Montoya5276 holotype	Mexico	MK211181	MK211190
	Lactifluus oedematopus	*Lactifluus oedematopus*	AV07-079 GENT	Belgium	JQ753835	JQ348270
	Lactarius volemus	*Lactifluus oedematopus*	RW1228 GENT	France	HQ318216	HQ318116
	Lactifluus oedematopus	*Lactifluus oedematopus*	KVP12-001 GENT neotype	Germany	KR364100	KR364232
	Lactarius clarkeae	***Lactifluus pagodicystidiatus* sp. nov.**	**MEL2320494**	**AU_VIC**	**MW134814**	**MW128160**
	Lactarius clarkeae	***Lactifluus pagodicystidiatus* sp. nov.**	**MEL2121979**	**AU_VIC**	**MW134815**	**MW128161**
	Lactarius clarkeae	***Lactifluus pagodicystidiatus* sp. nov.**	**MEL2150777 holotype**	**AU_VIC**	**MW134816**	**MW128162**
	Lactifluus sp.	*Lactifluus pallidilamellatus*	Leticia Montoya 4716	Mexico	JQ753824	JQ348268
	Lactarius pinguis	*Lactifluus pinguis*	LTH255 GENT	Thailand	HQ318263	HQ318178
	Lactarius pinguis	*Lactifluus pinguis*	LTH117 GENT holotype	Thailand	HQ318211	HQ318111
	Lactarius pinguis	*Lactifluus pinguis*	LTH169 GENT	Thailand	HQ318221	HQ318121
	***Lactarius* sp.**	***Lactifluus rugulostipitatus* sp. nov.**	**MEL2329677 holotype**	**AU_NT**	**MW134817**	**MW128163**
	***Lactarius* sp.**	***Lactifluus rugulostipitatus* sp. nov.**	**MEL2329678**	**AU_NT**	**MW134818**	–
	***Lactarius* sp.**	***Lactifluus rugulostipitatus* sp. nov.**	**MEL2329673**	**AU_NT**	**MW134819**	–
	Lactarius volemus	*Lactifluus* sp.	KIINA158 GENT	China	HQ318225	HQ318126
	Lactifluus dissitus	*Lactifluus* sp.	AV-KD-KVP09-134 GENT	India	JN388978	JN389026
	Lactarius cf. *volemus*	*Lactifluus* sp.	AV-KD-KVP09-125	India	–	JN389017
	Lactarius cf. *volemus*	*Lactifluus* sp.	AV-KD-KVP09-128	India	–	JN389020
	Lactarius cf. *volemus*	*Lactifluus* sp.	AV-KD-KVP09-137	India	–	JN389027
	Lactarius cf. *volemus*	*Lactifluus* sp.	AV-KD-KVP09-129	India	–	JN389021
	Lactarius volemus	*Lactifluus* sp.	OSA-My-3993	Japan	–	AB238645
	Lactarius volemus	*Lactifluus* sp.	OSA-My-3998	Japan	–	AB238650
	Lactarius volemus	*Lactifluus* sp.	OSA-My-4003	Japan	–	AB238655
	Lactarius corrugis	*Lactifluus* sp.	OSA-My-4016	Japan	–	AB238668
	Lactarius volemus	*Lactifluus* sp.	OSA-My-3994	Japan	–	AB238646
	Lactarius corrugis	*Lactifluus* sp.	OSA-My-4014	Japan	–	AB238666
	Lactarius corrugis	*Lactifluus* sp.	OSA-My-4015	Japan	–	AB238667
	Lactarius volemus	*Lactifluus* sp.	OSA-My-3995	Japan	–	AB238647
	Lactarius volemus	*Lactifluus* sp.	OSA-My-4000	Japan	–	AB238652
	Lactarius volemus	*Lactifluus* sp.	OSA-My-3999	Japan	–	AB238651
	Lactarius volemus	*Lactifluus* sp.	LTH313 GENT	Thailand	HQ318272	HQ318190
	Lactarius volemus	*Lactifluus* sp.	LTH133 GENT	Thailand	HQ318212	HQ318112
	Lactarius volemus	*Lactifluus* sp.	KVP08-006 GENT	Thailand	HQ318229	HQ318136
	Lactarius volemus	*Lactifluus* sp.	LTH231 GENT	Thailand	HQ318278	HQ318197
	Lactarius volemus	*Lactifluus* sp.	LTH123 GENT	Thailand	HQ318222	HQ318122
	Lactarius volemus	*Lactifluus* sp.	LTH294 GENT	Thailand	HQ318273	HQ318191
	Lactarius volemus	*Lactifluus* sp.	KVP08-021 GENT	Thailand	HQ318233	HQ318140
	Lactarius volemus	*Lactifluus* sp.	LTH170 GENT	Thailand	HQ318252	HQ318165
	Lactarius volemus	*Lactifluus* sp.	LTH230 GENT	Thailand	HQ318260	HQ318174
	Lactarius volemus	*Lactifluus* sp.	KVP08-004 GENT	Thailand	HQ318228	HQ318134
	Lactarius volemus	*Lactifluus* sp.	KVP08-011 GENT	Thailand	HQ318232	HQ318139
	Lactarius volemus	*Lactifluus* sp.	LTH264 GENT	Thailand	HQ318264	HQ318179
	Lactarius volemus	*Lactifluus* sp.	KVP08-008 GENT	Thailand	HQ318231	HQ318138
	Lactarius volemus	*Lactifluus* sp.	LTH247 GENT	Thailand	HQ318261	HQ318175
	Lactarius volemus	*Lactifluus* sp.	KVP08-005 GENT	Thailand	–	HQ318135

Table 1 (cont.)

(Infrageneric) taxon	Original identification	Revised identification	Herbarium number and type information	Country	GenBank acession number	
					ITS	LSU
subg. *Lactifluus* sect. *Lactifluus* (cont.)	*Lactarius volemus*	*Lactifluus* sp.	LTH249 GENT	Thailand	–	HQ318176
	Lactarius volemus	*Lactifluus* sp.	LTH284 GENT	Thailand	HQ318253	HQ318166
	Lactarius volemus	*Lactifluus* sp.	KVP08-026 GENT	Thailand	HQ318238	HQ318146
	Lactarius volemus	*Lactifluus* sp.	KVP08-043 GENT	Thailand	HQ318247	HQ318156
	Lactarius volemus	*Lactifluus* sp.	DED7577	USA	–	HQ318188
	Lactarius volemus	*Lactifluus* sp.	AV05-394 GENT	USA	GU258300	GU265660
	Lactifluus cf. *corrugis*	*Lactifluus* sp.	EIU-ASM10990	USA	JQ358921	JN940236
	Lactarius corrugis	*Lactifluus* sp.	AV04-209 GENT	USA	JN388977	JN388998
	Lactarius volemus	*Lactifluus* sp.	EIU-ASM11130	USA	JQ358938	JN940223
	Lactarius cf. *volemus*	*Lactifluus* sp.	SAM310809-02 TENN	USA	MF773609	–
	Lactifluus corrugis	*Lactifluus* sp.	MycoMap10398	USA	MH975019	–
	Lactifluus cf. *corrugis*	*Lactifluus* sp.	AV05-337 GENT	USA	JQ753821	–
	Lactifluus cf. *volemus*	*Lactifluus* sp.	AV04-167 GENT	–	JQ753827	JQ348273
	Lactarius cf. *volemus*	*Lactifluus* sp. 9	REH9320 NY	AU	KR364096	KR364228
	Uncultured fungus	*Lactifluus* sp. 9	environmental sample Toosoil58	AU_QLD	KC222838	–
	Uncultured fungus	*Lactifluus* sp. 8	environmental sample Toosoil17	AU_QLD	KC222797	–
	Uncultured fungus	*Lactifluus* sp. 8	environmental sample Toosoil13	AU_QLD	KC222793	–
	Uncultured fungus	*Lactifluus* sp. 8	environmental sample RFLP38	AU_QLD	DQ388845	–
	Uncultured fungus	*Lactifluus* sp. 8	environmental sample RFLP39	AU_QLD	DQ388846	–
	Uncultured fungus	*Lactifluus* sp. 8	environmental sample RFLP5	AU_QLD	DQ388812	–
	Lactarius volemus	*Lactifluus subvolemus*	AV07-082 GENT	Slovenia	HQ318218	HQ318118
	Lactifluus sp.	*Lactifluus subvolemus*	KVP08-048 GENT	Slovenia	JQ753927	JQ348379
	Lactifluus sp.	*Lactifluus subvolemus*	LAS75_092-A	Sweden	–	JQ348348
	Lactifluus versiformis	*Lactifluus versiformis*	AV-KD-KVP09-108 GENT	India	JN388961	JN389013
	Lactifluus versiformis	*Lactifluus versiformis*	AV-KD-KVP09-047 GENT	India	JN388964	JN389032
	Lactifluus versiformis	*Lactifluus versiformis*	AV-KD-KVP09-014 GENT holotype	India	JN388963	JN389029
	Lactarius vitellinus	*Lactifluus vitellinus*	LTH348 GENT	Thailand	HQ318251	HQ318164
	Lactarius vitellinus	*Lactifluus vitellinus*	KVP08-024 GENT holotype	Thailand	HQ318236	HQ318144
	Lactarius vitellinus	*Lactifluus vitellinus*	LTH269 GENT	Thailand	HQ318267	–
	Lactarius volemus	*Lactifluus volemus*	UE09.08.2004-5 UPS	–	DQ422008	DQ422008
subg. *Lactifluus* sect. *Piperati*	*Lactarius* aff. *piperatus*	*Lactifluus albopicri*	MDB_F12_18	AU_NT	MN598888	MN598864
	Lactarius piperatus	*Lactifluus albopicri*	AQ808493	AU_QLD	MN598878	MN598859
	Lactarius subclarkeae	*Lactifluus albopicri*	MEL2297391 type	AU_VIC	MN598874	MN598855
	Lactarius cf. *piperatus*	*Lactifluus austropiperatus*	PERTH07550324 type	AU_QLD	MN614115	MN614111
	Lactarius subclarkeae	*Lactifluus austropiperatus*	AQ808481	AU_QLD	MN614118	MN614113
	Lactarius subclarkeae	*Lactifluus austropiperatus*	MEL2150778	AU_VIC	MN614116	MN614112
	Lactifluus dwaliensis	*Lactifluus dwaliensis*	KD 612 GENT type	India	KR364042	–
	Lactifluus dwaliensis	*Lactifluus dwaliensis*	LTH67 GENT	Thailand	KF220108	KF220203
	Lactifluus dwaliensis	*Lactifluus dwaliensis*	LTH346 GENT	Thailand	KF220113	KF220206
	Lactifluus glaucescens	*Lactifluus glaucescens*	M.Lecomte_2002-20-9-3	France	KF220031	KF220134
	Lactifluus glaucescens	*Lactifluus glaucescens*	AV93-025 GENT	France	KF220062	KF220160
	Lactifluus glaucescens	*Lactifluus glaucescens*	M.Lecomte_2003-6-14-1	Italy	KF220117	KF220210
	Lactarius leucophaeus	*Lactifluus leucophaeus*	AV97-382 GENT	Papua New Guinea	GU258299	GU265640
	Lactifluus leucophaeus	*Lactifluus leucophaeus*	LTH-AV-RW 126.04-075 GENT	Thailand	KF220056	–
	Lactifluus lorenae	*Lactifluus lorenae*	Montoya5190 holotype	Mexico	MK211185	MK211194
	Lactarius piperatus	*Lactifluus piperatus*	M.Lecomte_2001-8-19-23	France	KF220120	KF220212
	Lactarius piperatus	*Lactifluus piperatus*	M.Lecomte_2001-8-19-65	France	KF220115	–
	Lactarius piperatus	*Lactifluus piperatus*	G.Zecchin 619	Italy	JF908270	–
	Lactarius piperatus	*Lactifluus piperatus*	UE09.08.2004-6 UPS	–	DQ422035	DQ422035
	Lactifluus roseophyllus	*Lactifluus roseophyllus*	JN2011-076 GENT	Vietnam	KF220107	KF220202
	Lactifluus aff. *piperatus*	*Lactifluus* sp.	AV-KD-KVP09-008 GENT	India	KF220095	KF220190
	Lactarius glaucescens	*Lactifluus* sp.	LTH66 GENT	Thailand	GU258298	GU265639
	Lactarius piperatus	*Lactifluus* sp.	Sunadda Yomyart	Thailand	AB451975	–
	Lactifluus aff. *piperatus*	*Lactifluus* sp.	LTH322 GENT	Thailand	KF220078	–
	Lactifluus aff. *subpiperatus*	*Lactifluus* sp.	LTH376 GENT	Thailand	KF220110	–

Table 1 (cont.)

(Infrageneric) taxon	Original identification	Revised identification	Herbarium number and type information	Country	GenBank acession number	
					ITS	LSU
subg. *Lactifluus* sect. *Piperati* (cont.)	*Lactarius glaucescens*	*Lactifluus* sp.	AV04-202 GENT	USA	HQ318280	HQ318203
	Lactifluus aff. *piperatus*	*Lactifluus* sp.	AV05-295 GENT	USA	KF220048	KF220149
subg. *Lactifluus* sect. *Tenuicystidiati*	*Lactifluus* aff. *tenuicystidiatus*	*Lactifluus* sp.	JN2011-074 GENT	Vietnam	KR364047	KR364173
	Lactifluus subpruinosus	*Lactifluus subpruinosus*	KUN_F76034	China	KC154110	KC154136
	Lactifluus subpruinosus	*Lactifluus subpruinosus*	KUN_F53356	China	KC154112	KC154138
	Lactifluus sp.	*Lactifluus subpruinosus*	JN2011-061 GENT	Vietnam	KR364046	KR364172
	Lactifluus tropicosinicus	*Lactifluus tropicosinicus*	KUN_F59626	China	KC154120	KC154146
	Lactifluus tropicosinicus	*Lactifluus tropicosinicus*	KUN_F75765	China	KC154119	KC154145
subg. *Pseudogymnocarpi*	*Lactifluus* sp.	*Lactifluus armeniacus*	EDC14-501 GENT holotype	Thailand	KR364127	–
	Lactifluus sp.	*Lactifluus* sp.	TENN065929	USA	KR364102	KR364233
	Lactifluus sp.	*Lactifluus* sp.	JN2011-012 GENT	Vietnam	KR364045	KR364171
	Lactarius clarkeae	***Lactifluus* sp. 7**	**AQ0797939**	**AU_QLD**	–	**MW128164**
	***Lactarius* sp.**	***Lactifluus* sp. 7**	**FG2018031**	**AU_QLD**	**MW134820**	**MW128165**
	Lactarius clarkeae	***Lactifluus* sp. 7**	**AQ0794627**	**AU_QLD**	**MW134821**	**MW128166**
	Lactifluus volemoides	*Lactifluus volemoides*	TS0705 holotype	Tanzania	KR364038	KR364165
subg. *Pseudogymnocarpi* sect. *Pseudogymnocarpi*	*Lactifluus flavellus*	*Lactifluus flavellus*	MD393 holotype	Togo	LK392594	–
	Lactifluus gymnocarpoides	*Lactifluus gymnocarpoides*	JD885	DR Congo	KR364074	–
	Lactifluus gymnocarpoides	*Lactifluus gymnocarpoides*	AV05-184 GENT	Malawi	KR364024	–
	Lactifluus sp.	*Lactifluus holophyllus*	ASIS19960	South Korea	MF611684	MF611659
	Lactifluus sp.	*Lactifluus holophyllus*	ASIS22632	South Korea	MF611685	–
	Lactifluus sp.	*Lactifluus holophyllus*	SFC20150812-63 holotype	South Korea	MF611683	–
	Lactarius hygrophoroides	*Lactifluus hygrophoroides*	AV05-251 GENT	USA	HQ318285	HQ318208
	Lactarius hygrophoroides	*Lactifluus hygrophoroides*	EIU-ASM10004	USA	JQ358912	JN940241
	Lactarius hygrophoroides	*Lactifluus hygrophoroides*	EIU-ASM10004 clone c4	USA	JQ358911	–
	Lactifluus longisporus	*Lactifluus longisporus*	AV94-557 GENT	Burundi	KR364118	KR364244
	Lactifluus cf. *longisporus*	*Lactifluus longisporus*	AV11-025 GENT	Tanzania	KR364054	–
	Lactarius longisporus	*Lactifluus longisporus*	AV99-197 GENT	Zimbabwe	DQ421971	DQ421971
	Lactifluus pseudoluteopus	*Lactifluus luteolamellatus*	MHHNU8297	China	MK167429	–
	Lactifluus sp.	*Lactifluus luteolamellatus*	SFC20150818-39	South Korea	MF611680	–
	Lactifluus sp.	*Lactifluus luteolamellatus*	ASIS12249	South Korea	MF611679	–
	Lactifluus luteopus	*Lactifluus luteopus*	AV94-463 GENT type	Burundi	KR364119	–
	Lactifluus luteopus	*Lactifluus luteopus*	EDC11-087 GENT	Tanzania	KR364049	KR364176
	Lactifluus medusae	*Lactifluus medusae*	EDC12-152 GENT	Cameroon	KR364069	–
	Lactifluus cf. *pseudogymnocarpus*	*Lactifluus* cf. *pseudogymnocarpus*	AV05-085 GENT	Malawi	KR364012	–
	Lactarius hygrophoroides	*Lactifluus pseudohygrophoroides*	environmental sample cloneX3-4	China	JN129397	–
	Lactifluus sp.	*Lactifluus pseudohygrophoroides*	SFC20140821-45 holotype	South Korea	MF611682	MF611657
	Lactifluus sp.	*Lactifluus pseudohygrophoroides*	SFC20150813-71	South Korea	MF611681	–
	Lactarius pseudoluteopus	*Lactifluus pseudoluteopus*	LTH155 GENT	Thailand	HQ318286	HQ318210
	Lactifluus pseudoluteopus	*Lactifluus pseudoluteopus*	FH12-026 GENT	Thailand	KR364084	–
	Uncultured *Lactarius*	*Lactifluus pseudoluteopus*	environmental sample CD15	Thailand	FJ644702	–
	Lactifluus cf. *pumilus*	*Lactifluus* cf. *pumilus*	EDC12-066 GENT	Cameroon	KR364067	–
	Lactifluus rugatus	*Lactifluus rugatus*	EP 1212_7 LGAM-AUA	Greece	KR364104	KR364235
	Lactifluus rugatus	*Lactifluus rugatus*	PA2010R	Greece	MH125243	–
	Lactifluus rugatus	*Lactifluus rugatus*	4_01_2015	Italy	KU885436	–
	Uncultured ECM	*Lactifluus* sp.	environmental sample L7524_Russ MAD37	Madagascar	FR731264	–
	Uncultured fungus	*Lactifluus* sp.	environmental sample T071b	Thailand	JN969388	–
	Lactifluus hygrophoroides	*Lactifluus* sp.	MycoMap6251	USA	MK560130	–
	Lactifluus hygrophoroides	*Lactifluus* sp.	MycoMap6284	USA	MK560131	–
	Lactifluus sp.	*Lactifluus* sp.	FLAS-F-61011	USA	MH016945	–
	Lactifluus pseudoluteopus	*Lactifluus* sp.	KUNF58696	–	KC154100	–
	Lactifluus sudanicus	*Lactifluus sudanicus*	AV11-174 MD105	Togo	HG426469	KR364186
	Lactifluus sp.	*Lactifluus sudanicus*	MD148	Togo	HG426476	–

Abbreviations used: AU - Australia, NZ - New Zealand, NCal - New Caledonia, WA - Western Australia, VIC - Victoria, TAS - Tasmania, SA - South Australia, NT - Northern Territory, NSW - New South Wales, QLD - Queensland, FrIsland - Fraser Island.

Molecular studies

Protocols for DNA extraction (Qiagen Plant Dneasy kit or EZNA forensic kit for samples older than 1995), PCR, and sequencing followed those in Lebel & Syme (2012) and Lebel et al. (2015) and the references therein.

Assembly, manual editing, and preliminary alignment of sequences were performed within Geneious v. 9.1.7 (Biomatters Ltd). Individual alignments for the internal transcribed spacer (ITS) and large ribosomal subunit (LSU) were then manually trimmed in BioEdit v. 7.1.3 (Hall 2011) and some editing done in Geneious v. 9.1.7. The concatenated alignment and phylogenetic trees are available from the Landcare Research datastore https://doi.org/10.7931/n4fc-4z93.

Sequences of the ITS representing a broad range of species within *Lactarius. Lactifluus*, *Multifurca*, and *Russula* were retrieved from GenBank and UNITE (Kõljalg et al. 2013), to aid in initial placement of sequences generated for this study. In this preliminary alignment, *Auriscalpium vulgare*, *Bondarzewia* sp., *Echinodontium tinctorium*, and *Stereum hirsutum* were included as outgroup (Stubbe et al. 2010, Van de Putte et al. 2016, De Crop et al. 2017). Two further alignments, one of ITS sequences and one of LSU sequences were then generated using the new sequences and a selection of publicly available sequences of closely related species and species representing the phylogenetic diversity of *Lactifluus*. This was done with the on-line version of MAFFT v. 7 (Katoh et al. 2019). Several species of *Lactarius*, *Multifurca*, and *Russula* were utilised as outgroup. Novel sequences representing collections from Australasia and other regions generated for this study are listed in Table 1 with relevant GenBank accession numbers, and all sequences utilised in analyses.

Phylogenetic analyses of the concatenated ITS+LSU were performed with Maximum Likelihood (ML) in RAxML v. 8.2.12 (Stamatakis 2014) using the CIPRES Science Gateway v. 3.3 (Miller et al. 2010). The final dataset comprised 425 specimens (392 ITS and 270 LSU sequences), consisting of 2234 bp. Gaps in alignments were treated as missing data. The tree was visualized in FigTree v. 1.4.2 (Rambaut 2009).

RESULTS

Molecular studies

General phylogeny

Sequences of collections labelled as *Lf. clarkeae*, *R. flocktoniae*, and *Lf. subclarkeae* were scattered across four sections in three subgenera within *Lactifluus*: subg. *Lactifluus* (sect. *Lactifluus*), subg. *Gymnocarpi* (sect. *Luteoli* and sect. *Tomentosi*), and an unnamed clade in subg. *Pseudogymnocarpi* (Fig. 2). We exclude the single true *Russula* collection (labelled as *R. flock-*

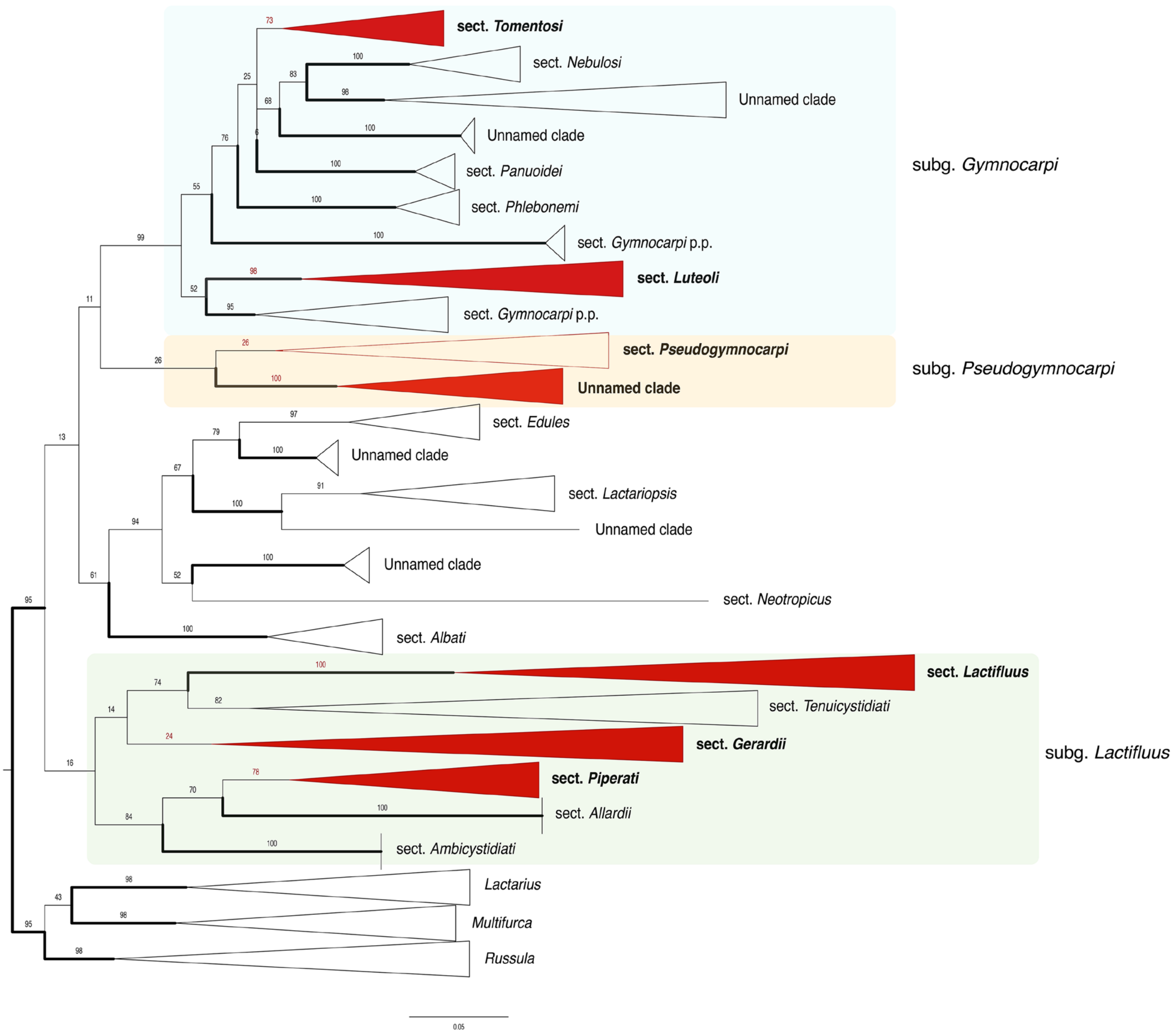

Fig. 2 Maximum Likelihood phylogeny of *Russulaceae*, based on ITS and LSU sequences, showing major subgenera and sections in which collections labelled as *Lf. clarkeae*, *Lf. flocktoniae*, and *Lf. subclarkeae* as discussed in this paper appear (red clades). Subgenera highlighted by a block of colour: *Gymnocarpi* (blue); *Pseudogymnocarpi* (orange); *Lactifluus* (green). Bolded lines ML support > 70 %.

Fig. 3 Maximum Likelihood tree based on ITS and LSU sequences for subg. *Gymnocarpi* (sects. *Tomentosi* and *Luteoli* highlighted blue boxes). Bold lines indicate ML support > 70 %. **Bold** text sequences generated this study. Red text: Australian specimens or sequences, blue text: New Zealand specimens, green text: New Caledonia specimens or sequences.

toniae), those falling in sect. *Piperati* (Crous et al. 2020) with basidiocarps on the white to very pale buff end of the spectrum for '*Lf. subclarkeae* sensu lato', and four provisional species in sect. *Gerardii* from any further discussion in this paper. Nine unnamed species that fit within the broad characteristics of the *Lactifluus clarkeae* complex, are provisionally indicated in sect. *Tomentosi* (6), subg. *Pseudogymnocarpi* (1), and sect. *Lactifluus* (2), suggesting further cryptic diversity to uncover in Australasia.

Unfortunately, we were unable to obtain usable sequences from holotypes or lectotypes for any of the published taxa. The name *Lactifluus subclarkeae* could not be applied to any of the material sampled, as none of the material labelled as such had a lamprotrichoderm pileipellis (De Crop et al. 2017) nor matched the type description, and nor did any of the material sequenced fall in sect. *Lactariopsis*.

Subgenus Gymnocarpi

Greatest diversity was shown in sect. *Tomentosi*, with six well-supported clades representing *Lf. clarkeae* s.str., *Lf. flocktoniae* s.str., *Lf. aurantioruber* comb. & stat. nov., *Lf. pseudoflocktoniae* sp. nov., *Lf. albens* sp. nov., and *Lf. psammophilus* sp. nov., three undescribed species from New Caledonia (*Lf.* sp. 1 New Caledonia, *Lf.* sp. 5 NCal, *Lf.* sp. 6 NCal), and three unnamed Australian species (*Lf.* sp. 2 New South Wales, *Lf.* sp. 3 Queensland FrIsland, *Lf.* sp. 4 QLD) (Fig. 3). Many of the undescribed taxa are currently only represented by a single collection or environmental sequence, however, where possible we have provided a simplified macro-morphological description, collection information, associated plants, and a photo. This section is sister to South and Central American sect. *Nebulosi* and sect. *Panuoidei* and some unassigned taxa including *Lf. brunellus* from Guyana (De Crop et al. 2017, Delgat et al. 2020). While each species in sect. *Tomentosi* is well-supported as distinct, relationships between species are generally not that strongly supported. In both *Lf. clarkeae* s.str. and *Lf. albens* there is more intraspecific molecular variation than typical (some branches with bootstrap support). However, we were unable to find any consistent morphological characters to support distinguishing these clades as distinct taxa at this time (see descriptions for further notes).

A single Australasian species, *Lf. russulisporus*, is currently known from sect. *Luteoli* (Dierickx et al. 2019). Previously known from two collections from Fraser Island and near Brisbane, Queensland, the known range of this species is extended considerably (1 000 km) with a third collection from central New South

Fig. 4 Maximum Likelihood tree based on ITS and LSU sequences for sect. *Pseudogymnocarpi* and related taxa (highlighted orange box). Bold lines indicate ML support > 70 %. Red text: Australian specimens.

Wales, near Lithgow. Our analyses support placement of this species sister to *Lf. caliendrifer* from Thailand, in sect. *Luteoli* with *Lf. luteolus* from North America, *Lf. brunneoviolascens* from Southern Europe, *Lf. rubrobrunnescens* from Indonesia, *Lf. longivelutinus* from China, and *Lf. nonpiscis* from Africa.

Subgenus Pseudogymnocarpi

A set of three Australian sequences (currently labelled as *Lf.* sp. 7), fall within a strongly supported clade with *Lf. armeniacus* from Thailand, *Lf. volemoides* from Tanzania, and singleton sequences from Vietnam and the USA, forming a potential new section within subg. *Pseudogymnocarpi* (Fig. 4). Further

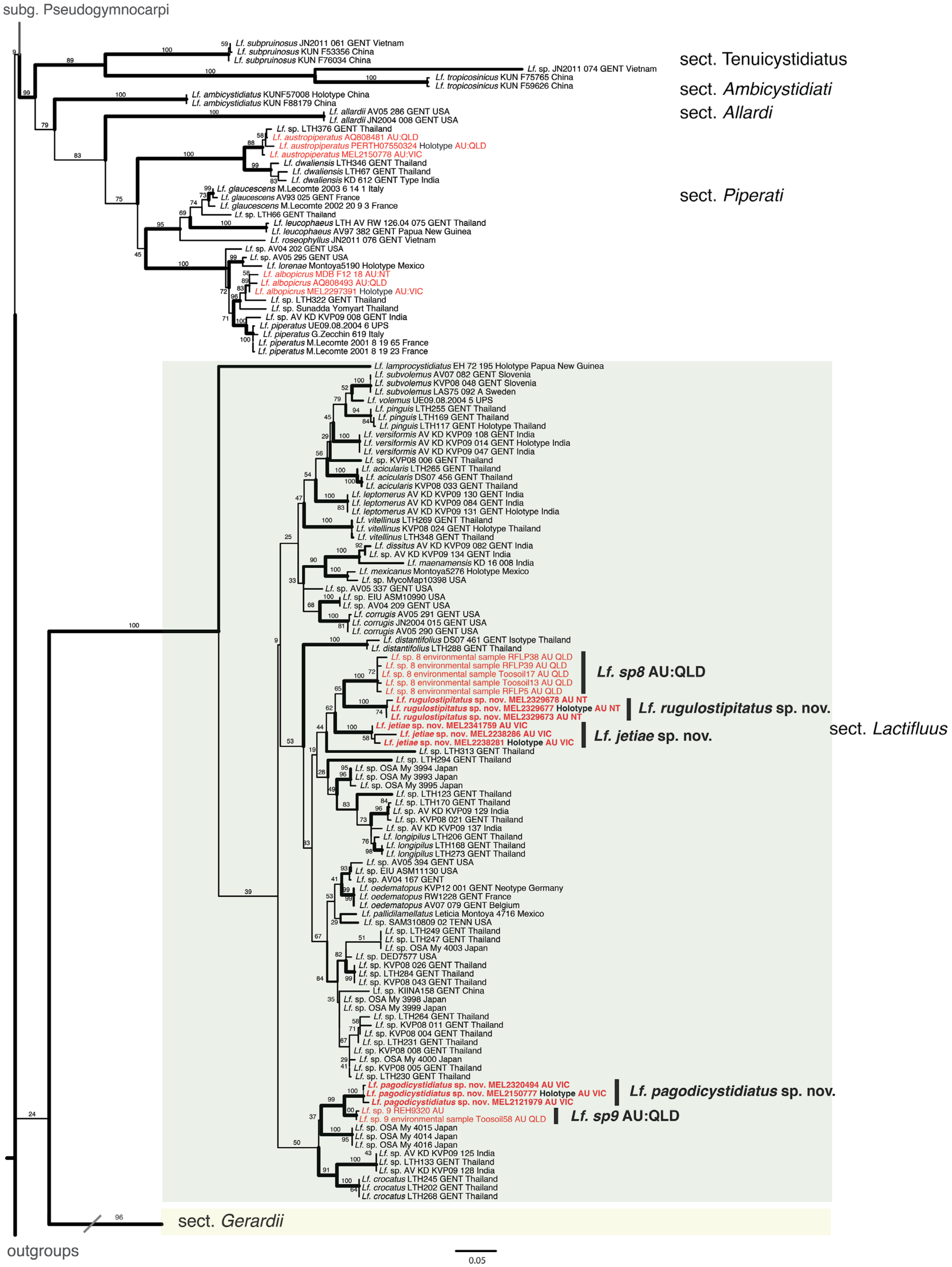

Fig. 5 Maximum Likelihood tree based on ITS and LSU sequences for subg. *Lactifluus* (sect. *Lactifluus* and sect. *Gerardii* (highlighted green box)). Bold lines indicate ML > 70 %. Red text: Australian specimens, blue text: New Zealand specimens, green text: New Caledonia specimens or sequences.

material is required to better determine species boundaries and support for this clade of mixed geographic origin.

Subgenus Lactifluus

Four clades representing sequences of Australian collections are well supported in sect. *Lactifluus* and are recognised as distinct species (Fig. 5). *Lactifluus jetiae* sp. nov. is genetically and morphologically distinct at the species level, although there are some minor variations in morphology and ITS sequences that may be explained by the geographical distance between collection sites. *Lactifluus rugulostipitatus* sp. nov. differs from *Lf.* sp. 8 (environmental QLD) by 34 bp, indicated by strong support values; they form a poorly supported subclade with a sequence from Thailand (LTH313). *Lactifluus rugulostipitatus* is morphologically different from the other species in this group by the more delicate appearance of the basidiomes and the longitudinally wrinkled stipe. These two new species are part of a larger clade including a mixture of taxa from Mexico, USA, Europe, Japan, Thailand, and Papua New Guinea; *Lf. oematodopus*, *Lf. pallidilamellatus*, *Lf. longipilus*, *Lf. lamprocystidiatus*, and *Lf. distantifolius* fall in this clade (Montoya & Bandala 1996, 2005, Van de Putte et al. 2010, 2016).

The fourth new Australasian species in sect. *Lactifluus*, *Lf. pagodicystidiatus* sp. nov., is sister to *Lf.* sp. 9, in a sub-clade with unnamed species from Japan and Thailand/India, and *Lf. crocatus* from Thailand.

Taxonomy

Differences between species are subtle and species delimitation requires close analysis of a combination of microscopic characters (Van de Putte et al. 2012).

KEY TO AUSTRALASIAN SPECIES OF LACTIFLUUS

1. Basidiomes pleurotoid, white to pale cream, small not exceeding 30 mm diam . . . . *Lf. genevievae*
1. Basidiomes agaricoid, pileus and stipe pale cream to pale buff, varying tones of orange, dark or pale brown 2
2. Pileus and stipe dark brown, context faintly and slowly turning pink when exposed 3
2. Pileus and stipe pale cream to pale buff, yellowish brown, yellow, or varying tones of orange; context unchanging or slowly pale brown rusty ochre, or staining bright vinaceous pink 4
3. Basidiospore ornamentation an almost complete reticulum composed of more or less acute, triangular ridges, 1–1.5 μm high . . . . *Lf. wirrabara* s.lat.
3. Basidiospore ornamentation a dense reticulum of low ridges, not higher than 1 μm . . . . *Lf. sepiaceus*
4. Injured context staining bright vinaceous pink *Lf. leonardii*
4. Injured context unchanging or staining pale brown or rusty ochre 5
5. Basidiomes pale cream to pale buff or pale yellow, when young with yellowish or pale orange tinges; taste mild or very acrid to peppery 6
5. Basidiomes varying tones of orange, reddish orange to brownish orange; taste mild or acrid to peppery 9
6. Fishy odour to basidiomes, and pileus, stipe and lamellae staining brown; lampropalisade pellis 7
6. Basidiomes lacking fishy odour, and either not staining or lamellae bruising slightly darker; hypoepithelial pellis . . . 8
7. Basidiomes large, pileus 55–120 mm diam; latex drying rusty-ochre; spores 8–11 × 5–9 μm, ornamentation mostly isolated verrucae with short lines to 1 μm high; WA, VIC . . . . *Lf. albens* sp. nov.
7. Basidiomes rather small, pileus to 40 mm diam; latex drying brown; spores 7–8.7 × 5.7–7 μm, ornamentation mostly isolated verrucae to 1.3 μm high; QLD, NSW . . . . *Lf. russulisporus*
8. Basidiomes 48–85(–120) mm diam, no bruising; spores small 6–8 × 5–6.5 μm, verrucae to 1 μm linked by short lines in partial retic; VIC, TAS, NT, QLD . . *Lf. albopicrus*
8. Basidiomes 30–50 mm diam, lamellae very pale orange bruising slightly darker; spores 7.5–9.5 × 6.5–8.5 μm, very fine verrucae < 0.5 μm high linked by fine lines in partial retic; NE NSW, QLD, NT . . . . *Lf. austropiperatus*
9. Odour mild to slightly fishy fresh, strongly fishy in dry basidiomes; lamellae cream to orange cream or pale fawn; latex typically scant; cheilocystidia common 10
9. Odour mild or spermatic when fresh, NOT fishy when dry; lamellae cream; latex scant or abundant; cheilocystidia rare 12
10. Pileus bright reddish orange or dark reddish brown, up to 75 mm diam; lamellae discolouring orange brown or brown; spore ornamentation robust retic to 2 μm high . . . . *Lf. jetiae* sp. nov. or *Lf.* sp. 9
10. Pileus dull pale orange-ochre or buff, up to 55 mm diam; lamellae discolouring pale brown; spore ornamentation robust retic to 1 μm high 11
11. Pileus dull pale orange ochre with dark yellow undertone, context golden orange-cream; stipe longitudinally wrinkled; basidia mostly 2-spored (some 3, 4); pleurolamprocystidia scarce, mucronate, constricted but not pagodaform; currently known only from NT . . . *Lf. rugulostipitatus* sp. nov.
11. Pileus orange-buff with red undertone, fading to dull orange buff; context cream-coloured; stipe NOT longitudinally wrinkled; basidia mostly 4-spored; pleurolamprocystidia common, distinctly pagodaform; currently known from VIC. . . . . *Lf. pagodicystidiatus* sp. nov.
12. Pileus bright orange; latex typically scant, rarely abundant; taste quickly acrid or peppery 13
12. Pileus brownish orange, sordid orange to orange-red drying greyish orange; latex typically abundant, taste mild or faintly acrid 15
13. Lamellae white to cream, bruising brown; pileus strongly wrinkling concentrically . . . . . *Lf. psammophilus* sp. nov.
13. Lamellae white to cream, not discolouring or staining; pileus not wrinkling concentrically or barely so 14
14. Pileus 30–63 mm diam; spores 9.5–12 × 7.5–9, fine warts part retic 0.2–0.5 μm high; associated with eucalypts (WA, VIC, NSW) . . . . *Lf. flocktoniae* s.str.
14. Pileus 50–103 mm diam; spores 8.5–9.5 × 6.5–7.5, low partial retic warts to 0.8; *Nothofagus* associated (TAS), or *Eucalyptus* associated (VIC) . . . . *Lf. pseudoflocktoniae* sp. nov.
14. . . . . *Lf.* sp. 3 or *Lf.* sp. 4
15. Pileus and stipe context pale orange-yellow; lamellae creamy white (AU) with pinkish tinge (NZ); stipe brownish orange, sordid orange with greyish bloom when dry but same colour throughout; spores 6–11 × 5–9, verrucae to 0.8 μm, linked by low partial retic; terminal elements of pileipellis up to 100 μm long; either *Nothofagus* associated (NZ) or sometimes *Eucalyptus* associated (AU) . . . . *Lf. aurantioruber*
15. Pileus and stipe context cream; lamellae white to cream; stipe pallid orange with greyish bloom when dry but with white patch at very base; spores smaller, 5–9 × 5–8 μm, verrucae up to 1 μm linked by low partial retic; terminal elements of pileipellis up to 306 μm long; *Leptospermum* associated (NZ), eucalypt associated (AU). . *Lf clarkeae* s.str.
15. . . . . *Lf.* sp. 2 or *Lf.* sp. 7

Subgenus *Gymnocarpi*

The discolouration of latex and context to brown when exposed to air, plus the absence of true pleurocystidia and a lampropalisade pileipellis, define subg. *Gymnocarpi* (De Crop et al. 2017).

Section *Tomentosi*

All species described here have white to pale cream lamellae that bruise or stain pale brown in patches or spotting.

Lactifluus albens T. Lebel, J. Douch & L. Vaughan, *sp. nov*. — MycoBank MB 837606; Fig. 6a, 7

Etymology. Meaning 'bleached', so named for the pale cream to buff colouration of basidiomes, which is unique to this clade among other Australian clades of *Lactifluus* subg. *Gymnocarpi* sect. *Tomentosi*, which come in variations of orange.

Typus. Australia, Western Australia, Dwellingup, Inglehope Forest Block Arboretum, mixed *Eucalyptus* spp., 31 May 2003, *K. Syme 1239/03* (holotype MEL 2231695).

Diagnosis — Differs from other species in sect. *Tomentosi* by the very pale cream to buff with hints of brown and yellow basidiomes that stain rusty-ochre, ventricose-rostrate or strangulated pleurocystidia and cheilocystidia, relatively moderate in length cylindrical pileal terminal elements and caulocystidia (to 117 and 153 µm, respectively), and taste very acrid or hot.

Pileus 55–120 mm diam, convex when immature, plane when mature, depressed at all stages, generally very pale cream to buff with hints of brown and yellow, in immature material may be pale yellow overall, drying pale yellow, staining rusty-ochre in some patches, margin entire, plane to partially upturned, becoming plicate, and subrimose when mature, downturned to slightly inrolled when immature, surface flocculent and finely velutinous to subtomentose, particularly towards centre; context cream, slightly moist, contiguous with stipe, staining rusty-ochre, up to 24 mm deep. *Lamellae* adnate or occasionally subdecurrent, close to subdistant (11 L + l/cm), thick, up to 8 mm deep, pale buff with rusty brown spotting mainly near edge of pileus when mature, readily staining brown when disturbed, splitting with age, forked mostly near stipe and margin, lamellulae present and intermixed (l = 20/half pileus). *Stipe* up to 55 × 25 mm, terete, almost equal but tapering slightly towards base, concolorous with pileus, readily staining brown when disturbed, surface flocculent and finely velutinous to subtomentose; context solid, chambered, concolorous with pileus context. *Latex* white to watery. *Odour* mild to acrid and fishy, mild in dried collections. *Taste* very acrid or hot. *Chemical tests*: $FeSO_4$ dull lead green.

Basidiospores 8–11 × 5–9 µm ($\bar{x}$ = 8.92 ± 0.70 × 7.48 ± 0.82, *n* = 25), globose to elongate (Q = 1.00–1.80 ($\bar{x}$ = 1.21 ±

Fig. 6 Subgenus *Gymnocarpi* sect. *Tomentosi*. Basidiomata of a. *Lf. albens* sp. nov.; b. *Lf. aurantioruber* NZ; c. *Lf. aurantioruber* AU. — Scale bars: 10 mm. — Photos: a by K. Syme; b by R.E. Halling; c by G. Lay.

0.17, n = 25)), walls amyloid, ornamentation amyloid and verrucose with some slight reticulation, verrucae rising up to 1 µm. *Basidia* 45–85 × 8–13 µm ($\bar{x}$ = 66.00 ± 9.10 × 10.58 ± 1.01, n = 20), 2–5 µm wide at base ($\bar{x}$ = 4.05 ± 0.83, n = 20), clavate, mostly 4-spored but occasionally 2- or 3-spored; sterigmata 3–9 × 2–4 µm ($\bar{x}$ = 6.70 ± 1.52 × 2.66 ± 0.57, n = 22); basidioles 33–71 × 6–11 µm ($\bar{x}$ = 50.40 ± 10.36 × 8.96 ± 1.43, n = 25), 3–6 µm wide at base ($\bar{x}$ = 3.92 ± 0.81, n = 25), clavate. *Hymenophoral trama* comprising interwoven hyphae 2–5 µm diam ($\bar{x}$ = 3.60 ± 1.14, n = 5), sinuous laticiferous hyphae 6–8 µm diam ($\bar{x}$ = 6.60 ± 0.89, n = 5), and sphaerocytes 22–53 × 17–40 µm ($\bar{x}$ = 32.92 ± 8.78 × 25.08 ± 7.01, n = 25); *subhymenium* composed of hyphae and round or angular polygonal cells 8–48 × 7–42 µm ($\bar{x}$ = 22.76 ± 11.36 × 15.80 ± 8.64, n = 25), sinuate laticiferous hyphae present and occasionally to frequently extending into hymenium as cystidia. *Pleuromacrocystidia* 45–86 × 2–11 µm ($\bar{x}$ = 69.20 ± 14.79 × 7.60 ± 1.57, n = 20), 1–2 µm wide at apex ($\bar{x}$ = 1.45 ± 0.51, n = 20), ventricose-rostrate, sometimes apically strangulated, slightly emergent above hymenium, thin-walled, hyaline. *Pleurolamprocystidia* and *pseudocystidia* absent. *Cheilomacrocystidia* up to 85 × 9 µm, 1 µm wide at apex,

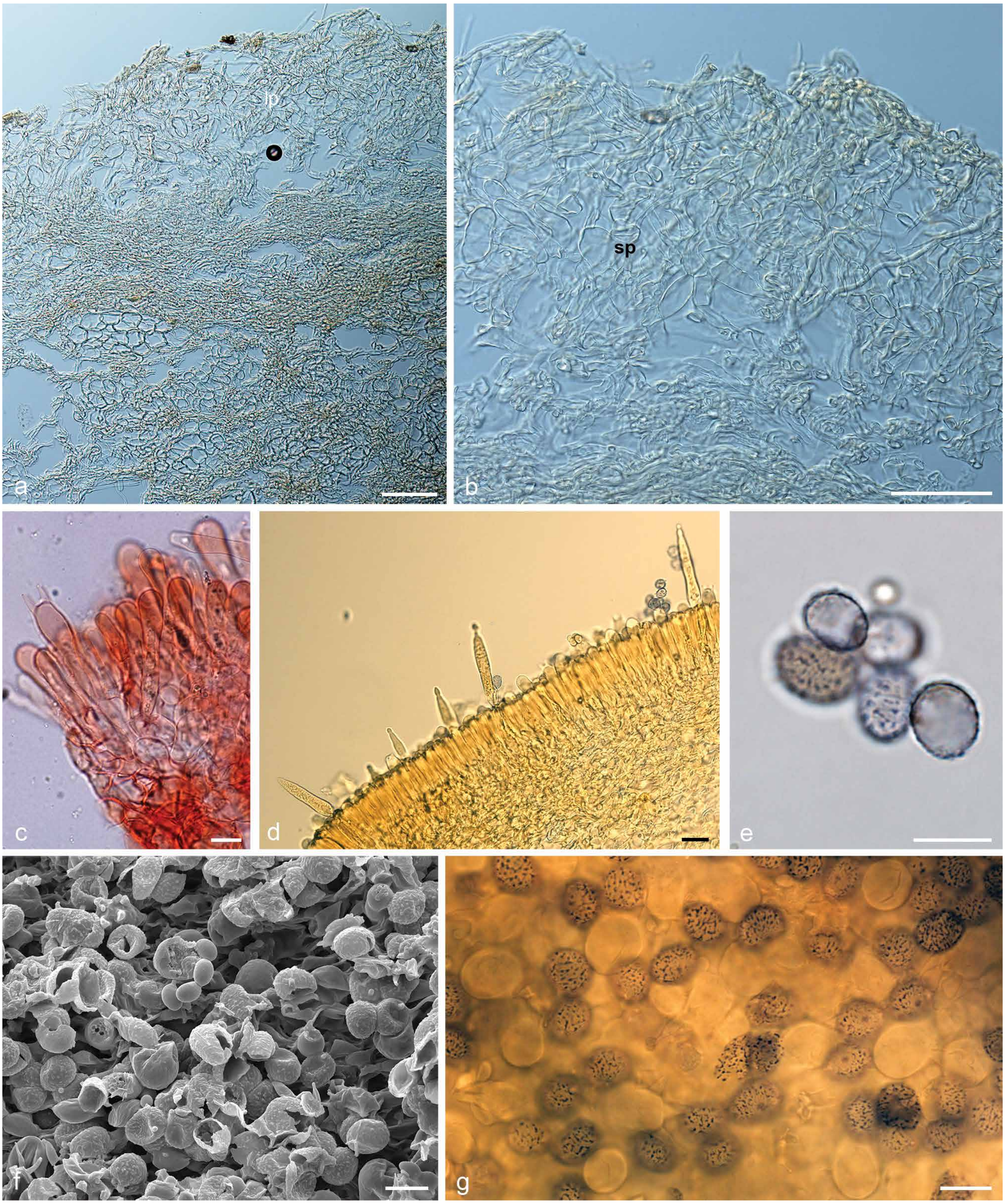

Fig. 7 *Lactifluus albens* sp. nov. a. Lampropalisade pileipellis, subpellis (sp) and terminal elements (te), heteromerous context (hc) (MEL2231695); b. pileipellis terminal elements and subpellis (sp); c. basidia and subhymenium; d. hymenial trama and pleurocystidia; e. basidiospores; f. SEM of basidiospores; g. basidiospores. — Scale bars: a–b = 50 µm; c–g = 10 µm.

ventricose-rostrate, sometimes mucronate, and strangulated, emergent above hymenium, thin-walled, hyaline. *Pileipellis* a lampropalisade; subpellis consisting of several layers of round or angular polygonal cells, 12–39 × 10–26 µm ($\bar{x}$ = 25.52 ± 7.30 × 17.44 ± 4.13, *n* = 25); terminal elements 33–117 × 3–6 µm ($\bar{x}$ = 58.00 ± 32.55 × 4.00 ± 0.96, *n* = 10), 2–5 µm wide at apex ($\bar{x}$ = 3.00 ± 1.05, *n* = 10), narrow-cylindrical, tapering towards apex, apex obtuse, septate, outline slightly sinuate, some appearing thick-walled; *pileus trama* similar to hymenophoral trama, heteromerous. *Stipitipellis* a lampropalisade; subpellis consisting of several layers of round or angular polygonal cells, 15–47 × 7–30 µm ($\bar{x}$ = 25.52 ± 8.87 × 17.08 ± 5.77, *n* = 25); terminal elements 22–158 × 3–10 µm ($\bar{x}$ = 67.12 ± 34.95 × 4.64 ± 1.89, *n* = 25), similar to pileal terminal elements with narrow-cylindrical shape; *stipe trama* similar to hymenophoral trama and pileus trama, heteromerous.

Distribution & Habitat — South-west Western Australia and eastern Victoria associated with *Eucalyptus* spp. in open woodland with varied understory of *Banksia spinulosa*, *B. nutens*, *Platylobium formosa*, *Hovea heterophylla*, *Pterydium esculenta*, *Lycopodium* spp., *Correa*, *Persoonia*, *Gahnia*, and *Adenanthos cuneatus*. Substrate is consistently described as loamy soil. May be gregarious or a singleton. Basidiomes emerge May–June.

Additional specimens examined. Australia, Western Australia, Mt Merivale, 20 km east of Esperance, 15 June 1996, *B. Archer 358* MEL 2036515; Manjimup, Dickson Rd, JF245, 11 July 2011, *R. Robinson*, *P. Leonard WA245* BRI. Victoria, Bunyip State Park, Tonimbuk, 90 m a.s.l., wet sclerophyll forest, 14 June 2004, *S. Miller 118-04* MEL 2322071; Cape Conran, about 20 km E of Marlo, 16 m a.s.l., 2 June 2006, *R.E. Halling & J.M. Trappe REH 8853* MEL 2297067; Cann River, 8 km south along Tamboon Rd, 25 May 2002, *J.E. Tonkin 984* MEL 2238278.

Notes — These collections were initially examined because some were labelled as *Lf. subclarkeae*. *Lactifluus albens* is unique in sect. *Tomentosi* in having very pale basidiomes, lacking any tinge of orange pigmentation. However, the subtomentose to flocculent pileus, pale lamellae that bruise or stain brown in patches, lampropalisade pileipellis and fine reticulate spores are all typical features of the section. This species could be confused in the field with the recently described *Lf. albopicri* from sect. *Piperati* (Crous et al. 2020), which also has pale cream basidiomes and peppery taste, but lacks a fishy odour, and thus far has a similar distribution. *Lactifluus russulisporus* also has pale creamy-yellow basidiomes but has a strong fishy odour; but is currently not known so far south or west.

Our analyses show two subclades that are geographically distinct, clade I is Western Australian and clade II is Victorian. The three WA collections tend to have larger basidiomes, in the range 75–120 mm diam, whereas the Victorian material is in the range 55–80 mm diam. Otherwise no other macro- or micro- differences were observed. Further gene regions and investigation is required before determining these as two distinct taxa.

Lactifluus aurantioruber (McNabb) J.A. Cooper, *comb. & stat. nov.* — MycoBank MB 837624; Fig. 6b–c, 8, 9

Basionym. Lactarius clarkeae var. *aurantioruber* McNabb (1971) The Russulaceae of New Zealand. 1. *Lactarius* DC ex S.F. Gray. New Zealand J. Bot. 9: 60. (MB 348303)

Etymology. For the colour of the basidiomes.

Typus. New Zealand, Tongariro National Park, Desert Road, Oturere Stream, Taupo, associated with *Nothofagus solandri*, 8 Apr. 1965, *R.F.R. McNabb* PDD 26381.

Diagnosis — This species is very similar to *Lf. clarkeae* but can be recognised by the more orange-red, pruinose to subtomentose pileus, sometimes pinkish tinted lamellae, and pallid orange-yellow flesh, and in New Zealand the strict association with *Nothofagus*.

Pileus up to 100 mm diam, centrally depressed at maturity, often finely rugulose near margins, pruinose to subtomentose under lens, variable in colour from brownish orange, sordid orange, or orange-red under wet conditions, paler when dry and then greyish orange or with a white to greyish bloom; context pallid orange-yellow, unchanging, firm. *Lamellae* adnate to subdecurrent, subdistant (15–17 L + l/cm), thick, simple or occasionally forked near stipe, to 8 mm deep, creamy white to pallid cream in Australian material and with pink tints in some New Zealand material, often discoloured with brownish spots where latex has dried; lamellulae present in 2–3 unequal series (l = 48/half pileus). *Stipe* up to 55 × 30 mm, ± equal or tapering basally, solid, longitudinally rugose to smooth, finely pruinose to subtomentose under lens, ± concolorous with pileus or slightly paler; flesh pallid orange-yellow, unchanging. *Latex* white, viscid, unchanging on immediate exposure to air, drying brown, known from lamellae and stipe-lamellae junction, not always observed. *Odour* not distinctive, mild in dried specimens. *Taste* lamellae mild to faintly acrid, context mild.

Basidiospores 6–11 × 5–9 µm ($\bar{x}$ = 8.34 ± 1.26 × 6.94 ± 1.08, *n* = 45), globose to ellipsoid (Q = 1.00–1.50 ($\bar{x}$ = 1.21 ± 0.14, *n* = 45)), walls amyloid, ornamentation verrucose with very slight reticulation, verrucae rising up to 1 µm. *Basidia* 38–74 × 6–14 µm ($\bar{x}$ = 56.31 ± 9.84 × 9.29 ± 1.93, *n* = 35), 1–7 µm wide at base ($\bar{x}$ = 3.37 ± 1.19, *n* = 35), clavate to almost cylindrical, mostly 4-spored but occasionally 1-, 2-, or 3-spored; sterigmata 4–18 × 1–4 µm ($\bar{x}$ = 7.74 ± 3.27 × 2.14 ± 0.69, *n* = 35); basidioles 36–73 × 5–10 µm ($\bar{x}$ = 53.46 ± 8.96 × 7.94 ± 1.43, *n* = 35), 2–5 µm wide at base ($\bar{x}$ = 3.49 ± 0.89, *n* = 35). *Hymenophoral trama* heteromerous in both proximal and distal halves of lamellae, comprising mostly interwoven, occasionally parallel hyphae 2–4 µm diam ($\bar{x}$ = 3.14 ± 0.90, *n* = 7), sinuous laticiferous hyphae 5–9 µm diam ($\bar{x}$ = 5.86 ± 1.46, *n* = 7), and sphaerocytes 14–77 × 14–44 µm ($\bar{x}$ = 34.40 ± 12.66 × 25.47 ± 7.67, *n* = 30); *subhymenium* composed of hyphae and round or angular polygonal cells 9–32 × 6–31 µm ($\bar{x}$ = 19.57 ± 6.50 × 12.80 ± 5.16, *n* = 30), sinuate laticiferous hyphae present and occasionally extending into hymenium as cystidia. *Pleurocystidia* and *cheilocystidia* not observed. *Pileipellis* a lampropalisade of thick-walled glassy cystidia forming the trichoderm; subpellis consisting of several layers of round or angular polygonal cells, 10–43 × 7–25 µm ($\bar{x}$ = 19.00 ± 6.18 × 12.57 ± 3.87, *n* = 35); terminal elements 24–104 × 2–5 µm ($\bar{x}$ = 54.77 ± 6.50 × 3.77 ± 1.04, *n* = 30), 1–4 µm wide at apex ($\bar{x}$ = 1.90 ± 0.76, *n* = 30), narrow and cylindrical, tapering towards apex, apex round, septate, outline slightly sinuate; *pileus trama* similar to hymenophoral trama, heteromerous. *Stipitipellis* a lampropalisade; subpellis consisting of several layers of round or angular polygonal cells, 7–40 × 5–33 µm; terminal elements 28–153 × 1–8 µm ($\bar{x}$ = 62.76 ± 31.59 × 3.64 ± 1.41, *n* = 25), similar to pileil terminal elements with narrow and cylindrical shape; *stipe trama* similar to hymenophoral trama and pileus trama, heteromerous.

Distribution & Habitat — Gregarious under *Nothofagus* in New Zealand. Australian collections gregarious or singletons have been found in association with *Nothofagus* or in wet *Eucalyptus* forest, sometimes emerging through leaf litter. Basidiomes emerge January–August.

Additional specimens examined. Australia, New South Wales, Tallaganda State Forest, small road off Captains Flat-Majors Creek Rd near Parkers Gap, 17 Apr. 1982, *T.W. May & K.E. Geering TWM 437* MEL 2036360. Victoria, Gembrook, Bunyip State Forest, Mortimer Nature Trail, 100 m south of Gembrook-Tonimbuk Road, 31 Mar. 2002, *J.E. Tonkin 912* MEL 2238211; Cement Creek, Acheron Way, between St. Fillans and Warburton, 17 Mar. 1984, *T.W. May*, *B.A. Fuhrer & C. Shankley TWM 504* MEL 2036369. Tasmania, Mt Field National Park, walk to Lady Barron Falls, 8 Apr. 1987, *T.W. May 87239* MEL 2036366; Derwent Bridge to Queenstown, Franklin Falls picnic area and nature trail, 1 Jan. 2012, *T. Lebel 2243* MEL 2362076; Mount Donaldson track, 3 May 2012, *T. Lebel*, *G.M. Lay*, *P.S. Catcheside & D.E.A Catcheside TL*

2459 MEL 2359409; Woodvine Nature Reserve, 20 June 2013, *G.M. Gates & D.A. Ratkowsky GMG 3027* MEL 2381530; Rivulet Track, 16 Feb. 1996, *A.V. Ratkowsky 0138* MEL 2257827. – New Zealand, Oturere stream, Desert Road, Tongariro National Park, under *Nothofagus solandri*, 8 Apr. 1965, *R.F.R. McNabb* PDD 26381, holotype; Waitonga Falls Track, Manawatu-Wanganui, under *Nothofagus cliffortioides*, 4 Apr. 2005, *P.K. Buchanan* PDD 80786; Wellington, Rimutaka Forest Park, under *Nothofagus fusca*, 14 May 2009, *P. Leonard 25509* PDD 95561; Coromandel, under *Nothofagus truncata*, 14 June 1984, *P.R. Johnston* PDD 45301; Westland, under *Nothofagus menziesii*, 2 Mar. 2012, *J.A. Cooper* PDD 96536; Taupo, under *Nothofagus fusca*, 6 Apr. 2005, *L. Fischer* PDD 82495; Taupo, 11 May 1996, *G.M. Taylor* PDD 84503; Nelson, under *Nothofagus truncata*, 6 Jan. 1970, *B.J. Denton* PDD 31183 (paratype); Nelson, 1 May 1971, *R.F.R. McNabb* PDD 31198, paratype; Nelson, Karamea, Oparara Arch Track, 6 Feb. 2011, *P. Leonard 380211* PDD 101410; Nelson, 1 May 2009, *P. Leonard* PDD 99297; Ngahere, Kopara, West Coast, under *Nothofagus*, 25 Apr. 2005, *E. Horak* PDD 82817; Canterbury, Glentui Bush, under *Nothofagus solandrii*, 8 Feb. 2014, *J.A. Cooper* PDD 105466; Southland, Te Anau, under *Nothofagus*, 2 May 2018,

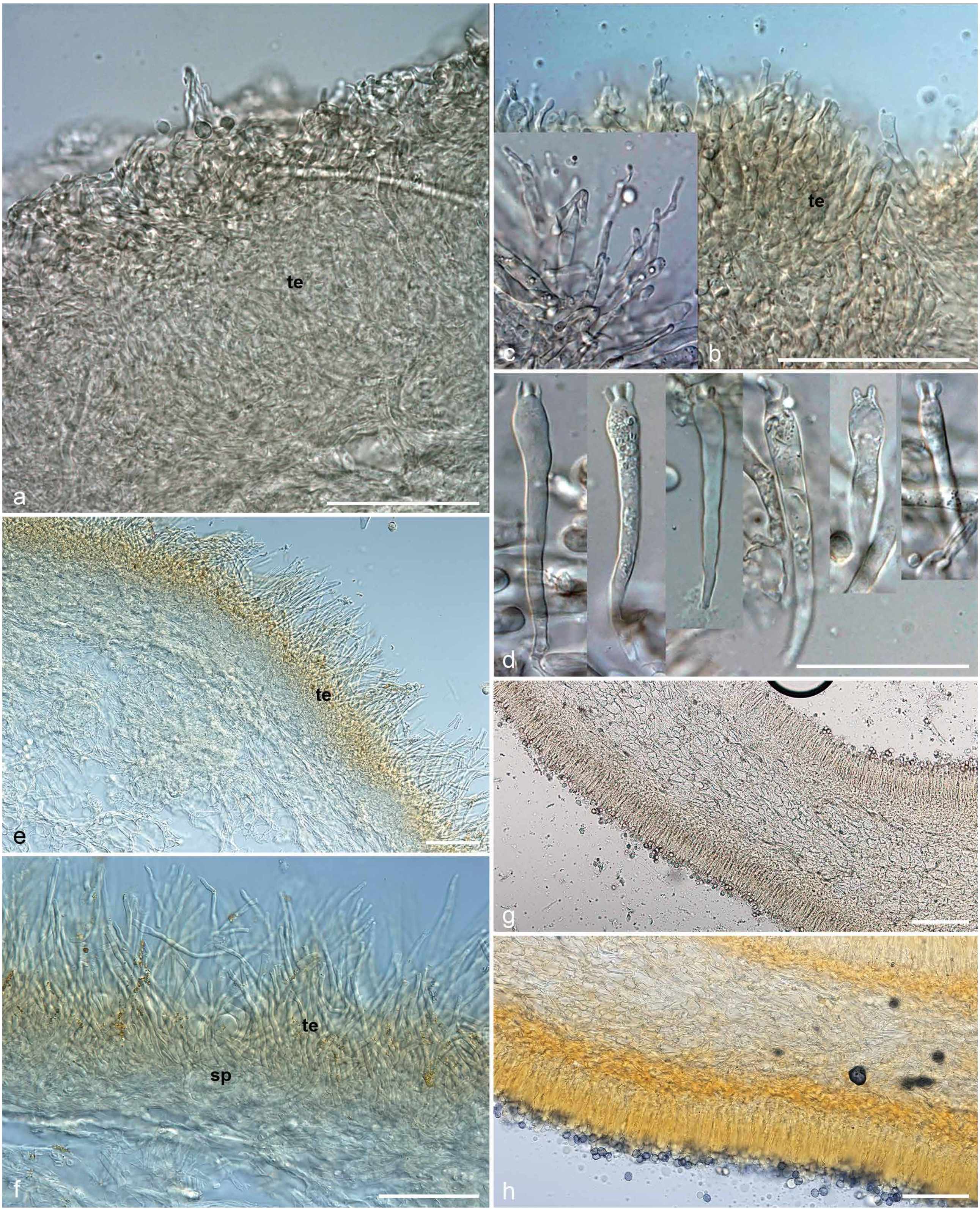

Fig. 8 *Lactifluus aurantioruber*. a. Lampropalisade pileipellis, with terminal elements (te) and context (NZ); b–c. pileipellis terminal elements (te) (NZ); d. basidia (NZ); e. lampropalisade pileipellis with terminal elements (te), and context (AU); f. pileipellis terminal elements (te) and subpellis (sp) (AU); g–h. hymenium, subhymenium and heteromerous trama (AU). — Scale bars: a = 125 µm; b–d = 75 µm; e–h = 50 µm.

N. Siegel PDD 112414; Buller, Punakaiki, Inland Trail, under *N. menziesii*, 8 May 2006, *I. Dickie* PDD 88985; Buller, 4 Jan. 1970, *R.F.R. McNabb* PDD 31194, paratype; Buller, Maruia, under *Nothofagus fusca*, 23 Mar. l966, *R.F.R. McNabb* PDD 26378, paratype; Buller, 23 Mar. 1966, *R.F.R. McNabb* PDD 26380, paratype; Buller, 14 Apr. 1968, *R.F.R. McNabb* PDD 26518, paratype; Buller, 13 Apr. 1968, *R.F.R. McNabb* PDD 26519, paratype; Buller, 14 Mar. 1968, *R.F.R. McNabb* PDD 26529; Buller, 11 Apr. 2005, *E. Horak & A. Horak* PDD 82758; Buller, 1 Feb. 1970, *Mulcock Family* PDD 31188, paratype; Buller, 1 Feb. 1970, *Mulcock Family* PDD 31189, paratype; Buller, St. Arnaud, next to Lake Rotoiti, 8 May 2014, *T. Lebel 2612* PDD 105131; Fiordland, under *Nothofagus menziesii*, 13 Feb. 1960, *R.F.R. McNabb* PDD 26379, paratype; Fiordland, 2 Mar. 1992, *H. Neda* PDD 62036; Fiordland, 22 Feb. 1990, *P.K.C. Austwick* PDD 76341; Fiordland, 29 Jan. 2011, *P. Leonard* PDD 101038; Fiordland, 15 Feb. 2009, *P. Leonard* PDD 104363.

Notes — McNabb (1971) cited the holotype as PDD 26381, 14 April 1968, Springs Junction, South Island. There are nine collections of this taxon deposited in PDD by McNabb on this date and from the area of Spring's Junction, but none were accessioned as PDD 26381. The notes associated with PDD 26381 indicate it was collected from the Tongariro National Park, North Island 8 April 1965 and we accept this collection as the holotype. All these collections represent the same taxon.

Apart from length of cuticular hairs, *Lf. aurantioruber* is microscopically indistinguishable from *Lf. clarkeae* s.str., and it is often difficult to separate dried specimens of the two taxa. In the field, *Lf. aurantioruber* can be recognised by the more orange, pruinose to subtomentose pileus, sometimes pinkish tinted lamellae, and pallid orange-yellow flesh. In New Zealand this species associates solely with *Nothofagus*. However, in Australia, while *Lf. aurantioruber* has been found in association with *Nothofagus* in Tasmania (MEL 2359409, MEL 2360276) and Victoria (MEL 2036369), it can also be found in association with species of *Eucalyptus* in wetter forests of Victoria (MEL 2238211), Tasmania (MEL 2381530, MEL 2036366), and New South Wales (MEL 2036360). While the Australian collections associated with *Eucalyptus* tend to be more orange than their New Zealand counterparts, our current analyses of ITS sequence data show only a few base pairs difference between the New Zealand and Australian material sequenced thus far.

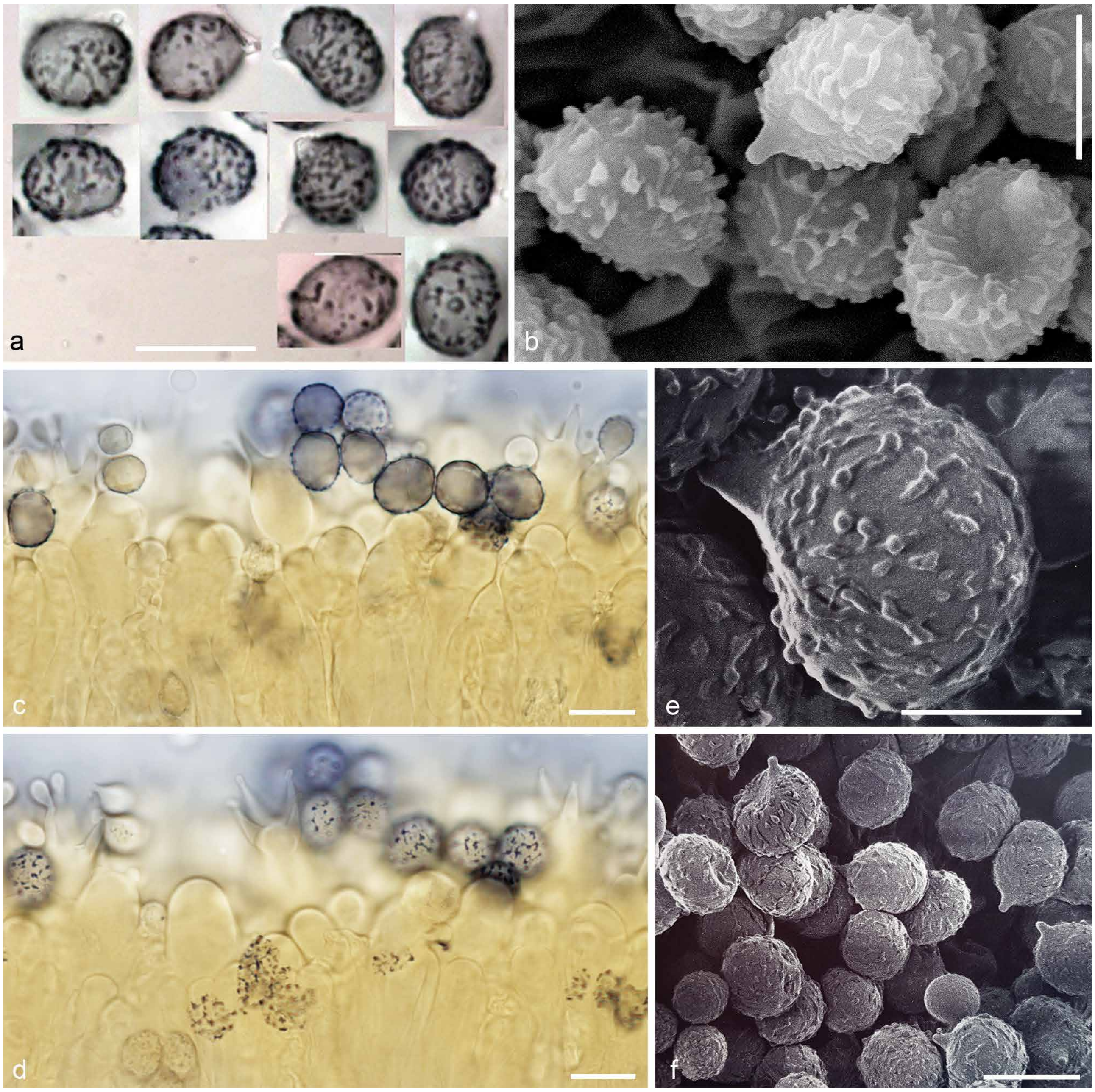

Fig. 9 *Lactifluus aurantioruber*. a. Basidiospores (NZ); b. SEM of basidiospores (NZ); c–d. basidiospores and basidia (AU); e–f. SEM of basidiospores (AU). — Scale bars: a–d, f = 10 μm; e = 5 μm.

Lactifluus clarkeae (Cleland) Verbeken, New combinations in *Lactifluus*. 3. *L.* subgenera *Lactifluus* and *Piperati*. Mycotaxon 120: 448. 2012 — MycoBank MB 564623; Cleland 1934, 1935; McNabb 1971; Grgurinovic 1997; Bougher & Syme 1998; Young & Smith 2000; Fig. 10, 11

Basionym. Lactarius clarkeae Cleland, Trans. Roy. Soc. South Australia 51: 302. 1927. (MB 261046).

Synonym. Lactarius clarkeae Cleland var. *clarkeae*, Trans. Roy. Soc. South Australia 51: 302. 1927. (MB 426689)

Etymology. Named after Miss M. Flockton's niece, Phyllis Clarke, who painted many NSW fungi.

Lectotype. AUSTRALIA, South Australia, Mount Lofty, 16 June 1917, *J.B. Cleland* AD 9801 (ADW 15299) (designated by McNabb 1971. (IF 597788)

Epitype designated here. AUSTRALIA, South Australia, Cleland Conservation Park, Mt Lofty-Cleland Wildlife Park Trail, c. 200 m from summit, 8 July 2001, *J.E. Tonkin*, *T. Lebel & A. Giachini JET 887* MEL 2101947. (MBT 10000641)

Diagnosis — Pileus pale orange to apricot, stipe colourous with pileus but paling towards base, pleurocystidia and cheilocystidia typically strangulated and cylindrical, pileicystidia and caulocystidia cylindrical and highly elongate (over 300 µm), taste mild, *Myrtaceae* associated.

Pileus to 77 mm diam, convex when immature becoming plane with maturity, centrally depressed, pallid orange to greyish orange, with pallid greyish overtones imparted by tomentose surface, more intensely coloured at margin, prone to staining when immature, margin entire or occasionally lobed, undulate, and downturned when immature, smooth to tomentose, hairs often matted or occasionally aggregated into poorly defined squamules, concentrically wrinkled; context cream, contiguous with stipe, immediately stains pale brown in Australian collections, unchanging pileus context in NZ material, 90–120 mm deep at lamellae-stipe junction. *Lamellae* adnate or occasionally subdecurrent, close to subdistant (16–20 L + l/cm), intermediate thickness, up to 6 mm deep, white to cream or cream with brown patches, becoming brown upon bruising or drying, forked mostly near stipe, lamellulae present and intermixed (l = 28/half pileus). *Stipe* to 41 mm long and 20 mm wide at base, 23 mm wide at apex, terete, tapering towards base, approximately concolorous with pileus but increasingly pallid towards base, extreme of base white or tinted light orange, surface velutinate to tomentose, context solid, slightly chambered, unchanging, and concolorous with pileus context. *Latex* white, viscid, unchanging on immediate exposure to air, aging brown, known to exude from lamellae. *Odour* fishy or spermatic, mild in dried collections. *Taste* typically mild.

Basidiospores 5–9 × 5–8 µm (AU $\bar{x}$ = 8.29 ± 1.01 × 6.32 ± 0.65, *n* = 40; NZ $\bar{x}$ = 9.11 ± 0.62 × 6.75 ± 0.6, *n* = 40), globose to ellipsoid (Q = 1.00–1.50 ($\bar{x}$ = 1.21 ± 0.16, *n* = 40)), walls amyloid, ornamentation verrucose with slight reticulation, verrucae up to 1 µm. *Basidia* 31–67 × 8–13 µm ($\bar{x}$ = 46.79 ± 9.08 × 9.59 ±

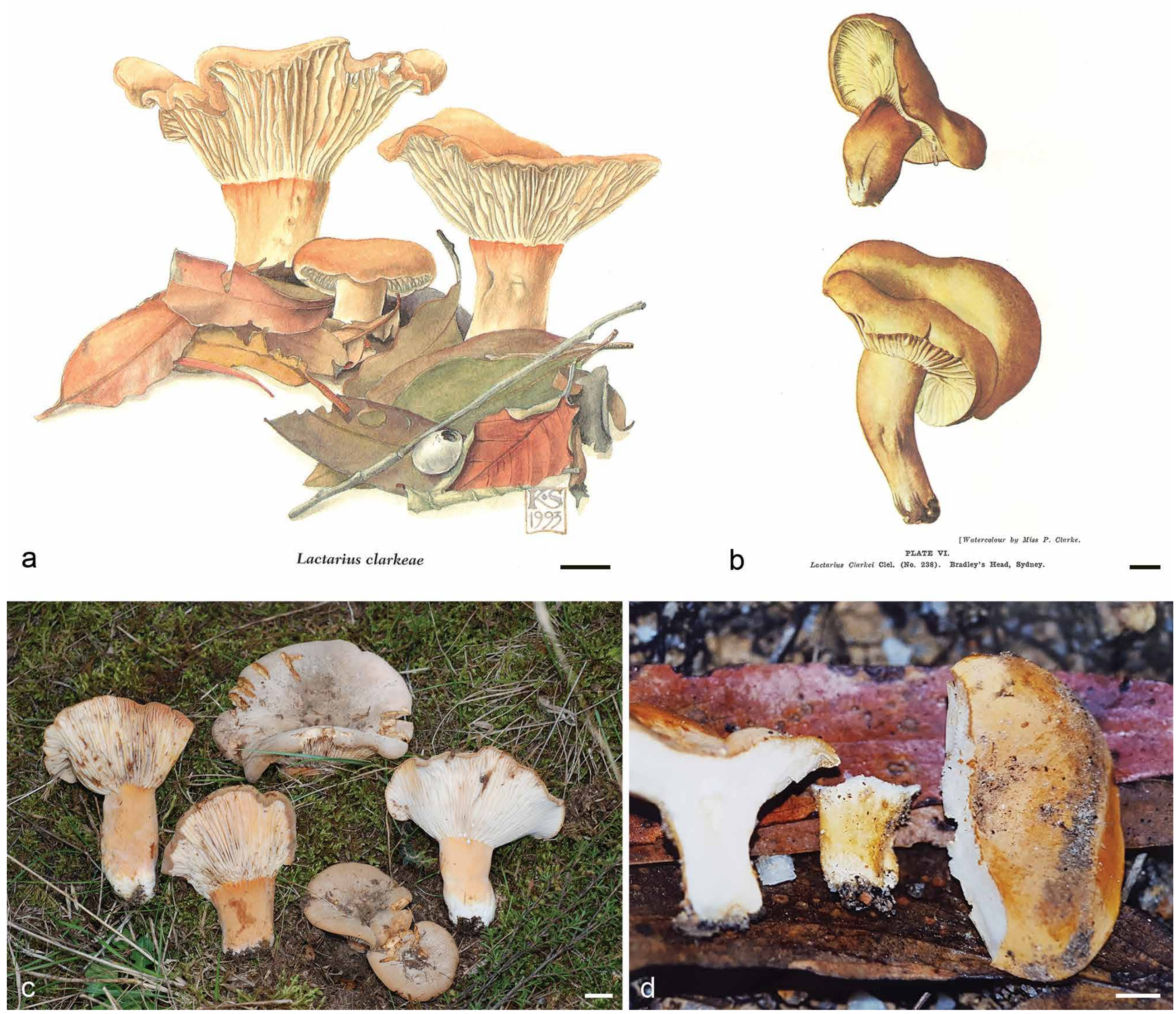

Fig. 10 Subgenus *Gymnocarpi* sect. *Tomentosi*. Basidiomata of *Lf. clarkeae*. a. Bougher & Syme (1998); b. Cleland (1934), Pl 6 watercolour by P. Clarke; c. *L. clarkeae* sensu NZ; d. *L. clarkeae* sensu AU. — Scale bars: 10 mm. — Photos: c by J.A. Cooper; d by J.E. Tonkin.

1.22, *n* = 37), 1–5 µm wide at base ($\bar{x}$ = 3.01 ± 1.03, *n* = 37), clavate, mostly 3-spored but occasionally 1-, 2-, or 4-spored; sterigmata 3–10 × 1–4 µm ($\bar{x}$ = 6.17 ± 1.50 × 2.11 ± 0.57, *n* = 39); basidioles 29–69 × 4–11 µm ($\bar{x}$ = 46.47 ± 11.65 × 8.36 ± 1.82, *n* = 40), 1–6 µm wide at base ($\bar{x}$ = 2.82 ± 1.07, *n* = 40). *Hymenophoral trama* comprising mostly interwoven, occasionally parallel hyphae 2–5 µm diam ($\bar{x}$ = 3.50 ± 0.93, *n* = 8), sinuous laticiferous hyphae 5–13 µm diam ($\bar{x}$ = 5.50 ± 1.31, *n* = 8), and sphaerocytes 15–92 × 14–37 µm ($\bar{x}$ = 34.67 ± 9.58 × 23.24 ± 6.76, *n* = 40), in well-defined layer 6–10 cells thick; *subhymenium* composed of hyphae and round or angular polygonal cells 10–29 × 5–21 µm ($\bar{x}$ = 19.25 ± 4.37 × 11.73 ± 3.04, *n* = 35), sinuate laticiferous hyphae present and occasionally extending into hymenium as cystidia. *Pleuromacrocystidia* 25–73 × 1–9 µm ($\bar{x}$ = 46.62 ± 11.77 × 3.64 ± 1.60, *n* = 28), 1–3 µm wide at apex ($\bar{x}$ = 1.69 ± 0.56, *n* = 36), single or double strangulations along cylinder with variable acuteness of strangulations within and between cells, or occasionally ventricose-rostrate and not strangulated, slightly emergent above hymenium, thin-walled, hyaline. *Pleurolamprocystidia* absent. *Cheilomacrocystidia* 27–39 × 3–5 µm ($\bar{x}$ = 32.50 ± 4.12 × 2.80 ± 1.03, *n* = 6), 1–3 µm wide at apex ($\bar{x}$ = 1.69 ± 0.56, *n* = 36), similar shape to pleurocystidia, or ventricose-rostrate and doubly strangulated, thin-walled, hyaline. *Pileipellis* a lampropalisade forming a trichoderm over periclinal filamentous layer 200 µm thick; subpellis consists of several layers of round or angular polygonal cells, 14–34 × 9–25 µm ($\bar{x}$ = 23.93 ± 5.30 × 15.64 ± 3.83, *n* = 40); terminal elements 36–306 × 2–6 µm ($\bar{x}$ = 114.70 ± 68.03 × 3.93 ± 0.96, *n* = 35), 1–4 µm wide at apex ($\bar{x}$ = 2.63 ± 0.73, *n* = 35), length variable but often highly elongate, narrow and cylindrical, tapering towards apex, apex obtuse or bluntly acuminate, septate, outline slightly sinuate, simple or basally branched; *pileus trama* similar to hymenophoral trama, heteromerous. *Stipitipellis* a lampropalisade; subpellis consists of several layers of round or angular polygonal cells, 12–34 × 7–26 µm; caulocystidia length variable of often highly elongate, 25–372 µm long ($\bar{x}$ = 143.22 ± 76.87, *n* = 40) and 2–7 µm wide at base ($\bar{x}$ = 4.11 ± 1.35, *n* = 40), similar shape to pileicystidia but not arising from a cellular layer; *stipe trama* similar to hymenophoral trama and pileus trama, heteromerous.

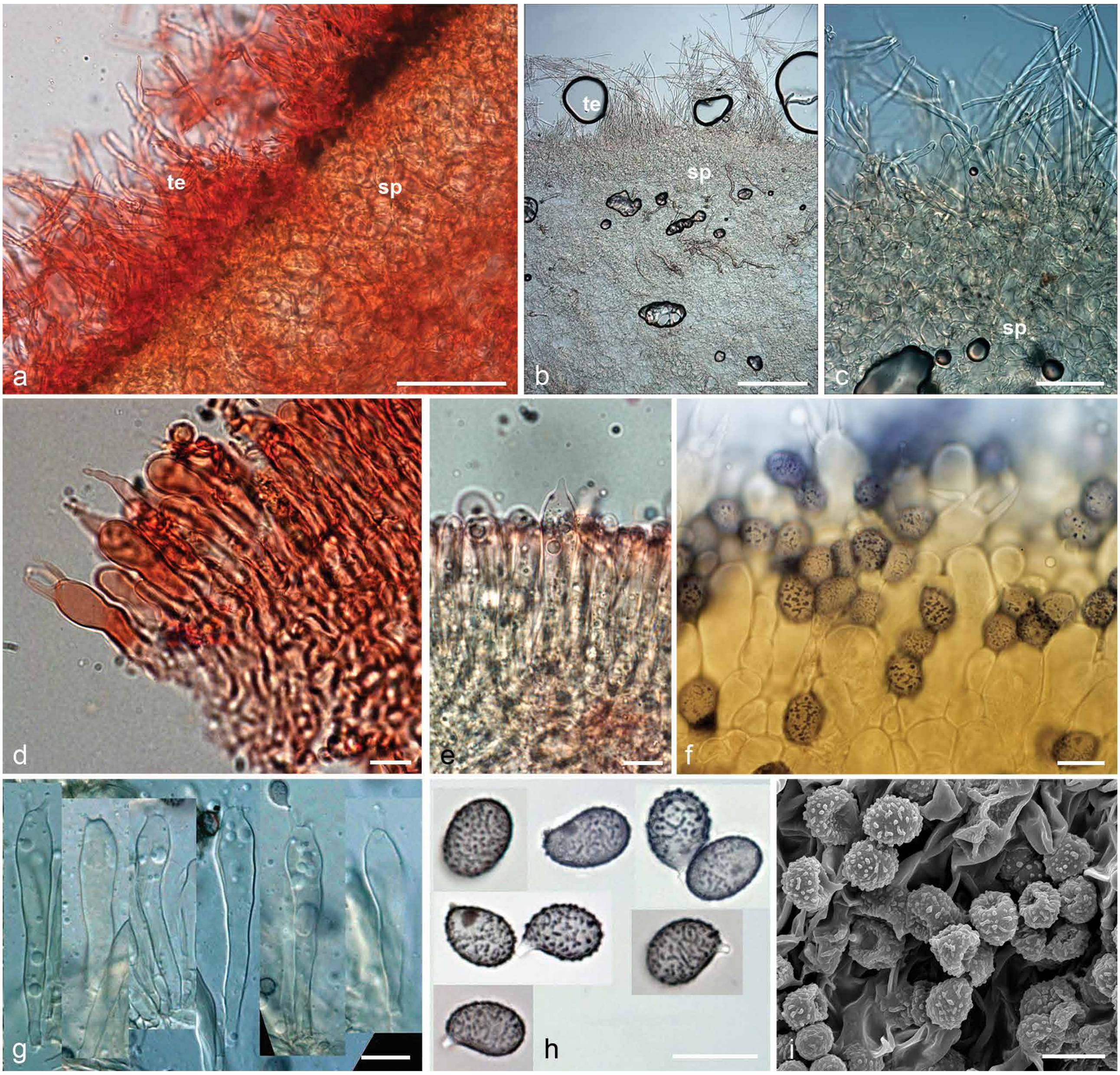

Fig. 11 *Lactifluus clarkeae*. a. Lampropalisade pileipellis, terminal elements (te), subpellis (sp) (AU); b. pileipellis, terminal elements (te), subpellis (sp), context (NZ); c. pileipellis terminal elements and subpellis (sp) (NZ); d–e. subhymenium, basidia, pleurocystidia (pc) and cheilocystidia (cc) (AU); f. basidiospores and basidia (AU); g. basidia (NZ); h. basidiospores (NZ); i. SEM of basidiospores (AU). — Scale bars: a = 150 µm; b = 200 µm; c = 50 µm; d–f, i = 10 µm; g = 30 µm; h = 20 µm.

Distribution & Habitat — In Australia this species is known from open *Eucalyptus* woodland with *Callitris* sp., *Allocasuarina* sp., and *Acacia* sp. in secondary canopy, low shrub layer, and *Lomandra* sp., bracken and grasses in understory. In New Zealand it is known from lowland scrub, where it is associated with *Kunzea* spp. and *Leptospermum scoparium*. Known from singleton specimens to groups of up to 6, emerging through shallow leaf litter. Not common where found. Basidiomes emerge January – July.

Additional specimens examined. Australia, South Australia, Southern Lofty Ranges, Kuitpo Forest near gate H07, 25 Apr. 2011, *P. Catcheside & D. Catcheside PSC3472* AD-C 56542; ibid., 24 Aug. 2013, *P. Catcheside & D. Catcheside PSC 3892* AD-C 58512; ibid., 24 Aug. 2013, *P. Catcheside & D. Catcheside PSC 3299* AD-C 56692; Mt Lofty, 18 June 1932, *J.B. Cleland*, AD-C 9803; ibid., 15 July 1922, *J.B. Cleland*, AD-C 9802; ibid., 25 Apr. 1924, *J.B. Cleland*, AD-C 9805; Greenhill Road, 1 July 1922, *J.B. Cleland*, AD-C 9804; Belair National Park, 29 June 1932, *J.B. Cleland*, AD-C 9806; Southern Lofty, 30 June 1971, *J.H. Warcup 263* MEL 2024762. Victoria, Anglesea, NW of Ironbark basin off Point Addis Rd, Otway Plain, likely collected June 1995, *H. Weatherhead 11* MEL 2320759; Cann River, 12 km south along the Tamboon Rd, 25 May 2002, *J.E. Tonkin 972* MEL2238268; Cann River, 8 km south along the Tamboon Rd, 25 May 2002, *J.E. Tonkin 981* MEL2238275. Tasmania, Lenah Valley Track, Mt Wellington, 720 m a.s.l., 27 Jan. 1996, *A.V. Ratkowsky 0136* MEL 2257826. Western Australia, Denmark, Walpole-Nordalup National Park, Cemetery Rd, approx. 1 km from SW Highway, Darling, 25 June 2001, *J.E. Tonkin 876* MEL 2101938; Westralia Conservation Park (near Collie), 11 July 2011, *N.L. Bougher 00785* PERTH 08318271; Worsley Alumina Pty Ltd, Bauxite Mine, Boddington, 3 July 2002, *G. Nener* PERTH 07676042; ibid., *G. MacNish* PERTH 07676026; Alcoa Mine, Nettleton Road, Dwellingup, 4 July 2000, *J. Tayler & N.L. Bougher* PERTH 07670400; Keswick Camp, Wattle Grove, Perth, 6 June 2005, *N.L. Bougher & J. Bracken E8196* PERTH 07680007; Marribup State Forest, E of Manjimup, Muir Highway, 22 June 2006, *R.E. Halling*, *N.L. Bougher & R. Robinson 8830* PERTH 08019274; Munglinup, Dallinup Creek, Rockhole Road, Ravensthorpe, 10 June 2006, *K. Syme 1459/06* PERTH 07574428; Manjimup, 20 June 1985, *N.L. Bougher* PERTH 07569041; Lot 406, W of Denmark, 21 Sept. 1993, *K. Syme 690/93* PERTH 05485568; Walpole-Nornalup National Park, corner Monastery and Gully Roads, Walpole, 8 June 1993, *N.L. Bougher*, *K. Syme & M.C. Brundrett KS 652/93* PERTH 07665385; Queensland, Central Forest Station, Wide Bay, Fraser Island, 100 m a.s.l., 25 June 2008, *P. Leonard 22608* MEL 2332064; Wide Bay District, Great Sandy National Park, Fraser Island, Smith Road, 6 Oct. 2009, *R.E. Halling 9231* NY 1115414, BRI; Lamington N.P., Bellbird area, 4 Apr. 2001, *A.M. Young & N. Fechner LNP01* BRI: AQ 808473. – New Zealand, Nelson, Wairau Bridge, 10 Jan. 2002, *P. Leonard 5102* PDD 76085; Canterbury Akaraoa, Hinewai Reserve, 29 Jan. 2011, *J.A. Cooper 11696* PDD 96000; Bankside Scenic Reserve, 15 Mar. 2010, *J.A. Cooper 11742* PDD 96149; Puketi, Northland, under Kunzea, 9 May 2017, *P.R. Johnston*, *J.A. Cooper 14568* PDD 106449. Nelson Crosby District, Kaihoka Lakes Track, 13 May 2014, *J.A. Cooper & D.A. Orlovich 13490* PDD 105741; Abel Tasman National Park, track to Anapai, 1 May 2013, *P. Leonard 4513* PDD 103505; Bankside Scientific Reserve, Canterbury, under *Kunzea serotina*, 22 Apr. 2011, *J.A. Cooper 11792* PDD 96189.

Notes — McNabb (1971) stated that the original type material of *Lf. clarkeae* (South Australia, Mt Lofty, June 1927) could not be traced in Cleland's herbarium and that the paratypes represented different species, one with warty and one with reticulate spores. McNabb selected 'ADW15299', the one with warty spores, as a lectotype for *Lf. clarkeae*. Grgurinovic (1997) states it might even be possible that this collection (ADW15299) is the holotype because the collection notes agree perfectly with the protologue and there might have been a typographical error. Verbeken et al. (2010) provided further microscopic details of this material. The reticulate spored species that was represented in Cleland's paratypes was later described by Grgurinovic (1997) as *Lf. mea* which, according to Verbeken et al. (2010), belongs to *Lactarius* subg. *Russularia.* McNabb (1971) described sect. *Tomentosi* to accommodate this species and *Lf. rubroviolascens* from Madagascar (McNabb 1971), based on the distinctive cuticular structure. De Crop et al. (2017) have since placed *Lf. rubroviolascens* in its own sect. *Rubroviolascentini* with three other African species. We were unable to obtain sequence data from the lectotype; the material is in poor condition, and morphological characters difficult to interpret. We feel morphological characters, both macro- and microscopic characters of the collections in the designated clade (*Lf. clarkeae* s.str.; Fig. 3) best fit the original description of *Lf. clarkeae*, and currently accepted species concept. In selecting an epitype, we have attempted to find a collection from a similar vegetation type, habitat and the type locality. Some geographic variation in the ITS is present within *Lf. clarkeae*, but for the moment we act conservatively in using a broad concept until further genes can be analysed. All Australian material examined have a slightly more pastel-orange wrinkled cap surface, often with greyish undertones, and shortish stout stipe. Morphologically, the New Zealand material has, on average, very slightly longer spores than Australian material (AU $\bar{x}$ = 8.29 ± 1.01 × 6.32 ± 0.65, *n* = 40; NZ $\bar{x}$ = 9.11 ± 0.62 × 6.75 ± 0.6, *n* = 40); however, no morphological differences between WA and SA-VIC-QLD Fraser Is. material could be found. *Lactifluus clarkae* is close to *Lf.* sp. 1 from New Caledonia and *Lf.* sp. 2 from NSW, two insufficiently known taxa.

Lactifluus flocktoniae (Cleland & Cheel) T. Lebel, Persoonia 38: 76. 2016 — MycoBank MB 839615; Cleland 1934, 1935; Griffiths 1985; Grgurinovic 1997; Bougher & Syme 1998; Fuhrer 2001, 2005; Fig.12a–e, 13

Basionym. Russula flocktoniae Cleland & Cheel, Trans. & Proc. Roy. Soc. South Australia 43: 274. 1919. (MB 648151)

Lectotype. Australia, New South Wales, The Spit, Sydney, 9 June 1912, *J.B. Cleland* AD 9871 (designated by Grgurinovic 1997: 81. MBT 10000759).

Epitype designated here. Australia, Victoria, East Gippsland, Colquhoun State Forest, Lake Tyers Forest Park, 15 km east of Lakes Entrance, 400 m along Burnt Ridge Rd from junction with LE-Nowa Nowa Rd, open stringy bark eucalypt woodland, 27 May 2002, *J.E. Tonkin 1006* MEL 2238290 (MBT 10000642).

Diagnosis — This species typically lacks latex production on cutting or bruising of cap or lamellae, has a bright orange pileus and very pale distant to subdistant lamellae, an acrid taste. cheilocystidia rare; thick-walled terminal elements in pellis and stipitipellis rare but often > 100 µm long.

Pileus 30–63 mm diam, becoming broadly convex with central depression, bright orange, generally more intense towards the centre but with paler flares irregularly across most basidiomes, margin entire inturned to straight, even; surface smooth, minutely pubescent to velvety (most obvious in younger specimens); context pale cream and densely spongy, eventually discolouring slightly pale brown, up to 9–12 mm deep at the lamellae/stipe junction. *Lamellae* decurrent, distant to subdistant (10–15 L + l/cm), thick (2–3 mm), up to 3.5 mm deep, white to pale cream, edge entire and not pigmented, forked infrequently mostly near stipe, with scattered, short, intermixed lamellulae (l = 3–5/half pileus). *Stipe* 10–22(–30) × 8–13(–25) mm, smooth to minutely pubescent, pale cream to pale apricot in upper and lower halves, context cream, densely spongy becoming hollow in age. *Latex* either absent or not abundant, white, unchanging; taste quickly acrid, hot. *Odour* not distinctive, or faintly spermatic. *Taste* peppery. *Chemical tests*: $FeSO_4$ dull greenish outside, salmon going slowly greenish inside.

Basidiospores 9.5–11.9 × 7.5–9.0 µm ($\bar{x}$ = 10.44 ± 0.57 × 8.25 ± 0.35, *n* = 39), subglobose to broadly ellipsoid (Q = 1.20–1.38 ($\bar{x}$ = 1.27 ± 0.04, *n* = 39)), ornamentation of fine warts connected by shallow, narrow lines in a low partial reticulum (appears not strongly ornamented and overall reaction in Melzers not strong), 0.2–0.5 µm in height, plage not obvious; hilar appendix 1–2 × 0.5–1 µm. *Basidia* 38.0–70.0 × 9.0–12.0 µm ($\bar{x}$ = 56.04 ± 8.05 × 11.04 ± 0.78, *n* = 31), 4.0–8.5 µm wide at base ($\bar{x}$ = 5.36 ± 1.62, *n* = 31), clavate to subfusiform or centrally inflated, mostly 4-spored; sterigmata 5.5–9.0 × 2.5–3.0 µm ($\bar{x}$ = 7.27 ± 0.89 × 2.70 ± 0.29, *n* = 31); basidioles 33.0–52.0 ×

9.0–12.5 µm ($\bar{x}$ = 41.91 ± 5.24 × 9.89 ± 1.43, *n* = 29), 3.5–6.5 µm wide at base ($\bar{x}$ = 4.08 ± 0.89, *n* = 29). *Hymenophoral trama* comprising interwoven hyphae 2–4 µm diam, sinuous and winding laticiferous hyphae 3–8 µm diam ($\bar{x}$ = 5.86 ± 1.10, *n* = 22), and abundant sphaerocytes 20.0–40.5 × 11.0–33.5 µm ($\bar{x}$ = 29.80 ± 4.72 × 19.33 ± 3.64, *n* = 25); *subhymenium* 61–85 µm wide, comprising interwoven hyphae and 3–5 layers of closely interconnected polygonal cells 8.0–18.0 × 5.0–14.0 µm ($\bar{x}$ = 11.67 ± 3.12 × 11.11 ± 2.26, *n* = 29), laticiferous hyphae present and arising from hymenophoral trama, sometimes extending through hymenium as cystidia. *Pleuromacrocystidia* 42.5–91.0 × 9.8–12 µm ($\bar{x}$ = 79.47 ± 12.99 × 10.69 ± 1.25, *n* = 16), 3.5–6 µm wide at base ($\bar{x}$ = 4.58 ± 0.75, *n* = 16), narrow-cylindrical but centrally inflated or subfusiform, tapering toward apex and base, tapering in strangulated, often rounded segments (2–3) narrowing toward apex, apex obtuse or capitulate, distinctly emergent above hymenium and often arising from subhymenium or hymenophoral trama, scattered to patchily abundant. *Pleuropseudocystidia* 44–71(–96.0) × 8–11 µm ($\bar{x}$ = 49.82 ± 11.77 × 9.84 ± 2.01, *n* = 28), 2–4.5 µm

Fig. 12 Subgenus *Gymnocarpi* sect. *Tomentosi* basidiomata of *Lf. flocktoniae*. a. Bougher & Syme (1998); b. Cleland & Cheel (1919), Pl 5 watercolour by M. Flockton; c–d. *Lf. flocktoniae*; e. Grgurinovic (1997), Pl 5b watercolour by P. Clarke; f. basidiomata of *Lf. psammophilus* sp. nov. — Scale bars: 10 mm. — Photos: c–d, f by J.E. Tonkin.

wide at base ($\bar{x}$ = 3.04 ± 1.20, *n* = 18), 1–3 µm wide at apex ($\bar{x}$ = 1.69 ± 0.56, *n* = 18), single or double strangulations along cylinder with variable acuteness of strangulations within and between cells, or occasionally ventricose-rostrate or mucronate and unstrangulated, slightly to obviously emergent above hymenium, hyaline. *Cheilomacrocystidia* very few observed in most collections; similar in appearance and size to pleuropseudocystidia. *Pileipellis* a lampropalisade; subpellis 28–42 µm wide, consisting of closely interlocked, rounded or angular, thick-walled polygonal cells 12–33 × 11–30.5 µm ($\bar{x}$ = 20.46 ± 6.47 × 16.05 ± 4.18, *n* = 28) interwoven with scattered hyphae 2–4 µm diam; terminal elements mostly 35.0–91.0 × 3.0–9.0 µm ($\bar{x}$ = 59.31 ± 17.34 × 6.40 ± 1.35, *n* = 28), 3–5 µm wide at base ($\bar{x}$ = 3.7 ± 0.51, *n* = 28), densely packed, thin-walled, cylindrical to clavate, sometimes fusiform, sometimes septate, tapering from base to apex, apex obtuse or acuminate, outline sometimes sinuate or wavy, hyaline, with scattered, rare thick-walled lamprocystidia protruding well beyond the palisade, 68.5–140 × 4–7 µm ($\bar{x}$ = 91.43 ± 22.16 × 5.92 ± 1.06, *n* = 17), 4–6 µm wide at base, 1–4 µm wide at apex, fusiform to cylindrical tapering to base, apex mucronate to acute; *pileus trama* heteromerous, similar to hymenophoral trama with larger sphaerocytes 24–49 × 13–36 µm and laticiferous hyphae occasionally present. *Stipitipellis* a short turf of hyphal tips and scattered cystidia; subpellis comprising mostly of interwoven hyphal elements 2–4 µm diam with scattered inflated ele-

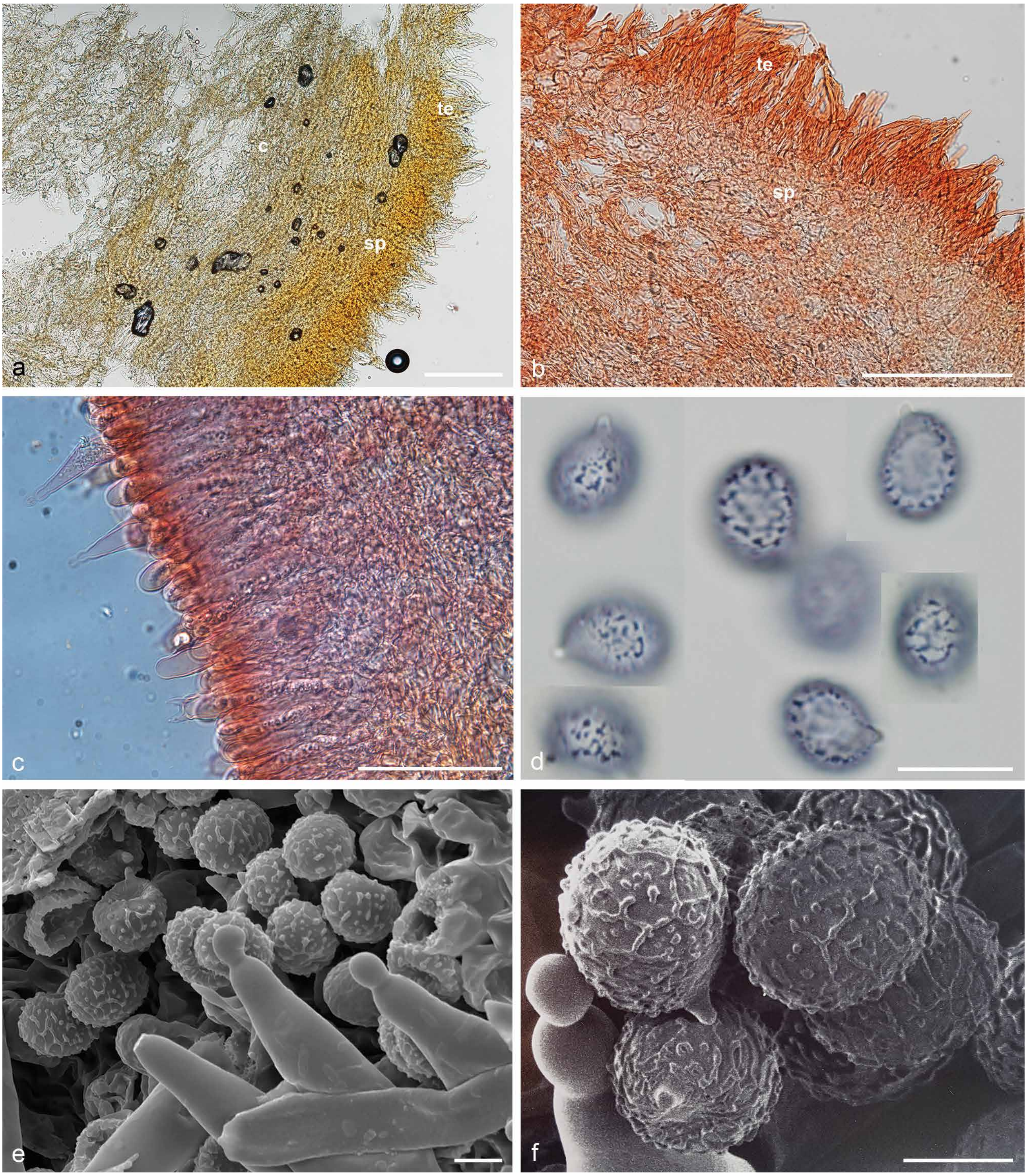

Fig. 13 *Lactifluus flocktoniae*. a. Lampropalisade pileipellis, terminal elements (te), subpellis (sp) and context (c); b. pileipellis terminal elements (te), subpellis (sp) and context; c. subhymenium, basidia, pleurolamprocystidia (plc) and pleuropseudocystidia (ppc); d. basidiospores; e–f. SEM of basidiospores. — Scale bars: a–b = 100 µm; c = 20 µm; d = 10 µm; e–f = 5 µm.

ments 5–11 × 4–9 µm; terminal elements 18.0–48.0 × 5–9.5 ($\bar{x}$ = 30.67 ± 9.88 × 6.45 ± 1.07, *n* =23), 3–4.5 µm wide at base ($\bar{x}$ = 3.8 ± 0.86, *n* = 5), loosely packed and tangled, narrow-cylindrical to clavate tapering from base to apex, apices obtuse, with scattered, rare thick-walled lamprocystidia protruding well beyond the palisade, 33.0–101.0 × 4–7 µm ($\bar{x}$ = 71.61 ± 21.84 × 3.41 ± 0.67, *n* = 12), 3–6 µm wide at base, 1–4 µm wide at apex, fusiform to cylindrical tapering to base, apex mucronate to acute; *stipe trama* consisting of interwoven hyphae 2–4 µm diam, laticiferous hyphae 3–7 µm diam ($\bar{x}$ = 4.98 ± 1.22, *n* = 12), and abundant sphaerocytes 20–48 × 10–32 µm ($\bar{x}$ = 29.1 ± 4.06 × 20.35 ± 5.70, *n* = 15).

Distribution & Habitat — Central and southern New South Wales, north-eastern Victoria, and south-west Western Australia. Associated with open sclerophyll woodland and coastal scrub with very little understory, dominated by *Eucalyptus* spp., *Banksia serrata*, *Acacia terminalis*, *Leptospermum* sp., *Pteridium esculentum*, and *Epacris impressa*. Grey sand with shallow layer of leaf litter. Basidiomes emerge May–June.

Additional specimens examined. Australia, New South Wales, The Spit, Sydney, 9 June 1912, *J.B. Cleland* AD-C 31547, isolectotype; Ryde, Sydney, 27 May 1916, *J.B. Cleland* AD-C 9876, syntype; Bradleys Head, 6 May 1917, *J.B. Cleland* AD-C 9877, syntype; Southern Tablelands, off Reef Rd east, 1.8 km from junction with Laings Rd, near Fire Trail junction with Reef Rd east, Plot SAO4, 28 May 2003, *S.H. Lewis 920* MEL 2218977; Victoria, Cape Conran, Swampy Creek Walk, 2 June 2004, *S. Miller 47-04* MEL 2322022; Cape Conran National Park, Cape Conran Cottages, East Gippsland, 6 June 2006, *J.E. Tonkin 1240* MEL 2298098; Baw Baw National Park and Tanjil Bren State Forest, Mountain Monarchs Walk, 17 May 1993, *J.E. Tonkin 1131* MEL 2239381; Western Australia, Darling, Denmark, Walpole-Nornalup National Park, Cemetery Rd, ± 1 km from SW Hwy, open woodland with *Allocasuarina fraseriana*, *E. marginata* and *C. calophylla*, low shrub layer, *Lomandra* sp. and grasses, 25 June 2001, *J.E. Tonkin 878* MEL 2101940; Darling, Denmark, Walpole-Nornalup National Park, Cemetery Rd, ± 1 km from SW Hwy, open woodland with *Allocasuarina fraseriana*, *E. marginata* and *C. calophylla*, low shrub layer, *Lomandra* sp. and grasses, 25 June 2001, *J.E. Tonkin 877* MEL 2101939; Worsley Alumina Pty Ltd, Bauxite Mine, Boddington, 17 June 2002, *J. Ray* PERTH 07650469; Alcoa Mine, Nettleton Road, Dwellingup, 24 June 2002, *M. Glen & J. Ray* PERTH 07673396; Cemetery Road near Walpole, Walpole-Nornalup National Park, 3 June 1992, *N.L. Bougher*, *K. Syme & M. Hart KS47/91* PERTH 07581726; Urea (Ammonia) plots, just N of Torrens Road, Dwellingup, 3 June 1997, *N.L. Bougher & A. Suzuki* PERTH 07599102; Alcoa (of Australia Ltd) Bauxite Mine, Nettleton Road, Jarrahdale, 13 June 2000, *D. Willyams & N.L. Bougher* PERTH 07676204; Worsley Alumina Pty Ltd, Bauxite Mine, Boddington, 2 July 2002, *I.C. Tommerup*, *M. Glen*, *G. Nener & N.L. Bougher* PERTH 07675917; Ledger Road Bushland, Gooseberry Hill, 26 June 2005, *N.L. Bougher*, *P & J Foss & M.C. Brundrett E8242* PERTH 07681011; Alcoa Mine, Nettleton Road, Dwellingup, 10 June 2002, *M. Glen & R. Armstead* PERTH 07650795; Wungong Catchment, ± 1 km west of Albany Highway just north of Jarrahdale Rd, 19 June 2008, *N.L. Bougher 00438* PERTH 08072728; Jarrahdale, Cobiac site 2, 25 June 1985, *N. Malajczuck* PERTH07587643.

Notes — The description in Cleland & Cheel (1919) and that of Grgurinovic (1997) for *Lf. flocktoniae* is very broad, and as we now know, incorporate several distinct but close taxa. Grgurinovic (1997) selected one of the five collections (syntypes) cited by Cleland & Cheel (1919), who did not indicate a holotype, as a lectotype (AD 9871). Cleland & Cheel (1919) mention a watercolour of a collection/syntype; however, there is no indication of which syntype was painted. A watercolour of '*R. flocktoniae*' was eventually printed in Cleland (1934); it is assumed to be the watercolour by 'P.Clarke no.A' (M. Flockton's niece) that is referred to in Grgurinovic (1997).While several of the syntypes cited by Grgurinovic (1997) are consistent with *Lf. flocktoniae*, macro- and microscopically (listed in additional specimens examined), the collections AD-C 9873 and AD-C 9874 are not. The spores are shorter and broader, the pileipellis structure not a lampropalisade, and pleuromacrocystidia are a different shape to those present in our current circumscription of *Lf. flocktoniae*; both AD-C 9873 and AD-C 9874 have been re-determined as *Lactifluus* sp.

More recent collections of this species complex from the broader region where the syntypes are from (NSW or SA) are few, and unfortunately little likely habitat remains. On close morphological examination and analysis of DNA data, none of the collections from the broader region where syntypes were collected are morphologically similar to this taxon. While the lectotype has some of the macro- and microscopic features of the original description, it is in poor condition, we were unable to obtain usable DNA data, and none of the other material we examined from South Australia match the currently accepted species concept.

The description provided in Bougher & Syme (1998) most closely fits the currently accepted concept of '*Lf. flocktoniae'*. In order to maintain stability of the current concept of *Lf. flocktoniae* we select a more recent collection MEL 2238290 from north eastern Victoria as epitype to provide a strong concept of the taxon.

Lactifluus flocktoniae strongly resembles *Lf. pseudoflocktoniae* sp. nov. However, *Lf. pseudoflocktoniae* typically has slightly larger basidiomes (50–103 mm vs up to 35–65 mm), smaller spores (8.5–9.2 × 6.1–7.3 µm vs 9.5–11 × 7.5–8.5 µm), and lacks pleurolamprocystidia. The velvety orange pileus, thick, well-spaced pale lamellae, pale orange stipe, hot peppery taste, and distinct lack of abundant latex production, combined with long pileal terminal elements and caulocystidia, are common in this species complex.

Lactifluus psammophilus T. Lebel, J. Douch & L. Vaughan, *sp. nov*. — MycoBank MB 837608; Fig. 12f, 14, 15

Etymology. Refers to the growth habit in sandy soils psammophillous = sand loving.

Typus. Australia, Victoria, Gembrook-Tonimbuk Road, Bunyip State Forest, c. 1 km from Mortimer Nature Trail, on roadside verge, 11 May 2003, *J.E. Tonkin*, *N. Klazenga & J.H. Ross JET 1116* (holotype MEL 2238407).

Diagnosis — Pileus orange, stipe pale orange, pleurocystidia typically strangulated, cheilocystidia absent, pileal terminal elements and caulocystidia cylindrical and relatively short (to 96 and 69 µm, respectively), taste quickly peppery or acrid, *Eucalyptus* associated.

Pileus to 80 mm diam, circular or occasionally asymmetric, undulate, planoconvex to plane, depressed, orange becoming darker and more intense near centre, margin entire, even, straight, inturned becoming plane or upturned, surface dry, surface smooth and velutinous to subtomentose, strongly wrinkled concentrically on drying, particularly at margins; context cream to white becoming pale buffy brown on exposure, solid, contiguous with stipe, to 13 mm deep at lamellae-stipe junction. *Lamellae* adnate to subdecurrent, subdistant to distant (24 L + l/cm), to 7 mm deep, cream with pale brown bruising on older specimens, margin entire, anastomosing infrequently, lamellulae variable in length (l = 29/half pileus). *Stipe* to 40 mm long and 23 mm wide, central or occasionally eccentric, slightly tapered to base or cylindrical, slightly rugulose to base, pale yellowish orange to brownish orange and may feature darker or bruised areas, pale orange to cream base, base rounded, smooth to minutely pubescent but velutinous to subtomentose in fissures; context solid, becoming chambered, cream-white. *Latex* absent or scarce, white. *Basal mycelium* white. *Odour* mild to very mushroomy, mild in dried material. *Taste* quickly peppery or acrid. *Chemical tests*: $FeSO_4$ quickly dull lead green context; surface salmon going green.

Basidiospores 6–10 × 5–9 µm ($\bar{x}$ = 8.23 ± 1.05 × 6.73 ± 0.91, *n* = 40), globose to ellipsoid (Q = 1.00–1.43 ($\bar{x}$ = 1.23 ± 0.14, *n* = 40)), walls amyloid, ornamentation amyloid and verrucose with some slight reticulation, rising up to 1 µm. *Basidia* 37–89 × 9–13 µm ($\bar{x}$ = 59.10 ± 11.46 × 10.07 ± 1.31, *n* = 33), 3–7 µm wide at base ($\bar{x}$ = 4.08 ± 1.00, *n* = 33), clavate, 1- to 4-spored, mostly 3-spored; sterigmata 4–10 × 2–4 µm ($\bar{x}$ = 7.03 ± 1.55 × 2.73 ± 0.61, *n* = 38); basidioles 28–85 × 6–13 µm ($\bar{x}$ = 49.58 ± 11.76 × 8.68 ± 1.80, *n* = 40), 2–6 µm wide at base ($\bar{x}$ = 3.90 ± 0.90, *n* = 40), clavate. *Hymenophoral trama* comprising interwoven hyphae 3–4 µm diam ($\bar{x}$ = 3.13 ± 0.35, *n* = 8), sinuous laticiferous hyphae 5–9 µm diam ($\bar{x}$ = 6.63 ± 1.41, *n* = 8), and sphaerocytes 17–52 × 11–34 µm ($\bar{x}$ = 26.58 ± 7.18 × 20.18 ± 5.83, *n* = 40); *subhymenium* composed of hyphae and round or angular polygonal cells 9–44 × 6–23 µm ($\bar{x}$ = 20.51 ± 8.24 ×

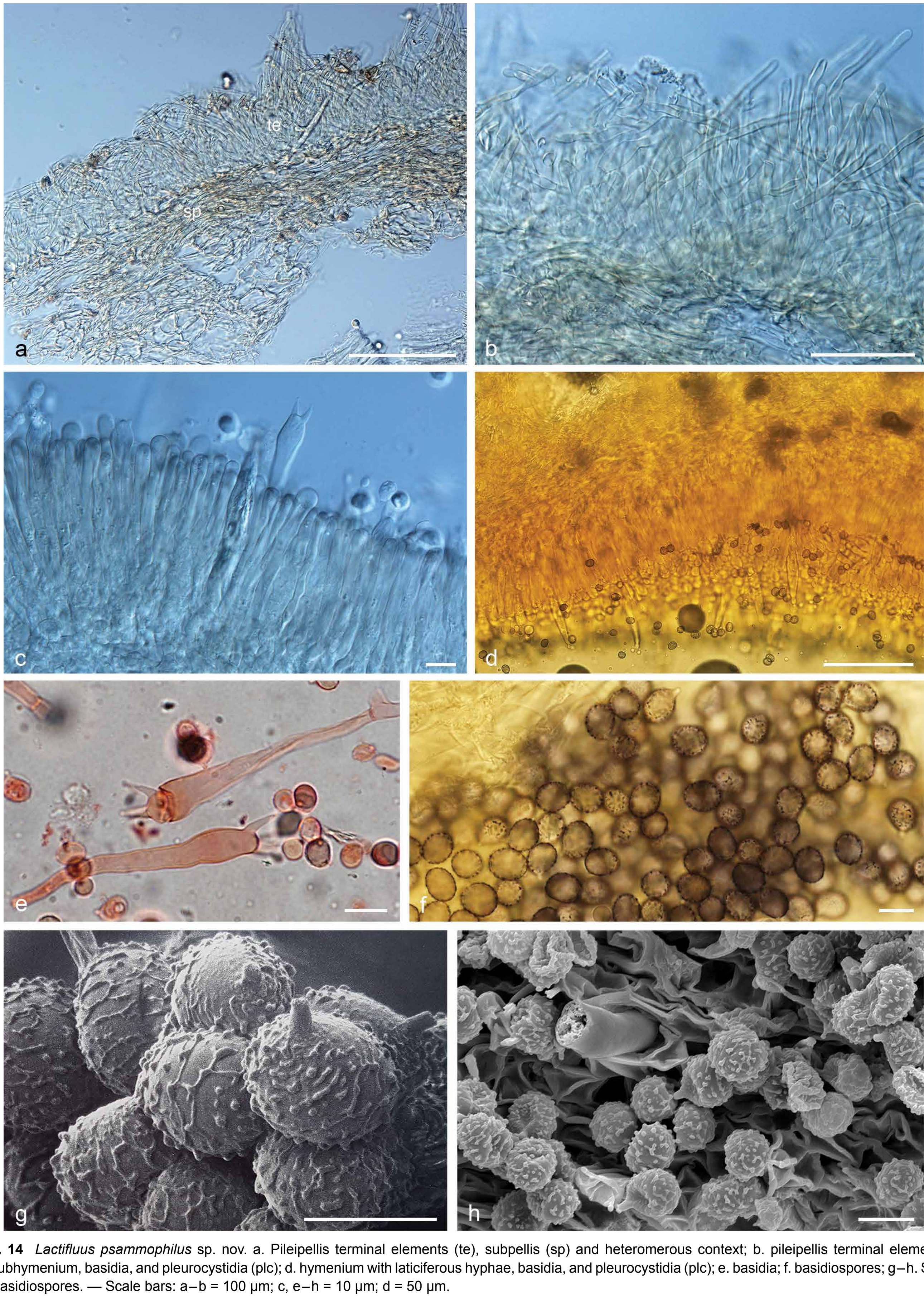

Fig. 14 *Lactifluus psammophilus* sp. nov. a. Pileipellis terminal elements (te), subpellis (sp) and heteromerous context; b. pileipellis terminal elements; c. subhymenium, basidia, and pleurocystidia (plc); d. hymenium with laticiferous hyphae, basidia, and pleurocystidia (plc); e. basidia; f. basidiospores; g–h. SEM of basidiospores. — Scale bars: a–b = 100 µm; c, e–h = 10 µm; d = 50 µm.

Fig. 15 *Lactifluus psammophilus* sp. nov. Concentrically wrinkled appearance of pellis on drying. — Scale bar: 10 mm.

12.63 ± 3.87, *n* = 35), sinuate laticiferous hyphae occasionally extending into hymenium as cystidia. *Pleuromacrocystidia* 32–61 × 2–7 µm ($\bar{x}$ = 48.85 ± 9.30 × 4.50 ± 1.68, *n* = 7), 1–2 µm wide at apex ($\bar{x}$ = 1.74 ± 0.50, *n* = 14), thin-walled, typically a doubly strangulated cylinder but occasionally triply strangulated or unstrangulated and ventricose-rostrate, slightly emergent above hymenium, hyaline. *Cheilocystidia* absent. *Pileipellis* subpellis not always obvious in older material, consisting of 2–4 layers of round or angular polygonal cells, 13–43 × 8–32 µm ($\bar{x}$ = 21.80 ± 7.17 × 14.83 ± 5.88, *n* = 30); pileicystidia 16–96 × 3–6 µm ($\bar{x}$ = 46.10 ± 18.13 × 4.03 ± 0.62, *n* = 40), 1–5 µm wide at apex ($\bar{x}$ = 2.60 ± 0.78, *n* = 40), septate, cylindrical, tapering towards apex, apex obtuse; *pileus trama* similar to hymenophoral trama, heteromerous. *Stipitipellis* subpellis consisting of several layers of round or angular polygonal cells, 18–66 × 10–36 µm ($\bar{x}$ = 30.71 ± 10.63 × 20.14 ± 5.53, *n* = 35); caulocystidia 21–69 × 2–8 µm ($\bar{x}$ = 41.17 ± 10.37 × 4.57 ± 1.45, *n* = 30), 1–5 µm wide at apex ($\bar{x}$ = 2.50 ± 0.73, *n* = 30), septate, cylindrical, tapering towards apex, apex obtuse; *stipe trama* similar to hymenophoral trama, heteromerous.

Distribution & Habitat — North eastern Victoria. Associated with open sclerophyll woodland or coastal scrub dominated by peppermint and stringy bark with understory of *Banksia spinulosa*, *B. serrata*, *Acacia terminalis*, *Leptospermum* sp., *Hovea heterophylla*, *Gahnia* sp., *Melaleuca* sp., *Platylobium formosa*, wire grass, *Pterydium esculentum*, *Lycopodium* sp., *Correa* sp., and *Persoonia* sp. Gregarious. Not common where found. Basidiomes emerge from May–July.

Additional specimens examined. Australia, Victoria, Gembrook-Tonimbuk Road, Bunyip State Forest, c. 1 km from Mortimer Nature Trail, on roadside verge, 11 May 2003, *J.E. Tonkin*, *N. Klazenga & J.H. Ross JET 1115* MEL 2238406; Cape Conran National Park, Cape Conran Cottages, East Gippsland, 6 June 2006, *J.E. Tonkin 1244* MEL 2298102; Wellington Road, Gippsland Plain, 1 May 1978, *F.M. Cole* MEL 2036361; Bunyip State Park, Tonimbuk, Eastern Highlands, 14 June 2004, *S. Miller 117-04* MEL 2322070; Cape Conran, Swampy Creek Walk, East Gippsland, 9 Apr. 2004, *S. Miller 59-04* MEL 2322029; Cape Conran, c. 20 km E of Marlo, East Gippsland, 2 July 2006, *R.E. Halling 8854* MEL 2297068.

Notes — *Lactifluus psammophilus* closely resembles *Lactifluus flocktoniae* but the slightly larger pilei (50–80 mm vs 40–60 mm diam), consistently wrinkle concentrically on drying (Fig. 15). Both species are generally to be found in coastal woodland or scrub, always on sandy soils. *Lactifluus psammophila* is sister to an unnamed taxon, *Lf.* sp. 3 from Fraser Island, QLD (AQ797938), which appears to lack the concentric wrinkling on drying (Fig. 16e).

Lactifluus pseudoflocktoniae T. Lebel, J. Douch, L. Tegart & L. Vaughan, *sp. nov.* — MycoBank MB 837609; Fig. 16a–b, 17

Etymology. In reference to the strong resemblance to *Lf. flocktoniae*.

Typus. Australia, Victoria, Cann River, 8 km south along the Tamboon Rd, 25 May 2002, *J.E. Tonkin 973* (holotype MEL 2238269).

Diagnosis — Resembles *Lf. flocktoniae* but with slightly larger basidiomes and slightly smaller spores, taste quickly peppery.

Pileus 50–103 mm diam, orange to apricot, paler at margin and deeper salmon orange at centre; apically depressed tending to infundibuliform, convex towards the margins at first and retaining this tendency into maturity, velvety fibrillose and a tendency towards wrinkling, especially near the margins; margins entire, plane, undulate and rivulose; context white to cream and quickly staining pale brown, up to 15 mm deep at lamellae/stipe junction. *Lamellae* cream, up to 7 mm deep, distant becoming subdistant and very thick at stipe juncture, adnate to decurrent, edge entire and strongly forked near the stipe, sometimes more than once for the same lamella; lamellulae intermixed. *Stipe* up to 40–50 × 20–25 mm, tapered at base, saffron or a pale orange throughout, lighter than the orange or apricot of the pileus and tinged with cream; context white, solid, contiguous with pileus context, quickly staining pale brown towards outer surface. *Latex* present, trace amounts or abundant white latex observed. *Taste* quickly peppery. *Odour* spermatic.

Basidiospores 8.5–9.5 × 6.4–7.4 µm ($\bar{x}$ = 8.89± 0.30 × 6.93 ± 0.39, *n* = 17), broadly ellipsoid to ellipsoid (Q = 1.18–1.42 ($\bar{x}$ = 1.29 ± 0.06, *n* = 17)), ornamentation verrucose, up to 0.8 µm high, with low short lines sometimes joining 4–5 verrucae. *Basidia* 50–60 × 9.5–10.8 µm ($\bar{x}$ = 54.24 ± 3.66 × 10.34 ± 0.52, *n* = 10), 4.5–5.3 µm wide at base ($\bar{x}$ = 4.83 ± 0.43, *n* = 10), clavate, mostly 4-spored but occasionally 2- or 4-spored; sterigmata 5.5–6.5 × 1.5–2.0 µm ($\bar{x}$ = 6.19 ± 0.08 × 1.87 ± .025, *n* = 8); basidioles 32.5–49.5 × 6.0–7.5 µm ($\bar{x}$ = 39.58 ± 6.21 × 7.06 ± 0.48, *n* = 15), 4.5–5.5 µm wide at base ($\bar{x}$ = 5.02 ± 0.44, *n* = 15). *Hymenophoral trama* comprising mostly interwoven, occasionally parallel hyphae 2–5 µm diam, sinuous laticiferous hyphae 5–13 µm diam, and sphaerocytes 15–35 × 12–32 µm ($\bar{x}$ = 28.56 ± 3.45 × 24.2 ± 2.33, *n* = 18); *subhymenium* composed of hyphae and round or angular polygonal cells 9.5–20.0 × 5.5–13.5 µm ($\bar{x}$ = 13.57 ± 2.91× 9.46 ± 2.27, *n* = 11), sinuate laticiferous hyphae present and occasionally extending into hymenium as cystidia. *Pleuromacrocystidia* 35–78 × 3.5–15 µm ($\bar{x}$ = 48.62 ± 8.77 × 7.67 ± 3.80, *n* = 20), 2–3.5 µm wide at apex, mostly cylindrical or ventricose-rostrate or capitate and not strangulated, slightly emergent above hymenium, thin-walled, hyaline. *Pleurolamprocystidia* absent. *Cheilocystidia* rare, similar shape and size to pleurocystidia. *Pileipellis* a lampropalisade forming a trichoderm; subpellis consists of several layers of round or angular polygonal cells, 24.5–34.0 × 20.5–34.0 µm ($\bar{x}$ = 26.34 ± 4.83 × 24.30 ± 5.08, *n* = 15); terminal elements 42–97.5 × 3–5.5 µm ($\bar{x}$ = 62.98 ± 19.78 × 4.64 ± 0.49, *n* = 16), 3.5–5 µm wide at apex, length variable but elongate, narrow and cylindrical, tapering slightly towards apex, apex obtuse or bluntly acuminate, often septate, arising from inflated subpellis cells; *pileus trama* similar to hymenophoral trama, heteromerous. *Stipitipellis* a short turf of hyphal tips and cystidia; subpellis consists of interwoven hyphae 2–5 µm diam; caulocystidia 29–46 µm long × 4–6 µm wide ($\bar{x}$ = 40.05 ± 4.46 × 5.05 ± 1.48, *n* = 14) and 2–4.5 µm wide at base ($\bar{x}$ = 4.05 ± 0.07, *n* = 14), similar shape to pileil terminal elements but not arising from a cellular layer; *stipe trama* similar to hymenophoral trama and pileus trama, heteromerous.

Distribution & Habitat — South-west Tasmania, south-east Victoria, and central southern South Australia. Typically associated with high rainfall forests. In Tasmania associated with cool tropical rainforest of *Nothofagus*, *Dacrydium* and *Atherosperma* with scattered *Eucalyptus.* In Victoria and South Australia found in association with wet sclerophyll forest of open *Eucalyptus* spp. woodland with dense tall shrub *Banksia* and *Xanthorrhea* understorey, or sandy heath. Basidiomes emerge February–July.

Additional specimens examined. Australia, Tasmania, Arve Valley, Huon River, Tahune Bridge, Huon Pine Reserve, 9 Apr. 1987, *T.W. May 87275* MEL 2036362; Mt Wellington, Kermandie Falls, Upper Track, 20 Feb. 2001, *D. Ratkowsky 0132* MEL 2257830. Victoria, Mornington Peninsula, 8 June 1978, *F.M Cole & A.A. Holland* MEL 2121981; Wannon, Lower Glenelg River area, c. 2.25 miles NW of Johnstone Swamp, near head of Gallas Creek, 14 June 1964, *J.H. Willis & A.C. Beauglehole* MEL 2030448; Huon Valley, Warra LTER, SST area, coupe WR001E, 16 June 2006, *G.M. Gates & D.A. Ratkowsky* MEL 2317147. South Australia, Kangaroo Island, Flinders Chase National Park, Mays Cottage, 26 June 2004, *P. Catcheside & D. Catcheside PSC1936c* AD-C 58323; Southern Lofty Ranges, Kuitpo Forest, 29 July 2017, *P. Catcheside & D. Catcheside PSC4551* AD-C 60165.

Notes — *Lactifluus pseudoflocktoniae* has a close resemblance to *Lf. flocktoniae* and *Lf. clarkeae*, but typically has slightly larger basidiomes and slightly smaller spores. Pleurocystidia in *Lf. pseudoflocktoniae* are typically cylindrical or ventricose-rostrate or capitate and not strangulated, slightly emergent above hymenium, rather than consistently strangulated and often emergent above hymenium as in *Lf. flocktoniae*. Hymenium lacking pleurolamprocystidia – but these are rare in *Lf. flocktoniae* so not a good character. Sequences of *Lactifluus* sp. 4 (Fig. 16f), with two collections from Southern QLD, and *Lf.* sp. 5 from New Caledonia (Fig. 18) are highly similar to *Lf. pseudoflocktoniae*.

Lactifluus sp. 1

Sequence data. New Caledonia, Col de Mouirange, Apr.–July 2012, *CM-My30M1 root tip* (ITS KY774240).

Notes — Sequence published in Carriconde et al. (2019), where they sampled from three different types of rainforest monodominant *Nothofagus aequilateralis* rainforest, monodominant *Arillastrum gummiferum* rainforest and mixed rainforest (most

Fig. 16 Subgenus *Gymnocarpi* sect. *Tomentosi* basidiomata. a–b. *Lf. pseudoflocktoniae* sp. nov. (type); sect. *Luteoli* basidiomata c. *Lf. russulisporus* (REH 9674) sect. *Tomentosi*; d. *Lf.* sp. 2; e. *Lf* sp. 3; f *Lf.* sp. 4 (PL59048). — Scale bars: 10 mm. — Photos: a–b by J.E. Tonkin; c, e by R.E. Halling; d by T. Lebel; f by P. Leonard.

abundant plant species *Archidendropsis granulosa* (*Fabaceae*), *Calophyllum caledonicum* (*Calophyllaceae*), *Codia jaffrei* (*Cunoniaceae*), *Gastrolepis austrocaledonica* (*Stemonuraceae*), *Montrouziera gabriellae* (*Clusiaceae*), *Myodocarpus fraxinifolius* (*Myodocarpaceae*) and *Syzygium brongniartii* (*Myrtaceae*). This sample was from mixed forest.

***Lactifluus* sp. 2** — Fig. 16d

Pileus dark orange to apricot, paler at centre; apically depressed tending to slightly infundibuliform, convex towards the margins at first and retaining this tendency into maturity, finely velvety, margins entire; context white to cream and quickly staining pale

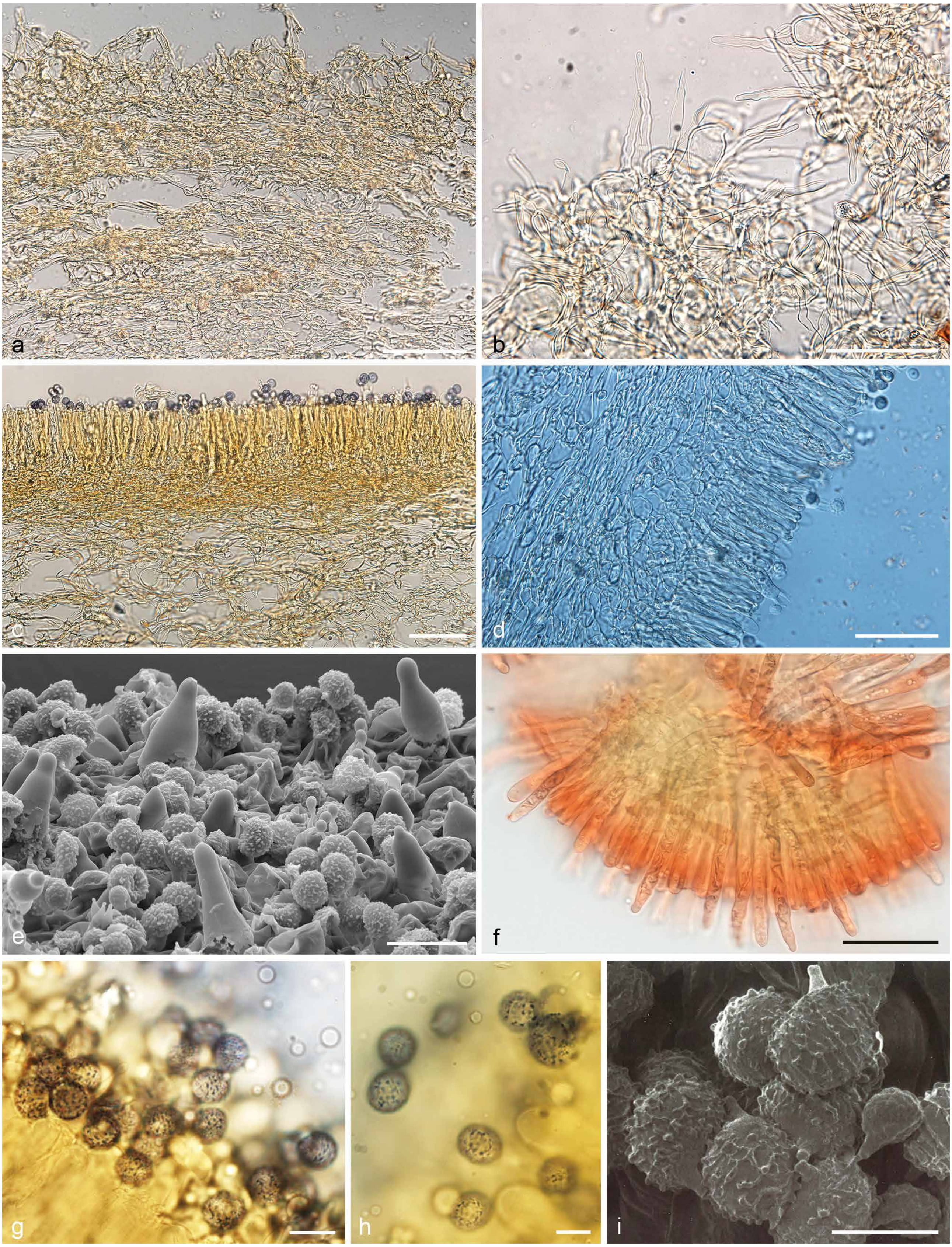

Fig. 17 *Lactifluus pseudoflocktoniae* sp. nov. a. Lampropalisade pileipellis terminal elements (te), subpellis (sp), context; b. pileipellis terminal elements and inflated cells of subpellis; c–d. subhymenium, basidia, and pleurocystidia; e. SEM of pleurocystidia (BRI796523) and spores; f. pleurocystidia and cheilocystidia; g–h. basidiospores; i. SEM of basidiospores. — Scale bars: a–d, f = 50 µm; e = 5 µm; g–i = 10 µm.

brown, up to 11 mm deep at lamellae/stipe junction. *Lamellae* cream staining dark brown where damaged, up to 5 mm deep, subdistant, thick, adnate to decurrent, edge entire; lamellulae intermixed. *Stipe* 30–45 × 15–21 mm, tapered slightly towards base, saffron or a pale orange throughout, only slightly lighter than the pileus; context white, solid, contiguous with pileus context, quickly staining brown towards outer surface. *Latex* abundant white. *Taste* and *odour* not recorded.

Distribution & Habitat — Northern New South Wales. Found in subalpine grassy woodland, mixed eucalypt with grassy understory. March.

Specimen examined. Australia, New South Wales, Narrabri, Mt Kaputar National Park, Kaputar Rd, S of Lindsay rock tops turnoff, plot index GW3, subalpine grassy woodland, alt. 1409 m, 4 Mar. 2008, *M. Danks 45*, MEL 2364071.

Notes — Strong orange colours, robust basidiomes and brown staining of lamellae all support placement in sect. *Tomentosi*.

Lactifluus **sp. 3** — Fig. 16e

Pileus orange to brownish orange, darker in younger basidiomes, dry, even to subcorrugate. *Lamellae* subdecurrent, white, close, staining brown. *Latex* copious, white, staining brown. *Stipe* white to orange as in pileus, tapering slightly towards base. *Odour* slightly fishy.

Distribution & Habitat — Southern Queensland. Found in mixed coastal sclerophyll forest of *Eucalyptus*, *Syncarpia*, *Allocasuarina* and *Leptospermum* species, on deep sandy soils. May.

Specimen examined. Australia, Queensland, Fraser Island, Lake Garawongera Rd, 21 May 2011, *R.E. Halling 9533*, *N. Fechner*, *T. Baroni* BRI: AQ 797938.

Notes — Not enough material to describe. The orange colours of the basidiomes, slight tomentum and microscopic characters support placement of this provisional species in this section of *Lactifluus*.

Lactifluus **sp. 4** — Fig. 16f

Pileus bright orange. *Lamellae* white. *Stipe* orange. *Latex* white, mild. *Odour* not recorded.

Distribution & Habitat — Southern Queensland. Wet sclerophyll forest. Basidiomes emerge April.

Specimens examined. Australia, Queensland, Maroochy Regional Bushland Botanic Garden, 25 m a.s.l., 19 Apr. 2008, *P. Leonard 59408* BRI: AQ 796523; Lamington N.P., Binna Burra, Upper Ballunjui Track, 4 Apr. 2002, *A.M. Young*, *N. Fechner LNP539* BRI: AQ 808472.

Fig. 18 *Lactifluus* sp. 5 basidiomes. — Photo: F. Calliconde.

Notes — Not enough material to describe. The orange colours of the basidiomes, slight tomentum and micro characters support placement of this provisional species in this section of *Lactifluus*.

Lactifluus **sp. 5** — Fig. 18

Sequence data. New Caledonia, Pic du Gran Kaori, Apr. 2013–Apr. 2014, *F. Carriconde PGK13-130* (ITS KP691436, LSU KR605507); ITS+LSU from sporocarp KY774241.

Notes — According to GenBank data for this sporocarp sample, the associated vegetation is *Nothofagus aequilateralis* forest. The collection date is taken from Carriconde et al. (2019); twelve sampling rounds for epigeal sporocarps were completed during the period April 2013–April 2014.

Lactifluus **sp. 6**

Sequence data. New Caledonia, Koniambo Mountain, 15 May 2017, *Trazy*, *A. Houles & F. Joussemet KT-26* (ITS LC271308); ibid., *Trazy*, *A. Houles & F. Joussemet KT-47* (ITS LC271325).

Notes — According to GenBank data for these root-tip samples, the associated vegetation is *Tristaniopsis guillainii*.

Section *Luteoli*

Lactifluus sect. *Luteoli* is a diverse group with widespread global distribution. Species are known from Asia, Australia, Africa, Europe, and North America, notably occurring in tropical rainforests of Togo, Zambia, Indonesia, and Thailand as well as more temperate Mediterranean regions of Europe and USA (De Crop et al. 2017). The section is characterised by capitate elements in the pileipellis and marginal cells (Verbeken & Walleyn 2010, De Crop et al. 2017).

Lactifluus russulisporus Dierickx & De Crop, Index Fungorum 392: 1. 2019 — Index Fungorum IF 829913; Fig. 16c, 19

Typus. Australia, Queensland, Fraser Island, Wanggoolba Creek Road, West of Central Station, alt. 90 m, S25°28' E153°2', 27 May 2010, leg.: *R.E. Halling*, *N. Fechner & M. Castellano R.E.H. 9398*, holotypus BRI, isotypus NY.

Distribution & Habitat — Gregarious on sand in dry sclerophyll forest with *Leptospermum* sp., *Syncarpia* sp., *Eucalyptus pilularis*, *E. microcorys*. Basidiomes emerge around May.

Additional specimens examined. Australia, New South Wales, Central Tablelands, Lithgow near Marrangaroo National Park, c. 1 km WNW of Cooerwull Road and Great Western Highway junction, 24 May 2009, *N. Fechner*, *R.E. Halling & P. Leonard PL11509* MEL 2336075; W of Brisbane, D'Aguilar National Park, Maiala Area walking tracks, 8 Mar. 2012, *R.E. Halling 9674* BRI, NY.

Notes — *Lactifluus russulisporus* was recently described from two Queensland collections REH 9398 and REH 9674 from Fraser Island and D'Aguilar National Park west of Brisbane (Dierickx et al. 2019). The known range of this species is extended considerably with a third collection from central New South Wales, near Lithgow. The basidiomes of MEL 2336075 are slightly larger (pileus 40–50 mm diam, stipe 40–60 × 5–11 mm), and appear to have a little more of a hint of apricot in colour. Microscopically, the only difference appears to be somewhat shorter suprapellis elements (up to 80 µm vs 180 µm in other collections). This species is strongly supported in subg. *Gymnocarpi* sect. *Luteoli* as sister to *Lf. caliendrifer* from Thailand (Fig. 3). Most species in sect. *Luteoli* have creamy-yellowish basidiomes, dry, finely velvety to pruinose pilei, crowded lamellae and copious latex that stains brown. *Lactifluus caliendrifer* has paler basidiomes and a stronger fruity smell than *Lf. rus-*

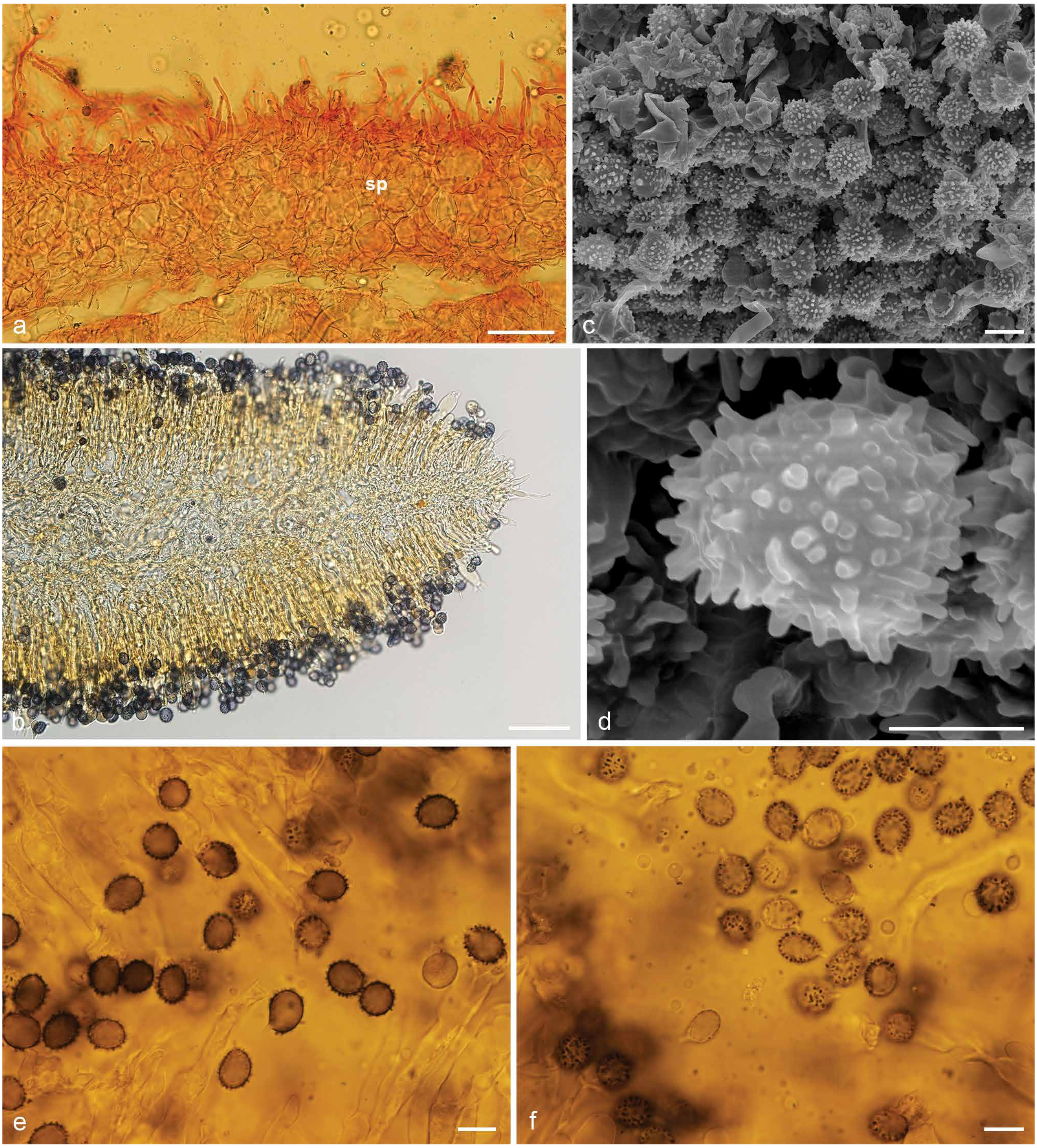

Fig. 19 *Lactifluus russulisporus*. a. Pileipellis terminal elements and polycystoderm subpellis (sp); b. hymenium with basidia, cystidia and spores; c–d. SEM of basidiospores; e–f. basidiospores. — Scale bars: a–b = 50 µm; c, e–f = 10 µm; d = 5 µm.

sulisporus which is more yellowish and has a strong unpleasant fishy odour (Dierickx et al. 2019). Micromorphologically, *Lf. caliendrifer* has longer pileipellis elements, larger spores and basidia, and numerous thick-walled marginal cells than can be found in *Lf. russulisporus*. Two recently described species of *Lactifluus* with pale basidiomes, *Lf. austropiperatus* and *Lf. albocpicri* differ in the lack of a fishy smell, tasting hot peppery rather than mild, and the finer ornamentation connected in short lines vs taller isolated warts.

Subgenus *Pseudogymnocarpi*

This subgenus is not easy to distinguish from other subgenera morphologically, as it appears to have a mixture of characters. De Crop et al. (2017) state that it is characterised by yellow, orange to reddish brown caps and a trichoderm to (lampro)(tricho) palisade as pileipellis. In some species, true pleurocystidia are absent, while others have pleurolamprocystidia or pleuromacrocystidia. Some species show striking colour reactions of the latex, but most species do not.

Unnamed clade

***Lactifluus* sp. 7** — Fig. 20

Pileus with deeply depressed centre, even in young basidiomes, 30–60(–80) mm diam, centre sienna (11; Edinburgh colour chart) to dark brick (20) shading to cinnamon (10) to rusty tawny orange (14) with paler margins (pale ochre (9H)) in some basidiomes, smooth to somewhat wrinkled or very finely felted,

Fig. 20 Subgenus *Pseudogymnocarpi Lactifluus* sp. 8 basidiomes.

margins sometimes uplifted, irregularly; context creamy to buff ochre. *Lamellae* adnate to subdecurrent, occasionally forking, white to cream, moderately spaced with 3–4 tiers lamellulae, coloured brown where latex dries. *Stipe* 30–40 by 8–12(–17) mm, rust (13) to sienna (11), longitudinally streaked, stuffed or solid in younger material; context white. *Spore print* cream. *Latex* white drying dark brown, copious; taste mild to slightly astringent but not hot. *Odour* and *taste* mild. *Chemical tests*: phenol faintly violet-pink after 5–10 mins; $FeSO_4$ greenish grey slowly.

Distribution & Habitat — Southern Queensland. Associated with *Eucalyptus* and *Melaleuca* spp. dominated vegetation in coastal open woodland and sometimes with regenerating subtropical rainforest with scattered eucalypts. Basidiomes emerging February–May.

Specimen examined. Australia, Queensland, Great Sandy National Park, Cooloola, Freshwater Rd, growing in association with *Melaleuca* and *Eucalyptus* sp., 23 May 2011, *R.E. Halling*, *T. Baroni*, *N.A. Fechner REH 9539* BRI: AQ797939; Great Sandy National Park, Fraser Island, Pile Valley Walking Track, 12 Feb. 2009, *N. Fechner 12209-26*, BRI: AQ797607; Mt Tambourine National Park, Palm Groves Track, in *Eucalyptus* forest, 1 Mar. 2009, *K. Querengasser*, *M. Prance*, *R. Thomson* BRI: AQ794627; Wide Bay District, Dilkusha Nature Refuge, Maleny, Hoya Track, under *Eucalyptus* and regenerating subtropical rainforest, 22 Mar. 2018, *F.E. Guard FG2018031* MEL 2458232; Taromeo, Playstowe Rd, 21 May 1989, *A. Young & D. Young 1457* BRI: AQ 808494; D'Aguilar National Park, Mount Mee, 3 Mar. 1990, *A. Young 1525* BRI: AQ808475.

Notes — The pileus surface of close relative *Lf. armeniacus* is also wrinkled, with an undulate margin and pruinose texture, and thus similar in morphology to *Lf.* sp. 7 (Fig. 19). This species will be fully described in another paper.

Subgenus *Lactifluus*

Section *Lactifluus*

Lactifluus sect. *Lactifluus* has a diversity of species in Asia, North America, and Europe, and is distinguished from other sections in subg. *Lactifluus* by the: reticulate basidiospore ornamentation, thick-walled or 'lampro' hymenial cystidia and thick-walled 'lampropalisade' pileipellis and stipitipellis structures; a distinctly fishy odour, white latex which stains brown on tissues, and velutinous pileus texture with colours ranging from orange to brown (Van de Putte et al. 2010, 2016, De Crop et al. 2017).

Dried material of all Australian taxa examined have a distinctly fishy odour, however fresh material may have a different or less distinctive odour.

Lactifluus jetiae L. Vaughan, L. Tegart, J. Douch & T. Lebel, *sp. nov.* — MycoBank MB 837610; Fig. 21a–b, 22

Etymology. The epithet '*jetiae*', acknowledges the meticulous work of Jennifer E. Tonkin (collector initials JET) who contributed many collections of *Lactarius*, *Lactifluus*, and *Russula* to the National Herbarium of Victoria (MEL), and completed preliminary research on these genera in Australia.

Typus. Australia, Victoria, East Gippsland, Cann River, 6 km west of Cann River, 100–200 m from Princes Highway, Reed Bed Road, open *Eucalyptus* sp. woodland with *Banksia* sp., *Acacia* sp., and *Leptospermum* sp., 26 May 2002, *J.E. Tonkin 987* (holotype MEL 2238281).

Diagnosis — Robust bright reddish orange basidiomes with plane to upturned pileus, decurrent white to pale fawn lamellae discolouring orange brown, and a cylindrical stipe that is slightly paler than the pileus with white to cream-coloured context; white latex not abundant. Strong fishy smell when dry. Basidiospores are globose to ellipsoid with robust reticulate ornamentation (ridges up to 2 μm high), hymenial cystidia are relatively short (less than 50 μm long).

Pileus up to 75 mm diam, convex to plane and centrally depressed, becoming evenly upturned, bright reddish orange with darker patch in central depression, margin straight and entire to slightly wavy; surface smooth or minutely rugulose from centre, minutely pubescent and occasionally rivulose; context whitish to pale yellow and solid. *Lamellae* decurrent, close to crowded (21–29 L + l/cm), moderately broad (0.1–0.4 mm), 2–2.5 mm deep, whitish cream to pale fawn, discolouring orange-brown when damaged, fragile, occasionally forked, lamellulae intermixed (l = 9–32/half pileus). *Stipe* up to 28 mm long and 10 mm wide at base, up to 15 mm wide at lamellae junction, cylindrical and tapering towards base, pale yellowish orange to reddish orange, mostly darker towards base, discolouring orange-brown when damaged, surface smooth and minutely pubescent; stipe context whitish to cream-coloured, solid and contiguous with that of pileus.l*atex* white, not abundant; observed only in one collection. *Odour* not distinctive when fresh; strong fishy when dry. *Taste* not obvious.

Basidiospores 7–10 × 6–9 μm ($\bar{x}$ = 8.55 ± 0.83 × 7.79 ± 0.95, *n* = 17), globose to ellipsoid (Q = 1.00–1.25 ($\bar{x}$ = 1.10 ± 0.08, *n* = 17)), ornamentation forming a wide and mostly complete reticulum with ridges up to 2 μm, isolated warts occasionally present, plage not or distally amyloid. *Basidia* 36–58 × 8–14 μm ($\bar{x}$ = 45.08 ± 7.63 × 10.25 ± 1.48, *n* = 22), 3–6 μm wide at base ($\bar{x}$ = 4.17 ± 0.94, *n* = 22), clavate to subfusiform, mostly 2-spored (70–75 % of basidia) but occasionally 3- or 4-spored; sterigmata 3–12 × 1–3 μm ($\bar{x}$ = 8.38 ± 2.90 × 2.00 ± 0.71, *n* = 18); basidioles 30–49 × 6–11 μm ($\bar{x}$ = 35.29 ± 4.86 × 9.14 ± 1.41, *n* = 19), 2–5 μm wide at base ($\bar{x}$ = 3.36 ± 0.74, *n* = 18). *Hymenophoral trama* comprising interwoven hyphae 2–3 μm diam, sinuous laticiferous hyphae 5–7 μm diam and

Fig. 21 Subgenus *Lactifluus* sect. *Lactifluus* basidiomata. a–b. *Lf. jetiae* sp. nov.; c. *Lf. pagodicystidatus* sp. nov.; d. *Lf.* sp. 9; e–f. *Lf. rugulostipitatus* sp. nov. — Scale bars: 10 mm. — Photos: a–b by J.E. Tonkin; c by K.R. Thiele; d by R.E. Halling; e–f by G. Lay.

sphaerocytes 32–56 × 17–32 µm; *subhymenium* up to 60 µm wide, composed of hyphae and 3–4 layers of inflated, round, or angular polygonal cells 8–30 × 6–24 µm ($\bar{x}$ = 16.40 ± 6.10 × 11.40 ± 5.62, *n* = 25), laticiferous hyphae present and occasionally extending into hymenium as cystidia. *Pleurolamprocystidia* 18–41 × 3–10 µm ($\bar{x}$ = 27.50 ± 7.56 × 6.63 ± 2.56, *n* = 8), narrow-cylindrical to subfusiform, tapering toward apex and base and occasionally pagodaform or nearly so, apex obtuse or capitate, slightly emergent above hymenium, abundant. *Pleuropseudocystidia* 2–6 µm diam ($\bar{x}$ = 4.25 ± 1.39, *n* = 8), subcylindrical or tortuose, sometimes branching, sometimes septate, apex obtuse or lobed and branched, rarely emergent above hymenium, scarce. *Cheilolamprocystidia* 23–36 × 3–12 µm ($\bar{x}$ = 30.60 ± 4.77 × 9.30 ± 2.75, *n* = 10), subcylindrical to subfusiform, tapering toward apex and base and occasionally pagodaform or nearly so, apex capitulate or obtuse and mostly narrowing in one or two segmented tiers, emergent above hymenium, often arising from subhymenium. *Pileipellis* a lampropalisade: subpellis a 3–7-layered epithelium consisting of round, angular or elongate thick-walled polygonal cells, 11–32 × 6–16 µm ($\bar{x}$ = 16.92 ± 5.68 × 10.00 ± 2.86, *n* = 12); terminal elements elongate, 16–41 × 3–7 µm ($\bar{x}$ = 25.88 ± 9.62 × 4.63 ± 1.20, *n* = 16), thick-walled, narrow-cylindrical, slightly swollen where attached to polygonal cells at base, tapering towards apex, apex acuminate to subobtuse, outline slightly sinuate; *pileus trama* similar to hymenophoral trama, heteromerous. *Stipitipellis* a lampropalisade: subpellis consisting of several layers of round or angular, thick-walled polygonal cells 7–12 × 4–7 µm; terminal elements elongate, 18–31 × 2–3 µm ($\bar{x}$ = 26.20 ± 5.54 × 2.40 ± 0.55, *n* = 5), narrow-cylindrical, tapering towards apex, apex acuminate or sharply pointed; *stipe trama* similar to hymenophoral trama, heteromerous and tightly packed.

Distribution & Habitat — South-eastern Victoria. Open eucalypt woodland with *Banksia*, *Acacia*, and low shrub understorey with herbaceous groundcover. Basidiomes emerging May–June.

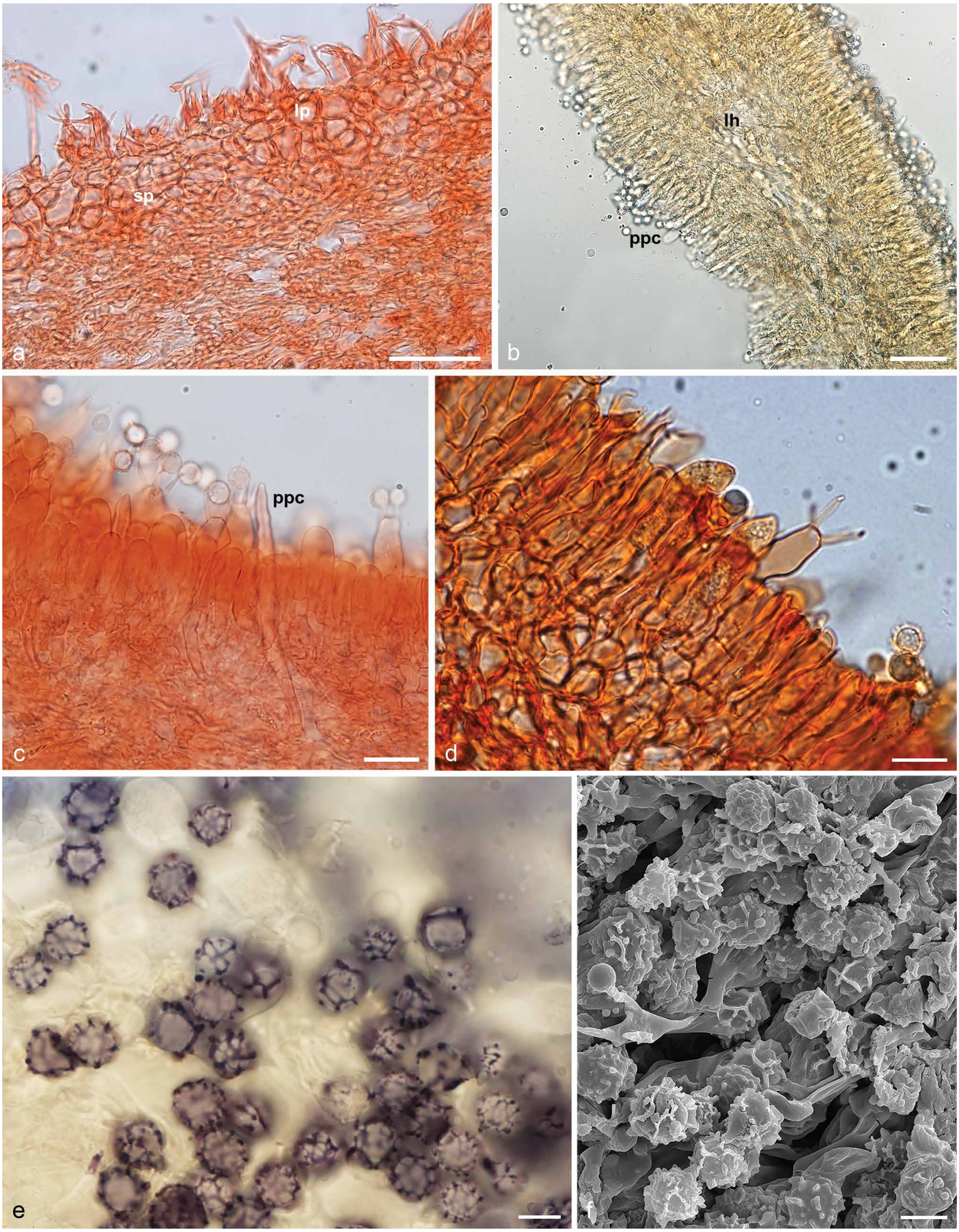

Fig. 22 *Lactifluus jetiae* sp. nov. a. Lampropalisade pileipellis terminal elements (te), subpellis (sp) and pellis context; b. hymenophoral trama with laticiferous hyphae (lh), cystidia; c. pleuropseudocystidia (ppc) and pleurolamprocystidium (plc); d. subhymenium, basidium, basidioles; e. basidiospores (MEL 2238281); f. SEM of basidiospores (MEL 2238281). — Scale bars: a, d–e = 20 µm; b = 50 µm; c, f = 10 µm.

Additional specimens examined. Australia, Victoria, Mornington Peninsula, Main Ridge Nature Reserve, near Mornington-Flinders Road carpark, 5 June 2010, *N.H. Sinnott 3827* MEL 2341759; East Gippsland, 500 m south of Club Terraces, 26 May 2002, *J.E. Tonkin 992* MEL 2238286.

Notes — *Lactifluus jetiae* is found in eucalypt forests of southern Victoria, likely in mycorrhizal association with species of *Myrtaceae*. It can be recognised by its striking bright reddish orange pileus, which becomes upturned without an incurved margin, basidiospores with robust ornamentation up to 2.0 µm high, relatively long sterigmata on mostly 2-spored basidia, relatively short hymenial cystidia (occasionally having pagodaform shape; see notes for *Lactifluus pagodicystidiatus* for explanation), and terminal elements of pileipellis less than 100 µm long. Microscopy is required to differentiate *Lf. jetiae*, as the relatively robust bright orange basidiocarps, pale lamellae that bruise orange brown, are easily confused with other taxa in the *Lf. clarkeae* species complex (see Key on p. 15). Laticiferous hyphae were observed in material from all three collections (MEL 2238281 (holotype), MEL 2232826, MEL 2341759); however, latex was only observed in the field on the lamellae tissue of MEL 2341759.

This species is morphologically similar to *Lf. longipilus* from Thailand (Van de Putte et al. 2010), *Lf. pallidilamellatus* from Mexico, and *Lf. oedematopus* from Europe.

Lactifluus pagodicystidiatus L. Vaughan, L. Tegart & J. Douch, *sp. nov.* — MycoBank MB 837611; Fig. 21c, 23, 24

Etymology. The epithet, 'pagodicystidiatus', refers to the shape of the portion of hymenial cystidia visible above the hymenium, which is distinctly stacked in narrowing strangulations resembling a pagoda tower.

Typus. Australia, Victoria, East Gippsland, 3 km WSW of Goongerah, Joys Creek Track near the summit of Mount Jersey, *Eucalyptus delegatensis*/*E. cypellocarpa* wet forest, 27 Mar. 2002, *K.R. Thiele 2703* (holotype MEL 2150777).

Diagnosis — Robust orange-buff becoming dull-orange pileus with strongly incurved margin, pale cream to pale orange decurrent lamellae discolouring to brownish buff when damaged, and stout orange-buff stipe. Basidiospore ornamentation finely reticulate (ridges less than 1 µm high), pleurolamprocystidia relatively long (up to 100 µm long), pagodaform with obtuse or capitulate apices; cheilocystidia similar shape and size.

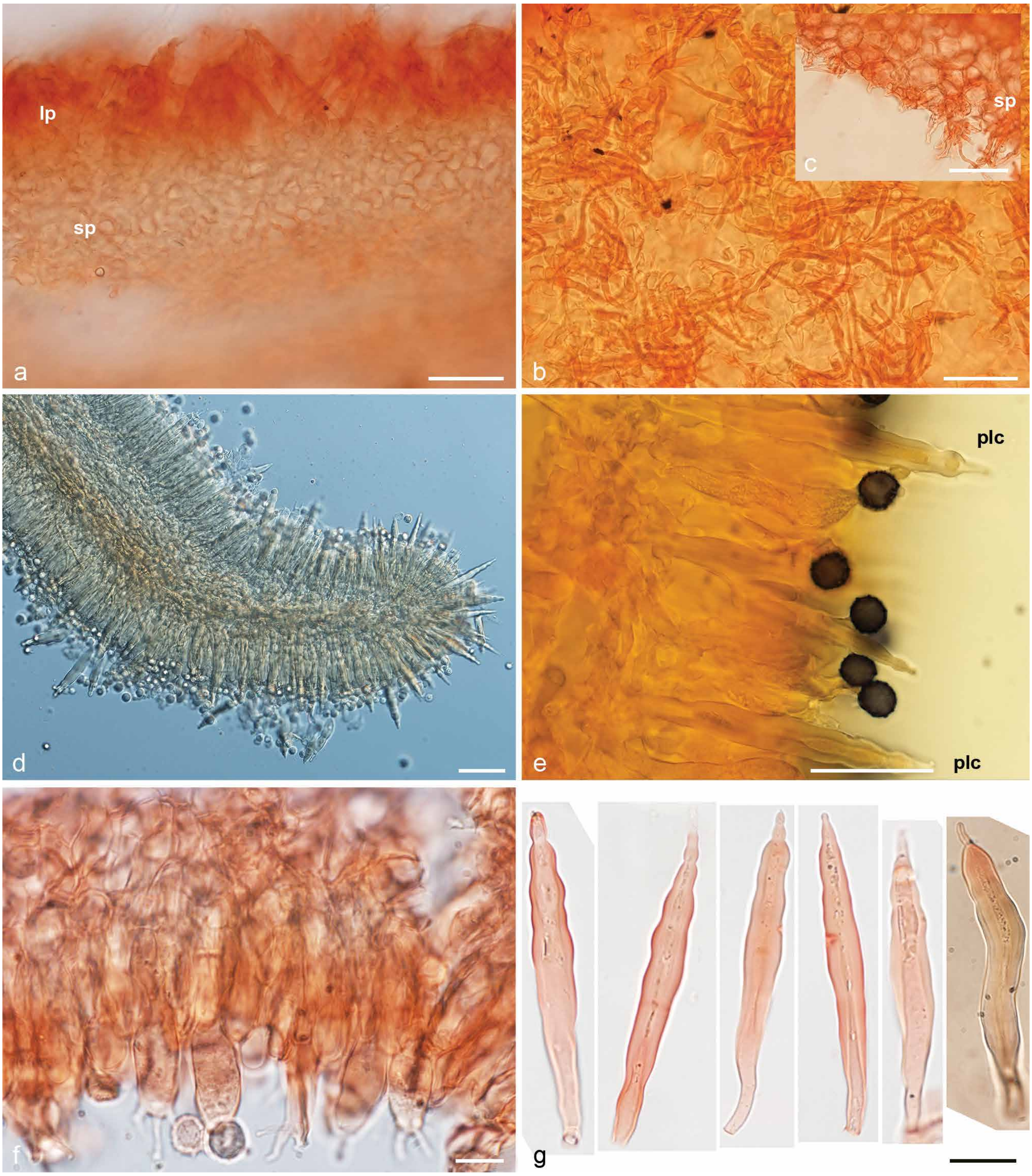

Fig. 23 *Lactifluus pagodicystidiatus* sp. nov. a. Lampropalisade pileipellis terminal elements and subpellis (sp); b. scalp section of pellis terminal elements (te); c. inflated cells of subpellis (sp); d. hymenial trama with cystidia; e. pleurolamprocystidium (plc) and spores; f. subhymenium and basidia; g. pleurolamprocystidia variation. — Scale bars: a–b, d–e = 50 µm; c, f–g = 10 µm.

Pileus 27–55 mm diam, younger specimens convex, centrally depressed, becoming rounded to plane and widely upturned with age, orange-buff with red undertone quickly fading to dull orange-buff, margin entire and thick, initially strongly incurved, persisting but becoming less so in mature basidiomes, distinctly smooth, minutely pubescent to velvety; context cream and solid. *Lamellae* subdecurrent to decurrent, close to crowded (22–27 L + l/cm), moderately broad (0.1–0.5 mm), up to 2.5 mm deep, pale cream to orange-cream, discolouring to brownish buff when damaged, brittle, sometimes forked, lamellulae occasional and intermixed (l = 5–8/half radius). *Stipe* 16–30 × 9–18 mm, stout cylindrical to faintly subfusiform, slightly tapering toward base and pileus, orange-buff similar to pileus and equally fading to dull, becoming dull orange-brown when damaged, surface distinctly smooth to minutely pubescent; context cream, spongy. *Latex* white, sparse, slightly sweet to taste. *Odour* not distinctive when fresh; strong fishy when dry. *Taste* not obvious.

Basidiospores 7.6–9.4 × 7.3–8.6 µm ($\bar{x}$ = 8.19 ± 0.68 × 7.57 ± 0.70, *n* = 30), globose to subglobose (Q = 1.00–1.19 ($\bar{x}$ = 1.08 ± 0.06, *n* = 30)), ornamentation robust reticulate, forming an even and narrow netting with ridge apices less than 1 µm, walls between ridges variably amyloid, plage faintly to completely amyloid; slightly elongate hilar appendix 1–2 µm. *Basidia* 40–68 × 8–12 µm ($\bar{x}$ = 55.92 ± 8.42 × 9.39 ± 1.76, *n* = 23), 3–5 µm wide at base ($\bar{x}$ = 4.00 ± 0.82, *n* = 21), clavate to subfusiform or centrally inflated, apex sometimes squared, mostly 2-spored but occasionally 3- or 4-spored; sterigmata 3–8 × 1–3 µm ($\bar{x}$ = 5.07 ± 1.27 × 1.93 ± 0.83, *n* = 24); basidioles 23–53 × 5–11 µm ($\bar{x}$ = 36.80 ± 10.00 × 7.47 ± 2.03, *n* = 15), 2–5 µm wide at base ($\bar{x}$ = 3.4 ± 0.91, *n* = 15). *Hymenophoral trama* cellular, comprising interwoven hyphae 2–4 µm diam, sinuous and winding laticiferous hyphae 2–8 µm diam, and sphaerocytes 20–32 × 10–20 µm; *subhymenium* 70–90 µm wide, comprising interwoven hyphae and 4–6 layers of closely interconnected polygonal cells 5–22 × 5–15 µm ($\bar{x}$ = 12.83 ± 4.82 × 8.42 ± 3.63, *n* = 12), laticiferous hyphae present and arising from hymenophoral trama, often extending through hymenium as cystidia. *Pleurolamprocystidia* 67–90 × 7–15 µm ($\bar{x}$ = 72.50 ± 13.81 × 11.00 ± 3.16, *n* = 6), 4–5 µm wide at base ($\bar{x}$ = 4.50 ± 0.55, *n* = 6), narrow-cylindrical to centrally inflated or subfusiform, tapering toward apex and base, mostly pagodaform, tapering in 2–4 tiers, strangulated segments narrowing toward apex, apex obtuse or capitulate, distinctly emergent above hymenium and often arising from subhymenium or hymenophoral trama, abundant. *Pleuropseudocystidia* 3–5 µm diam ($\bar{x}$ = 4.17 ± 0.75, *n* = 6), up to 55 µm long, narrow-cylindrical or tortuose, often septate, apex obtuse or acuminate or lobed and capitate, arranged among basidia and basidioles, rarely emergent, scarce to moderately abundant. *Cheilolamprocystidia* 60–95 × 8–13 µm ($\bar{x}$ = 77.14 ± 10.88 × 10.29 ± 1.80, *n* = 7), 2–5 µm wide at base ($\bar{x}$ = 3.14 ± 1.07, *n* = 7), thick-walled, narrow-cylindrical, sometimes with basal or central inflation, mostly pagodaform, tapering in 3–several tiers, strangulated segments narrowing toward sharp point, apex acute, distinctly emergent above hymenium at lamellae edge and often arising from subhymenium. *Pileipellis* a lampropalisade; subpellis 40–65 µm wide, consisting of closely interlocked, rounded or angular, thick-walled polygonal cells 9–25 × 5–13 µm ($\bar{x}$ = 14.23 ± 4.90 × 8.15 ± 2.88, *n* = 13); terminal elements 30–52 × 3–5 µm ($\bar{x}$ = 40.89 ± 7.98 × 4.22 ± 0.83, *n* = 9), narrow-cylindrical tapering from base to apex, apex obtuse or acuminate, outline often sinuate or wavy, densely packed, thick-walled; *pileus context* similar to hymenophoral trama, heteromerous with larger sphaerocytes 24–54 × 10–24 µm and less abundant laticiferous hyphae. *Stipitipellis* a lampropalisade; subpellis comprising several loosely arranged

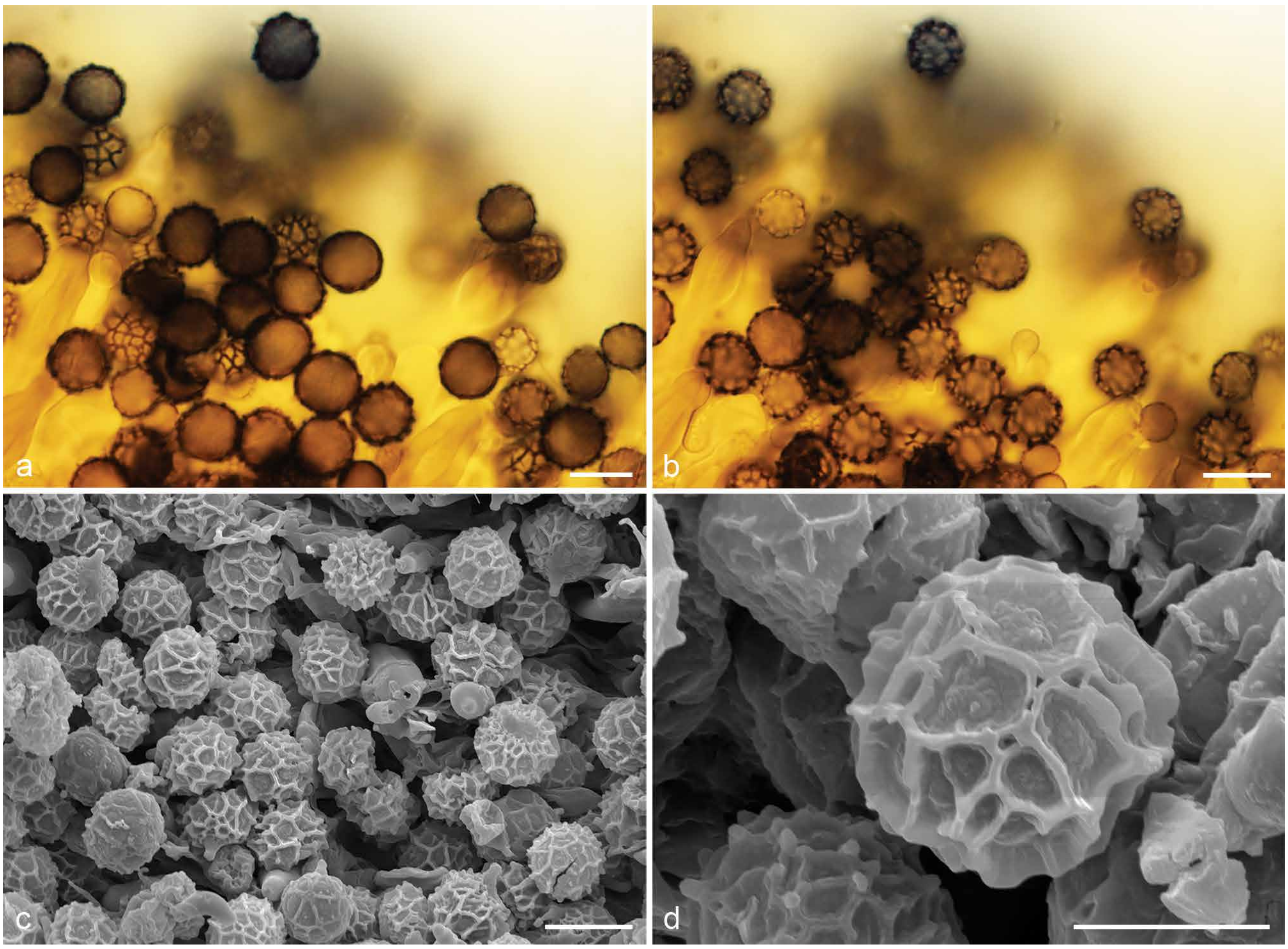

Fig. 24 *Lactifluus pagodicystidatus* sp. nov. a–b. Basidiospores; c–d. SEM of basidiospores. — Scale bars: a–d = 10 µm.

layers of round, angular or elongate, thick-walled polygonal cells 10–27 × 8–22 µm ($\bar{x}$ = 19.45 ± 5.56 × 14.45 ± 5.30, *n* = 11); terminal elements 18–50 × 2–6 µm ($\bar{x}$ = 40.3 ± 16.66 × 3.1 ± 1.29, *n* = 10), narrow-cylindrical tapering from base to apex or minutely subfusiform, apex acute or subacute, outline wavy or flexuose, densely packed and tangled, thick-walled; *stipe trama* similar to hymenophoral trama, heteromerous, sphaerocytes 20–58 × 10–30 µm.

Distribution & Habitat — South-eastern Victoria. *Eucalyptus* spp. wet forest. Mixed *Eucalyptus delegatensis*/*E. cypellocarpa* and *Syzygium smithii* or mixed *E. radiata*/*E. obliqua* wet forest. Basidiomes emerge March–June.

Additional specimens examined. Australia, Victoria, East Gippsland, Martins Creek, c. 48 km north of Orbost on Bonang Road, 28 Mar. 2005, *K.R. Thiele 3004* MEL 2320494; Mornington Peninsula, Main Ridge, c. 2 km north of Baldrys Road/Mornington-Flinders Road junction, c. 500 m east of Baldrys Road, 8 June 1978, *F.M. Cole* MEL 2121979.

Notes — *Lactifluus pagodicystidiatus* is found in moist *Eucalyptus* spp. sclerophyll forests of south-eastern Victoria. It is sister to an undescribed taxon (*Lf.* sp. 10 NSW/QLD) which appears to be distributed on Fraser Island, Queensland and northern New South Wales in association with *Eucalyptus* spp., and in a broader clade with *Lf. crocatus* from Thailand, and undescribed species from Thailand/India and Japan (Fig. 5). The *Lf.* sp. 10 NSW/QLD sequences are separated from the *Lf. pagodicystidiatus* node in the ITS phylogeny by 8 base pairs or around 1 % base pair difference.

Lactifluus pagodicystidiatus has similar macromorphology to various species around the world in the *Lf. volemus* s.lat. group, having a rather robust basidiome with a smooth, stout stipe and centrally depressed plano-convex pileus. In comparison to *Lf. crocatus*, *Lf. subvolemus*, and *Lf. volemus* sensu Van de Putte et al. (2016), which have a velutinous pileus texture and similar general morphology, *Lf. pagodicystidiatus* has distinctly shorter pileipellis cystidia and the strangulations of hymenial cystidia are more regular and symmetrical (Van de Putte et al. 2016).

Hymenial cystidia of this taxon are described as 'pagodaform'. Structures of similar morphology are described as 'strangulated' by Largent et al. (1977) or as 'gloeocystidia' by Hawksworth et al. (1995). Though structures described in the literature are somewhat comparable, the pagodaform elements described here are uniquely strangulated across the terminal third or quarter of the cystidia. The strangulations are regular, more or less symmetrical, and consistently found narrowing toward the apex in multiple tiers like a pagoda tower with multiple eaves. Pleurolamprocystidia taper in 2–4 tiers and terminate in a rounded apex, while cheilocystidia taper in 3–several tiers with a distinctly sharp-pointed apex. Cystidia are conspicuously emergent on lamellae edge and face, clearly exposing their pagodaform character in hymenial sections under light microscope and giving this species its name.

Lactifluus rugulostipitatus J. Douch, L. Tegart, L. Vaughan & T. Lebel, *sp. nov.* — MycoBank MB 837612; Fig. 21e–f, 25

Etymology. Lactifluus rugulostipitatus has a distinctly longitudinally wrinkled stipe surface texture in fresh material, which is a unique feature among the taxa described here.

Typus. Australia, Northern Territory, Gubara near Mount Bundley, near Arnhem Highway c. 2 km east of Old Jim Road, forest near fork in river c. 3 km north of Arnhem Highway, *Allosyncarpia ternata* rainforest, 14 Mar. 2009, *G.M. Lay 14* (holotype MEL 2329677).

Diagnosis — Dull, pale orange-ochre to dark yellow velvety pileus with faint concentric rings of wrinkles and darker orange colouration, lamellae pale cream to pale orange, stipe longitudinally rugulose and slightly velvety. Basidiospores subglobose with finely reticulate ornamentation, cystidia are mostly longer than 50 µm.

Pileus 25–42 mm diam (dried specimens), centrally depressed, convex to plane when immature to unevenly wide-upturned when mature, dull pale orange-ochre with dark yellow undertone, becoming paler orange-tinted cream towards margin, flesh thin, margin sharp and strongly incurved in younger or dried specimens, slightly so in mature fresh material, minutely pubescent to velvety and rugulose when young, becoming rugose in faint concentric rings of slightly darker orange pigmentation away from centre, more obvious in older specimens; context golden orange-cream and solid. *Lamellae* decurrent, close (12–24 L + l/cm), narrow (0.05–0.1 mm), up to 3 mm deep, pale yellowish cream to orange-cream, darker buff where bruised or damaged, whitish pruinose in older specimens, fragile, rarely forking, lamellulae intermixed (l = 11–17/half pileus). *Stipe* 23–42 × 3–9 mm (dried specimens), unevenly circular to approximately terete, slightly centrally tapering or tapering toward base, pale orange-ochre (similar to pileus, less orange), longitudinally wrinkled (rarely laterally) and minutely pubescent; context golden orange-cream and contiguous with pileus context. *Latex* not observed. *Odour* not distinctive when fresh; slightly fishy when dry. *Taste* not distinctive.

Basidiospores 6.8–9.0 × 6.0–8.4 µm ($\bar{x}$ = 8.18 ± 0.61 × 7.41 ± 0.73, *n* = 36), subglobose, Q = 1.00–1.21 ($\bar{x}$ = 1.11 ± 0.06, *n* = 36), ornamentation a robust almost complete reticulum with ridges up to 1 µm high, walls between ridges mostly amyloid, plage distally to completely amyloid; hilar appendix up to 2.5 µm. *Basidia* 39–63 × 9–12 µm ($\bar{x}$ = 53.00 ± 7.32 × 11.17 ± 1.03, *n* = 18), 2–5 µm wide at base ($\bar{x}$ = 3.79 ± 0.94, *n* = 15), clavate to subfusiform, commonly 2-spored but also 3- or 4-spored; sterigmata 6–10 × 2–4 µm ($\bar{x}$ = 8.00 ± 1.33 × 2.50 ± 0.82, *n* = 10); basidioles 21–51 × 6–12 µm ($\bar{x}$ = 37.35 ± 8.20 × 8.60 ± 1.69, *n* = 18), 3–5 µm wide at base ($\bar{x}$ = 4.09 ± 0.54, *n* = 18), cylindrical to clavate. *Hymenophoral trama* cellular, consisting of interwoven hyphae 2–4 µm diam, laticiferous hyphae 2–8 µm diam, and sphaerocytes 13–30 × 9–22 µm ($\bar{x}$ = 19.71 ± 4.66 × 13.71 ± 3.50, *n* = 17); *subhymenium* 20–40 µm wide, 3–5 layers of interconnected polygonal cells 7–13 × 5–12 µm ($\bar{x}$ = 9.71 ± 1.68 × 7.14 ± 1.96, *n* = 14), angular to almost spherical, thick-walled. *Pleurolamprocystidia* 57–90 × 5–9 µm ($\bar{x}$ = 69.78 ± 9.19 × 6.83 ± 0.92, *n* = 18), 2–5 µm at base ($\bar{x}$ = 2.96 ± 0.78, *n* = 18), narrow-cylindrical to narrow-subfusiform, tapering toward apex and base with widest point two thirds of the way towards apex, apex constricted or somewhat strangulated and tapering, emergent above hymenium and sometimes arising from subhymenium or hymenophoral trama, moderately to very abundant, outline sinuous or wavy. *Pleuropseudocystidia* 3–8 µm diam ($\bar{x}$ = 4.80 ± 2.19, *n* = 10), flexuose and cylindrical to fusiform, apex obtuse, rarely emergent above hymenium, scarce. *Cheilolamprocystidia* 55–95 × 5–9 µm ($\bar{x}$ = 70.40 ± 10.96 × 6.55 ± 1.23, *n* = 20), 2–5 µm wide at base ($\bar{x}$ = 2.91 ± 0.77, *n* = 20), thick-walled, narrow cylindrical to fusiform, occasionally somewhat pagodaform and tapering toward apex in narrowing tiers, apex acuminate, distinctly emergent above basidia. *Pileipellis* a lampropalisade; subpellis 20–70 µm wide, composed of 4–7 tiers of closely interconnected rounded, angular, or elongated thick-walled polygonal cells 6–15 × 4–10 µm ($\bar{x}$ = 10.70 ± 2.36 × 8.00 ± 1.94, *n* = 10); terminal elements 14–75 × 2–5 µm ($\bar{x}$ = 41.19 ± 17.26 × 4.01 ± 1.05, *n* = 21), 2–5 µm wide at base ($\bar{x}$ = 3.03 ± 0.95, *n* = 21), narrow-subcylindrical to fusiform or almost obclavate, swollen near attachment to polygonal cells, outline wavy to flexuose, tapering toward apex, apex acute or acuminate, thick-walled, contents in narrow thread when present; *pileus trama* similar to hymenophoral trama, heteromerous. *Stipitipellis* a lampropalisade; subpellis 30–50 µm wide, composed of 3–5 tiers of rounded, irregular, or elongated thick-walled polygonal cells, 6–16 × 4–10 µm ($\bar{x}$ = 11.40 ± 3.47 × 7.40 ± 2.07, *n* = 10); terminal elements sparse, 34–50 × 3–4 µm ($\bar{x}$ = 44.00 ± 8.72 ×

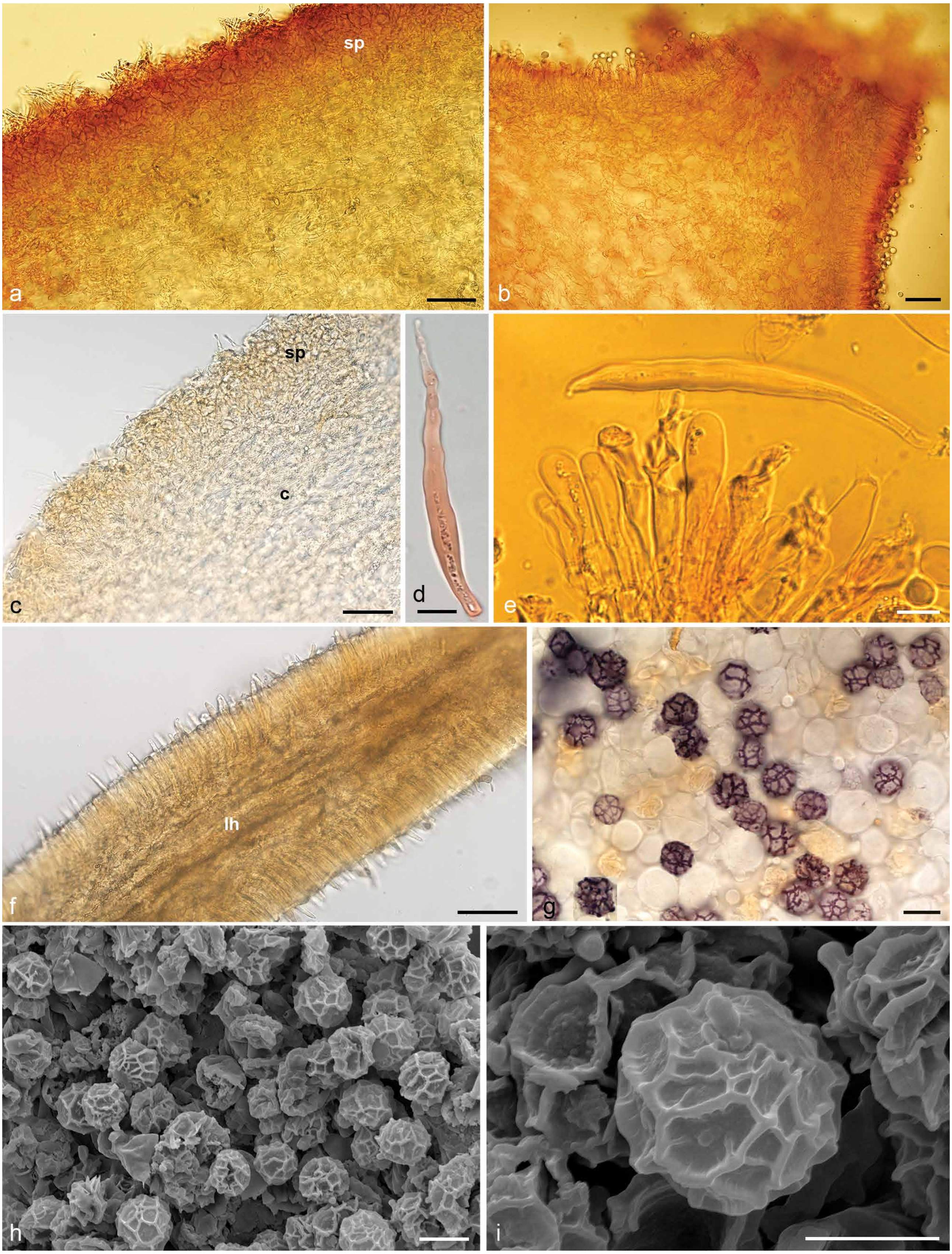

Fig. 25 *Lactifluus rugulostipitatus* sp. nov. a. Lampropalisade pileipellis terminal elements (te), subpellis (sp) and context (MEL 2329677); b. hymenophoral trama; c. pileipellis terminal elements (te), subpellis (sp) and conext (c); d. hymenial pleurolamprocystidium (MEL 2329677); e. pleuropseudocystidia, basidioles, basidium; f. hymenial trama with abundant laticiferous hyphae (lh); g. basidiospores (MEL 2329677); h–i. SEM of basidiospores (MEL 2329677). — Scale bars: a–c, f = 50 µm; d–e, g–i = 10 µm.

3.33 ± 0.58, $n = 5$), narrow-cylindrical to subfusiform, tapering towards apex, apex subobtuse or faintly capitulate; *stipe trama* similar to hymenophoral trama, heteromerous.

Distribution & Habitat — Northern Territory near Kakadu, subtropical monsoon rainforest associated with *Myrtaceae*, particularly *Allosyncarpia ternata*. Basidiomes emerging in March.

Additional specimens examined. Australia, Northern Territory, Gubara near Mount Bundley, near Arnhem Highway, c. 2 km east of Old Jim Road, forest near fork in river c. 3 km north of Arnhem Highway, 14 Mar. 2009, *G.M. Lay 15* MEL 2329678; Gubara near Mount Bundley, near Arnhem Highway c. 2 km east of Old Jim Road, forest near fork in river c. 3 km north of Arnhem Highway, *Allosyncarpia ternata* rainforest; 14 Mar. 2009, *G.M. Lay 10* MEL 2329673.

Notes — *Lactifluus rugulostipitatus* is distinctive among currently described Australasian *Lactifluus* species due to its dull basidiomes with pale orange-ochre to dark yellowish tones and longitudinally wrinkled stipe surface texture, plus its association with *Allosyncarpia ternata* (*Myrtaceae*) in subtropical Northern Territory. It also has a fairly small, delicate basidioma with narrow (0.05–0.1 mm) lamellae, fine partially reticulate basidiospore ornamentation (< 1 µm high), and hymenial lamprocystidia tapering to base and apex with the widest point between the midpoint and apex. It is macroscopically similar to several taxa from Thailand, Papua New Guinea, and India that also have longitudinally rugulose stipe texture, particularly *Lf. longipilus*, *Lf. vitellinus*, and *Lf. austrovolemus*, but differs primarily in its mycorrhizal host association with *Myrtaceae* and differences in size and shape of pleurolamprocystidia and pileipellis terminal elements. *Lactifluus rugulostipitatus* differs from *Lf. austrovolemus* in the lack of an inconspicuous papilla in the centre of the pileus, slightly smaller basidiomes with more orange tones, slight odour, and smaller spores with much lower ornamentation (Verbeken & Horak 2000). Unfortunately, there was no sequence of *Lf. austrovolemus* for comparison.

Lactifluus sp. 8

Sequence data. Australia, Queensland, Peachester State Forest, in wet sclerophyll forest, dominated by *Eucalyptus pilularis*, May 2004, RFLP5 (ITS DQ388812); RFLP38 (ITS DQ388845); RFLP39 (ITS DQ388846); Brisbane, Toohey Forest Conservation Park, off Nathan Ridge Track, in *Eucalyptus curtisii*, *E. planchoniana*, *E. microcorys*, *E. maculata*, *E. trachyphloia*, *E. umbra*, *E. henryi*, *E. drepanophylla*, *E. resinifera*, *E. baileyana*, *E. siderophloia*, Dec. 2011 (estimate), *E. Greenlaw toosoil 17* (ITS KC222797); ibid., *toosoil 13* (ITS KC222793).

Distribution & Habitat — Queensland near Brisbane, in wet sclerophyll and mixed *Eucalyptus* woodland.

Notes — Environmental sequences from soil samples (RFLPS) published in Bastias et al. (2006) and unpublished seqs in Greenlaw (MSc. 2012).

Lactifluus sp. 9 — Fig. 21d

Pileus 3.5–7 cm broad, plano-convex becoming depressed on the disc, then with uplifted margin, dry, matte to very finely subvelutinous, dark brown to dark reddish brown, becoming orange brown to brownish orange, cracking/ coarsely areolate with age and drying *in situ*, with margin incurved to decurved, rarely with a circumferential ridge and somewhat rugulose to subcorrugate. *Context* pale creamy white (4A3), staining pale brownish. *Lamellae* broadly adnate to nearly subdecurrent, crowded, light orange (5A5) at first, paler with age, staining brown from latex. *Stipe* 3–4.5 cm long, 1–2.5 cm broad, equal to tapered toward base, dry, matte, sometimes with a hoary aspect, dark brown to dark reddish brown, to pale brownish orange, white at base, with interior as in pileus. Extremely tough textured. *Latex* white, copious, staining tissues brown, with *taste* mild and a very slightly fishy-prawn *odour* with age.

Specimens examined. Australia, Queensland, Wide Bay District, Great Sandy National Park, Fraser Island, Cathedral Beach, alt. 40 m, 18 May 2010, *R.E. Halling*, *N. Fechner & M. Castellano REH 9320* BRI (ITS KR364096, LSU KR364228); North Maleny, Baroon Pocket Dam, Obi Obi Gorge track, 2 Oct. 2010, *P. Leonard 31010* BRI: AQ 796516; Brisbane, Toohey Forest Conservation Park, off Nathan Ridge Track, in *Eucalyptus curtisii*, *E. planchoniana*, *E. microcorys*, *E. maculata*, *E. trachyphloia*, *E. umbra*, *E. henryi*, *E. drepanophylla*, *E. resinifera*, *E. baileyana*, *E. siderophloia*, Dec. 2011 (estimate), *E. Greenlaw toosoil 58* (ITS KC222838). New South Wales, Watagan National Park, 11 Apr. 1983, *A. Young 722* BRI: AQ 808468.

Notes — Sequence from REH9320 published in De Crop et al. (2017). Quite a stocky basidiome, with deep dark brown, reddish orange brown to pale brownish orange pileus that cracks or is coarsely cracking/areolate with age or drying, light orange lamellae that stain brown with drying latex, stipe concolorous with pileus. Associated with *Eucalyptus* spp. in sandy soils.

DISCUSSION

In Australia, while distinct and highly visible, species in the *Lactifluus clarkeae* complex are generally not found in great abundance, nor are they the most common species found (species of *Lactarius eucalypti* group more typically observed). This is not the case in New Zealand, where *Lf. clarkeae* and *Lf. aurantioruber* are the most common lactarioid species found in *Leptospermum* and *Nothofagus* communities, respectively. The presence of mixed species syntypes listed in the original circumscriptions of *Lf. clarkeae* and *Lf. flocktoniae*, and variability in latex production observed in *Lf. flocktoniae* caused considerable confusion for field identification in Australia, and we believe led to the continuation of very broad species concepts being applied to any robust, yellow to orangish red tomentose *Lactarius* or *Russula*. A comparison of the distribution of all collections listed in Australian and New Zealand Herbaria/Fungaria under the names *Lf. clarkeae*, *Lf. flocktoniae*, *and Lf. aurantioruber* (Fig. 26b) and those differentiated in the course of this study (Fig. 26a), provide some indication of the complexity in this species complex. During this study we were able to delimit 19 taxa that were either named *Lf. clarkeae*, *Lf. flocktoniae*, or *Lf. subclarkeae* based on gross morphology, and/or analysis of ITS-LSU data places them as sister taxa to these species or within sect. *Tomentosi*. In order to stabilise species concepts in the *Lf. clarkeae* complex, we have chosen epitypes and provided full descriptions and images for all named species and partial details for some of the provisional species determined in this study.

Lactifluus section *Tomentosi*

The cryptic diversity discovered in this species complex is staggering, with three new taxa described and a further six unnamed provisional taxa uncovered in our analyses. Including the three previously known species, this brings the total species in sect. *Tomentosi* to 12. This whole section appears to be Gondwanan in origin, containing only southern hemisphere taxa. Section *Tomentosi* was originally advanced by McNabb (1971) for the genus *Lactarius*. De Crop et al. (2017) revised the sections in *Lactifluus*, also finding strong support for sect. *Tomentosi*, which in their concept included *Lf. clarkeae*, *Lf. subclarkeae*, and *Lf. flocktoniae* based on names applied to collections at the time. The extensive sampling for this study, enabled greater definition of species boundaries. Thus, the sequences in De Crop et al. (2017) named as *Lf. subclarkeae* (REH 9231) is now in *Lf. clarkeae* s.str., as *Lf. clarkeae* (MN 2004002; note there are two ITS GenBank numbers for this collection) is now in *Lf. pseudoflocktoniae*, and as *Lf. flocktoniae* (JET1006) remains as this species in our analyses (Fig. 3–5).

The closest relations to sect. *Tomentosi* are sections *Nebulosi* and *Panuoidei*, with a mixture of species from Mesoamerica including *Lf. putidus*, *Lf. nebulosus*, and *Lf. murinipes* from Martinique, *Lf. guadeloupensis* from Guadeloupe, *Lf. chiapanensis* from Mexico, the pleurotoid *Lf. panuoides* from French Guyana, and the pleurotoid *Lf. brunellus* from Guyana. It is curious that sect. *Tomentosi*, an Australasian group, appears to be most closely related to a Mesoamerican group rather than any other Australasian or Southeast Asian member of the genus. The recently described *Lactifluus* sect. *Nebulosi* (Delgat et al. 2020) contains only Neotropical collections and is characterised by dull, brown-grey sporocarp colours and spores with isolated,

Fig. 26 Distribution maps of *Lactifluus clarkeae* species complex showing: a. provisional, newly described and revised *Lactifluus clarkeae* complex species in this manuscript. Coloured dots representing: *Lf. clarkeae* (blue), *Lf. aurantioruber* (reddish brown), *Lf. flocktoniae* (light orange), *Lf. psammophilus* (dark green), *Lf. pseudoflocktoniae* (light blue), *Lf. albens* (bright purple), *Lf. jetiae* (lime green), *Lf. pagodicystidiatus* (brick red), *Lf. rugulostipitatus* (blue-grey NT), *Lf. russulisporus* (lilac), *Lf.* sp. 1 (dark purple NCAL), *Lf.* sp. 2 (emerald green (NSW), *Lf.* sp. 3 (dark grey QLD, Fraser Is.), *Lf.* sp. 4 (bright purple QLD), *Lf.* sp. 5 (dark blue NCAL), *Lf.* sp. 6 (dark orange NCAL), *Lf.* sp. 7 (green-blue QLD), *Lf.* sp. 8 (bright pink QLD), *Lf.* sp. 9 (brown QLD); b. all collections currently labelled as *Lf. clarkeae* (blue), *Lf. aurantioruber* (reddish brown), and *Lf. flocktoniae* (light orange) in Australian and New Zealand Herbaria.

rounded warts up to 1 µm high. This contrasts with the more brightly coloured *Tomentosi* that have verrucose spores with slight reticulation. Both sections do share the presence of pleuromacrocystidia in most species, while these are mostly absent in subg. *Gymnocarpi*. In both sections some species have a fishy odour. The species *Lf. panuoides* and *Lf. brunellus* may be readily distinguished by their pleurotoid basidiomata (Miller et al. 2000, 2002).

All species in sect. *Tomentosi* have a thick trichoderm layer on the pileus and stipe, resulting in a tomentose surface. *Lactifluus clarkeae* in particular has superlatively elongate terminal elements, with pileipellis and stipitipellis hairs reaching more than 300 µm in length. With the exception of *Lf. albens* sp. nov., which is coloured pale cream to pale yellow instead of orange as is typical among members of this section, the other species are difficult to distinguish from one another (see Key on p. 15). Three provisional taxa occurring in New Caledonia, are currently known only from ECM root-tips and a single basidiome collection (*Lf.* spp. 1, 5 and 6).

Other sections of Lactifluus

Lactifluus russulisporus is currently the only Australian species in subg. *Gymnocarpi* sect. *Luteoli*. The large range extension established for this species with the inclusion of a new collection indicates that it may be much more widely distributed than previously believed. It has a close genetic affinity with the Thai species *Lf. caliendrifer*, the European species *Lf. brunneoviolascens* and is morphologically similar to the Javanese species *Lf. rubrobrunnescens* in the nature of the capitate pileipellis and marginal cell elements, which confirms its placement in *Lf.* sect. *Luteoli* (Verbeken et al. 2001, Verbeken & Walleyn 2010, De Crop et al. 2017).

Also, a first for Australasia, is the discovery of a species in subg. *Pseudogymnocarpi*, *Lf.* sp. 7. Although DNA places it firmly in this clade, the subgenus shows very mixed morphological characters (De Crop et al. 2017), which makes it difficult to determine how well this taxon sits in this group. Detailed examination of microscopic data for all species currently placed here (Fig. 4), and further genes may help.

The single representative from Australia in subg. *Lactifluus* sect. *Lactifluus* known prior to this study, was from Fraser Island, Queensland (NY 1193969/REH9320); a sequence appeared in De Crop et al. (2017) multilocus phylogeny of subg. *Lactifluus* as *Lactifluus volemus* s.lat. This sequence still represents an undescribed species (*Lf.* sp. 9), but we now have a better framework to place it in context with *Lf. jetiae*, *Lf. rugulostipitatus*, and *Lf. pagodicystidiatus* as the first species to be described in sect. *Lactifluus* from Australasia. Although branch support values indicating relationships between species are not high, all of these new Australian species in sect. *Lactifluus* appear to show greater affinity to taxa from Thailand, Japan, and India than any other regions.

The combination of generally bright orange pileus, robust and high (up to 2 µm) basidiospore ornamentation, and relatively short lamprocystidia, aids in distinguishing *Lf. jetiae*. *Lactifluus rugulostipitatus* and *Lf. pagodicystidiatus* share similar micromorphology – with hymenial lamprocystidia in *Lf. rugulostipitatus* occasionally pagodaform or nearly so – however, *Lf. rugulostipitatus* basidiomes typically have a wrinkled stipe surface and are more delicate than the robust *Lf. pagodicystidiatus* basidiomes with a notably smooth and stout stipe. The delicate form in combination with a longitudinally rugose stipe surface is common to several Thai and Indian species including *Lf. longipilus* and *Lf. vitellinus*, but *Lf. rugulostipitatus* differs from *Lf. longipilus* in having much shorter pileicystidia, *Lf. vitellinus* in having a persistently incurved margin, and both in having mycorrhizal association with *Myrtaceae* flora (Van de Putte et al. 2010, 2012). The more robust form and plano-convex shape is characteristic of various species in the *Lf. volemus* s.lat. group from Europe, Asia, and North America (Van de Putte et al. 2016). In comparison to *Lf. subvolemus* and *Lf. volemus* sensu Van de Putte et al. (2016), *Lf. pagodicystidiatus* has distinctly shorter pileipellis hairs and the strangulations of hymenial cystidia are more regular and symmetrical (Van de Putte et al. 2016). The regularity and symmetry of pagodaform cystidia, and their consistency between tissues in different basidiomes and collections, appears to be unique to the Australian species (Van de Putte et al. 2010, 2012, 2016).

Biogeography and host patterns

In this study, we explored the diversity of the *Lf. clarkeae* complex species in Australia, New Zealand, and New Caledonia. All 28 Australasian *Lactifluus* species known so far and included in our phylogenetic analysis, are endemic to the region. No overlap in species with the under sampled island of New Guinea has been found so far, and overlap of species between land masses within Australasia is rare (Fig. 26).

At the sectional level, two distinct biogeographical patterns can be discerned: *Lactifluus* sect. *Tomentosi* has clear Gondwanan connections (mostly African, some Mesoamerican), while the other Australasian taxa are more closely related to South East Asian lineages (Fig. 3–5). The Gondwana distribution (McLoughlin 2001) of sect. *Tomentosi* is unlikely to be a consequence of ancient vicariance, a hypothesis that has been rejected for other mushroom groups such as *Lentinula* (Hibbett 2001) and *Cortinarius* (Harrower et al. 2015). The source landmass of this section could be distinguished from the other two landmasses by its relatively great genetic diversity, as landmasses that were colonised more recently by a small founding population will feature little diversity of genotypes. Support for this hypothesis comes from the fact that only negligible genetic divergence was found between populations from Australia and New Zealand, indicating that each species has not been reproductively isolated on each landmass for a sufficient length of time to allow for random mutation and local adaptation to significantly differentiate populations from one another. This finding indicates that the arrival of these species in New Zealand and New Caledonia from Australia, or the reverse, either occurred recently, or that gene flow has been maintained between landmasses since colonization.

Species in this complex and in other ectomycorrhizal lineages, do appear to have the capacity to switch hosts from *Nothofagaceae* to *Myrtaceae*, which could enable taxa to deal with changing climate, and aid dispersal patterns. Both *Lf. clarkeae* s.str. and *Lf. aurantioruber* comb. & stat. nov. are trans-Tasman species, occurring in both Australia and New Zealand. *Lactifluus clarkeae* shows one pattern, predominance in Western Australia and mainland Australia and New Zealand, with high genetic diversity apparent, suggestive of possible spore dispersal from mainland Australia to New Zealand. *Lactifluus aurantioruber* shows a different pattern with a strong association with *Nothofagus* across New Zealand, and in Australia a smaller geographic range and an association with mostly *Nothofagus* but also occurring with *Eucalyptus* spp. The fact that they are not sister taxa, in fact quite separate in our analysis, indicates two different dispersal and establishment events. Most authors suggest a mix of medium distance spore dispersal by various means (*Pisolithus*, Moyersoen et al. 2003, *Hysterangiales*, Hosaka et al. 2007, *Cyttaria*, Peterson et al. 2010) and post-cretaceous migration with hosts and a host shift (*Soliocassus*, Trappe et al. 2013, *Hydnum*, Feng et al. 2016, *Multifurca*, Wang et al. 2018).

This study has highlighted the need for further collections, particularly in Queensland and New Caledonia to complement the environmental sequence diversity uncovered, and in New South Wales where there appears to be a paucity of recent collections. This is also apparent in application of the name *Lf. subclarkeae*, as none of the material examined during this study matched the type; this species is still a puzzle. While some of the taxa can be differentiated morphologically, several will require further material and investigation to uncover macro-characters, plant community associations, or geographic distribution differences to aid in developing field characters for identification.

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