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A mixed bag of sequestrate fungi from five different families: Boletaceae, Russulaceae, Psathyrellaceae, Strophariaceae, and Hysterangiaceae

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Abstract: We describe several new genera and species of sequestrate fungi from different regions of the world that belong to five different basidiomycete families. New taxa include: *Amylotrama gen. nov.*, *Amylotrama clelandii comb. nov.*, *A. banrockensis sp. nov.*, *Boletus kundabungkid sp. nov.* (Boletaceae), *Russula crassibasidiata sp. nov.*, *R. danksiae sp. nov.* (Russulaceae), *Statesia gen. nov.*, *Statesia cazaresii sp. nov.*, *S. zelleri sp. nov.*, *S. pompholyx comb. nov.*, and *S. calcarea comb. nov.* (Hysterangiaceae). We also confirm the placement of two blue-green species from Australasia, one that was previously placed in "*Le Ratia*" and the other in *Weraroa*, and make the new combination *Agrocybe smaragdina comb. nov.* (Strophariaceae), and describe *Coprinopsis pulchricaerulea sp. nov.* (Psathyrellaceae) accordingly.

Keywords: truffle-like fungi, taxonomy, *Le-Ratia*, *Leratiomyces*, Xerocomoideae

Introduction

Numerous collections of sequestrate fungi have been made over the last 10 years in various parts of the world by the authors and other investigators. However, due to the cryptic habit (often hypogeal sporocarps) and patchy distribution of these fungi, many novel species are known from only one or a few collections. In the interest of advancing the taxonomy of these obscure and sometimes rare fungi, we provide descriptions and supporting data for several new taxa here. All of them are either from locations where fruiting is highly seasonal due to environmental conditions, thus rarely photographed or collected, or are unique in morphology and phylogenetic placement in genera that currently have no recorded sequestrate taxa.

In this paper we describe two new genera, seven new species, and make four new combinations for sequestrate (truffle-like) fungi from several different lineages. We utilise both molecular and morphological characters to determine their phylogenetic affinities with epigeal agaricoid, boletoid, or phalloid relatives.

Methods

Morphology

Macroscopic characters are based on examination of fresh material and field notes of dried collections. Colours are described in general terms. Fresh material was dried in a food dehydrator at 35°C for 12 h. Habitat, associated plant communities and fruiting season are based on field notes.

Hand-cut sections of fresh and dried material were either mounted in 5% aqueous solution of KOH, then stained with Congo red, or directly stained with Melzer's reagent. Measurements were made at ×400 or ×1000 with a calibrated ocular micrometer. Spore dimensions are given as length range × width range, mean ± standard deviation. The length:width ratio (Q) of individual spores is presented as the range of Q values and the Q_{mean}. Measurements do not include the apiculus. Dimensions of basidia and cystidia are given as length range × width range ($n = 15$). All drawings and illustrations are based on type material unless otherwise stated.

Molecular analyses

Taxon sampling. Based on preliminary blast searches of sequences generated for this study in GenBank and UNITE (Kõljalg *et al.* 2013), separate alignments were generated, with sequences representing a range of species within each lineage. Sister clade selection and appropriate reference outgroups for each lineage were based on various studies of each lineage (Matheny *et al.* 2006; Dentinger *et al.* 2010; Melzer *et al.* 2016; Vidal *et al.* 2019; Wachter & Melzer 2020). Names of taxa

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Table 1. GenBank numbers for sequences generated for new species and some related taxa. Newly generated sequences are in bold.

Genus	Species	Herbarium# or collection#	Country	GenBank ITS	GenBank LSU	GenBank atp6	GenBank tef1
Amylotrama	*clelandii*	MEL2432546	Australia	**MT007924**	**MT459235**	-	**MN413630**
Amylotrama	*clelandii*	AD-C58886	Australia	**MT007927**	**MN393698**	-	**MN413634**
Amylotrama	*clelandii*	AD-C58782	Australia	**MT007929**	-	-	**MN413631**
Amylotrama	*clelandii*	MEL2464313	Australia	**MT007928**	-	-	**MN413632**
Amylotrama	*clelandii*	MEL2464387	Australia	**MT007926**	-	-	**MN413633**
Amylotrama	*banrockensis*	AD-C58672	Australia	MT703615	-	-	**MN413637**
Boletus	*edulis*	MEL2363164	Australia	**MZ997390**	**MZ997376**	-	-
Boletus	*kundabungkid*	MEL2417154	Australia	**MZ997388**	**MZ997377**	**OK235707**	**OK323368**
Boletus	*semigastroideus*	PDD95796	New Zealand	**MZ997389**	-	-	-
Russula	*crassibasidiata*	MEL2364422	Australia	**MT893301**	**MT893304**	-	-
Russula	*crassibasidiata*	MEL2364389	Australia	**MT893302**	**MT893305**	-	-
Russula	*crassibasidiata*	MEL2364390	Australia	**MT893300**	**MT893307**	-	-
Russula	*danksiae*	MEL2363642	Australia	**MT893298**	**MT893306**	-	-
Russula	*danksiae*	OSC H5934	Australia	**MT893299**	**MT893303**	-	-
Russula	*danksiae*	MEL2363640	Australia	**MT913007**	-	-	-
Coprinopsis	*pulchricaerulea*	MEL2363910	Australia	**MZ997378**	**MZ997371**	-	-
Coprinopsis	*pulchricaerulea* *2nd basidiome	MEL2363910	Australia	**MZ997381**	-	-	-
Coprinopsis	*pulchricaerulea*	MEL2363909	Australia	**MZ997379**	**MZ997372**	-	-
Coprinopsis	*pulchricaerulea*	MEL2363911	Australia	**MZ997380**	**MZ997373**	-	-
Coprinopsis	*pulchricaerulea*	MEL2305158	New Caledonia	**MZ997383**	**MZ997374**	-	-
Coprinopsis	*pulchricaerulea*	MEL2305157	New Caledonia	**MZ997384**	**MZ997375**	-	-
Coprinopsis	*pulchricaerulea*	MEL2363908	Aus: Lord Howe Is	**MZ997382**	-	-	-
Coprinopsis	sp.	MEL2409229	Australia	**MZ997387**	-	-	-
Agrocybe	*smaragdina*	MEL2305149	New Caledonia	**MZ997385**	-	-	-
Agrocybe	*smaragdina*	TNS-F-34123	New Caledonia	**MZ997386**	-	-	-
Agrocybe	*smaragdina*	TNS-F-33732	New Caledonia	**OK147735**	**OK147739**	-	-
Agrocybe	*smaragdina*	TNS-F-34162	New Caledonia	**OK147736**	-	-	-
Statesia	*calcarea*	OSC159163	Germany	-	-	DQ218776	DQ219149
Statesia	*cazaresii*	OSC159158	Mexico	-	-	DQ218849	DQ219180
Statesia	*pompholyx*	OSC Gross495	France	-	-	DQ218783	DQ219163
Statesia	*zelleri*	OSC159159	United States	-	-	DQ218854	DQ219185

in phylogenies are as they currently appear in GenBank (i.e. not updated taxonomically).

For **Boletaceae**, six alignments were generated. A concatenated TEF1-α and LSU alignment with *Amylotrama gen. nov.* and related taxa of Xerocomoideae (subfamily of Boletaceae), with a *Suillus* exemplar as outgroup, consisted of 2107 sites (1202 sites for the TEF1-α portion of the alignment, 905 sites of the LSU portion). This alignment was analysed to confirm subfamily placement. Since only a limited number of specimens of *Amylotrama* were available from which both loci were retrieved, only a TEF1-α alignment with additional specimens of *Amylotrama* was analysed; the subsequent phylogenetic tree from this analysis is presented here. Partial ITS sequences were also retrieved for *Amylotrama*. For *Boletus kundabungkid sp. nov.*, four separate single gene analyses (ITS, LSU, TEF1-α, atp6) were performed, all of which corroborated the new species, however we were unable to obtain sufficient sequences of multiple loci across exemplars to produce a concatenated alignment. Thus, we present only the results from the TEF1-α alignment consisting of 604 sites, with *Tylopilus* as outgroup, as the best overall representation of placement.

For **Russulaceae** the alignment included closely related taxa in *Russula* subg. *Heterophyllidiae* sect. *Ingratae* and consisted of 1504 sites (847 sites for LSU, 657 sites for ITS), with *Lactarius* cf. *luculentus* Burl. as outgroup.

For **Psathyrellaceae** the concatenated ITS and LSU alignment representing a selection of sections within *Coprinopsis*, with *Parasola conopilea* (Fr.) Örstadius & E. Larss. as outgroup, consisted of 1448 sites (632 sites for ITS, 816 for LSU).

For **Strophariaceae** the ITS alignment including representative *Agrocybe*, *Psilocybe*, *Keuhneromyces* and *Protostropharia* species, with *Pholiota terrestris* Overh. as outgroup, consisted of 623 sites.

For **Hysterangiaceae** the concatenated ATP6 and TEF1-α alignment representing *Statesia gen. nov.* and related taxa, with *Geastrum fornicatum* (Huds.) Hook. as outgroup, consisted of 1387 sites (688 sites for ATP6, 699 sites for TEF1-α).

Novel sequences representing collections from Australasia and other regions generated for this study are listed in Table 1 with relevant GenBank accession numbers.

Nucleic acid preparation, amplification and sequencing. Genomic DNA was isolated with an E.Z.N.A. forensic DNA kit (Omega Biotek) for samples older than 1995, or the QIAGEN DNeasy Plant Mini Kit, following the manufacturer's protocol. The targeted regions were amplified from purified DNA with standard fungal primer pairs ITS1/ITS4 (White *et al.* 1990; Gardes & Bruns 1993); LROR/LR5 (Hopple & Vilgalys 1994); and ef1-983f/ef1-1567r (Binder & Hibbett 2003; Rehner & Buckley 2005) or atp6-1/atp6-2 (Kretzer & Bruns 1999). PCR protocols followed standard methods (Lebel & Tonkin 2007; Danks *et al.* 2010; Lebel & Syme 2012; Lebel *et al.* 2015; Davoodian *et al.* 2021). Assembly and manual editing of sequences for each region were performed with Geneious 9.1.3 (Biomatters Ltd).

Phylogenetic analyses. Analyses were performed with RAxML 8.2.12 (Stamatakis *et al.* 2014) and Bayesian likelihood with the Metropolis coupled Markov chain Monte Carlo (MCMC) search algorithm implemented in MrBayes 3.2.5 (Ronquist & Huelsenbeck 2003). Gaps in alignments were treated as missing data. Modeltest (Posada & Crandall 1998) was used to determine appropriate evolutionary models for the Bayesian analyses. Each search involved four chains (three heated to 0.2 and one cold) sampled every 1000 generations. The search ran until convergence between runs was achieved, measured by a standard deviation of split frequencies below 0.05 and observing when this was no longer decreasing. After discarding burn-in, consensus trees or ML trees were imported to FigTree 1.4.2 (Rambaut 2009) and are presented with posterior probabilities or ML bootstrap values at clades.

Nomenclature

Registration numbers are provided for new and existing names (with prefixes MB = MycoBank or IF = Index Fungorum) and new typifications (prefix MBT = MycoBank typification).

Results & Discussion

Single gene analyses were performed using Bayesian and Maximum likelihood approaches, and the same key relationships were recovered in all analyses. Where possible, concatenated alignments were analysed. However, in some cases there were insufficient sequences of multiple genes to produce a concatenated alignment; in these instances we present well supported single gene data.

Taxonomy

Boletaceae Chevall.

The family Boletaceae is a diverse, mostly ecto-mycorrhizal lineage which associates with a broad range of plant families. In the last decade, with the advent and expansion of molecular techniques, taxon concepts in the family have been revised considerably with the recognition of seven major clades at subfamily level and at least 62 generic lineages, and numerous new species have been described (Nuhn *et al.* 2013; Halling *et al.* 2014; Wu *et al.* 2014, 2016; Gelardi *et al.* 2015; Vadthanarat *et al.* 2019, 2021; Raghoonundon *et al.* 2021). The sequestrate habit has arisen multiple times and a large number of sequestrate genera have been described (Desjardin *et al.* 2009; Trappe *et al.* 2013; Castellano *et al.* 2016; Orihara *et al.* 2016; Orihara & Smith 2017; Crous *et al.* 2018; Vadthanarat *et al.* 2019). In Australia, taxonomic and phylogenetic revision of sequestrate Boletaceae is in its infancy, with many undescribed taxa to resolve.

Amylotrama Bloomfield, Davoodian, Trappe & T.Lebel, ***gen. nov.***

Typus: *Amylotrama clelandii* (G.Cunn.) Bloomfield, Davoodian, Trappe & T.Lebel

Registration identifier: IF557864.

Basidiomata subglobose, vaguely reniform, to irregular, 20–35 mm diam., 11–20 mm high; surface dry, cream to yellow to dull or dingy yellow, with either thin filamentous dark patches or gray rough patches; at times

Key to sequestrate Boletaceae mentioned in this paper and one unrelated but easily confused species

1. Basidiomes with a robust stipe to 20 mm long, 10 mm diam., in association with *Leptospermum* spp.; found in New Zealand . . . . ***Boletus semigastroideus***

1: Basidiomes lacking a stipe-columella or with a narrow < 1 mm diam. strand, in association with *Eucalyptus* spp.; found in Australia

  2. Basidiomes cream to dull yellow to yellow with either thin, filamentous darker patches that are easily rubbed off or overlying irregular gray filamentous rough patches, tramal hyphae amyloid, spores inamyloid

    3. Basidiomes become darker upon handling; pileipellis a thin undifferentiated cutis; spores 6.5–8.5 (–10.5) × 4.5–6.5 µm; basidia abundant, persistent, forming a conspicuous hymenial layer . . . . 1. ***Amylotrama clelandii***

    3: Basidiomes not darkening upon handling; pileipellis wide and distinctly two-layered; spores slightly larger, 8.0–10 µm × 5.5–7.2 µm; basidia readily collapsing, not forming a persistent hymenial layer . . . . 2. ***Amylotrama banrockensis***

  2: Basidiomes white to pale cream, either smooth without overlying patches or with fine pale brown fibrils, tramal hyphae inamyloid, spores dextrinoid

    4. Hymenophore initially pale cream becoming pale olive green, spores 15–19 × 6–7 µm . . . . ***Lepiota geogenia*** [Agaricaceae]

    4: Hymenophore remaining pale cream or becoming ochraceous, spores broader 12–15 (–17) × 8–11.5 (–13) µm . . . . 3. ***Boletus kundabungkid***

with rhizoids or basal attachment. *Hymenophore* cream to dull yellow to yellow to gray, at times oozing a clear liquid; loculate with chambers 2–4 mm wide, chambers may be more compressed towards the pileipellis. *Columella* present or absent; if present, white.

Pileipellis a thin cutis of dark yellow hyphae overlying a context composed of tangled, hyaline to pale yellow hyphae. *Hymenophoral trama* hyaline to yellowish, amyloid in Melzer's reagent. *Spores* statismosporic, hyaline to yellowish, subglobose to subovate, 6.5–10 × 4.5–7.2 µm, inamyloid, sometimes displaying oily inclusions. *Clamp connections* absent in all tissues.

Notes. The name "*Amylotrama*" appears in herbaria and various publications as a provisional name applied to a polyphyletic assemblage of sequestrate boletoid fungi, with amyloid hymenophoral and/or pileal context trama in Melzer's reagent. Here we formally introduce the name *Amylotrama*, restricting it to one of these monophyletic clades, and describe two species based on morphological and DNA data (Fig. 2). BLAST searches of TEF1-α, ITS and LSU and phylogenetic analyses of the loci singly and concatenated strongly support placement of *Amylotrama* in the Xerocomoideae. The portions of ITS sequences retrieved were insufficient to discriminate between species within *Amylotrama*, however they suggested subfamily placement in Xerocomoideae, with BLAST searches matching several Xerocomoideae sequences lodged in GenBank at 92–95% (e.g. GenBank: KP012700, *Hemileccinum* sp. from northern Australia; MF686530, *Heimioporus betula* from U.S.A.). Thus far, ITS sequences have not matched any sequences from root tips based on searches of GenBank and UNITE, though 97–98% matches have been detected in Australian soil metagenomic ITS1 data (Davoodian *et al.* 2020). *Amylotrama* is the only sequestrate member of the Xerocomoideae described from Australia thus far, and the sequestrate habit is uncommon worldwide in this subfamily (Trappe & Castellano 2000).

Morphologically, *Amylotrama* exhibits coloration and general appearance more or less consistent with other Xerocomoideae, however no other Xerocomoideae exhibits amyloid trama. A direct comparison is difficult to make since almost all known Xerocomoideae are epigeous bolete mushrooms. *Gastroboletus vividus* Trappe & Castellano, a hypogeous to subhypogeous bolete with sequestrate basidiomes that occurs in the western United States, may be in Xerocomoideae based on our preliminary analysis of one LSU sequence (GenBank: KF030245).

Amylotrama can be distinguished from other Australian boletoid sequestrate genera by the combination of small basidiomata, cream to yellow to gray hymenophore, amyloid trama, and inamyloid subglobose to subovate spores.

Etymology. The genus name refers to the amyloid reaction of the trama in Melzer's reagent.

1. *Amylotrama clelandii* (G.Cunn.) Bloomfield, Davoodian, Trappe & T.Lebel, *comb. nov.*

Registration identifier: IF557865.

Rhizopogon clelandii G.Cunn., *Proc. Linn. Soc. New South Wales* 59: 162 (1934), as "*clelandi*". MB374407. — *Alpova clelandii* (G.Cunn.) G.W.Beaton, Pegler & T.W.K.Young, *Kew Bull.* 40: 578 (1985). MB105028.

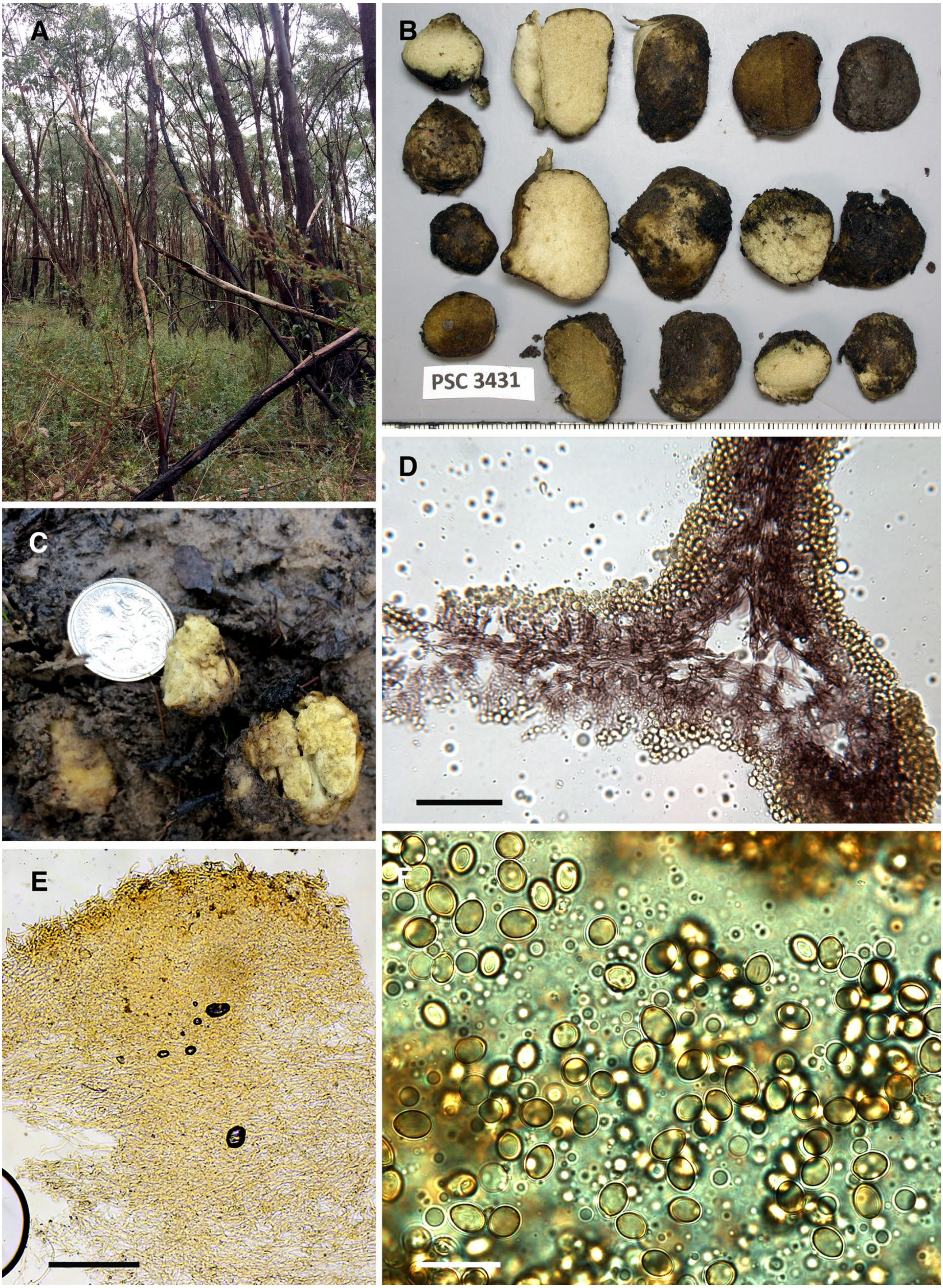

Fig. 1. *Amylotrama clelandii*. **A** Habitat image from epitype locality; **B** basidiomata fresh; **C** basidiomata *in situ*; **D** hymenophore tissue in Melzer's showing spores, basidia, basidioles, and amyloid subhymenial and tramal elements; **E** section of pileipellis and context through to the edge of the hymenophoral trama; **F** spores. Scale bars: D = 60 µm, E = 100 µm, F = 25 µm. — C–E *S.J.M. McMullan-Fisher 3140* (MEL2432546, epitype); B *P.S. Catcheside 3431* (AD-C58782). Photo: D. Catcheside (B).

— **Lectotype:** Australia, South Australia: Second Valley Forest Reserve, 6 June 1930, *J.B. Cleland s.n.* (AD-C58527; former accession number: ADW6009), *fide* G.W.Beaton, Pegler & T.W.K.Young, *Kew Bull.* 40: 579 (1985), as "holotype". **Epitype (here designated, MBT10003199):** Australia, South Australia: Mount Barker, Totness Recreation Park, 18 June 2018, *S.J.M. McMullan-Fisher 3140* (MEL2432546).

Basidiomata subglobose to elongate or reniform, sometimes lobed, becoming irregular, 20–35 mm diam., 11–20 mm high; surface dry when fresh, cream to dull yellow to yellow, becoming darker upon handling, with thin, filamentous darker patches that are easily rubbed off, drying tawny-brown; basal rhizoids rare (initially concolorous, becoming dark). *Hymenophore* cream to dull yellow to yellow, drying yellowish to tawny brown; loculate, empty, subglobose to irregular locules, up to 1–2 mm wide, locules occasionally more compressed towards the pileipellis. *Stipe* absent. *Columella*, when present, a percurrent narrow strand < 0.5 mm wide, white. *Odour* mild. *Taste* nondescript.

Pileipellis a thin layer 15–35 µm wide, composed of a patchy layer of dark yellow, interwoven hyphae 5.5–8.5 µm diam., easily missed in sectioning. *Context* 730–1000 µm wide, of hyaline to yellowish, septate hyphae, 2.5–5.0 µm diam., tangled and periclinal. *Hymenophoral trama* comprised of elongated, hyaline hyphae, 2.0–5.0 µm diam., and isodiametric subhymenial cells, the whole layer amyloid in Melzer's reagent. *Basidia* 28–36 × 9–11.5 µm, mean = 30.6 × 9.9 µm, abundant, persistent, forming a conspicuous hymenial layer, hyaline, sterigmata 2–4, 2.5–5 × 1–2.5 µm in size. *Spores* 6.5–8.5 (–10.5) × 4.5–6.5 µm, mean = 7.6 × 5.7 µm, Q = 1.1–1.7, $Q_{mean} = 1.3$, statismosporic, hyaline, smooth, subglobose to slightly elongated to subovate, inamyloid, usually with conspicuous oily inclusions, moderately thick-walled. **Fig. 1.**

Diagnosis. Distinguished from *Amylotrama banrockensis* by the poorly developed, thin pileipellis, slightly smaller spores, presence of persistent basidia and conspicuous hymenial layer, and smaller isodiametric cells in the subhymenium.

Ecology & distribution. *Amylotrama clelandii* is thus far recorded as occurring solitarily or in small groups, hypogeous or emergent, in association with *Eucalyptus* spp. in south-eastern South Australia and southern Tasmania (collected in association with *Eucalyptus obliqua* at the epitype locality).

Notes. *Rhizopogon clelandii* G.Cunn. (originally as "*clelandi*") was described by Cunningham (1934) from three collections of sequestrate fungi made by J.B. Cleland in June 1930 from Second Valley Forest Reserve in South Australia and held in Cleland's herbarium at the University of Adelaide. No accession numbers were cited in the protologue. Cleland's collections of macrofungi are now in AD, having been placed for a period in ADW (Waite Institute, University of Adelaide). Since no explicit type was specified, all three collections are syntypes. The Cleland material from Second Valley, currently at AD and identified originally as *R. clelandii*, is in two packets: AD-C58527 (formerly ADW 6009, collected 6 June 1930) and AD-C58528 (formerly ADW 6010). Within the latter packet, two collections made on different dates have been separated as AD-C58528A (4 June 1930) and AD-C58528B (6 June 1930). Beaton *et al.* (1985) cited the type as "Second Valley Forest Res., 5 June 1930, Cleland, Waites [sic] Agric. Inst. 6009 (holotype ADW 6009)". Although the date is incorrectly cited as 5 June, ADW 6009 corresponds to AD-C58527, which is the packet currently at AD that has not been subsequently divided. Grgurinovic (1997) cited the combined ADW 6010 collection but made no comment about typification. Because the existing collections are syntypes, and therefore a lectotype must be chosen, the designation by Beaton *et al.* (1985) of a "holotype" can be corrected to lectotype, following Article 9.10 of the *International code of nomenclature* (Turland *et al.* 2018). There is also a collection in the Landcare Research Fungarium (PDD) made by J.B. Cleland from Second Valley labelled "isotype of *Rhizopogon clelandii*" (PDD 8286) but the collection date is given only as June 1930, which means it is not clear which of the three AD collections it is a duplicate of.

Our molecular evidence supports the differentiation of two taxa, based upon data from recent collections (Fig. 2). The recent, sequenced collections of these two taxa also differ in some morphological features, in particular the width and differentiation of the pileipellis, the persistence of basidia and the presence of highly inflated cells in the subhymenium. Unfortunately, the original Cleland material of *Rhizopogon clelandii* (AD-C58527 and AD-C58528) is degraded, both for DNA (we were unsuccessful in obtaining sequences), and morphologically (e.g. collapsed spores, ruptured cells), preventing clear visualisation of features beyond the generic level. Based on morphological examination of the syntypes, we could not ascertain features that differentiate recent collections we have assigned to *A. clelandii* or *A. banrockensis*. Therefore it is necessary to select an epitype, above. Linking the recent, sequenced epitype to the lectotype solidifies the morphological and molecular interpretation of *A. clelandii*. Given the potential for the residual syntypes to represent *A. banrockensis*, we choose to leave them identified at the genus level only. In time, once the distribution of the two species is better understood, it may be possible to assign them to species based on locality and/or ecology.

Additional material examined

AUSTRALIA. SOUTH AUSTRALIA: **Kangaroo Island.** Flinders Chase, nr Platypus Waterholes Walk from Shackle Rd, 25 June 2017, *T. Lebel 2898* (MEL2464387); Flinders Chase, nr Rocky River Heritage Accommodation (off Cape du Couedic Rd), past heath into woodlands, 25 June 2016, *T. Lebel 2804* (MEL2464313); Flinders Chase, off W side of

Fig. 2. Phylogram from Bayesian analysis of partial TEF1-α sequences. Scale bar shows substitutions per site. Bayesian posterior probabilities (bpp) are shown at the nodes. Thickened lines indicate PP support ≥ 0.95. Included in the analysis but cropped from the image are sequences from four *Suillus* species (KU721557, KU721631, KU721709, KU721719); *Suillus sinuspaulianus* (KU721557) was specified as the outgroup. Xerocomoideae (node a), Boletaceae (node b), and Paxillaceae (node c, sister to Boletaceae) are indicated.

trail loop, 24 June 2014, *P.S. Catcheside 3985* (AD-C58886); Flinders Chase, nr Rocky River, 28 May 2010, *P.S. Catcheside 3431* (AD-C58782)

TASMANIA. Huon Valley, Garden Island Creek, 3 June 2000, *G.M Gates & D.A. Ratkowsky EB26* (MEL2360433).

Residual syntypes of A. clelandii*, identifiable only as* Amylotrama *sp.*

AUSTRALIA. SOUTH AUSTRALIA. Second Valley Forest Reserve, 4 June 1930, *J.B. Cleland ADW 6010* (AD-C58528A); Second Valley Forest Reserve, 6 June 1930, *J.B. Cleland ADW 6010* (AD-C58528B).

2. *Amylotrama banrockensis* Bloomfield, Davoodian & T.Lebel, *sp. nov.*

> **Holotypus:** Australia, South Australia: Banrock Station, Loxton Waikerie, 11 July 2014, *D. Catcheside, C. Tourenq, T. Field & P.S. Catcheside 4018* (AD-C58672).
>
> **Registration identifier: MB832366.**

Basidiomata subglobose or vaguely reniform, slightly indented at base, 30 × 24 × 20 mm; surface dry when fresh, with irregular gray to dark brown filamentous rough patches overlying smooth dingy yellow pellis, rhizomorphs absent or rare across pellis or at base. *Hymenophore* grey to yellow with very slight olive tinge,

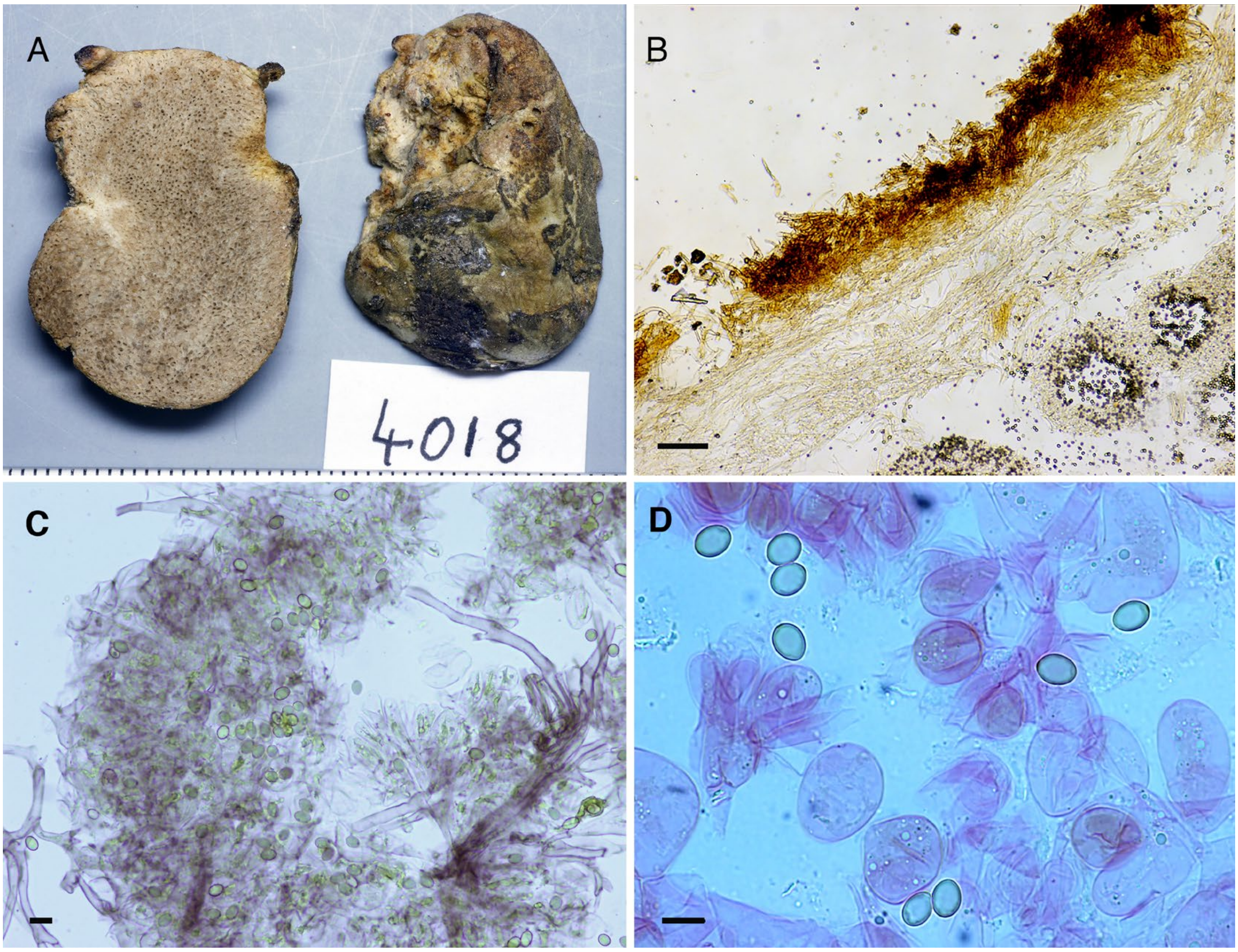

Fig. 3. *Amylotrama banrockensis*. **A** Basidiomata fresh; **B** section of pileipellis showing mixed suprapellis and subpellis, and context (in 3% KOH); **C** hymenophoral tissue showing amyloid inflated subhymenium elements, amyloid tramal tissues, and inamyloid spores (in Melzer's reagent); **D** spores, basidia, and inflated subhymenial elements (in phloxine). Scale bars: B–C = 50 µm, D = 10 µm. — A–C *D. Catcheside et al. 4018* (AD-C58672, holotype). Photo: D. Catcheside (A).

oozing clear liquid when squeezed; loculate, locules 2–3 mm, rounded. *Columella*, when present, small, not percurrent, slightly dendroid, extending 5 mm into basidiome, white. *Odour* of aniseed (in recent, dry material). *Taste* not recorded.

Pileipellis two-layered: a subpellis layer 70–180 µm wide, clearly differentiated from context, composed of golden brown hyphae, 5.4–12 µm diam., that are tangled and more or less periclinal, with obtuse apices; and overlying suprapellis, 20–65 µm wide, scattered in broad patches, composed of dark brown to greyish-brown filamentous septate hyphae, 6–14 µm diam., apices obtuse, partially erect to more or less flat, interwoven with subpellis hyphae. *Context* 215–430 µm wide, composed of hyaline to yellowish hyphae, 3–6 µm diam., mostly parallel. *Hymenophoral trama* hyaline to yellowish, composed of interwoven hyphae, 3–8 µm diam., and inflated to collapsing subhymenial cells, 12–31 × 9–26 µm diam., the whole layer amyloid in Melzer's reagent. *Basidia* 24–36 × 5–13 µm, narrowly clavate, thin-walled, hyaline, readily collapsing, few observed; sterigmata 2–4, 3–4 µm long. *Spores* 8.0–10.0 × 5.5–7.2 µm, mean = 8.98 × 6.61 µm, Q = 1.19–1.46 (–1.54), Q_{mean} = 1.36, statismosporic, hyaline to yellow-hyaline, smooth, subglobose (sometimes slightly elongated) to subovate, inamyloid, some spores displaying oily inclusions. **Fig. 3.**

Diagnosis. Distinguished from *Amylotrama clelandii* by the distinct differentiation of the wide two-layered pileipellis and context, slightly larger spores with a yellow tinge, lack of persistent basidia, highly inflated cells in the subhymenium, and aniseed odour when dried.

Ecology & distribution. Occurs solitarily in South Australia and Victoria, hypogeous to erumpent, in South Australia with *Eucalyptus camaldulensis* and *E. largiflorens* with Chenopodiaceae shrubby understory in the River Murray floodplain, with *Eucalyptus* sp. on Kangaroo Island, and in Victoria with *E. globulus*.

Notes. The aniseed odour was perceived by us in the holotype of *A. banrockensis*, which was collected and dried relatively recently (seven years ago). According to Cunningham (1934), "Although [*Rhizopogon clelandii*] is apparently without smell when fresh (according to the collection notes of Dr. Cleland), herbarium specimens have a strongly aromatic odour as of aniseed." However, such an odour is no longer detectable for any of the three Cleland collections originally identified as *R. clelandii* at AD. Further observations on fresh collections are required to ascertain if the aniseed odour is characteristic of *A. banrockensis* and if it can be detected in collections confirmed as *A. clelandii*. The collection *Beaton 32* from Victoria identified here as *A. banrockensis* was listed by Beaton *et al.* (1985) under *Alpova clelandii*; we place it under *A. banrockensis* based on morphology (presence of highly inflated subhymenial cells, lack of persistent basidia, amyloid trama, appearance of the spores, and pileipellis structure).

Morphologically, the highly inflated cells in the subhymenium, more obviously two-layered pileipellis and slightly larger spores enable differentiation of *A. banrockensis* from the more widespread *A. clelandii*. Our molecular analysis also supports *A. banrockensis* as distinct from *A. clelandii* (Fig. 2), with TEF1-α sequences diverging by 2–3%. Given the current distribution, the most likely areas to search for more material of this taxon would appear to be in eastern South Australia and Western Victoria.

Etymology. The specific epithet refers to the Banrock Station area, where the type was collected.

Additional material examined.

AUSTRALIA. VICTORIA. Colac-Otway, Grey River Reserve Rd, Kennett River, 3 July 1982, *G. Beaton 32* (MELU-F103764a).

3. *Boletus kundabungkid* T.Lebel, K.Syme & Davoodian, *sp. nov.*

> **Holotypus:** Australia, New South Wales: North of Grassy Head, Yarrahapinni State Forest, 20 Nov. 2015, *I. Dodd s.n.* (MEL2417154).
>
> **Registration identifier: MB841360.**

Basidiomata depressed globose or sub-turbinate, 10–18 mm tall, 10–25 mm diam., apex convex to occasionally planoconvex, base abruptly truncated, slightly excavated; white to pale cream coloured, drying pale tan, smooth, slightly viscid, sometimes irregularly areolate. *Stipe* highly reduced, 5–9 mm long, 2–5 mm diam., sharply tapering to base, at first white, becoming pale greyish or ochraceous, smooth, dry, cartilaginous in texture, barely inserted into hymenophore; context white, centrally hollow in some basidiomes. *Hymenophore* densely loculate, locules irregular in shape, less than 0.5 mm diam., empty, very pale cream initially becoming pale tan. No staining observed. *Odour* not distinctive. *Taste* mild.

Pileipellis composed of two layers, outer layer 80–175 µm thick, composed of septate hyphae, 4.5–7.2 µm diam., partly gelatinized and arranged in a vertical palisade 70–110 µm thick, the terminal elements are chains of inflated, globose to broadly clavate cells 19–48 µm long, 22–45 µm diam.; inner layer of hyaline, septate, interwoven hyphae 4.0–9.2 µm diam., to 200 µm thick, firm and compact. *Hymenophoral trama* 20–50 µm thick, pseudoparenchymatous, cells 5–11 × 5–9 µm. *Basidia* 23–40 × 12–15 µm, clavate to cylindrical, thin-walled, hyaline, 4-spored, embedded in a layer of obclavate to broadly clavate, thin-walled basidioles 16–24 × 10–17 µm. *Spores* (11.5–) 12–15 (–17) × 8–11.5 (–13) µm, mean = 13.83 ± 1.44 × 9.44 ± 1.2 µm (n = 40), Q = 1.2–1.8, Q_{mean} = 1.43, ovate-elliptical or ovate-fusiform, irregular in size and shape, bluntly acuminate or rounded, base bluntly pointed, apiculate, pallid ferruginous, smooth, wall 1 µm thick, strongly dextrinoid, lacking a germ pore. No cystidia observed. **Figs 4 & 5.**

Diagnosis. *Boletus kundabungkid* can be differentiated from *B. semigastroideus* Nuhn, Manfr. Binder, A.F.S. Taylor, Halling & Hibbett [replacement name for *Secotium areolatum* G.Cunn *non B. areolatus* Berk.; syn. *Notholepiota areolata* (G. Cunn.) E.Horak] by the smaller basidiomes, with a less-developed stipe, narrower spores and association with *Eucalyptus* spp. in Australia.

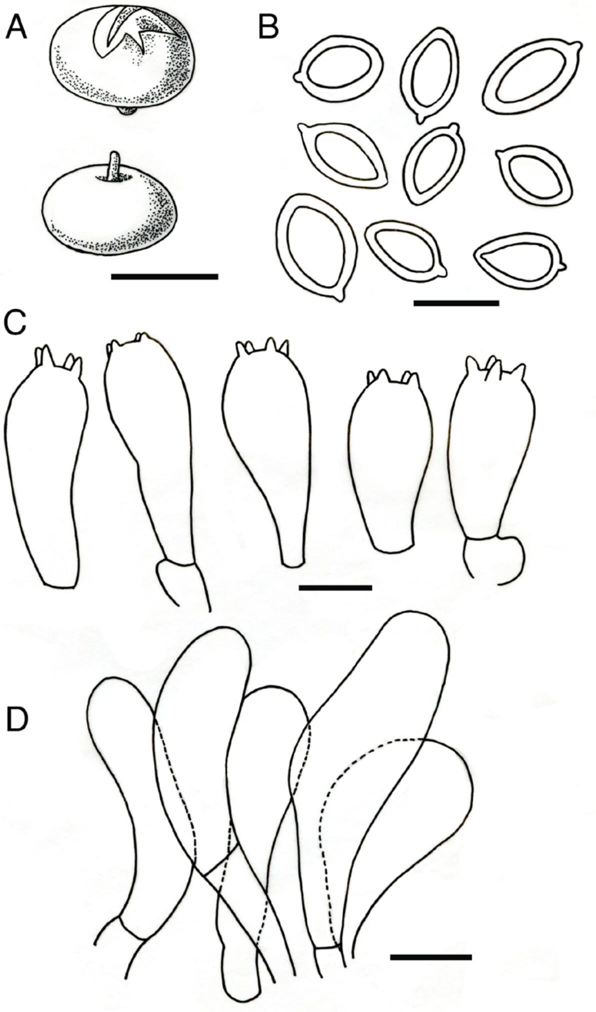

Fig. 4. *Boletus kundabungkid* illustration. **A** Basidiomata; **B** spores; **C** basidia; **D** pileipellis terminal elements. Scale bars: A = 10 mm, B–D = 10 µm. — Line drawing by K. Syme.

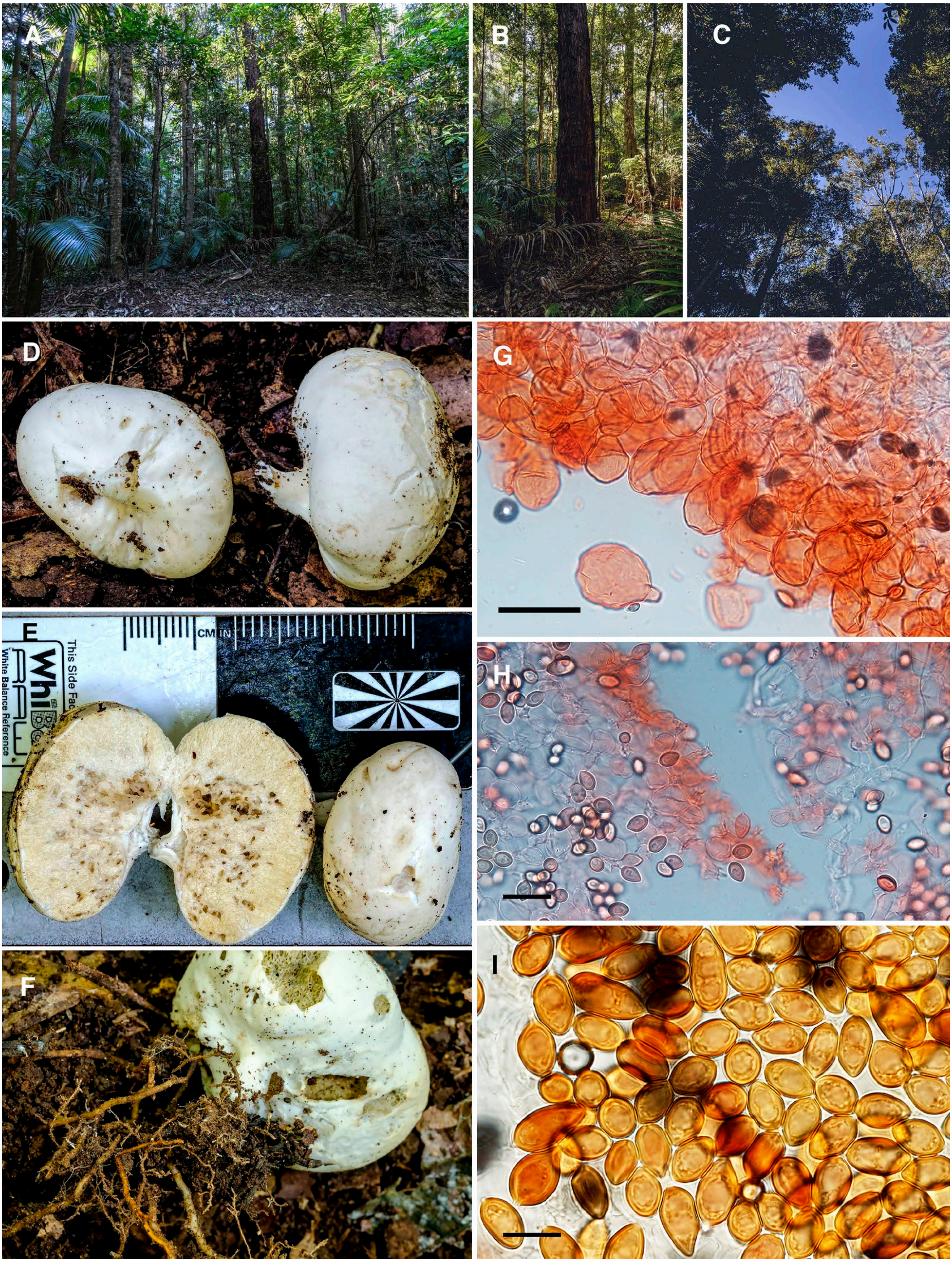

Fig. 5. *Boletus kundabungkid*. **A–C** Habitat images from type locality, showing dense bush and tall canopy; **D–F** basidiomata fresh; **G** palisade pileipellis chains of inflated terminal elements; **H** hymenophoral trama showing spores, basidia, basidioles and tramal elements; **I** spores. Scale bars: G = 40 µm, H = 20 µm, I = 10 µm. — D–F *I. Dodd s.n.* (MEL2417154, holotype). Photos: I. Dodd (A–F), T. Lebel (G–I).

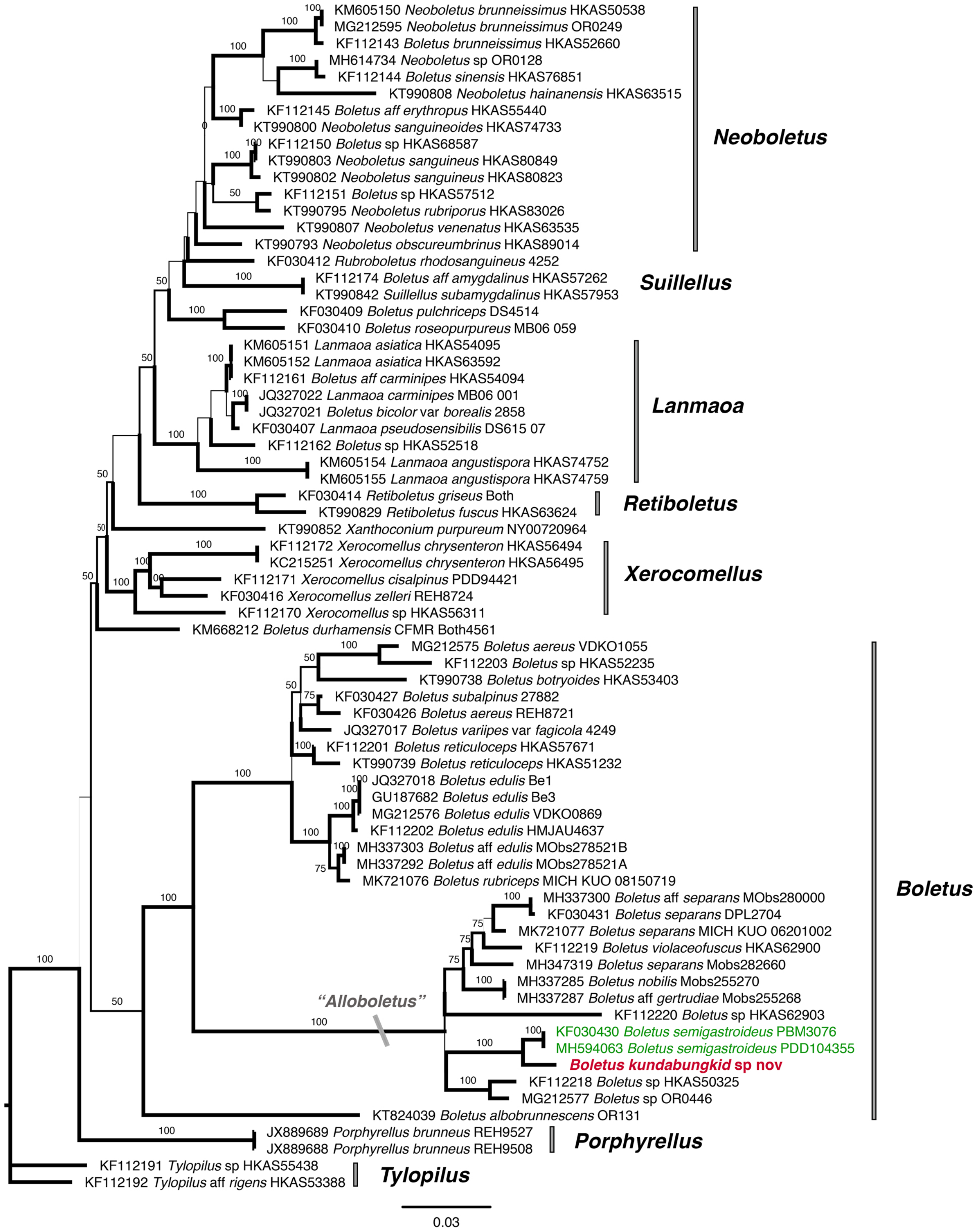

Fig. 6. Bayesian majority rule phylogram of partial TEF1-α sequences for *Boletus kundabungkid* and related taxa. Scale bar shows substitutions per site. Bayesian posterior probabilities (bpp) are shown at the nodes. Thickened lines indicate PP support ≥ 0.95.

Ecology & distribution. In small groups, hypogeous, in mixed rainforest in association with *Eucalyptus* spp.; Known only from type locality.

Notes. In the field this collection was initially thought to be a specimen of *Lepiota geogenia* T.Lebel & Vellinga, due to the small, pale cream basidiomes, and chambered pale hymenophore with somewhat cartilaginous texture. However, in maturity the hymenophore of *L. geogenia* becomes pale olive green, and microscopically the larger (14.5–) 19 × 6–7 µm, more ellipsoid, dextrinoid spores are distinctive (Lebel & Vellinga 2013). Both *L. geogenia*

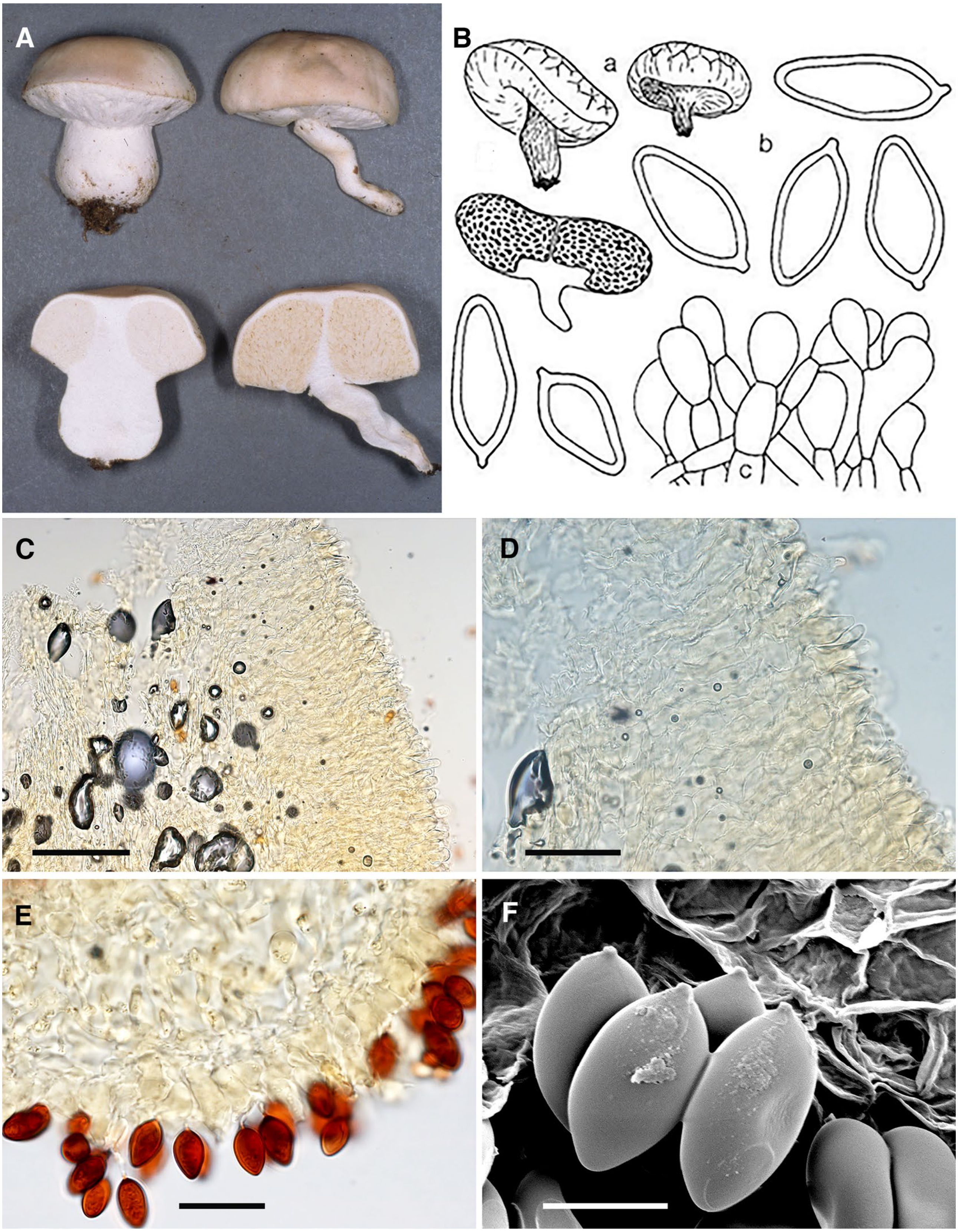

Fig. 7. *Boletus semigastroideus* (New Zealand). **A** Basidiomata; **B** illustration (as *Notholepiota areolata*), reproduced from Horak (1971); **C** pileus structure; **D** pileipellis; **E** hymenium, basidia, spores; **F** SEM of spores. Scale bars: C = 100 µm, D = 50 µm, E = 20 µm, F = 10 µm. — A *R.E. Beever* (PDD65276), C–E *R.E. Beever* (PDD68925); F *R.E. Beever* (PDD65277). Photos: T. Lebel (C–F).

and *Boletus kundabungkid* have been found in mixed lowland rainforest habitats in association with *Syzygium* spp. and *Eucalyptus* spp., in north eastern Australia.

Boletus kundabungkid is the first record from Australia of a sequestrate species in the almost entirely epigeous porcini clade (*B. edulis* Bull. and related species); it occurs in the "*Alloboletus*" subclade, comprising *B. violaceofuscus*, *B. separans*, and relatives (Dentinger *et al.* 2010; Nuhn *et al.* 2013; Fig. 6). *Boletus kundabungkid* is sister to the sequestrate *B. semigastroideus* from New Zealand based on independent analyses of 4 genes, and macro- and micro-characters. BLAST comparison of our *B. kundabungkid* ITS sequence matched publicly available ITS sequences of *B. semigastroideus* (GenBank: KP191796, JX258840) at 93.13%. *Boletus kundabungkid* typically has smaller basidiomes than *B. semigastroideus*, with a less-developed stipe, slightly wider spores and the pileipellis has chains of globose to broadly clavate terminal elements forming an epithelium-like layer. In *B. semigastroideus* the pileipellis is more palisadal to hymeniform (Fig. 7; Horak 1971, as *Notholepiota*). In Australia, *B. kundabungkid* is found in association with *Eucalyptus*, whereas in New Zealand *B. semigastroideus* is associated with *Leptospermum*.

Etymology. Specific epithet is a noun in apposition that refers to Ian Dodd the 'Kundabung Kid' who has made extensive collections and photos of intriguing fungi in an understudied area.

Russulaceae Lotsy.

Russula Pers. is an important ectomycorrhizal genus with high species diversity worldwide. The infrageneric classification of *Russula* is going through considerable change in light of recent multi-locus phylogenies with eight well-supported subgenera proposed (Looney *et al.* 2016; Bazzicalupo *et al.* 2017; Buyck *et al.* 2018, 2020). In Australia research on epigeal agaricoid *Russula* species remains limited, with only 24 species described in the last 20 years (Cleland 1976; Miller & Hilton 1986; Grgurinovic 1997). On the other hand, sequestrate *Russula* have been more extensively studied, with over 50 species described (Beaton *et al.* 1984; Bougher 1997; Elliott & Trappe 2019; Lebel & Trappe 2000; Lebel 2002a, b, 2003a, b; Trappe & Claridge 2003; Lebel & Tonkin 2007). However, placement of taxa in a phylogenetically stable section and subgeneric backbone of *Russula* as a whole remains to be completed.

Keys to Australian species of sequestrate *Russula* are available in Lebel & Castellano (2002), Lebel (2003a, b) and Lebel & Tonkin (2007). We place the two new species described below into a key to species that updates the key presented in Lebel (2003b: as *Gymnomyces*) with species names according to Lebel (2017). For further details of species not differentiated in the key below, see Lebel (2003b).

Updated key to Australian species of sequestrate *Russula*

Note that couplet numbers retain the numbering of the key in Lebel (2003b).

1. Spore ornamentation isolated, spinose
  2. Basidia with mostly 2 sterigmata
    3. Spore ornamentation 2–3 µm tall, many spines distinctly forked . . . . ***Russula furcatispina***
    3: Spore ornamentation 0.5–2 µm tall, of straight spines or of irregular rods, warts, and knobs
      3a. Hymenophore off-white to ivory initially, blackening in age, odour sharp of acetylene, pileipellis a trichoderm, basidia clavate to cylindrical, 24–39 × 6–12 µm. Currently known from New Zealand. . . . . ***Russula spinispora*** (= *Gymnomyces fuscus*)
      3b: Hymenophore initially off-white, becoming pale yellow, then eventually tan brown to brown, odour slightly fishy, pileipellis a patchy turf of hyphal tips and short cystidia, basidia broadly clavate to obovate, 22–28 × 12–16 (–20) µm. Currently known from New South Wales . . . . 4. ***Russula crassibasidiata***
  2: Basidia with (2, 3) 4 sterigmata . . . . ***Russula paneeroides*** (= *Gymnomyces pallidus*), ***R. eburnea*** & ***R. leucocarpa***

1: Spore ornamentation reticulate, partially reticulate or elements connected in distinct lines or ridges
  6. Spores ovate to ellipsoid (spore width 4–6 µm); ornamentation < 0.3 µm high, slowly amyloid (+ 10 min) . . . . ***Russula longispora***
  6: Spores globose or subglobose (spore width 7–14 µm); ornamentation mostly > 0.5 µm high, immediately amyloid
    7. Spore ornamentation 2–4 µm high, of branched, irregular ridges or isolated robust spines connected in a partial to complete reticulum, margins more strongly amyloid than sides . . . . ***Russula aurantirosea*** (= *Gymnomyces clelandii*), ***R. osphranticarpa*** (= *G. redolens*), ***R. leonardii*** (= *G. rodwayi*), ***R. costatispora***, ***R. korystospora*** (= *G. cristatus*) & ***R. pterosperma***

7: Spore ornamentation generally < 2 µm tall, of spines, rods or warts connected in a partial to complete reticulum
  13. Spore ornamentation 1–2 µm high; basidiomata white with brown patches . . . . ***Russula glarea***
  13: Spore ornamentation < 0.8 µm tall; basidiomata white to pale yellow or brown, with red to orange patches
    14. Hymenial cystidia absent; peridiopellis undifferentiated from context; basidia 35–50 µm long, cylindrical to narrowly clavate . . . . ***Russula wirrabarensis***
    14: Hymenial cystidia present; pileipellis a turf or trichodermium, which may be agglutinated and appressed in patches; basidia generally shorter, not as distinctively cylindrical
      15. Peridiopellis appearing as an ixocutis or in patches as an agglutinated turf of hyphal tips . . . . ***Russula parvisaxoides*** & ***R. eildonensis***
      15: Pileipellis a dense trichodermium or turf of cystidia
        17. Peridium pale yellow with orange to brick-red or brown streaks and patches or overall pale yellow; subhymenium of irregular elements 5–13 µm diam. . . . ***Russula westresi***
        17: Pileus white to pale yellow in youth, becoming brownish white with some brown to ochre mottling; subhymenium of isodiametric elements, 6–21 µm diam
          17a. Hymenophore cream-coloured to pale yellow, locules small, fine, odour mild, slightly spicy and fishy, taste slightly acrid, pileipellis a trichoderm with 2 or 3 tiers of cells, 6–25 × 7–12 µm, terminating in a golden turf of hyphal tips and cystidia. Known only from central New South Wales . . 5. ***Russula danksiae***
          17b: Hymenophore white to pale yellowish-orange, locules large, open, elongate, odour faintly of chlorine, taste mild, pileipellis a turf of hyphal tips and cystidia. Known only from southern WA. . . . . ***Russula boranupensis***

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4. ***Russula crassibasidiata*** T.Lebel, Davoodian & Castellano, ***sp. nov.***

Holotypus: Australia, New South Wales: Narrabri, Pilliga Nature Reserve, 18 July 2007, *M. Danks, J.M. Trappe, T. Lebel, K. Vernes KV631* (MEL2364422).

Registration identifier: IF557866.

Basidiomata sequestrate, subglobose to elongate, with a plane apex and incurved margins, 15–32 mm long and wide, 14–37 mm tall, hymenophore exposed for a few mm in some basidiomes. *Pileus* surface dry, smooth to minutely fibrillose, cracking into irregular patches in larger basidiomes, pale tan-yellow to pale orange-brown becoming darker ochre brown to brown with age. *Hymenophore* loculate, locules minutely labyrinthine, initially off-white, becoming pale yellow, then eventually tan brown to brown (becoming darker brown where insect damaged), firm in texture. *Stipe-columella* absent, or present as a very narrow percurrent strand < 1 mm wide, and a small inserted basal pad 3–5 mm wide, 2 mm tall. *Odour* slightly fishy. *Taste* mild.

Pileipellis 10–25 µm wide, a patchy turf of hyphal tips, 9–22 × 2–5 (–7) µm, septate, with short, cylindrical, narrowly clavate to fusoid cystidia, 7–15 × 2–5 µm, with obtuse or sometimes acute apices, contents golden in KOH, mostly repent; overlying a broad context, 50–200 µm wide, of hyaline, loosely interwoven hyphae, 3–5 µm wide, with rare scattered sphaerocytes up to 25 µm wide. *Hymenophoral trama* 20–48 µm wide, of hyaline, interwoven to parallel hyphae, 3–6 µm wide, with abundant endocystidia, golden in KOH; *subhymenium* narrow, pseudoparenchymatous to ramose, 1–2 tiers of cells, 3–11 × 4–9 µm. *Basidia* broadly clavate to obovate, 22–28 × 12–16 (–20) µm, mostly 2-spored (rarely 3–4); sterigmata 2–5 µm long. *Hymenial cystidia* abundant, arising from within trama, clavate to cylindrical, with obtuse or sometimes capitate apices, 20–25 × 2–5 µm, with oily contents that turn golden in KOH. Spores 8.5–10 × 8–10 µm ($Q_{mean} = 1.03$), orthotropic, globose to subglobose, irregularly amyloid ornamentation of isolated, irregular rods, warts, and knobs, 0.5–1 µm tall. **Fig. 8.**

Diagnosis. Differs from other sequestrate *Russula* species in the combination of a narrow, patchy turf pileipellis, mostly 2-spored, broadly clavate to obovate basidia, and spores with mostly isolated, irregular rods, warts and knobs.

Ecology & distribution. In small groups, hypogeous, in open ironbark woodlands of mixed *Eucalyptus sideroxylon*, *E. blakelyi*, *E. melliodora*, *Callitris endlicheri*, *Angophora floribunda*, and *Acacia* spp. Known only from Pilliga Nature Reserve.

Notes. *Russula crassibasidiata* is known only from a small, not easily accessible, area in the Pilliga Nature Reserve in central northern New South Wales. Extensive searches in nearby areas (2007–2011) were unsuccessful (Danks 2012). This is not altogether surprising given the cryptic nature of the basidiomata and the low rainfall in the region. *Russula crassibasidiata* resembles several other sequestrate *Russula* species, including *R. pilosella* T.Lebel and *R. paneeroides* T.Lebel in the pale cream to tan basidiomes that darken in age (Lebel & Tonkin 2007; Lebel 2017).

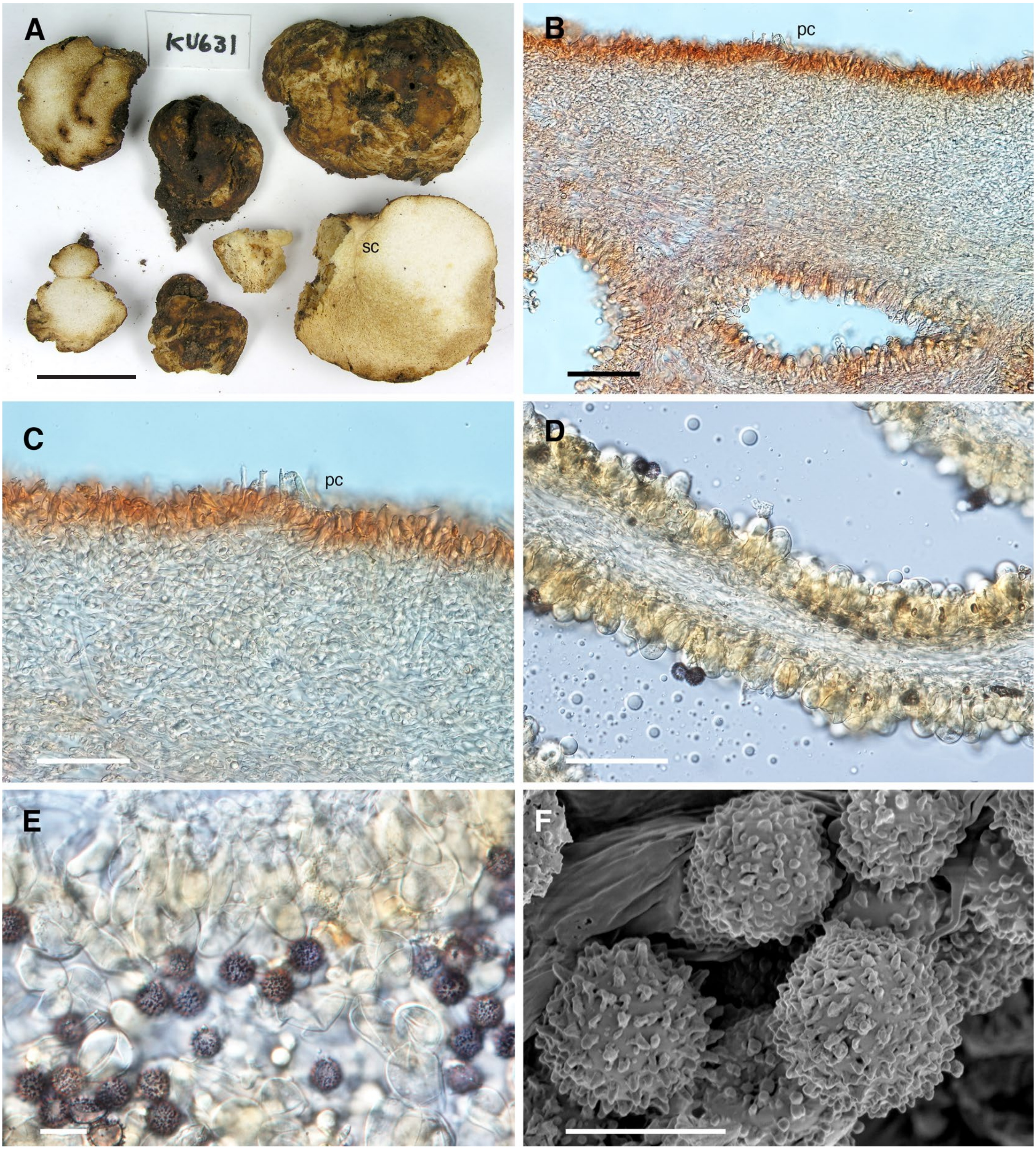

Fig. 8. *Russula crassibasidiata* (holotype). **A** Basidioma, sc = stipe-columella remnant; **B–C** pileipellis and context, pc = pileal cystidia; **D** hymenophoral trama showing broad basidia and cystidia; **E** spores, in Melzer's reagent; **F** SEM of spores. Scale bars: A = 10 mm, B–D = 50 µm, E–F = 10 µm. — A–F *M. Danks et al. KV631* (MEL2364422, holotype). Photo: K. Vernes (A), T. Lebel (B–F).

Russula crassibasidiata differs in the much-reduced stipe-columella, mostly 2-spored, broadly clavate basidia, single type of hymenophoral cystidia, and low, irregularly amyloid spore ornamentation (Fig. 8). In addition to morphological features, *R. crassibasidiata* is supported by molecular phylogenetic analysis (Fig. 9) as a distinct species, in sect. *Ingratae*, subsect. *Pectinatinae* with members of the *R. amoenolens* group (Vidal *et al.* 2019). The slightly fishy odour is consistent with the majority of other taxa in this subsection.

Etymology. The specific epithet refers to the short, broadly (*crassus*) clavate basidia (adj. *basidiata*).

Additional material examined.

AUSTRALIA. NEW SOUTH WALES. Narrabri, Pilliga Nature Reserve, 18 July 2007, *M. Danks, J.M. Trappe, T. Lebel, K. Vernes KV632* (MEL2364389); Narrabri, Pilliga Nature Reserve, 18 July 2007, *M. Danks, J.M. Trappe, T. Lebel, K. Vernes KV634* (MEL2364390).

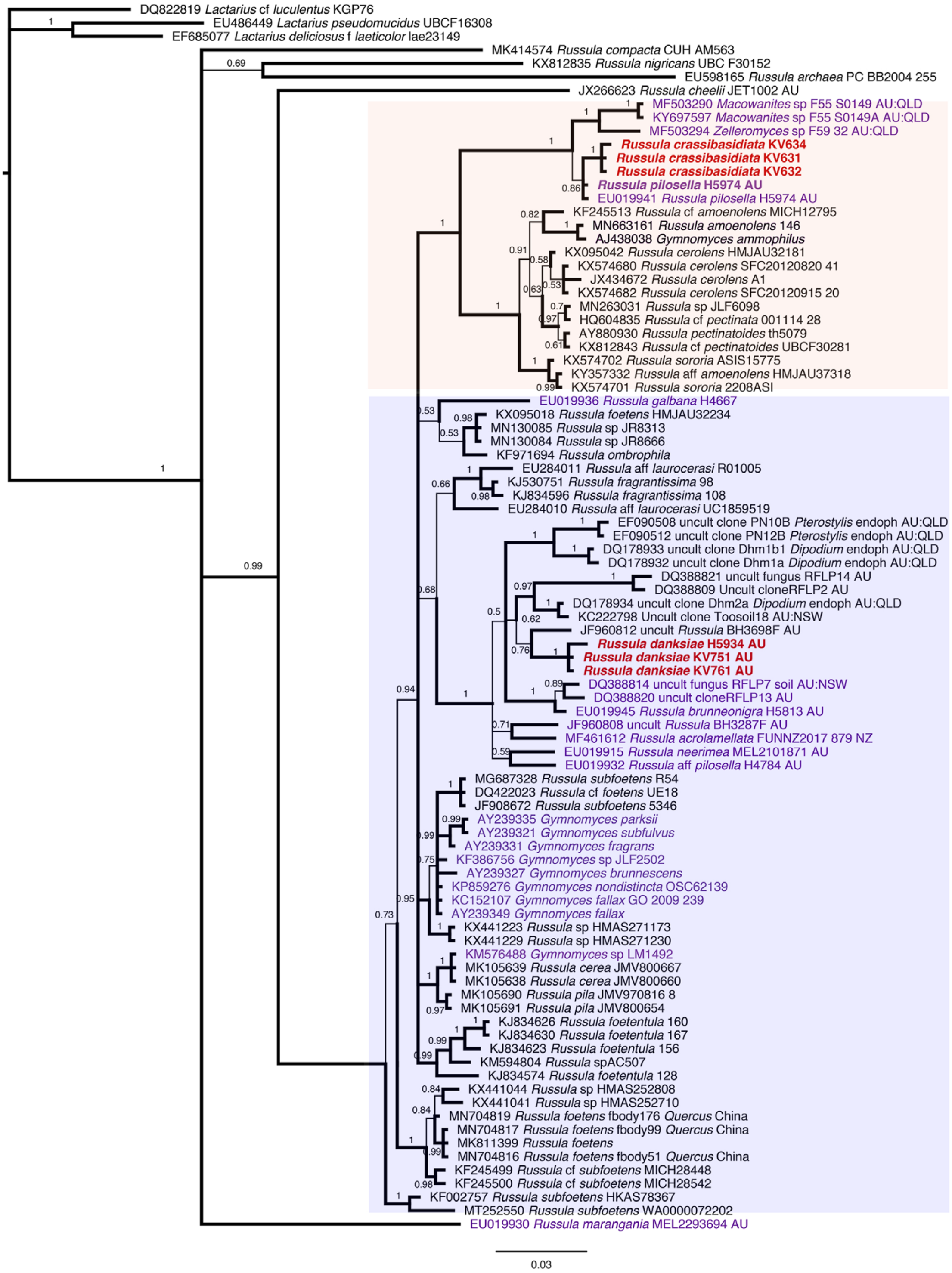

Fig. 9. Bayesian majority rule phylogram of concatenated LSU and ITS data for a selection of closely related taxa in *Russula* subgenus *Heterophyllidiae*, section *Ingratae*. Bayesian posterior probabilities (bpp) are shown at the nodes. Thickened lines indicate PP support ≥ 0.95. Taxon labels in red indicate the new taxa *R. crassibasidiata* and *R. danksiae*. Labels in purple indicate other sequestrate species.

5. *Russula danksiae* T.Lebel & Castellano, *sp. nov.*

Holotypus: Australia, New South Wales: Guy Fawkes National Park, horse exclusion experiment partial exclusion plot 1, 5 Aug. 2009, *K. Vernes, M. Danks & T. Lebel KV761* (MEL2363640).

Registration identifier: IF557867.

Basidiomata sequestrate, subglobose to ellipsoidal, to 12–20 mm long and wide, 15–20 mm tall. *Pileus* surface smooth, cream-coloured to dull yellow with brown spots; texture cottony to finely tomentose. *Hymenophore* loculate; locules small, cream-coloured to pale yellow. *Stipe-columella* absent or present as a narrow percurrent strand, to 0.5 mm wide, pale brownish yellow. *Odour* mild, slightly spicy and fishy. *Taste* slightly acrid.

Pileipellis 25–48 µm wide, a trichoderm with 2 or 3 tiers of cells, 6–25 × 7–12 µm, terminating in a turf of hyphal tips and cystidia, 18–40 × 3–9 µm, apices obtuse, capitate or fusoid, with some golden yellow pigment on outer surface of cells; overlying a context, 75–210 µm wide, of compact, short, septate, interwoven, parallel hyphae, 3–7 µm wide, and inflated hyphae up to 16 µm wide, with scattered clavate endocystidia, 17–20 × 5–6 µm. *Hymenophoral trama* 10–25 µm wide, of gelatinised hyphae, 2.0–4.5 µm wide; *subhymenium* 10–25 µm wide, well-developed, of 2–4 layers of hyaline, parenchymatous cells, 6–16 µm wide. *Basidia* clavate, (18–) 25–30 × (7–) 8–10 µm, mostly 4-spored; sterigmata up to 4–5 µm long. *Hymenial cystidia* rare, cylindrical to narrowly clavate, 16–30 × 4–6 µm, with granular contents. *Spores* subglobose to ellipsoidal, 8.5–10.0 × 7–8 µm (Q_{mean} = 1.37); ornamentation a partial to almost complete reticulum with scattered isolated warts, 0.3–0.5 µm tall, irregular in height. **Fig. 10.**

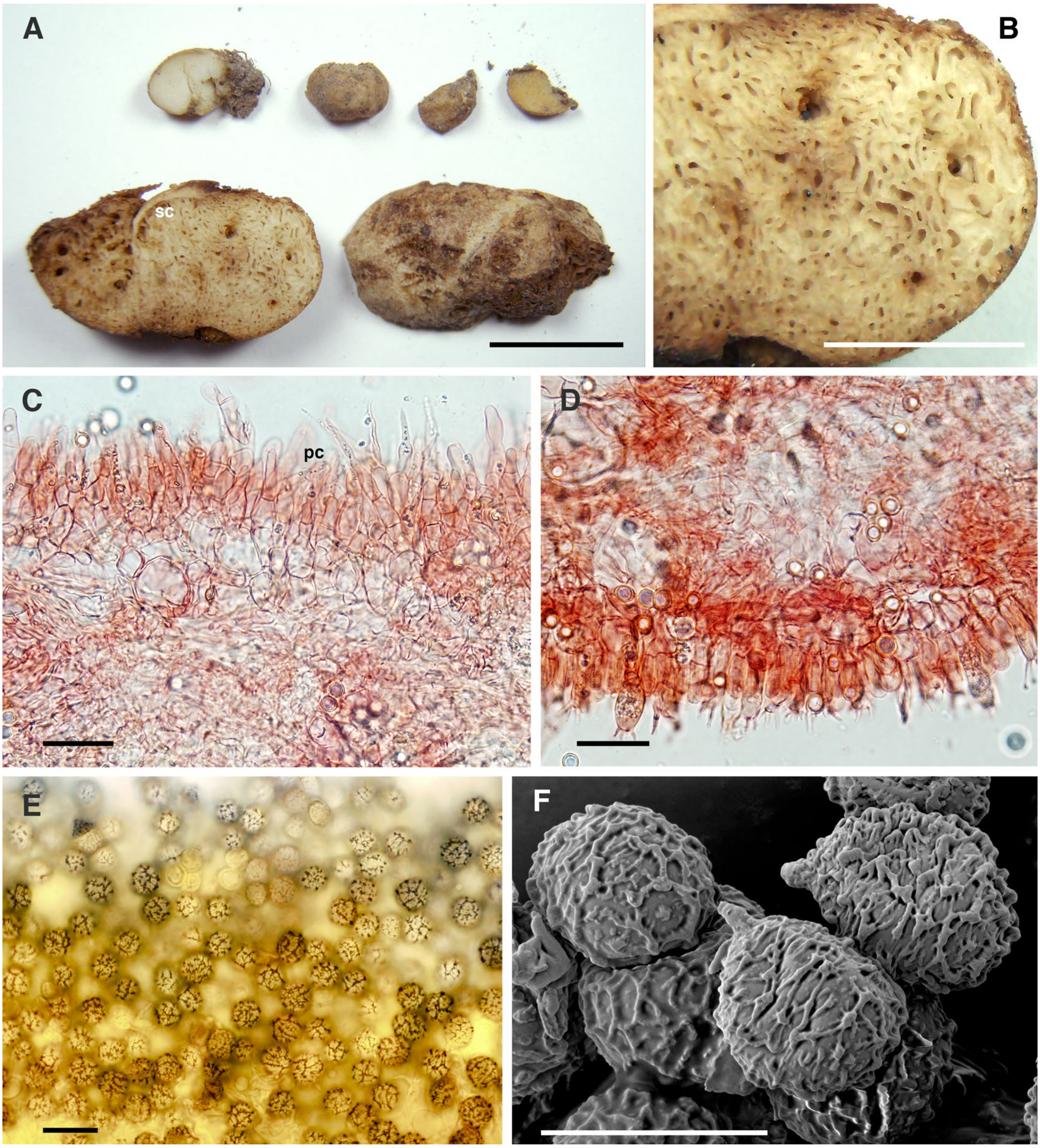

Fig. 10. *Russula danksiae* (holotype). **A** Basidiomata, sc = stipe-columella remnant; **B** closeup of loculate hymenophore; **C** pileipellis and context, pc = pileal cystidia; **D** hymenophoral trama showing basidia and cystidia; **E** spores, in Melzer's reagent; **F** SEM of spores. Scale bars: A = 10 mm, B = 5 mm, C–E = 20 µm, F = 10 µm. — A–F *K. Vernes et al. KV761* (MEL2363640). Photos: K. Vernes (A, B), T. Lebel (C–F).

Diagnosis. Differs from other sequestrate *Russula* species in the combination of large hymenophoral locules, a golden trichodermial pileipellis, and low, fine, distinctly reticulate spore ornamentation.

Ecology & distribution. Hypogeous in grassy eucalypt woodland in northeastern New South Wales.

Notes. *Russula danksiae* resembles *R. boranupensis* (T.Lebel) T.Lebel in the pale basidiomata that become mottled with brown and ochre, but differs in the quite large, empty hymenophoral locules, a trichodermial rather than cystidial turf pellis, and the spore ornamentation being distinctly more reticulate with fewer isolated elements (Lebel 2003b, 2017; Fig. 10). In the field this species was initially thought to be related to *Lactarius* rather than *Russula*, due to the texture of the basidiomes and hymenophore with larger, more open locules. It was thought that the basidiomata had dried out (no latex or moisture visible). However, analysis of ITS sequences (Fig. 9) places *Russula danksiae* in a strongly supported clade of Australasian *Russula* species, with *R. neerimea* Grgur., *R. acrolamellata* McNabb and *R. brunneonigra* T.Lebel (Lebel & Tonkin 2007), *R. aff. pilosella* (H4784), and several environmental sequences. The environmental sequences include soil sequences and sequences from orchid mycorrhizas. *Russula danksiae* is a member of sect. *Ingratae*, subsect. *Foetentinae*.

Etymology. Specific epithet refers to Melissa Danks, an excellent naturalist, ecologist, and collector of native truffle species.

Additional material examined.

AUSTRALIA. NEW SOUTH WALES. Guy Fawkes National Park, horse exclusion experiment control plot 1, 5 Aug. 2009, *K. Vernes, M. Danks & T. Lebel KV751* (MEL2363642); Gibraltar National Park, Gibraltar Gorge, 2 May 1992, *J.M. Trappe H5934* (OSC).

Psathyrellaceae Vilgalys, Moncalvo & Redhead

Redhead *et al.* (2001) introduced the family Psathyrellaceae to accommodate the genera *Psathyrella* (Fr.) Quél. and *Lacrymaria* Pat., together with related species in the polyphyletic genus *Coprinus sensu lato*, which were transferred to the genera *Coprinellus* P. Karst., *Coprinopsis* P.Karst. or *Parasola* Redhead, Vilgalys & Hopple. Kirk *et al.* (2008) broadened the concept of the family to include 12 genera. More recently, Wachter & Melzer (2020), proposed a new generic system for Psathyrellaceae, recognising an additional six new genera. *Coprinopsis* is a large genus with 20 subgenera, that contains around 200 species (Kirk *et al.* 2008; Wachter & Melzer 2020). They are saprotrophic and occur on soil, wood, vegetable refuse, dung or burnt ground, and produce agaricoid, rather fragile basidiomes which are often short-lived and/or deliquescent, with a blackish spore deposit. This is the first record in the genus *Coprinopsis* of a sequestrate basidiome form, or a species with pale spores.

6. *Coprinopsis pulchricaerulea* T.Lebel, Padamsee & T.W.May, ***sp. nov.***

> **Holotypus:** Australia, New South Wales: Booyong, 565 Houghlahans Creek Rd, 19 Oct. 2009, *S. Axford s.n.* (MEL2363909)
>
> **Registration identifier: MB841411.**
>
> *Le Ratia atrovirens* R.Heim, *Rev. Mycol.* 33: 143 (1968), *nom. inval.* — *Le Ratia atrovirens* R.Heim, *Rev. Mycol.* 33: 212 (1968), *nom. inval.* MB333316. — *Leratiomyces atrovirens* (R.Heim) Bresinsky & Manfr. Binder, *Z. Mykol.* 64(1): 80 (1998), *nom. inval.* MB446995.

Basidiomata 8–28 × 6–22 mm, spherical at first then ellipsoid to ovoid or sometimes turbinate, apex convex, margin remaining in-rolled though not necessarily attached to stipe, not completely covering hymenophore in most basidiomes, pale blue to bright sky blue or sometimes watery greenish blue, becoming dark greyish green when dry or in very old basidiomes, covered in tiny, fine, white warts/granular glistening spheres which wash off or erode as basidiome ages, otherwise appearing smooth, non-deliquescent. *Hymenophore* lamellate to sublamellate, with some labyrinthine fusions between lamellae, white to pale cream becoming pale tan, moderately packed. *Stipe* 5–20 mm long, 3–7 mm diam., variable, central, cylindrical, slightly bulbous at base tapering slightly to apex, dry, silky in age, white; context solid or hollow in some basidiomes, white or occasionally with pink tinge. *Partial veil* present, white, fibrillose to floccose remnants apparent on stipes of immature specimens, towards base. *Odour* strongly mushroom-like. *Taste* not distinctive. Basidiomata fragile, easily disintegrate on handling.

Pileipellis a thin cutis of hyaline hyphae, 4–12 µm diam., overlying inflated cells bunching into upright hyaline clusters to form small warts with elongated apices, 5–11 cells deep, composed of spherical, subglobose to oblong inflated elements, (18–) 25–48 (–72) × (16–) 32–45 (–60) µm, becoming interwoven with some cylindrical hyphae, 3–7 µm diam., in small parallel bundles, with occasional inflated elements, 10–16 µm diam., towards the base of the ‘warts’. *Pileus context* a broad layer 500–1100 µm thick, composed of interwoven hyphae 3–7 µm diam., with occasional inflated elements 8–19 µm diam. All hyphae in pileipellis and pileus context with scattered, irregular coating of pigment on outer surface; appears golden brownish in KOH and water in sections of dried material. *Hymenophoral trama* narrow, composed of loosely interwoven to occasionally parallel, hyaline, septate hyphae 4–8 µm diam.; *subhymenium* parenchymatous, 5–12 × 5–10 µm, with scattered hyphal elements. *Basidia* 18–32 × 6–12 µm, clavate to cylindrical, with slightly thickened wall, hyaline, mostly 4-spored, some 2-spored, squashed in between highly inflated basidioles, 26–58 × 18–52 µm, globose to obclavate, hyaline, thin-walled. *Hymenial cystidia* none observed. *Spores* (17–) 19–23 × 10–12.5 µm, mean = 19.07 ± 1.48 × 10.74 ± 1.42 µm, Q = 1.82–3.43, Q_{mean} = 2.19, ellipsoid to elongate, some misshapen, germ pore absent but some with pale lens at apex (otherwise no interruption), hyaline to very pale brown in KOH, inamyloid, nondextrinoid, smooth, thick-walled with a small apiculus. Clamps present at basidiole base. **Figs 11 & 12.**

Diagnosis. Differs from other *Coprinopsis* species in the blue coloration of the basidiomata, the sequestrate basidiome form, pale hymenophoral tissue and spores at all stages of maturity.

Fig. 11. *Coprinopsis pulchricaerulea*. **A–D** Examples of fresh basidiomata: **A–C** New South Wales; **D** New Caledonia. **E** Habitat (New South Wales). Scale bars: C = 5 mm, D = 10 mm. — Photos: S. Axford (A–C, E), T. Lebel (D).

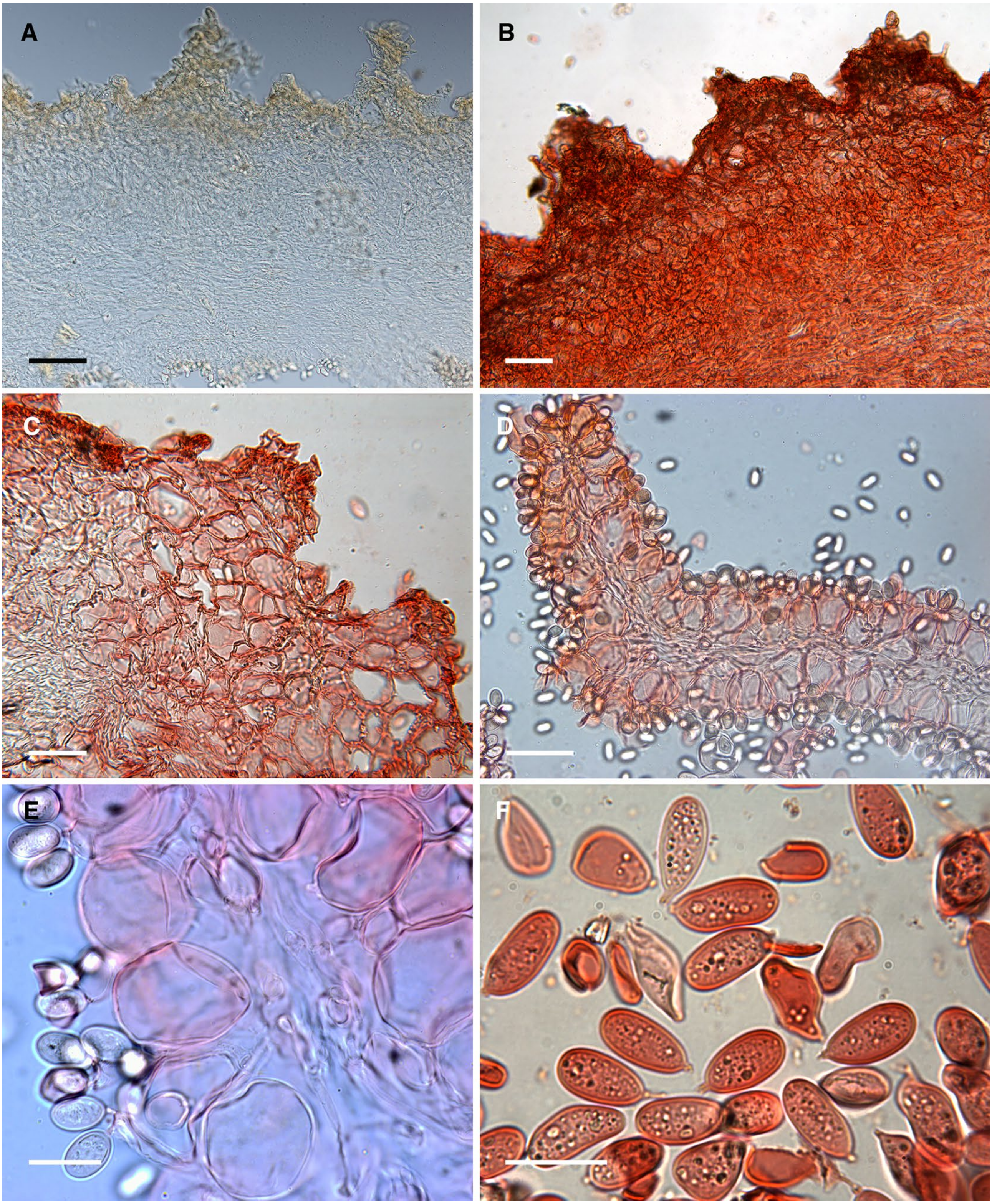

Fig. 12. *Coprinopsis pulchricaerulea* (paratype). **A–B** Pileipellis and context; **C** closeup of pileipellis showing granular structure; **D** hymenophoral trama showing basidia and inflated basidioles; **E** basidia, inflated basidioles and hymenophoral trama; **F** spores. Scale bars: A–D = 50 µm, E–F = 20 µm. — A–F *S. Axford B001* (MEL2363910). Photos: T. Lebel.

Ecology & distribution. Growing in small groups or solitary on soil and leaf litter and decaying branchlets in dense, wet forest or rainforest in northern New South Wales and New Caledonia; on Lord Howe Island on rocky path in wet dense forest, verging on rainforest, near paddock.

Notes. Redhead & McNeill (2008) discuss in detail the nomenclature of the name "*Le Ratia*" Pat. (invalid due to the space in the name), the illegitimate name *Le-Ratia* Pat. ex. Sacc. & Trotter (*non Leratia* Broth. & Paris) and efforts to introduce *Leratiomyces*, culminating in the valid publication of *Leratiomyces* Bresinsky &

Manfr. Binder ex Bridge, Spooner, Beever & D.-C. Park by Bridge *et al.* (2008). The type of *Leratiomyces* is *Leratiomyces similis* (Pat. ex Sacc. & Trotter) Bresinsky & Manfr. Binder ex Redhead & McNeill, a dull red, sequestrate taxon from New Caledonia; a second red sequestrate species from New Zealand is also accepted in the genus, *Leratiomyces erythrocephalus* (Tul. & C.Tul.) Beever & D.-C. Park (Bridge *et al.* 2008; Redhead & McNeill 2008). Two blue to green sequestrate species originally placed in "*Le Ratia*" were assigned to *Leratiomyces* by Bresinsky & Binder (1998) but excluded from the genus by Bridge *et al.* (2008) on the basis of sequence data, with *Leratiomyces atrovirens* suggested to belong in the /psathyrella clade and *L. smaragdinus* suggested to belong in the / agrocybe clade. Our phylogenetic analysis places recent collections from Australia and New Caledonia that match the original description of "*Le Ratia atrovirens*" within the genus *Coprinopsis* (Fig. 13).

According to Redhead & McNeill (2008) all three existing names with '*atrovirens*' as an epithet (see above in synonymy) are invalid. The material of "*Le Ratia atrovirens*" examined by Heim (1968) is apparently in poor condition [not seen by us: New Caledonia, in silva Thi, in foliis putridis, 21 June 1967, leg. *J.M. Veillon s.n.* (PC)]. Longstanding confusion exists between the two blue-green sequestrate species in New Caledonia originally named "*Le Ratia atrovirens*" and "*Le Ratia smaragdina*", with some considering basidiomes with the brown hymenophore of the latter as the mature stage of the former. This is not the case, basidiomes with a brown hymenophore belong to a different genus (see *Agrocybe smaragdina* below). This confusion persists among citizen science observations in iNaturalist and other sites. It is also possible that cryptic taxa remain to be uncovered. As a result, we have chosen to name this taxon as a new species, with a new epithet, and typify with a more recent Australian collection, which has sufficient material, images and molecular data.

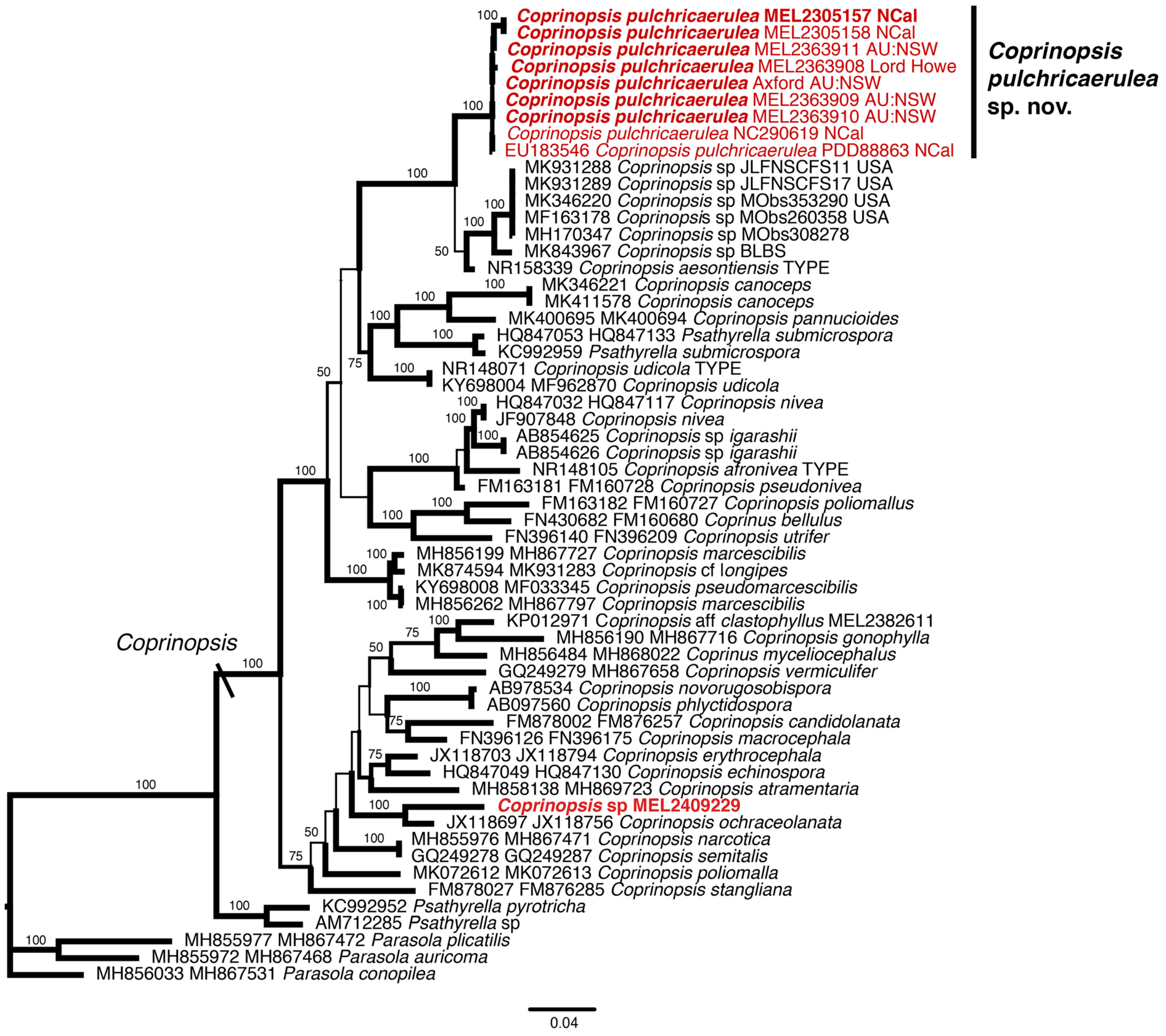

Fig. 13. Maximum Likelihood phylogram of concatenated ITS and LSU data representing a selection of sections within *Coprinopsis*, with *Parasola conopilea* as the outgroup. ML bootstrap support are shown at the nodes; thickened lines indicate ML support ≥ 80%. Taxon labels in red indicate *Coprinopsis pulchricaerulea*, and a novel agaricoid species (MEL2409229).

The tiny, fine, white warts/granular glistening spheres observed on the basidiome surface are not single cell structures. Rather they are chains of hyaline, inflated cells that form elongated pyramidal warts that allow light to pass through.

New Caledonian specimens of *Coprinopsis pulchricaerulea* had barely any white glistening structures visible, except in crevices and near the margin of the pileus of basidiomes. In two of these collections (MEL2305157, MEL2305158) the spores are slightly smaller and less ellipsoid-elongate: 17–20 × 10–12 µm, mean = 18.85 ± 0.74 × 11.40 ± 0.66 µm, Q = 1.58–1.90, Q_{mean} = 1.67. However, the differences are slight and could be due to maturity or age of material. Otherwise, microscopically these collections match other material in all details. In addition, sequences are very similar to those of collections from Australia, and the two New Caledonian collections do not form a distinct or well-supported clade. Therefore, one taxon is accepted, occurring in Australia and New Caledonia. Investigation of population genetic structure across this disjunct distribution will be of interest as there are few examples of sequestrate taxa with a distribution separated by large stretches of ocean.

Our DNA analysis (Fig. 13) places *Coprinopsis pulchricaerulea* close to *C. aesontiensis* A.Melzer, Ferisin & Dovana (Melzer *et al.* 2016), and an undescribed *Coprinopsis* sp. (California, USA; ITS: MK346220, MH170347; https://mushroomobserver.org/353290; https://mushroomobserver.org/308278) in what used to be section *Canoceps* (Wachter & Melzer 2020). *Coprinopsis pulchricaerulea* resembles *C. aesontiensis* and the *Coprinopsis* sp. (USA) in the pileus texture (but is blue not grey or white), absence of pleurocystidia, and growth on wood. The pileus of *C. pulchricaerulea* generally remains attached to the stipe, rarely exposing the hymenophore, unlike the other two taxa which form typical agaricoid basidiomata.

It is intriguing that the transition from dark to light spore colouration has occurred multiple times in the Agaricaceae, i.e., in *Coniolepiota* Vellinga and *Eriocybe* Vellinga (Vellinga *et al.* 2011), and in several sequestrate Australian *Agaricus* species (Lebel & Syme 2012). *Coprinopsis pulchricaerulea* occurs in subtropical rain forests with an often closed canopy and the spore mass is not exposed, so melanisation for protection of the spores may not be necessary. The bright basidiome colours of some sequestrate fungi from New Zealand have been postulated to be related to mycophagy by birds and reptiles rather than mammals (Beever & Lebel 2014); perhaps this is also the case for this brightly coloured wet forest inhabitant?

Thanks to the concerted efforts of local field naturalists, particularly S. Axford, this rare fungus has been found in three small remnants of lowland subtropical rainforest early settlers called 'the Big Scrub' in northern New South Wales. These small pockets are within a 25 km radius of Booyong Nature Reserve. Similarly, in both New Caledonia and on Lord Howe Island, all collections or iNaturalist records have been made within a restricted geographic area of 5–20 km^2.

Etymology. The specific epithet is from Latin *pulcher* (beautiful) and *caeruleus* (blue) referring to the striking colour of the basidiomes.

Additional material examined.

AUSTRALIA. NEW SOUTH WALES. Booyong, Tara Ridge, Dec. 2009, *S. Axford B001* (MEL2363910); Nightcap National Park, Big Scrub loop tk, Dec. 2009, *S. Axford B007* (MEL2363911); Lord Howe Island, c. 100 m inland of W end of Old Settlement Beach, July 2009, *J. Derkenne s.n.* (MEL2363908).

NEW CALEDONIA. Koghis, Cascade Track branch to giant Kauri in vicinity of kauri, 4 Dec. 2003, *P.R. Johnston & R.E. Beever 2202* (PDD88863); Parc Riviere Bleue, Le Geant Kaori walk trail, within first 100 m of trail, 29 Nov. 2000, *T. Lebel 820* (MEL2305157); Parc Riviere Bleue, Le Geant Kaori walk trail, within first 100 m of trail, 29 Nov. 2000, *T. Lebel 821* (MEL2305158).

Strophariaceae Singer & A.H.Sm.

Strophariaceae includes both decomposers growing on various kinds of organic matter, such as dung, soil and plant litter, as well as ectomycorrhizal species (Borovička *et al.* 2011; Cho *et al.* 2016; Frings *et al.* 2020; Lee *et al.* 2020). Species in the genus *Agrocybe* Fayod are decomposers, with a rusty brown, tobacco brown or dark brown spore print, typically the basidiospores have a broad germ pore, a hymeniform pileipellis composed of inflated cells and conspicuous cheilocystidia (Singer 1986; Largent & Baroni 1988; Niveiro *et al.* 2020). Vizzini *et al.* (2014) transferred several species, with larger basidiomes, a membranous annulus, and a rudimentary or absent germ pore to the genus *Cyclocybe* (V.Brig.) Vizzini. Sequestrate forms are not common, but have evolved more than once in the genus (Malysheva *et al.* 2019).

7. *Agrocybe smaragdina* (Pat. ex Sacc. & Trotter) T.Lebel, K.Hosaka, T.W.May & Padamsee, ***comb. nov.***

Registration identifier: MB841231.

Le-Ratia smaragdina Pat. ex Sacc. & Trotter, *Syll. Fung.* 21: 468 (1912). MB532576. — **Holotype:** New Caledonia: Ad truncus vetustos montis Dzumac, *Le Rat 108* (FH, Herb. Patouillard).

Le Ratia smaragdina Pat., *Bull. Soc. Mycol. France* 25: 133 (1909), *nom. inval.* (Art. 35.1). MB178862. — *Leratiomyces smaragdinus* (Pat.) Bresinsky & Manfr. Binder, *Z. Mykol.* 64(1): 80 (1998), *nom. inval.* (Art. 35.1). MB446998.

Pileus 8–14 mm tall, 6–30 mm diam., subglobose, apex convex to planoconvex, margin remaining incurved, bright turquoise green fresh, drying yellowish, somewhat crevassed, but otherwise smooth, dry. *Hymenophore* labyrinthine loculate, locules somewhat irregular shaped,

Fig. 14. *Agrocybe smaragdina*. **A** General habitat, Riviere Bleue P.P., New Caledonia; **B** dense mixed canopy forest, Riviere Bleue P.P., New Caledonia; **C–E** fresh basidiomes showing brown hymenophore, remnant stipe and partial veil (pv); **F** hymeniderm pileipellis and pileal context; **G** closeup of hymeniderm pileipellis; **I–J** spores. Scale bars: C–E = 10 mm, F–G = 50 µm, I–J = 20 µm. — Photos: K. Hosaka (A, C–E), T. Lebel (B, F–J).

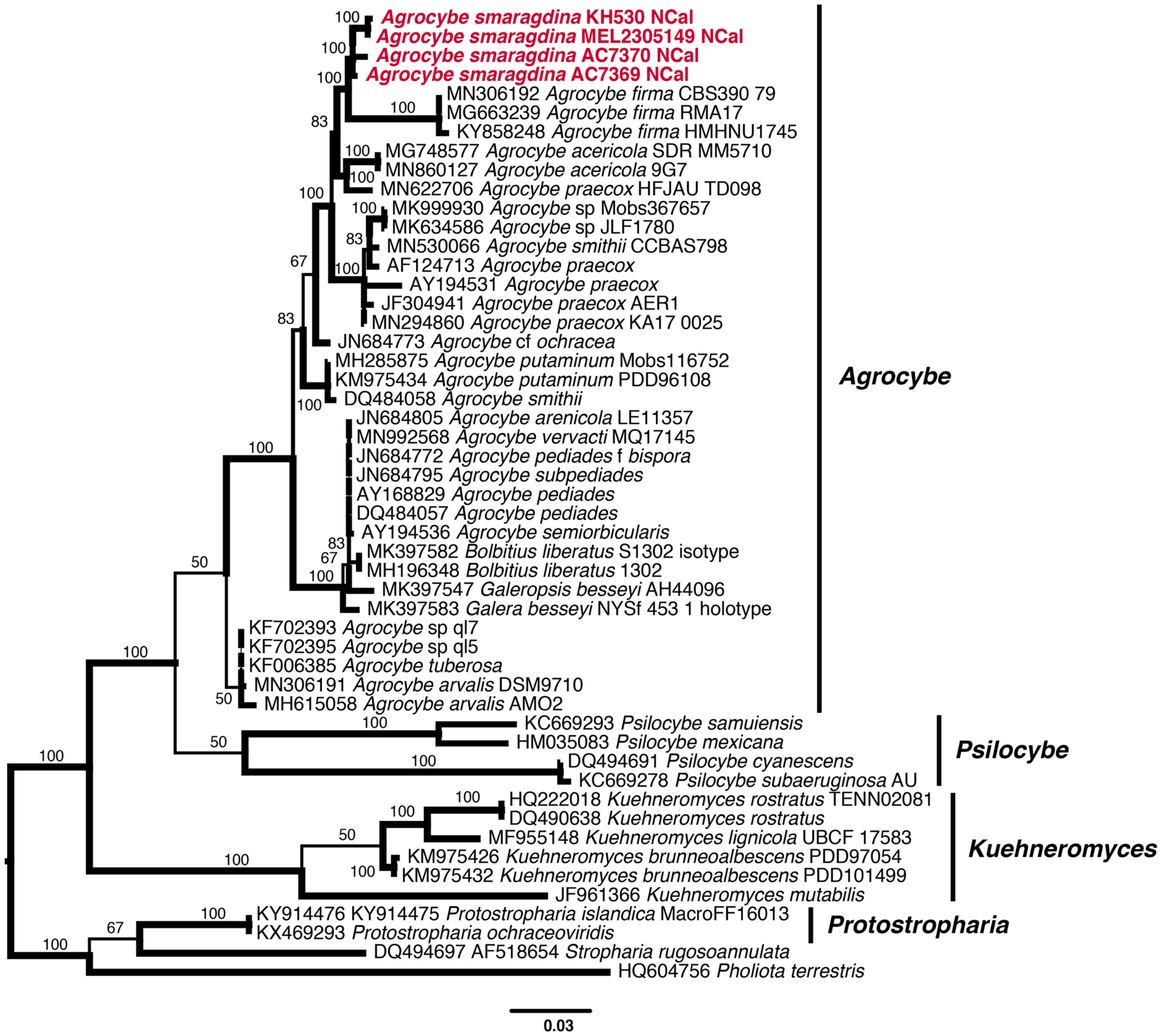

Fig. 15. Maximum Likelihood phylogram of ITS data including representative *Agrocybe* species, other Strophariaceae and *Pholiota terrestris* as outgroup. ML bootstrap support shown at the nodes; thickened lines indicate ML support ≥ 75%. Taxon labels in red indicate *Agrocybe smaragdina*.

empty, ochre brown. *Stipe-columella* 5–10 × 1–2.5 mm, percurrent, short, central with slight basal bulb, smooth, white with greenish tinge. *Partial veil* present, white, silky, remaining attached to pileus margin and stipe, enclosing hymenophore at base. *Basal rhizomorphs* white, abundant. *Odour* not distinctive. *Taste* mild.

Pileipellis thin, 45–60 µm thick, hymeniform, terminal cells clavate to cylindrical, 24–36 (–42) × 9–14 (–15) µm, hyaline, merging into a narrow layer of parenchymatous cells, 2–3 cells deep, 5–14 × 5–12 µm; context 50–80 µm wide, of interwoven inflated hyphae 5–12 µm diam., becoming more parallel towards hymenium. *Hymenophoral trama* 35–50 µm wide, of parallel, hyaline hyphae 4–7 µm diam., and scattered inflated elements to 14 µm diam. *Basidia* 18–29 × 6–12 µm, clavate, hyaline, 4-spored; basidioles similar size and shape. *Hymenial cystidia* none observed. *Spores* (12–) 14–15.5 (–17) × (6.5–) 7–8 µm, mean = 15.50 ± 0.94 × 7.18 ± 0.61, Q = 1.88–2.33, Q_{mean} = 2.17, broadly ellipsoid to ellipsoid, pale yellow to yellow-brown, smooth, thick-walled, with small germ pore, non-dextrinoid. **Fig. 14.**

Ecology & distribution. Growing in small groups or solitary, on soil and leaf litter and decaying branchlets in dense, wet forest. New Caledonia.

Notes. Redhead & McNeill (2008) point out that the designation "*Le Ratia smaragdina*" as introduced by Patouillard (1909) is invalid as is "*Leratiomyces smaragdinus* (Pat.) Bresinsky et Manfr. Binder", but *Le-Ratia smaragdina* Pat ex Sacc. & Trotter is a valid name that can serve as the basionym for the combination into *Agrocybe*. Although Redhead & McNeill (2008) use the masculine spelling "*smaragdinus*" for *Le-Ratia smaragdina*, *Le-Ratia* Pat. ex Sacc. & Trotter is feminine, following Patouillard (1907, 1909) who introduced "*Le Ratia similis*" and "*Le Ratia smaragdina*" and Saccardo

& Trotter (1912) who validated the generic name with species *Le-Ratia similis* and *L. smaragdina* with those spellings.

In addition to "*Le Ratia atrovirens*" (formally named above as *Coprinopsis pulchricaerulea*) and *Agrocybe smaragdina*, several dark-spored sequestrate taxa with blue to blue-green basidiomata have been variously placed in the genera *Secotium* Kunze, *Clavogaster* Henn. and *Weraroa* Singer. *Secotium novaezelandiae* G.Cunn. was described from New Zealand, and later placed in *Weraroa*, of which it is the type species. It is now recognised as a *Psilocybe* species (of which *Weraroa* is a synonym) under the replacement name *Psilocybe weraroa* Borov., Obornik & Noordel. *Clavogaster novozelandicus* Henn. was described from New Zealand as the type of *Clavogaster*, and later synonymised with *C. virescens* (Massee) J.A.Cooper (based on *Secotium virescens* Massee from New Zealand).

Agrocybe smaragdina differs from other blue-green sequestrate species from New Caledonia and New Zealand in both macro- and micro-morphology. *Coprinopsis pulchricaerulea* has larger basidiomata, a well-developed stipe, blue or blue-green colour, a pale mature hymenophore, and slightly larger spores that lack a distinct germ pore. Meléndez-Howell (1967: as "*Le Ratia smaragdina*") presents a transmission electron micrograph of the spore of *A. smaragdina* showing a distinct germ pore, with the ectospore markedly thinner at the truncate spore apex, and a germ pore is also visible under the light microscope.

The New Zealand species, *Psilocybe weraroa* (Bridge *et al.* 2008) and *Clavogaster virescens* have larger basidiomata (2–5 cm tall) that are irregularly roundish, elliptical or with a pyramidal/pointy apex, pale brown or pale blue when young, becoming pale blue grey to sky blue, with a dark brown spore mass, and cartilaginous stipe up to 4 cm long.

Phylogenetically, *A. smaragdina* is part of a strongly-supported clade (ML 100%) that includes *A. praecox* (Pers.) Fayod, *A. acericola* (Peck) Singer, *A. firma* (Peck) Singer and *A. smithii* Watling & H.E.Bigelow (Fig. 15). *Agrocybe firma* appears to be the closest agaricoid taxon (ML 100%). It appears that some names in this genus have been broadly applied based on morphological characters as some species are present in multiple places in the phylogenetic tree. Therefore, further analyses with more genes will be required to clarify species boundaries and relationships (Niverio *et al.* 2020). Nevertheless, the placement of *A. smaragdina* within the genus *Agrocybe* is confirmed from the phylogenetic analysis. Several species with sequestrate basidiome forms have recently been transferred from the genus *Galeropsis* Velen. or *Bolbitius* Fr. to *Agrocybe* (Malysheva *et al.* 2019). They all tend to have quite different appearing basidiomes, with small, partly enclosed conical to subconical pilei, partially anastamosed lamellae or loculate hymenophore, long slender stipe, ochre-brown spore mass, and a hymeniderm pileipellis. Most of the species are rare and occur in sandy, grass rich habitats rather than tropical rainforest as does *Agrocybe smaragdina*. These taxa, *A. liberata* (Kalchbr.) E.F.Malysheva and *A. besseyi* (Peck) E.F.Malysheva, G.Moreno & M.Villarreal, are more closely related to *A. pediades* (Fr.) Fayod, *A. vervacti* (Fr.) Singer and *A. arenicola* (Berk.) Singer, based on ITS data (Fig. 15; note names in phylogeny are those used in GenBank). It appears that the sequestrate basidiome form has evolved more than once in different clades within the genus, as is commonly observed for the origin of the sequestrate form in a number of genera in various orders, including Agaricales and Russulales (Sheedy *et al.* 2016).

Additional material examined.

NEW CALEDONIA. Northern Province, Mt Panie Massif nr Heinghen, 26 Nov. 2000, *T. Lebel 809* (MEL2305149); 1964, *B. Huguenin NC64227* (K(M)177208); Riviere Bleue Provincial Park, along Riviere Bleue, nr Pont Germain, 26

Key to blue-green sequestrate species of Psathyrellaceae and Strophariaceae in Australasia

1. Basidiomes blue or blue-green, with a pale hymenophore at maturity, spores lacking a distinct germ pore . . . . 6. ***Coprinopsis pulchricaerulea***

1: Basidiomes pale brown, pale blue, blue-grey, blue-green, bright turquoise green, with a dark brown hymenophore, spores with a narrow or broad germ pore

  2. Basidiomes 6–30 mm wide, 8–14 mm tall, bright turquoise green when fresh, stipe narrow < 3 mm diam.; occurs in New Caledonia . . . . 7. ***Agrocybe smaragdina***

  2: Basidiomes typically larger, 10–30 mm wide, 20–50 mm tall, pale brown, pale blue, blue-grey when fresh, stipe > 3 mm diam.; occurs in New Zealand

    3. Basidiomes with a reddish brown to rusty brown hymenophore and typically greyish blue or sky blue pellis, forming an elongated pouch often narrow and tapered at apex; spores with broad germ pore . . . . ***Clavogaster virescens***

    3: Basidiomes with a chocolate- or sepia-brown hymenophore and typically greyish blue becoming pallid-green pellis, with obtuse to slightly pointed apex ; spores with narrow barely visible germ pore . . . . ***Psilocybe weraroa***

Apr. 2004, *K. Hosaka KH-NC04-024* (TNS-F-34123; OSC122556); Reserve Speciale Botanique de Foret Nord, c. 5 km from Pic du Grand Kaori toward Goro, 30 Apr. 2004, *K. Hosaka KH-NC04-059* (TNS-F-33732; OSC122560); Reserve Speciale Botanique de Foret Nord, c. 5 km from Pic du Grand Kaori toward Goro, 30 Apr. 2004, *K. Hosaka KH-NC04-057* (TNS-F-34727; OSC122558); Reserve Speciale Botanique du Pic du Grand Kaori, Grand Lac, 2 May 2004, *K. Hosaka KH-NC04-081* (TNS-F-34162; OSC122561).

Hysterangiaceae E.Fisch.

We follow the current treatment of families in Hysterangiales according to Hosaka *et al.* (2006) and Davoodian *et al.* (2021). Based on DNA (ITS, atp6, TEF1-α) and morphological data, Davoodian *et al.* (2021) uncovered 26 provisional genera, established 2 new suborders, made 2 combinations and confirmed generic boundaries for 11 published taxa. The northern hemisphere genus name *Hysterangium* has been broadly applied worldwide to at least 9 clades/provisional genera, based on a few morphological characters (green or brown, gelatinised gleba, rubbery texture, spores with or without a utricle). The circumscription of *Hysterangium* and these 'hysterangioid' genera is in process; the new genus proposed here, *Statesia*, is one of these.

Statesia Castellano, T.Lebel, Davoodian & K.Hosaka, ***gen. nov.***

Typus: *Statesia cazaresii* Castellano, T.Lebel, Davoodian & K.Hosaka.

Registration identifier: IF557961.

Basidiomata hypogeous, sequestrate, subglobose, surface glabrous or tomentose, white, often staining brownish to reddish. *Peridium* single to double-layered, textura intricata, textura porrecta or textura angularis, hyaline to brownish. *Gleba* loculate, locules empty, partially filled or filled, reddish to brownish or olive. *Rhizomorphs* often numerous, adherent across the surface. *Columella* dendroid. *Basidia* 2-spored. *Basidiospores* ellipsoid, broadly ellipsoid, fusoid to broadly fusiform, surface somewhat smooth to verrucose, base pedicellate, utricle distinct or amorphous.

Notes. A phylogenetic analysis based on a combined dataset of ATP6 and TEF1-α DNA sequence data (Fig. 17) shows *Statesia* clusters with *Aroramyces* Castellano & Verbeken and two other unnamed genera designated *gen. prov.* 14 (Australian and New Zealand taxa) and *gen. prov.* 16 (western North America; *gen. prov.* numbers as per Davoodian *et al.* 2021; *Statesia* was listed as *gen. prov.* 15 in this reference). *Statesia* differs from these genera in having only 2-spored basidia and somewhat smooth to verrucose spores without spines embedded within a uniformly inflated utricle. Therefore, *Statesia* is described as a new genus based on phylogenetic and morphological comparison. As currently understood, *Statesia* is a northern hemisphere genus from temperate zones, typically occurring in association with species of *Quercus* or occasionally *Fagus*.

Etymology. In honor of Jack States, former Professor at Northern Arizona State University, mycologist and truffle enthusiast.

8. ***Statesia cazaresii*** Castellano, T.Lebel, Davoodian & K.Hosaka, ***sp. nov.***

Holotypus: Mexico: Guanajuato State, near Guanajuato, Hwy 110, Dolores Hidalgo-Guanajuato, at km post 83, elevation 7600 ft. [under *Quercus* sp. and *Arctostaphylos* sp.], 23 Sept. 1996, *J.M. Trappe 19263* (OSC159158).

Registration identifier: IF557962.

Basidiomata sequestrate, subglobose, up to 16 mm wide, surface glabrous when fresh, finely tomentose when dried with scattered individual or clusters of dark hyphae, white with some brown-tinged areas and slowly staining brown when exposed when fresh, mottled off-white and pale brown when dried. *Gleba* loculate, gelatinized, brown to dark cinnamon brown when mature, pale gray in youth, locules small, partially empty. *Rhizomorphs* scattered, appressed and emergent on sides and base, concolorous with peridium or pale brown. *Columella* dendroid, arising from base, brown gray to opaque, 1–2 mm wide at base. *Odour* medicinal, penetrating. *Taste* mild.

Key to species of *Statesia*

1. Peridium a single layer, 300–400 µm thick, of compact interwoven hyphae,
spores appearing smooth, 13.9–16.2 × 6.4–7.0 µm, $Q_{mean} = 2.2$ . . . . 11. ***Statesia zelleri***

1: Peridium with 1 or 2 layers, spores longer and thinner on average

  2. Spores distinctly verrucose beneath utricle, 16.8–18.6 x 5.8–7.0 µm,
  mean 18.1 x 6.2 µm, $Q_{mean} = 2.8$ . . . . 10. ***Statesia pompholyx***

  2: Spores appearing smooth or distinctly verrucose beneath utricle, and shorter
  and $Q_{mean} = 2.4–2.7$

    3. Spores 15–17 (–18) x 6–7 µm, mean 16.2 x 6.6 µm, $Q_{mean} = 2.4$;
    epicutis hyphae not in a gelatinised matrix and oxalate crystals absent . . . . 8. ***Statesia cazaresii***

    3: Spores 13.9–16.2 (–18.6) x 5.2–6.4 µm, mean 15.4 x 5.8 µm, $Q_{mean} = 2.7$;
    epicutis hyphae in a gelatinized matrix and abundant oxalate crystals present . . . . . . 9. ***Statesia calcarea***

Peridium readily separable from fresh and dried gleba, white in cross-section quickly staining pale brown when cut, 600–700 µm thick, two-layered; epicutis 100–150 µm thick, of sometimes granular, brown, branched, thin-walled, septate, interwoven hyphae, 5 µm wide, clamp connections present; subcutis 500–550 µm thick, of sometimes granular, hyaline, branched, thin-walled, septate, interwoven hyphae, irregular in width but up to 15 µm wide, clamp connections present. *Trama* 75–500 µm thick, of hyaline, gelatinized, compactly interwoven hyphae, up to 5 µm wide, clamp connections absent. *Basidia* cylindrical but slightly bent, 28–29 × 4–8 µm, hyaline, thin-walled, 2-spored; sterigmata thin-walled, hyaline, 2.3 × 2.3 µm. *Basidioles* clavate, thin-walled, hyaline, 8 × 23 µm. *Spores* fusiform, 15–17 (–18) × 6–7 µm, mean = 16.2 × 6.6 µm, Q = (2–) 2.1–2.6 (–2.8), $Q_{\text{mean}} = 2.4$, asymmetrical, smooth, apex slightly acuminate to mostly blunt, base pedicellate, 1.2 × 2.3 µm; spore wall up to 1 µm thick, particularly at apex; utricle absent but spores agglutinated when young to form clumps; in KOH individual spores appear hyaline but olive-brown in mass, in Melzer's reagent somewhat darker but inamyloid, non-dextrinoid. **Fig. 16 A–C.**

Diagnosis. *Statesia cazaresii* has a two-layered peridium, unique in the genus, and also has longer and wider spores than *S. calcarea*.

Ecology & distribution. Often caespitose, hypogeous, embedded throughout a mat of white rhizomorphs and mycelium, under *Quercus* sp. and *Arctostaphylos* sp. Known only from Mexico.

Notes. Based on our phylogenetic analysis (Fig. 17), *Statesia* belongs to the Hysterangiaceae and is sister to *Aroramyces*. The two-layered peridium of *Statesia cazaresii* is unique within *Statesia*. The spores are smooth but are somewhat agglutinated with one another as in *S. zelleri* (see below). *Statesia zelleri* has slightly smaller but wider spores (mean = 14.9 × 6.8 µm) to give the spores an overall squatter appearance compared to *S. cazaresii* (mean = 16.2 × 6.6 µm).

Etymology. The specific epithet is in honour of Efren Cázares, mycologist and truffle enthusiast.

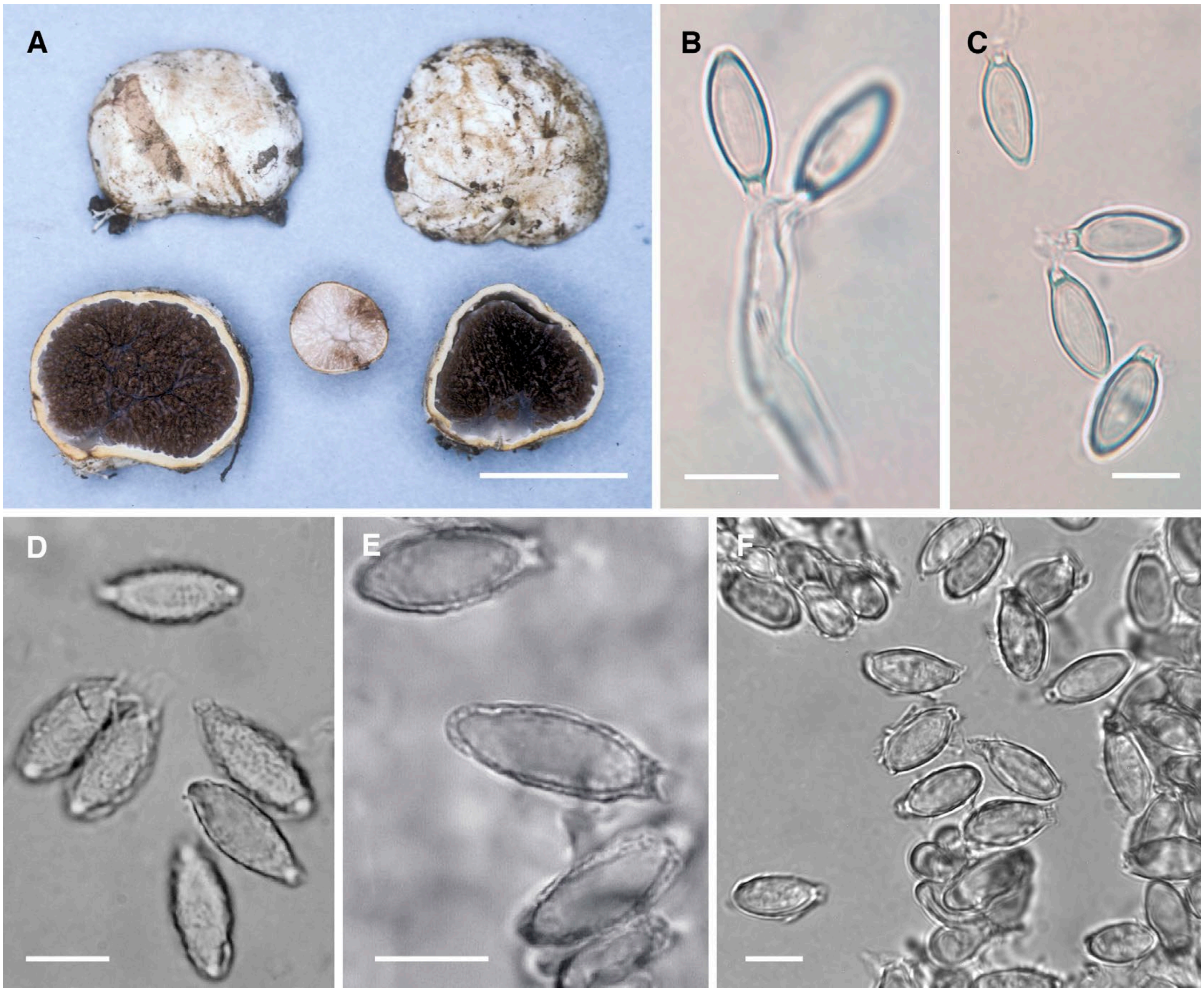

Fig. 16. **A–C** *Statesia cazaresii* (holotype): **A** Basidiomata; **B** bi-spored basidium; **C** spores. **D** *Statesia calcarea* spores. **E** *Statesia pompholyx* spores (isotype). **F** *Statesia zelleri* spores (holotype). Scale bars: A = 10 mm, B–F = 10 µm. — A–C *J.M. Trappe 19263* (OSC159158), D *A. Montecchi 2344* (OSC159163), E *L. Tulasne* (OSC159166), F *J. States AHF 602* (OSC159159).

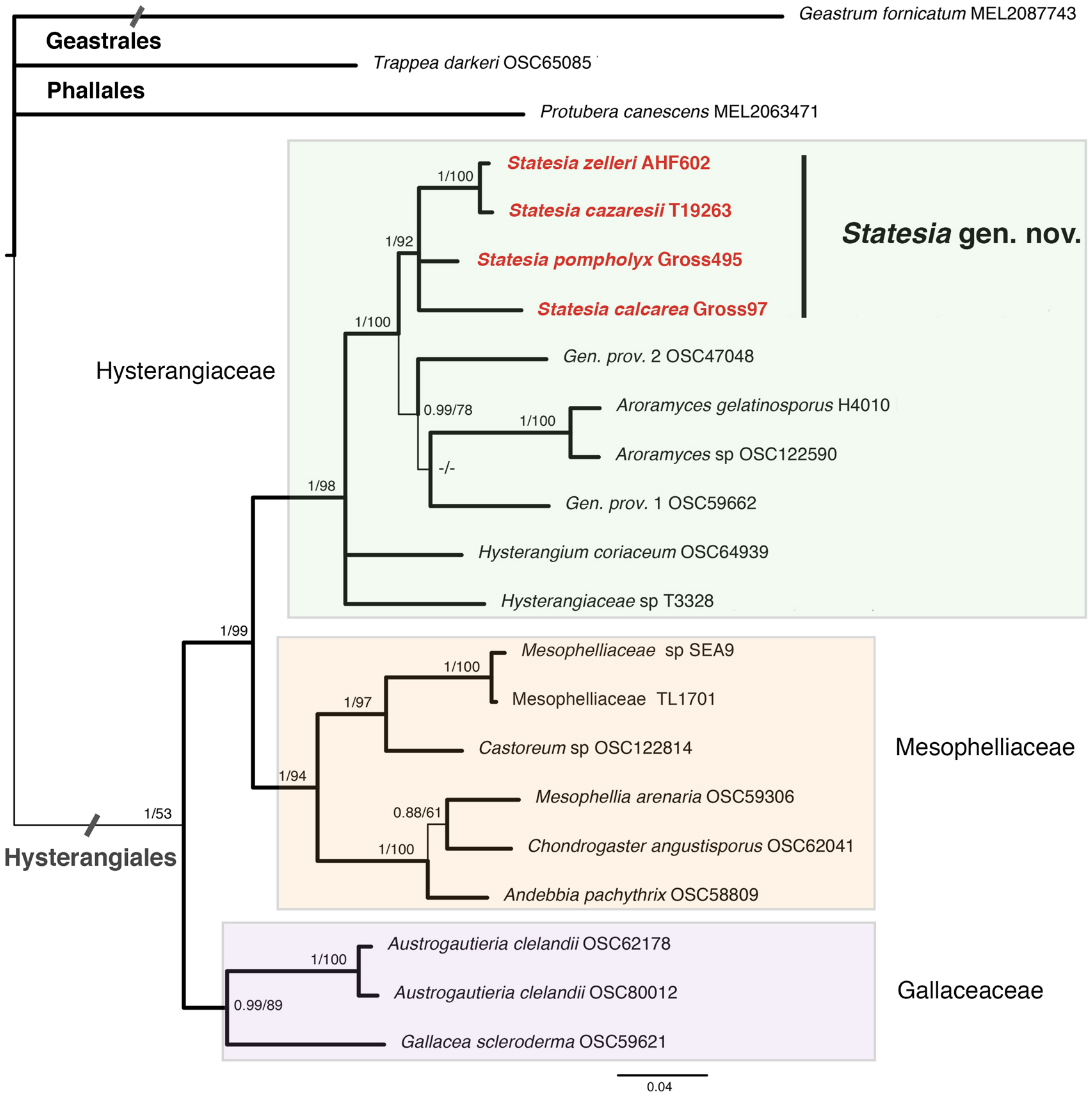

Fig. 17. Bayesian majority rule phylogram based on concatenated ATP6 and TEF1-α data representing *Statesia* and related taxa. Families are indicated by coloured boxes. Bayesian posterior probabilities > 0.90 and maximum likelihood bootstrap values > 50% are labeled on the nodes. Bold branches indicate support values at 0.99 (Bayesian) and 70% (maximum likelihood) or above. Scale bar shows substitutions/sites.

9. ***Statesia calcarea*** (R.Hesse) Castellano, T.Lebel, Davoodian & K.Hosaka, ***comb. nov.***

Registration identifier: IF557965.

Hysterangium calcareum R.Hesse, *Hypog. Deutschl.* 1: 97 (1891). MB173046. — **Lectotype (here designated, IF555906):** Germany: Cassel, 12 July 1881, *R. Hesse* (MB).

Description & illustration. See Montecchi & Sarasini (2000). **Fig. 16D.**

Basidiomata up to 2.5 cm, globose to subglobose, grayish white, surface floccose from covering of mycelium and mycelial strands, unchanging. *Gleba* bluish green to olive green; locules elongate, empty when young, filled at maturity. *Rhizomorphs* numerous, attached randomly on the peridial surface, commonly occurring in double strands, concolorous with peridium. *Columella* gelatinous, dendroid, stout, c. 1 μm thick, translucent when dried. *Peridium* easily separable from gleba, 500–600 μm thick, of two layers but the layers intergrade, epicutis of brownish yellow (on extreme outer edge) to hyaline, thin-walled, disorganized to periclinal hyphae, 2.5–3.5 μm wide, either agglutinated to each other or imbedded in a gelatinized matrix, abundant oxalate crystals across layer, subcutis of hyaline, thin-walled, interwoven hyphae (*textura intricata*), 4–6 μm wide with more hyphae in profile observed, crystals present but not abundant, the two layers clearly intergrade with each other in an irregular interzone, clamp connections absent. *Trama* variable in thickness, of hyaline, compactly interwoven hyphae, 2–3 μm wide, in a gelatinized matrix, clamp connections absent. *Basidia* rehydrating poorly, 2-spored. *Spores* broadly ellipsoid or occasionally subfusiform, 13.9–16.2 (18.6) × 5.2–6.4 μm, mean = 15.4 × 5.8 μm, Q = (2.4–) 2.5–2.7 (–3.2), Q_{mean} = 2.7, sometimes asymmetrical, smooth, apex blunt to occasionally papillate, base pedicellate, 1 × 2 μm wide. Spore wall 0.5–1 μm. Utricle absent, but outer spore wall irregular at times and with mucilage when mature. Spore colour in KOH hyaline singly, gray-green in mass.

Ecology & distribution. Hypogeous, usually in calcareous soil; under *Betula*, *Corylus*, *Fagus* and *Quercus* spp.; July through October. Known from Germany, Italy and Romania.

Notes. Hesse (1891) lists a collection from Hessen-Nassau province (Kingdom of Prussia) in Cassel (known as Kassel since 1926) from July 1886 and also a collection from near Kirchditmold (a suburb of Kassel) in August but does not designate a type. Zeller and Dodge (1928) state that the type is probably at MB but they did not study it and based their descriptive information on a collection from Czechoslovakia, studied by Hesse. Material from MB was not available by loan to us and we appreciate the efforts of Jim Trappe to secure data for this collection from an in-person visit he made to the herbarium a few decades ago. We designate the collection in MB labeled Germany, Cassel, 12 July 1881, *R. Hesse* as lectotype.

The peridium of *Statesia calcarea* is double-layered but intergrades to appear as one; it is readily separable from the gleba, which is more characteristic of a two-layered structure. The spores of *S. calcarea* are shorter and thinner with a slightly higher Q_{mean}.

Etymology. Probably in reference to the "calcareous" soil in which it is typically found (Hesse 1891).

Additional material examined.

GERMANY. Saar, Sitterswald, 8 Oct. 1967, *G. Gross 97* (M; OSC146868).

ITALY. Emilia Romagna, on eastern side of Monte Cusna, 7 Sep. 2001, *A. Montecchi 2344* (OSC).

ROMANIA. Dep. Harghita, pag. Ruganesti, 30 Aug. 1973, *Pap* (CLA).

10. ***Statesia pompholyx*** (Tul. & C.Tul.) Castellano, T.Lebel, Davoodian & K.Hosaka, ***comb. nov.***

Registration identifier: IF557964.

Hysterangium pompholyx Tul. & C.Tul., *Ann. Sci. Nat. Bot. ser.* 2, 19: 375 (1843). MB186665. — **Lectotype (here designated, IF555907):** France: Bois de Meudon, Apr. 1843, *L. Tulasne* (PC). **Isolectotypes:** FH; OSC159166.

Hysterangium rubricatum R.Hesse, *Jahrb. Wiss. Bot.* 15: 631–341, pl. XXXII (1884). MB183606.

Description & illustration. See Montecchi & Sarasini (2000). **Fig. 16E.**

Basidiomata 1–1.5 (–4) cm wide, reniform, globose to depressed, peridial surface white and yellow-brown, reddish brown to dark brown when fresh, floccose. *Gleba* at first white, then pale reddish brown, brown or olive brown when dried; locules elongate, partially filled. *Rhizomorphs* numerous, less than 1 mm thick, adherent to all areas of the peridium, concolorous with peridium. *Columella* gelatinous, distinct, dendroid, translucent.

Peridium not separable from gleba, a single layer, 200–250 µm thick, of dark reddish brown, thin-walled, polyhedral cells, up to 50–70 µm wide, abundant crystalline particles scattered throughout, some hyphal ends on outer edge with oxalate crystals, clamp connections common. *Trama* 25–100 µm thick, of hyaline, compactly interwoven hyphae, 2–4 µm wide, in a gelatinized matrix, clamp connections absent. *Basidia* not rehydrating well, hyaline, more or less cylindrical, 35–40 × 7–8 µm, 2-spored. *Spores* broadly fusiform, 16.8–18.6 × 5.8–7.0 µm, mean = 18.1 × 6.2 µm, Q = 2.5–2.9 (–3.2), Q_{mean} = 2.8, asymmetrical, at first smooth, verrucose at maturity, apex blunt, base distinctly pedicellate. Spore wall up to 1.0 µm thick, sometimes thicker at apex. Utricle distinct, roughened or wrinkled, 1 µm thick, spores often stuck together in pairs from mid-spore to base. Spore color in KOH pale brown singly, pale brown in mass.

Ecology & distribution. Hypogeous; probable mycorrhizal associates *Carpinus*, *Crataegus*, *Fagus*, *Corylus* and *Quercus*; March through November.

Notes. We studied authentic Hesse material identified as *Hysterangium rubricatum* from the Farlow herbarium and found it conspecific in all characters. Tulasne & Tulasne (1843) lists locations as Meudon (southwest suburbs of Paris) and Fleury (in southwest France) in April through August without designating a specific collection. We choose material available from PC from the first mentioned location in the appropriate year as the lectotype, isotypes are also in FH and OSC.

Statesia pompholyx has a single-layered peridium, similar to *S. zelleri* but the structure of the peridium in *S. pompholyx* is of polyhedral cells, while the peridium of *S. zelleri* is composed of compact hyphae 5–8 µm wide. In addition, the spores of *S. pompholyx* are much longer but thinner than spores of *S. zelleri*.

Etymology. Greek, "blister" or "bubble," possibly in reference to the roughened and wrinkled utricle surrounding the spore.

Additional material examined.

GERMANY. No locality (FH, Herb. Hesse, identified as *H. rubricatum* by Hesse; OSC159167). Saarland, Bierbach, 23 May 1972, *G. Gross 495* (OSC).

11. ***Statesia zelleri*** Castellano, T.Lebel, Davoodian & K.Hosaka, ***sp. nov.***

Holotypus: USA: Arizona, Cochise Co., Coronado National Forest, south of Cave Creek, elevation 7500 ft., 27 Apr. 1986, *J. States AHF 602* (OSC159159).

Registration identifier: IF557963.

Basidiomata up to 1.8 cm wide, subglobose, white with pale ochraceous patches, mottled white and brown when dried, surface tomentose with much adherent soil. *Gleba* bright ochraceous when fresh, cinnamon brown when dried; locules irregular, filled at maturity, $FeSO_4$ deep blue green, in KOH slightly sordid. *Rhizomorphs* few, small, attached to base, concolorous with peridium. *Columella* cartilaginous, dendroid, arising from a sterile base, narrow, greenish gray to translucent when fresh, reddish brown when dried. *Odour* not recorded. *Taste* not recorded.

Peridium separable from gleba, a single layer, 300–400 µm thick, of hyaline to pale brown, thin-walled, agglutinated, irregularly shaped, compactly interwoven hyphae, 5–8 µm in diam., numerous crystalline particles scattered across cells, clamp connections absent. *Trama* 20–40 µm thick, of hyaline, interwoven hyphae 1–3 µm in diam., in a gelatinized matrix, clamp connections absent. *Basidia* hyaline, elongate, thin-walled, clamped at base, 30 × 5 µm, 2-spored. *Spores* broadly ellipsoid to irregularly shaped; apex obtusely blunt to slightly papillate, base pedicellate, 1.2 × 2.3 µm, slightly asymmetrical, 13.9–16.2 × 6.4–7.0 µm, mean = 14.9 × 6.8 µm with base, Q = 2.0–2.3, Q_{mean} = 2.2, smooth, in KOH pale green singly, pale brown or buff in mass, walls up to 1 µm thick, slightly thicker at apex, utricle absent or inconspicuous, spores adherent to each other by way of what appears as a mucilaginous substance on the spore wall. **Fig. 16F.**

Diagnosis. *Statesia zelleri* has a single-layered peridium similar to *S. calcarea* and *S. pompholyx*, but the peridium of *S. pompholyx* is composed of parenchyma-like cells compared to the interwoven hyphae composition of the peridium of both *S. calcarea* and *S. zelleri*. The spores of *S. zelleri* (mean = 14.9 × 6.8 µm) are wider and thus squatter than those of *S. calcarea* (mean = 15.4 × 5.8 µm). In addition, the spores of both *S. calcarea* and *S. pompholyx* appear distinctly verrucose beneath the utricle while the spores of both *S. cazaresii* and *S. zelleri* appear smooth.

Ecology & distribution. Hypogeous, embedded throughout a mat of white rhizomorphs and mycelium, in association with *Quercus arizonica*, *Q. garryana* and other *Quercus* spp.; April, May in Arizona; October in Oregon.

Notes. *Statesia zelleri* occurs associated with *Quercus* spp. in dry habitats in Oregon and Arizona. *Statesia cazaresii* also occurs with *Quercus* spp. in Mexico. *Statesia calcarea* and *S. pompholyx* occur in Europe in more mesic habitats with *Fagus* spp.

Etymology. Specific epithet is in honour of Sanford M. Zeller, former Professor at Oregon State College (now University), preeminent truffle mycologist of his era.

Additional materials examined.

USA. Cochise Co., nr Nicksville, Carr Canyon, 11 May 1995, *B. Friedman F4875* (OSC159161); Coconino Co., Coconino National Forest, Oak Creek Canyon, 18 Sep. 1988, *J. States* (OSC159160); Oregon, Linn Co., Oct. 1922, *S.M. Zeller 2583* (NY; OSC159162).

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