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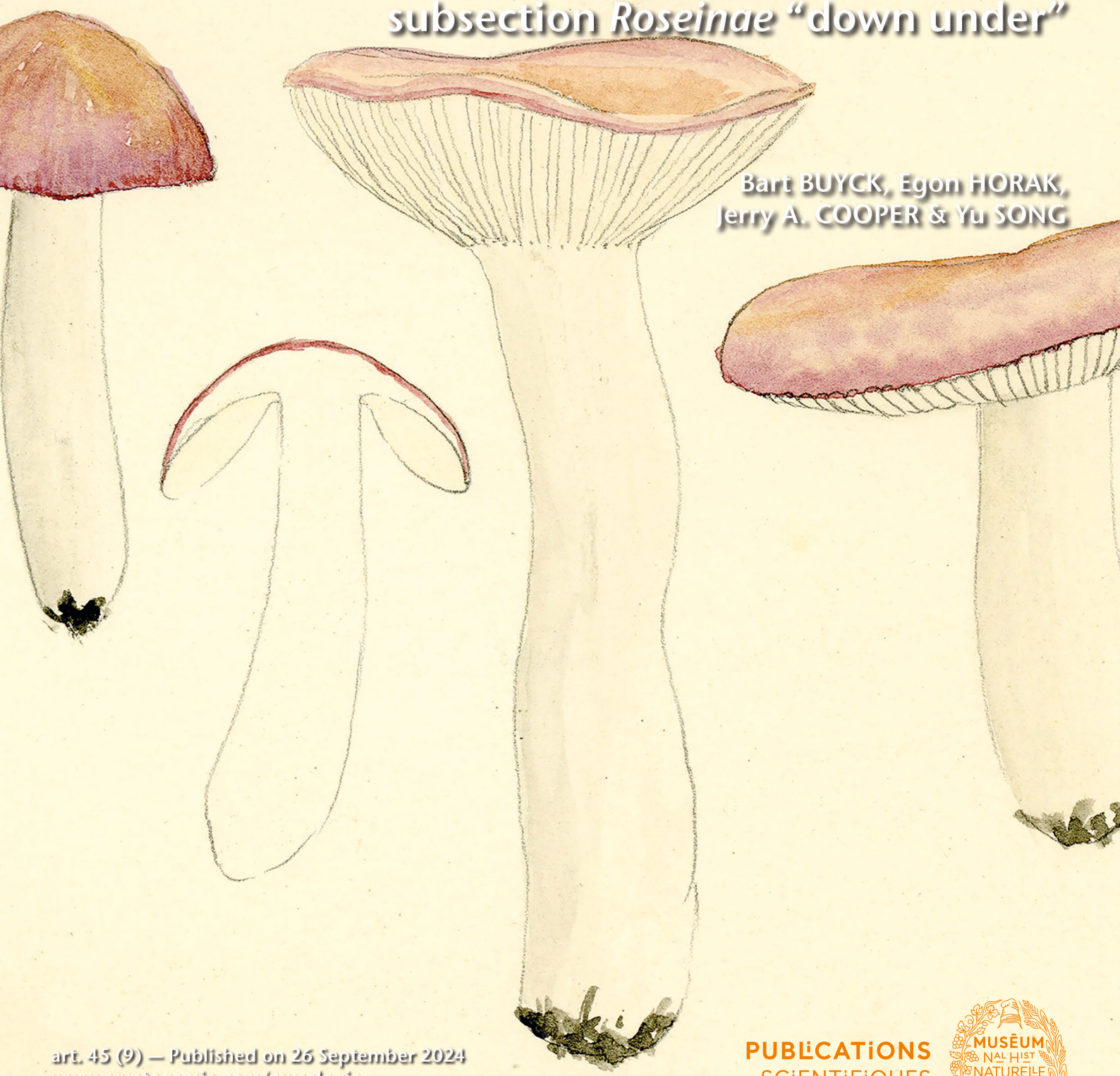

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Russula (Basidiomycota, Russulales, Russulaceae) subsection *Roseinae* "down under"

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ABSTRACT
The present contribution discusses species of *Russula* subsection *Roseinae* Singer ex Sarnari from the southern hemisphere. *Russula incrustata* Buyck, sp. nov. and *R. koniamboensis* Buyck, sp. nov. are described from New Caledonia, *R. purpureotincta* R.F.R. McNabb from New Zealand is redescribed based on new collections and two sequestrate species, *R. albobrunnea* T.Lebel from Australia and *R. kermesina* (R.F.R. McNabb) T.Lebel from New Zealand are shown to be the first known sequestrate taxa in *Roseinae*. The systematic placement and originality of these southern taxa is discussed. The definition of subsection *Roseinae* is emended.

KEY WORDS
Australia, New Caledonia, New Zealand, biogeography, phylogeny, new species.

RÉSUMÉ
Russula (Basidiomycota, Russulales, Russulaceae) sous-section Roseinae dans l'hémisphère sud.
La présente contribution discute les espèces de *Russula* sous-section *Roseinae* Singer ex Sarnari de l'hémisphère sud. *Russula incrustata* Buyck, sp. nov. et *R. koniamboensis* Buyck, sp. nov. sont décrits de la Nouvelle Calédonie, *R. purpureotincta* R.F.R. McNabb de la Nouvelle Zélande est redécrit sur la base d'autres collections et deux espèces sécotioïdes, *R. albobrunnea* T.Lebel d'Australie et *R. kermesina* (R.F.R. McNabb) T.Lebel de la Nouvelle Zélande sont les premières espèces sécotioïdes qui font partie des *Roseinae*. La position systématique ainsi que l'originalité de ces espèces de l'hémisphère sud sont discutées. La définition de la sous-section *Roseinae* est émendée.

MOTS CLÉS
Australie, Nouvelle Calédonie, Nouvelle Zélande, biogéographie, phylogénie, espèces nouvelles.

INTRODUCTION

Extant species of *Russula* subsection *Roseinae* Singer ex Sarnari were suggested to have diverged about three to one million years ago (Looney *et al.* 2020) and are part of the most diverse, major lineage of the genus in the northern hemisphere, viz. the crown clade of subgenus *Russula* (Looney *et al.* 2016). Species in subsection *Roseinae* are morphologically characterized by the pink to dark red pileus, the predominantly mild taste, the context and lamellae turning eosin red with sulfovanillin and their whitish to cream spore print. The North American *R. albida* Peck (synonym: *R. purpureomaculata* Shaffer) was so far the only exception having a combination of a whitish to yellowish pileus, a cream-coloured spore print and a pileipellis structure that was described as an epithelium. It was recently transferred to a subsection of its own (*Albidinae* Looney, Manz & Adamčík) together with morphologically similar red-capped collections that might correspond to *R. praeumbonata* Burl. (Looney *et al.* 2022). All these species share with several other lineages in the crown clade the fact that they possess "primordial hyphae", i.e., hyphal terminations that may have more or less similar contents as pileocystidia but possess acid-resistant incrustations (see Romagnesi 1967: 58-59).

In Europe, *Russula* subsection *Roseinae* is represented by merely two widely accepted species, *R. velutipes* Velen. (synonym: *R. rosea* Quél.) and *R. minutula* Velen., but the subsection as emended in the sense of Looney *et al.* (2022) is much more diverse in other regions of the northern hemisphere. Indeed, recent taxonomic studies on *Roseinae* (excl. *Albidinae*) report six described North American species and an additional four species that are still not formally described (Looney *et al.* 2020, 2022; Manz *et al.* 2021): *R. cordata* Looney, *R. rheubarbarina* Looney, *R. rubellipes* Fatto, *R. peckii* Singer, *R. pseudopeckii* Fatto and one undescribed relative, *R. cardinalis* Looney, one undescribed *R. minutula* aff., as well as two undescribed species in the '*magnarosea*'-lineage. In addition, four more species of *Roseinae* were described from the Central American montane forests in Western Panama (Manz *et al.* 2021): *R. cornicolor* Manz & F. Hampe, *R. zephyrovelutipes* Manz & F. Hampe, *R. oreomunneae* Manz, F. Hampe & Corrales and *R. cynorhodon* Manz & F. Hampe, now bringing the total of putative American species in *Roseinae* (*s.s.*) to 14 taxa. Manz *et al.* (2021) further confirmed or suggested the placement of an additional thirteen Asian phylogenetic species in *Roseinae*: *R. dhakuriana* K.Das, J.R.Sharma & S.L. Mill., *R. hakkae* G.J.Li, H.A.Wen & R.L.Zhao, *R. kewzingensis* K.Das, D. Chakr. & Buyck with one undescribed relative, *R. guangxiensis* G.J.Li, H.A.Wen & R.L.Zhao with one undescribed sister species, two undescribed Asian relatives to *R. velutipes*, two more undescribed Asian species close to *R. pseudopeckii*, two undescribed Asian relatives to *R. peckii*, as well as one sister species to *R. cynorhodon*.

Russula rimosa Murrill, again a North American species, is only known from the type collection and was placed in subsection *Roseinae* based on its morphology (Adamčík & Buyck 2012), but so far, any attempt of sequencing the DNA of this species has been unsuccessful. Sequence data are also needed for the Indian *R. sharmae* K.Das, Atri & Buyck, another potential member of subsection *Roseinae* based on its microscopic features, but it is unusual in producing an almost yellowish spore print (Das *et al.* 2013). This brings the total of potential northern hemisphere *Roseinae* close to 30 or about five times more than hardly a few years ago.

Looney *et al.* (2020) reported a northern hemisphere distribution for *Roseinae* and inferred an Appalachian origin for the subsection in North America, followed by *in situ* diversification of these species in the Appalachian Mountains roughly since the mid-Miocene. Whereas the subsection has not yet been recorded from Africa and South America, published sequence data suggested nevertheless the existence of several potential *Roseinae* in Oceania or Australasia (Lebel & Tonkin 2007; Cooper & Leonard 2014; Buyck *et al.* 2018; Cooper 2021), but these sequences were largely ignored (Looney *et al.* 2022) and none of these southern species has ever been discussed in a phylogenetic or systematic context. The aim of this study is to identify the actual taxonomic status and phylogenetic position of these southern hemisphere relatives.

MATERIAL AND METHODS

Studied material and morphological study

The southern hemisphere taxa that are here described or discussed are based on collections made in New Caledonia, New Zealand and Australia over the past 50-60 years by some of the authors or by other collectors. All of these specimens were documented with photographs taken in the field or in the lab and all benefited from descriptive notes taken on fresh specimens. Micromorphological characters were studied using a Nikon Eclipse E400 microscope under oil-immersion lens at a magnification of ×1000. All drawings of microscopical structures were made with a 'camera lucida' using a Nikon Y-IDT drawing attachment at a projection scale of ×2400. Contents of hymenial cystidia and pileocystidia in the figures are indicated schematically, with the exception of a few elements where contents are indicated as observed in Congo red preparations from dried material. Spores were observed in Melzer's reagent. All other microscopic observations were made in ammoniacal Congo red, after a short aqueous KOH pre-treatment near boiling temperature to improve tissue dissociation through gelatinous matrix dissolution. All tissues were also examined for the presence of ortho- or metachromatic contents or incrustations in Cresyl blue as explained in Buyck (1989).

DNA extraction, PCR and sequencing

Fungal genomic DNA was isolated from dried or fresh fruiting bodies (in the case of New Caledonian collections from tissue stored in cetyl-trimethyl-ammonium bromide buffer or CTAB 1×). Two loci were targeted for this study: *c.* 650 base pairs of the internal transcribed spacers (ITS) using primers ITS1f and ITS4 and 900 base pairs of the translation elongation factor 1-alpha (*tef*1) using primers EF1-F and EF1-R (Morehouse *et al.* 2003). Amplifications were performed

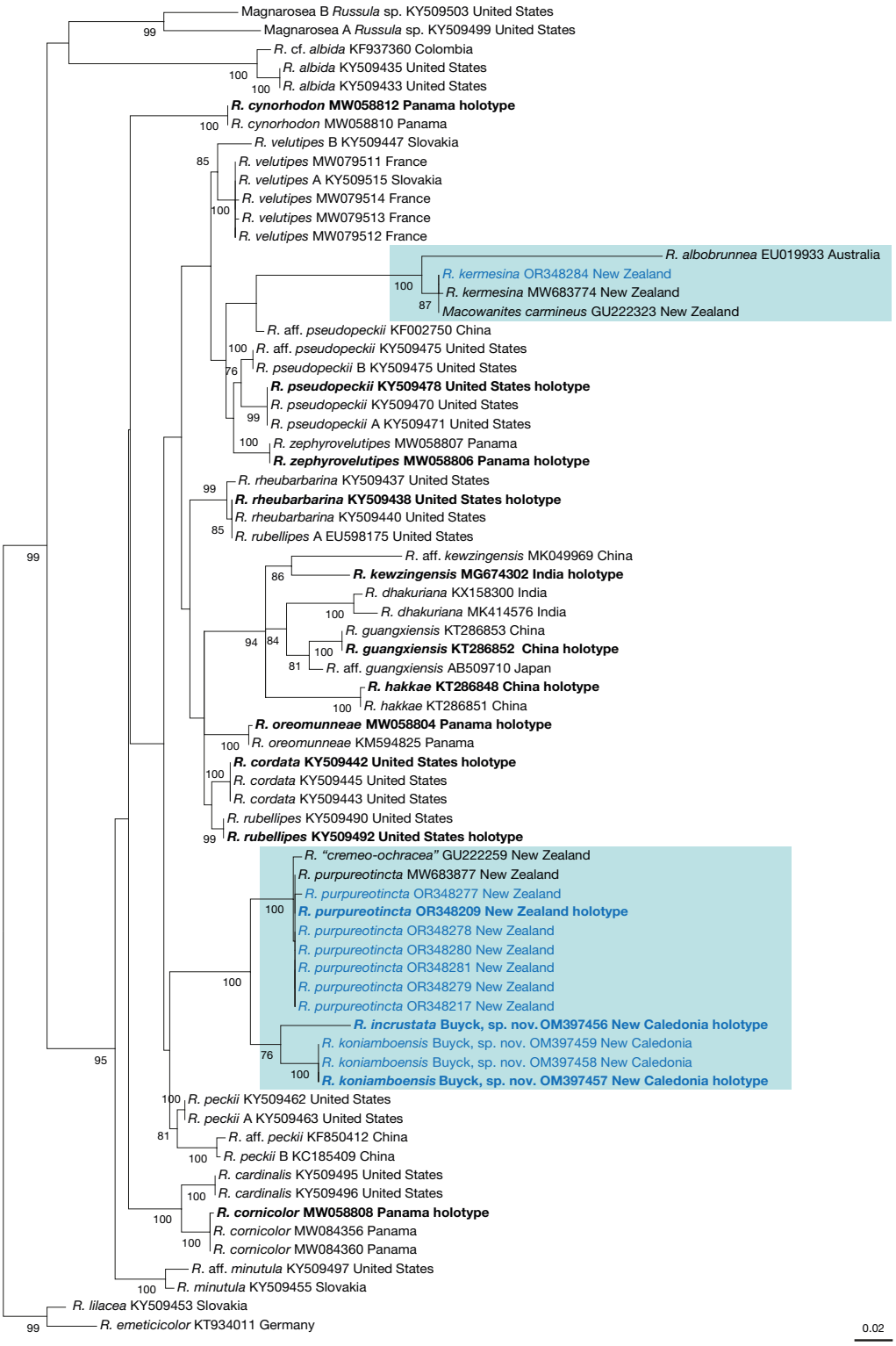

Fig. 1. — ITS phylogeny of *Russula* subsection *Roseinae* Singer ex Sarnari. Southern hemisphere species are indicated by **blue rectangles**. Type specimens are indicated in **bold**.

under the conditions and with the reagents of the Taq PCR core kit (QIAGEN, Inc., Valencia, California, United States). Sequencing used the amplification primers, reagents and conditions of the BigDye Terminator v3.1 Cycle sequencing Kit and an automated capillary sequencer ABI 3700 DNA analyzer (Perkin Elmer, Applied Biosystems, Foster City, CA, United States). The newly published sequences have all been deposited in GenBank (www.ncbi.nlm.nih.gov), viz. ITS (OM397456-OM397459) and *tef*1 (OM365994-OM365996, OM370807) for both new species from New Caledonia,

eight ITS sequences for *R. purpureotincta* R.F.R. McNabb (OR348209, OR348217, OR348277-OR348281), including one from the holotype, and a single ITS sequence for *R. kermesina* (R.F.R. McNabb) T.Lebel (OR348284).

Phylogenetic analysis

Separate phylogenetic analyses based on ITS and *tef*1 performed with Maximum Likelihood method were chosen in function of available sequence data for the southern species. The sampling of northern hemisphere taxa is based on Manz *et al.* (2021). Each dataset was automatically aligned by MAFFT v 7.427 (Katoh & Standley 2013), then manually adjusted and trimmed with BioEdit v7.0.9 (Hall 1999). The final ITS alignment consisted of 70 sequences and comprised 750 bp; the *tef*1 alignment was 921 bp long (excluding introns) and comprised 41 sequences; *Russula emeticicolor* (Jul.Schäff.) Singer and *R. lilacea* Quél. belonging to subsection *Lilaceinae* (Melzer & Zvára) Jul.Schäff. were chosen as the outgroup. A rapid bootstrapping (BS) algorithm of 1000 replicates was executed in RAxML 7.2.6 (Stamatakis 2006), followed by a heuristic ML search for the best tree using the GTRGAMMA model. All parameters in RAxML analysis were kept at default. Bootstrap value (BS) exceeding or equal to 70% was considered to represent significant support.

RESULTS

Phylogeny

The ITS phylogeny (Fig. 1) comprises 68 sequences representative of taxa in *Roseinae* and two sequences of *Lilaceinae* chosen as out-group. Southern *Roseinae* are represented by six previously deposited sequences in GenBank and twelve newly generated sequences (see above). In this phylogeny, the three New Caledonian specimens of *R. koniamboensis* Buyck, sp. nov. are placed sister with significant, although moderate support (MLbs = 76%) to our second new species from New Caledonia, *R. incrustata* Buyck, sp. nov. Both New Caledonian species are again placed sister with full support (MLbs = 100%) to a fully supported clade composed of all sequenes of *R. purpureotincta* from New Zealand (one was previously deposited under the misapplied name of *R. cremeoochracea* in GenBank). The relation between the clade composed of these three species and the other *Roseinae* remains unresolved. It is for the very first time that we also place two sequestrate species in subsection *Roseinae*: *R. kermesina* from New Zealand and *R. albobrunnea* from Australia. For both, only ITS sequence data are available and our analysis places these two taxa monophyletic with full support (MLbs = 100%), but also here the relationship with the other *Roseinae* remained unresolved.

The *tef*1 phylogeny (Fig. 2) comprises 41 sequences and places only the New Caledonian species as no *tef*1 sequences are available for the other southern species. Whereas the exact relationship of both New Caledonian species with the other species in the subsection remained unresolved in the ITS phylogeny (Fig. 1), the *tef*1 phylogeny offers now strong support (MLbs = 97%) to put both New Caledonian sister to the /cardinalis lineage as delimited in Manz *et al.* (2021). The latter lineage comprises merely two species, viz. *R. cornicolor* associated with *Oreomunnea* Oerst. (fam. Juglandaceae) in Western Panama and *R. cardinalis* associated with *Quercus* L. in the Appalachian Smoky Mts of Tennessee, United States. Other significantly supported clades in our *tef*1 phylogeny mirror strongly supported lineages in the multigene phylogeny of Manz *et al.* (2021).

Taxonomy

In the below paragraphs we provide descriptions for both new New Caledonian species, and also for the newly reported collections of the closely related *R. purpureotincta* from New Zealand.

Family Russulaceae Lotsy
Genus *Russula* Pers.
Subsection *Rosinae* Singer ex Sarnari

Russula incrustata Buyck, sp. nov.
(Figs 3; 5-8; 9D)

Differs from *R. koniamboensis* Buyck, sp. nov., the only other member of *Roseinae* in New Caledonia, in the vividly coloured larger pileus with pale brown, orange, pink, lilac, purple or vinaceous colours, pinkish stipe, the somewhat smaller spore size and its occurrence under endemic *Arillastrum gummiferum* (Brongn. & Gris) Pancher ex Baill. (family Myrtaceae).

Type material. — **New Caledonia** • Les Bois du Sud, near blockhut; 22°17'17.13"S, 166°76'01.03"E; *c.* 300 m alt.; on ultramafic soil in monodominant rain forest of endemic *Arillastrum gummiferum* (family Myrtaceae); 27.III.2009; *735/BB09.172*; holotype: PC0142414.

Etymology. — The epithet refers to the distinct incrustations present on the cell walls of the pseudoparenchyma in the lower pileipellis and other parts of the context.

GenBank. — OM370807 (ITS), KU237588 (LSU), KU237436 (mitSSU), KU237873 (*rpb*2), KU238015 (*tef*1), KU237728 (*rpb*1).

Index fungorum. — IF 901190.

Description

Pileus

Medium-sized, 64 mm diam., plane or very gently and widely depressed in the center, inconspicuously striate near margin; surface peeling ⅔ radius, dull, not hygrophanous, felty-velutinous, never viscid, not fragmenting in areolae or squamae but slightly concentrically pruinose, colour range from pale brown, orange, pink, lilac, purple or vinaceous, not paler in the center with age.

Stipe

51 × 11-12 mm, central, cylindrical; surface smooth, slightly longitudinally wrinkled, not pruinose, entirely pinkish but white at the extreme base, firm, context soft spongy without cavities, basal mycelium absent.

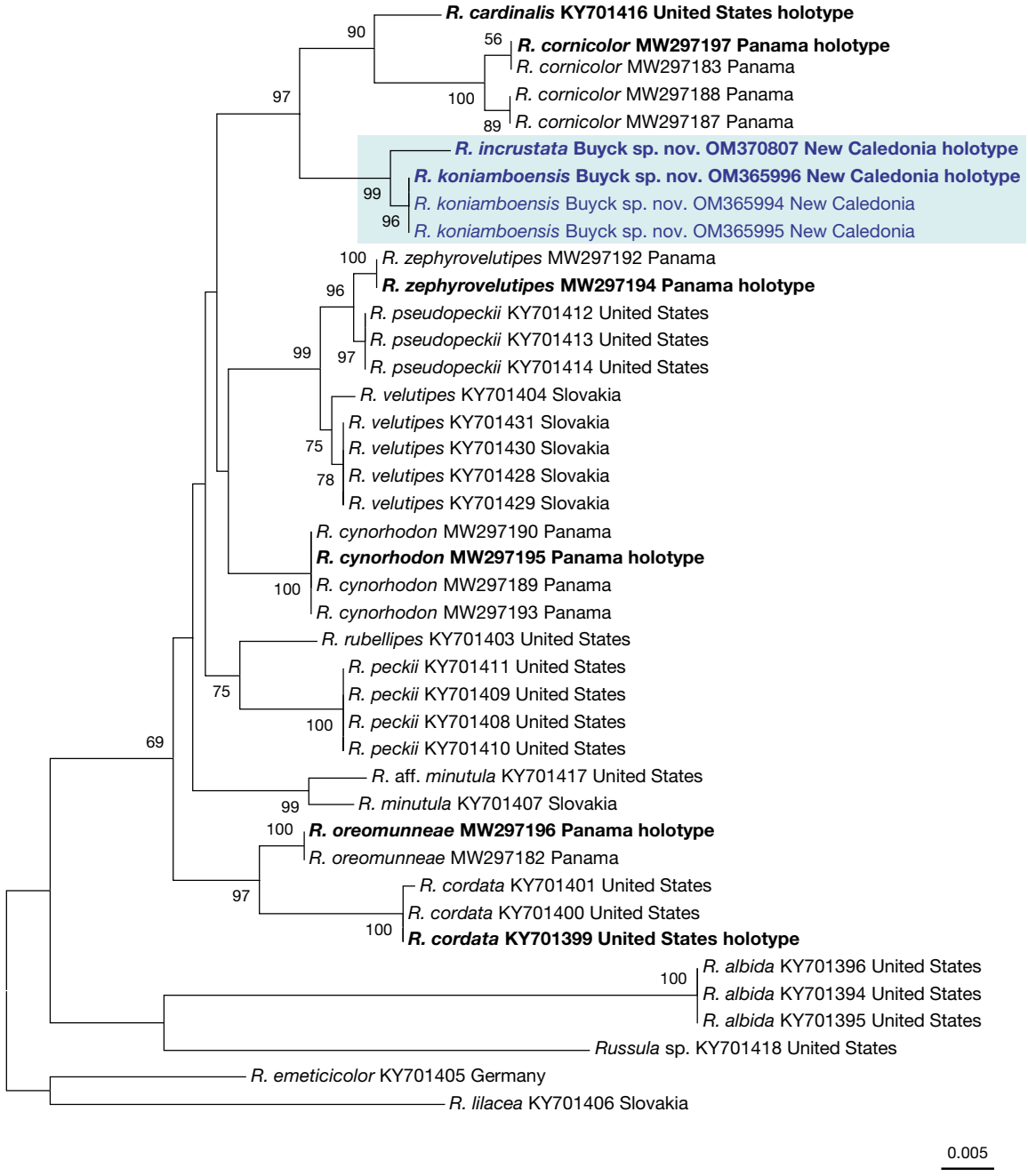

Fig. 2. — The *tef*1 phylogeny of *Russula* subsection *Roseinae* Singer ex Sarnari placing both New Caledonian species (**blue rectangle**). Type specimens are indicated in **bold**.

Lamellae
Equal in length, adnate, without anastomoses or forks, brittle, 8 mm high, off-white.

Context
Brittle, white, colour unchanging on injury or with age, about 6 mm thick in pileus above gill attachment to stipe, with $FeSO_4$ hardly changing colour, merely faintly grey inside stipe and weakly pinkish on stipe surface, no reaction with Guaiac. Taste and odour not distinctive.

Spore print
White.

Spores
(6.46)6.89-7.27-7.65(7.92) × (5.42)5.67-5.92-6.17(6.46) µm, broadly ellipsoid, Q = (1.10)1.17-1.23-1.29(1.36); ornamentation subreticulate, composed of large, prominent, moderately distant, conical and strongly amyloid spines, up to 1.5 µm high, connected by frequent fine lines into an incomplete network; suprahilar spot well-developed,

FIG. 3. — *Russula incrustata* Buyck, sp. nov. (holotype): fresh basidiomata. **A**, *in situ*; **B**, detail of the pileus surface; **C**, view of pileus and stipe surfaces, as well as stipe interior showing reaction to $FeSO_4$. Photo credit: B. Buyck. Scale bar: 10mm.

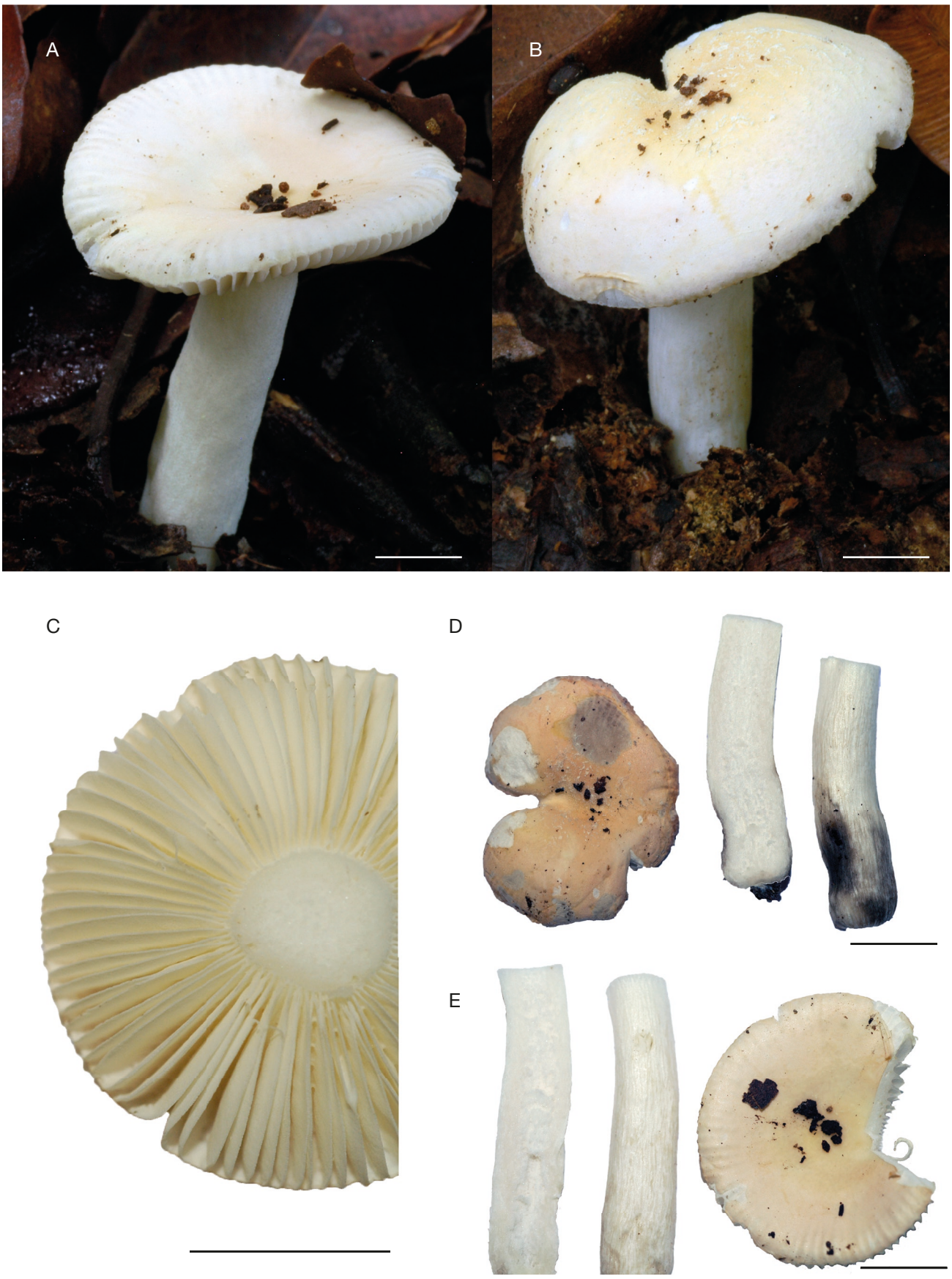

Fig. 4. — *Russula koniamboensis* Buyck, sp. nov.: fresh basidiomata. **A-C**, holotype; **D-E**, *730/BB09.170*. Photo credits: B. Buyck. Scale bar: 10mm.

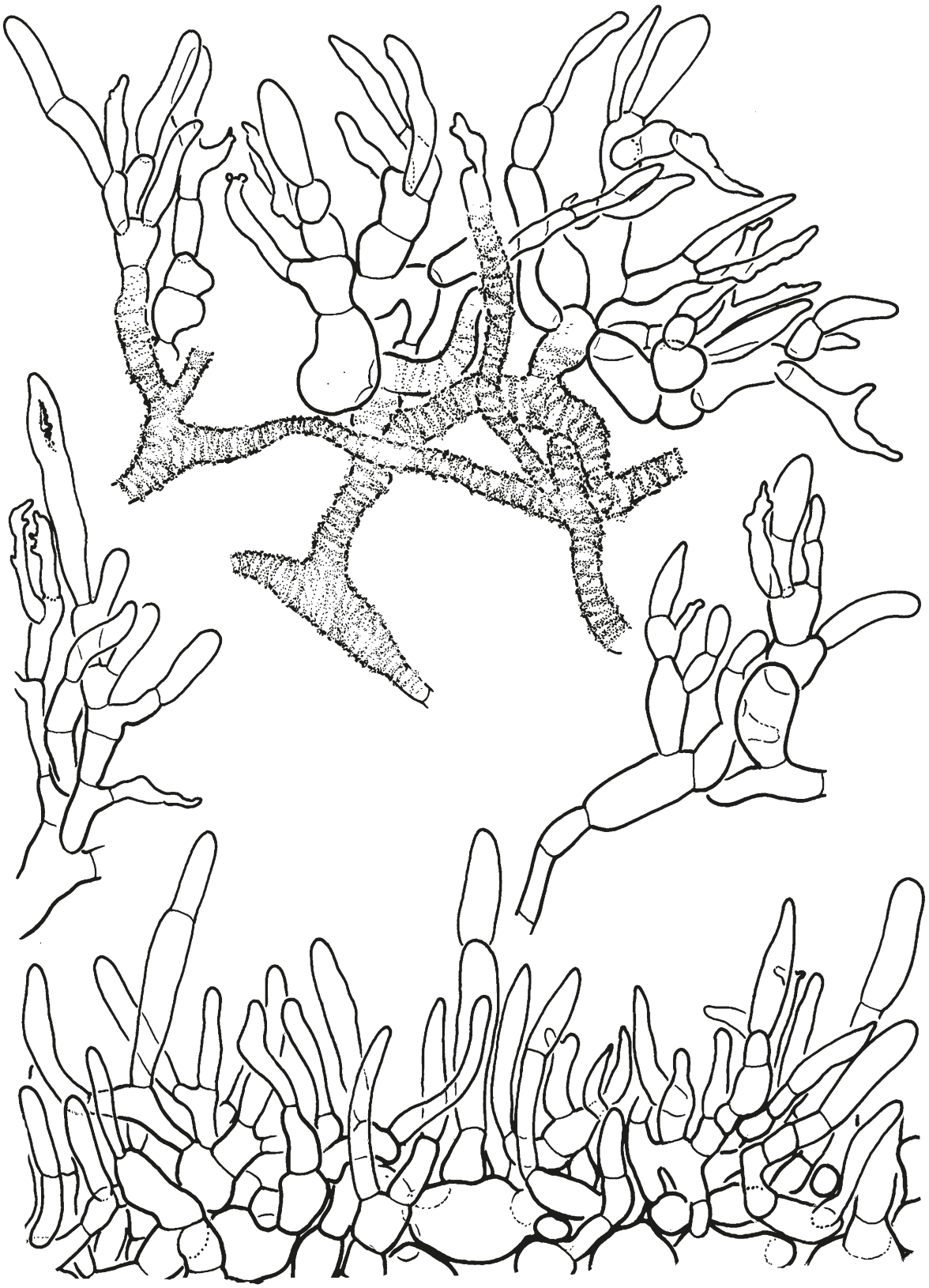

Fig. 5. — *Russula incrustata* Buyck, sp. nov. (holotype: *735/BB09.172*): details of the pileipellis. Drawings B. Duhem. Scale bar: 20 µm.

Fig. 6. — *Russula incrustata* Buyck, sp. nov. (holotype: *735/BB09.172*): hyphal terminations of the pileipellis, continued. Drawings B. Duhem. Scale bar: 20 µm.

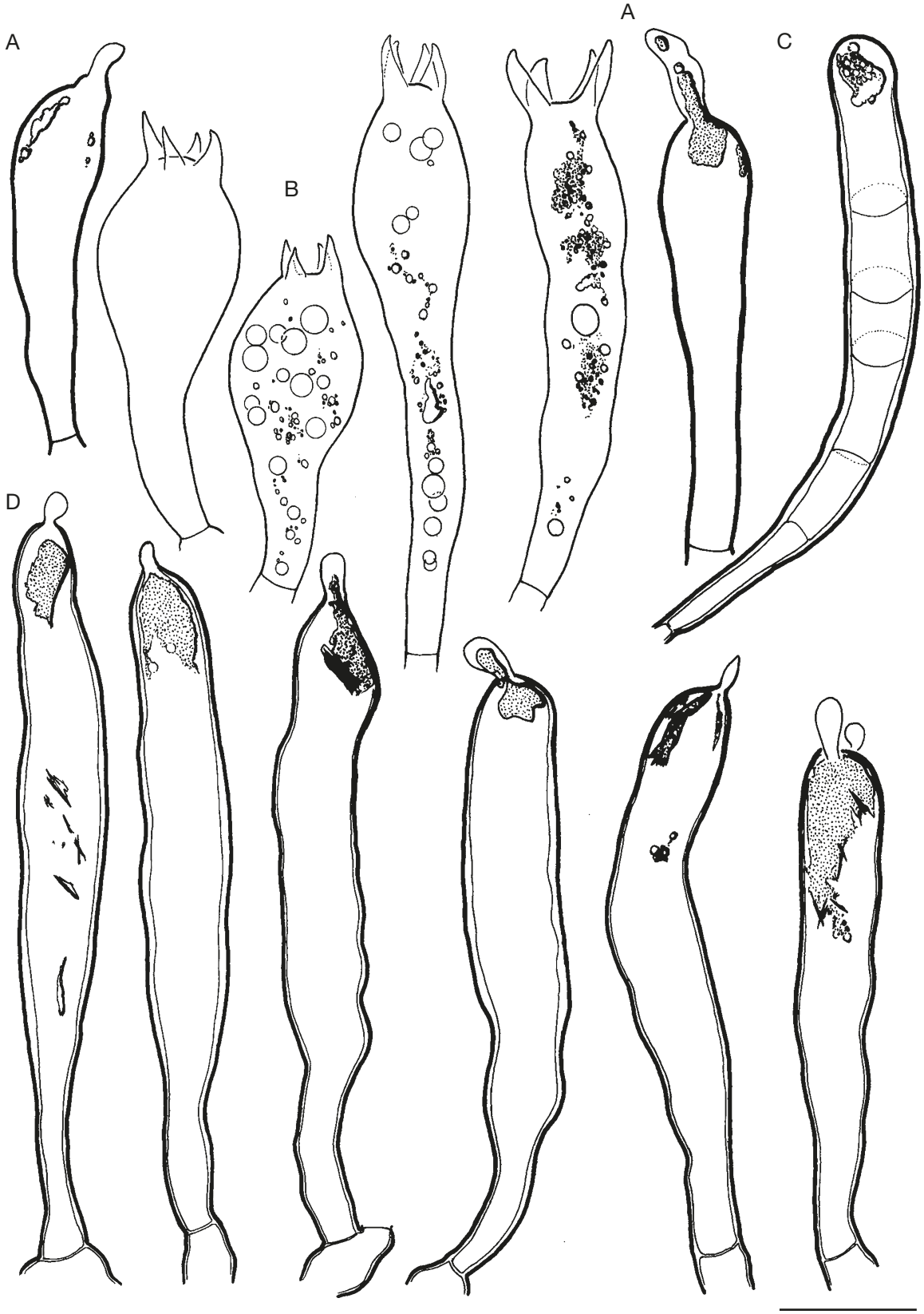

FIG. 7. — *Russula incrustata* Buyck, sp. nov. (holotype: *735/BB09.172*): details of the hymenium: **A**, cystidia on gill edge; **B**, basidia; **C**, cystidium with secondary septa; **D**, cystidia of gill sides. Drawings B. Duhem. Scale bar: 10 µm.

varying from strongly amyloid to verruculose, grayish and poorly amyloid.

Basidia
30-40(-58) × 11-15 µm, narrowly to broadly clavate, 4-spored with stout sterigmata; basidiola clavate.

Subhymenium
Pseudoparenchymatic.

Hymenial gloeocystidia
On lamella sides mostly 50-74 × 8-10 µm, clavate to fusiform, frequently mucronate to appendiculate at apex, up to 10 µm long, rarely obtuse rounded, originating in subhymenium and longer as basidia, walls up to 2(-2.5) µm thick; contents mainly restricted to some refringent inclusions at apex, not reacting to sulfovanillin, rarely with up to 5 secondary septa; cystidia near the lamellae edges smaller, up to 30 µm long.

Marginal cells
Occupying most of the lamellar edges, sitting on 1-2 basal cells, mostly 13-29 × (3-)5-9 µm, very variable in shape, several reminding of the terminal cells in the suprapellis (but smaller), but usually with 1-4 diverticulate pointed to obtuse-rounded outgrowths.

Pileipellis
Two-layered, not distinctly delimited from the underlying context; suprapellis composed in its lower part of a 60-80 µm thick, loose pseudoparenchyma of intertwined and strongly ramifying, ascending to erect, irregularly shaped cells, toward the loose subpellis carrying very distinct orthochromatic zebroid incrustations and with inflated basal cells up to 12(-15) µm wide; toward the pileus surface the pseudoparenchyma gives rise to short chains composed of 2-4(-5) smooth-walled, narrower cells; subterminal cells frequently branched, thin-walled, barrel-shaped or subcylindrical; terminal cells mostly longer in comparison and usually vertically oriented, (8-)16-23(-39) × 2-4(6) µm, often undulated in outline, typically attenuating towards a minutely capitate apex or with one subapical lateral diverticulum. Primordial hyphae difficult to distinguish because of the poor contents, sometimes clearly recognizable because of their slightly wider and more voluminous terminal cell measuring 15-31 × 3-5 µm and filled with some refringent, granular-heteromorphous contents in their very upper part. Subpellis ill-defined, forming a loose structure *c.* 100 µm deep before the larger sphaerocytes of the context are present. Cystidioid hyphae absent from subpellis and context. Oleiferous hyphae or hyphal fragments abundant in subpellis and upper context.

Clamp connections
Absent.

Notes
Russula incrustata Buyck, sp. nov. is a beautiful and colourful species that we found only once. There are no environmental sequences available for it, which could indicate that this taxon is rather rare, particularly since there are quite some environmental sequences available for many other New Caledonian *Russula* in GenBank. Perhaps its ectomycorrhizal association with the rare and endemic *Arrilastrum gummiferum* (Myrtaceae) is the explanation. This potential rarity and the fact that there is no ongoing mycological inventory in New Caledonia, justifies in our opinon the decision to describe this species formally. In the multigene phylogenetic analysis of worldwide *Russula* (Buyck *et al.* 2018), this species was already clearly placed in *Roseinae* as "*R. roseinae sp. ined*" with additional sequences for ncLSU, mit SSU, *rpb*2 and *rpb*1 deposited in GenBank (as *R. roseinae* sp. VH-2016 strain *735/BB09.172*).

Russula koniamboensis Buyck, sp. nov.
(Figs 4; 9A-C; 10-14)

Differs from *R. incrustata* Buyck, sp. nov. in the pale yellowish pileus, white stipe, the somewhat larger spore size and its occurrence under *Nothofagus* Blume; from *R. purpureotincta* again in the white yellowish pileus (which is pink, vinaceous and purple in *R. purpureotincta*) and its occurrence in New Caledonia, not New Zealand.

Type material. — **New Caledonia** • Northern Prov., Massif du Koniambo, near Voh, in the nickel mine exploitation site called 'Niko'; 21°00'22"S, 164°49'51"E; 724 m alt.; on ultramafic soil under *Nothofagus balansae*; 17.III.2009; leg. *B. Buyck*; *722/BB09.022*; holotype: PC0142407.

Etymology. — Named after the type locality.

GenBank. — OM397457, OM397457 (ITS), OM365994-OM365996 (*tef*1).

Index fungorum. — FI 90189

Additional examined material. — **New Caledonia** • Northern Prov., Massif du Koniambo, near Voh, in the "île nickel" mine exploitation site; 21°00'42"S, 164°49'50"E; 734 m alt.; on ultramafic soil under *Nothofagus balansae*; 19.III.2009; leg. *B. Buyck*; *730/BB09.117*; PC0714855 • Massif du Koniambo, near the Trazy entry of the nickel mine exploitation site; on ultramafic soil under *Nothofagus codonandra*; 9.IV.2009; leg. *B. Buyck*; *742/BB09.346*; PC0714856.

Pileus
25-30 mm diam., convex, slightly depressed in the center, near the margin striate over ⅓-¼ of the radius, surface dull, smooth to finely or even distinctly farinaceous in the center and more or less concentrically deposited, peeling ⅔ of the radius, pale yellowish in the center, cream towards margin.

Lamellae
Equal in length, adnate, distant and *c.* 1-2 L/mm at pileus margin, off-white to cream colour, obtusely rounded at the pileus margin; entire edge concolourous.

Stipe
30-34 × 6-8 mm, central, cylindrical to slightly obclavate, glabrous, smooth to finely longitudinally striate, white to ivory, pale greyish towards base, brittle, spongy inside, lacunes absent.

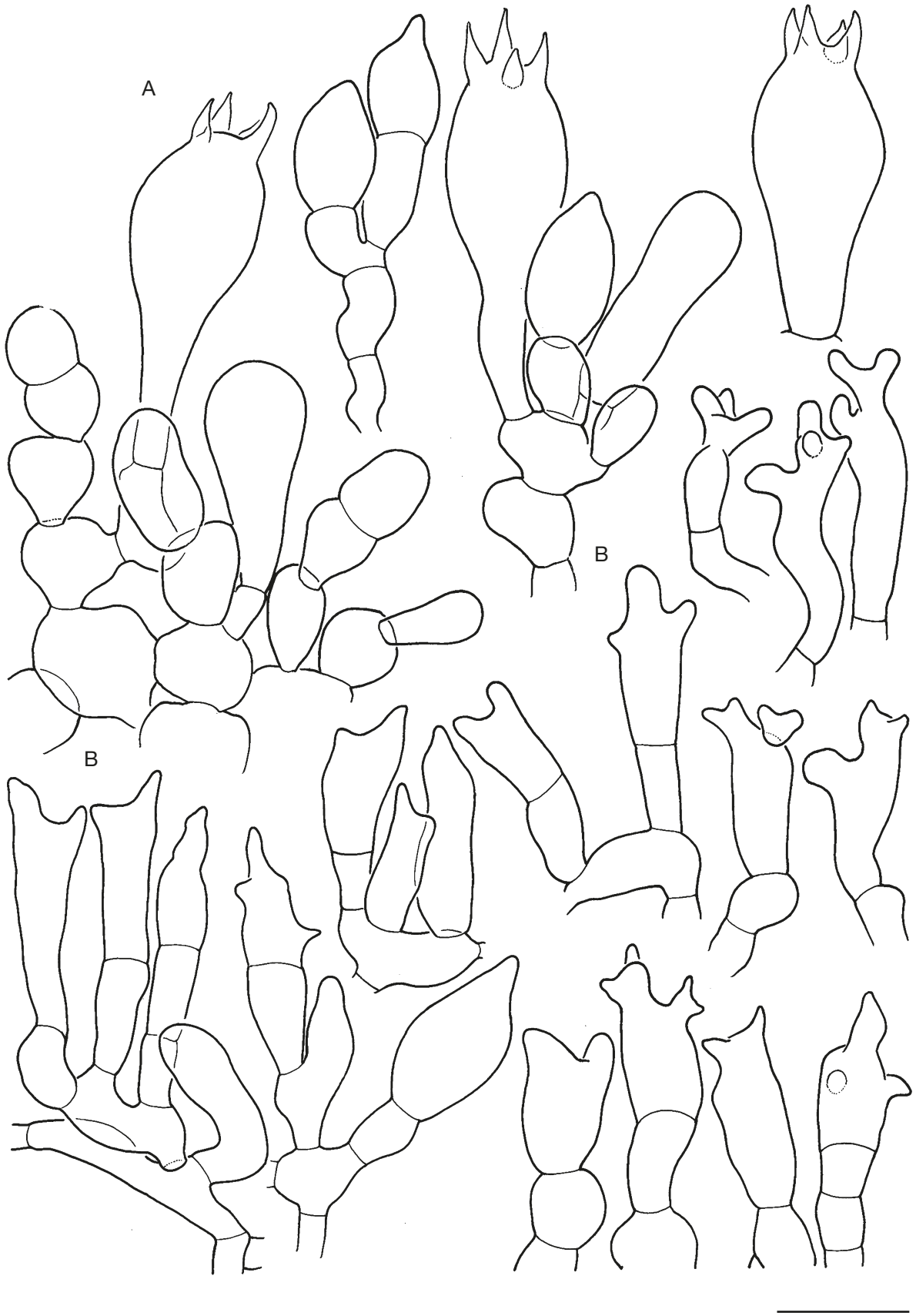

Fig. 8.— *Russula incrustata* Buyck, sp. nov. (holotype: *735/BB09.172*) details of the hymenium near the gill edge: **A**, basidiola and basidia; **B**, marginal cells. Drawings B. Duhem. Scale bar: 10 µm.

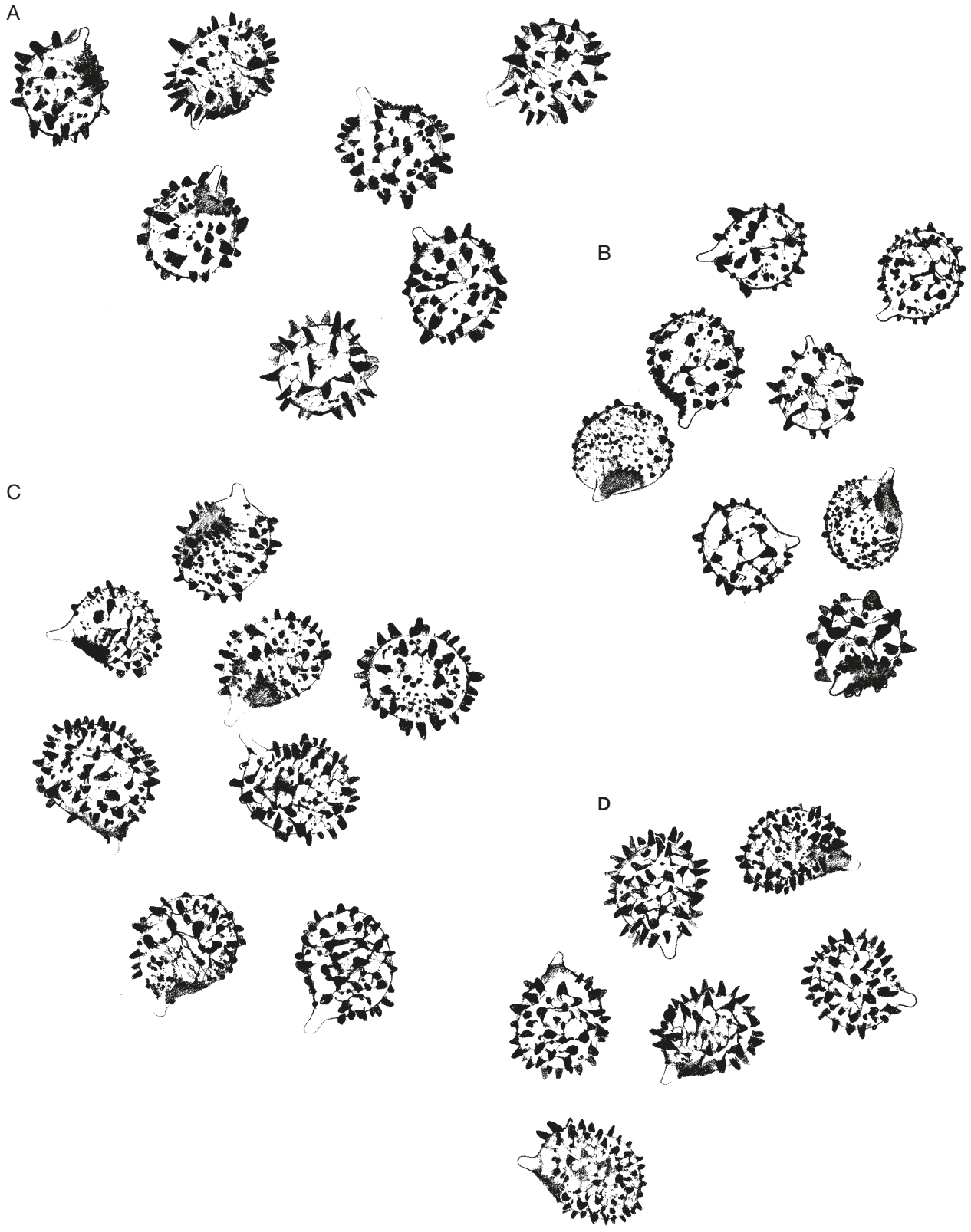

FIG. 9. — Spore clouds: **A**-**C**, *Russula koniamboensis* Buyck, sp. nov. (**A**, *730/BB09.11*; **B**, *742/BB09.346*; **C**, holotype: *722/BB09.022*); **D**, *Russula incrustata* Buyck, sp. nov. (holotype). Drawings B. Duhem. Scale bar: 10 µm.

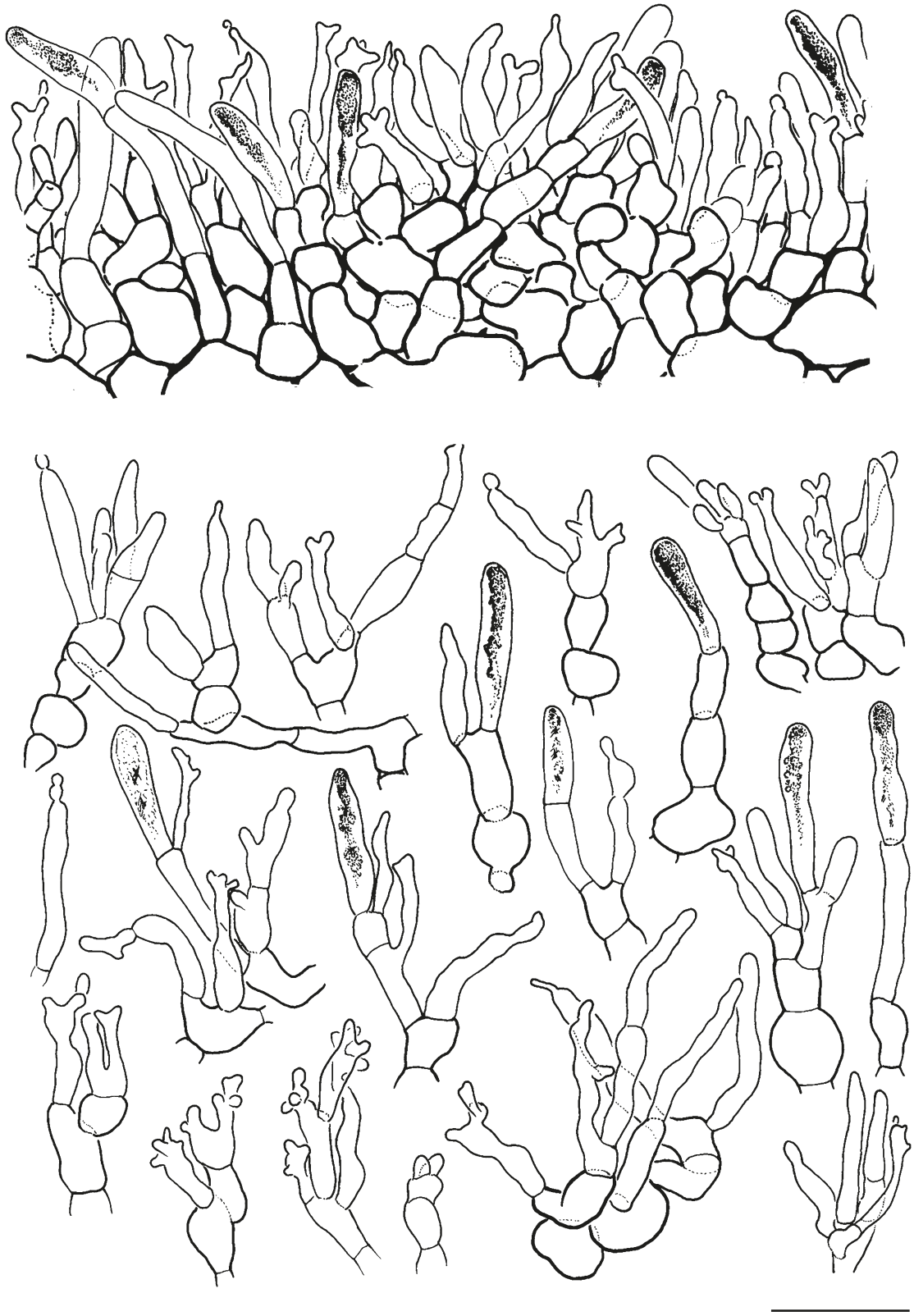

FIG. 10. — *Russula koniamboensis* Buyck, sp. nov. (holotype: *722/BB09.022*). Details of the pileipellis. Note that all capitate-mucronate endings are optically empty; these are not pileocystidia, notwithstanding they are morphologically very similar to the pileocystidia of species in subgenus *Heterophyllidiae Romagn.*, while all terminal cells of primordial hyphae are obtuse-rounded at their apex and possess refringent contents reminiscent of typical pileocystidia. Drawings B. Duhem. Scale bar: 20 µm.

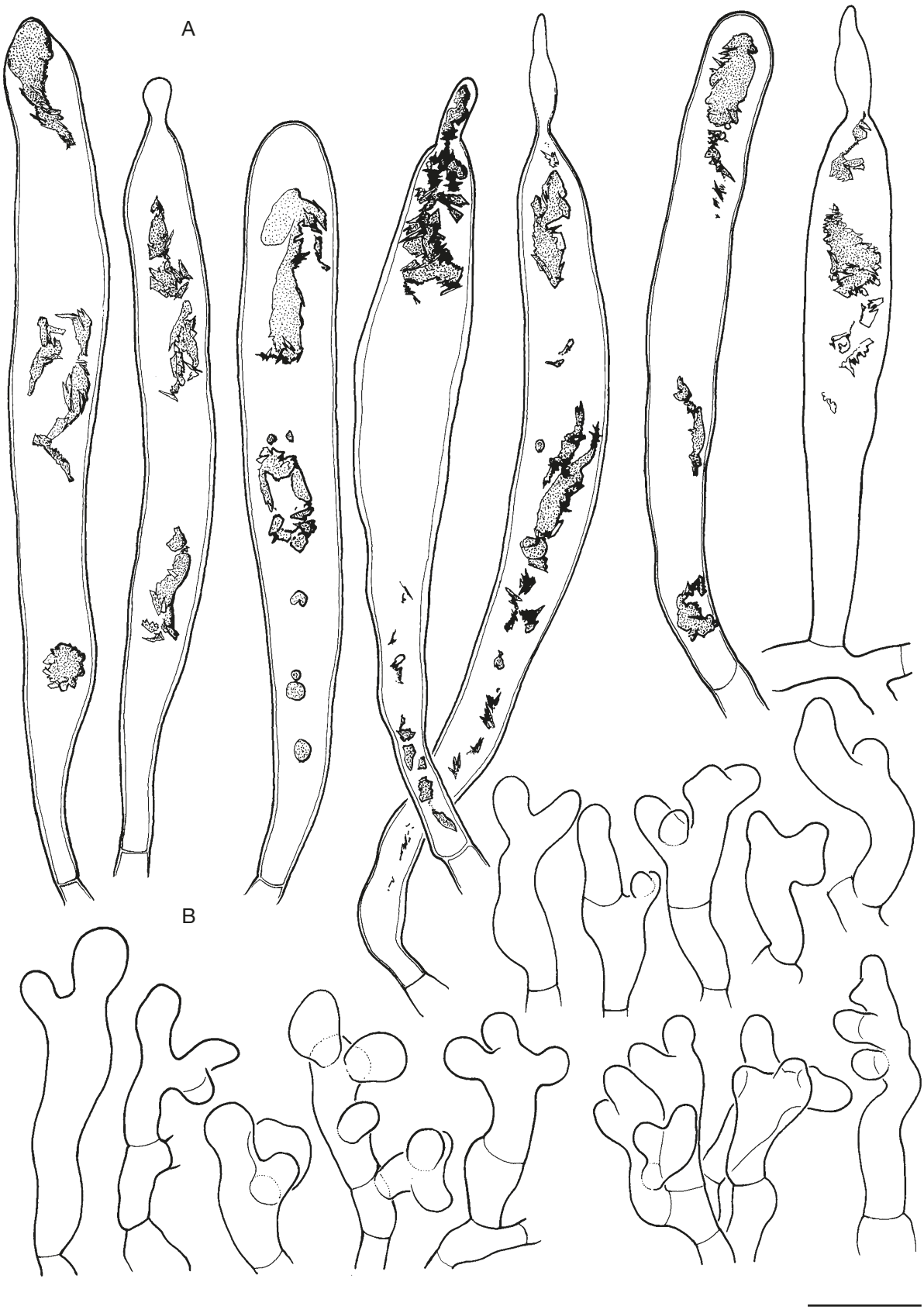

FIG. 11. — *Russula koniamboensis* Buyck, sp. nov. (holotype: *722/BB09.022*). Elements of the hymenium: **A**, cystidia with indication of contents; **B**, marginal cells. Drawings B. Duhem. Scale bar: 10 µm.

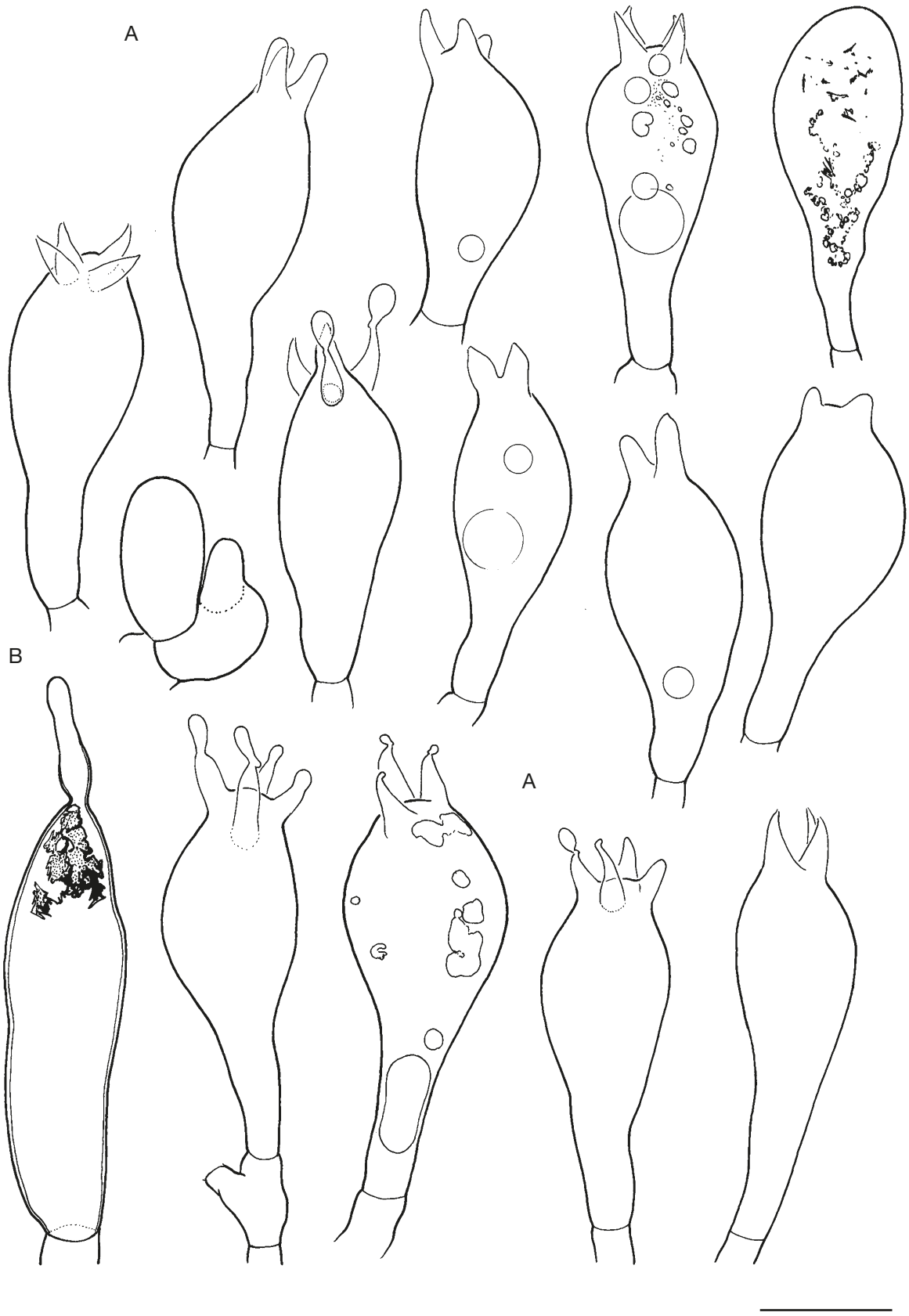

FIG. 12. — *Russula koniamboensis* Buyck, sp. nov. *(*holotype: *722/BB09.022*). Elements of the hymenium: **A**, basidia and basidiola; **B**, cystidium on gill edge. Drawings B. Duhem. Scale bar: 10 µm.

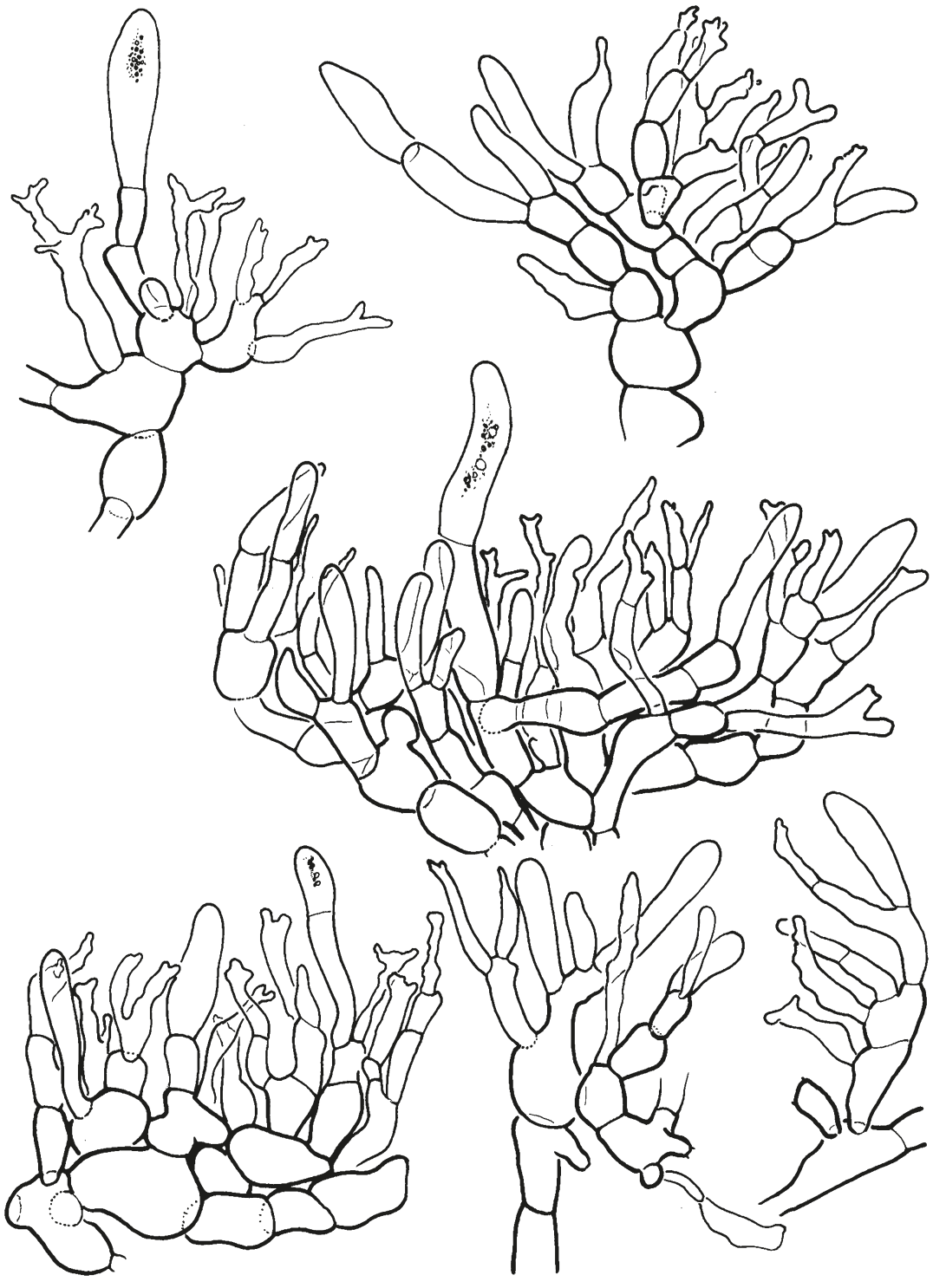

Fig. 13. — *Russula koniamboensis* Buyck, sp. nov. (holotype: *722/BB09.022*). Fragments of the suprapellis. Drawings B. Duhem. Scale bar: 20 µm.

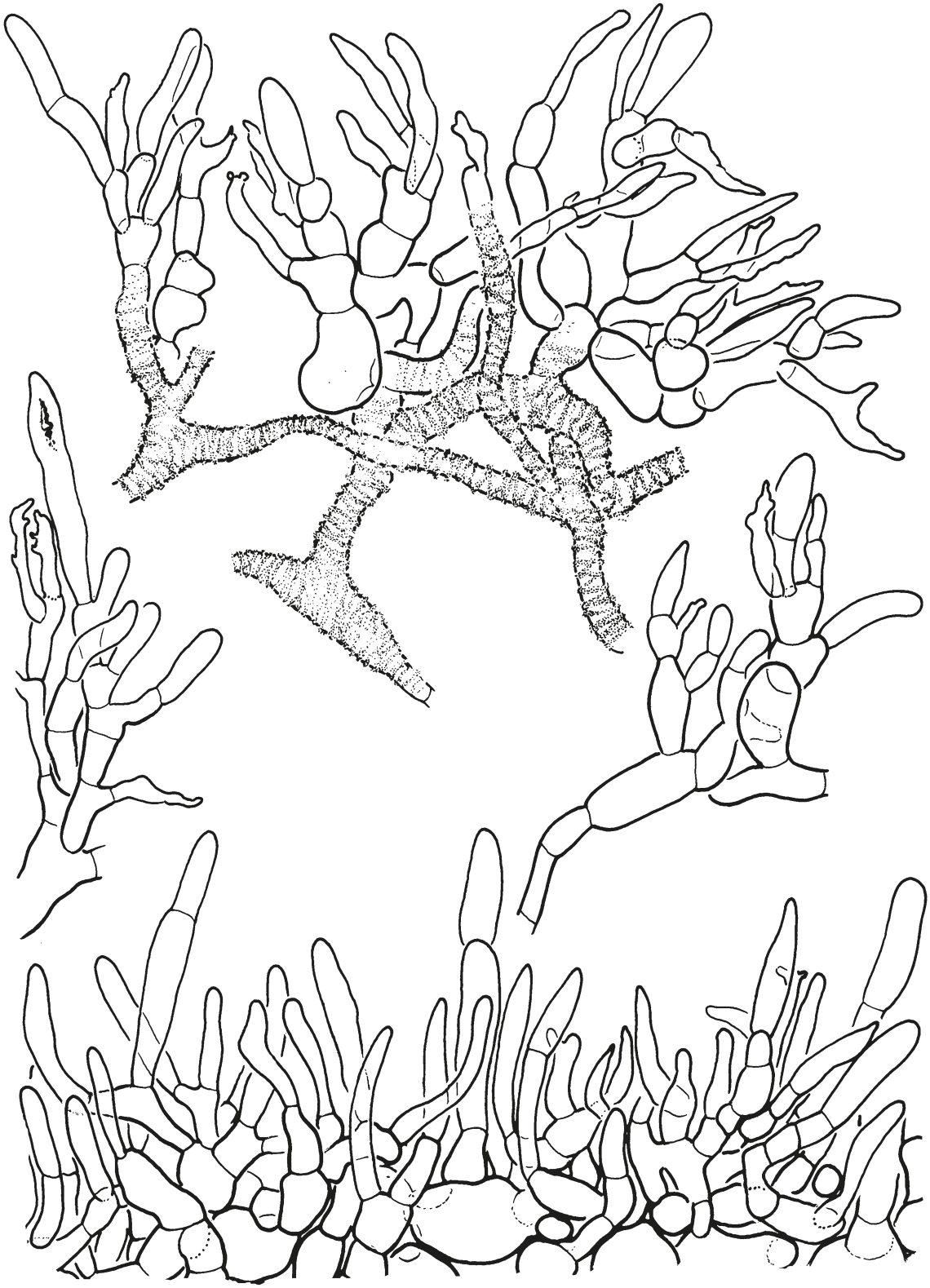

FIG. 14. — *Russula koniamboensis* Buyck, sp. nov. (*730/BB09.117*): details of the suprapellis. Drawings B. Duhem. Scale bar: 20 µm.

Context
Very thin toward the margin, white, distinctly greying in age. Taste and odor not distinctive.

Spore print
White.

Spores
(6.67)7.51-8.01-8.51(8.75) × (6.25)6.52-6.83-7.15(7.29) µm, Q = (1.06)1.10-1.17-1.24(1.31), subglobose to broadly ellipsoid; ornamentation subreticulate, composed of large, prominent, moderately distant, conical to hemispherical and strongly amyloid spines, up to 1(-1.5) µm long, connected by dispersed to frequent fine lines into a (very) incomplete network; suprahilar spot well-developed, varying from strongly amyloid to verruculose and grayish to poorly amyloid.

Basidia
30-42 × 12-17 µm, fusiformous to distinctly clavate, with (2-)4 stout sterigmata; basidiola clavate.

Subhymenium
Pseudoparenchymatic.

Hymenial gloeocystidia
68-94 × 7-12 µm on lamella sides, smaller near the lamella edges, up to 45 µm long, narrowly clavate to fusiform or subcylindrical, frequently mucronate to appendiculate at the apex, up to 14 µm long, originating in subhymenium and protruding beyond the basidia, thin-walled with walls up to 1 µm thick; contents in Congo red mainly restricted to dispersed refringent inclusions of variable size that do not react to sulfovanillin.

Marginal cells
15-26(-34) × 4-6(-9) µm, sitting on 1-2 short, subterminal cells, small, occupying most of the lamellar edges, extremely variable in shape, similar to the smaller terminal cells in the suprapellis in having 1-4 diverticulate, obtuse lobes or outgrowths.

Pileipellis
Two-layered; suprapellis composed in its lower part of hyphae with or without distinct orthochromatic incrustations, forming a 40-50 µm deep pseudoparenchyma of intertwined and strongly ramifying, irregularly shaped, thin-walled cells; basal cells sometimes up to 20(-25) µm wide; near the surface this suprapellis gradually transits into short chains composed of 2-4(-5) narrower cells that are slightly inflated and barrel-shaped or ellipsoid to subcylindrical, up to 10 µm wide; terminal cells of variable size are more or less arranged in a trichodermal structure, either longer or shorter than subterminal cells, (8-)16-23(-34) × 2-4(-6) µm, often very irregular or undulate in outline, slightly attenuating toward the frequently capitate, appendiculate or diverticulate apex. Primordial hyphae recognizable mostly by their somewhat more regular (i.e., cylindrical) outline, but especially by the refringent granular-heteromorphic contents of the terminal cell that mostly measures 15-25 × 4-5 µm, narrowly clavate to subcylindrical in outline, obtuse-rounded at the apex, diverticula or appendages absent, thin-walled; subpellis 60-70 µm deep, forming a loose structure above the first large sphaerocytes of the underlying context. Cystidioid hyphae absent in subpellis and context. Oleiferous hyphae rare in subpellis.

Clamp connections
Absent.

NOTES
The above description is based on the holotype collection. However, the two other collections of this species (having identical ITS sequences) clearly show that its microscopic features are quite variable among different collections (Fig. 14). For the pileipellis this variation concerns the size of the sphaerocytes in the lower suprapellis which are sometimes up to 35 µm diam., giving rise to 8-celled chains (as in *BB09.346*); observed variations apply also to the distinctiveness of the orthochromatic zebroid incrustations on the cell walls in the lower supra- and subpellis (as in *BB09.117*) and finally also to the form of the terminal cells on the hyphae, which can be either more regular in outline and thus similar to those of *R. incrustata* Buyck, sp. nov. (as in *BB09.346* and *BB09.117*) or they can be strongly diverticulate as in the type collection. On the lamella edge, cheilocystidia can be abundant and well-developed (as in *BB09.346*) or just widely dispersed among the other elements. The spores in *BB09.346* are near-identical in size and ornamentation to the holotype [(8.13)8.20-8.63-9.05(9.38) × (6.25)6.47-6.86-7.26(7.50) µm, Q = (1.11)1.17-1.26-1.35(1.40)], while spores in *BB09.117* produced several aberrant sizes and ornamentations indicating an unfavourable development. These spores were, therefore, not used for measurements.

Russula purpureotincta R.F.R. McNabb
(Figs 15-18)

New Zealand Journal of Botany 11: 711 (McNabb 1973).

TYPE MATERIAL. — **New Zealand** • Prov. Nelson, Springs Junction, Upper Grey, among *Sphagnum* under *Nothofagus* [*Fuscospora*] *solandri* var. *cliffortioides* and *Nothofagus* [*Lophozonia*] *menziesii*; 25.II.1968; E. Horak; *ZT 68-086* • Prov. Nelson, W of Tophonse Saddle, at the border of a swampy locality between moss (not Sphagnum) under *Nothofagus* [*Fuscospora*] *solandri* var. *cliffortioides* and *Nothofagus* [*Lophozonia*] *menziesii*; 3.III.1968; E. Horak; *ZT 68-105*.

PILEUS
Up to 75 mm diam., at first convex, becoming slightly depressed in the center with age, near the margin smooth to shortly striate; surface dull, when humid weakly viscid, at first reddish lilac to purplish, but rapidly discolouring, particularly between the center and the very margin, and then becoming

beige-brownish-pinkish to flesh-coloured, pileipellis separable up to mid-radius.

Stipe
36-80 × 10-19 mm, cylindrical or slightly narrowing towards apex, entirely white, smooth or finely striate lengthwise.

Lamellae
Equal in length or with rare lamellulae, 4-6 mm wide, normally spaced (*c.* 1L/mm at the pileus margin), white, becoming cream with age, not anastomosing in the dorsal interspaces, obtusely rounded at the pileus margin; gill edge smooth, concolourous.

Context
Brittle, spongy, white, unchanging on exposure. Odour not distinctive. Taste mild.

Spore print
White.

Spores
(8.13-)8.32-8.74-8.93-9.43(-10.21) × (6.67-)6.99-7.28-7.29-7.57(-7.92) µm, Q = (1.11-)1.14-1.20-1.23-1.28(-1.34), large, subglobose to broadly ellipsoid, densely ornamented with strongly to partly amyloid spines or cylindrical warts, these up to 2 µm high in many spores and frequently curved, often in pairs, with few smaller granular warts and rare interconnecting fine lines; suprahilar spot distinctly amyloid.

Basidia
40-48 × 12-15 µm, clavate, 4-spored; sterigmata stout, mostly 7-8 × 2-3 µm.

Hymenial gloeocystidia
Mostly 70-90 × 12-15 µm, abundant, on lamellar sides clavate to fusiform, thin- to slightly thick-walled; near lamellar edges distinctly thick-walled (up to 2-3 µm thick in middle portion) and smaller, mostly 40-60 × 7-12 µm, rarely with an additional septum in the upper part.

Marginal cells
Not differentiated.

Pileipellis
Two-layered. The suprapellis is forming at the pileus surface a trichodermal structure of densely packed, narrow and thin-walled, ascending hyphal extremities composed of 3-6 short cells which originate from a more disorganized pseudoparenchyma that constitutes its lower part; this 80-90 µm deep pseudoparenchyma is composed of strongly inflated, sausage-like, ellipsoid or spherical cells up to 30 µm diam., without zebroid incrustations on the cell walls; terminal cells of the trichoderma in the pileus center short to very short, rarely exceeding 20 × 3-5 µm, either narrowing in the upper part or clavate, often slightly undulate in outline, toward the pileus margin more irregular in outline and very frequently globose to moniliform at apex. Typical pileocystidia absent. Primordial hyphae emerging from the surface of the suprapellis, slightly more voluminous than the other hyphal extremities and composed of 3-6, thin-walled cells, usually more strongly septate in the pileus center; cells shortly cylindrical to barrel-shaped, up to 8 µm diam., mostly also containing distinctly refringent, granular contents in the one or two upper cells; their terminal cell frequently up to 35 µm long, more regular in outline compared to the other sometimes subcapitate hyphal extremities; subpellis ill-defined. Cystidioid and oleiferous hyphae lacking.

Clamp connections
Absent.

Notes
The description is based on two collections gathered by E. Horak one year before the species was officially described by R.F.R. McNabb (1973) as *R. purpureotincta*. Our description is highly similar to the original description, considering that the spore size given by McNabb (9-12 × 8.5-10.5 µm) includes the spore ornamentation. In addition, McNabb was probably not aware of the concept of 'primordial hyphae'.
This endemic species of New Zealand seems to be widely distributed and not rare at all as many records are reported online (e.g. on https://scd.landcareresearch.co.nz). The online available field images, illustrations of microscopic features and SEM pictures of the spores for these collections (including for the type collection) clearly confirm our own observations on Horak's specimens.

Russula purpureotincta is represented in our ITS phylogeny by nine sequences, including one newly produced sequence from the type specimen and one [GU222259 for PDD77740] that corresponds to a very pale collection initially identified as *Russula cremeo-ochracea* (and still deposited as such in GenBank). McNabb's species resembles our *R. incrustata* Buyck, sp. nov. because of the faint greyish magenta, greyish purple to reddish grey tints present in the pileus, but it lacks the warmer orange-red tints of our New Caledonian species which, in addition, has a coloured stipe. As evident from online published pictures for *R. purpureotincta*, the stipe can frequently be obclavate and can vary considerably in length between different specimens.

Russula purpureotincta is very variable in overall colour, but typically discolours very rapidly leaving a pale sordid whitish-isabelline pileus with only faint greenish-pinkish hues remaining in the center and at the very margin of the pileus. Such discoloured specimens are more reminiscent of equally discoloured forms of several (but acrid!) species in the *Russula* core clade, rather than of other species of subsection *Roseinae*.
Microscopic differences between *Russula purpureotincta* and both above-mentioned New Caledonian species are very subtle. Spore ornamentation in McNabb's species seems less reticulate, its cystidia on the gill edge more strongly thick-walled, and cystidial contents more abundant.

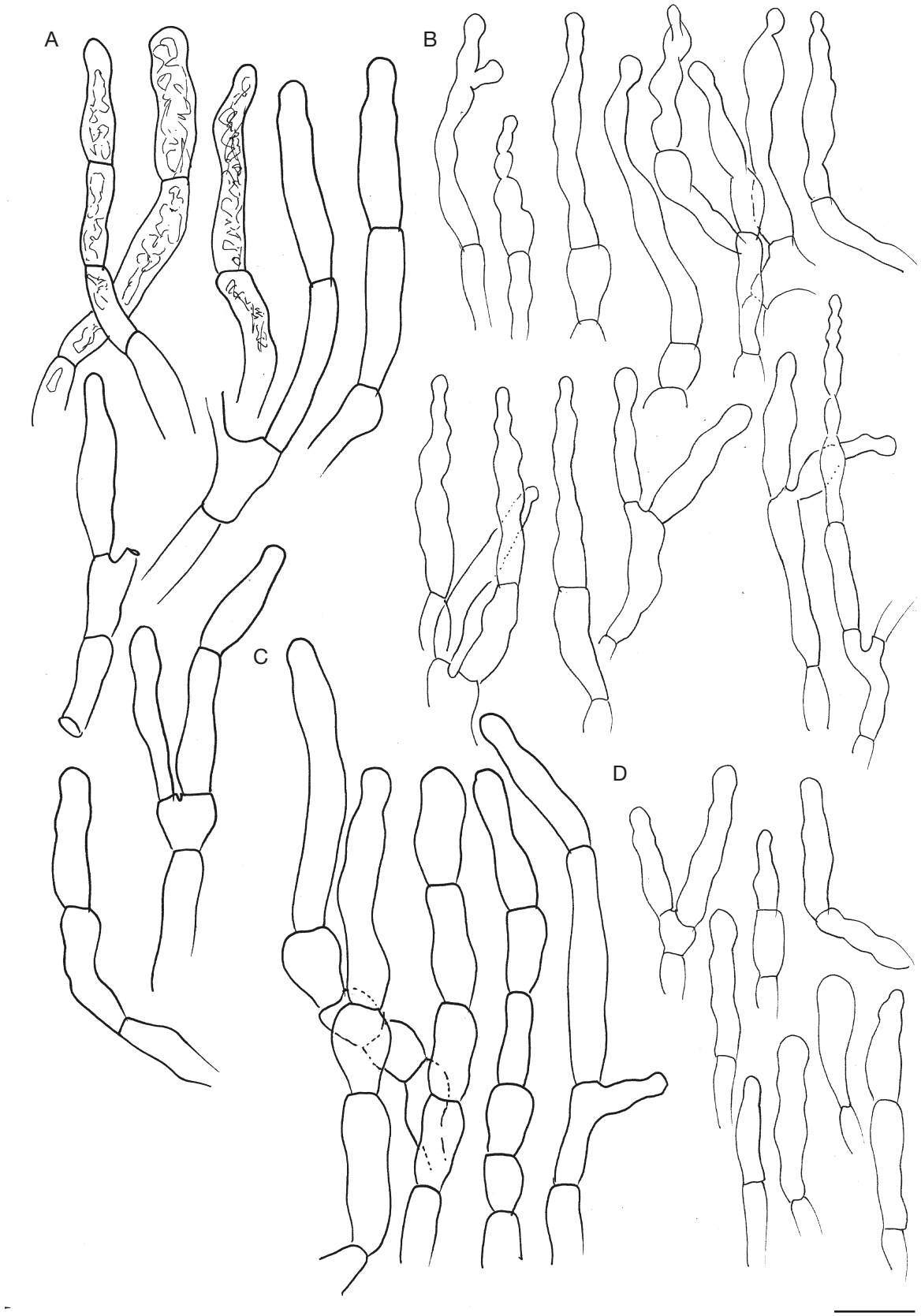

FIG. 15. — *Russula purpureotincta* R.F.R. McNabb (*ZT 68-105*): **A**-**B**, elements of the pileipellis near pileus margin: **A**, primordial hyphae with indication of contents in few cells; **B**, terminal cells of the other hyphal extremities. **C**-**D**, elements of the pileipellis in the pileus center: **C**, primordial hyphae without indication of contents; **D**, terminal cells of other hyphal extremities. Drawings B. Buyck. Scale bar: 10 µm.

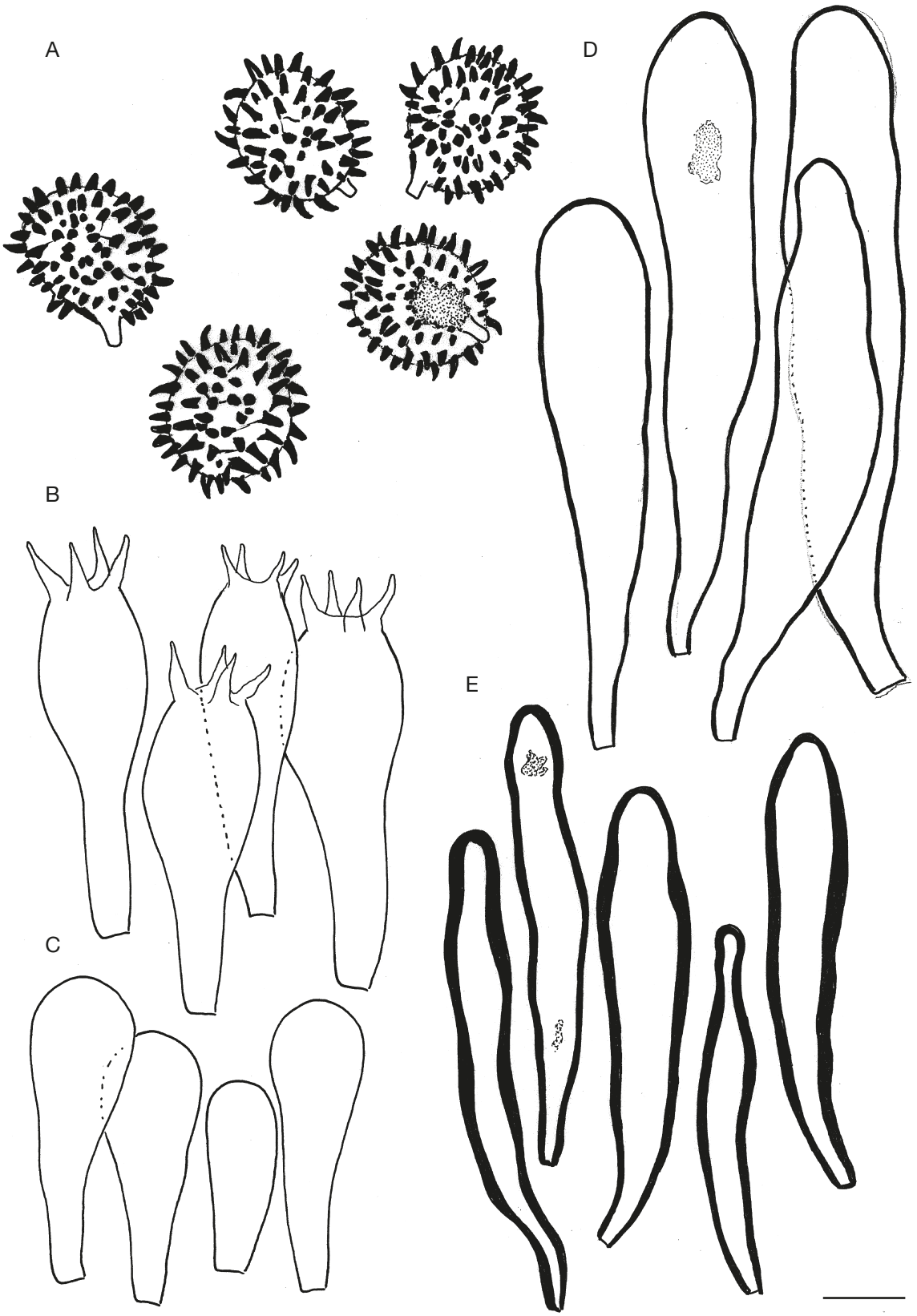

FIG. 16. — *Russula purpureotincta* RFR. McNabb. Elements of the hymenium (all from *ZT 68-105*, except **B** from *ZT 68-086*). **A**-**B**, basidiospores; **C**, basidia; **D**, basidiola; **E**, pleurocystidia; **F**, cheilocystidia. Drawings B. Buyck. Scale bar: 10 µm.

FIG. 17. — *Russula purpureotincta* R.F.R. McNabb. Fresh basidiomata (*ZT 68-105*). Photo E. Horak. Scale bar: 2 cm.

DISCUSSION

The concept of 'primordial hyphae' is not always very clear because the distinction with 'true' pileocystidia is very vague as already discussed recently for the /flavida lineage within subsection *Auratinae* (Ghosh *et al.* 2023). First of all, primordial hyphae are not 'hyphae' in the normal sense, but merely short chains of cells constituting terminal parts within larger ramifying hyphal extremities, just like regular pileocystidia. In *Roseinae*, the 'primordial hyphae' are typically composed of 1 to 4, 5 or 6 cells, also in the case of the southern hemisphere taxa. Even without the use of carbolfuchsin, most of these primordial hyphae are recognizable because the 1-2 terminal cells have very often refringent contents comparable to pileocystidia. Also, their general form is more regular with a terminal cell that is typically cylindrical to clavate and obtuse-rounded at the tip. The terminal cells of the other hyphal extremities are frequently irregularly lobed, capitulate or diverticulate at the tip.

The structure of the pileipellis is another subject of diverging interpretations. All known *Roseinae* possess a pileipellis that is composed of strongly branching hyphal extremities that are formed of inflated cells in their lower portion. These inflated cells usually compose a more or less well-developed pseudoparenchymatic layer. It is this pseudoparenchymatic layer that disrupts from drought or with continuing expansion of the cap, as is equally observed in all other subsections possessing such a pseudoparenchymatic layer (e.g. in subsections *Virescentinae* or *Castanopsidum* Buyck & X.H.Wang where the fragmentation is often very visible). For the first author (BB), this pseudoparenchyma is part of the suprapelllis which is the usual interpretation also in other subsections where a pseudoparenchyma is present. The much narrower (sub)terminal cells have more space and can, therefore, form a more or less trichodermal or epithelium-like structure at the pileus surface depending on their length-width ratio. In *Roseinae*, the transition between subpellis and underlying context is obscure as the hyphae of the subpellis are morphologically hardly differentiated from those of the context below. Here we have considered the subpellis to represent the layer between the pseudoparenchyma and the appearance of the first large sphaerocyte nests in the underlying context.

The above interpretation of the pileipellis layers differs considerably from the one adopted by other authors or even from the one used in papers co-authored earlier by the first author (e.g. Adamčík & Buyck 2012) in which the pseudoparenchymatic layer was referred to as subpellis. However, the uneasy consequence of the latter view is that: 1) the pseudoparenchyma of the pileipellis is differently interpreted within the same genus depending on the subsection; and 2) that when one considers

the pseudoparenchyma to represent the subpellis, this view reduces the suprapellis in *Roseinae* to the height of the terminal cell, not to a distinctive layer (e.g. as in Manz *et al.* 2021).

Subsection *Roseinae* was placed sister to subsection *Lilaceinae* with high support (MLbs = 91%) in the multilocus phylogeny by Buyck *et al.* (2018). Both subsections have always been considered – even in the traditional morphotaxonomic classifications (Romagnesi 1967; Sarnari 2005) – either as one single or as two extremely close species groups. In older morphology-based classifications, both subsections were part of subgenus *Incrustatula* Romagnesi (1967) together with other subsections having more coloured spore prints. In the first multilocus phylogeny that was more or less representative of world-wide *Russula* species, Buyck *et al.* (2018) demonstrated the artificial concept of subgenus *Incrustatula* with dark-spored subsection *Amethystinae* (Romagn.) Bon and *Chamaeleontinae* Singer of *Russula* subgenus *Incrustatula* being unrelated to the pale-spored taxa in subsection *Roseinae* and *Lilaceinae*. This was later confirmed with an identical multilocus approach by X.H.Wang & Buyck in Rossi *et al.* (2020) when providing significant support (MLbs = 80%) to group the northern hemisphere, dark-spored subsections *Amethystinae* and *Chamaeleontinae*, together with the Oceanian subsection *Tricholomopsidum* Buyck & V.Hofst. and the Asian subsection *Castanopsidum* Buyck & X.H.Wang and not with the *Roseinae* – *Lilaceinae* clade.

Arguing that the traditional interpretation of *Roseinae* should be considered at the section level, Looney *et al.* (2022) described subsection *Albidinae* Looney, Manz & Adamčik, for merely two species (*Russula albida* and a taxon that possibly corresponds to *R. praeumbonata*). The argumentation for this new subsection is in our opinion quite weak. Indeed, compared to other *Roseinae, Albidinae* no longer differ in pileus colour (especially now that there are more white southern taxa) and spore print colour (cream versus white). Other morphological differences are restricted to the fact that the cells of the suprapellis are very short compared to other *Roseinae*, giving thus rather an impression of an epithelium than a trichodermal structure at the cap surface, which is not a fundamental difference. Finally, the darker reaction with sulfovanillin was also observed for the still unsequenced *R. rimosa*, a species that morphologically fits *Roseinae s.s.* (Adamčík & Buyck 2012). The same authors also suggested that yet another separate subsection was needed for the American /magnarosea clade, another tiny subclade based so far on two undescribed collections. In our opinion, proposals to elevate the ranks of such extremely small entities within highly terminal clades should be postponed because these are bound to create problems in future. Gosh *et al.* (2023) and Buyck *et al.* (2023), therefore, considered different lineages, that were genetically equally different as the species groups discussed above, to be part of the same subsection *Auratinae* Bon.

Indeed, ongoing research clearly shows already that many tropical species, for example, appear to take rather basal positions in the crown clade. In the supposition that *Roseinae* becomes a section, then *Lilaceinae* should logically follow the same path, and then, so will probably many of the traditional subsections in the crown clade. Considering that most fungal genera typically have no additional ranks between section and subgenus, the problem of having no available ranks left for lineages that are in between section and subgenus in the crown clade is unavoidable (and the crown clade is not even a separate subgenus). It would be much better in our opinion to work with stirps, series, etc. within subsections.

Sequestrate *Roseinae* have not yet been reported from the northern hemisphere. We here placed in the subsection two southern species that conform to the morphological definition of the abandoned genus *Macowanites*: *R.* [*Macowanites*] *kermesina* from New Zealand and *R. albobrunnea* T.Lebel from Australia. Our ITS phylogeny suggests – although without any support – that these southern sequestrate taxa could be related to a different lineage of northern hemisphere *Roseinae* compared to the here studied agaricoid *Roseinae* from New Caledonia and New Zealand (Fig. 1). Indeed, the very high support obtained – both in ITS and *tef*1 phylogenies – for the grouping of the three agaricoid taxa, make it seem unlikely that both secotioid species would be their closest relatives considering their placement in the ITS phylogeny. Whereas the agaricoid southern hemisphere *Roseinae* belong to the /cardinalis lineage, the correct placement of the sequestrate species might be closer to a mixed American-Asian lineage. This hypothesis seems also corroborated by a BLASTn of the ITS of *R. kermesina*: the most similar sequences are from *R. albobrunnea* (96.7% similarity), followed by *R. peckii* (93%) and nearly all other *Roseinae* (91.7% down to 88.9%), while *R. cornicolor* (87.9%) from the /cardinalis lineage and the southern hemisphere *R. purpureotincta* (87.6%) are already less similar than species from other subsections (not *Lilaceinae*, but mostly dark-spored lineages, such as subsection *Chamaeleontinae*). Considering the bad quality of the two available ITS sequences for *R. albobrunnea* (particularly the holotype sequence) missing both the first 100 bp in ITS1, it would be good to obtain a better barcode sequence for this species.

Our ITS phylogeny grouped both sequestrate taxa with full support (MLbs = 100%) and this notwithstanding their important morphological differences. Several collections of *R. kermesina,* including the type specimen, have been illustrated on the Landcare Research website (https://scd.landcareresearch.co.nz). The species seems to conform to the general idea of northern hemisphere *Roseinae* because of the usually medium-sized, red pileus and the formation of a rather normal white or slightly pinkish stipe, a similar pileipellis structure and the subreticulate spore ornamentation (McNabb 1971; Lebel 2002). However, *R. kermesina* differs from all other *Roseinae* (incl. *R. albobrunnea*) in the fact that the strongly deformed hymenophore (prohibiting the full expansion of the pileus marginal zone) apparently resulted in the formation of statismospores lacking the distinct amyloid suprahilar spot, so typical for all other species in the subsection. No spore print could ever be obtained from this rather common species in New Zealand. *Russula albobrunnea* is not only very different in colour (white pileus) but also in size (only 1-2 cm diam.) and has a stipe which remains nearly entirely hidden within the pileus. Although described as a trichoderma, the pileipellis structure seems quite normal forming a pseudoparenchymatic layer that is perhaps a little bit less

Fig. 18. — *Russula purpureotincta* R.F.R. McNabb. Fresh basidiomata *(ZT 68-068)*. Watercolour by E. Horak.

developed compared to other *Roseinae* (Lebel & Tonkin 2007: fig. 4B); its spore ornamentation (Lebel & Tonkin 2007: fig. 5, not fig. 4F) is low and consists predominantly of isolated warts.

The southern *Roseinae* associate with different tree families compared to their relatives from the northern hemisphere: rarely Myrtaceae (so far only *R. incrustata* Buyck, sp. nov.) and normally *Nothofagaceae* (*R. purpureotincta, R. kermesina, R. koniamboensis* Buyck, sp. nov., *R. albobrunnea*). It is not clear whether these hosts have been more recently invaded by these fungi or not, but the fact that no *Roseinae* have yet been reported from *Nothofagus* forests in South America discards for the moment the hypothesis of an ancient vicariance within subsection *Rosinae*.

As a conclusion, we can state that southern *Roseinae* considerably impact the definition of the subsection as based on their northern hemisphere relatives. They expand features related to general colouration, host family associations, fruiting body and hymenophore development, as well as spore development and spore dispersal and types of spore ornamentation to name the most important. As a result, we present below an emended definition of the subsection.

Russula subsection ***Roseinae***
Singer ex Sarnari emend. Buyck

Monografia Illustrata del Genere Russula *in Europa* 1: 98 (Sarnari 1998).

Defined by agaricoid or more rarely secotioid fruiting bodies, mostly with red to pink pileus, more rarely also white or yellowish, or multicoloured with orange, brownish, vinaceous to purple and even greyish-greenish tints, with mild taste or rarely acrid, producing white to cream spore prints, context turning bright pink or red with sulfovanillin and surfaces magenta with PDAB (p-dimethylaminobenzaldehyde) in fresh and dry specimens, presence of primordial hyphae with acidresistant incrustations that turn pink in sulfovanillin, hyphal terminations in pileipellis composed of short chains of cylindrical to ellipsoid or more versiform cells that originate from inflated cells in the lower suprapellis, the latter forming a more or less well-developed pseudoparenchymatic layer; spores generally with distinct suprahilar amyloid spot, rarely without; spore ornamentation subreticulate or more rarely with isolated warts.

Type species. — *Russula velutipes* Velen.

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