Phytotaxa 668 (2): 117–129
https://www.mapress.com/pt/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

https://doi.org/10.11646/phytotaxa.668.2.1

Russulaceae of the Pakaraima Mountains of Guyana 5. Two newly described diminutive species in a novel lineage of the crown clade of *Russula* (Russulaceae)

STEVEN L. MILLER[1,4*], M. CATHERINE AIME[2,5] & TERRY W. HENKEL[3,6]
[1]*Department of Botany, University of Wyoming, Laramie, Wyoming 82071, USA*
[2]*Department of Botany and Plant Pathology, Purdue University, West Lafayette, Indiana 47907, USA*
[3]*Department of Biological Sciences, California State Polytechnic University, Humboldt, Arcata, California 95521, USA*
[4] *fungi@uwyo.edu; https://orcid.org/0000-0002-9741-0262*
[5] *maime@purdue.edu; https://orcid.org/0000-0001-8742-6685*
[6] *terry.henkel@humboldt.edu; https://orcid.org/0000-0001-9760-8837*
[*]*Corresponding author: fungi@uwyo.edu*

Abstract

Much of our previous work documenting fungal biodiversity in Guyana has been centered in forests of *Dicymbe corymbosa* Spruce ex Benth., which forms monodominant stands in the white sands region of Guyana. In order to begin to assess fungal biodiversity associated with other ectomycorrhizal host trees found in Guyana, expeditions were conducted to areas containing *Dicymbe altsonii* and *Pakaraimaea dipterocarpacea.* In this paper, we describe two new species of *Russula* from Guyana with diminutive basidiomata: *R. lilliputia* and *R. pakaraimaeae*, found in association with these tree hosts, using a combined approach of morphological characterization and molecular analyses. Together with *R. gelatinivelata*, which we previously described from Guyana, *R. lilliputia* and *R. pakaraimaeae* form what appears to be a new lineage within the crown clade of *Russula*, sister to the subsect. *Auratinae*. Synapomorphies for the lineage include a pruinose to subtomentose pileus in dry conditions, suprapellis comprised of inflated cells that give rise to long cylindrical or digitate, and sinuous, thin or thick-walled pileocystidia that are strongly emergent, easily disarticulate in microscopic preparations, and have contents that are acid resistant in Basic Fuchsin, pruinose to subomentose patches on the stipe, suprahilar plage on the basidiospores, spore ornamentation of mostly isolated verrucae, and geographic distribution restricted to the Pakaraima Mountains of Guyana. Full descriptions, photos, line drawings of microscopic features, and comparisons with related species are provided.

Key words: ectomycorrhizal fungi, new species, *Russula* crown clade, taxonomy, tropical fungal biodiversity

Introduction

Russula Pers. (1796) is one of the largest and most diverse genera within the Basidiomycota, with conservative estimates of the number of species ranging between 750 and 2000 on the low end (Adamčík *et al.* 2019; Mycobank 2024; Species Fungorum 2024) and an estimated 15,000 based on environmental sequences (Lücking & Hawksworth 2018). Owing to the work of R. Heim (*e.g.* 1937a,b, 1938, 1970, among many others), R. Singer (*e.g.* 1952, 1986, Singer *et al.*1983, and many others), B. Buyck (*e.g.* 1990a, b, 1994a, b, among many others), T.W. Henkel (Henkel *et al.* 2000; Henkel *et al.* 2011, Miller *et al.* 2002; Miller and Henkel 2004; Miller *et al.* 2012, and many others), the number of newly described taxa in tropical areas has been greatly expanded. However, the lack of complete sampling in many remote places around the world, along with disagreement between traditional morphological concepts and lineages recognized by phylogenetic studies, has led to uncertainty regarding the stability of characteristics for species delimitation and infrageneric classification (Miller and Buyck 2002; Adamčík *et al.* 2016 a, b; Caboň *et al.* 2017).

Much of our previous work documenting fungal biodiversity in Guyana has been in forests of *Dicymbe corymbosa* Spruce ex Benth., which forms monodominant stands in the white sands region of Guyana. While this work, some two decades on, is continuing, expeditions were conducted to other interesting areas of Guyana with the intent of beginning to assess fungal biodiversity associated with other ectomycorrhizal host trees found in Guyana. The present paper describes two new species of *Russula* from Guyana found in association with *Dicymbe altsonii* Sandwith and *Pakaraimaea dipterocarpacea* Maguire & P.S. Ashton: *R. lilliputia* and *R. pakaraimaeae,* with interesting ecological,

Accepted by Samantha C. Karunarathna: 25 Sept. 2024; published: 15 Oct. 2024

morphological and microscopic features. Together with *R. gelatinivelata* S.L. Mill., Aime & T.W. Henkel (2012: 248), which we previously described from Guyana, *R. lilliputia* and *R. pakaraimaeae* form what appears to be a new lineage within the crown clade of *Russula*, sister to subsect. *Auratinae* (Bon 1988: 115) *sensu* Gosh *et al.* (2023) supported by both molecular and morphological evidence.

Materials and methods

Collection and morphological analyses

Almost annual collecting expeditions have been made to the Upper Potaro River and Mazaruni River Basins of Guyana, in the south-central Pakaraima Mountains along the western border with Brazil between 2000 and 2024. *Russula lilliputia* described below was only encountered and collected in 2000. An expedition to the fringing forest surrounding the Pegaima savanna was made in 2010. Basidiomata were collected and examined in the field for fresh characteristics. Color characteristics were coded according to Kornerup & Wanscher (1981; code noted in parentheses) and described subjectively. Spore deposits were taken on acetate sheets and examined for fresh color characteristics. The $FeSO_4$ macrochemical test was performed using a large mineral crystal that was rubbed directly on the stipe, lamellae and flesh. Basidiomata were dried slowly using large bead silica gel and subsequently placed in re-sealable plastic bags with small bead silica gel to prevent spoilage in excessively humid conditions. In addition, basidiomata in various stages of development were immersed in ethanol for preservation and molecular analysis. Dried tissues were revived in ETOH and water, sectioned by hand using elder pith, and microscopic observation was made in 5% KOH + aqueous Congo-red. Sections of the pileus were examined both from near the disc and closer toward the margin. Reagents used included Sulfovanillin (SV) and Basic Fuchsin (BF) in their traditional formulation and methodology. Basidiospores from the spore print were observed and measured in Melzer's reagent in side view, excluding ornamentation and apiculus; basidiospore measurements were based on 20 spores and include: x = the mean of length by width; Q = the quotient of basidiospore length to width; and Qm = the mean of Q-values. All drawings were made with the aid of a drawing tube installed on an Olympus BH-2 microscope.

DNA extraction, PCR and sequencing

DNA extraction and PCR amplification with primers ITS1F and ITS4B and purification of the amplified product were generally those described in Miller *et al.* (2006). Sequencing was performed at the Nucleic Acid Exploration Facility at the University of Wyoming, USA.

Phylogenetic analyses

Two analyses were conducted in the present study. In the overall analysis the dataset included ITS sequences of 107 ingroup reference samples forming a representative scaffold of clades from the crown, core, and basal clades of *Russula* selected based on previous studies of Looney *et al.* (2016), Adamčik *et al.* (2019), and Zhou *et al.* (2022), which were used to analyze the phylogenetic position of our specimens within the genus *Russula*. In addition, we used a sequence similarity search for *R. lilliputia* and *R. pakaraimaeae* sequences in GenBank (Megablast option), defined as 98% similarity and above as a means of identifying close taxa (including environmental sequences), and verification that the fungi were undescribed. Sequences were retrieved from NCBI and UNITE databases. Two sequences of *Multifurca ochricompacta* (Bills & O.K. Mill.) Buyck & V. Hofst. in Buyck *et al.* (2008: 37) were used as outgroup taxa (Zhou 2022). In the second expanded analysis, 16 additional sequences representing taxa from the subsect. *Auratinae sensu* Gosh *et al.* (2023) recovered in the overall analysis were retrieved based on previous studies that included taxa in this clade (Adamčik *et al*. 2019; Vidal *et al*. 2019; Buyck *et al.* 2023; Gosh *et al.* 2023). Not all potential sequences used in these studies were equally complete; selected sequences were screened to match the level of completeness present in other sequences in our database. Four sequences of species from the core clade of *Russula* were used as outgroup taxa for the expanded analysis. Twelve ITS sequences are new sequences for the present study and can be found under GenBank accession numbers PP741561-PP741571 and PP747660. Accession numbers, voucher numbers, and locale are provided in the OTU line at the terminus of branches.

Sequences were firstly aligned in MAFFT (Katoh & Standley 2013), then manually adjusted in UniPro UGENE v. 50.0 2024 (Okonechnikov *et al.* 2012). The maximum likelihood (ML) and Bayesian approximation analyses were performed in IQ-TREE (Nguyen *et al.*2015; Trifinopoulos *et al.* 2016) using the web server and settings which included: automatic calculation of the best fit substitution model under Bayesian Information Criterion (BIC) (Kalyaanamoorthy *et al.* 2017), creation of an initial parsimony tree by Phylogenetic Likelihood Library (PLL), Ultrafast Bootstrap analysis (Hoang *et al.* 2018), number of bootstrap alignments = 1000, maximum iterations =1000, minimum correlation coefficient = 0.99 and approximate Bayes test, computing a BIONJ tree and optimizing candidate tree set, and computation of a bootstrap consensus tree. The resulting trees were displayed and adjusted in FigTree v 1.4.4 (A. Rambaut *et al.* http://tree.bio.ed.ac.uk/software/figtree/), and the final trees were rendered in Illustrator 2024 (Adobe, Inc., San Jose, CA).

Results

Phylogenetic analyses

The final scaffold ITS alignment contained 918 characters including gaps. The best-fit substitution model according to BIC was TIM2e+I+G4. The optimal log-likelihood of BIONJ tree was -18447.273. Tree search was completed after 236 iterations. Rate parameters were as follows: A-C: 1.45954 A-G: 2.65725 A-T: 1.45954 C-G: 1.00000 C-T: 5.80076 G-T: 1.00000. Base frequencies were: A: 0.250 C: 0.250 G: 0.250 T: 0.250. The log-likelihood of consensus tree was -18370.589. The ML consensus tree for the overall alignment is shown in Fig. 1. The alignment for the expanded sampling of subsect. *Auratinae* contained 917 characters including gaps. The best fit substitution model according to BIC was SYM+G4. The optimal log-likelihood of BIONJ tree was -5486.705. Tree search was completed after 102 iterations. Rate parameters were as follows: A-C: 1.632224 A-G: 1089333 A-T: 1.07598 C-G: 0.43672 C-T: 4.83503 G-T: 1.00000. Base frequencies were: A: 0.250 C: 0.250 G: 0.250 T: 0.250. The log-likelihood of consensus tree was -5479.042. The ML consensus tree for the expanded of subsect. *Auratinae* sampling is shown in Fig. 2. For both phylogenetic trees Bayes support greater than 0.95 and Bootstrap support values greater than 80% are indicated at the nodes.

The scaffold analysis of the ITS sequences (Fig. 1) retrieved essentially the same clades found in the other studies on which our taxon sampling was based and indicated that both *R. lilliputia sp. nova* and *R. pakaraimaeae sp. nova* are placed together with *R. gelatinivelata* S.L. Mill., Aime & T.W. Henkel (2012: 248) in a highly supported clade (Bayesian posterior probability 1, Bootstrap 100) within in the crown clade of *Russula* subgen. *Russula*, sister to a clade comprised of species typically referred to as the *R. wielangtae* and *R. aurea* lineages of subsect. *Auratinae sensu* (Gosh *et al.* 2023). The clade containing *Russula lilliputia* and *R. gelatinivelata* was highly supported (Bayesian posterior probability 1, Bootstrap 100) separate from the branch containing *R. pakaraimaeae.* The separation of *Russula lilliputia* from *R. gelatinivelata* was also highly supported (Bayseian posterior probability 0.966, Bootstrap 100).

The expanded analysis (Fig. 2) including sequences of *R. lilliputia, R. pakaraimaeae* and *R. gelatinivelata* and additional sequences from members of subsect. *Auratinae* indicated a well-supported relationship with subsect. *Auratinae,* but in a separate clade (Bayesian posterior probability 1, Bootstrap 100). There was sufficient evidence to hypothesize a new lineage called the *R. gelatinivelata* lineage. The clade containing *Russula lilliputia* and *R. gelatinivelata* was highly supported (Bayesian posterior probability 0.967, Bootstrap 94) separate from the branch containing *R. pakaraimaeae.* The separation of *Russula lilliputia* from *R. gelatinivelata* was also highly supported (Bayseian posterior probability 1, Bootstrap 99).

Taxonomy

Russula lilliputia S.L. Mill., Aime & T.W. Henkel ***sp. nov.*** (Fig 3)

Mycobank: 854388

Diagnosis: Russula lilliputia is characterized by the remarkably small size of its red pileus not exceeding 5 mm, its densely pruinose stipe, and pileus when dry, its restricted distribution in Guyana and basidiome production on the surface of trunks of *Dicymbe altsonii* trees, spores with relatively indistinct suprahilar plage and occasional scarce, low interconnections between verrucae, long hairlike pileocystidia arising from an epithelioid layer of swollen cells, and white spore print.

Etymology: in reference to the diminutive size of the basidiomata – these mushrooms could easily have been part of the mushroom flora of Lilliput encountered in Swift's Gulliver's Travels.

Holotype: GUYANA. Region 8 Potaro–Siparuni. Pakaraima Mountains, Upper Potaro River Basin, within 15 km radius of Potaro base camp located at 5°18′04.8″N 59°54′40.4″W, 710–750 m; 23 May 2000, *S.L. Miller 10046* (**holotype** BRG; **isotype** RMS). GenBank ITS PP741561.

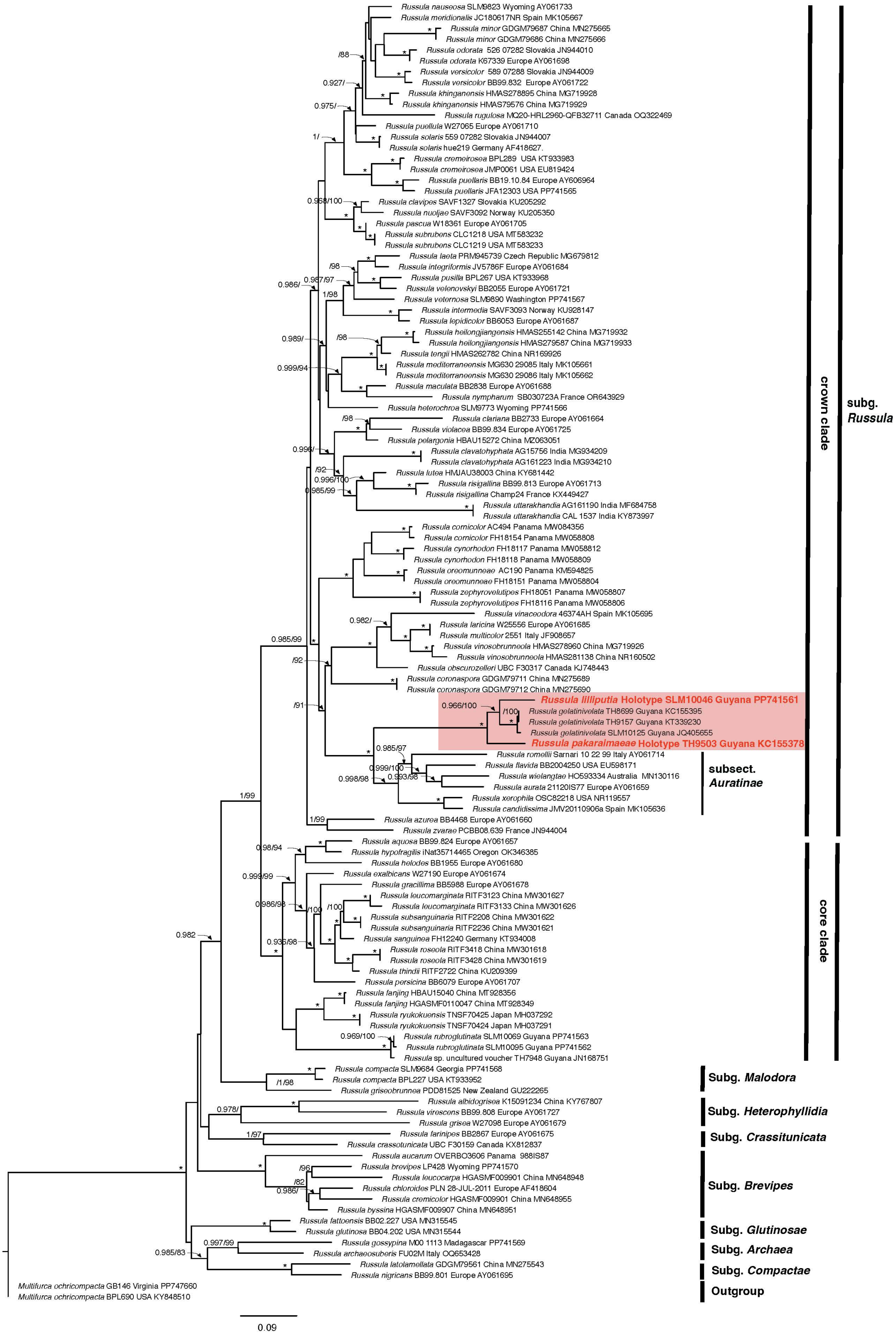

FIGURE 1. Maximum likelihood consensus tree showing the position of newly described *Russula lilliputia* (Holotype SLM 10046) and *Russula pakaraimaeae* (Holotype TWH 9503) within a representative *Russula* sampling scaffold inferred from ITS sequence alignments. The newly described taxa are indicated in red letters and the *R. gelatinivelata* clade is highlighted in red. The tree is rooted with *Multifurca ochricompacta*. Voucher designation, locale, and sequence accession numbers for GenBank and Unite are provided with the OTU designation at the terminus of each branch. Bayes branch support values equal to or greater than 0.95 (first number) and Bootstrap support values greater than or equal to 80% for maximum likelihood (second number) are given at the nodes. * Indicates Bayes support of 1 and Bootstrap support of 100%. The scale bar indicates expected changes per site.

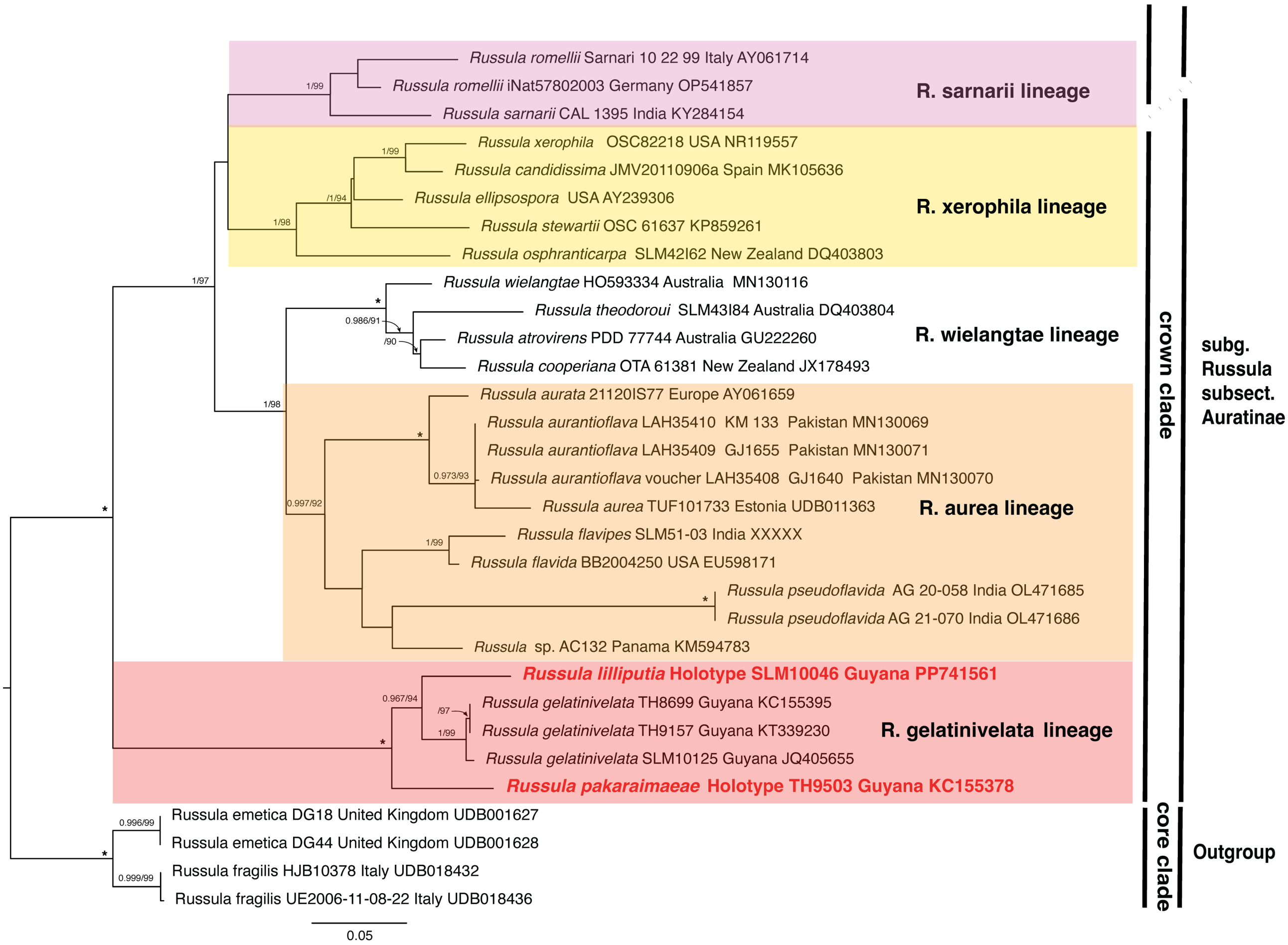

FIGURE 2. Maximum likelihood consensus tree showing the position of newly described *Russula lilliputia* (Holotype SLM 10046) and *Russula pakaraimaeae* (Holotype TWH 9503) within an expanded sampling of *Russula* species from the *R. aurea* and *R. wielangtae* lineages *fide* Adamčík *et al.* (2019) inferred from ITS sequence alignments. The newly described taxa are indicated in red letters and the *R. gelatinivelata* clade is highlighted in red. The tree is rooted with *R. emetica* and *R. fragilis* from the core clade of *Russula*. Voucher designation, locale, and sequence accession numbers for GenBank and Unite are provided with the OTU designation at the terminus of each branch. Bayes branch support values equal to or greater than 0.95 (first number) and Bootstrap support values greater than or equal to 80% for maximum likelihood (second number) are given at the nodes. * Indicates Bayes support of 1 and Bootstrap support of 100%. The scale bar indicates expected changes per site.

Macroscopic description:—*Pileus* 3–5 mm broad, convex young, then broadly convex, plane or slightly depressed; margin incurved at first, then decurved, entire when young, then frequently lacerate with age, not striate young, sulcate striate when older, striations 1–2 mm in length; pellis dry to moist, pruinose at margin when young, subvelutinous to scurfy in age, disk of primordia pale red to pastel red (9A3–4) with white margin, then brownish red (9C–6–8) overall or with center of disk reddish brown (9E–6–8; 9F6–8), cuticle separability not determined. *Lamellae* 1–2 mm broad at mid-radius, sinuate, subdistant, not forking at stipe, lamellulae absent but occasionally anastomosing near the cuticle, margin entire, white. *Stipe* 7.5–10 × 2–3 mm, equal slightly tapered to base, terete to straight cylindrical to slightly curving, attachment central, dry, densely pruinose to subhispid overall, white (i.e., concolorous with lamellae); trama in stipe stuffed, soft. *Context in pileus* 1 mm at mid-radius soft and pliant, white. *Odor* not detected. *Taste* mild, fungal. *$FeSO_4$* yellow on stipe surface. *Spore print* white.

Microscopic description:—*Basidiospores* 6.8–8 × 6.4–7.2 µm, (x = 7.4 x 6.8 µm, Q = 1.06–1.11, $Q_{m'}$ = 1.0), subglobose to broadly ellipsoid; ornamentation of widely distributed, mostly isolated, acute, narrowly conical elements that are occasionally broader at the base, 1.5(–2) µm high, with scarce low connections, amyloid; suprahilar plage large and verruculose, not decurrent on the apiculus. Basidia (24) 27–29 (–36) × 8–11 (13) µm, clavate to subcylindrical, 4-spored, sterigmata long, 8–12 × 1.6–2 µm. *Hymenial cystidia* 43–60 × 10–13 µm, subclavate to cylindrical, obtuse to capitate, thin-walled, some long, arising deep within the lamella trama, others shorter, arising in hymenium, emergent 10–35 µm above basidia, scattered to patchy (400–600/mm^2), greyish black in SV. *Marginal cells* 85–90 × 15–20

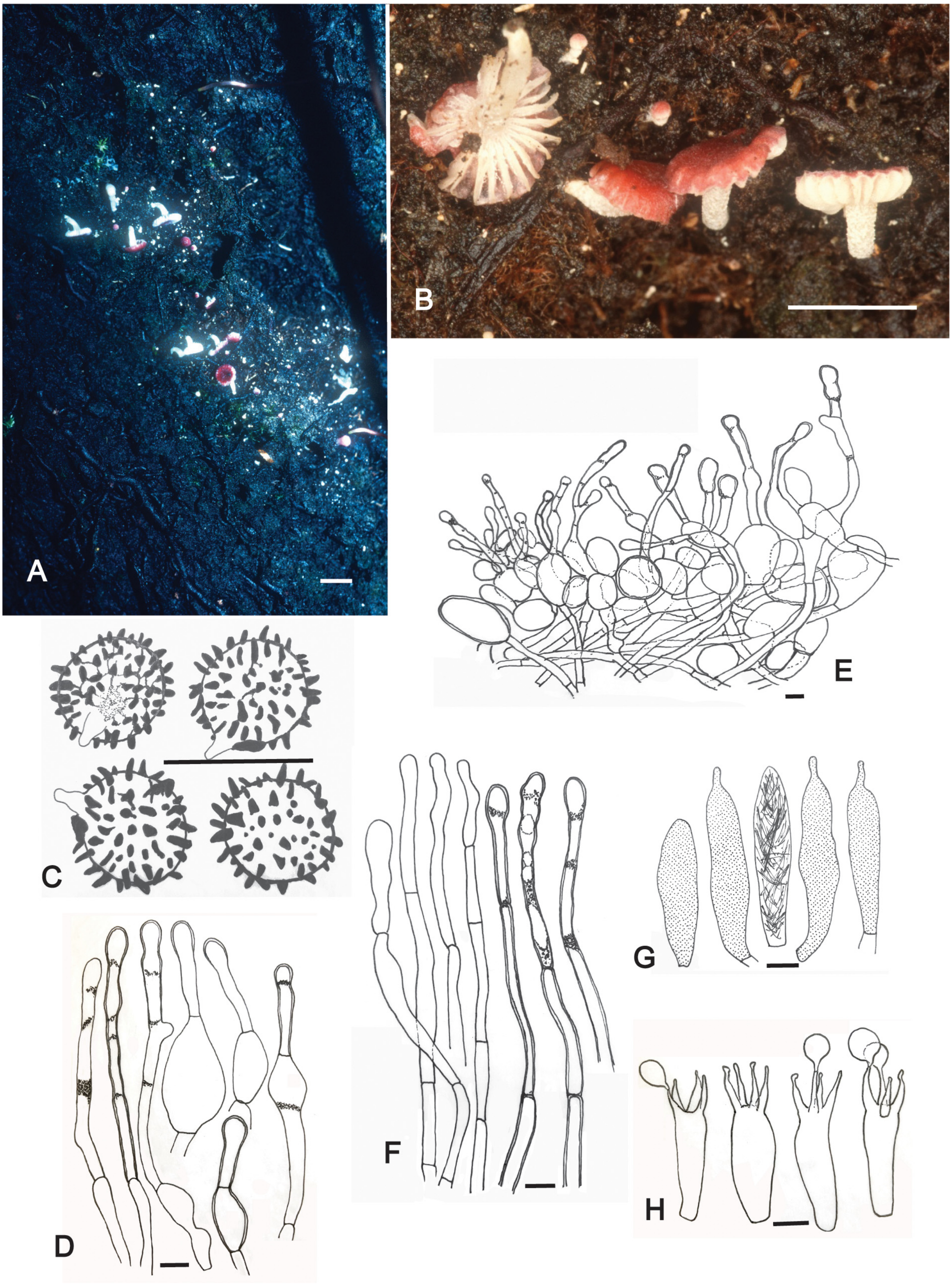

FIGURE 3. Macroscopic and microscopic features of ***Russula lilliputia*** (**holotype** SLM 10046). **A–B.** Macroscopic features. **A.** Primordia and mature basidiomata fruiting *in situ* on the trunk of *Dicymbe altsonii*; **B.** Macroscopic features of primordia and mature basidiomata. Scale bars = 5 mm. **C–H.** Microscopic characteristics **C.** Basidiospores; **D.** Pileocystidia; **E.** Diagram of a section of the pileipellis; **F.** Caulocystidia; **G.** Hymenial cystidia; **H.** Basidia and basidioles Scale bars = 10 µm.

µm, fusiform, mucronate, strongly emergent, mixing with small basidia, numerous. *Subhymenium* well developed of small tightly packed spherical cells of 10 µm diam *Lamellar trama* composed of many large sphaerocytes, and nests of relatively small, nearly isodiametrical sphaerocytes, interwoven with cylindrical hyphae. *Pileipellis* orthochromatic in Cresyl Blue, two-layered; subpellis of slightly gelatinized interwoven hyphae of 4–5 µm diam intergrading with discrete regularly spaced rosettes, these often encrusted with reddish brown pigment in KOH; suprapellis arranged in a loose trichoderm from pileus center to pileus margin, composed of frequently branching spindly, digitate hyphae, 5–12 µm diam, cylindrical to clavate, obtuse or capitate and often sinuous and irregularly constricted, often multi-septate, thin- or moderately thickened walls, arising from large inflated, ellipsoidal to spherical cells, 20–35 × 8–20µm, 2–6 deep in aggregate resembling an epithelium, these easily disarticulated in microscopic preparations; *Pileocystidia* 50–100 µm, long pedicellate, septate, irregularly constricted or swollen at the septum, banded with refringent contents particularly near the septa, moderately thick-walled, arising deep in the trama, SV– or turning pale grey, the contents or interior of the walls acid resistant in BF, no incrustations were observed. *Stipitipellis* resembling the pileipellis but lacking the swollen elements, composed of dense clusters of long branching, septate, digitate or slightly capitate to irregularly shaped hyphae, and pedicellate, septate, thick-walled caulocystidia that are cylindrical, clavate, obtuse and irregularly constricted.

Habit, habitat, and distribution:—Scattered across the trunk surface 1.5 m above the base of a *Dicymbe altsonii* Sandwith tree. Known only from a single large collection, Upper Potaro Basin of Guyana.

We feel confident for several reasons in describing *R. lilliputia* as a new taxon from a single collection. The type collection was comprised of all stages of basidiome development which included approximately thirty individual basidiomata and primordia distributed across a half-meter-square area of trunk surface 1.5 m above the base of a *Dicymbe altsonii* tree. The primordia were more numerous than the expanded basidiomata, and the largest basidiomata were never observed to be larger than 5 mm in diameter before beginning to senesce. Importantly, all of the largest basidiomata produced an easily observable white spore print on an acetate sheet, indicating that the basidiomata were mature and not just slightly expanded primordia. BLAST similarity searches on GenBank recovered no close matches. Further, our ITS analyses (not all of which are shown), including all of the red, reddish, or reddish orange *Russula* collections from our collecting sites in Guyana, along with another newly described red species, *R. rubroglutinata* S.L. Mill, T.W. Henkel & Aime, *ined*., included in the present analysis, indicated that *R. lilliputia* is distinct.

Russula pakaraimaeae S.L. Mill. & T.W. Henkel ***sp. nov.*** (Fig 4)

Mycobank: 854654.

Diagnosis: Russula pakaraimaeae is characterized by its small stature (pileus 5–17 (25) mm), its occurrence in the Upper Mazaruni Basin of Guyana in fringe forests surrounding the Pegaima savanna in association with *Pakaraimaea dipterocarpaceae* and possibly *Dicymbe jenmanii*, by its fruiting habit with branching or single rhizoidal base attached to large fallen leaves and organic debris, by its dark red to brownish violet pileus with pruinose white margin when young, stipe viscid in wet conditions wet then with appressed fibrillose squamules often flushed pinkish when conditions are dry, spores of isolated verrucae with no interconnections and a distinct suprahilar plage that occasionally forms a partial collar on the apiculus, by its long hairlike pileocystidia arising from scattered swollen cells.

Etymology: in reference to the occurrence in forests fringing savanna dominated by *Pakaraimaea dipterocarpacea* (Cistaceae).

Holotype: GUYANA. Pakaraima Mountains, Upper Mazaruni River Basin, fringing forest around the Pegaima savanna, 0.5 km S of Pegaima base camp located at 5° 26′ 21.3″ N; 60° 04′ 43.1″ W, ~800 m elevation; under *Pakaraimaea dipterocarpacea* and *Dicymbe jenmanii*, 21 December 2010, *T.W. Henkel 9503* (**holotype** BRG; **isotypes** HSCF 004453, RMS). GenBank ITS KC155378.

Macroscopic description:—*Pileus* 5–17(25) mm broad, first convex and sometimes mammilate, then broadly convex to slightly depressed, with or without umbo; margin decurved, entire but markedly pruinose when young, then frequently minutely lacerate or crenulate with age, smooth to obscurely striate when young, faintly plicate to subsulcate when older, striations 2–4 mm in length; pellis dull to shiny, heavily pruinose when young especially toward the margin, viscid when wet, subfloccose to subtomentose when dry, matted toward the margin, dark red (11C6–11C7) to brownish violet (11D7–8) to violet brown (11F7–8) with extreme margin white when young, then red to dark red or brownish red(10B7–10D7,8) when expanded, disk and umbo remaining violet brown (11E6–11F8). *Lamellae* 1–2 mm broad at mid-radius, adnate to slightly sinuate to subdecurrent, close to subdistant, entire, white when young, eventually pale yellow (3A 2–3); lamellulae rare to absent. *Stipe* 14–33 (48) × 1.5–3 (5) mm, equal or more typically tapered to single or branching rhizoid-like base, attachment central, even to slightly irregular, flattening, canaliculate with age, pruinose above, middle portions with white to pink appressed fibrillose squamules, base subtomentose, white to cream (3A 2–3) at apex (i.e. concolorous with lamellae, middle portions overlain with pale red areolae frequently in a stretch-mark like

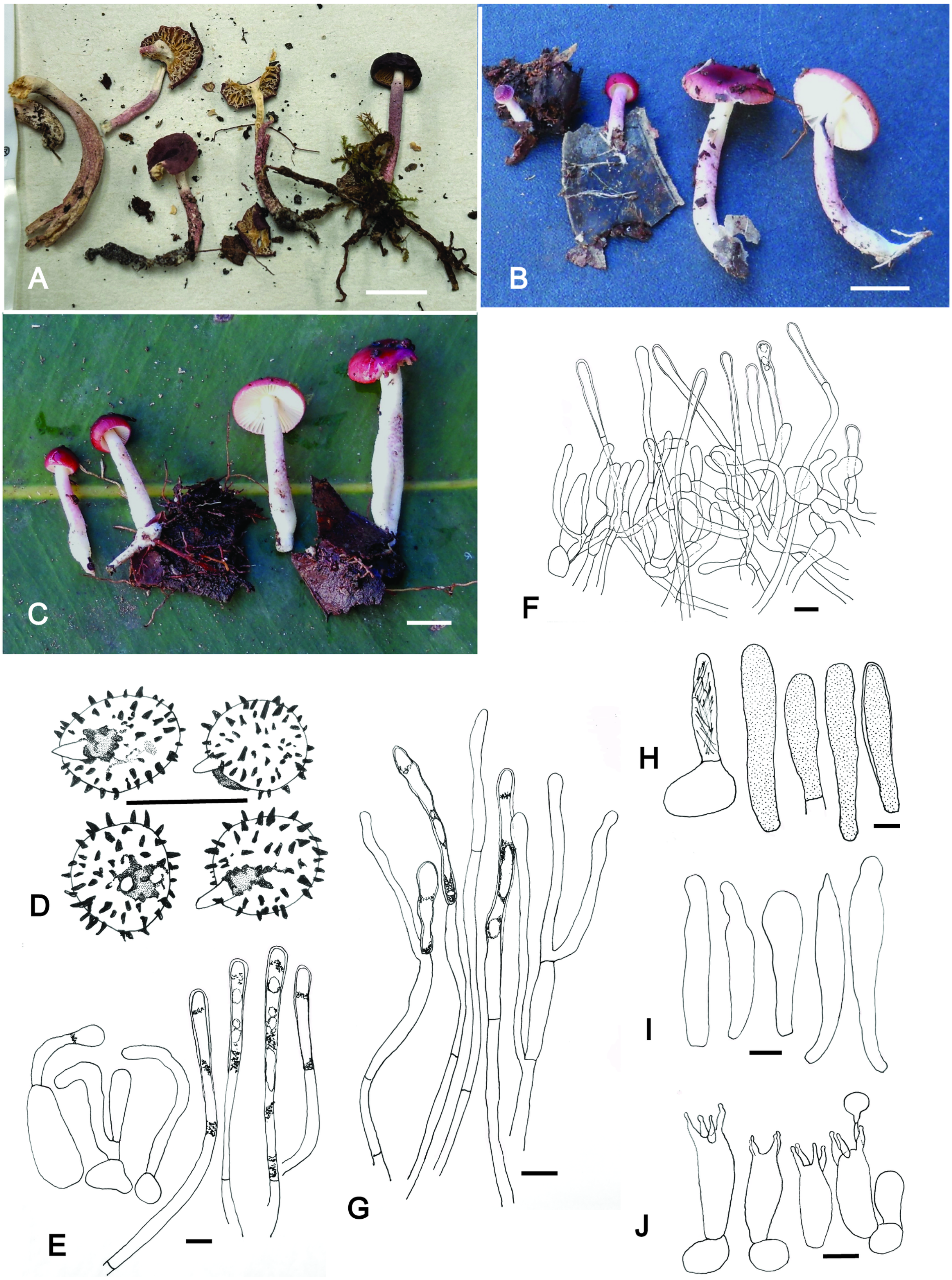

FIGURE 4. Macroscopic and microscopic features of ***Russula pakaraimaeae***. **A–C.** Macroscopic features. **A.** Dried herbarium collection of the holotype, TH9503; Note: no photos were taken of fresh basidiomata; **B.** Basidiomata developing from hyphal cords inhabiting coarse leaf litter of *Pakaraimaea dipterocarpacea*, TH9515; **C.** Basidiomata developing from hyphal cords inhabiting coarse leaf litter of *Pakaraimaea dipterocarpacea*, TH9548. Scale bars = 1 cm. **D–J.** Microscopic characteristics of ***Russula pakaraimaeae*** (holotype TH9503). **D.** Basidiospores; **E.** Pileocystidia; **F.** Diagram of a section of the pileipellis; **G.** Caulocystidia; **H.** Hymenial cystidia; **I.** Marginal cells; **J.** Basidia and basidioles. Scale bars = 10 µm.

pattern over a white or yellowish white (3A2) ground; the base concolorous with the apex; viscid in wet conditions. Context in pileus 1–1.5 mm at mid-radius pliant, white, pale pink immediately below cuticle, especially at disk; trama in stipe stuffed at maturity, outer cylinder pale yellow surrounding white central core; odor mild; taste mild to faintly sweet or slightly bitter; $FeSO_4$ not noted.

Microscopic description:—*Basidiospores* 7.2–8.8 × 5.8–7.04 (x= 7.96 × 6.4, Q = 1.25–1.3, Qm=1.25), broadly ellipsoid; ornamentation of widely distributed, isolated, acute, narrowly conical elements, 1.5–2(–2.5) µm high, amyloid, darkest near the apiculus; suprahilar plage large and verruculose, not or forming a collar on the apiculus. *Basidia* 25–3 × 8–10 µm, subcylindrical to clavate, 4-spored, sterigmata long, 6.4–10 × 1.5–1.9 µm. *Hymenial cystidia* 35–50 × 6–8 µm, cylindrical, subclavate to clavate, obtuse to capitate, or occasionally rostrate, mostly thin-walled, some thick-walled, some long, arising deep within the lamella trama, others shorter arising in hymenium, emergent 2–40 µm above basidia, scattered to numerous 800-1000 per mm^2, SV–. *Marginal cells* 45–75 × 7–13 µm, subclavate, fusiform, mucronate or irregular, strongly emergent, mixing with small basidia, moderately numerous. Subhymenium well developed of small tightly packed spherical cells of 10 µm diam. Lamellar trama composed of many large sphaerocytes,and nests of relatively small, nearly isodiametrical to globose sphaerocytes, interwoven with cylindrical hyphae. *Pileipellis*, two-layered; subpellis of slightly interwoven inflated to swollen hyphae of 6–15µm diam; suprapellis arranged in a loose trichoderm from pileus center to pileus margin composed of infrequently branching spindly hyphae, 5–12 µm diam, cylindrical to clavate or digitate, obtuse or sinuous and irregularly constricted, often multi-septate, thin- or thick-walled, often arising from inflated cells; *Pileocystidia* 50–250 µm × 3–5 µm obtuse digitate or capitate, pedicellate, septate, irregularly constricted or swollen at the septum, banded with refringent contents particularly near the septa, thin-or thick-walled, arising deep in the trama but extending 120–160 µm above the surface of the pellis, these easily disarticulated in microscopic preparations, SV- to pale grey, orthochromatic in Cresyl Blue, the contents or interior of the walls acid resistant in BF, no incrustations were observed. *Stipitipellis* resembling the pileipellis, composed of branching, septate, irregularly shaped hyphae that taper at the apex, and long pedicellate, septate, thick-walled caulocystidia that are cylindrical, digitate, clavate, obtuse or capitate and irregularly constricted 50–250 µm.

Habit, habitat, and distribution:—Solitary or in small troops in December on humic matter and large fallen leaves on forest floor in ECM *P. dipterocarpacea*/*Dicymbe jenmanii* savanna fringing forests, or in stands with only *P. dipterocarpacea*. Sequences corresponding to *R. pakaraimaeae* have also been found from the sampling of ectomycorrhizal roots at the Pegaima savanna (Smith *et al.* 2013). Known only from the type locality in the Upper Mazaruni Basin of Guyana.

Additional specimens examined:—GUYANA. Pakaraima Mountains, Upper Mazaruni River Basin, fringing forest around the Pegaima savanna, within a 1.5 km radius of Pegaima base camp located at 5° 26′ 21.3″ N; 60° 04′ 43.1″ W, ~800 m elevation; 0.1 km N of base camp in pure stand of *Pakaraimaea dipterocarpacea*, 22 December 2010, *T.W. Henkel 9515* (BRG; HSCF 004454; RMS); 1.5 km SW of base camp in pure stand of *Pakaraimaea dipterocarpacea*, 26 December 2010, *T.W. Henkel 9548* (BRG; HSCF 004455; RMS).

Discussion

Ectomycorrhizal fungi (ECM) historically were considered poorly represented in Neotropical forests; however, pockets of forests occupying the white sands region of the central Guiana Shield of Guyana are dominated by leguminous ECM trees that support a tremendous biodiversity of fungi (Henkel *et al.* 2012). Documenting this fungal biodiversity is not easy – requiring much planning, arduous travel, effort, and support, so documenting new additions to this fungal biodiversity is critical. In Guyana, Russulaceae comprise the greatest number of species in this area. The discovery of two new interesting species of *Russula* in Guyana expands our understanding of fungal diversity and the genus *Russula* in particular, along with the biogeography, and ecosystem dynamics in often under collected tropical forests.

The diminutive size of the mature *R. lilliputia* basidiomata and the fruiting habit at 1.5 height on a tree trunk makes this an unusual fungus. Heim (1970) referred to the African *R. annulata* and *R. radicans* species complexes as "lilliputiennes" because of their small size, which he detailed as "on the order of 1 to 2 cm". Buyck (1990a: 322) called attention to the small sizes of a number *Russula* species from Africa, which ranged between 15–20 mm. Based on the only collection we have ever encountered after over twenty years of collecting in this area, basidiomata of *R. lilliputia* are significantly smaller than those, making this new species likely the most diminutive species of *Russula* heretofore described.

Although distinct, *R. lilliputia* is most closely related to *R. gelatinivelata*. Macroscopically both are predominantly red with a subvelutinous or scurfy surface. However, the size difference is decidedly marked, with *R. lilliputia* not exceeding 5 mm in mature pileus diam, and *R. gelatinivelata* typically much larger, ranging from 3–5.5 cm in mature pileus diam. They differ in the margin of the pileus, with *R. gelatinivalata* having a thick gelatinous partial veil when young, while the margin of *R. lilliputia* is densely pruinose. The stipe of *R. lilliputia* is white with a densely pruinose surface overall, matching the ornamentation of the pileus margin when young, while the stipe of *R. gelatinivelata* is gelatinous over the lower one-half becoming subtomentose and conspicuously areolate below, often with a pinkish or reddish flush. The spore print in subsect. *Auratinae* can vary from white to dark ochre. Both *R. lilliputia* and *R. gelatinivelata* have a white spore print. Similarly, taste in members of subsect. *Auratinae* can vary from mild to strongly acrid. *Russula lilliputia* is mild in taste while *R. gelatinivelata* is slightly bitter.

Russula pakaraimaeae is overall very similar in appearance to *R. gelatinivelata* with the red pileus, and viscid stipe flushed with red, but is much smaller, and is intermediate in size to the pileus of *R. lilliputia*, which does not exceed 5 mm, and *R. gelatinivelata* which is larger. Both *R. gelatinivelata* and *R. lilliputia* have a bilayered pellis with a suprapellis that in many ways resembles an epithelium or lampropalisade found in *Lactifluus* due to the abundant layer of large inflated to spherical cells that give rise to long cylindrical or digitate and sinuous, thin or thick-walled pileocystidia. The suprapellis of *R. pakaraimaeae* contains similar long pileocystidia, which occasionally arise from somewhat inflated cells, but the appearance is more of a tangled trichoderm comprised of moderately to highly inflated hyphae that do not resemble an epithelium in section. The pileocystidia of all three species are uniquely similar in that they are all very long and hairlike, resulting in the subtomentose appearance in dry environmental conditions, and the interior wall or contents retain acid resistant red coloration in BF. While they do not form incrustations *per se* on the suprapellis elements as in some *Russula* species, *e.g.*, subgen. *Incrustatula* (Romagnesi 1985: 508), the BF reaction along with other distinctive elements of the suprapellis are obvious synapamorphies for the clade. The spores of all three species possess similar spore ornamentation comprised of isolated verrucae and a suprahilar plage. *Russula lilliputia* spores differ from those of the other two species in having a relatively indistinct suprahilar plage and scarce, very low connections on some spores, whereas the suprahilar plage on spores of the other two species is much larger and more distinct and the spores have no connections between verrucae. The suprahilar plage in *R. pakaraimaeae* often forms at least a partial collar on the apiculus.

All three species in the *R. gelatinivelata* lineage are regionally restricted to specific habitats within Guyana: both *R. lilliputia* and *R. gelatinivelata* have only been found in the Potaro River Basin in wet tropical forests in association with the ECM legume tree genus *Dicymbe* – *R. gelatinivelata* occurs with *D. corymbosa* and *D. altsonii*, while *R. lilliputia* has thus far only been found in association with *D. altsonii*; *R. pakaraimaeae* has thus far only been found in the Pegaima savanna fringe forests of the Mazaruni River Basin in association with ECM *P. dipterocarpacea* and possibly *D. jenmanii.*

Analyses of the internal transcribed spacer region (ITS) placed *R. lilliputia* and *R. pakaraimaeae* within the crown *Russula* clade *fide* Looney *et al.* (2016) with full support alongside *R. gelatinivelata*. The *R. gelatinivelata* lineage is highly supported as sister to subsect. *Auratinae sensu* Gosh *et al.* (2023). Among other features, species in this group often have multiple colors intermixed in the pileus, typically a red, orange, violet, or green mixed with yellow. *Russula gelatinivelata* occasionally expresses a red to reddish violet color with a mottled yellow disc, however, this feature is not exclusive to this group. The epithelioid pileipellis giving rise to distinctive thick-walled pileocystidia found in the three species in this lineage is different from most previously described taxa in subsect. *Auratinae,* which typically have no or indistinct pileocystidia (see for example *R. romellii* Maire 1910: 105) and oddly contorted "hyphal terminations" throughout the pileipellis or often only near the pileus margin (see for example *R. wielangtae* G.M Gates, Caboň, & Jančovičová (Adamčík *et al.* 2019), which the *R. gelatinivelata* lineage lacks. However, recent members of subsect. *Auratinae* described from Australia and New Zealand including: *R. discolor* Buyck & Bougher (Buyck *et al.* 2023: 8), and especially *R. atroviridis* Buyck (Buyck 1990: 202; but redescribed in Buyck *et al.* 2023: 14) have been described as having a pseudoparyenchymatic suprapellis with numerous swollen cells subtending hyphal extremities in chains. This type of suprapellis could be interpreted as having some similarity to the epithelioid suprapellis of the *R. gelatinivelata* lineage. In particular, the hyphal terminations of the pileipellis of *R. atroviridis* illustrated in Buyck *et al.* (2023: 15), are described as "forming 'hairs' that extend up to more than 100 µm and are strongly emergent, the uppermost 1–2 cells banded with refringent contents (pigments ?), particularly near the septa; the terminal cell mostly narrowing, up to 40 µm long, sometimes subcapitate (and reminiscent of mucronate pileocystidia)," and bear a resemblance to the pileocystidia found in the *R. gelatinivelata* lineage. Unfortunately, the exact placement of *R. atroviridis* is in a state of complex confusion because of potential synonymy, misinterpretation and use of misidentified or mislabeled sequences in GenBank in a number of papers. In attempting to resolve this confusion, Buyck *et al.*

(2023) suggests that the true *R. atroviridis* from New Zealand is best placed in subsect. *Tricholomopsidum* Buyck & V. Hofst. (Das *et al.* 2017: 532), which is far removed from subsect. *Auratinae* in the *Russula* phylogeny. It should be noted that *R. atroviridis* (=*R. roseostipitata?*) sequences did not turn up in our sequence similarity search in GenBank, so putative similarities of the pileipellis elements with those in the *R. gelatinivelata* lineage require further investigation. Singer *et al.* (1983: 203) described subsection *Epitheliosinae* to accommodate *R. epitheliosa* from Brazil, which has a suprapellis composed of densely arranged, sparsely ramified elements consisting of 2 or 3 ellipsoid to subglobose cells, giving the appearance of an epithelium, which is different than the suprapellis in the *R. gelatinivelata* lineage. Buyck (1990a) pointed out that several tropical African *Russula* spp. possess an epithelium-like pileipellis and described the subsection *Pseudoepitheliosinae* (1990a: 322) to accommodate them along with a newly described species, *R. moyersoenii* Buyck (1990a: 317), from Venezuela. The circumscription of subsect. *Pseudoepitheliosinae* indicated that the suprapellis is formed of closely arranged, erect elements composed of 1–3 spherical to ellipsoidal cells, with occasional rostrate or lageniform terminal cells, and are rarely thick-walled. Heim (1970, fig. 2) illustrated an epithelium-like pileipellis for *R. annulata* ssp. *parasitica* Heim (1970: 64) comprised of "large ellipsoid cystidiform cells that are beaked and filled with red frothy guttules when fresh", that somewhat resembles the suprapellis of members of the *R. gelatinivelata* lineage. Buyck (1990a: 322) combined *R. annulata* ssp. *parasitica* to *Russula parasitica* (Heim) Buyck and included it in his newly created *Pseudoepitheliosinae*. However, members of both subsect. *Epitheliosinae* and subsect. *Pseudoepitheliosinae* fall within subgen. *Heterophyllidia* (Romag.) Buyck & V. Hofst. (Buyck *et al.* 2018: 278), which occupies a more basal position in our *Russula* phylogeny and others previously published (*e.g.*, Looney *et al.* 2016; Adamčik *et al.* 2019; Vidal *et al.* 2019; Zhou *et al.* 2022) and are not closely related to the *R. gelatinivelata* lineage.

Acknowledgments

Funding was provided by the National Science Foundation grant DEB–1050292 to SLM. TWH received funding from the National Science Foundation DEB–0918591, the Smithsonian Institution's Biological Diversity of the Guiana Shield Program, the National Geographic Society's Committee for Research and Exploration, the Linnaean Society of London, and the Humboldt State University. Foundation. Funding from the Explorer's Club Exploration and Field Research grant, a field research gift from W.K. Smith, and NSF DEB–0732968 was provided to MCA. Research permits were granted by the Guyana Environmental Protection Agency. Dillon Husbands functioned as Guyanese local counterpart and assisted with field collecting, descriptions, and specimen processing. Expert field assistance was provided by C. Andrew, L. Edmund, D. Husbands, V. Joseph, P. Joseph, and L. Williams. We are grateful to Terry McClean at the Nucleic Acid Exploration Facility at UW for running the sequences used in this study and for fastidiously aligning an early version of our large *Russula* ITS database. This paper is number 189 in the Smithsonian Institution's Biological Diversity of the Guiana Shield Program publication series.

References

Adamčík, S., Caboň, M., Eberhardt, U., Saba, M,, Hampe, F., Slovák, M., Kleine, J., Marxmüller, H., Jančovičová, S., Pfister, D.H., Khalid, A.N., Kolařík, M., Marhold, K. & Verbeken, A. (2016a) A molecular analysis reveals hidden species diversity within the current concept of *Russula maculata* (Russulaceae, Basidiomycota). *Phytotaxa* 270 (2): 71–88. https://doi.org/10.11646/phytotaxa.270.2.1

Adamčík, S., Slovákm, M., Eberhardt, U., Ronikier, A., Jairus, T., Hampe, F. & Verbeken, A. (2016b) Molecular inference, multivariate morphometrics, and ecological assessment are applied in concert to delimit species in the *Russula clavipes* complex. *Mycologia* 108: 716–730. https://doi.org/10.3852/15-194

Adamčík, S., Looney, B., Caboň, M., Jančovičová, S., Adamčíková, K., Avis, P.G., Barajas, M., Bhatt, R.P., Corrales, A., Das, K., Hampe, F., Ghosh, A., Gates, G., Kälviäinen, V., Khalid, A.N., Kiran, M., De Lange, R., Lee, H., Lim, Y.W., Kong, A., Manz, C., Ovrebo, C., Saba, M., Taipale, T., Verbeken, A., Wisitrassameewong, K. & Buyck, B. (2019) The quest for a globally comprehensible *Russula* language. *Fungal Diversity* 99: 369–449. https://doi.org/10.1007/s13225-019-00437-2

Bon, M. (1988) Monographic key for European Russulae. *Documents Mycologiques* 18 (71–72): 1–125.

Buyck, B. (1990a) New taxa of tropical Russulae: *Pseudoepitheliosinae* subsect. nov. *Mycotaxon* 39: 317–327.

Buyck, B. (1990b) Nouveaux taxons infragénériques dans le genre *Russula* Persoon en Afrique centrale. *Bulletin Jardin Botanique National de Belgique* 60: 191–211.
http://dx.doi.org/10.2307/3668341

Buyck, B. (1994a) *Russula* I. (Russulaceae). *In* Rammeloo, J. & Heinemann, P. (Eds.) *Flore Illustrée des Champignons d'Afrique Centrale.* Vol. 15. pp. 335–408.

Buyck, B. (1994b) *Russula* II. (Russulaceae*). In:* Rammeloo, J. & Heinemann, P. (Eds.) *Flore Illustrée des Champignons d'Afrique Centrale.* Vol. 16. pp. 411–542.

Buyck, B., Hofstetter, V., Eberhardt, U., Verbeken, A. & Kauff, F. (2008) "Walking the thin line between *Russula* and *Lactarius*: the dilemma of *Russula* sect. *Ochricompactae*". *Fungal Diversity* 28: 15–40.

Buyck, B., Zoller, S. & Hofstetter, V. (2018) Walking the thin line ten years later: The dilemma of above-versus below-ground features to support phylogenies in the Russulaceae (Basidiomycota). *Fungal Diversity* 89: 267–292.
https://doi.org/10.1007/s13225-018-0397-5

Buyck, B., Hofstetter, V., Horak, E., Cooper, J. & Bougher, N. (2023) The search for Australian relatives of the eucalypt-associated *Russula prolifica* (Russulales) from Madagascar reveals new Oceanian taxa in subsection *Auratinae*. *Australian Journal of Taxonomy* 47: 1–25.
https://doi.org/10.54102/ajt.1rdyq

Das, K., Gosh, A., Bhatt, R.P., Chakraborty, D., Hofstetter, V. & Buyck, B. (2017) Fungal Biodiversity Profiles 41–50. *Cryptogamie, Mycologie* 38: 527–547.

Gosh, A., Buyck, B., Chakraborty, D., Hembrom, M.E., Bera, I. & Das, K. (2023) Three new species of genus *Russula* Pers. from Sal dominated forests of tropical India based on morphotaxonomy and multigene phylogenetic analysis. *Cryptogamie, Mycologie* 44 (3): 27–50.

Heim, R. (1937a) Les Lactario-Russulés du domaine oriental de Madagascar. *Prodrome à une flore mycologique de Madagascar et dépendances* 1: 1–196.

Heim, R. (1937b) Observations sur la flore mycologique malgache V. Les Lactario-Russules a anneau: Ontogenie et phylogenie III. *Revue de Mycologie (Paris)* 2: 61–75.

Heim, R. (1938) Diagnoses latine d'espèces et variéte Nouvelles de Lactario-russulés du domaine oriental de Madagascar. *Candollea* 7: 374–393.

Heim, R. (1970) Particularités remarquables des Russules tropicales Pellicularíae lilliputiennes; les complexes annulate et radicans. *Bulletin. Sociéte Mycologique de France* 86: 59–77.

Henkel, T.W., Aime, M.C. & Miller, S.L. (2000) Systematics of pleurotoid Russulaceae from Guyana and Japan, with notes on their ectomycorrhizal status. *Mycologia* 92: 1119–1132.
http://dx.doi.org/10.2307/3761479

Henkel, T.W., Aime, M.C., Chin, M., Miller, S.L., Vilgalys, R. & Smith, M. (2012) Ectomycorrhizal fungal sporocarp diversity and discovery of new taxa in *Dicymbe* monodominant forests of the Guiana Shield. *Biodiversity and Conservation* 21: 2195–2220.
http://dx.doi.org/10.1007/s10531-011-0166-1

Hoang, D.T., Chernomor, O., von Haeseler, A., Minh, B.Q. & Vinh, L.S. (2018) UFBoot2: Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution* 35 (2): 518–522.
https://doi.org/10.1093/molbev/msx281

Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K.F., von Haeseler, A. & and Jermiin, L.S. (2017) ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods* 14: 587–589.
https://doi.org/10.1038/nmeth.4285

Katoh, K. & Standley, D.M. (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30: 772–780.
https://doi.org/10.1093/molbev/mst010

Kornerup, A. & Wanscher, J.H. (1981) *Methuen handbook of colour.* 3rd ed. London: Eyre Methuen. 252 pp.

Looney, B.P., Ryberg, M., Hampe, F., Sánchez-García, M. & Matheny, P.B. (2016) Into and out of the tropics: global diversification patterns in a hyperdiverse clade of ectomycorrhizal fungi. *Molecular Ecology* 25: 630–647.

Lücking, R & Hawksworth, D.L. (2018) Formal description of sequence-based voucherless Fungi: promises and pitfalls, and how to resolve them. *IMA Fungus* 9: 143–165.

Maire, R. (1919) *Russula romellii*. *Bulletin de la Société mycologique de France* 26: 105.

Miller, S.L. & Buyck, B. (2002) Molecular phylogeny of the genus *Russula* in Europe with a comparison of modern infrageneric classifications. *Mycological Research* 106: 259–276.
https://doi.org/10.1017/S0953756202005610

Miller, S.L. & Henkel, T.W. (2004) Biology and molecular ecology of subiculate *Lactarius* species from Guyana. *In:* Cripps, C.L. (Ed.) *Fungi in Forest Ecosystems– Systematics, Diversity, and Ecology*. Memoirs of the New York Botanic Garden, vol. 89. pp. 297–313.

Miller, S.L., Aime, M.C. & Henkel, T.W. (2002) Russulaceae from the Pakaraima Mountains of Guyana. I. New species of pleurotoid *Lactarius*. *Mycologia* 94: 545–553.
http://dx.doi.org/10.2307/3761789

Miller, S.L., Aime, M.C. & Henkel, T.W. (2012) Russulaceae of the Pakaraima Mountains of Guyana 2. New Species of *Russula* and *Lactifluus*. *Mycotaxon* 121: 233–253.

Miller, S.L., Larsson, E., Larsson, K.-H., Verbeken, A. & Nuytinck, J. (2006) Perspectives in the new Russulales. *Mycologia* 98: 960–970.
http://dx.doi.org/10.3852/mycologia.98.6.960

MycoBank (2024) "*Mycobank: Russula*", International Mycological Association. Available from: https://www.mycobank.org (accessed 1 May 2024)

Nguyen, L.-T., Schmidt, H.A., von Haeseler, A. & Minh, B.Q. (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum likelihood phylogenies. *Molecular Biology and Evolution* 32: 268–274.
https://doi.org/10.1093/molbev/msu300

Okonechnikov, K., Golosova, O., Fursov, M. & the UGENE team (2012) Unipro UGENE: a unified bioinformatics toolkit. *Bioinformatics* 28: 1166–1167.
https://doi.org/10.1093/bioinformatics/bts091

Persoon, C.H. (1796) Descriptiones tam novorum quan notabilium fungorum. *Observations Mycologicae* 1: 1–221.

Romagnesi, H. (1985) *Les Russules d'Europe et d'Afrique du Nord*. Reprint with supplement. J. Cramer, Lehre. 1030 pp.

Singer, R. (1952) Russulaceae of Trinidad and Venezuela. *Kew Bulletin* 7: 295–301.
http://dx.doi.org/10.2307/4109329

Singer, R. (1986) *The Agaricales in modern taxonomy*. 4th ed. Koeltz Scientific Books, Koenigstein, Germany. 981 pp.

Singer, R., Araujo, I. & Ivory, M.H. (1983) The ectotrophically mycorrhizal fungi of the neotropical lowlands, especially central Amazonia. *Beihefte Nova Hedwigia* 77: 1–352.

Smith, M.E., Henkel, T.W., Uehling, J.K., Fremier, A.K., Clarke, H.D. & Vilgalys, R. (2013) The ectomycorrhizal fungal community in a neotropical forest dominated by the endemic dipterocarp *pakaraimaea dipterocarpacea*. *PLoS ONE* 8 (1): e55160.
https://doi.org/10.1371/journal.pone.0055160

Species Fungorum (2024) "Search Page", Royal Botanic Garden. Available from: www.speciesfungorum.org (accessed May 1 2024)

Trifinopoulos, J., Nguyen, L.-T., von Haeseler, A. & Minh, B.Q. (2016) W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research* 44 (W1): W232–W235.
https://doi.org/10.1093/nar/gkw256

Vidal, J.M., Alvarado, P., Loizides, M., Konstantinidis, G., Chachuła, P., Mleczko, P., Moreno, G., Vizzini, A., Krakhmalnyi, M., Paz, A., Cabero, J., Kaounas, V., Slavova, M., Moreno-Arroyo, B. & Llistosella, J. (2019) A phylogenetic and taxonomic revision of sequestrate Russulaceae in Mediterranean and temperate Europe. *Persoonia* 42: 127–185.
https://doi.org/10.3767/persoonia.2019.42.06

Zhou, H., Cheng, G.-Q., Wang, Q.-T., Guo, M.-J., Zhuo, L., Yan, H.-F., Li, G.-J. & Hou, C.-L. (2022) Morphological Characteristics and Phylogeny Reveal Six New Species in *Russula* Subgenus *Russula* (Russulaceae, Russulales) from Yanshan Mountains, North China. *Journal of Fungi* 8 (12): 1283–1316.
https://doi.org/10.3390/jof8121283