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Russula neoelpidensis, a new sequestrate species and member of the Badia subclade within the Integrae clade

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Abstract

In this paper, we describe a new species of sequestrate *Russula* (*Macowanites*), *R. neoelpidensis*, from the southeastern United States using a combined approach of morphological characterization and phylogenetic analyses. Our molecular analysis places *R. neoelpidensis* in the crown clade in a well-supported Badia subclade nested within Integrae. *Russula neoelpidensis* contains the pink or red staining of the incrustations in Sulfovanillin, which is present in the majority of the analyzed species of Integrae, as well as incrustations in Basic Fuchsin that are not acid resistant. *Russula neoelpidensis* was found in a mixed bottomland hardwood forest containing oaks which may be its ectomycorrhizal partner. *Russula neoelpidensis* is an interesting species with characteristics that both support and extend synapomorphies that could help refine and define formal subgeneric classification systems.

Key words: Badia subclade, *Macowanites*, Russulaceae, *Russula* crown clade, Taxonomy

Introduction

Agaricoid basidiomata are typical mushrooms characterized by the presence of a pileus that is clearly differentiated from the stipe, with gymnocarpic basidiospore formation on lamellae or in tubes on the underside of the pileus that are exposed to the environment (Kirk *et al.* 2008). Sequestrate basidiomata are typically intermediate between agaricoid and angiocarpic morphology and are characterized by production of basidiospores, to one degree or another, within tissue that is not exposed directly to the environment (Trappe & Claridge 2005; Kuhar *et al.* 2023).

Miller *et al.* (2001) were the first to use molecular evidence to show that the russuloid sequestrate genera *Arcangeliella* and *Zelleromyces* have been derived from within the agaricoid genus *Lactarius* and the sequestrate genus *Macowanites* has been derived from within the agaricoid genus *Russula*. For reasons centering on ballistospory *vs.* statismospory and a potential paraphyly conundrum Desjardin (2003) in a seminal paper took the radical step of describing a new sequestrate species as *Lactarius rubriviridis* (2003: 148). That paper arguably served as the turning point for placing sequestrate species within agaricoid genera. While a few authors continued to publish new sequestrate species under sequestrate genera (*e.g.* Josep 2004; Miller & Mitchell 2004; Xu *et al.* 2019) in an attempt to preserve historical, morphological and biological significance of basidiome morphology, others have moved instead to wholeheartedly subsume sequestrate taxa into agaricoid genera (Lebel & Tonkin 2007; Elliott & Trappe 2018). Vidal *et al.* (2019) showed convincingly using a multilocus phylogeny to support multiple convergent evolution of sequestrate basidiome anatomy that russuloid sequestrate taxa could be accommodated within specific subgenera, sections and subsections of the agaricoid genera *Lactarius* and *Russula*.

Based on our knowledge of hypogeous and sequestrate basidiomycetes from the southeastern United States (Miller & Mitchell 2004), along with a sequence similarity search for sequences in GenBank, we concluded that we had found a new undescribed species. This paper describes its phylogenetic relationships delimiting it as a new species.

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Materials and methods

Collection and morphological analyses

Fungi were included in a multi-taxa biodiversity survey of the New Hope Creek Bottomlands and adjacent areas in Durham County North Carolina in 2021–2022 (Hall *et al.* 2022). Over two hundred new fungal records (including lichenized fungi) were documented for this ecologically important area including two collections of the sequestrate *Russula* described herein as a new species.

Basidiomata were collected and examined in the field for fresh characteristics. Color characteristics were coded according to Kornerup & Wanscher (1981; code noted in parentheses). Basidiomata were dried slowly. 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 were observed and measured in Melzer's reagent in side view, excluding ornamentation and apiculus. Basidiospores of *R. neoelpidensis* were bimodal in both size and shape so measurements were based on 40 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 was generally as described in Miller *et al.* (2006). The ITS region of the nuclear ribosomal DNA (nrDNA) cistron was amplified using DreamTaq DNA polymerase according to the manufacturer's protocols (Thermo Fisher Scientific, Waltham, MA) with ITS1f and ITS4 primers. Extraction, amplification and sequencing were provided by the Vilgalys Mycology lab at Duke University.

Phylogenetic analysis

Initial analyses using a large and complete scaffold representing all known clades of *Russula* placed our collections in the crown clade of *Russula*. In order to focus on the most likely placement, the dataset for our phylogenetic analysis was pared down to include ITS sequences of 69 ingroup reference samples forming a minimal representative scaffold of clades from the crown clade of *Russula* based on previous studies *fide* Looney *et al.* (2016), Adamčík *et al.* (2019) and Zhou *et al.* (2022) which were used to analyze the phylogenetic position of our specimens within the genus *Russula*. A sequence similarity search for *R. neoelpidensis* sequences in GenBank (Megablast option), defined as 98% similarity and above was conducted as a means of identifying close taxa including environmental sequences. Sequences were also retrieved from the GenBank database in NCBI and from UNITE based on two recent papers which treated taxa in the Integrae clade and other related clades (Caboň *et al.* 2017, 2018). Six sequences from the core group of *Russula* were used as outgroup taxa. The two new ITS sequences for *R. neoelpidensis* in the present study were assigned GenBank accession numbers PP905596 and PP905597. Accession numbers, voucher numbers, and locale are provided in the OTU line at the terminus of branches. Sequences were first 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 the 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.* 2017), 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 tree was displayed and adjusted in FigTree v 1.4.4 (A. Rambaut *et al.* http://tree.bio.ed.ac.uk/software/figtree/), and the final tree was rendered in Illustrator 2024 (Adobe, Inc., San Jose, CA).

Results

Phylogenetic analyses

The final ITS alignment contained 924 characters including gaps and included 391 parsimony-informative characters. The best-fit substitution model according to BIC was TIM2e+I+G4. The tree search was completed after 236 iterations. Rate parameters were as follows: A–C: 1.5625 A–G: 3.3098 A–T: 1.5625 C–G: 1.0000 C–T: 6.9574 G–T: 1.0000. Base frequencies were: A: 0.250 C: 0.250 G: 0.250 T: 0.250. The log-likelihood of consensus tree was -12082.622045. The ML consensus tree is shown in Fig. 1; Bayes support greater than 0.95 and Bootstrap support values greater than 80% are indicated at the nodes.

The analysis of the ITS sequences (Fig. 1) recovered the Integrae clade *fide* Caboň *et al.* (2017, 2018) with a Bayesian support of 1. Both collections of *Russula neoelpidensis* were nested within the Integrae clade in what has been called the Badia subclade (Caboň *et al*. 2017, 2018) which was delimited at full support of 1/100.

Taxonomy

Russula neoelpidensis S.L. Mill. & Cotter *sp. nov.* (Figs. 2, 3)
MycoBank: 854612

Diagnosis: *Russula neoelpidensis* is characterized by a sequestrate basidiome morphology, cream to pale yellow translucent pileus, pale yellow gleba, percurrent to nearly percurrent stipe-columella, suprapellis and incrustations on the subglobose cells that give rise to pileocystidia that stain pink in Sulfovanillin, basidiospores ellipsoid to narrowly ellipsoid, heterotropic, bimodal in size and shape, ornamentation of isolated, blunt, broadly conical elements, occasionally interconnected with low faintly amyloid bands, suprahilar plage absent. Associated with oaks in the southeastern United States.

Etymology: Latin "neo" meaning "new" and Greek "elpida" meaning "hope" in reference to the New Hope Creek Bottomlands in North Carolina where the fungus was collected.

Macroscopic description:—*Basidiomata* russuloid, partially pseudoangiocarpic, stipitate. *Pileus* 2.2–4.4 cm wide, subglobose to hemispherical, smooth, shiny to mat, translucent, white to yellowish white (4A2), mottled in patches with pale yellow (4A3) where handled; margin closed or laterally open, sublamellate where exposed. *Hymenophore* loculate, yellowish white (3A2–4A2) to pale yellow (4A3), darkening to greyish orange (5B5) to golden yellow (5B8) or so where insect larvae have traveled, locules 0.7–1.8 × 0.15–1 mm (1–3 per mm), larger and more sinuous toward the base and where exposed, irregular, elongated, sinuous, deeply interdigitating with pileus cuticle; fresh spore mass in locules pale yellow to yellow (4A2–A3). *Stipe-columella* 1.5–2.6 × 0.6–1.1 cm, well developed, cylindrical, central, curved, mostly percurrent to percurrent, not branched, white with low rugulose texture on the surface, context white, translucent pale grey or mottled with white and translucent pale grey patches, darker where insect larvae have traveled, irregularly solid, minutely lacunose. Odor and taste not noted.

Microscopic description:—*Basidiospores* bi-modal in size, smaller spores 9.6–10.4 x 7.6–8 µm, x=10.2 x 7.8, Q=1.2–1.4. Qm=1.3, larger spores more numerous 11.2–13.2 x 8–9.6, x=11.9 x 8.6, Q=1.3–1.5, Qm=1.4, ellipsoid to narrowly ellipsoid, heterotropic, ornamentation of isolated, blunt, broadly conical elements, 1–1.5 µm high, occasionally interconnected with low faintly amyloid bands, in Melzer's reagent larger spores staining darker with thicker-walls, hilar appendix 1.3–1.8 × 1.2 µm, conical or cylindrical, straight, frequently with tear-marks at the apex; suprahilar plage absent or indistinct. *Basidia* 2 or 4-spored with 2-spored basidia more abundant, 25–35 × 8–15 µm, broadly clavate; sterigmata 4–7 x 1.3–1.5 µm, basidioles 20–35 × 8–15 µm, clavate. *Hymenial cystidia* common, 40–90 × 7–12 µm, cylindrical, lanceolate or fusiform, rostrate or irregular. *Subhymenium* composed of isodiametric cells 10–20 µm diam. *Hymenophoral trama* 30–50 µm wide, composed of hyaline hyphae 3–8 µm diam, with nests and columns of sphaerocytes 20–36 µm diam. *Pileipellis* two-layered, suprapellis consisting of a pseudoepithelium of loosely arranged subglobose and inflated cells 6–25 µm diam, and hyaline, pileocystidia near the disk cylindrical or clavate 30–80 × 6–10 µm with sand-colored grainy contents in KOH, heavily incrusted but not acid resistant in BF, purplish grey to grey with sparce pink incrustations in SV, entire suprapellis turning pink and spherical cells that give rise to pileocystidia with pink incrustations, hyphal terminations near the margin filamentous, obtuse, scarcely branching, 1–3 celled, 30–60 x 1–3 µm; subpellis consisting of tightly compacted, thick-walled subglobose cells, 8–40 µm diam, not colored or incrusted in SV. *Pileus context* 200–300 µm thick, heteromerous with hyaline hyphae 2–8 µm diam inflated hyphae and sphaerocytes up to 15 µm diam. *Stipitipellis* with numerous large clavate to subclavate dermatocystidial elements, 80–160 x 5–12 µm, medium brownish grey not incrusted in SV, incrusted but not colored in BF, sublayers strongly pink in SV.

Habit, habitat, and distribution—On the ground in mixed bottomland hardwood forest including oaks. Known only from North Carolina, USA.

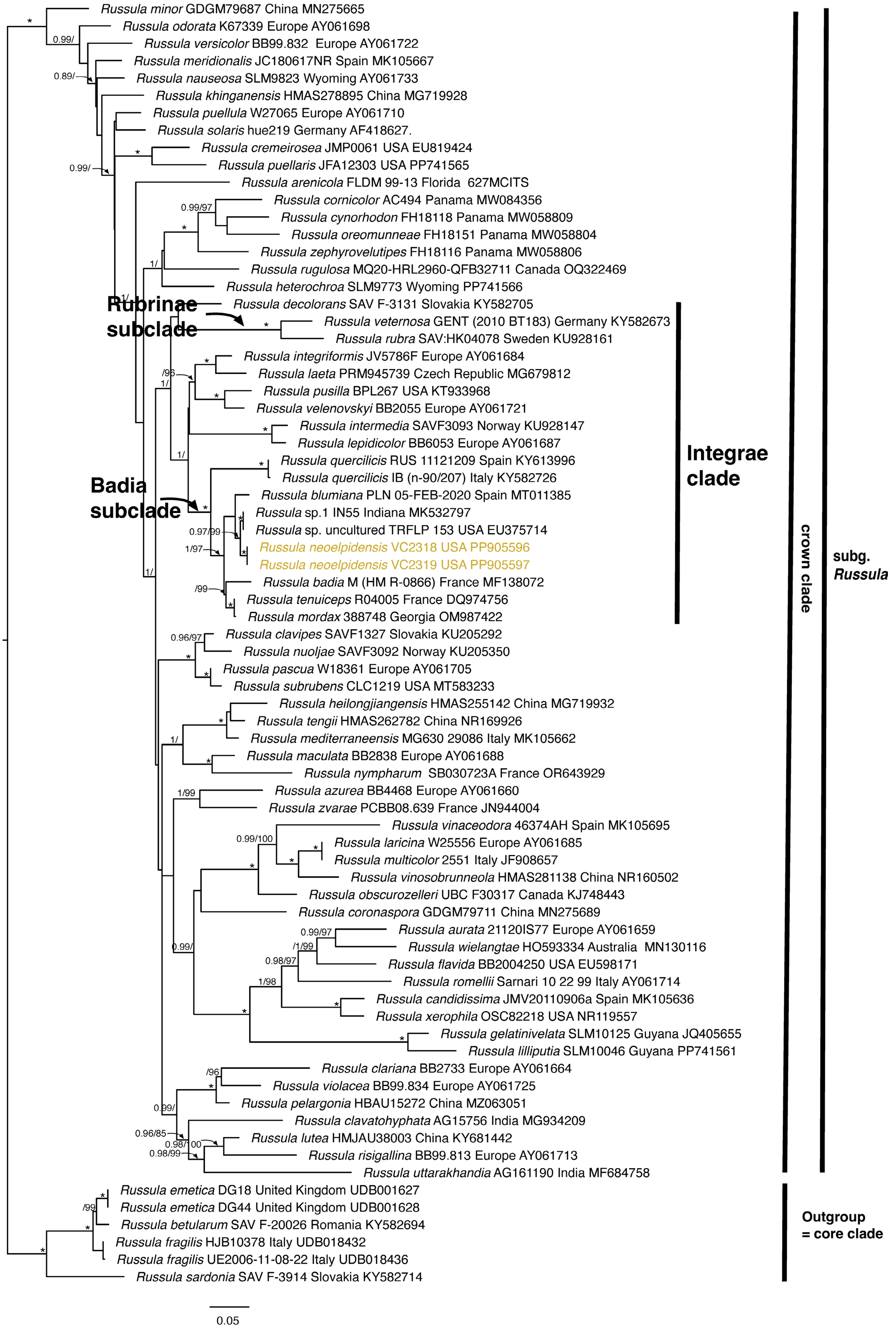

FIGURE 1. Maximum likelihood consensus tree showing the position of ***Russula neoelpidensis*** within a representative *Russula* sampling scaffold inferred from ITS sequence alignments. The newly described taxon, *R. neoelpidensis*, is indicated in orange and the *Russula* Integrae clade is indicated by the line to the right; the nodes for the Badia and Rubrinae subclades are highlighted in bold. The tree is rooted with six members of 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.

Material examined:—USA. Durham County, North Carolina. Along Bottomlands Trail, New Hope Creek Preserve; Latitude: 35.952747, Longitude: -78.981247; collected by H. Van T. Cotter and Meriel Goodwin, 11 October 2021, VC 2318 (holotype DUKE 0378456). GenBank ITS PP905596; same region, Latitude: 35.951033, Longitude:—78.9786; collected by H. Van T. Cotter and Meriel Goodwin, 11 October 2021, VC 2319 (DUKE 0378457). GenBank ITS PP905597.

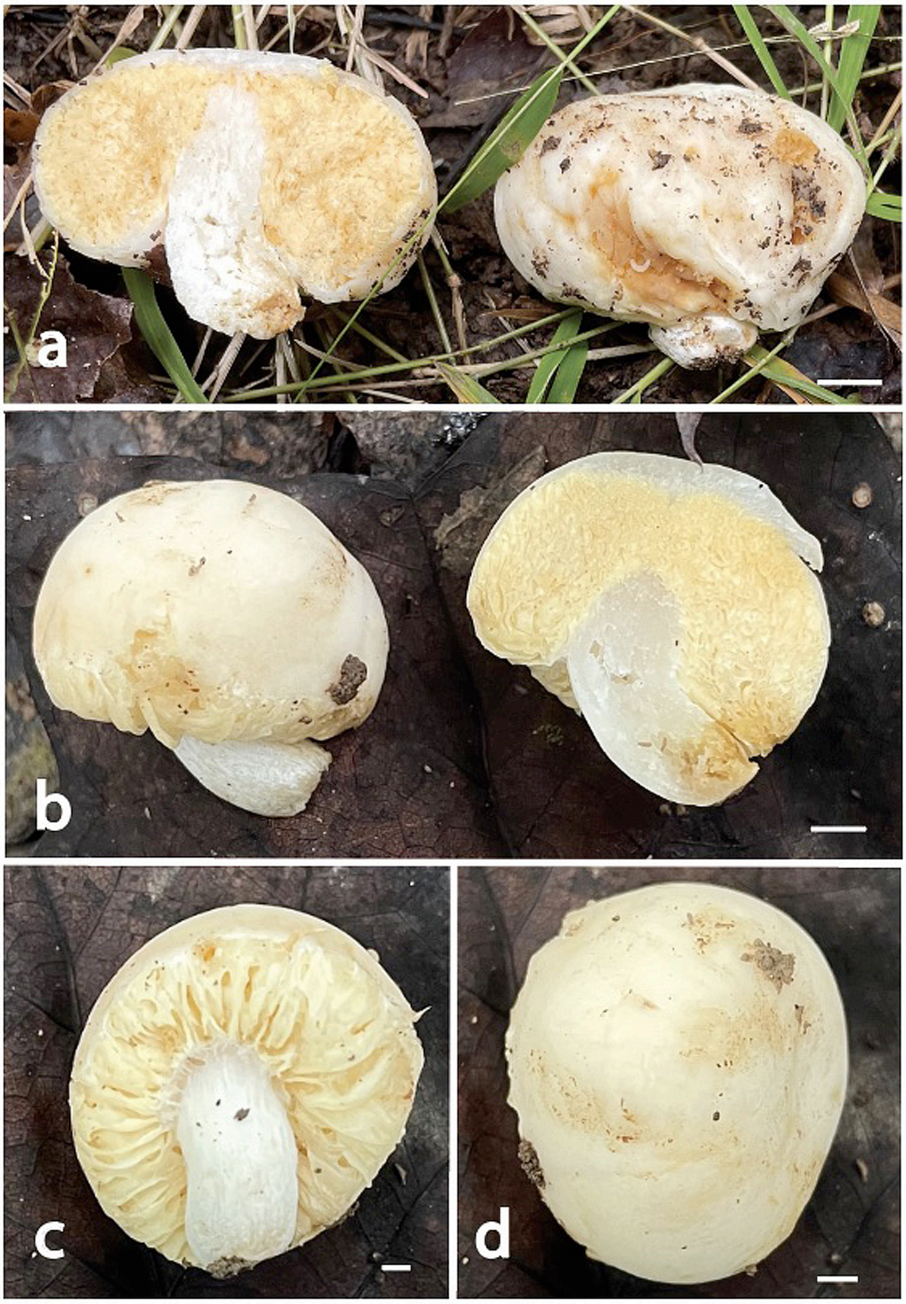

FIGURE 2. Macroscopic features of *Russula neoelpidensis*. A. Mature basidiomata sectioned vertically showing the gleba and stipe-columella (left) and outer surface (right) (holotype VC 2318); B. Mature basidiomata sectioned vertically showing outer surface (left) and gleba and stipe-columella (right), VC 2319; C–D. Macroscopic features of mature basidiomata, VC 2319, C. showing a ventral view of exposed hymenophore, D. Showing a dorsal view of the surface of basidioma. Scale bars = 1 cm.

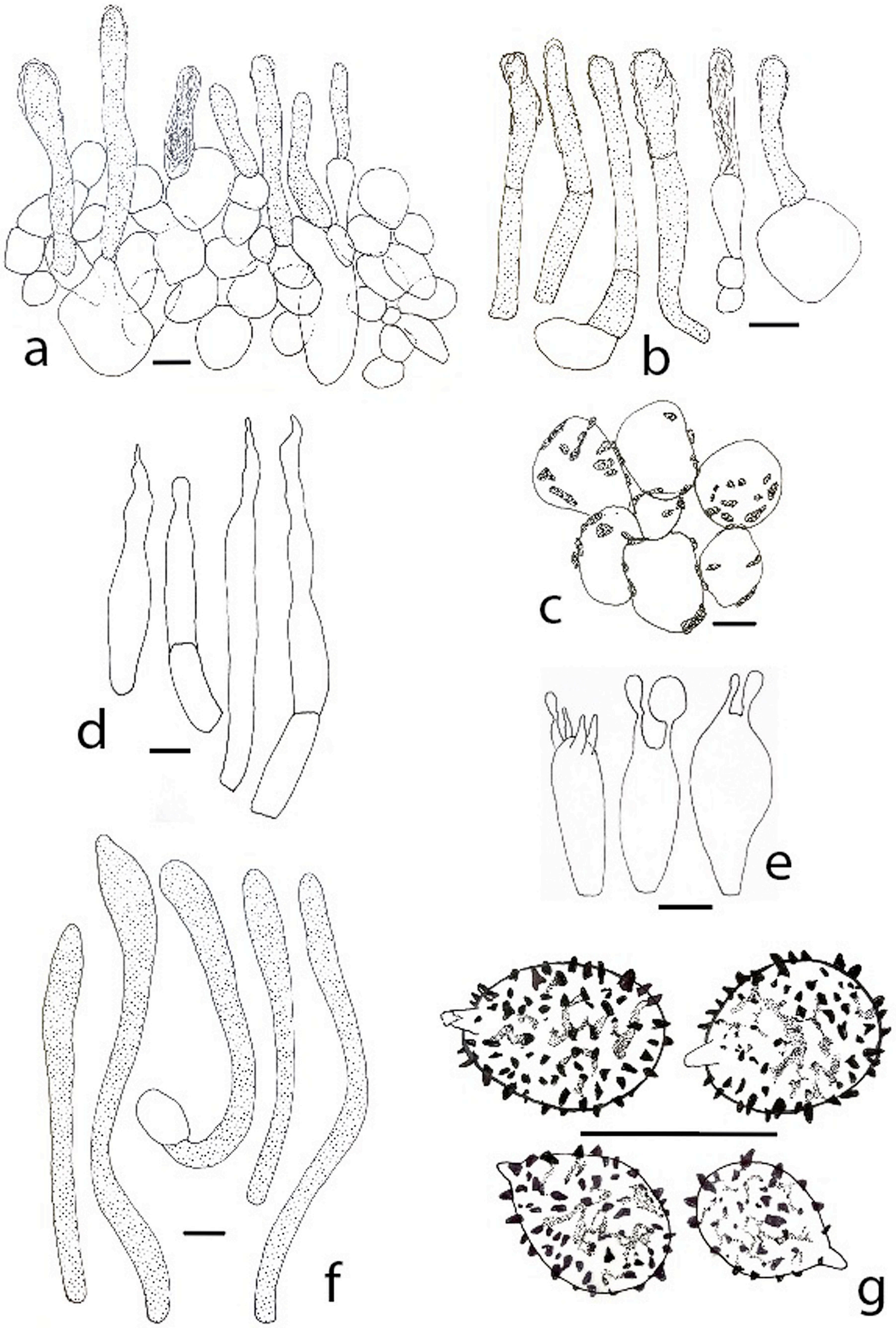

FIGURE 3. Microscopic characteristics of *Russula neoelpidensis* (holotype VC 2318). A. Diagram of a section of the pileipellis taken from near the disc; B. Pileocystidia in KOH taken from near the disc. C. Subglobose cells of the suprapellis showing incrustations in Sulfovanillin. D. Hymenial cystidia. E. Basidia; F. Elements of the stipitipellis in Sulfovanillin; G. Basidiospores in Melzer's reagent. Scale bars = 10 µm.

Discussion

Blast searches of the *Russula neoelpidensis* sequences in GenBank uncovered 98% plus similarity with a *R. blumiana* sequence, several environmental sequences and sequences labeled *R. mordax* and *R. tenuiceps* from ectomycorrhizal studies of California oak woodlands. A search of the literature for *R. blumiana* revealed that Caboň *et al.* (2017, 2018) in their testing of possible synonymies of some European *Russula* spp. found that *R. blumiana* Bon (1986: 299) belongs together with *R. badia* Quél. (Quélet 1881: 668; MB#156717) in a strongly supported Badia subclade of clade Integrae. Including the sequences of *R. badia* from Europe, and *R. mordax* and *R. tenuiceps* from California in our analysis allowed us to recover a Badia subclade but with poor support. High support was achieved for a Badia subclade, which included *R. neoelpidensis*, when the California *R. mordax* and *R. tenuiceps* sequences from GenBank were excluded, and verified *R. mordax* and *R. tenuiceps* sequences from Europe were used in the analysis. In addition to *R. blumiana*, the Badia subclade recovered by Caboň *et al.* (2018) also included *R. quercilicis* Sarnari (1990: 338; MB#129737). None of the previously described *Russula* species in the Badia subclade is sequestrate.

Species that have been found by molecular analyses to comprise the Badia subclade are traditionally classified into two morphologically separate subsections based on the presence of incrustations on the pileocystidia in Sulfovanillin (Caboň *et al.* 2017). Species placed thus far in the Badia subclade are characterized by acrid taste, yellow spore print and contents of pileocystidia turning grey to black in Sulfovanillin. However, this combination of characters is not exclusive to the Badia subclade and is present in other unrelated groups of the crown clade of *Russula*.

Russula neoelpidensis was placed squarely in the Integrae clade. Unfortunately, the Integrae clade is somewhat difficult to delimit exclusively. Among 14 species that form the Integrae clade in the analysis of Caboň *et. al*. (2017), nine had pink incrustations in Sulfovanillin, two had only acid-resistant incrustations and three had no incrustations. Members of *Russula* subsect. Rubrinae, thoroughly treated by Caboň *et. al.* (2017) as also nested withing the Integrae, all appear to possess pileocystidia with pink incrustations in Sulfovanillin. The Badia subclade, like the Integrae clade, contains members with different incrustation characteristics: *R. badia* lacks pink incrustations on pileocystidia in Sulfovanillin, while in *R. neoelpidensis* the pink incrustations are generally lacking on the pileocystidia, it was possible find scattered individual cystidial elements with scanty pink incrustations. Interestingly, the layer of subglobose cells in the suprapellis from which the pileocystidia arise had copious pink incrustations in Sulfovanillin, and it was these cells that resulted in the overall pink coloration of the suprapellis. The use of carbolfuchsin and Sulfovanillin and other reagents to visualize incrustations on various cell types and tissues in the pileipellis appear to form tantalizing synapomorphies for members of the crown clade of *Russula*. However, it remains insufficiently widely tested, and appears to be of limited use in defining morphological synapomorphies to support the placement of *R. neoelpidensis*. One reason might be that absence of visible incrustations in some species might be caused by a very thick gelatinous-slimy matter in which the hyphal terminations in the pileipellis are embedded or by inconsistent chemical composition of the reagents used (*e.g.* concentration of sulfuric acid used in the making of sulfovanillin) (Caboň *et. al*. 2018).

Among other interesting features of *R. neoelpidensis* is the translucent cuticle, which likely results from the layer of densely packed thick-walled globose cells forming the subpellis, that gives an almost crystalline appearance under the microscope. The basidiospore accumulations in the locules are yellow, further agreeing with that of other members of the Badia subclade. Unfortunately taste of the fresh basidiome tissue was not observed, so we are unable to verify the acrid taste found in other members of the Badia subclade. Vidal *et al.* (2019) reported several sequestrate Russulaceae from Mediterranean and temperate Europe with at least slightly acrid taste, so it is possible that *R. neoelpidensis* does indeed possess this feature. The closest relative, *R. blumiana* in our analysis, has a strongly pigmented red pileus whereas *R. neoelpidensis* is cream or pale yellow and lacks red pigments. *Russula quercilicis* is cream-colored, especially at the margin and has brownish red coloration at the disc (Mua *et al.* 2017), and does not fall close to *R. neoelpidensis* in our molecular analysis. Ecologically *R. quercilicis* is associated with oaks like *R. neoelpidensis*, while other members of the Badia subclade are primarily conifer associates. *Russula neoelpidensis* was found in a bottomland mixed hardwood forest with abundant oaks and is likely an ectomycorrhizal partner of oaks.

Vidal *et al.* (2019) found many sequestrate species in the crown clade of *Russula* on a long branch sister to, in part, the Integrae clade. Most are *Eucalyptus* associates from Australia and *Nothofagus* associates from New Zealand and lack identity with *R. neoelpidensis*. Unfortunately, many of these sequences are not complete in ITS1, ITS2 and 5.8s and likely clustered together in a single clade due to long branch attraction rather than within previously defined clades in the crown clade.

Russula neoelpidensis is an interesting species, with characteristics that both support and extend synapomorphies that could help refine and define formal subgeneric classification systems. It is critical that systematic studies of clades of *Russula* that apply both molecular and morphological analyses in the quest for synapomorphic characters should include sequestrate taxa.

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