

The study of *Russula* in the Western United States

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Abstract – A short history to the study of *Russula* in the Western United States is provided and for the first time an exhaustive list of all 49 taxa described from this part of the country has been compiled. As a start to a revision of these species, a first series of four holotypes (one from California and three from the Pacific Northwest) have here been studied microscopically, resulting in some very substantial changes concerning species concept and consequent systematic placement. *Russula flava* var. *pacifica* appears unrelated to the type variety. It is therefore excluded as member of *Integroidinae*, subgen. *Polychromidia*, and deserves probably to be upgraded to species level within subgen. *Russula*. The Californian *R. paxilloides* is lectotypified and is a good member of subgen. *Russula*, but is closer to sect. *Persicinae* than to the white-spored *Vinaceae* as previously suggested. *Russula maxima*, widely accepted as a species of subsect. *Subcompactinae* (subgen. *Heterophyllidia*), certainly does not belong there and has to be moved to subgen. *Polychromidia*. Finally, *R. inconstans* is here maintained as member of subg. *Polychromidia*.

Pacific West coast / lectotypification / *Russula flava* var. *pacifica* / *R. inconstans* / *R. maxima* / *R. paxilloides*

INTRODUCTION

When discussing the need for a more thorough and integrated approach in the study of the genus *Russula* in the United States, Buyck (2007) pointed out the urgency of modern, detailed and well-illustrated redescrptions of the micromorphology of the type specimens for nearly all of the 332 native, North American *Russula* species as a necessary prerequisite for a correct application of names, as well as for a sound basis for future molecular work. As most of the earlier mycologists in the USA lived and worked on the East coast, the large majority of the native American russulas have been described from the eastern part of the country and one might be inclined to think that the study of West Coast russulas started much later through regional taxonomic studies by PhD students such as D.W. Grund (1979) or regional

monographs such as the Russulaceae mycota of California by H.D. Thiers (1994, 1997b). However, when checking original descriptions of native American russulas, one realizes rapidly that the study of West Coast russulas started much earlier.

The first *Russula* published from the Western United States is *R. nigrodisca* Peck. This species was based on material collected on St. Paul Island in the Bering see (Macoun 1899), and still remains the only *Russula* described from the state of Alaska. It was soon followed by two species described from California by F.S. Earle (1902). A decennium later, G.S. Burlingham started her mycological career with a publication that listed species of *Russulaceae* deposited in the herbarium of the New York Botanical Garden but that had been collected on the Pacific coast (Burlingham 1913). She continued to publish new West Coast russulas first based on specimens sent to her for examination (Burlingham 1915, 1924), but later also as a result of her own collections made in Oregon (Burlingham 1936). With 14 new *Russulas* described from the Pacific Coast, Burlingham remains the mycologist who described the highest number of new *Russulas* from the area (Table 1). Also C.H. Kauffman collected several times in the Western states, but described no new species. He reported nine russulas from Siskiyou Mts. in Oregon (Kauffman 1930) including the new variety *R. flava* var. *pacifica* Kauffman. Western *Russula* collections made by Kauffman, and also by A.H. Smith, were later designated as holotypes for an additional nine new russulas described by R. Singer (1938, 1939a, 1939b, 1948) when he was still residing in Europe. Also R.L. Shaffer (1962, 1964, 1972, 1975) described eight new taxa, four of them at infraspecific rank, that were mainly based on *Russula* specimens collected by A.H. Smith.

During the past 50 years, *Russula* has attracted a not negligible interest from mycologists on the West Coast. Apart from H.D. Thiers (Thiers 1997b), who presented a *Russula* revision for California, there have been several mycology students focusing on this genus on the West Coast: H. Peters (1962) made her Master's thesis also on *Russula* in California, while D.W. Grund (1965) wrote for his PhD a very personal vision on *Russula* in Washington. More recently, C. Roberts (2007) presented a very thorough approach on *Russula* from coastal forests in Vancouver Island (British Columbia, Canada), integrating data derived from morphology, ecology, chromatography as well as from using molecular tools. Finally, it is worth mentioning that for the Pacific Northwest there is also a comprehensive key to the species of *Russula* published by B. Woo (1989). With the exception of the eight new *Russulas* resulting from Thiers' monograph for California (Thiers, 1997a) and the three new species described from Washington State by D.W. Grund (1979), none of these studies resulted in the description of new taxa and all report a relatively high number of European species for the area. Considering these many years of study devoted to western *Russulas*, one would suspect that at least the species originally described from this area would be well known by now, but this is absolutely not the case. As we will show below, there remains a huge confusion concerning the correct interpretation of native western russulas, mainly because modern published studies of the holotypes are still unavailable. Therefore, the correct assignment of these western taxa to particular subsections will make it possible to integrate them in identification keys and as such stimulate the interest in these poorly known species (Adamčík & Buyck 2014; Buyck & Adamčík 2013).

Extending the notion of "Western" russulas also to non-coastal states of the Western part of the United States seems quite legitimate when considering the phytogeographical division of North America (Cronquist 1982). In that case, 14 more *Russula* taxa can be accounted for: five from Wyoming (Burlingham 1915, 1924, 1936; Singer 1939b), four from Colorado (Burlingham 1915, Shaffer 1975,

Table 1. List of *Russula* taxa described based on material from Western US arranged chronologically. Their classification in a particular (sub)section is adopted from Singer (1986) or from the more recent original publications. Abbreviations: ss. – subsection, s. – section.

<i>Species</i>	<i>Publication year</i>	<i>US state</i>	<i>Classification fide Singer 1986 or later original descriptions</i>
<i>R. nigrodisca</i> Peck in Macoun	1899	Alaska	ss. <i>Russula</i>
<i>R. cremoricolor</i> Earle	1902	California	ss. <i>Cyanoxanthinae</i> Singer
<i>R. paxilloides</i> Earle	1902	California	?
<i>R. crenulata</i> Burl.	1913	Oregon	ss. <i>Russula</i>
<i>R. murrillii</i> Burl.	1913	Oregon	ss. <i>Amethystinae</i> Romagn.
<i>R. atroviolacea</i> Burl.	1915	Colorado	ss. <i>Urentes</i> Maire
<i>R. maxima</i> Burl.	1915	Washington	ss. <i>Subcompactinae</i> Singer
<i>R. robinsoniae</i> Burl.	1915	Wyoming	ss. <i>Sardoninae</i> Singer
<i>R. subalutacea</i> Burl.	1915	Colorado	ss. <i>Chamaeleontinae</i> Singer
<i>R. alcalinicola</i> Burl.	1924	Wyoming	? s. <i>Ingratae</i> Quéf.
<i>R. flava</i> var. <i>pacifica</i> Kauffman	1930	Oregon	?
<i>R. californiensis</i> Burl.	1936	California	ss. <i>Decolorantinae</i> Maire
<i>R. inconstans</i> Burl.	1936	Oregon	ss. <i>Lilaceinae</i> Melzer & Zvára
<i>R. marginata</i> Burl.	1936	Wyoming	?
<i>R. mordax</i> Burl.	1936	Washington	ss. <i>Sardoninae</i> Singer
<i>R. murina</i> Burl.	1936	Oregon	?
<i>R. placita</i> Burl.	1936	Washington	ss. <i>Betulinae</i> Romagn.
<i>R. zelleri</i> Burl.	1936	Oregon	ss. <i>Betulinae</i> Romagn.
<i>R. citrina</i> f. <i>separata</i> Singer	1938	Washington	ss. <i>Citrinae</i> Romagn.
<i>R. crassotunicata</i> Singer	1938	Washington	s. <i>Crassotunicatae</i> (Singer) Singer
<i>R. rosacea</i> var. <i>americana</i> Singer	1938	Washington	ss. <i>Sardoninae</i> Singer
<i>R. smithii</i> Singer	1938	Washington	ss. <i>Amoeninae</i> Singer
<i>R. persobria</i> Kauffman ex Singer	1939a	Oregon	ss. <i>Modestinae</i> Singer
<i>R. alutacea</i> subsp. <i>ambigua</i> Singer., nom. inval.	1939b	Wyoming	ss. <i>Polychromae</i> (Maire) Singer
<i>R. subveterosa</i> Singer	1939b	Wyoming	ss. <i>Urentes</i> Maire
<i>R. vinosa</i> subsp. <i>occidentalis</i> Singer	1948	Idaho	ss. <i>Vinosinae</i> Singer
<i>R. atrata</i> Shaffer	1962	Oregon	s. <i>Compactae</i> Fr.
<i>R. densifolia</i> f. <i>cremeispora</i> Shaffer	1962	Washington	s. <i>Compactae</i> Fr.
<i>R. densifolia</i> f. <i>dilatatoria</i> Shaffer	1962	Oregon	s. <i>Compactae</i> Fr.
<i>R. densifolia</i> f. <i>fragrans</i> Shaffer	1962	Washington	s. <i>Compactae</i> Fr.
<i>R. cascadenis</i> Shaffer	1964	Oregon	s. <i>Plorantes</i> Singer
<i>R. brevipes</i> var. <i>acrior</i> Shaffer	1964	Idaho	s. <i>Plorantes</i> Singer
<i>R. cerolens</i> Shaffer	1972	Oregon	ss. <i>Foetentinae</i> Melzer & Zvára
<i>R. montana</i> Shaffer	1975	Colorado	ss. <i>Russula</i>
<i>R. rosacea</i> var. <i>macropseudocystidiata</i> Grund	1979	Washington	ss. <i>Sardoninae</i> Singer
<i>R. stuntzii</i> Grund	1979	Washington	ss. <i>Russula</i>
<i>R. viridofusca</i> Grund	1979	Washington	ss. <i>Xerampelinae</i> Singer
<i>R. burgeae</i> Thiers	1997a	California	? ss. <i>Sanguineae</i> Singer
<i>R. ellenae</i> Thiers	1997a	California	ss. <i>Lepidinae</i> Melzer & Zvára
<i>R. grundii</i> Thiers	1997a	California	ss. <i>Xerampelinae</i> Singer
<i>R. mendocinensis</i> Thiers	1997a	California	ss. <i>Rubrinae</i> Melzer & Zvára
<i>R. pacifica</i> Thiers	1997a	California	?
<i>R. punicea</i> Thiers, nom. illeg.	1997a	California	?
<i>R. sierrensis</i> Thiers	1997a	California	? ss. <i>Integrae</i> Maire
<i>R. xanthoporphyræa</i> Thiers	1997a	California	ss. <i>Lilaceinae</i> Melzer & Zvára
<i>R. avellaneiceps</i> Fatto	1999	Colorado	ss. <i>Amethystinae</i> Romagn.
<i>R. cochisei</i> Fatto	2000	Arizona	ss. <i>Laetinae</i> Romagn.
<i>R. cinereovinosa</i> Fatto	2002	Arizona	ss. <i>Urentes</i> Maire
<i>R. cantharellicola</i> Arora & N.H. Nguyen	2014	California	s. <i>Compactae</i> Fr.

Fatto 1999) two from Arizona (Fatto 2000, 2002) and another two from Idaho (Singer 1948, Shaffer 1964). To the best of our knowledge, there are no russulas described from adjacent regions of Canada and Mexico, the only two species originating from Mexico being from the Southeastern part (Murrill 1911, Kong *et al.*, 2002). All in all, this very first compilation of all *Russula* described from the Western United States results in a total of 49 taxa, a number that is much higher than we suspected as most of these species have hardly ever been discussed in the literature. Thirty seven of these western taxa were described by mycologists from the eastern part of the country (Table 1).

As a start for a general revision of these western taxa we will present here detailed microscopical features of four type specimens of western russulas.

MATERIAL AND METHODS

Micromorphological characters were observed using Olympus CX-41 and Nikon Eclipse E400 microscopes using oil-immersion lenses at a magnification of 1000x. All drawings of microscopical structures, with the exception of spores, were made with a “camera lucida” using a Nikon Y-IDT drawing attachment at a projection scale of 2400x. Contents of hymenial cystidia and pileocystidia are indicated schematically in the illustrations, with the exception of a single element (in some cases a few elements) where contents are indicated as observed in Congo red preparations from dried material. Spores were observed on the gills in Melzer’s reagent. All other microscopic observations were made in ammoniacal Congo red, after a short treatment in warm, aqueous KOH to dissolve the gelatinous matrix and improve tissue dissociation. All tissues were also examined in Cresyl blue to verify presence of ortho- or metachromatic reactions as explained in Buyck (1989). Trama and cystidia were examined in sulfovanillin solution, acidoresistant incrustation of primordial hyphae was colored in karbolfuchsin and observed in distilled water after staining for a few seconds in a 10% solution of HCl (cf. Romagnesi 1967).

Spores were scanned with an Artray Artcam 300MI camera and measured by Quick Micro Photo (version 2.1) software. Enlarged, scanned pictures of spores were used for measuring with an accuracy of 0.1 μm and for making line drawings. Q gives length/width ratio of the spores. Measurements exclude ornamentation. Statistics for measurements of microscopical characters are based on 30 measurements and given as a mean value (underlined) plus/minus standard deviation; values in parentheses give measured minimum or maximum values. An estimate for spore ornamentation density in our descriptions is given following Adamčík & Marhold (2000). Herbarium abbreviations follow Holmgren *et al.* (1990).

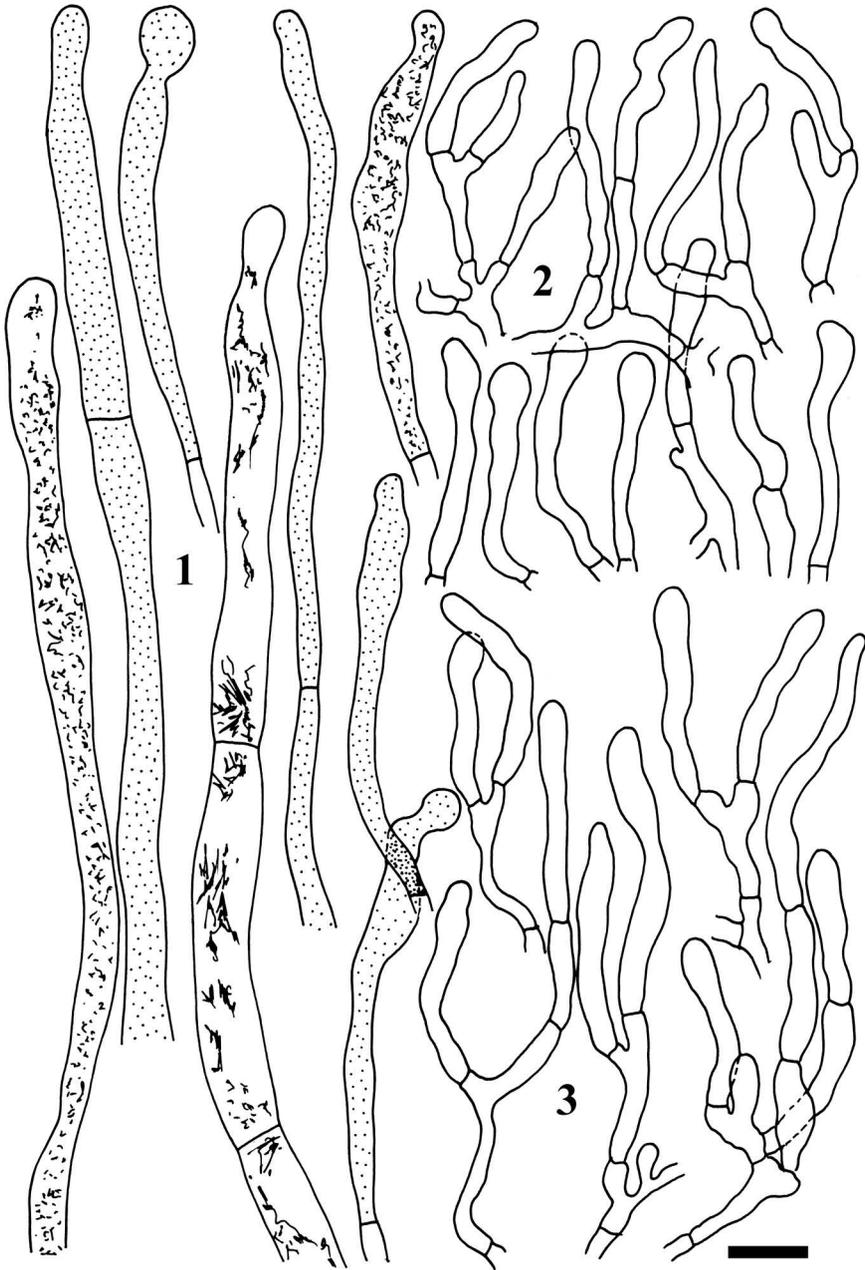
TAXONOMY

Russula flava var. *pacifica* Kauffman, Pap. Michigan Acad. Sci. 11: 205. 1930

Figs 1-9

Original description:

This has so much the general appearance of R. flava that I am loath to separate it entirely. The taste is slowly subacid, and the flesh does not, except indistinctly, show any

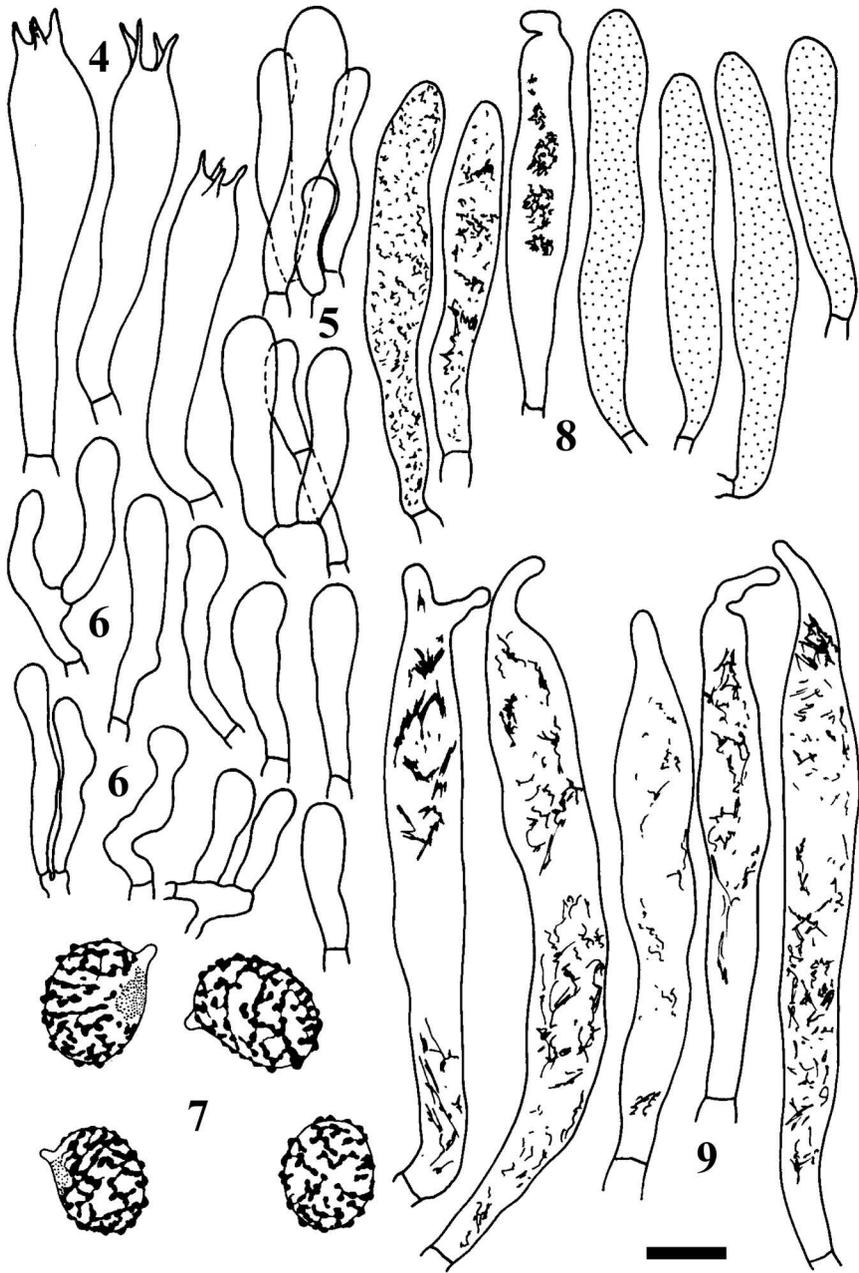


Figs 1-3. *Russula flava* var. *pacifica* (holotype). 1. Pileocystidia. 2. Hyphal terminations near the cap center. 3. Hyphal terminations near the cap margin. Cystidial contents as observed in Congo Red, but most elements with contents indicated schematically. Scale bar = 10 μ m.

cinerescent tendency. These are characters of the variety. The spores are subellipsoid, with large oil drop, and measure about 7-8 (10) × 6-7 (8) μ, almost smooth under dry high powers of microscope, and are almost hyaline with a faintly tinted exospore. The gills are forked here and there at base only, at first white, then "straw yellow" to "Naples yellow". The pileus varies from "straw yellow" to "Naples yellow"; the stem is white or whitish. I have it from Montana, Washington and Oregon, where it occurs in coniferous forests, usually singly.

The type was collected at Takilma, Oregon, December 2, 1925. It differs from R. ochroleuca (Pers.) Fr. in the stem' not becoming ashy, although in advanced age they may become watery-grayish, but this occurs in other old Russula stems with otherwise unchanging flesh. Lange (17) says of R. ochroleuca: "It is generally said to be acrid, but in Denmark the almost insipid form is present, - in fact I have never met with really acrid specimens. Common in woods of Fagus. The spore powder is white." Evidently our plant is in some respects very similar to this species of Lange, but the gills and spores are not pure white, as in his, and the plant is more acrid.

Spores broadly ellipsoid (7-)7.5-7.9-8.4(-8.9) × (5.6-)5.9-6.3-6.6(-7) μm, Q = (1.17-)1.22-1.27-1.31(-1.33), ornamentation zebrate, of low, obtuse, relatively numerous [(5-)6-8 in a 3 μm diam. circle] amyloid warts, 0.5-0.7 μm high, connected with occasional, short, fine line connections [0-2(-3) in the circle], frequently fused and forming parallel chains that are sometimes branched [(1-)2-5 fusions in the circle], without isolated warts; suprahilar plage amyloid, small. **Basidia** (38-)41-44-48(-56) × (6.5-)7.5-9-10(-11.5) μm, 4-spored, clavate-pedicellate; basidiola first cylindrical, then narrowly clavate, ca. 4-8 μm wide. **Subhymenium** pseudoparenchymatic. **Lamellar trama** mainly composed of large sphaerocytes that are mixed with cystidioid hyphae. **Hymenial cystidia** moderately numerous, ca. 800-1000/mm², fusiform or rarely clavate, pedicellate, measuring (72-)78-91-105(-125) × (8.5-)9.5-10.5-11.5(-12.5) μm on sides, mainly apically mucronate or appendiculate [appendage (2-)4-10(-16) μm long], occasionally with double appendage, mainly thin-walled, with heteromorphous to partly crystalline contents, in sulfovanillin staining dark to blackish brown. Hymenial cystidia near the gill edge numerous, narrowly clavate or fusiform, measuring (38-)44-50-56.5(-62) × (6-)6.5-7.5-8.5 μm, thin-walled, with obtuse tips, sometimes slightly constricted near the tips, with heteromorphous (granular-banded) contents. **Marginal cells** similar to basidioles, mostly clavate, often moniliform, measuring (15-)19.5-24.5-29.5(-35) × (4-)4.5-5.5-7(-8) μm. **Pileipellis** orthochromatic in Cresyl blue, not sharply delimited from the underlying sphaerocytes of the context, strongly gelatinized throughout, vaguely divided in rather dense, 60-70 μm deep suprapellis of ascending hyphal ends forming a palisade trichoderm, gradually passing into a dens, 60-80 μm deep subpellis of intricate, horizontally oriented hyphae that are ca. 2-5 μm wide. Acidoresistant incrustations not observed. Terminal cells of hyphae in pileipellis near the cap margin measuring 22-28-33(-40) × 3-4-4.5(-5.5) μm, mostly cylindrical, often also clavate, often slightly flexuous or moniliform, mostly obtuse and only occasionally slightly narrowed towards tips; subterminal cells equally wide, mostly irregular-nodulose, branched and intricate, some with lateral branches. Pileipellis near the cap margin similar, with terminal cells measuring (13-)22-27.5-33(-37) × (3-)3.5-4-5(-5.5) μm, mainly clavate or cylindrical, with subterminal cells building a very dense layer. Pileocystidia very numerous especially near the cap center, with terminal cells measuring (40-)48-81-113(-146) × (3.5-)4.5-6-7.5(-9) μm, usually very long, cylindrical or narrowly clavate, mostly one-celled, some multi-celled ones originating from deep in subpellis, in Congo red with heteromorphous, banded or crystalline contents, in sulfovanillin distinctly graying, thin-walled. Cystidioid hyphae in supellis and trama present. **Clamp connections** absent in all parts.



Figs 4-9. *Russula flava* var. *pacifica* (holotype). 4. Basidia. 5. Basidiola. 6. Marginal cells of the gill edge. 7. Spores as seen in Melzer's reagent. 8. Hymenial cystidia near the gill edge. 9. Hymenial cystidia on gill sides. Cystidial contents as observed in Congo Red, but some elements with contents indicated schematically. Scale bar = 10 μ m, but only 5 μ m for spores.

Examined material: UNITED STATES. **California.** Josephine Co., Takilma, 1 Dec 1925, C.H. Kauffman & C.A. Brown (MICH12213, holotypus).

Commentary: *Russula flava* var. *pacifica* has never been commented upon in later publications on American russulas. Kauffman accepted this yellow collection as a variety of *R. flava* Romell, an earlier synonym for *R. claroflava* Grove. The latter is a European species with distinctly greying to blackening context, without pileocystidia but with encrusted primordial hyphae and which is placed in subsect. *Integroidinae* Romagn. together with other greying species having similar pileipellis features, such as *R. vinosa* Lindbl.

The presence of abundant pileocystidia clearly excludes such a placement and, in our opinion, Kauffman's variety may represent a good species of *Russula* subgen. *Russula*. The strong SV+ reaction, acrid taste, colored spore print and presence of numerous, mainly one-celled pileocystidia that continue as cystidioid hyphae in the whole context of the fruiting body suggest possible affinities to subsect. *Sanguininae* Singer or subsect. *Sardoninae* Singer. Both subsections comprise several European representatives that are known to produce occasional yellow forms of otherwise darker, more reddish or purplish species.

Russula inconstans Burl., Mycologia 28 (3): 255. 1936

Figs 10-18

Original description:

Pileus broadly convex becoming plane to centrally depressed, from 5.5 cm. to 13 cm. broad; surface corinthian red on the margin toning into pale reddish lilac, mineral brown to maize yellow over the center, or vandyke brown in the center when young, fading with age, slimy viscid when wet, cuticle separable half way to the center; glabrous; margin pruinose when young, becoming striate tuberculate on the edge; context white, unchanging, acrid in young specimens, slowly acrid in the adult stage, without special odor; lamellae white at first, becoming pale ecru tone 4 to maize yellow tone 2, some short, some forking near the stipe or near or part way to the margin, depressed near the stipe and attached by a tooth, close not very broad; stipe white, sometimes with yellow strains at the base, spreading at the apex, firm becoming spongy, 1.5-3.5 cm. × 6-8 cm.; spores ochroleucous, 6.8-7.5 μ × 7.5-8.75 μ, exclusive on the apiculus, reticulate banded with some protuberances and some fine connecting lines.

TYPE LOCALITY: Woodcock's Hill, Corvallis, Oregon, Nov. 14, 1927. 255.

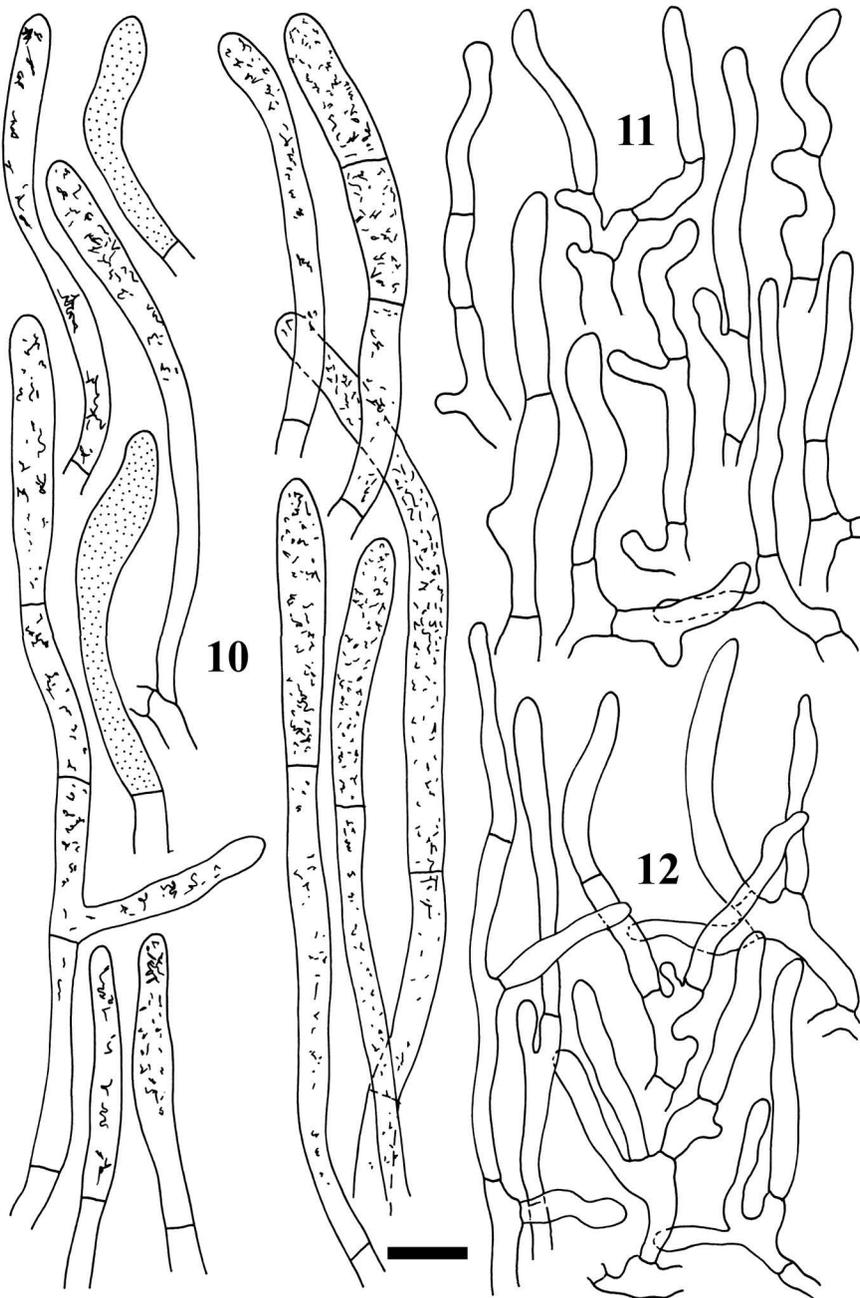
HABITAT: In needle soil under Douglas fir trees on the edge of woods.

DISTRIBUTION: In various localities near Corvallis, Oregon.

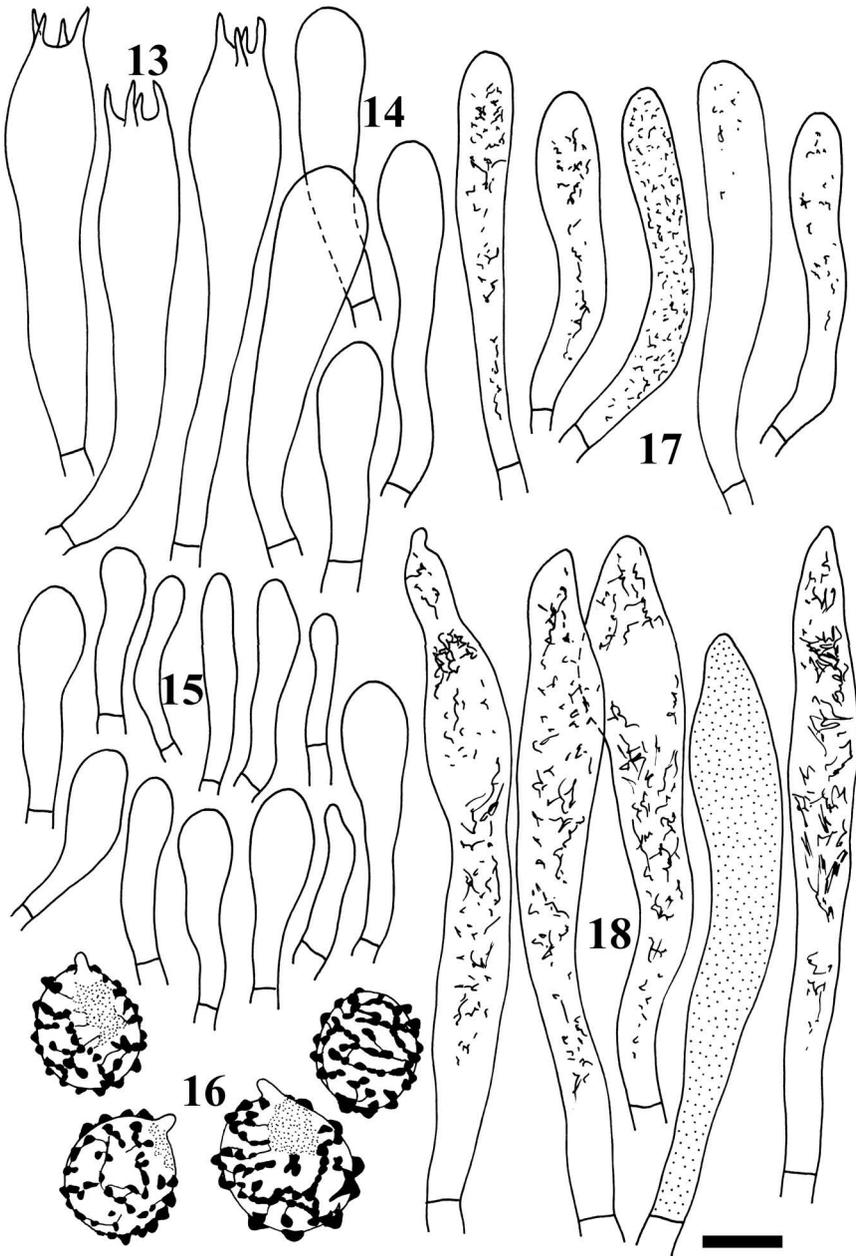
Pileo variegato firmulo, explanato depressove, jove pluvio viscoso, glabro; margine primum pruinoso, tum glabro, dein striatulo; carne alba, acri; lamellis ex albo gilvis, adnexis, confertis, immixtis brevioribus, furcatis; stipite albo e firmo spongioso; sporis ochroleucis, reticulatis, 6.8-7.5 μ × 7.5-8.75 μ.

*This species differs from *Russula placita* in the narrower forking lamellae, the firmer context, in the deeper yellow spores as well as in the color of the pileus and the less pronounced striate tuberculate margin. From *Russula maculata* Quél. it differs in the paler lamellae and the absence of red or bistre on the stipe, and in having smaller ellipsoid and reticulate banded spores.*

Spores subglobose, (8-)8.2-8.6-9.1(-9.9) × (6.9-)7.1-7.4-7.7(-8.2) μm, Q = (1.11-)1.13-1.16-1.2(-1.26); ornamentation subreticulate, of moderately distant [(4-)5-7(-8) in 3 μm circle] hemisphaerical to conical warts measuring 0.3-0.6(-0.7) μm high, occasionally connected by fine line connections [0-2(-3) connections in the circle] or fused in often long and branched chains [(1-)2-5(-6) fusions in the circle], rarely isolated; suprahillar spot amyloid, distinct. **Basidia** (50-)53-57-61.5(-66) × 11-12-13(-13.5) μm, 4-spored, rarely also 1-2 spored, broadly clavate, pedicellate; basidiola first cylindrical or ellipsoid than clavate. **Subhymenium**



Figs 10-12. *Russula inconstans* (holotype). **10.** Pileocystidia near the cap margin (right) and near the cap center (left). **11.** Hyphal terminations near the cap center. **12.** Hyphal terminations near the cap margin. Cystidial contents as observed in Congo Red, but some elements with contents indicated schematically. Scale bar = 10 μ m.



Figs 13-18. *Russula inconstans* (holotype). **13.** Basidia. **14.** Basidiola. **15.** Marginal cells of the gill edge. **16.** Spores as seen in Melzer's reagent. **17.** Hymenial cystidia near the gill edge. **18.** Hymenial cystidia on gill sides. Cystidial contents as observed in Congo Red, but some elements with contents indicated schematically. Scale bar = 10 μ m, but only 5 μ m for spores.

pseudoparenchymatic. **Lamellar trama** mainly composed of large sphaerocytes. **Hymenial cystidia** on gill sides dispersed, 500-600/mm², measuring (68-)74-86-97.5(-109) × (9-)10.5-12.5-14.5 μm, near the gill edge (32-)39.5-48-56.5(-63) × (6-)7-8.5-9.5(-11) μm, fusiform, more rarely clavate, pedicellate, apically narrowing to mucronate, thin-walled; contents oily, granular to crystalline in Congo red, sometimes optically empty near the gill edge, moderately graying in sulfovanillin. **Marginal cells** not differentiated. **Pileipellis** orthochromatic in Cresyl blue, without acidoresistant incrustations, not sharply delimited from the underlying context, 110-130 μm deep, two-layered and covered with up to 30 μm deep gelatinous matrix, composed of a 55-65 μm deep, strongly gelatinized suprapellis of ascending or erect hyphae and protruding pileocystidia that become repent near the surface and an equally deep subpellis of horizontally oriented, intricate, dense, less gelatinized, 2.5-7.5 μm wide hyphae; terminal cells near the cap margin measuring (14-)22-29-35.5(-43) × 3-4-4.5 μm, subcylindrical, slightly moniliform or flexuous, obtuse or apically slightly constricted, somewhat denser but very similar in the cap center; subterminal cells often branched and intricate, equally wide but often shorter than terminal cells. Pileocystidia cylindrical or narrowly clavate, 1-2(-3)-celled, obtuse, with terminal cells measuring (22-)34-55-75.5(-90) × (5-)5.5-6-7(-7.5) μm near the cap margin, and (28-)35-47-59(-67) × (4-)4.5-6-7(-8) μm near the cap center, some originating deep in the subpellis and very long; contents heteromorphous-granular in Congo red, hardly reacting in sulfovanillin. Cystidioid hyphae absent from trama. **Clamp connections** absent in all parts.

Examined material: UNITED STATES. **Oregon**, Woodcock's Hill, Corvallis, in needle soil under Douglas fir trees on the edge of woods, Nov. 14. 1927, G.S. Burlingham (NY00653577, holotypus).

Commentary: Burlingham compared this species to her own *R. placita* Burl., a supposedly close relative of *R. sphagnophila* Kauffman (Singer 1951, 1975).

The slightly acid taste, colored (probably cream-ochre) spore print and not-incrusted pileocystidia with weak SV⁺ contents suggest that *R. inconstans* belongs in subgen. *Polychromidia* Romagn. Spore ornamentation and cylindrical hyphal terminations in the pileipellis do not contradict the opinion of Singer, but are also reminiscent of *R. paludosa* Britzelm.

Russula maxima Burl., North American Flora 9: 229. 1915

Figs 19-27

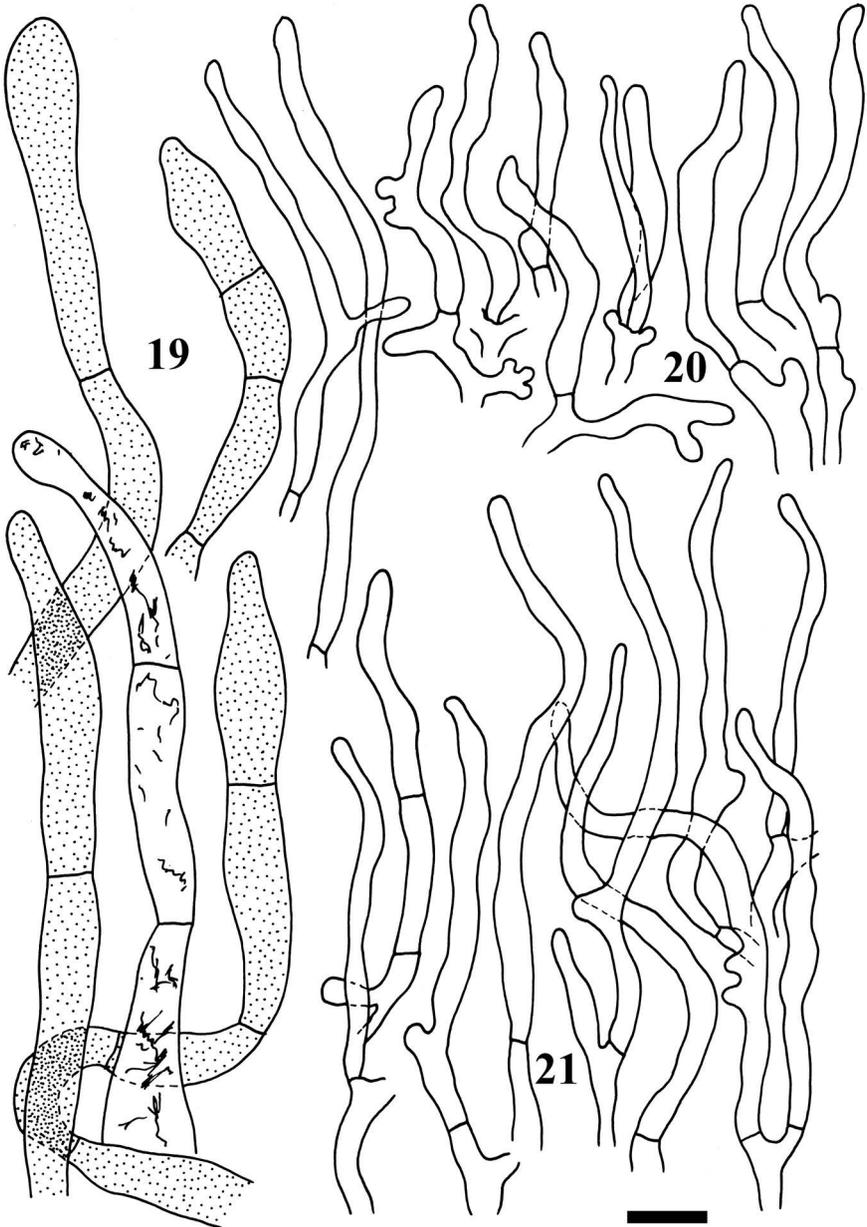
Original description:

Pileus convex to expanded, depressed in the center when mature, up to 22 cm. broad: surface smooth, viscid when wet, with pellicle separable in part, dark-purple, almost black on the disk, glabrous; margin even: context white, mild, without special odor; lamellae white, becoming pale-yellow, sinuate, close, broad, densely pruinose; stipe rose-colored, equal, solid, 10 cm. long, 2.5-3 cm. thick: spores cream-colored in mass, broadly elliptic, echinulate, 7-8.5 × 8.7-10.5 μ.

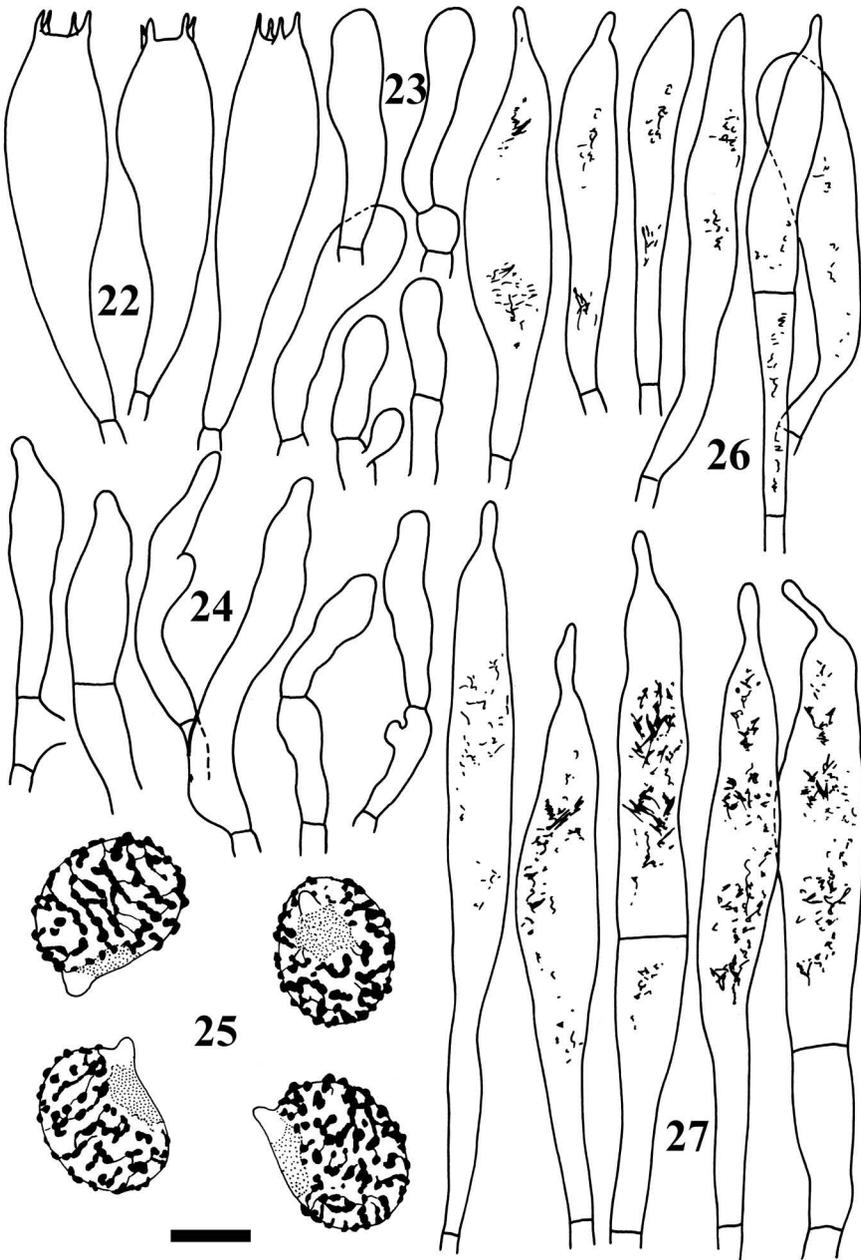
Type collected on the ground under evergreen and deciduous trees at Tacoma, Washington, October 26, 1911, W. A. Murrill 721 (herb. N. Y. Bot. Gard.).

DISTRIBUTION: Washington.

Spores broadly ellipsoid to ellipsoid (9.2-)9.4-9.9-10.4(-11.2) × (6.7-)7.1-7.5-8(-8.5) μm, Q = (1.22-)1.26-1.32-1.38(-1.44), ornamentation incompletely reticulate or zebrate, of low, dense [6-9(-10) in a 3 μm diam. circle] amyloid warts, 0.5-0.6(-0.8) μm high, connected with numerous fine line connections [(0-)1-4(-6) in the circle], often fused in short or long chains [0-)1-4(-6) fusions in the circle], rarely isolated; suprahilar plage amyloid, very large. **Basidia** (48-)51-54.5-58(-61)



Figs 19-21. *Russula maxima* (holotype). **19.** Pileocystidia. **20.** Hyphal terminations near the cap center. **21.** Hyphal terminations near the cap margin. Cystidial contents as observed in Congo Red, but most elements with contents indicated schematically. Scale bar = 10 μ m.



Figs 22-27. *Russula maxima* (holotype). 22. Basidia. 23. Basidiola. 24. Marginal cells of the gill edge. 25. Spores as seen in Melzer's reagent. 26. Hymenial cystidia near the gill edge. 27. Hymenial cystidia on gill sides. Cystidial contents as observed in Congo Red. Scale bar = 10 μ m, but only 5 μ m for spores.

× (13.5-)14-14.5-15.5(-16) μm, 4-spored, clavate-pedicellate; basidiola mostly clavate, rarely cylindrical with central constriction or utriform. **Subhymenium** pseudoparenchymatic. **Lamellar trama** mainly composed of large sphaerocytes. **Hymenial cystidia** probably numerous to abundant but not coloring in sulfovanillin and difficult to count, fusiform-pedicellate or clavate pedicellate, measuring (50-)66.5-80-92.5(-100) × (7.5-)8.5-10-11(-12) μm on sides, mostly mucronate-appendiculate, thin-walled or with slightly thickened wall in the central part (up to 0.5 μm), with heteromorphous to crystalline-granular contents that are sometimes dispersed, occasionally septate. Hymenial cystidia near the gill edge inconspicuous, fusiform or clavate, measuring ca. 37-65 × 5-11 μm, mostly acute and occasionally with a short appendage, thin-walled, optically empty or with dispersed granular inclusions. **Marginal cells** on the gill edge measuring ca. 20-42 × 4.5-9 μm, clavate, fusiform or cylindrical, often irregular, nodulose to moniliform or flexuous, usually apically constricted. **Pileipellis** orthochromatic in Cresyl blue, not sharply delimited from the underlying sphaerocytes of the context, 220-250 μm deep, strongly gelatinized, with a 60-70 μm deep gelatinous layer near surface, vaguely divided in loose, ca. 100 μm deep suprapellis of irregularly oriented, ascending hyphae and a more dense, 120-140 μm deep subpellis of almost parallel, horizontally oriented hyphae. Acidoresistant incrustations absent. Hyphal extremities thin-walled, slender, with mostly very long and flexuous terminal cells near the cap margin measuring (32-)48-62-77(-86) × (3-)3.5-4-5 μm, cylindrical or attenuated, moniliform, often also nodulose or with lateral branches; subterminal cells usually equally wide, nodulose and branched, toward the cap center similar, but shorter, more branching and irregular, measuring (22-)29-43-57(-92) × (2.5-)3-4-4.5(-5.5) μm. Pileocystidia large, long, abundant near surface, often in a large clusters, with terminal cells measuring (22-)31.5-40-48.5(-52) × (6.5-)7-8-9.5(-10) μm, subcylindrical, sometimes fusiform or clavate, mostly with obtuse tips, rarely constricted near apices, usually composed of several short cells with distinct heteromorphous contents that hardly react to sulfovanillin, descending and disappearing in the subpellis, but not continuing as cystidioid hyphae in the trama. **Clamp connections** absent in all parts.

Examined material: UNITED STATES. **Washington.** Pierce Co., Tacoma, border of Lake, under evergreen and deciduous trees, 26 Oct 1911, W.A. Murrill 721 (NY00653932, holotypus).

Commentary: Burlingham's species is characterized by a very robust stature, a dark purplish cap and pinkish stipe, mild taste, relatively pale gills producing a colored spore print, subreticulate spores having low warts and an amyloid suprahilar spot, a strongly gelatinized pileipellis with irregular and slender extremities and non-encrusted, weakly SV+ pileocystidia composed of several short cells.

Burlingham's commentary on this species placed it in *Integrae* Maire, which at that time (Maire 1910), meant not only close to *R. integra* (L.) Fr., but also side by side with other species such as *R. paludosa* Britzelm., *R. xerampelina* (Schaeff.) Fr., *R. romellii* Maire etc... It is difficult to understand why Singer, who originally accepted this placement, later (Singer 1951 and onwards) changed his mind and transferred *R. maxima* to subgen. *Heterophyllidia* near *R. grisea* Fr. and related species in subsect. *Subcompactinae* Singer, followed in this also by Woo (1989). The latter placement can absolutely be excluded by the amyloid suprahilar spot on the spores. We see for the moment no reason to doubt the original placement proposed by Burlingham (1915) and accept *R. maxima* as a member of subgen. *Polychromidia*.

Russula paxilloides Earle, Bull. N. Y. Bot. Garden 2(7): 341. 1902 **Figs 28-36**

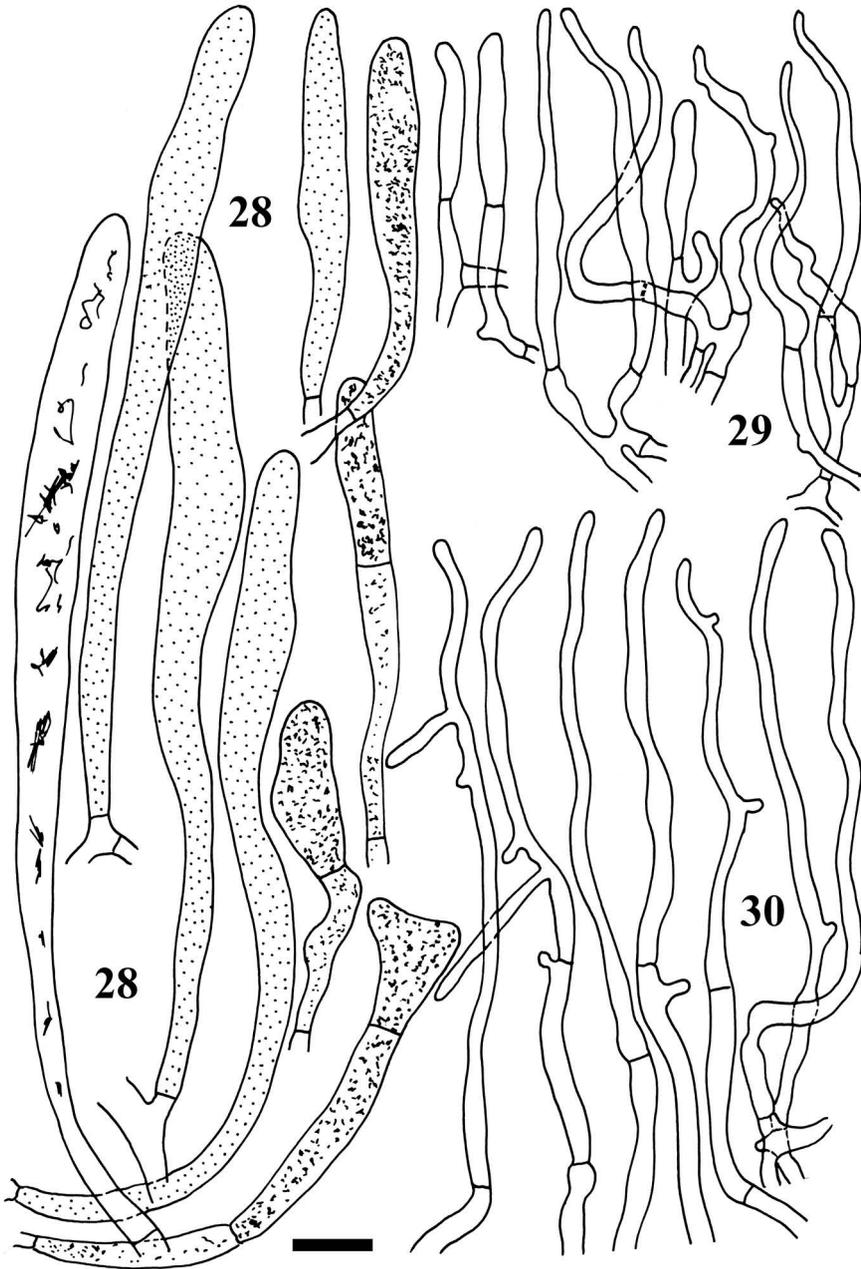
Original description:

In beds of decaying oak leaves; pileus 5-9 cm., thick and fleshy but with thin margin, expanded or subdepressed, disc whitish or pallid more or less deeply washed with carmine toward the margin, smooth, slightly viscid, margin entire; lamellae all equal, interveined and subanastomosing near the stipe, subsinuate, broad, nearly plane, white to cream yellow; spores pale yellow, globose, rough with sharp conical projections, 7-9 μ ; stipe variable in size, 5-11 \times 1½-3 cm., equal, smooth, white, spongy, stuffed with a loose pith; flesh white, unchanging, taste burning peppery, odor not noticeable.

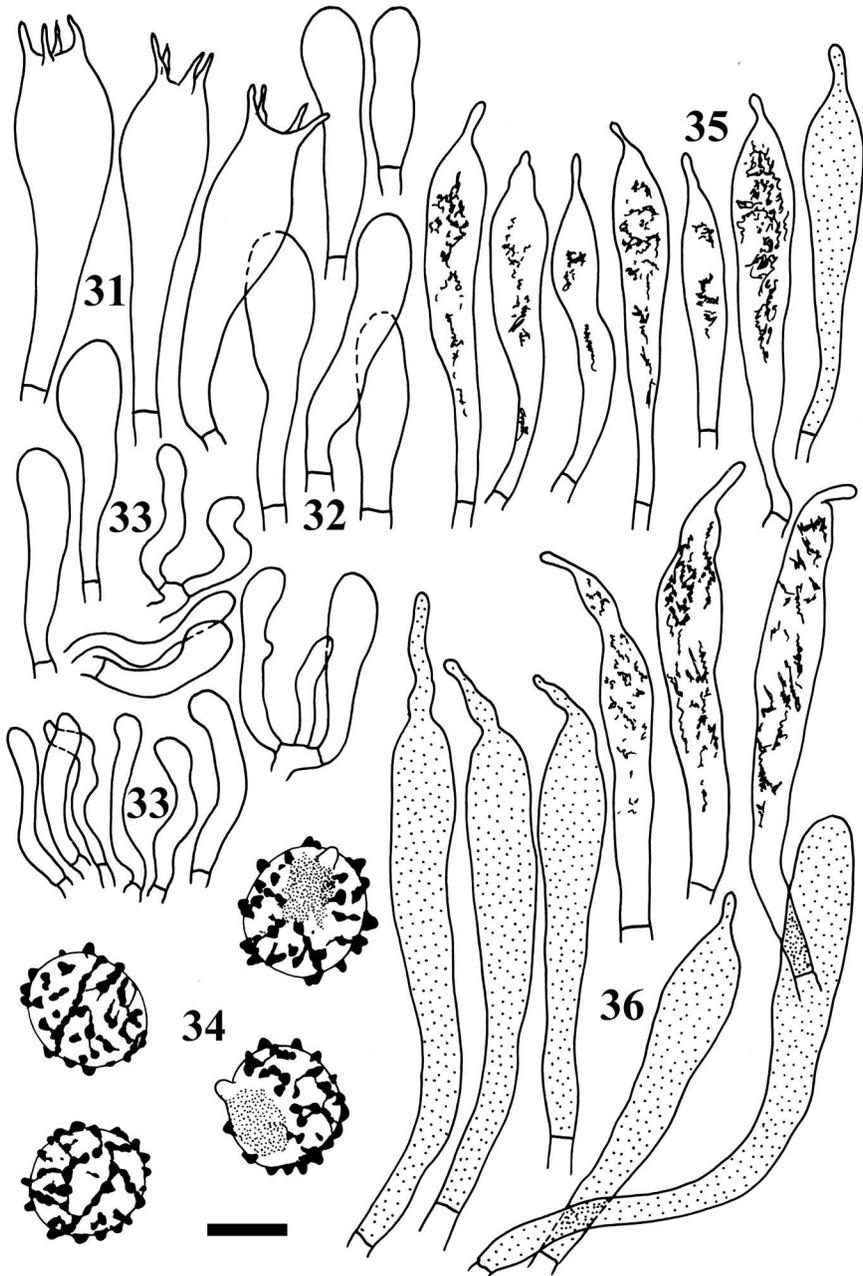
Stanford University, Calif., Nov. 10, 1901, C. F. Baker, no. 156.

*This showy species is somewhat nearly related to *R. veteriosa* Fr. but it may be distinguished by the equal subanastomosing lamellae. It belongs to the section *Fragiles*.*

Spores subglobose (7.9-)8.4-8.9-9.2(-9.5) \times (7-)7.4-7.7-8(-8.2) μm , $Q = (1.09-)1.11-1.14-1.18(-1.22), ornamentation of rather distant (3-5 in a 3 μm diam. circle) amyloid spines, 0.8-1 μm high, fused in often very long chains or crests (0-3 in the circle), with occasional, fine line connections (0-2 in the circle) or a few isolated spines; suprahilar spot amyloid, large. **Basidia** (35-)40.5-44-50 \times (10-)11-12-13 μm , 4-spored, clavate-pedicellate; basidiola first cylindrical than clavate, 4.5-9.5 μm wide. **Subhymenium** pseudoparenchymatic. **Lamellar trama** mainly composed of large sphaerocytes. **Hymenial cystidia** dispersed, ca. 350-400/mm², more numerous towards the gill edge, clavate or fusiform, pedicellate, measuring (54-)60-71-82.5(-91) \times (7-)8-9-9.5(-11) μm on sides, mostly mucronate and acute on tips, with 4-13(-17) μm long appendage, thin-walled, almost completely filled with heteromorphous contents that hardly change color in sulfovanillin. Hymenial cystidia near the gill edge numerous and smaller than pleurocystidia on sides, fusiform or clavate, measuring (34-)40.5-48-56(-60) \times 6-7-8(-9) μm , acute and mostly with 2-7(-10) μm long appendage, thin-walled. **Marginal cells** on the gill edge not well differentiated, similar to basidiola on the gills sides but often narrower and flexuous, obtuse, cylindrical or clavate, measuring (15-)18-22-27(-33) \times 3-4.5-6(-9) μm . **Pileipellis** orthochromatic in Cresyl blue, sharply delimited from trama, ca. 200 μm deep, gelatinized throughout, vaguely divided in approximately two, equally deep layers; suprapellis with very abundant pileocystidia and erect hyphae, gradually passing into irregularly to horizontally oriented, ca. 2-5 μm wide hyphae. Acidoresistant incrustations absent. Hyphal extremities in pileipellis near the cap margin long, filiform, intricate but not fasciculate; the terminal cell attenuated towards the apices, measuring (46-)57-75-94(-125) \times (2.5-)3-4 μm , narrowing apically and mostly slightly widened near the basal septum, flexuous, angulate, indistinctly moniliform, often with lateral nodules or branches, near the cap center often shorter and obtuse, measuring (15-)19.5-32-45(-70) \times 2-3-4.5 μm , often flexuous and nodulose, especially towards apices; subapical cells equal in width to terminal ones, mostly branched. Pileocystidia distinctly dark grey in sulfovanillin, very large and conspicuous, near the cap margin always one-celled, near the cap center occasionally also two and more celled, clavate, obtuse on apex, strongly narrowed towards base, very long, with heteromorphous to granular contents, thin-walled, with terminal cells measuring ca. (75-)120-163-200(-250) \times (7-)7.5-8.5-9.5(-10) μm near the cap margin, and (18-)28-50-73(-95) \times (5-)5.5-7.5-9.5(-13) μm near the cap center, continuing as cystidioid hyphae also in subpellis and trama. **Clamp connections** absent in all parts.$



Figs 28-30. *Russula paxilloides* (lectotype). **28.** Pileocystidia near the cap margin (longer on the left) and near the cap center (shorter on the right). **29.** Hyphal terminations near the cap center. **30.** Hyphal terminations near the cap margin. Cystidial contents as observed in Congo Red, but some elements with contents indicated schematically. Scale bar = 10 μ m.



Figs 31-36. *Russula paxilloides* (lectotype). 31. Basidia. 32. Basidiola. 33. Marginal cells of the gill edge. 34. Spores as seen in Melzer's reagent. 35. Hymenial cystidia near the gill edge. 36. Hymenial cystidia on gill sides. Cystidial contents as observed in Congo Red, but some elements with contents indicated schematically. Scale bar = 10 μ m, but only 5 μ m for spores.

Examined material: UNITED STATES. **California.** Santa Clara Co., foothills near Stanford University, in beds of decaying oak leaves, 30 Nov 1901, *C.F. Baker 156* (NY00654235, lectotypus, here designated; NY00654236).

Commentary: Burlingham (1915) placed this species in *Vinaceae* Burl., which is in agreement with her indication of a white spore print for this species, but not with Earle's original description which mentions a pale yellow spore print. *Russula paxilloides* may represent a good, native American species. In the mycological herbarium of NY there are two specimens, both belonging to the single collection cited in the protologue, one of which (NY00654235) is here designated as lectotype.

Earle (1902) compared *R. paxilloides* with *R. veternosa* Fr., but this relationship seems improbable because of the opposition between the "pale yellow" spore print for the first species and the "deep yellow" spore print of the latter (Romagnesi 1967).

In our opinion, several characters mentioned in the original description suggest that *R. paxilloides* could belong in *Russula* sect. *Persicinae* Romagn.: (1) it has a red cap cuticle that is easily discoloring to white in the center, (2) the spore print is neither yellow nor white but most likely cream to ochre as typical for *Persicinae*, (3) it has locally anastomosing gills as frequently encountered in *Persicinae*, (4) the taste is strongly acrid, (5) it has a fleshy cap becoming quickly thin toward the margin, and (6) it is associated with oak. This study now also reveals a spore ornamentation and mainly one-celled, long and strong SV+ pileocystidia that originate often deep in the subpellis, both being very similar to those of *R. persicina* Krombh., the type species of subsect. *Persicinae*.

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