# Type studies on some *Russula* species described by C.H. Peck

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Abstract – The authors present detailed descriptions of microscopic features for some of the more common *Russula* species described by C.H. Peck from the eastern United States. As a result of these analyses, *R. uncialis* is confirmed as good member of subsect. *Lilaceinae* of subgenus *Incrustatula*. *R. ventricosipes*, *R. pectinatoides* and *R. foetentula* are confirmed as members of subgenus *Ingratula*, with *R. ventricosipes* being closer related to the *R. foetens*-group in the strict sense (= *Foetentinae* sensu M. Bon); with *R. pectinatoides* being related to the *R. amoenolens* group (= *Pectinatinae* M. Bon) and having a different spore ornamentation from what is usually identified under that name in Europe, whereas *R. foetentula* is reinstated as a good, American species that is related to the *R. laurocerasi*-group because of its almond smell. The type of *R. modesta* is clearly different from what is commonly identified as such and is provisionally maintained in a monotypic subsection *Modestinae* within subgenus *Heterophyllidia*. Finally, *R. flaviceps* is transferred from subsection *Integroidinae* to *Chamaeleontinae* in subgenus *Incrustatula*.

Taxonomy / type studies / Russula flaviceps / Russula foetentula / Russula modesta / Russula pectinatoides / Russula uncialis / Russula ventricosipes

## INTRODUCTION

Charles Horton Peck, born March 30, 1833, was one of the earlier North American mycologists. His impact on North American mycology can probably be compared with the impact that the work of E.-M. Fries had in Europe. Very young, Peck developed a keen interest in botany, an interest he would pursuit until his death in 1917 and his career was characterized by an incredible productivity. He was appointed New York State Botanist between 1883 to 1915 (Atkinson 1918, Burnham 1919). Stimulated by his friend botanist, and later mycologist, E.C. Howe, Peck got interested in mycology and started his mycological career at the State Museum in Albany (NY) in May 1868, where he learned the profession from corresponding with senior American mycologists, such as M.A. Curtis, but also with foreign mycologists such as the British M.C. Cooke or the French C. Roumeguère and others. By the end of his career Peck had published some 2700 new fungal taxa (Gilbertson 1962, Petersen 1980), most of these based on his personal collections from New York State and published in the Annual Reports of the State Botanist (1868-1912).

Peck described forty six *Russulas*, including five varieties, most of these collected by himself in New York State, some brought to his attention by others (C.C. Frost, M.E. Banning, W.H. Ballou, F.S. Earle, Marshall & Anderson), sometimes from other parts of the United States. Peck's descriptions were for obvious reasons mainly limited to field characters, but contained sufficient detail and precision to allow for his taxa to be recognized and adopted by others, also because of his contacts with fellow mycologists, e.g. E.P. Morgan, G.F. Atkinson, W.A. Murrill or C.H. Kauffman.

Peck described his fungi based on a single collection that was deposited in his herbarium at the New York State Museum (NYS). These specimens represent "implicit holotypes", i.e. if this single collection and accompanying notes correspond to the protologue, the specimen is the holotype (Petersen 1980). The type of *R. subvelutina* Peck is not deposited in NYS, but in the herbarium of the New York Botanical Garden (NY, see Buyck & Adamčík 2013). During a recent visit to NYS herbarium by one of us (SA), we were unable to locate type specimens for *R. pulverulenta* Peck and also for *R. viridipes* Banning in Peck, the type of which is an illustration cited in the protologue (Peck 1891).

Many of Peck's Russula types have been re-examined in more recent years, but these studies rarely resulted in detailed published accounts of their microscopic features (Hesler 1960, Adamčík & Buyck 2011, 2012, Buyck & Adamčík 2013). Most often, his types were merely cited in "Material examined" with descriptions integrating mainly features of supposedly conspecific specimens (Singer 1958, Bills & Miller 1984, Shaffer 1990, Fatto 1998), a presumption that quite often turned out to be unjustified (e.g. for R. peckii Singer see Adamčík & Buyck 2011; for R. foetentula Peck and R. modesta Peck see below). In this paper, we comment on the type specimens of six widely accepted Russula species described by Peck: R. flaviceps Peck, R. foetentula, R. modesta, R. pectinatoides Peck, R. uncialis Peck and R. ventricosipes Peck.

### 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 sulfovanilin solution, acidoresistant incrustation of primordial hyphae was colored in carbol fuchsin and observed in distilled water after staining for as 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). Years of Peck's publications in Annual Reports of the State Botanist follows Petersen (1980).

### **TAXONOMY**

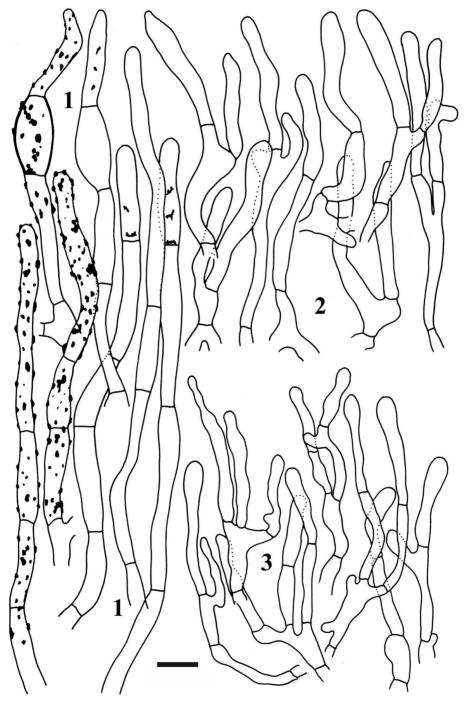
Russula flaviceps Peck, Ann. Rep. N.Y. St. Mus. Nat. Hist. 53: 843. 1902. Figs 1-7 Original description:

Pileus convex, centrally depressed, glabrous, viscid, even on the margin when young, slightly tuberculose striate when old, the thin pellicle separable, pale yellow, flesh white, taste mild or slightly acrid; lamellae close, narrow, adnate, slightly rounded behind, pale yellow becoming more yellow and dusted with spores; stem equal or nearly so, stuffed or spongy within, white; spores yellow, subglobose, .0003 of an inch broad.

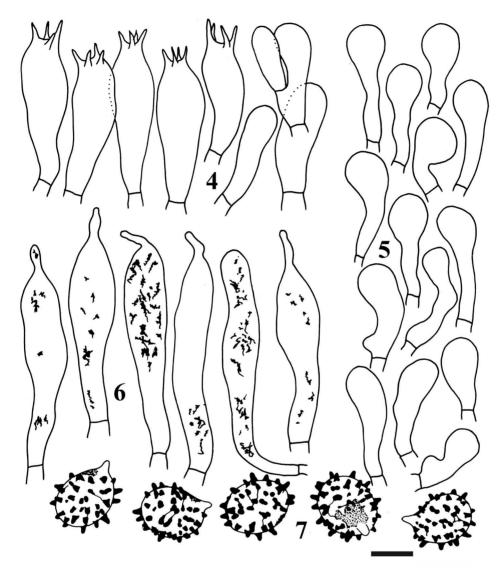
Pileus 2 to 4 inches broad; stem 1.5 to 2.5 inches long, 4 to 8 lines thick. Woods. Claryville. August.

This species belongs to the tribe Fragiles. From R. ochroleuca it may be separated by its yellow lamellae and spores.

**Spores** broadly ellipsoid 7.2- $\underline{7.7}$ -8(-8.4) × 5.8- $\underline{6.3}$ -6.6(-7)  $\mu$ m, Q = (1.17-) 1.20-1.23-1.28, with an ornamentation of moderately distant [4-6(-7) in a 3 μm diam. circle, conical, amyloid spines measuring 0.9-1.1 µm high, connected by infrequent fine line connections and occasionally also fused in pairs or short ridges [0-2(-3) fusions as well as line connections in the circle]; suprahilar plage distinctly amyloid. **Basidia** 28-34-41 × 9-10-12 µm, 4-spored, clavate, rarely fusiform; basidiola first ellipsoid, then clavate. Subhymenium pseudoparenchymatic. Lamellar trama mainly composed of large sphaerocytes. Hymenial cystidia on sides and edges of gills widely dispersed, ca.  $200-400/\text{mm}^2$ ,  $(42-)50-\underline{56.4}-66 \times 8-\underline{9.7}-10.5$ (-11.5) μm, fusiform or rarely clavate, with apices mostly acute and a 3-9(-11) μm long appendix, emerging, mostly pedicellate, thin-walled, in Congo red with few dispersed inclusions but sometimes almost completely filled with heteromorphous refringent contents that hardly react with sulfovanilin. Marginal cells measuring  $(17-)20-24-29) \times (5.5-)7-8.5-9.5(-10.5)$  µm, hardly differentiated from basidiola but slightly more inflated capitate and with an often flexuous, pedicellate, basal part. **Pileipellis** orthochromatic in Cresyl blue, sharply delimited from the underlying sphaerocytes of the context, up to 100 µm deep, including a 10-20 µm deep surface layer of hyaline, gelatinous matrix, vaguely divided in a 30-50 µm deep suprapellis of strongly gelatinized tissue of ascending hyphal terminations becoming more horizontally oriented and less gelatinized, 3-6(-8) µm wide, toward the context. Hyphal extremities of the suprapellis very short, with terminal cells measuring near the cap margin  $(19-)24-30-36(-41) \times (3-)4-4.6-5.5(-6)$  µm and in the cap center  $(15-)16.5-23-29(-38) \times (3-)3.5-4-5(-5.5)$  µm, cylindrical or clavate, obtuse or rarely slightly constricted at the tip, thin-walled; subapical cell branched or not, equal in width or wider, occasionally with lateral branches or nodules. Primordial hyphae comparatively longer than the other extremities and often protruding or repent



Figs 1-3. *Russula flaviceps* (holotype). **1.** Primordial hyphae at pileus surface as observed after karbolfuchsin treatment (on the left) and in Congo red (on the right). **2.** Hyphal terminations near the pileus margin. **3.** Hyphal terminations of the pileus center. Scale bar =  $10 \, \mu m$ .



Figs 4-7. Russula flaviceps (holotype). **4.** Basidia and basidiola. **5.** Marginal cells of the gill edge. **6.** Hymenial cystidia with contents as observed in Congo Red. **7.** Spores as seen in Melzer's reagent. Scale bar =  $10 \mu m$ , but only  $5 \mu m$  for spores.

on the cap surface, occurring singly or with a few clustered together, composed of (2-)3-5(-6) cylindrical cells, especially in the cap center sometimes slightly or distinctly ventricose, in Congo red optically empty or with few inclusions and having a fine glutinous coating especially on terminal cells, which are slightly flexuous, obtuse and measure  $24-\underline{35.5}-47(-76)\times(3.5-)4.5-\underline{5.5}-7$  µm near cap margin and  $(13-)18.5-\underline{32}-45.5(-67)\times3-\underline{4.5}-5.5$  µm in the center, with some more basal cells occasionally ventricose and slightly thick-walled (< 1 µm); incrustations hyaline in Cresyl blue, distinctly red acidoresistant, but with relatively small and dispersed

acidoresistant droplets after carbol fuchsine treatment, negative in sulfovanilin. Cystidioid hyphae in subpellis and trama absent. **Clamp connections** absent in all parts.

Examined material: UNITED STATES. **New York State**. Claryville, Sullivan Co., Aug., C. H. Peck (NYSf1229).

Commentary: Burlingham (1915) classified R. flaviceps in her "Luteae", a group of species with mild taste, yellow cap and yellow spore print. In this group, she classified also R. lutea (Huds.: Fr.) Gray, a species now generally accepted in subsect. Chamaeleontinae Singer of subgenus Incrustatula Romagn., a placement that is also in complete agreement with the characters of R. flaviceps mentioned in Peck's description, although the cap diam. is apparently larger than in European species.

Singer (1943) studied Peck's type and, based on the color and cap size, he concluded that *R. flaviceps* was a synonym of *R. flava* Romell, a species for which the currently accepted name is now *R. claroflava* Grove. The latter is a blackening species similar to *R. vinosa* Lindblad (both are placed in subsect. *Integroidinae* Romagn.) and both should be quite unrelated to Peck's species.

Our observations on the type specimen confirm Burlingham's placement of *R. flaviceps* close to *R. lutea*: yellow cap, fragile context, striated cap margin, yellow spore print, mild taste, primordial hyphae with acidoresistant incrustations and presence of clavate, obtuse hyphal terminations in the pileipellis all suggest subsect. *Chamaeleontinae*. Apart from its relatively large size, *R. flaviceps* differs also from most European *Chamaeleontinae* in its weaker incrusted primordial hyphae and the less distinctly clavate shape of hyphal terminations near the pileus margin.

Russula foetentula Peck, Bull. New York State Mus. Nat. Hist. 116: 85. 1907.

Figs 8-15a

## Original description:

Pileus thin, nearly plane, viscid, glabrous, striate on the margin, reddish yellow, flesh white, taste tardily acrid, odor like that of almonds; lamellae thin, narrow, close, adnexed or nearly free, whitish, the interspaces venose; stem equal, firm, cavernous, white or yellowish white, usually spotted or stained with reddish brown at the base; spores very pale yellow, globose, .0003-.00035 of an inch broad.

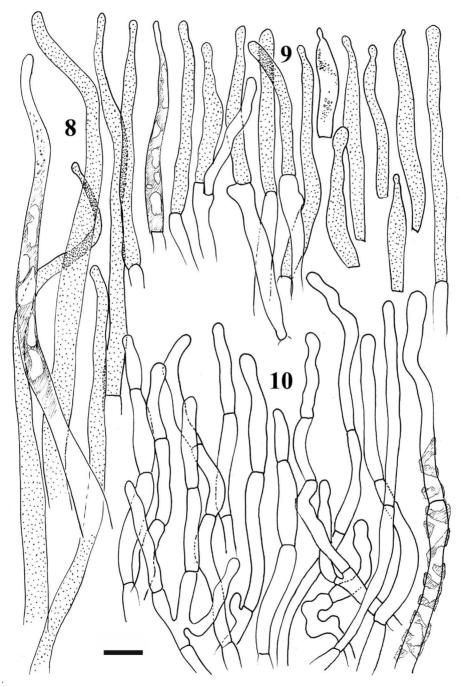
Pileus 1.5-3 inches broad, the stem 1–1.5 inches long, 3-5 lines thick.

Among fallen leaves in woods. Suffolk county. August.

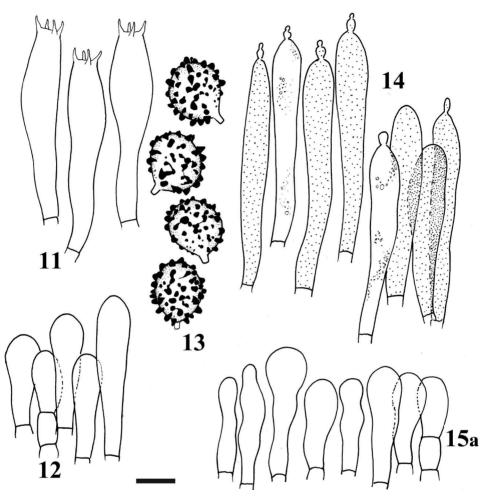
This species is related to R. foetens Fr., to which it is similar in odor but from which it differs in its closer lamellae and reddish brown or burnt sienna color at the base of the stem.

The species reported in State Museum Report 35, page 135 under the name Russula heterophylla Fr. are doubtful and the species is therefore omitted.

**Spores** subglobose to broadly ellipsoid,  $(6.7-)7-\underline{7.3}-7.8\times5.8-\underline{6.1}-6.3$  (-6.6) µm, Q=(1.11-)1.14- $\underline{1.19}$ -1.23(-1.27), ornamented with relatively distant [4-6(-7) in a 3 µm diam. circle], amyloid, conical warts, (0.5-)0.8-0.9 µm high and connected by occasional to rare line connections (0-2 line connections in the circle) or frequently fused in pairs or short ridges and crests [(0-)1-3(-5) fusions in the circle]. Suprahilar spot not amyloid but covered by small amyloid punctuations. **Basidia**  $40-\underline{47}-51(-54)\times9-\underline{10}-11(-12)$  µm, 4-spored, clavate; basidiola first cylindrical, then narrowly clavate. **Subhymenium** pseudoparenchymatic. **Lamellar trama** mainly composed of sphaerocytes, also with yellowish-oily, cystidioid hyphae. **Hymenial cystidia** on sides abundant, ca.  $3500-4000/\text{mm}^2$ , narrowly clavate to narrowly fusiform, thin-walled, with mucronate-appendiculate



Figs 8-10. *Russula foetentula* (holotype). **8.** Cystidioid hyphae in the lower subpellis. **9.** Pileocystidia in pileus center (on the left) and near the pileus margin (on the right). **10.** Hyphal terminations in pileus center (on the left) and near the pileus margin (on the right). Scale bar =  $10 \mu m$ .



Figs 11-15a. Russula foetentula (holotype). **11.** Basidia. **12.** Basidiola. **13.** Spores as seen in Melzer's reagent. **14.** Hymenial cystidia of gill sides (on the left) and on gill edge (on the right) with contents as observed in Congo Red for one element, schematically indicated for the others. **15a.** Marginal cells of the gill edge. Scale bar =  $10 \mu m$ , but only  $5 \mu m$  for spores.

tips up to 2-7 µm long, measuring (50-)54- $\underline{60}$ -65(-70) × 6.5- $\underline{7}$ -8(-8.5) µm, near the gill edge also clavate, obtuse-rounded, rarely longer than 60 µm and with refringent yellowish contents, on gill sides optically empty in Congo red, turning dark black in sulfovanilin, thin-walled. **Marginal cells** undifferentiated from basidiola, measuring (15-)19- $\underline{24}$ -29.5(-33) × 4.5- $\underline{7}$ -9(-10.5) µm. **Pileipellis** orthochromatic in Cresyl blue, not sharply delimited from the trama (underlying context of filamentous hyphae, and sphaerocytes gradually more numerous downward), ca. 300-380 µm deep; vaguely divided in a 40-100 µm deep suprapellis of strongly gelatinized, more or less ascending, sparingly ramified, ca. 3-4 µm wide hyphae, becoming increasingly more irregularly and finally nearly horizontally oriented and much less gelatinized towards the trama. Acidoresistant incrus-

tations absent. Suprapellis very similar between cap center and margin, composed of loosely arranged, repent hyphal terminations, with terminal cells measuring ca.  $17\text{-}30 \times 3\text{-}4~\mu\text{m}$ , or  $(13\text{-})18\text{-}\underline{24\text{-}}31(\text{-}35) \times 3\text{-}\underline{4\text{-}}5~\mu\text{m}}$  in the cap center, cylindrical, with obtuse tips, thin-walled, very flexuous, often moniliform; subapical cells equal in size and sparingly branched, more frequently branched and often with lateral branches or nodules in pileus center. Pileocystidia in pileus center usually one-celled, terminal, measuring  $27\text{-}61\text{-}91(>150) \times 3.5\text{-}4\text{-}4.5(-6)~\mu\text{m}$ , usually constricted to  $1\text{-}2.5~\mu\text{m}$  at the tips, mostly subulate, but some subcylin-drical, narrowly fusiform or lanceolate, thin-walled and toward base with fine glutinous coating visible in Congo red, near the cap margin and in subpellis often very long and with septa difficult to trace,  $4\text{-}7~\mu\text{m}$  wide, but attenuated toward apex; contents yellow, refringent, with negative reaction in sulfovanilin, dark blue-green in Cresyl blue. Cystidioid hyphae with yellowish-oily contents also abundant in subpellis and trama, especially so in lower subpellis, turning distinctly dark grey to black in sulfovanilin. **Clamp connections** absent in all parts.

Examined material: UNITED STATES. **New York State**. Wading River, Suffolk Co., Aug. 1906, C.H. Peck (NYSf1229, holotypus).

Commentary: This is a typical member of subsect. Foetentinae (Melzer & Zvára) Singer of subgenus Ingratula Romagn. as suggested by the viscid, yellow-red cap cuticle with striated margin, the cavernate stipe and also by all of its microscopic features, in particular those of spores and dermatocystidia. The latter are quite different from both other Ingratula here examined in the sense that the form of the pileocystidia that are terminal cells in the suprapellis, is much less distinctly and regularly conical.

R. foetentula is rarely reported from North America, perhaps because Singer (1943) synonymized it with R. foetens var. minor Singer, whereas Shaffer (1972) synonymized it with the European R. subfoetens W.G. Sm. Both these taxa, however, have a very unpleasant smell and different spores. Peck (1907) situated his species near R. foetens Pers., but the distinct almond odor mentioned in the protologue as well as its spore ornamentation suggest otherwise. Indeed, in our experience the presence of an almond smell is a good and reliable character for a Russula species, but the fact that R. foetentula possesses this odor seems largely ignored when considering it a synonym of R. subfoetens. In our opinion, R. foetentula is a good American species which is most likely often misidentified in the field as either R. laurocerasi Melzer or R. fragrantissima Romagn., two European taxa that are frequently reported from the United States but have different spore ornamentations.

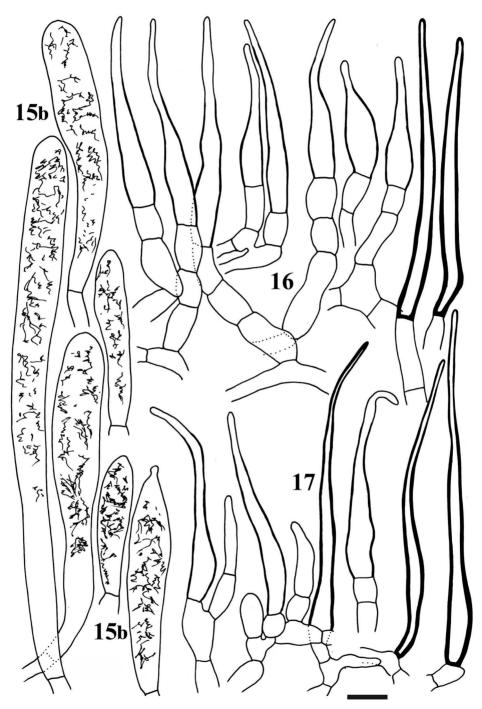
The fact that Peck refers also to the smell of *R. foetens* in the protologue of *R. foetentula* is probably due to a misconception of his, as he was of the opinion that the European *R. foetens* had a strong almond smell (Peck 1907, see also Shaffer 1972). This might also explain why Murrill, who corresponded with Peck, compared the smell of his *R. mutabilis* Murrill equally to *R. foetens* (Murrill 1940). The odor of *R. mutabilis* was later correctly appreciated by Singer, who compared it to maraschino cherries. Whether or not the types of *R. foetentula* and *R. mutabilis* are the same species remains to be examined, but at least in the present concept of *R. mutabilis*, the spore ornamentation of the latter is much more subreticulate.

Russula modesta Peck, Bull. New York State Mus. Nat. Hist. 116: 78. 1907.

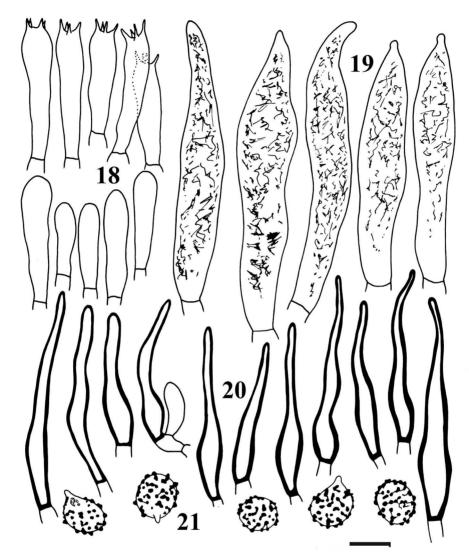
Figs 15b-23

### Original description:

Pileus firm but thin and flexible, broadly convex, becoming nearly plane or centrally depressed, dry, pruinose, even or obscurely striate on the margin, greenish gray,



Figs 15b-17. *Russula modesta* (holotype). **15b.** Pileocystidia with contents as observed in Congo Red. **16.** Hyphal terminations near the pileus margin. **17.** Hyphal terminations in the pileus center. Scale bar =  $10 \ \mu m$ .



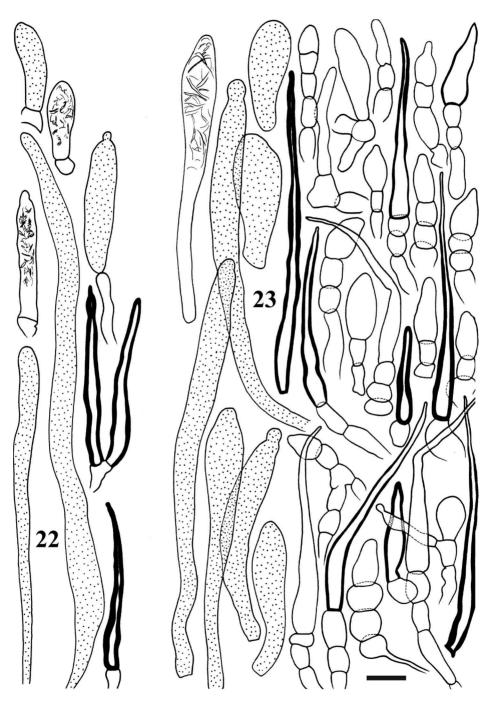
Figs 18-21. *Russula modesta* (holotype). **18.** Basidia (top) and basidiola (below). **19.** Hymenial cystidia with contents as observed in Congo Red. **20.** Marginal cells of the gill edge. **21.** Spores as seen in Melzer's reagent. 16. Scale bar =  $10 \mu m$ , but only  $5 \mu m$  for spores.

paler on the margin, flesh white, taste mild; lamellae thin, close, many forked at the base, a few short ones, narrowed toward each end, adnate or slightly decurrent, white becoming yellowish, the interspaces venose; stem short, cylindric, solid, glabrous, white; spores subglobose, pale yellowish, .00025–.0003 of an inch long, nearly as broad.

Pileus 1-2.5 inches broad, the stem 1-1.5 inches long, 3-5 lines thick.

Woods. Albany county. July.

This species differs from its allies in the pruinose appearance of the surface of the pileus. Under a lens, this is seen to be due to a minute whitish tomentose pubescence. A form of this species with the pileus more distinctly green has been received from Miss T.L. Smith who collected it under oak trees and reports it to be edible.



Figs 22-23. *Russula modesta* (holotype, different specimen). **22.** Caulocystidia and thick-walled terminal cells of stipe surface. **23.** Pileocystidia (on the left) and hyphal terminations in pileus center (on the right). Scale bar =  $10 \mu m$ .

**Spores** broadly ellipsoid, 5-5.4-5.7(-6.2)  $\times$  4.1-4.5-4.7(-5.1)  $\mu$ m, Q = (1.13) 1.16-1.21-1.26(-1.34), with a subreticulate ornamentation of dense, hemispherical to conical warts, [(6-)7-10(-11) warts in a 3 µm diam. circle], 0.3-0.5 µm high, connected by frequent line connections [(0-)1-3(-4) connections in the circle] or fused in short to long chains [(0-)1-4(-5) fusions in the circle]. Suprahilar spot indistinctive, small, inamyloid to rarely somewhat amyloid. **Basidia** 24-28-34 × 6-7-8(-9) µm, 4-spored, clavate; basidiola first cylindrical then clavate. **Sub**hymenium pseudoparenchymatic. Lamellar trama mainly composed of large sphaerocytes. Hymenial cystidia on sides of gills dispersed to numerous (500- $750/\text{mm}^2$ ),  $(52-)67-77-87(-93) \times (9-)10-12-13.5(-15) \, \mu\text{m}$ , mostly fusiform, often minutely capitate-mucronate at the apex, thin-walled; contents heteromorphous, graying in sulfovanilin. **Marginal cells** crowded,  $(32-)39-47-55(-60) \times 4.5-6-7$ (-8) μm, apically attenuated or constricted to 1-2.5(-3.5) μm, subulate to setoid and mostly distinctly thick-walled. Pileipellis orthochromatic in Cresyl blue (or with very weak metachromatic incrustation), sharply delimited from trama; vaguely divided in ca. 125-150 µm deep subpellis of strongly gelatinized, horizontally oriented, intricate, 3-6 µm wide hyphae; and 100-150 µm deep, loose suprapellis; acidoresistant incrustations absent. Hyphal extremities with tapering to aculeate terminal cells,  $(30-)38-\underline{49}-59(-78)\times(4)5-\underline{6.5}-7.5(-8.5)$  µm and in the cap center  $(20-)28-48-67(-92)\times(3.5-)4.5-5-6(-7)$  µm, 1-2(-3.5) µm wide at their apex, mostly with distinctly thickened wall (up to 1 µm), sitting on a short chain of one or more ellipsoid to subglobose cells, 6-10-13(-18) × 4.5-6-7.5(-9) µm, with sparse lateral ramifications particularly in the pileus center. Pileocystidia numerous and very voluminous, near the pileus margin  $50-\overline{78}-106(-140) \times 9.5-\underline{11}-12.5$  µm, and  $22-37-49(-72)\times(7-)8-9-10.5$  µm in the center, one-celled, clavate or ellipsoid, obtuse rounded or sometimes capitate toward the margin, thin-walled, mostly with heteromorphous-banded contents, graying in sulfovanilin. Cystidioid, SV positive hyphae absent from trama, but present in lower subpellis. Clamp **connections** absent in all parts.

Examined material: UNITED STATES. **New York State**. Menands, Albany Co., 20. July 1906, *C.H. Peck* (NYSf1962, holotypus).

Commentary: Because of its mild taste, pale spore print, non-amyloid suprahilar spot and many furcations of the gills (Peck 1907), all past authors agreed on placing R. modesta in what corresponds now to subgenus Heterophyllidia Romagn., but opinions on the most closely related species were less clear-cut. Burlingham (1915), for example, classified this species in her "Crustosae", together with R. crustosa Peck, R. mariae Peck and R. virescens (Schaeff.) Fr. because of the pruinose and minutely granulose appearance of its pileus surface. In his earliest monographs, Singer (1926-1935) inferred close affinities with subsection Lepidinae, but then moved R. modesta closer to R. parazurea Jul. Schaeff. (Singer 1939) and R. grisea (Singer, 1942), before finally adhering to Burlingham's view and placing R. modesta in subsect. Virescentinae Singer or Amoeninae (Singer 1943, 1951). Finally, Singer (1958 onwards) designated R. modesta as the type-species of a new subsection in his Rigidae, subsect. Modestinae Singer, erected for species differing from subsect. Griseinae Jul. Schaeff. either by a white spore print or by the presence of swollen elements in the subpellis (the latter is the case of R. modesta). Singer (1958 onwards), who had studied the type specimen and his own supposedly conspecific collections from Florida, considered R. modesta, although very similar, not closely related to R. parazurea. This is certainly true for the type collections, but not for the current species concept in North America (which is species that is very close related to the European R. parazurea – Buyck unpubl.). Much later, Bills (1984) published a detailed account on *R. modesta* based both on his own examination of the type as well as on many collections from the Southern Appalachians. Bills followed Singer in referring to the terminal cells of normal hyphal extremities in the pileipellis as "acicular to subulate dermatocystidia arising from inflated basal cells" and admitted to the difference in cell wall thickness of these cells between the holotype and all other studied material. We can also confirm Bills' observation that, even now, the holotype of *R. modesta* is still distinctly more yellow than other dried collections of what is commonly referred to as *R. modesta*. In addition, Bills (l.c.) was of the opinion that the *R. modesta* collections from Florida (Singer 1958) were again different from the Appalachian collections studied by himself, as well as from the holotype, having a.o. a different type of spore ornamentation. Bills' conclusion followed Singer's view that *R. modesta* was intermediate between subsections *Amoeninae*, *Virescentinae* and *Griseinae*, but that this species clearly did not fit in either of them.

Our observations on the type of *R. modesta*, as well as on a number of our own collections from the eastern United States, confirm those by Bills and Singer. The difference in length of the terminal cell of the hyphal extremities between different specimens of the same collection or belonging to the same species is not unexpected and has been observed earlier for related species (see Buyck & Ovrebo 2002). However, our long experience with *Russula* from different continents has learned us that the presence of distinctly thick-walled, aculeate elements is clearly an indication for a placement in subgenus *Heterophyllidia*, both in northern temperate and southern tropical countries (Buyck 1994), and that this feature has always revealed itself as extremely consistent with species delimitation. Therefore, we consider both the different aspect of the exsiccatum and the presence of thick-walled cells to be of great importance in deciding on conspecificity between the holotype and more recent collections of *R. modesta*, none of which seem to possess either feature.

In the northern hemisphere, the presence of thick-walled aculeate 'hairs' on the surface of the pileus is the exclusive character of *R. vesca* and *R. heterophylla* Fr. (subsect. *Heterophyllinae* (Fr.) Jul. Schaeff.), whereas in the southern hemisphere this species remarkably resembles the African *R. alveolata* R. Heim in its microscopic features (see Buyck 1994). Not only the overall structure of the pileipellis, but also the crowded, (and in this case thick-walled) ciliate marginal cells of the gill edge (not observed by Bills 1984) are, however, more reminiscent of *Amoeninae*; yet, the presence of typical macrocystidia and dermatocystidia is in conflict with such a placement and more reminiscent of the tropical subsection *Mimeticinae* Buyck (where *R. alveolata* was placed). Our measurements also demonstrate the distinctly smaller spores of the type specimen compared to spores of more recent specimens studied by either Bills or Singer. Therefore, we advise to maintain a monotypic subsection *Modestinae* for this species and to restrict the use of the name "*R. modesta*" only to the type specimen.

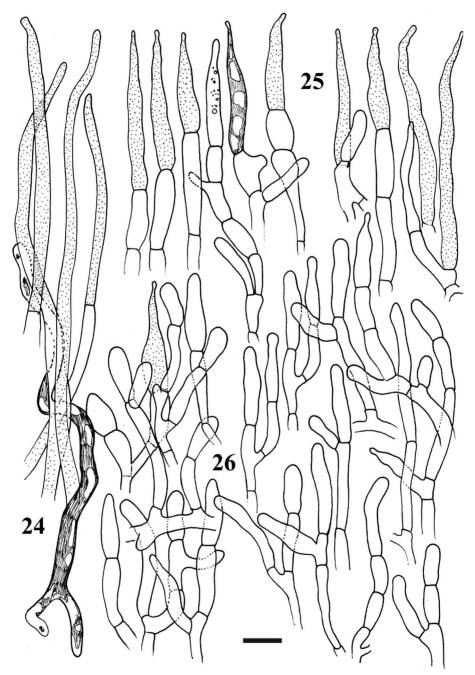
As Bills (1984) already mentioned, there is probably more than one species hiding under what is now commonly identified as *R. modesta*. Some of these species may have been described by Murrill who has named quite a number of species that come in shades of green.

Russula pectinatoides Peck, Bull. New York State Mus. Nat. Hist. 116: 43. 1907.

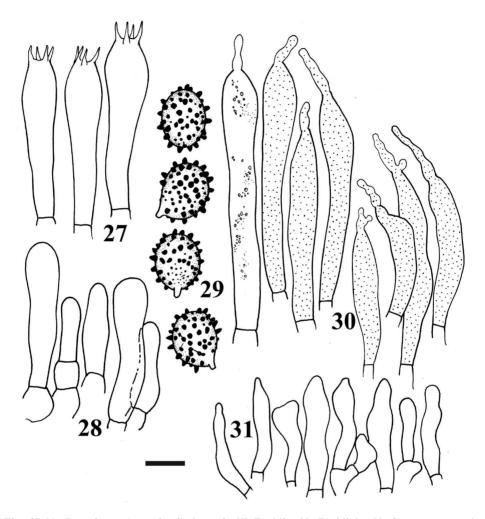
Figs 24-31

### Original description:

Pileus thin, broadly convex becoming nearly plane or centrally depressed, viscid when moist, widely tuberculose striate on the margin, brownish or yellowish brown,



Figs 24-26. Russula pectinatoides (holotype). **24.** Cystidioid hyphae in the lower subpellis. **25.** Pileocystidia in pileus center (on the left) and near the pileus margin (on the right). **26.** Hyphal terminations in pileus center (on the left) and near the pileus margin (on the right). Pileocystidia with contents as observed in Congo Red for one or two elements, schematically indicated for the others. Scale bar =  $10 \mu m$ .



Figs 27-31. Russula pectinatoides (holotype). 27. Basidia. 28. Basidiola. 29. Spores as seen in Melzer's reagent. 30. Hymenial cystidia of gill sides (on the left) and on gill edge (on the right) with contents as observed in Congo Red for one element, schematically indicated for the others. 31. Marginal cells of the gill edge. Scale bar =  $10 \mu m$ , but only  $5 \mu m$  for spores.

sometimes darker in the center, flesh white, grayish white under the separable cuticle, taste mild or slightly acrid; lamellae thin, a few forked at the base, occasionally a short one, adnate, white becoming pallid; stem equal, spongy within, even, glabrous, white; spores whitish, subglobose, .00025-.0003 of an inch long.

Grassy ground in groves or pastures. The pectenlike russula is similar to Russula pectinata (Bull.) Fr. from which it differs in its mild or slightly acrid flavor, its even stem, in its flesh being grayish white under the cuticle and in its adnate gills. It is gregarious or scattered in its mode of growth and is not plentiful. It closely resembles Russula sororia Fr. in its general appearance, but may be separated from it by its milder taste.

Its cap is 1-3 inches broad; its stem is 1-2 inches long and 3-4 lines thick. It appears in July and August. It is edible but not very highly flavored.

**Spores** ellipsoid,  $(6.1-)6.5-6.8-7.2(-7.7)\times(5.2-)5.4-5.6-5.9(-6.1) \mu m$ , Q = (1.14-)1.17-1.22-1.26(-1.38), ornamented with moderately distant [(4-)5-7(-8) in a 3 µm diam. circle] obtuse, amyloid warts, 0.5-0.7 µm high, occasionally connected by line connections [0-1(-2) line connections in the circle] or fused in pairs or short ridges [0-2(-4) fusions in the circle]. Suprahilar spot not or indistinctly amyloid, covered by minute, irregularly dispersed warts. **Basidia** 32-40-44.5(-49) × 7.5-9-10.5 µm, 4-spored, narrowly clavate, pedicellate; basidiola first cylindrical, then narrowly clavate. **Subhymenium** pseudoparenchymatic. **Lamellar trama** mainly composed of large sphaerocytes, also with cystidioid hyphae with yellowish-oily contents. **Hymenial cystidia** on gill sides moderately numerous, ca. 700-1100/mm<sup>2</sup>,  $(42-)54.5-\underline{63}-71.5(-77)\times(6-)6.5-\underline{7.7}-8.5(-9.5)$  µm, narrowly clavate to narrowly fusiform, thin-walled, with often repeatedly constricted, mucronate-appendiculate apices, 5-13 µm long, occasionally bearing also a lateral knob, on the gill edge rare, mostly fusiform and more attenuated apically, some slightly smaller; contents optically empty to yellowish refringent in Congo red, distinctly graying in sulfovanilin. Marginal cells crowded, little differentiated, measuring (10-)13-19- $24(-30) \times 3.5$ -5-6.5 µm. **Pileipellis** orthochromatic in Cresyl blue, sharply delimited from the underlying sphaerocytes of the context, ca. 100-140 µm deep; composed of 3-4 µm wide hyphae that are strongly gelatinized and more or less ascending near the surface, becoming more horizontal, denser and gradually less gelatinized towards the trama. Acidoresistant incrustations absent. Hyphal extremities with cylindrical or clavate, obtuse terminal cells, measuring (9-)12-18-24 × (3-)3.5-4-4.5(-5) µm, up to 36 µm long toward pileus margin, thin-walled, arising from cylindrical subapical cells with similar diam. and sometimes branched. Pileocystidia especially abundant and almost clustered in the pileus center, near margin more dispersed, one-celled,  $(19-)22-34-46(-62) \times (3-)3.5-4-5(-5.5)$  µm, up to 7 µm diam. in the pileus center, subulate to setiform and strongly narrowing toward the apex, mucronate towards the pileus margin, thin-walled, in Congo red with refringent (especially near tips) but not heteromorphous contents, often originating from one shorter unbranched basal cell, thin walled, weakly react in sulfovanilin. Cystidioid hyphae with yellowish-oily contents abundant in subpellis and trama, especially so in the lower subpellis. Clamp connections absent in all parts.

Examined material: UNITED STATES. **New York State**. Menands, Albany Co., Aug. 1906, *C.H. Peck* (NYSf2303, annotated as lectotype by R. Shaffer).

Commentary: The holotype of R. pectinatoides consists of approximately 19 basidiomata in the received material, one of which clearly belongs to a different species as already observed by Shaffer (1972). Since the original publication, published accounts of the re-examination of the type specimen were published by Singer (1958), Hesler (1960) and Shaffer (1972). Yet, apart from the short comments by Hesler, both other accounts presented a mixed description integrating also features observed on more recent collections that were presumed to be conspecific.

The present description of the type specimen is therefore the first modern revision exclusively based on the original material with all measurements based on a single basidioma annotated as such inside the type specimen. It is an essential first step toward the correct interpretation of a species that has been the subject of a lot of confusion since its original description, not only in America but in the whole northern hemisphere. *R. pectinatoides* is, for example, one of the few North American *Russula* that has been identified from Europe, where it was generally accepted as a common and widespread species (e.g. Einhellinger 1994, Romagnesi 1967), for which the principal characters seems the absence of a distinctly acrid taste. Singer's (1958) interpretation of *R. pectinatoides* most likely lumped more

than one species and the resulting variation in spore ornamentation covered easily also those of several European taxa. Also Romagnesi (1967) was well aware of the difficulty of delimiting taxa within this species-complex and his *Russula* monograph offered a key to eight distinct forms and varieties based on cap color, taste, spore print color, spore ornamentation and features of macrocystidia. Sarnari (1998) took an important step in the good direction by describing *R. praetervisa* Sarnari as a species corresponding to nearly identical specimens having distinctly subreticulate spores: the dominant taxon in the Mediterranean area. Nevertheless, the question still remains whether or not Peck's species occurs in Europe. Our observations on the type show a spore ornamentation composed of nearly always isolated, conical to almost cylindrical warts of variable size but, on average, relatively tall and stout. This type of ornamentation is rarely (ever?) encountered in European collections identified as Peck's species (Romagnesi, 1967).

There can be no doubt about the correct placement of *R. pectinatoides* in subgenus *Ingratula*, where Peck himself correctly situated it in the proximity of *R. sororia* Fr. and *R. pectinata* Fr. *R. pectinata* is also considered its closest match by Romagnesi, but it is not a commonly identified species in Europe (see Kibby 2005). It is recognized by strongly yellowish cap colors, a short, stout stipe with frequent reddish-brown stains at the base and lamellae with an extremely acrid taste allowing for an easy distinction from Peck's species.

Russula uncialis Peck, Bull. New York State Mus. Nat. Hist. 1 (2): 10. 1887.

Figs 32-39

## Original description:

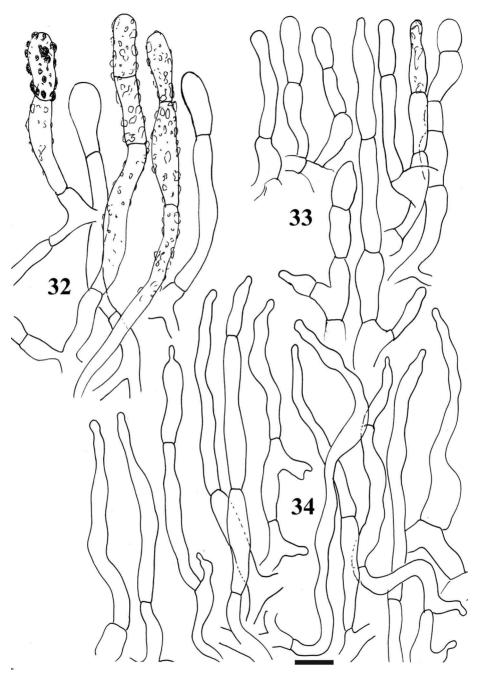
Pileus thin, convex, then expanded or centrally depressed, viscid when moist, glabrous or very minutely rivulose-granulose, red or pinkish-red, the margin obscurely tuberculose-striate, flesh white; lamellae moderately close, narrowed toward the stem, at which a few of them are sometimes forked, adnate or slightly emarginate, white, the interspaces venose; stem equal, glabrous, stuffed or spongy within, white or reddish; spores white, globose, rough, .0003 to .00035 in. in diameter; taste mild.

Plant 1 to 1.5 in. high, pileus 1 to 1.5 in. broad, stem 2 to 4 lines thick.

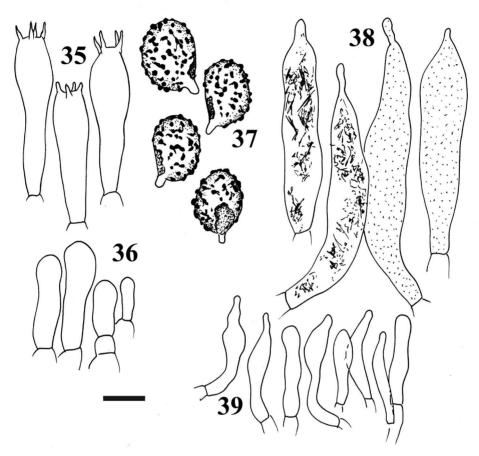
Thin woods. Sandlake. June and July.

A small species generally about 1 in. high, with the pileus about the same in breadth. Like the preceding species, to which it is closely related, it belongs to the whitespored group of the section FRAGILES, a group to which Europe contributes but a single mild species. The color of the pileus is nearly uniform and generally a pale-red or pinkishred. The lamellae in the fresh plant are white, but in the dried specimens they are pallid.

**Spores** narrowly ellipsoid,  $(6.9-)7.3-7.7-8.1(-8.7)\times5-5.5-5.8(-6.1)$  µm, Q=(1.29-)1.34-1.4-1.46(-1.56), with an ornamentation composed of dense [6-8(-9)] in a 3 µm diam. circle], low warts, 0.2-0.3 µm high, connected by occasional line connections [0-2 line connections in the circle], or merged in short chains [(1-)2-4(-6) fusions in the circle]. Suprahilar plage amyloid. **Basidia** 28-32.5-35(-39) × 8.5-9.4-10.5 µm, 4-spored, narrowly clavate; basidiola clavate or subcylindrical, ca. 4-8 µm wide. Subhymenium pseudoparenchymatic. Lamellar trama mainly composed of large sphaerocytes. **Hymenial cystidia** on sides of gills dispersed, ca. 600/mm<sup>2</sup>, fusiform, acute apices with short appendage, measuring ca. 44-68 × 9-11 µm, thin-walled, in Congo red with granulose-heteromorphous content, but sometimes with clear content, after a long time weakly react in sulfovanilin. Marginal cells on edge of gills not well differentiated, similar to basidiola but narrower and longer. Pileipellis orthochromatic in Cresyl blue, sharply delimited from the underlying sphaerocytes of the context, vaguely divided in a dens, ca. 60-80 µm deep subpellis of irregularly oriented and inflated hyphae that form pseudoparenchymatic structure and a less dense, ca. 50 µm deep suprapellis of



Figs 32-34. Russula uncialis (holotype). 32. Primordial hyphae at pileus surface (for some with indication of incrustations as observed after karbolfuchsin treatment. 33. Hyphal terminations of the pileus center. 34. Hyphal terminations near the pileus margin. Scale bar =  $10~\mu m$ .



Figs 35-39. *Russula uncialis* (holotype). **35.** Basidia. **36.** Basidiola. **37.** Spores as seen in Melzer's reagent. **38.** Hymenial cystidia of gill sides with contents as observed in Congo Red for two elements, schematically indicated for the others. **39.** Marginal cells of the gill edge. Scale bar =  $10 \mu m$ , but only  $5 \mu m$  for spores.

aeriferous, repent or erect hyphal tips. Incrustation present only in suprapellis on primordial hyphae, acidoresistant after treating in carbol fuchsin, visible also in Cresyl blue (hyaline and opalescent). Terminal cells of hyphae in pileipellis near margin of the cap measuring (15-)34-50.2-66.5(-93) × 3.5-4.8-5.5(-7.5) μm, mostly subulate-attenuated, flexuous, moniliform, always with distinctly constricted (1-3 μm) tips, sometimes slightly inflated in central or basal part, subapical cells usually broader, mostly branched, sometimes nodulose, usually implemented in subpellis. Hyphal endings in the center of pileipellis distinctly shorter, unbranched, with terminal cells measuring (8-)11-16.7-22.5(-29) × 4-4.6-5(-6) μm, cylindrical, blunt, regular, with one or two unbranched, cylindrical basal cells arising from pseudoparenchymatic subpellis. Primordial hyphae with mostly two septa, usually protruding over undifferenciated hyphae, thin-walled, with terminal cells measuring (12-)13-18.5-24(-33) × 4-5.1-6(-7) μm, near margin of cap in Congo

red with clear content, but in the center narrower and with heteromophousopalescent inclusions in the terminal cell, acido-resistant incrustation present in form of large red drops on surface, sulfovanilin negative. Cystidioid hyphae in subpellis and trama of cap absent. **Clamp connections** absent in all parts, trama not coloring bright red in sulfovanilin.

Examined material: UNITED STATES. **New York State**. Sandlake, Rensselaer Co. June, C.H. Peck (NYSf3274, holotypus).

Commentary: R. uncialis is one of the oldest names published for North American Russulas and it has been referred to in several publications as a good species of subsect. Lilaceinae (Melzer & Zvára) Jul. Schaeff. (Fatto 1998, Kibby & Fatto 1990, Singer 1951, 1975, 1986), a placement that seems indeed perfectly justified.

Mild taste, white spore print and strongly incrusted primordial hyphae are typical for *Russula* subsections *Roseinae* and *Lilaceinae* of subgenus *Incrustatula* Romagn. The typical bright red reaction of the trama to sulfovanilin is indecisive, but may be due to the old age of the type (see also for *R. nigrescentipes* in Adamčík & Buyck 2012). The strongly incrusted primordial hyphae are mostly two-celled and show a distinct acidorestistant reaction when treated with karbol-fuchsin contrary to the observations of Fatto (1998).

It is worth to mention that the spores of the type are narrowly ellipsoid (Q > 1.3) which is not a common character within the genus and may help in distinguishing this species from close allies.

Russula ventricosipes Peck, Bull. Torrey Bot. Club 29: 70. 1902. Figs 40-47

Original description:

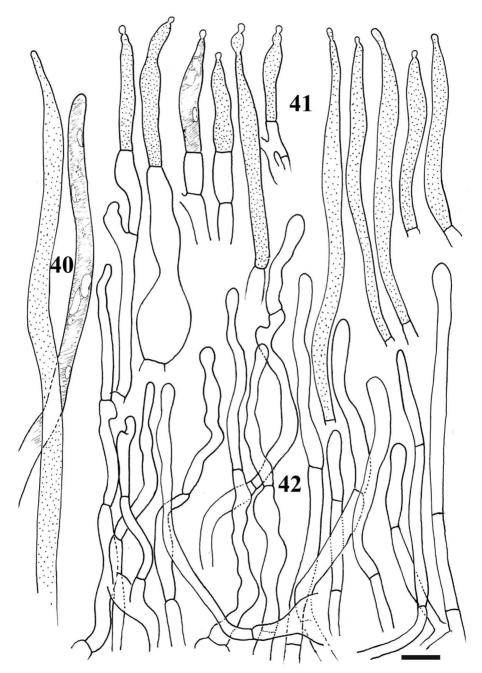
Pileus thin, broadly convex, nearly plane or sligtly depressed in the center, glabrous, varying in color from tawny yellow to pale alutaceous; flesh white; lamellae thin, narrow, close, slightly sinuate, adnate, white or whitish, becoming discolored in drying; stem stout, firm, ventricose, solid, or somewhat spongy within, subglabrous, whitish above, reddish toward the pointed base; spores broadly elliptic or subglobose, 6-8 µm long, 6 µm broad.

Pileus 5-7 cm. broad; stem 5-7 cm. long, about 2.5 cm. thick in the middle, more narrow toward each end.

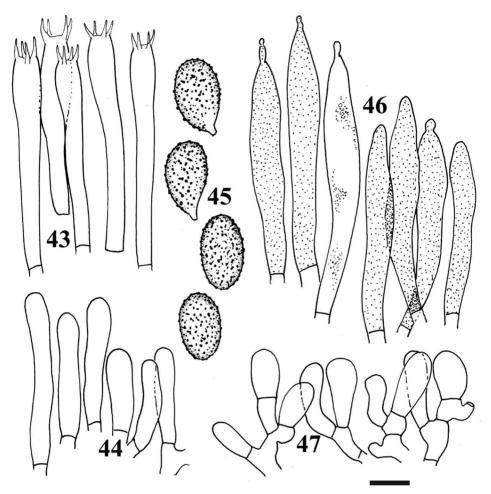
Sandy soil under or near pine trees. South Yarmouth, Mass. October. S. Davis.

A singular species resembling in some respects Tricholoma compactum, but apparently a Russula. Remarkable for the thin, slightly sinuate lamellae and the stout ventricose stem which seems out of proportion to the small thin pileus.

**Spores** narrowly ellipsoid to oblong,  $(7.4-)7.9-8.6-9.3(-10.5) \times 4.7-5.3-5.8$  $(-6.7) \mu m$ , Q = (1.47-)1.53-1.62-1.71(-1.84), with a dense ornamentation of mostly isolated, obtuse, low to hardly perceptible warts, [(7-)8-10(-11) in a 3 µm diam. circle], 0.1-0.2 µm high, and very rarely some hardly perceptible, short, line connections [0-1 line connection in the circle], more frequently with fusions in pairs or short ridges [0-4(-6) fusions in the circle]. Suprahilar plage indistinct, not amyloid. Basidia remarkably slender,  $(39-)44-50-55(-58) \times 6-6.5-7(-8)$  µm, fourspored, subcylindrical to narrowly clavate. Subhymenium pseudoparenchymatic. Lamellar trama mainly composed of sphaerocytes, with abundant, cystidioid hyphae with yellowish-oily contents, especially just underneath the subhymenium. **Hymenial cystidia** on sides numerous, ca.  $1800-3000/\text{mm}^2$ ,  $(49-)59-\underline{66}-76\times6.5-\underline{7.5}$ 8.5 µm, similar but slightly shorter on gill edge, narrowly fusiform, thin-walled, and except near the gill edge often with mucronate to appendiculate tips up to 7 µm long; contents yellowish-oily, strongly blackening in sulfovanilin. Marginal cells undifferentiated, somewhat shorter than basidiola, (11-)13-18-23(-27) × 4.5-5.5-7(-8) µm. Pileipellis orthochromatic in Cresyl blue, sharply delimited from the underlying sphaerocytes of the context, forming a 200-250 µm deep ixocutis,



Figs 40-42. Russula ventricosipes (holotype). **40.** Cystidioid hyphae in the lower subpellis. **41.** Pileocystidia in pileus center (on the left) and near the pileus margin (on the right). **42.** Hyphal terminations in pileus center (on the left) and near the pileus margin (on the right). Pileocystidia with contents as observed in Congo Red for one or two elements, schematically indicated for the others. Scale bar =  $10 \mu m$ .



Figs 43-47. Russula ventricosipes (holotype). **43.** Basidia. **44.** Basidiola. **45.** Spores as seen in Melzer's reagent. **46.** Hymenial cystidia of gill sides (on the left) and on gill edge (on the right) with contents as observed in Congo Red for one element, schematically indicated for the others. **47.** Marginal cells of the gill edge. Scale bar =  $10 \mu m$ , but only  $5 \mu m$  for spores.

strongly gelatinized throughout and vaguely divided in a 100-120  $\mu$ m deep suprapellis of irregularly and sparsely arranged hyphae; and a 100-130  $\mu$ m deep subpellis of more horizontally oriented hyphae. Acidoresistant incrustations absent. Hyphal terminations loosely arranged, slender, with distant septa and sparsely branched, with terminal cells measuring (18-)29-41-56(-72)  $\times$  3-4-4.5 (-5.5)  $\mu$ m, cylindrical, often slightly flexuous in the pileus center, thin-walled; subapical cells of equal diam., sometimes branching, the more basal cells of some larger hyphal terminations occasionally with glutinous incrustations in Congo red. Pileocystidia with terminal cells measuring (25-)29.5-48-67(-101)  $\times$  3-4.5-5.5(-8)  $\mu$ m, one celled (rarely two or more celled), narrowly fusiform, subulate, subcylindrical, lanceolate, thin-walled, mostly with 1-3(-5)  $\mu$ m large capitulum,

thin walled; contents in Congo red refringent, yellowish-oily, weakly reacting in sulfovanilin, dark blue-green in Cresyl blue. Cystidioid hyphae with yellowish-oily contents also abundant in subpellis and trama, especially so in lower subpellis. **Clamp connections** absent.

Examined material: UNITED STATES. Massachusetts. South Yarmouth, Barnstable Co., Oct., S. Davis (NYSf3345, holotypus).

Commentary: Peck (1902) described R. ventricosipes as a species with a remarkably tall, ventricose stipe in comparison with the small, thin pileus, something which, in our experience, corresponds to a rather atypical development for this species. Peck (1902) did not mention any closely related taxa and it was Burlingham (1915) who first suggested a placement in subgenus Ingratula (as "Pectinatae") and who correctly observed the narrowly ellipsoid to oblong spores, so unique for this species, as opposed to the "broadly elliptic to subglobose" spores mentioned in Peck's description (another indication for the unusual development).

Both Singer (1942) and Shaffer (1972) re-examined the type and have published very detailed descriptions for this species, but these were mainly based on other collections. *R. ventricosipes* is in fact a common and easily recognizable species that has a very specific habitat, being exclusively associated with pine on sandy soils. Its most evident field character lies in the very strong reddish tints that usually develop, particularly at the stipe base (Peck's description mentions the reddish stipe base), but even very young specimens can exude abundant blood red droplets all over the hymenophore (Buyck unpubl.). Singer (1942) noted the presence of an abundant incrusting pigment on dermatocystidia and hymenial cystidia of fresh specimens, but we were unable to detect this pigment in the type. However, whereas Shaffer (1972) admitted to complete absence of this pigment also in more recently dried specimens, we have observed sometimes abundant pigment incrustations turning the entire gill edge reddish in 15 year old herbarium specimens.

R. ventricosipes is clearly related to the R. foetens group (sensu stricto) where it occupies a special, probably quite basal position because of the abovementioned, unusual features. R. roseiisabellina Murrill (see Adamčík & Buyck 2011) has a very similar spore ornamentation, but less oblong spores and a white spore print (as opposed to the IIc-d spore print of R. ventricosipes [fide Shaffer]).

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