

**Type-studies in American *Russula*  
(Russulales, Basidiomycota): species of subsection  
*Decolorantinae* described by H.C. Beardslee,  
G.S. Burlingham and W.A. Murrill**

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**Abstract** – In this new contribution on russulas from the southeastern United States, the authors focus on four species that exhibit a blackening context: *R. burkei* Burl., *R. subdensifolia* Murrill, *R. cinerascens* Beardslee and *R. magna* Beardslee. In the past, every single one of these species has been related to *Russula* subgenus *Polychromidia* Romagn. subsection *Decolorantinae* R. Maire. Based upon the study of their type-specimens, all of the species here redescribed and illustrated are good members of *Decolorantinae* with a possible exception of *R. subdensifolia* which might be related to a group of pale-spored, blackening species that might be more tropical. Possible synonyms and related species are discussed. *R. burkei*, *R. cinerascens* and *R. magna* are here lectotypified.

***Russula magna* / *Russula subdensifolia* / *Russula cinerascens* / *Russula burkei* /  
lectotypification / United States / east coast**

## INTRODUCTION

This paper is part of an ongoing revision of the microscopic features of all existing type material of North American *Russula* Pers. (Agaricomycotina), an initiative that has already resulted in many remarkable changes in species concepts and their subsequent classification (Adamčík & Buyck 2010, 2011; Buyck & Adamčík 2011a,b,c). In this new contribution on russulas from the southeastern United States, the authors focus on four species that exhibit a blackening context: *R. burkei* Burl., *R. subdensifolia* Murrill, *R. cinerascens* Beardslee and *R. magna* Beardslee. In the past, every single one of these species has been considered as being related to the species group around *R. decolorans* (Fr.: Fr.) Fr, although Singer (1986), in the latest edition of his “Agaricales”, classified *R. magna* in subsection *Vinosinae* Singer (syn. subsection *Integroidinae* Bon), a group of taxa with strongly graying flesh that lack pileocystidia but possess instead “primordial hyphae” at the cap surface. Apart from *Decolorantinae* R. Maire and *Vinosinae*, strongly graying to blackening context is also typical for many species in subgenus *Compacta* (Fr.) Bon, whereas a distinctly weaker graying of the flesh is observed in several individual species belonging to various groups in the genus and seems in some cases accentuated by cold, wet weather conditions (e.g. *R. ochroleuca* Pers.).

## 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 of a few seconds in a 10% solution of HCl (cf. Romagnesi 1967).

Spores were scanned with an Olympus Artcam camera and measured using Quick Micro Photo (version 2.1) software. Enlarged scanned pictures of spores were used for measuring with an accuracy of 0.1  $\mu\text{m}$  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). The infrageneric classification of the genus *Russula* follows Romagnesi (1967, 1985).

## TAXONOMY

*Russula burkei* Burl., *Mycologia* 16 (1): 21. 1924

Figs 1-8

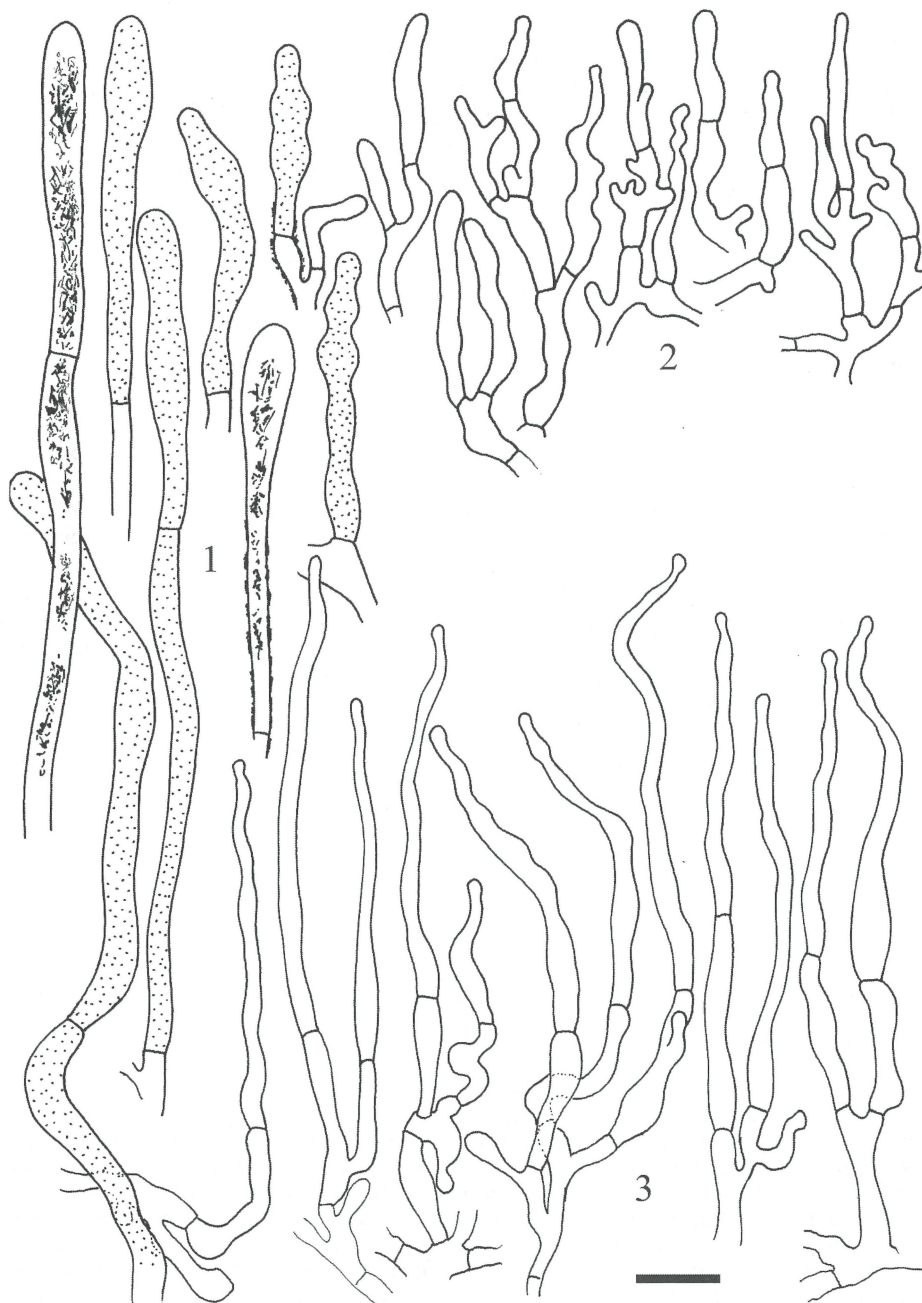
### Original description

*Pileus convex, becoming expanded with depressed, subumbilicate center, 5.5 to 7 cm. broad; surface madder-brown on the disk, shading outwards to tawny-olive, and occasionally clay-colored spots, the colors being somewhat intermingled over the central portion, viscid with pellicle separable part way to the center, glabrous, margin even, sometimes broadly undulate; context very compact and firm, white to smoky, becoming slowly vinaceous-drab where cut, slowly very acrid, odor somewhat like Russula foetens; lamellae white, not stained with spots, yellow in drying, equal, few or none forking, narrowed behind, rounded in front, crowded; stipe white becoming blackish-gray internally with age and somewhat discolored externally where bruised, slightly ridged, stuffed but not fragile, 4 cm. long, 1.8 cm. thick; spores pale-ecru (66, t. 1), nearly globose, very minutely tuberculate, apiculate,  $6.25\text{-}7.5 \times 7\text{-}8.75 \mu$ .*

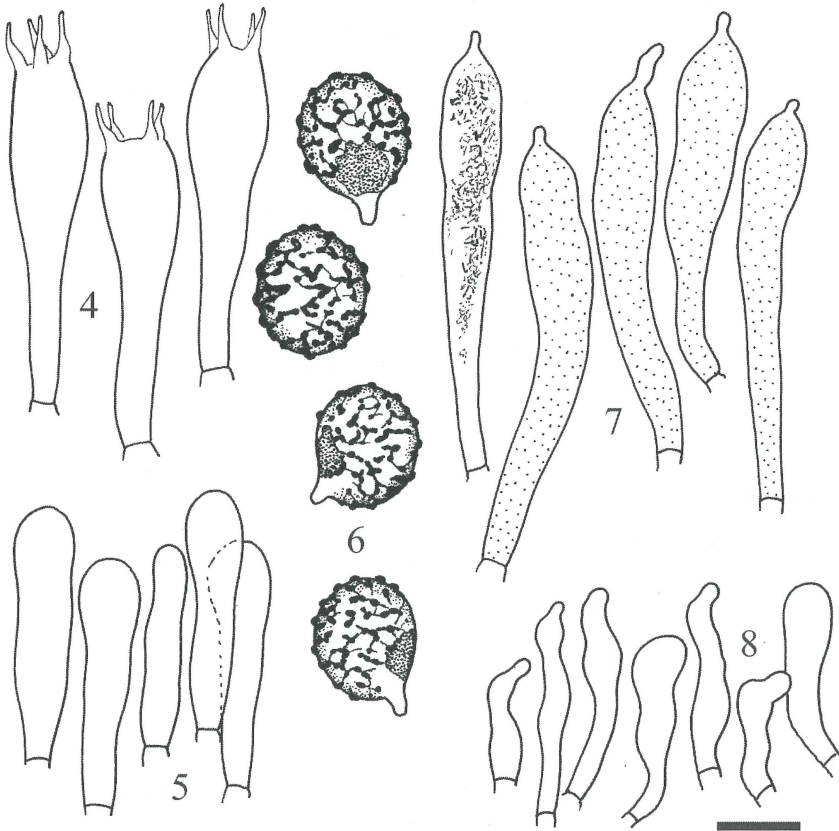
*TYPE LOCALITY:* Montgomery, Alabama.

*HABITAT:* Mixed woods. Type collected by Dr. R. P. Burke, July 23, 1921.

*This species resembles Russula obscura, and Russula rubescens and Russula cinerascens in the change in the color of the flesh. It differs in its acrid taste and disagreeable*



Figs 1-3. *Russula burkei* (lectotype). 1. Pileocystidia with contents indicated in one element as seen in Congo red. 2. Hyphal extremities in the cap center. 3. Hyphal extremities near the cap margin. Scale bar equals 10  $\mu$ m.



Figs 4-8. *Russula burkei* (lectotype). 4. Basidia. 5. Basidiola. 6. Basidiospores in Melzer's reagent. 7. Pleurocystidia with contents indicated in one element as seen in Congo red. 8. Marginal cells. Scale bar equals 10  $\mu\text{m}$ , but only 5  $\mu\text{m}$  for spores.

*odor from Russula cinerascens, in color, in taste, and in the spore markings from the others. In the dried state the pileus is brownish drab (302), except in the center, where it is nearly black. The lamellae in dried specimens are isabelline (309, t. 4). The flesh of the pileus shows blackish between the bases of the lamellae. The description has been arranged from notes made by Dr. Burke, and the colors of the fresh mushroom are named according to Ridgeway.*

**Spores** (7.2-)7.5-8-8.4(-9)  $\times$  6.3-6.7-7.1(-7.9)  $\mu\text{m}$ , Q=(1.13-)1.14-1.19-1.23(-1.36), ornamentation subreticulate, composed of numerous [(7-)8-11(-12) amyloid warts in a 3  $\mu\text{m}$  diam. circle on the spore surface] warts measuring 0.2-0.3  $\mu\text{m}$  high, connected with frequent line connections [2-4(-5) line connections in the circle], frequently fused in rather long chains or crests that are often branched [(1-)4-8(-9) fusions in the circle]; suprahilar plage amyloid. **Basidia** (36-)38.5-42.6-47(-49)  $\times$  (9.5-)10-11.3-12.5(-13)  $\mu\text{m}$ , 4-spored, clavate-pedicellate; basidiola first cylindrical, then narrowly clavate. **Subhymenium** pseudoparenchymatic. **Lamellar trama** mainly composed of large sphaerocytes. **Hymenial cystidia** numerous, ca. 1800/mm<sup>2</sup>, measuring (44-)49-57-65(-72)  $\times$  (7-)7.5-8.6-9.5(-10.5)  $\mu\text{m}$  on gill sides, clavate, pedicellate, mucronate to appendiculate with a 3-6.5(-13)  $\mu\text{m}$  long appendage,

thin-walled, almost completely filled with heteromorphous contents. **Marginal cells** very slender, small compared to the basidioles, mostly cylindrical or narrowly clavate, occasionally fusiform, slightly flexuous, with obtuse or narrowed tips, measuring  $(10.5\text{-})13\text{-}18.4\text{-}23.5\text{-}(27) \times 3\text{-}4.2\text{-}5\text{-}(6) \mu\text{m}$ . **Pileipellis** orthochromatic in cresyl blue, not sharply delimited from the underlying sphaerocytes of the context, vaguely divided in a 40-50  $\mu\text{m}$  deep, strongly gelatinized suprapellis of loosely intermixed, erect or ascending hyphal ends and dispersed pileocystidia, transforming gradually into a dense, 70-90  $\mu\text{m}$  deep subpellis of intricate, horizontally oriented hyphae, that are ca. 3-4  $\mu\text{m}$  wide. Near the cap margin with terminal cells measuring  $(17\text{-})33\text{-}44.7\text{-}56.5\text{-}(72) \times (2\text{-})2.5\text{-}3\text{-}3.5\text{-}(4.5) \mu\text{m}$ , mostly with long, narrow, attenuated tips, subulate or more rarely subcylindrical, flexuous, towards the apex only 1-2  $\mu\text{m}$  diam. and often subapically slightly constricted and subcapitulate; towards the pileus center hyphal endings are more dense, distinctly shorter, erect or ascending, forming almost a trichoderm of subcylindrical hyphal tips, some moniliformous or subapically constricted but generally more irregular tortuous-nodulose (especially the subapical cells), measuring  $(10\text{-})13.5\text{-}18.8\text{-}24\text{-}(32) \times 2.5\text{-}3\text{-}3.5 \mu\text{m}$ , more branched, optically empty or with distinctly yellowish-brownish contents. Pileocystidia measuring  $(23.5\text{-})27.5\text{-}42.2\text{-}56.5\text{-}(79) \times (4\text{-})5\text{-}5.6\text{-}6.5\text{-}(7) \mu\text{m}$  at the cap surface, usually narrowly clavate, sometimes also lanceolate or irregularly constricted, one(two)-celled, in Congo red with heteromorphous granular contents, in sulfovanillin hardly graying, thin-walled or nearly so, particularly near the basal septum sometimes minutely encrusted, longer when originating deep in the subpellis or underlying context, continuing as cystidioid hyphae in subpellis and cap trama. **Clamp connections** absent in all parts.

*Examined material:* UNITED STATES. **Alabama.** Montgomery Co., Montgomery, 23 July 1921, leg. *R.P. Burke* sub nr. 1038 in herbario *Burlinghamii* (NY00618791 **lectotypus hic designatus**, NY00618792 isotypus).

*Commentary:* Our study confirms the placement of Burlingham's species in *Decolorantinae*. Burlingham (1924) described *R. burkei* as a blackening species with relatively small to medium-sized basidiomata, a brown-olive to dark pileus without reddish tints, a distinct acrid taste and an unpleasant smell. Singer (from 1932 onwards) classified it in *Decolorantinae* reducing it to an acrid form of *R. cinerascens* Beardslee (see below) based both on his type study and on his own field observations, but in the later editions of his "Agaricales in Modern taxonomy" Singer (1951, 1975, 1986) listed both species separately again, perhaps as a result of Burlingham's (1944) observation regarding differences in spore ornamentation, which according to her was more distinctive in *R. burkei* and almost invisible in *R. cinerascens*.

***Russula cinerascens*** Beardslee, *J. Elisha Mitchell scient. Soc.* 33: 164. 1918

Figs 9-16

### Original description

Cap 8-12 cm. broad, convex, then depressed at the center, viscid when moist, dull flesh-red, to cinnamon buff, fading to sordid gray with olive and vinaceous tints at maturity, at length striate on the margin, cuticle separable to outer third. Flesh white becoming cinereous with age; taste mild.

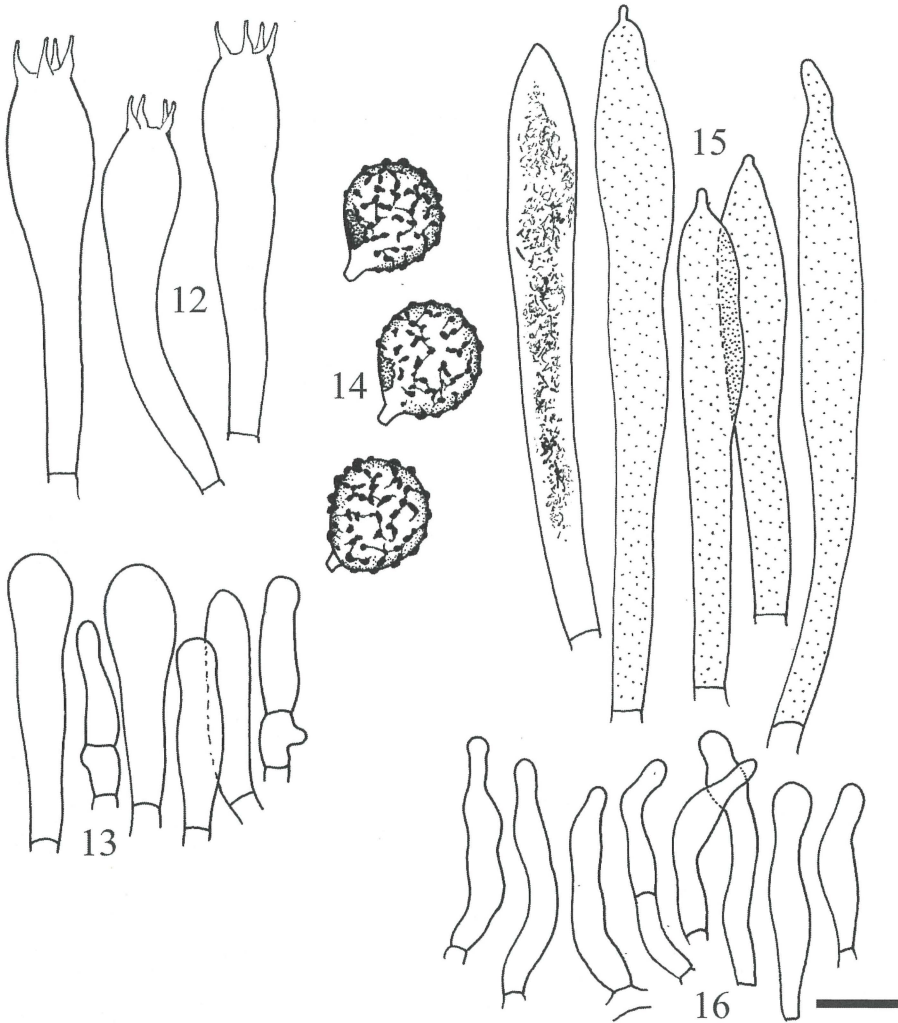
Gills rather close, white, then pale cream, forking 10 mm. broad at the center, attenuate toward the stem, a little rounded behind.

Stem white, spongy within, nearly equal, quickly becoming red, then black when wounded; in mature plants entirely cinereous within.

Spores pale maize yellow, nearly globose, nearly smooth 7-9 $\mu$ .



Figs 9-11. *Russula cinerascens* (lectotype). 9. Pileocystidia with contents indicated in one element as seen in Congo red. 10. Hyphal extremities in the cap center. 11. Hyphal extremities near the cap margin. Scale bar equals 10  $\mu\text{m}$ .



Figs 12-16. *Russula cinerascens* (lectotype). 12. Basidia. 13. Basidioli. 14. Basidiospores in Melzer's reagent. 15. Pleurocystidia with contents indicated in one element as seen in Congo red. 16. Marginal cells. Scale bar equals 10  $\mu$ m, but only 5  $\mu$ m for spores.

This is one of our most interesting species. The color is quite variable. In the numerous collections found this year the plants in woods are quite uniformly more or less red or dull vinaceous. In plants found in open places the red is almost entirely lacking and the plants are then almost Ridgway's cinnamon buff. As they reach maturity, the flesh of the entire plant becomes cinereous and the color of the cap becomes sordid gray with tints of olive and vinaceous.

The species seems to suggest *R. depallens* Fr., but a careful attempt to connect the two has not been successful. Several European specialists to whom our plant has been submitted are positive in their belief that it is unknown in Europe, and that it is not *R. depallens*. Only three red *Russulas* seem to have the curious change of flesh noted in this

*plant. The difference in the spore characters of this species and R. decolorans, to which it seems related, is very marked. In specimens of R. decolorans from North Carolina and Sweden the spores are elliptic, 9-11 $\mu$ , and coarsely tuberculate. Under a good immersion objective their contrast to the smaller nearly smooth spores of this species is very striking.*

**Spores** shortly ellipsoid, measuring (7.2-)7.4-7.6-7.9(-8.2)  $\times$  (6.2-)6.4-6.7-6.9(-7.2)  $\mu\text{m}$ ,  $Q=1.1-1.15-1.18(-1.22)$ ; ornamentation amyloid, subreticulate, consisting of numerous warts [7-9(-10) warts in a 3  $\mu\text{m}$  diam. circle on the spore surface], 0.3-0.4  $\mu\text{m}$  high, connected with frequent line connections [(1-)2-3(-4) line connections in the circle] or fused in chains or low crests that are often branched [(1-)3-6(-7) fusions in the circle]; suprahilar plage amyloid. **Basidia** (42-)44-48.6-53(-57)  $\times$  (9-)10-10.6-11(-12)  $\mu\text{m}$ , 4-spored, clavate-pedicellate; basidiola first cylindrical, then narrowly clavate. **Subhymenium** pseudoparenchymatic. **Lamellar trama** mainly composed of large sphaerocytes. **Hymenial cystidia** moderately numerous, ca. 1100/mm<sup>2</sup>, measuring (50-)62.5-74.8-87(-90)  $\times$  (7-)7.5-8.6-9.5(-11)  $\mu\text{m}$  on gill sides, clavate-pedicellate or fusiform, mostly mucronate with a short 1-3  $\mu\text{m}$  appendage, thin-walled, almost completely filled with heteromorphous contents. **Marginal cells** very slender, subcylindrical and subapically constricted or with narrowed tips, measuring (15-)20-25.8-31.5(-36)  $\times$  (2.5-)3.5-4.7-6(-7.5)  $\mu\text{m}$ . **Pileipellis** orthochromatic in cresyl blue, sharply delimited from the underlying sphaerocytes of the context, vaguely divided in a loose, 50-70  $\mu\text{m}$  deep and strongly gelatinized suprapellis of erect or ascending hyphal ends and pileocystidia, gradually passing into a dense, 85-130  $\mu\text{m}$  deep subpellis of intricate, mostly horizontally oriented hyphae, that are ca. 2-4  $\mu\text{m}$  wide. Incrustations not observed. Suprapellis composed of dispersed pileocystidia and erect or ascending, strongly branched hyphal extremities, arranged in a gradually denser trichodermal structure towards the cap center; terminal cells near cap margin mostly tapering to subulate, measuring (21-)24-30.1-36(-42.5)  $\times$  (2.5-)3-3.2-3.5(-4)  $\mu\text{m}$ , narrowing to 1-2  $\mu\text{m}$  diam. towards the tip; in the cap center densely arranged and not subulate, but subcylindrical to subclavate or repeatedly or subapically constricted, measuring (12.5-)17.5-22.1-27(-32.5)  $\times$  2.5-3.1-3.5  $\mu\text{m}$ . Pileocystidia mostly one-celled, some of the longer ones ascending from the subpellis with one septum, measuring (25-)33-56.1-79(-120)  $\times$  (3-)4-4.6-5.5(-6)  $\mu\text{m}$ , subcylindrical, narrowly clavate to narrowly fusiformous, often subapically or repeatedly constricted to moniliformous, in Congo red with heteromorphous banded contents that are hardly graying in sulfovanillin, thin-walled, continuing as cystidioid hyphae in context of cap. **Clamp connections** absent in all parts.

*Examined material:* UNITED STATES. **North Carolina.** Buncombe Co., Asheville, Aug. 1917, *Beardslee* (NY00618820 **lectotypus hic designates**).

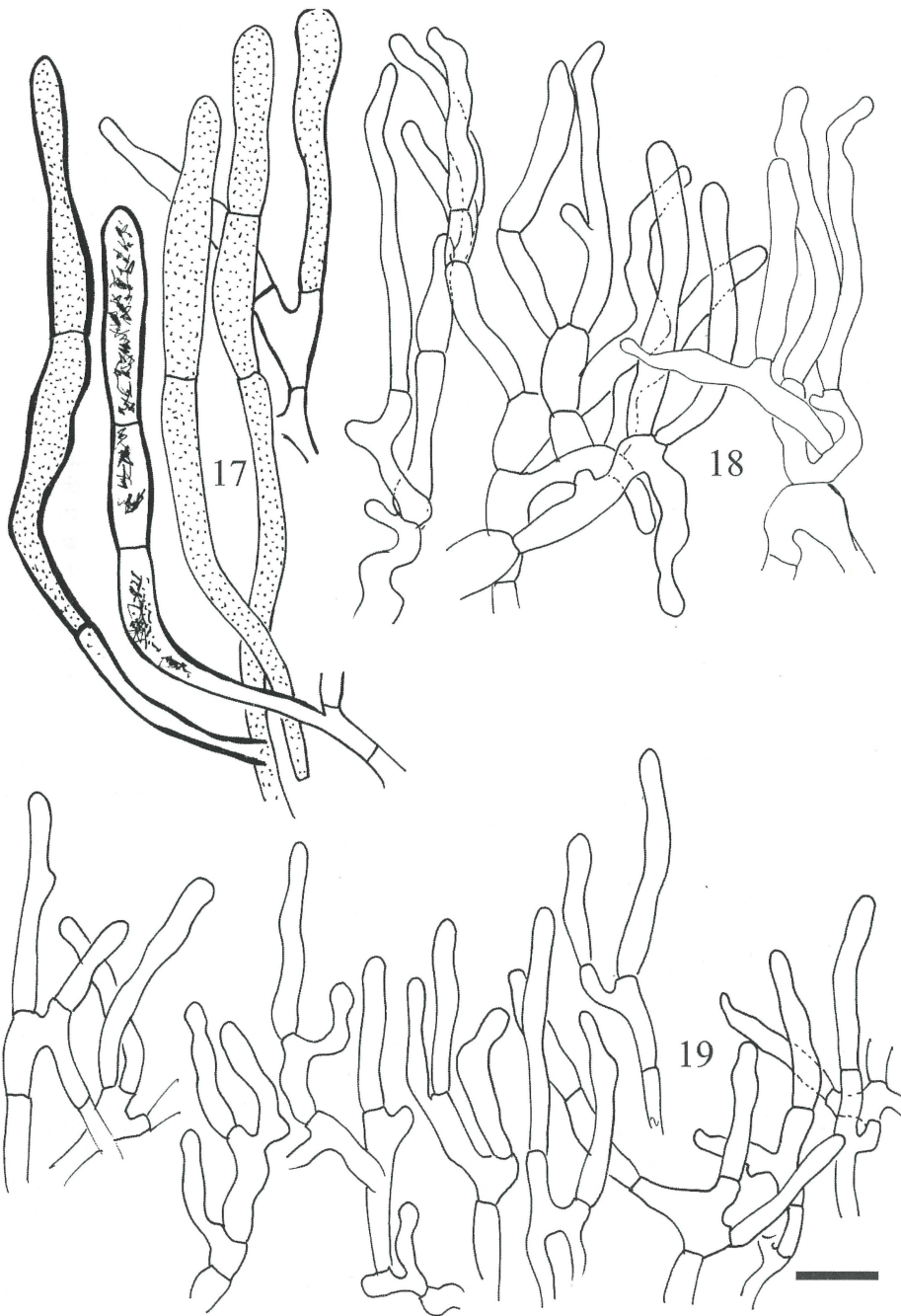
*Commentary:* Although *Beardslee* (1918) described *R. cinerascens* and *R. magna* in the same publication, he may have confused both species before that date as evident from the specimen deposited in NY in which the epithet "*magna*" was struck out and replaced by the epithet "*cinerascens*". As *R. cinerascens* has the same small spores with low reticulated ornamentation as in *R. burkei*, *Singer* (1942) synonymized both species.

***Russula magna*** *Beardslee*, J. Elisha Mitchell scient. Soc. 33: 183. 1918      Figs 17-24

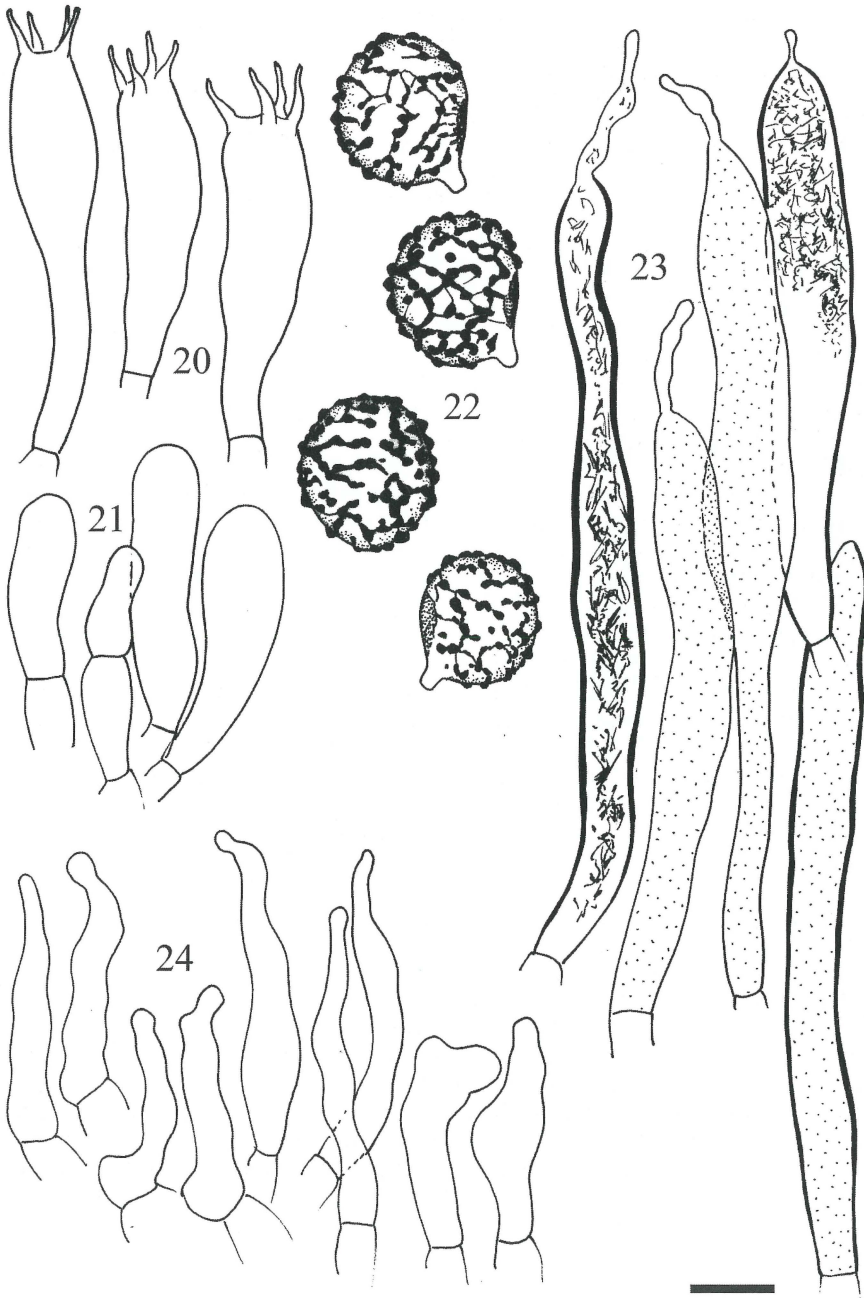
#### Original description

*Cap 8-15 cm. broad, round convex, then expanded, cream color to buff, darker at the center, smooth and shining, with a texture like kid as it dries, flesh white, becoming cinereous with age, very firm and solid. Gills 5-10 mm. wide, thick rather distant, a few forking*





Figs 17-19. *Russula magna* (lectotype). 17. Pileocystidia with contents indicated in one element as seen in Congo red. 18. Hyphal extremities near the cap margin. 19. Hyphal extremities in the cap center. Scale bar equals 10  $\mu$ m.



Figs 20-24. *Russula magna* (lectotype). 20. Basidia. 21. Basidiola. 22. Basidiospores in Melzer's reagent. 23. Hymenial cystidia with contents indicated in two elements as seen in Congo red. 24. Marginal cells. Scale bar equals 10  $\mu$ m, but only 5  $\mu$ m for spores.

and shorter, cream color, distant from the stem, rounded behind. Stem 5-8 cm. long, 2-3 cm. thick, white, enlarged above, often obscurely ridged, changing to red than black when wounded, becoming entirely cinereous within with age. Spores 7-9  $\mu$ , globose, nearly smooth, with delicate reticulating lines; pale buff-yellow.

In drying the cap and stem blacken more or less. The buff color of the cap often is left in patches, and the gills tend to blacken less than the other parts. In the main, however, it blackens much like *R. nigricans*. The fresh plant has a rather pungent smell, which becomes much stronger in drying and is then quite offensive. It is a strong "piggy" smell. Coker speaks of it as like the smell of sweaty horse. At all events it is very powerful and very bad. The dried specimens would probably be taken for *R. nigricans*, but it is amply distinct from that plant. The yellow spores, nearly equal gills, strong odor, at once distinguish it.

Asheville, as Nos. 15065, 12002, and 16083.

**Spores** subglobose, (8.1-)8.6-9.2-9.8(-10.1)  $\times$  (7.4-)7.7-8.2-8.8(-9.5)  $\mu$ m, Q=(1.06-)1.08-1.12-1.15(-1.2); ornamentation subreticulate, amyloid, composed of numerous warts [7-9(11) warts in a 3  $\mu$ m diam. circle on the spore surface], measuring 0.3-0.4  $\mu$ m high, connected with frequent line connections [(1-)2-4 line connections in the circle] or fused in short chains or crests [(2-)3-6(-8) fusions in the circle]; suprahilar spot amyloid. **Basidia** (36-)38.5-43.1-47.5(-53)  $\times$  (9-)10-11.2-12.5(-13)  $\mu$ m, 4-spored, clavate-pedicellate; basidiola first cylindrical, then narrowly clavate. **Subhymenium** pseudoparenchymatic. **Lamellar trama** mainly composed of large sphaerocytes. **Hymenial cystidia** dispersed, ca. 450/mm<sup>2</sup>, but more numerous and more protruding towards the gill edge, measuring (67-)79-103.3-127(-162)  $\times$  (7.5-)8-10-12(-13)  $\mu$ m on sides, clavate or fusiform, pedicellate, generally mucronate to appendiculate bearing a 3-20(-28)  $\mu$ m long appendage, mostly thick-walled, with abundant heteromorphous contents. **Marginal cells** measuring (22-)25-30.9-37(-42)  $\times$  (4-)5-6.3-7.5(-9)  $\mu$ m, irregular, often subulate or fusiform and moniliformous or constricted on tips. **Pileipellis** orthochromatic in cresyl blue, not sharply delimited from the underlying sphaerocytes of the context, vaguely divided in a 40-60  $\mu$ m deep, strongly gelatinized suprapellis of erect or ascending hyphal ends and dispersed pileocystidia, denser towards the cap center, gradually passing into a 50-65  $\mu$ m deep pseudoparenchymatic subpellis of intricate hyphae composed of irregular inflated cells. Suprapellis composed of repeatedly branched hyphal endings that do not remarkably narrow towards their tip; near the cap margin with terminal cells measuring (16-)22-31.4-41(-62)  $\times$  2.5-4.5-6.5(-10.5)  $\mu$ m, apically constricted or not, sometimes with distinctly yellowish-brownish contents, originating from mostly thicker, ca. 4-10  $\mu$ m wide basal cells; in the cap center more densely arranged, measuring (14-)17-22.9-28.5(-34)  $\times$  (2.5-)3-3.4-4  $\mu$ m, subcylindrical and more regular and less tapering. Pileocystidia measuring (22-)25-35.4-45.5(-60)  $\times$  5-5.9-6.5(-7.5)  $\mu$ m, one-celled or with 1(-2) septa, tapering downwards, in Congo red with heteromorphous granular contents that are weakly graying in sulfovanillin, with distinctly thickened walls (0.5-1  $\mu$ m) and often bearing a minute incrustation on their surface that is visible in cresyl blue and becomes more distinct downwards, some longer pileocystidia originating in the subpellis but not continuing in the underlying trama. **Clamp connections** absent in all parts.

*Examined material:* UNITED STATES. **North Carolina.** Buncombe Co., Asheville, 10 Aug. 1917, *Beardslee s.n.* (NY00653786 **lectotypus hic designatus**)

*Commentary:* Despite the combination of very striking characters (large and fleshy basidiomata, blackening flesh, yellow spores and a strong, very bad odor) *Beardslee's* species was never reported again in later literature. Our own examination of authentic material (which is here chosen as lectotype) leaves no doubt on its placement in *Decolorantinae*, and also Singer (1942) confirmed this same placement after having studied the type.

*Russula subdensifolia* Murrill, *Mycologia* 33: 441, 1941

Figs 25-32

### Original description

*Pileo convexo-depresso, 7 cm. lato, glabro, cremeo, tuberculato-striato, subnigricante, sapore grato; sporis albis, spinulosis, 7-8 μ longis; stipite glabro, albo ad cinereo, 7 × 1.5-2 cm.*

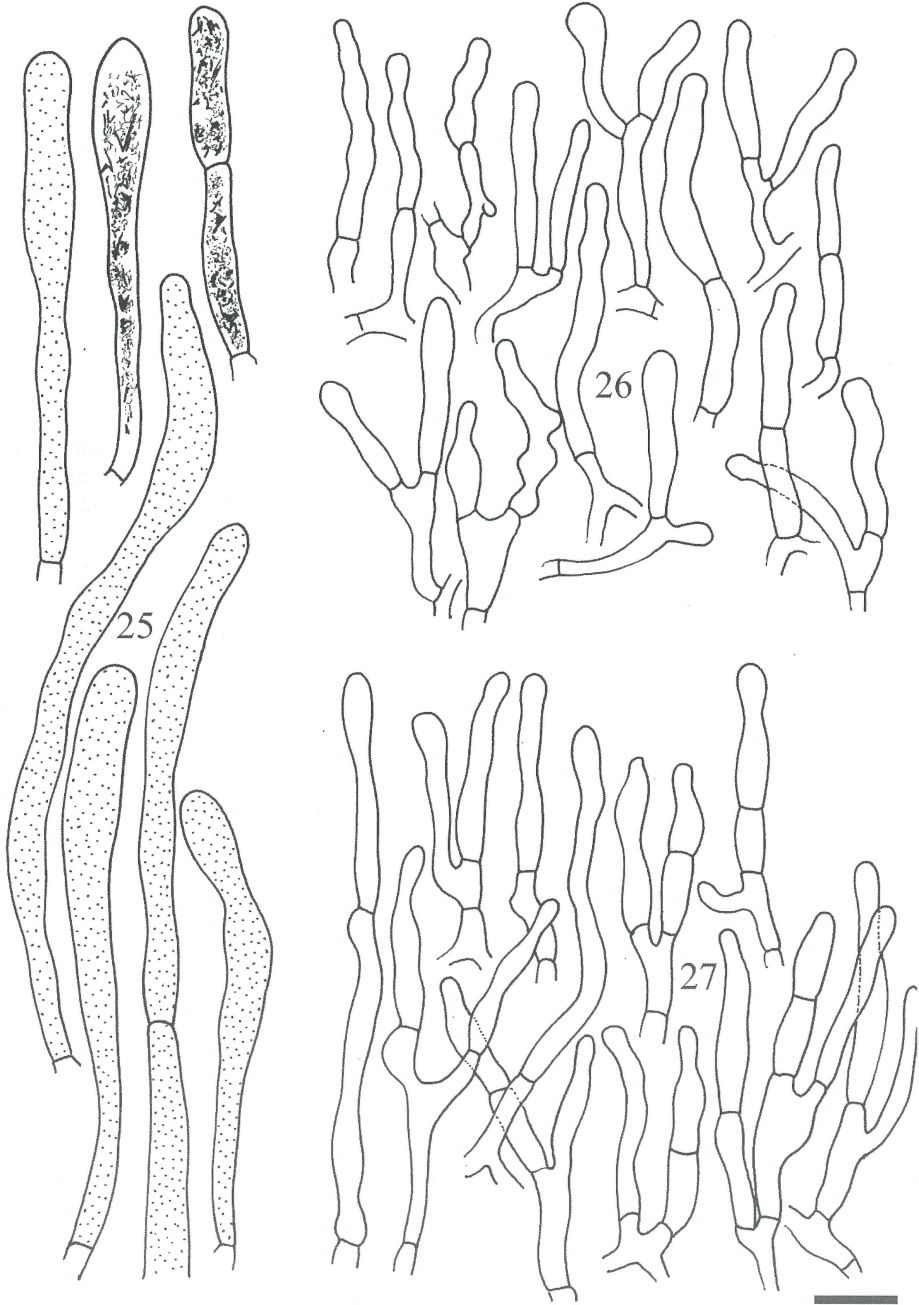
*Pileus convex to depressed, solitary, 7 cm. broad; surface slightly viscid when wet, glabrous, cremeous, margin entire, widely tuberculate-striate; context thin, white, mild, odorless; lamellae adnate, rather close, of medium width, mostly equal, entire, pallid; spores subglobose, spinulose, hyaline, 6-7 μ long; cystidia none; stipe subequal, smooth, glabrous, milk-white, 7 × 1.5-2 cm. On drying the surface of the pileus becomes pale umbrinous, while the lamellae and stipe become cinereous.*

*Type collected by W. A. Murrill under a live-oak in Gainesville, Fla., June 1, 1938 (F 16447). This species has characters in common with R. decolorans and also with the group to which R. densifolia belongs. The spores are conspicuously spinulose. One is hardly prepared for the entire change in color on drying.*

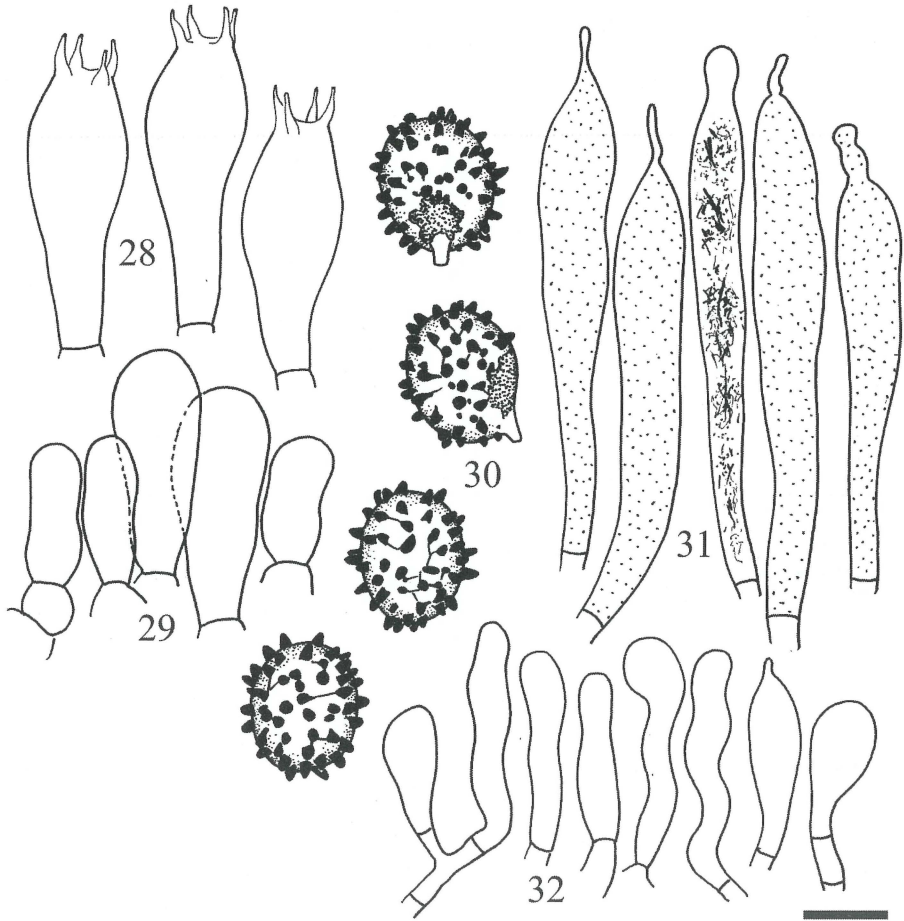
**Spores** (7.2-)7.7-8-8.3(-8.7) × (6-)6.3-6.6-6.9(-7) μm, Q=(1.14-)1.18-1.21-1.25(-1.29), ornamentation of mostly isolated, amyloid spines [4-6(-7) spines in a 3 μm diam. circle on the spore surface], measuring 0.8-1.1(-1.2) μm high, locally connected by scattered line connections [0-2 line connections in the circle] or occasionally fused in pairs or small groups [0-2(-3) fusions in the circle]; suprahilar spot amyloid. **Basidia** short, 30-33.5-36.5(-42) × (11-)11.5-12.5-13(-14) μm, 4-spored, clavate; basidiola cylindrical or ellipsoid, then clavate. **Subhymenium** pseudoparenchymatic. **Lamellar trama** mainly composed of large sphaerocytes. **Hymenial cystidia** dispersed, ca. 500/mm<sup>2</sup>, measuring (47-)54-62.7-71(-83) × (6.5-)8-8.8-10(-11) μm on sides, clavate-pedicellate or fusiformous, mucronate to shortly appendiculate (up to 8 μm), mostly with slightly thickened walls (0.5-1 μm thick), in Congo red usually with abundant heteromorphous contents. **Marginal cells** 15-28(-32) × 5-8(-10) μm, cylindrical, clavate-pedicellate or subcapitate, often flexuous or moniliformous. **Pileipellis** orthochromatic in cresyl blue, sharply delimited from the underlying sphaerocytes of the context, vaguely divided in a thin, rather poorly gelatinized, ca. 30 μm deep subpellis and a 45-50 μm deep, strongly gelatinized suprapellis of ascending hyphal ends and dispersed pileocystidia; terminal cells near the cap margin measuring (11-)17-24.6-32(-47) × (2-)3-3.5-4(-5.5) μm, not narrowing towards their tips, cylindrical to rarely subclavate, sometimes slightly or distinctly subapically or repeatedly constricted, originating from equally wide subapical cells that are usually shorter, towards the cap center measuring (13-)16-21.7-27(-35) × 2.5-3.4-4(-4.5) μm, more irregular, often flexuous or nodulose to moniliformous. Pileocystidia 1(-2)-celled, rarely multicelled, with terminal cells measuring (20-)45-63.7-83(-104) × (5-)5.5-6.1-7(-7.5) μm, subcylindrical to clavate-pedicellate, rarely fusiformous, with distinctly heteromorphous contents that turn not gray in sulfovanillin; walls thin- to slightly thickened, with a weak, indistinct incrustation in Cresyl blue. **Clamp connections** absent in all parts.

*Examined material:* UNITED STATES. **Florida.** Alachua Co., Sugarfoot Hammock, near Gainesville, under live oak, 1 June 1938, leg. West & Murrill, *Murrill* (FLAS F16447, holotype); Gainesville, 4 Aug. 1938, *Murrill* (TENN 21247 – part of FLAS18583).

*Commentary:* Singer (1951, 1958, 1975, 1986) classified Murrill's species in *Decolorantinae*, initially as a synonym of *R. subflava* Murrill, but later, following Hesler (1960), as an individual taxon. The amyloid suprahilar spot on the spores, presence of pileocystidia, together with the color change of context suggest affinities with *Decolorantinae*, being somewhat similar to the European *R. seperina* Dupain, but it differs from this species and other *Decolorantinae* in the white spores.



Figs 25-27. *Russula subdensifolia* (holotype). 25. Pileocystidia with contents indicated in two elements as seen in Congo red. 26. Hyphal extremities in the cap center. 27. Hyphal extremities near the cap margin. Scale bar equals 10  $\mu$ m.



Figs 28-32. *Russula subdensifolia* (holotype). 28. Basidia. 29. Basidiola. 30. Basidiospores in Melzer's reagent. 31. Hymenial cystidia with contents indicated in one element as seen in Congo red. 32. Marginal cells. Scale bar equals 10  $\mu\text{m}$ , but only 5  $\mu\text{m}$  for spores.

## DISCUSSION

All of the here examined species are clearly related to the European *R. decolorans* – group because of the blackening context, the amyloid suprahilar spot on the spores and the possession of well-differentiated pileocystidia. Whether or not they are all distinct taxa is another question. Microscopically speaking, there are no differences worth mentioning between *R. burkei* and *R. cinerascens* (the difference between the length of terminal cells between pileipellis in cap center versus cap margin of both types needs to be checked for reliability on more specimens – see Tab. 1). Singer's (1942) synonymy might therefore very well apply,

Table 1. Comparison of selected characters observed on type material of *R. burkei* and *R. cinerascens*. Values of microscopical characters are averages of 30 measurements. TC = terminal cells of hyphae in pileipellis. In shaded boxes are the distinguishing characters.

	<i>Burkei</i>	<i>Cinerascens</i>	
cap	<i>color</i>	madder-brown on the disk, shading outwards to tawny-olive, and occasionally clay-colored spots, the colors being somewhat intermingled over the central portion	dull flesh-red, to cinnamon buff, fading to sordid gray with olive and vinaceous tints at maturity
	<i>striation</i>	margin even	at length striate on the margin
	<i>surface</i>	with pellicle separable part way to the center, glabrous	viscid when moist, cuticle separable to outer third
	<i>size</i>	5.5-7 cm	8-12 cm
	<i>spore print</i>	pale-ecru	maize yellow
	<i>stipe size</i>	4 × 1.8	not defined
	<i>odor</i>	somewhat like <i>Russula foetens</i>	not defined
	<i>taste</i>	slowly very acrid	mild
	<i>flesh consistency</i>	very compact and firm	not defined
	<i>color change of flesh</i>	white to smoky, becoming slowly vinaceous-drab where cut	white becoming cinereous with age, stipe quickly becoming red, then black when wounded
spores	<i>size</i>	8 × 6.7	7.6 × 6.7
	<i>Q</i>	1.19	1.15
	<i>ornament.</i>	0.2-0.3 μm high	0.3-0.4 μm high
	<i>warts</i>	(7-)-8-11(-12)	7-9(-10)
	<i>lines</i>	2-4(-5)	(1-)-2-3(-4)
pileipellis	<i>TC margin</i>	44.7 × 3 μm	30.1 × 3.2 μm
	<i>suprapellis</i>	40-50 μm	50-70 μm
	<i>subpellis</i>	70-90 μm	85-130 μm
	<i>TC centre</i>	18.8 × 3 μm	22.1 × 3.1 μm
	<i>pileocystidia</i>	42.2 × 6 μm	56.1 × 4.6 μm

in which case Beardslee's name has priority. There has been some debate on the differences in height of the spore ornamentation between both species (Hesler 1960, Burlingham 1944, Singer 1942), but our study demonstrates that these are negligible (Tab. 1) and might have been caused by the observation of immature specimens present at NY. On the other hand, we can not ignore the important differences in field characters between the descriptions of *R. burkei* and *R. cinerascens*: a spore print that is "pale ecru" for the former and "maize yellow" for the latter, a distinctly acrid versus mild taste, a principally brown-olive versus reddish-vinaceous cap and finally also an important difference in size (a cap diam. of 5.5-7 versus 8-12 cm). For this reason, we maintain both species as separate taxa until new collections shed more light on their field characters. Nevertheless, when observing the color of the spore print deposit accompanying

the type collection (<http://sweetgum.nybg.org/vh/specimen.php?irn=330344>), it is clear that the “pale ecru” is a distinct yellowish color, probably in the “ochre” series of the Romagnesi color chart (1967) and may just as well apply to “maize yellow”.

*R. magna* is definitely a much more fleshy, compact species and seems particularly well characterized by an apparently very strong, disagreeable odor. The picture of the lectotype (<http://sweetgum.nybg.org/vh/specimen.php?irn=108229>) reminds one of the *R. nigricans* group, if it was not for the absence of polydymous gills. Microscopically, it seems different from *R. burkei* or *R. cinerascens* by the larger spores, the absence of subulate or clearly tapering hyphal ends near the pileus margin and the thickened walls of cystidioid elements. A good but apparently rare species.

In some of our descriptions and illustrations, the term incrustation is used. This does not refer to the type of acido-resistant incrustation such as in “primordial hyphae”. The precise nature of the here observed incrustations on some cells/dermatocystidia is uncertain and mentioned here only for completeness.

*R. subdensifolia* is quite different from all preceding species because of the spiny spores, the much shorter basidia and the “white” spore print (Murrill 1941), the latter being unknown for European or American *Decolorantinae*, but not for some exotic species with blackening context (Das *et al.* 2011, Buyck 1997) that are still of uncertain taxonomic position.

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