

## Type studies in *Russula* subsection *Nigricantes* from the Eastern United States

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**Abstract** – After a short historical summary of the species in *Russula* subgenus *Compacta* subsection *Nigricantes* in the United States, the microscopic features of the type specimens of four taxa from North America are described and discussed: *Russula decora*, *R. densifolia* var. *paxilloides*, *R. sordida* and *R. subsordida*. Previous suggestions of possible synonymies with European taxa are rejected.

***Russula densifolia* var. *paxilloides* / *Russula decora* / *Russula sordida* / *Russula* subgenus *Compacta* / *Russula subsordida* / taxonomy**

### INTRODUCTION

The often blackening species of *Russula* subsect. *Nigricantes* Maire were always part of subgenus *Compacta* (Fr.) Bon together with the other groups of *Russula* Pers. in the northern hemisphere that have unequal gills, such as the white Russulas of section *Lactarioides* (Bataille) Konrad & Joss. (Buyck & Adamčík 2013), and later also *Archaeinae* R. Heim for example. The type species of *Nigricantes*, *R. nigricans* Fr., was together with *R. adusta* Fr. among the first accepted species in the genus (Fries 1838), followed nearly forty years later by two other members of this group, i.e. *R. densifolia* Gillet and *R. albonigra* (Kromh.) Fr. It was around that same period that Peck (1873) described across the Atlantic the first native American species in this group, *R. sordida* Peck, and that Frost (in Peck 1879) published his *R. compacta*, later followed by *R. incarnata* Morgan 1883 non Quélet nom. inval. (the accepted name is now *R. morgani* Sacc. 1887), *R. polyphylla* (Peck 1898), *R. magnifica* (Peck 1903), *R. densifolia* var. *paxilloides* (Peck 1904), *R. subsordida* (Peck 1906) and *R. eccentrica* (Peck 1911). Both Peck (1907) and Burlingham (1915) recognized all of these taxa as good American species, but confirmed also the additional presence in the Eastern United States of the European *R. nigricans*, *R. adusta* (renamed *R. subusta* nom. illeg. by Burlingham in 1915) and *R. densifolia*.

Kauffmann (1918) was the first to suggest a very close relationship and possible synonymy of both Peck's *R. subsordida* and *R. sordida* with the European *R. albonigra*, but it was Singer (1926) who strongly simplified the situation in

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American *Nigricantes* by accepting not only the abovementioned synonymy of both Peck's species with the European *R. albonigra*, but also of Burlingham's *R. subusta* with the European *R. densifolia*, and later (Singer 1951) also of *R. magnifica* with *R. polyphylla*, while interpreting *R. eccentrica* as a mere subspecies of *R. nigricans* (Singer 1958). Singer's interpretations were followed by most subsequent American authors, also when he (Singer 1958) was of the opinion that *R. morgani* was a good species of section *Lactarioides*, transferred *R. compacta* out of subgenus *Compacta* to section *Crassotunicatae* Singer, and much later (Singer 1975) moved *R. polyphylla* to section *Rigidae* subsection *Polyphyllinae* Singer.

At the time that Shaffer (1962) started his revision of subsect. *Nigricantes*, the *R. nigricans* – group in the United States had therefore practically been reduced to the presumed presence of four common European species (*R. nigricans*, *R. adusta*, *R. albonigra* and *R. densifolia*). Shaffer's revision altered the existing situation considerably even though he still reported on the presence (in both Eastern and Western parts of the United States) of the European *R. adusta*, *R. albonigra* and *R. densifolia*. However, all American specimens previously identified as *R. nigricans* were transferred by him to a new native species, *R. dissimulans* Shaffer, based on closer gill placement and slightly larger spores. He also recognized four additional forms of *R. densifolia*: a form *dilatoria* from the West Coast with hardly changing context, another Western form, f. *fragrans*, with more spaced gills and distinct odor (a collection previously identified by Singer as *R. nigricans* ssp. *eccentrica*), a f. *cremeispora* with warm buff spore print from Idaho, and finally a f. *gregata* with a similar, warm buff spore print, but growing gregarious under pine in Michigan (the not white spore print of the latter two varieties is at least very surprising and has never been recorded from other *Nigricantes* anywhere in the world). In addition, Shaffer published three new species: the Western *R. atrata* Shaffer from Oregon differing from *R. albonigra* by the structure of its pileipellis, and two new species from Michigan, *R. decora* Shaffer with pink-cinnamon floccules on the cap, and *R. michiganensis* Shaffer, another supposedly close ally to *R. albonigra*. The only later addition to subsection *Nigricantes* in the United States was the description of *R. imitatrix* (Homola & Shaffer 1975).

Most of the new taxa described by Shaffer were based on very few specimens or even a single collection and apart from *R. imitatrix* and *R. michiganensis*, both reported from Québec (Canada) in recent years (<http://www.myc Quebec.org/bas.php?l=l&trie=R>), none of his new taxa seem to have been commented upon in the literature since their original description 50 years ago. Preliminary sequence data (Buyck unpubl.) suggest that none of the European taxa are present in the United States. In this first contribution on American *Nigricantes* we will document the microscopic characters of four taxa described from the Northeastern USA: *R. sordida*, *R. subsordida*, *R. densifolia* var. *paxilloides* and *R. decora*.

## MATERIAL AND METHODS

Micromorphological characters were observed with 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  $\mu\text{m}$  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).

## TAXONOMY

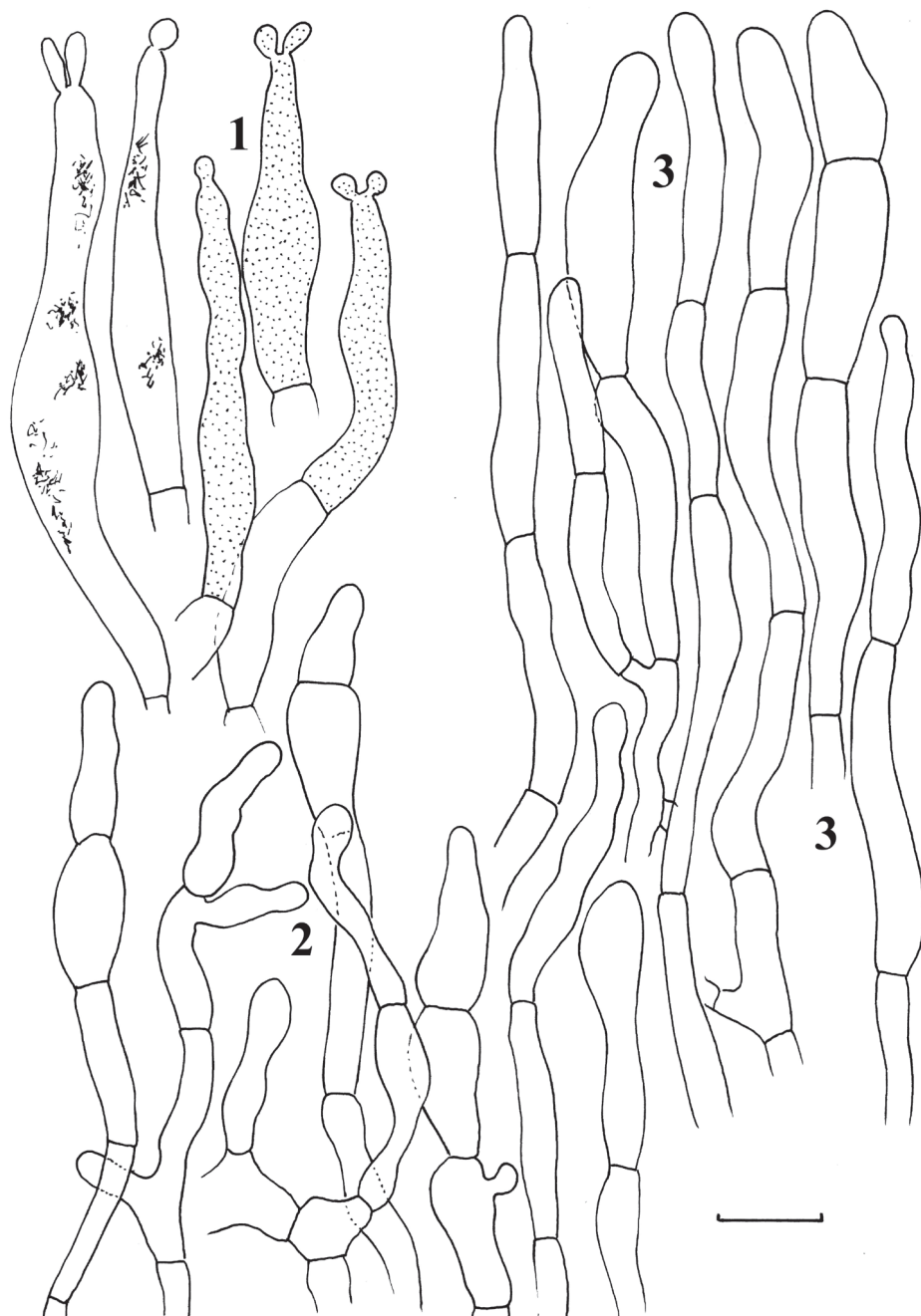
*Russula decora* Shaffer, *Brittonia* 14: 276. 1962

**Figs 1-8**

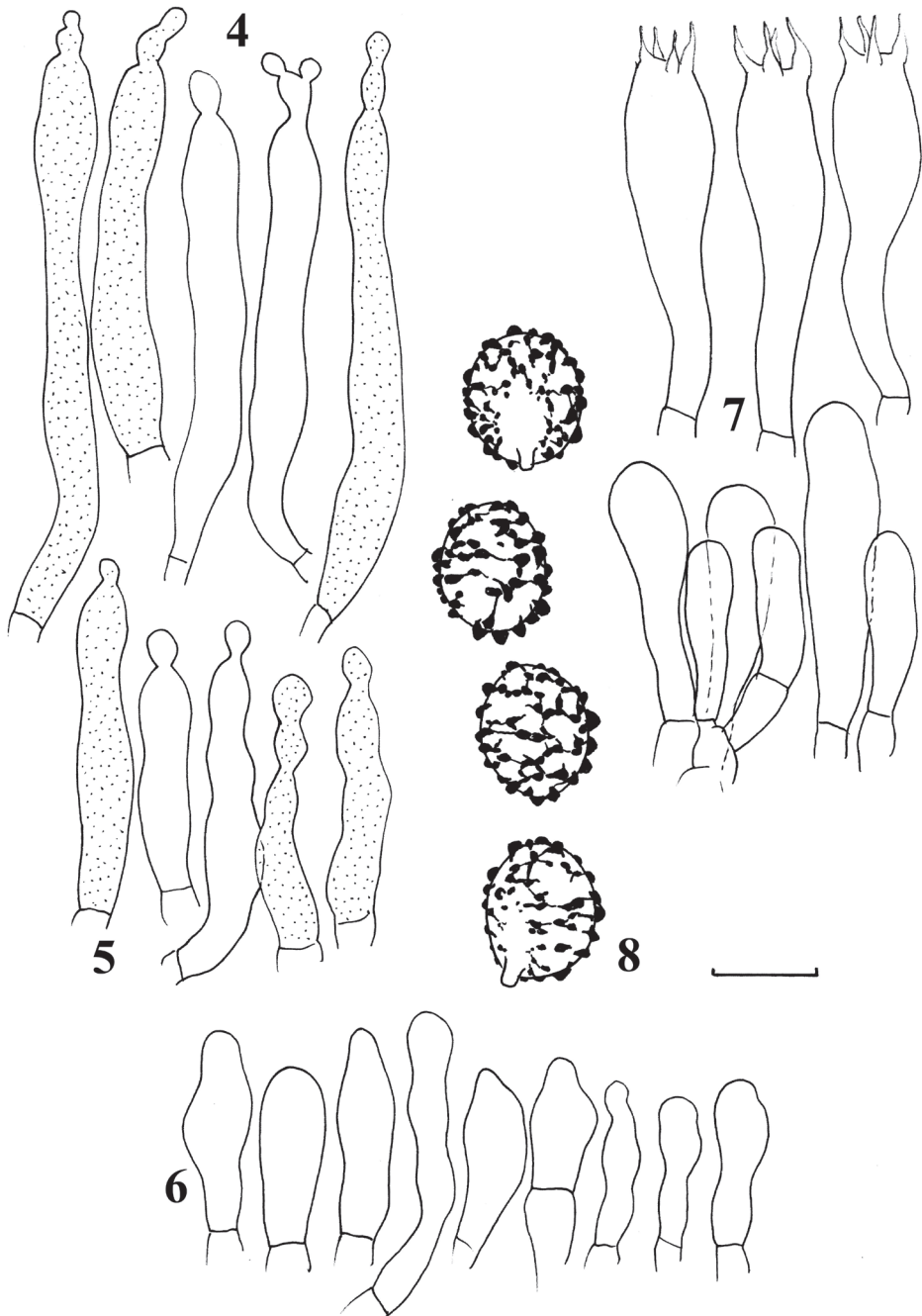
### *Original description:*

*Pileus maturitate siccus, virgulatus in ora, cum paucis panniculis rubicundulo-cinnamomeis, brunneus; trama rigida, albidula, secta fuscans, sapore nullo; lamellae angustae, decurrentes, confertae, pallido-luteae, obtritae nigrescentes; lamellulae numerosae; stipes glaber, obtritus fuscans; sporae in cumulo albae, 8.6-10  $\times$  7.3-8  $\mu$ , ornamentatione 0.3-0.6  $\mu$  alta, reticulo verrucoso patulo; cuticula pilei 230-310  $\mu$  crassa, ex hyphis intertextis 1.4-6.5  $\mu$  latis aliquando trichodermium laxum implicatum formantibus, etiam cum raris hyphis oleiferis 2.7-5.7  $\mu$  latis.*

**Spores** shortly ellipsoid, (7.3-)7.6-8.1-8.6(-9.1)  $\times$  (5.9-)6.2-6.6-6.9(-7.4)  $\mu\text{m}$ , Q = (1.14-)1.19-1.24-1.28(-1.39), subreticulate, with an ornamentation of relatively distant [(3-)4-5(-6)] in a circle of 3  $\mu\text{m}$  diam. on spore surface], obtuse, amyloid warts, measuring 0.5-0.8  $\mu\text{m}$  high, connected by numerous fine line connections [1-4(-5) line connections in the circle] and frequently also fused in short to longer ridges [(0-)1-3(-4) fusions in the circle]. Suprahilar spot not amyloid, smooth. **Basidia** (39-)42.5-45.2-49  $\times$  (8.5-)10-11-12.5  $\mu\text{m}$ , 4-spored, clavate to fusiform, pedunculate; basidiola first cylindrical, then narrowly clavate or fusiform. **Subhymenium** pseudoparenchymatic. **Lamellar trama** mainly composed of large sphaerocytes. **Hymenial cystidia** measuring (43-)57.5-67.2-77(-88)  $\times$  6.5-7.5-8.5  $\mu\text{m}$  and probably abundant on gill sides (without content and therefore impossible to count), cylindrical or narrowly fusiform, rarely lanceolate, with acute or rarely obtuse apices that are mucronate or appendiculate (often with double appendices), smaller but otherwise similar although typically strongly capitulate



Figs 1-3. *Russula decora* (holotype). 1. Pileocystidia. 2. Hyphal terminations near the pileus margin. 3. Hyphal terminations in the pileus center. Contents of cystidia are represented as observed in Congo Red for some elements only, the others are simply filled with dots to indicate their cystidial nature. Scale bar = 10  $\mu$ m.



Figs 4-8. *Russula decora* (holotype). 4. Hymenial pleurocystidia. 5. Hymenial cheilocystidia. 6. Marginal cells of the gill edge. 7. Basidia and basidiola. 8. Spores as seen in Melzer's reagent. Contents of cystidia are represented as observed in Congo Red for some elements only (in this particular case they are optically empty), the others are simply filled with dots to indicate their cystidial nature. Scale bar = 10  $\mu$ m, but only 5  $\mu$ m for spores.

on gill edge, measuring (33-)36.5-43.5-50.5(-57)  $\times$  5.5-7-8.5  $\mu\text{m}$ , thin-walled, optically empty, not graying in sulfovanilin. **Marginal cells** shorter but otherwise similar to basidioles, measuring (10-)14.5-20.5-26.5(-38)  $\times$  (5-)53.5-6.9-8.5  $\mu\text{m}$ . **Pileipellis** orthochromatic in Cresyl blue, many cells containing a dark brown, and then green brown vacuolar pigment, vaguely divided in a 100-130  $\mu\text{m}$  deep, strongly gelatinized, loosely structured suprapellis and a denser, less gelatinized, ca. 90-100  $\mu\text{m}$  deep subpellis. Suprapellis gradually more fragmented towards the cap margin, forming a tissue of irregularly oriented, intricate, frequently branched and anastomosing, subcylindrical hyphae and numerous pileocystidia, near the surface with extremities and pileocystidia aggregated locally in repent to erect fascicles; hyphal terminations sparsely branched, with terminal cells measuring (15-)24-35-46(-63)  $\times$  (3.5-)4-5.5-7(-8.5)  $\mu\text{m}$  near cap margin, and (12-)21-30.5-40(-48)  $\times$  (3.5-)4-5.5-6.5(-8.5)  $\mu\text{m}$  in the cap center, subregular or slightly flexuous, with blunt apices, subcylindrical, rarely utriform, fusiform or narrowly clavate to even short and inflated inside clusters; subapical cells usually equally wide. Subpellis composed of horizontally oriented, intricate and branched, ca. 3-7  $\mu\text{m}$  wide hyphae. Incrustations absent. Pileocystidia measuring (35-)41-52.5-63.5(-87)  $\times$  5-7-8.5(-12)  $\mu\text{m}$ , near centre of the cap also smaller, occurring only near the cap surface with rare longer ones descending closer to subpellis, but not continuing in subpellis nor in underlying trama as endocystidia, mostly one-celled, fusiform, subulate or rarely lanceolate, frequently very distinctly 1-2-capitulate, thin-walled, with yellowish contents that react weakly and indistinctly in sulfovanillin. Oleiferous hyphae frequent in subpellis and suprapellis, but absent or rare in trama. **Clamp connections** absent in all parts.

*Examined material:* UNITED STATES. **Michigan.** Cheboygan Co., Carp Creek near University of Michigan Biological Station, 3 Aug 1957, under pine, leg. A.H. Smith, *Shaffer 1741* (MICH 12203, holotype).

*Commentary:* Shaffer (1962) defined *R. decora* as a species of *Nigricantes* having spores with a moderately prominent, reticulate ornamentation, immediately blackening context and a flocculose cap surface. It undoubtedly belongs to subsect. *Nigricantes* because of the blackening context and unequal gills, the inamyloid suprahilar spot and the mucronate pileocystidia bearing frequently two, often sublaterally implanted, apical knobs. The presence of inflated cells in the pileipellis, especially near the cap centre, as well as the short pileocystidia and subreticulate spores with relatively distant but distinct warts are reminiscent of the European *R. densifolia*, from which it differs nevertheless by the floccules on the cap surface and the fact that the context is not reddening before turning black.

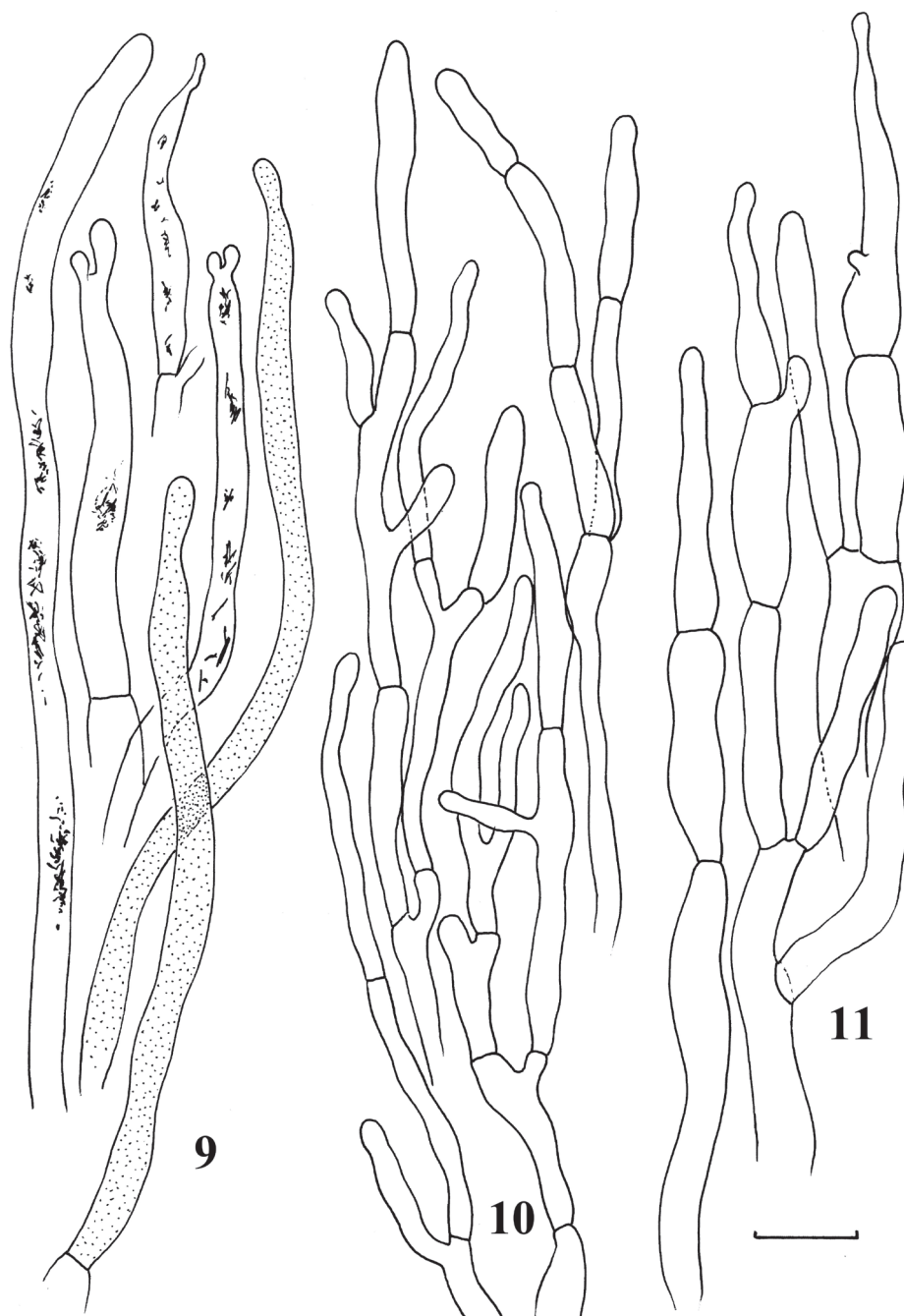
***Russula densifolia* var. *paxilloides*** Peck, Bull. New York State Mus. Nat. Hist. 75: 20. 1904 **Figs 9-15**

#### **Original description:**

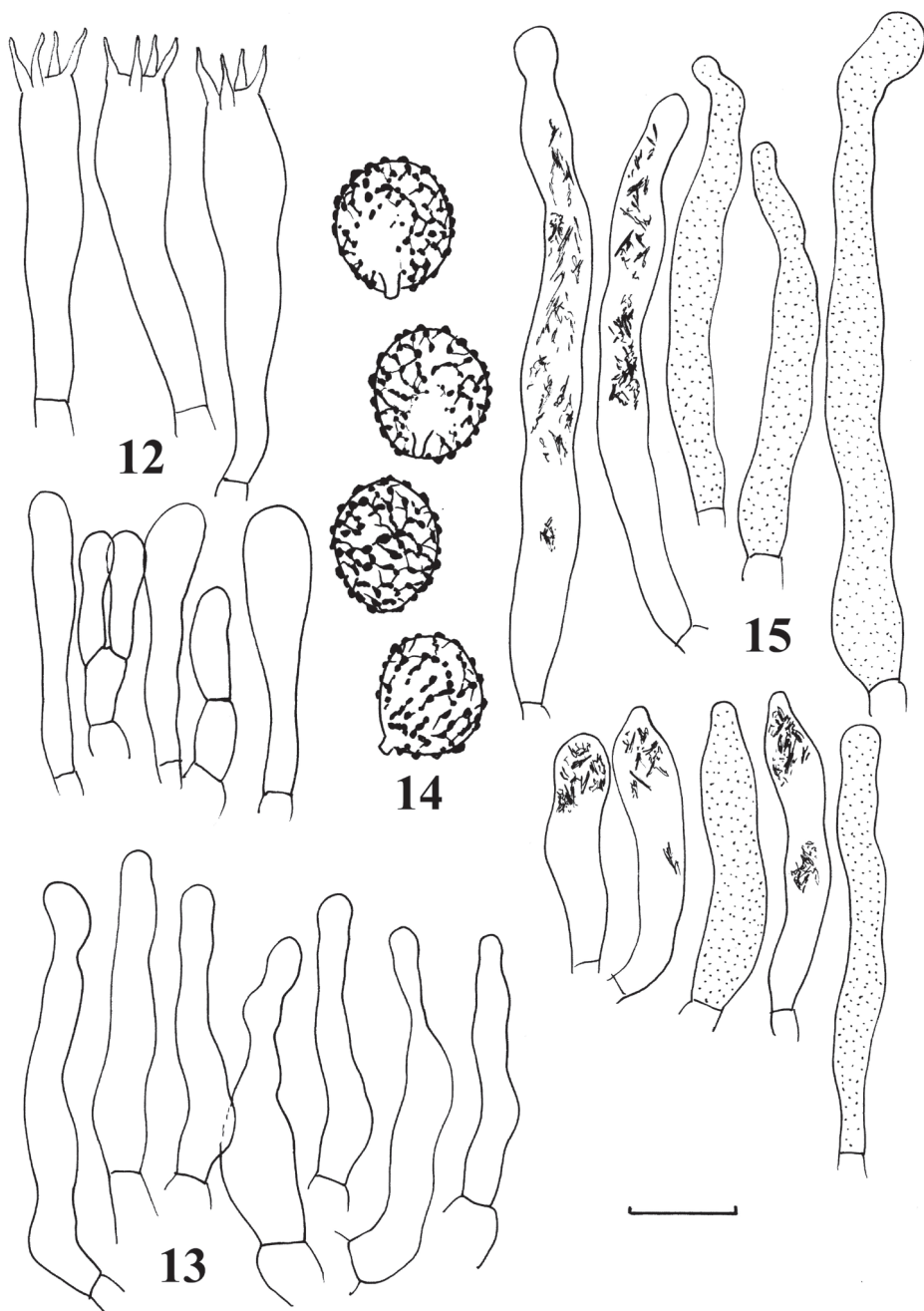
[...] Among decaying leaves in woods. Lake Pleasant. August. This species is closely related to *R. adusta* from which it may be separated by the slight reddening of the flesh where wounded. Our specimens are a peculiar form in which many of the lamellae are forked at the base. They also separate at the inner externity from the stem and pileus and curl outward revealing the hymenophore beneath. All the specimens found exhibited this character. It indicates a feeble attachment of the hymenium to the hymenophore and is suggestive of a relationship to the genus *Paxillus*. The white spores, however, show that it is not referable to that genus. It may be called variety *paxilloides*.

**Spores** subglobose to shortly ellipsoid, (7-)7.2-7.5-7.7(-8)  $\times$  (5.8-)6.1-6.4-6.7(-7)  $\mu\text{m}$ , Q = (1.09-)1.12-1.17-1.21(-1.26), ornamentation completely reticulate





Figs 9-11. *Russula densifolia* var. *paxilloides* (holotype). **9.** Pileocystidia. **10.** Hyphal terminations in pileus center. **11.** Hyphal terminations near the pileus margin. Contents of cystidia are represented as observed in Congo Red for some elements only, the others are simply filled with dots to indicate their cystidial nature. Scale bar = 10  $\mu$ m.



Figs 12-15. *Russula densifolia* var. *paxilloides* (holotype). **12.** Basidia and basidiola. **13.** Marginal cells of the gill edge. **14.** Spores as seen in Melzer's reagent. **15.** Hymenial pleurocystidia (above) and cheilocystidia (below). Contents of cystidia are represented as observed in Congo Red for some elements only, the others are simply filled with dots to indicate their cystidial nature. Scale bar = 10  $\mu$ m, but only 5  $\mu$ m for spores.



or almost so, composed of moderately close [6-8(-10) in a 3  $\mu\text{m}$  diam. circle on spore surface], obtuse, amyloid, low warts, measuring 0.2-0.4  $\mu\text{m}$  high, connected by fine line connections [2-4(-5) in the circle] or fused in short or long ridges [0-2(-4) fusions in the circle]. Suprahilar spot not amyloid, smooth. **Basidia** (40-)45.5-50-54(-55)  $\times$  (7.5-)8.5-9.5-10.5(-11)  $\mu\text{m}$ , 4-spored, narrowly clavate, pedicellate; basidiola first cylindrical, then narrowly clavate. **Subhymenium** pseudoparenchymatic. **Lamellar trama** mainly composed of large sphaerocytes. **Hymenial cystidia** moderately numerous [ca. 1200-1500/mm<sup>2</sup>] on gill sides, measuring (49-)52.5-62-71(-83)  $\times$  (5-)5.5-7-8(-10)  $\mu\text{m}$ , subcylindrical, rarely narrowly fusiform or subulate, often with 4-12  $\mu\text{m}$  long appendage or capitulum, thin-walled, usually optically empty in Congo red, but distinctly greying in sulfovanilin, near the gill edge shorter, measuring (29-)33.5-41-48(-52)  $\times$  (4.5-)5-6-7(-7.5)  $\mu\text{m}$  and usually without an apical appendage, often with some apical, crystalline contents in Congo red. **Marginal cells** well differentiated, measuring (21-)33.5-41-48.5(-54)  $\times$  (4-)5-6.5-8(-9)  $\mu\text{m}$ , usually subulate and lageniform, at the tip often moniliform or apically constricted and with yellowish contents. **Pileipellis** orthochromatic in Cresyl blue, vaguely divided in a 50-60  $\mu\text{m}$  deep suprapellis of strongly gelatinized, more or less repent hyphal endings and a 50-60  $\mu\text{m}$  deep, less gelatinized subpellis composed of denser, irregular-nodulose, branched, ca. 4-12  $\mu\text{m}$  wide hyphae. Acidoresistant incrustations absent. Hyphal extremities in cap center narrow, subcylindrical, sometimes more or less erect, densely aggregated and branching, with terminal cells measuring (15-)22-38-54(-69)  $\times$  (2.5-)3-4-4.5(-5)  $\mu\text{m}$ , near the cap margin becoming often wider, with terminal cells measuring (23-)29.5-43-56(-83)  $\times$  (3-)3.5-5-6.5(-9)  $\mu\text{m}$ , with obtuse tips, thin-walled. Pileocystidia dispersed near cap margin, even less numerous near cap centre, usually arising from deep in the subpellis where they are especially numerous near the subpellis-trama transition, more rarely continuing as endocystidia in the trama, one-celled, mostly longer than 100  $\mu\text{m}$  and 4.5-7  $\mu\text{m}$  wide, often narrowing at the tip, obtuse to 1-2 appendiculate, shorter and often 2-capitulate in the cap center, thin-walled, optically empty or with few, dispersed inclusions that do not react in sulfovanilin. **Clamp connections** absent in all parts.

*Examined material:* UNITED STATES. **New York.** Lake Pleasant, Hamilton co., Aug., C. H. Peck (NYSf2289, holotype).

*Commentary:* Shaffer (1962), who described four new forms of *R. densifolia*, does not discuss Peck's variety at all. The protologue of this variety (Peck 1904) does not contain any indication of reddish tinted gills or of a particular unpleasant smell, but in his later description of *R. densifolia* (Peck 1907) which includes also this variety, Peck described the gills as "sometimes tinged with red". Peck's taxon, which is certainly not a close relative of *R. densifolia*, might therefore possibly be better placed in subsect. *Polyphyllinae* Singer, also because of the long pileocystidia that arise from deep within the subpellis, especially near the cap margin, and are also present in the trama. The latter feature is also typical for *R. polyphylla* and *R. eccentrica* (Buyck *et al.*, 2004, Buyck & Halling 2004), both of which belong to *Polyphyllinae* (Buyck unpubl.).

Except for the long pileocystidia, this taxon differs from the other species included in this study in its subglobose spores, a pileipellis structure as in *R. sordida* but without protruding, attenuated, terminal cells near the cap centre, and finally also because of the well differentiated, lageniform or subulate marginal cells mixed with mostly obtuse cheilocystidia.

***Russula sordida*** Peck, Bull. Buffalo Soc. Nat. Sci. 1: 57. 1873

**Figs 16-23**

**Original description:**

*Pileus firm, convex, centrally depressed, dry, sordid white, sometimes clouded with brown; lamellae white, some of them forked; stem equal, solid, concolorous; spores globose, .0003'; taste acrid; flesh changing color when wounded, becoming black or bluish-black. Plant 4'-5' high, pileus 3'-5' broad, stem 6"-12" thick.*

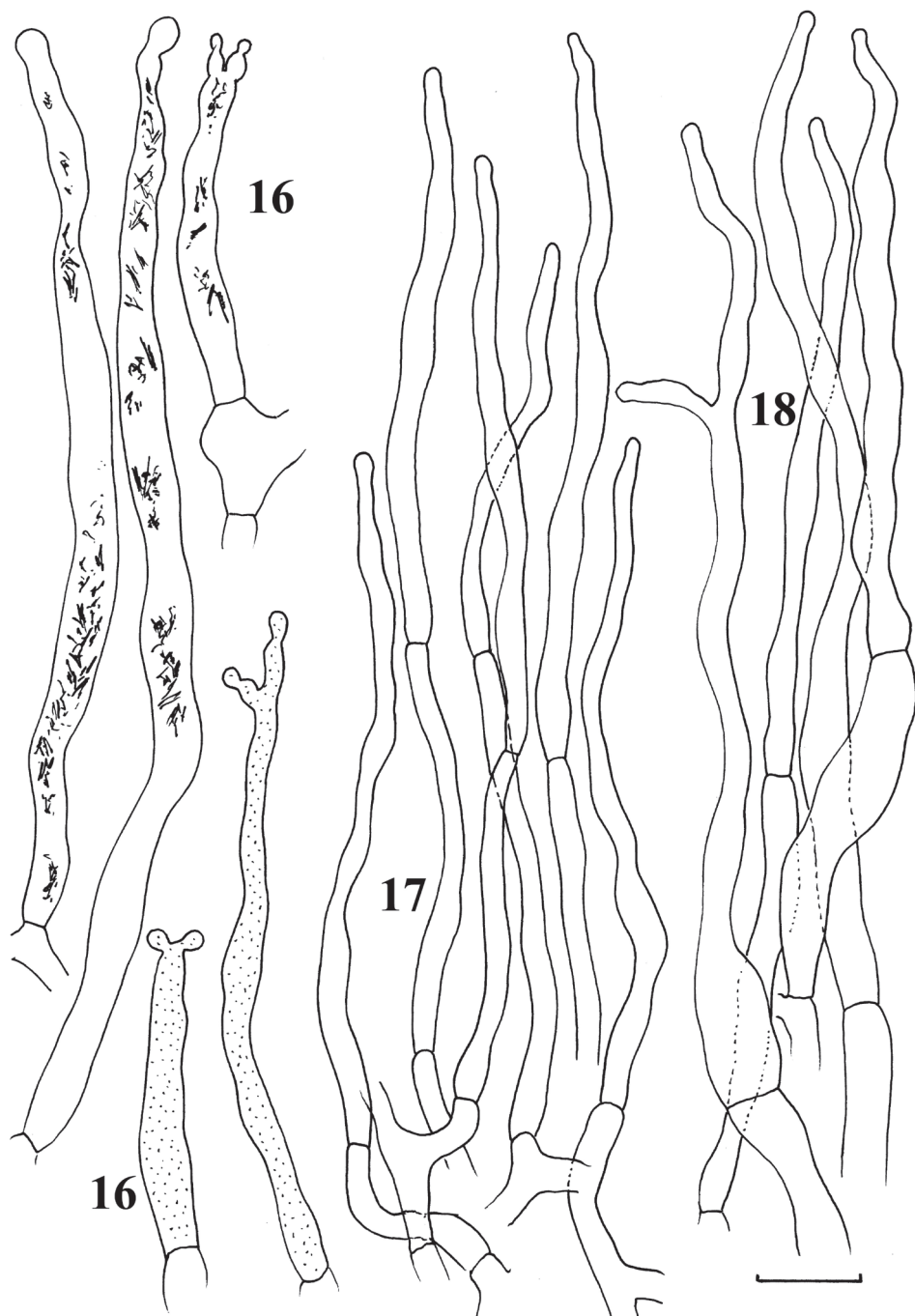
*Ground under hemlock tress. Worcester. July. The whole plant turns black in drying.*

**Spores** shortly ellipsoid, (7-)7.5-7.8-8.5 × (5.5-)6-6.3-6.9 μm, Q = (1.17-) 1.19-1.24-1.29(-1.32), with a reticulate ornamentation of numerous [6-9(-10) amyloid, fine warts in a 3 μm diam. circle on the spore surface], amyloid, low warts, measuring 0.3-0.5 μm high, connected by fine line connections [2-5(-6) in the circle] or merged in chains [2-5(-7) fusions in the circle]. Suprahilar plate not amyloid, small, smooth. **Basidia** (40-)41.5-44-47(-49) × (8-)8.5-9.5-11 μm, 4-spored, narrowly clavate, pedicellate; basidiola first cylindrical, then narrowly to broadly clavate. **Subhymenium** pseudoparenchymatic. **Lamellar trama** mainly composed of large sphaerocytes. **Hymenial cystidia** on gill sides abundant, ca. 3500-5000/mm<sup>2</sup>, narrowly fusiform, subcylindrical, subulate or rarely narrowly clavate, thin-walled, mucronate-appendiculate (appendix 2-7 μm long), measuring (49-)52-60-67(-74) × (5.5-)6-7-8 μm, near the gill edge smaller, (23-)25-30-35(-43) × (5-)5.5-6.5-7(-8) μm, almost completely filled with crystalline-heteromorphous contents, weakly reacting in sulfovanilin. **Marginal cells** measuring (18-)20-23-25(-27) × (5-)6-8-10(-12) μm, mostly lageniform or fusiform, often with darker vacuolar pigments. **Pileipellis** orthochromatic in Cresyl blue, with parietal pigments staining dark blue-green, divided in a 85-100 μm deep suprapellis of strongly gelatinized, more or less horizontal, dark-pigmented hyphae and a 30-45 μm deep subpellis of ca. 3-8 μm wide, horizontally oriented, intricate, less gelatinized, densely aggregated hyphae. Acidoresistant incrustations absent. Hyphal extremities in cap centre with distant septa, long and narrowly cylindrical, sparsely branching, thin-walled, with terminal cells measuring (43-)55-72.5-89.5(-111) × 3-4-5(-9) μm, near cap margin with terminal cells measuring (30-)55-84-112(-141) × 3-5-6.5(-10) μm, often wider in their lower part and more subulate or arising from more inflated subapical cells. Pileocystidia dispersed near the cap surface, some continuing in subpellis or as endocystidia in the trama as, (31-)40-74-108(-143) × 4-6-7 μm, one-celled or with one, rarely two septa, cylindrical, subulate or narrowly fusiform, often minutely capitate with one or two, 2-5 μm long appendages, thin walled, mostly with heteromorphous-crystalline contents hardly graying in sulfovanilin. **Clamp connections** absent in all parts.

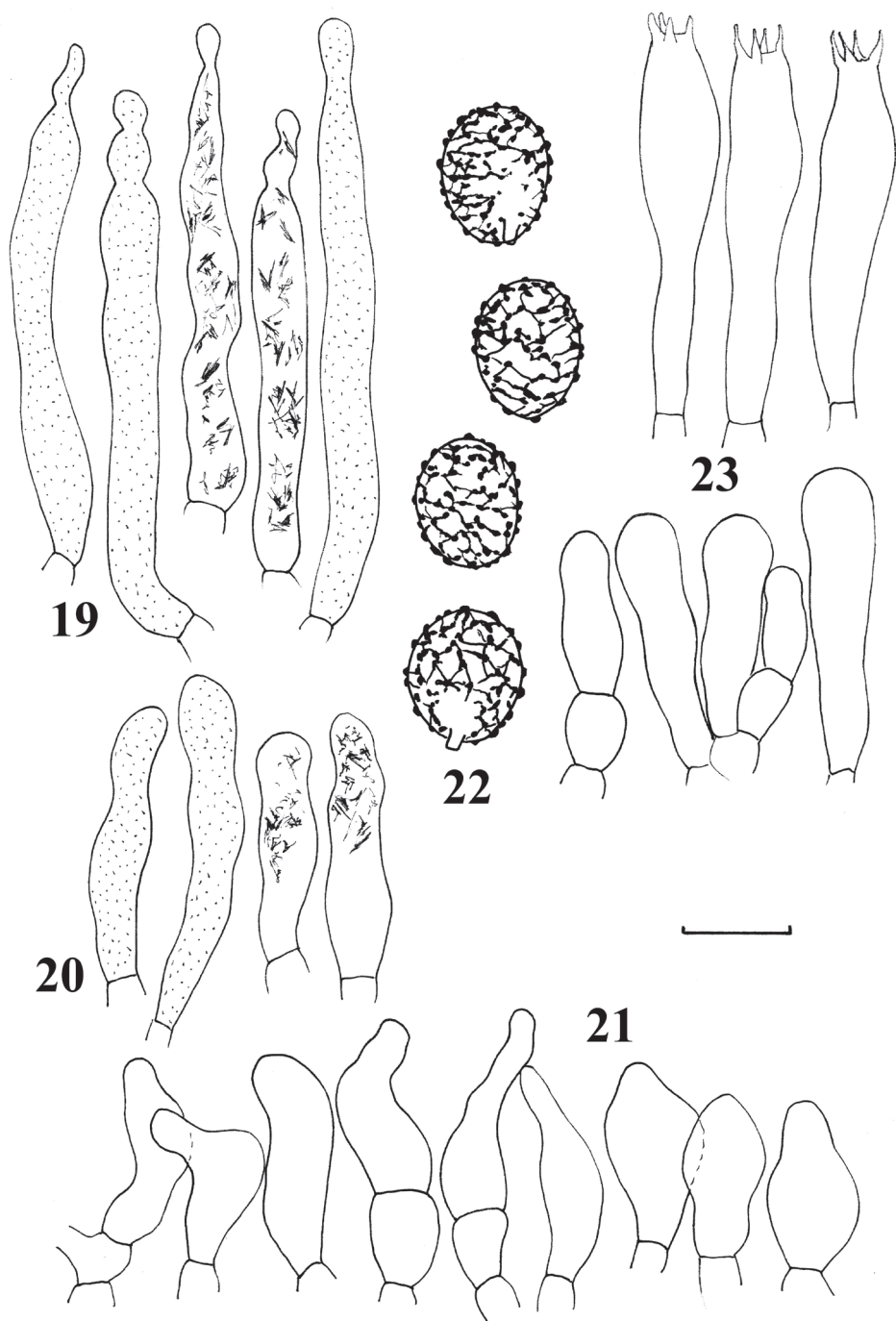
*Examined material:* UNITED STATES. **New York.** East Worcester, Otsego Co., Jul., C. H. Peck (NYSf2839, holotype).

*Commentary:* *R. sordida* seems a good species of subsect. *Nigricantes* because of the dark pigments in many elements of the pileipellis, the frequently double-capitulate pileocystidia and low reticulate spore ornamentation without an amyloid suprahilar spot. Singer (1926 and onwards), and later also Shaffer (1962), considered it a synonym of the European *R. albonigra*, but its appendiculate pileocystidia and higher spore ornamentation contradict this synonymy (see descriptions of *R. albonigra* in Sarnari 1998 and Romagnesi 1967).

When following the identification key to American *Nigricantes* by Shaffer (1962), this species seems to be similar to *R. michiganensis* because of the relatively prominent, reticulate spore ornamentation, the immediately blackening context and the dry pileus surface without any floccules. The type of *R. sordida* differs from the other taxa treated here in the very long, flexuous, attenuating terminal cells near the cap margin and the voluminous, short, lageniform or fusiform marginal cells on the gills.



Figs 16-18. *Russula sordida* (holotype). **16.** Pileocystidia. **17.** Hyphal terminations in the pileus center. **18.** Hyphal terminations near the pileus margin. Contents of cystidia are represented as observed in Congo Red for some elements only, the others are simply filled with dots to indicate their cystidial nature. Scale bar = 10  $\mu$ m.



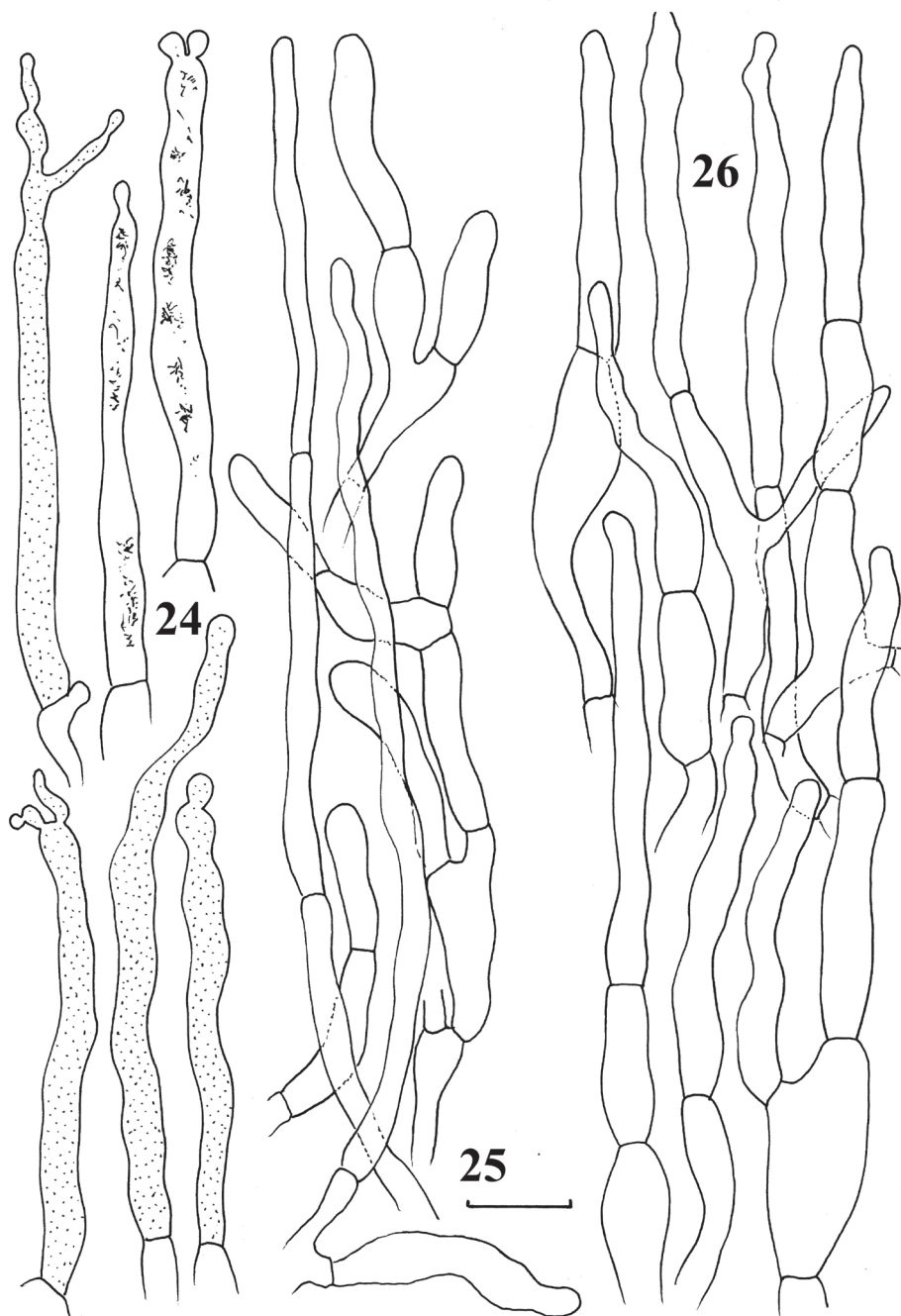
Figs 19-23. *Russula sordida* (holotype). **19.** Hymenial pleurocystidia. **20.** Hymenial cheilocystidia. **21.** Marginal cells of the gill edge. **22.** Basidia and basidiola. **23.** Spores as seen in Melzer's reagent. Contents of cystidia are represented as observed in Congo Red for some elements only, the others are simply filled with dots to indicate their cystidial nature. Scale bar = 10  $\mu$ m, but only 5  $\mu$ m for spores.

***Russula subsordida*** Peck, Bull. New York State Mus. Nat. Hist. 105: 40. 1906**Figs 24-31****Original description:**

*Pileus* fleshy, firm, convex becoming nearly plane or centrally depressed, glabrous, viscid when moist or young, even on the margin, whitish becoming smoky brown with age, sometimes with an olive-green tint, flesh grayish white, slowly changing to a darker or smoky brown color when cut or broken, taste mild or tardily and slightly acrid; lamellae thin, close, adnate, with many short ones intermingled, whitish; stem short, firm, glabrous, spongy within or sometimes cavernous, white slowly becoming smoky brown where wounded; spores white, globose, .0003 of an inch broad.

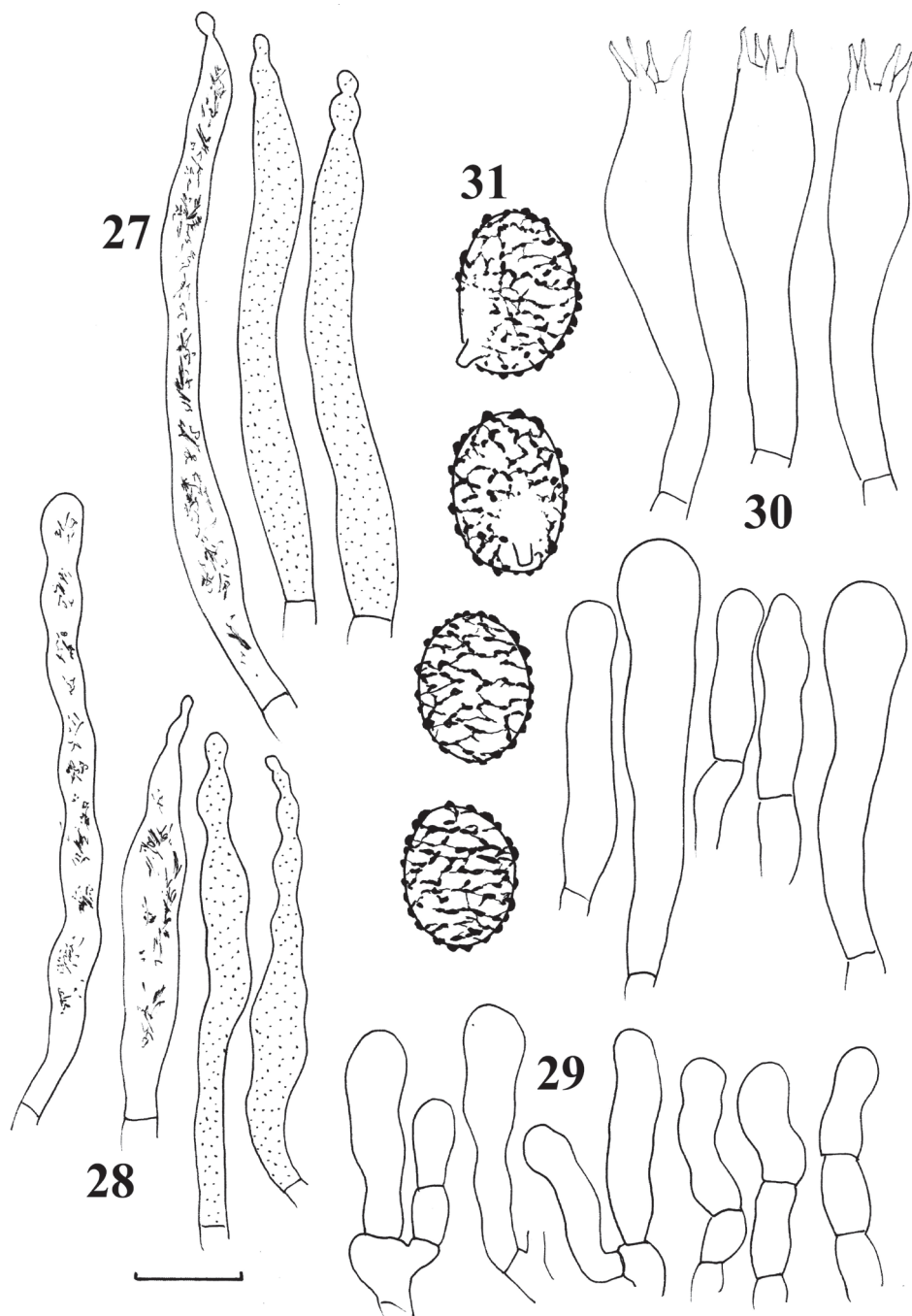
The subsordid russula is very similar to the sordid russula and grows in similar places. It is sometimes associated with it, growing in the same locality and at the same time. Hitherto it has been found in Horicon only, but occurred there in several stations. It may be distinguished from the sordid russula by its viscid cap which is also less white when young, by its less white gills and by its wounds more slowly assuming the smoky brown hue. Both are equally good to eat and equally unattractive in appearance. Both are apparently equally acceptable to insect larvae and both become black or nearly so in drying.

**Spores** (7.5-)8.1-8.7-9.3(-9.9)  $\times$  (5.8-)6.1-6.5-6.8(-7.1)  $\mu\text{m}$ , Q = (1.24-)1.29-1.35-1.41(-1.5), ornamentation of moderately numerous: (4-)6-7(-8) amyloid warts in the circle of diameter of 3  $\mu\text{m}$  on spore surface, warts measuring 0.2-0.4  $\mu\text{m}$  high, connected by numerous fine line connections [2-4(-5) line connections in the circle] and frequently also fused in short crests [(0-)1-4(-5) fusions in the circle], ornamentation completely reticulate or on some places with disconnected reticulum, isolated warts absent. Suprahilar plate inamyloid, smooth, small. **Basidia** (40-)44-47.8-52(-55)  $\times$  9-10.1-11(-12.5)  $\mu\text{m}$ , 4-spored, narrowly clavate or fusiform; basidiola first cylindrical, then narrowly clavate, 5-10  $\mu\text{m}$  wide. **Subhymenium** pseudoparenchymatic. **Lamellar trama** mainly composed of large sphaerocytes. **Hymenial cystidia** on sides moderately numerous, ca. 1000 per  $\text{mm}^2$ , subulate or narrowly fusiform, strongly mucronate, thin-walled, with small (2-7  $\mu\text{m}$ ) capitulum, measuring (64-)79-76.3-84(-92)  $\times$  6-6.8-7.5(-8)  $\mu\text{m}$ , in more than half of volume with crystalline-granulous contents, not graying in sulfovanilin or very indistinctly. **Marginal cells** undifferentiated, on gill edge cylindrical or clavate, obtuse, measuring (10-)14-19.7-25.5(-32)  $\times$  (4.5-)5-5.9-7(-7.5)  $\mu\text{m}$ . **Cheilocystidia** smaller than pleurocystidia, towards apices moniliform-mucronate, mostly with 1-5  $\mu\text{m}$  long appendage or capitulum, measuring (45-)50.5-58.8-67(-78)  $\times$  (5.5-)6-6.6-7.5(-8)  $\mu\text{m}$ , usually in major part with heteromorphous (often crystalline) contents, but sometimes optically almost empty. **Pileipellis** orthochromatic in Cresyl blue with brownish hyphal terminations, vaguely divided in a 75-85  $\mu\text{m}$  deep, strongly gelatinized suprapellis of ascending and near surface repent, pigmented hyphae and a denser, less gelatinized, 20-30  $\mu\text{m}$  deep subpellis of horizontally oriented, intricate, ca. 2-5  $\mu\text{m}$  wide, unpigmented hyphae. Incrustations absent. Pileipellis near margin with terminal cells of hyphae measuring (26-)32.5-43.8-55(-67)  $\times$  (3.5-)4-5.1-6(-7)  $\mu\text{m}$ , irregular in shape, subcylindrical or subulate, some long, distinctly attenuated, moniliform, mostly with distinct dark brown to black parietal pigments, thin-walled, but few distinctly thick-walled and very dark; subapical cells usually equally long, occasionally distinctly shorter, often distinctly wider [4-7.5(-10)  $\mu\text{m}$  wide], rarely branched, less moniliform and flexuous than terminal cells, lower basal cells also scarcely branched. Pileipellis in centre of pileus trichoderm composed of densely arranged short-celled hyphal terminations mixed with occasional protruding, long-celled and attenuated ones, terminal cells measuring (17-)19-41.4-68(-118)  $\times$  (3-)3.5-4.8-6(-8.5)  $\mu\text{m}$ , shorter ones cylindrical, longer ones attenuated, subapical cells branched or not. Pileocystidia dispersed, more numerous near centre of cap,



Figs 24-26. *Russula subsordida* (type, NYSf3077). **24.** Pileocystidia. **25.** Hyphal terminations in pileus center. **26.** Hyphal terminations near the pileus margin. Contents of cystidia are represented as observed in Congo Red for some elements only, the others are simply filled with dots to indicate their cystidial nature. Scale bar = 10  $\mu$ m.





Figs 27-31. *Russula subsordida* (type, NYSf3077). 27. Hymenial pleurocystidia. 28. Hymenial cheilocystidia. 29. Marginal cells of the gill edge. 30. Basidia and basidiola. 31. Spores as seen in Melzer's reagent. Contents of cystidia are represented as observed in Congo Red for some elements only, the others are simply filled with dots to indicate their cystidial nature. Scale bar = 10  $\mu$ m, but only 5  $\mu$ m for spores.

measuring (44-)53.5-80.3-107(-more than 150)  $\times$  (4-)4.5-5.3-6.5  $\mu\text{m}$ , even longer in deeper layers and also continuing as endocystidia in trama, subcylindrical, subulate or narrowly fusiform, very distinctly mucronate to appendiculate, often with two sometimes flexuous-moniliform appendages; contents in Congo red mostly crystalline-granular, not or hardly changing color in sulfovanilin. **Clamp connections** absent in all parts.

*Examined material:* UNITED STATES. **New York State.** Horicon, Warren Co., July 1905, C. H. Peck (NYSf3077, syntype).

*Commentary:* Kauffmann (1918) was the first to consider *R. subsordida* a likely synonym of *R. albonigra*, and was followed herein by Singer (from 1926 onwards) and also by Shaffer (1962), who did not publish a type study but annotated the type as such. We can use the same arguments as in our commentary on *R. sordida* to state that *R. subsordida* certainly belongs in *Nigricantes*, but cannot be a synonym of *R. albonigra*. Among the few types studied here, the type of *R. subsordida* is microscopically most similar to the type of *R. sordida*, but it has longer spores, comparatively shorter and wider terminal cells near the cap margin, a mixture of short and protruding, long terminal cells near the cap centre, subulate and mucronate cheilocystidia and, finally, lacks differentiated marginal cells.

Following Shaffer's key (1962), the most similar species would seem to be *R. adusta* sensu Shaffer because of the similar spore ornamentation, but *R. subsordida* has a gelatinized cutis and not a non-gelatinized trichoderm.

## DISCUSSION

As a result of this study we do not confirm the repeatedly suggested synonymies of Peck's species with European *Nigricantes*, nor between Peck's *R. sordida* and *R. subsordida*. It would honestly have been quite astonishing for the excellent mycologist Peck indeed was to describe twice the same species, especially considering the thirty year interval between the two publications. *R. sordida* was described as an acrid species, whereas *R. subsordida* is mild or merely tardily and weakly acrid. This could potentially be a good character to distinguish between both although Peck (1907) did not use taste in his key to *Compactae* and opposed both species more particularly by the strong viscosity of the cap of *R. sordida* in humid conditions and its strongly blackening context, whereas the cap of *R. subsordida* remains dry in all weather conditions and possesses only a slowly browning context. Both species differ from *R. nigricans* and *R. densifolia* (both sensu Peck) in the absence of an initially reddening context when cut. The latter feature is also found in Shaffer's mild *R. decora* which has a flocculose cap, particularly in the center. Under the microscope, Shaffer's species stands out from the other species studied here in the higher spore ornamentation, whereas *R. subsordida* has the most elliptical spores (mean  $Q = 1.35$ ) of all four species. *R. sordida* differs from *R. subsordida* – and even more so from *R. decora* – in the absence of shorter cells in the cap. *R. decora* is also the only species here that has pileocystidia that are restricted to the cap surface and absent from lower layers.

Finally, *R. densifolia* var *paxilloides* remains presently the most puzzling case as it might also belong in *Polyphyllinae* as suggested by Peck's observation

of the sometimes reddish gills (Peck 1907). It differs from the other species here by the considerable length of most pileicystidia and the well differentiated and longer marginal cells.

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