

***Phanerochaete filamentosa*-*Corticium radiculatum* species complex in North America**

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Phanerochaete filamentosa (Corticiaceae, Aphyllophorales) is a distinctive wood decay fungus found in eastern North America. *Corticium radiculatum* is phenotypically similar to *P. filamentosa* and has been placed in synonymy under *P. filamentosa*. Morphological evidence from basidiomata and cultures, however, shows that these species are distinct. The new combination *Phanerochaete radicata* is proposed. In addition, *Ceraceomyces americanus*, a new species possessing regularly clamped hyphae that bears a striking macroscopic resemblance to *P. radicata* and *P. filamentosa* is described. Basidioma and cultural descriptions are included for all taxa. The new combination *Ceraceomyces fouquieriae* is proposed.

Keywords: Corticiaceae, *Phanerochaete*, *Ceraceomyces*, cultural descriptions, new species, new combinations.

Phanerochaete filamentosa (Berk. & Curtis) Burds. is a distinctive resupinate wood decay species characterized by fragile, grayish orange basidiomata and cordons that turn purplish pink in potassium hydroxide. This species is common in the eastern United States on angiospermous wood and bark (Burdsall, 1985). The species was first described from Alabama by Berkeley (1873); 17 years later, it was redescribed from New York by Peck (1890) as *Peniophora unicolor* Peck. In 1895, Hennings described the new species *Corticium radiculatum* P. Henn. from South Africa. In both macroscopic and microscopic features, *P. filamentosa* is very similar to *C. radiculatum*, and Bresadola believed they were conspecific (v. Höhnelt & Litschauer, 1908: 1093). This synonymy has been generally accepted by other mycologists (Burt, 1925; Bourdot & Galzin, 1928; Talbot, 1951; Burdsall, 1985). However, our studies of basidiomata and cultures reveal that *C. radiculatum* and *P. filamentosa* are distinct taxa.

Fifteen years ago while examining specimens for a monograph on *Phanerochaete*, we noticed that a few collections of *P. fila-*

mentosa from North America possessed regular clamp connections. Since *Phanerochaete* species are characterized by simple septate hyphae with scattered clamps, these collections probably represented an undescribed taxon. Subsequently, in the early 1980s, collections of this same taxon were obtained and cultured from Minnesota.

In this paper, we resolve the *Phanerochaete filamentosa*-*Corticium radicatium* species complex and describe a new species, *Ceraceomyces americanus*. Basidioma and cultural descriptions of these phenotypically similar taxa are included.

Material and methods

Material and methods were those described in Nakasone (1990a). Color names are from Kornerup & Wanscher (1978), and herbarium designations follow Holmgren & al. (1990). For the temperature studies, starter plates were grown on 1.5% malt extract agar (MEA) at room temperature for 7 to 10 d. Plugs of inoculum 5 mm in diameter were taken from the advancing zone and placed mycelium side down in the center of 90 mm plastic Petri dishes containing approximately 25 ml of 1.5% MEA. Each isolate was inoculated in triplicate, and the dishes were placed in plastic bags and incubated at 12, 16, 20, 24, 28, 32, and 36 °C. Plates were removed after 7 d, and mat diameters were recorded and averaged. All available isolates were used and are listed after the cultural descriptions. For the cultural studies, the same protocol was followed except the plates were incubated at 25 °C. Gallic acid (GAA) and tannic acid (TAA) agars were prepared and scored as described by Davidson & al. (1938).

Results

Temperature studies

The three taxa, *Phanerochaete radicata*, *P. filamentosa*, and *Ceraceomyces americanus* responded similarly to the different temperatures which resulted in nearly identical curves (Fig. 1). Although *P. filamentosa* generally grew faster than the other species, there was considerable overlap in mat diameters; thus, standard deviation ranges are not shown in Fig. 1. The optimum temperature for all three species was between 24° and 28 °C. Both *Phanerochaete* species grew poorly at 32 °C while *C. americanus* grew somewhat better. No growth was observed at 36 °C.

Description of taxa

Phanerochaete radicata (P. Henn.) Nakasone, Bergman & Burdsall, comb. nov. – Fig. 2a–d.

= *Corticium radicatum* P. Henn., Pflanzenzw. Ost-Afrikas, Lieferung 1, Theil C, p. 54. 1895.

= *Peniophora radicata* (P. Henn.) v. Höhn. & Litsch., Sitzungsber. Kaiserl. Akad. Wiss. Math.-Naturwiss. Cl. Abt. 1, 116: 746. 1907.

= *Corticium byssogenum* Pat., Bull. Trimestriel Soc. Mycol. France 40: 32. 1924.

Basidiomata resupinate, effuse, loosely attached to substrate, up to 45 × 30 mm in extent, up to 1 mm thick, ceraceous to membranous, soft; hymenial surface continuous or interspersed with sterile areas, friable and pellicular but sometimes crustaceous or ceraceous, easily detached from subiculum, smooth, pilose and with a white cast from emergent cystidia, light yellow (4A4), pale orange (5A3), greyish orange (5B4), brownish orange (5C4), or orange white (6A2) then toward margins brownish orange (6C3–4), greyish orange (5B5), or light yellow (4A5), turning purplish red in KOH; margins sterile, cordonic, loose cobwebby or cottony–felty, cordons up to 1 mm diam, white, light yellow (4A5), or greyish orange (5B5), loosely attached or detached from substrate; context bilayered with a thin, subceraceous upper layer concolorous with hymenium and a thicker, lower layer of cottony, soft, light yellow (4A5) or greyish orange (5B6) to brownish orange (5C6) mycelium. – Hyphal system monomitic. – Subiculum a loose *textura intricata*, up to 450 µm thick, often with large, hyaline crystal clusters embedded throughout tissue; subicular hyphae 2–5.5(–9) µm diam, hyaline, simple septate with rare single clamp connections, sparingly to moderately branched, walls slightly thick to 1.5 µm thick, covered with tiny, brownish yellow, resinous-like granules (observed in Melzer's reagent) that dissolve in KOH, also sometimes encrusted with hyaline crystal clusters. – Subhymenium 50–230 µm thick, composed of embedded cystidia and dense, compact, vertically arranged, short-celled hyphae covered with tiny, brownish yellow, resinous-like granules that dissolve in KOH; subhymenial hyphae 3–4 µm diam, hyaline, simple septate, frequently branched, walls thin, smooth, occasionally brown in Melzer's reagent. – Hymenium a dense palisade of basidia and cystidia covered with tiny, brownish yellow, resinous-like granules that dissolve readily in KOH. – Cystidia arising from subhymenium and hymenium, at first clavate then fusiform, (40–)60–100 (–115) × 5–10(–12) µm, up to 15 µm diam including encrustations, tapering to a narrow stalk, 2–5 µm diam at base, hyaline, simple septate at base, embedded or projecting up to 45 µm, apex obtuse to acute, walls thin throughout or up to 3.5 µm thick then thinning

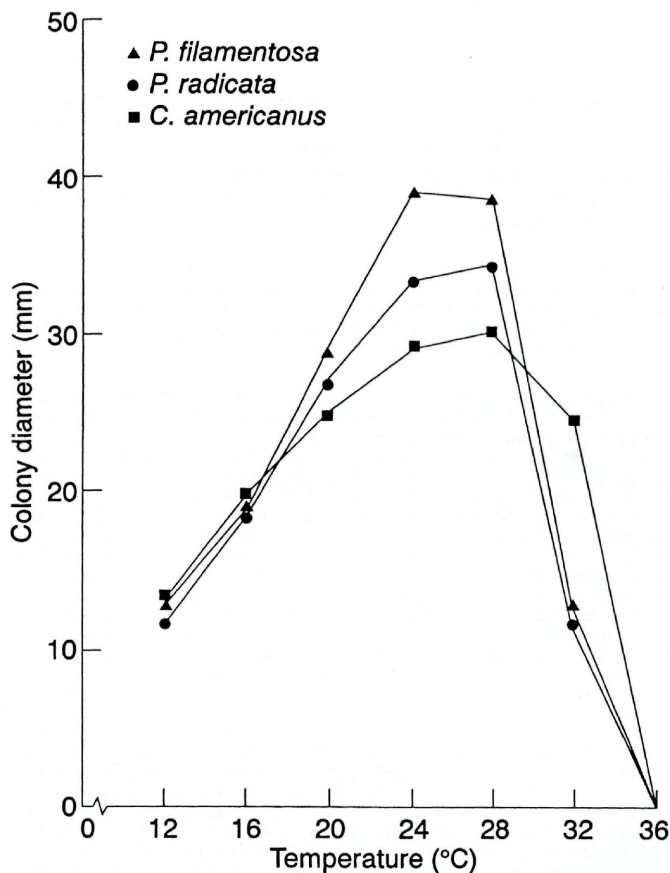


Fig. 1. – Average mat diameter of *Phanerochaete radicata*, *P. filamentosa*, and *Ceratomyces americanus* on malt extract agar after 7 d at different temperatures.

toward apex, smooth or encrusted with hyaline, resinous-like granules. – Basidia clavate, $19\text{--}35 \times 4.5\text{--}5.5 \mu\text{m}$, tapering to $3\text{--}3.5 \mu\text{m}$ at base, hyaline, simple septate at base, 4-sterigmate, walls thin or occasionally slightly thickened. – Basidiospores short cylindrical to ellipsoid, $4\text{--}5(5.5) \times (2.2\text{--})2.5\text{--}3 \mu\text{m}$, hyaline, walls thin, smooth, negative in Melzer's reagent.

Habitat. – On wood and bark of angiosperms, rarely on gymnosperms.

Distribution. – Eastern, midwestern, and southwestern United States, Cuba, Jamaica, Mexico, Costa Rica, Brazil, Sweden (Eriksson & al., 1978; as *P. filamentosa*), Denmark (Christiansen, 1960; as *P. filamentosa*), Germany, Switzerland (Breitenbach & Kränzlin, 1986, as *P. filamentosa*), Burundi, Uganda, India, Vietnam, Japan, New Zealand.

Type specimens examined. – VIETNAM: Tonkin, Nam-Kep, Juillet, M. Petelot No. 492, Patouillard Herb., sheet no. 2074 (HOLOTYPE of *C. byssogenum*: FH). – BURUNDI: [N]derema, Urwald, von Höhnel Herb., ut *Peniophora radicata* (LECTOTYPE of *Corticium radicum*: FH); Usumbara, Holst, von Höhnel Herb. sheet no. 1711 (ISOTYPE of *C. radicum*: FH).

Representative specimens examined. – BRAZIL: Rio Grande do Sul, Serro Azul, 1928, Rick 437, ut *Ph. filamentosa* (NY). – COSTA RICA: San Jose Province, Jardin, on hardwood bark, 9. Aug. 1963, J. L. Lowe 13398 (CFMR). – CUBA: C. G. Lloyd 420, ut *Peniophora filamentosa* (*Pen. filamentosa*) (BPI); Omaja, on hardwood limb, 18. Dec. 1914, C. J. Humphrey 2782, ut *Phanerochaete filamentosa* (*Ph. filamentosa*) (BPI). – GERMANY: Hannover, Misburg, on *Betula* sp., Aug. 1911, Engelke, Missouri Bot. Gard. Herb. 10076, ut *Pen. filamentosa* (BPI); Hamburg, on *Pinus sylvestris* L., 22. Sep. 1907, Jaap 446, ut *P. unicolor* (BPI). – INDIA: Himachal Pradesh, Simla Chail, on angiospermic wood, 5. Aug. 1971, S. S. Rattan 5588, ut *Pen. filamentosa* (BPI); Mahasu, Narkanda, on *Abies* sp., 17. Oct. 1967, S. S. Rattan 5360, ut *Pen. filamentosa* (BPI). – JAMAICA: St. Catherine Parish, on wood, 26. Aug. 1957, A. L. Welden 825 and 831, ut *Ph. filamentosa* (NO); St. Ann Parish, from Moneague to Hollymount via Union Hill, on wood, 6. Aug. 1957, A. L. Welden 568, ut *Ph. filamentosa* (NO). – JAPAN: Tottori Prefecture, Saihaku-gun, Mt. Daisen (Sannosawa), on *Fagus crenata* Blume, 14. Sep. 1983, N. Maekawa 571, ut *Ph. filamentosa* (TMI, CFMR); Okayama Prefecture, Maniwa-gun, Kuse-cho, on *Quercus serrata* Thunb., 17. Sep. 1986, N. Maekawa 1056, ut *Ph. filamentosa* (TMI, CFMR). – MEXICO: Jalapa, 5000 ft., on bark, 12–20. Dec. 1901, W. A. and E. L. Murrill 327, ut *Pen. filamentosa* (BPI, NY). – NEW ZEALAND: Auckland, Waitakere Ranges, Ruatwhenua, 300 m, 28. Dec. 1954, J. M. Dingley 14137, ut *Pen. filamentosa* (BPI). – SWEDEN: Halland, Släp par., Särö Vasterskog, on wood, 19. Sep. 1972, N. Hallenberg 0762, ut *Ph. filamentosa* (TENN). – UGANDA: Kyagwe, Forest Kipayo, 4000 ft., 5. 1915, R. A. Dummer 636, (BPI). – UNITED STATES: Arizona, Cochise County, Coronado Nat. Forest, Chiricahua Mts., Turkey Creek, on *Quercus arizonicus* Sarg., 18. Aug. 1972, R. L. Gilbertson 10719 (CFMR); Pima County, Coronado Nat. Forest, Santa Catalina Mts., Bear Wallow, on *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr., 19. Aug. 1971, H. H. Burdsall, Jr. 6146 (CFMR); Santa Cruz County, Coronado Nat. Forest, Santa Rita Mts., Madera Canyon, on *Platanus wrightii* Wats., 8. Sep. 1975, H. H. Burdsall, Jr. 8501 (CFMR). Florida, Alachua County, San Felasco Hammock, on *Quercus nigra* L., 28. 7. 1970, H. H. Burdsall, Jr. 4800 (CFMR). Iowa, West Okoboyi, on *Quercus macrocarpa* Michx., 10. Aug. 1932, D. P. Rogers, ISU 371736, ut *Ph. filamentosa* (ISC). Louisiana, Livingston Parish, near Walker, on woody angiosperm, 23. Aug. 1960, A. L. Welden, NO 00778, ut *Pen. filamentosa* (NO). Massachusetts, Wakefield, on twigs and bark on forest floor, 12. Jul. 1942, D. H. Linder and W. L. White, ut *Pen. filamentosa* (FH). New Jersey, Newfield, on old oak stump, 15. Feb. 1877, Ellis 1518,

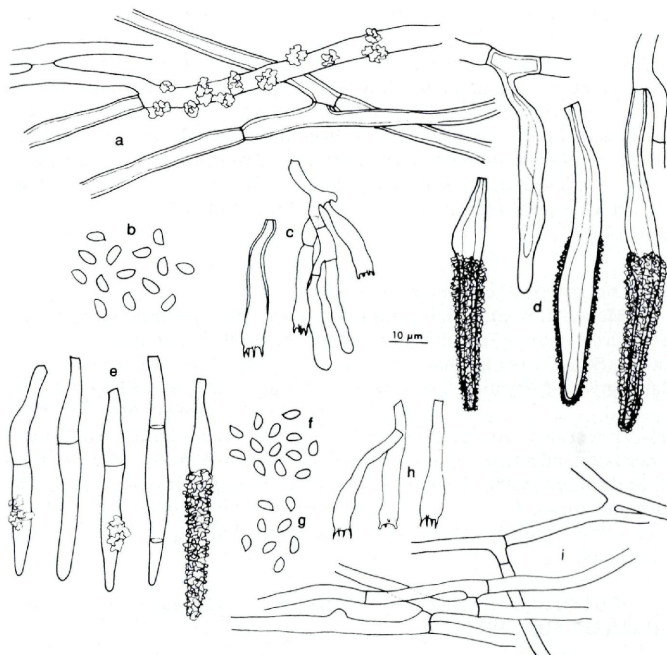


Fig. 2. – Microscopic elements of *Phanerochaete* species. – *P. radicata* (RLG 10719): (a) subicular hyphae, (b) basidiospores, (c) basidia, and (d) cystidia. – *P. filamentosa* (holotype of *Peniophora unicolor*): (e) cystidia, (f) basidiospores, (g) basidiospores (HHB 6822), (h) basidia, and (i) subicular hyphae (HHB 6822) (M93 0089).

ut *Pen. filamentosa* (FH). New York, Warrensburg, Pack Forest, on *Populus tremuloides* Michx., 9. Sep. 1963, R. L. Gilbertson 4217 (CFMR). North Carolina, Macon County, Coweeta Expt. Forest, Big Butt, on *Fagus* sp., 17. Aug. 1969, H. H. Burdsall, Jr. 3111 (CFMR); Highlands, Satula Mt. Trail, on *Quercus* sp., 5. Jul. 1969, H. H. Burdsall, Jr. 1909 (CFMR). Tennessee, Sevier County, Great Smoky Mtns. Nat. Park, along Roaring Fork, Cherokee Orchard, on *Liriodendron tulipifera* L., 10. Jul. 1970, H. H. Burdsall, Jr. 4329 (CFMR). Pennsylvania, Cambria County, Ehernsburg, Aug. 1916, D. R. Sumstine 5762, ut *Pen. filamentosa* (NY). Virginia, Giles County, Pembroke, on *Quercus* sp., 2. Aug. 1979, H. H. Burdsall, Jr. 10707 (CFMR).

Culture description

Growth on MEA 26–36 mm diam at 7 d; 66–80(–90+) mm diam at 14 d (Fig. 3a). Mats yellowish white (3A2) or pastel yellow (3A4) to pale yellow (3A3), thin to moderately thick, usually cottony

immediately around inoculum, then becoming silky-raised, downy to cottony-woolly toward margins in 2 wk, by 6 wk mats pale yellow (4A3) to greyish yellow (4B6), some isolates with patches of brownish orange (5C6), thin to moderately thick, silky-downy, slightly raised in some areas; in isolate RLG 10719 forming brownish orange (5C6) cordons up to 0.5 mm diam that grow up side of Petri dish; margins even, appressed; no agar discoloration at 2 and 6 wk; not fruiting by 6 wk. Oxidase reactions on GAA +++, rarely -, mat 0-6(-13) mm diam at 7 d, 0-12(-25) mm diam at 14 d; on TAA stain or +, no growth at 7 and 14 d.

Microscopic characters

Marginal hyphae 2.5-5 µm diam, thin walled, simple septate with scattered clamps, moderately branched, often branching below the septa. Submerged hyphae 2.5-8 µm diam, occasionally encrusted with large hyaline crystals (not dissolving in 3% KOH, as in Fig. 3e), thin walled, simple septate, typically with rare clamps, often forming H-connections. Aerial hyphae 2.5-7.5 µm diam, lightly to heavily encrusted with fine, yellow to yellowish brown, resinous-like granules that dissolve in 3% KOH (as in Fig. 3f) and large hyaline crystals that do not dissolve, simple septate with scattered clamps; by 6 wk becoming slightly thick-walled and hyphal tips often heavily encrusted.

Cultures studied. - HHB 1909, HHB 4329, HHB 10707, RLG 4217, RLG 10719.

Species code: (1).2.5.(12).(16).21.32.(36).(37).38.(44).45-47.54.(55).

Phanerochaete radicata is a widely distributed and easily recognized species. It is sympatric in eastern United States with the phenotypically similar species *P. filamentosa*. In the past, these two taxa were considered conspecific; however, there are morphological differences. For example, the cystidia of *P. radicata* have thick walls and no secondary septa while those of *P. filamentosa* have generally thin walls and frequently develop secondary septa. The basidiospores of *P. radicata* are slightly wider (2.2-3 µm diam) than those of *P. filamentosa* (2-2.5 µm diam). Furthermore, the hymenia of

Fig. 3. - Two-wk-old colonies grown at 25°C on malt extract agar: - (a) *Phanerochaete radicata* (RLG 4217), (b) *P. filamentosa* (HHB 3169), (c) *Ceraceomyces americanus* (HHB 11669), and (d) *C. americanus* (HHB 11540). Encrusted hyphae in 2-wk-old cultures: (e) submerged hypha with hyaline crystal clusters in *P. filamentosa*, (f) aerial hyphae with yellowish brown resinous-like granules and hyaline crystals (arrow) in *C. americanus*, and (g) terminal aerial hypha with yellowish brown resinous-like granules and larger hyaline crystals in *C. americanus* (M93 0088).



P. filamentosa have a more yellowish brown cast with a concolorous and homogeneous context. On the other hand, *P. radicata* has a white cast to the hymenia (in mature areas) and a bicolored context. In culture, *P. radicata* is very similar to *P. filamentosa*, but the species can be distinguished by dropping 3% KOH on 2-wk-old mats. *Phanerochaete filamentosa* develops a pink reverse discoloration overnight while *P. radicata* does not.

Some morphological characters of *P. radicata* vary. For example, some specimens from India have a distinct, thick, ceraceous hymenium and subhymenium that are lacking in specimens from the United States. In addition, in specimens examined from Cuba and Jamaica, cystidia are typically shorter (up to 45 μm long) with consistently thin walls.

Other descriptions and illustrations of *P. radicata* can be found under *Phanerochaete* or *Peniophora filamentosa* in Breitenbach & Kränzlin (1986: 156–157); Christiansen (1960: 182–183); Cunningham (1963: 125–126); Eriksson & al. (1978: 1000–1002); Hayashi (1974: 61–63); Lindsey & Gilbertson (1978: 91–93); Rattan (1977: 256–257). While the description of *P. filamentosa* in Burdsall (1975) is a composite of *P. radicata* and *P. filamentosa*, the illustration (p. 279) is that of *P. radicata* (specimen HHB 4203).

Although Hennings' collection is housed at Berlin, there is no type material of *C. radicatulum* (Burghard Hein, pers. comm.). However, the von Höhnelt collection at the Farlow Herbarium has two specimens of *P. radicata* that are stated on the packets to be "original". Both specimens are in good condition and represent the same species. The packet labeled *Peniophora radicata*, Derema, Urwald, ex Mus. bot. Berolin, is chosen here as the lectotype. The other specimen, *Corticium radicatulum*, Usambara, Holst, ex herbario J. Bresadola, is designated the isotype.

We also examined the type specimen of *Phanerochaete borneensis* Jülich, which was described from Borneo (Jülich, 1980). This species was placed in synonymy under *P. filamentosa* by Burdsall (1985). Our observations indicate that *P. borneensis* is closely related to *P. radicata* but is a distinct species. In particular, the cystidia of *P. borneensis* are unlike those of *P. radicata* in that they are consistently short ($20\text{--}33 \times (5\text{--})7\text{--}8 \mu\text{m}$) with slightly thickened walls and are encrusted apically with coarse, hyaline crystals. Additionally, the bright yellow context of *P. borneensis* is striking and contrasts with the duller, brownish orange context of *P. radicata* and *P. filamentosa*.

Cultural descriptions of *P. radicata* in Hayashi (1974: 63, as *Membranidium filamentosum*) and Nakasone (1990b: 230–231, as *P. filamentosa*) agree with our observations except for minor differences. Hayashi (1974) observed pale yellow to yellowish brown hyphae and heavy encrustations on all types of hyphae. However, his observations

were made from cultures grown on potato dextrose agar at 30 °C whereas our cultures were grown on MEA at 25 °C. Although Nakasone (1990b) observed cystidia in one culture, cystidia were not found in the study reported here. Possibly, the ability to form cystidia was lost upon storage or the structures observed were not cystidia but encrusted hyphal tips.

Phanerochaete filamentosa (Berk. & Curtis) Burds. in B. D. Parker & M. K. Roane, Distributional history of the biota of the southern Appalachians IV. Algae and fungi. p. 278. 1975. – Fig. 2e–i.

= *Corticium filamentosum* Berk. & Curtis in Berk., Grevillea 1: 178. 1873.

= *Peniophora filamentosa* (Berk. & Curtis) Burt in Coker, J. Elisha Mitchell Sci. Soc. 36: 162. 1921.

= *Grandiniella filamentosa* (Berk. & Curtis) Burds., *Taxon* 26: 329. 1977.

= *Peniophora unicolor* Peck, New York State Bot. Rep. 43: 69–70. 1890.

Basidiomata resupinate, effuse, loosely attached to substrate, up to 65 × 30 mm in extent, up to 0.5 mm thick, fragile and soft, membranous; hymenial surface continuous, smooth, easily detached from subiculum, light yellow (4A5), greyish yellow (4B5), reddish yellow (4A6), or brownish orange (5C5–6), with a few scattered cracks, turning purplish pink in KOH; margins abrupt and cordonic or thinning out and fibrillose, forming poorly organized, flattened, appressed, white to greyish yellow (4B5) cordons; cordons white to light yellow (3A4, 4A5), up to 1.5 mm diam, loosely attached or detached from substrate; context concolorous with hymenium, cottony, soft, homogeneous throughout, sometimes with a thin, white mycelial layer next to substrate. – **Hyphal system** monomitic. – **Subiculum** up to 400 µm thick, composed of two distinct sections: (a) basal layer next to substrate up to 90 µm thick, consisting of a dense layer of hyphae arranged parallel to substrate, and (b) upper layer, up to 300 µm thick, an open and loose *textura intricata*, with hyphae coated with tiny yellow granules that dissolve in KOH and hyaline, crystal clusters that do not dissolve in KOH; subicular hyphae of two types (a) 3.5–6(–8) µm diam, opaque, dark yellow, but staining deeply in phloxine, simple septate, rarely branched, walls thin to slightly thick, smooth, difficult to observe, found only in basal layer next to substrate; (b) 2–5 µm diam, hyaline, primarily simple septate with rare single clamps, sparingly to moderately branched, often forming H-connections, walls thin, encrusted with hyaline crystal clusters or tiny, yellow granules that dissolve in KOH, predominate hyphal type in subiculum. – **Subhymenium** up to 50 µm thick, composed of cystidia and hyphae arranged perpendicular to substrate to form a dense tissue; subhymenial hyphae 2–3.5 µm diam, hyaline, simple septate, short-celled, walls thin, smooth. – **Hymenium** a dense palisade of basidia and cystidia. – **Cystidia**

arising from hymenium and subiculum, cylindrical to narrowly obclavate, $(30\text{--}40\text{--}60 \times 5\text{--}7 \mu\text{m})$, up to $13 \mu\text{m}$ diam including encrustations, tapering to a short stalk $2\text{--}4 \mu\text{m}$ diam, hyaline, simple septate at base, often with one or more secondary septa, embedded or projecting up to $30 \mu\text{m}$, apex obtuse, walls thin, occasionally up to $2 \mu\text{m}$ thick then thinning toward apex, smooth or encrusted with persistent, hyaline crystals or lightly coated with small yellow granules that dissolve in KOH. – Basidia cylindrical to clavate, $20\text{--}33 \times 3.5\text{--}5 \mu\text{m}$, tapering to $2\text{--}2.5 \mu\text{m}$ at base, hyaline, simple septate at base, 4–sterigmate, walls thin, mature elements often non-staining in phloxine and collapsed. – Basidiospores short cylindrical, $4\text{--}5 \times 2\text{--}2.5 \mu\text{m}$, hyaline, walls thin, smooth, negative in Melzer's reagent.

Habitat. – On bark and wood of angiosperms.

Distribution. – East of the Mississippi River in the United States and eastern Canada.

Type specimens examined. – UNITED STATES: Alabama, Peters, Curtis no. 6119 (HOLOTYPE of *C. filamentosum*: FH); New York, Syracuse, Sep. 1889, L. M. Underwood (HOLOTYPE of *P. unicolor*: NYS, ISOTYPE: NY).

Representative specimens examined. – CANADA: Ontario, Renfrew County, near Eganville, Shaw Woods, on bark and wood of *Fagus grandifolia* Ehrh., 11. Aug. 1987, J. H. Ginns 8913 (DAOM, NY); Quebec, Cascades, on wood, 1. Oct. 1935, I. Mounce, F 7213 (DAOM, NO). – UNITED STATES: Alabama, Etowah County, Gadsden, on *Quercus* sp., 31. May 1975, A. L. Welden 8389 (NO). District of Columbia, Rock Creek Park, on *Fagus* sp., 18. Aug. 1938, K. D. Doak, FP 72170 (CFMR). Florida, Alachua County, Univ. Florida horticulture unit, on *Ostrya virginiana* (Mill) K. Koch, 10. Jul. 1972, H. H. Burdsall, Jr. 6454 (CFMR), and on *Quercus* sp., 28. Jul. 1972, H. H. Burdsall, Jr. 6822 (CFMR). Georgia, Clarke County, 5 mi SW Athens, branch of Oconee River, on decorticated fallen hardwood limb, 5. Oct. 1952, A. S. Rhoads, FP 103297 (CFMR). Illinois, Johnson County, Ferne Clyffe State Park, on *Acer* sp., 20. Oct. 1989, H. H. Burdsall, Jr. 12951 (CFMR). Indiana, Brown County State Park, Bloomington, on *Quercus* sp., 23. Aug. 1958, R. W. Davidson, FP 105240 (CFMR); Owen County, Spencer, on *Quercus* sp., 22. Aug. 1970, J. L. Lowe 15002 (CFMR). Maryland, Fredrick County, W Emmetsburg, Middle Creek, on hardwood bark, 2. Sep. 1969, H. H. Burdsall, Jr. 3169 (CFMR). Michigan, New Richmond, on *Fagus* sp., 9. Sep. 1914, C. H. Kauffman 49 (BPI); Berrien County, Stevensville, on *Quercus* sp., 4. Sep. 1955, R. F. Cain, Univ. Toronto No. 31858 (FH, NY). New Jersey, near Flemington, 3. Aug. 1935, D. R. Sumstine 10648 (NY). New York, Allegheny State Park, on *F. grandifolia*, 12. Sep. 1964, R. L. Gilbertson 5067 (CFMR); Onondaga County, Pratt's Falls Park, on *Acer saccharum* Marsh., 15. Sep. 1966, R. L. Gilbertson 6829 (CFMR); Rensseler County, West Schaghticoke, 1. Aug. 1910, C. H. Peck (NYS); Schuyler County, Van Etten, Arnot Forest, Banfield Rd., on *Ulmus americanus* L., 19. Sep. 1970, H. H. Burdsall, Jr. 4918 (CFMR). North Carolina, Chapel Hill, on *Cornus* sp., 31. Jul. 1920, J. N. Couch 4607 (BPI); Haywood County, Great Smoky Mtns. Nat. Park, above Big Creek Ranger Station, on deciduous log, 6. Jul. 1970, H. H. Burdsall, Jr. 4230 (CFMR). Ohio, Ross County, Scioto Trail State Forest, on hardwood, 31. Aug. 1968, W. B. & V. G. Cooke 7514 (NO). Pennsylvania, Mercer County, 5 mi NW Fairview, Half Moon Swamp, on

trunk of living *A. saccharum*, 9. Jul. 1947, L. K. Henry 14267 (NY). Tennessee, road to Cade's Cove, on underside of fallen tree, 7. Jun. 1975, G. W. Freeman 41005 and 28. Jul. 1975, G. W. Freeman 41054 (TENN). Virginia, Shenandoah County, George Washington Nat. Forest, Elizabeth Furnace Day Use Area, on *Quercus* sp., 9. Oct. 1970, H. H. Burdsall, Jr. 5003 (CFMR).

Culture description

Growth on MEA 26–42 mm diam at 7 d, 68–90+ mm diam at 14 d (Fig. 3b). Mats light yellow (3A5), pastel yellow (3A3) to pale yellow (3A4), moderately thin to moderately thick, cottony to downy around inoculum, silky-raised to cottony-woolly towards margins at 2 wk, by 6 wk mats pale yellow (4A3) to greyish yellow (4B5), moderate to thick, silky-downy, slightly raised, forming brownish orange (5C6) to greyish yellow (4C7) cordons up to 1 mm thick which grow out of plate; margins even, occasionally appressed to slightly raised; no agar discoloration at 2 and 6 wk, however, a drop of KOH on mats will develop a pink reverse discoloration overnight in 2-wk-old cultures; not fruiting by 6 wk. Oxidase reactions on GAA +++++, mat 8–12 mm diam at 7 d, 8–20 mm diam at 14 d; on TAA +, no growth at 7 and 14 d.

Microscopic characters

Marginal hyphae 2.5–5 µm diam, thin walled, simple septate with rare clamps, moderately branched often below septa. Submerged hyphae 2.5–7.5 µm diam, thin walled, sometimes encrusted with large hyaline crystals (not dissolving in 3% KOH), simple septate with scattered single clamps, occasionally with multiple branches below septa, some twisted hyphae, often forming H-connections. Aerial hyphae 2.5–5(–7) µm diam, simple septate with rare clamps, encrusted with fine yellow to yellowish brown resinous like granules that dissolve in 3% KOH and large hyaline crystals that do not dissolve (Fig. 3e), by 6 wk becoming slightly thick walled, hyphal tips heavily encrusted.

Cultures studied. – HHB 3169, HHB 4918, HHB 6454, HHB 6822, FP 103297, FP 105240.

Species code: (1).2.5.(12).16.21.31e.32.(36).(37).38.(44).45–47.54.

Phanerochaete filamentosa is phenotypically similar to *P. radicata* in both macroscopic and microscopic basidioma and cultural features. See remarks under *P. radicata* for further discussion on the differences between these taxa. The subhymenium–hymenium layer in *P. filamentosa* is never ceraceous; thus, it is difficult to obtain thin, free-hand sections through the basidioma. In contrast, *P. radicata* has a distinct ceraceous hymenial layer, and free-hand sections are often easily obtained.

Most published descriptions and illustrations of *P. filamentosa* actually refer to *P. radicata*. However, the description by Jung (1987: 50) is based on a specimen of *P. laevis* (Pers.: Fr.) Erikss. & Ryv. *Phanerochaete filamentosa* as described by Burdsall (1985: 75–79) is a composite of *P. filamentosa* and *P. radicata*, whereas the illustration on page 77 is that of *P. filamentosa*. Similarly, Burt's (1925: 320) description is a composite as he included not only specimens of *P. filamentosa* and *P. radicata* in the list of specimens examined but also at least three specimens of *C. americanus*.

Two specimens of *P. unicolor* at the Farlow Herbarium are labeled TYPE with the date Oct. 1889; however, the month on the holotype specimen at NYS and in the protologue is Sept. Therefore, the collections at FH cannot be types of *P. unicolor*.

Since some confusion has surrounded the name *Corticium petersii* Berk. & Curtis, we investigated it further. When Berkeley (1873) described this species, he indicated that it was represented by Curtis No. 4509 and Ravenel's Fungi Caroliniani, Fascicle V, no. 28. We examined Curtis No. 4509 from Berkeley's herbarium at Kew (holotype) and Curtis's herbarium at FH (isotype). Both these specimens are *Phanerochaete sanguinea* (Fr.) Pouzar. However, specimens of Ravenel's exsiccati from BPI, FH, NY and NYS are *P. filamentosa*. Our observations, therefore, agree with Burt (1925), who first identified and resolved this problem.

Ceraceomyces americanus K. K. Nakasone, C. R. Bergman & H. H. Burdsall, sp. nov. – Figs. 3c, d, f, g; 4.

Differt a *C. cystidiato* hymeniis olivaceis, marginibus funiculosis; cystidiis fusiformibus, $33\text{--}60 \times 5\text{--}9\text{--}(12) \mu\text{m}$, ochraceis materiis in KOH dissolventibus; basidiosporis $4\text{--}5 \times 2\text{--}2.5 \mu\text{m}$.

Holotypus: U.S.A., Minnesota, Clearwater County, Lake Itasca State Park, Bohall Trail, in ligno *Aceris sacchari* Marsh., leg. H. H. Burdsall, Jr. 11354, in herbario CFMR conservatus, isotypus in herbario BPI conservatus.

Basidiomata resupinate, adherent, effused, up to $25 \times 7 \text{ cm}$ in extent, up to 0.45 mm thick, soft, membranous; hymenial surface continuous, pelliculose, readily detached from subiculum, smooth but uneven from substrate, sometimes with numerous fine cracks, olive brown (4D4, 4E5–6), brownish orange (5C4), greyish brown (5D3) to yellowish brown (5D4–5), turning purplish red in KOH; margins up to 15 mm wide, sterile, deeply lacerate to fimbriate, yellowish brown (5D5), brownish orange (5C6), or yellowish brown (5D6), then white or pale orange (5A3) at the edges or abrupt and cordonic; cordons yellowish brown (6D5–6) with scattered white patches, loosely attached or detached from substrate; context bilayered with a thin top

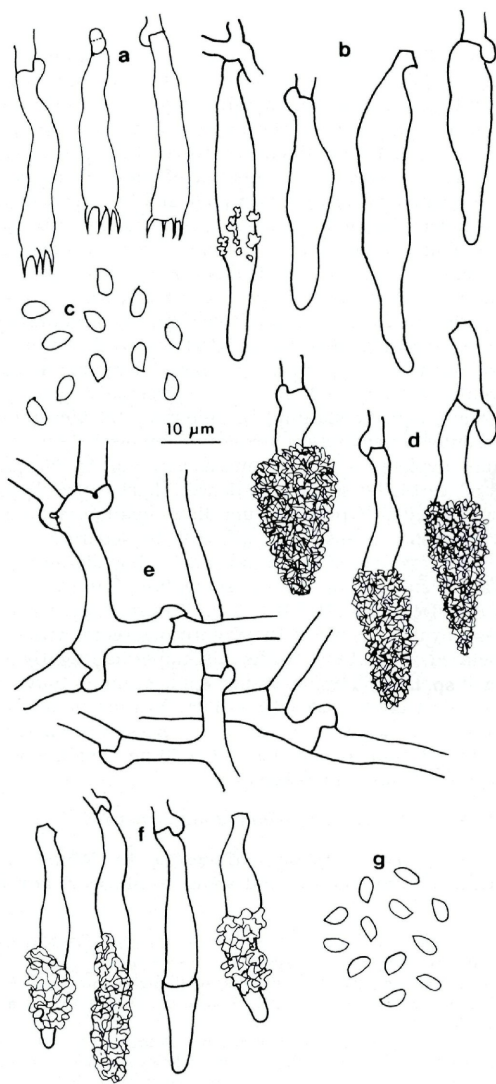


Fig. 4. – Microscopic elements of *Ceraceomyces americanus*. Holotype specimen, HHB 11354: (a) basidia, (b) cystidia (after KOH treatment), (c) basidiospores, and (d) encrusted cystidia. HHB 4317: (e) subicular hyphae, (f) cystidia, and (g) basidiospores (M93 0090).

layer concolorous with hymenium and a thin or thick bottom layer of cottony mycelium concolorous with sterile margin, occasionally observed with a thin, white, mycelial layer closely appressed to substrate near margins. – Hyphal system monomitic. – Subiculum up to 350 μm thick, composed of two layers: (a) next to substrate a *textura porrecta*, composed of parallel, dense, hyphae smooth or encrusted with hyaline crystals, and (b) a *textura intricata*, loose upper layer of hyphae encrusted with orange-brown granules; subicular hyphae 3–5 μm diam, hyaline, nodose septate, sparingly branched next to substrate but moderately branched in upper subiculum, walls thin, smooth or encrusted with hyaline crystal clusters or a thin to thick layer of yellowish brown granules (observed in Melzer's reagent) that dissolve in KOH. – Cordons up to 1 mm diam, inner core a *textura porrecta*, composed of hyphae 4–8 μm diam, nodose septate, walls up to 2 μm diam, occasionally some hyphae up to 20 μm diam, densely staining in phloxine and Melzer's reagent, walls thick, outer core a *textura intricata*, composed of hyphae similar to subicular hyphae. – Subhymenium up to 30 μm thick, composed of vertically arranged, dense, short-celled hyphae and cystidia; subhymenial hyphae 3–4 μm diam, hyaline, nodose septate, frequently branched, dense and difficult to separate, walls thin, smooth. – Hymenium a dense palisade of basidia and cystidia. – Cystidia arising from upper subiculum, subhymenium and hymenium, fusiform, 33–44(–60) \times 5–9(–12) μm , tapering to 2–3 μm diam at base, hyaline, rarely with adventitious septa, nodose, septate at base, enclosed, apex obtuse, walls thin, upper half lightly to heavily encrusted with yellowish brown resinous like granules that dissolve in KOH. – Basidia clavate, 22–36 \times 4–5 μm , hyaline, nodose septate at base, 4-sterigmate, walls thin, smooth. – Basidiospores short cylindrical to ellipsoid, 4–5(–5.5) \times 2–2.5(–3) μm , hyaline, walls thin, smooth, negative in Melzer's reagent.

Habitat. – On bark and wood of angiosperms.

Distribution. – From Minnesota to Maine, including southern Ontario and Quebec, and south to Missouri and northern Georgia.

Representative specimens examined. – CANADA: Ontario, Renfrew County, Shaw Woods near Eganville, on well-rotted log of *F. grandifolia*, 11. Aug. 1987, J. H. Ginns 8927, ut *Ph. filamentosa* (DAOM). Quebec, Ile Perrot, near Montreal, on *Acer* sp., 27. Aug. 1941, H. S. Jackson, DAOM 161447 and 161450 (DAOM). – UNITED STATES: Georgia, Rabun County, Chattahoochee Nat. Forest, Warwoman Dell, on bark and wood of hardwood branch, 8. Jul. 1969, H. H. Burdsall, Jr. 2004 (CFMR). Illinois, Edgar County, Foley's woods near Grand View, 14. Aug. 1965, R. F. Cain, TRTC 50018, ut *Ph. filamentosa* (BPI); Pope County, Shawnee Nat. Forest, Hunting Grounds Picnic Area, on *Quercus* sp., 16. Jun. 1984, K. K. Nakasone, FP 101981 (CFMR), and on hardwood, 4. Jun. 1986, K. K.

Nakasone, FP 102179 and FP 102188 (CFMR); Williamson County, east side of Devil's Kitchen Lake, on *Quercus* sp., 3. Jun. 1986, K. K. Nakasone, FP 102144 (CFMR). Kentucky, Crittenden, 1. Aug. 1910, C. G. Lloyd, Lloyd Herb. 10113, ut *Pen. filamentosa* (BPI). Maine, Kittery Pt., R. Thaxter 3489, ut *Pen. filamentosa* (FH). Minnesota, Clearwater County, Itasca State Park, maple grove along Bohall Trail, on *Acer saccharum* Marsh., 30. Jul. 1982, H. H. Burdsall, Jr. 11540 (CFMR), on *Ganoderma applanatum* (Pers.) Pat., 11. Sep. 1982, H. H. Burdsall, Jr. 11699 (CFMR), and on *U. americanus* bark, 6. Aug. 1981, H. H. Burdsall, Jr. 11351 (CFMR). Missouri, Columbia, on *Acer* sp., 26. Sep. 1903, B. M. Duggar 447, ut *Pen. filamentosa* (FH). New Hampshire, Franconia, Sep. 1905, W. G. Farlow 26, ut *Pen. filamentosa* (FH). New Jersey, Orange, Nov. 1899, L. M. Underwood, Missouri Bot. Gard. Herb. 61576, ut *Pen. filamentosa* (BPI, NY). New York, Bolton, on bark of *Tilia* sp., Aug. 1927, C. H. Peck, ut *Pen. filamentosa* (NYS); North Greenbush, on dead branches of *Ulmus* sp., 25. Nov. 1915, H. D. House, ut *Pen. filamentosa* (BPI, NY, NYS). North Carolina, Wake County, Raleigh, Schenck Res. Forest, on bark of *O. virginiana*, 21. Sep. 1982, L. F. Grand 3185 (CFMR). Ohio, Portage County, West Branch State Park, on wood and bark of hardwood, 5. Sep. 1978, S. J. Mazzer 9686 (CFMR). South Carolina, Union County, Union, Calhoun Expt. Forest, on wood of fallen hardwood limb, 8. Oct. 1952, A. S. Rhoads, FP 103304 (CFMR). Tennessee, Sevier County, Great Smoky Mtns. Nat. Park, along Roaring Fork, on bark of *Robinia pseudoacacia* L., 10. Jul. 1970, H. H. Burdsall, Jr. 4317 (CFMR), and near Fish Camp Prong, Little River, on hardwood, 25. Jul. 1970, H. H. Burdsall, Jr. 3987 (CFMR).

Culture description

Growth on MEA (17-)28–45 mm diam at 7 d; (40-)45–82(–90+) mm diam at 14 d (Fig. 3c,d). Mats variable, at 2 wk often light yellow (4A4) to greyish yellow (4B5), moderately thin to moderately thick, slightly raised, cottony around inoculum, then silky-cordonic toward margins, cordons greyish yellow (4B6) to brownish orange (5C6) with margins even to bayed; in some isolates cordonic only around inoculum, then becoming thin and appressed toward margin or sectoring, thin, silky with margins even to bayed; in other isolates yellowish white (1–2A2), moderately thin to moderately thick, slightly raised, cottony around inoculum and cottony-downy throughout with even margins; by 6 wk mats typically light yellow (4A4) to golden (4B5), moderately thin to moderately thick, slightly raised, silky-cordonic usually out to margin, at times irregularly cordonic or with tufted appearance, cordons greyish orange (5B4) to brownish yellow (5C7), occasionally growing up sides of Petri dish and fanning out or forming tree-like aerial tufts; no agar discoloration at 2 and 6 wk; not fruiting at 6 wk. Oxidase reactions on GAA – or stain, mat 9–18 mm diam at 7 d, 10–30 mm diam at 14 d; on TAA stain or +++, no growth at 7 and 14 d.

Microscopic characters

Marginal hyphae 2–5 µm diam, thin-walled, nodose septate, seldom having only rare clamps, occasionally branching from clamps, moderately branched, rarely extensively branched. Submerged hyphae 2–7 µm diam, thin-walled, nodose septate, moderately to

frequently branched, occasionally lightly encrusted with large hyaline crystals. Aerial hyphae 2–5 µm diam, thin-walled, nodose septate, moderately branched, lightly to heavily encrusted with fine, yellow to yellowish brown resinous like granules that dissolve in 3% KOH and large hyaline crystals that do not dissolve (Fig. 3f), by 6 wk usually heavily encrusted with both types of encrusting materials and developing numerous encrusted hyphal tips (Fig. 3g).

Cultures studied. – HHB 2004, HHB 3987, HHB 11351, HHB 11540, HHB 11668, HHB 11669, FP 101981, FP 102144, FP 102179, FP 102188.

Species code: (1).2.3c.12.16.21.32.(36).37.38.(44).45–47.54.59.

Ceraceomyces americanus is strikingly similar to *P. filamentosa* and *P. radicata* in basidioma morphology. These three taxa occur sympatrically in eastern United States and Canada. Most specimens of *C. americanus* have been identified as *P. filamentosa* or occasionally *Trechispora (Phlebiella) vaga* (Fr.) Liberta; thus, this taxon has not been recognized as a distinct and undescribed species. *Ceraceomyces americanus* typically has an olive green tint with a white basal mycelial layer next to the substrate. Microscopically, the presence of nodose septate hyphae readily distinguishes *C. americanus* from phenotypically similar *Phanerochaete* species that have primarily simple septate hyphae.

Ceraceomyces americanus is also similar to *C. sulphurinus* (Karst.) Erikss. & Ryv. and *C. cystidiatus* (Erikss. & Hjortst. in Jül.) Hjortst. All three taxa have nodose septate hyphae, encrusted cystidia, and smooth, pellicular hymenia that turn red-violet in KOH. However, basidiomata of *C. sulphurinus* are yellow to mustard yellow and those of *C. cystidiatus* are violaceous, in contrast to the olive to brown basidiomata of *C. americanus*.

Hyphoderma fouquieriae Nakas. & Gilbn., described on ocotillo from the Sonoran Desert in Arizona, is also quite similar to the species of *Ceraceomyces* described above. Although not mentioned in the description (Nakasone & Gilbertson, 1978), the hymenium of *H. fouquieriae* also turns red-violet in KOH and has a pelliculose structure. Thus, the new combination *Ceraceomyces fouquieriae* (Nakas. & Gilbn.) Nakasone, Bergman, & Burdsall (basionym: *Hyphoderma fouquieriae* Nakas. & Gilbn., Mycologia 70: 272. 1978) is proposed.

Discussion

Phanerochaete filamentosa, *P. radicata*, and *Ceraceomyces americanus* have phenotypically similar basidiomata and were all

identified as *Peniophora filamentosa* in the past. Eastern United States is the only area where these three taxa occur sympatrically. *Ceraceomyces americanus* and *P. filamentosa* appear to be restricted to North America, but *P. radicata* has a circumglobal distribution. All are characterized by fragile fruitbodies with fimbriate or cordonic margins, hymenia that turn red to purple in KOH, and encrusted cystidia. *Ceraceomyces americanus*, however, has nodose septate hyphae and olive green to brown basidiomata, while the *Phanerochaete* species are simple septate with yellow to brown basidiomata. Differences in the cystidia and basidiospores can be used to distinguish *P. radicata* and *P. filamentosa*. The cystidia of *P. radicata* are typically thick-walled whereas those of *P. filamentosa* have thin walls and frequently are secondarily septate. Although the basidiospores are very similar in shape and size, those of *P. radicata* are slightly broader than those of *P. filamentosa*.

Cultures of these three taxa are also very similar. However, *C. americanus* can be distinguished from *P. radicata* and *P. filamentosa* microscopically by the abundance of clamps and encrusted hyphal tips and macroscopically by its dark-colored, silky-cordonic mats at 2 wk. *Phanerochaete radicata* and *P. filamentosa* have many characters in common and therefore are difficult to distinguish culturally. They are most reliably distinguished by dropping 3% KOH on 2-wk-old mats; *P. filamentosa* develops a pink reverse overnight while *P. radicata* does not. Furthermore, *P. radicata* has scattered clamps in the margin whereas clamps are rarely observed in *P. filamentosa*.

Interestingly, all three taxa develop similar types of encrusting materials. The yellow to brown, resinous-like granules are found on hyphae and cystidia in the basidiomata as well as cultures. Because these granules dissolve instantly in KOH, they should be observed in Melzer's reagent or water. These granules are also responsible for the red to purple color change observed when a drop of KOH is applied to the hymenial surface. On the other hand, hyaline crystals are not affected by KOH. These crystals aggregate into clusters and are larger and coarser than the colored granules. The crystals are also found on hyphae and cystidia in basidiomata and cultures. While cystidia of both *Phanerochaete* species may be encrusted with these crystals, those of *C. americanus* are exclusively encrusted with resinous-like granules.

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