**Fomitopsis mounceae and F. schrenkii—two new species from North America in the *F. pinicola* complex**


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**ABSTRACT**

Two new species, *Fomitopsis mounceae* and *F. schrenkii* (Polyporales, Basidiomycota) in the *F. pinicola* species complex in North America, are described and illustrated. Previous molecular phylogenetic analyses identified three well-delimited lineages that represent *F. mounceae* and *F. ochracea* from Canada, the Appalachian Mountains, and the northern United States and *F. schrenkii* from western and southwestern regions of the United States. *Fomitopsis pinicola* sensu stricto is restricted to Eurasia and does not occur in North America. Morphological descriptions of basidiocarps and cultures for *F. mounceae*, *F. schrenkii*, and *F. ochracea* are presented. The three species are readily differentiated by nuc rDNA internal transcribed spacer (ITS1-5.8S-ITS2 = ITS) sequence, geographic distribution, and basidiospore size. *Polyporus ponderosus* H. Schrenk is an earlier illegitimate synonym of *F. schrenkii*. Both *F. mounceae* and *F. schrenkii* have a heterothallic multiallelic incompatibility system.

**INTRODUCTION**

*Fomitopsis pinicola* (Sw.) P. Karst. sensu lato is a common brown-rot decay fungus found on many softwood and hardwood trees throughout North America and Eurasia. Broadly defined, it is morphologically variable with respect to color and form and has been described many times, with 17 recognized heterotypic names listed in MycoBank (http://www.mycobank.org) and Index Fungorum (http://www.indexfungorum.org). All synonymous names are based upon European specimens or observations except for *Fomes subungulatus* Murrill from the Philippines and *Polyporus ponderosus* H. Schrenk from South Dakota. Subsequently, North American authors considered *Fomes marginatus* (Pers.) Gillet, *Fomes ungulatus* (Schaeff.) Sacc., *Polyporus ponderosus*, and *Fomes pinicola* (Sw.) Fr. to be synonymous (Murrill 1908; Hedgcock 1914; Lloyd 1915; Overholts 1953). Although Murrill (1908) used *F. ungulatus* for the North American taxon, other authors adopted the name *F. pinicola*, which is the correct name based on nomenclature rules involving sanctioned names.

Mounce’s (1929) comprehensive study of *F. pinicola* in North America included a review of nomenclature, occurrence, and geographic distribution, and a host list of 91 plant species. She examined basidiocarps, studied cultures, and determined that *F. pinicola* is heterothallic with a bipolar or unifactorial incompatibility system. After intensive morphological study and many crosses between monosporous isolates from Canada, France, and Sweden, she concurred with Lloyd (1915), Murrill (1908), and others that *F. ungulatus* (sensu North American authors) and *F. marginatus* were conspecific with *F. pinicola* (Mounce 1929). In the following study, Mounce and Macrae (1938) paired monosporous isolates of 20 strains in various combinations and uncovered two intersterile populations of *F. pinicola* in North America, Groups A and B. They reported that monosporous cultures from Groups A and B were completely or incompletely compatible, respectively, with those from Group C, composed of strains from Europe and Japan. Later, Höpberg et al. (1999) showed that European populations of *F. pinicola* were all members of one intersterility group.

Of all synonyms of *F. pinicola*, only *P. ponderosus* was originally described from North America. In 1903, von Schrenk introduced the new species *P. ponderosus* (an illegitimate later homonym, non *P. ponderosus* Kalchbr. 1882) for the causal agent of red rot of western yellow pine and ponderosa pine in South Dakota. He
described the development of decay in the trunk and butt of dead pines and the subsequent formation of basidiocarps. He recognized that *P. ponderosus* was similar to *F. pinicola* (as *Polyporus pinicola* (Sw.) Fr.) but noted differences in the color, surface texture, and resinous covering of the basidiocarp pileus (von Schrenk 1903).

Ryvarden and Stokland (2008) described *Fomitopsis ochracea* from Alberta on *Populus tremuloides* that was distinguished from *F. pinicola* by substrate preference, basidiospore morphology, and match flame test to the lacquered pileus surface. Although DNA sequence differences between the two taxa were noted, no reference sequences were cited or deposited.

In a phylogenetic and population genetic study of the *F. pinicola* species complex in North America, Haight et al. (2016) confirmed that *F. ochracea* was a distinct taxon from *F. pinicola* and identified two undescribed taxa using a three-gene molecular phylogenetic approach. They resolved four well-supported clades representing *F. pinicola* sensu stricto from Europe and three lineages from North America, namely, North America A (NAA), North America B (NAB), and Southwest (SW). They concluded that NAB and Mounce and Macrae’s (1938) Group B were conspecific with *F. ochracea*. In addition, NAA and Group A from Mounce and Macrae (1938) represented a taxon that is sympatric with *F. ochracea* in the northern United States and Canada, and SW occurs primarily in western and southwestern United States.

Kancherla et al. (2017) published the genome of *F. pinicola* from a monokaryon isolate obtained from basidiocarps on spruce logs in Sweden. Their multigene phylogenetic tree of *Fomitopsis* confirmed the conclusions of Haight et al. (2016). Earlier, Floudas et al. (2012) sequenced the genome of *F. pinicola* sensu lato (FP-58527) from a monokaryon isolate from a basidiocarp on *Pinus ponderosa* from South Dakota, where *P. ponderosus* was described.

This study is the natural sequel to the phylogenetic study of Haight et al. (2016) of the *F. pinicola* species complex in North America. We describe and illustrate the new taxa *Fomitopsis mounceae* and *F. schrenkii*, representing NAA and SW, respectively, as well as *F. ochracea*. Cultural descriptions of the three species are included. *Fomitopsis pinicola* from Eurasia and the three species of the *F. pinicola* complex from North America are morphologically similar but can be distinguished by nuc rDNA internal transcribed spacer (ITS1-5.8S-ITS2 = ITS) sequence, geographic distribution, basidiospore size, and cultural characters. As an aid to identifying these taxa, a table of diagnostic characters is provided.

**MATERIALS AND METHODS**

**DNA sequencing, phylogenetic inference, and ITS polymorphisms.**—See Haight et al. (2016) for detailed polymerase chain reaction (PCR) protocols and sequencing methods. To confirm the placement of type specimens of the new taxa described herein, a multispecies coalescent tree was estimated using MrBayes 3.2.6 (Ronquist et al. 2011) provided on the CIPRES Web site (Miller et al. 2010). The NEXUS input file contained 68 sequences; each a three-gene, 1739–base pair, concatenated alignment consisting of the nuc rDNA ITS1-5.8S-ITS2 (ITS) region, translation elongation factor 1-α (TEF1), and RNA polymerase II subunit 2 (RPB2). Analysis model settings (Ronquist et al. 2011) included in a MrBayes data block were speciespartitions = species, unlink topology = (all), prset topolgypr = speciestree, prset brlenspr = clock: speciestree, prset rpbr = variable, prset popsizepsilon = lognormal (4.6,2.3), and using nst = 6, rates = gamma, and run for 50 000 000 generations.

The ITS region is often used to characterize species; therefore, ITS sequences of 68 samples were analyzed for polymorphisms, including 28 new sequences. Some of these new sequences were obtained from isolates originally used by Mounce and Macrae (1938) and are deposited in the Canadian Collection of Fungal Cultures (CCFCC = DAOMC), Ottawa, Canada. The ITS data set was analyzed in MEGA5 (Tamura et al. 2011) and MrBayes 3.2 (Ronquist and Huelsenbeck 2003). Sequence alignments and all other phylogenetic information generated in this study were deposited in TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S23648). The ITS sequence of *F. pinicola* AFTOL-ID 770 (AY854083) was used as the reference sequence for the alignment. GenBank numbers for all sequences used in this study are listed in SUPPLEMENTARY TABLE 1.

**Monosporous cultures and mating type studies.**—Monosporous cultures were obtained directly from fresh basidiocarps by vigorous agitation of small pieces of hymenial tissue in a microfuge tube with 1 mL sterile distilled water. Aliquots of 100 µL were streaked onto 1% malt extract agar (MEA) plates and incubated at 25 C for 2 d. After 1 and 2 d, germinating spores were visualized using a dissecting scope with backlighting and transferred to MEA plates with a 20-µL pipette tip. After several weeks’ growth, cultures were checked for the presence of clamp connections. The mating systems for *F. schrenkii*, JEH-141a and JEH-142, and *F. mounceae*, JEH-219 and JEH-225, were determined.
by pairing nine to 14 monosporous cultures in all combinations on MEA, incubated for 4 wk at 25 C, then examined for clamp connections. After the mating types were determined, two or three cultures of each mating type were paired in all combinations to determine whether there were multiple mating type alleles.

**Morphological studies.**—About 215 specimens were examined, mostly from the herbarium at the Center for Forest Mycology Research (CFMR), Madison, Wisconsin. Other specimens were borrowed from BPI, CUW, H, NY, TRTC, and UTC. Herbarium code designations are from Index Herbariorum (Thiers [continuously updated]). Basidiocarp dimensions are given as length/breadth (measured from side to side) × width/depth (front to back) × height/thickness (top to bottom) in millimeters. Capitalized color names are from Ridgway (1912), and color codes follow Kornerup and Wanscher (1978). For microscopic studies, thin freehand sections from basidiocarps were mounted in 2% (w/v) aqueous potassium hydroxide (KOH) and 1% (w/v) aqueous phloxine or Melzer’s reagent (Kirk et al. 2008) and examined with an Olympus BH2 compound microscope (Shinjuku, Tokyo, Japan). Drawings were made with a camera lucida attachment. Cyanophily of basidiocarp and hyphal walls was observed in 0.1% cotton blue in 60% (w/v) lactic acid (Kotlaba and Pouzar 1964; Singer 1986). Average (x̄) basidiospore measurements were calculated from 30 spores and when followed by numbers in parentheses, indicate the number of specimens measured. Q values were obtained by dividing average basidiospore length by width of at least 30 spores (Kirk et al. 2008). Basidiospores are critical for identification but often are rare or absent. Representative specimens in which basidiospores were measured are included in the section “Other specimens examined” and were used to construct the graph (SUPPLEMENTARY FIG. 1) and accompanying table (SUPPLEMENTARY TABLE 2) that compare basidiospore sizes. Additional specimens examined are included in SUPPLEMENTARY MATERIALS. A species distribution map (FIG. 2) was constructed from specimens listed in SUPPLEMENTARY TABLE 3.

Several types of hyphae were observed in specimens examined in this study. The hyphal system of *F. mounceae*, *F. schrenkii*, and *F. ochracea* is dimitic, although it may appear to be trimitic with generative, skeletal, and binding hyphae. We believe, however, that the binding hyphae are best described as sclerified generative hyphae, as noted by Donk (1964, p. 237). There are two lines of evidence that support this interpretation. First, clamp connections were observed several times on the “binding hyphae,” although the clamps never became thick-walled and eventually disintegrated. Second, the diameter of the thick-walled, sparsely to moderately branched “binding hyphae” is identical to those of the thin-walled generative hyphae. Corner’s illustration (fig. 1 in Corner 1953) of a trimitic polypore hyphal structure is similar to what we observed for the North American taxa studied herein except that sclerified generative hyphae should be substituted for the binding hyphae.

Cultures of *Fomitopsis* species were obtained from the culture collection at CFMR; see SUPPLEMENTARY TABLE 1 for specific strain information. Detailed methods for cultural studies are described in Nakasone (1990). Briefly, the culture media used were 1.5 % malt extract agar (MEA), 0.5% gallic acid agar (GAA), and 0.5% tannic acid agar (TAA). Reactions of cultures on GAA and TAA range from negative, no brown discoloration (−) or weakly staining, to positive, with a brown diffusion zone just under inoculum to forming a wide corona (+ to +++++); see Nakasone (1990) for a more detailed discussion. The species code was developed by Nobles (1965) and expanded by others as a shorthand identification system for cultures of wood-inhabiting basidiomycetes. See Nakasone (1990) for a discussion on development of the code and description of what each number represents.

**RESULTS**

**Coalescent species tree.**—The coalescent species tree from the Bayesian inference (w) analysis is shown in FIG. 1. In this tree, *F. ochracea*, *F. mounceae*, *F. schrenkii*, and *F. pinicola* sensu stricto are distinct clades, supported by high posterior probabilities, and are congruent with ITS, RPB2, and TEF1 gene trees and the coalescent species tree in Haight et al. (2016). The type specimens for *F. mounceae* (JEH-78) and *F. schrenkii* (JEH-150) each reside within their respective clades. The type specimen for *F. ochracea*, Stokland 223, was not included in the analysis because we were unable to obtain a sequence for the RPB2 gene, but the ITS sequence places it in the *F. ochracea* lineage (data not shown). Sequences from an authentic specimen of *F. ochracea* from Newfoundland, LR48800 (TRTC 167845), were included in the analysis, and this strain is placed in the *F. ochracea* clade.
Figure 1. Bayesian coalescent, concatenated, three-gene species tree showing phylogenetic relationships among species in *Fomitopsis pinicola* sensu lato. The tree is midpoint rooted and branch support values (PP ≥ 0.95) are shown on individual branches. Type specimens are noted in bold type.
Figure 2. Distribution of *Fomitopsis* species in North America. Star indicates location of type specimens. Icons are stacked when locations are similar.
**ITS polymorphisms.**—The ITS alignment begins at position 71 of the AFTOL-ID 770 (MB-03-036, *F. mounceae*) reference sequence. The alignment consists of 563 nucleotides, including 14 variable characters, 12 of which are parsimony informative. At position 446 of the reference sequence, the nucleotide segment GTTTACTTTT begins, which is unique to *F. mounceae*, and at position 450 changes from A to G for *F. schrenkii* GTTTGTCTTTT. At this site, most strains of *F. pinicola* sensu stricto have the sequence ATTTGCTTTT, whereas in *F. ochracea* it is GTTTACTTTT. In six cases, however, the *F. pinicola* sequences were identical to those of *F. ochracea*. In these rare instances, *F. pinicola* (as well as *F. mounceae* and *F. schrenkii*) has the sequence GGTAACCTTGT at positions 489–498 and is readily differentiated from the unique motif GGTACCTTTG of *F. ochracea*. TABLE 1 summarizes these species-specific sequence segments.

**Mating type studies.**—Two mating types of *F. schrenkii* were found for JEH-141a (A1 = 1,2,4,5,7,9,11; A2 = 3,8,12) and JEH-142 (A3 = 1,3,4,7; A4 = 2,5,6,12,14); see SUPPLEMENTARY FIG. 2 for the mating type grids. When two monosporous cultures of each mating type from JEH-141a were paired in all combinations with three monosporous cultures of each mating type from JEH-142, all but one of the 24 pairings produced clamp connections, indicating that there are multiple alleles of each mating type gene. Thus, *F. schrenkii* is heterothallic with a multiallelic bipolar mating system or unifactorial incompatibility system. *Fomitopsis mounceae* is also bipolar, for two mating types were recovered from two samples: JEH-219 (A1 = 1,3,4,5,7,8,11,13; A2 = 2,9,10,12,14) and JEH-225 (A3 = 1,2,4,5,6,12; A4 = 3,7,8,9,10,11,14) (SUPPLEMENTARY FIG. 2). Two mating types from each of the two samples were paired in all combinations. Clamp connections were produced in all 16 pairings; thus, multiple mating type alleles are present in this species also.

**TAXONOMY**


Etymology: *mounceae* (Latin), named for Irene Mounce (1894–1987), a pioneering Canadian mycologist, for her contributions to mycology and *Fomitopsis* (fide Giinns 1988).

Diagnosis: Similar to *F. schrenkii* except with slightly narrower basidiospores, average size 5.8–6.6(–7.1) × (3.1–)3.4–4.1 μm, Q = 1.6–1.9, occurring on hardwood as well as coniferous hosts and distributed primarily across Canada, northern and eastern United States, including the Appalachian Mountains.

Basidiocarps perennial, woody, sessile, sometimes umbonate, occasionally imbricate, typically planate, 25–160(–170) mm across × 22–80(–150) mm deep × 25–90 mm thick, rarely triquetrous, (42–)80–160 × (22–)50–90 × (20–)35–95 mm, rarely ungulate. Pileus

| Table 1. Diagnostic characters that differentiate North American *Fomitopsis mounceae*, *F. ochracea*, and *F. schrenkii* and Eurasian *F. pinicola* s. str. |
|-----------------|-----------------|-----------------|-----------------|-----------------|
| Character       | *F. mounceae*   | *F. ochracea*   | *F. schrenkii*  | *F. pinicola* s. str. |
| Substrate/host  | Hardwoods and conifers | Hardwoods and conifers | Conifers, rarely hardwoods southwestern and western USA | Hardwoods and conifers, Eurasia |
| Distribution    | Canada, northern USA, Appalachian Mountains | Canada, northern USA, Appalachian Mountains | Sometimes present | Usually present |
| Pileus with reddish brown band | Usually present | None | Sometimes present | Rare |
| Pores per mm    | 3–5(–6)         | 3–5(–6)         | 3–5(–6)         | 3–5(–6)         |
| Receding pore surface | 5.8–6.6(–7.1)   | 5.1–5.9         | 5.7–6.7         | Data not available |
| Average basidiospore size (μm) | (3.1–)3.4–4.1 | (1.6–)1.7–1.9 | (3.4–)3.7–4.2 | 1.5–1.6–2.2 |
| Q values         | 1.7–1.9         | 1.7–1.9         | 1.7–1.9         | 1.8–2.2         |
| ITS sequence at position ~446–456 | GTTTACCTTTG | GTTTACCTTTG | GTTTACCTTTG | GTTTACCTTTG |
| Mycelial growth at 30 C at 3 wk (mm) | 17–62 | 0–4 | 13–53 | 13–69 |
| Cottony balls of mycelia at 6 wk | None | None | Sometimes | None |
| Irregularly thick-walled hyphae in aerial or surface mat at 6 wk | None | None | None | None |
glabrous, often with a sticky resinous coating, smooth to uneven, sulcate, colors varied but usually with a distinct, shiny, red or reddish brown, laccate band near margin. In young specimens, pileus smooth to uneven, at base black then brownish orange (7C7), reddish brown (8D–E8), Kaiser Brown, or Hay’s Brown, margin rounded, smooth,

Figure 3. Basidiocarps of *Fomitopsis* species. A–B. Top and side view of *F. mounceae* (JEH-78, holotype). C–D. Top view (DLL-2010-138) and bottom view showing receding hymenia (JEH-34) of *F. ochracea*. E–F. Top and side view of *F. schrenkii* (JEH-150, holotype). All bars = 2 cm.
pale orange (5A3) or grayish orange (5B6). In older specimens, pileus uneven often with rounded warts or bumps, at base and upper pileus black to brownish orange (5C3), grayish brown (5D3), yellowish brown [5(D–E)4], grayish brown [6(D–E)3, 7(E–F)3, 8F(3–4)], brown (6ES), or greenish gray (30C2), then at mid-pileus grayish brown (5E3), brownish orange [6C5, 7C(5–6)], reddish brown [8E7, 9(E–F)8, 9F6], Wood Brown, Buffy Brown, or Russet, sometimes with a narrow, reddish brown [8(D–E)8] band above the margin; margin a rounded, smooth, narrow to wide band of yellowish white (4A2), orange white (5A2), pale orange (5A3), orange white (6A2), or grayish orange [6B(3–4)]. Pore surface not receding or contracting, yellowish white [4A(2–3)], pale yellow (4A3), grayish yellow (4B3), orange white (5A2), pale orange (5A3), grayish orange [5B3(4)], or Light Ochraceous Buff, dried specimens bright reddish brown, red with 2% KOH at first then fading to a dull light brown or grayish brown. Pores circular, 3–5(–6) mm, 85–180 (–215) µm diam, eventually becoming filled with sclerified generative hyphae and fragments of thin-walled generative hyphae; dissepiments entire, composed of thin-walled skeletal hyphae; pore trama (45–)80–215 µm thick, composed primarily of thick-walled skeletal hyphae vertically arranged and intertwining sclerified generative hyphae, often with fragments of thin-walled generative hyphae and clusters of coarse hyaline crystals, in dried specimens reddish brown in 2% KOH at first then fading to light brown. Tube layers distinctly stratified, concordous with pore surface at first, older layers indistinct, becoming light brown (6D5), dried specimens brown in 2% KOH at first then fading to light brown. Context woolly, dense, azonate, brown (6D5), composed primarily of brownish yellow, thick-walled skeletal and dark yellow sclerified generative hyphae with remnants of thin-walled generative hyphae.

Hyphal system dimitic with clamped generative and skeletal hyphae. Generative hyphae 1.5–3.5(–4.5) µm diam, clamped, sparingly branched usually opposite clamp, walls hyaline, thin, smooth; behind leading edge, much branched hyphae with narrow, tapered branches developed from main hyphae. Submerged hyphae 1–6 µm diam, clamped, moderately branched, occasionally with ampullate clamps or ampullate adjacent to septa, walls hyaline, thin, smooth. Surface and aerial hyphae (i) similar to submerged hyphae except often evenly encrusted with a thin to moderately thick layer of hyaline crystals at 3 and 6 wk, also developing occasional, irregularly inflated segments up to 18 µm diam at 6 wk; (ii) 1–1.5 µm diam, clamped, sparingly to moderately branched at right angles, by 6 wk sometimes developing numerous short, lateral branches with walls hyaline, thin, sparsely encrusted with tiny, hyaline crystals, becoming more conspicuous and dominant with age; (iii) fiber/skeletal hyphae 1–2.5 µm diam, with a basal clamp connection, aseptate, sparingly to moderately branched at right angles, walls hyaline, slightly thickened to 0.5 µm thick but thinning toward apex, smooth, nonstaining, absent to numerous at 3 and 6 wk. Chlamydospores none; hyphal swellings described above may be interpreted as chlamydospores.

Incompatibility system: Heterothallic with a multiallelic, bipolar mating system; SUPPLEMENTARY FIG. 2A and B and Mounce 1929, tables IX–X, as F. pinicola.

Species code: 1(2).3c.8(9).26).31d.(32).34).36.38.43.44.45.54.55.59.
Type of rot: Brown cubical rot of dead hardwoods, especially aspen (Populus tremuloides), and conifers.

Distribution: Canada, northern United States including Alaska down the western cordillera to northern California, and down the Appalachian Mountains to Tennessee, also in Puerto Rico (FIG. 2).


Descriptions and illustrations: Gilbertson and Ryvarden (1986, p. 280, fig. 133 only); Mounce (1929, cultures plate III, figs. 6, 9; plate IV, figs. 5, 6; plate VIII, fig. 7); Voitk (2013, as F. pinicola).

Remarks: Fomitopsis mounceae is characterized by a variable basidiocarp form usually with a distinct red or reddish brown laccate band near the margin, dimitic hyphal system with clamped generative hyphae, and ellipsoid to cylindrical basidiospores. The pileus often has a shiny, resinous, or tacky surface and a reddish brown band. It is found on mainly on aspen and conifers across Canada and northern and eastern parts of the United States and is sympatric with F. schrenkii in Utah. It is most similar to F. schrenkii with respect to macro- and micromorphology. The two species can be readily distinguished by a combination of characters such as distribution (FIG. 2) (except where they occur sympatrically in Utah), basidiospore size (SUPPLEMENTARY TABLE 1, SUPPLEMENTARY FIG. 1), and in culture by the presence or absence of chlamydospores and irregularly thick-walled hyphae; see TABLE 1. In Utah F. mounceae occurs at lower elevations (~6000 ft) compared with F. schrenkii (~8000 ft). DNA polymorphisms at specific sites in the ITS region can be used to distinguish the two species (TABLE 1).

The illustration of F. pinicola in Gilbertson and Ryvarden (1986, p. 280, fig. 133) is that of F. mounceae, but the basidiospore measurement given is more similar to F. pinicola sensu stricto. The large cystidia described and illustrated (fig. 133d) were not observed in any specimen studied and appear to be young, developing skeletal hyphae observed in dissepiments. Voitk (2013, p. 17, as F. pinicola) noted that the “red laccate band ... melts” when in contact with a flame from a lighter or match.

It is possible to refer some strains used by Mounce (1929) and Mounce and Macrae (1938) to F. mounceae. Haigt et al. (2016) noted that ITS and RPB2 sequences from isolate 1264 in Group A (Mounce and Macrae 1938) placed it in the F. mounceae clade. The single-spore mating study by Mounce and Macrae (1938) directly links some of the published photographs in Mounce (1929) to Group A, and Group A (Mounce and Macrae 1938, table II, [forestry] “925”) itself is directly linked to F. mounceae by ITS sequence of DAOMC F69255 (formerly DAOM F6925 [culture]), including the characteristic nucleotide polymorphisms.

It is noteworthy from a forest pathology perspective that F. mounceae was isolated from Douglas fir bark beetles (Dendroctonus pseudotsugae) from Washington State (strain 32TT; DAOMC 250086 and 250087) by Castello et al. (1976). In Europe, bark beetles were implicated in the vectoring and associated decay by F. pinicola of Picea (Persson et al. 2011; Jacobsen et al. 2017; Vogel et al. 2017).


Basidiocarps perennial, woody, usually sessile, occasionally imbricate, usually planate, 40–230 × 25–130 (~300) × 25–130 mm, sometimes ungulate, 65–100 ×
40–65 × 45–110 mm, rarely triquetrous, 35–60 × 25–30 × 30–45 mm. Pileus glabrous, smooth to uneven, coarsely undulate or somewhat radially plicate, sulcate, sometimes rimose, colors varied. In young specimens, pileus with more or less with evenly pigmented bands—at base orange white (5A2) or grayish orange (5B3), then darkening to pale orange (5A3), grayish orange (5B4), or brown (7E6), then lightening to orange white (5A2), finally pale orange (5A3) at margin. Older specimens in even or mottled shades of black, brown and beige—base and upper pileus black, grayish orange (5B3), light brown (6D4), grayish brown (6E3), brown (6E7), brownish gray (7F2), or grayish brown (7F3), then at mid-pileus often orange (5A3), grayish orange (5B3), grayish brown (5D3, 8F3), brownish gray (6C2), light brown (6D4), brown [6F7, 7(E–F)(5–6)], reddish brown (8E8), or nearly black, sometimes with scattered black spots or irregular brown (6E6) lines, finally at margin rounded, smooth, dull yellowish white (4A2), pale yellow (4A3), orange white (5A2), pale orange (5A3), light orange (5A4), grayish orange [5B(3–4)], or brownish orange (6C3), rarely brown (6D8) or brownish orange (7C5). Pore surface sometimes receding, yellowish white [4A(2–3)], pale yellow (4A3), orange white (5A2), pale orange (5A3), grayish orange [5B(3–4)], or Light Ochraceous Buff, dried specimens reddish brown in 2% KOH at first then fading to light brown. Pores circular, (3–)4–5–(6) per mm, 85–130(–160) µm diam, concolorous with pore surface, becoming filled with a dense tangle of sclerified generative hyphae; disseipements entire, consisting of thin-walled skeletal hyphae; pore trama 85–165 µm thick, dominated by skeletal and sclerified generative hyphae, in dried specimens reddish brown in 2% KOH at first then fading to light brown. Tube layers distinctly stratified, concolorous with pore surface, older layers becoming indistinct, darker, light orange (5A4), grayish orange [5B(4–5)] or between Chamois and Honey Yellow, dried specimens reddish brown in 2% KOH at first then fading to light brown. Context woody, azonate, dominated by thick-walled skeletal hyphae also with sclerified and fragments of thin-walled generative hyphae, concolorous with tube layers, in dried specimens reddish brown in 2% KOH at first then fading to light brown.

Hyphal system dimitic with clamped generative and skeletal hyphae. Generative hyphae 2–4.5(–5.5) µm diam, clamped, sparingly to moderately branched, walls hyaline, thin to slightly thickened, smooth, observed in context, pore trama, and hymenium; often becoming sclerified with walls hyaline, up to 2 µm thick, irregular or strangled, dominant in mycelial stuffed pores, numerous in context and pore trama. Skeletal hyphae (4.5–)5–9(–10) µm diam, aseptate, rarely branched, even, straight, lumen may contain resinous-like aggregations, walls hyaline and slightly thickened at first then dark yellow to brownish yellow, up to 3.5 µm thick, wall thickness sometimes variable along hyphal length, smooth, dominant in context, disseipements, and pore trama. Hymenium up to 25 µm thick, a single layer of cystidia and basidia. Cystidia scarce to numerous, subfusiform with subacute, acuminate, or rounded apex, rarely obclavate to cylindrical with obtuse or slightly capitate apex, (14–)20–4(–60) × (3–)4–6.5 µm, clamped at base, protruding up to 40 µm, walls hyaline, thin, smooth. Basidia clavate, subclavate, or short cylindrical, (10–)15–25 × (5.5–)7–9 µm, clamped at base, 4-sterigmate, walls hyaline, thin, smooth. Basidiospores broadly ellipsoid, (4–)4.5–6.5(–7) × (3–)3.5–4.5(–5) µm, x (7) = 5.1–5.9 × 3.6–4(–4.4) µm, Q (7) = 1.3–1.4(–1.5), walls hyaline, thin to slightly thickened, smooth, acyanophilous, not reacting in Melzer’s reagent.

Cultural description: Mats similar to F. mounceae except odor absent or faintly sweet at 3 and 6 wk. Growth on MEA 10–20 mm radius at 1 wk, 20–45 mm radius at 2 wk; GAA negative, rarely ++++, 11–32 mm diam at 1 wk, negative, rarely +++, 31–65 mm diam at 2 wk; TAA negative or light brown stain under inoculum, <10–26 mm diam at 1 wk, negative or weakly staining, 12–52 mm diam at 2 wk.

Microscopic characters as in F. mounceae except as noted. Surface and aerial hyphae (i) as described above for F. mounceae except with occasional to numerous ampullate segments that sometimes develop into irregularly globose swellings, up to 18 µm diam, walls hyaline, slightly thick, smooth at 4 and 6 wk, also some hyphal segments developing irregularly thickened walls at 3 and 6 wk; (ii) as described above for F. mounceae except sparingly to moderately branched at right angles, walls thin to slightly thick, absent to numerous at 4 and 6 wk; (iii) fiber/skeletal hyphae 1.5–2.2(–3.5) µm diam, with a basal clamp connection, aseptate, rarely to moderately branched at right angles, some branches short, walls hyaline, slightly thick to 0.5 µm thick, smooth, nonstaining, absent to numerous at 3 and 6 wk. Chlamydospores globose to lemon-shaped, 6–13 × 4–8 µm, intercalary, walls hyaline, thin, smooth, staining or not in phloxine, absent to numerous in aerial mats at 3 and 6 wk.

Incompatibility system: Presumed heterothallic with a multiallelic bipolar mating system (see Mounce and Macrae 1938, table I).

Species code: 1.3.8.(31d),(32).34.36.38.43.44.45.54.55.59.
Type of rot: Brown cubical rot of dead hardwoods, especially Populus tremuloides, also P. balsamifera, Betula occidentalis, and conifers such as Abies balsamea, A. lasiocarpa, Picea mariana, and Tsuga, occasionally on living Picea sitchensis.

Distribution: Canada (British Columbia, Alberta, Manitoba, Nova Scotia, and Newfoundland Island) and northern United States (Washington, Oregon, Idaho, Wyoming, Utah, Minnesota, Wisconsin, Michigan, New York, New Hampshire, Maine) including the Appalachian Mountains down to Georgia (FIG. 1).


Description and illustration: Ryvarden and Stokland (2008, as F. populicola in fig. 1); Voitk (2013).

Remarks: Fomitopsis ochracea is characterized by a black-, brown-, and gray-colored pileate basidiocarp, dimitic hyphal system with clamped generative hyphae, and broadly ellipsoid basidiospores. It occurs sympatrically with F. mounceae across northern North America and the Appalachian Mountains on conifers and hardwoods. The two species can be distinguished readily by differences in basidiospore shape and size (TABLE 1, SUPPLEMENTARY TABLE 2, SUPPLEMENTARY FIG. 1). There are also some basidiocarp differences, but these are not consistent; for example, a receding pore surface (FIG. 3D) was observed sometimes in F. ochracea but never in F. mounceae. Ryvarden and Stokland (2008) report that F. ochracea has a trimitic hyphal system likely because they interpreted the sclerified generative hypha as binding hyphae.

The type specimen of F. ochracea, Stokland 223, was not included in the coalescent species analysis (FIG. 1) because the RPB2 sequence was unavailable, but it was confirmed by ITS sequence to be in the F. ochracea lineage (data not shown). Instead, an authentic specimen of F. ochracea, LR48800 from Newfoundland and identified by L. Ryvarden, is included in FIG. 1 to represent the taxon.

Cultures of F. ochracea sometimes develop irregularly thick-walled hyphal segments in the aerial and surface mats that were never observed in the other Fomitopsis species studied. In addition cultures of F. ochracea generally grew significantly slower or not at all at 30°C compared with most isolates of F. mounceae and F. schrenkii (TABLE 1, SUPPLEMENTARY FIGS. 3 and 4).

Fomitopsis ochracea was first detected as a biological entity by Mounce (1929) when she attempted matings between DAOMC 5778 and DAOMC 562C and discovered complete intersterility. Later, Mounce and Macrae (1938) showed that DAOMC 5778 was in Group A (= F. mounceae) whereas DAOMC 562C was a member of Group B (= F. ochracea). Group B itself is directly linked to F. ochracea by ITS sequence polymorphism of DAOMC F3249.

In the legend for their fig. 1, Ryvarden and Stokland (2008) used the name "Fomitopsis populicola," which may have been a preliminary name for F. ochracea. "Fomitopsis populicola" is an invalid name (nom. nud., International Code of Nomenclature for algae, fungi, and plants Art. 38.1; Turland et al. 2018) but was used in Europe in species lists of old growth taiga fungi (e.g., Romão 1996). The name "F. populicola" is considered to be a typographic error and is not in contradiction of Art. 36.3 (Turland et al. 2018). If it were interpreted as an alternative name, then both F. populicola and F. ochracea would be invalid (K. Bensch, P. Kirk, T. May, S. Pennycook, pers. comm. to S.A.R., March 2018).

Fomitopsis schrenkii J.-E. Haight & Nakasone, sp. nov. FIGS. 3E–F, 4K–O, 7

MycoBank MB826718


Typification: USA. SOUTH DAKOTA: Custer County, Black Hills, Custer, on Pinus ponderosa, Jul 2014, J.-E. Haight JEH-150 (holotype CFMR). Ex-type culture at CFMR. GenBank: ITS = KU169365; TEF1 = MK236356; RPB2 = MK208858.

Diagnosis: Similar to F. mounceae except with slightly broader basidiospores, average size 5.1–7(–7.5) × 3.3–4.3(–4.7) μm, Q = 1.5–1.6(–1.7), occurring primarily on coniferous hosts, occasionally on hardwoods, and distributed in the southwestern United States, Colorado, Utah, and South Dakota.
**Etymology: schrenkii** (Latin), named for Hermann von Schrenk (1893–1953), a pioneer in forest pathology (fide Peterson et al. 2000).

Basidiocarp perennial, woody, usually sessile, rarely imbricate, usually applanate, 40–180(–275) × 30–100 (–180) × 20–70(–110) mm, occasionally subungulate to ungulate, 35–55 × 45–80 × 35–55 mm, rarely triquetrous, 75 × 45 × 40 mm or effused-reflexed, 210 × 70 × 120 mm. Pileus glabrous, often with a shiny, black, resinous surface, smooth at first then uneven with irregular knobs and bumps, occasionally pitted, sulcate, sometimes rimose, colors varied. In young specimens, pileus with more or less evenly pigmented bands—at base orange white (5A2) or grayish orange (5B3), then darkening to pale orange (5A3), grayish orange (5B4), or brown (7E6), then orange white (5A2) near margins, finally at margin pale orange (5A3). Older specimens in even or mottled shades of black, brown or olive brown (4E4)—at base and upper pileus black, often with a thin, pale yellow (4A3), grayish yellow (4B3), or grayish orange (5B3), crustaceous film or layer, then mottled, dull brownish orange (6C3), reddish brown [8 (E–F)(6–8)], or grayish green [28(D–E)4], at mid-pileus often olive brown [4(D–E)4], brownish orange [5C (5–6)], light brown (5D5, 7D6), brownish orange (6C6), brown [6D8, 7D(7–8), 7E8], reddish brown [8D(5–6)], sometimes shiny reddish brown [9E(6–8)], finally margins rounded to subacute, smooth, with a thin or broad band of yellowish white (4A2), pale yellow (4A3), yellowish gray (4B2), grayish yellow [4(B–C)(3–5)], or grayish orange (5B5, 6B6), occasionally Ochraceous Buff, or brownish orange (6C6, 7C8). Pore surface rarely receding, yellowish white (4A2), pale yellow (4A3), grayish yellow (4B3), orange white (5A2), pale orange (5A3), grayish orange [5B(3–4)], occasionally light brown (5D5) or Cream Buff, dried specimens reddish brown in 2% KOH at first then fading to light brown. Pores circular, 3–4 per mm,

**Figure 5.** Microscopic elements from *Fomitopsis mounceae* (JEH-78, holotype). A. Dark brownish yellow skeletal hyphae from context. B. Dark yellow sclerified generative hyphae from context. C. Young skeletal hyphae from dissepiment. D. Hyaline sclerified generative hyphae from mycelial stuffed pores. E. Hymenial cystidia. F. Basidia. G. Basidiospores. A-D, upper scale bar; E-G, lower scale bar. Figure 6 add: A-B, upper scale bar; C-G, lower scale bar. Figure 7 add: A-B, upper scale bar; C-H, lower scale bar.
(150–)170–215 µm diam, eventually becoming filled primarily with sclerified and thin-walled generative hyphae with skeletal hyphae less abundant; dissepi- ments entire, composed of thin-walled skeletal hyphae; pore trama 70–240 µm thick, composed of vertically arranged, thick-walled skeletal hyphae intertwined with sclerified and thin-walled generative hyphae, in dried specimens reddish brown in 2% KOH at first then fading to light brown. Context woody to firm felty, azonate, composed of sclerified and thin-walled generative and skeletal hyphae, pale yellow (4A3), light yellow (4A4), grayish yellow [(4–5)B4], Warm Buff, in dried specimens reddish brown in 2% KOH at first then fading to light brown.

Hyphal system dimitic with clamped generative and skeletal hyphae. Generative hyphae 2–6(–9) µm diam, clamped, sparingly to moderately branched, walls hyaline, thin, smooth, observed in context, pore trama, and hymenium, becoming sclerified, often irregular or strangulated with walls up to 3

µm thick, dominant in stuffed pores, abundant in context and pore trama. Skeletal hyphae regular, even, 6–9(–12) µm diam, rarely inflated up to 20 µm diam, aseptate but often with adventitious septa, unbranched, walls at first hyaline, 0.5–1.5 µm thick, smooth, then light yellow to light brown, up to 4.5 µm thick, smooth or encrusted with resinous-like particles, dominant in context and pore trama, scattered in stuffed pores. Hymenium up to 30 µm thick, a single layer of cystidia and basidia. Cystidia scarce to numerous, cylindrical, subulate, or subfusiform with subacute or acuminate apex or clavate, rarely with an apical knob, 16–30(–48) × 3–8 µm, clamped at base, protruding up to 25 µm, walls hyaline, thin, smooth. Basidia clavate, subclavate, or short cylindrical, 12–22 × 6–8 µm, clamped at base, 4-sterigmate, walls hyaline, thin, smooth. Basidiospores ellipsoid to broadly cylindrical, 5.7–6.7 × 3.7–4.2(--4.3) µm, Q (11) = 1.5–1.7, walls hyaline, thin to slightly thickened, smooth, acyanophilous, not reacting in Melzer’s reagent.

Cultural description: Mats as for *F. mounceae* except often becoming moderately thick, developing white felty areas around inoculum and raised, woolly balls toward margins.

Growth on MEA 15–30 mm radius at 1 wk, 30–70 mm radius at 2 wk; GAA negative, <10–33 mm diam at 1 wk, negative, 40–88 mm diam at 2 wk; TAA
negative, 11–21 mm diam at 1 wk, negative, 21–45 mm diam at 2 wk.

Microscopic characters as described for *F. mounceae* except as noted. Surface and aerial hyphae (i) pronounced inflated hyphae absent at 4 and 6 wk; (ii) as in *F. mounceae*. Chlamydomospores globose to lemon-shaped, 8–12.5 × 5.5–8 μm, intercalary or terminal, walls hyaline, thin to slightly thickened, smooth, staining or not in phloxine, absent to numerous in aerial mat at 3 and 6 wk.

*Incompatibility system:* Heterothallic with a multiallelic, bipolar mating system; SUPPLEMENTARY FIG. 2C and D.

*Species code:* 1.3.8,(31d),(32).34.36.38.43.44.45.54.55.59.

*Type of rot:* Brown cubical rot of dead conifers, occasionally on hardwoods.

*Distribution:* Southern California, Arizona, New Mexico, Colorado, Utah, South Dakota (FIG. 2).


Description and illustration: von Schrenk (1903, p. 27–30, plate XIII).

Remarks: *Fomitopsis schrenkii* is characterized by a variable basidiocarp form, dimitic hyphal system with clamped generative hyphae, and ellipsoid to broadly cylindrical basidiospores. It occurs frequently on conifers in the southwestern United States, Utah, Colorado, and South Dakota and is sympatric with *F. mounceae* in Utah. It is most similar to *F. mounceae* with respect to macro- and micromorphology; see discussion under *F. mounceae* above. *Fomitopsis schrenkii* is primarily associated with conifers, rarely on hardwoods, whereas *F. mounceae* does not have a substrate preference. Slight differences in basidiospore shape and size between the two taxa and ITS sequence were observed (TABLE 1, SUPPLEMENTARY TABLE 2, SUPPLEMENTARY FIG. 1).

Culturally, *F. schrenkii* differs from the other *Fomitopsis* species studied herein, for its aerial mats often are denser, producing raised woolly balls toward the margins, and hyphal swellings are absent. The growth rates of *F. schrenkii* and *F. mounceae* are nearly identical (SUPPLEMENTARY FIGS. 3 and 4).

Floudas et al. (2012) based the whole genome sequence of *F. piniola* on monosporous isolate FP-58527 ss1, which is correctly named *F. schrenkii*. The ITS sequence, basidiocarp features, basidiospore size, host, and distribution of FP-58527 are all consistent with *F. schrenkii*. In addition, the monosporous culture of FP-58527 produced clamp connections when paired with *F. schrenkii* JEH-131 ss1 and ss2 and JEH-142 ss4 and ss6, indicating conspecificity (data not shown).

The holotype of *P. ponderosus* is in poor condition and sterile. The overall morphology of the specimen appears to be that of a young basidiocarp of *F. schrenkii*.

**DISCUSSION**

This study is the beneficiary and logical culmination of many years of research that began over 100 years ago with von Schrenk’s 1903 report on red rot of ponderosa pine in South Dakota caused by *Polyergus ponderosus*. Later, Mounce (1929) and Mounce and Macrae (1938) identified several intersterile groups of *Fomitopsis piniola* in North America that were mostly interfertile with the Eurasian taxon after the pairing of many monosporous cultures. In the latter study, Group A is recognized as *F. mounceae* described herein and Group B is *F. ochracea* that was described in 2008 by Ryvarden and Stokland. By employing molecular phylogenetic methods, Haight et al. (2016) validated the findings of Mounce (1929) and Mounce and Macrae (1938) and showed that *F. mounceae* (as NAA) and *F. schrenkii* (as
SW) are sister species that are closely related to *F. pinicola* sensu stricto and distinct from *F. ochracea* (as NAB). The Bayesian coalescent species analysis and resultant species tree (FIG. 1) show that a coalescent analysis can be an effective approach to delimit species when individual gene trees are incongruent, as in the case with species complexes. We show that the type specimens for *F. mounceae* and *F. schrenkii* as well as an authentic specimen of *F. ochracea*, LR48800, are embedded within their respective clades.

In this study, we formally describe the new species *F. mounceae* and *F. schrenkii*, two closely related species in the *F. pinicola* complex in North America. *Fomitopsis ochracea* is a similar species that occurs sympatrically with *F. mounceae* over much of its distribution, but the two species are reproductively isolated. These three North American taxa and *F. pinicola* sensu stricto from Eurasia have similar basidiocarp and cultural morphologies but can be differentiated by using a combination of characters that include distribution, substrate, basidiomycete size and shape, pileal and cultural features, and ITS sequence. These are summarized in TABLE 1. Successful identification of these species is challenging, for many of the characters overlap or are difficult to obtain. For example, it is often difficult to measure 30 spores in a sample to get a size range and Q value. Gathering information on as many characters as possible will increase the probability of arriving at a correct identification.

Temperature growth studies were undertaken, and methods and results are presented in SUPPLEMENTARY MATERIALS and SUPPLEMENTARY FIG. 3 and 4. Unfortunately, these studies were not useful in differentiating the species discussed herein except in one instance—growth at 30°C. None of the *F. ochracea* strains tested grew at 30°C, whereas most strains of *F. mounceae* and *F. schrenkii* grew significantly, except for one strain of each species tested.

Compatible matings between monokaryons and dikaryon-monokaryon (di-mom) strains can also be used to identify these closely related species. However, we obtained unexpectedly disappointing results with di-mom matings with *F. schrenkii* cultures. We undertook di-mom pairings with two to six monosporous cultures and about 30 dikaryotic cultures of *F. schrenkii* and obtained just 67% compatible pairings with monosporous strains of JEH-141a and 51% with JEH-142 (data not shown). Although a positive compatible result from di-mom pairings can be used to confirm conspecificity to *Fomitopsis* species described herein, a negative result is not informative. It is beyond the scope of this study to speculate on the reasons that there was such high failure rate of di-mom pairings, for this is a complex process that involves genes involved in somatic incompatibility, nuclear selection, nuclear migration, and clamp formation (Worrall 1997; Anderson and Kohn 2007).

Most of the North American literature has used a broad species concept of *F. pinicola*. The concepts of Gilbertson and Ryvarden (1986) and Nobles (1948) for *F. pinicola* is an amalgam of all three species as well as *F. pinicola* sensu stricto. Recently, Zhou et al. (2016) listed 11 species of *Fomitopsis*, including *F. pinicola*, in their checklist of polypores from North America. This list should be updated to 12 *Fomitopsis* species with the addition of *F. mounceae* and *F. schrenkii* and the removal of *F. pinicola*.

The geographic distribution of *F. mounceae*, *F. ochracea*, and *F. schrenkii* is probably wider than described above or shown in FIG. 2. It appears that the three taxa are sympatric in Utah, and the range of *F. ochracea* (isolate 6612 in Group B; Mounce and Macrae 1938) may extend into Arizona where *F. schrenkii* is prevalent. Targeted collecting at different elevations and various substrates in Utah, Colorado, Arizona, and Nevada may expand the range of these species.

*Fomitopsis mounceae*, *F. ochracea*, and *F. schrenkii* are important brown-rot fungi in North America. They are major decomposers of coarse woody debris in western forests and are responsible for sequestering large amounts of carbon as modified organic matter that may persist for hundreds of years and contribute 26% of the humus layer in northern forests (McFee and Stone 1966; Gilbertson 1980). Although most of the literature relating to *F. pinicola* in North America does not differentiate these three taxa, their importance to forest health and ecosystem processes is unchanged, since there appears to be little or no difference among the three species in pathogenicity, decay mechanisms, habitat specialization, and host preferences (Haight et al. 2016). Hepting (1971) reported that *F. pinicola* sensu lato caused heart rot in living conifers, black cherry, and occasionally on aspen and birch. It is likely that *F. mounceae* or *F. ochracea* is the dominant decay fungus associated with all decay classes of Lutz spruce (*Picea x lutzii*) on the Kenai Peninsula of southern Alaska after extensive mortality by the spruce bark beetle in the late 1990s (Glaeser et al. 2009). These two species may also be aggressive stem pathogens of living conifers in southern Alaska (Anonymous 2015) and have been suggested for use as inoculum for living trees for the generation of cavities for wildlife habitat (Brandeis et al. 2002; Bednarz et al. 2013).
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