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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.

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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, Högberg 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

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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 topologypr = speciestree, prset brlenspr = clock: speciestree, prset popvarpr = variable, prset popsizepr = 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 basidiospore and hyphal walls was observed in 0.1% cotton blue in 60% (*w*/*v*) lactic acid (Kotlaba and Pouzar 1964; Singer 1986). Average ($\bar{x}$) 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 (BI) 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.

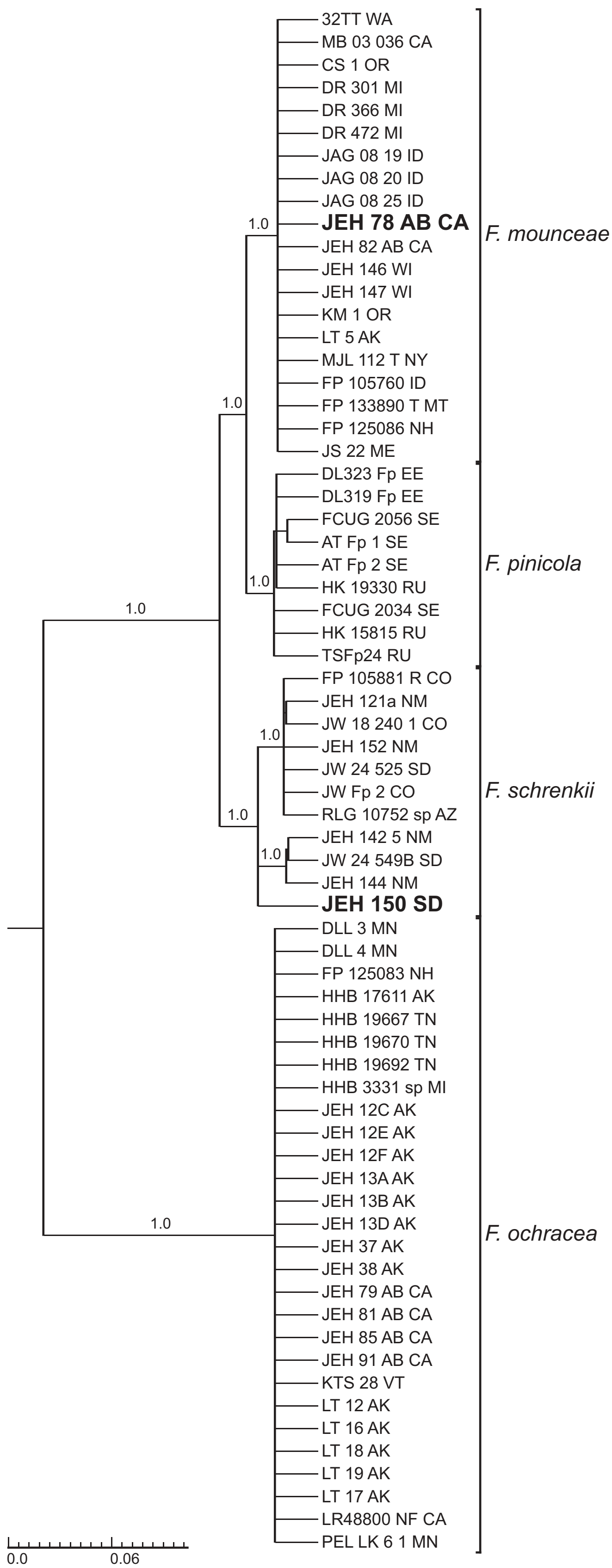

Figure 1. Bayesian coalescent, concatenated, three-gene species tree showing phylogenetic relationships among species in *Fomitopsis pinicola* sensu lato. The tree is midpoint rooted and branch support values (PP ≥ 0.95) are shown on individual branches. Type specimens are noted in bold type.

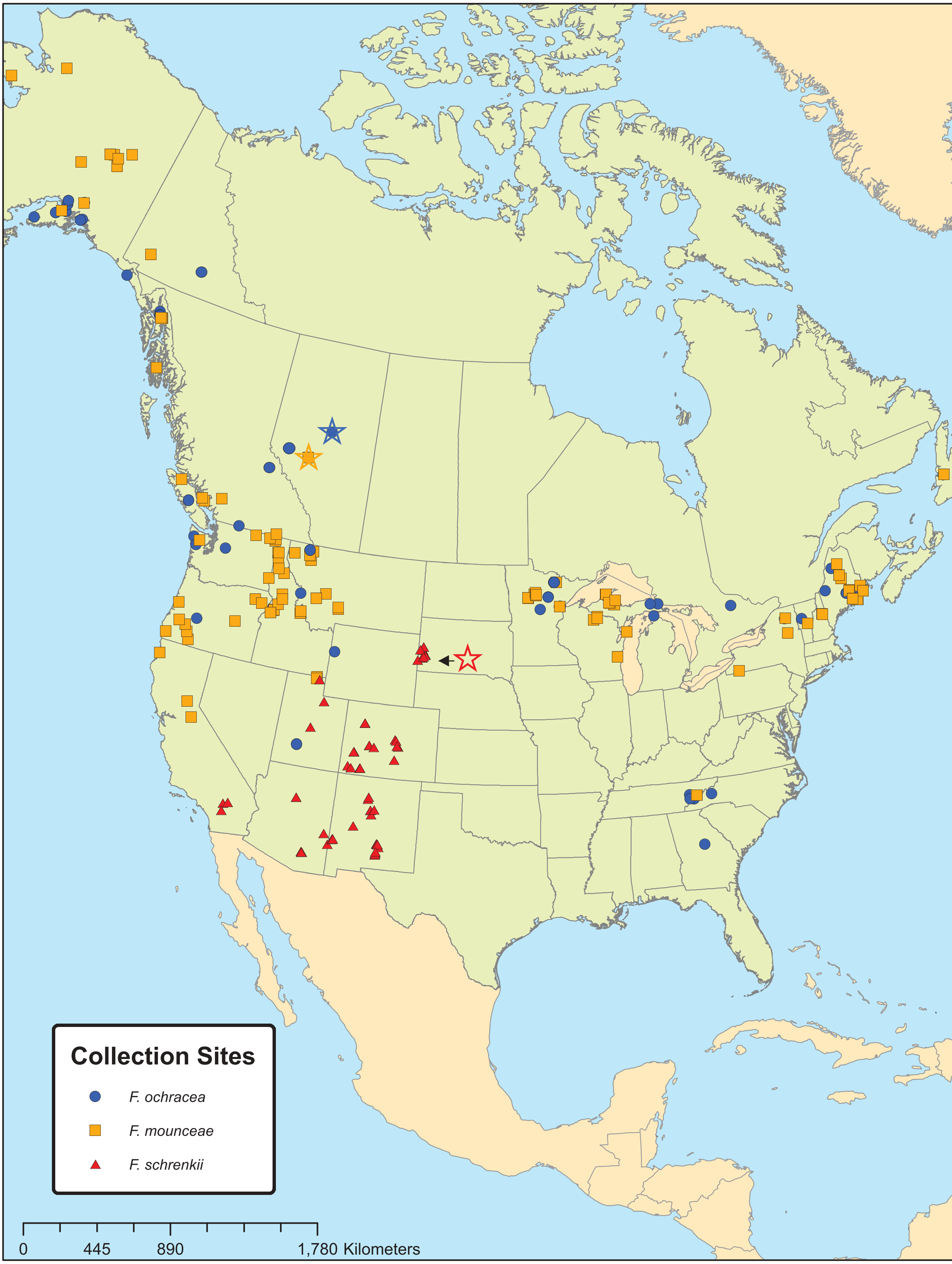

Figure 2. Distribution of *Fomitopsis* species in North America. Star indicates location of type specimens. Icons are stacked when locations are similar.

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 **G**TTT**A**CTTTT begins, which is unique to *F. mounceae*, and at position 450 changes from A to G for *F. schrenkii* **G**TTT**G**CTTTT. At this site, most strains of *F. pinicola* sensu stricto have the sequence **A**TTT**G**CTTTT, whereas in *F. ochracea* it is **A**TTT**A**CTTTT. 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 GGTAC**C**TGTG at positions 489–498 and is readily differentiated from the unique motif GGTAC**T**TGTG 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 (A_1 = 1,2,4,5,7,9,11; A_2 = 3,8,12) and JEH-142 (A_3 = 1,3,4,7; A_4 = 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 (A_1 = 1,3,4,5,7,8,11,13; A_2 = 2,9,10,12,14) and JEH-225 (A_3 = 1,2,4,5,6,12; A_4 = 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

Fomitopsis mounceae J.-E. Haight & Nakasone, sp. nov. FIGS. 3A–B, 4A–E, 5

MycoBank MB826717

Typification: CANADA. ALBERTA: Yellowhead County, Edson, 12 km E of Edson, rest area on Hwy 16 (53.5767, −116.1545), on *Populus tremuloides* snag, 9 Oct 2010, *J.-E. Haight JEH-78* (**holotype** CFMR). GenBank: ITS = KF169269; *TEF1* = KF178354; *RPB2* = KF169698.

Etymology: mounceae (Latin), named for Irene Mounce (1894–1987), a pioneering Canadian mycologist, for her contributions to mycology and *Fomitopsis* (fide Ginns 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 applanate, 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	Hardwoods and conifers
Distribution	Canada, northern USA, Appalachian Mountains	Canada, northern USA, Appalachian Mountains	southwestern and western USA	Eurasia
Pileus with reddish brown band	Usually present	None	Sometimes present	Usually present
Pores per mm	3–5(−6)	(3–)4–5(−6)	3–4	5–6
Receding pore surface	Never	Sometimes	Rare	Data not available
Average basidiospore size (µm)	5.8–6.6(−7.1) × (3.1–)3.4–4.1	5.1–5.9 × 3.6–4(−4.4)	5.7–6.7 × 3.7–4.2(−4.3)	6–9 × 3–4.5
Q values	(1.6–)1.7–1.9	1.3–1.4(−1.5)	1.5–1.6(−1.7)	1.8–2.2
ITS sequence at position ~446–456	**GTTTA**CTTTTG	**ATTTA**CTTTTG	**GTTTG**CTTTTG	**ATTTG**CTTTTG or **ATTTA**CTTTTG
ITS sequence at position ~489–498	GGTA**CCT**GTG	GTTA**CTT**GTG	GGTA**CCT**GTG	GGTA**CCT**GTG
Mycelial growth at 30 C at 3 wk (mm)	17 – 62 mm	0 – 4 mm	13 – 53 mm	13 – 69 mm
Cottony balls of mycelia at 6 wk	None	None	Sometimes	None
Irregularly thick-walled hyphae in aerial or surface mat at 6 wk	None	Sometimes	None	None

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.

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 [8(D–E)8], Kaiser Brown, or Hay's Brown, margin rounded, smooth, 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 (6E5), 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) per 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, concolorous 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 woody, 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 to moderately branched, walls hyaline, thin to slightly thickened, smooth, then becoming sclerified, up to 7 µm diam, with walls hyaline at first then dark yellow, thick with lumen lacking, smooth, dominant in pore trama and mycelial stuffed pores, scattered to numerous in context. Skeletal hyphae (4.5–)5–9(–10) µm diam, aseptate, sometimes with adventitious septa, rarely branched, even, straight, walls hyaline, thin at first, then brownish yellow, up to 4.5 µm thick, smooth, dominant in context, dissepiments, and pore trama. Hymenium up to 30 µm thick, a single layer of cystidia and basidia. Cystidia scarce to numerous, obclavate to subfusiform with subacute or rounded apices 16–35(–40) × 3–6.5 µm, clamped at base, enclosed or protruding up to 25 µm, walls hyaline, thin, smooth. Basidia clavate, sometimes with a stalk, 14–25 × 6–8 µm, clamped at base, 4-sterigmate, walls hyaline, thin, smooth. Basidiospores ellipsoid to cylindrical, (5.5–)6–7(–8) × (3–)3.5–4(–4.5) µm, $\bar{x}$ (based on 14 specimens) = 5.8–6.6(–7.1) × (3.1–)3.4–4.1 µm, Q (based on 14 specimens) = 1.6–1.9, walls hyaline, thin to slightly thickened, smooth, acyanophilous, not reacting in Melzer's reagent.

Cultural description: Mats white, thin, slightly raised, subfelty to downy throughout with occasional woolly patches, sometimes appressed around inoculum, subfelty, margins even to slightly uneven, appressed, thin; silky to fimbriate at 2 wk, similar at 4 and 6 wk except aerial mat sometimes slightly thicker; no odor at 4 and 6 wk; no agar discoloration at 2, 4, and 6 wk; not fruiting by 6 wk. Growth on MEA 11–28 mm radius at 1 wk, 34–57 mm radius at 2 wk; GAA negative, <10–36 mm diam at 1 wk, negative, 52–88 mm diam at 2 wk; TAA negative or light brown stain under inoculum, <10–21 mm diam at 1 wk, negative or weakly stained, 21–46 mm diam at 2 wk.

Microscopic characters: Hyphae in margin 3.5–5.5 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).

Other specimens examined (see also SUPPLEMENTARY MATERIALS): USA. CALIFORNIA: Humboldt County, Redwood National Park, N of Eureka, on conifer (probably not *Metasequoia* as on label), 8 Apr 2003, *M. Binder MB-03-036* (CUW). IDAHO: Valley County, Payette National Forest, Squaw Meadows, on *Picea engelmannii*, 17 Jun 1966, *Hope & O. K. Miller OKM-4065* (CFMR); on *Pseudotsuga*, no date or collector, *FP-9558* (CFMR). MAINE: Sunkhaze Trail County Road, on *Betula* sp., 8 Oct 2002, *J. Schilling JS-15* (CFMR). MICHIGAN: Houghton County, North Hancock, Salo Road, on dead *Populus tremuloides*, 22 Nov 2007, *D. Richter DR-07-016* (CFMR). MONTANA: Lake County, Flathead Lake State Park-West Shore Unit, on conifer trunk on ground, 7 Sep 2017, *K.K. Nakasone KKN-2017-01* (CFMR); Flathead Lake State Park, Yellow Bay Unit, on conifer snag, 7 Sep 2017, *K.K. Nakasone KKN-2017-02* (CFMR). OREGON: Union County, 14 miles NE of La Grande, on butt of *Abies grandis* snag, 24 Mar 2007, *C. Schmitt CS-001* (CFMR); Wallowa County, Wallowa-Whitman National Forest, Joseph, on *Abies*, 26 Jun 1960, *R.W. Davidson & R.W. Robertson FP-105543* (CFMR). PUERTO RICO (culture only): Caribbean National Forest, May 1991, *E. Setliff 241726* (DAOM). UTAH: Cache County, Wasatch-Cache National Forest, Smithfield Canyon, along Smith Creek, 3 miles E of Smithfield Campground, elev 4800–5000 ft, on conifer stump, 22 May 1999, *M.E. Piep no. 6* (UTC 00146586); Cache National Forest, Logan Canyon, Spring Hollow, 7.11 miles NE of Logan Ranger Station along Hwy 89, on live *Betula occidentalis*, 29 Jun 2011, *M.E. Piep s.n.* (UTC 00255982). WISCONSIN: Fond du Lac County, Kettle Moraine State Forest, North Unit, along Ice Age Trail, 1 mile S of pay booth, on *Larix* in cedar swamp, 18 Sep 2012, *A.D. Parker ADP-4, JEH-147* (CFMR). WYOMING: Jenny Lake, Paintbrush Canyon Trail, substrate unknown, 26 Jun 1956, *L.K. Henry* (NY 01966232).

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 FIG. 1, SUPPLEMENTARY TABLE 2), 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*. Haight 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] "6925") itself is directly linked to *F. mounceae* by ITS sequence of DAOMC F6925 (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).

Fomitopsis ochracea Ryvarden & Stokland, Synopsis Fungorum 25:46. 2008. FIGS. 3C–D, 4F–J, 6

Basidiocarps perennial, woody, usually sessile, occasionally imbricate, usually applanate, 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 [5B3-4)], 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; dissepiments 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 strangulated, 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, dissepiments, 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, $\bar{x}$ (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. 2).

Other specimens examined (see also SUPPLEMENTARY MATERIALS): CANADA. ALBERTA: Slave Lake, on dead *Populus tremuloides*, 8 Jun 2005, *J.N. Stokland 223* (**isotype** TRTC 167884). BRITISH COLUMBIA: Valemount, behind Best Western Motel, 6 Oct 2010, *G. DeNitto JEH-87* (CFMR). NEWFOUNDLAND and LABRADOR: Terra Nova National Park, Sandy Point, on *Picea mariana*, 9 Sep 2011, *L. Ryvarden 48800* (TRTC 167845). USA. ALASKA: Kenai Peninsula Borough, Granite Creek, substrate unknown, 14 Sep 2007, *L. Trummer 16* and *18* (CFMR). MINNESOTA: St Louis County, Orr, on aspen or birch, 9 Sep 2010, *D.L. Lindner 2010-138* (CFMR). UTAH: Sevier County, Fishlake National Forest, 16 miles E from boundary from Monroe, 4 miles E of junction of road to Fitzgerald Park, Monroe Creek, on *Abies lasiocarpa*, 29 Aug 1987, *C.T. Rogerson s.n.* (NY 01966249).

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 hyphae 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

= *Polyporus ponderosus* H. Schrenk, Bulletin, Bureau of Plant Industry, United States Department of Agriculture 36:30. 1903 (nom. illegit., non *P. ponderosus* Kalchbr. 1882).

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.

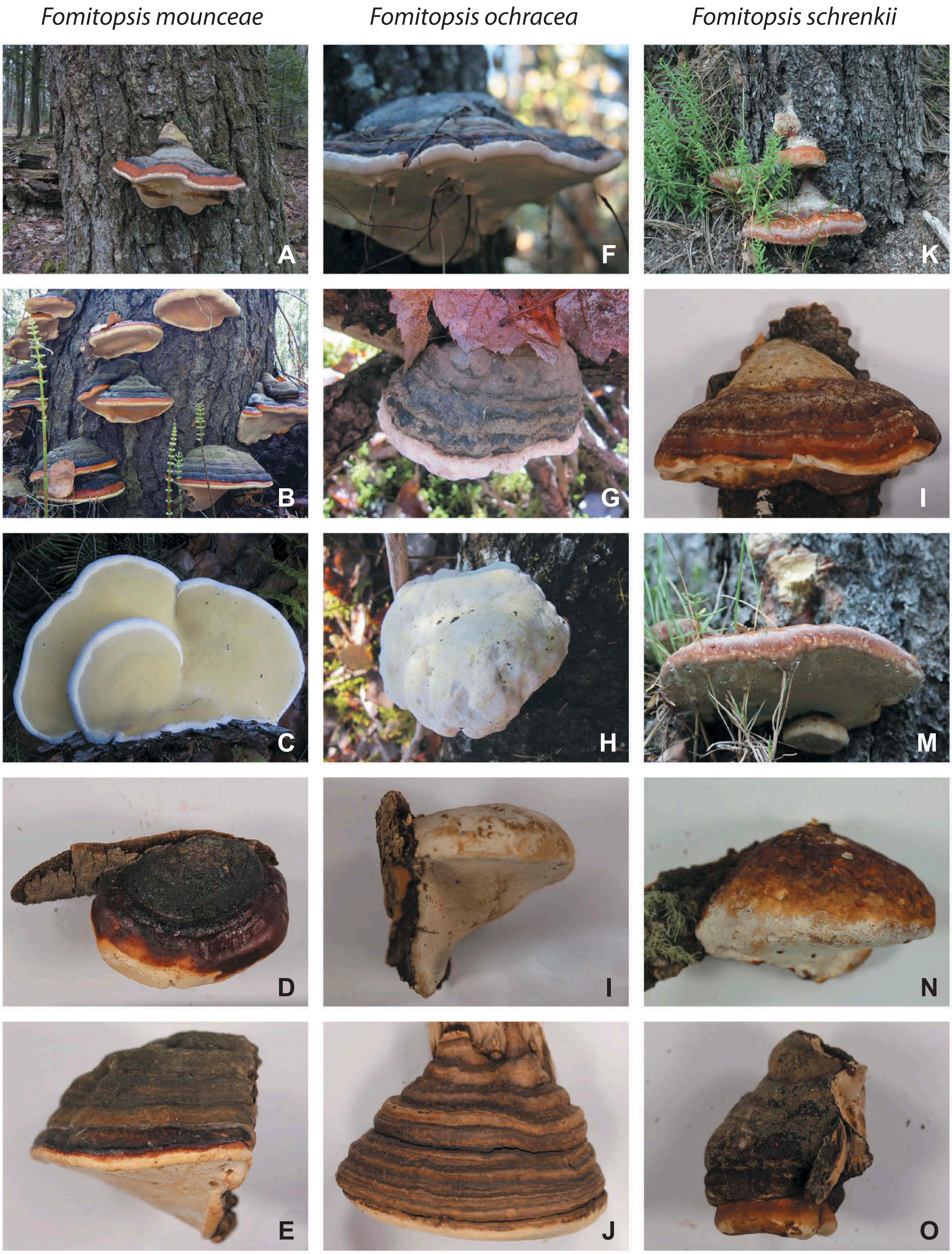

Figure 4. Basidiocarps of *Fomitopsis* species in situ and from herbarium specimens, displaying varied morphology and color. A–E. *Fomitopsis mounceae*. A. Mature basidiocarp from Illinois. B. Multiple basidiocarps on conifer snag from Alaska. C. Pore surface (14.11.03av01, Newfoundland). D. Shiny, resinous, reddish brown pileus (DR-07-016, Michigan). E. Older basidiocarp, side view with thin red band above margin (JEH-84, Alberta). F–J. *Fomitopsis ochracea*. F. Mature basidiocarp (JEH-81, Alberta). G. Mature basidiocarp (14.10.03av03, Newfoundland). H. Pore surface, (14.10.31av03, Newfoundland). I. Young basidiocarp side view (DLL-07-127, Minnesota). J. Older basidiocarp with multiple bands (AK91-18, Alaska). K–O. *Fomitopsis schrenkii*. K. Mature basidiocarps (JMGerring-3, South Dakota). L. Basidiocarp with wide, red-brown band (JEH-130, New Mexico). M. Mature basidiocarp, imbricate (JMGerring-4, South Dakota). N. Young basidiocarp, front view with reddish brown pileus (JEH-216, New Mexico). O. Ungulate basidiocarp with reddish brown band at margin (JEH-115, Colorado).

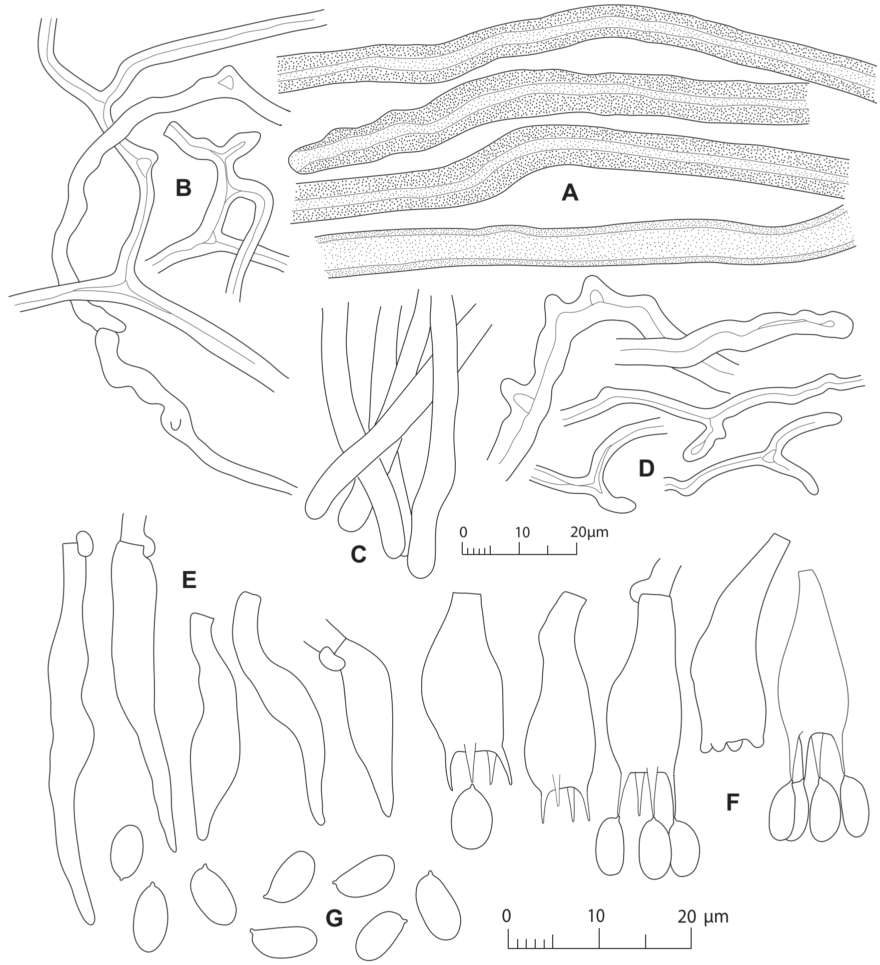

Figure 5. Microscopic elements from *Fomitopsis mounceae* (JEH-78, holotype). A. Dark brownish yellow skeletal hyphae from context. B. Dark yellow sclerified generative hyphae from context. C. Young skeletal hyphae from dissepiment. D. Hyaline sclerified generative hyphae from mycelial stuffed pores. 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.

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 triquertous, 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,

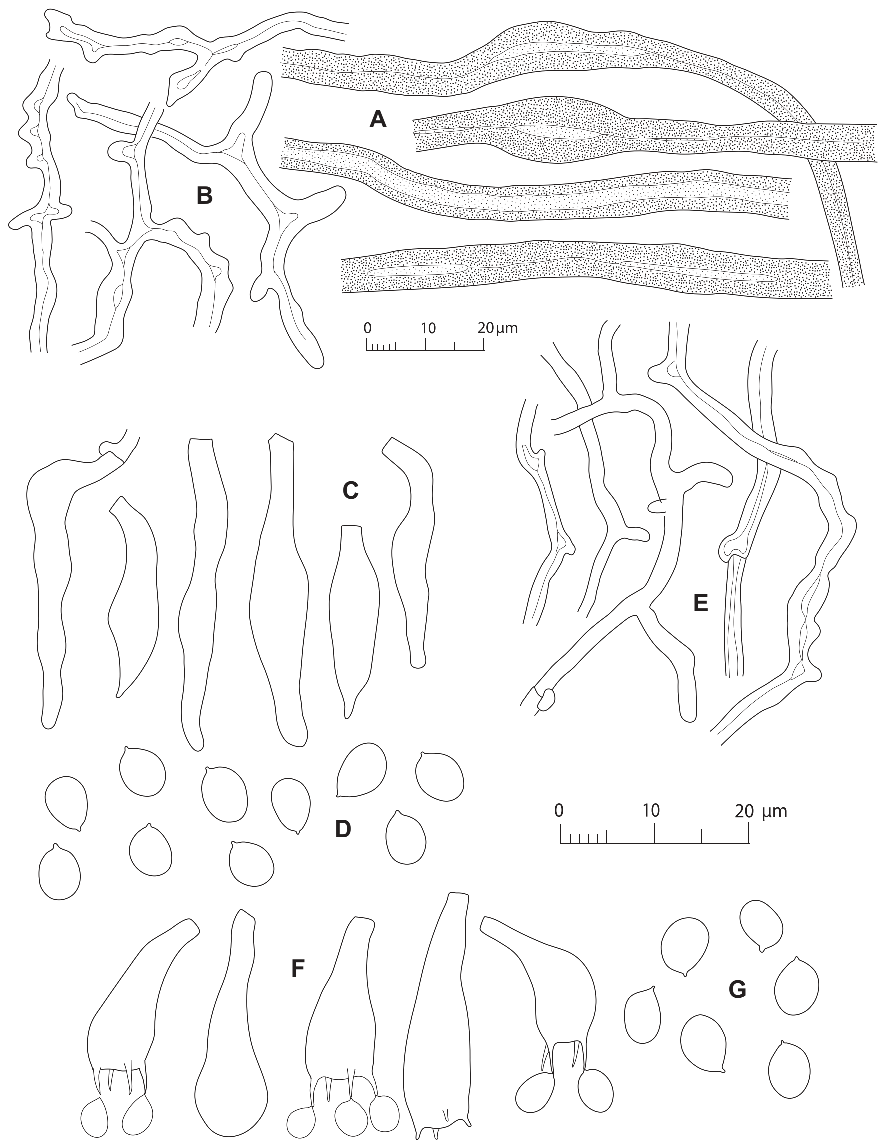

Figure 6. Microscopic elements from *Fomitopsis ochracea*. A. Dark brownish yellow skeletal hyphae from context (Stokland 223, isotype). B. Dark yellow sclerified generative hyphae from context (Stokland 223, isotype). C. Hymenial cystidia (Stokland 223, isotype). D. Basidiospores (Stokland 223, isotype). E. Hyaline sclerified generative hyphae from mycelial stuffed pores (DLL-2010-138). F. Basidia (LT-17). G. Basidiospores (LT-17).

(150–)170–215 µm diam, eventually becoming filled primarily with sclerified and thin-walled generative hyphae with skeletal hyphae less abundant; dissepiments 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. Tube layers distinctly stratified, concolorous with pore surface or pale yellow (4A3), light yellow (4A4), grayish yellow (4B4), or Warm Buff, 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

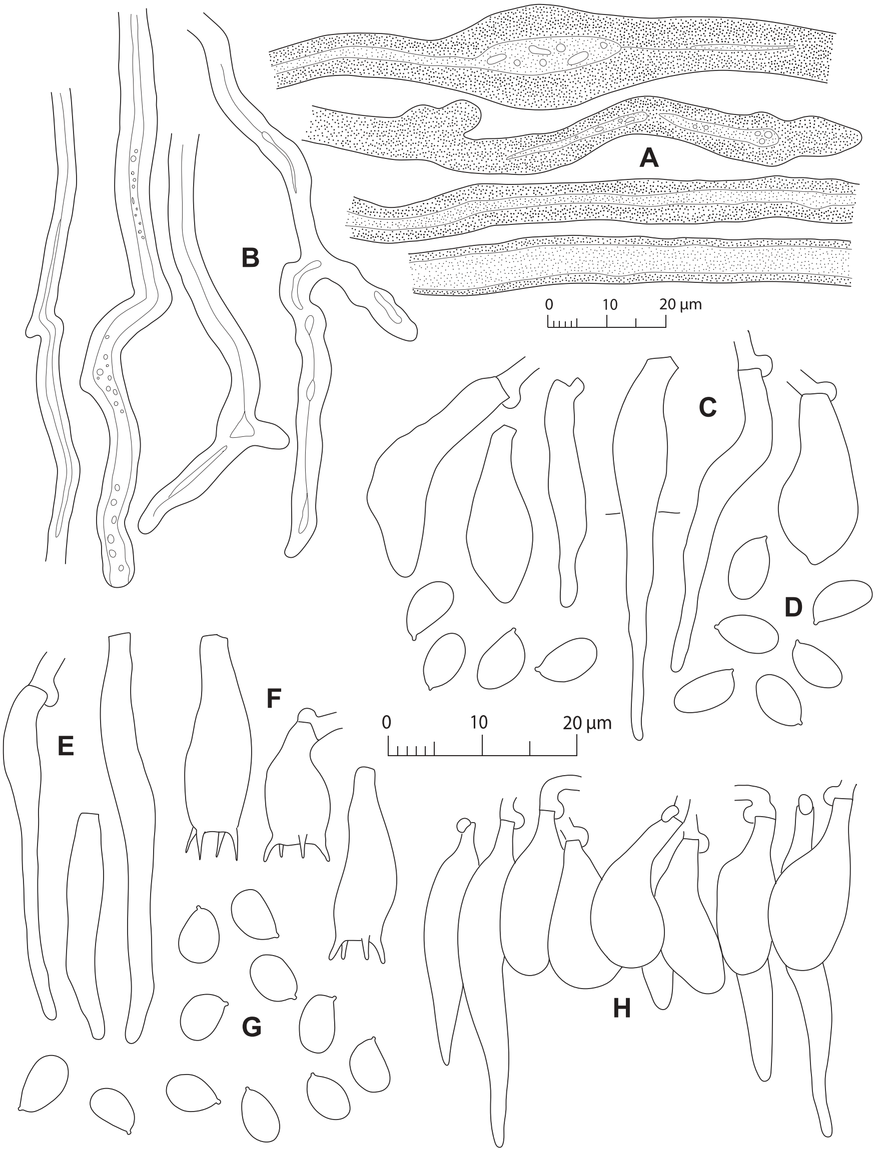

Figure 7. Microscopic elements and basidiocarp from *Fomitopsis schrenkii*. A. Dark brownish yellow skeletal hyphae from context (JEH-150, holotype). B. Dark yellow, sclerified generative hyphae from context (JEH-150, holotype). C. Hymenial cystidia (JEH-150, holotype). D. Basidiospores (JEH-150, holotype). E. Hymenial cystidia (JEH-122a). F. Basidia (JEH-122a). G. Basidiospores (JEH-122a). H. Hymenium section with immature basidia and hymenial cystidia (JEH-198).

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(–7.5) × 3.5–4.5 µm, $\overline{x}$ (11) = 5.7–6.7 × 3.7–4.2(–4.3) µm, Q (11) = 1.5–1.6(–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*. Chlamydospores 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).

Other specimens examined (see also SUPPLE MENTARY MATERIALS): USA. ARIZONA: Pima County, Coronado National Forest, Santa Catalina Mountains, Bigelow, *Pseudotsuga menziesii*, 31 Aug 1972, *R.L. Gilbertson RLG-10752* (CFMR). CALIFORNIA: Riverside County, Mt. San Jacinto State Park, Long Valley Nature Trail, elev 8500 ft, on old growth *Abies concolor* with snapped off trunk, fresh fruiting above residual snow banks, 4 Feb 2016, *S.A. Redhead, JEH-198* (CFMR). COLORADO: Archuleta County, San Juan National Forest, Opal Lake Trail, on *P. menziesii*, 19 Oct 2011, *D.L. Taylor, JEH-115* (CFMR). NEW MEXICO: Lincoln County, Lincoln National Forest, near Ruidoso, on conifer snag, 19 Oct 2011, *D.L. Taylor, JEH-122a* (CFMR); Otero County, off Road 244 between Cloudcroft and Ruidoso, on recently dead *Abies* sp., 31 May 2012, *J.-E. Haight JEH-173a* (CFMR). SOUTH DAKOTA: Black Hills, no date, *Schrenk s.n.* (**holotype** of *Polyporus ponderosus*, NY 00780681); Custer County, Black Hills National Forest, near Custer, on *Pinus ponderosa*, Oct 1914, *G.G. Hedgcock, FP-17044* (CFMR); Black Hills National Forest, on *P. ponderosa*, 25 Jul 1933, *R.W. Davidson, FP-58527* (CFMR). UTAH: Cache County, Cache National Forest, T.W. Daniels Experimental Forest, Logan Canyon summit, near headwaters of Spawn Creek, 5 miles S of US 89, elev 8400 ft, 41°51′N 111°29′W, on conifer stump, 9 Sep 1999, *S. McKibben 2* (UTC 00163339); Garfield County, Dixie National Forest, along Pine Creek near Blue Spruce Campground, on dead trunk of *Picea pungens*, 29 Aug 1989, *C.T. Rogers* (NY 01966294); Rich County, Cache National Forest, Logan Canyon summit on US 89, 5 miles SSW of Garden City along Limber Pine Trail, elev 8000 ft, 41°52′N 111°29′W, 26 Sep 1998, on conifer log, *M.E. Piep 6* (UTC 00163279).

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. pinicola* 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-141 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 *Polyporus ponderosus*. Later, Mounce (1929) and Mounce and Macrae (1938) identified several intersterile groups of *Fomitopsis pinicola* 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, basidiospore 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-mon) strains can also be used to identify these closely related species. However, we obtained unexpectedly disappointing results with di-mon matings with *F. schrenkii* cultures. We undertook di-mon 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-mon 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-mon pairings, for this is a complex process that involve 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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LITERATURE CITED

Anderson JB, Kohn LM. 2007. Dikaryons, diploids, and evolution. In: Heitman J, ed. Sex in fungi: molecular determination and evolutionary implications. Washington, DC: ASM Press. p. 333-348.

Anonymous. 2015. Forest health conditions in Alaska 2015. FS-R10-FHP Publication R10-PR-38. Anchorage, Alaska: US Forest Service, Alaska Region. 78 p.

Bednarz JC, Huss MJ, Benson TJ, Varland DE. 2013. The efficacy of fungal inoculation of live trees to create wood decay and wildlife-use trees in managed forests of western Washington, USA. Forest Ecology and Management 307:186-195.

Brandeis TJ, Newton M, Filip GM, Cole EC. 2002. Cavity-nester habitat development in artificially made Douglas fir snags. Journal of Wildlife Management 66:625-633.

Castello JD, Shaw CG, Furniss MM. 1976. Isolation of *Cryptoporus volvatus* and *Fomes pinicola* from *Dendroctonus pseudotsugae*. Phytopathology 66:1431–1434.

Corner EJH. 1953. The construction of polypores—introduction: *Polyporus sulphureus, P. squamosus, P. betulinus* and *Polystictus microcyclus*. Phytomorphology 3:152–163.

Donk MA. 1964. A conspectus of the families of Aphyllophorales. Persoonia 3:199–324.

Floudas D, Binder M, Riley R, Barry K, Blanchette RA, Henrissat B, Martínez AT, Otillar R, Spatafora JW, Yadav JA, Aerts A, Benoit I, Boyd A, Carlson A, Coutinho PM, de Vries RP, Ferreira P, Findley K, Foster B, Gaskell J, Glotzer D, Górecki P, Heitman J, Hesse C, Hori C, Igarashi K, Jurgens JA, Kallen N, Kersten P, Kohler A, Kües U, Kumar TKA, Kuo A, LaButti K, Larrondo LF, Lindquist E, Ling A, Lombard V, Lucas S, Lundell T, Martin R, McLaughlin DJ, Morgenstern I, Morin E, Murat C, Nagy LG, Nolan M, Ohm RA, Patyshakuliyeva A, Rokas A, Ruiz-Dueñas FJ, Sabat G, Salamov A, Samejima M, Schmutz J, Slot JC, St. John F, Stenlid J, Sun H, Sun S, Syed K, Tsang A, Wiebenga A, Young D, Pisabarro A, Eastwood DC, Martin F, Cullen D, Grigoriev IV, Hibbett DS. 2012. The paleozoic origin of enzymatic lignin decomposition reconstructed from 31 fungal genomes. Science 336:1715–1719, doi:10.1126/science.1221748

Gilbertson RL 1980. Wood rotting fungi of North America. Mycologia 72:1–49.

Gilbertson RL, Ryvarden L. 1986. North American polypores. Vol. 1. Oslo, Norway: Fungiflora. 433 p.

Ginns J. 1988. Irene Mounce, 1894–1987. Mycologia 80:607–608.

Glaeser JA, Lindner DL, Banik MT, Trummer L. 2009. Wood decay fungi associated with beetle-killed Lutz spruce (*Picea* × *lutzii*) from the Kenai Peninsula, AK: culture studies. In: Proceedings of the 56th Western International Forest Disease Work Conference, Missoula, MT, October 27-31, 2008. Logan, Utah: University of Southern Utah, Department of Wildland Resources. p. 61-70. Available from: http://www.fs.fed.us/foresthealth/technology/wif/proceedings/WIFDWC2008.pdf

Haight J-E, Laursen GA, Glaeser JA, Taylor DL. 2016. Phylogeny of *Fomitopsis pinicola*: a species complex. Mycologia 108:925–938, doi:10.3852/14-225R1

Hedgcock GG. 1914. Notes on some diseases of trees in our national forests. IV. Phytopathology 4:181–188.

Hepting GH 1971. Diseases of forest and shade trees of the United States. Agriculture Handbook Number 386. Washington, DC: US Department of Agriculture US Forest Service. 658 p.

Högberg N, Holdenreider O, Stenlid J. 1999. Population structure of the wood decay fungus *Fomitopsis pinicola*. Heredity 83:354–360.

Jacobsen RM, Kauserud H, Sverdrup-Thygeson A, Bjorbækmo MM, Birkemoe T. 2017. Wood-inhabiting insects can function as targeted vectors for decomposer fungi. Fungal Ecology 29:76–84.

Kancherla RP, Durling MB, Stenlid J, Högberg N. 2017. Draft genome of the brown-rot fungus *Fomitopsis pinicola* GR9-4. Data in Brief 15:496–500.

Kirk PM, Cannon PF, Minter DW, Stalpers JA. 2008. Ainsworth & Bisby's Dictionary of the Fungi. 10th ed. Wallingford, UK: CAB International. 771 p.

Kornerup A, Wanscher JH. 1978. Methuen handbook of colour. 3rd ed. London, UK: Eyre Methuen. 252 p.

Kotlaba F, Pouzar Z. 1964. Preliminary results on the staining of spores and other structures of Homobasidiomycetes in cotton blue and its importance for taxonomy. Feddes repertorium specierum novarum regni vegetabilis 69:131–142.

Lloyd CG. 1915. Synopsis of the genus *Fomes*. Mycological writings 4:209–288.

McFee WW, Stone EL. 1966. The persistence of decaying wood in the humus layers of northern forests. Soil Science of America Journal 30:513–516.

Miller MA, Pfeiffer W, Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE), New Orleans, LA, November 14, 2010. p. 1–8.

Mounce I. 1929. Studies in forest pathology. II. The biology of *Fomes pinicola* (Fr.) Cooke. Bulletin of the Department of Agriculture of the Dominion of Canada. New series. No. 111:1-56 + 10 pl. Ottawa, Ontario.

Mounce I, Macrae R. 1938. Interfertility phenomena in *Fomes pinicola* (Fr.). Canadian Journal of Research, Section C: Botanical Sciences 16:354–376.

Murrill WA. 1908. Polyporaceae. Part 2. North American Flora 9:73–131.

Nakasone KK. 1990. Cultural studies and identification of wood-inhabiting Corticiaceae and selected Hymenomycetes from North America. Mycological Memoir 15:1–412.

Nobles MK. 1948. Studies in forest pathology VI. Identification of cultures of wood-rotting fungi. Canadian Journal of Research, Section C: Botanical Sciences 26:281–431.

Nobles MK. 1965. Identification of cultures of wood-inhabiting Hymenomycetes. Canadian Journal of Botany 43:1097–1139.

Overholts LO. 1953. The Polyporaceae of the United States, Alaska, and Canada. Ann Arbor, Michigan: University of Michigan Press. 466 p.

Persson Y, Ihrmark K, Stenlid J. 2011. Do bark beetles facilitate the establishment of rot fungi in Norway spruce? Fungal Ecology 4:262–269.

Peterson PD, Griffith CS, Campbell C. 2000. Hermann von Schrenk and the rise of forest pathology in the United States. Plant Disease 84:586–591.

Ridgway R. 1912. Color standards and color nomenclature. Washington, DC: Published by the author. 43 p. + 53 pl.

Romão C. 1996. Interpretation manual of European Union habitats. Version EUR15. Natura 2000. European Commission, DG XI —Environment, Nuclear Safety and Civil Protection, Nature protection, coastal zones and tourism. 146 p.

Ronquist F, Hulsenbeck JP. 2003. MrBayes3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572–1574, doi:10.1093/bioinformatics/btg180

Ronquist F, Huelsenbeck J, Teslenko M. 2011. Draft MrBayes version 3.2 manual: tutorials and model summaries. [cited 2018 Oct 22] Available from: http://mrbayes.sourceforge.net/manual.php

Ryvarden L, Stokland J. 2008. *Fomitopsis ochracea* nova species. Synopsis Fungorum 25:44-46.

Singer R. 1986. The Agaricales in modern taxonomy. Koenigstein, Germany: Koeltz Scientific Books. 981 p. + 88 pl.

Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S. 2011. MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance and maximum parsimony methods. Molecular Biology and Evolution 28:2731–2739, doi:10.1093/molbev/msr121

Thiers B. [continuously updated]. Index Herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. [cited 2018 Nov 29]. Available from: http://sweetgum.nybg.org/ih/

Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber W-H, Li D-Z, Marhold K, May T, McNeill, J, Monro A, Prado J, Price, MJ, Smith GF. 2018. International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code). Königstein, Germany: Koeltz Scientific Books. 254 p.

Vogel S, Alvarez B, Bässler C, Müller J, Thorn S. 2017. The Red-belted Bracket (*Fomitopsis pinicola*) colonizes spruce trees early after bark beetle attack and persists. Fungal Ecology 27:182–188.

Voitk A. 2013. The genus *Fomitopsis* in Newfoundland & Labrador. Omphalina 4(7):14–17.

von Schrenk H. 1903. The "bluing" and the "red rot" of the western yellow pine, with special reference to the Black Hills forest reserve. Bulletin, Bureau of Plant Industry, United States Department of Agriculture No. 36: 1–40+ 14 pl. Washington, DC.

Worrall JJ. 1997. Somatic incompatibility in basidiomycetes. Mycologia 89:24–36.

Zhou L-W, Nakasone KK, Burdsall HH Jr,Ginns JH, Vlasák J, Miettinen O, Spirin V, Niemelä T, Yuan H-S, He S-H, Cui B-K, Xing J-H, Dai Y-C. 2016. Polypore diversity in North America with an annotated checklist. Mycological Progress 15:771–790, doi:10.1007/s11557-016-1207-7