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The Inocybe geophylla group in North America: A revision of the lilac species surrounding I. lilacina

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Abstract:	The Inocybe geophylla group is circumscribed based on phylogenetic analysis of DNA sequences largely sampled from North America and Europe. Twenty-nine phylogenetic species are uncovered after analysis of combined nuc 28S rDNA (28S) and RNA polymerase II second largest subunit (rpb2) DNA sequence data. Species in the I. geophylla group share the presence of a cortina, silky-fibrillose pileus and stipe, pruinose stipe apex, spermatic odor, thick-walled hymenial cystidia, and smooth amygdaliform or elliptical basidiospores. Within the group as many as five phylogenetic species attributable to I. lilacina and allies form a strongly supported clade based on analysis of nuc ITS1-5.8S-ITS2 rDNA (ITS), 28S, and rpb2 data. However, all lilac colored species do not form a monophyletic group. Sufficient morphological and ecological data are present to document four of the I. lilacina subgroup species, two of which are described from North America as new: I. ionocephala and I. sublilacina. Inocybe lilacina is re-circumscribed based on sequencing the holotype and is distributed in the eastern U.S. under pines and/or hardwoods. Inocybe pallidicremea is a widespread and common conifer-associate in mostly northern parts of North America, to which the name I. lilacina was previously applied. Descriptions, photographs, line drawings, and a taxonomic key to lilac species in the I. lilacina subgroup from North America are provided. Well-documented collections, especially notes on gross morphology and ecology, are needed to continue to assess and describe the high taxonomic variation in the I. lilacina subgroup and its allies worldwide.
Keywords:	Agaricales, Inocybaceae, new species, systematics, taxonomy, 2 new taxa
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Short title for running head: Revision of *Inocybe lilacina*

Title: The *Inocybe geophylla* group in North America: A revision of the lilac species surrounding *I. lilacina*

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ABSTRACT

The *Inocybe geophylla* group is circumscribed based on phylogenetic analysis of DNA sequences largely sampled from North America and Europe. Twenty-nine phylogenetic species are uncovered after analysis of combined nuc 28S rDNA (28S) and RNA polymerase II second largest subunit (*rpb2*) DNA sequence data. Species in the *I. geophylla* group share the presence of a cortina, silky-fibrillose pileus and stipe, pruinose stipe apex, spermatic odor, thick-walled hymenial cystidia, and smooth amygdaliform or elliptical basidiospores. Within the group as many as five phylogenetic species attributable to *I. lilacina* and allies form a strongly supported clade based on analysis of nuc ITS1-5.8S-ITS2 rDNA (ITS), 28S, and *rpb2* data. However, all lilac colored species do not form a monophyletic group. Sufficient morphological and ecological data are present to document four of the *I. lilacina* subgroup species, two of which are described from North America as new: *I. ionocephala* and *I. sublilacina*. *Inocybe lilacina* is re-circumscribed based on sequencing the holotype and is distributed in the eastern U.S. under pines and/or hardwoods. *Inocybe pallidicremea* is a widespread and common conifer-associate in mostly northern parts of North America, to which the name *I. lilacina* was previously applied. Descriptions, photographs, line drawings, and a taxonomic key to lilac species in the *I. lilacina* subgroup from North America are provided. Well-documented collections, especially notes on gross morphology and ecology, are needed to continue to assess and describe the high taxonomic variation in the *I. lilacina* subgroup and its allies worldwide.

KEY WORDS: Agaricales, Inocybaceae, new species, systematics, taxonomy, 2 new taxa

INTRODUCTION

The *Inocybe geophylla* (Fr.: Fr.) P. Kumm. group includes some of the most common and easily recognizable species in the genus *Inocybe* (Fr.) Fr. Classic species in this group, apart from *I. geophylla*, produce basidiomes that are white, lilac to lavender, or bear brownish yellow or dark gray fibrils. All of these species possess a cortina and feature smooth basidiospores, the apices of which are rounded or obtuse in some species. The surface texture of the pileus and stipe is silky-fibrillose with the upper part of the stipe pruinose and the lower part at times bearing agglutinated fibrils. The odor of basidiomes in this group is characteristically spermatic. In addition all species have thick-walled hymenial cystidia and caulocystidia at the stipe apex. Members of the *I. geophlla* group were first recognized as a monophyletic entity in Matheny (2005) as "clade 1b" and later by Ryberg et al. (2010) as clade XIIIb.

Species in the *I. geophylla* group have been variously classified within *Inocybe* since 19th century works. Heim (1931) treated the group as "stirpe geophylla" in section *Viscosae* R. Heim. Singer (1986) included the group in an unnamed section 5. Bon established subsection *Geophyllinae* Bon within section *Tardae* Bon. Jacobsson and Larsson (2012) did not include any subsectional treatments of *Inocybe* but retained *I. geophylla* and allies in section *Tardae*. Daniel E. Stuntz, in his unpublished works on smooth-spored Inocybes, recognized "stirps Geophylla" within his large encompassing but unpublished "section *Inocybium*".

Species in this group were subjected to broad morphological species interpretations (Kuyper 1986). However, Ryberg et al. (2008) demonstrated that, as then delimited, several species were not monophyletic, and that further taxonomic assessments were necessary to untangle the polyphyletic morphological taxa in the group. Here, we address the systematic treatment of the species *I. lilacina* (Peck) Kauffman, originally described from New York, the name of which has been broadly applied, based on morphological interpretations, to collections in North America, Europe, Asia, and Australia (Matheny and Bougher 2005).

Inocybe lilacina was first acknowledged as *Agaricus geophyllus* var. *lilacinus* Peck in a brief two-sentence statement (Peck 1874). Peck wrote: "AGARICUS GEOPHYLLUS Sow. The variety with the pileus of a beautiful lilac color occurs in Bethlehem. It is *Ag. affinis* Pers. and might appropriately be named var. *lilacinus*." Gillet (1879), a few years later, made the new combination based on Peck's variety as *I. geophylla* var. *lilacina* (Peck) Gillet [as "*lilacinus*"]. Kauffman (1918) was the first to establish *I. lilacina* at species rank distinct from the white *I. geophylla* noting that in Michigan the two species never co-occurred, and that the lilac-violaceous colored basidiomes were sufficiently diagnostic. In North America *I. lilacina* was recognized as an autonomous morphological species in its own right (Kauffman 1918, 1924; Hesler 1936; Smith et al. 1979; Lincoff 1981) or at the rank of a variety of *I. geophylla* (Smith 1949; Nishida 1989; Bessette et al. 1995; Evenson 1997; Bessette et al. 2007; Elliott and Stephenson 2018).

The purpose of our work is three-fold: (i) to circumscribe the *I. geophylla* group at large based on expanded sampling of North American taxa and estimate its taxonomic richness and highlight clades or taxa that deserve further taxonomic revision; (ii) to determine the identity of *I. lilacina* based on collecting efforts and by sequencing the holotype collected in the early 1870s; and (iii) to provide a taxonomic framework, with an evolutionary underpinning, to identify North American species of the *I. lilacina* species complex, a subgroup within the greater *I. geophylla* group. This work represents the first step to revise members of this group, or subsection *Geophyllinae*, in North America.

MATERIALS AND METHODS

***Field sampling*.**—Collections made in the field were documented when fresh using Kornerup and Wanscher (1967), Munsell Soil Color Charts (1954), or Ridgway (1912). Gross morphological descriptions were made from notes based on fresh material or reconstructed from photographs. Fresh tissues were subject to PDAB macrochemical tests when available (Matheny et al. 2013). Specimens were dehydrated and preserved at herbaria, abbreviations of which follow Thiers [continuously updated]. NYS provided digitized images of the holotype of *Agaricus geophyllus* var. *lilacinus* and a loan of the holotype.

***Microscopy*.**—Microscopic examinations were made on dried material. Sections were rehydrated in 5% KOH to study the morphology of basidiospores, basidia, hymenial cystidia, stipitipellis, and pileipellis. Terminology regarding use of the terms cheilocystidia, paracystidia, pleurocystidia, caulocystidia, and cauloparacystidia follows that of Kuyper (1986). Basidiospore dimensions in excess of two standard deviations from the mean are placed in parentheses. The number of total basidiospores measured (n) is indicated from *x* collections. Mean basidiospore lengths, widths, and Q values (quotients or lengths divided by widths measured in profile view) are italicized. Cell measurements and line drawings were done following the methods of Braaten et al. (2014).

***DNA extractions, PCR, and sequencing*.**—DNA extractions of dried material involved grinding 10–20 mg of material with a mortar and pestle in liquid N and use of an E.Z.N.A. fungal DNA extraction kit (Omega Bio-Tek, Norcross, Georgia). For type specimens we used a 'High Performance' HP Fungal DNA Kit (Omega Bio-Tek) and filtered pipette tips in a laminar flow hood to reduce chances for DNA cross contamination. Recent dried collections (<5 yr old) were placed in 40 μL of Extract-N-Amp solution (Sigma-Aldrich, St. Louis, Missouri) and incubated at RT for >10 min, then incubated at 95 C for 10 min, followed by mixing with an equal volume of 3% bovine serum albumin (BSA) dilution solution (Truong et al. 2017). After the addition of the BSA solution, samples were ready for PCR.

***Gene sampling*.**—Regions of nuc ITS1-5.8S-ITS2 rDNA (ITS), nuc 28S rDNA (28S), and the most variable region of RNA polymerase II second largest subunit (*rpb2*) were amplified, purified, and sequenced following protocols outlined in Sánchez-García et al. (2014). ITS1 and ITS2 were amplified and sequenced separately for types and historical collections >30 yrs. Sequence chromatograms were assembled in SEQUENCHER 5.0.1 (Gene Codes Corporation, Ann Arbor, Michigan).

***DNA alignments, taxon sampling, and phylogenetic analyses*.**—Taxa used in phylogenetic analyses and their corresponding GenBank accession numbers are provided in Table 1. Newly produced sequences are in bold and were added manually in MACCLADE 4.08 (Maddison and Maddison 2005) to curated alignments of 28S and *rpb2* produced originally in Matheny (2005) and Matheny et al. (2009). These alignments were supplemented with 28S sequences produced by various works, namely those of Ryberg et al. (2008, 2010). Taxa were pruned to those affiliated with "clade 1b" identified in Matheny (2005), which correspond to the *I. geophylla* and *I. flocculosa* groups at large. *Inocybe kauffmanii* A.H. Sm. was used for outgroup purposes. All sites were included for analyses. After inspection for intergene conflict, the 28S and *rpb2* alignments were concatenated. Phylogenetic analyses were conducted in RAXML 8.2.9 (Stamatakis 2014) under the Maximum Likelihood (ML) criterion using a GTRGAMMA model as recommended in the RAXML user manual. The concatenated alignment was partitioned by 28S, *rpb2* gene codon positions, and one *rpb2* intron region. 1000 bootstrap replicates were performed. Bootstrap values >50% are shown on resulting tree figures.

ITS+28S+*rpb2* sequences of members of the *I. lilacina* subgroup, as identified by the 28S+*rpb2* analysis, were aligned in CLUSTALX 2.0.9 (Larkin et al. 2007) and inspected in MACCLADE. This dataset was assembled to include nuc rDNA sequences from type collections and a selection of those available on GenBank. All sites were included in this analysis. For this alignment, sequences labeled as *I. lilacina* that clustered outside the *I. lilacina* group in the 28S+*rpb2* analysis were used for outgroup purposes. Phylogenetic analyses were conducted as described above but partitioned by ITS+28S+*rpb2*-intron 4 data and by *rpb2* codon position. Thus, four different partitions were used in analyses of this dataset. A third dataset was examined including 51 taxa but only ITS+28S data. This data set incorporated numerous ITS or 28S only sequences, including from environmental samples. For phylogenetic analyses, a single model partition was used.

Bayesian Inference (BI) phylogenetic analyses were also performed on the three alignments in MRBAYES 3.2.6 (Ronquist et al. 2012). Models were partitioned as in the RAXML analyses, but model selection was based on Matheny (2005). The 28S+*rpb2* dataset was run for five million generations sampling trees every 5000 steps. The ITS+28S+*rpb2* dataset was run for two million generations sampling trees every 500 steps. The ITS+28S dataset was run for one million generations sampling trees every 500 steps. Convergence diagnostics were observed and length of analyses run as recommended in the user manual. The first 25% of the trees from two independent runs for each dataset were discarded as the burnin prior to calculation of posterior probabilities (PP). PP values >0.95 are reported. Alignments and tree files are available at two locations: http://mathenylab.utk.edu/Site/Alignments_%26_Data_Sets.html and at TreeBASE as submission 21910.

Genetic distances were measured for the ITS and *rpb2* loci separately using the "showdist" command in PAUP 4.0b10 for Unix (Swofford 2002). This command produces a pairwise uncorrected or proportional ("p") distance matrix.

RESULTS

58 ITS, 43 28S, and 26 *rpb2* sequences were produced during this study (127 total; see Table 1). No strongly supported intergene conflict was detected when comparing individual gene topologies, thus the 28S and *rpb2* data were combined. The 28S+*rpb2* alignment contained 79 taxa and 2185 included sites. Each taxon was represented by a 28S sequence, and 52 taxa were represented by *rpb2* sequences. The combined ITS+28S+*rpb2* alignment included 33 taxa and 2960 sites. In this data set, 28 taxa were represented by ITS sequences, 27 by 28S, and 16 by *rpb2*. In the BI analyses, 15002 trees were sampled to calculate PPs for the 28S+*rpb2* dataset and 6002 trees sampled to calculate PPs for the ITS+28S+*rpb2* dataset after discarding the first 25% of trees sampled from both analyses.

Phylogenetic analysis of the 28S+*rpb2* dataset (FIG. 1) resulted in strong support for the *I. geophylla* group or clade Ib of Matheny (2005) as indicated by the bracket. Considerable taxonomic diversity amounting to 29 phylogenetic species in the *I. geophylla* group was detected from samples in North America, Europe, and east Asia. At least eleven morphological taxa are recognizable members of the *I. geophylla* group. These include *I. agglutinata* Peck, *I. fuscicothurnata* Grund & D.E. Stuntz, *I. fuscodisca* (Peck) Massee, *I. geophylla*, *I. insinuata* Kauffman, *I. lilacina*, *I. pallidicremea* Grund & D.E. Stuntz, *I. phaeodisca* var. *geophylloides* Kühner, *I. posterula* (Britzelm.) Sacc., *I. pudica* Kühner, and *I. xanthodisca* Kühner. Both *I. geophylla* and *I. lilacina*, however, comprise eight to nine phylogenetic species-level lineages each and are polyphyletic, reinforcing earlier finds of their non-monophyly by Ryberg et al. (2008). In contrast, the species *I. pudica*, although sampled from a wide geographic range including western North America and northern Europe, forms a cohesive monophyletic group. *Inocybe fuscicothurnata*, earlier names for which may be *I. virgata* G.F. Atk. and *I. fuscodisca* (Peck) Massee, is found to be sister to the remainder of the *I. geophylla* group with strong support.

Six separate phylogenetic lineages are recovered in what we call the *I. lilacina* subgroup, a strongly supported clade of mostly lilac-colored species occurring predominantly in North America (FIG. 1). This clade includes *I. lilacina* in the strict sense based on analysis of ITS sequences from the holotype collected in New York and collections from North Carolina and Tennessee (FIG. 2). Two single stem lineages, represented by 28S sequence data only, are labeled *I. lilacina* from British Columbia and Finland. These branch separately from the other species-level lineages. Three other clades that correspond to the North American species *I. pallidicremea*, *I. ionocephala* sp. nov., and *I. sublilacina* sp. nov. are recovered, each with high measures of branch support.

Phylogenetic analysis of the ITS+28S+*rpb2* dataset resulted in recovery of at least five phylogenetic species in the *I. lilacina* subgroup, all of which are characterized by basidiomes with lilac pigmentation (FIG. 2). Of these we have sufficient documentation to present four North American species, each receiving strong branch support, in taxonomic detail below.

Many samples attributed to *I. lilacina*, mainly from the northern U.S. and western and eastern Canada, cluster with type of *I. pallidicremea* described from Nova Scotia (FIGS. 1, 2, SUPPLEMENTARY FIG. 1). Most collections from the Rocky Mountains and Colorado Plateau labeled as *I. lilacina* also cluster with *I. pallidicremea* (SUPPLEMENTARY FIG. 1). A distinct clade of southeastern U.S. samples labeled *I. lilacina* is recovered with strong support together with a partial ITS sequence of the type of Peck's *Agaricus geophyllus* var. *lilacinus* from New York (FIG. 2). In all three datasets, samples of *I. sublilacina* cluster together with strong support from eastern Canada and the Rocky Mountains. In addition, samples from California form a monophyletic group with strong support — these are labeled *I. ionocephala* sp. nov. Sequences from environmental samples and basidiomes collected in pure conifer stands suggest *I. pallidicremea* is ectomycorrhizal with *Picea*, *Pseudotsuga*, and/or *Tsuga* (SUPPLEMENTARY FIG. 1). Similar environmental and ecological data suggest *I. lilacina* in the strict sense is ectomycorrhizal at least with *Pinus* (SUPPLEMENTARY FIG. 1) and with Fagales. TABLE 1 indicates the species assignment of all DNA sequences analyzed.

Infraspecific variation measured as uncorrected "p" distances at the *rpb2* locus for *I. ionocephala*, *I. lilacina*, *I. pallidicremea*, and *I. sublilacina* ranged from 0 to less than 1%. Interspecific variation or "p" distances at the *rpb2* locus ranged from 1–2.5%. Infraspecific variation at the ITS locus measured less than 1%, whereas interspecific distances ranged between 1.6–2.8% in all comparisons except for those between *I. lilacina* and *I. pallidicremea*, which exhibited low ITS variation between 0.2–0.8%.

TAXONOMY

Inocybe pallidicremea Grund & D.E. Stuntz, Mycologia 69:399. 1977. FIGS. 3A–B, 4A–B

Description: Pileus 10–40 mm wide, obtusely conical to broadly convex with a nipple-like umbo, becoming plane or even somewhat depressed with age, margin decurved; surface of umbo smooth or with agglutinated fibrils, silky-fibrillose towards the margin, becoming rimose, velipellis not observed, dry to tacky subviscid; in youth lilac to pale lilac (14B4–B3–C4; reddish-lilac to grayish-lilac) in entirety but fading with age; at times or in age the umbo yellowish brown to mustard brown or brown (5E8–E7–E6), rarely smoky gray (5YR 4/1–3/1), becoming grayish yellow to brownish orange (4B5–5C6) around the umbo, this dissipating towards the margin into a grayish-white color, at times maintaining grayish-lilac fibrillose streaks; context white, thin, up to 3–4 mm thick under the umbo, not changing color where cut or bruised, odor spermatic to strongly so; pileus surface negative with PDAB. Lamellae adnexed, uncinate, or adnate, close, with several tiers of lamellulae, light gray to gray when young becoming pale brown to brown (5D4–D5) with age, subventricose, edges white-fimbriate. Stipe 35–60 × 3–6 mm at the apex, flexuous, clavate-bulbous towards the base, this 7–9 mm wide, upper 1/6–1/8th pruinose; cortina present, cortinate fibrils collapsed and forming a ring-zone at times or fugacious, more or less smooth towards the base or finely-fibrillose; lilac to pale lilac at first, this soon fading and becoming whitish overall, rarely with grayish brown streaks (6D3) beneath the insertion of the cortina and above the base, or with agglutinated gray fibrils above the base, the base itself (pale) yellow or with brownish-orange or grayish-yellow tones (5C5–4B5); context solid, whitish.

Basidiospores (7–)7.5–*9.0*–10.5(–11) × 4.5–*5.3*–6.0 μm, Q = (1.40–)1.44–*1.70*–1.96(–2.11) (n=175/17), smooth, mostly amygdaliform to subamygdaliform, at times elliptical, apices often bluntly pointed or obtuse, apiculus small but distinctive, yellowish-brown, slightly thick-walled. Basidia 29–33 × 8–10 μm, 4-sterigmate, clavate, hyaline. Pleurocystidia 49–73 × 11–20 μm, fusiform-ventricose, often with a slender basal pedicel, thick-walled (walls 1.0–3.0 μm thick), hyaline, apices often bare or weakly crystalliferous. Cheilocystidia similar to pleurocystidia but some shorter and more ventricose or saccate, densely arranged, paracystidia infrequent. Caulocystidia similar to hymenial cystidia but subfusiform, ventricose, or clavate, these 30–110 × 9–18 μm, mixed occasionally with cauloparacystidia. Pileipellis an interwoven cutis of smooth, hyaline hyphae, these slightly thick-walled or thin-walled, mostly 4–8 μm wide, hyaline in mass. Clamp connections present.

Ecology and distribution: Scattered singly or in groups on soil in western states and provinces, Alaska, British Columbia, Washington, Oregon, Wyoming, Colorado, and Arizona, eastward to Michigan, New York, New England, and eastern provinces of Newfoundland and Labrador and Nova Scotia (type); associated with conifers including *Pseudotsuga*, *Picea*, *Tsuga*, and/or *Pinus*. Occurring Aug–Dec.

Illustrations: Smith (1949, as *I. geophlla* var. *lilacina*); Lincoff (1981, as *I. lilacina*); Baroni (2017, as *I. geophylla*).

Specimens examined: CANADA: NEWFOUNDLAND AND LABRADOR: Gros Morne National Park, Stuckless Pond (49.4299, -57.7103), in moss on ground under *Picea*, 4 Sep 2005, *M. Prior & D. Malloch GM5-300* (TENN 070835). Same locality as previous, on soil in coniferous woods, 18 Sep 2004, *N. Siegel & L.L. Norvell GM4-222* (TENN 070832). Twillingate Foray, on soil under *Abies* in coniferous woods, 11 Sep 2009, *MS10-007* (TENN 071726). NOVA SCOTIA: Kings Co., Kentville, Agricultural Experimental Station (45.0692, -64.4781), in wooded area under conifers, 7 Sep 1966, *D. Grund ACAD 11600* (isotype of *Inocybe pallidicremea*). ONTARIO: York Co., N. Summit Golf Club, 7 Oct 1936, *H.S. Jackson*

HSG9619 (TENN 010331). USA: ARIZONA: Coconino Co., Locket Meadow Trail (35.3586, -111.6208), on soil under conifers and *Populus*, 2896 m, 6 Aug 2015, *P.B. Matheny PBM4060a* (TENN 071254). COLORADO: White River National Forest, Braille Trail on Independence Pass (long, lat not available), on soil or dead wood under *Picea*, 9 Aug 2013, *H. Burgess* (DBG 027710). Summit Co., Keystone, River Run Lodge, 2150 m (39.60694, -105.94028). Eagle Co., White River National Forest, Sam's Ranch (39.573878, -106.61574), in moss and litter under *Picea*, 2745 m, 22 Jul 1967, *S. Mitchell* (DBG 001183). Gilpin Co., Roosevelt National Forest, Perigo, 2865 m (39.8922, -105.5303), 13 Aug 1974, *A.H. Smith, Mitchell, & Chapman* (DBG 004919). Pitkin Co., Elk Camp, Snomass Village, 2591 m, (39.1881, -106.9353), under *Picea*, 10 Aug 1979, *V.S. Evenson* (DBG 014326). Similar locality as previous, 2590 m, (39.2408, -106.9822), in moss under *Picea* and *Abies*, 28 Aug 1980, *V.S. Evenson* (DBG 017522). Teller Co., Clyde Campground (38.7308, -105.0254), on soil in grass near conifers, 10 Aug 2007, *L. Barzee* (DBG 023850). MAINE: Bar Harbor, Harbor Trail (44.3875, -68.20389), on ground next to trail under *Picea* and *Betula*, 18 Sep 2005, *P.B. Matheny PBM2744* (TENN 062552). MICHIGAN: Montmorency Co., northwest area (45.0993, -84.2233), in boggy area, 22 Aug 1967, *D.H. Mitchel & M. Wells* (DBG 001716). OREGON: Linn Co., Crescent Mountain Trail (44.42930, -122.03024), on soil under conifers, 23 Oct 1999, *P.B. Matheny PBM1743* (WTU). NEW YORK: South Bethlehem, Joralemon Memorial Park, 4.6 miles south of Brewer Station (42.53222, -73.84611), on soil in mixed woods under *Pinus strobus*, *Juniperus*, *Carya*, *Quercus*, 20 Sep 2006, *K. Bushley PBM2445* (TENN 063879). Same locality as previous, gregarious to scattered or in small pairs or clusters on soil under *Pinus strobus* on edge of mixed forest, 20 Sep 2006, *P.B. Matheny PBM2448* (TENN 062757). WASHINGTON: Island Co., Whidbey Island, Ebbey's Landing, 35 m, on soil under *Pseudotsuga*, 14 Nov 1998, *P.B. Matheny PBM1360*

(WTU). Island Co., Whidbey Island, Ebbey’s Landing, 35 m (48.2292, -122.7073), on soil under *Pseudotsuga*, 14 Nov 1998, *P.B. Matheny PBM1353* (WTU). King Co., Sammamish, Pine Lake State Park (47.58760, -122.04429), on ground under *Pseudotsuga*, 5 Nov 2000, *P.B. Matheny PBM2039* (WTU). King Co., Lincoln Park (47.5306, -122.3960), in mossy grass under *Abies grandis*, 21 Dec 2011, *J.M. Birkebak JMB122111-05* (TENN 066939). Kittitas Co., Crystal Springs Campround (47.30955, -121.31370), on soil under *Abies*, *Pseudotsuga*, *Thuja*, 12 Oct 1997, *P.B. Matheny PBM781* (WTU). Kitsap Co., Seabeck (47.6409, -122.8286), scattered to gregarious on soil under *Pseudotsuga*, *Tsuga*, *Rhododendron*, *Vaccinium*, 25 Oct 1997, *P.B. Matheny PBM817* (WTU). Same locality as previous, on soil under *Pseudotsuga*, *Tsuga*, 21 Nov 1998, *P.B. Matheny PBM1364* (WTU). Whatcom Co., Bellingham Fall Mushroom Show. 20 Oct 2007, *B. McAdoo BM381#10* (TENN 063535). San Juan Co., San Juan Island, Friday Harbor (48.5343, -123.0171), 12 Nov 1962 (TENN 026020). Same locality as previous, on soil under conifers, 3 Nov 2001, *P.B. Matheny PBM2237* (WTU). Same locality and date as previous, on soil under conifers, *P.B. Matheny PBM2238* (WTU). Thurston Co., Olympia, Priest Point Park (47.0723, -122.8954), on soil under *Pseudotsuga*, *Tsuga*, *Abies*, 31 Oct 1998, *P.B. Matheny PBM1334* (WTU). WYOMING: Teton Co., Flagg Ranch-Ashton Road, Teton National Forest, 2285 m, on soil near *Picea*, 30 Aug 1995, *V.S. Evenson* (DBG 018072).

Notes: Based on phylogenetic results and current sampling, *I. pallidicremea* appears to be known only from western and northern North America, associated with conifers, and can be misinterpreted for *I. geophylla* when faded. The species was long interpreted under the name *I. lilacina* or as *I. geophylla* var. *lilacina*. With age or in dry conditions, however, basidiomes of this species become pale yellow with a darker colored umbo (brown, brownish yellow, or even grayish) losing all lilac coloration including from the stipe. Indeed, *I. pallidicremea* was described based on specimens in which the lilac colors must have been completely lost (Grund and Stuntz 1977; as in FIG. 3B). The combination of a darker colored umbo and the yellow to cream-colored stipe base are clues that can be used to distinguish faded forms of *I. pallidicremea* from white-colored basidiomes of *I. geophylla* in the field.

Inocybe lilacina, documented below based on the type and southeastern specimens, can be distinguished from *I. pallidicremea* by the dark purple or dark violet colors that persist at the center of the pileus, smaller basidiome size, and eastern U.S. distribution (New York, North Carolina, Tennessee). The distribution of *I. pallidicremea* and *I. lilacina*, based on present collections confirmed by molecular data (SUPPLEMENTARY FIG. 1), overlaps only in New York. *Inocybe ionocephala*, described below, is known thus far only from the Coastal Redwood zone of northern California and distinguished morphologically by its white stipe and stipe base and larger basidiome size. *Inocybe sublilacina*, a second new species described below, is best distinguished from *I. pallidicremea* by genetic divergence at multiple loci. The basidiospores of *I. sublilacina* are somewhat larger than those of *I. pallidicremea* on average (9.4 × 5.7 μm versus 9.0 × 5.3 μm), a difference that is probably too subtle to detect for practical purposes. However, we did observe the basidiospores of *I. sublilacina* are more often elliptical than amygdaliform unlike those of *I. pallidicremea*, which is typically characterized by amygdaliform basidiospores. Basidiomes of *I. sublilacina* are lilac throughout when young except for the yellowish or cream colored stipe base and the brownish yellow to yellowish brown pileal disc. The geographic range of *I. sublilacina* overlaps with that of *I. pallidicremea*, where the former has thus far only been confirmed with molecular data from Colorado and Newfoundland and Labrador. Despite their morphological and ecological similarities (FIGS. 3, 4), the two species are rather distantly related (FIGS. 1, 2).

The photo of *I. lilacina* under *Tsuga* in Lincoff (1981) resembles specimens in which the lilac colors faded and thus match the description of *I. pallidicremea*. The photograph of *I. geophylla* in Baroni (2017) probably illustrates faded specimens of *I. pallidicremea.*

Two morphological variants among the specimens examined stand out. *PBM1334* was observed with pallid to pale vinaceous drab lamellae when young, and *PBM2238* had a whitish stipe throughout with no yellow or cream to the stipe base. In the overwhelming number of collections we studied of *I. pallidicremea*, the young lamellae are light gray to gray when young, and the stipe base is yellowish or cream-colored.

Inocybe lilacina (Peck) Kauffman, The Agaricaceae of Michigan I:466. 1918. FIGS. 3C–D, 4C–D

≡ *Agaricus geophyllus* var. *lilacinus* Peck, Ann Rep NY St Mus Nat Hist 26:90. 1874 [1873].

≡ *Inocybe geophylla* var. *lilacina* (Peck) Gillet [as '*lilacinus*'], Les Hyménomycètes ou Description de tous les Champignons quie Croisssent en France:520. 1876.

Description: Pileus 8–18 (–30) mm wide, obtusely conical in youth, expanding to plane with age, developing a small subacute umbo, margin incurved in youth becoming decurved; surface tacky, subviscid, margin entire; intense dark purple, dark violet, to blackish purple in youth (15F8–F7), this remaining so over the disc ("Raisin Black" to "Dull Violet-Black" or very dark purple) with purplish or dark violet fibrillose streaks towards the margin over a whitish background; context up to 2 mm thick, whitish but may be dull violet above the lamellae when water soaked, not changing color where cut or bruised, odor strongly spermatic. Lamellae adnexed to subsinuate, moderately close with several tiers of lamellulae, light gray in youth becoming pale brown to brown at maturity, edges pallid-fimbriate or indistinctly so with age, ventricose. Stipe 20–30 × 2–3 mm, even but with a swollen or slightly rounded bulbous base;

cortina mixed violet and whitish with the interior silky white; surface dark violet like the pileus with an underlying white background, white where expanding upwards leaving streaks of dark violet glutinous fibrils, cream colored at the extreme base mixed with white at point of attachment; context soft, interior white with a violet cortex when young, white in the base.

Basidiospores 8–*9*–9.5(–10) × 4.5–*5.2*–5.5 μm, Q = 1.45–*1.74*–1.90(–2.00) (n=31/2), smooth, subamygdaliform or elliptical with bluntly pointed or rounded apices, apiculus small but distinctive, yellowish brown in KOH. Basidia 24–30 × 8–9 μm, 4-sterigmate, clavate, hyaline. Pleurocystidia 45–60 × 14–18 μm, fusiform to fusiform-ventricose, apices obtuse and sparsely crystalliferous, tapered towards the base, thick-walled (walls 1.0–3.0 μm thick), hyaline. Cheilocystidia similar to pleurocystidia but often shorter, mixed with paracystidia that are pyriform to clavate, hyaline, and thin-walled. Caulocystidia restricted to the extreme apex or upper 1/8th of stipe surface, similar to cheilocystidia, at times mixed with shorter, thin-walled, hyaline cells; stipe surface covered with an interwoven superficial layer of hyaline hyphae, these thin-walled, smooth, and mostly 5–10 μm wide. Pileipellis an interwoven cutis, pale pinkish in mass, hyphae smooth, cylindrical, thin-walled, mostly 5–10 μm wide. Clamp connections present.

Ecology and distribution: Scattered singly or in small clusters on soil in the eastern U.S. – New York (type), North Carolina, Tennessee; in woods of *Pinus*, in mixed forests containing *Tsuga*, *Pinus, Fagus*, *Betula*, *Quercus, Juglans*, *Carya*, or in beech-oak-hickory forests (*Fagus*, *Quercus*, *Carya*). Occurring August through October.

Illustration: Elliott and Stephenson (2018, as *I. geophylla* var. *lilacina*).

Specimens examined: USA. NEW YORK: Bethlehem, Albany Co., no date, *C.H. Peck* (holotype NYSf1711). NORTH CAROLINA: Highlands (35.0525, -83.19694), 31 Aug 1939, *L.R. Hesler* (TENN 012367). Highlands, Franklin, Wayah Bald (35.18028, -83.56055), in deciduous woods, 21 Aug 1955, *L.R. Hesler* (TENN 022115). Great Smoky Mountains National Park, Kephart Prong Trail (35.58667, -83.35972), 17 Aug 2005, *E.B. Lickey TFB12747* (TENN 061204). Blue Ridge Parkway, Little Switzerland, 0.2 miles from the Little Switzerland Tunnel (35.82472, -82.10639), on soil under *Quercus* and *Betula*, 13 Sep 2013, *J.M. Birkebak & M. Sánchez-García PBM3982* (TENN 068443). TENNESSEE: Anderson Co., Norris Dam State Park, near Clear Creek Trail (36.2352, -84.1032), on soil in hardwood forest under *Fagus*, *Quercus*, *Carya*, 23 Oct 2017, *V.R. Harpe VRH13* (TENN 073103). Knoxville, New Hopewell (35.96055, -83.92083), on soil in pine woods, 21 Oct 1934, *L.R. Hesler* (TENN 006434). Knoxville, New Hopewell (35.92833, -83.80055), on soil in pine woods, 17 Nov 1935, *L.R. Hesler* (TENN 008431). Same locality as previous, on soil in pine woods, 17 Oct 1936, *L.R. Hesler* (TENN 009562). Same locality as previous, on soil in pine woods, 20 Oct 1937, *L.R. Hesler* (TENN 010926). Great Smoky Mountains National Park, near LeConte (35.655, -83.44111), in mixed woods, 29 Sep 1956, *T.H. Campbell* & *L.R. Hesler* (TENN 022423). Great Smoky Mountains National Park, Cades Cove (35.60194, -83.81138), on soil in pine woods, 23 Sep 1966, *L.R. Hesler* (TENN 029412). Great Smoky Mountains National Park, Greenbrier (35.73028, -83.40611), on ground under *Tsuga*, *Pinus*, *Liquidambar*, and other hardwoods (*Quercus* absent), 6 Sep 2004, *M.C. Aime & E. Lickey PBM2590* (TENN 062429). Great Smoky Mountains National Park, Cades Cove, Little Baptist Church area (35.60194, -83.81333), on soil under *Tsuga*, *Fagus*, *Quercus*, *Juglans*, *Carya*, 9 Sep 2004, *M.C. Aime & E. Lickey PBM2628* (TENN 062463). Same locality as previous, 9 Sep 2004, *E. Lickey PBM2629* (TENN 062464). Great Smoky Mountains National Park, Greenbrier area, Grapeyard Ridge Trail (35.70778, -83.38361), 25 Sep 2006, *E.B. Lickey TFB13384* (TENN 061647). Great Smoky Mountains

National Park, Greenbrier area, Ramsey Cascades Picnic Area (35.71056, -83.38306), in mixed forest, 13 Oct 2012, *E. Harrower EH212* (TENN 067734). Union Co., Big Ridge State Park (long, lat), on ground in mixed hardwood forest (*Fagus*, *Carya*, *Quercus*) with *Pinus virginiana*, 27 Sep 2011, *J.W. Bills JWB17* (UT EEB351 teaching collection). Great Smoky Mountains National Park, Cherokee Orchard Loop, Ogle Place (35.6829, -83.4898), on soil in mixed forest of *Tsuga*, *Pinus*, *Fagus*, *Betula*, 30 Aug 2013, *B. Looney PBM3940* (TENN 068443).

Notes: *Inocybe lilacina* differs morphologically from *I. pallidicremea* by the smaller basidiome size, more intense dark violet pigmentation, and pinkish colors that tend to persist after drying. It is comparatively much less frequent that *I. pallidicremea*, which is common in northern and western parts of North America based on molecular confirmation of specimens and environmental sequences. The two species are sister groups with strong measures of support (FIGS. 1, 2).

Inocybe lilacina has been recorded “in pine woods” but also in habitats without any Pinaceae. L.R. Hesler made several collections in the greater Knoxville area under pines (Hesler 1936). An environmental sequence (EF619676) that corresponds to *I. lilacina* was sampled from a *Pinus taeda* dominated forest in North Carolina (Parrent and Vilgalys 2007) (SUPPLEMENTARY FIG. 1). Associations with other trees (*Tsuga*, *Quercus*, *Fagus*, *Carya*), however, cannot be ruled out, and one collection (VR13) was made in a pure oak-hickory-beech forest.

ITS variation between *I. lilacina* and *I. pallidicremea* is very low (0.2–0.8%). Operational approaches that rely on ITS sequence dissimilarity (genetic distance thresholds) are not sufficient to distinguish these two species. The genetic distance at the *rpb2* locus is higher than in the ITS comparison (1.2–1.8%). Phylogenetic analyses of multiple loci serve to delineate the two species.

The collection HRL2223 referred to as *I. "lilacina"* (FIG. 1) was recorded from Montreal, Quebec at the Morgan Arboretum under planted *Abies*, *Salix*, and *Populus*. Despite its lilac coloration, the species is not closely related to the *I. lilacina* subgroup. We cannot exclude the possibility that this lilac colored taxon was introduced from outside North America. Phylogenetic analysis of molecular data from the sample strongly suggests a close relationship with a sample labeled *I. "lilacina"* from Sweden (EL12605).

A rare secondary metabolite, an ergostane triterpenoid, was reported from a culture of *I. lilacina* by Liu et al. (2014). The collection from which the culture was produced should be examined and placed within a phylogenetic context to confirm the identification.

Inocybe ionocephala Matheny, sp. nov. FIGS. 3E–F, 4E–F

MycoBank: MB822202

Typification: USA. CALIFORNIA: Mendocino Woodlands Camp area, Mycological Society of San Francisco Foray (39.3311, -123.7349), on soil in mixed woods including *Pseudotsuga*, *Notholithocarpus*, *Tsuga*, *Arbutus*, *Sequoia*, 15 Nov 2008, *P.B. Matheny PBM3049* (**holotype** TENN 062799). GenBank ITS = KY990551; 28S = KY990504; *rpb2* = MF416422.

Etymology: *ionocephala* (Greek), *ion*- purple, -*cephala* head, in reference to the pale lilac to light grayish lilac margin of the pileus.

Diagnosis: *Inocybe ionocephala* differs from *I. lilacina*, *I. pallidicremea*, and *I. sublilacina* by the larger basidiomata, less intense lilac coloration of the pileus, and the white stipe with a white base.

Description: Pileus 15–35 mm wide, obtusely conical with an obtuse (to broad) umbo, expanding with age but retaining umbo, margin incurved to decurved; surface slightly sticky or subviscid, smooth an unbroken over the disc, silky-fibrillose towards the margin, velipellis absent; center cream, brownish yellow, to light brown (5B4), margin pale lilac to light grayish lilac (14B2–B1); context white, thick, odor spermatic. Lamellae adnexed to sinuate, close with several tiers of lamellulae, light gray to avellaneous, becoming brown with age, edges pallid-fimbriate, ventricose. Stipe 25–45 × 4–7 mm at the apex, even or swollen at the base and up to 10 mm wide, cortina fugacious, apex pruinose, elsewhere finely-fibrillose, white throughout, apparently white even when young, context not observed.

Basidiospores 7.5–*8.5*–9.5(–10) × 4.5–*5.0*–5.5 µm, Q = 1.45–*1.68*–1.80 (n=31/2), smooth, subamygdaliform or elliptical with bluntly pointed or rounded apices, apiculus small but distinctive, yellowish brown in KOH. Basidia 25–30 × 8–9 µm, 4-sterigmate, clavate, hyaline. Pleurocystidia 58–70 × 12–19 µm, fusiform to fusiform-ventricose, less often subcylindrical, apices obtuse and crystalliferous, tapered towards the base, thick-walled (1.5–2.5 µm) or occasionally only slightly thick-walled (ca. 1.0 µm), hyaline. Cheilocystidia similar to pleurocystida, often shorter, mixed with hyaline paracystidia. Pileipellis a compact interwoven cutis of cylindrical hyphae, these thin-walled, smooth, hyaline, mostly 5–10 µm wide. Caulocystidia 79–108 × 10–11 µm, present on upper 1/8th of stipe surface (absent below), long and narrow ranging from slenderly fusiform to cylindrical, mixed with cauloparacystida and other intermediate clavate to subcylindrical cells; lower part of stipe covered with a superficial layer of hyaline, cylindrical, thin-walled, hyphae, mostly 5 × 12 µm wide. Clamp connections present.

457 *Ecology and distribution*: In small clusters or scattered singly on soil in the coastal redwood zone between Mendocino and San Mateo counties, northern California; associated with *Pseudotsuga*, *Notholithocarpus*, *Tsuga*, and/or *Arbutus*. Occurring Nov–Jan.

460 *Other specimens examined*: USA: CALIFORNIA: San Mateo Co., Butano State Park, Jackson Flat Trail (37.2227, -122.3033), on soil under *Pseudotsuga* in mixed woods, 2 Jan 1988, *M.T. Seidl MTS2488* (UC). Mendocino Co., Caspar, Caspar Little Lake Rd. (39.3600, -123.7860), scattered singly on soil under *Pseudotsuga*, *Notholithocarpus*, *Rhododendron*, 26 Dec 2001, *P.B. Matheny PBM2275* (WTU). Mendocino Co., Mendocino Woodlands Camp Area, Mycological Society of San Francisco Foray (39.3311, -123.7349), on soil in mixed woods including *Pseudotsuga*, *Notholithocarpus*, *Tsuga*, *Arbutus*, *Sequoia*, 15 Nov 2008, *P.B. Matheny PBM3043* (TENN 062794). Point Reyes National Seashore, Point Reyes Mycoblitz, collection route Stew (38.0666, -122.8844), 10 Dec 2005, *PtR21* (UC1859629). Point Reyes National Seashore, Point Reyes Mycoblitz, collection route OLEMA2 (38.0435, -122.7905), 10 Dec 2005 *PtR96* (UC1859626).

471 *Notes*: *Inocybe ionocephala* can be distinguished from other North American species in the *I. lilacina* subgroup by the light grayish lilac pileus with a brownish disc and often robust stipe that is white throughout. Other species in the group feature a lilac colored stipe when young but differ especially by the yellow to cream-colored stipe base. Collections cited by Nishida (1989) as *I. geophylla* var. *lilacina* most likely represent *I. ionocephala* as these originated from northern California under conifers, but molecular confirmation is lacking.

477 The description of *I. lilacina* in Siegel and Schwarz (2016), which corresponds well with *I. ionocephala* in terms of the white stipe base, basidiome size, and geographic distribution, states the stipe is pale lilac-gray and the lamellae pale lilac-gray in youth. These features should

be carefully examined in young material of *I. ionocephala*, as our documentation of multiple collections found the stipe to be consistently white throughout (including the base) and the young lamellae as light gray.

The photo of *I. lilacina* depicted under *Pinus* in Desjardin et al. (2015) in their California mycoflora more closely resembles the concept of *I. pallidicremea* because of the smaller basidiome size and lilac tinged stipe compared to *I. ionocephala*, which produces larger basidiomes and has an entirely white stipe.

Inocybe sublilacina Matheny & A. Voitk, sp. nov. FIGS. 3G–H, 4G–H

MycoBank: MB822203

Typification: UNITED STATES. COLORADO: Routt Co., Keystone, Montezuma Rd. (39.6081, -105.9228), on soil under *Picea*, 2775 m, 9 Aug 2005, *P.B. Matheny PBM2730* (**holotype** TENN 062542). GenBank 28S = KY990519; *rpb2* = MF416430.

Etymology: *sublilacina* (Latin), *sub*- almost, -*lilacina* lilac, so named because of the similar morphological appearance to *I. lilacina*.

Diagnosis: Most similar in morphology to *I. pallidicremea* but best distinguished from it by mostly somewhat larger and elliptical basidiospores and genetic divergence at ITS, 28S, and *rpb2* loci.

Description: Pileus 10–28 mm wide, conical at first but expanding with age, developing an obtuse to subacute umbo, margin incurved at first becoming decurved; surface dry to slightly tacky, finely-fibrillose at first and smooth and unbroken over the center, becoming silky-fibrillose to weakly rimose towards the margin with age; lilac at first (14C6–C5–C4) mostly throughout except at the disc that may be tinged yellowish or brownish yellow, the umbo becoming brownish with age and the margin fading to purplish white (14A2–B2), or the center pallid due to a heavy velipellis and the margin fading to brown; context not observed, odor spermatic. Lamellae adnexed to sinuate, moderately close; whitish to grayish with lilac tints when young, becoming grayish to brown; edges indistinctly pallid-fimbriate, ventricose. Stipe 17–35 × 3–6 mm at the apex, base slightly swollen and up to 7–8 mm wide; cortina fugacious; surface silky-fibrillose, tacky or subviscid, pruinose at the apex; colored like the pileus when young except for the stipe base, which is yellowish or cream-colored, in age fading to whitish mixed with streaks of pinkish-lilac; context not observed.

Basidiospores 8.0–*9.4*–10.5 × 5.0–*5.7*–6.5 μm, Q = 1.38–*1.65*–1.91 (n=63/3), smooth, elliptical with rounded apices or (sub)amygdaliform with bluntly pointed apices, at times with a slight ventral depression, apiculus small but distinctive, yellowish brown. Basidia 24–28 × 7–10 μm, 4-sterigmate (occasionally 2-sterigmate), clavate, hyaline. Pleurocystidia 50–75 × 11–14 μm, fusiform to subcylindrical, apices obtuse and crystalliferous; thick-walled (mostly 2.0–3.0 μm), pale yellow to hyaline. Cheilocystidia similar to pleurocystida, often shorter, mixed with hyaline paracystidia. Pileipellis a compact interwoven cutis of cylindrical hyphae, these thin-walled, smooth, hyaline, mostly 5–12 μm wide, subhyaline to light ochraceous-buff in mass. Caulocystidia 40–60 × 14–19 μm, similar to hymenial cystidia but slightly wider, fusiform to ventricose, at times thin-walled, mixed with cauloparacystidia or shorter clavate to cylindrical cells, present at only the extreme apex of the stipe. Clamp connections present.

Ecology and distribution: Singly on soil under *Picea*, *Abies*, *Pinus* at high elevation or high latitude, Newfound and Labrador and Colorado (type). Occurring Aug–Sep.

Other specimens examined: CANADA. NEWFOUNDLAND & LABRADOR: Gros Morne National Park, Stuckless Pond (49.4299, -57.7103), 18 Sep 2004, *A. Voitk GM5-302*

(TENN 071464). USA. COLORADO: Keystone, River Run Lodge, on soil under *Picea*, ca. 2800 m, 8 Aug 2005, *P.B. Matheny PBM2716* (TENN 062531).

Notes: *Inocybe sublilacina* is molecularly and microscopically distinct from *I. pallidicremea*, which it otherwise closely resembles. Phylogenetic analyses of three loci (ITS, 28S, *rpb2*), however, readily separate *I. sublilacina* and *I. pallidicremea* as different phylogenetic species. The two are very similar morphologically, however, the basidiospores of *I. sublilacina* are slightly larger on average than those of *I. pallidicremea*, and the basidiospores are more often elliptic in outline. Evenson (1997, as *I. geophylla* var. *lilacina*) ascribes lilac tints to the immature or young lamellae of Colorado specimens, but we are fairly certain this species lacks this feature after examination of numerous specimens from DBG. Both *I. sublilacina* and *I. pallidicremea* occur in Newfoundland and Labrador and Colorado as confirmed by DNA sequencing. Examination of additional interior western U.S. collections attributed to *I. lilacina* confirms their status as *I. pallidicremea* (SUPPLEMENTARY FIG. 1). Comparatively, *I. sublilacina* is rare.

KEY TO NORTH AMERICAN SPECIES OF THE INOCYBE LILACINA SUBGROUP

1. Stipe and stipe base white, robust, up to 10 mm wide; occurring in northern California in the coastal redwood zone ..... *I. ionocephala*

1. Stipe lilac or with lilac streaks, fading to whitish with age, base yellowish or cream-colored, more slender than above, up to 6 mm wide; occurring elsewhere and in different habitats 2

2. Pileus center persistently dark violet to dark purple when fresh, these colors not completely fading; stipe 2–3 mm thick at the apex

I. lilacina

2. Pileus center yellowish or becoming brownish-yellow, yellowish-brown, brown, or pallid, lilac completely fading; stipe 3–6 mm wide at the apex 3

3. Basidiospores on average <5.5 μm wide, mostly amygdaliform in outline; widely distributed, in northern and western regions of North America, common *I. pallidicremea*

3. Basidiospores on average >5.5 μm wide, mostly elliptical in outline; patchily distributed, known only from eastern Canada and the Rocky Mountains, uncommon *I. sublilacina*

DISCUSSION

This is the first treatment to revise the taxonomy of species in the *I. geophylla* group or subsect. *Geophyllinae* from North America within a molecular phylogenetic framework. Overall, nearly 30 species-level lineages that correspond to phylogenetic species were detected mainly from North America and Europe, increasing considerably the taxonomic diversity of the group. One particular well-supported subgroup surrounds the putative cosmopolitan species *I. lilacina* that became the focus of this study. Phylogenetic analysis of multigene data (FIG.1) recovered up to nine phylogenetic species within the broadly morphologically recognized but polyphyletic *I. lilacina*. Several of these have been shown to represent distinct morphological and phylogenetic species that occupy different geographical regions in North America.

European works have reported the occurrence of *I. lilacina* or *I. geophylla* var. *lilacina* since the late 1800s, however, our molecular analyses based on current sampling have yet to confirm the presence of *I. lilacina* in Europe. At least two different European clades ascribed to *I. lilacina* have been detected, neither of which groups with North American collections of *I. lilacina* (FIGS. 1, 2). New investigations of violet or lilac pigmented taxa described from Europe such as *I. geophylla* var. *violacea* (Pat.) Sacc. and *I. geophylla* var. *amethystina* Overeem, as well as taxa referred to by Heim (1931), are needed.

Future systematic revisions are also required to clarify the taxonomy and status of North American materials referred to as *I. geophylla*, which are highly polyphyletic, and unique but poorly known taxa such as *I. agglutinata*, *I. armeniaca* Huijsman, *I. fuscicothurnata*, *I. fuscodisca*, *I. insinuata*, *I. pudica*, *I. virgata*, *I. sambucella* G.F.Atk., and *I. whitei* (Berk. & Broome) Sacc., as well as lilac-pigmented taxa outside the *I. lilacina* subgroup.

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LEGENDS and FOOTNOTES

Figure 1. ML phylogeny of the *I. geophylla* group (in black bracket) based on combined 28S+*rpb2* nucleotide sequences. Numbers above or below branches are bootstrap proportions >50%. Branches that are thickened received a posterior probability >0.95. The *I. lilacina* subgroup is indicated in a box and is recovered with significant measures of branch support. *Inocybe kauffmanii*, used to root the tree, is pruned from the figure. The scale bar indicates the expected number of substitutions per site.

Figure 2. ML phylogeny of the *I. lilacina* subgroup based on combined ITS+28S+*rpb2* nucleotide sequences. Numbers above branches are bootstrap proportions >70%. Branches that are thickened received a posterior probability >0.95. The scale bar indicates the expected number of substitutions per site.

Figure 3. Basidiomes of the *Inocybe lilacina* subgroup in North America. A. *Inocybe pallidicremea* (*PBM2448*). B. Faded specimens of *I. pallidicremea* (*PBM1743*). C. *Inocybe lilacina* (*PBM3982*). D. *Inocybe lilacina* (*PBM3940*), photo B.P. Looney. E. *Inocybe ionocephala* (*PBM3049* holotype). F. *Inocybe ionocephala* (*UC1859626*), photo K. Peay. G. *Inocybe sublilacina* (*PBM2730* holotype). H. *Inocybe sublilacina* (*GM5-302*), photo A. Voitk. Bars = 10 mm.

Figure 4. Line drawings of pleurocystidia and basidiospores of four North American species in the *I. lilacina* subgroup. A–B. Pleurocystidia and basidiospores of *I. pallidicremea* (*PBM2448*). C–D Pleurocystidia and basidiospores of *I. lilacina* (*PBM3940*). E–F. Pleurocystidia and basidiospores of *I. ionocephala* (*PBM3049* holotype). G–H. Pleurocystidia and basidiospores of *I. sublilacina* (*PBM2730* holotype). Bars = 10 μm.

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Figure1

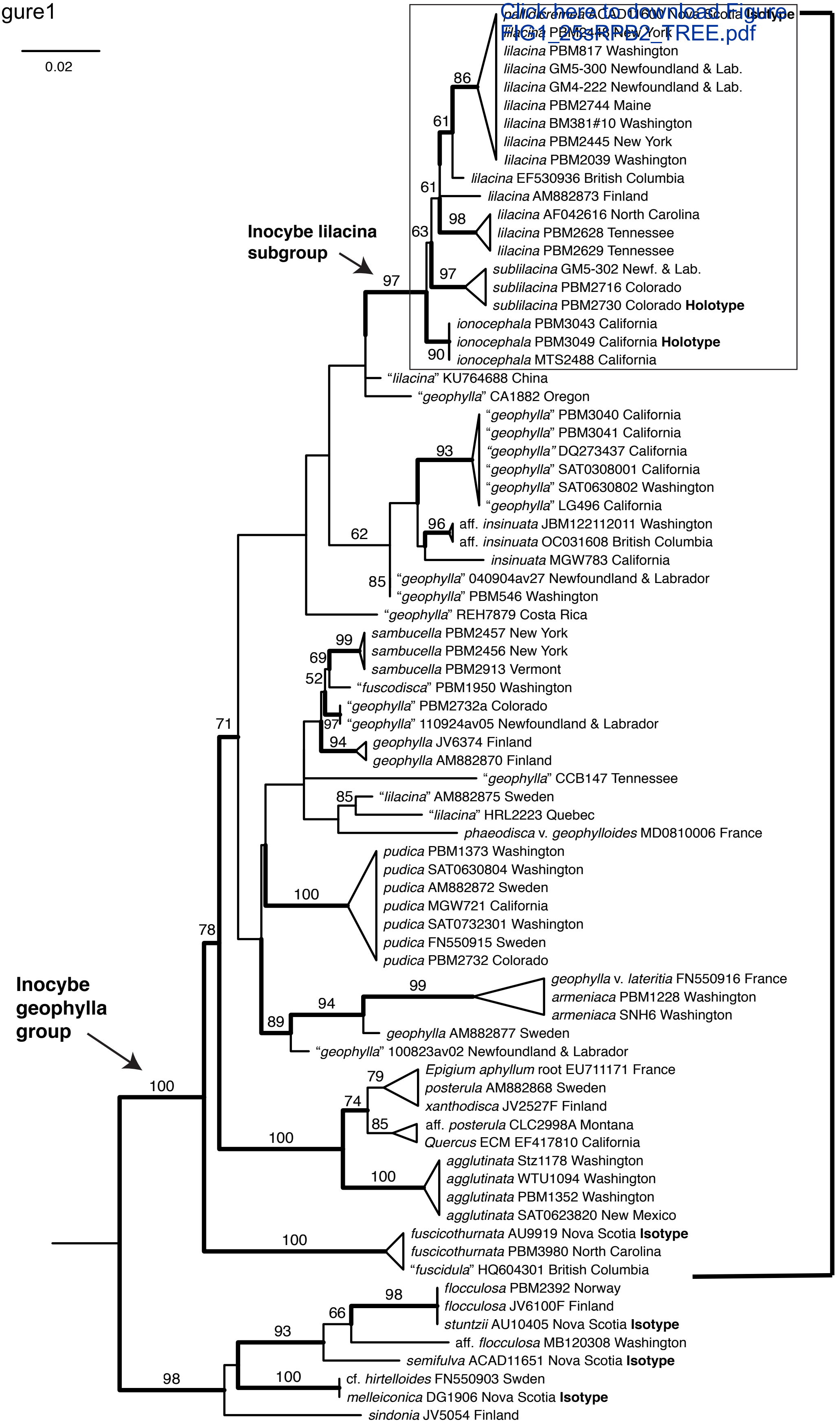
0.02
Inocybe lilacina subgroup
Inocybe geophylla group
pallidicremea ACAD11600 Nova Scotia Isotype
lilacina PBM2448 New York
lilacina PBM817 Washington
lilacina GM5-300 Newfoundland & Lab.
lilacina GM4-222 Newfoundland & Lab.
lilacina PBM2744 Maine
lilacina BM381#10 Washington
lilacina PBM2445 New York
lilacina PBM2039 Washington
lilacina EF530936 British Columbia
lilacina AM882873 Finland
lilacina AF042616 North Carolina
lilacina PBM2628 Tennessee
lilacina PBM2629 Tennessee
sublilacina GM5-302 Newf. & Lab.
sublilacina PBM2716 Colorado
sublilacina PBM2730 Colorado Holotype
ionocephala PBM3043 California
ionocephala PBM3049 California Holotype
ionocephala MTS2488 California
"lilacina" KU764688 China
"geophylla" CA1882 Oregon
"geophylla" PBM3040 California
"geophylla" PBM3041 California
"geophylla" DQ273437 California
"geophylla" SAT0308001 California
"geophylla" SAT0630802 Washington
"geophylla" LG496 California
aff. insinuata JBM122112011 Washington
aff. insinuata OC031608 British Columbia
insinuata MGW783 California
"geophylla" 040904av27 Newfoundland & Labrador
"geophylla" PBM546 Washington
"geophylla" REH7879 Costa Rica
sambucella PBM2457 New York
sambucella PBM2456 New York
sambucella PBM2913 Vermont
"fuscodisca" PBM1950 Washington
"geophylla" PBM2732a Colorado
"geophylla" 110924av05 Newfoundland & Labrador
geophylla JV6374 Finland
geophylla AM882870 Finland
"geophylla" CCB147 Tennessee
"lilacina" AM882875 Sweden
"lilacina" HRL2223 Quebec
phaeodisca v. geophylloides MD0810006 France
pudica PBM1373 Washington
pudica SAT0630804 Washington
pudica AM882872 Sweden
pudica MGW721 California
pudica SAT0732301 Washington
pudica FN550915 Sweden
pudica PBM2732 Colorado
geophylla v. lateritia FN550916 France
armeniaca PBM1228 Washington
armeniaca SNH6 Washington
geophylla AM882877 Sweden
"geophylla" 100823av02 Newfoundland & Labrador
Epigium aphyllum root EU711171 France
posterula AM882868 Sweden
xanthodisca JV2527F Finland
aff. posterula CLC2998A Montana
Quercus ECM EF417810 California
agglutinata Stz1178 Washington
agglutinata WTU1094 Washington
agglutinata PBM1352 Washington
agglutinata SAT0623820 New Mexico
fuscicothurnata AU9919 Nova Scotia Isotype
fuscicothurnata PBM3980 North Carolina
"fuscidula" HQ604301 British Columbia
flocculosa PBM2392 Norway
flocculosa JV6100F Finland
stuntzii AU10405 Nova Scotia Isotype
aff. flocculosa MB120308 Washington
semifulva ACAD11651 Nova Scotia Isotype
cf. hirtelloides FN550903 Swden
melleiconica DG1906 Nova Scotia Isotype
sindonia JV5054 Finland
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Figure2

Click here to download Figure FIg2_ITS_28S_rpb2_MLtree.pdf

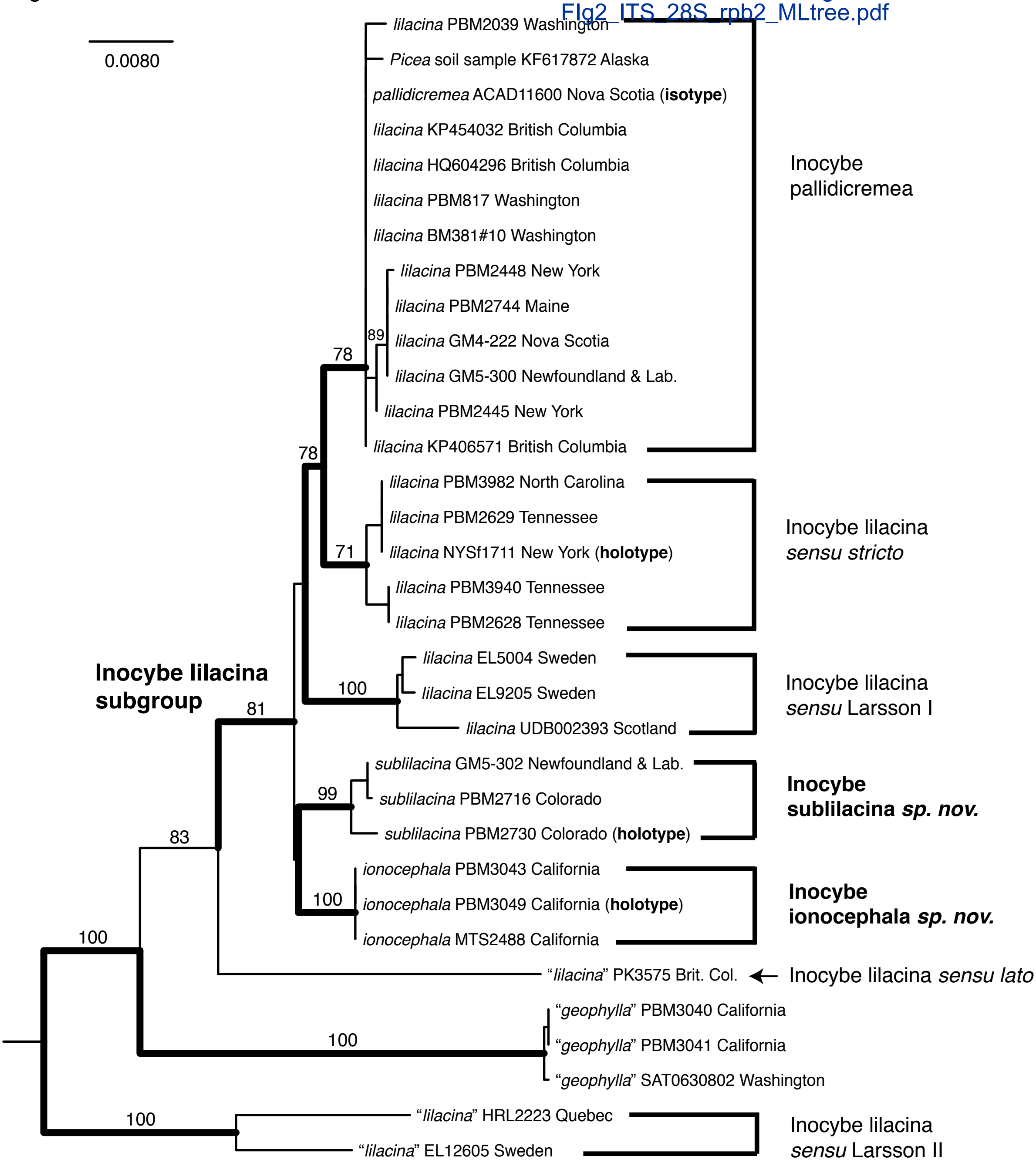
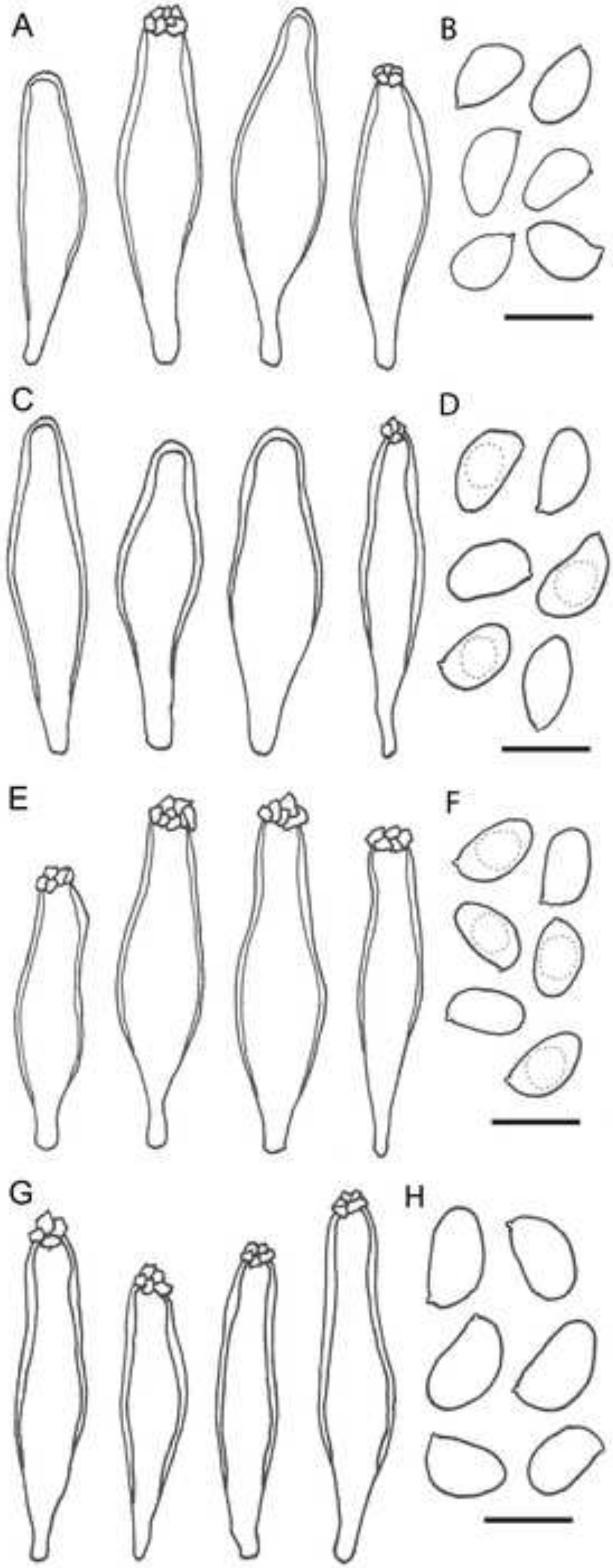


Figure3 Click here to download Figure FIG3_PHOTO_PLATE_2b.tif

Figure4

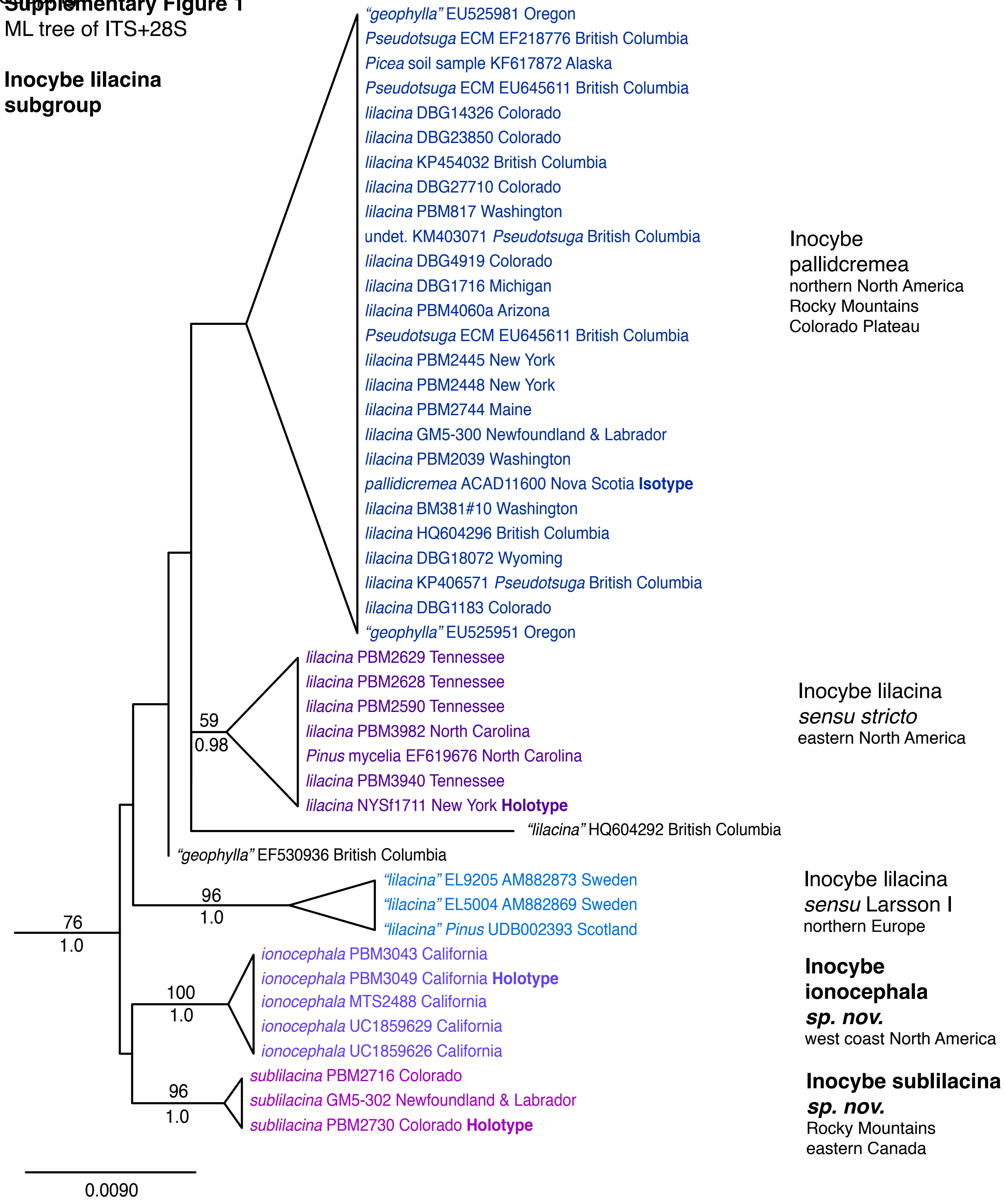
Click here to download Figure Fig4_LINE_DRAWINGS.tif



SuppFig1

Supplementary Figure 1
ML tree of ITS+28S

Inocybe lilacina subgroup



Supplementary Figure 1. ML phylogeny of the *Inocybe lilacina* subgroup based on 51 taxa and ITS+28S sequences. ML bootstrap values >50% are located above branches and Bayesian posterior probabilities >0.95 below branches. Outgroups have been pruned from the tree.

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Table 1. DNA sequences used in this study. Newly released sequences are highlighted in bold.

Taxon	**Collection (Herbarium)**	**Geographic origin**	**GenBank DNA sequences**		
			ITS	**nLSU-rRNA**	***rpb2***
I. agglutinata	WTU 1094	Washington	**KY990521**	**KY990479**	—
	Stz1178 (WTU)	Washington	**KY990522**	**KY990480**	—
	PBM1352 (WTU)	Washington	—	AY038312	AY509113
	SAT0623820 (WTU)	New Mexico	**KY990523**	**KY990481**	—
I. armeniaca	PBM1228 (WTU)	Washington	—	AY380367	AY337363
	SNH6 (WTU)	Washington	**KY990524**	**KY990482**	—
	EL24606 as *I. geophylla* var. *lateritia*	France	FN550916	FN550916	—
I. fuscicothurnata	PBM3980 (TENN 068940)	North Carolina	**MF487844**	**KY990485**	**MF416408**
	AU9919 (**isotype** WTU)	Nova Scotia	**KY923020**	**KY923039**	—
I. "*fuscodisca*"	PBM1950	Washington	—	AY380376	AY337376
I. geophylla I	EL9005	Sweden	AM882870	AM882870	—
	JV6374 (WTU)	Finland	—	AY380377	AY333777
I. geophylla II	EL8003	Sweden	AM882877	AM882877	—
I. "*geophylla*"	SAT0308001 (WTU)	California	**KY990530**	**KY990486**	—
	WT11	California	—	DQ273437	—
	MTS2811 (UC)	California	**KY990531**	—	—
	PBM3040 (TENN 062791)	California	**KY990532**	**KY990488**	**MF416409**
	PBM3041 (TENN 062792)	California	**KY990533**	**KY990489**	**MF416410**
	LG496 (WTU)	California	**KY990534**	**KY990490**	—
	SAT0630802 (TENN 071578)	Washington	**KY990535**	JN974952	**MF416411**
I. "*geophylla*"	CA1882 (WTU)	Oregon	**KY990536**	JN974951	—
I. "*geophylla*"	PBM546 (WTU)	Washington	**KY990537**	**KY990491**	—
	040904av27	Newfoundland and Labrador	**KY990538**	**KY990492**	—
I. "*geophylla*"	REH7879	Costa Rica	**KY990539**	JN974953	—
I. "*geophylla*"	110924av05 (TENN 070836)	Newfoundland & Labrador	**KY990542**	**KY990496**	**MF416415**
	PBM2732a (TENN 062544)	Colorado	**KY990543**	**KY990497**	**MF416416**
I. "*geophylla*"	CCB147 (TENN 068276)	Tennessee	**KY990544**	**KY990498**	**MF416417**
I. "*geophylla*"	100823av02 (TENN 071463)	Newfoundland & Labrador	**KY990545**	**KY990499**	**MF416418**
I. insinuata	MGW783 (TENN 063977)	California	**KY990546**	**KY990500**	**MF416419**
I. aff. *insinuata*	JMB122111-04 (TENN 066938)	Washington	**KY990547**	**KY990501**	**MF416420**
	OC031608 (TENN 063620)	British Columbia	**KY990548**	**KY990502**	—
I. ionocephala sp. nov.	MTS2488 (UC)	California	**KY990549**	JN974950	—
	PBM3043 (TENN 062794)	California	**KY990550**	**KY990503**	**MF416421**
	PBM3049 (**holotype** TENN 062799)	California	**KY990551**	**KY990504**	**MF416422**
	UC 1859626	California	**MF490439**	—	—
	UC 1859629	California	**KY990552**	—	—
I. lilacina	Peck s.n. (**holotype** NYSf1711)	New York	**MH024860**	—	—
	JM96/25	North Carolina	—	AF042616	—
	Pinus mycelia	North Carolina	EF619676	—	—
	PBM3982	North Carolina	**KY990527**	—	—

	(TENN 068443)				
	TFB12747 (TENN 061204)	North Carolina	**KY990526**	—	—
	PBM2590 (TENN 062429)	Tennessee	EU523556	—	—
	PBM2628 (TENN 062463)	Tennessee	**KY990525**	**KY990483**	**MF416406**
	PBM2629 (TENN 062464	Tennessee	**KY990528**	**KY990484**	**MF416407**
	PBM3940 (TENN 068443)	Tennessee	**KY990529**	—	—
	VRH13 (TENN 073103)	Tennessee	**MG663234**	—	—
I. lilacina sensu Larsson I	EL9205	Finland	AM882873	AM882873	—
	EL175-06 as *I. geophylla*	Scotland	UDB 002393	—	—
	EL5004 as *I. geophylla* var. *lilacina*	Sweden	AM882869	AM882869	—
I. lilacina sensu Larsson II	EL12605	Sweden	AM882875	AM882875	—
I. "*lilacina*"	PK3575 (UBC)	British Columbia	HQ604292	HQ604292	—
I. "*lilacina*"	Y55	China	—	KU764688	—
I. pallidicremea	*Picea* soil sample 3329H20	Alaska	KF61782	—	—
	PBM4060a (TENN 071254)	Arizona	**MG429695**	—	—
	DBG 001183	Colorado	**MG429696**	—	—
	DBG 004919	Colorado	**MG429697**	—	—
	DBG 014326	Colorado	**MG429698**	—	—
	DBG 023850	Colorado	**MG429699**	—	—
	DBG 027710	Colorado	**MG429700**	—	—
	PBM2744 (TENN 062552)	Maine	**KY990553**	**KY990505**	**MF416423**
	DBG 001716	Michigan	**MG429701**	—	—
	PBM2445 (TENN 063879)	New York	—	**KY990506**	**MF416424**
	PBM2448 (TENN 062757)	New York	HQ201357	HQ201357	**MF416425**
	OSC1064044 as *I. geophylla*	Oregon	EU525951	—	—
	OSC1064214 as *I. geophylla*	Oregon	EU525981	—	—
	BM381#10 (TENN 063535)	Washington	**KY990554**	**KY990507**	—
	PBM817 (WTU)	Washington	**KY990555**	**KY990508**	—
	PBM2039 (WTU)	Washington	—	AY380385	AY337388
	DBG 018072	Wyoming	**MG429702**	—	—
	Pseudotsuga ECM	British Columbia	EU645611	—	—
	Pseudotsuga ECM	British Columbia	EF218776	—	—
	UBC F16253 as *I. geophylla*	British Columbia	EF530936	EF530936	—
	UBC F19540	British Columbia	HQ604296	HQ604296	—
	ACAD 11600 (**isotype** *I. pallidicremea*)	Nova Scotia	**KY923033**	**KY923042**	—
	GM5-300 (TENN 070835)	Newfoundland & Labrador	—	**KY990509**	**MF416426**
	GM4-222 (TENN 070832)	Newfoundland & Labrador	—	**KY990510**	**MF416427**

I. phaeodisca var. *geophylloides*	MD08100106	France	—	**KY990511**	—
I. posterula	EBJ051120	Sweden	AM882868	AM882868	—
	EM6.1	France	EU711171	EU711171	—
	JV2527F (WTU) as *I. xanthodisca*	Finland	**KY990556**	**KY990512**	—
I. aff. *posterula*	CLC2998A (TENN 069518)	Montana	**MF490440**	**KY990513**	**MF416428**
	L3BD11	California	EF417810	EF417810	—
I. pudica	MGW721 (TENN 066724)	California	**KY990557**	**KY990514**	—
	PBM2732b (TENN 062544)	Colorado	**KY990558**	**KY990515**	—
	SAT0630804 (TENN 071580)	Washington	**KY990559**	**KY990516**	—
	SAT0732301 (TENN 071579)	Washington	**KY990560**	**KY990517**	—
	PBM1373 (WTU)	Washington	—	AY038323	AY337394
	EL15905	Sweden	AM882872	AM882872	—
	SJ06012 as *I. whitei*	Sweden	FN550915	FN550915	—
I. sambucella	PBM2913 (TENN 062774)	Vermont	—	**KY990493**	**MF416412**
	PBM2456 (TENN 063623)	New York	**KY990540**	**KY990494**	**MF416413**
	PBM2457 (TENN 062431)	New York	**KY990541**	**KY990495**	**MF416414**
Inocybe sp. QUE03	HRL2223 (TENN 071128)	Quebec	**KX897427**	**KY990518**	—
I. sublilacina sp. nov.	PBM2716 (TENN 062531)	Colorado	**KY990561**	JN974949	**MF416429**
	PBM2730 (**holotype** TENN 062542)	Colorado	—	**KY990519**	**MF416430**
	GM5-302 (TENN 071464)	Newfoundland and Labrador	**KY990562**	**KY990520**	**MF416431**

28S+rpb2 alignment

ITS+28S alignment

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Data Files

lilacina_52.nxs

ITS+28S+rpb2 alignment

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lilacina_3genes.nxs