

## *Inocybe* section *Rimosae* in Utah: phylogenetic affinities and new species

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**Abstract:** Results of a study on species of *Inocybe* section *Rimosae* sensu lato in Utah are presented. Eight species, seven from the Pseudosperma clade (section *Rimosae* sensu stricto) and one from the Inosperma clade (section *Rimosae* pro parte), are documented morphologically and phylogenetically. Five of the eight species, *I. aestiva*, *I. breviterincarnata*, *I. cercocarpi*, *I. niveivelata* and *I. occidentalis*—all members of the Pseudosperma clade—are described as new from Utah and other western states. Two European species, *I. spuria* and *I. obsoleta*, are confirmed from Utah. *Inocybe aurora*, originally described from Nova Scotia, is synonymized with *I. obsoleta*. The only member of the Inosperma clade recorded from Utah is *I. lanatodisca*, a widely distributed species for which three geographical clusters were detected. The phylogenetic analyses indicate that the Pseudosperma clade includes 53 clusters or species worldwide and that the Inosperma clade includes 47 such clusters. Many of these probably correspond to undescribed species. A key to species of section *Rimosae* sensu lato from Utah is provided together with illustrations of the eight species found in the state.

**Key words:** Agaricales, Basidiomycota, Inocybaceae, North America, systematics

### INTRODUCTION

Members of *Inocybe* section *Rimosae* (Fr.) Quél. sensu lato occur commonly in the western United States. This section of the genus is challenging taxonomically and has been demonstrated to be polyphyletic (Matheny 2005, Larsson et al. 2009, Matheny et al. 2009, Ryberg et al. 2010). One group of species

belonging to the section that centers around *I. rimosa* (Bull.:Fr.) P. Kumm. is monophyletic and has been referred to as either the Pseudosperma clade (Matheny 2005, Matheny 2009, Matheny et al. 2009) or as section *Rimosae* sensu stricto (Larsson et al. 2009). This clade is characterized by a number of unifying characters that includes the lack of metuloids and pleurocystidia with smooth, radially appressed-fibrillose to rimose pilei along with smooth, elliptical to indistinctly phaseoliform basidiospores, and usually cylindrical to clavate cheilocystidia. In contrast, residual taxa of section *Rimosae* pro parte, that are related to *I. maculata* Boud. and allies cluster in a separate major clade (Maculata clade; Larsson et al. 2009) together with section *Cervicolores*. This inclusive group of clades has been referred to as the Inosperma clade (Matheny et al. 2002, Matheny and Watling 2004). Morphological characters do not always clearly separate species of the Pseudosperma and Maculata clades. Nonetheless, members of the latter typically have more distinctly phaseoliform spores, more broadly clavate cheilocystidia, and a suite of different odors when compared with members of the Pseudosperma clade.

Because species of section *Rimosae* sensu lato are challenging taxonomically and some species in the western United States have been assigned names based on European literature, phylogenetic work is needed to clarify species concepts in the section. The objectives of this paper are to assess the phylogenetic placement of samples of section *Rimosae* sensu lato from Utah relative to European species, produce descriptions for species that occur in Utah and provide a key for their identification.

### MATERIALS AND METHODS

Basidiomata collected in the field were photographed in a natural setting or against a gray card before drying. Field notes were taken while material was fresh, and color notations were made with the Munsell Soil Color Charts or The Munsell Book of Color (Munsell Color 1976, 2000). Each specimen was dried and preserved as a herbarium voucher. Microscopic study of dried specimens was carried out in the laboratory with a light microscope after rehydrating sections of tissue in 5% NH<sub>4</sub>OH. Microscopic measurements were done with oil immersion at 1000× magnification, and drawings of microscopic characters were done with the aid of a drawing tube. Spore measurements were made for spores in lateral view and are given as an average of 20 spores per collection (indicated by parentheses) with ranges. Measurements of the other cells are given

as ranges. Each of the collections examined from Utah, including the holotype of each new species described, has been accessioned into the Intermountain Herbarium (UTC) at Utah State University. Other collections studied by us not deposited at UTC have been deposited in other herbaria, abbreviations of which follow Thiers (<http://sweetgum.nybg.org/ih/>).

DNA extractions and PCR protocols follow procedures outlined in Judge et al. (2010). For DNA isolates we amplified the 5' end (ca. 1400 bp) of the nuclear large subunit ribosomal rRNA (nLSU) using primers LR0R and LR7 (<http://www.biology.duke.edu/fungi/mycolab/>) and the most variable region of the *rpb2* gene between conserved domains six and seven. To sequence the nLSU region, we used LR0R, LR7 and internal primers LR16, LR5 and LR3R. We used b6F and b7.1R to amplify and sequence *rpb2* (Matheny 2005). We also sequenced the internal transcribed spacer region, including both spacers and the 5.8S ribosomal RNA gene (ITS), using ITS1F and ITS4 for amplification and sequencing (White et al. 1990, Gardes and Bruns 1993). For collections older than 50 y, we followed DNA extraction protocols and procedures outlined in Ammirati et al. (2007) whereby the individual spacer regions were amplified and sequenced separately. Sequences were annotated with Sequencher 4.9 (Gene Codes Corp., Ann Arbor, Michigan).

Because section *Rimosae* as traditionally conceived is not monophyletic, we prepared three different data matrices for phylogenetic analysis: (i) separate nucleotide datasets (nLSU, *rpb2*) for the *Pseudosperma* clade using *I. adaequata* and *I. subhirsuta* as outgroups; (ii) separate nucleotide datasets (nLSU, *rpb2*) of the *Inosperma* clade using *I. terrigena*, *I. dulcamara*, and *I. unicolor* as outgroups; and (iii) a combined nucleotide dataset (ITS and LSU) for the *I. lanatodisca-I. maculata* f. *fulva* clade in an attempt to investigate differences between these two taxa. Selection of outgroups is based on Matheny et al. (2009).

New nLSU and *rpb2* sequences generated for this study were merged manually in separate nexus files in MacClade (Maddison and Maddison 2005) with pre-existing aligned sequences taken from these studies: Matheny et al. (2002), Matheny and Watling (2004), Matheny (2005), Larsson et al. (2009), Matheny et al. (2009), Ryberg et al. (2010) and Ryberg and Matheny (2012). nLSU and/or ITS sequences of selected members of the *Inosperma* clade were downloaded from the taxonomy database of GenBank for phylogenetic analysis of *I. lanatodisca* and *I. maculata* f. *fulva* and aligned using Clustal X 2.0.9 (Larkin et al. 2007). ITS sequences, including those from environmental samples, were compiled in this latter alignment where BLAST similarities were > 90%. Ambiguously aligned sites were removed before phylogenetic analyses. All alignments used in this study were deposited in TreeBASE (accession numbers 13489, 13490, 13491, 13492, 13493). GenBank accession numbers for sequences produced by this study are provided (SUPPLEMENTARY TABLE I). All nexus files were converted to PHYLIP format with Seaview 4.2.4 (Gouy et al. 2010) before conducting maximum likelihood (ML) analyses using RAxML 7.0.3 (Stamatakis 2006, Stamatakis et al. 2008). One thousand rapid bootstraps were conducted

for each dataset followed by a thorough ML tree search. nLSU and *rpb2* gene regions were analyzed separately.

Model selection follows that of Larsson et al. (2009) for ribosomal RNA loci and Matheny (2005) for the *rpb2* gene region, which was partitioned by codon position. The intron 4 (Matheny et al. 2007) region of *rpb2* was excluded from the *Inosperma* phylogenetic analysis due to alignment ambiguities. Intron 4 was maintained in the *Pseudosperma rpb2* data matrix due to easier alignment and modeled according to a separate partition. A single model of nucleotide substitution (GTRGAMMAI) was applied to the *I. lanatodisca-I. maculata* f. *fulva* dataset composed of a supermatrix of ITS and LSU sequence data.

## RESULTS

*Sequencing results.*—200 new sequences were produced for this study: 60 of the nLSU region, 87 of the ITS region and 53 of the *rpb2* region (SUPPLEMENTARY TABLE I).

*Species from Utah in the Pseudosperma clade.*—Thirteen positions were removed from the LSU data matrix of the *Pseudosperma* clade due to alignment ambiguities. This resulted in a data matrix of 1377 aligned nucleotide characters. Within the *Pseudosperma* clade (FIGS. 1A1, 2), several large, inclusive strongly supported subclades can be identified, three of which correspond to clades A, B and D of Larsson et al. (2009). Clade F also was recovered as monophyletic but with marginal bootstrap support. Two smaller clades or lineages, C and E, are indicated as well. Overall, 53 terminal clusters and tips can be counted that correspond to individual morphological species, cryptic species, groups of closely related species or geographic units.

Two species from Utah are found nested in the *I. rimosa* complex (FIG. 1A1), *I. aestiva* sp. nov. and *I. niveivelata* sp. nov. Four other species reported here from Utah, *I. breviterincarnata* sp. nov., *I. occidentalis* sp. nov., *I. cercocarpi* sp. nov. and *I. spuria* Jacobsson & Larsson, join with clades D, E and F of Larsson et al. (2009) (FIG. 1A2), in addition to an unclarified species from eastern North America (*I. cf. rimosa* 3). *Inocybe spuria*, *I. cercocarpi*, and *I. occidentalis* form a moderately well supported monophyletic group.

A phylogenetic tree of *Pseudosperma rpb2* sequences (FIG. 1B) is less densely sampled and missing numerous European species. However, the results are mostly consistent with the analysis of the nLSU data. The *I. rimosa* complex is recovered with strong bootstrap support, but clades B and D of Larsson et al. (2009) are joined with species from Asia, North America, Australia and Papua New Guinea with marginal bootstrap support. Like the nLSU gene tree, the three species *I. occidentalis*, *I. cercocarpi*, and

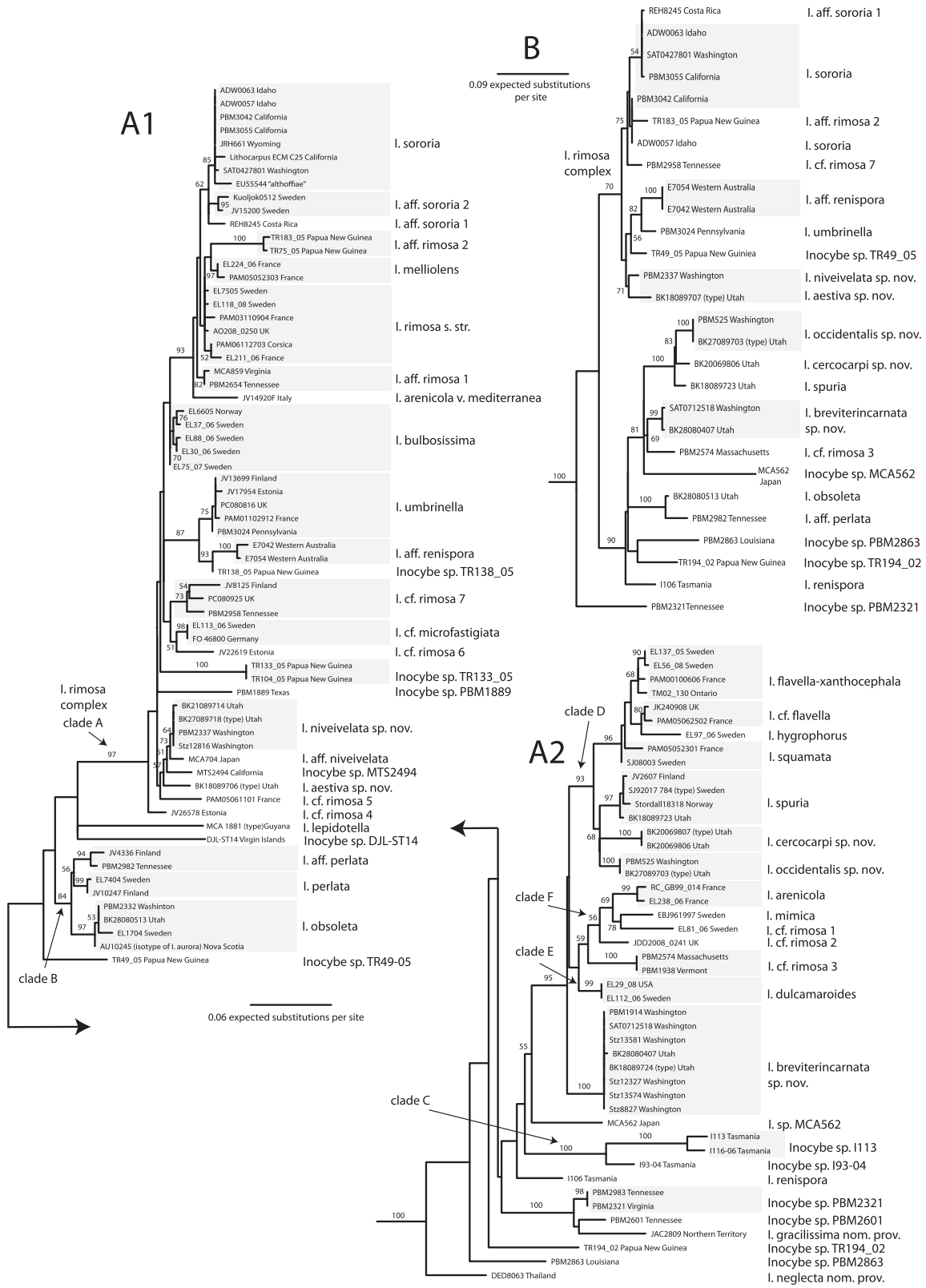


FIG. 1. Maximum likelihood trees of the *Pseudosperma* clade based on nLSU-rRNA sequences (A1–A2) and *rpb2* (B) nucleotide sequence data. The six clades recovered in Larsson et al. (2009; A–F) are indicated. Clade A corresponds to what is labeled here as the *I. rimosa* complex. Outgroups *I. adaequata* and *I. subhirsuta* (*Inosperma* clade) have been pruned. Values above or below branches indicate bootstrap proportions.

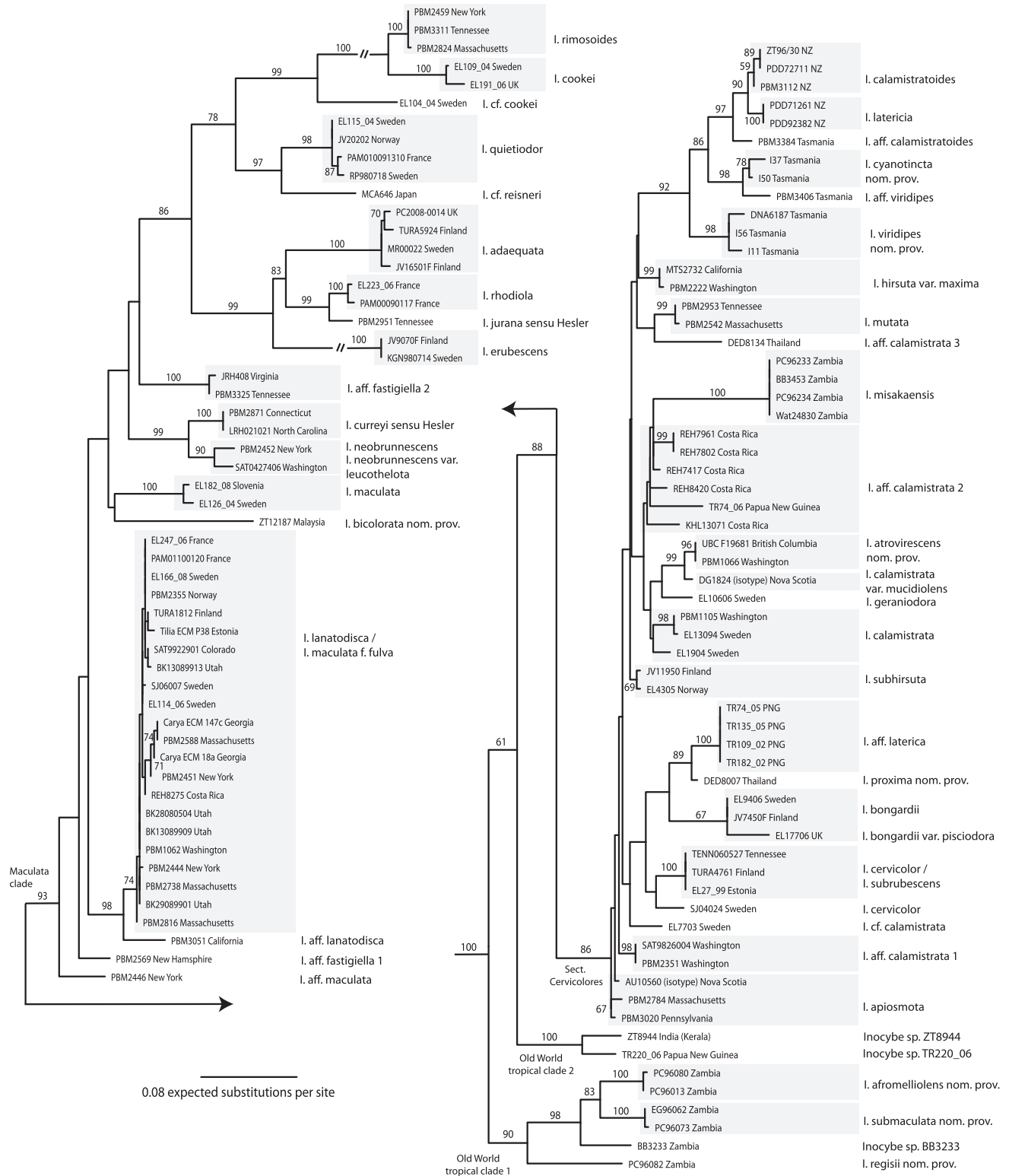


FIG. 2. Maximum likelihood tree of the *Inosperma* clade based on nLSU-rRNA nucleotide sequence data. Four major groups are recovered: two independent Old World tropical clades, section *Cervicolores* and the *Maculata* clade of Larsson et al. (2009). Outgroups *I. unicolor*, *I. terrigena* and *I. dulcamara* (*Mallocybe* clade) have been pruned. Values above or below branches indicate bootstrap proportions.

*I. spuria* form a monophyletic group with high (99%) bootstrap support.

Both phylograms indicated that the taxonomy of species in the Pseudosperma clade is complex and that a number of undescribed taxa occur worldwide within the lineage. Five undescribed taxa from Utah, and in some cases from other parts of western North America, are distinguished by molecular phylogenetic analyses, morphological characters and/or ecological characters.

*Species from Utah in the Inosperma clade.*—Similarly the Inosperma clade is divided into several well supported subclades that include at least 47 morphological species or geographic units or groups of closely related taxa. Independent analyses of nLSU and *rpb2* sequences indicated that additional undescribed species are to be found among representatives of the clade worldwide, including tropical Africa, Asia, Central America and temperate Australia (FIG. 2). Analysis of nLSU data recovered four inclusive robust monophyletic groups: the Maculata clade (Larsson et al. 2009), section *Cervicolores* and two Old World tropical clades. Analysis of *rpb2* sequences (FIG. 3) recovered similar groupings except for the placement of the tropical African species *I. misakaensis*, which lies in a position sister to the rest of the Inosperma clade.

Only one species from Utah is documented from the Inosperma clade, *I. lanatodisca* Kauffman. Representatives of *I. lanatodisca* (Maculata subclade) are common in both eastern and western North America, occur in Central America, and form a distinct group together with isolates from Europe labeled *I. maculata* f. *fulva* (FIG. 2). Resolution within the *lanatodisca-maculata* f. *fulva* clade using LSU and *rpb2* data was low, suggesting these two taxa might be conspecific.

To investigate the *lanatodisca* lineage in more detail, we analyzed a combination of available ITS and LSU data, including environmental sequences available from GenBank. A BLAST analysis of GenBank using an ITS sequence of a North American representative of *I. lanatodisca* (PBM2816, JQ408761) revealed 19 sequences with > 90% similarity not labeled *I. lanatodisca* or *I. maculata* f. *fulva*. We combined these sequences with those from collections and GenBank sequences labeled *I. lanatodisca* or *I. maculata* f. *fulva*. This exercise resulted in a supermatrix of 36 taxa and 1906 sites, all of which were included in a phylogenetic analysis using sequences of voucher PBM3051 (*I. aff. lanatodisca* from California) to root the phylogeny. As a result of this analysis, we detected three major groupings (FIG. 4) that we estimate correspond to three species

including two that are likely undescribed: *I. lanatodisca* and its variants, *I. aff. maculata* 2 (known only from Europe and southwest Asia) and *I. aff. lanatodisca* (known thus far only from California). Among the samples of *I. lanatodisca* reside three poorly supported lineages that appear to correspond to general geographic location (FIG. 4).

#### TAXONOMY

***Inocybe aestiva*** Kropp, Matheny & Hutchison, sp. nov. FIGS. 5, 13a

MycoBank MB564167

*Diagnosis:* This species differs from *I. rimosa* and from other members of the genus by its unique phylogenetic position.

*Holotype:* USA. UTAH. Cache County, Uinta-Wasatch-Cache National Forest, 19 Aug 1997, leg. B.R. Kropp, BK18-Aug-97-6 (UTC255656)

*Etymology:* *aestiva* refers to the summer fruiting habit of this taxon.

Pileus 30–65 mm diam, conical to broadly conical or nearly plane with uplifted margins, umbonate; surface appressed-fibrillose, dry, smooth, shiny, distinctly rimose with numerous whitish interstices; whitish veil remnants sometimes present at the margin; color yellowish to pale yellow toward the margins, yellow brown sometimes with coppery hues (2.5Y 8.5/4 to 10YR 6/6) toward the center. Lamellae close, adnate or adnexed, 3–5 mm deep; whitish to pale yellowish (2.5Y 8/2) when immature becoming olive yellow (2.5Y 6/6) at maturity; margins distinctly pallid. Stipe 40–70 × 5–12 mm, solid, equal, whitish, not pruinose, except lightly so at the stipe apex, the remainder fibrillose to lightly fibrillose. Context white. Odor spermatric.

Basidiospores 10.0 (11.2) 13.0 × 5.5 (6.2) 7.0 μm, smooth, ellipsoid to slightly phaseoliform. Basidia 28–34 × 10–12 μm, four-spored, clavate. Pleurocystidia none. Cheilocystidia 30–75 × 11–23 μm, numerous, thin-walled, clavate. Pileipellis a repent layer of compact, golden brown hyphae, 3–5 μm wide, some lightly encrusted. Lamellar trama of subparallel, hyaline slightly inflated hyphae 5–13 μm wide; subhymenium compact and narrow, of relatively short cells that are 3–6 μm wide. Stipitipellis at the apex consisting of nearly parallel, hyaline hyphae with a scant covering of loose hyphae, the lower stipe similar but with an abundant covering of loosely woven hyaline hyphae with some cystidioid hyphal tips. Clamps present.

*Habitat and distribution:* Fruiting during summer in montane conifer forests, Utah.

*Additional Specimens examined:* USA. UTAH. Rich County, Uinta-Wasatch-Cache National Forest, 10 Sep 1997, leg.

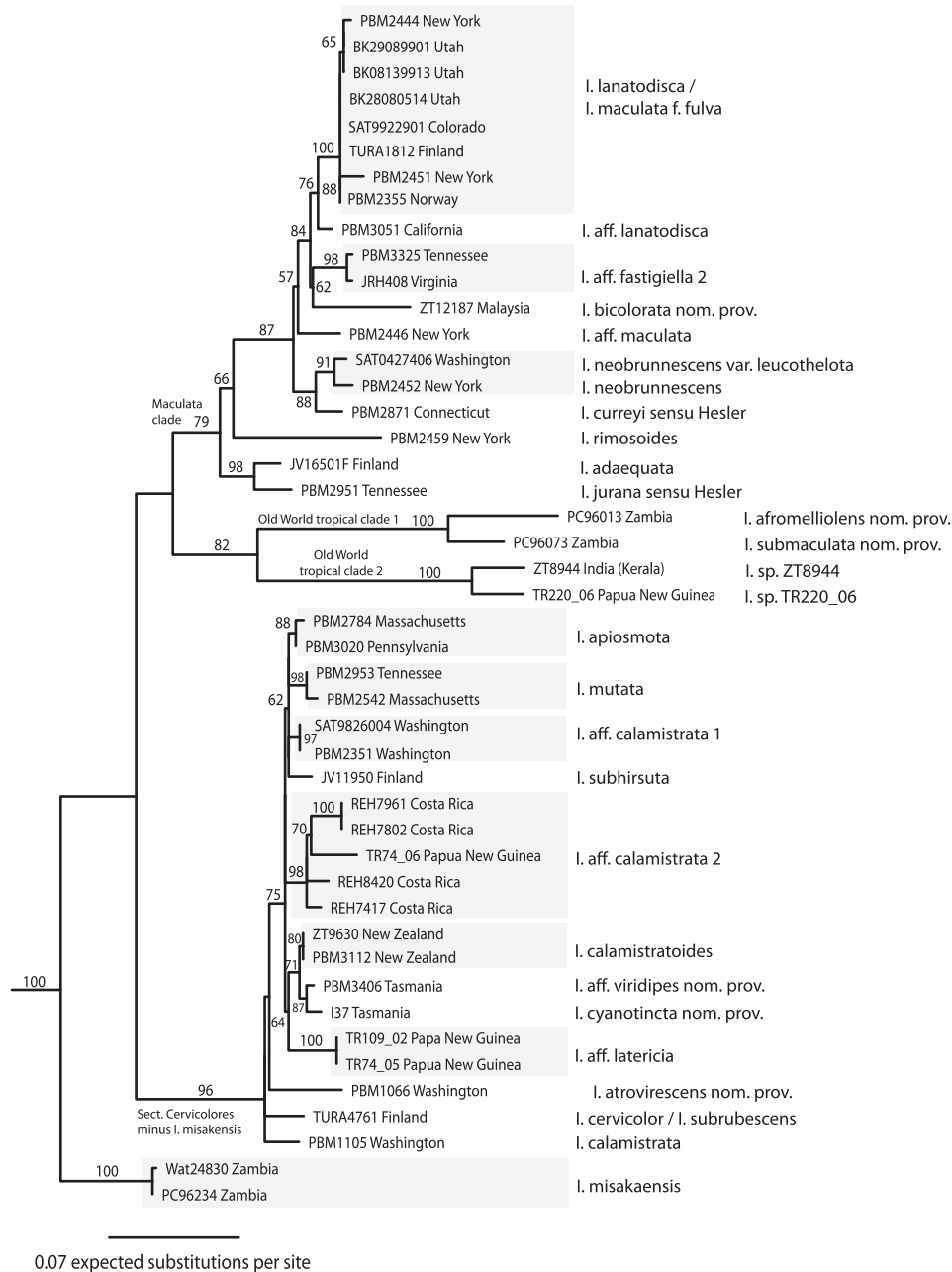


FIG. 3. Maximum likelihood tree of the *Inosperma* clade based on *rpb2* nucleotide sequence data. The *Maculata* clade, Old World tropical clade 1, Old World tropical clade 2 and section *Cervicolores* (minus *I. misakaensis*) are indicated. Outgroups *I. unicolor*, *I. terrigena* and *I. dulcamara* (Mallocybe clade) have been pruned. Values above or below branches indicate bootstrap proportions.

*B.R. Kropp, BK10-Sep-97-1* (UTC255657); *ibid.*, 21 Aug 1997, leg. *B.R. Kropp, BK21-Aug-97-17* (UTC255658); *ibid.*, 28 Aug 1995, leg. *B.R. Kropp, BK28-Aug-95-1* (UTC255659); Summit County, Uinta-Wasatch-Cache National Forest, 28 Aug 1994, leg. *B.R. Kropp, BK28-Aug-94-2* (UTC255660).

*Comments:* *Inocybe aestiva* is commonly encountered in Utah at 2500–3000 m in conifer forests. Based on its morphology, this species is often identified as *I. rimosa* and, until now, we have

routinely assigned that name to all specimens of this taxon. Our taxon represents a distinct monophyletic group independent of the other clades that correspond to material going by the name *I. rimosa*.

*Inocybe aestiva* can be recognized readily in the Rocky Mountains of North America because few other species in the *I. rimosa* complex have been found in this area that would confound its identification. However, it could be difficult to separate *I. aestiva*

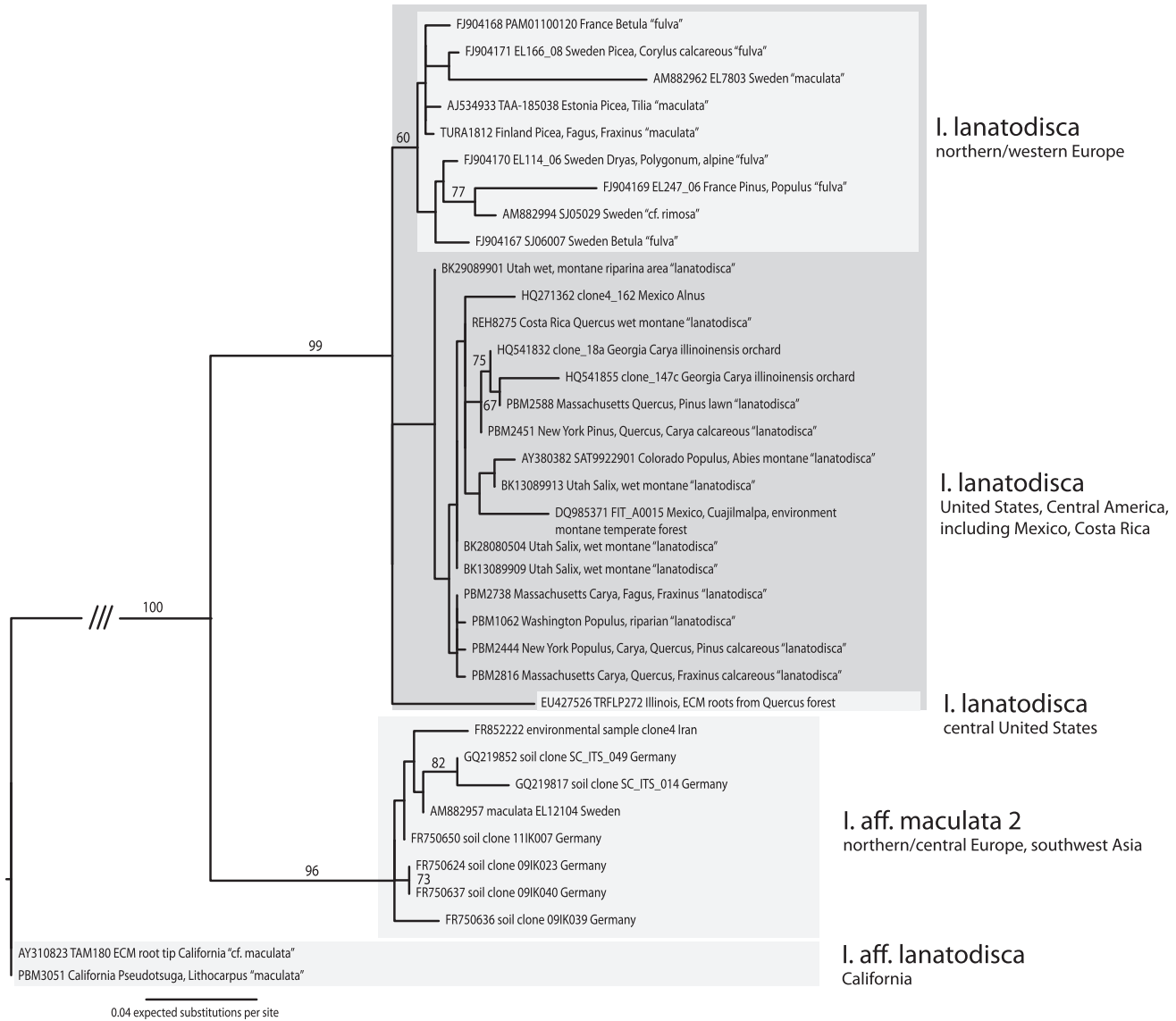


FIG. 4. Phylogram produced by a maximum likelihood analysis of combined ITS and LSU sequence data of members of the *I. lanatodisca* species lineage. Three putative populations within *I. lanatodisca* can be detected and appear to correspond by geographic area, but none receive robust bootstrap support. Values above or below branches indicate bootstrap proportions.

from members of *I. rimosa* sensu lato found in other geographical regions using morphology alone. Further work will be required to resolve this species complex worldwide, but it ultimately may prove impossible to derive a satisfactory morphological taxonomy for the group. Cryptic species may need to be recognized that can only be separated with the aid of molecular tools.

***Inocybe breviterincarnata*** Stuntz ex Kropp, Matheny & Hutchison, sp. nov. FIGS. 6, 13b  
MycoBank MB564163

**Diagnosis:** Pileus light brown. Lamellae pink when young. Basidiospores  $11.5(13.7)17.0 \times 5.5(6.6)8.5 \mu\text{m}$ .

Differs from *Inocybe niveivelata* by having lamellae that are pink when young and from *I. pseudo-orbata* by its brown pileus.

**Holotype:** USA. UTAH. Cache County, Uinta-Wasatch-Cache National Forest, 18 Aug 1997, leg. B.R. Kropp, BK18-Aug-97-24 (UTC255675).

**Etymology:** *breviterincarnata* refers to the briefly incarnate, or pinkish, color of the immature lamellae.

Pileus 9–45 mm diam, convex to broadly convex or plane with the margin sometimes uplifted in age; surface radially appressed-fibrillose, smooth at disk, not rimose or rarely slightly so in age; pale velipellis present on some but not all specimens; tan to light brown with some copper tones (7.5 YR 6/6, 10YR 6/

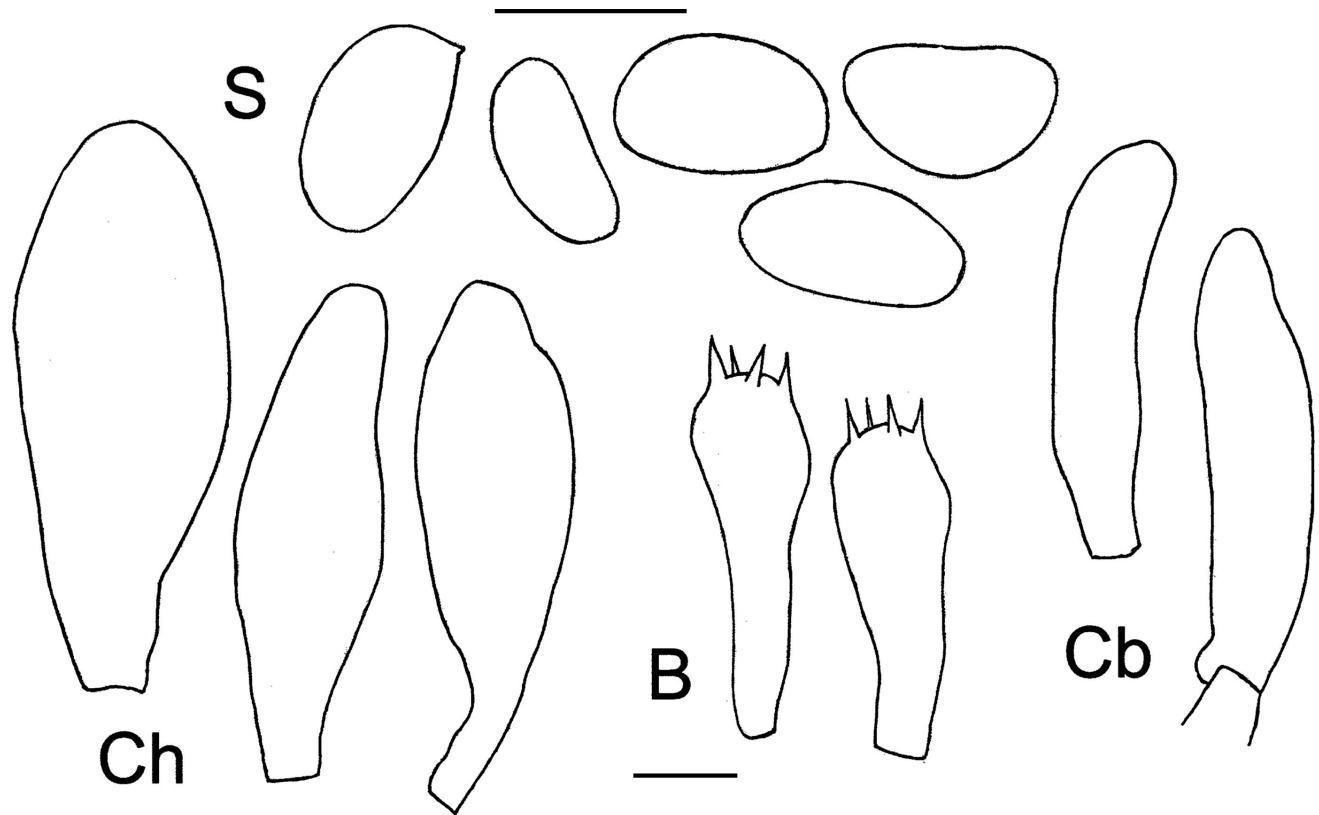


FIG. 5. Microscopic characters of *Inocybe aestiva*. S. Basidiospores. B. Basidia. Cb. Caulocystidioid hyphal tips at stipe base. Ch. Cheilocystidia. Bars = 10  $\mu$ m.

4). Lamellae close, adnexed, 2–7 mm deep, when young pink (10YR 8/3, 7.5YR 7/4) this quickly disappearing and becoming brown with age (10 YR 6/4–5/4); margins distinctly pallid. Stipe 12–45  $\times$  4–10 mm, solid, equal with base sometimes slightly enlarged; whitish, often with pale pinkish hues at the apex when young, pale brown in age (10 YR 8/4) with a white base; short-fibrillose to scurfy over the upper half of the disk with the remainder being longitudinally fibrillose. Context whitish. Odor spermiatic.

Basidiospores 11.5 (13.7) 17.0  $\times$  5.5 (6.6) 8.5  $\mu$ m, smooth, somewhat elongated and ellipsoid to phaseoliform. Basidia 35–42  $\times$  12–13  $\mu$ m, mostly four-spored, sometimes two-spored, clavate, some with a brownish internal pigment. Pleurocystidia none. Cheilocystidia 35–74  $\times$  10–17  $\mu$ m, thin-walled, clavate. Pileipellis a cutis of repent, golden brown hyphae with light incrustations, 2–4  $\mu$ m wide, in a fairly dense layer. Lamellar trama of nearly parallel enlarged smooth hyphae 5–16  $\mu$ m wide; subhymenium of more compact hyphae, 3–5  $\mu$ m wide. Stipitipellis with a few clusters of somewhat variable cystidia and cystidioid hyphal tips at the apex, otherwise of hyaline, compact hyphae covered with a loose covering of sparse interwoven hyphae. Clamps present.

*Habitat and distribution:* Fruiting in summer in montane environments with conifers and *Populus tremuloides*, Utah and Washington.

*Additional specimens examined:* USA. UTAH. Cache County, Uinta-Wasatch-Cache National Forest, 8 Jul 2004, leg. B.R. Kropp, BK8-Jul-04-2 (UTC255676); *ibid.*, 17 Aug 1998, leg. B.R. Kropp, BK17-Aug-98-10 (UTC255677); Wasatch County, Uinta-Wasatch-Cache National Forest, 28 Aug 2004, leg. B.R. Kropp, BK28-Aug-04-7 (UTC255680). WASHINGTON. County unknown, Boulder Creek Trail, 1680 m, 2 Aug 1954, leg. H.E. Bigelow (Stz8827, WTU, labeled "*I. rhodocianota*" nom. prov.); Kittitas County, Cle Elum Pine Flats, 21 May 1961, leg. Klett & D.E. Stuntz (Stz12327, WTU-F-5372 and UTC255681); Kittitas County near Ellensburg, Table Mountain, Reecer Canyon Road, 1500 m, 28 Jun 2000, leg. P.B. Matheny & S. Clark (PBM1914, WTU); Klickitat County, Fisher Hill Road, 5 May 2007, leg. S.A. Trudell (SAT0712518, TENN).

*Comments:* *Inocybe breviterincarnata* is distinctive and easily recognized in the field because of the pink lamellae that are present in young basidiomata. However, this character state is ephemeral and, as is expressed by the name "*breviterincarnata*", pink disappears as the basidiomata mature. One other species of *Inocybe* with pink lamellae is *I. pseudo-orbata* Esteve-Rav. & Garcia Blanco described from Spain (Esteve-Raventós et al. 2003). This



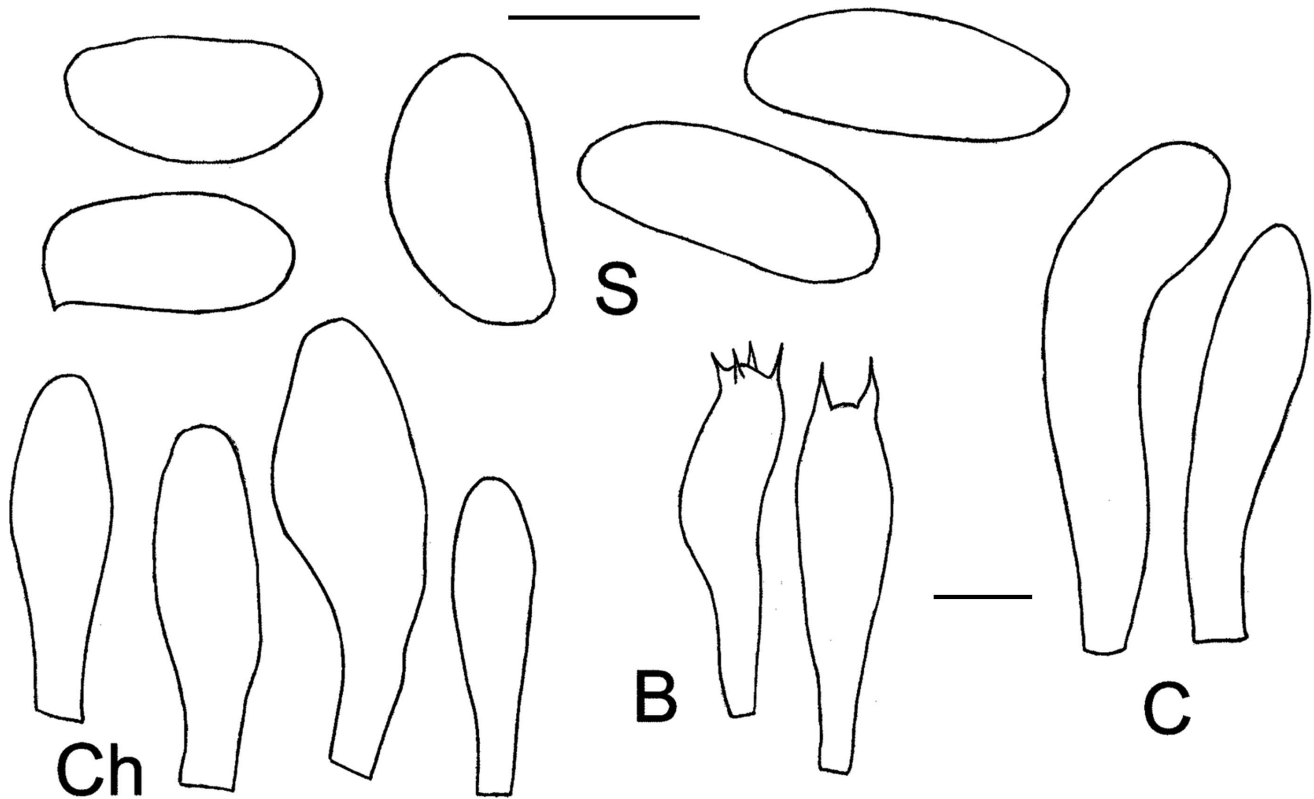


FIG. 6. Microscopic characters of *Inocybe breviterincarnata*. S. Basidiospores. B. Basidia. C. Caulocystidia. Ch. Cheilocystidia. Bars = 10  $\mu$ m.

species also has long spores similar to those of *I. breviterincarnata* but differs sharply in the larger and more robust basidiomata with whitish pilei.

The specific epithet “*breviterincarnata*” was coined by D.E. Stuntz, who never published the species but was the first to recognize it as an undescribed taxon in an unpublished manuscript. This species has been collected in Washington, and it fruits frequently in Utah at 2500–3000 m in mixed conifer-aspen forests. It has not yet been reported from other parts of western North America but, given its presence in both Utah and Washington, it can be expected in suitable environments in other western areas. Material suggested by Stuntz to be closely related to *I. breviterincarnata*, but possibly distinct from it and provisionally labeled “*I. rhodocianota*” (Stz8827), is indeed the same as *I. breviterincarnata* based on ITS and LSU sequence analysis (FIG. 1). Collections of mature specimens of *I. breviterincarnata* can be confused with *I. niveivelata* if the velipellis is relatively well developed and the lamellae are mature.

***Inocybe cercocarpi*** Kropp, Matheny & Hutchison, sp. nov. FIGS. 7, 13C  
Mycobank MB 564165

**Diagnosis:** Basidiomata robust with yellow to brownish pileus and a tendency to become caespitose.

Differs from *I. spuria* by having yellowish pileus, by its often caespitose basidiomata and by its association with *Cercocarpus ledifolius* and *Pinus monophylla*.

**Holotype:** USA. UTAH. Boxelder County, Sawtooth National Forest, 20 Jun 1998, leg. B.R. Kropp, BK20-Jun-98-7 (HOLOTYPE, UTC255669).

**Etymology:** *cercocarpi* refers to the association with *Cercocarpus ledifolius* (Rosaceae).

Pileus 30–65 mm diam, convex, to nearly plane with uplifted margins, often with a broad, low umbo at center; surface radially appressed-fibrillose, smooth, often somewhat shiny, not rimose but sometimes splitting in age; center occasionally whitish, becoming yellow to pale yellow (5Y 9/4 to 2.5Y 8.5/6) toward the margin and developing brownish hues in places, center and sometimes much of the pileus dark brown to brown (7.5YR 3/2–4/6) with age. Lamellae close, notched, 4–6 mm deep, pale yellow becoming olive yellow to light olive brown 2.5Y 5/4–6/6 to 5Y 8.5/4); margins lightly fimbriate and whitish. Stipe 40–90  $\times$  8–20 mm, equal solid, frequently but not always caespitose; white but becoming yellow to brownish yellow (2.5Y 6/6–10YR 8/8) in age sometimes due to spore deposits; not pruinose but longitudinally fibrillose or striated. Context white, with pale dull brownish hues present in the stipe context of some specimens. Odor spermatic.

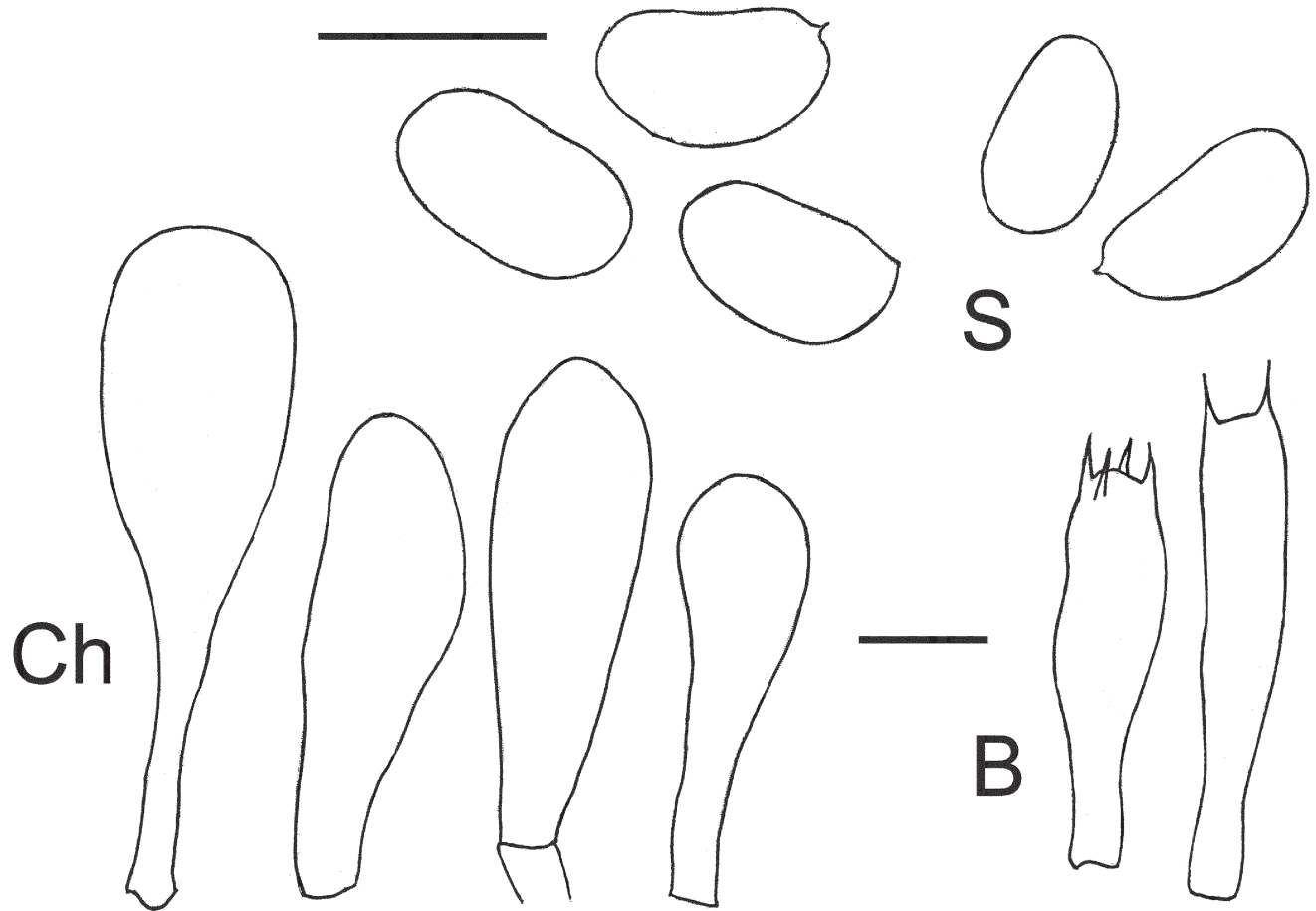


FIG. 7. Microscopic characters of *Inocybe cercocarpi*. S. Basidiospores. B. Basidia. Ch. Cheilocystidia. Bars = 10  $\mu$ m.

Basidiospores 8.0 (10.7) 12.0  $\times$  5.0 (5.6) 6.5  $\mu$ m, smooth, ellipsoid to phaseoliform. Basidia 33–43  $\times$  7–9.6  $\mu$ m, four-spored, sometimes two-spored, clavate. Pleurocystidia none. Cheilocystidia 33–60  $\times$  10–22  $\mu$ m, thin-walled, clavate. Pileipellis a thin cutis of repent, moderately compact, pale yellowish hyphae, 4.5–6.5  $\mu$ m wide. Lamellar trama subparallel to slightly interwoven hyaline hyphae, some inflated hyphae present, 4–10  $\mu$ m wide. Stipitipellis composed of appressed hyphae with some loose hyphae present over the surface of the stipe; hyphae light yellowish brown with scant light incrustations, similar at the stipe apex sometimes with scarce cystidioid hyphal tips. Clamps present.

*Habitat and distribution:* Fruiting in spring or early summer in mixed stands of *Cercocarpus ledifolius* and *Pinus monophylla*, often appearing as erumpent clumps of caespitose basidiomata, sometimes solitary, Utah.

*Additional specimens examined:* USA. UTAH. Boxelder County, Sawtooth National Forest, 20 Jun 1998, leg. B.R. Kropp, BK20-June-98-6 (UTC255670); *ibid.*, 20 Jun 1998, leg. B.R. Kropp, BK20-Jun-98-16 (UTC255671); *ibid.*, 28 Jun 1997, leg. B.R. Kropp, BK28-Jun-97-6 (UTC255672); *ibid.*, 2

Jun 2000, leg. B.R. Kropp and L.J. Hutchison, BK2-Jun-00-1 (UTC 255673); *ibid.*, 20 Jun 1998, leg. B.R. Kropp, BK20-Jun-98-1 (UTC255674).

*Comments:* *Inocybe cercocarpi* is known to date only from a single mountainside in northwestern Utah. It fruits abundantly over a large portion of the mountainside when conditions are moist, but further fieldwork is needed to determine whether it is more widely distributed. One of its putative ectomycorrhizal hosts, *Cercocarpus ledifolius*, grows in semi-arid regions across the western United States indicating that *I. cercocarpi* is potentially distributed across much of the continent. However, given the dry, rugged environments occupied by *C. ledifolius*, work on its fungal associates is challenging because fungal fruiting is unpredictable.

*Inocybe cercocarpi* is a robust species that is unusual for the genus not only because of its large size but also because the often caespitose basidiomata tend to have an erumpent fruiting habit. It is morphologically similar to *I. spuria* and is closely related to it. Yet, in spite of their close relationship, the two species are phylogenetically distinct. *Inocybe cercocarpi* differs morphologically from *I. spuria* by its yellowish pileus,

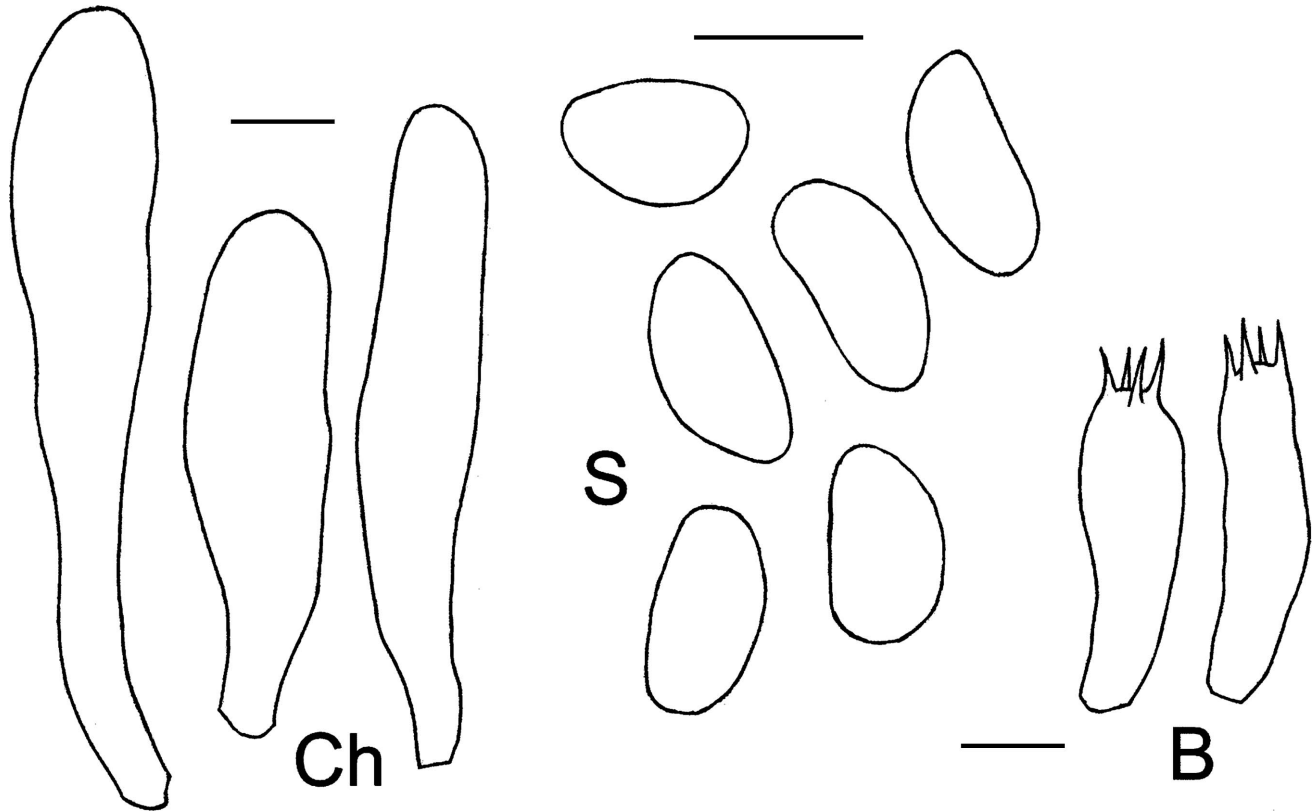


FIG. 8. Microscopic characters of *Inocybe lanatodisca*. S. Basidiospores. B. Basidia. Ch. Cheilocystidia. Bars = 10  $\mu$ m.

caespitose tendency and absence of scales on the pileus. *Inocybe cercocarpi* also differs ecologically from *I. spuria* which develops in the montane *Populus tremuloides* and mixed conifer forests.

*Inocybe lanatodisca* Kauffman, Agaricaceae of Michigan:459. 1918. FIGS. 8, 13d  
= *Inocybe maculata* f. *fulva* Bon, Docums Mycol 21(81):47. 1991.

Pileus 19–52 mm diam, conical to nearly plane, some with uplifted margins, distinctly umbonate; surface radially appressed-fibrillose, rimose, becoming radially split in age, veil remnants absent, shiny when dried; color yellow to yellow brown or orange brown (10YR 7/8) when young and ochraceous or yellowish (5Y8/6–9/4) in age. Lamellae close, narrowly attached and ventricose, 4–5 mm deep; whitish when young, becoming medium gray brown (10YR 5/4) when mature, with whitish margins. Stipe 32–65  $\times$  5–10 mm, equal, solid; white when young and smooth, remaining mostly white at maturity but with a few brownish tints; not pruinose but with a light covering of fibrils on some. Context white. Odor variable and often complex—in some collections aromatic and not spermatic, in others floral-like and aromatic when first cut then with a subtle

spermatic element, others aromatic with a green corn component, and others spermatic.

Basidiospores 8.0(9.8)11.5  $\times$  4.5(5.5)6.0  $\mu$ m, smooth, phaseoliform to ellipsoid. Basidia 29–34  $\times$  10–11  $\mu$ m, four-spored, clavate. Pleurocystidia none. Cheilocystidia 38–75  $\times$  11–16  $\mu$ m, numerous, thin-walled, clavate or at times variable comprising a mixture of cylindrical, utriform, and shorter clavate cells, these densely arranged on the lamellar edge. Pileipellis a thin cutis of compact, pale, yellow brown hyphae 2–5  $\mu$ m wide. Lamellar trama subparallel and consisting of somewhat inflated hyphae 5–17  $\mu$ m wide; subhymenium thin and consisting of relatively short cells that are 3–5  $\mu$ m wide. Stipitipellis of subparallel, mostly hyaline hyphae with a few loose superficial hyphae with light yellow pigment and some incrusting material; scattered cystidia present at the apex of some specimens. Clamps present.

*Habitat and distribution:* Highly varied and widely distributed from Europe to North and Central America. Mainly occurring during summer and early fall with a variety of hardwoods and conifers.

*Specimens examined:* COSTA RICA. San José, Dota, San Gerardo, about 5 km SW of Cerro de la Muerte, Albergue de la Montaña, Savegre, 9°32'2"N, 83°48'27"W, 9 Jul 2001, leg. R.E. Halling (REH8275, NY). NORWAY. Tømte, at the

farm near biology station grounds, 17 Aug 2002, leg. *T. Harrington* (PBM2355, TENN062753, as *I. maculata* f. *fulva*). USA. COLORADO. San Juan National Forest, Blanco Basin Road (Archuleta County Road 326), Ted Stampfer's cabin, 750 m, 17 Aug 1999, leg. *S.A. Trudell* (SAT9922901, WTU). MASSACHUSETTS. Worcester, Clark University Campus, 30 Aug 2004, leg. *P.B. Matheny* (PBM2588, TENN062427). NEW YORK. Near Albany, South Bethlehem, Joralemon Memorial Park, 20 Sep 2002, leg. *P.B. Matheny* (PBM2444, TENN062316); Rhinebeck, 23 Sep 2006, leg. *J.C. Slot* (PBM2827, TENN062618). UTAH. Cache County, Uinta-Wasatch-Cache National Forest, 13 Aug 1999, leg. *B.R. Kropp*, BK13-Aug-99-9 (UTC255687); *ibid.*, 13 Aug 1999, leg. *B.R. Kropp*, BK13-Aug-99-13 (UTC255688); *ibid.*, 28 Aug 2005, leg. *B.R. Kropp*, BK28-Aug-05-4 (UTC255689); Summit County, Uinta-Wasatch-Cache National Forest, 29 Aug 1999, leg. *B.R. Kropp*, BK29-Aug-99-1 (UTC255690). WASHINGTON. King County, Hazel Wolf Wetlands Preserve, 4 Jul 1997, leg. *P.B. Matheny* (PBM561, WTU); *ibid.*, 27 Sep 1997, leg. *P.B. Matheny* (PBM750, WTU); *ibid.* 28 Jun 1998, leg. *P.B. Matheny* (PBM1048, WTU); county unknown, lower Tahoma Creek, 19 Sep 1948, leg. A.H. Smith, E. Knowles, M. McKenny, D.E. Stuntz (St 4620, as *I. armoricana*).

*Comments:* *Inocybe lanatodisca* is a widely distributed species occurring in both eastern and western North America, as well as at high elevations in Mexico and Costa Rica. The species is fairly common in Utah where it tends to occur in riparian environments. *Inocybe lanatodisca* is a distinctive taxon that can be readily recognized by its rimose, conic pileus that is yellowish to orange brown or copper brown and by its white, unusually smooth stipe.

The material from Utah clusters with other diverse representatives (FIGS. 2–4) and corresponds well with the description of *I. lanatodisca* by Grund and Stuntz (1968) and by Smith and Stuntz (1950, as *I. armoricana* Heim). It should be noted that *I. armoricana* as described and illustrated by Heim (1931) is similar but differs by having a tawny stipe and somewhat smaller spores than our material. We have not included specimens going by the name *I. armoricana* in our analysis, but if molecular data were to show *I. armoricana* and *I. lanatodisca* to be conspecific then *I. lanatodisca* would have priority as the older name. Also, *I. lanatodisca* var. *phaeoderma* Grund & Stuntz was described to accommodate a variety with an umbrinous pileus (Stuntz 1954 as “*I. armoricana* var. *phaeoderma*”, Grund and Stuntz 1975). This variety has been recorded from Michigan and Nova Scotia, but we have not encountered it in Utah or elsewhere. However, future work should include material corresponding to both *I. armoricana* and *I. lanatodisca* var. *phaeoderma* to determine their relationship to the rest of section *Rimosae*.

As noted by Grund and Stuntz (1968), the original description of Kauffman (1918) must have been

based on lightly colored material. The pileus color that they refer to (“cadmium yellow” to “raw sienna” becoming “tawny”, see Smith and Stuntz 1950) and that we noted for our materials are relatively strong by comparison. *Inocybe rimosa* differs by its wider spores and fibrillose to floccose stipe surface.

Because both nLSU and *rpb2* gene trees support indiscriminate clusters of American *I. lanatodisca* and European *I. maculata* f. *fulva* Bon, we investigated this relationship further using ITS data from vouchered materials and sequences from GenBank. This analysis resulted in recognition of three lineages (FIG. 4). Even though none of these lineages are robustly supported relative to one another, these results indicate that at least three geographically separated variants may exist within *I. lanatodisca*: (i) one from northern/western Europe and southwestern Asia (including material labeled *I. maculata* f. *fulva*), (ii) one widely distributed in North and Central America and (iii) a third known only from a single ectomycorrhizal sample from oak roots in the central United States. The Eurasian population appears to be going by the name *I. maculata* f. *fulva* and because *I. maculata* and *I. maculata* f. *fulva* fail to form a monophyletic group here and in Larsson et al. (2009), we have placed *I. maculata* f. *fulva* in synonymy with *I. lanatodisca*. Kuyper (1986) also noted that *I. lanatodisca* fell within the range of variation for *I. maculata* and that more work would be needed to assess their relationship.

***Inocybe niveivelata*** Stuntz ex Kropp, Matheny & Hutchison, sp. nov. FIGS. 9, 13e  
Mycobank MB564164

*Diagnosis:* Pileus white. Lamellae brownish yellow to pale yellowish. Basidiospores  $11.5(13.9)18.5 \times 6.0(6.4)7.5 \mu\text{m}$ . Differs from *Inocybe breviterincarnata* by its white pileus, lack of pinkish young lamellae.

*Holotype:* USA. UTAH. Cache County, Uinta-Wasatch-Cache National Forest, 27 Aug 1997, leg. *B.R. Kropp*, BK27-Aug-97-18 (UTC255662).

*Etymology:* *niveivelata* refers to the white, abundant velipellis covering the pileus.

Pileus 12–50 mm diam, convex to broadly convex with the margin sometimes slightly inrolled, sometimes with a slight umbo; surface not rimose, smooth and sericeous due to the presence of a white, abundant velipellis that covers the pileus and leaves veil remnants at the margin; white overall due to the velipellis with an underlying appressed-fibrillose surface that is pale brown or having yellow hues when exposed (10YR 8/4, 2.5Y 9/4–7/4). Lamellae close, narrowly attached, 3–5 mm wide; dull brownish yellow to pale yellowish (10YR 6/4, 2.5Y 7/4); margins

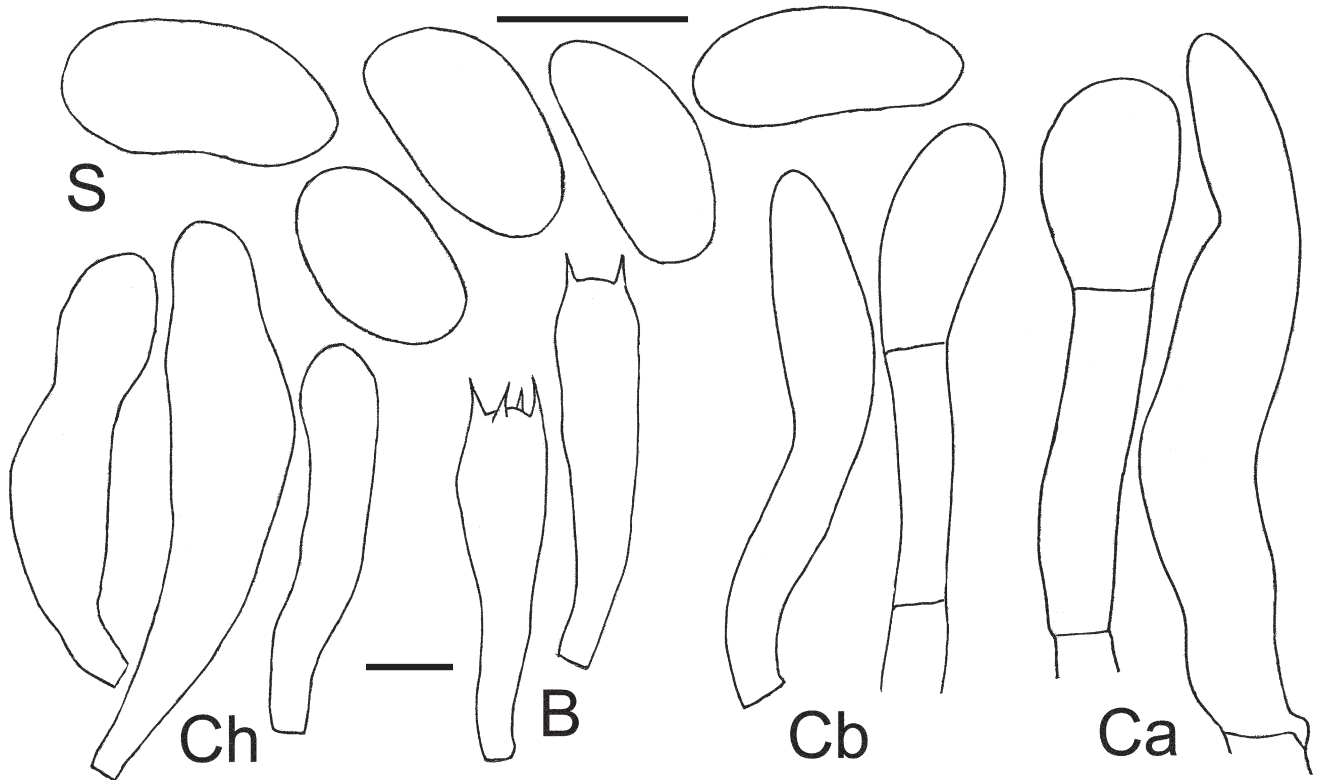


FIG. 9. Microscopic characters of *Inocybe niveivelata*. S. Basidiospores. B. Basidia. Ca. Apical caulocystidia and caulocystidioid hyphal tips. Cb. Caulocystidioid hyphal tips at stipe base. Ch. Cheilocystidia. Bars = 10  $\mu$ m.

white, fimbriate. Stipe 20–50  $\times$  2–10 mm, solid, equal or sometimes with a basal bulb; surface of the stipe apex short-fibrillose to scurfy or silky floccose, white sometimes turning brownish in places from spore deposition. Context white. Odor spermiatic.

Basidiospores 11.5 (13.9) 18.5  $\times$  6.0 (6.4) 7.5  $\mu$ m, smooth, ellipsoid to phaseoliform. Basidia 37–40  $\times$  10–12  $\mu$ m, four-spored, clavate. Pleurocystidia lacking. Cheilocystidia 27–60  $\times$  7–17  $\mu$ m, abundant, mostly thin-walled, somewhat variable in size and shape, clavate to utriform. Pileipellis a cutis of hyaline, compact hyphae 3–5  $\mu$ m wide that gradually blends into a subtending pale tan layer. Lamellar trama subparallel, hyphae 5–17  $\mu$ m wide, hyaline; subhymenium of compact hyphae 2–5  $\mu$ m wide. Stipitipellis consisting of parallel, hyaline hyphae with a loose superficial covering of hyphae present from the apex to the base that often have cystidioid hyphal tips that vary in size and shape, 21–107  $\times$  10–15  $\mu$ m. Clamps present.

*Habitat and distribution:* Fruiting during summer with conifers or with *Populus tremuloides* and conifers in montane environments in the western United States.

*Additional specimens examined:* USA. IDAHO. Heavens Gate Road, near Riggins, 1220 m, 30 Jul 1954, leg. D.E. Stuntz

& A.H. Smith, Stz8810 (WTU, UTC255668); *ibid.*, 30 Jul 1954, leg. D.E. Stuntz & A.H. Smith, Stz8811 (WTU, UTC255667). OREGON. Wallowa County Wallowa-Whitman National Forest, 19 Jun 1997, leg. B.R. Kropp, 19-Jun-97-2 (UTC255661). UTAH. Cache County, Uinta-Wasatch-Cache National Forest, 17 Aug 1998, leg. B.R. Kropp, BK17-Aug-98-6 (UTC 255663); *ibid.*, 18 Aug 1997, leg. B.R. Kropp, BK18-Aug-97-25 (UTC255664); Rich County, Uinta-Wasatch-Cache National Forest, 21 Aug 1997. Leg. B.R. Kropp, BK21-Aug-97-14 (UTC255665); *ibid.*, 21 Aug 1997, leg. B.R. Kropp, BK21-Aug-97-16 (UTC255666). WASHINGTON. Kittitas County, near Ellensburg, Table Mountain, Reecer Canyon Road, 13 Jul 2002, leg. P.B. Matheny (PBM2337, WTU); Kittitas County, Cle Elum Flats, 27 May 1962, leg. D.E. Stuntz (Stz12816, WTU-F-5373).

*Comments:* *Inocybe niveivelata* has a wide distribution in western North America and is known thus far from Idaho, Washington, Oregon and Utah. The name was suggested by D.E. Stuntz for a species he recognized as undescribed but did not publish. *Inocybe niveivelata* stands out both in dried material and in the field because of its white, sericeous pileus and its white stipe. It is also set apart by its long basidiospores. ITS and nLSU sequence data from Stz12816 (labeled *I. niveivelata* by Stuntz) are the same as sequences produced from our more recent samples from Utah and Washington.

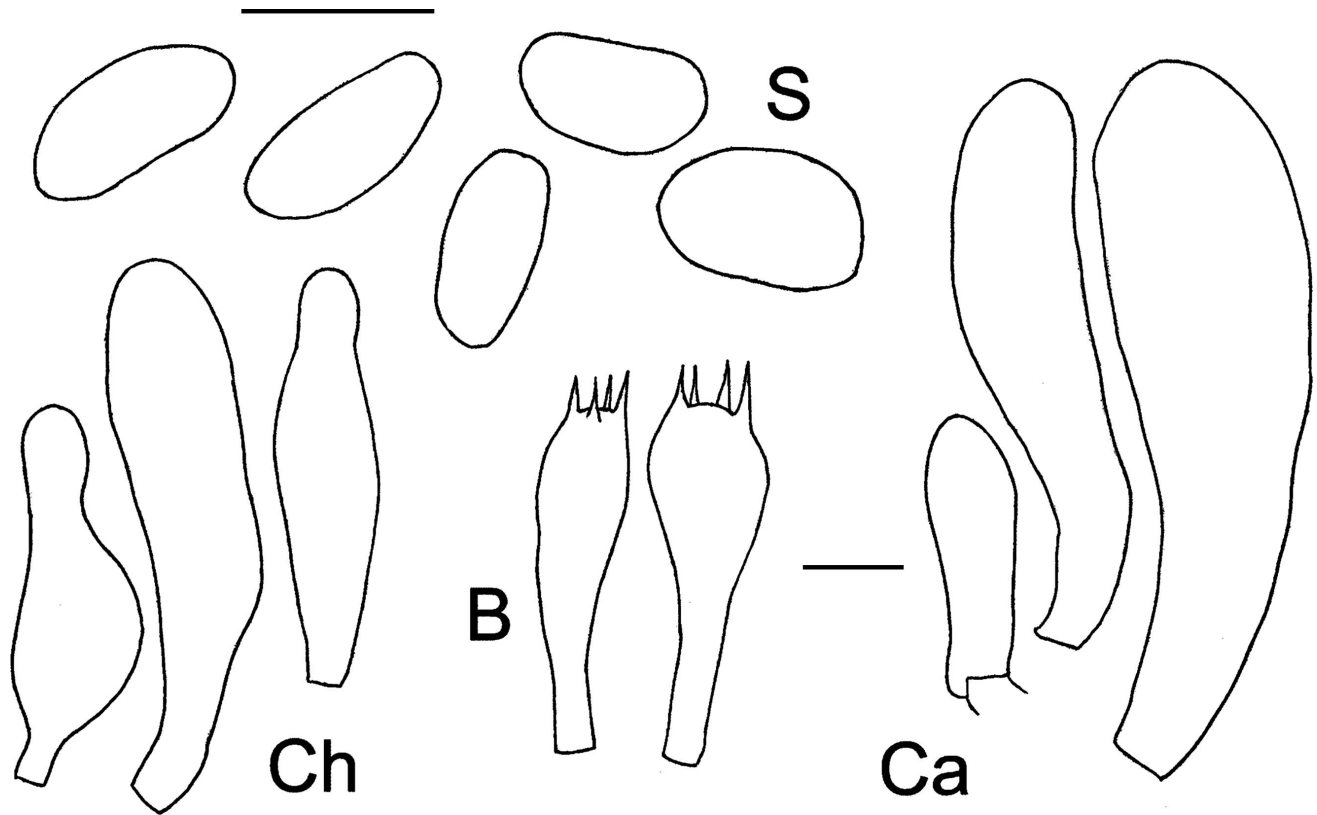


FIG. 10. Microscopic characters of *Inocybe obsoleta*. S. Basidiospores. B. Basidia. Ca. Caulocystidia at stipe apex. Ch. Cheilocystidia. Bars = 10  $\mu$ m.

*Inocybe niveivelata* can be separated from *I. breviterincarnata* by its white color and the lack of the distinctive young pink gills characteristic of *I. breviterincarnata*. Old material or herbarium specimens of these two taxa that lack either the pink lamellae of *I. breviterincarnata* or the white pileus of *I. niveivelata* can be difficult to separate because their microscopic characters are similar.

White forms of *I. arenicola* (R. Heim) M. Bon are similar to *I. niveivelata* based on descriptions of the former (Kuyper 1986), and one would be hard-pressed to differentiate between them morphologically. However, the two species are not closely related phylogenetically (FIG. 1) and they have different ecological associations. *Inocybe niveivelata* occurs in montane environments in western North America, whereas *I. arenicola* is reported from coastal sand dunes in Europe.

*Inocybe obsoleta* Romagn., Bull. Trimest. Soc Mycol Fr 74:145–148. 1958. FIGS. 10, 13f  
= *Inocybe aurora* Grund & Stuntz, Mycologia 67:24. 1975.

Pileus 34 mm diam, conical and sharply umbonate with uplifted margins; surface radially appressed-fibrillose and rimose, smooth, shiny, lacking a velipel-

lis; uniformly gray brown to pinkish gray (7.5YR 7/4) when fresh, gray brown when dry. Lamellae notched, 1–1.5 mm deep, gray brown with whitish margins. Stipe 50  $\times$  5 mm, solid, equal, whitish fresh, with faint gray hues when dry; pruinose at the extreme apex, short-fibrillose to mid stipe then somewhat shiny and smooth with scattered fibrils. Context whitish. Odor distinctive, faintly of Pelargonium.

Basidiospores 9.0 (10.8) 13.0  $\times$  5.0 (5.5) 6.0  $\mu$ m, smooth, ellipsoid to phaseoliform. Basidia 32–33  $\times$  10–12  $\mu$ m, four-spored, clavate. Pleurocystidia none. Cheilocystidia 35–50  $\times$  9–14  $\mu$ m, abundant, thin-walled, clavate to utriform. Pileipellis a cutis of pale tan lightly encrusted hyphae, 4–10  $\mu$ m wide. Lamellar trama subparallel, of hyaline somewhat enlarged hyphae that are 8–17  $\mu$ m wide, with a more compact subhymenium of hyphae that are 2–3  $\mu$ m wide. Stipitipellis at the apex of compact, smooth, parallel hyaline hyphae with clusters of variable caulocystidia 20–59  $\times$  9–22  $\mu$ m, the lower stipe is similar but without caulocystidia and with scant loosely woven, lightly encrusted superficial hyphae. Clamps present.

*Habitat and distribution:* Fruiting in summer in a montane environment with *Populus tremuloides* and conifers in Utah; under conifers during late summer

in Nova Scotia; under hardwoods and conifers during summer in Washington.

*Specimens examined:* CANADA. NOVA SCOTIA. Kings County, south side of Gaspereaux Valley, two miles east of Gaspereaux, 24 Aug 1972, leg. D.W. Grund (AU10245, isotype of *Inocybe aurora*). USA. UTAH. Summit County, Uinta-Wasatch-Cache National Forest, 28 Aug 2005, leg. B.R. Kropp, BK28-Aug-2005-13 (UTC 255686). WASHINGTON. King County, North Bend, Little Si Trail, 7 Jul 2002, leg. P.B. Matheny (PBM2332, WTU); *ibid.*, 7 Jul 2002, leg. P.B. Matheny (PBM2333, WTU).

*Comments:* Although our collection from Utah initially was identified as *I. aurora* Grund & Stuntz, its morphology and phylogenetic affinities indicate that instead it should be referred to as *I. obsoleta*. The above description is based on the specimen from Utah. The material from Utah corresponds in most respects with the protolog for *I. obsoleta* in Romagnesi (1958) but differs by lacking the whitish velipellis described by Romagnesi and the somewhat darker pileus. In spite of these differences, there can be little doubt that our material is conspecific with *I. obsoleta* given the phylogenetic affinity between North American and European samples (FIG. 1). In addition, the description of *I. aurora* given by Grund and Stuntz (1975) agrees well with the protolog for *I. obsoleta*. It should be noted that, even though our isotype material of *I. aurora* from Nova Scotia and material identified as *I. obsoleta* are somewhat divergent, they are nonetheless closely related with low bootstrap support for the branch separating them (FIG. 1). Thus, a good case can be made for synonymizing *I. aurora* and *I. obsoleta*. Of the two names, *I. obsoleta* has priority.

It should also be noted that *I. obsoleta* has been treated by some workers as a synonym of *I. rimosa* (Kuyper 1986). However, the representatives of *I. obsoleta* in our study cluster on our phylogram (FIG. 1) and are well separated from representatives of *I. rimosa* sensu stricto, indicating that *I. obsoleta* should be maintained as an independent taxon, a result first reported by Larsson et al. (2009).

This report extends the range of *I. obsoleta* from Europe to North America and it extends the range within North America from Nova Scotia to the western United States. *Inocybe obsoleta* can be separated from the other members of section *Rimosae* that are present in Utah by its rimose, sharply umbonate pileus with grayish brown or pinkish gray hues. The aromatic or faint odor of *Pelargonium*, when present, is also unusual for species of section *Rimosae* and is also distinct from the other members of section *Rimosae* sensu stricto found in Utah. However, Grund and Stuntz (1983) described a variety of *I. aurora* that lacked an odor (*I. aurora* var. *inodorata*).

***Inocybe occidentalis*** Kropp, Matheny & Hutchison, sp. nov. FIGS. 11, 13g

MycoBank MB564166

*Diagnosis:* Pileus convex and smooth, not rimose, lacking umbo. Basidiospores relatively narrow, 8.0(9.1)11.0 × 4.5(4.9)5.5 μm.

*Holotype:* USA. UTAH. Cache County, Uinta-Wasatch-Cache National Forest, 27 Aug 1997, leg. B.R. Kropp, BK27-Aug-97-3 (UTC255682).

*Etymology:* *occidentalis* refers to presence of the species in western North America.

Pileus 28–30 mm diam, broadly convex to nearly plane; surface smooth, appressed-fibrillose, not rimose or with tiny interstices visible near the margin, often shiny, sometimes with scant whitish, silky veil remnants present especially toward the disk; light tan with some copper tints (2.5Y 8.5/6–10YR 6/8). Lamellae close, notched, 4–5 mm deep, pallid when young becoming light brown (10YR 7/4) at maturity with distinctly pallid margins. Stipe 25–28 × 8–10 mm, solid, almost equal but swollen at the base, white but developing brownish hues due to spore deposition; longitudinally fibrillose, appearing pruinose to the base. Context white. Odor spermatric or, at times, featuring a pleasant truffle-like component.

Basidiospores 8.0 (9.1) 11.0 × 4.5 (4.9) 5.5 μm, smooth, ellipsoid to phaseoliform. Basidia 31–34 × 9–12 μm, four-spored, clavate. Pleurocystidia none. Cheilocystidia 22–33 × 12–19 μm, abundant, thin-walled, clavate. Pileipellis an appressed, dense layer of golden brown hyphae 2–6 μm wide. Lamellar trama of nearly parallel, hyaline hyphae 4–20 μm wide; subhymenium more compact of hyphae with relatively short cells, 2–4 μm wide. Stipitipellis apex of dense parallel hyphae overlain by loosely woven superficial hyphae with numerous cystidioid hyphal tips that are longer and more irregular than the cheilocystidia, with fewer cystidioid tips further down the stipe. Clamps present.

*Habitat and distribution:* Fruiting in summer in montane environments with conifers.

*Additional specimens examined.* USA. WASHINGTON. Chelan County, Lake Wenatchee, Tall Timbers, 14 Jun 1997, leg. P.B. Matheny (PBM525, WTU).

*Comments:* *Inocybe occidentalis* is rarely encountered, and as a result it is not well known. To date, it has been found only once in Utah in 1997 in a *Picea-Abies* forest near 3000 m. Repeated visits to the same locality have not yielded more collections, although it has been collected in Washington during the same year, indicating that it could potentially range across much of western North America. More observations are needed to know the geographical distribution and the morphological variation that can be expected for this species.

*Inocybe occidentalis* can be recognized by its smooth, broadly convex pileus that does not become rimose

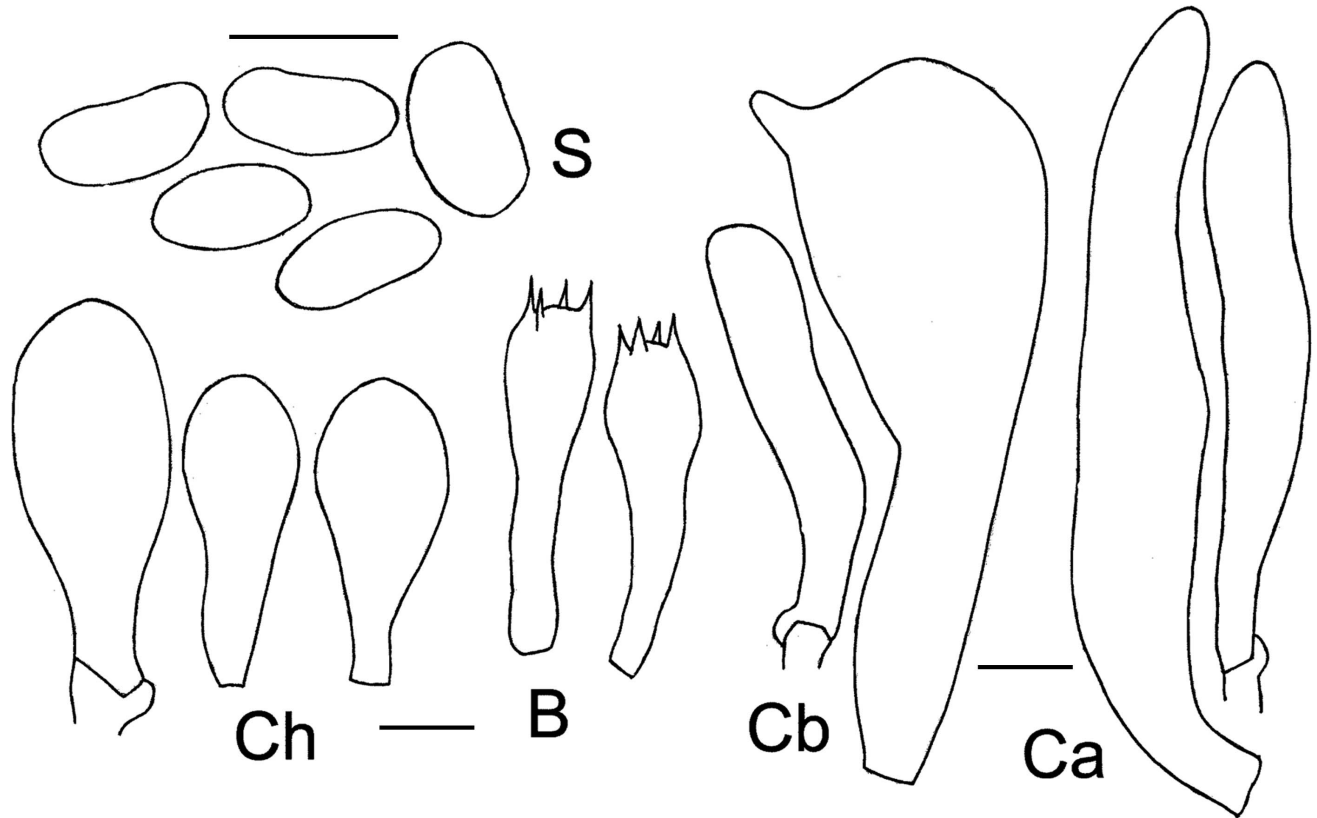


FIG. 11. Microscopic characters of *Inocybe occidentalis*. S. Basidiospores. B. Basidia. Ca. Apical caulocystidioid hyphal tips. Cb. Caulocystidioid hyphal tips at stipe base. Ch. Cheilocystidia. Bars = 10  $\mu$ m.

and by its small basidiospores. The species was mislabeled *I. maculata* in Matheny et al. (2002) and later referred to as *I. cf. maculata* in Matheny (2005).

*Inocybe spuria* Jacobsson & Larsson, Mycotaxon 109:204. 2009. FIGS. 12, 13h

Pileus 30–65 mm diam, conical becoming broadly conical, sometimes with umbo, margin incurved; surface radially appressed-fibrillose, smooth, somewhat shiny when dried, disk often but not always with small scales; color uniformly light tan (2.5Y 8/6–7/6) when young becoming reddish tan (7.5YR 6/8), dark yellow brown (10YR 4/4), or yellow brown (10YR 7/6) and tending to crack when mature. Lamellae close, notched, 3–7 mm deep, pale yellow brown (5Y 9/4) when young becoming dull yellow brown (2.5Y 7/4–5Y 8/6) at maturity with whitish margins. Stipe 40–80  $\times$  10–18 mm, equal, solid, occasionally joined at the base, longitudinally striate; white when young, becoming light brown (7.5YR 7/6–6/6) at maturity with a pallid or pale yellow brown to yellow brown (10YR 7/6–8/6) apex, sometimes with a white base. Context white. Odor spermiatic.

Basidiospores 8.0(9.7)11.5  $\times$  4.5(5.4)6.0  $\mu$ m, smooth, ellipsoid to phaseoliform. Basidia 31–38  $\times$

9–11  $\mu$ m, four- or two-sterigmate, clavate. Pleurocystidia none. Cheilocystidia 23–55  $\times$  13–25  $\mu$ m, numerous, thin-walled, varying in size, broadly clavate to elliptical. Pileipellis a dense layer of repent, golden brown hyphae that are 3–5  $\mu$ m wide and either smooth or sometimes lightly encrusted. Lamellar trama subparallel, hyaline hyphae that are 4–10  $\mu$ m wide, with a more compacted subhymenium of hyphae that are 2–4  $\mu$ m wide. Stipitipellis at the apex of parallel hyaline hyphae covered with loosely arranged light brownish hyphae, the remainder of the stipe is similar but having a more abundant covering of loose hyphae with golden brown pigmentation. Clamps present.

*Habitat and distribution:* In Utah appearing in summer in montane environments with mixed *Populus tremuloides* and onifers.

*Specimens examined:* USA. UTAH. Cache County, Uinta-Wasatch-Cache National Forest, 18 Aug 1997, leg. B.R. Kropp, BK18-Aug-97-23 (UTC255683); Rich County, Uinta Wasatch-Cache National Forest, 21-Aug-1997, leg. B.R. Kropp, BK21-Aug-97-20 (UTC255684); *ibid.*, 21-Aug-1997, leg. B.R. Kropp, BK18-Aug-97-26 (UTC255685).

*Comments:* This robust and striking species appears occasionally in Utah in montane forests but is not common. In North America, *I. spuria* is known thus far



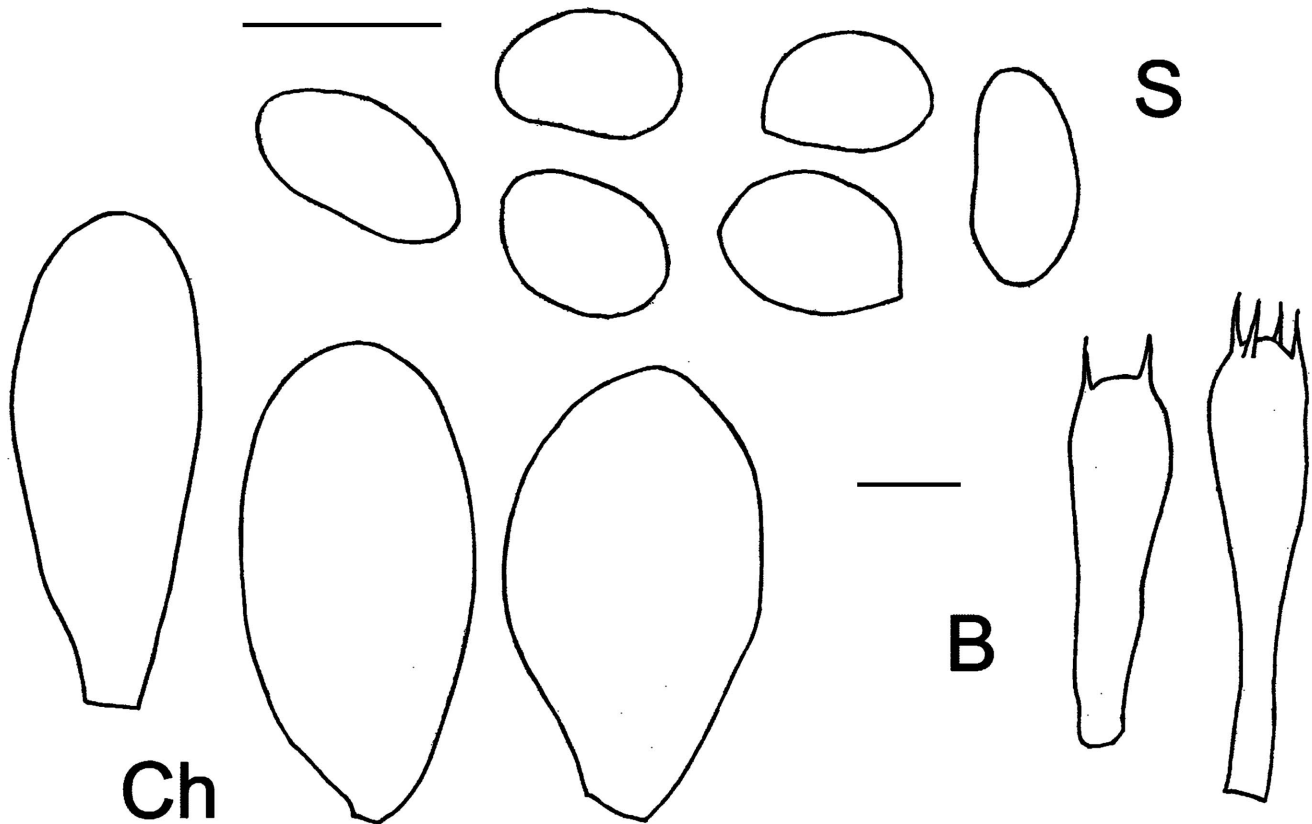


FIG. 12. Microscopic characters of *Inocybe spuria*. S. Basidiospores. B. Basidia. Ch. Cheilocystidia. Bars = 10  $\mu$ m.

from Utah and British Columbia even though the Canadian samples were identified from sequences obtained during soil sampling (GenBank Nos. FJ554451, FJ553958) (Jacobsson and Larsson 2009). As far as we know, no basidiomata have been reported from British Columbia.

The material from Utah compares very well with the description of Jacobsson and Larsson (2009) who were the first to point out the high sequence similarity between North American and European sequences. Until these workers showed *I. spuria* to be an independent taxon, it had been identified as *I. squamata* J.E. Lange (Matheny et al. 2009). The two species closely resemble one another and are not easily separated morphologically. However, *I. spuria* can be separated from *I. squamata* by its narrower spores that tend to be predominantly phaseoliform rather than mostly ellipsoid as in *I. squamata* (Jacobsson and Larsson 2009). Thus far, *I. squamata* has not been found in Utah, and further work will be required to determine whether it occurs anywhere in North America. It should be pointed out that before the discovery of *I. spuria*, a fungus was reported as *I. squamata* from *Populus tremuloides* stands in Montana by Cripps (1997). Molecular data for this material probably will answer the question of whether it belongs to *I. squamata* or *I. spuria*.

TAXONOMIC KEY TO SPECIES OF *INOCYBE* SECTION  
*RIMOSAE* SENSU LATO IN UTAH

- 1a. Pileus white or lamellae pink when young; pileus not rimose; basidiospores on average  $\geq$  13  $\mu$ m long . . . . . 2
- 1b. Pileus not white and lamellae not pink when young; pileus rimose or not; basidiospores on average  $\leq$  13  $\mu$ m long . . . . . 3
- 2a. Lamellae pinkish when young; pileus light brown; velipellis usually absent but sometimes present; stipe whitish or pinkish at apex when young . . . . . *I. breviterincarnata*
- 2b. Lamellae not pink when young; pileus whitish and sericeous due to a heavy velipellis; stipe whitish . . . . . *I. niveivelata*
- 3a. Basidiomata robust (pileus 30–65 mm wide, stipe 40–90  $\times$  8–20 mm); pileus not rimose; lamellae with yellow hues when young; odor spermatic . . . . . 4
- 3b. Basidiomata typically less robust than above; pileus either rimose or not; lamellae with or without pale yellow hues when young; odor more varied—aromatic, pleasant, or spermatic . . . . . 5
- 4a. Associated with *Cercocarpus ledifolius* and *Pinus monophylla*; basidiomata often caespitose and



FIG. 13. Basidiomata of *Inocybe* species section *Rimosae* sensu lato from Utah. A. *I. aestiva*. B. *I. breviterincarnata*. C. *I. cercocarpi*. D. *I. lanatodisca*. E. *I. niveivelata*. F. *I. obsoleta*. G. *I. occidentalis*. H. *I. spuria*. Bars = 1 cm.

- erumpent; pileus with distinct yellow tones and fibrillose surface . . . . . *I. cercocarpi*
- 4b. Associated with *Populus* and mixed conifers; basidiomata usually single and not erumpent; pileus lacking distinct yellow tones and often squamulose . . . . . *I. spuria*
- 5a. Pileus convex, lacking a distinct umbo; spores on average  $\leq 5.0 \mu\text{m}$  wide . . . . . *I. occidentalis*
- 5b. Pileus conical, with a distinct umbo; spores on average  $\geq 5.0 \mu\text{m}$  wide . . . . . 6
- 6a. Pileus gray brown to pinkish gray . . . . . *I. obsoleta*
- 6b. Pileus yellowish to yellow brown . . . . . 7
- 7a. Stipe smooth and white; spores on average  $\leq 10.0 \mu\text{m}$  long; widespread throughout North America and Central America, mainly associated with hardwoods . . . . . *I. lanatodisca*
- 7b. Stipe surface fibrillose; spores on average  $\geq 10.0 \mu\text{m}$  long, associated with Pinaceae . . . . . *I. aestiva*

#### DISCUSSION

The primary objective of this study was to determine which species of section *Rimosae* sensu lato occur in Utah. Based on morphological and phylogenetic evidence, we are able to identify eight species that occur in the state. Several of these fungi also occur elsewhere in North America, Central America and/or Europe. Of these eight species, seven are placed phylogenetically in the Pseudosperma clade (*Rimosae* sensu stricto). These include two species known from Europe, *I. obsoleta* and *I. spuria*, as well as five species described here as new: *I. aestiva*, *I. breviterincarnata*, *I. cercocarpi*, *I. niveivelata* and *I. occidentalis*. Based on DNA sequence comparisons from isotype material of *I. aurora*, originally described from Nova Scotia, we conclude that this species is a later synonym of *I. obsoleta*, a species with a broad geographic distribution in North America and Europe.

*Inocybe rimosa* sensu lato deserves discussion because it is a variable taxon that has been treated as an aggregate species comprising numerous taxa or divided variously into different species or varieties depending on the author. As many as 31 species or varietal names have been synonymized with *I. rimosa* (Kuyper 1986). Because species concepts in the complex often overlap, adopting a broad concept that places these overlapping variants under one name was a reasonable approach to the problem of morphologically classifying this group of fungi. However, our work concurs with that of Larsson et al. (2009) in that *I. rimosa* sensu lato is highly polyphyletic and that at least some of the taxa, such as *I. umbrinella* Bres., *I. perlata* (Cooke) Sacc. and *I.*

*bulbosissima* (Kühner) Bon, that have either been placed in synonymy with *I. rimosa* or assigned varietal rank should be retained as independent species. In some cases, it will probably prove impossible to clearly separate phylogenetic species in this group using morphological characteristics alone, but ecology and/or geography could provide important clues to species identity.

Our work had a regional focus and, thus, was not designed to resolve the *I. rimosa* complex in either Europe or eastern North America. However, examination of FIG. 1 reveals that specimens collected in Europe and North America labeled *I. cf. rimosa* do not cluster together, indicating that additional work needs to be done to thoroughly resolve this species complex. Even though the name *I. rimosa* is often used for material found in western North America, we have no evidence yet that *I. rimosa* sensu stricto even occurs there.

The eighth species we report from Utah, *I. lanatodisca*, belongs to the Inosperma clade (Matheny and Watling 2004). This species originally was described from Michigan (Kauffman 1918). Our studies of unpublished notes taken from the holotype by D.E. Stuntz and various other descriptions of this species as *I. armoricana* R. Heim by Smith and Stuntz (1950) and Stuntz (1954), and as *I. lanatodisca* in Grund and Stuntz (1968) leave little doubt as to the identity of our material from Utah. We also have observed the species in the field in Washington, New York and Massachusetts. Heim (1931) suggested the possibility that *I. lanatodisca* was a taxonomic synonym of *I. maculata*. Grund and Stuntz (1968), however, disagreed with this assessment. We have not studied or sequenced materials cited as *I. maculata* by Grund and Stuntz, and their identity is questionable given the polyphyletic nature of *I. maculata* observed here and by Larsson et al. (2009). The latter study recovered two groups representing samples identified as *I. maculata* and *I. maculata* f. *fulva*, and as mentioned above *I. maculata* f. *fulva* corresponds with *I. lanatodisca* as circumscribed here.

#### ACKNOWLEDGMENTS

Financial support for this work was provided to Bradley Kropp by the Utah Agricultural Experiment Station and to Brandon Matheny by the National Science Foundation (DEB-0949517). Support for laboratory work also were provided by the Hesler Endowment Fund at the University of Tennessee. We thank Aaron Wolfenbarger, Kathryn Allen, Emily Giles, Whitaker Hoskins and Sarah Sprague for laboratory assistance. This is UAES paper 8479. Dr Karen Hughes is thanked for providing unpublished sequence data to us for use in our phylogenetic analyses. We thank Joe Ammirati, Dennis Oliver, Roy Halling, Bart Buyck, Roland Treu, Cathie

Aime, Dennis Desjardin, Genevieve Gates, David Ratkowsky, Neale Bougher, Judith Curnow, Heino Lepp and other herbarium staff for arranging or providing loans or gifts of material from WTU, NY, P, LSUM, SFSU, CANB, PERTH and M.

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