

Basidiospore homoplasy and variation in the *Inocybe chelanensis* group in North America

Bradley R. Kropp¹

Department of Biology, Utah State University, Logan, Utah 84322

P. Brandon Matheny

Department of Biology, Box 351330, University of Washington, Seattle, Washington 98195-5325

Abstract: We present a morphological and phylogenetic study of *Inocybe chelanensis* and other North American species of *Inocybe* that have unusually elongated nodulose spores. Taxonomy and illustrations of these species are provided, along with a key to these and similar species found in Europe and North America. The species concept of *I. chelanensis* is broadened to include the range of variation occurring for the species in North America. Despite similar basidiospore morphologies, *I. chelanensis* and *I. candidipes* are not closely related. *Inocybe chelanensis* is related more closely to *I. stellatospora* and *I. candidipes* is related to *I. glabrodisca* based on RPBI and nLSU-rDNA nucleotide sequences. Distal elongation of *Inocybe* basidiospores was achieved independently in at least two separate lineages of *Inocybe*. *Inocybe candidipes* and *I. sierraensis* are described as new.

Key words: Agaricales, Basidiomycota, RPBI, species concepts, systematics

INTRODUCTION

Although several monographic treatments of *Inocybe* have been done for Europe and keys to species have been written for other parts of the world (Alessio and Rebaudengo 1980, Horak 1977, 1979, 1980, Kobayasi 1952, Kobayashi 2002, Kuyper 1986, Losa Quintana 1960, Perez-Silva 1967, Stangl 1989), much of the work done on the genus in North America still consists of scattered reports and species descriptions. An early monograph by Kauffman (1924), together with a series of papers by Smith and Stuntz (1950), Stuntz (1947, 1954) and Grund and Stuntz (1968, 1970, 1975, 1977, 1980, 1981, 1983, 1984), provide an important platform for work on the genus within the

continent. In addition, recent papers focused on North American taxa have provided keys to species from California (Nishida 1989), species associated with *Populus tremuloides* Michx. (Cripps 1997) and species within the *Inocybe lanuginosa* (Bull.: Fr.) Kummer group (Matheny and Kropp 2001). In many parts of North America, the species of *Inocybe* remain poorly documented and it is likely that at least some new taxa will be found as these areas are studied.

While working on species of *Inocybe* in western North America, we discovered several interesting specimens sharing similar characters with the *Inocybe chelanensis* Stuntz group. Members of this group either are uncommon or rare, often occur in montane to subalpine settings in association with *Abies* and *Pinus* and are characterized by having spores with an elongated apex and one to several basal nodules that give them a distinctive rocket shape. Within North America, three species that appear to belong to this group, *Inocybe chelanensis*, *I. rainierensis* Stuntz and *I. texensis* Thiers, have been described. Outside North America, only two other species that share affinities with the group have been reported thus far. These are *I. dolichospora* Malençon, a species associated with *Cedrus* in North Africa, and *I. ortegae* Esteve-Raventós, reported with *Quercus* from Spain. *Inocybe rennyi* (Berk. & Broome) Sacc. is another similar species with unusual spores that occurs in North America and Europe. Although its spores are elongated and angular to nodulose, they typically lack the basal nodules that impart the rocket shape of the other species mentioned above.

Specimens from Utah and Arizona appear to belong to the *I. chelanensis* group because of their unusual spores, but they seem unique because their spores and, to a lesser degree, their cheilocystidia differ in length from those reported for the holotype of *I. chelanensis* (Stuntz 1947); in addition, the stipe covering of the Arizona material is different than is typical for *I. chelanensis*. A preliminary examination of herbarium specimens representing *I. chelanensis* indicated that more variation occurs within this species than anticipated. Thus, to determine the status of the Utah and Arizona collections, it was necessary to examine the holotype of each member of the group and to document morphological and phylogenetic variation among existing collections.

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¹ Corresponding author. E-mail: brkropp@biology.usu.edu

Species concepts in *Inocybe* have relied strictly upon gross morphological and anatomical data (Kuyper 1986). However, Matheny et al (2002) demonstrated that sufficient variability exists at the species level within *Inocybe* at the RPB1 locus, a gene that encodes the largest subunit of RNA polymerase II, to separate species. Less variation among species of *Inocybe* occurs at the nLSU-rDNA (nLSU) locus, yet the region also appears suitable to separate many samples at the species level (Matheny et al 2002, Matheny data unpubl).

In this paper, we present the results of a systematic study of *I. chelanensis* and similar species in North America, including species descriptions, known geographical distributions, phylogenetic data and a key to species that are either phenotypically similar to *I. chelanensis* or might be confused with it.

MATERIALS AND METHODS

The microscopic characters of herbarium specimens prepared from dried, fresh material or obtained from F, K, MICH, UTC, WTU and SFSU were studied with light microscopy (herbarium abbreviations according to Holmgren et al 1990). Samples from all specimens were rehydrated and examined directly in 10% NH₄OH (or 3% KOH for *I. texensis*). Microscopic measurements were made under oil immersion at 1000 \times , and line drawings were made with the aid of a drawing tube. When possible, measurements of basidiospores were done using spores that had been deposited on stipes to avoid measuring immature spores. Spore measurements are given as averages and ranges for length and width with outlying measurements indicated in parentheses. Dimensions for basidia and hymenial cystidia are given as ranges. Spore colors were taken from microscopic preparations in 10% NH₄OH using the Munsell book of color (Munsell Color 1976). Color notes from fresh material were taken from several different color standards (Ridgway 1912, Kornerup and Wanscher 1967, Munsell Color 1976). For the purposes of this paper, all colors used in notes from fresh material or given in previously published species descriptions have been converted to the nearest equivalent in the Munsell book of color by direct comparison. The other color designations used are our own. When only herbarium specimens were available, colors and other macroscopic characters either were obtained directly from the specimen or from field notes enclosed with the specimen.

The sampling strategy includes only nodulose-spored taxa of subgenus *Inocybe* (Kuyper 1986) and the minimally angular to smooth-spored species *I. lacera* so that we could evaluate both the placement of collections of an unknown taxonomic status and test the monophyly of *Inocybe* species with apically elongated nodulose-basidiospores. The inclusion of *I. lacera* is warranted based on the suggestion of others (Kühner 1980, Kuyper 1986) that *I. lacera* might be related to some goniosporous species such as *I. curvipes*. The two do share similar cystidial characters and oblong basidiospores. Whereas the spores of *I. lacera* are oblong-

smooth, subfusiform, to minimally angular, those of *I. curvipes* are oblong angular-nodulose, generally with few to several low obtuse nodules. In addition, several caulocystidiate taxa that lack a cortina (i.e., *I. calospora*, *I. praetervisa* and *I. glabrodisca*) were included to assess the taxonomic and phylogenetic utility of apically elongated basidiospores. Both Kuyper (1986) and Matheny et al (2002) have suggested the polyphyly of *Inocybe* species with angular-nodulose basidiospores, thus phylogenetic conclusions about nodulose-spored taxa in general are not addressed. We were unable to extract DNA successfully from the holotype of *I. rainierensis*, which was collected in 1948.

DNA was extracted from dried basidiomata (samples listed in TABLE I), and nucleotide sequences were obtained for both RPB1 and nLSU following Matheny et al (2002). Primers A forward, C reverse, and B reverse were used to directly sequence the 5' end of RPB1 that includes conserved domains A to C; primers 5.8SR and LR7 were used to amplify the 5' nLSU region with internal primers LR0R, LR3R, LR16 and LR5 used for direct sequencing. Sequences were aligned using ClustalX (Thompson et al 1997), adjusted by eye and analyzed with PAUP* (Swofford 2002). The alignment is available at TreeBASE (S917) or from the second author on request.

The RPB1 and nLSU datasets were included as a single file for maximum-parsimony (MP) analysis with gaps treated as missing data. Separate analysis of the individual partitions showed no topological incongruence using the partition-homogeneity test in PAUP* ($P = 0.483$) (Farris et al 1994); hence, the two datasets were combined for further analysis. We used heuristic searches to find the optimal (MP) trees and 1000 bootstrap replicates (Felsenstein 1985) to evaluate branch strength. All searches for optimal trees employed 30 random-addition sequence replicates holding one tree at each step during stepwise addition and the tree-bisection-reconnection (TBR) branch-swapping algorithm. *Inocybe ayangannae*, a neotropical nodulose-spored species with a cortina (Matheny, Aime and Henkel 2003), was used to root the trees. Combined analysis of RPB1, nLSU, and an additional locus, RPB2, suggests *I. ayangannae* and several newly described species from the neotropics form a clade sister of the remainder of subgenus *Inocybe sensu* Kuyper (Matheny unpubl data).

We generated unconstrained and constrained maximum-likelihood (ML) trees under a best-fit model selected by Modeltest 3.0 (Posada and Crandall 1998, 2001) to evaluate suboptimal trees using the Shimodaira-Hasegawa test (SH-test) (Shimodaira and Hasegawa 1999). This permits testing of alternative (suboptimal) phylogenetic hypotheses to determine if they are significantly worse than the optimal ML topology ($\alpha = 0.05$) (Goldman, Anderson and Rodrigo 2000). A Tamura-Nei model was chosen as best fit to the combined RPB1 and nLSU data (base frequencies equal; a rate matrix of 5.1873 and 9.9843 for AG and CT transitions, respectively, and 1.0000 for all transversions; a 0.4351 proportion of invariable sites and a gamma distribution shape parameter of 1.3616). Under this model of DNA substitution, we then constrained the monophyly of taxa with a rocket-shaped basidiospore outline (two *I. chelanensis* collections, *I. sierraensis* sp. nov. and *I. candidipes* sp. nov.) and

TABLE I. DNA sequences used in the phylogenetic analysis, collection data, and GenBank accession numbers

Species	Origin	Collection/Herbarium	GenBank (RPB1)	GenBank (nLSU)
<i>Inocybe ayangannae</i> Matheny, Aime & Henkel	Guyana	MCA 1232 (WTU)	AY239028	AY239018
<i>Inocybe calospora</i> Quél.	Sweden	JFA 12539 (WTU)	AF389535	AY038313
<i>Inocybe candidipes</i> sp. nov.	Ariz., USA	BK 240799-7 (UTC)	AY239029	AY239019
<i>Inocybe chelanensis</i> Stuntz	Calif., USA	PBM 491 (WTU)	AY239030	AY239020
<i>Inocybe chelanensis</i> Stuntz	Wash., USA	PBM 2314 (WTU)	AY239031	AY239021
<i>Inocybe curvipes</i> P. Karst.	Wash., USA	PBM 2401 (WTU)	AY239032	AY239022
<i>Inocybe glabrodisca</i> P. D. Orton	Wash., USA	PBM 2109 (WTU)	AY239033	AY239023
<i>Inocybe lacera</i> (Fr. : Fr.) Kumm.	Wash., USA	PBM 1462 (WTU)	AF389540	AY038318
<i>Inocybe lanuginosa</i> (Bull. : Fr.) Kumm.	Wash., USA	PBM 956 (WTU)	AF389541	AY038319
<i>Inocybe leptophylla</i> Atk.	Utah, USA	BK 090797-19 (UTC)	AF389542	AY038320
<i>Inocybe napipes</i> J. Lange	Norway	PBM 2376 (WTU)	AY239034	AY239024
<i>Inocybe praetervisa</i> Quél.	Wash., USA	PBM 1021 (WTU)	AF389544	AY038322
<i>Inocybe relicina</i> (Fr.) Rick.	Finland	JV 10258 (WTU)	AF389546	AY038324
<i>Inocybe sierraensis</i> sp. nov.	Calif., USA	DED 6101 (SFSU)	AY239035	AY239025
<i>Inocybe sierraensis</i> sp. nov.	Calif., USA	DED 6477 (SFSU)	—	AY239026
<i>Inocybe stellatospora</i> (Peck) Masee	Wash., USA	PBM 963 (WTU)	AF389550	AY038328
<i>Inocybe teraturgus</i> M. M. Moser	Finland	JV 4290 (WTU)	AY239036	AY239027

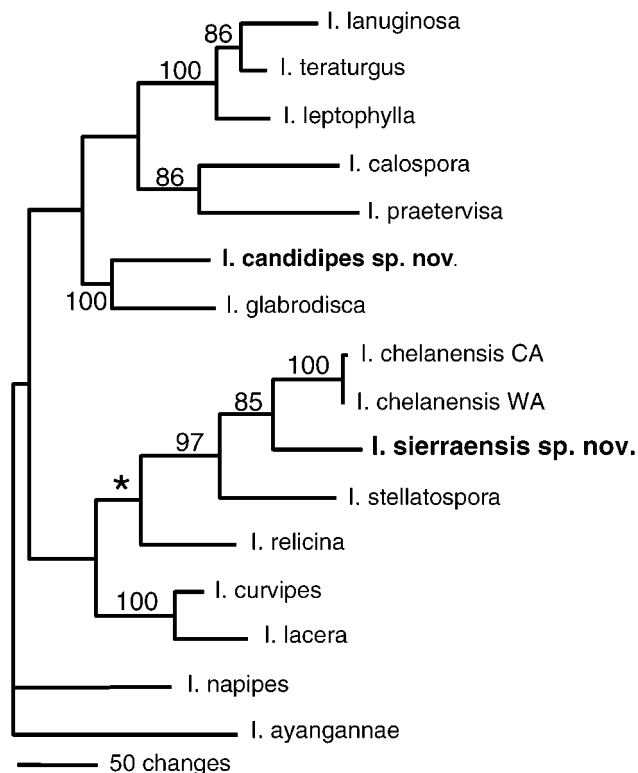


FIG. 1. One of three most-parsimonious trees using RPB1 and nLSU nucleotide sequences ($L = 1230$; $CI = 0.645$). The two new species, *Inocybe candidipes* and *I. sierraensis*, are in boldface type. Numbers above or below branches indicate bootstrap support $>50\%$. The asterisk indicates the collapse of that branch in the strict consensus of the three most-parsimonious trees.

of the taxa belonging to the *I. lanuginosa* group (*I. lanuginosa*, *I. leptophylla*, *I. teraturgus* and *I. stellatospora*). The SH-test then was used to determine if our constrained topologies significantly were worse than the optimal ML topology ($\alpha = 0.05$).

RESULTS

MP analysis of combined RPB1 and nLSU sequences yielded three equally optimal trees, one of which is shown (FIG. 1). Branches that collapse in the strict consensus of the three trees are indicated by an asterisk. Bootstrap support also is shown above or below branches to indicate branch support. The RPB1 partition contributed 1227 total sites; nLSU contributed 1422 sites. The combined dataset totaled 2649 characters, of which 2028 are constant, 259 parsimony uninformative and 362 parsimony informative. Of the parsimony-informative characters, RPB1 contributed 269 and nLSU 93. The RPB1 region analyzed included two introns, introns 2 and 3 of Matheny et al (2002) and three exon regions. Intron 2 is composed of 536 sites and intron 3 has 52 sites, including gaps. No indels were present in the exon regions.

Samples of *I. chelanensis* from California (PBM 491) and from Washington (PBM 2314) differ at only two of 1227 sites across RPB1 and at two of 1422 sites across nLSU. Two samples of *I. sierraensis* do not differ across the nLSU region. An RPB1 sequence for the second *I. sierraensis* sample (DED 6477) was not obtained, hence its exclusion from the phylogenetic dataset.

Species with rocket-shape basidiospores cluster in

two separate clades (FIG. 1). *Inocybe chelanensis* is sister with strong bootstrap support (85%) of *I. sierraensis*. Both species share similar basidiospore morphologies but differ in other morphological characters. However, *I. candidipes*, which has the distinctive rocket-shape basidiospore outline similar to *I. chelanensis*, occurs in a separate clade sister of the caulocystidiate species, *I. glabrodisca* (= *I. oblectabilis* Britz. f. *decemgibbosa* Kühn. & Bours.), with 100% bootstrap support. Like *I. glabrodisca*, *I. candidipes* appears to lack a cortina and has caulocystidia on the lower part of the stipe, although not in abundance. When we constrained the monophyly of taxa with this peculiar spore shape under maximum likelihood conditions, the ML constraint tree was rejected ($P < 0.05$) ($T_1 = 9881.7031$; $T_{BEST} = 9771.7970$). This further supports the homoplastic status of this spore outline. Nodulose- to spinose-spored species with caulocystidiate stipes (and that lack a cortina) appear paraphyletic, although this result is weakly supported (<50% bootstrap support).

Inocybe lanuginosa, *I. leptophylla* and *I. teratargus* are strongly supported as monophyletic (100% support). However, *I. stellatospora* (= *I. longicystis* Atk.), also thought to be a member of this group, is excluded (Matheny and Kropp 2001). The strongly supported (97%) sister position of *I. stellatospora* to the *I. chelanensis* group is unexpected because *I. stellatospora* has nodulose spores that are merely subangular to subelliptic. When we constrained the monophyly of members of this group, the constrained topology ($T_2 = 9798.4200$; $T_{BEST} = 9771.7970$) is statistically worse ($P < 0.05$) than the optimal topology using the SH-test. This result substantiates the strong bootstrap support for the sister position of *I. stellatospora* and the *I. chelanensis* group.

The sister relationship of *I. curvipes* and *I. lacera* also is supported strongly (100%), and this is the first phylogenetic work that supports a smooth-spored species as sister of an angular-nodulose-spored species. Although it should be said that *I. lacera* often has slightly angular spores and thus is somewhat atypical of the smooth-spored group.

ARTIFICIAL KEY TO *INOCYBE* SPECIES WITH APICALLY ELONGATED NODULOSE BASIDIOSPORES

- 1a. At least some basidiospores spurred at the base with 1–4 nodules, distal end often distinctly elongated into a rocket or bullet-shape or oblong-triangular in outline 2
- 1b. Basidiospores usually entirely gibbous, distal end somewhat elongated or outline trapeziform or polymorphic 7
 - 2a. Small percentage of basidiospores with basal nodules, mostly oblong and smooth to irregular in outline; known only from type locality under *Pinus* in east Texas *I. texensis* Thiers
 - 2b. Most basidiospores spurred with 1–4 basal nodules 3
- 3a. Basidiospores usually spurred with 1 basal nodule; hymenial cystidia mostly thin-walled ($\leq 0.5 \mu\text{m}$); pileus whitish with cream areas to light brown; velipellis absent *I. sierraensis* sp. nov.
- 3b. Basidiospores usually spurred with 3–4 basal nodules; hymenial cystidia mostly thick-walled ($\geq 0.5 \mu\text{m}$); pileus yellowish brown, grayish brown, avellaneous, or dark brown; velipellis often present 4
 - 4a. Pileus dark brown; known only from type locality under conifers including *Abies*, Mount Rainier National Park, Washington *I. rainierensis* Stuntz
 - 4b. Pileus yellowish brown, grayish brown, or avellaneous; widespread 5
- 5a. Caulocystidia descending at least to lower half of stipe; stipe with whitish ground color, appearing glabrous but lightly pruinose apically or over entire length; spores $11\text{--}14 \times 5\text{--}6 \mu\text{m}$ *I. candidipes* sp. nov.
- 5b. Caulocystidia absent or restricted to extreme apex; stipe with pinkish, pinkish cinnamon, or cinnamon ground color, rarely whitish; spores $11\text{--}17 \times 5\text{--}6.5 \mu\text{m}$ 6
 - 6a. Known only from North Africa; basidiomata remaining whitish or pale ochraceous until maturity; under *Cedrus* in Morocco *I. dolichospora* Malençon (see Malençon & Bertault 1970, Esteve-Raventós 2001)
 - 6b. Occuring in western North America under *Pinus* and *Abies*; basidiomata with a yellowish brown or avellaneous pileus *I. chelanensis* Stuntz
- 7a. Hymenial cystidia often papillate or with subacute apices and long basal pedicel 8
- 7b. Hymenial cystidia with obtuse to well-rounded apices usually without a long basal pedicel 9
 - 8a. Basidiospore outline trapeziform with 5–10 low obtuse nodules, these at times projecting more strongly, $9\text{--}12 \times 6\text{--}7 \mu\text{m}$; under hardwoods and conifers; relatively common *I. curvipes* P. Karst. (see Stuntz 1947 [as *I. decipientoides* Peck], Stangl 1989)
 - 8b. Basidiospores with highly variable outline, often much elongated, $7.5\text{--}17 \times 4.5\text{--}7 \mu\text{m}$, plant associates unclarified; rare *I. rennyi* (Berk. & Broome) Sacc.
- 9a. Pileus umber brown; in arctic and alpine habitats with *Salix* but also in stands of *Populus tremuloides* in subalpine areas; basidiospores mostly $10\text{--}11 \times 5\text{--}6.5 \mu\text{m}$ *I. giacomii* Favre (see Cripps 1997)
- 9b. Pileus lighter in color, with ochraceous, grayish brown, clay brown, to brown colors; if in subalpine areas, then under conifers, or habitat not as above 10
 - 10a. Pileus distinctly rimose as in *I. rimosa*; stipe pallid with reddish brown tinges; basidiospores $11\text{--}13 \times 5\text{--}6.5 \mu\text{m}$, indistinctly nodulose *I. undulatospora* Kuyp. (see Kuyper 1989)

- 10b. Pileus not distinctly rimose; stipe lacking reddish brown tinges; spores broader than above 11
- 11a. Basidiospore outline not distorted, usually with 7–9 moderate-size nodules, 8.5–11.5 × 5.5–8 μm; pileus grayish brown *I. cicatricata* Ellis & Everh. (see Stangl 1989, Esteve-Raventós 2001)
- 11b. Basidiospore outline often distorted by few prominent nodules, 10–13.5 × 5.5–8 μm; pileus grayish buff to clay brown *I. ortegae* Esteve-Raventós (see Esteve-Raventós 2001)

TAXONOMY

Inocybe texensis Thiers, *Mycologia* 51:52. 1959.

FIG. 2a

Pileus 20–25 mm diam, convex to broadly conical with a slightly incurved margin, becoming straight and sometimes undulate with age; surface dry, coarsely appressed-fibrillose, sometimes rimose with age, fibrils forming suberect scales near the disk, color more or less uniform through all developmental stages, tan to yellowish brown (10YR 7/8, 6/8; 7.5YR 6/8) when fresh; on dried specimen medium reddish brown (5YR 5/4–4/4); context thin (1–2 mm) and concolorous with the surface; odor not distinctive; taste slightly bitter. *Lamellae* ascending adnate, close to subdistant, 4–5 mm broad, narrow, thin, white when young becoming medium yellow brown (10YR 5/6) at maturity; dull rusty brown (7.5YR 4/4) on dried specimen; margins entire and concolorous with the gill faces; lamellulae of three lengths. *Stipe* 30–35 × 6–7.5 mm, equal except for a slight enlargement at the base, stuffed; surface dry, covered with short fibrils that usually are appressed to the surface but sometimes become slightly recurved, the dried

specimens appear pruinose for the upper ¼–½ of stipe length, with dense sand-filled mycelium at the base; stipe lavender (or vinaceous, 7.5R 8/4) in all developmental stages. *Basidiospores* 12.0–13.8–15.5 (–16.5) × (4.0–)4.5–4.9–6.5 (–9.5) μm, variable in outline from smooth and elongated to irregular, a relatively small proportion (approximately 10–15%) more-or-less rocket-shaped with 1–4 basal nodules and an elongated apex; spore color yellowish under the microscope (2.5Y 9/2–9/4). *Basidia* 29–39 × 8.4–12 μm, clavate, mostly 4-spored with a few 2-spored basidia present. *Pleurocystidia* 52–71 × 14–25 μm, walls mostly less than or equal to 0.5 μm, sometimes up to 1.0 μm thick, walls hyaline or pale yellowish, mostly fusiform-ventricose usually above a basal pedicel, occasionally nearly pyriform with a tapered apex, apices obtuse, often crystalliferous at the apex. *Cheilocystidia* 40–74 × 14–25 μm, similar to pleurocystidia, mostly fusiform-ventricose, occasionally subcylindrical, usually with a basal pedicel, apices obtuse, mostly crystalliferous at the apex, no paracystidia seen. *Lamellar trama* hyaline, parallel hyphae about 8 μm diam. *Pileipellis* a cutis of repent hyphae

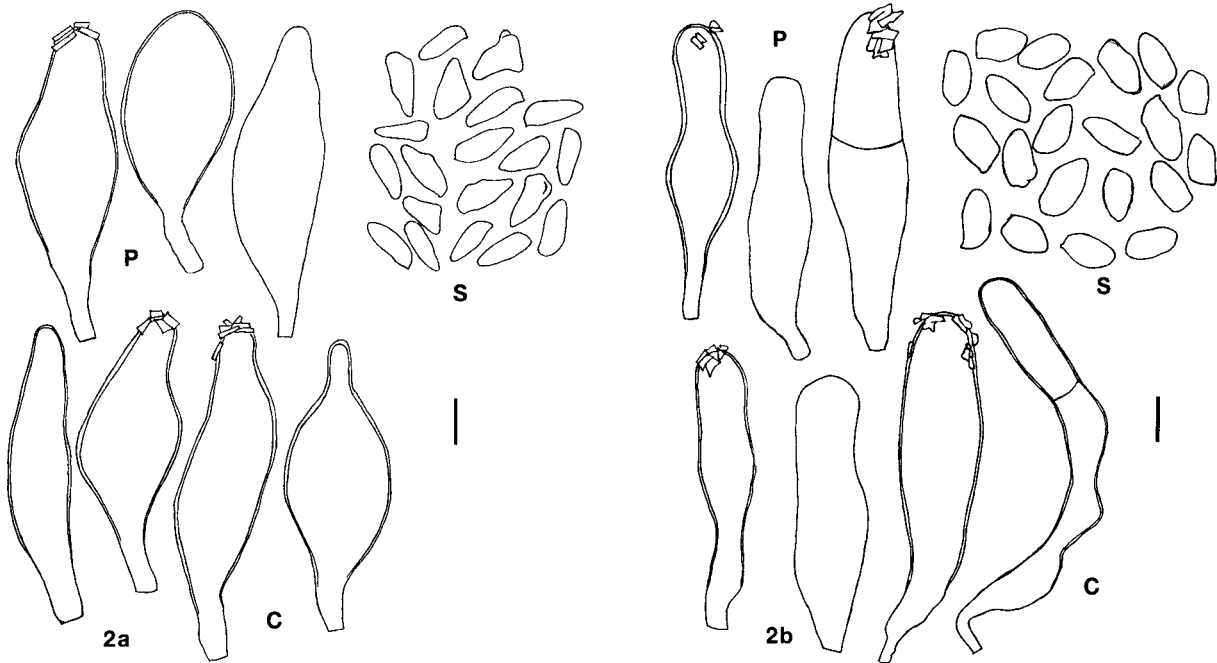


FIG. 2. a) *Inocybe texensis* (H. D. Thiers 1508 HOLOTYPE), b) *Inocybe sierraensis* (DED 6101 HOLOTYPE). Symbols used: S = spores, C = cheilocystidia, P = pleurocystidia. Bar = 10 μm.

up to 22 μm diam that are lightly incrustated and golden brown, incrustations pale yellowish. *Stipitipellis* apex (upper $\frac{1}{4}$ – $\frac{1}{3}$) covered by a superficial layer of hyphae 3–18 μm diam that often are lightly incrustated with pale yellowish material, many of the hyphae terminate in thin-walled cystidioid cells that tend to be clustered, cauloparacystidia not observed; the remainder of the stipe covered by a superficial layer of tangled hyphae similar to those at the apex but lacking cystidioid hyphal tips. *Clamps* present.

Habit, habitat and distribution. Solitary on sandy soil, associated with loblolly pine (*Pinus taeda* L.) The only known specimens were collected in eastern Texas during April.

Specimens examined. USA. TEXAS. Walker County, Sam Houston National Forest, near Huntsville, 19 Apr 1952, leg. H.D. Thiers, *H.D. Thiers 1508* (HOLOTYPE MICH).

Comments. *Inocybe texensis* is known only from the holotype that consists of two single halves of different basidiomata. The location of the complementary halves of these specimens is unknown. One of the pieces appears to have partially decayed before being dried and, although its microscopic characters are identical to the remaining specimen, it is not useful for macroscopic study. The other piece is in good condition and all microscopic measurements presented above, except for the details on the lamellar trama, were taken from it. Details on the lamellar trama presented above were taken from Thiers' protologue to minimize sampling from the holotype.

The macroscopic description given above is a modification of Thiers' original description from fresh material with added notes from the holotype. Our microscopic observations agreed with those presented in the original description, with the exception of a few minor details. We observed a wider range in the length of the hymenial cystidia than was given by Thiers, and the pileus cuticle did not stain dark brown in KOH as originally described.

A relatively low 10–15% of the spores of *I. texensis* have the rocket-shape outline characteristic of *I. chelanensis*. The majority of spores are somewhat variable in outline, and many resemble the rather unusual spores of *I. hotsoniana* Stuntz (Stuntz 1947) by being elongated and more-or-less amygdaliform with a narrowed apex. However, *I. hotsoniana* differs from *I. texensis* macroscopically and by lacking rocket-shaped *chelanensis*-type spores. It also is characterized by having distinctive cap-like pleurocystidial apices, although we are uncertain how consistent this trait is. *Inocybe texensis* differs from *I. chelanensis* and *I. dolichospora* by having a lavender stipe along with a pileus that tends to become scaly. In addition, the pleurocystidia and cheilocystidia of *I. texensis* are thin-walled, unlike those of *I. chelanensis*. The hy-

menial cystidia of *I. sierraensis* are thin-walled, but this species has been found only soon after snowmelt in the Sierra Nevada. It differs sharply from *I. texensis* by its overall whitish to cream coloration and glabrous to finely fibrillose pileus surface. *Inocybe rennyi* and *I. ortegae* both have very polymorphic spores.

To our knowledge, no one has reported *I. texensis* aside from the holotype and it is probably quite rare. Examination of nearly 100 unidentified specimens of *Inocybe* from eastern Texas housed at the Field Museum of Natural History (F) failed to turn up any additional material of this species. Additional collections are needed to further document the variation and distribution of this fungus, but the holotype is distinctive enough that, until more material can be studied, its status as an autonomous species is warranted.

***Inocybe sierraensis* Kropp et Matheny sp. nov.**

FIG. 2b

Pileus 20–40 mm latus, convexus vel applanatus, siccus et glaber, albus interdum laete brunneus, marginem versus leviter fibrillosus et cremi-color. Lamellae albae vel pallide brunneae, adnatae vel basi rotundato-adnatae. Stipes 10–30 mm longus, 5–10 mm crassus, aequalis, albus, interdum laete cinero-brunneolus tinctus, leviter fibrillosus. Sporae 10.5–12.8–16.5(–17.5) \times (5.0–)5.5–6.8–7(–8.0) μm amygdaliformes vel angulatae vel triangulares; nodulis basalibus 1–3 plerumque solitaribus. Basidia 37–49 \times 9–14 μm , clavata. Pleurocystidia 51–99 \times 9–20 μm , subventricosa vel clavata, interdum septata, tenuitunicata. Cheilocystidia 60–112 \times 10–21 μm , subventricosa vel clavata, interdum septata, tenuitunicata. Caulocystidia nulla. HOLOTYPE: DED 6101, SFSU.

Pileus 20–40 mm diam, broadly convex to nearly plane at maturity, margin incurved to straight and sometimes lobed; surface dry and dull, disk smooth and glabrous, usually white, becoming finely, radially fibrillose toward the margin, this region cream (10YR 9/4) with pale ochraceous to tan fibrils, velipellis absent, occasionally the pileus color may appear mostly light brown to medium yellow brown with whitish areas, in some cases adhering soil may obscure the ground color; context thick, soft, white; odor not distinctive. *Lamellae* close, bluntly adnate to very shallowly adnexed, white to pale grayish white becoming pale brown or grayish brown; light brown on dried specimens (10YR 7/6–8/6), margins entire and faintly whitish; lamellulae one tier. *Stipe* 10–30 \times 5–10 mm, equal, cylindrical, solid, lacking a bulb, white mycelium at the base; surface lightly covered with white, longitudinally arranged fibrils, most specimens not pruinose anywhere, although some may have a scurfy appearance near the stipe apex; stipe color entirely white becoming pale grayish brown on some

specimens; cortina fugacious. *Basidiospores* 10.5–12.8–16.5(–17.5) × (5.0–)5.5–6.8–7(–8.0) μm, varying from angular to smooth with a slightly amygdaliform outline, most spores spurred, many with a single nodule at the base giving the spores a blunt triangular appearance, the number of nodules varies from 1–3 but relatively few spores have more than one nodule; spore yellowish under the microscope (2.5Y 8.5/4–9/4). *Basidia* 37–49 × 9–14 μm, clavate, mostly 4-spored with a few 2-spored basidia present. *Pleurocystidia* 51–99 × 9–20 μm, sometimes septate, thin-walled, fusiform-ventricose, narrowly utriform, to clavate, some but not all above a basal pedicel, apices obtuse, often crystalliferous, walls pale yellowish mostly less than or equal to 0.5 μm thick, occasionally up to 1.0 μm. *Cheilocystidia* 60–112 × 10–21 μm, sometimes septate, walls mostly less than or equal to 0.5 μm, mostly clavate to narrowly utriform, some but not all with a basal pedicel, apices obtuse, often crystalliferous, no paracystidia observed. *Lamellar trama* hyaline, smooth, parallel hyphae, 4–15 μm diam. *Pileipellis* a fairly dense cutis of repent hyphae 2.5–6 μm diam with incrusting and adhering yellowish or brownish yellow material; velipellis not present in cross sections. *Stipitipellis* covered by a sparse superficial layer of yellowish hyphae 3.0–9.0 μm diam, this scant on some specimens; hyphae sometimes with adhering and incrusting material; some cystidioid hyphal tips present, these solitary or in clusters and most common apically, decreasing in abundance toward the base, sometimes absent at the base; cauloparacystidia nowhere observed. *Clamps* present.

Habit, habitat and distribution. Gregarious, subhyphogeous on soil soon after snowmelt, early June. Some basidiomata joined at the stipe base. Associated with *Abies* sp. or with mixed *Ceanothus* sp. and *Abies* sp. in montane fir-pine forests. Known only from the Sierra Nevada of California.

Specimens examined. USA. CALIFORNIA. Sierra County, Haskell Peak Road about 11 km from junction with Gold Lake Road, 6 Jun 1994, leg. D.E. Desjardin, *DED 6101* (as *I. chelanensis*) (HOLOTYPE, SFSU); Sierra County, Chapman Creek Campground on California 49, 3 Jun 1996, leg. D.E. Desjardin, *DED 6471* (as *I. chelanensis*) (SFSU); Sierra County, on California 49 at Yuba Pass, 4 Jun 1996, leg. D.E. Desjardin, *DED 6483* (as *I. chelanensis*) (SFSU).

Comments. *Inocybe sierraensis* is a snowbank fungus (Cooke 1955) characterized by its unusual whitish basidiomata that have cream-to-tan fibrillose areas on the pileus, especially near the margin. The combination of thin-walled, sometimes septate, hymenial cystidia and spurred spores is both distinctive and characteristic of this species. Other than *I. sierraensis*, none of the species of *Inocybe* with both nodulose

spores and whitish basidiomata occurs as a snowbank fungus and all differ, in one or more ways, microscopically from *I. sierraensis*.

Inocybe dolichospora is whitish but generally only during early development (Malençon and Bertault 1970). The spores of *I. dolichospora* are fairly similar in size to those of *I. sierraensis* but have basal nodules below an elongated apex that give them the more typical rocket-shaped appearance of members of the *I. chelanensis* group. The spores of *I. sierraensis* differ by having fewer nodules than those of either *I. dolichospora* or *I. chelanensis*. In many cases, its spores either are entirely smooth or have only a single nodule, which gives the spores a spurred or triangular appearance. In addition, the cystidia of *I. dolichospora* are thick-walled and the species is known only from North Africa, where it associates with *Cedrus* species (Malençon and Bertault 1970).

Phylogenetically, *I. sierraensis* is sister of *I. chelanensis* (FIG. 1) that, like *I. sierraensis*, frequently occurs around melting snow in montane environments in western North America. A second sample of *I. sierraensis* was sequenced for nLSU and found to match the holotype but is not included in the phylogenetic analysis due to the lack of an RPB1 sequence.

***Inocybe rainierensis* Stuntz, Mycologia 42:109. 1950.**

FIG. 3a

Pileus 15–45 mm diam, convex to broadly convex, some with a broad umbo, margin broadly rounded with pallid veil remnants often present; surface smooth, dry, uniformly covered with fine, radially appressed fibrils, disk sometimes becoming slightly areolate to subscaly, color uniformly dark brown with faint reddish hues (7.5YR 5/4, 4/4; 10YR 5/6) somewhat lighter in places due to the coating of surface fibrils, dry specimens umber to dull medium dark brown (7.5YR 4/4, 3/2); context 2–3 mm thick at the disk and pallid or tinged with brown, unchanging; odor none or faintly raphanoid. *Lamellae* close, broadly to narrowly attached, ventricose and sometimes rounded at the stipe, 4.5–7 mm broad, pallid at first becoming olive brown, on dried specimens of young material rusty brown (7.5YR 6/6) darker on older material, margins entire and whitish; lamellulae one tier. *Stipe* 20–45 × 3.5–8.0 mm, solid, equal, usually with a napiform basal bulb, terete to compressed; surface pruinose for the upper 1/10–1/3 of the stipe, otherwise longitudinally silky-fibrillose becoming streaked, bulb with veil remnants present, stipe color at first uniformly light pinkish tan (7.5YR 8/4), later gradually darkening to dark reddish or yellowish brown (7.5YR 5/4, 4/6) below a pallid apex; context unchanging. *Basidiospores* (11.0–)11.5–12.7–14.0

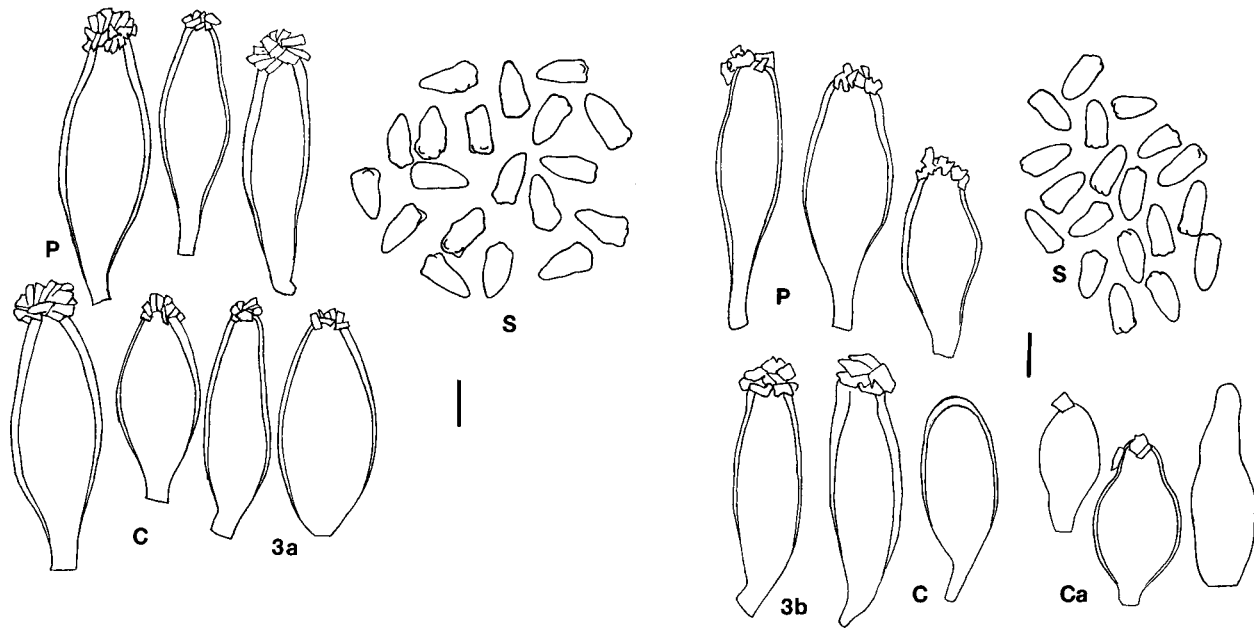


FIG. 3. a) *Inocybe rainierensis* (Stuntz 4200 HOLOTYPE), b) *Inocybe candidipes* (BK23-Jul-99-26, HOLOTYPE). Symbols used: S = spores, C = cheilocystidia, Ca = caulocystidia, P = pleurocystidia. Bar = 10 μ m.

(-14.5) \times (4.5-)5.0-5.8-6.5(-7.0) μ m, mostly rocket-shaped in outline with 2-4 basal nodules and an elongated apex, some spores vary in outline from the typical rocket shape by having one or two lateral nodules, occasional spores are nearly square due to lateral nodules, and a few are nearly smooth in outline or have an elongated triangular shape; spore color yellowish under the microscope (2.5Y 9/4-9/6). *Basidia* 29.0-41.0 \times 10.0-12.0 μ m, 4-spored. *Pleurocystidia* 53.0-75.0 \times 14.0-23.0 μ m, cell walls mostly 0.5-2.5 μ m thick, and pale yellowish in 10% NH_4OH , fusiform-ventricose above a short pedicel, apices obtuse and usually crystalliferous. *Cheilocystidia* 40.0-72.0 \times 16.5-25.0 μ m, similar to pleurocystidia, usually with a short basal pedicel, no paracystidia observed. *Lamellar trama* fairly dense trama, of parallel, mostly hyaline, smooth hyphae up to 10 μ m diam. *Pileipellis* a cutis of compact, repent, smooth hyphae up to 5.0 μ m diam that are reddish brown to yellowish brown; no velipellis seen. *Stipitipellis* apex covered with golden brown hyphae, having some incrusting material; caulocystidia present, these variable and usually but not always thin-walled, with or without apical crystals; middle of the stipe and stipe base covered with a superficial layer of golden brown hyphae with some incrusting material, up to 12 μ m diam, cystidioid hyphal tips sometimes present. *Clamps* present.

Habit, habitat and distribution. Associated with conifers in late August. Known only from Mount Rainier NP in the Cascade Mountains of western Washington.

Specimens examined. USA. WASHINGTON. Lewis County, Mount Rainier National Park, at Reflection Lake, 28 Aug 1948, leg. A.H. Smith, *Stuntz 4200* (HOLOTYPE WTU); Lewis County, Eagle Peak, 26 Aug 1948, leg. A.H. Smith, *Stuntz 4161* (WTU).

Comments. The gross morphological description above has been modified from Stuntz (1947). In his description of *I. rainierensis*, Stuntz mentions the similarities between this species and *I. chelanensis*. He also emphasized that, at the time, *I. chelanensis* was known only from the type collection. As a result, little could be said about the extent of its variability with respect to the characters that define *I. rainierensis*. Since then, enough additional collections of *I. chelanensis* have been made to allow a better assessment of its variability and relationship to *I. rainierensis*, and these two taxa do not appear to intergrade with one another. Thus, we consider *Inocybe rainierensis* an autonomous species.

Inocybe rainierensis is distinguished from *I. chelanensis* by having a uniformly dark brown pileus, a stipe that is darker brown at maturity and a bulbous stipe base. It also lacks a velipellis, while one is typically, although not always, present in the material representing *I. chelanensis*. In addition, all known material of *Inocybe rainierensis* was collected in late August, while *I. chelanensis* usually appears in the spring just after snowbanks have melted, although it sometimes can be found throughout the summer.

Inocybe rainierensis and *I. chelanensis* differ little in their microscopic characters such that the two taxa only can be separated macroscopically. The hymenial

cystidia of *I. rainierensis* and *I. chelanensis* are virtually identical, and their spores are also indistinguishable in outline. The spores of the *I. rainierensis* holotype are relatively short, only 11.5–14 μm in length compared to 14–19.5 μm for the holotype of *I. chelanensis*. However, they fall within the relatively wide range of variation for *I. chelanensis* as circumscribed here.

It should be pointed out that one collection (Stz 6241, WTU) made by Dr. Stuntz subsequent to the publication of *I. rainierensis* appears to be somewhat intermediate between *I. rainierensis* and *I. chelanensis* in exhibiting darker colors close to those of *I. rainierensis*. However, this collection lacks a bulbous stipe base and has the velipellis that usually is found on *I. chelanensis*. Dr. Stuntz (unpublished) noted this but did not assign the collection to either taxon, and it is unknown how he intended to interpret the material. This collection is considered by us to be a color variant of *I. chelanensis*.

Inocybe rainierensis is rare and is known only from two collections from montane environments in western Washington. Little is known about its geographical distribution or ecology.

***Inocybe candidipes* Kropp et Matheny sp. nov.**

FIGS. 3b, 6c

Pileus 10–34 mm latus, conicus vel convexus demum appanatus, umbonatus, siccus, centrum pellicula pallida, marginem versus fibrillosus et brunneus. Lamellae albae vel brunneae, adnatae vel sinuatae; acie leviter fimbriata. Stipes 27–40 mm latus, 3–6 mm crassus, albus interdum laete brunneus, aequalis, basi leviter bulbosus, paene glaber, ad apicem leviter pruinosis, caulocystidiis communibus, ad basim caulocystidia sparsa, interdum omnis leviter pruinosis. Sporae (10.0–)11.5–12.8–14.0(–14.5) \times 5.0–5.6–6.0(–6.5) μm , plerumque triangularis et elongata; apicibus elongatis et nodulis basalibus 1–4. Basidia 36 \times 8–14 μm , clavata. Pleurocystidia et Cheilocystidia 44–69 \times 14–26 μm , late fusiformia vel ventricosa, interdum ovata. HOLOTYPE: BK 23-Jul-99-26, UTC.

Pileus 10–34 mm diam, conic to convex or nearly plane with an umbo; surface dry, disk covered with a pallid velipellis, radially fibrillose toward the margin, not rimose, somewhat felty, occasionally with appressed squamules in age; color of areas beyond the velipellis medium grayish brown (10YR 8/4, 7/4, 7/6, 6/6, 4/4); context white; odor faint, spermatic to acidulous. *Lamellae* close, adnate to sinuate, ventricose, up to 4 mm broad; color whitish when young, becoming gray-brown at maturity (2.5Y 6/4, 10YR 7/6); margins entire, faintly white-fimbriate; lamellulae one tier. *Stipe* 27–40 \times 3–6 mm, solid, equal to the base that usually has a slight nonmarginate bulb; surface appearing nearly glabrous but lightly pruinose at the apex and sometimes lightly pruinose over

the entire stipe, cortina not observed; color white when young becoming somewhat yellowish brown (2.5Y 8.5/4) on some specimens in age, this at least partly due to spore deposits; context white in young material developing gray brown tints (2.5Y 8/4, 7/4) in age. *Basidiospores* (10.0–)11.5–12.8–14.0(–14.5) \times 5.0–5.6–6.0(–6.5) μm , mostly rocket-shaped in outline with 1–4 basal nodules and an elongated apex; occasional spores vary in outline from the typical rocket shape by having an elongated triangular outline or one or two lateral nodules that sometimes give a rectangular outline; spore color yellowish under the microscope (2.5Y 8.5/4). *Basidia* 27–36 \times 8–14 μm , clavate, 4-spored, sometimes 2-spored. *Pleurocystidia* 49–69 \times 14–24 μm , slightly thick-walled, walls 1.0–2.5 μm thick, pale yellowish, fusiform-ventricose, occasionally ovate, usually above a short pedicel, apices obtuse and often crystalliferous. *Cheilocystidia* 44–68 \times 16–26 μm , walls 0.5–3.0 μm , similar to pleurocystidia, mixed with smaller and variably shaped cells. *Lamellar trama* parallel, mostly hyaline, smooth hyphae up to 16 μm diam. *Pileipellis* a cutis of repent hyphae that are brown, incrustated, and up to 12 μm diam; velipellis visible in section, composed of hyaline, sometimes lightly incrustated hyphae up to 12 μm diam. *Stipitipellis* nearly glabrous, a very light superficial layer of hyaline to yellowish, sometimes incrustated hyphae, can be seen especially near the base; caulocystidia present at the apex, these similar to the cheilocystidia but variable and often clustered, thick or thin-walled, with or without apical crystals, caulocystidia scattered over the remaining length of the stipe but very infrequent on the lower portion, at times mixed with short cylindrical cells. *Clamps* present.

Habit, habitat and distribution. Gregarious on soil and associated with *Pinus ponderosa* in montane environments. Thus far, known only from Arizona. Appearing in midsummer.

Specimens examined. USA. ARIZONA. Apache County, 23 Jul 1999, leg. B.R. Kropp, BK 23-Jul-99-26 (HOLOTYPE UTC); Coconino County, 24 Jul 1999, leg. B.R. Kropp, BK 24-Jul-99-7 (UTC).

Comments. *Inocybe candidipes* thus far has been found along the Mogollon Rim of Arizona in association with *Pinus ponderosa*. The taxon is known only from the material cited here, but the collections were found at sites widely separated from one another. Extensive collecting of *Inocybe* species has not been done in the southwestern United States. However, it is likely that *I. candidipes* will be found throughout that region and perhaps in adjacent parts of Mexico. *Inocybe chelanensis* occasionally occurs in association with *Pinus ponderosa* in parts of Washington, but ma-

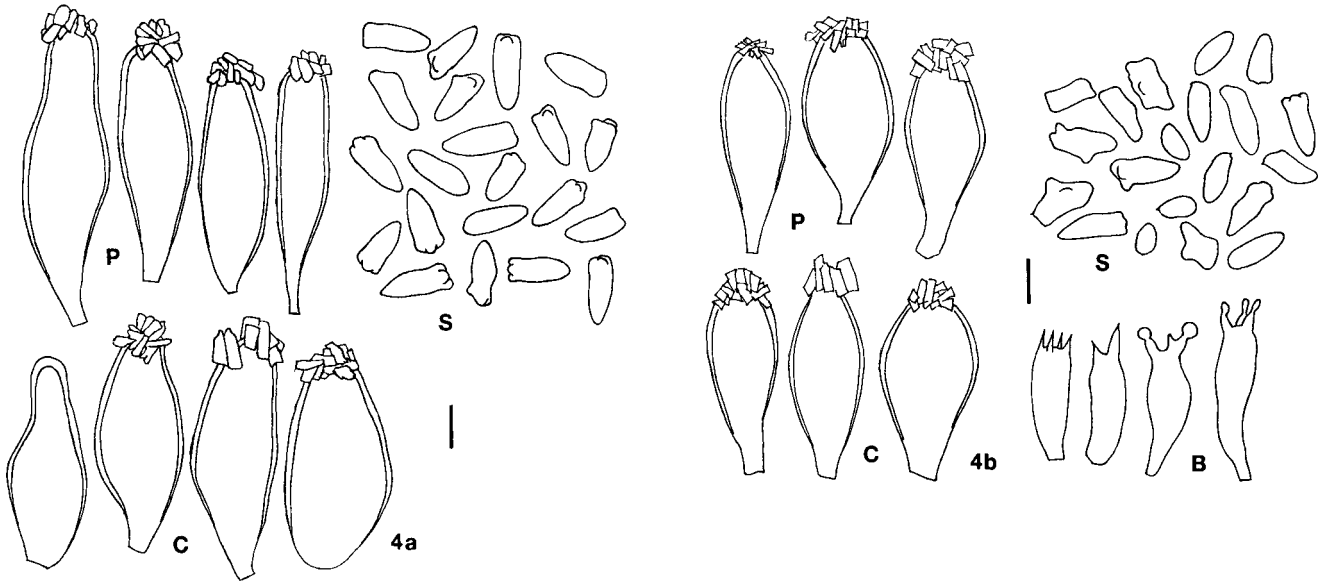


FIG. 4. a) *Inocybe chelanensis* (Stuntz 659 HOLOTYPE), b) *Inocybe chelanensis* (PBM 1870, atypical). Symbols used: S = spores, C = cheilocystidia, P = pleurocystidia, B = basidia. Bar = 10 μ m.

terial corresponding to *I. candidipes* has not been confirmed in that area.

Although *I. candidipes* has a spore outline similar to *I. chelanensis*, it is rather distinctive in the field because of its sometimes lightly pruinose stipe, which is usually white especially when young, and the lack of a rimose pileus. The stipe usually has a weak non-marginate bulb. Brownish hues may be present on the stipe in age. The basidiospore length of *I. candidipes* also occurs at the lower end of the range for *I. chelanensis* as circumscribed here. Moreover, both RPBI and nLSU sequence data confirm that *I. candidipes* is not closely related to *I. chelanensis* (FIG. 1), and that the rocket-shape outline of their basidiospores has arisen more than once independently over the course of evolution within *Inocybe*.

***Inocybe chelanensis* Stuntz, Mycologia 39:26. 1947.**

FIGS. 4a, b and 6a, b

Pileus 14–45 mm diam, convex to broadly convex or campanulate with or without a low umbo, sometimes obtusely conic, becoming almost plane, margin inrolled at first, sometimes even, and rounded or becoming undulating; surface dry, disk usually covered with a pallid to light gray velipellis, often becoming coarsely to finely radially fibrillose toward the margin, often rimulose to rimose or occasionally with minute squamules; velipellis occasionally lacking, in other cases it is rather copious, covering most of the pileus and imparting a whitish overall appearance to the pileus (FIGS. 6a, b), rarely forming appressed-squamulose patches; color of areas beyond the veli-

pellis light yellowish brown, brown, medium grayish brown (10YR 8/4, 7/4, 7/6, 6/6, 5/6, 5/4, 4/4) sometimes with reddish hues (7.5YR 7/6, 6/8, 6/6, 5/4, 4/4) or avellaneous; context usually whitish to pallid and unchanging; odor varying from spermatic to fungoid, faintly raphanoid, like *Pelargonium* (one collection), or not distinctive; taste mild. *Lamellae* close to somewhat distant, adnate to adnexed, often sinuate, ventricose; color whitish to light gray (10YR 7/2) when young, becoming dull, light yellowish brown, tan, or sometimes dark yellowish brown (10YR 7/4, 6/4, 5/6, 5/4, 4/4) in age; margins entire, often white-fimbriate but usually faintly so, sometimes not at all; occasionally more than one tier of lamellulae. *Stipe* 15–45 \times 3–2 mm, solid, equal or tapering to base that is sometimes slightly swollen, terete to compressed; cortina fugacious, surface usually scanty pruinose for the upper $\frac{1}{4}$ – $\frac{1}{3}$, below this covered with a pallid silky fibrillose layer that is usually thin but is sometimes thick enough to impart an overall whitish color to the stipe (FIGS. 6a, b), occasionally nearly glabrous; ground color usually yellowish brown, or dull pinkish brown, sometimes dark reddish or yellowish brown (10YR 7/4–6/4; 7.5YR 8/4, 8/2, 6/4, 5/4, 4/6; 5YR 7/4, 5/4), rarely white, often having light rose or grayish pink hues (2.5YR 8/6, 6/6; 5YR 5/4, 8/6) near the apex which also may be pallid; stipe base usually white; context pallid or with weak flesh tones, unchanging. *Basidiospores* (10.0–)11.0–14.1–17.0(–19.5) \times (4.5–)5.0–5.7–6.5(–7.5) μ m, mostly rocket shaped in outline with 2–4 basal nodules and an elongated apex, some are near-

ly smooth in outline or have an elongated triangular outline, occasional spores vary in outline from the typical rocket shape by having one or two lateral nodules, rarely quite polymorphic; spore color yellowish under the microscope (2.5Y 9/4, 8.5/6, 8.5/4, 8.5/2). *Basidia* 25–47 × 8–14 μm, clavate, mostly 4-spored. *Pleurocystidia* 41–81 × 25–12 μm, slightly thick-walled to thick-walled, walls 1.0–2.5 μm thick, pale yellowish, fusiform-ventricose, sometimes narrowly so, occasionally ovate, usually above a short pedicel, apices obtuse and crystalliferous. *Cheilocystidia* 29–85 × 10–27 μm, similar to pleurocystidia, no paracystidia observed. *Lamellar trama* parallel, hyaline, mostly smooth hyphae 4–21 μm diam. *Pileipellis* a cutis of repent hyphae that are reddish brown or dark to golden brown, either incrustated or smooth, up to 12 μm diam; velipellis usually visible in section, composed of hyaline, smooth hyphae 2.5–11 μm diam, velipellis sometimes lacking. *Stipitipellis* apex usually with a light covering of hyaline or yellowish hyphae 2–9 μm diam, with or without light incrusting material; caulocystidia usually but not always present at the apex, versiform, usually thin-walled and often occurring in clusters, with or without apical crystals; the remainder of the stipe usually covered with a light superficial layer of hyphae, cystidioid hyphal tips often present. *Clamps* present.

Habit, habitat and distribution. Associated with *Pinus* and *Abies* in montane environments throughout western North America. Solitary to gregarious, sometimes caespitose on soil. Appearing from spring to mid-August and occasionally found near melting snowbanks at high elevations.

Specimens examined. USA. CALIFORNIA. Sierra County at SFSU field campus, 4 Jun 2000, leg. D.E. Desjardin, *DED 7165* (SFSU); Sierra County, SFSU field campus, 1 Jun 1997, leg. P.B. Matheny, *PBM 491* (WTU); IDAHO. Idaho County, Seven Devils Mountains, 30 Jul 1954, leg. Stuntz, Smith, Bigelow, Kennedy, *Stuntz 8804* (MICH); OREGON. Baker County, Wallowa-Whitman National Forest, 2 Jul 1995, leg. S. Albee, *BK 2-Jul-95-1* (UTC); UTAH. Rich County, 27 Jul 1997, leg. B.R. Kropp, *BK 27-Jul-97-21* (WTU); Rich County, 27 Jul 1997, leg. B.R. Kropp, *BK 27-Jul-97-22* (WTU); Rich County, 15 Jul 1997, leg. B.R. Kropp, *BK 15-Jul-97-16a* (WTU); Rich County, 15 Jul 1997, leg. B.R. Kropp, *BK 15-Jul-97-16b* (WTU); WASHINGTON. Chelan County, Chesapeake Saddle, 8 Jul 1938, leg. D.E. Stuntz, *Stuntz 659* (HOLOTYPE WTU); Chelan County, Wenatchee Lake State Park, 27 May 1951, leg. D.E. Stuntz, *Stuntz 6241* (atypical) (WTU); Kittitas County, Table Mountain, Naneum Meadows, 15 Aug 1999, leg. P.B. Matheny, *PBM 1583* (WTU); Yakima County, near confluence of American and Bumping rivers, 23 May 2000, leg. R. Halling, *PBM 1870* (atypical) (WTU); Kittitas County, Table Mountain, 28 Jun 2000, leg. P.B. Matheny, *PBM 1917* (WTU); Kittitas County, Table Mountain, 28 Jun 2000, leg. P.B. Matheny, *PBM 1918* (WTU); Kittitas County, Table Moun-

tain, 23 Jun 2000, leg. P.B. Matheny, *PBM 1919* (WTU); Kittitas County, Table Mountain at Naneum Meadows, 15 Aug 1999, leg. P.B. Matheny, *PBM 1583* (WTU); Kittitas County, Table Mountain, 12 Jul 2000, leg. P.B. Matheny, *PBM 1930* (WTU); Chelan County, Fish Lake, 8 Jun 2002, leg. P.B. Matheny, *PBM 2314* (WTU); Kittitas County, Table Mountain, Reecer Canyon Road, 30 Jun 2002; leg. P.B. Matheny, *PBM 2329* (WTU).

Comments. Of the species treated, *Inocybe chelanensis* is the most common and widespread. It is reported thus far from montane to subalpine environments in much of the western United States and probably also occurs in similar habitats in adjacent Canada and Mexico. To our surprise, both RPBI and nLSU sequences (FIG. 1) reveal a close relationship between *I. chelanensis* and the umber brown scaly *I. stellatospora*, despite their markedly different outward appearances and differences in basidiospore and cystidia morphologies.

Most collections of *I. chelanensis* macroscopically fit the protologue of Stuntz (1947) quite well and are characterized by having a light yellowish brown to medium gray-brown pileus with a pallid velipellis over the disk. Typical collections have stipes with a brownish overall ground color and incarnate reflections at the apex. They are lightly pruinose at the apices and are covered by a relatively light whitish, silky-fibrillose superficial layer below. However, variation occurs for pileus and stipe color as well as for the degree to which the velipellis and stipe covering are developed. The velipellis of some specimens is entirely lacking while in others, it is exceptionally thick and imparts a whitish overall appearance to the pileus. The incarnate hues typically seen at the stipe apices also may be absent and, in this case, the ground color of the stipe is brownish. A few of these variants, if considered individually, are fairly distinctive in appearance but fit within *I. chelanensis* as circumscribed here when all characters are considered together.

Most microscopic characters of *I. chelanensis* exhibit relatively little variation and the structure of the pileipellis, lamellar trama, and stipe surface remain quite constant between collections. Our measurements of the basidiospores and hymenial cystidia from the holotype of *I. chelanensis* agree well with those given by Stuntz (1947). However, the dimensions of the basidiospores were found to vary markedly among the collections representing this taxon. The basidiospores from the holotype were the longest encountered, while spores from the specimens from Utah were among the smallest and were nearly nonoverlapping in length with those of the holotype. A comparison of the available collections shows that their basidiospore measurements thoroughly intergrade and there is no correlation between spore size

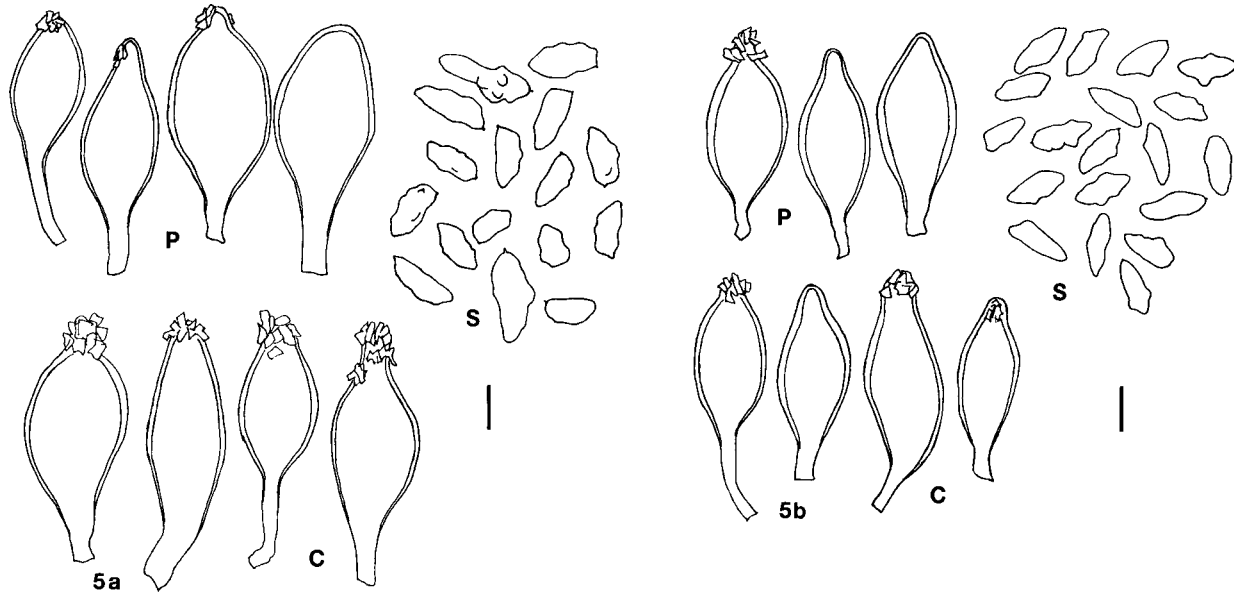


FIG. 5. a) *Inocybe rennyi* (K 60274 HOLOTYPE), b) *Inocybe rennyi* (MICH 00041356). Symbols used: S = spores, C = cheilocystidia, P = pleurocystidia. Bar = 10 μ m.

and any of the other characters. None of the variants of *I. chelanensis* studied warrants formal taxonomic recognition.

The basidiospores of a number of the collections of *I. chelanensis* are somewhat polymorphic but with the typical rocket-shaped outline exhibiting basal nodules and an elongated apex clearly predominant. However, certain collections, (i.e., PBM 1870, WTU) produce basidiospores that are strongly polymorphic, exhibiting outlines that ranged from the typical rocket shape to ovate, amygdaliform, rectangular or very irregular with lateral and/or apical nodules present in addition to the typical basal nodules (FIG. 4b). This atypical material agrees in all other respects with *I. chelanensis*. It is interesting to note that quite a few of the basidia present were malformed and some produced two or three sterigmata rather than four (FIG. 4b). Spores still attached in microscopic mounts to these odd basidia sometimes were quite unusual in outline. The polymorphic spores from these collections probably resulted from abnormalities in basidial development. Because of the variation in spore outline, the range in spore size and differences in macroscopic characters among collections of *I. chelanensis*, variants of the species should be interpreted cautiously.

The spores of *I. ortegae* (Esteve-Raventós 2001) also are polymorphic, although their outlines differ somewhat from the atypical collections of *I. chelanensis*. *Inocybe ortegae* differs from *I. chelanensis* primarily in the outline of its spores, although it also differs somewhat in pileus color. In addition, it occurs with species of *Quercus* and *Cistus* rather than with conifers

(Esteve-Raventós 2001). We have not studied *I. ortegae*, but it is only known from the type collection and additional material needs to be found before an assessment of its variability and relationship to *I. chelanensis* can be made.

Inocybe dolichospora is another species occurring outside North America that appears very similar to *I. chelanensis*. The only substantial differences between these two species are that *I. dolichospora* is associated with *Cedrus* in North Africa and that its basidiomata are reported to remain whitish or pale ochraceous until maturity (Malençon and Bertault 1970).

Inocybe rennyi (Berk. & Broome) Sacc., Sylloge Fungorum 5:788. 1887.

FIGS. 5a, b
= *Agaricus rennyi* Berk. & Broome, Ann. Mag. Nat. Hist. Ser. 5, III, p 205. 1879.

Pileus 6–25 mm, broadly convex to nearly plane at maturity, margins not inrolled, most specimens umbonate, sometimes acutely so when young, becoming broadly umbonate in age; surface coarsely radially fibrillose except disk, which is nearly glabrous; context thin; color of herbarium specimens dark, reddish brown to dark brown at disk (7.5YR 3/2–7.5YR 4/4) becoming lighter brown (7.5YR 5/4) toward the margin, some nearly uniform in color. *Lamellae* close, adnate to somewhat adnexed, ventricose; color rusty brown (7.5YR 5/6–4/6) as observed on herbarium specimens; margins fimbriate; lamellulae one tier. *Stipe* 14–30 \times 0.5–2 mm (45–50 mm long for holotype), equal, base with matted mycelium; cortina present, longitudinally fibrillose along entire length, oc-

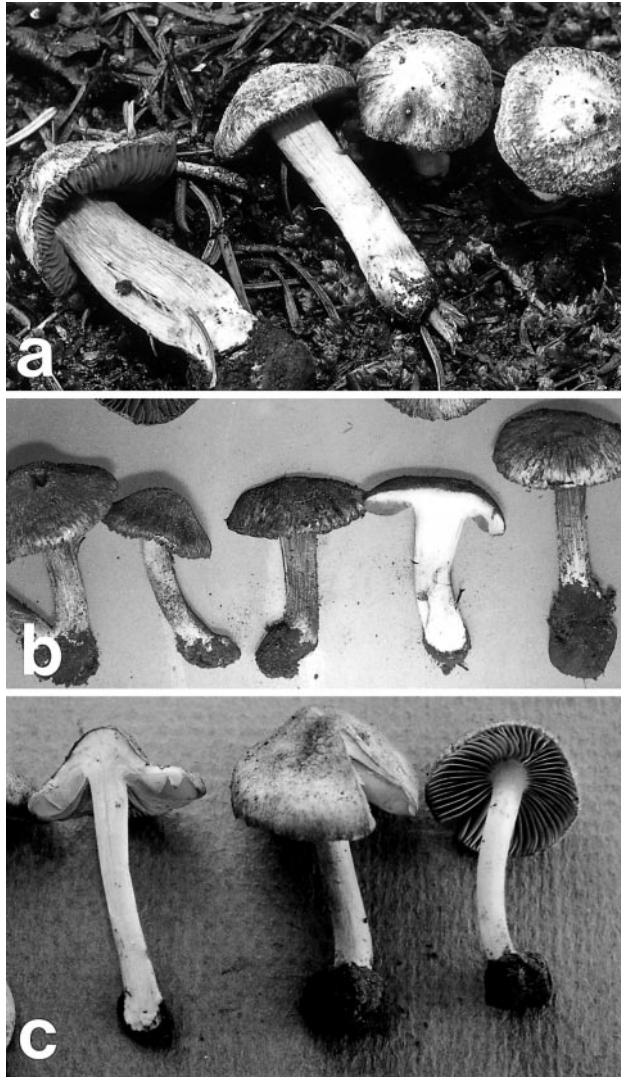


FIG. 6. a) *Inocybe chelanensis* with a heavily developed velipellis and stipe vestiture giving a superficial whitish appearance. b) *Inocybe chelanensis* with a moderately developed velipellis and typical stipe pigmentation. c) *Inocybe candidipes* basidiomata (BK23-Jul-99-26, HOLOTYPE).

asionally lightly pruinose at apex in herbarium specimens; nearly concolorous with the pileus for most specimens except at the apex which is light grayish on herbarium specimens. *Basidiospores* (7.5–)9.5–13.3–16.0(–17) \times 4.5–5.3–6.5(–7.0) μm , (10.5–13.9–19.5 [–22.5] \times 5.0–5.8–7.5 [–9.0] μm for holotype), oddly shaped, extremely polymorphic in size and outline, usually greatly elongated apically, with numerous irregularly formed low nodules and occasional large nodules present along the spore outline; spore color pale yellowish under the microscope (2.5Y 9/4). *Basidia* 24–29 \times 7–9 μm (28–32 \times 9–11 μm for holotype), mostly 4-spored, some producing two spores, poorly reviving and difficult to measure. *Pleurocystidia* 42–62 \times 12–21 μm (53–58 \times 16–24 μm for

holotype), cell walls mostly 1.0–2.0 μm thick and pale yellowish, some thinner (0.5 μm) or thicker (3.0 μm), cellular contents of some also pale yellowish, ovate to fusiform-ventricose with apices that are somewhat papillate to obtuse and often crystalliferous, pedicels often long but sometimes short. *Cheilocystidia* 40–65 \times 13–25 μm (50–62 \times 14–23 μm for holotype), nearly identical to pleurocystidia, cell walls 0.5–1.5 μm thick, some up to 2.5 μm , often pale yellowish, some with yellowish contents, ovate to fusiform-ventricose with papillate to obtuse apices, often with crystals at the apex, pedicels either long or short. *Lamellar trama* of parallel hyphae, 7–15 μm diam, smooth and light yellow as revived in NH_4OH , poorly reviving. *Pileipellis* a dense cutis of poorly reviving hyphae 2–4 μm diam (up to 8 μm for the holotype); hyphae yellowish brown to golden yellow with some light incrustations. *Stipitipellis* apex covered with loosely tangled, mostly hyaline smooth hyphae, 2–5 μm diam, clusters of versiform caulocystidia present at the apex of some specimens, these usually thin-walled, sometimes thick-walled, with or without apical crystals; the stipe middle and base are covered with fairly dense, tangled hyphae that are mostly hyaline, some with light incrustations. *Clamps* present.

Habit, habitat and distribution. Known both from Europe and North America. Collected during spring and summer on the ground in woodlands.

Specimens examined. ENGLAND. Herefordshire, leg. J. Renny, K 60274 (HOLOTYPE K). USA. MASSACHUSETTS. Suffolk County 10 Jul 1916, leg. S. Davis (MICH 00041358); Suffolk County 19 Jul 1918, leg. S. Davis (MICH 00041357), Suffolk County 16 Sep 1918, leg. S. Davis (MICH 00041356).

Comments. *Inocybe rennyi* is a rare species that is known to occur in Europe and is represented in North America by very few collections (Smith 1939). Except where indicated, the above description is based on North American material housed at MICH that agrees very closely with the holotype of *I. rennyi*.

Inocybe rennyi is an unusual fungus that is readily recognized by its polymorphic and oddly shaped spores. In addition to the distinctively elongated, nodulose shape of its spores, *I. rennyi* differs from *I. chelanensis* by its coarsely fibrillose pileus that consistently lacks a velipellis. It differs from *I. texensis* by lacking lilac hues on its stipe and by having thick-walled cystidia. *Inocybe sierraensis* differs from *I. rennyi* by having both whitish basidiomata and thin-walled cystidia. Little information is available about the habitat or hosts of *I. rennyi* because none of the specimens examined contained notes on habitat. Heim (1931) indicates that it might occur in montane environments or, in one instance, on the ground

in "Dinedor Fir Wood", while Alessio and Rebaudengo (1980) list hardwoods as associated hosts.

We are aware of only five specimens from North America that have been identified as *I. rennyi* (Smith 1939, Stuntz 1947). Three of these, collected in Massachusetts, are housed in MICH, and these are the only North American specimens that agree accurately with the holotype for this species. Many of the basidiomata in the MICH collections have caulocystidia at the stipe apices. We could not confirm the presence of caulocystidia on the holotype because the specimens are glued to a cardboard card and the surface of the stipe apex has now almost disappeared from the specimen. However, caulocystidia were nicely illustrated by Stangl (1975) from holotype material. He indicates their presence on the upper third of the stipe, while on the MICH material they are present only on the extreme apex.

The other two North American specimens were reported by Stuntz from Washington (Stuntz 1947). These specimens both vary to differing degrees from the holotype of *I. rennyi* and they also are quite different from one another. One of them (Stz 610, WTU) has a dark brown, squarrose to lanuginose, convex pileus that, as was noted by Stuntz, strongly resembles that of *I. lanuginosa* (Bull. : Fr.) Kummer. Except for its spores, we do not believe that this collection fits the type-concept of *I. rennyi* and have excluded it from our description. It might be an aberrant developmental form of one of the species in the *I. lanuginosa* group. The other collection (Stz 438, WTU) more closely resembles the holotype of *I. rennyi* but differs by having longer hymenial cystidia, somewhat different colors and by being more robust.

The status of *I. rennyi* has been somewhat controversial. Most authors have retained it as an autonomous taxon while pointing to its strong similarity to *I. cicatricata* Ellis & Everh. or *I. curvipes* P. Karst. Heim (1931), for example, emphasized that *I. rennyi* differs from *I. cicatricata* only in its elongated spores. Stangl and Enderle (1983) also indicated that the two species can be separated only microscopically. Alessio and Rebaudengo (1980) go further and, although they treat *I. rennyi* as an autonomous species, they pose the question of whether *I. rennyi*, *I. cicatricata* and *I. lanuginella* Schroet. (= *I. curvipes*) all are synonyms. Esteve-Raventós (2001) more recently discussed the similarities between *I. rennyi* and *I. curvipes*, expressing the view that an elongation of *I. curvipes* spores would give rise to spores like those of *I. rennyi*. Esteve-Raventós also indicates that the smaller spores present in the holotype of *I. rennyi* resemble the spores of *I. curvipes*. Our observations of the *I. rennyi* holotype agree with those of Esteve-Raventós (2001). We concur that the presence of *curvipes*-type

spores in specimens of *I. rennyi*, the macroscopic similarities between the two, and the similarities between the cystidia of *I. rennyi* and *I. curvipes* call the recognition of two taxa into question.

Two of the collections of *I. rennyi* housed at MICH (00041356, 00041358) are mixed and contain basidiomes that correspond to both *I. rennyi* and *I. curvipes*. Except for the topology of the spores, the basidiomes in these collections are indistinguishable. Under the assumption that the basidiomes in these mixed collections were produced from the same mycelium, the unusual mix of these particular species within two separate collections suggests once again that the two names could represent a single taxon.

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