

Phylogenetic taxonomy of the *Inocybe splendens* group and evolution of supersection “Marginatae”

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Abstract: A phylogenetic and taxonomic study of the *Inocybe splendens* complex in western North America is presented. Our analysis indicates that western North American and European specimens referable to *I. splendens sensu lato* cluster into eight clades and that European and western North American representatives of this taxon are not conspecific. Section *Splendentes* and supersection “Marginatae” of *Inocybe*, smooth-spored taxa characterized by a syndrome of unique developmental characters (entirely or mostly pruinose stipe, absence of cortina, frequent presence of marginate basal bulb) are not monophyletic. The species concept for *I. splendens* is discussed, and a lectotype for *I. splendens sensu Heim* is designated. Two new species, *I. monticola* and *I. praecox*, are illustrated and described. The poorly known species *I. bakeri* is redescribed from type material, and a key for 22 species is provided for identification of these and other non-reddening species with smooth spores and a caulocystidiate stipe reported from North America and Europe.

Key words: Agaricales, Basidiomycota, Inocybaceae, species, systematics

INTRODUCTION

Our understanding of the systematics of agarics in North America often lags behind that for other parts of the world. Genus *Inocybe* is an especially good example of this. Even though a number of studies have examined specific taxonomic groups within *Inocybe* (Matheny and Kropp 2001, Kropp and Matheny 2004) or documented species within certain parts of the continent (Cripps 1997; Grund and

Stuntz 1968, 1970, 1975, 1977a, b, 1980, 1981, 1983, 1984; Nishida 1989; Stuntz 1947, 1954) there is no comprehensive monograph of the genus for North America. Partly as a consequence many of the names applied to North American species of *Inocybe* are based on European monographs or floristic treatments such as Kuyper (1986), Stangl (1986) or Moser (1983). Even though European specimens of *Inocybe* often are used to help characterize morphological species from North America relatively few studies have taken advantage of molecular phylogenetic analyses to help assess the fit between European species concepts and North American taxa. For certain species of *Inocybe* that encompass an especially wide range of variation, molecular data may be very useful for sorting out species recognition (Taylor et al. 2000, Taylor et al. 2006).

Inocybe splendens Heim is an example of a species found in Europe and reported from western North America (Nishida 1989) that has a broad morphological species concept. It is also of some economic importance because it has been reported to be a potential contaminant in truffle production. Thus sorting out species recognition within the *I. splendens* complex is pertinent to the truffle industry (Iotti et al. 2005). The most current and widely accepted concept for *I. splendens* is that held by Kuyper (1986) and Stangl (1989). As circumscribed by both of these authors *I. splendens* comprises two varieties, var. *splendens* Kuyper and var. *phaeoleuca* (Kühner) Kuyper, and encompasses a broad range of morphological variation. Indeed Horak (2005) treats *I. phaeoleuca* as a synonym of *I. splendens* in a mycofloristic treatment of European Agaricales. The species as a whole can be roughly characterized as having smooth spores, metuloids on the edges and sides of the lamellae, the absence of cortina, an almost entirely caulocystidiate stipe and a basal bulb (FIG. 1a). However much macroscopic variation has been attributed to individual specimens of *I. splendens* (FIG. 1b) and individuals vary greatly in stature and pileus ranges from dark reddish brown to ochraceous (Kuyper 1986, Stangl 1989 color plates 21, 22).

In his monograph of smooth-spored species of *Inocybe* in Europe Kuyper (1986) notes that, even though extreme macroscopic variations sometimes can be found within *I. splendens*, all variants are identical microscopically. Assuming the phenotype of *I. splendens* is influenced by environmental factors,

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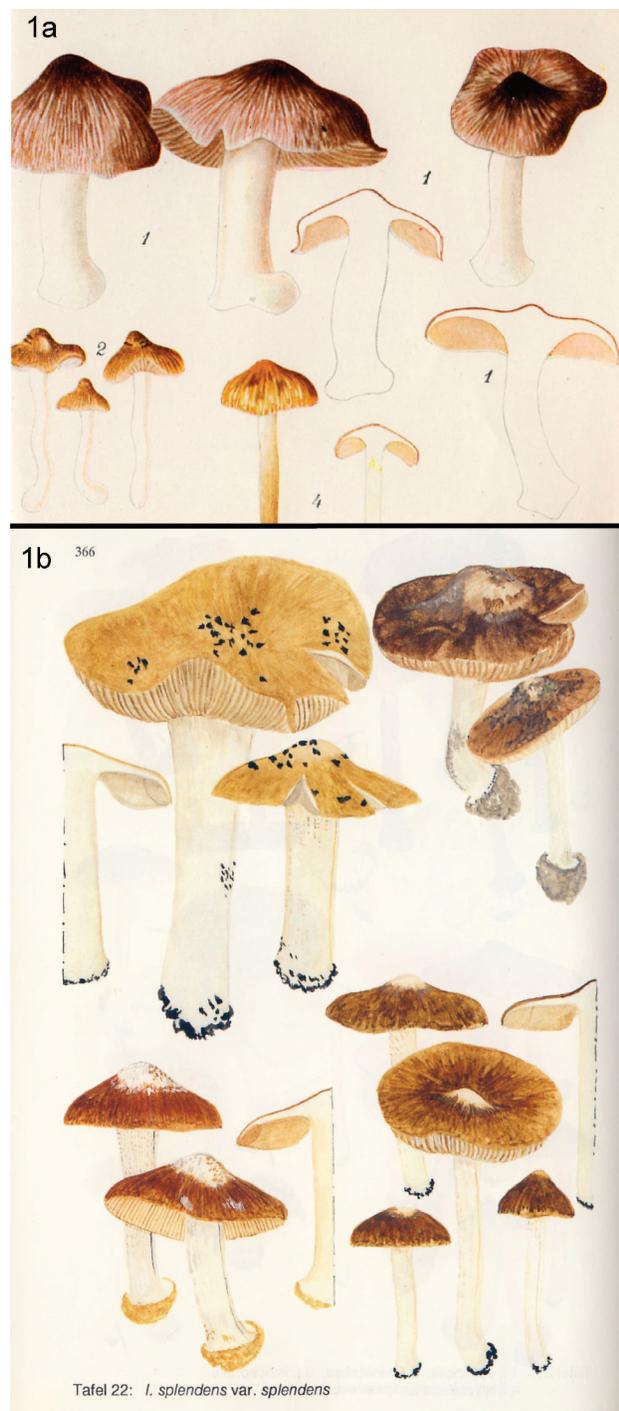


FIG. 1. Illustrations of *Inocybe splendens* from Europe. a. Heim plate XVI. Reproduction of the original icons of *I. splendens* (labeled 1) in Heim (1931). b. Icons of different color and developmental forms attributed to *I. splendens* in Stangl (1989). Note differences in basal bulb morphology, pileus color and presence or absence of a velipellis on the pileus.

Kuyper logically concludes that only one species with two well delimited varieties should be accepted and that recognizing each of the variants at a species level would produce an unnecessarily large number of species. However not all authors agree with such a broad species concept for *I. splendens* (Esteve-Raventós and Ortega 1995, Bon 1997).

Inocybe splendens serves as the type of *Inocybe* section *Splendentes* in Singer (1986). Section *Splendentes* encompasses taxa having an entirely or mostly pruinose stipe, an often marginate bulb and a veil, which if visible connects the pileus margin and stipe base. Characters such as these often are used to classify species within *Inocybe* (Kuyper 1986, Stangl 1989), presumably because they are thought to reflect basidiome ontogeny. However, as Singer (1986) pointed out, the use of ontogenetic criteria in agaric taxonomy is still provisional and relatively little has been done to learn how well such characters reflect evolutionary trends. Obtaining molecular data for the *I. splendens* complex is not only useful for sorting out the taxonomy of the group it also provides an opportunity to analyze evolutionary origins of the pruinose stipe and associated group of traits (absence of cortina, caulocystidiate stipe) that is both characteristic of section *Splendentes* and other taxa and widely used in *Inocybe* systematics.

Our fieldwork in western North America confirms Kuyper's observation that material referable to *I. splendens* indeed is variable macroscopically and that different collections of the species show relatively little variation for microscopic characters. In this article we carry out a preliminary evaluation of the species concept for *I. splendens* in North America by subjecting material from the western United States and Europe to a phylogenetic analysis. We also reconstruct the evolution of *Inocybe* species that bear entirely pruinose or caulocystidiate stipes and show this character is derived within *Inocybe* and evolved independently on several occasions.

MATERIALS AND METHODS

North American specimens referable to *I. splendens* var. *splendens* and var. *phaeoleuca* were collected from different parts of the western United States. Examples of European material were obtained as a loan from TUR (Herbarium, University of Turku, Finland). Material representing *I. leiocephala* Stuntz and *I. bakeri* Peck also was studied because of the morphological similarity these species have to *I. splendens*. Herbarium abbreviations follow Holmgren et al. (1990).

Microscopic study of specimens was done with a light microscope after rehydrating and examining material in 10% NH_4OH . All microscopic measurements were done with oil immersion at 1000 \times , and whenever possible

basidiospores were measured from spores deposited on stipes to avoid measuring immature spores. Spore measurements are given as averages and ranges while measurements of the other cells are given as ranges. Color notes from fresh material were taken from the Munsell book of color (Munsell Color 1976), Ridgway (1912) and Kornerup and Wanscher (1967).

DNA was extracted at Utah State University from the dried herbarium specimens with standard protocols (Kropp et al. 1996). Partial DNA sequences were obtained for the nuclear large ribosomal subunit (nLSU) between primers LROR and LR5 (Moncalvo et al. 2000). Direct sequencing of the PCR products in both directions was done with primers LROR and LR5 with internal primers LR22 and LR3R (Moncalvo et al. 2000). Protocols for DNA extraction, PCR and DNA sequencing at Clark University follow Frøslev, Matheny, Hibbett (2005) and Matheny et al. (2007). Sequence chromatograms were edited with Sequencher software 4.7 (Gene Codes Corp., Ann Arbor, Michigan). All sequences were checked for accuracy with the reverse sequences and deposited in GenBank.

Taxon sampling focused on members of section *Splendentes* (Singer 1953, 1986) and other taxa with smooth or nodulose spores and caulocystidiate stipes in the *Inocybe* clade (phylogenetic nomenclature follows Matheny and Bougher (2006)). A total of 43 of the 44 accessions represent the *Inocybe* clade and one the *Pseudosperma* clade. The latter was used for outgroup purposes, together with sequences of *I. calamistrata* of the *Inosperma* clade. Previously published nLSU sequences (*I. "geophylla"*, EF530936; *I. geophylla* "var. *lilacea*", AF042616; *Inocybe* sp. WT11, DQ273437; *I. fibrosa*, AY586681; *Inocybe* sp., AF33545; and *I. petiginosa*, AF261510) were merged with 47 taxa from the 84-taxon dataset of Matheny (2005) and four taxa from Kropp and Matheny (2004). To this we added 81 new sequences produced from 48 accessions (TABLE I). In total sequences from 101 specimens were sampled.

Sequence data of the first 900–1400 base pairs of nLSU, *rpb1* domains A and C, *rpb1*-intron2 and 3 and *rpb2* between domains 6 and 7 were aligned manually in MacClade 4.0 (Maddison and Maddison 2000). The dataset is available at http://www.bio.utk.edu/matheny/Site/Alignments_%26_Data_Sets.html. These data then were assembled into an interleaved supermatrix with PAUP* 4.0b10 (Swofford 2003). Sequences of nLSU, *rpb1* and *rpb2* were separated into eight partitions to enable separate model estimates for nLSU sites, *rpb1*-intron2 and intron3 sites, and first, second and third codon positions from both *rpb1* and *rpb2* coding regions. The eight partitions then were analyzed with the parallel version of MrBayes 3.1.1 (Ronquist and Huelsenbeck 2003, Altekar et al. 2004). The dataset was subject to two independent runs of 10 000 000 generations each followed by a subsequent run of 20 000 000 generations. This procedure ensured that the average standard deviation of split frequencies reached less than 0.01, a convergence diagnostic that measures similarity of tree samples from different runs. Trees were sampled every 10 000 or 20 000 generations, and those that reached stationarity according to the convergence diagnostic were pooled to compute

posterior probabilities. Five hundred bootstrap replicates were performed with maximum parsimony (MP) and a full heuristic search with 10 random addition sequences, SPR swapping algorithm and MULTREES off.

Ancestral state reconstruction analysis.—Taxa that demonstrate a "caulocystidiate" stipe (metuloid caulocystidia descending to the base of the stipe or at least beyond the stipe center and with the exception of *I. sindonia* lacking cortina) were scored 1; those with metuloid caulocystidia restricted to the stipe apex or lacking them entirely were scored 0 in the data editor of MacClade. The character state for outgroups of the *Inocybe* clade is 0. These data are based on personal observations of specimens sequenced and from literature sources (Moser 1983, Stangl 1986, Kuyper 1986) for species retrieved from NCBI. Bayesian trees sampled from the MCMC posterior distribution then were stored in the MacClade file. The caulocystidiate character was charted on all trees, and the number of transitions of this character was counted after resolving all polytomy. Character states were equally weighted and unordered.

Testing alternative tree topologies.—Species of section *Splendentes* (Singer 1996) and supersection "Marginatae" (Kuyper 1986) were constrained to be monophyletic in MacClade. These two constraint topologies then were loaded and filtered in PAUP* against all trees sampled from the MCMC posterior distribution. If less than 5% of the unconstrained trees matched a constraint ($P < 0.05$) we considered the constraint topology significantly rejected (Yang et al. 2005).

RESULTS

Forty-eight nLSU, 19 *rpb1* and 14 *rpb2* sequences were newly generated for this study. A total of 3480 characters were assembled for phylogenetic analysis (TABLE I). A total of 1481 characters were used from nLSU, 616 characters from *rpb1*-intron2 and intron3, 678 exon characters from *rpb1* and 705 exon characters from *rpb2*. Nine ambiguously aligned characters of *rpb1*-intron2 were excluded. All taxa (101) were represented by nLSU sequences. Sixty-five taxa were represented by *rpb1*-intron2 and 3, 66 taxa by *rpb1* exons and 57 taxa by *rpb2* exons. Of the 3480 total sites, 1094 were parsimony informative. The average standard deviation of split frequencies did not reach < 0.01 until generation 18 414 000 in the MCMC runs set to 20 000 000 generations (this metric was not achieved at all in the analysis set to 10 000 000 generations). Thus 793 trees were sampled from the last 1 586 000 generations from two independent runs in this analysis for a total of 1586 trees sampled from the posterior distribution. We produced a Bayesian 50% majority rule consensus tree (FIG. 2). Significantly supported nodes are indicated by filled circles. If the PP for a given node is < 0.95 , but the bootstrap

TABLE I. Newly generated DNA sequences^a used in the phylogenetic analysis with collection data and GenBank numbers

Species ^b	Origin	Collection ^c	GenBank		
			nLSU	rpb1	rpb2
<i>Inocybe albidisca</i>	Washington, USA	PBM1390 WTU	EU307819	EU307820	EU307821
<i>Inocybe "asterospora"</i>	New York, USA	PBM2453 CUW	AY702015	DQ447914	—
<i>Inocybe alabamensis</i>	Texas, USA	PBM1892 WTU	AY536280	AY536282	AY536281
<i>Inocybe actinospora</i> nom prov	Argentina	D25 WTU	AY536280	AY536282	AY536281
<i>Inocybe bakeri</i>	California, USA	ST0207701 WTU	EU307827	—	—
<i>Inocybe fraudans</i>	Washington, USA	JFA11831 WTU	EU433887	EU433888	EU433889
<i>Inocybe griseolilacina</i>	Tennessee, USA	PBM2661 CUW	EU307828	EU307829	EU307830
<i>Inocybe fibrillosibrunnea</i>	W. Australia, Australia	E5971 WTU	EU307848	EU307849	EU307850
<i>Inocybe fuliginеоatra</i>	Tennessee, USA	PBM2662 CUW	EU307831	EU307832	EU307833
<i>Inocybe hirtella</i>	Tennessee, USA	PBM2650 CUW	EU307822	EU307823	—
<i>Inocybe</i> cf. <i>hirtella</i>	Tennessee, USA	PBM2594 CUW	EU307826	—	—
<i>Inocybe</i> cf. <i>hirtella</i>	Tennessee, USA	PBM2619 CUW	EU307825	—	—
<i>Inocybe</i> cf. <i>hirtella</i>	Tennessee, USA	PBM2624 CUW	EU307824	—	—
<i>Inocybe intricata</i>	Tennessee, USA	PBM2600 CUW	EU307835	EU307836	—
<i>Inocybe luteifolia</i>	Tennessee, USA	PBM2642 CUW	EU307814	EU307815	EU307816
<i>Inocybe leioccephala</i> (= <i>I. catalaunica</i>)	Utah, USA	UTC 248129	EU499605	—	—
<i>Inocybe leioccephala</i> (= <i>I. catalaunica</i>)	Washington, USA	UTC 248128	EU499607	—	—
<i>Inocybe olympiana</i>	Washington, USA	PBM2219 WTU	EU307841	EU307842	—
<i>Inocybe paludinella</i>	New Hampshire, USA	PBM2552 WTU	AY32209	EU307843	EU307844
<i>Inocybe phaeoleuca</i>	Germany	TURA171481	EU499618	—	—
<i>Inocybe "phaeoleuca"</i> (= <i>I. catalaunica</i>)	Utah, USA	UTC 248131	EU499604	—	—
<i>Inocybe "phaeoleuca"</i> (= <i>I. catalaunica</i>)	Wyoming, USA	UTC 248130	EU499606	—	—
<i>Inocybe "phaeoleuca"</i>	Utah, USA	UTC 248119	EU499617	—	—
<i>Inocybe queletii</i>	Finland	JV19682F CUW	EU307813	—	—
<i>Inocybe rimosa</i>	Massachusetts, USA	PBM2574 CUW	EF561633	EU307857	EU307858
<i>Inocybe</i> cf. <i>sindonia</i>	Washington, USA	UTC 248126	EU499601	—	—
<i>Inocybe</i> cf. <i>sindonia</i>	Washington, USA	UTC 248127	EU499602	—	—
<i>Inocybe</i> sp.	New York, USA	PBM2449 CUW	EU307818	—	—
<i>Inocybe</i> sp.	Argentina	GDa TENN	EU600895	—	—
<i>Inocybe</i> sp.	Australia	PBM2181 CUW	EU307851	EU307852	EU307853
<i>Inocybe</i> sp.	Ontario, Canada	NI250904 CUW	EU307834	—	—
<i>Inocybe</i> sp.	Slovakia	SA100602A CUW	EU307837	—	—
<i>Inocybe</i> sp.	Slovakia	SA100602B CUW	EU307838	—	EU307839
<i>Inocybe splendens</i>	Latvia	TURA147681	EU499612	—	—
<i>Inocybe splendens</i>	Latvia	TURA147679	EU499611	—	—
<i>Inocybe "splendens"</i>	Washington, USA	UTC 248118	EU499603	—	—
<i>Inocybe "splendens"</i> (= <i>I. monticola</i>)	Utah, USA	UTC 248120	EU499608	—	—
<i>Inocybe "splendens"</i> (= <i>I. monticola</i>)	Utah, USA	UTC 248121	EU499609	—	—
<i>Inocybe "splendens"</i> (= <i>I. monticola</i>)	Oregon, USA	UTC 248122	EU499610	—	—
<i>Inocybe "splendens"</i> (= <i>I. praecox</i>)	Washington, USA	UTC 248123	EU499614	—	—
<i>Inocybe "splendens"</i> (= <i>I. praecox</i>)	Washington, USA	UTC 248124	EU499615	—	—
<i>Inocybe "splendens"</i> (= <i>I. praecox</i>)	Washington, USA	UTC 248125	EU499616	—	—
<i>Inocybe stellatospora</i>	Minnesota, USA	PRL 2716 MIN	EU307840	—	—
<i>Inocybe subexilis</i>	Tennessee, USA	PBM2620 CUW	EU307845	EU307846	EU307847
<i>Inocybe terrifera</i> (= <i>Inocybe</i> sp. ^d)	Germany	TURA171482	EU499613	—	—
<i>Inocybe tubarioides</i>	North Carolina, USA	PBM2550 CUW	AY732211	EU307854	EU307855
<i>Inocybe tubarioides</i>	New Hampshire, USA	PBM2570 CUW	AY732210	EU307856	—
<i>Inocybe violaceocaulis</i>	W. Australia, Australia	PBM2164 WTU	AY732208	EU307817	—

^a See Kropp and Matheny 2004, Matheny 2005 for additional sequences used in generating Fig 2.

^b Species name as given in FIG. 2 refers to the original identity on the herbarium specimen; new names assigned to the specimen as a result of the phylogenetic analysis are given in parentheses.

^c Collection or herbarium accession number used in FIG. 2; Herbarium abbreviations follow Holmgren et al. (1990).

^d Examination of the specimen labeled *Inocybe terrifera* indicates that this is not the correct species name for the specimen.

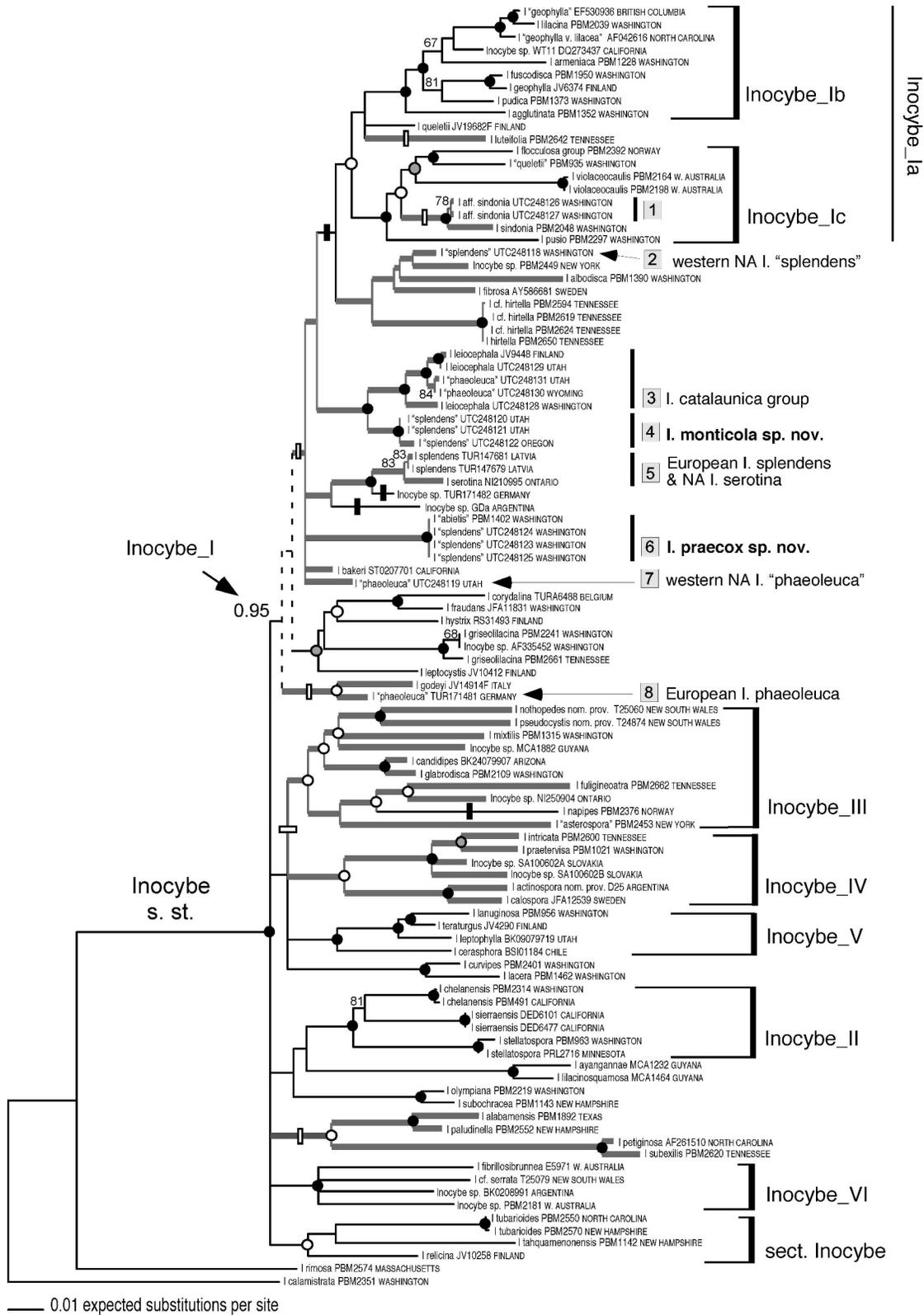


FIG. 2. A Bayesian 50% majority rule consensus tree of *Inocybe* sensu stricto clade. Black-filled circles indicate nodes that receive > 0.95 PP and > 70% BP; gray-filled circles indicate nodes that receive > 0.95 PP and 50–69% BP; white-filled circles indicate nodes that receive > 0.95 PP but < 50% BP. Internodes that receive > 50% BP but < 0.95 PP are indicated with the BP value for that node. At least eight clades that conform to a broad morphological species concept of *I. splendens* are

proportion (BP) is greater than 50%, then the BP value is indicated for that node. Species with caulocystidiate stipes are indicated by gray branches.

North American and European exemplars referable to the broad morphological concept of *I. splendens sensu* Kuyper are distributed in at least eight labeled lineages (FIG. 2). At least two of these lineages (clades 4 and 6) represent undescribed taxa, and two more are potentially undescribed but currently lack sufficient material to be accurately described. All eight lineages are clustered in Inocybe_I of *Inocybe sensu stricto* (Matheny et al. 2002, Matheny 2005). Inocybe_I receives a PP of 0.95 but weak bootstrap support (BP < 50%) in our supermatrix analysis but is now composed of at least 38 species of *Inocybe*, 36 of which bear smooth basidiospores, as opposed to angular or nodulose spores. This is the first result where nodulose-spored species *I. albodisca* and *I. fibrosa*, two caulocystidiate species, cluster in what is otherwise the predominantly smooth-spored Inocybe_I.

Section *Splendentes* is not monophyletic. European exemplars of *I. phaeoleuca* (lineage 8) and *I. splendens* (lineage 5), the North American *I. luteifolia* (clade Inocybe Ia) and European and North American exemplars of *I. catalaunica* fail to cluster in a single cohesive group. Constraint topologies that enforced the monophyly of section *Splendentes* and supersection “Marginatae” received *p*-values of 0.00; that is none of the 1586 trees sampled from the MCMC posterior distribution produced a topology that matched the two topological constraints.

Fifty-one taxa were scored with the non-caulocystidiate state and 50 with the caulocystidiate state. A parsimony ancestral state reconstruction (ASR) analysis of all trees sampled from the MCMC posterior distribution indicates the caulocystidiate state has undergone 9–11 transitions. The average gain of the caulocystidiate condition was 5.4 times. The average loss (reversal) of the caulocystidiate condition was 4.4 times. *Inocybe napipes* represents an unambiguous instance where the caulocystidiate state has been reversed. *Inocybe* sp. GDa, a *Salix* associate and indigenous to Argentina, represents a reversal of this condition as well. Many species of Inocybe_Ia evolved

from caulocystidiate ancestors. We recorded 10 transitions (six gains, four losses) of the caulocystidiate state under a parsimony procedure of a random tree drawn from the MCMC posterior distribution (FIG. 2).

Significant support also is generated for a clade of smooth-spored species of *Inocybe* with a temperate distribution in the South Pacific. This clade is labeled Inocybe_VI (FIG. 2).

DISCUSSION

Evolution of caulocystidiate species of Inocybe.—Species of *Inocybe* with caulocystidia distributed beyond the center of the stipe and often to the stipe base are not monophyletic. Indeed strong statistical support rejects the monophyly of section *Splendentes* and supersection “Marginatae”. This result was reported originally in Matheny et al. (2002) in discussion of the nonmonophyly of supersections “Marginatae” and “Cortinatae” of Kuyper (1986). This result was upheld by expanded taxon and gene sampling in Matheny (2005). A total of 49 of 101 species in our dataset that produce caulocystidia as metuloids beyond the stipe center also do not produce cortina. Thus it is likely these two character states are highly correlated (Kuyper 1986). At least one exception occurs in the development of *I. sindonia*, discussed in detail by Kuyper (1986).

It is clear from our current understanding of Inocybaceae systematics that the evolution of caulocystidiate species, coupled with the absence of cortina, are derived character states. Although at least two species of *Auritella* (Matheny and Bougher 2006) have never been observed with cortina none of the early diverging major clades outlined by Matheny (2005) include taxa that bear metuloids anywhere on the basidiomata. However it is clear from the ASR analysis that the caulocystidiate condition has been lost (reversed) repeatedly, including in *I. napipes*, *Inocybe* sp. GDa from Argentina, *Inocybe* sp. TUR171482, and the common ancestor of at least 20 species in clade Inocybe_Ia. At least two independent transitions to the caulocystidiate state are observed among nodulose-spored clades (considering Inocybe_III and Inocybe_IV are monophyletic) and in the weakly supported

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indicated. Species with caulocystidiate stipes are marked with thickened gray branches. Internodes are reconstructed as caulocystidiate, according to an ASR analysis of a random tree drawn from the MCMC posterior distribution. This reconstruction illustrates at least 10 transitions (six gains as white bars and four losses as black bars) of the caulocystidiate character in the *Inocybe sensu stricto* clade. However as many as 11 transitions are possible depending on the tree topology. The taxa sampled are identified by collection numbers and location (see Table I; Kropp and Matheny 2004, Matheny 2005) except for six previously published sequences available on GenBank that are listed by their accession numbers in the text.

clade represented by *I. subexilis*, *I. petiginosa*, *I. alabamensis* and *I. pahudinella*.

Species concept for Inocybe splendens.—Our species concept for *I. splendens* corresponds to the original description of the species by Heim (1931) instead of the broader concept of Stangl (1989) and Kuyper (1986), which placed several species in synonymy.

European specimens of *I. splendens* and *I. phaeoleuca* occur in two separate clades (5 and 8). This suggests that Kühner's concept for *I. phaeoleuca* as a taxon distinct from *I. splendens* should be retained (Kühner 1955). Although we did not obtain DNA sequence data from the examined holotype of *I. phaeoleuca*, the specimen of this species from Germany (TUR 171481) included in our phylogenetic analysis corresponds very well to the holotype and accurately represents the species.

Our studies of type material of both *I. alluvionis* Stangl & Veselský and *I. terrifera* Kühner, which had been synonymized by Kuyper (1986) and Stangl (1989) with *I. splendens*, indicate that the two taxa are very similar microscopically to one another and to *I. splendens* Heim. However both taxa differ macroscopically from *I. splendens sensu* Heim (1931) by having an ochraceous to yellow-brown pileus compared to the darker brown pileus of *I. splendens* (Kühner 1955, Stangl and Veselský 1976). An additional difference between *I. terrifera* Kühner and *I. splendens* Heim is that *I. splendens* possesses a marginately bulbous bulb while *I. terrifera* does not. Further work on European representatives of these taxa will be necessary to determine fully whether they should be kept separate or synonymized. We treat them here as distinct taxa because of our finding that *I. splendens* and *I. phaeoleuca* should not be synonymized and because of morphological differences among *I. alluvionis* Stangl & Veselský, *I. terrifera* Kühner and *I. splendens* Heim.

No type specimen exists for *I. splendens* because Heim's material in P (Muséum National d'Histoire Naturelle) has been lost (Dr Bart Buyck, Muséum National d'Histoire Naturelle, Paris, pers comm). Thus we designate Heim's watercolor painting of this species in Heim (1931) as the lectotype for the species (FIG. 1a is reproduction). Either the collection of *I. splendens* from Latvia (TUR 147679) used in our phylogenetic analysis or a collection from France (AF 3130) cited below could serve as an epitype for the species. A comparison of the nuclear LSU sequences from these two specimens reveals that they have 99 percent similarity to one another. However Heim's description and painting are unambiguous and are sufficient to represent *I. splendens* without being supported by an epitype.

Specimens examined. *Inocybe alluvionis* Stangl & Veselský. GERMANY. Augsburg, Göggingen, 28 Jun 1968, leg. J. Stangl, det. J. Stangl & J. Veselský (HOLOTYPE, PRM 756100). *Inocybe phaeoleuca* Kühner. FRANCE. Paris, Bois de Vincennes, 5 Sep 1934, leg./det. R. Kühner (LECTOTYPE, G 451876); GERMANY, Baden-Württemberg, Inzigkofen, 30 Sep 1980, leg. J. Vauras, revid. J. Stangl. (TUR 171481). *Inocybe splendens* Heim. FRANCE. Metz, 28 Aug 2006, leg./det. A. Ferville et J. Guinberteau (Herb. A. Ferville No. AF3130) (GenBank GO892828); FRANCE. Oise, Forêt de Laigue, Sep 1999, leg. G. Tassi, det. G. Tassi & R. Courtecuisse (Herb. G. Tassi No. 99090); LATVIA. Jūrmala, Kemerī, 27 Sep 1996, leg. I. Krastina, det. J. Vauras (TUR 147681); LATVIA. Jūrmala, Kemerī, 25 Sep 1996, leg. I. Avota, det. J. Vauras (TUR 147679). *Inocybe terrifera* Kühner. FRANCE. Paris, Bois de Vincennes, 9 Aug 1931, leg./det. R. Kühner (LECTOTYPE, G 388274).

North American taxa.—The finding that none of the western North American material referable to *I. splendens* clustered together with material from Europe was unexpected. We would have expected at least some of the European and North American material to cluster together in spite of the fact that *I. splendens sensu lato* in western North America is clearly polyphyletic. Because only western North America was sampled in our study it eventually might turn out that specimens from other parts of the continent do in fact cluster with their European counterparts. Nonetheless our data indicate that exemplars referable to *I. splendens* from Europe and western North America are not conspecific. Thus neither *I. splendens* nor *I. phaeoleuca* can yet be applied to taxa found in western North America. We are aware of one report of *I. phaeoleuca* from eastern North America (Grund and Stuntz 1968). Our study did not include this material, but it should be noted that its submarginate basal bulb on the stipe is more consistent with specimens from clade 7 in this study than it is with *I. phaeoleuca*. Kühner's original description of *I. phaeoleuca* is explicit in saying that the stipe of *I. phaeoleuca* is equal and without a marginate bulb (Kühner 1955).

The material in clades 4 and 6 both represent undescribed taxa that differ phylogenetically and morphologically from other accepted species of *Inocybe*. Each is described as new species below and included in a key that allows them to be separated from similar taxa. Another of the specimens from western North America that was identified as *I. splendens* var. *phaeoleuca* in clade 7 is different from European material going by this name based on sequence data. It is also different from any of the other material from western North America that we studied although it might be related to *I. bakeri*. Although it corresponds in many ways to *I. phaeoleuca* Kühner it differs by having a submarginate to

marginate bulb at the stipe base. It potentially represents an undescribed taxon although more specimens are required before a formal species description can be made.

In contrast to the material assigned to *I. splendens sensu lato* specimens representing *I. catalaunica* Sing. (= *I. leiocephala* Stuntz, according to Esteve-Raventós 1997) from both Europe and western North America are monophyletic (FIG. 2, clade 3). However even though exemplars of this taxon form a robust monophyletic group this lineage encompassed a broader range of morphological variation than expected and included material that we originally had considered to be representatives of *I. splendens* var. *phaeoleuca*.

A detailed examination of both of *I. phaeoleuca* and *I. catalaunica* reveals relatively few morphological differences between them beyond stipe color and size of the pileus. *Inocybe catalaunica* is characterized by a reddish-brown stipe, while *I. phaeoleuca* tends to have a whitish stipe, although the stipe in this species ranges from white to pale ochraceous or even brown at the base. Another difference is that the spore apices of *I. phaeoleuca* are subconical while they often are described as being obtuse for *I. catalaunica* even though Bon (1984) recognized a variant of *I. catalaunica* with subconical spore apices (as *I. subbrunnea* Kühner var. *subconicospora*, = *I. leiocephala sensu* Kuyper 1986). Given the normal range in stipe coloration for *I. phaeoleuca* and the variation in the form of the basidiospore apices within *I. catalaunica*, our finding that specimens referable to both taxa cluster together in a single clade is perhaps not surprising.

The lineage represented by clade 3 includes material from both Europe and North America that is quite typical of the species as described by Singer (Esteve-Raventós 1997) and Stuntz as *I. leiocephala* (1950) in having a dark brown pileus with a brownish to incarnate stipe. However the other exemplars in the lineage are morphologically variable and differ to varying degrees from the currently accepted species concept for *I. catalaunica*. Certain specimens in clade 3 have white to pale brownish stipes while their pilei range from tan to medium yellow-brown. The spore apices range from obtuse to subconical although the predominant shape is subconical.

Based on our results, the species concept for *I. catalaunica* could be broadened to include specimens with both obtuse and subconical spore apices. It also could be expanded to include variants with stipe ranging from white to reddish brown, as well as variants in pileus ranging from dark brown to tan. Under this broadened concept most of the material that we originally had referred to *I. splendens* var. *phaeoleuca* in the western United States instead would

be referred to *I. catalaunica*. Our sequence data indicate that *I. phaeoleuca* equivalent to that in Europe may not occur in the western United States. However, because the type of *I. leiocephala* is from Washington state and the specimen sequenced from Washington is strongly supported as sister of sequences of collections from Utah, Wyoming and Finland (FIG. 2), it might be that *I. leiocephala sensu* Stuntz occurs in the Pacific Northwest as an autonomous species. Further work will be required to dissect species concepts for this clade, and for now we simply treat it as the *I. catalaunica* "group".

Two of our specimens originally thought to be *I. splendens* var. *phaeoleuca* clustered with *I. sindonia* (clade 1). The stipe covering in *I. sindonia* is variable and may be either partially or completely pruinose (Kuyper 1986). Therefore mature specimens with an entirely pruinose stipe might be misidentified. Our material is characterized by a darker pileus than that normally reported for *I. sindonia* along with broader cystidia and slightly larger spores. The specimens also had cystidia to the base of the stipe. Although a detailed study of *I. sindonia* is beyond the scope of our study our data suggest that further work on the variation within *I. sindonia* and its allies is needed.

TAXONOMY

KEY TO NON-REDDENING NORTH AMERICAN² SPECIES OF *INOCYBE* WITH SMOOTH SPORES AND A CAULOCYSTIDIATE STIPE

- | | |
|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------|
| 1. Pileus whitish to buff. | 2 |
| 1. Pileus some shade of yellow or brown | 3 |
| 2. Pleurocystidia rare, flavor minty; pileus
–38 mm, convex, smooth and silky; stipe
entirely pruinose, 120 × 9 mm; spores 9–10 ×
5.5–6 μm | <i>Inocybe menthi-gustans</i> Nishida |
| 2. Pleurocystidia common and long and narrow;
flavor not minty; stipe often only pruinose
halfway to base, 25–100 × 2–8 mm; pileus 10–
70 mm, convex to nearly plane, silky sometimes
becoming excoriolate to subsquamulose; spores 7–
9.5 × 4–5.5 μm | <i>Inocybe sindonia</i> (Fr.) P. Karst. |
| 3. Spores > 11 μm long on average | 4 |
| 3. Spores < 11 μm long. | 5 |
| 4. Stipe whitish, not always pruinose to base, at
times subradicating, 25–80 × 5–6 mm; pileus
uniformly light brown, or sometimes appearing
pallid due to a velipellis but then chamois to
yellow-brown ground, 25–55 mm, convex, nearly
plane, matte; spores 11–15 × 5–7 μm; with
<i>Quercus</i> in California. | <i>Inocybe bakeri</i> Peck |

²Species reported for North America by Kuyper (1986), Nishida (1989) and Grund and Stuntz (1968, 1970, 1975, 1977a, b, 1981, 1983, 1984). Some extralimital species are included for clarity.

4. Stipe yellow-brown darkening toward base, entirely pruinose, 22–74 × 2–9 mm; pileus 8–40 mm, dark brown at center, becoming ochraceous brown to orange brown toward margin, initially with a velipellis, coarsely fibrillose to subsquamulose; spores 8–10 × 6.5–9 μm; with mixed broadleaf trees *Inocybe vulpinella* Bruylants
5. Spores less than 8 μm on average 6
5. Spores more than 8 μm on average 7
6. Lamellae yellow to bright yellowish brown, edges bruising brown, narrow; stipe discoloring bister on lower half, 30–55 × 3–5 mm, equal; pileus 10–30 mm, dark sordid yellowish brown, with the center tinged reddish tawny in age, fibrillose to appressed squamulose in age; pleurocystidia short, dark yellow, mostly 35–45 × 10–15 μm; spores 6–8 × 4–5 μm. *Inocybe luteifolia* A. H. Smith
6. Spores 6.5–8 × 4–5 μm; pileus 23–31 mm convex to nearly plane, dark red brown, becoming rimose; stipe 31–45 × 3–4 mm, entirely pruinose, without a distinct bulb *Inocybe albomarginata* Velen.
7. Stipe discoloring olive black in lower half, 17–52 × 2–6 mm; pileus 10–32 mm, lacking a velipellis, dark brown at center, lighter toward margin, becoming squamose; spores 7–9.5 × 4.5–6 μm *Inocybe tenebrosa* Quéf.
7. Stipe not discoloring olive black 8
8. Pileus yellow, orange-brown or ochraceous 9
8. Pileus duller, some shade of brown 18
9. Stipe typically lacking a marginate basal bulb 10
9. Stipe typically with a marginate basal bulb 17
10. Velipellis present and persistent at least at center 11
10. Velipellis absent 12
11. Pileus ochraceous, 45–70 mm diam, nearly glabrous, with a velipellis in early stages; stipe 30–60 × 5–19 mm, often pale brownish, equal or rarely with a bulb, entirely pruinose; spores 8.5–11 × 5–7 μm *Inocybe terrifera* Kühner
11. Pileus fulvous to orange brown, 30–60 mm diam, conic to convex, smooth to very finely squamulose; stipe 30–70 × 3.5–8 mm, light orange-brown; spores 8–10 × 5–6 μm *Inocybe vaccina* Kühner
12. Pileus smooth 13
12. Pileus not smooth, becoming rimose, squamulose, or squarrulose 14
13. Pileus, golden orange and darker at center, 12–25 mm, broadly conical to convex; stipe 35–60 × 3–6 mm, yellowish; spores 10–11 × 5.5–6 μm, *Inocybe chrysocephala* Nishida
13. Pileus ochraceous (ranging to dark reddish brown in some specimens), uniform in color, 9–35 mm, convex to nearly plane, velipellis indistinct if present, typically smooth; stipe 12–51 × 4–5 mm, pallid to orange brown, with or without a bulb; spores 9.5–10.5 μm long *Inocybe catalaunica* group
14. Pileus rimose 15
14. Pileus not rimose, becoming squamulose or squarrulose 16
15. Pileus rimose and becoming squamulose to excoriolate, fulvous at center yellowish toward margin, 10–17 mm, campanulate; stipe 20–30 × 1.5–2.5 mm, yellowish; spores 10–11 × 5–5.5 μm; under hardwoods or mixture of hardwoods and conifers in eastern North America *Inocybe microteroxantha* Grund & Stuntz
15. Pileus rimose but not squamulose or only slightly so at disk, uniformly cream to isabelline, 30–60 mm, subconical with umbo; stipe 40–80 × 4–10 mm, concolorous with pileus, entirely pruinose; spores 8.5–10.5 × 5–6 μm; under conifers in western North America *Inocybe kauffmanii* A.H. Smith
16. Cystidia clavate, pileus becoming squamulose to squarrulose, 15–31 mm, ochraceous to brownish yellow; stipe 20–58 × 3–4 mm, equal to subbulbous, apically yellowish to ochraceous, pallid below; spores 8–10.5 × 5–6 μm *Inocybe hirtella* Bres.
16. Cystidia lageniform to fusiform, pileus felt-like becoming squarrose at disk only, ochraceous brown to ochre yellow; stipe 20–59 × 2–5 mm, apically reddish brown becoming yellowish below; spores 8.5–12 × 5–6.5 μm *Inocybe muricellata* Bres.
17. Pileus with a velipellis, 30–50 mm, campanulate to applanate, yellow brown becoming umbrinous; stipe 30–40 × 5–8 mm; spores 9–10.5 × 5–6 μm *Inocybe alluvionis* Stangl & Veselský
17. Pileus without a velipellis, 20–60 mm, convex to nearly plane, slightly greasy, matted fibrillose, uniformly medium yellow brown; stipe 20–70 × 5–13 mm, entirely pruinose, pallid to pale tan; spores 7.5–10 × 4.5–5.5 μm *Inocybe praecox* sp. nov.
18. Stipe with red-brown or flesh tones 19
18. Stipe lacking red-brown or flesh tones 21
19. Pileus uniformly dark brown, not rimose 20
19. Pileus brown at the disk with a brassy yellow margin, rimose, 20–35 mm, smooth, campanulate to plane; stipe 25–70 × 2.5–5.5 mm, flesh-colored with a whitish base; spores 9–11 × 5.5–6 μm *Inocybe laetior* Stuntz
20. Pileus small (9–35 mm diam), dark reddish brown to ochraceous in some specimens, uniform in color, convex to nearly plane, typically smooth, velipellis indistinct if present; stipe 12–51 × 4–5 mm, pallid to orange brown, with or without a bulb; spores 9.5–10.5 μm long *Inocybe catalaunica* Singer
20. Pileus larger (25–62 mm diam), convex to nearly plane, chestnut brown to ochraceous brown, velipellis often present and distinct; stipe 28–60 × 4–10 mm, reddish brown, with a distinct marginate bulb; spores on average 8.2–9.0 μm long *Inocybe amblyspora* Kühner
21. Stipe with a marginate basal bulb, 30–35 × 7–11 mm, white; pileus conic to convex, 30–50 mm,

- brown to dark brown; spores $9.5\text{--}11 \times 5.5\text{--}6 \mu\text{m}$ *Inocybe splendens* Heim
21. Stipe without a marginate basal bulb 22
22. Basidiomes typically robust in stature ($IS \leq 5\text{--}5.5$)³; pileus 13–60 mm, convex to nearly plane, dark reddish brown to brown, velipellis often present; stipe 20–70 × 6–15 mm, white to pale tan; spores $8\text{--}10.5 \times 5\text{--}6.5 \mu\text{m}$; known from montane forests in western North America *Inocybe monticola* sp nov
22. Basidiomes typically slender in stature ($IS = 5\text{--}18$); pileus 12–46 mm, conic campanulate to nearly plane, ochraceous to dark brown, often with a velipellis; stipe 21–59 × 2–7 mm, whitish becoming yellowish or pale brown; spores $8\text{--}11.5 \times 5\text{--}6.5 \mu\text{m}$; known from Europe and reported from eastern North America
 *Inocybe phaeoleuca* Kühner

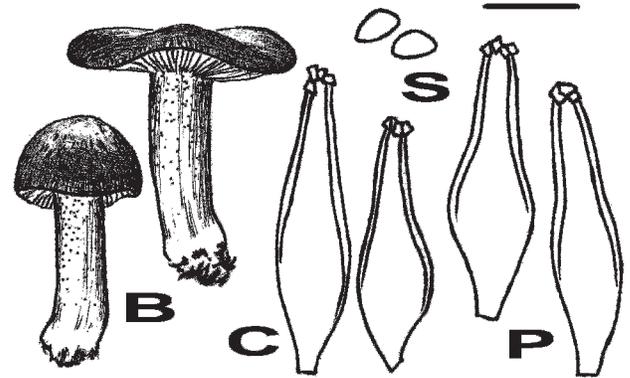


FIG. 3. *Inocybe monticola* (HOLOTYPE); B = basidiomata, S = basidiospores, C = cheilocystidia, P = pleurocystidia. Bar = 20 μm .

Inocybe monticola Kropp, Matheny et Nanagyulyan
 sp. nov. FIG. 3

Mycobank MB 515176

Etymology: monticola = mountain dweller.

Pileus 13–60 mm, latus, convexus, demum paene applanatus, parum lubricus vel siccus, marginem versus fibrillosus et brunneus vel castaneus, centrum pellicula tenui. Lamellae adnatae vel sinuatae, albae demum brunneae. Stipes 23–45 mm longus, 6–8 mm crassus, aequalis, basin versus interdum parum inflatus aut decrescens, pruinosis, praeter fundus leviter pruinosis, albus vel laete avellaneus; basi albida. Sporae $(8.0\text{--})9.5\text{--}(10.5) \times (5.0\text{--})5.9\text{--}(6.5) \mu\text{m}$, amygdalinae. Basidia $25\text{--}34 \times 8\text{--}11 \mu\text{m}$, clavata. Pleurocystidia et cheilocystidia $13\text{--}20 \times 48\text{--}75 \mu\text{m}$, fusiformia vel ventricosa. A *Inocybe splendens* sensu Heim et *Inocybe phaeoleuca* genetice differt. Holotypus hic designatus BK 28-Jun-98-3 (UTC248120) in Herbario Intermontanis (UTC) conservatus.

Pileus 13–60 mm diam, convex to nearly plane or with upswept margins, sometimes with a broad umbo at maturity, either dry or slightly greasy and glistening when first collected, center often covered with a thin, pale velipellis, becoming radially appressed-fibrillose and mostly smooth toward the margin, sometimes developing fine squamules, dark reddish brown to brown (5YR 5/4–4/4, 7.5YR 4/4). Context white. Odor slightly spermatic to raphanoid. *Lamellae* close and adnate to slightly notched, pallid when young, becoming light brown at maturity, margins obscurely pallid for some specimens. *Stipe* 20–70 × 6–15 mm, solid, equal, some narrowing toward the base, others slightly enlarged toward the base but not bulbous, white to light tan (10YR 9/4–8/6), base often remaining white, pruinose along most of the length

but not appearing pruinose at the base. *Basidiospores* $(8.0\text{--})9.5\text{--}(10.5) \times (5.0\text{--})5.9\text{--}(6.5) \mu\text{m}$, smooth, amygdaliform, apices mostly subconical, yellowish brown. *Basidia* $25\text{--}34 \times 8\text{--}11 \mu\text{m}$, four-spored, clavate. *Pleurocystidia* $53\text{--}75 \times 13\text{--}20 \mu\text{m}$, fusiform-ventricose, crystals usually present at apices, cell walls 1.0–2.5 μm thick and pale yellowish in NH_4OH . *Cheilocystidia* $48\text{--}70 \times 13\text{--}18 \mu\text{m}$, fusiform-ventricose, crystals usually present at the apices, cell walls 1.0–2.5 μm thick and pale yellowish in NH_4OH . *Lamellar trama* subparallel, hyphae 5–16 μm wide. *Stipitipellis* caulocystidia present as metuloids and mostly occurring in clusters near the apex and down to the middle of the stipe, becoming less frequent or absent and sometimes more irregular in form at the stipe base. *Clamps* present.

Habitat and distribution. Fruiting during spring (May and June) in loose clusters on soil in montane environments. Occurring with mixed conifers and *Populus tremuloides* Michx.

Specimens examined. USA. UTAH. Cache County, Beaver Mountain Ski Area, 28 Jun 1998, leg. B. Kropp, BK 28-June-98-3 (HOLOTYPE, UTC248120); Cache County, Beaver Mountain Ski Area, 28 Jun 98, leg. B. Kropp, BK 28-June-98-1 (UTC248121); OREGON. Wallowa County, Wallowa-Whitman National Forest, 28 May 1996, leg. B. Kropp, BK 28-May-96a (UTC248122).

Comments. Even though the collections of *Inocybe monticola* were made in late May or June at the relatively high elevations represented, this is early in the growing season and can be considered vernal. *Inocybe monticola* thus far has been found only in montane habitats at intermediate elevations in the western United States. How common or widespread this taxon is remains unknown. It has not been seen fruiting again at the type locale in the 10 y since it was first collected there. For the time being we can say only that it occurs in Oregon and Utah and that it does not

³ $IS = l^2/d \times D$, where l = stipe length, d = stipe diameter and D = pileus diameter (see Kuyper 1986).

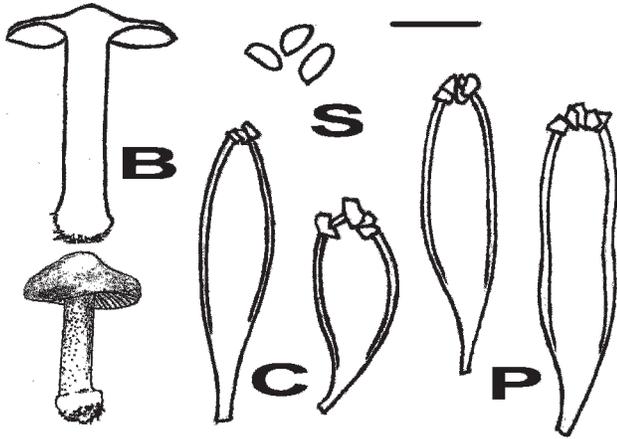


FIG. 4. *Inocybe praecox* (HOLOTYPE); B = basidiomata, S = basidiospores, C = cheilocystidia, P = pleurocystidia. Bar = 20 μ m.

appear to be part of the mycoflora that is seen annually.

I. monticola material originally was identified as *I. splendens* var *splendens sensu* Kuyper (1986) who synonymized *I. splendens* Heim, *I. alluvionis* Stangl & Veselský, and *I. terrifera* Kühner. *Inocybe monticola* fits the concept for *I. splendens sensu lato* reasonably well, but based on our sequence data it differs phylogenetically from European material representing the species. The European material that we used in our phylogenetic work best fits *I. splendens sensu* Heim (1931) that is characterized by dark pileus colors and a distinct basal bulb on the stipe. *Inocybe monticola* differs from Heim's concept of *I. splendens* by lacking a distinct basal bulb on the stipe. *Inocybe alluvionis* is characterized by a lighter pileus color than *I. monticola* and by having a submarginate basal bulb on the stipe that is not present on *I. monticola*. *Inocybe terrifera* lacks a basal bulb but can be separated from *I. monticola* by its lighter pileus colors. *Inocybe monticola* comes closest to *I. phaeoleuca* Kühner in having dark pileus colors and lacking a basal bulb. However its DNA sequences differ sharply from that of the European exemplar of *I. phaeoleuca* Kühner and its stature is considerably more robust than that of *I. phaeoleuca*. In addition a velipellis is present on most of the material of *I. monticola* and this is usually absent from *I. phaeoleuca*. One rare European species, *I. glabrescens* Velen, also has some similarity to *I. monticola* but differs by having a rimose pileus margin and a more slender stipe that discolors yellowish in age.

The material on which *I. monticola* is based does not belong to either *I. splendens sensu* Heim or *I. phaeoleuca sensu* Kühner, and as mentioned above there are morphological reasons to exclude it from both *I. alluvionis* and *I. terrifera*.



FIG. 5. *Inocybe praecox* basidiomata (PBM 1402).

***Inocybe praecox* Kropp, Matheny et Nanagyulyan, sp. nov.**

FIGS. 4, 5

Mycobank MB 515177

Etymology: praecox = developing early.

Pileus 20–60 mm latus, convexus demum appplanatus et late umbonatus, parum sebosus, appressus fibrillosus, avellaneus. Lamellae adnexae, pallide brunneae. Stipes 20–70 mm longus, 5–11 mm crassus, aequalis, ad apicem pruinosis, basin versus leviter pruinosis, laete fulvus tinctus; basi bulbosa. Sporae (7.5–)8.6(–10.0) \times (4.5–)4.9(–5.5) μ m, ellipsoideae vel amygdalinae. Basidia 25–30 \times 6–10 μ m, clavata. Pleurocystidia et Cheilocystidia 32–70 \times 12–18 μ m, fusiformia vel ventricosa. A *Inocybe splendens sensu* Heim (1931) et *Inocybe monticola* genetic differt. Holotypus hic designatus BK 21-Apr-99-6 (UTC248123) in Herbario Intermontanis (UTC) conservatus.

Pileus 20–60 mm diam, convex to nearly plane at maturity sometimes with a broad umbo at maturity and the margin straight or remaining incurved in some specimens; surface slightly greasy, radially appressed or matted fibrillose, not rimose, occasionally with small appressed squamulose areas in age, velipellis absent; uniformly medium yellow-brown (10YR 7/6–6/6 to 5/8–4/4; 5D5–5D6–5E7) or “tawny-olive”, “Buckthorn brown” to “Dresden brown”, context pallid, odor none, not spermatic, flavor mild. *Lamellae* close, narrowly attached, 2.5–6 mm deep, pallid when young becoming light gray-brown (10YR 8/2, 6/4), edges pallid and indistinctly fimbriate. *Stipe* 20–70 \times 5–13 mm, solid, equal to a marginate basal bulb, young specimens may be pruinose over the entire length but lightly so near the base, at maturity the color is visible only part way down the stipe; pallid to light tan (10YR 9/2) with faint apical incarnate hues when young becoming light yellow-brown with a pallid apex at maturity; basal bulb and stipe context pallid. *Basidiospores* (7.5–)8.6(–10.0) \times (4.5–)4.9(–5.5) μ m, smooth, mostly amygdaliform to elliptical in outline, apices subconical to obtuse, yellowish-brown. *Basidia* 25–30 \times 6–10 μ m, four-

spored, clavate. *Pleurocystidia* 44–70 × 12–18 μm, clavate to fusiform-ventricose with obtuse apices, crystals usually present at the apices, cell walls 1–1.5 μm thick and pale yellowish in NH₄OH. *Cheilocystidia* 32–65 × 12–17 μm, clavate to fusiform-ventricose, occasionally ovate, crystals usually present at apices, cell walls 0.5–2 μm thick and pale yellowish in NH₄OH. *Lamellar trama* subparallel, hyphae 2–12 μm wide. *Stipitipellis* caulocystidia present as metuloids near the apex and either appearing in clusters or individually scattered, mostly thin-walled or with slightly thickened walls, cauloparacystidia present on the upper half of the stipe, metuloids scattered over the remaining length of the stipe but becoming less frequent and often fewer toward the stipe base; cauloparacystidia infrequent or absent toward the stipe base. *Clamps* present.

Habitat and distribution. Fruiting in loose clusters or solitary on soil during spring (April, May, June) in conifer forests or parks under *Pseudotsuga menziesii* (Mirb.) Franco, *Alnus rubra* Bong., *Tsuga heterophylla* (Raf.) Sarg., or *Arbutus menziesii* Pursh. Known only from western Washington state in the United States. Fruiting near sea level to 1200 feet (400 m).

Specimens examined. USA. WASHINGTON. Clallam County, Elwah River Campground, 21 Apr 1999, leg. J.F. Ammirati, BK 21-Apr-99-6 (HOLOTYPE, UTC248123); Clallam County, near Wolf Creek Trail, 21 Apr 1999, leg. B. Kropp, BK 21-Apr-99-8 (UTC248125); Clallam County, Elwah River Campground, trail to Cascade Rock, 21 Apr 1999, leg. P.B. Matheny, PBM 1402 (WTU). Clallam County, Whiskey Bend Road, 28 May 2000, leg. S. Trudell, ST 00-146-05 (WTU). Island County, Camano Island, leg. B. Kropp, BK 3-Jun-99-1 (UTC248124). King County, University of Washington Arboretum, under *Pseudotsuga menziesii*, 14 Apr 2001, leg. P.B. Matheny, PBM 2092 (WTU). King County, Seward Park, north end of Ridge Trail, 25 Mar 2003, leg. B. Woo, PBM 2413 (WTU). Kitsap County, under *Tsuga*, *Pseudotsuga* and ericaceous shrubs, main road of the Clark property, Seabeck, 10 Jun 2001, leg. P.B. Matheny & S. Clark, PBM 2107 (WTU). Kitsap County, under *Tsuga*, *Pseudotsuga*, 30 Apr 2000, leg. S. Clark, SC000430_11 (WTU). Pierce County, Hugo Peak Trail in Pack Experimental Forest, 18 May 2003, leg. J.F. Ammirati & M.T. Seidl, PBM 2418 (WTU). Pierce County, same locality and date as above, leg. M.T. Seidl, PBM 2420 (WTU). Snohomish County, Forest Service Road 6024, north of Baring, about 1 mile from U.S. 2 in mature second growth conifer woods of *Tsuga* and *Pseudotsuga*, 27 Apr 2003, leg. M.T. Seidl, PBM 2414 (WTU).

Comments. *Inocybe praecox* is thus far known only from the Pacific Northwest of the United States. It is characterized by its vernal fruiting habit and its relatively light yellow-brown, slightly greasy pileus that lacks a velipellis and by having a basal bulb on the stipe. Specimens of *I. praecox* fit within *I. splendens sensu lato* but differ from it phylogenetically. It differs

from *I. alluvionalis* primarily by lacking a velipellis and by lacking the umbrinous pileus that develops in *I. alluvionalis*. *Inocybe splendens sensu* Heim (1931) has a darkly pigmented pileus, while *I. terrifera* lacks a basal bulb on its stipe and has a velipellis. A number of North American species also fit within section *Spendentes* of *Inocybe* that could be potentially interpreted as *I. praecox*. Among these *I. bakeri* is differentiated by its larger spores while *I. kauffmanii* has a cream-colored pileus and lacks a basal bulb on the stipe. The single specimen in clade 2 from Washington that is identifiable as *I. splendens sensu lato* is also at first glance strikingly similar to *I. praecox*. This fungus fruits in spring in the same region and has a stature and coloration similar to *I. praecox*. Yet it is phylogenetically distinct from *I. praecox* and, even though more material is required to fully characterize or formally describe this taxon, a closer examination indicates that some morphological differences exist that allows it to be distinguished from *I. praecox*. The taxon represented by clade 2 has a distinct velipellis and its pileus becomes rimose toward the margin, while *I. praecox* lacks both characters. This taxon is probably undescribed, however more collections are required before we can fully characterize or formally describe it. It should be pointed out that the name *Inocybe abietis* Kühner originally was applied to some of the material we now refer to as *I. praecox* in Matheny et al. (2002) and Matheny (2005).

Inocybe bakeri Peck, Bull. Torrey Bot. Club 36:332. 1909. Figs. 6, 7

Pileus 25–55 mm, convex to nearly plane, dry, surface finely felt-like or matte and smooth not becoming rimose or scaly, uniformly light brown, or sometimes appearing pallid due to a velipellis but then usually with a chamois to yellow-brown background, conspicuous odor lacking *Lamellae* close, adnexed to notched and pale brownish with pallid margins. *Stipe* 25–80 × 5–6 mm, white, solid, smooth but becoming striated at the apex, pruinose at the apex but not obviously pruinose below, slightly enlarging towards the base and with a somewhat radicating base, context white. *Basidiospores* (11–) 11.24(–15) × (5–)5.86(–7) μm, smooth elliptical with an obtuse apex, light brownish. *Basidia* 31–29 × 11 μm, four-spored, clavate. *Pleurocystidia* 64–80 × 16–23 μm, fusiform-ventricose, crystals usually present at the apices, cell walls 1–1.5 μm thick and pale yellowish in NH₄OH. *Cheilocystidia* 52–65 × 17–20 μm, fusiform-ventricose, crystals usually present at the apices, cell walls 1–1.5 μm thick and pale yellowish in NH₄OH. *Stipitipellis* caulocystidia among lightly woven hyphae at the stipe apex, mostly thin-walled with

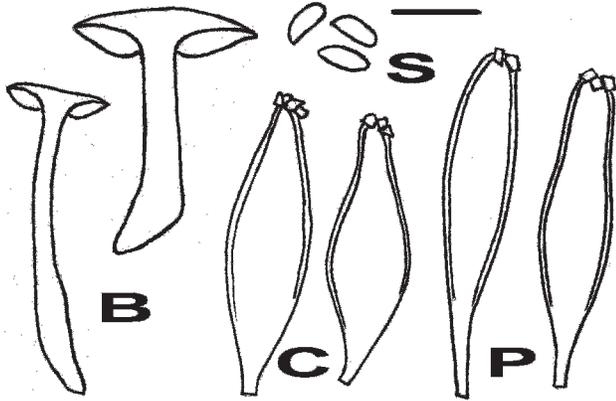


FIG. 6. *Inocybe bakeri* (HOLOTYPE); B = basidiomata copied from original sketch enclosed with the holotype, S = basidiospores, C = cheilocystidia, P = pleurocystidia. Bar = 20 μ m.

some thick-walled representatives, mostly lacking apical incrustations, becoming scarce or completely absent at the base. *Clamps* present.

Habitat and distribution. Known only from California, fruiting in late winter or early spring with *Quercus*.

Specimens examined. USA. CALIFORNIA. Los Angeles County, Claremont, California, Jan 1909, leg. C.F. Baker (HOLOTYPE, NYS 413); San Luis Obispo County, Los Osos Baywood Park, 18 Mar2002, leg. S. Trudell, ST02-077-01 (WTU).

Comments. This is a poorly known species that we redescribe and illustrate here based on our studies from fresh material and the holotype. This species appears to be relatively rare, and we know of only a handful of collections that represent it. In addition to the two collections cited above Nishida (1989) reports *I. bakeri* from southern California. Thus far *I. bakeri* is known only from southern California where it associates with *Quercus* sp. and fruits in late winter and spring.

Inocybe bakeri is a relatively robust species that is characterized mainly by its large basidiospores, and Peck's protolog describes the stipe as "more or less radicating". The caulocystidiate nature of the stipe surface appears to be variable. In her key to species of *Inocybe* from California Nishida (1989) places *I. bakeri* in two different places, once in subsection "*Holoconiatae*" and another time in subsection "*Acroconiatae*" reflecting the variation in this character. Our examination of the holotype for the species indicated that no caulocystidia are present on the lower half of the stipe although a few caulocystidiate hairs were present at the middle of the stipe. Yet the second specimen (ST-02-077-01) studied had scarce but distinct caulocystidia present at the base of the stipe. In spite of this difference the two collections are very similar in all other regards and at the moment we



FIG. 7. *Inocybe bakeri* basidiomata. Photo courtesy Steve Trudell (ST02-077-01).

regard them as the same species. The European species, *I. inodora* Velen., differs from *I. bakeri* by its nonradicating stipe and somewhat smaller spores.

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