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## Nodulose-spored *Inocybe* from the Rocky Mountain alpine zone molecularly linked to European and type specimens

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### ABSTRACT

*Inocybe* (Inocybaceae) is one of the most diverse ectomycorrhizal genera in arctic and alpine habitats where the primary hosts are *Salix*, *Betula*, and *Dryas*. Subgenus *Inocybe* is common in these habitats and typically characterized by the presence of thick-walled pleurocystidia. Here, we focus on species that have angular or nodulose spores. Historically, over 30 taxa from this group have been reported from arctic and alpine habitats. Many names have been synonymized, whereas molecular analysis has revealed new species. Nuc rDNA internal transcribed spacer ITS1-5.8S-ITS2 (ITS) sequence data of 26 type specimens in this group now allow for further taxonomic clarification and comparison across continents of disjunct populations. Here, we compare ITS sequence data and the D1–D2 portion of nuc 28S rDNA (28S) from Rocky Mountain specimens with those of types and European reference material. We report 10 species from the Rocky Mountain alpine zone, all of which are conspecific with known European boreal, montane, or alpine species, and four are described as new; all have inter-continental distributions. Nodulose-spored *Inocybe* taxa that occur in the Rocky Mountain alpine zone include *I. alpinomarginata*, sp. nov., *I. arctica*, *I. giacomii*, *I. leonina*, *I. murina*, sp. nov., *I. occulta*, *I. paragiacomii*, sp. nov., *I. phaeocystidiosa*, *I. purpureobadia*, and *I. subgiacomii*, sp. nov. Remarkably, these species occur at elevations up to 4000 m and at latitudes as low as 36°N, hundreds of miles from the Arctic, the European alpine, and original type localities. Distributions are explained in part by host distributions and historical glaciation patterns. A key and full descriptions for Rocky mountain species are provided to promote species recognition.

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## INTRODUCTION

Species of Agaricales (Basidiomycota) have been reported from arctic and alpine habitats for over 60 years (Favre 1955; summarized in Brunner et al. 2017). *Inocybe* (Fr.) Fr. (Inocybaceae Jülich; Matheny 2009) is one of the most diverse ectomycorrhizal genera in these cold-dominated habitats at arctic latitudes and above tree line on high mountain tops (Timling et al. 2012). *Salix*, *Betula*, *Dryas*, and *Bistorta* (*Persicaria*) *vivipara* are the primary potential ectomycorrhizal hosts in these treeless areas (Cripps and Eddington 2005). Many *Inocybe* species produce small brown basidiomata with conical radially fibrous pilei that exude a spermiac odor; however, some species lack these macroscopic traits (Stangl 1986). Microscopic features are more reliable in helping to distinguish species, the most definitive being the production of brown thick-walled basidiospores that lack a true germ pore (Peglar and Young 1972; Largent and Baroni 1988) and exhibit an angular, amygdaliform, elliptical, nodulose, spinose, or

phaseoliform outline. Spore shape has been a useful diagnostic feature to distinguish groups within *Inocybe*. Whatever the overall shape, *Inocybe* spores are smooth, and never verrucose as in *Cortinari* or roughened as in some *Hebeloma* (Largent and Baroni 1988), the two other common brown-spored ectomycorrhizal genera in arctic and alpine habitats.

Of the three subgenera of *Inocybe* (Kuyper 1986), subgenus *Inocybe* is the most diverse, delineated by the presence of thick-walled pleurocystidia often termed metuloids. In northern Europe, *I.* subg. *Inocybe* is divided into eight sections, half of which have angular or nodulose spores (Jacobsson and Larsson 2012). Of the nodulose-spored species, most in section *Inocybe* (= *I.* sect. *Cortinatae* Kühner & Boursier) possess a cortina. Noncortinate species are in sections *Marginatae* Kühner (marginate stipe base), *Petiginosae* R. Heim (equal stipe base), or *Calosporae* J.E. Lange

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(spiny spores) (Jacobsson and Larsson 2012). Here, we focus on the nodulose-spored species in sections *Inocybe* (= *Cortinatae*) and *Marginatae* of Jacobsson and Larsson (2012). Although these two groups are not monophyletic, the presence or absence of a cortina is useful for morphological distinction of taxa presented. This section has been further refined by Matheny and Kudzma (2019). It remains a small monophyletic group, quite different from the artificial morphology-based classification of section *Inocybe* in *Funga Nordica*.

One of the first substantial reports of agarics in alpine habitats included 10 nodulose-spored species of *Inocybe* from the Swiss Alps, primarily with dwarf willows *Salix herbacea*, *S. retusa*, and *Dryas* (Favre 1955; Brunner et al. 2017). Jules Favre described several new species for this group, including new alpine varieties and forms of known subalpine taxa. Favre's notebooks and collections list at least 14 names for *Inocybe* species with nodulose spores over his years of collecting in the alpine zone (Brunner et al. 2017); 32 years later, Horak (1987) placed Favre's alpine nodulose-spored *Inocybe* taxa in the previously described genus *Astrosporina* J. Schröt. based on their unique spore shape. He also added new species to the list and reported 30 historical names that have been used to identify nodulose-spored *Inocybe* from arctic and alpine habitats. Contemporaneously, Kühner (1988) described eight new species in this group from above tree line in the French Alps.

In 1994, a review by Graf listed 19 nodulose-spored species previously reported with *Salix herbacea* alone from arctic and alpine areas (Graf 1994). Bon (1997) included most Favre, Horak, and Kühner species in his key to alpine species of nodulose-spored *Inocybe* under subgenus *Clypeus* Britzelm. Jacobsson and Larsson (2012) documented 17 taxa occurring at least occasionally in arctic-alpine habitats of northern Europe. We estimate that over 30 names have been used to delineate species of this group in arctic and alpine habitats in the Northern Hemisphere. Synonymy has reduced the number of names; however, new research that includes molecular data has revealed new or cryptic species (Kokkonen and Vauras 2012; Larsson et al. 2014, 2017, 2018; Esteve-Raventós et al. 2016, 2018).

Sequence data from 28 type specimens of *Inocybe* with nodulose spores, newly generated for this study, or from recent publications, allow for identification of collections from arctic and alpine habitats across the Northern Hemisphere. For the Rocky Mountain alpine zone south of the Canadian border, there has been only one unconfirmed report (Cripps and Horak 2008) and a few molecularly confirmed occurrences of

*Inocybe* species above tree line (Cripps et al. 2010; Larsson et al. 2014, 2018). Here, we present phylogenetic comparisons of sequence data of specimens from the Rocky Mountain alpine zone originating hundreds of miles from the Arctic, the European alpine, and original type locations using nuc rDNA internal transcribed spacer region ITS1-5.8S-ITS2 (ITS) and about 1200 bp of the 5' end of the nuc 28S rDNA (28S). We document 10 nodulose-spored species of *Inocybe* (four as new) from the Rocky Mountain alpine zone between latitudes 36°N and 45°N at elevations between 3000 and 4000 m, along with hosts, distributions, and a key to taxa. A phylogenetic tree with reference to types and European specimens is included for species confirmation.

## METHODS AND MATERIALS

**Collections.**—North American specimens (TABLE 1) were collected from 1997 to 2017 in alpine areas above tree line, primarily on the Beartooth Plateau in Wyoming/Montana (45°N, 109°W) at 3000–3400 m and in the southern Rocky Mountains (37°–39°N) at elevations between 3700 and 4000 m. The various locations in Colorado included Cottonwood Pass, Cumberland Pass, Independence Pass, Loveland Pass, and the San Juan Mountains. Potential host associations in these areas included *Salix arctica*, *S. reticulata*, *S. planifolia*, *S. glauca*, *Dryas octopetala*, and *Bistorta vivipara* (Cripps and Horak 2008). For location details, see Osmundson et al. (2005). European specimens (TABLE 1) and type specimens (TABLE 2) were included as reference specimens.

In all, 67 specimens of nodulose-spored *Inocybe* from the arctic and alpine zones of North America and northern Europe were sequenced for this study. In addition, in order to present species in a phylogenetic context, sequence data were included from previous studies of section *Inocybe* sensu Matheny and Moreau (2009) and from other works (Kokkonen and Vauras 2012; Esteve-Raventós et al. 2015, 2016; Vauras and Larsson 2015; Larsson et al. 2017, 2018). For the herein newly described species, each ITS sequence type was also blasted in GenBank (Clark et al. 2016) and the UNITE database (Kõljalg et al. 2013) to search for additional data. In all, eight sequences, mainly from soil and ectomycorrhizal studies, were found and added to the data set. *Inocybe rimosa* (Bull.) P. Kumm. and *I. flavella* P. Karst. were selected for rooting purposes (Matheny 2009; Matheny et al. 2009; Ryberg et al. 2010).

**Table 1.** Nodulose-spored *Inocybes* of the Rocky Mountain alpine zone and European reference specimens.

Species	Collection no.	Original location	Putative host	GenBank	
<b>Marginatae</b>					
<i>I. alpinomarginata</i>	CLC 1303/ZT 8798	Loveland Pass, Colorado, USA	<i>S. glauca</i>	MK153644	
	CLC 1334	Independence Pass, Colorado, USA	<i>S. reticulata/S. glauca</i>	MK153646	
	CLC 1354a	Independence Pass, Colorado, USA	Dwarf/shrub <i>Salix</i>	MK153645	
	CLC 1698	San Juan Mountains, Colorado, USA	<i>S. arctica</i>	MK153647	
	EL207-13 holotype	Torne lappmark, SWEDEN	<i>S. herbacea, S. reticulata</i>	MK153648	
<i>I. arctica</i>	—	ITALY	Environmental sample	JF908229	
	CLC 1923	Nordenskiold, SVALBARD	<i>D. octopetala, S. polaris</i>	KY033826	
	CLC 1804	San Juan Mountains, Colorado, USA	<i>Salix arctica</i>	MK153628	
	EL18-15	Longyearbyen, SVALBARD	<i>D. octopetala, S. polaris</i>	KY033830	
	EL80-09	Adventsdalen, SVALBARD	<i>Dryas octopetala</i>	KY033832	
<i>I. bufonia</i>	EL72-07	Torne lappmark, SWEDEN	<i>S. reticulata</i>	KY033839	
	CLC 2791	Branham Lakes, Montana, USA	<i>Abies, Picea, Pinus</i>	MK153681	
<i>I. leonina</i>	CLC 1349	Independence Pass, Colorado, USA	Dwarf and shrub <i>Salix</i>	MG574396	
<i>I. occulta</i>	CLC 1147/ZT 7279	Niwot Ridge, Colorado, USA	Dwarf <i>Salix</i>	MK153693	
	CLC 1756/ZT 9840	Independence Pass, Colorado, USA	<i>S. glauca, S. planifolia</i>	MK153692	
<i>I. phaeocystidirosa</i>	EL272-13	Troms, Storfjord, NORWAY	<i>Dryas, S. reticulata</i>	MK153695	
	EL102-12	Oppland, Grimsdalen, NORWAY	<i>Salix</i> spp., <i>Betula nana</i>	MK153694	
	EH 7473	Independence Pass, Colorado, USA	<i>Salix</i> spp.	MK153696	
	CLC 1133/ZT 6091	Beartooth Plateau, Wyoming, USA	dwarf <i>Salix</i>	MK153630	
	CLC 1204/ZT 6416	Beartooth Plateau, Wyoming, USA	<i>S. reticulata, Salix</i> sp.	MK153632	
	CLC 1645	Cottonwood Pass, Colorado, USA	<i>S. glauca/spruce</i>	MK153633	
	CLC 1738	San Juan Mountains, Colorado, USA	<i>S. reticulata/arctica</i>	MK153631	
	CLC 3107	Beartooth Pass, Wyoming/Montana, USA	<i>Salix</i> spp.	MK153637	
	CLC 3108	Beartooth Pass, Wyoming/Montana, USA	<i>Salix</i> spp.	MK153636	
	CLC 3293	Cooke City, Montana, USA	Conifers, <i>Vaccinium</i>	MK153635	
<i>I. cortinatae</i>	EL39-07	Torne lappmark, SWEDEN	<i>S. reticulata, S. polaris</i>	MK153639	
	EL289-13	Enontekiön Lappi, FINLAND	—	MK153634	
	JV 29937	Torne lappmark, SWEDEN	<i>Dryas, S. reticulata, S. herbacea</i>	MK153638	
	<i>I. giacomii</i>	CLC 1229/ZT 7281	Loveland Pass, Colorado, USA	Dwarf and shrub <i>Salix</i>	MK153654
		CLC 1359	Independence Pass, Colorado, USA	<i>S. planifolia</i>	MK153653
		CLC 1700	San Juan Mountains, Colorado, USA	<i>Salix arctica</i>	MK153652
		CLC 1702	San Juan Mountains, Colorado, USA	<i>Salix reticulata</i>	MK153651
		CLC 3600	Beartooth Plateau, Wyoming, USA	<i>Salix reticulata</i>	MK153668
		EL80-12	Sör-Tröndelag, NORWAY	<i>B. nana, S. herbacea</i>	MK153657
		JV 21543	Satakunta, FINLAND	<i>Picea, Betula, Pinus</i>	MK153656
ZT 9790		San Juan Mountains, Colorado, USA	—	MK153659	
ZT 9820		San Juan Mountains, Colorado, USA	—	MK153658	
CLC 1226		Beartooth Plateau, Wyoming, USA	Shrub <i>Salix</i> , krummholz	MK153679	
<i>I. murina</i>	EL15-05	Hordaland, NORWAY	<i>S. herbacea</i>	MK153673	
	EL45-05	Hordaland, NORWAY	<i>S. herbacea, Dryas</i>	MK153674	
	EL183-12	Inari Lapi, FINLAND	<i>Salix</i> sp., <i>B. pubescens</i>	MK153676	
	EL228-13	Torne lappmark, SWEDEN	<i>S. herbacea</i>	MK153677	
	EL230-17 holotype	Torne lappmark, SWEDEN	<i>Betula pubescens</i>	MK153678	
	FA-11435	ICELAND	<i>Salix</i> spp.	MK153675	
	—	Alaska, USA	<i>Picea</i> , environmental	KF617310	
	—	ESTONIA	<i>Populus</i> , environmental	JX316526	
	CLC 3117	Beartooth Pass, Wyoming, USA	Shrub <i>Salix</i> , krummholz	MK153672	
	EL64-11 holotype	Torne lappmark, SWEDEN	<i>S. herbacea, B. nana</i>	MK153670	
<i>I. paragiacomii</i>	EL116-15	Lycksele lappmark, SWEDEN	<i>Salix</i> sp., <i>B. nana</i>	MK153671	
	—	ITALY	Environmental	JF008219	
	—	Alaska, USA	<i>Picea</i> , environmental	KF618034	
	CLC 1205 = ZT 6418	Beartooth Pass, Wyoming, USA	Dwarf <i>Salix</i>	MK153689	
	CLC 2982	Mount Evans, Colorado, USA	<i>S. arctica, S. glauca</i>	MK153686	
	CLC 3106	Beartooth Pass, Wyoming, USA	Dwarf and shrub <i>Salix</i>	MK153688	
	CLC 3109	Beartooth Pass, Wyoming, USA	<i>S. planifolia, S. glauca</i>	MK153687	
	EH 6412	Beartooth Pass, Wyoming, USA	—	MK153690	
	EL215-06	Hauts-de-France, FRANCE	<i>Betula nana</i>	MK153691	
	—	—	Environmental	JN580876	
<i>I. subgiacomii</i>	CLC 1239/ZT 7282?	Independence Pass, Colorado, USA	<i>S. reticulata</i>	MK153661	
	CLC 1330/ZT 8852	Independence Pass, Colorado, USA	<i>Salix reticulata</i>	MK153664	
	CLC 1346/ZT 8800	Independence Pass, Colorado, USA	Dwarf <i>Salix</i>	MK153663	
	CLC 1402/ZT 8851	Beartooth Pass, Wyoming, USA	<i>S. reticulata</i>	MK153667	
	CLC 3113	Beartooth Pass, Wyoming, USA	<i>S. reticulata</i>	MK153669	
	CLC 3116	Beartooth Plateau, Wyoming, USA	Shrub <i>Salix</i> , krummholz	MK153660	
	CLC 3600	Beartooth Plateau, Wyoming, USA	<i>Salix reticulata</i>	MK153668	
	EL9-08	Beartooth Plateau, Wyoming, USA	<i>Salix reticulata</i>	MK153666	
	JV 29938F holotype	Torne lappmark, SWEDEN	<i>Dryas, S. reticulata, S. herbacea</i>	MK153665	
	EH 6215	Beartooth Pass, Wyoming, USA	<i>Salix</i> spp.	MK153662	

**Morphological examination.**—Specimens were photographed and described while fresh, dehydrated, and accessioned into herbaria, primarily the Fungal Herbaria at

Montana State University (MONT), the University of Turku (TUR), and University of Gothenburg (GB). Abbreviations of herbaria follow Thiers (continuously

**Table 2.** Type specimens, synonyms, countries of origin, and GenBank numbers.

Species	Type collection no.	Country	GenBank no.
<i>I. arctica</i> E. Larss. Vauras & C.L. Cripps	JV 2238F holotype	NORWAY	KY033843
<i>I. bufonia</i> Kokkonen & Vauras	JV 25043 paratype	FINLAND	JN580823
<i>I. candidipes</i> Kropp & Matheny	UTC00236599 holotype	USA	MG833870
	paratype	USA	AY239019
<i>I. caprimulgi</i> Vauras & E. Larss.	JV 5808F holotype	FINLAND	KT958924
<i>I. favrei</i> Bon	BON 84095 holotype	FRANCE	KY033786
= <i>I. taxocystis</i> J. Favre	J. Favre 122a lectotype	SWITZERLAND	JN580884ITS1
<i>I. flavobrunnescens</i> Esteve-Rav., G. Moreno & Bizio	AH 29883 holotype	PORTUGAL	KJ938784
<i>I. giacomii</i> J. Favre	J. Favre 124b ITS1 lectotype	SWITZERLAND	JN580864
= <i>I. johannae</i> Kühner	K 65-117 ITS1 holotype	FRANCE	JN580865
= <i>I. striaepes</i> Kühner	Kühner 72 70 holotype	FRANCE	JN580867
<i>I. hirculus</i> Vauras	JV 5974F holotype	FINLAND	FJ531872
<i>I. krieglsteineri</i> Fern. Sas.	RFS031213 03 holotype	SPAIN	KJ958915
<i>I. lacunarum</i> Vauras & E. Larss.	JV 12244F holotype	FINLAND	KT958908
<i>I. leonina</i> Esteve-Rav. & A. Caball.	AH 36128 isotype	SPAIN	MN275014
<i>I. lemmi</i> E. Larss., Vauras & C.L. Cripps	JV 31462F holotype	SWEDEN	MG574394
<i>I. mixtilis</i> (Britzelm.) Sacc.	M-O219661 epitype	GERMANY	NR153144
<i>I. occulta</i> Esteve-Rav., Bandini, B. Oertel & G. Moreno	AH 36443 holotype	SPAIN	KX290787
<i>I. phaeocystidiosa</i> Esteve-Rav., Moreno, Bon	AH 9154 holotype	SPAIN	KT203789
= <i>I. salicis-herbaceae</i> Kühner	Kühner 66-49 FR holotype	FRANCE	MK153629
<i>I. populnea</i>	Paratype	JAPAN	KT958911
<i>I. praetervisiva</i> Quél.	S-F229598 epitype	ITALY	KT203792
<i>I. praetervisoides</i> Esteve-Rav., G. Moreno & Olariaga	AH 29863 holotype	SPAIN	KT203794
<i>I. purpureobadia</i> Esteve-Rav. & A. Caball.	18.V.2008 paratype	SPAIN	JN580875
<i>I. rivularis</i> Jacobsson & Vauras	JV 3610F paratype	FINLAND	JN580885
= <i>I. tundrae</i> E. Ludw.	Ludwig 3896 holotype	SWEDEN	MK153627
<i>I. substellata</i> Kühner	K73 218 holotype	FRANCE	KT958928

updated). “L” denotes the approximate number of full-length lamellae on a basidiome.

Microscopic examination was completed on dried specimens in 10% NH<sub>4</sub>OH. The size of basidiospores is given as length × width with nodules included. The number of spores measured is given under each taxon; means are placed between range limits. Q denotes the quotient of length divided by width for each spore, and Q values are averaged and the mean values presented. Measurements of basidia are for length × width but exclude sterigmata. Measurements of cystidia are given as length × width, without inclusion of crystals at the apex.

**Sequencing and phylogenetic analysis.**—Sequences of ITS and 28S were generated for most specimens. For some older type specimens, only the ITS region was generated. DNA extractions, polymerase chain reaction (PCR) reactions, primers used, and sequencing were performed as described in Larsson et al. (2018). Sequences were edited and assembled using Sequencher 5.1 (Gene Codes, Ann Arbor, Michigan). Alignment was performed using the L-INS-i strategy as implemented in MAFFT 7.017 (Kato and Standley 2013). The alignment was adjusted using AliView 1.17.1 (Larsson 2014). The DNA alignment is available at TreeBASE (S24162).

For inferring phylogenetic relationships among species, heuristic searches for the most parsimonious trees were performed under the maximum parsimony (MP) criterion in PAUP\* (Swofford 2003). All transformations were considered unordered and equally weighted. Variable regions

with ambiguous alignment were excluded, and gaps were treated as missing data. Heuristic searches with 1000 random-addition sequence replicates and tree bisection reconnection (TBR) branch swapping were performed, saving at most 25 trees in each replicate. Relative robustness of clades was assessed by the bootstrap method using 1000 heuristic search replicates with 10 random taxon addition sequence replicates and TBR branch swapping, the latter saving at most 25 trees in each replicate. Bootstrap values >70% and posterior probabilities >0.95 were considered to be evidence for strong support of clades. In addition, a Bayesian inference (BI) analysis was carried out in MrBayes 3.2.6 (Ronquist et al. 2012), with a best-fit model of nucleotide evolution supplied by MrModeltest 2.2 (Nylander 2004). Eight default-setting Metropolis-coupled Markov chain Monte Carlo (MCMCMC) chains were run for 5 million generations, with trees sampled every 2500 generations and an initial burn-in of 500 samples (25%). The MCMC analysis converged well in advance of the burn-in threshold, and chain mixing was found to be satisfactory, as assessed by using Tracer 1.5 (Drummond et al. 2012). After discarding the trees prior to the burn-in threshold, a 50% majority-rule consensus phylogram was computed from the remaining trees.

## RESULTS

**DNA sequences analysis.**—A total of 67 ITS-28S sequences were produced for this study and submitted to GenBank (MK153627–MK153696, MN275014, MN296110–MN296111). Sequences from 26 type

specimens were included, of which eight were newly generated for this study (TABLE 2). The concatenated alignment consisted of 150 sequences and 2268 characters. After exclusion of ambiguous regions, mainly from the beginning and the end of the data set, 2219 characters remained for analysis. Of these, 1493 were constant, 107 were variable but parsimony uninformative, and 619 (26.7%) were parsimony informative. The MP analysis retained 4840 equally most parsimonious trees (length = 2217 steps, consistency index [CI] = 0.5165, and retention index [RI] = 0.9145). The bootstrap analysis recovered 29 terminal clades with low to strong bootstrap support and three single branches that correspond to 32 recognized nodulose-spored species. The clade including the ITS sequence data of the isotype of *I. leonina* Esteve-Rav. & A. Caball., and a sequence originating from the arctic-alpine zone in North America was not supported (FIG. 1A–C). However, comparison of the ITS regions shows the two to be conspecific, and we conclude that *I. leonina* occurs in North America and is a closely related sister species to *I. candidipes* Kropp & Matheny, and to the alpine *I. lemni* E. Larss., Vauras & C.L. Cripps described from Fennoscandia.

The 50% majority-rule consensus tree obtained from the BI analysis recovered the same terminal supported clades and single branches (FIG. 1A–C). Of these supported clades and terminal branches, 10 species were recognized from the Rocky Mountain alpine zone (FIG. 1A–C). Six were conspecific with known European boreal, montane, or alpine species, and four were described as

new species with intercontinental distributions. *Inocybe bufonia* Kokkonen & Vauras is also reported from the Rocky Mountains. It is included in the phylogenetic tree but is not in the key because it is a subalpine species with conifers; it was originally described from boreal Finland (Kokkonen and Vauras 2012).

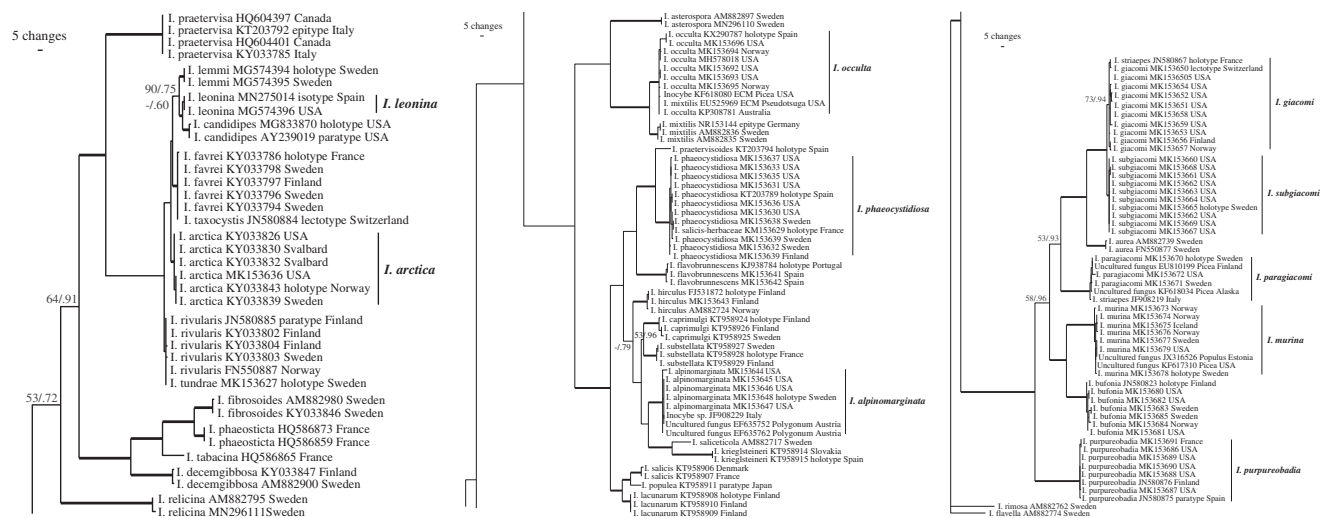
## TAXONOMY

*Inocybe alpinomarginata* C.L. Cripps, E. Larss. & Vauras, sp. nov. **FIGS. 2A, 4**

Mycobank MB832701

**Typification:** SWEDEN. Torne lappmark, Jukkasjärvi, Björkliden, close to Rakkasjokka, alpine heath with *Salix herbacea*, *S. reticulata*, and *Bistorta vivipara*, on calcareous soil, ca. 650 m above sea level (a.s.l.), 24 Aug 2013, E. Larsson & J. Vauras EL207-13 (**holotype** GB-0156958, **isotype** TUR-A 204817). GenBank: ITS-28S = MK153648.

**Diagnosis:** Pileus yellowish brown, conic-convex, fibrous; lamellae grayish brown; stipe whitish to watery orange, smooth, totally pruinose with marginate base; cortina absent; spores with 6–12 nodules, av. 11.0 × 8.0 μm; with *Salix* in alpine zone. The most closely related species, *I. substellata*, has larger, more nodulose spores, and molecular divergence is 6 substitutions and one 15-bp, one 14-bp, and six single-bp insertion/deletion events in the ITS1; 10 substitutions and one 3-bp and three single-bp insertion/deletion events in the ITS2; 16 substitutions and one 3-bp and one single-bp insertion/deletion events in the 28S loci.



**Figure 1.** Phylogram showing the phylogenetic relationships among nodulose species of *Inocybe* based on ITS and 28S sequence data. Branches of clades with bootstrap values greater than 70% and posterior probabilities >0.95 are marked in bold. Other values are indicated. Clades of the North American arctic-alpine species dealt with in this study are marked with a bar and species epithet. Sequences originating from type specimens are indicated. *Inocybe rimosa* and *Inocybe flavella* are used as outgroups.



**Figure 2.** Macromorphology of marginate group. A. *Inocybe alpinomarginata* EL207-13, holotype. B. *I. leonina* CLC 1349. C, D. *I. arctica* EL34-09 and CLC 1804. E, F. *I. occulta* EL102-12 and CLC 1756. G, H. *I. phaeocystidiosa* JV 2712F and CLC 3293 (subalpine). Bar = 1 cm.

*Etymology:* *alpinomarginata* (Latin), in reference to the marginate stipe base and high elevation habitat.

Pileus 15–30 mm wide, conico-convex to convex, with down-turned slightly rimulose margin, pale yellow-brown, golden brown, brown, appearing smooth but radially fibrous, greasy. Lamellae sinuate, slightly separated, L = 50 plus lamellulae, buff becoming pale gray to grayish brown, with white edges. Stipe 15–40 × 2–4 mm, equal down to the marginate or submarginate base, a bit curved, pruinose for whole length but appearing rather smooth, whitish becoming watery orange in age. Cortina absent. Flesh all white to cream, sometimes with yellow tinge in stipe base. Odor absent. Exsiccata: pileus brown; lamellae darker brown; stipe buff or darkening.

Basidiospores (9.5–)10.0–11.0–12.0(–12.5) × (6.5–)7.0–8.0–8.5 μm, range of mean values 10.5–11.5 × 7.5–8.0 μm, Q = (1.20–)1.30–1.40–1.55(–1.65), range of mean Q values 1.40–1.42 (n = 60, from 3 collections), nodulose with 6–12 distinct nodules, somewhat sunken below apiculus. Basidia (24–)28–38–48(–54) × 10–12–14(–16) μm (n = 50), clavate, mainly 4-spored. Pleurocystidia (55–)61–74–90(102) × (14–)16–19–23(–24) μm (n = 64, from 3 collections), subfusiform to fusiform with a long and slim neck and short pedicel; walls pale to pale yellowish, 2–5 μm thick; crystals often abundant. Cheilocystidia (39–)42–65–93(–100) × 14–17–19(–26) μm (n = 46), similar to pleurocystidia but shorter and more variable in shape; paracystidia (13–)15–22–30 × 8–9–13 μm, mainly clavate to oval (n = 30). Caulocystidia (38–)40–61–94(–98) × (12–)14–18–22(–24) μm (n = 54), variable, often crystalliferous at apex, rarely yellow brown inside, present on whole stipe; cauloparacystidia 12–23–37(–38) × (7–)9–13–16(–18) μm, clavate, oval to spherical, some thick-walled (n = 32).

*Ecology and distribution:* In alpine zone with dwarf willow *S. arctica* and shrub willow *S. glauca*, North America (Colorado), also Sweden (type), Italy, and Austria (the latter based on environmental samples). Aug.

*Specimens examined:* SWEDEN. Torne lappmark, Jukkasjärvi, Abisko, Björkliden, Rakkasjåkka, with *Betula nana*, *Salix herbacea*, *S. reticulata*, and *Bistorta vivipara*, 24 Aug 2013, E. Larsson & J. Vauras 30005, 30006F (TUR-A). USA. COLORADO: Loveland Pass, with *S. glauca*, 7 Aug 1999, C. Cripps CLC 1303 (MONT); Independence Pass, with dwarf and shrubby *Salix*, 10 Aug 1999, C. Cripps CLC 1334 (MONT); loc. cit., with dwarf and shrubby willows, 12 Aug 1999, C. Cripps CLC 1354a (MONT); San Juan Mountains, Cinnamon Pass, with *Salix arctica*, 10 Aug 2001, C. Cripps CLC 1698 (MONT).

*Observations:* The macromorphology of *Inocybe alpinomarginata* is rather similar to that of

*I. phaeocystidiosa* Esteve-Rav., G. Moreno & Bon except that the pileus is not appressed scaly, the margin is more rimulose, and the cystidia are subfusiform without yellowish brown contents. The two likely have been confused in alpine habitats. A difference was originally detected because pleurocystidia appeared to lack the more prominent yellow-brown coloration found in cystidia of *I. phaeocystidiosa*. In the phylogenetic analysis, they were found to be well separated (FIG. 1C).

*Inocybe arctica* E. Larss., Vauras & C.L. Cripps, Mycoscience 59:279. 2017. **FIG. 2C–D**

Pileus 10–35 mm wide, when young conical to plano-convex, later more applanate and indistinctly umbonate, with deflexed, often somewhat undulate margin, dirty brown with yellowish tinge, or dark brown, often with dark brown fibrils, subtomentose to smooth around the disc, outward radially fibrillose-felty, often with frosty or more abundant whitish velipellis that sometimes cracks into squares. Lamellae narrowly adnate to adnexed, moderately crowded, up to 6 mm broad, initially pale yellowish, then pale grayish brown with yellow tinge, becoming yellowish brown. Stipe 10–35 × 3–7 mm, often equal or base bulbous but not clearly marginate, yellowish but apex often with reddish tint and whitish at the base; surface distinctly pruinose at the apex and on the upper half, but not evidently so on the lower part, longitudinally striate, silky shiny. Cortina fugacious, scarce, whitish, present in young basidiomata. Context whitish to pale brown, in stipe also pale yellowish brown, sometimes with reddish tint at apex. Smell indistinct to slightly spermiatic. Exsiccata: pileus dark brown; lamellae dark brown; stipe buff.

Basidiospores (10.5–)11.0–12.0–13.0(–14.0) × (6.5–)7.0–7.5–8.5(–9.0) μm, range of mean values 11.5–12.0 × 7.0–8.0 μm, Q = (1.35–)1.40–1.5–1.8(–2.0), range of mean Q values 1.5–1.7 (120 spores from 6 collections), nodulose, heterodiametric, fairly dark yellow-brown. Basidia (29–30–35–43(–44) × 11–13–14(–16) μm, generally 4-spored (47 basidia from 6 collections). Pleurocystidia (50–)56–70–82(8–8) × (11–)13–17–22(–28) μm, range of mean values 65–77 × 14–20 μm (100 pleurocystidia from 6 collections), cylindrical to narrowly utriform, with crystals; walls up to 4 μm thick, pale yellow. Cheilocystidia 44–59–72 × 13–19–26 μm (n = 26), with crystals, abundant; paracystidia 10–32 × 9–13 μm (n = 11). Caulocystidia (30–)38–49–62(–65) × (12–)14–18–21(–22) μm (n = 21), at stipe apex thick-walled, abundant, often with crystals, present but more rare toward the stipe base. Cauloparacystidia more rare but present at stipe base, 17–38 × 11–16 μm (n = 8), a few thick-walled.

*Ecology and distribution:* With *Salix arctica*, North America (Colorado), also Sweden, Norway (type), Svalbard and Jan Mayen. Jul to Aug.



*Specimens examined:* NORWAY. Troms, Parasdalen, fjeld Paras, alpine zone in snow bed with *Salix polaris* and *Bistorta vivipara*, 12 Aug 1986, J. Vauras JV 2238F (**holotype** TUR-A 147440); SVALBARD and JAN MAYEN: Svalbard, Nordenskiöld Land, Adventsdalen, Endalen, with *Dryas octopetala*, 14 Aug 2009, E. Larsson EL80-09 (GB); Svalbard, Nordenskiöld Land, Longyearbyen, with *Dryas octopetala* and *S. polaris*, 7 Aug 2015, E. Larsson EL18-15 (GB); Nordenskiöld Land, Longyearbyen, with *Dryas octopetala* and *S. polaris*, 21 Aug 2002, C. Cripps CLC 1923 (MONT). SWEDEN. Torne Lappmark, Jukkasjärvi, Latnajaure, in moist area with *Salix reticulata*, 10 Aug 2007, E. Larsson EL72-07 (GB, TUR-A); Lule lappmark, Jokkmokk, Padjelanta National Park, Vielggisbakte on northwest side of Vastenjaure Lake, near *Salix herbacea* and *S. reticulata*, 12 Aug 2016, J. Vauras JV 31471 (GB, TUR-A); Lule lappmark, Jukkasjärvi, Padjelanta National Park, Slahpejaure North East, with *Salix herbacea*, 14 Aug 2016, E. Larsson EL117-16 (GB). USA. COLORADO: San Juan Mountains, Cinnamon Pass, with *Salix arctica*, 27 Jul 2002, C. Cripps CLC 1804 (MONT).

*Observations:* This is the first report of *Inocybe arctica* for North America, and it is from the southern Rockies, thousands of kilometers from the type locality and at an elevation of 3800 m in contrast to sea-level specimens from Svalbard. Other reports are from Fennoscandia where it occurs primarily with *Salix polaris*, *S. reticulata*, and *Dryas octopetala* but also with *Bistorta vivipara* and *S. herbacea*. *Inocybe arctica* is positioned in the *I. praetervisa* clade close to *I. favrei* Bon (= *I. taxocystis* (J. Favre) Singer (Larsson et al. 2018), a species with smaller spores and cystidia that has not been found in the Rockies. Microscopic details of *I. favrei* are illustrated in Larsson et al. (2018). Spore size for North American specimens differs slightly from other collections (Larsson et al. 2018).

***Inocybe giacomii*** J. Favre, Res Rech Scient Parc Nat Swiss 5:115. 1955 **FIGS. 3F, 8A**

= *Inocybe hinnulea* Kühner, Doc Mycol 20(74):20. 1988.

= *Inocybe johanna* Kühner, Doc Mycol 21(74):21. 1988.

= *Inocybe striaepes* Kühner, Doc Mycol 24(74):24. 1988.

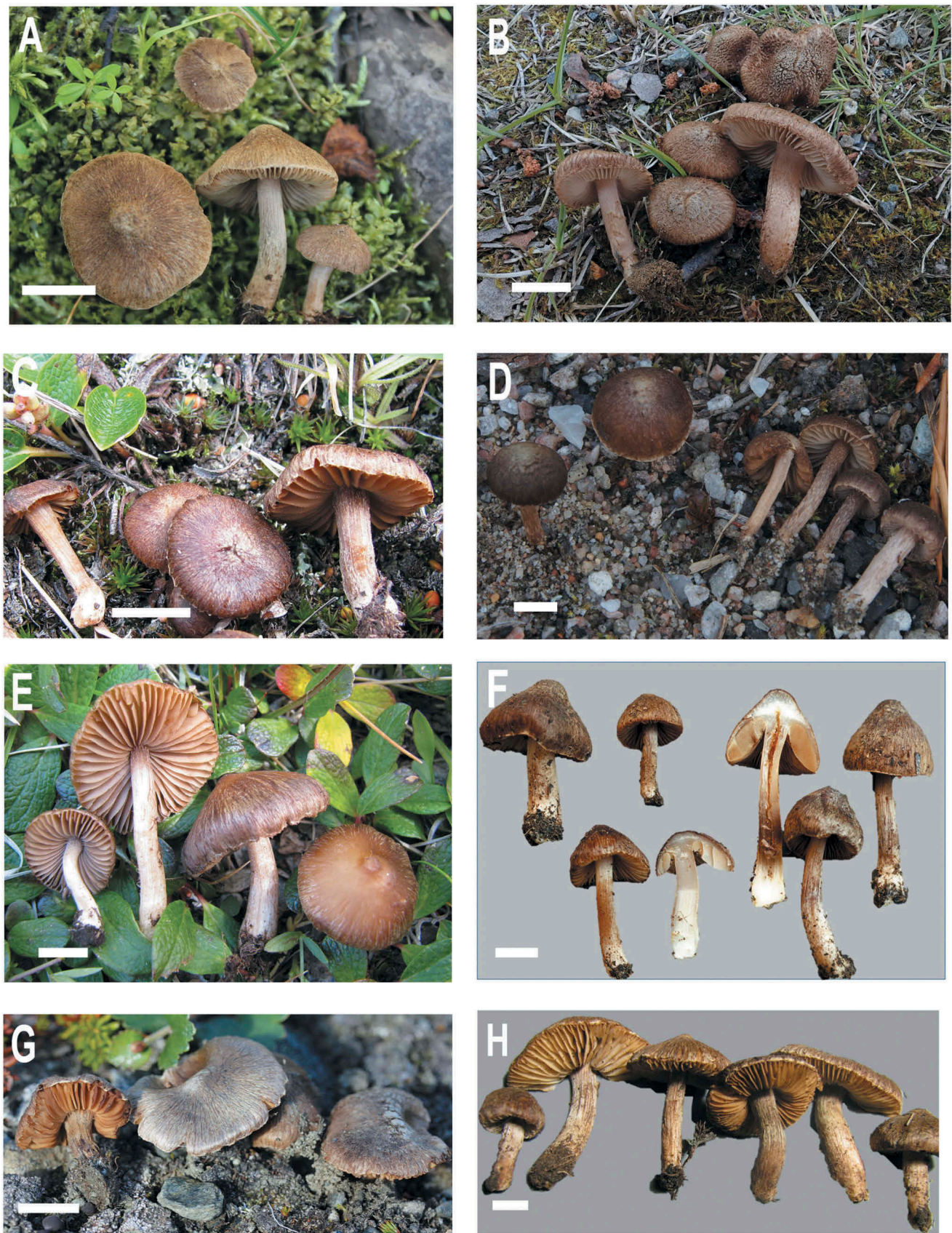
Pileus 10–35 mm wide, shape variable—conic-convex, often rather tall conic-convex, convex-umbonate, with rounded umbo, or campanulate, with margin typically persistently turned inward or down and entire or occasionally split, medium to dark brown often with a gray component or darkening to black, often with paler gray-brown margin, dry, sometimes shiny, innately streaked, outward radially fibrous,

sometimes hoary, with fibers diverging at margin, at center typically finely scurfy or rough, more rarely smooth or areolate. Lamellae narrowly attached, typically sinuate or rounded out, a bit broad, L = 40–50, cream at first, then pale gray, gray brown, or milk coffee; edges concolorous. Stipe 20–45 × 2–5 mm wide, mostly equal, or slightly larger toward base, not marginate, at first appearing whitish because of a covering of longitudinal white fibrils, then pale orange brown, pink brown (incarnate) especially in top half, fibrillose at apex, longitudinally fibrous to base. Cortina as a few fibrils on young specimens or not observed. Context white in pileus, usually incarnate (pink) in stipe. Odor not strong but subspermatic when cut. Exsiccata: pileus brown; lamellae orange brown; stipe buff or darker.

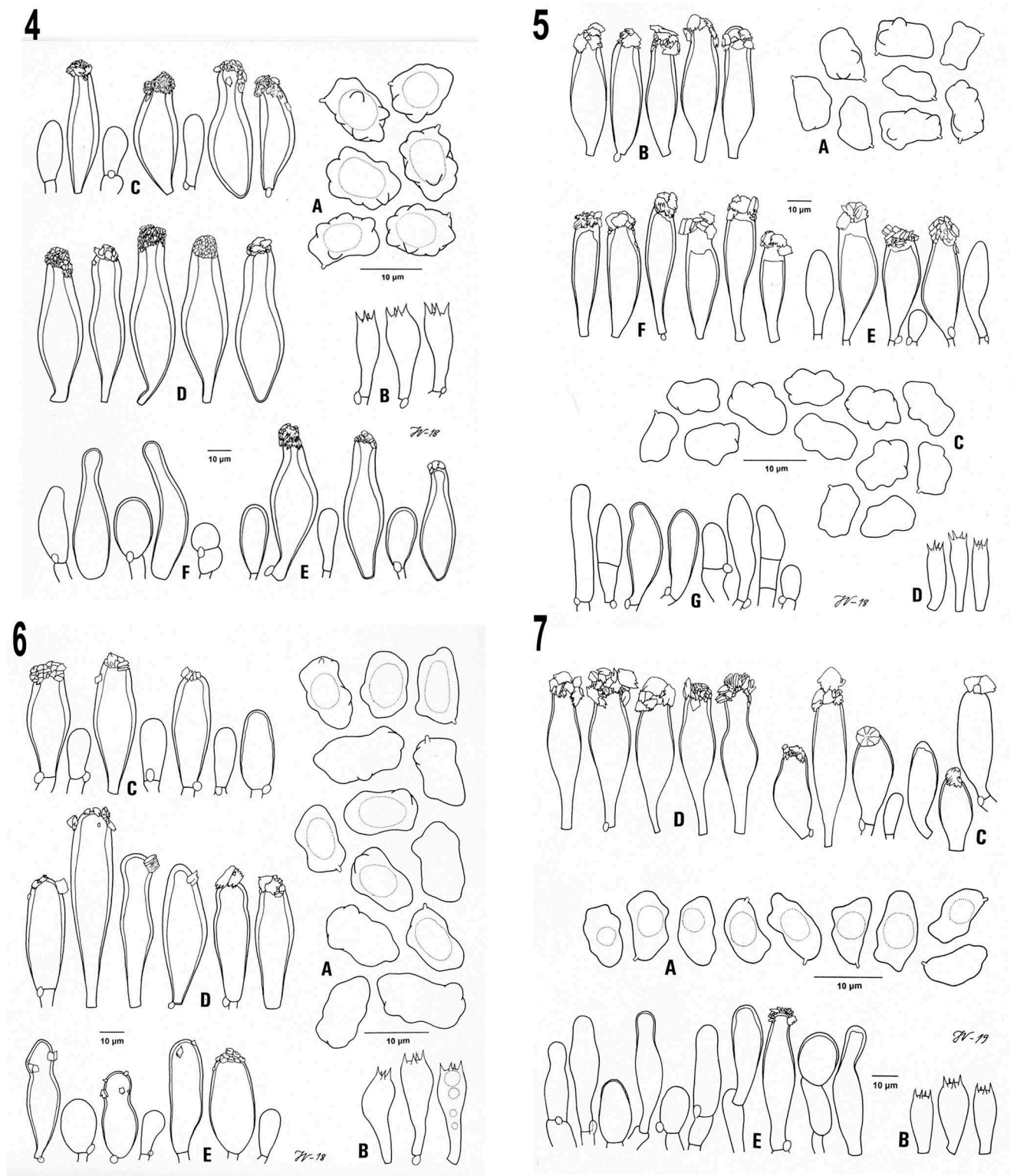
Basidiospores 9.0–9.5–10.5–11.5 μm × 5.5–6.0–6.5–7 (–7.5) μm, Q = 1.50–1.60, nodulose with 6–8 indistinct nodules and a tiny apiculus, somewhat rectangular in outline. Basidia 30–45 × 9–13 μm, clavate, 4-spored (occasionally 2-spored). Pleurocystidia 55–80 × 15–25 (–30) μm, narrowly lageniform with short pedicel or not, some with slight neck; walls 1–3 μm thick, mostly pale, a few pale yellow, with crystals at apex; paracystidia not observed. Cheilocystidia similar to pleurocystidia, some with pale yellow contents; walls 1–3 μm thick, mostly pale; paracystidia scarce. Caulocystidioid hairs, 40–100(–150) × 5–20 μm, mostly thin-walled, more rarely as caulocystidia with slightly thickened walls and crystals at apex; paracystidia also present.

*Ecology and distribution:* With shrub willow *Salix planifolia* and dwarf willows *S. arctica* and *S. reticulata*, North America (Colorado), frequent in forested and arctic-alpine areas of Europe. Jul to Aug.

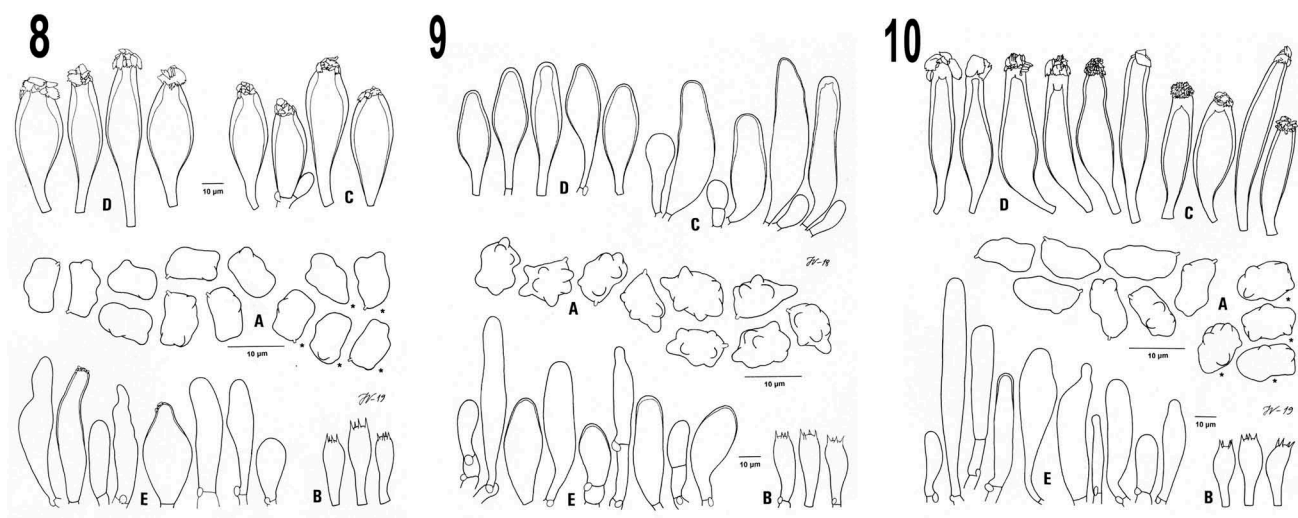
*Specimens examined:* FINLAND. Satakunta, Alastaro commune, Virttaankangas, near Lohensuon lähteikkö, heath forest on sandy soil, with *Pinus sylvestris*, *Betula*, *Picea abies*, and *Salix caprea* with *Pinus* as most likely hosts, by path, 30 Jul 2004, J. Vauras JV 21543 (TUR-A). FRANCE. Pralognan, Col de la Valette, near *Salix serpyllifolia*, 26 Aug 1965, R. Kühner K65-117 (**holotype** *I. johanna* (G)); SAVOIE: Alpes Francaises, Parc National de la Vanoise, near *Salix serpyllifolia*, 8 Aug 1972, R. Kühner K72-70 (**holotype** *I. striaepes* (G)). NORWAY. Sør-Trøndelag, Dovre, Dovrefjell National Park, Hjerkin, Geitberget, with *Betula nana* and *S. herbacea*, 20 Aug 2012, E. Larsson, J. Vauras & S. Jacobsson EL80-12 (GB). SWITZERLAND. KT. GRAUBÜNDEN: Val S-charl, Munt Plazèr, 1951, J. Favre 124a (**lectotype** *I. giacomii* (GC)). USA. COLORADO: Independence Pass, with *S. planifolia*, 13 Aug 1999, C. Cripps CLC 1359 (MONT, ZT8141 (ZT)); Loveland Pass, with dwarf and shrub willows,



**Figure 3.** Macromorphology of cortinate group. A, B. *I. murina* EL183-12 and EL230-17. C, D. *I. purpureobadia* CLC 3109 and JV32571 (subalpine). E. *Inocybe subgiacomii* CLC 360. F. *I. giacomii* CLC 1359. G, H. *I. paragiacomii* EL64-11 and CLC 3117. Bar = 1 cm.



**Figures 4–7.** Microscopic features. Figure 4. *Inocybe alpinomarginata* (from holotype, EL207-13). A. Basidiospores. B. Basidia. C. Cheilocystidia and paracystidia. D. Pleurocystidia. E. Caulocystidia and cauloparacystidia at stipe apex. F. Caulocystidia and cauloparacystidia at stipe base. Figure 5. *Inocybe murina*. A–B. Basidiospores and pleurocystidia from holotype (EL230-17). C–G. Basidiospores, basidia, cheilocystidia and paracystidia, pleurocystidia, and caulocystidia and cauloparacystidia from stipe apex (from paratype EL228-13). Figure 6. *Inocybe leonina* (CLC 1349). A. Basidiospores. B. Basidia. C. Cheilocystidia and paracystidia. D. Pleurocystidia. E. Caulocystidia and cauloparacystidia at stipe apex. Figure 7. *Inocybe purpleobadia* (from JV32571). A. Basidiospores. B. Basidia. C. Cheilocystidia and paracystidia. D. Pleurocystidia. E. Caulocystidia and cauloparacystidia at stipe apex.



**Figures 8–10.** Giacomii group. Figure 8. Microscopic characters of *Inocybe giacomii* (from EL80–12, but basidiospores indicated with asterisk from JV 21543). A. Basidiospores. B. Basidia. C. Cheilocystidia and paracystidia. D. Pleurocystidia. E. Caulocystidia and cauloparacystidia at stipe apex. Figure 9. *Inocybe paragiacomii* (from holotype, EL64–11). A. Basidiospores. B. Basidia. C. Cheilocystidia and paracystidia. D. Pleurocystidia. E. Caulocystidia and cauloparacystidia at stipe apex. Figure 10. *Inocybe subgiacomii* (from holotype, EL and JV 29938). A. Basidiospores (spores indicated with asterisk from EL9–08). B. Basidia. C. Cheilocystidia. D. Pleurocystidia. E. Caulocystidia at stipe apex.

12 Aug 1998, *C. Cripps CLC 1229* (MONT); loc. cit., with *S. reticulata*, *S. arctica*, and *S. planifolia*, 12 Aug 1998, *C. Cripps CLC 1321* (MONT); San Juan Mountains, Cinnamon Pass, with *S. arctica*, 10 Aug 2001, *C. Cripps CLC 1700* (MONT); loc. cit., with *S. reticulata* and other willows, 10 Aug 2001, *C. Cripps CLC 1702* (MONT); San Juan Mountains, Stony Pass, 9 Aug 2001, *E. Horak ZT 9790* (ZT), San Juan Mountains, Black Bear Pass, 10 Aug 2001, *E. Horak ZT 9820* (ZT).

**Observations:** The North American material of *Inocybe giacomii* described above falls phylogenetically with the Favre type of *I. giacomii* and Kühner types of *I. hinnulea*, *I. johannaea*, and *I. striaepes*, although there is some controversy as to the reference material that should be used (Kokkonen and Vauras 2012). The species occurs in forested as well as alpine habitats. Rocky Mountain collections are characterized by a streaky grayish brown pileus, gray lamellae, and pink tinged stipe, and spores that are indistinctly nodulose. Stipes are not consistently pinkish in European specimens. Three Kühner species, *I. hinnulea*, *I. johannaea*, and *I. striaepes* were tentatively synonymized with *I. giacomii* (Kokkonen and Vauras 2012), and here we confirm this. *Inocybe subgiacomii* and *I. giacomii* are closely related sister species and differ by two substitutions in the ITS1 region and two substitutions and one 10-bp and one single-bp insertion/deletion events in the ITS2 region. *Inocybe paragiacomii*, sp. nov., is evolutionarily more distant

(FIG. 1C). Most Rocky Mountain collections are characterized by a pileus that is tall conic-convex or tall umbonate. For morphological distinctions, the pileus of *I. paragiacomii* is more convex, and the lamellae are pale orange rather than gray; the stipe usually is not incarnate, but this can vary, and the spores are more nodulose. It also lacks the spermatic odor of *I. giacomii*. *Inocybe subgiacomii* is more difficult to differentiate morphologically, but the pileus is convex, even sunken in center, and brown; it shares pink tints in the stipe and a spermatic odor with *I. giacomii*.

***Inocybe leonina*** Esteve-Rav. & A. Caball., *Fungi Non Delineati* 47:33. 2009. **FIGS. 2B, 6**

Pileus 10–20 mm wide, conic-convex, hemispherical, with an entire margin that is slightly turned in or not; yellow brown, golden, medium brown; smooth when young (type), then scaly-fibrillose with some scales uplifted or recurved, without velipellis (type) or with conspicuous whitish velipellis patches on each scale, sometimes striking in contrast. Lamellae attached, sinuate, rather thick; white at first, then gray or gray brown; L = 40 plus lamellulae; edges pale. Stipe 15–20 × 3–5 mm, equal, squared-off at base, or with slight bulb, or very indistinctly submarginate, shining white, then watery brown, pruinose to base, also indistinctly longitudinally fibrous in lower part. Cortina not observed. Context completely white. Odor faint, unusual, fruity (type), not spermatic. Exsiccata: pileus brown; stipe buff.

Basidiospores (10.5–)11.0–12.0–13.0(–13.5) × (6.0–)6.5–7.0–8.0(–8.5) μm, Q = 1.55–1.70–1.85 (–1.9) (n = 40), oblong, barely nodulose, with small apiculus, generally rectangular in outline. Basidia 33–37–42 × 12–12–13 μm clavate, 4-spored (N = 16). Pleurocystidia (47–)56–60–66(–70) × 14–17–21 μm (20 pleurocystidia), clavate to short-fusoid, some tending toward subcapitate, with or without crystals at apex, wall mostly pale yellow up to 3 μm thick; rather scarce. Cheilocystidia 38–50–60 × 16–19–24 μm (n = 12), similar to pleurocystidia, some with yellow contents, abundant, with abundant pyriform to clavate paracystidia interspersed, 21–26–31 × 9–13–15 μm (n = 10). Caulocystidia at stipe apex (32–)38–49–61(–63) × (11–)12–16–20(–22) μm (n = 31), even a few to the base, mostly hyphal-like and thin-walled, cylindrical, but some with thicker walls to 1 μm thick; cauloparacystidia at stipe apex mainly clavate, 18–28–38 × 9–11–12 μm (n = 10), scarce.

*Ecology and distribution:* Alpine zone in North America (Colorado), where dwarf and shrub *Salix* occur, also in European subalpine (Spain, type). Aug.

*Specimen examined:* USA. COLORADO: Sawatch Range, Independence Pass, 12 Aug 1999, C. Cripps CLC 1349 (MONT, TUR-A).

*Observations:* *Inocybe leonina* was collected in an alpine locality in the mountains of Colorado, where both dwarf and shrubby willows occur. Remarkably, it is only the second known collection of this species, and the type is from a mountainous locality with *Pinus sylvestris* at 1300 m in Spain. The type description matches our collection in ITS-LSU sequence and in morphology except that in the type a velipellis was not observed, the stipe base appears to be more consistently bulbous, and the spores are smaller than originally reported (9–10.6–12.2 × 5–6.3–7.8 μm in Esteve-Raventós and Caballero Moreno 2009). Also, the closely related species *I. candidipes* Kropp & Matheny has been found with *Pinus ponderosa* in montane environments in Arizona (Kropp and Matheny 2004). Microscopically, *I. leonina* has wider spores than *I. candidipes* (5.0–5.6–6.0(–6.5) μm), and the spore outline is not rocket-shaped. The closest alpine species, *I. lemmi* E. Larss., Vauras & C.L. Cripps, is similar in color but differs by slightly larger spores and by seven substitutions and three insertion/deletion events in the ITS region, and by two substitutions, one ambiguous site, and one insertion/deletion event in the 28S region (Larsson et al. 2017). The sequence difference from *I. candidipes* is somewhat larger for the ITS region, with seven substitutions, three insertion/deletion events, and one 13-bp insertion. For the 28S, the sequence difference includes one substitution and one insertion/deletion event.

*Inocybe murina* E. Larss., C.L. Cripps & Vauras, sp. nov. FIGS. 3A–B, 5

MycBank MB832703

*Typification:* SWEDEN. Torne lappmark, Karesuando, Karesuando Cemetery close to entrance, among grasses and herbs under *Betula pubescens* and *Pinus sylvestris* on sandy poor soil, ca. 325 m a.s.l., 23 Aug 2017, E. Larsson & J. Vauras EL230-17 (**holotype** GB-0156960, **isotype** TUR-A 204710). GenBank: ITS-28S = MK153678.

*Diagnosis:* Pileus woolly, brown or smoother with a silvery white velipellis; lamellae brown; stipe pale brown, equal; spores on average 8.7 × 5.2 μm, rectangular with 4–6 low nodules; pleurocystidia short, on average 51 × 14 μm. Closest morphologically to *I. purpureobadia* Esteve-Rav. & A. Caball., which has a smoother pileus. Closest molecularly to *I. bufonia* Kokkonen & Vauras, a boreal/subalpine species distinguished by larger basidiomata and more strongly nodulose spores. Differs from *I. bufonia* at ITS and 28S loci.

*Etymology:* *murina* (Latin), in reference to the furry mouse-like texture and color of the pileus that is brownish with a grayish overlay.

Pileus 10–25 mm wide, conic-convex or broadly convex with a blunt or sharp umbo, or almost hemispherical when young, with slightly down-turned margin that is entire and covered with tissue in young specimens, medium brown, dark brown, rusty brown, woolly when young, then minutely scurfy or squamulose, or rough in center and outward radially fibrous, with conspicuous white-silvery velipellis in center or not. Lamellae emarginate or with small tooth on stem, broadest in center, L = 50–60, white at first, then pale grayish brown. Stipe 15–25 × 2–5 mm, equal, straight or a bit curved, pale brown covered with longitudinal fibrils, pinkish tint in top half (sometimes) and floccose at extreme apex. Cortina fugacious. Context whitish, usually incarnate in stipe apex, brownish in base. Odor subspermatoc, faint. Exsiccata: pileus grayish brown; lamellae grayish brown, rusty brown; stipe buff.

Basidiospores (6.5–)7.5–8.5–10.0(–10.5) × 4.0–5.0–6.5 μm, range of mean values 7.8–9.1 × 4.6–5.6 μm, Q = (1.4–)1.45–1.66–1.95(–2.15), range of mean Q values 1.61–1.71 (n = 100, from 5 collections), angular-subnodulose with 3–6 low nodules and tiny apiculus, rather rectangular in outline, pale. Basidia (16–)19–33 × 7–9(–10) μm, clavate, most 4-spored (n = 40). Pleurocystidia (38–)43–51–61(–68) × (10–)11–14–17(–18) μm (n = 80, from 5 collections), fusoid, often with pedicel, mostly with large crystals at apex, sparse, rather small; walls 1–2 μm thick, slightly yellowish. Cheilocystidia 35–80(–90) × 8–10 μm (n = 40), variable, clavate, cylindrical, fusiform, with or without crystals, some yellowish brown inside, fairly numerous; walls up to 1 μm thick, pale; paracystidia sparse.

Caulocystidioid hairs at stipe apex, 30–60 × 6–12 µm, with pale yellow-brown contents; walls thin or occasionally slightly thickened, sometimes with yellow contents.

*Ecology and distribution:* One collection with dwarf and shrub *Salix* from alpine zone at 3355 m in North America (Colorado). Also with *Salix herbacea*, *S. reticulata*, and *Dryas octopetala* in alpine and with *Betula pubescens*, often in company with *Salix* in sub-alpine areas of Europe (Fennoscandia). Aug.

*Specimens examined:* FINLAND. Inari Lapland, Utsjoki, Kevo, Kevo Strict Nature Reserve, the island between Kevojoki and Tsarsjoki, lake shore with *Salix* spp. and *Betula pubescens*, 30 Aug 2012, *E. Larsson & J. Vauras* EL183-12 (GB, TUR-A). ICELAND. S.-Múl., Fjarðarheiði, 25 Aug 1987, *H. Hallgrímsson* FA-11435 (AMNH). NORWAY. Hordaland, Ulvik, Finse, Lilla Finsenuten, with *S. herbacea*, 10 Aug 2005, *E. Larsson* EL15-05 (GB); Ulvik, Finse, Sanddalsnut, with *Dryas octopetala* and *S. herbacea*, 12 Aug 2005, *E. Larsson* EL45-05 (GB, TUR-A). SWEDEN. Torne lappmark, Jukkasjärvi, Abisko NP, between Nuolja and Slättatjåkka, with *S. herbacea*, 25 Aug 2013, *E. Larsson & J. Vauras* EL228-13 (GB, TUR-A). USA. COLORADO: Loveland Pass, with dwarf and shrub *Salix*, 12 Aug 1998, *C. Cripps* CLC 1226 (MONT).

*Observations:* *Inocybe murina* is recognized by a brown scurfy pileus sometimes covered with a grayish velipellis, pale lamellae, and light brown fibrillose to subsquamulose stipe. The spores are pale and small (on average 8.7 × 5.2 µm), with a few indistinct nodules and almost rectangular. The short cystidia distinguish it from *I. alpinigenes* (E. Horak) Bon and *I. purpurobadia*, which also have small brown basidiomata and rectangular spores. The related *I. pseudoteratargus* Vauras & Kokkonen and *I. bufonia* are found in forested habitats, and both have more nodulose spores (Kokkonen and Vauras 2012). Species of the *I. lanuginosa* group can have a rather similar pileus, but they have a scallier stipe.

***Inocybe occulta*** Esteve-Rav., Bandini, B. Oertel & G. Moreno, *Persoonia* 41:229. 2018. [FIG. 2E–F](#)

Pileus 15–25 mm, conic-convex, campanulate, with indistinct umbo, and a margin that is entire and turned down or not, ocher, yellow brown, a bit greasy, appearing smooth, but can be scurfy in center and outward radially fibrous. Lamellae with narrow attachment, sinuate, depressed at apex, pale gray, gray brown, gray yellow brown, gray yellow buff, staining yellow; edges floccose, concolorous or brown. Stipe 20–30 × 2–4 mm, equal down to distinctly marginate base, straight or curved, shining white or tinged ocher, pruinose to the base, more obvious at apex and more fibrous in lower part. Cortina absent. Context white in pileus, buff in stipe. Odor

spermatic, subspermatic, especially when cut open. Exsiccata: pileus golden brown; stipe buff.

Basidiospores (8.5–)9.0–9.5–10.0(–10.5) × (5.5–)6.0–6.5–7.0(–7.5) µm, range of mean values 9.3–9.7 × 6.2–6.5 µm, Q = (1.25–)1.35–1.49–1.65, range of mean Q values 1.47–1.50 (n = 60, from 3 collections), thick-walled, nodulose with 6–8 nodules, narrowing toward apiculus, occasionally with 1 or 2 prominent nodules at opposite end. Basidia (19–)20–23–27(–28) × (7–)8–10–11 µm, clavate, 4-spored (n = 20). Pleurocystidia (36–)41–48–54(–58) × (14–)15–18–22(–23) µm (n = 63, from 3 collections), abundant, short, subfusiform (or fusiform) with crystals at apex, some broadly clavate with rounded apex and not crystalliferous, mostly without long pedicels; walls 2–3 µm thick, pale or pale yellow. Cheilocystidia similar to pleurocystidia, more often subfusiform with crystals at apex; walls 2–3 µm thick, some with pale yellow contents. Caulocystidia similar to cheilocystidia, or larger, up to 70 × 18 µm, with pale walls.

*Ecology and distribution:* Alpine habitats with dwarf *Salix* species and shrub species *S. planifolia* and *S. glauca* in North America (Colorado), and in alpine and boreal habitats of northern Europe (Fennoscandia) but widespread in North America and Europe predominantly in forested habitats—west coast of North America, Nova Scotia, Mexico, with pine in North Carolina piedmont according to environmental samples, introduced in Australia with pine.

*Specimens examined:* FINLAND. Varsinais-Suomi, Kustavi, Iso-Rahi, dry heath forest, near *Pinus sylvestris* and *Picea abies*, 29 Jul 2007, *J. Vauras* JV 24871F (TUR-A), Kainuu, Paltamo, Itkonpuro Nature Reserve, moist herb-rich forest, 27 Aug 2018, *K. Kokkonen* 312/18 (TUR-A); Enontekiön Lappi, Enontekiö, Kilpisjärvi, rather moist forest with mountain birch *Betula pubescens* subsp. *Czerepanovi*, 15 Aug 1990, *J. Vauras* JV 4811 (TUR-A). NORWAY. Sør-Trøndelag, Dovre, Grimsdalen, Grimsdalshytta, with *Salix* spp. and *Betula nana*, 21 Aug 2012, *I.-L. Fonneland* EL102-12 (GB); Troms, Storfjord, Sallorassa, southeast of Rassajavrit and Goallarrassa, with *Dryas octopetala* and *S. reticulata*, 28 Aug 2013, *E. Larsson* EL272-13 (GB). USA. COLORADO: Niwot Ridge, with dwarf *Salix*, 17 Aug 1997, *E. Horak* CLC 1147 (MONT, ZT 7279); Independence Pass, with *S. glauca* and *S. planifolia*, 14 Aug 2001, *C. Cripps* CLC 1756 (MONT, ZT 9840).

*Observations:* Most specimens collected above tree line determined as *I. mixtilis* likely represent the recently described species *I. occulta* (Esteve-Raventós

et al. 2018). In the phylogenetic analyses, *I. occulta* comes out as sister species to *I. mixtilis* (Britzelm.) Sacc., which occurs in forested habitats. Sequence data of the holotype of *I. occulta* are identical to those of our collections. The ITS sequence of the epitype of *I. mixtilis* is also included in our data set. *Inocybe occulta* has also been reported from a montane forest in the Pacific Northwest and from pine forests of Mexico in Esteve-Raventós et al. (2018).

Although *I. occulta* is not molecularly close to the *I. phaeocystidiosa* group, it is included in the key because of convergent morphological characters. Both are characterized by a yellow-brown pileus, a strongly marginate stipe that is entirely pruinose, and distinctly nodulose spores. However, the spores and cystidia are smaller (or the spores more narrow) than in *I. occulta*. In the field, they can sometimes be distinguished by odor that is spermatic (at least when cut open) in *I. occulta* and absent or faintly fruity in *I. phaeocystidiosa*. In addition, dried specimens of *I. occulta* do not darken as much as those of *I. phaeocystidiosa*. Its lower elevation range overlaps with that of the similar *I. ceskae* Bandini, Esteve-Rav. & Oertel found with *Betula* and conifers (Esteve-Raventós et al. 2018) in the Pacific Northwest and Canada. Microscopic illustrations of *I. ceskae* and *I. occulta* can be found in Esteve-Raventós et al. (2018)—these two species are rather similar both macroscopically and microscopically. Also, molecular results of *I. abundans* Murrill should eventually be considered, but its morphology is not similar. Spore widths for Rocky Mountain collections are recorded as narrower than those of the type.

***Inocybe paragiacomii*** E. Larss., C.L. Cripps & Vauras, sp. nov. FIGS. 3G–H, 9  
Mycobank MB832705

**Typification:** SWEDEN. Torne lappmark, Jukkasjärvi, Abisko, Latnja, alpine heath with *Salix herbacea* and *Betula nana*, on bare soil, ca. 1000 a.s.l. 30 Jul 2011, E. Larsson & B. Larsson EL64-11 (**holotype** GB-0156959, **isotype** TUR-A 203732). GenBank: ITS-LSU = MK153670.

**Diagnosis:** Pileus slightly conic-convex, brown, with roughened radial fibrils and slight velipellis; lamellae pale orange; stipe equal, pale brown, fibrous; not pruinose, not usually incarnate. Spores rectangular, slightly nodulose, on average  $10.5 \times 6.5 \mu\text{m}$ ; pleurocystidia on average  $64 \times 16 \mu\text{m}$  long with thick walls. In contrast to *I. giacomii* and *I. subgiacomii*, the lamellae are pale orange instead of gray, the stipe is not incarnate, and the odor is not spermatic. *Inocybe paragiacomii* is

separated from *I. giacomii* and *I. subgiacomii* in phylogenetic analyses.

**Etymology:** *paragiacomii* (Greek), in reference to the similar species *Inocybe giacomii*.

Pileus 15–40 mm wide, slightly conic-convex at first, then broadly convex, with or without a small low umbo, and turned down at margin, which splits and is rimose, brown, with roughened radial fibrils, at center sometimes with slight pale vellipellis. Lamellae adnexed, rather thick, well separated, L = 40 plus lamellulae, pale old gold, pale orange, light brown, with brown edges. Stipe 20–30 mm  $\times$  3–5 mm, equal, brownish with a longitudinal fibrous silvery overlay, not pruinose. Cortina fibrillose in young basidiomata, fugacious, often not observed. Context cream throughout, not incarnate. Odor absent. Exsiccata: pileus dark brown; lamellae medium brown with rusty tone; stipe pale to dark brown.

Basidiospores  $(8.5\text{--})9.0\text{--}10.5\text{--}12.0 \times (5.5\text{--})6.0\text{--}6.5\text{--}7.5$  ( $-8.0$ )  $\mu\text{m}$ , range of mean values  $10.0\text{--}10.5 \times 6.5\text{--}7.9 \mu\text{m}$ ,  $Q = (1.3\text{--})1.35\text{--}1.56\text{--}1.8(-1.85)$ , range of mean Q values  $1.54\text{--}1.58$  ( $n = 60$ , from 3 collections), with a few very low nodules, irregular or rectangular, some constricted in the middle. Basidia  $(32\text{--})34\text{--}44 \times 10\text{--}13 \mu\text{m}$  ( $n = 20$ ), clavate, 4-spored. Pleurocystidia  $(48\text{--})52\text{--}64\text{--}80(-90) \times (12\text{--})13\text{--}16\text{--}21(-25) \mu\text{m}$  ( $n = 63$ , from 3 collections), subfusiform with short pedicel, crystals or not at apex; walls  $2 \mu\text{m}$  thick, mostly pale. Cheilocystidia similar to pleurocystidia but more variable in shape,  $(40\text{--})41\text{--}59\text{--}77(-98) \times (10\text{--})13\text{--}17\text{--}21(-22) \mu\text{m}$ , often yellow brown inside ( $n = 37$ ); paracystidia  $(13\text{--})14\text{--}24\text{--}32(-37) \times (7\text{--})8\text{--}12\text{--}13(-14) \mu\text{m}$ , clavate to oval, some yellow brown inside ( $n = 37$ ). Caulocystidia  $(29\text{--})35\text{--}53\text{--}67(-79) \times (8\text{--})10\text{--}13\text{--}19(-20) \mu\text{m}$ , thick-walled at apices only, often yellow brown inside ( $n = 21$ ); caulocystidioid hairs thin-walled, with end cells  $36\text{--}56 \times 8\text{--}9 \mu\text{m}$ ; cauloparacystidia  $10\text{--}27 \times 6\text{--}11 \mu\text{m}$ , scarce.

**Ecology and distribution:** Low alpine, in shrub *Salix* with krummholz nearby, on rocky slope, North America (Montana) and Europe (Sweden, type).

**Specimens examined:** SWEDEN. Lycksele lappmark, Tärna, Laisaliden, with *Salix* spp. and *Betula nana*, 19 Aug 2015, E. Larsson & P.-A. Moreau EL116-15 (GB, TUR-A). USA. MONTANA: Beartooth Plateau, Frozen Lakes, with shrub *Salix* and near conifer krummholz, 17 Aug 2014, C. Cripps CLC 3117 (MONT).

**Observations:** *Inocybe paragiacomii* is characterized by basidiomata that are rather stout, with dark brown pilei and stipes covered with silvery longitudinal fibrils that are all reminiscent of *I. giacomii*. However, the stipe apparently is not incarnate in North American collections, the lamellae have a pale orange coloration, and

the pileus is not tall conic-convex. *Inocybe giacomii* and *I. subgiacomii* typically have reddish tints in the stipe, and the spores are narrower and less nodulose.

***Inocybe phaeocystidiosa*** Esteve-Rav., G. Moreno & Bon, *Doc Mycol* 17(67):18. 1987. **FIG. 2G–H**

GenBank: ITS = KT203789

Pileus 15–35 mm (15–60 mm in subalpine collection) wide, conic-convex, convex, slightly campanulate, with rounded smooth apex, with entire margin that is not rimulose, yellow brown, golden brown, orange brown, often with darker, appressed scales, radially fibrous, greasy. Lamellae narrowly attached, sinuate or notched, up to 5.5 mm broad, L = 60+, whitish, pale cream, pale gray, grayish brown, some with yellow stains; edges fimbriate white or dark. Stipe 20–50 mm × 3–5 mm (up to 100 × 12 mm in subalpine collections), curved, equal down to marginate or submarginate base, and rounded at base, cream, some with orange tint, appearing smooth but pruinose for whole length. Cortina absent. Context all white to yellowish brown. Odor none or faintly fruity. Exsiccata: pileus brown; stipe buff; flesh graying.

Basidiospores (9.5–)10.0–11.0–12.0(–12.5) × 7.0–8.0–9.0(–9.5) μm, range of mean values 10.8–11.2 × 7.7–8.6 μm, Q = (1.15)–1.2–1.55, on average 1.35, range of mean Q values 1.26–1.43 (60 spores from 3 collections), nodulose, with 10–14 round knobs, sunken near apex. Basidia clavate, mostly 4-spored, 25–40 × 8–12 μm. Pleurocystidia (60–)61–73–86(87) × 14–17–22(–25) μm, range of mean values 69–76 × 16–18 μm (50 pleurocystidia from 3 collections), subfusiform, some with long necks and a short pedicel, crystals at apex, a few rounded clavate with no crystals, sometimes with yellow-brown contents; walls 1–4 μm thick, colorless, or very pale yellow. Cheilocystidia similar, some with yellow-brown contents. Paracystidia clavate. Caulocystidia similar to pleurocystidia, with paracystidia present.

**Ecology and distribution:** In alpine zone with dwarf willows *S. reticulata*, *S. arctica*, and shrub willow *S. glauca* in North America (Colorado, Montana) and in alpine and forested areas of Europe (Finland, Sweden, and Spain, type).

**Specimens examined:** FINLAND. Enontekiön Lappi, Enontekiö, Kilpisjärvi, Tsahkaljohka, with *Betula pubescens* subsp. *czerepanovii*, 15 Aug 1990, *J. Ruotsalainen & J. Vauras* 4798F (TUR-A, GB), same area, Jeähkkas, E slope, 29 Aug 2013, *E. Larsson & K. Bendiksen* EL289-13 (GB); Perä-Pohjanmaa, Tornio, Kalkkimaa, on forest track with *Betula*, *Picea abies*, and *Populus tremula*, 11 Aug 1987, *J. Ruotsalainen & J. Vauras* 2712F (TUR-A). SWEDEN. Torne Lappmark, Jukkasjärvi, Latnjajaure, 7 Aug 2007, with *Salix reticulata* and *S. polaris*, *E. Larsson*

EL39-07 (GB); with *Dryas octopetala*, *Salix reticulata*, and *S. herbacea*, 18 Aug 2013, *P.-A. Moreau, E. Larsson & J. Vauras* 29937F (TUR-A, GB). SPAIN. Segovia, San Rafael, in *Pinus sylvestris* forest, 29 May 1985, *G. Moreno & F. Esteve-Raventós* (**holotype** AH 9154). SWITZERLAND. S-charl, 1966, in *Salix herbacea* (**holotype** *I. salicis-herbaceae* Kühner GR-66-49, G00110923). USA. COLORADO: Cottonwood Pass, 4 Aug 2001, with *S. glauca*, *C. Cripps* CLC 1645 (MONT); Independence Pass, with *S. reticulata* and *S. arctica*, 12 Aug 2001, *C. Cripps* CLC 1738 (MONT); MONTANA: Beartooth Plateau, site 1, with dwarf *Salix*, 27 Jul 1997, *C. Cripps* CLC 1133 (MONT, ZT 6091); Beartooth Plateau, Highline Trail, with *S. reticulata*, 8 Aug 1998, *C. Cripps* CLC 1204 (MONT); Cooke City, Miller Creek, with *Picea*, *Abies*, and *Vaccinium cf. canadensis*, 25 Aug 2016, *C. Cripps* CLC 3293 (MONT).

**Observations:** Our description fits that of *I. phaeocystidiosa*, and the ITS sequences of the Rocky Mountain specimens match that of the holotype. The stipe of *I. phaeocystidiosa* is entirely pruinose as in our specimens (which is not true of *I. praetervisa*), the cystidia are quite large, and sometimes have yellowish brown contents, and the flesh turns gray on drying. The Rocky Mountain collection from the subalpine is much larger (**FIG. 2H**) than typical alpine collections.

*Inocybe praetervisa* previously has been reported from alpine habitats (Favre 1955; Horak 1987; Brunner et al. 2017). However, a newly designated epitype and molecular data confirm it to be found primarily in subalpine areas of Europe with conifers (Esteve-Raventós et al. 2016). There are several recognized arctic-alpine species in the *I. praetervisa* clade (*I. favrei*, *I. arctica*, *I. rivularis*) (Larsson et al. 2017, 2018), and *I. salicis-herbaceae* has been found to be synonymous with *I. phaeocystidiosa* through type sequencing. Therefore, reports of *I. praetervisa* in arctic and alpine habitats need to be compared with *I. phaeocystidiosa* and these other species.

***Inocybe purpureobadia*** Esteve-Rav. & A. Caball., *Fungi Non Delineati* 47:90. 2009. **FIGS. 3C–D, 7**

Pileus 5–15 mm wide, conic-convex with small rounded umbo or without umbo, with turned-down margin that is mostly entire or rimulose, umber brown to purple brown with yellowish gray velipellis in center of some specimens, appearing sericeous smooth but roughened on close inspection, outward radially fibrous with fibrils diverging slightly at margin. Lamellae narrowly attached, emarginate, well separated, L=30–40, thickish, with only tiny lamellulae, cream or pale brown, brown, yellow brown, tobacco brown, or rusty brown; edges paler, concolorous or dark brown. Stipe 5–20 × 1–3 mm, equal



or clavate, pale brown or darker brown with pinkish tint, darker at apex and lighter below, covered with longitudinal white fibrils for the length, floccose-pruinose at very apex. Cortina fugacious. Flesh white in cap, buff in stipe, slightly incarnate in some. Odor not distinct. Exsiccata: tiny; pileus umber brown; lamellae rusty brown; stipe buff.

Spores (8)8.5–10.0–11.5(–12.5) × (5)5.5–6.0–6.5 μm, slightly angular in outline or angular-subnodulose. Basidia 30–40 × 9–12 μm, clavate, 4-spored. Pleurocystidia 40–80 × 12–19 μm, cylindrical-subfusiform, some with a slight neck, some subcapitate, typically with a pedicel, often with abundant crystals at apex; walls up to 2 μm thick, pale to pale yellow. Cheilocystidia similar but on average shorter. Caulocystidia 30–56 × 8–18 μm, as metuloids at stipe apex numerous, utriform, cylindrical or slightly clavate, subglobose, often with brown contents, some with crystals, walls up to 1 μm thick, a few with encrusted pigment.

**Ecology and distribution:** Scattered on soil between rocks on slopes in alpine zone with dwarf *Salix reticulata* and shrub *Salix* in the vicinity in North America (Colorado and Montana). Occurring in Europe (Finland, France, Spain, type) with several hosts, typically on sandy soils. Aug and Oct.

**Specimens examined:** FINLAND. Koillismaa, Kuusamo, Oulanka National Park, near Kiutaköngäs, with *Pinus sylvestris*, 14 Aug 2009, J. Vauras & K. Kokkonen 64/09 (TUR-A), Oulanka National Par, near Jäkäläniemi, with *Pinus sylvestris*, 19 Aug 2018, J. Vauras JV 32571F (TUR-A). FRANCE. HAUTS-DE-FRANCE: Wallery, Mare à Goriot, with *Betula pendula*, 31 Oct 2006, E. Larsson & P.-A. Moreau EL215-06 (GB). USA. COLORADO: Mount Evans, Summit Lake, with *S. arctica* and *S. glauca*, 11 Aug 2013, C. Cripps CLC 2982 (MONT); WYOMING: Beartooth Plateau, Highline Trail: with dwarf willows, 8 Aug 1998, C. Cripps CLC 1205 (MONT, ZT 6418); loc. cit., 8 Aug 8 1998, E. Horak ZT 6412 (ZT); loc. cit., 15 Aug 2014, C. Cripps CLC 3106 (MONT); loc. cit., with *S. reticulata*, *S. planifolia*, and *S. glauca*, 16 Aug 2014, C. Cripps CLC 3109 (MONT).

**Observations:** *Inocybe purpureobadia* was originally described from Spain in forested areas with *Quercus ilex* on sandy soil (Esteve-Raventós and Gaballero Moreno 2009). Then, it was reported from boreal and hemiboreal habitats in Finland and Estonia (Kokkonen and Vauras 2012). The species is reminiscent of a tiny species of *Cortinari* subg. *Telamonia* because of the dark brown pileus and rusty brown lamellae of older fruiting bodies; however, the spores are not dark colored. The velipellis appears to be a variable character. Microscopic details of *I. purpureobadia* are illustrated in Esteve-Raventós and Gaballero Moreno (2009) and Kokkonen and Vauras (2012).

The basidiomata of *I. purpureobadia* are on average smaller and darker than those of *I. murina*, but microscopically they are rather similar. However, the spores of *I. purpureobadia* are on average larger, pleurocystidia have thinner walls, and there are metuloid caulocystidia at the stipe apex. *Inocybe alpigenes* (E.Horak) Bon (syn. *I. tetragonospora* Kühner) also has quadrangular spores similar to the two species mentioned above. However, the spores and Q values are smaller, and the cystidia shape is different (Horak 1987; Kokkonen and Vauras 2012).

***Inocybe subgiacomii*** C.L. Cripps, Vauras & E. Larss., sp. nov. FIGS. 3E, 10

MycoBank MB832707

**Typification:** SWEDEN. Torne lappmark, Jukkasjärvi, Abisko, southeast-east of Latnjajaure, south slope of the fjeld Latnjatjärro, alpine heath with *Dryas octopetala*, *Salix reticulata*, and *S. herbacea*, on calcareous soil, ca. 1100 a.s.l., 18 Aug 2013, E. Larsson & J. Vauras JV 29938F (**holotype** TUR-A 199032, **isotype** GB). GenBank: ITS-LSU = MK153665.

**Diagnosis:** Similar to *I. giacomii*, but the pileus not as tall and with a smoother center that can be indistinctly umbonate to sunken; pileus margin more rimose and less persistently incurved. Spores less nodulose than those of *I. paragiacomii*, and the lamellae gray (not orange). *Inocybe subgiacomii* and *I. giacomii* are closely related sister species but differ slightly at ITS and 28S loci.

**Etymology:** *subgiacomii* (Greek), in reference to the similar species *Inocybe giacomii*.

Pileus 10–32 mm wide, conic-convex, not umbonate or with indistinct umbo, or sunken in center, with splitting margin, light brown, brown, dark brown to black brown in center, radially fibrillose. Lamellae adnexed or submarginate, well spaced, up to 6.5 mm broad, whitish at first, then pale gray, brown gray, pale orange brown, brown; edges concolorous. Stipe 15–35 mm × 2–6.5 mm, equal, but slender clavate to tapering toward the base; whitish at first, then pale brown, often with a reddish brown tinge, whitish at the base; pruinose at the apex, with longitudinal whitish fibrils below. Cortina not observed. Context whitish, shiny in stipe, at times weakly incarnate at stipe apex. Odor spermatic. Exsiccata: pileus brown to dark brown; lamellae medium brown; stipe pale to dark brown.

Basidiospores (9.0–)9.5–10.5–12.0(–12.5) × (5.5–)6.0–6.5–7.0 μm, range of mean values 10.2–11.4 × 6.4–6.5 μm, Q = 1.4–1.65–1.9(–2.05), range of mean Q values 1.57–1.79 (n = 60, from 3 collections), irregular, often only slightly nodulose, or nodulose with 6–8 small nodules, somewhat rectangular to elongate.

Basidia (25–)27–31–35(–36) × 9–11(–12) μm (n = 21), clavate, 4-spored. Pleurocystidia (50–)63–70–79(–83) × (11–)12–15–18(–19) μm (n = 38, from 3 collections), subfusiform, several with pedicel, often with large or abundant crystals at apex; walls up to 3 μm thick, mostly pale yellow. Cheilocystidia like pleurocystidia but more variable, (50–)51–72–78(–87) × (11–)13–18–21(–22) μm, some yellow brown inside (n = 25); paracystidia scarce. Caulocystidia: metuloids 58–64–70 × 12–15–17 μm, subfusiform, scarce (n = 5); caulocystidioid hairs mainly thin-walled, 27–102 × 6–17 μm (n = 15); cauloparacystidia scarce.

*Ecology and distribution:* In alpine areas of North America (Colorado, Montana, Wyoming) with dwarf and shrub *Salix*, also northern Europe (Sweden, type). Aug.

*Specimens examined:* SWEDEN. Torne lappmark, Jukkasjärvi parish, Abisko, southeast-east of Latnjajaure, south slope of fjeld Latnjatjärro, alpine site with *Dryas octopetala*, *Salix reticulata*, and *S. herbacea*, ca. 1100 m a.s.l., 18 Aug 2013, *E. Larsson* & *J. Vauras* 29938F (**holotype** TUR-A, **isotype** GB). USA. COLORADO: Independence Pass: with dwarf *Salix*, 13 Aug 1998, *C. Cripps* CLC 1239 (MONT); loc. cit., with *S. reticulata*, 9 Aug 1999, *C. Cripps* CLC 1330 (MONT); loc. cit., with dwarf willows, 11 Aug 1999, *C. Cripps* CLC 1346 (MONT); MONTANA: Beartooth Plateau, Birch Quad Creek, with *S. reticulata*, 4 Aug 2008, *E. Larsson* EL9-08 (GB, TUR-A); East Summit, 3460 m, with *Salix* spp., 1 Aug 1997, *E. Horak* ZT 6215 (ZT); Frozen Lakes, with shrub *Salix* and near conifer krummholz, 17 Aug 2014, *C. Cripps* CLC 3116 (MONT); WYOMING: Beartooth Plateau, with *S. reticulata*, 21 Aug 1999, *C. Cripps* CLC 1402 (MONT); with *S. reticulata*, 16 Aug 2016, *C. Cripps* CLC 3113 (MONT); 22 Aug 2017, *C. Cripps* CLC 3600 (MONT).

*Observations:* *Inocybe subgiacomii* is morphologically similar to *I. giacomii*, but differences were noted in the field. The pileus of *I. subgiacomii* is typically not as tall as in *I. giacomii*, the pileus margin is not as persistently incurved, and the odor is more strongly spermatic. *Inocybe paragiacomii* lacks the reddish incarnate tints found in the stipe of the other two species. Microscopically, the spores of all three taxa are similar in size, but those of *I. paragiacomii* appear to be more nodulose, and the cystidia lack crystals more often. The sequence difference between *I. giacomii* and *I. subgiacomii* includes two substitutions in the ITS1 and two substitutions and one 10-bp and one single-bp insertion/deletion event in the ITS2, and two substitutions in the 28S region. The sequence difference between *I. giacomii* and *I. paragiacomii* is much larger (FIG. 1C).

## KEY TO *INOCYBE* WITH NODULOSE SPORES FROM THE ROCKY MOUNTAIN ALPINE ZONE

1. Stipe marginate, submarginate, pruinose to middle or base; pileus yellow brown or medium brown; cortina clearly absent or fugacious ..... 2
- 1'. Stipe not marginate, pruinose only at apex or not at all; pileus pale brown, dark brown, purple brown; cortina present but can be fugacious ..... 6
2. Pileus typically small (<20 mm), minutely scaly, yellow brown with white vellipellis (can be absent) on each scale; stipe equal to submarginate, distinctly striate; odor faint; spores angular-rectangular, 11–13 × 6–8 μm ..... *I. leonina*
- 2'. Pileus larger than above (>20 mm), smooth or with appressed scales; spores more nodulose.... 3
3. Pileus brown with frosty vellipellis; stipe base submarginate to swollen, pruinose in top half, pinkish at apex; cortina fugacious; odor slightly spermatic or not; spores 11–13 × 7–8.5 μm ..... *I. arctica*
- 3'. Pileus yellow brown, brown, with or without slight vellipellis; stipe with marginate base, white, smooth, pruinose to base; cortina absent; spores smaller ..... 4
4. Pileus smooth, radially fibrous; odor spermatic; spores 9–10.5 × 6–7 μm; pleurocystidia rather short, 40–55 × 15–22 μm (molecularly distant to others in group) ..... *I. occulta*
- 4'. Pileus smooth or appressed scaly; odor not spermatic; spores wider; pleurocystidia longer ..... 5
5. Pileus smooth or appressed scaly; odor absent or faintly fruity; spores 9.5–12 × 7–9 μm; pleurocystidia 60–85 × 14–22 μm, mainly sublageniform with crystals at top, some with yellow-brown contents ..... *I. phaeocystidiosa*
- 5'. Pileus smooth or radially fibrillose; odor absent; spores 10–12 × 7–8.5; pleurocystidia 60–90 × 16–23 μm, mainly subfusiform with crystals at top and also at neck, without yellow-brown contents ..... *I. alpinomarginata*
6. Basidiomata typically fairly small; pileus 5–25 mm, gray brown to dark brown, purple brown, smooth, woolly or rough, often with distinct vellipellis; stipe often short, 5–25 mm; pleurocystidia walls 1–2 μm thick ..... 7
- 6'. Basidiomata larger; pileus 10–40 mm, dark brown, gray brown, streaky, smooth to roughened; vellipellis mostly absent; stipe usually longer, 20–45 mm; pleurocystidia walls 2–3 μm thick ..... 8
7. Pileus dark brown, purple brown with pale vellipellis or not, smooth or roughened; lamellae brown or

- rusty brown; stipe white over brownish red, fibrous; odor indistinct; spores angular or weakly nodulose,  $8.5\text{--}11.5 \times 5\text{--}6.5 \mu\text{m}$ .....*I. purpureobadia*
- 7'. Pileus dark brown, gray brown, woolly-rough to smoother with pale vellipellis; lamellae pale brown, gray brown, brown; stipe brown with white fibers; odor subspermatic; spores angular to weakly nodulose,  $7.5\text{--}10.5 \times 4\text{--}6.5 \mu\text{m}$  .....*I. murina*
8. Pileus convex, often with small umbo, brown, grayish brown, streaky; lamellae pale orange; stipe not usually with pinkish tint; context cream; odor absent; spores more nodulose,  $9\text{--}12 \times 6\text{--}7.5 \mu\text{m}$  .....*I. paragiacomii*
- 8'. Stipe usually with pinkish tints; lamellae grayish brown; odor weak or strong spermatic; spores less nodulose, more rectangular ..... 9
9. Pileus often tall with rounded umbo or campanulate, with incurved margin, often scurfy in center, brown, grayish brown, dark brown, streaky; lamellae grayish brown; stipe typically with pinkish apex; context usually pink; odor subspermatic; spores rectangular,  $9.5\text{--}10.5 \times 6.0\text{--}6.5 \mu\text{m}$ ; pleurocystidia narrowly lageniform . .....*I. giacomii*
- 9'. Pileus conic-convex or sunken in center, light brown, brown, with smooth center and rimulose margin; lamellae grayish brown, brown; stipe pale brown with pinkish tints; context with or without pink tints; odor spermatic; spores rectangular to elongate,  $9.5\text{--}12 \times 6\text{--}7 \mu\text{m}$ ; pleurocystidia subfusiform .....*I. subgiacomii*

## DISCUSSION

Considering all the historical data from Favre (1955), Horak (1987), Kühner (1988), and Bon (1997), only *Inocybe giacomii* is reported here, even though all Rocky Mountain species are molecularly confirmed to have an intercontinental distribution. However, four of our species are new (*I. alpinomarginata*, *I. murina*, *I. paragiacomii*, *I. subgiacomii*), and six occur in North America and Europe (*I. arctica*, *I. giacomii*, *I. leonina*, *I. occulta*, *I. phaeocystidiosa*, *I. purpureobadia*) and are also known from boreal or subalpine habitats.

Favre's original reports included *I. casimiri* Velen., *I. concinnula* J. Favre, *I. decipiens* Bres. (var. *megacystis* and var. *mundula* J. Favre.), *I. decipientoides* Peck sensu Kühner (var. *taxocystis* J. Favre), *I. egenula* J. Favre, *I. giacomii*, *I. napipes* J.E. Lange, *I. oreina* J. Favre, *I. praetervisa* Quél. sensu Kühner & Bours., (and f. *rufofusca* J. Favre), and *I. pseudohiulca* Kühner.

Thirty-two years after Favre first documented this group of *Inocybe* from the alpine, Horak (1987) placed Favre's alpine nodulose-spored *Inocybe* taxa in the previously described genus *Astrosporina* J. Schröt. because of spore shape. In addition, *A. alpigenes* E. Horak was described as new; *A. aurea* (Huijsman) E. Horak. and *A. humilis* J. Favre & E. Horak were added as alpine taxa; *A. mundula* J. Favre & E. Horak and *A. taxocystis* J. Favre & Horak were raised to species rank; *I. napipes* J.E. Lange sensu J. Favre was determined to be *A. asterospora* (Quél.) Rea; and *I. decipientoides* sensu Kühner became *A. lanuginella* Schröt. Most taxa have since been placed back in genus *Inocybe* because the designation *Astrosporina* has not been well accepted and is unsupported by molecular phylogenetic analyses (e.g., Matheny et al. 2009; Ryberg et al. 2010).

At nearly the same time as Horak's work, in his treatise on *Inocybe* from the French Alps, Kühner (1988) described eight new species, six of which have since been synonymized with previously named taxa. Original taxa described by Kühner from the French Alps included *I. hinnulea*, *I. johannaea*, *I. obtusiuscula*, *I. polytrichi-norvegici*, *I. salicis-herbaceae*, *I. striaepes*, *I. substellata*, and *I. tetragonospora*. Bon (1997) included most Kühner, Favre, and Horak species in his inclusive key to alpine species of *Inocybe* subg. *Clypeus* Britzelm. His additions included *I. albofibrillosa* Stangl. & Schmid.-Heckel., *I. umbrinodisca* Kühner, and *I. rennyi* sensu M. Lange. Over time, synonymy has reduced the number of names: *Inocybe hinnulea*, *I. johannaea*, and *I. striaepes* have been synonymized with *I. giacomii* (Kokkonen and Vauras 2012); *I. tetragonospora* is now *I. alpigenes* (Kokkonen and Vauras 2012; Larsson et al. 2018); *I. taxocystis* is confirmed as *I. favrei* (Larsson et al. 2018); and *I. salicis-herbaceae* has been synonymized with *I. phaeocystidiosa* (Esteve-Raventós et al. 2016).

New research that includes molecular data has revealed new or cryptic species from arctic and alpine areas. *Inocybe praetervisa* Quél. has been commonly reported from such areas, but a new epitype has been established and sequenced, and the species appears to be associated primarily with conifers in southern Europe (Esteve-Raventós et al. 2016; Larsson et al. 2018). At least one of the "praetervisa-like" taxa reported from arctic and alpine habitats appears to be *I. phaeocystidiosa*, which we report from the Rocky Mountain alpine zone. This species has abundant caulocystidia down to the stipe base as described for most alpine collections. In *I. praetervisa*, the caulocystidia are sparse or absent on the lower stipe, and the species has larger basidiomata. In this same study, *I. salicis-herbaceae*, a name used for arctic-alpine specimens, was synonymized with *I. phaeocystidiosa* (which was

described a year earlier) based on ITS data (Esteve-Raventós et al. 2016).

A closer look at the *I. praetervisa* group revealed a complex of at least four species, including *I. rivularis* Jacobsson & Vauras, *I. favrei* (= *I. taxocystis*), and *I. arctica*, all of which have been reported from alpine or arctic habitats, although the last two appear restricted to them (Larsson et al. 2018). Also, *I. lemmi* E. Larss., Vauras & C.L. Cripps, described from an alpine area of Sweden, occurs in the *I. praetervisa* clade closely related to *I. favrei* (Larsson et al. 2018). From this group, we report only *I. arctica* and *I. leonina* from the Rocky Mountain alpine zone.

*Inocybe mixtilis* has been reported occasionally from arctic-alpine habitats, although it is primarily a species of forested areas. It is morphologically somewhat similar to *I. phaeocystidiosa* due to the smooth, yellowish pileus, white stipe with a marginate base, and distinctly nodulose spores. An epitype has been proposed for *I. mixtilis* (Marchetti et al. 2014), and molecular results show it to be distantly related to the *I. praetervisa* clade (Ryberg et al. 2010; Esteve-Raventós et al. 2016). In the recent study by Esteve-Raventós et al. (2018), *I. mixtilis* was revealed to constitute of a complex of six species based on molecular data. The species occurring in the arctic-alpine zone was described as *I. occulta*, which we report from the Rockies.

A few of the new nodulose-spored *Inocybe* species described from boreal habitats in Europe also have been reported with dwarf willow in alpine areas; these include *I. acuta* Boud. (= *I. acutella* Bon), *I. borealis* M. Lange (= *I. heterochrominea* Grund & D.E. Stuntz), and *I. purpureobadia* (Esteve-Raventós and Gaballero Moreno 2009; Kokkonen and Vauras 2012). Of these, we confirm *I. purpureobadia* from the Rocky Mountain alpine zone. *Inocybe leonina* is reported from low elevations in Spain, but here we report the second collection of this species from the Colorado alpine.

It is difficult to estimate the number of nodulose-spored *Inocybe* taxa that occur in arctic and alpine habitats, but the number is certainly greater than the small subset reported here from the Rocky Mountains despite our extensive collecting efforts. Moreover, data from Canada and Alaska are still scant. Of the 10 *Inocybe* species reported here from the Rocky Mountain alpine zone, all have intercontinental distributions and most occur in alpine or arctic areas of northern continental Europe and Svalbard (Kokkonen and Vauras 2012; Esteve-Raventós et al. 2018; Larsson et al. 2018). *Inocybe leonina* has been found in the Colorado alpine, and its sister species, *I. lemmi*, was described from an alpine zone in Sweden (Larsson et al.

2018); another close relative, *I. candidipes*, was reported from montane Arizona (Kropp and Matheny 2004). Interestingly, most that have long distance disjunct distributions are from the southern Rocky Mountains at latitudes reaching south to 36°N and at elevations as high as 4000 m, in contrast to the lower latitudes and elevations of the arctic and the alpine habitats of northern Europe. Seven species (*I. arctica*, *I. giacomii*, *I. leonina*, *I. murina*, *I. occulta*, *I. phaeocystidiosa*, and *I. purpureobadia*) also occur in subalpine, montane, or boreal habitats in Europe and thus have potential to occur below tree line in North America.

Three of the four newly described species (*I. alpinomarginata*, *I. paragiacomii*, *I. subgiacomii*) are thus far only reported from alpine habitats, but data are scarce. There is some but not total overlap in host species between North America and Europe, with *Salix reticulata* and *Dryas octopetala* listed here as common hosts. *Salix herbacea* and *S. polaris* do not occur in the areas of the Rocky Mountains studied, and *Betula nana* is rare. Conversely, *S. planifolia* and *S. glauca* occur in the low alpine of the Rockies and also Fennoscandia but are not mentioned for the alpine of Europe. Hosts for subalpine habitats include *Betula* and *Pinus*. Therefore, most of these *Inocybe* species appear to occur with more than one host, and some are widespread.

Other genera and other *Inocybe* species from the Rocky Mountain alpine zone also have been confirmed to have intercontinental distributions in disjunct cold habitats according to DNA analysis, i.e., *Lactarius* (Barge and Cripps 2016; Barge et al. 2016), *Hebeloma* (Beker et al. 2016; Cripps et al. 2019), *Cortinarius* (Peintner 2008), and *Inocybe* (Cripps et al. 2010; Larsson et al. 2014, 2018). At least morphology and ITS sequences show consistent match across continents within these cold-dominated habitats, which is attributed primarily to the distribution of willows, birches, and other hosts (*Dryas*) that can survive in arctic-alpine habitats and glaciation.

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## LITERATURE CITED

- Barge EG, Cripps CL. 2016. New reports, phylogenetic analysis, and a key to *Lactarius* Pers. in the Greater Yellowstone Ecosystem informed by molecular data. *MycKeys* 15:1–58.
- Barge EG, Cripps CL, Osmundson TW. 2016. Systematics of the ectomycorrhizal genus *Lactarius* in the Rocky Mountain alpine zone. *Mycologia* 108:414–440.
- Beker HJ, Eberhardt U, Vesterholt J. 2016. *Hebeloma* (Fr.) P. Kumm. *Fungi Europaei* 14. Lomazzo, Italy: Edizioni Tecnografica. 1217 p.
- Bon M. 1997. Clé monographique des *Inocybes* alpins. Bulletin trimestriel de la Fédération Mycologique Dauphiné-Savoie 144:71–109.
- Brunner I, Frey F, Hartmann M, Zimmerman S, Graf F, Suz L, Niskanen T, Bidartondo M, Senn-Irlet B. 2017. Ecology of alpine macrofungi—combining historical with recent data. *Frontiers in Microbiology* 8:2066.
- Clark K, Karsch-Mizrachi I, Lipman DJ, Ostell J, Sayers E. 2016. GenBank. *Nucleic Acids Research* 44(Database issue): D67–D72, doi:10.1093/nar/gkv1276
- Cripps CL, Eberhardt U, Schütz N, Beker HJ, Evenson VS, Horak E. 2019. The genus *Hebeloma* in the Rocky Mountain alpine zone. *MycKeys* 46:1–54.
- Cripps CL, Eddington LE. 2005. Distribution of mycorrhizal types among alpine vascular plant families on the Beartooth Plateau, Rocky Mountains, USA, in reference to large-scale patterns in arctic-alpine habitats. *Arctic, Antarctic and Alpine Research* 37:77–188.
- Cripps CL, Horak E. 2008. Checklist and Ecology of the Agaricales, Russulales and Boletales in the alpine zone of the Rocky Mountains (Colorado, Montana, Wyoming) at 3000–4000 m a.s.l. *Sommerfeltia* 31: 101–123 (*Arctic and Alpine Mycology* 7).
- Cripps CL, Larsson E, Horak E. 2010. Subgenus *Mallocybe* (*Inocybe*) in the Rocky Mountain alpine zone with molecular reference to European arctic–alpine material. *North American Fungi* 5: 97–126 (*Arctic and Alpine Mycology* 8).
- Drummond AJ, Suchard MA, Xie D, Rambaut A. 2012. Bayesian Phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution* 29:1969–1973.
- Esteve-Raventós F, Bandini D, Oertel B, González V, Moreno G. 2018. Advances in the knowledge of the *Inocybe mixtilis* group (*Inocybaceae*, *Agaricomycetes*), through molecular and morphological studies. *Persoonia* 41:213–226.
- Esteve-Raventós F, Cabellero Moreno A. 2009. Especies nuevas e interesantes del género *Inocybe* (*Inocybaceae*, *Basidiomycetes*) en la Comunidad de La Rioja (España Peninsular). *Fungi non Delineati* 47:1–128.
- Esteve-Raventós F, Moreno G, Alvarado P, Olariaga I. 2016. Unraveling the *Inocybe praetervisoides* group through type studies and ITS data: *Inocybe praetervisoides* sp. nov. from the Mediterranean region. *Mycologia* 108: 123–134.
- Esteve-Raventós F, Moreno G, Bizio E, Alvarado P. 2015. *Inocybe flavobrunnescens*, a new species in section *Marginatae*. *Mycological Progress* 14:14.
- Favre J. 1955. Les champignons supérieurs de la zone alpine du Parc National Suisse. *Ergebnisse der Wissenschaftlichen Untersuchungen des Schweizerischen National Parks* 5:1–212.
- Graf F. 1994. Ecology and sociology of macromycetes in snow-beds with *Salix herbacea* L. in the alpine Valley of Radönt (Grisons, Switzerland). Berlin, Germany: J. Cramer. 242 p.
- Horak E. 1987. *Astrosporina* in the alpine zone of the Swiss National Park (SNP) and adjacent regions. In: Laursen G, Ammirati J, Redhead R, eds. *Arctic and alpine mycology II. Proceedings of the Second International Symposium of Arctic and Alpine Mycology*; Aug 26–Sep 2; Fetan, Switzerland. New York: Plenum Press. p. 205–234.
- Jacobsson S, Larsson E. 2012. *Inocybe* (Fr.) Fr. In: Knudsen H, Vesterholt J, eds. *Funga Nordica. Agaricoid, boletoid, cyphelloid and gasteroid genera*. Copenhagen, Denmark: Nordsvamp. p. 981–1021.
- Katoh K, Standley DM. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30:772–780.
- Kokkonen K, Vauras J. 2012. Eleven new boreal species of *Inocybe* with nodulose spores. *Mycological Progress* 11:299–341.
- Köljalg U, Nilsson RH, Abarenkov K, Tedersoo L, Taylor AFS, Bahram M, Bates SB, Bruns TD, Bengtsson-Palme J, Callaghan TM, Douglas B, Drenkhan T, Eberhardt U, Dueñas M, Griffith TGW, Hartmann M, Kirk PM, Kohout P, Larsson E, Lindahl BD, Lücking R, Martín RMP, Matheny PB, Nguyen NH, Niskanen T, Oja J, Peay KG, Peintner U, Peterson M, Pöldmaa K, Saag L, Saar I, Schüssler A, Scott JA, Senés C, Smith ME, Suija A, Taylor DL, Telleria T, Weiss M, Larsson K-H. 2013. Towards a unified paradigm for sequence-based identification of fungi. *Molecular Ecology* 22:5271–5277.
- Kropp BR, Matheny PB. 2004. Basidiospore homoplasy and variation in the *Inocybe chelanensis* group in North America. *Mycologia* 96:295–309.
- Kühner R. 1988. Diagnoses de quelques nouveaux *Inocybes* récoltés en zone alpine de la Vanoise (Alpes françaises). *Documents Mycologique* 19:1–27.
- Kuyper T. 1986. A revision of the genus *Inocybe* in Europe. I. Subgenus *Inosperma* and the smooth-spored species of subgenus *Inocybe*. *Persoonia Supplement* 3:1–247.
- Largent DL, Baroni TJ. 1988. How to identify mushrooms to genus VI: modern genera. *Eureka, California: Mad River Press*. 277 p.
- Larsson A. 2014. AliView: a fast and lightweight alignment viewer and editor for large data sets. *Bioinformatics* 22:3276–3278.
- Larsson E, Vauras J, Cripps CL. 2014. *Inocybe leiocephala*, a species with an intercontinental distribution range—disentangling the *I. leiocephala*–*subbrunnea*–*catalaunica* morphological species complex. *Karstenia* 54:15–39.
- Larsson E, Vauras J, Cripps CL. 2017 [2018]. *Inocybe lemni*, a new species of section *Marginatae* from the alpine region of Sweden. *Karstenia* 57:1–9.

- Larsson E, Vauras J, Cripps CL. 2018. *Inocybe praetervisa* group—a clade of four closely related species with partly different geographical distribution ranges in Europe. *Mycoscience* 59:277–287.
- Marchetti M, Franchi P, Consiglio G. 2014. Tipificazione di alcune *Inocybe* di Britzelmayr. *Rivista di Micologia* 2:27–178.
- Matheny PB. 2009. A phylogenetic classification of the Inocybaceae. *McIlvainea* 18:11–21.
- Matheny PB, Aime MC, Bougher NL, Buyck B, Desjardin DE, Horak E, Kropp BR, Lodge DJ, Soyong K, Trappe JM, Hibbett DS. 2009. Out of the palaeotropics? Historical biogeography and diversification of the cosmopolitan ectomycorrhizal mushroom family Inocybaceae. *Journal of Biogeography* 36:577–592.
- Matheny PB, Kudzma LV. 2019. New species of *Inocybe* (Inocybaceae) from eastern North America. *Journal of the Torrey Botanical Society* 146:213–235.
- Matheny PB, Moreau PA. 2009. A rare and unusual lignicolous species of *Inocybe* (Agaricales) from eastern North America. *Brittonia* 61:163–171.
- Nylander JAA. 2004. MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden.
- Osmundson TW, Cripps CL, Mueller GM. 2005. Morphological and molecular systematics of Rocky Mountain alpine *Laccaria*. *Mycologia* 97:949–972.
- Pegler DN, Young TWK. 1972. Basidiospore form in the British species of *Inocybe*. *Kew Bulletin* 26: 499–537, 24 plates.
- Peintner U. 2008. *Cortinarius alpinus* as an example for morphological and phylogenetic species concepts in ectomycorrhizal fungi. *Sommerfeltia* 31:161–177.
- Ronquist F, Teslenko M, Van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Heulsenbeck JP. 2012. MrBayes 3.2, efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61:539–542.
- Ryberg M, Larsson E, Jacobsson S. 2010. An evolutionary perspective on morphology and ecological characters in the mushroom family Inocybaceae (Agaricomycotina, Fungi). *Molecular Phylogenetics and Evolution* 55:431–442.
- Stangl J. 1986. Die Gattung *Inocybe* in Bayern. *Hoppea, Denkschriften der Regensburgische Botanische Gesellschaft* 46:5–388.
- Swofford DL. 2003. PAUP\*: Phylogenetic Analysis Using Parsimony (\*and other methods). Version 4. Sunderland, Massachusetts: Sinauer Associates.
- Thiers B. (continuously updated). Index Herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. [cited 2019 Jan 15]. Available from: <http://sweetgum.nybg.org/ih/>
- Timling I, Dahlberg A, Walker DA, Gardes M, Charcosset JY, Welker JM, Taylor DL. 2012. Distribution and drivers of ectomycorrhizal fungal communities across the North American Arctic. *Ecosphere* 3:111.
- Vauras J, Larsson E. 2015 (2016). *Inocybe caprimulgi* and *I. lacunarum*, two new nodulose-spored species from Fennoscandia. *Karstenia* 55:1–18.