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Subgenus *Mallocybe* (*Inocybe*) in the Rocky Mountain alpine zone with molecular reference to European arctic-alpine material

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Abstract: The genus *Inocybe* (including subgenus *Mallocybe*) is a significant component of the ectomycorrhizal community in arctic and alpine habitats in terms of both diversity and distribution. Species are associated primarily with low woody shrubs of *Salix*, *Betula* and *Dryas*. There is evidence that shrubs are expanding in arctic-alpine habitats making the ectomycorrhizal fungi that support them of high interest. Here we provide the first detailed report for six *Mallocybe* taxa with willows from the Rocky Mountain alpine zone (WY, MT, CO) including: *Inocybe arthrocytis*, *I. dulcamara*, *I. leucoloma*, *I. leucoblema* and in the *I. fulvipes* group, *I. substraminipes* and other taxa. Phylogenetic analysis matched Rocky Mountain specimens to arctic-alpine specimens from Scandinavia. ITS sequences of Kühner and Favre type specimens were used as references for several clades. Data suggest that these species have a broad intercontinental range in arctic-alpine habitats and a few are known from the subalpine. A key to *Mallocybe* species in the Rocky Mountains is provided along with type information.

Key words: Key Words: Arctic-alpine, fungi, *Inocybaceae*, Kühner types, Rocky Mountains, Sweden

Introduction: The genus *Inocybe* is a significant component of the ectomycorrhizal community in arctic and alpine habitats in terms of both diversity and distribution (Cripps & Horak 2009). Of the approximately 200+ ectomycorrhizal fungi reported in northern cold-dominated regions, over half are concentrated in just two genera, *Cortinarius* and *Inocybe* (Cripps & Horak 2009). In arctic-alpine habitats, they are primarily associated with the low woody shrubs *Salix*, *Betula*, *Dryas* and the herbal plant *Bistorta* (Polygonaceae), although there are scattered reports with other hosts. Recent studies suggest that there is evidence that woody shrubs are expanding in both arctic and alpine areas due to changes in climate (Sturm et al. 2001, Walker et al. 2006, Ryberg et al. 2009). Chapin and Korner (1995) suggest that as few as 20 genera of vascular plants account for most of the biomass in the circumpolar arctic, and that in most alpine areas less than ten species make up 90% of the biomass; in both cases a significant portion are woody shrubs. Therefore, the ectomycorrhizal fungi that support the physiological processes

and survival of arctic and alpine shrubs should be of high interest.

Over 60 species of *Inocybe* (including subgenus *Mallocybe* Kuyper) have been reported in Arctic and alpine habitats (reviewed in Graff 1994 and Cripps & Horak 2009). Of these, approximately 20 taxa in subgenus *Mallocybe* have been reported in arctic and alpine habitats worldwide, with around 13 reported consistently and from more than one area (Table 1).

The genus *Inocybe* was previously considered part of the Cortinariaceae, but is now regarded as an independent family *Inocybaceae* as interpreted from molecular phylogenetic analysis (Matheny 2005, Matheny et al. 2006, Ryberg et al. 2010). *Mallocybe* is traditionally considered a subgenus of *Inocybe* (Kuyper 1986, Stangl 1989, Jacobsson 2008), although recent work suggests raising it to genus rank (Matheny 2009, Matheny et al. 2009). Here we maintain it as a subgenus within *Inocybe* for practical reasons and reserve taxonomic changes for a subsequent paper.

Table 1. Species in subgenus *Mallocybe* (*Inocybe*) reported from arctic and alpine habitats with decreasing latitude from North (Svalbard) to South (Rocky Mountains).

Species	Svalbard	Greenland	Scandinavia	Pyrenees	Alps	Rocky Mts
<i>I. arthrocystis</i> Kühner	X		X	X	X	X
<i>I. dulcamara</i> (Alb & Schw) Kumm. v. <i>parcelosquamosa</i> J. Favre		X	X	X	X	X
v. <i>peronata</i> J. Favre	X	X		X	X	X?
v. <i>pygmaea</i> J. Favre			X		X	
<i>I. fulvipes</i> group* Kühner	X		X	X	X	X
<i>I. fuscomarginata</i> Kühner	X		X		X	
<i>I. leucoblema</i> Kühner	X	X	X	X	X	X
<i>I. leucoloma</i> Kühner	X		X	X	X	X
<i>I. solidipes</i> Kühner	X			X	X	
<i>I. squarrosoannulata</i> Kühner			X		X	X
<i>I. umbrinofusca</i> Kühner					X	

**I. fulvipes* group includes: *I. fulvipes*, *I. substraminipes* and *I. paludosa*.

Not included are Kühner species: *I. hebelomoides*, *I. leucolepis*, *I. pelargoniodora*, *I. sericiepes*, *I. subannulata*.

Most species of *Inocybe* are characterized by smooth or nodulose brown spores that lack a germ pore; most have distinctive thick-walled pleurocystidia (metuloids) often with crystals at the apex. Subgenus *Mallocybe* is differentiated by a lack of metuloids (along with subgenus *Inosperma sensu* Stangl 1989). *Mallocybe* species in general are recognized macroscopically by a fibrous or scaly often flattened pileus, a short stipe (for many), ocher, brown, or red brown coloration, a cortina (with a few exceptions), adnate lamellae (most) and the absence of a spermatic odor (odor typically of burnt sugar, honey or absent). Microscopically spores are smooth, pleurocystidia absent, cheilocystidia thin-walled without crystals, and necropigment can be observed in basidia of fresh and dried specimens (Kuyper 1986, Stangl 1989, Jacobsson 2008).

Historically, Favre (1955) in his excellent work on alpine fungi reported eight taxa of *Mallocybe* from the Swiss National Park, five as forms of *I. dulcamara*. Several of his forms have since been raised to the rank of species. Over thirty years later, Kühner reported 15 taxa of *Mallocybe* from the French Alps, 11 of which were new (Kühner 1988). Some of his new species are poorly understood. Since this time, arctic and alpine *Mallocybes* have been reported at least from: Svalbard (Huhtinen 1987, Gulden & Torkelsen 1996, E. Larsson, pers. observation), Greenland (Borgen et al. 2006), Scotland (Watling 1987), Pyrenees and Spain (Corriel 2008), Scandinavia (Vauras and Huhtinen 1986, Gulden 2005), Alps (Kühner 1988, Kühner and Lamoure 1986, Bon 1989, 1990, 1991, 1992, 1997, Graf 1994, Jamoni & Bon 1995, Bizio 1995, 1997, Moreau 2002, Jamoni 2008), Canada (Ohenoja et al. 1998), Alaska (Miller 1987) and the Rocky Mountains, USA (Cripps & Horak 2008). These references were used to develop Table 1; not included are reports from Iceland, Scotland and Russia.

Here we report at least six taxa of *Mallocybe* from the Rocky Mountain alpine region in the lower USA in association with *Salix* and *Dryas* species. This includes: *Inocybe arthrocytis* Kühner, *I. dulcamara v. typique* (Alb. & Schwein.) P. Kumm., *I. leucoloma* Kühner, *I. leucoblema* Kühner and in the *I. fulvipes* Kühner group, *I. aff. substraminipes* Kühner and other taxa. These are compared molecularly to taxa from arctic and alpine habitats in Europe. Type material was included when possible for molecular analysis and a key to North American alpine taxa is provided (Addendum 1).

Materials and Methods

NORTH AMERICAN COLLECTIONS: North American specimens were collected between 1999 and 2008 in alpine areas above treeline on the Beartooth Plateau (Wyoming/Colorado border) and at various locations in Colorado (Cottonwood Pass, Cumberland Pass, Independence Pass, Loveland Pass and the San Juan Mountains). All were collected within the alpine vegetation zone in association with shrub willows *Salix glauca* L. and *S. planifolia* Pursh., dwarf willows *S. reticulata* L. and *S. arctica* Pall., and/or species of *Dryas*. The Beartooth Plateau is in the middle Rocky Mountain floristic zone at lat. 45°N and long. 109°W with minimum alpine zone elevations of 3,000 m a.s.l. For Colorado at latitudes of 37°-39°N, collections were made above treeline at 3,700 m a.s.l. or higher in the southern Rocky Mountains.

Each collection was photographed, described, drawn, and identified on subsequent completion of microscopic examination. Spores and other microscopic features were examined in 3% KOH after rehydration. Colors are from Kornerup and Wanscher (1967). Voucher specimens are in herbaria at Montana State University, Bozeman, MT (MONT) and the Institute of Integrative Biology, ETH, Zurich, Switzerland (ZT). Dried tissue samples in small vials were subjected to

molecular analysis. North American collections are described in detail and compared molecularly to European material.

Kühner's type collections from G (Geneva) were the basis for the microscopic details drawn by Egon Horak (E.H.) and translations of Kühner's protologues were also done by E.H. This author comments that the large range of Kühner's spore measurements were derived from both 1-, 2-, and/or 4-spored basidia; E.H. measurements of Kühner's types are derived from 4-spored basidia. Kühner's Latin protologues were composed several years after his death by other authors and E.H. took the liberty in translations to delete repetitions, meaningless references, and to take into account missing data.

Apparently gaps exist in macrodescriptions that may have been present in Kühner's original notes. Also, all measurements were converted from cm to mm in the text.

TAXON SAMPLING: Sixty-nine specimens of *Inocybe* subgenus *Mallocybe* from arctic/alpine and sub-alpine environments originating from USA and Europe were sequenced (Tab. 2). Seven type specimens of arctic/alpine species (*I. leucoloma* Kühner, *I. substraminipes* Kühner, *I. fuscocomarginata* Kühner, *I. solidipes* Kühner, *I. umbrinofusca* Kühner, *I. squarrosannulata* Kühner and *I. dulcamara* f. *pymaea* J. Favre) were available at Herbarium G and permission for sequencing granted. Based on results from earlier molecular phylogenetic studies of Agaricales (Matheny et al 2006) *Crepidotus* (AM882996, FJ904178) was selected as the out-group. In addition LSU sequences from the *Mallocybe*, *Mallocybella* and *Auritella* clades (Matheny et al 2009) were downloaded from GenBank and include AY380403, EU568855, EU600887, AY380371 and AY380403.

DNA EXTRACTION, PCR AND SEQUENCING: Sequences of the complete ITS region, 1200 base pairs of the 5' end of the nuclear LSU ribosomal

DNA were generated. DNA extractions, PCR reactions and sequencing for recently collected specimens were performed as described in Larsson and Örstadius (2008). Type specimens were extracted using a modified CTAB method and PCR and sequencing follow protocols described in Larsson and Jacobsson (2004).

PHYLOGENETIC ANALYSES: Sequences were edited and assembled using Sequencher 3.1 (Gene Codes, Ann Arbor). Sequences were aligned automatically using the software MAFFT (Katoh et al. 2005) and adjusted manually using the data editor in PAUP* (Swofford 2003). Sequences have been deposited in GenBank and accession numbers are listed in Table 2.

Heuristic searches for most parsimonious trees were performed using PAUP*. 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 TBR branch swapping were performed, saving 100 trees in each replicate. Relative robustness of clades was assessed by the bootstrap method using 1000 heuristic search replicates with 100 random taxon addition sequence replicate, TBR swapping, saving 100 trees in each replicate.

Results: For five of the seven type specimens, we succeeded in generating useful sequences. The complete ITS region was recovered for *I. leucoloma*, *I. squarrosoannulata* and *I. dulcamara* f. *pymaea*. For *I. substraminipes*, the ITS2 region was recovered and for *I. umbrinofusca* the ITS1 region. The aligned dataset comprised 78 taxa and had 2294 characters. After exclusion of ambiguous regions 1950 characters remained for the analysis. Of these 1384 were constant, 142 were variable and parsimony uninformative, and 424 were

Table 2. Data of specimens sequenced in this study. Specimens with CLC numbers are deposited in Herbarium MONT. EL, SM, SJ and BJ numbers in Herbarium GB (Sweden). Type specimens are from Herbarium G (Geneva).

Species	Coll No.	Original location	Putative host	Genbank	
<i>I. arthrocytis</i>	CLC 1141	Independence Pass CO, USA	Shrub <i>Salix</i>	GU980653	
	CLC 1356	Independence Pass CO, USA	Dwarf <i>Salix</i>	GU980649	
	CLC 1357	Independence Pass CO, USA	Dwarf & shrub <i>Salix</i>	GU980652	
	CLC 1688	San Juans, Stony Pass CO, USA	<i>S. glauca</i> & <i>S. arctica</i>	GU980651	
	CLC 1752	Independence Pass CO, USA	<i>S. planifolia</i>	GU980650	
	EL62-07	Sweden	<i>S. herbacea</i>	FN550941	
	SJ06-011	Sweden	<i>Salix</i> sp.	GU980654	
	BJ900815	Sweden	<i>Salix</i> sp.	GU980655	
<i>I. dulcamara</i>	CLC 1131	Beartooth Pass, MT, USA	Dwarf & shrub <i>Salix</i>	GU980639	
	CLC 1160	Beartooth Pass, MT, USA	Dwarf & shrub <i>Salix</i>	GU980642	
	CLC 1241	Independence Pass CO, USA	<i>S. glauca</i>	GU980637	
	CLC 1295	Loveland Pass CO, USA	<i>S. glauca</i>	GU980636	
	CLC 1333	Independence Pass CO, USA	Dwarf <i>Salix</i>	GU980635	
	CLC 1364	Independence Pass CO, USA	<i>S. glauca</i> , <i>S. reticulata</i>	GU980641	
	CLC 1408	San Juans, Cinnamon Pass CO, USA	Dwarf <i>Salix</i>	GU980647	
	CLC 1421	San Juans, Engineer Pass CO, USA	<i>S. planifolia</i>	GU980646	
	CLC 1458	Independence Pass, CO, USA	Shrub	GU980638	
	CLC 1581	Beartooth Pass, WY, USA	<i>Salix</i> near	GU980634	
	CLC 1664	San Juans, Horseshoe Pass, USA	<i>Dryas?</i> <i>S.</i>	GU980640	
	CLC 1841	San Juans, Imogene Pass, USA	<i>S. arctica</i> <i>S. planifolia</i>	GU980644	
	EL59-05	Norway	<i>Betula</i> sp.	GU980643	
	EL33-05	Norway	<i>S. glauca</i>	GU980645	
	EL89-06	Sweden	<i>S. glauca</i> , <i>Betula</i>	FJ904122	
	<i>I. dulc. v pygmaea</i>	EL48-05	Norway	<i>Dryas</i> , <i>S. reticulata</i>	GU980628
GK13103		Type Favre	Dwarf <i>Salix</i>	GU980629	
<i>I. fulvipes group A</i>	CLC 1375	Independence Pass CO, USA	Shrub <i>Salix</i>	GU980605	
	CLC 2292	Loveland Pass CO, USA	<i>Salix</i> spp.	GU980604	
	EL30-07	Sweden	<i>Dryas</i> , <i>S. reticulata</i>	GU980599	
	EL37-05	Norway	<i>Dryas</i> , <i>Salix</i> p.	AM882858	
	EL83-07	Sweden	<i>S. herbacea</i> , <i>S. polaris</i>	FN550935	
	EL99-07	Sweden	<i>S. polaris</i>	GU980600	
	CLC 1649	Cumberland Pass CO, USA	<i>Dryas</i> sp.	GU980602	
	CLC 1731	Independence Pass CO, USA	<i>Dryas</i> & <i>Salix</i>	GU980603	
	(<i>I. substraminipes</i>)	K 70-148	Type Kühner (group A)	<i>Dryas</i>	GU980601
	<i>I. fulvipes group B</i>	CLC 1490	Loveland Pass CO, USA	<i>Salix</i> spp.	GU980612
CLC 1566		Beartooth Pass, WY, USA	<i>S. reticulata</i>	GU980606	
CLC 1580		Beartooth Pass, WY, USA	<i>S. reticulata</i>	GU980608	
CLC 1844		Mineral Basin CO, USA	<i>S. arctica</i> <i>S. planifolia</i>	GU980611	
EL12-08		Beartooth Pass, WY USA	<i>S. reticulata</i>	GU980607	
SJ84030		Sweden	<i>Salix</i> sp.	GU980609	
BJ890718		Sweden	<i>Salix</i> sp.	GU980656	
EL109-06		Sweden	<i>S. herbacea</i>	FN550940	
<i>I. fuscomarginata</i>	EL77-07	Sweden	<i>Dryas</i> sp.	GU980657	
	CLC 1721	Cottonwood Pass CO, USA	<i>Dryas</i> sp.	GU980632	
<i>I. leucoblema</i>	EL66-07	Sweden	<i>Dryas</i> , <i>S. reticulata</i>	FN550936	
	SEB97-09	Sweden	<i>Pinus</i> sp.	GU980631	
	SM2324	Sweden	<i>Picea</i> sp.	GU980630	
	TAA 128324	Estonia	<i>Salix</i> sp.	GU980633	
	<i>I. leucoloma</i>	CLC 1223	Loveland Pass CO, USA	Dwarf & shrub <i>Salix</i>	GU980624
CLC 1355		Independence Pass CO, USA	Shrub <i>Salix</i>	GU980623	
CLC 1431		San Juans, Emma Lake CO, USA	<i>S. planifolia</i>	GU980619	
CLC 1442		San Juans, Black Bear CO, USA	<i>S. planifolia</i>	GU980620	
CLC 1703		San Juans, Cinnamon Pass CO, US	<i>S. reticulata</i>	GU980617	
CLC 1869		San Juans, Emma Lake CO, USA	<i>S. planifolia</i>	GU980618	
CLC 1877		San Juans, Mineral Basin CO, USA	<i>S. arctica?</i>	GU980621	

Table 2 (continued).

Species	Coll No.	Original location	Putative host	Genbank
<i>I. leucoloma</i>	EL40-07	Sweden	<i>S. reticulata</i>	GU980622
	EL41-07	Sweden	<i>S. reticulata</i>	GU980615
	EL50-05	Norway	<i>Dryas, S. reticulata</i>	AM882855
	EL69-05	Norway	<i>Dryas, S. reticulata</i>	GU980616
	EL 1-06	Norway	<i>Salix</i>	GU980626
	EL106-07	Sweden	<i>S. hastata</i>	GU980627
	EL 107 07	Sweden	<i>S. hastata</i>	GU980625
	K 63 36	TYPE Kühner	<i>Dryas, S. retusis</i>	GU980614
<i>I. squarrosoannulata</i>	K 63-236	TYPE Kühner	<i>S. foetida</i>	HM209795
<i>I. terrigena</i>	EL22-99	Estonia	<i>Picea, calcareous</i>	AY586680
	EL117-04	Sweden	<i>Picea, calcareous</i>	AM882864
	EL24-08	Beartooth Plateau, WY, USA	<i>S. reticulata</i>	GU980648
<i>I. umbrinofusca</i>	K 70-38	Type Kühner	<i>S. reticulata</i>	GU980613

parsimony informative. The maximum parsimony analysis yielded 95300 equally most parsimonious trees (length=983, CI= 0.7447, RI= 0.9031) one of which is presented in Fig 1. Bootstrap values above 50% are indicated above branches.

Bootstrap analysis recovered eight clades with support corresponding to species or species groups: *I. arthrocytis* (97%), *I. fuscomarginata* (100%), *I. terrigena*-group (100%), *I. dulcamara*-group (99%), *I. dulcamara* f. *pygmaea* (99%), *I. leucoloma* (97%), *I. leucoblema* (99%) and *I. fulvipes/substraminipes*-group (85%). *Inocybe umbrinofusca* and *I. squarrosoannulata* occur on single branches and represent unique sequence types (Fig 1). Six of the clades include North American as well as European specimens.

Taxonomy

Taxa with smooth to rough stipes, no yellow in stipe base

***Inocybe arthrocytis* Kühner** (Figs. 2, 3)
 Docums. Mycol. 19(no. 74): 17 (1988)

Pileus 10-25(30) mm in diameter (small), mostly conic-convex, almost bell-shaped, a few convex,

with or without boss, not flat in center, ocher, dark ocher, uniformly minutely pubescent over whole cap, appearing velvety; margin turned under a bit when young, entire, not splitting, usually clean of remnants. *Lamellae* narrow adnate or emarginate, strikingly white or cream at first, milk coffee, then yellow brown, can be lighter at edges. *Cortina* not noted for most specimens, or possibly as a few fibrils. *Stipe* 10-25(-40) mm long, 2-4(-6) mm wide, slim, equal, straight or bit curved, dingy white at first, then pale ocher, whiter at base, surface roughened with a few longitudinal fibrils, hollow or stuffed, rubbery. *Context* dingy white to pale watery brown. *Odor* absent.

Spores brown, (8)9.5-12(-14) x 4.5-5.5(-6.5) μ m, on average 11 x 5 μ m, long and narrow, quotient of length to width around 2, regular, tending towards narrowly cylindrical, subphaesoliform, some with broad conic apex, length variable. *Basidia* 35-40(-50) x 8-11(-13) μ m, clavate, 4-sterigmate, a few 2-sterigmate. *Pleurocystidia* absent. *Cheilocystidia* articulated, in chains, mostly clavate, a few broader, 10-30 x 8-18 μ m, abundant, with pale or brown contents; walls thin, some slightly encrusted. *Clamp connections* present and obvious on articulated cystidia.

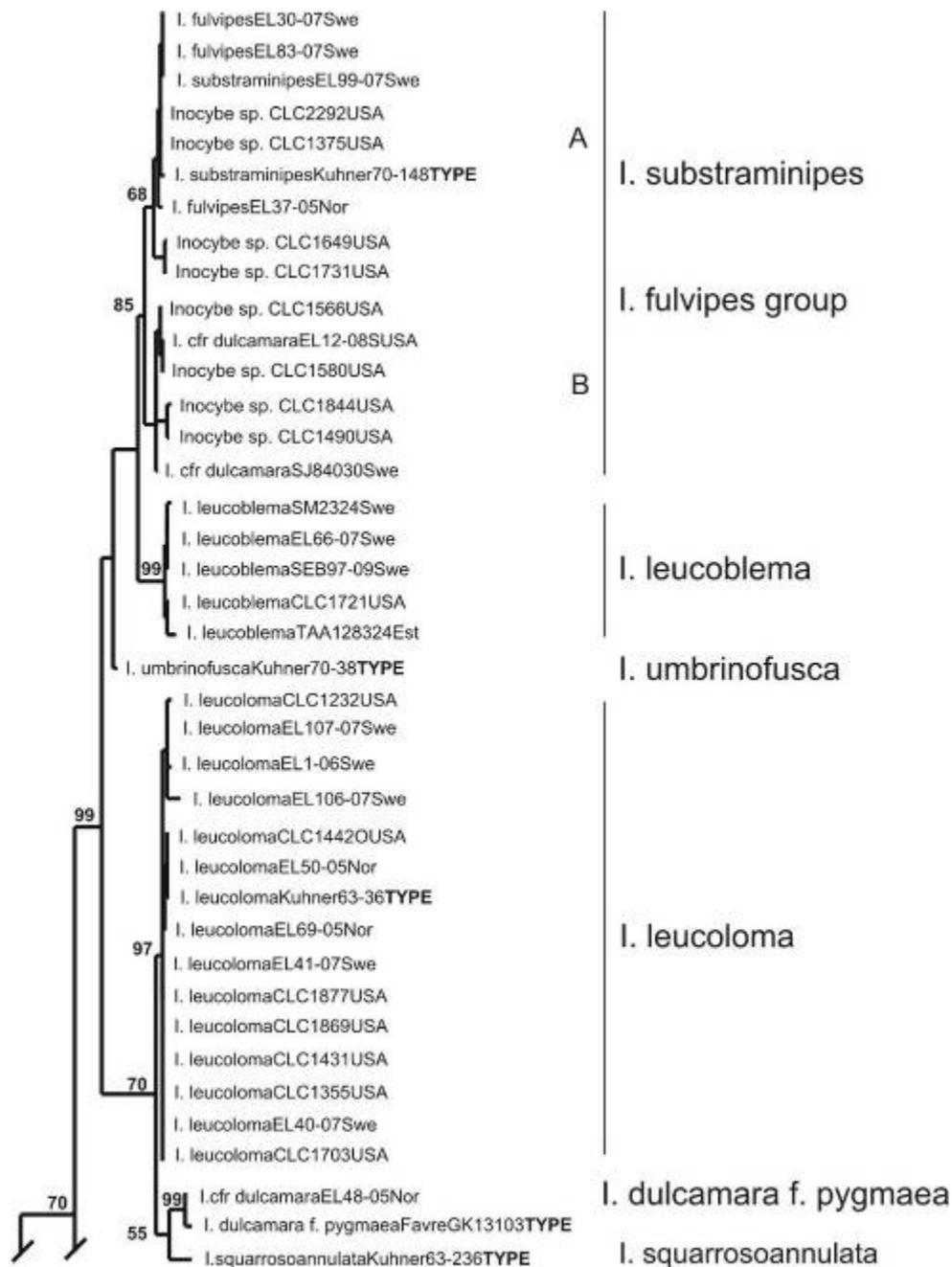


Fig. 1A. Upper part. One of the equally most parsimonious trees obtained from the maximum parsimony analysis, presented as a phylogram. Bootstrap values are indicated on branches. The nine recovered clades have been marked and named.

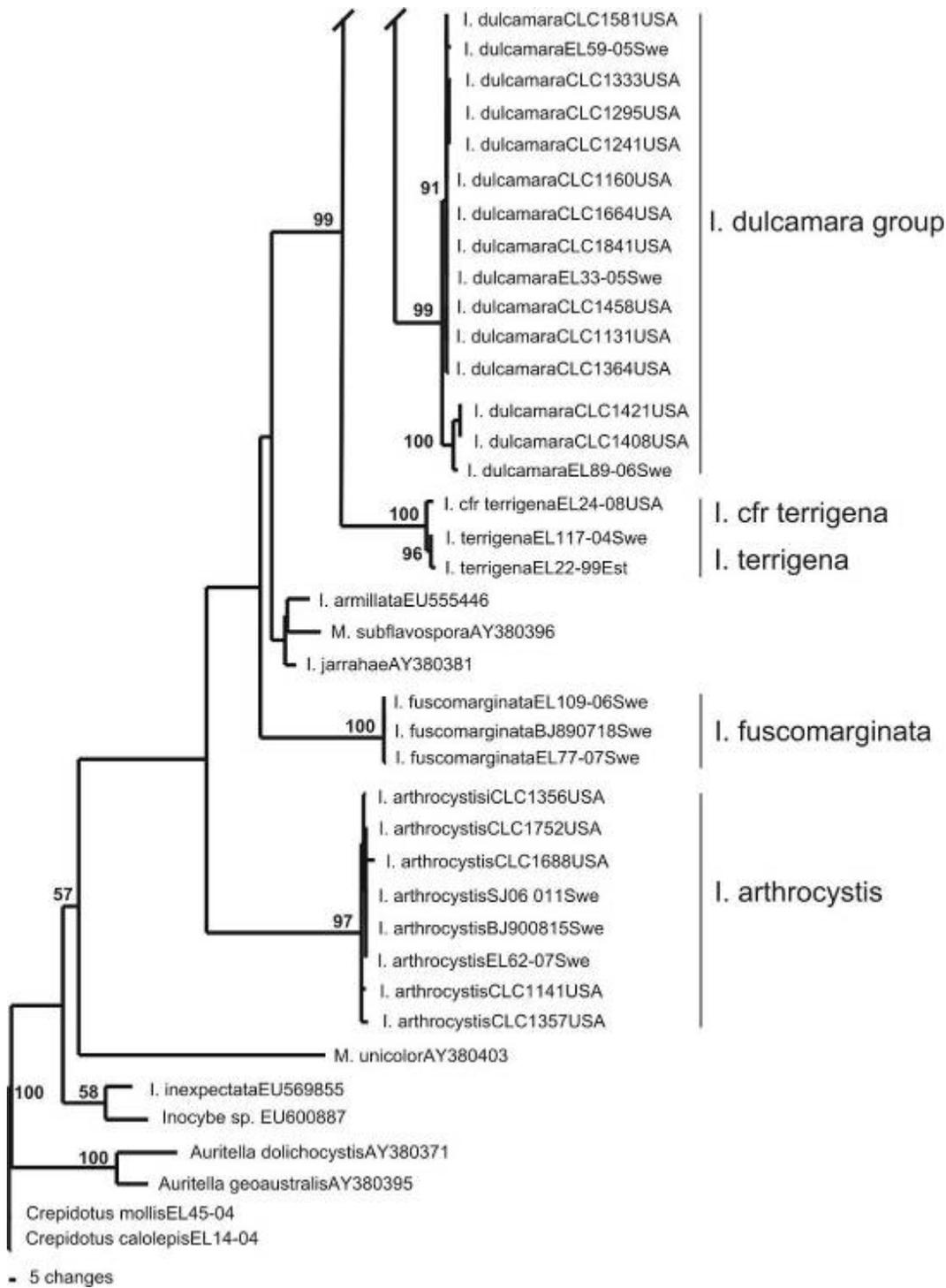


Fig. 1B. Lower part. One of the equally most parsimonious trees obtained from the maximum parsimony analysis, presented as a phylogram. Bootstrap values are indicated on branches. The nine recovered clades have been marked and named.



Fig. 2. Alpine *Inocybe* (*Mallocybe*) species. Row 1: *I. arthrocytis* CLC 1293(USA), EL 62-07(Sweden). Row 2: *I. dulcamara* CLC 1752 (USA), CLC 1241 (USA). Row 3: *I. leucoblema* CLC 1721(USA), EL 66-07(Sweden). Row 4: *I. leucoloma*, CLC 1431(USA), EL 41-07c(Sweden). CLC specimens are from the Rocky Mts and EL specimens from Northern Europe. Bar = 1 cm (rows 1, 4, 6); bar = 2 cm (rows 2, 3, 5).



Fig. 2. Alpine *Inocybe* species (continued). Taxa with scaly stipes and/or or yellow in stipe base. Row 5: *Inocybe fulvipes* clade A: CLC 2292 (USA) , EL 30-07c (Sweden) . Row 6: *I. fulvipes* clade B: CLC 1844(USA), CLC 1441 (USA). *Inocybe terrigena* EL 195-09 (USA). Bar = 1 cm (rows 1, 4, 6); bar = 2 cm (rows 2, 3, 5).

Material examined: USA. Colorado, Pitkin /Lake County, Independence Pass, CLC 1141(MONT), 14 Aug, 1997, CLC 1356(MONT), 12 Aug. 1999, CLC 1357(MONT), 12 Aug. 1999, CLC 1752(MONT), 14 Aug. 2001, San Juan County, San Juan Mountains, Stony Pass, CLC 1688(MONT), 9 Aug. 2001. All collected by C.L. Cripps.

Ecology: alpine zone, associated with dwarf and shrub willows, including mixes of *Salix reticulata*, *S. planifolia*, *S. glauca*, and *S. arctica*. All collections are from Colorado.

Remarks: This *Mallocybe* possesses a bell-shaped, uniformly pubescent ocher pileus and white to pale ocher stipe; the lamellae are often strikingly white but can be more yellow brown. For all specimens, the cortina was not apparent (clean margin) and an odor was lacking. This taxon is microscopically similar to *I. malenconii* which has a flatter cap with more brown coloration and wider cystidia. Our specimens fit Kühner's Type description and micro-features (Fig. 3). This is the first report of *I. arthrocytis* from the Rocky Mountain alpine, although it is known from arctic-alpine areas of Europe and Greenland.

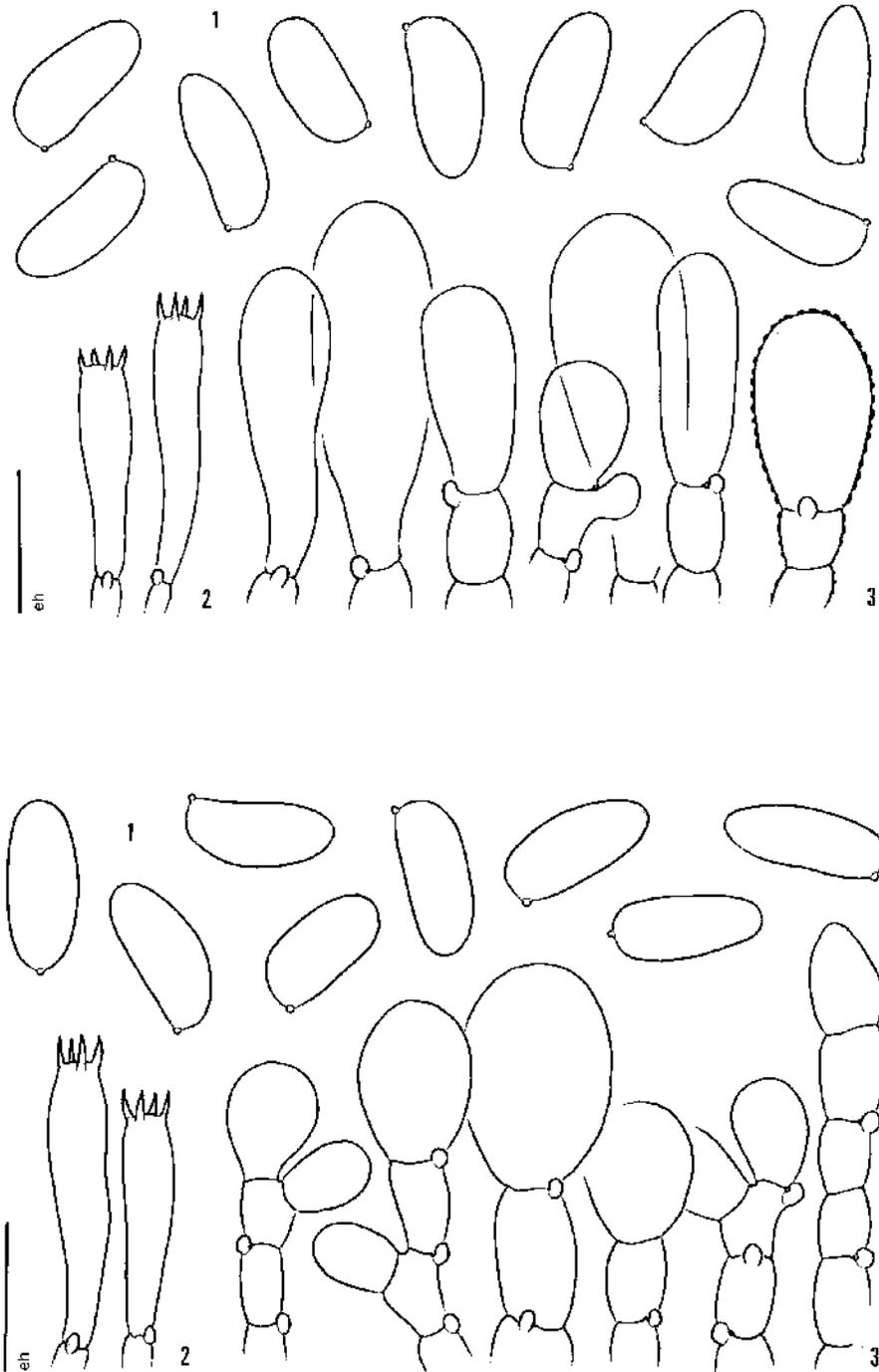


Fig. 3. Micro-features of Alpine *Inocybe* (*Mallocybe*) species from the Rocky Mountain alpine zone and holotypes. Top: *I. arthrocytis* CLC 1357, 1-spores, 2-basidia, 3-cheilocystidia. Bottom: *I. arthrocytis* G-C (R. Kühner nr. 73-310, holotype), 1= spores, 2= basidia, 3= cheilocystidia. Bar = 10 μm. Spores 2000x, basidia & cystidia 1000x.

Inocybe dulcamara (Alb. & Schwein) P.

Kumm. Fuhr. Pilzk (Swickau): 79 (1871)

(Figs. 2, 4)

Agaricus dulcamara Alb. & Schwein. Sacc. Syll. Fung.

763, 1887

Pileus 15-45 mm in diameter, at first hemispheric or with low umbo, becoming broadly convex, umbo remaining or not, to appanate with low boss, or flat or sunken in center, uniformly pale ocher (dull yellow brown) but not dark colors, often with olive tint, rather smooth to indistinctly radially fibrous; margin incurved when young, later turned down or in, and entire. *Lamellae* broadly adnate or subdecurrent when young, often narrow, pale yellow brown at first, then yellow brown (ocher) with olive tint, edges can be paler. *Cortina* cobwebby, pale whitish buff, pale yellowish, fugacious or leaving a few fibrils that can adhere to margin of young specimens. Stipe 15-40(60) mm long x 3-6(8) mm wide, equal, can be rather long, undulating slightly or not, dull yellow brown, whiter at base, surface rough-fibrous, somewhat floccose at apex, in some collections with persistent white peronate sheath that flares upward, white at base in most cases, stuffed or hollow, tough. *Context* white in cap, watery yellow brown in stipe; *odor* of burnt sugar, honey-like. Basidiomes dry pale yellow brown with olive tint (no yellow at base).

Spores brown, 8.5-11.5 x 5-6 μm , on average 10.7 x 5.4 μm , larger for 2-spored basidia up to 17 x 7.5 μm , smooth, subphaesoliform to sub-amygdaliform, with conic or obtuse apex.

Basidia long, clavate, 30-60(85) x 8-12(19) μm , mostly 4-sterigmate, in some collections mixed with 2-sterigmate basidia. *Pleurocystidia* absent.

Cheilocystidia clavate, cylindrical, 15-35(-50) x 6-15(-28) μm , pale, thin-walled.

Clamp connections present.

Material examined: USA. Colorado: Pitkin/Lake County, Independence Pass, CLC 1241(MONT), 12 Aug. 1998, CLC 1333 (MONT), 10 Aug. 1999, CLC 1364(MONT), 13 Aug. 1999, Summit County, Loveland Pass, CLC 1295(MONT), 7 Aug. 1999, San Juan County, San Juan Mountains, Horseshoe Lake, CLC 1664, 6 Aug. 2001; Montana, Carbon County, Beartooth Plateau, CLC 1131(MONT), 30 July 1997, CLC 1160(MONT), 30 Aug. 1997, CLC 1581(MONT), 20 July, 2001 (Beartooth collections have peronate veil and 2-spored basidia). All collected by C.L. Cripps.

Ecology: alpine zone with mixed dwarf (*S. reticulata*) and shrubby willow (*S. glauca*, possibly *S. planifolia*), CLC 1581 was possibly with *Dryas*.

Remarks: Our specimens fit nicely into the *I. dulcamara* clade described in the broad sense (Favre's *forme Typique*). Specimens are typically pale ocher with rather smooth cap, olive yellowish gills, fibrous ocher stipe, white stipe base, with an odor of burnt sugar. The Beartooth specimens with a white peronate sheath and 2-spored basidia group molecularly with 4-spored specimens. This taxon is apparently widespread in the Rocky Mountains alpine zone and is known from other arctic-alpine areas with willows. It is also reported from subalpine areas and with aspen in the Rockies (Cripps 1997). There is sequence variation within the *I. dulcamara* group clade indicating that there are possibly two or more taxa hidden in this morphotype. The different sequence types occur in both Europe and North America.

One specimen from Norway matched molecularly to Favre's type of *I. dulcamara f. pygmaea*, but no North American specimens are reported. Interestingly this form appears outside the *I. dulcamara* clade.

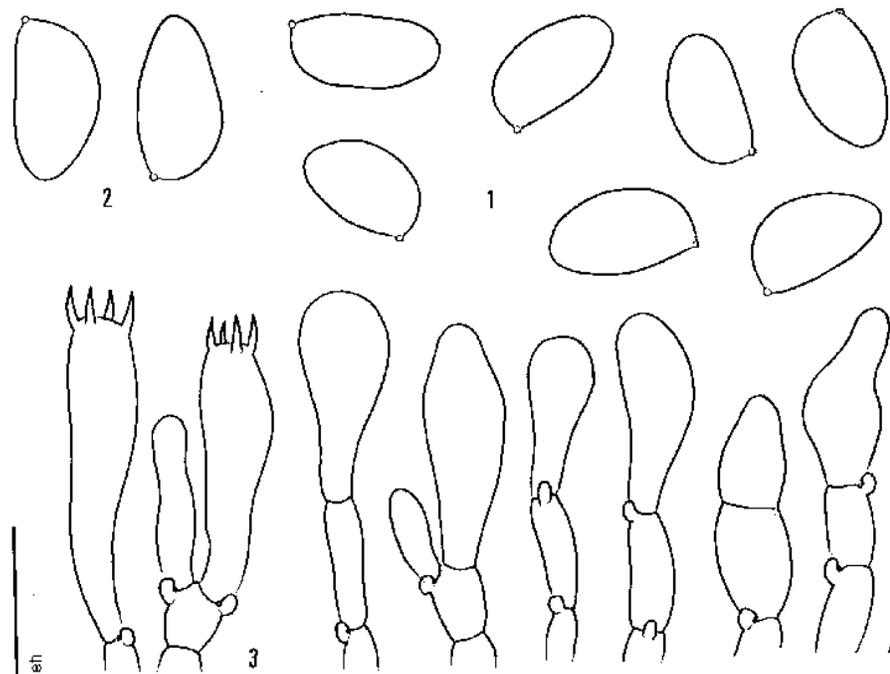


Fig. 4. Micro-features of Alpine *Inocybe* (*Mallocybe*) species from the Rocky Mountain alpine zone. *I. duclamara* CLC 1241, 1-spores, 2-spores from 2-spored basidia), 3-basidia, 4- cheilocystidia. Bar = 10 μ m. Spores 200x,

Inocybe leucoblema Kühner (Figs. 2, 5)
Bull. Trimmest. Soc. Mycol. Fr. 71(3): 294 (1956)
[1955]

Pileus 25-55 mm in diameter, robust, fleshy, convex, slightly domed when young, with margin strongly incurved at first, then curved downwards, or almost plane with slight dome, ocher, brownish yellow, appearing smooth but indistinctly fibrous, a bit greasy when wet, covered with patchy whitish tissue when young, leaving a band or pieces at cap margin; margin entire, not splitting. **Cortina** white, soon gone. **Lamellae** subdecurrent, narrowly adnate, pale yellow, olive, then olive brown, somewhat well-spaced. **Stipe** 25-50 mm long x 8-12 mm wide,

robust, whitish, covered with longitudinal white fibrils and velar material, pale ocher underneath, at apex with conspicuous white floccules.

Context very pale yellow, tough, rubbery. **Odor** faint, not strong.

Spores brown, smooth, indistinctly subphaesoliform, flattened in one aspect, 9-11 x 5-6 μ m, on average 9.7 x 5 μ m. **Basidia** clavate, 30 x 8 μ m, 4-sterigmate. **Pleurocystidia** absent. **Cheilocystidia** 25-35 x 10-15 μ m, broadly clavate to subpyriform, a few with thickened walls, pale. **Clamps connections** present.

Material examined: USA. CO. Chafee/Gunnison County, Sawatch Range, Cottonwood Pass, MONT CLC 1721, 12 Aug. 2001, collected by C.L. Cripps.

Ecology: alpine habitat, our one collection from Colorado was with *Dryas octopetala*.

Remarks: The robust specimens found in *Dryas* are covered with white fibrils when young and conform to the type description of *I. leucoblema* by Kühner; this includes the somewhat domed pileus when young and thick flesh plus spore size and cystidial shape (Kühner and Romagnesi 1953). This is the first report of this species from the Rocky Mountain alpine zone. It is reported from other arctic-alpine areas of the world as well as from boreal to subalpine habitats in both Europe and North America.

Inocybe leucoloma Kühner (Figs. 2, 6)
Docums. Mycol. 19(no. 74): 22 (1988)

Pileus 15-45 mm in diameter, at first hemispherical with inrolled margin, conic-convex, convex, shallow convex, with small umbo (on some), pale yellow brown with olive tint at first, darkening to yellow brown, pale or medium brown, covered with copious whitish velipellis when young, underneath surface woolly, rough-fibrous, fibrous; margin typically turned down, occasionally lifted up, with bits of white tissue. *Lamellae* decurrent, subdecurrent to adnate (and pulling away), somewhat crowded, pale olive yellow gray when young, then mustard yellow, yellow-brown, brown, edges paler or concolorous. *Cortina* white, copious, cobwebby, obvious on young specimens. *Stipe* 15-45 mm x 2-6 mm, equal, bit curved, slim, mostly rather long in relation to pileus, pale brown base color, covered with patches of white longitudinal fibrils or bands of white tissue that rub off and are less obvious in older specimens, hollow or stuffed.

Context pale watery yellow brown. *Odor* faint, fungoid.

Spores brown, smooth, indistinctly subphaesoliform to regularly elliptical, apex obtuse, occasionally subconic, (8.5)9-11 x 4.5-5.5(6) μm , on average 9-10 x 5.2 μm . *Basidia* clavate, long and narrow, 35-45(60) x 8-10 μm , some with yellow granular contents, most 4-sterigmate, a few with 2-sterigmata up to 7 μm long. *Pleurocystidia* absent. *Cheilocystidia* 15-40 x 8-14 μm , clavate to subpyriform, with thin, pale walls. *Clamp connections* present. Velar hyphae noted in pileipellis on microscopic examination.

Material examined: USA. Colorado: Pitkin/Lake County, Independence Pass, CLC 1355(MONT), 12 Aug. 1999; San Juan County, San Juan Mountains, Emma Basin CLC 1431(MONT), 1 Aug. 2000, CLC 1869(MONT), 31 July 2002, Black Bear Basin, CLC 1442(MONT), 2 Aug. 2000, Cinnamon Pass, CLC 1702(MONT), 10 Aug. 2001, Mineral Basin, CLC 1877(MONT), 30 July 2002, Summit County, Loveland Pass, CLC 1232(MONT), 12 Aug. 1998, all collected by C.L. Cripps.

Ecology: alpine habitat, often in wet areas, noted with both shrub (*S. planifolia*) and dwarf (*S. reticulata*) willows.

Remarks: When young, the slim delicate fruiting bodies are covered with copious white tissue, making this taxon distinctive. In older specimens, tissue is apparent only at the cap margin and on the stem as bands of white fibrils. *Inocybe leucoblema* is also covered with white tissue but is a more robust species. Older specimens that lack white tissue might be mistaken for a small *I. dulcamara*. This species is known from the European alpine and this is the first record for the Rocky Mountains. Our specimens were matched molecularly to Kühner's Type, fit Kühner's Type description, and match microscopic features of Type (Fig. 6).

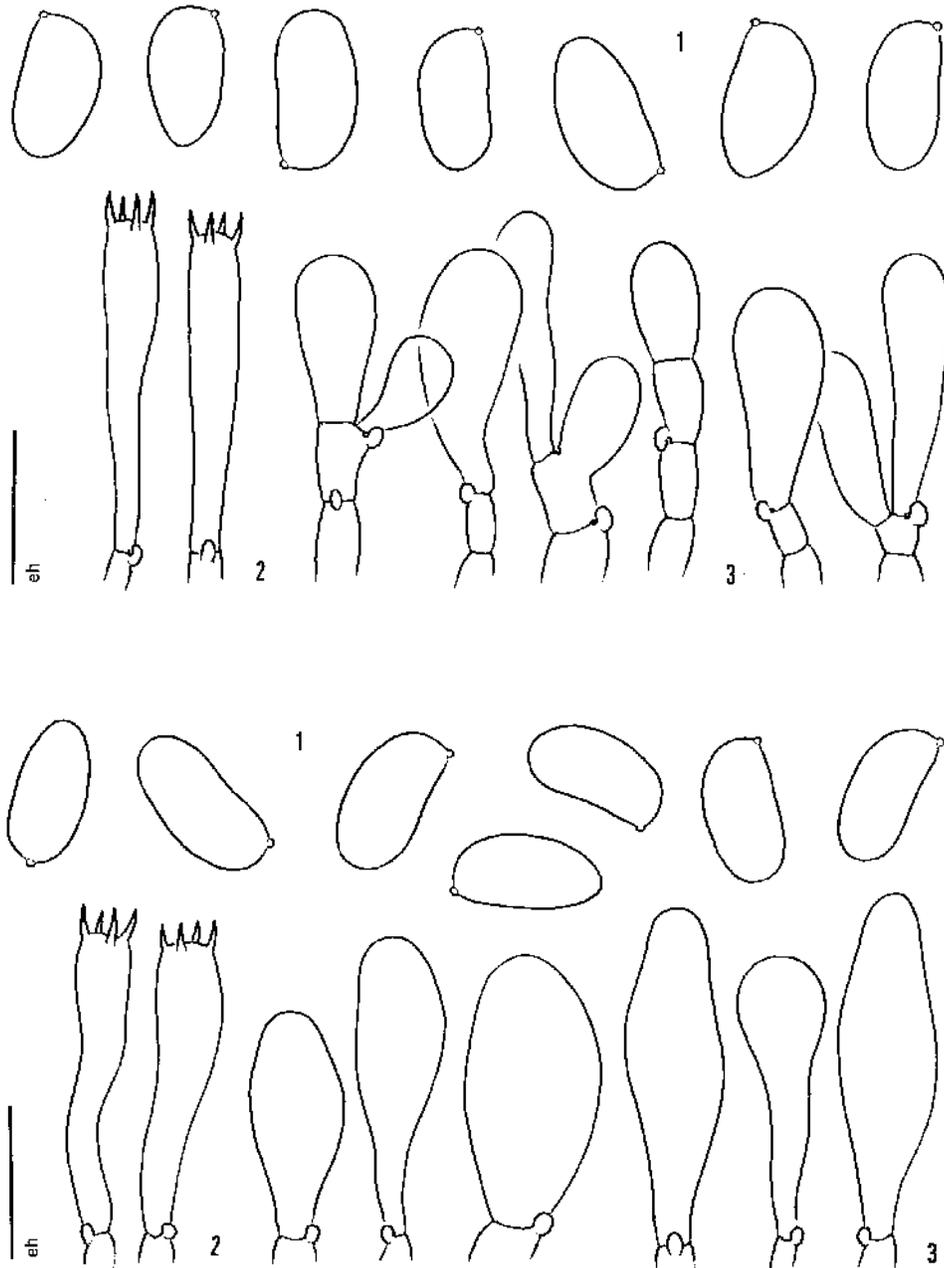


Fig. 5. Micro-features of Alpine *Inocybe* (*Mallocybe*) species from the Rocky Mountain alpine zone and holotypes. Top: *I. leucoblema* CLC 1721, 1-spores, 2-basidia, 3-cheilocystidia. Bottom: *I. leucoblema* G-C (R. Kühner, 20-8, holotype), 1= spores, 2= basidia, 3= cheilocystidia. bar = 10 um. Spores 2000x, basidia & cystidia 1000x.

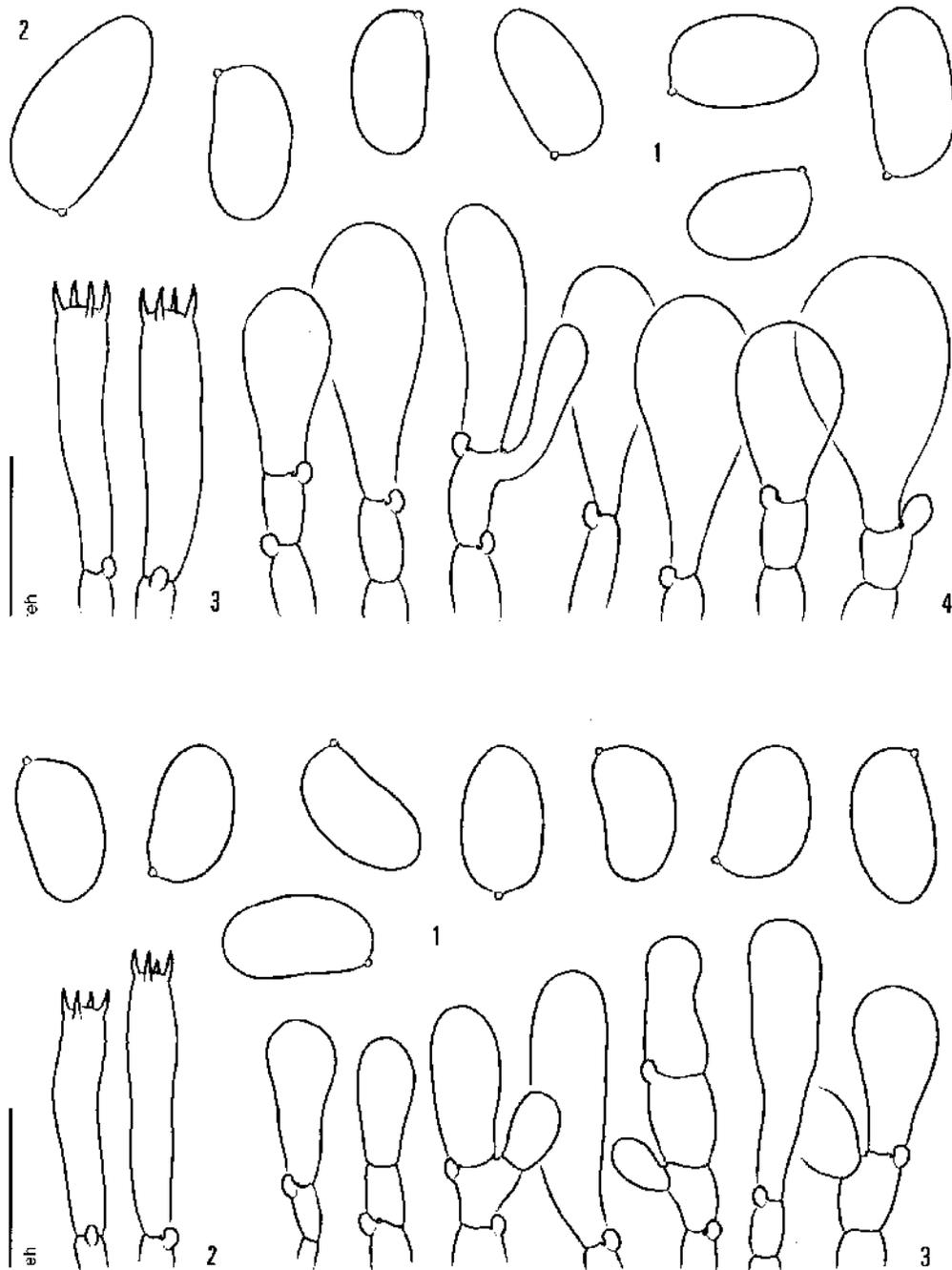


Fig. 6. Micro-features of Alpine *Inocybe* (*Mallocybe*) species from the Rocky Mountain alpine zone and holotypes. Top *I. leucoloma*, CLC 1431, 1-spores, 2-larger spores from 2-spored basidia, 3-basidia, 4-cheilocystidia. Bottom: *I. leucoloma* G-C (R. Kühner nr. 63-36, holotype). Bar = 10 μ m. Spores 2000x, basidia & cystidia 1000x.

Taxa with scaly or upward fibrils on stipe, yellow or ocher inside base

Inocybe fulvipes clade

Subclade A (Figs. 2, 7, 8)

Inocybe aff. substraminipes Kühner

I. substraminipes Kühner Docums. Mycol. 19(no.74):26(1988)

I. fulvipes Kühner Docums. Mycol. 19(no. 74): 18 (1988)

[possibly *I. paludosa* Kühner Docums. Mycol. 19(no. 74):23(1988)]

Pileus (robust) 20-50 mm in diameter, robust, convex, shallow convex, ocher, golden brown, orange brown, appressed fibrillose scaly, tomentose, occasionally areolate in center; margin curves down, often rolls under, with yellowish (appendiculate) veil tissue overhanging lamellae or not. *Lamellae* adnate, narrow or broad attachment, narrow to broad, golden yellow, golden brown, orange brown, paler when young. *Cortina* cottony whitish yellow, leaving tissue on cap margin and superior zone on stipe. *Stipe* robust, firm, up to 15-40 mm long x 5-10 mm wide, equal, covered with dingy whitish yellow floccules or scales that flare upward, pale cap color, ocher, yellow brown, white at base exterior, hollow or stuffed, rubbery. *Context* pale yellowish, yellow, golden brown, ocher, more golden or yellow at base. *Odor* faint. Basidiomes dry yellow brown (flesh dries pale orange) in NA collections.

Spores brown, (8)9-11 x 4.5-5.5 μm , on average 9.8 x 5 μm , smooth, regular or subphaesoliform. *Basidia* 25-40 x 7-10 μm , clavate, some with yellow granular contents, mostly 4-sterigmate, a few 2-sterigmate. *Pleurocystidia* absent. *Cheilocystidia* clavate, narrowly clavate, in some collections cylindrical and attenuated, variable,

10-50(60) μm x 5-10 μm , pale, thin-walled (not to be confused with sphaeropedunculate paracystidia interspersed with basidia on gill sides. *Clamp connections* present. Velar hyphae noted in CLC 135 on microscopic examination.

Material examined. USA. CO, Pitkin/Lake County, Independence Pass, CLC 1375 (MONT), 14 Aug. 1999, collector E. Horak, Summit County, Loveland Pass, CLC 2292 (MONT), 8 Aug., 2006 collector C.L. Cripps.

Ecology: In the alpine zone, associated with dwarf and shrubby willows.

Remarks: North American collections are robust with variable golden to orange brown colors, a stout scaly stem, and golden to yellow flesh that is brighter inside the stipe base. If stipe base color is interpreted as yellow, this fits Kühner's alpine group with this characteristic, i.e., *I. fulvipes*, *I. substraminipes* and *I. paludosa*, although synonymy may be involved. Our NA specimens fit molecularly with specimens from Europe. However, there is variation in the scaly/smooth aspect of the stem, coloration of the basidiome, and cystidial shape within the group. NA specimens (at least) dry a yellow brown color making them distinguishable from Subclade B that dries a red brown color.

We have a sequence from the type specimen of *I. substraminipes* for direct comparison, but those for *I. fulvipes* and *I. paludosa* were not available for comparison.

North American specimens differ somewhat in micro-anatomy to Kühner's original Type of *I. substraminipes* and *I. fulvipes* (Fig. 7, 8). Pleurocystidia for NA specimens are thinner and can be more attenuated, although they are variable in areas of the hymenium. Kühner included rare sphaeropedunculate cells in his Type description which are presented as paracystidia on gill sides in ours.

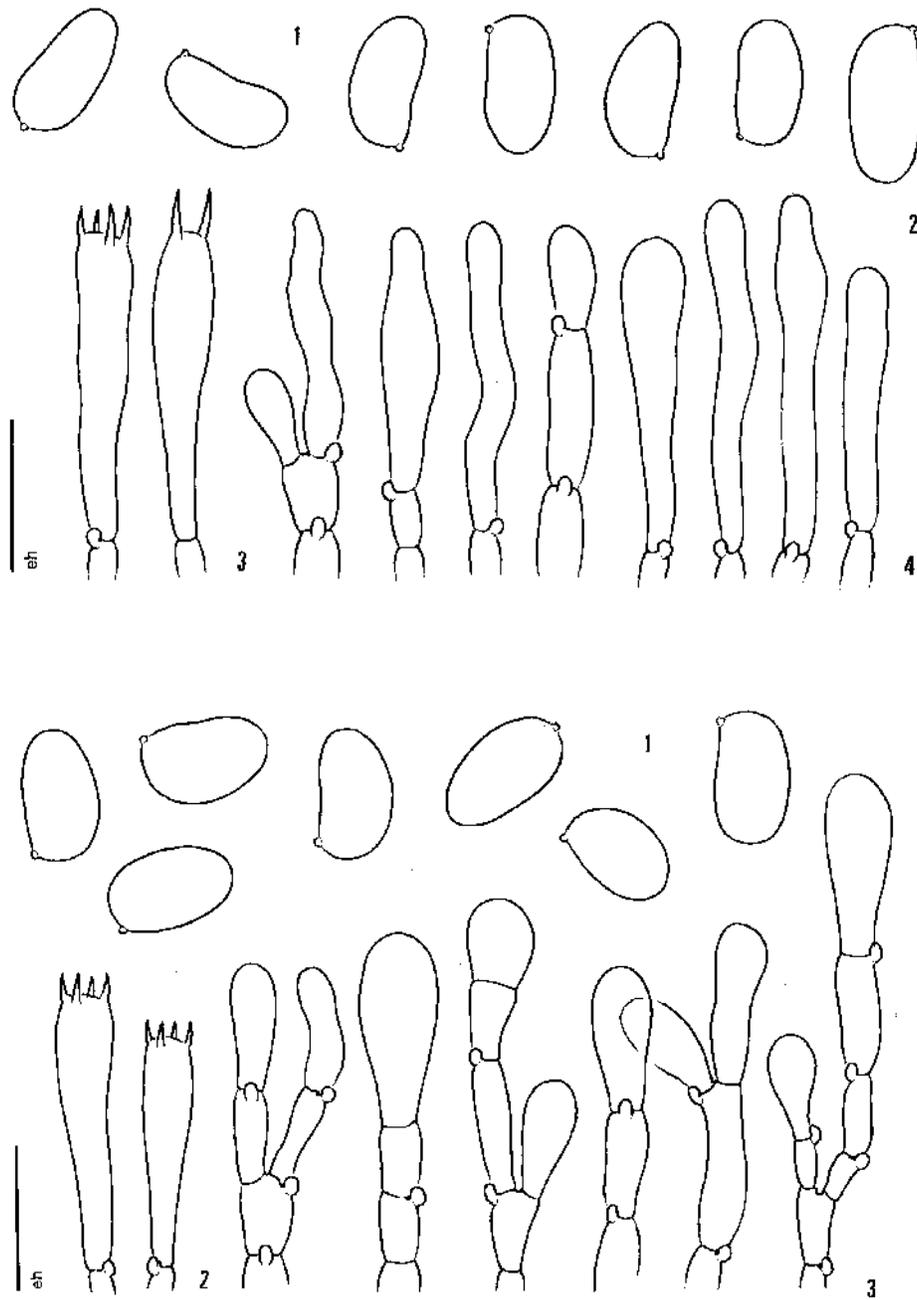


Fig. 7. Micro-features of Alpine *Inocybe* (*Mallocybe*) species from the Rocky Mountain alpine zone. Top: *I. fulvipes* group A (affinity *I. substraminipes*), CLC 1375, 1-spores, 2-larger spores, 3-basidia, 4-cheilocystidia. Bottom: *I. substraminipes* G-C 452068 (R. Kühner nr. 70-148, holotype), 1-spores, 2-basidia, 3-cheilocystidia. Scale bars = 10 μ m. Spores 2000x, basidia & cystidia 1000x.

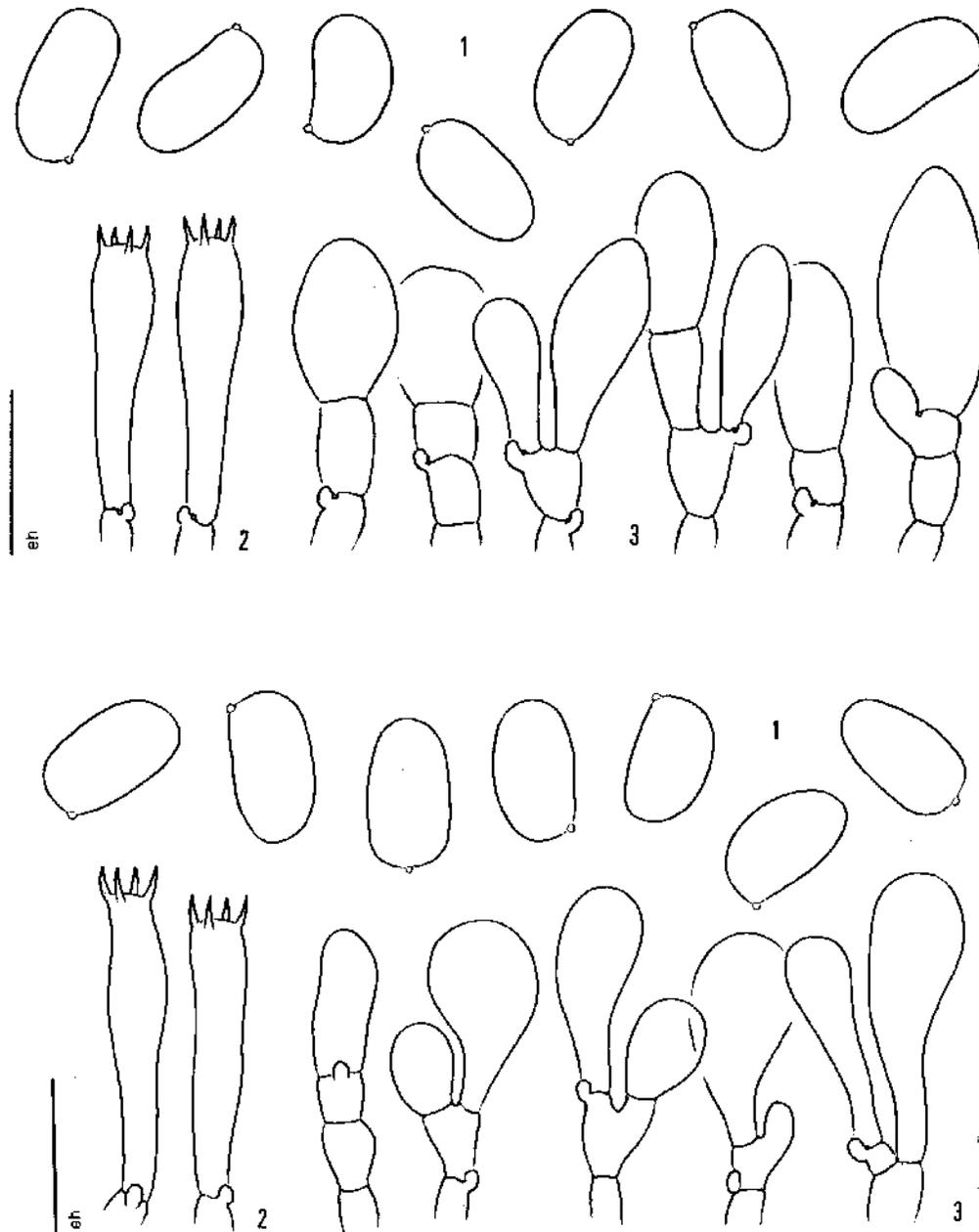


Fig. 8. Micro-features of Alpine *Inocybe* (*Mallocybe*) species holotypes, *I. fulvipes* group (continued). Top: *I. fulvipes* s.l. G-C 452063 (R. Kühner nr. 71-2, Va-2, holotype), 1-spores, 2-basidia, 3-cheilocystidia. Bottom: *I. paludosa* G-C (R. Kühner, nr. 63-236, holotype), 1-spores, 2-basidia, 3-cheilocystidia. Bottom: Scale bars = 10 μ m. Spores 2000x, basidia & cystidia 1000x.

The morphological variation is also reflected in the sequence data of the *I. fulvipes* clade with at least four sequence types. There is no clear correlation between sequence data and morphology except for the two taxa described here. More data and further analysis is needed to disentangle the entities within this species complex, also see discussion in Eyssartier (2006).

Outliers CLC 1649 and CLC 1731 were both with *Dryas*; specimens were immature and did not provide quality data, but stipes appeared smoother.

Inocybe fulvipes clade

Subclade B: Inocybe sp. (taxon B)

(Figs. 2, 9)

Pileus 10-35 mm in diameter, conic-convex when young, then broadly convex, some flat in center, occasionally with low boss, orange brown, red brown, brown, umber brown, occasionally more ochre brown, center rough-woolly, scurfy, appressed scaly, outwards roughened striate, smooth when wet, roughened when dry; margin turned down, occasionally splitting, often with rim of tissue. *Lamellae* adnate, with narrow or broad attachment, pale gray yellow at first, then medium to dark yellow brown, red brown, with slight olive tints. *Cortina* cobwebby, dingy yellow, soon gone (absent on older specimens). *Stipe* 10-35 mm long x 2-6(8) mm wide, slim, equal, straight or slightly curved, yellow brown, becoming darker yellow brown, red brown, covered with tufts of rough fibrils (sparse in some) that flare upwards, white at base, hollow or stuffed, rubbery.

Context pale yellow brown, yellow inside stipe base of some specimens. *Odor* faint to faint dulcamara-like. Basidiomes dark dry orange brown or red brown, yellow in stipe base (if present) can persist in dried specimens.

Spores brown, 9-12 x 5-6 µm, on average 9.8 x 5.3 µm, smooth, subphaesoliform with rounded apex. *Basidia* 25-30 x 8-10 µm, clavate, some with yellow granular contents, mostly 4-sterigmate, a few 2-sterigmate. *Pleurocystidia* absent. *Cheilocystidia* clavate, some tending towards pyriform, occasionally with slightly thickened walls, some with golden contents, 20-40 x 9-12 µm. *Clamp connections* present.

Material examined: USA. Colorado: Summit County, Loveland Pass, CLC 1490 (MONT), 9 Aug. 2000, San Juan county, San Juan Mountains, Mineral Basin, CLC 1844 (MONT), 30 July 2002. Wyoming, Park County, Beartooth Plateau (site 2), CLC 1566 (MONT), 14 July 2001, CLC 1580 (MONT), 20 July 2001, all collected by C.L. Cripps.

Ecology: In the Rocky Mountain alpine zone mostly with *Salix reticulata*, one collection with mixed *S. arctica* and *S. planifolia*. Two collections recorded near streams.

The North American collections typically have a dark red brown coloration, appressed scaly pileus and upward directed fibrils on the stipe. It could be confused with other dark Mallocybes with scaly aspects (Fig. 2, part 2) such as: *I. fuscomarginata* (Fig. 9b), *I. umbrinofusca* (Fig. 10b), *I. terrigena*, and *I. squarrosoannulata* (Fig. 10a). Also compare morphological characteristics in the Key and microscopic features on the reference sheet (Fig. 11). Rocky Mountain specimens have bright yellow flesh in the stipe base (especially when frozen), but this was not a consistent character for each basidiome. Yellow would be expected inside the stipe base of the *I. fulvipes* group. Our specimens dried red brown in contrast to subclade A that dries more yellow brown (at least for NA collections). When yellow does occur in the stipe base of specimens in subclade B, it can persist on drying. Since the types of

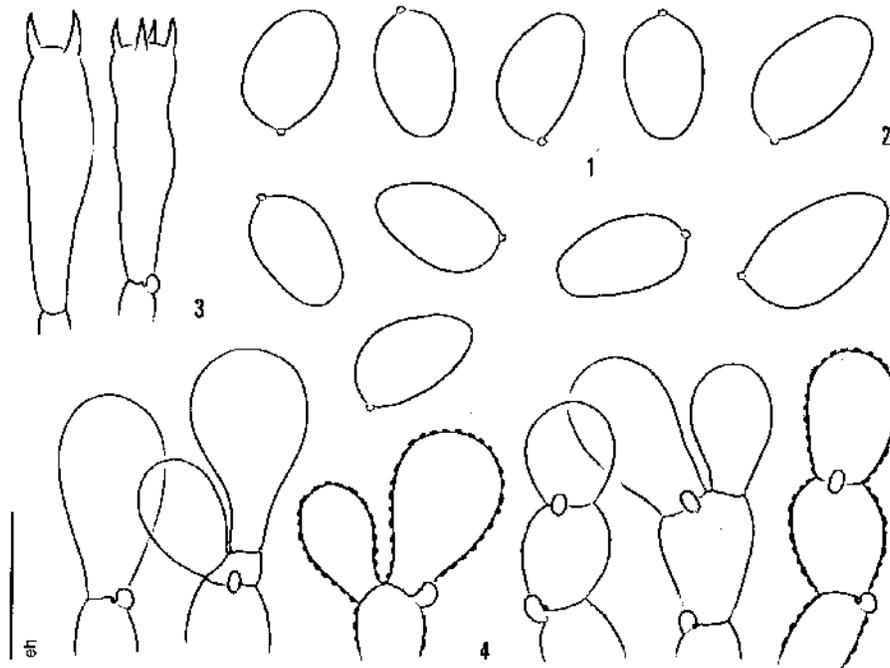


Fig. 9. Micro-features of Alpine *Inocybe* (*Mallocybe*) species, holotypes. Top: *I. Fulvipes* clade, *Inocybe* sp. (Taxon B), CLC 1844, 1-spores, 2-larger spores, 3-basidia, 4-cheilocystidia. Bottom: *I. fuscomarginata* G-C (31 Aug. 1927, R. Kühner, holotype, 1-spores, 2-basidia, 3-cheilocystidia. Scale bars = 10 um. Spores 2000x, basidia & cystidia 1000x.

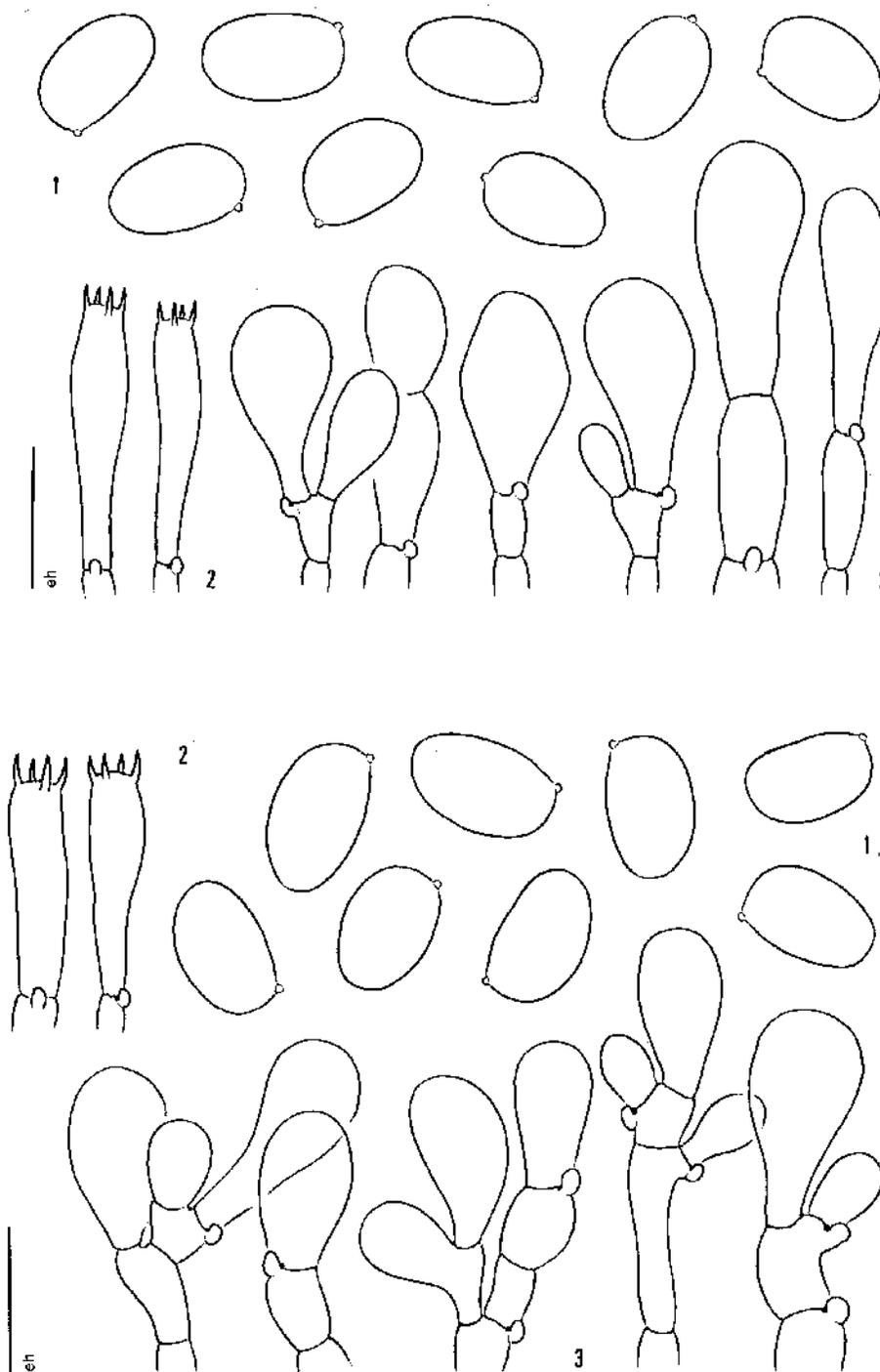


Fig. 10. Micro-features of Alpine *Inocybe* (*Mallochybe*) species, holotypes. Top: *I. squarrosoannulata* G-C (R. Kühner, nr. 63-236, holotype), 1-spores, 2-basidia, 3-cheilocystidia. Bottom: *I. umbrinofusca* G-C 452075 (R. Kuhner nr. 7(B)-38, holotype), 1-spores, 2-basidia, 3-cheilocystidia. Scale bars = 10 μ m. Spores 2000x, basidia & cystidia 1000x.

other taxa in the *I. fulvipes* group such as *I. fulvipes* (Fig. 8a) and *I. paludosa* (Fig. 8b) are not available we cannot yet name this rather distinctive taxon in subclade B, but the microscopic features do not appear to fit either of these taxa.

***Inocybe terrigena* (Fr.) Kühner**

This species is known from boreal to hemiboreal areas associated with *Picea abies* on calcareous ground in Europe and subalpine areas of the Rocky Mountains. We can here report one collection from the Rocky Mountain alpine zone with morphology similar to *I. terrigena*. The fruiting bodies are distinctly smaller and the ITS sequence differ in a few base pairs from the boreal specimens indicating that it may be different. We need more data before giving a detailed description of this species.

Discussion: Of eight resolved clades within *Mallocybe*, six contain North American material and all are matched with European material at the species level (Fig. 1). These are *I. arthrocytis*, *I. dulcamara s.l.*, *I. leucoloma*, *I. leucoblema*, *I. terrigena* and in the *I. fulvipes* group, *I. aff. substraminipes*. These matches between Rocky Mountains alpine collections and those from Scandinavia coupled with data from arctic-alpine habitats in other countries (Table 1) reveal broad intercontinental ranges for these species. Interestingly, a majority of North American collections are from the southern Rocky Mountains in Colorado, far from the arctic. These sites may harbor more varied habitats with the calcareous soil preferred by some *Inocybe* species than northern sites on the Beartooth Plateau (Cripps & Horak 2009).

Type material for *I. leucoloma* and *I. substraminipes* provided reference sequences for these respective taxa. The *I. fulvipes* group likely includes at least *I. fulvipes*, *I. substraminipes* and *I. paludosa* (Kühner

1988) and synonymy may be involved. Color and ‘scaliness’ within the *I. fulvipes* group appears somewhat variable as are cystidia. There was some confusion within the clade as to the character “chrome yellow in base” originally described for *I. fulvipes*, *I. substraminipes* and *I. paludosa* as it does not appear to be consistent for all basidiomes within collections from NA. However, it was not possible to obtain Types for *I. fulvipes* and *I. paludosa*, so further resolution was not possible at this time, but warrants further study. In addition, micro-morphology matches of types and NA specimens were made for *I. arthrocytis*, *I. leucoblema* and *I. leucoloma*. Micro-morphology of types in the *I. fulvipes* group and similar taxa is provided for comparison (Figs. 7, 8 and 11). Comparisons suggest that *I. fulvipes* and *I. substraminipes* may be congeneric.

Type material for *I. dulcamara* f. *pygmaea* matched one collection from Norway outside the *dulcamara* clade. The Types for *I. umbrinofusca* and *I. squarrosoannulata* did not match any of our collections and came out on separate single branches. Micro-anatomy of *I. umbrinofusca* T (70(B)-38 and *I. squarrosoannulata* T (69-236) types are substantially similar. However, ITS sequence data indicate that they should be regarded as separate species. Additional material is needed to get a broader knowledge of these species. One collection of *I. terrigena* is reported from the Beartooth Plateau that matched European material but is not reported in detail due to insufficient data.

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material. International Symposia on Arctic-alpine Mycology (ISAM) helped initiate the international collaboration on this project.

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Addendum 1: Key to subgenus *Mallocybe* in the Rocky Mountain alpine zone*

1. Spores long and narrow, more than twice as long as wide, pleurocystidia articulated, clavate. Pileus bell-shaped, uniformly pubescent, ocher; lamellae strikingly white at first, cortina not apparent, margin clean; stipe dingy white or pale ocher; odor absent.....**I. arthrocytis**
- *I. malenconii* has similar spores, wider cystidia, a cortina, flatter, brown pileus**
 - *I. gymnocarpa* lacks a cortina, is larger (up to 6 cm) with wider spores**
1. Spores less than twice as long as wide, cystidia not articulated as above, cortina more apparent.....**2**
2. Basidiomes covered with white tissue when young that can remain on pileus margin or stipe in age; cortina white, often copious..... **3**
2. Basidiomes not obviously covered with white tissue (u.v. remnants) when young (may have white peronate sheath on stipe); cortina pale yellow, ocher, dark ocher, golden.....**4**
3. Pileus robust (25-55 mm), context thick, margin incurved, pale brown covered with white tissue; lamellae pale yellow or olive brown; cortina white; stipe robust and covered with whitish tissue; odor faint.....**I. leucoblema**
3. Pileus (15-45), context thinner, margin can be incurved, ocher or pale brown beneath white u.v. tissue or white tissue only at margin; lamellae pale then yellow brown; cortina white copious; stipe slim, covered with white fibrils in bands; odor faint**I. leucoloma**
4. Pileus smooth fibrous, ocher with olive tint; lamellae ocher with olive tint; cortina pale yellow or ocher; stipe ocher, slightly roughened (white peronate sheath for some); context pale yellow; odor honey-like or of burnt sugar; dries pale ocher with olive tint.....**I. dulcamara f. typique**
- *I. dulcamara* var. *pygmaea* – smaller with larger spores**
 - *I. dulcamara* var. *peronata* – with white peronate sheath**
4. Pileus scaly, rough or smoother; stipe often scaly, squamose or with upward flaring fibrils (sometimes sparse); context white, buff, ocher, pale yellow, yellow; yellow in base or not.....**5**
5. Pileus (20-50 mm), appressed tomentose, radially fibrous, yellow brown, golden brown, orange brown; lamellae golden to orange brown; cortina yellow, can be appendiculate or leave zone on stipe; stipe robust(15-40 x 5-10 mm), ocher, with white base (exterior), fibrillose, with armillate, flocculose scaly or smoother; context pale yellow, bright yellow, ocher; stipe base interior golden or yellow color; odor faint; basidiomes dry yellow brown color..... **I. fulvipes group subclade A (incl. I. substraminipes)**
5. Pileus (10-35 mm), rough woolly, appressed fibrous, slightly scaly, ocher, red brown, brown, umber brown; lamellae yellow brown, red brown; cortina yellow; stipe rough, slim (10-35 x 2-6 mm); base flesh yellow in some specimens; odor faint; basidiomes dry red brown color...**I. fulvipes group subclade B**

Other taxa with dark colors and scaly stipes, but lacking yellow in stipe base include:

- *I. fuscomarginata* has a scaly pileus, wide pigment-encrusted cystidia**
- *I. squarrosoannulata* has finely squamose pileus, wider different spores**
- *I. terrigena* has appressed scaly pileus, more definitive annulus**
- *I. umbrinofusca* has pubescent pileus, wider different spores**

* spores sizes for Rocky Mountain collections in descriptions and for Types in Addendum.

**not recorded in Rocky Mountain alpine to date or not described here.

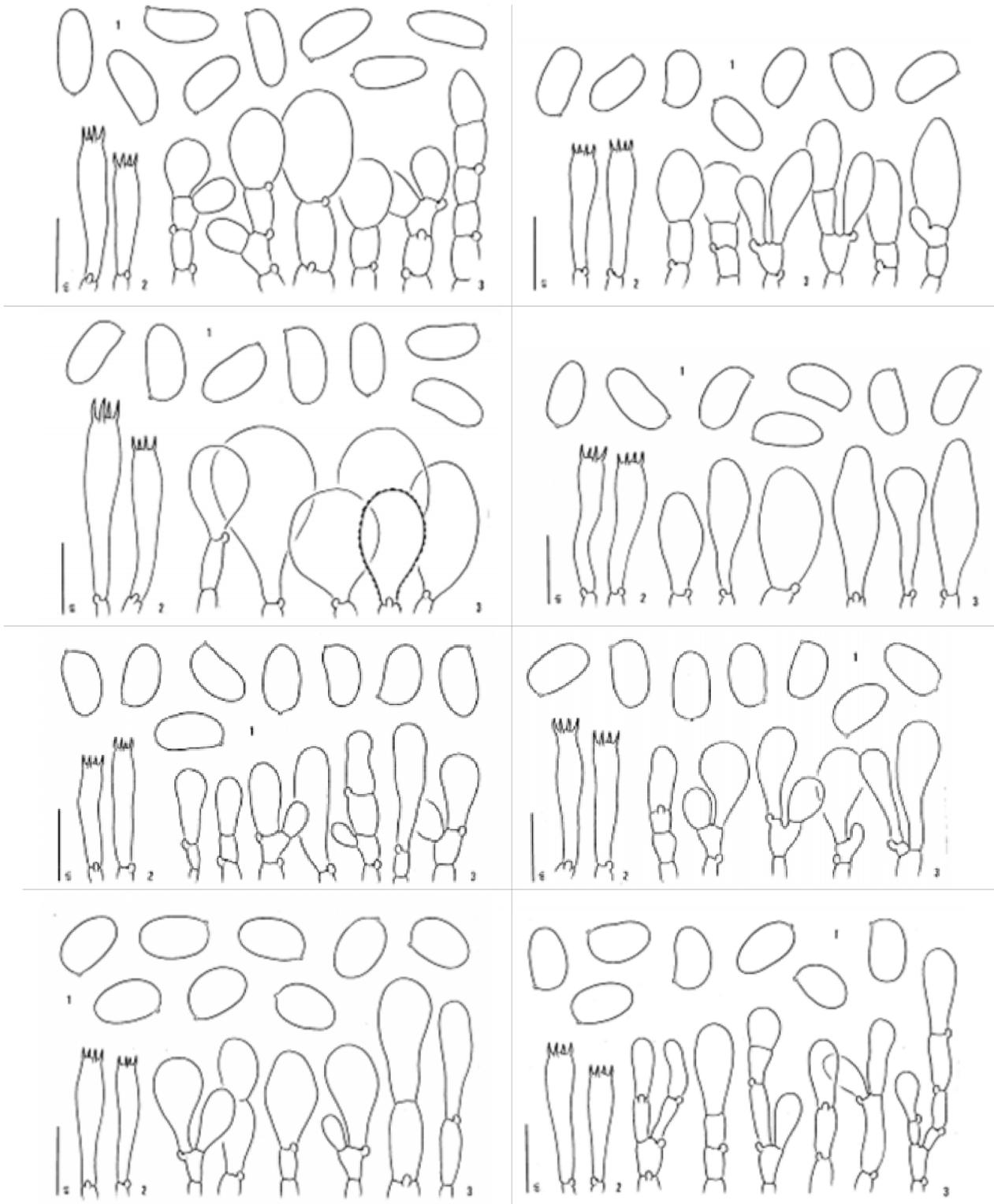


Fig. 11. Kühner holotype reference comparisons: **Row 1:** *I. arthrocytis* Kühner, *I. fulvipes* Kühner. **Row 2:** *I. fuscomarginata* Kühner, *I. leucoblema* Kühner. **Row 3:** *I. leucoloma* Kühner, *I. paludosa* Kühner. **Row 4:** *I. squarrosoannulata* Kühner and *I. substraminipes* Kühner. 1= spores, 2= basidia, 3= cheilocystidia. Bar = 10 μ m. Spores 1500x, basidia & cystidia 750x.

Addendum 2: Information on Type Specimens and translations of protologues of *Inocybe* described by R. Kühner

Note: E.H. personal measurements of microcharacters deviate from those publ. in Kühner (see explanation in methods). Also, it is interesting to note that Kühner often refers to “negative information“ instead of giving actual facts [e.g.: not white!]. Original text is re-adjusted with reference to sequence of macro-then microcharacters.

***Inocybe arthrocystis* Kühner**
(holotype examined by EH) (Figs. 3 & 11)

Docums. Mycol. 19(no. 74): 18 (1988)

Translated protologue:

Pileus expanded, broadly obtuse, ochre-brown, occasionally velutinous-floccose (as observed by naked eye, recalls *Cystoderma*), under lens minute, appressed or individual squamules reddish brown. Lamellae dirty yellowish or olive-brown. Stipe up to 5 mm in diam., straw-yellow becoming ochre, covered with longitudinal, (not whitish) fibrils, base not chrome yellow. Cortina inconspicuous, evanescent. Odor not distinctive (“subinodorous“?).

Spores smooth [not gibbous], (9.5-)10.2-10.6(-11.7) μm , (Q ca. 2). Metuloids absent. Cheilocystidia catenulate, broadly sessile, unstalked, globose-elliptical, terminal cells 12-23 x 9-18 μm .

Associated with *Salix herbacea*.

France: Savoie, Parc National de la Vanoise, near Col de l’Iseran, between the creek Cema and Pays Désert, 2600 m alt., 06.08.1973, Kühner 73-310 (holotype, GC).

***Inocybe fulvipes* Kühner**
(holotype examined by EH, lost?) (Figs. 8 & 11)

Docums. Mycol. 19: 18 (1988).

Translated protologue:

Pileus 12-28 mm diam., dark ochre or ochre-brown, 10 YR 7/5 becoming 7.5 YR 5/5 or 5 YR 4/4, covered with appressed, agglutinated, minute fibrils. Lamellae pale brownish. Stipe 2-5 mm in diam., pale brown-ochre becoming ochre-brown, 10 YR 7/5.6/6, occasionally also reddish

ochre Y,5, YR 6/7.5/5, fibrillose-woolly, often plus/minus flocculose or floccose-squamulose, under lens rarely with minute, erect, not recurved squamules. Cortina pale yellow (not white!), fibrillose-woolly, in young specimens margin of pileus covered with appendiculate, fibrillose veil remnants. Distinctive annulus or ring-like remnants of cortina absent. Context in base of stipe often yellow. Odor like *Inocybe cervicolor* or *Cystoderma carcharias*.

Spores smooth [not gibbous], (8.5-)8.8-11.2(-12) x (5-)5.5-6.5(-6.7) μm . Metuloids absent. Cheilocystidia (17-)20-35 x /7-)11-15(-18) μm , claviform or pyriform, rarely clavate-stipitate, wall pallid, yellow or brown [plasmatic] pigment present.

Associated with dwarf-*Salix* in alpine zone, France, Savoie. Herbarium G-C 452063. (R. Kühner nr. 71-2, Va. 2, holotype) (cf. contaxic with *I. substraminipes*)

***Inocybe fuscomarginata* Kühner**
(holotype examined by EH) (Fig. 9)

BSMF 71: 169. 1956.
Herb. G-C (31 Aug. 1927, R. Kühner, holotype).

***Inocybe leucoblema* Kühner**
(holotype examined by EH)

BSMF 71: 294. 1956.

Herb. G-C (France, Oct. 1986, R. Kühner 20-8, holotype).

***Inocybe leucoloma* Kühner**
(holotype examined by EH) (Figs. 6 & 11)

Docums. Mycol. 19: 22 (1988).

Translated protologue:

Pileus 12-25 mm diam., becoming convex, brownish ochre, covered with radial fibrils. Lamellae at first brownish becoming brown. Stipe 2.5-4.5 mm in diam., at first pallid white from veil remnants becoming pale brownish, most parts covered and striate from \pm longitudinal pallid fibrils. Cortina conspicuous, fibrillose, white. Odor not distinctive (subinodorous).

Spores [not gibbous], (9.7-)10.1(-10.5) x (5.2-)5.5-6(-6.5), Q 1.7-1.8. Metuloids absent. Cheilocystidia 16-25 x 7-14 μ m, often pyriform.

Associated with *Dryas* and *Salix retusa*.
France: Savoie, Parc National de la Vanoise, Le Moriond, near Pralognan, 2200 m alt., 23.07.1963, Kühner 63-36 (holotype, GC).

Inocybe paludosa Kühner (Fig. 8)
(holotype examined by EH)
Docums. Mycol. 19: 23. 1988.

France, Savoie, P.N. Vanoise, Pralognan, Arcellin, among moss in bog with *Salix reticulata*, *S. retusa*, 2300 m alt., 10 Sept. 1970. Herb. G-C (R. Kühner nr. 70-123, holotype).

Inocybe squarrosoannulata Kühner
(holotype examined by EH)

Docums. Mycol. 19: 24. 1988.

France, Savoie, P.N. Vanoise, Pralognan, Arcellin, among moss in bog with *Salix foetida*, 2300 m alt. 29 Aug. 1963, Herb. G-C (R. Kühner, nr. 63-236, holotype).

Inocybe substraminipes Kühner
(holotype examined by EH)

Docums. Mycol. 19(no. 74): 26 (1988)

HOLOTYPE "70-148"
F – savoie, Region de Pralognan, Haute vallee de champagny, Parc de la Vanoise, moraine du glacier de l'Epena. 14.09.1970.
6 exemplaires, -don't 1 ferme, parmi les *Dryas*.
Alt: 2000 – 2100 m. GENIEVE, 19 G N° 452068.

According to Esteve-Raventós *I. fulvipes* is supposed to be identical with *Inocybe substraminipes* Kühner (holotype material examined by EH).

Inocybe umbrinofusca Kühner
(holotype examined by EH)

Docums. Mycol. 19: 26. 1988.

France, Savoie, Maurienne, Plan des Evettes, among moss in moist habitat, associated with *Salix reticulata*, 2500 m. alt., 18 Aug. 1970, Herb. G-C 452075 (R. Kühner nr. 7(B)-38, holotype).



Fig. 12. Alpine *Inocybe* habitat (green areas) on the Beartooth Plateau and collectors E. Larsson, D. Bachman and C. Cripps, ISAM 8, 2008. Photo by P.-A. Moreau.