

A revision of the *Inocybe lanuginosa* group and allied species in North America

P. Brandon Matheny¹ & Bradley R. Kropp²

¹ Dept. of Botany, Box 351330, University of Washington, Seattle, Washington 98195-5325, USA

² Department of Biology, Utah State University, Logan, Utah 84322-5305, USA

Matheny, P.B. & B. R. Kropp (2001). A revision of the *Inocybe lanuginosa* group and allied species in North America. – *Sydowia* 53(1): 93–139.

A morphological evaluation of the *Inocybe lanuginosa* group and allied species is presented for North American taxa. 425 collections from herbaria in North America and Europe representing putative taxa within the group have been studied. 39 collections were subject to phenetic analysis using two clustering procedures, UPGMA and Neighbor-Joining. Four species are recognized in the *I. lanuginosa* group: *I. lanuginosa*, *I. leptophylla*, *I. teraturgus* and *I. stellatospora*. Taxonomy, illustrations and the North American distribution of these species are provided including two allied species, *I. tahquamenonensis* and *I. diminuta*. *Inocybe stellatospora* is an earlier name for *I. longicystis*. *Inocybe nodulospora* is an earlier name for *I. ovatocystis*, both of which are synonyms of *I. lanuginosa*. *Inocybe lanuginosa* var. *alpina* is synonymous with *I. lanuginosa*. *Inocybe sabuletorum* is not a synonym of any member of the *I. lanuginosa* group but rather a member of sect. *Petiginosae*. A key to nodulose-spored species of *Inocybe* with a scaly pileus and a scaly to wooly-fibrillose stipe is included. We consider the name *I. lanuginosa* to represent the synonymous species *I. nodulospora* and *I. ovatocystis*. We fix this interpretation by designation of an epitype for *I. lanuginosa*.

Keywords: Agaricales, *Inocybe*, systematics, fungi, taxonomy, nomenclature.

The exact identity of Bulliard's *Agaricus lanuginosus* has been subject to several interpretations by various workers once it was recognized that a significant amount of variation existed at the microscopic level (Bresadola, 1892; Ricken, 1915; Atkinson, 1918; Kauffman, 1924; Konrad & Maublanc, 1924, 1925; Boursier & Kühner, 1928; Heim, 1931; Pearson, 1946; Moser, 1955, 1967, 1978a; Grund & Stuntz, 1968; Stangl, 1976, 1989; Stangl & Enderle, 1983). Even Fries (1857, 1874) doubted which name to apply. Confusion resulted since several different concepts, viz. *I. ovatocystis* Boursier & Kühner, *I. longicystis* Atk., non Velen. 1920, *I. leptophylla* Atk., *I. plumosa* (Bolt. : Fr.) Quélet and *I. sabuletorum* (Berk. & M. A. Curtis) Sacc. have been suggested as representing Bulliard's *Agaricus lanuginosus*, for which no holotype collection exists save a

plate (the lectotype) and brief macroscopic diagnosis (Bulliard, 1780–1795).

Members of the *I. lanuginosa* group are distinguished by the brown squarrose to squamulose pileus; young lamellae that are pallid and become brown with age; brown squamulose, floccose to wooly-fibrillose stipe; nodulose basidiospores; and occurrence on soil, among *Sphagnum* or on rotten wood under members of the *Pinaceae* in the northern hemisphere. The latter substrate is particularly unusual in *Inocybe* (Fr.) Fr. since the genus is ectomycorrhizal based on general observation (Trappe, 1962; Molina & al., 1992) and some experimental evidence (Zerova, 1966; Chu-Chou & Grace, 1981; Agerer, 1987–98; Cripps & Miller, 1995). However, it has not been determined whether lignicolous members of *Inocybe* behave saprotrophically or ectotrophically. Peck (1887), Murrill (1912, as *Naucoria jalapensis*) and Horak (1977) described additional species of *Inocybe* outside or possibly allied with the *I. lanuginosa* group that can occur on rotten wood or woody debris.

Recognition of morphological species in the *I. lanuginosa* group has not been without controversy. Several authors (Boursier & Kühner, 1928; Grund & Stuntz, 1968; Moser, 1978a; Singer, 1986) considered members of the *I. lanuginosa* group to be distinct species. However, other authors placed one or more species at an infraspecific rank. Heim (1931) admitted three infraspecific taxa (*I. lanuginosa*, *I. lanuginosa* f. *longicystis* and *I. lanuginosa* var. *casimiri*) into stirps Lanuginosa. Stangl (1989), however, considered Heim's var. *casimiri* (as *I. leptophylla*) an autonomous species but *I. longicystis* as a varietal taxon of *I. lanuginosa*.

Singer (1986) recognized Heim's concepts as separate species and redefined the stirps to exclude *I. leptophylla*, a species that lacks pleurocystidia, and *I. casimiri* Velen., the latter now considered synonymous with *I. leptophylla*. Kobayashi (1993) formally recognized Singer's proposal and created subgenus *Leptocybe* to accommodate non-smooth spored species with thin-walled cheilocystidia and absence of metuloids. Singer, additionally, included in stirps Lanuginosa *I. relicina* (Fr.) Ricken, *I. carelica* Singer and *I. cerasphora* Singer. *Inocybe relicina* has not been recorded from North America and differs from other members of the *I. lanuginosa* group by its young yellow lamellae, differently shaped basidiospores and restricted distribution to Fennoscandia. *Inocybe carelica* was described from the former USSR and has not been studied by us but is suggested by Singer (1986) to be very close to *I. longicystis* Atk. *Inocybe cerasphora* was described from Tierra del Fuego, Argentina in the southern hemisphere. These three species, *I. relicina*, *I. carelica* and *I. cerasphora* are excluded from this study.

Two additional species not included by Singer (1986) are *I. sublanuginosa* Rick, which was originally described from Brazil; and *I. paralanuginosa* Pegler, described from the Lesser Antilles but with a pallid ochraceous salmon pileus and fibrillose striate stipe (Rick, 1938; Pegler, 1983). Both of these species are excluded from the *I. lanuginosa* group as well because of the geographical distribution (*I. sublanuginosa*) or color of the pileus and nature of the stipe covering (*I. paralanuginosa*). We consider Singer's classification of stirps Lanuginosa to be heterogeneous given the inclusion of *I. relicina* and *I. cerasphora* and omission of *I. leptophylla*. We intend to evaluate stirps Lanuginosa ss. Heim, or what we refer to as the *I. lanuginosa* group.

From the outset we considered stirps Lanuginosa to be composed of three taxa in North America: *I. ovatocystis*, *I. longicystis* and *I. leptophylla*. However, during the course of study, we uncovered one cryptic taxon, heterogeneous holotype collections and several surprising synonyms, the results of which have upset the nomenclature of members of this group. To afford some stability, we concluded that a prudent course of action would be to epitypify *I. lanuginosa*. At the end, we thus recognize four species in the *I. lanuginosa* group: *I. lanuginosa* (= *I. nodulospora* and *I. ovatocystis*), *I. leptophylla*, *I. teraturgus* M. Moser and *I. stellatospora* (= *I. longicystis* and *I. lanuginosa* ss. Moser, Stangl).

Unfortunately, *Agaricus lanuginosus* Bull. cannot be neotypified. Bulliard's plate (Pl. 370) serves as the lectotype, and according to the International Code of Botanical Nomenclature (ICBN) Art. 9.6, a neotype cannot be designated as long as materials of the original type remain extant (Greuter & al., 2000). However, Art. 9.7 permits the designation of an 'epitype' to serve as an interpretive type in this instance. Previous examples of epitypification among agarics can be found for *Melanotus horizontalis* (Bull. : Fr.) P. Orton (Sime & Petersen, 1999) and in *Tricholoma* (Christensen & Noordeloos, 1999). Accordingly, 'the author who first designates an epitype must be followed' (Art. 9.18) (Greuter & al, 2000). We epitypify *A. lanuginosus* with the concept of *Inocybe ovatocystis* Boursier & Kühner.

We present here a systematic study of members of the *I. lanuginosa* group in North America along with an analysis of taxa using UPGMA and Neighbor-Joining distance-based analyses. Complete descriptions, illustrations and North American biogeographical data are provided along with a key to distinguish taxa and species that may be confused with members of the group. The purpose of this study is to evaluate the taxonomy and nomenclature of members of the *I. lanuginosa* group and to contribute towards future systematic studies of *Inocybe*.

Materials and methods

Materials

425 herbarium collections that included specimens identified as *I. lanuginosa*, *I. leptophylla*, *I. longicystis*, *I. ovatocystis*, *I. relicina*, *I. sabuletorum* and *I. stellatospora* were surveyed from the following North American herbaria: ACAD, BPI, CUP-A(local), CUP-A(general), DAOM, F, KHD, MEXU, MICH, MIN, MONT, NY, NYS, OSC, SFSU, TENN, UTC, VPI and WTU (abbreviations according to Holmgren & al., 1990 except for CUP-A). Holotypes and isotypes of *I. leptophylla* Atk., *I. leptophylla* var. *cystomarginata* Atk. and *I. longicystis* Atk. were also studied. In addition, comparisons with the holotypes of *I. sabuletorum* (Berk. & M. A. Curtis) Sacc. (K), *I. stellatospora* (Peck) Masee (NYS), *I. tahquamenonensis* Stuntz (WTU), *I. nodulospora* (Peck) Sacc. (NYS) and *I. diminuta* Peck (Isotype; WTU) were made. European material, necessary for taxonomic comparisons, was provided by M, depository of Johann Stangl's collections of *Inocybe*. Collections were also examined from individuals who kindly loaned their material: Rob Countess, Ray Fatto, Pam Janszen, Steve Miller, and Lorelei Norvel (denoted by PNW-MS). Tissues of exsiccata were rehydrated either directly in 10% NH₄OH or wetted with 95% ETOH, placed in a drop of distilled water and then mounted in 10% NH₄OH, unless where specified. Line drawings were made with the assistance of a drawing tube. Magnification of basidiospores was drawn at 2000x; other cells were drawn at 800x.

Macroscopic descriptions

Fresh North American material of *I. lanuginosa*, *I. leptophylla* and *I. stellatospora* was collected by both authors and is located at WTU and UTC. Fresh material of *I. tahquamenonensis* has been studied by the first author (WTU). Color notes of gross morphological features and spore pigment were taken with the aid of several color references (Ridgway, 1912; Maerz & Paul, 1930; Munsell Soil Color Charts, 1954; Kornerup & Wanscher, 1967; Munsell Book of Color, 1976). Ridgway colors such as 'Mummy Brown' are capitalized and placed in quotation marks. Munsell colors such as yellowish brown (10YR 5/4) are in lower case and followed by the chart, value and chroma in parentheses. Kornerup & Wanscher colors such as (6F6) are merely indicated in parentheses. Maerz & Paul color references are also included in parentheses and used only in the description of *I. teraturgus*. Any other color designations are our own.

Descriptive statistics

Statistics of basidiospores, number of spore nodules (determined by counting number of nodules per spore that entered into view while turning the fine focus up and down), basidia, cheilocystidia and pleurocystidia include: the range of cell length by cell width where applicable with the lower and upper 5% of that range bound in parentheses for n cells measured from a single collection (specimen); \bar{x}_r , the range of means of cell length by width where applicable for n means from m collections; \bar{x}_m , the mean of the mean values \pm the standard deviation; quotient of basidiospore length by basidiospore width (Q), \bar{Q}_r , the range of means of Q , and \bar{Q}_m , the mean of Q mean values \pm the standard deviation, where applicable. Materials examined are deposited in herbaria identified by abbreviation according to Holmgren & al. (1990).

Phenetic analyses

Exemplar taxa of stirps Lanuginosa ss. Heim (1931) (*I. lanuginosa*, *I. leptophylla* and *I. stellatospora*), and a putative cryptic taxon later determined as *I. teraturgus* M. M. Moser), were included in the phenetic analyses. 425 collections were determined to species after microscopic examination followed by selection of 9–10 randomly selected OTUs (operational taxonomic units, cf. Sneath & Sokal, 1973). OTUs were randomly chosen by a geographic block design (with exception of *I. teraturgus*). Blocks were defined as the west coast of North America, the Rocky Mountains, eastern North America and Europe. European OTUs were included in the analysis because potential taxonomic differences would have nomenclatural consequences (see Tab. 1). Of the 425 collections, 187 were represented by *I. lanuginosa*, 104 by *I. leptophylla*, 68 by *I. stellatospora*, 9 by *I. tahquamenonensis*, 9 by *I. teraturgus*, 2 by *I. diminuta* and 1 by *I. sabuletorum*; the remaining collections represent other species.

Thirteen characters studied from fresh material and exsiccata were employed in the phenetic analyses (Tab. 2). Six qualitative and seven quantitative characters comprise the total 13 characters used. Secondary characters of pleurocystidia, absent from 10 of the 39 OTUs, were excluded to ensure uniformity throughout the data matrix (Tab. 1). 10 basidiospores, 10 basidia and 10 cheilocystidia were observed per OTU. The number sampled (10) has been shown to be generally sufficient, at least for basidiospores (Corner, 1947; Bas, 1977; Høiland, 1984). Of the qualitative characters, substrate was determined by collector information or by study of the material. Cystidial shape was scored according to Bas & al. (1988). For definitions of paracystidia and cauloparacystidia, see Kuyper (1986).

Tab. 1. – 37 OTUs used in the phenetic analysis. Herbaria are abbreviated according to Holmgren & al., 1990.

OTU	Data matrix	Accession no.	Geographic origin	Herbarium
	0000000001111 1234567890123			
stella01*	0000111101111	Stz. 4263	Washington, USA	WTU
stella02	0000111111111	ACAD 14308	Nova Scotia, Canada	ACAD
stella03	0000111111011	DAOM 186960	Quebec, Canada	DAOM
stella04	0000110011011	PBM 963	Washington, USA	WTU
stella05	0000111111111	Sm. 29499	Washington, USA	WTU
stella06	0000111111111	Grund 1811	Nova Scotia, Canada	ACAD
stella07	0000111011011	MICH 36280	New York, USA	MICH
stella08	0000111111111	Stangl 1027	Germany, Europe	M
stella09	2000111111111	Stangl 1018	Germany, Europe	M
stella10	0000111001011	TENN 13954	Tennessee, USA	TENN
lepto01 [¶]	2110110000010	ACAD 13520	Nova Scotia, Canada	M
lepto02	0101110001010	Stangl 1081	Austria, Europe	M
lepto03	2100110001110	UTC 163351	Utah, USA	UTC
lepto04	2101000001110	UTC 163355	Quebec, Canada	UTC
lepto05	0111110101110	C. Ardrey 3-26-78	Oregon, USA	WTU
lepto06	2100000001010	MICH 36296	Washington, USA	MICH
lepto07	0100110001110	HDT 12746	California, USA	SFSU
lepto08	2101010001110	LN 93.06.30-1	Washington, USA	WTU
lepto09	2100110001110	MTS 4410	Wyoming, USA	WTU
lepto10	0100110001110	Stangl 1078	Sweden, Europe	M
tera01 [¶]	1110110111011	DAOM 17429	Ontario, Canada	DAOM
tera02	1111111111011	Stangl 1030	Norway, Europe	M
tera03	1111110011011	Stz. 11470	Michigan, USA	WTU
tera04	1110110100001	Sm. 4040	Ontario, Canada	WTU
tera05	1100110010001	Stangl 1044	Sweden, Europe	M
tera06	1111110111111	DAOM 56914	Ontario, Canada	DAOM
tera07	1111110111111	DAOM 197814	Ontario, Canada	DAOM
tera08	1111110111011	MICH 36299	Minnesota, USA	MICH
tera09	2111110111111	Sm. 26307	Ontario, Canada	WTU
lanu01 [¶]	2000000011111	Stz. 2201	Oregon, USA	WTU
lanu02	2000000010101	DAOM 165900	NB, Canada	DAOM
lanu03	2000000010101	M. Gilliam 1127	Michigan, USA	MICH
lanu04	2000000110101	Largent 468	Idaho, USA	WTU
lanu05	2000000010101	DAOM 192128	BC, Canada	DAOM
lanu06	2000000110101	Stz. 20453	Washington, USA	WTU
lanu07	2000000010101	HDT 21717	California, USA	SFSU
lanu08	2000100110101	UTC 163357	Idaho, USA	UTC
lanu09	1000000110001	Stangl 1038	Germany, Europe	M
lanu10	0100000010111	Stangl 1046	Finland, Europe	M

* = *I. stellatospora*; [¶] = *I. leptophylla*; [¶] = *I. teraturgus*; [¶] = *I. lanuginosa*

Tab. 2. – 13 characters and character states used in the phenetic analysis. Quantitative character states were partitioned for character coding as explained in the text. The number of OTUs with a particular character state is shown in the four righthand columns. For example, for character no. 1 (substrate), nine *I. stellatospora* OTUs are recorded with character state 0, none with character state 1, and one with character state 2.

Character no.	Characters	Character states	No. OTUs with character state			
			<i>I. stellatospora</i>	<i>I. leptophylla</i>	<i>I. turgus</i>	<i>I. lanuginosa</i>
1	Substrate	0 = on soil 1 = in sphagnum 2 = on wood	0 ← 9 1 ← 0 2 ← 1	0 ← 4 1 ← 0 2 ← 6	0 ← 0 1 ← 8 2 ← 1	0 ← 1 1 ← 1 2 ← 8
2	Basidiospore length	0 = $\bar{x} < 9.75 \mu\text{m}$ 1 = $\bar{x} > 9.75 \mu\text{m}$	0 ← 10 1 ← 0	0 ← 0 1 ← 10	0 ← 0 1 ← 9	0 ← 9 1 ← 1
3	Basidiospore width	0 = $\bar{x} < 7.8 \mu\text{m}$ 1 = $\bar{x} > 7.8 \mu\text{m}$	0 ← 10 1 ← 0	0 ← 8 1 ← 2	0 ← 1 1 ← 8	0 ← 10 1 ← 0
4	Nodule number per spore	0 = $\bar{x} < 12.8$ 1 = $\bar{x} > 12.8$	0 ← 10 1 ← 0	0 ← 6 1 ← 4	0 ← 3 1 ← 6	0 ← 10 1 ← 0
5	Basidia length	0 = $\bar{x} < 27.3 \mu\text{m}$ 1 = $\bar{x} > 27.3 \mu\text{m}$	0 ← 0 1 ← 10	0 ← 3 1 ← 7	0 ← 0 1 ← 9	0 ← 9 1 ← 1
6	Basidia width	0 = $\bar{x} < 9.6 \mu\text{m}$ 1 = $\bar{x} > 9.6 \mu\text{m}$	0 ← 0 1 ← 10	0 ← 2 1 ← 8	0 ← 0 1 ← 9	0 ← 10 1 ← 0
7	Cheilocystidia length	0 = $\bar{x} < 52.5 \mu\text{m}$ 1 = $\bar{x} > 52.5 \mu\text{m}$	0 ← 1 1 ← 9	0 ← 10 1 ← 0	0 ← 8 1 ← 1	0 ← 10 1 ← 0
8	Cheilocystidia width	0 = $\bar{x} < 15.6 \mu\text{m}$ 1 = $\bar{x} > 15.6 \mu\text{m}$	0 ← 7 1 ← 3	0 ← 9 1 ← 1	0 ← 2 1 ← 7	0 ← 6 1 ← 4
9	Cheilocystidia wall thickness	0 = thin-walled 1 = slightly thickened (0.5 < 1.5 μm)	0 ← 8 1 ← 2	0 ← 10 1 ← 0	0 ← 1 1 ← 8	0 ← 0 1 ← 10
10	Cheilocystidia apical morphology	0 = evenly rounded, none subcapitate 1 = subcapitate present	0 ← 0 1 ← 10	0 ← 1 1 ← 9	0 ← 2 1 ← 7	0 ← 9 1 ← 1
11	Cheilocystidia apices crystalliferous	0 = none 1 = present	0 ← 4 1 ← 6	0 ← 3 1 ← 7	0 ← 6 1 ← 3	0 ← 1 1 ← 9
12	Cheilocystidia shape	0 = majority obovate to ovate 1 = majority utriform, fusiform or oblong	0 ← 0 1 ← 10	0 ← 0 1 ← 10	0 ← 2 1 ← 7	0 ← 8 1 ← 2
13	Pleurocystidia	0 = absent 1 = present	0 ← 0 1 ← 10	0 ← 10 1 ← 1	0 ← 0 1 ← 10	0 ← 0 1 ← 10

The quantitative characters were partitioned by frequency distributions of mean values of the 39 OTUs and examination of the resultant graphs for abrupt troughs (Abbot & al., 1985). If abrupt troughs were present (as was the case in 2 of 7 characters), then character states were partitioned at the midpoint of the bottom of the trough. If abrupt troughs did not occur (as was the case in 5 of 7 characters), then character states were partitioned by dividing the range of the data in two. The data matrix included the first two columns of Tab. 1. For the number of OTUs with a particular character state, see Tab. 2. UPGMA (Sneath & Sokal, 1973) and Neighbor-Joining (Saitou & Nei, 1987) were used to analyze the data matrix in PAUP 4.0* (Swofford, 1999). The format datatype of the data matrix was set to 'standard' and symbols to '012'. The simple matching coefficient is invoked when using UPGMA in PAUP 4.0*.

Gross morphological characters were not sampled due to the overall similarity of the material in dried condition. Also, many samples lacked descriptions of their fresh states and several were damaged.

Results

Phenetic Cluster Analysis

The objective of the analysis was to determine whether or not the combination of characters used in the data matrix could resolve any separation among the OTUs of the *I. lanuginosa* group into discrete clusters that could be referred to as individual taxa. UPGMA and Neighbor-Joining were used to analyze the data matrix. Both the UPGMA rectangular cladogram (Fig. 1) and the Neighbor-Joining unrooted cladogram (Fig. 2) indicate four main clusters that support the separation of four taxa (*I. stellatospora*, *I. teraturgus*, *I. leptophylla* and *I. lanuginosa*). Only in one instance (the UPGMA analysis) does a single OTU cluster outside its hypothesized species cluster, i.e., *I. lepto05* (*I. leptophylla*) nests within the *I. teraturgus* cluster. However, this relationship is not supported by the Neighbor-Joining analysis. UPGMA supports a greater similarity between *I. stellatospora* and *I. teraturgus*, whereas Neighbor-Joining supports a greater similarity between *I. leptophylla* and *I. teraturgus*. Thus, the relationship of the four taxa to each other remains unclear. The monophyly of *Stirps Lanuginosa* ss. Heim or ss. Singer has yet to be established.

Among the 13 characters used in the phenetic analysis (Tab. 2), a number possess character states that appear relatively constant for a species cluster, i.e., the number of OTUs per species that share a

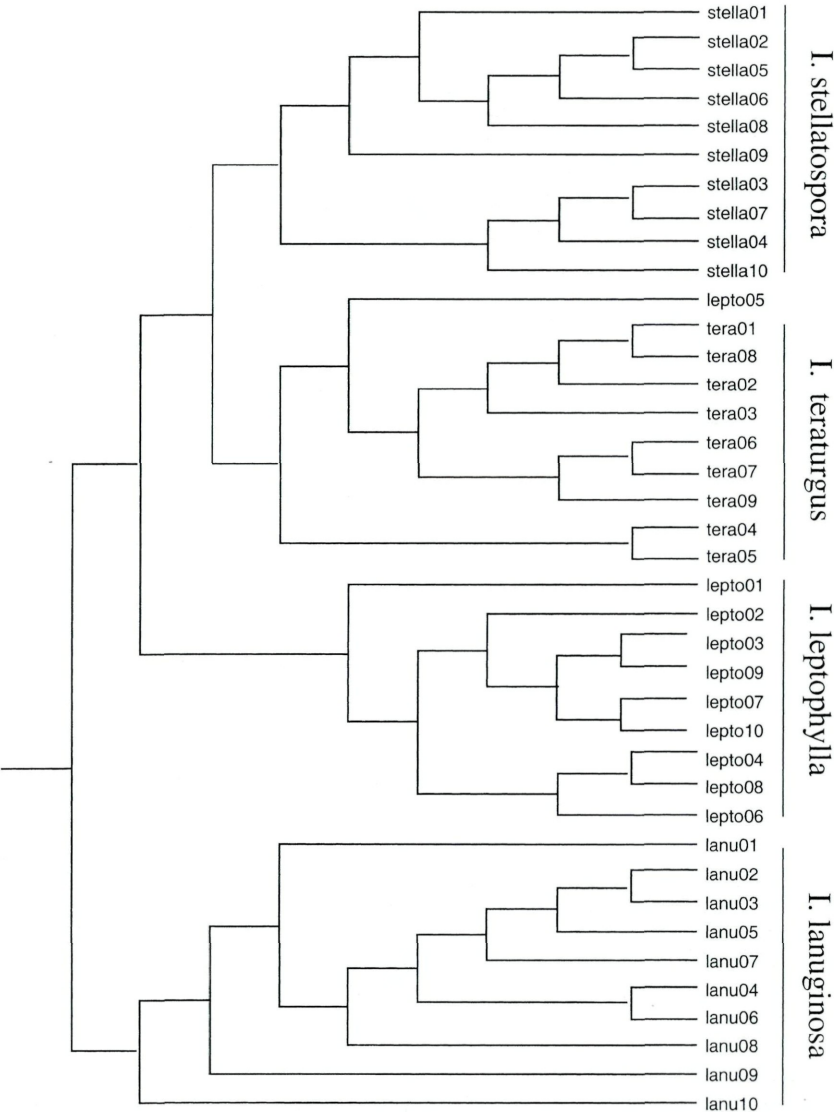


Fig. 1. - UPGMA rectangular cladogram (phenogram) generated by PAUP 4.0* showing relationship of 39 OTUs representing four different putative morphological taxa within the *I. lanuginosa* group based largely on microscopic data. Similarity increases from left to right. Four main clusters are recognized and referred to as species. The position of lepto05 is not supported in the Neighbor-Joining analysis (lanu = *I. lanuginosa*; lepto = *I. leptophylla*; tera = *I. teraturgus*, stella = *I. stellatospora*).

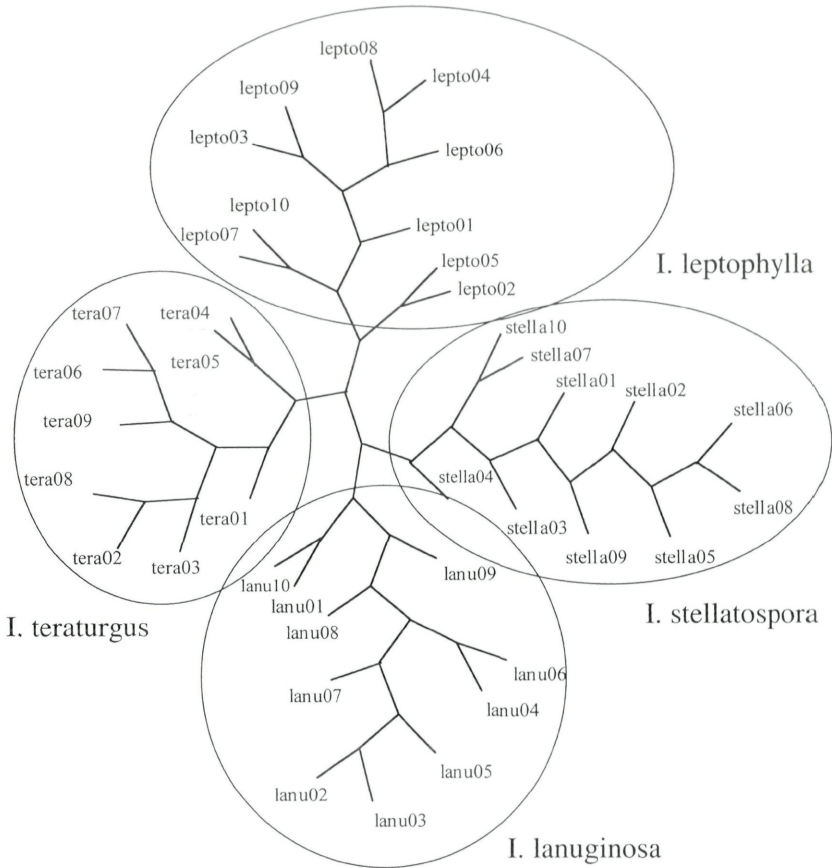


Fig. 2. – Neighbor-Joining unrooted cladogram (phenogram) generated by PAUP 4.0* showing relationship of 39 OTUs representing four different putative morphological taxa within the *I. lanuginosa* group based largely on microscopic data. The network is unrooted. Four main clusters are recognized and referred to as species. The position of lepto05 falls within the *I. leptophylla* cluster in contrast to the UPGMA phenogram of Fig. 1. (lanu = *I. lanuginosa*; lepto = *I. leptophylla*; tera = *I. teraturgus*, stella = *I. stellatospora*).

particular character state is >70%. Characters that are useful to distinguish members of the *I. lanuginosa* group include substrate, basidiospore length and width, basidia length and width, cheilocystidia length, cheilocystidia wall thickness, cheilocystidia apical morphology, cheilocystidia shape and the presence of pleurocystidia. In the dichotomous key below, we emphasize pleurocystidia length. Generally, characters considered too variable to be reliable species specific indicators include nodule number per

basidiospore, cheilocystidia width and crystalliferous cheilocystidia apices.

Artificial key to nodulose-spored species of *Inocybe* in North America with scaly pileus and scaly to woolly-fibrillose stipe

1. Basidiomes very small, pileus 7–13 mm diam, stipe 9–17 × 1–2 mm; center of pileus squarrose, fibrillose towards margin; stipe pallid above, grayish brown and subsquamulose towards the base; on soil, eastern North America. 1. *I. diminuta*
1. Basidiomes larger, pileus 10–40 mm diam, stipe 2–6 (10) mm diam 2
2. Pileus pallid ochraceous salmon; on soil in xerophytic forests of the Lesser Antilles.
. *I. paralanuginosa* (Pegler, 1983; not treated here)
2. Pileus brown, dark brown to dark purplish-fuscous; on various substrates, under conifers or mixed hardwoods. 3
3. Stipe fibrillose to coarsely-fibrillose; pileus fibrillose-tomentose to squamulose on the disc; fibrillose towards margin; lamellae pallid for long durations *I. subcarpta* sensu lato (*I. boltonii* R. Heim, 1931; *I. subcarpta* Kühner & Boursier, 1932; *I. subcarpta* sensu Stangl, 1989; not treated here)
3. Stipe squarrose, squamulose, floccose to woolly-fibrillose; pileus squarrose to squamulose on the disc; squamulose towards margin; lamellae soon brown or olivaceous 4
4. Basidiomes dark purplish-fuscous; lamellae purplish-vinaceous; on soil, eastern North America in mixed hardwood stands
. 2. *I. tahquamenonensis*
4. Basidiomes brown to dark brown; lamellae pallid, yellow, brown or olivaceous; on soil, wood or among *Sphagnum* under conifers 5
5. Young lamellae yellow, olivaceous with age; basidiospores at times cruciate, among *Sphagnum*; known only from Finland, Norway and Sweden.
. *I. relicina* (Moser, 1978b; Stangl, 1989; not treated here)
5. Young lamellae pallid to very pale brown, yellowish brown with age; basidiospores nodulose with an angular to (sub)elliptic outline, not cruciate, geographic distribution broad 6
6. Pleurocystidia absent. 3. *I. leptophylla*
6. Pleurocystidia present 7

7. On rotten wood; pleurocystidia obovate to ovate, short, 30–45 μm long; center of pileus hispid–squamose 4. *I. lanuginosa*
7. On soil (or occasionally on rotten wood) or in *Sphagnum*; pleurocystidia elongate or utriform, 55–80 μm long; center of pileus squarrose to squamulose 8
8. On soil (occasionally on rotten wood); basidiospores 7.5–10 \times 6–7.5 μm , distinctly nodulose with a subelliptic to subangular outline (similar to *I. lanuginosa*), 8–14 nodules 5 *I. stellatospora*
8. Among *Sphagnum*; basidiospores 10–12.5 \times 7.5–10 μm , coarsely-nodulose with an elliptic outline (similar to *I. leptophylla*), 11–20 nodules 6. *I. teraturgus*

Taxonomy

1. *Inocybe diminuta* Peck, Bull. N.Y. St. Mus. 105: 23. 1906. – Fig. 3.

Pileus 7–13 mm diam, thin, hemispheric becoming convex or nearly plane, squamose with hairy, erect or squarrose scales in the center, fibrillose on the margin, grayish brown. – Lamellae subdistant, broadly sinuate, adnexed, ventricose, at first whitish, then brownish or rusty brown. – Stipe 9–17 \times 2 mm diam, cylindric,

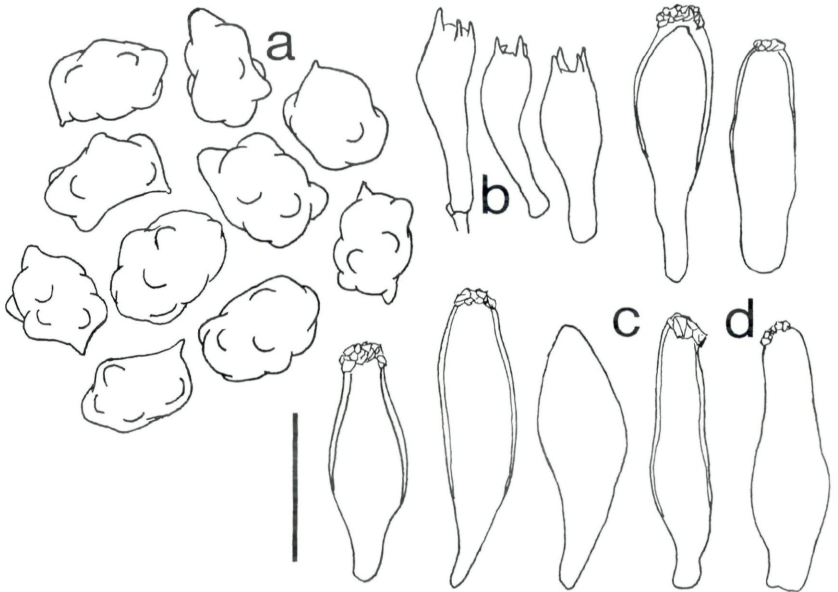


Fig. 3. – *Inocybe diminuta* (Peck; Holotype). – a. Basidiospores. – b. Basidia. – c. Six pleurocystidia. – d. One cheilocystidium. – Scale bar: a = 10 μm ; b–d = 25 μm .

short, firm, solid, silky fibrillose, whitish in the upper part, grayish brown and subsquamulose towards the base.

Basidiospores (7.5–)8–10(–10.5) \times 6–7(–7.5) μm [\bar{x} = 8.8 \pm 0.77 \times 6.4 \pm 0.46 μm , Q_r = 1.14–1.62, Q = 1.37 \pm 0.12, n = 32 spores], nodulose with (sub)angular to subelliptic outline, nodules small to moderate, not distinctly nodulose as in *I. lanuginosa*, 'Ochraceous-Buff'. – Basidia 25–32 \times 9–12 μm , 4-sterigmate, clavate, hyaline. – Pleurocystidia 38–63 \times 14–22 μm , moderately frequent, thin- to thick-walled apically, walls up to 2.0 μm thick, hyaline, (narrowly) utriform, subcylindric to fusiform, apices crystalliferous, necks not well-developed at times, with a basal pedicel. – Cheilocystidia similar to pleurocystidia. – Caulocystidia not observed. – Lamellar trama regular, yellowish brown in mass to hyaline, central hyphae inflated, up to 17 μm diam. – Pileipellis on the disc composed of fascicles of trichodermial elements, thin- to (slightly) thick-walled (–1.0 μm); hyphae cylindric, up to 17 μm diam, incrustated yellowish brown or ochraceous-tawny; subpellis of regularly arranged hyphae otherwise similar to the trichodermial elements; tramal hyphae much lighter in color, regular, cylindric to inflated. – Stipe vestiture at the base composed of hyphae that are thin-walled, yellowish brown, irregular, faintly incrustated or with smooth appearance, up to 13 μm diam, tramal hyphae regular, compact, refractive hyphae present. – Clamps frequent.

Habit, habitat and distribution. – On soil. New York and Michigan, July and August.

Material examined. – USA. MICHIGAN: Ann Arbor, leg. L. V. Baxter, 21 July 1920, MICH 36269 (MICH). NEW YORK: Wading River, August (Isotype; WTU).

The macroscopic description is taken from Peck's protologue. The basidiomes (Isotype; WTU) are very small with a pileus barely 1 cm in diameter and with a narrow stipe about 1–2 mm thick and were recorded from bare compact soil. Peck considered the species to belong to section *Laceri* rather than *Squarrosi*, two Friesian delimited groups that differed by gross morphological details. However, the microscopic characters in combination with brownish colors and squarrose disc could indicate an affinity to the *I. lanuginosa* group. The Michigan collection agrees very well with the isotype. Kauffman (1924) excluded *I. diminuta* from his monograph in the North American Flora. Boursier & Kühner (1928) were unsure of the placement of this taxon. We include the description here with the hope that it may be recollected and its relationship to the *I. lanuginosa* group better ascertained.

2. *I. tahquamenonensis* Stuntz, Pap. Mich. Acad. Sci. Arts Lett. 39: 78. 1954. – Fig. 4.

Pileus 17–24 mm diam, obtusely conical to campanulate, margin decurved to upturned, surface dry, squarrose especially on the disc and squamose towards the margin, or squarrose throughout, dark vinaceous-brown or purple-fuscous (no comparable Methuen color), context pale vinaceous (10D5), odor none, taste not remarkable. – Lamellae close, adnate, up to 3 tiers of lamellulae, dark vinaceous-brown to dark brown (8F7), edges somewhat darker and fimbriate. – Stipe 30 mm × 4.5 mm at the apex, terete, even, straight or somewhat flexuous, surface dry, subsquarrose the entire length, nowhere visibly pruinose, colored like the pileus, context dull vinaceous-brown, solid, firm, cortina fugacious.

Basidiospores (5.5–)6–7.5(–8) × 4.5–6(–6.5) μm [$\bar{x}_r = 6.7\text{--}7 \times 5.2\text{--}5.6 \mu\text{m}$, $\bar{x}_m = 6.8 \pm 0.6 \times 5.4 \pm 0.5 \mu\text{m}$, $Q = (1.08\text{--})1.09\text{--}1.50$ (–1.56), $\bar{Q}_r = 1.25\text{--}1.30$, $\bar{Q}_m = 1.28 \pm 0.12$, $n = 10\text{--}30$ spores per 3 collections], nodulose with 5–9 subconic nodules, at times cruciate, a few nodules occasionally blunt or truncate and/or notched, apiculus small, ‘Ochraceous-Buff’, brown in deposit. – Basidia 26–39 × 8–9 (13) μm , 4-sterigmate, clavate to subcylindric, light reddish brown or testaceous in mass, (sub)hyaline when isolated. – Pleurocystidia frequent, (50–) 58–74 (–95) × (13–) 14–20 (–25) μm , fusiform to subcylindric, apices obtuse to rounded and lacking crystals, at times subcapitate, usually with a slender basal pedicel, thin- to slightly thick-walled, walls hyaline to rose or pale testaceous, smooth, at times faintly incrustated with pigment. – Cheilocystidia abundant, variable, similar to pleurocystidia but also saccate, cylindric, clavate or at times globose to vesiculose forming short chains of concatenated elements, walls pale rose or testaceous, often smooth but occasionally faintly incrustated with pigment, up to 20 μm diam. – Caulocystidioid elements infrequent, thin-walled, subcylindric at the (extreme) apex, rose in KOH, stipe hyphae cylindric, up to 15 μm diam, smooth or incrustated with pigment, bright reddish-vinaceous to vinaceous in KOH. – Lamellar trama regular, compact, pale rose to pale apricot-tawny in mass, hyphae cylindric to inflated, up to 18 (25) μm diam, subhymenial elements narrow and cylindric, walls smooth, refractive hyphae present. – Pileipellis composed of fascicles of trichodermial elements, thin- to slightly thick-walled, with ‘Vinaceous-Tawny’ or testaceous membranal pigment, cells inflated to cylindric, up to 27 μm diam, occasionally elliptic with frequent septa, cells also incrustated with pigment; subpellis not readily differentiated, subtended by the largely hyaline tramal zone; inter-hyphal yellow pigment deposits present in pileal trama, observed in dried tissue rehydrated in 3% KOH. Clamps frequent.

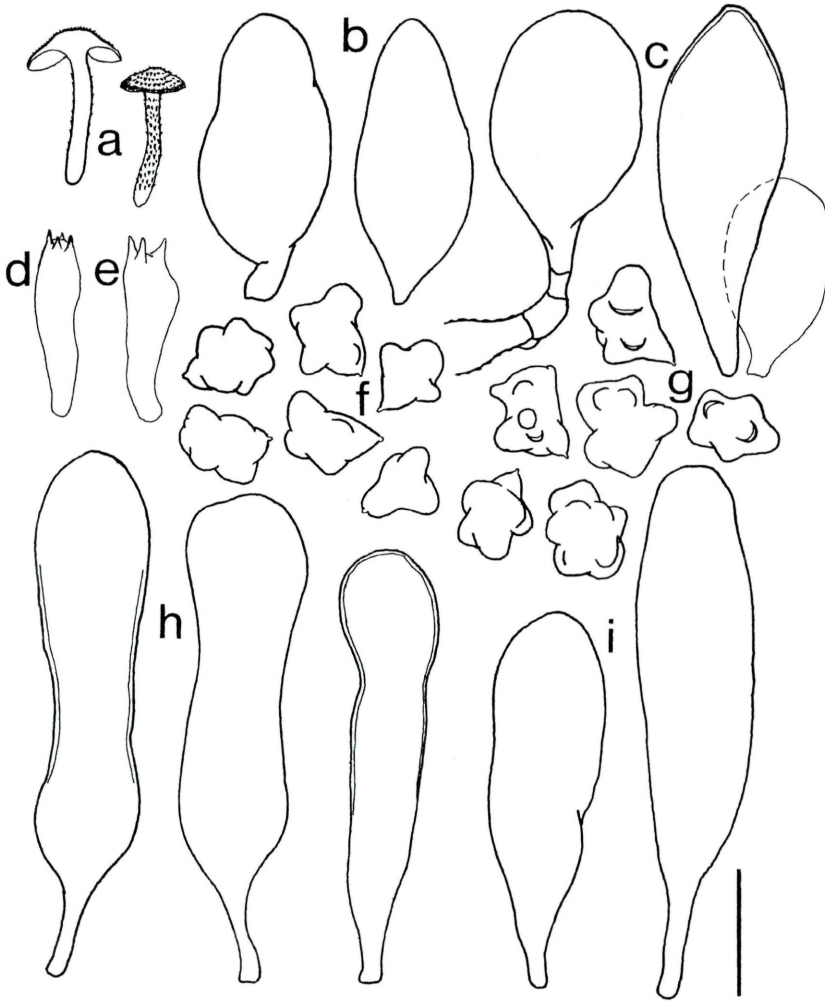


Fig. 4. *Inocybe tahquamenonensis*. – a. Basidiomes (PBM 1142). – b. Three cheilocystidia (Stz. 5555; Holotype). – c. Two cheilocystidia (*I. stellatospora* 'dark'; holotype). – d. Basidium (Stz. 5555). – e. Basidium (*I. stellatospora* 'dark'). – f. Six basidiospores (Stz. 5555). – g. Six basidiospores (*I. stellatospora* 'dark'). – h. Three pleurocystidia (Stz. 5555). – i. Two pleurocystidia (*I. stellatospora* 'dark'). – Scale bar: a = 3 cm; b–e, h, i = 25 μ m; f, g = 10 μ m.

Habit, habitat and distribution. – Single to scattered in small groups on the ground under mixed hardwoods in eastern North American deciduous forests. The species occurs in the Great Lakes region, the White Mountains and south through the deciduous forests of New England into the Appalachians reaching elevations of 1,500 m. Endemism is rare among temperate species of *Inocybe*

(Kuyper 1986), but *I. tahquamenonensis* has yet to be recorded outside North America and, furthermore, is restricted to eastern North American deciduous forests. *Inocybe tahquamenonensis* appears from July through September.

Material Examined. – USA. CONNECTICUT: Westport, 10 July 1977, leg. G. Lincoff, NY s.n., (NY). GEORGIA: Testatnee-Hogpen Gap, no date, leg. G. Walker, GRW 399 (WTU). MICHIGAN: Upper Tahquamenon Falls, on ground under mixed hardwoods, 6 Sept 1949, Stz. 5555 (Holotype; WTU); Douglas Lake, UMBS, 18 Aug 1965, leg. A. H. Smith, KHD 560 (KHD). NEW HAMPSHIRE: Grafton Co., Mt. Moosilauke, on ground under *Fagus*, *Betula* and *Acer* in beech-maple woods, 2 Sept 1998, leg. P. B. Matheny, PBM 1142 (WTU). NEW YORK: Lewis Co., Croghan, on ground in woods, Sept, (*Agaricus stellatosporus*, ‘3 dark carpophores’; Holotype; non Lectotype; NYS). PENNSYLVANIA: east of Rector, Laurel Hill, Forbes Forest, 6 Sept 1947, leg. L. K. Henry, NY 14267 (NY). TENNESSEE: Cades Cove, Great Smoky Mtns NP, 17 Sept 1985, DED 3459 (SFSU). VIRGINIA: Mountain Lake, 1200-1400 m elev, in moist oak-chestnut and hemlock woods and rhododendron thickets, 8-14 July 1909, leg. W. A. Murrill, no. 79 (NY).

The dark fuscous-purple or dark vinaceous-brown colors in combination with the squarrose pileus and (sub)squarrose stipe characterize *I. tahquamenonensis* in the field. This combination of color and vestiture is unusual for *Inocybe*. Overmature specimens might be mistaken for the dark brown to sepia colored members of the *I. lanuginosa* group. Microscopically, *I. tahquamenonensis* is noteworthy because of the cheilocystidia that may be composed of concatenated chains of cylindrical to swollen cells that are rose or vinaceous tinged, angular to cruciate basidiospores with occasional blunt to wedge-shaped nodules and yellow interhyphal pigment deposits in exsiccata. Because of the combination of these unusual characters, we do not consider *I. tahquamenonensis* as a member of *Stirps Lanuginosa*.

Stuntz (1954) described *I. tahquamenonensis* after examination of a ‘...fragment of the type of *I. stellatospora* among Atkinson’s collections at Cornell University...’. Because no purple colors and vinaceous pigments were noted, he concluded the two species to be distinct. However, Peck’s holotype (NYS) of *I. stellatospora* is heterogeneous and consists of two species: (1) a single ‘light’ specimen that corresponds to *I. longicystis* Atk. and (2) three ‘dark’ specimens that match *I. tahquamenonensis*. When tissues of the ‘dark’ specimens are mounted in weak alkali solutions, a pale vinaceous pigment dissolves in the solution, characteristic of the holotype of *I. tahquamenonensis* (WTU). The similarity in microscopic characters shared by *I. stellatospora* ‘dark’ and *I. tahquamenonensis* indicate they are conspecific (Fig. 4). It would appear that *I. stellatospora* would have nomenclatural priority over *I. tahquamenonensis* if not for the protologue of the former, which

fails to mention the dark purple or vinaceous shades so characteristic of *I. tahquamenonensis*. Furthermore, a subsequent collection of Peck's at NYS that is labeled *Agaricus stellatosporus* is conspecific with *I. longicystis*. Lastly, a small painting of the holotype of *A. stellatosporus* (NYS) depicts a fungus without any purple or dark vinaceous-brown colors. A smaller separate sketch of basidiospores does represent those of *I. tahquamenonensis*. However, in accordance with ICBN Art. 9.12 (Greuter & al., 2000), the 'light' specimens of Peck's holotype of *I. stellatospora* must serve as the lectotype. *I. tahquamenonensis* is the valid name for the 'dark' specimens.

Inocybe relicina (Fr.) Ricken, known only from the countries of Fennoscandia, shares similar spore characters with *I. tahquamenonensis* but has yellow pigmented lamellae when young. Moser (1978b) provides a complete description of *I. relicina*, the type species of *Inocybe*.

The yellow interhyphal pigment deposits in *I. tahquamenonensis* that are located in the pileal trama of exsiccata have not been reported among other species of *Inocybe*. Deposits become more conspicuous as exsiccata increase in age. The deposits are scarcely seen in recently collected material.

Good color photographs of *I. tahquamenonensis* can be found in Phillips (1991) and in Bessette & al. (1997).

3. *Inocybe leptophylla* Atk., Am. J. Bot. 5: 212. 1918. – Figs. 5, 10.

= *Inocybe casimiri* Velen., České Houby: 369. 1920.

≡ *Inocybe lanuginosa* var. *casimiri* (Velen.) R. Heim, Genre *Inocybe*: 365. 1931.

≡ *Astrosporina casimiri* (Velen.) Horak, Arctic Alpine Mycology II: 223. 1987.

= *Inocybe leptophylla* var. *cystomarginata* Atk., Am. J. Bot. 5: 213. 1918.

Pileus up to 30 mm diam, obtusely conic to plano-convex, without an umbo, margin slightly incurved when very young, to decurved, arched slightly with age, surface dry, densely hispid-squarrose on the disc and towards the margin or recurvately-squamulose towards the margin, coarsely-fibrillose on decurved portion of the margin, not rimose, dark brown (10YR 3/3) or 'Mummy Brown', to very dark brown, context white, unchanging where bruised, thick, firm, up to 5 mm thick, odor not remarkable, taste same as odor or slightly acidulous. – Lamellae close, narrowly adnate to sinuate or uncinata, rounded towards the stipe, with several tiers of lamellulae, light brown with flesh tone (7.5YR 6/4) or 'Avellaneous' when young, to pale brown and brown (10YR 6/3–5/3) or 'Cinnamon-Brown' to 'Snuff Brown' with age, edges pallid, fimbriate, becoming ventricose, up to 4 mm diam. – Stipe

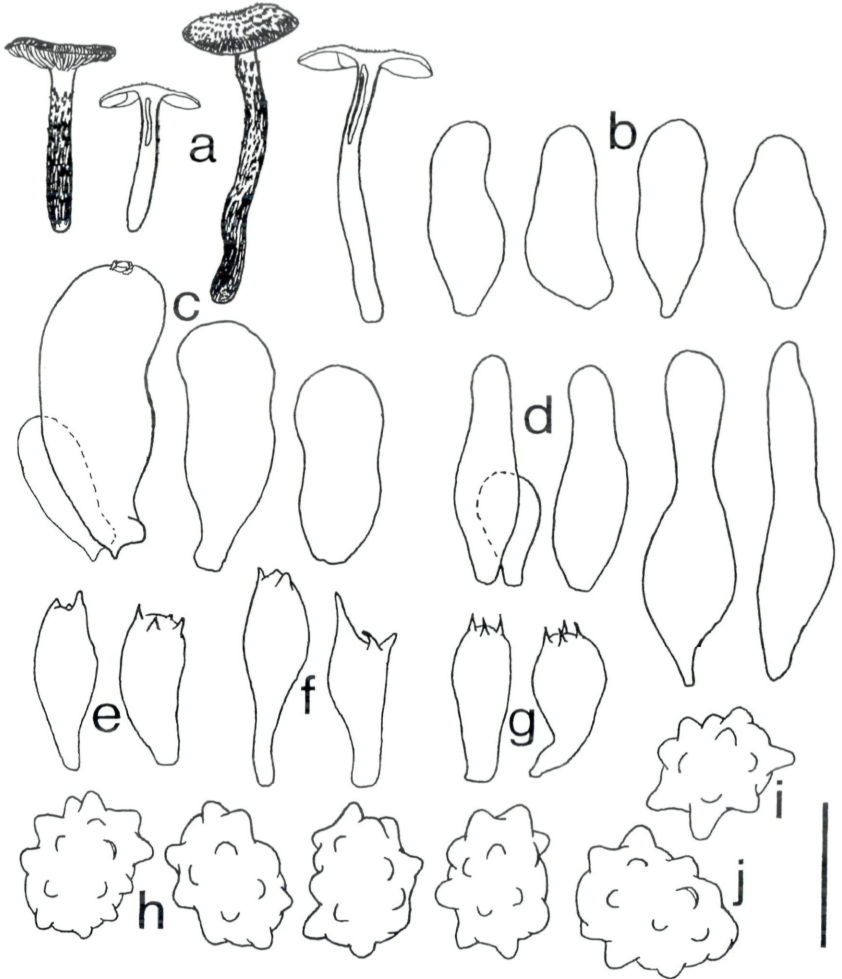


Fig. 5. *Inocybe leptophylla*. – a. Basidiomes, *I. leptophylla* (PBM 1550). – b. Four cheilocystidia, *I. leptophylla* (Atk. 13372; Holotype). – c. Three cheilocystidia, one paracystidium, *I. leptophylla* (PBM 1616). – d. Four cheilocystidia, var. *cystomarginata* (Atk. 24164; Holotype). – e. Two basidia, *I. leptophylla* (Atk. 13372). – f. Two basidia, var. *cystomarginata* (Atk. 24164). – g. Two basidia, *I. leptophylla* (PBM 1616). – h. Four basidiospores, *I. leptophylla* (Atk. 13372). – i. One basidiospore, var. *cystomarginata* (Atk. 24164). – j. One basidiospore, *I. leptophylla* (PBM 1616). – Scale bar: a = 3 cm; b–g = 25 μ m; h–j = 10 μ m.

20–55 mm \times 3–6 mm diam, terete, even or tapering somewhat towards the base, cortina fugacious, apex white pruinose, pallid, below appressed-(sub)squamulose to floccose or wooly-fibrillose, colored like the pileus, vestiture occasionally separating to reveal

pallid flesh beneath, context solid, firm, pallid, cortex brownish below.

Basidiospores (8–)9.0–12.0(–12.5) × (6–) 7–9 (–9.5) μm [$\bar{x}_r = 10.0\text{--}11.1 \times 7.2\text{--}8.4 \mu\text{m}$, $\bar{x}_m = 10.5 \pm 0.8 \times 7.7 \pm 0.7 \mu\text{m}$, $Q = (1.11\text{--})1.22\text{--}1.53(–1.69)$, $\bar{Q}_r = 1.30\text{--}1.44$, $\bar{Q}_m = 1.37 \pm 0.11$, $n = 10$ spores per 10 collections], nodulose, distinctly elliptic in outline, with (9–) 10–16 (–18) nodules [$\bar{x}_m = 12.6 \pm 1.92$ nodules per spore], ‘Ochraceous-Buff’, brown in deposit. – Basidia (22–) 24–35 (–38) μm [$\bar{x}_r = 25.6\text{--}33.0 \times 9.5\text{--}11.4$, $\bar{x}_m = 29.3 \pm 3.7 \times 10.3 \pm 1.0 \mu\text{m}$], 4-sterigmate, clavate, hyaline to pale ochraceous. – Pleurocystidia absent. – Cheilocystidia abundant, lamellar edge sterile, (19–) 29–53 (–61) μm [$\bar{x}_r = 31.4\text{--}43.9 \times 11.9\text{--}16.3 \mu\text{m}$, $\bar{x}_m = 39.2 \pm 7.1 \times 13.5 \pm 2.3 \mu\text{m}$, $n = 10$ cystidia per 10 collections], utriform to cylindrical, sublageniform or fusiform, apices well-rounded to subcapitate, occasionally crystalliferous but usually bare, thin-walled, hyaline; paracystidia smaller, clavate to vesiculose, thin-walled, hyaline. – Caulocystidia restricted to the (extreme) apex, similar to cheilocystidia in shape but also (sub)cylindrical, intermixed with cauloparacystidia, hyphae of the stipe vestiture thin- to slightly thick-walled, brown, incrusting pigments faint to not evident. – Lamellar trama regular, compact, hyphae cylindrical to inflated, up to 17 μm diam. – Pileipellis a trichoderm of subcylindrical to fusiform hyphae, faintly incrustated, brown, with walls up to 1.5 μm thick, end cells undifferentiated; tramal hyphae parallel to somewhat interwoven, hyaline to pale yellow. – Clamps frequent.

Habit, habitat and distribution. – Solitary to scattered or in small groups on rotten coniferous stumps and less often on the ground under conifers (*Picea*, *Abies*, *Pseudotsuga*, *Pinus*), rarely in *Sphagnum* bogs. *Inocybe leptophylla* appears to be the most widely distributed member of the *I. lanuginosa* group extending from the 60th parallel south into the North American Cascade and Rocky Mountain ranges. Its distribution in North America appears disjunct by virtue of two Veracruz collections in Mexico that are recorded in pine-oak forests (*Pinus* and *Quercus*). Samples from the southern Rocky Mountains are few, but we would predict its occurrence at least into northwest New Mexico and likely Arizona thereby indicating a western cordilleran distribution. *Inocybe leptophylla* is chiefly montane extending into subalpine areas in western North America but also occurs in the maritime provinces of New Brunswick and Nova Scotia, the Great Lakes region and the Adirondacks. Within Washington state *I. leptophylla* is encountered on the leeward slopes of the Cascades and the Olympic Mountain ranges. It is rare in the coastal areas of the Pacific Northwest and absent from the Appalachians in the east. Horak (1987) states that

I. leptophylla (as *Astrosporina casimiri* (Velen.) Horak) is rare in arcto-alpine habitats but verified its occurrence on the west coast of Greenland. The species is recorded from Asia (Kobayashi, 1993) and appears to have a circumboreal distribution.

Inocybe leptophylla, like *I. lanuginosa*, predominantly fruits in the summer months, July through September. It occurs less often in spring, March–June, and as late as November. However, no members of the *I. lanuginosa* group are snow-bank fungi.

Material examined. – AUSTRIA. TIROL: Kramsach, in damp *Picea* forest, on the ground, 31 July 1979, leg. J. Stangl, St. 1081 (M); near Götzens, on wet soil under *Picea* and *Alnus*, 30 July 1950, leg. M. Moser, 25099 (TENN). CANADA. ALBERTA: Brown-Lowery Prov Park(sic) (Natural Area), on base of rotten stump of *Picea glauca*, 8 April 1974, leg. R. M. Danielson, 145654 (DAOM). BRITISH COLUMBIA: Takla Lake, Takla Landing, on moss covered *Picea* stump, 17 July 1940, leg. T. McCabe, 114006 (DAOM); St. Elmo, 24 July 1932, leg. J. E. Davidson, 36308 (MICH). MANITOBA: Winnipeg, Victoria Beach, 19 Sept 1928, leg. G. R. Bisby, 25218 (DAOM); Winnipeg, Victoria Beach, 7 Sept 1927, leg. G. R. Bisby, 157220 (DAOM); Winnipeg, Victoria Beach, 8 Aug 1928, leg. G. R. Bisby, 173367 (DAOM). NEW BRUNSWICK: Kouchibouguac NP, Black River near HWY 117, scattered on mossy sides of stumps & logs, 23 Sept 1977, leg. S. A. Redhead, 166066 (DAOM). NORTHWEST TERRITORIES: Fort Smith, on the ground, 8 Aug 1950, 25857 (DAOM). NOVA SCOTIA: West Gaspereaux, in conifers, 21 July 1980, leg. K. A. Harrison, 13520 (ACAD part; WTU part; Colchester Co., Upper Brookside, on rotten coniferous wood, 1 July 1931, leg. A. H. Smith, 36282 (MICH); Colchester Co., Upper Brookside, on old wood, 27 July 1931, leg. A. H. Smith, 36286 (MICH). ONTARIO: Lake Timagami, Ko-Ko-Ko Bay, on moist ground, 11 Sept 1936, leg. R. F. Cain, 80433 (DAOM); Lake Timagami, Bear Is, 4 Sept 1936, leg. H. A. Jackson, 36293 (MICH). QUÉBEC: L'Islet Co., St. Aubert, Adrien Morin's woods, in low damp woods, mossy ground, 1 Aug 1946, leg. H. A. C. Jackson, 87166 (DAOM); MSA Foray, on wood, BK 2-Aug-97-1, UTC163355 (UTC). FINLAND. Koillismaa, Salla, Naruska, Sätsivaara N., G. 27-E 74643:6024, *Pinus sylvestris* forest, 16 Aug 1993, leg. H. Väre, 225191 (DAOM); Pohjois-Savo, Kuopio, Neulaniemi, Neulalahi (?), *Picea-Abies* forest, 14 Aug 1979, leg. J. Vauras, 515 / St. 1084 (M). GERMANY. BAYERN: Ammersee region, Riederwald, MTB 7932, in *Picea* forest, 4 Sept 1983, leg. Grünert, St. 1082 (M); München, in low-lying bog (Flachmoor), 6 July 1974, leg. A. Einhellinger, St. 1083 (M). BERLIN: among thickets in a park under *Alnus* and *Quercus*, leg. E. Gerhardt, early June, St. 1079/EG 160a (M). MEXICO. VERACRUZ: El Paraje, caminoa, Rancho Quemado, Huayarocotla, in woods of *Quercus* and *Pinus*, 1950 msnm, leg. R. Hernández & R. C. Trigos, 23 Oct 1970, 7542 (MEXU); entre Los Mangos & J. D. Covarrubias, *Quercus* forest, 300 msnm, leg. J. Trappe, 12 July 1972, 9168 (MEXU). NORWAY. Telemark, Bamble, Gjoemle, on black soil under *Corylus*, *Fraxinus* but also *Pinus* and near *Picea*, leg. Ö. Weholt, 9 July 1983, St. 1076 / OW I17/83 (atypical) (M); Sör-Trøndelag, Trondheim, Byneset, Onsøy, under conifers, *Picea*, *Virtellus myrtilinus*, leg. Ö. Weholt, 18 July 1982, St. 1077 / OW I12/82 (M). SWEDEN. Tönnersa, edge of *Pinus* forest, in a moist gully, gregarious and clustered on bare sandy soil, leg. E. Ludwig, 3 July 1980, St. 1078/EL 605a (many spores albinistic) (M). SWITZERLAND. Lavin, Engadine, under *Picea*, 17 Sept 1975, leg. R. L. Shaffer, 36322 (MICH). USA. CALIFORNIA: Lassen Volcanic National Park, Reflection Lake, in humus under *Alnus*, 1900 m elev, 24 June 1965, leg. H. D. Thiers, HDT 12746 (SFSU). COLORADO: Clear Creek Co., Chicago Forks Picnic Area, Rt. 103, under *Populus*, *Pinus* and *Picea*, 10 Aug 1997, leg. J. Sommer, VTMH 4377 (VPI); Jones Pass Road,

1 mi from Climax bldgs, on wood, 28 Aug 1970, leg. Chapman, 2835 (KHD); Chicago Forks, under *Picea* and *Populus*, 22 Aug 1974, leg. A. H. Smith, 5187 / Sm. 85076 (KHD); Gilpin Co., Perigo, on moss mixed with wood, 27 Aug 1970, leg. Chapman, 2816 (KHD); in mts NW of Apex, in moss, 21 Aug 1997, leg. R. L. & R. D. Brace, 19878 / 97-63 (KHD); east of Basalt, Frying Pan Creek, on dead *Picea* stump, 26 July 1978, leg. H. D. Thiers, HDT 38766 (SFSU); Dolland, 3000 m elev, 17 Sept 1920, 36277 (MICH); Leal, on decayed debris under *Pinus*, 18 Aug 1917, leg. C. H. Kauffman, 36321 (MICH). IDAHO: south of Priest Lake, on dead log, 21 July 1964, leg. H. D. Thiers, HDT 11411 (SFSU); McCall, Boulder Lake Trail, 31 July 1941, leg. A. H. Smith, Sm. 15865 (WTU); Payette Lake, on old logs, 6 Aug 1941, leg. A. H. Smith, Sm. 16055 (WTU); 29 July 1954, leg. Bigelow & Stuntz, Stz. 8800 (WTU); Payette NF, under *Larix*, *Abies*, *Pinus*, on rotten wood debris, 30 June 1993, leg. O. K. Miller, VTMH 1655 (VPI); Brundage Mt, 2000 m elev, on well decayed wood under *Picea*, 3 Aug 1993, leg. O. K. Miller, VTMH 2471 (VPI); Valley Co., Payette Lakes, 29 July 1954, leg. D. E. Stuntz, 36279 (MICH). MICHIGAN: Cheboygan Co., in woods in gorge N of Burt Lake, 31 July 1947, leg. H. Iltis, 18206 (TENN). Hermit Bog, 23 Aug 1953, Stz. 8423 (WTU); Hermit Bog, 2 Aug 1959, leg. D. E. Stuntz, Stz. 11384 (WTU); Mud Lake Bog, 29 Aug 1953, Stz. 8497 (WTU); Mud Lake, 12 July 1957, Stz. 10166 (WTU); 15 Aug 1957, leg. D. E. Stuntz, Stz. 10581, 10582 & 10583 (WTU); Harbor Springs, on wood, 7 July 1953, leg. S. C. Hoare, 40269 (DAOM); Jackson & Lakeland, 9 & 18 July 1915, on moss beds and rotten wood, leg. C. H. Kauffman, 36283 (MICH); Lower Tahquamenon Falls, 10 July 1953, leg. A. H. Smith, Stz. 7834 (WTU); Oakland Co., La Badie Lake, on debris, 21 June 1940, leg. A. H. Smith, 36287 (MICH); Bay View, 5 Sept 1905, leg. C. H. Kauffman, det. J. F. Atkinson 36295 (authentic material; MICH); MONTANA: Carbon Co., Custer NF, Red Lodge, Parkside, along Rock Creek, 2300 m elev, on rotten wood under *Picea*, *Pinus*, *Abies*, 3 Aug 1999, PBM 1502 (WTU); Glacier NP, N side of Kintla Lake, on ground (on buried wood), 8 July 1970, leg. O. K. Miller, VTMH 5448 (VPI); Rt. 209 along Swan River, on ground, 16 July 1968, leg. O. K. Miller, VTMH 5452 (VPI); near Swan River, July 1968, leg. O. K. Miller, VTMH 5453 (VPI); Flathead Co., Flathead Lake, Yellow Bay, station grounds, 1 Aug 1968, leg. J. P. Bennett, 36318 (MICH); Flathead NF, near Swan Lake, Peterson Cr Rd, 25 June 1975, leg. O. K. Miller, VTMH 5454 (VPI); Yellow Bay, Yellow Bay Creek, on ground (buried wood), 7 July 1968, leg. O. K. Miller, VTMH 5455 (VPI); near Mission L. O., S of Swan Lake, terrestrial, 2 July 1970, leg. H. & O. K. Miller, VTMH 5458 (VPI); Echo Lake, Flathead NF, on rotten log, 14 July 1928, leg. C. H. Kauffman, 36314 (MICH); on rotten conifer wood, 18 July 1928, leg. C. H. Kauffman, 36290 (MICH); 19 July 1928, leg. C. H. Kauffman, 36281 (MICH); 19 July 1928, leg. C. H. Kauffman, 36285 (MICH); Glacier NP, on trail along Bowman Lake under *Pinus*, *Larix* and *Pseudotsuga*, 4 July 1989, leg. O. K. Miller, VTMH 5456 (VPI); Josephine Lake, on trail, 9 July 1969, leg. O. K. Miller, VTMH 5457 (VPI). NEW HAMPSHIRE: Hanover, 28 Aug 1937, leg. H. C. Beardslee, 36294 (MICH). NEW YORK: Coy Glen, near Ithaca, on the ground, 7 Aug 1902, leg. W. Bradfield, Atk. 13372 (Holotype; CUP-A(local)); Atk. 13372 (Isotype; WTU); Enfield Gorge, Cayuga Lake Basin, on very rotten moss covered log, 8 Nov 1902, leg. C. H. Kauffman, Atk. 14281 (authentic material; CUP-A(local)); north side of Fall Creek, near Forest Home, on the ground in woods, 8 July 1917, leg. J. H. Faull, Atk. 24164, *I. leptophylla* var. *cystomarginata* (Holotype; CUP-A(local)); Atk. 24164, *I. leptophylla* var. *cystomarginata* (Isotype; WTU). OREGON: Benton Co., Green Peak, 28 Oct 1998, leg. L. L. Norvel, GP 1981028H2-07 (PNW-MS); Coos County Forest, on rotten log, 20 Mar 1978, leg. C. Audrey, CA 3/20/78 (WTU); Coos County Forest, on duff on ground under *Pseudotsuga*, 26 March 1978, leg. C. Audrey, CA 3/26/78 (WTU); Lane Co., H. J. Andrews Experimental Forest, lower watershed II, 17 June 1971, leg. F. Rhoades, 32134 (OSC); PENNSYLVANIA: Mt. Gretna, on ground around wood and moss, 9 Sept 1926, leg. C. H. Kauffman, 36297

(MICH). UTAH: Uintah Mtns, leg. B. Kropp, BK 24-Aug-96-1 (UTC); on wood, leg. B. Kropp, BK 2-Aug-98-6, UTC163354 (UTC); on wood, leg. B. Kropp, BK 7-Sept-97-19, UTC163351 (UTC); on wood, leg. B. Kropp, BK 30-Aug-97-13, UTC163353 (UTC); School Forest, on wood, leg. B. Kropp, BK 17-Aug-98-5, UTC163356; WASHINGTON: Chelan Co., Maple Pass, under *Abies lasiocarpa*, elev. 2020 m, 29 Aug 1989, leg. J. Trappe, 58797 (OSC); Clallam Co., Olympic Peninsula, Heart O'Hills, under conifers, 28 June 1939, leg. A. H. Smith, 36296 (MICH); Kittitas Co., Teanaway River, 27 Sept 1963, leg. J. L. Maas, 773053 (BPI); Table Mtn, Naneum Meadows, on wood under conifers, leg. B. Kropp, BK 18-Sept-98-14, UTC163358 (UTC); Lewis Co., Randle, Cispus area, 22 Oct 1972, Stz. 17496 (WTU); Mount Rainier NP, Eagle Peak Trail, 1100 m elev, on old log, 12 July 1948, leg. A. H. Smith, Sm. 28983 (WTU); Mount Rainier NP, Tahoma Creek Trail, on conifer wood, 18 July 1948, leg. A. H. Smith, Sm. 29126 (WTU); Mount Rainier NP, Wonderland Trail, below Ricksecker Point, 28 Aug 1948, leg. D. E. Stuntz, Stz. 4211 (WTU); Longmire, 28 Aug 1948, leg. D. E. Stuntz, Stz. 4212 (WTU); 10 July 1969, leg. D. Hosford, Stz. 15498 (WTU); Okanogan Co., west of Mazama, Monument Trail, on woods under mixed conifers, 19 June 1998, leg. P. B. Matheny, PBM 1009 (WTU); Pasayten Wilderness area, Lake Creek Trail to Black Lake, 3300 m elev, on rotten coniferous wood under *Abies*, *Picea*, *Pinus* and *Pseudotsuga*, 21 June 1998, PBM 1030 (WTU); on moss and coarse soil under *Pseudotsuga* and *Picea*, 22 Aug 1999, PBM 1616 (WTU); Whatcom Co., Mount Baker area, 16 Sept 1960, Stz. 11934 (WTU); Lick Creek Rd, 10 Sept 1976, leg. F. Van de Bogart, FVDB 3747 (WTU). WYOMING: Targhee NF, Grassy Lake, on very rotten wood under *Pinus*, *Picea*, 7 Aug 1987, leg. J. F. Ammirati, JFA 9418 (WTU); Yellowstone NP, Sand Point picnic area, N 44° 29.818', W 110° 25.162', 2500 m elev, on wood, 4 Aug 1997, leg. M. T. Seidl, MTS 4410 (WTU); Sand Point area, on soil under *Picea*, *Pinus*, *Abies*, 10 Aug 1999, leg. B. Kropp, PBM 1550 (WTU); Teton Co., Bridger-Teton NP, Buffalo Valley Rd., near Turpin Meadow, on rotten wood under *Picea*, *Pinus*, *Abies*, 3 Aug 1999, leg. M. Moser, PBM 1503 (WTU); 4 Aug 1999, PBM 1504 (WTU); on well-decayed conifer wood under *Picea*, *Pseudotsuga*, 7 Aug 1999, PBM 1532 (WTU); Medicine Bow Mts, North Fork, Little Laramie, on *Abies* stump, 10 Aug 1950(?), leg. A. H. Smith, Sm. 35598 (WTU).

In the field, *I. leptophylla* is indistinguishable from *I. lanuginosa*. Dried herbarium samples of the two species cannot be distinguished without the aid of a microscopic examination. The lack of pleurocystidia, in combination with larger spores with more nodules, and differently shaped cheilocystidia serve to differentiate *I. leptophylla* from *I. lanuginosa*, *I. stellatospora* and *I. teraturgus*. Both UPGMA and Neighbor-Joining analyses (Figs. 1 & 2) support the recognition of *I. leptophylla*. This result does not contradict previous taxonomic hypotheses of *I. leptophylla* (= *I. casimiri*) as a morphological species (Atkinson, 1918; Velenovsky, 1920; Boursier & Kühner, 1928; Horak, 1987; Stangl, 1989).

The reference to collection 'no. 13370' (Atkinson 1918) as the holotype (Atk. 13372; CUP-A(local)) is, ostensibly, a mistake in the original publication. The holotype sheet contains two packets of *I. leptophylla* var. *leptophylla*, (1) 13372 leg. W. Bradfield 7 Aug. 1902, and (2) 14281 leg. C. H. Kauffman 8 Nov. 1902. Both collections occurred in the Cayuga Lake Basin of New York. Notes on fresh material exist for both collections. Evidently, Atkinson's macroscopic

diagnosis is a composite of both collections since only Kauffman's description mentions the pileus as 'purple seal brown', which led Atkinson to describe the pileus as '...pileo brunneo vel umbrino frequenter purpureo tincto...'. This aspect of the diagnosis led Boursier & Kühner (1928) in part to continue the application of *I. casimiri*. In their current condition, the two Cornell collections are not unlike the colors and texture of other exsiccata of *I. leptophylla* that we have examined.

Atkinson (1918) described *I. leptophylla* var. *cystomarginata* differing primarily by the presence of subampullaceous [sublageniform) cystidia on the lamellar edge. The holotype [Atk. 24164; CUP-A(local)] does indeed possess such scattered cheilocystidia, but these are mixed with other cystidial shapes typical for the species. We do not consider var. *cystomarginata* as an autonomous taxon.

Kobayasi (1993) placed *I. leptophylla* in subgenus *Leptocybe* Kobayasi primarily due to the lack of metuloid cystidia. Though we consider *I. leptophylla* to be closely related to other members of stirps *Lanuginosa* based on overall phenetic similarity, we are not in a position to test Kobayasi's hypothesis at this time.

Inocybe squarrosula (P. Karsten) Sacc. is conspecific with *I. leptophylla* (J. Vauras, pers. comm.). The occurrence on wood, the range of spore size and the absence of cystidia as described by Karsten (as *Clypeus squarrosulus*, 1893) certainly are suggestive of *I. leptophylla*. We have not studied the holotype of *I. squarrosula*, but this species would hold nomenclatural priority over *I. leptophylla*.

4. *Inocybe lanuginosa* (Bull. : Fr.) Kummer, Fürh. Pilzkd.: 80. 1871. – Figs. 6, 11.

Lectotype (Icon): *Agaricus lanuginosus* Bull., Herb. France. Pl. 370. 1789.

Epitype (design. here): Finland, Oulun Pohjanmaa, Oulu, Hietasaari, near Kansankenttä, 8 Sept 1965, leg. Tauno Ulvinen, F50698 (OULU); Isoepitype (WTU).

≡ *Agaricus lanuginosus* Bull., Herb. France. Pl. 370. 1789.

≡ *Agaricus (Inocybe) lanuginosus* Bull. : Fr., Syst. mycol. 1: 257. 1821.

= *Agaricus (Inocybe) nodulosporus* Peck, Rep. N.Y. State Mus. 32: 28. 1880.

≡ *Inocybe nodulospora* (Peck) Sacc., Syll. Fung. 9: 95. 1891, non *nodulospora* Kobayasi, 1952.

= *Inocybe ovatocystis* Boursier & Kühner, Bull. Soc. Myc. Fr. 44: 181. 1928.

≡ *Inocybe lanuginosa* var. *ovatocystis* (Boursier & Kühner) Stangl, Z. Pilzkd. 42: 19. 1976.

= *Inocybe lanuginosa* ss. Bresad. Fung. Trid. II: 12. 1892.

= *Inocybe sabuletorum* ss. Pearson & Dennis, Trans. Br. Mycol. Soc. 31: 182. 1948, non Berk. & M. A. Curtis, 1890.

= *Inocybe plumosa* ss. Konrad & Maublanc, Icon. Fung., Pl. 102, fig. II. 1924–1932.

= *Inocybe lanuginosa* var. *alpina* Schmid-Heckel, Nationalpark Berchtesg. 15: 95. 1988.

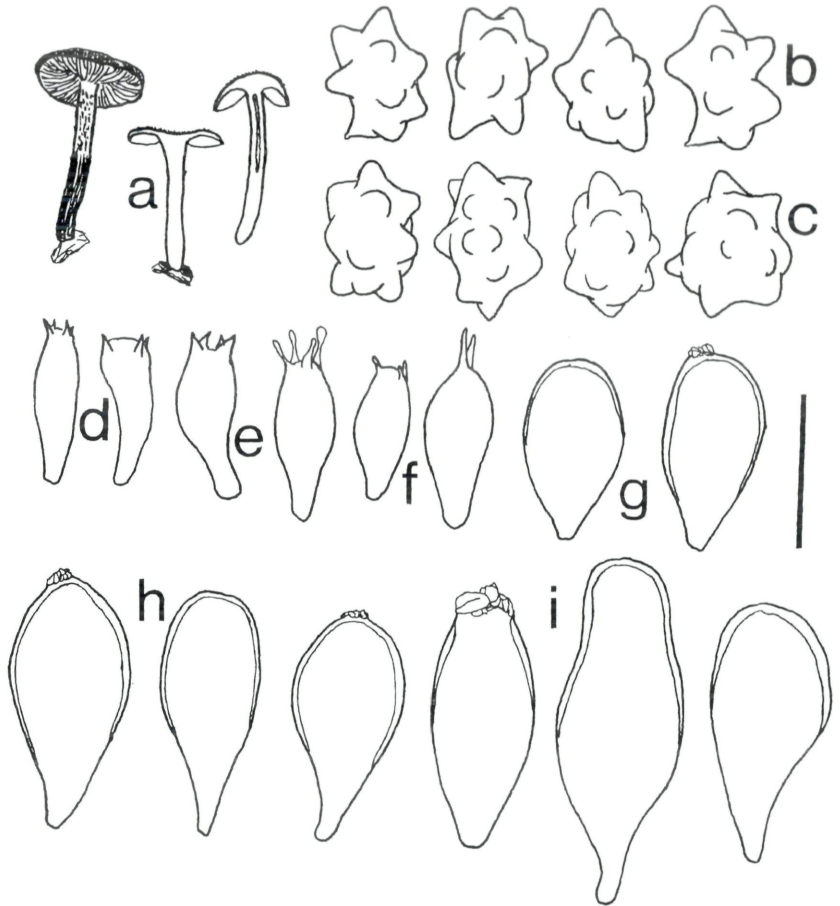


Fig. 6. *Inocybe lanuginosa*. – a. Basidiomes, *I. lanuginosa* (PBM 1552). – b. Four basidiospores, *Agaricus (Inocybe) nodulosporus* (NYS; Holotype). – c. Four basidiospores, *I. lanuginosa* var. *alpina* (SH 5115; Isotype). – d. Two basidia, *A. nodulosporus*. – e. One basidium, *I. lanuginosa* (HDT 21717). – f. Three basidia, *I. lanuginosa* var. *alpina* (SH 5115). – g. Two cheilocystidia, *A. nodulosporus*. – h. Three pleurocystidia, *A. nodulosporus*. – i. Three pleurocystidia, *I. lanuginosa* var. *alpina*. – Scale bar: a = 3 cm; b–c = 10 μ m; d–i = 25 μ m.

Pileus 10–35 mm diam, conic, obtusely conic to convex, applanate with age, usually with a low, obtuse umbo when plane, margin incurved to decurved, surface dry, disc with small, crowded, hispid squarreae; squamulose or recurvately-squamulose towards the margin; tearing with age but not rimose, neither shaggy nor revealing a pallid ground color, center dark brown (5F6), towards the margin brown (5E6/E5) or ‘Prout’s Brown’ to ‘Sepia’, context whitish, unchanging where bruised, to 3 mm thick, odor

not remarkable, taste same as odor or slightly acidulous. – Lamellae close, adnate to uncinata, with several tiers of lamellulae, even to (sub)ventricose, to 3 mm broad, pallid at first, ‘brownish orange’, ‘light brown’ to ‘brown’ (5C4/D4/E6), edges pallid, fimbriate. – Stipe 20–45 mm × 3–7 mm diam, equal to slightly enlarged at the base, terete, surface dry, cortina fugacious, extreme apex pruinose, pallid, lower half woolly-fibrillose or floccose to appressed-(sub)squamulose, less so towards the apex, concolorous with the pileus, extreme base at times with white mycelium, context solid at first but may become hollow with age, pallid to dingy.

Basidiospores 8–10.5(–11) × (5–)5.5–7.5(–8) μm [$\bar{x}_r = 8.6\text{--}10.4 \times 6.0\text{--}7.2 \mu\text{m}$, $\bar{x}_m = 9.3 \pm 0.7 \times 6.4 \pm 0.6 \mu\text{m}$, $Q = (1.07\text{--})1.27\text{--}1.64$ (–1.80), $\bar{Q}_r = 1.32\text{--}1.55$, $\bar{Q}_m = 1.45 \pm 0.13$, $n = 10$ spores per 10 collections], distinctly nodulose, outline often subelliptic, typically with (8–) 9–13 (–14) nodules [$\bar{x}_m = 10.7 \pm 1.3$ nodules per spore], ‘Ochraceous-Buff’, brown (5E4) in deposit. – Basidia (14–)19–30 (–34) μm , 4-sterigmate, clavate to cylindrico-clavate, hyaline to nearly so [$\bar{x}_r = 20.7\text{--}29.2 \times 7.3\text{--}9.5 \mu\text{m}$, $\bar{x}_m = 24.8 \pm 3.5 \mu\text{m}$, $n = 10$ basidia per 10 collections]. – Pleurocystidia frequent to infrequent, (26–)29–46(–48) μm [$\bar{x}_r = 32.4\text{--}41.8 \times 14.8\text{--}18.5 \mu\text{m}$, $\bar{x}_m = 37.0 \pm 5.1 \times 16.4 \pm 2.0 \mu\text{m}$, $n = 10$ pleurocystidia per 10 collections], obovate, pyriform to broadly clavate, less often elliptic or utriform, walls thin to slightly thickened, < 2.0 μm thick, hyaline, apices crystalliferous, basal pedicel brief. – Cheilocystidia abundant, similar to pleurocystidia though somewhat shorter, also some ventricose to utriform, (17–)22–43(–56) × (10–)11–20(–22) μm [$\bar{x}_r = 28.0\text{--}38.0 \times 13.8\text{--}18.8 \mu\text{m}$, $\bar{x}_m = 31.6 \pm 6.2 \times 15.7 \pm 2.58 \mu\text{m}$, $n = 10$ cheilocystidia per 10 collections], paracystidia broadly clavate, pyriform to subelliptic, thin-walled, hyaline. – Caulocystidia present at the (extreme) apex, generally utriform, obovate to subcylindric, hyaline to pale brown, usually thin-walled, apices crystalliferous or not, well-rounded to subcapitate, in dense clusters. – Lamellar trama regular, pale yellowish brown in mass, hyphae cylindric to inflated, up to 28 μm diam. – Pileipellis on the disc a trichoderm of russet to rust-brown, thick-walled (up to 1.0 μm), cylindric to swollen hyphae, 10–23 μm diam; tramal hyphae inflated, up to 25 μm diam, pale grayish brown to hyaline in mass. – Clamps frequent.

Habit, habitat and distribution. – In North America *I. lanuginosa* appears restricted to rotten woody substrates, either on stumps of conifers or terrestrially on buried rotten wood. It is found under conifers (*Abies*, *Picea*, *Pinus*, *Pseudotsuga*, *Thuja* and *Tsuga*) or in mixed woods where conifers (*Abies*, *Picea*) are present. In

Europe, it is cited more frequently on the ground and at times under hardwoods (*Betula*, *Populus* and *Alnus*).

Inocybe lanuginosa occurs both in Europe and North America and likely has a circumboreal distribution. In North America the distribution appears bimodal. *Inocybe lanuginosa* occurs in coastal areas of North America but extends into montane or subalpine habitats in the Adirondack, Appalachian, Coastal, Columbian, Cascade, northern Rocky Mountain and Sierra Nevada ranges. It is also conspicuous in the Great Lakes region. To date, the species is noticeably absent from the southern Rocky Mountains and the coastal plain of the southeast United States. We have not seen any collections from Mexico where putative hosts (*Abies*, *Pinus* and *Pseudotsuga*) occur, although Luz (1998) reports *I. lanuginosa* in *Abies* forests. Perez-Silva (1967) mistakenly cites 1620 (MEXU) as *I. lanuginosa* ss. Pat. (= *I. ovatocystis*, *I. nodulospora*); however, this collection represents a species outside the *I. lanuginosa* group. We have no reason to suspect *I. lanuginosa* does not occur in Mexico.

Inocybe lanuginosa peaks in appearance from July through September but is recorded from March through December. Its occurrence is skewed towards the summer months.

Material examined. – CANADA. ALBERTA: 20 m NW of Edmonton, Sandy Lake, on old wood, 14 Aug 1976, leg. H. M. E. Schalkwyk, 162834 (DAOM). BRITISH COLUMBIA: Saturna Is, 101 E. R., 5 Apr 1998, leg. P. Janszen, pers. herb.; Vancouver Is, leg. R. Countess, RC 2461/252, RC 2505/308, RC 2612/386, RC 2684/527 (UVIC); Seymour Watershed, greater Vancouver regional district, leg. S. Gamiet, 8 Sept 1994, SG 62090894-2 (WTU); 31 Aug 1994, SG 54083194-3 (WTU); 18 July 1994, SG 42071897-1 (WTU); 9 Oct 1996, SG 1341100996 (WTU); 3 Sept, SG 440903-1 (WTU); 4 Oct 1994, SG 41100494-129 (WTU); 14 Sept 1994, SG 21091494-8 (WTU); 31 Aug 1994, SG 44083194-11 (WTU); above Clearwater, in mature *Pseudotsuga* forest, on decaying *Pseudotsuga*, 7 Sept 1982, leg. T. Goward, 192128 (DAOM); Vancouver Is, Upper Carmanah Valley, in old growth *Picea*, *Thuja*, *Abies* forest, 30 Sept 1993, leg. S. A. Redhead et al, 208863 (DAOM). NEW BRUNSWICK: Kouchibouguac NP, *Thuja* swamp W of Callander Beach, on moss and liverwort covering humus-like stump, greg under *Acer*, *Alnus*, *Picea*, *Betula*, *Thuja*, 7 July 1977, leg. S. A. Redhead, 165900 (DAOM). NOVA SCOTIA: Colchester Co., Salmon River, on old log, 15 July 1931, leg. A. H. Smith, 36268 (MICH). ONTARIO: Merivale, on rotten wood, 24 July 1952, leg. J. W. Groves, 28923 (DAOM); Lake Timagami, Bear Is, on humus, 11 Aug 1937, leg. R. F. Cain, 48123 (DAOM); Fallowfield, on ground, 12 Sept 1956, leg. J. W. Groves et al, 51929 (DAOM); Lake Timagami, on humus, 11 Aug 1937, leg. R. F. Cain, 80432 (DAOM); Lake Timagami, Bear Is, on mossy, very rotten log, 11 Aug 1936, leg. R. F. Cain, 80621 (DAOM). QUÉBEC: Gatineau Park, Hermit Trail, on rotten wood, 12 July 1945, leg. J. W. Groves, 16337 (DAOM); Meach L., on ground (on buried wood), 1 Oct 1950, leg. E. Groves, 24692 (DAOM); near Tourville, Elgin Rd, 25 July 1957, leg. Groves & Jackson, 56561 (DAOM); L'Islet Co., St. Aubert, Adrien Morin's woods, on rotten wood, 1 Aug 1946, leg. H. A. C. Jackson, 87733 (DAOM); Lachute, on wood, 20 Sept 1980, leg. R. McNeil, 197432 (DAOM). FINLAND. Varsinais-Suomi, Nauvo, S of Turku, Seili, Högholmen, in *Picea abies* forest, 669:21, 31 July 1977, leg. J. Vauras, 854 / St. 1040 (M); Varsinais-Suomi, Kustavi, Rahi, Leonsaari,

dry place on rock, near *Pinus sylvestris* on *Cladonia*, 6733:193, 24 July 1980, leg. J. Vauras, 623 / St. 1046 (M); Varsinais-Suomi, Houtskär commune, Hypppeis, Jungfruskär, Storlandet island, middle part, Southwestern Archipelago National Park, open pastured, fairly moist forest with *Betula pubescens*, *Populus tremula* and *Alnus glutinosa*, 27 E: 6684: 171, 31 Aug 1998, leg. J. Vauras, 14268F (TURA 7701; WTU); Oulun Pohjanmaa, Oulu, Hietasaari, near Kansankenttä, grassy path in a heath forest with *Pinus sylvestris*, grid 27 °E: 72141:4262, 8 Sept 1965, leg. Tauno Ulvinen, F50698 (Epitype; OULU; Isoepitype; WTU). FRANCE. Barbizon, 1906, leg. C. G. Lyold, 839498 (BPI); near Coye-la-forêt, Forêt de Coye, on humus under *Pinus sylvestris*, 19 Oct 1965, leg. R. L. Shaffer, 36300 (MICH); Forêt de Coye, near Coye-la-forêt (Oise), on sandy soil in open *Quercus* woods, 8 Aug 1965, leg. R. L. Shaffer, 36319 (MICH). GERMANY. on soil under *Pinus*, 1923, leg. P. Sydow, 773043 (BPI); BADEN-WÜRTTEMBERG: Igelsberg bei Freudenstadt, MTB 7416, under *Abies* and *Picea*, 16 Aug. 1979, leg. J. Stangl, St. 1038 (M). BAYERN: 'München?', in a glade (Schneise) in a *Picea* planting, on boggy ground, with *Betula* in the area, 11 Oct 1973, leg. A. Einhellinger, St. 1039 (M); Ammersee-Ufer, Herrsching, MTB 7933, on old wood, 24 Aug 1985, leg. J. Stangl, St. 1048 (M); Haltepunkt Streitheim, before Welden, MTB 7529, am Holzlagerplatz, in *Picea* forest, 8 Aug 1987, leg. J. Stangl, St. 1049 (M); Alpenpark Berchtesgaden, Watzmannhaus, in humus under *Arctostaphylos*, 2000 m, 16 Aug 1985, leg. Schmid-Heckel, S-H 5115 (= St. 1007 & St. 1008), (*Inocybe lanuginosa* var. *alpina*, Isotypes; M). BERLIN: Grunewald, under *Pinus*, on bare sand, single and clustered, no date, leg. E. Ludwig, St. 1041 / EL 605b (M); BRANDENBURG: Sophienstädt, Ruhlsdork, Nieder-Barnim, on moorland, 1923, leg. P. Sydow, 36323 (MICH). NIEDERSACHSEN: Bardowick, Lüneburger Heide, 12 Aug 1979, leg. R. Bregazzi, St. 1042 (M); Schwarmstedt, Hannover, under *Pinus*, 22 June 1981, leg. Weber, St. 1043 / W 5(M); Bardowick, Lüneburger Heide, in moss under *Pinus*, 7 Aug 1979, leg. R. Bregazzi, St. 1045 (M). ITALY. South Tirol, Region Bozen, Dolomiten, Welschenhofen, at Karrer-See, under *Picea* near rotten wood, leg. J. Stangl, 19 July 1982, St. 1080. (M). SWEDEN. Femsjö, in a *Fagus* wood, 24 Sept 1947, leg. A. Melderis, 64828 (DAOM). SWITZERLAND. near Lavin, 17 Sept 1975, leg. K. Scates, Stz. 19205 (*lanuginosa* s. l.; atypical) (WTU). USA. ALASKA: Glacier Bay Nat. Monument, upper trail to Bartlett Lake, on the ground, 14 July 1980, leg. W. B. & V. G. Cooke, WBC 58880 (WTU). CALIFORNIA: Humboldt Co., near rotting wood, 15 Nov 1998, leg. C. Cripps, CLC 1260 (MONT); Mendocino Co., Jackson State Forest, on rotten logs, 21 Mar 1965, leg. H. D. Thiers, HDT 12250 (SFSU); place/date undet, leg. H. D. Thiers, HDT 12635B (SFSU); Yosemite NP, Red Fir (*Abies*) forest near Porcupine Flat, HWY 120, on very rotten *Abies* log, 13 Sept 1967, leg. H. D. Thiers, HDT 21053 (SFSU); Shasta Co., Castle Crags State Park, on rotten stump in mixed woods, 24 Nov 1967, leg. H. D. Thiers, HDT 21717 (SFSU); Trinidad, on humus, 10 Dec 1935, leg. A. H. Smith, 36272 (MICH). IDAHO: Higg-Nibley Canyon, on wood, under conifers, leg. B. Kropp, BK 14-Aug-97-8, UTC163357 (UTC); McCall, Aug 1962, leg. O. K. Miller, VTMH 5443 (VPI); on wood, 4 July 1962, , leg. H. H. Miller, VTMH 5445 (VPI); VTMH s.n. (VPI); Big Payette Lake, 9 Sept 1956, leg. A. H. Smith, 36311 (MICH); McCall, SIMA Foray, June 1997, teach. coll. (MONT); east side of Payette Lake, scattered in humus in dense mixed conifers, leg. D. Largent, DLL 468 (SFSU); 10 Sept 1976, Stz. 19497 (WTU); Little Payette Lake, 17 Sept 1946, Sm. 23557 (WTU); Fork Guard Station, Payette NF, 30 June 1993, VTMH 1655 (VPI); Payette NF, Lick Creek Guard St, on well-decorticated rotten log breaking up with brown cubical rot, 24 June 1992, leg. O. K. Miller, VTMH 5442 (VPI); Priest Lake district, on decomposed log, 6 July 1964, leg. H. D. Thiers, HDT 11298 (SFSU); Copeland, 11 Sept 1922, leg. Wehmeyer, 36312 (MICH). ILLINOIS: Glencoe, on decaying wood in woods, 23 Aug 1905, leg. W. S. Moffatt, 1229431 / WSM 1247 (F). MICHIGAN: Cheboygan Co., Burt Lake, Colonial Pt, on wood, 30 July 1947, leg. M. Lange, 18205; Oakland Co.,

Haven Hill, 17 Sept 1937, leg. A. H. Smith, 36289 (MICH); Brutus, Lower Maple River, leg. B. Isaacs, IS 818 (WTU); Lower Maple River, 6 July 1947, leg. A. H. Smith & Stuntz, Stz. 2606 (WTU); 7 July 1947, leg. A. H. Smith & Stuntz, Stz. 2643 (WTU); 26 July 1957, Stz. 10422 (WTU); West Maple River, 3 July 1959, leg. B. Isaacs, Stz. 11097 (WTU); Burt Lake, 30 July 1947, 18205 (TENN); Stew. Swamp, 1 July 1947, Stz. 2523 (WTU); Wolf Bog, 1 July 1947, leg. A. H. Smith & Stuntz, Stz. 2525 (WTU); Grapevine Point, Douglas Lake area, 10 July 1947, Stz. 2694 (WTU); Gorge, Douglas Lake area, 11 July 1947, Stz. 2708 (WTU); Cascadilla Gorge, 31 July 1947, Stz. 3012 (WTU); Douglas Lake, 5 July 1953, leg. R. Singer, Stz. 7702 (WTU); Reflection Lake, 28 Aug 1948, leg. A. H. Smith, Stz. 4194 (WTU); Douglas Lake, on decayed log, 17 July 1953, leg. S. C. Hoare, 40085 (DAOM); Douglas Lake, on decaying log, 7 July 1953, leg. S. C. Hoare, 40218 (DAOM); Manitou Campground, 8 July 1949, Stz. 5133 (WTU); French Lake, 11 July 1949, leg. A. H. Smith, Stz. 5156 (WTU); Cross Village, 26 July 1953, 'pale form', Stz. 7969 (WTU); Wilderness, 5 Aug 1953, leg. K. McKnight, Stz. 8129 (WTU); Whitmore Lake, Mud Lake Bog, 22 July 1929, leg. A. H. Smith, 36266 (MICH); New Richmond, on rotten log, 29 Sept 1911, leg. C. H. Kauffman, 36298 (MICH); Emmet Co., Mackinaw City, on mossy log in *Fagus-Acer* woods, 8 July 1971, leg. M. Gilliam, 36320 (MICH); 2 July 1953, leg. H. D. Thiers, Stz. 7669 (WTU); Bois Blanc Is, 27 July 1947, leg. M. Lange, L-1486 (WTU); Luce Co., Tahquamenon (Upper) Falls, on very rotten conifer log, 23 June 1953, leg. R. Singer, 1095715 / N156 (F). MINNESOTA: Scenic State Park, T016N R25W S32 NW of NE, old-growth (200 yr) red pine forest with *Pinus* spp., *Abies*, *Betula* and *Picea*, transect 10, near circle at 25 m, 7 Aug 1994, leg. P. R. Leacock, 839875 (MIN); 16 July 1994, 839915 (MIN); 3 Sept 1995, 840248 (MIN). MONTANA: Gallatin Co., Hyalite Canyon, under mixed conifers, 24 July 1993, leg. C. Cripps, CLC 695 (MONT); Big Sky, Gallatin Co., on wood under conifers, 25 Aug 1997, PBM 662 (WTU); Flathead NF, Noisy Creek, in moss (and rotten wood), 7 July 1989, leg. L. Bailey & J. Olsen, VTMH 5449 (VPI); mixed conifer and hardwoods, 9 July 1975, leg. O. K. Miller, VTMH 5451 (VPI); Flathead Lake, 2 Aug 1998, leg. L. L. Norvell, LLN1980802-21 (PNW-MS); 6 Aug 1998, leg. L. L. Norvell, LLN1980806-14 (PNW-MS); Mission Lake, on well-rotted stump, 8 July 1985, leg. H. & O. K. Miller, VTMH 5459 (VPI); Glacier NP, trail to Gunsight Lake, on ground on rotten wood, 6 July 1969, leg. O. K. Miller, VTMH 5450 (VPI). NEW HAMPSHIRE: Grafton Co., Mt. Moosilauke, on soil and rotten wood under *Betula*, *Picea* and *Tsuga*, 2 Sept 1998, PBM 1149 (WTU); NEW YORK: Paul Smith's, 20 Aug 1993, leg. R. M. Fatto, RMF 743; Coy Glen, Ithaca, 16 Oct 1903, leg. C. Thom, 773050 (BPI); New York City, West Park, 7 Aug 1903, leg. F. S. Earle, 36288 (MICH); Ithaca, Coy Glen, 24 July 1903, leg. C. H. Kauffman, 36292 (MICH); 7th Lake, Adirondacks, on very decayed log, 21 Aug 1934, leg. A. H. Smith, 36310 (MICH); Gansevoort, on decaying wood in woods, August, leg. C. H. Peck (*Agaricus (Inocybe) nodulosporus*, Holotype; NYS). NORTH CAROLINA: Great Smoky Mts NP, Indian Gap, on decaying *Picea* stump, 7 July 1946, leg. H. H. & A. J. Sharp, 17643 (TENN) (= 36307 MICH). OREGON: Benton Co., Rock Creek Watershed, Chintimini Creek, on class 5 rotten logs with *Tsuga* seedlings in old growth forest, 20 July 1982, leg. M. Castellano, 41118 (OSC); Green Peak, under *Pseudotsuga*, 28 Oct 1998, leg. L. L. Norvell, GP1981028U2-04 (PNW-MS); Clackamas Co., Rhododendron, on rotten wood, 22 Oct. 1946, Sm. 2007 (WTU); 5 miles up Salmon River from Welches, 13 Oct. 1946, Stz. 2201 (WTU); Mt. Hood NF, Bull Run Watershed, under *Pseudotsuga* and *Tsuga*, 8 July 1998, leg. L. L. Norvell, LLN1980708A1h2 (PNW-MS); LLN1980722A3d (PNW-MS); LLN1980722B2j (PNW-MS); LLN1980722B2m1 (PNW-MS); 22 July 1998, LLN1980722A3a (PNW-MS); LLN1980722B4 (PNW-MS); Coos County Forest, on wood, 29 Mar 1984, leg. C. Ardrey, CA 678 (WTU); Douglas Co., Bureau of Land Management, Irwin Rocks RNA, central area, on soil under *Pseudotsuga menziesii* and *Calocedrus decurrens*, 1750 ft elev, 6 May 1997, leg. M. Trappe, 60027 (OSC).

TENNESSEE: Great Smoky Mts NP, Clingman's Dome, in *Abies* woods, 27 Sept 1936, leg. L. Hesler, 9494 (TENN); Clingman's Dome, around stump of *Abies*, 8 Aug 1943, leg. Meyer, 15809 (TENN). VERMONT: Grand View Mt., on mossy ground under *Picea*, 1 July 1898, ex E. A. Burt, 773188 (BPI). WASHINGTON: Chelan Co., Chesapeake Saddle, 5 Aug 1940, Stz. 905 (WTU); Lake Ann Trail, on debris (soil & wood) under *Tsuga*, *Abies*, *Picea*, *Pseudotsuga* and *Pinus*, 3 Aug 1993, det. T. Kuyper, JFA 11069 (WTU); Glacier View Ridge, 1900 m elev, under *Abies lasiocarpa*, 1 Sept 1989, leg. J. Trappe, 58805 (OSC); Clallam Co., Olympic Peninsula, Heart O'Hills, on old logs, 25 June 1939, leg. A. H. Smith, 36278 (MICH); Lake Crescent, 2 June 1939, leg. A. H. Smith, 36305 (MICH); 4 June 1939, on wood, Sm. 14043-A (WTU part) & Sm. 104043-B (WTU part); Joyce, on conifer logs, 9 June 1939, leg. A. H. Smith, 36326 (MICH); Grays Harbor Co., Olympic Peninsula, Quinault NRA, on decayed wood in *Tsuga* stand, 14 Oct 1993, leg. G. Walker, GRW 533 (WTU); 2nd growth transect, on wood, 2 Nov 1993, leg. G. Walker & M. Puccio, GRW 642 (WTU); Jefferson Co., Dosewallips River, Olympic Pen., 10 Oct. 1971, leg. F. van de Bogart, FVDB 772 (WTU); (WTU); King Co., Hazel Wolf Wetlands, *Pseudotsuga*, on rotten wood, 19 April 1997, leg. P. B. Matheny, PBM 401 (WTU); second growth *Pseudotsuga* woods, on very rotten wood, 9 May 1997, PBM 438 (WTU); on rotten wood, 16 Apr 1998, PBM 956 (WTU); on rotten wood under *Pseudotsuga*, *Thuja* and *Alnus*, 10 May 1998, PBM 965 (WTU); on wood under *Pseudotsuga* and *Thuja*, 28 June 1998, PBM 1045 (WTU); Lee Forest, Apr 1963, Stz. 12956 (WTU); Kittitas Co., Lake Kachess Campground, on rotten wood, 24 Oct 1978, Stz. 20453 (WTU); Teanaway River, on wood, 27 Sept 1963, leg. J. L. Maas, 773189 (BPI); Lewis Co., Cispus Center, 25 June 1971, leg. G. Hosford, Stz. 16667 (WTU); Mason Co., Mason Lake Corner, Rt. 3, on wood, 5 Nov. 1972, leg. J. Williams, JWL 1565 (WTU); Mount Rainier NP, Longmire, 10 July 1948, Sm. 28949 (WTU); 14 July 1948, leg. W. B. Gruber, Sm. 29004 (WTU); on log, 21 July 1948, Sm. 29232 (WTU); 4 Sept 1948, Stz. 4281 (WTU); on conifer log, 19 Sept 1948, Sm. 29175 (WTU); Stz. 3752 (WTU); on rotten conifer log, 2 Aug 1948, Stz. 3806 (WTU); Mount Rainier, Frying Pan Creek, 29 Aug 1937, Stz. 615 (WTU); Lower Tahoma, 18 Aug 1948, Stz. 4033 (WTU); on rotten wood, 11 Sept 1948, leg. M. McKenney & Morris, Stz. 4408 (WTU); Eagle Peak, 1300 m elev, 26 Aug. 1948, Stz. 4149 (WTU); Ranger Creek Airstrip above the Dalles Campground, along river trail inside the NP boundary, gregarious on very rotten wood in old growth mixed conifer forest of *Thuja*, *Abies* and *Tsuga*, 15 Sept 1989, leg. N. Laycock, NL 9/15/89 (atypical; WTU); Pend Oreille Co., Colville NF, HWY 20, under mixed conifers, 30 June 1993, leg. Norvell & Redhead, LLN 93.06.30-1 (WTU); San Juan Co., Friday Harbor, 19 Nov 1976, leg. F. van de Bogart, FVDB 3837 & 3841; Snohomish Co., Point Wells, 26 May 1934, leg. D. E. Stuntz, Stz. 48 (WTU); Barlow Pass, on rotten wood under *Abies* and *Tsuga*, 25 Aug 1990, leg. J. F. Ammirati, JFA 10154 (WTU); on rotten wood, *Abies* and *Tsuga* old growth, 29 June 1992, JFA 10546 (WTU); Kennedy Hot Springs, Glacier Peak area, 5 July 1969, leg. J. Williams, JWL 205 (WTU); Barclay Lake, on rotten wood, 22 July 1998, 700 m elev, leg. P. B. Matheny & al., PBM 1084, 1085 & 1090 (WTU); on wood under *Tsuga* and *Abies*, leg. B. Kropp, BK 16-Sept-98-18, UTC163352 (UTC); 3 miles west of Crystal Creek, on rotten wood, 5 Oct. 1958, Stz. 10698 (WTU); Thurston Co., Millersylvania, on rotten wood, 26 Oct 1968, Stz. 15075 & 15113 (WTU); N of Hawk Prairie, 12 Nov 1950, Stz. 6134 (WTU); Whatcom Co., Mt. Baker, 1100 m elev, 17 Aug 1941, Sm. 16227 (WTU); Shuksan Inn, 18 Aug 1941, Sm. 16253 (WTU); 13 Oct. 1969, Stz. 15636 (WTU); 10 Sept 1976, on rotten wood, Stz. 19497 (WTU); on rotten wood, leg. B. McAdoo, BM 30#14 (WTU); Washburn Pass, on soil and rotten log under *Picea* and *Pinus*, leg. H. D. Thiers, 6 Aug 1987, JFA 9410 (WTU); in woods east of Clease Lake, 2 May 1941, Stz. 970 (WTU); Pacific Crest Trail, 27 Sept 1981, Stz. 21395 (WTU); Port Defiance, on slash and dirt in woods of *Pseudotsuga*, early May 1946, Stz. 7025 (WTU); Bench Mtn. Trail, on wood, 10 July

1993, leg. G. Walker, GRW 429 (WTU). WYOMING: Yellowstone NP, west side of Yellowstone Lake, gregarious on rotten conifer log, 2 Aug 1989, leg. H. D. Thiers, HDT 52252 (SFSU); Lewis Lake, Yellowstone NP, on moss covered rotten wood and organic debris, 10 Aug 1999, leg. M. T. Seidl, PBM 1552 (WTU); Grand Teton NP, Leigh Lake, on rotten wood under *Picea* and *Abies*, 6 Aug. 1999, PBM 1524 (WTU); Teton Co., Turpin Meadow area, on very rotten wood under *Picea* and *Abies*, 7 Aug 1999, PBM 1531 (WTU).

Inocybe lanuginosa differs from *I. leptophylla* by the smaller basidiospores with fewer nodules, the presence of small, obovate (pyriform) to ovate pleurocystidia and the somewhat smaller basidia. The two species share similar gross morphological characters such as the hispid-squarrose pileus and wooly-squamulose stipe. In North America *I. lanuginosa* is restricted in most instances to woody substrates. On the other hand, *I. leptophylla* is less restricted to woody substrates. Species determination, however, must be made by microscopic analysis. *Inocybe stellatospora* occurs predominantly on soil, less often on woody debris, and differs subtly from *I. lanuginosa* by the squamulose pileus that is shaggy and non-hispid, and the tendency for the squamules to separate and reveal the pallid context beneath. Stangl (1976, 1989) concluded that *I. lanuginosa* and *I. stellatospora* of central Europe could only be differentiated in the field in the rarest of instances. This homogeneity does not hold among North American material. Both UPGMA and Neighbor-Joining analyses (Figs. 1 & 2) warrant the specific separation of *I. lanuginosa* and *I. stellatospora* and support the hypotheses of Boursier & Kühner (1928) and Grund & Stuntz (1968). Additionally, our findings fail to corroborate the observations of Trigeaux (1980).

We consider *I. lanuginosa* var. *alpina* Schmid-Heckel (Schmid-Heckel, 1988) a synonym of *I. lanuginosa* despite its alpine occurrence under *Arctostaphylos*. No microscopic differences were detected between var. *alpina* (Isotypes; M) and *I. lanuginosa* other than occasional 2-sterigmate basidia in the former that appear to produce spores of unusual shape or size and with more or fewer nodules. The gross morphological differences described by Schmid-Heckel are not significant in our opinion because they are inseparable from collections of *I. lanuginosa*.

Inocybe nodulospora (Peck) Sacc. (non *nodulospora* Kobayasi, 1952), appears to be the earliest eptithet available from North American material applicable to *I. lanuginosa*. Thus, *I. nodulospora* has nomenclatural priority over *I. ovatocystis*. Peck's protologue and the holotype (NYS) are in perfect agreement with *I. ovatocystis* including the occurrence on wood. Kauffman (1921) cited '*I. nodulosa*' as a synonym of *I. lanuginosa*, but this clearly is an error as *I. nodulosa* was described by Kauffman in the North

American Flora (1924) and is an entirely different species. In the same publication, Kauffman considered *I. nodulispora* (sic) as a doubtful name.

5. *Inocybe stellatospora* (Peck) Masee, Ann. Bot. 18: 469. 1904. –
Figs. 7, 12.

Lectotype (design. here): single 'light' basidiome (Holotype, Peck; NYS)

≡ *Agaricus* (*Hebeloma*) *stellatosporus* Peck, Ann. Rep. N.Y. St. Mus. 26: 57. 1874.

≡ *Hebeloma stellatosporum* (Peck) Sacc., Syll. Fung. 5: 98. 1887.

= *Inocybe longicystis* Atk., Am. J. Bot. 5: 213. 1918, non *longicystis* Velen., 1920.

≡ *Inocybe plumosa* var. *longicystis* (Atk.) Konrad & Maublanc, Icon. Fung. VI: 137. 1924.

≡ *Inocybe lanuginosa* f. *longicystis* (Atk.) R. Heim, Genre *Inocybe*: 364. 1931.

≡ *Inocybe lanuginosa* var. *longicystis* (Atk.) Stangl & Enderle, Z. Mykol. 49(1): 120. 1983.

= *Inocybe lanuginosa* (Bull. : Fr.) Kummer, ss. Moser, Kleine Krypt. II/b: 165. 1955.

= *Inocybe lanuginosa* (Bull. : Fr.) Kummer, ss. Stangl, Hoppea 46: 284. 1989.

Pileus 15–40 mm diam, parabolic to plano-convex to depressed and arched towards the margin, umbo generally absent or low and obtuse, margin decurved to straight, undulating with age, surface dry, matted fibillose-squamulose to squarrose, scales recurved or squarrose with age; color dark brown (6F8–6F7) when young or exceedingly moist, to brown (5E5–5F5) or 'Dresden Brown' to 'Saccardo's Umber', subrimose revealing the pallid context beneath separating squamules in age; context solid, up to 3 mm thick, watery to pallid, may become brown, odor none to weakly spermatic, taste same as odor. – Lamellae close, adnate to uncinata, up to 3 tiers of lamellulae, pallid when young to grayish (4B4), light brown (5D6) or dark yellowish brown or 'Dresden Brown' with age, up to 4 mm broad, (sub)ventricose, edges pallid, fimbriate. – Stipe 25–45 mm × 3–5 mm diam, equal, terete, straight to somewhat flexuous, surface dry, cortina fugacious, extreme apex pruinose, pallid, fibrillose below to mid-length, lower half fibrillose-squamulose, squamules recurved when fresh, finely-squamulose with age; color brown (5E6–5E5), base may become bister with age; context pale dingy brown, solid, unchanging where cut or bruised.

Basidiospores (7–)7.5–10(–11) × (5.5–)6–7.5(–8) μm [$\bar{x}_r = 8.2$ – 9.3×6.1 – 7.0 μm, $\bar{x}_m = 8.8 \pm 0.8 \times 6.6 \pm 0.6$ μm, $Q = (1.07$ –) 1.21 – 1.50 (– 1.58), $\bar{Q}_r = 1.31$ – 1.40 , $\bar{Q}_m = 1.35 \pm 0.10$, $n = 10$ spores per 10 collections], distinctly nodulose, outline subangular to subelliptic, (8–) 9–13 (–14) nodules [$\bar{x}_m = 11.0 \pm 1.5$ nodules per spore], 'Ochraceous-Buff', brown ('Prout's Brown' or near 10YR 4/3) in deposit. – Basidia (25–)28–35(–38) μm [$\bar{x}_r = 29.2$ – 33.5×9.7 – 10.6 μm, $\bar{x}_m = 31.63 \pm 2.84 \times 10.09 \pm 1.53$ μm, $n = 10$ basidia per 10

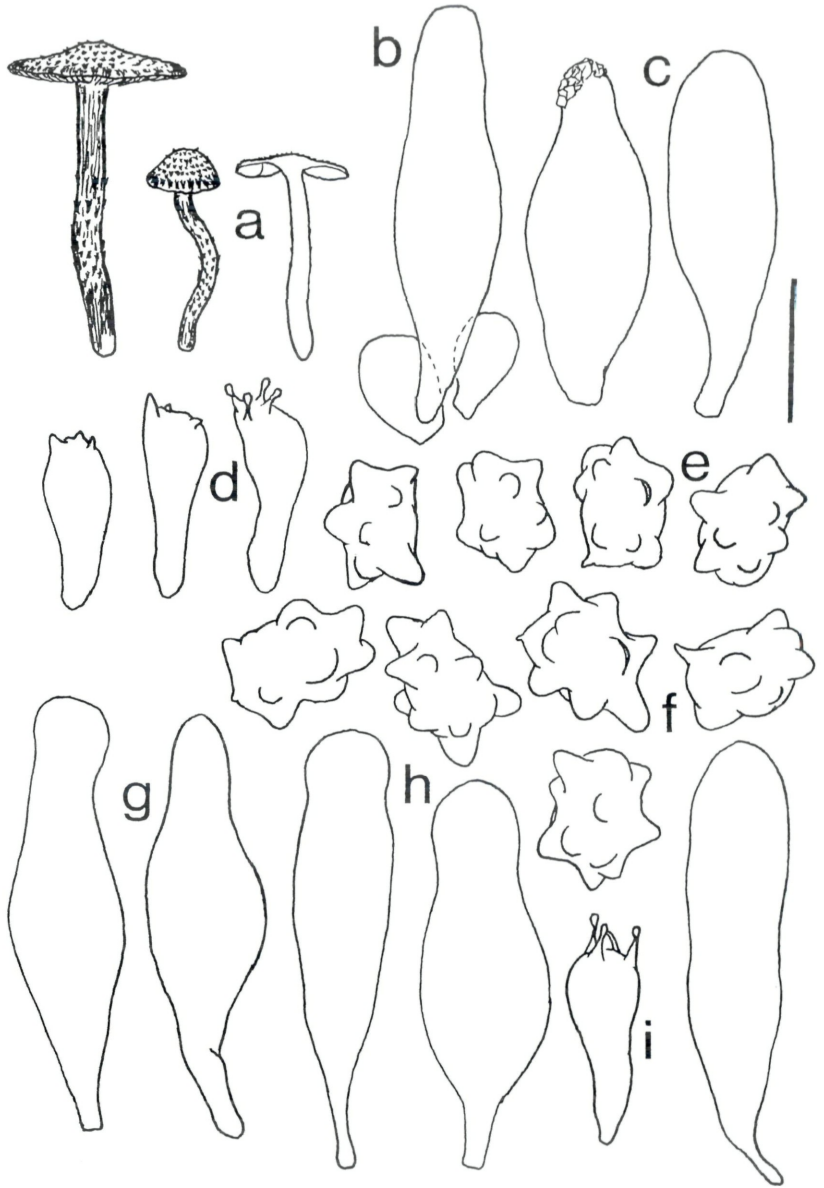


Fig. 7. *Inocybe stellatospora*. – a. Basidiomes (PBM 1436). – b. Two cheilocystidia, two paracystidia, *I. longicystis* (Atk. 24321; Holotype). – c. Cheilocystidium (*stellatospora* 'light'; Lectotype). – d. Three basidia, *I. longicystis* (Atk. 24321). – e. Four basidiospores, *I. longicystis* (Atk. 24321). – f. Five basidiospores (*stellatospora* 'light'). – g. Two pleurocystidia, *I. longicystis* (Atk. 24321). – h. Three pleurocystidia (*stellatospora* 'light'). – i. Basidium (*stellatospora* 'light'). – Scale bar: a = 3 cm; b–d, g–i = 25 µm; e–f = 10 µm.

collections], 4-sterigmate, (sub)clavate, hyaline or nearly so. – Pleurocystidia frequent, (46–)55–79(–88) × (13–)13.2–20(–24) μm [$\bar{x}_r = 57.0\text{--}77.1 \times 14.0\text{--}18.0$ μm, $\bar{x}_m = 66.02 \pm 8.66 \times 16.08 \pm 2.42$ μm, n = 10 pleurocystidia per 10 collections], (narrowly) utriform, subcylindric to fusiform usually above a slender basal pedicel, apices well-rounded, at times subcapitate, occasionally crystalliferous but usually bare, thin-walled. – Cheilocystidia abundant, (35–)40–80 (–90) × (10–)13–23(–25) μm [$\bar{x}_r = 48.9\text{--}62.6 \times 13.0\text{--}19.3$ μm, $\bar{x}_m = 59.30 \pm 11.48 \times 16.56 \pm 3.25$ μm, n = 10 cheilocystidia per 10 collections], similar to pleurocystidia, often utriform though variable in shape, paracystidia clavate to vesiculose, thin-walled, hyaline, 17–20 × 10–14 μm. – Caulocystidia variable but often similar to hymenial cystidia–subcylindric, utriform, pyriform to clavate, with well-rounded to subcapitate apices, thin-walled (up to 1.0 μm thick), hyaline to pale brown, restricted to the extreme apex. – Lamellar trama regular, pale yellowish brown in mass, hyphae cylindric to inflated, up to 25 μm diam. – Pileipellis a cutis giving rise to fascicles of trichodermial elements, hyphae cylindric, up to 19 μm diam, incrustated with ‘Tawny’ to rust brown pigment; tramal hyphae pale yellowish brown to hyaline, hyphae cylindric to inflated, up to 20 μm diam, refractive hyphae present. – Clamps frequent.

Habit, habitat and distribution. – Scattered singly or in small groups on soil, humus and occasionally woody debris, terrestrial under conifers such as *Abies*, *Picea*, *Pinus*, *Pseudotsuga*, *Thuja* and *Tsuga*; in mixed woods of *Pseudotsuga*, *Tsuga*, *Thuja* and *Alnus*; in northern hardwood successional forests under *Acer*, *Betula*, *Populus* and *Tilia* mixed with seedlings of *Abies*, *Picea* and *Fagus*; and in Mexico under *Abies* and *Pinus*.

Inocybe stellatospora (= *I. longicystis*) is known from Europe and North America and appears to have a circumboreal distribution. However, in North America *I. stellatospora* has been reported from only two locations in Washington, one location in Mexico, a few scattered locations in the Great Lakes region, the Maritime provinces, the Adirondacks and the Appalachians. The biogeographical pattern is disjunct. *Inocybe stellatospora* ranges from sea level to montane areas (Mount Rainer National Park and Mexico). However, it is absent from the Rocky Mountains and Sierra Nevada. Hesler (1937) cites 9494 (TENN) as *I. longicystis*, but this collection represents *I. lanuginosa*. Nishida (1989) records *I. stellatospora* (as *I. longicystis*) in a checklist of California *Inocybes*, yet the collection on which the record was made (HDT 12747; SFSU) is heterogeneous (specimens correspond to *I. lacera* (Fr. : Fr) Kummer and *I. subcarpta sensu lato*) and includes specimens with thick-walled hymenial cystidia. The exsiccata also

deviate in their appearance from *I. stellatospora*. Thus, we cannot accept the western extension of the range of *I. stellatospora* into California based on these data. Luz (1998) cites *I. lanuginosa* as a common species in *Abies* forests of Tlaxcala, but we have not examined these collections and cannot be sure which concept is being applied.

Inocybe stellatospora occurs most often in the summer months from July through September but can fruit in late spring at low elevations in the Pacific Northwest. We consider it uncommon in North America.

Material examined. – CANADA. ONTARIO: Lake Timagami, Ko-Ko-Ko Bay, 2 Sept 1936, leg. A. H. Smith, 36274 (MICH). NOVA SCOTIA: Kings Co., Scott's Bay, 10483 (ACAD); 29 Aug 1973, 10521 (ACAD); Gospel Wood Road, 5 Aug 1982, leg. K. A. Harrison, 14116 (ACAD) (atypical); Lunenburg Co., Gifford Is, 28 Aug 1982, leg. D. Grund, 14294 (ACAD); in *Picea* forest, 28 Aug 1982, 14308 (ACAD); Ironbound Is, *Abies* forest, 21 Aug 1966, leg. H. Stewart, DWG 1805 (ACAD); in duff in *Abies* forest, 21 Aug 1966, leg. H. Stewart, DWG 1811 (ACAD); DWG 1937 (ACAD). QUEBEC: Albanel 48°54'N 92°23'(sic)W, under conifers on sandy soil, 25 Aug 1982, leg. Y. Dalpé, 186960 (DAOM). FINLAND. Pohjois-Savo, Siilinjauri, 20 km N of Kuopio, Toivala, rich *Picea abies* forest, near to e.g., *Lactarius badiosanguineus*, 20 Aug 1977, leg. J. Vauras, 183 / St. 1026 (M). GERMANY. BADEN-WÜRTTEMBERG: Freudenstadt district, Igelsberg, MTB 7416, under *Abies*, in moss, 19 Aug 1979, leg. J. Stangl, St. 1025 (M). BAYERN: Augsburg district, Lauterbrunn, MTB 7530, in *Picea* forest in moss bed on rotten wood on the ground, 15 Aug 1986, leg. J. Stangl, St. 1009 (M); Lauterbrunn, in *Picea* forest on conifer duff in peat moss (*Sphagnum*), 15 Aug 1986, leg. J. Stangl, St. 1010 (M); Lützelburg, near Parkplatz, MTB 7530, in peat moss (*Sphagnum*), gregarious about an old hardwood branch, 21 Aug 1982, leg. J. Stangl, St. 1012 (M); Schwabegg, MTB 7830, in *Picea* forest, 5 Aug 1978, leg. H. Bertold, St. 1014 (M); MTB 7830, in *Picea* forest, 11 Aug 1984, leg. H. Bertold, St. 1019 (M); Mickhausen, MTB 7729, in *Picea* forest on tree stump, leg. J. Stangl, 16 Sept 1977, St. 1018 (M); Mödishofen, Mödishofer Moor, MTB 7629, under *Picea* in moss, leg. K. Pfaff, 25 Oct. 1987, St. 1020 (M); MTB 7629, on grassy but very wet trail under *Picea* and *Pinus*, leg. J. Stangl, 15 Aug 1979 (15 Oct 1979?), St. 1027 (M); Horgau, MTB 7529, in *Picea* forest on old wood, leg. Lindemeier, 3 Oct 1982, St. 1021 (M); district of Fürstenfeldbruck, Hörbach (near Haspelmoor), MTB 7732, on edge of trail in *Picea* forest, leg. J. Stangl, 26 Sept 1981, St. 1022 (M); Bayerischer Wald, Regen, MTB 7044, on slope of sandy soil under *Picea*, *Abies* and *Fagus*, leg. J. Stangl, 17 July 1981, St. 1023 (atypical) (M); district of Bamberg, 'Stammberg', near Pünzendorf, MTB 6032, in mixed woods on moss covered stump, leg. J. Stangl, 9 Aug 1981, St. 1024 (atypical) (M); Haspelmoor, MTB 7732, under *Picea* and *Pinus* in 'Spießmoor', leg. J. Stangl, 28 Aug 1976, St. 1028 (M); between Unterfahlheim and Leipheim, MTB 2527, in *Picea* forest, 'Lechfeld', among needle litter, leg. M. Enderle, 20 July 1979, St. 1029 (M); Haltepunkt Streitheim, before Welden, MTB 7529, in *Picea* forest, leg. J. Stangl, 8 Aug 1987, St. 1031 (M); Mertingen, Mertinger Gemeinwald, MTB 7330, under *Picea*, in conifer duff, also on rotten wood, 28 Aug. 1987, leg. G. Sedlmeir, St. 1032 (M); Augsburg-Bergheim, MTB 7630, in *Picea* forest, near an old stump, 9 Nov 1984, leg. J. Stangl, St. 1033 (atypical); Augsburg district, Lützelburg, MTB 7530, in *Picea* forest, 10 Sept 1983, leg. J. Stangl, St. 1034 (M); Fürstenfeldbruck district, Haspelmoor-Nord, MTB 7732, in peat moss (*Sphagnum*) under *Pinus*, 19 July 1980, leg. J. Stangl, St. 1035 (M); Haspelmoor-Süd, MTB 7732, in moss under *Pinus*, 14 July 1979, leg. J. Stangl,

St. 1036 (M); Lindgraben, MTB 7629, in *Picea* forest on conifer duff, 12 May 1987, leg. J. Stangl, St. 1037 (M). HESSEN: Kassel, Falkenstein, MTB 4721, *Fagus* forest, 5 Sept 1979, leg. D. Laber, St. 1047 (M). NORDRHEIN-WESTFALEN: Arnsberg-Nord, MTB 4514, under *Fagus*, 1 Sept 1979, leg. E. Kavalir, St. 1015 (M); Borlo-Vardingholter Venn, MTB 4007 (Oeding)?, in dried out bog, 17 July 1979, leg. A. Borcken-Gemen, St. 1016 (M). MECKLENBURG-VORPOMMERN: Rügen, Glowe, Dünen, under *Pinus*, *Picea* and *Betula*, between needles and moss, 22 June 1980, leg. R. Rauschert, St. 1017 (doubtful, = *I. subcarpta*?) (M). GREAT BRITIAN. England, Ashdown Forest, on ground, 1 Aug 1954, leg. J. W. Groves, 48057 (DAOM). MEXICO. MEXICO: km 70 carr. Toluca-Litácuaro, under *Abies* and *Pinus*, 2 Nov 1981, leg. E. Pérez-Silva, et al., 19709 (MEXU). SWEDEN. near Femsjö, under *Betula*, *Populus*, *Fagus*, *Picea* and *Pinus*, 19 Sept 1964, leg. M. Moser, 29092 (TENN); Drottningholm, 1905, leg. C G. Lloyd, 840118 (BPI). USA. MICHIGAN: Duck Bldg, 10 July 1949, leg. A. H. Smith, Stz. 5145 (WTU); Tahquamenon Falls area, 23 July 1953, leg. D. E. Stuntz, Stz. 7951 (WTU). MINNESOTA: Tettegouche State Park, T56N R07W S08 NW of NW, successional northern hardwood forest (Old-Growth Project) with *Acer*, *Betula*, *Populus*, *Tilia* and seedlings of *Abies*, *Picea* and *Fagus*, transect 13, near circle at 55 m, 3 Aug 1994, leg. P. R. Leacock, 839873 (MIN); 25 Sept 1996, 863923 (MIN). NEW JERSEY: Hutchinson Forest, in mixed woods, old-growth, 10 July 1996, leg. R. Fatto, RMF 944 (atypical) (pers. herb.). NEW YORK: Adirondack Mts, Endogone Ravine, Seventh Lake, leg. F. C. Stewart, 13 Aug 1917, Atk. 24321 (Holotype; CUP-A (general)); Atk. 24321, *I. longicystis* (Isotype; WTU) Lewis Co., Croghan, on ground in woods, Sept, Peck, *Agaricus stellatosporus* ('light specimen' Lectotype; NYS); Hakima Co., Old Forge, Peck, Old Forge, '*Agaricus (Inocybe) stellatosporus*' (authentic material; NYS); 12 Sept 1914, leg. C. H. Kauffman, 36280 (MICH); TENNESSEE: Great Smoky Mts NP, Clingman's Dome, in deep moss, 24 Aug 1941, leg. L. Hesler, 13954 (TENN). VIRGINIA: Mt. Rogers, Grayson Co., scattered under *Picea* and *Abies*, 10 Sept 1983, leg. R. Vilgalys, 900406 (BPI). WASHINGTON: King Co., Hazel Wolf Wetlands, 100 m elev, on soil under *Alnus*, *Pseudotsuga*, *Thuja*, 16 May 1997, leg. P. B. Matheny, PBM 470 (WTU); on soil under *Pseudotsuga* and *Alnus*, 4 July 1997, PBM 569 (WTU); on soil under *Pseudotsuga*, *Tsuga* and *Alnus*, 28 June 1998, PBM 1044 (WTU); on soil under *Pseudotsuga* and *Alnus*, 12 July 1998, PBM 1067 (WTU); four basidiomes on soil but two on woody debris, in mixed woods of *Pseudotsuga*, *Tsuga*, *Thuja*, *Alnus*, 5 June 1999, PBM 1436 (WTU part); Mount Rainier NP, Lower Tahoma, 24 July 1948, leg. A. H. Smith, Sm. 29387 (WTU); on soil, 26 July 1948, leg. A. H. Smith, Sm. 29499 (WTU); 9 Aug 1948, leg. Simmons, Stz. 3921 (WTU); 19 Sept 1948, leg. D. E. Stuntz et al, Stz. 4623 (WTU); Mount Rainier NP, Tahoma Creek, 29 July 1948, leg. A. H. Smith, Stz. 3760 (WTU); 28-31 July 1948, Stz. 3766, 3780 & 3784 (WTU); 31 July 1948, leg. D. E. Stuntz, Stz. 3785 (WTU); 31 July 1948, leg. Smith & Imsh., Stz. 3789 (WTU); Mount Rainier NP, Longmire, 14 Aug 1948, Stz. 3953.5 (atypical) (WTU).

Inocybe stellatospora is recognized in the field by its shaggy squamulose pileus, floccose-squamulose stipe and typical occurrence on soil. We have observed a few basidiomes on woody debris. Diagnostic microscopic characters include the thin-walled, elongate hymenial cystidia with well-rounded to subcapitate apices that may or may not be crystalliferous. The basidiospores are smaller and less elliptic in appearance than in either *I. leptophylla* or *I. teraturgus* and are similar to those of *I. lanuginosa*. The subtle gross morphological features in combination with the differently shaped and larger hymenial cystidia and larger basidia readily distinguish

Inocybe stellatospora from *I. lanuginosa*. Both clustering procedures, UPGMA and Neighbor-Joining analyses (Figs. 1, 2) support the taxonomic separation of *I. stellatospora* and *I. lanuginosa*, in agreement with Boursier & Kühner (1928) and Grund & Stuntz (1968).

Inocybe subcarpta sensu lato lacks the squamulose stipe, but weathered specimens could be confused with *I. stellatospora*. In most cases *I. subcarpta* can be distinguished in the field by the pileus that is fibrillose-tomentose to squamulose at the center, lamellae that are pallid for a long time and fibrillose to coarsely-fibrillose stipe. We have made collections of the *I. subcarpta* complex on rotten wood in western North America. Microscopically, some members of the *I. subcarpta* complex can be distinguished by the differently shaped hymenial cystidia that are attenuated towards the apices, thick-walled and crystalliferous. These taxa could be referred to as *I. boltonii* ss. Heim. Fewer collections, however, exhibit cystidia similar to those of *I. stellatospora*, but these lack the floccose-squamulose stipe of the latter. Kuyper (1985), despite the absence of type material, considered *I. mirabilis* Velen. an earlier name for *I. subcarpta*. Given the absence of the holotype and Pilát's latin translation (1948), which describes the spores in part as '... parvis, 5-8 μ ...', we are reluctant to accept this synonymy and consider *I. mirabilis* as doubtful until the holotype is recovered or a neotype designated that matches the original diagnosis.

Kauffman (1924) held a broad concept of *I. longicystis* that included forms of *I. subcarpta* sensu lato. His reference to *I. stellatospora*, '...becoming blackish on drying...', is a misinterpretation of the heterogeneous appearance of the holotype (NYS) collection. Masee (1904) evidently did not observe the mixed condition of Peck's type. Hesler's citation of *I. longicystis* (1937) actually represents *I. lanuginosa* (9494, TENN). Bon (1998) misinterprets *I. stellatospora* as a member of sect. *Petiginosae* R. Heim; the basidiospores do not possess short spines as he suggests, nor is the stipe covering entirely pruinose.

6. *Inocybe teraturgus* M. M. Moser, Persoonia 14(4): 574 (1992). – Fig. 8.

Pileus 15–55 mm diam, obtusely campanulate to convex then appanate with age, with or without a low obscure umbo, margin decurved to briefly so, surface dry, everywhere densely squarrose-scaly with rather small pointed erect fibrillose squarreae, especially on the disc, elsewhere the scales appressed, more sparse towards the margin where it becomes fibrillose-lacerate; color 'Cinnamon-Brown' on the disc, 'Tawny-Olive' to 'Snuff Brown' towards the

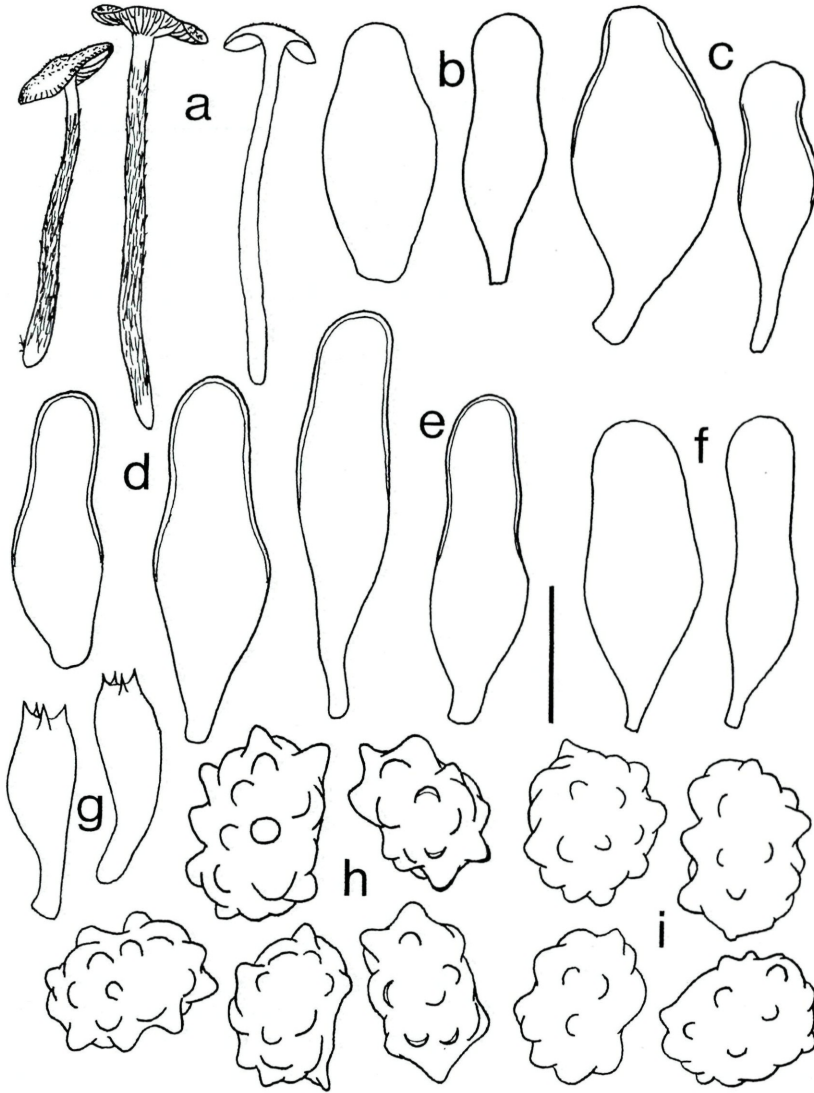


Fig. 8. *Inocybe teraturgus*. – a. Basidiomes (Stz. 11470). – b. Two cheilocystidia (Stz. 11470). – c. Two cheilocystidia (MICH 36299). – d. Three pleurocystidia (Stz. 11470). – e. Pleurocystidium (MICH 36299). – f. Two caulocystidia (Stz. 11470). – g. Two basidia (Stz. 11470). – h. Five basidiospores (Stz. 11470). – i. Four basidiospores (MICH 36299). – Scale bar: a = 3 cm; b–g = 25 μ m; h–i = 10 μ m.

margin (13C7/D7-14B9/C9); context 1–2.5 mm thick, pallid to white below the brown cuticle, unchanging when cut, odor rather strongly like *Lycoperdon*, taste the same. – Lamellae adnate, shallowly rounded sinuate towards the stipe, pointed towards the margin,

moderately broad, up to 4.5 mm, moderately close, color at first white with subtle pinkish tinge to brownish gray, then slightly darker and becoming olivaceous (13D6-E7), edges pallid. – Stipe 55–130 mm × 2.5–8 mm diam, terete to slightly flattened, equal, cortina fugacious, surface dry, apex pruinose, ‘Pinkish Buff’ (11B3), below floccose-squamulose to floccose-fibrillose; ‘Cinnamon-Brown’ shaded ‘Snuff Brown’ below; context solid, in age tending to become hollow upwards, context fibrous (but fragile), pallid, unchanging where cut.

Basidiospores (9.5–)10–12.5(–13.5) × (7–)7.5–10(–11) μm [$\bar{x}_r = 10.4\text{--}12.0 \times 7.6\text{--}9.6 \mu\text{m}$, $\bar{x}_m = 11.0 \pm 0.8 \times 8.4 \pm 0.8 \mu\text{m}$, $Q = (1.10\text{--}) 1.14\text{--}1.50$ (–1.63), $\bar{Q}_r = 1.22\text{--}1.42$, $\bar{Q}_m = 1.33 \pm 0.11$, $n = 10$ spores per 9 collections], coarsely-nodulose, outline elliptic, with (9–) 11–17 (–20) nodules [$\bar{x}_m = 13.77 \pm 2.11$ nodules per spore, $n = 10$ spores per 9 collections], ‘Ochraceous-Buff’. – Basidia (25–)26–36(–38) × (9–) 10–13 (–14.5) μm [$\bar{x}_r = 28.4\text{--}34.5 \times 10.7\text{--}11.9 \mu\text{m}$, $\bar{x}_m = 31.04 \pm 3.04 \times 11.29 \pm 1.03 \mu\text{m}$, $n = 10$ basidia per 9 collections]. – Pleurocystidia frequent, (36–) 41–70 (–88) × (15–) 15.6–24 (–30) μm [$\bar{x}_r = 43.4\text{--}64.0 \times 17.8\text{--}22.0 \mu\text{m}$, $\bar{x}_m = 54.92 \pm 9.63 \times 19.22 \pm 2.83 \mu\text{m}$, $n = 10$ pleurocystidia per 9 collections], often utriform to nearly lageniform, thin- to somewhat thick-walled apically (up to 2.0 μm), hyaline, apices lacking crystals, obtuse to subcapitate, base with a brief pedicel. – Cheilocystidia abundant, (25–)31–66 (–76) × (11–)13–20(–25) μm [$\bar{x}_r = 42.4\text{--}53.6 \times 15.1\text{--}18.1 \mu\text{m}$, $\bar{x}_m = 45.1 \pm 10.8 \times 16.8 \pm 2.7 \mu\text{m}$, $n = 10$ cheilocystidia per 9 collections], similar to pleurocystidia but more often narrowly utriform or ventricose and somewhat smaller, mostly thin-walled, apices bare, often subcapitate, paracystidia clavate to pyriform, thin-walled, hyaline, 22–25 × 11–14 μm . – Caulocystidia restricted to the (extreme) apex of stipe, often in clusters, similar to cheilocystidia, hyaline, thin-walled, cauloparacystidia not differentiated, vestiture hyphae often cylindrical and elongated but similar in color and wall thickness to pileipellis hyphae, stipe hyphae up to 15 μm diam, refractive hyphae present. – Lamellar trama regular, up to 17(–25) μm diam, central hyphae inflated to cylindrical, elements narrower in subhymenium, hyaline, light yellowish brown in mass, golden refractive hyphae present. – Pileipellis a loose trichoderm of tangled or upturned thick-walled hyphae arising from a regularly arranged layer, septa frequent, walls up to 1.0(–1.5) μm thick, with light ochraceous-brown pigment, also (faintly) incrustated, inflated, up to 18 μm diam; tramal hyphae subhyaline to pale ochraceous, inflated, up to 20 μm diam, thin- to slightly thick-walled, regular. – Clamps frequent.

Habit, habitat and distribution. – Scattered to gregarious in *Sphagnum* under *Pinus resinosa* and *P. strobus*, also under other conifers such as *Picea* and *Larix*, at times mixed with

hardwoods like *Alnus* or *Betula*, exceptionally on rotten wood but then in *Sphagnum* bogs. In North America *I. teraturgus* occurs most often in August and is recorded only from the Great Lakes region. In Europe it is recorded from Sweden, Norway and Finland.

Material examined. – CANADA. ONTARIO: Petawawa For. Exp. St, among *Sphagnum*, 7 Sept 1947, leg. A. H. Smith, DAOM 17429 (DAOM); Mer Bleue, among *Sphagnum*, 15 Aug 1957, leg. J. W. Groves, DAOM 56914 (DAOM); between Upper and Lower Selwyn L., Thunder Bay Dist., 49°28'N, 90°51'W, on mossy soil in bog under *Picea*, *Pinus*, *Alnus* and *Larix*, 7 Aug 1987, leg. G. Gilbert, DAOM 197814 (DAOM); Lake Timagami, on *Sphagnum*, 20 Aug 1936, leg. A. H. Smith, Sm. 4044 (WTU); Petawawa, P.O.W. Camp., on rotten log among mosses under *Picea* and *Pinus*, 29 Aug 1947, leg. A. H. Smith, Sm. 26307 (WTU). FINLAND: Varsinais-Suomi, Koski Tl commune, Vähäsorvasto, Sulkalammi, on *Sphagnum* near a small lake, near *Pinus sylvestris*, *Betula* and *Salix* bushes; grid 27 °E: 6735:292, 11 Aug 1990, leg. P. Heinonen & J. Vauras, TURA 986 (TURA; WTU). NORWAY. Sör-Trøndelag, Melhus, Lundemo, in a bog, deep in moss under *Picea* and *Betula*, 21 July 1983, leg. Ö. Weholt, St. 1030 / I39/83 (M). SWEDEN. Helsingbo, 'im Hochmoor' on *Sphagnum*, 3 Aug 1983, leg. E. Ludwig, St. 1044 (M). USA. MICHIGAN: Luce Co., Pike Lake, in *Sphagnum* in a grove of *Pinus resinosa* and *P. strobus*, 10 Aug 1959, leg. A. H. Smith, Stz. 11470 (WTU; UTC163350). MINNESOTA: Minneapolis, substrate not specified, but *Spagnum* at base of stipe, Aug 1921, leg. M. S. Whetstone, MICH 36299 (MICH).

The application of the name *I. teraturgus* M. M. Moser was considered after correspondence with Jukka Vauras, who kindly provided notes of the holotype and Finnish material. A remark is necessary, however, concerning the protologue (Moser, 1992) that describes the stipe as fibrillose with an aspect similar to that of the *I. dulcamara* group. Collections from North America generally possess an elongate stipe and a floccose to squamulose stipe covering. The elongate stipe is likely attributable to growth in *Sphagnum* bogs and probably a variable character. Finnish material likewise possesses a squamulose stipe covering (J. Vauras, pers. comm.) More critically, Vauras' observations of the holotype are in complete agreement with our observations of North American and additional material from Fennoscandia. Thus, we find it justifiable to expand Moser's concept of this species, where one collection is cited, to include collections with a squamulose stipe covering.

Inocybe teraturgus appears similar to other members of the *I. lanuginosa* group in terms of coloration ('Cinnamon-Brown' to 'Snuff Brown'), squarrose to squamulose pileus and floccose-squamulose stipe. However, it differs by its occurrence in *Sphagnum* bogs and microscopically by the larger spores. Stangl & Enderle (1983) included a sphagnicolous form of *I. longicystis* in their key to European nodulose-spored *Inocybes* but chose not to recognize it formally. Their description did not mention the conspicuously large spores so characteristic of *I. teraturgus*, but two collections among

Stangl's material (M) correspond well to this species. *Inocybe cerasphora* Singer (Singer, 1953) shares similar characters with *I. teraturgus* (viz. spore size) but is recorded on rotten *Nothofagus* wood in Tierra del Fuego, Argentina. Singer raised the possible affinity of *I. cerasphora* to *I. subcarpta*. *Inocybe paracerasphora* (Horak) Garrido (Horak, 1977, as *Astrosporina*) differs by the smaller size, occurrence on rotten *Nothofagus* wood in New Zealand, thick-walled hymenial cystidia and smaller basidia. *Inocybe sublanuginosa* Rick is described with large basidiospores (10–12 × 7–8 µm) but occurs on soil in Brazil (Rick, 1938). Fries' concept of *I. plumosa* (Bolt.: Fr.) Quélet (Fries, 1821–1832; 1836–1838; 1857; 1874) is certainly close to that of *I. teraturgus* including the elongate stipe, except that the former is not recorded in *Sphagnum* and lacks a pruinose stipe apex. The concept of *I. plumosa* is certainly not clear.

UPGMA and Neighbor-Joining analyses (Figs. 1 & 2) support the recognition of *I. teraturgus* as a morphological species.

Excluded taxa

Inocybe sabuletorum (Berk. & M. A. Curtis) Sacc., Syll. Fung. 11: 51 (1895). – Fig. 9.

Lectotype (design. here): two 'umbrinous' basidiomes (Holotype, Brown 857, 64221; K)

≡ *Agaricus sabuletorum* Berk. & M. A. Curtis in Cooke, Grevillea 19(89): 103 (1890).

Basidiospores 8–9(–10) × 5–6(6.5) µm [\bar{x} = 8.6 × 5.5 µm, Q = 1.33–1.63, \bar{Q} = 1.56, n = 20 measured from lamellae], angular-nodulose, often pentagonal in outline, with a distinct apical nodule, apiculus small but distinct, with 5–8 low, obtuse nodules, pigmentation pale yellowish-brown. – Basidia 20–21 × 7–8 µm, 4-sterigmate, clavate. – Pleurocystidia frequent, 42–58 × 11–15 µm, (sub)lageniform, occasionally fusiform to cylindrical, sessile, i.e., without a basal pedicel, apices obtuse, crystalliferous, thick-walled, walls up to 4.0 µm thick, walls (pale) yellow to subhyaline. – Cheilocystidia similar to pleurocystidia, at times shorter, paracystidia broadly clavate, not reviving well. – Caulocystidia frequent at the apex, present near the base but scarce, similar to cheilocystidia, refractive hyphae present among the stipe hyphae. – Pileipellis a cutis of rusty-ochraceous hyphae that appears to be surmounted by filamentous, slightly thick-walled hyaline hyphae, subtending tissues not reviving well. – Clamps frequent.

The two blackish basidiomes have the following microscopic characters:

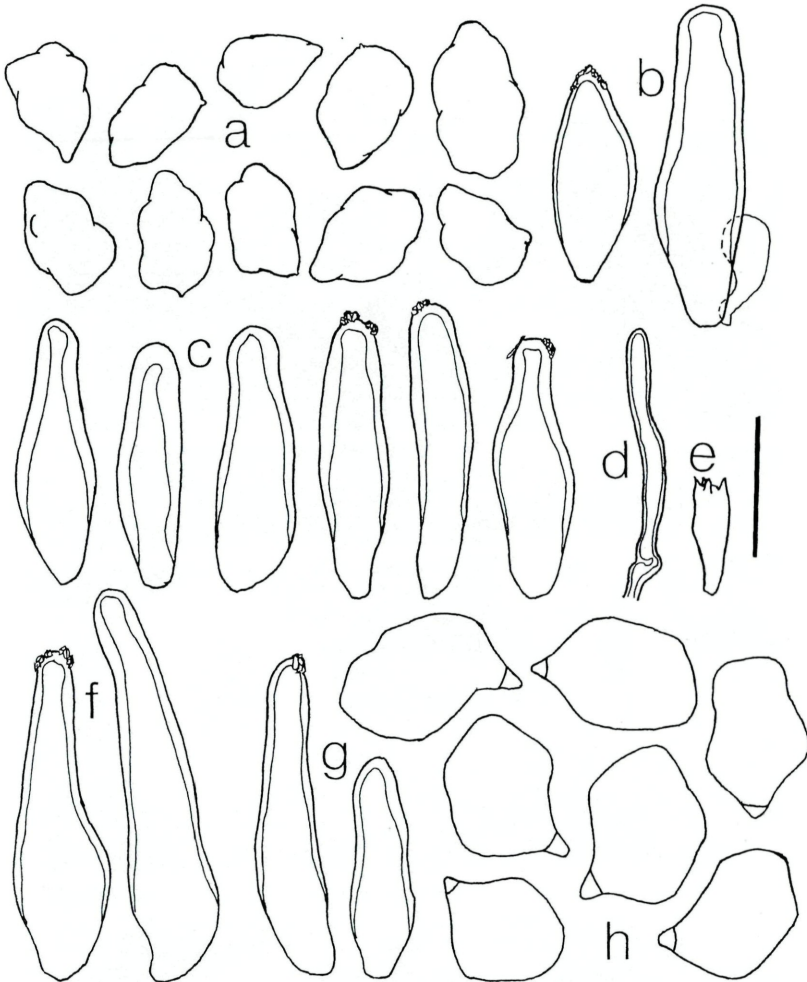


Fig. 9. *Inocybe sabuletorum*. – a. Basidiospores ('light'; Lectotype). – b. Two cheilocystidia, paracystidium ('light'). – c. Pleurocystidia ('light'). – d. Pileipellis element ('light'). – e. Basidium ('light'). – f. Two apical caulocystidia ('light'). – g. Two basal caulocystidia ('light'). – h. Basidiospores ('dark'; Holotype = *Entoloma sensu lato* sp.). – Scale bar: a, h = 10 μ m; b–g = 25 μ m.

Basidiospores 9–11 \times 7–8 μ m [\bar{x} = 9.9 \times 7.3 μ m, n = 13], heterodiametric, 5–8 sided, with faint pigmentation and a prominent apiculus (Fig. 9, h). – Hymenial cystidia not observed. – Pileipellis a cutis, presence of clamps not confirmed, pigments believed to be incrusting but not confirmed. – Stipe hyphae with scattered aggregations of blackish minute granular pigment, these appear exterior to the hyphae, otherwise stipe hyphae brownish yellow in mass. – Caulocystidia not observed. – Clamps present.



Figs. 10–12. Basidiomes of *Inocybe* species. – 10. *Inocybe leptophylla* (CA 3/20/73). – 11. *Inocybe lanuginosa* (CA 3/3/86). – 12. *Inocybe stellatospora* (PBM 569). – Scale bars: 10, 11 = 1 cm; 12 = 3 cm.

Based on the protologue *I. sabuletorum* hardly represents a member of the *I. lanuginosa* group as pointed out by Boursier & Kühner (1928). Masee (1904) had considered *I. sabuletorum* a synonym of *I. lanuginosa*. Consequently, subsequent authors (Rea, 1922; Kauffman, 1924; Pearson & Dennis, 1948) followed Masee. An examination of the holotype reveals that it is heterogeneous consisting of four mounted specimens, two of which are umbrinous or 'Snuff Brown' throughout and approach *I. sapinea* Velen., a member of sect. *Petiginosae* R. Heim; the other two are blackish with angular basidiospores up to 11.5 µm long and represent a species of *Entoloma sensu lato*. We designate the two umbrinous *Inocybe* specimens as the lectotype, which agree reasonably well with the protologue. *Inocybe sabuletorum* would seem to be an earlier name for *I. sapinea* (fide Stangl & Kuyper, 1985; Stangl, 1989) in that the two taxa share similar spore and cystidial characters. However, Velenovsky's latin diagnosis of *I. sapinea* (Velenovsky, 1939) in combination with Kuyper's holotype basidiospore illustrations (Kuyper, 1985) contain a few incongruencies with later interpretations of *I. sapinea* (Stangl & Kuyper, 1985; Stangl, 1989), namely '...zona marginali notato, dense squamuloso, centro fusco, ad marginem alutaceo. St... pallidus...' and basidiospores with 8–12 nodules. The fuscous center of the pileus is similar to that described for *I. nigrodisca* Peck (Peck, 1888; Stuntz, 1954), but the spores of *I. nigrodisca* (Isotype; WTU) are smaller and have more pronounced nodules compared to *I. sabuletorum* and to descriptions of *I. sapinea* (Velenovsky, 1939; Stangl & Kuyper, 1985; Stangl, 1989).

Conclusions

The taxonomy and nomenclatural history of the *Inocybe lanuginosa* group is complex. Early workers operated with broad species concepts often based only on gross morphological characters. In North America, however, a taxonomy based largely on microscopic characters serves to distinguish members of the *I. lanuginosa* group readily. UPGMA and Neighbor-Joining analyses support the segregation of 39 OTUs into four discrete clusters that we recognize as morphological species: *I. lanuginosa*, *I. leptophylla*, *I. teraturgus* and *I. stellatospora*. The recognition of *I. lanuginosa*, *I. lanuginosa* var. *casimiri* and *I. lanuginosa* f. *longicystis* as infraspecific taxa (cf. Heim, 1931) or *I. lanuginosa* and *I. lanuginosa* var. *ovatozystis* (cf. Stangl, 1989) as infraspecific taxa is not supported by these analyses. Both qualitative and quantitative characters comprised the data matrix used in the analyses. Partitioning of quantitative characters into scoreable states was determined by the examination of mean value histograms.

Decision over which concept to apply *I. lanuginosa* is not without debate because Bulliard's plate of *Agaricus lanuginosus* lacks the necessary features to make a determination, i.e., application of the name is ambiguous. A neotype cannot be designated because a lectotype exists. However, ICBN Art. 9.7 allows the designation of an epitype in such instances to fix the interpretation of the lectotype. We choose the concept represented by *I. ovatocystis* to fix the application of *I. lanuginosa* for several reasons: (1) this concept was accepted by North American workers such as Atkinson, Kauffman, A. H. Smith, O. K. Miller and Stuntz. In fact, application of *I. lanuginosa* (= *I. ovatocystis*) in North America has been stable; (2) several European workers also applied the concept of *I. ovatocystis* to *I. lanuginosa*, viz. Bresadola and purportedly Patouillard; (3) application of *I. longicystis* as *I. lanuginosa* was done only in accordance with the rules of the ICBN when 1821 served as the nomenclatural starting point for agarics. Since the starting date has been modified to 1753, Fries' interpretation of *I. lanuginosa* as *I. longicystis* is superseded. Stangl's interpretation of *I. lanuginosa* stems from the consequences of the 1821 nomenclatural starting date.

Additional work on European taxa such as *I. squarrosula* (P. Karsten) Sacc. and *I. subornata* (Britzelm.) is required before nomenclature within the *I. lanuginosa* group is settled. *Inocybe squarrosula* has priority over *I. leptophylla* and *I. subornata* but not *I. lanuginosa* nor *I. stellatospora*. *Inocybe longicystis* Atk. and *I. ovatocystis* do not have nomenclatural priority under any scenario.

Fries (1836–1838) cites two post-Bulliard names as synonyms of *I. lanuginosa*: *Agaricus flocculentus* Pollini and *A. horridulus* Lasch. However, Fries (1857) reapplied *A. flocculentus* to his concept of *A. lanuginosus* only to reverse his decision later (1874). We consider *A. flocculentus* and *A. horridulus* as nomina dubia.

At the moment we hesitate to make any supraspecific systematic judgements in absence of phylogenetic analyses. The monophyly of the *I. lanuginosa* group has not been established.

Acknowledgments

The authors are grateful for the assistance of many people with various aspects of this project. We would especially like to thank Jukka Vauras, Joe Ammirati, John Haines, Bob Fogel, Meinhard Moser, Roy Halling, Dick Olmstead, Jean-Claude Maire and the University of Washington Map Library. We thank Catherine Ardrey for use of slides of *I. leptophylla* and *I. lanuginosa*. We also thank the following individuals for supplying us with herbarium material: Cathie Aime, Rob Countess, Cathy Cripps, Dennis Desjardin, Vera Evenson, Ray Fatto, Sharmin Gamiet, Pam Janszen, Richard Korf, Steve Miller, Greg Mueller, Lorelei Norvell, Ron Petersen, Scott Redhead, Michelle Seidl and Brian Spooner. The following

institutions were instrumental in this study, and we thank their curators and staff for the loan of material: BPI, CUP, DAOM, F, K, KHD, M, MEXU, MICH, MIN, NY, NYS, OSC, SFSU, TENN, UVIC, VPI and WTU. The first author was supported by a departmental systematic fellowship and the Daniel E. Stuntz Memorial Foundation for financial assistance. We thank Dennis Desjardin, an anonymous reviewer and the editors of *Sydowia* for their careful criticisms and improvement of the manuscript.

References

- Abbot, L.A., F. A. Bisby & D. J. Rogers (1985). *Taxonomic Analysis in Biology*. – Columbia University Press, New York, 336 pp.
- Agerer, R. (1987–98). *Colour atlas of ectomycorrhizae*. – Einhorn-Verlag, Schwäbisch Gmünd.
- Atkinson, G. F. (1918). Some new species of *Inocybe*. – *Am. J. Bot.* 5: 210–218.
- Bas, C. 1977. Species-concept in *Amanita* sect. *Vaginatae*. – In: Clemençon, H. (ed.), *The Species Concept in Hymenomycetes*, J. Cramer, Vaduz: 79–91.
- T. W. Kuyper, M. E. Noordeloos, E. C. Vellinga (eds.) (1988). *Flora Agaricina Neerlandica*. – Balkema Publishers, Rotterdam, Vol. 1, 182 pp.
- Bessette, A. E., A. R. Bessette & D. W. Fischer (1997). *Mushrooms of Northeastern North America*. – Syracuse University Press, 582 pp.
- Bon, M. (1998). Clé monographique du genre *Inocybe* (Fr.) Fr. 3ième partie (esp. gibbosporées, = ss-g. *Clypeus*). – *Doc. Mycol.* 28(111): 1–40.
- Boursier, J. & R. Kühner (1928). Notes sur le genre *Inocybe*. – *Bull. Soc. Myc. Fr.* 44: 170–189.
- Bresadola, G. (1892). *Fungi Tridentini*. II. – Tridenti, 4–106 pp.
- Bulliard, P. (1780–1795). *Herbier de la France*. – Paris.
- Christensen, M. & M. E. Noordeloos (1999). *Notulae ad floram agaricinam neerlandicam – XXXVI Tricholoma*. – *Persoonia* 17(2): 295–317.
- Chu-Chou, M. & L. J. Grace (1981). Mycorrhizal fungi of *Pseudotsuga menziesii* in the north island of New Zealand. – *Soil. Biol. Biochem.* 13: 247–249.
- Corner, E. J. H. (1947). Variation in the size and shape of spores, basidia and cystidia in basidiomycetes. – *New Phytol.* 46: 195–228.
- Cripps, C. & O. K. Miller, Jr. (1995). Ectomycorrhizae formed in vitro by quaking aspen: including *Inocybe lacera* and *Amanita pantherina*. – *Mycorrhiza* 5: 357–370.
- Fries, E. M. (1821–1832). *Systema mycologicum, sistens fungorum ordines, genera et species hucusque cognitae*. – Gryphiswaldiae.
- (1836–1838). *Epriocrisis systematis mycologici*. – Upsaliae et Lundae.
- (1857). *Monographia Hymenomycetum Sueciae*. – Upsaliae.
- (1874). *Hymenomycetes Europaei*. – Upsaliae.
- Greuter, W., J. McNeil, F. R. Barrie, H. M. Burdet, V. Demoulin, T. S. Filgueiras, D. H. Nicolson, P. C. Silva, J. E. Scog, P. Trehane, N. J. Turland & D. L. Hawksworth (eds.) 2000. *International code of botanical nomenclature (Saint Louis Code)*. – Koeltz Scientific Books, Königstein, Germany, 474 pp.
- Grund, D. W. & D. E. Stuntz (1968). *Nova Scotian Inocybes*. I. – *Mycologia* 60(2): 406–425.
- Heim, R. (1931). *Le Genre Inocybe*, *Encyclopédie mycologique* 1. – Paris, 429 pp.
- Hesler, L. R. (1937). Notes on southern appalachian fungi, II. – *J. Tenn. Acad. Sci.* 12(3): 239–254.
- Høiland, K. (1984). *Cortinariarius* subgenus *Dermocybe*. – *Opera Bot.* 71: 1–112.
- Holmgren, P. K., N. H. Holmgren & L. C. Barnett (1990). *Index herbariorum*. 8th ed. – Bronx, New York Botanical Garden, New York, 693 pp.
- Horak, E. (1977). *Fungi agaricini Novaezelandiae VI. Inocybe* (Fr.) Fr. and *Astrosporina* Schroeter. – *N. Z. J. Bot.* 15: 713–747.

- (1987). *Astrosporina* in the alpine zone of the Swiss National Park (SNP) and adjacent regions. – In: Laursen, G. A. & al. (eds.). Arctic Alpine Mycology II. Plenum Press, New York: 205–234.
- Karsten, P. A. (1893). *Symbolae ad mycologiam fennicam*, pars XXXII. – Acta Soc. pro Fauna et Flora Fenn. 9(1): 3–11.
- Kauffman, C. H. (1921). Studies in the genus *Inocybe*. I. The species of *Inocybe* in Peck's collections. – Bull. N. Y. St. Mus. 223–224: 43–60.
- (1924). *Inocybe*. – N. Am. Flora 10: 227–260.
- Kobayashi, T. (1993). A new subgenus of *Inocybe*, *Leptocybe* from Japan. – Mycotaxon 48: 459–469.
- Kobayasi, Y. (1952). On the genus *Inocybe* from Japan. – Nagaoa 2: 76–114.
- Konrad, P. & A. Maublanc (1924). *Icones selectae Fungorum*. VI. – Paris, 558 pp.
- (1925). *Icones selectae Fungorum*. – II: Pl 101–109. Paris.
- Kornerup, A. & J. H. Wanscher (1967). *Methuen handbook of colour*. – London.
- Kuhner, R. & J. Boursier (1932). Notes sur le genre *Inocybe*. 1. Les *Inocybes* goniospores. – Bull. Soc. Mycol. Fr. 48: 118–161.
- Kuyper, T. W. (1985). Studies in *Inocybe*–1: Revision of the new taxa of *Inocybe* described by Velenovsky. – Persoonia 12(4): 375–400.
- (1986). A revision of the genus *Inocybe* in Europe. I. Subgenus *Inosperma* and the smooth-spored species of subgenus *Inocybe*. – Persoonia, Suppl. 3: V–247.
- Luz, A. K. (1998). Ectomycorrhizal Agaricales of Tlaxcala, Mexico. – *McIlvainea* 13(2): 13–24.
- Maerz, A. & M. R. Paul (1930). *A Dictionary of color*. 1st Ed. – McGraw-Hill, New York, 207 pp., 55 pl.
- Massee, G. (1904). A monograph of the genus *Inocybe* Karsten. – *Ann. Bot.* 18: 459–504.
- Molina, R., H. Massicotte & J. M. Trappe (1992). Specificity phenomena in mycorrhizal symbioses: community-ecological consequences and practical implications. – In: Allen, M. F. (ed.). *Mycorrhizal functioning: an integrated plant-fungal process*. Chapman & Hall, New York: 357–423.
- Moser, M. (1955). *Kleine Kryptogamenflora II b*. 2nd Ed. – Gustav Fischer Verlag, Stuttgart, 327 pp.
- (1967). *Kleine Kryptogamenflora IIB/2*. 3rd Ed. – Gustav Fischer Verlag, Stuttgart, 443 pp.
- (1978a). *Klein Kryptogamenflora IIB/2*. 4th Ed. – Gustav Fischer Verlag, Stuttgart, 532 pp.
- (1978b). *Fungorum rariorum icones coloratae* 7: 1–48.
- (1992). On two interesting species of *Inocybe* from Sweden. – *Persoonia* 14(4): 571–576.
- Munsell book of color (1976). – Munsell Color. Baltimore, Maryland.
- Munsell soil color charts. (1954). – Munsell Color Company, Inc. Baltimore 18, Maryland.
- Murrill, W. A. (1912). The Agaricaceae of tropical North America–V. – *Mycologia* 4(2): 72–83.
- Nishida, F. (1989). Key to the species of *Inocybe* in California. – *Mycotaxon* 34(1): 181–196.
- Pearson, A. A. (1946). New records and observations. III. – *Trans. Br. Mycol. Soc.* 29(4): 191–210.
- & R. W. G. Dennis. (1948). Revised list of British agarics and boleti. – *Trans. Br. Myc. Soc.* 31: 145–190.
- Peck, C. H. (1887). Report of the botanist. – *Rep. N. Y. St. Mus.* 38: 77–138.
- (1888). Report of the botanist. – *Rep. N. Y. St. Mus.* 41: 51–122.
- Pegler, D. (1983). *Agaric flora of the Lesser Antilles*. – *Kew Bulletin Additional Series IX*. Royal Botanic Gardens, Kew, 668 pp.

- Perez-Silva, E. (1967). Les *Inocybes* du Mexique. – An. Inst. Biol. Univ. Nat. Autón. México 38, Ser Bot. 1: 1–60.
- Phillips, R. (1991). Mushrooms of North America. – Little, Brown & Co., Boston, 319 pp.
- Pilát, A. (1948). Velenovskyyi species novae Basidiomycetum. – Opera Bot. Cechica 6: 5–301.
- Rea, C. (1922). British basidiomycetes: a handbook to the larger British fungi. – Cambridge University Press, London, 799 pp.
- Rick, J. (1938). Agarici riograndenses. – Lilloa 3: 399–455.
- Ricken, A. (1915). Die Blätterpilze. Vols. I–II. – Verlag von Theodor Oswald Weigel, Leipzig. 480 pp., 112 pl.
- Ridgway, R. (1912). Color standards and color nomenclature. – Publ. by the author, Washington, D. C., 43 pp., 53 pl.
- Saitou, N. & M. Nei. (1987). The neighbor-joining method: a new method for reconstructing phylogenetic trees. – Mol. Biol. Evol. 4: 406–425.
- Schmid-Heckel, H. (1988). Pilze in den Berchtesgadener Alpen. – Nationalpark Berchtesgaden, Forschungsbericht 15: 1–136 pp.
- Sime, A. D. & R. H. Petersen (1999). Intercontinental interrelationships among disjunct populations of *Melanotus* (Strophariaceae, Agaricales). – Mycotaxon 71: 481–492.
- Singer, R. (1953). The agarics of the Argentine sector of Tierra del Fuego and limitrophous regions of the Magallanes area. Part 2. The brown-spored genera (except *Cortinarius*). – Sydowia 7: 206–265.
- (1986). The Agaricales in modern taxonomy. 4th Ed. – Koenigstein, Koeltz Scientific Books, Germany, 981 pp.
- Sneath, P. H. A. & R. R. Sokal (1973). Numerical Taxonomy. – W. H. Freeman & Co., San Francisco, 573 pp.
- Stangl, J. (1976). Die eckigsporigen Rißpilze (2). – Z. Pilzk. 42: 15–32.
- (1989). Die Gattung *Inocybe* in Bayern. – Hoppea 46: 5–388.
- & M. Enderle (1983). Bestimmungsschlüssel für europäische eckigsporige Rißpilze. – Z. Mykol. 49(1): 111–136.
- & T. W. Kuyper (1985). Neue and seltene Rißpilz-Arten in der Bundesrepublik Deutschland. – Z. Mykol. 51(2): 257–268.
- Stuntz, D. E. (1954). Studies on the genus *Inocybe* II. New and noteworthy species from Michigan. – Pap. Mich. Acad. Sci. Arts Lett. 39: 53–84.
- Swofford, D. L. (1999). PAUP*: Phylogenetic analysis using parsimony (*and other methods). Version 4. – Sinauer Associates, Sunderland, Mass.
- Trappe, J. M. (1962). Fungus associates of ectotrophic mycorrhizae. – Bot. Rev. 28: 538–606.
- Trigaux, A. (1980). Variabilité d'*Inocybe ovatocystis* Kühn.-Bours. – Doc. Mycol. 11(41): 1–8.
- Velenovsky, J. (1920). České Houby. – Pragae.
- (1939). Novitates mycologicae. – Pragae.
- Zerova, M. Y. (1966). *Inocybe boltoni* Heim var. *ionipes* Boud. (*I. ionipes* Boud.), a mycorrhizal symbiont of the oak (*Quercus robur* L.) and the black poplar (*Populus nigra* L.). – J. Ukrainian Bot. 23(5): 62–66.

(Manuscript accepted 29th October 2000)