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ORIGINAL ARTICLE

Eleven new boreal species of *Inocybe* with nodulose spores

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Abstract The diversity and characteristics of species within *Inocybe* section *Inocybe* Singer were investigated in Finland. As a result, 11 species are described here as new: *Inocybe acutoides*, *I. amicta*, *I. boreocarelica*, *I. bufonia*, *I. ericetorum*, *I. kittilensis*, *I. lapponica*, *I. paludicola*, *I. porcorum*, *I. pseudoteraturgus*, and *I. silvae-herbaceae*. Detailed macroscopic and microscopic descriptions, habitat information, and ITS sequence data are included. The new species are compared with each other and with similar species within the section, and a key is provided for the European boreal species. The types of *Inocybe acuta*, *I. alpigenes*, *I. borealis*, *I. cicatricata*, *I. giacomi*, *I. heterochrominea*, *I. hinnulea*, *I. johannae*, *I. proximella*, *I. purpureobadia*, *I. putilla*, *I. striaepes*, *I. taxocystis*, *I. teraturgus*, *I. tetragonospora*, and *I. umbrinodisca* are treated. The often poorly understood *Inocybe acuta*, *I. borealis*, *I. giacomi,* and *I. proximella*, as well as the recently described *I. purpureobadia*, are characterised on the basis of our own material. *Inocybe borealis*, *I. giacomi,* and *I. purpureobadia* are reported from the boreal zone for the first time. *Inocybe borealis* appears to be a remarkably variable species. *Inocybe striata* and *I. umbrinodisca* are reduced to synonyms of *I. proximella*, *I. heterochrominea* is reduced to a synonym of *I. borealis*, and *I. tetragonospora* to a synonym of *I. alpigenes*. In addition, *Inocybe hinnulea* and *I. striaepes* are reduced to synonyms of *I. giacomi*, and the previously supposed synonymy of *I. johannae* with *I. giacomi* is supported by ITS analysis.

Keywords *Agaricales* · Finland · *Inocybe* · ITS · Taxonomy

Introduction

The large ectomycorrhizal genus *Inocybe* (*Agaricales*, *Inocybaceae*) includes mostly fairly small, inconspicuously brown species. It has been divided into subgenera and sections primarily on the basis of microscopic characteristics, the presence of cortina, and the amount of pruinosity on the stipe. The species in subgenus *Inocybe* section *Inocybe* Singer, or section *Cortinatae* Kühner & Boursier, have typically angular/nodulose spores, thick-walled pleurocystidia, a cortina, and a stipe that is not pruinose or only slightly pruinose at the apex. The phylogenetic studies of Matheny and Moreau (2009) and Ryberg et al. (2010) have indicated that section *Inocybe* is polyphyletic, and Matheny and Moreau (2009) restricted this section to a small clade of three species. For practical reasons, we have used Singer's concept of section *Inocybe* based on morphology. This section is one of the largest within the genus. Its species occur worldwide including the tropics (e.g. Buyck and Eyssartier 1999; Horak 1979; Matheny et al. 2003; Singer et al. 1983), but a large majority seems to be temperate, boreal or arctic/alpine (Matheny et al. 2003; Singer 1962). In a recent key to section *Inocybe* in the Nordic countries, Jacobsson (2008) included 22 species. Of these, 13 species were recorded from the temperate zone, 18 from both the hemiboreal and boreal zones, and 8 from the arctic/alpine zone.

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In the past, European mycologists have often been confused about the identities and separation of species within section *Inocybe*. Species may have been interpreted differently because of morphological similarity, intraspecific variation, and the use of old, vague descriptions, sometimes without type specimens. For this reason, a species may have been described as new several times. We, too, were confronted with identification problems. Our study began from our disagreement about the identity of *I. acutoides*; whether it should be a separate species on the basis of its morphology. Molecular methods involving ITS (internal transcribed spacer) analysis proved invaluable. ITS analyses had previously been successful for identification of *Inocybe* species (E. Larsson, personal communication), as well as species in many other fungal genera. We found that most of our specimens could be grouped using ITS in accordance with their morphology and, consequently, could be recognized as species. Of the 11 new species described here, 6 were identified by this means, whereas *I. acutoides*, *I. ericetorum*, *I. paludicola, I. porcorum,* and *I. pseudoteraturgus* were identified prior to our use of ITS. The ITS sequences usually diverged considerably at species level, thus supporting the observations of Larsson et al. (2009) that ITS is well suited for the identification of *Inocybe* species. Despite the morphological similarities between most species presented in this paper, only a few were closely related according to the ITS data. However, we doubt whether all specimens with identical or nearly identical ITS but surprisingly different morphology can be conspecific, as appeared in a few cases discussed later in this paper.

An essential part of our study was to compare our material with the type specimens, type descriptions, and other specimens of morphologically similar species. We worked in particular on taxa that were more or less similar to *Inocybe acuta* Boud. or *I. proximella* P.Karst., and later included *I. purpureobadia* Esteve-Rav. & A.Caball., *I. ericetorum, I. pseudoteraturgus,* and *I. porcorum.* We found that the study of cheilocystidia or caulocystidia often gives important clues to identification. A problem was that some specimens had abortive spores, i.e. the spores had not been well-formed.

In summary, the identification of many species described in this paper is difficult without molecular annotation. Observation of many characters is required, and habitat information is often crucial. A new key based on the most recently published key of the Nordic species of section *Inocybe* (Jacobsson 2008) is provided.

Materials and methods

Our descriptions of the new species, as well as of *Inocybe acuta*, *I. borealis* M.Lange, *I. giacomi* J.Favre, *I. proximella,* and *I. purpureobadia*, were based on fresh collections and herbarium specimens from TUR, TUR-A, H and OULU. Enrico Bizio provided collections of *I. striata* Bres., and Fernando Esteve-Raventós provided an isoparatype of *I. purpureobadia*. Type specimens of the following species were also examined: *I. acuta*, *I. alpigenes* E.Horak, *I. borealis*, *I. cicatricata* Ellis & Everh., *I. giacomi*, *I. heterochrominea* Grund & Stuntz, *I. hinnulea* Kühner, *I. johannae* Kühner, *I. proximella*, *I. putilla* Bres., *I. striaepes* Kühner, *I. striatorimosa* P.D.Orton, *I. taxocystis* (J.Favre & E.Horak) Senn-Irlet, *I. teraturgus* M.M.Moser, *I. tetragonospora* Kühner, and *I. umbrinodisca* Kühner. Drawings showing significant new microscopic information are included. Types of *I. carelica* Singer, *I. radiata* Peck, and *I. umboninota* Peck could not be obtained for loan. Thus, these species were compared from literary descriptions alone. The examined specimens were deposited in TUR-A, unless otherwise stated.

Macroscopic features were noted, and cross-sections were drawn from fresh fruitbodies. The colour codes refer to Küppers (1981, 1999), or Cailleux (1981). Vegetation, especially trees and bushes, was observed at the collection sites. Microscopic features were measured and drawn from dried material mounted in 10% NH_4OH solution at ×1,000 magnification. Numbers of structures measured and numbers of collections are included in descriptions. Spore lengths included nodules, cystidial lengths excluded crystals, and basidial lengths excluded sterigmata. The sizes of spores, basidia and cystidia are given as length × width. The range is in parentheses; between the parentheses is the 90% confidence interval with the mean underlined. When fewer structures have been measured the interval is the range. The Q value means the ratio of spore length to spore width (calculated for each spore).

The ITS region including 5.8S rDNA was analysed from the holotypes of the new species, from several other specimens marked * in the descriptions, and from all other treated types except *Inocybe acuta*, *I. putilla* and *I. teraturgus*. Of these three species, ITS was analysed from some TUR-A herbarium specimens. In addition, the 5′ end of the LSU (large subunit) region of rDNA was analysed from the type and one Finnish collection of *I. borealis* to compare ITS because of divergence in spores. Amounts of 0.1–2.3 mg of dried lamella were sampled. To prevent contamination between samples, benches, pincers, and gloves were cleaned with ethanol, and the pincers were also flamed between samplings. Samples were frozen in liquid nitrogen and then ground. DNA was extracted from most specimens and from all old types using a NucleoSpin Tissue XS kit (Macherey-Nagel). Although this kit is made for human or animal material, it worked well for these fungi. A NucleoSpin Plant kit (Macherey-Nagel) was used for some specimens. For specimens that were several decades old, ITS1 and ITS2 were analysed separately. The PCR primers were ITS1-F, ITS4-B (Gardes and Bruns 1993), ITS2, ITS3 (White et al.

1990), LROR (Cubeta et al. 1991), and LR5 (Rehner and Samuels 1995). The PCR was run using a GeneAmp PCR system 9700 (PE Applied Biosystems), with Pure Taq Ready-To-Go PCR beads (GE Healthcare). The reaction volume was 25 µl. The PCR procedure consisted of 5 min at 94°C, 30–38 cycles of 1 min at 94°C, 1 min at 55°C, and 1 min at 72°C, and then a final extension step of 7 min at 72°C. PCR products were purified using GFX PCR DNA and Gel Purification kit (GE Healthcare), Ezna Cycle Pure Kit (Omega), or the service provided by Macrogen. Sequencing was done by Macrogen. The primers ITS1, ITS4 (White et al. 1990), ITS2, ITS3, LR3, and LR3R (Rehner and Samuels 1995) were used for sequencing. Sequences were edited using Seqman (DNAStar), aligned using ClustalW (www.ebi.ac.uk/clustalw/), and compared visually. Loci with ambiguous bases were usually excluded from comparisons. Sequences from all the types, sequences that show intraspecific divergence, and some additional sequences, have been submitted to GenBank and one sequence to EMBL-Bank; in total, ITS sequences of 84 specimens and two LSU sequences. All related species with rather similar sequences are indicated in the comments.

The phylogenetic analysis was performed using MEGA5 (Tamura et al. 2011). In addition to the species within this paper, two nodulose-spored species from sect. *Marginatae* Kühner (GenBank FJ755798, FJ531872) and three smooth-spored species from other sections (FJ436328, FJ436331, JN580886) were included. Only sequences of types were accepted, apart from those of our own collections. Some outgroups were tested, but were discarded from the final run. Sequences were aligned using MUSCLE, adjusted manually, and run by the maximum likelihood (ML) analysis with 500 bootstrap replicates, a GTR model, uniform rates, the NNI heuristic method, and an automatically obtained initial tree. Using a tree from the maximum parsimony (MP) run as an initial tree did not improve the log likelihood value. Gaps were included as missing data.

The vegetation zones and biogeographical provinces used are following Knudsen and Vesterholt (2008), and the zones within the boreal zone are following Sjörs (2004).

Key to *Inocybe* section *Inocybe* Singer in boreal and hemiboreal zones of Europe: key modified from *Funga Nordica* (Jacobsson 2008)

1. Spores ± smooth, elongate . . . . . . *I. lacera*
   - Spores angular to nodulose 2
2. Pileus golden yellow . . . . . . *I. aurea*
   - Pileus other colour 3
3. Pileus scaly. 4
   - Pileus fibrillose 11
4. Lamellae distinctly yellow when young; spores 6–7×5–6 µm, with few nodules . . . . . . *I. relicina*
   - Lamellae white to pale grey when young 5
5. Pleurocystidia absent (but thin-walled cheilocystidia abundant) . . . . . . *I. leptophylla*
   - Pleurocystidia present 6
6. Stipe fibrillose without scales 7
   - Stipe scaly. 8
7. Pleurocystidia thin-walled and mostly without crystals . . . . . . *I. subcarpta*
   - Pleurocystidia thick-walled and mostly with crystals . . . . . . *I. porcorum* sp. nov.
8. Spores 9.5–12.5×7–9.5 µm; in fens amongst *Sphagnum* . . . . . . *I. teraturgus*
   - Spores on average smaller; in forests, rarely in *Sphagnum* 9
9. Pleurocystidia short, clavate to pyriform. . . . . . . *I. lanuginosa*
   - Pleurocystidia cylindrical to lageniform. 10

10. Pleurocystidia mostly without crystals, walls up to 1 μm thick; usually in moist *Picea* forests . . . . *I. stellatospora*

- Pleurocystidia mostly with crystals, walls up to 3(−4) μm thick; habitat variable . . . . *I. pseudoteraturgus* sp. nov.

11. Stipe base ± bulbous 12

- Stipe base not bulbous 17

12. Stipe apex abundantly pruinose . . . . *I. rivularis*

- Stipe not at all pruinose or only at extreme apex 13

13. Pileus typically with acute umbo 14

- Pileus with obtuse umbo 15

14. With *Salix*; stipe dark; spores rather dark yellow brown . . . . *I. acuta*

- Not restricted to *Salix*; stipe paler; spores rather pale yellow brown . . . . *I. bufonia* sp. nov.

15. Stipe base subbulbous; spores 9.5−12×6−8 μm. . . . . *I. porcorum* sp. nov.

- Stipe base distinctly bulbous 16

16. Spores 8.5−11×6−8 μm, with very prominent nodules, nearly star-shaped . . . . *I. napipes*

- Spores 7−9×5−7 μm, nodules not very prominent . . . . *I. assimilata*

17. Pileus with distinct velipellis; on sandy soil 18

- Pileus without velipellis 19

18. Spores angular to very weakly nodulose; pileus not rimose. . . . . *I. purpureobadia*

- Spores distinctly nodulose; pileus margin often rimose . . . . *I. ericetorum* sp. nov.

19. Pleurocystidia fusiform with subacute apex. . . . . *I. curvipes*

- Pleurocystidia otherwise shaped 20

20. Spores distinctly elongate 21

- Spores not or somewhat elongate 24

21. Spores 8−15 (−20)×5−7 μm, irregular . . . . *I. rennyi*

- Spores shorter and not as irregular 22

22. Pileus strongly rimose; pleurocystidia slightly thick-walled (to 1 μm) . . . . *I. undulatospora*

- Pileus not strongly rimose; pleurocystidia thick-walled (to 2−3 μm); occasionally with distinctly elongate spores. 23

23. With *Salix* on alluvial lake and river shores; pileus typically rather dark grey brown; metuloid caulocystidia usually infrequent at stipe apex . . . . *I. acutoides* sp. nov.

- Not restricted to *Salix* and alluvial sites; pileus colour more variable; metuloid caulocystidia usually frequent at stipe apex . . . . *I. borealis*

24. Spores with large nodules, often quadrangular star-shaped, 6.5−10×5−7.5 μm . . . . *I. pseudoasterospora* var. *microsperma*

- Spores otherwise shaped 25

25. Pleurocystidia thin-walled or slightly thick-walled 26

- Pleurocystidia distinctly thick-walled. 27

26. Spores 6−8×5−6.5 µm; pileus rarely somewhat scaly . . . . *I. soluta*

- Spores 8−11×5−7 µm; pileus often scaly . . . . *I. subcarpta*

27. With *Quercus* or *Tilia*, up to the southern boreal zone . . . . *I. putilla*

- Not restricted to *Quercus* or *Tilia* 28

28. Stipe apex abundantly pruinose . . . . *I. rivularis*

- Stipe not at all pruinose or only at extreme apex 29

29. Stipe distinctly white flocculose to felted. 30

- Stipe not or weakly flocculose 33

30. In fens amongst *Sphagnum* . . . . *I. paludicola* sp. nov.

- In other habitat. 31

31. Pleurocystidia mostly fusiform; in dry sandy habitats . . . . *I. ericetorum* sp. nov.

- Pleurocystidia mostly lageniform 32

32. Stipe typically strongly white felted; spores usually with medium-sized nodules, 8−10×5.5−7 µm . . . . . . *I. amicta* sp. nov.

- Stipe not as strongly white felted; spores usually with small nodules, 7−9×5−7 µm . . . . *I. boreocarelica* sp. nov.

33. Pileus dark brown 34

- Pileus paler: brown, grey brown, yellow brown or red brown 40

34. Umbo usually acute; often with dark fibres at stipe base; spores usually with many nodules; in moist habitats . . . . *I. bufonia* sp. nov.

- Umbo not or rarely somewhat acute; no dark fibres at stipe base; spores usually with not so many nodules 35

35. Walls of hymenial cystidia up to 3−4 µm thick, often distinctly thickened in neck . . . . *I. giacomi*

- Walls of hymenial cystidia up to 2−3 µm thick, not or weakly thickened in neck. 36

36. With *Salix* on alluvial lake and river shores . . . . *I. acutoides* sp. nov.

- Not restricted to *Salix* 37

37. Pleurocystidia mostly fusiform . . . . *I. ericetorum* sp. nov.

- Pleurocystidia mostly lageniform to utriform 38

38. Spores angular to very weakly nodulose; pileus often with velipellis . . . . *I. purpureobadia*

- Spores distinctly nodulose; pileus without velipellis 39

39. Spores 8−10×5.5−7 µm, with medium-sized to rather large nodules; metuloid caulocystidia frequent . . . *I. borealis*

- Spores 9.5−12×6.5−8 µm, with rather small nodules; metuloid caulocystidia scarce . . . . . *I. porcorum* sp. nov.

40. Spores weakly nodulose to angular 41

- Spores distinctly nodulose 46

41. Many hymenial cystidia with subcapitate apex . . . . *I. kittilensis* sp. nov.

- Hymenial cystidia rarely with subcapitate apex 42

42. Some spores with a strongly protruding apical nodule 43
    - Spores without or rarely with strongly protruding nodules 44
43. With *Salix* on alluvial lake and river shores; metuloid caulocystidia usually infrequent; pileus not yellow brown . . . . . *I. acutoides* sp. nov.
    - Not restricted to *Salix* and alluvial sites; metuloid caulocystidia usually frequent; pileus often yellow brown . . . . . *I. borealis*
44. Pleurocystidia mostly fusiform . . . . . *I. ericetorum* sp. nov.
    - Pleurocystidia mostly lageniform to utriform 45
45. Umbo rather acute; in moist habitats . . . . . *I. lapponica* sp. nov.
    - Umbo obtuse; in drier habitats . . . . . *I. giacomi*
46. In fens amongst *Sphagnum*; spores with many small nodules . . . . . *I. paludicola* sp. nov.
    - In other habitat. 47
47. Spores usually with many medium-sized to rather large ± hemispherical nodules; with *Picea* 48
    - Spores with fewer or smaller nodules 49
48. Caulocystidia very variable; spores 8−10×5.5−7 μm . . . . . *I. silvae-herbaceae* sp. nov.
    - Caulocystidia not so variable, typically with tapering apex; spores 8.5−11×6.5−8 μm . . . . . *I. proximella*
49. Hymenial cystidia mostly fusoid; on sandy soil. . . . . . *I. ericetorum* sp. nov.
    - Hymenial cystidia mostly lageniform 50
50. Umbo usually acute; in moist habitats, often in *Sphagnum* . . . . . *I. bufonia* sp. nov.
    - Umbo usually obtuse; rarely in *Sphagnum*. 51
51. Walls of hymenial cystidia often distinctly thickened in neck, up to 4 μm thick; stipe usually distinctly felted or flocculose . . . . . *I. boreocarelica* sp. nov.
    - Walls of hymenial cystidia weakly or not thickened in neck, stipe rarely flocculose 52
52. Spores 9.5−12×6.5−8 μm, usually with rather small nodules . . . . . *I. porcorum* sp. nov.
    - Spores on average smaller and with medium-sized to rather large nodules. 53
53. With *Salix* on alluvial lake and river shores; metuloid caulocystidia usually infrequent; pileus not yellow brown . . . . . *I. acutoides* sp. nov.
    - Not restricted to *Salix* and alluvial sites; metuloid caulocystidia usually frequent; pileus often yellow brown . . . . . *I. borealis*

Taxonomy

Inocybe acuta Boud., *Bull. Soc. Mycol. France* 33: 8 (1917)

Figs. 1 and 2

Synonym: *Inocybe acutella* Bon, *Doc. mycol.* 6: 45 (1976).

Pileus 0.7–4.2 cm in diameter, conical, conico-convex or applanate, umbo usually prominently acute or rather acute, rarely obtuse; dark brown (30S, 30 T, 30R, 33S, 53R, 70S, 70T), at times reddish brown (57P), usually blackish brown in the centre and palest at the outer margin; slightly viscid or dry, centre smooth, outwards radially fibrillose, at times rather villose, sometimes breaking up, velipellis lacking, rarely scant remnants of cortina at margin. *Lamellae* rather broad, up to 5 mm, ventricose, adnexed, moderately crowded or sometimes rather distant; pale grey, yellow grey to grey brown, dark brown when old, edge concolorous or paler. *Stipe* 1.5–7.5 cm long, 1.5–6 mm wide, widening slightly downwards, base subbulbous to non-marginately bulbous, rarely base only slightly wider; usually intensely red brown turning darker lower down, at times dark brown or yellow brown or vividly colourful:

Fig. 1 *Inocybe acuta*. Finland, Oulu, Ruotsalainen & Vauras 2151F. Photograph J. Vauras

whitish apex turns yellow lower down and then gradually red brown, apex and base usually whitish; usually faintly fibrillose striate, rarely somewhat felted, apex pruinose. *Cortina* present in young specimens. *Context* in pileus whitish, yellowish, or pale brownish grey, in stipe somewhat shiny, grey, or in the upper part whitish to yellowish and lower down red brown, paler than surface, in bulb often whitish. Smell indistinct to slightly spermatic. No specific taste.

Spores (8.3) 9.0–10.2–11.8 (12.3)×(5.8) 6.0–6.6–7.2 (7.4) µm, total range of mean values 9.2–10.9×6.5–6.7 µm, Q=(1.25) 1.3–1.54–1.8 (1.85), total range of mean Q values 1.41–1.68 (100 spores from 5 Finnish collections); weakly nodulose with a few obtuse nodules, or angular, rather dark yellow brown. *Basidia* (22) 25–31–36 (37)×(8) 9–11–13 (14) µm (*n*=40), clavate, 4-spored. *Pleurocystidia* (47) 55–63–72 (75)×(12) 14–18–22 (26) µm (*n*=52); narrowly to rather broadly lageniform with cylindrical, conical or weakly subcapitate apex, rarely utriform or fusoid, apex usually crystalliferous, wall up to 2 (rarely −3.5) µm thick, pale yellow. *Cheilocystidia* generally shorter and wider than pleurocystidia, apex often subcapitate, a few with thin walls; rarely with yellowish contents, typical paracystidia rare. *Caulocystidia*: metuloids rather rare to frequent at stipe apex, similar to pleurocystidia, rarely fusoid or ellipsoid; long hyphoid thin-walled cystidia abundant, flexuous or cylindrical, at times with protuberances or short branches; rarely with brownish or yellow contents; cauloparacystidia with thin or slightly thick walls, numerous.

Habitat: Moist places with *Salix*, usually *Salix* thickets on alluvial shores of lakes, rivers, or ponds, also margins of fens, moist depressions in forests and old sand-pits, amongst mosses like *Sphagnum* or leaf litter, also above timberline in

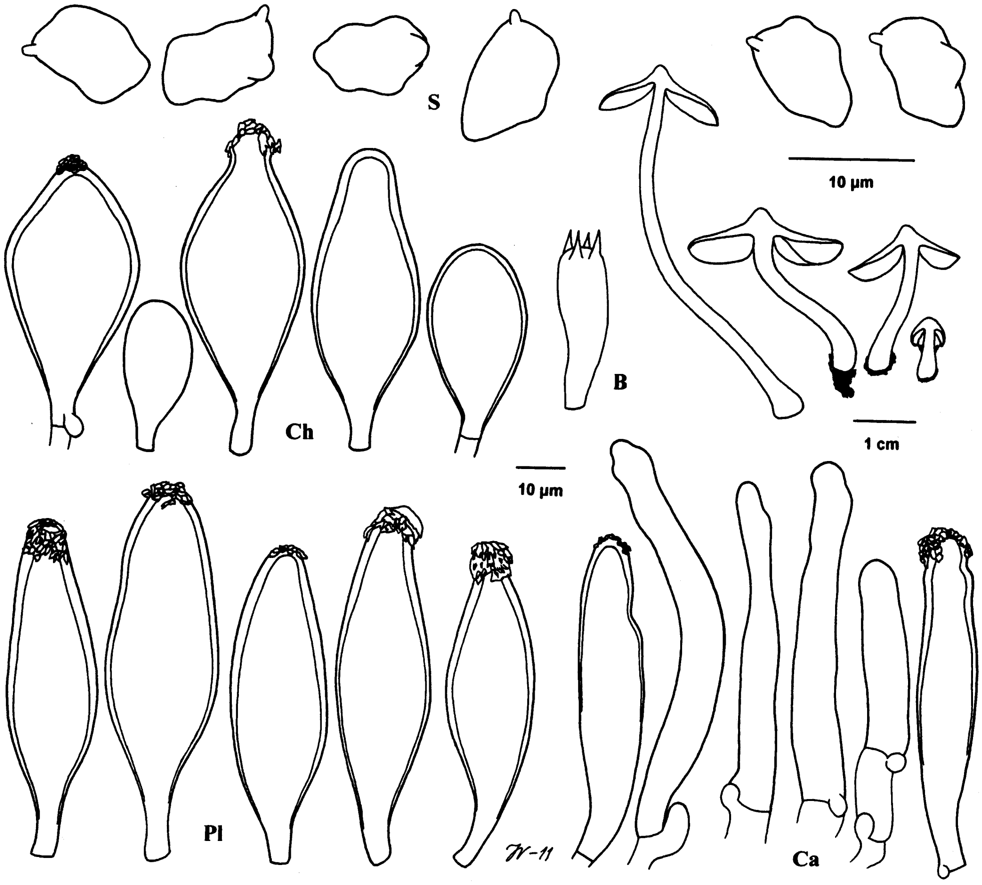


Fig. 2 *Inocybe acuta*. Holotype: spores, cheilocystidia and pleurocystidia. Ruotsalainen & Vauras 2151F: caulocystidia and *left* cross-section of a fruitbody. Vauras 2247F: other fruitbodies. *B* basidium/basidia, *Ca* caulocystidia at apex of stipe, *Ch* cheilocystidia, *Pl* pleurocystidia, *S* spores

snow beds with *Salix herbacea*. At least *S. phylicifolia* or *S. myrsinifolia* is a host in the lowlands of Finland.

Distribution: Western and northern Europe, from temperate to arctic/alpine zone.

Phenology: Mid-July to early October.

Holotype: *Inocybe acuta*. France, Montmorency, inter Sphagna, Septembro 1892 (PC). – Spores 8.5–9.2–10.2 (10.5)×5.6–6.2–6.5 (6.8) µm, Q=1.35–1.49–1.7 (*n*=20). Pleurocystidia 58–73×17–22 µm (*n*=6), wall up to 2.5 µm thick, pale yellow. Cheilocystidia 37–63×20–26 µm (*n*=5), some yellow brown inside. Paracystidia thin-walled, ellipsoid. Basidium 31×10 µm, 4-spored. Caulocystidia not studied.

Comments: To be characterised shortly within the section *Inocybe*, *I. acuta* has a dark appearance with prominent umbo, stipe with whitish bulb at base, and rather dark spores.

The identity of *Inocybe acuta* has been constantly misunderstood since Kühner and Boursier (1932) regarded it as a variable species of montane spruce forests. The confusion, involving, for example, the wrong habitat ("bei Nadelbäumen, auf kalkhaltigen Boden"), can be found in literature such as the key provided by Stangl and Enderle (1983). And still, recently, Breitenbach and Kränzlin (2000) synonymised *I. striata* with *I. acuta*.

Boudier saved a type specimen, remarked on its growth among *Sphagnum*, and described this species well. One reason for the misunderstandings has probably been that *Salix* thickets have largely been ignored as collection sites. Also, Lange (1917) regarded *I. acuta* as synonymous with *I. umboninota* Peck. Adding to the confusion, Bon (1976) described *I. acutella*, a species resembling *I. acuta* and growing in *Sphagnum* near *Salix* and *Alnus*. He stated that *I. acutella* differs from *I. acuta* (and the separate *I. umboninota*) in spores and habitat, but did not state whether he had studied the type of *I. acuta* (Bon 1976, 1979). Romagnesi (1989) did study the type of *I. acuta* and regarded it as a synonym of *I. acutella*; a conclusion we share. In microscopic features, the type of *I. acuta* clearly coincided with our collections from *Salix* thickets and with Bon's detailed descriptions of *I. acutella*. The macroscopic features also matched.

Peck (1884) offered a scanty description of *Inocybe umboninota* from the United States, but fortunately saved a type. Esteve-Raventós (1987) found the spores of Peck's type to be star-shaped, and thus clearly deviating from the spores of *I. acuta* Boud., judging from his photographs. Kauffman (1924) described *I. prominens* from one of Peck's collections of *I. umboninota*. The microscopic features of *I. prominens* do not fit *I. acuta* either: the spores are smaller, 6–8×4–6 µm, sometimes irregularly subglobose, and the cystidia have thin walls (Kauffman 1924).

All the studied five ITS sequences were identical apart from two loci, where the collection JR&JV2151F had ambiguous bases C or T (GenBank JN580803), three collections had bases T (KK293/03 in the phylogram - JN580804) and the Estonian collection had bases C (JN580805).

Specimens examined: **DENMARK**. **Western Jylland.** West of Ribe, Staunsager Plantage, 28.IX.1996 Nielsen 96–51. **ESTONIA**. **Viljandimaa**. Kolga-Jaani, Alam-Pedja Nature Reserve, 25.VIII.1997 Põldmaa. **Võrumaa**. Haanja, Väikjärv E, 1.X.1997 Vauras 12960*. **FINLAND**. **Varsinais-Suomi**. Kemiönsaari, Dragsfjärd, Holma, 27.IX.1995 Vauras 10866. Koski Tl., Vähä-Sorvasto, Sulkalammi, 2.IX.1991 Heinonen & Vauras 5983. Kustavi, Puorenjärvi, 31.VII.1993 Vauras 8016 (TUR). **Satakunta**. Pori, Kankaanpään lehtokorpi, 11.IX.1996 Vauras 11916*, Noormarkku, Finpyy, 21.IX.2006 Kokkonen & Vauras 24296. **Etelä-Häme**. Tampere, Peltolammi, 15.VII.1976 Söderholm 124 (TUR). Urjala, Raikko, 22.VIII.2003 Vauras 20096. **Etelä-Savo**. Kerimäki, Hautaniemi, 8.IX.2006 Ruotsalainen & Toivonen 6234 (TUR). **Pohjois-Häme**. Äänekoski, Parantala, 31.VII.1986 Storbacka & Vauras 2133. **Pohjois-Savo**. Kuopio, Kolmisoppi, 22.VII.1984 Vauras 1640F, 1.VIII.1985 Vauras 1886F, 2.VIII.1986 Vauras 2145, Karhonsaari, 30.IX.1984 Ruotsalainen, 3.X.1985 Ruotsalainen. **Pohjois-Karjala**. Nurmes, Metelinmäki, 23.IX.2002 Kokkonen, Metsä-Vastimo, 30.VIII.2002 Kokkonen, 30.VIII.2003 Kokkonen 293/03*, Pahakala, 4.VIII.2003 Kokkonen. Valtimo, Mahalanniemi, 29.VIII.2002 Kokkonen, 18.IX.2002 Kokkonen, 17.IX.2003 Kokkonen 677/03. **Oulun Pohjanmaa**. Oulu, Sanginsuu, 4.VIII.1986 Ruotsalainen & Vauras 2151F* (TUR, TUR-A). **Koillismaa**. Kuusamo, Juuma, 1.IX.1996 Vauras 11727, Petäjäkangas, 1.9.2008 Kokkonen & Vauras 222/08. **Kittilän Lappi**. Kittilä, southeast side of church village, 27.8.2008 Kokkonen 178/08. **Enontekiön Lappi**. Enontekiö, Kilpisjärvi, Goallarrassa, 11.VIII.1986 Metsänheimo, Leutsuvaara, 14.VIII.1986 Vauras 2247F, Maunu, 14.VII.2006 Toivonen 6054 (TUR), Palojärvi, Galdotieva, 11.VIII.2004 Höijer 3651 (TUR), Vähäniva, 8.VIII.1986 Vauras 2194, 2195. **Inarin Lappi**. Utsjoki, Kevo, 18.VIII.1995 Vauras 10520, Pappila, 16.VIII.1961 Kallio et al. (TUR), Pulmankijoki, 28.VIII.2005 Kokkonen*. **FRANCE**. Montmorency, IX.1892 (holotype, PC). **NORWAY**. **Finnmark**. Tana, Gæidnogaissa, 20.VIII.1963 Kankainen (TUR).

Inocybe acutoides Kokkonen & Vauras, **sp. nov.**

Figs. 3 and 4

MycoBank number: MB 563068

Etym.: resembles *Inocybe acuta* in macroscopic and microscopic features and in habitat.

Pileo 0.9–4.2 cm lato, umbonato, fusco-brunneo vel brunneo, fibrilloso. Lamellis usque ad 7 mm latis et

Fig. 3 *Inocybe acutoides*. Type locality, Kokkonen 124/09. Photograph K. Kokkonen

ventricosis. Stipite 3.0–7.9 cm longo, 2–7 mm crasso, sine bulbo. Inodora. Sporis (7.5) 8.3–10.8 (11.7)×(5.0) 5.6–7.1 (7.4) µm, angulato-nodulosis. Pleurocystidiis (48) 51–73 (76)×(13) 15–24 (28) µm, lageniformibus. Cum Salicibus.

Holotypus: **Finland**, Koillismaa, Kuusamo Municipality, Oulanka National Park, Jäkälämutka, Jäkälämutkanlampi, *Salix* thicket by the Oulankajoki River, near *S. phylicifolia, S. lapponum, Ranunculus repens, Filipendula ulmaria, Potentilla palustris, Calamagrostis canescens, Galium palustre*, and *Scutellaria galericulata*; amongst leaf litter, *Climacium dendroides* and *Calliergon cordifolium*, Grid 27°E: 73581:36182, alt. ca. 138 m, 1.IX.2007 *K. Kokkonen* 575/07 (TUR-A 190464, isotypi GB, H, WTU), GenBank JN580806.

Pileus 0.9–4.2 cm in diameter, 0.5–1.3 cm high, conical to conico-convex when young, then campanulate to applanate, margin often reflexed when old, prominently umbonate, umbo obtuse, usually somewhat hemispherical, rarely nearly acute; rather dark, getting paler towards margin, chestnut brown ($S_{70}Y_{90}M_{50}$) or grey brown (near $S_{50}Y_{70}M_{40}$, $S_{60}Y_{50}M_{50}$, $S_{40}Y_{60}M_{40}$), umbo dark brown ($S_{90}Y_{90}M_{60}$-$S_{70}Y_{60}M_{40}$); very weakly viscid, centre smooth, outwards radially fibrillose, at times breaking up, velipellis lacking. *Lamellae* rather broad, up to 7 mm, ventricose, adnexed or narrowly adnate, often with a small decurrent tooth, moderately crowded; when young pale grey or pale grey brown (near $S_{20}Y_{30}M_{10}$), later grey brown ($S_{20}Y_{50}M_{30}$, $S_{30}Y_{40}M_{10}$, $S_{40}Y_{50}M_{20}$), edge concolorous or paler, even or minutely fimbriate. *Stipe* 3.0–7.9 cm long, 2–7 mm wide, equal or widening slightly downwards, base roundish; when young whitish, then pale brown having at times a red or grey tinge ($S_{20}Y_{50}M_{30}$, near $S_{00}Y_{30}M_{10}$, $S_{10}Y_{30}M_{10}$), base often white; dry, faintly fibrillose striate, rarely slightly flocculose, apex pruinose; solid. *Cortina* whitish. *Context* in pileus whitish to pale grey or pale grey brown; in stipe whitish to pale brown with a red tinge (near $S_{00}Y_{30}M_{10}$), usually paler than surface, longitudinally striate. Smell indistinct or rarely slightly spermatic. No specific taste.

Spores (7.5) 8.3–9.5–10.8 (11.7)×(5.0) 5.6–6.2–7.1 (7.4) µm, total range of mean values 8.8–9.9×6.0–6.7 µm, Q=(1.25) 1.35–1.53–1.75 (1.9), total range of mean Q values 1.45–1.65 (120 spores from 5 collections); weakly nodulose with a few obtuse nodules or angular, often somewhat quadrangular or with a protruding apical nodule, rarely all spores elongated, rather pale yellow brown. *Basidia* 26–33–40 (41)×9–11–13 µm (n=22), clavate, 4- or rarely 2-spored. *Pleurocystidia* (48) 51–60–73 (76)×(13) 15–19–24 (28) µm (n=41); narrowly to rather broadly lageniform with cylindrical, conical or weakly subcapitate apex, rarely fusiform, apex crystalliferous, base tapered or with a pedicel, wall up to 2 (rarely −3) µm thick, pale yellow, very rarely walls thin. *Cheilocystidia*: metuloids 37–59×16–24 µm (n=17), rather similar to pleurocystidia, but shorter, more often fusiform or subcapitate, apex usually crystalliferous, wall rarely up to 3.5 µm thick in neck; rarely with yellow contents; thin-walled cystidia, some of which hyphoid and long, up to 81 µm long and 19 µm wide (n=9), fairly abundant; typical paracystidia very rare. *Caulocystidia*: metuloids at stipe apex rather rare, wall thin at base, shape more or less similar to hymenial cystidia, crystalliferous; hyphoid thin-walled cystidia abundant, flexuous or cylindrical, apex tapering or clavate, at times with protuberances or short branches; cauloparacystidia hyphoid and short, numerous.

Habitat: Inland shores, usually *Salix* thickets on alluvial lake or river shores, always with *Salix*. *S. phylicifolia* is the most likely host, possibly also mycorrhizal with *S. myrsinifolia* and *S. lapponum*.

Distribution: Known only from Finland, from southern to northern boreal zone, but more common in the north.

Phenology: Late July to early September, mainly collected from mid- to late August.

Comments: *Inocybe acutoides* can be recognized by its association with *Salix* and its paler, equal stipe and more obtuse umbo than *I. acuta*, which grows in similar habitats. Sometimes they share a site. However, the distribution of *I. acutoides* is concentrated in the northern boreal zone, whereas *I. acuta* has a wide distribution from France to the alpine zone of northern Fennoscandia. The most distinct microscopic differences from *I. acuta* are paler spores and frequent thin-walled cheilocystidia. These two species show clear divergence in their ITS; there were 98 base pair differences and 17 insertions/deletions (1–19 bases in length) between *I. acuta* and the holotype of *I. acutoides*.

Inocybe borealis is close to *I. acutoides* in both microscopic features and in ITS. The holotypes differed only in 11 bases and 3 insertions/deletions (1–3 bases in

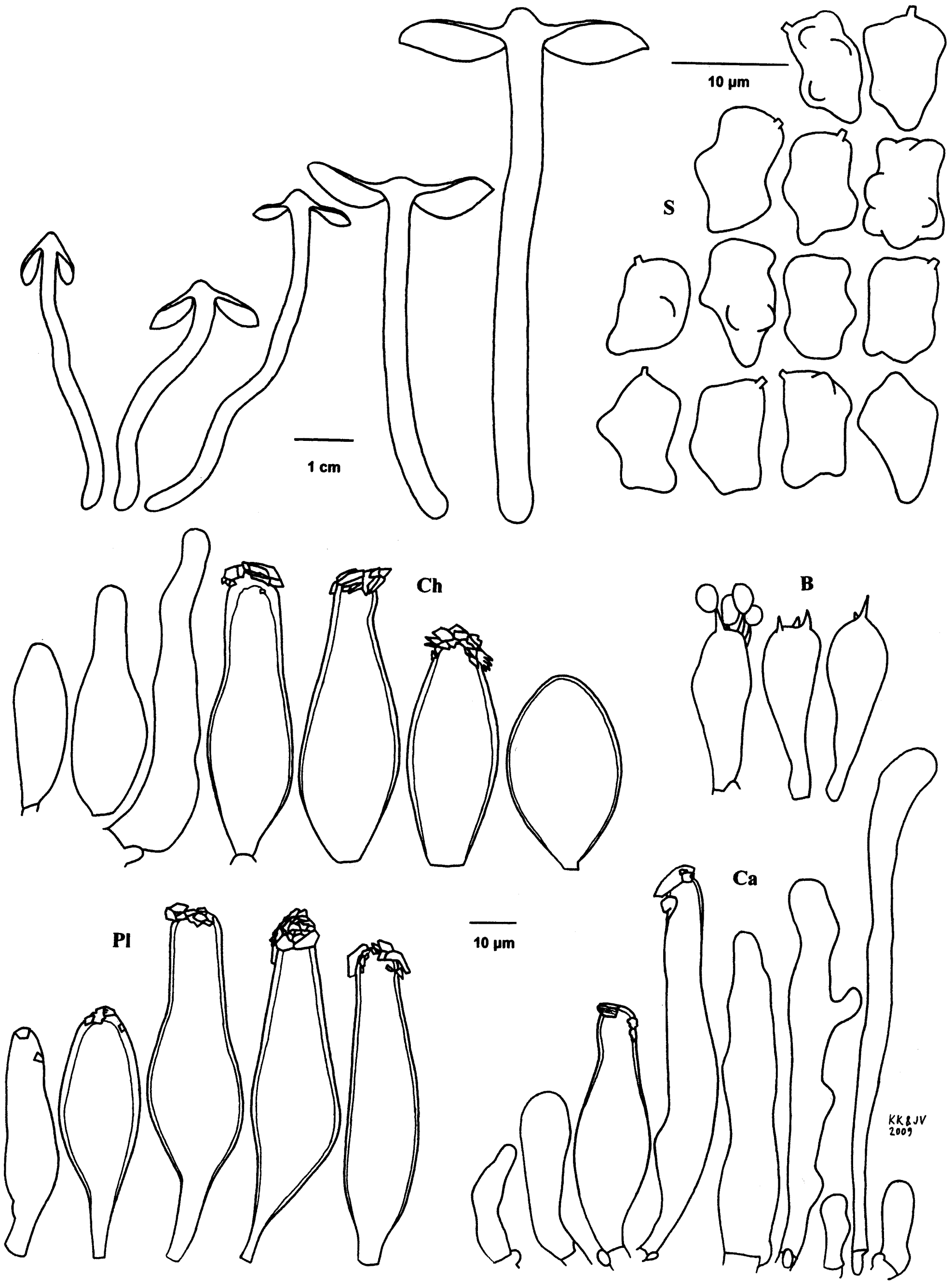


Fig. 4 *Inocybe acutoides*. Holotype: microscopic characters, *left* three cross-sections of fruitbodies. Kokkonen 318/03: second fruitbody from the *right*. Kokkonen 290/03: fruitbody on the right. For symbols, see Fig. 2

length). Though *I. borealis* might grow in shore forests, it is not associated with *Salix* according to our observations. In addition, it looks somewhat different from *I. acutoides*; the pileus, for example, often has a yellow tinge. The most useful microscopic difference from *I. acutoides* seems to be the numerous thick-walled caulocystidia.

Inocybe lapponica can be confused with *I. acutoides* in the northern boreal zone. These fungi resemble each other in both macroscopic and microscopic characteristics. However, the spores of *I. lapponica* usually lack prominent apical nodules and are more rarely elongated. *I. lapponica* also grows on shores, but is not restricted to *Salix*.

The ITS sequences of the examined 12 *Inocybe acutoides* specimens were identical, except for one different base in collection KK464/07 (GenBank JN580807) and a gap of one base in JV11737 (JN580808), and excluding three loci with ambiguous bases. The type had two ambiguous bases (C or T). Another ambiguous base was in six collections T (KK272/06 in the phylogram - JN580809), in three collections C (KK290/03 - JN580810), and in two collections C or T (KK&JV19280 - JN580811).

Specimens examined: **FINLAND**. **Pohjois-Häme**. Saarijärvi, Ranta-Hännilä, 14.VIII.1998 Vauras 13966*. **Pohjois-Savo**. Nilsiä, Huutavanholma, 29.VIII.1994

Ruotsalainen 3723a*. **Pohjois-Karjala**. Nurmes, Vastimo, 1.IX.2003 Kokkonen 318/03. Valtimo, Mahalanniemi, 19. VIII.2002 Kokkonen & Vauras 19280*, 29.VIII.2003 Kokkonen 290/03*. **Perä-Pohjanmaa**. Kemijärvi, Vuostimo, 23.VIII.2005 Kokkonen, 31.VIII.2005 Kokkonen. Pello, Konttajärvi, 29.VII.1976 Ulvinen* (OULU). Rovaniemi, Muurola, 22.VIII.1990 Reiniharju. **Koillismaa**. Kuusamo, Juuma, 1.IX.1996 Vauras 11737*, Jäkälämutka 1.IX.2007 Kokkonen 575/07* (holotype, TUR-A), 584/07, 16.VIII.2009 Kokkonen 76/09, 24. VIII.2009 Kokkonen 124/09, Vuotunki, 31.VIII.2007 Kokkonen 545/07. **Kittilän Lappi**. Kittilä, Hossa, 26. VIII.2008 Kokkonen 148/08, Sirkka, 25.VIII.2007 Kokkonen 459/07, 464/07*, 470/07. **Enontekiön Lappi**. Enontekiö, Karesuvanto, 20.VIII.2006 Kokkonen 272/06*. **Inarin Lappi**. Utsjoki, Kevo, 15.VIII.1995 Kytövuori 95-451* (H), Vauras 10444, 29.VIII.2005 Kokkonen 431/05*, k12*, k7vas.

Inocybe borealis M.Lange, *Meddelelser om Grønland* 148 (2): 19 (1957)

Figs. 5 and 6

Synonym: *I. heterochrominea* Grund & Stuntz, *Mycology* 72: 259 (1983).

Pileus 1.3–4.5 cm in diameter, conical or conico-convex or applanate, margin at times slightly undulating or later reflexed, umbo usually rather small, obtuse or rather acute, often somewhat conical, rarely absent; colour variable, most strikingly variable between populations: yellow brown or pale brown having sometimes a red tinge or grey brown (near $S_{50}Y_{60}M_{40}$, 49N) to dark brown, umbo darker, up to blackish brown (30T, 30R), in one collection umbo paler (60N), the darkest collections are from Lapland; weakly viscid to dry, centre smooth or cracked to small appressed scales, outwards radially fibrillose, rarely somewhat felted, often breaking up, velipellis lacking. *Lamellae* up to 7 mm wide, ventricose, narrowly adnate or adnexed or emarginate with decurrent teeth, moderately crowded; brown grey (71L) or yellowish grey when young, later brown grey or grey brown ($S_{20}Y_{30}M_{10}$, $S_{20}Y_{40}M_{20}$), edge concolorous or paler, even or slightly fimbriate. *Stipe* 1.6–9.5 cm long (15.2 cm in one dry specimen), 3–6.5 mm wide, equal or widening slightly downwards; usually pale brown, at times pale brownish yellow or reddish or grey brown with sporadic red brown fibres, base at times white or yellowish; dry or slightly viscid, whitish fibrillose, shiny, rarely flocculose, apex pruinose or rarely not; solid. *Context* in pileus whitish or grey in the middle and concolorous with pileus surface above lamellae; in stipe concolorous with stipe surface to whitish, often shiny. Smell weakly acidulous−spermatic or indistinct. No specific taste or slightly spermatic or bitter.

Fig. 5 *Inocybe borealis*. Finland, Nurmes, Kokkonen & Vauras 26120F. Photograph J. Vauras

Spores (7.2) 7.8–$\underline{8.8}$–10.0 (10.7)×(5.0) 5.3–$\underline{6.0}$–6.8 (6.9) µm, total range of mean values 8.3–9.4×5.6–6.4 µm, Q=(1.3) 1.35–$\underline{1.49}$–1.65 (1.9), total range of mean Q values 1.44–1.56 (100 spores from 5 boreal collections); weakly to moderately nodulose or angular, sometimes with a strongly protruding apical nodule, nodularity varies rather much between collections, rarely all spores distinctly elongated; rather pale yellow brown. Svalbard collection: mean 10.3×6.5 µm, mean Q=1.58, angular or with few low nodules. *Basidia* (24) 29–$\underline{32}$–37 (40)×9–$\underline{10}$–12 (13) µm (*n*=34 boreal), clavate, 4- or rarely 2-spored. Svalbard: 32–50×11–12 µm (*n*=7). *Pleurocystidia* (41) 48–$\underline{62}$–73 (89)×(12) 13–$\underline{18}$–23 (26) µm (*n*=88 boreal); narrowly to broadly lageniform with cylindrical or rarely conical neck, rarely subcapitate, at times fusiform, apex usually crystalliferous, base tapered or with pedicel, wall up to 2.5 (rarely −3) µm thick, pale yellow, sometimes apex with thick-walled "cap". Svalbard: 51–75×10–20 µm (*n*=10). *Cheilocystidia* similar to pleurocystidia but at times slightly shorter and wider, some thin-walled; rarely with yellow contents; paracystidia cannot be distinguished: intermediate forms between basidioles, possible paracystidia, thin-walled cystidia and even thick-walled cystidia exist suggesting that they are developmental stages of the same structure. *Caulocystidia*: metuloids at stipe apex usually more numerous than thin-walled cystidia, usually rather long and narrow, more or less cylindrical or tapering towards apex, more seldom similar to hymenial cystidia or clavate, in some specimens chain-like with septae, apex crystalliferous or not, wall up to 2 µm thick, pale yellow; thin-walled cystidia usually hyphoid and tapering towards apex; cauloparacystidia with thin walls; often in clusters.

Habitat variable: herb-rich forests, brookside forests, mesic mixed forests, pastured forests, forest margins, parks, subarctic mountain birch (*Betula pubescens* ssp. *czerepa-*

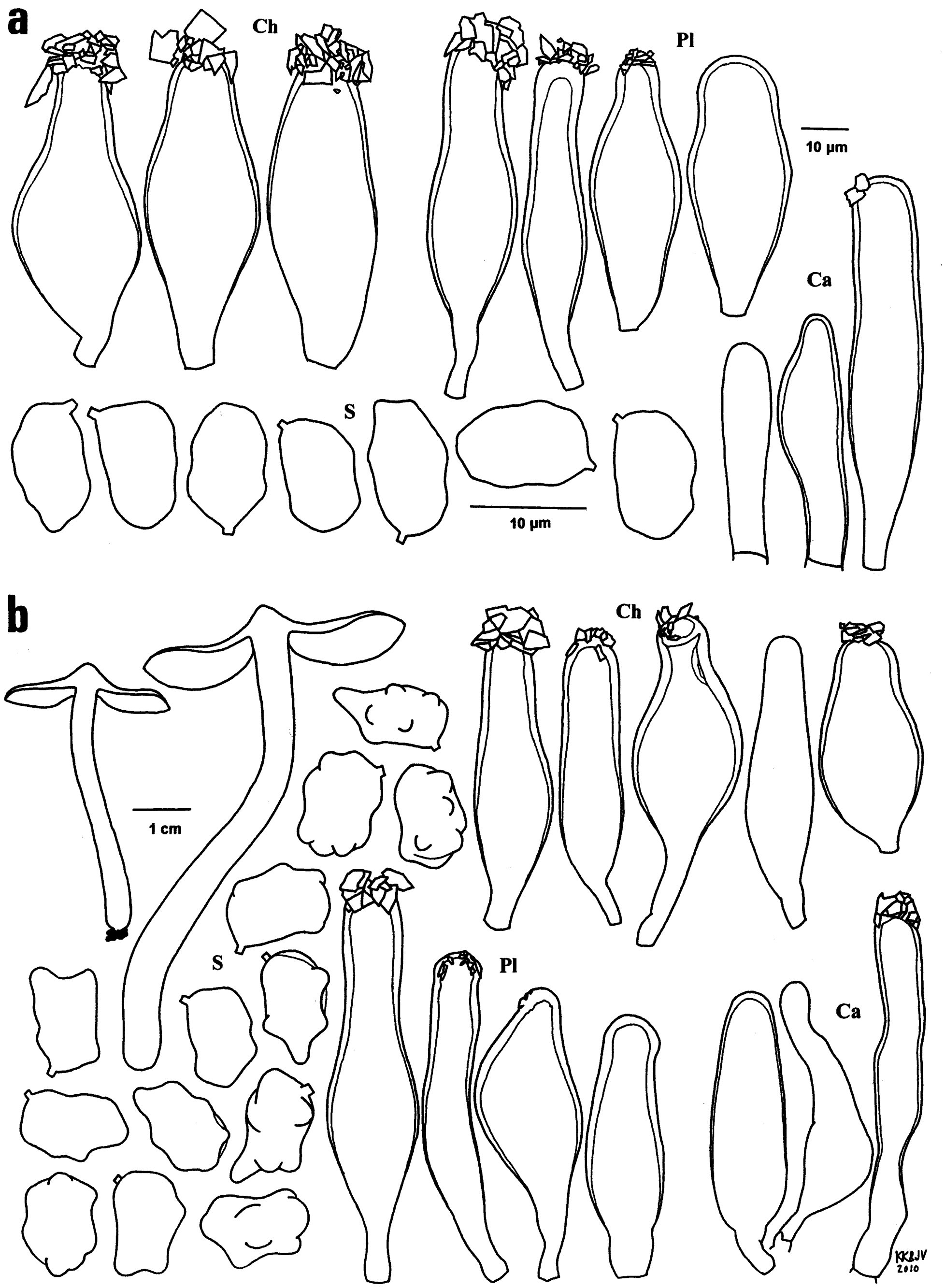


Fig. 6 *Inocybe borealis*. **a** Holotype of *I. borealis*, **b** Kokkonen & Vauras 26120F: microscopic characters, *left* cross-section of fruitbody. Kokkonen 191/08: *right* fruitbody. For symbols, see Fig. 2

novii) forests and arctic habitats, from mull to sandy soils. Not calcicolous, but avoiding poor soils. In most cases growing near *Picea abies* and *Betula*.

Distribution: Known from Finland, Greenland (holotype), Svalbard, Sweden, and North America (Nova Scotia, Michigan, Washington; Grund and Stuntz 1983); southern to northern boreal zone, subarctic and arctic zones.

Phenology: Early July to late September, mostly collected in August.

Holotype: *Inocybe borealis*. Greenland, Sdr. Strömfjord, Sandflugtdalen near Ice Cap, in deep moss on north slope, ML 387, 26 Aug. 1946 (C). – Specimen in small pieces. Spores (8.7) 9.4–$\underline{10.3}$–12.0 (12.5)×(5.7) 6.0–$\underline{6.5}$–7.0 µm, Q=(1.45) 1.5–$\underline{1.61}$–1.75 (1.9), (*n*=20); angular, elongated, rarely a few low nodules. Basidia 4-spored, 27–45×9.5–13 µm (*n*=4). Pleurocystidia (37) 51–$\underline{62}$–78 (80)×(13) 15–$\underline{18}$–22 µm (*n*=16), wall up to 3 µm thick, pale yellow to yellow, apex usually crystalliferous. Cheilocystidia 62–70×21–27 µm (*n*=4), wall up to 2.5 µm thick. No paracystidia observed. A few caulocystidia observed, wall thick or thin. ITS GenBank JN580812, LSU JN580888.

Holotype: *Inocybe heterochrominea*. U.S.A., Michigan, Chippewa Co., Sugar Island, University Reserve, in sylva arborum frondosum, STZ 11492 (WTU). – Piece of pileus as loan. Spores (8.0) 8.5–8.9–9.6 (10.5)×5.7–6.3–6.9 μm, Q=(1.25) 1.35–1.42–1.5 (1.65), (*n*=20); rather strongly nodulose, rather pale yellow brown. Basidia 4-spored. Pleurocystidia 47–60×14–20 μm (*n*=9), wall up to 3 μm thick, yellowish, apex often densely covered with small crystals. Cheilocystidia similar to pleurocystidia, some short and thin-walled cystidia or paracystidia. ITS1 GenBank JN580821, ITS2 JN580822.

Note: The protologue (McNeill et al. 2006) of *I. heterochrominea* is controversial in the type citation. According to the Latin description, the holotype is in ACAD and isotype in WTU, and in "Collections examined… HOLOTYPE in WTU, ISOTYPE in ACAD". The type was collected by D.E. Stuntz and deposited at WTU, where it is indicated as the holotype. Furthermore, according to Curator Ruth Newell, the type at ACAD is the isotype. For this reason, we propose the holotype resides at WTU and the isotype at ACAD.

Comments: *Inocybe borealis* is a variable species in many aspects. Our identifications of boreal collections, a subarctic collection, and *I. heterochrominea* are primarily based on ITS and LSU sequences, because the spores diverged so much from the *I. borealis* type. They were consistently smaller (except in KK141/03), paler, and more strongly nodulose. The Nordic ITS sequences were identical with the type sequence of *I. borealis* in two specimens (KK190/08 - GenBank JN580813, KK&JV27051F - JN580814), or deviated from the type by one gap (JV9244 - JN580815), by one common base in nine specimens (KK&JV26120F - JN580816), by one other base in JV15250F (JN580817), by one base and a gap of 12 bases (KK141/03 - JN580818), or by two bases (Heinonen 307–95 - JN580819). The *I. heterochrominea* type deviated from the *I. borealis* type by one base and a gap of one base, when 42 bases were lacking in the middle of the *I. heterochrominea* sequence and three loci with ambiguous bases were ignored. The LSU sequences of the type of *I. borealis* and a collection with one different base in ITS (KK&JV26120F - JN580889) diverged by one base as well.

An arctic collection from Svalbard (Online Resource Fig. S3) resembled the Greenland type in its spores, the presence of velipellis (absent in the other collections), and identical ITS (in the phylogram, JN580820). These specimens thus seem to form their own group. They both also have dark brown pilei seemingly unlike most boreal collections (the colours may have changed in exsiccata). Still, the two boreal collections with the type ITS also have dark brown pilei (Online Resource Fig. S2), but in spores they resemble other boreal specimens rather than the type; thus forming an intermediate group. Overall, the strength of nodularity varies rather much among the boreal specimens, and rarely the spores are elongated (KK141/03) as in the type of *Inocybe borealis*.

We were unable to find more distinct morphological boundaries between the specimens differing in ITS or between arctic and boreal/subarctic collections, and thus we tentatively determine them all to be the same very variable species. The observed morphological differences may have been caused by environment, or may be genetically intraspecific. The amount of velipellis, for example, often varies within species and seems to increase in arctic and alpine environments.

The microscopic and macroscopic features of *Inocybe heterochrominea* agreed with our Nordic collections of *I. borealis*. Accordingly, we have reduced it to a synonym. The walls of the cystidia of the *I. heterochrominea* holotype (a piece of a pileus) seemed thinner than in the drawings of Grund and Stuntz (1983), and the spores did not seem quite as strongly nodulose. *I. heterochrominea* was described from mixed and conifer forests of Michigan, Nova Scotia, and Washington. In Finland, *I. borealis* grows in various habitats, and we assume *Betula* to be one host. Lange (1957) did not mention any plant species from the type site, but he described the vegetation and fungi of the northern slopes, for example, stating that *Betula nana* was the dominant shrub and *Salix glauca* was scattered.

Inocybe acutoides is a closely related sibling species associated with *Salix*. See our comments regarding *I. acutoides*, and the diagnostic key.

Specimens examined: **DENMARK. Greenland.** Sdr. Strömfjord, 26.VIII.1946 Lange 387* (holotype, C). **FINLAND. Varsinais-Suomi.** Marttila, Karhunpääntie, 8. VII.1995 Issakainen & Vauras 10219*. **Uusimaa.** Vantaa, Mustavuori, 18.VIII.1988 Saarenoksa 17488* (TUR). **Satakunta.** Karvia, Kantti, 25.VII.1990 Vauras 4490*. **Pohjois-Savo.** Kuopio, Riistavesi, Laajalahti, 28.VII.2003 Ruotsalainen & Toivonen 3067* (TUR), Vehmersalmi, Huttujärvi, 20.VII.1989 Ruotsalainen, Litmaniemi, 20. VII.1989 Ruotsalainen, 11.VIII.1994 Vauras 9197F. Nilsiä, Tarpinen, 12.VIII.1994 Vauras 9244*. Siilinjärvi, Toivala, Haapamäki, 12.VIII.1994 Vauras 9233, 6.VIII.2003 Vauras 19818*. **Pohjois-Karjala.** Nurmes, Porokylä, Pitkämäki, 15.VIII.2003 Kokkonen 141/03F*, 22.IX.2003 Kokkonen 786/03, 16.VIII.2008 Kokkonen & Vauras 70/08, Kokkonen & Vauras 26120F*, 4.VIII.2009 Kokkonen 38/09. Tohmajärvi, Värtsilä, Savikko, 3.IX.1993 Väre* (OULU). **Koillismaa.** Kuusamo, Oulanka National Park, Ampumavaara, 16.VIII.1993 Pynssi, Talvilampi, 15.VIII.2009 Kokkonen & Vauras 26948F, 22.VIII.2009 Kokkonen & Vauras 27051F*. Posio, Korouoma, 28.VIII.2007 Toivonen & Kytövuori 07–903 (H). **Perä-Pohjanmaa.** Rovaniemi, Jaatilanvaara, 20.VIII.1999 Vauras 15250F*, Kalkkimaa, 18. VIII.1990 Vauras 4866. **Kittilän Lappi.** Kittilä, southeast side of church village, 28.VIII.2008 Kokkonen 190/08*, 191/08, 208/08, 209/08. **Inarin Lappi.** Utsjoki, Kevo, 15. VIII.1995 M.-L. & P. Heinonen 307-95* (TUR), 18.

VIII.1995 Vauras 10516*. **NORWAY. Svalbard.** Longyearbyen, 7.VIII.1983 Huhtinen 83/281* (TUR). **SWEDEN. Torne Lappmark.** Jukkasjärvi, Abisko, Björkliden, 17.VIII.1999 Vauras 15215*. **UNITED STATES. Michigan.** Chippewa, Stuntz 11492* (holotype of *I. heterochrominea*, WTU).

Inocybe bufonia Kokkonen & Vauras, **sp. nov.**

Figs. 7 and 8

MycoBank number: MB 563069

Etym.: *bufonia* (Latin) refers to the moist habitat with frogs and toads.

Pileo 1.4–4.0 cm lato, umbone plus minusque acuto praedito, fusco-brunneo, margine cano-brunneo, fibrilloso, paulum viscido. Lamellis usque ad 6 mm latis, ventricosis. Stipite 1.4–10.3 cm longo, 2–7 mm crasso, pallido brunneo vel subrubero. Sporis (7.2) 7.6–10.0 (10.5)×(5.3) 5.7–7.0 (7.5) μm, nodulosis. Pleurocystidiis (39) 43–72 (82)×(9) 11–20 (26) μm, lageniformibus. In locis humidis.

Holotypus: **Finland**, Pohjois-Karjala, Nurmes Municipality, Tervavaara, west slope, spruce swamp, near *Picea abies, Betula, Equisetum sylvaticum, Maianthemum bifolium* and *Dryopteris expansa,* amongst *Sphagnum girgensohnii*, Grid 27°E: 7058:3605, alt. ca. 116 m, 5.VIII.2009 *K. Kokkonen* 45/09 (TUR-A 190477, isotypus WTU), GenBank JN580823.

Pileus 1.4–4.0 cm in diameter, conical when young, then conical to conico-convex or applanate, umbo prominent, rather acute, rarely obtuse, margin at times weakly undate; dark brown or rather dark brown ($S_{80}Y_{60}M_{50}$, $S_{60}Y_{60}M_{50}$, near $S_{50}Y_{50}M_{30}$, near $S_{40}Y_{50}M_{40}$), rarely grey brown, centre up to blackish brown ($S_{80}Y_{50}M_{50}$, $Y_{99}M_{99}C_{99}$), outermost margin sometimes pale; weakly viscid, rarely dry, centre smooth or rarely with indistinctly appressed scales, outwards usually weakly fibrillose, rarely somewhat villose, margin at times slightly breaking up, velipellis lacking. *Lamellae* up to 6 mm wide, ventricose, adnexed or adnate, rarely with small decurrent teeth, moderately or rather densely crowded; yellowish pale brown or grey brown ($Y_{20}M_{10}C_{10}$, $S_{20}Y_{40}M_{20}$–$S_{20}Y_{50}M_{30}$), when old entirely dark brown ($S_{40}Y_{60}M_{30}$-$S_{60}Y_{60}M_{50}$) or with dark spots, edge concolorous or paler, even. *Stipe* 1.4–10.3 cm long, 2–7 mm wide, equal or widening slightly downwards, sometimes base subbulbous; pale brown (near $S_{00\text{-}10}Y_{30}M_{10}$) or reddish (near $S_{10}Y_{40}M_{20}$), upper part at times whitish, lower part usually darker, up to dark brown, and often with dark brown bundles of fibres resembling appressed scales, base usually white; slightly viscid or dry, usually faintly fibrillose striate, apex slightly pruinose, solid. *Cortina* whitish. *Context* in pileus brown grey or grey brown ($S_{40}Y_{30}M_{00\text{-}10}$) to whitish; in stipe concolorous with stipe surface to whitish, faintly striate, base usually white, rarely yellowish. Smell weakly spermatic or indistinct. No specific taste.

Fig. 7 *Inocybe bufonia*. Holotype. Photograph K. Kokkonen

Spores (7.2) 7.6–$\underline{8.8}$–10.0 (10.5)×(5.3) 5.7–$\underline{6.3}$–7.0 (7.5) μm, total range of mean values 8.5–9.1×6.2–6.4 μm, Q=(1.15) 1.25–$\underline{1.40}$–1.55 (1.8), total range of mean Q values 1.37–1.47 (100 spores from 5 collections); usually rather strongly nodulose, nodules small to medium-sized, pale or rather pale yellow brown. *Basidia* (24) 27–$\underline{34}$–40 (42)×9–$\underline{11}$–14 μm (*n*=51), clavate, 4- or rarely 2-spored. *Pleurocystidia* (39) 43–$\underline{56}$–72 (82)×(9) 11–$\underline{15}$–20 (26) μm (*n*=100), narrowly to moderately broadly lageniform with short or long neck, in some specimens nearly all narrow with long neck, rarely short ellipsoid or utriform, crystalliferous or not, tapered or with a pedicel, wall up to 3 μm thick, pale yellow, rarely walls thin. *Cheilocystidia* up to 78 μm long and 21 μm wide (*n*=28), similar to pleurocystidia, rarely subglobose, apex crystalliferous or mucilaginous or without cover, rarely with yellow contents; thin-walled cystidia scarce, sometimes short and fusoid resembling paracystidia. *Caulocystidia*: metuloids numerous at stipe apex, more or less similar to pleurocystidia or with long hyphoid apex or cylindrical or flexuous, rarely with protuberances or short branches or septae, crystalliferous or not, up to 116 μm long (*n*=24), wall up to 3 μm thick, pale yellow, some with thin walls, often in clusters with numerous cauloparacystidia.

Habitat: Moist forests dominated by *Picea abies*, spruce-hardwood swamps, shore forests, moist depressions and ditches in mixed forests.

Distribution: Known from southern to northern boreal zone of Finland. A collection with deviating ITS (see Comments) was from a moist site under *Betula glandulosa* in Canada.

Phenology: Mid-July to late August.

Comments: Typical *Inocybe bufonia* can be initially recognized by its dark, rather acutely umbonate pileus, pale stipe, and its growth in moist habitats. However, it has

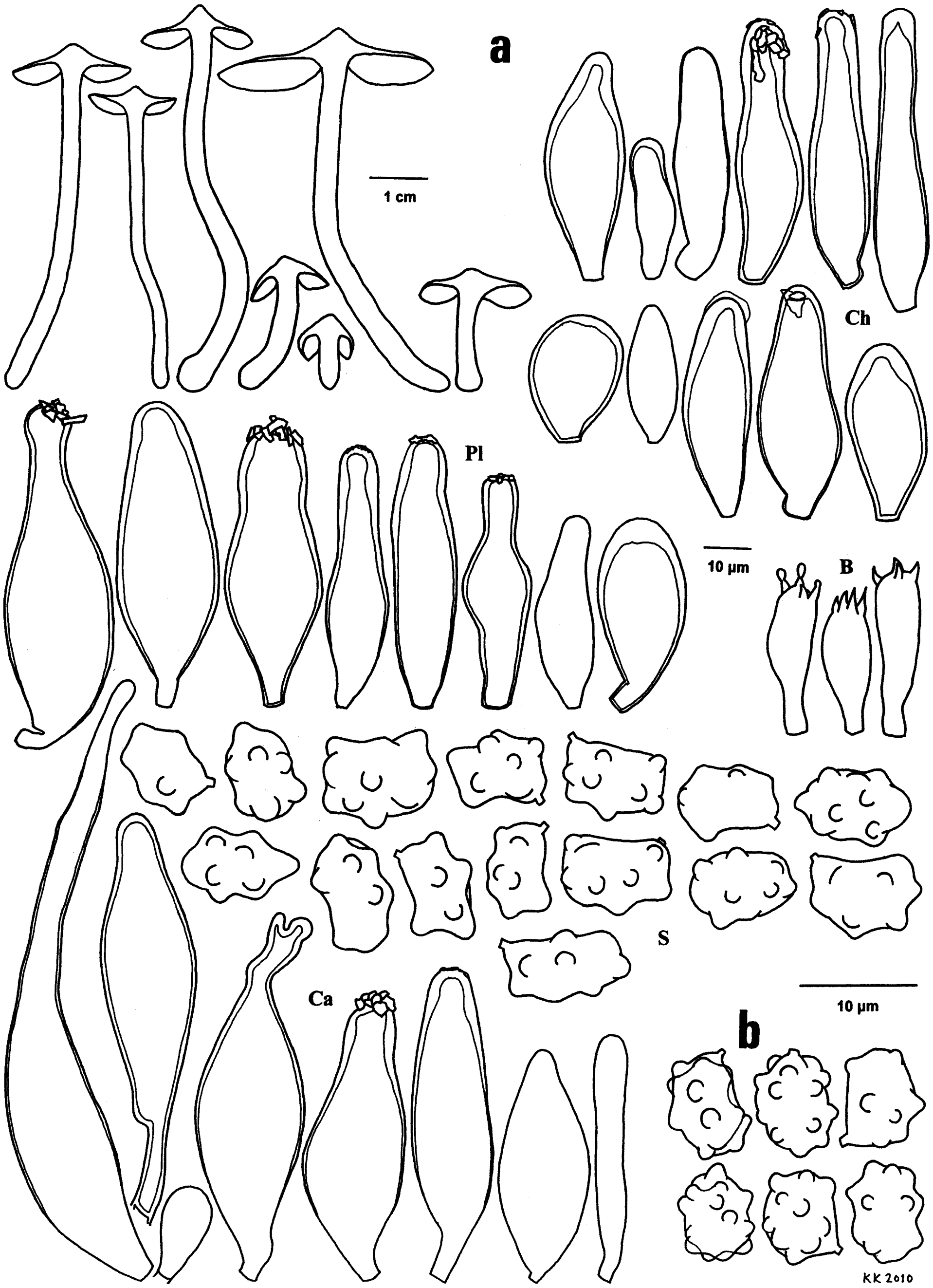


Fig. 8 *Inocybe bufonia*. **a** Holotype: microscopic characters, two cross-sections of fruitbodies on the *left*. Other fruitbodies from the *right*: Vauras & Kokkonen 69/09, 67/09, 111/09, 107/09, Kokkonen 23/09, **b** Kokkonen 165/03: spores. For symbols, see Fig. 2

never been found in *Salix* thickets like *I. acuta*, from which it can be easily distinguished microscopically by its paler spores. *Picea abies* or *Betula* seems to be the host.

The limits of variation of *Inocybe bufonia* were difficult to define. Two subgroups could be recognized. Subgroup 1 (four sequenced specimens - GenBank JN580825, JN580826, JN580827, JN580828) differed from "the type group" (nine sequenced specimens, insertion of a base in KK60/05 - JN280824) in more strongly nodulose spores (Fig. 6b), as well as by 6–8 bases and 1–2 insertions/deletions in the ITS region. Subgroup 2 (five specimens - JN580830, JN580831, JN580832, JN580833, one from Canada on the basis of ITS1 - JN580829) differed from "the type group" solely by seven bases and 0–1 gap in the ITS (one specimen was an intermediate to the type on the basis of ambiguous bases in four loci). These subgroups deviated from each other by 3–7 bases and 0–2 insertions/deletions. All grew in moist habitats, but the pilei in the subgroups often seemed paler (Online Resource Figs. S6 and S7). Because we could not find more distinct differences between the groups, all are treated here as *Inocybe bufonia*. However, the subgroups have been excluded from the microscopic and macroscopic descriptions, and are listed below as additional specimens.

Specimens examined: **FINLAND. Varsinais-Suomi.** Vihti, Salmenkartano, 20.VIII.1997 Kytövuori 97-218* (H). **Satakunta.** Säkylä, Harjunkylä, 12.VII.1995 Vauras 10274*. **Pohjois-Karjala.** Nurmes, Tervavaara, 1.VIII.2005 Kokkonen 60/05*, 13.VIII.2005 Kokkonen & Vauras 23057*, 30.VII.2009 Kokkonen 23/09, 5.VIII.2009 Kokkonen 45/09* (holotype, TUR-A), 23.VIII.2010 Vauras & Kokkonen 60/10*, 62/10. **Koillismaa.** Kuusamo, Oulanka National Park, Talvilampi, 27.VIII.2007 Vauras 25043*, 15.VIII.2009 Kokkonen & Vauras 26947, Vauras & Kokkonen 67/09, 69/09, 22.VIII.2009 Vauras & Kokkonen 107/09*, 111/09. **Perä-Pohjanmaa.** Rovaniemi, Suolijoki, 28.VII.1978 Ulvinen* (OULU).

Additional specimens examined: Subgroup 1: **FINLAND. Varsinais-Suomi.** Kustavi, Rahi, 28.VII.2004 Vauras 21516*. **Etelä-Häme.** Joutsa, Leivonmäki, Selänpohja, Joutsiniemi, 15.VIII.1993 Kytövuori 93-180* (H). Jyväskylä, Korpilahti, Ristisuo, VIII.1986 Storbacka. **Pohjois-Karjala.** Valtimo, near Hoikanvaara, 21.VIII.2003 Kokkonen 165/03*, 5.VIII.2009 Kokkonen 44/09. **Koillismaa.** Kuusamo, Iivaara, 13.VIII.2009 Kokkonen 58/09*. Subgroup 2: **CANADA. Quebec.** Schefferville, 1.VIII.1963 Kallio 208* (TUR). **FINLAND. Pohjois-Häme.** Saarijärvi, Linnankylä, 31.VII.1986 Storbacka & Vauras 2129F*. **Pohjois-Savo.** Kuopio, Vehmersalmi, Rytökylä, 19.VII.1992 Ruotsalainen & Vauras 2558*, 13.VIII.1994 Vauras 9291*. **Koillismaa.** Kuusamo, Oulanka National Park, Nurmisaarenrinne, 15.VIII.2009 Vauras & Kokkonen 73/09*.

Inocybe boreocarelica Kokkonen & Vauras, **sp. nov.**

Figs. 9 and 10

MycoBank number: MB 563070

Etym.: *boreocarelica* (Latin) refers to the biogeographical province of Karelia borealis.

Pileo 1.4–3.5 cm lato, subumbonato, brunneo, fibrilloso, paulum viscido. Lamellis usque ad 5.5 mm latis, ventricosis. Stipite 2.8–6.0 cm longo, 3.0–5.5 mm crasso, sine bulbo, rufobrunneolo. Sporis (7.0) 7.3–9.1 (10.1)×(5.0) 5.3–7.0 (7.5) µm, nodulosis. Pleurocystidiis (45) 50–77 (82)×(11) 13–23 (26) µm, lageniformibus.

Fig. 9 *Inocybe boreocarelica*. Holotype. Photograph K. Kokkonen

Holotypus: **Finland**, Pohjois-Karjala, Nurmes Municipality, Tervavaara, west slope, old-growth heath forest dominated by *Picea abies,* near *Picea, Betula, Sorbus aucuparia, Vaccinium myrtillus* and *Maianthemum bifolium,* amongst *Hylocomium splendens*, Grid 27°E: 7058:3606, alt. ca. 125 m, 30.VII.2009 *K. Kokkonen* 25/09 (TUR-A 190468, isotypus WTU), GenBank JN580834.

Pileus 1.4–3.5 cm in diameter, conico-convex when young, then applanate with deflexed margin or later sometimes margin reflexed, rather prominent obtuse umbo or subumbonate; grey brown (near $S_{50}Y_{60\text{-}70}M_{40}$) or rather dark reddish brown (near $S_{60}Y_{50}M_{50}$), rarely yellow brown, centre usually redder and darker, up to blackish brown ($S_{50}Y_{50\text{-}70}M_{50}$-$S_{90}Y_{60}M_{40}$); weakly viscid, centre smooth, outwards radially fibrillose, margin sometimes breaking up and with darker bundles of fibres, velipellis lacking. *Lamellae* rather broad, up to 5.5 mm, ventricose, adnexed or narrowly adnate, moderately crowded; pale grey brown (near $Y_{20}M_{10}C_{10}$) or grey brown ($Y_{30}M_{20}C_{20}$, $S_{30}Y_{30}M_{10}$, $S_{30}Y_{40}M_{20}$), edge concolorous or when young paler, even. *Stipe* 2.8–6.0 cm long, 3.0–5.5 mm wide, equal or widening slightly downwards, base tapering or roundish; pale red brown (near $S_{30}Y_{30}M_{30}$), usually darker in the lower part (near $Y_{60}M_{50}C_{30}$, up to $S_{70}Y_{50}M_{40}$), base white; slightly viscid or dry, fibrillose, whitish flocculose to felted entirely or only weakly in the upper part, apex pruinose, solid. *Cortina* whitish. *Context* in pileus greyish pale brown or concolorous with surface above and whitish deeper; in stipe greyish or slightly paler than surface, striate, base white. Smell weakly acidulous or indistinct. No specific taste.

Spores: (7.0) 7.3–8.3–9.1 (10.1)×(5.0) 5.3–6.1–7.0 (7.5) µm, total range of mean values 8.0–8.4×5.8–6.3, Q=(1.2) 1.25–1.37–1.5 (1.75), total range of mean Q values 1.34–1.42 (80 spores from 4 collections); rather weakly to rather strongly nodulose, nodules usually small, sometimes spores slightly bent, rather pale yellow brown. *Basidia* (24) 25–31–36 (38)×8–10–11 (12) µm (*n*=29), clavate, 4-spored. *Pleurocystidia* (45) 50–60–77 (82)×(11) 13–17–23 (26) µm (*n*=52), narrowly to broadly lageniform with short or long neck, apex usually crystalliferous, base tapered or with pedicel; wall often distinctly thickened in neck, up to 4 µm thick, rarely wall totally thin, pale yellow or at times bright yellow. *Cheilocystidia* usually slightly wider and shorter than pleurocystidia, crystalliferous or not; thin-walled lageniform or ellipsoid cystidia or paracystidia scarce. *Caulocystidia*: metuloids at stipe apex very rare to frequent, usually lageniform with short neck, rarely fusoid or cylindrical or clavate, crystalliferous or not, wall up to 2 µm thick, pale yellow; narrow hyphoid or cylindrical

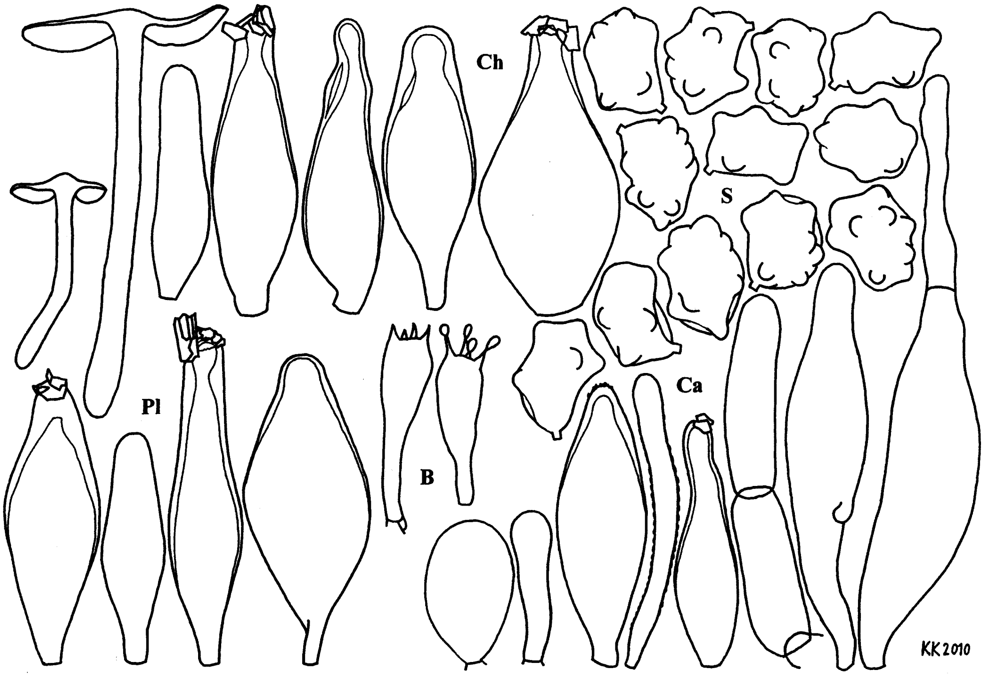


Fig. 10 *Inocybe boreocarelica*. Holotype: microscopic characters. Kokkonen 19/09: cross-sections of fruitbodies. For symbols, see Fig. 2

thin-walled cystidia abundant, some inflated at base and with a septum, some with encrusted walls, also short lageniform, subglobose, ellipsoid, fusoid or clavate cystidia or paracaulocystidia.

Habitat variable: heath forest mainly with *Picea abies*, cemetery with mixed stand, brookside forest with *Picea*, *Betula,* and *Alnus incana*, subarctic pastured mountain birch (*Betula pubescens* ssp. *czerepanovii*) forest.

Distribution: Known from three localities in the province North Karelia in Finland near the boundary of southern and middle boreal zones, and from one locality at the timberline on a fjeld in Norway.

Phenology: Late July to mid-August.

Comments: *Inocybe boreocarelica* may be difficult to identify, but it is characterised by its reddish brown, flocculose stipe and rather small spores. It may resemble *I. borealis* both in morphology and habitat. Both sometimes have a yellow brown pileus cracked into scales at umbo, as observed in an old cemetery (Pitkämäki, Nurmes) where they grow near each other. However, the cystidial walls of *I. boreocarelica* are often distinctly thickened in the neck.

Inocybe boreocarelica also resembles *I. bufonia* microscopically, but the spores of *I. bufonia* are more often elongated. *I. bufonia* differs more distinctly in its darker appearance and moister habitat. The ITS sequence of the Norwegian specimen deviated from the others by one base (GenBank JN580835).

Specimens examined: **FINLAND. Pohjois-Karjala.** Lieksa, Koli National Park, 11.VIII.1995 Vauras 10384*. Nurmes, Porokylä, Pitkämäki, 27.VII.2009 Kokkonen 19/09*, Ylikylä, Tervavaara, 30.VII.2009 Kokkonen 25/09* (holotype, TUR-A). **NORWAY**. **Sör-Tröndelag**. Oppdal, Vinstradalen, 9.VIII.1991 Vauras 5707*.

Inocybe lapponica Kokkonen & Vauras, **sp. nov.**

Figs. 11 and 12a

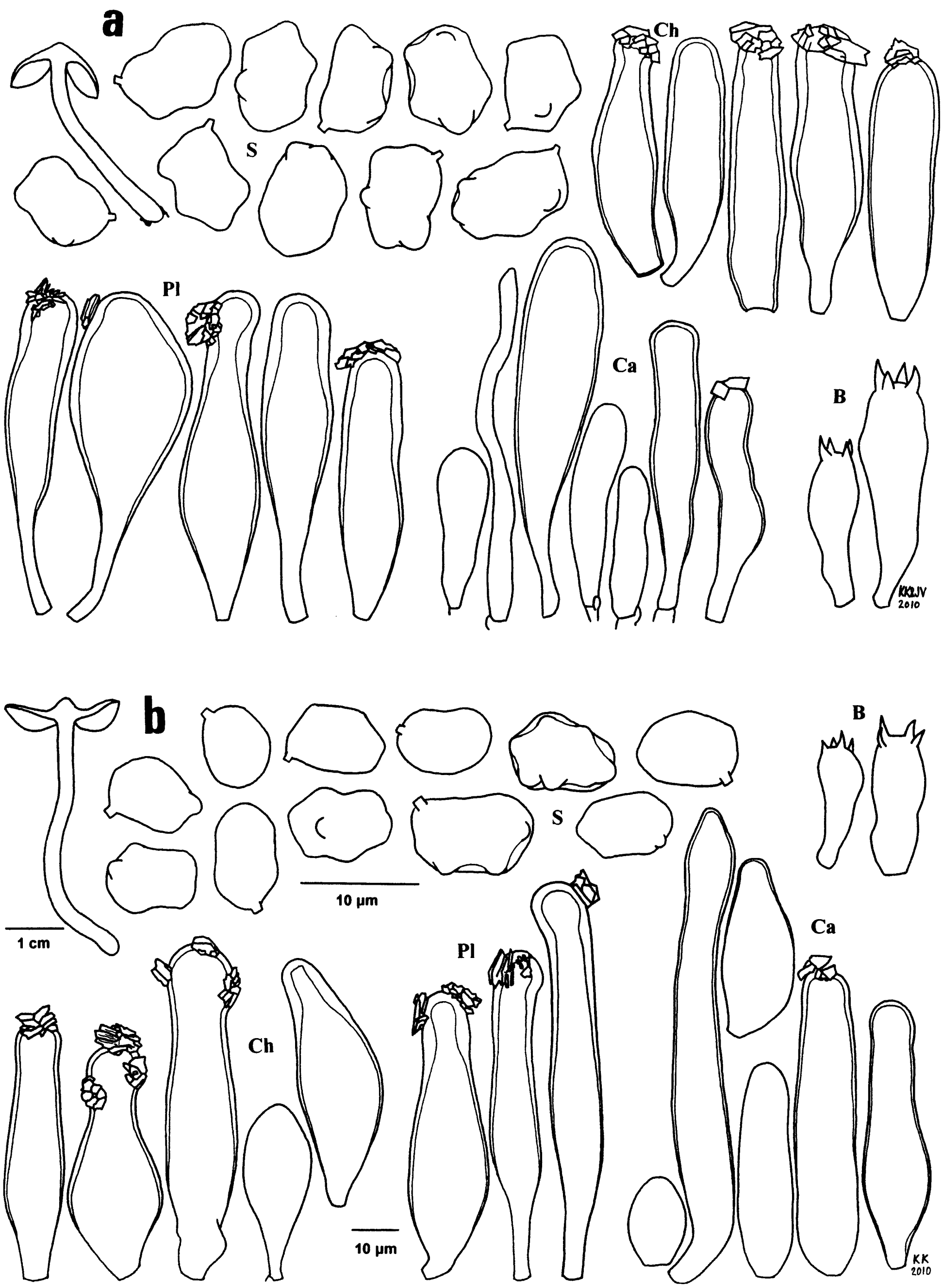
MycoBank number: MB 563071

Etym.: *lapponica* refers to the known main distribution area in Lapland.

Pileo 1.0–2.5 cm lato, umbone plus minusque acuto praedito, brunneo, fibrilloso. Lamellis usque ad 5 mm latis, ventricosis. Stipite 2.5–4.5 cm longo, 2.5–5 mm crasso, sine bulbo, pallido brunneo vel brunneo-subrubero, ad apicem paulum albo-pruinoso, in reliqua parte fibrillis albis fuscisque signato. Sporis (8.0) 8.3–10.6 (11.8)×(5.7) 5.9–7.3 (8.0) µm, nodulosis. Pleurocystidiis (43) 54–73 (79)×

Fig. 11 *Inocybe lapponica*. Holotype. Photograph J. Vauras

Fig. 12 Microscopic characters and cross-sections of fruitbodies: **a** *Inocybe lapponica*, holotype; **b** *Inocybe kittilensis*, holotype. For symbols, see Fig. 2



(10) 11–20 (27) µm, utriformibus vel cylindraceis. Imprimis in Lapponia.

Holotypus: **Finland**, Inarin Lappi, Utsjoki Municipality, Kevo, north of Kutuniemi, south of the mouth of the river Rássejohbohki, at the foot of a northern slope, in a moist site with *Betula pubescens* subsp. *czerepanovii* and *Salix,* amongst scattered mosses (e.g. *Polytrichum*) and *Betula* litter. Grid 27°E: 7743:3500, alt. ca. 76 m, 18.VIII.1995 *J. Vauras* 10521F (TUR-A 162944), GenBank JN580836.

Pileus 1.0–2.5 cm in diameter, conico-convex or conical, margin straight or deflexed, umbo prominent, rather acute; dirty brown (50P–R) or reddish to yellowish brown, often partly blackish, outermost margin the palest; centre smooth, outwards usually rather finely fibrillose, at times breaking up, velipellis lacking. *Lamellae* rather broad, up to 5 mm, ventricose, adnexed or free, moderately crowded; when young pale grey, later pale brown, edge concolorous and even. *Stipe* 2.5–4.5 cm long, 2.5–5 mm wide, equal or widening slightly downwards, base tapering or roundish, not bulbous; pale brown red or pale brown, red tinge most distinct at apex; fibrillose, sometimes coarsely so and with white and dark brown fibres, apex slightly pruinose. *Context* whitish to pale yellow reddish or in stipe pale red brown. Smell indistinct.

Spores (8.0) 8.3–9.4–10.6 (11.8)×(5.7) 5.9–6.6–7.3 (8.0) µm, total range of mean values 9.1–9.9×6.4–6.8 µm, Q=(1.2) 1.3–1.43–1.55 (1.75), total range of Q values 1.40–1.46 (100 spores from 5 collections); angular or with few nodules, pale or rather pale yellow brown. *Basidia* (21) 22–31–38 (46)×9–10–13(14) µm (*n*=50), clavate, 4- or rarely 2-spored. *Pleurocystidia* (43) 54–63–73 (79)×(10) 11–15–20 (27) µm (*n*=80), narrowly to broadly utriform or lageniform with short to rather long neck or cylindrical, rarely fusiform or clavate, apex usually crystalliferous, base tapered or with pedicel, wall up to 3 (rarely 3.5) µm thick, pale yellow or nearly hyaline. *Cheilocystidia* similar to pleurocystidia, sometimes with yellow or brownish contents. *Caulocystidia*: metuloids at stipe apex rare, clavate, narrowly lageniform, narrowly utriform or cylindrical, apex crystalliferous or not, wall up to 2 µm thick, pale yellow; thin-walled cystidia hyphoid, cylindrical or clavate or tapering towards apex, often short resembling cauloparacystidia, abundant; at times with brownish contents.

Habitat: Alluvial river and lake shore forests, also in moist depressions and along brooksides in subalpine forests, moist sites and snow bed areas on fjelds. Possibly associated with *Betula,* but *Salix* species often present also.

Distribution: Known from Finland and Sweden, from northern boreal to low-alpine zones.

Phenology: Collected only in August.

Comments: *Inocybe lapponica* is a small northern species much resembling *I. acuta* and *I. acutoides*, but it is not restricted to *Salix* (see Comments relating to *I. acutoides* and the key for differential diagnosis). The most distinct difference from *I. bufonia* is that its spores have fewer nodules. The ITS sequences of *I. lapponica* specimens were identical except for one with a different base (Ruots. 1985 - GenBank JN580837) and one with a gap (Kallio 1962 - JN580838).

Specimens examined: **FINLAND. Koillismaa.** Kuusamo, Oulanka National Park, near the Research Station, 14.VIII.2009 Vauras 26942*. **Sompion Lappi.** Pelkosenniemi, Jaurujoki 12.VIII.1994 U. & P. Salo* (OULU). **Enontekiön Lappi.** Enontekiö, Kilpisjärvi, Goallarrassa, 11.VIII. 1986 Metsänheimo & Ruotsalainen, Pikku-Malla, 5.VIII.1985 Ruotsalainen*. **Inarin Lappi.** Utsjoki, Kevo, 14.VIII.1962 Kallio et al.*, 15.VIII.1995 Vauras 10430, 18. VIII.1995 Heinonen & Heinonen 444-95F* (TUR, GB, WTU), Vauras 10517, Vauras 10521F* (holotype, TUR-A). **SWEDEN. Jämtland.** Undersåker, Renfjellet, 25. VIII.2001 Vauras 17522*.

Inocybe kittilensis Kokkonen & Vauras, **sp. nov.**

Figs. 13 and 12b

MycoBank number: MB 563072

Etym.: *kittilensis* – referring to the Kittilä Municipality in the biogeographical province of Lapponia kittilensis.

Pileo 1.9–2.9 cm lato, applanato circa umbonem obtusum, brunneo, fibrilloso. Lamellis usque ad 4 mm latis, ventricosis. Stipite 4.2–5.4 cm longo, 2–3.5 mm crasso, pallido brunneo. Inodora. Sporis (8.1) 8.6–10.6 (11.1)×(5.7) 5.8–7.0 (7.1) µm, nodulis exiguis ornatis. Pleurocystidiis (50) 55–81 (90)×(10) 11–17 (21) µm, lageniformibus, apicis saepe subcapitatis.

Holotypus: **Finland**, Kittilän Lappi, Kittilä Municipality, southeast side of the village with a church, south of the camping place, near the swimming shore, ca. 120 m east of the river Ounasjoki, in a pastured wood grazed by sheep, near *Salix phylicifolia, Betula, Picea abies, Pinus sylvestris, Salix caprea* and *Populus tremula,* amongst leaf litter, Grid 27°E: 75080:34124, alt. ca. 176 m, 28.VIII.2008 *K. Kokkonen* 188/08 (TUR-A 190480, isotypus H), GenBank JN580839.

Pileus 1.9–2.9 cm in diameter, 5–7 mm high, with age more or less applanate with prominent obtuse umbo; medium to rather dark brown (near $Y_{80}M_{50}C_{50}$), margin paler; dry, centre smooth, outwards somewhat villose fibrillose, velipellis lacking, scant remnants of cortina at margin. *Lamellae* up to 4 mm wide, ventricose, narrowly adnate or adnexed, moderately crowded; grey brown (near $Y_{70}M_{50}C_{40}$), edge concolorous and even or minutely fimbriate. *Stipe* 4.2–5.4 cm long, 2–3.5 mm wide, equal, solid; pale brown with faint reddish tinge, base whitish; dry, fibrillose, delicately pale flocculose, slightly shiny, apex slightly pruinose. *Context* whitish. Smell indistinct. No specific taste.

Spores (8.1) 8.6–9.3–10.6 (11.1)×(5.7) 5.8–6.2–7.0 (7.1) µm, total range of mean values 9.3×6.1–6.4 µm, Q=(1.3) 1.4–1.49–1.65 (1.8), total range of Q values 1.46–1.52 (40 spores from 2 collections); weakly angular or weakly nodulose or nearly ellipsoid, rather pale yellow brown. *Basidia* 24–28–31 (34)×(8) 9–10–11 (12) µm, clavate, 4-spored (*n*=31). *Pleurocystidia* (50) 55–69–81 (90)×(10) 11–13–17 (21) µm (*n*=52), narrowly to moderately broadly

Fig. 13 *Inocybe kittilensis*. Holotype. Photograph K. Kokkonen

lageniform, often with widened or capitate apex, crystalliferous or not, base tapered or with pedicel, wall up to 5 µm in neck, elsewhere up to 2 µm thick, pale yellow, rarely apex with yellow contents. *Cheilocystidia*: metuloids 37–69 × 13–20 µm (n=13), similar to pleurocystidia, but some shorter and with thinner walls, wall up to 3.5 µm thick in neck, some short thin-walled cystidia or paracystidia. *Caulocystidia*: metuloids at stipe apex numerous, up to 95 µm and 22 µm wide (n=33), narrowly lageniform, narrowly utriform, cylindrical or fusiform, apex often subcapitate, rarely crystalliferous, wall up to 2 µm thick, pale yellow; thin-walled short cystidia and cauloparacystidia scarce.

Habitat and *distribution*: known only from the type locality, a pastured wood in the northern boreal zone in Finland.

Comments: *Inocybe kittilensis* appears to be a rare, fairly small species. It is best recognized by the combination of fairly long, subcapitate cystidia and weakly nodulose spores.

Specimens examined: **FINLAND**. **Kittilän Lappi**. Kittilä, southeast side of the village with a church, 28. VIII.2008 *Kokkonen* 188/08* (holotype, TUR-A), same locality 189/08.

Inocybe proximella P.Karst., *Symb. Mycol. Fenn.* 9: 44 (1882)

Figs. 14 and 15

Synonyms: *I. striata* Bres., *Iconogr. Mycol.* 16: 759 (1930).

I. umbrinodisca Kühner, *Doc. Mycol.* 74: 26 (1988).

Pileus 1.8–4.8 cm in diameter, convex to conical when young, then campanulate, conico-convex to rather applanate, margin sometimes reflexed when old, usually prominently umbonate, umbo obtuse or rarely rather acute; pale grey brown to medium grey brown, rarely yellow brown, umbo darker being sometimes even red brown to blackish, usually paler towards margin, at times dark striae on pale background; weakly viscid, centre smooth, outwards weakly radially fibrillose, rarely coarsely fibrillose, rarely breaking up, velipellis lacking. *Lamellae* rather broad, up to 7.5 mm, ventricose, narrowly adnate or adnexed, moderately crowded; when young pale grey, later pale grey brown to grey brown, edge usually slightly fimbriate and concolorous to paler. *Stipe* 2.0–13.5 cm long, 2.5–10 mm wide, widening slightly downwards; when young whitish, then pale reddish brown or pale grey brown, often quite dark in the middle part, base whitish or yellowish to ochre when old; in exsiccata stipe is sometimes partly greyish dark brown to blackish, and base often ochre; dry or slightly viscid, fibrillose, often floccose, apex slightly pruinose or not; solid. *Cortina* whitish to pale brownish grey. *Context* whitish, at times greyish, pale brown or reddish, rarely base brown, sometimes longitudinally striate and slightly shiny. Smell weakly acidulous‒spermatic or indistinct. No specific taste.

Fig. 14 *Inocybe proximella*. Finland, Mikkeli, Vauras 2822F. Photograph J. Vauras

Spores (7.8) 8.7–9.9–11.2 (11.8) × (6.2) 6.4–7.3–8.0 (8.7) µm, total range of mean values 9.4–10.5 × 7.0–7.6 µm, Q=(1.1) 1.2–1.35–1.55 (1.65), total range of mean Q values 1.27–1.39 (110 spores from 5 collections); usually rather strongly nodulose with hemispherical, medium-sized to rather large nodules, rather pale yellow brown. *Basidia* (25) 26–31–36 (41) × (9) 10–11–12 µm (n=43), clavate, 4-spored. *Pleurocystidia* (50)54–65–77(85) × (14)16–19–23 (29) µm (n=80), usually moderately to broadly lageniform with cylindrical or conical neck, some fusoid, rarely weakly subcapitate, apex usually crystalliferous, wall up to 2.5 µm thick, at times thickened in neck, pale yellow or nearly hyaline, sometimes apex with thick-walled "cap". *Cheilocystidia* variable, often shorter and wider than pleurocystidia, at times very broad with mucronate apex, wall up to 3 µm thick, thin-walled cystidia usually short, typical paracystidia mostly thin-walled. *Caulocystidia*: metuloids at stipe apex frequent, fusiform, with broad base and typically narrow, tapering apex, also some cylindrical, clavate, flexuous, mucronate or globose, sometimes septae especially at the base; wall usually rather thin, up to 2 µm thick, pale yellow or nearly hyaline, some with thin walls; contents at times brownish; cauloparacystidia numerous.

Habitat: Mainly in forests with *Picea abies*, rarely in parks; calciphilous in Fennoscandia, because most were collected in calcareous and other fertile areas.

Distribution wide; examined specimens from the northern boreal zone of Finland to Croatia and northern Italy. For further details on its European distribution, see *I. striata* in Gminder (2010).

Phenology: *I. proximella* has a long fruiting period, from mid-June to early October.

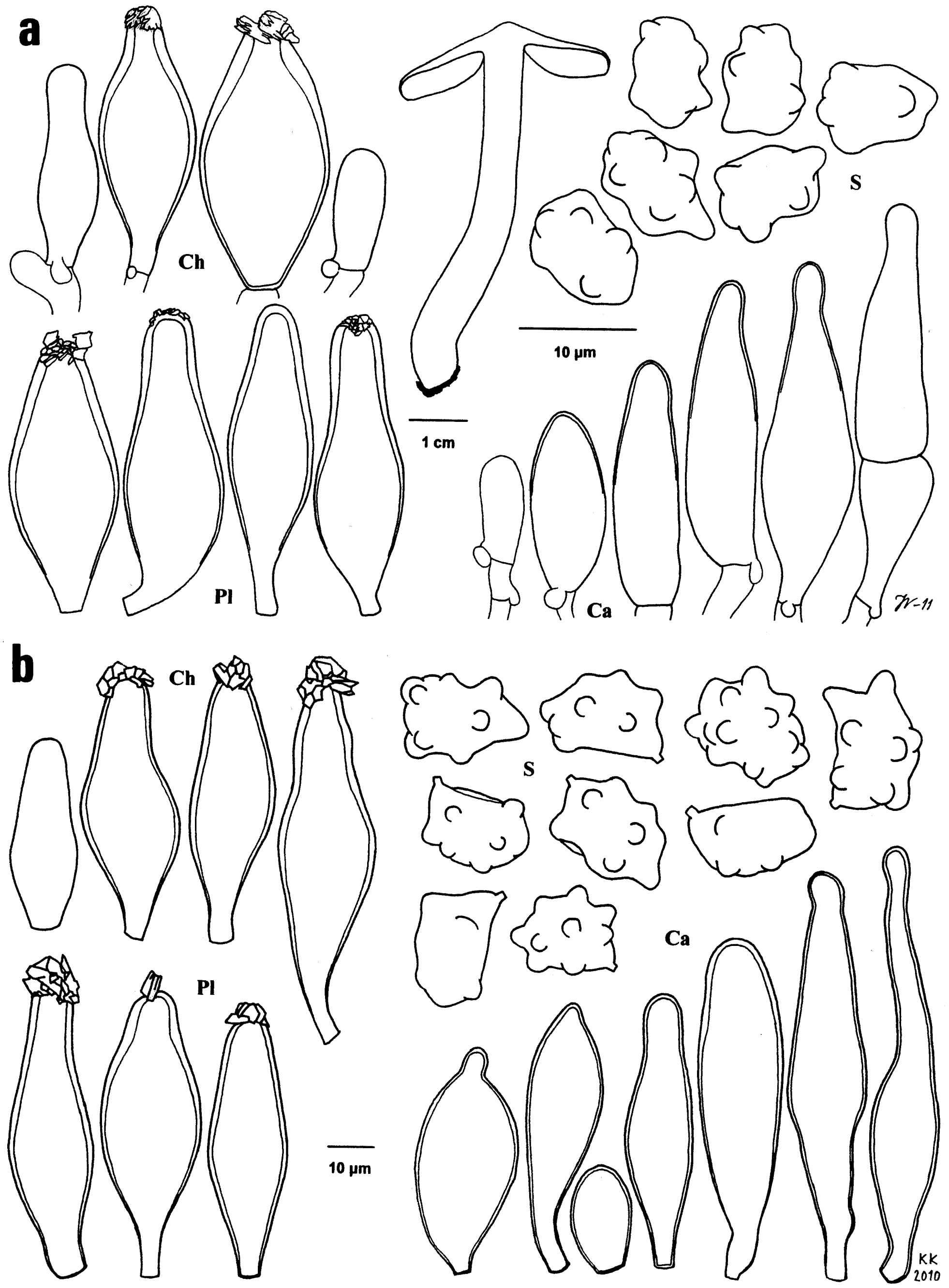


Fig. 15 *Inocybe proximella*. **a** Holotype of *I. proximella*: spores and pleurocystidia. Karsten 896: caulocystidia. Vauras 26381: cheilocystidia and cross-sections of fruitbody. **b** Holotype of *I. umbrinodisca*. For symbols, see Fig. 2

Holotype: *I. proximella*. Finland, Tammela, Syrjä, Herb. P.A.K. No 893, 16.VIII.1881 (H). – Four fruitbodies in good condition. Spores (9.2) 9.8–10.2–11.0 (11.5)×(6.6) 7.2–7.3–8.0 (8.2) µm, Q=(1.2) 1.3–1.39–1.4 (1.6), (*n*=20). Pleurocystidia 54–65×16–23 µm (*n*=10), apex crystalliferous or not, wall up to 2.5 µm thick, hyaline or yellowish. Caulocystidia with broad base and tapering apex. GenBank JN580840. – Note: It is still possible to collect *I. proximella* in the type locality (the last specimen 19.IX.2007, Vauras 25490).

Holotype: *I. umbrinodisca*. France, Bois du Praz, sub Piceis, R. Kühner "A-69", 12.IX.1969 (G). – In small pieces. Spores (8.1) 9.0–9.9–11.0 (11.2)×6.2–7.1–7.9 (8.1) µm, Q=(1.15) 1.2–1.40–1.55 (1.6), (*n*=20). Basidia 4-spored. Pleurocystidia 51–64×12–23 µm (*n*=9), apex crystalliferous, wall up to 2.5 µm thick, pale yellow. Cheilocystidia 53–79×13–23 µm (*n*=8), wall up to 2.5 µm thick, pale yellow, short to rather long thin-walled cystidia or paracystidia rare. Caulocystidia: usually with broad base, tapering neck and subcapitate or clavate apex, some shorter fusoid or clavate, without crystals, numerous; wall thick, up to 1.5 µm, pale yellow; cauloparacystidia rare. ITS1 GenBank JN580851.

Comments: *Inocybe proximella* has been known by Finnish mycologists as a spruce forest species, but the limits of its variation have been obscure. *I. striata* has had much the same status in southern Europe. It appeared conspecific with *I. proximella* in our examinations, as did *I. umbrinodisca*. We thus reduce these to synonyms.

We have not studied the type of *Inocybe striata*, but have relied on type descriptions by Bresadola (1927–33) and Bizio and Marchetti (1998), and considered how the Bizio's collections agree with these descriptions. Bizio sent us four recent collections of *I. striata* that we subjected to ITS analysis. Of these, two Italian and the Croatian specimen agreed in cystidia and reasonably well in spores with the type descriptions of *I. striata*, as well as with *I. proximella*. They deviated from the type of *I. proximella* in their ITS sequences by one or two bases and a gap of three bases (GenBank JN580841, JN580842, JN580843). However, the Croatian and an Italian sequence were identical with some other Finnish sequences of *I. proximella*. Compared with the type, all the other *I. proximella* sequences had the same gap of three bases including a collection of Karsten from 1895 (from that collection only the ITS1 succeeded - JN580844). The fourth analysed specimen sent by Bizio from Italy had shorter fusiform cystidia and spores with smaller, irregular nodules, and it diverged greatly in the ITS from the *I. proximella* type, representing an unknown species. In further support, Bizio and Marchetti (1998) mentioned that the stipe bases of the type fungi of *I. striata* were ochraceous. This fits our observations of *I. proximella*.

According to Stangl (1976), both *Inocybe striata* and *I. striatorimosa* P.D.Orton possibly belong to the *I. acuta* complex. We have studied a part of the holotype of *I. striatorimosa* (K). This belongs to the *I. soluta* Velen. complex, differing from all the species we describe here. The ITS2 sequence of *I. umbrinodisca* failed, but the ITS1 was identical with most Finnish sequences of *I. proximella*. Microscopic and macroscopic features and habitat information agreed, except that the odour of *I. umbrinodisca* was mentioned as fruity-acidulous or at times subpelargonious (Kühner 1988). Kühner collected *I. umbrinodisca* under *Picea*.

In conclusion, *Inocybe proximella* is a rather variable species with a wide distribution. It has typically a rather robust appearance, a weakly fibrillose and rather pale, grey brown cap, often a yellow to ochre tinge at the stipe base, and fairly large spores with rather large nodules. It is likely that it is the most common of all species treated in this paper. However, it is not a common species in Finland. It can be confused with *I. silvae-herbaceae*, for example. See our comments about *I. silvae-herbaceae* for comparison. The ITS sequences of the examined one Swedish and 20 Finnish collections of *I. proximella*, excluding the type, were identical (JV26381 in the phylogram – GenBank JN580845), except for one base difference in collection JV15349 (JN580846), and an insertion/deletion of one base in two specimens (JV21832 - JN580847, KK223/08 - JN580850). An Estonian (JN580848) and a Norwegian (JN580849) specimen both differed by one (different) base from most Finnish specimens. *I. proximella* is rather closely related to *I. giacomi*: the ITS sequences of *I. giacomi* deviated by 22–23 bases and 5 insertions/deletions from the sequence of *I. proximella* type.

Specimens examined: **CROATIA**. Delnice, 19.IX.2007 Bizio*. **ESTONIA**. **Hiiumaa**. Käina, Männamaa, 13.IX.2009 Vauras 27145. **Läänemaa**. Vormsi, Saxby, 19.IX.2010 Vauras 27819. **Lääne-Virumaa**. Vihula, Lahemaa National Park, Käsmu, 18.IX.2009 Kollom. **Saaremaa**. Veere, 19.VI.1995 Kytövuori 95-22* (H). **FINLAND**. **Åland**. Eckerö, Skag, 27.VIII.1984 Vauras 1725, Finström, Ekö, 8.IX.1992 Vauras 7292, Emkarby, 3.IX.1993 Vauras 8572. Jomala, Jomalön, 23.VIII.2000 Vauras 16780, Önningby, 23.VIII.2000 Vauras 16784. **Varsinais-Suomi**. Karkkila, Haavisto, Iitalampi, 13.VIII.2003 Vauras 20006* (TUR). Kemiönsaari, Västanfjärd, Svinberget, 15.VII.2004 Vauras 21458. Lohja, Torhola, 29.VIII.1993 Kytövuori 93–589 (H). Paimio, Huso, 4.X.2005 Vauras 23679. Parainen, Åntala, 5.IX.1990 Vauras 5132. Salo, Suomusjärvi, Lemulanrinne Nature Reserve, 1.IX.2009 Vauras 28149. Turku, Ruissalo, 25.IX.2006 Kokkonen 984/06, Iso-Pukki, 2.VIII.2007 Kokkonen & Vauras 103/07*, Uittamo, 19.VII.1996 Vauras 11279. **Satakunta**. Alastaro, Virttaankangas, Lohensuon lähteikkö, 12.VII.1995 Vauras 10279, 24.VII.2000 Vauras 16160F. Loimaa, Pappinen, Isolähde, 20.VII.1990 Vauras 4387*. **Etelä-Häme**. Hattula, Nihattula, 19.VIII.1993 Kytövuori 93- 340* (H). Ruovesi, Ryövärinkuoppa, 17.VII.1995 Kytövuori 95–034 (H). Tammela, Mustiala, Syrjä, 16.VIII.1881 Karsten, Herb. P.A.K. 893* (holotypus, H), 23.VII.1892 Karsten P.A.K. 894 (H), 13.VIII.1892 Karsten P.A.K. 895 (H), 20.VII.1895 Karsten P.A.K. 896* (H), 19.IX.2007 Vauras 25490. Urjala, Kivijärvi Nature Reserve, 9.IX.2010 Issakainen & Vauras 27777. Vilppula, Elämänmäki, 23.VIII.2004 Vauras 21832*. **Etelä-Savo**. Imatra, Linnansuo E, 10.VIII.1987 Kytövuori 87208 (H). Mikkeli, town, 8.VIII.1987 Vauras 2677, 20.VIII.1987 Vauras 2822F (TUR, TUR-A). **Pohjois-Savo**. Kuopio, Matkusjärvi, 2.VIII.1986 Vauras 2148F, 21.VIII.1987 Vauras 2846*, Niirala, Huuhanmäki, 23.VI.1981 Vauras 878*, Pitkälahti, Kylmälahti, 5.IX.1989 Ruotsalainen*, Puijo 12.08.2011 Kokkonen 157/11, Riistavesi, Laajalahti, 18.VII.1998 Ruotsalainen 4612*. **Pohjois-Karjala**. Nurmes, Ylikylä, Lehmilampi, 16.VIII.2008 Kokkonen & Vauras 26137F*, 2.IX.2008 Kokkonen 223/08*. Valtimo, Haapakylä, Hujalansärkkä, 8.VIII.2004 Kokkonen 18/04*. **Kainuu**. Paltamo, Itkonpuro, 4.IX.2001 Vauras 17622*, Mieslahti, 4.IX.1996 Vauras 11827, Tololanmäki, Kylmänpuro, 20.VIII.2010 Vauras 27645. Ristijärvi, Kivikylä, Lehtipuron lehto, 19.VIII.2010 Lahti & Vauras 27624. **Oulun Pohjanmaa**. Kiiminki, Keskikylä, Isohalmeenmaa, 2.

VIII.1985 Vauras 1889, 28.VII.1988 E. Ohenoja (OULU). **Koillismaa**. Kuusamo, Iivaara, 24.VIII.1992 Vauras 7034* (TUR-A, GB), Oulanka National Park, Talvilampi, 15. VIII.2009 Vauras & Kokkonen 68/09*. **Perä-Pohjanmaa**. Rovaniemi, Jaatilanvaara, Savioja, 24.VIII.1991 Vauras 5826, Meltaus, 23.VIII.1999 Vauras 15349*. Tervola, Vähäjoki, Kuusikkokivalo, 4.IX.1992 Kytövuori 92–1737 (H). **Kittilän Lappi**. Muonio, Pallastunturi, Pyhäjoki, 18.VIII.2009 Vauras & Kokkonen 85/09*. **Sompion Lappi**. Pelkosenniemi, Suvanto, Niskakorpi, 28.VIII.2008 Vauras 26381*. **GERMANY**. **Baden-Württemberg**. Freiburg, Seedorfer Wald, 22.IX.1996 Kytövuori 96–926 (H). **ITALY**. **Belluno**. Falcade, 21.VI.2008 Bizio*. **Trentino**. Valfredda, 19.VII.2008 Bizio*. **NORWAY**. **Buskerud**. Övre Eiker, near Sirikirke, 30. VIII.2003 Vauras 20269. **Vestfold**. Hof, Eidsfoss, 31. VIII.2003 Vauras 20316*. **SWEDEN**. **Medelpad**. Torp, Getberget E, 29.VIII.2001 Vauras 17564. **Norbotten**. Övertorneå, Pello, 12.VIII.1999 Kuusela & Vauras 15099*.

Inocybe silvae-herbaceae Kokkonen & Vauras, **sp. nov.**

Figs. 16 and 17

MycoBank number: MB 563073

Etym.: *silvae-herbaceae* (Latin) refers to the habitat of rich spruce forests.

Pileo 1.0–4.3 cm lato, umbone plus minusque acuto praedito, brunneo, paulum fibrilloso, viscido. Lamellis usque ad 5.5 mm latis, ventricosis. Stipite 1.8–11 cm longo, 2–9 mm crasso, sine bulbo, paulum fibrilloso, viscido. Sporis (7.2) 8.0–9.9 (10.4)×(5.1) 5.5–6.9 (8.0) µm, cum nodulis obtusis ornatis. Pleurocystidiis (40) 48–65 (73)× (11) 12–18 (20) µm, lageniformibus.

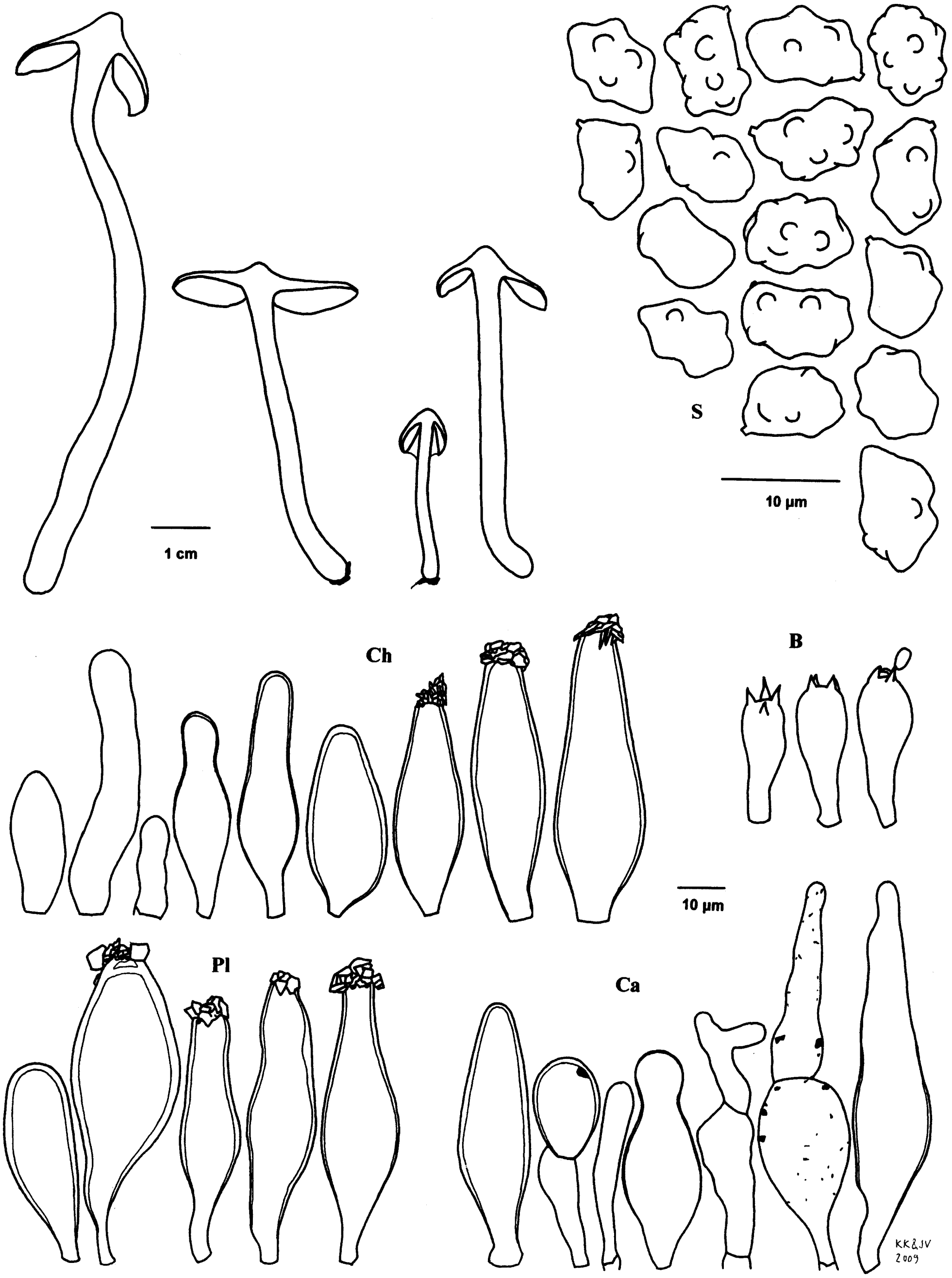
Holotypus: **Finland**, Pohjois-Savo, Kuopio Municipality, Pitkälahti, eastern side of the northern Lake Matkusjärvi, on the western slope, in moist herb-rich forest with mainly *Picea abies, Populus tremula* and *Salix caprea,* by the path, Grid 27°E: 6970:3529, alt. ca. 105 m, 16.VIII.1986 *J. Vauras* 2268F (TUR-A 175344, isotypi GB, WTU), GenBank JN580852.

Fig. 16 *Inocybe silvae-herbaceae*. Finland, Nurmes, Kokkonen & Vauras 23073. Photograph J. Vauras

Pileus 1.0–4.3 cm in diameter, 0.4–1.2 cm high, conical to conico-convex when young, then campanulate or applanate or low conical, margin at times reflexed when old, prominently umbonate, umbo rather acute to obtuse; grey brown (near $S_{40}Y_{50}M_{20}$), medium or yellow brown (near $S_{30}Y_{50}M_{30}$, 50M, 50N), umbo dark to medium brown ($S_{50}Y_{70}M_{50}$, 50T, 33S, 47S, 69S, 47R), outermost margin often the palest; usually distinctly viscid, centre smooth, outwards usually weakly fibrillose, rarely breaking up, velipellis lacking, sometimes remnants of cortina at margin. *Lamellae* up to 5.5 mm wide, ventricose, narrowly adnate to free, moderately crowded; when young pale grey, later grey brown ($S_{30}Y_{30}M_{20}$), rarely pale yellow brown, edge concolorous or paler, usually even. *Stipe* 1.8–11 cm long, 2–9 mm wide, widening slightly downwards or equal, base usually subclavate; when young whitish, then pale brown, often with red tinge (near $S_{00}Y_{30}M_{20}$), base whitish or yellowish; finely fibrillose, rarely delicately flocculose, often shiny, apex slightly pruinose; distinctly to weakly viscid, solid. *Cortina* whitish. *Context* in pileus whitish to pale brown; in the upper part of stipe reddish pale brown, in the lower part whitish to pale brown usually without red tinge, base whitish or rarely yellowish. Smell spermatic to acidulous, rarely indistinct. No specific taste.

Spores (7.2) 8.0–9.0–9.9 (10.4)×(5.1) 5.5–6.2–6.9 (8.0) µm, total range of mean values 8.5–9.3×5.8–6.6 µm, Q=(1.2) 1.3–1.46–1.6 (1.7), total range of mean Q values 1.40–1.49 (100 spores from 5 collections); rather strongly nodulose with somewhat hemispherical, usually medium-sized to rather large nodules, often a prominent hilar nodule, at times spores slightly bent, rather pale yellow brown. *Basidia* (19) 26–31–36 (40)×(8) 9–10 (12) µm (*n*=56), clavate, 4-spored. *Pleurocystidia* (40) 48–56–65 (73)×(11) 12–14–18 (20) µm (*n*=86), narrowly to moderately broadly lageniform, rarely fusiform or clavate, apex usually crystalliferous, base tapered or with pedicel, wall up to 2 µm thick, yellowish, rarely apex with thick-walled "cap". *Cheilocystidia* rather similar to pleurocystidia, but apex more often conical or subcapitate, apex crystalliferous or not, wall up to 2 µm thick but usually thinner, wall yellowish, at times with yellow contents, sometimes apex with thick-walled "cap"; some thin-walled, hyphoid often with broader base, or fusiform cystidia without distinct border with paracystidia. *Caulocystidia* at stipe apex various; metuloids fusiform, also some capitate, subglobose, cylindrical or utriform, wall up to 2 µm thick, yellowish; abundant thin-walled, multiform cystidia, often hyphoid, sometimes with inflated base or transverse walls or branches and protuberances; apex at times crystalliferous, rarely scattered crystals. Cauloparacystidia thin-walled, numerous.

Fig. 17 *Inocybe silvae-herbaceae*. Holotype: microscopic characters, two cross-sections of fruitbodies on the *right*. Vauras 3135F: second fruitbody from the *left*. Kokkonen 327/08: *left* fruitbody. For symbols, see Fig. 2



Habitat: Rich forests with *Picea abies*, often moist depressions. Calciphilous.

Distribution: Known from Finland, Norway and Sweden, from hemiboreal to northern boreal zone.

Phenology: Early August to late September, mainly mid-August.

Comments: *Inocybe silvae-herbaceae* can be easily confused with *I. proximella*. They both grow in spruce forests, preferring calcareous localities, sometimes sharing the site, and resemble each other in appearance and microscopic features. However, *I. silvae-herbaceae* is not as greyish as *I. proximella*, it has somewhat smaller spores, cheilocystidia with thinner walls, and perhaps the best distinguishing feature is the more variable caulocystidia. ITS sequencing shows that these fungi are not closely related. *I. silvae-herbaceae* can also be confused with the related *I. amicta*; see for comparison our comments about *I. amicta*.

Compared with the type sequence, one collection deviated by a base and a gap (JV9200 - GenBank JN580853), three collections by an insertion of a base (KK&JV23073 - JN580854, Kytövuori 93–146 - JN580855, Heinonen 353–94 - JN580857), and one collection by two gaps (JV4983 - JN580858), when loci with ambiguous bases were ignored.

The type had one ambiguous base (T or G), and in that locus six specimens had base G and three had T (Kytövuori 95–2143 in the phylogram - JN580856).

Specimens examined: **FINLAND**. **Varsinais-Suomi**. Paimio, Kurki, Koivula, 16.IX.1992 Vauras 7572. Parainen, Valoniemi, 29.VIII.1990 Vauras 4983*. Salo, Kiikala, Hirvelä, 25.IX.1994 Heinonen 353-94* (TUR). **Etelä-Häme**. Somero, Häntälä, 12.IX.1994 Vauras 9592. **Pohjois-Häme**. Uurainen, Jokihaara, 15.VIII.1993 Kytövuori 93-146* (H). Äänekoski, Parantala, 13.VIII.1988 Storbacka & Vauras 3175. **Pohjois-Savo**. Kuopio, Neulaniemi, 11.VIII.1994 Vauras 9200*, Pitkälahti, Matkusjärvi, 21.VIII.1980 Vauras 2845, 16.VIII.1986 Vauras 2268F* (holotype, TUR-A), 11.VIII.1988 Vauras 3135F, 13.VIII.1992 Heinonen 69–92 (TUR), Puijo, Antikkalanrinne, 12.IX.2009 Kokkonen 266/09. Nilsiä, Haluna, Halunanranta, 12.VIII.1994 Vauras 9261, east side of lake Karankainen, 13.VIII.2002 Vauras 19130*, Kangas, Loutteispuro, 6.VIII.2003 Vauras 19833*. **Pohjois-Karjala**. Juankoski, Huosiaisniemi, 15.VIII.2002 Vauras 19220, 16.IX.2008 Kokkonen 327/08*. Nurmes, Ylikylä, Lehmilampi, 13.VIII.2005 Kokkonen & Vauras 23073*. **Kainuu.** Paltamo, Itkonpuro, 17.VIII.2010 Vauras 27582F. **Perä-Pohjanmaa.** Keminmaa, Kallinkangas, 13.IX.1988 Tammilehto (OULU). **Kittilän Lappi.** Muonio, Pyhäjoki, 18.VIII.2009 Kokkonen & Vauras 86/09. **NORWAY**. **Buskerud**. Ringerike, Hönefoss, Grunntjern, 28.VIII.2003 Vauras 20222. **SWEDEN**. **Medelpad**. Borgsjö, Bergåsen, 13.IX.1995 P. & I. Kytövuori 95-2143* (H), Granbodaåsen, 3.IX.1997 Kytövuori 97–658 (H).

Inocybe amicta Kokkonen & Vauras, **sp. nov.**

Figs. 18 and 19

MycoBank number: MB 563074

Etym: *amicta* (Latin) refers to the white cover of the stipe.

Fig. 18 *Inocybe amicta*. Holotype. Photograph J. Vauras

Pileo 1.1–3.8 cm lato, umbonato, brunneo, paulum viscido. Lamellis usque ad 7 mm latis. Stipite 1.8–7 cm longo, 2.5–8 mm crasso, sine bulbo, plerumque distincte albo-villoso. Sporis (7.2) 8.0–9.9 (10.4)×(5.5) 5.6–7.0 (7.6) µm, nodulosis. Pleurocystidiis (42) 47–64 (74)×(12) 13–21 (24) µm, lageniformibus.

Holotypus: **Finland**, Koillismaa, Kuusamo Municipality, Oulanka National Park, northwest of Kiutaköngäs, on the north side of the Oulankajoki River, near the Oulanka Research Station, by a path in the shore forest, near *Pinus sylvestris, Betula, Populus tremula, Alnus incana, Prunus padus, Sorbus aucuparia, Juniperus communis, Ribes spicatum, Vaccinium vitis-idaea, Rubus saxatilis, Thymus serpyllum* ssp. *tanaënsis, Solidago virgaurea, Fragaria vesca, Melica nutans, Campanula rotundifolia, Galium boreale, Maianthemum bifolium, Achillea millefolium*, and *Angelica sylvestris*, amongst litter and mosses, a few on bare ground, soil with mull and fine sand, Grid 27°E: 73660:36037, alt. ca. 158 m, 14.VIII.2009 *Vauras* & *Kokkonen* 61/09 (TUR-A 190466, isotypi H, GB, WTU), GenBank JN580859.

Pileus 1.1–3.8 cm in diameter, conical when young, then conico-convex or applanate, margin sometimes reflexed or weakly undate, umbo obtuse to rather acute; colour variable, greyish yellow brown ($S_{40}Y_{70}M_{40}$) or reddish yellow brown (near $S_{30}Y_{60}M_{40}$) with darker, red brown or grey brown centre ($S_{40}Y_{60}M_{50}$, near $S_{50}Y_{60}M_{40}$), or predominantly rather dark grey brown ($S_{50}Y_{60}M_{40}$, near $S_{50}Y_{80}M_{50}$), sometimes paler yellow brown, rarely dark brown or very pale grey brown with brown yellow umbo, umbo usually the darkest and outermost margin the palest; weakly to distinctly viscid, centre smooth or cracked to small appressed scales, outwards radially fibrillose, at times breaking up, velipellis lacking, sometimes with remnants of cortina at margin. *Lamellae* rather broad, up to 7 mm, moderately crowded, ventricose, adnexed or narrowly adnate or emarginate, often with a long decurrent tooth; when young pale grey or pale grey brown, later grey brown ($Y_{20}M_{10}C_{10}$–$S_{30}Y_{40}M_{20}$, near $Y_{40}M_{20}C_{10}$), rarely pale yellow brown, edge concolorous or slightly paler, even or slightly fimbriate. *Stipe* 1.8–7.0 cm long, 2.5–8 mm wide, equal to slightly widening downwards, base round to tapering; very weakly viscid, entirely distinctly white felted to floccose or only weakly in the upper part, rarely entirely nearly smooth, at times striate, base yellowish or white, ground colour pale red brown (near $S_{00}Y_{30}M_{20}$), pale brown, or at apex reddish ($S_{00}Y_{20}M_{10}$), in exsiccata sometimes darkened, solid. *Cortina* whitish. *Context* in pileus pale brown or pale grey or whitish; in stipe same as the surface ground colour or whitish, striate, base white or yellowish. Smell weakly spermatic to acidulous or indistinct. No specific taste.

Spores (7.2) 8.0–$\underline{8.8}$–9.9 (10.4)×(5.5) 5.6–$\underline{6.3}$–7.0 (7.6) µm, total range of mean values 8.3–9.2×6.1–6.5 µm,

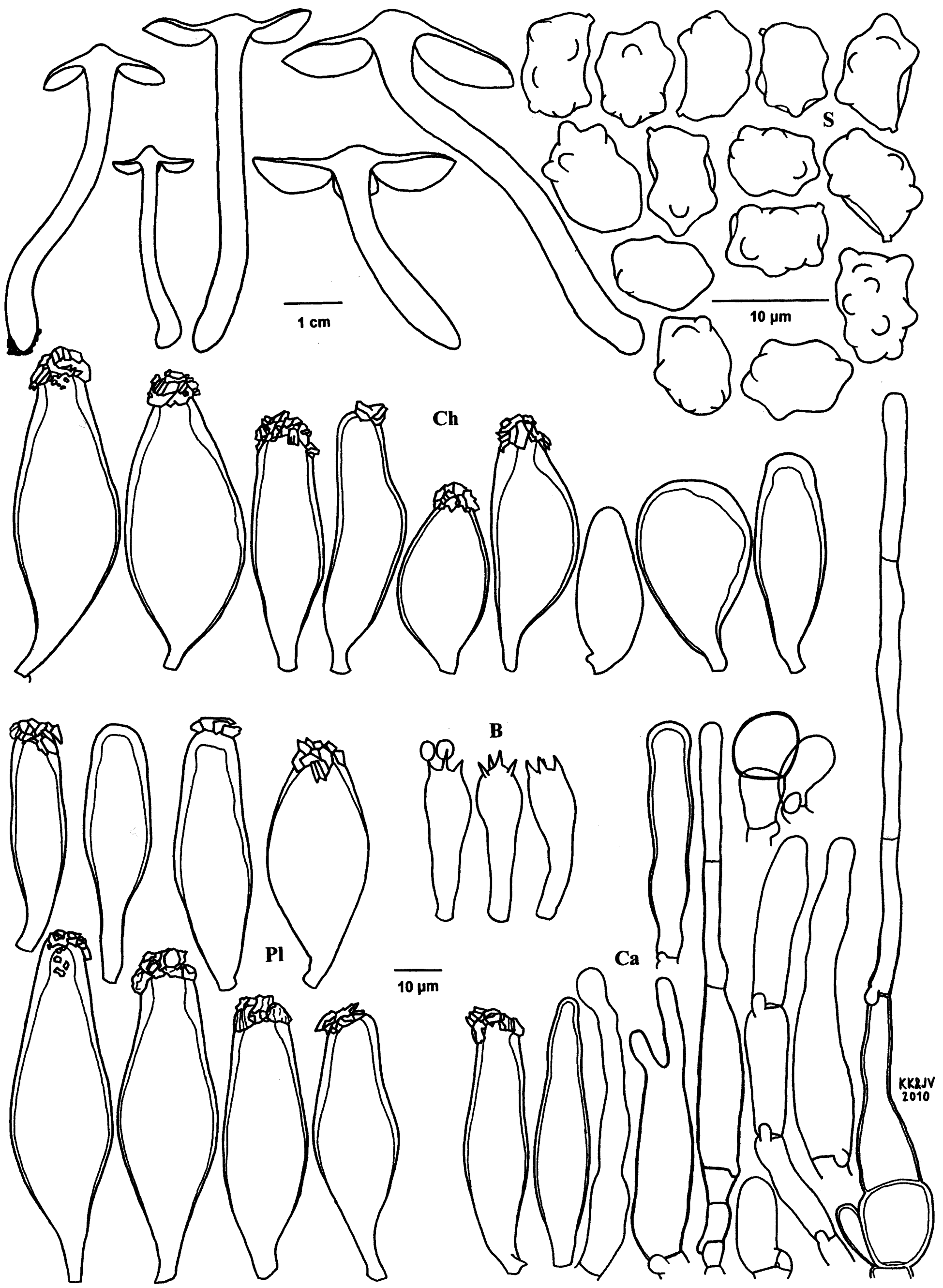


Fig. 19 *Inocybe amicta*. Holotype: microscopic characters, three fruitbodies in the *middle*. Ruotsalainen & Vauras 7015: fruitbody on the *left*. Vauras & Kokkonen 62/09: fruitbody on the *right*. For symbols, see Fig. 2

Q=(1.2) 1.3–1.41–1.6 (1.7), total range of mean Q values 1.35–1.51 (100 spores from 5 collections); weakly to rather strongly nodulose (moderately nodulose in the holotype), nodules usually medium-sized to rather large, some spores slightly bent with protruding hilar nodule, rather pale yellow brown. *Basidia* (22) 24–28–32 (33)×9–11–12 µm (*n*=37), clavate, 4-spored. *Pleurocystidia* (42) 47–56–64 (74)×(12) 13–17–21 (24) µm (*n*=81); narrowly to rather broadly lageniform with short to rather long neck, utriform or nearly cylindrical, rarely fusiform, apex usually crystalliferous, base tapered or with pedicel; wall at times distinctly thickened in neck, up to 3 µm thick, pale yellow, sometimes apex with thick-walled "cap". *Cheilocystidia* usually slightly shorter and wider than pleurocystidia, rarely subglobose; short thin-walled cystidia or paracystidia rare. *Caulocystidia*: metuloids at stipe apex rather rare, subfusiform, cylindrical or flexuose, apex with crystals or not, wall up to 2 µm thick; hyphoid thin-walled cystidia abundant, often with septae, at times walls thick at base or with protuberances or branches; cauloparacystidia thin-walled or slightly thick-walled, numerous.

Habitat: On richer, but mainly sandy soils. River bank with mixed stand; old church park with *Betula*, *Picea abies*, and *Pinus sylvestris*; rich forest mainly with *Picea abies*.

Distribution: Known from only three localities in Finland, from southern and northern boreal zones.

Phenology: Collected from mid-July to late August.

Comments: The most distinctive feature of *Inocybe amicta* is the white cover of the stipe. Otherwise, it can be macroscopically quite variable. The ITS sequences of five *I. amicta* specimens were otherwise identical (JR&JV7015 in the phylogram - GenBank JN580861), but there was a gap of three bases in the holotype sequence, and one different base in KK45/10 (JN580860).

Inocybe amicta is closely related to *I. silvae-herbaceae*. The ITS sequences of the holotypes of these two species differed only by 14 bases and 4 insertions/deletions (1 base in length). These species also microscopically resemble each other. However, *I. amicta* typically has thicker walls in its hymenial cystidia with distinct thickenings at the neck, and does not have as multiform caulocystidia as *I. silvae-herbaceae*.

Inocybe putilla Bres., which is a southern species in Finland and probably mycorrhizal with *Quercus robur*, resembles *I. amicta*, for example, in its pale stipe cover and some microscopic features (see Additional type studies, Fig. 33b). However, the ITS sequence of a typical Finnish *I. putilla* collection (Turku, Ruissalo, KK&JV23972, GenBank JN580862) deviated greatly from the *I. amicta* sequences.

Specimens examined: **FINLAND. Pohjois-Savo.** Kuopio, Vuorilampi Nature Reserve, 5.VIII.1980 Vauras 570*. Leppävirta, church village, 12.VII.1996 K. & J. Ruotsalainen 4108*. **Koillismaa.** Kuusamo, Oulanka National Park, near Kiutaköngäs, 23.VIII.1992 Ruotsalainen & Vauras 7015*, 14.VIII.2009 Vauras & Kokkonen 61/09* (holotype, TUR-A), 62/09, 63/09, 22.VIII.2009 Kokkonen 110/09, 14.VIII.2010 Kokkonen 28/10, 32/10, 16.VIII.2010 Kokkonen 44/10*, 45/10*.

Inocybe porcorum Vauras & Kokkonen, **sp. nov.**

Figs. 20 and 21

MycoBank number: MB 563075

Etym.: *porcorum* (Latin) means "of the pigs". The name refers to the type locality Svinberget (in Swedish meaning "pig rock").

Pileo 1.5–3.5 cm lato, umbonato, brunneo, fibrilloso, plerumque etiam squamuloso. Lamellis usque ad 7 mm latis. Stipite 2.5–4.5 cm longo, 2.5–4 mm crasso, saepe subbulboso, brunneo, non pruinoso. Sporis (9.6) 9.7–11.8 (12.1)×(6.2) 6.4–7.8 (7.9) µm, nodulosis. Pleurocystidiis (53) 58–83 (96)× (11) 13–22 (24) µm, angusto-fusiformibus.

Holotypus: **Finland**, Varsinais-Suomi, Kemiönsaari Municipality, Västanfjärd, Billböle, Svinberget, Åkerbacka, on eastern slope, on bank of the main road at margin of open forest with *Pinus sylvestris, Betula, Picea abies*, and *Salix caprea,* Grid 27°E: 66677:32617, alt. ca. 19 m, 15. VII.2004 *J. Vauras* 21444 F (TUR-A 111926, isotypi H, GB, WTU), GenBank JN580863.

Fig. 20 *Inocybe porcorum*. Holotype. Photograph J. Vauras

Pileus 1.5–3.5 cm in diameter, conico-convex, with a low broad umbo, later plano-convex, dark brown to brown around disc, outwards slightly paler, around disc smooth, squamulose or moderately cracked, outwards radially fibrillose to slightly squamulose, margin often with darker bundles of fibres, velipellis lacking. *Lamellae* up to 7 mm wide, ventricose, narrowly adnate, moderately crowded, when young pale grey, later brownish grey, then fairly dark brown, edge slightly fimbriate, uneven and paler. *Stipe* 2.5–4.5 cm long, 2.5–4 mm wide, equal, often curved and subbulbous, when young pale, slightly brownish, later brown to fairly dark brown, not pruinose, whitish fibrillose, at times part of the fibrils fairly dark brown; slightly shiny, solid. *Cortina* brownish grey, soon disappearing. *Context* in pileus whitish, pale brown under surface, in stipe pale, slightly yellow-brown, with stronger brown to red-brown tinge under surface, longitudinally fibrillose striate, shiny. Smell acidulous.

Spores (9.6) 9.7–$\underline{10.6}$–11.8 (12.1)×(6.2) 6.4–$\underline{7.0}$–7.8 (7.9) µm, total range of mean values 10.6–10.7×6.9–7.1 µm, Q=(1.3) 1.35–$\underline{1.51}$–1.65 (1.75), total range of mean Q values 1.50–1.53 (60 spores from 2 collections), nodulose to angular-nodulose, with several hemispherical, fairly small nodules, rather pale yellow brown. *Basidia* (26) 28–$\underline{33}$–37 (41)×9–$\underline{11}$–12 (13) µm (*n*=36), clavate, 4-spored. *Pleurocystidia* (53) 58–$\underline{70}$–83 (96)×(11) 13–$\underline{17}$–22 (24) µm (*n*=51), slenderly fusiform or lageniform to cylindrical, usually with abundant crystals, base tapered or with pedicel, wall up to 2 µm thick, pale yellow. *Cheilocystidia* similar to pleurocystidia but more variable, up to 78 µm long and 25 µm wide, rarely with brown contents; paracystidia scarce. *Caulocystidia*: metuloids at stipe apex very scarce to absent; caulocystidioid hairs up to 92 µm long, mostly tapering to the apex or slightly capitate,

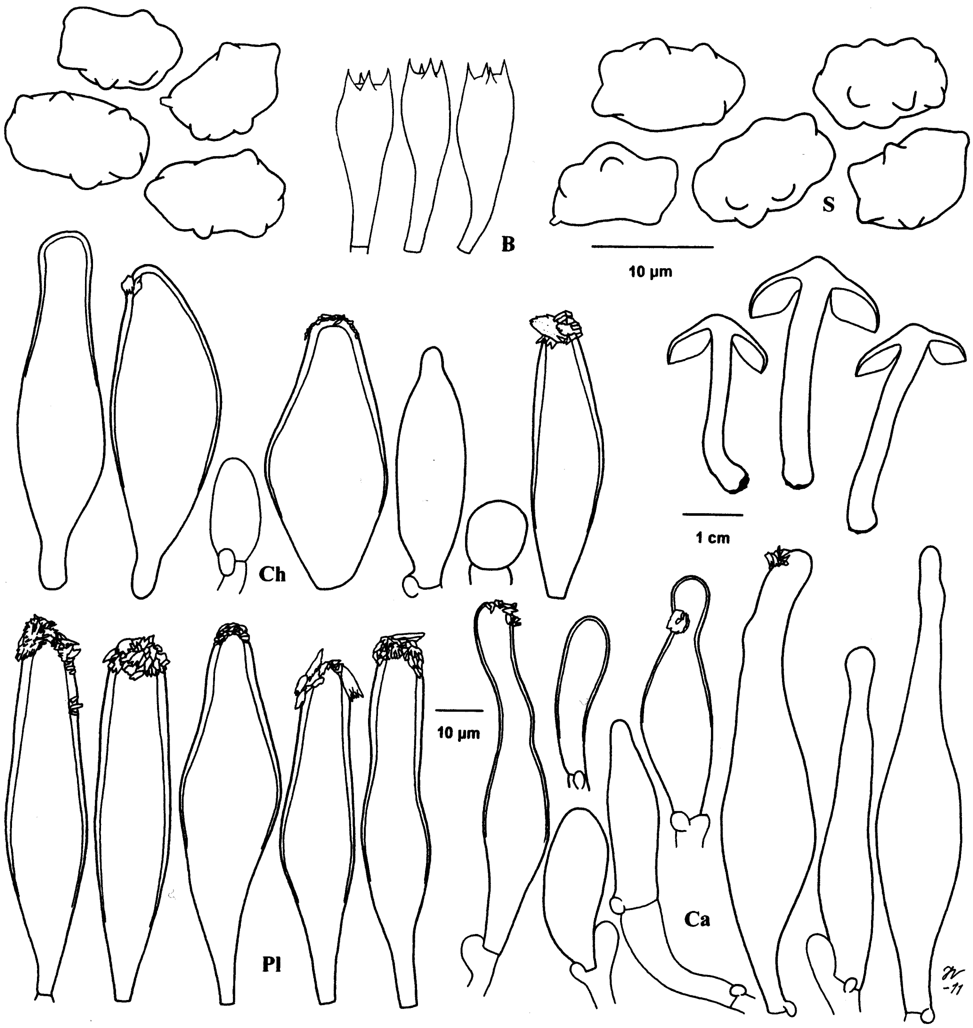


Fig. 21 *Inocybe porcorum*. Holotype: microscopic characters and cross-sections of fruitbodies. For symbols, see Fig. 2

some with crystals, some slightly thick-walled; cauloparacystidia not observed.

Habitat: Margin of forest with *Pinus sylvestris* and scattered *Picea abies, Betula*, and *Salix caprea*, on fairly bare moraine sandy mull at road bank. The rock underlying this forest is partly limestone. The locality is known as the place in Finland where the vascular plant *Saxifraga adscendens* is most abundant. Calciphilous macrofungi of the locality include *Cantharellus aurora* and several *Cortinarius* species of subgenus *Phlegmacium*. These data suggest that *Inocybe porcorum* may be a demanding species, restricted to calcareous areas.

Distribution: Known only from the type locality in the hemiboreal zone of southern Finland.

Comments: *Inocybe porcorum* is characterised by fairly large spores and pleurocystidia, which to some extent resemble those of *I. decipiens* Bres. However, the latter species has larger spores and caulocystidia over half-way down the stipe. *I. curvipes* P.Karst., a common species in southern Finland, differs, for example, in its silvery grey-brown colour at the stipe base and its pleurocystidia with subacute apices. *I. proximella*, a species with caulocystidioid hairs tapering to their apices, is more greyish and usually paler in colour, not squamulose, has somewhat smaller spores with larger nodules and smaller Q values, and wider and shorter pleurocystidia on average. In our material of sequenced species, *I. proximella* is the closest to *I. porcorum*, but showed as many as 35 deviating bases and 12 insertions/deletions.

Specimens examined: **FINLAND**. **Varsinais-Suomi**. Kemiönsaari, Västanfjärd, Billböle, 15.VII.2004 Vauras 21444F* (holotype, TUR-A), 30.IX.2004 Vauras 22758.

Inocybe giacomi J.Favre, *Rés. Rech. Scient. Parc Nat. Suisse* 5: 115 (1955)

Figs. 22, 23 and 24

Synonyms: *I. hinnulea* Kühner, *Doc. Mycol.* 74: 20 (1988).

I. johannae Kühner, *Doc. Mycol.* 74: 21 (1988).

Fig. 22 *Inocybe giacomi*. Finland, Kuopio, Vauras 9198F. Photograph J. Vauras

I. striaepes Kühner, *Doc*. *Mycol*. 74: 24–25 (1988).

Pileus 2.0–4.5 cm in diameter, 1.0–1.6 cm high, convex when young, then applanate, margin usually deflexed, often undate, subumbonate or with broad obtuse umbo; centre smooth, outwards villose fibrillose, often breaking up, velipellis not observed; dark brown (47S, 47R) fibres on pale grey brown (49N–50N) background or rather evenly coloured, centre brown (49R), or when young also tinged red (47R), and margin pale grey brown. *Lamellae* up to 6 mm wide, ventricose, narrowly adnate, moderately crowded to rather distant; when young pale brown grey, later pale brown, edge concolorous or paler, even or slightly fimbriate. *Stipe* 4.0–4.8 cm long, 7–10 mm wide, equal, base roundish or tapering; fibrillose striate, very finely white to brownish felted; ground colour pale brown with reddish tinge (30K) to whitish. *Context* whitish or in stipe sporadically tinged reddish. Some damaged spots turn brown red (47N). Smell acidulous.

Spores (8.5) 8.9–9.9–11.1 (11.5)×(5.5) 5.8–6.5–7.2 (7.3) µm, total range of mean values 9.9×6.2–6.6 µm, Q=(1.3) 1.4–1.54–1.75 (1.9), total range of mean Q values 1.50–1.59 (80 spores from four Nordic collections); angular or with few nodules, often somewhat quadrangular, rather pale yellow brown. *Basidia* (28) 29–32–36 (38)×10–11–12 µm (*n*=35), clavate, 4-spored. *Pleurocystidia* (42) 47–59–74 (84)×(14) 15–18–24 (25) µm (*n*=42); narrowly to rather broadly lageniform with short neck, rarely narrowly fusoid, apex usually crystalliferous, wall often distinctly thickened in neck, up to 4 (rarely −6) µm thick, yellowish. *Cheilocystidia*: metuloids similar to pleurocystidia, few with long neck, often crystalliferous, some thin-walled. *Caulocystidia*: metuloids at stipe apex resembling pleuro-

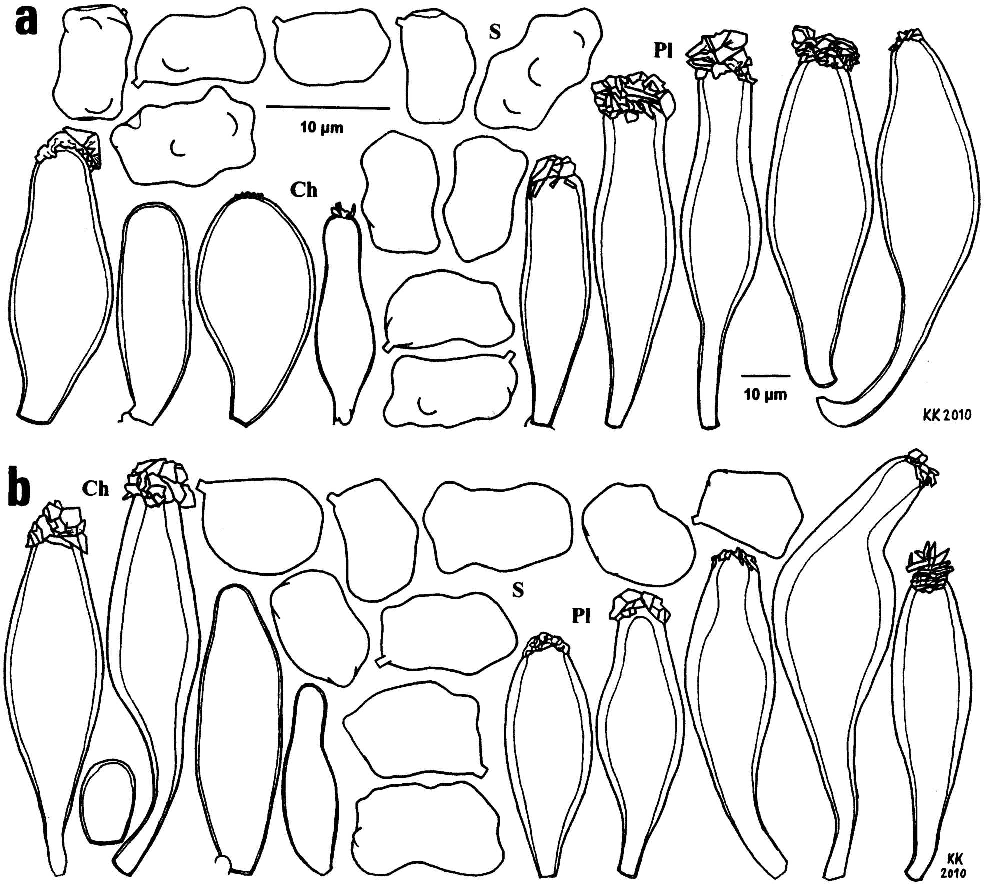


Fig. 23 *Inocybe giacomi*: microscopic characters. **a** Lectotype of *I. giacomi*. **b** Holotype of *I. johannae*. For symbols, see Fig. 2

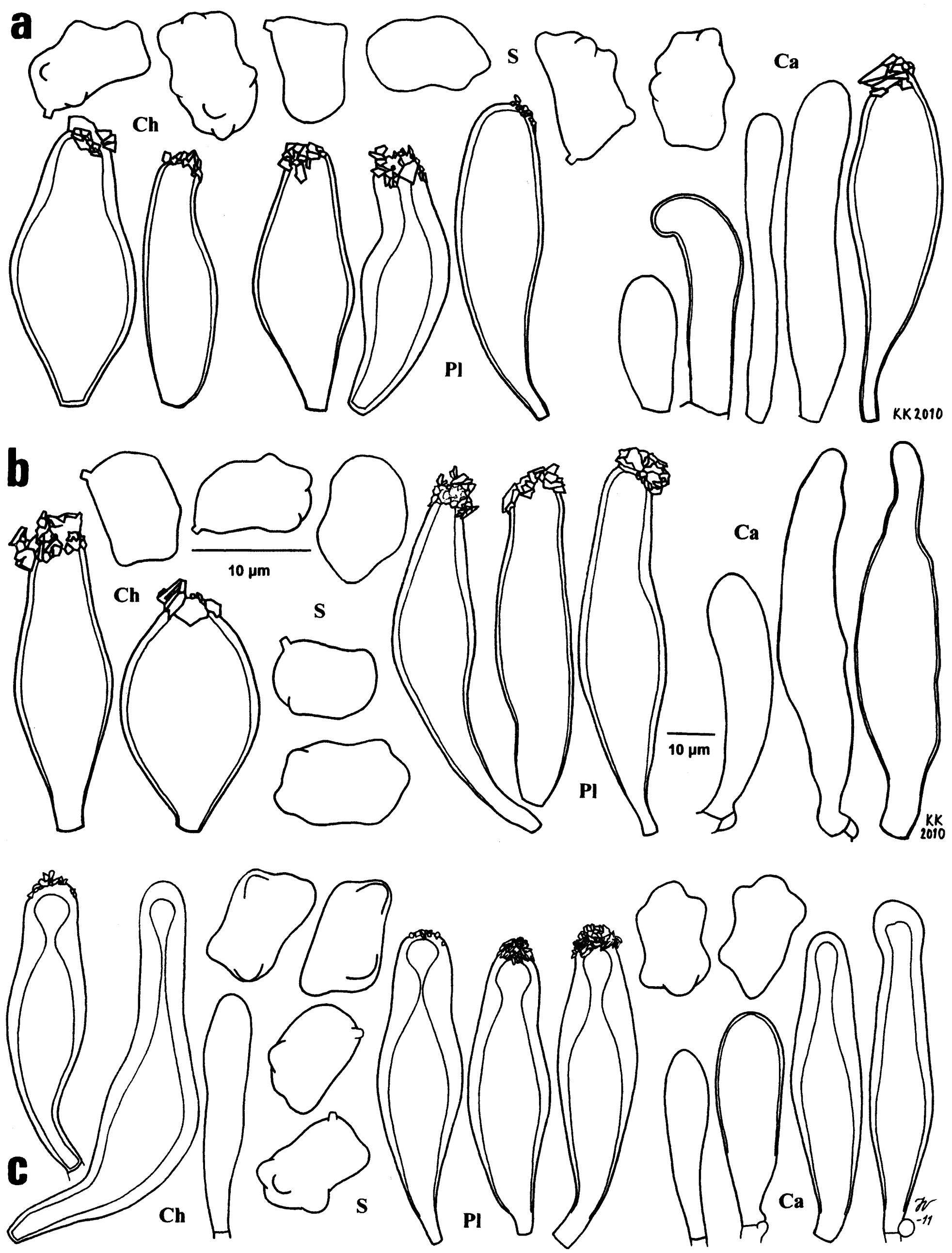


Fig. 24 *Inocybe giacomi*: microscopic characters. **a** Holotype of *I. hinnulea*. **b** Holotype of *I. striaepes*. **c** Vauras 9198F. For symbols, see Fig. 2

cystidia but at times larger and some clavate or cylindrical, some with thin walls, cauloparacystidia thin-walled or slightly thick-walled.

Habitat: This species favours sandy soils and areas of human influence in the boreal zone of Finland. Collected from dry, pine heath forest with sandy soil, from margin of yard with *Betula* and *Pinus sylvestris*, and on fjeld near *Dryas octopetala* and *Salix reticulata*.

Distribution: Widely distributed based on the examined specimens; the southern boreal zone of Finland, alpine zones of Norway, France and Switzerland.

Phenology: Late July to mid-September.

Lectotype: *I. giacomi*. Switzerland, Ofenpass, Entre le col du Gialet et le marais superieur de Buffalora, prairie alpine, J. Favre 124b, 13.VIII.1941 (G). – Only one fruitbody. Spores (8.7) 8.9–10.1–12.0 (12.5)×(5.5) 5.7–6.2–7.3 (7.4) µm, Q=(1.4) 1.5–1.64–1.8 (2.0), (*n*=20). Basidia 4-spored, 31–34×10–12.5 (*n*=6). Pleurocystidia 48–68–91×15–17–21 µm (*n*=16), often with long pedicel, apex crystalliferous, wall up to 2.5 (rarely 3) µm thick, slightly yellowish. Cheilocystidia 32–55×11–25 µm (*n*=8), wall up to 2.5 (rarely 3) µm thick, slightly yellowish or hyaline. Caulocystidia not examined. ITS1 GenBank JN580864.

Holotype: *I. hinnulea*. France, Savoie, Pralognan, Pâtures de la Motte, Parmi les Hélianthimes et les Genévriers, Alt. 1,950 m, R. Kühner "K68-125", 16. VIII.1968 (G). – Two fruitbodies. Spores 8.5–9.7–10.5 (11.9)×5.5–6.3–6.8 (6.9) µm, Q=(1.35) 1.4–1.55–1.7 (1.75), (*n*=20). Basidia 4-spored. Pleurocystidia 50–57–64×16–18–22 µm (*n*=11), wall up to 5 µm thick, yellowish or hyaline. Cheilocystidia 46–58×15–27 µm (*n*=6), wall up to 3 µm thick, yellowish or hyaline, no typical paracystidia. Caulocystidia −70×−22 µm (*n*=6), often clavate, crystalliferous or not, nearly all thin-walled, wall up to 1.5 µm thick, yellowish; cauloparacystidia rather numerous. ITS1 EMBL-Bank HE582395, ITS2 GenBank JN580866.

Holotype: *I. johannae*. France, Savoie, Pralognan, Col de la Valette, sur terre moussue et lichénisée parmi *Salix serpyllifolia*, Alt. 2,550 m, R. Kühner "K65-117", 26. VIII.1965 (G). – Ca. four fruitbodies. Spores (8.2) 8.8–10.2–11.9 (13.5)×(5.7) 5.9–6.6–7.8 (8.0) µm, Q=(1.25) 1.3–1.55–1.7 (1.8), (*n*=20). Basidia 4- or rarely 2-spored, 31–40×10.5–13.5 µm (*n*=8). Pleurocystidia 42–55–84×13–17–24 µm (*n*=8), wall up to 4 µm thick, hyaline, at times contents yellow. Cheilocystidia 37–74×11–21 µm (*n*=7), wall up to 3.5 µm thick, yellow, contents yellow, apex crystalliferous or not. A paracystidium rather thick-walled, yellowish. Caulocystidia not examined. ITS1 GenBank JN580865.

Holotype: *I. striaepes*. France, Savoie, Alpes Francaises, Parc National de la Vanoise, R. Kühner "K72-70", 8. VIII.1972 (G). – Ca. four fruitbodies. Spores (8.1) 9.0–9.9–11.1 (11.2)×(5.6) 6.5–6.9–7.6 (8.2) µm, Q=1.25–1.43–1.6, (*n*=20). Basidia 4-spored. Pleurocystidia 60–69–77×17–19–22 µm (*n*=5), wall up to 2.5 µm thick, hyaline. Cheilocystidia 43–67×18–28 µm (*n*=7), wall up to 3 µm thick, hyaline, typical paracystidia absent. Caulocystidia −93×−18.5 µm (*n*=9), often narrow, apex tapering or clavate, without crystals, wall thick or thin, up to 1.5 µm, yellowish; typical cauloparacystidia not observed. ITS1 GenBank JN580867.

Comments: Our specimens and the types of *Inocybe hinnulea*, *I. johannae* and *I. striaepes* were identified mainly on the basis of ITS1 and/or ITS2 sequences. All the ITS1 sequences were identical with the *I. giacomi* type sequence except for an insertion of two bases in *I. striaepes*, an end shortage in *I. hinnulea*, and a locus where *I. giacomi* had A, *I. johannae* had an ambiguous base A or T, and the others had T. The ITS2 sequences of types other than *I. hinnulea* failed. ITS2 sequences differed from each other by one or two bases at the most (the Nordic specimens - GenBank JN580868, JN580869, JN580870, JN580872, in the phylogram Holtan & Larsen 28–2008 - JN580871). A Finnish specimen collected from a park (KK370/03) deviated from the others in appearance having a large, weakly fibrillose, pale yellow brown pileus, and frequent utriform cystidia. For these reasons, we hesitated to identify it as *I. giacomi* and excluded it from the description. The macroscopic and microscopic features of the other collections matched. Ferrari (2006) considered *I. johannae* a synonym of *I. giacomi* based on morphology. He also reported a collection from a subalpine locality. Further, Rödel and Vesper (2009) found *I. giacomi* from elsewhere than mountains, in a German hilly region.

The identification of *Inocybe giacomi* has been to some extent problematic. Favre (1955) did not have any type, but he renamed his collections of *I. carpta* Scop. sensu Bresadola as *I. giacomi*. Stangl (1976) chose a holotype (this should have been a lectotype), which Horak (1987) rejected in favour of a new lectotype (Favre 124a), corresponding to the drawing information of Favre. We, however, regard the first lectotype as valid, because its microscopic features agree with Favre's description, and the herbarium G has not rejected it. Kühner and Romagnesi (1953) and Moser (1978) regarded *I. giacomi* a synonym of *I. boltonii* Heim (1931), and Miller (1987) regarded it as a subspecies of *I. boltonii* from boreal Alaska. Indeed, the spores and cystidia of *I. giacomi* and Heim's description of *I. boltonii* greatly resemble each other, although the cystidia of *I. boltonii* are shorter. More importantly, the pileus of *I. boltonii* is scaly. That almost certainly indicates a different species. Heim does not seem to have chosen a type, but he mentioned having collected the specimens from a French pine forest; a possible habitat for *I. giacomi* based on our present knowledge. Unfortunately, we did not manage to get his collections on loan. Jacobsson (2008) gave different spore measurements from ours for *I. giacomi* (longer and narrower, with Q values 2–2.3).

In summary, *Inocybe giacomi* has a wide ecological amplitude and distribution. It seems to be characterised by a somewhat robust appearance and an inconspicuously umbonate pileus. Our macroscopic description was based on collection “Vauras 9198F”, which had an exceptional feature of some damaged parts turning brown red. This collection fits well with the photograph “raccolta 2001” in Bizio and Rossi (2002). *I. giacomi* is rather closely related to *I. proximella*: the ITS sequences of *I. giacomi* deviated by 22–23 bases and 5 insertions/deletions from the sequence of the *I. proximella* type. For differential diagnosis see key.

Specimens examined: **FINLAND**. **Satakunta**. Loimaa, Alastaro, Virttaankangas, Lohensuon lähteikkö, 30. VII.2004 Vauras 21543*. **Etelä-Savo**. Punkaharju, Vaara, 20.IX.2003 Vauras 20844* (TUR). **Pohjois-Savo**. Kuopio, Vehmersalmi, Litmaniemi, 11.VIII.1994 Vauras 9198F, 19. VIII.1996 Vauras 11409*. **Pohjois-Karjala**. Nurmes, town, 4.IX.2003 Kokkonen 370/03* (TUR). **FRANCE**. **Savoie**. Alpes Francaises, Parc National de la Vanoise, 8.VIII.1972

R. Kühner 72-70* (holotype of *I. striaepes*, G), Région de Pralognan, Col de la Valette, 26.VIII.1965 R. Kühner K.65-117* (holotype of *I. johannae*, G), Pâtures de la Motte, 16. VIII. 1968 R. Kühner 68-125* (holotype of *I. hinnulea*, G). **NORWAY**. **Nordland**. Ballangen, Håfjället, 26.VII.2008 Holtan & Larsen 28-08*. **SWITZERLAND.** Region de l′ Ofenpass, Entre le col du Gialet et le marais superior de Buffalora, 13.VIII.1941 Favre 124b* (lectotype, G).

Inocybe paludicola Kokkonen & Vauras, **sp. nov.**

Figs. 25 and 26

MycoBank number: MB 563076

Etym.: *paludicola* (Latin) refers to the boggy habitat.

Pileo 2.2–4.5 cm lato, primum conico, dein expanso circa umbonem minimum acutumque, brunneo, paulum viscido. Lamellis usque ad 6 mm latis, ventricosis, brunneolis. Stipite 6.5–10 cm longo, 6–9 mm crasso, basim versus paulatim incrassato, pallide brunneo. Sporis (8.2) 8.6–11.1 (12.7)×(5.9) 6.0–7.6 (8.1) µm, nodulosis. Pleurocystidiis (44) 49–76 (79)×(11) 12–22 µm, plerumque lageniformibus, tunicis crassis. In paludibus.

Holotypus: **Finland**, Pohjois-Karjala, Nurmes Municipality, Ylikylä, 120 m south of Lake Viitajärvi, pine fen, beside an overgrown ditch, near *Pinus sylvestris, Betula pubescens, B. nana, Alnus incana, Salix phylicifolia, Picea abies* seedling, *Menyanthes trifoliata, Andromeda polifolia, Chamaedaphne calyculata, Carex pauciflora* and *Vaccinium oxycoccos*, amongst *Sphagnum*, Grid 27°E: 70625:36053, alt. ca. 98 m, 30.VII.2009*K. Kokkonen* 21/09 (TUR-A 190488, isotypus WTU), GenBank JN580873.

Pileus 2.2–4.5 cm in diameter, conical when young, then campanulate to applanate with small and rather acute umbo; yellow brown (near $S_{30}Y_{60}M_{30}$) to medium brown (near $S_{40}Y_{60\text{-}70}M_{40}$), often red brown near umbo ($S_{40}Y_{70}M_{50}$), umbo dark brown ($S_{50}Y_{60}M_{40}$, $S_{70}Y_{60}M_{40}$), rarely with patches of darker fibres; weakly viscid, centre smooth, outwards radially fibrillose, at times breaking up, velipellis lacking, margin sometimes with scant remnants of cortina. *Lamellae* rather broad, up to 6 mm, ventricose, narrowly adnate or adnexed, rather crowded; when young pale grey brown (near $S_{10}Y_{40}M_{10}$), later grey brown ($S_{20}Y_{30}M_{10}$) or yellow brown ($S_{30}Y_{60}M_{30}$), edge paler or concolorous, slightly fimbriate especially in young lamellae or even. *Stipe* 6.5–10.0 cm long, 6–9 mm wide, widening gradually downwards, base round; reddish pale brown (near $Y_{20}M_{10}C_{00}$), paler and often yellowish in the upper part, the lower part at times with grey tinge, base whitish; dry, fibrillose, often flocculose especially in the lower part, apex rarely slightly pruinose; solid. *Cortina* whitish. *Context* in pileus pale grey or pale brown or above lamellae concolorous with pileus surface; in stipe whitish to pale brown with stronger red tinge under the surface, base white and sometimes above it reddish, longitudinally fibrillose striate. Smell indistinct or slightly spermatic. No specific taste.

Fig. 25 *Inocybe paludicola*. Holotype. Photograph K. Kokkonen

Spores (8.2) 8.6–$\underline{9.8}$–11.1 (12.7)×(5.9) 6.0–$\underline{6.8}$–7.6 (8.1) µm, total range of mean values 9.3–10.2×6.4–7.1 µm, Q=(1.2) 1.3–$\underline{1.43}$–1.6 (1.75), total range of mean Q values 1.38–1.46 (100 spores from 5 collections); rather strongly nodulose mostly with small nodules, rather pale yellow brown. *Basidia* (21) 24–$\underline{32}$–37 (42)×9–$\underline{11}$–13 (15) µm (*n*=73), clavate, 4-spored. *Pleurocystidia* (44) 49–$\underline{64}$–76 (79)×(11) 12–$\underline{16}$–22 µm (*n*=61), narrowly to rather broadly lageniform with short or rather long neck, some cylindrical or fusoid, usually without crystals, base tapered or with pedicel; wall up to 5 µm thick, pale yellow or rarely bright yellow, rarely with brown contents. *Cheilocystidia* generally shorter than pleurocystidia, some shortly clavate, wall up to 5.5 µm thick; paracystidia thick-walled or thin-walled, numerous; rarely with yellow or brown contents. *Caulocystidia*: metuloids at stipe apex numerous, more or less cylindrical often with tapering apex, clavate, fusoid, or with inflated base, often with septae resembling chains, apex rarely crystalliferous; wall up to 3 µm thick, pale yellow or bright yellow, some with brown contents.

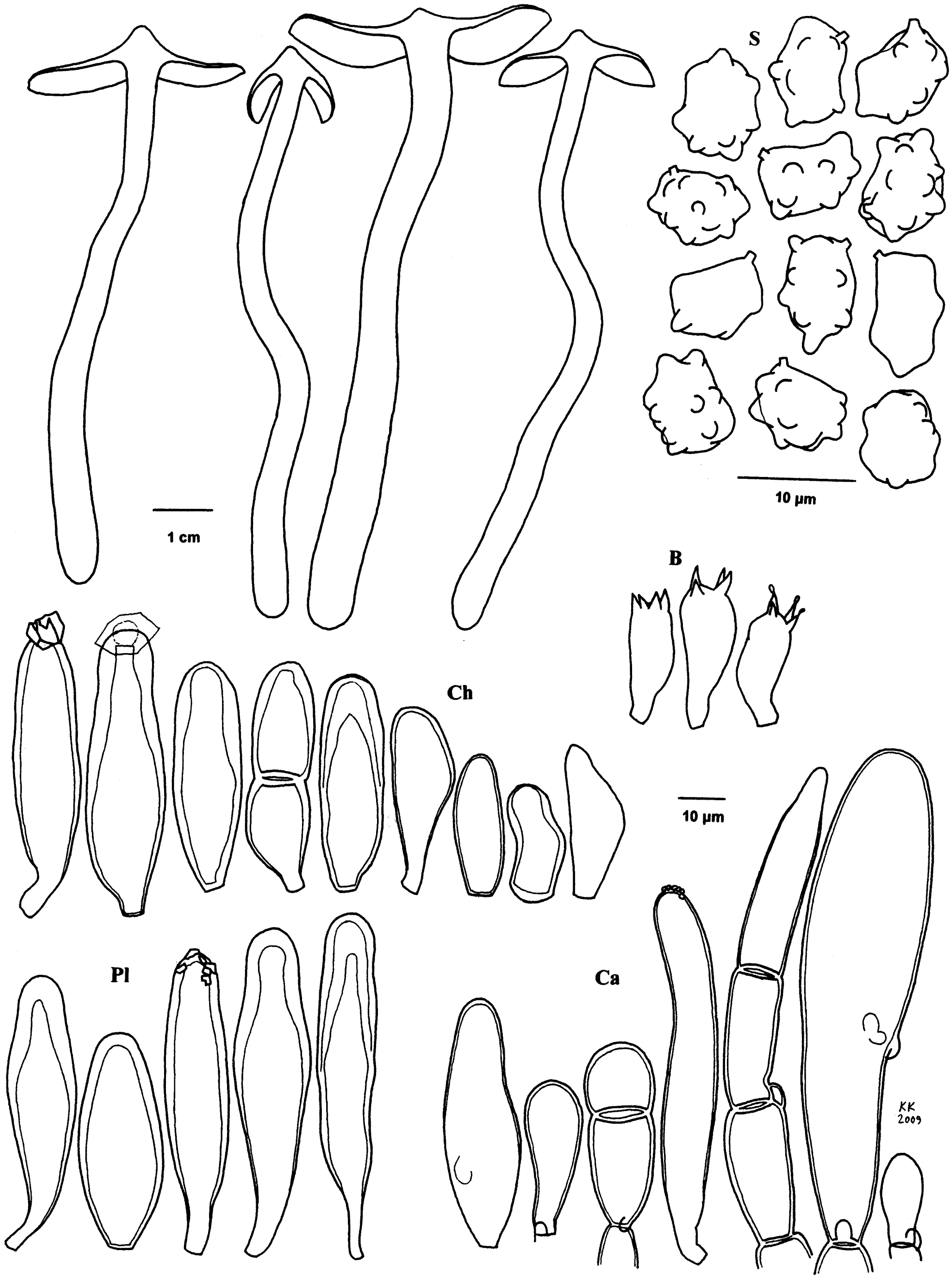
Habitat: Mesotrophic to eutrophic *Pinus sylvestris* fens with *Betula*, *Alnus*, *Salix,* and *Picea*. Found growing close to *I. teraturgus*.

Distribution: Known from four localities in Finland, from southern, middle, and northern boreal zones.

Phenology: *I. paludicola* fruits fairly early in the season. It has been collected from early July to early August.

Comments: *Inocybe paludicola* is a rather large species like *I. proximella* and *I. silvae-herbaceae*. It can be easily identified by its characteristic thick-walled caulocystidia, spores with numerous small nodules, small umbo, and specific habitat. In the sequence data, the specimen from Koski Tl. (GenBank JN580874) deviated from the type by a gap of one base.

Fig. 26 *Inocybe paludicola*. Holotype: microscopic characters, cross-sections of three fruitbodies on the *right*. Kokkonen 22/09: *left* fruitbody. For symbols, see Fig. 2



Specimens examined: **FINLAND**. **Varsinais-Suomi**. Koski Tl., Vähäsorvasto, Sulkalammi, 11.VII.1990 Vauras 4287, 5.VIII.1992 Vauras 6722, 29.VII.1993 Vauras 8005F* (TUR), 8.VII.1995 Issakainen & Vauras 10251. **Pohjois-Karjala**. Nurmes, Ylikylä, S of Viitajärvi, 4. VIII.2005 Kokkonen 68/05* (TUR), 30.VII.2009 Kokkonen 21/09* (holotype, TUR-A), 22/09, 28/09. **Oulun Pohjanmaa**. Kiiminki, Huttukylä, Ruostesuo, 21.VII.1992 Kaukonen (OULU). Pudasjärvi, Sarajärvi, Syöte National Park, Isovaara, 24.VII.1999 E. Ohenoja (OULU).

Inocybe purpureobadia Esteve-Rav. & A.Caball., *Fungi Non Delineati* 47: 90–91 (2009)

Figs. 27 and 28

Pileus 0.6–2.2 cm in diameter, conico-convex to low convex, subumbonate or with low obtuse umbo; dark brown (near $S_{70}Y_{50}M_{40}$), with central pale greyish yellow brown (near $S_{30}Y_{50}M_{20}$) patch of velipellis; dry, centre somewhat felty, margin weakly radially fibrillose with darker bundles of fibres and slightly breaking up. *Lamellae*

Fig. 27 *Inocybe purpureobadia*. Finland, Kuusamo, Vauras & Kokkonen 64/09. Photograph K. Kokkonen

up to 4 mm wide, segmentiform to subventricose, narrowly adnate to adnate, moderately crowded; when young pale grey brown or pale brown, later grey brown ($S_{20}Y_{30}M_{20}$), edge concolorous or paler, even. *Stipe* 1.0–3.0 cm long, 1–4 mm wide, equal, base sometimes slightly wider; pale brown with red tinge ($Y_{40}M_{30}C_{10}$); dry, whitish fibrillose, often somewhat villose or floccose, weakly shiny, not pruinose, solid. *Context* in pileus whitish to grey brown ($Y_{40}M_{30}C_{20}$), in stipe whitish to brownish with red tinge (near $S_{00}Y_{20}M_{10}$), weakly shiny. Cortina not observed. Smell indistinct to weakly acidulous.

Spores (8.1) 8.5–9.4–10.5 (11.4)×(4.8) 5.0–5.6–6.2 (6.4) µm, Q=(1.4) 1.5–1.68–1.9 (2.1), (80 spores from 3 collections; Finland, Estonia); weakly angular or with few low nodules, at times a bit undulating, some elongated, rather pale yellow brown. *Basidia* 23–29–35 (38)×(7) 8–10–12 (13) µm (*n*=39), clavate, 4-spored. *Pleurocystidia* (39) 45–53–64 (75)×(10) 11–13–16 (21) µm (*n*=31), narrowly to broadly lageniform with short neck, utriform or clavate, apex crystalliferous, base tapered or with pedicel, wall up to 2.5 µm thick, pale yellow; scarce. *Cheilocystidia* numerous, often larger than pleurocystidia, metuloids 40–66×9–19 µm (*n*=18), apex crystalliferous; wall up to 2.5 µm, pale yellow or at times bright yellow; rarely with brown contents; some thin-walled cystidia lageniform, fusoid or clavate. *Caulocystidia*: often with brown contents, metuloids at stipe apex numerous, up to 71 µm long and 19 µm wide (*n*=14), flexuous, cylindrical, lageniform with short neck, utriform or subglobose, apex crystalliferous or not, wall up to 1.5 µm thick, pale or bright yellow; thin-walled cystidia numerous.

Habitat: in forests with *Pinus sylvestris* on somewhat calcareous, sandy soils; the Spanish collections from a *Quercus ilex* forest on sandy soil; possibly also occurring in the alpine zone in Austria (see our comments).

Distribution: Known from hemiboreal and northern boreal zones of Finland, Estonia, and Spain.

Phenology: *I. purpureobadia* fruits in northern Europe from mid-August to late September, and in Spain from mid-May to early July (Esteve-Raventós and Caballero Moreno 2009).

Comments: *Inocybe purpureobadia* is distinguished by its small, dark brown fruitbodies with pale velipellis and weakly angular spores. Our collections lacked the purple tinge often seen in Spanish fruitbodies (Esteve-Raventós and Caballero Moreno 2009). The sequenced Finnish specimen (GenBank JN580876) deviated from the isoparatype (JN580875) by five bases, a deletion and an insertion, but clearly matched in morphology. Drawings of the microscopic features of both are included. The specimens we studied had normal cheilocystidia and not the heterogeneous lamellar edge with violaceous brownish cystidia observed by Esteve-Raventós and Caballero Moreno. Except for the different colour of also other cystidia, our observations agreed with theirs.

Pinus sylvestris seems to be the host in Finland and Estonia, and *Quercus ilex* in Spain. A common feature of the habitats seems to be sandy soils. We found that GenBank had ITS sequences of unidentified fungi collected from an alpine habitat in Austria that deviated by only 6–7 bases and 2–3 gaps from the sequence of the isoparatype of *I. purpureobadia* (Oberkofler et al. unpublished, GenBank EU516939, EU516943).

Specimens examined: **ESTONIA**. **Ida-Viru**. Illuka, Kurtna, near Martiska lake, 28.IX.2006 Heinonen & Vauras 24198. **FINLAND**. **Uusimaa**. Hanko, Lappohja, 3.IX.2004 Kytövuori & Toivonen 4128 (TUR). **Koillismaa**. Kuusamo, Oulanka National Park, near the Research Station, 14.VIII.2009 Vauras & Kokkonen 64/09*, 14.VIII.2010 Kokkonen 29/10. **SPAIN**. **La Rioja**. Villarroya, 18.V.2008 Caballero (isoparatype*, TUR-A).

Inocybe ericetorum Vauras & Kokkonen, **sp. nov.**

Figs. 29 and 30a

MycoBank number: MB 563077

Etym.: *ericetum* (Latin, *ericetorum* plur. gen.), refers to a community characterised by plants of *Erica/Calluna* on dry, often sandy soil.

Pileo 0.9–2.0 cm lato, circa umbonem obtuso, fusco-brunneo vel brunneo, fibrilloso. Lamellis usque ad 4 mm latis, ventricosis. Stipite 1.8–2.3 cm longo, 1.5–2.5 mm crasso, nigrescente, cum flocculis albidis. Sporis (7.5) 7.9–9.6 (10.6)×(5.4) 5.5–6.9 (7.2) µm, nodulosis. Pleurocystidiis (45) 48–75 (81)×(10) 12–19 (22) µm, fusiformibus. In locis arenosis.

Typus: **Finland**, Inarin Lappi, Utsjoki Municipality, Kevo, Kutuniemi, dry heath forest with *Betula pubescens*

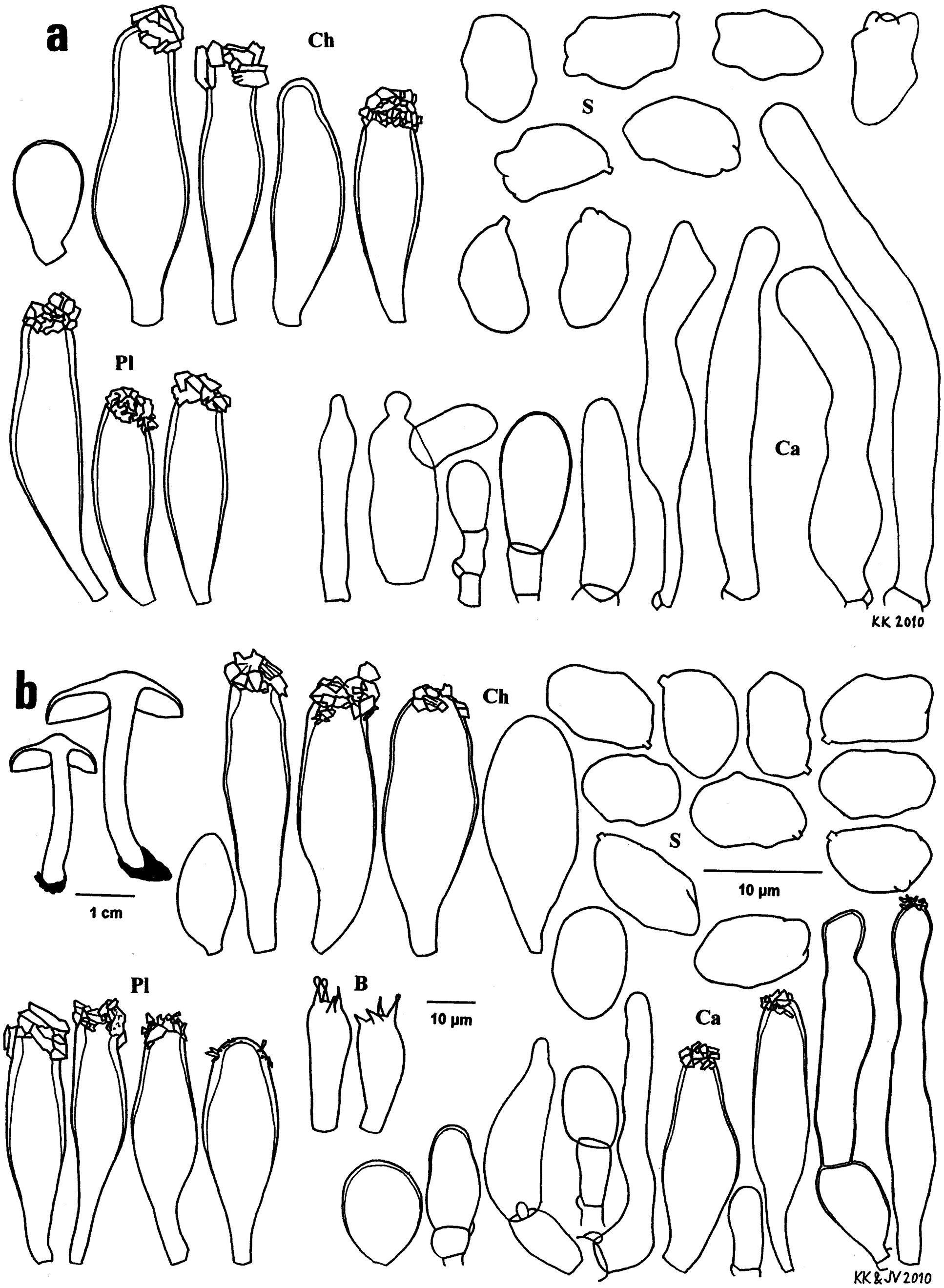


Fig. 28 *Inocybe purpureobadia*: microscopic characters. **a** Isoparatype, Caballero 18.V.2008. **b** Vauras & Kokkonen 64/09, also cross-sections of fruitbodies. For symbols, see Fig. 2

subsp. *czerepanovii* and *Pinus sylvestris* on sandy soil, on old forest track, Grid 27°E: 7742:3500, alt. ca. 90 m, 18. VIII.1995 *J. Vauras 10522 F* (TUR-A 177504, holotypus), GenBank JN580877.

Pileus 0.9–2.0 cm in diameter, hemisphaerical to conico-convex when young, then plano-convex with broad, low umbo and deflexed margin, dark brown to blackish brown around disc, outwards brown (e.g. $S_{60}Y_{70}M_{50}$), smooth at centre, outwards radially fibrillose, fibrils diverging, margin often cracking; at times with pale velipellis at centre. *Lamellae* up to 4 mm wide, ventricose, narrowly adnate, moderately crowded, pale greyish brown, then grey-brown to brown, edge paler or concolorous. *Stipe* 1.8–2.3 cm long, 1.5–2.5 mm wide, equal to subbulbous, pale yellow-brown when young, soon darkening and then red-brown at apex, downwards dark brown to blackish brown or blackish red-brown, extreme apex white pruinose, downwards weakly white flocculose to fibrillose, longitudinally striate, solid. *Cortina* not observed. *Context* in pileus whitish to pale brown, in stipe pale brown, pale reddish brown, at base even blackish brown, shiny. Smell indistinct or weakly acidulous.

Spores (7.5) 7.9–$\underline{8.8}$–9.6 (10.6)×(5.4)5.5–$\underline{6.1}$–6.9 (7.2) µm, total range of mean values 8.5–8.9×5.9–6.5 µm,

Fig. 29 *I. ericetorum*. Holotype. Photograph J. Vauras

Q=(1.2) 1.25–1.43–1.65 (1.7), total range of mean Q values 1.35–1.52 (80 spores from 4 collections); with a few obtuse, medium-sized to large nodules, pale to rather pale yellow brown. *Basidia* (22) 23–28–34 (40)×(8) 9–10–11 µm (*n*=42), clavate, 4-spored. *Pleurocystidia* (45) 48–64–75 (81)×(10) 12–16–19 (22) µm (*n*=69), slenderly to broadly fusiform, often with pedicel, slightly thick-walled, with up to 2 µm thick, yellowish wall, often strongly crystalliferous at apex. *Cheilocystidia* shorter and more variable than pleurocystidia; paracystidia clavate to pyriform, thin-walled, colourless, fairly scarce to fairly abundant. *Caulocystidia*: metuloids at stipe apex very scarce, more or less similar to cheilocystidia, caulocystidioid hairs up to 65 µm long, often with crystals and tapering to the apices, at times pale brown inside, often in clusters with cauloparacystidia.

Habitat: On small sandy roads and road banks in dry heath forests with *Pinus sylvestris* and *Betula* on fine sandy soil.

Distribution: Known from southern Sweden to Lapland in Finland. From temperate, hemiboreal, boreal and subalpine zones.

Phenology: Mid-July to late September.

Comments: *Inocybe ericetorum* is a small species characterised by fairly dark colours, pileus with rimulose margin and often velipellis around centre, distinctive spore shape, pleurocystidia often with remarkably abundant crystals, and its habitat on sandy soils.

Inocybe purpureobadia is also a small, dark species found on sand, but its pileus margin is not rimulose, its spores are only weakly angular or with few low nodules and have a larger average Q value. This species prefers more calcareous soils.

Inocybe ericetorum also resembles somewhat *I. assimilata* (Britzelm.) Sacc., a more southern species. It has not been found in Finland, but is common in forests, for example, with *Fagus sylvatica* in the temperate zone of southern Sweden and Denmark (own observations, J.V.), and in the spruce forests of Germany (Gminder 2010). It is a slightly larger species with a bulbous stipe base and different microscopic characters.

Inocybe giacomi may grow in similar habitats to *I. ericetorum*. The former is larger, and with larger spores and cystidia.

In the two phylogenic trees created by Ryberg et al. (2010), *Inocybe ericetorum* (as *I.* cf. *assimilata*, EL 23–04) grouped with *I. acuta*, *I. napipes*, *I.* cf. *assimilata*, and *I. assimilata*. In our phylogram, *I. ericetorum* grouped with *I. acuta* and *I. alpigenes*, but these were not close relatives.

Specimens examined: **FINLAND**. **Varsinais-Suomi**. Salo, Perniö, Lupaja, Alhonmäki, 11.VII.2004 Vauras 21377, 8.IX.2004 Vauras 21972. **Satakunta**. Loimaa, Alastaro, Virttaankangas, 1.VIII.2007 Vauras 25005. **Pohjois-Karjala**. Kesälahti, Kermola, 23.IX.2004 Vauras 22506F (TUR). **Inarin Lappi**. Utsjoki, Kevo, 15.VIII.1995 Vauras 10429, 18.VIII.1995 Vauras 10522F* (holotype, TUR-A). **SWEDEN**. **Bohuslän**. Grinneröd, Backamo, 25.VII.2004 Larsson 23–04 (GB).

Inocybe pseudoteraturgus Vauras & Kokkonen, **sp. nov.**

Figs. 31 and 30b

MycoBank number: MB 563078

Etym.: the microscopic characters resemble those of *Inocybe teraturgus* M.M.Moser as originally illustrated.

Pileo 1.2–3.3 cm lato, paulum umbonato, cano-brunneo, fusco-brunneo, squamuloso, tomentoso fibrillosoque. Lamellis usque ad 6 mm latis. Stipite 1.5–5 cm longo, 2–7 mm crasso, brunneolo, ad basim subsquamuloso. Sporis (7.7) 8.3–9.8 (11.1)×(6.0) 6.4–7.9 (8.0) µm, nodulosis. Pleurocystidiis (49) 54–72 (73)×(11) 13–24 (25) µm, angusto-fusiformibus.

Holotypus: **Finland**, Åland, Jomala Municipality, Möckelö, southwest of Kovaberget, at a camping place, on a mossy lawn near *Picea abies* and *Pinus sylvestris,* Grid 27°E: 6685:3106, alt. ca. 3 m, 23.IX.1992 *J. Vauras* 7676F (TUR-A 177550, isotypi GB, H, WTU), GenBank JN580878.

Pileus 1.2–3.3 cm in diameter, conico-convex when young, later plano-convex to almost applanate, broadly umbonate, around centre dark brown (30S-50T), brown (30P, 70R), pale brown (69P, 69N) to yellowish brown (65P), outwards dark brown, brown, greyish brown, greyish red-brown (49N, 49P) or yellowish brown, disc subtomentose or with small squarrae, towards margin with appressed scales to tomentose-fibrillose, at margin often radially fibrillose, with dark bundles of fibres and slightly breaking up, velipellis lacking. *Lamellae* up to 6 mm wide, narrowly adnate to adnate, often subventricose, moderately crowded, when young pale grey, later grey brown (70M) to yellow

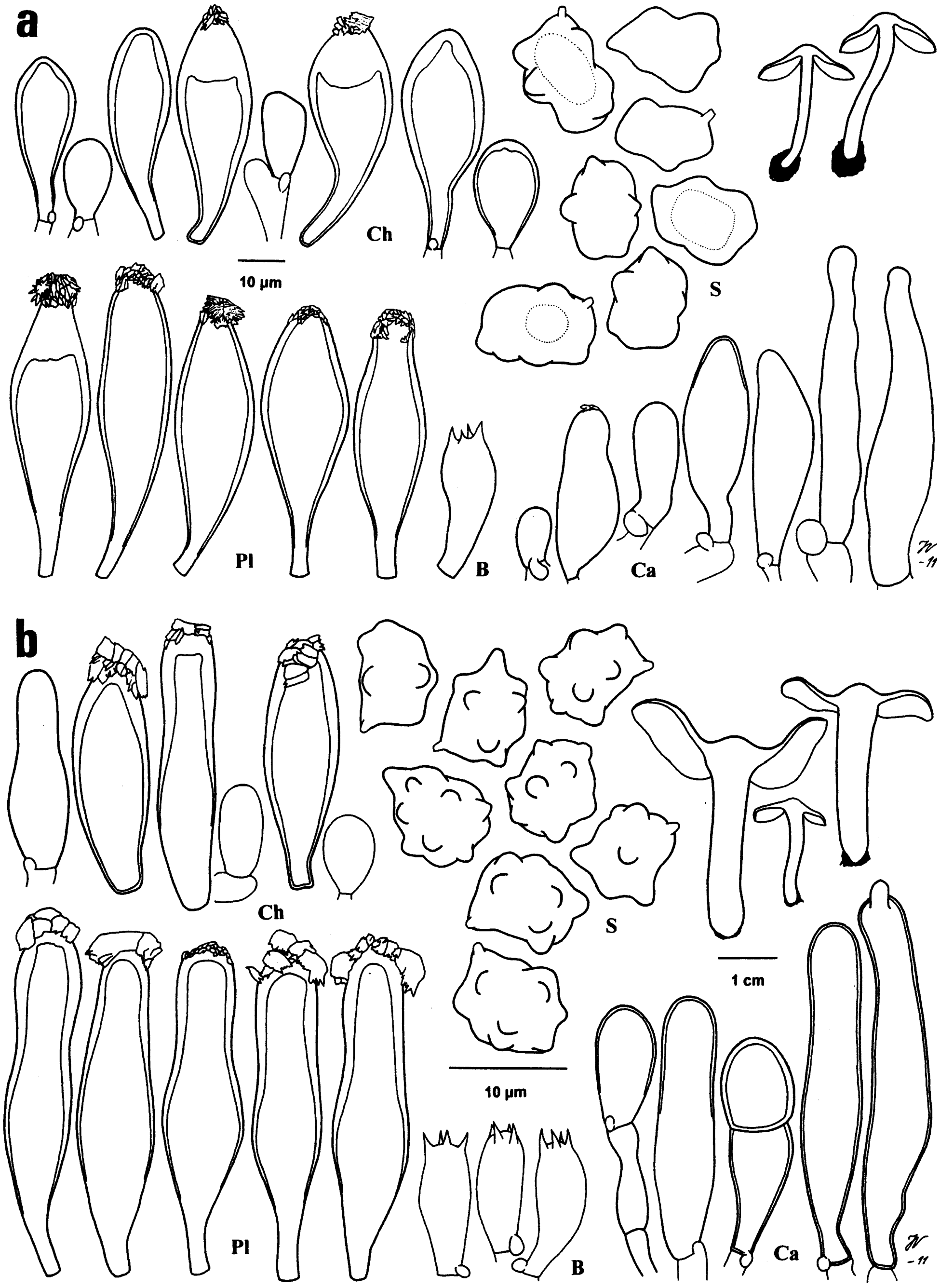


Fig. 30 Microscopic characters and cross-sections of fruitbodies: **a** *Inocybe ericetorum*, holotype; **b** *Inocybe pseudoteraturgus*, holotype. For symbols, see Fig. 2

brown, then brown (60P), edge concolorous. *Stipe* 1.5–5.0 cm long, 2–7 mm wide, equal to somewhat enlarged at base, or base tapering; often flexuous; pale brown, base brown; woolly-fibrillose, often striated with pale and brown fibres, base subsquamulose; slightly shiny, solid. *Context* in pileus whitish to very slightly yellowish, in stipe whitish with red or brown tinge, cortex the darkest, base whitish; weakly shiny. Cortina soon disappearing. Smell acidulous, weakly spermatic to indistinct.

Spores (7.7) 8.3–9.1–9.8 (11.1)×(6.0) 6.4–7.1–7.9 (8.0) µm, total range of mean values 8.9–9.4×6.8–7.2 µm, Q=(1.05) 1.15–1.29–1.4 (1.5), total range of mean Q values 1.26–1.34 (100 spores from 5 collections), rather strongly nodulose, rather pale yellow brown. *Basidia* 23–29–33×9–11–12 (14) µm (n=32), clavate, 4-spored. *Pleurocystidia* (49) 54–64–72 (73)×(11) 13–17–24 (25) µm (n=48), narrowly utriform to lageniform, fusiform, some cylindrical, usually with abundant crystals, base tapered or with pedicel, wall up to 3 (−4) µm thick, pale yellow. *Cheilocystidia* similar to pleurocystidia but more variable, some thin-walled, mostly shorter, up to 57 µm long and 20 µm wide, rarely with brown contents, paracystidia

Fig. 31 *Inocybe pseudoteraturgus*. Holotype. Photograph J. Vauras

scarce. *Caulocystidia*: at stipe apex hyphoid, mostly more or less cylindrical and long, often with septae and narrow apical cell, attenuating to apex, up to 110 µm long, without crystals, majority slightly thick-walled, wall often bright yellow, up to 1 µm thick; several pale brown inside; cauloparacystidia rather abundant.

Habitat: In dry, mesic, and moist forests, often dominated by *Pinus sylvestris* or *Picea abies*. Two finds were from deciduous forests without any coniferous trees nearby. Usually at least scattered *Betula* were growing close to collection sites. Often found on sandy soil by forest tracks and paths, on bare soil, on litter, but also on mosses, even on *Sphagnum*. It is clearly not a demanding species, although it also grows in herb-rich forests.

Distribution: Known from Finland, Sweden, and Estonia, from hemiboreal to northern boreal zones.

Phenology: Early July to late October, mostly early August to mid-September.

Comments: *Inocybe pseudoteraturgus* has a scaly pileus and belongs to the *Inocybe lanuginosa* group. The pileus colour varies from grey brown to dark brown (Online Resource Fig. S16). It can be collected as *I. lanuginosa* (Bull.: Fr.) P.Kumm., *I. leptophylla* G.F.Atk., *I. relicina* (Fr.) Quél. or *I. teraturgus*, but distinctly differs from them in its spores and cystidia.

The first collections made by J.V. were identified as *Inocybe teraturgus*, but the type study revealed that the latter species does not have exactly the spores originally drawn by Moser (1992). The ITS sequences of *I. pseudoteraturgus* and a Finnish collection of *I. teraturgus* (M.-L. & P. Heinonen 214-95F (TUR), GenBank JN580887) deviated greatly from each other.

Inocybe pseudoteraturgus seems to greatly resemble the North American species *I. diminuta* Peck (Peck 1906), known only from two old collections (Matheny and Kropp 2001). *I. pseudoteraturgus* differs from the latter in its larger fruitbodies, wider spores with slightly smaller Q-values, and on average longer pleurocystidia with slightly thicker walls.

The two other sequenced specimens differed from the type of *Inocybe pseudoteraturgus* by three common bases and two common insertions, and another also differed by a deletion (GenBank JN580879, JN580880).

Specimens examined: **ESTONIA**. **Hiiumaa**. Käina, Männamaa, 13.IX.2009 Vauras 27142. **FINLAND**. **Åland**. Jomala, Möckelö, 20.IX.1989 Vauras 4020F, 23.IX.1992 Vauras 7676F* (TUR-A, holotype); Ytterby, Jomalön**,** 30. VII.1991 Huhtinen & Vauras 5598. **Varsinais-Suomi**. Lieto, Vanhalinna, Satiaismäki, 28.VIII.1988 Vauras 3265. Parainen, Houtskari, Jungfruskär, 31.VIII.1998 Vauras 14266F. Salo, Kiikala, Hyyppärä, 8.VII.2003 Vauras 19698 (TUR). Turku, Ruissalo, 26.X.2006 Kokkonen 1485/06. **Etelä-Häme**. Vilppula, Elämänmäki, 23. VIII.2004 Vauras 21837. Ylöjärvi, Teivaala, 18.VIII.1993 Järvenpää 155 (OULU). **Pohjois-Häme**. Toivakka, Paloskylä, 24.VIII.1986 Ulvinen (OULU). **Pohjois-Savo**. Nilsiä, Haluna, Loutteispuro, 13.VIII.2002 Vauras 19141. Siilinjärvi, Vuorela, 16.IX.1984 Ruotsalainen. **Pohjois-Karjala**. Nurmes, Ylikylä, Muusarinvaara, 16.VIII.2005 Kokkonen 148/05 (TUR). **Oulun Pohjanmaa**. Kiiminki, Juuansydänmaa, Kolomaa, 2.VIII.1966 Ulvinen (OULU), Pyssyvaara, 3.IX.1975 Ulvinen (OULU); Keskikylä, Pöksälänkangas, 16.VIII.2007 Rahko (OULU). Ylikiiminki, Vepsä, Villinkangas, 11.IX.1989 Ohenoja (OULU). **Koillismaa**. Kuusamo. Oulanka National Park, Ampumavaara, 14.VIII.2009 Vauras 26939F*, Kiutaköngäs, 22. VIII.1983 Ohenoja (OULU), Tulilammenpuro, 3.IX.2007 Vauras 25252. **Perä-Pohjanmaa**. Keminmaa, Kallinkangas, 4.IX.1988 Tammilehto (OULU). Rovaniemi, Jaatilanvaara, 19.VIII.1992 Ruotsalainen & Vauras 6898. Tornio, Kalkkimaa, 16.IX.1986 Ohenoja (OULU). **Sompion Lappi**. Sodankylä, Luosto, 25.VIII.2008 Lahti. **Inarin Lappi**. Utsjoki, Kevo, Jesnalvaara, 16.VIII.1995 Vauras 10465, Tsieskuljohka, 17.VIII.1995 Vauras 10490*. **SWEDEN**. **Värmland**. Grava, Skåre, Älvåker, 8.VIII.1990 Jansson. Norra Råda, Råbäcken, Nollaberget, 11.VIII.1990 Jansson.

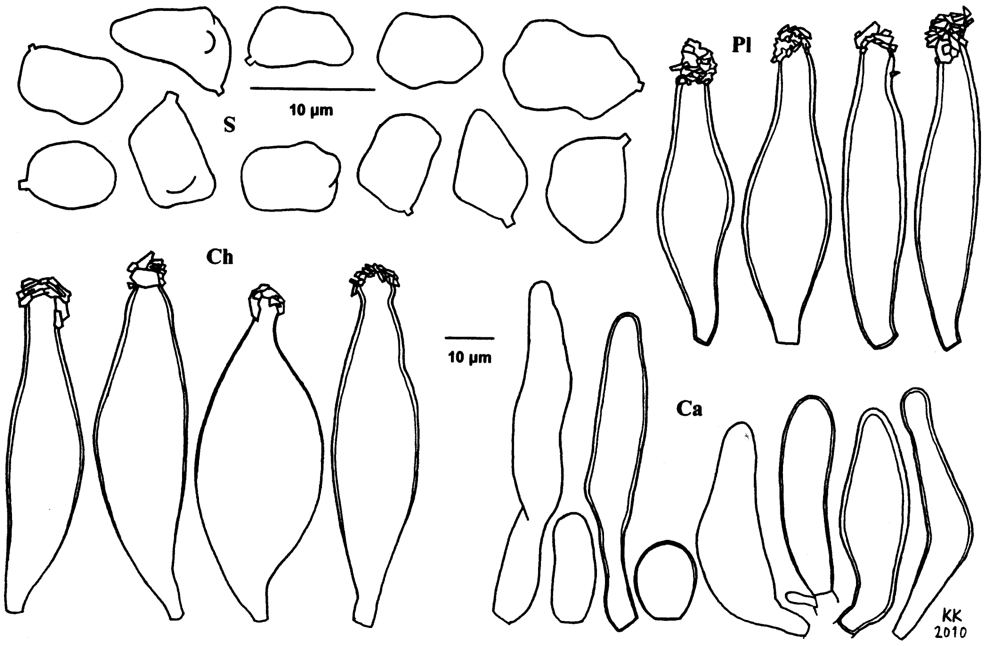
Additional type examinations

Inocybe alpigenes (E.Horak) Bon, *Bulletin Trim. Féd. Mycol. Dauphiné-Savoie* 37(144): 99 (1997). – *Astrosporina alpigenes* E.Horak, *Arctic and alpine mycology* 2: 212 (1987).

Synonym: *I. tetragonospora* Kühner, *Doc. Mycol.* 74: 26 (1988). (Fig. 32)

Holotype: *Inocybe alpigenes.* Switzerland, Kt. Graubünden, SNP, Val Zeznina (near Lavin), Macun, snow-bed: *Salix herbacea-retusa*, on soil, 5.IX.1983 Horak 2266 (ZT). −

Fig. 32 *Inocybe tetragonospora*. Holotype: microscopic characters. For symbols. see Fig. 2



Four small fruitbodies. *Spores* 7.3−8.2−9.0×(4.9) 5.0−5.5−5.9 (6.0) µm, Q=(1.35) 1.4−1.49−1.65 (1.7), (*n*=20), angular or with few low nodules, often rather quadrangular, rather pale yellow brown. *Basidia* 4-spored. *Pleurocystidia* 43−81×15.5−18 µm (*n*=6), wall up to 2.5 µm thick, yellowish. *Cheilocystidia* 42−60×14−18 µm (*n*=4), similar to pleurocystidia; paracystidia absent. *Caulocystidia* at stipe apex more or less similar to hymenial cystidia, wall up to 1.5 (rarely 2) µm thick; paracaulocystidia thin-walled, numerous. Analysis of the ITS2 sequence failed. ITS1 GenBank JN580881.

Holotype: *Inocybe tetragonospora*. France, Savoie, Région de Pralognan, Le Vallonnet, tranchée d'effondrement du torrent, non loinde *Salix herbacea*, 6.IX.1973 R. Kühner "K.73-378" (G452165). − *Spores* (7.0) 7.4−8.2−9.7 (9.9)×(4.9) 5.0−5.5−6.2 (6.9) µm, Q=(1.15) 1.3−1.49−1.65 (1.7), (*n*=20), angular or with few low nodules, rarely ellipsoid, often rather quadrangular, rather pale yellow brown. *Pleurocystidia* 49−62×11−17 µm (*n*=9), wall up to 2 µm thick, pale yellow. *Cheilocystidia* 53−77×15−25 µm (*n*=6), usually broader than pleurocystidia, wall up to 1.5 (rarely 2) µm thick, rarely walls thin; paracystidia absent. *Caulocystidia* at stipe apex often fusoid, usually with thick walls, wall up to 1.5 µm thick, pale yellow; paracaulocystidia scarce. Analysis of the ITS2 sequence failed. The ITS1 (GenBank JN580882) was identical with the sequence of the holotype of *I. alpigenes*. These specimens also matched microscopically, and rather well in macroscopic features. The pileus of *I. alpigenes* was described as minutely scurfy or squamulous in the centre, unlike in *I. tetragonospora*.

Inocybe cicatricata Ellis & Everh., *J. Mycol*. 5: 25 (1889). (Fig. 33a)

Isotype: *Inocybe cicatricata*. U.S.A., Gloucester Co., Newfield, on gravelly ground in open fields, Oct. 1887 (MICH11045). − One fruitbody and a piece of pileus as a loan. Stipe sandy and partly mouldy, at apex flocculose pruinose, at base indistinctly pruinose. *Spores* (8.5) 8.9−9.9−11.6 (11.7)×6.0−6.6−7.2 (7.4) µm, Q=(1.3) 1.35−1.52−1.65 (1.85), (*n*=20); rather pale yellow brown. *Basidia* 4-spored, 17−29×8−12 µm (*n*=6). *Pleurocystidia* 41−46−61×17−21−27 µm (*n*=13), mostly fusiform, some with short neck or clavate, wall up to 4 µm thick, yellowish. *Cheilocystidia* similar to pleurocystidia or short subglobose, wall up to 3 µm thick, pale yellow. *Caulocystidia* at stipe apex similar to hymenial cystidia or clavate, paracaulocystidia thin-walled; at base many paracaulocystidia and a slightly thick-walled cystidium were observed. GenBank JN580883.

Inocybe putilla Bres., *Fungi tridentini* 1(6–7): 81 (1887). (Fig. 33b)

Holotype: [Italia, Trento, Val di Sole, Malè,] sopra Arnago, estate 1883 leg. Inzenga (S). − *Spores* (8.1) 8.6−9.6−10.4 (11.0)×(6.3) 6.4−6.8−7.2 (7.7) µm, Q=(1.2) 1.25−1.42−1.6 (1.7), (*n*=20).

Pleurocystidia 59−83×19−29 µm (*n*=7), subfusiform to subutriform, often with long pedicel, wall up to 4.5 µm thick, yellowish to yellow. *Caulocystidia* impossible to study.

Note: The Nordic specimens we studied matched the holotype of *Inocybe putilla* very well except that the pleurocystidia were not as thick-walled. The supplementary material to Fig. 33b was drawn from Vauras 2074F (Finland, Varsinais-Suomi, Kaarina, Rauhalinna, 20.VII.1986, TUR-A).

Inocybe taxocystis (J.Favre & E.Horak) Senn-Irlet, *Botanica Helvetica* 102(1): 55 (1992).

– *Inocybe decipientoides* Peck var. *taxocystis* J.Favre. *Rés. Rech. Scient. Parc Nat. Suisse* 33: 113 (1955).

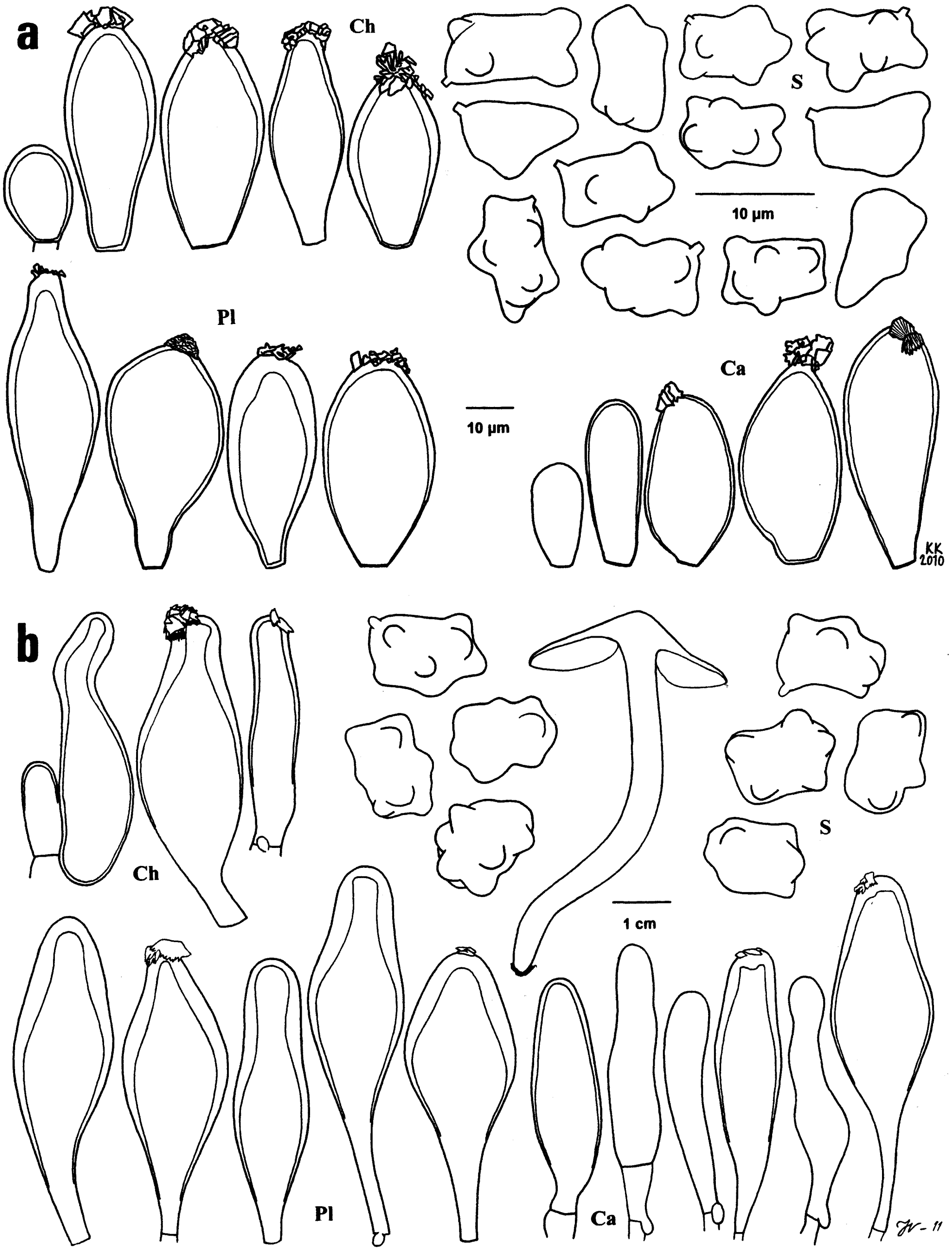


Fig. 33 Microscopic characters: **a** *I. cicatricata*, holotype; **b** *I. putilla*, holotype: spores and pleurocystidia, Vauras 2074F: caulocystidia, cheilocystidia and cross-section of fruitbody. For symbols, see Fig. 2

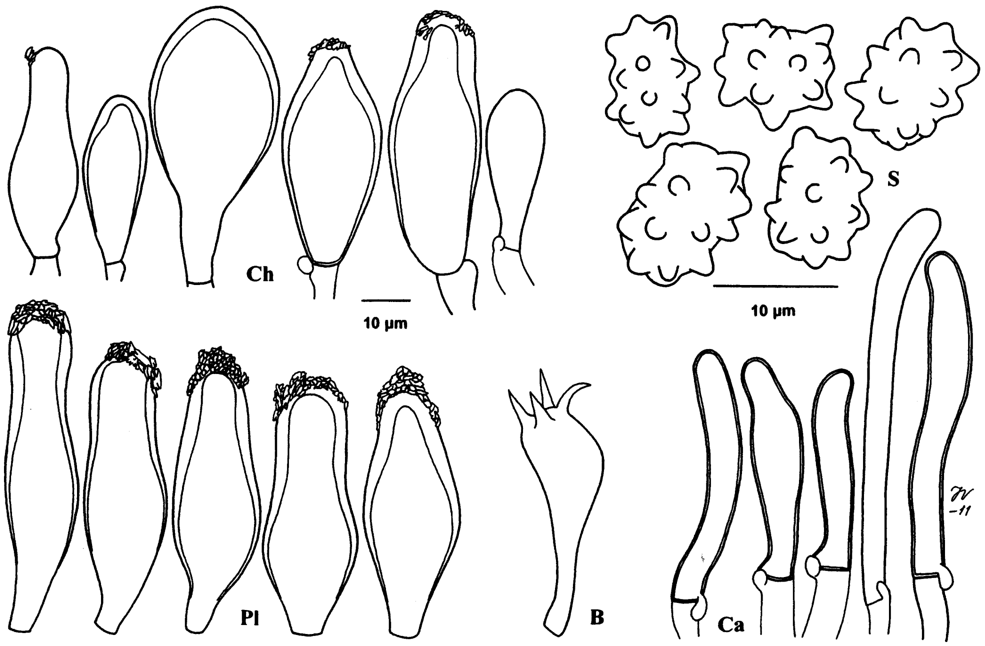
– *Astrosporina taxocystis* J.Favre & E.Horak, *Arctic and Alpine Mycology* 2: 230 (1987).

Lectotype: Switzerland, Munt da la Bescha sur Tarasp, Grisons, 2550 m, sur tapis de *Salix herbacea*, 8 Sept 1945 J. Favre 122a (G13208). − Stipe pruinose at apex rather long way down. *Spores* (8.8) 9.2−10.3−11.8 (12.0)× (5.6) 5.8−6.7−7.9 µm, Q=(1.3) 1.45−1.53−1.7 (1.85), (*n*=20); angular to rather weakly nodulose, elongated. *Basidia* 4-spored, 31−35×11−13 µm (*n*=2). *Pleurocystidia* 45−65×18−25 µm (*n*=9), utriform, ellipsoid or obovoid, crystalliferous or not, wall up to 3 µm thick, yellowish.

Cheilocystidia 40−56×17−24 µm (*n*=8), similar to pleurocystidia, wall up to 2.5 µm thick, yellowish, no distinct paracystidia or few fusoid to obovoid. *Caulocystidia* at stipe apex similar to hymenial cystidia, but range wider, 17−68×12−24 µm (*n*=6), wall up to 2.5 µm thick, yellowish; also near base thick-walled, usually utriform or obovoid cystidia.

Note: The ITS sequence of the *Inocybe taxocystis* lectotype (GenBank JN580884) differed by only 8 bases and 5 insertions/deletions (1−4 bases in length) from the ITS sequence of the *I. rivularis* Jacobsson & Vauras

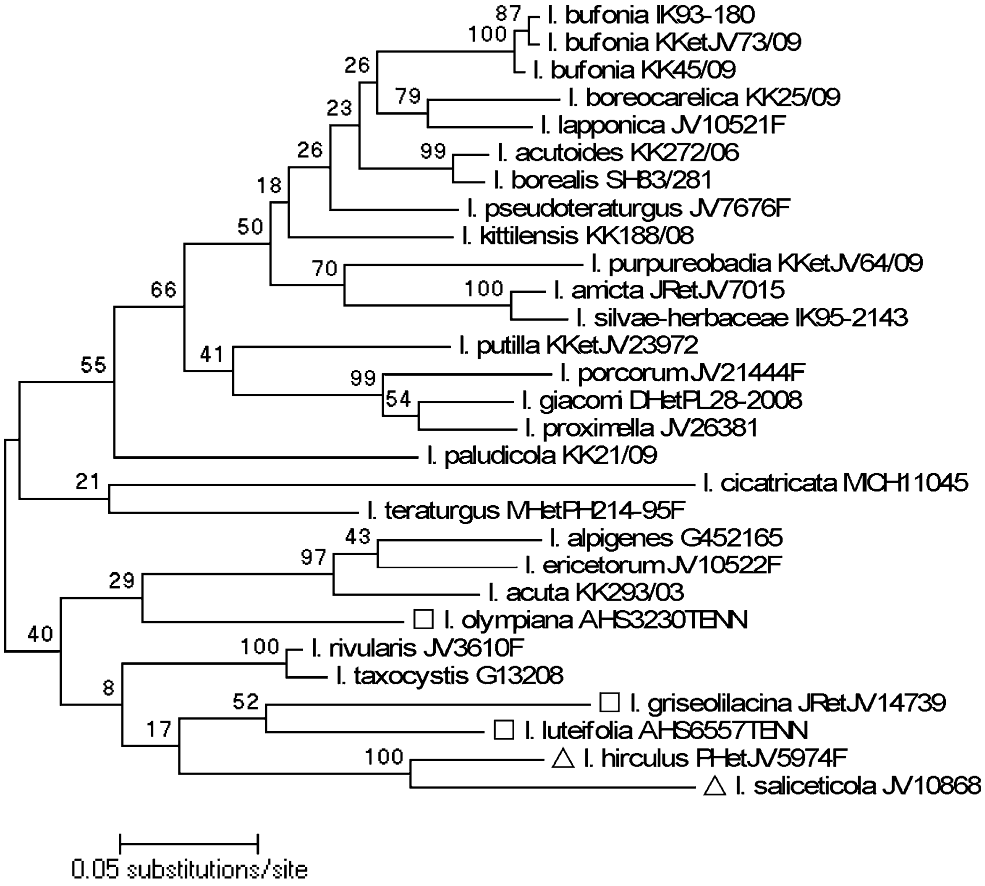
Fig. 34 *Inocybe teraturgus*. Holotype: microscopic characters. For symbols, see Fig. 2



paratype (Vauras 3610F - JN580885). These species also resemble each other morphologically, for example, in their abundantly pruinose stipe apices, subbulbous stipe bases and similar hymenial cystidia. However, we assume them separate species on the basis of dissimilar spore morphologies, pileus colours, and habitats.

Inocybe teraturgus M.M.Moser, *Persoonia* 14: 574 (1992). (Fig. 34)

Fig. 35 An unrooted maximum likelihood tree with log likelihood −6688.13. ML bootstrap values are given at nodes. Species within section *Marginatae* are marked with Δ, smooth-spored species are marked with □, and the others belong to section *Inocybe* Singer



Holotype: Schweden, Värmland, bei Narensjö, zwischen *Sphagnum fuscum* (?) im Tümpel, 8.VIII.1982 Moser 82/95 (IB). − *Spores* (9.1) 9.5−$\underline{10.8}$−12.0 (12.6)×(6.8) 7.1−$\underline{8.3}$−9.4 (9.5) µm, Q=(1.1) 1.25−$\underline{1.30}$−1.4 (1.5), (*n*=20). *Basidium* 4-spored, 46×14 µm. *Pleurocystidia* rather few, 50−67×15−19 µm (*n*=5), wall up to 3.5 µm thick, yellowish. *Cheilocystidia* similar or broadly ellipsoid, some thin-walled, paracystidia thin-walled. *Caulocystidia* at stipe apex long hyphoid, slightly thick-walled or thin-walled, brown inside.

Note: For the *Inocybe teraturgus* holotype description, see also Kobayashi (2002). The species has also been reported from *Sphagnum* bogs in North America by Matheny and Kropp (2001).

Phylogeny

The maximum likelihood (ML) phylogram is presented in Fig. 35. The evolutionary structure among *Inocybe* lineages remains uncertain because of low bootstrap values at ancestral nodes. Distinctly separate clades were only formed by species pairs or triplets. When a *Crepidotus* species was used as an outgroup the structure was almost identical, but the log likelihood and some bootstrap values were slightly lower, and we therefore discarded this. *Crepidotus*, and a *Naucoria* sp. as an outgroup, did not separate from *Inocybe*, indicating phylogenetic remoteness among *Inocybe* lineages as well as nearness to these genera. The *Crepidotaceae* has been reported to be a sister family to *Inocybaceae* based on molecular phylogenies (Matheny 2005). When *Volvariella volvacea* was used as an outgroup the reliability values were also lower.

The species within section *Inocybe* Singer were mostly but not distinctly separated from the species within section *Marginatae* and the group of smooth-spored species. Similarly, these groups have not appeared as separate in previous studies based on larger datasets including LSU, RPB1, RPB2 (e.g. Matheny 2005) or ITS sequences (Ryberg et al. 2010). On the basis of its morphology, *I. rivularis* has been regarded as an intermediate between sections *Inocybe* and *Marginatae* (Jacobsson and Vauras 1989). It has a very fugacious cortina and abundantly pruinose stipe apex. *I. rivularis* and the sibling species *I. taxocystis* were also placed between these sections in our tree, although with low support. *I. cicatricata* appeared the most distant to the other species. Further comparisons are needed, using a larger dataset, preferably with types or other reliably identified specimens, to clarify the place of *I. cicatricata* and the other newly sequenced species within *Inocybe*.

Electronic supplementary material includes additional photographs of the following species: *Inocybe acutoides*, *I. borealis*, *I. bufonia*, *I. boreocarelica*, *I. silvae-herbaceae*, *I. amicta*, *I. ericetorum*, and *I. pseudoteraturgus*.

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