

# Inocybe leiocephala, a species with an intercontinental distribution range – disentangling the *I. leiocephala* – *subbrunnea* – *catalaunica* morphological species complex

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Sequence data and morphological characteristics of specimens determined as *Inocybe leiocephala* were compared with six type specimens. We confirm *I. leiocephala*, *I. lindrothii*, *I. subbrunnea*, *I. fuscetipes*, *I. subpaleacea* and *I. catalaunica* as separate independent species. All species except *I. subpaleacea* and *I. catalaunica* were shown to have a broad intercontinental distribution range. *Inocybe leiocephala* has its main distribution in arctic-alpine and subalpine habitats, and *I. lindrothii* in hemiboreal – boreal zones. *Inocybe subbrunnea* is confined to nutrient rich, often more calcareous soils and mixed coniferous forests. Both *I. fuscetipes* and *I. subpaleacea*, described from the alpine zone, also grow in boreal forests. *Inocybe catalaunica* is a species well separated from *I. leiocephala*, *I. lindrothii* and *I. subbrunnea* in molecular data and it appears to be more related to *I. tjallingiorum* and *I. phaeoleuca* despite macro-morphological similarities to the *I. leiocephala* group. The new species *I. ohenojae* is described here based on material from the alpine zone in Canada. The new combination *Inocybe lindrothii* is proposed and an epitype is designated. *Inocybe saponacea* is regarded as a synonym of *I. lindrothii*. A key to the species is provided.

Key words: *Inocybe*, Agaricales, taxonomy, morphological species complex, molecular systematics, arctic-alpine mycology

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## Introduction

*Inocybe* (Agaricales, Inocybaceae) is one of the most diverse and dominating genera in arctic and alpine habitats. While some northern species appear restricted to alpine ectomycorrhizal

hosts such as dwarf *Salix* and *Dryas*, others appear to have a wider distribution extending into subalpine habitats and boreal coniferous forests (Ryberg et al. 2010). Smith & Stuntz (1950) de-

scribed *Inocybe leiocephala* D.E. Stuntz from subalpine conifer forests in Washington State (USA). The species has smooth spores, metuloids, fairly smooth pileus, lacks a cortina and has a totally pruinose stipe which places it in section Splendentes, in supersection "Marginatae" (Stangl 1989). However, in contrast to many species in "Marginatae", the stipe is not marginate or rimmed at the base, but is either cylindrical or only slightly swollen. Senn-Irlet et al. (1990) reported *I. leiocephala* from open calcareous alpine tundra heath with *Dryas octopetala* in the low alpine zone of Switzerland. It was reported as *I. leiocephala* partly because of the distinguishing features mentioned. These features, especially a totally pruinose non-marginate stipe, have made it relatively easy to identify this species in the field, with the need to only eliminate a few other taxa that possess these characteristics.

In 1955, Kühner described the similar *I. subbrunnea* Kühner which is distinguished, according to Senn-Irlet et al. (1990), from *I. leiocephala* by a lack of a spermatric smell and the presence of small grains below the crown of calcium crystals at the apex of the cystidia. The species was described from a *Picea* forest in France. Kuyper (1986) later suggested that the two species are identical and synonymized them and cited a wide range of possible hosts including *Picea*, *Quercus*, *Pinus mugo*, *Salix retusa*, *Dryas octopetala* and other shrubs in the alpine zone. In addition, Kuyper described a new species, *I. tjallingiorum* Kuyper which occurs both in alpine and subalpine habitats and on lowlands, differing by somewhat smaller spores and shorter cystidia. He considered this new taxon a synonym of "*I. ovalispora-subbrunnea* f. *brunneola*" J. Favre (1955). In the revision he also described *I. saponacea* Kuyper from boggy, rather acid soil with *Betula nana* and *Salix* species, based on a single specimen from the subalpine region in Kevo, Finland. This species is similar in macro- and micromorphology and related to the species above but is unique in having a strong smell of soap. Esteve-Raventós (1997) also concluded that *I. leiocephala* and *I. subbrunnea* were synonymous, but also that both were conspecific with the earlier *I. catalaunica* Singer (1947). The type collection originates from a montane region of the Pyrenees in Spain, and is likely to be associated with *Abies alba*.

Another species with similar characteristics was described by Karsten (1898) under the

name *Hebeloma lindrothii* P. Karst. As Karsten described the species in the genus *Hebeloma* the name was not associated with *Inocybe* for a long time, but Jan Vesterholt discovered this when studying the type specimens of *Hebeloma* (Vesterholt 1989). Like many descriptions from older times, the description by Karsten is not unambiguous, but the type specimen is well preserved and the micromorphology confirms its affinity to the species described above. The name *Inocybe lindrothii* has already been invalidly used by Kytövuori et al. (2005). The species was stated to grow in forests and parks on nutritious soils with *Betula* and *Picea abies* and to be a common species in whole Finland.

The names *I. leiocephala*, *I. subbrunnea* and *I. catalaunica* have been used inconsistently by mycologists over the years and *I. leiocephala* (s.l.) has been reported from numerous arctic-alpine habitats (Cripps & Horak 2008, Ohenoja & Ohenoja 2010) but also from a wide range of other forest habitat types (Stridvall et al. 1989, Vauras 1992, Jacobsson & Larsson 2012).

Here we use ITS and LSU sequence data in the attempt to get support for determining the limits of *I. leiocephala* and to sort out these morphologically similar taxa. We used specimens collected during fieldwork from the arctic-alpine, subalpine and boreal zones in Europe and North America together with the type specimens. The aim was also to infer the distribution range and ecology of these species and to see if the information can be of help in discriminating between the entities in this morphological species complex.

We also included the type specimens of two morphologically similar species, *I. fuscescens* Kühner and *I. subpaleacea* Kühner, described from *Dryas* vegetation in the alpine zone (Kühner 1988), and of which we have little knowledge. Also included are the type of *I. monticola* Kropp, Matheny & Nanagy recently described from a subalpine community of *Abies*, *Pinus contorta* and *Populus tremuloides* in Utah (Kropp et al. 2010) and specimens of *I. tjallingiorum*, to evaluate morphological characters and their phylogenetic position in relation to the *I. leiocephala* – *subbrunnea* – *catalaunica* morphological species complex. This article is part of the proceedings of the 9<sup>th</sup> International Symposium of Arctic and Alpine Mycology (ISAM) held at Kevo Subarctic Research Station in Inari Lapland, Finland, 26.08. – 01.09.2012.

## Material and methods

Stuntz's type material and 15 additional specimens determined as *Inocybe leiocephala* by Stuntz were obtained from the University of Washington Herbarium (WTU). Loan of the type specimens of *I. fuscuscentipes*, *I. subbrunnea*, *I. subpaleacea*, *I. catalaunica*, *I. monticola* and *Hebeloma lindrothii* were available at G, LE, UTC and H respectively. Permission for sequencing was granted. The main portion of the specimens was collected by the authors in Northern Europe (Fennoscandia and Svalbard) and western North America but additional specimens were also included from OULU, AH, GB, TUR-A and TUR. Macroscopical characters and ecology were noted and selected specimens were photographed in the field. Microscopical characters were measured and drawn from dried material mounted in 10% NH<sub>4</sub>OH solution and at 1000 × magnifications following the methodology described in Vauras & Kokkonen (2009).

In this study, eighty specimens of *Inocybe* section Splendentes from arctic-alpine, subalpine, boreal and hemiboreal zones were targeted, including the type specimens mentioned above. In addition, sequences from earlier molecular phylogenetic studies of supersection "Marginatae" and Inocybaceae respectively (Kropp et al. 2010, Ryberg et al. 2010) were retrieved from GenBank and added to the data set. *Crepidotus* was selected as the out-group. Each unique ITS sequence generated from the specimens in the *I. leiocephala* – *subbrunnea* – *catalaunica* complex was also blasted in GenBank and the UNITE database (Abarenkov et al. 2010) to explore the occurrence of additional sequence data relevant for the study. From this six ITS sequences generated from ectomycorrhizal root tips were added. Data of specimens sequenced in this study are provided in Table 1.

Sequences of the complete ITS region, 1400 base pairs of the 5' end of the nuclear ribosomal LSU DNA were generated. DNA extractions, PCR reactions and sequencing were performed as described in Larsson & Örstadius (2008). Type specimens were extracted using a modified CTAB method and PCR and sequencing follow protocols described in Larsson & Jacobsson (2004). Sequences were edited and assembled using Sequencher 5.1 (Gene Codes, Ann Arbor, Michigan). Sequences were aligned automatically using the L-INS-i strategy as implemented in MAFFT v. 7.017 (Katoh & Standley, 2013). The alignment was adjusted manually using the data editor in PAUP\* (Swofford 2003). Sequences have been deposited in GenBank and accession numbers are listed in Table 1.

Heuristic searches for most parsimonious trees were performed using PAUP\*. All transformations were considered unordered and equally weighted. Variable regions with ambiguous alignment were excluded and gaps were treated as missing data. Heuristic searches with 1000 random-addition sequence replicates and TBR branch swapping were performed, saving 25 trees in each replicate. Relative robustness of clades was assessed by the bootstrap method using 1000 heuristic search replicates with 100 random taxon addition sequence replicate, TBR swapping, saving 100 trees in each replicate.

## Results

For six of the seven type specimens, we succeeded in generating useful sequence data. The complete ITS and about 900 bp of the LSU was recovered for *Inocybe leiocephala*, the 5.8S and ITS2 for *I. subbrunnea*, the 5.8S and ITS2 for *I. catalaunica* and the complete ITS for *I. fuscuscentipes*, *I. subpaleacea* and *I. monticola*. From the *Hebeloma lindrothii* type we failed to get sequence data. Also the type specimen of *I. saponacea* was requested but because of reorganisation of Herbarium L it was not available for this study. The aligned complete dataset, including sequences downloaded from GenBank, consisted of 93 taxa and 2206 characters. After exclusion of ambiguous regions, mainly from the 5' and 3' ends and the ITS1 and ITS2 regions, 2018 characters remained for the analysis. Of these, 1526 were constant, 100 were variable but parsimony uninformative, and 392 (19%) were parsimony informative. The maximum parsimony analysis yielded 21425 equally parsimonious trees (length=909 steps, CI= 0.7052, and RI= 0.9086). One of the equally parsimonious trees is presented as a phylogram in Fig. 1.

The bootstrap analysis recovered specimens named *I. leiocephala*, *I. subbrunnea*, and *I. catalaunica* in three main supported clades, corresponding to *I. leiocephala* (100%), *I. lindrothii* (81%) and *I. subbrunnea* (100%) (Fig. 1). *Inocybe leiocephala* and *I. lindrothii* came out as sister clades and the two seem to be separated by an ecological differentiation and host preferences where *I. leiocephala* has a main distribution in arctic-alpine to sub-alpine habitats whereas *I. lindrothii* occurs from the hemiboreal to northern boreal areas up to the sub-alpine zone. Within the clade representing *I. lindrothii*, the sequence data of specimens with European and North American origin are separated into two supported clades, suggesting they may represent two different taxa with separate distribution ranges. More data from North America is needed to evaluate this trend (Fig. 1, Tab. 1).

*Inocybe subbrunnea* is clearly segregated from *I. leiocephala* and *I. lindrothii* and seems to be a species restricted to more herb-rich coniferous forests on nutrient rich and often calcareous soils. All specimens included in our study originate from Europe but the two included sequences that were retrieved from

GenBank originated from the North American continent, one from an ectomycorrhizal (ECM) root tip study on serpentine soil in the Chicago area and the other from a fruiting body collected in an *Abies* forest in Mexico. This suggests that *I. subbrunnea* occurs on both continents.

None of the sequences from the included specimens matched the ITS 2 sequence generated from the type specimen of *I. catalaunica*. To confirm the sequence, a second DNA extraction from a different fruiting body from the type specimen was done, resulting in identical sequences for the 5.8S and ITS2 regions. The only ITS sequence with a close match in GenBank, originating from an ECM root tip in a *Quercus* forest in California, was similar but not identical. We conclude that *I. catalaunica* is a species well separated from *I. leiocephala*, *I. lindrothii* and *I. subbrunnea* in sequence data and that it seems to be more related to *I. tjallingiorum* and *I. phaeoleuca* Kühner, and the sequences of the three species form a clade with 91% bootstrap support (Fig. 1).

*Inocybe fuscescencipes* described from *Dryas* vegetation in the alpine zone of France is a species rather close to *I. leiocephala*, *I. lindrothii* and *I. subbrunnea*. Sequence data from one of Stuntz specimens (STZ6459), a specimen from Finland, and an ITS sequence originating from an ECM root tip in a mixed temperate forest in Canada were identical with the type sequence and form a clade with 100% support. Our data suggest that this species has a broad intercontinental distribution range and that it occurs in both temperate and boreal forests as well as in the subalpine and alpine zones (Fig. 1, Tab. 1).

*Inocybe subpaleacea* came out as a sister species to *I. monticola* and sequences of the two species form a supported clade (81%). Sequence data of two specimens from Spain and one from Russia matched the type sequence (96%). The specimens originating from Spain were both collected in *Dryas* vegetation like the type, but the Russian specimen originates from a *Larix gmelinii* forest mixed with *Betula platyphylla*, *Pinus sylvestris*, a few *Populus tremula* and *Alnus fruticosa*.

The sequence data of one specimen first determined to *I. cf. leiocephala* originating from *Dryas* vegetation with *Salix* in Canada and a sequence retrieved from GenBank originating from an ECM root tip of *Salix arctica* from North America form a clade with 100% support. This species is distinct in morphology and is therefore de-

scribed here as a new species, *I. ohenojae*.

The sequence data of Stuntz specimen STZ6549 was basal in the phylogeny and this specimen is more close to *I. nitidiuscula* (Britzelm.) Sacc. than *I. leiocephala*.

## Discussion

In this study we show that the sequence data of specimens determined as *Inocybe leiocephala* are spread out in seven evolutionary lineages discussed separately below.

*Inocybe leiocephala* seems to have its main distribution in arctic-alpine and subalpine habitats but one of our specimens was collected in a hemiboreal coniferous forest in Estonia suggesting that it has a broader ecological range. The species has a wide intercontinental distribution and the included specimens were collected in North America, Scandinavia, Greenland, Svalbard, Russia and Italy. The result is in line with the findings in Cripps et al. (2010) where species of subgenus *Mallocybe* from the arctic-alpine zones of North America and Europe were compared. It is clear that Stuntz used a rather broad morphological species concept of his species but it was restricted to the subalpine zone, coniferous forests and *Pseudotsuga menziesii*. In addition to the *I. leiocephala* clade, the sequences generated from his specimens were also found e.g. in the *I. fuscescencipes* and in the *I. subpaleacea* – *monticola* clades. One sequence came out on a basal place in the phylogeny. It seems to be related to a species group around *I. nitidiuscula*, which is rather similar to *I. leiocephala* in macromorphology but has caulocystidia only at the stipe apex.

The sister clade to *I. leiocephala* is here named *I. lindrothii*. Most specimens in this clade were collected in hemiboreal and boreal mixed forests but several specimens originate from subalpine *Betula* forest in the Kevo area in Finland. An alternative name for this clade could also be *I. saponacea*, but no soapy smell was noted from the included specimens. We selected *I. lindrothii* as it is an older name and the morphology of the included specimens is in congruence with that of the type specimens. The ecology also fits with the area in Mustiala from where Karsten's specimen originates. As we were not able to generate sequence data out of the type specimen an



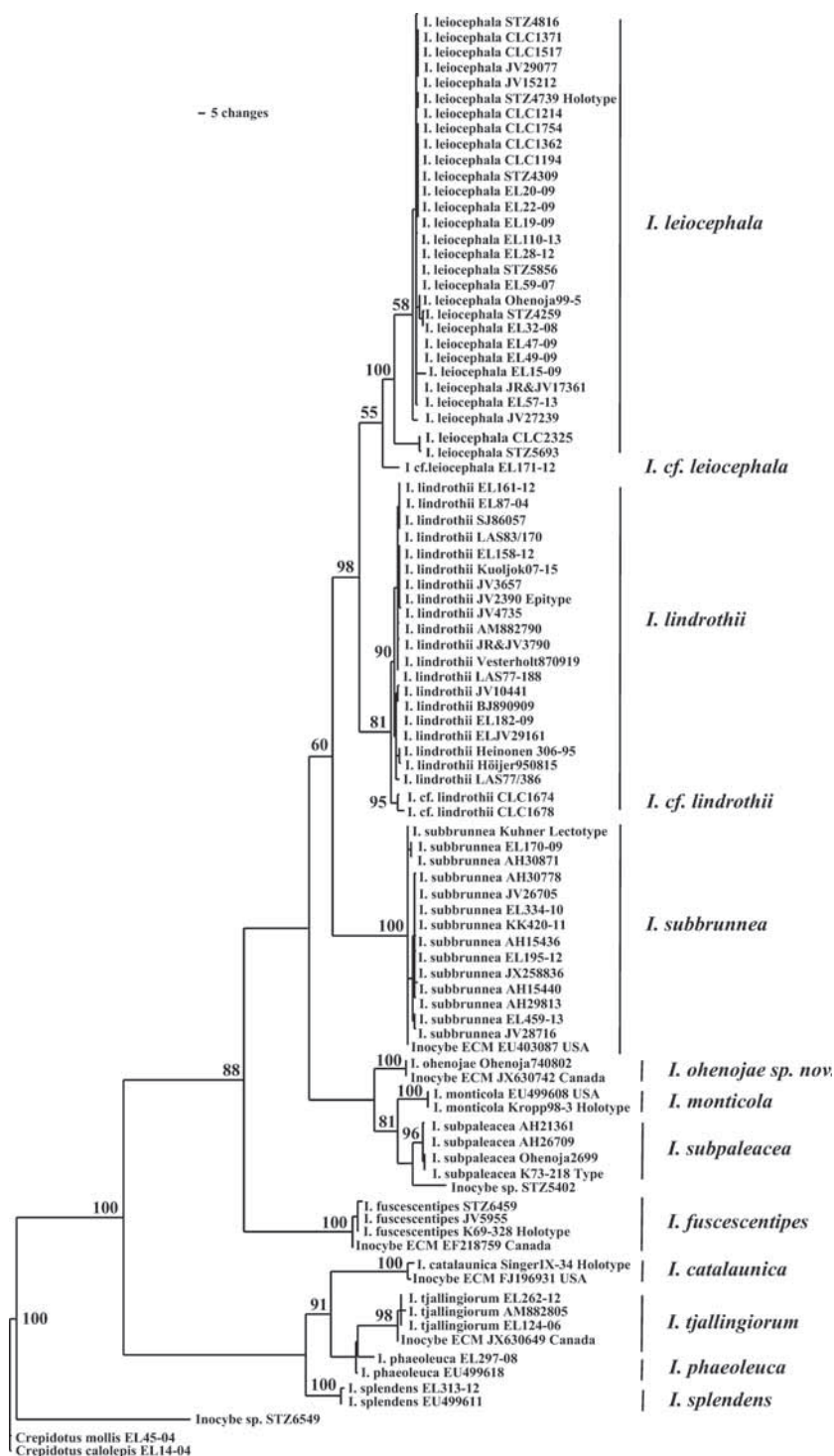


Fig. 1. One of the most parsimonious trees obtained from the MP analysis based on ITS and LSU sequence data. Bootstrap values are indicated on branches.

epitype originating from Finland is selected (Table 1 and the description below). Unfortunately the type of *I. saponacea* was not available for us to sequence because of the reorganisation of the Leiden Herbarium. Therefore, it was not possible to determine if the soapy smell is a distinct and unique character. However, the morphology of the type specimen was studied at an earlier occasion and based on morphology and ecology we regard *I. saponacea* as a synonym of *I. lindrothii*. Sequence data of the two specimens originating from Colorado, USA, and from the alpine zone came together on a separate branch in the *I. lindrothii* clade (Fig. 1). These sequences differ in 5 substitutions and two insertion/deletion events in the ITS region from the European *I. lindrothii* specimens. However no morphological differences were observed.

The sequences in the clade representing *I. subbrunnea* are all rather homogeneous, with only few substitution differences in the ITS region. The included specimens were collected in disparate geographic areas in Europe (Tab. 1), whereas the two sequences retrieved from GenBank originate from the American continent. We believe that more representatives of this species are to be found in North America and should be searched for in open mixed coniferous forests on more nutrient-rich, calcareous soils.

For *I. catalaunica* we have very little information. According to the morphological description it should be a species close to *I. leiocephala* and *I. subbrunnea*. However, it seems to be a somewhat misinterpreted species and may be rather rare, or it has a more southern distribution and is therefore not encountered in Northern Europe. Neither of the sequences generated from the specimens originating in Spain, also from *Abies alba* forests, matched the ITS 2 sequence from the type specimen. We first thought the generated ITS2 sequence was erroneous so a second DNA extraction and sequencing was performed from a different fruiting body, but it confirmed the first sequence. In micro-morphology *I. catalaunica* has slightly narrower spores with a mean value of  $Q=1.80$  in comparison to *I. leiocephala* ( $Q=1.60$ ), *I. lindrothii* ( $Q=1.58$ ) and *I. subbrunnea* ( $Q=1.57$ ), and with a slight suprahilar depression that is not so pronounced in the other species (Figs. 10, 12, 13, 14, 15, 16, 17, 18). The confusion in interpretation of *I. leiocephala*, *I. subbrunnea* and *I. catalaunica* is rather easy to under-

stand. As many mycologists before us, we found only few differences in the micro-morphology. In contrast, when observing photographs taken from the different collections within the clades, they differ very much in macro-morphology. This can often be explained by the fact that pilei are heavily affected by weather conditions, especially in the arctic-alpine zone (Figs. 2, 3, 4, 5, 6). But there is also a rather large variation among specimens from the hemiboreal and boreal forests. The great variation in macro-morphology and appearance of the fruiting bodies has led to the description of varieties of *I. subbrunnea* where the authors have referred to differences in pileus and lamellae colour and also to differences in spore measurements and ecology (Bon & Chevassut 1973, Bon 1984, Ferrari 2006). The types of these varieties were not included in this study.

*Inocybe fuscuscentipes* seems to be a species growing both in the alpine and boreal zones. It can be segregated from the others by the occurrence of white fibrils on the pileus margin and stipe, which is rather easy to observe on younger fruiting bodies (Fig. 7). *Inocybe subpaleacea* is a rather small species with a pileus not more than 20 mm in diam. As with *I. fuscuscentipes*, it has been found in alpine and boreal zones. The pileus colour is more yellowish brown and the stipe has a yellowish tint (Fig. 8). *Inocybe ohenojae* is distinct by having rather thick-walled and large, subamygdaloid to ovoid spores. The species is so far only known from North America from the alpine zone in association with *Dryas* and *Salix* (Fig. 17).

It is known that several species in section *Splendentes* are very similar in micro-morphology. This has caused problems when applying European names to North American specimens and vice versa. In Kropp et al. (2010) molecular methods were used to compare species concepts in the *I. splendentes* group from Europe and North America. In their study the included representative taxa were shown not to be conspecific between the continents and the sequences of *I. leiocephala* s.l. (in their study as *I. catalaunica*) failed to form a single clade. In this study we confirm that *I. leiocephala* is not monophyletic and consists of at least seven separate species, and we also show that five of these appear to have a broad intercontinental distribution range. For *I. catalaunica* and *I. subpaleacea* we have a rather limited num-



Fig. 2. *Inocybe leiocephala* in the alpine zone, Sweden, Torne Lappmark, Abisko mountains, with *Salix herbacea* and *Bistorta vivipara*, 20.VIII.2013 Larsson & Vauras 29954F (TUR-A, GB). – Photo: J. Vauras.



Fig. 3. *Inocybe leiocephala* in the arctic heath tundra, Norway, Svalbard, Longyearbyen, with *Bistorta vivipara*, 12.VIII.2009 Larsson 47-09 (GB). – Photo: E. Larsson.





Fig. 4. *Inocybe lindrothii* in southern boreal zone, Finland, Pohjois-Savo, Varkaus, Ruokokoski, on garden lawn under *Betula*, 6.IX.1986 Vauras 2390F, epitype). – Photo: J. Vauras.



Fig. 5. *Inocybe lindrothii* in northern boreal zone, Finland, Perä-Pohjanmaa, Rovaniemi, Pisavaara, at brookside under *Betula*, 4.IX.2013 Vauras 30110F (TUR-A, GB). – Photo: J. Vauras





Fig. 6. *Inocybe subbrunnea* in a mountainous coniferous forest with *Pinus sylvestris* in Spain, Madrid, Bustarviejo, Puerto de Canencia, 31.X.2013 Larsson 459-13 & Jeppson (GB, TUR-A). – Photo: E. Larsson.



Fig. 7. *Inocybe fuscetipipes* in middle boreal zone, Finland, Keski-Pohjanmaa, Vimpeli, Vesterbacka, in mixed forest near limestone quarries, 27.VIII.1991 Vauras 5955F (TUR-A, GB). – Photo: J. Vauras.





Fig. 8. *Inocybe subpaleacea* in the alpine zone in Spain, Girona, Núria, ras de l'Ortigar, growing with *Dryas* and *Salix retusa*, 10.VIII.1999 Esteve-Raventós (AH 26709). – Photo: J. V. Garcia.



Fig. 9. *Inocybe tjallingiorum* in northern boreal zone, Finland, Kittilän Lappi, Kolari, Kalkkikangas, near a limestone processing plant, on sandy soil near *Salix*, *Pinus sylvestris*, *Betula* and *Picea abies*, 8.VIII.1986 Vauras 2187F (TUR-A, GB). – Photo: J. Vauras.

ber of specimens and sequence data available so future studies may well show that these are also present on the North American continent.

There are few distinct morphological characters that with confidence can be used to differentiate between species in this group. The characteristic of having small grains below the crown of crystals at the apex of cystidia, is not a unique character for *I. subbrunnea*. It is here shown to occur more or less frequently in seven of the species treated. We have also found that habitat preferences offer support in species identification. A key to the species included in this study is provided and is based on a combination of morphological characters and ecological preferences.

For *I. catalaunica* we need more information to be able to better characterize the species. It should be searched for in the area of the Pyrenees from where it was first discovered and described.

## Taxonomy

***Inocybe leiocephala*** D.E. Stuntz, Mycologia 42: 98 (1950) – Figs. 2, 3, 10

**Holotype:** **USA. Washington**, Mt. Rainier National Park, Longmire, in moss under Douglas fir, 24.IX.1948 Stuntz 4739 (WTU, examined). GenBank acc. no. KJ399884

This seems to be a relatively common species in the arctic-alpine zone, especially on more calcareous soils. Spores (type and one collection from Estonia, Norway, Svalbard and Sweden):  $(8.5\text{--}8.8\text{--}11.4\text{--}12.0) \times (5.4\text{--}5.6\text{--}7.0\text{--}8.0)$   $\mu\text{m}$ , mean  $10.0 \times 6.2$   $\mu\text{m}$ ,  $Q = (1.35\text{--}1.5\text{--}1.75\text{--}1.85)$ , mean  $Q = 1.60$  ( $n = 130$ ), pleurocystidia  $(51\text{--}53\text{--}81\text{--}86) \times (11\text{--}12\text{--}21\text{--}26)$   $\mu\text{m}$ , mean  $64 \times 16$   $\mu\text{m}$  ( $n = 89$ ). The spore size seems to be larger at higher elevations and arctic habitats. Spores from Sweden, Abisko mountains, measured  $9.7\text{--}10.6\text{--}12.0 \times (5.7\text{--}5.8\text{--}6.4\text{--}7.1)$   $\mu\text{m}$ , and those from Svalbard  $(9.4\text{--}9.5\text{--}10.5\text{--}11.5\text{--}12.0) \times (5.7\text{--}5.9\text{--}6.7\text{--}7.8\text{--}8.0)$   $\mu\text{m}$ . In the specimen from Svalbard also pleurocystidia were longer than in other collections:  $64\text{--}75\text{--}84\text{--}86) \times 11\text{--}13\text{--}16$   $\mu\text{m}$ .

***Inocybe lindrothii*** (P. Karst.) Vauras & E. Larss. **comb. nov.** – Figs. 4, 5, 11, 12

MycoBank no.: MB808606

**Basionym:** *Hebeloma lindrothii* P. Karst., Kritisk Öfersigt af Finlands Basidsvampar, Tillägg 3: 8. 1898. – Holotype: **Finland. Etelä-Häme**. Tammela, Mustiala, Syrjä IX.1897 Lindroth (H, PAK 2888, examined).

**Epiletype** (selected here): **Finland. Pohjois-Savo**. Varkaus, Ruokokoski. On lawn with *Betula*, 6911:3542, 6.IX.1986 Vauras 2390F (TUR-A 144764;–isoeotypeGB). GenBankno. KJ399915.

**Synonym:** *Inocybe saponacea* Kuyper, Persoonia, Suppl. 3: 195. 1986.

**Pileus** 1.5–4.5(–6) cm in diam, first conico-convex or campanulato-convex, then plano-convex, distinctly umbonate, margin somewhat inflexed when young, pale reddish yellow, ochraceous brown, pale yellow brown to dark brown, umbo often dark brown to blackish brown, sometimes with whitish remnants of velipellis on umbo and cap margin, smooth, somewhat shiny when moist, at margin slightly radially fibrillose, somewhat breaking up with age, then the whitish context contrasts with the darker surface of the pileus, sometimes subsquamulose. **Lamellae** up to 6 mm broad, moderately crowded to subdistant, when young pale grey, grey brown with age, edge concolorous or paler. **Stipe** 2–6(–12) long, 0.3–0.7 cm wide, cylindrical, base mostly sub-bulbous to bulbous; pale yellow-brown, sometimes partly pale reddish yellow, dark brown to blackish brown, apex pale, base often whitish; pruinose all over, longitudinally striate. **Cortina** not seen. **Context** whitish, in stipe partly slightly reddish, yellowish to orange. **Smell** acidulous to spermiatic. **Taste** mild. **Spores**  $(7.3\text{--}8.0\text{--}9.1\text{--}10.2\text{--}10.8) \times (4.8\text{--}5.1\text{--}5.8\text{--}6.5\text{--}7.0)$   $\mu\text{m}$ , range of mean values  $8.2\text{--}10.0 \times 5.4\text{--}6.1$   $\mu\text{m}$ ,  $Q = (1.25\text{--}1.4\text{--}1.58\text{--}1.75\text{--}1.95)$ , range of mean  $Q$  -values 1.49–1.69 (320 spores from 15 collections); smooth, subamygdaloid to ovoid. **Basidia**  $(22\text{--}23\text{--}28\text{--}35\text{--}39) \times 8\text{--}9\text{--}12$



$\mu\text{m}$ , clavate, 4-spored (22 basidia from 3 collections). *Pleurocystidia* (43–)52–60–70(–80)  $\times$  (11–)14–18–22(–25)  $\mu\text{m}$  (82 pleurocystidia from 14 collections), subfusiform to lageniform, thick-walled, wall up to 4.5  $\mu\text{m}$  thick, colourless to slightly yellowish; usually with both larger and small crystals at apex. *Cheilocystidia* similar to pleurocystidia but more utriform, often with rounded base; paracystidia ovoid to clavate, thin-walled. *Caulocystidia* present on the whole stipe, similar to cheilo- and pleurocystidia, some with rounded base, up to 72  $\mu\text{m}$  long; cauloparacystidia ovoid to clavate, thin-walled.

The species has its main distribution in the hemiboreal to subalpine zones, associated mainly with *Betula* on better soils, but is also found in mixed *Picea* forests and parks. Together with *I. sindonia* (Fr.) P. Karst. it is the most common species of section Splendentes in Finland. We have never met any specimen of this species with a soapy smell.

**Additional specimens studied: FINLAND.** **Varsinais-Suomi.** Turku, Luolavuori, 31.VIII.1988 Vauras 3268F (TUR-A). **Uusimaa.** Porvoo, Ilola, 13.IX.1989 Kytövuori 89-712 (H). **Etelä-Häme.** Tammela, Mustiala, Syrjä, IX.1897 Lindroth (H, holotype). **Etelä-Savo.** Taipalsaari, Pönniälä, 16.IX.1989 Kytövuori 89-924 (H). **Pohjois-Savo.** Siilinjärvi, Toivala, 16.VIII.1986 Vauras 2259 (TUR-A). **Keski-Pohjanmaa.** Ruukki, Revonlahti, 26.VIII.1989 Vauras 3667 (TUR-A, GB). **Perä-Pohjanmaa.** Rovaniemi, Pisavaara, 4.IX.2013 Vauras 30110F (TUR-A, GB, MONT). **Koillismaa.** Kuusamo, near Kiutaköngäs, 10.IX.1970 Ulvinen (OULU); Korvasvaara, 21.VIII.1974 Ulvinen (OULU). **Enontekiön Lappi.** Enontekiö, Kilpisjärvi, 12.VIII.1990 Ruotsalainen & Vauras 4735F (TUR-A, GB). **Inarin Lappi.** Utsjoki, Ailigas, 20.VIII.1966 Suominen (TUR); Kevo, 5.IX.1970 Ulvinen (OULU), 27.VIII.1973 Bas 6048 (L, holotype of *Inocybe saponacea*), 28.VIII.1973 Ulvinen (OULU). **SWEDEN. Västergötland.** Norra Kyrketorp, Hene, 13.IX.1986 Jacobsson 86057b (GB); Trollhättan, Kronogården, 8.X.1991 Olsson (TUR-A). **Dalarna.** Leksand, Hjortnäs, 22.VIII.1978 Morander & Jacobsson 78127 (GB).

*Inocybe subbrunnea* Kühner, Bull. Soc. Nat. Oyonnax 9 (Suppl. (Mém. hors sér. 1)): 6 (1955). – Figs. 6, 13

Mycobank no.: MBT177720

**Lectotype:** Designated by Jukka Vauras 1996; published here. **France. Savoie.** Praz, in *Picea* forest, 29.VIII.1941 Kühner “1941 AB / type subbrunnea” (G388231, examined). GenBank acc. no. KJ399934

The species has a more southern distribution and seems to be confined to herb-rich mixed coniferous forests on nutrient rich and often more calcareous soils. In Northern Europe it is typically encountered in open herb rich *Picea* forests, but it is also found in Spain at higher altitudes associated with *Pinus sylvestris*. Spores and pleurocystidia (lectotype and one collection from Estonia, Greece, Norway and Spain): spores (8.0–)8.5–10.4(–11.4)  $\times$  (5.2–)5.4–6.5(–7.0)  $\mu\text{m}$ , mean 9.4  $\times$  6.0  $\mu\text{m}$ ,  $Q = (1.3–)1.4–1.75(–1.85)$ , mean  $Q = 1.57$  ( $n = 100$ ); pleurocystidia (65–)66–82(–88)  $\times$  13–24(–25)  $\mu\text{m}$ , mean 73  $\times$  18  $\mu\text{m}$  ( $n = 36$ ), the small crystals below the crown mostly spine like.

*Inocybe fuscescentipes* Kühner, Docums Mycol. 19, 74: 18 (1988) – Figs. 7, 14

**Holotype:** **France. Savoie.** Haute vallée de Champagne Pierre, moraninique calcaire, glacier de l'Epéna, in *Dryas*, 16.IX.1969 Kühner 69-238 (G, examined). GenBank acc. no. KJ399947

The species is an exceptional member of the section Splendentes, as it has a white thin fugacious cortina at pileus margin and white fibrils on stipe. However, it has caulocystidia on the whole stipe. It may be overlooked but seems to have a more northern but wide intercontinental distribution range. According to the original diagnosis (Kühner 1988), spores of *I. fuscescentipes* measure 8.7–9.7–10.5  $\times$  5–5.7–6.2  $\mu\text{m}$  and metuloids 60–65–75  $\times$  13–15  $\mu\text{m}$ . Our measurements from the holotype are: spores (9.0–)9.1–11.9  $\times$  (5.4–)5.5–6.3(–7.0)  $\mu\text{m}$ , mean 10.1  $\times$  6.0  $\mu\text{m}$ ,  $Q = (1.5–)1.55–1.9(–2.05)$ , mean  $Q = 1.70$  ( $n =$

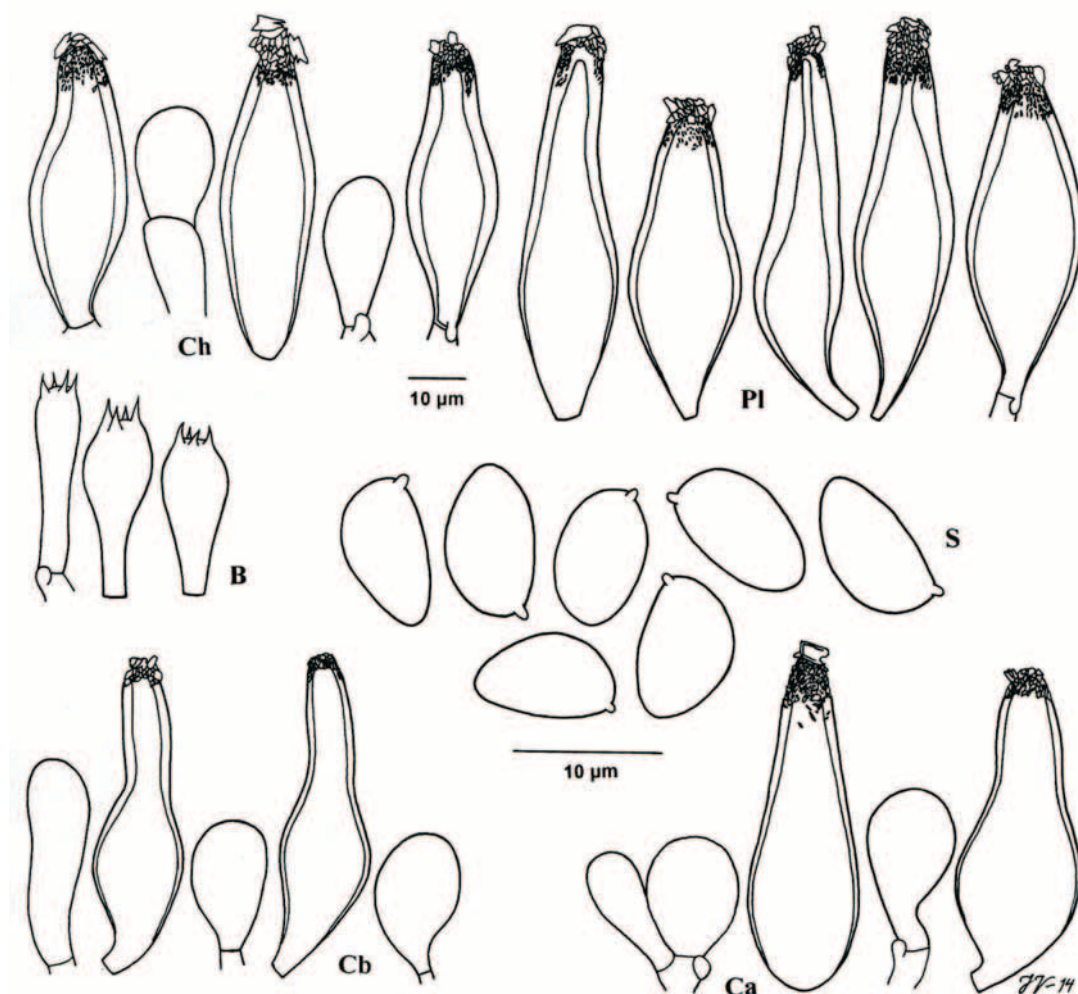


Fig. 10. Microscopical characters of *I. leiocephala* (holotype). B = basidia, Ca = caulocystidia and paracystidia at stipe apex, Cb = caulocystidia and paracystidia at stipe base, Ch = cheilocystidia and paracystidia, Pl = pleurocystidia, S = spores.

20); pleurocystidia  $65\text{--}82 \times 15\text{--}20\text{ }\mu\text{m}$ , mean  $74 \times 18\text{ }\mu\text{m}$  ( $n = 4$ ). The collection from Finland (*Vauras 5955F*) has smaller spores, measuring  $8.0\text{--}10.2(-11.1) \times (4.6\text{--})4.9\text{--}5.9(-6.2)\text{ }\mu\text{m}$ , mean  $9.3 \times 5.4\text{ }\mu\text{m}$ ,  $Q = (1.5\text{--})1.55\text{--}1.8(-2.05)$ , mean  $Q = 1.71$  ( $n = 40$ ), and shorter pleurocystidia with often rounded base, measuring  $(45\text{--})48\text{--}64(-66) \times (12\text{--})15\text{--}22\text{ }\mu\text{m}$ , mean  $56 \times 18\text{ }\mu\text{m}$  ( $n = 30$ ).

**Additional specimen studied: FINLAND.** Keski-Pohjanmaa. Vimpeli, Vesterbacka, 27.VIII.1991 *Vauras 5955F* (TUR-A, GB).

*Inocybe subpaleacea* Kühner, *Docums Mycol.* 19, 74: 25 (1988) – Figs. 8, 15

**Holotype: France. Savoie.** Parc National de la Vanoise, plan de Bellecombe, 2300 m, avec *Helianthemum*, *Dryas* et *Salix serpyllifolia*, 30.X.1973 Kühner 73-346 (G, examined). GenBank acc. no. KJ538548

A small species with yellowish brown to brown pileus and stipe. So far only found in Europe. It seems to have its main distribution in

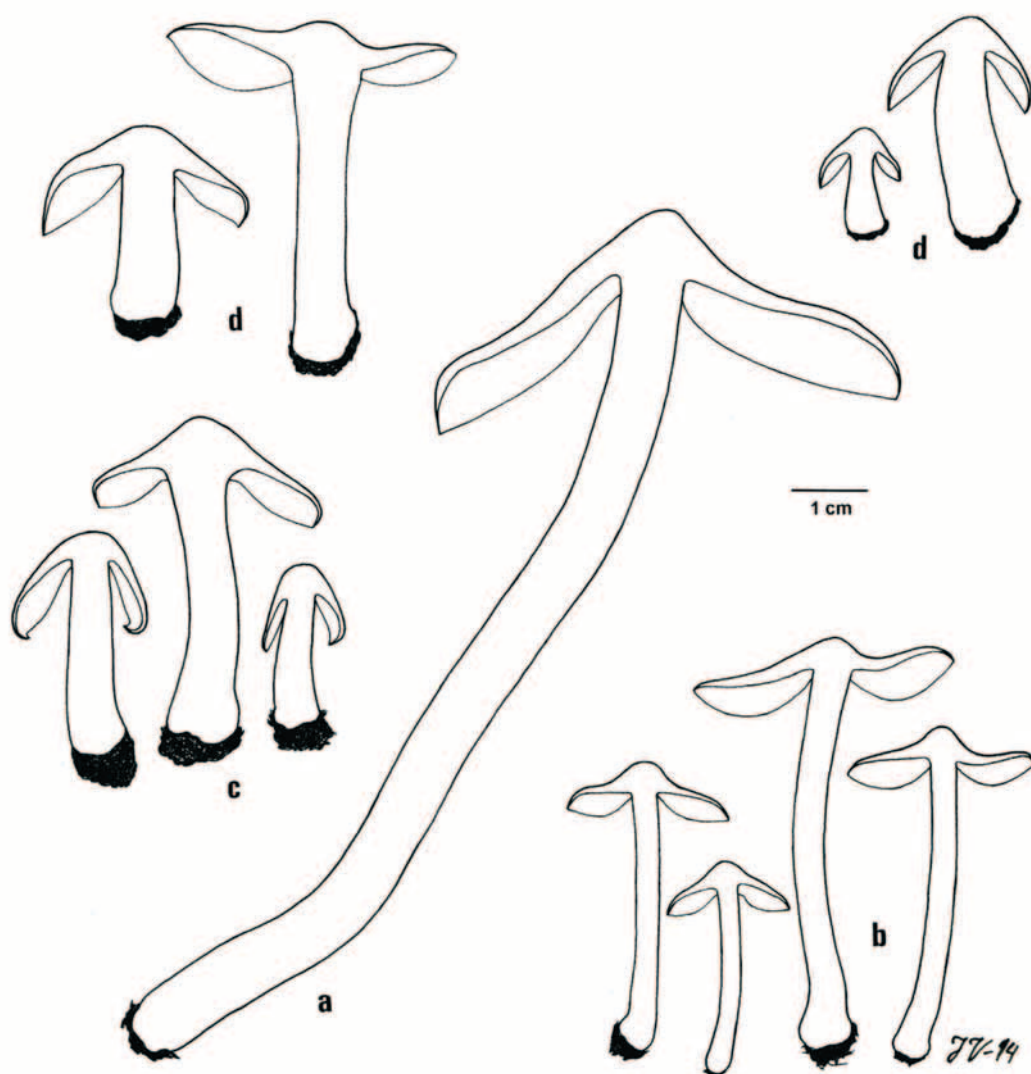


Fig. 11. Cross-sections of fruiting bodies of *I. lindrothii*. - a) Large fruit body amongst grasses, from *Vauras* 3667, b) from epitype, c) from *Ruotsalainen & Vauras* 4735F, d) from *Vauras* 3268F.

the alpine zone and with *Dryas* vegetation. Further, it has also been found in northern Russia in a dry *Larix gmelinii* forest with *Betula platyphylla*, *Pinus sylvestris* and few *Populus tremula* and *Alnus fruticosa*, and in northern Finland in mixed forest with *Picea abies*, *Pinus sylvestris*, *Betula* and *Populus tremula*, on a calcareous rocky outcrop. According to the original diagnosis (Kühner 1988), spores of *I. subpaleacea* measure  $10\text{--}11.5 \times 6\text{--}7 \mu\text{m}$  and metuloids  $43\text{--}58 \times 14\text{--}16 \mu\text{m}$ . Our measurements from four

collections are: spores  $(8.2\text{--})8.7\text{--}11.1(\text{--}11.4) \times (5.4\text{--})5.7\text{--}6.7(\text{--}7.2) \mu\text{m}$ , mean  $9.8 \times 6.2 \mu\text{m}$ ,  $Q = (1.35\text{--})1.4\text{--}1.8(\text{--}1.9)$ , mean  $Q = 1.57$ , total range of mean  $Q$  values =  $1.48\text{--}1.67$  ( $n = 80$ ); pleurocystidia  $(44\text{--})48\text{--}68(\text{--}72) \times 12\text{--}19 \mu\text{m}$ , mean  $59 \times 16 \mu\text{m}$  ( $n = 38$ ).

**Additional specimens studied:** FINLAND. **Perä-Pohjanmaa.** Tornio, Arpela, Korkeamaa, Runteli, 6.IX.2012 *Vauras* 29282F (TUR-A, GB); GenBank acc. No KJ849311. **RUS-**



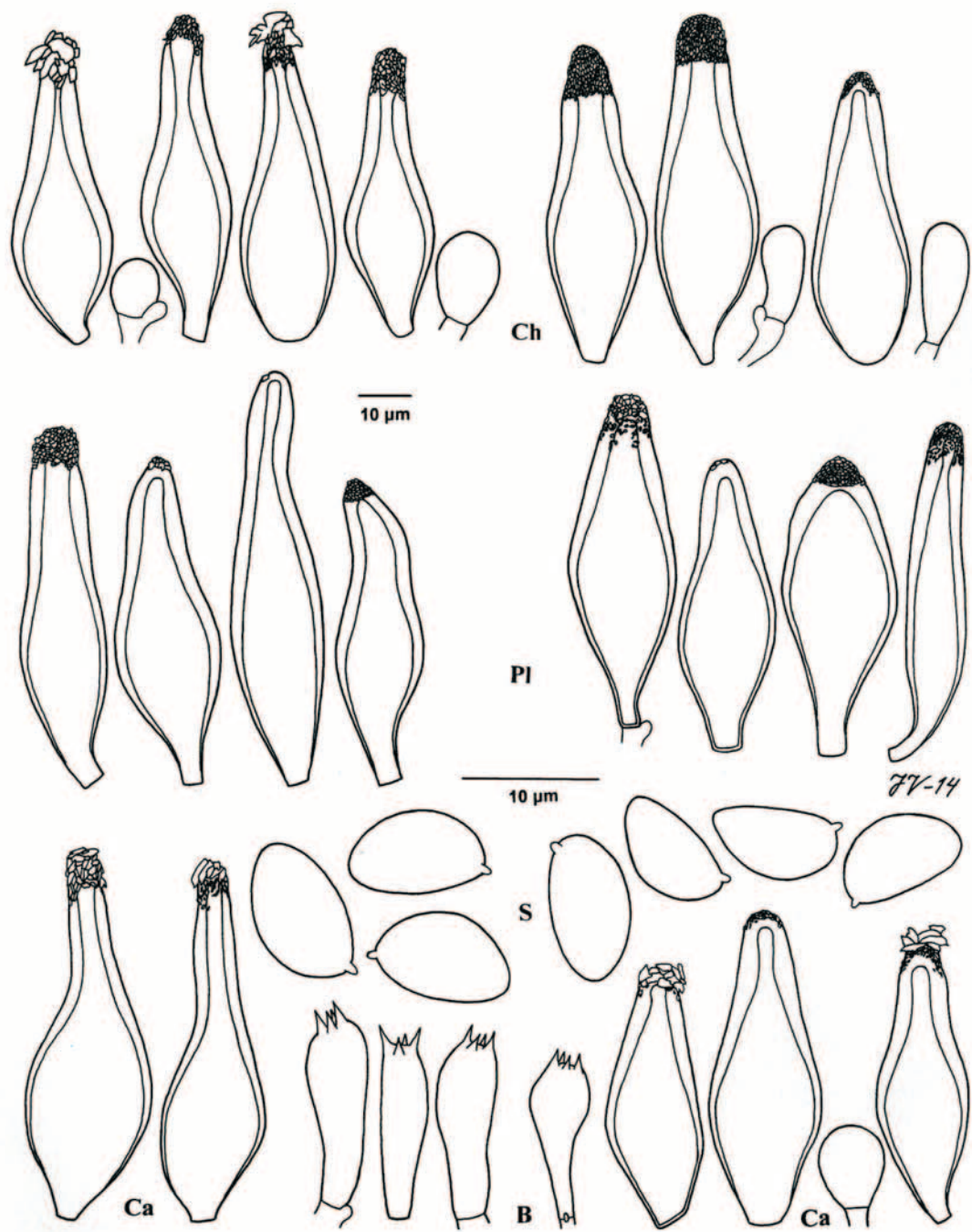


Fig. 12. Microscopical characters of *I. lindrothii* (from holotype of *Hebeloma lindrothii*, on the left, from holotype of *Inocybe saponacea*, on the right). For symbols, see Fig. 10.

**SIA. Sakha.** Magan, near Magan airport, 4.VIII.1999 *Ohenoja* 26 (OULU, GB). **SPAIN.** Huesca, Bielsa, Pala de Montiner, 28.VIII.1996 *Esteve-Raventós* (AH21361). Girona, Núria, ras de l'Ortgar, 10.VIII.1996 *Esteve-Raventós* (AH26709).

*Inocybe catalaunica* Singer, Collectanea Bot., Barcinone Bot. Instit. 1: 245 (1947).

– Fig. 16

**Holotype: Spain. Catalonia.** Pyrenees, Valle De Arán, Bosc de Baricauba, in Abieto, IX.1934 *Singer* (LE 12646, examined). GenBank acc. no. KJ399954

Our knowledge of this species is restricted to the type specimen. This species can be separated from the other similar species by the amygdaloid spores with a suprahilar depression, and caulocystidia that are fairly thin walled. Singer (1947)

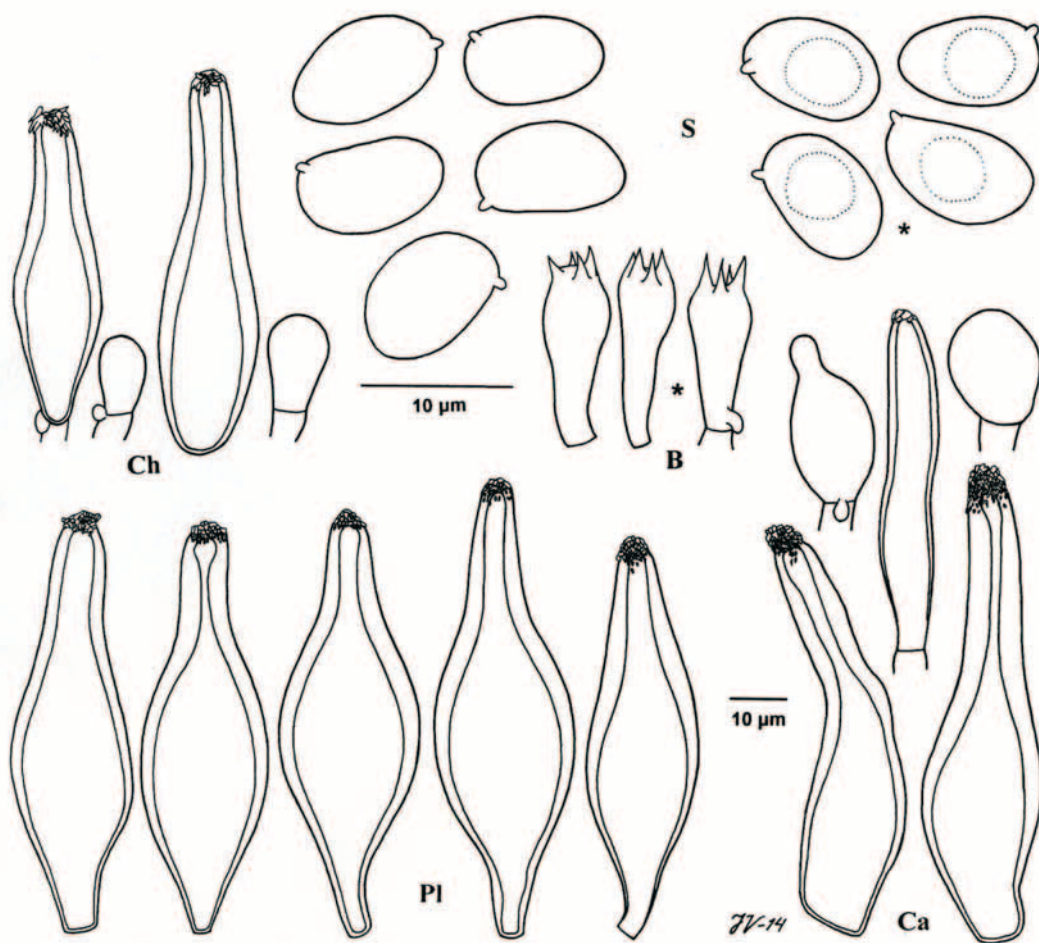


Fig. 13. Microscopical characters of *I. subbrunnea* (holotype; all basidia and spores indicated with asterisk from *Larsson 459-13*). For symbols, see Fig. 10.

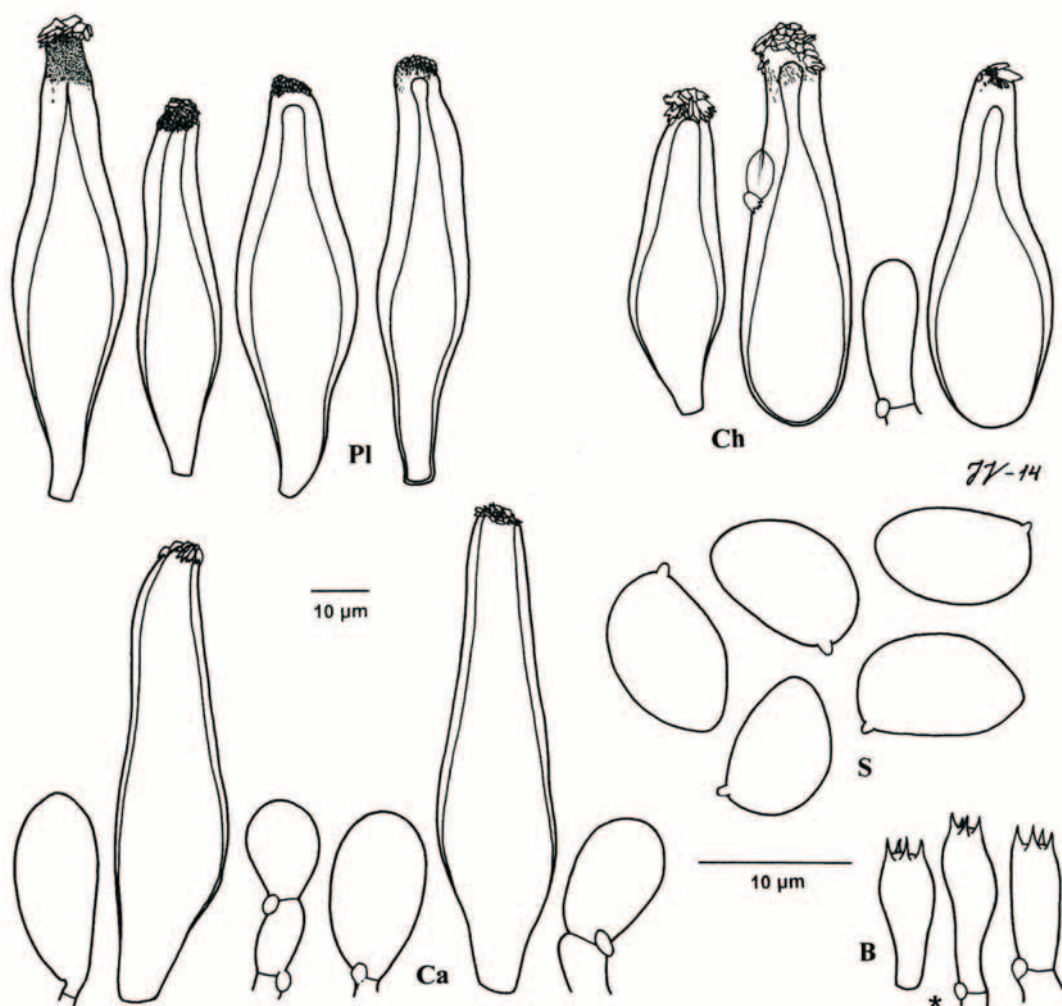


Fig. 14. Microscopical characters of *I. fuscescens* (holotype, basidia from *Vauras 5955F*). For symbols see Fig. 10.

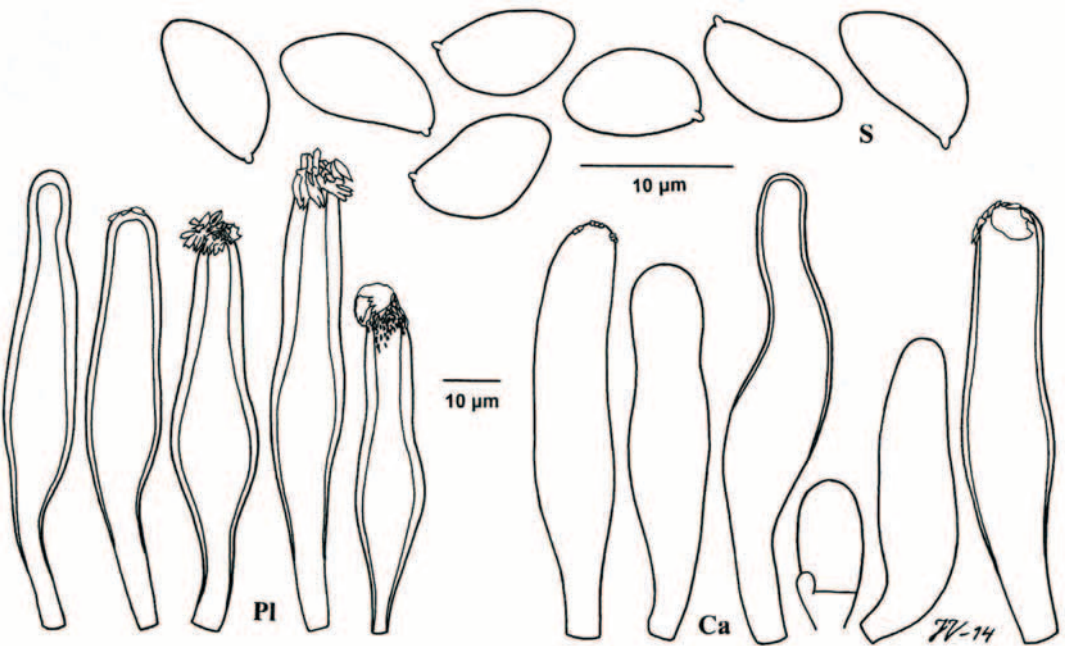
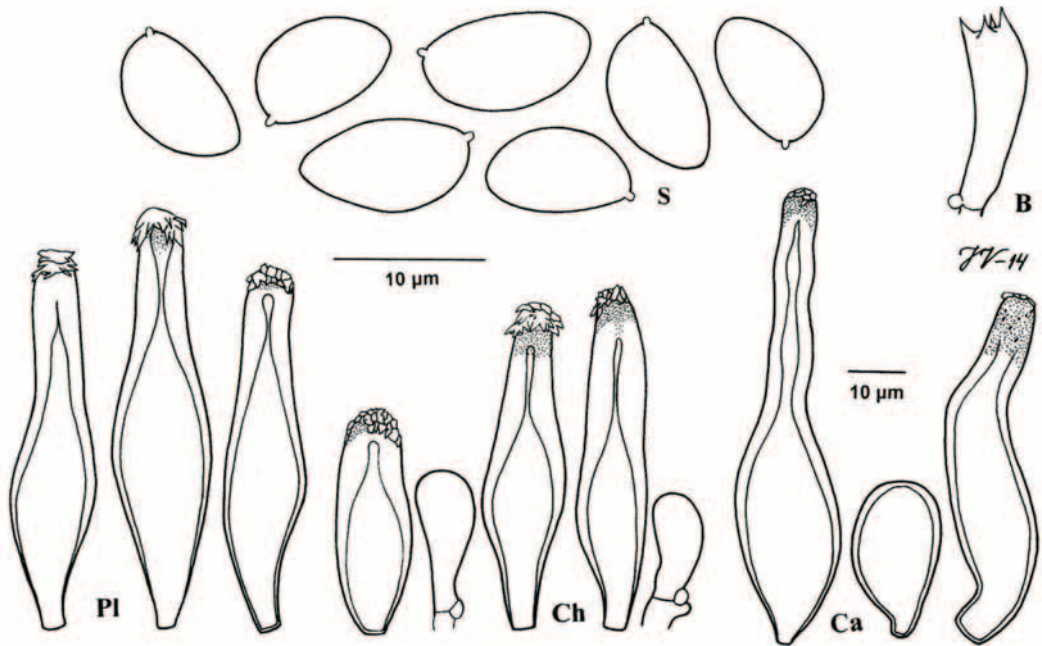
gave the spore size as  $8.3\text{--}10.3 \times 5\text{--}6 \mu\text{m}$  and Esteve-Raventós (1997) as  $9\text{--}11 \times 5\text{--}6.2 \mu\text{m}$ . Our measurements are:  $(8.6\text{--})8.8\text{--}10.3\text{--}(11.1) \times (4.5\text{--})4.8\text{--}5.7 \mu\text{m}$ , mean  $9.7 \times 5.3 \mu\text{m}$ ,  $Q = 1.6\text{--}2.05\text{--}(2.25)$ , mean  $Q = 1.83$  ( $n = 30$ ). Pleurocystidia were reported by Singer as  $50\text{--}80 \times 11\text{--}13.5\text{--}(15) \mu\text{m}$  and by Esteve-Raventós as  $55\text{--}70 \times 13\text{--}16 \mu\text{m}$ . Our measurements are:  $52\text{--}81 \times 11\text{--}15 \mu\text{m}$ , mean  $66 \times 13 \mu\text{m}$  ( $n = 16$ ).

***Inocybe ohenojae* Vauras & E. Larss., sp. nova**  
– Fig. 17

MycoBank no.: MB808487

**Diagnosis:** Macroscopically fairly similar to *Inocybe leiocephala*, *I. lindrothii* and *I. subbrunnea*. *Inocybe ohenojae* differs from all these species by having larger, subamygdaloid to ovoid thick-walled spores with an average  $Q = 1.39$ .





Figs. 15–16. – 15 (Above). Microscopical characters of *I. subpaleacea* (Esteve-Raventós, AH 26709). – 16 (Below). Microscopical characters of *I. catalaunica* (holotype). For symbols see Fig. 10.

**Typus: Canada. Nunavut.** Melville Peninsula, Repulse Bay, 200 m N of the settlement, between the radio link and the road to the north, moist depression under a rocky outcrop, on hummock in *Dryas integrifolia* – *Carex* vegetation with *Salix* sp., with *Callicladium haldanianum*, *Campylium stellatum*, *Trichostomum arcticum*, *Bryum pseudotriquetrum* and *B. pallescens*, 66°31', 86°15', 2.VIII.1974, E. & M. Ohenoja 2.8.1974/1 (OULU – holotypus; GB – isotypus, GenBank no. KJ399955).

**Etymology:** In honour of the Finnish mycologist Dr. Esteri Ohenoja who has explored the Mycota in arctic and alpine habitats around the world.

**Pileus** 1.5–2.8 cm diam, dirty grey-brown, at centre dark brown, subtomentose-smooth, at margin slightly radially fibrillose, somewhat breaking up with age, then the whitish context contrasts with the brown surface of the pileus; velipellis present or absent. **Lamellae** up to 4 mm broad, cinnamon-brown with age. **Stipe** up to 2 × 0.4 cm, cylindrical, base slightly bulbous; yellow-brown, apex and base whitish, pruinose all over. **Cortina** not observed. **Smell** indistinct. **Taste** mild. **Spores** (10.4–)10.8–11.7–12.8(–14.8) × (7.5–)7.7–8.4–9.1(–9.4) µm, Q = (1.25–)1.3–1.39–1.5(–1.7) (50 spores); smooth, very thick-walled, broadly subamygdaloid to ovoid. **Basidia** 29–34–38(–40) × 10–12–13 µm (n = 27), clavate, 4-spored. **Pleurocystidia** (64–)65–74–87(–90) × (13–)14–17–19(–21) µm (n = 23), lageniform to fusiform, some with pedicel, thick-walled, with up to 4 µm thick, pale yellowish wall, usually with abundant crystals, part of these small and narrow, below the larger ones, frequent. **Cheilocystidia** similar to pleurocystidia but more variable, 54–68–80 × 13–18–31 µm (n = 12), some with yellow-brown contents, some with wide, fairly rounded base; paracystidia fairly abundant, oval to clavate, 18–23–27 × 7–11–13 µm (n = 11). **Caulocystidia** on whole stipe, similar to cheilo- and pleurocystidia, some with a rounded base, up to 80 µm long; cauloparacystidia pyriform to clavatae, 29–34 × 10–17 µm, some thick-walled.

*Inocybe ohenojae* is macroscopically fairly similar to several species of the *I. leiocephala* group. It differs from these by having significantly thick-walled, larger spores. The species is so far only known from the arctic areas of North America. We know only the type collection of it, but the sequence data of the type matched with an ectomycorrhizal sample from root tips of *Salix arctica* in GenBank.

**Inocybe tjallingiorum** Kuyper Persoonia, Suppl. 3: 192 (1986) – Figs. 9, 18

**Holotype: The Netherlands.** IJsselmeerpolders, Roggeboezand, 9.X.1981 Kuyper 1902, (L, examined).

This species differs from the other species by its quite small fruiting bodies characterised by dark reddish brown colour and the velipellis covering the young pilei. The stipe is first pale with a reddish tint but soon turns dark reddish brown. The lamellae are first white but turn ochraceous brown with age. The species is encountered in Nordic countries typically in the hemiboreal to subalpine zone e.g. along roadsides under *Salix*, *Betula*, *Populus* and *Pinus*, preferably on more calcareous soils, also on the coast on sandy soil with clam shells. In Central Europe it is also found in the Alps with *Salix herbacea* and *Dryas octopetala* (Kuyper 1986). Spores (type, five collections from Finland, one from Sweden): (7.4–)7.6–10.0(–10.5) × (4.7–)5.2–6.6(–7.2) µm, mean 8.7 × 5.8 µm, Q = (1.25–)1.3–1.8(–1.9), mean Q = 1.52, total range of mean Q values = 1.36–1.66 (n = 120); pleurocystidia (38–)41–62 × 11–21(–22) µm, mean 50 × 16 µm (n = 28).

**Additional specimens studied: FINLAND. Etelä-Savo.** Kerimäki, Louhi, 18.VIII.1987 Vauras 2775F (TUR-A). **Kittilän Lappi.** Kolari, Kalkkikangas, 4.VIII.1985 Ruotsalainen & Vauras 1898F, 1900F (TUR-A), 8.VIII.1986 Vauras 2187F (TUR-A, GB), 12.VIII.1987 Vauras 2727 (TUR-A). **SWEDEN. Jämtland.** Mörsil, 22.VII.1981 Stridvall 81-54 (GB).

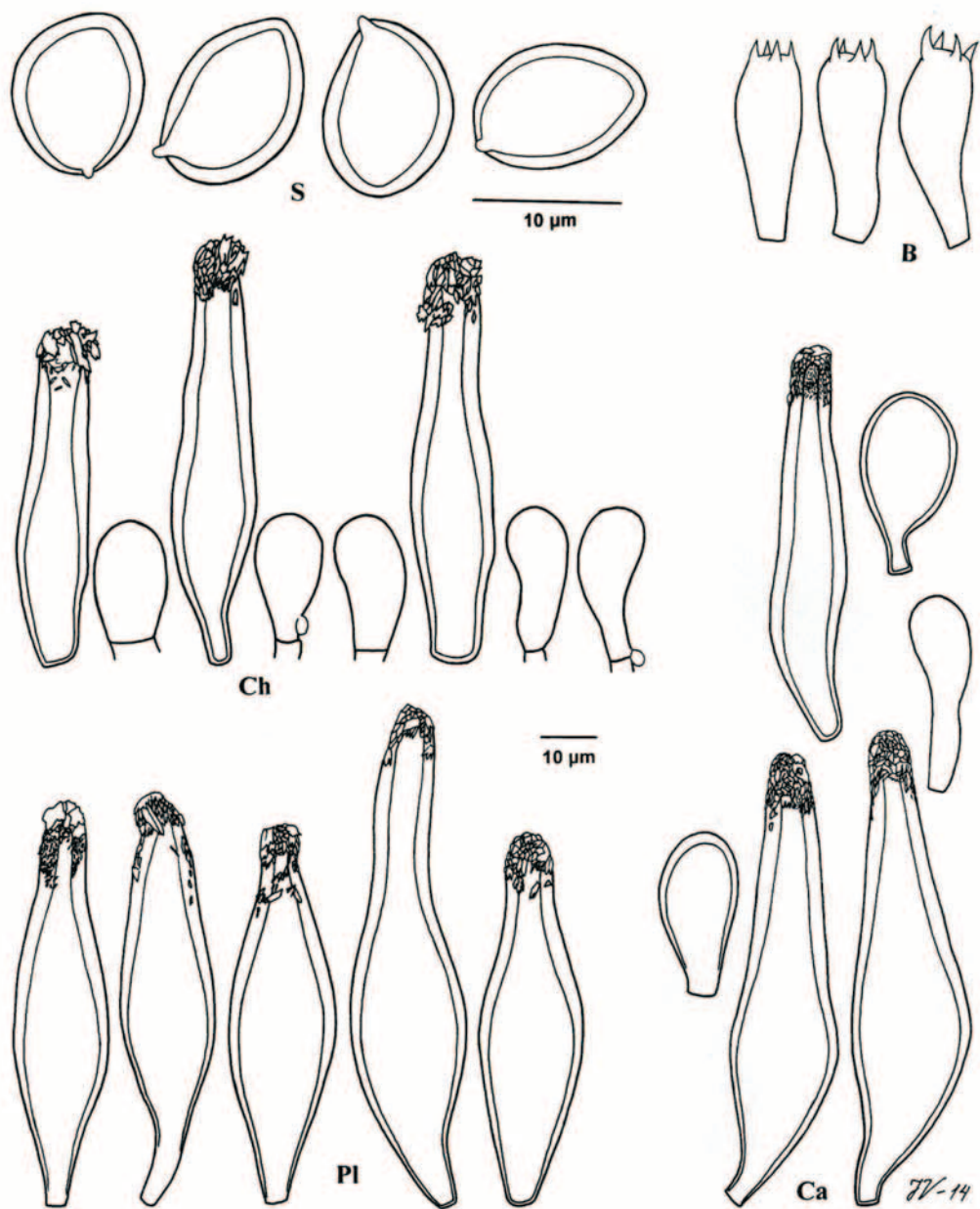


Fig. 17. Microscopical characters of *I. ohenojae* (holotype). For symbols see Fig. 10.



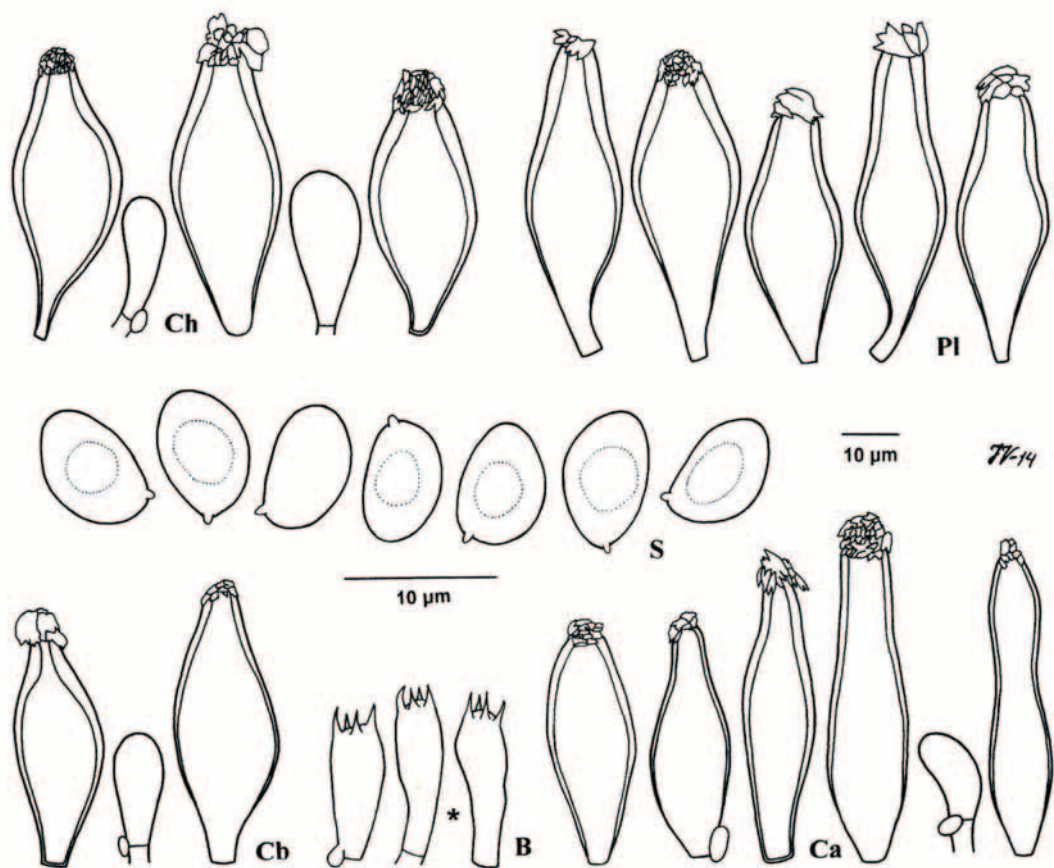


Fig. 18. Microscopical characters of *I. tjallingiorum* (holotype; basidia from *Vauras 2187F*) For symbols see Fig. 10.

**Key to smooth-spored species in this study with a totally pruinose and bulbous to sub-bulbous (non-marginate) stipe and with metuloid cystidia:**

- 1a Fruiting bodies rather small and slender, pleurocystidia on average 50 µm long and without small grains below the crown of crystals ..... *I. tjallingiorum*
- 1b Fruiting bodies on average larger and stouter, cystidia longer, often with small grains below the crown of crystals ..... 2
- 2a Spores thick-walled, large (average 11.7 × 8.4 µm), average Q = 1.4 ..... *I. ohenojae*
- 2b Spores not as thick-walled, smaller, average Q = 1.5–1.8 ..... 3
- 3a Pileus margin and stipe with white fibrils, with a fugacious cortina ..... *I. fuscescentipes*

- 3b Pileus margin finely radially fibrillose, without cortina ..... 4
- 4a Pleurocystidia narrow (average 13  $\mu$ m broad), caulocystidia rather thin-walled, spores  
amygdaloid to ellipsoid, often with a suprahilar depression, average Q = 1.8 ..... *I. catalaunica*
- 4b Pleurocystidia broader, spores without suprahilar depression, average Q = 1.5–1.7 ..... 5
- 5a Spores with an almost obtuse apex, pleurocystidia large (average 73  $\times$  18  $\mu$ m), with a more  
southern distribution ..... *I. subbrunnea*
- 5b Spores mainly with indistinctly subconical apex, pleurocystidia smaller, with a more  
alpine/northern distribution ..... 6
- 6a Mostly in hemiboreal to subalpine zones, usually with *Betula*, not strongly calciphilous,  
fruiting bodies rather large and stout ..... *I. lindrothii*
- 6b Mostly in arctic-alpine and subalpine zones, calciphilous species ..... 7
- 7a Pileus 15–25(–35) mm, stipe with a pinkish tint ..... *I. leiocephala*
- 7b Pileus 10–20 mm, stipe with a yellowish tint ..... *I. subpaleacea*

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**Table 1.** Data on specimens sequenced in this study. Specimens with CLC numbers are deposited in Herbarium MONT; STZ in Herbarium WTU; EL, BJ, Kuoljok, SJ and LAS in Herbarium GB; JV, Heinonen, Höijer, JR&JV, Vesterholt, KK in Herbarium TUR-A/TUR; AH in Herbarium AH. Abbreviations: *Abies alba* = A. alba, *Betula nana* = B. nana, *B. pendula* = B. pen, *B. pubescens* subsp. *czerepanovii* = B. pub, *Bistorta vivipara* = B. vivi, *Dryas octopetala* = Dryas, Dwarf *Salix* = S. dwa, *Helianthemum* sp. = Heli, *Picea abies* = Picea, *Pinus pinea* = P. pin, *P. sylvestris* = P. syl, *P. uncinata* = P. unc, *Pseudotsuga menziesii* = Pseudots. menz, *Salix caprea* = S. cap, *S. glauca* = S. gla, *S. herbacea* = S. herb, *S. planifolia* = S. pla, *S. polaris* = S. pol, *S. reticulata* = S. ret, *S. serpyllifolia* = S. ser.

Species	Coll. ID. / Origin	Ecology / putative host	Genbank No. ITS/LSU
I. leiocephala	<b>STZ4739 Type</b> , WA, USA	Subalpine, Pseudts. menz	KJ399884
	STZ4816, WA, USA	Subalpine, Pseudts. menz	KJ399883
	STZ4259, WA, USA	Subalpine, Pseudts. menz	KJ399901
	STZ5856, WA, USA	Subalpine, in grass	KJ399902
	STZ4309, WA, USA	Subalpine, Pseudts. menz	KJ399887
	CLC1517, Greenland	Arctic, S. dwa	KJ399900
	CLC1214, CO, USA	Alpine, S. ret, S. pla	KJ399899
	CLC1754, CO, USA	Alpine, S. gla, S. pla	KJ399906
	CLC1362, CO, USA	Alpine, S. gla, S. dwa	KJ399886
	CLC1194, MT/WY, USA	Alpine, S. ret	KJ399888
	CLC1371, CO, USA	Alpine, S. dwa	KJ399885
	CLC2325, MT/WY, USA	Alpine, S. dwa	KJ399911
	EL19-09, Svalbard	Arctic, S. pol	KJ399896
	EL20-09, Svalbard	Arctic, S. pol, B. vivi	KJ399894
	EL22-09, Svalbard	Arctic, B. vivi	KJ399895
	EL110-13, Sweden	Alpine, S. herb	KJ399897
	EL28-12, Sweden	Subalpine, S. herb	KJ399898
	EL59-07, Sweden	Alpine, S. pol	KJ399889
	EL32-08, WY, USA	Alpine, S. dwa	KJ399890
	EL47-09, Svalbard	Arctic, S. pol, B. vivi	KJ399891
	EL49-09, Svalbard	Arctic, S. pol, B. vivi	KJ399892
	EL15-09, Svalbard	Arctic, S. pol, B. vivi	KJ399905
	EL57-13, Sweden	Alpine, Dryas	KJ399909
	JV29077, Norway	Alpine, B. nana, S. dwa	KJ399903
	JV15212, Sweden	Subalpine, B. pub, S. sp.	KJ399904
	JV27239, Estonia	P. syl, Picea, Betula	KJ399893
	Ohenoja99-5, Russia	Alpine, S. herb, Dryas	KJ399907
	JR&JV17361, Italy	Alpine	KJ399908
	STZ5693, unknown, WA, USA	Subalpine, unknown	KJ399912
I. cf. leiocephala	EL171-12, Norway	Subalpine, S. gla	KJ399910
I. lindrothii	<b>JV2390 Epitype</b> , Finland	Betula	KJ399915
	JV3667, Finland	Betula	KJ399914
	JR&JV4735, Finland	Subalpine, B. pub	KJ399920
	JV10441, Finland	Suybalpine, B. pub	KJ399922
	BJ890909, Sweden	Meadow with Picea, B. pen	KJ399923
	Heinonen306-95, Finland	Subalpine, B. pub, S. sp.	KJ399927
	Höijer950815, Finland	Subalpine, B. pub	KJ399928
	JR&JV3739, Sweden	Mixed coniferous	KJ399919
	LAS77/188, Sweden	Mixed forest	KJ399926
	LAS77/386, Sweden	Mixed Quercus	KJ399929
	LAS83/170, Sweden	Mixed coniferous	KJ399918
	EL182-09, Norway	Picea	KJ399924
	EL&JV29161, Finland	Subalpine, B. pub, S. sp.	KJ399925
	EL161-12, Finland	Subalpine, B. pub	KJ399932
	EL158-12, Finland	Subalpine, B. pub	KJ399933
	EL87-04, Sweden	Mixed deciduous	KJ399916
	SJ86057, Sweden	S. cap	KJ399917
	Kuoljok07-15, Sweden	Picea forest	KJ399913

I. cf. lindrothii	Vesterholt870919, Sweden CLC1674, CO, USA CLC1678, CO, USA	Mixed coniferous Alpine	KJ399921 KJ399930
I. subbrunnea	<b>Kühner G388231 Type</b> , France AH15440, Spain AH30871, Spain AH30778, Spain AH15436, Spain AH29813, Portugal EL170-09, Norway EL334-10, Sweden EL195-12, Sweden EL459-13, Spain JV26705, Estonia JV28716, Sweden KK420-11, Italy	Alpine, S. gla Picea forest P. syl A. alba, P. unc A. alba, P. unc P. syl, Quercus ilex P. pinaster Mixed Picea Mixed Picea Mixed Picea P. syl, Cistus sp. P. syl, Betula P. syl, Picea Picea, Fagus, Corylus	KJ399931 KJ399934 KJ399946 KJ399936 KJ399937 KJ399943 KJ399940 KJ399935 KJ399939 KJ399945 KJ399941 KJ399938 KJ399944 KJ399942
I. fuscescentipes	<b>Kühner K69-328 Type</b> , France STZ6459, WA, USA JV5955, Finland	Alpine, Dryas Subalpine, coniferous Mixed coniferous	KJ399947 KJ399949 KJ399948
I. ohenojae sp. nov	<b>Ohenoja740802/1 Type</b> , Canada	Alpine, Dryas, Salix	KJ399955
I. monticola	<b>Kropp UTC248120 Type</b> , USA	Subalpine fir, Populus sp.	KJ538547
I. subpaleacea	<b>Kühner K73-346 Type</b> , France AH21361, Spain AH26709, Spain Ohenoja99-26, Russia	Alpine, Dryas, S. ser, Heli. Alpine, Dryas Alpine, Dryas, S. retusa Mixed Larix forest	KJ538548 KJ399950 KJ399951 KJ399952
I. catalaunica	<b>Singer IX34 Type</b> , Spain	A. alba	KJ399954
I. tjallingiorum	EL262-12, Sweden EL124-06, Sweden EL297-08, Hungary	Pinus, Populus Subalpine Salix, B. pub Mixed Pinus forest	KJ399956 KJ399957 KJ399958
I. phaeoleuca	EL313-12, France	Populus	KJ399959
I. splendens	STZ6549, WA, USA	Subalpine	KJ399960
Inocybe sp.	STZ5402, WA, USA	Subalpine	KJ399953

