Fibre caps across Europe: type studies and 11 new species of Inocybe (Agaricales, Basidiomycota)

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RESEARCH ARTICLE

Fibre caps across Europe: type studies and 11 new species of *Inocybe* (Agaricales, Basidiomycota)

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Abstract

Based on detailed morphological and genetic investigation, 11 new species of *Inocybe* (*I. abdita*, *I. alcis*, *I. carissima*, *I. cryptica*, *I. culicis*, *I. mecoana*, *I. mortenii*, *I. orioli*, *I. rangiferi*, *I. sepiana* and *I. turfae*) are described. Six of the new species are smooth-spored and five are nodulose-spored. The new species are compared to 18 type specimens, all of which are described here and for seven of which (partial) ITS sequences have been generated. For six species, namely *I. griseovelata*, *I. lacera*, *I. soluta*, *I. subcarpta, I. tarda* and *I. transitoria*, a lectotype, epitype or neotype was selected, and a description and a figure plate are provided for each of them. Based on our studies, we are convinced that *I. albofibrillosa* and *I. striatorimosa* are synonymous with *I. soluta*, while *I. aurantioumbonata* is synonymous with *I. tarda*. Furthermore, we affirm that *I. longicystis* is synonymous with *I. stellatospora.* All of the new species are supported by phylogenetic analyses. In summary, we here describe as new, verify the taxonomic status of, or provide or corroborate morphological concepts for 29 species of *Inocybe*.

Keywords: alpha taxonomy, epitypification, Inocybaceae, *Inocybe*, molecular systematics, neotypification nrITS, nrLSU, *RPB2*, type studies.

Zusammenfassung

Auf der Basis detaillierter morphologischer und genetischer Untersuchungen werden 11 neue Arten von *Inocybe* beschrieben (*I. abdita*, *I. alcis*, *I. carissima*, *I. cryptica*, *I. culicis*, *I. mecoana*, *I. mortenii*, *I. orioli*, *I. rangiferi*, *I. sepiana* and *I. turfae*). Sechs Arten sind glattsporig, fünf höckersporig. Die neuen Arten werden mit 18 Typusbelegen verglichen, die alle hier beschrieben werden. Für sieben von ihnen wurden ITS-Sequenzen generiert. Für sechs Arten, *I. griseovelata*, *I. lacera*, *I. soluta*, *I. subcarpta*, *I. tarda* und *I. transitoria* wurden Lecto- und/oder Epi-, respektive Neotypen ernannt und von allen wurde jeweils eine Beschreibung und Abbildungstafel vorgelegt. Auf Grund unserer Untersuchungen sind wir davon überzeugt, dass *I. albofibrillosa* und *I. striatorimosa* synonym sind mit *I. soluta*, während *I. aurantioumbonata* synonym ist mit *I. tarda*. Außerdem bestätigen wir, dass *I. longicystis* synonym ist mit *I. stellatospora*. Alle neuen Arten werden durch phylogenetische Analysen gestützt. Zusammenfassend werden in dieser Arbeit 29 Arten von *Inocybe* entweder neu beschrieben, ihr taxonomischer Status überprüft, beziehungsweise deren morphologisches Artkonzept erarbeitet oder bestätigt.

Contents

Introduction

The formerly large genus *Inocybe* (Fr.) Fr. was recently divided into seven genera (Matheny et al. 2020) within the monophyletic family *Inocybaceae* Jülich. Of these genera, *Inocybe* is still by far the largest with an estimated 850 species worldwide (Matheny et al. 2020)—a number that will undoubtedly rapidly increase as further studies proceed from parts of the world such as Africa (e.g., Aïgnon et al. 2021a, 2021b, 2021c; Buyck et al. 2021, 2022), India (Latha & Manimohan 2015, 2016, 2017; Latha et al. 2016) and China (Fan & Bau 2010, 2013, 2020; Fan et al. 2018; Mao et al. 2022), where DNA-based *Inocybe* studies only started recently. Only in the last five years, more than 200 new species have been described in the genus considering molecular data from all over the world (e.g., Bandini et al. 2017, 2019a, 2019b, 2019c, 2020a, 2020b, 2020c, 2021a, 2021b, 2021c, 2022a, 2022b; Esteve-Raventós et al. 2017, 2018; Matheny & Bougher 2017; Larsson et al. 2018a, 2018b; Matheny & Swenie 2018; Cripps et al. 2019b; Cervini 2021; Dovana et al. 2021; Mešić et al. 2021; Larsson & Vauras 2021).

In this article, only species of the genus *Inocybe* characterized by the presence of cheilocystidia and generally also pleurocystidia with more or less thick walls are treated. Species with this combination of characters do not occur in the other six genera of the family (Matheny et al. 2020). Six new species with smooth spores and five with nodulose spores are described here. In making this distinction, we remain fully aware of the fact that there is no clear morphological or genetic delimitation between species with smooth or with nodulose spores (see, e.g., Matheny 2009; Ryberg et al. 2010). Species with spores that can neither be called smooth nor nodulose are for instance the already described *I. ambigua* Romagn., *I. helobia* (Kuyper) Bandini, B. Oertel & U. Eberh, *I. pluppiana* Bandini, B. Oertel & U. Eberh., or *I. diabolica* Vauras. Nevertheless, the presence or absence of nodulose spores is a good, major character used in keys, although a third category with intermediate spores ought to be included in future keys based on morphological characteristics. Up to now, such a category is lacking in keys of this genus (see, e.g., Kuyper 1986; Stangl 1989; Bon 1997a, 1997b, 1998).

Just as the distinction between smooth-spored and nodulose-spored species can be fluent, the distinction between species that have metuloid cystidia only near the apex or in the upper half of the stipe and those that have such cystidia over the entire length of the stipe—a crucial question in existing keys (Kuyper 1986; Stangl 1989; Bon 1997a, 1997b, 1998)—is in several cases quite difficult. In fact, there are species that are pruinose over the entire length but only very sparely so in the lower half, sometimes giving the impression of being pruinose only near the apex. This is for instance the case of *I. perchtana* Bandini & B. Oertel (Bandini et al. 2020a) or *I. beatifica* Bandini & B. Oertel (Bandini et al. 2021c). Furthermore, there are species, such as *I. sindonia* (Fr.) P. Karst., the stipes of which are sometimes densely covered with metuloid caulocystidia down to the base and sometimes not (see Kuyper 1986; Bandini et al. 2022a). Strangely enough, this question is less a problem with nodulose-spored species, since the differentiation between species with an entirely pruinose stipe and those with metuloid caulocystidia only in the upper part is generally easier—at least where European species are concerned (DB, personal observation).

Even within its current limits (Matheny et al. 2020), *Inocybe* is a genus that includes species that are rather variable in their nuclear ribosomal genes. A satisfactory, comprehensive, modern infrageneric classification based on phylogeny has not been reached so far. Thus, we continue to refer to Bon's (1997a, 1997b, 1998) classification as a guide through this large genus.

The present article includes smooth- and nodulose-spored species which are pruinose only near the apex of the stipe and some that are pruinose over the entire stipe length. These would be classified in different sections according to the key of Bon (1997a, 1997b, 1998, see Discussion).

We observed in our own studies of species occurring in Central and Northern Europe that the biodiversity on more or less basic soils is far greater than on acidic soils (Bandini & Oertel 2021). In fact, the number of species occurring on strictly acidic soil—in woods, sandy heathland areas or in bogs—is quite limited. Characteristic species of those habitats are, for instance, *I. napipes* J.E. Lange, *I. stellatospora* (Peck) Massee, *I. lanuginosa* (Bull.) P. Kumm. and allies, or *I. pluppiana* and *I. soluta* Velen.—strangely enough, often species with nodulose spores. Species occuring on basic as well as on superficially (e.g., through needle litter) acidic soils, such as, e.g., *I. flocculosa* Sacc., *I. nitidiuscula* (Britzelm.) Lapl. or *I. ochroalba* Bruyl., thus presumably the most adaptable ones, are, not surprisingly, also among the most common and widespread ones, at least in Central Europe (DB, personal observation). Species that can only be found on strictly basic soil, such as for instance *I. tricolor* Kühner, *I. woglindeana* Bandini, Vauras & Weholt or *I. tiburtina* Bandini & G. Bandini, are again much less numerous, but in Central Europe still far more numerous than species restricted to acidic soil. In the North European boreal taiga, on the other hand, acidic pozolic soils and oligotrophic forests of the *Vaccinium myrtillus* type are much more frequent than basic/calcareous ones, and species such as *I. napipes*, *I. lacera* (Fr.) P. Kumm. and of the *I. lanuginosa* group rule the region (TEB, personal observation).

Despite many years of *Inocybe* studies, even in Central Europe it is still possible to find new species in strictly acidic habitats. *Inocybe lacera* is a species that tends to grow on acidic soil, and it is therefore often quite common in (raised) bogs or in sandy heathlands. Because of its laceroid spores it is one of the few species of the genus *Inocybe* that are included in illustrated mushroom books (e.g., Bresadola 1930; Michael et al. 1985; Phillips 1990; Breitenbach & Kränzlin 2000; Bon 2005; Consiglio & Papetti 2008; Gminder 2010; Arnolds et al. 2015). However, things are not as easy as they may seem, and even for this characteristic species there is another morphologically and genetically closely related species, *I. moravica* Hruby. This species was already described in 1930 by Hruby, but since it has almost been forgotten or has been mistaken for *I. lacera*, we here give a portrait of *I. moravica*, which can be found in the same habitat as *I. lacera*. Since no type existed of *I. lacera*, we here designate a neotype for this species.

Another species found on acidic soil, often in bogs with *Sphagnum* in Europe, is *I. turfae*, which is described below. Morphologically, it is similar to *I. lanuginosa* and *I. stellatospora*. The smooth-spored *I. mortenii* is probably also restricted to acidic soils, whereas *I. abdita*, *I. orioli* and *I. rangiferi* seem to prefer more basic soils. The holotypes of the species described below as new are from Finland, Germany, the Netherlands, Norway, Portugal and Spain, with paratypes from (besides the named countries) Austria, Malta and Sweden.

The selection of taxa considered in the analyses was largely driven by the species mentioned here, emended with taxa used by Matheny et al. (2020) to delimit the genus. Although the molecular infrageneric classification of the genus remains a challenge, in our experience, good, morphologically distinguishable *Inocybe* species do not share the same ITS sequence with other species of *Inocybe* [see Marchetti et al. (2021) for a diverging opinion, based however on data concerning other genera, such as, e.g., *Hebeloma*, *Cortinarius*, *Pluteus*].

Species delimitation followed the same principles used in earlier publications (Bandini et al. 2021c, 2022a), namely that species are described as new if they differ from existing species by the combination of at least three independent characters that are constant among representatives of the new species, and the representatives of the new species are monophyletic in phylogenetic ITS (ITS + LSU) analyses. Constant ecological differences between new and existing species are considered as meaningful, but neither ecological nor ITS differences were used unless supported by morphological differences. Taxa were considered as synonymous if the overall impression of the species was very similar, if no constant characters could be found that separated the two species, and if neither pronounced ecological preferences nor molecular data (if available) indicated that the two species might be cryptic (Bandini et al. 2021c).

Epitypifications were carried out in cases in which the appraisal of the status of more recent names required the clarification of old names and the existing types did not show sufficient characters for species distinction. Important characters for species identification and delimitation that are often not observable in old material and not explicitly mentioned in species descriptions are associated with the caulocystidia at the top of the stipe. The features of the caulocystidia directly below the lamellae form a character that we started to use relatively recently (Bandini et al. 2017), but that we have since found to be very useful for species recognition in *Inocybe*. For all species newly epitypified, holo- or lectotype studies were published in Bandini et al. (2021c) or are published here. Studies of the selected epitypes are included here, mentioning all characters that are important for the recognition of the species. Although DNA sequence data are not crucial for the delimitation of the species epitypified here (and thus not permissible as a reason for epitypification), we took care to select material from which sequence data had been generated.

Material and methods

Morphological study

Fresh materials were obtained on forays in Austria, Finland, Germany, Malta, the Netherlands, Norway, Portugal, Sweden, Spain and Switzerland between 1986 and 2021. Type specimens were borrowed from various herbaria (see Acknowledgements). For fresh collections, the relevant macroscopic details, i.e., habit, size and shape of the basidiomata, colour and surface of the pileus, number and colour of the lamellae, size, colour, surface and base of the stipe, smell and colour of flesh, colour of exsiccata, habitat and surrounding trees, were noted.

For all collections—if possible in the fresh, otherwise in the dried state—basidia, spores, hymenial cystidia, caulocystidia, etc. were examined by D. Bandini with a Leica DM-750 microscope in a water and 3% KOH solution, at 400 and 1000 magnifications. Photographs of microscopic details were taken by D. Bandini with a Zeiss AxioCam ERc5s. Measurements of spores and cystidia were determined using a Zeiss Axiovision version 4.8. Cystidia were measured without crystals and basidia without sterigmata. The size of all elements measured is given as length × width. The Q value equals the ratio of spore length to spore width (calculated for each spore). The number of spores or cystidia measured is included in the descriptions.

Unless indicated otherwise, all pictures of fresh collections were taken by by D. Bandini with a Panasonic Lumix GH2 with Leica DG Macro-Elmarit 1:2.8/45 mm lens. For the determination of the colour temperature, a calibration card was photographed together with the fresh collections at the collection site. The RAW files were developed with Silkypix Developer Studio 4.0.

Other photographs were taken by: J. Vauras with an Olympus OM-1 N equipped with an O=M Zuiko Macro 1:3.5 50 mm lens (Figs. 3b, 14b); F. J. Rodríguez with a Nikon D300S equipped with a Micro-Nikkor 105 mm lens (Fig. 5a, b); V. Fachada with a Canon EOS Kiss X4 equipped with a Tamron SP 1:2.5/90 mm lens (Fig. 9a); S. Mifsud with a Canon EOS 750D equipped with a Canon EFS 18-135mm lens (Fig. 9b); Ø. Weholt with an Olympus Tough Tg-5 (Fig. 11a).

All drawings of microscopic details were done by D. Bandini, with the exception of those of *I. decipiens* Bres. (Fig. 21f) and *I. pholiotinoides* Romagn. (Fig. 22c), which were done by J. Vauras.

Colour codes are taken from Munsell (2009, as “Mu”), terminology follows Vellinga (1988) and Kuyper (1986).

Molecular study

DNA extraction, PCR and sequencing of nrDNA ITS and LSU followed protocols published by Cripps et al. (2019a) and Bandini et al. (2021c). For *Inocybe lacera* and *I. moravica*, *RPB2* sequences were obtained (if possible) according to the protocol given in Bandini et al. (2022a). For epitypes and other material processed in Stuttgart, DNA extracts are available at the Staatliches Museum für Naturkunde for the generation of sequences from other DNA regions as needed.

Bidirectional sequencing was carried out by LGC Genomics (Berlin, Germany). Sequence editing and assembly was done in Sequencher v. 4.9 (Genecodes). Newly generated sequences were submitted to GenBank with acc. no. MF782552, MK584751, MN319698, OM760512, OM760514, OM971871, OM971872, OM985894, ON000207, ON010592, ON010593, ON359948, OP164016–OP164108, OP186965–OP186975 and OP218359. Sequences for GenBank acc. no. OM760512, OM760514, OM971871, OM971872, OM985894, ON000207, ON010592, ON010593 and OP218359 were generated by Alvalab (Oviedo, Spain).

Sequences were blasted against GenBank (Johnson et al. 2008) and UNITE (Kõljalg et al. 2005) in order to find additional records for the species treated here and putative close relatives. For every species (or species hypothesis—see Kõljalg et al. 2005) included, we selected representative sequences for the tree analyses by length (inclusion of LSU), quality and preferred, if available, sequences from studied material, i.e., from other molecular systematic studies. Sequence similarity or identity values were directly copied from BLAST results. Percent values given in the text refer to ITS1-5.8S-ITS2 or fewer positions if the complete sequence was unavailable for at least one of the sequences. Conspecificity between public sequences and sequences of types was assumed if sequence variation was 1% or less. This value was selected to be smaller than the 98.5% cut-off value proposed by several authors (Lücking et al. 2020 and references therein), to be used as general cut-off values for ITS variation to distinguish between species. Sequence variation attributed to long indels, stretches of N (i.e., in cases in which the ITS was obtained in two amplicons, not allowing to read the entire ITS) or obviously wrong sequence reads in the beginnings or ends of published sequences were ignored. BLAST searches were done on 6 May 2021. In contrast to earlier publications, we did not normally report on EcM (ectomycorrhizae) or soil sample sequences unless environmental sequences were the only matches available. Information on distribution in excess to the information from our own data was obtained from UNITE species hypotheses (sh, Kõljalg et al. 2013, vs 8.3, Abarenkov et al. 2021). Correspondence of species with UNITE sh was assumed if the query sequence had a 100% or 99.7% matching sequence present in the sh.

For species described as new, we aimed at having at least three collections sequenced for ITS and LSU, provided sufficiently many collections were available for sequencing. Representatives of published sequences from collections putatively belonging to these taxa or very close relatives of these taxa (i.e., > 97% similar in BLAST results) were also included. For species that were synonymized here, we included sequence data from types (if available) or from material that had been morphologically analyzed and considered to represent the same species.

The initial alignment was carried out in Mafft vs. 7 using the E-INS-i option (Katoh et al. 2005, 2019), adding the ITS and LSU sequences considered by Matheny et al. (2020) for *Inocybe* to our dataset. Sequences from Matheny et al. (2020) that did not help to further elucidate the phylogenetic position of the taxa considered in our study were removed for the final analysis, without changing the alignment. *Pseudosperma spurium* (Jacobsson & E. Larss.) Matheny & Esteve-Rav. was used for rooting.

The entire alignment was treated as a single partition. Because our main goal was species recognition and not phylogenetic reconstruction, all positions were retained in the analysis. ML analyses were run in IQ-TREE v. 1.6 (Nguyen et al. 2015) online (Trifinopoulos et al. 2016), with standard settings apart from setting the perturbation strength to 0.3 and the stopping rule to 200. Branch support was obtained through 5000 replicates of UFBoot (Minh et al. 2013; Hoang et al. 2018) and SH-aLRT (Guindon et al. 2010).

Bayesian inference (BI) was done in MrBayes 3.2.7a (Ronquist et al. 2012) using BEAGLE (Ayres et al. 2012) on CIPRES (Miller et al. 2010). The BI analysis was carried out in two runs with four chains including one heated chain each, using the GTRINVGAMMA model and a uniform prior and sampling one tree of each run every 1000 generations. The analysis was stopped employing default stoprule parameters after 3.205 million generations when convergence was reached (Ronquist et al. 2011). The first 25% of trees were discarded as burn-in.

The tree was visualized using FigTree v. 1.4.4 (Rambaut 2006–2018). Support values were noted as SH-aLRT support [%], ultrafast bootstrap (ufb) support [%] and BI posterior probability (pp). SH-aLRT support ≥85% and ufb support ≥95% and pp ≥0.95 are indicated. Alignment and tree files are available via TreeBASE (study id TB2:S29819).

Specimen depositories

Herbarium acronyms are according to Holmgren et al. (1990) except D. B., which refers to the private herbarium of Ditte Bandini.

Results

In the taxonomy section, all species are listed that were either newly described, newly typified or for which type material has been re-studied and illustrated. Species that are synonymized with other taxa are listed under the name accepted here.

Sequences included in the phylogenetic analyses (Fig. 1) are listed in Appendix 1. The final alignment included 278 sequences and 2045 positions. The result of the ML analysis is depicted in Fig. 1. The consensus tree resulting from the BI analysis was generally similar to the ML result and differed only in clades not supported in either of the analyses. Differences were located mainly in the backbone of the tree and in the clade around *Inocybe lacera*. All species described here were resolved as *Inocybe* species. The relationships between several of the subclades indicated in Fig. 1 remained unresolved. Despite this, in the upper part of the tree, from *I. prisca* Bandini & B. Oertel (Fig. 1 part 1, close to the top) to the bottom of Fig. 1 part 3, all species have nodulose or laceroid spores, with the exception of the members of the smooth-spored temperate austral clade (“STAC”) ss. Matheny et al. (2020). The clade starting with *I. perchtana* (top of Fig. 1 part 3 right down to the bottom of the tree, *I. mortenii*) includes only smooth-spored species, including the members of what Matheny et al. (2020) termed the smooth-spored temperate boreal clade (STBC). The clade starting in Fig. 1 part 4 received 99%/97%/1 support. However, the main focus of this study is on species recognition and delimitation.

One of the newly described species, *I. mecoana*, was not monophyletic in relation to sequences (two environmental sequences and a sequence identified as *I. pruinosa* R. Heim) in the BI tree. Although there is a clade corresponding to *I. mecoana* in the ML tree in Fig. 1, it is lacking support. All other species described here as new were monophyletic in relation to their closest known relatives and all received support from at least two of the three support measures used. All species apart from *I. abdita* and *I. alcis* received full (100%/1) support at least from ufb and pp. *Inocybe abdita* received full support only from ufb and *I. alcis* received support from all three criteria, albeit not full.

Among the previously described species recognized here as current, only the distinction between *I. lacera* and *I. moravica* is somewhat precarious. While the core groups of sequences for each species (nearly all with ITS and LSU) are fully supported by ufb and pp, there is a group of ITS-only sequences tentatively named *I.* cf. *moravica* that form a clade with the core of *I. moravica* only supported by 95% ufb and no other support. From the material we had available for further study, for five collections of *I. lacera* and six of *I. moravica*, *RPB2* data were obtained. The respective collections are indicated in Fig. 1 by diamond symbols. In a single locus ML analysis of the *RPB2* data (result not shown), the same clades formed as in Fig. 1 and the split was fully supported. Three positions were in the alignment that were constant within clades and different between clades, but the overall variation in the dataset was much higher (66 positions out of 783with sequence variation).

Taxonomy

Inocybe abdita Bandini & U. Eberh., **sp. n.**
(Fig. 2; MycoBank: MB 845160)

Etymology

Named “abdita” (Latin “hidden”), because the species was until now hidden and as such undetected as a new species.

Diagnosis

Inocybe abdita **sp. n.** has a brownish to nut-brown pileus colour, a whitish velipellis, a rather smooth to minutely innately fibrillose pileus surface, rather small spores, measuring 6.2–9.3 µm (av. 7.8 µm) × 5.0–7.3 µm (av. 5.9 µm), and rather short, predominantly (sub)fusiform hymenial cystidia and pleurocystidia measuring 29–61 µm (av. 45 µm) × 10–20 µm (av. 14 µm). It can be recognized by the combination of the above characters and differs in its ITS sequence from other species, such as the closely related *I. transitoria*.

Holotype

GERMANY, Baden-Württemberg, Karlsruhe, TK25 6916/3, alt. 117 m, *Picea abies*, 14 Sep. 2014, leg. D. Bandini (holotype STU SMNS-STU-F-0901691; isotypes priv. herb. D. B. DB14-9-14-14, TUR-A 209531).

Description

Pileus 15–30 mm wide, at first (sub)conical, later convex or expanded, with more or less prominent broad umbo, margin decurved when young, with age straight or uplifted and then depressed around the centre; young basidiomata covered with a thin layer of a whitish velipellis, visible

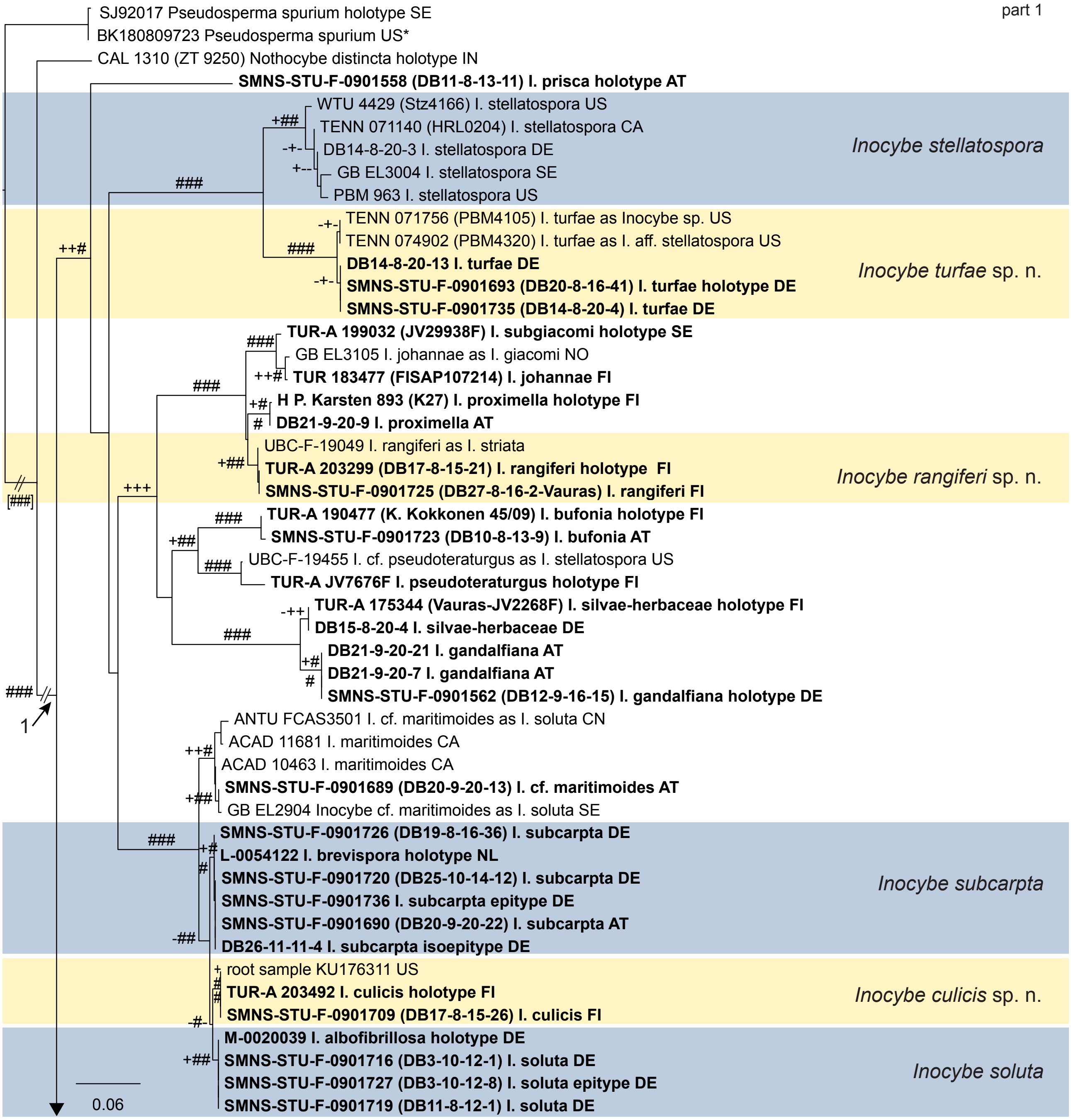

Fig. 1. ML topology ITS and partial LSU sequences of the species of *Inocybe* treated or discussed here. *Pseudosperma spurium* (Jacobsson & E. Larss.) Matheny & Esteve-Rav. was used for rooting. Clades of species that are described here as new are highlighted in yellow; species clades for which type material is described here are highlighted in blue. Sequences taken from Matheny et al. (2020) are indicated by *. For collections indicated by ♦, *RPB2* data is available. Material studied is in bold font. Arrow 1: *Inocybe* (genus). Support values from 5,000 replicates of the SH-like approximate likelihood ratio test (SH-aLRT), 5,000 replicates of ultrafast bootstrap (ufb) and BI posterior probabilities (pp) are indicated at the branches in that order, with # indicating 100% or 1 support and + indicating values ≥ 80 % (SH-aLRT), ≥ 95% (ufb) or ≥ 0.95 (pp).

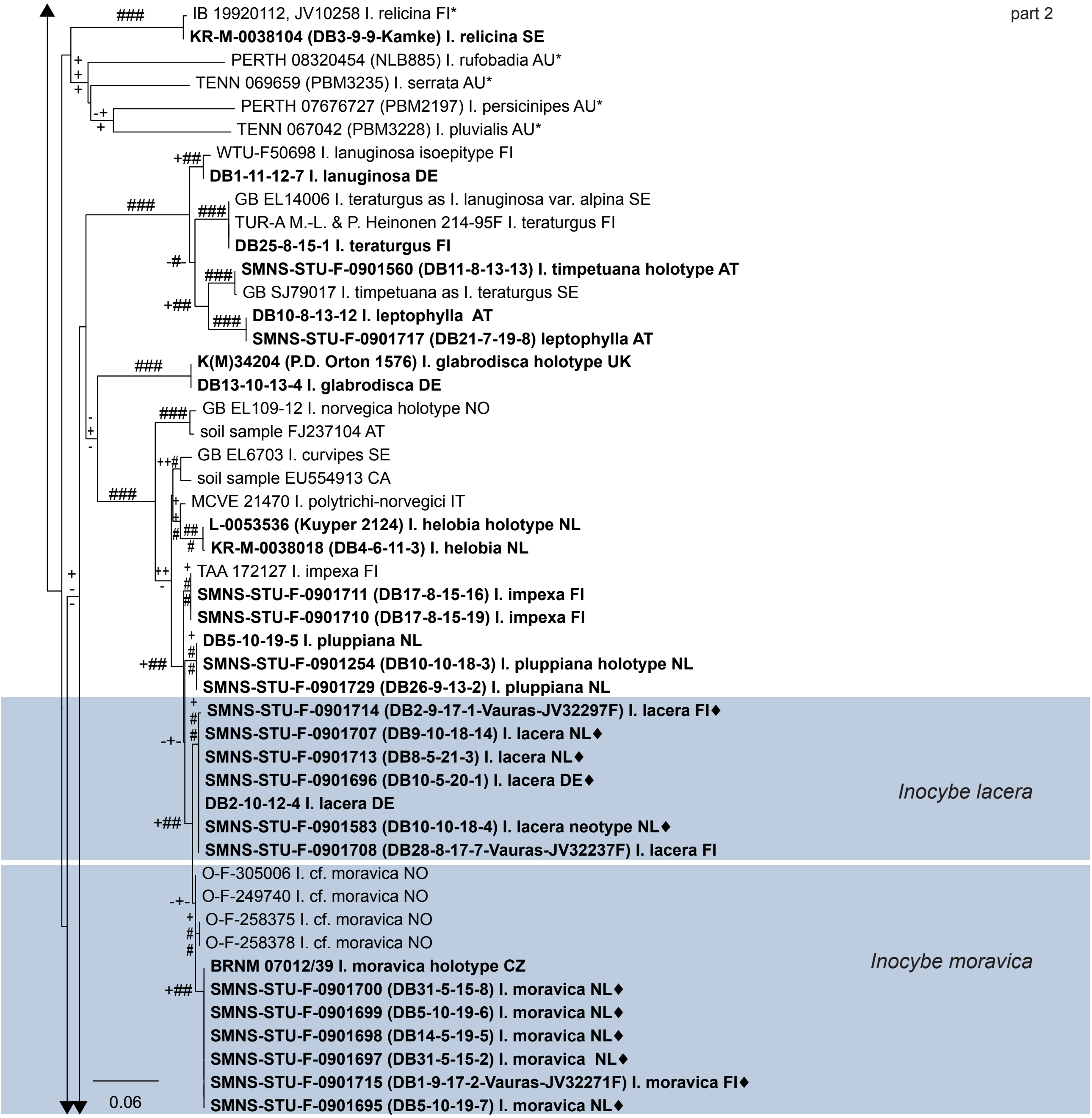

Fig. 1 (cont.)

also later at the centre; colour often uniformly brownish to nut-brown in different nuances (Mu 5YR 6/3–6/6, 5/3–5/6; 7.5YR 6/4–6/6), mostly without reddish tinge, but sometimes with greyish tinge or fine darker fibrils on paler ones; surface glabrous or shiny even when old, otherwise finely rim(ul)ose to minutely innately fibrillose; young basidiomata rimmed with a whitish cortina; often a bit greasy and therefore with adhering soil particles. *Lamellae* rather crowded (c. 70–80, l = 1–3), adnate to emarginate adnate with (sub)decurrent tooth, (sub)ventricose, whitish to greyish-brown, edge fimbriate, whitish. *Stipe* 30–60 × 3–6 mm, cylindrical or widening towards the base, base with a more or less marginate bulb, when young entirely covered with whitish tomentum appearing like pruina, later glabrous, whitish to light brown, lower part sometimes brownish, bulb whitish; pruinose only

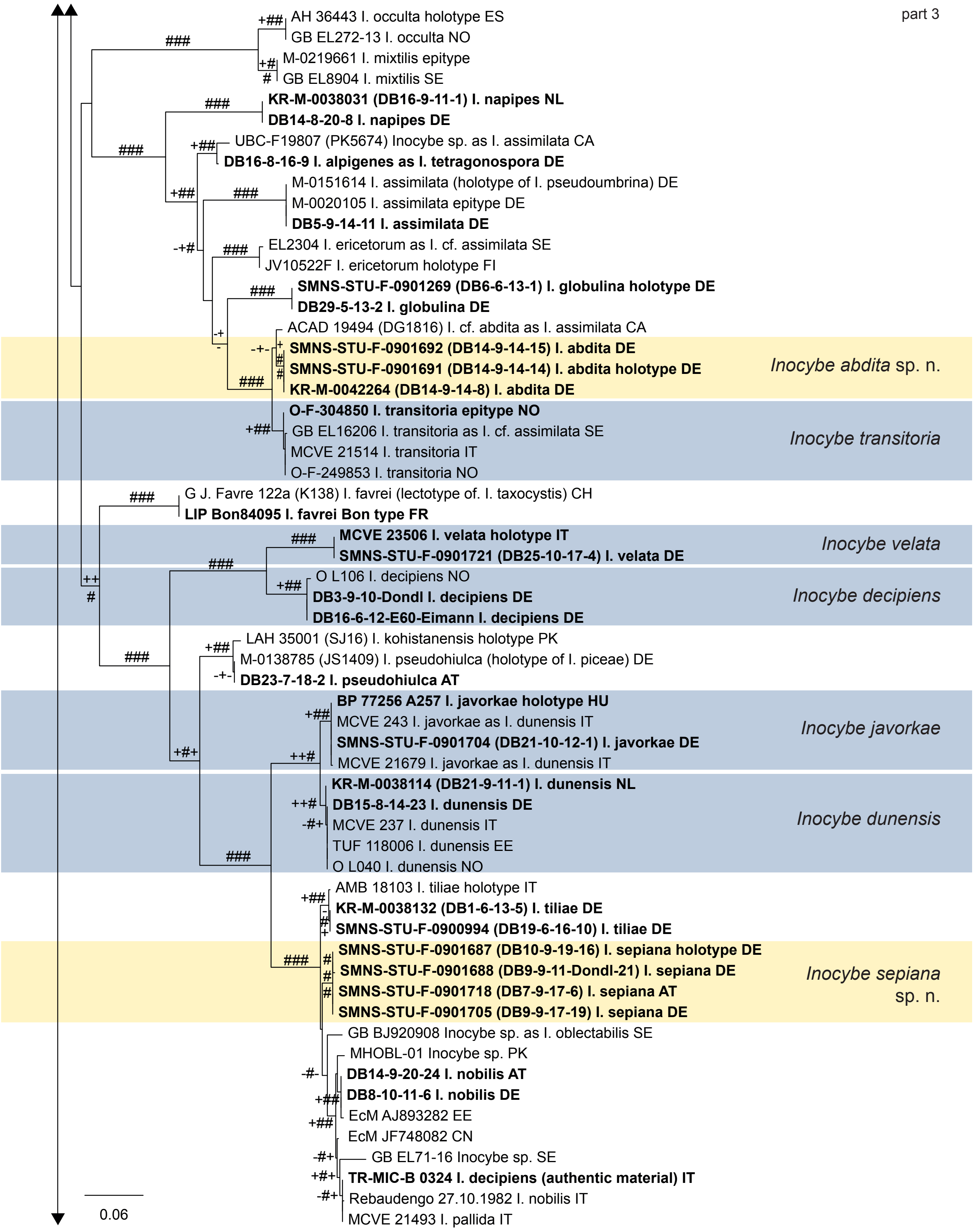
part 3
AH 36443 I. occulta holotype ES
GB EL272-13 I. occulta NO
M-0219661 I. mixtilis epitype
GB EL8904 I. mixtilis SE
KR-M-0038031 (DB16-9-11-1) I. napipes NL
DB14-8-20-8 I. napipes DE
UBC-F19807 (PK5674) Inocybe sp. as I. assimilata CA
DB16-8-16-9 I. alpigenes as I. tetragonospora DE
M-0151614 I. assimilata (holotype of I. pseudoumbrina) DE
M-0020105 I. assimilata epitype DE
DB5-9-14-11 I. assimilata DE
EL2304 I. ericetorum as I. cf. assimilata SE
JV10522F I. ericetorum holotype FI
SMNS-STU-F-0901269 (DB6-6-13-1) I. globulina holotype DE
DB29-5-13-2 I. globulina DE
ACAD 19494 (DG1816) I. cf. abdita as I. assimilata CA
SMNS-STU-F-0901692 (DB14-9-14-15) I. abdita DE
SMNS-STU-F-0901691 (DB14-9-14-14) I. abdita holotype DE
KR-M-0042264 (DB14-9-14-8) I. abdita DE
Inocybe abdita sp. n.
O-F-304850 I. transitoria epitype NO
GB EL16206 I. transitoria as I. cf. assimilata SE
MCVE 21514 I. transitoria IT
O-F-249853 I. transitoria NO
Inocybe transitoria
G J. Favre 122a (K138) I. favrei (lectotype of. I. taxocystis) CH
LIP Bon84095 I. favrei Bon type FR
MCVE 23506 I. velata holotype IT
SMNS-STU-F-0901721 (DB25-10-17-4) I. velata DE
Inocybe velata
O L106 I. decipiens NO
DB3-9-10-Dondl I. decipiens DE
DB16-6-12-E60-Eimann I. decipiens DE
Inocybe decipiens
LAH 35001 (SJ16) I. kohistanensis holotype PK
M-0138785 (JS1409) I. pseudohiulca (holotype of I. piceae) DE
DB23-7-18-2 I. pseudohiulca AT
BP 77256 A257 I. javorkae holotype HU
MCVE 243 I. javorkae as I. dunensis IT
SMNS-STU-F-0901704 (DB21-10-12-1) I. javorkae DE
MCVE 21679 I. javorkae as I. dunensis IT
Inocybe javorkae
KR-M-0038114 (DB21-9-11-1) I. dunensis NL
DB15-8-14-23 I. dunensis DE
MCVE 237 I. dunensis IT
TUF 118006 I. dunensis EE
O L040 I. dunensis NO
Inocybe dunensis
AMB 18103 I. tiliae holotype IT
KR-M-0038132 (DB1-6-13-5) I. tiliae DE
SMNS-STU-F-0900994 (DB19-6-16-10) I. tiliae DE
SMNS-STU-F-0901687 (DB10-9-19-16) I. sepiana holotype DE
SMNS-STU-F-0901688 (DB9-9-11-Dondl-21) I. sepiana DE
SMNS-STU-F-0901718 (DB7-9-17-6) I. sepiana AT
SMNS-STU-F-0901705 (DB9-9-17-19) I. sepiana DE
Inocybe sepiana sp. n.
GB BJ920908 Inocybe sp. as I. oblectabilis SE
MHOBL-01 Inocybe sp. PK
DB14-9-20-24 I. nobilis AT
DB8-10-11-6 I. nobilis DE
EcM AJ893282 EE
EcM JF748082 CN
GB EL71-16 Inocybe sp. SE
TR-MIC-B 0324 I. decipiens (authentic material) IT
Rebaudengo 27.10.1982 I. nobilis IT
MCVE 21493 I. pallida IT
0.06

Fig. 1 (cont.)

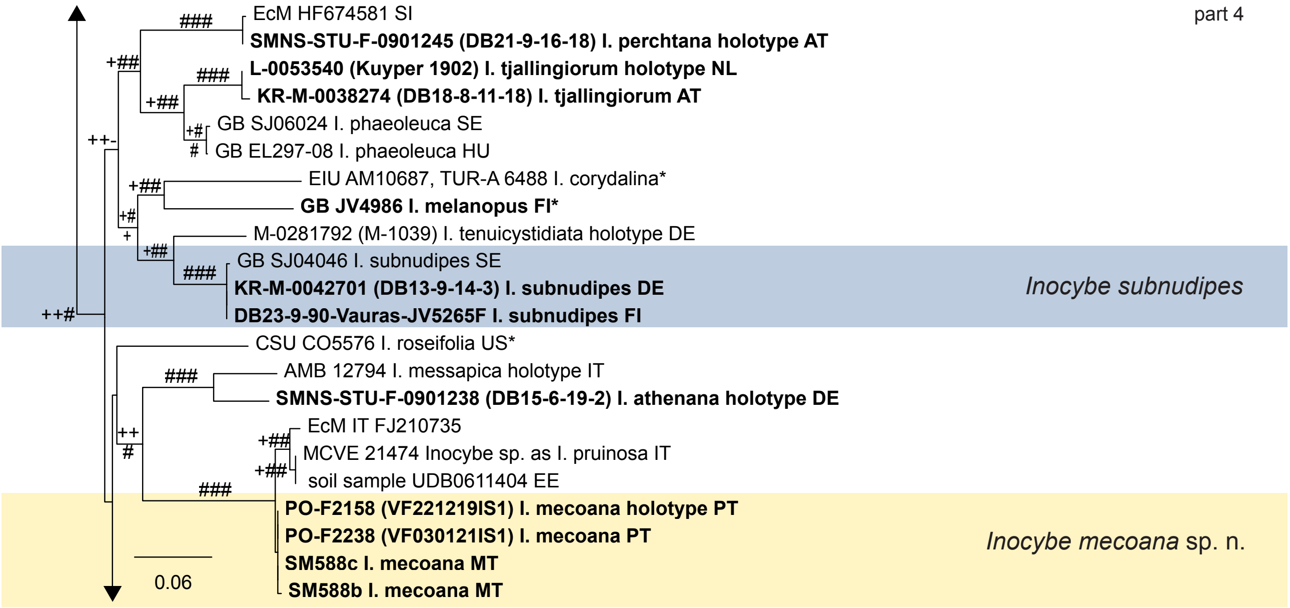

Fig. 1 (cont.)

near the apex of the stipe. *Context* whitish in the pileus, brownish in the cortex of the stipe. *Smell* agreeable, faintly aromatic. *Colour of exsiccata* pileus brown with reddish hue (Mu 7/5YR 4/4–4/6), lamellae and stipe concolourous or a little lighter in colour, no darkening or blackening on drying.

Spores 6.2–9.3 µm (av. 7.8 µm, SD 0.5 µm) × 5.0–7.3 µm (av. 5.9 µm, SD 0.4 µm); Q = 1.1–1.6 (av. 1.3, SD 0.1) (n = 120 of 3 coll.) (n = 40)], nodulose with 7–11 rather strongly protruding obtuse nodules. *Basidia* 24–30 × 9–13 µm, generally 4-spored. *Lamella edge* composed of cheilocystidia and numerous colourless, (sub)clavate or subglobose, thin-walled paracystidia. *Pleurocystidia* 29–61 µm (av. 45 µm, SD 8 µm) × 10–20 µm (av. 14 µm, SD 2 µm); Q = 1.7–4.7 (av. 3.2, SD 0.5) (n = 45 of 3 coll.), predominantly (sub)fusiform, but also (sub)clavate, seldom subcylindrical, mostly neckless and with short pedicel, mostly with crystals, walls often quite thick, up to 3.5 (4.5) µm thick at the apex, almost colourless to very pale yellowish-greenish with 3% KOH. *Cheilocystidia* similar in appearance and size. *Pileipellis* constituted by an epicutis made up of parallel hyphae 4–10 µm wide, with encrusting and parietal brownish pigment, subcutis with wider and paler to colourless elements. *Caulocystidia* only near the extreme apex of the stipe, hyphoid segmented elements with subconical apex, last element sometimes with thickened walls. *Clamp connections* abundant in all tissues.

Habitat and distribution

Inocybe abdita **sp. n.** was found in a park-like environment on basic soil. The type collection was associated with *Picea abies* as the only possible host, while *Carpinus betulus* was also present in the vicinity of the other two collections. Apart from our own collections, we do not know of other specimens.

Additional specimens examined

GERMANY, Baden-Württemberg, Karlsruhe, TK25 6916/3, alt. 117 m, *Picea abies*, *Carpinus betulus*, 14 Sep. 2014, leg. D. Bandini (DB14-9-14-8). Ibidem, at some distance from former location, *Picea abies*, *Carpinus betulus*, 14 Sep. 2014, leg. D. Bandini (SMNS-STU-F-0901692, dupl. DB14-9-14-15).

Notes

Inocybe abdita **sp. n.** is characterized by a brownish to nut-brown pileus colour, whitish velipellis, rather smooth, up to finely rim(ul)ose to minutely innately fibrillose pileus surface, comparatively small spores and rather short, predominantly (sub)fusiform hymenial cystidia. On first sight it could be mistaken for *I. assimilata* Britzelm., which however differs, e.g., by a greyish velipellis, a (sub)hygrophanous pileus surface and on average longer hymenial cystidia (see, e.g., Britzelmayr 1881; Saccardo 1887; Stangl 1989; Bandini et al. 2017). *Inocybe globulina* Bandini & B. Oertel usually has a darker brown pileus colour, a (sub)globose bulb, on average longer spores and longer hymenial cystidia (Bandini et al. 2020c), and *I. napipes* differs, e.g., by a napiform bulb, larger spores with more prominent nodules, larger hymenial cystidia with thinner walls and habitat generally on moist acidic soil (see, e.g., Lange 1917; Stangl 1989; Ludwig 2017). *Inocybe gandalfiana* Bandini & B. Oertel can be distinguished from *I. abdita*, e.g., by a prominent umbo, a (sub)-

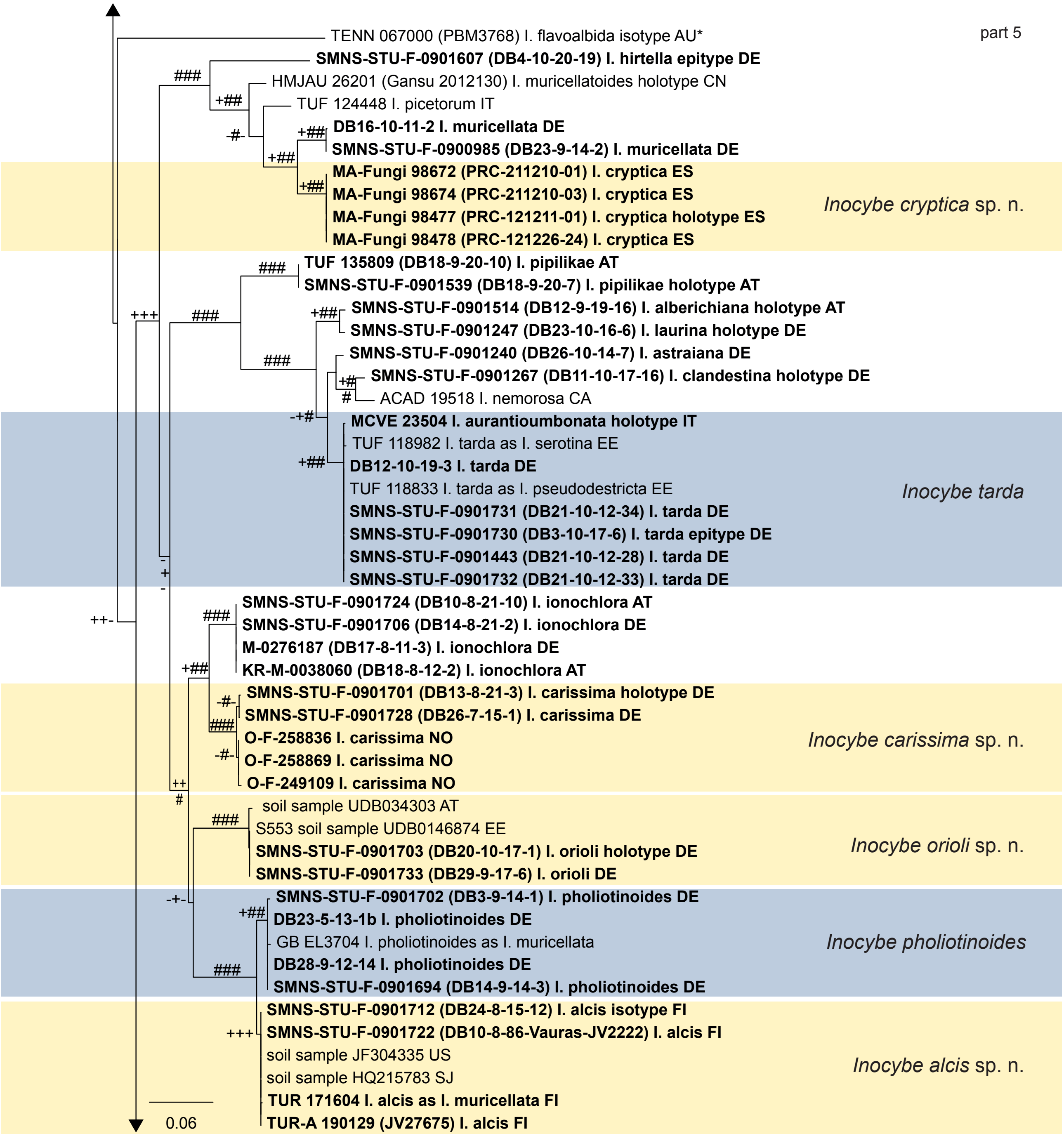

Fig. 1 (cont.)

hygrophanous pileus surface, and larger spores (Bandini et al. 2021a), whereas *I. silvae-herbaceae* Kokkonen & Vauras differs, e.g., by the missing velipellis, larger spores and often subutriform hymenial cystidia with thinner walls. Furthermore, this species normally occurs on acidic moist terrain (Kokkonen & Vauras 2012; DB, personal observation). *Inocybe glabrodisca* P.D. Orton has a greyish velipellis, on average larger spores and longer

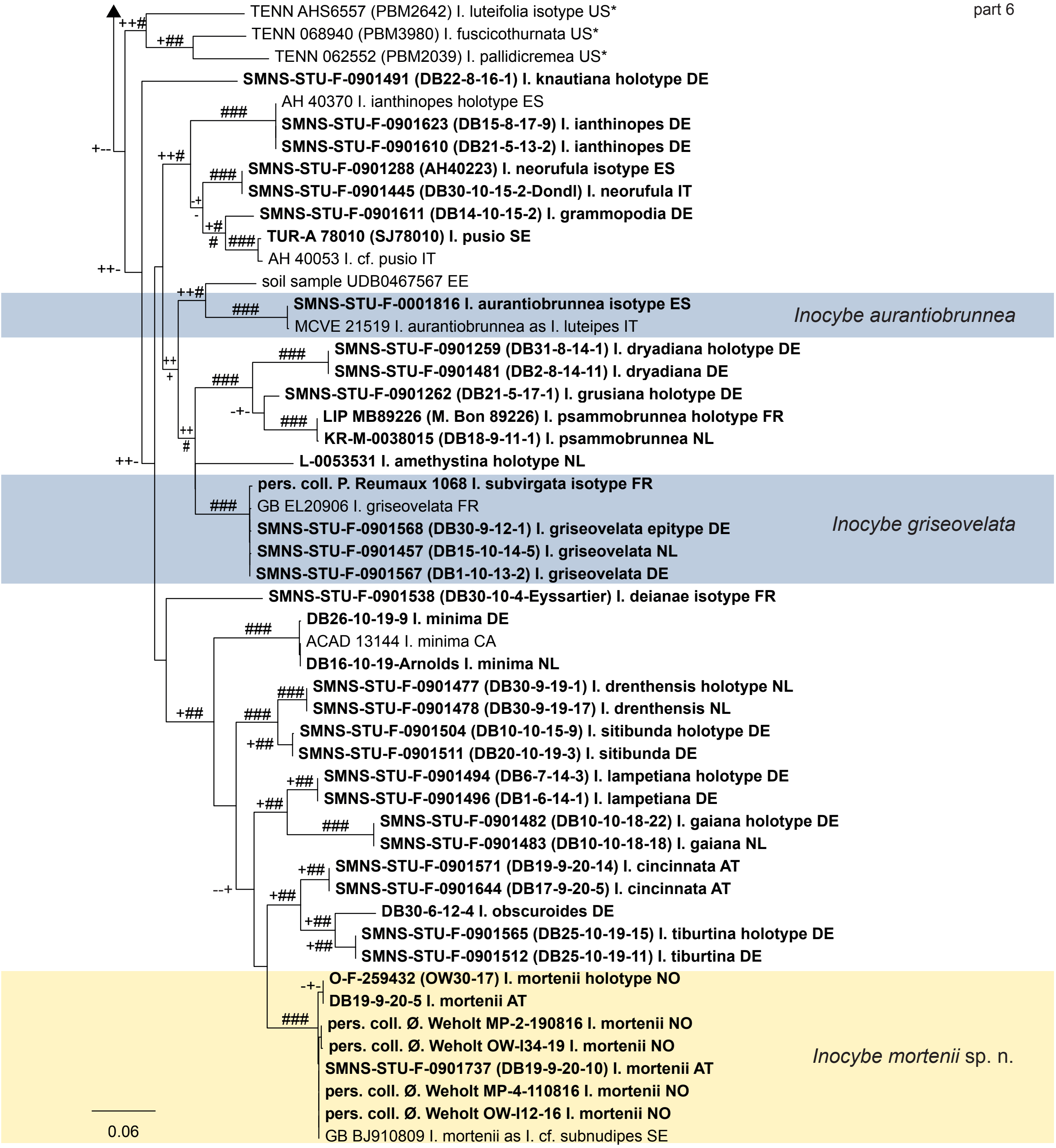

Fig. 1 (cont.)

hymenial cystidia as well as non-segmented caulocystidia (ORTON 1960). *Inocybe transitoria* (Britzelm.) Sacc., distinguishable by its darker brown pileus colour, a subhygrophanous pileus surface, on average narrower spores and shorter hymenial cystidia, is the species most similar morphologically as well as in terms of ITS similarity (just below 98.5%). *Inocybe transitoria* grows with frondose trees (BRITZELMAYR 1881; STANGL 1989).

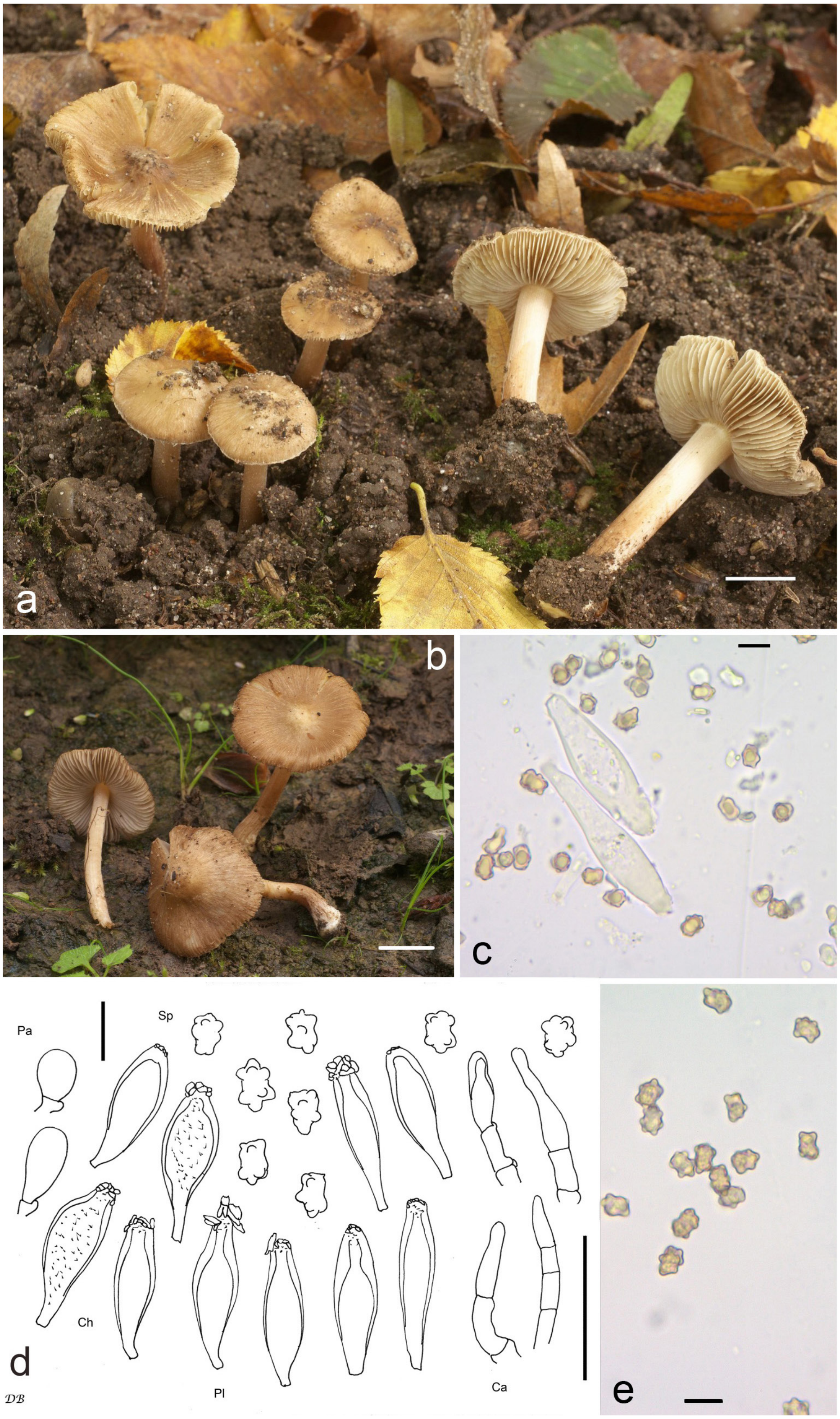

Fig. 2. *Inocybe abdita* **sp. n.** – **a.** Holotype; scale bar: 1 cm. **b.** Coll. DB14-9-14-15; scale bar: 1 cm. **c.** Cheilocystidia (coll. DB14-9-14-8); scale bar: 10 µm. **d.** Microscopic characters (holotype); Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm. **e.** Spores (coll. DB14-9-14-8); scale bar: 10 µm.

Inocybe albofibrillosa → ***Inocybe soluta***

(Fig. 21a)

Inocybe alcis Bandini, Vauras & B. Oertel, **sp. n.**

(Fig. 3; MycoBank: MB 845161)

Etymology

Named "alcis" because of the moist northern habitat of the species where elks (*Alces alces*) roam.

Diagnosis

Inocybe alcis **sp. n.** has dark red brown to reddish tinged dark brown, sometimes bicoloured pileus, a glabrous to minutely rimulose pileus surface, at first strikingly white lamellae, smooth spores measuring 8.5–11.6 µm (av. 9.8 µm) × 5.0–7.0 µm (av. 5.9 µm) and (sub)lanceolate to (sub)fusiform hymenial cystidia, pleurocystidia measuring 51–82 µm (av. 71 µm) × 10–18 µm (av. 14 µm), and walls which strongly react with 3% KOH. It can be recognized by the combination of the above characters and differs in its ITS sequence from other smooth-spored species, such as *I. pholiotinoides*.

Holotype

FINLAND, Kuusamo municipality, Vuotunki, at riverside of Kuusinkijoki river, S of Naavakangas, *Pinus sylvestris*, *Betula* sp., *Picea abies*, *Alnus incana*, *Prunus padus*, alt. 220 m, WGS84 66.18971, 29.59218, 24 Aug. 2015, leg. D. Bandini, B. Oertel & J. Vauras (holotype TUR-A 203433; isotypes STU SMNS-STU-F-0901712, priv. herb. D. B. DB24-8-15-12).

Description

Pileus 5–15 mm wide, at first (sub)conical, later subconical to expanded, at first without, later with rather low large umbo, margin at first slightly incurved, later straight or even uplifted, and then pileus depressed around the umbo; young basidiomata with faint greyish remnants of a velipellis at least at the umbo; colour dark red brown to dark brown with reddish hue (Mu 5YR 4/3–4/6, 3/3–3/4; 7.5YR 4/4–4/6, 3/4), but sometimes much paler up to (almost) ochraceous towards the margin and therefore appearing bicoloured; surface entirely glabrous to minutely rimulose also when older, but towards the margin sometimes slightly effaced; no remnants of a cortina observed. *Lamellae* (sub)distant (c. 20–25, l = 1–3), emarginate adnate, (sub)ventricose, at first pure white, later greyish, then ochraceous with greyish hue; edge fimbriate, whitish to concolourous. *Stipe* 10–25 × 1–1.5 mm, cylindrical or curved, sometimes slightly thickened towards the base, glabrous to slightly longitudinally striate, at first beige, later pale yellowish to pale brownish, in parts even darker brown to red-brown; pruinose on the entire length of the stipe. *Context* whitish to pale brown in the pileus and the stipe. *Smell* (sub)spermatic, at least when cut. *Colour of exsiccata* pileus brown to dark brown (Mu 10YR 5/3–5/4, 3/4–3/6), lamellae and stipe concolourous or a little lighter in colour, no darkening or blackening on drying.

Spores 8.5–11.6 µm (av. 9.8 µm, SD 0.6 µm) × 5.0–7.0 µm (av. 5.9 µm, SD 0.4 µm); Q = 1.4–2.0 (av. 1.7, SD 0.1) (n = 120 of 3 coll.), smooth, (sub)amygdaloid, partially oblong and partially almost ovoid, without or with only faint suprahilar depression, apex mostly (sub)obtuse, sometimes with indistinct pseudoporus. *Basidia* 22–28 × 7–9 µm, generally 4-spored, seldom also 2-spored, and then spores up to 12.5 µm. *Lamellae edges* composed of cheilocystidia and numerous colourless, (sub)clavate, cylindrical or subglobose, thin-walled paracystidia. *Pleurocystidia* 51–82 µm (av. 71 µm, SD 7 µm) × 10–18 µm (av. 14 µm, SD 2 µm); Q = 3.5–7.2 (av. 5.1, SD 0.9) (n = 45 of 3 coll.), mostly (sub)lanceolate (sub)fusiform, with short or long, sometimes undate neck and short pedicel, at the apex generally wide, apex usually crystalliferous, walls up to 4.0 µm thick at the apex, but quite incoherently, sometimes rather thin- and sometimes thicker-walled, intensely yellow-green with 3% KOH. *Cheilocystidia* similar in size, but somewhat more variable in shape. *Pileipellis* constituted by an epicutis made up of parallel hyphae 4–10 µm wide, with encrusting and parietal brownish pigment, subcutis with wider and paler to colourless elements. *Caulocystidia* on entire length of the stipe, 45–70 × 10–15 µm, mostly somewhat misshaped (sub)fusiform, with short or longer neck and with short pedicel, apex usually crystalliferous, walls up to 1.5 (2.0) µm thick at the apex, intensely yellow-green with 3% KOH; intermixed with numerous (sub)clavate to subglobose cauloparacystidia. *Clamp connections* abundant in all tissues.

Habitat and distribution

Inocybe alcis **sp. n.** was found in Finland from middle to northern boreal zones, and in Sweden in the alpine zone. At one locality it occurred with only *Betula* and *Salix*, at one alpine site only with dwarf *Salix* (*S. herbacea*); at the others with both broadleaved trees and conifers present. All collections were found on rather moist localities, therefore in most cases *Salix* and *Betula*, and in the type locality *Alnus* were present. *Salix* spp. seem to be the preferential hosts. The species corresponds to SH1522282.08FU (1.5%) of the UNITE database, assembling sequences from collections, EcM or soil samples from Canada, Estonia, Finland, Norway (Svalbard) and the United States.

Additional specimens examined

FINLAND, Enontekiön Lappi, Enontekiö commune, Kilpisjärvi, Tsahkaljohka, *Salix glauca*, *Salix myrsinifolia*, *Betula pubescens* subsp. *czerepanovii*, alt. 520 m, 10 Aug. 1986, leg. J. Vauras (TUR-A 171597, JV2222F, dupl. DB10-8-86-Vauras). Ibidem 13 Aug. 1990, leg. J. Vauras (TUR-A 171602, JV4746). Ibidem, 15 Aug. 1990, leg. J. Vauras (TUR-A 171604, JV4784F). Kainuu, Sotkamo municipality, Pökkelöperä, brookside forest with *Alnus incana*, *Salix phylicifolia*, *Salix myrsinifolia*, *Betula* sp., *Picea abies*, alt. 218 m, 24 Aug. 2010, leg. K. Kokkonen & J. Vauras (TUR-A 190129, JV27675).

Fig. 3. *Inocybe alcis* **sp. n.** – **a.** Holotype; scale bar: 1 cm. **b.** Coll. TUR-A 171604l (photo: J. Vauras); scale bar: 1 cm. **c.** Cheilocystide (holotype); scale bar: 10 µm. **d.** Microscopic characters (holotype); Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm. **e.** Spores (holotype); scale bar: 10 µm.

Notes

Inocybe alcis **sp. n.** is characterized by a dark red brown to reddish tinged dark brown, sometimes bicoloured pileus, a glabrous to minutely rimulose pileus surface, at first strikingly white lamellae, (sub)lanceolate to (sub)fusiform hymenial cystidia with strong reaction with 3% KOH. The distribution of the examined collections is boreal. The species belongs to the "*pholiotinoides*-group", which is characterized by, e.g., often (sub)lanceolate and rather narrow hymenial cystidia the walls of which react strongly with KOH. *Inocybe pholiotinoides* differs from *I. alcis* sp. n., e.g., by the bright yellow-ochraceous pileus colour with a more or less intense orange to orange-coppery tinge, the often minutely (sub)squamulose pileus surface with age and on average smaller spores (Romagnesi 1979; DB, personal observation and see below). The same can be said with respect to *I. fissuratula* E. Ludw. (Ludwig 2017; Eberhardt et al., in prep.). Furthermore, *I. pholiotinoides* is more thermophilic and the two species hardly show an overlapping distributional range. *Inocybe carissima* (see below) has a paler pileus colour especially at the centre of the pileus, not strikingly white lamellae and smaller spores. Besides, it grows with *Picea abies*. *Inocybe orioli* (see below) can be distinguished from *I. alcis*, e.g., by paler pileus colours, the often finely tomentose pileus surface, the somewhat thickish lamellae and smaller spores, and from *I. ionochlora* Romagn., e.g., by the much paler centre and paler margin of the pileus, near the apex violet stipe and on average longer, but narrower spores (Romagnesi 1979; Bandini et al. 2013). *Inocybe muricellata* Bres. usually has a more orange-reddish centre of the pileus, a tomentose-lanose, subquamulose to squarrose pileus surface and smaller spores (Bresadola 1905; Kuyper 1986; Stangl 1989; DB, personal observation). The sister species of *I. alcis* is *I. pholiotinoides* (Fig. 1), which is also the species with the most similar ITS (97% similarity). *Inocybe alcis* received 86%/98%/1 support in the analyses.

Inocybe aurantiobrunnea Esteve-Rav. & García Blanco *in* Esteve-Raventós, García Blanco, Sanz Carazo & Del Val, *Öst. Z. Pilzk.* 12: 90 (2003)

(Fig. 21b)

Description and iconography: Esteve-Raventós et al. (2003).

Type specimen examined

Isotype: SPAIN, Valladolid, Castromonte, La Espina, sandy, calcareous soil, *Pinus halepensis*, *Quercus ilex*, subsp. *ballota*, 30 Apr. 2003, [leg. not indicated] (STU SMNS-STU-F-0001816). *Spores* 9.9–12.6 µm (av. 10.5 µm, SD 0.5 µm) × 5.7–7.0 µm (av. 6.4 µm, SD 0.3 µm); Q = 1.5–1.9 (av. 1.7, SD 0.1) (n = 40), smooth, broadly amgydaliform to (sub)ovoid, with (sub)obtuse to subacute apex. *Basidia* usually 4-spored, rarely 2-spored. *Pleurocystidia* 46–70 µm (av. 61 µm, SD 6 µm) × 10–14 µm (av. 12 µm, SD 1 µm); Q = 4.2–6.2 (av. 5.0, SD 0.5) (n = 15), mostly (sub)cylindrical, apex usually crystalliferous, walls up to 1.0 (1.5) µm thick at the apex, pale yellowish-greenish with 3% KOH. *Cheilocystidia* similar in appearance and size. *Paracystidia* not observed. *Caulocystidia* similar in size to hymenial cystidia, (sub)cylindrical to (sub)fusiform, walls up to 0.5 µm.

Notes

Inocybe aurantiobrunnea is a Mediterranean species, with dark brown pileus, caulocystidia only near the apex of the stipe and usually (sub)cylindrical hymenial cystidia (see Esteve-Raventós et al. 2003 and below). It is not a well-known species up to now. In GenBank, there is only one ITS sequence from a collection from Italy (JF908212) labelled as "*I.* cf. *luteipes*", putatively belonging to *I. aurantiobrunnea*; otherwise, there are currently no ITS sequences more similar than around 91%. In Fig. 1, *I. aurantiobrunnea* is sister to a soil sample sequence, but both are on relatively long branches. The clade of the two sequences assigned to *I. aurantiobrunnea* received full support in the analyses.

Inocybe aurantioumbonata → ***Inocybe tarda***

(Fig. 21c)

Inocybe bresadolana Bon [as "*bresadoliana*"], *Docums Mycol.* 12(no. 48): 44 (1983) [1982]

(Fig. 21d)

Description and iconography: Bresadola (1930; as "*I. fuscidula*").

Specimen examined

FRANCE, environs Bellème, muddy ground with *Salix* ("Saulaie fangeuse"), 25 Sep. 1982, [leg. M. Bon] (LIP-MB8209251). Description: *Spores* 11.6–16.0 µm (av. 13.3 µm, SD 1.0 µm) × 4.6–6.6 µm (av. 5.7 µm, SD 0.5 µm); Q = 1.9–2.7 (av. 2.4, SD 0.2) (n = 40), slender elongate (sub)laceroid, sometimes with slightly undate walls and often with truncate base, with (sub)obtuse to (sub)acute apex. *Basidia* usually 4-spored. *Pleurocystidia* 38–60 µm (av. 52 µm, SD 7 µm) × 14–22 µm (av. 16 µm, SD 2 µm); Q = 2.3–4.3 (av. 3.3, SD 0.6) (n = 15), mostly ventricose (sub)fusiform or subutriform, without or with only short neck, apex usually crystalliferous, walls up to 2.0 (3.0) µm thick at the apex, pale yellowish-greenish with 3% KOH. *Cheilocystidia* similar in appearance and size. *Paracystidia* not observed. *Caulocystidia* not studied (to preserve the material).

Notes

Bresadola (1930) described a species with elongate and slim spores under the name *I. fuscidula* (see Bresadola 1930, pl. 735). Since the name *I. fuscidula* was not available anymore at the time—Velenovský (1920–1922) had used it already—the name was invalid. Bon later described a species as new under the name *I. bresadoliana* Bon (Bon & Van Haluwyn 1983), which he thought to be the species described by Bresadola as *I. fuscidula*. In the herbarium of LIP are two collections of this species from different years (MB8209251; MB780191403; see above). By examining both of Bon's collections, we could exclude that *I. bresadolana* sensu Bon is *I. lacera*, because the spores are longer and regular in shape and often with slightly undate walls, and the cystidia are clearly shorter. However, it could be a species in the neighborhood of *I. helobia*. Since the spores of the latter species are on average shorter and there is no macroscopic description of the species by Bon, and since sequence generation from the collections of Bon failed, we cannot say if his concept of *I. bresadolana* is synonymous with *I. helobia* or not. In the protologue, the cystidia are, with 70–90 µm (Bresadola 1930), much longer than what was measured in the collections of *I. bresadolana* as well as of a different shape; thus, we do not think that what Bon described as *I. bresadolana* is indeed the *I. fuscidula* of Bresadola, which could have been *I. lacera*.

Inocybe brevispora → ***Inocybe subcarpta***
(Fig. 21e)

Inocybe carissima Bandini, Hussong & Brandrud, **sp. n.**
(Fig. 4; MycoBank: MB 845162)

Etymology

Named "carissima" (Latin) because the species is a very dear one.

Diagnosis

Inocybe carissima **sp. n.** has a yellow-tinged ochraceous to brownish-tinged ochraceous pileus colour, smooth to fine velvety or tomentose pileus surface, only very faint and fugacious velipellis, whitish to pale yellow up to ochraceous brownish lamellae, on average rather narrow smooth spores measuring 7.0–10.0 µm (av. 8.7 µm) × 4.0–5.4 µm (av. 4.8 µm), and mostly long and narrow (sub)fusiform to sublageniform hymenial cystidia, pleurocystidia measuring 49–96 µm (av. 71 µm) × 10–16 µm (av. 13 µm), and intensely yellow-green walls of the cystidia with 3% KOH.

Holotype

GERMANY, Bayern, Ostallgäu, Halblech, Niederbleick, TZK25 8331/3, alt. 1432 m, *Picea abies*, 13 Aug. 2021, leg. D. Bandini, A. Hussong, J. Christan, B. Oertel & M. Dondl (holotype STU SMNS-STU-F-0901701; isotype priv. herb. D. B. DB13-8-21-3).

Description

Pileus 5–30 mm wide, at first (sub)conical, later subconical, and then expanded; at first without, later with more or less prominent umbo; margin at first slightly incurved to decurved, later straight and slightly uplifted with age, and then somewhat depressed around the centre; young basidiomata with very faint and fugacious remnants of a pale velipellis; colour pale ochraceous with yellowish hue to ochraceous or ochraceous with faint brownish tinge (Mu 10YR 6/5–6/6, 5/6–5/8), sometimes somewhat orange reddish at the umbo or, when young, sometimes somewhat paler due to the velipellis; surface at first almost smooth, later finely to thickly velvety to tomentose, rarely subrimulose towards the margin and sometimes with age somewhat lacerate; no remnants of a cortina observed. *Lamellae* subdistant (c. 25–35, l = 1–3), emarginate adnate, subventricose, whitish to pale yellowish, with age sometimes pale ochraceous to pale ochraceous brownish, with or without greyish tinge; edge fimbriate, whitish. *Stipe* 15–50× 1–3 mm, cylindrical or slightly curved, at first covered by a very thin whitish tomentum, vanishing soon and then longitudinally striate to smooth, whitish to beige, whitish-yellowish and more intensely yellowish with age; pruinose on the entire length of the stipe; sometimes the pruina becomes slightly greenish to greyish olivaceous with age. *Context* whitish in the pileus, at first creamy, with age pale yellowish in the stipe. *Smell* indifferent. *Colour of exsiccata* pileus ochraceous brownish to brown (Mu 10YR 6/4–6/6, 5/4–5/8), lamellae and stipe concolourous or a little lighter in colour, no darkening or blackening on drying.

Spores 7.0–10.0 µm (av. 8.7 µm, SD 0.6 µm) × 4.0–5.4 µm (av. 4.8 µm, SD 0.3 µm); Q = 1.6–2.1 (av. 1.8, SD 0.1) (n = 120 of 3 coll.), smooth, oblong (sub)amygdaloid, without or with only faint suprahilar depression, apex subacute, subobtuse, in some collections with indistinct pseudoporus. *Basidia* 23–28 × 7–9 µm, generally 4-spored, rarely also 2-spored and then spores up to 11.0 µm. *Pleurocystidia* 49–96 µm (av. 71 µm, SD 13 µm) × 10–16 µm (av. 13 µm, SD 2 µm); Q = 4.1–7.4 (av. 5.5, SD 0.9) (n = 45 of 3 coll.), mostly lanceolate, narrow fusiform, usually with rather long and sometimes undate neck, with short pedicel, sometimes also without pedicel and then (sub)lageniform, apex usually crystalliferous, walls up to 3.5 (4.5) µm thick at the apex, intensely yellow-green with 3% KOH. *Cheilocystidia* similar in size, but somewhat more variable in shape, intermixed with numerous colourless, (sub)clavate to subcylindrical, thin-walled paracystidia. *Pileipellis* constituted by an epicutis made up of parallel hyphae 4–10 µm wide, with encrusting and parietal ochraceous brownish pigment, subcutis with wider and paler to colourless elements. *Caulocystidia* on the entire length of the stipe, 45–65 × 10–15 µm, (sub)utriform, (sub)fusiform, apex usually crystalliferous, walls up to 1.5 µm thick at the apex, intensely yellow-green with 3% KOH; intermixed with numerous (sub)clavate to subglobose cauloparacystidia. *Clamp connections* abundant in all tissues.

Habitat and distribution

Inocybe carissima **sp. n.** was found by us at subalpine altitudes in Germany and in the middle boreal zone in SE

Fig. 4. *Inocybe carissima* **sp. n.** – **a.** Holotype; scale bar: 1 cm. **b.** Coll. O-F-258869 (photo: T. E. BRANDRUD); scale bar: 1 cm. **c.** Cheilocystidia (Coll. DB26-7-15-1); scale bar: 10 µm. **d.** Microscopic characters (holotype); Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm. **e.** Spores (Coll. DB26-7-15-1); scale bar: 10 µm.

Norway, next to a brook. All collections where close to *Picea abies*. The Norwegian finds were from dense, luxuriant tall herb vegetation, at a slightly calcareous site. The species corresponds to UNITE SH1384674.08FU (2.0%), including some sequences from EcM or soil samples from China, Estonia and the Russian Federation.

Additional specimens examined

GERMANY, Bayern, Ostallgäu, Halblech, near Kenzenhütte, TK25 8431/1, alt. 1350 m, *Picea abies*, 26 Jul. 2015, leg. A. Hussong (SMNS-STU-F-0901728, dupl. DB26-7-15-1). Ibidem, at some distance from former location, alt. 1432 m, *Picea abies*, 24 Jul. 2019, leg. A. Hussong & J. Christan (DB24-7-19-Hussong). NORWAY, Oppland, Valdres, Nord-Aurdal, Fodnes, Hilmeshaugen, next to a brook with *Picea abies*, 9 Aug. 2021, leg. T. E. Brandrud, B. Dima & A. Nagy (O-F-258836). Ibidem, at some distance from former location, next to a brook with *Picea abies*, slightly calcareous, with dense, tall herb vegetation, 9 Aug. 2021, leg. T. E. Brandrud, B. Dima & A. Nagy (TEB 174-21, O-F-258869).

Notes

Inocybe carissima **sp. n.** is characterized by a yellow-tinged pale ochraceous, ochraceous to brownish-tinged ochraceous pileus colour, smooth to finely velvety or tomentose pileus surface, only very faint and fugacious velipellis, whitish to pale yellow up to ochraceous brownish lamellae, mostly long and narrow (sub)fusiform to sublageniform hymenial cystidia and intensely yellow-green walls of the cystidia with 3% KOH. The species can be mistaken for *I. pholiotionoides* and *I. orioli*, which differ, e.g., by a more intense or brighter pileus colour, on average larger spores, and habitat usually with frondose trees (Romagnesi 1979; DB, personal observation and see below). The same can be said with respect to *I. fissuratula* (Ludwig 2017; Eberhardt et al., in prep.). *Inocybe alcis* has a much darker, often red-brown centre of the pileus, at first strikingly whitish lamellae and larger spores. Besides, it grows with frondose trees. *Inocybe ionochlora* can be distinguished from *I. carissima* by a stipe that is violet near the apex, longer spores and on average shorter hymenial cystidia (Romagnesi 1979; Bandini et al. 2013), and *I. muricellata* differs, e.g., by a tomentose-lanose, subquamulose to squarrose pileus surface, at first often strikingly whitish lamellae, on average wider spores and shorter hymenial cystidia (Bresadola 1905; Kuyper 1986; Stangl 1989; DB, personal observation). The pileus surface of the recently described *I. pallidolutea* Carteret & Reumaux is (sub)squamulose, and the stipe is pinkish to reddish in the upper part according to the protologue, the hymenial cystidia are on average smaller and the reaction of the cystidia walls with KOH is weaker (Carteret & Reumaux 2017; Bandini et al. 2022a). *Inocybe ionochlora* is the sister species of *I. carissima* in Fig. 1; it is also the species most similar in its ITS to *I. carissima*, although only with 91% sequence similarity, followed by *I. orioli* (see below) with around 90%. The clade of *I. carissima* received full support in the analyses.

Inocybe cryptica Rodr.-Campo & Bandini, **sp. n.**

(Fig. 5; MycoBank: MB 845163)

Etymology

Named “cryptica” (Latin “*crypticus*”, “not visible”) because the species is camouflaged by the surrounding plants and soil.

Diagnosis

Inocybe cryptica **sp. n.** has a rather small size (< 3 cm), dark brown to red-brown pileus colour, fibrillose to (sub)lanose pileus surface, an ample whitish velipellis, stipe pruinose only near the apex, smooth spores measuring 7.7–11.3 µm (av. 9.1 µm) × 4.5–6.4 µm (av. 5.4 µm), mostly narrow (sub)fusiform hymenial cystidia measuring 58–86 µm (av. 68 µm) × 9–18 µm (av. 12 µm), and up to almost 100 µm long and narrow caulocystidia. The species can be recognized by the combination of the above characters and differs in its ITS sequence from other superficially similar smooth-spored species, such as *I. costinitii*.

Holotype

SPAIN, Comunidad de Madrid, Villa del Prado, 40.256959 / -4.281102, alt. 376 m, sandy soil, under *Quercus ilex* subsp. *ballota*, close to *Cistus ladanifer*, 11 Dec. 2012, leg. J. A. Rodea-Butragueño & A. Díaz-Fernández (holotype MA-Fungi 98477; isotypes priv. herb. F. J. Rodríguez-Campo PRC-121211-01, priv. herb. D. B. DB11-12-12-Rodr.-Campo).

Description

Pileus 13–30 mm wide, at first (sub)campanulate or (sub)conical, later convex to expanded, mostly without umbo or with a broad and rather low umbo, margin at first involute, later more or less deflected and finally straight to even faintly uplifted and then somewhat depressed around the centre, young basidiomata with ample remnants of a whitish velipellis, visible mainly as a thick patch at the centre of young basidiomata but spreading like a cobweb towards the margin, and still visible in mature basidiomata, colour brown with or without a reddish hue, greyish brown, chestnut-brown to dark brown, sometimes with faint olivaceous tinge (Mu 10YR 4/3–4/6, 3/4–3/6; 7.5YR 5/6–5/8, 4/4–4/6, 3/4); surface mostly (sub)fibrillose to (sub)lanose at least towards the margin and in some cases slightly squamulose at the centre, sometimes with adhering soil debris; young basidiomata with remnants of a whitish cortina. *Lamellae* moderately crowded (c. 32–48, l = 1–3), narrowly adnate, (sub)ventricose; whitish when young, then pale brownish to brown and finally reddish brown; edge irregular, fimbriate, concolourous. *Stipe* 20–40 × 2–7 mm, cylindrical or curved, sometimes widening towards the base, when young covered with whitish tomentum, later longitudinally striate, at first

Fig. 5. *Inocybe cryptica* **sp. n.** – **a.** Holotype (photo: F. J. Rodríguez-Campo); scale bar: 1 cm. **b.** Coll. MA-Fungi 98478 (photo: F. J. Rodríguez-Campo); scale bar: 1 cm. **c.** Cheilocystide (holotype); scale bar: 10 µm. **d.** Microscopic characters (holotype); Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm. **e.** Spores (holotype); scale bar: 10 µm.

whitish or pale cream, later yellow-brown, brown, reddish brown to intensely red-brown; pruinose only near the apex of the stipe and with whitish fibrils towards the base. *Context* whitish or brown in pileus and stipe, unchanged when cut. *Smell* indistinct or very slightly spermatic. *Colour of exsiccata* pileus brown or dark brown (Mu 10YR 4/3–4/6, 3/4–3/6), lamellae and stipe concolourous, no darkening on drying.

Spores 7.7–11.3 µm (av. 9.1 µm, SD 0.7 µm) × 4.5–6.4 µm (av. 5.4 µm, SD 0.3 µm); Q = 1.4–2.1 (av. 1.7, SD 0.2) (n = 160 of 4 coll.), smooth, (sub)amygdaloid, ellipsoid, sometimes with a faint suprahilar depression, apex subobtuse. *Basidia* 27–36 × 7–11 µm, generally 4-spored. *Lamellae edges* composed of cheilocystidia and numerous colourless, (sub)clavate or (sub)cylindrical, thin-walled paracystidia. *Pleurocystidia* 58–86 µm (av. 68 µm, SD 5.8 µm) × 9–18 µm (av. 12 µm, SD 2 µm); Q = 3.9–8.3 (av. 5.7, SD 1.0) (n = 60 of 4 coll.), mostly narrow (sub)fusiform, sometimes also subutriform or subcylindrical, generally without neck, sometimes with short neck, and with short pedicel, usually wide at the apex, sometimes subcapitate, apex usually crystalliferous, walls up to 3.0 µm thick at the apex, yellow-green with 3% KOH. *Cheilocystidia* similar in size, but somewhat more variable in shape. *Pileipellis* constituted by an epicutis made up of parallel hyphae 4–7 µm wide, with encrusting and parietal brownish pigment, subcutis with wider and paler to colourless elements. *Caulocystidia* only near the apex of the stipe, 61–95 × 9–16 µm, narrow (sub)cylindrical, (sub)fusiform, (sub)utriform, sometimes with undate walls, usually without neck, sometimes subcapitate, and with short pedicel, apex without or with only small crystals, walls up to 1.5 µm thick at the apex, yellow-green with 3% KOH; intermixed with numerous (sub)clavate or subglobose cauloparacystidia. *Clamp connections* abundant in all tissues.

Habitat and distribution

Inocybe cryptica **sp. n.** was found in winter, on acidic and sandy soil, under evergreen Mediterranean oaks (*Quercus ilex* subsp. *ballota*) mixed with *Cistus ladanifer* shrubs in Spain. No other collections or sequences from collections or EcM-sequences are known to us.

Additional specimens examined

SPAIN, Comunidad de Madrid, Villa del Prado, 40.256959 / -4.281102, alt. 376 m, sandy soil, under *Quercus ilex* subsp. *ballota*, close to *Cistus ladanifer*, 26 Dec. 2012, leg. A. Díaz-Fernández, J. A. Rodea-Butragueño, N. Núñez-Mauriz & F. J. Rodríguez-Campo (MA-Fungi 98478, dupl. priv. herb. F. J. Rodríguez-Campo PRC-121226-24). Ibidem, 10 Dec. 2021, leg. F. J. Rodríguez-Campo (MA-Fungi 98672, dupl. priv. herb. PRC-211210-01 and MA-Fungi 98674, dupl. priv. herb. PRC-211210-03).

Notes

Inocybe cryptica **sp. n.** is characterized by a rather stout habit, brown to dark brown pileus colour with or without a reddish hue, an ample whitish velipellis, fibrillose to (sub)lanose pileus surface, with age brown to intensely red-brown stipe pruinose only near the apex, mostly narrow (sub)fusiform hymenial cystidia, the walls of which react strongly with KOH, and up to almost 100 µm long and narrow caulocystidia. Species of the "*cincinnata*-group", such as *I. cincinnata* (Fr.) Quél. or *I. minima* Peck, have long and narrow hymenial cystidia with walls reacting strongly to KOH, but the shape is more lanceolate and the stipes of all members of the group are more or less intensely violet at least near the apex of the stipe when young, and the caulocystidia are shorter on average (see Peck 1913; Bandini et al. 2021c). Furthermore, no species of the group has such an ample whitish velipellis in combination with the shape and size of the hymenial cystidia. An ample whitish velipellis is usually characteristic of *I. costinitii* Bizio, Ferisin & Dovana, another Mediterranean species. This species differs from *I. cryptica*, e.g., by a smoother pileus surface, on average larger spores and a less strong reaction of the cystidia walls to KOH (Bizio et al. 2016; Bandini et al. 2021c). Such a large patch of velipellis at the centre of the pileus is also characteristic for *I. psammobrunnea* Bon, which differs from *I. cryptica*, e.g., by the often larger basidiomata, on average larger spores and ventricose cystidia as well as shorter caulocystidia. Furthermore, it is mostly associated with *Pinus* (Bon 1990; Bandini et al. 2021c). *Inocybe griseovelata* Kühner and *I. grusiana* Bandini & B. Oertel often have (sub)cylindrical hymenial cystidia, but their velipellis is greyish, the pileus surface is smoother, the spores on average are longer and the reaction of the walls of the cystidia to KOH is much weaker (Kühner 1955; Bandini et al. 2021c). *Inocybe subnudipes* Kühner may have similar hymenial cystidia, but the pileus colour is ochraceous, dull fallow to brownish and the pileus surface is innately fibrillose (Kühner 1955; DB, personal observation). *Inocybe tenuicystidiata* E. Horak & Stangl has no such ample whitish velipellis, the pileus surface is smoother and the spores are smaller (see, e.g., Horak & Stangl 1980; Stangl 1989, as "*I. obscurobadia*"; Bandini et al. 2021c). The dark pileus colour and the velipellis of *I. cryptica* may remind of *I. tjallingiorum* Kuyper, which differs, e.g., by a more glabrous pileus surface, an entirely pruinose stipe and shorter and mostly neckless hymenial cystidia (Kuyper 1986; Bandini et al. 2021c). In Fig. 1, *I. cryptica* is the sister species of *I. muricellata*, but the two species are, with only 91% similarity, by no means easy to confuse molecularly. *Inocybe muricellata* differs from *I. cryptica*, e.g., by the often lanose, subquamulose to squarrose pileus surface, stipe entirely and densely pruinose down to the base, and shorter caulocystidia (Bresadola 1905; Kuyper 1986; Stangl 1989; DB, personal observation). It seems that *I. cryptica* is a very rare species. The clade of *I. cryptica* received 99%/100/1 support.

Inocybe culicis Bandini, Vauras & B. Oertel, **sp. n.**
(Fig. 6; MycoBank: MB 845164)

Etymology

Named "culicis" because of the presence of swarms of mosquitoes (Culicidae) next to the locations where the species was found.

Diagnosis

Inocybe culicis **sp. n.** has an abundant silvery beige velipellis, brownish to nut-brown pileus colour and tomentose to (innately) fibrillose pileus surface, rather pale nodulose spores, measuring 5.1–7.9 µm (av. 6.2 µm) × 3.8–5.9 µm (av. 4.8 µm) and mostly (sub)utriform, rather thin-walled and with rather short hymenial cystidia, pleurocystidia measuring 36–58 µm (av. 50 µm) × 10–18 µm (av. 14 µm). The species can be recognized by the combination of the above characters and differs in its ITS sequence from other nodulose-spored species, such as the genetically closely related *I. soluta*.

Holotype

FINLAND, Koillismaa, Kuusamo municipality, parking place at the road Liikasenvaarantie, SWW of Kiutaköngäs, S of the Guidance Center of Oulanka National Park, WGS84: 66.3653:29.3147, alt. 172 m, on sand near *Pinus sylvestris*, *Betula* sp., *Picea abies*, 21 Aug. 2015, leg. D. Bandini, J. Vauras & B. Oertel (holotype TUR-A 203492; isotypes STU SMNS-STU-F-0901258, priv. herb. D. B. DB21-8-15-27).

Description

Pileus 10–20 mm wide, (sub)campanulate when young, later broadly convex or expanded, with a more or less prominent large umbo, margin at first slightly incurved, later decurved; when young, covered by a silvery beige velipellis; colour at first (due to the velipellis) silvery beige with faint orange-ochraceous hue, later pale brown to nut-brown (Mu 10YR 7/3–7/4, 6/3–6/4, 5/4–5/6), at the umbo darker and more intense in colour; surface densely tomentose to innately fibrillose or fibrillose with appressed fibres; young basidiomata with faint remnants of a pale brownish cortina. *Lamellae* moderately crowded (c. 30–40, l = 1–3), adnate with subdecurrent tooth, ventricose, at first whitish, later pale brownish with cinnamon tinge; edge fimbriate, whitish to concolourous. *Stipe* 15–25 × 2–3 mm, stout, curved, at first entirely covered with whitish tomentum, later longitudinally striate to glabrous, reddish brown to dark brown with reddish tinge; very roughly and sparely pruinose near the apex. *Context* whitish in the pileus and the upper half of the stipe, brownish at the cortex of the stipe, and brownish towards the base. *Smell* indifferent. *Colour of exsiccata* pileus and stipe silvery greyish-brownish, light brown (Mu 10YR 6/4–6/6, 5/3–5/4), lamellae without silvery tinge, no darkening or blackening on drying.

Spores 5.1–7.9 µm (av. 6.2 µm, SD 0.5 µm) × 3.8–5.9 µm (av. 4.8 µm, SD 0.5 µm); Q = 1.0–1.7 (av. 1.3, SD 0.1) (n = 80 of 2 coll.), rather pale, nodulose, with 6–9 differently protruding, mostly obtuse nodules occasionally appearing quadrangular or even triangular. *Basidia* 22–30 × 7–9 µm, generally 4-spored. *Lamella edges* composed of cheilocystidia and numerous colourless, (sub)clavate, thin-walled paracystidia. *Pleurocystidia* 36–58 µm (av. 50 µm, SD 5 µm) × 10–18 µm (av. 14 µm, SD 2 µm); Q = 2.6–4.5 (av. 3.6, SD 0.5) (n = 30 of 2 coll.), mostly (sub)utriform, sometimes subfusiform, also (sub)-cylindrical, seldom (sub)clavate, mostly with (only faint) short neck, sometimes without neck, generally with short pedicel, apex usually crystalliferous, usually thin-walled, with walls only up to 0.5 (1.0) µm thick at the apex, pale yellowish-greenish with 3% KOH. *Cheilocystidia* similar in appearance and size. *Pileipellis* constituted by an epicutis made up of parallel hyphae 5–12 µm wide, often but not always with finely encrusting and parietal orange-brownish pigment, subcutis with wider and paler to colourless elements. *Caulocystidia* only near the apex of the stipe, 30–60 × 10–20 µm, (sub)utriform or (sub)clavate, without or with only a short neck, with short pedicel, apex usually without crystals, often filled with colourless amorphous content, thin-walled or walls up to 0.5 µm thick at the apex, pale yellowish-greenish in 3% KOH. *Clamp connections* abundant in all tissues.

Habitat and distribution

The only two collections we had were found in dry locations among moss and lichens, one in a parking lot, the other on the side of a street next to another parking lot. Thus, possibly, the soil was somewhat basic. Apart from our own collections we are not aware of other collections or sequences from collections apart from a root sample sequence from Alaska likely to belong to *I. culicis* (Fig. 1). The species corresponds to SH1691884.08FU (1%) of UNITE database, which currently only includes the said root sample sequence (KU176311).

Additional specimen examined

FINLAND, Koillismaa, Kuusamo municipality, Liikasenvaara, near Jäkälämutkanlampi, wayside with *Pinus sylvestris*, *Betula* sp., *Picea abies*, 17 Aug. 2015, leg. D. Bandini, J. Vauras & B. Oertel (DB17-8-15-26).

Notes

Inocybe culicis **sp. n.** is characterized by abundant silvery beige velipellis, brownish to nut-brown pileus colour and tomentose to (innately) fibrillose pileus surface, rather pale spores, which often appear triangular or quadrangular in outline, mostly (sub)utriform, rather thin-walled, and rather short hymenial cystidia. On first sight it could be mistaken for *I. soluta* Velen., which has equally pale and similar shaped spores. However, *I. soluta* differs by often larger basidiomata, velipellis missing, often almost blackish-brown centre of pileus, on average longer spores

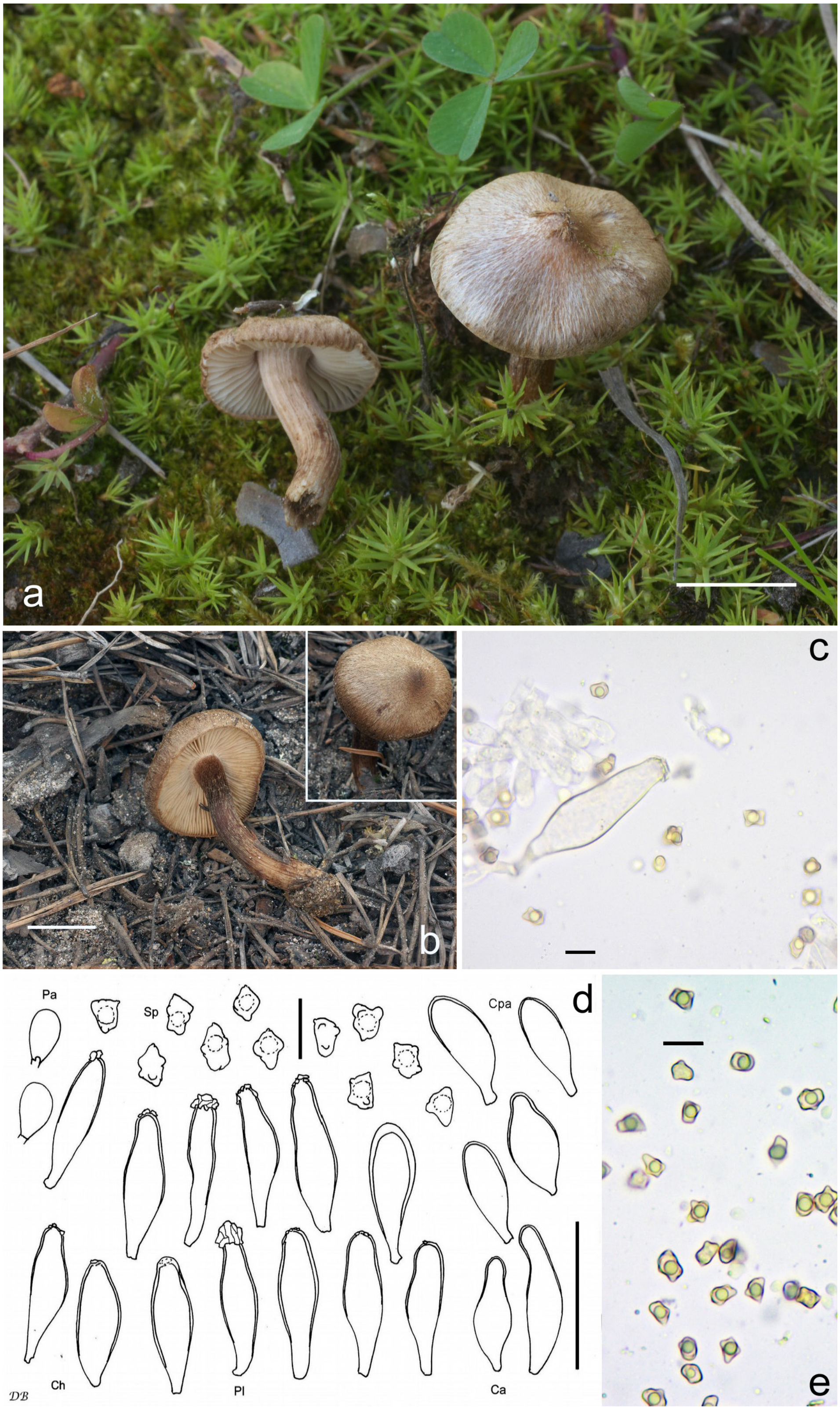

Fig. 6. *Inocybe culicis* **sp. n.** – **a.** Holotype; scale bar: 1 cm. **b.** Coll. DB17-8-15-26; scale bar: 1 cm. **c.** Cheilocystide (holotype); scale bar: 10 µm. **d.** Microscopic characters (holotype); Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm. **e.** Spores (coll. holotype); scale bar: 10 µm.

and longer hymenial cystidia (see, e.g., VELENOVSKÝ 1920–1922; KUYPER 1985; STANGL 1989; BIZIO & FERRARI 1999; ARMADA et al. 2007; FERRARI et al. 2014; LUDWIG 2017; and see below). *Inocybe subcarpta* Kühner & Boursier can be distinguished from *I. culicis*, e.g., by the less abundant and fugacious velipellis, larger spores and longer, often (sub)capitate hymenial cystidia often with undate walls (KÜHNER & BOURSIER 1932; HUIJSMAN 1955 (as "*I. brevispora*"); STANGL & VESELSKÝ 1974 (as "*I. brevispora*"); STANGL 1975, 1989; FERRARI 2006; FERRARI et al. 2014; LUDWIG 2017), and *I. prisca* has a more lanose surface of pileus, a greyish velipellis, larger spores and longer hymenial cystidia. Besides, *I. prisca* was found in a very moist location (BANDINI et al. 2021c). Two species are very similar in their ITS to *I. culicis*: *I. soluta* with, based on currently available sequence data, almost 99% similarity in the ITS and an 8 bp difference in the LSU, and *I. subcarpta* with a bit less than 98.5% similarity in the ITS and a 6 bp difference in the LSU. In spite of this, the monophyly of all three species received support: 91%/100%/1 for *I. culicis* and similar values for the other two species. Not very different from these three are sequences of two collections that were identified as *I. maritimoides* (Peck) Sacc. by STUNTZ (MH024862 and MH024867). Judging from PECK's (1885) and GRUND & STUNTZ's (1977) descriptions, *I. maritimoides* is morphologically similar to *I. culicis*, differing in the longer hymenial cystidia and oblong spores (GRUND & STUNTZ 1977). In Fig. 1, the clade including these sequences also includes sequences from two European collections, tentatively referred to as *I.* cf. *maritimoides*. We do not know where species limits in this clade may be, but judging from Fig. 1 it does not interfere with the integrity of either *I. culicis*, *I. soluta* or *I. subcarpta*.

Inocybe decipiens Bres., *Fung. trident.* 2(8–10): 13 (1892) (Fig. 21f)

Selected descriptions and iconography: BRESADOLA (1892); BIZIO & MARCHETTI (1997).

Type specimen examined

Holotype: ITALY, Villazzano, ad marginem camporum. Jul. 1888, leg. G. BRESADOLA (S-F-14450). *Spores* 10.4–16.0 µm (av. 13.1 µm, SD 1.2 µm) × 6.3–7.5 µm (av. 6.9 µm, SD 0.3 µm); Q = 1.5–2.4(av. 1.9, SD 0.2) (n = 30), oblong with sinuous outline to subnodulose, sometimes almost smooth. *Basidia* 4-spored. *Pleurocystidia* 58–65 µm (av. 61 µm, SD 4 µm) × 17–19 µm (av. 18 µm, SD 1 µm); Q = 3.1–3.8 (av. 3.4, SD 0.4) (n = 3, to preserve the material), mostly (sub)fusiform walls up to 3.5 µm thick at the apex, colourless with 3% KOH. *Cheilocystidia* not observed. *Paracystidia* not observed. *Caulocystidia* not studied (to preserve the material) [type-study by J. V.].

Selected additional specimens examined

AUSTRIA, Oberösterreich, Braunau am Inn, Oberrothenbuch, „Riviera", ÖK25V 3321-Ost, alt. 355 m, *Pinus sylvestris*, *Salix* sp., *Betula pendula*, *Picea abies*, 26 Jul. 2018, leg. D. BANDINI (DB26-7-18-9). GERMANY, Bayern, Bad Tölz-Wolfratshausen, Puppling, TK25 8034/4, alt. 580 m, *Salix* sp., *Pinus sylvestris*, 3 Sep. 2010, leg. M. DONDL (DB3-9-10-Dondl). Bayern, Garmisch-Partenkirchen, Werdenfelser Land, *Picea abies*, *Salix* sp., 16 Jun. 2012, leg. P. & W. EIMANN (DB16-6-12-E60-Eimann).

Notes

Inocybe decipiens was described by BRESADOLA (1892), and a water colour plate of the species was given with it (Pl. CXVIII). Apart from the holotype (see above), which is deposited in Stockholm (S), remnants of two collections (no. 284 and no. 324) of a much later date are deposited in Trient (TR).

Microscopic details of one of them (no. 324) were portrayed by BIZIO & MARCHETTI (1997) and the specimen was also examined and sequenced by us (see Fig. 1). The watercolour plate of *I. decipiens* by BRESADOLA (1892, Pl. CXVIII) shows dark brown pilei. While no velipellis is visible at the pileus of one older basidiome, the centre of the pileus of the basidiome to the left is paler than the rim. The spores are oblong and two of them almost rectangular, and the cystidia depicted are well in the range of cystidia we have observed in our own collections of a species, which might be *I. decipiens*.

The holotype of *I. decipiens* is currently unavailable for examination. The only observations we have are from three pleurocystidia of the holotype that could have been examined and measured by J. VAURAS. Based on this admittedly meagre evidence, we consider the clade labelled "*I. decipiens*" in Fig. 1 (support 99%/100%/1) and sister to *I. velata* Franchi & M. Marchetti as the real *I. decipiens*. Whether this assumption is correct, we could not test. The authentic collection no. 324 of *I. decipiens* is very similar in its ITS to *I. nobilis* (R. Heim) Alessio, a species with similar macroscopic and microscopic aspect (HEIM 1931, as "*I. fibrosa* var. *nobilis*"; ALESSIO 1980; DB, personal observation), even though the spores are shorter on average. Nevertheless, with the data currently available to us, we cannot entirely rule out the possibility that *I. decipiens* is synonymous with the younger *I. nobilis*. However, the clade including *I. nobilis* in Fig. 1 is difficult to interpret as to whether subclades could represent further species or not. In the same multi-species clade are also included *I. dunensis* P.D. Orton and *I. sepiana*, discussed below, which differ from *I. decipiens* by microscopic details in the shape and size of the spores and the shape of the hymenial cystidia (see below).

Inocybe dunensis P.D. Orton, *Trans. Br. mycol. Soc.* 43(2): 277 (1960) (Fig. 21g)

Selected descriptions and iconography: ORTON (1960); STANGL (1989); BREITENBACH & KRÄNZLIN (2000); FERRARI (2006); LUDWIG (2017).

Type specimen examined

Holotype: UNITED KINGDOM, South Lancashire, Formby, Freshfield, on sandy soil, 9 Jul. 1956, [leg. P. D. Orton] (K(M): 60273). *Spores* 10.2–12.7 µm (av. 11.4 µm, SD 0.6 µm) × 5.6–7.1 µm (av. 6.5 µm, SD 0.3 µm); Q = 1.5–1.9 (av. 1.7, SD 0.1) (n = 40), nodulose with only faintly protruding nodules. *Basidia* 4-spored. *Pleurocystidia* 45–69 µm (av. 57 µm, SD 6 µm) × 17–25 µm (av. 21 µm, SD 2 µm); Q = 2.1–3.5 (av. 2.7, SD 0.4) (n = 15), mostly broadly fusiform or subutriform, apex usually crystalliferous, walls up to 5.0 (6.0) µm thick at the apex, almost colourless with 3% KOH. *Cheilocystidia* similar in appearance and size. *Paracystidia* not observed. *Caulocystidia* not studied (to preserve the material).

Selected additional specimens examined

GERMANY, Baden-Württemberg, Rhein-Neckar-Kreis, Sandhausen, near Nature Reserve Pflege Schönau-Galgenbuckel, TK25 6617/2, alt. 110 m, *Pinus sylvestris*, *Helianthemum nummularium*, 25 Oct. 2017, leg. D. Bandini (DB25-10-17-7). Bayern, Rottal-Inn, Julbach, TK25 7743/2, alt. 360 m, *Pinus sylvestris*, 15 Aug. 2014, leg. A. Hussong (DB15-8-14-23). Hessen, Bergstrasse, Viernheim, near Viernheimer Heide, TK25 6417/1, alt. 100 m, *Pinus sylvestris*, 28 Oct. 2016, leg. D. Bandini (DB28-10-16-1). NETHERLANDS, Friesland, Ameland, Hollum, alt. 2–3 m, *Salix repens*, *Pinus sylvestris*, *Ammophila arenaria*, 21 Sep. 2011, leg. D. Bandini (KR-M-0038114, dupl. DB21-9-11-1).

Notes

Inocybe dunensis is a fairly common species apparently preferring sandy and somewhat calcareous soil, often growing in dune sand with *Salix repens* and/or *Pinus sylvestris*. It is characterized by usually rather stout basidiomata with whitish velipellis at the centre of the sticky pileus, which is therefore mostly covered by soil particles, and oblong and nodulose spores when observed under the microscope (Orton 1960; DB, personal observation). The stipe is entirely pruinose when young but often rubbed off with age in the lower half due to the sand. We were not allowed to sequence the holotype, but the microscopic details fit very well to some of our own collections, sequences of which are included in the tree (see Fig. 1). The clade labelled "*I. dunensis*" received 89%/99%/1 support.

Inocybe griseovelata Kühner, *Bull. Soc. nat. Oyonnax* 9(Suppl. (Mém. hors sér. 1)): 4 (1955)

(Fig. 7)

Heterotypic synonym: *Inocybe subvirgata* Reumaux, *Docums Mycol.* 31(no. 121): 9 (2001).

Selected descriptions and iconography: Kühner (1955); Kuyper (1986); Stangl (1989).

Typification

FRANCE, Paris, Bois de Vincennes, 14 Jul. [1927], leg. R. Kühner (G00058738), lectotype designated by Bandini et al. (2021c).

Epitypus hic designatus (MBT 10008601)

GERMANY, Sachsen-Anhalt, Harz, Ilsenburg, TK25 4130/1, *Picea abies*, 30 Sep. 2012, leg. D. Bandini & B. Oertel (STU SMNS-STU-F-0901568, dupl. priv. herb. DB DB30-9-12-1).

Description

Pileus 15–40 (45) mm wide, subglobose to (sub)campanulate or subconical, later broadly convex or expanded, mostly without umbo or with a usually rather flat, large umbo, margin inflexed at the extreme border, soon decurved to straight, sometimes deeply torn when older and sometimes somewhat uplifted and then depressed around the centre; when young entirely covered by abundant remnants of a whitish-greyish velipellis; colour from almost straw-coloured, pale light brown, nut-brown to brown, sometimes with a more or less intense reddish hue (Mu 7.5YR 5/4–5/8, 6/4–6/8; 10YR 5/6–5/8; 5YR 3/2–3/4), sometimes appearing speckled because of scattered velipellis; surface at first, and sometimes rather long, smooth or minutely tomentose, later rim(ul)ose to innately fibrillose towards the margin and there then sometimes with diverging fibres so that the paler trama beneath is visible, rarely somewhat tomentose; with age sometimes subsquamulose or somewhat areolate diffracted at the centre; young basidiomata with remnants of a pale cortina. *Lamellae* moderately crowded to subdistant (c. 40–50, l= 1–3), adnate to emarginate adnate with decurrent tooth, (sub)ventricose, at first whitish, then greyish to greyish-brownish or brownish; edge fimbriate, sometimes uneven, whitish to concolourous. *Stipe* 20–50 × 2–5 mm, mostly rather stout, cylindrical or curved, and sometimes slightly widening towards the base, when young entirely and thickly covered with whitish tomentum, later longitudinally striate or glabrous, pale beige to pale wood-coloured, often more or less intensely pinkish towards the apex; sparely pruinose at the extreme apex. *Context* whitish in the pileus, whitish or faintly brownish in the cortex of the stipe, sometimes faintly pinkish near the apex of the stipe. *Smell* (sub)spermatic, at least when cut. *Colour of exsiccata* pileus grey-brown (Mu 10YR 4/3–4/4, 3/3–3/6), lamellae and stipe concolourous or a little lighter in colour, no darkening or blackening on drying.

Spores 8.5–12.5 µm (av. 10.4 µm, SD 0.8 µm) × 4.9–6.7 µm (av. 5.7 µm, SD 0.3 µm); Q = 1.6–2.1 (av. 1.8, SD 0.1) (n = 120 of 3 coll.), smooth, (sub)amygdaloid, often with a more or less explicit suprahilar depression, apex usually (sub)acute, with indistinct pseudoporus. *Basidia* 25–35 × 9–10 (12) µm, generally 4-spored, but occasionally also 2-spored, and then up to 13.7 µm. *Lamella edge* composed of cheilocystidia and numerous colourless, (sub)clavate to (sub)cylindrical, thin-walled paracystidia. *Pleurocystidia* 49–88 µm (av. 66 µm, SD 10.6 µm) × 10–21 µm (av. 15 µm, SD 2.6 µm); Q = 2.8–7.2 (av. 4.4, SD 0.9) (n = 45 of 3 coll.), often subcylindrical, also (sub)utriform, in some collections sometimes (sub)lageniform,

Fig. 7. *Inocybe griseovelata* **sp. n.** – **a.** Epitype; scale bar: 1 cm. **b.** Coll. SMNS-STU-F-0901567; scale bar: 1 cm. **c.** Cheilocystidia (epitype); scale bar: 10 µm. **d.** Microscopic characters (epitype); Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm. **e.** Spores (coll. epitype); scale bar: 10 µm.

with short or longer, always wide neck, with short pedicel, apex usually crystalliferous, walls up to 1.5 (2.0) µm thick at the apex, almost colourless to pale yellowish-greenish with 3% KOH. *Cheilocystidia* similar in appearance and size. *Pileipellis* constituted by an epicutis made up of parallel hyphae 5–13 µm wide, often but not always with coarsely encrusting and parietal brown pigment, subcutis with wider and brownish to paler elements. *Caulocystidia* only sparely at the extreme apex of the stipe, 40–100 × 10–15 µm, long and narrow and curved, mostly subcylindrical to subfusiform, apex usually only with few crystals, walls up to 1.0 (1.5) µm thick at the apex, almost colourless to pale yellowish-greenish with 3% KOH. *Clamp connections* abundant in all tissues.

Habitat and distribution

Inocybe griseovelata was found by us always on calcareous soil, along waysides or in parks or cemeteries. It is associated with both frondose trees and conifers. The species is widespread in Europe. It corresponds to SH1472941.08FU (2.0%) of the UNITE database, in which are assembled some sequences from collections, EcM or soil samples, if names are given then labelled *I. griseovelata* (e.g., FN550931, from France).

Type specimen examined

Epitype (Fig. 7a, c–e): *Spores* 9.5–12.5 µm (av. 10.5 µm, SD 0.6 µm) × 5.2–6.7 µm (av. 5.9 µm, SD 0.3 µm); Q = 1.6–2.0 (av. 1.8, SD 0.1) (n = 40), smooth (sub)amygdaloid, often with suprahilar depression, apex (sub)acute. *Basidia* usually 4-spored, rarely 2-spored. *Pleurocystidia* 51–74 µm (av. 63 µm, SD 8 µm) × 13–21 µm (av. 16 µm, SD 2 µm); Q = 3.3–4.8 (av. 3.9, SD 0.4) (n = 15), (sub)cylindrical, sometimes (sub)utriform, apex usually crystalliferous, walls up to 1.5 (2.0) µm thick at the apex, almost colourless to pale yellowish-greenish with 3% KOH. *Cheilocystidia* similar in appearance and size. *Paracystidia* not observed. *Caulocystidia* near the extreme apex of the stipe, 45–90 × 10–15 µm, long and narrow and curved, mostly subcylindrical to subfusiform, apex crystalliferous, walls up to 1.0 (1.5) µm thick at the apex, almost colourless to pale yellowish-greenish with 3% KOH.

Notes

Bandini et al. (2021c) synonymized *Inocybe griseovelata* with *I. subvirgata* and described *I. grusiana*, a species that is rather similar to *I. subvirgata*. One important character distinguishing *I. griseovelata* and *I. grusiana* from each other and from other species is the shape of the caulocystidia near the top of the stipe (Kuyper 1985, Bandini et al. 2021c). These could not be observed in the lectotype material of *I. griseovelata* (or in the holotype material of *I. subvirgata*). It also appears that American authors (Braaten et al. 2014; S. D. Russell, evidenced by MK532850, submitted 13 Oct. 2017 from Indiana) have a different concept of *I. griseovelata* from that of European authors. Therefore, we decided to epitypify *I. griseovelata* here.

Inocybe griseovelata is characterized by an abundant whitish-greyish velipellis, a usually rather smooth to at mostly innately fibrillose pileus surface, stipe only sparely pruinose at the extreme apex, rather large spores, often (sub)cylindrical hymenial cystidia with wide necks and long and narrow caulocystidia. It occurs on calcareous soil with frondose trees as well as with conifers (Kühner 1955; Bandini et al. 2021c). The clade of *I. griseovelata* received full support. A type study of *I. subvirgata* Reumaux was published by Bandini et al. (2021c).

Inocybe javorkae Babos & Stangl,
Annls hist.-nat. Mus. natn. hung. 77: 113 (1985)
(Fig. 21h)

Description and iconography: Babos & Stangl (1985); Nagy & Nagy (2011).

Type specimen examined

Holotype: HUNGARY, Kiskunság Nat. Park, Bugac (9382), “Ösborókás”, Komikt. Bács-Kiskun, in Junipero-Populetum albae festucetosum vaginatae, 13 Nov. 1977, leg. Babos & Friesz (BP77256). *Spores* 11.7–16.0 µm (av. 13.2 µm, SD 0.8 µm) × 6.1–8.9 µm (av. 7.5 µm, SD 0.5 µm); Q = 1.5–2.0 (av. 1.8, SD 0.1) (n = 40), oblong, often almost rectangular, with sinuous outline or subangular to subnodulose. *Basidia* generally 4-spored, sometimes also 2-spored. *Pleurocystidia* 58–76 µm (av. 64 µm, SD 5 µm) × 16–23 µm (av. 20 µm, SD 2 µm); Q = 2.7–3.9 (av. 3.3, SD 0.4) (n = 15), mostly (sub)clavate, also (sub)fusiform, apex usually crystalliferous, walls up to 3.0 (4.0) µm thick at the apex, pale yellowish-greenish with 3% KOH. *Cheilocystidia* somewhat more variable in shape and size. Paracystidia not observed. *Caulocystidia* mostly (sub)clavate, similar in size to pleurocystidia.

Additional specimens examined

GERMANY, Baden-Württemberg, Rhein-Neckar-Kreis, Sandhausen, TK25 6617/4, alt. 115 m, *Pinus sylvestris*, *Helianthemum nummularium*, *Quercus robur*, 21 Oct. 2012, leg. D. Bandini & B. Oertel (SMNS-STU-F-0901704, dupl. DB21-10-12-1). Baden-Württemberg, Rhein-Neckar-Kreis, Walldorf, TK25 6617/4, alt. 120 m, *Pinus sylvestris*, 6 Nov. 2021, leg. D. & G. Bandini (DB6-11-21-1).

Notes

Inocybe javorkae has large basidiomata sticking deep in the sand, and the pileus is almost entirely covered by sand and thus at first very difficult to observe—not without reason, in the protologue they were called “sand-digger” (Babos & Stangl 1985; DB, personal observation). The base of the stipe is bulbous and externally dark brown to blackish, as if it has been stuck in boggy ground. The spores are large, oblong, often almost rectangular, with a sinuous to nodulose outline and pleurocystidia often subclavate. The habitat is calcareous sand. It appears to be a fairly rare species easily confused with *I. sepiana* because of the outwards dark to almost blackish base of the stipe (for differences see notes on *I. sepiana*, below). Such confusion might have happened in a publication by Krisai-Greilhuber (1992), where collections of *I. javorkae* are described. However, judging from the photograph of the basidiomata and the drawings of the microscopic details, it seems that in fact *I. sepiana* was described—the basidiomata are rather small, the pilei are not covered by sand and the spores are smaller. Thus, these collections should be re-examined. We were able to obtain an ITS1 sequence of the holotype of *I. javorkae*, matching with the ITS of our own collections. The clade of *I. javorkae* is sister to the clade of *I. dunensis* and received 98%/100%/1 support (see Fig. 1).

Inocybe lacera (Fr.) P. Kumm, *Führ. Pilzk. (Zerbst)*: 79 (1871) (Fig. 8)

Basionym: *Agaricus lacerus* Fr., *Syst. mycol. (Lundae)* 1: 257 (1821).

Neotypus hic designatus (MBT 10008602)

NETHERLANDS, Drenthe, Eursinge, alt. 22 m, *Salix* sp, *Quercus robur*, *Pinus sylvestris*, *Betula pendula*, 10 Oct. 2018, leg. D. Bandini (STU SMNS-STU-F-0901583, dupl. priv. herb. D. B. DB10-10-18-4).

Description

Pileus 15–40 mm wide, at first subglandular, (sub)campanulate or subconical, later broadly convex or expanded, without or with only a low large umbo, margin at first incurved, later decurved to straight, and often uplifted when old and then pileus depressed around the umbo; young basidiomata covered with sometimes abundant and sometimes rather faint whitish remnants of a velipellis; colour pale brown, nut-brown, greyish brown, dull brown to dark brown (Mu 10YR 5/4–5/8, 4/4–4/6, 3/4–3/6; 7.5YR 5/4–5/6); surface mostly coarsely (sub)lanose, sometimes fibrillose or villose towards the margin, sometimes (sub)squamulose around the centre, seldom scaly; young basidiomata with beige to pale straw-coloured cortina. *Lamellae* rather crowded, moderately crowded to rather distant (c. 30–70, l = 1–3), adnate to broadly adnate with (sub)decurrent tooth, (sub)ventricose, at first whitish, later beige to ochraceous with reddish hue to reddish brown with or without olivaceous hue; edge fimbriate, whitish to concolourous. *Stipe* 20–70 × 2–7 mm, cylindrical or curved, sometimes widened towards the apex, when young entirely covered with rather coarse, whitish, beige to pale straw-coloured tomentum, later reticulate, longitudinally striate or seldom glabrous, sometimes brown, reddish brown to dark brown, but mostly already when young at least in the lower part almost blackish brown beneath the tomentum; extremely sparely pruinose directly below the lamellae, sometimes vanishing with age. *Context* whitish to watery beige in the pileus, whitish to brownish in the stipe, especially in the cortex of the stipe. *Smell* indefinite. *Colour of exsiccata* pileus pale to darker greyish brown, dark brown with greyish hue (Mu 10YR 5/4–5/6, 4/4–4/6, 3/4–3/6), lamellae concolourous or a little lighter in colour, stipe concolourous in the upper half, below dark greyish to greyish with blackish hue, but no obvious darkening or blackening on drying.

Spores 9.8–14.5 µm (11.9 µm, SD 1.1 µm) × 3.7–5.3 µm (av. 4.5 µm, SD 0.3 µm); Q = 2.1–3.6 (av. 2.6, SD 0.2) (n = 120 of 3 coll.), mostly elongate and very narrow (sub)laceroid, but sometimes also oblong (sub)amygdaloid, rather rarely somewhat heterogenous in shape, often with a more or less explicit suprahilar depression, apex mostly subacute to subobtuse, often with small indistinct pseudoporus. *Basidia* 25–35 × 7–10 µm, generally 4-spored, occasionally 2-spored, and then spores up to > 20 µm. *Lamella edge* composed of cheilocystidia and numerous colourless, (sub)clavate or (sub)cylindrical paracystidia, often in different intermediate states with slightly thick walls and often filled with brownish amorphous content. *Pleurocystidia* 34–78 µm (av. 59 µm, SD 8 µm) × 11–27 µm (av. 17 µm, SD 3 µm); Q = 2.0–5.8 (av. 3.6, SD 0.6) (n = 45 of 3 coll.), mostly (sub)fusiform, also (sub)utriform, or somewhat misshaped, generally without or with only a short neck, at the apex often mammiform, often with undate walls, with short or with a rather long, sometimes undate pedicel, apex usually crystalliferous, but sometimes also without crystals, walls up to 2.5 µm thick near the apex, very differently thick from collection to collection, yellow(ish)-green(ish) with 3% KOH. *Cheilocystidia* more variable in shape, and often filled with brownish amorphous content. *Pileipellis* constituted by an epicutis made up of parallel hyphae 5–15 µm wide, with finely to roughly encrusting and parietal light brown to dark brown pigment, subcutis with wider and paler to colourless elements. *Caulocystidia* extremely rarely and only near the extreme apex of the stipe, sometimes vanishing with age, 50–80 × 10–15 (20) µm, mostly oblong, somewhat misshaped subfusiform, and sometimes with slightly undate walls, without or with only a short neck, usually with a short pedicel, with or without small crystals, walls up to 1.0 (1.5) µm thick near the apex, yellow(ish)-green(ish) with 3% KOH; intermixed with narrow, segmented hyphoid elements. *Clamp connections* abundant in all tissues.

Habitat and distribution

Inocybe lacera is a very common and well-known species, which may occur in sandy dunes of the North Sea coast as well as at alpine altitudes above 2300 metres. It occurs in dry sandy terrain as well as in moist and boggy locations. Most often it is observed on acidic soil. Our own collections are from Austria, Finland, Germany, the Netherlands and Switzerland. The species probably corresponds to SH1955848.08FU (0.5%) of the UNITE database, assembling sequences from collections or from EcM from Canada, Estonia, Finland, Germany, Japan, New Zealand, Norway, Korea, Sweden and the United States.

Fig. 8. *Inocybe lacera* – **a.** Neotype; scale bar: 1 cm. **b.** Coll. DB2-10-12-4; scale bar: 1 cm. **c.** Cheilocystidia (coll. DB2-10-12-4); scale bar: 10 µm. **d.** Microscopic characters (neotype); Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm. **e.** Spores (neotype); scale bar: 10 µm.

These sequences are mostly labelled as *I. lacera* or (incorrectly) as *I. lacera* var. *helobia*. Sequence metadata list as mycorrhizal partners Pinaceae or Salicaceae, which corresponds to our own collections that were mostly from places where *Pinus sylvestris* was present, but sometimes also *Salix* or *Picea*. Judging from the entries in the databases, *I. lacera* is a much more common species than *I. moravica*.

Type specimen examined

Neotype (Fig. 8d, e): *Spores* 10.2–14.5 µm (av. 12.4 µm, SD 1.2 µm) × 3.7–5.2 µm (av. 4.5 µm, SD 0.3 µm); Q = 2.2–3.6 (av. 2.8, SD 0.3) (n = 40), generally elongate (sub)laceroid. *Basidia* 4-spored. *Pleurocystidia* 34–69 µm (av. 57 µm, SD 10 µm) × 12–20 µm (av. 16 µm, SD 2 µm); Q = 2.0–4.6 (av. 3.6, SD 0.7) (n = 15), mostly (sub)fusiform, also (sub)utriform, or somewhat misshaped, apex usually crystalliferous, walls up to 2.5 µm thick at the apex, yellow(ish)-green(ish) with 3% KOH. *Cheilocystidia* more variable in shape. *Paracystidia* (sub)clavate or (sub)cylindrical, sometimes in intermediate states and then slightly thick-walled. *Caulocystidia* mostly oblong, somewhat misshaped subfusiform, and sometimes with slightly undate walls, in size similar to hymenial cystidia, intermixed with narrow segmented hyphoid elements.

Selected additional specimens examined

FINLAND, Koillismaa, Kuusamo municipality, Oulanka National Park, Ampumavaara, *Pinus sylvestris, Betula, Picea abies*, 22 Aug. 2015, leg. D. Bandini, J. Vauras & B. Oertel (DB22-8-15-6). Kainuu, Paltamo, Saarinen, Lehtoharju, 27°E:71576;35389, *Pinus sylvestris*, *Picea abies*, *Betula*, 28 Aug. 2017, leg. J. Vauras (TUR-A204903, dupl. SMNS-STU-F-0901708, dupl. DB28-8-17-7-JV32237F). Pohjois-Häme, Äänekoski, Konginkangas, 27° E: 69641: 34392*, Pinus sylvestris*, *Betula*, 2 Sep. 2017, leg. J. Vauras (TUR-A204914, dupl. SMNS-STU-F-0901714, dupl. DB2-9-17-1-JV32297F). GERMANY, Baden-Württemberg, Heidelberg, Stadtwald, TK25 6518/3, alt. 210 m, *Pinus sylvestris*, *Quercus robur*, *Fagus sylvatica,* 15 Apr. 2014, leg. D. Bandini (DB15-4-14-2). Bayern, Kelheim, Abensberg-Offenstetten, TK25 7137/3, alt. c. 380 m, inland-dunes with *Pinus sylvestris*, 11 Oct. 2017, leg. D. Bandini & B. Oertel (DB11-10-17-2). Nordrhein-Westfalen, Kleve, Geldern, near Walbeck, TK25 4503/1, alt. 29 m, *Betula pendula*, *Pinus sylvestris*, *Salix* sp, 10 May 2020, leg. D. Bandini (SMNS-STU-F-0901696, dupl. DB10-5-20-1). Rheinland-Pfalz, Kaiserslautern, Enkenbach-Alsenborn, Nature Reserve Mehlinger Heide, TK25 6512/2, alt. c. 330 m, heath with *Pinus sylvestris*, 24 Oct. 2013, leg. P. & B. Behrens (DB24-10-13-1-Behrens). Sachsen-Anhalt, Harz, Oberharz am Brocken, Kramershai, TK25 4229/4, c. 680 m, *Picea abies*, 2 Oct. 2012, leg. D. Bandini & B. Oertel (DB2-10-12-4). Sachsen-Anhalt, Börde, Angern, Bertingen, TK25 3636/2, sandy terrain with *Pinus sylvestris*, 3 Nov. 2012, leg. D. Bandini & B. Oertel (DB3-11-12-1). NETHERLANDS, Limburg, Wellerloi, near De Hamert, alt. 20 m, *Salix caprea*, *Betula* sp., 7 May 2016, leg. D. Bandini (DB7-5-16-9). Ibidem, at some distance from former location, alt. 20 m, *Salix caprea*, *Betula*, 7 May 2016, leg. D. Bandini (DB7-5-16-12). Drenthe, Kraloo, alt. 15 m, *Salix* sp, *Quercus robur*, *Pinus sylvestris*, *Betula pendula*, 9 Oct. 2018, leg. D. Bandini (SMNS-STU-F-0901707, dupl. DB9-10-18-14). Ibidem, at some distance from former location, alt. 15 m, *Salix* sp, *Quercus robur*, *Pinus sylvestris*, *Betula pendula*, 9 Oct 2018, leg. D. Bandini (DB9-10-18-15). Limburg, Wellerloi, alt. 29 m, *Pinus sylvestris*, *Betula* sp., *Salix* sp., 8 May 2021, leg. D. Bandini (SMNS-STU-F-0901713, dupl. DB8-5-21-3). SWITZERLAND, Graubünden, east from Piz da las Trais Linguas, TK25 1239, alt. 2840 m, *Salix herbacea*, 9 Aug. 2015, leg. B. Oertel (DB9-8-15-1b). Graubünden, Albulapass near La Punt, near Albula-Hospiz, TK25 1237/3, alt. 2300 m, *Dryas octopetala*, *Salix reticulata*, 1 Sep. 2016, leg. B. Oertel (DB1-9-16-8b).

Notes

No type existed for *I. lacera*. The first collection of *I. lacera* in the databases of Sweden's six largest herbaria (http://herbarium.emg.umu.se/index.html) is from 1852, and the first depiction of *I. lacera* (S0663) is from 1849 by E. Pettersen (https://herbarium.nrm.se/specimens/S0663). We therefore chose the neotype of the most common species of the *I. lacera*-group from specimens with the characteristically elongate laceroid spores, which, based on labels in public sequence databases, are most often labelled *I. lacera*.

A number of descriptions and images exist for *I. lacera* (Bresadola 1930; Kuyper 1986; Ferrari 2006; Stangl 1989; Ludwig 2017); however, as *I. lacera* is very similar to *I. moravica* described below, it is impossible to tell whether they refer to *I. lacera* as circumscribed here, to *I. moravica* or to a mixture of both.

Inocybe lacera is characterized by (fugacious) whitish velipellis when young, a fibrillose to scaly brown to dark brown pileus surface, at first whitish lamellae, mostly at least in the lower half up to a blackish brown stipe beneath the tomentum, usually oblong and very narrow laceroid-shaped spores and mostly oblong somewhat misshaped (sub)fusiform hymenial cystidia. The caulocystidia are rare and with age often rubbed off and generally oblong, somewhat misshaped subfusiform. Morphologically and genetically most closely related to *I. lacera* is *I. moravica*, which differs, e.g., by the not whitish but grey(ish) velipellis, often more (sub)squamulose to (sub)squarrose pileus surface, on average wider and usually heterogenously shaped spores and shorter fusiform caulocystidia. *Inocybe helobia* differs, e.g., by the generally smaller size of the basidiomata, smoother surface of pileus, wider spores with an often undulate to subangular outline and on average shorter hymenial cystidia (Kuyper 1986, as "*I. lacera* var. *helobia*"; Bandini et al. 2020a) and *I. impexa* (Lasch) Kuyper, e.g., by abundant arachnoid velipellis and on average longer and much wider spores (Lasch 1829; Kuyper 1986). *Inocybe pluppiana* can be distinguished from *I. lacera*, e.g., by the subangular-shaped and on average shorter spores and shorter hymenial cystidia (Bandini et al. 2020a), and from *I. norvegica* Vauras & E. Larss., e.g., by the smaller size of the basidiomata, smooth and much wider spores and on average shorter hymenial cystidia (Vauras & Larsson 2021; see also notes on *I. moravica*).

We could only locate the type of *I. infelix* var. *brevipes* Peck in NYS, but not the type of *I. infelix* Peck, a species which according to the original description (Peck

1887) seems to be similar to *I. lacera* or even conspecific. A question to P. Brandon Matheny on this matter was kindly answered by the following information: "Peck indicates type specimens of *I. infelix* var. *brevipes* at NYS and an isotype of *infelix* at WTU. Stuntz, however, never examined the type of *infelix*, but he does have notes for var. *brevipes*. Hesler examined all possible Peck types but has no data for *infelix*. Same for Stuntz. I think the "*infelix*" type at WTU is a small piece of the type of var. *brevipes*. My guess is Peck never designated a type specimen for *infelix*, and no one has published on it since Kauffman 1918 (Agaricaceae of Michigan) that I can find." (P.B. Matheny, email to DB, Oct. 4th, 2021). Massee (1904) stated that he had examined the type of *I. infelix*, but possibly this was the type of *I. infelix* var. *brevipes*.

Collections that we consider to be *I. lacera* form a supported (95%/100%/1) monophylum in Fig. 1; using ITS data, the most likely confusion is with *I. moravica*.

Inocybe longicystis → ***Inocybe stellatospora***
(Fig. 22a)

Inocybe mecoana Fachada, Bandini & Mifsud, **sp. n.**
(Fig. 9; MycoBank: MB 845165)

Etymology

Named "mecoana" after "Meco", with the suffix -anus, meaning "from or belonging to Meco", a local Portuguese village by that name, near which the holotype was found.

Diagnosis

Inocybe mecoana **sp. n.** has a dark brown to almost blackish brown pileus, smooth and glabrous pileus surface, ample whitish velipellis visible as a patch at the centre of young basidiomata, an entirely pruinose stipe, rather large spores measuring 8.9–15.4 µm (av. 12.2 µm) × 5.3–8.0 µm (av. 6.8 µm) and rather long (sub)fusiform to (sub)utriform pleurocystidia measuring 59–87 µm (av. 72 µm) × 16–24 µm (av. 19 µm), and inhabitats Mediterranean coastal shores. The species can be recognized by the combination of the above characters and differs in its ITS sequence from other superficially similar smooth-spored species, such as *I. tarda* or *I. aurantiobrunnea*.

Holotype

PORTUGAL, Sesimbra, Praia da Amieira, near Aldeia do Meco, 38°30′06.0″N 9°10′50.5″, alt. 25 m, *Pinus pinea*, *Helichrysum italicum*, 22 Dec. 2019, leg. V. Fachada (PO-F2158).

Description

Pileus 24–65 mm wide, at first hemispherical to (sub)conical, later expanded, margin at first slightly decurved, soon straight and slightly uplifted with age, and then depressed around the umbo, which can be absent or low and irregular; young basidiomata with ample remnants of a whitish velipellis, visible at least as a patch at the centre, sometimes also at the margin as a whitish rim; colour dark brown, sometimes almost chestnut-brown to sometimes almost blackish towards the margin, at the centre beige to brownish or ochraceous brownish due to remnants of the velipellis (Mu 10YR 3/4–3/6, 2/2; 7.5YR 3/2–3/4); surface smooth and almost sericeous, with age getting rimulose to somewhat lacerate towards the margin. *Lamellae* moderately to rather crowded (c. 50–70(80), l = 1–3), adnate, (sub)ventricose; edge fimbriate, initially light grey, later light brown, finally caramel-brown. *Stipe* 40–85 × 5–14 mm, cylindrical or curved, base often somewhat recurved, even to very slightly enlarged but never abruptly bulbose, at first covered with fine whitish tomentum, later longitudinally striate to glabrous, mostly whitish beige to yellowish, at the apex often somewhat darker, pale wood-coloured to brownish, sometimes with clear flushes of bright orange, paler at the base, densely pruinose on its entire length. *Context* whitish, unchanging in the stipe, rather translucid in the pileus, rather brittle. *Smell* spermatic. *Colour of exsiccata* pileus the same dark brown as in fresh state (Mu 10YR 3/4–3/6, 2/2, 7.5YR 3/2–3/4), lamellae paler, stipe light brown to beige, no significant darkening on drying.

Spores 8.9–15.4 µm (av. 12.2 µm, SD 1.2 µm) × 5.3–8.0 µm (av. 6.8 µm, SD 0.6 µm); Q = 1.3–2.4 (av. 1.8, SD 0.2) (n = 190 of 3 coll.), rather variable from ovoid-ellipsoid, (sub)amygdaloid, to somewhat navicular, often with conical apex. *Basidia* 27–44 × 8–11 µm, generally 4-spored. *Lamellae edges* composed of cheilocystidia and colourless, subclavate to subglobose, thin-walled paracystidia. *Pleurocystidia* 59–87 µm (av. 72 µm, SD 6 µm) × 16–24 µm (av. 19 µm, SD 2 µm); Q = 2.7–4.9 (av. 3.8, SD 0.4) (n = 44 of 2 coll.), (sub)fusiform to (sub)utriform, more rarely clavate-fusiform and then less crystalliferous, very rarely cylindrical-(sub)lageniform, generally without or with only a short wide neck, occasionally with (sub)capitate apex, usually quite crystalliferous, without or with only a short pedicel, apex usually with often rather small crystals, walls up to 3.0 (3.8) µm thick at the apex, usually colourless to weakly yellowish-greenish with 3% KOH. *Cheilocystidia* abundant, often somewhat shorter than the pleurocystidia, and more variable in shape. *Pileipellis* consisting of a very thin epicutis made up of parallel hyphae 5–15 µm wide, with finely encrusting and parietal brownish pigment, subcutis with wider and paler to colourless elements. *Caulocystidia* on entire length of the stipe, 40–87 × 13–27 µm, mostly (sub)fusiform, sometimes (sub)utriform or somewhat misshaped with undate walls, without or with only a short neck, without or with only a short pedicel, walls up to 2.0 (2.5) µm, intermixed with numerous (sub)clavate to subglobose cauloparacystidia, colourless to yellowish-greenish with 3% KOH. *Clamp connections* present in all tissues.

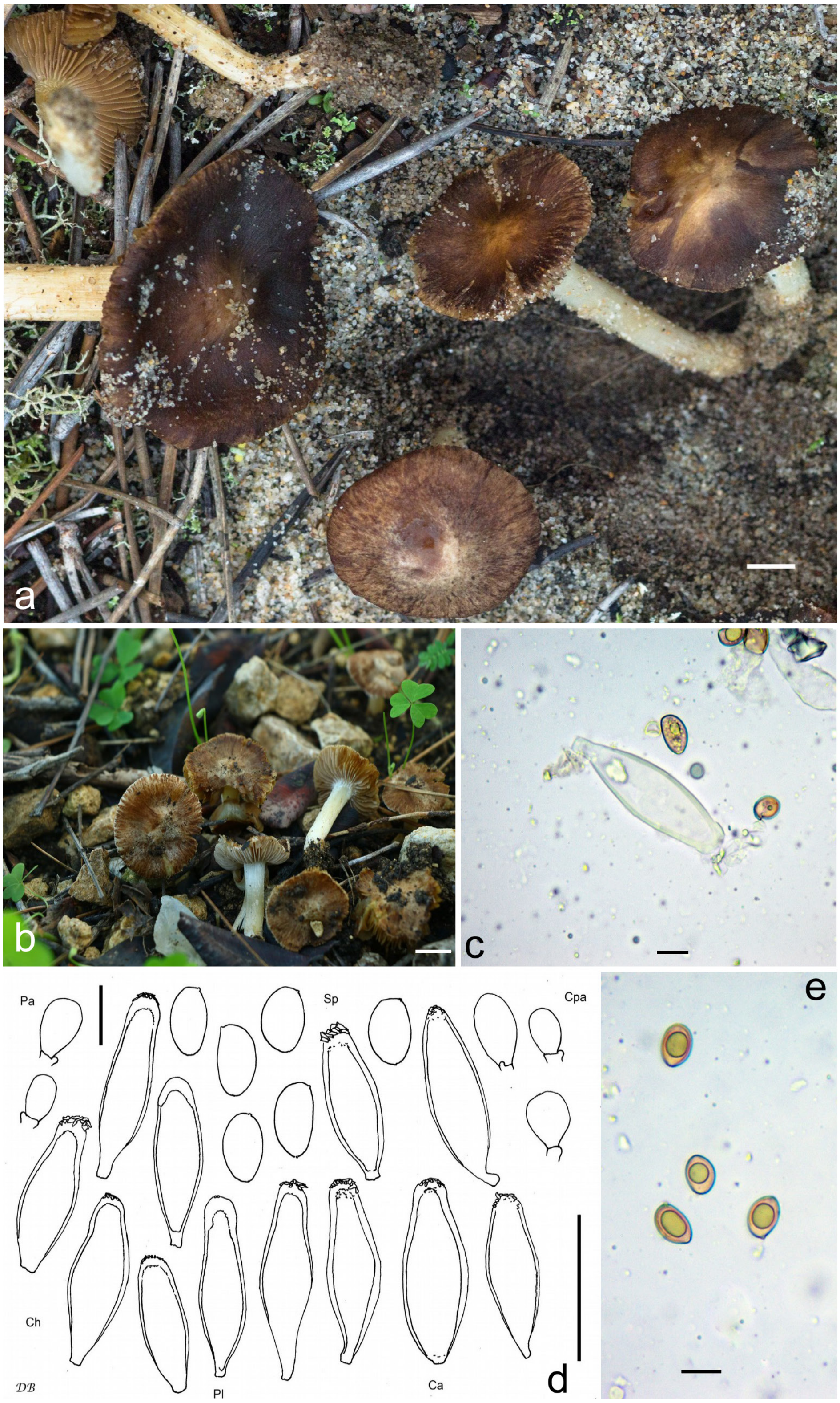

Fig. 9. *Inocybe mecoana* **sp. n.** – **a.** Holotype (photo: V. Fachada); scale bar: 1 cm. **b.** Coll. SM588a (photo: S. Misfud); scale bar: 1 cm. **c.** Cheilocystide (holotype); scale bar: 10 µm. **d.** Microscopic characters (holotype); Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm. **e.** Spores (holotype), scale bar: 10 µm.

Habitat and distribution

The holotype collection of *I. mecoana* **sp. n.** was found directly behind the white dunes in Praia da Amieira, Southwest Portugal, occurring in sand in the vicinity of *Pinus pinea*, *Pinus pinaster*, *Juniperus* sp. and native sandy bushes (*Corema album*, *Helichrysum italicum*), in troops, often deeply buried in the sand, in clearings where the trees first appear, but sometimes completely exposed on the dunes. The collections from Malta were found on Gozo (Maltese Islands) in the Chambray pinetum (Għajnsielem), an afforested area about 100 m from the coast composed primarily of *Pinus halepensis* but also with pockets of *Ceratonia siliqua* and *Prunus dulcis* trees and, further away, few *Eucalyptus gomphocephala* and *Acacia saligna*. The pinetum is found on the clay slopes below Fort Chambray, the soil of which is rich with organic matter from the existing trees over the last five decades. There are also elements of coralline limestone rocks crumbling down from the layer above the clay slopes. The soil is calcareous and slightly alkaline in pH and predominantly clayey. The location is about 10–20 m above sea level. Apart from our own collections, no other sequences or collections from the same environment are known to us.

Additional specimens examined

MALTA, Gozo, Għajnsielem, Chambray pinetum, alt. 20 m, *Ceratonia siliqua*, *Pinus halepensis*, 24 Dec. 2020, leg. S. Mifsud (SM588a). Ibidem, at some distance from former location, alt. 20 m, *Pinus halepensis*, *Ceratonia siliqua*, 24 Dec. 2020, leg. S. Mifsud (SM588b). Ibidem, at some distance from former location, alt. 20 m, *Pinus halepensis*, *Ceratonia siliqua*, 24 Dec. 2020, leg. S. Mifsud (SM588c). PORTUGAL, Sesimbra, Praia da Amieira, 38°29′50.2″N 9°10′52.4″W, alt. 26 m, *Pinus pinea, Helichrysum italicum*, 3 Jan. 2021, leg. V. Fachada (PO-F2238).

Notes

Inocybe mecoana **sp. n.** is characterized by a dark brown to almost blackish brown pileus, with smooth and glabrous surface, a whitish velipellis visible as patch at the centre of young basidiomata, an entirely pruinose stipe, rather large spores and rather long (sub)fusiform to (sub)utriform pleurocystidia as well as a habitat along shallow Mediterranean shores, namely calcareous sand dunes and calcareous soil. The species might be mistaken for *I. tarda* Kühner, which is often found on sandy inland dunes with *Pinus* and which often has an equally dark pileus. It differs from *I. mecoana*, e.g., by a stipe which is only sparely pruinose in the lower half and which mostly is somewhat pinkish near the apex and with age often becomes entirely reddish in different intensity and smaller spores, which often have a characteristic bulgy shape (Kühner 1955; Bandini et al. 2021c). *Inocybe psammobrunnea* occurs in the same kind of habitat, and the young basidiomata of this species often have, like in *I. mecoana*, a patch of velipellis at the centre of the pileus. The pileus, however, is paler, the stipe is often pinkish to intensely pinkish-reddish and pruinose only near the apex, and the spores are smaller (Bon 1990; Poirier 2002, as "*I. griseotarda*"; Bandini et al. 2021c). *Inocybe aurantiobrunnea*, a Mediterranean species associated with *Pinus*, has a very dark brown pileus like *I. mecoana*, but the surface is more finely fibrillose, the context is entirely orange or orange-yellow, the stipe is pruinose only near the apex and the hymenial cystidia are mostly (sub)cylindrical (Esteve-Raventós & García Blanco 2003). *Inocybe phaeoleuca* Kühner may be found in dune sand next to *Pinus* (DB, personal observation), its surface is often quite smooth and the stipe is entirely pruinose. The pileus, however, is paler brown, the stipe remains whitish for a long time, the spores are much smaller and the pleurocystidia are on average shorter (Kühner 1955; Bandini et al. 2019c; DB, personal observation). *Inocybe deianae* Eyssart. has a paler, villose to strongly lanose to (sub)squamulose or lacerate squamulose pileus, the spores are pruinose only in the upper part and smaller (Eyssartier 2007; Bandini et al. 2022a), and *I. messapica* Cervini differs by, e.g., a paler pileus, less "patchy" velipellis, smaller spores and shorter pleurocystidia as well as in the habitat (Cervini 2021). *Inocybe neorufula* Esteve-Rav., Macau & Ferville has a paler and more reddish-tinged pileus, the pileus surface is not as glabrous and the spores are clearly smaller (Esteve-Raventós et al. 2012; Bandini et al. 2020c). As pointed out in the Results section, *I. mecoana* is the species with the least support from the phylogenetic analysis, assuming that the sister clade, with a sequence wrongly identified as *I. pruinosa* and two environmental sequences (receiving 95%/100%/1 support), represents another taxon. This assumption is based on direct comparison of the sequences, which showed that the soil sample clone FJ237104 is quite different from the other sequences (artefact?), while the sequence from "*I. pruinosa*" and the other environmental sequence differ constantly in 13 alignment positions in the ITS from *I. mecoana*. Thus, although we cannot explain the weak support for *I. mecoana* in the tree results, we suspect that it was a rogue result which may be related to the composition of the alignment, most probably with the inclusion of FJ237104.

Inocybe moravica Hruby, *Hedwigia* 70: 279 (1930) (Figs. 10, 22b)

Description and iconography: Hruby (1930).

Description

Pileus 15–50 mm wide, at first (sub)campanulate or subconical, later broadly convex or expanded, generally without or with a rather low, large umbo, margin often strongly involute when young or even when older, later decurved or straight to uplifted when old; young basidio-

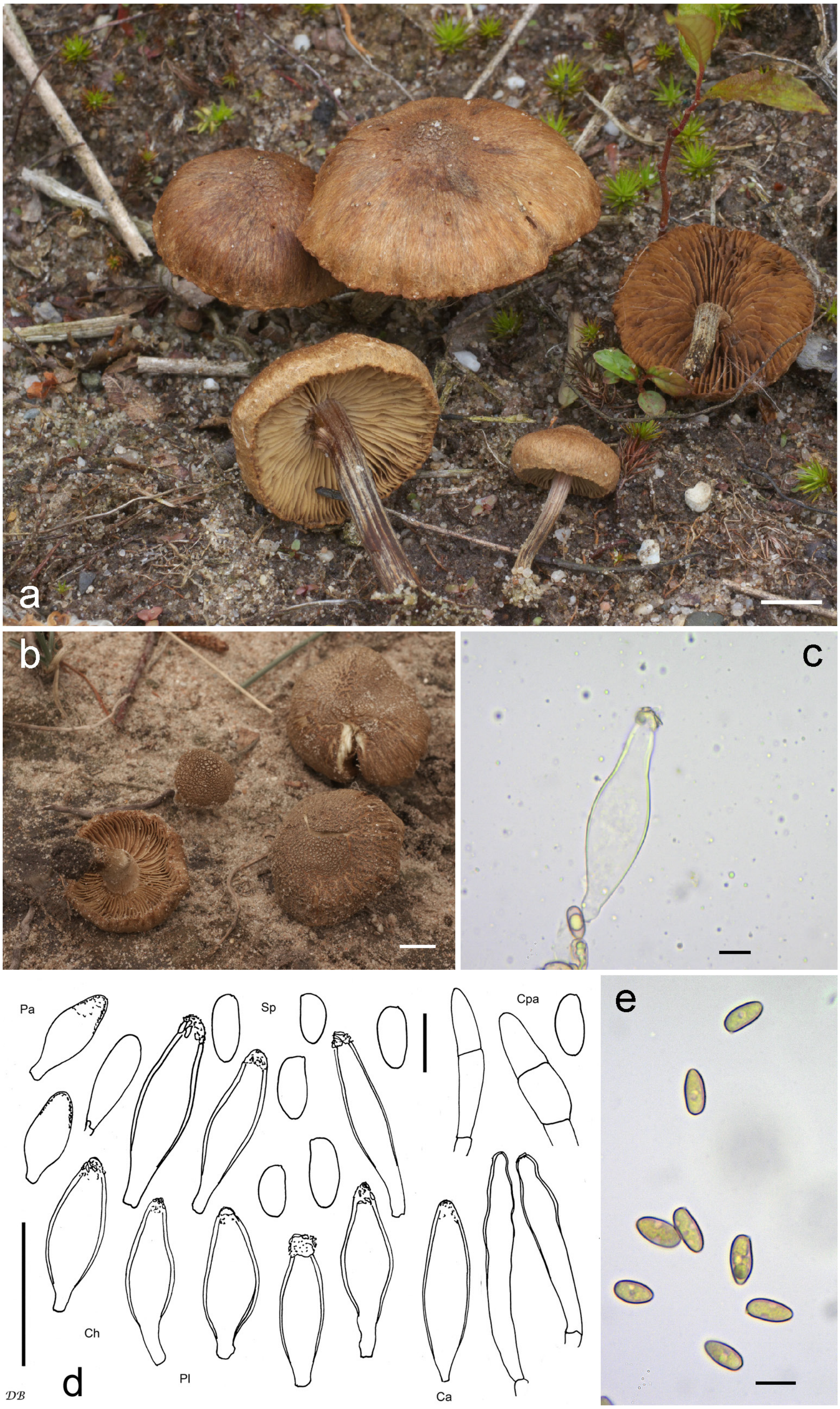

Fig. 10. *Inocybe moravica* **sp. n.** – **a.** Coll. DB31-5-15-8; scale bar: 1 cm. **b.** Coll. DB31-5-15-7; scale bar: 1 cm. **c.** Cheilocystide (Coll. DB31-5-15-7); scale bar: 10 µm. **d.** Microscopical characters (Coll. DB31-5-15-8); Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm. **e.** Spores (Coll. DB31-5-15-7); scale bar: 10 µm.

mata with fugacious grey(ish) remnants of velipellis; colour dull brown to dark brown, often with greyish tinge (Mu 10YR 4/4–4/6, 3/2–3/6; 7.5YR 3/2–3/4), often almost blackish at the centre; surface usually coarsely lanose to (sub)squamulose and often minutely (sub)squarrose at least around the centre, at the centre, with age, often deeply areolate diffracted; young basidiomata with pale ochraceous cortina. *Lamellae* moderately crowded (c. 35–50, l = 1–3), broadly adnate with (sub)decurrent tooth, even to subventricose, beige to ivory-coloured, later sometimes intensely ochraceous or brownish with olivaceous tinge or reddish brown; edge (sub)fimbriate, often notchy, whitish to concolourous with age. *Stipe* 20–80 × 2–7 (10) mm, cylindrical or up to strongly widened towards the apex, when young entirely covered with rather coarse beige to pale straw-coloured tomentum, later longitudinally striate and greyish brown to dark brown, sometimes with reddish tinge in the upper half and up to blackish brown in the lower half and, when older, on entire length beneath the tissue; sparely pruinose only near the extreme apex of the stipe, pruina often vanishing with age. *Context* whitish to watery brownish in pileus and stipe, reddish-brownish in the cortex of the stipe. *Smell* indistinct to faintly fungoid. *Colour of exsiccata* pileus dark brown, dark greyish brown (Mu 10YR 3/2–3/6; 7.5YR 3/2–3/4), lamellae and stipe concolourous or a little lighter in colour, no darkening or blackening on drying.

Spores 9.3–17.0 µm (av. 11.8 µm, SD 1.4 µm) × 4.5–6.7 µm (av. 5.2 µm, SD 0.5 µm); Q = 1.7–3.1 (av. 2.3, SD 0.2) (n = 120 of 3 coll.), usually extremely variable in shape and size, from elongate (sub)laceroid to elongate subamygdaloid, subcylindrical or subovoid, boletoid or even subangular, seldom uniformly laceroid, often with a more or less explicit suprahilar depression, apex subacute, subobtuse, with indistinct pseudoporus. *Basidia* 25–33 × 7–10 µm, generally 4-spored, seldom also 2-spored and then spores up to > 20 µm. *Lamella edge* composed of cheilocystidia and numerous colourless, (sub)clavate or (sub)cylindrical paracystidia, often in intermediate states with slightly thickened walls and often filled with brownish amorphous content. *Pleurocystidia* 35–98 µm (av. 62 µm, SD 12 µm) × 9–22 µm (av. 16 µm, SD 3 µm); Q = 2.5–6.5 (av. 4.1, SD 1.1) (n = 45 of 3 coll.), mostly (sub)fusiform, but also (sub)utriform or (sub)clavate and often somewhat deformed, generally without or with only a short neck, at the apex sometimes mammiform, and sometimes with undate walls, usually with a short, but occasionally rather long, sometimes undate pedicel, apex usually crystalliferous, walls up to 1.5 (2.5) µm thick near the apex, yellow(ish)-green(ish) with 3% KOH. *Cheilocystidia* more variable in shape and often filled with brownish amorphous content. *Pileipellis* constituted by an epicutis made of parallel hyphae 3–13 µm wide, with only faintly encrusting and parietal brown(ish) pigment, subcutis with wider and paler to colourless elements. *Caulocystidia* sparely only near the extreme apex of the stipe of young basidiomata, 35–60 (70) × 8–20 µm, mostly rather short fusiform, without a neck and without or with only a short pedicel, walls up to 1.0 (1.5) µm near the apex, yellow(ish)-green(ish) with 3% KOH; often intermixed with rather wide catenate hyphoid elements. *Clamp connections* abundant in all tissues.

Habitat and distribution

Inocybe moravica was found by us in Finland, Germany and the Netherlands. Due to the similarity with *I. lacera*, *I moravica* is impossible to match with the UNITE species hypotheses, because the sequence divergence is so small that even small sequence errors can obscure the distinction between the two taxa. UNITE SH1955853.08FU (0.5%) includes sequences from EcM collections respectively from Canada and the United States, mostly labelled as *I. lacera* or *I. lacera* var. *helobia* but which probably correspond to *I. moravica*. Some more sequences can be found in GenBank from Estonia, Germany, Japan, Norway and Sweden. Most of our own collections were associated with *Pinus sylvestris*, some originated from very dry acidic sandy heathland terrain next to *Calluna vulgaris*, others from the border of lakes, not directly on the edge of the water but on a slightly higher sandy and acidic soil. The holotype collection was found in a mossy oakwood.

Type specimen examined

Holotype (Fig. 22b): CZECH REPUBLIC, Kromau [now Moravský Krumlov], urban forest on mossy ground with *Quercus*, Aug. 1927, [leg. J. Hruby] (BRNU-07012-39). *Spores* 10.0–13.8 µm (av. 11.9 µm, SD 1.1 µm) × 4.6–6.0 µm (av. 5.1 µm, SD 0.4 µm); Q = 0.9–2.7 (av. 2.3 SD 0.2) (n = 40), variable in shape and size, from elongate (sub)laceroid to elongate subamygdaloid, subcylindrical subovoid or (sub)boletoid. *Basidia* 4-spored. *Pleurocystidia* 50–74 µm (av. 62 µm, SD 7 µm) × 15–27 µm (av. 18 µm, SD 3 µm); Q = 2.7–4.3 (av. 3.5, SD 0.5) (n = 15), mostly (sub)fusiform, apex usually crystalliferous, walls up to 1.5 (2.5) µm thick at the apex, yellowish-greenish with 3% KOH. *Cheilocystidia* similar in appearance and size. *Paracystidia* oblong (sub)clavate to subcylindrical. *Caulocystidia* not studied (to preserve the material).

Selected additional specimens examined

FINLAND, Pohjois-Savo, Suonenjoki, town, Tervala, 27°E:69471:35061, *Betula*, *Pinus sylvestris*, *Picea abies*, 1 Sep. 2017, leg. J. Vauras (TUR-A204911, dupl. SMNS-STU-F-0901715, dupl. DB1-9-17-2-Vauras-JV32271F). Koillismaa, Kuusamo municipality, Oulanka National Park, Pähkänä, *Pinus sylvestris*, *Betula* sp., *Picea abies*, 21 Aug. 2015, leg. D. Bandini, J. Vauras & B. Oertel (DB21-8-15-2). GERMANY, Nordrhein-Westfalen, Kleve, Weeze, gravel pit, TK25 4402/2, alt. 30 m, *Salix caprea*, *Pinus sylvestris*, *Betula* sp., 24 May, 2017, leg. D. Bandini (DB24-5-17-2). Nordrhein-Westfalen, Kleve, Kevelaer, Wemb, TK25 4403/1, alt. 30 m, *Betula* sp., *Salix* sp., *Pinus sylvestris*, 13 Oct. 2018, leg. D. Bandini (DB13-10-18-1). Rheinland-Pfalz, Kaiserslautern, Enkenbach-Alsenborn, Nature

Reserve Mehlinger Heide, TK25 6512/2, ca. 330 m, *Pinus sylvestris*, 9 Nov. 2013, leg. B. Oertel (DB9-11-13-2b). Sachsen-Anhalt, Harz, Oberharz am Brocken, Kramershai, TK25 4229/4, alt. c. 600 m, *Picea abies*, 2 Oct. 2012, leg. D. Bandini & B. Oertel (DB2-10-12-1). NETHERLANDS, Limburg, Wanssum, near Maasduinen, alt. 25 m, sandy terrain with *Betula* sp., *Salix caprea*, 30 May 2015, leg. D. Bandini (DB30-5-15-1). Ibidem, at some distance from former location, sunny sandy terrain with *Pinus sylvestris*, *Betula* sp., *Calluna vulgaris*, 31 May 2015, leg. D. Bandini (SMNS-STU-F-0901697, dupl. DB31-5-15-2). Ibidem, at some distance from former location, sunny sandy terrain with *Pinus sylvestris*, *Betula* sp., *Calluna vulgaris*, 31 May 2015, leg. D. Bandini (DB31-5-15-7). Limburg, Wanssum, near Maasduinen, alt. 25 m, sandy terrain with *Salix caprea*, *Pinus sylvestris Betula* sp., 31 May 2015, leg. D. Bandini (SMNS-STU-F-0901700, dupl. DB31-5-15-8). Limburg, near Wellerloi, alt. 25 m, *Betula* sp., *Salix* sp., *Pinus sylvestris*, 5 Oct. 2019, leg. D. Bandini (DB5-10-19-3). Ibidem, at some distance from former location, alt. 22 m, *Betula* sp., *Salix* sp., *Pinus sylvestris*, 5 Oct. 2019, leg. D. Bandini (SMNS-STU-F-0901695, dupl. DB5-10-19-6). Ibidem, at some distance from former location, alt. 22 m, *Betula* sp., *Salix* sp., *Pinus sylvestris*, 5 Oct. 2019, leg. D. Bandini (SMNS-STU-F-0901698, dupl. DB5-10-19-7). Drenthe, Stuifzand, alt. 15 m, *Betula pendula*, *Salix caprea*, 14 May 2019, leg. D. Bandini (SMNS-STU-F-0901698, dupl. DB14-5-19-5).

Notes

It seems that *I. moravica* is only known from the protologue by Hruby (1930), and no entries in GenBank were found with this name. According to the protologue the pileus with papillate umbo is dark grey-brown, the surface at the centre is fibrillose-squamulose, the stipe is grey brownish, the lamellae pale cinnamon brownish and the spores are long and cylindrical with a size of 15–18 µm. Our examination of the holotype suggests that the species is a close neighbour, both morphologically as well as molecularly, to *I. lacera*.

Our own collections of the species are characterized by (fugacious) grey(ish) velipellis when young, coarsely fibrillose to coarsely lanose or minutely (sub)squamulose, at the centre often areolate diffracted pileus surface, at first beige to ivory-coloured lamellae, mostly at least in the lower half up to the blackish brown stipe beneath the tomentum, usually heterogenous shaped spores and generally fusiform caulocystidia. The species can easily be mistaken for *I. lacera*, which can be distinguished from *I. moravica*, e.g., by whitish velipellis when young, usually more uniformously (sub)lanose to villose pileus surface, mostly on average narrower elongate (sub)laceroid spores and longer, misshaped subfusiform caulocystidia. *Inocybe pluppiana* has subangular shaped and on average shorter spores and shorter hymenial cystidia (Bandini et al. 2020a), and *I. helobia* can usually be distinguished by its smaller sized basidiomata, smoother surface of pileus, wider spores with often undulate to subangular outline and on average shorter hymenial cystidia (Kuyper 1986, as "*I. lacera* var. *helobia*"; Bandini et al. 2020a). *Inocybe impexa* has an abundant arachnoid velipellis, on average longer and much wider spores (Lasch 1829; Kuyper 1986), and *I. norvegica* differs, e.g., by the smaller size of the basidiomata, smooth and much wider spores and on average shorter hymenial cystidia (Vauras & Larsson 2021).

Inocybe lacera and *I. moravica* are very similar in macroscopic as well as in microscopic aspects and may occur at the same locations. In collections with young and older basidiomata in good condition, the differentiation between the two species is feasible without major problems. However, it is sometimes extremely difficult to determine either species from one single or aged basidiomata, because then some of the distinguishing features such as presence or colour of a velipellis or the shape and length of the caulocystidia cannot be checked anymore, and the spore width and shape alone is not in all cases a reliable feature, since in some collections of *I. lacera* the spores may be quite heterogenous in shape as well. Thus, the literature cited under *I. lacera* may refer as well to *I. moravica*.

If we had been in a position to describe either species as new, we would have hesitated to do so. However, as both species have been described before, and morphological as well as sequence characters from different markers support each other, we hesitate to synonymize *I. moravica* with *I. lacera*. The ambiguous placement of the Norwegian collections in the tree and the lack of support (the clade including *I. moravica* as well as sequences from *I.* cf. *moravica* received -/98/-) is at least in part due to missing data; indeed, there are more alignment positions supporting the split between *I. lacera* and *I moravica* in the LSU than in the ITS dataset (11 differences including gaps in the LSU vs. 5 differences in the ITS) and for the Norwegian sequences the only marker available was ITS. The clade including only sequences labelled *I. moravica* received 94%/100%/1 support, is further supported by *RPB2* (see Results), but was not reciprocally monophyletic in relation to the sequences labelled *I.* cf. *moravica*. Although we tentatively recognize *I. moravica* here, the distinction from *I. lacera* needs further observations.

Inocybe mortenii Weholt & Bandini, **sp. n.**

(Fig. 10; MycoBank: MB 845166)

Etymology

Named "mortenii" after Morten Pettersen, an ardent Norwegian collector of *Inocybe* and collector of the first Norwegian collection of the species in 2015.

Diagnosis

Inocybe mortenii **sp. n.** mostly has a tomentose-sublanose, pale brown to chestnut-brown pileus with an often areolate diffracted centre with age, often with thick layer of greyish velipellis when young, thickish lamellae, stipe entirely or only near the apex reddish-pinkish

Fig. 11. *Inocybe mortenii* **sp. n.** – **a.** Holotype (photo: Ø. Weholt); scale bar: 1 cm. **b.** Coll. DB19-9-20-5; scale bar: 1 cm. **c.** Cheilocystide (Coll. DB19-9-20-6); scale bar: 10 µm. **d.** Microscopic characters (holotype); Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm. **e.** Spores (holotype); scale bar: 10 µm.

to dark pinkish violaceous, smooth spores measuring 8.5–10.5 µm (av. 9.3 µm) × 4.7–5.7 µm (av. 5.1 µm), rather narrow hymenial cystidia with a wide neck and sometimes subcapitate, pleurocystidia measuring 45–80 µm (av. 61 µm) × 9–16 µm (av. 12 µm). It grows on acidic, moist soil. The species can be recognized by the combination of the above characters and differs in its ITS sequence from other superficially similar smooth-spored species, such as *I. cincinnata* or *I. subnudipes*.

Holotype

NORWAY, Viken county, Østfold, Fredrikstad municipality, near Søndre Haugen, alt. c. 60 m, prevailing *Populus tremula*, mixed with *Picea abies*, 1 Sep. 2017, leg. Ø. Weholt (holotype O-F-259432; isotypes priv. herb. Weholt OW30-17, priv. herb. D. B. DB1-9-17-Weholt).

Description

Pileus 5–30 mm wide, at first (sub)conical, later conico-convex, broadly convex or expanded, mostly with a more or less pronounced, sometimes even (sub)papillate umbo, margin at first slightly incurved, later decurved to straight or even uplifted, and then pileus depressed around the umbo; young basidiomata with often a thick layer of a greyish velipellis; colour pale brown, nut-brown to brown or even chestnut-brown (Mu 10YR 5/6–5/8, 4/4–4/6; 7.5YR 4/4–4/6), young basidiomata due to the velipellis sometimes pale greyish-brownish; surface densely tomentose to tomentose-sublanose, sometimes also (sub)-squamulose, at the centre often areolate diffracted; young basidiomata with remnants of a pale cortina. *Lamellae* subdistant (c. 25–40, l = 1–3), thickish, almost free to adnate, (sub)ventricose, at first whitish, later dingy whitish to pale ochraceous, often with brownish to pinkish-reddish blotches with age; edge fimbriate, whitish to concolourous. *Stipe* 20–50 × 2–4 mm, cylindrical or curved, when young covered with whitish tomentum, later longitudinally striate, at first sometimes entirely pinkish but sometimes also reddish-pinkish to dark pinkish violaceous only near the apex and somewhat straw-coloured beneath, sometimes entirely brownish to dark reddish brown with age; pruinose only near the apex of the stipe. *Context* (watery) whitish in the pileus, whitish in the stipe, but pinkish-reddish or violaceous near the apex of the stipe, at least in the cortex of the stipe when young. *Smell* indistinct to subspermatic, at least when cut. *Colour of exsiccata* pileus brown to dark brown with or without reddish hue (Mu 10YR 4/4–4/6; 7.5YR 4/4–4/6), lamellae and stipe concolourous or a little lighter in colour, no darkening or blackening on drying.

Spores 8.5–10.5 µm (av. 9.3 µm, SD 0.4 µm) × 4.7–5.7 µm (av. 5.1 µm, SD 0.2 µm); Q = 1.6–2.1 (av. 1.8, SD 0.1) (n = 120 of 3 coll.), smooth, (sub)amygdaloid, sometimes (sub)ellipsoid, usually without a suprahilar depression, apex (sub)acute, with indistinct pseudoporus. *Basidia* 23–29 × 7–9 µm, generally 4-spored, seldom also 2-spored. *Lamellae edges* composed of cheilocystidia and numerous colourless, (sub)clavate, sometimes catenate, thin-walled paracystidia. *Pleurocystidia* 45–80 µm (av. 61 µm, SD 10 µm) × 9–16 µm (av. 12 µm, SD 2 µm); Q = 3.3–7.6 (av. 5.1, SD 1.0) (n = 45 of 3 coll.), mostly rather narrow (sub)fusiform, (sub)cylindrical or (sub)utriform, with a short or long, sometimes undate neck, and occasionally with geliferous cap and subcapitate, at the apex generally wide, usually with short pedicel, sometimes with truncate base, apex usually crystalliferous, walls generally rather thin, up to 1.0 (1.5) µm thick at the apex, yellowish-greenish with 3% KOH. *Cheilocystidia* similar in size, but somewhat more variable in shape. *Pileipellis* constituted by an epicutis made of parallel hyphae 4–15 µm wide, with encrusting and parietal brownish pigment, subcutis with wider and paler to colourless elements. *Caulocystidia* only near the apex of the stipe, 50–100 × 10–15 µm, generally long and narrow (sub)lageniform, subutriform, usually with undate walls, without or with only a short pedicel, apex usually crystalliferous, walls up to 1.0 µm thick at the apex, yellowish-greenish with 3% KOH; intermixed with numerous, oblong (sub)clavate cauloparacystidia. *Clamp connections* abundant in all tissues.

Habitat and distribution

Inocybe mortenii **sp. n.** was collected by us in Austria, Germany and Norway, from rather moist to shady habitats; in Austria always in *Picea abies* forests, in Norway in mixed forests, but apparently mainly with *Populus tremula* and in Germany with frondose trees. The species corresponds to SH1239177.08FU (3.0%) of the UNITE database, including sequences of soil samples, only one sequence from a collection from Sweden, labelled "*I.* cf. *subnudipes*", and some EcM-sequences from Estonia, for which "*Populus*" was indicated as host.

Additional specimens examined

AUSTRIA, Salzburg, Tamsweg, ÖK25V 3230-Ost, alt. 1490 m, *Picea abies*, 19 Sep. 2020, leg. D. Bandini (DB19-9-20-5). Ibidem, at some distance from former location, alt. 1470 m, *Picea abies*, 19 Sep. 2020, leg. D. Bandini (DB19-9-20-6). Ibidem, at some distance from former location, alt. 1470 m, *Picea abies*, 19 Sep. 2020, leg. D. Bandini (SMNS-STU-F-0901737, dupl. DB19-9-20-10). GERMANY, Baden-Württemberg, Rhein-Neckar-Kreis, near Epfenbach, TK256619/1, alt. 260 m, shady path with *Fagus sylvatica*, *Quercus robur*, 6 Aug 2016, leg. D. Bandini (DB6-8-16-3). NORWAY, Viken county, Østfold, Fredrikstad municipality, Søndre Haugen, *Populus* sp., some *Picea abies*, *Betula* sp., 13 Sep. 2015, leg. M. Pettersen (MP-11-130915). Ibidem, at some distance from former location, *Populus* sp., some *Picea abies*, *Betula* sp., 31 Jul. 2016, leg. M. Pettersen (MP-9-310716). Ibidem, at some distance from former location, *Populus* sp., some *Picea abies*, *Betula* sp., 5 Aug. 2016, leg. Ø. Weholt (OW-I12-16). Ibidem, at some distance from former location, *Populus* sp., some *Picea abies*, *Betula* sp., 10 Aug. 2016, leg. M. Pettersen (MP-2-100816).

Ibidem, at some distance from former location, *Populus* sp., some *Picea abies*, *Betula* sp., 11 Aug. 2016, leg. M. Pettersen (MP-4-110816). Ibidem, at some distance from former location, *Populus* sp., some *Picea abies*, *Betula* sp., 19 Aug. 2016, leg. M. Pettersen (MP-2-190816). Ibidem, at some distance from former location, *Populus* sp., some *Picea abies*, *Betula* sp., 24 Aug. 2016, leg. M. Pettersen (MP-2-240816). Ibidem, at some distance from former location, *Populus* sp., some *Picea abies*, *Betula* sp., 21 Aug. 2018, leg. M. Pettersen (MP-7-210818). Viken county, Østfold, Fredikstad municipality, Tofteberg, in *Sphagnum*, *Picea abies*, *Betula* sp., 3 Sep. 2019, leg. Ø. Weholt (OW-I34-19). Ibidem, at some distance from former location, *Populus* sp., some *Picea abies*, *Betula* sp. 2 Aug. 2020, leg. Ø. Weholt (OW-I54A-20).

Notes

Inocybe mortenii **sp. n.** is characterized by the mostly tomentose-sublanose pileus surface with often areolate diffracted centre with age, often a thick layer of greyish velipellis when young, thickish lamellae often with brownish to pinkish-reddish blotches with age, sometimes entirely pinkish, but sometimes only near the apex reddish-pinkish to dark pinkish violaceous stipe and rather narrow hymenial cystidia with a wide, often undate neck and sometimes subcapitate and geliferous cap. It occurs on acidic, moist soil. The species could be mistaken for *I. subnudipes*, which also has hymenial cystidia with often slightly undate walls. However, in this species the pileus surface is not lanose but innately fibrillose without a velipellis, and the hymenial cystidia are usually not subcapitate (Kühner 1955; DB, personal observation; and see below). *Inocybe mortenii* may further be mistaken for one of the several other species with a violet pinkish stipe. *Inocybe amethystina* Kuyper differs, however, e.g., by a more squamulose to scaly pileus centre, thinner and blotchy lamellae, on average larger spores and wider walls of the hymenial cystidia (Kuyper 1986; Bandini et al. 2021c); *I. cincinnata* differs, e.g., by an outwards mostly finely fibrillose pileus surface, thinner and blotchy lamellae, on average shorter spores and longer hymenial cystidia with narrower apex (Bandini et al. 2021c); and *I. drenthensis* Bandini & B. Oertel differs, e.g., by the speckled pileus sometimes with an orange hue, on average shorter spores and more heterogeneously shaped hymenial cystidia with thicker walls (Bandini et al. 2021c). *Inocybe gaiana* Bandini & B. Oertel can be distinguished from *I. mortenii*, e.g., by the dull clayish or greyish brown pileus colour even in older basidiomata, not thickish and blotchy lamellae, on average shorter spores and shorter and more ventricose caulocystidia (Bandini et al. 2021c); *I. lampetiana* Bandini & B. Oertel can be distinguished, e.g., by the usually darker brown pileus colour, habitat with *Alnus*, on average larger spores and longer hymenial cystidia (Bandini et al. 2021c); and *I. minima* can be distinguished, e.g., by a beige-coloured velipellis, thinner and blotchy lamellae and on average shorter spores (Peck 1913). *Inocybe obscuroides* P.D. Orton differs from *I. mortenii*, e.g., by a usually squamulose-squarrose pileus surface that in the centre is areolate diffracted with age, on average wider spores and longer hymenial cystidia with narrower necks (Orton 1960; Bandini et al. 2021c); *I. pusio* P. Karst differs, e.g., by the smoother pileus surface, not blotchy lamellae and ventricose hymenial cystidia (Karsten 1889; Kuyper 1986; Bandini et al. 2021c); and *I. sitibunda* Bandini, B. Oertel & U. Eberh. differs, e.g., by the not blotchy lamellae, on average wider hymenial cystidia with thicker walls and shorter and not as narrow caulocystidia (Bandini et al. 2021c). Finally, *Inocybe tiburtina* has an abundant beige-coloured velipellis, on average wider spores and wider hymenial cystidia, and is found on calcareous soil (Bandini et al. 2021c). The most similar known species in terms of ITS, but still quite dissimilar, is *Inocybe cincinnata* (90% similarity). The species clade of *I. mortenii* received full support.

Inocybe orioli Bandini, B. Oertel & U. Eberh., **sp. n.**

(Fig. 12; MycoBank: MB 845167)

Etymology

From the Latin name of the golden oriole (*Oriolus oriolus*), because of the yellowish colour of the pileus and lamellae.

Diagnosis

Inocybe orioli **sp. n.** has a bicoloured pileus with orange-tinged centre and yellowish margin, pale yellow lamellae when young, smooth spores measuring 8.0–10.2 µm (av. 9.2 µm) × 4.4–6.0 µm (av. 5.4 µm), mostly long and narrow (sub)fusiform to sublageniform hymenial cystidia, pleurocystidia measuring 51–88 µm (av. 67 µm) × 10–19 µm (av. 13 µm), and intensely yellow-green walls of the cystidia with 3% KOH. The species can be recognized by the combination of the above characters and differs in its ITS sequence from *I. pholiotinoides*.

Holotype

GERMANY, Baden-Württemberg, Rhein-Neckar-Kreis, Mauer, border of Nature-Reserve Sandgrube Grafenrain, TK25 6618/2, alt. 150 m, shady and rather moist wayside with *Salix* sp., *Quercus robur*, 20 Oct. 2017, leg. D. Bandini (holotype STU SMNS-STU-F-0901703; isotypes priv. herb. D. B. DB20-10-17-1, TUR-A 209532).

Description

Pileus 15–30 mm wide, at first (sub)campanulate, later broadly convex, then expanded, when older with pronounced large umbo, margin at first decurved, later straight or even uplifted, and then pileus deeply depressed around the umbo; when young with remnants of a pale greyish velipellis; colour at the centre warm to bright yellow-orange to ochraceous brownish or brown with orange tinge (Mu 5YR 6/6–6/8; 10YR 7/6–7/8, 6/6–6/8, 5/6–5/8; 7.5YR 6/6–6/8, 5/6–5/8), yellow(ish) towards the margin; surface at first smooth and glabrous, with very fine fibres, later subrimulose towards the margin, but fibres

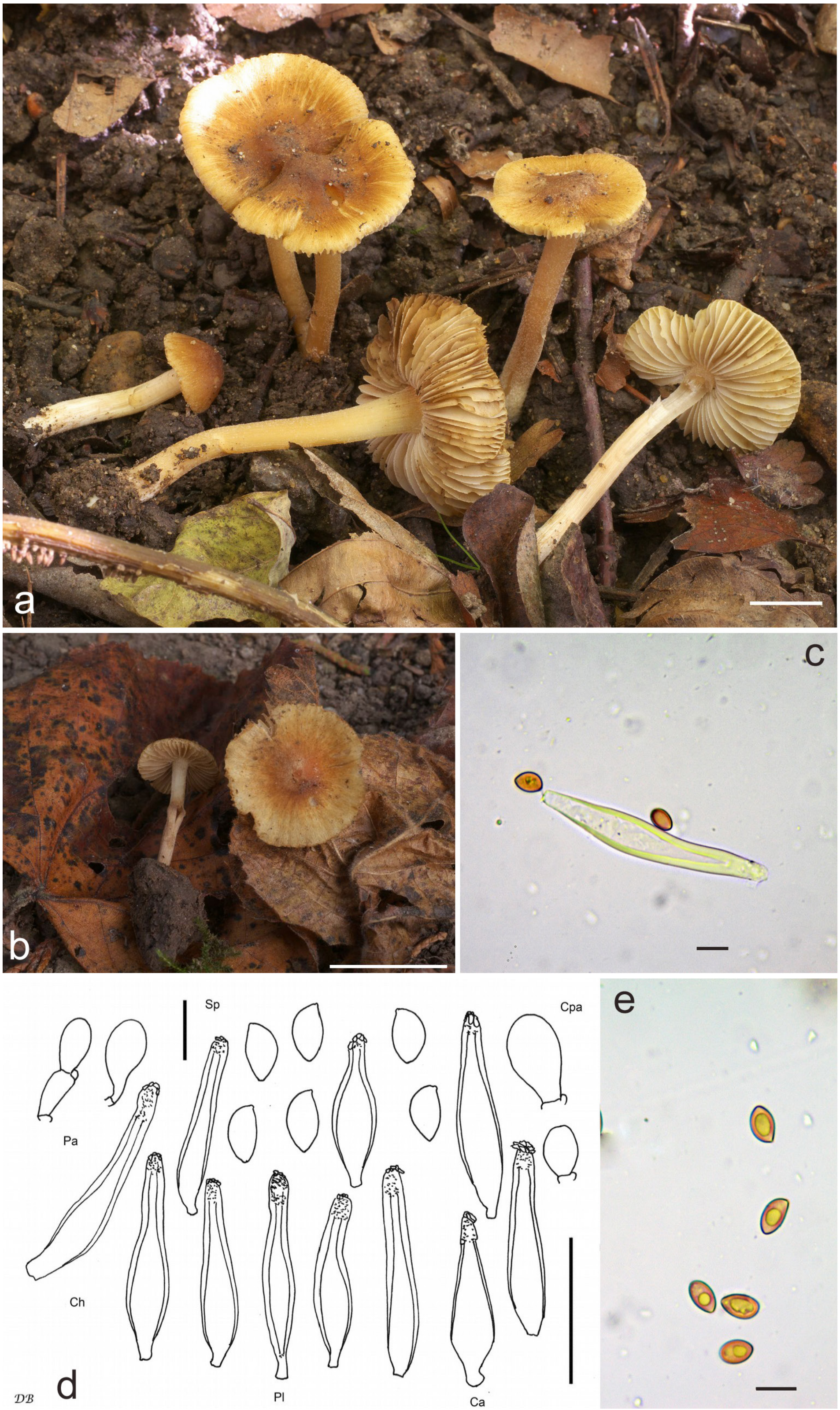

Fig. 12. *Inocybe orioli* **sp. n.** – **a.** Holotype; scale bar: 1 cm. **b.** Coll. DB29-9-17-6; scale bar: 1 cm. **c.** Cheilocystide (holotype); scale bar: 10 µm. **d.** Microscopic characters (holotype); Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm. **e.** Spores (holotype); scale bar: 10 µm.

not diverging; no remnants of a cortina observed. *Lamellae* rather distant (c. 40–50, l = 1–3), almost free to narrowly adnate, subventricose, at first pale yellowish, later pale greyish with yellowish hue; edge fimbriate, whitish to concolourous. *Stipe* 4–100 (150) × 2–4 (5) mm, cylindrical or curved, sometimes widening towards the apex, glabrous, yellowish to a different degree depending on the age of the basidiomata, base covered by whitish tomentum; pruinose on the entire length of the stipe. *Context* whitish in the pileus, whitish to pale yellowish in the stipe. *Smell* subspermatic, at least when cut. *Colour of exsiccata* pileus brown with reddish hue (Mu 7/5YR 4/4–4/6, 3/4), lamellae and stipe concolourous or a little lighter in colour, no darkening or blackening on drying.

Spores 8.0–10.2 µm (av. 9.2 µm, SD 0.5 µm) × 4.4–6.0 µm (av. 5.4 µm, SD 0.3 µm); Q = 1.4–2.0 (av. 1.7 SD 0.1) (n = 120 of 3 coll.), smooth, (sub)amygdaloid, often with a more or less explicit suprahilar depression, apex subacute, sometimes also subpapillate, with indistinct pseudoporus. *Basidia* 21–25 × 7–9 µm, generally 4-spored. *Lamellae edges* composed of cheilocystidia and numerous colourless, (sub)clavate, sometimes catenate, thin-walled paracystidia. *Pleurocystidia* 51–88 µm (av. 67 µm, SD 8 µm) × 10–19 µm (av. 13 µm, SD 2 µm); Q = 3.3–6.9 (av. 5.2, SD 0.9) (n = 45 of 3 coll.), mostly narrow subfusiform, sometimes also sublageniform, with a short or longer neck and short pedicel, apex usually crystalliferous with small crystals and often appearing "sandy" (i.e., with very small crystals around the apex), walls up to 3.0 (3.5) µm thick at the apex, intensely greenish with faint yellowish hue with 3% KOH. *Cheilocystidia* similar in appearance and size. *Pileipellis* constituted by an epicutis made up of parallel hyphae 4–10 µm wide, with encrusting and parietal brownish to dark brown pigment, subcutis with wider and paler to colourless elements. *Caulocystidia* on entire length of the stipe, 50–80 × 10–15 µm, mostly (sub)fusiform to (sub)lageniform, with rather longer neck and short pedicel, apex usually crystalliferous, walls up to 2.5 µm thick at the apex, intensely greenish with faint yellowish hue with 3% KOH. *Clamp connections* abundant in all tissues.

Habitat and distribution

Inocybe orioli **sp. n.** was collected in shady and thus rather moist locations with frondose trees in Germany. The species corresponds to SH1155135.08FU (3.0%) of the UNITE database, with only a small number of sequences from EcM or soil samples from Austria, Estonia and Germany.

Additional specimen examined

GERMANY, Baden-Württemberg, Rhein-Neckar-Kreis, Langenzell, TK25 6618/2, alt. 170 m, *Fagus sylvatica*, *Corylus avellan*a, 29 Sep. 2017, leg. D. Bandini (SMNS-STU-F-0901733, dupl. DB29-9-17-6).

Notes

Inocybe orioli **sp. n.** is characterized by a bicoloured pileus with orange-tinged centre and yellowish margin, pale yellow lamellae when young, mostly long and narrow (sub)fusiform to sublageniform hymenial cystidia and intensely yellow-green walls of the cystidia with 3% KOH. The species can be mistaken for *I. pholiotionoides*, which differs, e.g., by the minutely squamulose pileus surface with age, pileus centre often red(dish) with age, less yellowish lamellae and on average longer spores (Romagnesi 1979; DB, personal observation; and see below). The same can be said of *I. fissuratula* (Ludwig 2017; Eberhardt et al., in prep. The sister species *I. carissima* differs by its habitat in boreal-subalpine *Picea* forests, less intense pileus colours and on average smaller spores. *Inocybe alcis* can be distinguished from *I. orioli*, e.g., by a much darker, often red-brown centre of the pileus with less pale margin, at first strikingly whitish lamellae and on average larger spores. *Inocybe ionochlora* has a violet stipe near the apex and on average longer but narrower spores (Romagnesi 1979; Bandini et al. 2013). *Inocybe muricellata* differs from *I. orioli*, e.g., by the tomentose-lanose, subquamulose to squarrose pileus surface, at first whitish lamellae, on average shorter spores and shorter hymenial cystidia (Bresadola 1905; Kuyper 1986; Stangl 1989; DB, personal observation). The pileus of the recently described *I. pallidolutea* is pale ochraceous to yellowish (sub)squamulose and the stipe pinkish to reddish in the upper part according to the protologue, the spores are on average smaller and the reaction of the cystidia walls with KOH is weaker (Carteret & Reumaux 2017; Bandini et al. 2022a). The most similar taxon in terms of its ITS sequence is *I. carissima*, but the similarity is only around 90%, followed by *I. pholiotinoides* with 89%. The species clade of *I. orioli*, including two environmental sequences, received full support in Fig. 1.

Inocybe pholiotinoides Romagn. *Beih. Sydowia* 8: 355 (1979) (Figs. 13, 22c)

Selected descriptions and iconography: Romagnesi (1979); Kuyper (1986); Jacobsson & Larsson (2012; as "*I. muricellata*"); Ludwig (2017).

Description

Pileus 5–30 mm wide, at first mostly (sub)conical, later broadly conico-convex, convex or expanded, with a more or less pronounced, large umbo, margin slightly incurved, later decurved, straight or even uplifted, and then pileus depressed around the umbo; young basidiomata usually without, sometimes with very faint traces of a pallid velipellis at the umbo; colour bright yellow-ochraceous, sometimes dull ochraceous (Mu 5YR 5/6–5/8; 7.5YR 6/8, 5/6–5/8; 10YR 6/6–6/8), but often orange, orange-coppery to more or less intensely reddish to red

Fig. 13. *Inocybe pholiotinoides* – **a.** Coll. SMNS-STU-F-0901702; scale bar: 1 cm. **b.** Coll. DB5-10-18-1; scale bar: 1 cm. **c.** Cheilocystidia (coll. SMNS-STU-F-0901702); scale bar: 10 µm. **d.** Microscopic characters (coll. SMNS-STU-F-0901702); Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm. **e.** Spores (coll. DB5-10-18-1); scale bar: 10 µm.

at the centre, therefore appearing bicoloured; surface at first almost glabrous to very fine felty with minutely fine fibres, soon breaking up with very small excoriate, sometimes subsquarrose small areolate diffracted fibres outside the centre, and appressed finely fibrillose at the margin; no remnants of a cortina observed. *Lamellae* rather distant (c. 20–30 (35), l = 1–3), adnate to broadly adnate with (sub)decurrent tooth, subventricose, at first whitish with faint greyish hue, beige, greyish with yellowish tinge to intensely ochraceous with orange tinge or ochraceous brownish with olive tinge; edge fimbriate, whitish to concolourous. *Stipe* 25–60 × 1–3 mm, cylindrical or curved, base thickened to (sub)bulbous, glabrous, at first whitish, dingy whitish, beige with faint yellowish hue to yellowish ochraceous, sometimes with fine, darker fibres; pruinose on entire length of the stipe. *Context* whitish in the pileus, whitish to yellowish or faintly reddish in the stipe, somewhat darker in the cortex of the stipe. *Smell* (sub)spermatic, at least when cut. *Colour of exsiccata* pileus brown with coppery to reddish hue (Mu 5YR 4/4–4/6; 7.5YR 4/4–4/6), lamellae concolourous or a little lighter or darker in colour, stipe a little paler, no darkening or blackening with drying.

Spores 8.6–10.9 µm (av. 9.7 µm, SD 0.5 µm) × 4.9–6.2 µm (av. 5.5 µm, SD 0.2 µm); Q = 1.5–2.1 (av. 1.8, SD 0.1) (n = 120 of 3 coll.), smooth, (sub)amygdaloid, often with more or less explicit suprahilar depression, apex subacute, subobtuse, in some collections with indistinct pseudoporus. *Basidia* 24–28 × 7–9 µm, generally 4-spored, but in some collections also 2-spored and then spores up to 12.5 µm and sometimes almost laceroid in shape. *Lamellae edges* composed of cheilocystidia and numerous colourless to ochraceous brownish to brownish, (sub)clavate, thin-walled paracystidia. *Pleurocystidia* 53–90 µm (av. 74 µm, SD 9 µm) × 10–29 µm (av. 16 µm, SD 3 µm); Q = 2.6–7.2 (av. 4.6, SD 1.0) (n = 45 of 3 coll.), mostly (sub)fusiform, also (sub)utriform, often with rather long neck, with short or longer pedicel, sometimes with roundish base, apex usually crystalliferous, walls up to 3.5 (5.0) µm thick at the apex, intensely yellow-green with 3% KOH, often filled with amorphous content of almost the same or darker colour. *Cheilocystidia* similar in appearance and size. *Pileipellis* constituted by an epicutis made up of parallel hyphae 5–14 µm wide, with barely encrusting and parietal yellowish to yellow-ochraceous pigment, subcutis with wider and paler to colourless elements. *Caulocystidia* on entire length, 50–90 × 10–15 µm, shaped like hymenial cystidia, but often somewhat misshaped and often with slightly undate walls, walls up to 2.0 µm thick at the apex, intensely yellow-green with 3% KOH; intermixed with numerous (sub)clavate to subglobose cauloparacystidia. *Clamp connections* abundant in all tissues.

Habitat and distribution

Inocybe pholiotinoides is mostly found in deciduous forests, often with *Carpinus betulus* and *Corylus avellana*, but also with *Quercus* spp., *Tilia cordata* and *Salix* spp. In South Scandinavia it is most frequently encountered in calcareous *Corylus* woodlands. In montane Central Europe it may occur also in *Abies alba* forests (which often include deciduous forest species). The species seems widespread and not rare, as verified by ITS sequences from montane Central Spain, via Austria-Germany to the boreo-nemoral zone of South Scandinavia.

Type specimen examined

Holotype (Fig. 22c): FRANCE, La-Neuville en Hez (Oise), in moss on sandy soil, at a moist wayside, 20 Sep. 1958, H. Romagnesi (PC, Romagnesi n° 58.298). *Spores* 8.5–11.4 µm (av. 9.5 µm, SD 0.6 µm) × 4.8–6.0 µm (av. 5.4 µm, SD 0.3 µm); Q = 1.5–2.0 (av. 1.8, SD 0.1) (n = 40), smooth, (sub)amygdaloid, with (sub)acute apex. *Basidia* 4-spored. *Pleurocystidia* 52–88 µm (av. 68 µm, SD 9 µm) × 12–18 µm (av. 14 µm, SD 2 µm); Q = 4.0–5.8 (av. 4.9, SD 0.5) (n = 15), mostly (sub)fusiform, apex usually crystalliferous, walls up to 2.0 (2.5) µm thick at the apex, yellow-green with 3% KOH. *Cheilocystidia* somewhat more variable in shape and size. *Paracystidia* (sub)clavate, sometimes in intermediate states with slightly thickened walls. *Caulocystidia* on entire length of the stipe, similar in size and appearance to hymenial cystidia, sometimes with somewhat undate neck, intermixed with oblong (sub)clavate cauloparacystidia [type-study by J. V].

Selected additional specimens examined

AUSTRIA, Oberösterreich, Braunau am Inn, Oberrothenbuch, „Riviera“, ÖK25V 3321-Ost, alt. 355 m, riparian forest, 26 Jul. 2018, leg. D. Bandini (DB26-7-18-26). GERMANY, Baden-Württemberg, Rhein-Neckar-Kreis, Wiesenbach, TK25 6618/2, alt. 170 m, *Corylus avellana*, *Fagus sylvatica*, *Betula pendula*, 28 Sep. 2012, leg. D. Bandini (DB28-9-12-14). Baden-Württemberg, Rhein-Neckar-Kreis, Bammental, TK25 6618/2, alt. 130 m, *Alnus glutinosa*, *Salix* sp., 3 Sep 2014, leg. D. Bandini (SMNS-STU-F-0901702, dupl. DB3-9-14-1). Baden-Württemberg, Ortenaukreis, Sasbachwalden, Brandmatt, TK25 7314/1, alt. 800 m, *Abies alba*, *Picea abies*, 14 Sep. 2014, leg. D. Bandini (SMNS-STU-F-0901694, dupl. DB14-9-14-3). Nordrhein-Westfalen, Bonn, TK25 5208/3, *Carpinus betulus*, 23 May 2013, leg. B. Oertel (DB23-5-13-1b).- Nordrhein-Westfalen, Olpe, Attendorn, Biggesee, TK25 4913/1, alt. 363 m, *Salix* sp., *Alnus glutinosa*, 5 Oct. 2018, leg. D. Bandini (DB5-10-18-1). Nordrhein-Westfalen, Märkischer Kreis, Plettenberg, TK25 4813/1, alt. 270 m, *Salix* sp., *Alnus glutinosa*, *Carpinus betulus*; 6 Oct. 2018, leg. D. Bandini (DB6-10-18-25). SPAIN, Madrid, La Acebeda, 3.616842 / 41.088434, alt. 1195 m, *Corylus avellana*, *Quercus pyrenaica*, 25 Jun. 2018, leg. A. Díaz-Fernández, G. Coello-Yuste, L. Barrio-de la Pena & F. J. Rodríguez-Campo (DB 25-6-18-Rodr.-Campo).

Notes

Inocybe pholiotinoides usually has a bright yellow-ochraceous, at the centre often more or less intense orange to orange-coppery to reddish or red pileus colour. The pileus surface is at first glabrous to very finely felty with minutely fine fibres, but soon breaking up with very small squamules or excoriate around the centre and appressed, finely fibrillose at the margin. The stipe is entirely pruinose and the hymenial cystidia are mostly (sub)fusiform, often with a rather long neck and with intense reaction to 3% KOH. It often grows on calcareous, somewhat humid terrain with frondose trees. It is macroscopically, microscopically and also genetically closely related to *I. alcis* sp. n. (see above).

Since we could not borrow the type material of *I. pholiotinoides* from PC, and in the absence of a type sequence, we had to rely on the morphological examination previously done by J. VAURAS and the quite detailed original description by ROMAGNESI (1979) to decide which of the species in the group is the "true" *I. pholiotinoides* and which one is a new species. Our concept of *I. pholiotinoides*, described above, is based on the colour of the pileus, which according to ROMAGNESI is a "bel ocre roux à ocre brunâtre" with the centre generally of a more or less intense red ("roux"), and pileus towards the margin breaking up in somewhat excoriate small "plaques", which is quite typical for our collections of what we think is *I. pholiotinoides*—while this is not the case with *I. orioli*. In addition, the pilei of *I. orioli* are usually paler in colour, and the spores are on average somewhat shorter than those of the holotype of *I. pholiotinoides* and of our own collections of what we consider to be *I. pholiotinoides*. To judge from our own data, it seems that *I. pholiotinoides* is more frequent than *I. orioli*. *Inocybe pholiotinoides* in the sense of collection STU SMNS-STU-F-0901702 is a quite common species, in South Scandinavia as well as in Germany or Spain. The pileus colour of *I. carissima* is less intense, the surface smoother and the spores on average smaller. The pileus colour of *I. alcis* sp. n. is darker, the surface smoother, the lamellae at first strikingly white and the spores on average wider. In Fig. 1, the clade of *I. pholiotinoides* is supported by 97%/100%/1; the species is reciprocally monophyletic in relation to *I. alcis*, which has the most similar ITS (97%). It should be noted that the present species has been interpreted as *I. muricellata* by Ellen Larsson and other Scandinavian authors (see, e.g., JACOBSSON & LARSSON 2012). *Inocybe muricellata* can be distinguished by often abundant velipellis, usually tomentose-lanose to entirely (sub)squarrose pileus surface and usually lacking yellow tinges on the stipe and pileus (margin).

Inocybe rangiferi Bandini, Vauras & B. Oertel, **sp. n.**

(Fig. 14; MycoBank: MB 845168)

Etymology

Named "rangiferi" after the reindeer (*Rangifer tarandus*), because the species was found in an area where reindeer occur.

Diagnosis

Inocybe rangiferi **sp. n.** has a rather stout habit in comparison with its small size, streaky brown to at the centre dark brown pileus colour, almost glabrous to minutely rim(ul)ose or minutely innately fibrillose pileus surface, stipe pruinose only near the apex, irregular protruding nodulose spores measuring 8.5–11.2 µm (av. 9.9 µm) × 6.0–8.0 µm (av. 6.9 µm) and on average rather short, mostly (sub)fusiform hymenial cystidia, pleurocystidia measuring 41–64 µm (av. 52 µm) × 11–21 µm (av. 15 µm). It can be recognized by the combination of the above characters and differs in its ITS sequence from other superficially similar species, such as *I. proximella*.

Holotype

FINLAND, Koillismaa, Kuusamo municipality, Liikasenvaara, Jäkäläniemi, WGS84: 66.2924, 29.6244, margin of a small sandy road, on sandy, somewhat calcareous soil near *Pinus sylvestris*, alt. 140 m, 17 Aug. 2015, leg. J. VAURAS, D. BANDINI & B. OERTEL (holotype TUR-A 203299, JV31300; isotypes STU SMNS-STU-F-0901252, priv. herb. D. B. DB17-8-15-21).

Description

Pileus 4–22 mm wide, at first (sub)conical, later conico-convex or expanded, with pronounced umbo, margin at first incurved, later decurved; with faint remnants of a greyish velipellis at the centre of the pileus, visible often as very small patches; colour brown to dark brown with reddish hue (Mu 7.5YR 4/4–4/6; 5YR 4/4–4/6), darker at the centre and somewhat streaky, with darker fibres on paler ones; surface at first almost glabrous, later minutely rim(ul)ose or minutely innately fibrillose; young basidiomata with faint remnants of a pale cortina. *Lamellae* moderately crowded to subdistant (c. 30–50, l = 1–3), adnate, (sub)ventricose, at first beige with greyish hue, later brownish-greyish to red-brown; edge fimbriate, whitish to concolourous. *Stipe* 15–35 × 1–5 mm, cylindrical, when young covered with pale tomentum, later longitudinally striate to (almost) glabrous, pale brownish to brown with reddish hue; sparely pruinose only near the apex of the stipe. *Context* whitish in the pileus and the stipe, faintly brownish in the cortex of the stipe. *Smell* acidulous, aromatic. *Colour of exsiccata* pileus dark brown with faint reddish hue (Mu 5YR 3/3–3/4; 7.5YR 3/4), lamellae and stipe concolourous or a little lighter in colour, no darkening or blackening on drying.

Spores 8.5–11.2 µm (av. 9.9 µm, SD 0.6 µm) × 6.0–8.0 µm (av. 6.9 µm, SD 0.4 µm); Q = 1.2–1.6 (av. 1.4, SD 0.1) (n = 80 of 2 coll.), nodulose with 8–12 irregular protruding obtuse nodules. *Basidia* 23–29 × 7–10 µm, generally 4-spored. *Lamellae* composed of cheilocystidia and numerous colourless, (sub)clavate thin-walled, sometimes in intermediate states and then slightly thick-walled paracystidia. *Pleurocystidia* 41–64 µm (av. 52 µm, SD 5 µm) × 11–21 µm (av. 15 µm, SD 2 µm); Q = 2.7–4.3 (av. 3.5, SD 0.4) (n = 30 of 2 coll.), mostly broadly (sub)fusiform, sometimes (sub)utriform or subclavate, usually without neck and with short pedicel, at the apex generally

Fig. 14. *Inocybe rangiferi* **sp. n.** – **a.** Holotype; scale bar: 1 cm. **b.** Coll. TUR-A 204103 (photo: J. Vauras); scale bar: 1 cm. **c.** Cheilocystidia (holotype); scale bar: 10 µm. **d.** Microscopic characters (holotype); Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm. e. Spores (Coll. TUR-A 204103); scale bar: 10 µm.

wide, apex usually crystalliferous, walls up to 1.5 (2.0) µm thick at the apex, pale yellowish-greenish with 3% KOH. *Cheilocystidia* similar in size, but somewhat more variable in shape. *Pileipellis* constituted by an epicutis made up of parallel hyphae 4–15 µm wide, with encrusting and parietal brownish pigment, subcutis with wider and paler to colourless elements. *Caulocystidia* only near the apex of the stipe, 40–65 × 10–25 µm, ventricose and somewhat misshaped (sub)fusiform or slender subclavate, without or with only short neck and pedicel, apex crystalliferous or not, walls up to 1.0 (1.5) µm thick at the apex, pale yellowish-greenish with 3% KOH; intermixed with subclavate cauloparacystidia. *Clamp connections* abundant in all tissues.

Habitat and distribution

Inocybe rangiferi **sp. n.** was collected by us in northeast Finland, in a sandy area next to *Pinus sylvestris*. The species corresponds to UNITE SH1223194.08FU (3.0%), including only one sequence from a specimen from Canada (HQ604258) under the name of "*I. striata*", as well as two sequences of soil samples from Estonia, which might belong to this species. We consider *I. rangiferi* a rare species.

Additional specimen examined

FINLAND, Koillismaa, Kuusamo municipality, Liikasenavaara, Jäkäläniemi, *Pinus sylvestris*, 24 Aug. 2016, leg. J. Vauras (TUR-A 204103, JV31661F, dupl. SMNS-STU-F-0901725, dupl. priv. herb. D. B. DB24-8-16-2-Vauras).

Notes

Inocybe rangiferi **sp. n.** is characterized by a rather stout habit in comparison with its small size, a streaky brown to at the centre dark brown pileus colour, almost glabrous to minutely rim(ul)ose or minutely innately fibrillose pileus surface, stipe pruinose only near the apex, nodulose spores with irregular protruding nodules, and on average rather short, mostly (sub)fusiform hymenial cystidia. Both examined collections are very similar in all these details. The species may be mistaken for *I. proximella* P. Karst. which may have a similar macroscopic aspect. It differs from *I. rangiferi*, e.g., by the missing velipellis, stipe becoming dark brown to almost blackish brown in the lower half with age, larger hymenial cystidia, and habitat with *Picea abies* (see, e.g., Karsten 1883; Stangl 1989; Kokkonen & Vauras 2012; Ferrari et al. 2014; Ludwig 2017). *Inocybe bufonia* Kokkonen & Vauras can be distinguished, e.g., by the less glabrous pileus surface, often with age areolate pileus centre and much smaller spores (Kokkonen & Vauras 2012); *I. glabrodisca* can be distinguished, e.g., by the paler pileus colour, much smaller spores and longer hymenial cystidia (Orton 1960; Stangl 1989; Ferrari 2006); and *I. johannae* can be distinguished, e.g., by the less glabrous pileus surface, narrower, oblong to rectangular or trapezoid polygonal or subentolomoid spores and larger hymenial cystidia (Kühner 1988; Kokkonen & Vauras 2012). *Inocybe napipes* differs, e.g., by the napiform bulb and shorter spores with more strongly protruding nodules as well as growth mostly in moist ground with *Picea abies* (Lange 1917; Stangl 1989; Ferrari 2006; Ludwig 2017), while in Finland it is found also with *Betula*. *Inocybe subgiacomi* C.L. Cripps, Vauras & E. Larss. can be distinguished from *I. rangiferi*, e.g., by the missing velipellis, longer, often almost rectangular, almost sinuate or subentolomoid spores and longer hymenial cystidia (Cripps et al. 2019b), and from *I. acuta* Boud., by, e.g., a (sub)bulbous base of stipe, hymenial cystidia with often (sub)capitate apex, mostly rather narrow (sub)cylindrical or (sub)fusiform caulocystidia mixed with thin-walled elements often with protuberances, and moist habitat with *Salix* (Boudier 1917; Kokkonen & Vauras 2012). In terms of the ITS region, *Inocybe rangiferi* is, with only 93% similarity, most closely but only fairly distantly related to *I. proximella*. The two species are sisters in Fig. 1 and *I. rangiferi* received 95%/100%/1 support. This comparatively low support might have been caused by missing data. For *I. proximella*, we only had ITS data available.

Inocybe ravenelii Massee [as "*raveneli*"], *Revue mycol., Toulouse* 18: 485 (1904)
(Fig. 22d)

Description and iconography: Massee (1904).

Type specimen examined

Holotype: UNITED STATES, Georgia, Darien, damp places, 14 Apr. 1878, leg. Ravenel (K(M): 264841). *Spores* 10.4–14.5 µm (av. 12.3 µm, SD 1.0 µm) × 5.0–6.6 µm (av. 5.8 µm, SD 0.4 µm); Q = 1.8–2.7 (av. 2.1, SD 0.2) (n = 40), smooth, mostly oblong (sub)ellipsoid, but also (sub)cylindrical or sublaceroid, with obtuse apex. *Basidia* 4-spored. *Pleurocystidia* 38–56 µm (av. 49 µm, SD 5 µm) × 14–19 µm (av. 16 µm, SD 2 µm); Q = 2.5–4.0 (av. 3.1, SD 0.4) (n = 15), mostly (sub)fusiform or subutriform, apex usually crystalliferous, walls up to 2.0 (3.0) µm thick at the apex, yellowish-greenish with 3% KOH. *Cheilocystidia* similar in appearance and size. *Paracystidia* not observed. *Caulocystidia* not studied (to preserve the material).

Notes

In the protologue, Massee describes the pileus as having an acute umbo, the colour as brown and the pileus surface as silky-floccose, the stipe as hollow and of the same colour or paler as the pileus, and the spores as elliptic-oblong, obliquely apiculate with a size of 15 (18) × 5 µm, and the cystidia as thin-walled fusoid or subventricose (Massee 1904). This description may point to a species of the "*lacera-helobia*-group", an assumption which was confirmed by the examination of the holotype. Kauffman (1924) synonymized the species with *I. lacera*. The shape and size of the hymenial cystidia suggests that the species is morphologically related to *I. helobia*. *Inocybe helobia* differs from *I. ravenelii* by the often (sub)ellipsoid spores and cystidia with wider and often roundish apex, while the spores of *I. lacera* and *I. moravica* are narrower on average and the hymenial cystidia longer with at least sometimes a mammiform apex. We were not permitted to extract DNA from the type.

Inocybe sepiana Bandini, Dondl & Dima, **sp. n.**

(Fig. 15; MycoBank: MB 845169)

Etymology

Named "sepiana" (from Latin "*sepia*", "ink") because of the blackish rim at the base of the stipe.

Diagnosis

Inocybe sepiana **sp. n.** has rather small basidiomata, a usually blackish-brown pileus centre with age, tomentose to (sub)lanose or squamulose pileus surface, entirely pruinose stipe the base of which is blackish-brown at the rim, nodulose, often rather wide and differently shaped spores measuring 9.2–12.9 µm (av. 10.8 µm) × 5.9–9.7 µm (av. 7.6 µm), often (sub)capitate hymenial cystidia, pleurocystidia measuring 30–83 µm (av. 57 µm) × 15–29 µm (av. 20 µm), and it is to be found on calcareous gravelly or sandy terrain. The species can be recognized by the combination of the above characters and differs in its ITS sequence from *I. tiliae* and other similar species.

Holotype

GERMANY, Bayern, Garmisch-Partenkirchen, Mittenwald, TK25 8533/2, alt. 880 m, *Pinus mugo*, *Dryas octopetala*, *Helianthemum nummularium*, 10 Sep. 2019, leg. D. Bandini (holotype STU SMNS-STU-F-0901687; isotypes priv. herb. D. B. DB10-9-19-16, TUR-A 209533).

Description

Pileus 5–20 (25) mm wide, at first (sub)campanulate to subglobose, later broadly convex or expanded, without or with only a faint, large umbo, margin at first slightly incurved, later decurved to straight or even uplifted, and then pileus depressed around the umbo; young basidiomata with faint pale greyish remnants of a velipellis; colour nut-brown to dark brown, sometimes with a coppery or faintly reddish hue (Mu 10YR 5/6–5/8, 4/3–4/6, 3/4–3/6; 7.5YR 5/4–5/6, 4/4–4/6), at the centre usually becoming blackish-brown with age; surface finely tomentose when young, soon finely lanose to lanose or (sub)squamulose with appressed or subquarrose fibre bundles, sometimes villose; at the centre diffracted to areolate diffracted with age; no remnants of a cortina observed. *Lamellae* moderately crowded to subdistant (c. 30–45, l = 1–3), somewhat thickish, sometimes uneven, mostly broadly adnate, sometimes with subdecurrent tooth, (sub)ventricose, at first ivory-coloured, then greyish-brownish or pale brownish with ochraceous hue to brown with greyish hue, sometimes with rusty patches; edge fimbriate, whitish to concolourous. *Stipe* 20–40 × 2–4 mm, mostly cylindrical, sometimes slightly curved, base even to faintly thickened or with a small bulb, glabrous, at first beige, later pale brownish, ochraceous brownish, also reddish brown, sometimes darker to dark brown in some parts; pruinose on the entire length, but in many basidiomata difficult to observe in the lower half of the stipe because of the pruina often being rubbed off by sand or gravel. *Context* whitish to cream-coloured in the pileus, pale flesh-coloured to reddish in the stipe, especially at the apex and in the cortex of the stipe, rim of the base of the stipe blackish brown. *Smell* spermatic, at least when cut. *Colour of exsiccata* pileus dark brown (Mu 10YR 3/3–3/6), lamellae and stipe concolourous or a little lighter in colour, no darkening or blackening on drying.

Spores 9.2–12.9 µm (av. 10.8 µm, SD 0.8 µm) × 5.9–9.7 µm (av. 7.6 µm, SD 0.8 µm); Q = 1.0–1.9 (av. 1.4, SD 0.2) (n = 120 of 3 coll.), nodulose, from isodiametric to oblong, quite different in shape, with 8–12 often only weakly protruding obtuse nodules, always also some spores with one more protruding nodule, and also always spores which are almost merely entolomoid. *Basidia* 25–35 × 8–12 µm, generally 4-spored, but sometimes also 2-spored and then spores up to 14.5 µm. *Lamellae edges* composed of cheilocystidia and numerous colourless, (sub)clavate to subglobose, thin-walled paracystidia. *Pleurocystidia* 30–83 µm (av. 57 µm, SD 11 µm) × 15–29 µm (av. 20 µm, SD 4 µm); Q = 1.7–4.5 (av. 3.0, SD 0.7) (n = 45 of 3 coll.), mostly (sub)utriform to subfusiform, also (sub)cylindrical, seldom (sub)clavate, transition between bulge and neck often clearly demarcated, often (sub)capitate, usually with only a short neck or even without neck, at the apex usually wide, mostly with only a short pedicel, apex usually crystalliferous, walls up to 3.0 (3.5) µm thick at the apex, yellowish-greenish with 3% KOH. *Cheilocystidia* similar in size, but somewhat more variable in shape. *Pileipellis* constituted by an epicutis made up of parallel hyphae 5–14 µm wide, with encrusting and parietal dark brown pigment, subcutis with wider and paler elements. *Caulocystidia* on entire length of the stipe, but often sparely towards the base due to being rubbed off by sand/gravel, 30–55 × 15–20 µm, (sub)fusiform to (sub)utriform, (sub)cylindrical or even (sub)clavate, apex usually crystalliferous, walls up to 2.5 µm thick at the apex, yellowish-greenish with 3% KOH; intermixed with slightly thick-walled, oblong (sub)cylindrical elements and numerous (sub)clavate to subglobose cauloparacystidia. *Clamp connections* abundant in all tissues.

Habitat and distribution

Inocybe sepiana **sp. n.** was collected by us in Germany and Austria, always on calcareous, sandy to gravelly soil on the banks of rivers or lakes, in a quite special and rare

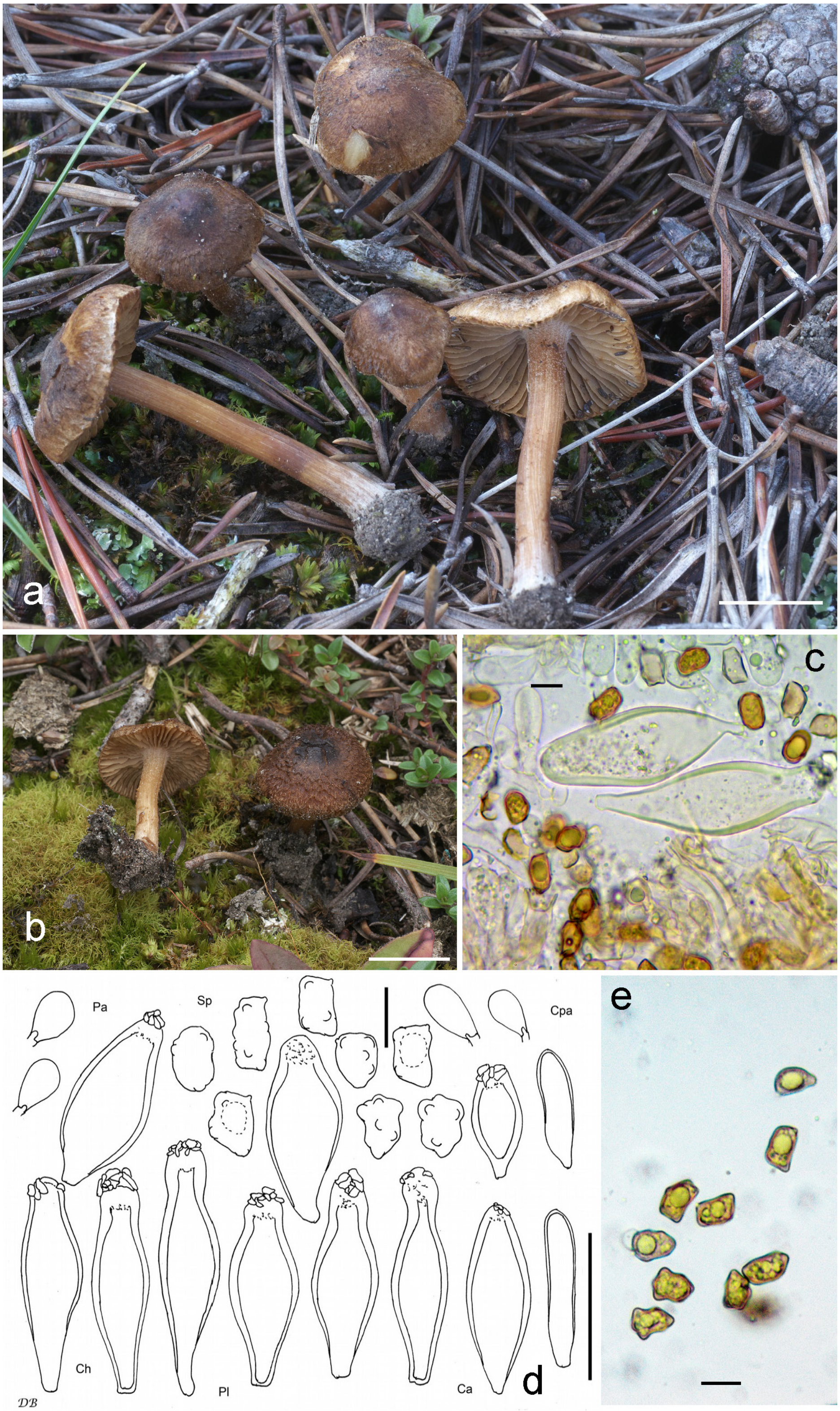

Fig. 15. *Inocybe sepiana* **sp. n.** – **a.** Holotype; scale bar: 1 cm. **b.** Coll. DB9-9-17-19; scale bar: 1 cm. **c.** Cheilocystidia (coll. DB9-6-12-E15-Eimann); scale bar: 10 µm. **d.** Microscopic characters (holotype); Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm. **e.** Spores (holotype); scale bar: 10 µm.

habitat where the little ringed plover (*Charadrius dubius*) nests. In most cases *Pinus* and often also *Salix* were present. There are no sequences of collections, EcM or soil samples in GenBank or the UNITE database.

Additional specimens examined

AUSTRIA, Tirol, Reutte, Weißenbach, border of river Lech, ÖK25V 2214-Ost, alt. 760 m, *Salix* sp., *Juniperus* sp., *Dryas octopetala*, *Pinus sylvestris*, *Alnus* sp., 7 Sep. 2017, leg. D. Bandini (SMNS-STU-F-0901718, dupl. DB7-9-17-6).- Tirol, Reutte, Forchach, ÖK25V 2215-West, alt. 910 m, *Salix* sp., 11 Sep. 2018, leg. D. Bandini (DB11-9-18-11).- Tirol, Reutte, Rieden, border of river Lech, ÖK25V 2215-West, alt. 890 m, *Salix* sp., *Pinus sylvestris*, 21 Sep. 2018, leg. D. Bandini (DB21-9-18-16). GERMANY, Baden-Württemberg, Markgräflerland, Grißheim, TK25 8111/1, alt. 208 m, *Populus tremula*, 12 Oct. 2014, leg. H. Obenauer (DB12-10-14-1-Obenauer).- Bayern, Garmisch-Partenkirchen, Griesen, Naidernach, TK25 8531/2, alt. 835 m, *Salix* sp., *Pinus mugo*, *Pinus sylvestris*, *Picea abies*, 9 Sep. 2011, leg. M. Dondl (SMNS-STU-F-0901688, dupl. DB9-9-11-Dondl).- Bayern, Garmisch-Partenkirchen, Werdenfelser Land, TK25 8434/7, *Picea abies*, *Salix* sp., 9 Jun. 2012, leg. P. & W. Eimann (KR-M-0038099, dupl. DB9-6-12-E14-Eimann,).- Bayern, Bad Tölz-Wolfratshausen, Vorderriß, TK25 8434/2, alt. 810 m, *Salix* sp., *Alnus* sp., 23 Jun. 2012, leg. M. Dondl (DB23-6-12-Dondl).- Bayern, Garmisch-Partenkirchen, Mittenwald, near Scharnitz, TK25 8533/3, alt. 940 m, *Juniperus* sp., *Pinus mugo*, *Dryas octopetala*, 9 Sep. 2017, leg. D. Bandini (SMNS-STU-F-0901705, dupl. DB9-9-17-19).- Bayern, Garmisch-Partenkirchen, Mittenwald, TK25 8533/3, alt. 920 m, *Pinus sylvestris*, *Pinus mugo*, *Dryas octopetala*, 12 Sep. 2017, leg. D. Bandini (DB12-9-17-16).- Ibidem, at some distance from former location, alt. 880 m, *Pinus mugo*, *Dryas octopetala*, *Helianthemum nummularium*, 10 Sep. 2019, leg. D. Bandini (DB10-9-19-12).- Ibidem, at some distance from former location, alt. 880 m, *Pinus mugo*, *Dryas octopetala*, *Helianthemum nummularium*, 10 Sep. 2019, leg. D. Bandini (DB10-9-19-13).- Ibidem, at some distance from former location, alt. 880 m, *Pinus mugo*, *Dryas octopetala*, *Helianthemum nummularium*, 10 Sep. 2019, leg. D. Bandini (DB10-9-19-17).- Ibidem, at some distance from former location, alt. 880 m, *Pinus mugo*, *Dryas octopetala*, *Helianthemum nummularium*, 10 Sep. 2019, leg. D. Bandini (DB10-9-19-18).- Ibidem, at some distance from former location, alt. 880 m, *Pinus mugo*, *Dryas octopetala*, *Helianthemum nummularium*, 10 Sep. 2019, leg. D. Bandini (DB10-9-19-19).

Notes

Inocybe sepiana **sp. n.** is characterized by rather small basidiomata, a usually blackish-brown pileus centre with age, tomentose to (sub)lanose or squamulose pileus surface, entirely pruinose stipe the base of which is blackish brown at the rim, nodulose, often rather wide and different shaped spores, often (sub)capitate hymenial cystidia and habitat on calcareous gravelly or sandy terrain, e.g., at the edge of alpine rivers. Because of the blackish rim at the stipe base, *I. sepiana* may on first sight be mistaken for *I. javorkae*, which differs from *I. sepiana*, however, by the larger basidiomata, sticky pileus surface thus often almost entirely covered by sand, more elongate and larger spores and larger hymenial cystidia. Furthermore, the base of the stipe of *I. javorkae* is externally dark brown to almost blackish as if it had been stuck in dark wet mud, but there is no small blackish brown rim, best visible when cut, as is the case with *I. sepiana*. *Inocybe dunensis* can be found in the same habitat, but it can be distinguished from *I. sepiana*, e.g., by larger basidiomata, no blackish brown rim at the stipe base, more elongate and larger spores and not subcapitate hymenial cystidia (see above and below). *Inocybe decipiens* has no blackish brown rim at the stipe base, more elongate and larger spores and non-subcapitate hymenial cystidia (Bresadola 1892; Bizio & Marchetti 1997, 1998; and see above). *Inocybe pseudohiulca* Kühner differs, e.g., by larger basidiomata, no blackish brown rim at the stipe base, on average larger spores and non-subcapitate hymenial cystidia as well as a different habitat with *Picea abies* (Kühner 1933; Horak 1987, as "*Astrosporina pseudohiulca*"), and *I. nobilis* differs, e.g., by larger basidiomata, no blackish brown rim at the stipe base, on average shorter spores and a different habitat, often with *Picea abies* (Heim 1931, as "*I. fibrosa* var. *nobilis*"; Alessio 1980; DB, personal observation). *Inocybe favrei* Bon can be distinguished from *I. sepiana*, e.g., by the often more reddish brown pileus colour, no blackish brown rim at the stipe base, on average narrower spores with a different Q-value, and the (sub)boreal or alpine habitat (Bon 1985; Riva 2009). Finally, *I. tiliae* Franchi, M. Marchetti & Papetti, which is genetically the closest related species to *I. sepiana* with 96% identity in the ITS region, has larger basidiomata, mostly at least near the apex a reddish-pinkish stipe, no blackish brown rim at the stipe base, smaller spores, and entirely different habitat, since it is often found in parks with *Tilia* or *Quercus* (Franchi et al. 2016; DB, personal observation). It is not entirely clear whether *I. tiliae* (95%/100%/1) forms the sister clade to *I. sepiana* or an unsupported clade including, among others, what we consider *I. nobilis* and the *I. decipiens* collection of Bresadola (see above).

Inocybe soluta Velen. *České Houby* 2: 365 (1920) (Figs. 16, 21a, 22e, g)

Heterotypic synonyms: *Inocybe striatorimosa* P.D. Orton, *Trans. Br. mycol. Soc.* 43(2): 279 (1960); *Inocye albofibrillosa* Stangl & Schmid-Heckel *in* Schmid-Heckel, *Forschungsberichte Nationalpark Berchtesgarden* 8: 159 (1985).

Selected descriptions and iconography: Velenovský (1920–1922); Kuyper (1985); Stangl (1989); Bizio & Ferrari (1999); Armada et al. (2007); Ferrari (2014); Ludwig (2017).

Lectotype

[Designated by Kuyper (1985).] CZECH REPUBLIC, at the ridge of the giant mountains, Jul. 1918, leg. Kavina (PRC bottle n° 385).

Epitypus hic designatus (MBT 10008604)

GERMANY, Sachsen-Anhalt, Harz, Ilsenburg, near Nature Reserve Kramershai, TK25 4229/4, alt. c. 800 m, *Picea abies*,

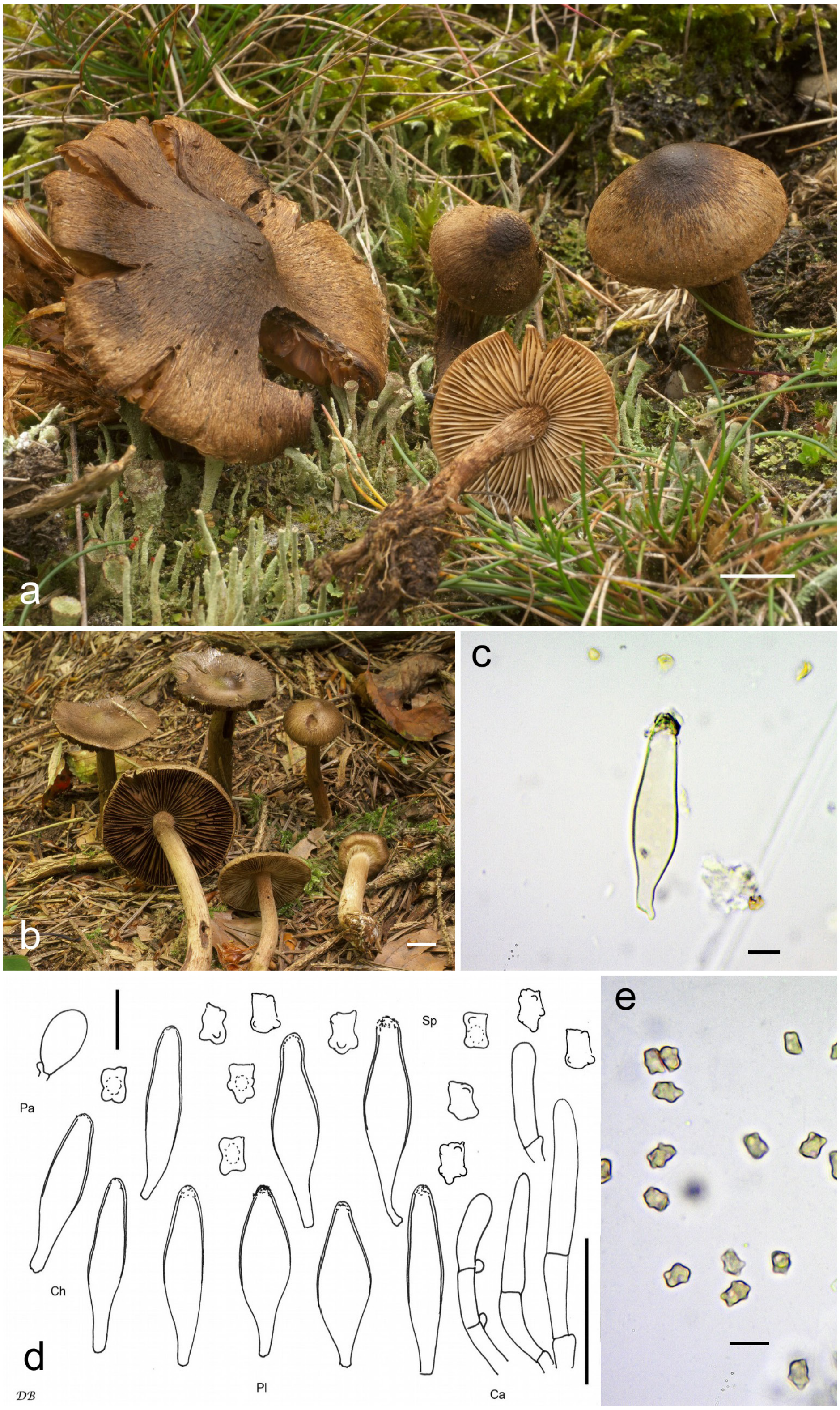

Fig. 16. *Inocybe soluta* – **a.** Epitype; scale bar: 1 cm. **b.** Coll. DB11-8-12-1; scale bar: 1 cm. **c.** Cheilocystide (coll. DB11-8-12-1); scale bar: 10 µm. **d.** Microscopic characters (epitype); Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm. **e.** Spores (coll. DB22-8-12-6); scale bar: 10 µm.

3 Oct. 2012, leg. D. Bandini (STU SMNS-STU-F-0901727; dupl. priv. herb. D. B. DB3-10-12-8).

Type specimens examined

Lectotype of *I. soluta* (Fig. 22e): *Spores* 5.4–8.3 µm (av. 6.8 µm, SD 0.6 µm) × 3.9–6.1 µm (av. 5.1 µm, SD 0.4 µm); Q = 1.1–1.6 (av. 1.3, SD 0.1) (n = 40), nodulose, with few obtuse nodules, often only almost with sinuous outline. *Basidia* 4-spored. *Pleurocystidia* 50–73 µm (av. 58 µm, SD 5.8 µm) × 13–18 µm (av. 16 µm, SD 1.3 µm); Q = 2.8–4.3 (av. 3.6, SD 0.4) (n = 15), mostly ventricose (sub)cylindrical, (sub)fusiform or plump sac-shaped, apex usually without crystals, walls up to 0.5 (1.0) µm thick, pale yellowish-greenish with 3% KOH. *Cheilocystidia* similar in appearance and size. *Paracystidia* not observed. *Caulocystidia* not observed, because stipe was in a bad condition.

Epitype of *I. soluta* (Fig. 16a, d): *Spores* 6.2–8.0 µm (av. 7.0 µm, SD 0.5 µm) × 4.3–6.6 µm (av. 5.2 µm, SD 0.5 µm); Q = 1.1–1.6 (av. 1.4, SD 0.1) (n = 40), with few obtuse nodules, often almost rectangular in outline. *Basidia* 4-spored. *Pleurocystidia* 49–79 µm (av. 65 µm, SD 8 µm) × 10–22 µm (av. 16 µm, SD 3 µm); Q = 3.2–6.4 (av. 4.3, SD 0.9) (n = 15), rather ventricose (sub)cylindrical or (sub)fusiform, sometimes plump sac-shaped, apex usually without crystals, walls up to 0.5 (1.0) µm thick, pale yellowish-greenish with 3% KOH. *Cheilocystidia* similar in appearance and size. *Paracystidia* (sub)clavate. *Caulocystidia* only near the extreme apex of the stipe, hyphoid, often segmented.

Holotype of *I. albofibrillosa* (Fig. 21a): GERMANY, Bayern, Nationalpark Berchtesgaden, above Watzmannhaus, TK25 8443/2, alt. 1970 m, with *Pinus mugo*, 22 Sep. 1982, leg. H. Schmid-Heckel (M-0020039). *Spores* 5.2–8.0 µm (av. 6.8 µm, SD 0.7 µm) × 4.4–6.1 µm (av. 4.9 µm, SD 0.3 µm); Q = 1.1–1.6 (av. 1.4, SD 0.1) (n = 40), nodulose, with few differently and faintly protruding obtuse nodules. *Basidia* 4-spored. *Pleurocystidia* 48–64 µm (av. 58 µm, SD 3.8 µm) × 10–16 µm (av. 12 µm, SD 1.6 µm); Q = 3.8–6.3 (av. 4.8, SD 0.7) (n = 15), mostly (sub)cylindrical, also subutriform or sac-shaped, sometimes with slightly undate walls, apex usually crystalliferous, walls up to 1.0 µm thick, pale yellowish-greenish with 3% KOH. *Cheilocystidia* similar in appearance and size. *Paracystidia* not observed. *Caulocystidia* mostly hyphoid.

Holotype of *I. striatorimosa*, Fig. 22g: ENGLAND, Surrey, Hindhead, 23 Sep. 1942, leg. A. A. Pearson (K(M): 68622). *Spores* 6.0–7.8 µm (av. 7.0 µm, SD 0.5 µm) × 4.5–6.2 µm (av. 5.1 µm, SD 0.4 µm); Q = 1.1–1.6 (av. 1.4, SD 0.1) (n = 40), nodulose, with few faintly protruding obtuse nodules. *Basidia* 4-spored. *Pleurocystidia* 41–65 µm (av. 57 µm, SD 7 µm) × 10–15 µm (av. 12 µm, SD 1 µm); Q = 3.7–5.8 (av. 4.6, SD 0.6) (n = 15), mostly (sub)fusiform, also sublageniform or sac-shaped, apex without or with few very small crystals, walls up to 0.5 µm thick, pale yellowish-greenish with 3% KOH. *Cheilocystidia* similar in appearance and size. *Paracystidia* not observed. *Caulocystidia* not observed, to prevent damage.

Description

Pileus 10–50 mm wide, at first (sub)conical or subglobose, later convex to expanded, with a more or less prominent large umbo, margin at first strongly involute, later decurved to straight, and often uplifted when old, and then depressed around the centre; usually no or only faint remnants of a velipellis observed; colour brown to dark greyish brown, sometimes with darker fibres on paler ones (Mu 10YR 4/3–4/6, 3/3–3/6; 7.5YR 3/2–3/4), often almost blackish brown or even blackish at the centre and therefore sometimes intensely contrasting in colour; surface innately fibrillose, appressed fibrillose, tomentose-fibrillose to strongly lanose-fibrillose, at the centre occasionally verrucous, young basidiomata with abundant brownish cortina. *Lamellae* moderately crowded (c. 40–60, l = 1–3), narrowly adnate to adnate, even to subventricose, at first whitish, later brown to dark brown or reddish dark brown, often somewhat darkening when bruised; edge fimbriate, whitish to concolourous. *Stipe* 20–70 × 3–10 mm, cylindrical or curved, sometimes widening towards the base, when young entirely covered with whitish tomentum, later longitudinally striate to glabrous, pale brown to almost blackish brown; faintly pruinose only near the extreme apex of the stipe. *Context* whitish in the pileus, pale brown in the stipe, especially in the cortex and at the base of the stipe. *Smell* weakly spermatic, at least when cut. *Colour of exsiccata* pileus and stipe greyish dark brown to almost blackish brown (Mu 7.5YR 3/2; 10YR 3/3–3/6, 2/2), lamellae lighter in colour and with an ochraceous tinge, no darkening or blackening on drying.

Spores 5.1–8.7 µm (av. 6.7 µm, SD 0.7 µm) × 4.0–6.6 µm (av. 5.0 µm, SD 0.5 µm); Q = 1.1–1.6 (av. 1.4, SD 0.1) (n = 120 of 3 coll.), rather pale, nodulose, sometimes almost rectangular in outline, with 6–9 obtuse nodules. *Basidia* 20–30 × 7–10 µm, generally 4-spored. *Lamella edge* composed of cheilocystidia and numerous colourless, (sub)clavate, thin-walled paracystidia. *Pleurocystidia* 40–79 µm (av. 63 µm, SD 7.2 µm) × 10–23 µm (av. 15 µm, SD 2.7 µm); Q = 2.1–6.4 (av. 4.3, SD 0.7) (n = 45 of 3 coll.), mostly (sub)fusiform, also (sub)utriform or plump sac-shaped, without or with only a short neck, generally with a rather short pedicel, sometimes with brownish amorphous content, apex, if at all crystalliferous, with only small crystals, usually thin-walled or up to 0.5 µm thick near the apex, but occasionally also walls up to 1.5 µm thick near the apex, pale yellowish-greenish in 3% KOH. *Cheilocystidia* similar in appearance and size. *Pileipellis* constituted by an epicutis made up of parallel hyphae 6–14 µm wide, often but not always with finely encrusting and parietal brownish to brown pigment, subcutis with wider and paler to colourless elements. *Caulocystidia* only near the extreme apex of the stipe, hyphoid, often segmented, occasionally with brownish amorphous content. *Clamp connections* abundant in all tissues.

Habitat and distribution

Inocybe soluta generally prefers mountainous woods with *Picea abies* or *Abies* on acidic, often moist ground, but it can be found also on dry acidic sandy terrain with *Pinus sylvestris*. Our own collections are from Austria, Germany and Switzerland. The species corresponds to SH1691880.08FU (1.0%) of the UNITE database, in which are assembled some sequences from collections (all labelled "*I. soluta*"), EcM or soil samples from Austria, Canada, Estonia, Finland, Slovakia, Sweden and Switzerland.

Selected additional specimens examined

AUSTRIA, Tirol, Imst, Silz, Kühtai, ÖK25V 2221-Ost, *Picea abies*, 22 Aug. 2012, leg. D. Bandini & B. Oertel (DB22-8-12-6). Salzburg, Tamsweg, ÖK25V 3230-Ost, alt. 1510 m, *Picea abies*, 20 Sep. 2020, leg. D. Bandini (DB20-9-20-2). GERMANY, Baden-Württemberg, Freudenstadt, Baiersbronn, Hornisgrinde, Nature Reserve Wilder See, TK25 7415/1, alt. 914 m, *Picea abies*, 13 Sep. 2014, leg. D. Bandini (KR-M-0042245, dupl. DB13-9-14-13). Bayern, Freyung-Grafenau, St. Oswald-Riedlhütte, Stadtschneiderseige, TK25 7046/4, alt. 720 m, moist terrain near brook with *Picea abies*, *Fagus sylvatica*, *Abies alba*, 17 Aug. 2016, leg. P. Püwert (DB17-8-16-17). Bayern, Regen, Lindberg, Zwiesler Waldhaus, Ruckowitzhänge, TK25 6845/4, alt. c. 900 m, moist terrain with *Picea abies*, *Fagus sylvatica*, *Abies alba*, 20 Aug. 2016, leg. D. Bandini, C. Bässler, C. Hahn, J. Christan & B. Oertel (DB20-8-16-40). Bayern, Kelheim, Abensberg-Offenstetten, TK25 7137/3, alt. c. 380 m, *Pinus sylvestris*, *Pseudotsuga menziesii*, 9 Oct. 2017, leg. D. Bandini, B. Oertel & J. Christan (DB9-10-17-12). Nordrhein-Westfalen, Hochsauerlandkreis, Meschede, near Nature Reserve Lattenberg, TK25 4515/3, alt. 435 m, *Picea pungens*, 7 Oct. 2018, leg. D. Bandini & J. Christan (DB7-10-18-1). Rheinland-Pfalz, Kaiserlautern, Frankenstein, TK25 6513/4, alt. c. 380 m, near brook with *Carpinus betulus*, *Fagus sylvatica*, 11 Aug. 2012, leg. D. Bandini & B. Oertel (SMNS-STU-F-0901719, dupl. DB11-8-12-1). Sachsen-Anhalt, Harz, Oberharz am Brocken, Kramershai, TK25 4229/4, alt. 660 m, *Picea abies*, 3 Oct 2012, leg. D. Bandini (SMNS-STU-F-0901716, dupl. DB3-10-12-1). SWITZERLAND, Graubünden, Engadin, above Muottas Muragl, near Pontresina, TK25 1257/2, alt. 2620 m, *Salix herbacea*, 31 Aug. 2016, leg. B. Oertel (DB31-8-16-3b).

Notes

The lectotype of *I. soluta* was preserved in a bottle with formaldehyde mixed with species of other genera; pieces putatively belonging to the same collection had to be separated out from a kind of sludge at the bottom of the bottle. It is impossible to know exactly which fragment belonged to which basidiome and sequenceable DNA can normally not be extracted from formaldehyde-preserved material. The two later synonyms of *I. soluta* and the confusion around *I. brevispora* are evidence that the species has not been sufficiently clear based on existing evidence. Therefore, we here chose an epitype that matches the lectotype in the microscopic details as far as they could be recovered and that allows the analysis of those that could not. *Inocybe soluta* is characterized by dark brown to at the centre almost blackish brown pileus colour, usually missing velipellis, fibrillose to fibrillose-lanose pileus surface, rather pale small spores with often almost rectangular outline. It is generally associated with conifers, especially with *Picea* or *Pinus*. *Inocybe culicis* differs from *I. soluta*, e.g., by the silvery beige velipellis, paler centre of the pileus, on average even shorter spores and shorter hymenial cystidia, and *I. subcarpta* differs, e.g., by the larger spores and longer, often (sub)capitate hymenial cystidia, often with undate walls (see, e.g., Kühner & Boursier 1932; Huijsman 1955, as "*I. brevispora*"; Stangl & Veselský 1974, as "*I. brevispora*"; Stangl 1975, 1989; Marchetti & Franchi 2003; Ferrari 2006; Ludwig 2017). *Inocybe prisca* has a more lanose surface of the pileus, a greyish velipellis, larger spores and longer hymenial cystidia (Bandini et al. 2021a).

The holotype of *I. albofibrillosa* was examined and sequenced by us. The macroscopic description stresses that the pileus towards the margin is overgrown with whitish fibres (hence the name "*albofibrillosa*", see Schmid-Heckel 1985), which deviates from the usual appearance of *I. soluta*. We have not seen anything like that ourselves, but the microscopic details drawn by Schmid-Heckel and the data we gained from our examination of the holotype fit very well to those of *I. soluta*, as does the ITS sequence of the holotype, which is a perfect match with that of the epitype of *I. soluta*. We thus consider the two species as synonymous. The protologue of *I. striatorimosa* is well in accordance with the usual appearance of *I. soluta* with an almost blackish centre of the pileus and an equally very dark stipe in the lower part (Orton 1960), and also the microscopic details proved to be the same as those of *I. soluta*. We were not permitted to extract DNA from the holotype.

The clade of *I. soluta* received 89%/100%/1 support. The species with the most similar ITS is *I. culicis*, which is almost 99% similar in the ITS region but differs by 8 bp in the LSU region.

Inocybe stellatospora (Peck) Massee, *Ann. Bot., Lond.* 18: 469 (1904) (Fig. 22a, f)

Heterotypic synonym*: Inocybe longicystis* G.F. Atk., *Am. J. Bot.* 5: 213 (1918)

Selected descriptions and iconography: Peck (1873; as "*Agaricus stellatosporus*"); Atkinson (1918; as "*I. longicystis*"); Stangl (1989); Matheny & Kropp (2001); Ludwig (2017).

Type specimens examined

Lectotype of *I. stellatospora* [designated by Matheny & Kropp (2001)] (Fig. 22f): UNITED STATES, New York, Lewis County, Croghan, Sep. [no year indicated], leg. C. H. Peck (NYS-f-2936.1). *Spores* 8.0–11.3 µm (av. 9.4 µm, SD 0.6 µm) × 5.6–9.5 µm (av. 7.0 µm, SD 0.7 µm); Q = 1.0–1.6 (av. 1.4, SD 0.1) (n = 40), nodulose, with strongly protruding (sub)obtuse to subacute nodules. *Basidia* 4-spored. *Pleurocystidia* 45–70 µm (av. 57 µm, SD 7 µm) × 15–22 µm (av. 19 µm, SD 2 µm); Q = 2.5–4.1 (av. 3.1, SD 0.5) (n = 15), mostly (sub)utriform, apex usually without crystals, often subcapitate, walls thin or up to 0.5 µm thick at the apex, (almost) colourless with 3% KOH. *Cheilocystidia* similar in appearance and size. *Paracystidia* not observed. *Caulocystidia* not studied (to preserve the material).

Holotype of *I. longicystis* (Fig. 22a): UNITED STATES, New York, Adirondack Mts., Seventh Lake, Endogone Ravine, on leaf mold on hillside in mixed forest, 13 Aug. 1917, leg. F. C. Stewart (CUP-A-024321). *Spores* 8.1–10.3 µm (av. 9.1 µm, SD 0.5 µm) × 6.1–7.9 µm (av. 6.9 µm, SD 0.4 µm); Q = 1.2–1.6

(av. 1.4, SD 0.1) (n = 40), nodulose with rather protruding obtuse nodules. *Basidia* 4-spored. *Pleurocystidia* 56–83 µm (av. 66 µm, SD 7 µm) × 14–25 µm (av. 19 µm, SD 3 µm); Q = 2.6–4.9 (av. 3.5, SD 0.7) (n = 15), mostly (sub)utriform, often subcapitate, apex with or without small crystals, walls thin, or up to 0.5 µm thick at the apex, almost colourless with 3% KOH. *Cheilocystidia* similar in appearance and size. Paracystidia not observed. *Caulocystidia* not studied (to preserve the material).

Selected additional specimens examined

AUSTRIA, Oberösterreich, Braunau am Inn, Schalchen, Kobernausser Wald, ÖK25V 3328-Ost, alt. 550 m, *Picea abies*, *Abies alba*, *Larix decidua*, 18 Aug. 2014, leg. D. Bandini, J. Christan and L. Quecke (DB18-8-14-16). GERMANY, Bayern, Ostallgäu, Roßhaupten, Senkele, TK25 8330/1, alt. 860 m, *Picea abies*, *Betula* sp., *Sphagnum* sp., 14 Aug. 2020, leg. D. Bandini, J. Christan, B. Oertel & A. Hussong (DB14-8-20-3). NETHERLANDS, Drenthe, Dwingeloo, alt. 20 m, *Betula* sp., *Quercus robur*, 11 Oct. 2018, leg. D. Bandini (DB11-10-18-20).

Notes

Inocybe stellatospora has a brown to dark brown pileus colour, and young basidiomata are covered with lanose to squarrose fibre bundles. The spores are nodulose with strongly protruding nodules and the hymenial cystidia are often subcapitate and almost or entirely thin-walled. The microscopic details of the holotypes of *I. longicystis* G.H. Atkinson and *I. stellatospora* are very much alike and the protologues of both species do not contradict each other. Furthermore, Atkinson, in his protologue of *I. longicystis*, explicitly mentions that the cystidia are subcapitate (“frequenter subcapitatis”, Atkinson 1918). We were not permitted to extract DNA from either of the types, but our own concept of *I. stellatospora* matches in all respect with the protologue and the microscopic details of the lectotype of *I. stellatospora*. We agree with the conclusion of Matheny & Kropp (2001) that *I. longicystis* and *I. stellatospora* are synonymous. Sequences assigned to *I. stellatospora* from North America and Europe form a clade (97%/100%/1 support, although one of the sequences lacks ITS data) that is sister to the *I. turfae* clade (see also the notes to *I. turfae*). *Inocybe stellatospora* looks very similar to *I. turfae*, which differs, e.g., by the generally paler pileus colour, on average wider spores with a lower Q-value and on average shorter, seldom subcapitate hymenial cystidia (see below).

Inocybe striatorimosa → ***Inocybe soluta***
(Fig. 22g)

Inocybe subcarpta Kühner & Boursier, *Bull. trimest. Soc. mycol.* Fr. 48(1): 137 (1932)
(Figs. 17, 21e)

Heterotypic synonym: *Inocybe brevispora* Huijsman, *Fungus, Wageningen* 25: 23 (1955).

Selected descriptions and iconography: Kühner & Boursier (1932); Huijsman (1955; as “*I. brevispora*”); Stangl & Veselský (1974; as “*I. brevispora*”); Stangl (1975, 1989); Luhmann & Vesper (1998); Eyssartier et al. (2002); Marchetti & Franchi (2003); Ferrari (2006); Ludwig (2017).

Typification

FRANCE, Haute-Savoie, Bois du Praz, under *Picea*, 9 Aug. 1924, leg. R. Kühner, s.n. holotype (lost).

Lectotypus hic designatus (MTB 10008605)

Kühner & Boursier, *Bull. trimest. Soc. mycol. Fr.* 48(1) (figs. 20a, 21 (top), pp. 38, 140).

Epitypus hic designatus (MBT 10008606)

GERMANY, Hessen, Bergstraße, Viernheim, Viernheimer Heide, TK25 6417/3, alt. 110 m, *Pinus sylvestris*, 26 Nov. 2011, leg. D. Bandini & B. Oertel (STU SMNS-STU-F-0901736; dupl. priv. herb. D. B. DB26-11-11-4).

Description

Pileus 20–60 mm wide, (sub)conical, later broadly convex or expanded, with more or less flat, large umbo, margin incurved to decurved, later straight or uplifted and then depressed around the umbo; when young with remnants of a fugacious whitish to beige velipellis; colour dull brown to dark brown or brown with reddish tinge (Mu 10YR 4/3–4/6, 3/3–3/6, 7.5YR 4/4–4/6), at the umbo often somewhat darker to almost blackish brown; surface at first smooth to minutely tomentose, later tomentose to appressed felty-fibrillose; young basidiomata with remnants of a pale cortina. *Lamellae* moderately crowded (c. 40–50, l = 1–3), somewhat thickish, almost free to adnate or emarginate adnate with decurrent tooth, even to subventricose, whitish to reddish or rusty brown; edge notchy and uneven, fimbriate, whitish to concolourous. *Stipe* 30–60 × 3–5 mm, cylindrical or widening towards base or sometimes also towards the apex, at first entirely covered with whitish tomentum, later longitudinally striate or glabrous, pale brownish, reddish brownish, to dark brown or almost blackish brown with or without a reddish hue; pruinose only sparely at the extreme apex of the stipe. *Context* watery-beige in the pileus, brownish in the stipe, especially in the cortex of the stipe. *Smell* often strangely somewhat like bugs. *Colour of exsiccata* pileus and stipe dark brown (Mu 7.5YR 3/2, 10YR 3/4–3/6, 2/2), lamellae somewhat a little lighter in colour, no darkening or blackening on drying.

Spores 6.6–10.1 µm (av. 8.2 µm, SD 0.7 µm) × 4.8–7.3 µm (av. 6.0 µm, SD 0.5 µm); Q = 1.1–1.8 (av. 1.4, SD 0.1) (n = 120 of 3 coll.), rather pale in colour, nodulose, sometimes (sub)trapezoid in shape, with 8–10 differently protruding (sub)obtuse to subacute nodules. *Basidia* 20–27 × 8–13 µm, generally 4-spored. *Lamella edge* composed of cheilocystidia and numerous colourless, (sub)clavate or (sub)cylindrical, thin-walled paracystidia. *Pleurocystidia* 40–87 µm (av. 65 µm, SD 10 µm) × 9–17 µm (av. 13 µm, SD 2 µm); Q = 2.4–8.2 (av. 5.2, SD 1.4) (n = 45 of 3 coll.), mostly rather long and narrow (sub)fusiform, subcylindrical or sac-shaped or (sub)clavate, often narrowing towards

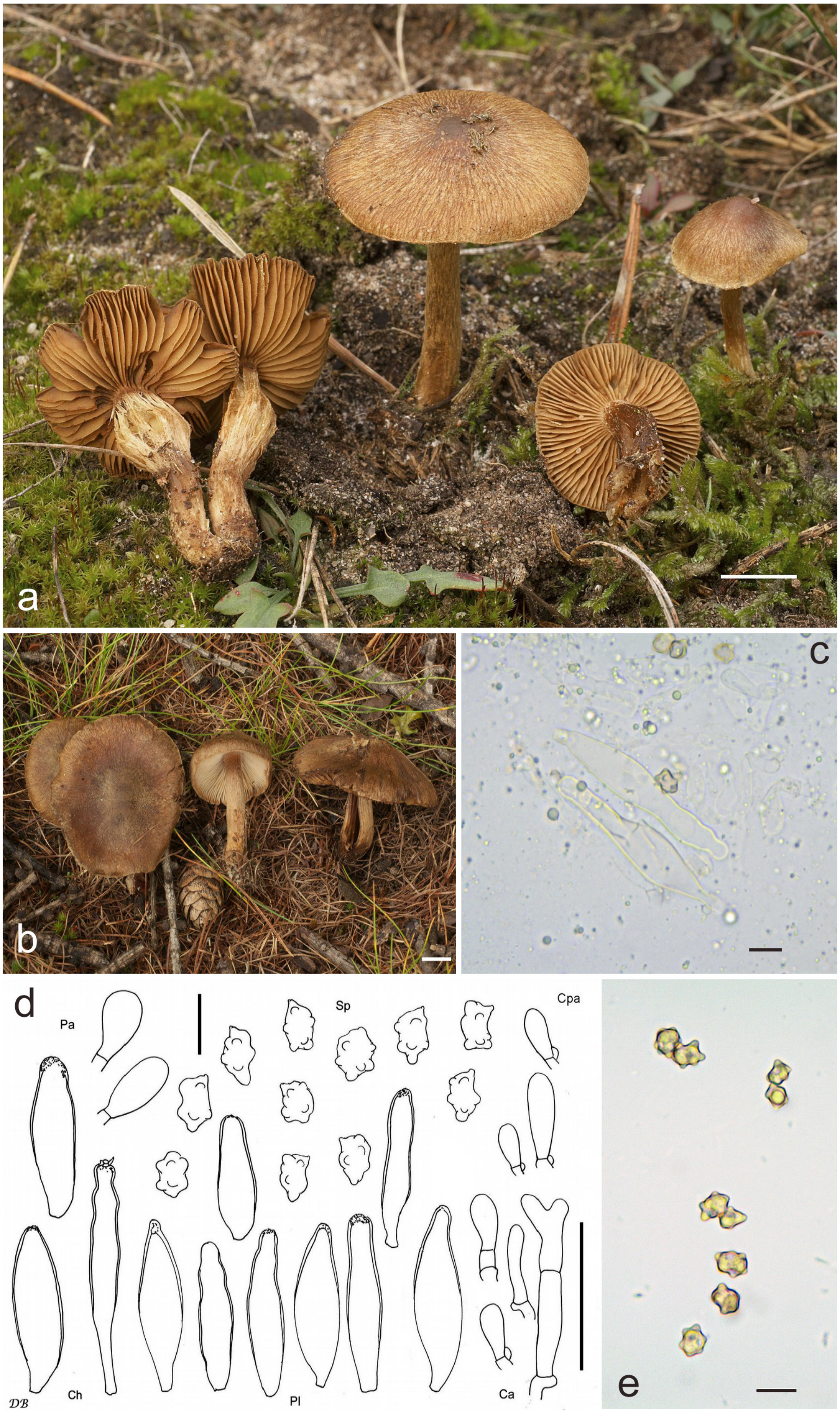

Fig. 17. *Inocybe subcarpta* – **a.** Epitype; scale bar: 1 cm. **b.** Coll. DB26-8-14-2b; scale bar: 1 cm. **c.** Pleurocystidia (coll. DB20-9-15-1); scale bar: 10 µm. **d.** Microscopic characters (epitype); Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm. **e.** Spores (coll. DB25-10-14-12); scale bar: 10 µm.

the apex and thus often (sub)capitate, often with more or less undate walls, apex with only small crystals or without crystals, mostly rather thin-walled with walls only up to 0.5 (1.0) µm at the apex, almost colourless to pale yellowish-greenish in 3% KOH. *Cheilocystidia* similar in appearance and size. *Pileipellis* constituted by an epicutis made up of parallel hyphae 4–11 µm wide, often but not always with finely encrusting and parietal brownish pigment, subcutis with wider and paler to colourless elements. *Caulocystidia* only sparely near the extreme apex of the stipe, hyphoid subclavate or sometimes catenate and forked, thin-walled elements, colourless in 3% KOH, intermixed with oblong (sub)clavate, thin-walled colourless caulo-paracystidia. *Clamp connections* abundant in all tissues.

Habitat and distribution

Inocybe subcarpta is mostly found on acidic soil, in bogs or heathland, but sometimes also on more basic or even calcareous soil that is only slightly acidified by needle litter, as was the case with the epitype. Our own collections are from Austria, Germany, Italy and Switzerland, the authentic collection of Kühner is from France, and the holotype of *I. brevispora* is from the Netherlands. The species corresponds to SH1691879.08FU (1%) of the UNITE database, in which are assembled some sequences from collections (labelled "*I. subcarpta*"), EcM or soil samples from Canada, Finland, Germany and Switzerland.

Authentic collection and type specimens examined

Authentic collection of *I. subcarpta* (Fig. 22h): FRANCE, Haute-Savoie, environs de Samoëns, Mouille Rousse, sur terre moussue, 8 Sep. 1959, leg. R. Kühner (G-00566264). *Spores* 6.9–9.2 µm (av. 8.2 µm, SD 0.6 µm) × 5.1–6.7 µm (av. 5.7 µm, SD 0.4 µm); Q = 1.3–1.8 (av. 1.4, SD 0.1) (n = 40), nodulose, sometimes subtrapezoid in shape, with differently protruding obtuse nodules. *Basidia* 4-spored. *Pleurocystidia* 57–78 µm (av. 66 µm, SD 6.0 µm) × 11–20 µm (av. 15 µm, SD 2.2 µm); Q = 3.6–5.7 (av. 4.3, SD 0.6) (n = 15), mostly (sub)cylindrical, sac-shaped or subutriform, apex if with crystals then with small ones, walls up to 1.0 (1.5) µm thick, almost colourless, to weakly positive with 3% KOH. *Cheilocystidia* similar in appearance and size. Paracystidia not observed. *Caulocystidia* not observed, because fear of damage.

Epitype of *I. subcarpta* (Fig. 17a, d): *Spores* 7.3–10.0 µm (av. 8.3 µm, SD 0.8 µm) × 5.1–7.1 µm (av. 6.1 µm, SD 0.5 µm); Q = 1.1–1.8 (av. 1.4, SD 0.1) (n = 40), nodulose, occasionally subtrapezoid with differently protruding, mostly obtuse nodules. *Basidia* 4-spored. *Pleurocystidia* 40–80 µm (av. 63 µm, SD 10 µm) × 10–17 µm (av. 14 µm, SD 2.3 µm); Q = 2.7 –7.0 (av. 4.7, SD 1.3) (n = 15), mostly (sub)cylindrical, sac-shaped or subutriform, apex without or with only small crystals, walls up to 1.0 (1.5) µm thick, almost colourless, to weakly positive with 3% KOH. *Cheilocystidia* similar in appearance and size. Paracystidia not observed. *Caulocystidia* near the extreme apex of the stipe, hyphoid subclavate or subclavate sometimes catenate and occasionally forked, thin-walled elements.

Holotype of *I. brevispora,* Fig. 21e: NETHERLANDS, Gelderland, Vorden, c. 30 km ENE from Arnheim, Kiefskamp, *Pinus*, 24 Oct. 1953, leg. H. S. C. Huijsman (L-0054122). *Spores* 6.7–9.1 µm (av. 8.1 µm, SD 0.5 µm) × 4.8–6.4 µm (av. 5.7 µm, SD 0.4 µm); Q = 1.2–1.8 (av. 1.4, SD 0.1) (n = 40), nodulose, sometimes subtrapezoid in shape. *Basidia* 4-spored. *Pleurocystidia* 35–74 µm (av. 58 µm, SD 9 µm) × 13–25 µm (av. 17 µm, SD 3 µm); Q = 2.7–4.4 (av. 3.5, SD 0.5) (n = 15), mostly (sub)-fusiform to subcylindrical, apex usually crystalliferous, thin-walled or walls up to 0.5 µm thick at the apex, pale yellowish-greenish with 3% KOH. *Cheilocystidia* similar in appearance and size. *Paracystidia* not observed. *Caulocystidia* hyphoid and some misshaped elements.

Selected other specimens examined

AUSTRIA, Salzburg, Tamsweg, ÖK25V 3230-Ost, alt. 1510 m, *Picea abies*, 20 Sep. 2022, leg. D. Bandini (SMNS-STU-F-0901690, dupl. DB20-9-20-22). GERMANY, Baden-Württemberg, Freudenstadt, Baiersbronn, Nature Reserve Wilder See, Hornisgrinde, TK25 7415/1, alt. 1031 m, near path with *Abies alba*, *Picea abies*, 20 Sep. 2015, leg. D. Bandini & B. Oertel (KR-M-0042662, dupl. DB20-9-15-1). Bayern, Freyung-Grafenau, Mauther Forst, TK25 7047/4, alt. 1200 m, *Picea abies*, 19 Aug. 2016, leg. A. Huber (SMNS-STU-F-0901726, dupl. DB19-8-16-36). Rheinland-Pfalz, Kaiserslautern, Mehlingen, Mehlinger Heide, TK25 6512/2, alt. c. 330 m, *Pinus sylvestris,* 25 Oct. 2014 leg*,* J. Siembida (SMNS-STU-F-0901720, dupl. DB25-10-14-12). ITALY, South-Tirol, Melag pass, alt. 1910 m, *Pinus strobus*, *Larix decidua*, 26 Aug. 2014, leg. B. Oertel (DB26-8-14-2b). SWITZERLAND, Graubünden, Maloja, Bergell, alt. 1805 m, *Larix*, 23 Aug. 2014, leg. B. Oertel & G. Schmidt-Stohn (DB23-8-14-1b).

Notes

Boursier & Kühner (1932) described *I. subcarpta* based on four collections, one considered the "forme type" and three others considered variants, "formes", pointing out the differences between the "forme type" and the variants. The "forme type" would have to be considered the holotype of *I. subcarpta*, collected by R. Kühner on 9 Aug. 1924 (see above). The material appears to be lost; according to P. Clerc (in an email to DB, Nov. 2nd, 2018), no material of *I. subcarpta* from Kühner collected in or prior to 1932 survived. Accordingly, we selected here the microscopic drawings accompanying the species description as the lectotype.

Two later collections of Kühner's identified as *I. subcarpta* survived. One, G-00566265, collected in France, Haute-Savoie, Bois du Praz, by R. Kühner, 14 Aug. 1941 as "1941C", was identified as *I. stellatospora* by DB. The second, from France, Haute-Savoie, environs de Samoëns, Mouille Rousse, collected by R. Kühner in Sept. 1959, is described in some detail here and fits perfectly in its microscopic details to the protologue of *I. subcarpta*. The protologue is fairly detailed and the typical long, thin-walled cystidia are depicted in the lectotype figures as well as the subtrapezoid shaped spores, which we have found in every collection we examined, including the epitype (see also Stangl 1989; Breitenbach & Kränzlin 2000; Ferrari 2006; Ludwig 2017).

Judging from herbarium slips accompanying Kühner's material *I. subcarpta* was considered by him as a younger synonym of *I. stellatospora* rather than a species in its own right. On the other hand, in our view, *I. subcarpta* has a younger synonym, *I. brevispora*, which Kuyper (1983) and Armada et al. (2007) considered to be the same as *I. soluta*. The drawings selected as lectotype do not show all characters necessary to solve this confusion. Thus, we decided to select one of our own collections as epitype—the rationale being that a modern collection, better documented, with all microscopic characters still present and amenable to molecular studies, could fulfil the functions of an epitype better than a historical collection for which we did not have the permission for DNA extraction and which might no longer possess amplifiable DNA.

The holotype of *I. brevispora* was also examined by us. We do not agree with Kuyper (1983), who considered the size and shape of the spores of the type to be similar to those of *I. soluta*; in contrast, we found the spores and the hymenial cystidia of *I. brevispora* to be like those of *I. subcarpta*. The protologue fits to *I. subcarpta* as well. The ITS of the holotype of *I. brevispora* differs from the ITS of the epitype of *I. subcarpta* by 1 bp. In terms of ITS similarity, *I. subcarpta* is most similar to *I. culicis* and *I. soluta*, but both are less similar than 98.5%. The clade of *I. subcarpta* is shown as reciprocally monophyletic and received 92%/100%/1 support; the sister clade includes *I. culicis* and *I. soluta*.

Inocybe subnudipes Kühner, *Bull. Soc. nat. Oyonnax* 9 (Suppl. (Mém. hors sér. 1)): 6 (1955)

(Fig. 23a)

Description and iconography: Kühner 1955.

Type specimen examined

Lectotype [designated by Poirier (2016)]: FRANCE, Savoie, Tarentaise, bois du Praz de Saint Bon, alt. 1500-1 700 m, *Picea*, 12 Sep. 1941, leg. R. Kühner (G-00262332). *Spores* 8.0–9.7 µm (av. 8.9 µm, SD 0.4 µm) × 4.5–5.6 µm (av. 4.9 µm, SD 0.3 µm); Q = 1.6–2.0 (av. 1.8, SD 0.1) (n = 40), smooth, oblong (sub)amygdaloid, with (sub)acute apex. *Basidia* usually 4-spored, rarely 2-spored. *Pleurocystidia* 47–64 µm (av. 57 µm, SD 4 µm) × 8–14 µm (av. 12 µm, SD 2 µm); Q = 4.0–7.3 (av. 5.0, SD 0.8) (n = 15), mostly narrow (sub)fusiform, sometimes with slightly undate walls, apex usually crystalliferous, walls up to 1.5 (2.0) µm thick at the apex, yellowish-greenish with 3% KOH. *Cheilocystidia* similar in appearance and size. *Paracystidia* (sub)clavate. *Caulocystidia* not studied (to preserve the material).

Selected other specimens examined

FINLAND, Pärnu rajooni, ca. 40 km S of Pärnu, Kabli, 58°00′N, 24°25′E, *Pinus sylvestris*, 23 Sep. 1990, leg. J. Vauras (DB23-9-90-Vauras-JV5265F). GERMANY, Baden-Württemberg, Kreis Freudenstadt, Baiersbronn, Wilder See, Hornisgrinde, TK25 7415/1, alt. 1000 m, *Abies alba*, *Picea abies*, 13 Sep. 2014, leg. D. Bandini (KR-M-0042701). Bayern, Oberallgäu, Bad Hindelang, Untergschwend, TK25 8428/2, alt. 1100 m, *Picea abies*, 15 Sep. 2018, leg. D. Bandini (DB15-9-18-3).

Notes

Inocybe subnudipes is a quite common species, but it is not often portrayed in the literature and when so it is mostly not clear whether *I. subnudipes* in the sense of the original description is referred to (see, e.g., Cullington 2013; Ludwig 2017). *Inocybe subnudipes* is characterized by the usually rather dull pale ochraceous, ochraceous brownish, fallow or pale nut-brown pileus colour and strongly innately fibrillose pileus surface. Also characteristic are the often slightly undate walls of the rather narrow, mostly (sub)fusiform hymenial cystidia, as well as the on average rather slim spores (Kühner 1955; DB, personal observation). The species is associated with conifers and can be found mostly in montane to subalpine or (sub)boreal habitats. The collections representing the species in Fig. 1 formed a fully supported clade. The species is sister to *I. chondroderma* D.E. Stuntz ex Matheny, Norvell & E.C. Giles as shown in Matheny et al. (2013). *Inocybe chondroderma* differs from *I. subnudipes*, e.g., by a smoother and subhygrophanous pileus surface, often bicolourous pileus aspect and on average somewhat shorter spores (Matheny et al. 2013). All sequence data published to date for *I. chondroderma* originated from America; the UNITE species hypothesis most likely corresponding to *I. chondroderma* also includes the holotype sequence of *I. submuricellata* var. *stenospermia* Grund & D.E. Stuntz (MH577999, submitted by Matheny and Hobbs on 4 Jul. 2018), which, judging from the original description (Grund & Stuntz 1983), differs by the same characters as *I. chondroderma* from *I. subnudipes.*

Inocybe tarda Kühner, *Bull. Soc. nat. Oyonnax* 9 (Suppl. (Mém. hors sér. 1)): 6 (1955)

(Fig. 18)

Heterotypic synonym: *Inocybe aurantioumbonata* Franchi & M. Marchetti *in* Marchetti & Franchi, *Riv. Micol.* 51(4): 315 (2008) (Fig. 21c).

Selected descriptions and iconography: Kühner (1955); Poirier (2012); Marchetti & Franchi (2008; as "*I. aurantioumbonata*").

Holotype

FRANCE, Paris, Bois de Vincennes, *Pinus* (G00058745).

Epitypus hic designatus (MBT 10008607)

GERMANY, Rheinland-Pfalz, Rhein-Pfalz-Kreis, near Dudenhofen, TK25 6616/3, alt. 105 m, sandy soil with *Quercus robur*, *Corylus avellana*, *Pinus sylvestris*, 3 Oct. 2017, leg. D. Bandini (STU SMNS-STU-F-0901730, dupl. DB3-10-17-6).

Description

Pileus 20–40 (50) mm wide, (sub)conical or subcampanulate when young, later broadly convex or expanded, mostly with a rather prominent, sometimes even subpapil-

Fig. 18. *Inocybe tarda* – **a.** Epitype; scale bar: 1 cm. **b.** Coll. DB21-10-12-34; scale bar: 1 cm. **c.** Cheilocystide (coll. DB21-10-12-34); scale bar: 10 µm. **d.** Microscopic characters (epitype); Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm. **e.** Spores (epitype); scale bar: 10 µm.

late umbo, margin at first slightly incurved to decurved, later straight, and often uplifted when old and then depressed around the umbo; young basidiomata usually with a thin layer of a whitish-greyish velipellis giving older basidiomata a mottled appearance; colour usually dark brown, greyish brown to almost blackish brown, with or without a reddish hue (Mu 10YR 3/2–3/6; 7.5YR 4/4–4/6, 3/2–3/4; 5YR 3/2–3/4, 2.5/2), sometimes somewhat orange with or without a reddish hue at the centre, sometimes somewhat paler towards the margin with age, but not (sub)hygrophanous; surface smooth to finely felty, also rimulose with fibres only minutely diverging towards the margin, often having a somewhat "combed" aspect and margin often finely dentate; young basidiomata with remnants of a pale cortina. *Lamellae* rather distant to moderately crowded (c. 30–50, l = 1–3), adnate, (sub)ventricose, at first whitish, then greyish-brownish, brownish, coffee-brown to brown; edge fimbriate, whitish. *Stipe* 30–70 × 3–7 mm, cylindrical or curved, sometimes slightly widening towards the base, when young entirely covered with whitish tomentum, later longitudinally striate or glabrous, at first beige to flesh-coloured or brownish, near the apex mostly with a more or less intense pinkish hue and with age often entirely reddish of different intensity; pruinose either only in the upper half of the stipe or entirely but then only sparely in the lower half. *Context* watery-beige in pileus and stipe, with pinkish hue near the apex of the stipe, sometimes with yellowish ochraceous tinge. *Smell* spermatic, at least when cut. *Colour of exsiccata* pileus dark brown with greyish hue (Mu 10YR 3/2–3/6, 7.5YR 3/2), lamellae and stipe lighter in colour, no darkening or blackening on drying, but stipe often getting more reddish.

Spores 9.1–13.5 µm (av. 10.6 µm, SD 0.9 µm) × 5.2–7.2 µm (av. 6.0 µm, SD 0.4 µm); Q = 1.5–2.1 (av. 1.8, SD 0.1) (n = 120 of 3 coll.), smooth, (sub)amygdaloid, in all collections with some unusual, abruptly bulgy spores with a more or less explicit suprahilar depression, apex (sub)obtuse to subacute, sometimes almost subpapillate, mostly with a small pseudoporus. *Basidia* 25–40 × 7–12 µm, generally 4-spored, but also 2-spored. *Lamella edge* composed of cheilocystidia and abundant colourless, (sub)clavate, (sub)cylindrical, (sub)utriform or somewhat deformed, thin- or slightly thick-walled paracystidia, very often in intermediate states. *Pleurocystidia* 35–94 µm (av. 64 µm, SD 11 µm) × 10–21 µm (av. 15 µm, SD 2 µm); Q = 2.3–7.2 (av. 4.3, SD 1.0) (n = 45 of 3 coll.), (sub)cylindrical to (sub)fusiform, sometimes (sub)utriform, without or with a short or longer neck, walls sometimes slightly undate, at the apex generally wide, usually with only short pedicel or even with a truncate base, apex usually crystalliferous, walls up to 3.0 (4.0) µm thick at the apex, pale yellowish-greenish with 3% KOH. *Cheilocystidia* usually similar in appearance and size, but sometimes also more variable due to weather conditions or age. *Pileipellis* constituted by an epicutis made up of parallel hyphae 4–15 µm wide, with encrusting and parietal brownish pigment, subcutis with wider and paler to colourless elements. *Caulocystidia* 35–100 × 10–15 (20) µm, mostly somewhat deformed subcylindrical, subfusiform or subutriform, often with undate walls, apex usually crystalliferous, walls up to 2.5 µm thick at the apex, pale yellowish-greenish with 3% KOH, intermixed with thin-walled (sub)clavate to oblong subcylindrical colourless cauloparacystidia. *Clamp connections* abundant in all tissues.

Habitat and distribution

Inocybe tarda usually occurs on calcareous sandy soil with *Pinus*, as for instance in dunes at the seashore or in inland dunes. It usually appears quite late in the year. The species corresponds to SH1419562.08FU (2.0%) of the UNITE database, including EcM sequences and sequences of soil samples from Estonia, Italy and Poland.

Type specimens examined

Epitype of *I. tarda* (Fig. 18a, d, e): *Spores* 9.5–12.4 µm (av. 10.6 µm, SD 0.7 µm) × 5.2–6.5 µm (av. 5.9 µm, SD 0.3 µm); Q = 1.6–2.0 (av. 1.8, SD 0.1) (n = 40), smooth, (sub)amygdaloid, in sometimes with abruptly bulgy spores, usually with suprahilar depression, apex (sub)obtuse to subacute. *Basidia* 4-spored. *Pleurocystidia* 35–79 µm (av. 61 µm, SD 11 µm) × 13–21 µm (av. 16 µm, SD 2 µm); Q = 2.3–5.3 (av. 4.0, SD 0.8) (n = 15), mostly (sub)cylindrical to subfusiform, apex usually crystalliferous, walls up to 3.5 (4.0) µm thick, pale yellowish-greenish with 3% KOH. *Cheilocystidia* similar in appearance and size. *Paracystidia* in different shape, sometimes slightly thick-walled. *Caulocystidia* mostly subcylindrical, subfusiform or subutriform, sometimes deformed, often with undate walls, intermixed with thin-walled (sub)clavate, subcylindrical colourless cauloparacystidia.

Holotype of *I. aurantioumbonata* (Fig. 21c): ITALY, Orbetello, Tombolo di Giannella, sandy terrain with *Pinus pinaster*, *Pinus pinea*, 21 Nov. 2008, leg. P. Franchi & M. Marchetti (MCVE-23504). *Spores* 9.5–11.5 µm (av. 10.4 µm, SD 0.5 µm) × 5.2–6.7 µm (av. 5.7 µm, SD 0.4 µm); Q = 1.5–2.1 (av. 1.8, SD 0.1) (n = 40), smooth, (sub)amygdaloid, sometimes abruptly bulgy, with (sub)obtuse to subacute to sometimes almost subpapillate apex. *Basidia* 4-spored, rarely 2-spored. *Pleurocystidia* 54–74 µm (av. 64 µm, SD 6 µm) × 15–21 µm (av. 17 µm, SD 2 µm); Q = 3.2–4.3 (av. 3.7, SD 0.3) (n = 15), mostly (sub)fusiform, also subcylindrical, sometimes subutriform, apex usually crystalliferous, walls up to 3.0 (3.5) µm thick at the apex, pale yellowish-greenish with 3% KOH. *Cheilocystidia* similar in appearance and size. *Paracystidia* numerous, differently shaped, often in intermediate states with slightly thick walls. *Caulocystidia* not studied (to preserve the material).

Selected additional specimens examined

GERMANY, Baden-Württemberg, Rhein-Neckar-Kreis, Sandhausen, TK25 6617/4, alt. 110 m, *Pinus sylvestris*, *Quercus robur, Helianthemum nummularium*, 21 Oct. 2012, leg. D. Bandini & B. Oertel (SMNS-STU-F-0901443, dupl. DB21-10-12-28). Ibidem, at some distance from former location, alt. 110 m, *Pinus sylvestris*, *Helianthemum nummularium*, *Quercus robur*, leg. D. Bandini & B. Oertel (SMNS-STU-F-0901732, dupl. DB21-10-12-33). Ibidem, at some distance from former location, alt. 110 m, *Pinus sylvestris*, *Helianthemum nummularium*, *Quercus robur*, leg. D. Bandini & B. Oertel (SMNS-STU-F-0901731, dupl. DB21-10-12-34). Rheinland-Pfalz, Bad Dürkheim, Haßloch, TK25 6615/4, alt. 122 m, *Quercus robur*, *Pinus sylvestris*, *Corylus avellana*, 12 Oct. 2019, leg. D. Bandini (DB12-10-19-3).

Notes

The holotype of *Inocybe tarda* was described in some detail by Bandini et al. (2021c), but sequencing was not permitted nor was it possible to analyse the caulocystidia at the top of the stipe (for fear of damage). *Inocybe tarda* is the type species of *I.* sect. *Tardae* Bon and is thus, at least historically, an important species in the infrageneric classification of the genus, but there has been confusion in the past as to what *I. tarda* actually is. Kuyper (1983), for example, considered *I. tarda* a synonym of *I. nitidiuscula*, which is quite a different species from what we consider here as *I. tarda* (see Marchetti et al. 2014; Bandini et al. 2021c). *Inocybe aurantioumbonata* was described without even mentioning *I. tarda* in the discussion of similar taxa, but mentioning the caulocystidia as an important character for the diagnosis of the species. To end the confusion around *I. tarda*, we decided to designate an epitype here in which this character could be observed.

Inocybe aurantioumbonata is a species with a dark brown, rather smooth pileus surface, velipellis, spores usually > 10 µm long, and a stipe that is at least pruinose down to the middle. It was described from Italy, from sandy ground with *Pinus* (Marchetti & Franchi 2008). The species is macroscopically reminiscent of *I. tarda*, with the same pileus colour and surface and similar average spore size. Furthermore, *I. aurantioumbonata* (see Marchetti & Franchi 2008 and below) has the same typical shape of spores, i.e., unusually bulgy with a sometimes almost subpapillate apex, which we also observed in every single one of our own collections of *I. tarda* (see Bandini et al. 2021c, pl. 27c). The cystidia of *I. tarda* are usually (sub)cylindrical to (sub)fusiform—in some collections more (sub)fusiform, in others more subcylindrical—usually with rather wide necks and short pedicels, which is also the case with the cystidia of *I. aurantioumbonata* (see Bandini et al. 2021d and below). In addition, the habitat is the same: sandy soil with *Pinus*, often in inland dunes. Figure 1 shows the clade of *I. tarda*, including the epitype selected here and *I. aurantioumbonata* in a joint clade (98%/100%1), reciprocally monophyletic in relation to the clade of *I. astraiana* Bandini & B. Oertel, *I. clandestina* Bandini, B. Oertel & U. Eberh. and *I. nemorosa* (R. Heim) Grund & D.E. Stuntz, which also received support (99%/100%/-). The ITS of the holotype of *I. aurantioumbonata* shows in a qualitatively very good Sanger result evidence of some intragenomic variation (four ambiguous bp reads, an indel that was read as an insertion in the published sequence), but no consistent difference to the epitype sequence of *I. tarda*. Thus, we consider *I. aurantioumbonata* as synonymous with *I. tarda*.

Inocybe transitoria (Britzelm.) Sacc., *Syll. fung. (Abellini)* 5: 788 (1887)

(Fig. 19)

Basionym: *Agaricus transitorius* Britzelm., *Ber. naturhist. Augsburg* 26: 137 (1881).

Selected descriptions and iconography: Britzelmayr (1881); Saccardo (1887); Stangl & Kuyper (1985); Stangl (1989).

Holotype

GERMANY, Bayern, Krumbach, Britzelmayr, Hyporhodii und Leucospori aus Südbayern. Ber. Natur. Ver. Augsburg 26, S. 137. Abb. 11 (= Hymenomyceten aus Südbayern 2), 1881.

Epitypus hic designatus (MBT 10008608)

NORWAY, Telemark, Kragerø, Kammerfossåsen, *Tilia*, *Fraxinus*, *Populus* forest on clay ground, margin of meadow, under *Tilia* and *Populus*,15 Jul. 2016, leg. T. E. Brandrud TEB-45-16 (O-F-304850).

Type specimen examined

Epitype (Fig. 19a, c–e): *Spores* 6.9–8.6 µm (av. 7.6 µm, SD 0.4 µm) × 5.1–6.5 µm (av. 5.7 µm, SD 0.4 µm); Q = 1.2–1.5 (av. 1.3, SD 0.1) (n = 40), nodulose, with prominent obtuse nodules. *Basidia* 4-spored. *Pleurocystidia* 31–45 µm (av. 39 µm, SD 5 µm) × 12–17 µm (av. 14 µm, SD 2 µm); Q = 2.4–3.5 (av. 2.8, SD 0.3) (n = 15), mostly (sub)fusiform to subclavate, apex usually crystalliferous, walls up to 2.5 (3.0) µm thick at the apex, pale yellowish-greenish with 3% KOH. *Cheilocystidia* similar in appearance and size. *Paracystidia* not observed. *Caulocystidia* at the apex of the stipe, narrow subfusiform to subutriform with undate walls.

Description

Pileus 5–30 mm wide, at first (sub)campanulate, later broadly convex or expanded, without or with only a low umbo, margin at first incurved, later decurved to straight or even uplifted, and then pileus depressed around the umbo; young basidiomata with remnants of a faint whitish-greyish velipellis, mostly centred at the umbo; colour nut-brown to dark red-brown (Mu 7.5YR 5/6, 4/4–4/6, 3/4), somewhat paling towards the margin with age; surface at first glabrous, later rimulose to rimose towards the margin; young basidiomata with remnants of a whitish cortina. *Lamellae* moderately crowded (c. 50–65, l = 1–3), almost free to adnate, subventricose, at first whitish, later pale milkcoffee-brownish to brown, with or without a reddish tinge; edge fimbriate, whitish to concolourous. *Stipe* 20–40 × 1–3 mm, cylindrical or curved, base with (sub)marginate bulb, when young covered with whitish tomentum, later longitudinally striate or glabrous, pale brownish to brownish with a reddish hue; pruinose only near the apex. *Context* pale watery brownish in the pileus, somewhat darker in the stipe. *Smell* (sub)spermatic, at least when cut. *Colour of exsiccata* pileus dark brown (Mu 7/5YR 3/4), lamellae and stipe concolourous or a little lighter in colour, no darkening or blackening on drying.

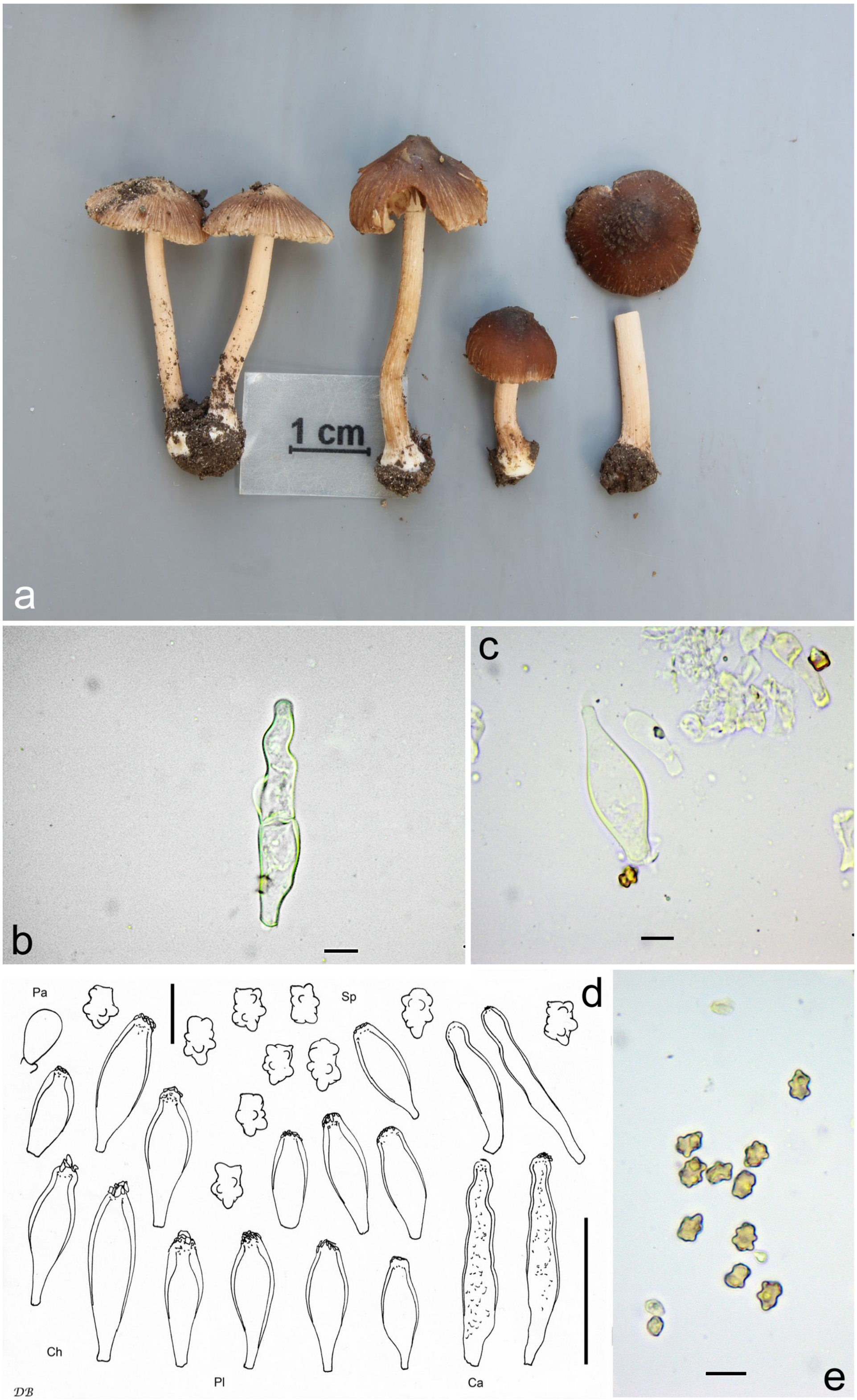

Fig. 19. *Inocybe transitoria* – **a.** Epitype (photo: T. E. BRANDRUD); scale bar: 1 cm. **b.** Caulocystide (coll. O-F-249853); scale bar: 10 µm. **c.** Cheilocystide (epitype); scale bar: 10 µm. **d.** Microscopic characters (epitype); Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm. **e.** Spores (epitype); scale bar: 10 µm.

Spores 6.3–8.6 µm (av. 7.7 µm, SD 0.5 µm) × 4.8–6.5 µm (av. 5.6 µm, SD 0.4 µm); Q = 1.2–1.7 (av. 1.4, SD 0.1) (n = 80 of 2 coll.), nodulose, with 7–10 often rather prominent obtuse nodules. *Basidia* 23–28 × 7–9 µm, generally 4-spored. *Lamellae edges* composed of cheilocystidia and numerous colourless, (sub)clavate, thin-walled paracystidia. *Pleurocystidia* 31–60 µm (av. 41 µm, SD 6 µm) × 11–17 µm (av. 14 µm, SD 2 µm); Q = 2.4–4.6 (av. 3.0, SD 0.5) (n = 30 of 2 coll.); mostly (sub)fusiform to subclavate, at the apex generally wide, mostly without a neck, sometimes (sub)capitate, with a short pedicel or truncate base, apex usually crystalliferous, walls up to 2.5 (3.0) µm thick at the apex, mostly abruptly thickened towards the apex, pale yellowish-greenish with 3% KOH. *Cheilocystidia* similar in size and shape. *Pileipellis* constituted by an epicutis made up of parallel hyphae 4–11 µm wide, with encrusting and parietal brownish pigment, subcutis with wider and paler to colourless elements. *Caulocystidia* only at the apex of the stipe, 50–80 × 10–15 µm, narrow subfusiform to subutriform with undate walls, sometimes (sub)capitate, with a short pedicel, apex usually without or with only very small crystals, walls up to 0.5 µm thick at the apex, pale yellowish-greenish with 3% KOH. *Clamp connections* abundant in all tissues.

Habitat and distribution

Inocybe transitoria was collected with frondose trees in Norway. The species corresponds to UNITE SH1731462.08FU (1%), including data from collections (labelled *I. transitoria* or *I.* cf. *assimilata*), EcM or soil samples from Germany, Estonia, France, Italy, Japan, Latvia and Sweden. In EcM sequences the symbionts *Fagus*, *Quercus* and *Tilia* were indicated.

Additional specimens examined

NORWAY, Møre og Romsdal, Ålesund, Hegrestien, rich *Corylus* forest with some *Betula* sp., 62.43868°N 6.42974 E, 6 Aug. 2011, leg. P. G. Larsen (O-F-249853). SWEDEN, Öland, Borga Hage near Borgholm, *Quercus robur*, *Corylus avellana*, 2 Oct 2020, leg. G. Schmidt-Stohn & B. Oertel (SSt20-080; BOe 2-10-20-2b).

Notes

No exsiccatum of *I. transitoria* survived from Britzelmayr (Killermann [1939, cited by https://pilzeaugsburg.de/mykologen__britzelmayr/]; Enderle et al. 1986), but the holotype, represented by a watercolour of *I. transitoria*, is mentioned in the protologue (Britzelmayr 1881, fig. 11), which however does not allow a reliable assignment to a certain species. Depicted are three basidiomata, one with a brownish pileus with smooth surface and clearly bulbous base of stipe, one without a coloured pileus and the third in cross-section without colours as well. Christian Volbracht, owner of a very comprehensive mycological library ("MykoLibri"), kindly sent to DB not only this watercolour (Britzelmayr 1881, fig. 11), but also another watercolour of "*Clypeus transitorius*" (Britzelmayr 1881, fig. 277, short for *Agaricus* [subgen. *Clypeus*] *transitorius*) in which two basidiomata are depicted: one with a rather glabrous brown subcampanulate pileus and one in cross section. The bases of the stipes are thickened to bulbous. Three oblong nodulose spores were illustrated as well (email by C. Vollbracht to DB, Oct. 26th, 2021). Because no more special features were visible in the listed illustrations, we assigned an epitype, which agrees well with the traditional interpretation of *I. transitoria*, most importantly with the concept of Stangl (1989), also expressed in an earlier article (Stangl & Kuyper 1985).

Inocybe transitoria is characterized by a nut-brown to dark red-brown pileus colour, paling towards the margin with age, a faint whitish-greyish velipellis, glabrous to rim(ul)ose pileus surface, rather small spores with an average length of < 8 µm and predominantly (sub)fusiform to (sub)clavate, and on average rather short hymenial cystidia. Based on available data, it seems to associate mainly with frondose trees such as *Tilia* and *Corylus*. The species might on first sight be mistaken for *Inocybe assimilata*, which differs, e.g., by a greyish velipellis, more (sub)-hygrophanous pileus surface, on average longer hymenial cystidia and habitat on acidic ground, often with *Picea abies* (see, e.g., Britzelmayr 1881; Saccardo 1887; Stangl 1989; Bandini et al. 2017). *Inocybe glabrodisca* can be distinguished from *I. transitoria*, e.g., by a greyish velipellis, on average larger spores and longer hymenial cystidia (Orton 1960; Stangl 1989; Ferrari 2006); from *I. gandalfiana*, e.g., by a prominent umbo, clearer hygrophanous pileus surface and larger spores (Bandini et al. 2021a); and from *I. globulina*, e.g., by usually darker brown pileus colour, (sub)globose bulb, on average longer spores and longer hymenial cystidia (Bandini et al. 2020 c). *Inocybe napipes* has a napiform bulb, larger spores with more prominent nodules and larger hymenial cystidia with thinner walls (Lange 1917; Stangl 1989; Ferrari 2006; Ludwig 2017), while *I. silvae-herbaceae* has no velipellis, larger spores and longer, often subutriform hymenial cystidia with thinner walls (Kokkonen & Vauras 2012). The species morphologically and, with almost 98% sequence similarity in the ITS, also genetically most similar to *I. transitoria* is *I. abdita*, which differs, e.g., by the paler pileus colour, not paling pileus surface with age, on average wider spores and longer hymenial cystidia. In Fig. 1, *I. abdita* and *I transitoria* were supported as reciprocally monophyletic sister clades, *I. transitoria* receiving 96%/100%/1 support.

Inocybe turfae Bandini, B. Oertel & U. Eberh., **sp. n.**
(Fig. 20; MycoBank: MB 845170)

Etymology

Named "turfae" (from Latin "*turfa*" "peat") because the species grows in wet peat hollows.

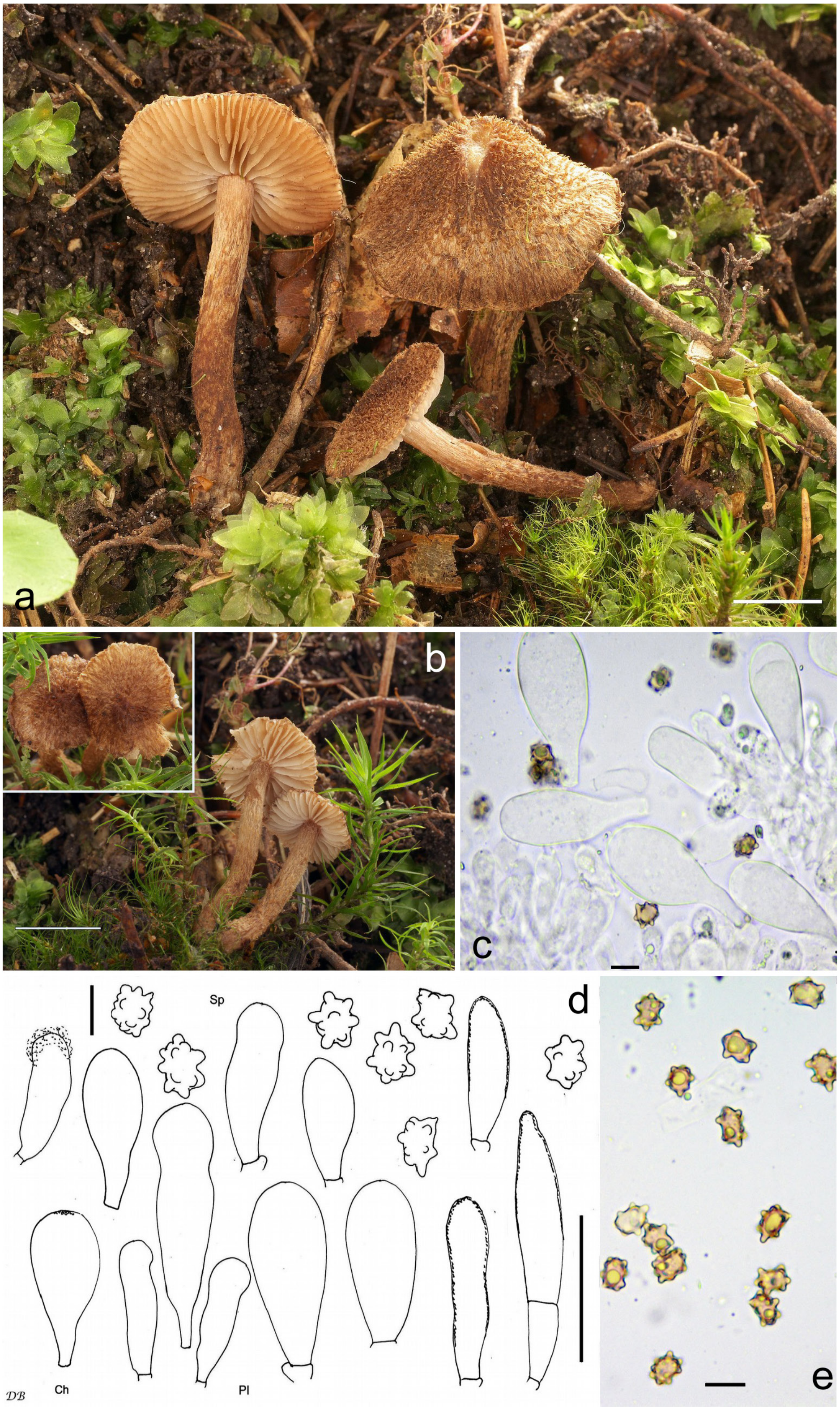

Fig. 20. *Inocybe turfae* **sp. n.** – **a.** Holotype; scale bar: 1 cm. **b.** Coll. DB20-8-16-42; scale bar: 1 cm. **c.** Cheilocystidia (coll. DB14-8-20-13); scale bar: 10 µm. **d.** Microscopic characters (holotype); Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm. **e.** Spores (coll. DB20-8-16-42); scale bar: 10 µm.

Diagnosis

Inocybe turfae **sp. n.** is characterized by a pale brown to brown pileus colour, lanose-squarrose pileus surface, distant thickish lamellae, strongly nodulose spores measuring 7.8–11.5 µm (av. 9.6 µm) × 6.2–10.8 µm (av. 7.8 µm), usually thin-walled hymenial cystidia, pleurocystidia measuring 32–96 µm (av. 55 µm) × 12–25 µm (av. 16 µm), oblong subclavate, intermixed with segmented hyphoid caulocystidia with brownish walls and habitat usually in acid, very moist boggy terrain with conifers. The species can be recognized by the combination of the above characters and differs in its ITS sequence from similar species, such as *I. stellatospora*.

Holotype

GERMANY, Bayern, Regen, Lindberg, Zwieslerwaldhaus, Ruckowitzhänge, TK25 6845/4, alt. c. 900 m, *Picea abies*, *Fagus sylvatica*, *Abies alba*, *Sphagnum* sp., 20 Aug. 2016, leg. D. Bandini, J. Christan, C. Bässler, C. Hahn & B. Oertel (holotype STU SMNS-STU-F-0901693; isotypes priv. herb. D. B. DB20-8-16-41, TUR-A 209534).

Description

Pileus 10–30 mm wide, at first (sub)conical, later broadly convex to expanded, generally without umbo, margin at first slightly incurved or decurved, later straight to even uplifted, and then pileus depressed around the umbo; no remnants of a velipellis observed; colour pale brown, nut-brown to brown (Mu 10YR 5/6–5/8, 4/6; 7.5YR 5/4–5/8), at the centre sometimes somewhat darker; surface usually squamulose-squarrose with fibre bundles at the centre, and lanose towards the margin; young basidiomata with brownish remnants of a cortina. *Lamellae* distant (c. 20–30, l = 1–3), thickish, adnate to broadly adnate, ventricose, at first pale greyish, later cream coloured with brownish tinge or pale brownish to brown(ish) with age; edge fimbriate, whitish to concolourous or even darker brown. *Stipe* 10–45 × 2–3 mm, cylindrical, when young roughly covered with cream-coloured to very pale brownish tomentum, later lanose to (sub)squamulose or even subsquarrose or villose, brown beneath the tomentum, sometimes dark brown towards the base with age; pruinose only at the extreme apex of the stipe. *Context* in the pileus watery whitish, in the stipe with brownish hue. *Smell* indistinct. *Colour of exsiccata* pileus dark greyish brown, dark brown (Mu 10YR 3/3–3/6), lamellae somewhat lighter in colour, stipe concolourous, no darkening or blackening on drying.

Spores 7.8–11.5 µm (av. 9.6 µm, SD 0.7 µm) × 6.2–10.8 µm (av. 7.8 µm, SD 0.7 µm); Q = 1.0–1.5 (av. 1.2, SD 0.1) (n = 120 of 3 coll.); nodulose, with 9–14 strongly protruding obtuse or subacute nodules. *Basidia* 25–33 × 7–13 µm, generally 4-spored, seldom also 2-spored. *Lamella edge* composed of cheilocystidia and rare colourless, (sub)clavate, sometimes somewhat brownish, thin-walled paracystidia. *Pleurocystidia* 32–96 µm (av. 55 µm, SD 20 µm) × 12–25 µm (av. 16 µm, SD 4 µm); Q = 1.8–5.6 (av. 3.4, SD 1.1) (n = 45 of 3 coll.), variable in shape, but mostly subclavate to broadly sac-shaped, also almost balloon-shaped or subutriform, sometimes filled with brownish amorphous content, apex usually without crystals, usually thin-walled or walls only up to 0.5 µm thick near the apex, and then pale yellowish in 3% KOH. *Cheilocystidia* similar, but even more variable in shape. *Pileipellis* constituted by an epicutis made up of parallel unusual hyphae 6–14 µm wide, with thick walls and joints and parietal brownish pigment, subcutis with wider and paler elements. *Caulocystidia* only near the apex of the stipe, oblong subclavate elements, intermixed with segmented hyphoid elements, generally with brownish to dark brown walls and sometimes amorphous brown content in 3% KOH. *Clamp connections* abundant in all tissues.

Habitat and distribution

Our collections were from Germany, in montane regions, all in very moist habitats near small brooks or in very wet peat hollows always with *Sphagnum*, and always with *Picea abies* nearby, on acidic ground, and among other morphologically similar species, such as *I. stellatospora*, or in association with *I. napipes*. The species corresponds to UNITE SH1159943.08FU (3.0%), including sequences from collections or from EcM and soil samples from Denmark, Estonia, France, Japan, United Kingdom and United States. With a collection from North Carolina (MG773840, as "*Inocybe* sp.") from the Great Smoky Mountains National Park, there is a note that the collection grew "at the base of old *Acer* tree under *Picea*, *Fagus*, *Betula*". With a further collection from North Carolina (MT196976, as "*I.* aff. *stellatospora*"), Mt. Mitchell State Park, the symbionts *Abies fraseri* and *Picea rubens* are noted. As hosts of the EcM sequences, *Pinus sylvestris*, *Abies*, *Picea abies*, *Quercus petraea* and *Fagus sylvatica* were indicated.

Additional specimens examined

GERMANY, Bayern, Regen, Lindberg, Zwieslerwaldhaus, Ruckowitzhänge, TK25 6845/4, alt. c. 900 m, *Picea abies*, *Fagus sylvatica*, *Abies alba, Sphagnum* sp., 20 Aug. 2016, leg. D. Bandini, J. Christan, C. Bässler, C. Hahn and B. Oertel (DB20-8-16-42).- Bayern, Ostallgäu, Roßhaupten, Senkele, TK25 8330/1, alt. 860 m, *Picea abies*, *Alnus glutinosa*, *Betula* sp., *Sphagnum* sp., 14 Aug. 2020, leg. D. Bandini & B. Oertel (SMNS-STU-F-0901735, dupl. DB14-8-20-4).- Ibidem, at some distance from former location, *Picea abies*, *Alnus glutinosa*, *Betula* sp., *Sphagnum* sp., 14 Aug. 2020, leg. D. Bandini & B. Oertel (DB14-8-20-13).- Bayern, Ostallgäu, Halblech, Buchenberg, TK25 8430/2, alt. c. 1155 m, *Picea abies*, *Fagus sylvatica*, *Sphagnum* sp., 15 Aug. 2020, leg. D. Bandini, B. Oertel & J. Christan (DB15-8-20-8).

Notes

Inocybe turfae **sp. n.** is characterized by pale brown to brown pileus colour, lanose-squarrose pileus surface, dis-

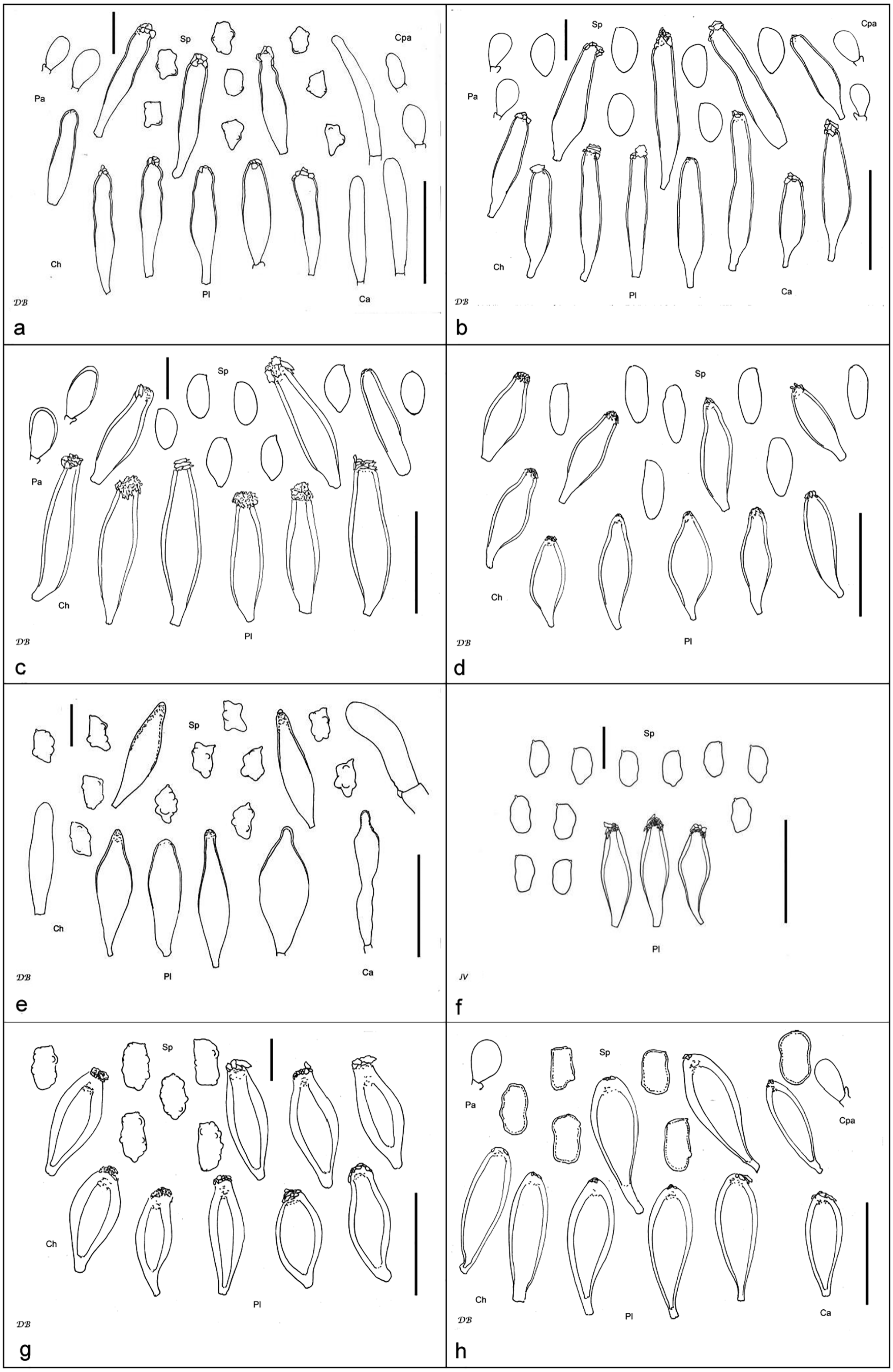

Fig. 21. Microscopic characters of type collections – **a.** *Inocybe albofibrillosa* (M_M_0020039). **b.** *I. aurantiobrunnea* (SMNS-STU-F-0001816). **c.** *I. aurantioumbonata* (MCVE-23504). **d.** *I. bresadolana* (LIP-MB8209251). **e.** *I. brevispora* (L-0054122). **f.** *I. decipiens* (S-F-14450). **g.** *I. dunensis* (K(M): 60273). **h.** *I. javorkae* (BP77256). Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm.

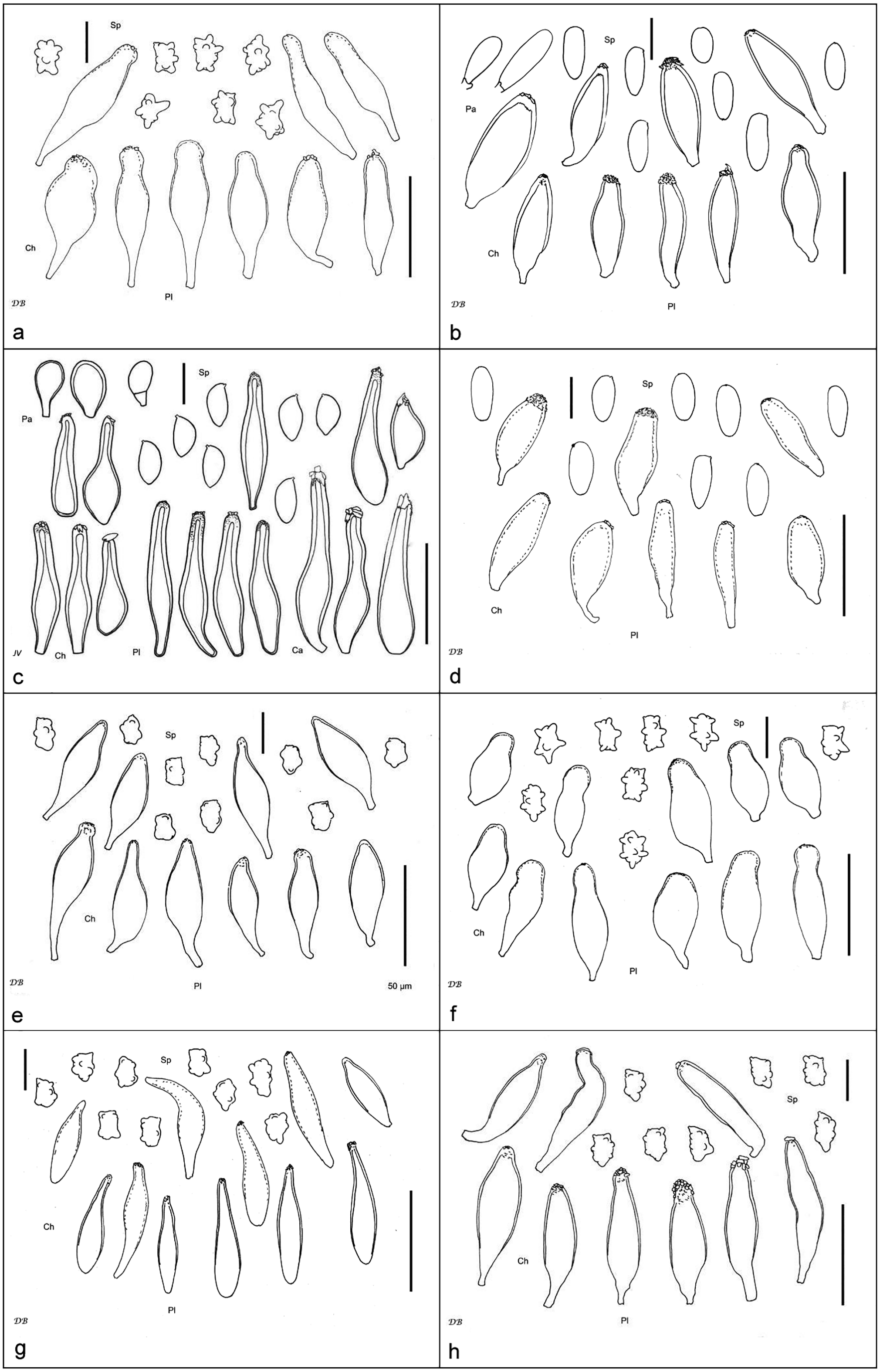

Fig. 22. Microscopic characters of type collections – **a.** *Inocybe longicystis* (CUP-A-024321). **b.** *I. moravica* (BRNU-07012-39). **c.** *I. pholiotinoides* (PC, Romagnesi n° 58, 298). **d.** *I. ravenelii* (K(M): 264841). **e.** *I. soluta* (PRC-bottle n° 385). **f.** *I. stellatospora* (NYS-f-2936.1). **g.** *I. striatorimosa* (K(M): 68622). **h.** *I. subcarpta* (G-00566264). Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm.

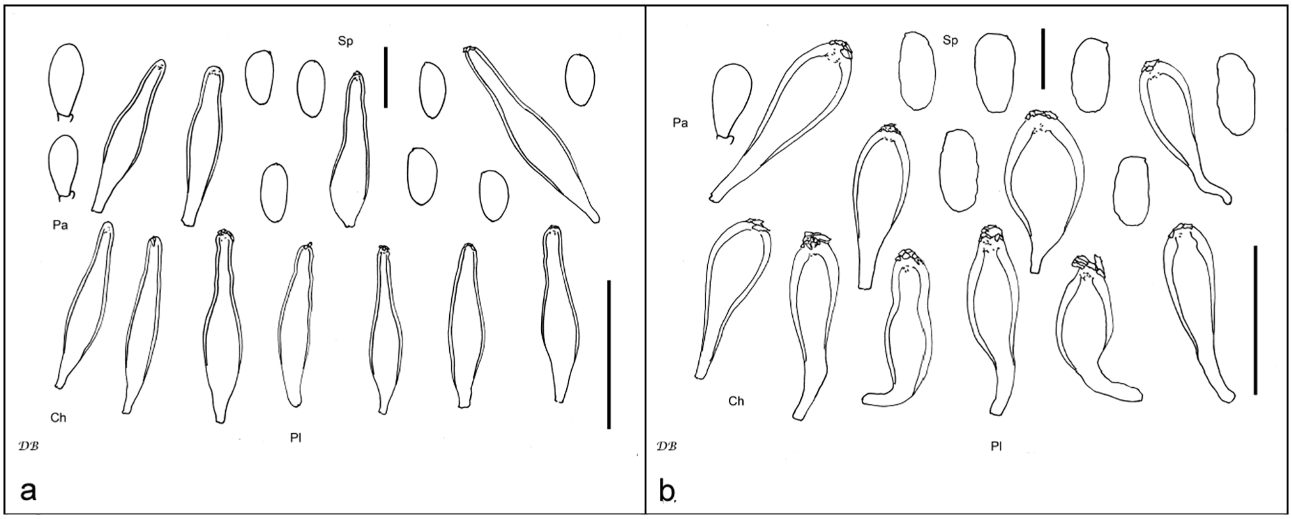

Fig. 23. Microscopic characters of type collections – **a.** *Inocybe subnudipes* (G-00262332). **b.** *I. velata* (MCVE-23506). Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm.

tant thickish lamellae, strongly nodulose spores, usually thin-walled hymenial cystidia, oblong subclavate intermixed with segmented hyphoid caulocystidia with brownish walls and a habitat usually in acidic, very moist boggy terrain with conifers. The species looks very similar to *I. stellatospora*, which differs, e.g., by the generally darker pileus colour, on average narrower spores with a higher Q-value and on average longer, often subcapitate hymenial cystidia (Massee 1904; Matheny & Kropp 2001; DB, personal observation). *Inocybe lanuginosa* (Bull.) P. Kumm. can be distinguished from *I. turfae*, e.g., by longer spores, shorter hymenial cystidia and shorter (sub)clavate caulocystidia (Bulliard 1788; Stangl 1989 (as "*I. lanuginosa* var. *ovatocystis*"); Matheny & Kropp 2001), and *I. leptophylla* G.F. Atk. can be distinguished, e.g., by the usually darker pileus colour, missing pleurocystidia, longer spores and on average shorter cheilocystidia (Atkinson 1918; Horak 1987 as "*Astrosporina casimiri*"; Stangl 1989; Matheny & Kropp 2001; Kobayashi 2002 and notes therein; Ferrari et al. 2014; DB, personal observation). *Inocybe parcecoacta* Grund & D.E. Stuntz has a smoother pileus surface, smaller spores with less prominent nodules and on average longer hymenial cystidia (Grund & Stuntz 1977; DB, personal observation), *I. prisca* differs, e.g., by the smoother pileus surface, smaller spores with much less protruding nodules and on average longer hymenial cystidia (Bandini et al. 2021a) and *I. relicina* differs, e.g., by the darker pileus colour, yellow(ish) lamellae and much smaller spores (Fries 1821; Quélet 1873; Ferrari et al. 2014). *Inocybe teraturgus* M.M. Moser has a smoother subhygrophanous pileus surface, larger spores and on average shorter, often near the apex thickened hymenial cystidia and habitat in eutrophic swamps (Moser 1992; Matheny & Kropp 2001; DB, personal observation), while *I. timpetuana* Bandini & B. Oertel can be distinguished from *I. turfae*, e.g., by the generally darker pileus colour, larger spores and longer hymenial cystidia mostly with a long neck (Bandini et al. 2021a). The species with the most similar ITS in comparison to *I. turfae* is *I. stellatospora*, but the similarity is only 89%. The clade of *I. turfae* received full support and is supported as sister to the clade of *I. stellatospora*. The split within the *I. turfae* clade is based on three constant SNP positions in the ITS; none of the sequences downloaded from GenBank includes the LSU, which might have influenced the support values. We suspect that all four sequences belong to *I. turfae*.

Inocybe velata Franchi & M. Marchetti, *in* Marchetti & Franchi, *Riv. Micol*. 51(4): 345 (2008)
(Fig. 23b)

Description and iconography: Marchetti & Franchi (2008).

Type specimen examined

Holotype: ITALY, Tombolo di Giannella, near Orbetello, *Pinus pinaster*, *Pinus pinea*, *Pinus halepensis*, 21 Nov. 2008, leg. P. Franchi & M. Marchetti (MCVE-23506). *Spores* 11.1–14.5 µm (av. 12.6 µm, SD 0.8 µm) × 5.4–7.6 µm (av. 6.7 µm, SD 0.5 µm); Q = 1.7–2.2 (av. 1.9, SD 0.1) (n = 40), oblong, mostly with sinuous to entolomoid, sometimes almost smooth outline. *Basidia* 4-spored. *Pleurocystidia* 39–70 µm (av. 56 µm, SD 8 µm) × 14–25 µm (av. 18 µm, SD 3 µm); Q = 2.4–3.6 (av. 3.2, SD 0.4) (n = 15), mostly ventricose (sub)fusiform or (sub)clavate, apex usually crystalliferous, walls up to 3.0 (4.0) µm thick at the apex, pale yellowish-greenish with 3% KOH. *Cheilocystidia* similar in appearance and size. *Paracystidia* not observed. *Caulocystidia* not studied (to preserve the material).

Additional specimen examined

GERMANY, Baden-Württemberg, Rhein-Neckar-Kreis, Sandhausen, near Nature Reserve Düne Pferdstrieb, TK25 6617/4, alt. 113 m, *Pinus sylvestris*, 25 Oct. 2017, leg. D. Bandini (SMNS-STU-F-0901721, dupl. DB25-10-17-4).

Notes

Inocybe velata is, according to the protologue, characterized by abundant whitish velipellis, a quite glabrous, rather pale pileus, which becomes somewhat lacerate with age at the margin, large oblong spores with undulate outline and mostly (sub)fusiform to (sub)clavate hymenial cystidia (Marchetti & Franchi 2008). It is a Mediterranean species growing in sandy maritime habitats with *Pinus*. Almost all this information, in combination with the photographs given with the original description, reminds of *I. dunensis*, as already noted by the authors themselves.

The difference, according to the authors, consists of the shape of the spores of *I. dunensis*, which is "più o meno angoloso". Furthermore, the stipe of *I. velata* is pruinose only near the apex of the stipe. We examined the holotypes of both species and, apart from the named differences, found that the spores of *I. dunensis* were also on average shorter (see above). In Fig. 1, *I. velata* (fully supported) is supported as sister clade to what we consider to be *I. decipiens*, which is also the species with the most similar—though in fact rather dissimilar—ITS (85% similarity). *Inocybe dunensis* is included in the same supported multi-species clade as *I. velata*, but fairly distant.

Discussion

The present article offers a small glimpse into the enormous diversity of the genus *Inocybe*. We here present species the holotypes of which are from northern, central, and southern Europe, and in two cases from North America (New York and Georgia). Given the great divergence of the species included in the molecular analysis and the small number of markers used in combination with the large number of species in the genus, the tree presented as Fig. 1 cannot represent the phylogenetic history of the genus. In spite of that, the nodulose or laceroid species cluster in several clades in the upper portion of the tree, closer to the root, while the smooth-spored taxa from Europe are all in the lower portion of the tree. The backbone of the tree is not supported. Therefore, this arrangement should not be mistaken for phylogenetic signal with regard to spore shapes. We would like to stress again that our focus was not on resolving the evolutionary history of *Inocybe*, but on supporting the species concepts presented here. It stands to reason that, as ITS-LSU data from additional collections become available, the molecular support of species could become less, even in an analysis including the same set of species, because larger samples are likely to include more infraspecific sequence variation. But on the other hand, as additional markers become available, the support might be raised. As the great majority of species and all of the newly described species are well supported by the available data, we consider our conclusions, i.e., new taxa, typified taxa and synonymized taxa, as well supported.

The habitats of the species are as diverse as their distribution: *Inocybe mecoana* was found in Portugal and Malta at or near the seashore with *Pinus* nearby, in sand or clayish calcareous ground, while *I. turfae* is a species that grows in acidic boggy soil often in association with *Sphagnum* and was found by us in montane woods in Germany. *Inocybe sepiana*, too, is restricted to a very specific and rare habitat: sandy or pebbly calcareous shores of rivers or lakes, always with *Salix* nearby; *I. orioli* prefers rather rich humid soil, and *I. abdita* was found in a city at different places in a park-like location.

Furthermore, the described species are morphologically very different. There are smooth-spored species, as *I. mortenii*, the stipes of which have caulocystidia only near the apex, while others, such as *I. alcis* and *I. orioli*, have an entirely pruinose stipe. *Inocybe abdita* and *I. turfae* have nodulose spores and stipes which are pruinose only near the apex, while the equally nodulose-spored *I. sepiana* has an entirely pruinose stipe. Besides, there are species with rather small spores, such as *I. abdita*, while the spores of *I. sepiana* are quite large. All this in combination with the different shapes and sizes of the cystidia and the different colours and textures of the pilei and stipes, gives a good impression of the morphological diversity of the genus.

Thus, in a key based on morphological criteria, the newly described species would have to be classified predominantly in different groups. According to the keys of Bon (1997a, 1997b, 1998), which are still in use even though they are in many respects long outdated, *I. mortenii* would belong to *I.* sect. *Lilacinae* R. Heim because of its violet stipe. *Inocybe cryptica* would be part of sect. *Inocybe*, even though in Fig. 1 it is resolved within the clade that includes members of the "*hirtella*-group". *Inocybe mecoana*, *I. alcis* and *I. orioli* belong to the *Splendentes*, and *I. mecoana* can be attributed to the subsection *Phaeoleucinae* Bon, which includes species with whitish or subconcolourous but not pinkish-reddish stipes. In Fig. 1, a close relationship with *I. phaeoleuca* was not supported. Bon listed *I. pholiotinoides* in this subsection, which species is at least morphologically related to *I. alcis*, *I. carissima* and *I. orioli*, but Fig. 1 suggests a closer relationship to *I. pholiotinoides* only for *I. carissima*. We would not include these four species in the subsection *Phaeoleucinae* since, in our opinion, and in the result shown in Fig. 1, all four species, and likewise *I. ionochlora* and *I. muricellata*, should be united in a new group because of their characteristic common features, such as the narrow (sub)-fusiform cystidia with walls strongly reacting on KOH.

The species with nodulose spores can be divided between the artificial *I.* sect. *Cortinatae* Kühner & Boursier, with species with stipes pruinose only near the apex, and the artificial *I.* sect. *Marginatae* Kühner, with species with entirely pruinose stipes. *Inocybe abdita* has to be assigned to the former section and therein to *I.* subsect. *Napipedinae* (J.E. Lange) Bon because of the bulbous base of the stipe. *Inocybe culicis* and *I. rangiferi* also belong to *I.* sect. *Cortinatae*, but not to *I.* subsect. *Napipedinae* but either to *I.* subsect. *Brevisporinae* Bon, which includes species with a non-bulbous stipe base, or to the subsection *Cortinatae* (Kühner & Boursier) Bon, including species with a glabrous or squamulose-fibrillose pileus surface. Since the delimitation of both subsections (*Brevisporinae* and *Cortinatae*) is not clear and morphologically closely related species like *I. soluta* and *I. subcarpta* would have to be assigned to different subsections using this delimitation, a new classification is called for. *Inocybe turfae* would be assigned to *I.* sect. *Cortinatae* as well, and there to the stirps *Lanuginosa* Singer ex Bon, since it is morphologically similar to species of this group such as *I. stellatospora*. Finally, *Inocybe sepiana* is part of *I.* sect. *Marginatae*, where it would be included in *I.* subsect. *Oblectabiles* Bon, which is defined by stipes with more or less intense pinkish-reddish or subconcolourous tinges.

In addition to the 11 species described as new, we presented portraits of eight species. For five of them, *I. griseovelata*, *I. soluta*, *I. subcarpta*, *I. tarda* and *I. transitoria*, we assigned epitypes, and for *I. lacera* a neotype. *Inocybe lacera* and *I. moravica* are very similar to each other and may be found in the same habitat. We consider the acceptance of *I. moravica* as a good species, independent of *I. lacera*, as tentative, hoping that further evidence will emerge for a better supported decision. *Inocybe transitoria* is morphologically and genetically closely related to *I. abdita*, and at least the latter-named species is surely quite rare judging from the missing entries in databases and from our own few collections. *Inocybe soluta* is closely related to *I. culicis* as well as *I. subcarpta*, but the three species are not too difficult to distinguish morphologically from each other because of the different macroscopic aspect of the pileus and size and shape of the spores and cystidia.

Given the fact that, by now, more than 10,000 sequences of the genus *Inocybe* are available in the GenBank and UNITE databases and that we ourselves (i.e., DB) have herbarium holdings with more than 8,000 morphologically examined and partly sequenced collections, most of the species here described as new seem to be comparatively rare. For several of the species, we cannot yet determine if they are truly rare, because it seems quite possible that they have been mistaken for other species in the past. This is the case of *I. turfae*, which resembles the common and rather well-known *I. stellatospora* in many respects. *Inocybe alcis*, *I. carissima* and especially *I. orioli* could have easily been mistaken for *I. pholiotinoides*, and *I. mortenii* could have been mistaken for several species with violet stipes, such as *I. pusio* or *I. amethystina* (Kuyper 1986; Stangl 1989; Bon 1997a; Bandini et al. 2021c). *Inocybe mecoana* has probably been mistaken for *I. tarda* and, judging from its absence from sequence databases, *I. cryptica* seems to be a rare species.

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Appendix 1. Sequences used in this study. Herbarium abbreviations follow Index Herbariorum (http://sweetgum.nybg.org/science/ih/), with the exception of DB = private herbarium of Ditte Bandini. Accession numbers in bold print were obtained in the context of this study. EcM – ectomycorrhizae.

Species	Herbarium	Voucher no.	Other voucher numbers	Origin	GenBank_ UNITE acc. no. ITS	Genbank acc. no. LSU or *RPB2* (with *)	Published in
Inocybe abdita	STU	SMNS-STU-F-0901691 (holotype)	DB14-9-14-14	Germany	**OP164062**	**OP164062**	
I. abdita	DB	DB14-9-14-8	KR-M-0042264	Germany	**OP164107**	**OP164107**	
I. abdita	STU	SMNS-STU-F-0901692	DB14-9-14-15	Germany	**OP164063**	**OP164063**	
I. alberichiana	STU	SMNS-STU-F-0901514 (holotype)	DB12-9-19-16	Austria	MW845855	MW845855	Bandini et al. 2021c
I. albofibrillosa	M	M-0020039 (holotype)	HSH1889, JS126	Germany	**OP164105**		
I. alcis	STU	SMNS-STU-F-0901712 (isotype)	DB24-8-15-12	Finland	**OP164083**	**OP164083**	
I. alcis	TUR	TUR-A 190129	JV27675	Finland	**OP164046**		
I. alcis	STU	SMNS-STU-F-0901722	DB10-8-86-Vauras-JV2222	Finland	**OP164055**		
I. alcis as *I. muricellata*	TUR	TUR 171604		Finland	**UDB022385, FISAP987-14**		
I. alpigenes as *I. tetragonospora*	DB	DB16-8-16-9		Germany	MG136899		Bandini et al. 2019b
I. amethystina	L	L-0053531 (holotype)		Netherlands	MW845932		Bandini et al. 2021c
I. assimilata	M	M-0151614 (holotype of I. pseudoumbrina)		Germany	**MF782552**		
I. assimilata	M	M-0020105 (epitype)		Germany	KM873366 (= NR_153148)		Marchetti et al. 2014
I. assimilata	DB	DB5-9-14-11		Germany	MG136880	MG137006	Bandini et al. 2019b
I. astraiana	STU	SMNS-STU-F-0901240	DB26-10-14-7	Germany	MN512321	MN512321	Bandini et al. 2020a
I. athenana	STU	SMNS-STU-F-0901238 (holotype)	DB15-6-19-2	Germany	MN512320	MN512320	Bandini et al. 2020a
I. aurantiobrunnea	STU	SMNS-STU-F-0001816 (isotype)		Spain	**OP164016**	**OP164016**	
I. aurantiobrunnea as *I. luteipes*	MCVE	21519		Italy	JF908212		Osmundson et al. 2013
I. aurantioumbonata	MCVE	MCVE 23504 (holotype)		Italy	**OP164048**		
I. brevispora	L	L-0054122		Netherlands	**MN319698**		
I. bufonia	TUR-A	TUR-A 190477 (holotype)	K. Kokkonen 45/09	Finland	JN580823 (= NR_119988)		Kokkonen & Vauras 2012

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I. bufonia	STU	SMNS-STU-F-0901723	DB10-8-13-9	Austria	**OP164053**	**OP164053**	
I. carissima	STU	SMNS-STU-F-0901701 (holotype)	DB13-8-21-3	Germany	**OP164058**	**OP164058**	
I. carissima	O	O-F-249109		Norway	NOBAS1023-15		NORBOL
I. carissima	O	O-F-258836		Norway	NOBAS8397-21		NORBOL
I. carissima	O	O-F-258869		Norway	NOBAS8417-21		NORBOL
I. carissima	STU	SMNS-STU-F-0901728	DB26-7-15-1	Germany	**OP164087**	**OP164087**	
I. cf. *abdita* as *I. assimilata*	ACAD	ACAD 19494	DG1816	Canada	MT237516		MATHENY et al. unpublished, submitted 12 Mar-2020
I. cf. *maritimoides*	STU	SMNS-STU-F-0901689	DB20-9-20-13	Austria	**OP164076**	**OP164076**	
I. cf. *moravica*	O	O-F-249740		Norway	NOBAS1429-15		NORBOL
I. cf. *moravica*	O	O-F-258375		Norway	NOBAS8253-21		NORBOL
I. cf. *moravica*	O	O-F-258378		Norway	NOBAS8256-21		NORBOL
I. cf. *moravica*	O	O-F-305006		Norway	NOBAS5402-18		NORBOL
I. cf. *pseudoteraturgus* as *I. stellatospora*	UBC	UBC-F-19455		USA	HQ604223		BERBEE et al. unpublished, submitted 4 Nov 2010
I. cf. *pusio*	AH	AH 40053		Italy	OL352057	OL352057	MUÑOZ et al. 2022
I. cincinnata	STU	SMNS-STU-F-0901571	DB19-9-20-14	Austria	MW845946	MW845946	BANDINI et al. 2021c
I. cincinnata	STU	SMNS-STU-F-0901644	DB17-9-20-5	Austria	**OP164069**	**OP164069**	
I. clandestina	STU	SMNS-STU-F-0901267 (holotype)	DB11-10-17-16	Germany	MW845865	MW845865	BANDINI et al. 2021c
I. corydalina	EIU, WTU	EIU AM10687, TURA6488		Russula	MH216083	AY038314	MATHENY et al. 2002, MATHENY et al. 2020
I. cryptica	MA	MA-Fungi 98677 (holotype)	PRC-121211-01	Spain	**OM985894**		
I. cryptica	MA	MA-Fungi 98478	PRC-121226-24	Spain	**ON000207**		
I. cryptica	MA	MA-Fungi 98672	PRC-211210-01	Spain	**ON010592**		
I. cryptica	MA	MA-Fungi 98674	PRC-211210-03	Spain	**ON010593**		
I. culicis	TUR-A	TUR-A 203492 (holotype)	SMNS-STU-F-0901258/ DB21-8-15-27 (isotypes)	Finland	**OP164108**	**OP164108**	
I. culicis	STU	SMNS-STU-F-0901709	DB17-8-15-26	Finland	**OP164068**	**OP164068**	

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I. curvipes	GB	EL6703		Sweden	AM882813.2	AM882813.2	Ryberg et al. 2008
I. decipiens	TR	TR-MIC-B 0324 (authentic material)		Italy	**OP164050**		
I. decipiens	DB	DB16-6-12-E60-Eimann		Germany	**OP164018**	**OP164018**	
I. decipiens	DB	DB3-9-10-Dondl		Germany	**OP164017**		
I. decipiens	O	L106		Norway	UDB017679		Høiland, dataset 2012
I. deianae	STU	SMNS-STU-F-0901538 (isotype)	DB30-10-4-Eyssartier; double of G. Eyssartier pers. coll. 04-095	France	OK057117		Bandini et al. 2022a
I. drenthensis	STU	SMNS-STU-F-0901477 (holotype)	DB30-9-19-1	Netherlands	MW845869	MW845869	Bandini et al. 2021c
I. drenthensis	STU	SMNS-STU-F-0901478	DB30-9-19-17	Netherlands	MW845871	MW845871	Bandini et al. 2021c
I. dryadiana	STU	SMNS-STU-F-0901259 (holotype)	DB31-8-14-1	Germany	MW845873	MW845873	Bandini et al. 2021c
I. dryadiana	STU	SMNS-STU-F-0901481	DB2-8-14-11	Germany	MW845875	MW845875	Bandini et al. 2021c
I. dunensis	DB	DB15-8-14-23		Germany	**OP164020**		
I. dunensis	KR	KR-M-0038114	DB21-9-11-1	Netherlands	**OP164019**	**OP164019**	
I. dunensis	MCVE	237		Italy	JF908092		Osmundson et al. 2013
I. dunensis	O	L040		Norway	UDB017616		Høiland, dataset 2012
I. dunensis	TUF	TUF 118006		Estonia	UDB015288		Liiv, dataset 2010
I. ericetorum	TUR-A	JV10522F (holotype)		Finland	JN580877		Kokkonen & Vauras 2012
I. ericetorum as *I.* cf. *assimilata*	GB	EL2304		Sweden	AM882930	AM882930	Ryberg et al. 2008
I. favrei	G	G J. Favre 122a (lectotype of. *I. taxocystis*)	K138	Switzerland	JN580884		Kokkonen & Vauras 2012
I. favrei Bon	LIP	Bon84095 (type)		France	NR_158506,KY033786		Larsson et al. 2018b
I. flavoalbida	TENN	TENN 067000 (isotype)	PBM3768	Australia	KJ729873,	KJ729901	Matheny et al. 2020; Matheny & Bougher 2017
I. fuscicothurnata	TENN	TENN 068940	PBM3980	USA	MF487844	KY990485	Matheny & Swenie 2018
I. gaiana	STU	SMNS-STU-F-0901482 (holotype)	DB10-10-18-22	Germany	MW845876	MW845876	Bandini et al. 2021c
I. gaiana	STU	SMNS-STU-F-0901483	DB10-10-18-18	Netherlands	MW845877	MW845877	Bandini et al. 2021c

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I. gandalfiana	STU	SMNS-STU-F-0901562 (holotype)	DB12-9-16-15	Germany	MW647626	MW647626	Bandini et al. 2021a
I. gandalfiana	DB	DB21-9-20-21		Austria	**OP164021**		
I. gandalfiana	DB	DB21-9-20-7		Austria	**UDB01004651**		
I. glabrodisca	K	K(M)34204 (holotype)	P.D. Orton 1576	UK	**MK584751**		
I. glabrodisca	DB	DB13-10-13-4		Germany	**OP164022**		
I. globulina	STU	SMNS-STU-F-0901269 (holotype)	DB6-6-13-1	Germany	MN625274	MN625274	Bandini et al. 2020a
I. globulina	DB	DB29-5-13-2		Germany	**OP164023**		
I. grammopodia	STU	SMNS-STU-F-0901611	DB14-10-15-2	Germany	OK057203	OK057203	Bandini et al. 2022a
I. griseovelata	STU	SMNS-STU-F-0901568 (epitype)	DB30-9-12-1	Germany	MW845942	MW845942	Bandini et al. 2021c
I. griseovelata	GB	EL20906		France	FN550931	FN550931	Ryberg et al. 2010
I. griseovelata	STU	SMNS-STU-F-0901457	DB15-10-14-5	Netherlands	MW845883	MW845883	Bandini et al. 2021c
I. griseovelata	STU	SMNS-STU-F-0901567	DB1-10-13-2	Germany	MW845944	MW845944	Bandini et al. 2021c
I. grusiana	STU	SMNS-STU-F-0901262 (holotype)	DB21-5-17-1	Germany	MW845884	MW845884	Bandini et al. 2021c
I. helobia	L	L-0053536 (holotype)	Kuyper 2124	Netherlands	MN319699		Bandini et al. 2020a
I. helobia	KR	KR-M-0038018	DB4-6-11-3	Netherlands	**OP164024**	**OP164024**	
I. hirtella	STU	SMNS-STU-F-0901607 (epitype)	DB4-10-20-19	Germany	OK057200	OK057200	Bandini et al. 2022a
I. ianthinopes	AH	AH 40370 (holotype)		Spain	OL352086 (= NR_176185)		Muñoz et al. 2022
I. ianthinopes	STU	SMNS-STU-F-0901610	DB21-5-13-2	Germany	OK057202	OK057202	Bandini et al. 2022a
I. ianthinopes	STU	SMNS-STU-F-0901623	DB15-8-17-9	Germany	OK057181	OK057181	Bandini et al. 2022a
I. impexa	STU	SMNS-STU-F-0901710	DB17-8-15-19	Finland	**OP164066**	**OP164066**	
I. impexa	STU	SMNS-STU-F-0901711	DB17-8-15-16	Finland	**OP164065**	**OP164065**	
I. impexa	TAA	TAA 172127		Finland	AM882821.2	AM882821.2	Ryberg et al. 2008
I. ionochlora	KR	KR-M-0038060	DB18-8-12-2	Austria	**OP164025**	**OP164025**	
I. ionochlora	M	M-0276187	DB17-8-11-3	Germany	MF804316	**OP218359**	Bandini et al. 2013
I. ionochlora	STU	SMNS-STU-F-0901706	DB14-8-21-2	Germany	**OP164061**	**OP164061**	

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I. ionochlora	STU	SMNS-STU-F-0901724	DB10-8-21-10	Austria	**OP164054**	**OP164054**	
I. javorkae as *I. dunensis*	MCVE	21679		Italy	JF908262		Osmundson et al. 2013
I. javorkae	BP	BP 77256 A257 (holotype)		Hungary	**ON359948**		
I. javorkae	STU	SMNS-STU-F-0901704	DB21-10-12-1	Germany	**OP164078**	**OP164078**	
I. javorkae as *I. dunensis*	MCVE	243		Italy	JF908093		Osmundson et al. 2013
I. johannae	TUR	TUR 183477		Finland	**OP164045**, **FISAP107214**		
I. johannae as *I. giacomi*	GB	EL3105		Norway	AM882742.2	AM882742.2	Ryberg et al. 2008
I. knautiana	STU	SMNS-STU-F-0901491 (holotype)	DB22-8-16-1	Germany	MW845887	MW845887	Bandini et al. 2021c
I. kohistanensis	LAH	LAH 35001 (holotype)	SJ16	Pakistan	KP316243		Jabeen et al. 2016
I. lacera	STU	SMNS-STU-F-0901583 (neotype)	DB10-10-18-4	Netherlands	OK057130	OK057130, **OP186969***	Bandini et al. 2022a
I. lacera	DB	DB2-10-12-4		Germany	OK057120	OK057120	Bandini et al. 2022a
I. lacera	STU	SMNS-STU-F-0901696	DB10-5-20-1	Germany	**OP164052**	**OP164052,** **OP186966***	
I. lacera	STU	SMNS-STU-F-0901707	DB9-10-18-14	Netherlands	**OP164102**	**OP164102,** **OP186973***	
I. lacera	STU	SMNS-STU-F-0901708	DB28-8-17-7-Vauras-JV32237F	Finland	**OP164090**	**OP164090**	
I. lacera	STU	SMNS-STU-F-0901713	DB8-5-21-3	Netherlands	**OP164101**	**OP164101,** **OP186972***	
I. lacera	STU	SMNS-STU-F-0901714	DB2-9-17-1-Vauras-JV32297F	Finland	**OP164073**	**OP164073,** **OP186975***	
I. lampetiana	STU	SMNS-STU-F-0901494 (holotype)	DB6-7-14-3	Germany	MW845891	MW845891	Bandini et al. 2021c
I. lampetiana	STU	SMNS-STU-F-0901496	DB1-6-14-1	Germany	MW845893	MW845893	Bandini et al. 2021c
I. lanuginosa	WTU	WTU-F50698 (isoepitype)		Finland	HQ201356	HQ201356	Matheny & Wolfenbarger unpublised, submitted 29 Aug 2010
I. lanuginosa	DB	DB1-11-12-7		Germany	MH366601.2		Bandini et al. 2019b
I. laurina	STU	SMNS-STU-F-0901247 (holotype)	DB23-10-16-6	Germany	MN512325	MN512325	Bandini et al. 2020a

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I. leptophylla	DB	DB10-8-13-12		Austria	MH366599.2		Bandini et al. 2019b
I. leptophylla	STU	SMNS-STU-F-0901717	DB21-7-19-8	Austria	**OP164081**	**OP164081**	
I. luteifolia	TENN, CUW	TENN AHS6557 (isotype)	PBM2642	USA	FJ436331	EU307814	Matheny et al. 2020; Kropp et al. 2010
I. maritimoides	ACAD	ACAD 10463		Canada	MH024862		Matheny et al., unpublished, submitted 3 Mar 2018
I. maritimoides	ACAD	ACAD 11681		Canada	MH024878, MH024867		Matheny et al., unpublished, submitted 3 Mar 2018
I. mecoana	PO	PO-F2158 (holotype)	VF221219IS1	Portugal	**OM971872**		
I. mecoana		SM588b		Malta	**OM760514**		
I. mecoana		SM588c		Malta	**OM760512**		
I. mecoana	PO	PO-F2238	VF030121IS1	Portugal	**OM971871**		
I. melanopus	GB	JV4986		Finland	AM882727.2	AM882727.2	Ryberg et al. 2008
I. messapica	TR	AMB 12794 (holotype)		Italy	MT386024	MT476738	Cervini 2021
I. minima	ACAD	ACAD 13144		Canada	MH578003		Matheny & Hobbs, unpublished, submitted 4 Jul 2018
I. minima	DB	DB16-10-19-Arnolds		Netherlands	MW856431		Bandini et al. 2021c
I. minima	DB	DB26-10-19-9		Germany	**OP164026**		
I. mixtilis	M	M-0219661 (epitype)			KJ938767	KJ938767	Esteve-Raventós et al. 2018
I. mixtilis	GB	EL8904		Sweden	AM882836.2	AM882836.2	Ryberg et al. 2008
I. moravica	BRNM	BRNM 07012/39 (holotype)		Czechia	**OP712321**		
I. moravica	STU	SMNS-STU-F-0901695	DB5-10-19-7	Netherlands	**OP164099**	**OP164099, OP186965***	
I. moravica	STU	SMNS-STU-F-0901698	DB14-5-19-5	Netherlands	**OP164059**	**OP164059, OP186968***	
I. moravica	STU	SMNS-STU-F-0901699	DB5-10-19-6	Netherlands	**OP164098**	**OP164098, OP186970***	
I. moravica	STU	SMNS-STU-F-0901700	DB31-5-15-8	Netherlands	**OP164097**	**OP186971***	
I. moravica	STU	SMNS-STU-F-0901715	DB1-9-17-2-Vauras-JV32271F	Finland	**OP164051**	**OP164051, OP186974***	
I. moravica	STU	SMNS-STU-F-0901697	DB31-5-15-2	Netherlands	**OP164096**	**OP164096, OP186967***	

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I. mortenii	DB	DB19-9-20-5		Austria	**OP164049**	**OP164049**	
I. mortenii	personal collection Ø. Weholt	MP-2-190816		Norway	**OP164044**		
I. mortenii	personal collection Ø. Weholt	MP-4-110816		Norway	**OP164042**		
I. mortenii	personal collection Ø. Weholt	OW-I12-16		Norway	**OP164041**		
I. mortenii	personal collection Ø. Weholt	OW-I34-19		Norway	**OP164043**		
I. mortenii	STU	SMNS-STU-F-0901737	DB19-9-20-10	Austria	**OP164072**	**OP164072**	
I. mortenii	O	O-F-259432 (holotype)	OW30-17	Norway	**OP164040**		
I. mortenii as *I.* cf. *subnudipes*	GB	BJ910809		Sweden	AM882983		Ryberg et al. 2008
I. muricellata	DB	DB16-10-11-2		Germany	MW856432		Bandini et al. 2021c
I. muricellata	STU	SMNS-STU-F-0900985	DB23-9-14-2	Germany	MW845931	MW845931	Bandini et al. 2021c
I. muricellatoides	HMJAU	HMJAU 26201 (holotype)	Gansu 2012130	China	KY402220	KY402216	Fan & Bau 2020
I. napipes	DB	DB14-8-20-8		Germany	**OP164027**		
I. napipes	KR	KR-M-0038031	DB16-9-11-1	Netherlands	MG136884	MG137005	Bandini et al. 2019b
I. nemorosa	ACAD	ACAD 19518		Canada	MH586780, MH586817		Matheny & Hobbs, unpublished, submitted 5 Jul 2018
I. neorufula	STU	SMNS-STU-F-0901288 (isotype)	AH40223	Spain	MT101890		Bandini et al. 2020b
I. neorufula	STU	SMNS-STU-F-0901445	DB30-10-15-2-Dondl	Italy	MT101876	MT101876	Bandini et al. 2020b
I. nobilis		Rebaudengo 27.10.1982		Italy	KX592683		Franchi et al. 2016
I. nobilis	DB	DB14-9-20-24		Austria	**UDB0799561**		
I. nobilis	DB	DB8-10-11-6	DB8-10-11-6	Germany	**OP164028**	**OP164028**	
I. norvegica	GB	EL109-12 (holotype)		Norway	MW617340	MW617340	Larsson & Vauras 2021
I. obscuroides	DB	DB30-6-12-4		Germany	MW856433		Bandini et al. 2021c

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I. occulta	AH	AH 36443 (holotype)		Spain	KX290787		Esteve-Raventós et al. 2018
I. occulta	GB	EL272-13		Norway	MK153695		Cripps et al. 2019b
I. orioli	STU	SMNS-STU-F-0901703 (holotype)	DB20-10-17-1	Germany	**OP164074**	**OP164074**	
I. orioli	STU	SMNS-STU-F-0901733	DB29-9-17-6	Germany	**OP164091**	**OP164091**	
I. pallida	MCVE	21493		Italy	JF908198		Osmundson et al. 2013
I. pallidicremea	TENN, WTU	TENN 062552	PBM2039	USA	KY990553	AY380385	Matheny et al., 2020; Matheny 2005
I. perchtana	STU	SMNS-STU-F-0901245 (holotype)	DB21-9-16-18	Austria	MN512326	MN512326	Bandini et al. 2020a
I. persicinipes	PERTH	PERTH 07676727	PBM2197	Australia	KF977215	EU600837	Matheny & Bougher 2017
I. phaeoleuca	GB	EL297-08		Hungary	KJ399958	KJ399958	Larsson et al. 2014
I. phaeoleuca	GB	SJ06024		Sweden	FN550907	FN550907	Ryberg et al. 2010
I. pholiotinoides	STU	SMNS-STU-F-0901702	DB3-9-14-1	Germany	**OP164095**	**OP164095**	
I. pholiotinoides	DB	DB23-5-13-1b		Germany	**OP164029**		
I. pholiotinoides	DB	DB28-9-12-14		Germany	OK057125	OK057125	Bandini et al. 2022a
I. pholiotinoides	STU	SMNS-STU-F-0901694	DB14-9-14-3	Germany	**OP164064**	**OP164064**	
I. pholiotinoides as *I. muricellata*	GB	EL3704			AM882915.2	AM882915.2	Ryberg et al. 2008
I. picetorum	TUF	TUF 124448		Italy	UDB028399	UDB028399	Saitta, dataset 2016
I. pipilikae	STU	SMNS-STU-F-0901539 (holotype)	DB18-9-20-7	Austria	MW647629	MW647629	Bandini et al. 2021a
I. pipilikae	TUF	TUF 135809	DB18-9-20-10	Austria	**UDB01004650**		
I. pluppiana	STU	SMNS-STU-F-0901254 (holotype)	DB10-10-18-3	Netherlands	MN512327		Bandini et al. 2020a
I. pluppiana	DB	DB5-10-19-5		Netherlands	**OP164030**		
I. pluppiana	STU	SMNS-STU-F-0901729	DB26-9-13-2	Netherlands	**OP164088**	**OP164088**	
I. pluvialis	TENN	TENN 067042	PBM3228	Australia	KF871777	KF853401	Matheny & Bougher 2017
I. polytrichi-norvegici	MCVE	MCVE 21470		Italy	JF908185		Osmundson et al. 2013
I. prisca	STU	SMNS-STU-F-0901558 (holotype)	DB11-8-13-11	Austria	MW647623	MW647623	Bandini et al. 2021a
I. proximella	H	P. Karsten 893 (holotype)	K27	Finland	JN580840		Kokkonen & Vauras 2012

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I. proximella	DB	DB21-9-20-9		Austria	**UDB0799559**		
I. psammobrunnea	LIP	LIP MB89226 (holotype)	M. Bon 89226	France	MW845926		Bandini et al. 2021c
I. psammobrunnea	KR	KR-M-0038015	DB18-9-11-1	Netherlands	MT101889		Bandini et al. 2020b
I. pseudohiulca	M	M-0138785 (holotype of I. piceae)	JS1409	Germany	**OP164106**		
I. pseudohiulca	STU	SMNS-STU-F-0901738	DB23-7-18-2	Austria	**OP164082**	**OP164082**	
I. pseudoteraturgus	TUR-A	JV7676F (holotype)		Finland	JN580878		Kokkonen & Vauras 2012
I. pusio	TUR-A	TUR-A 78010	SJ78010	Sweden	KJ432286		Esteve-Raventós et al. in Crous et al. 2014
I. rangiferi	TUR-A	TUR-A 203299 (holotype)	DB17-8-15-21	Finland	**OP164067**	**OP164067**	
I. rangiferi	STU	SMNS-STU-F-0901725	DB27-8-16-2-Vauras, JV31661F	Finland	**OP164089**	**OP164089**	
I. rangiferi as *I. striata*	UBC	UBC-F-19049			HQ604258		Berbee et al. unpublished, submitted 4 Nov 2010
I. relicina	IB, WTU	IB 19920112; JV10258		Finland	AF325664	AY038324	Peintner et al. 2001
I. relicina	KR	KR-M-0038104	DB3-9-9-Kamke	Sweden	**OP164031**	**OP164031**	
I. roseifolia	CSU	CO5576		USA	MH578026	MK421968	Matheny et al. 2020
I. rufobadia	PERTH	PERTH 08320454	NLB885	Australia	KF977213	KF915290	Matheny & Bougher 2017
I. sepiana	STU	SMNS-STU-F-0901687 (holotype)	DB10-9-19-16	Germany	**OP164056**	**OP164056**	
I. sepiana	STU	SMNS-STU-F-0901688	DB9-9-11-Dondl-21	Germany	**OP164103**	**OP164103**	
I. sepiana	STU	SMNS-STU-F-0901705	DB9-9-17-19	Germany	**OP164104**	**OP164104**	
I. sepiana	STU	SMNS-STU-F-0901718	DB7-9-17-6	Austria	**OP164100**	**OP164100**	
I. serrata	TENN	TENN 069659	PBM3235	Australia	KP636810	KP171012	Matheny & Bougher 2017
I. silvae-herbaceae	TUR-A	TUR-A 175344 (holotype)	Vauras 2268F	Finland	JN580852 (= NR_119991)		Kokkonen & Vauras 2012
I. silvae-herbaceae	DB	DB15-8-20-4		Germany	**OP164032**		
I. sitibunda	STU	SMNS-STU-F-0901504 (holotype)	DB10-10-15-9	Germany	MW845918	MW845918	Bandini et al. 2021c

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I. sitibunda	STU	SMNS-STU-F-0901511	DB20-10-19-3	Germany	MW845921	MW845921	Bandini et al. 2021c
I. soluta	STU	SMNS-STU-F-0901727 (epitype)	DB3-10-12-8	Germany	**OP164093**	**OP164093**	
I. soluta	STU	SMNS-STU-F-0901716	DB3-10-12-1	Germany	**OP164092**	**OP164092**	
I. soluta	STU	SMNS-STU-F-0901719	DB11-8-12-1	Germany	**OP164057**	**OP164057**	
I. stellatospora	DB	DB14-8-20-3		Germany	**OP164033**		
I. stellatospora	GB	EL3004		Sweden	AM882747.2	AM882747.2	Ryberg et al. 2008
I. stellatospora	TENN	TENN 071140	HRL0204	Canada	KX897445		Mattheny et al., unpublished, 23 Sep. 2016
I. stellatospora	WTU	PBM 963		USA		AY038328	Matheny et al. 2002
I. stellatospora	WTU	WTU 4429	Stz4166	USA	MF977664, MF977986		Matheny & Swenie 2018
I. subcarpta	DB	DB26-11-11-4 (isoepitype)		Germany	**OP164039**	**OP164039**	
I. subcarpta	STU	SMNS-STU-F-0901736 (epitype)	DB26-11-11-4	Germany	**OP164086**	**OP164086**	
I. subcarpta	STU	SMNS-STU-F-0901690	DB20-9-20-22	Austria	**OP164077**	**OP164077**	
I. subcarpta	STU	SMNS-STU-F-0901720	DB25-10-14-12	Germany	**OP164084**	**OP164084**	
I. subcarpta	STU	SMNS-STU-F-0901726	DB19-8-16-36	Germany	**OP164071**	**OP164071**	
I. subgiacomi erroneously as *I.* cf. *giacomi*	TUR-A	TUR-A 199032 (holotype)	JV29938F	Sweden	MK153665	MK153665	Cripps et al. 2019b
I. subnudipes	DB	DB23-9-90-Vauras	JV5265F	Finland	**OP164034**		
I. subnudipes	GB	SJ04046		Sweden	FN550925	FN550925	Ryberg et al. 2010
I. subnudipes	KR	KR-M-0042701	DB13-9-14-3	Germany	MH732915		Bandini & Oertel 2021
I. subvirgata	Personal collection P. Reumaux	PR1068 (isotype)		France	MW856436		Bandini et al. 2021c
I. tarda	STU	SMNS-STU-F-0901730 (epitype)	DB3-10-17-6	Germany	**OP164094**	**OP164094**	
I. tarda	DB	DB12-10-19-3		Germany	**OP164035**		
I. tarda	STU	SMNS-STU-F-0901443	DB21-10-12-28	Germany	MW845922	MW845922	Bandini et al. 2021c
I. tarda	STU	SMNS-STU-F-0901731	DB21-10-12-34	Germany	**OP164080**	**OP164080**	
I. tarda	STU	SMNS-STU-F-0901732	DB21-10-12-33	Germany	**OP164079**	**OP164079**	

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I. tarda as *I. pseudo-destricta*	TUF	TUF 118833		Estonia	UDB019506		Liiv, dataset 2013
I. tarda as *I. serotina*	TUF	TUF 118982		Estonia	UDB023543		Liiv, dataset 2014
I. tenuicystidiata	M	M-0281792 (holotype)	M-1039	Germany	MW856454, MW856453		Bandini et al. 2021c
I. teraturgus	DB	DB25-8-15-1		Finland	MH366600.2		Bandini et al. 2019b
I. teraturgus	TUR-A	M.-L. & P. Heinonen 214-95F		Finland	JN580887		Kokkonen & Vauras 2012
I. teraturgus as *I. lanuginosa var. alpina*	GB	EL14006		Sweden	FN550879	FN550879	Ryberg et al. 2010
I. tiburtina	STU	SMNS-STU-F-0901565 (holotype)	DB25-10-19-15	Germany	MW845939	MW845939	Bandini et al. 2021c
I. tiburtina	STU	SMNS-STU-F-0901512	DB25-10-19-11	Germany	MW845936	MW845936	Bandini et al. 2021c
I. tiliae	TR	AMB 18103 (holotype)		Italy	KX592681		Franchi et al. 2016
I. tiliae	KR	KR-M-0038132	DB1-6-13-5	Germany	**OP164036**	**OP164036**	
I. tiliae	STU	SMNS-STU-F-0900994	DB19-6-16-10	Germany	**OP164070**	**OP164070**	
I. timpetuana	STU	SMNS-STU-F-0901560 (holotype)	DB11-8-13-13	Austria	MW647622		Bandini et al. 2021a
I. timpetuana as *I. teraturgus*	GB	SJ79017		Sweden	AM882789	AM882789	Ryberg et al. 2008
I. tjallingiorum	L	L-0053540 (holotype)	Kuyper 1902	Netherlands	MW845929		Bandini et al. 2021c
I. tjallingiorum	KR	KR-M-0038274	DB18-8-11-18	Austria	**OP164037**	**OP164037**	
I. transitoria	O	O-F-304850 (epitype)		Norway	NOBAS4147-17		NORBOL
I. transitoria	MCVE	21514		Italy	JF908209		Osmundson et al. 2013
I. transitoria	O	O-F-249853		Norway	NOBAS1546-15		NORBOL
I. transitoria as *I.* cf. *assimilata*	GB	EL16206		Sweden	FN550881	FN550881	Ryberg et al. 2010
I. turfae	STU	SMNS-STU-F-0901693 (holotype)	DB20-8-16-41	Germany	**OP164075**	**OP164075**	
I. turfae	DB	DB14-8-20-13		Germany	**OP164038**		
I. turfae	STU	SMNS-STU-F-0901735	DB14-8-20-4	Germany	**OP164060**	**OP164060**	
I. turfae as *I. aff. stellatospora*	TENN	TENN 074902	PBM4320	USA	MT196976		Matheny et al., unpublished, submitted 12 Mar-2020

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I. turfae as *Inocybe* sp.	TENN	TENN 071756	PBM4105	USA	MG773840		Matheny et al., unpublished, submitted 7 Dec 2017
I. velata	MCVE	MCVE 23506 (holotype)		Italy	**OP164047**		
I. velata	STU	SMNS-STU-F-0901721	DB25-10-17-4	Germany	**OP164085**	**OP164085**	
Inocybe cf. *maritimoides* as *I. soluta*	ANTU	FCAS3501		China	MN314589		Fan, unpublished, submtted 15 Aug 2019
Inocybe cf. *maritimoides* as *I. soluta*	GB	EL2904		Sweden	AM882755.2	AM882755.2	Ryberg et al. 2008
Inocybe sp.		MHOBL-01		Pakistan	JF927857		Hanif et al. unpublished, submitted 8 May 2011
Inocybe sp.	GB	EL71-16		Sweden	MH310758		Wurzbacher et al. 2019
Inocybe sp. as *I. assimilata*	UBC	UBC-F19807	PK5674	Canada	HQ604561	HQ604561	Berbee et al. unpublished, submitted 4 Nov 2010
Inocybe sp. as *I. oblectabilis*	GB	BJ920908		Sweden	AM882831	AM882831	Ryberg et al. 2008
Inocybe sp. as *I. pruinosa*	MCVE	21474		Italy	JF908187		Osmundson et al. 2013
Nothocybe distincta	CAL	CAL 1310 (holotype)	ZT 9250	India	KX171343	KX171344	Latha et al. 2016b
Pseudosperma spurium	GB	SJ92017 (holotype)		Sweden	AM882784.2	AM882784.2	Ryberg et al. 2008
P. spurium	UTC	BK180809723		USA	JQ408794	EU600868	Kropp et al. 2013; Matheny et al. 2009
EcM				China	JF748082		Zhang et al. 2013
EcM				Italy	FJ210735		Iotti et al. 2010
EcM				Estonia	AJ893282		Tedersoo et al. 2006
EcM				Slovenia	HF674581		Masek 2013
root sample				USA	KU176311		Hewitt et al. 2017
soil sample				Austria	UDB034303		Tedersoo et al. 2020
soil sample				Estonia	UDB0611404		Tedersoo et al. 2020
soil sample				Canada	EU554913		Stefani et al. 2009
soil sample				Austria	FJ237104		Kühnert et al. 2012
soil sample				Estonia	UDB0467567		Tedersoo et al. 2020
soil sample				USA	JF304335		Geml et al. 2012
soil sample				Svalbard	HQ215783		Geml et al. 2012
soil sample				Estonia	UDB0146874		Tedersoo et al. 2020