Inocybe woglindeana, a new species of the genus Inocybe, thriving in exposed habitats with calcareous sandy soil

Ditte Bandini*1, Jukka Vauras 2, Øyvind Weholt 3, Bernd Oertel 4 and Ursula Eberhardt 5

We describe a smooth-spored species of Inocybe, the basidiomes of which have been encountered growing with Salix in exposed habitats, often with calcareous sandy soils in Germany and Fennoscandia. The species is presented with a detailed description, photographs and microdrawings. Its relationship to similar taxa growing in the same environments is illustrated with ITS and LSU data. Morphologically the species would be keyed out as a member of I. sect. Tardae. For comparison, the types of somewhat similar species occurring in similar habitats as I. woglindeana, i.e. I. subpelargonium, I. rufuloides, I. inodora, I. neorufula and I. variispora, were examined morphologically; from the latter ITS and mtSSU V6 data were obtained. Molecular data supported a very close relationship between I. woglindeana and I. variispora. The two species are also morphologically similar, but differ in colour of pileus, in shape and details of hymenial cystidia, and also in their host and habitat. None of the other species, represented by our own collections or sequences from the public domain, are phylogenetically closely related to I. woglindeana.
Introduction

Until recently the genus *Inocybe* has been divided into three subgenera – *Malocybe*, *Inosperma* and *Inocybe* – (Kuyper 1986, Stangl 1989, Bon 1997, 1998), or according to Matheny and Kudzma (2019) into five major clades, *Inocybe*, *Pseudosperma*, *Inosperma*, *Malocybe* and *Nothocybe*. In a recent study, Matheny et al. (2019) raised those clades to the rank of genera, thus, the genus *Inocybe* is reduced to what used to be *I.* subgenus *Inocybe*, characterised by e.g. mostly thick-walled hymenial cystidia. This character is not shared by the newly created genera for the other former subgenera or clades of the former circumscription of *Inocybe*.

Species of the genus *Inocybe* may be smooth- or nodulose-spored or show a mixture of both, for instance in *I.* diabolica Vauras, *I.* ambigua Romagn., or the recently described *I.* pluppiana Bandini, B. Oertel & U. Eberh. (Bandini et al. 2020). An important criterium in keys for the identification of species of *Inocybe* is the question whether the metuloid caulocystidia descend down to the base of the stipe, or whether they are restricted to the apex, or the upper third/fourth of the stipe, and the species are classified respectively in different sections and subsections. According to the classification system used by Marcel Bon in his keys (Bon 1997, 1998), the species described here would have to be assigned to *I.* sect. *Tardae*, defined by Bon as comprising smooth-spored species, the stipes of which are pruinose down to a fourth or third of the stipe.

Whereas in our experience most species of *Inocybe* preferably grow along shady path- or roadsides, in parks, in cemeteries etc., the basidiomes of *Inocybe* may be smooth- or nodulose-spored, or show a mixture of both, for instance in *I.* diabolica Vauras, *I.* ambigua Romagn., or the recently described *I.* pluppiana Bandini, B. Oertel & U. Eberh. (Bandini et al. 2020). An important criterium in keys for the identification of species of *Inocybe* is the question whether the metuloid caulocystidia descend down to the base of the stipe, or whether they are restricted to the apex, or the upper third/fourth of the stipe, and the species are classified respectively in different sections and subsections. According to the classification system used by Marcel Bon in his keys (Bon 1997, 1998), the species described here would have to be assigned to *I.* sect. *Tardae*, defined by Bon as comprising smooth-spored species, the stipes of which are pruinose down to a fourth or third of the stipe.

Materials and methods

Fresh material was obtained on a number of forays in Finland, Germany and Norway between 1991 and 2017. Type material was loaned from various herbaria. For fresh collections, the relevant macroscopic details, i.e. habit, size and shape of the basidiomes, colour and surface of the pileus, number, colour and edge-type of lamellae, size, colour, surface and base of the stipe, smell and colour of flesh, colour of exsiccate, 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 in water and 3% KOH solution, with a Leica DM-750 microscope in water and 3% KOH solution, at 400 and 1000 magnifications (German collections of D. Bandini), and with a Leitz Laborlux D microscope in 10% NH$_4$OH solution, at 500 and 1250 magnification (Finnish collections of J. Vauras). Photographs of microdetails have been taken with a Zeiss Axiocam ERC5s. The measurements of spores and cystidia were determined using Zeiss Axiovision version 4.8. Cystidia were measured without crystals and cystidia without sterigmata. The size of all elements measured is given as length × width. The Q value means the ratio of spore length to spore width (calculated for each spore). The number of spores or cystidia measured is included in the description.

The pictures of fresh collections on Figure 3 were taken by D. Bandini with a Panasonic Lumix GH2 with a 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. The photographs of fresh collections in Figures 4-5 were taken by J. Vauras with a Olympus OM-1 N with O= M Zuiko Macro 1:3.5 50 mm lens, using Fuji Velvia RVP film, and scanning the slides with a Nikon Coolscan V ED.

Colour codes are taken from Munsell (2009, as “Mu”) for the German collections, and from Küppers (1981, as “Kü”) and Cailleux (1981, as “Ca”) for the Finnish collections. Terminology follows Vellinga (1988) and Kuyper (1986). Herbarium acronyms are according to Holmgren et al. (1990), the acronym
DB refers to the private herbarium of Ditte Bandini.

DNA was extracted from dried material following the protocol described by Cripps et al. (2019). PCR amplification of the ITS follows Cripps et al. (2019), for recent collections the same PCR conditions were used to amplify larger fragments of ITS and nrLSU with standard primers (ITS1F, ITS4, LROR, LR5; Vilgalys & Hester 1990, White et al. 1990, LoBuglio et al. 1991, Gardes & Bruns 1993). The same PCR conditions were also applied to amplify the variable region 6 (V6) of the mtSSU of selected collections. Primers were v6u and v6r (Gonzalez & Labarère 1998). Bidirectional Sanger sequencing was carried out at LGC (Berlin, Germany). Sequences were assembled and edited using Sequencher vs. 4.8 (Genecodes). Newly generated sequences were submitted to GenBank with acc. no. MN319696 and MT101872–MT101896. Raw data for sequences MT101888–MT101896 were generated by Alvalab.

Collections and sequences included in the analyses were selected to represent *I. woglindeana*, its closest relatives in terms of sequence similarity, recovered through BLAST searches against GenBank and UNITE (Altschul et al. 1990; downloaded Dec. 2019), and species discussed as morphologically similar. To allow for easier comparison with other published work, we added some sequences from public collections assigned to species discussed here, although we have not seen the material. Following Matheny et al. (2019) sequences of *I. reliquina* (Fr.) Quéhl. (the type species of the genus *Inocybe*), *Nothocybe distincta* (K.P.D. Latha & Manim.) Matheny & K.P.D. Latha and as outgroup *Pseudosperma spurium* (Jacobsson & E. Larss.) Matheny & Esteve-Rav. were added. Metadata of sequences used in the analysis are summarized in Table 1.

Alignments were viewed and reformatted using AliView 1.26 (Larsson 2014). Sequences were aligned using the online version of Mafft with the E-INS-i option (Katoh et al. 2005, 2019). The final alignment encompasses 46 collections and 1797 positions (ITS & nrLSU) plus 201 positions mtSSU. For all collections, the complete ITS fragment was available, apart from *I. variispora* for which only 5.8S & ITS2 could be amplified and a downloaded sequence, originally identified as *I. queletii* (EU307813) includes only LSU. Twenty-two sequences in the alignment included nrLSU (see Table 1) and five mtSSU data (*I. variispora* and four collections of *I. woglindeana*).

Distance values were calculated as p-distances in PAUP* vs. 4.0a build 167 (Swofford 2002) considering only the ITS between the primers ITS1F and ITS4 or 58SF and ITS4. Maximum Likelihood analyses were done in RAxML vs. 8.2 (Stamatakis 2014) locally or on CIPRES (Miller et al. 2010) with the GTR+GAMMA option, 10 searches for the best ML tree with 1000 replicates. The tree was drawn in FigTree 1.4.2 (Rambaut 2006-2018).

Results

Figure 1 shows the result of the ML analysis. Apart from collections studied morphologically and assigned to *Inocybe woglindeana*, some of these originally identified as *I. queletii*, the *I. woglindeana* clade includes the type of *I. variispora* and sequences from basidiome, soil or ectomycorrhiza samples from Sweden, Estonia and Alaska. Its sister branches, presumably representing two putative species, consist of sequences for which no names could be found. These include, apart from environmental samples, a collection of ours (DB25-5-13-5) and a collection from Thailand (DED8054a).

Species that could be confused with *I. woglindeana*, including *I. queletii*, are all very distinct from *I. woglindeana*. What we consider a representative of *I. queletii*, occurs as sister to *I. exilis*. Sequences of specimens that were selected to represent species for which no type sequence exists, occur in the same clades as their conspecifics (if they have any). Thus, the species delimitation is in most taxa clear in the tree, but there are exceptions (*I. pruinosa* and *I. inodora*, *I. involuta* and *I. nitidiuscula*). The placement of downloaded sequences is in all cases within the same clade as conspecifics selected by us, whether or not all of the alleged conspecifics are indeed conspecific is a different question and not part of this study.

The *I. woglindeana* clade is not supported by bootstrap, although distance values show that the similarity within the clade (98.2–100%) is much larger than to the clade of *Inocybe* sp. DB25-5-13-5 (92.9–94.5) and to *Inocybe* sp. DED8054a from Thai-
Table 1. Sequences included in the analyses. Accessions include the ITS and LSU, unless indicated otherwise. * = ITS only, ** = ITS2 only, *** = LSU only; DB = private herbarium Ditte Bandini, SMG-GME = Collection Sociedad Micologica Gallarta-Gallarta Mikologia Elkarte.

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*Notes:*** Unpublished; **Here; ***Published; **V6**
Fig. 1. ML topology calculated under the GTRGAMMA model. Branch support from 1000 replicates of bootstrap. Collection numbers in bold refer to material studied by us. T – type. AL – Alaska, AUS – Austria, AUT – Australia, CZE – Czech Republic, DEN – Denmark, ESP – Spain, EST – Estonia, FIN – Finland, FRA – France, GER – Germany, IND – India, ITA – Italy, NED – Netherlands, NOR – Norway, SWE – Sweden, UT – Utah.
land (87.8–93.4%). The sequence similarity between the ITS sequences of studied collections of *I. woglindeana* is 100%, including also sequence data from Estonia, from collection EL404 (Sweden) and environmental sequences 99.7–100%.

The split between *I. variispora* and the other members of the *I. woglindeana* clade is only weakly supported (Fig. 1). For the comparisons with *I. variispora* only the ITS2 fragment is available (430 positions). All studied collections of *I. woglindeana*, collection EL404 and all European soil or root derived sequences are identical in terms of p-values. These sequences are 98.3–98.5% similar to *I. variispora*, with missing data being responsible for the lower values. The Alaskan soil clone (without missing data) is 98.2% similar to *I. variispora*, and 99.7% to the former group. The *I. variispora* ITS2 has an insertion of 5 bp compared to the other sequences from the *I. woglindeana* cluster. The Alaskan sample has an insertion of 2 bp and another one of 4 bp compared to all of the other sequences in the *I. woglindeana* clade, including *I. variispora*. For the sequences for which we have the raw data (i.e. data submitted in the context of this study), we know that these insertions are unambiguously absent from *I. woglindeana*; also, the raw data of *I. variispora* is unambiguous with a view to these indels. There are 7 substitutions in the V6 variable region of the *I. variispora* type compared to the four sequences of *I. woglindeana*.

In conclusion, based on the molecular analyses, we consider *I. woglindeana* as a species distinct from *I. variispora*. We consider it very likely that the sequences from northern European samples that cluster with the studied collections of *I. woglindeana* are also members of this species. The same is true, albeit with some reservation, for the Alaskan sequence.

**Taxonomy**

*Inocybe woglindeana* Bandini, Vauras & Weholt sp. nov. – Figs. 2–5

MycoBank number: MB834803; ITS GenBank MT101882

**ETYMOLOGY:** “woglindeana”, after Woglinde the Rhinemaiden in the "Ring der Nibelungen" of Richard Wagner, because the holotype of the species was collected on the border of a lake next to the river Rhine.

**DIAGNOSIS:** Most basidiomes fairly small with ochraceous to ochraceous brownish felty-lanose pileus, when young usually with ample whitish velipellis and cortina, a stipe that is sparsely pruinose only at the extreme apex, spores that on average are longer than 10 µm, hymenial cystidia that are mostly ventricose with rather thin walls and often with a truncate or roundish base. It grows on exposed locations, mostly with *Salix* and also *Populus* nearby. The most similar species morphologically as well as molecularly is *I. variispora*. From this and other species it differs by the above-named combined characteristics and by ITS sequence data.


**DESCRIPTION – PILEUS** 15–30 (45) mm wide, at first almost globulose, soon mostly (sub)conical, more rarely (sub)campanulate, later broadly convex or expanded, often without umbo, seldom with more or less pronounced large umbo, margin at first involute, then deflexed, later straight to uplifted, and then pileus slightly depressed around the centre; when young entirely or radially covered with a whitish velipellis, later still visible mostly on or around the centre; colour because of the velipellis dingy beige or pale straw-coloured, straw-coloured, later ochraceous to ochraceous brownish in different nuances (Mu 10YR 7/4–7/8, 6/6–6/8, 5/4–5/6, also 8/4–8/6, 7.5YR 6/6–6/8, Kü S 10Y40M30, S 10Y30M20, Ca 77M, 77N), at the umbo often somewhat paler due to the velipellis, sometimes with a faint orange hue; surface at first finely felty, then thickly felty or felty-lanose with appressed fibres, when old or due to weather-circumstances, also with lacerate fibrous bundles especially towards the margin; at the centre occasionally areolate-diffracted or subscaly; young...
basidiomata with ample whitish cortina. LAMEL-LAE mostly (sub)distant (ca. 30–45 (50), l = 1–3), to 8 mm broad, adnate or emarginate adnate, or subdecurrent, ventricose, at first and for long time conspicuously whitish, beige or ivory-coloured, near the margin also yellowish, then greyish light brown (Mu 10YR 5/4–5/6, Ca 70M) to grey-brown (Mu 10YR 4/4–4/6, Kü S 30Y50M30, Ca 70N), sometimes with pale pinkish hue, when old also with rusty-brownish blotches; edge fimbriate, whitish. STIPE 20–50 × 1.5–8 mm, cylindrical or slightly widening towards the base, when young entirely covered with whitish tomentum, later longitudinally white-fibrillose, striate or glabrous, at first whitish, then with faint yellowish or ochraceous tinge or slightly flesh-coloured beneath the tomentum, sometimes faintly yellowish, especially towards the base, when older yellow-brown (Kü S 10Y40M30, Ca 65N); only sparsely pruinose at the extreme apex of the stipe. CONTEXT whitish in the pileus near the centre, watery above the lamellae, in the stipe whitish, pale yellowish, pale brown or partially brownish, in the base of the stipe whitish or yellowish, sometimes stipe with faint pinkish tinge. SMELL weak, acidulous to agreeably fragrant when in good condition, not at all spermatic. COLOUR OF EXSICCATA: pileus pale brown to nutbrown, sometimes with faint reddish hue (Mu 7.5YR 5/4–5/8, 5YR 4/4–4/6, Ca 77M, 75N, 75P), lamellae and stipe concolorous or a little lighter in colour, rarely darkening on drying.

SPORES: German collections 8.0–13.0 µm (av. 10.2 µm, SD 0.7 µm) × 4.9–7.1 µm (av. 5.9 µm, SD 0.4 µm); Q = 1.4–2.2 (av. 1.7, SD 0.1) (n = 240 of 6 coll.); Finnish collections 9.0–14.3 µm (av. 11.3 µm) × 5.3–7.4 µm (av. 6.3 µm); Q = 1.5–2.2 (av. 1.8) (n = 160 of 4 coll.), smooth, mostly oblong (sub)amyladoid or (sub-)ellipsoid or subcylindrical, sometimes with faint suprahilar depression, apex subacute, subobtuse or obtuse, occasionally with indistinct pseudopore. BASIDIA 25–30 (32) × 7–10 µm, generally 4-spored. LAMELLA EDGE sterile, composed of cheilocystidia and numerous colourless, (sub)clavate, cylindrical or subglobose, thin-walled paracystidia, sometimes also in intermediate states. PLEUROCYSTIDIA: German collections 35–77 µm (av. 57 µm, SD 11 µm) × 12–31 µm (av. 19 µm, SD 4 µm); Q = 1.3–4.9 (av. 3.3, SD 0.6) (n = 90 of 6 coll.); Finnish collections 51–82 µm (av. 67 µm) × 15–30 µm (av. 20 µm); Q = 2.1–4.9 (av. 3.3) (n = 90 of 6 coll.), rather ventricose subfusiform, (sub)utiform, often characteristically elongate (sub)ellipsoid, somewhat sac-shaped or subcylindrical, usually without or with only a short neck and wide or rounded apex, mostly without pedicel and often with rounded or truncate base, apex mostly crystalliferous, walls usually only up to 1.0 µm (neck) thick at the apex, pale yellow in 3% KOH. CHEILOCYSTIDIA similar in size, but more variable in shape. PILEIPELLIS constituted by an epicutis
Fig. 3.

*Inocybe woglindeana*

made up of parallel hyphae 6–12 µm wide, with finely encrusting and parietal ochraceous pigment; subcutis with wider and paler but often also pigmented to hyaline elements, up to 25 µm; epicutis in young basidiomata often covered with thin (sub)hyphae, with scattered free ends (belonging to velipellis remnants). **STIPITIPPELLIS** consisting of a cutis bearing numerous bundles of rather thin-walled caulocystidia at the extreme apex of the stipe, intermixed with thin-walled colourless cauloparacystidia. **CAULOCYSTIDIA** 35–75 × 10–20 (25) µm, quite variable in shape, (sub)fusiform, (sub)utriiform, (sub)cylindrical, (sub)clavate or deformed, apex usually not crystalliferous and rather thin-walled, walls usually only up to 1.0 µm thick at the apex, pale yellow in 3% KOH. **CLAMP-CONNECTIONS** abundant in all tissues; **REFRACTIVE HYphae** occasionally present in trama of stipe, lamellae and pileus.

**ECOLOGY AND ASSOCIATED FUNGIFlora** – All German collections of *Inocybe woglindeana* were found on exposed dry gravellous and/or sandy poor soil – some collections near the shore of a river or a lake, two on a renaturated railway-terrain and some others next to a calcareous inland-dune-terrain, in a renaturated sand-and gravel-quarry. All locations are sunny and open, thus especially in summer they are quite hot and for long periods near the surface very dry, but nevertheless all with *Salix*, mostly *Salix caprea* nearby. Also *Betula* and/or *Populus* were noted next to several collections. *Pinus sylvestris* was noted with several collections as well.

In Finland, *I. woglindeana* is known from four localities from Southern to Central Finland. These all are human influenced areas with limestone processing plants, limestone quarry or brick-works.
Further, all are fairly open, in every place with Salix, mostly Salix caprea, and often with other deciduous trees, mostly Populus tremula and Betula pendula. The soil of these localities is sandy and calcareous. The terrain is generally open or somewhat open to direct sun and is quickly warmed and dried – in spite of the presence of Salix. The species I. exilis (Kuyper) Jacobsson & E. Larss. grows nearby in Germany as well as in Finland, where other accompanying species were e.g. I. vulpinella Bruylants and Malloccybe latispora (Bon) Matheny & Esteve-Rav.

Also in Norway, I. woglindeana was found associated with deciduous trees including Salix sp. The locality is influenced by past industrial activities (paper industry), and the area also is habitat for a rich flora of Morchella-species. Inocybe woglindeana was found in an area of about 1000 m². It seems to reappear there annually like Malloccybe dulcamara, which is common in this area.

**Phenology:** Inocybe woglindeana is apparently not restricted to a certain season, as it has been found in spring (May), summer (June – August) as well as in autumn (September – October). However, it is one of the earliest species of Inocybe.

Collections studied (Sequenced specimens indicated with asterisk) – FINLAND. Varsinais-Suomi.


ADDITIONAL TYPES STUDIED: HOLOTYPE: INOCYBE INODORA Velen. 1920, Czech Republic, Bilichov, frondose trees, leg. Vinklár, Jun. 1920 (PR, bottle no 156). SPORES 9.0–12.8 µm (av. 11.0 µm, SD 0.9 µm) × 5.2–7.4 µm (av. 6.2 µm, SD 0.5 µm); Q = 1.4–2.1 (av. 1.8, SD 0.1) (n = 40), smooth, with subacute to (sub)obtuse apex, some with indistinct pseudopore. BASIDIA 4-spored. PLEUROCYSTIDIA 44–68 µm (av. 59 µm, SD 6 µm) × 12–25 µm (av. 18 µm, SD 3 µm); Q = 2.6–5.2 (av. 3.4, SD 0.6) (n = 15), mostly (sub)fusiform or subutriform, with short neck and short pedicel, apex usually crystaliferous, walls up to 3.0 (3.5) µm thick, yellowish-greenish with 3% KOH. CHEILOCYSTIDIA similar in appearance and size. PARACYSTIDIA not observed. CAULOCYSTIDIA in the upper part of the stipe, similar in form and size to hymenial cystidia, walls up to 1 µm thick.

HOLOTYPE: Inocybe involuta Kuyper, Netherlands, Terschelling, 6 Oct. 1988, under Pinus nigra in dune sand, leg. E. Arnolds (L-0017086). SPORES 9.0–13.0 µm (av. 10.5 µm, SD 1.0 µm) × 5.3–7.2 µm (av. 6.2 µm, SD 0.4 µm); Q = 1.5–2.0 (av. 1.7, SD 0.1) (n = 40), smooth, (sub)amgydaloid, with (sub)acute apex, with indistinct pseudopore. BASIDIA 4-spored. PLEUROCYSTIDIA 50–77 µm (av. 64 µm, SD 7 µm) × 19–30 µm (av. 24 µm, SD 4 µm); Q = 2.0–4.2 (av. 2.8, SD 0.6) (n = 15), mostly (sub)fusiform or subutriform, apex usually crystaliferous, walls up to 3.0 (3.5) µm thick, pale yellowish with 3% KOH. CHEILOCYSTIDIA similar in appearance and size. PARACYSTIDIA not observed. CAULOCYSTIDIA only in the upper third of the stipe, similar to hymenial cystidia, but somewhat thinner-walled.

ISOTYPE: Inocybe neorufa Esteve-Rav., Macau & Ferville 2012, Spain, Catalonia, Girona, Torroella de Montgrí, Fraxinus angustifolia, Pinus pinea, leg. J. Carbó & N. Macau, 6 Dec. 2010 (SMNS-STU-F-0901287). SPORES 9.3–14.3 µm (av. 10.9 µm, SD 1.0 µm) × 4.9–6.7 µm (av. 5.9 µm, SD 0.4 µm); Q = 1.6–2.3 (av. 1.9, SD 0.2) (n = 40), smooth, (sub)amgydaloid, with suprahilar depression and (sub)acute to papillate apex. BASIDIA 4-spored. PLEUROCYSTIDIA 55–74 µm (av. 61 µm, SD 6 µm) × 12–21 µm (av. 15 µm, SD 2 µm); Q = 3.2–5.5 (av. 4.2, SD 0.6) (n = 15), (sub)fusiform, (sub)utriform, also (sub)cylindrical, apex usually crystaliferous, with short pedicel, walls up to 1.5 (2.0) µm thick, pale yellowish with 3% KOH. CHEILOCYSTIDIA similar in appearance and size. PARACYSTIDIA not observed. CAULOCYSTIDIA in the upper part of the stipe, similar in form and size to hymenial cystidia, walls up to 1 µm thick.

HOLOTYPE: Inocybe rufaloides Bon 1984, France, Somme, Cayeux-sur-Mer, Brighton-La Mollière, Pinus, leg. M. Bon, J. Vast & Claus, 18 May 1983 (LIP-MB83038). SPORES 8.6–11.3 µm (av. 9.9 µm, SD 0.7 µm) × 5.2–7.0 µm (av. 6.0 µm, SD 0.3 µm); Q = 1.4–2.0 (av. 1.7, SD 0.1) (n = 40), smooth, with subacute to (sub)obtuse apex, with indistinct pseudopore. BASIDIA 4-spored. PLEUROCYSTIDIA 37–65 µm (av. 54 µm, SD 7 µm) × 9–17 µm (av. 15 µm, SD 2 µm); Q = 3.0–4.2 (av. 3.7, SD 0.3) (n = 15), mostly (sub)fusiform or subutriform, sometimes with rather long and slightly undulate neck, with short pedicel, apex usually crystaliferous, walls up to 2.0 (3.0) µm thick, yellowish-greenish with 3% KOH. CHEILOCYSTIDIA similar in appearance and size. PARACYSTIDIA not observed. CAULOCYSTIDIA not studied (to preserve the material).

HOLOTYPE: Inocybe subpelargonium Beller 1982, France, Madirac, Créon, Gironde, frondose trees, 14 Oct. 1979 (LIP-7910142). SPORES 7.9–10.4 µm (av. 9.1 µm, SD 0.6 µm) × 4.5–6.0 µm (av. 5.1 µm, SD 0.3 µm); Q = 1.6–1.9 (av. 1.8, SD 0.1) (n = 40), smooth, (sub)amgydaloid, (sub)ellipsoid, apex (sub)obtuse, (sub)acute, sometimes subpapillate. BASIDIA 4-spored. PLEUROCYSTIDIA 45–63 µm (av. 53 µm, SD 6 µm) × 11–16 µm (av. 14 µm, SD 2 µm); Q = 2.8–5.3 (av. 3.9, SD 0.7) (n = 15), (sub)fusiform, subutriform (sub)cylindrical, with rather short neck and short pedicel, apex usually crystaliferous, walls up to 2.0 (2.5) µm thick, yellowish-greenish with 3% KOH. CHEILOCYSTIDIA similar in appearance and size. PARACYSTIDIA not observed. CAULOCYSTIDIA not studied (to preserve the material).

ISOTYPE: Inocybe variispora Fern. Sas., 2002, Spain, Muskiz, province Biscay, 30T WN 8995, garden with Pseudotsuga menziesii (No 980504-01, Sociedad Micológica Gallarta-Gallarta Mikologia
Elkartea). **SPORES** 9.1–12.6 µm (av. 10.4 µm, SD 0.7 µm) × 5.4–6.2 µm (av. 5.7 µm, SD 0.2 µm); Q = 1.6–2.0 (av. 1.8, SD 0.1) (n = 40), smooth, (sub)amygdaloid, apex (sub)acute, with faint pseudopore. **BASIDIA** 4-spored, seldom also 2-spored. **PLEUROCYSTIDIA** 45–70 µm (av. 54 µm, SD 8 µm) × 11–22 µm (av. 15 µm, SD 2 µm); Q = 2.7–5.5 (av. 3.7, SD 0.5) (n = 15), mostly subfusiform to subutriform, without or with short neck, usually with short pedicel, apex usually very finely crystalliferous, walls up to 2.0 (2.5) µm thick, pale yellowish with 3% KOH. **CHEILOCYSTIDIA** similar in appearance and size. **PARACYSTIDIA** not observed. **CAULOCYSTIDIA** not present.

**Discussion**

The molecular support for *Inocybe woglindeana* as a species distinct from *I. variispora* is not strong and rests heavily on distance data from a single collection, albeit the type. The evidence includes a locus (V6) that has not been tested for the genus and for which we have data for no other species. We have analysed the available data in a multitude of ways and combinations: different sets of species and sequences; only ITS; with gap recoding [FastGap, vs. 1.2, Borchsenius 2009, Simmons & Ochoterena 2000], Baysian Inference with MrBAYES 3.2.7a [Ronquist et al. 2012] on CIPRES [Miller et al. 2010]; ML with better fitting models, ultrafast bootstrap and SH-arl-tests in IQ-TREE [Guindon et al. 2010, Nguyen et al. 2015, Kalyaanamoorthy et al. 2017, Hoang et al. 2018]; analyses other than ML-based methods are less well suited to deal with missing data. However, the result was essentially the same – generally concordant results and very little, if at all, support for the monophyly of *I. woglindeana* against *I. variispora*. Responsible for the lack of support for the split between *I. variispora* and *I. woglindeana*, are presumably missing data and the fact that
only a single collection of this species is available. The bootstrap support for the *I. woglindeana* clade, below 75% in Fig. 1, increases to 98% when the sequence of the Thai collection DED8054a is removed from the analysis (details not shown). Although in terms of similarity one of the closest relatives of the *I. woglindeana* clade, homology assessment aka sequence alignment is not self-evident between DED8054a and the members of the *I. woglindeana* clade. Thus, the lack of support here could be an alignment issue. The collection DED8054a was a singleton in the study by Horak et al. (2015) and not further investigated.

Considering the molecular results in combination with morphological and ecological differences, we are confident that *I. variispora* and *I. woglindeana* are separate species. We expect that when sequence data for additional loci and collections or full genomes will become available, the support for this conclusion will increase.

*Inocybe woglindeana* has been found in exposed places: sandy and/or gravelly terrain with *Salix* and often *Populus* in Germany, Finland and Norway. Ectomycorrhiza or soil sample sequences suggest that the species occurs in Estonia (all samples are from places where *Salix fragilis* or *Salix caprea* were the only available ectomycorrhizal hosts, from an urban site as well as agricultural wasteland and a juniper woodland on limestone ;Tedersoo, unpubl.) and possibly also in the Tundra of Prudhoe Bay, Alaska, which is also known for calcareous habitats, presumably with *Salix arctica* or *Dryas integrifolia* (Tidling et al. 2014). Whether this last sample is indeed a member of *I. woglindeana* cannot be determined based on the available information. There could well be a species complex around *I. variispora* as e.g. observed in *Hebeloma* (Cripps et al. 2019) or *Lactarius* (Barge et al. 2016), where temperate and arctic-alpine species are hard to separate molecularly and morphologically, and when representatives of different continents are considered, it becomes even harder to delimit species. However, even if this was the case, it would be an advantage to have a name, *I. woglindeana*, available for the set of collections.

![Fig. 6. Inocybe variispora, holotype, photograph R. Fernández Sasia.](image)
distinguished by certain morphological features, habitat and molecular markers.

*Inocybe woglindeana* is characterised by often rather stout but usually rather small basidiomata, ochraceous to ochraceous brownish lanose pilei with ample whitish velipellis and cortina and conspicuously whitish lamellae when young, oblong smooth spores that can be ellipsoid or subcylindrical and have a length of more than 10 µm on average. The hymenial cystidia are rather ventricose, mostly without neck and with a wide apex, quite thin-walled and often with truncate or roundish base. So far, in every collection elongate (sub)ellipsoid cystidia have been found (see microplate in Fig. 3, second cystidium from the left). It is worth noting, that spores and hymenial cystidia of the German collections are on average smaller than those of the Finnish collections, a phenomenon we already came across in another species, *I. leochroma* Bandini, Vauras & B. Oertel (see Bandini et al. 2019), irrespective of examiner and microscope.

We are not aware of any other species that possesses all of the named characteristics, and there are only very few species that can possibly be confused with *Inocybe woglindeana*, owing to the colour of pileus, the habitat and the size of the spores etc. One of them, *I. subpelargonium* Beller, is according to Bon (1997) also fond of sandy terrain, as stated in Beller’s original description (1982). It is subhygrophile, grows with frondose trees, and its smell reminds of *Pelargonium* leaves, being thus somehow sweetish-aromatic. However, the pileus of this species is according to the original description not lanose but fibrillose to subrimose, and the colour is ochraceous brownish, but darker near centre, resembling thus *I. phaeodisca* (Bon 1997) rather than *I. woglindeana*. No such colour contrast was observed in any of the collections of *I. woglindeana* – in this species, the umbo is not darker but paler in colour in older specimens. Furthermore, the examination of the holotype of *I. subpelargonium* confirmed that the microdetails are entirely different from those of *I. woglindeana*: The spores are much smaller, and the hymenial cystidia are shorter and narrower (Beller 1982, for details of the holotype see above and Fig. 7e). We do not have sequence data for this species available.

A species with rather long spores and sometimes growing on sandy ground is *Inocybe involuta* Kuyper. It was originally found on the Dutch island of Terschelling by Eef Arnolds. However, as originally described and observed in many own collections (Kuyper 1989, Bandini et al. 2020), the colour of the pileus usually is reddish brown, and the stipe is often reddish. The hymenial cystidia are very different in shape compared to those of *I. woglindeana*, subfusciform and thick-walled (for details of holotype see above and Fig. 7b).

*Inocybe inodora* Velen., another species growing in sandy or gravelly, calcareous habitats, may look similar to *I. woglindeana*, and is also furnished with a pale velipellis, but the stipe is entirely pruinose, the spores are on average somewhat larger, the hymenial cystidia smaller and never almost “sac-shaped” or (sub)ellipsoid with apex and base looking almost or entirely alike (e.g. Kuyper 1986, Stangl 1989; for details of lectotype see above and Fig. 7a).

*Inocybe pruinosa* R. Heim, another species that superficially may resemble *I. woglindeana*, is also found on sandy ground. However, the former often has a more yellowish pileus colour, the stipe is entirely pruinose, the spores are larger and the hymenial cystidia are clearly more thick-walled (Heim 1931, and e.g. Kuyper 1986, Stangl 1989).

*Inocybe queletii* Konrad, for which *I. woglindeana* was mistaken (see Table 1 and Kuyper 1986), is again similar in aspect, the pileus colour is yellowish, the surface rather smooth and the stipe is only pruinose at the apex (Konrad 1927, 1929, and e.g. Kuyper 1986, Stangl 1989). However, the basidiomes are larger, the spores are on average somewhat smaller, the hymenial cystidia are on average slimmer, with thicker walls and not with a roundish or truncate base. And the habitat is quite different: mountainous regions with *Abies*.

*Inocybe neorufula* Esteve-Rav., Macau & Ferrville is, like *I. woglindeana*, fond of sandy calcareous ground. It has a whitish velipellis and rather large spores, too, but the pileus is more foxy brown with a reddish tinge, and the hymenial cystidia do not have a roundish or truncate base (for details of isotype see above and Fig. 7c). Only *Pinus*, not *Salix*, is mentioned as potential mycorrhizal associate in the original description (Esteve-Raventós et al. 2012).

*Inocybe exilis* (Kuyper) Jacobsson & E. Larss. was found in the neighbourhood of *I. woglindeana* both in Germany and in Finland. The pileus of this
The species is reddish brown in colour, the spores are on average larger, and the hymenial cystidia are usually more thick-walled and have no truncate or roundish base (Kuyper 1986). The same holds true for *I. rufuloides* Bon (Bon 1984, Kuyper 1986). For details of the holotype see above and Fig. 7d.

We also found *I. nitidiuscula* (Britzelm.) Lapl. in exposed sandy-gravelly locations with *Salix* nearby. Its pileus is normally somewhat reddish or at least with reddish tinges, but exceptionally it is also almost ochraceous. The species has rather long spores like *I. woglindeana*, but the hymenial cystidia are very different in shape, with rather narrow long necks, thicker walls and narrow apex.

The species that is most closely related genetically and in microscopical details to *I. woglindeana* is *I. variispora*. However, the hymenial cystidia of the latter are normally somewhat narrower, they are mostly pedicellate and the walls are generally somewhat thicker. And the elongate (sub)ellipsoidal shaped cystidia – typical for *I. woglindeana* – are missing. The macroscopical aspect, too, is quite different, since the pilei of *I. variispora* are dark brown – and not yellow-ochraceous (see Fig. 6). As Fernández Sasia (2002) highlights in his description, the general aspect of *I. variispora* reminds strongly of a small *I. lacera* (“l’aspect général rappelle fortement un *I. lacera* de petite taille”), which cannot at all be said about the basidiomes of *I. woglindeana*. Also, the typical whitish velpellis, visible in young basidiomes of *I. woglindeana*, is missing in *I. variispora*, and the odour is described as spermatic (“spermatoire évident”), while the odour of *I. woglindeana* is agreeable aromatic and never spermatic. The type of *I. variispora* was found next to *Pseudotsuga menziesii* in a garden (Fernández Sasia 2002), thus with a different host than *I. woglindeana*.

The number and size of the collections listed for *I. woglindeana* show that in the appropriate habitat, the species can often be found in large numbers. Such habitats are quite rare, at least in Central and Northern Europe, which probably is the reason why such a characteristic species has been overlooked in both Germany and adjacent areas as well as in the Nordic countries, or was misinterpreted as *I. queletii* or perhaps also as *I. inodora*.

**Acknowledgements**

We are grateful to the curators Javier Rejos (AH), Nicolien Sol (L) and Régis Courteceisse (LIP) for the loan of specimens in their keeping, to Holger Thüs (STU) for handling the loans on our side, to Roberto Fernández Sasia (Muskiz, Biskay, Spain) for sending a part of an isotype of *I. variispora* and for the kind permission to print his photograph of the holotype of *I. variispora* and to Fernando Esteve-Raventós (Alcalá, Spain) for his help regarding *I. neorufula*. Leho Tedersoo (University of Tartu) is thanked for sharing with us unpublished collection information of Estonian soil samples. We also thank FinBOL for support and are grateful that Bálint Dima (Eötvös Loránd University Budapest) allowed us to use two sequences of the FinBOL project. The contribution of U. Eberhardt was financed through the German Barcode of Life (GBOL) project, supported by the German Federal Ministry of Education and Research (BMBF FKZ 01LI1501l) as research for sustainable development (FONA; http://www.fona.de).

We finally thank Morten Pettersen (Fredrikstad, Norway) for his contribution to the study with valuable material and Ellen Larsson (Gothenburg, Sweden) for drawing our attention to *I. variispora*.

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