

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

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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 – *Mallocybe*, *Inosperma* and *Inocybe* – (Kuyper 1986, Stangl 1989, Bon 1997, 1998), or according to Matheny and Kudzma (2019) into five major clades, *Inocybe*, *Pseudosperma*, *Inosperma*, *Mallocybe* 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 *I. woglindeana* have been found in more extreme habitats that are sun-exposed locations with calcareous soil, as for instance at old limestone quarries and limestone processing plants (see below). Based on the currently known material, it is always associated with *Salix*, often with *Salix caprea*, and also often with *Populus*. As such locations are comparatively rare in temperate and boreal Europe, *I. woglindeana* probably has been overlooked, despite its striking combination of characters or it has been mistaken for other species growing in the same habitat or for *I. queletii* Konrad.

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 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 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% NH₄OH 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 basidia 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 Silkipix 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, LR0R, 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. relicina* (Fr.) Quél. (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 (Kato 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 ITS1 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 GTRGAMMA 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.

SPECIES	VOUCHER NO.	OTHER NUMBERS	HERBARIUM	COUNTRY	GENBANK/ UNITE	PUBLISHED
<i>Inocybe exilis</i> (Kuyper) Jacobsson & E. Larss.	DB25-5-13-11	BAN386	DB	Germany	MT101888*	here
<i>I. exilis</i>	SMNS-STU-F-0901441	DB28-9-15-16, BAN2857	STU	Austria	MT101873	here
<i>I. exilis</i>	JVe06575			Denmark	FN550919	Ryberg et al. 2010
<i>I. griseotarda</i> Poirier (holotype)	J. Poirier 19901119-01		GK	France	MF361839*	Bizio et al. 2017
<i>I. griseotarda</i>	KR-M-0038015	DB18-9-11-1, BAN148	KR	Netherlands	MT101889*	here
<i>I. inodora</i> Velen.	SMNS-STU-F-0901439	DB26-9-15-14, BAN2855	STU	Austria	MT101875	here
<i>I. inodora</i>	EL2405		GB	Norway	AM882834.2	Ryberg et al. 2008
<i>I. inodora</i>	SMNS-STU-F-0901438	DB24-9-15-11, BAN2854	STU	Austria	MT101874	here
<i>I. involuta</i>	SMNS-STU-F-0901270	DB13-10-16-19, BAN2849	STU	Austria	MN512329	Bandini et al. 2020
<i>I. involuta</i> Kuyper (holotype)	L 0017086		L	Netherlands	MN319696*	here
<i>I. neorufula</i> Esteve-Rav., Macau & Ferville (isotype)	SMNS-STU-F-0901287	AH40223, BAN2357	STU	Spain	MT101890*	here
<i>I. neorufula</i>	SMNS-STU-F-0901445	DB30-10-15-2-Dondl, BAN2861	STU	Italy	MT101876	here
<i>I. nitidiuscula</i> (Britzelm.) Lapl. (epitype)	M-0229745		M	Germany	KM873364*	Marchetti et al. 2014
<i>I. nitidiuscula</i>	DB16-8-11-15	BAN140	DB	Germany	MT101891*	here
<i>I. pruinosa</i> R. Heim	SMNS-STU-F-0900987	DB13-10-12-11, BAN2336	STU	Germany	MT101877	here
<i>I. pruinosa</i>	EL24106		GB	France	FN550904	Ryberg et al. 2010
<i>I. pseudodistricta</i> Stangl & J. Veselský (holotype)	PRM716231		PRM	Czech Republic	MG012468	Bandini et al. 2019
<i>I. pseudodistricta</i>	KR-M-0043223	DB6-5-12-10, BAN102	KR	Netherlands	MT101892*	here
<i>I. queletii</i> Konrad	KR-M-0038286	DB22-5-12-1, BAN160	KR	Germany	MT101893*	here
<i>I. relicina</i>	JV10258, IB19920112		WTU, IB	Finland	AF325664, AY038324	Peintner et al. 2001, Matheny et al. 2002
<i>I. rufuloides</i> Bon	SMNS-STU-F-0901442	DB13-10-12-4, BAN2858	STU	Germany	MT101878*	here
<i>I. rufuloides</i>	JVe061110			Italy	FN550921	Ryberg et al. 2010
<i>I. rufuloides</i>	PERTH 7700598	E8353	PERTH	Australia	JN035292, JN035295	Boughner & Matheny 2011
<i>I. subporospora</i> Kuyper	RP950618			Sweden	AM882931.2	Ryberg et al. 2008
<i>I. subporospora</i> Kuyper	DB2-10-12-2	BAN266	DB	Germany	MT101895*	here

<i>I. variispora</i> Fern. Sas. (isotype)	980504-01	BAN2804	SMG-GME	Spain	MT101872**, MT101883 (V6)	here
<i>I. woglindeana</i> Bandini, Vauras & Weholt (holotype)	SMNS-STU-F-0901435	DB12-5-13-2, BAN2851	STU	Germany	MT101882, MT101887 (V6)	here
<i>I. woglindeana</i>	DB25-5-13-1	BAN373	DB	Germany	MT101896*	here
<i>I. woglindeana</i>	SMNS-STU-F-0901448	JV26781	STU	Finland	MT101880, MT101885 (V6)	here
<i>I. woglindeana</i>	SMNS-STU-F-0901449	JV29347	STU	Finland	MT101881, MT101886 (V6)	here
<i>I. woglindeana</i>	SMNS-STU-F-0901434	DB10-10-17-19, BAN2850	STU	Germany	MT101879, MT101884 (V6)	here
<i>I. woglindeana</i> (soil sample)		G4776		Estonia		Tedersoo et al. Global soil samples unpublished
<i>I. woglindeana</i> (soil sample)		G4231		Estonia		Tedersoo et al. Global soil samples unpublished
<i>I. woglindeana</i> (soil sample)		G3562		Estonia		Tedersoo et al. Global soil samples unpublished
<i>I. woglindeana</i> (soil sample)		G3564		Estonia		Tedersoo et al. Global soil samples unpublished
<i>I. woglindeana</i> as <i>I. queletii</i>	TUR 147244	JV13784F, FI-PUT476-14	TUR-A	Finland	UDB022396*	Bálint Dima, unpublished
<i>I. woglindeana</i> as <i>I. queletii</i>	JV19682F		CUW	Finland	EU307813***	Kropp et al. 2010
<i>I. woglindeana</i> as <i>Inocybe</i> sp.	EL404		GB	Sweden	AM882968	Ryberg et al. 2008
<i>I. woglindeana</i> as <i>Inocybe</i> sp.	TUR 182154	JV5898F, FI-PUT578-14	TUR-A	Finland	UDB022408*	Bálint Dima, unpublished
<i>Inocybe</i> sp.	DB25-5-13-5	BAN384	DB	Germany	MT101894*	here
<i>Inocybe</i> sp.	DED8054a		SFSU	Thailand	GQ892998, GQ892953	Horak et al. (2015)
<i>Inocybe</i> sp. (ectomycorrhiza)		morphotype 12, isolate 140		Austria	EU326161*	Mühlmann & Peintner 2008
<i>Inocybe</i> sp. (soil sample)		clone 87_NA11_P31_E1/ OTU470		USA, Alaska	KC965603*	Timling et al. 2014
<i>Inocybe</i> sp. (soil sample)		clone IIS4-12		Austria	EU517033*	Oberkofler & Peintner 2008
<i>Nothocybe distincta</i>	ZT 9250, CAL 1310		ZT, CAL	India	KX171343, EU604546	Latha et al. 2016, Matheny et al. 2009
<i>Pseudosperma spurium</i> (holotype)	SJ92-017		GB	Sweden	AM882784.2	Ryberg et al. 2008
<i>Pseudosperma spurium</i>	BK180809723		UTC	USA, Utah	JQ408794, EU600868	Kropp et al. 2013, Matheny et al. 2009



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.

Holotype – Germany, Rheinland-Pfalz, Rhein-Pfalz-Kreis, Altrip, TK25 6516/4, alt. 95 m, sandy lake shore with *Salix* sp., *Populus* sp., *Betula pendula*, *Pinus sylvestris*, 12 May 2013, leg. D. Bandini & B. Oertel (Holotype STU SMNS-STU-F-0901435, BAN2851; Isotypes personal collection D. Bandini DB12-5-13-2, TUR-A 208610, AH 46945).

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

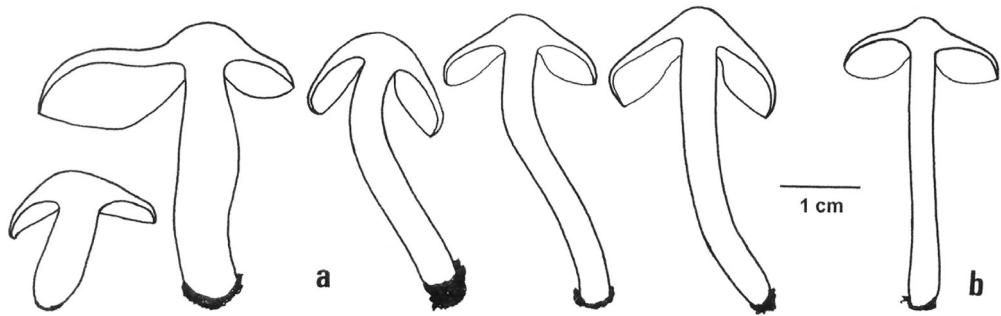
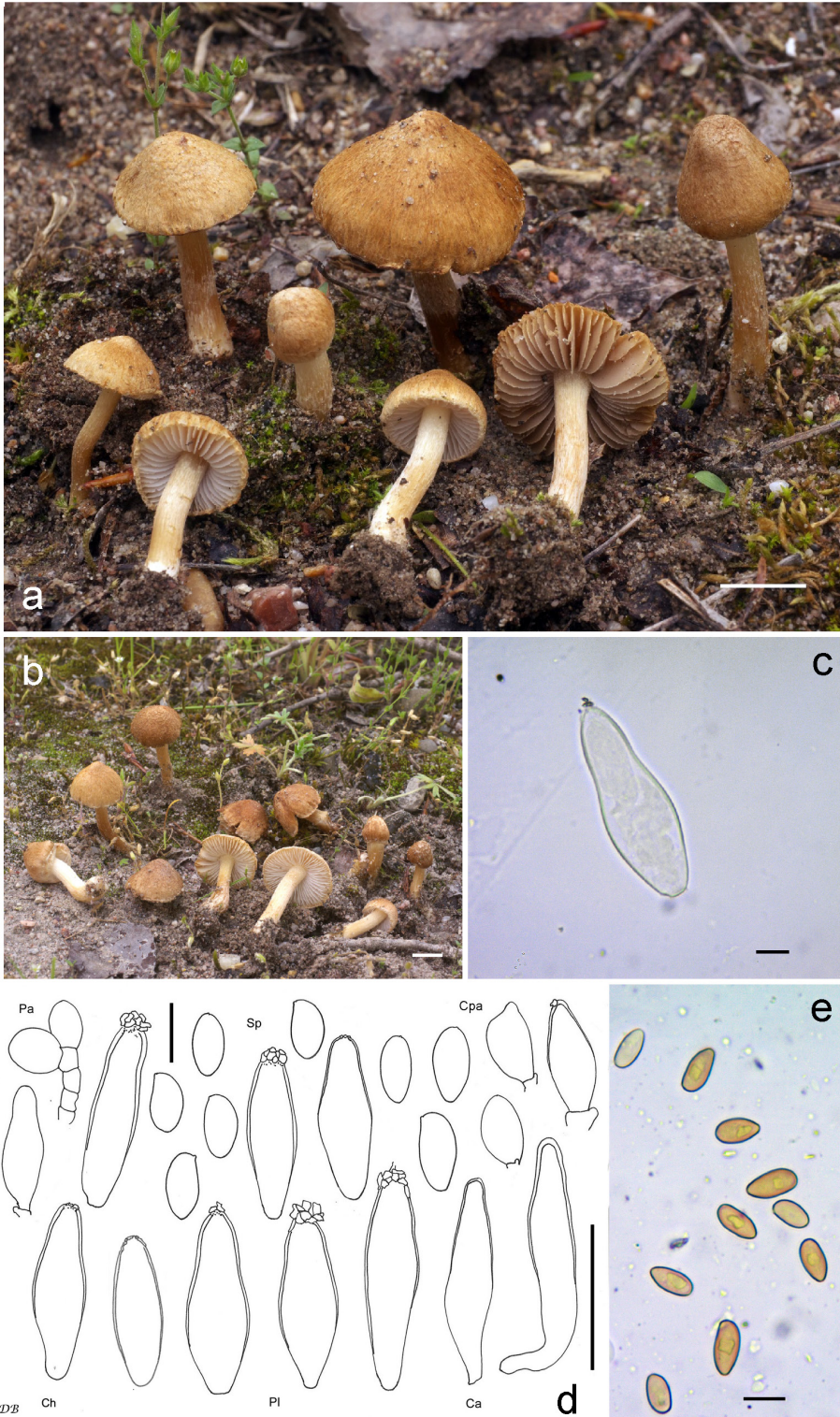


Fig. 2. *Inocybe woglindeana*. Basidiomes a: coll. Vauras 13558F. b: coll. Vauras 5898F; drawing J. Vauras.

basidiomata with ample whitish cortina. **LAMELLAE** 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 spermat-ic. **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)amygdaloid 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)utriform, 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
 a: coll. DB12-5-13-2, Holotype, scale bar: 1 cm. b: coll. DB25-5-13-1, scale bar: 1 cm. c: Cheilocystidia (coll. DB25-5-13-1), scale bar: 10 μm . d: Microscopic characters (coll. DB12-5-13-2), Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, PI = Pleurocystidia, Sp = Spores; scale bar spores: 10 μm , scale bar cystidia: 50 μm . e: Spores (coll. DB25-5-13-1), scale bar: 10 μm ; photographs and drawing D. Bandini.



Fig. 4. *Inocybe woglindeana*, coll. Vauras 13616F; photograph J. Vauras.

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 \times 10–20 (25) μm , quite variable in shape, (sub)fusiform, (sub)utriform, (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 gravelly 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 *Mallocybe 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 *Mallocybe 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. Lohja, Virkkala, near old limestone plant, margin of meadow, near *Salix caprea* and *Populus tremula*, 22 Jun. 1998, leg. *J. Vauras* 13556 (TUR-A), 13558F (TUR-A), 1 Jul. 1998, leg. *J. Vauras* 13616F (TUR-A, H), 16 Jul. 1998, leg. *J. Vauras* 13704 (TUR-A), 13705F (TUR-A, DB), 31 Jul. 1998, leg. *J. Vauras* 13784F* (TUR-A), 25 Aug. 1998, leg. *J. Vauras* 14123 (TUR-A), 1 Jul. 2003, leg. *J. Vauras* 19682F* (TUR-A, GB, WTU).- At margin of road in herb-rich forest with *Populus tremula*, *Betula pendula*, *Salix caprea* and *Pinus sylvestris*, 1 Jul. 2003, leg. *J. Vauras* 19665 (TUR-A).- Near Evästorppa, margin of sandy yard, near *Betula pendula*, *Salix* sp. and *Populus tremula*, 20 Sep. 2012, leg. *J. Vauras* 29347* (TUR-A, STU SMNS-STU-F-0901449, DB), 23 Sep. 2013, leg. *J. Vauras* 30246 (TUR-A).- Parainen, Storgård, Malmnäs, near limestone processing plant, 17 Jun. 2009, leg. *J. Vauras* 26781* (TUR-A, STU SMNS-STU-F-0901448, DB).- Uusimaa. Hanko, Tvärminneby, at abandoned brick-works, old yard with *Salix caprea*, *Populus tremula* and *Betula*

pendula, 30 Jun. 1998, leg. *J. Vauras* 13603 (TUR-A, H, DB).- Keski-Pohjanmaa.- Vimpeli, Koskela, abandoned limestone quarry and limestone plant, near *Betula* sp., *Salix* sp., *Pinus sylvestris* and *Alnus incana*, 26 Aug. 1991, leg. *J. Vauras* 5898F* (TUR-A).

GERMANY. Baden-Württemberg, Heidelberg, Südstadt, TK25 6618/1, alt. 110 m, former railway terrain, sandy ground with *Salix caprea*, *Betula pendula*, 30 May 2016, leg. *D. Bandini* (DB30-5-16-1*).- *Ibidem*, 5 Jun. 2016, leg. *D. Bandini* (DB5-6-16-1).- Rheinland-Pfalz, Rhein-Pfalz-Kreis, Neuhofen, wayside near Kistnerweiher, TK25 6516/4, alt. 95 m, in some distance to type-collection, alt. 90 m, sandy terrain with *Populus* sp., *Salix* sp., 12 May 2013, leg. *D. Bandini* & *B. Oertel* (DB12-5-13-6).- Rheinland-Pfalz, Rhein-Pfalz-Kreis, Ludwigshafen am Rhein, TK25 6516/4, alt. 93 m, sandy shore with *Populus* sp., *Salix* sp., 25 May 2013, leg. *D. Bandini* & *B. Oertel* (DB25-5-13-1*).- Rheinland-Pfalz, Rhein-Pfalz-Kreis, Neuhofen, wayside near Kistnerweiher, TK25 6516/4, alt. 95 m, *Salix* sp., *Populus* sp., *Pinus sylvestris*, *Betula pendula*, 25 May 2013, leg. *D. Bandini* & *B. Oertel* (DB25-5-13-3).- Bayern, Kelheim, Abensberg-Offenstetten, TK25 7137/3, alt. 380 m, *Pinus sylvestris*, *Salix* sp., 10 Oct. 2017, leg. *D. Bandini* (DB10-10-17-18*).- *Ibidem*, in some distance to former location, *Salix* sp., *Pinus sylvestris*, 10 Oct. 2017, leg. *D. Bandini* (DB10-10-17-19, STU SMNS-STU-F-0901434*).- *Ibidem*, in some distance to former location, *Salix* sp., *Pinus sylvestris*, 10 Oct. 2017, leg. *D. Bandini* (DB10-10-17-20).- *Ibidem*, in some distance to former location, *Pinus sylvestris*, *Salix* sp., 10 Oct. 2017, leg. *D. Bandini* (DB10-10-17-21).- *Ibidem*, in some distance to former location, *Salix caprea*, *Pinus sylvestris*, *Populus tremula*, 11 Oct. 2017, leg. *D. Bandini* & *B. Oertel* (DB11-10-17-15*).- *Ibidem*, in some distance to former location, *Salix caprea*, *Pinus sylvestris*, *Populus tremula*, 12 Oct. 2017, leg. *D. Bandini*, *B. Oertel* & *J. Christian* (DB12-10-17-17*).

NORWAY. Østfold. Fredrikstad, Torp Bruk, with various deciduous trees, among them *Salix* sp., *Alnus* sp., 29 Jun. 1985, leg. Ø. *Weholt*. First record of the species, originally identified as *I. queletii* by Th.W. Kuyper and cited in Kuyper (1986, probably deposited in L).- *Ibidem*, 2 Sep. 2014, leg. *M. Pettersen*.- *Ibidem*, 2 Aug. 2015, leg. *M. Pettersen* (O).- *Ibidem*, 25

May 2017, leg. *M. Pettersen* (O).- *Ibidem*, 24 May 2019, leg. *M. Pettersen*.- *Ibidem*, 5 Jun. 2019, leg. *Ø. Weholt* (now lost).

ADDITIONAL TYPES STUDIED: HOLOTYPE: INOCYBE INODORA Velen. 1920, Czech Republic, Bilichov, frondose trees, leg. Viniklář, Jun. 1920 (PR, bottle no 156). **SPORES** 9.0–12.8 μm (av. 11.0 μm , SD 0.9 μm) \times 5.2–7.4 μm (av. 6.2 μm , SD 0.5 μm); $Q = 1.4\text{--}2.1$ (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) \times 12–25 μm (av. 18 μm , SD 3 μm); $Q = 2.6\text{--}5.2$ (av. 3.4, SD 0.6) ($n = 15$), mostly (sub)fusiform or subutriform, with short neck and short pedicel, apex usually crystalliferous, walls up to 3.0 (3.5) μm thick, yellowish-greenish with 3% KOH. **CHEILOCYSTIDIA** similar in appearance and size. **PARACYSTIDIA** (sub)clavate to subovoid. **CAULOCYSTIDIA** not studied (to preserve the material).

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) \times 5.3–7.2 μm (av. 6.2 μm , SD 0.4 μm); $Q = 1.5\text{--}2.0$ (av. 1.7, SD 0.1) ($n = 40$), smooth, (sub)amygdaloid, with (sub)acute apex, with indistinct pseudopore. **BASIDIA** 4-spored. **PLEUROCYSTIDIA** 50–77 μm (av. 64 μm , SD 7 μm) \times 19–30 μm (av. 24 μm , SD 4 μm); $Q = 2.0\text{--}4.2$ (av. 2.8, SD 0.6) ($n = 15$), mostly (sub)fusiform or subutriform, apex usually crystalliferous, 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 neurufula Esteve-Rav., Macau & Ferville 2012, Spain, Catalonia, Girona, Torroella de Montgrí, *Fraxinus angustifolia*, *Pinus pinaster*, 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) \times 4.9–6.7 μm (av. 5.9 μm , SD 0.4 μm); $Q = 1.6\text{--}2.3$ (av. 1.9, SD 0.2) ($n = 40$), smooth, (sub)amygdaloid, with suprahilar depression and (sub)acute to papillate apex. **BASIDIA** 4-spored. **PLEUROCYSTIDIA** 55–74 μm (av. 61 μm , SD 6 μm) \times 12–21 μm

(av. 15 μm , SD 2 μm); $Q = 3.2\text{--}5.5$ (av. 4.2, SD 0.6) ($n = 15$), (sub)fusiform, (sub)utriform, also (sub)cylindrical, apex usually crystalliferous, 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 rufuloides 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) \times 5.2–7.0 μm (av. 6.0 μm , SD 0.3 μm); $Q = 1.4\text{--}2.0$ (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) \times 9–17 μm (av. 15 μm , SD 2 μm); $Q = 3.0\text{--}4.2$ (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 crystalliferous, 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) \times 4.5–6.0 μm (av. 5.1 μm , SD 0.3 μm); $Q = 1.6\text{--}1.9$ (av. 1.8, SD 0.1) ($n = 40$), smooth, (sub)amygdaloid, (sub)ellipsoid, apex (sub)obtuse, (sub)acute), sometimes subpapillate. **BASIDIA** 4-spored. **PLEUROCYSTIDIA** 45–63 μm (av. 53 μm , SD 6 μm) \times 11–16 μm (av. 14 μm , SD 2 μm); $Q = 2.8\text{--}5.3$ (av. 3.9, SD 0.7) ($n = 15$), (sub)fusiform, subutriform (sub)cylindrical, with rather short neck and short pedicel, apex usually crystalliferous, 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



Fig. 5. *Inocybe woglindeana*, coll. Vauras 13558F; photograph J. Vauras.

Elkartea). **SPORES** 9.1–12.6 μm (av. 10.4 μm , SD 0.7 μm) \times 5.4–6.2 μm (av. 5.7 μm , SD 0.2 μm); $Q = 1.6\text{--}2.0$ (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) \times 11–22 μm (av. 15 μm , SD 2 μm); $Q = 2.7\text{--}5.5$ (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 & Ochoteren 2000], Bayesian 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, Kalyanamoorthy 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



Fig. 6. *Inocybe variispora*, holotype, photograph R. Fernández Sasía.

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 ;Tedesoo, 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* (Timling 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

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*, subfusiform 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 & Fer-ville 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

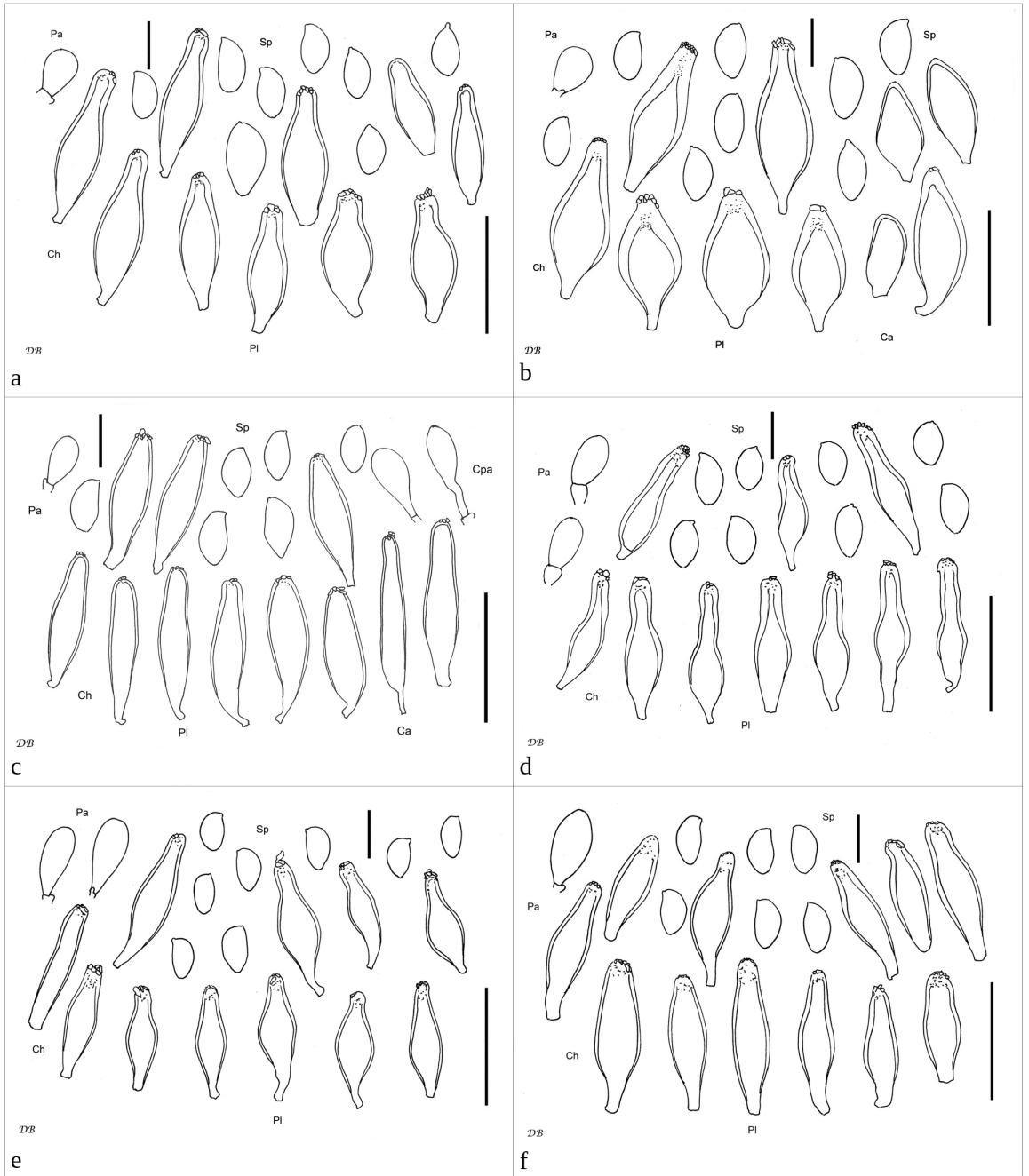


Fig. 7. Microscopic characters of type collections. a: *Inocybe inodora* (PR, bottle no. 156). b: *I. involuta* (L-0017086). c: *I. neorufula* (SMNS-STU-F-0901287). d: *I. rufuloides* (LIP-MB83038). e: *I. subpelargonium* (LIP-7910142). f: *I. variispora* (No 980504-01). Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm; drawings D. Bandini.

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. rufiloides* 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 velipellis, visible in young basidiomes of *I. woglindeana*, is missing in *I. variispora*, and the odour is described as spermatic (“spermatique 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*.

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