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ORIGINAL ARTICLE

Revision of some central European species of *Inocybe* (Fr.: Fr.) Fr. subgenus *Inocybe*, with the description of five new species

Ditte Bandini[1] · Bernd Oertel[2] · Sebastian Ploch[2] · Tahir Ali[2] · Jukka Vauras[3] · Anja Schneider[4] · Markus Scholler[4] · Ursula Eberhardt[5] · Marco Thines[2,6]

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Abstract

The subgenus *Inocybe* is widespread in the Holarctic but, due to a superficially similar appearance of the species, much of its diversity has been overlooked. In this study, a revision of some Central European species of the subgenus is carried out. On the basis of detailed morphological and phylogenetic investigation, five new species of *Inocybe,* subgenus *Inocybe* are described. Three of these are smooth-spored (*I. venustissima, I. curcumina,* and *I. leochroma*), and two are nodulose-spored (*I. strickeriana* and *I. villosa*). The new species are compared to the type specimens of *I. alluvionis*, *I. angulatosquamulosa*, *I. hirtelloides*, *I. pelargonium*, *I. salicis*, *I. splendentoides*, *I. straminipes*, and *I. terrifera*. *Inocybe derbschii* is confirmed, and a comprehensive description with photographs is given. The morphological species complex consisting of *I. furfurea*, *I. rufotacta,* and *I. sandrae* is disentangled and it is shown that the three names are synonyms. Finally, it is shown that *I. stenospora* does not belong to the subgenus *Mallocybe* but to the subgenus *Inocybe*. All new species and most type specimens were included in molecular phylogenetic analyses. The phylogenetic analyses are well in line with the current perception of species boundaries in *Inocybe* subg. *Inocybe*.

Keywords Agaricales · Inocybaceae · Taxonomy · Molecular systematics · Type specimens · ITS

Introduction

The genus *Inocybe* (Agaricales, Inocybaceae) comprises small, medium-sized, or even large mushrooms with mainly brown, but also whitish, yellowish, ochraceous, reddish, violaceous or greyish caps and has a global distribution, with an assumed diversity hot-spot in the temperate Holarctic (Larsson et al. 2009). Based on own taxonomical and molecular studies (Bandini, Oertel and Thines unpublished), there are more than 450 species in Germany and adjacent countries (France, Netherlands, Austria, and Switzerland). Thus, *Inocybe* appears to be more species-rich than it had been assumed some years ago (Kirk et al. 2008; Larsson et al. 2009; Matheny et al. 2009; Seress et al. 2016). *Inocybe* has been divided by different authors in varying numbers of subgenera, sections, and subsections on the basis of morphological characteristics, e.g. thin- or thick-walled hymenial cystidia, presence of cortina or presence of metuloid caulocystidia near the base of stipe, shape of spores and hymenial cystidia. The phylogenetic-based classification proposed by Matheny (2009) is largely consistent with traditional classifications. This suggests that even though there is not a full congruence,

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✉ Marco Thines
m.thines@thines-lab.eu

[1] Panoramastr. 47, 69257 Wiesenbach, Germany

[2] Senckenberg Biodiversität und Klima Forschungszentrum, Senckenberganlage 25, 60325 Frankfurt am Main, Germany

[3] Biological Collections of Åbo Akademi University, Herbarium, Biodiversity Unit, University of Turku, FI-20014 Turku, Finland

[4] Staatliches Museum für Naturkunde Karlsruhe, Erbprinzenstr. 1, 76133 Karlsruhe, Germany

[5] Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, 70191 Stuttgart, Germany

[6] Department of Biological Sciences, Institute of Ecology, Evolution and Diversity, Goethe University, Max-von-Laue-Str. 13, 60483 Frankfurt am Main, Germany

many of the morphological characters used in the traditional classifications are reliable and phylogenetically informative.

The species of *Inocybe* subg. *Inocybe* usually have more or less thick-walled hymenial cystidia and, with only few exceptions, pleurocystidia (see also Matheny 2009; Ryberg 2009). The subgenus has been divided into two informal "supersections", based on the presence/absence of a cortina and metuloid cystidia, the "Cortinatae" and the "Marginatae" (Kühner and Boursier 1932; Kühner 1933; Kuyper 1986), a division that is not monophyletic (Matheny et al. 2002; Ryberg 2009; Ryberg et al. 2010). Thus, the assignment of the species to these groups in this manuscript is solely meant in terms of morphology along the lines of Heim (1931), Malençon and Bertault (1970), Alessio and Rebaudengo (1980), Kuyper (1986), Singer (1986), Stangl (1989), Bizio (1997), Bon (1997, 1998), Ferrari (2006, 2010), Jacobsson and Larsson (2012), and Ferrari et al. (2014).

The stipes of the species characterised as "Cortinatae" are not pruinose, only pruinose near apex or only in the upper half of the stipe, the base of the stipe is mostly not bulbous and remnants of a cortina are often present on the margin of young pilei. The stipes of the species characterised as "Marginatae" are entirely pruinose, and they have a somewhat bulbous base (Matheny et al. 2002; Matheny 2005; Kropp et al. 2010).

Of the aforementioned ca. 450 species of *Inocybe* found in Germany and adjacent areas, more than 350 belong to subgenus *Inocybe*, about 30 belong to the subgenus *Mallocybe* and the rest to subgenus *Inosperma*. Of the 350 species of the subgenus *Inocybe*, more than the half are smooth-spored species. These observations are in agreement with the keys of Bon (1997, 1998). The choice of species presented here was based on the following criteria: *I. strickeriana* and *I. villosa* belong to a complex of nodulose species that has been recently treated in detail (Esteve-Raventós et al. 2015; Esteve-Raventós et al. 2016; Larsson et al. 2018), and with these two species this complex will be still more complete. One species, *I. venustissima,* has a striking appearance, and therefore it was appropriate to present it here. The other two species, *I. curcumina* and *I. leochroma*, were chosen because they are closely related to species which had to be compared to *I. venustissima*. Other species presented here where chosen along the same lines, in order to investigate the diversity of *Inocybe* subg. *Inocybe*, with a focus on species that might easily be overlooked, misinterpreted, or neglected, challenging earlier, doubtful synonymy. For this, both detailed morphological comparisons focussing on type material and phylogenetic analyses were carried out in order to investigate their relationships in *Inocybe* subg. *Inocybe*.

Material and methods

Specimens

All species descriptions in this study were supported by fresh collections. The type collections studied were obtained from the fungaria in Genève (G), Karlsruhe (KR), Lille (LIP), Munich (M), Paris (PC), Prague (PRM), and Turku (TUR-A) (Thiers 2017). Type specimens of the following species were studied: *I. alluvionis, I. angulatosquamulosa, I. derbschii*, *I. furfurea*, *I. hirtelloides*, *I. pelargonium*, *I. pseudodestricta*, *I. rufotacta*, *I. salicis, I. sandrae*, *I. splendentoides*, *I. stenospora*, *I. straminipes,* and *I. terrifera*. Permission for sampling for phylogenetic analysis was granted in all cases, except for *I. salicis* and *I. straminipes*. From the types of *I. alluvionis* and *I. terrifera* no amplifiable DNA could be obtained. Fresh collections of these species were studied and sequenced, instead. All specimens sequenced are listed in Table 1.

Morphology

As far as fresh collections are concerned, the relevant macroscopical details, i.e. habit, size and shape of the basidiomata, 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 associated trees, were noted. Of all species—if possible in the fresh, otherwise in the dried state—basidia, spores, hymenial cystidia, caulocystidia etc. were examined with a Leica DM-750 microscope (Leica, Wetzlar, Germany) in water and 3% KOH solution, at × 400 (0.17, HI Plan40 ×/0.65; Leica, Wetzlar, Germany) and × 1000 (0.17 C Plan 100 ×/1.25 OIL; Leica, Wetzlar, Germany) magnifications. Photographs were taken with a Zeiss AxioCam ERc5s. The measurements of spores and cystidia were done using Zeiss Axiovision version 4.8. Spore length includes nodules, and cystidia were measured without crystals and basidia without sterigmata. The size of all organs 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 descriptions.

Most pictures of fresh collections were photographed by D. Bandini with a Panasonic Lumix GH2 with a Leica DG Macro-Elmarit 1:2,8/45 mm lens. For the determination of colour temperature a greycard has been photographed together with the fresh collections at the site where they were found. The RAW files were developed with Silkypix Developer Studio 4.0. *Inocybe strickeriana* was photographed by Anja Schneider, *I. stenospora* by Reinhard Geiter, and DB13-8-13-25 of *I. leochroma* by Wolfgang Dämon.

Table 1 Specimens investigated in this study. The original identification (orig. ident.) is given if the current species name is deviating

Species (*I.* = *Inocybe*)	Voucher	Herbarium	Additional number	Country	Genbank/ UNITE (ITS)
I. alluvionis	DB7-9-14-11	DB	BAN814	Germany	MH807259
I. alluvionis	DB10-10-15-3	DB	BAN1338	Germany	MH807260
I. amblyospora Kühner	DB12-7-13-1	DB	BAN394	Germany	MH366616*
I. amblyospora	JFA12538	WTU		Sweden	KJ729872
I. angulatosquamulosa Stangl	M-028791 **holotype**	M		Germany	MG012474
I. angulatosquamulosa	KR-M-0042369	KR	DB1-8-14-6, BAN670	Germany	MH366613
I. angulatosquamulosa	KR-M-0042370	KR	DB8-8-14-4, BAN683	Germany	MH366614
I. angulatosquamulosa	KR-M-0042371	KR	DB29-8-14-2, BAN797	Germany	MH366615
I. angulatosquamulosa	TUR190216	TUR	FIRUS204-13	Finland	UDB022322
I. angulatosquamulosa	TUR137165	TUR	FIRUS213-13	Finland	UDB022324
I. casimirii Velen.	DB10-8-13-12	DB	BAN448	Austria	MH366599
I. catalaunica Singer	DB5-9-14-9	DB	BAN805	Germany	MH366576
I. chalcodoxantha Grund & D.E. Stuntz	WTU DG1817 **isotype**	WTU		Canada	NR_119900 (HQ201341)
I. curcumina Bandini, B. Oertel & U. Eberh. sp. nov.	KR-M-0042332 **holotype**	KR	DB30-6-12-1, BAN200	Germany	MH366621
I. curcumina	KR-M-0042335	KR	DB2-10-14-4, BAN836	Germany	MH366622
I. curcumina	KR-M-0042360	KR	DB7-8-11-2, BAN1516	Germany	MH366620
I. curcumina	KR-M-0042333	KR	DB5-9-16-2, BAN1828	Germany	MG012480
I. derbschii Schwöbel & Stangl	KR-M-0005011 **holotype**	KR		Germany	MG012466
I. derbschii orig. ident. *I. pseudodestricta*	PRM716232 *I. pseudodestricta*-**paratype**	PRM		Germany	MG012469
I. derbschii	DB30-5-13-2	DB	BAN1478	Germany	MH366593
I. derbschii	KR-M-0042367	KR	DB25-10-15-3, BAN1909	Germany	MH366592
I. erythospilota Grund & D.E. Stuntz	ACAD 11699 **holotype**	ACAD		Canada	MG489947
I. flavoalbida Matheny & Bougher	PBM3768 **isotype**	TENN		Australia	KJ729873
I. flocculosa	EL10605			Finland	AM882992
I. furfurea Kühner	G00053152 **lectotype**	G		France	MG012472
I. furfurea orig. ident. *I. rufotacta*	KR-M-0005010 *I. rufotacta*-**holotype**	KR		Germany	MG012467
I. furfurea orig. ident. *I. sandrae*	KR-M-0042355 *I. sandrae*-**isotype**	KR		Germany	MH366610
I. furfurea	KR-M-0042337	KR	DB4-7-12-3, BAN213	Germany	MH366607*
I. furfurea	KR-M-0042339	KR	DB2-6-13-3, BAN372	Germany	MH366608*
I. furfurea	KR-M-0042341	KR	DB25-5-13-9, BAN388	Germany	MH366609*
I. furfurea orig. ident. *Inocybe* sp.	GDa	TENN		Argentina	EU620230
I. fuscidula	EL9505			Finland	AM882886
I. grammopodia Malençon	KR-M-0044138	KR	BAN1023	Germany	MH366590
I. grammopodia	DB14-10-15-2	DB	BAN1405	Germany	MH366591

Table 1 (continued)

Species (*I.* = *Inocybe*)	Voucher	Herbarium	Additional number	Country	Genbank/ UNITE (ITS)
I. grammopodia	IMG 1632				KY680785
I. griseotarda	J. Poirier n 19901119-01 **holotype**	G		France	MF361839
I. griseovelata	EL20906			France	FN550931
I. hirculus	TUR-A 2577 **holotype**	TUR-A	Vauras 5974F	Finland	FJ531872
I. hirtelloides Stangl & J. Veselský	PRM727125 **holotype**	PRM		Germany	MG012471
I. hirtelloides	KR-M-0042354	KR	DB1-8-14-4, BAN668	Germany	MH366618
I. hirtelloides	KR-M-0042359	KR	DB8-8-14-7, BAN684	Germany	MH366617
I. hirtelloides orig. ident. *I. pelargonium*	TK04063			Sweden	AM882936
I. hygrophana Glowinski & Stangl	MTB 2130 **holotype**	M		Germany	JX983593
I. krieglsteineri Fern. Sas.	DB29-9-15-1-Zinke	DB	BAN1283	Germany	MH366602
I. krieglsteineri	EL202-09				KT958916
I. lacera	EL805			Norway	AM882818
I. lacunarum	TUR-A 171771 **holotype**	TUR-A	JV12244F	Finland	KT958908
I. langei	EL7705			Sweden	AM882919
I. lanuginosa (Bull.: Fr.) P. Kumm.	DB1-11-12-7	DB	BAN447	Germany	MH366601
I. lanuginosa	OUC99161				DQ367905
I. leochroma Bandini, Vauras & B. Oertel sp. nov.	KR-M-0042372 **holotype**	KR	DB25-9-15-21, BAN1215	Austria	MH366611
I. leochroma	KR-M-0042373	KR	DB13-8-13-25, BAN404	Austria	MH366612*
I. leochroma orig. ident. *I. angulatosquamulosa*	TUR-A 142765	TUR	FIPUT475-14	Finland	UDB022323
I. leochroma orig. ident. *I. pelargonium*	TUR-A 190230	TUR	FIPUT606-14	Estonia	UDB022390
I. mallopus (*mallopoda*) Matheny & Bougher	PERTH 08092214 **holotype**	PERTH	NLB258	Australia	KP308774
I. mystica	M-0208610 **holotype**	M		Germany	KY349131
I. nigricans Matheny, Bougher & Ryberg	TENN 066635 **holotype**	TENN	PBM3697	Australia	KP308787
I. ochroalba	EL5704			Sweden	AM882882
I. pelargonium Kühner	KR-M-0042334	KR	DB29-6-12-7, BAN201	Germany	MH366623*
I. pelargonium	KR-M-0042363	KR	DB11-8-14-21, BAN694	Germany	MH366624
I. pelargonium	KR-M-0042361	KR	DB5-9-16-8, BAN1829	Germany	MG012479
I. pelargonium	21637	MCVE			JF908252
I. phaeoleuca	SJ06024			Sweden	FN550907
I. populea	TAKK15655 **paratype**	TUR-A		Japan	KT958911
I. cf. *praetervisa* Quél.	EL7206			Sweden	FN550890
I. pseudodestricta Stangl & J. Veselský	PRM716231 **holotype**	PRM		Czech Republic	MG012468
I. pseudodestricta	KR-M-0043223	KR	DB6-5-12-10, BAN102	Netherlands	MH366594*
I. pseudodestricta	KR-M-0042344	KR	DB17-8-15-13, BAN1050	Finland	MH366595
I. pseudodestricta	KR-M-0042350	KR	DB25-8-15-13, BAN1167	Finland	MH366596

Table 1 (continued)

Species (*I.* = *Inocybe*)	Voucher	Herbarium	Additional number	Country	Genbank/ UNITE (ITS)
I. pseudodestricta orig. ident. *I. glabrescens*	UBC F19517	UBC		Canada	HQ604513
I. pseudoreducta Stangl & Glowinski	M-0138786 **holotype**	M		Germany	KY213955
I. pseudoreducta	KR-M-0042676	KR	DB20-9-15-20, BAN1005	Germany	MH366630
I. pseudoreducta	5057	MCVE		Italy	JF908125
I. cf. *pusio* P. Karst.	DB14-7-12-4	DB	BAN215	Germany	MH366589*
I. cf. *pusio*	DB16-8-14-24	DB	BAN1359	Germany	MH366588
I. roseipes Malençon	9856	MCVE		Italy	JF908143
I. rufescens Matheny & Bougher	PERTH 08318468 **holotype**	PERTH	NLB834	Australia	KP308818
I. saliceticola Vauras & Kokkonen	Kokkonen & Vauras 19738F **holotype**	TUR-A		Finland	FJ755796
I. salicis Kühner	DB1-6-12-2	DB	BAN293	Germany	MH366575*
I. salicis	DB14-6-15-1	DB	BAN1042	Netherlands	MH366574
I. salicis	PAM07051802				KT958907
I. serotina Peck	KR-M-0038266	KR	DB19-9-11-1, BAN196	Netherlands	MH366584*
I. serotina	L036	O		Norway	UDB017612
I. splendens R. Heim	DB16-10-15-1b	DB	BAN1786	Germany	MH366583
I. splendentoides Bon	MB89165 **holotype**	LIP		France	MG012470
I. splendentoides	KR-M-0042351	KR	DB16-10-11-1, BAN145	Germany	MH366585*
I. splendentoides	KR-M-0042352	KR	DB21-10-15-1, BAN1834	Germany	MH366586
I. splendentoides	KR-M-0042353	KR	DB4-10-13-1, BAN1839	Germany	MH366587
I. splendentoides orig. ident. *I. splendens*	EL22506			France	FN550911
I. stenospora Stangl & Bresinsky	M-0151619 **holotype**	M		Germany	MG012473
I. stenospora	KR-M-0042356	KR	DB24-10-12-Geiter, BAN321	Germany	MH366597*
I. stenospora	KR-M-0042357	KR	DB7-10-13-Geiter, BAN714	Germany	MH366598
I. strickeriana Bandini, Anja Schneider & M. Scholler sp. nov.	KR-M-0044749 **holotype**	KR		Germany	MG012477
I. strickeriana	KR-M-0044126	KR		Germany	MH366572
I. strickeriana	KR-M-0044133	KR		Germany	MH366573
I. strickeriana	KR-M-0044132	KR		Germany	MG012481
I. strickeriana orig. ident. *I.* aff. *xanthomelas*	PAM07062202	LIP		France	HQ586861
I. substellata	Kühner73_218 **holotype**	G		France	KT958928
I. teraturgus M.M. Moser	DB25-8-15-1	DB	BAN1160	Finland	MH366600
I. teraturgus	M.-L. & P. Heinonen 214-95F	TUR		Finland	JN580887
I. terrifera Kühner	KR-M-0042366	KR	DB31-8-14-6, BAN802	Germany	MH366582
I. terrifera	KR-M-0044140	KR	BAN1018	Germany	MH366578
I. terrifera	KR-M-0044137	KR	BAN1027	Germany	MH366580

Table 1 (continued)

Species (*I.* = *Inocybe*)	Voucher	Herbarium	Additional number	Country	Genbank/ UNITE (ITS)
I. terrifera	KR-M-0044175	KR	BAN1028	Germany	MH366579
I. terrifera	KR-M-0044139	KR	BAN1030	Germany	MH366581
I. vaccina Kühner	DB30-9-13-7	DB	BAN1514	Germany	MH366619
I. venustissima Bandini & B. Oertel sp. nov.	KR-M-0042322 **holotype**	KR	DB22-8-12-8, BAN230	Austria	MH366625*
I. venustissima	KR-M-0042323	KR	DB15-8-13-17, BAN414	Austria	MH366626
I. venustissima	KR-M-0042326	KR	DB16-8-13-9, BAN503	Austria	MH366627
I. venustissima	KR-M-0042325	KR	DB16-8-13-2, BAN510	Austria	MH366628
I. venustissima	KR-M-0042324	KR	DB16-8-13-13, BAN538	Austria	MH366629
I. venustissima orig. ident. *I.* aff. *pelargonium*	BJ910808			Sweden	AM882977
I. venustissima orig. ident. *I. auricoma*	UBC F19796	UBC		Canada	HQ604526
I. villosa Bandini, B. Oertel & U. Eberh. sp. nov.	KR-M-0042327 **holotype**	KR	DB29-9-13-2, BAN407	Germany	MH366605
I. villosa	KR-M-0042329	KR	DB22-9-15-13, BAN1177	Germany	MH366606
I. villosa	KR-M-0042328	KR	DB12-10-16-13, BAN1420	Austria	MG012478
I. villosa	KR-M-0042374	KR	DB15-10-17-1, BAN1942	Germany	MH366604
I. cf. *xanthomelas* Boursier & Kühner	DB15-9-15-3-Dondl	DB	BAN1302	Germany	MH366571
Inocybe sp.	DB22-8-14-21	DB	BAN779	Germany	MH366577
Inocybe sp.	DB3-6-13-3	DB	BAN1481	Germany	MH366603
Outgroup					
I. arthrocystis Kühner	EL9207			Sweden	FN550941
I. leucoblema Kühner	SEB97-09				GU980631
I. leucoblema	SM2324				GU980630

An asterisk (*) indicates sequences generated by Alvalab (Oviedo, Spain)

Colour codes are taken from Munsell (2009). Terminology follows Vellinga (1988) and Kuyper (1986). Herbarium acronyms are according to Holmgren et al. (1990), the acronym DB means the private herbarium of Ditte Bandini.

DNA extraction, PCR and sequencing

The DNA of a small part of the basidiomata was extracted using the BioSprint 96 Plant Kit (Qiagen, Hilden, Germany) on a KingFisher Flex robot (Thermo Fisher Scientific, Waltham, MA, USA) following the manufacturer's instructions. The PCR reaction was conducted on a Thermocycler ProS (Eppendorf, Hamburg, Germany) equipped with a vapoprotect lid using MangoTaq DNA polymerase (Bioline, Luckenwalde, Germany). Each PCR reaction contained 1× MangoTaq colourless reaction buffer, 200 μM dNTPs, 2 mM $MgCl_2$, 0.5 U MangoTaq Polymerase as well as 0.8 μg ml^{-1} BSA (bovine serum albumin, Carl Roth GmbH, Karlsruhe, Germany) and 0.4 mM of each primer (Sigma-Aldrich, part of Merck KGaA, Darmstadt, Germany). The ITS region (containing the internal transcribed spacer 1, 5.8S rDNA, and the internal transcribed spacer 2) was amplified using ITS1-F and ITS4-B (Gardes and Bruns 1993) following the amplification program described in the manuscript introducing the primers. The fragments were bidirectionally sequenced by the laboratory centre of Senckenberg Biodiversity and Climate Research Centre (S-BiK-F, Frankfurt, Germany) using the primers used for PCR or the ITS1 and ITS4 primers designed by White et al. (1990).

Extraction of DNA from type specimens, older or otherwise difficult material was carried out using the PureGene kit (Qiagen, Hilden, Germany) as described in Eberhardt et al. (2016). Amplification was done with the primers ITS1-F and ITS2 for ITS1; and 58sf forward ITS4 reverse for ITS2 (White et al. 1990; Gardes and Bruns 1993; Martin and Rygiewicz 2005) with an annealing temperature of 55 °C for 45 s and elongation time of 30–90 s in 35 cycles using MyTaq Red (Bioline, Luckenwalde, Germany). For further details see Eberhardt (2012). Bi-directional sequencing was done with the PCR primers at LGC (Berlin, Germany).

The DNA of 13 of the specimens was extracted and the ITS region sequenced by Alvalab (Oviedo, Spain, http://alvalab.es/). These samples are marked in Table 1.

Sequence processing and phylogenetic analyses

Sequences were assembled and edited using Sequencher (version 4.9, Gene Codes, Ann Arbor) or Geneious (version 5.6, Biomatter Ltd., Auckland, New Zealand). Sequences were submitted to GenBank with accession numbers given in Table 1. Forward and reverse sequences were merged, edited if necessary and a consensus sequence was generated for every sample. The sequences were aligned with MAFFT version 7 (https://mafft.cbrc.jp/alignment/server/, Katoh et al. 2017) with the G-INS-i algorithm. All other parameters were set to default. Phylogenetic reconstructions were conducted on the TrEase webserver (Mishra et al. unpublished), using the maximum likelihood algorithm with RAxML (GTRGAMMA model with 1000 bootstrap replicates). Bayesian Inference was done using MrBayes (Huelsenbeck 2012) as implemented in siMBa (Mishra and Thines 2014), using the GTR model, 10 M generations, sampling every 100th tree, and discarding the first 30% of trees generated as burn-in.

Results

Our phylogenetic and morphological investigations based on the specimens given in Table 1 revealed the presence of five previously undescribed lineages of *Inocybe* subg. *Inocybe* that warrant description as new species.

The phylogenetic (Fig. 1) and morphological analyses of *Inocybe derbschii* showed that it is clearly distinct from *I. pseudodestricta*, with which it had been synonymised, perhaps based on a paratype not belonging to *I. pseudodestricta*. Sometimes, these two species share the same habitat but *I. pseudodestricta* can be distinguished from *I. derbschii* by its buttery shiny pileus and by caulocystidia that sometimes exceed 100 μm. *Inocybe derbschii* has been recorded from Estonia, otherwise only from Germany, while *I. pseudodestricta* is recorded from several European countries, including Russia and Finland, but also from Canada.

The very common species *I. furfurea*, which often grows in parks or cemeteries, has proven synonymous with *I. sandrae* and *I. rufotacta*. In some collections or basidiomata a magnifying glass suffices to see that the stipes are pruinose on the entire length, while in others they seem to be pruinose only in the upper half or only near the apex, and only upon microscopic examination metuloid caulocystidia can be observed also in the lower half of the stipe. Similarly, lamellae when bruised are reddening to different degrees in different collections and sometimes also not at all. Thus, there is apparently significant gradual variation in this species, which, in terms of ITS sequences, was found to be highly homogenous.

Inocybe venustissima sp. nov. has an unusual appearance with a big bulb. Apparently, it was previously overlooked in moist coniferous woods of montane or subalpine regions. Apart from its unusual morphology, it was also well-differentiated from its Canadian sister species *I. chalcodoxantha* in the ITS-based phylogeny (Fig. 1). One sequence from a specimen determined as *I. auricoma* (Batsch) Sacc. is almost identical to the ITS sequence of *I. venustissima*. However, *I. venustissima* can be readily distinguished from *I. auricoma* on the basis of its habit, larger size of basidiomata and a big bulb, whereas *I. auricoma* has no bulb at all, as can be seen in the original publication by Batsch (1783, Ic. jen. XXI).


73/0.98
I. angulatosquamulosa M-028791 holotype
I. angulatosquamulosa KR-M-0042371
92/0.75
I. angulatosquamulosa TUR190216
I. angulatosquamulosa KR-M-0042370
I. angulatosquamulosa TUR137165
100/1.0
I. angulatosquamulosa KR-M-0042369
I. angulatosquamulosa
I. leochroma sp. nov. TUR190230
I. leochroma sp. nov. KR-M-0042373
100/1.0
I. leochroma sp. nov. KR-M-0042372 holotype
I. leochroma sp. nov. TUR142765
I. leochroma sp. nov.
88/0.99
100/1.0
I. amblyospora DB12-7-13-1
98/1.0
-/0.99
I. amblyospora JFA12538
I. flavoalbida TENN 067000 holotype
I. pseudoreducta M-0138786 holotype
100/1.0
I. pseudoreducta KR-M-0042676
I. pseudoreducta 5057
I. pelargonium KR-M-0042363
-/0.93
I. pelargonium KR-M-0042334
100/1.0
I. pelargonium 21637
-/0.99
I. pelargonium KR-M-042361
I. pelargonium
99/1.0
I. curcumina sp. nov. KR-M-042332 holotype
I. curcumina sp. nov. KR-M-002360
100/1.0
I. curcumina sp. nov. KR-M-042335
I. curcumina sp. nov. KR-M-042333
I. curcumina sp. nov.
94/1.0
86/0.95
I. hirtelloides KR-M-042354
79/0.96
I. hirtelloides KR-M-042359
86/0.91
I. hirtelloides PRM727125 holotype
-/0.80
100/1.0
I. pelargonium TK04063
I. hirtelloides
I. vaccina DB30-9-13-7
I. langei EL7705
I. grammopodia KR-M-044138
100/1.0
I. grammopodia DB14-10-15-2
-/0.76
I. grammopodia IMG 1632
100/1.0
I. cf. pusio DB16-8-14-24
-/0.85
I. cf. pusio DB14-7-12-4
84/0.99
99/1.0
I. derbschii KR-M-0005011 holotype
I. derbschii KR-M-0042367
100/1.0
I. pseudodestricta PRM716232 paratype
I. derbschii
91/1.0
I. derbschii DB30-5-13-2
I. roseipes 9856
I. pseudodestricta KR-M-043223
I. pseudodestricta PRM716231 holotype
100/1.0
I. pseudodestricta KR-M-042350
I. pseudodestricta KR-M-042344
I. pseudodestricta
I. glabrescens UBC F19517
100/1.0
I. griseotarda J. Poirier n 19901119-01 holotype
I. fuscidula EL9505
86/0.99
I. cf. flocculosa EL10605
73/0.93
I. griseovelata EL20906
I. ochroalba EL5704
I. venustissima sp. nov. KR-M-0042324
I. venustissima sp. nov. KR-M-0042323
I. venustissima sp. nov. KR-M-0042325
88/-
I. venustissima sp. nov. KR-M-0042326
99/1.0
I. venustissima sp. nov. KR-M-0042322 holotype
I. venustissima sp. nov.
I. aff. pelargonium BJ910808
100/1.0
I. auricoma UBC F19796
-/0.97
I. chalcodoxantha WTU DG1817 isotype
I. splendentoides KR-M-0042351
I. splendentoides KR-M-0042352
97/1.0
I. splendentoides KR-M-0042353
I. splendentoides
I. splendens EL22506
97/0.99
I. splendentoides MB89165 holotype
100/1.0
I. serotina KR-M-0038266
71/1.0
I. serotina L036
99/1.0
I. alluvionis DB10-10-15-3
77/0.95
I. alluvionis DB7-9-14-11
95/1.0
I. splendens DB-16-10-15-1b
I. terrifera KR-M-0044137
84/0.97
I. terrifera KR-M-0044139
I. terrifera KR-M-0042366
I. terrifera
-/0.99
100/1.0
I. terrifera KR-M-0044175
I. terrifera KR-M-0044140
I. sandrae KR-M-0042355 isotype
I. furfurea KR-M-0042341
-/0.86
I. furfurea KR-M-0042339
100/1.0
I. rufotacta KR-M-0005010 holotype
I. furfurea
I. furfurea G00053152 lectotype
92/1.0
I. furfurea KR-M-0042337
Inocybe sp. GDa
83/1.0
-/1.0
I. hygrophana MTB 2130 holotype
-/0.99
I. rufescens PERTH 08318468 holotype
Inocybe sp. DB22-8-14-21
84/1.0
100/1.0
I. catalaunica DB5-9-14-9
I. erythospilota ACAD 11699 holotype
I. phaeoleuca SJ06024
I. mystica M-0280610 holotype
100/1.0
I. teraturgus DB25-8-15-1
I. teraturgus M.-L. & P. Heinonen 214-95F
-/0.86
I. lanuginosa DB1-11-12-7
-/0.99
100/1.0
I. lanuginosa var. lanuginosa OUC99161
-/0.92
I. stenospora M-0151619 holotype
100/1.0
I. stenospora KR-M-0042356
I. stenospora
-/0.99
I. stenospora KR-M-0042357
98/1.0
I. casimirii DB10-8-13-12
I. mallopoda PERTH 08092214 holotype
100/1.0
I. nigricans TENN 066635 holotype
I. lacera EL805
I. villosa sp. nov. KR-M-0042328
96/0.92
I. villosa sp. nov. KR-M-0042374
72/0.99
I. villosa sp. nov. KR-M-0042327 holotype
I. villosa sp. nov.
I. villosa sp. nov. KR-M-0042329
97/1.0
I. cf. praetervisa EL7206
100/1.0
Inocybe sp. DB3-6-13-3
100/1.0
I. krieglsteineri DB29-9-15-1-Zinke
89/0.99
I. krieglsteineri EL202_09
I. saliceticola Kokkonen & Vauras 19738F holotype
I. substellata Kühner73_218 holotype
I. strickeriana sp. nov. KR-M-0044133
I. strickeriana sp. nov. KR-M-0044126
100/1.0
I. strickeriana sp. nov. KR-M-0044132
I. strickeriana sp. nov.
-/0.93
I. aff. xanthomelas PAM07062202
93/1.0
I. strickeriana sp. nov. KR-M-0044749 holotype
I. salicis DB14-6-15-1
98/1.0
I. salicis PAM07051802
100/1.0
I. salicis DB1-6-12-2
98/-
I. populea TAKK15655 paratype
100/1.0
I. lacunarum TUR-A 171771 holotype
I. hirculus TUR-A 2577 holotype
I. xanthomelas DB15-9-15-3
100/1.0
I. leucoblema SEB97-09
100/1.0
I. leucoblema SM2324
outgroup (Mallocybe clade)
I. arthrocystis EL9207
0.05

◀ **Fig. 1** Phylogenetic tree of ITS sequences (encompassing partial internal transcribed spacer 1, 5.8S rDNA, and partial internal transcribed spacer 2) inferred using the Maximum Likelihood criterion. Numbers on the branches indicate Maximum Likelihood bootstrap support and posterior probabilities from Bayesian inference greater than 50% and 0.75, respectively. The tree is rooted with three specimens from the *Mallocybe* clade. The bar indicates the amount of substitutions per site

While phylogenetically clearly distinct, *I. pelargonium* is morphologically similar to the newly described *I. curcumina*. However, the pileus of the latter has a mottled appearance and is less coppery and greasy than in the former species, and the spores and hymenial cystidia are larger on average. *Inocybe hirtelloides* is phylogenetically related to these species but it can be distinguished from both on the basis of its shorter hymenial cystidia and normally long and narrow caulocystidia.

Inocybe leochroma sp. nov. is a species with rather small spores and both morphologically and phylogenetically closely related to *I. angulatosquamulosa*, from which it differs by a brighter "leonine" and less speckled pileus, by a "rough" pruina of the stipe, larger spores and smaller hymenial cystidia, and by its affinity to coniferous trees.

Even though the molecular analysis of the type of *I. terrifera* failed, it can be readily distinguished from the related species *I. splendentoides* and *I. serotina*, e.g. by different pileus colour and habitat—*I. splendentoides* preferring moist locations with *Salix* nearby and *I. serotina* growing on sandy soils, in particular dunes, while *I. terrifera* preferably grows in park-like terrain, often with *Quercus*. In addition, the species differ in the reaction of hymenial cystidia with KOH. *Inocybe splendentoides* and *I. serotina* differ by seven base pairs and three gaps.

The phylogenetic analysis revealed that *I. stenospora* does not belong to the subgenus *Mallocybe*, but to the subgenus *Inocybe* and therein to the group around *I. lanuginosa*, from which other species it differs morphologically mainly by its long projectile-shaped spores.

The species *I. strickeriana* and *I. villosa*, which are introduced in this study, group together with *I. salicis*, *I. lacunarum* and *I. populea*. *Inocybe strickeriana* apparently prefers habitats with *Quercus* spp., while *I. villosa* is a species of alluvial terrain or at least moist ground with *Salix* spp. and species of *Alnus*. One sequence labelled "*I.* cf. *praetervisa*" groups together with *I. villosa*; however, this was erroneously labelled that way (Esteve-Raventós et al. 2016).

Taxonomy *Inocybe derbschii* Schwöbel & Stangl 1982

Figure 2

Pileus 15–45 (50) mm wide, campanulate or subconical when young, then becoming broadly convex to expanded; when young sometimes without, but mostly with a more or less pronounced broad umbo, sometimes depressed around the centre, margin incurved or deflexed to almost or entirely straight, but when old also uplifted, regular or slightly undulate, margin sometimes deeply torn in older specimens; some, mostly young, specimens with ample remnants of a greyish velipellis especially at the centre; colour ranging from light coffee-brown to chestnut-brown, greyish brown to dark brown, sometimes with a faint reddish tinge (Mu 10YR 5/4–5/6, 4/3–4/6, 3/4–3/6, or 7.5YR 4/4–4/6, 3/4), in one collection also with faint olive hue; surface glabrous or finely felty when young, then becoming rimulose or innately fibrillose, sometimes also breaking up or being minutely squamulose in and around the centre; in some basidiomata pileipellis disappearing towards margin with age, as a result are lighter in colour and thus appearing subhygrophanous; young basidiomata with remnants of a cortina. **Lamellae** moderately distant (ca. 40–60, l: 1–3), almost free to adnate, even to (sub)ventricose, whitish when young, then greyish to greyish-brownish; edge even, whitish. **Stipe** 30–60 (70) × 3–7 mm, cylindrical to slightly widening towards the base, base seldom with an inconspicuous small bulb, glabrous, when young entirely covered with whitish tissue, vanishing with age, and stipe thus often appearing streaky flesh-coloured or reddish brown; pruinose in the upper half of the stipe, but rather sparse towards the middle. **Context** whitish in pileus and stipe, cortex of stipe with brownish tinge. **Smell** faintly aromatical to subspermatical, at least when cut. **Colour of exsiccata** pileus brown to dark brown (Mu 10YR 3/4–3/6, 3/2–3/3), in the centre also darker (Mu 10YR 2/1–2/2), lamellae somewhat lighter in colour, stipe with slight greyish tinge, but no obvious darkening or blackening with drying.

Spores 7.5–11.3 μm (av. 9.6 μm, SD 0.8 μm) × 4.7–7.3 μm (av. 5.8 μm, SD 0.4 μm); $Q = 1.3–1.9$ (av. 1.6, SD 0.2) ($n = 120$ from 3 coll.), smooth, (sub)amygdaloid, apex obtuse to subacute, seldom also (sub)papillate, sometimes with a rather indistinct pseudopore. **Basidia** 25–30 × 7–10 μm, usually 4-spored, seldom also 2-spored, and then spores up to 13.3 μm. **Lamellae edges** sterile, composed of cheilocystidia and numerous hyaline, thin-walled paracystidia, mostly (sub)clavate or subglobose, but occasionally also in intermediate forms with slightly thick walls (− 0.5 μm). **Pleurocystidia** 36–72 μm (av. 54 μm, SD 7.4 μm) × 10–18 μm (av. 15 μm, SD 3.1 μm); $Q = 2.4–5.8$ (av. 3.7, SD 0.8) ($n = 45$ from 3 coll.), (sub)utriform, (sub)fusiform or (sub)cylindrical, walls sometimes not reaching the apex and sometimes slightly undate, usually with rather short pedicel, apex usually with rather small crystals, walls 0.5 (bulge)–3.5 μm (neck) thick, weak reaction with 3% KOH. **Cheilocystidia** similar in appearance and size, in one collection (DB12-10-13-11) sometimes with brownish content and resinous exudate around the apex and then reminding of cystidia of *I. leptocystis* G.F. Atk. **Pileipellis** consisting of an epicutis made up of parallel hyphae 4–10 (13) μm wide, with a finely encrusted and parietal yellowish-brownish pigment, subcutis with wider, often shorter and paler elements, up to 25 μm wide, epicutis in young basidiomata sometimes

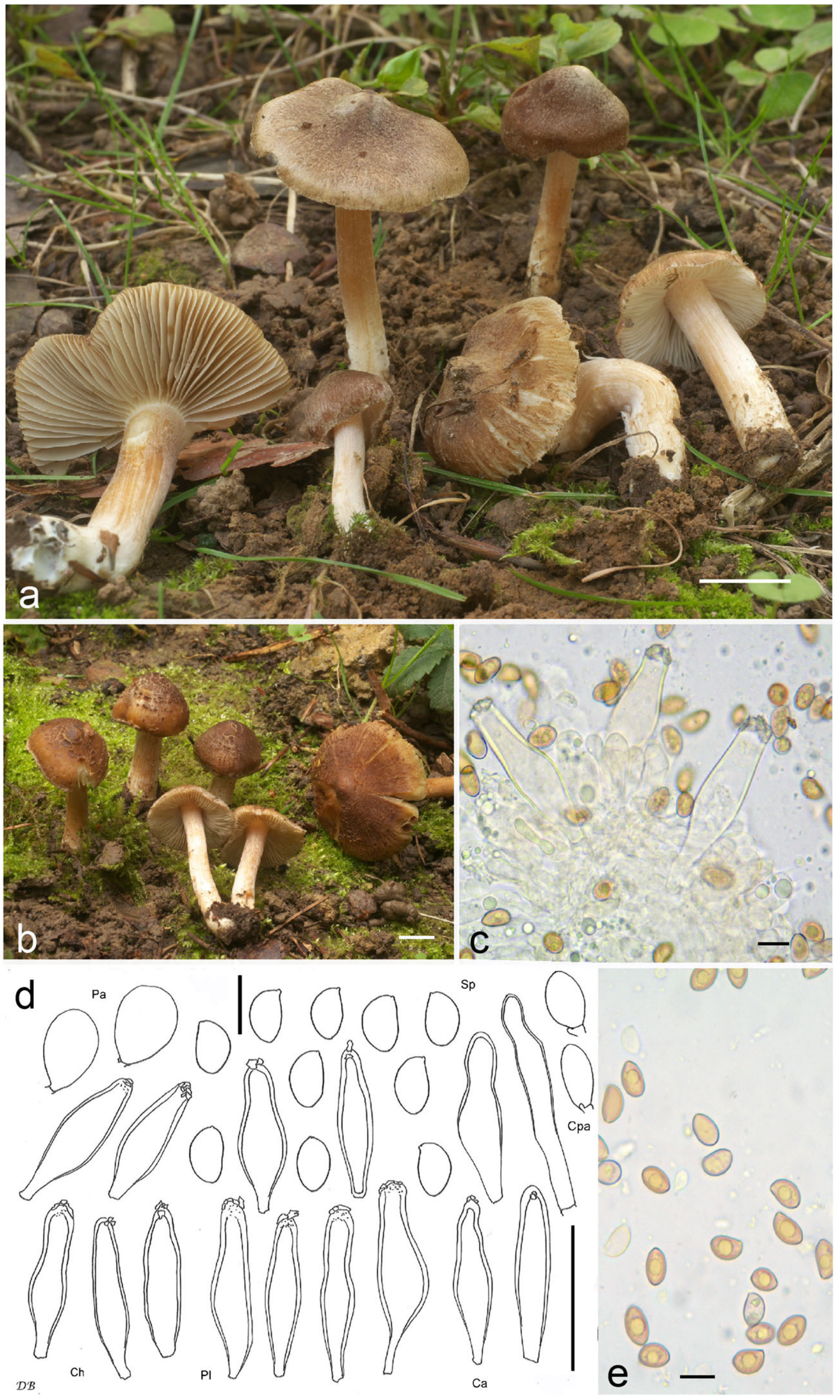


Fig. 2 *Inocybe derbschii* **a** DB1-8-14-11, scale bar: 1 cm. **b** DB12-10-13-11, scale bar: 1 cm. **c** Hymenial cystidia (DB1-8-14-11), scale bar: 10 µm. **d** Microscopical characters (DB1-8-14-11), Ca Caulocystidia, Cpa Cauloparacystidia, Ch Cheilocystidia, Pa Paracystidia, Pl Pleurocystidia, Sp Spores; scale bar spores 10 µm, scale bar cystidia 50 µm. **e** Spores (DB1-8-14-11), scale bar 10 µm

covered with thin hyaline hyphae, with scattered free ends (belonging to velipellis remnants). **Stipitipellis** consisting of a cutis bearing numerous bundles of metuloid caulocystidia mainly at the apex, but more sparsely down to the middle of the stipe, intermixed with subclavate or subcylindrical, thin-walled paracystidia. **Caulocystidia** 40–75 × 10–15 (20) µm, (sub)fusiform, (sub)cylindrical or (sub)utriform or even (sub)clavate, walls often undate, apex with or without small crystals, walls 0.5 (bulge)–2.5 µm (neck) thick, weak reaction with 3% KOH. **Clamp-connections** abundant in all tissues.

Habitat and known distribution: The type was collected in Germany, and up to now, collections verified by ITS sequencing are only known to us from Germany (Heidelberg and Karlsruhe) and from Estonia, from the island Saaremaa (UNITE database UDB024611; Saare maakond, Triigi, 58.59031670 22.71351670, leg. Vello Liiv, 24 Sep 2015, deposited in the herbarium of Tartu, TU120277). The German collections were collected in urban surroundings, on a churchyard, on a meadow near a churchyard, on park-like terrain on lawn and in a garden on lawn. Triigi is a very small port with just a few inhabitants and only very few trees. On the photograph of the collection lawn-like grass can be seen as well as some needles of *Pinus*. Conifers were growing near four of the German collections as well, whereas the type collection was associated exclusively with broadleaf trees.

Phenology: From May to October.

Collections studied: GERMANY, Baden-Württemberg, Rhein-Neckar-Kreis, Bammental, near churchyard, TK25 6618/2, alt. 147 m, meadow with *Picea abies*, 30 May 2013, leg. *D. Bandini*; det. *D. Bandini & B. Oertel* (DB30-5-13-2, BAN1478, MH366593).- Ibidem, in some distance of former location, alt. 146 m, lawn with *Picea abies,* 12 Oct 2013, leg. *D. Bandini*; det. *D. Bandini & B. Oertel* (KR-M-0042331, DB12-10-13-11, BAN563).- Baden-Württemberg, Heidelberg, war cemetery, TK25 6618/1, alt. 292 m, lawn with *Quercus robur*, *Pinus sylvestris*, *Fagus sylvatica*, 1 Aug 2014, leg. *D. Bandini*; det. *D. Bandini, B. Oertel & U. Eberhardt* (KR-M-0042330, DB1-8-14-11, BAN674).- Bayern, Göggingen near Augsburg, 2 Jun 1970, leg. *J. Stangl*, paratype (erroneously referred to as isotype in Stangl and Veselský 1973) of *I. pseudodestricta* (PRM-716232, MG012469).- Rheinland-Pfalz, Mainz, Mainz-Lerchenberg, TK25 6015/1, alt. 235 m, *Picea abies*, *Pinus* sp., 25 Oct 2015, leg. *D. Bandini*; det. *D. Bandini & B. Oertel* (KR-M-0042367, DB25-10-15-3, BAN1909, MH366592).

For holotype of *I. derbschii* see below.

Comments: *Inocybe derbschii* is characterised by a rather stout habit, a finely felt-like to innately fibrillose, brown pileus, a stipe that is pruinose only near the apex of the stipe, spores that are on average smaller or not much larger than 10 μm and hymenial cystidia on average shorter than 60 μm, most often without or with only short neck. In some basidiomata the pileipellis vanishes with age towards the margin and the surface appears therefore subhygrophanous. Some pilei show an olivaceous hue. Occasionally greyish remnants of the velipellis are to be seen at the umbo. A photograph of an Estonian collection shows almost glabrous uniformly dark brown pilei and, in contrast, almost whitish lamellae, and the same is the case in one of our own collections (DB25-10-15-3). Thus, one feature, that is stressed in the original description of *I. derbschii,* the olive tinge in the pileus colour, does not seem to be a constant trait. According to Schwöbel and Stangl (1982) the species has no further conspicuous characteristics and is placed close to *I. pseudodestricta* Stangl & J. Veselský and *I. virgatula* Kühner. In fact, the paratype of *I. pseudodestricta*, deposited in Prague, has turned out to be *I. derbschii*, both morphologically and according to its ITS.

The microscopic details of the examined collections match quite well with those of the type collection, only the cystidia of the latter are on average a little wider. The spores of the paratype of *I. pseudodestricta* are on average 10.2 (SD 0.7) × 5.7 (SD 0.4) μm ($n = 40$) and thus a bit larger and slightly narrower, yet the cystidia are similar in size and appearance.

It seems quite likely that *I. derbschii* is not a rare species, but that it has previously been overlooked. It can, for instance, be mistaken for *I. pseudodestricta, I. fuscidula* Velen. or, when a greyish velipellis is present, for *I. griseovelata* Kühner. The hymenial cystidia of the two latter named species however are longer, and those of *I. griseovelata* often are (sub)cylindrical and the spores are on average larger (Kuyper 1986). *Inocybe pseudodestricta* often has a shiny "buttery" pileus of coppery reddish colour with diverging fibres that do not disappear with age towards margin, on average larger hymenial cystidia and especially longer caulocystidia and narrower spores. Molecularly, too, *I. derbschii* is not contiguous to any of the mentioned species but to species with often more or less pinkish stipes so as *I. grammopodia* Malençon and the species around *I. pusio* P. Karst.

Inocybe pseudodestricta Stangl & J. Veselský 1973
Figure 3

Pileus 20–45 (60) mm wide, conical or campanulate when young, then convex or almost applanate, mostly with a pronounced broad umbo, margin involute, inflexed or deflexed when young, later straight or even uplifted; young basidiomata sometimes loosely covered all over with a greyish velipellis and then almost shiny silvery or only greyish in the centre of the pileus; colour mostly reddish chestnut-brown or coppery-brown in different shades (Mu 5YR 3/3–3/4, 4/4–4/6, 5/6–5/8), sometimes with a greyish tint, seldom greyish brown with or sometimes without a very slight reddish hue (Mu 10YR 4/4–4/6, 7.5YR 4/2–4/4, or 5YR 4/2–4/3); surface at the umbo often slightly verrucose to subsquamulose, outwards glabrous when young, then rimose or minutely lanose, but mostly innately fibrillose with appressed but diverging fibres, showing the lighter context of the pileus beneath, often—but not always—with a buttery shiny appearance; margin of young specimens often with remnants of a whitish cortina. **Lamellae** moderately crowded (ca. 40–60, l: 1–3 (5), often thickly, (sub)ventricose, narrowly to broadly adnate, sometimes emarginate with decurrent tooth, first whitish or pale creamy or greyish to light brown, then blotchy rusty-brown, sometimes with olive tint, edge fimbriate, whitish to concolorous. **Stipe** 20–65 × 3–10 mm, cylindrical to slightly thickening towards the base or with subbulbous base, when young covered with whitish tissue, later glabrous, or streaky flesh-coloured or yellowish to brownish, sometimes with slightly reddish hue, especially near the apex; pruinose only in the upper half of the stipe. **Context** whitish in pileus and stipe, slightly flesh-coloured at cortex of stipe. **Smell** spermatical, at least when cut. **Colour of exsiccata** pileus different shades of brown, with or without reddish tinge (Mu 7.5 YR 4/2–4/4, 5YR 3/3–3/4,

Fig. 3 *Inocybe pseudodestricta* **a** DB17-8-15-13, scale bar: 1 cm. **b** DB20-8-15-12, scale bar: 1 cm. **c** Pleurocystide (DB17-8-15-13), scale bar 10 µm. **d** Microscopical characters (DB20-8-15-16), Ca Caulocystidia, Cpa Cauloparacystidia, Ch Cheilocystidia, Pa Paracystidia, Pl Pleurocystidia, Sp Spores; scale bar spores 10 µm, scale bar cystidia 50 µm. **e** Spores (DB17-8-15-13), scale bar 10 µm

or 10YR 4/3–4/6), in the centre sometimes also darker (Mu 10YR 2/1–2/2), lamellae and stipe somewhat lighter in colour, no obvious darkening or blackening with drying.

Spores 7.6–12.2 µm (av. 9.7 µm, SD 1.0 µm) × 4.8–6.8 µm (av. 5.6 µm, SD 0.4 µm); Q = 1.4–2.0 (av. 1.7, SD 0.1) (*n* = 120 from 3 coll.), smooth, (sub)amygdaloid, sometimes with indistinct suprahilar depression, apex subconical. **Basidia** 25–30 × 7–10 µm, generally 4-spored. **Lamellae edges** sterile, composed of cheilocystidia and numerous hyaline (sub)clavate or subglobose, thin-walled paracystidia. **Pleurocystidia** 35–80 µm (av. 59 µm, SD 9.9 µm) × 9–23 µm (av. 17 µm, SD 9.9 µm); Q = 1.9–5.5 (av. 3.6, SD 0.7) (*n* = 45 from 3 coll.), mainly (sub)fusiform or (sub)lageniform, seldom also (sub)cylindrical, (sub)utriform or even (sub)clavate, sometimes with tapering walls at the neck, without or with only short pedicel, apex usually crystalliferous, walls 0.5 (bulge)–2 (seldom −4.5) µm (neck) thick, weak reaction with 3% KOH. **Cheilocystidia** similar in appearance and size.

Pileipellis consisting of an epicutis made up of parallel hyphae 6–12 (15) µm wide, with finely encrusting and parietal yellowish-brownish pigment, subcutis with wider and paler elements, up to 20 µm wide, epicutis in young basidiomata sometimes covered with thin hyaline hyphae, with scattered free ends (belonging to velipellis remnants). **Stipitipellis** consisting of a cutis bearing numerous bundles of caulocystidia in the upper half of the stipe, intermixed with subclavate or subcylindrical paracystidia. **Caulocystidia** 35–115 × 10–15 µm, usually long and slim, (sub)cylindrical, (sub)fusiform, (sub)lageniform, (sub)utriform or even (sub)clavate, sometimes with tapering walls, apex usually crystalliferous, walls 0.5 (bulge)–1.5 (2) µm (neck) thick, weak reaction with 3% KOH. **Clamp-connections** abundant in all tissues.

Habitat and known distribution: With broadleaf and coniferous trees on pathsides, on dry ground but also on moist sandy-pebbly terrain near lakesides. According to the original description (Stangl and Veselský 1973) preferably with *Quercus*, *Betula* and *Pinus*. The species is obviously widespread, since apart from Germany, the Czech Republic, the Netherlands, and Finland, it is confirmed through the UNITE data base (Kõljalg et al. 2013) also for further European countries such as France, Russia (Ural), and is also known from Canada. Kobayashi (2005) describes the species also from Japan. The only trees indicated with the sequences in the UNITE database are *Salix arctica*, *Salix caprea,* and *Populus alba*.

Phenology: Own collections from May to August.

Collections studied: FINLAND, Koillismaa, Kuusamo, Oulanka National Park, near Research Station, alt. ca. 165 m, roadside with *Pinus sylvestris*, *Betula* sp., *Picea abies*, 17 Aug 2015, leg./det. *D. Bandini, J. Vauras & B. Oertel* (KR-M-0042343, DB17-8-15-6, BAN1046).- Ibidem, 17 Aug 2015, leg./det. *D. Bandini, J. Vauras & B. Oertel* (KR-M-0042344, DB17-8-15-13, BAN1050, MH366595).- Koillismaa, Kuusamo, Oulanka National Park, Runsuniitty, roadside with *Pinus sylvestris*, *Betula* sp., *Picea abies*, 18 Aug 2015, leg./det. *D. Bandini, J. Vauras & B. Oertel* (KR-M-0042345, DB18-8-15-18, BAN1067).- Koillismaa, Kuusamo, Oulanka National Park, Ampumavaara, roadside with *Pinus sylvestris*, *Betula* sp., *Picea abies*, 20 Aug 2015, leg./det. *D. Bandini, J. Vauras & B. Oertel* (KR-M-0042346, DB20-8-15-12, BAN1097).- Ibidem*,* 20 Aug 2015, leg./det. *D. Bandini, J. Vauras & B. Oertel* (KR-M-0042347, DB20-8-15-16, BAN1100).- Ibidem*,* 21 Aug. 2015, leg./det. *D. Bandini, J. Vauras & B. Oertel* (KR-M-0042348, DB21-8-15-22, BAN1114).- Ibidem*,* 22 Aug 2015, leg./det. *D. Bandini, J. Vauras & B. Oertel* (KR-M-0042349, DB22-8-15-13, BAN1125).- Koillismaa, Kuusamo, Oulanka National Park, Liikasenvaara, lawn near house with *Pinus sylvestris*, *Betula* sp., *Picea abies*, 25 Aug 2015, leg./det. *D. Bandini, J. Vauras & B. Oertel* (KR-M-0042350, DB25-8-15-13, BAN1167, MH366596).- NETHERLANDS, Gelderland, Druten, Deest, alt. ca. 4 m, moist gravelly shore of lake with *Salix caprea* and *Salix* sp., 6 Mai 2012, leg./det. *D. Bandini & B. Oertel* (KR-M-0043223, DB6-5-12-10, BAN102, MH366594).

For holotype of *I. pseudodestricta* see below.

Comments: *Inocybe pseudodestricta* is characterised by a reddish or chestnut-brown more or less buttery shiny pileus, an innately fibrillose covering with diverging fibres showing the lighter context below, and subcylindrical usually very long caulocystidia (> 110 µm), with occasionally tapering walls. Young basidiomata, however, may entirely or partially be covered with a velipellis and therefore appear almost silvery. One of our collections shows extremely long and undate necks of hymenial cystidia (DB6-5-12-10). Thus, *I. pseudodestricta* is not always easy to recognise. The suggestion of Stangl and Veselský (1973), that *I. pseudodestricta* most probably is a thermophilous species, is now that it was found several times in Northern Finland (Oulanka National Park), to be denied. Macroscopically certain collections of *I. pseudodestricta* could be mistaken for *I. derbschii* or also for *I. griseotarda* Poirier, a rather frequent species, often associated with *Pinus sylvestris* (Bizio et al. 2017). The texture of the pileus of the named species, however, is different, the buttery shiny appearance is missing, the caulocystidia are not so long and of a different shape, and the hymenial cystidia of *I. derbschii* are shorter. Bon (1997) has listed *I. pseudodestricta* as synonym of *I. destricta* (Fr.) Quél. in *I.* subsect. *Tardinae* Bon. *Inocybe pseudodestricta* shares 98–99% sequence identity to sequences from specimens identified as *I. abjecta*, *I. glabrescens*, and *I. flocculosa.* However, to name only some major differences, *I. abjecta* has larger spores, the stipe of *I. glabrescens* is entirely pruinose, and the pileus of *I. flocculosa* is more fibrillose-lanose and the hymenial cystidia show a strong reaction with KOH.

Inocybe furfurea Kühner 1955

= *I. rufotacta* Schwöbel and Stangl 1982

≡ *I. furfurea* var. *rufotacta* (Schwöbel & Stangl) Kuyper 1986

≡ *I. furfurea* f. *rufotacta* (Schwöbel & Stangl) Gminder 2010

= *I. sandrae* Zitzmann 2002

Figure 4

Pileus 5–30 (40) mm wide, subconical, subcampanulate, then convex to expanded, often with a more or less pronounced broad umbo, sometimes depressed around the umbo, margin at first inflexed to deflexed, then straight or even uplifted, not seldom undate; young basidiomata sometimes with remnants of a greyish velipellis; colour varies considerably from collection to collection from ochraceous, ochraceous orange-brown to brown or red-brown in different shades with a more or less intense reddish or cinnamon or amber tinge (Mu 7.5YR 5/6–5/8, 3/4–3/6, 5YR 5/6–5/8, 4/4–4/6, or 10YR 6/6–6/8), at the umbo often considerably

Fig. 4 *Inocybe furfurea* **a** DB25-5-13-9, scale bar: 1 cm. **b** DB4-7-12-3, scale bar: 1 cm. **c** Pleurocystidia (DB4-7-12-3), scale bar 10 µm. **d** Microscopical characters (DB2-6-13-3), Ca Caulocystidia, Cpa Cauloparacystidia, Ch Cheilocystidia, Pa Paracystidia, Pl Pleurocystidia, Sp Spores; scale bar spores 10 µm, scale bar cystidia 50 µm. **e** Spores (DB4-7-12-3), scale bar 10 µm

darker, there up to blackish brown (Mu 2.5YR 2.5/2–2.5/4, 5YR 4/4–4/6, 3/3–3/4), in some collections—due to weather conditions or when older—towards the margin much lighter; surface at the umbo at first mostly glabrous to finely velvety, later grindy, cracked and/or fissured, towards the margin glabrous, finely rimulose or rimose to innately fibrillose when young, with age also subsquamulose to squamulose; margin often undate and rimulose to innately fibrillose with appressed fibres; seldom with faint remnants of a cortina. **Lamellae** rather distant (ca. 25–40, l: 1–3), thickly, adnexed, adnate or emarginate with decurrent tooth, (sub)ventricose, long time whitish, then greyish, greyish-brownish, later especially towards the margin of the pileus also greyish ochraceous, sometimes with brownish, rusty or reddish spots, especially when bruised; edge fimbriate, whitish. **Stipe** 15–35 × 2–4 (5) mm, often quite straight and rigid and cylindrical, but in some collections also flexuous and/or twisted or flattened, base not thickened to slightly thickened or subbulbous, when young entirely covered with fine whitish tissue, later more or less streaky to glabrous from slightly flesh-coloured to intensely reddish or reddish brown, base often covered with whitish mycelium; pruinose mostly—though sometimes— very—on the entire length of the stipe. **Context** whitish or watery greyish in the pileus, flesh-coloured or reddish to reddish brown in the stipe, especially near the apex and in the cortex of the stipe. **Smell** (sub)spermatical, at least when cut. **Colour of exsiccata** pileus brown to dark brown (Mu 5YR 4/4–4/6, 3/3–3/4, 7.5YR 3/4), in the centre sometimes also slightly darker, lamellae lighter in colour, stipe in some collections with more or less intense reddish tinge, no obvious darkening or blackening with drying.

Spores 6.6–10.6 μm (av. 8.2 μm, SD 0.8 μm) × 4.6–6.3 μm (av. 5.4 μm, SD 0.4 μm); Q = 1.3–1.9 (av. 1.5, SD 0.1) (*n* = 120 from 3 coll.), smooth, subelliptic or (sub)amygdaloid, apex (sub)obtuse to subacute or with papilla. **Basidia** 20–33 × 7–10 μm, usually 4-spored, but occasionally also 2-spored, and then spores up to 12 μm. **Lamellae edges** sterile, composed of cheilocystidia and numerous hyaline, thin-walled paracystidia, normally (sub)clavate or subglobose, but also in intermediate forms. **Pleurocystidia** 42–78 μm (av. 54 μm, SD 7.4 μm) × 11–25 μm (av. 16 μm, SD 3.1 μm); Q = 2.5–4.8 (av. 3.7, SD 0.7) (*n* = 45 from 3 coll.), differently shaped in every collection, often (sub)cylindrical, but also (sub)fusiform, (sub)utriform or even (sub)clavate, and not seldom deformed or sac-shaped, sometimes with a truncate base and so either without or with only short pedicel, apex usually crystalliferous, walls 0.5 (bulge)–1.5 (2.5) μm (neck), sometimes slightly undate; weak reaction with 3% KOH. **Cheilocystidia** similar in appearance and size, but in some basidiomata somewhat narrower and more variably shaped. **Pileipellis** consisting of an epicutis made up of parallel hyphae 4–10 μm wide, with finely encrusting and parietal brownish pigment, subcutis with wider and paler elements, up to 20 (25) μm wide. **Stipitipellis** consisting of a cutis usually bearing numerous bundles of caulocystidia at the apex or descending to the middle, but rather sparsely—also down to the base of the stipe, intermixed with subclavate or subcylindrical, sometimes also catenate thin-walled cauloparacystidia. **Caulocystidia** 50–90 × 10–20 μm, (sub)cylindrical, (sub)fusiform, (sub)lageniform or deformed, apex with or without crystals, walls 0.5 (bulge)–2.0 μm (neck), usually though rather thin-walled; weak reaction with 3% KOH. **Clamp-connections** abundant in all tissues.

Habitat and known distribution: Usually in large numbers on the lawn in parks or cemeteries, occasionally also on sandy ground near rivers or lakes, but not in moist terrain, mostly with different broadleaf trees such as *Quercus*, *Tilia*, and *Salix*, *Populus*, etc., but also with conifers nearby. The type collection was found in France, and the species probably is common also in countries other than Germany, Austria, and France. Sequences putatively belonging to *I. furfurea*, though only from ectomycorrhiza samples, not from basidiomata, were published from Italy and Argentina, in the latter case with *Salix humboldtiana*.

Phenology: Quite early in May or June, but also found in October at the same locations as in spring and summer.

Collections studied: AUSTRIA, Oberösterreich, Braunau am Inn, Weng im Innkreis, ÖK25V 3327-Ost, alt. ca. 400 m, wayside with *Picea abies* and different broadleaf trees, 13 Aug 2014, leg. *D. Bandini*, *J. Christan* & *L. Quecke;* det. *D. Bandini* (KR-M-0042336, DB13-8-14-18, BAN705).- GERMANY, Baden-Württemberg, Heidelberg, war cemetery, TK25 6618/1, alt. 290 m, lawn with *Quercus robur*, *Pinus sylvestris*, *Fagus sylvatica*, 4 Jul 2012, leg./det. *D. Bandini* (KR-M-0042337, DB4-7-12-3, BAN213, MH366607). - Ibidem, 18 Jul 2014, leg./det. *D. Bandini* (KR-M-0042338, DB18-7-14-4, BAN650).- Baden-Württemberg, Karlsruhe, Erzbergerstraße, TK25 6916/3, alt. 114 m, lawn with *Quercus* sp., *Fagus sylvatica*, *Betula pendula*, 2 Jun 2013, leg./det. *D. Bandini* & *B. Oertel* (KR-M-0042339, DB2-6-13-3, BAN372, MH366608).- Bayern, Rottal-Inn, Simbach a. Inn, TK25 7744/1, alt. 360 m, lawn with *Tilia* sp., 16 Aug 2014, leg./det. *D. Bandini* (KR-M-0042340, DB16-8-14-16, BAN619).- Rheinland-Pfalz, Rhein-Pfalz-Kreis, Neuhofen, Kistnerweiher, TK25 6515/4, alt. 90 m, dry sandy riverside with *Salix* sp., *Populus* sp., *Betula pendula*, *Pinus sylvestris*, 25 May 2013, leg./det. *D. Bandini* & *B. Oertel* (KR-M-0042341, DB25-5-13-9, BAN388, MH366609).- Rheinland-Pfalz, Rhein-Pfalz-Kreis, Böhl-Iggelheim, TK25 6616/3, alt. 105 m, dry sandy wayside with *Pinus sylvestris*, *Quercus* sp., *Corylus avellana*, 29 Jun 2013, leg./det. *D. Bandini* & *B. Oertel* (KR-M-0042342, DB29-6-13-3, BAN396) (only those of totally 22 collections of which a DNA extraction has been prepared are listed here).

For holotypes of *I. furfurea* and *I. rufotacta* as well as isotype of *I. sandrae* see below.

Comments: *Inocybe furfurea* is characterised by mostly rather small or slender basidiomata, often conspicuous red-brown or amber- or cinnamon-tinged pileus colours, with typically fissured, grindy or cracked surface mainly on and around umbo, conspicuous colour contrast of stipe with whitish lamellae in young basidiomata, rather distant lamellae and often but not always by reddish spots on the lamellae when bruised. The spores are less than 9 μm on average (so also Stangl and Veselský 1976).

Inocybe furfurea is sometimes referred to as either *I. furfurea, I. rufotacta* (e.g. Ferrari 2006), *I. furfurea* var. *rufotacta* (Kuyper 1986; Bušek 2012) or *I. furfurea* f. *rufotacta* (Gminder 2010). The comparative examination of both types has shown almost identical microscopic details and, in addition, they were indistinguishable on the basis of ITS sequences. However, the name-giving phenomenon of *I. rufotacta*, the reddening of bruised lamellae, is not a constant feature—not even within the same collection. The comparative molecular analysis supports the opinion that both species are identical and thus should be treated as synonyms.

According to Schwöbel and Stangl (1982), caulocystidia can only rarely be found at the apex of the stipe in *I. rufotacta*. But a thorough examination of the type collection of *I. rufotacta* has revealed the existence of sparse metuloid caulocystidia even near the base of the stipe—which fits quite well to our observations regarding other collections of *I. furfurea*. The type material of *I. furfurea* consists of small portions of pilei and only a part of a stipe. Kühner (1955) describes the pruina towards the base as rare and "éparse", an indication that matches with our own observations. The average value of the spores of the lectotype of *I. furfurea* is slightly higher, but otherwise the microscopic details fit well with those of our own collections.

In his Bavarian monograph Stangl (1989) has described a smooth-spored species as *Inocybe* sp., which later has been described as a new species and named *I. sandrae* by Zitzmann (2002). The photograph of the type of *I. sandrae*, the drawing of Stangl (1989) as well as the descriptions are well in line with typical characteristics of *I. furfurea* listed above: reddish brown pileus, darker centre of pileus, broad umbo, towards margin smooth (velvetlike) but in centre subsquamulose surface of pileus, colour contrast between reddish stipe and whitish lamellae, rather distant lamellae. Besides, the basidiomata are described as quite small (up to max. 4 cm) and the form of the cystidia is alike. Only the spores are, on average, slightly larger. Furthermore, Stangl himself points out the similarity of this *Inocybe* sp. with *I. furfurea.* Our re-examination of the isotype of *I. sandrae* revealed sparse metuloid caulocystidia below the centre of the stipe. In accordance with the microscopic features, the ITS of *I. furfurea* is identical with that of *I. sandrae* as well as with the ITS of *I. rufotacta.* Thus, we conclude that *I. sandrae* should be regarded as a synonym of *I. furfurea*.

Inocybe venustissima Bandini & B. Oertel sp. nov**.**

Figure 5

MycoBank number: MB 827575, ITS barcode GenBank: MH366625.

Etymology: "venustissima", Latin, "most beautiful, lovely".

Short description: Rather large species with a honey-yellow or light brown smooth to rimose pileus and a big bulb. The stipe is either only in the upper half or entirely pruinose, the spores are smooth, measuring 7.3–10.9 × 4.6–6.7 μm, the hymenial cystidia are mainly (sub)fusiform, pleurocystidia measuring 35–76 × 11–23 μm.

Diagnosis: *Inocybe venustissima* is similar to *I. chalcodoxantha* Grund & D.E. Stuntz, but can be distinguished from this species by its larger size, smaller spores, differently formed hymenial cystidia, and on the basis of ITS sequence data.

Holotype: AUSTRIA, Tirol, Imst, Silz, Kühtai (Krainhof), ÖK25V 2221-Ost, 10.9857 E 47.2185 N, alt. 1795 m, northern slope, moist place with springs, with *Picea abies*, *Pseudotsuga menziesii*, *Pinus cembra*, 22 Aug 2012, leg. D. Bandini & B. Oertel (holotype KR-M-0042322; isotypes DB22-8-12-8, BAN230, SMNS-STU-F-0900968, TUR-A 199166).

Detailed description

Pileus 20–50 mm wide, when young glandiform or conical, then subcampanulate to convex or expanded, with acute or broad umbo, margin slightly inflexed when young, then deflexed to straight or even uplifted and then often depressed around the centre; when young with whitish-greyish patches of a velipellis, later still sometimes visible in the centre of the pileus; colour honey-yellow, yellowish ochraceous to ochraceous (Mu 10YR 8/6–8/8, 7/6–7/8), or ochraceous-brownish to light hazel-brown (Mu 10YR 6/6–6/8, 5/6–5/8) with or without slightly golden or even olive hue; surface shiny glabrous or silky smooth to appearing almost waxy or as if a little moist, later some basidiomata also rimulose to rimose with appressed yet diverging fibres so that the lighter context beneath is visible. **Lamellae** moderately to rather crowded (ca. 60–80, l = 1–3), almost free to adnexed, even to (sub)ventricose, whitish when young, then greyish brown, also speckled with rusty blotches; edge fimbriate, sometimes undate, whitish. **Stipe** 30–100 × 3–7 mm, cylindrical, sometimes tortuous, base mostly with a quite huge roundish bowl-shaped bulb (up to 18 mm wide) with a recessed, not marginate border, stipe imbedded in the bulb, glabrous or finely grooved, when young covered with whitish tissue, then striate beige or flesh-coloured, later also glabrous light wood-coloured or with yellowish ochraceous tinge, bulb creamy, but also brownish, probably due to muddy earth; pruinose only in the upper half or on the entire length of the stipe, but rather sparse in the lower half. **Context** whitish in the pileus, creamy in stipe and bulb. **Smell** subnull or spermatical when cut. **Colour of exsiccata** pileus ochraceous brownish (Mu 10YR 5/6–5/8, 4/6), in older basidiomata also somewhat darker, lamellae lighter in colour or concolorous, stipe slightly darker, but never conspicuously darkening or blackening with drying.

Spores 7.3–10.9 μm (av. 8.9 μm, SD 0.8 μm) × 4.6–6.7 μm (av. 5.3 μm, SD 0.4 μm); Q = 1.4–2.0 (av. 1.7, SD 0.1) (*n* = 200 from 5 coll.), smooth, (sub)amygdaloid, mostly with suprahilar depression, apex (sub)conical, often with indistinct pseudopore. **Basidia** 20–30 × 8–13 μm, usually 4-spored, but sometimes also 2-spored, and then up to 12 μm, clavate. **Lamellae edges** sterile, composed of cheilocystidia and numerous hyaline, (sub)clavate, cylindrical or subglobose, thin-walled paracystidia. **Pleurocystidia** 35–76 μm (av. 50 μm, SD 8.9 μm) × 11–23 μm (av. 16 μm, SD 2.7 μm); Q = 1.9–4.8 (av. 3.1, SD 0.5) (*n* = 75 from 5 coll.), mostly (sub)fusiform, more seldom subutriform,

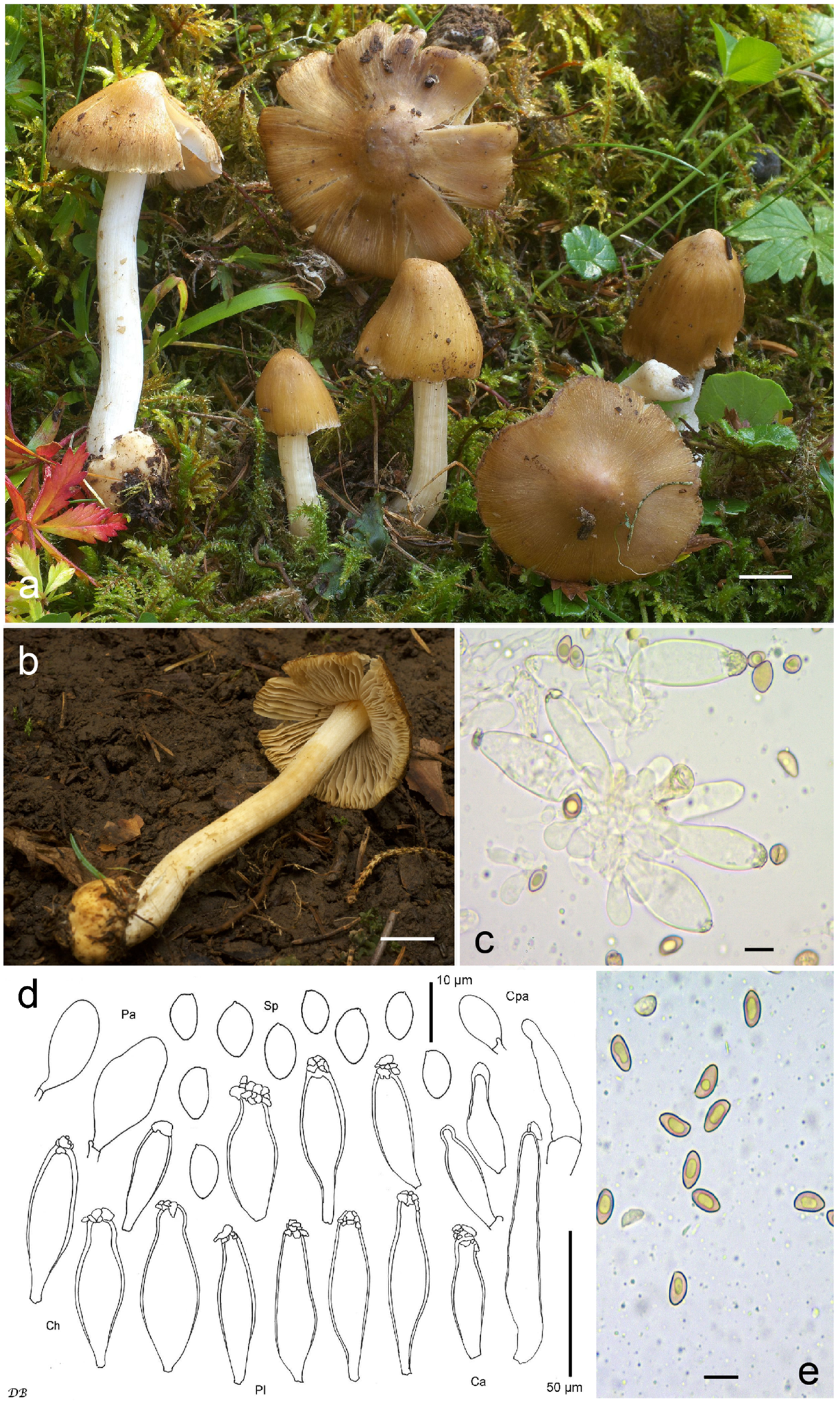


Fig. 5 *Inocybe venustissima*, holotype (DB22-8-12-8) **a**, **b** Basidiomata, scale bar 1 cm. **c** Cheilocystidia, scale bar 10 µm. **d** Microscopical characters, Ca Caulocystidia, Cpa Cauloparacystidia, Ch Cheilocystidia, Pa Paracystidia, Pl Pleurocystidia, Sp Spores; scale bar spores 10 µm, scale bar cystidia 50 µm. **e** Spores, scale bar 10 µm

subcylindrical or (sub)clavate, generally with none or only short neck, sometimes deformed or with undate walls, mostly with short, but sometimes with long pedicel, apex usually with crystals, not seldom as an amorphous lump, walls 0.5 (bulge)–1.5 (2.0) µm (neck) thick, weak reaction with 3% KOH. **Cheilocystidia** generally similar in appearance and size, sometimes a little shorter. **Pileipellis** consisting of an epicutis made up of parallel hyphae 4–8 (10) µm wide, with finely encrusting and parietal yellowish-brownish orange pigment, subcutis with wider and paler elements, up to 17 (20) µm wide, epicutis in young basidiomata sometimes covered with thin hyaline hyphae, with scattered free ends (belonging to velipellis remains). **Stipitipellis** consisting of a cutis bearing numerous bundles of metuloid caulocystidia in the upper half or on the entire length of the stipe, but then in the lower half rather sparse, intermixed with thin-walled colourless cauloparacystidia, partially in different intermediate states or catenate. **Caulocystidia** 35–80 × 10–20 µm, (sub)fusiform, (sub)lageniform, (sub)cylindrical, sometimes (sub)capitate, with or without crystals, walls 0.5 (bulge)–1.5 µm (neck) thick, weak reaction with 3% KOH. **Clamp-connections** abundant in all tissues.

Habitat and known distribution: All examined collections of *I. venustissima* were found in *Picea abies* forests in montane to subalpine regions in Austria on moist ground near small brooks or rivulets. Apparently, the species has also been found in Canada, British Columbia, on the Queen Charlotte Islands archipelago (GenBank HQ604526, F19796; UBC Herbarium, online), labelled "*I. auricoma*". The climate of these islands is oceanic with cool summers and mild winters. On the specimen label of UBC (F19796) it is noted: "wet hypermaritime". The only basidioma has been found with Western Hemlock (*Tsuga heterophylla*). Another unpublished collection is known from Sweden (GenBank AM88297, BJ910808, leg. *Bo Jansson*) and has been labelled "aff. *I. pelargonium*", but it is not known to us where exactly it was found. We are not aware of any further sequences or collections.

Phenology: In Europe up to now only found in August, the Canadian specimen was found in September (8 Sep 2006, by Oluna Ceska). The date of the Swedish collection is not known to us.

Additional collections studied: AUSTRIA, Salzburg, Tamsweg, road to Seetal, ÖK25V 3104-Ost, alt. 1230 m, moist terrain near small brook with *Picea abies,* 15 Aug 2013, leg. *U. Österle*; det. *D. Bandini & B. Oertel* (KR-M-0042323, DB15-8-13-17, BAN414, MH366626).- Ibidem, in ca. 500 m distance of former location, *Picea abies*, 16 Aug 2013, leg./det. *D. Bandini & B. Oertel* (KR-M-0042325, DB16-8-13-2, BAN510, MH366628).- Salzburg, Tamsweg, Lessach, Lasshoferalm, ÖK25V 3230-West, alt. 1270 m, *Picea abies*, 16 Aug 2013, leg. *D. Laber*; det. *D. Bandini & B. Oertel* (KR-M-0042326, DB16-8-13-9, BAN503, MH366627).- Ibidem, in some distance of former location, alt. ca. 1250 m, *Picea abies*, 16 Aug 2013, leg. *I. Krisai-Greilhuber*; det. *D. Bandini & B. Oertel* (KR-M-0042324, DB16-8-13-13, BAN538, MH366629).

Comments: At least when young, *I. venustissima* resembles in habit *Porpolomopsis calyptriformis* (Berk. & Broome) Bresinsky, whereas the big bowl-shaped bulb, in which the stipe is immersed, reminds of some species in the genus *Amanita*. Because of these characteristics and its size, the often honey-yellow colour and shiny silky smooth or even waxen pileus it is undoubtedly an eye-catching species. Taken all this into consideration it does not seem likely, even on first sight, to confound it with some other yellowish-brownish bulbous *Inocybe* species—as for instance *I. cookei* Bres. or one of the nodulose-spored members of *Inocybe* as *I. mixtilis* (Britzelm.) Sacc. In addition, no smooth-spored bulbous species of *I.* subgen. *Inocybe* known up to now from European countries possesses all the named characteristics. *Inocybe pelargonium,* with which a Swedish collection of *I. venustissima* has been confounded (see above), has a different habit, different colour of pileus, smaller bulb and smaller spores. *Inocybe hirtelloides* is a smaller species with a different habit, different bulb and entirely different short cystidia. *Inocybe splendentoides* Bon normally does not show a clear defined bulb, the colour of pileus is different; the texture of pileus is characteristically excoriated near the margin. Although *I. splendentoides* grows in moist terrain like *I. venustissima*, *I. splendentoides* prefers lowland sites with *Salix*. Furthermore, its spores and hymenial cystidia are larger and in form quite different from those of *I. venustissima*. The same holds true for *I. terrifera*, which is also known from a different habitat and has no such bulb and another habit.

One species however, found in Canada, is very close to *I. venustissima* in many respects: *I. chalcodoxantha* Grund & D.E. Stuntz. Unfortunately, we could neither obtain the type nor the isotype on loan for own taxonomical studies. Luckily it was described in detail by Grund and Stuntz (1968): conical pileus with prominent umbo and appressed silky, shining surface, rimose towards the margin, colour brassy yellowish brown, stipe entirely pruinose. The basidiomata are much smaller than those of *I. venustissima*—only 2.5 cm in diam. maximum—, the bulb is flat-margined and only up to 11 mm wide. Its cystidia show a clearly defined neck, their walls are thicker, and the spores are smaller and with an obtuse apex, whereas in *I. venustissima* the apex of spores mostly is subconical to conical. *Inocybe chalcodoxantha* has been found "gregarious in moss or needle" with conifers. No mention however is made of it growing in moist places as is the case with all Austrian collections of *I. venustissima*. In summary, *I. venustissima* morphologically is similar but not identical with *I. chalcodoxantha*, and also in terms of ITS sequence data, there is a significant divergence between the two species.

In the UBC Herbarium of the University of British Columbia, Vancouver, Canada, a specimen is deposited (F19796), the ITS of which is identical with the sequences from the Austrian collections. The photograph of the only basidioma (https://bit.ly/2IrBMhn) shows the typical strongly conical habit, yellow colour and smooth surface of pileus. The stipe is widened towards the base, but the base itself has not been preserved. The size of spores is indicated with 8–10 × 5–5.5 (6.0) µm, which lies in the range of those of *I. venustissima*. The shape of the roughly pencil-drawn two cystidia can be observed in *I. venustissima* too. Oluna Ceska has noted that the stipe is not pruinose and the species has been determined as *I. auricoma*—probably due to the fact that the bulb is missing. The base of the stipe of *I. auricoma* is not bulbous at all and the basidiomata are smaller than those of *I. venustissima* (see Batsch 1783; Lange 1917; Kuyper 1986; Kuyper and Weholt 1988).

Inocybe curcumina Bandini, B. Oertel & U. Eberh. sp. nov.

Figure 6

MycoBank number: MB 827576, ITS barcode GenBank: MH366621.

Etymology: “curcumina”, because the yellow-ochraceous colours of the pileus remind of curcuma powder.

Short description: Rather stout species. Pileus generally with darker fibres on lighter ground and therefore appearing mottled yellow-ochraceous or ochraceous brownish; often a little sticky and then covered with soil particles. Stipe entirely pruinose and with bulbous or at least clearly widened base. Spores smooth, measuring 7.4–10.4 × 4.1–5.8 µm, hymenial cystidia mostly (sub)utriform or subcylindrical, pleurocystidia measuring 40–70 × 12–21 µm.

Diagnosis: *Inocybe curcumina* resembles *I. pelargonium* Kühner, but differs from this species by stouter habit, generally less intense colours without or with less coppery tinge,

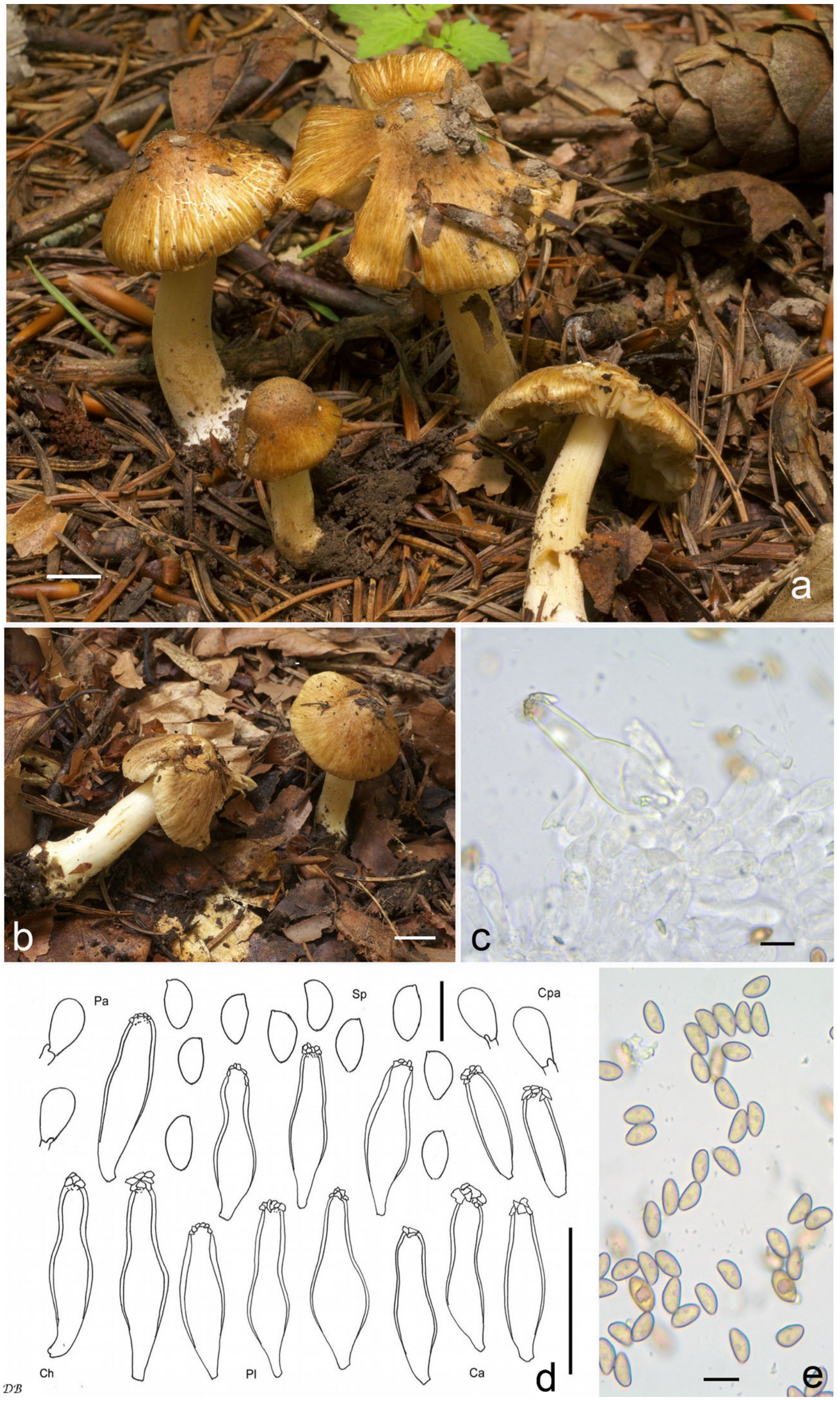


Fig. 6 *Inocybe curcumina* **a** Holotype (DB30-6-12-1), scale bar 1 cm. **b** DB5-9-14-2, scale bar 1 cm. **c** Pleurocystide (DB5-9-14-2), scale bar 10 µm. **d** Microscopical characters (DB30-6-12-1), Ca Caulocystidia, Cpa Cauloparacystidia, Ch Cheilocystidia, Pa Paracystidia, Pl Pleurocystidia, Sp Spores; scale bar spores 10 µm, scale bar cystidia 50 µm. **e** Spores (DB5-9-14-2), scale bar 10 µm

less glabrous surface of pileus, larger spores and larger cystidia as well as by ITS sequence data.

Holotype: GERMANY, Baden-Württemberg, Rhein-Neckar-Kreis, Schönbrunn, TK25 6519/4, 8.9548 E 49.4052 N, alt. 360 m, wayside with *Fagus sylvatica*, *Picea abies*, *Pseudotsuga menziesii,* 30 Jun 2012, leg. *D. Bandini & B. Oertel* (holotype KR-M-0042332; isotype DB30-6-12-1, BAN200).

Detailed description

Pileus 20–40 mm wide, (sub)campanulate, paraboloid or (sub)conical when young, later broadly convex or expanded, with more or less pronounced broad umbo, sometimes depressed around the centre, margin slightly inflexed or deflexed, later straight, regular or somewhat undate, sometimes torn in old specimens; with fugacious greyish velipellis remnants especially when young; colour in different shades of yellow-ochraceous, but also ochraceous brownish to hazel-brown (Mu 10YR 6/6–6/8, 5/6–5/8, 7.5YR 6/6–6/8) sometimes with faint coppery or orange tinge especially towards centre when moist, generally appearing somehow mottled or streaky, some basidiomata seem to be subhygrophanous and therefore colour then not uniformous but paler towards the margin; surface glabrous to rimose or (innately) fibrillose with appressed, but diverging fibres, showing the paler flesh underneath; in wet conditions slightly sticky and then with soil particles on the umbo; no cortina observed. **Lamellae** moderately crowded (ca. 40–60, l = 1–3), almost free to adnate, subventricose, whitish or creamy when young, later yellowish-greyish with or without olive tinge to greyish or grey-brown; with age also with rusty patches, edge fimbriate, whitish to concolorous. **Stipe** 20–50 × 3–5 mm, cylindrical or widening towards the base, with age sometimes hollow, more or less—not marginate—bulbous or at least conspicuously widened (up to 10 mm), glabrous, first creamy to faintly yellowish, light wood-brown beneath whitish pruina; pruinose on the entire length of the stipe. **Context** whitish, also watery in the pileus, whitish in the stipe, with yellowish or brownish tinge in the cortex of the stipe. **Smell** subspermatical at least when cut, one basidioma with a fruity note. **Colour of exsiccata** pileus warm brown with ochraceous-orange tinge (Mu 7.5YR 5/6, 4/4–4/6, 5YR 4/4–4/6), lamellae and stipe concolorous or a little lighter in colour, no darkening or blackening with drying.

Spores 7.4–10.4 μm (av. 8.7 μm, SD 0.6 μm) × 4.1–5.8 μm (av. 4.8 μm, SD 0.3 μm); Q = 1.5–2.0 (av. 1.8, SD 0.1) (*n* = 160 from 4 coll.), smooth, (sub)amygdaloid, sometimes with faint suprahilar depression, apex subacute, subobtuse, in some collections with indistinct pseudopore. **Basidia** 23–28 × 7–10 μm, generally 4-spored, seldom also 2-spored, and then spores up to 11.6 μm. **Lamellae edges** sterile, composed of cheilocystidia and numerous hyaline, (sub)clavate, cylindrical or subglobose, thin-walled paracystidia. **Pleurocystidia** 40–70 μm (av. 54 μm, SD 7.2 μm) × 12–21 μm (av. 16 μm, SD 2.3 μm); Q = 2.1–4.5 (av. 3.4, SD 0.5) (*n* = 60 from 4 coll.), mostly (sub)utriform, also (sub)cylindrical or (sub)lageniform, rarely also (sub)clavate, not seldom neck clearly demarcated, at apex generally wide, mostly with short pedicel, apex usually crystalliferous, walls (0.5) 1.0 μm (bulge)–2.5 (3.0) μm (neck) thick, weak reaction with 3% KOH. **Cheilocystidia** similar in appearance and size. **Pileipellis** constituted by an epicutis made up of parallel hyphae 4–8 (10) μm wide, often but not always with finely encrusting and parietal yellowish pigment, subcutis with wider and paler to hyaline elements, up to 35 (38) μm wide, epicutis in young basidiomata sometimes covered with thin hyaline hyphae, with scattered free ends (belonging to velipellis remnants). **Stipitipellis** consisting of a cutis bearing numerous bundles of metuloid caulocystidia on the entire length of the stipe, intermixed with thin-walled colourless cauloparacystidia. **Caulocystidia** (30) 35–60 × 10–20 μm, (sub)utriform, (sub)cylindrical or even (sub)clavate, apex usually crystalliferous, walls 1.0 (bulge)–2.5 μm (neck) thick, weak reaction with 3% KOH. **Clamp-connections** abundant in all tissues.

Habitat and known distribution: All collections were found at gravelled waysides in the same submontane region with *Fagus sylvatica* and *Picea abies* or also with *Picea abies* only. Up to now only known from Germany. We are not aware of further sequences or collections.

Phenology: End of June to October.

Additional collections studied: GERMANY, Baden-Württemberg, Neckar-Odenwald-Kreis, Aglasterhausen, TK25 6619/2, alt. 395 m, wayside with *Picea abies*, *Fagus sylvatica*, 7 Aug 2011, leg. *D. Bandini*; det. *D. Bandini & B. Oertel* (KR-M-002360, DB7-8-11-2, BAN1516, MH366620).- Baden-Württemberg, Neckar-Odenwald-Kreis, Schwarzach, TK25 6619/2, alt. 380 m, wayside with *Fagus sylvatica* & *Picea abies*, 5 Sep 2014, leg. *D. Bandini*; det. *D. Bandini & B. Oertel* (KR-M-0042333, DB5-9-14-2, BAN1828, SMNS-STU-F-0900966, MG012480).- Ibidem, in some distance, alt. 390 m, *Picea abies*, 2 Oct 2014, leg. *D. Bandini*; det. *D. Bandini & B. Oertel* (KR-M-0042335, DB2-10-14-4, BAN836, MH366622).

Comments: *Inocybe curcumina* is mainly characterised by its yellow-ochraceous or ochraceous brownish pileus and generally mottled or streaky appearance because of diverging fibres. The stipe base is more or less bulbous and the stipe is entirely pruinose. The spores are on average smaller than 9 μm and the hymenial cystidia on average smaller than 60 μm. According to the classification system of Bon (1997) *I. curcumina* would belong to *I.* sect. *Splendentes*, and there to *I.* subsect. *Splendentinae* Bon. But phylogenetically it is not related to the name-giving species of the *splendens* group, but to *I. pelargonium, I. hirtelloides* and *I. vaccina,* a species listed by Bon in *I.* subsect. *Phaeoleucinae* Bon, while *I. hirtelloides* and *I. pelargonium* are listed by him in *I.* subsect.

Splendentinae. Of these, the most similar to *I. curcumina* in taxonomical as well as in genetical respect is *I. pelargonium*, which also can be found in the same habitat and possibly has been mixed up with *I. curcumina* in the past. *Inocybe pelargonium* however is normally less stout and has a different habit, the pileus very often has a coppery orange tinge, and the surface is mostly more glabrous, even shiny or somehow "greasy" (Stangl 1971) or finely felty, and not rimose-fibrillose as in case of *I. curcumina.* Furthermore the stipe is—different from *I. curcumina*— often quite rigid, the spores are on average smaller and the hymenial cystidia shorter and wider. Yet some basidiomata of *I. pelargonium* may show a similar streaky appearance as *I. curcumina,* and, especially when moist, the two species might be confused.

A confusion with *I. hirtelloides* is less probable, because of differences in growth habit, colour and pileus texture as well as in the size of spores and hymenial cystidia. The same can be said with reference to *I. terrifera* and *I. splendentoides.* The basidiomata of these species are normally larger. The colour of pileus of *I. terrifera* is more yellowish, the colour of the pileus of *I. splendentoides* more brownish and the pileipellis does not normally reach the edge of the pileus. Moreover, *I. curcumina* and *I. splendentoides* do not seem to grow in the same habitats, since the latter species appears to favour moist terrain near *Salix*. The pileus of the molecularly related *I. vaccina* is more reddish or foxy brown, the surface of pileus is minutely squamulose (see also Kühner 1955), and the shape of the hymenial cystidia is different.

Inocybe pelargonium Kühner 1955.

Figure 7

Pileus 15–40 (50) mm wide, campanulate or subconical when young, to convex or expanded, without or with low broad umbo, margin in young specimens inflexed or deflexed, often remaining deflexed, but also almost straight to uplifted and then pileus depressed around the umbo, margin regular or slightly undate, when old also deeply torn; when young covered with fugacious remnants of a whitish velipellis; colour in some collections rather uniformously coppery-brownish or coppery-ochraceous or ochraceous brownish (Mu 7YR 5/6–5/8, 6/6–6/8, 10YR 7/6–7/8, 5/6–5/8), but also speckled orange brownish or in the centre brown with orange hue (Mu 7.5YR 4/4–4/6) and then quite contrasting to the margin; surface mostly glabrous, not seldom even satiny shiny or sericeous in appearance, later finely felty or rimulose and in some collections also minutely squamulose with darker squamules on lighter ground and in the centre of the pileus fissured or grindy, somewhat sticky in wet conditions; no cortina observed. **Lamellae** moderately crowded (ca. 40–60, l = 1–3), narrowly to broadly adnate, also emarginate adnate, even to subventricose, at first whitish or creamy, later greyish-brownish, ochraceous brownish, often with orange brownish speckles when old; edge even to fimbriate, whitish to concolorous. **Stipe** 20–70 × 2–9 mm, often conspicuously rigid, cylindrical or widening towards the base, base often subbulbous to (sub)marginate bulbous, glabrous, whitish to pale yellow; pruinose on the entire length of the stipe. **Context** whitish in the pileus, whitish to faintly yellowish in the stipe, especially in the cortex of the stipe. **Smell** fruity or as *Pelargonium* leaves, when cut often (sub)spermatical. **Colour of exsiccata** pileus brown to dark brown with reddish tinge (Mu 7.5YR 4/4–4/6, 3/4), lamellae concolorous, stipe lighter in colour, not seldom rather light greyish, no darkening or blackening with drying.

Spores 5.8–10.0 μm (av. 7.6 μm, SD 0.8 μm) × 3.9–5.7 μm (av. 4.6 μm, SD 0.4 μm); Q = 1.4–1.9 (av. 1.6, SD 0.1) (*n* = 120 from 3 coll.), smooth, (sub)amygdaloid, sometimes elliptic, seldom almost ovoid, apex obtuse to subacute. **Basidia** 25–33 × 8–10 μm, generally 4-spored. **Lamellae edges** sterile, composed of cheilocystidia and numerous hyaline, (sub)clavate, cylindrical or subglobose, thin-walled paracystidia. **Pleurocystidia** 28–65 μm (av. 48 μm, SD 8.4 μm) × 10–21 μm (av. 14 μm, SD 2.1 μm); Q = 2.3–4.8 (av. 3.4, SD 0.7) (*n* = 45 from 3 coll.), mostly (sub)utriform, also (sub)fusiform, (sub)cylindrical, seldom also (sub)lageniform or (sub)clavate, often with short clearly demarcated neck, with short pedicel or even without pedicel, apex usually crystalliferous, walls 0.5 μm (bulge)–1.5 (2.0) μm (neck) thick, weak reaction with 3% KOH. **Cheilocystidia** similar in appearance and size. **Pileipellis** constituted by an epicutis made up of parallel hyphae 4.5–10 (12) μm wide, often but not always with finely encrusting and parietal pale yellow or yellowish-brownish pigment, subcutis with wider and paler to hyaline elements, up to 20 (25) μm wide, epicutis in young basidiomata sometimes covered with thin hyaline hyphae, with scattered free ends (belonging to velipellis remnants). **Stipitipellis** consisting of a cutis bearing numerous bundles of metuloid caulocystidia on the entire length of the stipe, intermixed with thin-walled colourless cauloparacystidia. **Caulocystidia** 45–80 × 10–15 (20) μm, differently formed, from quite long and subcylindrical to (sub)fusiform, (sub)utriform or even (sub)clavate, apex with or without crystals, walls 0.5 (bulge)–1.0 (2.0) μm (neck) thick, weak reaction with 3% KOH. **Clamp-connections** abundant in all tissues.

Habitat and known distribution: With coniferous as well as with frondose trees, often with *Picea abies*, *Fagus sylvatica* or *Quercus*; along calcareous influenced waysides as well as in montane regions on meadows beneath solitary *Picea* trees or in *Picea* forests, in lowland to subalpine regions. The type collection was found in France, and the species most probably is widely distributed, at least in Central Europe, and there is an ITS sequence putatively belonging to this species (HF674563) in the databases isolated from ectomycorrhizal roots in Slovenia ("environmental sample from sub-Mediterranian beech forest").

Phenology: July to October.

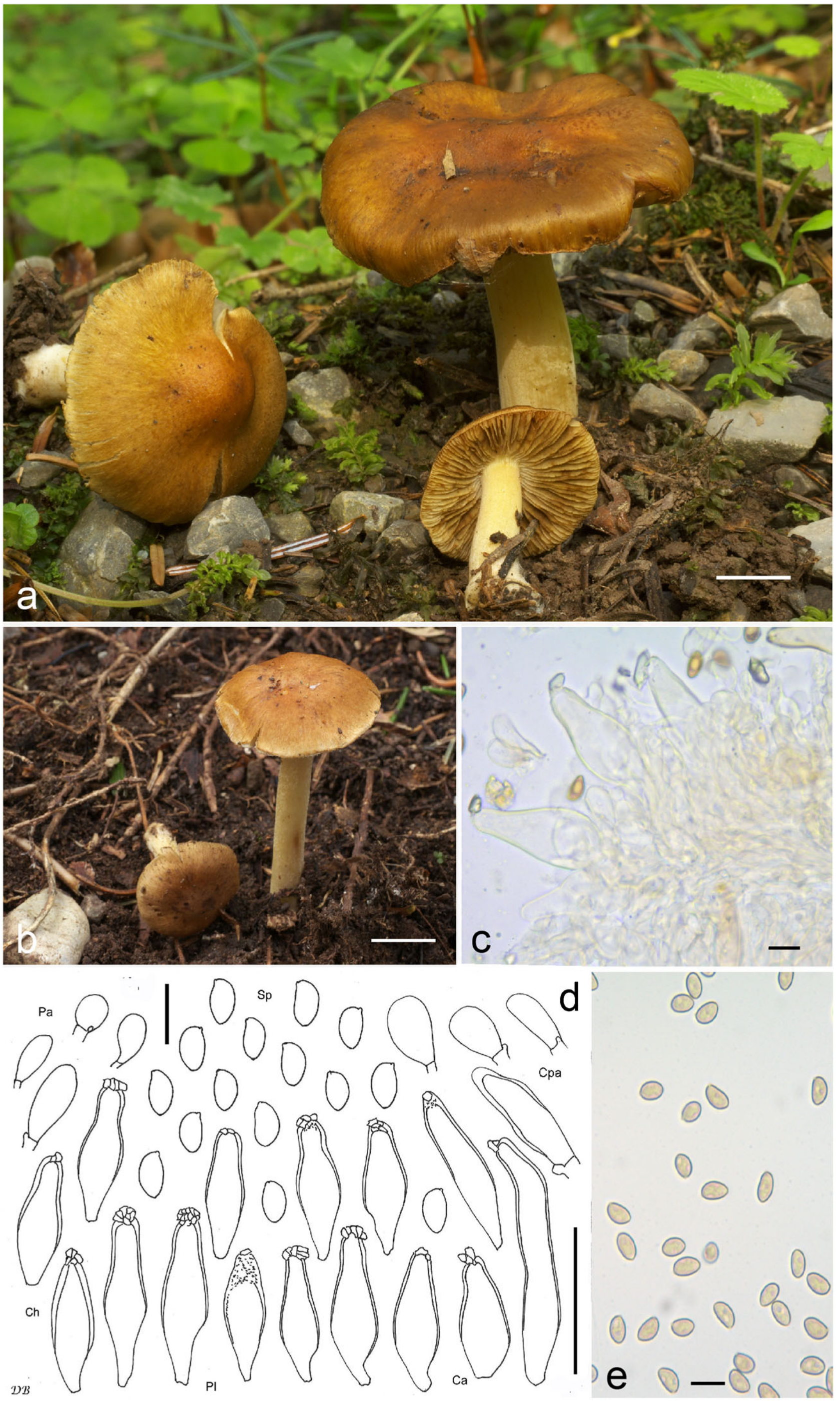


Fig. 7 *Inocybe pelargonium* **a** DB29-6-12-7, scale bar 1 cm. **b** DB14-10-16-5, scale bar 1 cm. **c** Cheilocystidia (DB12-9-16-1), scale bar 10 µm. **d** Microscopical characters (DB29-6-12-7), Ca Caulocystidia, Cpa Cauloparacystidia, Ch Cheilocystidia, Pa Paracystidia, Pl Pleurocystidia, Sp Spores; scale bar spores 10 µm, scale bar cystidia 50 µm. **e** Spores (DB29-6-12-7), scale bar 10 µm

Collections studied: GERMANY, Baden-Württemberg, Rhein-Neckar-Kreis, Schönbrunn, TK25 6519/4, alt. 380 m, *Picea abies*, *Abies alba*, *Fagus sylvatica*, 29 Jun 2012, leg./det. *D. Bandini* (KR-M-0042334, DB29-6-12-7, BAN201, MH366623).- Baden-Württemberg, Neckar-Odenwald-Kreis, Aglasterhausen, TK25 6619/2, alt. 395 m, *Picea abies*, 5 Sep 2014, leg. *D. Bandini*; det. *D. Bandini, B. Oertel* & *U. Eberhardt* (KR-M-0042361, DB5-9-14-8, BAN1829, SMNS-STU-F-0900969, MG012479).- Bayern, Miesbach, Osterwarngau, Taubenberg, TK25 8136/3, alt. ca. 750 m, *Picea abies*, *Abies alba*, *Pinus sylvestris*, 7 Jul 2007, leg. *M. Dondl*; det. *M. Dondl, D. Bandini* & *B. Oertel* (KR-M-0042362, DB7-7-7-1-Dondl, BAN638).- Bayern, Miesbach, Bayrischzell, Geitau, TK25 8337/2, alt. 850 m, *Picea abies*, 17 Sep 2008, leg./det. *M. Dondl* (KR-M-0038058, DB17-9-8-Dondl, BAN331).- Bayern, Ostallgäu, Pfronten, Breitenberg, TK25 8429/3, alt. ca. 1750 m, *Picea abies*, *Pinus mugo*, 11 Aug 2014, leg./det. *D. Bandini* (KR-M-0042363, DB11-8-14-

21, BAN694, MH366624).- Bayern, Weilheim-Schongau, Wessobrunn, Nature Reserve "Paterzeller Eibenwald", TK25 8132/1, alt. ca. 700 m, *Fagus sylvatica*, *Picea abies*, *Alnus incana*, 12 Sep 2016, leg./det. *D. Bandini & B. Oertel* (KR-M-0042364, DB12-9-16-1, BAN1618).- Bayern, Ostallgäu, Füssen, Hopfen am See, Hopfener Wald, TK25 8330/3, alt. 870 m, *Picea abies*, *Fraxinus excelsior*, *Corylus avellana*, 14 Oct 2016, leg. *D. Bandini, B. Oertel & J. Christan*; det. *D. Bandini & B. Oertel* (KR-M-0042365, DB14-10-16-5, BAN1760) (listed here are only those of totally 30 collections of which an DNA-analysis has been made).

For lectotype of *I. pelargonium* see below.

Comments: *Inocybe pelargonium* is characterised by the mostly (sub)glabrous to sometimes satiny shiny coppery-brownish or orange-tinged pileus, typical smell like *Pelargonium* leaves or sweet fruits, totally pruinose (sub)bulbous, stipe, small spores and relatively short cystidia. Kuyper (1986) gives average measurements of the spores of 7.3–9.4 μm, the spores of the collections measured here have an average value of 7.6 μm, and the spores of the lectotype examined by us are, have an average of 7.9 μm. The hymenial cystidia of the type are on average < 50 μm as in our own collections. *Inocybe pelargonium* is quite often presented in the literature (e.g. Kuyper 1986; Stangl 1989; Breitenbach and Kränzlin 2000; Ferrari 2010; Armada 2015; Arnolds et al. 2015), however it is doubtful, whether really *I. pelargonium* has been described and/or depicted in all cases (i.e. regarding the photograph of *I. pelargonium* in Gminder 2010). *Inocybe langei* R. Heim also has quite small spores and cystidia, but the pileus generally is always yellower, the cystidia are shaped differently, have thicker walls and show a stronger reaction with KOH. *Inocybe hirtelloides,* another species with a totally pruinose stipe and small spores, has a differently structured pileus surface and differently shaped and shorter hymenial cystidia. *Inocybe claviger* E. Horak & Bas, a species described from the Himalayan regions was synonymised with *I. pelargonium* by Kuyper (1986). However, as Horak pointed out in the original description of *I. claviger* (Horak 1981), the cystidia of the latter species "distinctly" separate the two species. The cystidia in *I. claviger* are "ovoid-vesiculose to broadly clavate" which they are not in *I. pelargonium*. Molecularly *I. pelargonium* is related to *I. vaccina* and *I. curcumina*. The latter normally has a more rimose to fibrillose and more dull ochraceous brownish pileus, on average larger spores and larger cystidia. And *I. vaccina* has a subsquamulose pileus surface, the colour is more reddish foxy brown and the hymenial cystidia and spores are on average larger and different in shape (see also Kuyper 1986; Stangl 1989).

Inocybe hirtelloides Stangl & J. Veselský 1974

Figure 8

Pileus 15–30 mm wide, subconical or (sub)campanulate when young, later convex to expanded, with a more or less pronounced broad umbo, margin inflexed to deflexed when young, later even to uplifted and then pileus depressed around the centre; colour yellow-ochraceous, ochraceous, at the centre slightly darker and with coppery or orange hue (Mu 7.5YR 7/6–7/8, 10YR 7/6–7/8, 6/6–6/8), towards margin lighter in colour, even straw-coloured; surface especially at the umbo almost glabrous, outwards glabrous when young, later finely innately fibrillose or fibrillose with adherent fibres. **Lamellae** moderately crowded (ca. 40–50, l = 1–3), adnexed to adnate, ventricose, young whitish, creamy to greyish, later ochraceous-brown to light brown; edge fimbriate, whitish. **Stipe** 20–35 × 2–4 mm, more or less cylindrical, base with a small roundish bulb, sometimes hidden in the ground and therefore difficult to be observed, glabrous, wax-coloured to yellowish, apex and bulb whitish; pruinose on the entire length of the stipe, but pruina sparse towards the base. **Context** whitish in the pileus, in the stipe light wood-coloured, rather brittle. **Smell** (sub)spermatical, at least when cut, with faint fruity tinge. **Colour of exsiccata** pileus, lamellae and stipe light brown, nut-brown, ochraceous-brown (Mu 10YR 5/6–5/8, 4/6), no darkening or blackening with drying.

Spores 6.9–9.8 μm (av. 8.2 μm, SD 0.6 μm) × 4.1–5.8 μm (av. 5.0 μm, SD 0.4 μm); Q = 1.4–1.9 (av. 1.6, SD 0.1) ($n = 80$ from 2 coll.), smooth, amygdaloid, often with faint apical depression, apex subacute to subobtuse, sometimes also obtuse. **Basidia** 25–30 × 7–9 μm, generally 4-spored. **Lamellae edges** sterile, composed of cheilocystidia and numerous, mostly (sub)clavate, subcylindrical or subglobose thin-walled paracystidia. **Pleurocystidia** 35–56 μm (av. 44 μm, SD 5.3 μm) × 11–20 μm (av. 15 μm, SD 6.2 μm); Q = 2.2–4.6 (av. 3.0, SD 0.6) ($n = 30$ from 2 coll.), mostly (sub)utriform or (sub)fusiform, seldom also subclavate, apex usually crystalliferous, base without or with short pedicel, sometimes with rounded base, walls 0.5 μm (bulge)–3.0 (5.0) μm (neck) thick, often abruptly thickened towards the neck, occasionally a little undate, weak reaction with 3% KOH. **Cheilocystidia** similar in appearance and size. **Pileipellis** consisting of an epicutis 4–10 (12) μm wide, with finely encrusting and parietal yellowish pigment, subcutis with wider and paler elements, up to 20 (25) μm wide, epicutis in young basidiomata sometimes covered with thin hyaline hyphae, with scattered free ends (belonging to velipellis remnants). **Stipitipellis** consisting of a cutis bearing numerous bundles of caulocystidia down to the base of the stipe, but sparse towards the base, intermixed with thin-walled colourless cauloparacystidia. **Caulocystidia** 30–80 × 10–15 (20) μm, at the apex of the stipe mostly long and narrow and almost cylindrical, subfusiform or deformed, occasionally with tapering walls, towards the base resembling in shape and size the hymenial cystidia, apex usually crystalliferous, wall 0.5 μm (bulge)–2.5 (3.0) μm (neck) thick; weak reaction with 3% KOH.

Fig. 8 *Inocybe hirtelloides* **a** DB1-8-14-4, scale bar 1 cm. **b** DB8-8-14-7, scale bar 1 cm. **c** Cheilocystide (DB1-8-14-4), scale bar 10 µm. **d** Microscopical characters (DB1-8-14-4), Ca Caulocystidia, Cpa Cauloparacystidia, Ch Cheilocystidia, Pa Paracystidia, Pl Pleurocystidia, Sp Spores; scale bar spores 10 µm, scale bar cystidia 50 µm. **e** Spores (DB1-8-14-4), scale bar 10 µm

Habitat and known distribution: The type collection was found in the Wittelsbacher Park (Augsburg, Bayern) in Germany with *Tilia.* Stangl (1989) is citing other collections in parks with broadleaf trees. The collections described by us were found on a war cemetery with *Quercus robur*, *Fagus sylvatica,* and *Pinus sylvestris*. Apart from a sequence of a collection from Sweden (TK04063, GenBank AM882936.2) putatively belonging to this species, we are not aware of any other confirmed collection. Unconfirmed records of *I. hirtelloides* are reported from different countries, for instance from Poland and France, and some places in Germany (Derbsch and Schmitt 1984/1987; Hansen and Knudsen 1992; Bon 1995; Wojewoda 2003; Gminder 2010).

Phenology: According to Stangl (1989) from June to August.

Collections studied: GERMANY, Baden-Württemberg, Heidelberg, war cemetery, TK25 6618/1, alt. 290 m, lawn with *Quercus robur*, *Pinus sylvestris*, *Fagus sylvatica*, 1 Aug 2014, leg. *D. Bandini*; det. *D. Bandini* & *B. Oertel* (KR-M-

0042354, DB1-8-14-4, BAN668, MH366618).- Ibidem, in some distance, alt. 292 m, lawn with *Quercus robur*, *Pinus sylvestris*, *Fagus sylvatica*, 8 Aug 2014, leg./det. *D. Bandini* (KR-M-0042359, DB8-8-14-7, BAN684, MH366617).

For holotype of *I. hirtelloides* see below.

Comments: Main characteristics of *I. hirtelloides* are the rather small basidiomata, the yellow-ochraceous colour with orange hue at the pileus centre, the entirely pruinose stipe with a small bulb and small hymenial cystidia, whereas the caulocystidia near the stipe apex are generally long and narrow (so also Enderle 1995).

Inocybe hirtelloides is included in the books of Stangl (1989) and Kuyper (1986). Kuyper only had examined collections of Stangl, thus no own collections. Consequently, it seems that the species is either rather rare and/or sometimes misidentified. A reason for this might be the ambiguity in the specifications of the size of the hymenial cystidia. In the original description (Stangl and Veselský 1974) the size is noted as 40–70 μm, without indicating an average value. This may have led to the wrong impression that *I. hirtelloides* is a species with cystidia in the normal size range. According to our own measurements the mean value of the type collection however is 49 μm, the maximum size indicated for the type collection measured by Kuyper is 55 (56) μm, and the average value of the collections from Heidelberg is even only 44 μm. Bon (1995), in one of the rare detailed descriptions of *I. hirtelloides* in literature, gives the size of hymenial cystidia as 45–55 μm, and in his Bavarian monograph Stangl (1989) gives measurements of 40–60 μm. Therefore it can be assumed, that in the past *I. hirtelloides* was sometimes mistaken for another species with entirely pruinose stipe, yellow-ochraceous pileus and short cystidia, as for instance *I. mystica* Stangl & Glowinski. The hymenial cystidia of this species are however still smaller than those of *I. hirtelloides*. The assumption that *I. hirtelloides* has occasionally been mistaken for other species is also supported by the fact, that in keys the short cystidia are not mentioned as characteristic for *I. hirtelloides* (see Kuyper 1986; Stangl 1989; Horak 2005). It also appears that the species named and discussed as *I. hirtelloides* by Jacobsson and Stridvall 1979 is not *I. hirtelloides,* because of its very long-necked hymenial cystidia.

Bon (1997) assigned *I. hirtelloides* to *I.* sect. *Splendentes* and there to *I.* subsect. *Splendentinae*. However, it differs from the typical members of this group, as *I. splendens*, *I. alluvionis*, *I. splendentoides*, in many respects as for instance smaller basidiomata, spores and hymenial cystidia. Molecularly, it is not closely related to any of the above-mentioned species but is placed in the vicinity of *I. vaccina* Kühner, a species differing from *I. hirtelloides* molecularly only by two base pairs and ten gaps, but morphologically in many respects, as for instance in the colour and texture of the pileus and size and form of the hymenial cystidia.

Inocybe leochroma Bandini, Vauras, & B. Oertel sp. nov.
Figures 9 and 10

MycoBank number: MB 827577, ITS barcode GenBank: MH366611.

Etymology: “leochroma”, because of the warm “lion-colour” of the pileus.

Short description: Up to fairly large smooth-spored species with bright orange-ochraceous, copper-tinged brown pileus, long and entirely pruinose bulbous stipe, rather small spores, measuring 6.6–9.5 × 4.1–5.9 μm and pleurocystidia measuring 35–74 × 10–22 μm.

Diagnosis: *Inocybe leochroma* is morphologically and molecularly similar to *I. angulatosquamulosa,* but differs from this species by its brighter colours, different and less speckled surface of the pileus, different pruina of the stipe, on average larger spores, smaller hymenial cystidia, and its association with coniferous trees.

Holotype: AUSTRIA, Tirol, Reutte, near Grän, above Achtal in direction to Pfronten, ÖK25V 2214-Ost, 10.5423 E 47.5320 N, alt. 1120 m, border of dry rivulet, calcareous soil with *Picea abies*, 25 Sep 2015, leg. *D. Bandini* (holotype KR-M-0042372; isotypes TUR-A, DB25-9-15-21, BAN1215).

Detailed description

Pileus 15–47 mm wide, (sub)conical or (sub)campanulate when young, later broadly convex or expanded and then with a broad more or less pronounced umbo, margin at first slightly inflexed or deflexed, later straight to uplifted, often depressed around the umbo, sometimes undate; some basidiomata with usually rather inconspicuous remnants of a greyish velipellis at the centre; colour mostly warm to intense ochraceous-orange in different shades and sometimes indistinctly speckled with small darker fibres on lighter ground and at the centre more intense and darker bright and warm golden orange to ochraceous-orange or orange-amber to orange reddish (Mu 5YR 5/6–5/8, 6/6–6/8, 7.5YR 6/8, 5/8), sometimes at the centre also greyish brown because of particles of soil; surface glabrous or finely felty when young, later becoming felty-lanose to lanose with appressed fibres, but occasionally also becoming (sub)squamulose with lacerate fibre bundles especially towards the margin whereas the centre remains glabrous to finely felty; in wet conditions slightly sticky; no cortina observed. **Lamellae** moderately crowded (ca. 40–60, l = 1–3), up to 7 mm broad, almost free to adnexed, adnate or adnate with decurrent tooth, (sub)ventricose, at first whitish, pale grey, later greyish ochraceous to ochraceous; edge sometimes notchy, fimbriate, whitish to concolorous. **Stipe** 20–50 × 2–11 mm, cylindrical or widening slightly towards the base, base mostly with a more or less marginate, up to 13 mm wide bulb, when young covered with fine whitish tissue, later striate or glabrous, whitish, then flesh-coloured, reddish-brownish or pale yellow-brown, remaining whitish at the extreme apex and at the base; pruinose on the entire length of the stipe; pruina unusually rough. **Context** in the pileus whitish, directly

Fig. 9 *Inocybe leochroma* **a** Holotype (DB25-9-15-21), scale bar 1 cm. **b** DB13-8-13-25, scale bar 1 cm. **c** Cheilocystide (DB25-9-15-21), scale bar 10 µm. **d** Microscopic characters (DB25-9-15-21), Ca Caulocystidia, Cpa Cauloparacystidia, Ch Cheilocystidia, Pa Paracystidia, Pl Pleurocystidia, Sp Spores; scale bar spores 10 µm, scale bar cystidia 50 µm. **e** Spores (DB25-9-15-21), scale bar 10 µm

below the surface yellowish, above the lamellae watery, in the stipe striate, whitish to pale yellow-brown, at the cortex of the stipe faintly flesh-coloured. **Smell** subnull to subspermatical, at least when cut. **Colour of exsiccata** pileus nut-brown, brown with slight orange reddish hue (Mu 7.5YR 5/4–5/6, 4/4–4/6), lamellae and stipe concolorous or a little lighter in colour, occasionally some darkening of stipes with drying.

Spores 6.6–9.5 µm (av. 8.0 µm, SD 0.6 µm) × 4.1–5.9 µm (av. 4.9 µm, SD 0.3 µm); Q = 1.3–2.1 (av. 1.6, SD 0.1) (*n* = 160 from 4 coll.), smooth, (sub)amygdaloid, apex subacute or subobtuse, sometimes also obtuse. **Basidia** 25–30 × 7–9 µm, generally 4-spored. **Lamellae edges** sterile, composed of cheilocystidia and numerous hyaline, (sub)clavate, cylindrical or subglobose, thin-walled paracystidia. **Pleurocystidia** 35–74 µm (av. 56 µm, SD 8.4 µm) × 10–22 µm (av. 15 µm, SD 2.9 µm); Q = 2.7–5.5 (av. 3.8, SD 0.7) (*n* = 90 from 4 coll.), (sub)cylindrical, (sub)utriform or subfusiform, rarely (sub)clavate, sometimes slightly constricted towards the apex,

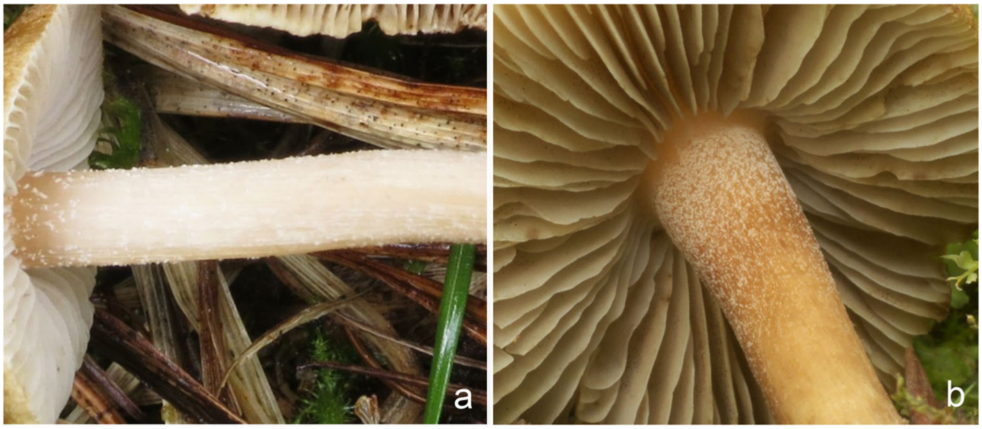


Fig. 10 **a** Stipe of *Inocybe leochroma* (DB13-8-13-25). **b** Stipe of *I. angulatosquamulosa* (DB1-8-14-6)

at the apex generally wide, without or with short to long pedicel, sometimes almost rounded at the base, apex usually crystalliferous, walls (0.5) 1.0 (bulge)–2.0 (2.5) μm (neck) thick, weak reaction with 3% KOH. **Cheilocystidia** similar in appearance and size, but more variable in form. **Pileipellis** constituted by an epicutis made up of parallel hyphae 4.5–13 μm wide, often with strongly encrusting and parietal yellowish or yellowish-orange-brownish pigment, subcutis with wider and paler to hyaline but partly also encrusting elements, up to 17 (20) μm wide, epicutis in young basidiomata sometimes sparely covered with thin hyaline hyphae, with scattered free ends (belonging to velipellis remnants). **Stipitipellis** consisting of a cutis bearing numerous bundles of metuloid caulocystidia on the entire length of the stipe, intermixed with thin-walled colourless cauloparacystidia. **Caulocystidia** (30) 35–55 (65) × 10–15 μm, mostly (sub)cylindrical, but also subfusiform, subutriform or even (sub)clavate, apex usually crystalliferous, walls 0.5 (bulge)–1.5 (2.0) μm (neck) thick, weak reaction with 3% KOH. **Clamp-connections** abundant in all tissues.

Habitat and known distribution: The two collections from Austria investigated in this study were found in montane regions, one collection with *Picea abies* near a rivulet, the other collection also near a rivulet, with *Picea* but also with *Salix* and *Larix* nearby. The collections from Estland and Finland are from lowlands in the hemiboreal zone. In Estland the species was collected fairly close to the seashore, on a mossy, herb-rich lawn near *Pinus sylvestris*. In Finland the collecting site is circa 55 m above the sea level, near an abandoned limestone factory, in mixed forest with *Picea abies*, *Pinus sylvestris*, *Betula pendula*, *Populus tremula,* and *Salix caprea*. The species seems to be calciphilous, since all the localities are on calcareous soil.

Phenology: August to September.

Additional collections studied: AUSTRIA, Salzburg, Lungau, Zederhaus, Riedingtal, ÖK25V 3229-Ost, alt. ca. 1500 m, *Picea abies*, *Larix decidua*, *Alnus incana, Salix* sp., 13 Aug 2013, leg. *W. & M. Dämon*; det. *D. Bandini & B. Oertel* (KR-M-0042373, DB13-8-13-25, BAN404, MH366612, as *I. angulatosquamulosa* in Dämon et al. 2013).- ESTONIA, Hiiumaa, Pühalepa, Heltermaa, near the ferry harbour, at the road to Sarve, mossy lawn with *Pinus sylvestris*, on calcareous soil, with *Hebeloma edurum*, *Lactarius sanguifluus*, *Tricholoma albobrunneum,* and *Chroogomphus rutilus*, 22 Sep 2011, leg. *J. Vauras* 27875F; det. *D. Bandini, J. Vauras & B. Oertel* (TUR-A, TU).- FINLAND, Varsinais-Suomi, Lohja, Virkkala, Kyrkstad, Grid 27° E: 6679:3333, S of the old limestone processing plant, between Tynninharjuntie and Torikuja, mixed forest on calcareous mull soil, with *Picea abies, Pinus sylvestris, Betula, Populus tremula,* and *Salix caprea*, 25 Aug 1998, leg. *J. Vauras* 14,182; det. *D. Bandini, J. Vauras & B. Oertel* (TUR-A).

Comments: *Inocybe leochroma* is characterised by its warm and bright, sometimes intensely ochraceous-orange pileus colours, the entirely pruinose stipe, the bulbous base, and the rather small spores (on average < 9 μm long). Fairly conspicuous is the unusually rough pruina of the stipe, sometimes appearing as if grains of salt had been loosely sprinkled on the entire length of the stipe (see Fig. 10a). This phenomenon has been noted with every single basidioma from both Austrian collections when describing the fresh collections and is visible also on the exsiccata of the Estonian collection. Whereas in the type collection the surface of the pileus was glabrous to felty, the surface of the pilei of the other examined collections was felty-lanose to lanose and in older basidiomata also (sub)squamulose to lacerate near the border of the pileus. Glabrous basidiomata of *I. leochroma* might on first sight be confused with *I. pelargonium*, but the colour of pileus of the latter is more copper-tinged, the lamellae are often speckled rusty, the spores and hymenial cystidia on average are smaller. If the pileus surface is as felty-lanose or subsquamulose and indistinctly speckled as in the other two collections examined, *I. leochroma* reminds of *I. angulatosquamulosa,* to which it is also most closely related moleculary. *Inocybe angulatosquamulosa* however has a less brightly coloured pileus, the colours are duller ochraceous or ochraceus brownish to hazel-brown, and most often the pileus is in and around the centre speckled with brownish fibre bundles or squamules on golden-ochraceous ground and then looking somewhat similar to *I. margaritispora* (Berk.) Sacc. (see also the plate in Stangl 1984). The squamules can be observed also in dried specimens which is not the case in *I. leochroma*. The pruina of the stipe is finer, and the stipe is, other than in case of *I. leochroma,* clearly more pruinose near the apex and the pruina is fading conspicuously towards the middle and the base of the stipe (see Fig. 10b), the lamellae edges are mostly irregularly undate, the spores are on average smaller and the hymenial cystidia on average are slightly larger than those of *I. leochroma*. It is noteworthy that the spores of the central European collections of *I. leochroma* were on average larger than those of *I. angulatosquamulosa*, whereas in the nordic collections the opposite was the case. However more data are necessary for general conclusions.

According to the original description, *I. angulatosquamulosa* is associated with deciduous trees, in line with collections from Finland and Estonia**,** whereas at least the type collection of *I. leochroma w*as found with *Picea abies* and no deciduous trees nearby, and the Estonian collection with *Pinus sylvestris*. Molecularly the two species form a clade with *I. amblyospora* Kühner, *I. flavoalbida* Matheny & Bougher and *I. pseudoreducta* Stangl & Glowinski and in the key of Bon (1997) the latter two taxa as well as *I. angulatosquamulosa* belong to *I.* sect. *Splendentes* and there to *I.* subsect. *Splendentinae*. Morphologically, *Inocybe leochroma* cannot be confused with either of them because of differences in the colour of the pileus and in the micro-details.

Inocybe angulatosquamulosa Stangl 1984
Figure 11

Pileus 15–40 (45) mm wide, (sub)conical or (sub)campanulate, later differently shaped to broadly convex or expanded, with more or less pronounced broad umbo, margin slightly inflexed to deflexed, later straight to uplifted, not seldom undate; when young, some basidiomata with remnants of a greyish velipellis; colour mostly dull ochraceous to ochraceous brownish or hazel-brown, often speckled brown on lighter, sometimes almost golden or yellow-ochraceous to ochraceous ground, at the centre sometimes with orange hue (Mu 10YR 6/6–6/8, 5/6–5/8, 7.5YR 6/8, 5/8), seldom at the centre also brown to dark brown; surface almost glabrous or innately fibrillose when young, then around the centre becoming (sub)squamulose with darker fibre bundles on lighter ground, towards the margin innately fibrillose; no cortina observed. **Lamellae** moderately crowded (ca. 40–60, l = 1–3), adnexed to adnate, or adnexed with decurrent tooth, ventricose, when young from whitish beige with greyish hue or greyish, later brownish, edge often conspicuously irregularly undate or notched, even, whitish. **Stipe** 20–40 × 3–5 (8) mm, cylindrical or widening towards the base and the extreme apex, base generally with a (sub)marginate or roundish bulb, when young covered with fine whitish tissue, later striate or glabrous, beige to faintly brownish, also entirely or at least towards the apex pinkish-brownish or reddish-brownish; pruinose on the entire length of the stipe, but pruina mostly concentrating near the apex, thus appearing sometimes as if the stipe were pruinose only at the apex. **Context** whitish in the pileus, whitish to faintly brownish in the stipe especially in the cortex of the stipe, whitish in the base. **Smell** mostly (sub)spermatical, at least when cut, sometimes also somehow aromatic. **Colour of exsiccata** pileus yellow-brown with darker centre, to brown or dark brown (Mu 7.5YR 4/4–4/6, 3/4, 10YR 3/4–3/6), the pruina, in contrast to some basidiomata of *I. leochroma* not visible on the stipes, lamellae and stipe concolorous, no darkening or blackening with drying.

Spores 5.9–9.8 μm (av. 7.4 μm, SD 0.7 μm) × 3.8–6.0 μm (av. 4.7 μm, SD 0.7 μm); Q = 1.3–1.9 (av. 1.6, SD 0.1) (*n* = 180 from 7 coll.), smooth, (sub)amygdaloid, also almost ovoid or elliptic, apex mostly subobtuse to obtuse. **Basidia** 25–35 × 7–10 μm, generally 4-spored. **Lamellae edges** sterile, composed of cheilocystidia and numerous hyaline, (sub)clavate, subcylindrical or subglobose, thin-walled paracystidia. **Pleurocystidia** 37–84 μm (av. 59 μm, SD 10 μm) × 10–22 μm (av. 14 μm, SD 1.0 μm); Q = 2.2–7.1 (av. 4.4, SD 1.0) (*n* = 105 from 7 coll.), (sub)cylindrical or (sub)fusiform, also (sub)utriform, seldom subclavate, sometimes undate, sometimes filled with yellowish amorphous content, apex usually crystalliferous, without or with only short pedicel and sometimes with rounded base, walls very variable from (0.5) 1.0 (bulge)–3.0 (4.5) μm (neck) thick, weak reaction with 3% KOH. **Cheilocystidia** similar in appearance and size. **Pileipellis** constituted by an epicutis made up of parallel hyphae 6–13 μm wide, with finely encrusting and parietal brownish pigment, subcutis with wider and paler to hyaline elements, up to 15 (20) μm wide, epicutis in some young basidiomata with rather spare thin hyaline hyphae, with scattered free ends (belonging to velipellis remnants). **Stipitipellis** consisting of a cutis bearing numerous bundles of metuloid caulocystidia on the entire length of the stipe, but vanishing abruptly towards the base, intermixed with thin-walled colourless cauloparacystidia. **Caulocystidia** 30–65 × 10–15 μm, mostly (sub)cylindrical or subfusiform, (sub)clavate, apex usually crystalliferous, walls 0.5 (bulge)–2.5 μm (neck) thick, weak reaction with 3% KOH. **Clamp-connections** abundant in all tissues.

Habitat and known distribution: *Inocybe angulatosquamulosa* has been found both on park-like terrain on the lawn near deciduous trees, and on at times rather moist terrain, at a dam along the river Isar, with *Salix* nearby. In the original description Stangl (1984) also mentions a collection found on alluvial terrain near *Salix*, *Populus*, *Fraxinus,* and *Alnus*, whereas the type collection was found in a park with *Corylus*, *Quercus*, *Fagus,* and other deciduous trees. The type

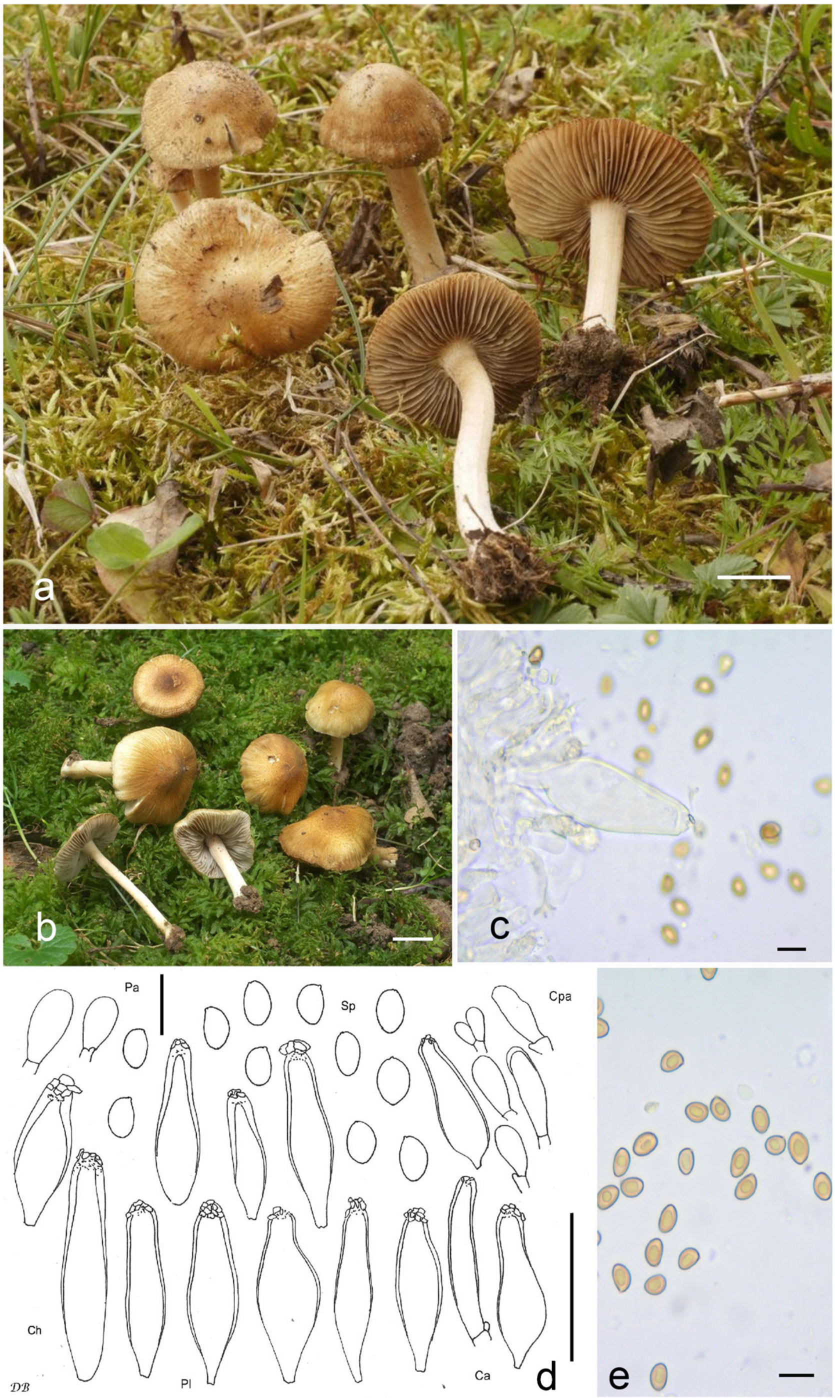


Fig. 11 *Inocybe angulatosquamulosa* **a** DB1-10-13-7, scale bar 1 cm. **b** DB8-8-14-4, scale bar 1 cm. **c** Pleurocystide (DB1-10-13-7), scale bar 10 µm. **d** Microscopical characters (DB1-10-13-7), Ca Caulocystidia, Cpa Cauloparacystidia, Ch Cheilocystidia, Pa Paracystidia, Pl Pleurocystidia, Sp Spores; scale bar spores 10 µm, scale bar cystidia 50 µm. **e** Spores (DB1-10-13-7), scale bar 10 µm

collection and some of our collections were found in Germany, but the species has also been collected in Finland and Estonia in parks with deciduous trees (*Quercus robur*, *Tilia*, and *Betula pendula*). In mixed forests often the presence of *Picea abies* alongside deciduous trees has been noted. It appears to be a calciphilous species, but maybe not as demanding *as I. leochroma.*

Phenology: July to October.

Collections studied: FINLAND, Varsinais-Suomi, Lohja, Virkkala, Pähkinäniemi, Grid 27° E: 6680:3332, E slope, deciduous forest with *Betula*, *Fraxinus excelsior*, *Populus tremula,* and *Alnus glutinosa*, *Aegopodium podagraria* abundant, on mull, calcareous soil, with *Cystolepiota adulterina*, 3 Aug 2000, leg./det. *J. Vauras* 16,389 (TUR-A; FinBOL 606-14).- Etelä-Häme, Urjala, Raikonkulma, Raikko, NE of Kalkkimäki, Grid 27° E: 67701:3080, E of the field, rich forest with *Picea abies*, *Betula*, *Alnus incana,* and *Populus tremula,* on mull soil in calcareous area, 9 Sep 2010, leg./det. *J. Issakainen* & *J. Vauras* 27,775 (TUR-A).- GERMANY, Baden-Württemberg, Heidelberg, war cemetery, TK25 6618/1, alt. 292 m, lawn with *Quercus robur*, *Fagus sylvatica*, 1 Aug 2014, leg./det. *D. Bandini* (KR-M-0042369, DB1-8-14-6, BAN670, MH366613).- Ibidem, at some distance of former location, alt. 290 m, *Fagus sylvatica, Quercus robur*, 8 Aug 2014, leg./det. *D. Bandini* (KR-M-0042370, DB8-8-14-4, BAN683, MH366614).- Ibidem, at some distance, alt. 300 m, *Quercus robur*, 29 Aug 2014, leg./det. *D. Bandini* (KR-M-0042371, DB29-8-14-2, BAN797, MH366615).- Bayern, Dingolfing-Landau, Mamming, TK25 7341/2, alt. 350 m, base of dam near river Isar, with *Salix caprea*, *Salix alba*, 1 Oct 2013, leg./det. *D. Bandini* & *B. Oertel* (KR-M-0038277, DB1-10-13-7, BAN440).

For holotype of *I. angulatosquamulosa* see below.

Comments: *Inocybe angulatosquamulosa,* first described by Stangl (1984) and later rarely re-described in literature (e.g. by Ferrari 2004, 2006), is mainly characterised by the mostly speckled fibrillose to subsquamulose pileus reminding—as already Stangl points out—of *I. margaritispora* (Berk.) Sacc. or *I. squamata* J.E. Lange, as well as by the entirely pruinose stipe with a bulbous base and the small smooth spores. *Inocybe angulatosquamulosa* has been synonymised by Kuyper (1986) with *I. ochroalba,* and in accordance to this, in the posthumously published monograph by Stangl (1989) the species has been treated as *I. ochroalba,* but with a separate description (see also Gminder 2010). In a later article Kuyper (1990) revokes this synonymisation on the basis of the examination of some additional material and of distinguishing morphological features.

Morphologically, *I. ochroalba* can be distinguished from *I. angulatosquamulosa* by the paler colour of the pileus, the missing speckles, the often ample velipellis, the different texture of the pileus, the more greyish lamellae, the pinkish-reddish colour of the stipe, the missing bulb, larger spores and especially the differently shaped hymenial cystidia. Molecularly, *I. ochroalba* and *I. angulatosquamulosa* are not even contiguous (see comments to *I. leochroma*).

Inocybe langei R. Heim, another species with small spores, differs from *I. angulatosquamulosa* by generally brighter colours of the pileus, smoother pileus surface, scarcer caulocystidia, and differently shaped hymenial cystidia with a stronger KOH reaction. *Inocybe leochroma* has a more intense and brighter pileus colour, a more lanose and less speckled texture of the pileus, a rougher pruina of the stipe, and on average larger spores and smaller hymenial cystidia. The microscopic details of the type of *I. angulatosquamulosa* largely fit the measurements of our own collections. The spores are a bit wider though, and due to two-spored basidia some spores with a size up to 11.2 μm were found. In terms of ITS sequences, our collections were identical with the one derived from the type specimen.

Inocybe splendentoides Bon 1990
Figure 12

Pileus 30–80 (100) mm wide, (sub)conical, (sub)campanulate, convex or expanded, with more or less pronounced large umbo, when old depressed around the centre, when young margin usually deflexed, rarely slightly inflexed, later straight to uplifted and occasionally undate, sometimes torn; when young with greyish remnants of a velipellis; mostly slightly sticky when wet and therefore covered with particles of soil at least around the umbo; colour light brown, nut-brown and different shades of brown, often with slight reddish, sometimes with ochraceous tinge towards the umbo, sometimes darker when the velipellis is vanished (Mu 5YR 4/3–4/6, 7.5YR 5/6–5/8, 4/4–4/6); surface at first entirely glabrous, towards the margin later finely rimose to innately fibrillose with diverging fibres and near or at the margin pileipellis with age entirely disappearing or excoriated and therefore there showing the cream-coloured flesh—sometimes in a strip of almost 10 mm; no cortina observed. **Lamellae** moderately crowded (ca. 50–75, l = 1–3), (sub)ventricose, narrowly adnate, to adnate with decurrent tooth; whitish when young, then greyish-brownish to light brown; edge fimbriate, sometimes rather undate, whitish. **Stipe** 50–100 × 5–12 mm, cylindrical or widening towards the base, base widened to (sub)bulbous (there up to 150 mm), glabrous, at first whitish or creamy, later flesh-coloured; pruinose on the entire length of the stipe. **Context** whitish in the pileus, in the stipe at first creamy, then slightly flesh-coloured. **Smell** aromatical with fruity tinge, but subspermatical when cut. **Colour of exsiccata** pileus brown with reddish hue (Mu 5YR 4/4–4/6, 7.5YR 4/4–4/6), lamellae and stipe somewhat lighter in colour and sometimes more ochraceous brown, no darkening or blackening with drying.

Spores 8.1–13.0 μm (av. 10.0 μm, SD 0.8 μm) × 4.7–7.4 μm (av. 6.0 μm, SD 0.4 μm); Q = 1.4–1.9 (av. 1.7, SD 0.1) (*n* = 120 from 3 coll.), smooth, (sub)amygdaloid, often with more or less explicit suprahilar depression, apex subacute or (sub)obtuse. **Basidia** 25–35 (40) × 7–10 μm, generally 4-spored. **Lamellae edges** sterile, composed of cheilocystidia and numerous hyaline, (sub)clavate, cylindrical or subglobose paracystidia, not seldom catenate or with septate base and sometimes in intermediate states. **Pleurocystidia** 40–76 μm (av. 57 μm, SD 8.7 μm) × 11–26 μm (av. 17 μm, SD 3.7 μm); Q = 2.4–5.6 (av. 3.5, SD 0.8) (*n* = 45 from 3 coll.), sometimes rather ventricose, mostly (sub)utriform, also (sub)cylindrical, occasionally with short clearly demarcated neck, at the apex wide, without or with short pedicel, apex usually crystalliferous, walls (0.5) 1.0 (bulge)–2.5 (3.0) μm (neck) thick, positive reaction with 3% KOH. **Cheilocystidia** similar

Fig. 12 *Inocybe splendentoides* **a** DB4-10-13-1, scale bar 1 cm. **b** DB16-10-11-1, scale bar 1 cm. **c** Cheilocystide (DB4-10-13-1), scale bar 10 µm. **d** Microscopical characters (DB4-10-13-1), Ca Caulocystidia, Cpa Cauloparacystidia, Ch Cheilocystidia, Pa Paracystidia, Pl Pleurocystidia, Sp Spores; scale bar spores 10 µm, scale bar cystidia 50 µm. **e** Spores (DB4-10-13-1), scale bar 10 µm

in appearance and size, sometimes with yellowish content. **Pileipellis** constituted by an epicutis made up of parallel hyphae 5–10 µm wide, often but not always with finely encrusting and parietal yellowish to orange brownish-yellowish pigment, subcutis with wider and paler elements, in deeper layers not seldom strongly inflated and then up to 60 µm wide, epicutis covered with thin hyaline hyphae, with scattered free ends (belonging to velipellis remnants). **Stipitipellis** consisting of a cutis bearing numerous bundles of metuloid caulocystidia on the entire length of the stipe, intermixed with thin-walled colourless cauloparacystidia. **Caulocystidia** 35–60 × 10–20 µm, (sub)utriform, (sub)-cylindrical or even (sub)clavate, apex usually crystalliferous, walls 1.0 (bulge)–2.5 µm (neck) thick, positive reaction with 3% KOH. **Clamp-connections** abundant in all tissues.

Habitat and known distribution: Known from moist places, either swampy ground or near riversides, with *Salix* nearby. The type collection was found in France, our collections are from Germany, and putative *I. splendentoides* sequences are known from France (EL22506 as *I. splendens*; FN550911), from Italy (voucher 15698 as *I. pseudoreducta*; JF908156), and from China (e.g. HMJAU26127 as *I. splendens*; KU359779).

Phenology: The type collection was found in October and our collections were found in October and November.

Collections studied: GERMANY, Baden-Württemberg, Rhein-Neckar-Kreis, Bammental, TK25 6618/2, alt. ca. 160 m, swampy ground with *Salix* sp., *Populus* sp., 16 Oct 2011, leg./det. *D. Bandini* (KR-M-0042351, DB16-10-11-1, BAN145, MH366585).- Ibidem, at several hundred metres distance, alt. 125 m, shadowy meadow near rivulet, with *Salix* sp., *Populus* sp., *Alnus glutinosa*, 21 Oct 2015, leg./det. *D. Bandini* (KR-M-0042352, DB21-10-15-1, BAN1834, MH3665586).- Bayern, Dingolfing-Landau, Mamming, TK25 7341/2, alt. 350 m, riverside with *Salix* sp., *Populus* sp., 4 Oct 2013, leg. *D. Bandini*, *B. Oertel* & *L. Quecke*; det. *D. Bandini* & *B. Oertel* (KR-M-0042353, DB4-10-13-1, BAN1839, MH366587).

For holotype of *I. splendentoides* see below.

Comments: *Inocybe splendentoides* is mainly characterised by its often large size, stout habit, typically excoriated margin of the brown(ish) pileus, often with reddish tinges in older specimens, entirely pruinose stipe with bulbous base, spores up to 13 μm, on average rather short hymenial cystidia (in our collections < 60 μm, in type collection 62 μm) and catenate paracystidia. As already Bon points out in the original description (Bon 1990), the species is very close to *I. splendens* R. Heim and might initially be confounded with it. However, *I. splendens* is not only smaller (pileus 3–5 cm, see Heim 1931), the colour of the pileus is described and depicted by Heim as orange-dark-brown, violet or purple blackish ("bistre-orangé, lilacines ou purpurin-noirâtre"). And the watercolour painting of the species in the monograph of Heim (1931), which has been chosen as lectotype by Kropp et al. (2010), (see also Consiglio et al. 2014), shows a strongly rimose surface. The spores usually have a very typical navicular shape or, if not, often are at least papillate. No mention is made of the catenate paracystidia and no mention of an excoriated margin of the pileus. The habitat seems to be different as well. The colour of *I. terrifera* is yellow-ochraceous, the margin of the pileus is usually not excoriated, the reaction of the walls of the hymenial cystidia with KOH is weak to subnull, and the habitat is not the same, since *I. terrifera* can fairly often be found on lawn in parks or cemeteries. The type collection of *I. terrifera* was found in the Bois de Vincennes in Paris. *Inocybe alluvionis* Stangl & J. Veselský shows a different pileus colour and surface, ample velipellis at the centre of the pileus, it has furthermore on average somewhat smaller and narrower spores and smaller cystidia (Stangl and Veselský 1976). The molecular analysis of the type of *I. alluvionis* failed, but the morphological examination showed that in all details own collections fit well to the description of Stangl and Veselský, including form and size of spores and hymenial cystidia (for holotype of *I. alluvionis* see below).

There are only few references to *I. splendentoides* in the literature, one of them to a collection from dunes in Cantabria in Spain (Picón Gonzáles 2008). A photograph of a collection from France has been published by the Société mycologique du Poitou (2009). It seems that *I. splendentoides* is not a common species or has been mistaken for *I. splendens* or *I. terrifera* (see below)—but in appropriate terrain it can be found in large numbers, as has been the case in 2013 at the riverside of the Isar near Mamming. Molecularly it is most closely related to *I. alluvionis* and *I. serotina* Peck, the latter being a common species in sand-dune areas of the southern North Sea coast, with large basidiomata with ample whitish velipellis at the centre of the pileus, often (sub)clavate hymenial cystidia and large thick-walled spores. *Inocybe splendentoides* differs from *I. alluvionis* molecularly by fifteen base pairs and sixteen gaps.

Inocybe terrifera Kühner 1955

Figure 13

Pileus 30–80 (100) mm wide, when young (sub)-campanulate or even undate subglobose, later broadly convex to expanded, but very often somehow deformed, with more or less pronounced large umbo, margin involute or incurved when young, later also decurved, straight or undate uplifted when old; young basidiomata inconsistently covered with a whitish-greyish velipellis, being slightly sticky, later sometimes as scattered remnants to be observed also on older basidiomata; colour very often unequally and sometimes speckled dingy yellowish, yellowish ochraceous, ochraceous or ochraceous brownish, brownish, sometimes with slight orange hue (Mu 10YR 7/6–7/8, 6/6–6/8, 5/6–5/8, 7.5YR 6/6–6/8), towards the umbo also much darker or greyish because of velipellis and adhering soil particles; surface at the umbo first glabrous then often somehow cracked, fissured or torn, towards the margin glabrous, finely felty to innately fibrillose, seldom subrimulose, but mostly fibres not or only at the margin diverging; very young basidiomata at the margin sometimes whitish from remnants of a velipellis. **Lamellae** moderately crowded (ca. 40–60, l = 1–3), adnexed to adnate, also emarginate with decurrent tooth, ventricose, whitish, greyish, later greyish-brownish, brownish or rusty brownish, occasionally speckled; edge even or fimbriate, often notchy, whitish to concolorous. **Stipe** 40–100 × 4–15 mm, cylindrical or widening towards the base, base mostly (sub)bulbous, seldom also with a marginate bulb (up to 20 mm), glabrous, whitish, then with yellowish tinge, flesh-coloured or slightly brownish; pruinose on the entire length of the stipe. **Context** whitish in pileus and stipe, cortex of the stipe later sometimes flesh-coloured or brownish. **Smell** faintly aromatic, also slightly

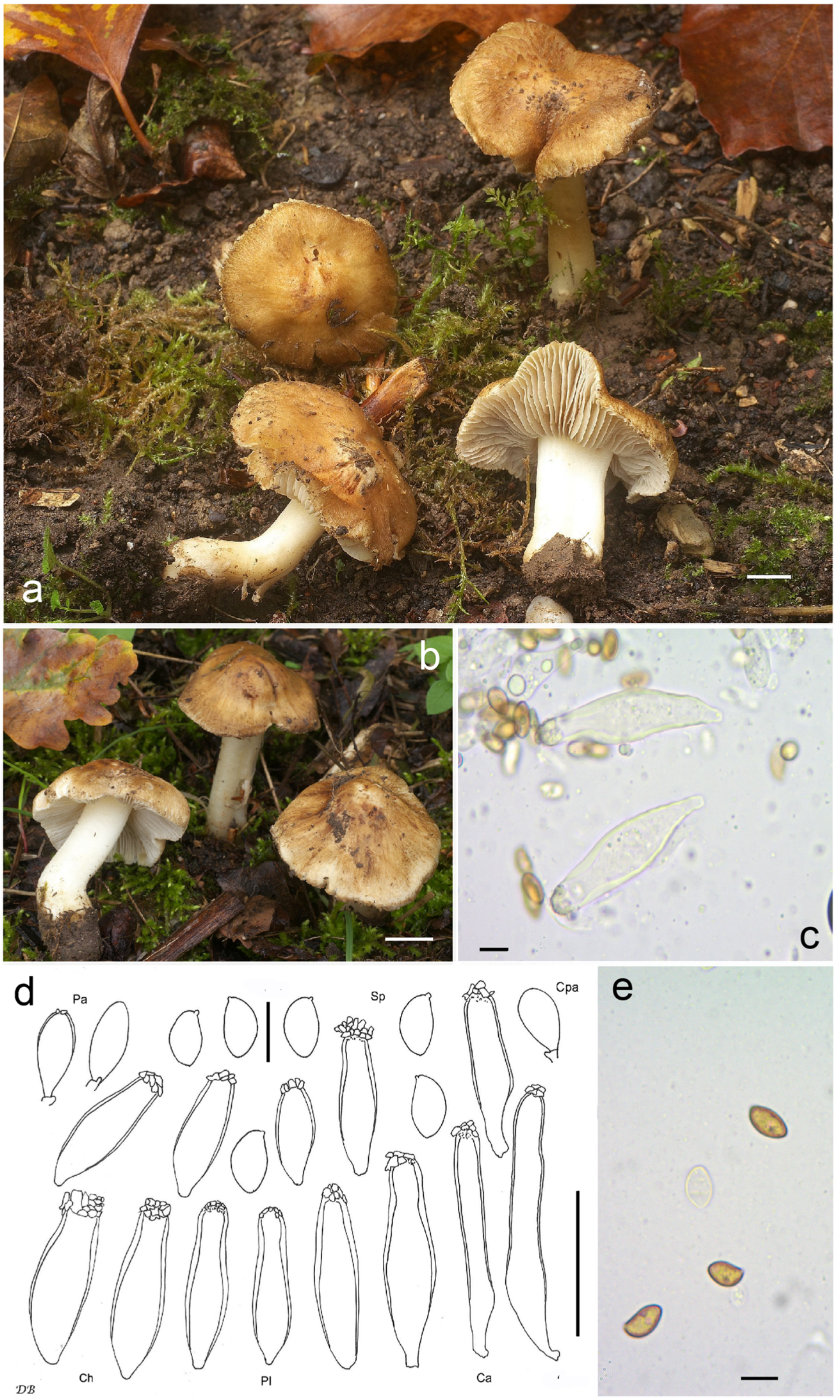


Fig. 13 *Inocybe terrifera* **a** DB15-9-13-2, scale bar 1 cm. **b** DB31-8-14-6, scale bar 1 cm. **c** Cheilocystidia (DB15-9-13-2), scale bar 10 µm. **d** Microscopical characters (DB12-9-11-1), Ca Caulocystidia, Cpa Cauloparacystidia, Ch Cheilocystidia, Pa Paracystidia, Pl Pleurocystidia, Sp Spores, scale bar spores 10 µm, scale bar cystidia 50 µm. **e** Spores (DB15-9-13-2), scale bar 10 µm

fruity or (sub)spermatical, at least when cut. **Colour of exsiccata** pileus nut-brown, brown with faint reddish hue or greyish brown (Mu 7.5YR 5/6–5/8, 4/4–4/6, 10YR 4/4–4/6), lamellae and stipe concolorous or a little lighter in colour, no darkening or blackening with drying.

Spores 8.6–12.3 µm (av. 10.3 µm, SD 0.7 µm) × 4.7–7.3 µm (av. 6.0 µm, SD 0.4 µm); Q = 1.4–2.0 (av. 1.7, SD 0.1) (*n* = 120 from 3 coll.), smooth, (sub)amygdaloid, with or without slight suprahilar depression, apex (sub)obtuse to subacute, sometimes with indistinct pseudopore. **Basidia** 25–35 × 8–12 µm, usually 4-spored, seldom also 2-spored, and then spores often greater than 14 µm. **Lamellae edges** sterile, composed of cheilocystidia and numerous hyaline, (sub)clavate, cylindrical or subglobose, thin-walled paracystidia, but also in different intermediate states, and then with walls up to 1 µm. **Pleurocystidia** 38–80 µm (av. 59 µm, SD 11 µm) × 12–23 µm (av. 17 µm, SD 2.9 µm); Q = 2.3–5.4 (av. 3.5, SD 0.8) (*n* = 45 from 3 coll.), usually (sub)utriform, but also subfusiform, (sub)cylindrical, seldom (sub)clavate, mostly with rather short neck, at the apex usually wide, apex usually crystalliferous, without or with only short pedicel, walls (0.5) 1.0 (bulge)–2.5 (3.0) µm (neck) thick, almost colourless or weak reaction with 3% KOH. **Cheilocystidia** similar in appearance and size. **Pileipellis** constituted by an epicutis made up of parallel hyphae 3.5–8 µm wide, often but not always with finely encrusting and parietal yellowish or yellowish-brownish pigment, sometimes also entirely yellowish-brownish, subcutis with wider and paler to hyaline elements, up to 25 (30) µm wide, epicutis in young basidiomata sometimes covered with thin hyaline hyphae, with scattered free ends (belonging to velipellis remnants). **Stipitipellis** consisting of a cutis bearing numerous bundles of metuloid caulocystidia on the entire length of the stipe, intermixed with thin-walled colourless cauloparacystidia, sometimes in intermediate states, and then slightly thick-walled (−0.5 µm). **Caulocystidia** 35–80 × 10–15 (20) µm, often long and narrow (sub)cylindrical, also (sub)fusiform, (sub)utriform, (sub)clavate or deformed, apex usually crystalliferous, walls 0.5 (bulge)–2.0 (2.5) µm (neck) thick, almost colourless or only weak reaction with 3% KOH. **Clamp-connections** abundant in all tissues.

Habitat and known distribution: Often in large numbers preferably on lawn in parks and in cemeteries or similar places, also near waysides. *Inocybe terrifera* is mostly associated with frondose trees, often with *Quercus*, but sometimes there are also conifers near by. The type collection stems from France. Our collections are from Germany. Probably widespread but may be sometimes mistaken for *I. splendens.* No further sequences are known.

Phenology: From August to October.

*Collections studied***:** GERMANY, Baden-Württemberg, Rhein-Neckar-Kreis, Wiesenbach, TK25 6619/1, alt. 173 m, wayside with *Picea abies*, *Quercus robur*, *Fraxinus excelsior*, 12 Sep 2011, leg. *D. Bandini*; det. *D. Bandini & B. Oertel* (KR-M-0038272, DB12-9-11-1, BAN105).- Baden-Württemberg, Rhein-Neckar-Kreis, Heidelberg, war cemetery, TK25 6618/1, alt. 290 m, lawn with *Quercus robur*, *Picea abies*, *Fagus sylvatica*, 15 Sep 2013, leg./det. *D. Bandini* (KR-M-0042368, DB15-9-13-2, BAN438).- Baden-Württemberg, Rhein-Neckar-Kreis, Wiesloch, cemetery, TK25 6718/1, alt. 123 m, lawn with *Quercus robur*, 31 Aug 2014, leg. *D. Bandini*; det. *D. Bandini & B. Oertel* (KR-M-0042366, DB31-8-14-6, BAN802, MH366582).- Baden-Württemberg, Karlsruhe, Innenstadt, E Engler-Bunte Ring, TK25 7016/1, alt. 115 m, lawn with *Quercus robur*, 15 Oct 2015, leg. *A. Schneider*; det. *D. Bandini & B. Oertel* (KR-M-0044137, BAN1027, MH366580).- Baden-Württemberg, Karlsruhe, Südweststadt, Beiertheimer Allee, N Schnetzlerstraße, TK25 7016/1, alt. 115 m, lawn with *Tilia cordata*, 15 Oct 2015, leg. *T. Bernauer*; det. *D. Bandini & B. Oertel* (KR-M-0044139, BAN1030, MH366581).- Ibidem*,* at some distance, lawn with *Quercus cerris* and *Quercus robur*, 15 Oct 2015, leg. *A. Schneider*; det. *D. Bandini & B. Oertel* (KR-M-0044140, BAN1018, MH366578).- Ibidem*,* in some distance, lawn with *Tilia cordata*, 15 Oct 2015, leg. *A. Schneider*; det. *D. Bandini & B. Oertel* (KR-M-0044175, BAN1028, MH366579) (here only those of totally 14 collections of which an DNA-analysis has been made are listed).

For holotype of *I. terrifera* see below.

Comments: *Inocybe terrifera* is characterised by stout, often large and deformed basidiomata, occasionally hidden deep in the ground. It has mostly yellow-ochraceous pilei that are almost always covered with particles of soil because of the sticky velipellis. The stipe is entirely pruinose and the spores on average are smaller than 11 µm. The species belongs to the *I.* sect. *Splendentes* and has been included in *I.* subsect. *Phaeoleucinae* by Bon (1997), thus together with species with a usually non-bulbous stipe base like *I. phaeoleuca* Kühner. Since the stipe base of *I. terrifera* is almost always somewhat bulbous and since also molecularly the species is similar to other species of the *I.* subsect. *Splendentinae*, it should be listed there. – It can be distinguished from *I. splendentoides* mainly by the more ochraceous pileus colour, the usually not excoriated margin of the pileus, the weaker reaction of the walls of the hymenial cystidia with KOH and the different habitat. The colour of the pileus of *I. splendens,* synonymised with *I. terrifera* by Kuyper (1986) and in consequence also by Stangl (1989), is darker brown with a purple hue, without a thick velipellis, the spores are often navicular or at least papillate and the cystidia have a different shape (see above). Colour and texture of the pileus of *I. alluvionis* are unlike *I. splendentoides.* The velipellis of *I. alluvionis* mostly centres in the middle of the pileus in older basidiomata, the pilei are usually less deformed than in *I. terrifera*, the spores on average are smaller, and the cystidia are differently shaped and on average also smaller. Furthermore, *I. alluvionis* grows in moist habitat often near *Alnus*. Sequencing of the type of *I. terrifera* failed, but morphologically the type falls within the character ranges of the collections described here. The spores are on average a little smaller, but have the same shape, and the hymenial cystidia have the same shape and size. *Inocybe terrifera* is occasionally mentioned in literature (e.g. Stangl 1985; Bizio and Consiglio 2003; Ferrari 2006). Apparently, however, the species described as *I. terrifera* not always *is I. terrifera*. For instance the description—moist habitat, excoriated margin of pileus, brown colour of pileus—as well as the colour drawing of "*I. terrifera*" in Stangl and Veselský (1971) point to *I. splendentoides* (see hereto Kuyper 1986). All named species of *I.* subsect. *Splendentinae* can also be distinguished molecularly (see above).

Inocybe stenospora Stangl & Bresinsky 1983
Figure 14

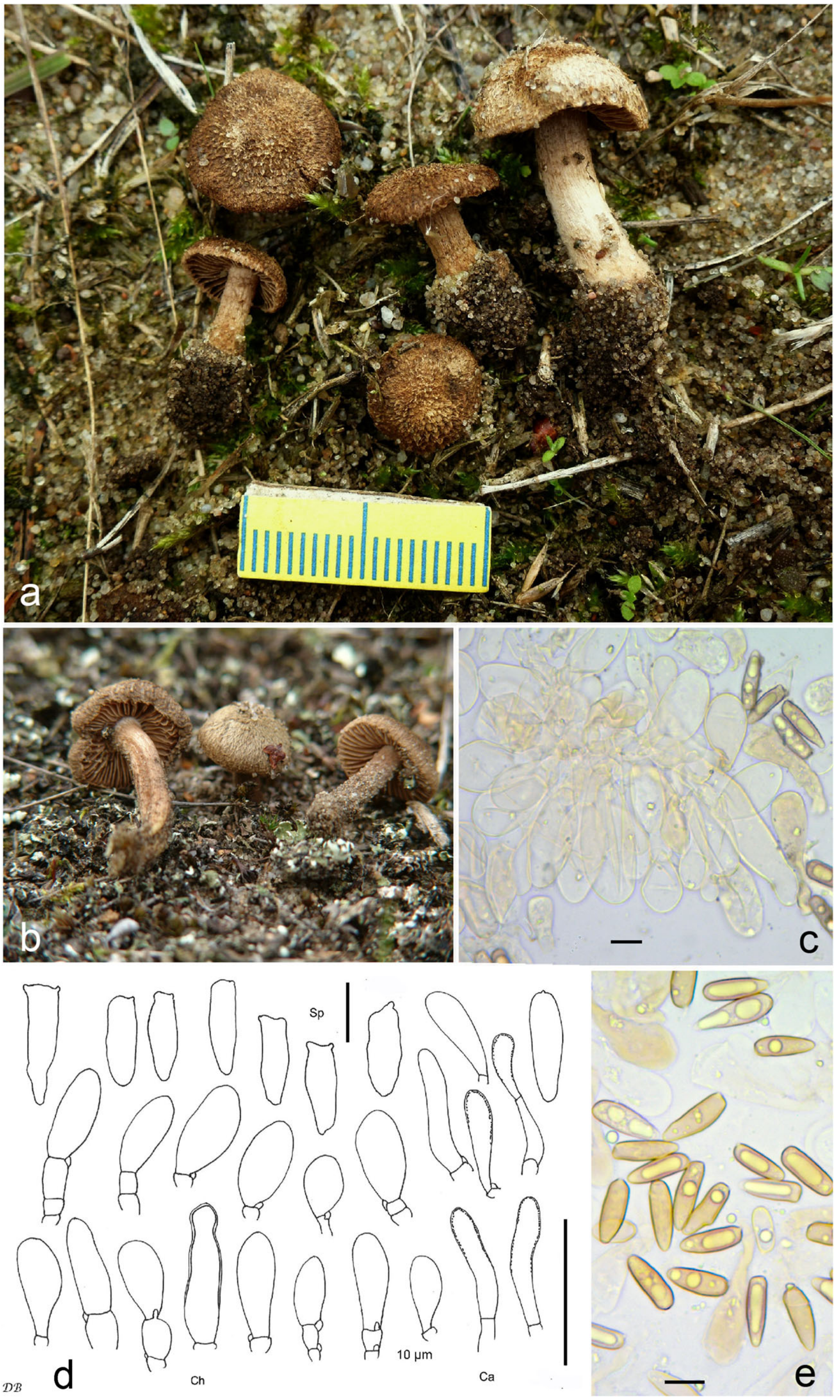


Fig. 14 *Inocybe stenospora* **a** DB7-10-13-Geiter. **b** DB24-10-12-Geiter. **c** Cheilocystidia (DB7-10-13-Geiter), scale bar 10 µm. **d** Microscopical characters (DB7-10-13-Geiter), Ca Caulocystidia, Ch Cheilocystidia, Sp Spores; scale bar spores 10 µm, scale bar cystidia 50 µm. **e** Spores (DB7-10-13-Geiter), scale bar 10 µm

Pileus 10–30 mm wide, subglobose or campanulate to convex, later expanded, without or with low broad umbo, sometimes depressed around the centre, margin incurved to more or less abruptly decurved, often even when old; young basidiomata with scattered remnants of a greyish velipellis; colour light brown, hazel-brown to dark brown with greyish or even darker tinge, sometimes with faint reddish hue (Mu 10YR 4/3–4/6, 3/3–3/6, 7.5YR 3/3–3/4); surface thickly lanose-fibrillose to subquamulose or scrubby, often with erect fibre bundles in or around the centre, but also with appressed fibres especially towards the border; young basidiomata sometimes with remnants of a brownish cortina. **Lamellae** moderately distant (ca. 30–40, l: 1–3), adnate to emarginate with decurrent tooth or deeply decurrent, (sub)ventricose, brown to dark greyish brown with faint reddish hue; edge fimbriate, at first whitish, later sometimes almost concolorous. **Stipe** 15–30 × 3–6 mm, stout, cylindrical to widened towards the base and sometimes also towards the apex, when young thickly covered with whitish tissue, later streaky or light brown, lighter in colour at the extreme apex and at the base; pruinose only at the apex of the stipe. **Context** whitish in the pileus, light brown in the stipe, especially in the cortex of the stipe; with age getting darker brown. **Smell** subnull. **Colour of exsiccata** pileus brown to dark brown (Mu 10YR 4/3–4/4, 3/3–3/6), lamellae and stipe somewhat lighter in colour, no obvious darkening or blackening with drying.

Spores 9.3–21.0 μm (av. 15.1 μm, SD 2.0 μm) × 4.2–6.5 μm (av. 5.2 μm, SD 0.5 μm); Q = 1.9–3.7 (av. 2.9, SD 0.3) (*n* = 120 from 3 coll.), truncate projectile-formed or almost smooth to slightly sinuose or undate, seldom with hint of nodules. **Basidia** 30–43 × 7–12 μm, usually 4-spored, but sometimes also 2-spored, and then with sterigmata up to 10 μm. **Lamellae edges** sterile, composed of cheilocystidia and numerous, mostly (sub)clavate or subglobose thin-walled paracystidia. **Cheilocystidia** 14–65 μm (av. 33 μm, SD 10.4 μm) × 9–20 μm (av. 14 μm, SD 2.9 μm); Q = 1.3–4.4 (av. 2.4, SD 0.8) (*n* = 45 from 3 coll.), mostly subglobose or balloon-shaped or (sub)clavate to subcylindrical, not seldom also deformed or sac-shaped, usually thin-walled, but sometimes also slightly thick-walled, walls then around 0.5 μm, often brownish; no reaction with 3% KOH. **Pleurocystidia** not observed. **Pileipellis** consisting of an epicutis made up of parallel hyphae 5–12 (15) μm wide, with finely encrusting and parietal brownish pigment, subcutis with wider and paler elements, up to 18 (20) μm wide, epicutis in young basidiomata sometimes covered with thin hyaline hyphae, with scattered free ends (belonging to velipellis remnants). **Stipitipellis** consisting of a cutis bearing rather sparse bundles of thin-walled caulocystidia at the apex of the stipe. **Caulocystidia** (15) 20–50 × 10–15 μm, (sub)cylindrical or subclavate to (sub)ovoid, no reaction with 3% KOH. **Clamp-connections** abundant in all tissues.

Habitat and known distribution: Sandy inland-dunes, sandy heath terrain (as for instance former restricted military areas) with *Calluna vulgaris* and *Pinus sylvestris*. The type collection and other collections were found in Germany in the states Sachsen-Anhalt, Nordrhein-Westfalen and Bayern. The species is also known from Finland (Kytövuori et al. 2005), Denmark and Hungary (Maarbjerg 2017).

Phenology: August to October.

Collections studied: GERMANY, Sachsen-Anhalt, Jerichower Land, Gommern, Düne Fuchsberg, TK25 3936/2, alt. 50 m, sand-dune-terrain with *Pinus sylvestris*, *Betula* sp., *Quercus rubra*, *Helianthemum nummularium*, 24 Oct 2012, leg./det. *R. Geiter* (KR-M-0042356, DB24-10-12-Geiter, BAN321, MH366597).- Ibidem, 7 Oct 2013, leg./det. *R. Geiter* (KR-M-0042357, DB7-10-13-Geiter, BAN714, MH366598).- Ibidem, 20 Aug 2014, leg./det. *R. Geiter* (KR-M-0042358, DB20-8-14-Geiter).

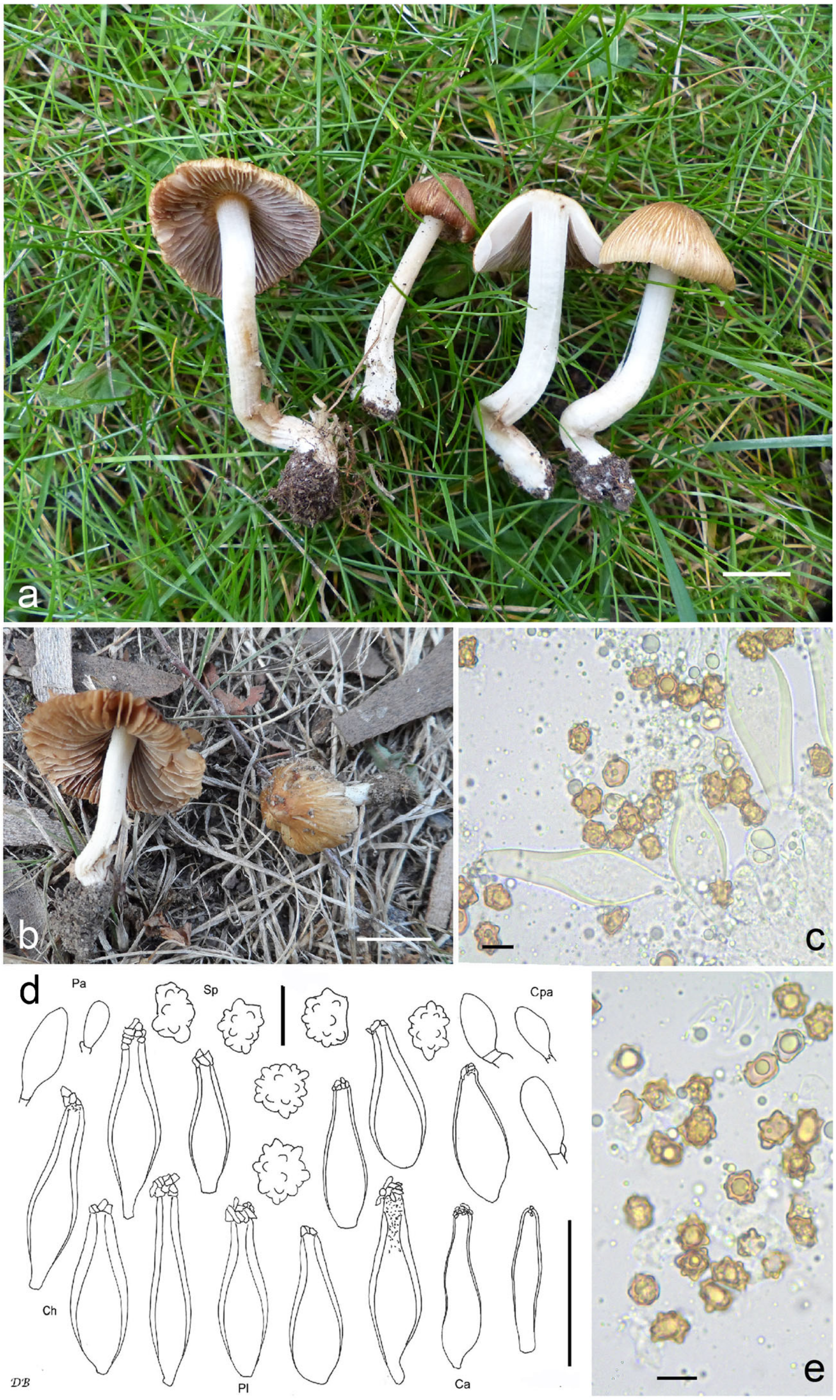
For holotype of *I. stenospora* see below.

Comments: *Inocybe stenospora,* a rather small species with brown pileus, is easily recognised by its unique spores, reminding of those of *I. lacera* (Fr.: Fr.) P. Kumm., but having a more or less pronounced "spur", which typically cannot be observed in *I. lacera*, but—as already noted by Stangl and Bresinsky in their original description (1983)—reminds of certain species of *Lepiota* subsect. *Stenosporae.* Similar spores, however, can also be seen in other species of *Inocybe* viz. *I. dolichospora* Malençon as well as in species of the group around *I. chelanensis* D.E. Stuntz (see Kropp and Matheny 2004), known from North America. Macroscopically *I. stenospora* can easily be mistaken for *I. lacera*, or for a species of the nodulose-spored members of the clade Lanuginosae as for instance *I. lanuginosa* (Bull.: Fr.) P. Kumm.. - In addition, the pileus of the latter species might be as lanose-fibrillose-squamulose as the pileus of *I. stenospora*. Microscopically though *I. stenospora* is probably unique because of its spore shape and size in combination with its ovoid, subglobose, subcylindrical or differently formed thin-walled, sometimes also slightly thick-walled cheilocystidia and the lack of pleurocystidia. *Inocybe stenospora* is rarely mentioned in the literature. In Germany it is only known from a few locations (see Krieglsteiner 1991; Wöldecke 1998; Kasparek 2000; Ludwig 2017), mostly sandy inland-dunes e.g. in restricted military areas. The collections examined fit the description of Stangl and Bresinsky (1983) in every detail, and the micro-details of the holotype are largely similar to the measurements given above, only the spores are on average a little narrower and the cheilocystidia a little larger. The type collection too has been found in inland-dunes (near Offenstetten in Bayern). *Inocybe stenospora* is not listed in the fungi databases of Austria (http://austria.mykodata.net/, Switzerland (https://www.wsl.ch/de/biodiversitaet/artenvielfalt/pilze/swissfungi/verbreitungsatlas.html, and the Netherlands (https://www.verspreidingsatlas.nl/paddenstoelen). So it seems that *I. stenospora* is as rare as it is reported to be, although it was perhaps sometimes macroscopically mistaken for *I. lacera.* This species is known from the same location, where the examined collections of *I. stenospora* were found. As our molecular analyses have shown, *I. stenospora* does not belong to *I.* subgen. *Mallocybe,* but was placed in *I.* subgen. *Inocybe*. *Inocybe casimirii* Velen. (Kobayashi 2002), another species without pleurocystidia included in this clade, has entirely different spores than *I. stenospora*. The same holds true for the other known species included in this clade, as for instance *I. teraturgus* M. M. Moser, a species that macroscopically easily can be mistaken for a *Mallocybe* as is the case also with some other species so as with *I. mallopoda* Matheny & Bougher (Matheny and Bougher 2017).

Inocybe strickeriana Bandini, Anja Schneider & M. Scholler sp. nov.

Figure 15

Fig. 15 *Inocybe strickeriana* **a** Holotype (KR-M-0044749), scale bar 1 cm. **b** KR-M-0044126, scale bar 1 cm. **c** Cheilocystidia (KR-M-0044749), scale bar 10 µm. **d** Microscopical characters (KR-M-0044749), Ca Caulocystidia, Cpa Cauloparacystidia, Ch Cheilocystidia, Pa Paracystidia, Pl Pleurocystidia, Sp Spores; scale bar spores 10 µm, scale bar cystidia 50 µm. **e** Spores (KR-M-0044749), scale bar 10 µm



MycoBank number: MB827578, ITS barcode GenBank: MG012477.

Etymology: The species is named in honour of Paul Stricker (1878–1956), a schoolteacher and popular mycologist from Karlsruhe (Germany).

Short description: Fairly small and gracile species with often amber-coloured, but also light brown, when old red-brown rimose pileus, entirely pruinose stipe with a small bulb, nodulose spores, measuring 7.5–13.9 × 6.6–11.6 µm and mostly (sub)fusiform hymenial cystidia, pleurocystidia measuring 37–71 × 10–23 µm.

Diagnosis: *Inocybe strickeriana* is related to *I. salicis* and *I. lacunarum.* It differs from both genetically in ITS sequence data, and micro-morphologically from *I. salicis* by a a less moist habitat, more roundish spores with more pronounced nodules and longer caulocystidia, and from *I. lacunarum* by a different pileipellis, smaller spores and hymenial cystidia.

Holotype: GERMANY, Baden-Württemberg, Karlsruhe, Stadtgarten, N Schwanensee, TK25 7016/1, 8.4008 E 48.9973 N, alt. 115 m, near *Quercus cerris*, in some distance also *Quercus robur*, 14 Oct 2016, leg. *A. Schneider* (holotype KR-M-0044749).

Detailed description

Pileus 10–25 mm wide, campanulate or subconical when young, to convex or expanded, sometimes slightly undate, mostly without, but sometimes with low broad umbo, border slightly inflexed or deflexed when young, later straight, in old basidiomata even uplifted; when young centre of the pileus with faint remnants of a greyish velipellis; often amber-coloured (Mu 7.5YR 5/6–5/8, 5YR 5/6–5/8), also light brown (10YR 5/6–5/8), more intense in the centre of the pileus, some basidiomata even when young with reddish tinge, to almost dark red-brown when old or due to certain weather conditions (Mu 10R 3/4–3/6), and then towards the border nearly blackish; surface at first glabrous, then finely radially rimose with appressed fibres, diverging often from almost the centre of the pileus and thus showing the lighter context beneath, when old sometimes deeply torn; pileipellis in some—even young—basidiomata, because of being quite thin, in some places of the pileus entirely vanished; no remnants of a cortina observed. **Lamellae** moderately crowded (ca. 40–60, l = 1–3), ventricose, almost free to adnexed, at first whitish or greyish, then unequally light brown with greyish tinge to almost rusty-brown; edge even to fimbriate, whitish. **Stipe** 15–40 × 2–5 mm, often twisted or crooked towards the base, base usually with a small almost marginate bulb, hidden mostly deep in the ground, glabrous, long time entirely whitish or beige, when old partly brownish; pruinose on the entire length of the stipe. **Smell** not perceived. **Colour of exsiccata** pileus streaky nut-brown or reddish brown (Mu 5YR 4/3–4/6, or 2.5YR 3/4–3/6), lamellae light brown, stipe also light brown, yet darkened in some places—but not blackening with drying.

Spores 7.5–13.9 μm (av. 10.4 μm, SD 0.9 μm) × 6.6–11.6 μm (av. 8.5 μm, SD 0.8 μm); Q = 1.0–1.4 (av. 1.2, SD 0.1) (*n* = 200 from 5 coll.), nodulose, (sub)isodiametrical, with predominantly strongly protruding nodules, with obtuse to (sub)conical apex. **Basidia** 25–35 × 7–10 μm, generally 4-spored. **Lamellae edges** sterile, composed of cheilocystidia and numerous hyaline, (sub)clavate or subglobose, thin-walled paracystidia. **Pleurocystidia** 37–71 μm (av. 54 μm, SD 9.0 μm) × 10–23 μm (av. 16 μm, SD 2.8 μm); Q = 2.3–5.4 (av. 3.5, SD 0.7) (*n* = 75 from 5 coll.), rather ventricose, mostly (sub)fusiform, but also (sub)lageniform or (sub)utriform or even (sub)clavate, without or with only short pedicel, and sometimes filled with yellowish or orange brownish amorphous content, apex usually crystalliferous, walls 1.5 (bulge)–4.0 (4.5) μm (neck) thick, almost colourless or only weak reaction with 3% KOH. **Cheilocystidia** similar in appearance and size. **Pileipellis** constituted by an epicutis made up of parallel hyphae 4–10 μm wide, with finely encrusting and parietal orange brownish pigment, often slightly darker at joints of hyphae, subcutis with wider and paler elements, up to 15 (20) μm wide, epicutis in young basidiomata sometimes covered by thin hyaline hyphae, with scattered free ends (belonging to velipellis remains). **Stipitipellis** consisting of a cutis bearing numerous bundles of metuloid caulocystidia down to the base of the stipe, intermixed with thin-walled colourless cauloparacystidia. **Caulocystidia** 45–100 × 10–25 μm, mostly (sub)fusiform, but also (sub)lageniform, (sub)cylindrical or (sub)utriform, (sub)clavate or deformed, apex usually crystalliferous, walls 1.0 (bulge)–2.5 μm (neck) thick, weak reaction with 3% KOH. **Clamp-connections** abundant in all tissues.

Habitat and known distribution: The species is only known from the type locality in Germany and from the north of France. Basidiomata of the type specimen and the other German collections were found in 2015 and 2016 between two about 30- to 50-year-old oak trees (*Quercus cerris*, *Q. robur*) in an urban park, on regularly mowed and watered lawn 115 m N and 1 m above an artificial pond. Associated plants are *Festuca rubra* ssp. *rubra* as dominant, furthermore *Agrostis capillaris*, *Bellis perennis*, *Potentilla indica*, *Glechoma hederacea*, *Poa angustifolia, Veronica serpyllifolia*, cf. *Prunella vulgaris,* and finally the calciphilous moss *Brachythecium rivulare*. Probably, *Q. cerris* is the mycorrhizal partner, because the basidiomata were closer to this species (5 m to *Q. cerris* vs. 8 m to *Q. robur*). *Quercus cerris*, the "Turkey oak", is native to south-eastern Europe and Asia Minor and a rather common tree grown in Central European parks. In Karlsruhe, numerous indigenous/native ectomycorrhizal species of different genera are associated with *Quercus cerris* (A. Schneider, T. Bernauer, M. Scholler, unpublished data). The French specimen of *I. strickeriana* has been collected at Thumeries, "bois des 5-Tailles" by P.-A. Moreau on 22 June 2007, under *Quercus* and *Carpinus* on acidic soil (as "*I.* aff. *xanthomelas*", Genbank HQ586861; PAM07062202(LIP)). According to P.-A. Moreau (personal communication, 8 Jan 2017) this species is not rare in the Lille area (Northern France), where it has always been found growing near large *Quercus* trees, along paths. Further collections and studies are necessary to gain more information on the ecology and distribution of *I. strickeriana*.

Phenology: Found in June, September and October.

Additional collections studied: FRANCE, Thumeries (59), Bois des 5-Tailles, border of sandy moist way with *Quercus*, *Carpinus*, 22 Jun 2007, leg. *C. van Wontherghem*; det. *P.-A. Moreau* as *I.* aff. *xanthomelas* Boursier & Kühner (PAM07062202).- GERMANY, Baden-Württemberg, Karlsruhe, Stadtgarten, N Schwanensee, TK25 7016/1, alt. 115 m, lawn with *Quercus cerris*, in some distance also *Quercus robur* (= type locality), 9 Sep 2015, leg. *T. Bernauer*; det. *D. Bandini & B. Oertel* (KR-M-0044126, MH366572).- Ibidem, 8 Oct 2015, leg. *A. Schneider*; det. *D.*

Bandini & *B. Oertel* (KR-M-0044133, MH366573).- Ibidem, 8 Oct 2015, leg. *A. Schneider*; det. *D. Bandini* & *B. Oertel* (KR-M-0044132, MG012481).

Comments: *Inocybe strickeriana* is characterised macroscopically by a relatively small size of the basidiomata, an amber-coloured to light brown finely rimose surface of the pileus with diverging fibres, and the whitish often twisted stipe with a bulbous base, and microscopically by its often (sub)isodiametrical spores and hymenial cystidia with thick walls and caulocystidia up to 100 μm.

All German collections examined were growing in the same site, and the morphological details do hardly vary. Morphologically, the French basidioma matches the German collections in its measurements. In terms of ITS sequences, the collections are identical.

Macroscopically, *I. strickeriana* might be mistaken for *I. salicis* Kühner, the species that is also molecularly closest related to *I. strickeriana*. Normally, however, the pileus of *I. salicis* is more yellow, or yellow-ochraceous to ochraceous brownish, the spores are of a different shape—rarely isodiametrical—and the nodules are normally less pronounced (see also Kühner 1956). Furthermore, the caulocystidia are shorter than those of *I. strickeriana* and the habitat of *I. salicis* is different, since this species usually grows on rather moist to very wet terrain in or near *Salix*-thickets. The species differ genetically by 24 base pairs and 21 gaps.

The holotype of *I. straminipes* Romagn. has been examined for this study. Our own morphological examination supports the conclusions of Vauras and Kokkonen (2009) that *I. straminipes* is conspecific with *I. salicis* and thus to be treated as a synonym of *I. salicis* (for holotype see below). Unfortunatly, the DNA-analysis attempted by Vauras and Kokkonen (2009), yielded no result and a further attempt has not been allowed, due to the smallness of the type material. Our attempt to generate sequence data of the type of *I. salicis* also failed, but morphologically the measurements of spores and cystidia match those of own collections (for holotype see below).

Another species, morphologically rather similar to *I. strickeriana,* is the only recently described *I. lacunarum* Vauras & E. Larss., known only from Finland and Sweden. It shows a yellow-brown pileus with appressed rimulose to rimose fibres, and a bulbous stipe. The pileipellis, however, is not as thin and finely rimose as is the case with *I. strickeriana*; moreover, the fibres do not diverge almost from the pileus centre, and on average the hymenial cystidia are longer and differently shaped. *Inocybe lacunarum* has been found in deciduous forests with *Betula pendula*, *Populus tremula,* and *Quercus robur* (Vauras and Larsson 2016). Also phylogenetically *I. strickeriana* differs by thirty-seven basepairs and twenty-three gaps clearly from *I. lacunarum*.

Inocybe substellata Kühner differs from *I. strickeriana* e.g. by the colour of pileus, the on average larger spores and cystidia, and the alpine habitat (Kühner 1988; Vauras and Larsson 2016). *Inocybe populea* Takah. Kobay. & Courtec., is morphologically likewise and molecularly close to *I. strickeriana* but differs in surface structure of the pileus, which is described as having small recurved squamules. In addition, the spores show "crown-shaped double nodules" (see original description, Vauras and Larsson 2016), which could not be observed in case of *I. strickeriana*. Also spores and cystidia of *I. populea* are smaller and *I. populea* has both, catenate paracystidia and cauloparacystidia.

Confirming the close relationship, the species *I. lacunarum*, *I. strickeriana*, *I. salicis,* and *I. populea* form a strongly supported clade (Fig. 1).

Inocybe villosa Bandini, B. Oertel & U. Eberh. sp. nov.

Figure 16

MycoBank number: MB 827579, ITS barcode GenBank: MH366605.

Etymology: "villosa", because of the villose texture of pileus.

Short description: Fairly small and gracile species with villose, copper-tinged brown pileus, long and entirely pruinose bulbous stipe, nodulose spores, measuring 9.0–13.4 × 5.7–8.5 μm, long and rather narrow pleurocystidia, measuring 45–93 × 9–21 μm. The species seems to be calciphilous.

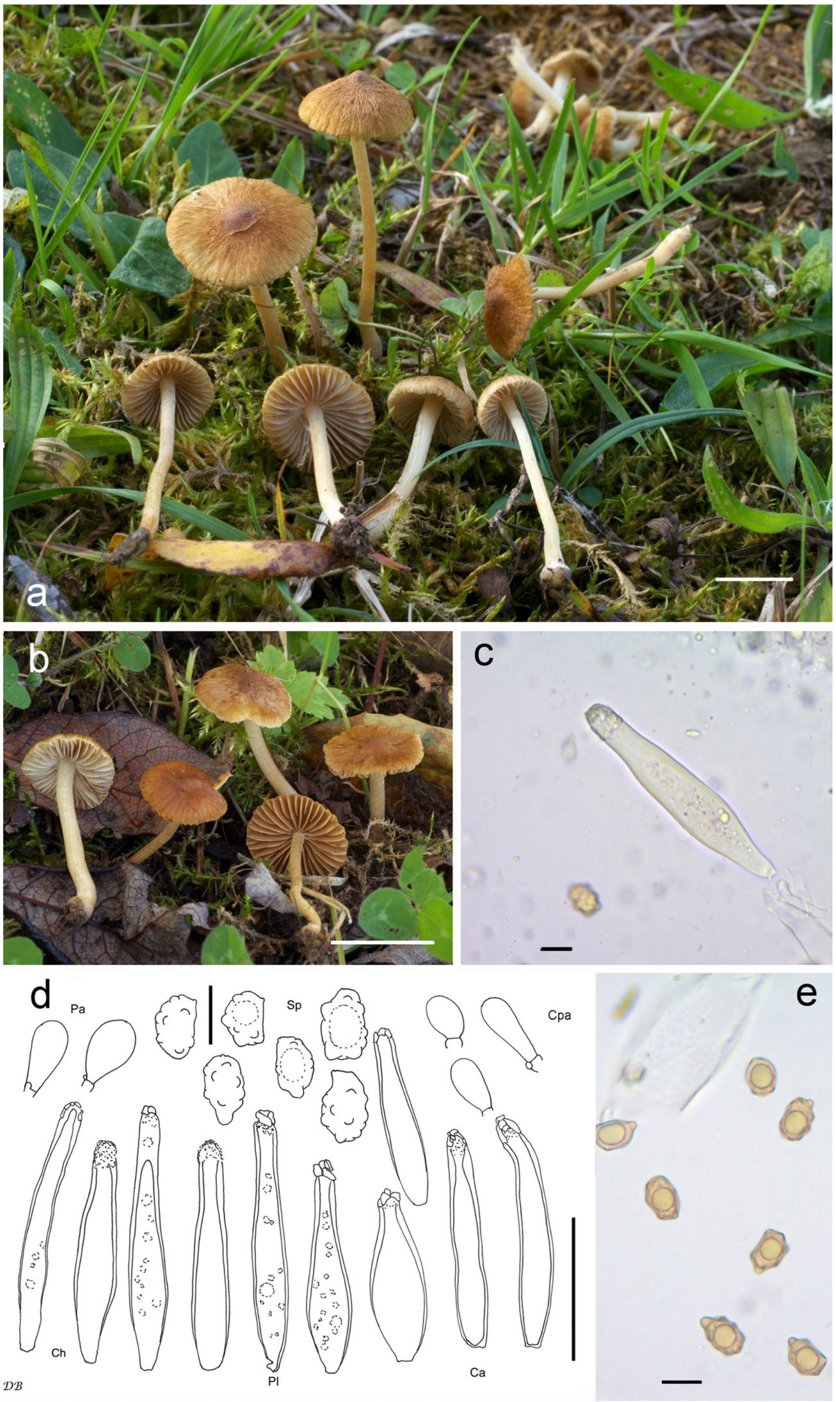
Diagnosis: *Inocybe villosa* is related to several species of the *I. xanthomelas* group, but differing from all by its unique combination of micro-morphological characterics, e.g. coppery villose pileus, long stipe, small bulb, rather large spores with often one visibly protruding nodule, large hymenial cystidia—as well as by ITS sequence data.

Holotype**:** GERMANY, Bayern, Dingolfing-Landau, Mamming, TK25 7341/2, 12.6111 E 48.6626 N, alt. 348 m, on dam near river Isar with *Salix* sp., *Betula pendula*, *Populus* sp., 29 Sep 2013, leg. *D. Bandini* & *B. Oertel* (holotype KR-M-0042327; isotypes DB29–9–13-2, BAN407, SMNS-STU-F-0900967).

Detailed description

Pileus 5–20 mm wide, (sub)campanulate or subconical or hemispherical when young, later expanded, often with more or less pronounced, rather acute or large umbo, but some basidiomata also without any umbo at all, margin deflexed when young, then straight or even uplifted when old, sometimes uneven to undate; some younger basidiomata with faint remnants of a greyish velipellis in the centre of the pileus; colour ochraceous brownish or light brown, most often with a conspicuous shiny coppery sometimes also amber-coloured tinge (Mu 5YR 5/6–5/8, 6/6–6/8, 7.5YR 5/6–5/8), in some basidiomata somewhat darker at the umbo when old; surface normally villose-lanose with appressed fibres, when old or due to rainy weather also only fibrillose or finely grooved and almost glabrous at the umbo or partially subsquarrose; no cortina observed. **Lamellae** rather distant (ca. 25–40, l =

Fig. 16 *Inocybe villosa*, **a** Holotype (DB29-9-13-2), scale bar 1 cm. **b** DB15-10-17-1, scale bar 1 cm. **c** Pleurocystide (DB29-9-13-2), scale bar 10 µm. **d** Microscopical characters (DB29-9-13-2), Ca Caulocystidia, Cpa Cauloparacystidia, Ch Cheilocystidia, Pa Paracystidia, Pl Pleurocystidia, Sp Spores; scale bar spores 10 µm, scale bar cystidia 50 µm. **e** Spores (DB29-9-13-2), scale bar 10 µm



1–3), ventricose, adnate to emarginate with decurrent tooth, first whitish or creamy, then greyish to ochraceous light brown, rusty-brown or red-brown when old; edge fimbriate, whitish to concolorous with age. **Stipe** 20–50 × 1–3 mm, cylindrical to slightly widening towards the base, base mostly bulbous, with a rounded not marginate bulb or not roundish with a small marginate bulb, seldom stipe only thickened at the base, glabrous, when young whitish, cream-coloured or yellowish, then faintly ochraceous or light brown especially when old; pruinose on the entire length of the stipe. **Context** whitish in the pileus, whitish or with faintly ochraceous hue in the stipe, later brownish towards the base. **Smell** spermatical, at least when cut. **Colour of exsiccata** pileus uniformely nut-brown or with slightly reddish tinge (Mu 7.5YR 5/6–5/8, 5YR 4/3–4/6), lamellae almost concolorous, stipe partially with slight greyish tinge, but no obvious darkening or blackening with drying.

Spores 9.0–13.4 μm (av. 11.1 μm, SD 0.9 μm) × 5.7–8.5 μm (av. 7.2 μm, SD 0.5 μm); Q = 1.3–1.8 (av. 1.5, SD 0.1) (*n* = 200 from 5 coll.), nodulose, with differently protruding nodules, often with one conspicuously protruding nodule, apex obtuse. **Basidia** 25–33 × 8–12 μm, usually 4-spored, seldom also 2-spored. **Lamellae edges** sterile, composed of cheilocystidia and numerous hyaline, (sub)clavate or cylindrical, thin-walled paracystidia. **Pleurocystidia** 45–93 μm (av. 70 μm, SD 11 μm) × 9–21 μm (av. 16 μm, SD 2.4 μm); Q = 2.8–7.9 (av. 4.7, SD 0.9) (*n* = 75 from 5 coll.), usually rather narrow (sub)fusiform, (sub)cylindrical, also subutriform or sublageniform, sometimes with guttules with greenish content, without or with only short pedicel, sometimes with truncate base, apex usually crystalliferous and not seldom granulose ("sandy"), walls 0.5 (1.0) (bulge)–2.5 (3.0) μm (neck) thick; sometimes abruptly thickened at the neck, weak reaction with 3% KOH. **Cheilocystidia** similar in appearance and size. **Pileipellis** consisting of an epicutis made up of parallel hyphae 5–12 μm wide, with finely encrusting and parietal ochraceous yellow-orange pigment, subcutis with wider and paler elements, up to 20 (25) μm wide. **Stipitipellis** consisting of a cutis bearing numerous bundles of metuloid caulocystidia down to the base of the stipe, intermixed with subclavate or subcylindrical, thin-walled paracystidia. **Caulocystidia** 45–80 × 10–20 μm, (sub)cylindrical or (sub)fusiform, also (sub)lageniform or (sub)utriform, apex usually crystalliferous, walls 0.5 (1.0) (bulge)–2.0 (2.5) μm (neck) thick, weak reaction with 3% KOH. **Clamp-connections** abundant in all tissues.

Habitat and known distribution: Up to now *I. villosa* was found only in Germany (Bayern and Baden-Württemberg) and Austria (Tirol); no further sequences or specimens are known to us. The collections of Austria and Bayern were found next to rivers, on rather moist, at times even flooded alluvial terrain, the two collections of Baden-Württemberg grew in a disused quarry on at times quite dry calcareous terrain. Whereas the type collection and the two collections of Baden-Württemberg grew exclusively with broadleaf trees—*Salix*, *Alnus*, *Populus,* and *Betula* –, next to the other two collections conifers, *Pinus,* respectively *Picea*, have also been noted. The species seems to be calciphilous, since all the localities are on calcareous soil. Further collections are necessary to gain more information on the ecology and distribution of *I. villosa*.

Phenology: September and October.

Additional collections studied: AUSTRIA, Tirol, Reutte, Pinswang, ÖK25V 2215-West, alt. ca. 800 m, with *Alnus glutinosa*, *Picea abies*, *Fraxinus excelsior*, *Pinus sylvestris*, *Populus* sp., *Salix* sp., 12 Oct 2016, leg./det. *D. Bandini* (KR-M-0042328, DB12-10-16-13, BAN1420, MG012478).- GERMANY, Bayern, Ostallgäu, Füssen, TK25 8430/1, alt. 800 m, on pathside near the river Lech, with *Salix* sp. *Betula pendula*, *Picea abies*, *Populus* sp., 22 Sep 2015, leg./det. *D. Bandini* (KR-M-0042329, DB22-9-15-13, BAN1177, MH366606).- GERMANY, Baden-Württemberg, Rhein-Neckar-Kreis, Eschelbronn, Nature Reserve Kallenberg, TK25 6619/3, alt. 190 m, *Salix caprea*, *Alnus glutinosa*, 15 Oct 2017, leg./det. *D. Bandini* (KR-M-0042374, DB15-10-17-1, BAN1942, MH366604).- Ibidem, 21 Oct 2017, leg./det. *D. Bandini* (DB21-10-17-2).

Comments: *Inocybe villosa* is characterised by its mostly striking copper-coloured villose pileus, in relation to the pileus diameter rather long, entirely pruinose stipe, small bulb, spores with often differently protruding nodules—often with one visible conspicuously protruding knob—and mostly rather narrow and long hymenial cystidia. Because of its moist habitat with *Salix I. villosa* could perhaps be mistaken for *I. salicis*. The pileus of the latter taxon can sometimes be brownish as in ageing *I. villosa*. However, the texture of the pileus of the *I. salicis* is normally not villose, but smooth, finely felty to subsquarrose. Furthermore, the two species differ in carpophore proportions, the shape of spores and shape and size of the hymenial cystidia. Another species that needs to be mentioned in the context of *I. villosa* is *I. saliceticola* Vauras & Kokkonen. The latter shows a yellow-brown to pale brown colour of pileus—often strongly contrasting with the red-brown centre –, the surface of the pileus is radially fibrillose, but not villose, and the shape and size of the spores and the shape of the cystidia differ from those of *I. villosa* (Vauras and Kokkonen 2009*)*. The third species growing on moist ground that could be mistaken for *I. villosa* is *I. hirculus* Vauras. Its pileus is woolly-fibrillose, and the colour yellow-brown, brown or red-brown. The size of basidiomata of *I. hirculus* is with up to 45 mm larger than the size of *I. villosa,* and the spores and cystidia have a different shape (Vauras 1994). *Inocybe villosa* belongs to the Phaeocystidiosa clade and there to a subclade which includes *I. krieglsteineri* Fernández Sas. and *I. saliceticola.* Whereas, for instance, the stipes of *I. krieglsteineri*, *I. salicis* and *I. lacunarum* (Vauras and Larsson 2016) in accordance with the definition of Esteve-Raventós et al. (2015), see also Esteve-Raventós et al. 2016) turn brown—according to Kühner (1956) with respect to *I. salicis* even "fortement"—or even blackish during the drying process, this is not the case in the examined collections of *I. villosa*. May be due to its uncommon habitat, at least in Central Europe, *I. villosa* seems to be a fairly rare species.

Additional type specimens

Figures 17 and 18

Holotype: ***I. alluvionis*** Stangl 1976, Germany, Bayern, Augsburg-Göggingen, near river Wertach, 20 Jun 1968, leg. *J. Stangl* (PRM-756100). Spores 8.6–11.3 μm (av. 9.6 μm, SD 0.6 μm) × 4.7–5.9 μm (av. 5.2 μm, SD 0.6 μm), Q = 1.6–2.1 (av. 1.8, SD 0.1) (*n* = 40), smooth, often with suprahilar depression, apex (sub)obtuse to (sub)acute. Basidia generally 4-spored. Pleurocystidia 42–69 μm (av. 55 μm, SD 7.4 μm) ×

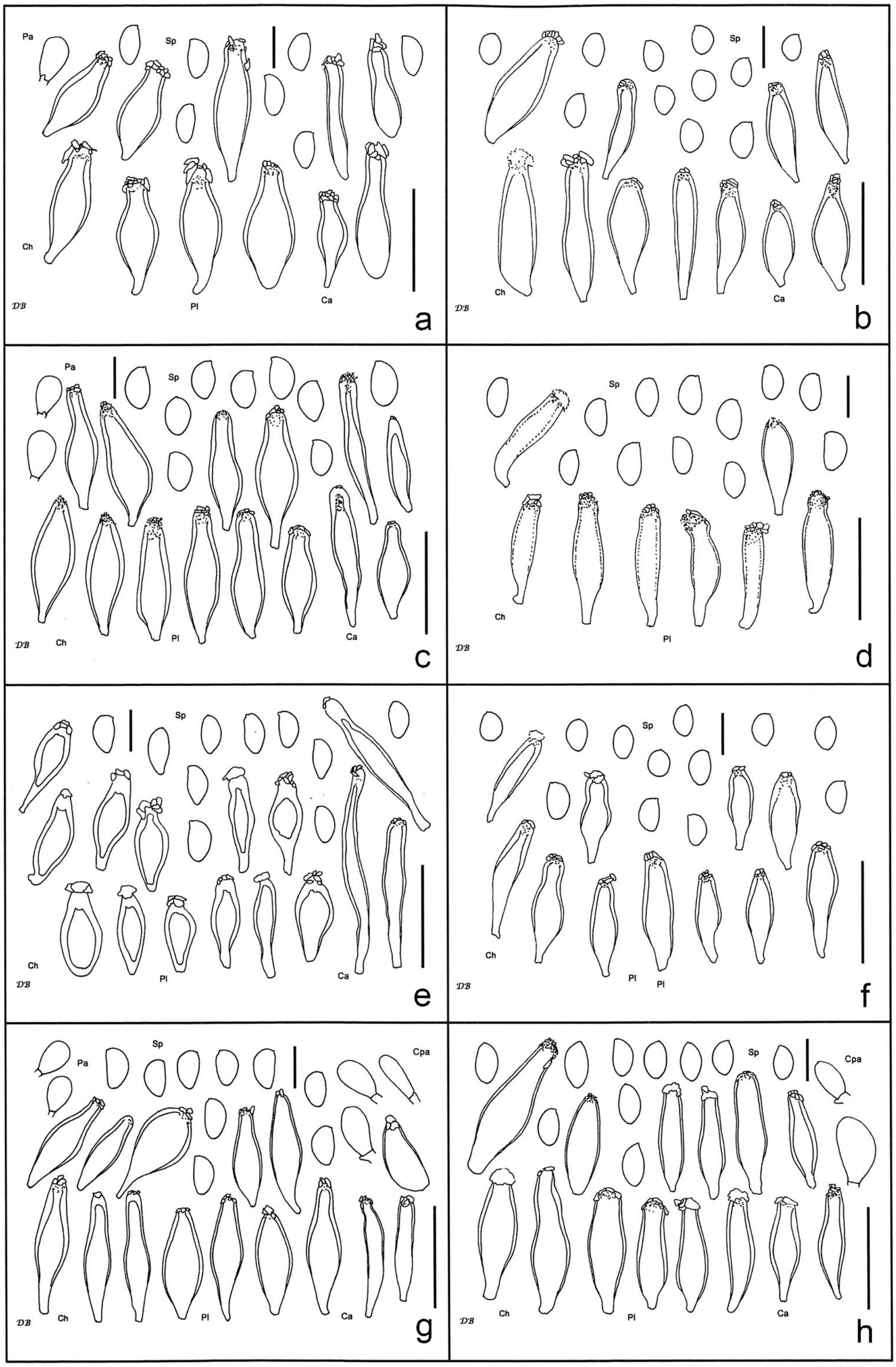


Fig. 17 Microscopical characters of type collections **a** *Inocybe alluvionis* (PRM-756100). **b** *I. angulatosquamulosa* (M-0281791). **c** *I. derbschii* (KR-0005011). **d** *I. furfurea* (G00053152). **e** *I. hirtelloides* (PRM-727125). **f** *I. pelargonium* (G00118409). **g** *I. pseudodestricta* (PRM-716231). **h** *I. rufotacta* (KR-0005010). Ca Caulocystidia, Cpa Cauloparacystidia, Ch Cheilocystidia, Pa Paracystidia, Pl Pleurocystidia, Sp Spores; scale bar spores 10 μm, scale bar cystidia 50 μm

13–21 μm (av. 18 μm, SD 2.8 μm); Q = 2.4–4.5 (av. 3.1, SD 0.5) (*n* = 15), mostly (sub)utriform, also (sub)fusiform or subcylindrical, apex usually crystalliferous, walls up to 3.0 (3.5) μm thick, weak reaction with 3% KOH. Cheilocystidia similar in appearance and size. Paracystidia subclavate thin-walled. Caulocystidia metuloid down to the base of the stipe, more variable in form than hymenial cystidia, apex mostly crystalliferous, walls up to 2.0 (2.5) μm thick, weak reaction with 3% KOH. Cauloparacystidia not observed.

Holotype: ***I. angulatosquamulosa*** Stangl 1984, Germany, Bayern, Augsburg, Wittelsbacher Park, 1 Oct 1983, leg. *J. Stangl* (M-0281791). **Spores** 6.4–8.9 μm (av. 7.5 μm, SD 0.6 μm) × 4.7–5.8 μm (av. 5.2 μm, SD 0.6 μm); Q = 1.3–1.7 (av. 1.4, SD 0.6) (*n* = 40), smooth, apex (sub)obtuse. **Basidia**

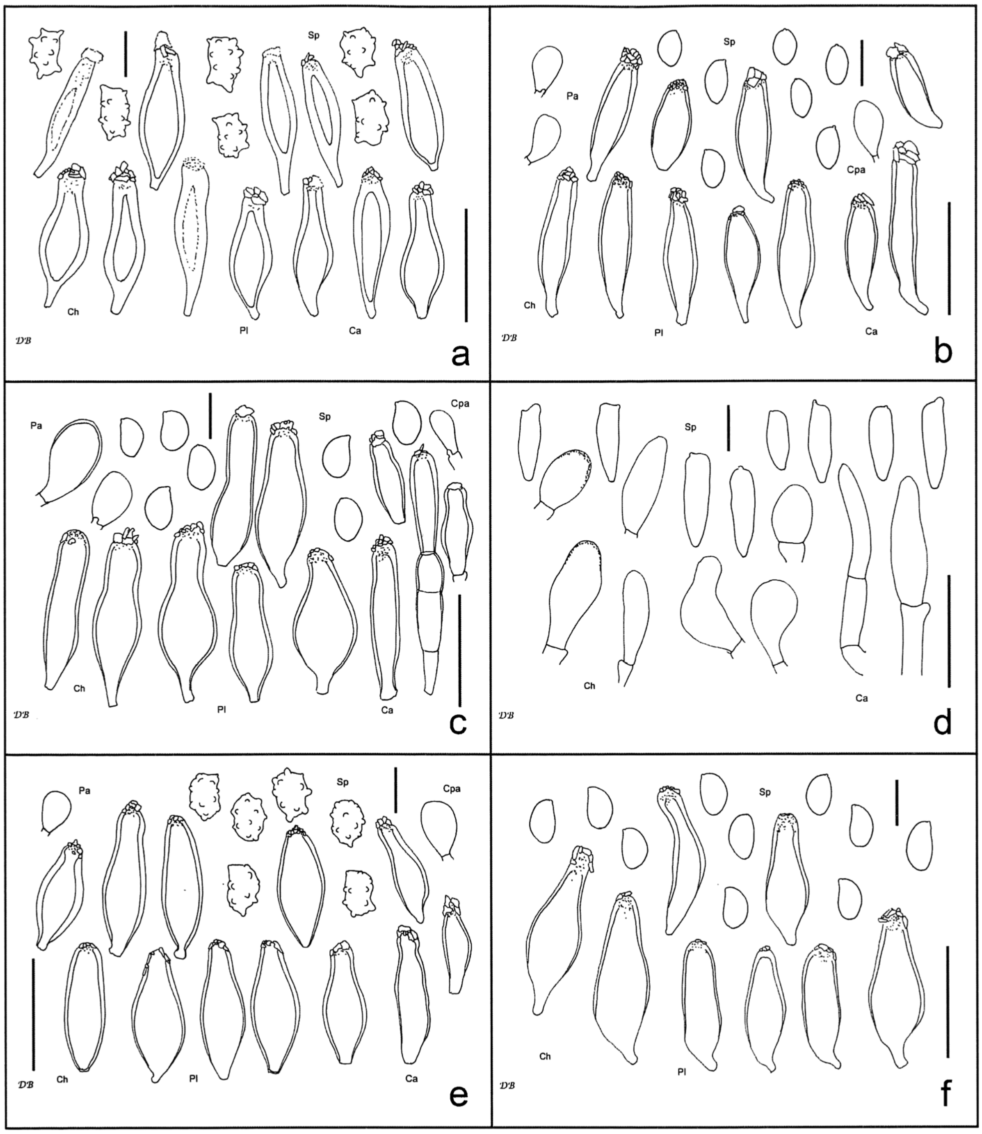


Fig. 18 Microscopical characters of type collections **a** *Inocybe salicis* (G00052219). **b** *I. sandrae* (KR-M-0042355). **c** *I. splendentoides* (LIP-89165). **d** *I. stenospora* (M-0151619). **e** *I. straminipes* (PC0705254). **f** *I. terrifera* (G00058743). Ca Caulocystidia, Cpa Cauloparacystidia, Ch Cheilocystidia, Pa Paracystidia, Pl Pleurocystidia, Sp Spores; scale bar spores 10 μm, scale bar cystidia 50 μm

usually 4-spored, but seldom also 2-spored, and then spores up to 11.2 μm. **Pleurocystidia** 47–75 μm (av. 62 μm, SD 8.1 μm) × 10–28 μm (av. 18 μm, SD 5.0 μm); Q = 2.2–6.6 (av. 3.6, SD 0.9) (*n* = 28), mostly (sub)utriform, also subcylindrical or (sub)fusiform, apex usually crystalliferous, walls up to 3.0 (3.5) μm thick, weak reaction with 3% KOH. **Cheilocystidia** similar in appearance and size. **Paracystidia** oval, pyriform to sphaerical, thin-walled. **Caulocystidia** metuloid down to the base of the stipe, (sub)fusiform, (sub)utriform or (sub)cylindrical, apex mostly crystalliferous, walls up to 2.0 (2.5) μm thick, weak reaction with 3% KOH. Cauloparacystidia present. ITS MG012474.

Holotype: ***I. derbschii*** Schwöbel & Stangl 1982, Germany, Baden-Württemberg, Karlsruhe, Erzbergerstraße, with *Quercus* and *Carpinus*, 19 Jul 1980 (KR-0005011). **Spores** 7.4–11.0 μm (av. 9.5 μm, SD 0.7 μm) × 5.0–6.8 μm (av. 5.8 μm, SD 0.5 μm); Q = 1.4–1.9 (av. 1.6, SD 0.1) (*n* = 40), smooth, sometimes with suprahilar depression, apex subacute or even with apical papilla, sometimes with indistinct germpore. **Basidia** 4-spored. **Pleurocystidia** 40–67 μm (av. 54 μm, SD 7.8 μm) × 12–22 μm (av. 17 μm, SD 2.9 μm); Q = 2.6–4.1 (av. 3.3, SD 0.6) (*n* = 20), mostly (sub)fusiform or subutriform, often with rather long pedicel, apex crystalliferous, walls up to 2.5 (3.0) μm thick, almost colourless with 3% KOH. **Cheilocystidia** similar in appearance and size. **Paracystidia** (sub)clavate to subglobose, thin-walled. **Caulocystidia** metuloid only in the upper half of the stipe, similar in shape to hymenial cystidia, but usually narrower and sometimes deformed or with undate walls, apex with or without small crystals, walls up to 2.5 μm thick, almost colourless with 3% KOH. **Cauloparacystidia** mostly subclavate. ITS MG012466.

Lectotype: ***I. furfurea*** Kühner 1955, France, Paris, Bois de Vincennes, on mossy earth, on lawn on right side of the Porte

Jaune, 16 basidiomata, 17 Aug 1931, leg. *R. Kühner* (G00053152). **Spores** 7.3–10.2 μm (av. 8.7 μm, SD 1.5 μm) × 4.3–5.8 μm (av. 5.2 μm, SD 0.3 μm); Q = 1.3–2.0 μm (av. 1.7, SD 0.3) (*n* = 40), smooth, apex subacute to (sub)obtuse. **Basidia** generally 4-spored. **Pleurocystidia** 45–66 μm (av. 57 μm, SD 10.7 μm) × 10–16 μm (av. 13 μm, SD 3.3 μm); Q = 3.4–5.5 (av. 4.4, SD 0.6) (*n* = 15), mostly subcylindrical or (sub)fusiform, apex usually crystalliferous, walls usually not in a good state, presumably up to 2.5 μm, thus weak reaction with 3% KOH. **Cheilocystidia** similar in appearance and size. **Paracystidia** not observed. **Caulocystidia** not observed. ITS MG012472.

Holotype: ***I. hirtelloides*** Stangl & J. Veselský 1974, Germany, Bayern, Augsburg, Wittelsbacher Park, 17 Jun 1971, leg. *J. Stangl* (PRM-727125). **Spores** 7.8–11.9 μm (av. 9.3 μm, SD 0.9 μm) × 4.7–5.7 μm (av. 5.2 μm, SD 0.3 μm); Q = 1.5–2.1 (av. 1.8, SD 0.1) (*n* = 40), smooth, sometimes with suprahilar depression, apex (sub)acute or even papillate, sometimes with indistinct germpore. **Basidia** 4-spored. **Pleurocystidia** 36–61 μm (av. 49 μm, SD 5.7 μm) × 13–20 μm (av. 16 μm, SD 1.7 μm); Q = 2.1–3.9 (av. 3.1, SD 0.5) (*n* = 20), mostly (sub)fusiform or subutriform, apex usually crystalliferous, walls up to 2.5 (3.0) μm thick, almost colourless with 3% KOH. **Cheilocystidia** similar in appearance and size. **Paracystidia** not observed. **Caulocystidia** metuloid down to the base of the stipe, often narrow and quite long (up to 80 μm) and mostly subcylindrical, not seldom with undate walls, apex with or without small crystals, walls up to 2 μm thick, almost colourless with 3% KOH. Cauloparacystidia rare. ITS MG012471.

Lectotype: ***I. pelargonium*** Kühner 1955, France, Savoie, St. Bon - Tarentaise, Forêt du Praz, on earth strewn with needles, alt. 1600–1800 m, 5 Sep 1927, leg. *R. Kühner* (G00118409). **Spores** 6.7–9.4 μm (av. 7.9 μm, SD 0.7 μm) × 4.5–5.6 μm (av. 5.0 μm, SD 0.3 μm); Q = 1.2–1.9 (av. 1.6, SD 0.2) (*n* = 40), smooth, apex mostly (sub)obtuse. **Basidia** 4-spored. **Pleurocystidia** 43–58 μm (av. 48 μm, SD 10.2 μm) × 11–15 (av. 14 μm, SD 4.7 μm); Q = 3.1–4.4 (av. 3.6, SD 0.6) (*n* = 30), mostly (sub)utriform, subcylindrical, apex usually crystalliferous, walls up to 4.0 (4.5) μm thick, weak reaction with 3% KOH. **Cheilocystidia** similar in appearance and size. **Paracystidia** not observed. **Caulocystidia** not seen, because no stipe existent in type material.

Holotype: ***I. pseudodestricta*** Stangl & J. Veselský 1973, Čechoslovakia (Moravia inter septentriones et orientem solem spectans), Ostrava, 30 Aug 1970, leg. *J. Veselský* (PRM-716231). **Spores** 8.2–12.1 μm (av. 9.6 μm, SD 0.9 μm) × 4.9–6.3 μm (av. 5.6 μm, SD 0.4 μm); Q = 1.5–2.0 (av. 1.7, SD 0.1) (*n* = 40), smooth, sometimes with indistinct suprahilar depression, apex subacute. **Basidia** mostly 4-spored, seldom also 2-spored, and then spores up to 13.3 μm. **Pleurocystidia** 40–76 μm (av. 61 μm, SD 8.3 μm) × 12–26 μm (av. 16 μm, SD 3.1 μm); Q = 3.0–4.7 (av. 3.8, SD 0.6) (*n* = 20), mostly subfusiform or subutriform, apex usually crystalliferous, walls up to 3.0 (3.5) μm, weak reaction with 3% KOH. **Cheilocystidia** similar in appearance and size. **Paracystidia** mostly subclavate to subglobose, thin-walled. **Caulocystidia** metuloid only in the upper half of the stipe, often sublageniform or subcylindrical, but also subfusiform or subutriform, sometimes deformed and with undate walls, apex with or without crystals, walls up to ca. 2.5 μm thick, weak reaction with 3% KOH. **Cauloparacystidia** mostly subclavate or subglobose. ITS MG012468.

Paratype (wrongly called Isotype in Stangl and Veselský 1973) of ***I. pseudodestricta*** = ***I. derbschii***, Göggingen prope Augsburg, 2 Jun 1970, leg. *J. Stangl* (PRM-716232). See above discussion to *I. derbschii*. ITS MG012469.

Holotype: ***I. rufotacta*** Schwöbel & Stangl 1982 (= ***I. furfurea***), Germany, Baden-Württemberg, Karlsruhe, Erzbergerstraße, with *Quercus* and *Carpinus*, 12 Jul 1980 (KR-0005010). **Spores** 6.9–10.4 μm (av. 8.6 μm, SD 0.8 μm) × 4.8–6.2 μm (av. 5.4 μm, SD 0.3 μm); Q = 1.4–1.8 (av. 1.6, SD 0.1) (*n* = 40), smooth, apex (sub)obtuse to subacute, sometimes with indistinct germpore. **Basidia** 4-spored. **Pleurocystidia** 40–67 μm (av. 54 μm, SD 8.2 μm) × 12–21 μm (av. 17 μm, SD 3.5 μm); Q = 2.6–4.1 (av. 3.3, SD 0.7) (*n* = 20), mostly (sub)fusiform, (sub)cylindrical or subutriform, but also sac-shaped, apex usually crystalliferous, walls up to 3.0 (3.3) μm thick, occasionally weakly undate, weak reaction with 3% KOH. **Cheilocystidia** similar in appearance and size. **Paracystidia** not observed. **Caulocystidia** metuloid in the upper half of the stipe, but sometimes also found near the base, similar in shape to the hymenial cystidia, apex with or without small crystals, walls up to 2.5 μm thick, weak reaction with 3% KOH. **Cauloparacystidia** mostly subclavate to subglobose. ITS MG012467.

Holotype: ***I. salicis*** Kühner 1956, France, Rhône, Marais des Échets near Lyon, in a thicket of *Salix alba*, 6 Oct 1944, leg. *R. Kühner* (G00052219). **Spores** 8.9–13.4 μm (av. 12.0 μm, SD 1.2 μm) × 6.5–10.2 μm (av. 8.3 μm, SD 0.8 μm); Q = 1.3–1.8 μm (av. 1.5, SD 0.1) (*n* = 40), nodulose, apex (sub)acute to (sub)obtuse. **Basidia** 4-spored. **Pleurocystidia** 48–69 μm (av. 60 μm, SD 5.7 μm) × 10–21 μm (av. 16 μm, SD 2.4 μm); Q = 3.5–5.9 (av. 3.8, SD 0.7) (*n* = 15), mostly (sub)fusiform or (sub)utriform, seldom also (sub)cylindrical, apex usually crystalliferous, walls up to 5.5 (6.0) μm thick, weak reaction with 3% KOH. **Cheilocystidia** similar in appearance and size. **Paracystidia** not observed. **Caulocystidia** metuloid on the entire length of the stipe, similar in shape and length to the hymenial cystidia, apex usually with crystals, walls up to 5.0 (5.5) μm thick, weak reaction with 3% KOH. **Cauloparacystidia** not observed.

Isotype: ***I. sandrae*** Zitzmann 2002 (= ***I. furfurea***), Germany, Bayern, Bad Abbach (TK 7038/3), with *Betula*, *Populus*, *Salix*, 24 Jul 1993, leg. *H. Zitzmann* (KR-M-0042355, DB21–7-93-Zitzmann). **Spores** 7.7–11.3 μm (av. 9.0 μm, SD 0.8 μm) × 4.6–6.5 μm (av. 5.4 μm, SD 0.5 μm); Q 1.5–1.9 (av. 1.7, SD 0.6) (*n* = 40), smooth, apex (sub)obtuse to subacute. **Basidia** 4-spored. **Pleurocystidia** 40–67 μm (av. 54 μm, SD 5.0 μm) × 12–23 μm (av. 17 μm, SD 1.7 μm); Q = 2.6–4.1 (av. 3.3, SD 0.6) (*n* = 20), mostly (sub)fusiform, (sub)cylindrical or subutriform, seldom also subclavate, apex usually crystalliferous, walls up to 3.0 μm thick, weak reaction with 3% KOH. **Cheilocystidia** similar in appearance and size. **Paracystidia** (sub)clavate to subglobose, mostly thin-walled. **Caulocystidia** metuloid in the upper half of the stipe, but with one specimen also below the middle, similar in shape to the hymenial cystidia, apex with or without small crystals, walls up to 2.5 μm thick, weak reaction with 3% KOH. **Cauloparacystidia** mostly subclavate to subglobose. ITS MH366610.

Holotype: ***I. splendentoides*** Bon 1990, France, Parc du Marquenterre, moist grassy sandy thicket, with *Populus*, *Salix*, *Buxus*, 22 Oct 89, leg. *M. Bon* (LIP-89165). **Spores** 8.0–12.6 μm (av. 10.1 μm, SD 1.1 μm) × 5.0–7.2 μm (av. 6.3 μm, SD 0.4 μm); Q = 1.3–1.9 (av. 1.6. SD 0.2) (*n* = 40), smooth, apex (sub)obtuse to subacute, not seldom with suprahilar depression. **Basidia** 4-spored. **Pleurocystidia** 37–79 μm (av. 62 μm, SD 12.2 μm) × 12–26 μm (av. 20 μm, SD 3.8 μm); Q = 2.2–4.3 (av. 3.1, SD 0.6) (*n* = 20), mostly (sub)utriform, (sub)cylindrical or sublageniform, towards the apex not seldom with clearly demarcated short neck, apex usually crystalliferous, walls up to 2.5 (3.0) μm thick, almost colourless with 3% KOH. **Cheilocystidia** similar in appearance and size. **Paracystidia** (sub)clavate to subglobose, thin-walled. **Caulocystidia** metuloid on the entire length of the stipe, similar in shape to the hymenial cystidia, but usually not as wide, apex with or without small crystals, walls up to 2.5 μm thick, almost colourless with 3% KOH. **Cauloparacystidia** mostly subclavate to subglobose. ITS MG012470.

Holotype: ***I. stenospora*** Stangl & Bresinsky 1983, Germany, Offenstetten, near Abendsberg, inshore-dunes, 5 Oct 1978 leg. *A. Bresinsky* (M-0151619). **Spores** 12.3–19.7 μm (av. 15.8 μm, SD 1.5 μm) × 4.4–6.2 μm (av. 5.0 μm, SD 0.3 μm); Q = 2.2–3.9 (av. 3.2, SD 0.3) (*n* = 40), truncate projectile-formed to almost smooth. **Basidia** generally 4-spored. **Pleurocystidia** not observed. **Cheilocystidia** 25–61 μm (av. 42 μm, SD 10.7 μm) × 11–22 μm (av. 17 μm, SD 3.3 μm); Q = 1.3–3.4 (av. 2.5, SD 0.5) (*n* = 15), subglobose or balloon-shaped, (sub)clavate, subcylindrical or deformed, thin-walled. **Paracystidia** not observed. **Caulocystidia** on apex of stipe, hyphoid. ITS MG012473.

Holotype: ***I. straminipes*** Romagn., France, Coye-la-Forêt (Oise), 18 Jul 1952, leg. *H. Romagnesi* 52.46 (PC0705254). **Spores** 10.3–13.0 μm (av. 11.5 μm, SD 0.6 μm) × 6.9–9.0 μm (av. 8.0 μm, SD 0.5 μm); Q = 1.2–1.6 (av. 1.4, SD 0.1) (*n* = 40), nodulose, with only small nodules, apex (sub)acute to (sub)obtuse. **Basidia** generally 4-spored. **Pleurocystidia** 48–69 μm (av. 58 μm, SD 5.9 μm) × 17–24 μm (av. 19 μm, SD 4.4 μm); Q = 2.5–3.9 (av. 3.0, SD 0.4) (n = 20), mostly (sub)fusiform, also subutriform or subcylindrical, apex often with small crystals, walls up to 4.0 (4.5) μm thick, almost colourless with 3% KOH. **Cheilocystidia** similar in appearance and size. **Paracystidia** (sub)clavate to subglobose, thin-walled. **Caulocystidia** metuloid also near base of stipe, similar in form to hymenial cystidia, but usually not as wide, up to 70 μm, apex with or without small crystals, walls up to 2.5 μm thick, weak reaction with 3% KOH. **Cauloparacystidia** subclavate to subglobose or subcylindrical.

Lectotype: ***I. terrifera*** Kühner 1955, France, Paris, Bois de Vincennes, border of avenue Dame Blanche, between Fontenay and Vincennes, six basidiomata on soil with frondose trees, 8 Aug 1931, leg. *R. Kühner* (G00058743). **Spores** 8.3–11.0 μm (av. 9.7 μm, SD 0.5 μm) × 5.3–6.6 μm (av. 5.9 μm, SD 0.4 μm); Q = 1.4–1.9 (av. 1.7, SD 0.1) (*n* = 40), smooth, apex (sub)obtuse. **Basidia** generally 4-spored. **Pleurocystidia** 45–79 μm (av. 61 μm, SD 10.0 μm) × 13–26 μm (av. 20 μm, SD 4.4 μm); Q = 2.3–4.5 (av. 3.2, SD 0.7) (*n* = 15), mostly (sub)utriform, also subcylindrical or (sub)fusiform, apex usually crystalliferous, walls up to 3.0 (3.5) μm thick, weak reaction with 3% KOH. **Cheilocystidia** similar in appearance and size. **Paracystidia** not observed. **Caulocystidia** not seen, because no stipe was contained in the type material.

Discussion

Articles on European *Inocybe* spp. based on both morphological and molecular evidence are often aiming to elucidate a certain species complex, e.g. the *I. leiocephala*-complex (Larsson et al. 2014) or the *I. praetervisa*-complex (Esteve-Raventós et al. 2015, 2016; Larsson et al. 2018), or are about species belonging to a group in a wider sense, as the nodulose-spored *Cortinatae* (Kokkonen and Vauras 2012). As there are more than 450 central European species of *Inocybe* it seems useful to deal with larger amounts of taxa at a time, in order to speed up the revision of the genus, similar to Matheny and Bougher (2017), who revised the *Inocybe* spp. of Australia.

Only very few of those 450 species are considered as "semicryptic" (Bickford et al. 2006; Brandrud et al. 2015), because the distinguishing features are overlapping with sister species in some of the collections. This means that by far most species can be discriminated by several morphological features and often also by different habitat preferences as well as by differences in ITS sequences. This is also the case for the often neglected species investigated within this study.

If a species is not described in much detail and without a diagnosis highlighting distinguishing features, it may happen that this species is either not recognised as such and therefore neglected, or synonymised with a similar one. This happened to *I. terrifera* and *I. derbschii*, being synonymised with *I. splendens* and *I. pseudodestricta*, respectively (Kuyper 1986). In both cases no colour picture was given in the original description, and as a consequence, differences were overlooked.

As exemplified by *I. hirtelloides*, misinterpretations can also arise from other omissions. One of the main characteristics of *I. hirtelloides* is the very small size of the hymenial cystidia. However, in the original description the crucial average value is missing and so the maximum value of 70 μm seems to point to a quite normal size, hiding the fact that large hymenial cystidia are very rare and small hymenial cystidia are rather common in this species.

Converse to omissions that lead to an underestimation of the number of species, there can be an overestimation of the number of species, if they are based on features thought to be constant, but in fact are not. This is the case with the reddening of lamellae or of other parts of the basidiomata when bruised. In basidiomata of *I. bongardii* (Weinm.) Quél. or *I. cervicolor* (Pers.: Fr.) Quél. this phenomenon cannot always be observed even within the same collection (Stangl 1989). And also in *I. furfurea* this character is apparently variable. In one collection we found only one basidioma with reddening lamellae, while the bruised lamellae of the other basidiomata did not change colour. Some other collections did not redden at all. Similarly, *I. vulpinella* var. *fuscolamellata* Bon, has been characterised on the basis of brown lamella edges. These were observed only in one or two basidiomata of several own fresh collections, while in other basidiomata of the same collection the edges remained whitish. This highlights that colour and colour changes might not always be good indicators of species identity.

The widely used classification of species in the "supersections" "Cortinatae" and "Marginatae" in keys has been a major reason why the conspecific species *I. rufotacta* and *I. sandrae* were described as separate species based on metuloid caulocystidia only near the apex or in the upper half of the stipe and not easily assignable to any of the "supersections". The species *Inocybe furfurea*, which is conspecific with the above two has been grouped into the subsection *Subbrunneinae* Bon in Bon (1997), and Kuyper (1986) placed it in the group of species with metuloid caulocystidia descending to the base of the stipe. However, in some collections cystidia are rather sparse below the centre, and thus, those collections are not always recognised as *I. furfurea*. Also in *I. venustissima* the distribution of metuloid cystidia is variable. This underpins that the distribution of metuloid cystidia is of limited taxonomic value and should be used with caution when discriminating species. As the boundaries between the "Cortinatae" and the "Marginatae" are blurred, their recognition as "supersections" should be discontinued, and when using their main characteristics in keys, the introduction of an intermediate category should be considered, or at least species in which the character is variable should be keyed in both groups.

In conclusion, for the *Inocybe* species treated in this study morphological circumscriptions matched well with phylogenetic groups, highlighting that a careful morphological investigation considering constant characters can lead to the formation of natural groups. These should, however, always be confirmed by sequence data, as homoplasy cannot be ruled out for any character combination. In addition, phylogenetic analyses also help with the placement of aberrant species, as exemplified by *I. stenospora*, which, because of its unusual spores, could only by ascertained as a member of the lanuginosa group based on phylogenetics.

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