

# *Inocybe antoniniana*, a new species of *Inocybe* section *Marginatae* with nodulose spores

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*Inocybe antoniniana*, a new species of *Inocybe* section *Marginatae* is described in detail along with illustrations of its macro- and micromorphology. It is a nodulose-spored species with yellowish-ochraceous pileus colour and smooth to (sub)rimulose pileus surface, that was found up to now in Turkey, Austria and Germany. It differs from other species of the group with equally coloured pilei (e.g. *I. xanthomelas*, *I. phaeocystidiosa* or *I. krieglsteineri*) by smaller, often (sub)isodiametrical basidiospores, rather short and slim hymenial cystidia, and ITS sequence data.

Keywords: Agaricales, Inocybaceae, *Inocybe*, taxonomy, molecular phylogeny. – 1 new species.

Up to now the family Inocybaceae was constituted by the genera *Inocybe* (Fr.: Fr.) Fr., *Auritella* Matheny & Bougher and *Tubariomyces* Esteve-Rav. & Matheny (see e.g. Latha et al. 2016). The genus *Inocybe* itself was divided into the three subgenera *Mallocybe* Kuyper, *Inosperma* Kühner and *Inocybe* (Kuyper 1986; Stangl 1989; Bon 1997, 1998), or according to Matheny & Kudzma (2019) in five major clades, namely *Inocybe*, *Inosperma*, *Mallocybe*, *Nothocybe* and *Pseudosperma*. Recently, these five clades were introduced as genera by Matheny et al. (2019) by treating the former subg. *Inocybe* on genus level thereby using this genus in a much narrower sense but finally as a monophyletic group, by raising the two subgenera *Inosperma* and *Mallocybe* to genus level as genera *Inosperma* (Kühner) Matheny & Esteve-Rav. and *Mallocybe* (Kuyper) Matheny, Vizzini & Esteve-Rav., by erecting the new genus *Nothocybe* Matheny & K.P.D. Latha for *Inocybe distincta* K.P.D. Latha & Manim., now *Nothocybe distincta* (K.P.D. Latha & Manim.) Matheny & K.P.D. Latha, and finally by erecting the new genus *Pseudosperma* Matheny & Esteve-Rav. for *Inocybe* sect. *Rimosae* (Fr.) Quél. Thus, according to Matheny et al. (2019), the family Inocybaceae now comprises seven genera.

During recent years numerous articles with new species of the family Inocybaceae were published

from all over the world, many of them from Asia, North America or Australia (e.g. Horak et al. 2015, Latha & Manimohan 2017, Matheny & Bougher 2017, Cripps et al. 2019, Matheny & Kudzma 2019), but also from Europe (see e.g. Kokkonen & Vauras 2012; Esteve-Raventós et al. 2015, 2016, 2018; Larsson et al. 2014; Franchi et al. 2016; Vauras & Larsson 2016a, b; Bizio et al. 2017; Larsson et al. 2018; Bandini et al. 2017, 2019a, b, c, 2020). Yet many parts of the world, e.g. China, are not even approximately evaluated regarding the actual number of species occurring there (see e.g. the list in Fan & Bau 2010), and thus the number of species worldwide, estimated at 1050 by Matheny et al. (2019), probably will be exceeded by far.

Our new species belongs to *Inocybe* ss. str., characterised e.g. by mostly thick-walled cheilocystidia and the presence of also mostly thick-walled pleurocystidia. The genus can be further divided into species that have no metuloid caulocystidia or only near the apex and those that have metuloid caulocystidia on the entire length of the stipe. *Inocybe antoniniana* belongs to this latter group, the section *Marginatae* Kühner. According to the key of Bon (1998) it is divided into the three subsections, *Rubellae* (Kühner & Boursier) Bon with reddish-pinkish (“rosé”) tinges on pileus or stipe, *Praetervisae* Bon, characterised by a white or yellowish stipe,

and *Oblectabiles* Bon with a more or less reddish-pinkish (“rosé”) or subconcolorous stipe. *Inocybe antoniniana* has to be attributed to subsect. *Praetervisae* according to these morphological criteria.

### Materials and methods

Notes were taken of relevant macroscopic characters, including especially those that change through drying, e.g. colour and smell, from fresh basidiomata, of habitat and surrounding trees, and in the following of the exsiccatum colour. Microscopic characters were examined and photographed in water and 3 % KOH solution with a Leica DM-750 and a Zeiss Axio Imager A2 at 400× and 1000× magnifications. Measurements were made with Zeiss Axiovision version 4.8. Basidiospore length includes nodules; cystidia were measured without crystals and basidia without sterigmata. The size of all characters measured is given as length by width. The Q value is the ratio of basidiospore length to width for each spore.

The photos of the fresh collections on Figures 2 and 3 were taken by E. Sesli with an Apple Iphone XS Max, those on Fig. 4 with a Canon EOS 600 D with EF-S 60 mm Canon macro lens, and those on

Fig. 5 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 calibration card has been photographed together with the fresh collections at the site where they were found. The RAW files were developed with Silkipix Developer Studio 4.0. Colour codes are taken from Munsell (2009, as “Mu”). Herbarium acronyms are according to Holmgren et al. (1990), the acronym DB means the private herbarium of Ditte Bandini.

The DNA of specimen KATO fungi 4064 was extracted in Trabzon University Mycology Laboratory. The DNA of specimen DB16-9-13-1 was extracted and the ITS region sequenced by Alvalab (Oviedo, Spain, <http://alvalab.es/>). The ITS sequence of WU\_20047 was generated following Hahn et al. (2019).

Sequences were assembled and edited using Geneious (version 6.1.2, Biomatters Ltd., Auckland, New Zealand). Forward and reverse sequences were merged, edited if necessary and a consensus sequence was generated for every sample. Sequences were submitted to GenBank (Tab. 1). FASTA sequences were studied and edited in MEGA 6.0 (<https://megasoftware.net/>) (Tamura et al. 2013). The comparative evaluation of the ITS sequences to record the adjacent species of *I. antoniniana* were

**Tab. 1.** Specimens investigated in this study. The original identification (orig. ident.) is given if the current species name is deviating. *Pseudosperma spurium* is used as outgroup. Newly generated sequences are in bold. The acronym DB means the private herbarium of Ditte Bandini.

<i>Inocybe</i> species	Voucher	Herbarium	additional voucher number	Country	GenBank/ UNITE (ITS)
<i>I. alnea</i> Stangl	M-147 holotype	M	K64	Germany	FJ755801 (ITS1)/ FJ755802 (ITS2)
<i>I. alnea</i> , orig. ident. <i>I. ochracea</i> Stangl	Stangl-88 <i>I.-ochracea</i> -holotype	M	K65	Germany	FJ755803
<i>I. alpinomarginata</i> C.L. Cripps, E. Larss. & Vauras	EL207-13 holotype	GB		Sweden	MK153648
<b><i>I. antoniniana</i> E. Sesli, Bandini &amp; Krisai</b>	<b>Fungi 4064 holotype</b>	<b>KATO</b>		<b>Turkey</b>	<b>MN988712</b>
<b><i>I. antoniniana</i></b>	<b>DB16-9-13-1</b>	<b>DB</b>		<b>Germany</b>	<b>MN989294</b>
<b><i>I. antoniniana</i></b>	<b>WU 20047</b>	<b>WU</b>		<b>Austria</b>	<b>MN989310</b>
<i>I. bombina</i> Bandini & B. Oertel	DB14-10-12-1 holotype	FR	FR-0246007/ BAN247	Germany	MK929267
<i>I. caprimulgi</i> Vauras & E. Larss.	JV5808F holotype	TUR-A	TUR-A 176158	Finland	KT958924
<i>I. decemgibbosa</i> (Kühner) Vauras	G00126469 lectotype	G		France	KT203784
<i>I. diabolica</i> Vauras	JV5712F isotype	WTU		Norway	HQ201350
<i>I. fibrosoides</i> Kühner	PAM01100301	LIP	TENN063562	Switzerland	HQ586857

<i>Inocybe</i> species	Voucher	Herbarium	additional voucher number	Country	GenBank/ UNITE (ITS)
<i>I. flavobrunnescens</i> Esteve-Rav., G. Moreno & Bizio	AH 29883 holotype	AH		Portugal	KJ938784
<i>I. hirculus</i> Vauras	JV5974F holotype	TUR-A	TUR-A 2577/K51	Finland	FJ531872
<i>I. intricata</i> Peck	Stz2822	WTU	WTU:34911	USA	MH024844
<i>I. invadens</i> Matheny, Bougher & G.M. Gates	PBM3746	TENN	TENN:066978	Australia	JX258832
<i>I. krieglsteineri</i> Fern. Sas.	RFS031213-03 holotype			Spain	KJ938768
<i>I. lacunarum</i> Vauras & E. Larss.	JV12244F holotype	TUR-A	TUR-A 171771	Finland	KT958908
<i>I. mixtilis</i> (Britzelm.) Sacc.	M-0219661 epitype	M		Germany	KJ938767 or KM873369
<i>I. obtusiuscula</i> Kühner	Kühner 60-56 holotype	G	K63	France	FJ755800
<i>I. occulta</i> Esteve-Rav., Bandini, B. Oertel & G. Moreno	AH 36443 holotype	AH	KR-M-0046550 (isotype)	Spain	KX290787
<i>I. oreina</i> J. Favre	DB25-8-11-3b	DB	BAN398	Switzerland	MK929270
<i>I. phaeocystidiosa</i> Esteve-Rav., G. Moreno & Bon	AH 9154 holotype	AH		Spain	KT203789
<i>I. phaeocystidiosa</i> , orig. ident. <i>I. salicis-herbaceae</i> Kühner	Kühner 66-49 <i>I.-salicis-herbaceae</i> -holotype	G		Switzerland	KM226889
<i>I. populea</i> Takah. Kobay. & Courtec.	TAKK15655 isoparatype	TUR-A	TUR-A 171763	Japan	KT958911
<i>I. praetervisiva</i> Quél.	SF229598 epitype	S		Italy	KT203792
<i>I. praetervisoides</i> Esteve-Rav., G. Moreno & Olariaga	AH 29863 holotype	AH		Spain	KT203794
<i>I. rivularis</i> Jacobsson & Vauras	JV3610F paratype	TUR-A	TUR-A 147424/K262	Finland	JN580885
<i>I. salicicola</i> Vauras & Kokkonen	KK&JV19738F holotype	TUR-A	TUR-A 163509/K11	Finland	FJ755796
<i>I. salicis</i> Kühner	PAM07051802	LIP			KT958907
<i>I. cf. similis</i> Bres. orig. ident. <i>I. sp.</i>	MCVE 29287	MCVE		Italy	KY848217
<i>I. strickeriana</i> Bandini, Anja Schneid. & M. Scholler	KR-M-0044749 holotype	KR		Germany	MG012477
<i>I. substellata</i> Kühner	Kühner 73-218 holotype	G		France	KT958928
<i>I. tabacina</i> Furrer-Ziogas	DB28-8-14-1	FR	FR-0246016/BAN616	Germany	MK929272
<i>I. undinea</i> Bandini, P.-A. Moreau & B. Oertel	DB6-7-14-1 holotype	KR	BAN2362/KR-0043293	Germany	MK929265
<i>I. urbana</i> Alessio	AMB 17142 holotype	AMB		Italy	KT229613
<i>I. villosa</i> Bandini, B. Oertel & U. Eberh.	DB29-9-13-2 holotype	KR	BAN407/KR-M-0042327	Germany	MH366605
<i>I. xanthomelas</i> Boursier & Kühner	DB15-9-15-3-Dondl	DB	BAN1302	Germany	MH366571

<i>Inocybe</i> species	Voucher	Herbarium	additional voucher number	Country	GenBank/ UNITE (ITS)
<i>I. sp. orig. ident.</i> <i>I. cf. praetervisa</i>	EL7206	GB		Sweden	FN550890
<i>I. sp. orig. ident.</i> <i>I. praetervisa</i>	EL8506	GB		Sweden	FN550892
<i>I. sp. orig. ident.</i> <i>I. straminipes</i>	PAM95081306	LIP		France	HQ586858
<i>I. sp. orig. ident.</i> <i>I. mixtilis</i>	PK5861	UBC	UBC:F19817	Canada	HQ604593
<i>Inocybe sp.</i>	SA100602A			Slovakia	KP636858
<i>Inocybe sp.</i>	FISAP971-14	TUR-A	TUR175302	Finland	UDB022394
<i>Pseudosperma spurium</i> (Jacobsson & E. Larss.) Matheny & Esteve-Rav.	SJ92-017 holotype	GB		Sweden	AM882784.2

made by BLAST analysis (Altschul et al. 1990). If necessary, the sequences were trimmed to the exact length of ITS. In Genbank (<https://www.ncbi.nlm.nih.gov/genbank/>) the setting “Optimize for somewhat similar sequences, blastn” and in UNITE (<https://unite.ut.ee/>) the massBLASTer was used. Unpublished private ITS sequence data of DB and collaborators were used for comparison.

The sequences were aligned with MAFFT version 7 (Katoh et al. 2019) (<https://mafft.cbrc.jp/alignment/server/>). The most suitable MAFFT-algorithm for *Inocybe* ITS sequences was found to be G-INS-i. All other parameters were set to default. Phylogenetic reconstructions were conducted on the CIPRES Portal (San Diego Supercomputer Center, [http://www.phylo.org/sub\\_sections/portal/](http://www.phylo.org/sub_sections/portal/)) (Miller et al. 2010), using the maximum likelihood algorithm RAxML with GTRGAMMA model and 1000 bootstrap replicates (Exelixis Lab, Heidelberg Institute for Theoretical Studies, Heidelberg, Germany) (Stamatakis 2014).

### Taxonomy

***Inocybe antoniniana*** E. Sesli, Bandini & Krisai, sp. nov. – Figs. 2–8  
Mycobank no.: MB 834091, Genbank MN988712 (holotype)

**Diagnosis.** – *Inocybe antoniniana* is a nodulose-spored species with yellowish-ochraceous pileus colour and smooth to (sub)rimulose pileus surface, an entirely pruinose stipe with (sub)bulbous base, rather small basidiospores, measuring 7.1–9.8 µm (av. 8.5 µm) × 5.7–8.7 µm (av. 7.0 µm), and usually rather short hymenial cystidia, pleurocystidia measuring 44–71 µm (av. 56 µm) × 9–19 µm (av. 14 µm). It differs from *I. xanthome-*

*las* e.g. by smaller and differently shaped spores, and from other species of the group with equally coloured pilei, as *I. phaocystidiosa* or *I. krieglsteineri* e.g. by smaller often (sub)isodiametrical spores, shorter and on average often slimmer hymenial cystidia, and from the named and other species also by ITS sequence data.

**Holotypus.** – TURKEY. Trabzon, Akcaabat, Fengo Yaylasi, N 40° 55' 23.54", E 39° 24' 51.64", alt. 1625 m, *Picea orientalis*, *Fagus orientalis*, *Alnus glutinosa*, 8 September 2019, leg. E. Sesli (Holotype KATO Fungi 4064).

**Description.** – Pileus 20–50 mm wide, at first (sub)conical, later broadly convex or expanded, with more or less pronounced large umbo, margin at first slightly involute, later decurved to straight or even uplifted, and then pileus depressed around the umbo; young basidiomata with faint remnants of a pallid velipellis, to be observed especially at the centre; colour yellowish, yellow-ochraceous, golden, or yellow with orange to faintly reddish or brownish hue (Mu 10YR 7/6–7/8, 6/6–6/8 or 5/6–5/8; 7.5YR 7/6–7/8); surface at first entirely glabrous, then finely rim(ul)ose towards margin, while remaining glabrous at the centre; no remnants of a cortina observed. – Lamellae moderately crowded (ca. 40–50(60), l = 1–3) a bit thickly, emarginate adnate, (sub)ventricose, at first whitish, then dingy beige to very pale coffee-brown; edge irregular, fimbriate, whitish, but in some basidiomata slightly brownish where bruised. – Stipe 30–65 × 3–6(10) mm, cylindrical or curved, with thickened to bulbous base, but not explicitly marginate bulbous, covered with fine whitish tomentum when young, later striate or glabrous, at first white or whitish, later still whitish or very pale brownish; entirely pruinose on the entire length of the stipe. – Context whitish in pileus and stipe. Smell none to

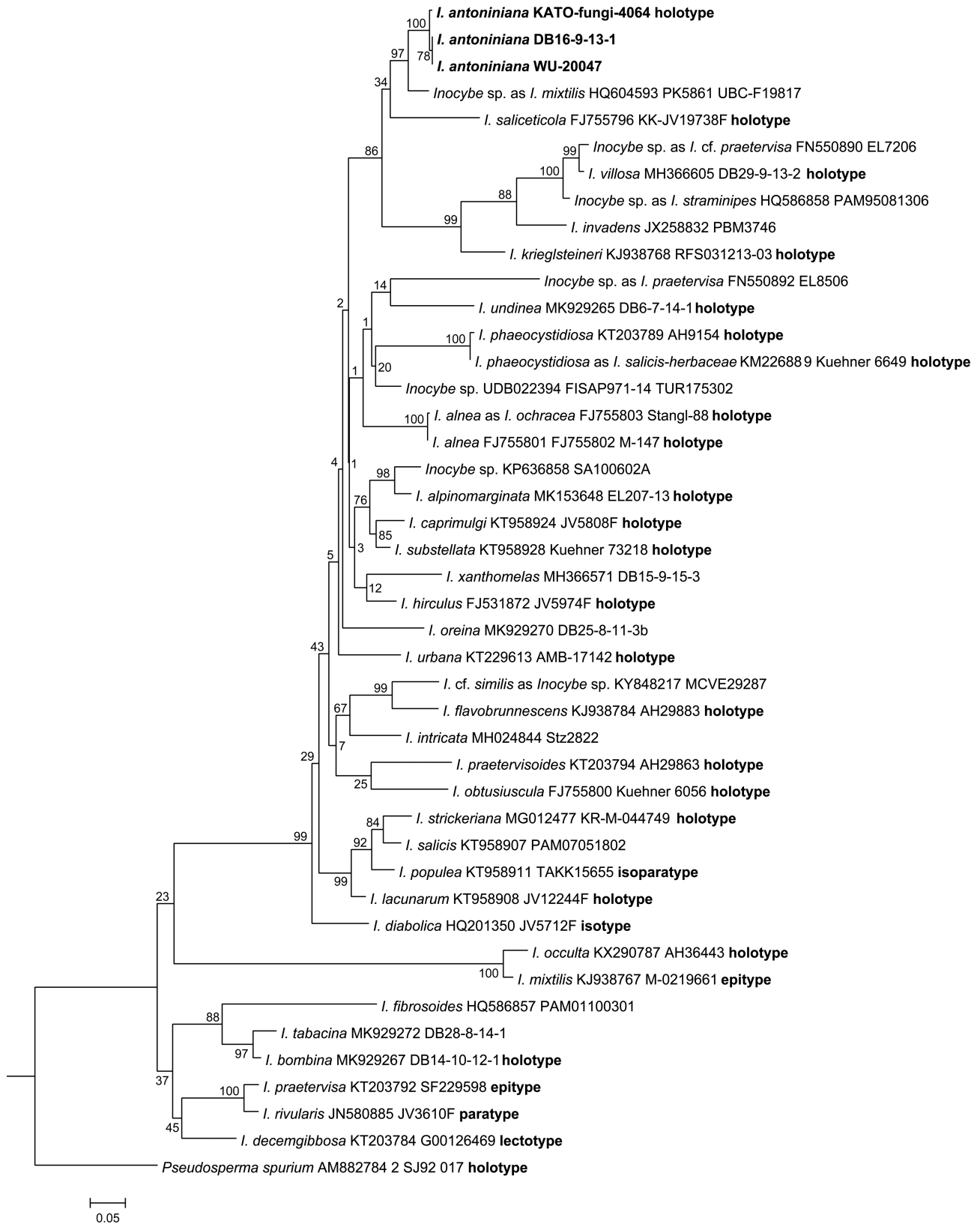


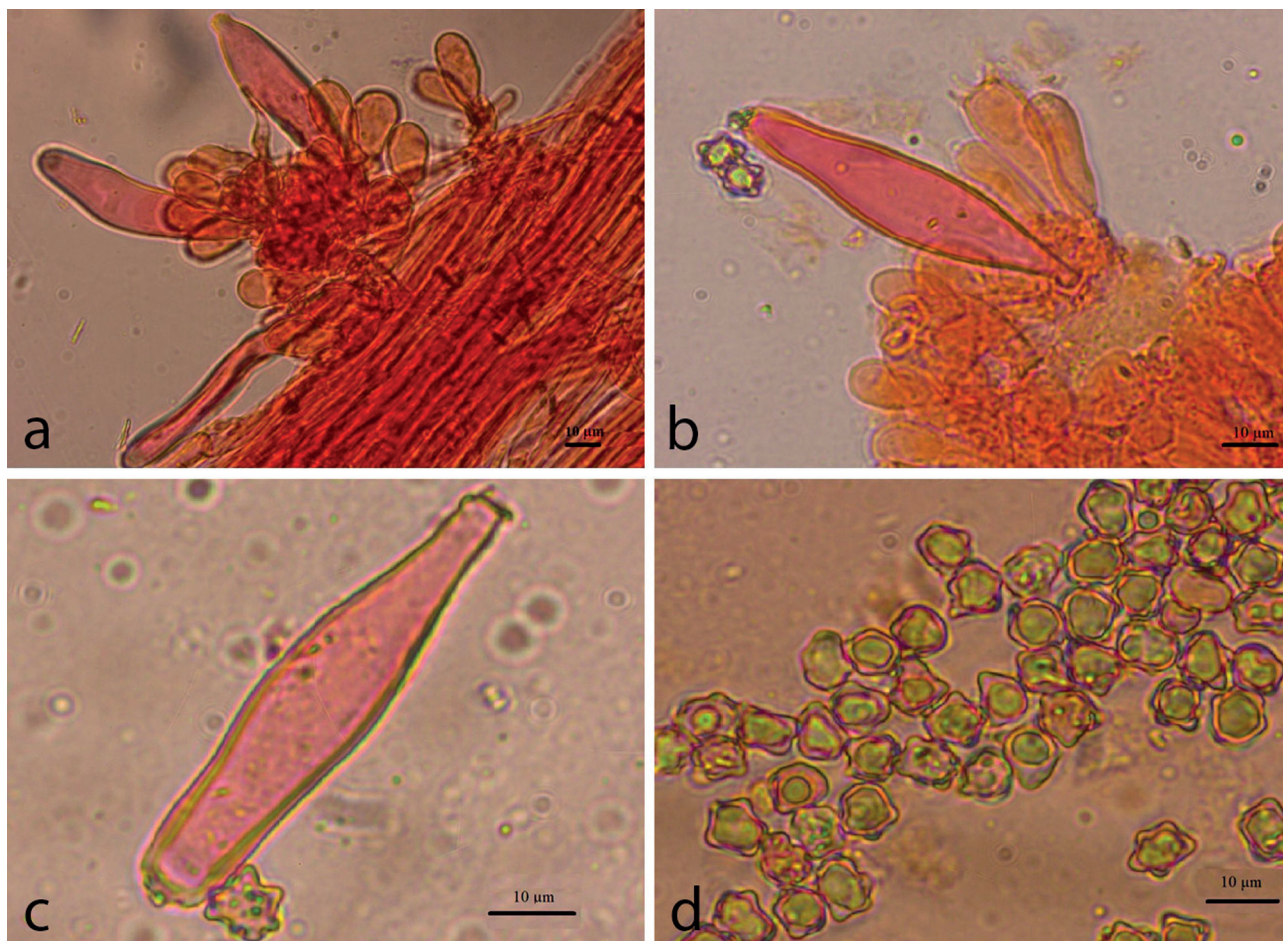
Fig. 1. Phylogenetic reconstruction based on ITS sequences with the Maximum Likelihood algorithm RAxML.



**Figs. 2–3.** *Inocybe antoniniana* (holotype, coll. KATO Fungi 4064), phot. E. Sesli. **Fig. 4.** *Inocybe antoniniana* (coll. KATO Fungi 3221), phot. E. Sesli. **Fig. 5.** *Inocybe antoniniana* (coll. DB16-9-13-1), phot. D. Bandini.

subspERMATICAL, at least when cut. – Colour of exsiccata pileus greyish brown, dark brown with reddish hue (Mu 10YR 4/2–4/4, 7.5YR 3/2–3/6),

lamellae concolorous or a little lighter, stipe concolorous or greyish brown, but not always obviously darkening, and not blackening on drying.



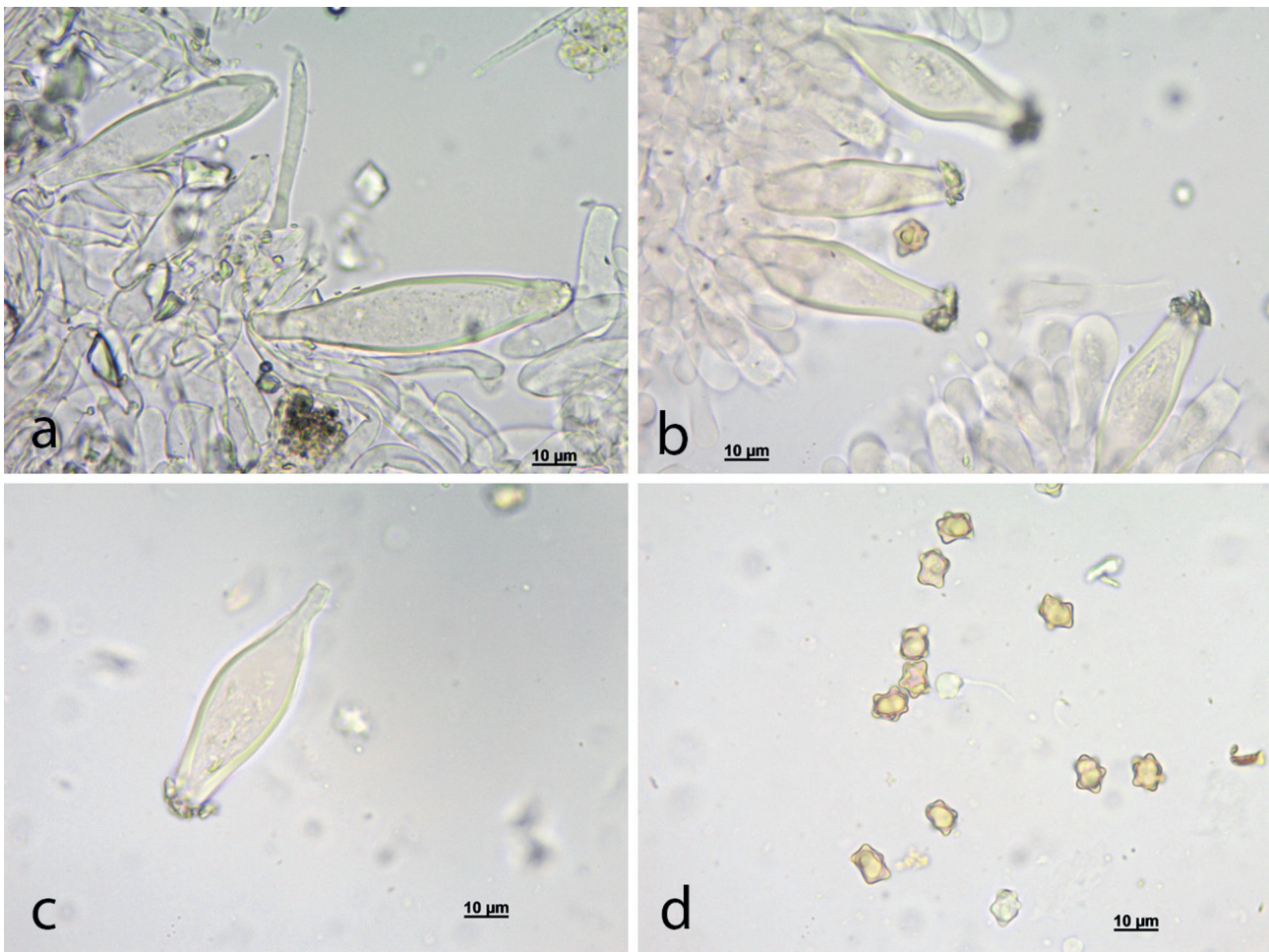
**Fig. 6.** *Inocybe antoniniana*, microscopical characters in Congo red (holotype); **a.** Caulocystidia, **b.** Cheilocystide, **c.** Hymenial cystide, **d.** spores; phot. E. Sesli.

Basidiospores  $7.1\text{--}9.8\ \mu\text{m}$  (av.  $8.5\ \mu\text{m}$ , SD  $0.6\ \mu\text{m}$ )  $\times$   $5.7\text{--}8.7\ \mu\text{m}$  (av.  $7.0\ \mu\text{m}$ , SD  $0.6\ \mu\text{m}$ );  $Q = 1.0\text{--}1.5$  (av.  $1.2$ , SD  $0.1$ ) ( $n = 120$  of 3 coll.), nodulose, often (sub)isodiametrical, with 7–10 often, but not in all collections strongly pronounced obtuse nodules. – Basidia  $25\text{--}33 \times 7\text{--}10\ \mu\text{m}$ , generally 4-spored, seldom also 2-spored and then basidiospores up to  $10.5\ \mu\text{m}$  long. – Lamellae edge sterile, composed of cheilocystidia and hyaline, (sub)clavate, cylindrical or subglobose, thin-walled paracystidia. – Pleurocystidia  $44\text{--}71\ \mu\text{m}$  (av.  $56\ \mu\text{m}$ , SD  $1\ \mu\text{m}$ )  $\times$   $9\text{--}19\ \mu\text{m}$  (av.  $14\ \mu\text{m}$ , SD  $2\ \mu\text{m}$ );  $Q = 2.6\text{--}6.7$  (av.  $4.2$ , SD  $0.8$ ) ( $n = 45$  of 3 coll.); mostly (sub)fusiform, also (sub)utriform, at the apex wide or narrow, usually without or with only short neck, with short pedicel, sometimes with truncate base, apex usually crystalliferous, walls up to  $2.0(2.5)\ \mu\text{m}$  thick at the apex, often abruptly thickened towards the apex, pale yellowish-greenish with 3% KOH. –

Cheilocystidia similar in appearance and size. Pileipellis constituted by an epicutis made up of parallel hyphae  $5\text{--}12\ \mu\text{m}$  wide, with encrusting and parietal ochraceous brownish pigment, subcutis with wider and paler to hyaline elements. Caulocystidia present on the entire stipe length,  $45\text{--}75 \times 10\text{--}15\ \mu\text{m}$ , mostly (sub)fusiform, often with truncate base, apex usually crystalliferous, walls up to  $1.5\ \mu\text{m}$  thick at the apex, pale yellowish-greenish with 3% KOH; intermixed with numerous (sub)clavate to subglobose cauloparacystidia. – Clamp connections abundant in all tissues.

**Etymology.** – Named “antoniniana” in honour of the Czech mycologist Vladimír Antonín.

**Habitat and associated trees.** – The German specimens grew next to *Fagus sylvatica* on a wayside at a south-west exposed slope with direct sunlight. The type and paratype material from Turkey also grew next to *Fagus* (*Fagus orientalis*), with



**Fig. 7.** *Inocybe antoniniana*, microscopical characters in 3 % KOH (paratype, coll. DB16-9-13-1); **a.** Caulocystidia, **b.** Cheilocystidia, **c.** Pleurocystidia, **d.** Spores; phot. D. Bandini.

*Picea orientalis* nearby. The Turkish collection sites are on highlands located in the East Black Sea region. In this region, mountain ranges, running parallel to the Black Sea, create a barrier for rain clouds moving inland, which is an important factor in determining the ecological conditions. Typical vegetation type of the region is beech-spruce mixed forests due to the mild and rainy climate even in the summer months. The collection site is favourable for mushroom growing and has a lot of old trees, such as *Fagus orientalis* and *Picea orientalis*, and some interesting species have been described from the region recently (Sesli & Liimatainen 2018, Sesli et al. 2018). The Austrian collection grew next to *Fagus sylvatica* in a young to middle-aged Central European beech forest, mixed with *Acer pseudoplatanus* and some *Picea abies* trees, on a locally south-east exposed small slope, this site lies in the Atlantic or Central

European transition climate with mild winters and moderately hot summers and mean annual rainfall between 1400 and 1800 mm (<https://www.land-oberoesterreich.gv.at/18479.htm>).

Thus we can cautiously assume that *I. antoniniana* is mainly associated with *Fagus* species.

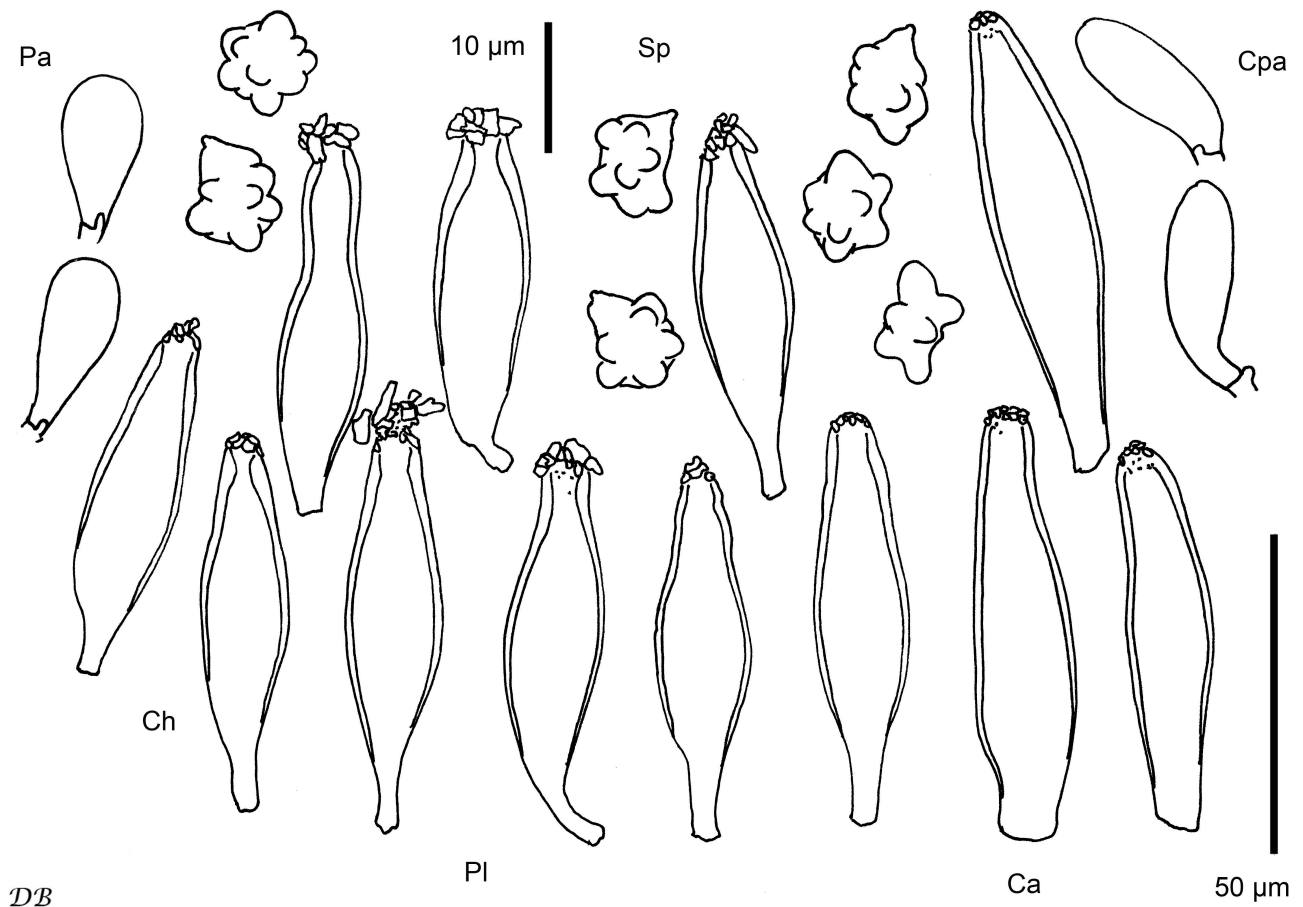
**Distribution.** – Up to now known from Turkey, Germany and Austria.

**Material examined** (besides holotype). – AUSTRIA. Oberösterreich, Vöcklabruck, Zell am Moos, Kolomansberg, Ruine Wildeneck, TK25 8045/5, N 47°55'30" E 13°17'30", alt. 680 m, *Fagus sylvatica*, 5 September 1999, leg. T. Bardorf (WU 20047).

GERMANY. Baden-Württemberg, Heidelberg, TK25 6518/3, alt. 250 m, *Fagus sylvatica*, 16 September 2013, leg. D. Bandini (DB16-9-13-1).

TURKEY. Trabzon, Akcaabbat, Hidirnebi Yaylasi, N 40°58'15.88", E 39°25'44.51", alt. 1413 m, *Picea orientalis*, *Fagus orientalis*, 11 Sep 2013, leg. E. Sesli (KATO Fungi 3221).





**Fig. 8.** *Inocybe antoniniana*, drawing of microscopical characters (paratype, coll. DB16-9-13-1), Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores, drawing D. Bandini.

## Discussion

### Morphology and ecology

*Inocybe antoniniana* has a smooth to finely rim(ul)ose ochraceous-yellow pileus surface and an entirely pruinose stipe with (sub)bulbous base. The nodulose basidiospores are often (sub)isodiametrical in shape and on average only 8.5 µm long; the pleurocystidia are on average < 60 µm; the base of the caulocystidia is often truncate; and the habitat are forests with *Fagus sylvatica* or *Fagus orientalis*. Thus *I. antoniniana* is clearly distinguishable from other yellow to ochraceous or ochraceous brownish species of sect. *Marginatae*. One of them is *I. phaeocystidiosa* Esteve-Rav., G. Moreno & Bon, that often has a yellow smooth pileus surface, but its spores and hymenial cystidia are on average much larger (see Esteve-Raventós & Moreno 1987). Furthermore, it grows mostly in mountainous to alpine regions with *Picea abies* or *Salix* sp. nearby and not with

*Fagus sylvatica*. *Inocybe xanthomelas* Boursier & Kühner is often associated with frondose trees, and the pileus may show the same colour and texture as *I. antoniniana*, but the basidiospores are larger on average (Kühner 19333) and shaped differently. *Inocybe krieglsteineri* Fern. Sas., a species that may also look similar to *I. antoniniana* macroscopically, has larger and not or only very rarely (sub)isodiametrical basidiospores, and larger hymenial cystidia (see e.g. Esteve-Raventós et al. 2015; Vauras & Larsson 2016a). Furthermore, it is mostly found with *Pinus sylvestris* or *Picea abies*. *Inocybe lacunarum* Vauras & E. Larss. and *I. saliceticola* Vauras & Kokkonen, two northern species (Vauras & Kokkonen 2009, Vauras & Larsson 2016a), that are not known from Germany, Austria or Turkey up to now, have much larger basidiospores and larger hymenial cystidia – as well as *I. praetervisoides* Esteve-Rav., G. Moreno & Olariaga, a Mediterranean species, only known from Spain up to now, growing in

evergreen oak forests (Esteve-Raventós et al. 2016). *Inocybe alpinomarginata* C.L. Cripps, E. Larss. & Vauras is an alpine species with larger basidiospores and hymenial cystidia (Cripps et al. 2019) and *I. substellata* Kühner grows mainly in the alpine region and the basidiospores are stellate and also much larger than those of *I. antoniniana* (see Kühner 1988, Vauras & Larsson 2016a). *Inocybe undinea* Bandini, P.-A. Moreau & B. Oertel as well has stellate and much larger spores, and it is a species which seems to be associated with *Alnus*, thus occurring in moist habitats (see Bandini et al. 2019a) – and so do *I. alnea* Stangl and *I. bombina* Bandini & B. Oertel. In addition, their spores are larger than those of *I. antoniniana*, and the hymenial cystidia are larger (*I. alnea*) or shorter (*I. bombina*) (Stangl 1989, Vauras & Kokkonen 2009, Bandini et al. 2019a). *Inocybe salicis* is associated with *Salix* in moist habitats, its basidiospores are larger than those of *I. antoniniana* and the hymenial cystidia are wider (see e.g. Vauras & Kokkonen 2009, Bandini et al. 2019b). *Inocybe caprimulgi* Vauras & E. Larss. finally has a coarse lanose-felty pileus texture and the hymenial cystidia are much wider than those of *I. antoniniana* (Vauras & Larsson 2016a). This species furthermore is not known from Central Europe up to now and it grows on sandy sites with *Pinus* and *Picea*. Several other species of the section *Marginatae*, such as *I. mixtilis* (Britzelm.) Sacc. (Esteve-Raventós et al. 2018), *I. hirculus* Vauras (Vauras 1994), *I. villosa* Bandini, B. Oertel & U. Eberh. (Bandini et al. 2019b), *I. praetervisa* Quél. (Esteve-Raventós et al. 2016), *I. rivularis* Jacobsson & Vauras (Jacobsson & Vauras 1990), or *I. oreina* J. Favre (Favre 1955) are that much different from *I. antoniniana* either in colour or texture of pileus and/or in microscopical aspect as well as genetically, that a confusion is unlikely. Of all these species in macroscopical and microscopical respect the most similar seems to be *I. xanthomelas*. Possibly *I. antoniniana* has been identified as this species up to now, but it is probably also rather rare.

Several of the species listed above, e.g. *I. phaeocystidiosa*, *I. xanthomelas*, *I. krieglsteineri* and *I. lacunarum* belong to a group of the *Marginatae* defined by pronounced darkening or even blackening of the stipes when drying and “elongate or slender sublageniform cystidia with a well-defined and protruding neck” (Esteve-Raventós et al. 2016). The stipes of some of them, especially of *I. krieglsteineri* and *I. xanthomelas* are actually often blackening when drying. The stipes of *I. antoniniana*, are sometimes greying when drying, but not blackening, and the hymenial cystidia are usually without or only

with a short neck. None of the above species is genetically closely related to *I. antoniniana*. The most closely related species but with only 94 % ITS identity (see Fig. 1) is yet undescribed.

### Molecular genetics

At present there are no further sequences from *I. antoniniana* in GenBank and UNITE. Therefore, many nodulose-spored *Inocybe* species should be compared to *I. antoniniana* (Fig. 1). Most species in Fig. 1 as well as *I. antoniniana* belong to the *phaeocystidiosa* section-clade (Esteve-Raventós et al. 2016) with a bootstrap support of 99.

Besides the MOTU (molecular operational taxonomic unit) HQ604593 there are another eight species/ MOTU's matching with the ITS of *I. antoniniana* in the BLASTn analyses: *I. alpinomarginata* C.L. Cripps, E. Larss. & Vauras (Cripps et al. 2019), *I. caprimulgi* Vauras & E. Larss., *I. hirculus* Vauras, *I. saliceticola* Vauras & Kokkonen, *I. substellata* Kühner, *I. xanthomelas* Boursier & Kühner, the MOTU KP636858, and the MOTU UDB022394.

“*I. sp. orig. ident. I. mixtilis* HQ604593” is in need of a new interpretation, because *I. mixtilis* is epitypified and a species of a different section-clade of *Inocybe* (Fig. 1) (Stangl 1984; Esteve-Raventós et al. 2018). “*I. sp. orig. ident. I. mixtilis* HQ604593” is the species with the highest ITS similarity value (94 %) of all nine neighbouring species of *I. antoniniana*. It occurs in North America, and a documentation of the dried specimens can be found on the UBC website ([https://herbweb.botany.ubc.ca/herbarium/images/fungi\\_images/Large\\_web/F19817.jpg](https://herbweb.botany.ubc.ca/herbarium/images/fungi_images/Large_web/F19817.jpg)). “*Inocybe sp. KP636858*” and “*Inocybe sp. UDB022394*” are further matches of the ITS of *I. antoniniana*. Also for these species a suitable name has to be worked out in future.

Further comments to the species in Fig. 1

As the differences between the holotype ITS sequences of *I. ochracea* Stangl and *I. alnea* Stangl are minor, these species were declared synonymous by Vauras & Kokkonen (2009).

*Inocybe phaeocystidiosa*, the core species of the *phaeocystidiosa* section-clade (Esteve-Raventós et al. 2016), can be found in Europe in alpine and also montane habitats. In some cases the ITS has the base pair motif CTGGAGTTTTGGT, but the alpine habitat is not correlated with the presence of this ITS motif (Bandini & Oertel, unpubl.). The ITS of the *I. salicis-herbaceae* Kühner holotype from an alpine habitat is identical to the sequence of the *I. phaeocystidiosa* holotype, which did not grow in an

alpine habitat. Therefore, they are synonyms (Esteve-Raventós et al. 2016). In both holotype ITS sequences the motif CTGGAGTTTGGT is lacking. An example for a sequence of *I. phaeocystidiosa* with this motif is KT203790 from a Swiss specimen. Two alpine samples collected by B. Oertel in Italy and Switzerland contained both types of ITS in equal parts. The author (BO) of this study guesses therefore that the presence of the motif has no taxonomic importance at all and should be seen as part of the natural ITS variability.

Comments to taxonomically still to be clarified MOTUs in Fig. 1

“*Inocybe* sp. orig. ident. *I. praetervisa* FN550892” and “*Inocybe* sp. orig. ident. *I. cf. praetervisa* FN550890” are in need of new names, because *I. praetervisa* is an epitypified species from quite another section-clade (Fig. 1) (Esteve-Raventós et al. 2016).

“*I. sp. orig. ident. I. straminipes* HQ586858” is something else, because microscopic studies of the holotype of *I. straminipes* Romagn. done by J. Vauras and ourselves (Bandini et al. 2019b) made clear, that this species is a synonym of *I. salicis* Kühner (Vauras & Kokkonen 2009).

A further MOTU is KY848217. Here the authors of this publication presently are working with the hypothesis, that this could be *I. similis* Bres. (therefore depicted as *I. cf. similis* in Fig. 1).

With the aid of molecular genetical studies, four different section-clades for the species morphologically similar to *I. antoniniana* could be differentiated:

1. The *phaeocystidiosa* section-clade (e.g. *I. antoniniana*, *I. saliceticola* & *I. phaeocystidiosa*, Esteve-Raventós et al. 2016).
2. The *mixtilis* group (e.g. *I. mixtilis* & *I. occulta*, Esteve-Raventós et al. 2018).
3. The group around *I. tabacina* (e.g. *I. tabacina* & *I. bombina*, Bandini et al. 2019a).
4. The *praetervisa* group (e.g. *I. praetervisa* & *I. rivularis*, Esteve-Raventós et al. 2016; Larsson et al. 2018).

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