Inocybe viscida (Inocybaceae: Agaricomycetes), a new species from Mediterranean forests of Turkey

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Abstract: *Inocybe viscida* sp. nov., a novel species found in a forest with old trees of *Pinus brutia* and tertiary relict endemic *Liquidambar orientalis* in coastal area of southwestern Turkey, is described and illustrated. We present this new species based on morphological and molecular data from nuclear rDNA internal transcribed spacer region (ITS1-5.8SITS2 = ITS) and the portions of nuc 28S rRNA (LSU) gene. Comprehensive description, field photographs, line drawings of the microscopic features and comparisons with phenetically similar taxa and phylogenetically related species are discussed.

Key words: Agaricales, Basidiomycota, *Inocybe*, molecular systematics, taxonomy, ITS, LSU

1. Introduction

The family Inocybaceae Jülich consisted of the genera *Inocybe* (Fr.) Fr., *Auritella* Matheny & Bougher and *Tubariomyces* Esteve-Rav. & Matheny (Latha et al., 2016) as yet. Broad taxonomic studies and phylogenetic analyses of six gene (18S, 28S, 5.8S, *tef1*, rpb1, and rpb2) regions made through the last decade have established a global overview of phylogenetic relationships in the Inocybaceae family (Matheny et al., 2020). According to it, the family comprises of seven genera as primarily described *Inocybe*, *Auritella* and *Tubariomyces*, recently elevated to generic rank *Inosperma* (Kühner) Matheny & Esteve-Rav. and *Mallocybe* (Kuyper) Matheny, Vizzini & Esteve-Rav.*,* and newly described *Nothocybe* Matheny & K.P.D. Latha and *Pseudosperma* Matheny & Esteve-Rav. (Matheny et al., 2020). Among them *Inocybe* has a worldwide distribution and is frequently encountered, also known as species rich with an estimated number of 1050 species (Matheny and Kudzma, 2019; Matheny et al., 2020). Thanks to genetic examinations in the world new species from this genus are continuously described (Bandini et al., 2019; Cripps et al., 2019; Matheny and Kudzma, 2019; Bandini and Oertel, 2020; Bandini et al., 2020a, 2020b; Bandini et al., 2021a, 2021b; Caiafa et al., 2021; Li et al., 2021; Mešić et al., 2021).

The characteristic feature of *Inocybe* is mostly thick-walled hymenial cystidia (Kuyper, 1986), including pleurocystidia, which are absent in the other genera in the family (Matheny et al., 2019; Bandini et al., 2020a, 2021a). The members of *Inocybe* are characterized by small, often brown basidiomes with a smooth, rimose, fibrillose, squamulose to squarrose pileus surface, with age often brownish lamellae, and often distinctive odor (Matheny and Kudzma, 2019). Their basidiospores are smooth or nodulose or rarely a mixture of both (Bandini et al., 2021a), pigmented, slightly thick-walled, and typically lack a true germ pore (Matheny and Kudzma, 2019; Matheny et al., 2020). Species of *Inocybe* occur on all continents except Antarctica, in most terrestrial biomes, associated with more than 23 ectomycorrhizal angiosperm and conifer families (Larsson et al., 2014; Matheny et al., 2020; Bandini et al., 2021a; Caiafa et al., 2021).

So far, *Inocybe* is known to have more than 85 species in Turkey (Altuntaş et al., 2019; Sesli, 2019; Sesli and Bandini, 2019; Sesli et al., 2020; Doğan et al., 2021; Oruç et al., 2021; Çevik et al., 2021; Solak and Türkoğlu, 2022), among them *Inocybe antoniniana* E. Sesli, Bandini & Krisai was recently described as new species (Bandini et al., 2020c). During the mycological exploration conducted between 2018 and 2022, the *Inocybe* species were gathered from Mediterranean forests. As a result of morphological and molecular analyzes, it was realized that the new *Inocybe* species did not match any of the known species

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517

of the genus, and it is therefore described here as *Inocybe viscida* sp. nov.

2. Materials and methods

2.1. Morphological studies

The macroscopic descriptions were based on field notes and photographs of fresh basidiomata. The microcharacters of the dried material were observed, measured and drawn from rehydrated tissues in 3% KOH, 10% NH$_4$OH or Congo red in 10% ammonia. The following abbreviations were used: L$_m$ - the average length, W$_m$ - the average width, Q - the quotient of length and width of all the measured elements, and Q$_m$ - the average of all calculated Q values. Measurements of basidiospores, basidia and cystidia were presented based on at least 30 measurements. Morphological terminology follows Vellinga (1988) and basidiospore shape was described according to Bas (1969).

2.2. Molecular studies and phylogenetic analysis

Genomic DNA was extracted from fresh specimens using ZR Fungal/Bacterial DNA MiniPrep kit (Zymo research, Irvine, California). The primer pairs ITS1F/ITS4 (White et al., 1990) and LR0R/LR5 (Vilgalys and Hester, 1990) were used to amplify nrITS and nrLSU gene regions, respectively. Positive PCR products were further sequenced from both ends (Source Bioscience, Berlin, Germany). Sequence chromatograms were checked and edited using in BioEdit 7.0.5 (Hall, 1999). Sequences for phylogenetic analysis retrieved from GenBank[1] (Table 1), with most of them generated by Matheny et al. (2002), Matheny (2005), Ryberg et al. (2008, 2010), Kropp et al. (2010), Ryberg and Matheny (2012), Kranabetter et al. (2013), Marchetti et al. (2014), Timling et al. (2014), Matheny and Bougher (2017), Matheny and Swenie (2018), Crous et al. (2020) and Bandini et al. (2021a, 2021b), were selected based on the results of BLAST and morphological similarities. For this study, all the generated sequences were compared with other sequences retrieved from the NCBI molecular database to estimate their phylogenetic placement. Phylogenetic tree was inferred from maximum likelihood (ML) and Bayesian inference (BI) methods using a concatenated dataset.

Phylogenetic tree inference was performed for the concatenated dataset with both ML and BI methods. The ML analysis was performed through the Cipres Science Gateway v.3.3 interface[2] (Miller et al., 2010) using RAxML v.8.2.10 (Stamatakis, 2014) employing the GTRGAMMA model with 1000 ML bootstrap replicates and default settings for other options. The BI was carried out employing a Markov chain Monte Carlo (MCMC)

algorithm using MrBayes version 3.2.2 (Ronquist et al., 2012). Four independent chains of MCMC were run for 1,000,000 generations, sampling every 1000 steps, with two runs per analysis. The initial 2500 trees (25%) recovered were excluded as a burn-in, and a 50% majority consensus tree of the remaining trees was then used to calculate the Bayesian posterior probabilities (BPP) of the group. Only maximum likelihood bootstrap (MLB) values of ≥ 85% and Bayesian posterior probability (BPP) values ≥ 0.90 are considered in the resulting tree (Figure 1). Branch lengths were estimated as mean values over the sampled trees. The phylogram inferred from both analyses were displayed with FigTree v.1.4.3[3] (Rambaut, 2016).

3. Results

3.1. Phylogeny

The combined nuclear dataset (nrITS and nrLSU) included 45 taxa with *Inocybe tenebrosa* Quél. (JV14910) and *I. luteifolia* A.H. Sm. (PBM2642 CUW) as the external group (Figure 1, Table 1). The results of the ML and BI analyzes showed similar topology, therefore only ML phylogeny (Figure 1) with both MLB and BPP bootstrap values is presented. The combined dataset consisted of 2300 characters, of which 1847 were constant characters, 159 were variable parsimony-uninformative characters, and 294 were parsimony-informative characters.

The multilocus analysis suggests *Inocybe viscida* sp. nov. in a well-supported clade with a long branch (MLB = 98%, BPP = 1.0, Figure 1) that is clearly distinct from all other sampled species of the *Inocybe geophylla*-group. The collections of *I. viscida* from Turkey were nested together forming a clade that is sister to *I.* aff. *geophylla* P. Kumm. (REH7879/NY:01034368) from Costa Rica, with high statistical support (MLB = 97%, BPP = 0.98, Figure 1).

3.2. Taxonomy

Inocybe viscida Kaygusuz, Knudsen & Bandini sp. nov. (Figures 2–5)

MycoBank: MB843492

Diagnosis: *Inocybe viscida* is characterized by pale straw to light yellow pileus, often with more or less distinct orange to reddish tinge at the center, often somewhat viscid pileus surface. Smooth spores, measuring on av. 8.5 × 5.2 μm, often narrowly fusiform to fusiform and narrowly lageniform to lageniform pleurocystidia, measuring on av. 65 × 13 μm, subfusiform to lageniform caulocystidia and growth with *Pinus brutia* Ten. and tertiary relict endemic *Liquidambar orientalis* Mill. By these combined characteristics as well as by nrITS and nrLSU sequence data it differs from, e.g., *I. posterula* (Britzelm.) Sacc., *I.*

Table 1. Information of taxa, specimens, and GenBank accession numbers of sequences used in this study. The newly released sequences are given in boldface.

| Species | Voucher or collection number | GenBank accession number | | Region |
		nrITS	nrLSU	
I. aff. geophylla	TENN:062544 (PBM2732a)	KY990543	KY990497	USA
I. aff. geophylla	TENN:070836	KY990542	KY990496	Canada
I. aff. geophylla	REH7879/NY:01034368	KY990539	JN974953	Costa Rica
I. aff. geophylla	TENN:071463	KY990545	KY990499	Canada
I. aff. geophylla	PBM546 (WTU)	KY990537	KY990491	USA
I. aff. insinuata	TENN:063620	KY990548	KY990502	Canada
I. aff. posterula	TENN:069518	—	KY990513	USA
I. agglutinata	Stz1178 (WTU)	KY990522	KY990480	USA
I. armeniaca	PBM 1228 (WTU)	—	AY380367	USA
I. armeniaca	SNH6 (WTU)	KY990524	KY990482	USA
I. bellidiana	STU:SMNS-STU-F-0901473 (Holotype)	MW845860	MW845860	Germany
I. fuscicothurnata	AU9919 (Isotype)	KY923020	KY923039	Canada
I. fuscodisca	PBM 1950 (WTU)	—	AY380376	USA
I. geophylla	JV 6374 (WTU)	—	AY380377	Finland
I. geophylla	UBC F28461	KP406546	—	Canada
I. geophylla	DAVFP 28144	HQ650749	—	Canada
I. geophylla	UBC:F19537	HQ604300	HQ604300	Canada
I. geophylla	EL9005	AM882870	AM882870	Sweden
I. geophylla	CA1882	KY990536	JN974951	USA
I. geophylla	TENN:062792	KY990533	KY990489	USA
I. geophylla	STU:SMNS-STU-F-0901531 (Epitype)	MW845949	MW845949	Austria
I. geophylla	DB9-11-11-12	MW856426	—	Germany
I. insinuata	TENN:063977	KY990546	KY990500	USA
I. ionocephala	TENN:062799 (Holotype)	KY990551	KY990504	USA
I. ionolepis	KM236689 (Holotype)	MT909818	MT909818	United Kingdom
I. lilacina	NYS:f1711 (Holotype)	MH024860	—	USA
I. luteifolia	PBM2642 (CUW)	—	EU307814	USA
I. miranda	EL8003	AM882877	AM882877	Sweden
I. miranda	X. Carteret private collection XC2012-02 (Isotype)	MW845954	—	France
I. orionis	SMNS-STU-F-0901455 (Holotype)	MW845898	MW845898	Germany
I. pallidicremea	WTU:F:038286 (Holotype)	KY923033	KY923042	Canada
I. phaeodisca var. *geophylloides*	MD08100106	—	KY990511	France
I. posterula	UBC:F18957	HQ604298	HQ604298	Canada
I. posterula	JV2527F (WTU)	KY990556	KY990512	Finland
I. posterula	M-0151615 (Epitype)	KM873368	—	Germany
I. pudica	TENN:062544 (PBM2732b)	KY990558	KY990515	USA
I. pudica	PBM 1373 (WTU)	—	AY038323	USA
I. pudica	EL15905	AM882872	AM882872	Sweden

Table 1. (Continued).

I. sambucella	TENN:063623	KY990540	KY990494	USA
I. sambucella	TENN:062762	KY990541	KY990495	USA
I. sublilacina	TENN:062542 (Holotype)	—	KY990519	USA
I. tenebrosa	JV14910	—	JN974945	Italy
I. viscida	**OKA-TR1717 (Holotype)**	**ON074702**	**ON074741**	**Turkey**
I. viscida	**OKA-TR1718**	**ON074703**	**ON074742**	**Turkey**
I. whitei	SJ06012	FN550915	FN550915	Sweden
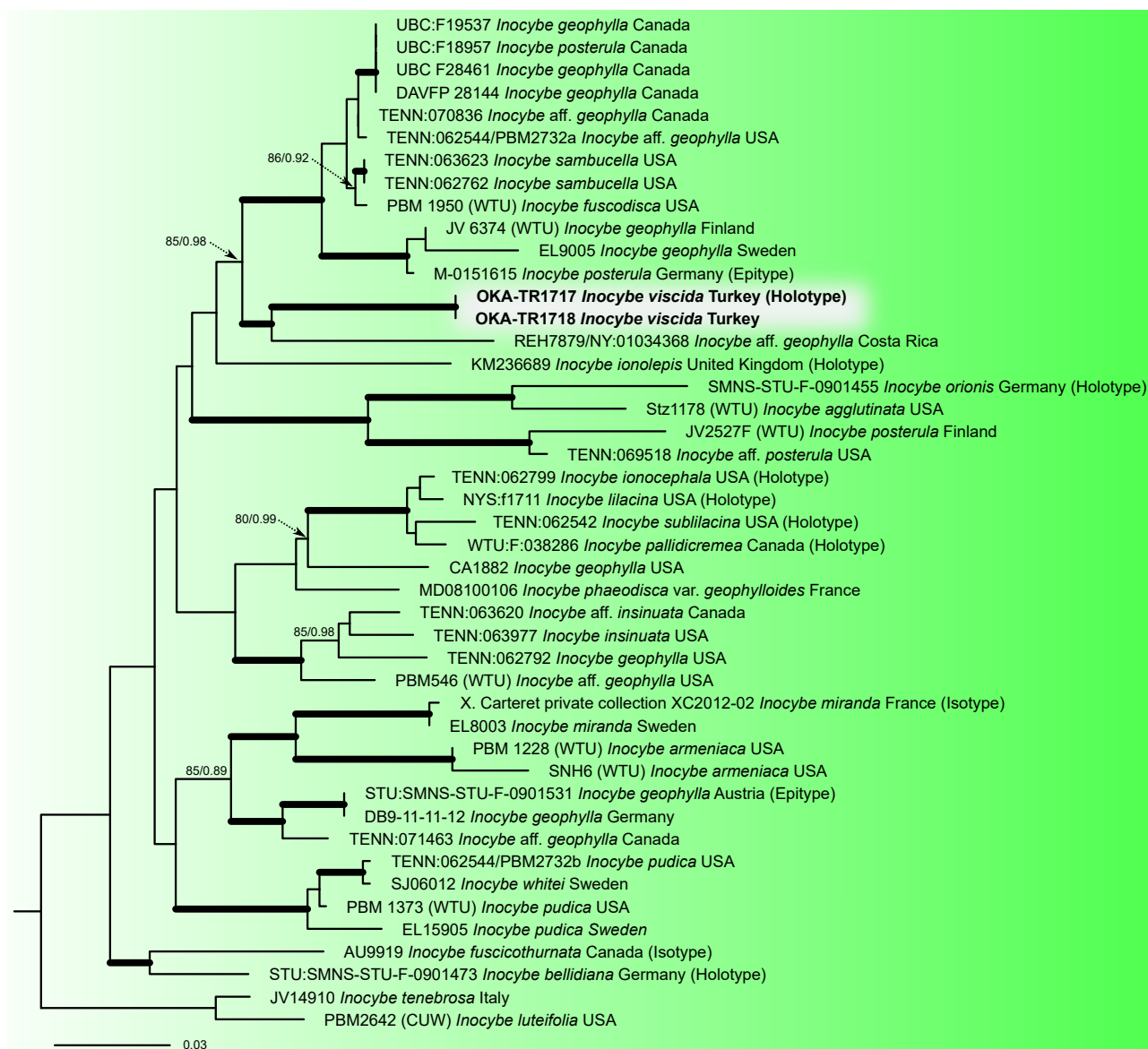
Figure 1. Maximum likelihood (ML) tree illustrating the phylogeny of *Inocybe* species based on concatenated dataset of nrITS and nrLSU sequences with *Inocybe tenebrosa* (JV14910) and *I. luteifolia* (PBM2642 CUW) as outgroup. The maximum likelihood bootstrap support values (MLB ≥ 85%) and Bayesian posterior probabilities (BPP ≥ 0.90) are shown at nodes. Branches with MLB ≥ 0.90% and BPP ≥ 0.95 are bolded. The newly generated sequences are displayed in boldface.
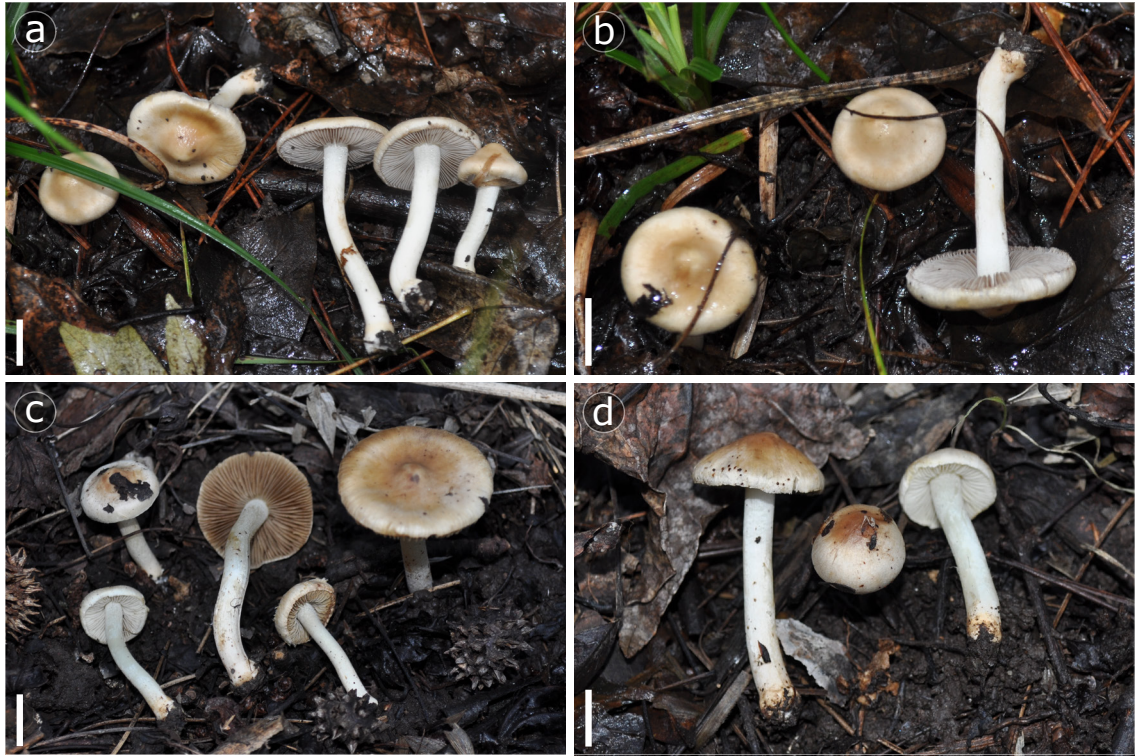
Figure 2. *Inocybe viscida*: basidiomes growing in its natural habitat. a. Collection *OKA-TR1717* (holotype), b. Collection *OKA-TR1718*, c. Collection *OKA-TR0230*, d. Collection *OKA-TR0231*. Scale bars = 10 mm.
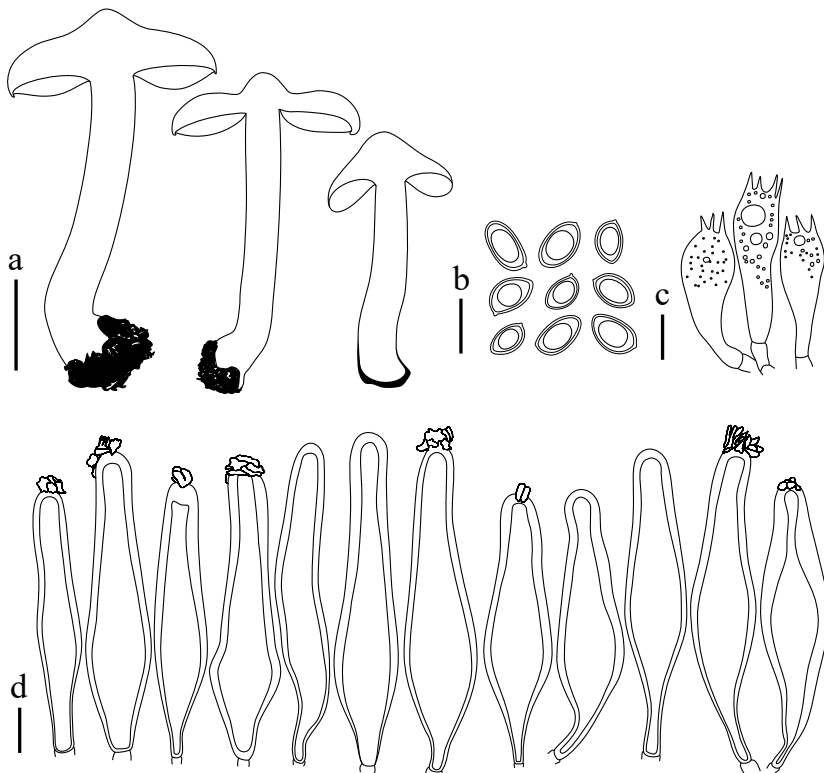

Figure 3. *Inocybe viscida* (*OKA-TR1717*, holotype): a. Crosssections of basidiomata, b. Basidiospores, c. Basidia, d. Pleurocystidia. Scale bars: a = 10 mm, b–d = 10 μm.
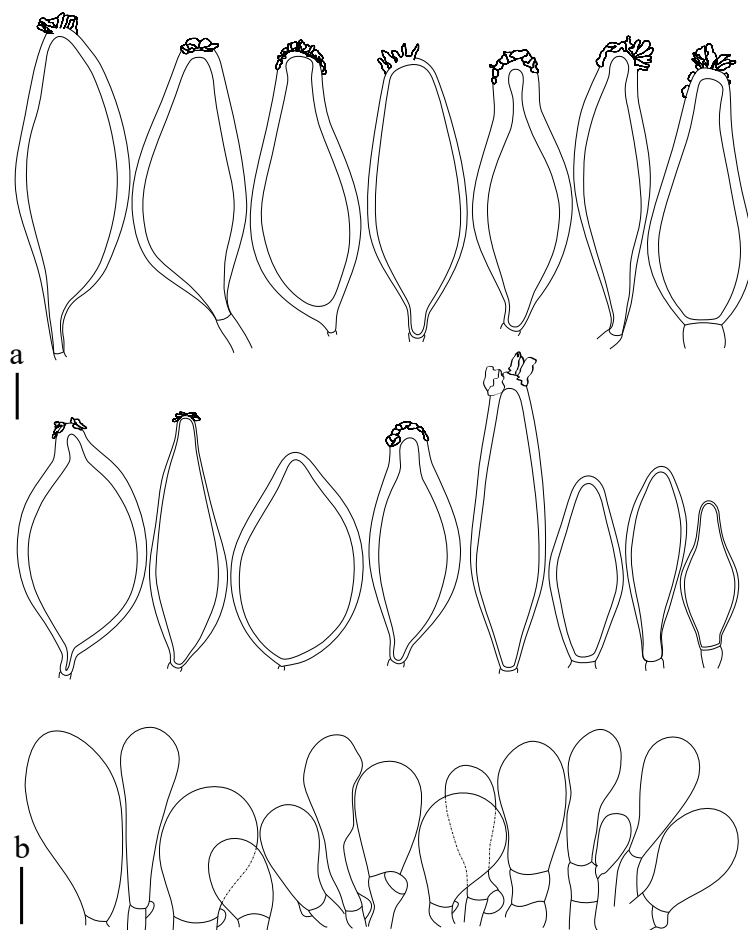
Figure 4. *Inocybe viscida* (*OKA-TR1717*; holotype): a. Cheilocystidia, b. Paracystidia. Scale bars = 10 μm.

geophylla P. Kumm., *I. armeniaca* Huijsman or *I. pudica* Kühner and other species.

Holotype: TURKEY. Muğla Province, Köyceğiz district, around Döğüşbelen town, under *Pinus brutia* and *Liquidambar orientalis*, at 36°59′12.7″N, 28°35′12.8″E, alt. 2 m, 10 March 2018, *O. Kaygusuz*, OKA-TR1717; GenBank: ON074702 for nrITS, ON074741 for nrLSU.

Etymology: *viscida* (Latin), viscid, referring to the adhesive nature of the pileus surface when fresh.

Description: *Pileus* 15–30 mm diam, conical to obtusely conical when young, then campanulate to broadly conical, finally plano-convex to applanate with an obtuse umbo, or even prominently umbonate, with incurved or deflexed margin, and then gradually straight when mature, often depressed around the center, surface shiny, sericeous-smooth, subtly innately radially fibrillose, often viscid, pale straw, straw yellow or light yellow, somewhat darker at the center, and there often with more or less distinct orange to reddish tinge, usually paler towards margin. *Lamellae* crowded, 3.5 mm broad, adnexed, ventricose, pale grey to

light beige, edge concolorous and even. *Stipe* 25–45 × 2.5–3.5 mm, equal, curved or widening slightly downwards, base often subbulbous to bulbous, up to 6 mm wide, solid, whitish, only at the base straw yellow, pruinose only near the apex. *Context* light yellow or whitish in pileus and stipe. *Smell* weakly spermatic or indistinct. *Taste* indistinct.

Basidiospores (7.1–)7.7–9.7(–11.0) × (4.2–)4.8–5.6(–6.3) μm (n = 130 of 3 coll.), $L_m \times W_m$ = 8.5 × 5.2 μm, Q = (–1.4)1.5–1.8(–2.0), Q_m = 1.6, ellipsoid to oblong or amygdaliform, often guttulate, hyaline, thick-walled. *Basidia* 28–35 × 7–9 μm, clavate, 4- or rarely 2-spored, hyaline and thin-walled. *Pleurocystidia* numerous, (55–)60–70(–75) × (10–)11–14(–17) μm (n = 60 of 3 coll.), $L_m \times W_m$ = 65 × 13 μm, Q = (–4.0)4.5–6.0(–6.8), Q_m = 5.1, narrowly fusiform to fusiform or narrowly lageniform to lageniform, often with rather long neck, often with widened apex, base tapered or with short pedicel, apex covered with abundant crystals or without crystals, walls up to 2.5 μm thick, colorless. *Cheilocystidia* abundant, (33–)36–68(–81) × (11–)15–23(–27) μm (n = 60 of 3 coll.), $L_m \times W_m$ = 54 ×
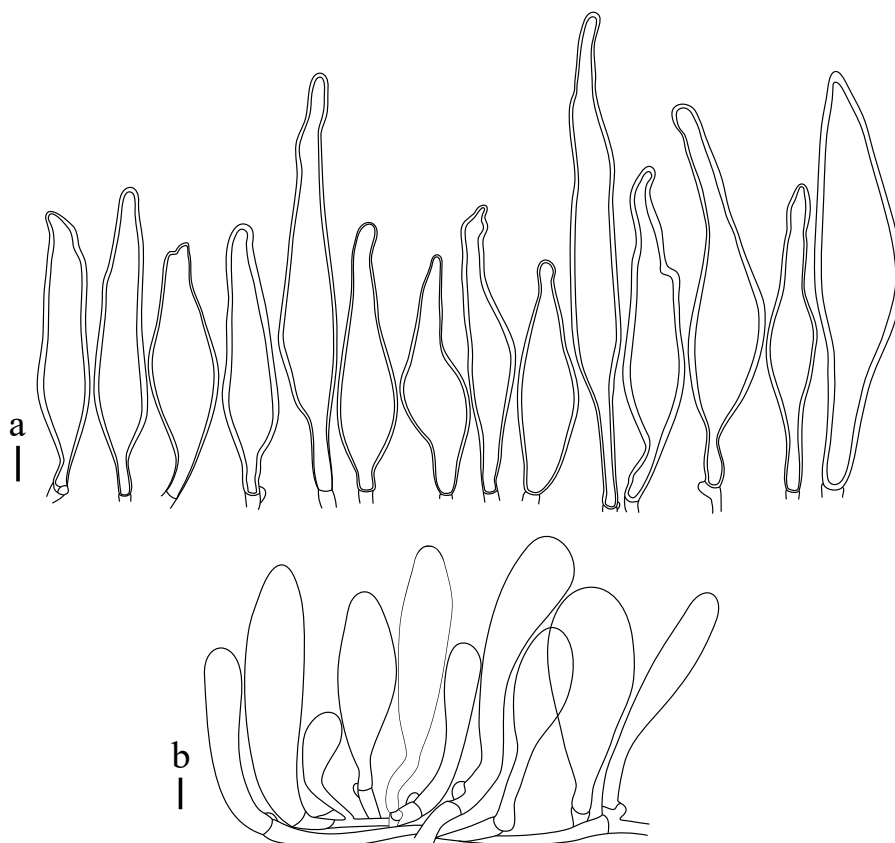
Figure 5. *Inocybe viscida* (*OKA-TR1717*; holotype): a. Caulocystidia, b. Cauloparacystidia. Scale bars = 10 μm.

19 μm, Q = (-1.6)2.1-3.8(-6.0), Q_m = 2.9, variable in shape, ventricose subutriform, subfusiform to sublageniform or subglobose, often with widened apex and short pedicel, usually crystalliferous at apex, walls up to 3.5 μm thick, hyaline. *Paracystidia* moderately frequent, (11-)16-30(-38) × (6-)8-13(-14) μm (n = 30 of 3 coll.), $L_m \times W_m$ = 22 × 10 μm, Q_m = 2.3, clavate to broadly clavate, hyaline, thin-walled. *Pileipellis* a cutis made up of radially arranged, cylindrical hyphae, 6.0–10.0 μm wide, thin-walled, smooth or slightly incrusted, hyaline. *Caulocystidia* in the upper part of stipe, (64-)72-125(-151) × (13-)15-23(-27) μm (n = 30 of 3 coll.), $L_m \times W_m$ = 100 × 18 μm, Q_m = 5.7, subfusiform to lageniform with tapering neck and obtuse to acuminate apex, thick-walled, hyaline. *Cauloparacystidia* numerous, occurring in clusters, (32-)45-75(-90) × (9-)11-16(-19) μm (n = 30 of 3 coll.), $L_m \times W_m$ = 60 × 14 μm, Q_m = 4.4, clavate to cylindric-clavate to cylindrical, thin-walled, hyaline. *Clamp connections* present in all tissue.

Ecology, phenology and distribution: Gregarious or in small scattered groups, in springtime and winter, wet ground, in a forest with an understorey of *Ruscus* sp. and old trees of *Pinus brutia* and *Liquidambar orientalis*, which are distributed along the coastal zones of southwestern Turkey, on sandy soil with a pH of 8.2 to 8.6 and calcium carbonate (6.20%). Basidiomata so far only known from Turkey.

Additional materials examined: TURKEY. Muğla Province, Köyceğiz district, around Döğüşbelen town, under *Pinus brutia* and *Liquidambar orientalis*, at 36°59′13.1″N, 28°35′11.1″E, alt. 5 m, 5 March 2020, O. Kaygusuz, OKA-TR1718 (GenBank: ON074703 for nrITS, ON074742 for nrLSU); *ibid.*, under *P. brutia* and *L orientalis*, at 36°59′12.7″N, 28°35′8.5″E, alt. 4 m, 19 January 2022, *O. Kaygusuz*, OKA-TR0230; *ibid.*, under *P. brutia* and *L orientalis*, at 36°59′12.0″N, 28°35′7.5″E, alt. 5 m, 20 January 2022, *O. Kaygusuz*, OKA-TR0231.

4. Discussion

Our multigene analyses confirmed that *I. viscida* is a member of the *Inocybe* "*geophylla*-group", which can also be recognized as *I.* subsect. *geophyllinae* Bon. In the phylogenetic tree, *I. viscida* is located as a sister to a yet undescribed species *I.* aff. *geophylla* (REH7879/ NY:01034368) from Costa Rica, and both species are grouped in the same clade with high support of MLB (97%) and BPP (0.98) (Figure 1).

No described genetically closely related species of the *geophylla*-group are known. With less than 90% similarity in the nrITS only very distantly genetically related to *Inocybe viscida* are e.g., *I. armeniaca*, *I. bellidiana* Bandini, B. Oertel & U. Eberh., *I. fuscodisca* (Peck) Massee, *I. geophylla*, *I. ionolepis* Cullington & E. Larss., *I. miranda* Carteret & Reumaux, *I. posterula*, *I. pudica*, *I. sambucella* G.F. Atk. and *I. whitei* (Berk. & Broome) Sacc. *Inocybe armeniaca* differs from *I. viscida*, e.g., by pileus fibres that with age or when bruised or on drying get more or less orange to orange reddish, on average slightly smaller basidiospores, much shorter hymenial cystidia, and growth often on sandy soil with conifers (Huijsman, 1974; Kuyper, 1986 as *I. whitei* f. *armeniaca* (Huijsman) Kuyper). *Inocybe bellidiana*,

recently described from Germany (Bandini et al., 2021a), can be separated from *I. viscida* by its typically small whitish or dingy beige pileus with yellowish center, less glabrous and not viscid pileus surface, basidiospores with characteristically bulgy dorsal side, shorter caulocystidia and growth very often with *Fagus sylvatica* L. in more loamy soil (Bandini et al., 2021a). *Inocybe fuscodisca* described from United States can be distinguished from *I. viscida* by the whitish pileus with the disc remaining blackish-brown, and spermatic smell (Peck, 1875; Massee, 1904). *Inocybe geophylla*, differs from *I. viscida*, e.g., by the whitish to pale yellowish pileus without orange to reddish tinge, sticky but not viscid pileus surface, on average smaller basidiospores, on average smaller and narrower

Figure 6. Views from the mixed forest in Köyçeğiz (Muğla Province, Turkey), the type locality of *Inocybe viscida* sp. nov.

pleurocystidia, and mostly (sub)utriform much shorter caulocystidia (Bandini et al., 2021b). *Inocybe ionolepis*, recently described from Great Britain, differs from the new species mainly by the dark purple and brown pileus with a brown umbo, pale yellowish stipe at the base and much shorter caulocystidia (Crous et al., 2020, and pers. observation of D. Bandini). The other abovementioned genetically related species, *I. miranda*, described from France, shows no orange-reddish tinges in the pileus color, the pileus surface is not viscid, the basidiospores are on av. narrower and the hymenial cystidia and the caulocystidia are shorter (Carteret and Reumaux, 2013; Bandini et al., 2021a). *Inocybe posterula* often has a (sub)campanulate shaped pileus, which is not viscid and without orange-reddish tinges, shorter hymenial, lageniform cystidia and much shorter caulocystidia (Britzelmayr, 1882; Saccardo, 1887; Kuyper, 1986, and pers. observation of D. Bandini). *Inocybe pudica* can be distinguished from *I. viscida* by often strongly reddening pilei or stipes with age or when bruised and especially on drying, on av. shorter hymenial cystidia and shorter caulocystidia (Kühner, 1947, and pers. observation of D. Bandini). *Inocybe sambucella* differs by missing orange-reddish tinges in the pileus, not viscid pileus surface, shorter hymenial cystidia and much shorter caulocystidia (Atkinson, 1918; Bandini et al., 2021a). *Inocybe whitei* differs in the reddening pilei and/or stipes when bruised or old, dry pileus surface and on average shorter hymenial cystidia and shorter caulocystidia (Berkeley and Broome, 1876; Saccardo, 1887; Kuyper, 1986 as *I. whitei* f. *whitei* (Berk. & Broome) Sacc., and pers. observation of D. Bandini).

The presented new species was found in the mixed forest dominated by *Liquidambar orientalis* (Figure 6), but we concluded that it forms an ectomycorrhizal association with *Pinus brutia*. When considering the soil moisture conditions, generally sweet gum forests in warm Mediterranean climate are characterized by the hydromorphic alluvial areas with ground water (Ketenoğlu and Kurt, 2008). Therefore, this habitat which is mostly preferred by fungi was characteristic for the new *Inocybe* species.

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