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Two new species of *Inocybe* (Inocybaceae: Agaricomycetes) from Türkiye based on morphological characteristics and phylogenetic evidence

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Abstract: During a survey of agarics in the Mediterranean region of southwestern Türkiye, some noteworthy mushrooms were collected. Among the specimens, we discovered two new species of *Inocybe*, which are proposed and illustrated in this study as *Inocybe pseudogeophylla* and *I. succinea*. Molecular phylogenetic analyses based on a nuc rDNA ITS1-5.8S-ITS2 (ITS) and partial 28S rDNA (LSU) dataset reveal that these species belong to the *Inocybe geophylla* group. The sequences of the new species form two independent lineages and differ from the known species of *Inocybe* by a unique combination of morphological characteristics. Detailed macro- and micromorphological features, colour photographs, habitat, and distribution data for the two novel species are provided, and their relationships with closely related species are discussed.

Key words: Basidiomycota, Agaricales, nrITS DNA, nrLSU DNA, taxonomy, molecular systematics

1.Introduction

The family Inocybaceae Jülich is one of the largest groups within Agaricales (Basidiomycota), and was recently estimated to comprise 1050 species (Matheny and Kudzma, 2019; Matheny et al., 2020). They mostly form ectomycorrhizal associations with diverse species of angiosperms and gymnosperms in tropical to temperate regions (Matheny and Kudzma, 2019; Matheny et al., 2020). The family initially included three genera, namely *Auritella* Matheny & Bougher, *Inocybe* (Fr.) Fr., and *Tubariomyces* Esteve-Rav. & Matheny (Latha et al., 2016). Based on extensive taxonomic and phylogenetic analyses of a multigene dataset (5.8S, 18S, 28S, rpb1, rpb2, and *tef1*), a global understanding of the phylogenetic relationships within the family has been provided (Matheny et al., 2020). Consequently, the family is now recognized to consist of seven genera, namely *Auritella*, *Inocybe*, *Inosperma* (Kühner) Matheny & Esteve-Rav., *Mallocybe* (Kuyper) Matheny, Vizzini & Esteve-Rav., *Nothocybe* Matheny & K.P.D. Latha, *Pseudosperma* Matheny & Esteve-Rav., and *Tubariomyces* (Matheny et al., 2020).

Inocybe contains more than 850 species described worldwide (Matheny et al., 2020; Bandini et al., 2022), and members of the genus have been prevalently recorded in terrestrial biomes on all continents except Antarctica (Larsson et al., 2014; Matheny et al., 2020; Bandini et al., 2021). Members of the genus are characterized by small, often brown basidiomata with a smooth, rimose, fibrillose, squamulose to squarrose pileus surface, lamellae that become brownish with age, a distinctive odour, smooth or nodulose basidiospores, usually thick-walled pleurocystidia, and the presence of cheilocystidia (Kuyper, 1986; Matheny and Swenie, 2018; Matheny and Kudzma, 2019; Matheny et al., 2020; Bandini et al., 2020, 2021).

Over a decade of surveys focusing on inocyboid agarics in Türkiye led to the identification of three new *Inocybe* species (Bandini et al., 2020; Kaygusuz et al., 2022a, 2022b), and some new records (Altuntaş et al., 2019; Sesli et al., 2020; Doğan et al., 2021; Oruç et al., 2021; Çevik et al., 2021; Sesli, 2022; Solak and Türkoğlu, 2022). In the continuation of these explorations, two *Inocybe* species were repeatedly collected in southwestern Türkiye and the detailed examination of the specimens showed that these species could not be assigned to any recognized species within the *Inocybe geophylla* group. This group, which can also be recognized as *Inocybe*

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subsect. *Geophyllinae* Bon., is known to exhibit a high level of phylogenetic diversity (Ryberg et al., 2008; Matheny and Swenie, 2018). Two new species of *Inocybe* are presented here based on detailed morphological and multigene phylogenetic analyses of the nrITS and nrLSU DNA data.

2. Materials and methods

2.1. Morphological observations

For this investigation, thirteen fungal specimens, mostly collected in 2018–2023 from cedar forests in southwestern Türkiye, were studied. Fresh specimens were used to record macroscopical characteristics. Basidiomata coloration was determined with the Munsell Soil Color Charts (Munsell 1975). All microscopic features were studied from dried specimens and mounted with 3% potassium hydroxide (KOH) and stained with 1% Congo red. For basidiospore size, at least thirty basidiospores of each basidioma were measured in profile view. The mean lengths and widths of the basidiospores are expressed as $L^m \times W^m$, the ratio of length to width as Q, and the mean of the Q values for individual basidiospores as Q^m. All descriptions were based on Vellinga (1988) and Bas (1969). Holotypes are deposited at the fungarium at Isparta University of Applied Sciences (ISUF) in Türkiye.

2.2. DNA extraction, PCR, and sequencing

The genomic DNA from *Inocybe* specimens was extracted from dry samples following the protocols of Kaygusuz et al. (2022a). For PCR amplification, the following two barcodes and corresponding primers were used: ITS1F/ITS4 (White et al., 1990; Gardes and Bruns, 1993) for the Internal Transcribed Spacer (ITS) region, and LR0R/LR5 (Vilgalys and Hester, 1990; Rehner and Samuels, 1994) for a fragment of the nuclear ribosomal Large Subunit (28S) region. The protocols for PCR amplification and sequencing followed Kaygusuz et al. (2020).

2.3. Sequence alignments

The raw DNA sequence data were processed with Chromas Lite 2.1.1[1] and assembled with BioEdit 7.2.5 (Hall, 1999). The generated ITS and 28S rDNA sequences in this study were subjected to BLASTn searches, and all the other reference sequences for conducting the phylogenetic analyses were downloaded from GenBank[2] and UNITE[3] database (Nilsson et al., 2019). Nucleotide sequence alignments were done using MAFFT 7.110 web tool[4] (Katoh et al., 2019) for each region separately and manually adjusted via BioEdit 7.2.5.

2.4. Phylogenetic analyses

Phylogenetic trees of *Inocybe* spp. were constructed from concatenated ITS+28S rDNA data sets with maximum likelihood (ML) as implemented in RAxML 8.2.10 (Stamatakis, 2014) on the Cipres Science Gateway 3.3 interface[5] (Miller et al., 2010), and Bayesian Inference (BI) as implemented in MrBayes 3.2.2 (Ronquist et al., 2012). The best-fit substitution model for nucleotides was estimated using the MrModelTest 2.3 (Nylander, 2004) and selected the GTR+I+G model for ITS and 28S rDNA. In the resulting phylogenetic tree, only ML bootstrap (MLB) values of 75% or higher and Bayesian posterior probabilities (BPP) values of 0.90 or higher were indicated (Figure 1). Mean values of branch lengths are calculated from the trees sampled. The trees generated from both ML and BI methods were visualized in FigTree v1.4.3[6].

3. Results

3.1. Phylogenetic analyses

The analyses of 100 sequences (51 for nrITS and 49 for nrLSU) of *Inocybe* spp. using both ML and BI methods resulted in topologies that were nearly identical. Therefore, only the ML trees, including MLB and BPP values, are shown (Figure 1). The dataset for this study consisted of a combined ITS/28S rDNA sequence from various *Inocybe* taxa, with *Nothocybe distincta* (K.P.D. Latha & Manim.) Matheny & K.P.D. Latha (CAL 1310) as an outgroup taxon, comprised 55 taxa with a total of 2268 nucleotides (848 for nrITS and 1420 for nrLSU), of which 1759 characters were constant, 355 parsimony-informative, and 154 parsimony-uninformative. The optimal tree, as determined by RAxML analysis, achieved a final ML optimization likelihood value of –993.673286. There were 760 unique patterns in the combined alignment, with 27.18% of gaps and characters that were completely undetermined. The following were the estimated base frequencies; A = 0.267816, C = 0.197988, G = 0.258594, T = 0.275603. Substitution rates were as follows: AC = 1.721541, AG = 3.663875, AT = 3.748515, CG = 0.437251, CT = 6.407080, and GT = 1.000000.

The tree inferred from the two-locus dataset reveals that sequences of the two new species, *Inocybe pseudogeophylla* and *I. succinea*, each form a monophyletic lineage within the genus *Inocybe* (Figure 1). Both ML and Bayesian phylogenetic analyses confirm that *I. pseudogeophylla* and *I.*

[1]http://technelysium.com.au/wp/chromas/

[2]https://www.ncbi.nlm.nih.gov/genbank/

[3]https://unite.ut.ee/

[4]http://mafft.cbrc.jp/alignment/server/

[5]http://www.phylo.org/portal2/

[6]Rambaut A (2016). FigTree v1.4.3: Tree figure drawing tool. Website http://tree.bio.ed.ac.uk/software/figtree/ [accessed 1 October 2023].

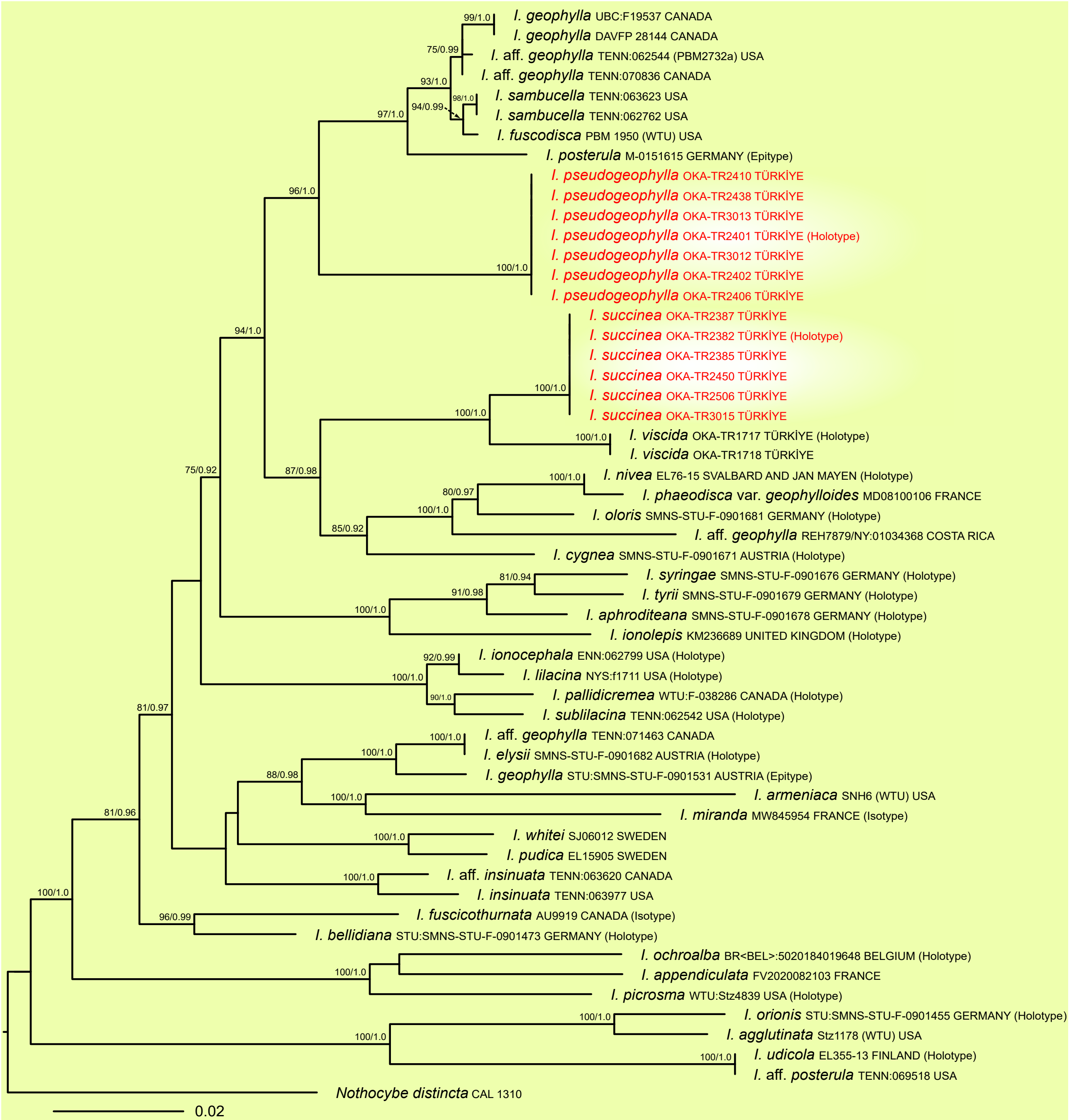

Figure 1. Phylogenetic reconstruction of the *Inocybe geophylla* group based on maximum likelihood (ML) analyses of the alignment of the nrITS and nrLSU DNA regions. MLB ≥ 75% and BPP ≥ 0.90 values are given on the branches, respectively. The tree is rooted with *Nothocybe distincta* (CAL 1310). Newly generated sequences are shown in bold red. The scale bar indicates the estimated nucleotide substitutions per site.

succinea have sequences clearly distinct from corresponding available sequences of other *Inocybe* species.

The new species *Inocybe pseudogeophylla* clustered together with *I. fuscodisca* (Peck) Massee, *I. geophylla* P. Kumm., *I. posterula* (Britzelm.) Sacc., *I. sambucella* G.F. Atk., and two undescribed taxa (*I.* aff. *geophylla* TENN:062544 and *I.* aff. *geophylla* TENN:070836), with high statistical support (MLB = 96%, BPP = 1.0, Figure 1). *Inocybe pseudogeophylla* is shown to be sister to the species in this clade. The other new species, *Inocybe succinea*, is found on a separate lineage within a statistically supported clade (MLB = 87%, BPP = 0.98, Figure 1) consisting of *I. cygnea* Bandini, B. Oertel & U. Eberh., *I. nivea* E. Larss., *I. oloris* Bandini & B. Oertel, *I. viscida* Kaygusuz, Knudsen & Bandini, *I. phaeodisca* var. *geophylloides* Kühner and *I.* aff. *geophylla*. *Inocybe succinea* is closely related to *I. viscida*, with high statistical supports (MLB = 100%, BPP = 1.0, Figure 1). The pairwise identity value among the nrITS sequences of these two species is 92.7%.

3.2. Taxonomy

Inocybe pseudogeophylla Kaygusuz, Bandini, Knudsen & M. Piepenbr., sp. nov.
(Figures 2 and 3)

MycoBank: MB851348

Diagnosis: Similar to *I. geophylla* but differs from it by longer basidiospores (9.3 × 5.5 µm on average) usually with subacute apex, longer hymenial cystidia (66 × 15 µm on average), longer caulocystidia with walls up to 3 µm thick, and by distinct nrITS and nrLSU DNA sequences.

Holotype: TÜRKİYE. Isparta Province, Şarkikaraağaç District, in Kızıldağ National Park, under *Cedrus libani* A.Rich., at 38°02′24.5″N, 31°21′55.8″E, 1790 m a.s.l., 10 May 2018, OKA-TR2401, *O. Kaygusuz*, GenBank nrITS OR898275, GenBank nrLSU OR898262.

Etymology: Named for its morphological resemblance to *I. geophylla.*

Description: *Pileus* 10–40 mm in diameter, (sub)conical to subcampanulate when young, then conico-convex to expanded, with or without rather low broad umbo, margin sometimes involute, but later straight or even uplifted, pileus depressed around the umbo; young basidiomata with faint and fugacious remnants of a whitish velipellis; colour mostly dingy whitish (2.5Y 8/2–4), beige or (dingy) ivory (2.5Y 8/6, 5Y 8/2–6), sometimes pale straw-coloured (5Y 8/8–10); surface first silky smooth, with age sometimes minutely innately fibrillose, sometimes areolate diffracted at the centre; surface somewhat sticky and therefore sometimes sullied by soil particles; young basidiomata with remnants of a cortina. *Lamellae* moderately crowded to crowded, adnate to emarginate adnate, (sub)ventricose, at first whitish or dingy whitish, then greyish tinge to ochraceous brownish with age; edge fimbriate, whitish. *Stipe* 25–40 × 2–5 mm, straight or curved, sometimes widening somewhat towards the base, base sometimes

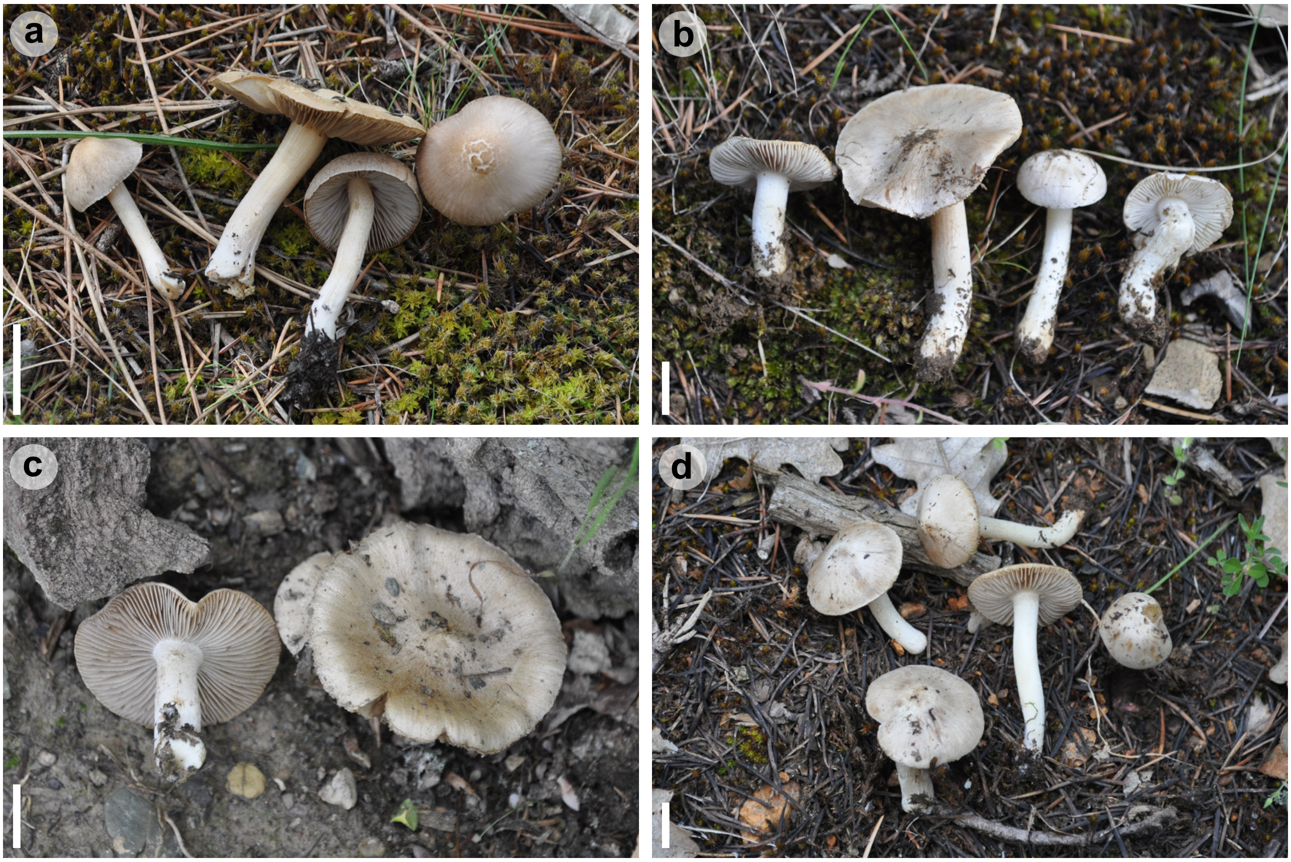

Figure 2. Fresh basidiomata of *Inocybe pseudogeophylla* in its natural habitat in Kızıldağ National Park. a. Collection OKA-TR2401 (holotype), b. Collection OKA-TR2402, c. Collection OKA-TR2410, d. Collection OKA-TR2438. Bars: 10 mm.

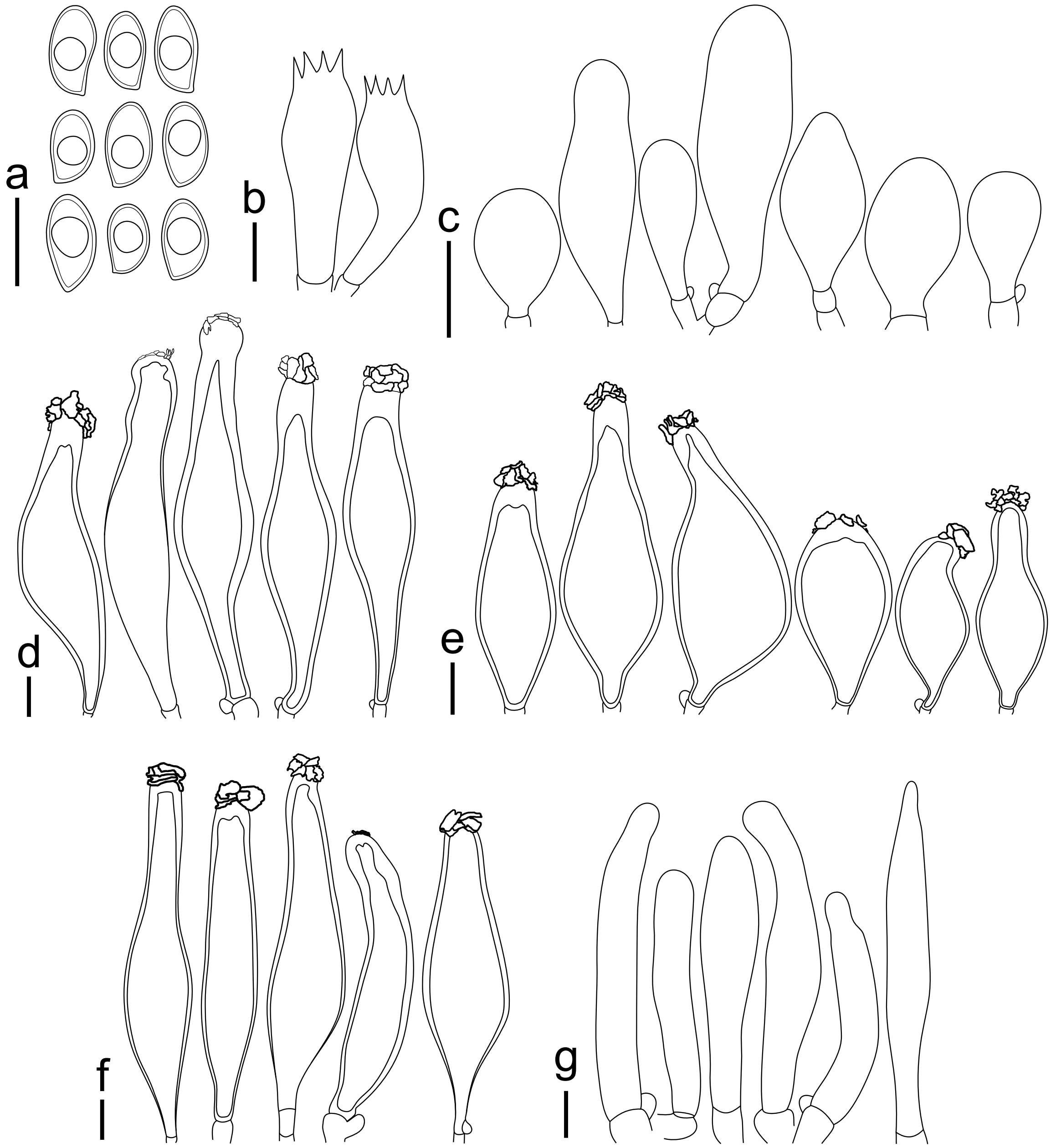

Figure 3. Microscopic features of *Inocybe pseudogeophylla* as seen by light microscopy (OKA-TR2401, holotype). a. Basidiospores, b. Basidia, c. Paracystidia, d. Pleurocystidia, e. Cheilocystidia, f. Caulocystidia, g. Cauloparacystidia. Bars: 10 µm.

bulbous, covered with whitish tomentum, at first whitish, then pale greyish-brownish; pruinose only near the apex. *Context* whitish to straw-coloured in stipe and pileus. *Smell* faintly spermatic. *Colour of exsiccata* pileus dingy ivory-coloured, lamellae and stipe a little lighter or concolorous, no darkening when dried.

Basidiospores 7.5–12 µm (av. 9.3 µm, SD 0.6 µm) × 4.3–6.5 µm (av. 5.5 µm, SD 0.5 µm); Q = 1.4–2.3 (av. 1.6, SD 0.1) (n = 210 of 5 coll.), subellipsoid to (sub)amygdaloid, usually with or without or faint suprahilar depression, apex mostly subacute, rarely subobtuse, smooth, yellowish-brown, thick-walled. *Basidia* 25–36 × 8–12 µm, clavate, generally 4-spored, rarely 2-spored. *Pleurocystidia* 50–100 µm (av. 66 µm, SD 5.2 µm) × 11–22 µm (av. 13 µm, SD 1.0 µm); Q = 3.7–5.5 (av. 4.3, SD 0.5) (n = 65 of 3 coll.), mostly (sub)fusiform, also (sub)utriform, rarely (sub)lageniform, usually with or without rather short neck, with short or longer pedicel, sometimes with truncate base, apex crystalliferous or not, walls often up to 3.5–4 µm thick at the apex, pale yellowish-greenish in 3% KOH. *Cheilocystidia* 40‑60 × 11‑26 µm (n = 65 of 3 coll.), (sub)clavate, (sub) utriform to subovoid, usually abundant with crystals at apex, intermixed with numerous colourless, walls up to 4.0 µm thick. *Paracystidia* frequent, 13.0‑30 × 5.5‑16.0 µm (n = 50 of 3 coll.), narrowly utriform to clavate to broadly clavate, hyaline, thin-walled. *Pileipellis* a cutis consisting of parallel cylindrical hyphae, 5–13 µm wide, smooth, hyaline, thin-walled. *Caulocystidia* only near the apex of the stipe, 60–90 × 10–20 µm, mostly (sub)fusiform to (sub) utriform, also subcylindrical or sublageniform, without or with only short and sometimes wide and rounded apex, with short or longer pedicel, without or with crystals, walls up to 2–3 µm thick at the apex, pale yellowish-greenish in 3% KOH. *Cauloparacystidia* numerous, occurring in clusters, 40‑85 × 6‑13 µm, often oblong, (sub)cylindrical, (sub)utriform to (sub)clavate, sometimes with subcapitate apex, hyaline, thin-walled. *Clamps* present in all septa.

Habitat and distribution: Basidiomata gregarious or in small groups, from early May to mid-June, mostly present at 1790 m a.s.l., under *Cedrus libani* A. Rich, on rocky, calcareous ground. Currently known from Türkiye.

Additional specimens examined: All associated with *Cedrus libani*: TÜRKİYE. Isparta Province, Şarkikaraağaç District, in Kızıldağ National Park, at 38°02′25.4″N, 31°21′58.1″E, 1779 m a.s.l., 07 May 2020, OKA-TR2402, *O. Kaygusuz*, GenBank nrITS OR898276, GenBank nrLSU OR898263; ibid., at 38°02′25.6″N, 31°22′04.0″E, 1786 m a.s.l., 20 May 2021, OKA-TR2406, *O. Kaygusuz*, GenBank nrITS OR898277, GenBank nrLSU OR898264; ibid., at 38°02′29.5″N, 31°22′04.4″E, 1791 m a.s.l., 18 May 2022, OKA-TR2410, *O. Kaygusuz*, GenBank nrITS OR898278, GenBank nrLSU OR898265; ibid., at 38°02′23.2″N, 31°22′19.5″E, 1795 m a.s.l., 23 May 2023, OKA-TR2438, *O. Kaygusuz*, GenBank nrITS OR898279, GenBank nrLSU OR898266; ibid., at 38°01′49.4″N, 31°22′06.9″E, 1788 m a.s.l., 02 June 2023, OKA-TR3012, *O. Kaygusuz*, GenBank nrITS OR898280, GenBank nrLSU OR898267; ibid., at 38°01′49.0″N, 31°22′06.1″E, 1784 m a.s.l., 09 June 2023, OKA-TR3013, *O. Kaygusuz*, GenBank nrITS OR898281, GenBank nrLSU OR898268.

Remarks: Phylogenetically, the sequences generated for *Inocybe pseudogeophylla* form a distinct terminal lineage and show a close relationship with sequences available for *I. geophylla*, *I. posterula*, *I. sambucella*, *I. fuscodisca*, and some undescribed taxa (Figure 1). *Inocybe geophylla* differs from *I. pseudogeophylla* by its shorter basidiospores (7.5–9.3 × 4.1–5.5 µm) with an obtuse apex, shorter hymenial cystidia (up to 65 µm long), and its association with a different plant species as a mycorrhizal symbiont (Bandini et al., 2021). The nrITS sequences of the new species show only 85% similarity with the corresponding sequence of the epitype of *I. geophylla* from Germany.

Inocybe posterula differs from *I. pseudogeophylla* by its usually not orange or brownish tinged centre of pileus, on average shorter and oblong basidiospores (8–9 × 4–5 µm) and shorter hymenial cystidia (up to 60 µm long) (Saccardo, 1887; Stangl and Veselský, 1980; Bandini et al., 2021). Compared to *Inocybe pseudogeophylla*, *I. sambucella* has shorter basidiospores (7–10 × 4–6 µm), shorter hymenial cystidia (40–50 × 11–15 µm), and a habitat with more acidic soil, usually in zones with a more moderate climate (Atkinson, 1918; Bandini et al., 2021). *Inocybe fuscodisca* has a pileus with a blackish-brown fibrillose disc against a pallid ground colour, shorter basidiospores (8–10 × 5–5.5 µm), and it smells like chestnut flowers (Peck, 1875; Bandini et al., 2021).

Morphologically, *Inocybe pseudogeophylla* is close to *I. cygnea*, *I. elysii* Bandini & B. Oertel, *I. huijsmanii* Kuyper, *I. jacobssonii* Vauras & E. Larss., *I. nivea*, *I. oloris*, *I. orionis* Bandini, B. Oertel & U. Eberh., and *I. udicola* E. Larss. & Vauras. *Inocybe cygnea* differs from *I. pseudogeophylla* by the presence of a velipellis, shorter basidiospores (on av. 8.8 × 5.2 µm) with obtuse apex, shorter hymenial cystidia (on av. 56 × 16 µm), usually with thinner walls, and growth in zones with a more moderate climate (Bandini et al., 2022). *Inocybe elysii* recently described from Austria, differs by a usually more yellowish pileus colour often with golden or pale ochraceous or pinkish hue, shorter basidiospores (on av. 8.1 × 4.9 µm) with obtuse apex, shorter, mostly rather ventricose (sub)utriform hymenial cystidia (on av. 55 × 15 µm), and growth on acidic soil in subalpine altitudes or in the subboreal zone (Bandini et al., 2022). *Inocybe huijsmanii* differs by usually smaller basidiomata, often less smooth pileus surface, shorter basidiospores (on av. 9.6 × 5.2 µm), shorter hymenial cystidia (on av. 62 × 15 µm), and growth with frondose trees in more moderate climatic zones (Kuyper, 1986; Stangl, 1989; Bandini et al., 2021). *Inocybe jacobssonii* differs by stouter basidiomata, an often bicoloured pileus, an often strongly areolate diffracted pileus centre, shorter basidiospores (on av. 8.4 × 5.4 µm) and shorter hymenial cystidia (on av. 57 × 17 µm) (Crous et al., 2023). *Inocybe nivea* differs by smaller basidiomata (up to 20 mm in diameter), basidiospores usually with (sub)obtuse apex, shorter hymenial cystidia (45–65 × 11–18 µm), and growth in montane to alpine altitudes (Crous et al., 2021). *Inocybe oloris* differs by abundant whitish velipellis, narrower basidiospores (on av. 9.4 × 5.1 µm) usually with obtuse apex, shorter hymenial cystidia (on av. 59 × 17 µm), and growth in (sub)alpine altitudes (Bandini et al., 2022). *Inocybe orionis* differs by often more intensive blurred orange or orange or greyish brownish coloured pileus centre, shorter basidiospores (on av. 8.3 × 4.7 µm), much shorter hymenial cystidia (on av. 45 × 11 µm), and growth with frondose trees (Bandini et al., 2021). *Inocybe udicola* differs by shorter basidiospores (on av. 8.8 × 5.3 µm), usually with (sub)obtuse apex, much shorter hymenial cystidia (40–60 × 12–18 µm), and growth in the midboreal zone (Tan et al., 2022).

In addition, *Inocybe viscida* differs from other morphologically similar species, recently described from Türkiye, by pilei that usually have a distinct orange to reddish tinged centre, shorter basidiospores (on av. 8.5 × 5.2 µm), and longer caulocystidia (on av. 65 × 13 µm) (Kaygusuz et al., 2022a). *Inocybe succinea* differs by longer basidiospores (on av. 10 × 5.7 µm) usually with (sub) obtuse apex, and shorter hymenial cystidia (on av. 54 × 12 µm) that have a sometimes subcapitate apex, sometimes with abruptly thickened walls.

Inocybe succinea Kaygusuz, Bandini, Knudsen & M. Piepenbr., sp. nov. (Figures 4 and 5)

MycoBank: MB851349

Diagnosis: Similar to *I. viscida* but differs from it by a smooth pileus surface, longer basidiospores measuring on average 10 × 5.7 µm, shorter hymenial cystidia (54 × 12 µm on average), shorter caulocystidia (up to 85 µm in length), and by distinct nrITS and nrLSU DNA sequences.

Holotype: TÜRKİYE. Isparta Province, Şarkikaraağaç district, in Kızıldağ National Park, under *Cedrus libani*, at 38°02′24.5″N, 31°21′55.8″E, 1835 m a.s.l., 15 May 2018, OKA-TR2382, *O. Kaygusuz*, GenBank nrITS OR898282, GenBank nrLSU OR898269.

Etymology: The epithet "*succinea*" refers to the orange-tinged pileus.

Description: *Pileus* 20–37 mm in diameter, (sub)conical to subcampanulate when young, then conico-convex, broadly convex to expanded, without or with rather low, large umbo, often involute margin, becoming straight or even uplifted, pileus depressed around the umbo; no remnants of a velipellis observed; mostly straw-coloured or pale yellowish in different intensity (2.5Y 8/8–10, 5Y 8/8–12), when older pale brownish ochraceous (7.5YR 7–6/8–10), often with orange tinge at the centre (5YR 7/8–10); surface silky smooth, even when old; young basidiomata with remnants of a cortina. *Lamellae* moderately crowded to crowded, adnate to emarginate adnate, (sub)ventricose, at first whitish or dingy whitish, then with greyish tinge or a faintly orange hue, brownish when old; edge fimbriate, whitish or concolorous. *Stipe* 40–50 × 3–6.5 mm, straight or curved, sometimes widened to subbulbous at the base,

Figure 4. Fresh basidiomata of *Inocybe succinea* in its natural habitat in Kızıldağ National Park. a. Collection OKA-TR2382 (holotype), b. Collection OKA-TR2385, c. Collection OKA-TR2387, d. Collection OKA-TR2506. Bars: 10 mm.

when young covered with a whitish tomentum, at first whitish, later discolouring to yellow-orange, pruinose in the upper part. *Context* whitish to pale yellowish in stipe and pileus. *Smell* indistinct to faintly spermatic, especially when bruised. *Colour of exsiccata* pileus dingy ivory-coloured, lamellae and stipe concolorous or a little lighter than the pileus, no darkening when dried.

Basidiospores 8.5–12.7 µm (av. 10.0 µm, SD 0.4 µm) × 4.8–6.8 µm (av. 5.7 µm, SD 0.2 µm); Q = 1.4–2.4 (av. 1.7, SD 0.1) (n = 260 of 6 coll.), oblong (sub)amygdaloid to (sub)navicular, with more or less evident suprahilar depression, apex (sub)acute to subpapillate, with indistinct pseudoporus, often guttulate, smooth, yellowish-brown, thick-walled. *Basidia* 27–36 × 8–9.5 µm, clavate, generally 4-spored, rarely also 2-spored, hyaline, thin-walled. *Pleurocystidia* 40–65 µm (av. 54 µm, SD 4.5 µm) × 8.0–15 µm (av. 12 µm, SD 1.1 µm); Q = 3.9–5.7 (av. 4.5, SD 0.2) (n = 65 of 3 coll.), mostly (sub)fusiform, also (sub)utriform or sublageniform, rarely subcylindrical, without or with only short, sometimes subcapitate neck, with short pedicel or with truncate base, apex crystalliferous, walls up to 2.5–3 µm thick at the apex, pale yellowish-greenish in 3% KOH. *Cheilocystidia* similar in size, variable in shape, (sub) utriform, (sub)clavate, to broadly subfusiform, hyaline, thick-walled. *Paracystidia* frequent, 14‒40 × 6.5‒14 µm, narrowly utriform with narrow neck, clavate to ellipsoid, fusiform, hyaline, thin-walled. *Pileipellis* a cutis consisting of parallel cylindrical hyphae, 3–10 µm wide, smooth, hyaline, thin-walled. *Caulocystidia* only in the upper part of the stipe, 45–85 × 8–16 µm, mostly (sub)fusiform, also (sub)utriform, rarely subclavate, without or with only short neck, with short or longer pedicel, or with truncate or rounded base, apex usually crystalliferous, walls up to 2–2.5 µm thick at the apex, pale yellowish-greenish in 3% KOH. *Cauloparacystidia* numerous, occurring in clusters, 30‒60 × 10‒18 µm, (sub)clavate to (sub)ovoid, hyaline, thin-walled. *Clamps* present in all septa.

Habitat and distribution: Basidiomata (sub)gregarious or in small groups on the ground, from early May to early June, mainly collected from mid to late May, at heights of mostly 1800 m, under *Cedrus libani*, on calcareous clay loam soils. Currenly only known from the type locality, an area in the *Cedrus* forest in Kızıldağ National Park in Türkiye.

Additional specimens examined: All associated with *Cedrus libani*: TÜRKİYE. Isparta Province, Şarkikaraağaç District, in Kızıldağ National Park, at 38°02′26.7″N, 31°22′03.3″E, 1810 m a.s.l., 07 May 2020, OKA-TR2385, *O. Kaygusuz*, GenBank nrITS OR898283, GenBank nrLSU OR898270; ibid, at 38°02′24.1″N, 31°22′14.1″E, 1805 m a.s.l., 09 May 2021, OKA-TR2387, *O. Kaygusuz*, GenBank nrITS OR898284, GenBank nrLSU OR898271; ibid, at 38°02′08.8″N, 31°22′19.3″E, 1830 m a.s.l., 16 May 2021, OKA-TR2450, *O. Kaygusuz*, GenBank nrITS OR898285, GenBank nrLSU OR898272; ibid, at 38°02′08.7″N, 31°22′03.4″E, 1825 m a.s.l., 21 May 2022, OKA-TR2506, *O. Kaygusuz*, GenBank nrITS OR898286, GenBank nrLSU OR898273; ibid, at 38°02′18.6″N, 31°21e58.0″E, 1836 m a.s.l., 28 May 2022, OKA-TR3015, *O. Kaygusuz*, GenBank nrITS OR898287, GenBank nrLSU OR898274.

Remarks: The closest relative of *Inocybe succinea* in the molecular phylogenetic tree is *I. viscida* (Kaygusuz et al., 2022a), with strong bootstrap support (MLB = 100%, BPP = 1.0, Fig. 1). However, *I. viscida* is distinctive due to its typically viscid pileus surface, shorter basidiospores measuring on average 8.5 × 5.2 µm, longer hymenial cystidia (on av. 65 × 13 µm), and longer caulocystidia (up to 150 µm in length). The genetic distance between *I. succinea* and *I. viscida* is 4%, indicating 16 base differences out of 400 nucleotides, which suggests that they are distinct species. Another genetically closely related species is *Inocybe pseudogeophylla*, but this species differs from *I. succinea* by shorter basidiospores (on av. 9.3 × 5.5 µm) typically with subacute apex, longer hymenial cystidia (on av. 66 × 15 µm) that usually lack a subcapitate apex and often have abruptly thickened walls at the apex.

Several species within the *Inocybe "geophylla* group", i.e., *I. cygnea*, *I. elysii*, *I. geophylla*, *I. nivea*, *I. oloris*, *I. posterula*, and *I. sambucella*, are genetically and morphologically closely related to *I. succinea*. *Inocybe cygnea*, originally described from Austria (Bandini et al., 2022), differs from *I. succinea* by the presence of a velipellis, notably shorter basidiospores (on av. 8.8 × 5.2 µm), and narrower hymenial cystidia (on av. 56 × 16 µm) typically lacking a subcapitate neck. *Inocybe elysii* differs from *I. succinea* by its often brighter, sometimes golden or pale pinkish hued pileus colour, distinctly shorter basidiospores (on av. 8.1 × 4.9 µm) with a lower Q-value (Q = 1.6), wider (on av. 55 × 15 µm) and mostly rather ventricose (sub)utriform hymenial cystidia, and growth on acidic soil in subalpine altitudes or in the subboreal zone (Bandini et al., 2022). *Inocybe geophylla* is distinct due to its shorter basidiospores (8.3 × 4.8 µm) with a lower Q-value (Q = 1.4–2), broader hymenial cystidia (up to 18 µm in width), usually not with subcapitate apex, and its preference for growth in more moderate climatic zones (Bandini et al., 2021). *Inocybe nivea*, recently described from Norway, has smaller basidiomata with a pileus measuring 5–20 mm in diameter, the presence of a whitish velipellis, usually a lack of an orange tinged pileus centre, wider hymenial cystidia (up to 18 µm in width), and growth in montane to alpine altitudes (Crous et al., 2021). *Inocybe oloris* has a whitish velipellis, shorter basidiospores (on av. 9.4 × 5.1 µm), longer hymenial cystidia (up to 78 µm in length), and grows at (sub)alpine altitudes (Bandini et al., 2022). *Inocybe posterula* has a usually not orange tinged pileus centre, shorter oblong basidiospores (8–9 × 4–5 µm) often with a (sub)acute apex, and shorter hymenial cystidia (Saccardo, 1887; Kühner, 1955; Stangl, 1985; Bandini et al., 2021). *Inocybe sambucella*, originally described from the USA, has larger basidiomata with a pileus measuring 40–50 mm in diameter, a whitish velipellis, distinctly shorter basidiospores (7–10 × 4–6 µm), shorter hymenial cystidia (40–50 × 11–15 µm), and grows on more acidic soil, usually in more moderate climatic zones (Atkinson, 1918; Bandini et al., 2021).

Inocybe orionis and *I. udicola*, which are genetically quite distant, are morphologically somewhat similar to *I. succinea*. *Inocybe orionis* differs by a whitish velipellis, often displaying a more intensively blurred orange, orange or greyish brownish coloured pileus centre, distinctly shorter basidiospores (on av. 8.3 × 4.7 µm), shorter caulocystidia (up to 55 µm), and a preference for growth with frondose trees (Bandini et al., 2021). *Inocybe udicola* differs by shorter basidiospores (on av. 8.8 × 5.3 µm), longer caulocystidia (up to 120 µm), and grows in the mid-boreal zone (Tan et al., 2022).

Inocybe succinea also resembles *I. huijsmanii* and *I. jacobssonii*. However, *Inocybe huijsmanii* differs from *I. succinea* by usually smaller basidiomata (13–20 mm in diameter), a less smooth pileus surface, a stipe that is pinkish lilac near the apex, shorter basidiospores (on av. 9.6 × 5.2 µm), and growth with frondose trees in moderate climatic zones (Kuyper, 1986; Bandini et al., 2021). *Inocybe jacobssonii* differs from *I. succinea* by its stouter basidiomata, an often distinctly bicoloured pileus, an often strongly areolate diffracted pileus centre, distinctly shorter basidiospores (on av. 8.4 × 5.4 µm), longer and wider hymenial cystidia (on av. 57 × 17 µm), and longer caulocystidia (up to 92 µm) (Crous et al., 2023).

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