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Inocybe messapica (Inocybaceae, Agaricales, Basidiomycota), a new species in section *Splendentes*, from Mediterranean oak woods

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Abstract

Inocybe messapica sp. nov., collected in Apulia (Italy) under *Quercus coccifera* and *Quercus ilex*, is presented with description, colour photographs, and line-drawings of the microscopic features. This species is proposed as new based on both morphology and molecular phylogenetic analysis. It is characterized by the stout habit, a dark castaneous brown pileus covered with a whitish velipellis, a non-marginate bulbous stipe base, and smooth amygdaliform spores. A comparison of *I. messapica* with *I. athenana* and similar species is also provided.

Keywords: ectomycorrhizal fungi, new species

Introduction

The genus *Inocybe* (Fr.) Fr. (1843: 346) has a worldwide distribution and includes about 850 species (Matheny *et al.* 2019). Macroscopically, it is characterized by small- to medium-sized, yellow to brown, rarely greyish or whitish basidiomata with a fibrillose or pruinose stipe. The genus is divided into subgenera and sections based on presence/absence of cortina, distribution of caulocystidia along the stipe, and spore morphology. The historical subgenera devoid of metuloid pleurocystidia have been recently elevated to genus rank (Matheny *et al.* 2019) on the base of morphologic and phylogenetic analysis: *Mallochybe* (Kuyper) Matheny, Vizzini & Esteve-Rav. (2019: 12), *Inosperma* (Kühner) Matheny & Esteve-Rav. (2019: 12), and *Pseudosperma* Matheny & Esteve-Rav. (2019: 11); and the genus *Inocybe sensu stricto* is currently confined only to the taxa with metuloid cystidia. *Tubariomyces* Esteve-Rav. & Matheny (2010: 1390), *Nothocybe* Matheny & K.P.D. Latha (2019: 11) and *Auritella* Matheny & Bougher (2006: 232) complete the overview of the family *Inocybaceae* Jülich. The aim of this paper is to propose a new species of *Inocybe*, from specimens collected in November 2019 during a mycological study of fungal diversity in Salento (Apulia, Italy).

Material and methods

Collecting site

Bosco di Cardigliano (Specchia, LE) is an important and well-preserved nature site on the Serre Salentine plateau, located in the highest area (160 m asl.) of Salento and about 30 km far from Capo d'Otranto, the easternmost point of the Italian territory. The zone, ca. 54 ha, is characterized by a stony and calcareous substrate, a dry and windy microclimate and a Mediterranean flora including the presence of *Quercus ilex*, *Quercus coccifera* and scrubs of *Cistus* spp.

Morphological studies

The collected basidiomata were geolocated in situ with the Android app Field Nature Mapping (Cervini 2019) and photographed using a NIKON D5100 reflex photo camera with a 40 mm Nikkor macro lens. The macrodescription of

the basidiomata was based on fresh specimens and photo observation, using the colour classification of the Munsell Soil Color Charts (1975). The microscopic analysis was performed with a trinocular OPTIKA B500-TPL compound microscope equipped with a camera, both on fresh and dried material using water, 3% ammonia, Congo Red, and 3% KOH for the rehydration of the tissues in the case of dried samples. The acquired images were used for the measurement of micro details with the software Optika Lite 2.1 and Piximètre (Henriot 2020), properly calibrated. The plate of microscopic features has been produced with Photoshop CS2, obtaining it from layers superimposed on the photos of the single details, suitably scaled to the correct dimensions. The nomenclature refers to Mycobank (2020). The holotype is retained in the fungal collection of the National Mycological Herbarium of Associazione Micologica Bresadola (AMB 12794).

DNA extraction, PCR and sequencing

Total DNA was extracted from dry specimens by ALVALB Laboratory employing a modified protocol based on Murray & Thompson (1980). PCR reactions (Mullis & Faloona 1987) included 35 cycles with an annealing temperature of 54 °C. Primers ITS1F and ITS4 (White *et al.* 1990, Gardes & Bruns 1993) were used to amplify the ITS rDNA region, while LR0R and LR5 (Vilgalys & Hester 1990, Cubeta *et al.* 1991) were used for the 28S rDNA region. PCR products were checked in 1% agarose gels, and positive reactions were sequenced with one or both PCR primers. Chromatograms were checked searching for putative reading errors, and these were corrected. The obtained sequences in this study are deposited in the NCBI GenBank under the accession numbers MT386024 (ITS) and MT476738 (LSU).

Phylogenetic analysis

The sequences of *Inocybe* species with the highest score of percent identity with our new taxon were downloaded from GenBank and UNITE by their BLASTn algorithm. Additional sequences of comparable taxa were also chosen and added to the dataset. Finally, the sequences of *Pseudosperma salentinum* Cervini, Bizio & P. Alvarado (2020: 3) and *Pseudosperma melleum* Cervini, Bizio & P. Alvarado (2020: 3) were used as outgroups, obtaining a global dataset of 27 collections (Table 1). The dataset was aligned with Clustal W application using MEGA-X software (Tamura *et al.* 2019) and then manually adjusted. The final alignments included 276/859 variable sites in ITS rDNA and 141/1374 variable sites in LSU rDNA. A maximum likelihood phylogram was then produced using the Gamma distributed with invariant sites (G+I) model of rate heterogeneity and 1000 bootstrap replicates as implemented in the same MEGA-X software (Fig. 1).

Results

Phylogenetic and morphological analyses indicate that none of the compared taxa match the new species. The phylogenetic analysis (Figure 1) places the sequence of *Inocybe messapica* *sp. nov.* in a strongly supported clade, clustered with several sequences from Estonian soil samples and sister to *Inocybe athenana* Bandini, B. Oertel & U. Eberh. (2020: 33) with which it also shares some basic morphological characters.

Taxonomy

Inocybe messapica Cervini, *sp. nov.* (Figs. 1–4)

Mycobank: MB835459

Type:—ITALY. Apulia: Specchia, Cardigliano di Sopra (LE), 160 m asl, 22 November 2019, on soil under *Quercus ilex* and *Quercus coccifera*, M. Cervini and G. Schirinzi (holotype AMB 12794!).

Diagnosis:—*Inocybe messapica* is characterized by the stout habit, the dark castaneous brown pileus, the pruinose stipe with pink shades and the bulbous base. The cortina is absent, but a whitish velipellis is present in young specimens, remaining on the pileus surface, especially at the margin. Smell is weak and spermatic. Spores are smooth, mostly amygdaliform, on average $10.6 \times 5.9 \mu\text{m}$. Metuloidal pleurocystidia, cheilocystidia and caulocystidia are present. Holotypus: Italy, Apulia, Specchia, Cardigliano di Sopra (LE), 160 m asl., 22/11/2019, in open path under *Quercus ilex*

and *Quercus coccifera*, Legit *M. Cervini* and *G. Schirinzi*. Stored in Herbarium AMB 12794. Etymology: the epithet *messapica* (from *Messapi*) refers to the name of the historical inhabitants of the Central Southern Apulia, Italy.

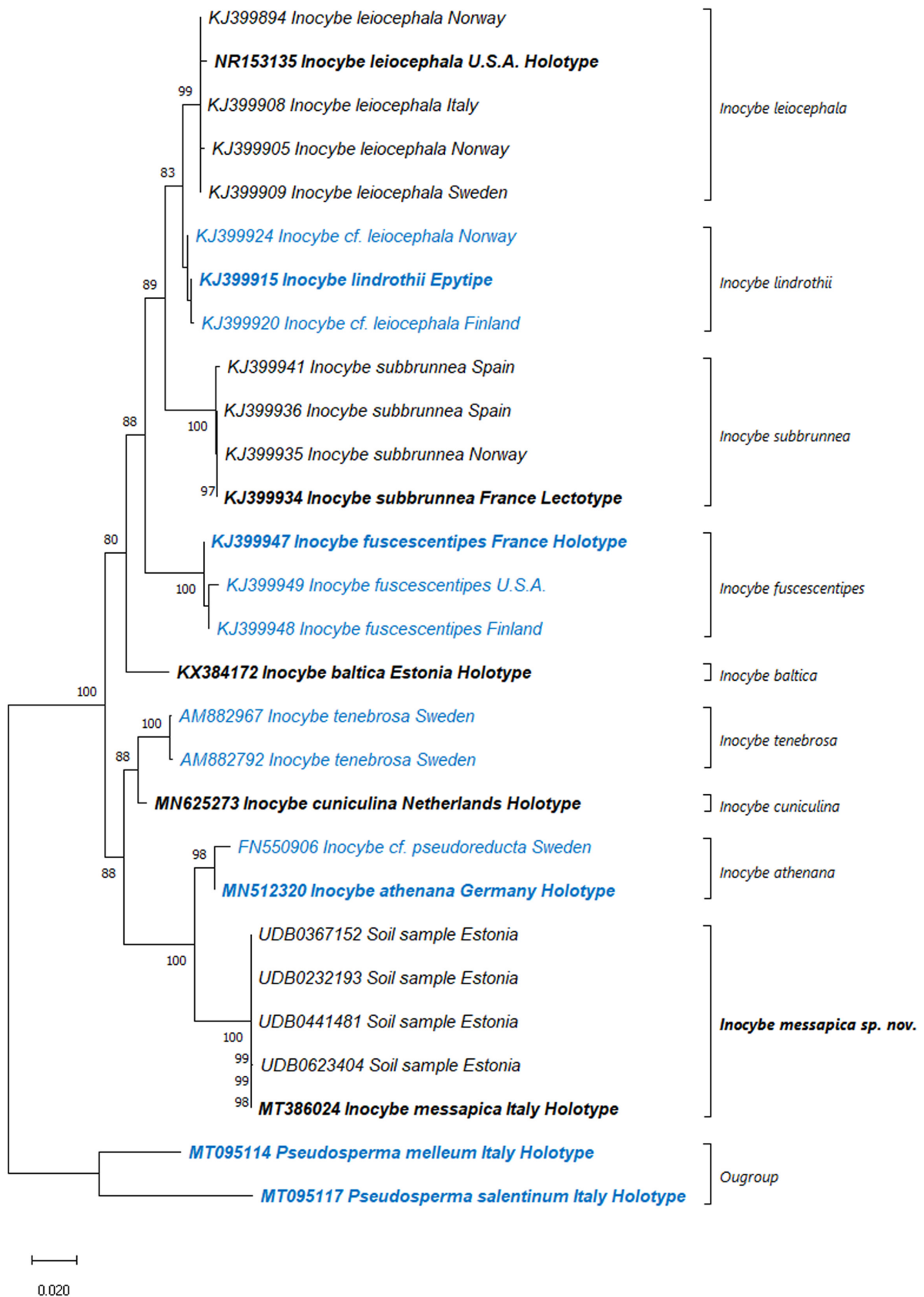


FIGURE 1. Phylogram inferred from maximum likelihood analysis of ITS and LSU sequences of *Inocybe*. Species names are provided by GenBank/Unite accession numbers and country of collection. The type species is in bold. Bootstrap support values of the ML analysis $\geq 80\%$ are displayed near each node.



FIGURE 2. *Inocybe messapica*: basidiomata in habitat (AMB 12794!, holotype). Photo M. Cervini.

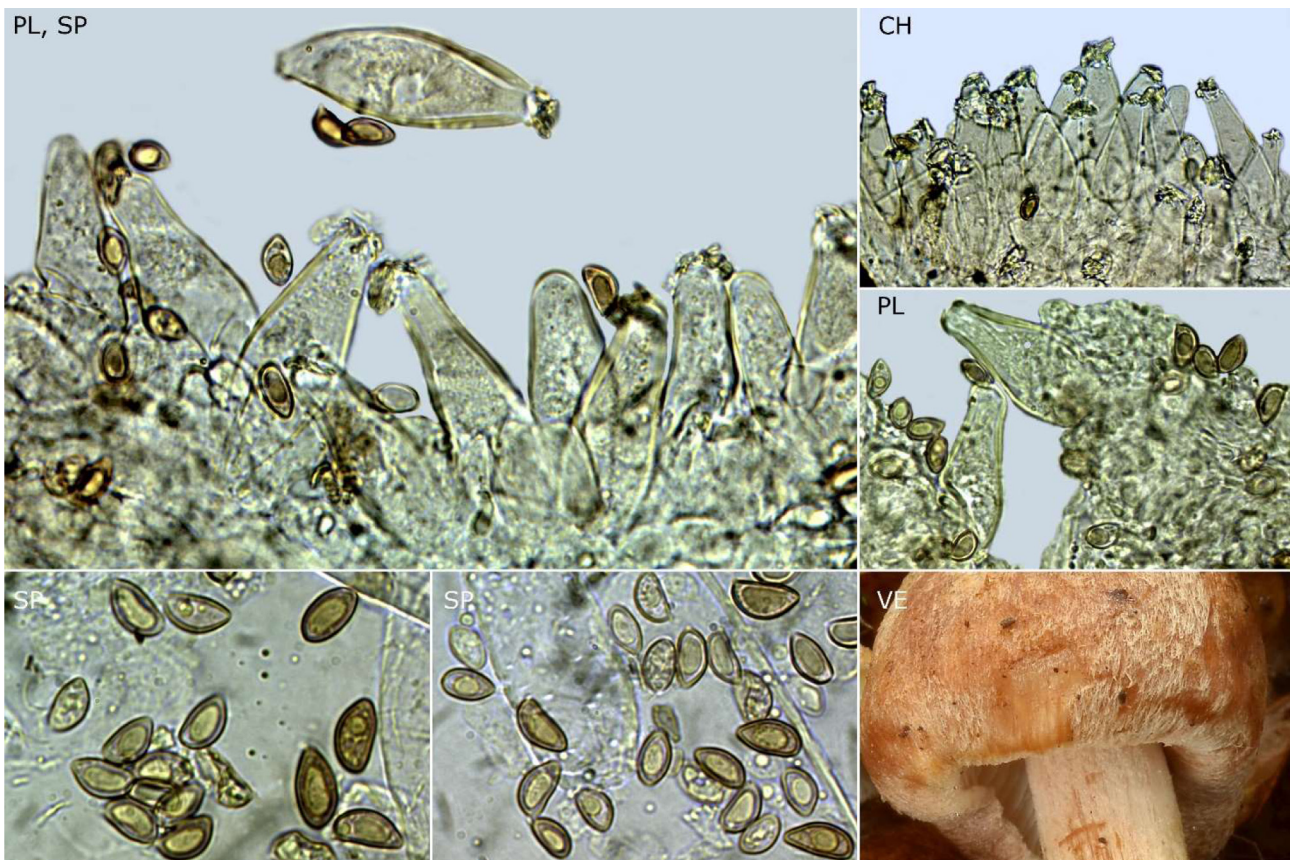


FIGURE 3. *Inocybe messapica*: CH) Cheilocystidia PL); Pleurocystidia; SP) Basidiospores; VE) detail of velipellis (AMB 12794!, holotype). Photos by M. Cervini.

TABLE 1. List of taxa and their GenBank/Unite accession numbers used in the phylogenetic analysis. The new species is in bold.

Taxa	Country	Herbarium - Voucher n°	Accession ITS	Accession LSU	
<i>Inocybe athenana</i>	Germany	STU:SMNS-STU-F-0901238	MN512320	MN512320	Holotype
<i>Inocybe baltica</i>	Estonia	EL34-09	KX384172	KX384172	Holotype
<i>Inocybe</i> cf. <i>leiocephala</i>	Finland	JV4735	KJ399920	KJ399920	
<i>Inocybe</i> cf. <i>leiocephala</i>	Norway	EL182-09	KJ399924	KJ399924	
<i>Inocybe</i> cf. <i>pseudoreducta</i>	Sweden	EL24B07	FN550906	FN550906	
<i>Inocybe cuniculina</i>	Netherlands	KR-M-0043257	MN625273	MN625273	Holotype
<i>Inocybe fuscescentipes</i>	France	K69328	KJ399947	KJ399947	Holotype
<i>Inocybe fuscescentipes</i>	U.S.A.	STZ6459	KJ399949	KJ399949	
<i>Inocybe leiocephala</i>	Norway	EL20-09	KJ399894	KJ399894	
<i>Inocybe leiocephala</i>	Italy	JR&JV17361	KJ399908	KJ399908	
<i>Inocybe leiocephala</i>	Sweden	EL57-13	KJ399909	KJ399909	
<i>Inocybe leiocephala</i>	USA	WTU:Stuntz 4739	NR153135	-	Holotype
<i>Inocybe lindrothii</i>	Finland	JV2390	KJ399915	KJ399915	Epitype
<i>Inocybe messapica</i>	Italy	AMB 12794	MT386024	MT476738	Holotype
<i>Inocybe subbrunnea</i>	France	G388231	KJ399934	-	Lectotype
<i>Inocybe subbrunnea</i>	Norway	EL170-09	KJ399935	KJ399935	
<i>Inocybe subbrunnea</i>	Spain	AH30871	KJ399936	KJ399936	
<i>Inocybe subbrunnea</i>	Spain	EL459-13	KJ399941	KJ399941	
<i>Inocybe tenebrosa</i>	Sweden	EL8204	AM882967	AM882967	
<i>Inocybe tenebrosa</i>	Sweden	RGC97087	AM882792	-	
<i>Pseudosperma melleum</i>	Italy	MCVE 30145	MT095090	MT095114	Outgroup
<i>Pseudosperma salentinum</i>	Italy	MCVE 30342	MT095093	MT095117	Outgroup
Soil sample	Estonia	m54032_171018_142128/34145137/ccs	UDB0623404	-	
Soil sample	Estonia	EST1447603	UDB0367152	-	
Soil sample	Estonia	EST16_40636	UDB0232193	-	
Soil sample	Estonia	EST18_256818	UDB0441481	-	

Description:—*Pileus* up to 55 mm, convex to hemispherical, not umbonate, dark castaneous brown (Mu 5YR 4/4–4/8; 7.5YR 3/4–3/6), glabrous to very minutely felty with involute felted margin in young specimens. *Velipellis* present, whitish, abundantly covering the pileus especially at the margin. *Lamellae* adnate-emarginate, close, whitish then ochre-argillaceous with whitish fimbriate margin. *Stipe* stout, central, fistulose, at first covered by the velipellis, beneath pruinose, pinkish (Mu 5YR 7/3–7/4; 7.5YR 3/4–3/6), up to 60 × 15 mm, until 22 mm at the non marginate bulb, slightly darkening at the base. *Flesh* white. *Odor* weak, spermatic.

Basidiospores (8.8)9.8–11.4(12.8) × (4.9)5.5–6.4(7.2) µm, Q = (1.4)1.6–2.0(2.5), on average 10.6 × 5.9 µm (n=106) smooth, asymmetrical, mainly amygdaliform, with subconical apex. *Basidia* 29–39 × 8–14 µm, tetrasporic, clavate. *Pleurocystidia* (36)44–57(65) × (12)16–20(24) µm, on average 51 × 19 µm (n=30) Q = (2.1)2.5–3.3(3.7), abundant, variable, slightly ventricose or subfusiform, rarely elongated, thick-walled up to 3.1 µm especially at the apex, with abundant apical crystals; ammonia reaction positive. *Cheilocystidia* frequent, similar to pleurocystidia. *Paracystidia* 19–26 × 5–11 µm, subcylindric to clavate, abundant. *Caulocystidia* 38–54 × 13–19 µm, on average 46 × 16 µm (n = 15) similar in shape to hymenial cystidia, present all over the stipe surface, more concentrated in the upper half; arranged in tufts and mixed with cauloparacystidia. *Clamp connections* present in all tissues.

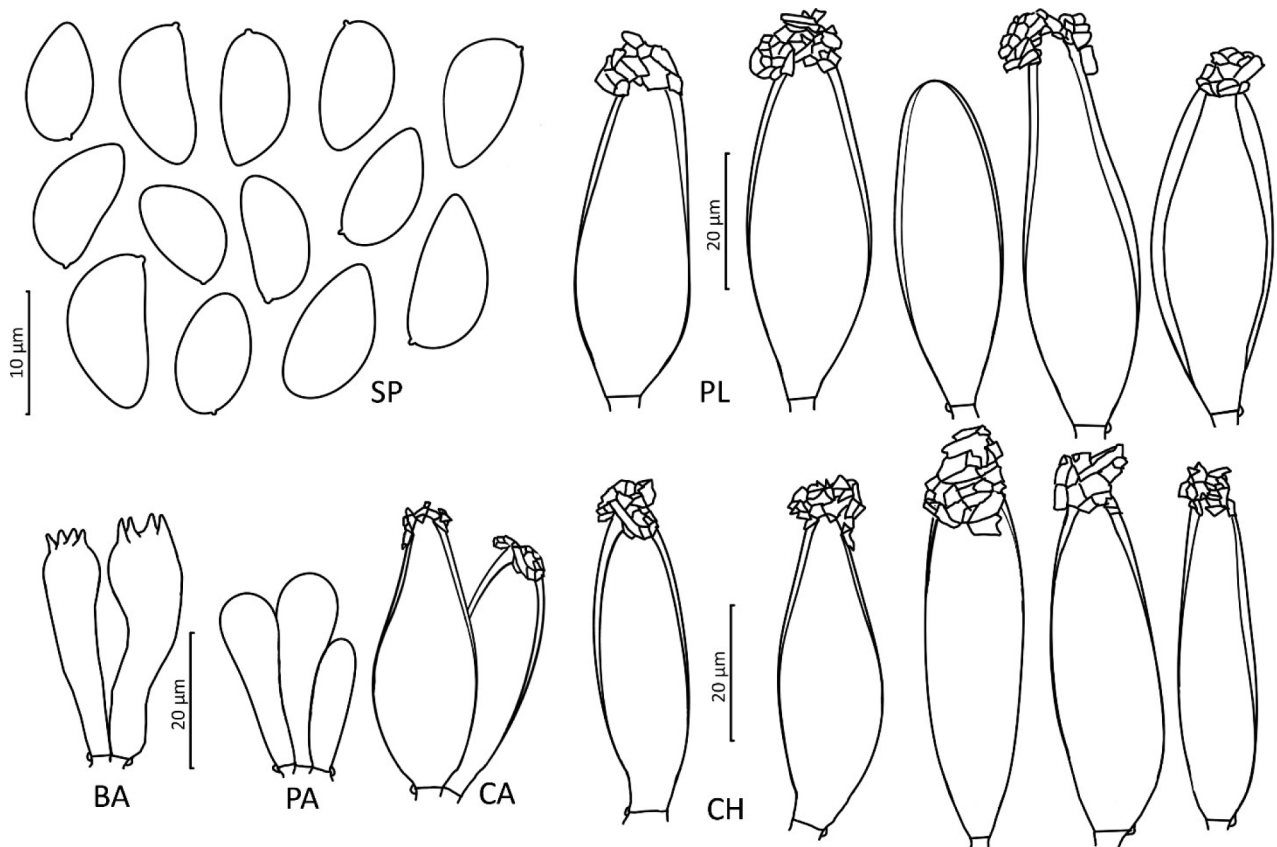


FIGURE 4. *Inocybe messapica*: BA) Basidia; CA) Caulocystidia; CH) Cheilocystidia; PA) Paracystidia; PL) Pleurocystidia; SP) Basidiospores (AMB 12794!, holotype). Drawings by M. Cervini.

Specimen:—AMB 12794! ITALY. Apulia, Specchia, Cardigliano di Sopra (LE), 22 November 2019, 160 m asl., N: 39,944°27,035 E: 18,26722941°66,666. Legit *M. Cervini* and *G. Schirinzi*.

Ecology:—On open path, on calcareous soil under *Quercus ilex* and *Quercus coccifera*. Other occurring species: *Inocybe oblectabilis* (Britzelm.) Sacc., *Lactarius zugazae* G. Moreno, Montoya, Band.-Muñoz & Heykoop, *Russula messapica* Sarnari.

Etymology:—The chosen epithet *messapica* (from *Messapi*) refers to the historical inhabitants of that area, corresponding to the actual Salento. Other tributes having the same specific name are *Russula messapica* Sarnari ex Sarnari (1990: 42) and *Clavaria messapica* Agnello, Kautman. & M. Carbone (2015: 197).

Inocybe athenana Bandini, B. Oertel & U. Eberh. (Fig. 5)
Mycologia Bavarica. 20:13-101 (2020)

Isotype collection DB15-6-19-2:—*Basidiospores* (7.7)8.2–9.6(11.2) × (4.5)5.1–6.0(6.4) µm, Q = (1.3)1.6–2.0(2.1), in average 8.9 × 5.5 µm (n = 100) smooth, asymmetrical, from ellipsoid to subamygdaliform, at most without conical apex. *Basidia* 24–32 × 7–12 µm, tetrasporic, clavate. *Pleurocystidia* (53)58–72(77) × (16)18–28(32) µm, on average 65 × 23 µm (n = 30) Q = (2.1)2.2–3.6(3.7), abundant, fusiform or ventricose-clavate, thin-walled up to 1.7 µm, with apical crystals; ammonia reaction positive. *Cheilocystidia* similar to pleurocystidia. *Paracystidia* 15–28 × 6–17 µm, subcylindrical to clavate, abundant. *Caulocystidia* 48–72 × 12–19 µm, on average 59 × 15 µm (n = 15) slender in respect to the hymenial cystidia, present all over the stipe surface, mixed with some cauloparacystidia. *Clamp connections* present in all tissues.

Specimen:—DB15-6-19-2! (isotype). GERMANY, Baden-Württemberg, Rhein-Neckar-Kreis, Schönbrunn, 15 June 2019, 390 m asl., *Abies alba*, *Fagus sylvatica*, leg. *D. Bandini*.

Discussion

The species belonging to *Inocybe*, supersection *Marginatae* (Kuyper 1986, Stangl 1989), section *Splendentes* R. Heim ex Singer are characterized by smooth spores, pruinose stipe and, in most cases, absence of cortina. According to the systematic arrangement proposed by Bon (1997) this section is divided into subsections *Subbrunneinae* M. Bon (without marginate bulb and with pinkish stipe), *Phaeoleucinae* M. Bon (without marginate bulb and with no pinkish stipe), and *Splendentinae* M. Bon (with marginate bulb). Subsequently Jacobsson (2008) did not give any formal subdivision in his key G about *Splendentes*, and later the studies carried out by Kropp *et al.* (2010) and by Bandini *et al.* (2018) demonstrated that this section is not monophyletic. In our phylogenetic analysis *I. messapica* is placed in a strongly supported clade that is different from the representative species of the *Subbrunneinae s.l.* complex, even though it shows the two above mentioned key-characters.

The distinguishing features of *I. messapica* are the stout habit, the dark castaneous brown pileus covered with a conspicuous whitish velipellis, the pruinose stipe with pink colorations and darkening bulb (Fig. 2), the amygdaliform spores, and the subusiform, rather short and thick-walled cystidia (Figs. 3, 4).

Comparisons with the species in the phylogenetic tree (Fig. 1)

I. athenana Bandini, B. Oertel & U. Eberh. (2020: 33) is the closest species to *I. messapica* with which it shares the pileus and stipe colors and the abundant velipellis. However, *I. athenana* differs in having a different habitat (so far found with *Fagus sylvatica* and *Abies alba*), the less bulbous stipe base, and an areolate to scaly pileus cuticle. Moreover, the microscopic analysis (Fig. 5) done on dried material of an *I. athenana* isotype showed significantly smaller spore size (on average 8.9×5.5 vs. 10.6×5.9 μm) with a more rounded apex, and bigger, differently shaped, mostly globose-ventricose cystidia, up to 32 μm wide with thinner walls (in average 1.3 vs. 2.8 μm). Genetically, the two species differ by 61 base pairs in the ITS and LSU rDNA sequence (89.07 of percent identity with BLASTn algorithm). According to Bandini *et al.* (2020) the sequence FN550906 from Sweden originally identified as *I. cf. pseudoreducta* Stangl & Glowinsky, most likely is a specimen of *I. athenana*.

Inocybe cuniculina Bandini & B. Oertel (2020: 42) is a well-differentiated species because of the fulvous foxy-tinged colour of lamellae, the whitish stipe, the spores that measure on average 9.7×5.7 μm and the habitat in sand dunes with *Salix repens* and *Ammophila arenaria*.

Inocybe tenebrosa Quél. (1885: 279) shares with *I. messapica* the habitat under evergreen oaks in the Mediterranean area but it is without a veil and has yellowish colors. Moreover, the stipe is whitish and darkens with olivaceous tinges and it often has a banana-like odour.

Inocybe baltica Vauras & E. Larss. (2016: 16) can be compared with *I. messapica* because of its robust habit, the pileus colour and the bulbous stipe (Vauras & Larsson 2016); however, it lacks the velipellis and has much smaller spores, on average 8.2×5.1 vs. 10.6×5.9 μm , and a lower Q ratio (1.6 vs. 1.8).

Inocybe catalaunica Singer (1947: 245), *Inocybe leioccephala* D.E. Stuntz (1950: 98), and *Inocybe subbrunnea* Kühner (1955: 6) were, for a long time, confused with each other or considered as conspecific (Kuyper 1986, Stangl 1989, Esteve-Raventos 1997). Later, Larsson *et al.* (2014) demonstrated, by studying the holotypes, their autonomy and revealed that the available sequences of the so-classified *I. leioccephala* were spread in different evolutionary lineages, indicating that at least seven different species have been identified under this name. Besides, *I. catalaunica*, despite the strict resemblance to the other two, was discovered to be more phylogenetically related to *Inocybe phaeoleuca* Kühner (1955: 5) and *Inocybe tjallingiorum* Kuyper (1986: 2).

Inocybe fuscetipes Kühner (1988: 18), and *Inocybe lindrothii* (P. Karst.) Vauras & E. Larss. (2014: 25) typically occur in a (sub) alpine habitat; in addition, *I. fuscetipes* has a white fugacious cortina at the pileus margin, which is an exceptional character in the section *Splendentes*.

In comparison with *I. messapica* this species complex has a boreal and/or montane to alpine habitat under coniferous trees or *Betula*, generally lacks a markedly white velipellis and typically shows characteristic granules at the apex of the cystidia, immediately below the apical crown of crystals.

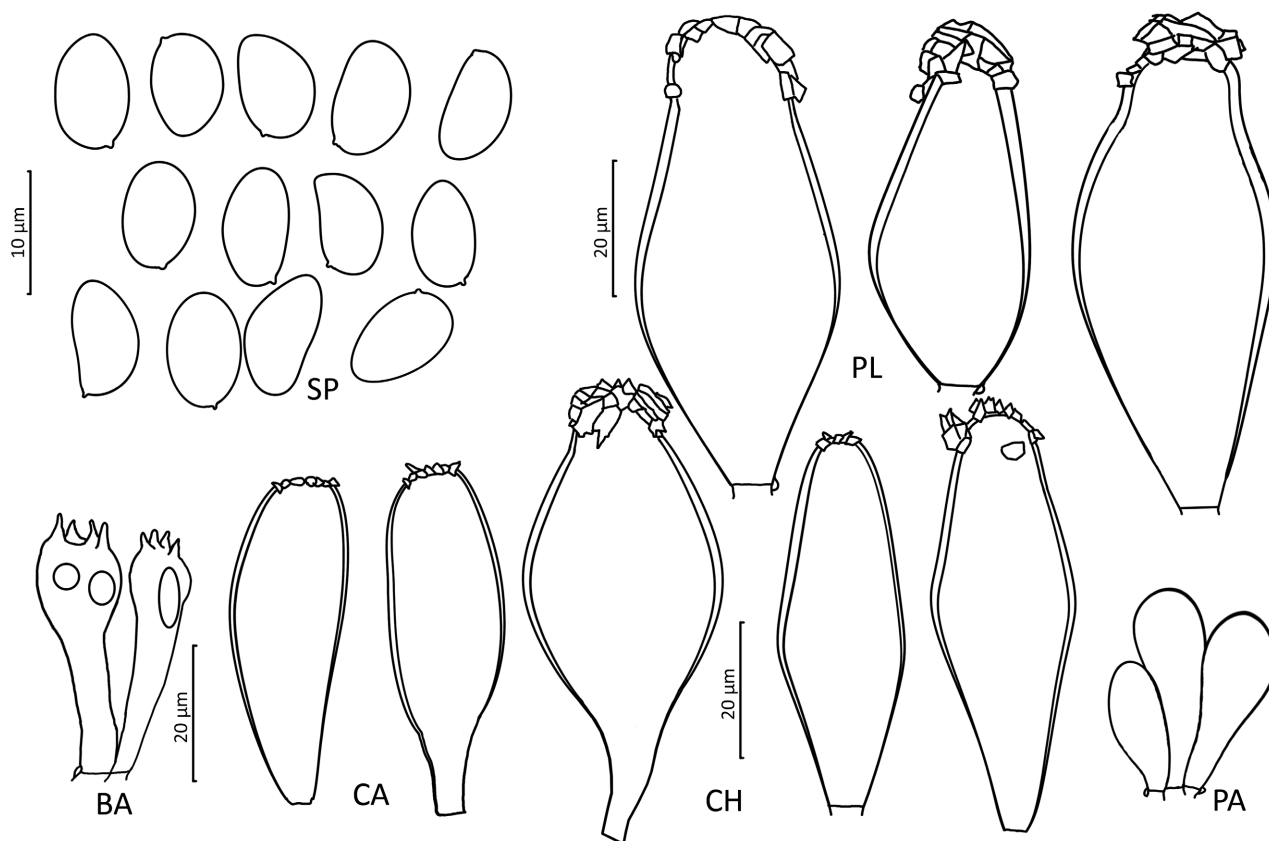


FIGURE 5. *Inocybe athenana*: BA) Basidia; CA) Caulocystidia; CH) Cheilocystidia; PA) Paracystidia; PL) Pleurocystidia; SP) Basidiospores; VE) detail of velipellis (DB15-6-19-2!, isotype). Drawings by M. Cervini.

Comparisons with other species of Sect. Splendentes

Inocybe phaeoleuca Kühner has been for a long time misinterpreted since mostly it was considered a variety of *Inocybe splendens* R. Heim without the marginate bulbous base (Kuyper 1986, Stangl 1989, Jacobsson 2008). Subsequently, Larsson *et al.* (2014) stated its autonomy, showing that this species is more related to *I. tjallingiorum* Kuyper rather than to the *splendens* complex.

Inocybe pararubens Carteret & Reumaux (2012:49) is close both in phylogeny and morphology to *I. phaeoleuca*, from which it differs by the presence of a marginate bulb and by having slender spores with a Q ratio around 2. The recent work of Vauras & Larsson (2020) revealed that *Inocybe castaneicolor* A. La Rosa, Bizio, Saitta & Tedersoo (2017: 79) published from Sicily (La Rosa *et al.* 2017) is a synonym of *I. pararubens*. *Inocybe tjallingiorum* Kuyper is described as a small and slender species with white to pale ochraceous stipe, and spores with rounded apex on average $5.9\text{--}9.7 \times 5.2\text{--}5.7\ \mu\text{m}$ (Kuyper 1986, Larsson *et al.* 2014). This species has been correctly placed by Bon (1997) close to *I. phaeoleuca*, which seems to be phylogenetically a sister species.

In comparison with *I. messapica*, this complex of species can be differentiated by the spore morphology and dimensions, the whitish stipe with no pink shades, and the absence of a universal veil.

Inocybe splendens R. Heim (1932:328), *I. terrifera* Kühner (1955: 33), *I. alluvionis* Stangl & J. Veselský (1976: 77) and *I. splendentoides* (Bon 1990: 61) constitute a homogeneous complex inside *Splendentinae*. They have been variously interpreted or considered as synonyms (Kuyper 1986) until subsequent works based on molecular and morphological data have clarified their autonomy (Kropp *et al.* 2010, Bandini *et al.* 2018, Bandini *et al.* 2019, Bandini *et al.* 2020).

Inocybe heidelbergensis Bandini & B. Oertel is a related taxon from Germany, described in Bandini *et al.* (2019). In this paper the authors provide an exhaustive review of the group through a phylogenetic tree and a determination key.

This whole complex of species, in comparison with *I. messapica*, differs in having a whitish stem and/or a clearly marginate bulbous base.

Inocybe vulpinella Bruyl. (1970: 341) could be similar to *I. messapica* in regard to size, colors, veil and tendency of the stipe to darken, but it has a marginate bulb, felted pileus and bigger spores with a very particular, subangular outline.

Inocybe pseudoreducta Stangl & Glowinsky (1981: 26) is characterized by robust size, entirely and strongly pruinose stipe with an abruptly marginate bulb and intense brownish pink colors. It has been variously interpreted since several sequences under this epithet do not match the type material (La Rosa *et al.* 2017). *Inocybe amblyospora* Kühner (1953: 200) is similar to *pseudoreducta* but differs in the smaller size and in the shape of the spores which have a rounded rather than acute-elongated apex.

In comparison with *I. messapica*, both can be differentiated by the spore morphology and dimensions, the presence of a marginate bulb, and the absence of a marked whitish velipellis.

Acknowledgments

I am very grateful to Gianni Schirinzi who guided me to the site of this new species and also Ditte Bandini for the useful advice and for providing me with the isotype of *I. atehana* for comparison. I also thank the two anonymous reviewers for their corrections and suggestions to improve my work.

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