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ALBERTO MUA, MASSIMO SANNA, MARIO MELIS, MARCO CASULA,
ARIADNE N.M. FURTADO, ANDREA C. RINALDI

TWO NEW SPECIES OF *INOCYBACEAE* *INOCYBE PARVIUMBONATA* AND *INOCYBE ILICICOLA*

Abstract

Inocybe parviumbonata and Inocybe ilicicola, two new species collected in Sardinia (Italy), the latter also in Spain, are described. The study is accompanied by photographs of the main macro- and micromorphological characters. The new species are compared with other similar taxa. A phylogenetic tree including the new species and other species of the genus Inocybe is also proposed.

Riassunto

Vengono descritte Inocybe parviumbonata e Inocybe ilicicola, due nuove specie raccolte in Sardegna (Italia), quest'ultima anche in Spagna. Lo studio è corredato da fotografie dei principali caratteri macro- e micromorfologici. Le nuove specie vengono confrontate con altri taxa simili. Viene inoltre proposto un albero filogenetico che include le nuove specie e altre specie del genere Inocybe.

Keywords *Agaricales, Agaricinae, Inocybaceae, Inocybe.*

Introduction

The family *Inocybaceae* Jülich (Jülich 1982), belonging to the order *Agaricales*, comprises numerous ectomycorrhizal species that live in association with various host plants and are distributed in temperate and tropical habitats. Recently, the family has undergone significant taxonomic changes based on multilocus phylogenetic analyses. Consequently, seven main clades have been identified, each elevated to genus level, as follows*: Auritella* Matheny & Bougher (Matheny & Bougher 2006), *Inocybe*, *Inosperma* (Kühner) Matheny & Esteve-Rav. (Matheny *et al.* 2019), *Mallocybe* (Kuyper) Matheny, Vizzini, Esteve-Rav. (Matheny *et al.* 2019), *Nothocybe* Matheny & K.P.D. Latha (Matheny *et al.* 2019), *Pseudosperma* Matheny & Esteve-Rav. (Matheny *et al.* 2019) and *Tubariomyces* Esteve-Rav. & Matheny (Alvarado *et al.* 2010).

Diversity within the *Inocybaceae* is remarkable. In the genus *Inocybe* alone, more than 1000 species are currently known, but the number is constantly increasing due to the continuous description of new taxa. This increase is mainly driven by the application of molecular tools, particularly useful in a morphologically rather homogeneous group of fungi. Worldwide, the estimated number of species belonging to *Inocybe* sensu stricto ranges between 3000 and 5000 (Bhunjun *et al.* 2022).

Sardinia remains largely unexplored with regard to the diversity of *Inocybaceae*; in recent years, several species have been described from this region (Cervini *et al.* 2020; Sanna *et al.* 2024a, 2024b; Dong *et al.* 2025), some of which were subsequently found in other territories.

Matheny (Matheny *et al.* 2019) defines the genus *Inocybe* as characterized by pleurocystidia frequently thick-walled, with a crystalline apex or lacking crystals due to their loss; basidia hyaline, not necropigmented; spores typically amygdaliform (more rarely ellipsoid or globose), angular, nodulose or spinose; many species present a distinct hilar appendix and only a few are sequestrate. These fungi establish ectomycorrhizal relationships with a wide range of plant families.

Historically, the genus *Inocybe* s.s. was divided into two main groups: subgenus *Clypeus* (Britzelm.) Fayod, including species with nodulose spores, and subgenus *Inocybe*, characterized by smooth spores. A third group, subsection *Lacerinae* (Fr.) Bon, included within subgenus

Inocybe, shows spores intermediate between the first two. All species of *Inocybe* possess metuloid hymenial cystidia, often topped with apical crystals. Many species also have caulocystidia, sometimes confined to the stipe apex, sometimes extending further down to the base. This character, once considered taxonomically relevant (Bon 1997), is now regarded as having minor systematic value, since phylogenetically related species may differ markedly in the presence or absence of caulocystidia. Most species of the genus *Inocybe* are toxic and unsuitable for human consumption (Sitta *et al.* 2021).

In the present contribution, we describe two new species of *Inocybe*, illustrating their evolutionary relationships inferred from a phylogenetic analysis based on the rDNA ITS1-5.8S-ITS2 and LSU markers.

Holotypes were deposited in the *herbarium* of the University of Cagliari (CAG, Italy), isotypes in the Mua (M, Quartu Sant'Elena, Italy) and Mario Melis (MM, Quartu Sant'Elena, Italy) private *herbaria*, while paratypes of *I. ilicicola* are preserved in the *herbarium* of the University of Alcalá (AH, Alcalá de Henares, Spain). *Herbarium* acronyms follow Holmgren *et al.* (1990).

Materials and methods

Morphological observations

Sporocarps were preliminarily subjected to macro- and micromorphological observations prior to molecular analysis. Collections were carried out in Mediterranean environments.

Macromorphological features were described on fresh basidiomata, photographed in situ. Color determination followed Ridgway (1912), and morphological terminology follows Kuyper (1986).

Microscopic observations

Micromorphological study was conducted on fresh and dried material using Optika B-383 PLi (Optika Italy, Ponteranica, BG, Italy) and Motic BA 400 (Motic Europe, Barcelona, Spain) trinocular microscopes, both equipped with integrated digital cameras, as well as an Optech B4 binocular microscope (Optech Technology, Taipei City, Taiwan) equipped with a Nikon Coolpix SQ digital camera (Nikon Europe B.V., Campi Bisenzio, FI, Italy).

Exsiccata were rehydrated with 5% KOH, 3% NH_4OH, or distilled water. The pileipellis was observed in water and 2% anionic Congo Red; hymenial cystidia were examined in NH_4OH and 2% anionic Congo Red.

Spore measurements were made on at least 32 spores from spore deposits, according to Parmasto & Parmasto (1987). Basidiospore dimensions are expressed as (min-) mean - standard deviation - mean - mean + standard deviation (-max), for both length and width; the mean value is underlined. The spore quotient (Q = length/width) is reported as minimum - mean - maximum. Qm (mean quotient) corresponds to the arithmetic mean of the quotients of individual spores, with the mean underlined. The hilar appendix was excluded from spore measurements, as were sterigmata from basidia measurements. Basidia and cystidia dimensions may also be expressed as minimum - maximum range.

DNA extraction, amplification and sequencing

Total DNA was extracted at Molecular Solutions laboratory (Portland, OR, USA). DNA was extracted from fungal tissue by heating with Chelex extraction buffer (100 mM Tris pH 8.5, 4% Chelex 100 and 1% Triton X-100) at 99 °C for 20 minutes, followed by freezing. After thawing, the supernatant was used for PCR.

PCR was performed in 25 mL reactions with 1 μL DNA extract, 0.4 mM of each primer, 0.2 mM dNTP mix, 5 μg bovine serum albumin, and 0.5 U OneTaq Hot Start DNA polymerase (New England Biolabs, Ipswich, MA, USA) in 1X OneTaq standard buffer. PCR conditions were: 94 °C for 30 s; 36 cycles of 94 °C for 15 s, 57 °C for 30 s, and 68 °C for 60 s; final extension at 68 °C for 5 min.

Primers ITS1F (Gardes & Bruns 1993) and ITS4 (White *et al.* 1990) were used for ITS amplification; LR0R (Rehner & Samuels 1994) and LR5 (Vilgalys & Hester 1990) for LSU.

Sequencing was carried out at Eurofins Genomics (Louisville, KY, USA) using the same primers. Forward and reverse reads were aligned using Geneious 10.2.4 and manually edited when necessary.

Phylogenetic analysis **(Fig. 1)**

Nucleotide sequences were first compared using BLASTn (Altschul *et al.* 1990) on the NCBI website to verify absence of contamination and obtain preliminary taxonomic assignment (MEGABLAST). Comparative sequences were downloaded from GenBank.

Two datasets were constructed: ITS (83 sequences) and LSU (51 sequences). Alignments were performed with MUSCLE (Edgar 2004) in MEGA 12 (Kumar *et al.* 2024), trimmed and concatenated with Mesquite v. 3.61 (Maddison & Maddison 2019).

Maximum Likelihood (ML) analysis was performed with RAxMLGUI 2.0 using 1000 bootstrap replicates and the GTR+GAMMA model for both partitions. Bayesian Inference (BI) was conducted with MrBayes v. 3.2.7, with 1×10^7 generations, burn-in 0.25, sampling every 1000 generations and 4 MCMC chains. Final parameters yielded Average standard deviation of split frequencies = (0.004049), Average PSRF= 1 and ESS > 200. The tree was edited with TREEGRAPH2.

Sequence of *Mallocybe terrigena* (HQ604783, ITS and LSU), was used as outgroup. Support thresholds were set at ≥0.95 for Bayesian posterior probabilities (BPP) and ≥70% for ML bootstrap support (MLBS).

The sequences used for phylogenetic reconstruction are listed in **Tab. 1**.

Table 1. Taxa, vouchers, locations, GenBank accession numbers and references of the DNA sequences used in the phylogenetic analyses. Newly sequenced collections are bold-faced.

Species	Voucher	ITS	LSU	Typus	Country
Inocybe ahmadii	LAH 14215	NR_156308	–	T	Pakistan
Inocybe alluvionis	GB13M	PZ008091	–	–	Italy_Sardinia
Inocybe alluvionis	DB7-9-14-11	MH807259	–	–	Germany
Inocybe aurantiobrunnea	STU-F-0001816	OP164016	OP164016	T	Italy
Inocybe aurantiobrunnea	FH04M	PX957279	–	–	Italy_Sardinia
Inocybe beatifica	STU-F-0901261	NR_174853	–	T	Germany
Inocybe beatifica	STU-F-0901472	MW845859	MW845859	–	Germany
Inocybe bonii	STU-F-0901743	OR102473	OR102473	T	Germany
Inocybe brijunica	PUL F27673	NR_172782	NG_075311	T	Croatia
Inocybe brijunica	GK18M	PZ008092	–	–	Italy_Sardinia
Inocybe castorina	STU-F-0901250	MN512319	MN512319	T	Germany
Inocybe chondroderma	Stz4771	GU949572	–	T	USA
Inocybe chondroderma	Stz502	MK607028	–	–	USA

Species	Voucher	ITS	LSU	Typus	Country
Inocybe chondroderma	PBM2028		PQ600550	–	USA
Inocybe cistophila	FW13M	PX961192	PX961193	–	Italy_Sardinia
Inocybe cistophila	AH 56407	NR_198632	NG_243915	T	Spain
Inocybe comis	STU-F-0901599	OK057190	OK057190	T	Austria
Inocybe costinitii	PRC-181203-01	PP794435	–	–	Spain
Inocybe costinitii	McVe n. 28974	KX686581	–	T	Italy
Inocybe cryptica	FF05M	PZ008095	–	–	Italy_Sardinia
Inocybe cryptica	MA Fungi:98477	NR_185706	–	T	Spain
Inocybe dagamae	GK12M	PX972506	–	–	Italy_Sardinia
Inocybe dagamae	POF2740	OR439021	OR439021	–	Portugal
Inocybe dagamae	POF2611	OR439020	–	T	Portugal
Inocybe demetris	STU-F-0901593	OK057184	OK057184	T	Germany
Inocybe demetris	HB07M	PZ011875	–	–	Italy_Sardinia
Inocybe devina	STU-F-0901659	ON003423	ON003423	T	Germany
Inocybe flocculosa	STU-F-0901628	OK057165	OK057165	–	Netherlands
Inocybe ghibliana	FH03M	PX960897	–	–	Italy_Sardinia
Inocybe ghibliana	STU-F-0901256	MW845878	MW845878	T	Germany
Inocybe glabripes	STU-F-0900979	MW845881	MW84588	T	Germany
Inocybe griseovelata	STU-F-0901568	MW845942	MW845942	T	Germany
Inocybe grusiana	STU-F-0901262	MW845884	MW845884	T	Germany
Inocybe halimiphila	CAG B/5.6.4	PP941799	PP941805	T	Italy_Sardinia
Inocybe hamadryadis	MA Fungi:98476	NR_198291	–	T	Spain
Inocybe hamadryadis	MA-Fungi 98651	OP480838	OP494213	–	Spain
Inocybe hamadryadis	MA-Fungi 98707	OP480840	–	–	Spain
Inocybe ilicicola	**CAG B/5.6.6**	**PX607987**	**PX607985**	**T**	**Italy_Sardinia**
Inocybe ilicicola	AH 60168	PX855139	–	–	Spain
Inocybe jacobssonii	GZ18M	PZ008096	–	–	Italy_Sardinia
Inocybe jacobssonii	JV33634	OQ520012	OQ520012	T	Finland
Inocybe juturnae	STU-F-0901767	OQ324780	OQ324780	T	Germany
Inocybe lacera	STU-F-0901707	OP164102	OP164102	–	Netherlands
Inocybe laurina	FX11M	PX960876	PX960866	–	Italy_Sardinia
Inocybe laurina	STU-F-0901247	MN512325	MN512325	T	Germany
Inocybe minimispora	STU-F-0901264	MW845934	MW845934	–	Austria
Inocybe minimispora	F-3436	PQ639073	PQ639073	–	Sweden
Inocybe obscurobadia	SJ03008	AM882802	AM882802	–	Sweden

Species	Voucher	ITS	LSU	Typus	Country
Inocybe othini	STU-F-0901622	OK057180	OK057180	T	Austria
Inocybe parviumbonata	**CAG B/5.6.7**	**PX607988**	**PX859766**	**T**	**Italy_Sardinia**
Inocybe phaeodisca	STU-F-0901574	MW845950	MW845950	–	Germany
Inocybe plurabellae	STU-F-0901260	MW845901	MW845901	T	Germany
Inocybe pinophila	FE01M	PZ008097	–	–	Italy_Sardinia
Inocybe pinophila	AMB 19334	PP065586	PP065586	T	Italy
Inocybe posterula	2024-61-n	PZ017188	–	–	Italy_Sardinia
Inocybe posterula	M 0151615	KM873368	KM873368	T	Germany
Inocybe psammobrunnea	GA03M	PZ012032	PZ012034	–	Italy_Sardinia
Inocybe psammobrunnea	LIP:LIL-89226	MW845926	–	T	France
Inocybe psammobrunnea	KR:KR-M-0038015	MT101889	OR100607	–	France
Inocybe pseudorubens	GZ14M	PX972503	–	–	Italy_Sardinia
Inocybe pseudorubens	XC2000-103	MW845952	–	T	France
Inocybe pudica	KR-M-0042243	MH732923	–	–	Germany
Inocybe rocabrunae	1833MS	PP935492	PP935502	–	Italy_Sardinia
Inocybe romana	FV17M	PZ012031	PZ016048	–	Italy_Sardinia
Inocybe romana	MAF-Fungi 2201	PX219989	–	–	Spain
Inocybe roseobulbipes	FC20M	PZ008372	–	–	Italy_Sardinia
Inocybe roseobulbipes	AH 56204	OQ300086	OQ300086	T	Spain
Inocybe rubripes	CAG B/5.6.5	PP941801	PP941847	T	Italy_Sardinia
Inocybe rufuloides	STU-F-0901753	OR102470	OR102470	T	Germany
Inocybe rufuloides	FV11M	PZ012032	PZ019398	–	Italy_Sardinia
Inocybe semifulva	STU-F-0901000	MW845916	MW845916	–	Germany
Inocybe semifulva	WTU ACAD11651	NR_119905	NG_057195	T	Canada
Inocybe sp.	isolate DLM_625	PX309547	–	–	UK
Inocybe subnudipes	DB23-9-90	OP164034	–	–	Finland
Inocybe subnudipes	F-2939	PQ652928	PQ652928	–	Sweden
Inocybe tenuicystidiata	M:M-0281792	MW856453	MW856453	T	Germany
Inocybe tenuicystidiata	2024-77-n	PZ008012	PZ008014	–	Italy_Sardinia
Inocybe tenuicystidiata	2024-77-m	PZ008001	PZ008013	–	Italy_Sardinia
Inocybe thrudiae	STU-F-0901771	OQ324784	OQ324784	T	Austria
Inocybe tigrina	STU-F-0901532	MW845933	MW845933	T	Germany
Inocybe tigrina	EV06M	PP946889	PP946893	–	Italy_Sardinia
Inocybe whitei	2024-61-f	PZ008375	–	–	Italy_Sardinia
Mallocybe terrigena	UBC:F19404	HQ604783	HQ604783	–	Canada



Figure 1. Phylogram illustrating the evolutionary relationships of the new *Inocybe* species and its relatives. The topology represented was obtained according to a Bayesian model using MrBayes, nrITS, and nrLSU sequence data. Posterior probability (PP) and Bootstrap support (BP) values are represented on the branches leading to the nodes. New species are highlighted in red.

TAXONOMY

Inocybe parviumbonata Mua, M. Sanna, M. Melis, Marc. Casula, A.N.M. Furtado & A.C. Rinaldi sp. nov.
MycoBank: 862583

Etymology referring to the small umbo on the cap.

Holotype 26/03/2011, Italy, Sardinia, Ballao (CA), Parco Interacquas, in *Populus alba* L. woodland on acidic soil; *leg.* Alberto Mua and Marco Casula; *herbarium* CAG B/5.6.7; isotype in Mua *herbarium* (DI04M). GenBank ITS PX607987.1; LSU PX607985.1.

Original diagnosis

Characterized by a small central umbo, strongly fibrillose cuticle, smooth spores, metuloid cystidia yellowing in NH_4OH, and absence of caulocystidia. Combined morphological and ITS/LSU data distinguish it from I. beatifica, I. costinitii and I. othini.

Description of macroscopic characters

Pileus up to 3 cm, conical-campanulate, then convex with a distinct central papilla; surface dry, fibrillose, fissured, ochre-brown in color with a darker center [P.L. XVI, 19′. yo-y, k (Buffy citrine), P.L. XV, 17′. o-y, k (Dresden brown)], margin whitish. In young specimens, ephemeral whitish remnants of velipellis may be observed.

Lamellae ventricose, broad, adnexed, uncinate, moderately spaced, pale ochre then darker, with few lamellulae (L1/l1-3); edge whitish, slightly crenulate.

Stipe 3-5 × 0.3-0.5 cm, cylindrical, slightly broadened toward the base; surface whitish, slightly pinkish above, fibrillose, bearing scant remnants of cortina.

Context whitish, scant, odorless.



Inocybe parviumbonata. Holotypus. Photo by Alberto Mua

Description of microscopic characters

Spores (7.6) 8.1-8.7-9.8 (10.3) × (4.3) 4.6-5.0-5.3 (6.1) µm, Q = (1.5) 1.6-1.7-1.9 (2.1); N = 64; amygdaliform, with apical callus, smooth, with wall 0.6-0.8 µm thick, yellow-brownish.

Basidia 23.6-27.4 × 9.0-9.5 µm, clavate, tetrasporic.

Cheilocystidia (35.7) 38.8-46.1-53.5 (64.7) × (13.1) 13.5-16.6-19.8 (21) µm, very abundant, muricate, utriform, less frequently lecythiform, with thick walls (2) 1.5-1.9 (3) µm, turning yellow in NH_4OH.

Paracystidia numerous, pyriform, 30.1-38.4 × 11-14.5 µm, with thin or slightly thickened walls.

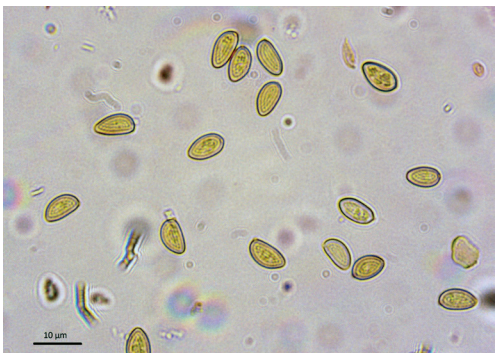
Pleurocystidia similar to cheilocystidia.

Caulocystidia absent.

Suprapellis of cutis type with hyphae (1.6) 2.0-5.0 (6.8) µm wide, wall pigment finely encrusting and intracellular, yellow-brownish, especially in deeper layers.

Clamp connections present throughout.

Habitat and distribution so far, it has been reported only from *Populus alba* woodlands, on very moist soil, in Sardinia. For another collection, cited below and originating from the United Kingdom (Scotland, Dryburgh Abbey), whose sequence has been deposited in GenBank, the growth habitat is unknown.



I. parviumbonata. Spore 100×. Photo by Alberto Mua

Observations

Observing the phylogram obtained in the present study, it is evident that the sequence of *Inocybe parviumbonata* is associated with an additional sequence identified as *Inocybe* sp. isolate DLM_625 (GenBank accession number: PX309547.1), clearly referable to the same species. For this sequence, the geographic origin (United Kingdom) is known, whereas no information is available regarding the origin of the material (basidiome, mycorrhiza, environmental sequence, or other).

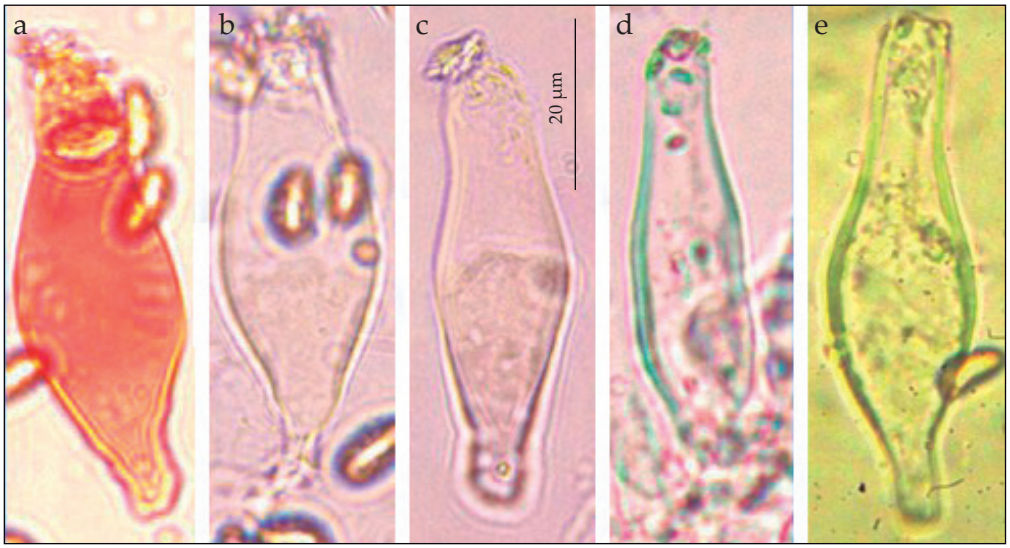
The two sequences form a well-supported clade, as indicated by high MLBS and BPP values, in association with *Inocybe beatifica* (to be considered the sister species) and *Inocybe costinitii*. In a slightly more distant but still phylogenetically close position lies *Inocybe othini*, with which they form a broader, well-supported clade.

From a morphological standpoint, *Inocybe parviumbonata* is characterized by the presence of a small central umbo on the cap, a strongly fibrillose cuticle, metuloid cystidia that yellow in NH_4OH, and absence of caulocystidia.

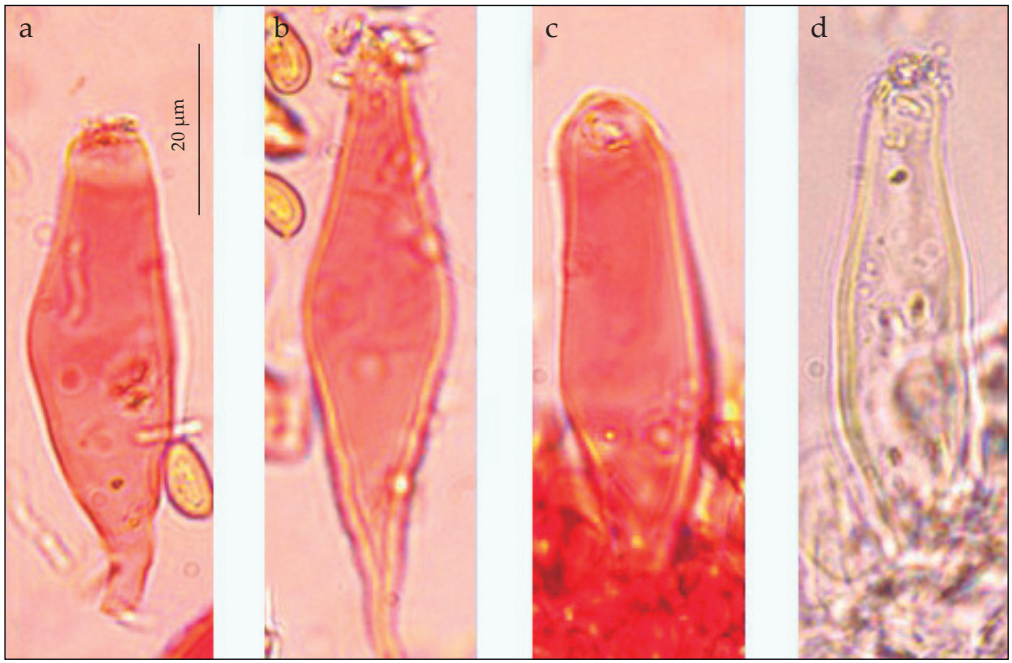
Inocybe beatifica Bandini & B. Oertel (Bandini *et al.* 2021) differs by the absence of a papilla on the cap, larger hymenial cystidia that only weakly yellow in alkaline solutions, the presence of caulocystidia along the entire length of the stipe, and a preferred habitat in association with *Picea abies* (L.) H. Karst.

Inocybe costinitii Bizio, Ferisin & Dovana (Bizio *et al*. 2016) differs by the presence of an abundant and persistent pileal veil, a broad umbo, spermatic odor, stipe with a small basal bulb, presence of caulocystidia, and growth in association with *Pinus halepensis* Mill.

Inocybe othini Bandini & B. Oertel (Bandini *et al.* 2022) differs by its broad umbo surrounded by a depression, spermatic odor, longer and more slender cheilocystidia, and presence of caulocystidia at the stipe apex.



I. parviumbonata. Cheilocystidia. Staining: **a**. Congo red; **b-c**: H_2O; **d-e**: NH_4OH. Photo by Alberto Mua



I. parviumbonata. Pleurocystidia. Staining: **a-b-c**: Congo red; **b-c**: H_2O; **d**: NH_4OH. Photo by Alberto Mua/Mario Melis

Inocybe parviumbonata presents a complex taxonomic placement, especially when considering certain historical classifications, such as that proposed by Bon (1997), based mainly on the presence of caulocystidia and their distribution along the stipe. More recent phylogenetic investigations have shown that closely related species from an evolutionary standpoint may differ markedly precisely in this morphological character.

In the present study as well, it is observed that *I. parviumbonata*, lacking caulocystidia, *I. beatifica*, with caulocystidia distributed along the entire stipe, and *I. costinitii* and *I. othini*, characterized by caulocystidia limited to the apical portion of the stipe, are nevertheless closely related phylogenetically. This confirms the poor systematic reliability of this character when considered in isolation.

Following the systematics proposed by Bon (1997), now considered outdated, *I. parviumbonata* should be placed in subgenus *Inocybe*, section *Lacerae*, due to the absence of green or reddish coloration, lack of reddening reaction, and absence of caulocystidia; within this, in subsection *Mesosporinae*, on account of its medium-sized spores.

According to Stangl's classification (Stangl 1980), the species should instead be placed in supersection *Cortinatae*, section A1, due to the presence of cortina remnants, absence of caulocystidia, and smooth spores.

Both of these systematic frameworks are now outdated; Matheny *et al*., already in 2002, asserted the polyphyly of the supersections *Cortinatae* and *Marginatae* (Matheny *et al*. 2002).

Inocybe ilicicola Mua, M. Sanna, M. Melis, Marco Casula, A.N.M. Furtado & A.C. Rinaldi sp. nov.

MycoBank: 862554

Etymology referring to the habitat of the holotype collection.

Holotype 13/05/2022, Italy, Sardinia, Sinnai (CA), Musui, 792 m a.s.l., in *Quercus ilex* L. and *Arbutus unedo* L. woodland on acidic soil, *leg.* Alberto Mua and Marco Casula; *herbarium* CAG B/5.6.6; isotype FR16M. GenBank ITS PX607987.1; LSU PX607985.1.

Additional material 03/03/2024, Spain, Comunidad de Madrid, Cenicientos, Las Tejoneras, 695 m a.s.l., under *Quercus suber* L., *Q. rotundifolia* L., *Pinus pinea* L., *P. pinaster* Aiton; *leg.* F. Pancorbo, C. Aramendi, J.C. Campos, F. Cifuentes, M.A. Ribes, & M. Villareal, *herbarium* AH 60168. GenBank ITS PX855139.1.

Original diagnosis

Characterized by a broad low umbo; whitish-grey velipellis persistent at the pileus margin; mature lamellar edge brown-dotted; pruinose stipe apex; absence of cortina; smooth spores; and cystidioid hairs at stipe apex. Distinguished from I. tenuicystidiata and I. hamadryadis by combined morphology and ITS/LSU data.

Description of macroscopic characters

Pileus 1.5-4.5 cm in diameter, initially hemispherical-campanulate, then convex with a broad, low central umbo; velipellis whitish-grey, evident in young basidiomata, fading early during development but persisting at the cap margin; surface dry, smooth, later covered with small scales toward the periphery, while the center remains smooth; often brown at maturity [PL. XL 17'''. o-y, i (buffy brown), PL. XL 17'''. o-y (wood brown), PL. XL 13'''. o-y-o, i (army brown)], margin fissured.

Lamellae whitish at first, then beige-ochre, ochre-yellowish, finally ochre-brown; adnexed or adnate, sometimes emarginate; fairly crowded, up to 4 mm broad, ventricose at maturity; interspersed with few lamellulae (L1/l1-3); edge initially white, then typically brown-dotted, in old age concolorous with the faces, finely eroded.

Stipe 3-6 × 0.3-0.6 cm, fibrous, cylindrical, often flexuous, base not bulbous but sometimes slightly broadened; fibrillose, pruinose at the apex, cream-ochre, covered with a whitish coating that disappears upon handling. Cortina absent.

Context whitish, ochraceous in the stipe, odor weak with tones reminiscent of geraniums, taste mild.

Description of microscopic characters

Spores (8.4) 8.7-9.4-10.2 (10.9) × (4.8) 5.2-5.5-6 (6.2) μm, Q = (1.5) 1.6-1.7-1.9 (2.1); N = 43; amygdaliform or ellipsoid, with walls 0.6-2 μm thick, yellowish in water, generally with apical callus, partly mono- or biguttulate.

Basidia (20) 28.6-30.4-32.3 (32.6) × (6,3) 7.1-8.2-8.9 (9.6) μm, tetrasporic, clavate.

Lamellar edge sterile.

Cheilocystidia (32.6) 38.1-44-49.8 (63.9) × (7.7) 8.6-10.5-12.4 (13.3) μm, (3.03) 3.66-4.21-4.95 (5.88); N = 15; very numerous, metuloid but with rather thin walls, sometimes thicker near the apex and not yellowing in NH_4OH; variable in shape, lageniform, cylindroid, fusiform, often capitate, mostly muricate, frequently provided with a short peduncle.

Paracystidia numerous, clavate, brown-pigmented, 15-20 × 7-9 μm.

Pleurocystidia (41.3) 47-52.6-58.7 (67) × (12.2) 12.8-14.4-16.2 (17.9) μm, N = 78, scattered, few, similar in shape to cheilocystidia but larger.

True caulocystidia very rare or absent; only a few tufts of cystidioid hairs present at the extreme apex of the stipe.

Pileipellis composed of a cutis of parallel hyphae, 3-6 μm wide, with brown encrusting pigment.

Clamp connections present throughout.

Habitat and distribution So far, *I. ilicicola* has been found in oak woodlands (*Quercus ilex*, *Q. suber*, *Q. rotundifolia*), also with the presence of *Pinus pinea* and *P. pinaster*, on acidic soil. Current knowledge of its distribution is limited to Italy (Sardinia) and central Spain.



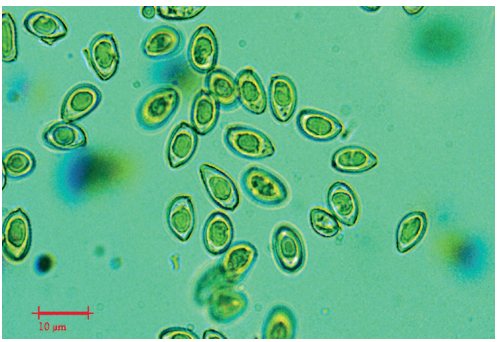
Inocybe ilicicola. Holotypus. Photo by Alberto Mua



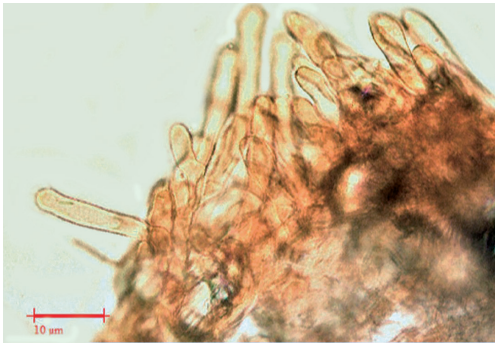
Inocybe ilicicola. Spain. Photo by Fermín Pancorbo



I. ilicicola. Edge brown-dotted. Spain. Photo by Fermín Pancorbo



I. ilicicola. Spores. Photo by Alberto Mua



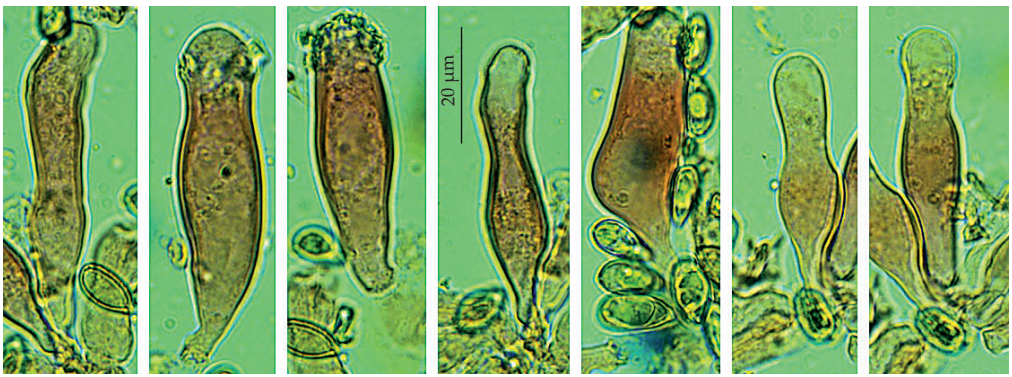
I. ilicicola. Caulocistydia. Foto di Alberto Mua

Observations

The data on the Spanish collection were kindly provided by Férmin Pancorbo following correspondence between him and one of us (M. Sanna), during which Pancorbo stated that he had collected and was in possession of a sequence similar to the one we deposited as the holotype, to which he had not assigned a name. *Inocybe ilicicola* is phylogenetically related to *Inocybe tenuicystidiata* E. Horak & Stangl (Horak & Stangl 1980), with which it shares the reduced wall thickness of the hymenial cystidia. However, *I. tenuicystidiata* differs by



I. ilicicola. Cheilocystidia in Congo red. Photo by Alberto Mua



I. ilicicola. Pleurocystidia in Congo red. Photo by Alberto Mua

its smaller size, lamellar edge not brown-dotted, habitat in coniferous forests (particularly with *Picea*), slightly larger spores lacking an apical callus, cheilocystidia on average smaller, and pleurocystidia on average larger.

Inocybe hamadryadis Rodr.-Campo, Bandini & Olariaga (Rodríguez-Campo *et al.* 2023), also phylogenetically related to our species and growing with *Q. ilex* subsp. *ballota* (Desf.) Samp. and *Cistus ladanifer* L., differs by the presence of a cortina in young specimens, lamellar edge not brown-dotted, smaller spores, larger cheilocystidia and paracystidia, and numerous pleurocystidia with walls that in KOH assume yellowish or greenish tones.

From the phylogram presented in the present study, it is also evident that *I. ilicicola*, *I. tenuicystidiata*, and *I. hamadryadis* form a distinct clade, well supported by the values obtained in Maximum Likelihood (ML) and Bootstrap (BP) analyses.

Similarly to *I. parviumbonata, I. ilicicola* would have been assigned, according to Bon's classification (Bon 1997), to section *Lacerae*, subsection *Mesosporinae*; however, in light of current phylogenetic evidence, this placement lacks real evolutionary significance.

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Authors' addresses

Alberto Mua
A.M.B., Gruppo 'Sette Fratelli', Via Famagosta 13, 09134 Cagliari, Italy.
E-mail: albermua@gmail.com

Massimo Sanna
A.M.B., Gruppo 'Sette Fratelli', Via Famagosta 13, 09134 Cagliari, Italy.
E-mail: massanfungo@gmail.com

Mario Melis
A.M.B., Gruppo 'Sette Fratelli', Via Famagosta 13, 09134 Cagliari, Italy.
E-mail: mariomelis02@gmail.com

Marco Casula
A.M.B., Gruppo 'Sette Fratelli', via Famagosta 13, 09134 Cagliari, Italy.
E-mail: casula.mek@gmail.com

Aradne N.M. Furtado,
Dipartimento di Scienze Biomediche, Sezione di Biochimica, Biologia e Genetica,
Università degli Studi di Cagliari, I-09042, Monserrato (CA), Italy.
E-mail: ariadnemf@gmail.com

Andrea C. Rinaldi
Dipartimento di Scienze Biomediche, Sezione di Biochimica, Biologia e Genetica,
Università degli Studi di Cagliari, I-09042, Monserrato (CA), Italy.
A.M.B., Gruppo 'Sette Fratelli', Via Famagosta 13, 09134 Cagliari, Italy.
E-mail: rinaldi.ac.2@gmail.com

References

Altschul S.F., Gish W., Miller W., Myers E.W. & Lipman D.J. – 1990: Basic local alignment search tool. *Journal of Molecular Biology* 215: 403-410.

Alvarado P., Manjón J.L., Matheny P.B. & Esteve-Raventós F. – 2010: *Tubariomyces*, a new genus of *Inocybaceae* from the Mediterranean region. *Mycologia* 102 (6): 1389-1397.

Bandini D., Oertel B. & Eberhardt U. – 2021: A fresh outlook on the smooth-spored species of *Inocybe*: type studies and 18 new species. *Mycological Progress* 20 (9): 1019-1114.

Bandini D., Oertel B. & Eberhardt U. – 2022: More smooth-spored species of *Inocybe* (*Agaricales, Basidiomycota*): type studies and 12 new species from Europe. *Persoonia, Molecular Phylogeny and Evolution of Fungi* 48 (1): 91-149.

Bhunjun C.S., Niskanen T., Suwannarach N., Wannathes N., Chen Y.J. *et al.* – 2022: The numbers of fungi: are the most speciose genera truly diverse? *Fungal Diversity* 114 (1): 387-462.

Bizio E., Ferisin G. & Dovana F. – 2016: *Inocybe costinitii*, a new species from the Istrian coast. *Micologia e Vegetazione Mediterranea* 31 (2), 95-102.

Bon M. – 1997: Clé monographique du genre *Inocybe* (Fr.) Fr. [2ème partie: sous-genre *Inocybe* = *Inocybium* (Earle) Singer]. *Documents Mycologiques* 27 (108): 1-69.

Cervini M., Bizio E. & Alvarado P. – 2020: Quattro nuove specie italiane del Genere *Pseudosperma* (*Inocybaceae*) con odore di miele. *Rivista di Micologia* 63 (1): 3-36.

Dong W., Hyde K.D., Jeewon R., Karunarathna S.C. & Zhang H. – 2025: Fungal diversity notes 2017-2122: taxonomic and phylogenetic contributions to freshwater fungi and other fungal taxa. *Fungal Diversity* 185-189.

Edler D., Klein J., Antonelli A. & Silvestro D. – 2021: raxmlGUI 2.0: a graphical interface and toolkit for phylogenetic analyses using RAxML. *Methods in Ecology and Evolution* 12 (2): 373-377.

Edgar R.C. – 2004: MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32 (5): 1792-1797.

Gardes M. & Bruns T.D. – 1993: ITS primers with enhanced specificity for *Basidiomycetes*—Application to the identification of mycorrhizae and rusts. *Molecular Ecology* 2: 113-118.

Jülich W – 1982 [1981]: Higher Taxa of *Basidiomycetes*. *Bibliotheca Mycologica* 85, Vaduz.

Holmgren P.K., Holmgren N.H. & Barnett L.C. – 1990: *Index herbariorum*. Part I: The herbaria of the world. 8th edition. *New York Botanical Garden.* Biodiversity Information Standards (TDWG).

Horak E. & Stangl V. – 1980: Notizen zur Taxonomie und Verbreitung von *Inocybe leptocystis*. *Sydowia* 33: 145-151

Kozlov A.M., Darriba D., Flouri T., Morel B. & Stamatakis A. – 2019: RAxML-NG: a fast, scalable and user-friendly tool for maximum likelihood phylogenetic inference. *Bioinformatics* 35 (21): 4453-4455.

Kumar S., Stecher G., Suleski M., Sanderford M., Sharma S. & Tamura K. – 2024: MEGA12: Molecular Evolutionary Genetic Analysis version 12 for adaptive and green computing. *Molecular Biology and Evolution* 41 (12): msae 263.

Kuyper T.W. – 1986: A revision of the genus *Inocybe* in Europe. I: Subgenus *Inosperma* and the smooth-spored species of subgenus *Inocybe*. *Persoonia Supplement* 3: 1-247.

Maddison W.P. & Maddison D.R. – 2019: Mesquite: a modular system for evolutionary analysis. Version 3.61.

Matheny P.B., Liu Y.J., Ammirati J.F. & Hall B.D. – 2002: Using RPB1 sequences to improve phylogenetic inference among mushrooms (*Inocybe*, *Agaricales*). *American Journal of Botany* 89 (4): 688-698.

Matheny P.B. & Bougher N.L. – 2006: The new genus *Auritella* from Africa and Australia (*Inocybaceae*, *Agaricales*): molecular systematics, taxonomy and historical biogeography. *Mycological Progress* 5 (1): 2-17.

Matheny P.B., Hobbs A.M. & Esteve-Raventós F. – 2019: Genera of *Inocybaceae*: New skin for the old ceremony. *Mycologia* 112 (1): 83-120.

Parmasto E. & Parmasto I. – 1987: Variation in basidiospores in the *Hymenomycetes* and its significance to their taxonomy. *Bibliotheca Mycologica*, Band 115. J. Cramer, Berlin.

Rehner S.A. & Samuels G.J. – 1994: Taxonomy and phylogeny of *Gliocladium* analysed from nuclear large subunit ribosomal DNA sequences. *Mycological Research* 98 (6): 625-634.

Ridgway R. – 1912: *Color standards and color nomenclature*. The Author, Washington D.C.: 172 pp.

Ronquist F., Teslenko M., van der Mark P., Ayres D.L., Darling A., Höhna S., Larget B., Liu L., Suchard M.A. & Huelsenbeck J.P. – 2012: MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539-542.

Rodríguez-Campo F.J., Bandini D. & Olariaga I. (2023). *Inocybe hamadryadis* (*Inocybaceae, Agaricales*), a new smooth-spored species from Europe and West Asia. *Phytotaxa* 594 (3): 191-203.

Sanna M., Mua A., Porcu G., Casula M., Rinaldi A.C., Mifsud S. & Garrido-Benavent I. – 2024a: *Pseudosperma calciphilum* (*Inocybaceae*), a new Mediterranean species from Sardinia (Italy), Malta, and Valencia (Spain). *Phytotaxa* 633 (3): 253-264.

Sanna M., Mua A., Casula M. & Rinaldi A.C. – 2024b: *Inocybaceae* (*Basidiomycota*) in ectomycorrhizal symbiosis with *Halimium* (*Cistaceae*), and the description of two new species of *Inocybe* from Sardinia (Italy). *Diversity* 16 (8): 505.

Sitta N., Davoli P., Floriani M. & Suriano E. – 2021: *Guida ragionata alla commestibilità dei funghi*. Reg. Piemonte: 1-180.

Stamatakis A. – 2006: RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688-2690.

Stangl J. – 1980: *Guida alla determinazione dei funghi*. Saturnia.

Vilgalys R. & Hester M. – 1990: Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* 172 (8): 4238-4246.

White T.J., Bruns T., Lee S. & Taylor J. – 1990: *Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics*. In PCR Protocols: A Guide to Methods and Applications; Innis M.A., Gelfand D.H., Sninsky J.J., White T.J., Eds.; Academic Press: New York, NY, USA, 315-322.