Phytotaxa 633 (3): 253–264
https://www.mapress.com/pt/
Copyright © 2024 Magnolia Press

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

https://doi.org/10.11646/phytotaxa.633.3.5

Pseudosperma calciphilum (*Inocybaceae*), a new Mediterranean species from Sardinia (Italy), Malta, and Valencia (Spain)

MASSIMO SANNA[1,5*], ALBERTO MUA[1,6], GIUSEPPE PORCU[1,7], MARCO CASULA[1,8], ANDREA C. RINALDI[2,9], STEPHEN MIFSUD[3,10] & ISAAC GARRIDO-BENAVENT[4,11]

[1]*Associazione Micologica Bresadola, Gruppo 'Sette Fratelli', Via Cavaro 45, 09131 Cagliari (CA), Italy.*
[2]*Department of Biomedical Sciences, University of Cagliari, 09042 Monserrato (CA), Italy.*
[3]*EcoGozo Directorate, Ministry for Gozo, VCT1335 Victoria, Gozo, Malta.*
[4]*Departament de Botànica i Geologia, Facultat de Ciències Biològiques, Universitat de València, C/ Doctor Moliner 50, E-46100 Burjassot, València, Spain.*
[5] *massanfungo@gmail.com; https://orcid.org/0000-0002-3427-702X*
[6] *albermua@tiscali.it; https://orcid.org/0000-0002-9586-0403*
[7] *pinoporcu.ss@gmail.com; https://orcid.org/0000-0001-7872-0153*
[8] *casula.mek@tiscali.it; https://orcid.org/0009-0008-8898-5778*
[9] *rinaldi@unica.it; https://orcid.org/0000-0002-9352-1037*
[10] *info@maltawildplants.com; https://orcid.org/0000-0002-9352-1037*
[11] *Isaac.Garrido@uv.es; https://orcid.org/0000-0002-5230-225X*
**Correspondence author*

Abstract

A complete description is provided for *Pseudosperma calciphilum* (*Inocybaceae*, *Agaricales*), a new basidiomycete species from Sardinia (Italy), Malta, and Valencia (Spain) in Europe, along with colour photographs of its macro- and microscopic characters and a comparative study of the similarities and differences from its closest allies. The new species occurs on calcareous soils in Mediterranean habitats preferably under *Quercus ilex* subsp. *ilex* and *Q. ilex* subsp. *rotundifolia*. *Pseudosperma conviviale* resembles *P. calciphilum* in some macro- and microscopic features, but the latter is distinguished by having white velar remnants on pileus, larger spores and by its ecology, as it apparently grows exclusively on calcareous soils. The phylogenetic analyses based on nrITS and nrLSU nucleotide sequence data confirmed that the new species is a member of the former *Inocybe* section *Rimosae sensu stricto*, whose species are currently placed in the genus *Pseudosperma*. The closest relatives are *P. melleum*, *P. conviviale*, *P. melliolens* and *P. umbrinellum*, from which the new Mediterranean species is well distinguished both morphologically and genetically.

Key words: *Agaricomycetes*, *Basidiomycota*, fungal biogeography, molecular systematics, taxonomy

Introduction

The family *Inocybaceae* Julich (1981: 374) has recently undergone significant taxonomic changes based on multi-locus phylogenetic analyses. The former genus *Inocybe* (Fries 1821: 254) Fries (1863: 346) subgenera *Inocybe sensu stricto*, *Inosperma* (Kühner 1980: 898) Matheny & Esteve-Raventós in Matheny *et al*. (2020: 94) and *Mallocybe* (Kuyper 1986: 22) Matheny, Vizzini & Esteve-Raventós in Matheny *et al.* (2020: 94) have been raised to genus level, and the same has occurred to the monospecific *Nothocybe* Matheny & K.P.D. Latha in Matheny *et al*. (2020: 93). Also, the former *Inocybe* sect. *Rimosae* (Fries) Quélet (1888: 98) has emerged as a well-supported clade, and therefore it has been erected to the new genus *Pseudosperma* Matheny & Esteve-Raventós in Matheny *et al*. (2020: 93).

Species in *Pseudosperma* usually produce fruiting bodies with fibrillose to squamulose, often rimose pilei, stipe apices often distinctly pruinose, furfuraceous or somewhat flocculose, and stipe bases usually even, while the context does not change color when bruised and the odor is often spermatic, although some species smell like green corn or honey (Matheny *et al*. 2020). Microscopically, *Pseudosperma* species are characterized by usually producing elliptic to phaseoliform basidiospores and by lacking pleurocystidia. Currently, *Pseudosperma* comprises nearly 100 taxa at the species and below-species levels according to Index Fungorum [www.indexfungorum.org/Names/Names.asp (accessed

Accepted by Francesco Dovana: 18 Dec. 2023; published: 9 Jan. 2024

on 3 August 2023), most of which occur in European ecosystems. Several new species have been described in recent years in this continent (e.g., Jacobsson & Larsson 2009, Carteret & Reumaux 2015, Cervini *et al.* 2020, Bandini & Oertel 2020, Bandini *et al*. 2021, 2022), but also in Australia (Matheny & Bougher 2017), and a large Asian area that includes Pakistan, India and China (Latha & Manimohan 2017, Ullah *et al.* 2018, Bau & Fan 2018, Saba *et al.* 2020, Mao *et al.* 2022). Despite that little is known of the mycorrhizal biology of *Pseudosperma* besides field observations, the variety of habitats where species of this genus thrive, such as boreal coniferous and broad-leaved forests, coastal dunes, and river banks (e.g., Cervini *et al.* 2020, Bandini & Oertel 2020, Saba *et al.* 2020, Bandini *et al*. 2021, 2022, Mao *et al.* 2022), suggests that species in this genus can establish ectomycorrhizal symbioses with a vast array of plant hosts (Matheny *et al*. 2020). Some *Pseudosperma* species seem to be specialists, i.e., engaged with symbiosis with a single plant host or a group of strictly related plants (Bandini & Oertel 2020, Yu *et al*. 2020). Moreover, as noted by Bandini & Oertel (2020), the geographic distribution of most species is poorly known, leaving large possibilities for exploring the ecological flexibility of *Pseudosperma*.

The aim of the present work is to describe a new species of *Pseudosperma* that was collected under holm oaks on calcareous soils in two areas of the western Mediterranean basin. We will discuss the main morphological and ecological characters that separate the new species from closely related ones and will unveil their evolutionary relationships by inferring a phylogeny based on multiple loci.

Materials and methods

Field work and morphological study

The present work considered four basidiomata collections from the municipality of Cagliari (Sardinia, Italy), which were collected in 2021 and 2022, two from Quatretonda (Valencia, Spain) in 2011 and 2012, and one from Verdala area (limits of Siġġiewi, Malta) in 2022. The description of the macromorphological characters was carried out on fresh basidiomata, which were photographed in the field using Canon 450D and Canon 1100D digital cameras. The study of the micromorphological characters was carried out on dried specimens using Optika B-383 PLi and Motic BA 400 trinocular microscopes equipped with integrated digital cameras and with an Optech B4 binocular microscope equipped with a Nikon Coolpix SQ Optec digital camera. The following dyes and reagents were also used for slide preparation: 2% anionic Congo Red, Phloxin and 6% NH_4OH. Rehydration of sample fragments was done with 5% KOH or with distilled H_2O. The pileipellis was observed in both water and 2% anionic Congo Red. Sporal measurements were taken from at least 32 spores obtained from the spore deposit of several collections (186 spores in total), as recommended by Parmasto & Parmasto (1987). Dimensions of the basidiospores are given as (minimum–) average minus standard deviation–*average*–average plus standard deviation (–maximum) of length × (minimum–) average minus standard deviation–*average*–average plus standard deviation (–maximum) of width. Spore quotient (Q; length/width ratio) and its minimum–maximum values are also reported. The Qm (= average quotient) is given by the arithmetic mean of single spore quotients. The hilar appendix was excluded from the sporal measurements; sterigmata were excluded from basidia measurements. The dimensions of the basidia, cystidia and their Qs are expressed as the minimum-maximum values, followed by the average value. The color code of Ridgway (1912) was used, whereas the work of Kuyper (1986) was followed for the description of morphological traits. Studied collections have been deposited at CAG (Cagliari Herbarium, Italy) with the number CAG B/5.8.1 (holotype) and the herbarium of the University of Valencia (acronym VAL_Myco). Duplicates of the collections are found in the private herbaria of Alberto Mua (M, Quartu St. Elena, Italy), Massimo Sanna (MS, Cagliari, Italy), Andrea Rinaldi (ACR, Monserrato, Italy) and Stephen Mifsud (SM, Gozo, Malta).

Laboratory procedures and phylogenetic inference

Total DNA was extracted in the Alvalab laboratory (Oviedo, Spain) using a standard cetyltrimethylammonium bromide (CTAB) method (Murray & Thompson 1980), and the nuclear ribosomal internal transcribed spacer (nrITS), the 28S nuclear large ribosomal region (nrLSU) and the protein-encoding second largest subunit of RNA polymerase II (*rpb2*), were amplified and sequenced using the primer pairs ITS-1F/ITS-4B (White *et al*. 1990), LR0R/LR5 (Vilgalys & Hester 1990, Cubeta *et al*. 1991) and b6F/b7.1R (Matheny *et al*. 2020), respectively. Further details on laboratory procedures, including PCR conditions, electrophoresis and purification may be consulted in Alvarado *et al.* (2010,

2021). The nucleotide sequences obtained in this study were first compared to those available in GenBank using the BLASTn algorithm (Altschul *et al*. 1990) to check for PCR product contamination and to obtain a preliminary genus-level taxonomic circumscription of our specimens within the family *Inocybaceae*. Next, we assembled two nucleotide sequence datasets (nrITS and nrLSU) with sequences available in recent phylogenetic studies that focused on the genus *Pseudosperma* (Bandini & Oertel 2020, Bandini *et al*. 2022, Cervini *et al.* 2020, Jabeen & Khalid 2020, Larsson *et al*. 2009, Latha & Manimohan 2016, Latha *et al*. 2016, Mao *et al*. 2022, Matheny *et al*. 2009, Matheny & Kudzma 2019, Osmundson *et al*. 2013, Ryberg *et al*. 2008, Saba *et al*. 2020, Yan *et al*. 2022). The final nrITS and nrLSU datasets consisted of 51 and 32 sequences, respectively, including nrITS and nuLSU sequences of *Inocybe oblectabilis* (Britzelmayr 1890: 23) Saccardo in Saccardo (1895: 54) and *Nothocybe distincta* (K.P.D. Latha & Manimohan 2016: 43) Matheny & K.P.D. Latha in Matheny *et al*. (2020: 93) which were used to root phylogenetic trees. We did not assemble a *rpb2* sequence dataset because most selected specimens for the previous two markers lacked *rpb2* data in public sequence repositories.

MAFFT v. 7.308 (Katoh 2002, Katoh & Standley 2013) was used to generate a multiple sequence alignment independently for each marker with the FFT-NS-I x1000 algorithm and the 200PAM / k = 2 scoring matrix, and the following additional parameters: a gap open penalty of 1.5 and an offset value of 0.123. The resulting alignments were manually optimised in Geneious v. 9.0.2 to (a) replace gaps at the ends of shorter sequences with an IUPAC base representing any base ("N"), and (b) trim ends of longer sequences in the nrITS alignment that included part of the 18S–28S ribosomal subunits. The online version of RAxML-HPC2 v. 8.2.12 hosted at the CIPRES Science Gateway (Stamatakis 2006, Stamatakis *et al*. 2008, Miller *et al*. 2010) was used to estimate a multi-locus phylogeny under a Maximum Likelihood (ML) framework. Prior to concatenation of the two markers, and to test for topological incongruence among sequence datasets, we inferred ML trees independently for each locus with RAxML-HPC2 v. 8.2.12, using 1000 bootstrap pseudoreplicates, and assumed bootstrap values ≥ 70% as significant for conflicting relationships among the same set of taxa (Mason-Gamer & Kellogg 1996). Because no conflicts were detected, the RAxML analysis was conducted using the GTRGAMMA substitution model for the three delimited partitions (nrITS1+2, 5.8S, nrLSU) and 1000 rapid bootstrap pseudoreplicates were implemented to evaluate nodal support. Next, we inferred an additional phylogeny in a Bayesian context using MrBayes v. 3.2.6 (Ronquist *et al*. 2012). Optimal substitution models and partition schemes for the above-mentioned sequence data partitions were estimated with PartitionFinder v. 1.1.1 (Lanfear *et al*. 2012) considering a model with linked branch lengths and the Bayesian Information Criterion (BIC). This analysis favoured the GTR+Γ model for the nrITS1+2 partition, and the K80+I+Γ for the 5.8S and for the nrLSU. The analysis was then conducted with two parallel, simultaneous four-chain runs executed over 5×10^7 generations starting with a random tree, and sampling after every 500th step. The first 25% of data were discarded as burn-in, and the 50% majority-rule consensus tree and corresponding posterior probabilities were calculated from the remaining trees. Average standard deviation of split frequencies (ASDSF) values below 0.005 and potential scale reduction factor (PSRF) values approaching 1.00 were considered as indicators of chain convergence. Tree nodes showing bootstrap support (BP) values equal or higher than 70% (RAxML analysis) and Bayesian posterior probabilities (PP) equal or higher than 0.95 (MrBayes analysis) were regarded as significantly supported. Phylogenetic trees were visualised in FigTree v. 1.4 (Rambaut 2012) and Adobe Illustrator CS5 was used for artwork.

Results

Molecular sequence datasets

Four nrITS and two nrLSU sequences were generated *de novo* from the Sardinian and Valencian collections (Table 1). The final nrITS alignment of 51 sequences was 782 bp long; 444 positions were variable and 136 were singleton sites. The nrLSU alignment comprised 32 sequences and was 1408 bp in length; the number of variable and singleton sites were 218 and 98, respectively. Last, the concatenated multi-locus (nrITS1+2, 5.8S and nrLSU) dataset used for inferring ML and Bayesian phylogenies, which consisted of 51 specimens, had a total number of 2190 bp, including 662 variable and 234 singleton sites.

TABLE 1. Specimens included in phylogenetic analyses. Data about collections (country, type specimens and/or herbarium no.) as well as GenBank accession numbers for nrITS and nrLSU loci are provided. "n/a" indicates the lack of data in public sequence databases. Sequences in bold have been obtained during this study.

Species	Voucher/Strain	Country	GenBank nrITS Accession Number	GenBank nrLSU Accession Number
Nothocybe distincta	CAL 1310 type	INDIA	NR_173156	NG_057278
Inocybe oblectabilis	JV13699	ITALY	FJ904165	FJ904165
Pseudosperma amabile	DB8-9-12-2b holotype	GERMANY	MW010031	n/a
Pseudosperma amoris	SMNS-STU-F-0901462 holotype	GERMANY	MW010038	n/a
Pseudosperma arenicola	EL238_06	FRANCE	FJ904133	FJ904133
Pseudosperma aestivum	UTC:BK18089706 holotype	USA	EU600847	n/a
Pseudosperma aureocitrinum	DB21-11-12-Esteve-Raventós isotype	SPAIN	MW010047	n/a
Pseudosperma bulbosissimum 4	EL37_06	SWEDEN	FJ904161	FJ904161
Pseudosperma bulbosissimum 2	EL30_06	SWEDEN	FJ904158	FJ904158
Pseudosperma bulbosissimum 1	EL6605	NORWAY	AM882765	AM882765
Pseudosperma bulbosissimum 3	EL75_07	SWEDEN	FJ904160	FJ904160
***Pseudosperma calciphilum* 1**	CAG B/5.8.1 holotype	ITALY	ON799406	OQ341419
***Pseudosperma calciphilum* 2**	CAG 5/3.63	ITALY	ON799411	OQ341322
***Pseudosperma calciphilum* 3**	IGB213 (VAL_Myco 1671)	SPAIN	OQ341418	n/a
***Pseudosperma calciphilum* 4**	IGB166 (VAL_Myco 1672)	SPAIN	OQ341420	n/a
Pseudosperma citrinostipes	FHMU3150 holotype	CHINA	MT072898	n/a
Pseudosperma conviviale	AMB 18243 holotype	ITALY	MT095091	MT095115
Pseudosperma fascinosum	SMNS-STU-F-0901666 holotype	GERMANY	ON003426	ON003426
Pseudosperma flavellum	EL56_08	SWEDEN	FJ904131	FJ904131
Pseudosperma flavorimosum	LAH:35042 holotype	PAKISTAN	NR169927	n/a
Pseudosperma friabile	TENN:068384 holotype	USA	MH216095	n/a
Pseudosperma gilvum	BJTC FM 1941 (holotype)	CHINA	OM801910	n/a
Pseudosperma guttuliferum	21581	ITALY	JF908233	n/a
Pseudosperma huginii	STU:SMNS-STU-F-0901564 holotype	AUSTRIA	MW647628	MW647628
Pseudosperma keralense	K(M):191712 holotype	INDIA	NR160442	NG_064382.1
Pseudosperma mediterraneum	JV14920F	ITALY	JQ408748	n/a
Pseudosperma melleum	MCVE:30145 holotype	ITALY	NR_171959	MT095114
Pseudosperma melliolens 1	G00110921 holotype	FRANCE	MN901255	n/a
Pseudosperma melliolens 2	MCVE 30343	ITALY	MT095094	n/a
Pseudosperma minutulum	AMB 18919 holotype	ITALY	ON202637	ON202637
Pseudosperma napaeanum	SMNS-STU-F-0901463 holotype	GERMANY	MW010040	n/a
Pseudosperma neoumbrinellum	HMJAU:25742 holotype	CHINA	NR160608	n/a
Pseudosperma niveivelatum	UTC:BK27089718 holotype	USA	EU600831	EU600831
Pseudosperma obsoletum	EL1704	SWEDEN	AM882769	AM882769
Pseudosperma perlatum	EL7404	SWEDEN	AM882771	AM882771
Pseudosperma permelliolens	XC2000-20	FRANCE	ON129680	n/a
Pseudosperma ponderosum	MCVE:30144 holotype	ITALY	MT095092	MT095116

.....continued on the next page

TABLE 1. (Continued)

Species	Voucher/Strain	Country	GenBank nrITS Accession Number	GenBank nrLSU Accession Number
Pseudosperma rimosum 2	SJ04007	SWEDEN	AM882763	AM882763
Pseudosperma rimosum 3	PAM06112703	FRANCE	FJ904143	FJ904143
Pseudosperma rimosum 1	EL7505	SWEDEN	AM882762	AM882762
Pseudosperma salentinum	MCVE:30342 holotype	ITALY	NR171961	MT095117
Pseudosperma solare	STU:SMNS-STU-F-0901563 holotype	GERMANY	MW647627	MW647627
Pseudosperma sororium 1	TENN:062793	USA	JQ408780	JQ319704
Pseudosperma sororium 2	JV15200	SWEDEN	FJ904151	FJ904151
Pseudosperma spectrale	SMNS-STU-F-0901669 holotype	GERMANY	ON003429	ON003429
Pseudosperma spurium	STORDAL18318	NORWAY	FJ904139	FJ904139
Pseudosperma squamatum	TK96109	SWEDEN	AM882780	AM882780
Pseudosperma umbrinellum 1	F14488TypeS holotype	ITALY	HM209796	n/a
Pseudosperma umbrinellum 2	4375	ITALY	JF908116	n/a
Pseudosperma umbrinellum 3	JV13699	FINLAND	FJ904165	FJ904165
Pseudosperma ushae	SMNS-STU-F-0901677 holotype	GERMANY	ON003433	ON003433

Phylogenetic inference

The multi-locus phylogeny produced with RAxML had a lnL value of -11370.7549, whereas the MrBayes analysis reached an average standard deviation of split frequencies of 0.005 after 2.4×10^6 generations. Average Estimated Sample Sizes (EESs) were well above 200 in the Bayesian analysis. Because the obtained phylogenies showed no supported conflicts, the topology inferred under a Bayesian framework is presented in Figure 1. A well-delimited and highly supported (PP= 1; BP= 96%) clade in Figure 1 represented the new species described in the present work (see section Taxonomy below). The nrITS sequences of two Valencian collections were identical, whereas the two Sardinian collections segregated by three nucleotide substitutions and six indel positions. The nrITS sequence of the holotype from Sardinia (GenBank accession ON799406) separated from the Valencian specimens by three nucleotide substitutions and five indel positions. Furthermore, the phylogeny indicated that the clade representing the new species was close to several species which were grouped into a clade only supported by the Bayesian analysis (PP= 0.99; BP < 70%), such as *P. bulbosissimum* (Kühner 1988: 24) Matheny & Esteve-Raventós in Matheny *et al*. (2020: 110), *P. ponderosum* Cervini, Bizio & P. Alvarado (2020: 441), *P. minutulum* Cervini (2022: 1), *P. aureocitrinum* (Esteve-Raventós 2014: 378) Matheny & Esteve-Raventós in Matheny *et al*. (2020: 109) and *P. mediterraneum* (Kuyper 1986: 56) Bandini, B. Oertel & U. Eberhardt (2022: 43). The nrITS genetic distances of all these species from the new species' type specimen, considering the whole length of the nrITS region (782 bp), ranged between 2.2% in *P. bulbosissimum* to 3% or higher in the other taxa. Other *Pseudosperma* species close to the clade including the new species were *P. conviviale* Cervini, Bizio & P. Alvarado (2020: 441), *P. melleum* Cervini, Bizio & P. Alvarado (2020: 441), and a supported clade (PP= 1; BP= 92%) including the nrITS type sequences of *P. umbrinellum* (Bresadola 1905: 161) Matheny & Esteve-Raventós in Matheny *et al*. (2020: 114), *P. napaeanum* Bandini & B. Oertel (2020: 241) and *P. melliolens* (Kühner 1988: 22) Matheny & Esteve-Raventós in Matheny *et al*. (2020: 112). The distance of the nrITS sequence of the new species' type compared with the types of the latter three species ranged from 3 to 3.6%.

Finally, we also compared the nrITS sequence of the type specimen of the new species with several still not published sequences of *Pseudosperma rimosum* (Bulliard 1798: pl. 388) Matheny & Esteve-Raventós in Matheny *et al*. (2020: 113) [including "*Inocybe fastigiata"* (Schaeffer 1774: 13) Quélet in Quélet (1872: 180)] and the typus of "*Inocybe rimosa* f. *marginatobulbosa*" E. Ludwig (2017: 189), kindly shared with us by Prof. Dr. Fernando Esteve-Raventós (Universidad de Alcalá de Henares, Spain; herbarium codes AH49047, AH00628, AH30688; AH is the acronym of the herbarium of the Universidad de Alcalá de Henares). In this case, the comparisons showed nrITS genetic distances ranging from 4.3% to more than 6%.

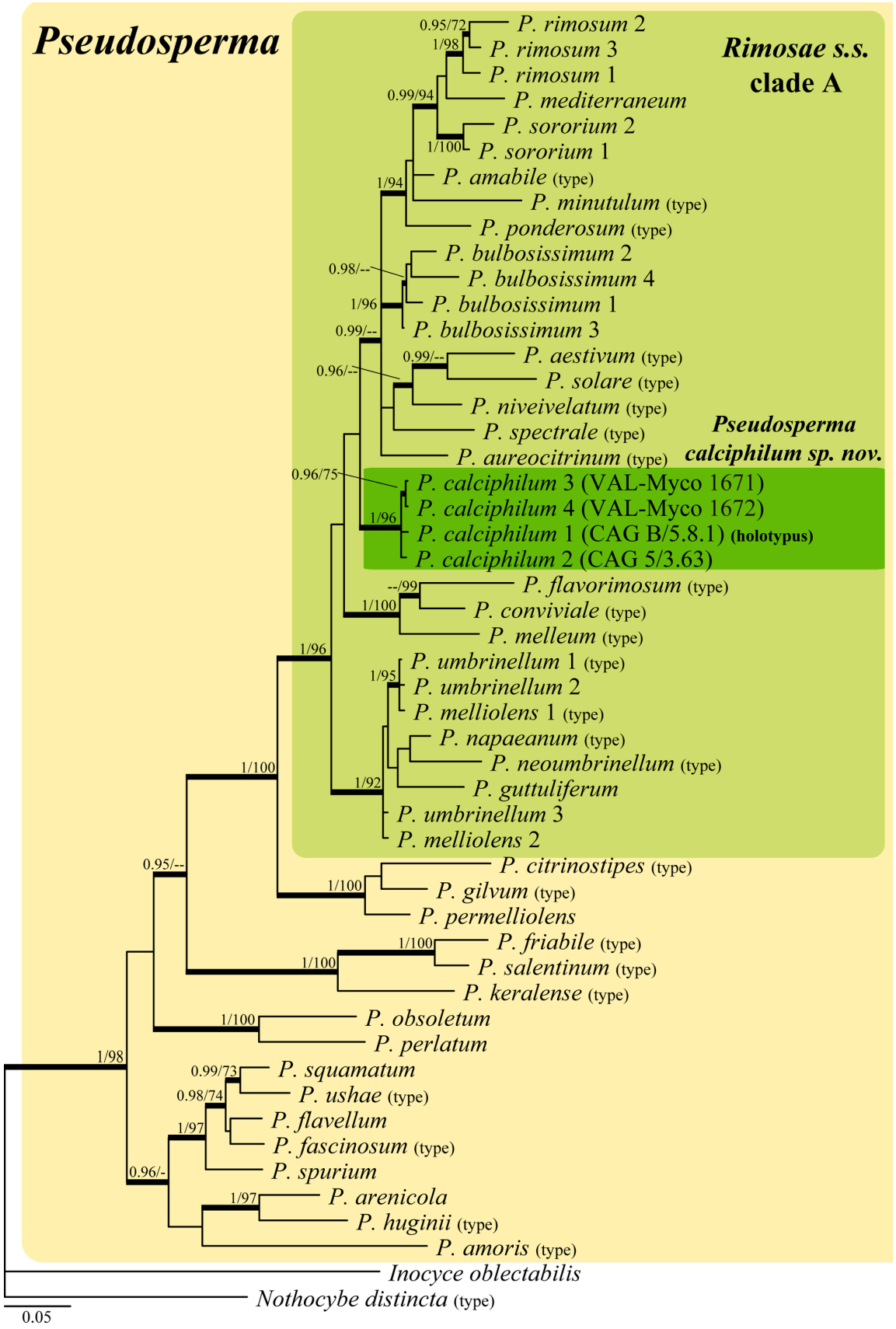

FIGURE 1. Phylogram depicting the evolutionary relationships of the new *Pseudosperma* species and its relatives. The represented topology was obtained under a Bayesian framework using MrBayes and nrITS and nrLSU sequence data. Posterior Probabilities (PP) and Bootstrap support (BP) values are represented on branches leading to nodes. *Inocybe oblectabilis* and *Nothocybe distincta* were used as outgroup taxa. The types are indicated were appropriate. The clade A of "*Rimosae sensu stricto*" as delimited by Larsson *et al.* (2009) is highlighted in a greenish box.

Taxonomy

Pseudosperma calciphilum Sanna, Mua, Porcu, Casula, Rinaldi, Mifsud & Garrido-Benavent, *sp. nov*. (Figures 2-3)
MycoBank MB 850154

Etymology:—The species epithet "calciphilum" refers to the apparently strict growth of this species on calcareous soils.

Diagnosis:—*Pseudosperma calciphilum* is macroscopically characterized by its medium to large basidiomata composed of yellow-amber, brown-ochre to brown pileus, with an obtuse umbo and with fibrillose-rimose margin surfaces that frequently show white velar remnants; lamellae at first white with a slight yellowish hue, then grayish-white and finally light brownish-olive with a white lamellar edge. Stipes enlarged at the base but not bulbous, with a pruinose-fibrillose surface, slightly scaled in the upper half. Context white and smell with mixed components: herbaceous-sourish, oily-honey, and slightly spermatic. Microscopically, it is characterized by the presence of ellipsoid to subphaseoliform spores with size (9–)10.76–*12.55*–14.34(–17.62) × (5.91–)6.7–*7.39*–8.09(–9.91) µm, Q= 1.29–2.17, Qm= 1.70, thin-walled cylindric-claviform to claviform cheilocystidia, some septate at the base and with size 26–*48.4*–71 × 10–*16*–23 µm, Q= 2.4–3.5, Qm= 3, and long catenate hairs with cheilocystidioid terminal elements mixed with caulocystidioid-like elements in the upper part of the stipes, with size 45–*78*–110 × 11–*16.9*–21 µm. Its nrITS region has more than 3% genetic distance from the nrITS type sequences of *P. umbrinellum* (GenBank nrITS accession number HM209796), *P. melleum* (NR_171959) and *P. conviviale* (MT095091).

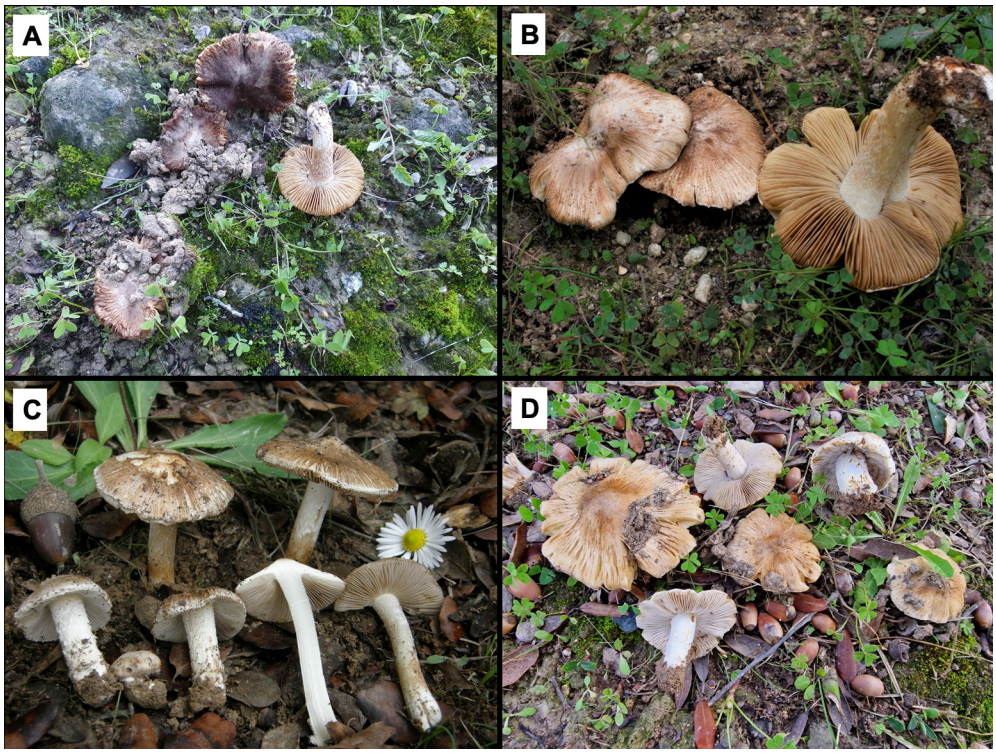

FIGURE 2. *Pseudosperma calciphilum*. Fresh basidiomata in the field. **a** Holotype-CAG B/5.8.1; **b** Coll. CAG 5/3.63; **c** Coll. VAL_Myco 1672; **d** Coll. n° 1569 MS. Photos: M. Sanna, A. Mua and I. Garrido-Benavent.

Holotype:—ITALY: Cagliari, Parco Colle San Michele, urban park with planted *Quercus ilex* subsp. *ilex*, on calcareous soil, 39º14'33.12" N, 9º06'30.94" E, 55 m above sea level, 6 December 2021, leg. *A. Mua* & *M. Sanna* (CAG! B/5.8.1). GenBank accession numbers: ON799406 (nrITS), OQ341419 (nrLSU) and OQ348110 (*rpb2*).

Description:—*Pileus* small to moderately large, 25–55 (80) mm in diameter, initially conical-convex, then convex up to flat-convex with a low, obtuse umbo; margin initially rounded, then straight, sometimes cracked; surface colour amber yellow (pl. XVI, 21', b – code Ridgway 1912), brown-ochre (pl. XV, 17' O–Y, i – code Ridgway 1912), brown (pl. XV, 17'O–Y, m – code Ridgway 1912), slightly darker at the center, smooth, fibrillose-rimose, splitting longitudinally near the edge, exposing the white flesh underneath; white velipellis present over the disc and the margin, here with a cortiniform appearance. *Lamellae* crowded, adnate-emarginated, L= (40–)50–90(–110), l=1(–3), at first

white with a slight yellowish hue, then grayish-white, pale grey and finally light brownish-olive (pl. XXX, 19'', k - code Ridgway 1912); lamellar edge white, fimbriate in places. *Stipes* 25–60 × 6–16 mm, cylindrical, enlarged towards the base but not bulbous, full; surface white, pruinose-fibrillose, with scales in the upper half; colour initially white with a yellowish tinge, then becoming beige-chamois (pl. XXX, 19'', b - code Ridgway 1912), paler near the apex. *Context* firm, white, slightly yellow at the upper part. *Smell* with mixed components: herbaceous-sourish, oily-honey, and slightly spermatic. *Basidiospores* (9–)10.76–*12.55*–14.34(–17.62) × (5.91–)6.7–*7.39*–8.09(–9.91) µm, Q= 1.29–2.17, Qm= 1.70 (n= 186), smooth, brown, ellipsoidal, also subphaseoliform in dorsiventral profile, ovoid in front profile, apex rounded, hilar appendices slightly pronounced, guttulate. *Basidia* 30.5–*37*–44 × 10–*12.5*–15 µm, claviform, tetrasporic, occasionally bisporic; sterigmata 3–5.5 µm long. *Cheilocystidia* 26–*48.4*–71 × 10–*16*–23 µm, Q= 2.4–3.5, Qm= 3, thin-walled, cylindrical-claviform, claviform, even pyriform, some subutriform, some septate at the base with one septum. Lamellar edge sterile. *Pleurocystidia* absent. At the upper third of the stipe there are long catenate hairs grouped in tufts and caulocystidioid hairs mixed with caulocystidia-like elements, 45–*78*–110 × 11–*16.9*–21 µm, Q= 3.3–6.5, Qm= 4.7. *Pileipellis* with cylindrical hyphae arranged in a cutis, sometimes slightly intermingled, 3–5 µm wide, slightly jellified, pigment brownish, encrusting, intracellular yellowish to brown-ochraceous pigment also present. *Stipitipellis* formed by cylindrical parallel hyphae, occasionally intermingled, 5–10 µm wide, with the presence of intracellular and encrusting brownish-yellowish pigment.

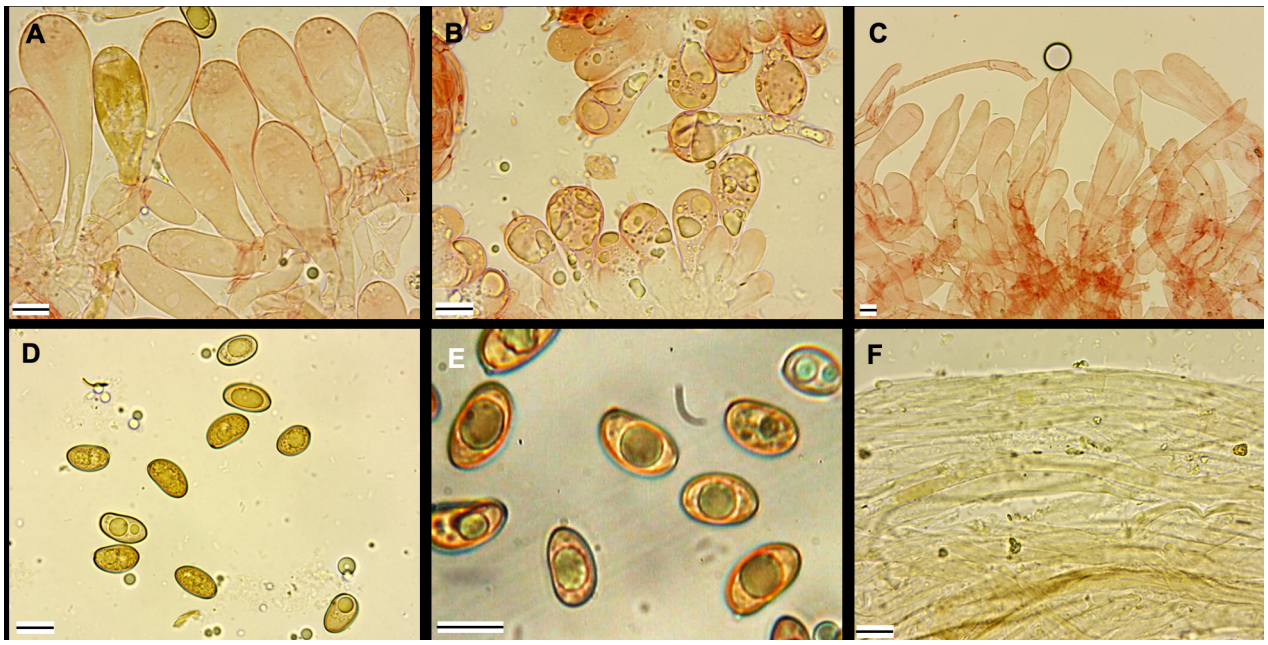

FIGURE 3. *Pseudosperma calciphilum* (all holotype except E, from IGB166). Micromorphological features. **A** Cheilocystidia 1000x; **b** Basidia 1000x; **c** Caulocystidioid hairs 400x; **d** Spores 1000x; **e** Spores 1000x; **f** Pileipellis 1000x. **a**–**c** in Congo Red; **d**, **f** in KOH; **e** in H_2O. Photos: G. Porcu and I. Garrido-Benavent. All bars = 10 µm.

Habitat and distribution:—Terrestrial, gregarious under *Quercus ilex* subsp. *ilex* and *Q. ilex* subsp. *rotundifolia*, in Mediterranean climate, on calcareous soil, in late autumn. At present it is known only from the islands of Sardinia (Italy) and Malta, and Valencia (eastern Iberian Peninsula, Spain). Interestingly, the Maltese locality was dominated by *Pinus halepensis* and *Pistacia lentiscus*. However, pollen records indicate that *Quercus* spp. were present throughout most of the Maltese landscape a few thousand years ago (Gambin *et al*. 2016).

Collections of Pseudosperma calciphilum examined:—ITALY: Cagliari, Parco Colle San Michele, urban park with planted *Quercus ilex* subsp. *ilex*, on calcareous soil, 39°14'33.12"N, 9°06'30.94"E, 55 m above sea level, 6 December 2021, leg. *A. Mua* and *M. Sanna* (CAG! B/5.8.1), holotypus; ITALY: Cagliari, Parco Colle San Michele, urban park with planted *Q. ilex* subsp. *ilex*, on calcareous (marly) soil, 39°14'33.67"N, 9°06'30.53"E, 55 m above sea level, 6 December 2021, leg. *A. Mua* and *M. Sanna* (CAG! 5/3.63), GenBank accession numbers: nrITS ON799411, nrLSU OQ341322, *rpb2* OQ348109; *ibidem*, 1 December 2022, leg. *A. Mua* and *M. Sanna* (n° 1569 MS); *ibidem*, 12 December 2022, 39°14'38.06"N, 9°06'46.50"E, 75 m above sea level, leg. *A. Rinaldi* (n° ACR-2022-66); SPAIN: Valencia, Quatretonda, Barranc de les Fontetes, Assut Nova, under *Q. ilex* subsp. *rotundifolia*, on calcareous (marly) soil, 38°55'53.73"N, 0°24'22.80"W, 200 m above sea level, 8 December 2011, leg. *I. Garrido-Benavent*, IGB213, VAL_Myco 1671, GenBank accession number: nrITS OQ341418; *ibidem*, under *Q. ilex* subsp. *rotundifolia* and *Pinus*

halepensis, on calcareous (marly) soil, 38°55'54.65"N, 0°24'22.97"W, 192 m above sea level, 4 November 2012, leg. *I. Garrido-Benavent*, IGB166, VAL_Myco 1672, GenBank accession number: nrITS OQ341420; MALTA: Siġġiewi, Verdala, five fruiting bodies in a maquis composed mainly of *Pinus halepensis* accompanied by a few *Pistacia lentiscus*, on calcareous soil, 35°51'38.16"N, 14°23'53.84"E, 180 m above sea level, 15 December 2022, leg. *S. Mifsud,* SM743, GenBank accession number: nrITS OR603126.

Discussion

The multi-locus phylogenetic analyses showed that the new Mediterranean species is placed within "*Inocybe*" section *Rimosae sensu stricto* clade A (Larsson *et al*. 2009). The main morphological features that characterize *Pseudosperma calciphilum*, whose basidiomata tend to fruit on calcareous soils in association with holm oaks, are the presence of white velar remnants on the pileus surface, the yellow amber to brown-ochre colour of pilei, the progressively widened stipes towards the non-bulbous bases, the pruinose-fibrillose stipe surfaces with scales in the upper half, and the herbaceous-acidulous to oily-honeyish smell with a slight spermatic component.

These traits of the new species resemble those of *P. conviviale* and *P. umbrinellum* (Cervini *et al.* 2020). The former species was originally described from Sardinia and does not show a velipellis on the pileus surface, which is more yellowish-ochraceous than that of the new species. Furthermore, stipes in *P. conviviale* are slenderer, 50–110 × 8–12 mm in size, and the smell is honey-like, reminiscent of that of *Inosperma cookei* (Bresadola 1892: 17) Matheny & Esteve-Raventós in Matheny *et al*. (2020: 102); it also shows smaller spores (11.7 × 7.2 µm on average) than the new species and cheilocystidia with dimensions 30–73 × 11–23 µm (Cervini *et al.* 2020). *Pseudosperma umbrinellum*, which might be conspecific to *P. melliolens* (see Cervini *et al*. 2020 for a detailed discussion), is a widely distributed species in Europe that produces dark to lurid gray pilei with a cinnamon dark center, whitish to argillaceous lamellae with white edges, and white stipes with a brownish sub-bulbous base, 30–50 × 4–6 mm in size, with a fibrillose-pruinose to furfuraceous or sub-floccose apices, and a white cortiniform veil. In addition, this species has a whitish, odorless flesh and, microscopically, the spores are different from those of the new species, because they are reniform, 10–14 × 5.5–6.5 µm in size, and the marginal cells are clavate to subfusiform, 40–65 ×10–16 µm in size. Furthermore, basidiomata of *P. umbrinellum* occur under *Populus nigra* (Bresadola 1905). According to the descriptions made by Kühner (1988) and Cervini *et al.* (2020) of *P. melliolens*, this species would have a slenderer habit than that of *P. calciphilum*, more bulbous stipe bases, lamellae stained with a yellow-brown tinge, persistent smell of honey, smaller basidia, 24–38 × 12–14 µm in size, slightly smaller spores, (9)9.9–12.2(13.5) × (6)6.3–7.2(8) µm in size, and mainly clavate and smaller cheilocystidia, 20–55 × 8–19 µm, [32–55 × 8–16 µm, on average 39 × 12 µm, Qm= 3.4 in Cervini *et al*. (2020)]. Despite the macro- and micromorphological similarities among *P. calciphilum*, *P. conviviale* and *P. umbrinellum*, nrITS sequence data clearly distinguish them, either considering genetic distances or at the phylogenetic level.

A further Mediterranean species is *Pseudosperma melleum* which produces pilei with ochraceous-orange tinges, slenderer stipes than *P. calciphilum*, up to 10 cm high, and a strong honey-like smell (Cervini *et al*. 2020); microscopically, it differs from the new species by its smaller spores (average 10.6 × 6 µm, Qm= 1.8) and cheilocystidia (31–54 × 10–17 µm, Qm= 42 × 13 µm). *Pseudosperma permelliolens* (Carteret & Reumaux 2015: 20) Matheny & Esteve-Raventós in Matheny *et al*. (2020: 113) has strong honeyed or virous-honeyed smell, spores on average longer and narrower than those of *P. calciphilum*, (11)11.5–15.5 (16) × 6–8 µm in size, with a Q= 1.8–1.9, cheilocystidia cylindrical or slightly utriform, longer on average than the new species, 25–75 (95) × (6)10–20(25) µm in size, and grows under broadleaved (*Fagus*, *Quercus* and *Betula*) and coniferous (*Picea*, *Larix* and *Pinus*) trees in temperate ecosystems (Carteret & Reumaux 2015). Another species from temperate ecosystems in Europe is the recently described *P. napaeanum*, which was originally described from Germany under *Pinus mugo*, *Dryas octopetala* and *Helianthemum nummularium* (Bandini & Oertel 2020). Compared to the new species, it has smaller pilei, 10–25 mm in size, yellow to yellow-ochre lamellae, smaller (sub)amygdaliform spores, on average 10.6 × 7.2 µm in size, with a Qm= 1.5, shorter basidia, 24–35 × 7–11 µm in size, smaller and often (sub)capitate cheilocystidia, 23–60 × 7–17 µm in size (average 37 ×10 µm), and often (sub)capitate or papillate caulocystidia (Bandini & Oertel 2020).

Pseudosperma guttuliferum (Kühner 1988: 19) Matheny & Esteve-Raventós in Matheny *et al*. (2020: 111) is another European species that grows in alpine areas in association with *Salix retusa* and *S. reticulata* (Kühner 1988), which is characterized by its olive-colored lamellae and odorless flesh, and it is further distinguished from the new species by its shorter cheilocystidia, on average (27)34–46(55) × (10)11–16(22) µm in size, as well as its slightly

shorter spores, (10)11.7–12.7(14.5) × 6.7–8.7 µm (Kühner 1988). In addition, stipes of *P. guttuliferum* may show a conspicuously bulbous base and cheilocystidia with yellow-refractive content in NH_4OH (Ferrari 2006). Finally, *P. flavorimosum* Jabeen & Khalid (2020: 187) is a species described from Pakistan that is distinguishable by the prominent pileus umbo, lamellae initially yellow-brown, then dark brown, stipe surfaces also dark brown, and by its spores (7.8–)9.5–12.8(–13.31) × (5.7–)6.3–7.8(–8.9) µm in size, Qm= 1.62; it produces smaller basidia, (14.8)26.4–31.2(36.7) × (10)10.5–10.8(11.8) µm and smaller cheilocystidia, (18.5)19.2–21.7(25.3) × (7.5)7.7–8.6(9.1) µm than *P. calciphilum*, and a non-encrusted trichoderm-like pileipellis (Jabeen & Khalid 2020).

Acknowledgments

The authors thank Prof. Dr. Fernando Esteve-Raventós (Universidad de Alcalá de Henares, Madrid, Spain) for his valuable suggestions and for sharing unpublished data, and Fermín Pancorbo (Madrid, Spain) for providing relevant bibliographic information.

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.
https://doi.org/10.1016/S0022-2836(05)80360-2

Alvarado, P., Manjón, J.L., Matheny, P.B. & Esteve-Raventós, F. (2010) *Tubariomyces*, a new genus of *Inocybaceae* from the Mediterranean region. *Mycologia* 102: 1389–1397.
https://doi.org/10.3852/10-041

Alvarado, P., Cabero, J., Moreno-Mateos, D., Vizzini, A., Alonso, J., Lebeuf, R., Siquier, J.L. & Vidal, J.M. (2021) Phylogenetic relationships among false truffle genera of *Paxillaceae—Alpova*, *Melanogaster*, *Neoalpova*, and *Paralpova*, gen. nov. *Mycologia* 113: 828–841.
https://doi.org/10.1080/00275514.2021.1911552

Bandini, D. & Oertel, B. (2020) Three new species of the genus *Pseudosperma* (*Inocybaceae*). *Czech Mycology* 72: 221–250.
https://doi.org/10.33585/cmy.72205.

Bandini, D., Oertel, B. & Eberhardt, U. (2021) Nochmehr Risspilze (2): Dreizehnneue Arten der Familie *Inocybaceae*. *Mycologia Bavarica* 21: 27–98.

Bandini, D., Oertel, B. & Eberhardt, U. (2022) Nochmehr Risspilze (3): Einundzwanzig neue Arten der Familie *Inocybaceae*. *Mycologia Bavarica* 22: 31–138.

Bau, T. & Fan, Y.G. (2018) Three new species of *Inocybe* sect. *Rimosae* from China. *Mycosystema* 37: 609–702.
https://doi.org/10.13346/j.mycosystema.180033

Bresadola, G. (1892) *Fungi Tridentini novi, vel nondum delineati, descripti, et iconibus illustrati*. II. J. Zippel, Trento, 384 pp.

Bresadola, G. (1905) Hymenomycetes novi velminus cogniti. *Annales Mycologici* 3: 159–164.

Bulliard, J.B.F. (1789) *Herbier de la France.* 9. Paris.

Carteret, X. & Reumaux, P. (2015) Miettes sur les inocybes (8^{e} série). Inocybes jaunes ou jaunâtres. *Bulletin de la Société Mycologique de France* 131: 1–96.

Britzelmayr, M. (1890) Hymenomyceten aus Südbayern. VI. Teil. *Bericht des Naturwissenschaftlichen Vereins für Schwaben und Neuburg (a.V.) in Augsburg* 30: 1–34.

Cervini, M. (2022) Nomenclatural novelties. *Index Fungorum* 520: 1–1.

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

Cubeta, M.A., Echandi, E., Abernethy, T. & Vilgalys, R. (1991) Characterization of anastomosis groups of binucleate *Rhizoctonia* species using restriction analysis of an amplified ribosomal RNA gene. *Phytopathology* 81: 1395–1400.
https://doi.10.1094/Phyto-81-1395

Esteve-Raventós, F. (2014) *Inocybe aureocitrina* (*Inocybaceae*), a new species of section *Rimosae* from Mediterranean evergreen oak forests. *Plant Biosystems* 148: 377–383.
https://doi.org/10.1080/11263504.2013.877532

Ferrari, E. (2006) *Inocybe alpine e subalpine. Fungi non delineati* 34–36. Edizioni Candusso, Alassio, 457 pp.

Gambin, B., Andrieu-Ponel, V., Médail, F., Marriner, N., Peyron, O., Montade, V., Gambin, T., Morhange, C., Belkacem, D. & Djamali, M. (2016) 7300 years of vegetation history and climate for NW Malta: a Holocene perspective. *Climate of the Past* 12: 273–297. https://doi.org/10.5194/cp-12-273-2016

Jabeen, S. & Khalid, A.N. (2020) *Pseudosperma flavorimosum* sp. nov. from Pakistan. *Mycotaxon* 135: 183–193. https://doi.org/10.5248/135.183

Fries, E.M. (1821) *Systema Mycologicum*. Lund, 520 pp.

Fries, E.M. (1863) *Monographia Hymenomycetum Sueciae*. C.A. Leffler, Uppsala, 355 pp.

Jacobsson, S. & Larsson, E. (2009) *Inocybe spuria*, a new species in section *Rimosae* from boreal coniferous forests. *Mycotaxon* 109: 201–207. https://doi.org/10.5248/109.201

Julich, W. (1981) Higher taxa of *Basidiomycetes*. *Bibliotheca Mycologica* 85: 1–485.

Katoh, K. (2002) MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* 30: 3059–3066. https://doi.org/10.1093/nar/gkf436

Katoh, K. & Standley, D.M. (2013) MAFFT: Iterative Refinement and additional methods. *Methods in Molecular Biology* 1079: 131–146. https://doi.org/10.1007/978-1-62703-646-7_8

Kuhner, R. (1980) Les *Hyménomycetès* agaricoides. *Bulletin Mensuel de la Société Linnéenne de Lyon* 49: 1–1027. https://doi.org/10.3406/linly.1980.10422

Kühner, R. (1988) Diagnoses de quelques nouveaux Inocybes récoltés en zone alpine de la Vanoise (Alpes françaises). *Documents Mycologiques* 19: 1–27.

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.

Lanfear, R., Calcott, B., Ho, S.Y.W. & Guindon, S. (2012) Partition Finder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* 29: 1695–1701. https://doi.org/10.1093/molbev/mss020

Larsson, E., Ryberg, M., Moreau, P.-A., Delcuse Mathiesen, Å. & Jacobsson, S. (2009) Taxonomy and evolutionary relationships within species of section *Rimosae* (*Inocybe*) based on ITS, LSU and mtSSU sequence data. *Persoonia* 23: 86–98. https://doi.org/10.3767/003158509X475913

Latha, K.P.D. & Manimohan, P. (2016) Five new species of *Inocybe* (Agaricales) from tropical India. *Mycologia* 108: 110–122. https://doi.org/10.3852/14-358

Latha, K.P.D. & Manimohan, P. (2017) *Inocybes of Kerala*. Spore Print Books, Calicut, 181 pp.

Latha, K.P.D. & Manimohan, P. & Matheny, P.B. (2016) A new species of *Inocybe* representing the Nothocybe lineage. *Phytotaxa* 267: 40–50. https://doi.org/10.11646/phytotaxa.267.1.4

Ludwig, E. (2017) *Pilzkompendium*, Band 3. Fungicon-Verlag, Berlin, 272 pp.

Mao, N., Xu, Y.-Y., Zhao, T.-Y., Lv, J.-C. & Fan, L. (2022) New species of *Mallocybe* and *Pseudosperma* from North China. *Journal of Fungi* 8: 256. https://doi.org/10.3390/jof8030256

Mason-Gamer, R.J. & Kellog, E.A. (1996) Testing for phylogenetic conflict among molecular data sets in the tribe *Triticeae* (*Gramineae*). *Systematic Biology* 45: 524–545. https://doi.org/10.1093/sysbio/45.4.524

Matheny, P.B. & Bougher, N.L. (2017) *Fungi of Australia*: *Inocybaceae*. ABRS-CSIRO Publishing, Canberra-Melbourne, 582 pp.

Matheny, P.B. & Kudzma, L.V. (2019) New species of *Inocybe* (Inocybaceae) from eastern North America. 1. *Journal of the Torrey Botanical Society* 146: 213–235. https://doi.org/10.3159/TORREY-D-18-00060.1

Matheny, P.B., Aime, M.C., Bougher, N.L., Buyck, B., Desjardin, D.E., Horak, E., Kropp, B.R., Lodge, D.J., Soytong, K., Trappe, J.M. & Hibbett, D.S. (2009) Out of the Palaeotropics? Historical biogeography and diversification of the cosmopolitan ectomycorrhizal mushroom family Inocybaceae. *Journal of Biogeography* 36: 577–592. https://doi.org/10.1111/j.1365-2699.2008.02055.x

Matheny, P.B., Hobbs, A.M. & Esteve-Raventós, F. (2020) Genera of *Inocybaceae*: New skin for the old ceremony. *Mycologia* 112: 83–120. https://doi.org/10.1080/00275514.2019.1668906

Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for Inference of Large Phylogenetic Trees.

Conference: Gateway Computing Environments Workshop (GCE). *2010 Gateway Computing Environments Workshop (GCE)*, pp. 1–8.

Murray, M.G. & Thompson, W.F. (1980) Rapid isolation of high molecular weight plant DNA. *Nucleic Acids Research* 8: 4321–4325. https://doi.10.1093/nar/8.19.4321

Osmundson, T.W., Robert, V.A., Schoch, C.L., Baker, L.J., Smith, A., Robich, G., Mizzan, L. & Garbelotto, M.M. (2013) Filling gaps in biodiversity knowledge for macrofungi: contributions and assessment of an herbarium collection DNA barcode sequencing project. *PLoS ONE* 8: e62419. https://doi.org/10.1371/journal.pone.0062419

Parmasto, E. & Parmasto, I. (1987) Variation in basidiospores in the *Hymenomycetes* and its significance to their taxonomy. *Bibliotheca Mycologica*, Band 115. J. Cramer, Berlin. 168 pp.

Quélet, L. (1872) Les Champignons du Jura et des Vosges. *Mémoires de la Société d'Émulation de Montbéliard* Ser. 2, 5: 43–332.

Quélet, L. (1888) *Flore mycologiquede la France et des payslimitrophes*. Octave Doin Éditeur, Paris: 492 pp.

Rambaut, A. (2012) *FigTree,* v1. 4.0. University of Oxford, Oxford, UK. [http://tree.bio.ed.ac.uk/software/figtree]

Ridgway, R. (1912) *Color standards and color nomenclature*. The Author, Washington D.C., 172 pp. https://doi.org/10.5962/bhl.title.144788

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. https://doi.org/10.1093/sysbio/sys029

Ryberg, M., Nilsson, R.H., Kristiansson, E., Topel, M., Jacobsson, S. & Larsson, E. (2008) Mining metadata from unidentified ITS sequences in GenBank: a case study in Inocybe (Basidiomycota). *BMC Evolutionary Biology* 8: 50. https://doi.org/10.1186/1471-2148-8-50

Saba, M., Haelewaters, D., Pfister, D.H. & Khalid, A.N. (2020) New species of *Pseudosperma* (Agaricales, *Inocybaceae*) from Pakistan revealed by morphology and multi-locus phylogenetic reconstruction. *MycoKeys* 69: 1–31. https://doi.org/10.3897/mycokeys.69.33563

Saccardo, P.A. (1895) Supplementum Universale, Pars III. *Sylloge Fungorum* 11: 1–753.

Shaeffer, J.C. (1774) *Fungorum qui in Bavaria et Palatinatu circa Ratisbonam nascuntur icones, nativis coloribus expressae*. 4. Zunckel, Ratisbonae.

Stamatakis, A. (2006) RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690. https://doi.org/10.1093/bioinformatics/btl446

Stamatakis, A., Hoover, P. & Rougemont, J. (2008) A fast bootstraping algorithm for the RAxML web-servers. *Systematic Biology* 57: 758–771. https://doi.org/10.1080/10635150802429642

Ullah, Z., Jabeen, S., Ahmad, H. & Khalid, A.N. (2018) *Inocybe pakistanensis*, a new species in section *Rimosae*s.str. from Pakistan. *Phytotaxa* 348: 279–288. https://doi.org/10.11646/phytotaxa.348.4.4

Vilgalys, R. & Hester, M. (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* 172: 4238–4246. https://doi.org/10.1128/jb.172.8.4238-4246.1990

White, T.J., Bruns, T., Lee, S. & Taylor, J. (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. *In:* Innis, M.A., Gelfand, D.H., Sninsky, J.J. & White, T.J. (Eds.) *PCR protocols: a guide to methods and applications*. Academic Press, New York, pp. 315–322. https://doi.org/10.1016/B978-0-12-372180-8.50042-1

Yan, Y.Y., Zhang, Y.Z., Vauras, J., Zhao, L.N., Fan, Y.G., Li, H.J. & Xu, F. (2022) *Pseudosperma arenarium* (*Inocybaceae*), a new poisonous species from Eurasia, based on morphological, ecological, molecular, and biochemical evidence. *MycoKeys* 92: 79–93. https://doi.org/10.3897/mycokeys.92.86277

Yu, W.J., Chang, C., Qin, L.W., Zeng, N.K., Wang, S.X. & Fan, Y.G. (2020) *Pseudosperma citrinostipes* (*Inocybaceae*), a new species associated with *Keteleeria* from southwestern China. *Phytotaxa* 450: 8–16. https://doi.org/10.11646/phytotaxa.450.1.2