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# *PSEUDOSPERMA EQUESTRE* SP. NOV. (*INOCYBACEAE*): A MEDITERRANEAN SPECIES ASSOCIATED WITH *QUERCUS ILEX* FROM SARDINIA

**Abstract**

*The new species Pseudosperma equestre from Sardinia, Italy, is described based on morphological characters and nrITS/nrLSU sequence data. It was collected in a Mediterranean habitat in association with Quercus ilex. The morphological and molecular differences between the newly described species and closely related taxa are also discussed. The study is accompanied by color photographs illustrating its macro- and micromorphological features of the species and a phylogenetic tree showing the phylogenetic placement between the new species and other species of the genus Pseudosperma.*

**Riassunto**

*La nuova specie Pseudosperma equestre proveniente dalla Sardegna, Italia, viene descritta sulla base di caratteri morfologici e dati di sequenze nrITS/nrLSU. La specie è stata raccolta in un habitat mediterraneo in associazione con Quercus ilex. Vengono inoltre discusse le differenze morfologiche e molecolari tra il nuovo taxon e le specie strettamente correlate. Lo studio è corredato da fotografie a colori che illustrano le caratteristiche macro- e micromorfologiche della specie e da un albero filogenetico che ne mostra la posizione all'interno del genere Pseudosperma.*

**Key words** *Agaricales*, Ectomycorrhizal fungi, *Inocybaceae*, Mediterranean fungi, nrITS, nrLSU, Taxonomy.

## Introduction

Recent phylogenetic studies demonstrated that the traditional concept of *Inocybe* (Fr.) Fr. was polyphyletic, leading to the recognition of several independent genera within *Inocybaceae* Jülich, including *Pseudosperma* Matheny & Esteve-Rav. and *Inosperma* (Kühner) Matheny & Esteve-Rav. (Larsson *et al*. 2009; Matheny 2009; Matheny *et al*. 2020).

*Pseudosperma* Matheny & Esteve-Rav. [= *Inocybe* Sect. *Rimosae* (Fr.) Quél. p.p.] is a genus which comprises overall a total of 133 among species and infraspecific levels worldwide, which can be found in different European ecosystems, according to what is reported on the website Index Fungorum [www.indexfungorum.org/names/names.asp (access carried out on 03 May 2026)]. This genus comprises ectomycorrhizal species with cheilocystidia derived from modified basidia, basidia hyaline and devoid of necropigments, by the absence of pleurocystidia, pileus fibrillose, often rimose, rarely squamulose, stipe with apex distinctly pruinose, furfuraceous or sometimes floccose, stipe base generally uniform, context not changing colour on rubbing, odour often spermatic, of green maize or honey, occasionally absent, spores from ellipsoidal to indistinctly phaseoliform (Matheny *et al*. 2020). Numerous new taxa of this genus have been described in recent years in Europe in the works of Jacobsson & Larsson (2009), Carteret & Remaux (2015), Cervini *et al*. (2020), Cervini (2022), Bandini & Oertel (2020), Bandini *et al*. (2021, 2022, 2023, 2024), Sanna *et al*. (2024, 2026), Dong *et al*. (2025), Kleine *et al*. (2025).

The mycorrhizal biology of the genus *Pseudosperma* is little known beyond those which have been the observations made in the field. However the wide range of habitats in which the species of this genus thrive, such as boreal forests of conifers and broadleaves, coastal dunes and riverbanks (Cervini *et al*. 2020; Bandini & Oertel 2020; Saba *et al*. 2020; Bandini *et al*. 2021, 2022;

Mao *et al*. 2022), suggests that they may establish ectomycorrhizal symbioses with a wide variety of host plants (Matheny *et al*. 2020). Some species of *Pseudosperma* seem to be specialised, that is engaged in symbiosis with a single host plant or a group of closely related plants (Bandini & Oertel 2020; Yu *et al*. 2020), but it is presumable that generalist species also exist. Furthermore, as observed by Bandini & Oertel (2020), the geographical distribution of most species is little known, leaving ample possibilities to explore the flexibility of this genus.

The rapid increase in newly described taxa within *Pseudosperma* highlights both the hidden diversity of the genus and the taxonomic challenges associated with species delimitation in morphologically similar groups. In this context, the integration of morphological and molecular data has become essential for the recognition and circumscription of species within the genus.

Extensive surveys conducted in different habitats of Sardinia resulted in the collection of several *Pseudosperma* specimens that could not be assigned to any currently known species based on morphological characters alone.

In this work, *Pseudosperma equestre* sp. nov. is described based on morphological and molecular evidence. Its phylogenetic placement within *Pseudosperma* is inferred using nrITS and nrLSU sequence data, and comparisons with morphologically and phylogenetically related species are provided.

## MATERIALS AND METHODS

### *Macroscopic and microscopic examination*

Macromorphological characters were studied from fresh material, whereas micromorphological analyses were performed on dried specimens (exsiccata). Microscopic preparations were examined using Optika B-383 PLi and Motic BA400 microscopes equipped with digital imaging systems.

Microscopic structures were mounted in 2% Congo red and 6% $NH_4OH$. Dried material was rehydrated in 5% KOH or distilled water prior to observation. The cuticle was observed both in water and in 2% anionic Congo red.

Spore measurements are the result of a number equal to or greater than 32 measurements obtained from spore deposit, according to what is recommended by Parmasto & Parmasto (1987); spore measurement was carried out on spores belonging to different specimens of the collection.

The data relating to basidiospores dimensions is expressed as (minimum-) mean minus standard deviation - mean– mean plus standard deviation (–maximum) of length × (minimum–) mean minus standard deviation – mean – mean plus standard deviation (–maximum) of width. Qm (= Mean Quotient) is given by the arithmetic mean of the quotients of the single spores; the quotient of a spore (Q) is the ratio length/width. From spore measurements the apiculus was excluded; from basidia measurements the sterigmata were excluded. The data relating to cystidia dimensions is expressed as (minimum-) mean minus standard deviation – mean plus standard deviation (–maximum); sometimes the value of the mean is also present, which is underlined. The dimensions of the basidia are expressed with the minimum and maximum values.

For the description of morphological characters the work of Kuyper (1986) was used, whereas the colour code of Ridgway (1912) was used for their definition.

The studied collections were deposited in the Herbaria of the Department of Life and Environmental Sciences, sect. Botany, of the University of Cagliari (CAG) in Italy. Duplicates specimens are preserved in the private herbaria of Alberto Mua (M, Quartu Sant'Elena, Italy) and Massimo Sanna (MS, Cagliari, Italy).

### *Laboratory procedures and phylogenetic inference*

Total DNA was extracted from dried material and sequenced by *Alvalab* (Oviedo, Spain) following standardized protocols based on CTAB extraction methodology (Murray & Thompson 1980). The nrITS and nrLSU regions were amplified and sequenced using standard

fungal primers (White *et al*. 1990; Vilgalys & Hester 1990). PCR products were visualized on 1% agarose gels, and chromatograms were manually checked and edited when necessary. Additional details regarding PCR conditions and purification procedures are available in Alvarado *et al*. (2010, 2021).

The newly generated sequences were initially compared against GenBank (National Center for Biotechnology Information -NCBI), using BLASTn (Altschul *et al*. 1990) to verify possible contamination and confirm their placement within *Inocybaceae*. Additional comparisons were performed using the UNITE database through PlutoF. Representative sequences from recent phylogenetic studies of *Pseudosperma* were selected from GenBank and UNITE for phylogenetic analyses.

The final nrITS and nrLSU datasets comprised 67 and 20 sequences, respectively, including sequence of *Inocybe oblectabilis* (Britzelm.) Sacc, the outgroup taxon.

Sequence alignments for nrITS and nrLSU were generated separately using the MUSCLE implemented in MEGA X (Edgar 2004; Kumar *et al*. 2018). Alignments were manually inspected, and poorly aligned regions and sequence overhangs were trimmed prior to phylogenetic analyses. The two datasets were concatenated using MESQUITE v. 4.02 (Maddison *et al*. 2025). Maximum Likelihood (ML) analyses were performed using RAxMLGUI 2.0 (Stamatakis 2006; Edler *et al*. 2020) under the GTR+GAMMA substitution model, with two partitions (nrITS1+5.8S+nrITS2 and nrLSU). Nodal support was assessed through 1000 rapid bootstrap replicates.

Bayesian Inference (BI) analyses were performed in MrBayes v. 3.2.7 (Ronquist *et al*. 2012) using the GTR+I+Γ model, with four Markov chains run for 10 million generations and sampling every 1000 generations. The first 25% of trees were discarded as burn-in. Nodes with ML bootstrap support (BS) ≥ 70% and Bayesian posterior probabilities (PP) ≥ 0.95 were considered significantly supported. Trees were visualized and edited using TreeGraph2 v. 2.15.0-887 (Stöver & Müller 2010). *Inocybe oblectabilis* JV32005 (GenBank ON754370) was selected as outgroup.

## RESULTS

### *Dataset of molecular sequences*

One nrITS sequence and one nrLSU sequence were newly generated from the Sardinian collection studied here (**Tab. 1**). The final nrITS and nrLSU alignments comprised 2326 bp and 1443 bp, respectively. The concatenated multi-locus dataset (nrITS1+5.8S+nrITS2, nrLSU) used for the inference of ML and Bayesian phylogenetic analyses, composed of 67 sequences, comparesed 3769 bp, including 770 variable sites of which 400 singleton sites.

### *Phylogenetic inference*

The multi-locus phylogeny produced with RAxML had a Final ML Optimization Likelihood (Final Log-Likelihood) value equal to −13874.920891, whereas the Bayesian analysis produced with MrBayes reached an Average Standard Deviation of Split Frequencies (avgstddev) of 0.005 after $3.76 \times 10^6$ generations: the final avgstddev value turned out to be 0.00257, meaning an excellent convergence between the chains. The estimated mean sizes of independent samples (Effective Sample Size - EES) were > 200 for all parameters, with actual values that were generally > 1000. Therefore, summarising, the convergence of the MCMC chains was evaluated by means of the Average Standard Deviation of Split Frequencies (< 0.01) and the Effective Sample Size, which turned out to be > 200 for all parameters, with values generally > 1000 thus demonstrating the reliability of the analysis carried out. Since the phylogenies obtained did not show supported conflicts, the topology inferred according to a Bayesian framework is presented in **Fig. 1**.

ML and Bayesian analyses produced congruent topologies without strongly supported conflicts. Convergence of the Bayesian analyses was confirmed by average standard deviation of

**Table 1**. List of the species included in the phylogenetic analysis. Collections are provided (species, herbarium number, country, GenBank number for the loci nrITS and nrLSU loci), n/d indicates the lack of data in public databases. The sequences in bold were obtained during this study.

| "Species" | "Orginal specimen identification" | Voucher/Strain | "Country" | "Genbank/ Unite (U) ITS Accession Number" | "Genbank/ Unite (U) LSU Accession Number" |
|---|---|---|---|---|---|
| *Inocybe oblectabilis* | *Inocybe oblectabilis* | "JV32005" | Italy | "ON754370 " | ON754370 |
| *Pseudosperma aestivum* | *Inocybe aestiva* | UTC:BK18089706 holotype | Usa | EU600847 | — |
| *Pseudosperma amabile* | *Pseudosperma* sp. BO-2020a | DB8-9-12-2b holotype | Germany | MW010031 | — |
| *Pseudosperma amabile* | *Pseudosperma* sp. BO-2020a | DB9-9-17-16 | Germany | MW010033 | — |
| *Pseudosperma arenarium* | *Pseudosperma* sp. | NXYC20201005_01 holotype | China | OM304278 | OM304287 |
| *Pseudosperma aureocitrinum* | *Pseudosperma aureocitrinum* | DB21-11-12-Esteve-Raventos isotype | Spain | MW010047 | — |
| *Pseudosperma bulbosissimum* | *Inocybe bulbosissima* | EL30_06 | Sweden | FJ904158 | — |
| *Pseudosperma bulbosissimum* | *Inocybe bulbosissima* | EL6605 | Norway | AM882765 | — |
| *Pseudosperma calciphilum* | *Pseudosperma calciphilum* | "CAG B/5.8.1 holotype" | "Italy" | ON799406 | "OQ341419" |
| *Pseudosperma calciphilum* | *Pseudosperma calciphilum* | "CAG 5/3.63 paratype" | Italy | "ON799411" | "OQ341322" |
| *Pseudosperma citrinostipes* | *Pseudosperma citrinostipes* | FHMU3150 holotype | China | MT072898 | — |
| *Pseudosperma californicum* | *Pseudosperma californicum* | NY:NY 814859 holotype | Usa | "OP162981" | — |
| *Pseudosperma coloniense* | *Pseudosperma coloniense* | "CAG B/5.8.3 holotype" | Italy | PX607989 | PX607990 |
| *Pseudosperma coloniense* | *Pseudosperma coloniense* | GP09M | Italy | PX607986 | PX607991 |
| *Pseudosperma coloniense* | *Inocybe fastigiata* | AH49047 | Spain | PZ019234 | — |
| *Pseudosperma coloniense* | *Inocybe rimosa* | AH00628 | Spain | PZ017929 | PZ017932 |
| *Pseudosperma conviviale* | *Pseudosperma conviviale* | AMB 18243 holotype | Italy | MT095091 | MT095115 |
| *Pseudosperma conviviale* | *Inocybe* sp. | TUF120558 | Estonia | UDB032063(U) | — |
| *Pseudosperma dominariense* | *Pseudosperma dominariense* | "CAG B/5.8.4 holotype" | Italy | PX607992 | PX607993 |
| *Pseudosperma dulcamaroides* | *Inocybe dulcamaroides* | EL112_06 | Sweden | FJ904126 | — |

| "Species" | "Orginal specimen identification" | Voucher/Strain | "Country" | "Genbank/ Unite (U) ITS Accession Number" | "Genbank/ Unite (U) LSU Accession Number" |
|---|---|---|---|---|---|
| ***Pseudosperma equestre* sp. nov.** | ***Pseudosperma equestre* sp. nov.** | **CAG B/5.8.6 holotype** | **Sardinia (Italy)** | **PZ500408** | **PZ500409** |
| *Pseudosperma flagellatum* | *Pseudosperma flagellatum* | "CAG B/5.8.5 holotype" | Italy | PX607994 | PX607995 |
| *Pseudosperma flavorimosum* | *Pseudosperma favorimosum* | LAH:35042 holotype | Pakistan | NR169927 | — |
| *Pseudosperma franchettii* | *Pseudosperma franchettii* | PERU-m_4473 holotype | Italy | PQ563302 | PQ563296 |
| *Pseudosperma gemellum* | *"Pseudosperma* sp. JMB-2022a" | "XC2002-81 isotype" | France | "ON129689 " | — |
| *Pseudosperma gilvum* | *"Pseudosperma* sp. NM-2022c" | BJTC FM 1941 holotype | China | OM801910 | — |
| *Pseudosperma guttuliferum* | *Pseudosperma guttiliferum* | 21581 | Italy | JF908233 | — |
| *Pseudosperma guttuliferum* | *Pseudosperma guttuliferum* | 373 | Italy | JF908100 | — |
| *Pseudosperma maggiorii* | *Pseudosperma* sp. MG-2022a | LUG 19804 holotype | Switzerland | ON212489 | — |
| *Pseudosperma mediterraneum* | *Pseudosperma mediterraneum* | L: L0054120 holotype | Italy | MZ700321 | — |
| *Pseudosperma mediterraneum* | *Inocybe arenicola var. mediterranea* | JV14920F | Italy | JQ408748 | — |
| *Pseudosperma melleum* | *Pseudosperma melleum* | MCVE: 30145 holotype | Italy | NR_171959 | MT095114 |
| *Pseudosperma melliolens* | *Inocybe melliolens* | G00110921 holotype | France | MN901255 | — |
| *Pseudosperma musilii* | *Pseudosperma musilii* | DB25-9-20-3b isotype | Sweden | OQ355040 | — |
| *Pseudosperma musilii* | *Inocybe rimosa* | EL12704 | Sweden | AM882768 | — |
| *Pseudosperma napaeanum* | *Pseudosperma* sp. BO-2020c | "SMNS-STU-F-0901463 holotype" | Germany | MW010040 | — |
| *Pseudosperma niveivelatum* | *Inocybe niveivelata* | UTC:BK27089718 holotype | Usa | EU600831 | — |
| *Pseudosperma niveivelatum* | *Inocybe niveivelata* | WTU:F5373 paratype | Usa | JQ408764 | — |
| *Pseudosperma obsoletum* | *Pseudosperma obsoletum* | Strain PBM2332 | Usa | JQ408766 | "JQ319697" |
| *Pseudosperma obsoletum* | *Inocybe obsoleta* | EL1704 | Sweden | AM882769 | — |
| *Pseudosperma ponderosum* | *Pseudosperma ponderosum* | MCVE:30144 holotype | Italy | MT095092 | MT095116 |

| "Species" | "Orginal specimen identification" | Voucher/Strain | "Country" | "Genbank/ Unite (U) ITS Accession Number" | "Genbank/ Unite (U) LSU Accession Number" |
|---|---|---|---|---|---|
| *Pseudosperma permelliolens* | *Pseudosperma permelliolens* | "XC2000-20 isotype" | France | "ON129680" | — |
| *Pseudosperma permelliolens* | *Pseudosperma permelliolens* | "XC2006-05" | France | "ON129682" | — |
| *Pseudosperma pinophilum* | *Inocybe* sp. MS-2018b | MSM 0047 holotype | Pakistan | MG742417 | MG742415 |
| *Pseudosperma rimosum* | *Inocybe rimosa* | PAM03110904 | France | FJ904144 | — |
| *Pseudosperma rimosum* | *Inocybe rimosa* | EL7505 | Sweden | "AM882762" | — |
| *Pseudosperma rimosum* | *Pseudosperma rimosum* | "STU:SMNS-STU-F-0901777 ITS variant a epitype" | Germany | "OQ324790" | — |
| *Pseudosperma rimosum* | *Pseudosperma rimosum* | "STU:SMNS-STU-F-0901777 ITS variant b epitype" | Germany | "OQ324791" | — |
| *"Pseudosperma schwetzingense"* | *Pseudosperma schwetzingense* | "SMNK:KR-M-0052968 holotype" | Germany | "PV487656" | "PV487787" |
| *Pseudosperma solare* | *Pseudosperma solare* | STU:SMNS-STU-F-0901563 holotype | Germany | MW647627 | — |
| *Pseudosperma spectrale* | *Pseudosperma spectrale* | SMNS-STU-F-0901669 holotype | Germany | ON003429 | — |
| *Pseudosperma subvolvatum* | *Pseudosperma* sp. CAG B/5.8.2 | " CAG B/5.8.2 holotype" | Italy | OR248647 | OR248673 |
| *Pseudosperma tiliae* | *Pseudosperma tiliae* | OKA-TR3501 holotype | Turkey | PP060399 | PP060414 |
| *Pseudosperma tiliae* | *Pseudosperma tiliae* | OKA-TR3502 | Turkey | PP060400 | — |
| *Pseudosperma umbrinellum* | *Inocybe umbrinella* | F14488TypeS holotype | "Submitted University Of Gothenburg-Sweden Collected In Italy" | HM209796 | — |
| *Pseudosperma umbrinellum* | *Pseudosperma umbrinellum* | 4375 | Italy | JF908116 | — |
| *Pseudosperma* sp. | *Pseudosperma* sp. | "mushroomobserver.org/482695" | USA | "ON866523" | — |
| *Pseudosperma* sp. | *Inocybe rimosa* | AH30688 | Spain | PZ017935 | — |

| "Species" | "Orginal specimen identification" | Voucher/Strain | "Country" | "Genbank/ Unite (U) ITS Accession Number" | "Genbank/ Unite (U) LSU Accession Number" |
|---|---|---|---|---|---|
| *Pseudosperma* sp. | *Pseudosperma* sp. | FYG9503 | China | PX745002 | — |
| *Pseudosperma* sp. | *Pseudosperma* sp. | FYG9501 | China | PX745001 | — |
| *Pseudosperma* sp. | *Pseudosperma* sp. | FYG10498 | China | PX745000 | — |
| *Pseudosperma* sp. | *Pseudosperma* sp. | FYG10525 | China | PX744997 | — |
| *Pseudosperma* sp. | *Pseudosperma* sp. | FYG10526 | China | PX744998 | — |
| *Pseudosperma* sp. | *Pseudosperma* sp. | FYG10496 | China | "PX744999" | — |
| *Pseudosperma* sp. | *Pseudosperma* sp. | BJTC FM1865 | China | OM756774 | OM756780 |
| *Pseudosperma* sp. | *Pseudosperma* sp. | FYG11166 | China | PX745169 | — |
| *Pseudosperma* sp. | *Pseudosperma* sp. | MO#616775 | Usa | PZ195449 | — |

split frequencies values < 0.01 and ESS values > 200 for all parameters. The Bayesian phylogeny is presented in **Figure 1**. *Pseudosperma equestre* formed a distinct lineage within the *P. aestivum-P. solare* complex, supported by high Bayesian posterior probability and moderate ML bootstrap support (PP = 0.99; BS = 71). The species was phylogenetically differentiated from *P. solare* and several unnamed *Pseudosperma* collections from China. The broader *P. aestivum-solare-equestre* complex was recovered as a coherent clade (PP = 0.99; BS = 87). The nrITS genetic distance of *P. equestre* with that of the closest species deposited in the NCBI dataset falls within the range 4.2-3.3%.

## TAXONOMY

***Pseudosperma equestre*** M. Sanna, A. Mua, M. Melis, M. Casula, A.N.M. Furtado & A.C. Rinaldi sp. nov.

MykoBank number: MB# 864016

**Original diagnosis**

*Pseudosperma equestre is characterized by a medium-small pileus from campanulate to plane-convex with low obtuse umbo and an white-pale yellow to pale yellow cuticle, darker at the disc, with a surface breaking into fibrils and presence of whitish velar remnants. The stipe, whitish at first and later becoming light ochre, is not bulbous and shows pruinosity only at the apex. The spores are smooth, broadly ellipsoidal, occasionally (sub)phaseoliform, measuring (10) 10.8 -11.6-12.3 (14.1) × (5.2) 6.6-7.1-7.6 (8.5) µm. The cheilocystidia are thin-walled, (sub)cylindrical, claviform, measuring (24) 30-37-43 (52) × (7) 8-10-11 (12) µm. Thin-walled from(sub)cylindrical to claviform caulocystidia are present at the stipe apex. Phylogenetically, the species belongs to the P. aestivum–P. solare complex but differs from P. solare and P. aestivum by its morphology, ecology, and nrITS/nrLSU sequence data.*

**Holotype** Italy, Sardinia, Laconi (OR), Loc. *Su Dominariu*, under *Quercus ilex* L., 20 October 2022, *leg.* A. Mua, M. Casula, M. Sanna & S. Costantini, herbarium CAG B/5.8.6 (holotype), GenBank: ITS (PZ500408), LSU (PZ500409).

**Etymology** The epithet refers to the "*Su Dominariu*" racecourse near the type locality.

**Macroscopic characters**

**Pileus** 3-4.6 cm, initially campanulate, then convex finally plane-convex provided with low obtuse umbo, cuticle of white-pale yellow colour (Pl. IV, 23, Y, f - Code Ridgway 1912), pale yellow (Pl. IV, 19, YO-Y, f - Code Ridgway 1912), darker at the disc, brown (Pl. XXIX, 15'', Y-O, k -

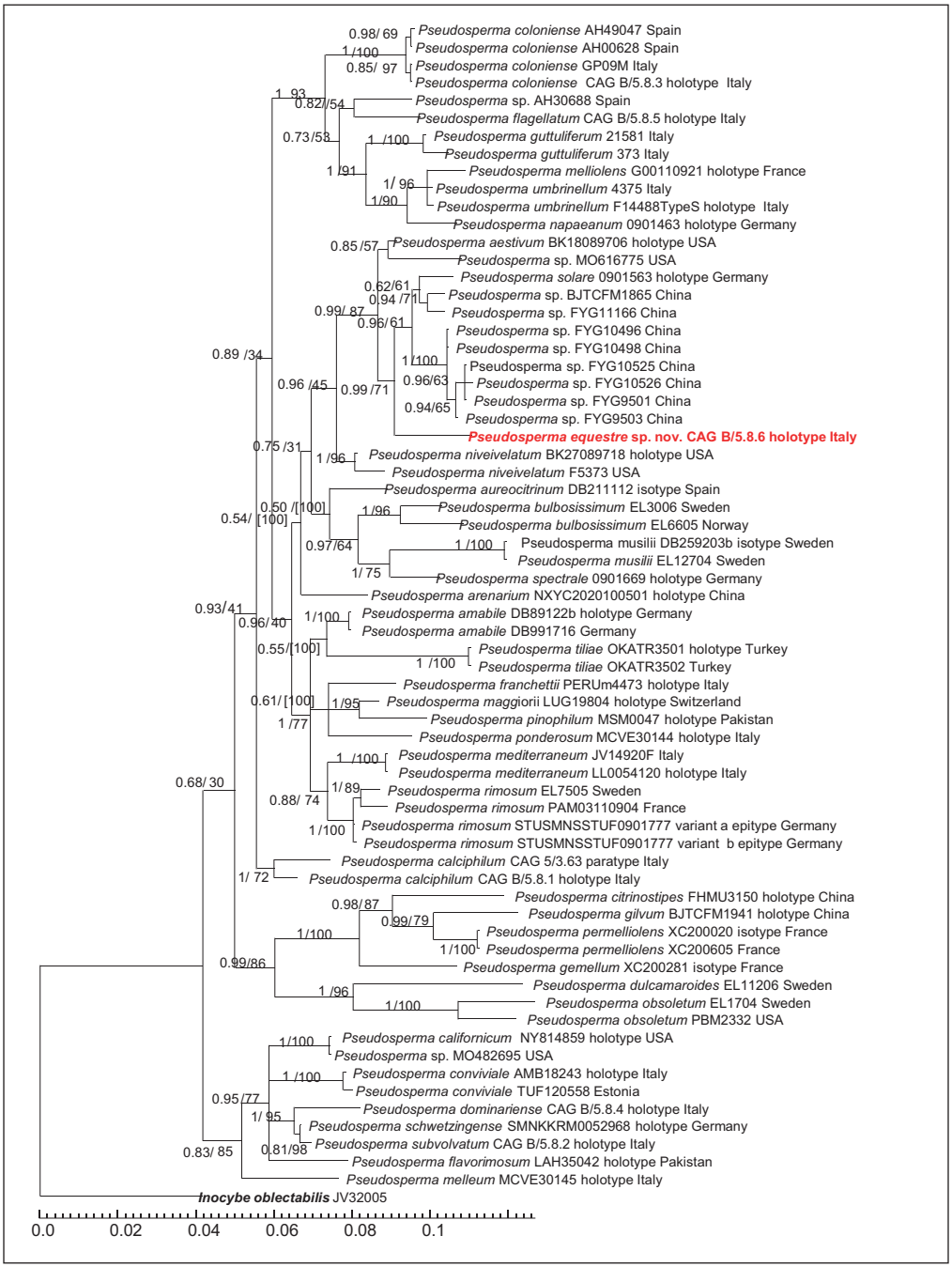



**Figure 1**. Phylogenetic tree. Bayesian phylogeny inferred from concatenated nrITS and nrLSU datasets showing the position of Pseudosperma equestre within *Pseudosperma*. Bayesian posterior probabilities (PP) and ML bootstrap support values (BS) are indicated at the nodes. *Inocybe oblectabilis* JV32005 was used as outgroup. Voucher numbers are indicated after species names. Newly generated sequences are shown in bold.

Code Ridgway 1912), or brown-ochre (Pl. XXX, 19'', YO-Y, k - Code Ridgway 1912), surface initially compact then broken into fibrils especially on the periphery, with ephemeral whitish velar remnants. Margin initially involute then plane.

**Lamellae** rather crowded, emarginate or adnate, initially whitish then whitish-greyish (Pl. LI, 23'', f - Code Ridgway 1912), then grey-ochre (Pl. XLVI, 21'', O-YY, b - Code Ridgway 1912) finally brownish (Pl. XXX, 19'', YO-Y, k - Code Ridgway 1912) without olive shade, with not numerous lamellulae; edge eroded, white.

**Stipe** 3.5-5.5 × 0.4-0.9 cm, cylindrical, slightly enlarged at the base, not bulbous, surface of whitish colour then light ochre (Pl. XXX, 23'',Y, I - Code Ridgway 1912), slightly fibrillose along its length, but pruinose in the apical part.

**Context** fibrous, whitish. Odour slightly spermatic. Taste acidulous.

**Microscopic characters**

**Spores** smooth, brown, from ellipsoidal to broadly ellipsoidal, also (sub)phaseoliform, with obtuse apex and central guttule or 2-guttulate, (10) 10.8-11.6-12.3 (14.1) × (5.2) 6.6-7.1-7.6 (8.5) μm, Qm = 1.63, n = 100.

**Basidia** tetrasporic, rarely bisporic, 32-42 × 11-14 μm, claviform, provided with basal clamp connections.

**Cheilocystidia** thin-walled, (sub)cylindrical, claviform, with rounded, rarely capitate apex, some of them provided with 1 septum, (24) 30-37-43 (52) × (7) 8-10-11 (12) μm, with some pyriform elements 8-9 μm wide.

**Pleurocystidia** absent.

**Caulocystidia** thin-walled, (sub)cylindrical, (sub)claviform or claviform, with rounded, rarely capitate or papillate apex, (36) 43-52-62 (72) × (8) 9-11-13 (15) μm, only present at the stipe apex; presence of septate piliform elements, 5-11 μm wide, with rounded terminal element.

**Suprapellis** cutis formed by hyphae 4-8 μm wide provided with encrusting and parietal pigment of brown colour and presence of cytoplasmic pigment of yellow-brownish colour especially in the deeper layers.

**Clamp connections** present.

**Studied collections** Italy, Sardinia, Laconi (OR), Loc. *Su Dominariu*, under *Quercus ilex* L., in small groups, 20 October 2022, *leg.* A. Mua, M. Casula, M. Sanna & S. Costantini, herbarium CAG B/5.8.6 (holotype), isotype in private herbarium Sanna (1623MS), GenBank: ITS (PZ500408), LSU (PZ500409).

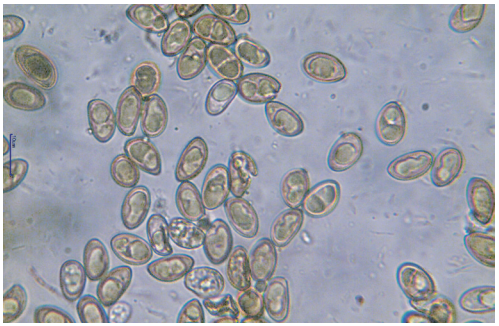
**Discussion**

*Pseudosperma equestre* is a small-medium sized species characterised macroscopically by the presence of ephemeral whitish velar remnants on the pileus, cuticle initially compact then broken into fibrils especially on the periphery, of yellowish colour, darker at the disc, with low obtuse umbo, stipe slightly enlarged at the base but not bulbous, grey-ochre-brownish lamellae without olive shade in adult specimens, and context with spermatic odour. Microscopically it is characterized by the presence of leiospores from ellipsoidal to (sub)phaseoliform, thin-walled cheilocystidia, with different morphologies, from (sub)cylindrical to claviform, some septate, caulocystidia present at the apex of the stipe, mostly (sub)clavate, growth under *Quercus ilex* L.

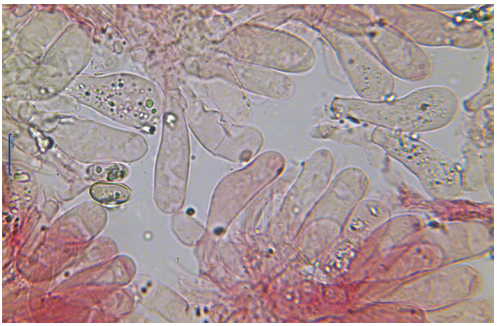
Phylogenetically *P. equestre* belongs to the *P. aestivum*–*P. solare* complex and appears closely related to *Pseudosperma solare* Bandini, B. Oertel & U. Eberh., and several unnamed *Pseudosperma* collections from China. BLASTn searches of the nrITS sequence showed the highest similarity (96.3%) with the holotype sequence of *Pseudosperma solare* (MW647627).



*Pseudosperma equestre* sp nov. 201022 Su Dominariu CAG B5.8.6 holotype. Photo by Alberto Mua



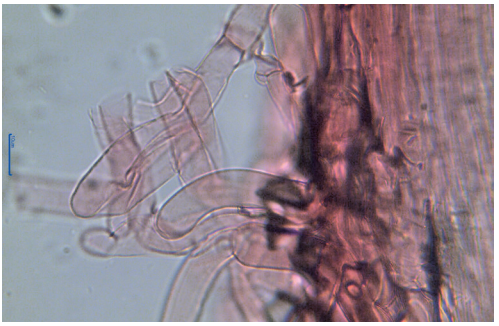
*P. equestre.* Spores 1000× in Congo red.
Photo by Massimo Sanna



*P. equestre.* Cheilocystidia 1000× in Congo red.
Photo by Massimo Sanna



*P. equestre.* Caulocystidia 1000× in Congo red.
Photo by Massimo Sanna



*P. equestre.* Caulocystidia 1000× in Congo red.
Photo by Massimo Sanna

*Pseudosperma flavorimosum* Jabeen & Khalid, a Pakistani species, is distinguishable from *P. equestre* by the prominent umbo, lamellae initially yellow-brown then dark brown, stipe also dark-brown, smaller spores, (7.8) 9.5-12.8 (13.31) × (5.7) 6.3-7.8 (8.9) µm, smaller basidia, (14.8) 26.4-31.2 (36.7) × (10) 10.5-10.8 (11.8) µm, smaller cheilocystidia, (18.5) 19.2-21.7 (25.3) × (7.5) 7.7-8.6 (9.1) µm, and a non-encrusted trichodermal pileipellis (Jabeen & Khalid 2020).

*Pseudosperma schwetzingense* Kleine, F. Hampe & M. Scholler (= *Pseudosperma subvolvatum* M. Sanna, Mua, Porcu, M. Casula & A.C. Rinaldi) recently published, is a medium-sized species, with more compact cuticle, lamellae initially whitish-greyish then brown-olivaceous, longer stipe, with basal velar remnants forming a pseudo-volva, complex odour with herbaceous notes reminiscent of potato peel and rancid oil, and only slight spermatic note, slightly smaller spores, (9.5) 10.4-11.4-12.4 (15) × (5.5) 6.1-6.7-7.2 (8) µm, bigger cheilocystidia, (25.7) 32.8-38.2-42.7 (62.7) × (9.2) 11.6-16-19.6 (24.9) µm, slightly gelatinised cutis, growth under *Populus alba* L. and *Quercus* spp. (Kleine *et al*., 2025; Dong *et al*. 2025; Mua *et al.* 2025).

*Pseudosperma californicum* (Murrill) Beker & U. Eberh., a Californian species found under *Quercus* sp., recently recombined in *Pseudosperma* from *Hebeloma*, has spores that range from cylindrical to ellipsoidal, on average longer, 11-14 × 6-7.5 µm, sometimes with constrictions, and clavate cheilocystidia (Eberhardt *et al.* 2023).

*Pseudosperma umbrinellum* (Bres.) Matheny & Esteve-Rav. [= *P. melliolens* (Kühner) Matheny & Esteve-Rav. (2019)] has pileus dark or lurid grey and a cinnamon dark centre, gills from white to argillaceous with white edges, white stipe with a brownish (sub)bulbous base, 30-50 × 4-6 mm, fibrillose-pruinate with furfuraceous, (sub)floccose apex, cortiniform white veil, white flesh, reniform spores of 10-14 × 5.5-6.5 µm, cheilocystidia clavate or (sub)fusiform, 40-65 × 10-16 um, under *Populus nigra* L. (Bresadola 1905). In the descriptions made by Kühner (1988) and Cervini *et al.* (2020) as *P. melliolens*, the species is described as having a slenderer habit, bulbous stipe bases, gills stained with yellow-brown, persistent odour of honey, smaller basidia, 24-38 × 12-14 µm, slightly smaller spores, (9) 9.9-12.2 (13.5) × (6) 6.3-7.2 (8) µm, mainly clavate and wider cheilocystidia, 20-55 × 8-19 µm, [32-55 × 8-16 µm, on average 39 × 12 µm, Qm = 3,4 by Cervini *et al.* (2020)].

*Pseudosperma melleum* Cervini, Bizio & P. Alvarado, also a Mediterranean species, is characterized by an ochraceous-orange pileus, a more slender stipe up to 10 cm high, a distinctive strong honey-like odour, smaller spores (average 10.6 × 6 µm, Qm = 1.8), and bigger cheilocystidia (31-42-54 × 10-13-17 µm. (Cervini *et al.* 2020).

*Pseudosperma permelliolens* (Carteret & Reumaux) Matheny & Esteve-Rav. has white abundant veil, strong honeyed or virous honeyed smell, spores on average longer and narrower, (11) 11.5-15.5 (16) × 6-8 µm, Q = 1.8 -1.9, cheilocistydia cylindrical or slightly utriform, longer on average, 25-75 (95) × (6) 10-20 (25) µm, growing under *Fagus sylvatica* L., *Quercus* sp., *Picea abies* (L.) H. Karst., *Larix decidua* Mill., *Betula* sp., *Pinus* sp. (Carteret & Reumaux 2015).

*Pseudosperma rimosum* (Bull.) Matheny & Esteve-Rav. has a larger basidiomata, straw-yellow, tawny or ochre-brown pileus, brown gills with a distinct olive tone, whitish flesh, straw-coloured on the stipe with spermatic odour (at least when cut), smaller spores, on average, 9-10.8-13 × 5.4-6.7-7.7 µm, (sub)cylindrical, (sub)phaseoliform or (sub)amygdaliform; longer cheilocystidia, 28-47-70 × 9-12-18 µm, from (sub)cylindrical to (sub)claviform. (Bandini *et al.* 2024).

*Pseudosperma guttuliferum* (Kühner) Matheny & Esteve-Rav. is an alpine species distinguishable by lamellae with olivaceous tones, inodorous context, slightly larger cheilocystidia, (27) 34-46 (55) × (10) 11-16 (22) µm, guttulate in $NH_4OH$, slightly longer and wider spores, (10) 11.7-12.7 (14.5) × 6.7-8.7 µm, growth under *Salix retusa* L. and *Salix reticulata* L. (Kühner 1988); according to Ferrari (2006) the stipe of this species would be conspicuously bulbous and the cheilocystidia with refractive yellow content in $NH_4OH$.

*Pseudosperma napaeanum* Bandini & B. Oertel, recently published species found in Germany under *Pinus mugo* Turra, *Dryas octopetala* L., *Helianthemum nummularium* (L.) Mill., is characterized

by a smaller pileus, 1-2.5 cm, lamellae from yellow to yellow-ochre, spores on average slightly wider, 9.1-14.1 × 5.9-9.3 μm, on average 10.6 × 7.2 μm, Qm = 1.5, (sub)amygdaliform, slightly shorter basidia, 24-35 × 7-11 μm, often (sub)capitate cheilocystidia of slightly bigger dimensions, 23-60 × 7-17 μm, on average 37 × 10 μm, often (sub)capitate or papillate caulocystidia (Bandini & Oertel 2020).

*Pseudosperma ponderosum* Cervini, Bizio & P. Alvarado is recognisable by its stocky, massive shape, by its initially copper-brown and not yellowish colouring, as well as by a more abundant cortina, often woolly-floccose in young specimens, by the lamellae and cuticle which frequently tend to become yellow-spotted, complex odour, by the cylindrical-clavate cheilocystidia, relatively narrow and short (Cervini, Bizio & Alvarado 2020).

*Pseudosperma conviviale* Cervini, Bizio & P. Alvarado originally described from Sardinia does not show a velipellis on the pileus, which is yellowish-ochraceous, the stipe is slender 50-110 × 8-12 mm, and the odour is honey-like, reminiscent of that of *Inosperma cookei* (Bres.) Matheny & Esteve-Rav.; it also shows slightly bigger spores (11.7 × 7.2 μm on average) and bigger cheilocystidia with dimensions 30-73 × 11-23 μm (Cervini *et al.* 2020).

*Pseudosperma calciphilum* Sanna, Mua, Porcu, Casula, A.C. Rinaldi, Mifsud & Garrido-Ben, recently found in Sardinia, is characterized by a low umbo and evident velar remnants on the pileus, lamellae of beige colour in adult specimens, slightly more robust stipe, with beige-chamois shading and also spotted with rust-brown at the base, context with honeyed-oily odour with herbaceous and spermatic notes, longer and larger spores, (9) 10.76-12.55-14.34 (17.62) × (5.91) 6.7-7.39-8.09 (9.91) μm with Qm = 1.70, basidia, 30.5-44 × 10-15 μm, bigger cheilocystidia, 26-71 × 10-23 μm, on average 48.4 × 16 μm, of cylindro-claviform, claviform but also pyriform shape, longer and wider caulocystidia, 45-78-110 × 11-16.9-21 μm, present also in the median third, slightly gelatinised pileipellis (Sanna *et al.* 2024; Mua *et al.* 2025).

*Pseudosperma solare* Bandini, B. Oertel & U. Eberh. is characterized by an intensely yellow pileus, smaller spores, catenulated and narrower caulocystidia, and occurs under coniferous trees, like *Picea abies* (L.) H. Karst. and *Pinus sylvestris* L. (Bandini *et al.* 2021).

*Pseudosperma aestivum* (Kropp, Matheny & Hutchison) Matheny & Esteve-Rav., a species recorded from North American coniferous forests, has a yellowish to pale yellow cap at the margin and yellow-brown, also with coppery shades at the centre, whitish to yellowish gills when young then yellow-olive, stem whitish, spermatic odour, narrower spores (11.2 × 6.2 μm on average) and shorter basidia (28-34 × 10-12 μm) (Kropp *et al.* 2013).

*Pseudosperma flagellatum* Sanna, Mua, Melis, Casula, A.N.M. Furtado & A.C. Rinaldi, recently described, has cuticle of brown, brown-yellowish colour, strongly rimose, ephemeral velar remnants on pileic margin, light ochre lamellae with slight olive shading in mature specimens, stipe initially whitish then of ochraceous colour, smaller spores, (7.4) 9.2-10.4-12.5 (13.7) × (5.4) 5.9-6.9-7.6 ( 8.4) μm, on average bigger cheilocystidia (22) 28-43-44 (47) × (7) 8.5-12-16 (17) μm, also (sub)ventricose or (sub)utriform, longer caulocystidia, (43) 45-61-86 (90) × (5) 6-8-11 μm, with presence of pyriform caulocystidioid elements (Sanna *et al.* 2026) (**Tab. 2**).

## CONCLUSIONS

The present study contributes to the growing knowledge of Mediterranean *Pseudosperma* diversity and highlights the importance of integrating morphological and molecular evidence in the delimitation of closely related taxa within *Inocybaceae* Jülich. Based on the currently available evidence, *Pseudosperma equestre* is interpreted as a distinct species within the *P. aestivum-P. solare* complex; although the species is currently represented by a single sequenced collection, the combination of morphological features and molecular differentiation supports its recognition as a distinct taxon within of the same complex Additional collections and multilocus datasets will be important to further clarify species boundaries within this complex.

**Table 2**. Comparative diagnostic table of species related

| Species | Pileus | Lamellae colour | Odour | Spores | Cheilocystidia |
|---|---|---|---|---|---|
| *Pseudosperma equestre* sp. nov. | Whitish–pale yellow, yellow, darker brown to brown-ochre disc | Whitish –> greyish –> grey-ochre –> brownish, without olive shades | Slightly spermatic | (10) 10.6-12.4 (14.1) × (5.2) 6.6-7.8 (8.5) µm | (Sub)cylindrical to claviform, 26-51 × 7-12 µm |
| *P. flavorimosum* | Brownish, prominently umbonate | Initially yellow-brown then dark brown | — | (7.8) 9.5-12.8 (13.31) × (5.7) 6.3-7.8 (8.9) µm | Smaller, (18.5) 19.2-21.7 (25.3) × (7.5) 7.7-8.6 (9.1) µm |
| *P. schwetzingense (= P. subvolvatum)* | More compact cuticle | Whitish-greyish then brown-olivaceous | Herbaceous, potato peel, rancid oil, slightly spermatic | (9.5) 10.4-12.4 (15) × (5.5) 6.1-7.2 (8) µm | Larger, (25.7) 32.8-42.7 (62.7) × (9.2) 11.6-19.6 (24.9) µm |
| *P. californicum* | — | — | — | 11–14 × 6-7.5 µm | Clavate |
| *P. umbrinellum* | Dark/lurid grey with cinnamon-dark centre | White to argillaceous | Odourless | 10–14 × 5.5-6.5 µm | Clavate to (sub) fusiform, 40-65 × 10-16 µm |
| *P. melleum* | Ochraceous-orange | — | Strong honey-like | Avg. 10.6 × 6 µm | Larger, 31-54 × 10-17 µm |
| *P. permelliolens* | — | — | Strong honeyed or virous-honeyed | (11) 11.5-15.5 (16) × 6-8 µm | Cylindrical to slightly utriform, 25-75 × 10-20 µm |
| *P. rimosum* | Straw-yellow, tawny or ochre-brown | Brown with olive tones | Spermatic | 9-13 × 5.4-7.7 µm | Longer, 28-70 × 9-18 µm, (sub) cylindrical/ (sub)clavate |
| *P. guttuliferum* | — | With olivaceous tones | Inodorous | (10) 11.7-12.7 (14.5) × 6.7-8.7 µm | Larger, (27) 34-46 (55) × (10) 11-16 (22) µm |
| *P. napaeanum* | Small pileus, yellow to yellow-ochre | Yellow to yellow-ochre | — | 9.1-14.1 × 5.9-9.3 µm | Often (sub)capitate, 23-60 × 7-17 µm |
| *P. ponderosum* | Initially copper-brown | Yellow-spotted with age | Complex | — | Cylindrical-clavate, short and narrow |
| *P. conviviale* | Yellowish-ochraceous, without velipellis | — | Honey-like | Avg. 11.7 × 7.2 µm | 30-73 × 11-23 µm |
| *P. calciphilum* | Low umbo, evident velar remnants | Beige in adults | Honeyed-oily with herbaceous and spermatic notes | (9) 10.76-14.34 (17.62) × (5.91) 6.7-8.09 (9.91) µm | Wider, 26-71 × 10-23 µm |

| Species | Pileus | Lamellae colour | Odour | Spores | Cheilocystidia |
|---|---|---|---|---|---|
| *P. solare* | Intensely yellow | — | — | Smaller | — |
| *P. aestivum* | Pale yellow margin, yellow-brown centre with coppery shades | Whitish/ yellowish then yellow-olive | Spermatic | Avg. 11.2 × 6.2 µm | — |
| *P. flagellatum* | Brown to brown-yellowish, strongly rimose | Light ochre with slight olive shades | — | (7.4) 9.2-12.5 (13.7) × (5.4) 5.9-7.6 (8.4) µm | Larger, (22) 28-44 (47) × (7) 8.5-16 (17) µm |

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