Five new species of Pseudosperma (Inocybaceae, Agaricales) from Benin and Turkey based on morphological characteristics and phylogenetic evidence

Oğuzhan Kaygusuz

okaygusuz03@gmail.com

Goethe-Universität Frankfurt am Main: Goethe-Universitat Frankfurt am Main https://orcid.org/0000-0003-3455-2965

Ditte BANDINI

Panorama str 47, Wiesenbach

Adrian RÜHL

Goethe-Universität Frankfurt am Main: Goethe-Universitat Frankfurt am Main

Sepas SARAWI

Goethe-Universität Frankfurt am Main: Goethe-Universitat Frankfurt am Main

Nourou S. YOROU

Université de Parakou: Universite de Parakou

Meike PIEPENBRING

Goethe-Universität Frankfurt am Main: Goethe-Universitat Frankfurt am Main

Research Article

Keywords: Ectomycorrhizal fungi, Biodiversity, Agarics, Molecular systematics, Biogeography, Taxonomy

Posted Date: February 20th, 2024

DOI: https://doi.org/10.21203/rs.3.rs-3937122/v1

Version of Record: A version of this preprint was published at Mycological Progress on April 3rd, 2024.
See the published version at https://doi.org/10.1007/s11557-024-01964-2.

Abstract

Species of *Pseudosperma* (Inocybaceae) are widely distributed from temperate to tropical regions. In this study, we describe and illustrate five new species of *Pseudosperma*: *P. beninense*, *P. cremeo-ochraceum*, *P. squarrosofulvum*, *P. stramineum*, and *P. tiliae*, based on comprehensive analyses of morphological and molecular data derived from specimens collected in Benin (West Africa) and Turkey (Western Eurasia). These new species have been found in forests with *Isoberlinia* spp. and other ectomycorrhizal tree species in Benin and in association with *Tilia platyphyllos* in Turkey. The phylogenetic relationships of the new species were inferred through analyses of nuclear rDNA sequences, encompassing the internal transcribed spacer (ITS1-5.8S-ITS2) and 28S rDNA regions. Phylogenetic analyses revealed that *P. beninense*, *P. cremeo-ochraceum*, *P. squarrosofulvum*, and *P. stramineum* from Benin cluster with species from Australia, China, and India within a clade formed exclusively by species known from the palaeotropics and Australia, whereas *P. tiliae* from Turkey clustered with *P. mediterraneum* from Italy. Detailed descriptions are provided, supplemented by illustrations and line drawings of key micromorphological features. In addition, a comparative analysis with morphologically similar and phylogenetically closely related species is presented and discussed in detail.

Introduction

By a recent molecular investigation based on several independent genetic loci, seven genera were identified within the family Inocybaceae Jülich: *Auritella* Matheny & Bougher, *Inocybe* (Fr.) Fr., *Inosperma* (Kühner) Matheny & Esteve-Rav., *Mallocybe* (Kuyper) Matheny, Vizzini & Esteve-Rav., *Nothocybe* Matheny & K.P.D. Latha, *Pseudosperma* Matheny & Esteve-Rav., and *Tubariomyces* Esteve-Rav. & Matheny (Matheny et al. 2020). The newly established genus *Pseudosperma* was initially classified as *Inocybe* section *Rimosae* sensu stricto (= *Pseudosperma* clade) (Matheny 2005; Larsson et al. 2009) in the subgenus *Inosperma* (Kuyper 1986; Bon 1997).

Species of *Pseudosperma* are characterized by a rimose pileus, a furfuraceous or pruinose stipe, smooth, elliptical to indistinctly phaseoliform basidiospores, hyaline, non-necropigmented basidia, cylindrical to clavate cheilocystidia with thin walls, and absence of pleurocystidia (Bandini and Oertel 2020; Cervini et al. 2020; Matheny et al. 2020; Saba et al. 2020). *Pseudosperma* species form ectomycorrhizal symbioses with both angiosperm or gymnosperm trees and occur in a variety of habitats, including temperate forests dominated by spp. of *Betula*, *Cedrus*, *Picea*, *Pinus*, *Populus*, *Quercus*, and *Salix* (Kuyper 1986; Stangl 1989; Jacobsson 2008).

Currently 80 species of *Pseudosperma* are described worldwide (Bandini et al. 2022, 2023), including species recently introduced from Austria (Bandini et al. 2021), Australia (Matheny and Bougher 2017), China (Yu et al. 2020; Mao et al. 2022; Yan et al. 2022; Zhao et al. 2022), Germany (Bandini and Oertel 2020; Bandini et al. 2021, 2022, 2023), India (Latha et al. 2023), Italy (Cervini et al. 2020; Sanna et al. 2024), Pakistan (Jabeen and Khalid 2020; Saba et al. 2020; Jabeen et al. 2021; Naseer et al. 2023), Spain (Sanna et al. 2024), Sweden (Bandini et al. 2023) and Turkey (Kaygusuz et al. 2023). Despite this

progress, the diversity of *Pseudosperma* species, particularly in tropical regions such as West Africa, remains poorly explored and documented. In addition to this, there are numerous cryptic and semi-cryptic species waiting for discovery (Ryberg et al. 2008; Matheny and Bougher 2017; Yan et al. 2022).

West Africa is a region of species rich ecosystems with forests ranging among the 25 world hotspots that deserve top conservation priorities (Myers et al. 2000). The mycological exploration of West Africa, however, shows that the identified fungal species diversity in six countries in this region does not exceed 2% of the existing diversity (Piepenbring et al. 2020). For Benin, only 432 fungal species have been documented in (Piepenbring et al. 2020). To date, the only species of *Pseudosperma* reported from Benin is *Pseudosperma squamatum* (J.E. Lange) Matheny & Esteve-Rav., historically called *Inocybe squamata* J.E. Lange (Lange 1917; Boa 2004; Piepenbring et al. 2020). No further species of *Pseudosperma* has ever been cited for any African country according to the literature available to us.

This study aims to increase the knowledge of the species diversity of *Pseudosperma*, with particular emphasis on the description of four new species from Benin and one from Turkey. Thereby, we contribute to the knowledge of morphological diversity, ecology, biogeography, and phylogeny of these hidden fungal treasures of Western Eurasia and West Africa.

Materials and methods

Sampling and Morphological Studies

The specimens from Benin were collected during a mycological survey conducted from June to August 2022. In Turkey, samples were picked up during fieldwork in the Isparta Province in 2022 and 2023. The macroscopic characteristics were obtained from fresh specimens, field notes and photographs taken in situ. Standardized colour values were documented using the Munsell Soil Color Charts (Munsell 1975). Microscopic features were observed using 1% Congo red (w/v) or 5% potassium hydroxide (KOH) (w/v). All samples were analysed and photographed with a light microscope. A minimum of thirty basidiospores were measured for each collection. Q values (ratio of length to width of basidiospore) and average values (length and width of basidiospore or cystidia) are presented. SD is the abbreviation for the standard deviation of the length × width. The terminology of Vellinga (1988) is used for macro- and micro-characters. Index Fungorum (http://www.IndexFungorum.org) and the International Index of Plant Names (https://www.ipni.org) were used as sources for taxonomic names and nomenclature. The samples from Benin are deposited in the fungarium of the Staatliches Museum für Naturkunde Stuttgart (STU) or the mycological herbarium of the University of Parakou (UNIPAR). The Turkish specimens are stored in the fungarium of the Isparta University of Applied Sciences (ISUF).

Molecular Analyses

Genomic DNA was isolated from *Pseudosperma* specimens using the innuPREP Plant DNA Kit (Analytik Jena, Jena, Germany) and the Fungi/Yeast Genomic DNA Isolation Kit (Norgen Biotek Corp, Ontario, Canada). For amplification of nuclear rDNA internal transcribed spacer region ITS1-5.8S-ITS2 (ITS) the

primer pair ITS1F/ITS4 (White et al. 1990; Gardes and Bruns 1993), and for the nuclear 28S rDNA (LSU) the primer pair LR0R/LR5 (Vilgalys and Hester 1990; Rehner and Samuels 1994) were used. Polymerase chain reaction (PCR) procedures were performed according to the methods described by Kaygusuz et al. (2020). The PCR products were sequenced at Microsynth Seqlab (Göttingen, Germany) and the Sanger DNA sequencing service of Source Bioscience (Berlin, Germany), using the same primers. The obtained DNA sequences were aligned and analysed using ClustalX (Thompson et al. 1997) and MEGA X v.10.0.5 (Kumar et al. 2018) and subsequently submitted to GenBank.

A total of 18 DNA sequences (nine from the nrITS and nine from the nrLSU) from nine collections were newly generated. BLASTn searches were conducted in the NCBI GenBank. For phylogenetic analyses, sequences with high similarity (with maximum identities larger than 82%) to the new sequences were retrieved from GenBank (www.ncbi.nlm.nih.gov) and UNITE (https://unite.ut.ee/, Kõljalg et al. 2005) databases, along with sequences from recent publications (Ryberg et al. 2008; Larsson et al. 2009; Matheny 2009; Matheny et al. 2009; Vauras and Larsson 2011; Sjökvist et al. 2012; Kropp et al. 2013; Osmundson et al. 2013; Pradeep et al. 2016; Matheny and Bougher 2017; Tibpromma et al. 2017; Bau and Fan 2018; Li et al. 2018; Ullah et al. 2018; Matheny and Kudzma 2019; Matheny et al. 2020; Bandini and Oertel 2020; Cervini et al. 2020; Jabeen and Khalid 2020; Saba et al. 2020; Yu et al. 2020; Bandini et al. 2021, 2022, 2023; Mao et al. 2022; Zhao et al. 2022; Kaygusuz et al. 2023; Latha et al. 2023; Naseer et al. 2023). The nrITS and nrLSU rDNA sequences were separately aligned using MAFFT 7.11 (Katoh et al. 2019) applying the E-INS-i iterative method, followed by manual corrections in AliView V.1.28 (Larsson 2014). *Mallocybe agardhii* (N. Lund) Matheny & Esteve-Rav. (AB980912) and *M. picea* L. Fan & N. Mao (BJTC FM555) were designated as outgroups. Multiple sequence alignments were inspected using MEGA X 10.0.5 prior to subsequent analyses. A single combined dataset of nrITS-nrLSU rDNA sequences was assembled for phylogenetic analysis. The optimal evolutionary model for each segment was determined using MrModeltest 2.3 (Nylander 2004). Phylogenetic assessments employed both Maximum Likelihood (ML) and Bayesian Inference (BI) approaches on the concatenated genes. The ML analysis was conducted with IQ-TREE v.1.6.12 (Minh et al. 2020), using the Ultrafast Bootstrap (UFBoot) (Hoang et al. 2018) approach with five thousand bootstrap iterations. The BI analysis using the Markov Chain Monte Carlo (MCMC) method was conducted in MrBayes 3.2.5 (Ronquist et al. 2012) over 1×10^7 generations, sampling trees every thousand generations. Phylogenetic trees were visualized using FigTree v1.4.4 (Rambaut 2018), with only Maximum Likelihood Bootstrap (MLB) values above 75% and Bayesian Posterior Probabilities (BPP) exceeding 0.90 being indicated.

Results

Phylogeny

The combined nrITS and nrLSU rDNA sequence dataset for *Pseudosperma* species, including 18 new sequences of the specimens from Benin and Turkey, consisted of 107 taxa with 2480 characters, of which 631 were parsimony-informative, 274 singleton sites, and 1575 constant sites. The best models in ML were TVM+F+I+G4 for nrITS and nrLSU rDNA, and GTR+I+G in the BI analysis. This matrix exhibited

1222 unique alignment patterns. The estimated nucleotide substitution rates were as follows: A-C = 1.06255, A-G = 5.05462, A-T = 1.63234, C-G = 0.42882, C-T = 5.05462, G-T = 1.00000. Base frequencies were determined as A = 0.263, C = 0.190, G = 0.247, T = 0.300. The gamma distribution shape parameter α was calculated to be 0.617. Phylogenetic trees derived from ML and BI analyses showed largely congruent topologies. The topology resulting from the ML analysis was selected for presentation, with statistical support values indicated by Maximum Likelihood Bootstrap (MLB) and Bayesian Posterior Probabilities (BPP) values (Fig. 1).

Molecular analyses based on the combined dataset revealed that *Pseudosperma* specimens from Benin and Turkey are genetically distinct from other species within the genus represented by molecular sequences data. Their sequences form part of five independent lineages, as shown in Fig. 1. The first lineage with high statistical support (MLB = 100%, BPP = 1.0) consists of three specimens of the new species called *Pseudosperma tiliae* together with *P. mediterraneum* (Kuyper) Bandini, B. Oertel & U. Eberh. from Italy in the same subclade. The second lineage (MLB = 99%, BPP = 1.0) consists of *Pseudosperma stramineum* andfive undescribed and unpublished sequences (HLA0707, HLA0386, 486ad3d1, 79c39691 and ASV_39) from Benin. The third lineage is formed by a single sequence labelled as *Pseudosperma squarrosofulvum* (AR-22-024) from Benin. The fourth lineage (MLB = 100%, BPP = 1.0) includes the new species *Pseudosperma beninense* (AR-22-037) from Benin and an undescribed and unpublished sequence from an uncultured fungus (ASV_330). *Pseudosperma beninense*, *P. squarrosofulvum*,and *P. stramineum* form a distinct, statistically highly supported clade of exclusively Beninese species (MLB = 100%, BPP = 1.0). The last lineage (MLB = 100%, BPP = 1.0) comprises the new species *Pseudosperma cremeo-ochraceum* (AR-22-088) and three undescribed and unpublished sequences (HLA0454, ASV_313, 881fdb9c) from Benin. The new sequences from Benin are located in a clade formed by a total of ten known species that all originate from the palaeotropics (and subtropics).The sequences of the recently collected *Pseudosperma* specimens consistently form distinct lineages in all phylogenetic analyses and can not be assigned to any existing *Pseudosperma* species concept by morphological characteristics. Therefore, we propose them as species new to science and provide detailed descriptions of these species in the following.

Figure 1 [near here]

Taxonomy

Pseudosperma beninense Kaygusuz, Bandini, Rühl, Sarawi, Yorou & M. Piepenbr., sp. nov. (Figs. 2 and 3)

MycoBank:MB 851970

Etymology: The specific epithet refers to the locality where the type specimen was collected.

Holotype:Benin, Borgou Department, Fôret Classée de l'Ouémé Supérieur, on soil in savannah forest dominated by *Isoberlinia doka* Craib & Stapf, *I. tomentosa* (Harms)Craib & Stapf, *Monotes kerstingii* Gilg and *Uapaca togoensis* Pax, at 09°15'37.9"N, 002°11'03.9"E, 340 m asl., 18 June 2022, leg. A. Rühl, C.

Manz, D. Dongnima, F. Hampe & S. Sarawi (AR-22-037, STU). GenBank accession numbers PP060393 (nrITS) and PP060408 (nrLSU).

Diagnosis: Differs from *P. squamatum* by smaller basidiomata with brown to straw-brown pileus, whitish to light yellow stipe, longer basidiospores (on average 12.5 × 7.0 µm) mostly with acute apex, longer (on av. 51 × 14 µm) and oblong to cylindrical or narrowly clavate cheilocystidia, and by distinct nrITS and nrLSU rDNA sequences.

Description: Pileus 7–14 mm diam., when young paraboloid, later hemispherical to convex, with or without low and broad umbo, margin inflexed when young, later long deflexed, surface dry, tomentose-lanose to subtomentose, radially fibrillose to rimulose outwards, colour light brown (2.5Y 8–7/6, 8/8) to straw brown (2.5Y 6/4–6), slightly darker at the centre (2.5Y 6/8). Lamellae moderately crowded, adnexed, subventricose, whitish to yellowish-white or light yellow, edge slightly eroded, whitish. Stipe 17–25 × 1.2–1.8 mm, central, cylindrical with subbulbous base up to 2.5 mm diam., solid, surface whitish to light yellow, pruinose only near the apex. Colour of exsiccate: pileus very light yellow to light straw yellow (5Y 8/2–4, 7/4), lamellae and stipe whitish. Smell unrecorded.

Basidiospores 10.7–14.7 µm (av. 12.5 µm, SD ± 0.4 µm) × 6.2–8.3 µm (av. 7.0 µm, SD ± 0.5 µm); Q = 1.4–2.1 (av. 1.8, SD ± 0.1) (n = 90 of 1 coll.), mainly (sub)amgydaliform with acute apex, also subcylindrical and subellipsoid, with guttules, smooth, thick-walled, dark yellowish brown in 5% KOH. Basidia 35–42 × 10–13 µm, clavate, 4-spored, thin-walled, hyaline. Cheilocystidia 37–65 µm (av. 51 µm, SD ± 7.0 µm) × 9–20 µm (av. 14 µm, SD ± 2.3 µm); Q = 2.4–5.8 (av. 4.2, SD ± 0.6) (n = 45 of 1 coll.), mostly oblong to cylindrical or narrowly clavate, sometimes with subcapitate apex, sometimes in chains of 1–3 cells, thin-walled, hyaline or very pale yellowish-brown in 5% KOH. Paracystidia 20–35 × 9–14 µm, cylindrical to broadly clavate, in chains of 2–4 cells, thin-walled, hyaline or very pale yellowish-brown in 5% KOH. Pileipellis cutis, consisting of long cylindrical or narrowly fusiform terminal cells, with sharply pointed apex, 60–170(220) × 11–25 µm, smooth, thin-walled, pale yellowish-brown in 5% KOH. Caulocystidia a cutis with transitions to a trichoderm composed predominantly of multiseptate cylindrical to inflated hyphae, 10–100 × 6.5–12 µm, sometimes with subcapitate apex, often in bundles, smooth, thin-walled, hyaline in 5% KOH. Stipitipellis a cutis of parallel hyphae, 5–18 µm wide, thin-walled, hyaline in 5% KOH. Clamp connections present in all parts examined.

Figure 2 [near here]

Habitat and distribution: Basidiomata solitary, terrestrial, on wet and sandy soils, growing in a forest dominated by species of Caesalpiniaceae (*Isoberlinia* spp.), Dipterocarpaceae (*Monotes kerstingii*), and Phyllanthaceae (*Uapaca togoensis*). Currently known only from Benin.

Additional specimen examined: Based on the phylogenetic analysis, one further specimen from West Africa (ASV_330) belongs to *Pseudosperma beninense*.

Figure 3 [near here]

Discussion: Phylogenetic analyses inferred from nrITS and nrLSU rDNA sequences show that *Pseudosperma beninense* forms a monophyletic subclade within *Pseudosperma* and is closely related to *P. squarrosofulvum* and *P. stramineum*, two other new species presented in this study. When the nrITS DNA sequences generated from *Pseudosperma beninense* are compared with the sequences of *P. squarrosofulvum* and *P. stramineum*, 56 nucleotide differences (83% similarity) were observed in the nrITS DNA sequences of *P. squarrosofulvum* and 52 differences (85% similarity) in the sequences of *P. stramineum*.

Morphologically, *Pseudosperma squarrosofulvum* differs from *P. beninense* by its pileus surface, which is covered by yellow ochre to brownish-yellow fibrillose scales, longer basidiospores (on av. 12.9 × 6.2 µm), somewhat shorter and narrower cheilocystidia(on av. 44 × 11 µm), mostly utriformparacystidia, pileipellis hyphae often with encrusted walls, and mostly cylindrical or narrowly clavate caulocystidia. *Pseudosperma stramineum* has a predominantly straw-yellow to buff pileus with a distinct squamulose-squarrose surface, pale brown lamellae when old, mostly oblong basidiospores, smaller cheilocystidia (on av. 40 × 14 µm), a pileipellis with strongly incrusted walls, and somewhat shorter caulocystidia (up to 90 µm in length).

Morphologically, the species closest to the new species*Pseudosperma beninense* is *P. squamatum*, which differs mainly by larger basidiomata, with a pileus measuring 30–70 mm in diameter, yellowish to yellow-ochraceous pileus, often with orange tinged, a longer stipe (up to 70 mm), shorter basidiospores (on av. 9.9 × 6.1 µm), shorter cheilocystidia (on av. 44 × 14 µm) that are subclavate to subglobose, and a habitat with a clay soil as well as an associated with *Populus* sp. (Lange 1917; pers. observation of D. Bandini). In addition, *P. beninense* is distant from *P. squamatum* following phylogenetic analyses (Fig. 1).

Other tropical or subtropical species that are morphologically somewhat similar to *Pseudosperma beninense* are *P. fissuratum* (Matheny & Bougher) Matheny & Esteve-Rav., *P. gracilissimum* (Matheny & Bougher) Matheny & Esteve-Rav., *P. palaeotropicum* (E. Turnbull & Watling) Matheny & Esteve-Rav. and *P. renisporum* (E. Horak) Matheny & Esteve-Rav. *Pseudosperma fissuratum*, originally described from Australia, differs from *P. beninense* by a typically bicoloured pileus, the presence of a velipellis, shorter basidiospores (on av. 11.4 × 6.2 µm), longer cheilocystidia (up to 72 µm in length), and ecologically by an association with *Eucalyptus* sp.(Matheny and Bougher 2017). Another Australian species, *Pseudosperma gracilissimum*, has a markedly conical pileus, slightly shorter basidiospores (on av. 9.9 × 5.9 µm), and is associated with *Acacia*, *Allocasuarina, Corymbia*, *Eucalyptus, Lophostemon*,and *Melaleuca* (Matheny and Bougher 2017). *Pseudosperma palaeotropicum*, initially discovered from Singapore and later reported from Australia and Malaysia, has larger basidiomata with a pileus measuring 20–40 mm in diameter, a longer stipe (40–70 × 4.0–6.0 µm), considerably shorter basidiospores (7.0–8.3 × 4.8–6.5 µm), and is typically associated with species of Dipterocarpaceae (Turnbull 1995). *Pseudosperma renisporum*, originally described from New Zealand, has a squamulose pileus centre, bean-shaped and shorter basidiospores (9.0–12.0 × 4.5–6.5 µm), and is associated with species of *Leptospermum* and *Nothofagus* (Horak 1978).

Pseudosperma cremeo-ochraceum Kaygusuz, Bandini, Rühl, Sarawi, Yorou & M. Piepenbr., sp. nov. (Figs. 4 and 5)

MycoBank: MB 851972

Etymology: The specific epithet refers to the cream to ochraceous colour of the surface of the pileus.

Holotype: Benin, Borgou Department, Fôret l'Ouémé Supérieur, on the soil in savannah forest dominated by *Isoberlinia doka*, *I. tomentosa*, *Monotes kerstingii* and *Uapaca togoensis*, at 08°36'04.7"N, 002°36'00.7"E, 340 m asl., 28 June 2022, leg. A. Rühl, C. Manz, D. Dongnima, F. Hampe & S. Sarawi (AR-22-088, STU). GenBank accession numbers PP060394 (nrITS) and PP060409 (nrLSU).

Diagnosis: Most similar to the tropical Australian species *Pseudosperma gracilissimum*, but differing by a silky fibrillose pileus, longer basidiospores (on av. 12.9 × 7.8 µm), mostly narrowly utriform to utriform cheilocystidia with subcapitate apex, pileipellis elements without encrusted walls, the presence of caulocystidia, a different habitat dominated by *Isoberlinia* spp., *M. kerstingii* and *U. togoensis*, and by distinct nrITS and nrLSU rDNA sequences.

Figure 4 [near here]

Description: Pileus 10–15 mm diam., broadly conical to hemispherical, expanded plano-convex, usually with a low umbo, with a straight and translucently striate margin reaching up to 1/4 or 2/4 of the radius, colour cream (2.5Y 8–7/2) to yellowish brown (2.5Y 7/6–10) or ochraceous (2.5Y 6/6–8), becoming darker at the centre with age, always creamy white (2.5Y 8/2–4) to ivory white (2.5Y 7/2) at the edge, surface dry, radially silky-fibrillose. Lamellae moderately crowded to subdistant, adnexed, subventricose, pale ivory white to pale yellow grey, becoming yellowish white, edge somewhat eroded, whitish. Stipe 12–20 × 0.6–1.2 mm, central, cylindrical, sometimes subbulbous at the base, straight or curved towards the base of the stipe, surface sordid white or cream to light brown when old, slightly pruinose only near the apex. Colour of exsiccate: pileus sordid white coloured, lamellae and stipe whitish. Smell unrecorded.

Basidiospores 11.0–16.0 µm (av. 12.9 µm, SD ± 1.2 µm) × 6.5–9.3 µm (av. 7.8 µm, SD ± 0.6 µm); Q = 1.4–1.9 (av. 1.7, SD ± 0.1) (n = 100 of 2 coll.), mostly oblong, with central germ pore, with guttules, smooth, thick-walled, yellowish brown in 5% KOH. Basidia 35–45 × 11–13 µm, clavate, 4-spored, thin-walled, hyaline. Cheilocystidia 40–80 µm (av. 51 µm, SD ± 6.0 µm) × 10–17 µm (av. 13.0 µm, SD ± 2.0 µm); Q = 3.1–5.3 (av. 4.1, SD ± 0.6) (n = 40 of 1 coll.), scattered, narrowly utriform to utriform mostly with subcapitate apex, hyaline or very pale yellowish-brown in 5% KOH. Paracystidia 25–40 × 10–18 µm, utriform with obtuse or subcapitate apex or fusiform, thin-walled, hyaline or very pale yellowish-brown in 5% KOH. Pileipellis a hymeniderm to epithelium formed by broadly fusiform to cylindrical terminal elements, with obtuse to mucronate apex, 47–95 × 20–40 µm, smooth, thin-walled, pale yellowish-brown in 5% KOH. Caulocystidia 15–35 × 10–15 µm, narrowly clavate, on clusters of erect hyphae, smooth, thin-

walled, hyaline in 5% KOH. Stipitipellis a cutis of subparallel hyphae, 6–12 µm wide, thin-walled, hyaline in 5% KOH. Clamp connections present in all parts examined.

Figure 5 [near here]

Habitat and distribution:Basidiocarpsgregarious, usually terrestrial, on wet and sandy soils, in woodlands dominated by Caesalpiniaceae (*Isoberlinia* spp.), Dipterocarpaceae (*Monotes kerstingii*), and Phyllanthaceae (*Uapaca togoensis*). Currently only known from Benin.

Additional specimen examined: Benin, Borgou Department, Fôret Classée de l'Ouémé Supérieur, on the soil in savannah forest dominated by *Isoberlinia* spp., 08°36'04.7"N, 002°36'00.7"E, 340 m asl., 28 June 2022, leg. A. Rühl, C. Manz, D. Dongnima, F. Hampe & S. Sarawi (AR-22-089, UNIPAR). According to the phylogenetic analysis, one further specimen from Benin (HLA0454) collected by H.L. Aignon and two sequences obtained from soil (ASV_313 and 881fdb9c) in Benin also belong to *Pseudosperma cremeo-ochraceum*.

Discussion

In the concatenated nrITS-nrLSU rDNA phylogeny (Fig. 1), *Pseudosperma tiliae* is sister to *P. mediterraneum* and nested with *P. holoxanthum* (Grund & D.E. Stuntz) Matheny & Esteve-Rav., *P. melliolens* (Kühner) Matheny & Esteve-Rav., *P. rimosum* (Bull.) Matheny & Esteve-Rav., and *P. sororium* (Kauffman) Matheny & Esteve-Rav. However, morphologically *P. mediterraneum*, originally described from Italy, differs from *P. tiliae* by a pale buff to ochraceous pileus, slightly longer basidiospores (on av. 13.2 × 6.6 µm) with a higher Q-value (Q = 2), shorter cheilocystidia (36–57 × 13–26 µm), and a habitat on dune sand associated with *Pinus pinea* (Kuyper 1986). The genetic distance between *Pseudosperma tiliae* and *P. mediterraneum* is 3%, corresponding to 18 base divergences in 600 nucleotides, indicating that these are different species. *Pseudosperma holoxantha*, originally described from the USA, differs from *P. tiliae* by a longer (up to 100 mm in length) and pale yellow to straw yellow stipe, shorter basidiospores (9.0–13.0 × 6.0–8.0 µm), longer cheilocystidia (up to 110 µm in length), and growth with conifers (Grund and Stuntz 1981). *Pseudosperma melliolens* differs by a brown to brownish coloured pileus, greyish or reddish stipe, shorter basidiospores (9.0–13.5 × 6.0–8.0 µm) and shorter cheilocystidia (up to 55 µm in length) (Kühner 1988). *Pseudosperma rimosum* differs by usually less stout habitus, often dull fallow pileus colour, only faint and fugacious greyish velipellis (Bulliard 1789). *Pseudosperma sororium*, originally described from the USA, has larger basidiomata (up to 70 mm in diam.) with a subconical to conical-campanulate pileus, and distinctly longer basidiospores (9.0–16.0 × 5.0–8.0 µm) (Murrill et al. 1924).

Other European species that are morphologically similar to *Pseudosperma tiliae* are *P. arenicola* (R. Heim) Matheny & Esteve-Rav., *P. mimicum* (Massee) Matheny & Esteve-Rav., *P. musilii* Bandini, B. Oertel & Schmidt-Stohn, *P. pamukkalense* Kaygusuz, Bandini & Knudsen, *P. pseudoorbatum* (Esteve-Rav. & García Blanco) Matheny & Esteve-Rav, and *P. spectrale* Bandini & B. Oertel. *Pseudosperma arenicola* differs by larger pileus (up to 68 mm in diam.) and stipe (up to 75 mm long), distinctly longer basidiospores (on av.

13–15.4 × 6.3–8.0 µm), longer (up to 105 µm) and mostly cylindrical cheilocystidia, cylindrical caulocystidia, and a habitat associated with *Salix repens* L, *Populus canadensis* Moench, or sometimes *Pinus maritima* Mill. (Kuyper 1986). *Pseudosperma mimicum* differs by larger pileus (up to 80 mm in diam.), yellow-brown lamellae, much longer basidiospores (14.0–16.0 × 6.0–8.0 µm), and the absence of cystidia (Massee 1904). *Pseudosperma musilii* differs by its dingy straw to dark brown pileus with a strongly rimose surface, shorter basidiospores (on av. 11.3 × 6.7 µm), and shorter cheilocystidia (on av. 48 × 12 µm) (Bandini et al. 2023). *Pseudosperma pamukkalense* differs by subphaseoliform basidiospores, a predominant association with *Pinus nigra* subsp. *pallasiana* (Lamb.) Holmboe, and genetic differences (nrITS locus 81.5% identity) (Kaygusuz et al. 2023). *Pseudosperma pseudoorbatum* has a white to ivory-white pileus, notably longer basidiospores (on av. 14.6 × 7.1 µm), and a habitat with *Pinus* forests (*Pinus pinaster* Aiton and *P. pinea* L.) (Esteve-Raventós et al. 2003). *Pseudosperma spectrale* has a whitish to straw-coloured pileus, slightly shorter basidiospores (on av. 12.1 × 7.0 µm), and a habitat with conifers (Bandini et al. 2022).

Conclusions

It was previously suggested that species of Inocybaceae began to spread over large areas of northern and southern South America, Australia, and New Zealand during the Palaeogene or later periods (Matheny 2009; Matheny et al. 2009). Recent multi-gene phylogenetic analyses confirmed close affinities between *Pseudosperma* taxa from tropical Asia, tropical Australia, and tropical China (Zhao et al. 2022). Similarly, in the present study, phylogenetic analyses generated from nrITS and nrLSU rDNA sequences revealed rather close phylogenetic relationships among *Pseudosperma* species indigenous to the tropical regions of Benin, Australia, India, and China. The new species *Pseudosperma beninense*, *P. cremeo-ochraceum*, *P. squarrosofulvum*, and *P. stramineum* were found in ectomycorrhizal forests with tropical climate of Benin and are phylogenetically close to each other in a clade that in addition to the species from Benin includes six further species from tropical regions of the palaeotropics and Australia. These six species are *P. araneosum* from Australia (Matheny and Bougher 2017), *Pseudosperma brunneosquamulosum*, *P. luteobrunneum*, and *P. rubrobrunneum* from India (Tibpromma et al. 2017), and *Pseudosperma fulvidiscum* and *P. singulare* from China (Zhao et al. 2022). The ongoing discovery and characterization of tropical to subtropical taxa within the genus will improve our understanding of their biogeographical distribution and evolutionary history.

Declarations

Acknowledgements

We would like to thank Frank Lappe and Anika Rüb for their technical assistance, and Cathrin Manz, Felix Hampe, Boris Olou, and Sylvestre Badou for their support in the field. We are grateful to Daouda Dognima for careful driving through Benin´s ecosystems. This study results from the project FunTrAf that is generously supported by the German Federal Ministry of Education and Research (BMBF, 01DG20015FunTrAf). The first author also acknowledges the financial support of the Scientific and

Technical Research Council of Turkey (TUBITAK) for the 2219 International Postdoctoral Research Fellowship Programme (Grant No. 1059B192202880).

Author contribution

All authors contributed to the conception and design of the study. Oğuzhan Kaygusuz, Adrian Rühl, Sepas Sarawi, Nourou S. Yorou, and Meike Piepenbring contributed to material preparation and data collection. Morphological characteristics were examined by Oğuzhan Kaygusuz and Ditte Bandini. Molecular lab work and phylogenetic analyses were conducted by Oğuzhan Kaygusuz, Adrian Rühl, and Sepas Sarawi. The first draft of the manuscript was written by Oğuzhan Kaygusuz and Meike Piepenbring, which was then improved by changes, edits, suggestions, and comments from Ditte Bandini, Adrian Rühl, Sepas Sarawi and Nourou S. Yorou. All authors read and approved the final manuscript.

Funding

FunTrAf by the German Federal Ministry of Education and Research (BMBF, 01DG20015FunTrAf) and 2219 International Postdoctoral Research Fellowship Programme (Grant No. 1059B192202880) by the Scientific and Technical Research Council of Turkey (TUBITAK).

Data availability

The DNA sequences produced in this study are available on NCBI GenBank (https://www.ncbi.nlm.nih.gov).

Code availability

Not applicable.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Informed consent was obtained from all individual participants included in the study.

Competing interests

The authors declare no competing interests.

References

1. Bandini D, Oertel B (2020) Three new species of the genus *Pseudosperma* (Inocybaceae). Czech Mycol 72(2):221–250. https://doi.org/10.33585/cmy.72205

2. Bandini D, Oertel B, Eberhardt U (2021) Even more fibre-caps (2): Thirteen new species of the family Inocybaceae. Mycologia Bavarica 21:27–98
3. Bandini D, Oertel B, Eberhardt U (2022) Noch mehr Risspilze (3): Einundzwanzig neue Arten der Familie Inocybaceae. Mycologia Bavarica 22:31–138
4. Bandini D, Oertel B, Eberhardt U (2023) Even more fibre-caps (4): Fourteen new species of the family Inocybaceae. Mycologia Bavarica 23:1–50
5. Bau T, Fan Y-G (2018) Three new species of *Inocybe* sect. *Rimosae* from China. Mycosystema 37:693–702
6. Boa E (2004) Wild edible fungi: A global overview of their use and importance to people. Non-wood forest products, Vol 17. Food and Agriculture Organization of the United Nations, Rome
7. Bon M (1997) Clé monographique du genre *Inocybe* (Fr.) Fr. (1čre partie). Documents Mycologiques 27(105):1–51
8. Cervini M, Bizio E, Alvarado P (2020) Quattro nuove specie italiane del Genere *Pseudosperma* (Inocybaceae) con odore di miele. RdM 63(1):3–36
9. Esteve-Raventós F, García Blanco A, Sanz Carazo M, Del Val JB (2003) *Inocybe aurantiobrunnea* and *I. pseudoorbata*, two new mediterranean species found in the Iberian Peninsula. Österreichische Zeitschrift für Pilzkunde 12:89–100
10. Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for Basidiomycetes-Application to the identification of mycorrhizae and rusts. Molecular Ecology 2:113–118. https://doi.org/10.1111/j.1365-294X.1993.tb00005.x
11. Grund DW, Stuntz DE (1981) Nova Scotian *Inocybes*. VI. Mycologia 73(4):655–674. https://doi.org/10.1080/00275514.1981.12021393
12. Hoang DT, Chernomor O, von Haeseler A, Minh BQ, Vinh LS (2018) UFBoot2: Improving the Ultrafast Bootstrap Approximation. Molecular Biology and Evolution 35:518–522. https://doi.org/10.1093/molbev/msx281
13. Horak E (1978) Fungi Agaricini Novaezelandiae, New Zealand Journal of Botany 15(4):713–747. https://doi.org/10.1080/0028825X.1977.10429642
14. Jabeen S, Khalid AN (2020) *Pseudosperma flavorimosum* sp. nov. from Pakistan. Mycotaxon 135(1):183–193. https://doi.org/10.5248/135.183
15. Jabeen S, Zainab Bashir H, Khalid AN (2021) *Pseudosperma albobrunneum* sp. nov. from coniferous forests of Pakistan. Mycotaxon 136(2):361–372. https://doi.org/10.5248/136.361
16. Jabeen S, Khalid AN (2020) *Pseudosperma flavorimosum* sp. nov. from Pakistan. Mycotaxon 135(1):183–193. https://doi.org/10.5248/135.183
17. Jacobsson S (2008) Key to *Inocybe*. In: Knudsen H, Vesterholt J (eds) Funga Nordica: Agaricoid, Boletoid and Cyphelloid Genera, Nordsvamp, Copenhagen, Denmark, pp 868–906
18. Katoh K, Rozewicki J, Yamada KD (2019) MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. Briefings in Bioinformatics 20(4):1160–1166.

https://doi.org/10.1093/bib/bbx108

19. Kaygusuz O, Bandini D, Knudsen H, Türkekul I (2023) *Pseudosperma pamukkalense* (Inocybaceae: Agaricomycetes), a new species from Turkey. Phytotaxa 599(4):225–238. https://doi.org/10.11646/phytotaxa.599.4.2
20. Kaygusuz O, Knudsen H, Türkekul İ, Çolak ÖF (2020) *Volvariella turcica*, is a new species from Turkey, and multigene phylogeny of *Volvariella*. Mycologia 112(3):577–587. https://doi.org/10.1080/00275514.2020.1724048
21. Karsten PA (1889) Symbolae ad Mycologiam Fennicam. Pars XXIX. Meddelanden af Societas pro Fauna et Flora Fennica 16:84–106
22. Kõljalg U, Larsson K-H, Abarenkov K, Nilsson RH, Alexander IJ, Eberhardt U, Erland S, Høiland K, Kjøller R, Larsson E, Pennanen T, Sen R, Taylor AFS, Tedersoo L, Vrålstad T, Ursing BM (2005) UNITE: a database providing web-based methods for the molecular identification of ectomycorrhizal fungi. New Phytologist 166(3):1063–1068. https://doi. org/10.1111/j.1469-8137.2005.01376.x
23. Kropp BR, Matheny PB, Hutchison LJ (2013) *Inocybe* section *Rimosae* in Utah: phylogenetic affinities and new species. Mycologia 105:728–747. https://doi.org/10.3852/12-185
24. Kühner R (1988) Diagnoses de quelques nouveaux *Inocybes* récoltés en zone alpine de la Vanoise (Alpes françaises). Documents Mycologiques 19(74):1–27
25. Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: molecular evolutionary genetics analysis across computing platforms. Mol Biol Evol 35:1547–1549. https://doi.org/10.1093/molbev/msy096
26. Kuyper TW (1986) A revision of the genus *Inocybe* in Europe. I. Subgenus *Inosperma* and the smooth-spored species of subgenus *Inocybe*. Persoonia Supplement 3(1):1–247
27. Lange JE (1917) Studies in the Agarics of Denmark. Part III, *Pluteus*, *Collybia*, *Inocybe*. Dansk botanisk Arkiv 2(7):1–50
28. Larsson A (2014) AliView: A fast and lightweight alignment viewer and editor for large data sets. Bioinformatics 30:3276–3278. https://doi.org/10.1093/bioinformatics/btu531
29. Larsson E, Ryberg M, Moreau PA, Mathiesen ÅD, 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
30. Latha KPD, Haridev P, Anil Raj KN, Manimohan P (2023) *Pseudosperma indicum* sp. nov. (Inocybaceae, Agaricales) from India. Phytotaxa 620(1):47–58. https://doi.org/10.11646/phytotaxa.620.1.4
31. Liu L-N, Razaq A, Atri NS et al (2018) Fungal systematics and evolution: FUSE 4. Sydowia 70:211–286
32. Mao N, Xu YY, Zhao TY, Lv JC, Fan L (2022) New Species of *Mallocybe* and *Pseudosperma* from North China. *J. Fungi 8*:256. https://doi.org/10.3390/jof8030256
33. Massee G (1904) A monograph of the genus Inocybe Karsten. Annals of Botany 18:459–504

34. Matheny PB (2005) Improving phylogenetic inference of mushrooms with *RPB1* and *RPB2* nucleotide sequences (Inocybe, Agaricales). Mol Phylogenet Evol 35:1–20. http://dx.doi.org/10.1016/j.ympev.2004.11.014
35. Matheny PB (2009) A phylogenetic classification of the Inocybaceae. McIlvainea 18:11–21
36. Matheny PB, Aime MC, Bougher NL, Buyck B, et al (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
37. Matheny PB, Bougher NL (2017) Fungi of Australia: Inocybaceae. Australian Biological Resources Study, Canberra. CSIRO Publishing, Melbourne, Australia
38. Matheny PB, Hobbs AM, Esteve-Raventós F (2020) Genera of Inocybaceae: New skin for the old ceremony. Mycologia 112(1):83–120. https://doi.org/10.1080/00275514.2019.1668906
39. Matheny PB, Kudzma LV (2019) New species of *Inocybe* (Agaricales) from eastern North America. J Torrey Bot Soc 146:213–235
40. Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, von Haeseler A, Lanfear R (2020) IQ-TREE 2: New Models and Efficient Methods for Phylogenetic Inference in the Genomic Era. Molecular Biology and Evolution 37:1530–1534. https://doi.org/10.1093/molbev/msaa015
41. Munsell AH (1975) Munsell soil color charts. Baltimore, Munsell Color Inc., Baltimore
42. Murrill WA, Kauffman CH, Overhotts LO (1924) North American Flora. The New York Botanical Garden 10: 227–260
43. Myers N, Mittenmerier RA, Mittenmeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403(6772):853–858. https://doi.org/10.1038/35002501
44. Naseer A, Jabeen S, Ashfaq A, Akbar M, Hussain SI, Khalid AN (2023) *Pseudosperma quercinum* sp. nov. (Inocybaceae) from the Himalayan forests of Pakistan. Phytotaxa 622(4):260–270. https://doi.org/10.11646/phytotaxa.622.4.3
45. Nylander JAA (2004) MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden
46. Osmundson TW, Vincent RA, Schoch CL, Baker LJ, Smith A, Robich G, Mizzan L, Garbelotto MM (2013) Filling gaps in biodiversity knowledge for macrofungi: contributions and assessment of a herbarium collection DNA barcode sequencing project. PLoS One 8(4):e62419. https://doi.org/10.1371/journal.pone.0062419
47. Piepenbring M, Maciá-Vicente JG, Codjia JEI, Glatthorn C, Kirk P, Meswaet Y, Minter D, Olou BA, Reschke K, Schmidt M, Yorou NS (2020) Mapping mycological ignorance - Checklists and diversity patterns of fungi known for West Africa. IMA fungus 11(1):13. https://doi.org/10.1186/s43008-020-00034-y
48. Pradeep CK, Vrinda KB, Varghese SP, Korotkin HB, Matheny PB (2016) New and noteworthy species of *Inocybe* (Agaricales) from tropical India. Mycological progress 15(3):24. https://doi.org/10.1007/s11557-016-1174-z

49. Rambaut A (2018) Molecular evolution, phylogenetics and epidemiology. FigTree ver.1.4.4 software. http://tree.bio.ed.ac.uk/software/figtree/. Accessed 1 October 2023
50. Rehner SA, Samuels GJ (1994) Taxonomy and phylogeny of *Gliocladium* analysed from nuclear large subunit ribosomal DNA sequences. Mycological Research 98:625–634
51. Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A et al (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61:589–542. https://doi.org/10.1093/sysbio/sys029
52. Ryberg M, Nilsson RH, Kristiansson E, Töpel M, Jacobsson S, Larsson E (2008) Mining metadata from unidentified ITS sequences in GenBank: A case study in *Inocybe* (Basidiomycota). BMC Evol Biol 8:50. https://doi.org/10.1186/1471-2148-8-50
53. Saba M, Haelewaters D, Pfister DH, Khalid AN (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
54. Sanna M, Mua A, Porcu G, Casula M, Rinaldi AC, Mifsud S, Garrido-Benavent I (2024) *Pseudosperma calciphilum* (Inocybaceae), a new Mediterranean species from Sardinia (Italy), Malta, and Valencia (Spain). Phytotaxa 633(3):253–264. https://doi.org/10.11646/phytotaxa.633.3.5
55. Singer R, Araujo I, Ivory MH (1983) The ectotrophically mycorrhizal fungi of the neotropical lowlands, especially Central Amazonia. Beih Nova Hedwigia 77:1–339
56. Sjökvist E, Larsson E, Eberhardt U, Ryvarden L, Larsson KH (2012) Stipitate stereoid basidiocarps have evolved multiple times. Mycologia 104(5):1046–1055. https://doi.org/10.3852/11-174
57. Stangl J (1989) Die Gattung *Inocybe* in Bayern. Hoppea 46:5–388
58. Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG (1997) The CLUSTAL_X windows interface: Flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Res 25:4876–4882. https://doi.org/10.1093/nar/25.24.4876
59. Tibpromma S, Hyde KD, Jeewon R et al (2017) Fungal diversity notes 491–602: taxonomic and phylogenetic contributions to fungal taxa. Fungal Divers 83(1):1–261. https://doi.org/10.1007/s13225-017-0378-0
60. Turnbull E (1995) *Inocybe* in Peninsular Malaysia. Edinburgh Journal of Botany 52(3):351–359. https://doi:10.1017/s0960428600002043
61. Ullah Z, Jabeen S, Ahmad H, Khalid AN (2018) *Inocybe pakistanensis*, a new species in section *Rimosae* s. str. from Pakistan. Phytotaxa 348(4):279–288. https://doi.org/10.11646/phytotaxa.348.4.4
62. Vauras J, Larsson E (2011) *Inocybe myriadophylla*, a new species from Finland and Sweden. Karstenia 51(2):31–36. https://doi.org/10.29203/ka.2011.446
63. Vellinga EC (1988) Glossary. In: Bas C, Kuyper ThW, Noordeloos ME, Vellinga EC (eds). Flora Agaricina Neerlandica, Vol. 1, A.A. Balkema, Rotterdam, the Netherlands, pp 54–64

64. 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
65. White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (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
66. 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
67. Yu WJ, Chang C, Qin LW, Zeng NK, Wang SX, Fan YG (2020) *Pseudosperma citrinostipes* (Inocybaceae), a new species associated with Keteleeria from southwestern China. Phytotaxa 450(1):8–16. https://doi.org/10.11646/phytotaxa.450.1.2
68. Zhao LN, Yu WJ, Deng LS, Hu JH, Ge YP, Zeng NK, Fan YG (2022) Phylogenetic analyses, morphological studies, and muscarine detection reveal two new toxic *Pseudosperma* (Inocybaceae, Agaricales) species from tropical China. Mycological Progress 21(75). https://doi.org/10.1007/s11557-022-01822-z

Figures

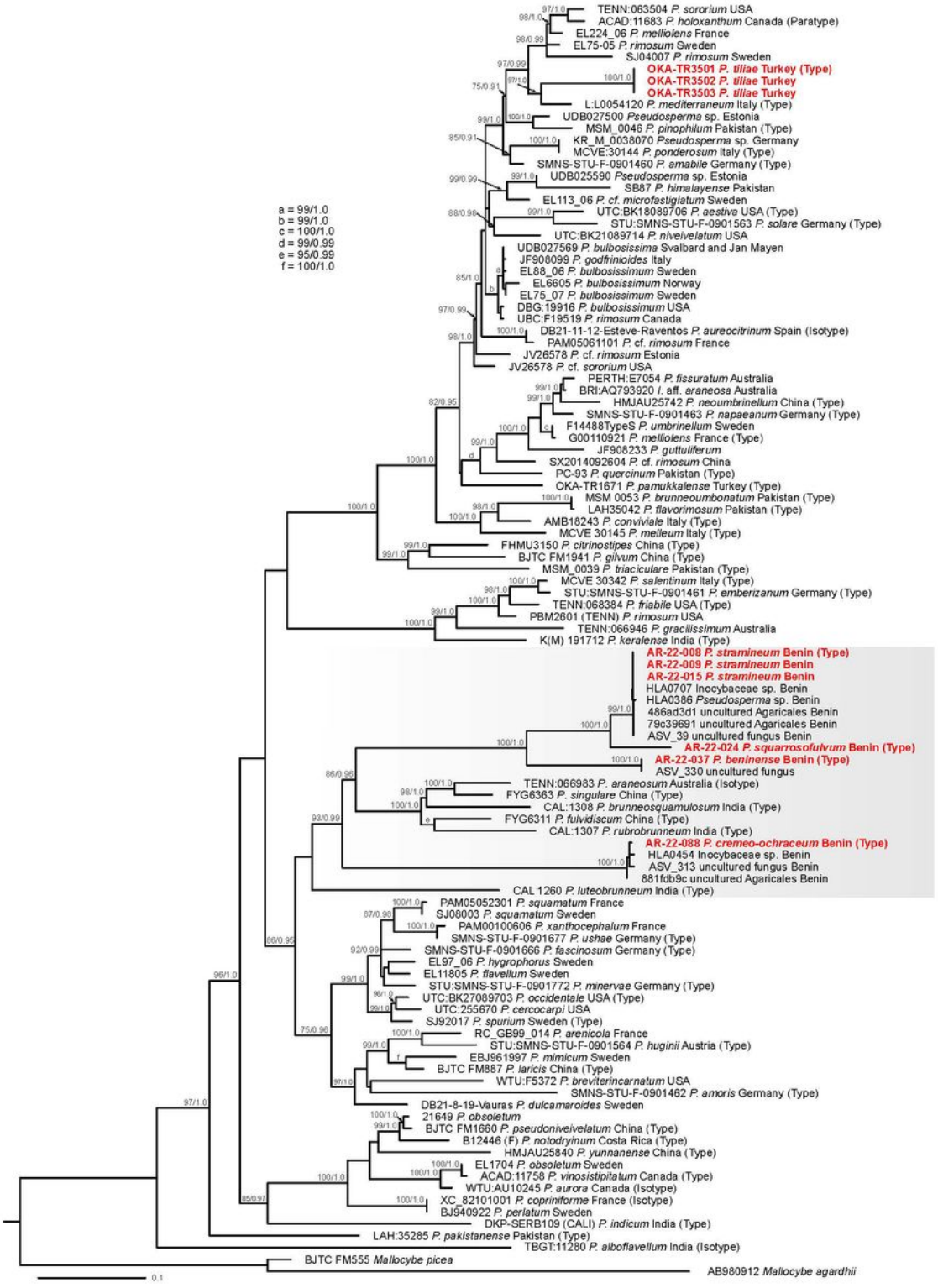

Figure 1

Phylogenetic position of the Beninese and Turkish collections of *Pseudosperma*based on nrITS and nrLSU rDNA sequences using Maximum Likelihood (ML) and Bayesian analyses. MLB ≥ 75% and BPP ≥ 0.90 values are indicated on the branches. *Mallocybe agardhii* (AB980912) and *M.picea* (BJTC FM555) were selected as outgroups. The newly generated sequences are marked in red bold. A clade formed by species from the palaeotropics and Australia is marked by a grey background.

Figure 2

Basidiomata of *Pseudosperma beninense* (AR-22-037, holotype). Bar = 5 mm.

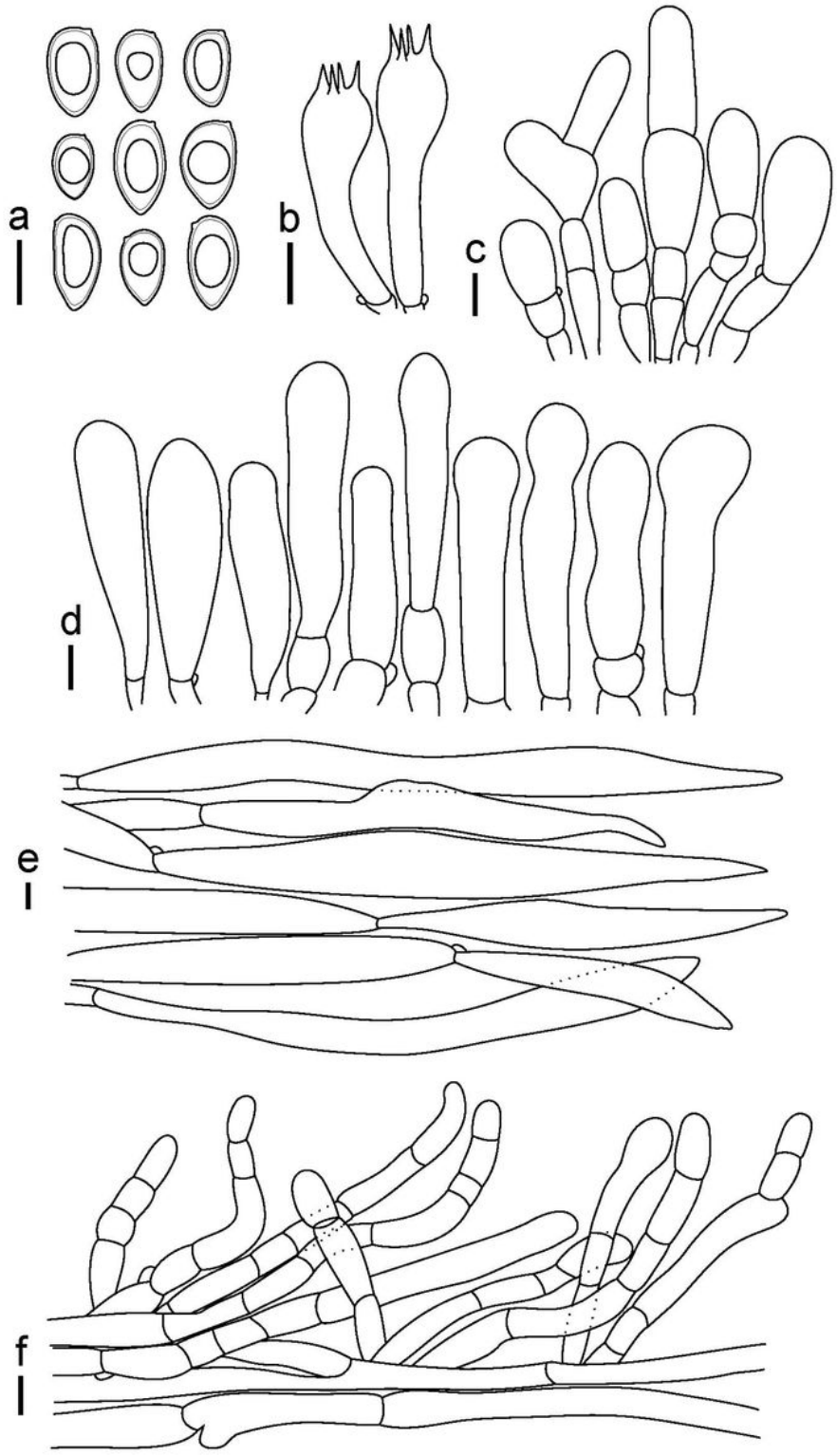

Figure 3

Microscopic features of *Pseudosperma beninense* (AR-22-037, holotype). **a-** Basidiospores. **b-** Basidia. **c-** Paracystidia. **d-** Cheilocystidia. **e-** Pileipellis. **f-**Caulocystidia. Bars = 10 µm.

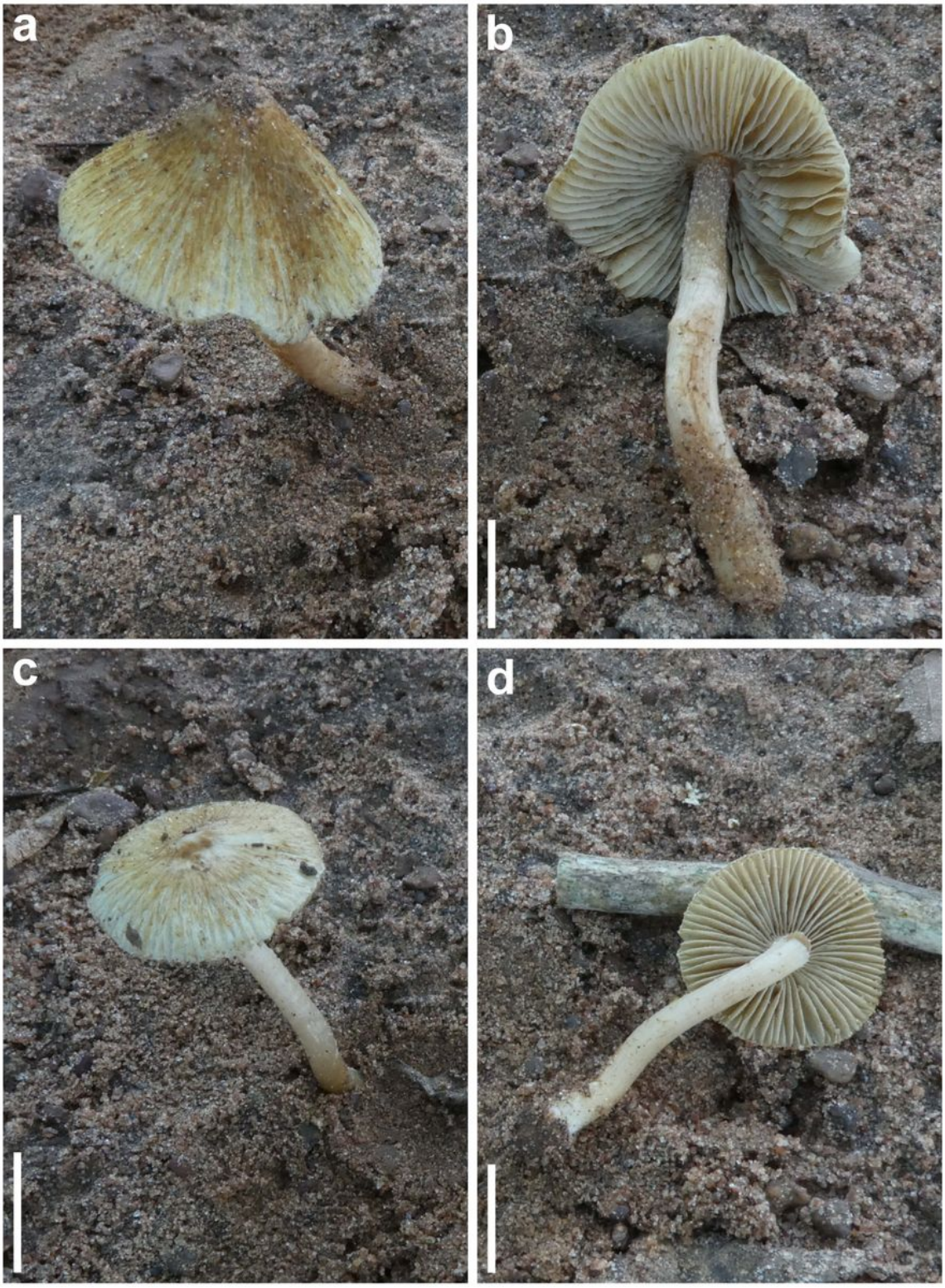

Figure 4

Basidiomata of *Pseudosperma stramineum*. **a-** Collection AR-22-008 (holotype). **b-** Collection AR-22-009. **c-** Collection AR-22-015. Bars = 10 mm.

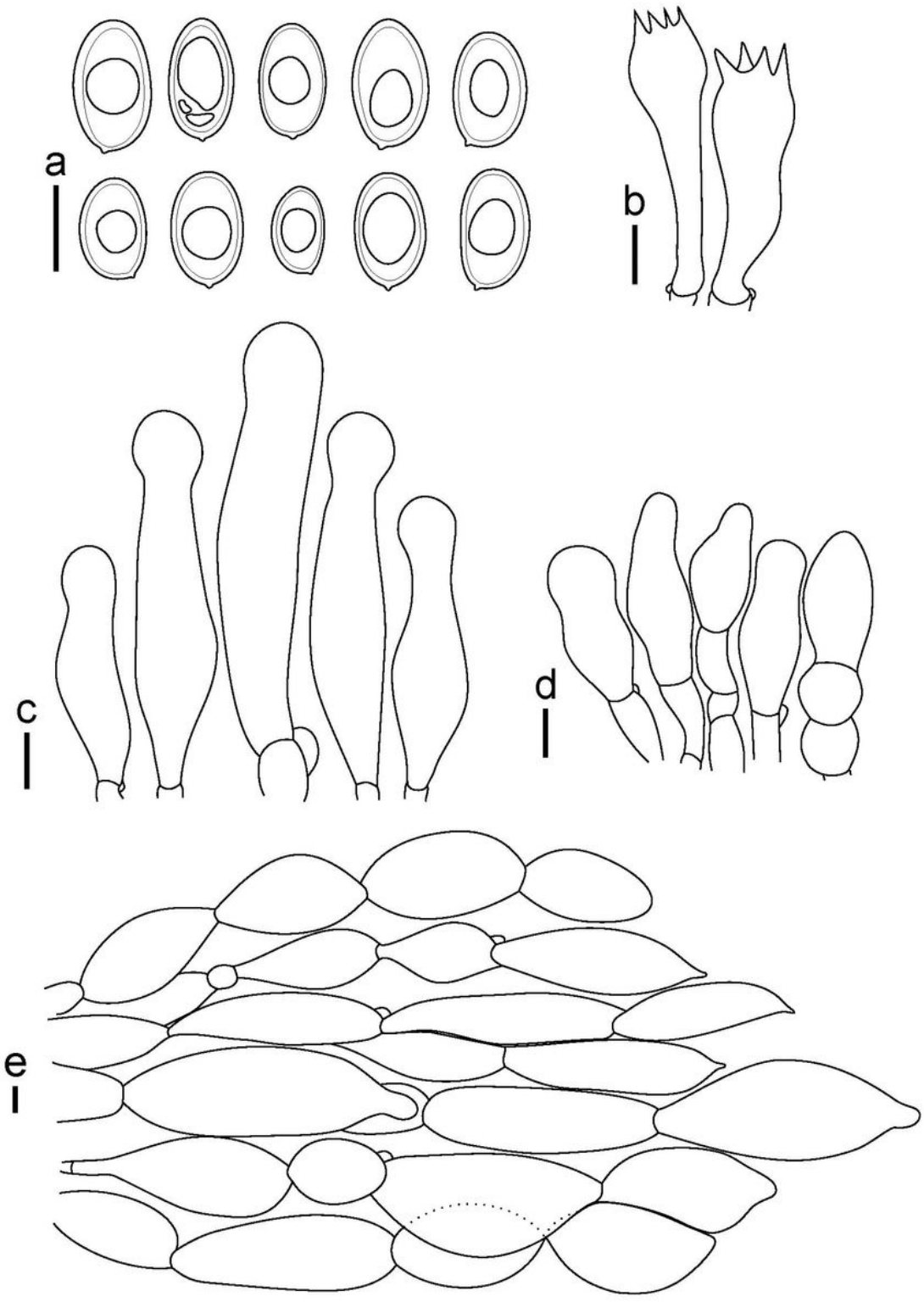

Figure 5

Microscopic features of *Pseudosperma stramineum*(AR-22-008, holotype). **a-** Basidiospores. **b-**Basidia. **c-** Caulocystidia. **d-** Cheilocystidia. **e-**Paracystidia. **f-** Pileipellis. Bars = 10 µm.

Figure 6

Basidiomata of *Pseudosperma squarrosofulvum* (AR-22-024, holotype). Bar = 10 mm.

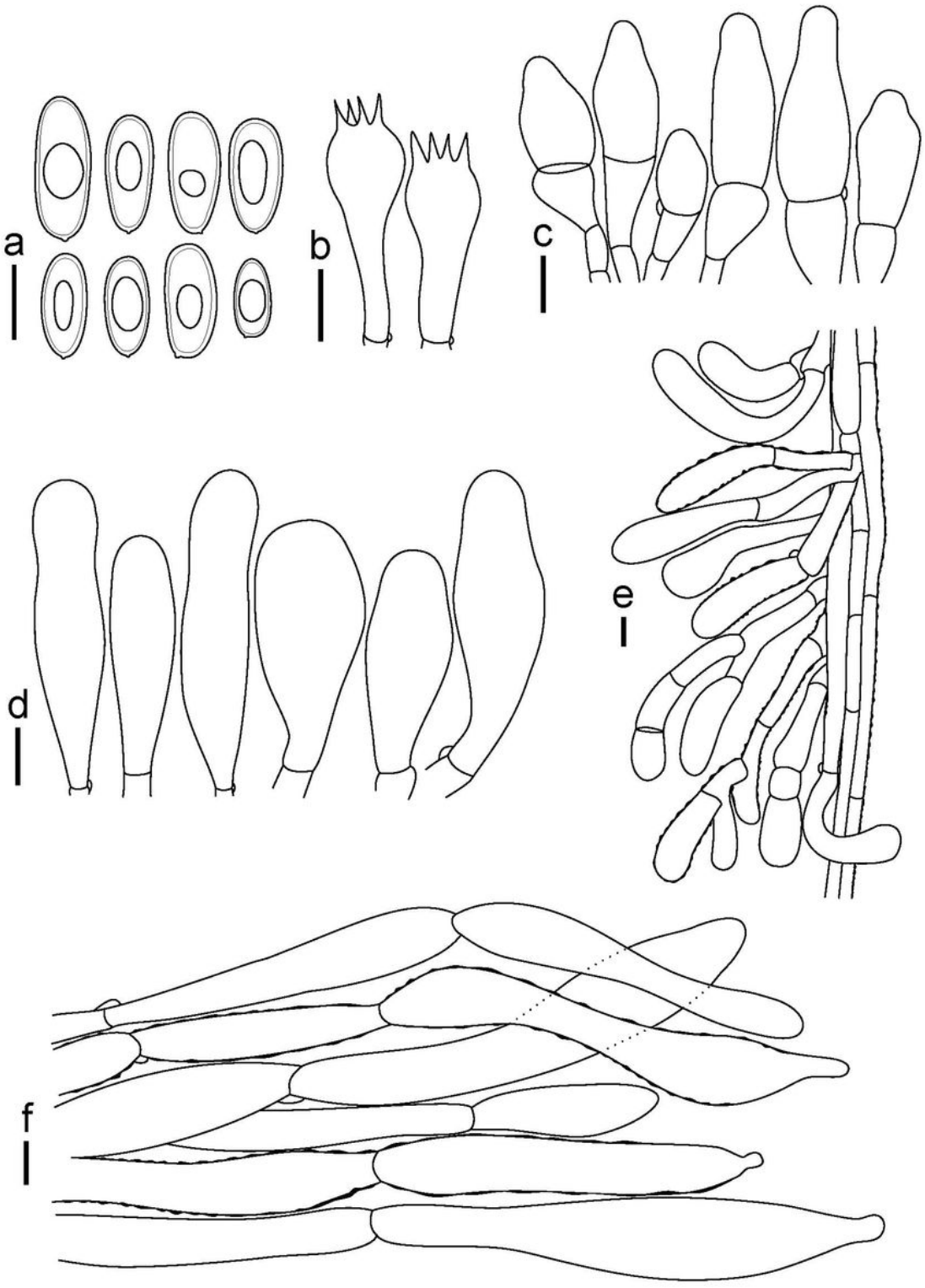

Figure 7

Microscopic features of *Pseudosperma squarrosofulvum* (AR-22-024, holotype). **a-** Basidiospores. **b-** Basidia. **c-**Paracystidia. **d-** Cheilocystidia. **e-** Caulocystidia. **f-**Pileipellis. Bars = 10 µm.

Figure 8

Basidiomata of *Pseudosperma cremeo-ochraceum*. **a, b-** Collection AR-22-088 (holotype). **c, d-** Collection AR-22-089. Bars = 5 mm.

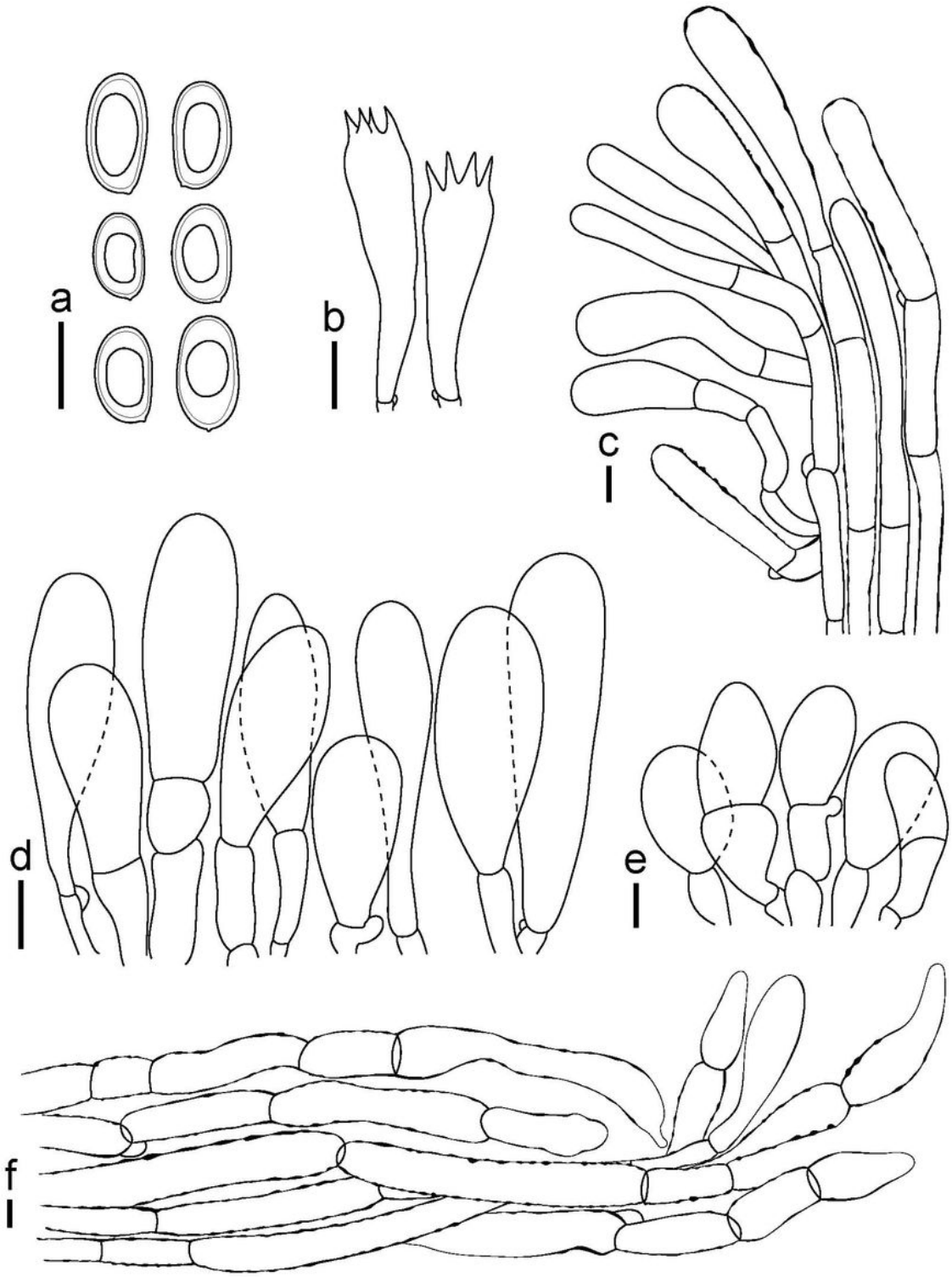

Figure 9

Microscopic features of *Pseudosperma cremeo-ochraceum*(AR-22-088, holotype). **a-** Basidiospores. **b-** Basidia. **c-** Cheilocystidia. **d-** Paracystidia. **e-**Pileipellis. Bars = 10 µm.

Figure 10

Basidiomata of *Pseudosperma tiliae* in the field. **a-**Collection OKA-TR3501 (holotype). **b-** Collection OKA-TR3502. **c-** Collection OKA-TR3503. Bars = 10 mm.

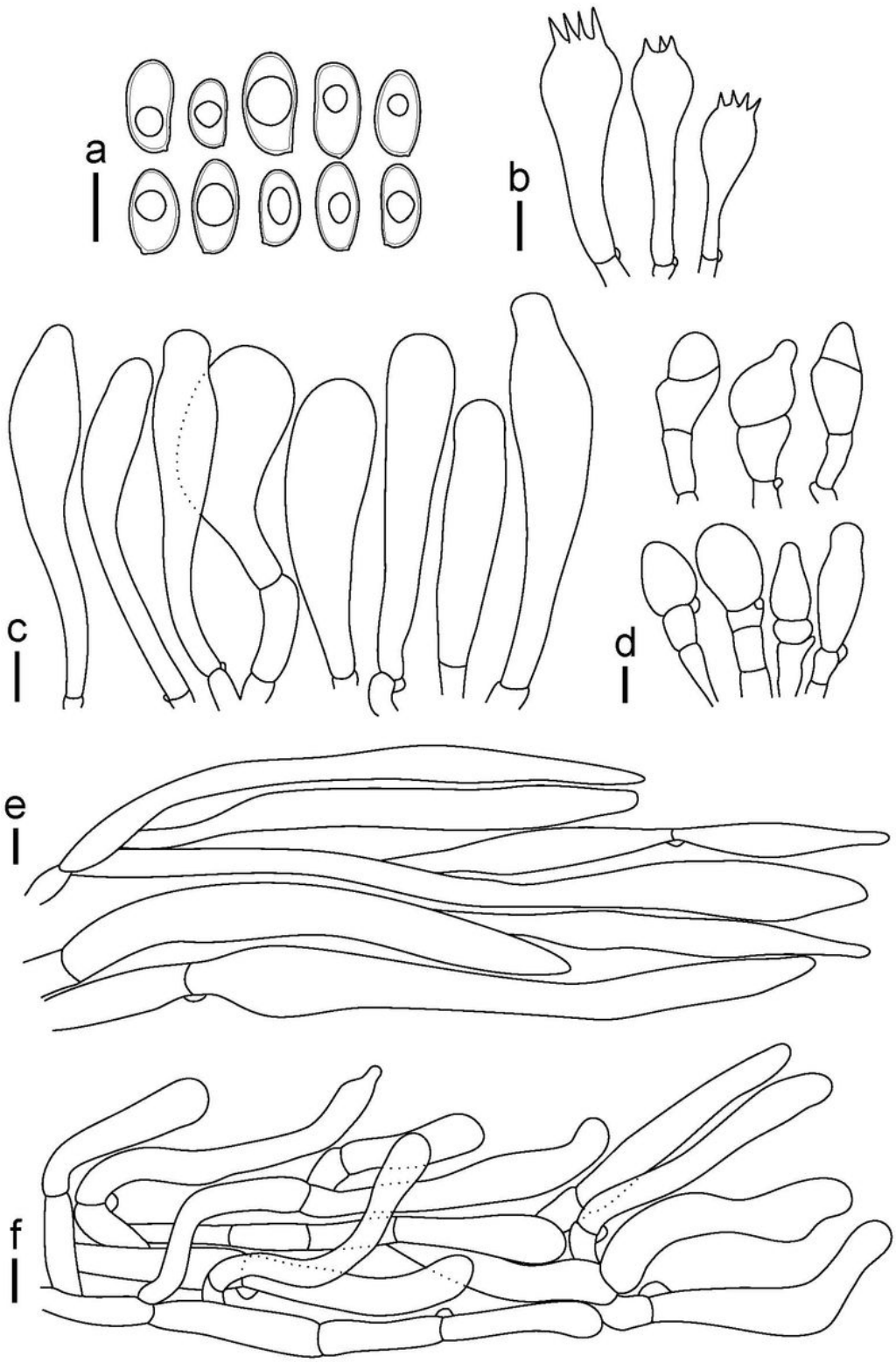

Figure 11

Microscopic features of *Pseudosperma tiliae*(OKA-TR3501, holotype). **a-** Basidiospores. **b-**Basidia. **c-** Cheilocystidia. **d-** Paracystidia. **e-**Pileipellis. **f-** Caulocystidia. Bars = 10 µm.