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ORIGINAL ARTICLE

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

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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 (ITS), 28S rDNA, and RNA polymerase II second largest subunit (*RPB2*) region. 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.

Keywords Ectomycorrhizal fungi · Biodiversity · Agarics · Molecular systematics · Biogeography · Taxonomy

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 earlier 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 stipe, smooth, elliptic to phaseoliform basidiospores, hyaline non-necropigmented basidia, cylindric 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 species of angiosperms and rarely gymnosperms and occur in a variety of habitats, including temperate forests (Kuyper 1986; Stangl 1989; Jacobsson 2008).

Currently 80 species of *Pseudosperma* are known worldwide (Bandini et al. 2022, 2023), including species recently described from Austria (Bandini et al. 2021), Australia

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(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), Turkey (Kaygusuz et al. 2023) and USA (Kropp et al. 2013; Matheny and Kudzma 2019). Despite this progress, the diversity of *Pseudosperma* species, particularly in tropical regions such as West Africa and Mediterranean areas of Western Eurasia, is poorly studied. 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 of fungi (Piepenbring et al. 2020). For Benin, only 432 fungal species have been listed by Piepenbring et al. (2020). To date, there are two species of *Pseudosperma* reported from Benin, namely *Pseudosperma squamatum* (J.E. Lange) Matheny & Esteve-Rav., formerly known as *Inocybe squamata* J.E. Lange (Lange 1917; Boa 2004; Piepenbring et al. 2020), and *Pseudosperma rimosum* (Bull.) Matheny & Esteve-Rav. previously called *Inocybe fastigiata* var. *brevispora* R. Heim (Heim 1931; Matheny et al. 2020), which was described from Madagascar. 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), for the nuclear 28S rDNA (LSU) the primer pair LR0R/LR5 (Vilgalys and Hester 1990; Rehner and Samuels 1994), and for *RPB2* the primer pair RPB2-5F/RPB2-7cR (Song et al. 2016) were used. Polymerase chain reaction (PCR) procedures were performed according to the methods described by Matheny (2005) and 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 27 DNA sequences (nine from the ITS, nine from the LSU, and nine from the *RPB2*) 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 the sequences listed in Table 1. The ITS, LSU, and *RPB2* 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

Table 1 List of taxa included in the molecular analyses, with voucher specimen numbers, country of origin, GenBank accession numbers of ITS, LSU, and *RPB2* gene sequences, and references to literature. Information on newly generated sequences is written in bold

Species	Voucher	Country	GenBank / UNITE accession number			References
			ITS	LSU	*RPB2*	
P. aestivum	UTC:BK18089706	USA	EU600847	EU600847	EU600846	Matheny et al. 2009
P. aff. *araneosa*	BRI:AQ793920	Australia	KJ729879	KJ729905	KJ729936	Matheny and Bougher 2017
P. alboflavellum	TBGT:11280	India	KP636859	KP171058	KM656097	Matheny and Bougher 2017
P. amabile	SMNS-STU-F-0901460	Germany	MW010031	—	—	Bandini and Oertel 2020
P. amoris	SMNS-STU-F-0901462	Germany	MW010038	—	—	Bandini and Oertel 2020
P. araneosum	TENN:066983	Australia	KJ729878	KJ729904	KJ729935	Matheny and Bougher 2017
P. arenicola	RC_GB99_014	France	FJ904134	FJ904134	—	Larsson et al. 2009
P. aureocitrinum	DB21-11–12-Esteve-Raventos	Spain	MW010047	—	—	Bandini and Oertel 2020
P. aurora	WTU:AU10245	Canada	HQ201337	HQ201338	—	GenBank, unpublished
P. beninense	**AR-22–037**	**Benin**	**PP060393**	**PP060408**	**PP430968**	**This study**
P. breviterincarnatum	WTU:F5372	USA	JQ408751	JQ319679	—	Kropp et al. 2013
P. brunneosquamulosum	CAL:1308	India	KX073582	KX073586	KX073589	Tibpromma et al. 2017
P. brunneoumbonatum	MSM#0053	Pakistan	MG742419	MG742420	—	Saba et al. 2020
P. bulbosissimum	TUF113526	Svalbard and Jan Mayen	UDB027569	—	—	UNITE, unpublished
P. bulbosissimum	EL88_06	Sweden	FJ904159	FJ904159	—	Larsson et al. 2009
P. bulbosissimum	EL6605	Norway	AM882765	AM882765	—	Larsson et al. 2009
P. bulbosissimum	EL75_07	Sweden	FJ904160	FJ904160	—	Larsson et al. 2009
P. bulbosissimum	DBG:19916	USA	MH024849	MH024885	MH249788	Matheny and Kudzma 2019
P. cercocarpi	UTC:255670	USA	MK421964	—	—	Matheny et al. 2020
P. cf. *microfastigiatum*	EL113_06	Sweden	FJ904156	FJ904156	—	Larsson et al. 2009
P. cf. *rimosum*	PAM05061101	France	FJ904155	FJ904155	—	Larsson et al. 2009
P. cf. *rimosum*	JV26578	Estonia	FJ904154	FJ904154	—	Larsson et al. 2009
P. cf. *rimosum*	SX2014092604	China	KR733590	—	—	GenBank, unpublished
P. cf. *sororium*	src60	USA	DQ974802	DQ974802	—	Smith et al. 2007
P. citrinostipes	FHMU3150	China	MT072898	MT071203	MT086749	Yu et al. 2020
P. conviviale	AMB:18243	Italy	MT095091	MT095115	—	Cervini et al. 2020
P. copriniforme	XC_82101001	France	MW010046	—	—	Bandini and Oertel 2020
P. cremeo-ochraceum	**AR-22–088**	**Benin**	**PP060394**	**PP060409**	**PP430969**	**This study**
P. dulcamaroides	DB21-8–19-Vauras	Sweden	MW010042	—	—	Bandini and Oertel 2020
P. emberizanum	STU:SMNS-STU-F-0901461	Germany	MW647630	—	—	Bandini et al. 2021
P. fascinosum	SMNS-STU-F-0901666	Germany	ON003426	ON003426	—	Bandini et al. 2022
P. fissuratum	PERTH:E7054	Australia	JQ408770	—	JQ421069	Kropp et al. 2013
P. flavellum	EL11805	Sweden	AM882782	AM882782	—	Ryberg et al. 2008
P. flavorimosum	LAH 35042	Pakistan	MG495391	—	—	Jabeen and Khalid 2020
P. friabile	TENN:068384	USA	MH216095	MH220272	—	Matheny and Kudzma 2019
P. fulvidiscum	FYG6311	China	OM135592	OM349998	OM747849	Zhao et al. 2022
P. gilvum	BJTC FM1941	China	OM801910	OM801914	—	Mao et al. 2022
P. godfrinioides	371	Italy	JF908099	—	—	Osmundson et al. 2013
P. gracilissimum	TENN:066946	Australia	KP171123	KJ801179	KJ729947	Matheny and Bougher 2017
P. guttuliferum	21581	—	JF908233	—	—	Osmundson et al. 2013
P. himalayense	SB87	Pakistan	HG796995	—	—	Liu et al. 2018
P. holoxanthum	ACAD:11683	Canada	MH024853	MH024884	—	GenBank, unpublished
P. huginii	STU:SMNS-STU-F-0901564	Austria	MW647628	MW647628	—	Bandini et al. 2021
P. hygrophorus	EL97_06	Sweden	FJ904137	FJ904137	—	Larsson et al. 2009
P. indicum	DKP-SERB109	India	OR243200	OR243199	OR253891	Latha et al. 2023
P. keralense	KM:191712	India	KM924523	KM924518	KY553243	Latha and Manimohan 2016

Table 1 (continued)

Species	Voucher	Country	GenBank / UNITE accession number			References
			ITS	LSU	*RPB2*	
P. laricis	BJTC FM887	China	OM801905	OM801912	—	Mao et al. 2022
P. luteobrunneum	CAL 1260	India	KX073580	KX073584	KX073588	Tibpromma et al. 2017
P. mediterraneum	L:L0054120	Italy	MZ700321	—	—	Bandini et al. 2022
P. melleum	MCVE:30145	Italy	MT095090	MT095114	—	Cervini et al. 2020
P. melliolens	EL224_06	France	FJ904149	FJ904149	—	Larsson et al. 2009
P. melliolens	G00110921	France	MN901255	—	—	GenBank, unpublished
P. mimicum	EBJ961997	Sweden	FJ904124	FJ904124	—	Larsson et al. 2009
P. minervae	STU:SMNS-STU-F-0901772	Germany	OQ324785	OQ324785	—	Bandini et al. 2023
P. napaeanum	SMNS-STU-F-0901463	Germany	MW010040	—	—	Bandini and Oertel 2020
P. neoumbrinellum	HMJAU25742	China	MH047249	MG844977	—	Bau and Fan 2018
P. niveivelatum	UTC:BK21089714	USA	JQ319695	JQ319695	—	Kropp et al. 2013
P. notodryinum	B12446 F	Costa Rica	MK607030	—	—	GenBank, unpublished
P. obsoletum	21649	—	JF908256	—	—	Osmundson et al. 2013
P. obsoletum	EL1704	Sweden	AM882769	AM882769	—	Ryberg et al. 2008
P. occidentale	UTC:BK27089703	USA	EU600893	EU600893	EU600892	Kropp et al. 2013
P. pakistanense	LAH:35285	Pakistan	MF588965	—	—	Ullah et al. 2018
P. pamukkalense	OKA-TR1671	Turkey	ON468479	ON468481	—	Kaygusuz et al. 2023
P. perlatum	BJ940922	Sweden	AM882772	AM882772	—	Ryberg et al. 2008
P. pinophilum	MSM 0046	Pakistan	MG742414	MG742418	—	Saba et al. 2020
P. ponderosum	MCVE:30144	Italy	MT095092	MT095116	—	Cervini et al. 2020
P. pseudoniveivelatum	BJTC FM1660	China	OM801909	OM801915	—	Mao et al. 2022
P. quercinum	PC-93	Pakistan	MZ314058	MZ314078	—	Naseer et al. 2023
P. rimosum	EL75-05	Sweden	JN649349	JN649349	—	Sjökvist et al. 2012
P. rimosum	SJ04007	Sweden	AM882763	AM882763	—	Ryberg et al. 2008
P. rimosum	UBC:F19519	Canada	HQ604622	HQ604622	—	GenBank, unpublished
P. rimosum	PBM2601 TENN	USA	—	EU600852	—	Matheny et al. 2009
P. rubrobrunneum	CAL:1307	India	KX073583	KX073587	KX073590	Tibpromma et al. 2017
P. salentinum	MCVE 30342	Italy	MT095093	MT095117	—	Cervini et al. 2020
P. singulare	FYG6363	China	OM135606	OM149381	OM780123	Zhao et al. 2022
P. solare	STU:SMNS-STU-F-0901563	Germany	MW647627	MW647627	—	Bandini et al. 2021
P. sororium	TENN:063504	USA	JQ408781	JQ319705	JQ421075	Kropp et al. 2013
P. spurium	SJ92017	Sweden	AM882784	AM882784	—	Ryberg et al. 2008
P. squamatum	PAM05052301	France	FJ904132	FJ904132	—	Larsson et al. 2009
P. squamatum	SJ08003	Sweden	FJ904136	FJ904136	—	Larsson et al. 2009
P. squarrosofulvum	**AR-22–024**	**Benin**	**PP060395**	**PP060410**	**PP430970**	**This study**
P. stramineum	**AR-22–008**	**Benin**	**PP060396**	**PP060411**	**PP430971**	**This study**
P. stramineum	**AR-22–009**	**Benin**	**PP060397**	**PP060412**	**PP430972**	**This study**
P. stramineum	**AR-22–015**	**Benin**	**PP060398**	**PP060413**	**PP430973**	**This study**
P. tiliae	**OKA-TR3501**	**Turkey**	**PP060399**	**PP060414**	**PP430974**	**This study**
P. tiliae	**OKA-TR3502**	**Turkey**	**PP060400**	**PP060415**	**PP430975**	**This study**
P. tiliae	**OKA-TR3503**	**Turkey**	**PP060401**	**PP060416**	**PP430976**	**This study**
P. triaciculare	MSM#0039	Pakistan	MG742423	MG742424	—	Saba et al. 2020
P. umbrinellum	F14488TypeS	Italy	HM209796	—	—	GenBank, unpublished
P. ushae	SMNS-STU-F-0901677	Germany	ON003433	ON003433	—	Bandini et al. 2022
P. vinosistipitatum	ACAD:11758	Canada	MH586818	—	—	GenBank, unpublished
P. xanthocephalum	PAM00100606	France	FJ904130	FJ904130	—	Larsson et al. 2009
P. yunnanense	HMJAU25840	China	MH047250	MG844975	—	Bau and Fan 2018
Pseudosperma sp.	TUF113459	Estonia	UDB027500	UDB027500	—	UNITE, unpublished

Table 1 (continued)

Species	Voucher	Country	GenBank / UNITE accession number			References
			ITS	LSU	*RPB2*	
Pseudosperma sp.	KR-M-0038070	Germany	MW009050	—	—	Bandini and Oertel 2020
Pseudosperma sp.	TUF116810	Estonia	UDB025590	UDB025590	—	UNITE, unpublished
Pseudosperma sp.	HLA0386	Benin	MT367616	—	—	GenBank, unpublished
uncultured *Agaricales*	486ad3d1	Benin	HG995718	—	—	GenBank, unpublished
uncultured *Agaricales*	79c39691	Benin	HG995912	—	—	GenBank, unpublished
uncultured *Agaricales*	881fdb9c	Benin	HG995969	—	—	GenBank, unpublished
uncultured fungus	ASV_39	Benin	LR993356	—	—	GenBank, unpublished
uncultured fungus	ASV_330	Benin	LR993647	—	—	GenBank, unpublished
uncultured fungus	ASV_313	Benin	LR993630	—	—	GenBank, unpublished
Inocybaceae sp.	HLA0707	Benin	OQ437997	—	—	GenBank, unpublished
Inocybaceae sp.	HLA0454	Benin	MN096193	MN097885	—	GenBank, unpublished
Mallocybe agardhii	AB980912	Sweden	HM209790	HM209790	—	Vauras and Larsson 2011
Mallocybe picea	BJTC FM555	China	OM801896	OM801901	OM780096	Mao et al. 2022

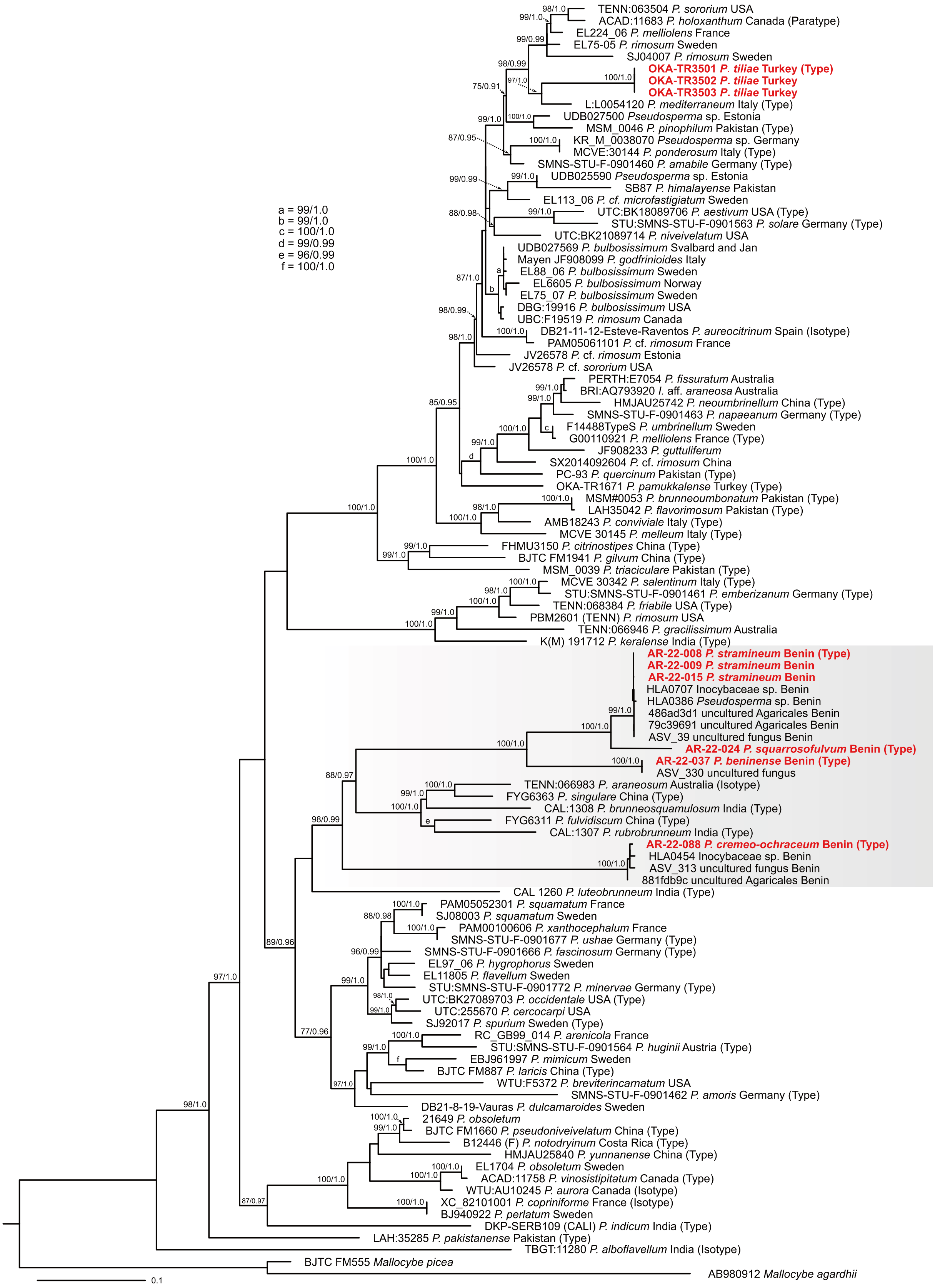
alignments were inspected using MEGA X 10.0.5 prior to subsequent analyses. A single combined dataset of ITS-LSU-*RPB2* sequences was assembled for phylogenetic analysis. The optimal evolutionary model for each segment was determined using MrModeltest 2.3 (Nylander 2004). Phylogenetic assessments employed both Maximum Likelihood (ML) and Bayesian Inference (BI) approaches on the concatenated gene regions. The ML analysis was conducted with RAxML 8.2.9. (Stamatakis 2014), using the ML + rapid bootstrap setting and the GTRGAMMAI substitution model with one 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 1 900 000 generations, sampling trees every thousand generations. The mean standard deviation of the split frequencies < 0.01 was an indication of convergence. 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 ITS, LSU, and *RPB2* sequence dataset for *Pseudosperma* species, including 27 new sequences of the specimens from Benin and Turkey, consisted of 107 taxa with 3574 characters, of which 850 were parsimony-informative, 594 parsimony-uninformative, and 2130 constant sites. The best model, GTR + I + G, was used for all the loci (ITS, LSU, and *RPB2*). This matrix exhibited 1725 unique alignment patterns. The estimated nucleotide substitution rates were as follows: A-C = 1.033265, A-G = 3.791763, A-T = 1.430448, C-G = 0.427887, C-T = 5.497537, G-T = 1.00000. Base frequencies were determined as A = 0.266, C = 0.191, G = 0.256, T = 0.287. The gamma distribution shape parameter α was calculated to be 0.282. 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* and five 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)


98/1.0
TENN:063504 P. sororium USA
99/1.0
ACAD:11683 P. holoxanthum Canada (Paratype)
EL224_06 P. melliolens France
99/0.99
EL75-05 P. rimosum Sweden
98/0.99
SJ04007 P. rimosum Sweden
OKA-TR3501 P. tiliae Turkey (Type)
100/1.0
97/1.0
OKA-TR3502 P. tiliae Turkey
75/0.91
OKA-TR3503 P. tiliae Turkey
L:L0054120 P. mediterraneum Italy (Type)
99/1.0
100/1.0
UDB027500 Pseudosperma sp. Estonia
MSM_0046 P. pinophilum Pakistan (Type)
87/0.95
100/1.0
KR_M_0038070 Pseudosperma sp. Germany
MCVE:30144 P. ponderosum Italy (Type)
SMNS-STU-F-0901460 P. amabile Germany (Type)
99/1.0
99/0.99
UDB025590 Pseudosperma sp. Estonia
SB87 P. himalayense Pakistan
EL113_06 P. cf. microfastigiatum Sweden
a = 99/1.0
b = 99/1.0
c = 100/1.0
d = 99/0.99
e = 96/0.99
f = 100/1.0
99/1.0
88/0.98
UTC:BK18089706 P. aestivum USA (Type)
STU:SMNS-STU-F-0901563 P. solare Germany (Type)
UTC:BK21089714 P. niveivelatum USA
UDB027569 P. bulbosissimum Svalbard and Jan
Mayen JF908099 P. godfrinioides Italy
a
EL88_06 P. bulbosissimum Sweden
87/1.0
EL6605 P. bulbosissimum Norway
b
EL75_07 P. bulbosissimum Sweden
98/0.99
DBG:19916 P. bulbosissimum USA
UBC:F19519 P. rimosum Canada
100/1.0
DB21-11-12-Esteve-Raventos P. aureocitrinum Spain (Isotype)
98/1.0
PAM05061101 P. cf. rimosum France
JV26578 P. cf. rimosum Estonia
JV26578 P. cf. sororium USA
PERTH:E7054 P. fissuratum Australia
99/1.0
BRI:AQ793920 I. aff. araneosa Australia
99/1.0
HMJAU25742 P. neoumbrinellum China (Type)
85/0.95
SMNS-STU-F-0901463 P. napaeanum Germany (Type)
100/1.0
F14488TypeS P. umbrinellum Sweden
c
G00110921 P. melliolens France (Type)
99/1.0
JF908233 P. guttuliferum
100/1.0
d
SX2014092604 P. cf. rimosum China
PC-93 P. quercinum Pakistan (Type)
OKA-TR1671 P. pamukkalense Turkey (Type)
100/1.0
MSM#0053 P. brunneoumbonatum Pakistan (Type)
100/1.0
98/1.0
LAH35042 P. flavorimosum Pakistan (Type)
100/1.0
AMB18243 P. conviviale Italy (Type)
MCVE 30145 P. melleum Italy (Type)
99/1.0
FHMU3150 P. citrinostipes China (Type)
99/1.0
BJTC FM1941 P. gilvum China (Type)
MSM_0039 P. triaciculare Pakistan (Type)
100/1.0
MCVE 30342 P. salentinum Italy (Type)
98/1.0
STU:SMNS-STU-F-0901461 P. emberizanum Germany (Type)
100/1.0
TENN:068384 P. friabile USA (Type)
99/1.0
PBM2601 (TENN) P. rimosum USA
100/1.0
TENN:066946 P. gracilissimum Australia
K(M) 191712 P. keralense India (Type)
AR-22-008 P. stramineum Benin (Type)
AR-22-009 P. stramineum Benin
AR-22-015 P. stramineum Benin
HLA0707 Inocybaceae sp. Benin
HLA0386 Pseudosperma sp. Benin
99/1.0
486ad3d1 uncultured Agaricales Benin
100/1.0
79c39691 uncultured Agaricales Benin
ASV_39 uncultured fungus Benin
100/1.0
AR-22-024 P. squarrosofulvum Benin (Type)
100/1.0
AR-22-037 P. beninense Benin (Type)
ASV_330 uncultured fungus
88/0.97
100/1.0
TENN:066983 P. araneosum Australia (Isotype)
99/1.0
FYG6363 P. singulare China (Type)
100/1.0
CAL:1308 P. brunneosquamulosum India (Type)
e
FYG6311 P. fulvidiscum China (Type)
98/0.99
CAL:1307 P. rubrobrunneum India (Type)
AR-22-088 P. cremeo-ochraceum Benin (Type)
HLA0454 Inocybaceae sp. Benin
100/1.0
ASV_313 uncultured fungus Benin
881fdb9c uncultured Agaricales Benin
CAL 1260 P. luteobrunneum India (Type)
100/1.0
PAM05052301 P. squamatum France
88/0.98
SJ08003 P. squamatum Sweden
100/1.0
PAM00100606 P. xanthocephalum France
SMNS-STU-F-0901677 P. ushae Germany (Type)
89/0.96
96/0.99
SMNS-STU-F-0901666 P. fascinosum Germany (Type)
EL97_06 P. hygrophorus Sweden
EL11805 P. flavellum Sweden
99/1.0
97/1.0
STU:SMNS-STU-F-0901772 P. minervae Germany (Type)
98/1.0
UTC:BK27089703 P. occidentale USA (Type)
99/1.0
UTC:255670 P. cercocarpi USA
SJ92017 P. spurium Sweden (Type)
77/0.96
100/1.0
RC_GB99_014 P. arenicola France
99/1.0
STU:SMNS-STU-F-0901564 P. huginii Austria (Type)
f
EBJ961997 P. mimicum Sweden
BJTC FM887 P. laricis China (Type)
97/1.0
WTU:F5372 P. breviterincarnatum USA
SMNS-STU-F-0901462 P. amoris Germany (Type)
98/1.0
DB21-8-19-Vauras P. dulcamaroides Sweden
100/1.0
21649 P. obsoletum
99/1.0
BJTC FM1660 P. pseudoniveivelatum China (Type)
B12446 (F) P. notodryinum Costa Rica (Type)
HMJAU25840 P. yunnanense China (Type)
100/1.0
EL1704 P. obsoletum Sweden
100/1.0
100/1.0
ACAD:11758 P. vinosistipitatum Canada (Type)
WTU:AU10245 P. aurora Canada (Isotype)
100/1.0
XC_82101001 P. copriniforme France (Isotype)
87/0.97
BJ940922 P. perlatum Sweden
DKP-SERB109 (CALI) P. indicum India (Type)
LAH:35285 P. pakistanense Pakistan (Type)
TBGT:11280 P. alboflavellum India (Isotype)
BJTC FM555 Mallocybe picea
0.1
AB980912 Mallocybe agardhii

◂**Fig. 1** Phylogenetic position of the Beninese and Turkish collections of *Pseudosperma* based on the combined ITS, LSU, and *RPB2* gene 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. The araneosum subclade formed by species from the palaeotropics and Australia is marked by a grey background

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.

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 country 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 (ITS), PP060408 (LSU), and PP430968 (*RPB2*).

Diagnosis: Most similar to *P. squamatum* but differs from it 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 ITS, LSU, and *RPB2* 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, velipellis absent, 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, cortina not observed, 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)amygdaliform 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 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.

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 from Benin and an environmental sequence of a soil sample from West Africa (ASV_330).

Discussion: Phylogenetic analyses inferred from the combined ITS, LSU, and *RPB2* sequences show that *Pseudosperma beninense* forms a monophyletic subgroup within *Pseudosperma* and is closely related to *P. squarrosofulvum* and *P. stramineum*, two other new species presented in this study. When the ITS 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 ITS 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 utriform paracystidia, pileipellis hyphae often with encrusted walls,

Fig. 2 Basidiomata of *Pseudosperma beninense* (AR-22–037, holotype). Bar = 5 mm

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 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 (ITS), PP060409 (LSU), and PP430969 (*RPB2*).

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 ITS, LSU, and *RPB2* sequences.

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, without velipellis, 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, cortina not observed, surface sordid white or cream to light brown when old, slightly pruinose only near the apex.

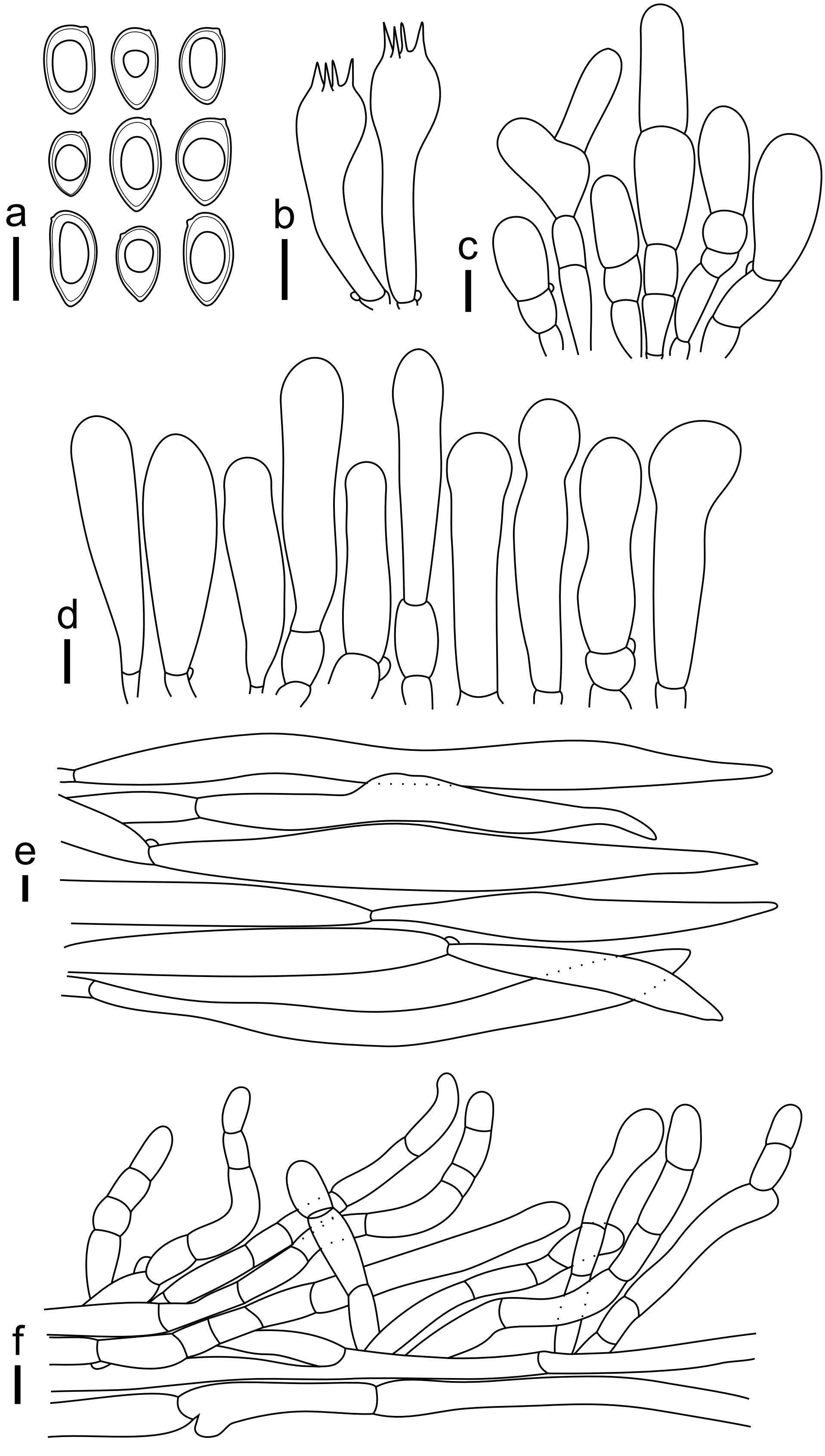


Fig. 3 Microscopic features of *Pseudosperma beninense* (AR-22–037, holotype). **a** Basidiospores. **b** Basidia. **c** Paracystidia. **d** Cheilocystidia. **e** Pileipellis. **f** Caulocystidia. Bars = 10 µm

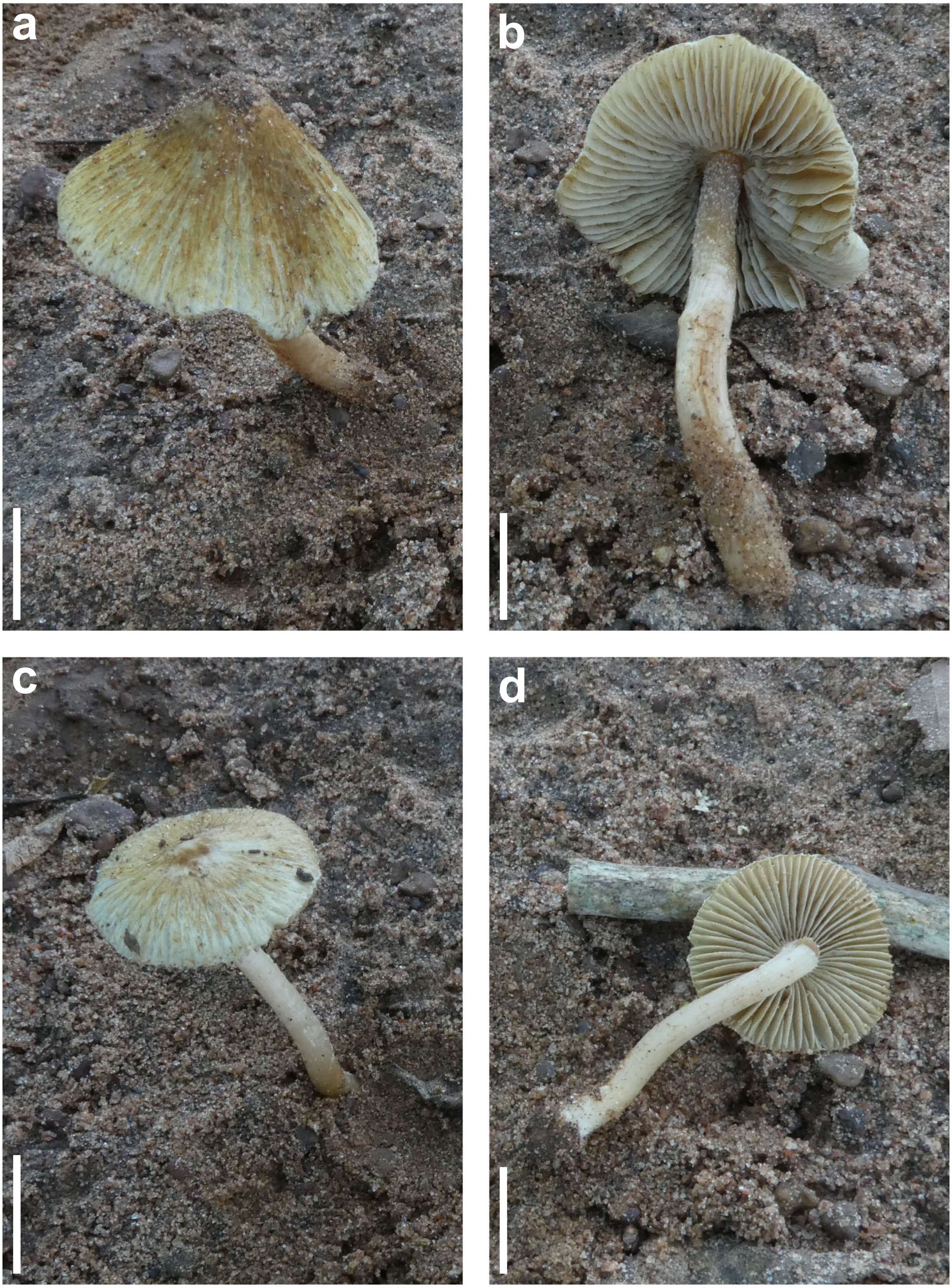


Fig. 4 Basidiomata of *Pseudosperma cremeo-ochraceum*. **a**, **b** Collection AR-22-088 (holotype). **c**, **d** Collection AR-22-089. Bars = 5 mm

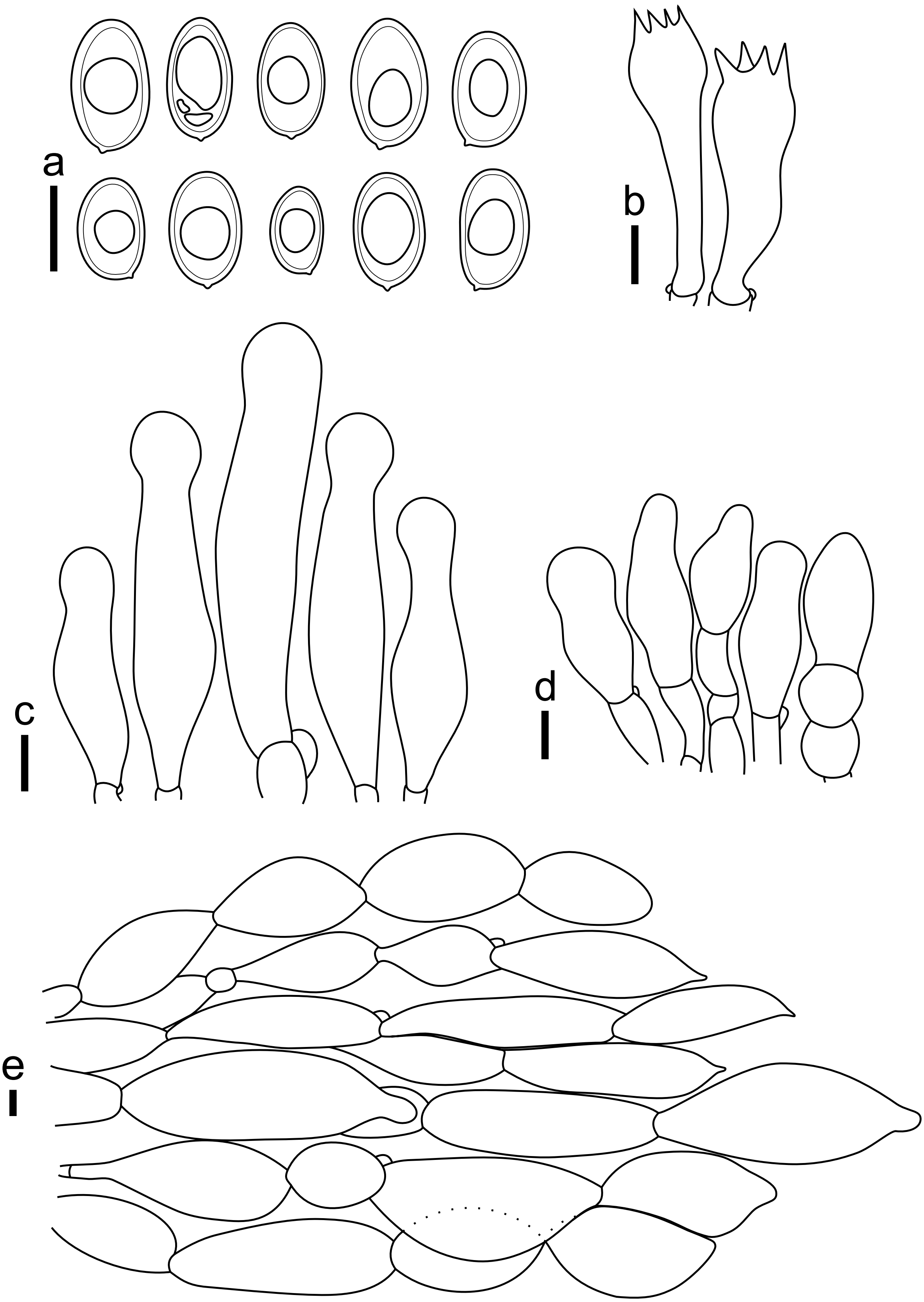


Fig. 5 Microscopic features of *Pseudosperma cremeo-ochraceum* (AR-22-088, holotype). **a** Basidiospores. **b** Basidia. **c** Cheilocystidia. **d** Paracystidia. **e** Pileipellis. Bars = 10 µm

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.

Habitat and distribution: Basidiocarps gregarious, usually terrestrial, on wet and sandy soils, in woodlands dominated by *Caesalpiniaceae* (*Isoberlinia* spp.), *Dipterocarpaceae* (*Monotes kerstingii*), and *Phyllanthaceae* (*Uapaca togoensis*). Currently known from Benin and from two environmental sequences of soil samples from West Africa (ASV_313 and 881fdb9c).

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).

Discussion: The molecular analyses revealed that *Pseudosperma cremeo-ochraceum* belongs to a distinct phylogenetic branch within the araneosum subclade that is strongly supported (MLB = 100%, BPP = 1.0). This subclade comprises species that are distributed in the tropics, in Australia, South Asia, and West Africa.

Pseudosperma cremeo-ochraceum is most closely related to several tropical species, including *P. araneosum* (Matheny & Bougher) Matheny & Esteve-Rav., *P. beninense*, *P. brunneosquamulosum* (K.P.D. Latha & Manim.) Matheny & Esteve-Rav., *P. fulvidiscum* Y.G. Fan, L.N. Zhao & W.J. Yu, *P. rubrobrunneum* (K.P.D. Latha & Manim.) Y.G. Fan, *P. singulare* Y.G. Fan, L.N. Zhao & W.J. Yu, *P. squarrosofulvum*, and *P. stramineum*. *Pseudosperma araneosum* differs from *P. cremeo-ochraceum* by lamellae that are very pale brown to brown when young, shorter basidiospores (on av. 10.2 × 6.1 µm), absence of caulocystidia, mostly cylindrical cheilocystidia, and habitats in lowland tropical sclerophyll swamps (Matheny and Bougher 2017). *Pseudosperma beninense* differs from *P. cremeo-ochraceum* by a lightly brown to straw brown pileus, a tomentose-lanose to subtomentose surface of its pileus, (sub)amygdaliform basidiospores with an acute apex, mostly oblong to cylindrical or narrowly clavate cheilocystidia and longer pileipellis elements (up to 220 µm in length). *Pseudosperma brunneosquamulosum* and *P. rubrobrunneum*, originally described from tropical India, differ from *P. cremeo-ochraceum* by notably shorter basidiospores (on av. 9.0 × 5.9 µm and av. 8.3 × 5.5 µm, respectively), versiform cheilocystidia, and associations with *Vateria indica* L. and *Hopea ponga* (Dennst.) Mabb., respectively (Tibpromma et al. 2017). Other similar Asian species are *Pseudosperma fulvidiscum* and *P. singulare* from tropical China. These species differ from *P. cremeo-ochraceum* by much shorter basidiospores (on av. 9.3 × 5.6 µm and on av. 9.1 × 6.1 µm, respectively) and an association with *Carpinus londoniana* var. *lanceolata* (Zhao et al. 2022). *Pseudosperma squarrosofulvum* has a brown-orange pileus and oblong, clavate or fusiform cheilocystidia. *Pseudosperma stramineum* has a straw-yellow or buff pileus, a squamulose-squarrose or lanose surface of its pileus, and shorter basidiospores (on av. 11.3 × 6.8 µm).

Pseudosperma renisporum known from New Zealand differs from *P. cremeo-ochraceum* by a squamulose pileus, kidney-shaped and shorter basidiospores (9.0–12.0 × 4.5–6.5 µm), cylindrical to clavate cheilocystidia, absence of caulocystidia, and a habitat in mixed forests with *Leptospermum* or *Nothofagus* (Horak 1978).

Pseudosperma brunneoumbonatum Saba & Khalid, *P. pinophilum* Saba & Khalid and *P. triaciculare* Saba & Khalid from Pakistan superficially resemble *P. cremeo-ochraceum*. However, *Pseudosperma brunneoumbonatum* differs by a strongly brown pileus, phaseoliform or ellipsoid basidiospores, clavate cheilocystidia, and an ecological association with *Pinus* sp. (Saba et al. 2020). *Pseudosperma pinophilum* differs by a pale to light yellow stipe, clavate or cylindrical cheilocystidia, and absence of caulocystidia (Saba et al. 2020). *Pseudosperma triaciculare* differs by a brownish-orange to fulvous pileus, the presence of a velipellis, shorter basidiospores (on av. 10.2 × 6.9 µm), cylindrical to clavate cheilocystidia, and a habitat with *Pinus* sp. (Saba et al. 2020).

Pseudosperma squarrosofulvum Kaygusuz, Bandini, Rühl, Sarawi, Yorou & M. Piepenbr., sp. nov. (Figs. 6 and 7).

MycoBank: MB 851973.

Etymology: The specific epithet refers to the *squarrosus* (Latin), squarrose; *fulvum* (Latin), brown-orange pileus.

Holotype: Benin, Atacora Province, Natitingou district, close to Kota Waterfall, on the ground in a gallery forest dominated by *Berlinia grandiflora* Hutch. &

Fig. 6 Basidiomata of *Pseudosperma squarrosofulvum* (AR-22–024, holotype). Bar = 10 mm

Dalziel and *Uapaca guineensis* Müll. Arg., at 10°12′43.5″N, 001°26′36.6″E, 500 m asl., 15 June 2022, leg. A. Rühl, C. Manz, D. Dongnima, F. Hampe & S. Sarawi (AR-22–024, STU). GenBank accession numbers PP060395 (ITS), PP060410 (LSU), and PP430970 (*RPB2*).

Diagnosis: Differs from *P. beninense* by a brownish-yellow to brown-orange pileus with conical fibrillose to squarrose scales, distinctly larger basidiospores (on av. 12.9 × 6.2 µm), shorter cheilocystidia (on av. 44 × 11 µm), narrow utriform to utriform paracystidia, pileipellis elements with incrusted walls and caulocystidia (up to 60 µm in length), as well as distinct ITS, LSU, and *RPB2* sequences.

Description: Pileus 5–12 mm diam., paraboloid to hemispherical, later convex to plano-convex, finally almost applanate, with or without a low small papilla, with deflexed margin when young, later even straight, velipellis absent, colour mostly brownish yellow (2.5Y 7/8–10, 7.5YR 6/8–10) to brown-orange (5YR 5/6–10), gradually darkening towards the centre, with paler margin, the entire surface covered by yellowish ochre (5YR 5/6–8, 4/6) to brownish-yellow (7.5YR 5/6–8), erect, conical scales, with persistent fibrillose veil remnants at the margin. Lamellae moderately crowded, adnexed, ventricose, creamy white to pale yellow when young, becoming light brown with age, margin eroded, whitish. Stipe 8–15 × 0.8–2 mm, central, cylindrical, with subbulbous at the base, cortina not observed, surface whitish to straw-yellow, pruinose only near the apex. Colour of exsiccate: pileus pale dirty straw-yellow to pale yellow–brown, lamellae and stipe whitish. Smell unrecorded.

Basidiospores 11.0–18.0 µm (av. 12.9 µm, SD ± 1.7 µm) × 5.1–8.3 µm (av. 6.2 µm, SD ± 0.6 µm); Q = 1.8–2.6 (av. 2.1, SD ± 0.2) (n = 90 of 1 coll.), mostly oblong to subcylindrical, with guttules, smooth, slightly thick-walled, yellowish brown in 5% KOH. Basidia 25–30 × 8–11 µm, clavate, 4-spored, thin-walled, hyaline or very pale brown in 5% KOH. Cheilocystidia 37–55 µm (av. 44 µm, SD ± 6.0 µm) × 8.5–14 µm (av. 11 µm, SD ± 1.5 µm); Q = 2.9–6.1 (av. 4.2, SD ± 1.0) (n = 40 of 1 coll.), usually oblong, clavate or fusiform, hyaline or very pale yellowish-brown in 5% KOH. Paracystidia 15–35 × 8–17 µm, narrowly utriform

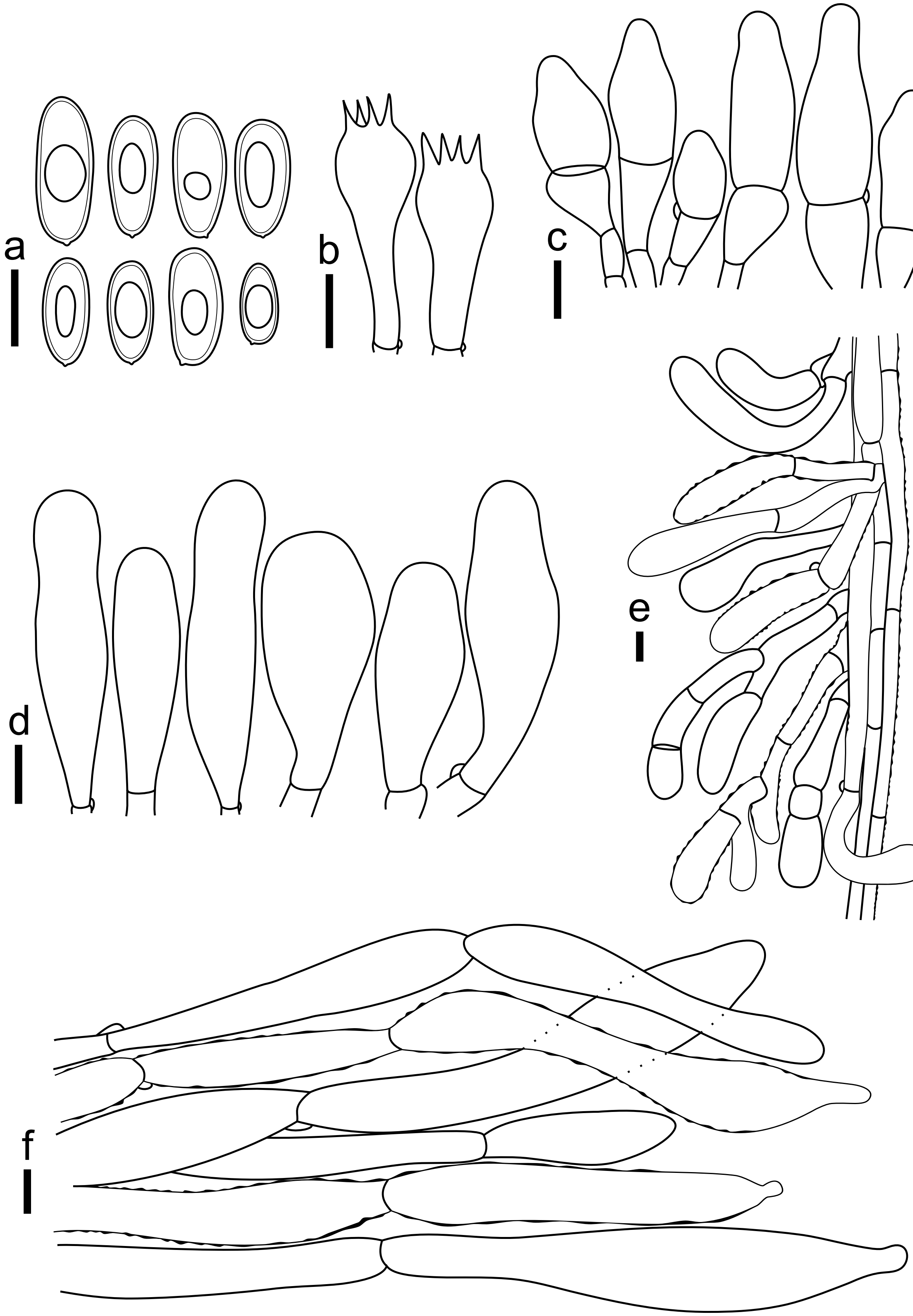


Fig. 7 Microscopic features of *Pseudosperma squarrosofulvum* (AR-22–024, holotype). **a** Basidiospores. **b** Basidia. **c** Paracystidia. **d** Cheilocystidia. **e** Caulocystidia. **f** Pileipellis. Bars = 10 µm

to utriform, thin-walled, hyaline or very pale yellowish-brown in 5% KOH. Pileipellis a cutis, formed by cylindrical to fusiform elements with subcapitate to rostrate apex or clavate terminal elements, (35)50–110 × 8–20 µm, often with incrusted walls, yellowish-green in 5% KOH. Caulocystidia (18)35–60 × 8–18 µm, mostly cylindrical or narrowly clavate, in clusters on erect hyphae, with often slightly incrusted walls, pale brownish yellow in 5% KOH. Stipitipellis a cutis of slender, cylindrical hyphae, 5–14 µm wide, thin-walled, colourless in 5% KOH. Clamp connections present in all parts examined.

Habitat and distribution: Basidiomata gregarious, usually terrestrial, on wet and sandy soils, under *Berlinia grandiflora* and *Uapaca guineensis*. Hitherto only known from Benin.

Discussion: Phylogenetic analyses of the combined ITS-LSU-*RPB2* sequences (Fig. 1) indicate that *Pseudosperma squarrosofulvum* is closely related to *P. stramineum* and *P. beninense*. Morphologically, *P. stramineum* differs from *P. squarrosofulvum* by its straw-yellow or buff pileus, a squamulose-squarrose or lanose surface of its pileus, shorter basidiospores (on av. 11.3 × 6.8 µm) with a lower Q-value (Q = 1.7), and broadly clavate to ellipsoid or obovoid paracystidia. *P. beninense* has a lightly brown to straw brown pileus, a tomentose-lanose to subtomentose surface of its pileus, shorter basidiospores (on av. 12.5 × 7.0 µm), slightly longer cheilocystidia (on av. 51 × 14 µm), cylindrical to broadly clavate paracystidia and longer pileipellis cells reaching up to 220 µm.

Other tropical species with genetic affinities to *Pseudosperma squarrosofulvum* are *P. araneosum*, *P. brunneosquamulosum*, *P. rubrobrunneum*, *P. fulvidiscum*, and *P. singulare*. Morphologically, *P. araneosum* from tropical Australia differs from *P. squarrosofulvum* by a strongly radially rimose pileus, notably shorter basidiospores (on av. 10.2 × 6.1 µm), predominantly cylindrical cheilocystidia, absence of caulocystidia, and growth on soil in *Melaleuca* swamp in lowland tropical mixed forests with *Acacia*, *Corymbia*, *Eucalyptus* and *Lophostemon* (Matheny and Bougher 2017). *Pseudosperma brunneosquamulosum* and *P. rubrobrunneum*, originally described from tropical India, differ from *P. squarrosofulvum* by significantly shorter basidiospores (on av. 9.0 × 5.9 µm and av. 8.3 × 5.5 µm, respectively), versiform cheilocystidia, and associations with *Vateria indica* and *Hopea ponga*, respectively (Tibpromma et al. 2017). *Pseudosperma fulvidiscum* and *P. singulare*, recently described from tropical China, differs by shorter basidiospores (on av. 9.3 × 5.6 µm and 9.1 × 6.1 µm, respectively), and an association with trees of *Carpinus londoniana* var. *lanceolata* (Hand.-Mazz.) P.C.Li (Zhao et al. 2022).

Pseudosperma stramineum Kaygusuz, Bandini, Rühl, Sarawi, Yorou & M. Piepenbr., sp. nov. (Figs. 8 and 9).

MycoBank: MB 851975.

Etymology: The epithet refers to the straw-yellow colour of the pileus.

Holotype: Benin, Borgou Department, Fôret de l'Okpara, on the ground in a savannah forest dominated by *Isoberlinia doka*, *I. tomentosa*, *Monotes kerstingii* and *Uapaca togoensis*, at 09°14′11.6″N, 002°43′26.0″E, 201 m asl., 12 June 2022, leg. A. Rühl, S. Badou, C. Manz, D. Dongnima, F. Hampe, B. Olou & S. Sarawi (AR-22–008, STU). GenBank accession numbers PP060396 (ITS), PP060411 (LSU), and PP430971 (*RPB2*).

Diagnosis: Similar to *P. amoris* Bandini & B. Oertel, but differs by the combination of smaller basidiomata (up to 15 mm in diam.), often squamulose-squarrose pileus surface, larger basidiospores (on av. 11.3 × 6.8 µm), predominantly oblong to narrowly clavate to clavate cheilocystidia, the presence of paracystidia, mostly narrowly cylindrical to narrowly clavate caulocystidia, association with a savannah forest, and by distinct ITS, LSU, and *RPB2* sequences.

Description: Pileus 5–15 mm diam., paraboloid to hemispherical when young, later convex to plano-convex, with subumbo to obtuse umbo, undulate with age, with inflexed margin when young, later even deflexed, velipellis absent, colour predominantly straw-yellow (2.5Y 8–7/6) or buff (2.5Y 7/8–10, 6/8), evenly coloured but darker with age, surface felty to lanose, strongly squamulose-squarrose or lanose around the centre with bundles of fibre. Lamellae moderately crowded to crowded, adnexed, (sub)ventricose, yellowish when young, pale brown with age, edge fimbriate to eroded, whitish. Stipe 10–20 × 0.6–1.5 mm, central, cylindrical, usually slightly curved, with subbulbous or distinctly bulbous base, cortina not observed, surface whitish to straw-yellow, pruinose only near the apex. Colour of exsiccate: pileus whitish to pale straw-yellow (2.5Y 8/4–6), lamellae and stipe concolorous. Smell unrecorded.

Basidiospores 10.0–14.0 µm (av. 11.3 µm, SD ± 0.9 µm) × 5.9–8.3 µm (av. 6.8 µm, SD ± 0.5 µm); Q = 1.5–1.9 (av. 1.7, SD ± 0.1) (n = 130 of 3 coll.), mostly oblong, rarely ellipsoid, with guttules, smooth, slightly thick-walled, pale brown to yellowish brown in 5% KOH. Basidia 30–40 × 8.0–11.0 µm, clavate, 4-spored, thin-walled, very pale brown or hyaline in 5% KOH. Cheilocystidia 30–55 µm (av. 40 µm, SD ± 6.6 µm) × 10–20 µm (av. 14 µm, SD ± 1.8 µm); Q = 1.6–4.5 (av. 2.7, SD ± 0.6) (n = 55 of 3 coll.), mostly oblong to narrowly clavate to clavate, thin-walled, pale yellowish-brown in 5% KOH. Paracystidia 20–35 × 10–17 µm, broadly clavate to ellipsoid or obovoid, thin-walled, slightly pale yellowish-greenish in 5% KOH. Pileipellis a cutis, made up of conical, clavate or cylindrical terminal elements with rostrate to obtuse apex, 40–100 × 8–18 µm, walls often strongly incrusted, pale brownish yellow in 5% KOH. Caulocystidia 25–90 × 7.5–15 µm, mostly narrowly cylindrical to narrowly clavate often

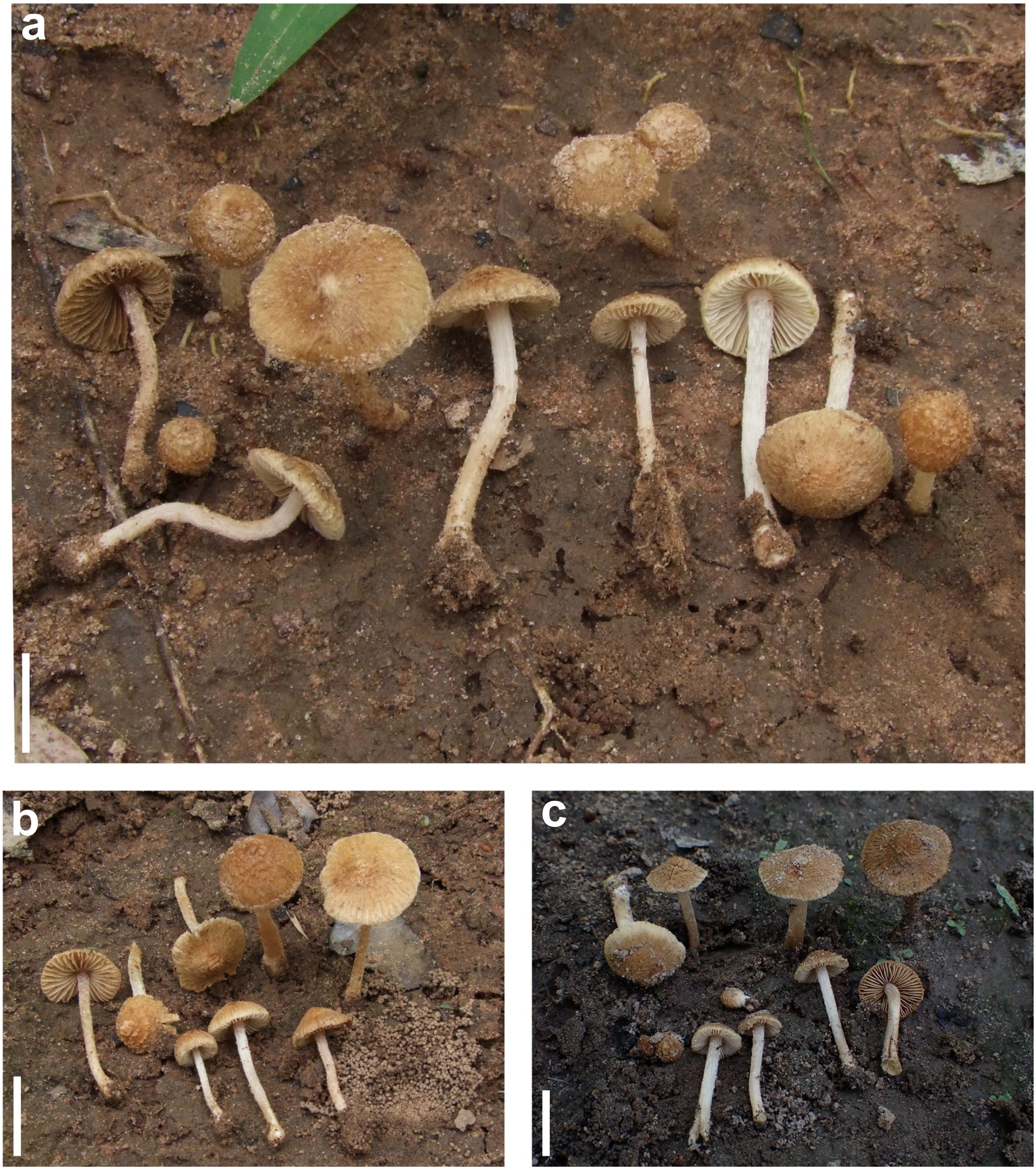


Fig. 8 Basidiomata of *Pseudosperma stramineum*. **a** Collection AR-22-008 (holotype). **b** Collection AR-22-009. **c** Collection AR-22-015. Bars = 10 mm

with slightly incrusted walls, pale brownish yellow in 5% KOH. Stipitipellis a cutis of cylindrical hyphae, 5–12 µm wide, thin-walled, colourless in 5% KOH. Clamp connections present in all parts examined.

Habitat and distribution: Basidiocarps gregarious to subgregarious usually on sandy soils, associated with *Caesalpiniaceae* (*Isoberlinia* spp.), *Dipterocarpaceae* (*Monotes kerstingii*), and *Phyllanthaceae* (*Uapaca togoensis*).

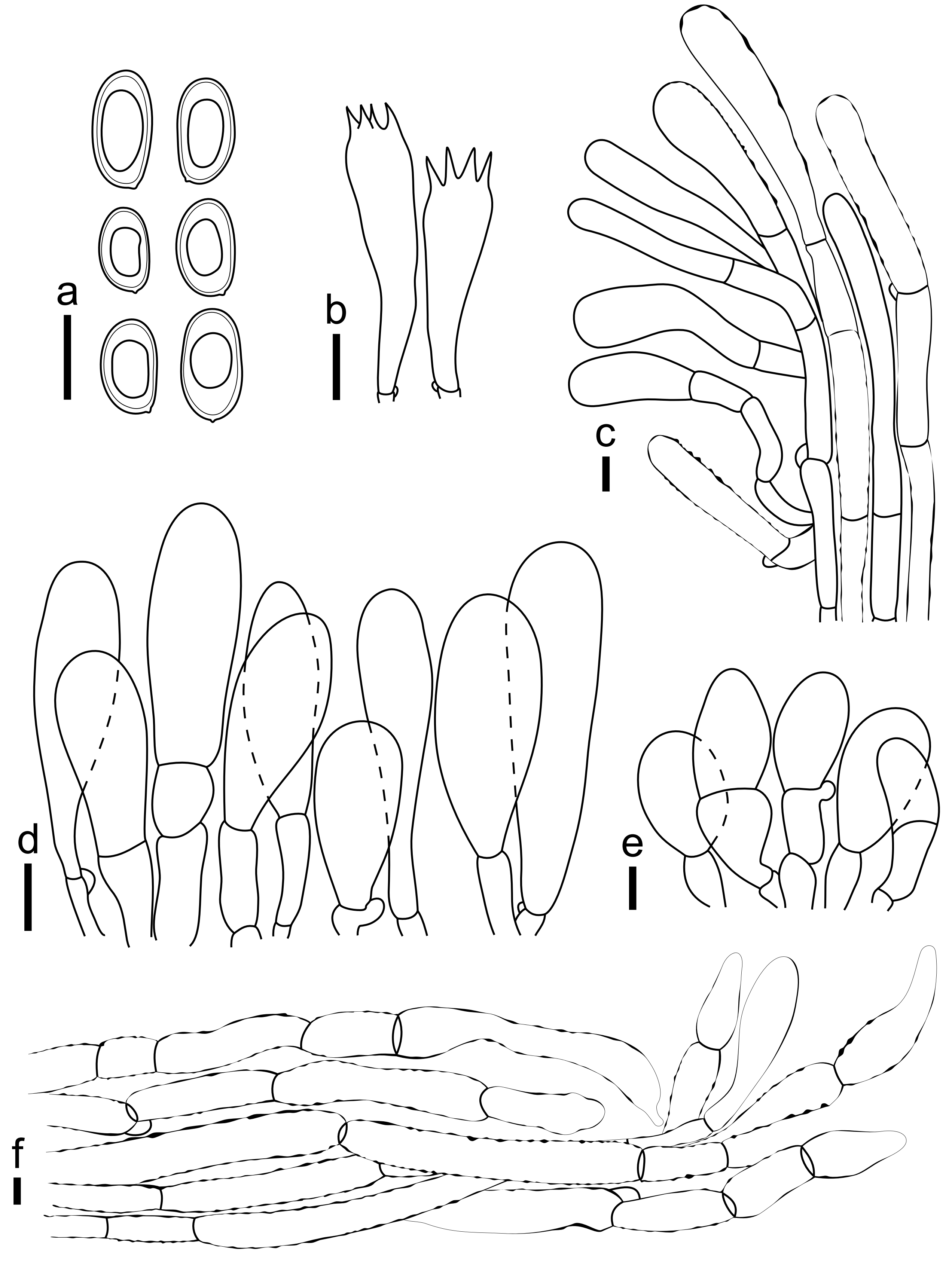


Fig. 9 Microscopic features of *Pseudosperma stramineum* (AR-22-008, holotype). **a** Basidiospores. **b** Basidia. **c** Caulocystidia. **d** Cheilocystidia. **e** Paracystidia. **f** Pileipellis. Bars = 10 µm

Hitherto known from Benin and from environmental sequences of soil samples from West Africa (486ad3d1, 79c39691, and ASV_39).

Additional specimens examined: Benin, Borgou Department, Fôret de l'Okpara, on soil in savannah forest dominated by *Isoberlinia* spp., *Monotes kerstingii* and *Uapaca togoensis*, at 09°14′11.6″N, 002°43′26.0″E, 201 m asl., 12 June 2022, leg. A. Rühl, S. Badou, C. Manz, D. Dongnima, F. Hampe, B. Olou & S. Sarawi (AR-22–009, UNIPAR); *ibid.,* Borgou Department, N'Dali, on soil in savannah forest dominated by *Isoberlinia* spp., *Monotes kerstingii* and *Uapaca togoensis*, at 09°44′38.5″N, 002°41′26.3″E, 350 m asl., 13 June 2022, leg. A. Rühl, C. Manz, D. Dongnima, F. Hampe & S. Sarawi (AR-22–015, UNIPAR).

Discussion: Phylogenetically, *Pseudosperma stramineum* is closely related to *P. squarrosofulvum* and *P. beninense*, but these species form three independent lineages nested in a tropical subclade of *Pseudosperma* (MLB = 100%, BPP = 1.0, Fig. 1). *Pseudosperma squarrosofulvum* differs from *P. stramineum* by its brownish yellow to brown-orange pileus, conical fibrillose scaly pilei surface with yellow ochre to brownish yellow tinge, longer basidiospores (on av. 12.9 × 6.2 µm), narrowly utriform to utriform paracystidia, and shorter caulocystidia (18–60 × 8.0–18 µm). *Pseudosperma beninense* has a tomentose-lanose to subtomentose pileus surface, mainly (sub)amygdaliform basidiospores with an acute apex, longer cheilocystidia (on av. 51 × 14 µm) and longer pileipellis elements (up to 220 µm in length).

Based on the ITS-LSU-*RPB2* phylogeny, *Pseudosperma stramineum* is also somewhat related to further tropical *Pseudosperma* species, namely *P. araneosum* and *P. gracilissimum* from Australia (Matheny and Bougher 2017), *P. brunneosquamulosum*, *P. rubrobrunneum* and *P. luteobrunneum* (K.P.D. Latha & Manim.) Matheny & Esteve-Rav. from India (Tibpromma et al. 2017), and *P. fulvidiscum* and *P. singulare* from China (Zhao et al. 2022). Apart from different geographical locations and different plant associations, *Pseudosperma stramineum* is easily distinguished from these species by its significantly longer basidiospores, which are av. 11.3 × 6.8 µm.

Pseudosperma notodryinum (Singer, I.J.A. Aguiar & Ivory) Matheny & Esteve-Rav., described from tropical Costa Rica, differs from *P. stramineum* by a brown to umbrious pileus with a distinct umbo, a slender stipe, shorter basidiospores (on av. 7.0–9.0 × 4.0–5.0 µm), and a habitat in *Quercus oleoides* Schltdl. & Cham. forests (Singer et al. 1983).

Further species morphologically similar to *Pseudosperma stramineum* in terms of the pileus colour are *P. amoris, P. flavellum* (P. Karst.) Matheny & Esteve-Rav. and *P. minervae* Bandini & G. Bandini. *Pseudosperma amoris*, described from Germany, differs from *P. stramineum* by the presence of a velipellis, and shorter basidiospores (on av. 10.3 × 6.2 µm) (Bandini and Oertel 2020). The European species *Pseudosperma flavellum* has shorter basidiospores (on av. 10.6 × 4.9 µm), mostly (sub)cylindrical to subutriform cheilocystidia, and no paracystidia (Karsten 1889; Bandini and Oertel 2020). *Pseudosperma minervae*, recently described from Germany, has a rimulose pileus, shorter basidiospores (on av. 10.4 µm in length) and generally (sub)clavate cheilocystidia (Bandini et al. 2023). These species are genetically very distant from *Pseudosperma stramineum* (Fig. 1).

Pseudosperma tiliae Kaygusuz, Bandini, Rühl, Sarawi, Yorou & M. Piepenbr., sp. nov. (Figs. 10 and 11).

MycoBank: MB 851976.

Etymology: The specific epithet refers to *Tilia*, the genus of the trees, which are probably ectomycorrhizal (ECM) partners of this fungal species.

Holotype: Turkey, Isparta Province, Atabey district, İslamköy village, on soil under *Tilia platyphyllos*, at 37°56′11.0″N, 30°38′46.9″E, 1000 m asl., 17 June 2022, leg. O. Kaygusuz (OKA-TR3501, ISUF). GenBank accession numbers PP060399 (ITS), PP060414 (LSU), and PP430974 (*RPB2*).

Diagnosis: Similar to *P. mediterraneum*, but differing by basidiomata with a broad subumbo, pale yellow to chrome yellow pileus often with brownish-red tinge at the centre, somewhat smaller basidiospores measuring on average 12.5 × 7.0 µm (on av. Q = 1.8), distinctly longer cheilocystidia (on av. 57 × 14 µm), association with *Tilia platyphyllos*, and by distinct ITS, LSU, and *RPB2* sequences.

Description: Pileus 30–45 mm diam., paraboloid to hemispherical when young, later convex, with low broad umbo, margin first often inflexed, later even deflexed or straight, with abundant remnants of a dingy whitish velipellis, colour predominantly pale yellow or chrome yellow (5Y 8/4–8, 2.5Y 7–5/6), transitioning to brown towards the centre, (5YR 5–4/6), often with dark brown to brownish-red tinge at the centre (10R 4/4–8), outwards paler, background whitish to whitish yellow towards the margin, surface dry, mate, appressed fibrillose and strongly rimose, splitting deeply radially, velipellis mostly present as a whitish to dingy whitish patch in the centre of the pileus, fugacious or not. Lamellae moderately crowded to crowded, adnexed, (sub) ventricose, at first creamy white or dingy whitish, then with a faintly orange tint, brownish when old, edge fimbriate to eroded, whitish. Stipe 35–50 × 4–10 mm, central, cylindrical, straight or sometimes curved at the base, with equal diam. but sometimes widened to subbulbous at the base, cortina not observed, surface whitish to ivory, covered by light orange-brown (7.5YR 7/4–6) fibrils downwards, pruinose near the apex, with white particles like the remains of a volva at the base. Colour of exsiccate: pileus whitish to ivory, lamellae and stipe concolorous or slightly lighter, slightly darker on drying. Smell faintly spermatic.

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

Basidiospores 10.0–14.5 µm (av. 12.5 µm, SD ± 1.4 µm) × 6.0–8.0 µm (av. 7.0 µm, SD ± 0.5 µm); Q = 1.4–2.3 (av. 1.8, SD ± 0.2) (n = 150 of 3 coll.), mostly oblong, rarely ellipsoid, sometimes with slight suprahilar depression, with guttules, smooth, slightly thick-walled, pale brown to brown in 5% KOH. Basidia 25–45 × 10–15 µm, clavate, generally 4-spored, rarely 2-spored, thin-walled, hyaline in 5% KOH. Cheilocystidia 45–75 µm (av. 57 µm, SD ± 1.5 µm) × 10–18 µm (av. 14 µm, SD ± 1.1 µm); Q = 2.8–5.8 (av. 4.3, SD ± 0.9) (n = 47 of 3 coll.), mostly narrowly clavate to clavate or narrowly utriform, with rounded apex, sometimes cylindrical, in clusters, thin-walled, pale yellowish-greenish in 5% KOH. Paracystidia 20–35 × 9–14 µm, fusiform, narrowly utriform, ellipsoid or subglobose, sometimes divided by septa,

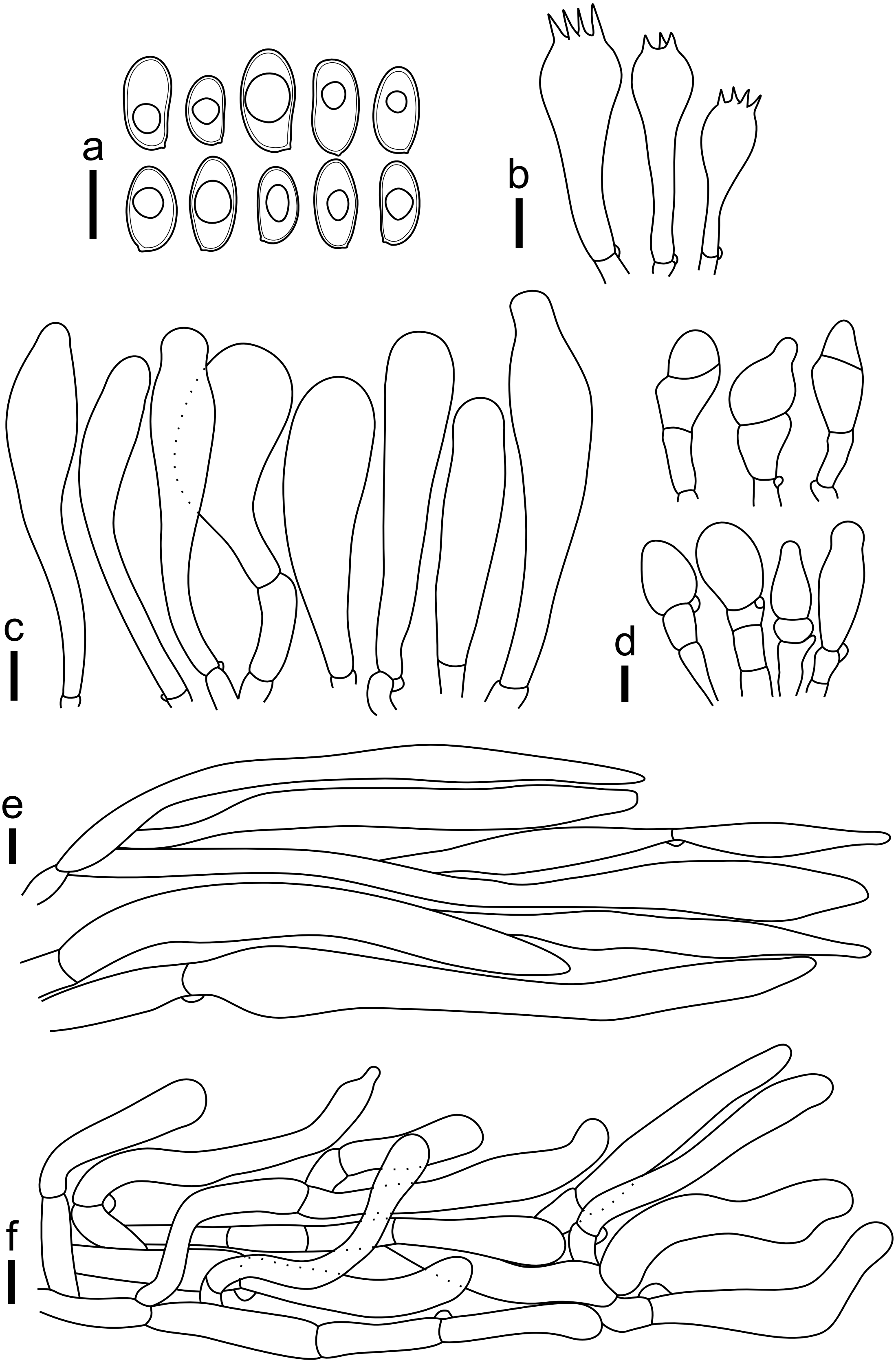


Fig. 11 Microscopic features of *Pseudosperma tiliae* (OKA-TR3501, holotype). **a** Basidiospores. **b** Basidia. **c** Cheilocystidia. **d** Paracystidia. **e** Pileipellis. **f** Caulocystidia. Bars = 10 µm

thin-walled, pale yellowish-greenish in 5% KOH. Pileipellis a cutis, composed of narrowly fusiform or cylindrical cells with acute to obtuse apex, with somewhat ascending terminal elements, 100–330 × 8–20 µm, thin-walled, pale brownish yellow in 5% KOH. Caulocystidia 50–90(120) × 6–14 µm, mostly narrowly clavate to cylindrical, sometimes with mucronate apex, thin-walled, hyaline. Stipitipellis a cutis of cylindrical hyphae, 3–10 µm wide, thin-walled, colourless in 5% KOH. Clamp connections present in all parts examined.

Habitat and distribution: Basidiocarps subgregarious, usually on humus-rich soils, from early to late June, generally present at 1000 m asl., under *Tilia platyphyllos*. Currently known from the Mediterranean region of Turkey.

Additional specimens examined: Turkey, Isparta Province, Çünür district, Süleyman Demirel University East Campus, on soil under *T. platyphyllos*, at 37°49′43.3″N, 30°32′24.3″E, 1020 m asl., 04 June 2023, leg. O. Kaygusuz (OKA-TR3502, ISUF); *ibid.,* Atabey district, around Atabey-İslamköy road, on soil under *T. platyphyllos*, at 37°53′45.1″N, 30°37′40.2″E, 1005 m asl., 12 June 2023, leg. O. Kaygusuz (OKA-TR3503, ISUF); *ibid.,* Aksu district, on soil under *T. platyphyllos*, at 37°48′40.2″N, 31°05′22.7″E, 1210 m asl., 21 June 2023, leg. O. Kaygusuz (OKA-TR3504, ISUF).

Discussion: In the concatenated ITS-LSU-*RPB2* 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 holoxanthum*, 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 (ITS 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 the combined ITS, LSU, and *RPB2* dataset 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 subclade that in addition to the species from Benin includes five further species from tropical regions of the palaeotropics and Australia. These five species are *P. araneosum* from Australia (Matheny and Bougher 2017), *Pseudosperma brunneosquamulosum* 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.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11557-024-01964-2.

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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.

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Data availability The DNA sequences produced in this study are available on NCBI GenBank (https://www.ncbi.nlm.nih.gov). The combined DNA dataset used for phylogenetic analyses is available in a supplementary file.

Code availability Not applicable.

Declarations

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.

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