

Three new species of the genus *Pseudosperma* (*Inocybaceae*)

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Bandini D., Oertel B. (2020): Three new species of the genus *Pseudosperma* (*Inocybaceae*). – Czech Mycol. 72(2): 221–250.

As a result of molecular phylogenetic and morphological analyses, three new species of the genus *Pseudosperma*, namely *P. amabile*, *P. amoris* and *P. napaeenum*, are described in detail along with illustrations of their macro- and micromorphology and a phylogenetic tree. In addition, to ensure a correct interpretation of the species identity in comparison with morphologically similar species, the holotype of *P. flavellum*, as well as an isoparatype of *P. spurium* and isotypes of *P. aureocitrinum* and *P. copriniforme* have been examined, and of the latter two species also an ITS sequence was obtained. A drawing of the microscopical details of all four type specimens is given.

Key words: *Agaricales*, *Inocybe*, taxonomy, molecular phylogeny, ITS.

Article history: received 18 July 2020, revised 11 September 2020, accepted 17 September 2020, published online 15 October 2020.

DOI: <https://doi.org/10.33585/cmy.72205>

Bandini D., Oertel B. (2020): Tři nové druhy rodu *Pseudosperma* (*Inocybaceae*). – Czech Mycol. 72(2): 221–250.

Jako výsledek molekulárně fylogenetické a morfologické analýzy jsou popsány tři nové druhy rodu *Pseudosperma*, konkrétně *P. amabile*, *P. amoris* a *P. napaeenum*. Je podán jejich podrobný popis spolu s ilustracemi jejich makro- a mikromorfologie, doplněný fylogenetickým stromem celé skupiny. Kromě toho byly studovány typové položky morfologicky podobných druhů – holotyp *P. flavellum*, isoparatyp *P. spurium* a isotypy *P. aureocitrinum* a *P. copriniforme* – pro srovnání s novými druhy a potvrzení správné interpretace jejich identity; od posledních dvou zmíněných druhů byly též získány sekvence ITS. Srovnání je doplněno kresbou mikroskopických detailů všech čtyř typových položek.

INTRODUCTION

The family *Inocybaceae* was until recently constituted by the genera *Inocybe* (Fr.) Fr., *Auritella* Matheny & Bougher and *Tubariomyces* Esteve-Rav. & Matheny (see e.g. Latha et al. 2016). The genus *Inocybe* itself was divided into the three subgenera *Mallocybe* Kuyper, *Inosperma* Kühner and *Inocybe* (Kuyper

1986, Stangl 1989, Bon 1997a, 1997b, 1998), or according to Matheny & Kudzma (2019) into five major clades, namely *Inocybe*, *Inosperma*, *Mallocybe*, *Nothocybe* and *Pseudosperma*. However, the former subgenera *Inocybe*, *Inosperma* and *Mallocybe* have been raised by Matheny et al. (2020) to genus level as *Inocybe*, *Inosperma* (Kühner) Matheny & Esteve-Rav. and *Mallocybe* (Kuyper) Matheny & Esteve-Rav., respectively. *Nothocybe*, too, was established at the rank of a genus as *Nothocybe* Matheny & K.P.D. Latha, and the former *Inocybe* sect. *Rimosae* (Fr.) Quél. has become the genus *Pseudosperma* Matheny & Esteve-Rav. Thus, according to Matheny et al. (2020), the family *Inocybaceae* now comprises seven genera.

The present article deals with three new species of the recently established genus *Pseudosperma*, which Matheny et al. (2020) define by the following characteristics: “Cheilocystidia arising from modified basidia, pleurocystidia absent, basidia hyaline or not necropigmented; lamellae adnexed to sinuate; pileus fibrillose or rarely squamulose, often rimose; stipe apex often distinctly pruinose, furfuraceous, or somewhat flocculose, stipe base usually even, stipe context not changing color where bruised; odor often spermatic, like green corn, or honey, occasionally nil; spores usually elliptic to indistinctly phaseoliform. Ectomycorrhizal with wide range of plant families.” The former *Inocybe sororia* Kauffman, now *P. sororium* (Kauffman) Matheny & Esteve-Rav., has been taken as the type of *Pseudosperma*.

Compared to the new genus *Inocybe* with presently an estimated number of 850 species worldwide (Matheny et al. 2020), *Pseudosperma* is a rather small genus, at present comprising nearly 70 described species worldwide (see the enumeration of species in Matheny et al. 2020). Of these, more than 40 species are known to occur also in Europe or are originally described from a European country (see the key in Bon 1997a, the list in Matheny et al. 2020 and for recently described new species e.g. Jacobsson & Larsson 2009, 2012, Esteve-Raventós 2014, Carteret & Reumaux 2017). In the past few years, also many new species of the genus *Pseudosperma* were described from e.g. Pakistan (Ullah et al. 2018), India, especially Kerala (Latha et al. 2016, Latha & Manimohan 2017), China (Bau & Fan 2018), USA (Kropp et al. 2013) and Australia (Matheny & Bougher 2017). The number of new species will certainly increase, since in many parts of the world genetic examination of species has only just begun.

Species of the genus *Pseudosperma* occur in quite diverse habitats, on dry sandy soil in lowland dunes at the sea-coast, for instance *P. arenicola* (R. Heim) Matheny & Esteve-Rav., on high mountains, such as *P. bulbosissimum* (Kühner) Matheny & Esteve-Rav., in tropical regions, like *P. alboflavellum* (C.K. Pradeep & Matheny) Haelew., in arctic realms, e.g. *P. nanum* (F.H. Möll.) Matheny & Esteve-Rav., and on acid as well as on calcareous soil. In spite of this ecological diversity, the macro- and micro-features are often very similar. For this reason several of the species of this genus were subsumed by Kuyper (1986) under the name

Inocybe rimosa, for instance the former *I. perlata*, *I. umbrinella*, *I. obsoleta*, *I. orbata*, *I. holoxantha* and *I. cerina* (as *I. fastigiata* var. *cerina*), which are in fact all good, separate species [Dermek & Veselský 1977 (as subspecies), Grund & Stuntz 1981, Bon 1997a]. Thus, during the last 30 years, this broad concept of *I. rimosa* may have resulted in several other new species considered to be *P. rimosum*. This perhaps was the case with two of the three species described in the present article, too, while the third, *P. amabile*, might macroscopically have been mistaken for *Inosperma maculatum* (Boud.) Matheny & Esteve-Rav. The latter species however belongs to the genus *Inosperma*, which is defined by Matheny et al. (2020) as follows: “Basidiospores often phaseoliform, basidia hyaline or necropigmented, cheilocystidia with cyanophilous contents in some species, pleurocystidia absent; stipe base even or bulbous in some species, context often reddening where bruised; odor often distinctive. Ectomycorrhizal with wide range of plant families.”

The aim of this study is to improve the knowledge of the genus *Pseudosperma* by adding descriptions of three new species.

MATERIAL AND METHODS

Notes were taken of relevant macroscopic traits of fresh basidiomata, especially those which change by drying, e.g. colour and smell, of habitat and surrounding trees, and, later on, of the exsiccata colour. Microscopic traits were examined and photographed in water and 3% KOH solution with a Leica DM-750 at magnifications of 400× and 1000×. Measurements were made with Zeiss Axiovision version 4.8. Basidia were measured without sterigmata. All sizes measured are given as length by width. 120 spores and 45 basidia or cystidia from 3 collections were measured for the new species, as well as 40 spores and 15 basidia or cystidia from additional type specimens of other species. The Q value is the ratio of spore length to width.

Photos of the fresh collections were taken by D. Bandini with a Panasonic Lumix GH2 with a Leica DG Macro-Elmarit 1:2.8/45 mm lens. For the determination of colour temperature, a calibration card was photographed together with the fresh collections at the site where they were found. The RAW files were developed with Silkypix Developer Studio 4.0. Colour codes are taken from Munsell (2009, cited as “Mu”). Herbarium acronyms are used according to Holmgren et al. (1990), the acronym DB means the private herbarium of Ditte Bandini.

TK25 and ÖK25V are German and Austrian mapping grids, 1:25,000.

The DNA of specimens was extracted and the ITS region sequenced by Alvalab (Oviedo, Spain, <http://alvalab.es/>).

Sequences were assembled and edited using Geneious (version 6.1.2, Biomatters Ltd., Auckland, New Zealand). Forward and reverse sequences were merged, edited if necessary and a consensus sequence was generated for every sample. Sequences were submitted to GenBank (Tab. 1).

FASTA sequences were studied in MEGA 5.2 (<https://megasoftware.net/>; Tamura et al. 2013).

For better anchoring of alignment procedures, the start of each ITS sequence was defined by the last conserved SSU motive GGAAGGATCATT and the continuation of the ITS with the first motive of LSU, TTGACCTCAAATCA (or with its similar species- or genus-specific variants of this region respectively), has been preserved for all analyses. All other parts of SSU and LSU were trimmed.

The comparative evaluation of the ITS sequences to record the adjacent species of the three new *Pseudosperma* species were made with BLAST analysis (Altschul et al. 1990). If necessary, the sequences were trimmed to the exact length of ITS. In GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) the setting “Optimize for somewhat similar sequences, blastn” and in UNITE (<https://unite.ut.ee/>) the massBLASter was used. Collections of unpublished private ITS sequences were used for comparison using the GenBank tool “Align two or more sequences”, the so-called “Local BLAST” method, using only ITS sequences of full length as references. This avoids the frequent BLAST errors which occur when comparing with reference sequences that are too short.

The sequences were aligned with MAFFT version 7 (Katoh et al. 2019; <https://mafft.cbrc.jp/alignment/server/>). The most suitable MAFFT-algorithm for *Inocybaceae* ITS sequences was found to be G-INS-i. All other parameters were set to default.

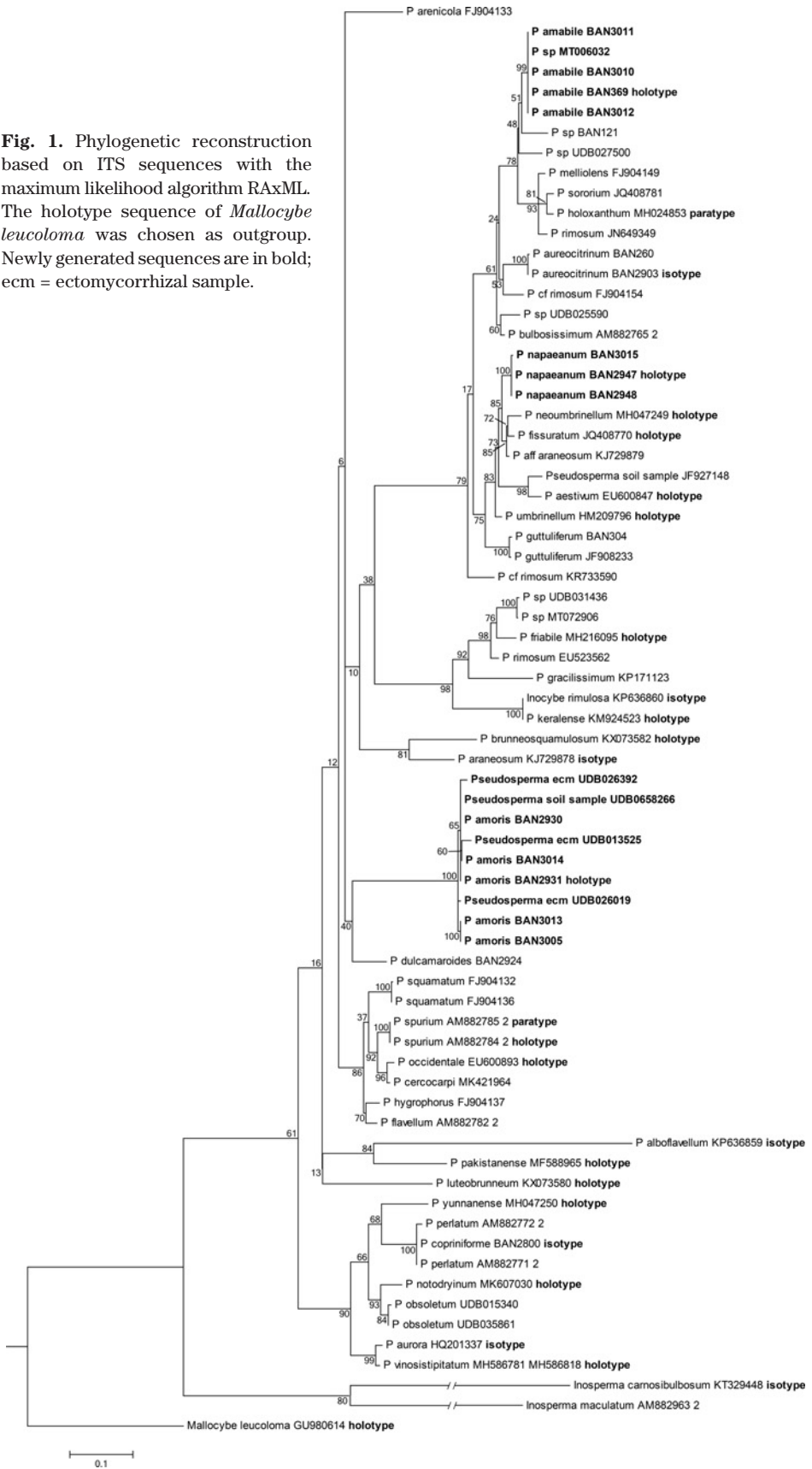
Phylogenetic reconstructions were conducted on the CIPRES Portal (San Diego Supercomputer Center, <http://www.phylo.org/>; Miller et al. 2010), using the maximum likelihood algorithm RAxML with the GTRGAMMA model and 1000 bootstrap replicates (Exelixis Lab, Heidelberg Institute for Theoretical Studies, Heidelberg, Germany; Stamatakis 2014).

RESULTS AND DISCUSSION

MOLECULAR STUDY

All three new species and the studied type specimens belong to the recently established genus *Pseudosperma*. Therefore, their molecular positions and the relations to the other species of this genus can be shown in a single phylogenetic reconstruction (Fig. 1). The metadata of these specimens are presented in Tab. 1.

Fig. 1. Phylogenetic reconstruction based on ITS sequences with the maximum likelihood algorithm RAxML. The holotype sequence of *Mallocybe leuocoloma* was chosen as outgroup. Newly generated sequences are in bold; ecm = ectomycorrhizal sample.



Tab. 1. Specimens investigated in this study. The original name is given if the current name is deviating. Abbreviations: DB = private herbarium of Ditte Bandini; ecm = ectomycorrhizal sample.

Species	Voucher	Herbarium	Additional voucher number	Country	GenBank / UNITE (ITS)
(<i>I. = Inocybe</i> ; <i>P. = Pseudosperma</i>)					
<i>I. rimulosa</i> C.K. Pradeep & Matheny	TBGT:12854 isotype	TBGT		India	KP636860
<i>Inosperma carnosibulbosum</i> (C.K. Pradeep & Matheny) Matheny & Esteve-Rav.; orig. name <i>I. carnosibulbosa</i>	TBGT:12047 isotype	TBGT		India	KT329448
<i>Inosperma maculatum</i> (Boud.) Matheny & Esteve-Rav.; orig. name <i>I. maculata</i>	EL5803	GB		Sweden	AMS82963.2
<i>Malloeybe leucoloma</i> (Kühmer) Matheny & Esteve-Rav.; orig. name <i>I. leucoloma</i>	Kühner 63-36 holotype	G		France	GU980614
<i>P. aestivum</i> (Kropp, Matheny & Hutchison) Matheny & Esteve-Rav.; orig. name <i>I. aestiva</i>	UTC:BK18089706 holotype	UTC		USA	EU600847
<i>P. alboflavellum</i> (C.K. Pradeep & Matheny) Haelew.; orig. name <i>I. alboflavella</i>	TBGT:11280 isotype	TBGT		India	KP636859
<i>P. amabile</i> Bandini, B. Oertel & Wehr sp. nov.	SMNS-STU-F-0901460 holotype	STU	DB8-9-12-2b / BAN369	Germany	MW010031
<i>P. amabile</i> sp. nov.	DB17-8-14-Wehr	TUR-A / AH	BAN3011; isoparatypes: TUR-A 209001; AH46947	Germany	MW010035
<i>P. amabile</i> sp. nov.	DB25-9-15-3	DB	BAN3010	Austria	MW010036
<i>P. amabile</i> sp. nov.	DB9-9-17-16	DB	BAN3012	Germany	MW010033
<i>P. amoris</i> Bandini & B. Oertel sp. nov.	SMNS-STU-F-0901462 holotype	STU / TUR-A / AH	DB1-8-14-12 / BAN2931; isotypes: TUR-A 209000; AH46946	Germany	MW010038
<i>P. amoris</i> sp. nov.	DB29-7-14-2	DB	BAN3013	Germany	MW010037
<i>P. amoris</i> sp. nov.	DB31-7-14-7	KR	KR-M-0038260 / BAN3014	Germany	MW010030
<i>P. amoris</i> sp. nov.	DB16-8-14-11	DB	BAN3005	Germany	MW010034
<i>P. amoris</i> sp. nov.	DB1-7-16-4	DB	BAN2930	Germany	MW010032
<i>P. arancosum</i> (Matheny & Bougher) Matheny & Esteve-Rav.; orig. name <i>I. araneosa</i>	TENN:066983 isotype	TENN	PEM3755	Australia	KJ729878
<i>P. arenicola</i> (R. Heim) Matheny & Esteve-Rav.; orig. name <i>I. arenicola</i>	EL238_06	GB		France	FJ904133

Species	Voucher	Herbarium	Additional voucher number	Country	GenBank / UNITE (ITS)
<i>(I. = Inocybe; P. = Pseudosperma)</i>					
<i>P. aureocitrinum</i> (Esteve-Rav.) Matheny & Esteve-Rav.; orig. name <i>I. aureocitrina</i>	DB21-11-12-Esteve-Raventós isotype	STU	BAN2903	Spain	MW010047
<i>P. aureocitrinum</i>	DB6-7-12-5	DB	BAN260	Germany	MW010041
<i>P. aurora</i> (Grund & D.E. Stuntz) Matheny & Esteve-Rav.; orig. name <i>I. aurora</i>	WTU:AUI0245 isotype	WTU		Canada	HQ201337
<i>P. brumeosquamulosum</i> (K.P.D. Latha & Manim.) Matheny & Esteve-Rav.; orig. name <i>I. brumeosquamulosa</i>	CAL 1308 holotype	CAL		India	KX073582
<i>P. bulbosissimum</i> (Kühner) Matheny & Esteve-Rav.; orig. name <i>I. bulbosissima</i>	EL6605	GB		Norway	AM882765.2
<i>P. cercocarp</i> (Kropp, Matheny & Hutchison) Matheny & Esteve-Rav.; orig. name <i>I. cercocarp</i>	UTC:255670	UTC	BK2006986	USA	MK421964
<i>P. copriniforme</i> (Reumaux) Matheny & Esteve-Rav.; orig. name <i>I. copriniformis</i>	XC_82101001 isotype	priv. herb. X. Carteret	DB20-10-82-Reumaux / BAN2800	France	MW010046
<i>P. dulcamaroides</i> (Kühner) Matheny & Esteve-Rav.	DB21-8-19-Yauras	DB	JV32865F / BAN2924	Sweden	MW010042
<i>P. fissuratum</i> (Matheny & Bougher) Matheny & Esteve-Rav.; orig. name <i>I. fissurata</i>	PERTH:E7054 holotype	PERTH	PBM2206	Australia	JQ408770
<i>P. flavellum</i> (P. Karst.) Matheny & Esteve-Rav.; orig. name <i>I. flavella</i>	EL11805	GB		Sweden	AM882782.2
<i>P. friabile</i> (Matheny & Kudzma) Haelew.; orig. name <i>I. friabilis</i>	TENN:068384 holotype	TENN	PBM3914	USA	MH216095
<i>P. gracilissimum</i> (Matheny & Bougher) Matheny & Esteve-Rav.; orig. name <i>I. gracilissima</i>	TENN:066946	TENN	PBM3738	Australia	KP171123
<i>P. guttuliferum</i> (Kühner) Matheny & Esteve-Rav.	DB4-8-12-1b	DB	BAN304	Switzerland	MW010043
<i>P. guttuliferum</i> ; orig. name <i>I. guttulifer</i>	MCVE 21581	MCVE		Italy	JF908233
<i>P. holocanthum</i> (Grund & D.E. Stuntz) Matheny & Esteve-Rav.; orig. name <i>I. holocantha</i>	ACAD:11683 paratype	ACAD		Canada	MH024853
<i>P. hygrophorus</i> (Kühner) Matheny & Esteve-Rav.; orig. name <i>I. hygrophorus</i>	EL97-06	GB		Sweden	FJ904137
<i>P. keratense</i> (K.P.D. Latha & Manim.) Matheny & Esteve-Rav.; orig. name <i>I. keratense</i>	K(M) 191712 holotype	K		India	KM924523

Species	Voucher	Herbarium	Additional voucher number	Country	GenBank / UNITE (ITS)
(<i>I. = Inocybe</i> ; <i>P. = Pseudosperma</i>)					
<i>P. luteobrunneum</i> (K.P.D. Latha & Manim.) Matheny & Esteve-Rav.; orig. name <i>I. luteobrunnea</i>	CAL 1260 holotype	CAL		India	KX073580
<i>P. melioliens</i> (Kühner) Matheny & Esteve-Rav.; orig. name <i>I. melioliens</i>	EL224-06	GB		France	FJ904149
<i>P. napaeaeum</i> Bandini & B. Oertel sp. nov.	SMNS-STU-F-0901463 holotype	STU	DB10-9-19-11 / BAN2947	Germany	MW010040
<i>P. napaeaeum</i> sp. nov.	DB12-9-17-12	DB	BAN3015	Austria	MW010045
<i>P. napaeaeum</i> sp. nov.	DB10-9-19-22	DB	BAN2948	Germany	MW010044
<i>P. necumbrinellum</i> (T. Bau & Y.G. Fan) Matheny & Esteve-Rav.; orig. name <i>I. necumbrinella</i>	HMJAU25742 holotype	HMJAU		China	MH047249
<i>P. notodryinum</i> (Singer, I.J. Araujo & Ivory) Matheny & Esteve-Rav.; orig. name <i>I. notodryina</i>	B12446 (F) holotype	F		Costa Rica	MK607030
<i>P. obsoletum</i> (Romagn.) Matheny & Esteve-Rav.; orig. name <i>I. obsoleta</i>	O-F-249256	O	NOBAS1084-15	Norway	UDB035861
<i>P. obsoletum</i> ; orig. name <i>I. obsoleta</i>	TU118148	TU(M)		Estonia	UDB015340
<i>P. occidentale</i> (Kropp, Matheny & Hutchison) Matheny & Esteve-Rav.; orig. name <i>I. occidentalis</i>	UTC:BK27089703 holotype	UTC		USA	EU600893 (ITS2)
<i>P. pakistanense</i> (Z. Ullah, S. Jabeen, H. Ahmad & A.N. Khalid) Matheny & Esteve-Rav.; orig. name <i>I. pakistanensis</i>	LAH35285 holotype	LAH	AR 23	Pakistan	MF588965
<i>P. perlatum</i> (Cooke) Matheny & Esteve-Rav.; orig. name <i>I. perlata</i>	Bj940922			Sweden	AM882772.2
<i>P. perlatum</i> ; orig. name <i>I. perlata</i>	EL7404	GB		Sweden	AM882771.2
<i>P. rimosum</i> (Bull.: Fr.) Matheny & Esteve-Rav.; orig. name <i>I. rimosa</i>	EL75-05	GB		Sweden	JN649349
<i>P. sororium</i> (Kauffman) Matheny & Esteve-Rav.; orig. name <i>I. sororia</i>	TENN:063504	TENN	PBM3055	USA	JQ408781
<i>P. spurium</i> (Jacobsson & E. Larss.) Matheny & Esteve-Rav.; orig. name <i>I. spuria</i>	SJ92017 holotype	GB		Sweden	AM882784.2
<i>P. spurium</i> [name in this very old GenBank entry erroneously <i>I. "squamata"</i> ; this had been already corrected to <i>I. spuria</i> in Jacobsson & Larsson 2009]	SJ92010 paratype	GB	isoparatype: DB14-7-87-Vauras-JV2607 / TUR-A-175730	Sweden	AM882785.2

Species	Voucher	Herbarium	Additional voucher number	Country	GenBank / UNITE (ITS)
<i>I. = Inocybe; P. = Pseudosperma</i> <i>P. squamatum</i> (J.E. Lange) Matheny & Esteve-Rav; orig. name <i>I. squamata</i>	PAM05052301			France	FJ904132
<i>P. squamatum</i> ; orig. name <i>I. squamata</i>	SJ08003			Sweden	FJ904136
<i>P. umbrinellum</i> (Bres.) Matheny & Esteve-Rav; orig. name <i>I. umbrinella</i>	F14488TypeS holotype	S		Italy	HM209796
<i>P. vinosistipitatum</i> (Grund & D.E. Stuntz) Matheny & Esteve-Rav; orig. name <i>I. vinosistipitata</i>	ACAD:11758 holotype	ACAD		Canada	MH586781 (ITS1) / MH586818 (ITS2)
<i>P. gunnanense</i> (T. Bau & Y.G. Fan) Matheny & Esteve-Rav; orig. name <i>I. gunnanensis</i>	HMJAU25840 holotype	HMJAU		China	MH047250
<i>Pseudosperma</i> sp.	DB23-9-11-4-Rave	KR	KR-M-0038070 / BAN121	Germany	MW009050
<i>Pseudosperma</i> sp.	FYG1120		FCAS1120	China	MT072906
<i>Pseudosperma</i> sp.; orig. name <i>I. aff. araneosa</i> / <i>P. aff. araneosum</i>	BRI: AQ793920	BRI	PL42609	Australia	KJ729879
<i>Pseudosperma</i> sp.; orig. name <i>I. cf. rimosa</i> / <i>P. cf. rimosum</i>	JV26578	TUR-A		Estonia	FJ904154
<i>Pseudosperma</i> sp.; orig. name <i>I. cf. rimosa</i> / <i>P. cf. rimosum</i>	SX2014092604			China	KR733590
<i>Pseudosperma</i> sp.; orig. name <i>I. rimosa</i> / <i>P. rimosum</i>	PBM2601			USA	EU523562
<i>Pseudosperma</i> sp.; orig. name <i>Inocybe</i> sp.	KR-M-0044827	KR		Germany	MT006032
<i>Pseudosperma</i> sp.; orig. name <i>Inocybe</i> sp.	TU113459	TU(M)		Estonia	UD027500
<i>Pseudosperma</i> sp.; orig. name <i>Inocybe</i> sp.	TU116810	TU(M)		Estonia	UD025590
<i>Pseudosperma</i> sp.; orig. name <i>Inocybe</i> sp.	TU120412	TU(M)		Estonia	UD031436
<i>Pseudosperma</i> ecm	L8802	-		Estonia	UD026019
<i>Pseudosperma</i> ecm	L8203	-		Estonia	UD026392
<i>Pseudosperma</i> ecm	TS1180	-		Estonia	UD013525
<i>Pseudosperma</i> soil sample	OTU79-S-122- VNQM-c	-		Italy	JF927148
<i>Pseudosperma</i> soil sample	G4245	-		Estonia	UD0887520
<i>Pseudosperma</i> soil sample	G4706	-		Estonia	UD0658266

All three species, *P. amabile*, *P. amoris* and *P. napaeaanum*, are very well supported by their species-clades in Fig. 1.

To date, we have not been able to find ITS sequences of *P. napaeaanum* in GenBank and UNITE, whereas in the case of *P. amabile* the ITS sequence MT006032 (as “*Inocybe* sp.”, Germany), and in the case of *P. amoris* the ITS sequences UDB013525 (ectomycorrhizal sample, Estonia), UDB026019 (ectomycorrhizal sample, Estonia), UDB026392 (ectomycorrhizal sample, Estonia) and UDB0658266 (soil sample, Estonia) have been found.

All three new species are genetically well-delimited from their neighbouring species: *P. amoris* is a singleton in the genus *Pseudosperma* and the other two new species have 3 to 6% ITS differences (94 to 97% ITS congruence) compared with their neighbours, as is also mentioned in the taxonomical part below.

As a result of their positions in Fig. 1, some names of the sequences of GenBank have to be annotated:

- AM882785.2 (Sweden) is a very old GenBank entry from the years before 2009, named therein *Inocybe* “*squamata*”. Its name had been already corrected in Jacobsson & Larsson (2009) to *Inocybe spuria* (now *Pseudosperma spurium*), but the species name has not been corrected in GenBank so far. In Fig. 1 we label this sequence *P. spurium* in accordance with Jacobsson & Larsson (2009).
- *Inocybe* aff. *araneosa* (*Pseudosperma* aff. *araneosum*) KJ729879 (Queensland, Australia) has quite a different position in comparison to the isotype sequence KJ729878 of *P. araneosum* in Fig. 1. This is therefore a yet unnamed species, *Pseudosperma* sp.
- *Inocybe* cf. *rimosa* (*Pseudosperma* cf. *rimosum*) FJ904154 (Estonia) should be better named *Pseudosperma* sp. (with our fungal MOTU nomenclature system we call this MOTU “*Pseudosperma* sp. FJ904154”; MOTU = molecular operational taxonomic unit).
- *Inocybe* cf. *rimosa* (*Pseudosperma* cf. *rimosum*) KR733590 (China) should also be named *Pseudosperma* sp. (with our fungal MOTU nomenclature system we call this MOTU “*Pseudosperma* sp. KR733590”).
- *Inocybe rimosa* (*Pseudosperma rimosum*) EU523562 (USA) is not *P. rimosum*, because the real *P. rimosum* has an entirely different position in Fig. 1. It represents a yet unnamed *Pseudosperma* sp. (with our fungal MOTU nomenclature system we call this MOTU “*Pseudosperma* sp. EU523562”).

Fig. 1 shows that *P. amabile* sp. nov. and *P. napaeaanum* sp. nov. belong to a relatively large and well-supported clade also containing *P. aestivum*, *P. aureocitrinum*, *P. bulbosissimum*, *P. fissuratum*, *P. guttuliferum*, *P. holoxanthum*, *P. melliolens*, *P. neoumbrinellum*, *P. rimosum*, *P. sororium* and *P. umbrinellum*. This clade corresponds to subclade A in Larsson et al. (2009). *Pseudosperma*

rimosum is a well-known species of the genus, but not its type species. Instead, *Pseudosperma sororium* was chosen as the type of the genus (Matheny et al. 2020). However, discussing single internal nodes with good bootstrap values in this subclade would certainly stress the method of ITS cladograms too much.

The clade with 98% bootstrap support, which was named “Gracilissima clade” in Matheny & Kudzma (2019) (now to be named correctly Gracilissimum clade) contains *P. friabile*, *P. gracilissimum*, *P. keralense* and two other species, represented by the sequences EU523562 on the one hand and MT072906 / UDB031436 on the other (Fig. 1).

Pseudosperma copriniforme (basonym *Inocybe copriniformis*) turned out to be a synonym of *P. perlatum* in this study. *Pseudosperma perlatum* is part of a rather well-supported clade containing *P. aurora*, *P. notodryinum*, *P. obsoletum*, *P. perlatum*, *P. vinosistipitatum* and *P. yunnanense*, species occurring in Europe, North America and Asia (Fig. 1). This clade corresponds to subclade B in Larsson et al. (2009) and Kropp et al. (2013).

The clade containing *P. cercocarpi*, *P. flavellum*, *P. hygrophorus*, *P. occidentale*, *P. spurium* and *P. squamatum* is somewhat insufficiently supported in Fig. 1, but this may relate to taxon sampling. This clade was named subclade D in Larsson et al. (2009), but with *P. spurium* treated in Jacobsson & Larsson (2009) (see also clade D in Kropp et al. 2013).

Typical of cladograms with only one or two considered DNA loci, many species behave like singletons: *P. alboflavellum*, *P. araneosum*, *P. arenicola*, *P. brunneo-squamulosum*, *P. dulcamaroides*, *P. luteobrunneum* and *P. pakistanense* (Fig. 1) (see also the phylogenetic reconstruction in Matheny & Bougher 2017, Fig. 136). In phylogenetic reconstructions based on more than two DNA loci, some of such singletons of ITS cladograms should find a supported place in some clade, even if hundreds of species of a single big genus were analysed (see e.g. Soop et al. 2019).

It is interesting that we have found another singleton species without genetic connection to the other species of the genus, namely *P. amoris* sp. nov. Whether *P. amoris* is a very old species or only the lack of other studied DNA loci is responsible for the isolated position of *P. amoris*, should be the subject of future studies.

TAXONOMY

Pseudosperma amabile Bandini, B. Oertel & Wehr, **sp. nov.**

Fig. 2

Mycobank MB 837447

Ety m o l o g y. The epithet “amabile” refers to the fact that the species appeared to be particularly lovable to the collectors.

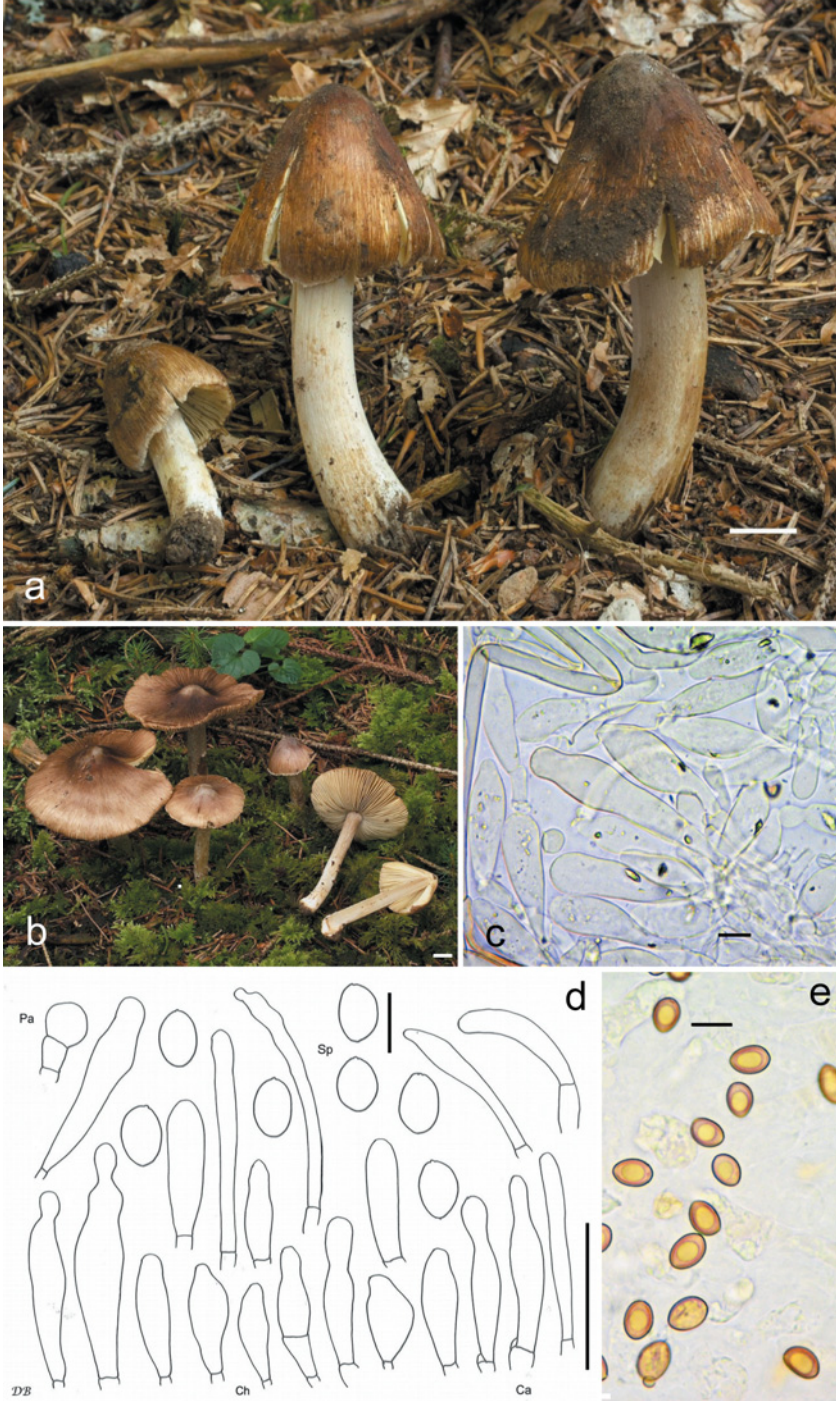
D i a g n o s i s. *Pseudosperma amabile* is a stout species with a brown to dark brown pileus colour, greyish velipellis and smooth to rim(ul)ose or innately fibrillose pileus surface. The smooth spores measure 8.5–12.2 µm (av. 10.0 µm) × 5.3–7.4 µm (av. 6.4 µm), and the thin-walled cheilocystidia are often (sub)capitate, measuring 32–70 µm (av. 42 µm) × 9–23 µm (av. 14 µm). It grows on calcareous soil with frondose trees or conifers. In these combined characteristics it differs from other species of the genus *Pseudosperma*. No closely genetically related species are known.

H o l o t y p e. Germany, Bayern, Oberallgäu, Oberstaufen, Steibis, near Obere-Lauch-Alm, TK25 8526/1, alt. 1490 m, NW slope with *Picea abies*, on calcareous soil, 8 Sep 2012, leg. B. Oertel (SMNS-STU-F-0901460, GenBank MW010031; isotype priv. herb. DB, DB8-9-12-2b).

Description

Macroscopic characters. Pileus 15–80 mm wide, at first (sub)campanulate to (sub)conical, later conico-convex or expanded, without umbo or with more or less pronounced large umbo, margin at first slightly incurved, later straight or even uplifted and then depressed around the centre; young basidiomata with pale greyish to greyish remnants of a velipellis, especially at the centre of the pileus; colour hazel-brown to dark brown (Mu 10YR 5/4–5/8, 5/4–5/6 or 3/4–3/6, 7.5YR 3/4), at the umbo either darker or greyish because of the velipellis, with age sometimes somewhat discolouring towards the margin; surface at first glabrous and smooth, later rimulose to rimose or finely or even innately fibrillose; young basidiomata with fine remnants of a whitish cortina. L a m e l l a e rather crowded (c. 60–70, l = 1–3), narrowly adnate, even, at first faintly yellowish, or yellowish with faint olive tinge, later yellow-ochraceous to ochraceous with more or less intense olive hue, edge fimbriate, whitish. Stipe 40–100 × 2–7 mm, cylindrical or curved, mostly widening towards the base, thickly covered with whitish tomentum for a long time, later longitudinally striate, pale brownish to brownish beneath; pruinose only near the apex of the stipe. C o n t e x t whitish to pale yellowish in the pileus, whitish in the stipe. S m e l l somewhat sweetish aromatic to (sub)spermatic. C o l o u r o f e x s i c c a t a pileus brown to dark brown with or without reddish hue (Mu 7/5YR 4/4–4/6, 3/4, 10YR 4/4–4/6, 3/6), lamellae and stipe a little brighter in colour, no darkening or blackening on drying.

Fig. 2. *Pseudosperma amabile*. **a** – coll. DB8-9-12-2b (holotype), **b** – coll. DB17-8-14-Wehr; scale bars = 1 cm. **c** – cheilocystidia (DB8-9-12-2b); scale bar = 10 µm. **d** – microscopic characters (DB8-9-12-2b), Ca = caulocystidia, Ch = cheilocystidia, Pa = paracystidia, Sp = spores; scale bar spores = 10 µm, scale bar cystidia = 50 µm. **e** – spores (DB8-9-12-2b), scale bar = 10 µm. Photographs B. Oertel (a), K. Wehr (b), D. Bandini (c, e); drawing D. Bandini. ►



Microscopic characters. Spores 8.5–12.2 μm (av. 10.0 μm , SD 0.7 μm) \times 5.3–7.4 μm (av. 6.4 μm , SD 0.3 μm); $Q = 1.3\text{--}1.9$ (av. 1.6, SD 0.1), smooth, subamygdaloid, (sub)ellipsoid, (sub)ovoid, also subcylindrical, usually without suprahilar depression, apex obtuse, in some collections with indistinct pseudoporus. Basidia 26–37 \times 8–14 μm , generally 4-spored, but in some basidiomata also 2-spored. Lamellae edges sterile, composed of cheilocystidia and some colourless, subglobose to (sub)clavate, thin-walled paracystidia. Cheilocystidia 32–70 μm (av. 42 μm , SD 9 μm) \times 9–23 μm (av. 14 μm , SD 3 μm); $Q = 2.1\text{--}5.2$ (av. 3.2, SD 0.6); (sub)clavate, (sub)utriform or (sub)cylindrical, often (sub)capitate, also (sub)papillate, mostly with truncate base, sometimes segmented with low base segment, sometimes intermixed with long hyphoid elements, colourless. Pileipellis constituted of an epicutis made up of parallel hyphae 4–10 μm wide, without or only barely encrusting and parietal brownish pigment, subcutis with wider and paler to colourless elements. Caulocystidia only near the apex, mostly rather long, (sub)utriform, (sub)cylindrical, often (sub)capitate, thin-walled. Clamp-connections abundant in all tissues.

Ecology and distribution

Ecology. Our own collections of *P. amabile* are from calcareous soil in Austria and Germany, in both cases exclusively with *Fagus sylvatica* or exclusively with *Picea abies*, at altitudes of c. 400 m up to more than 1400 m, in August and September. In the neighbourhood of the type collection, *Cortinarius varius* (Schaeff.) Fr. was noticed. The sequence of another collection found next to frondose trees in Bavaria as well as another sequence of EcM from Austria [alt. 1000 m; MK627281 (ITS)] is deposited in GenBank (KR-M-0044827 as *Inocybe* sp., leg. T. Bernauer; MT006032).

Distribution. Besides our own finds and the abovementioned collection from Bavaria, no other finds of *P. amabile* are known to us.

Other studied specimens

Austria. Tirol, Reutte, Tannheimer Tal, near Grän, ÖK25V 2214-Ost, alt. 1200 m, *Picea abies*, 25 Sep 2015, leg. D. Bandini, det. D. Bandini & B. Oertel (DB25-9-15-3, GenBank MW010036). – Tirol, Reutte, Tannheimer Tal, near lake Haldensee, ÖK25V 2214-Ost, alt. 1100 m, *Picea abies*, 20 Sep 2016, leg. & det. D. Bandini (DB20-9-16-4).

Germany. Bayern, Landkreis Garmisch-Partenkirchen, Mittenwald, TK25 8533/3, alt. 1080 m, *Fagus sylvatica*, 9 Sep 2017, leg. D. Bandini, det. D. Bandini & B. Oertel (DB9-9-17-16, GenBank MW010033); ibidem at some distance from the former location, alt. 1100 m, *Fagus sylvatica*, 11 Sep 2019, leg. & det. D. Bandini (DB11-9-19-18); ibidem at some distance from the former location, alt. 1100 m, *Fagus sylvatica*, 11 Sep 2019, leg. & det. D. Bandini (DB11-9-19-23). – Rheinland-Pfalz, Landkreis Vulkaneifel, Mürlenbach, Remmelbachtal, TK25 5805/2, alt. 420 m, *Picea abies*, 17 Aug 2014, leg. K. Wehr, det. D. Bandini & B. Oertel (DB17-8-14-Wehr, GenBank MW010035; isoparatypes TUR-A 209001, AH 46947).

Notes

Pseudosperma amabile is characterised by often large and stout basidiomata, a greyish velipellis, a smooth to rim(ul)ose or innately fibrillose pileus surface, often almost (sub)ovoid spores and cheilocystidia with often a (sub)capitate to even (sub)papillate apex, and occurrence on calcareous soil under *Picea* and *Fagus*. Some collections may macroscopically be mistaken for *Inosperma maculatum* because of the size, the often dark brown rimose pileus and a similar habitus. However, the latter named species has much smaller spores and a whitish, often radially scattered velipellis. Paler collections may be confused with *P. melliolens* (Kühner) Matheny & Esteve-Rav., the basidiomata of which are however smaller and the spores larger (Kühner 1988, and personal observations). *Pseudosperma rimosum* differs in e.g. a paler, more fallow pileus colour, absence of a greyish velipellis (see plate 388 in Bulliard 1789), larger spores and mostly lacking (sub)capitate or (sub)papillate cheilocystidia (Stangl 1989, and personal observations).

Another stout and large species is *P. perlatum* (Cooke) Matheny & Esteve-Rav. Even though the pileus colour of this species at the umbo is brownish to dark brown, it is always much paler to almost whitish towards the margin, and the stipe is very stumpy and turns brown with age towards the base (Cooke 1886, and personal observations), which is not the case in *P. amabile*. The same holds true for *P. copriniforme* (Reumaux) Matheny & Esteve-Rav. (see Reumaux 2004), an isotype of which we examined. Since the microscopic details are similar and the ITS is even identical, we here declare the latter synonymous with *P. perlatum* (for microscopic details of an isotype, see below).

Genetically somewhat related to *P. perlatum* is the recently described *P. pakistanense* (Z. Ullah, S. Jabeen, H. Ahmad & A.N. Khalid) Matheny & Esteve-Rav., from the Swat District in Pakistan. It differs from *P. amabile* in e.g. a missing velipellis, differently shaped and larger spores, and lacking subcapitate to (sub)papillate cheilocystidia (Ullah et al. 2018). *Pseudosperma neoumbrinellum* (T. Bau & Y.-G. Fan) Matheny & Esteve-Rav. is newly described from the Jilin Province in China. It is to be distinguished from *P. amabile* by e.g. a smaller size of basidiomata, an acute umbo and a missing velipellis (Bau & Fan 2018).

Inocybe rimulosa C.K. Pradeep & Matheny, a species described from Kerala (India) – synonymous with *Pseudosperma keralense* (K.P.D. Latha & Manim.) Matheny & Esteve-Rav. (see Matheny et al. 2020) – differs in e.g. a smaller size of basidiomata, larger spores and occurrence in tropical habitats (Pradeep et al. 2016, Latha & Manimohan 2017). *Pseudosperma brunneosquamulosum* (K.P.D. Latha & Manim.) Matheny & Esteve-Rav., a species likewise described from Kerala, differs from *P. amabile* in e.g. smaller basidiomata, smaller spores and occurrence in tropical habitats (Tibpromma et al. 2017, Latha & Manimohan 2017).

Pseudosperma notodryinum (Singer, I.J. Araujo & Ivory) Matheny & Esteve-Rav., described from Costa Rica, differs from *P. amabile* in e.g. much smaller spores and also its occurrence in tropical habitats (Singer et al. 1983). However, it also occurs in warm temperate areas of the USA (see Matheny et al. 2020). *Pseudosperma araneosum* (Matheny & Bougher) Matheny & Esteve-Rav. was found in Queensland, Australia. It differs in a missing velipellis, smaller spores, missing (sub)capitate cheilocystidia and occurrence in tropical lowland forests (Matheny & Bougher 2017). *Pseudosperma gracilissimum* (Matheny & Bougher) Matheny & Esteve-Rav., is also described from Queensland, Australia. It differs in e.g. a missing velipellis, smaller spores and a different habitat (Matheny & Bougher 2017).

Pseudosperma avellaneum (Kobayasi) Matheny & Esteve-Rav. finally, a Japanese species, has much smaller spores (Kobayasi 1952, Kobayashi 2002).

No species genetically closely related to *P. amabile* are known. Two *Pseudosperma* spp. are 95% congruous in the ITS, while *P. rimosum* and *P. melliolens* are 94% congruous in the ITS (see Fig. 1).

***Pseudosperma amoris* Bandini & B. Oertel, sp. nov.**

Fig. 3

Mycobank MB 837448

Etymology. The epithet “*amoris*” refers to the basidiomata being fragile and therefore as cautiously to handle as love (Latin “*amor*”).

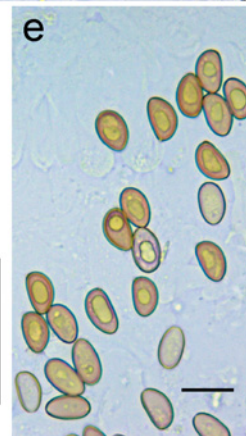
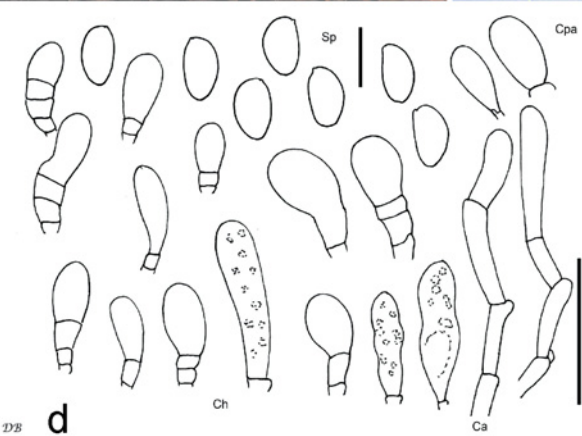
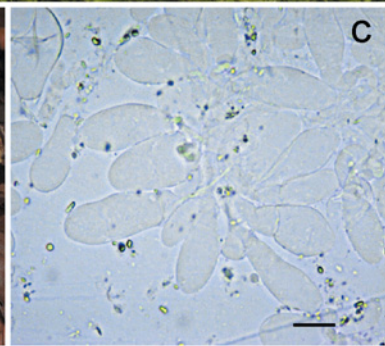
Diagnosis. *Pseudosperma amoris* has a yellowish to yellow-ochraceous pileus colour with often an orange-reddish hue at the centre and a smooth to innately fibrillose pileus surface. The stipe is finely floccose and the context often very brittle. The smooth spores measure 9.0–12.6 µm (av. 10.3) × 5.0–7.2 µm (av. 6.2 µm), and the thin-walled cheilocystidia are usually rather short, measuring 21–42 µm (av. 31 µm) × 9–18 µm (av. 13 µm). It grows on calcareous soil, preferably with frondose trees. In these combined characteristics it differs from other species of the genus *Pseudosperma*. No closely genetically related species are known.

Holotype. Germany, Baden-Württemberg, Heidelberg, War Cemetery, TK25 6618/1, alt. 292 m, lawn with *Quercus robur*, *Fagus sylvatica*, *Pinus sylvestris*, 1 Aug 2014, leg. D. Bandini (SMNS-STU-F-0901462, GenBank MW010038; isotypes TUR-A 209000, AH 46946 and priv. herb. DB, DB1-8-14-12).

Description

Macroscopic characters. Pileus 10–40 mm wide, at first (sub)conical, later conico-convex or expanded, when young without, later with more or less pronounced large umbo, margin at first incurved, later decurved to straight or even uplifted, and then pileus depressed around the umbo; young basidiomata

Fig. 3. *Pseudosperma amoris*. **a** – coll. DB1-8-14-12 (holotype), **b** – coll. DB1-7-16-4; scale bars = 1 cm. **c** – cheilocystidia (DB1-7-16-4); scale bar = 10 µm. **d** – microscopic characters (DB1-8-14-12), Ca = caulocystidia, Ch = cheilocystidia, Cpa = cauloparacystidia, Sp = spores; scale bar spores = 10 µm, scale bar cystidia = 50 µm. **e** – spores (DB1-7-16-4); scale bar = 10 µm. Photographs and drawing D. Bandini. ►



without or with only very faint whitish remnants of a velipellis; colour pale straw, straw to yellowish or bright, almost golden yellow (Mu 10YR 8/3–8/8, 7/4–7/8) at the centre often with more or less intense orange to reddish hue or even pale reddish, sometimes somewhat streaky towards the margin; surface of young basidiomata often glabrous, then finely innately fibrillose with fibres mostly hardly diverging, sometimes darker fibres partly covering paler ones; young basidiomata with faint remnants of a cortina. Lamellae moderately crowded (c. 45–60, $l = 1-3$), adnate to emarginate-adnate, even to subventricose, at first whitish, with or without yellowish tinge, then beige with yellowish hue and ochraceous when old; edge sometimes uneven, fimbriate, whitish. Stipe 30–60 × 2–6 mm, often rather stout, cylindrical or curved, sometimes widening towards the base, when young entirely covered with whitish tomentum, later longitudinally striate and then entirely finely floccose, at first whitish to dingy whitish, later pale straw-coloured; pruinose only near the apex of the stipe. Context whitish in the pileus and the stipe; extremely brittle in most collections. Smell weak, not spermatic. Colour of *exsiccata* pileus pale straw to pale ochraceous (Mu 10YR 7/4–7/8, 6/4–6/8), in lamellae and stipe concolorous or a little brighter in colour, no darkening or blackening on drying.

Microscopic characters. Spores 9.0–12.6 μm (av. 10.3 μm , SD 0.5 μm) × 5.0–7.2 μm (av. 6.2 μm , SD 0.3 μm); $Q = 1.4-2.1$ (av. 1.7, SD 0.1), smooth, (sub)ellipsoid, subamygdaloid to subcylindrical, rather rarely with faint suprahilar depression, apex obtuse, mostly with very small and indistinct pseudoporus. Basidia 25–34 × 8–11 μm , generally 4-spored, but sometimes also 2-spored. Lamellae edges sterile, composed of cheilocystidia, explicit paracystidia not observed. Cheilocystidia 21–42 μm (av. 31 μm , SD 5 μm) × 9–18 μm (av. 13 μm , SD 2 μm); $Q = 1.6-3.4$ (av. 2.4, SD 0.5); mostly subcylindrical to (sub)clavate, sometimes (sub)ovoid, often catenate with much shorter elements below the terminal element, thin-walled, often filled with almost colourless amorphous guttules. Pileipellis constituted of an epicutis made up of parallel hyphae 4–14 μm wide, with encrusting and parietal yellowish pigment, subcutis with wider and paler to colourless elements. Caulocystidia only near the apex, consisting of hyphoid segmented elements. Clamp-connections abundant in all tissues.

Ecology and distribution

Ecology. *Pseudosperma amoris* was found on calcareous soil in July and August, some collections exclusively with frondose trees. *Fagus sylvatica* was noted almost always close to our own collections, all from Germany. Equally, frondose trees were noted in relation with EcM sequences from Estonia.

Distribution. No other evidence of revised collections is known to us. UNITE, however, includes some EcM sequences from Estonia matching those of *P. amoris* (*Corylus avellana*, UDB026019, ITS; *Salix caprea*, UDB026392, ITS and *Tilia*, UDB013525, ITS).

Other studied specimens

Germany. Baden-Württemberg, Rhein-Neckar-Kreis, Wiesenbach, Judenwald, TK25 6619/1, alt. 170 m, *Fagus sylvatica*, 29 Jul 2014, leg. & det. D. Bandini (DB29-7-14-12). – Baden-Württemberg, Rhein-Neckar-Kreis, Wiesenbach, Herrenwald, TK25 6618/2, alt. 185 m, *Fagus sylvatica*, *Corylus avellana*, *Betula pendula*, 29 Jul 2014, leg. D. Bandini, det. D. Bandini & B. Oertel (DB29-7-14-2, GenBank MW010037). – Baden-Württemberg, Heidelberg, Johanneskirche, TK25 6518/3, alt. 117 m, *Betula pendula*, *Picea omorika*, 31 Jul 2014, leg. D. Bandini, det. D. Bandini & B. Oertel (DB31-7-14-7 / KR-M-0038260, GenBank MW010030). – Baden-Württemberg, Rhein-Neckar-Kreis, Haag, direction towards Schwanheim, TK25 6519/4, alt. 400 m, *Fagus sylvatica*, 1 Jul 2016, leg. D. Bandini, det. D. Bandini & B. Oertel (DB1-7-16-4, GenBank MW010032). – Baden-Württemberg, Neckar-Odenwald-Kreis, Schwarzach, TK25 6619/2, alt. 350 m, *Fagus sylvatica*, *Picea abies*, *Pseudotsuga menziesii*, 19 Aug 2017, leg. & det. D. Bandini (DB19-8-17-8). – Baden-Württemberg, Rhein-Neckar-Kreis, Wiesenbach, near Langenzell, TK25 6619/1, alt. 210 m, *Fagus sylvatica*, *Carpinus betulus*, *Corylus avellana*, 24 Jul 2020, leg. D. & G. Bandini, det. D. Bandini (DB24-7-20-1). – Baden-Württemberg, Rhein-Neckar-Kreis, Wiesenbach, TK25 6618/2, alt. 170 m, *Fagus sylvatica*, *Corylus avellana*, *Carpinus betulus*, *Picea abies*, 29 Aug 2020, leg. D. & G. Bandini, det. D. Bandini (DB29-8-20-1). – Bayern, Landkreis Altötting, Mehring, Mehring-Lengthal, TK25 7842/2, alt. 413 m, *Betula pendula*, 16 Aug 2014, leg. D. Bandini & L. Quecke, det. D. Bandini & B. Oertel (DB16-8-14-11, GenBank MW010034).

Notes

Pseudosperma amoris is characterised by its straw to honey-yellow or yellow-ochraceous pileus colour, often with orange to reddish tinges at the centre, its usually very brittle context, smooth to innately fibrillose pileus surface and entirely finely floccose stipe. It grows on calcareous soil, apparently preferably with frondose trees. Collections which are only yellow without orange hue could perhaps be mistaken for *P. aureocitrinum* (Esteve-Rav.) Matheny & Esteve-Rav., a species recently described from Spain, which we also found in Germany, in the neighbourhood of *P. amoris*, often also next to *Fagus sylvatica*. Young basidiomata, however, are glandiform, which is not the case with *P. amoris*. Furthermore abundant whitish velipellis is characteristic for *P. aureocitrinum*, and its cheilocystidia are longer than those of *P. amoris* (Esteve-Raventós 2014, and personal observations; for microscopic details of an isotype, see below).

When the basidiomata show orange-reddish hues at the centre of the pileus, they may resemble *P. squamatum* (J.E. Lange) Matheny & Esteve-Rav., which has however often larger and stouter basidiomata, smaller spores and longer cheilocystidia than *P. amoris*, and the habitat of *P. squamatum* is generally somewhat moister (Lange 1917, Kuyper 1986, Stangl 1989, and personal observations). *Pseudosperma flavellum* (P. Karst.) Matheny & Esteve-Rav. and *P. hygrophorus* (Kühner) Matheny & Esteve-Rav., both species with a yellowish to

ochraceous pileus colour not only have a different habitus, resembling the genus *Hygrophorus*, but also a smoother pileus surface and distinctly more slender spores with a higher average Q-value (Karsten 1889, Kühner 1956, and personal observations; for microdata and a microplate of *P. flavellum*, see below). *Pseudosperma cerinum* (Malençon) Matheny & Esteve-Rav. has larger basidiomata, yellow lamellae and larger spores and cheilocystidia (Malençon & Bertault 1970). The basidiomata of *Pseudosperma rimosum* are usually larger, the pileus colour is more fallow or buff brownish but not intensely yellowish, and the surface is strongly innately fibrillose (see plate 388 in Bulliard 1789).

The recently described species *P. permelliolens* (Carteret & Reumaux) Matheny & Esteve-Rav. from France, too, has larger, initially glandiform basidiomata, and is characterised by an abundant whitish velipellis. Furthermore, both its spores and cheilocystidia are larger (Carteret & Reumaux 2017).

The pileus of *P. aurora* (Grund & D.E. Stuntz) Matheny & Esteve-Rav., a North American species originally described from Nova Scotia, Canada, is tinged with pallid pinkish hues (Grund & Stuntz 1975) and the spores and cheilocystidia are larger than those of *P. amoris*. Another species described by the same authors, *P. holoxanthum* (Grund & D.E. Stuntz) Matheny & Esteve-Rav., differs from *P. amoris* in e.g. longer spores and much longer cheilocystidia (Grund & Stuntz 1981). *Pseudosperma vinosostipitatum* (Grund & D.E. Stuntz) Matheny & Esteve-Rav., equally described from Canada, has an incarnate tinge in the pileus and a purplish vinaceous stipe (Grund & Stuntz 1983). *Pseudosperma sororium* (Kauffman) Matheny & Esteve-Rav., described from Michigan, USA, differs from *P. amoris* in larger basidiomata with a paler pileus colour and conspicuously rimose surface, as well as longer and variably shaped spores (Kauffman 1924, Stuntz 1947).

Pseudosperma aestivum (Kropp, Matheny & Hutchison) Matheny & Esteve-Rav. and *P. cercocarpi* (Kropp, Matheny & Hutchison) Matheny & Esteve-Rav. are both species with a yellowish to yellow-brown cap described from Utah, USA. Their basidiomata are however larger and their cheilocystidia longer than those of *P. amoris*. *Pseudosperma aestivum* also differs in its whitish velipellis and longer spores, and *P. cercocarpi* in its cespitose growth under mountain mahogany (*Cercocarpus*), an ectomycorrhizal associate in the *Rosaceae* (Kropp et al. 2013). *Pseudosperma alboflavellum* differs from *P. amoris* in e.g. a paler to almost cream-coloured or whitish pileus, more slender and smaller spores, respectively, and occurrence in tropical habitats (Pradeep et al. 2016), and *P. yunnanense* (T. Bau & Y.-G. Fan) Matheny & Esteve-Rav., newly described from Yunnan Province, China, is distinguished from *P. amoris* by e.g. much stouter and larger basidiomata and much larger spores (Bau & Fan 2018).

No genetically closely related species are known so far (see Fig. 1).

***Pseudosperma napaeum* Bandini & B. Oertel, sp. nov.**

Fig. 4

Mycobank MB 837449

Etymology. The epithet “napaeum” refers to the Greek nymph of the valley (Napaea), because the species was found in the valley of the river Isar.

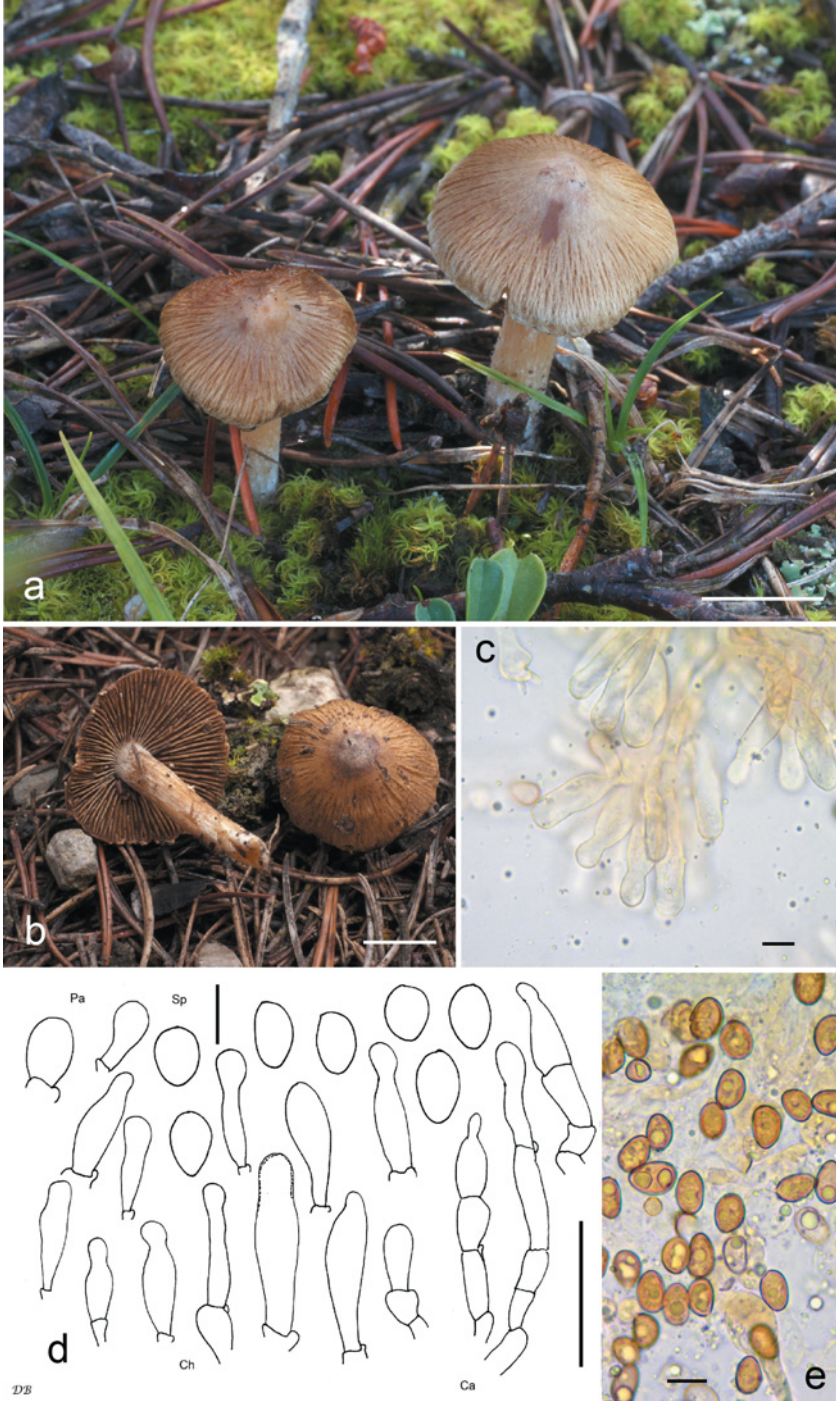
Diagnosis. *Pseudosperma napaeum* has a pale brownish to brown pileus colour, the pileus surface is strongly innately fibrillose and covered by ample whitish velipellis patches, the lamellae are rather thick. The smooth spores measure 9.1–14.1 μm (av. 10.6 μm) \times 5.9–9.3 μm (av. 7.2 μm), and the usually (sub)clavate, thin-walled cheilocystidia are often (sub)capitate and measure 23–60 μm (av. 37 μm) \times 7–17 μm (av. 10 μm). It was found on pebbly calcareous soil, accompanied by *Pinus mugo*, *Dryas octopetala* and *Helianthemum*. In these combined characteristics it differs from *P. umbri-nellum*, the genetically most closely related species, as well as other species of the genus *Pseudosperma*.

Holotype. Germany, Bayern, Garmisch-Partenkirchen, near Mittenwald, TK25 8533/2, alt. 880 m, *Pinus mugo*, *Dryas octopetala*, *Helianthemum nummularium*, 10 Sep 2019, leg. D. Bandini (SMNS-STU-F-0901463, GenBank MW010040; isotype priv. herb. DB, DB10-9-19-11).

Description

Macroscopic characters. Pileus 10–25 mm wide, at first (sub)conical, later conico-convex or expanded, with more or less pronounced large umbo, margin at first decurved, later straight; young basidiomata entirely covered with ample whitish remnants of a velipellis, later often still visible at the centre; colour pale brown, nut-brown to brown with ochraceous reddish tinge (Mu 10YR 6/4–6/8, 7.5YR 5/4–5/8, 5YR 5/4–5/8), at the centre either paler because of the velipellis or more intense in colour when old; surface glabrous at the centre, outwards strongly innately fibrillose or fissured, with fibres diverging towards the margin; young basidiomata with remnants of a whitish cortina. Lamellae moderately crowded to crowded (c. 50–60, l = 1–3), thickly adnate or even sub-ventricose, yellowish to intensely yellow-ochraceous with or without faint olive hue; edge fimbriate, whitish to concolorous. Stipe 25–40 \times 2–4 mm, cylindrical or curved, when young covered with whitish tomentum, later longitudinally striate or glabrous, ochraceous brownish in different intensity; pruinose near the apex of the stipe. Context whitish in the pileus, with yellowish tinge in the stipe. Smell faintly aromatic, at least when cut. Colour of exsiccata pileus dark brown (Mu 10YR 4/2–4/4), in lamellae concolorous or a little darker, stipe somewhat paler, no darkening or blackening on drying.

Microscopic characters. Spores 9.1–14.1 μm (av. 10.6 μm , SD 0.9 μm) \times 5.9–9.3 μm (av. 7.2 μm , SD 0.6 μm); Q = 1.1–1.8 (av. 1.5, SD 0.1), smooth, (sub)amygdaloid, (sub)ellipsoid, (sub)ovoid or pear-shaped, mostly without suprahilar depression, apex obtuse. Basidia 24–35 \times 7–11 μm , generally 4-spored, seldom also 2-spored. Lamellae edges sterile, composed of cheilocystidia and hyaline to pale ochraceous, (sub)clavate, cylindrical or subglobose, thin-walled paracystidia. Cheilocystidia 23–60 μm (av. 37 μm , SD 7 μm) \times 7–17 μm



(av. 10 µm, SD 2 µm); Q = 2.4–4.7 (av. 3.6, SD 0.6), mostly (sub)cylindrical, also subclavate, often with (sub)capitate apex, thin-walled, sometimes filled with brownish amorphous content. Pileipellis constituted of an epicutis made up of parallel hyphae 4–12 µm wide, with encrusting and parietal yellowish to ochraceous pigment, subcutis with wider and paler to colourless elements. Caulocystidia only near the apex, mostly consisting of catenate elements; the uppermost element often with (sub)capitate or papillate apex. Clamp connections abundant in all tissues.

Ecology and distribution

Ecology. *Pseudosperma napae anum* has to date only been found on the banks of the river Isar in pebbly calcareous terrain in Austria and Germany in September.

Distribution. No other sequences or collections are known to us.

Other studied specimens

Austria. Tirol, Bezirk Innsbruck-Land, Scharnitz, ÖK25V 2222-Ost, alt. ca. 980 m, *Pinus sylvestris*, *Pinus mugo*, *Dryas octopetala*, 12 Sep 2017, leg. D. Bandini, det. D. Bandini & B. Oertel (DB12-9-17-12, GenBank MW010045).

Germany. Bayern, Landkreis Garmisch-Partenkirchen, near Mittenwald, TK25 8533/2, alt. 920 m, *Pinus mugo*, *Dryas octopetala*, *Helianthemum nummularium*, 10 Sep 2019, leg. D. Bandini; det. D. Bandini & B. Oertel (DB10-9-19-22, GenBank MW010044).

Notes

Pseudosperma napae anum is characterised by its rather small size of basidiomata, ample whitish velipellis when young, strongly innately fibrillose pileus surface, rather large spores and cheilocystidia which often have a (sub)capitate apex. The morphologically and genetically most similar species, *P. umbrinellum* (Bres.) Matheny & Esteve-Rav., differs by e.g. only faintly whitish greyish velipellis, on average more slender spores and often catenate cheilocystidia without (sub)capitate apex (Bresadola 1905, and personal observations). *Pseudosperma melliolens* has a faintly greyish velipellis, and the cheilocystidia are mostly clavate without (sub)capitate apex (Kühner 1988, Bon 1997a, and personal observations). *Pseudosperma bulbosissimum* has a bulbous stipe base, the pileus colour is pale, the surface is not as strongly innately fibrillose, the ample velipellis is missing and the spores are larger. Besides, in Europe it is to be found in higher

Fig. 4. *Pseudosperma napae anum*. **a** – coll. DB10-9-19-11 (holotype), **b** – coll. DB12-9-17-12; scale bars = 1 cm. **c** – cheilocystidia (DB10-9-19-11); scale bar = 10 µm. **d** – microscopic characters (DB10-9-19-11), Ca = caulocystidia, Ch = cheilocystidia, Pa = paracystidia, Sp = spores; scale bar spores = 10 µm, scale bar cystidia = 50 µm. **e** – spores (DB10-9-19-22); scale bar = 10 µm. Photographs and drawing D. Bandini. ◀

montane regions (Kühner 1988, Bon 1997a, and personal observations). *Pseudosperma rimosum* differs in e.g. larger basidiomata with different habitus, missing velipellis (see plate 388 in Bulliard 1789), and mostly missing (sub)capitate cheilocystidia (Stangl 1989). *Pseudosperma perlatum* is a stout species, its pileus colour is brownish to dark brown at the umbo and paler to almost whitish towards the margin of the pileus, the stipe is very stumpy and turns brown towards the base with age (Cooke 1886). The same holds true for *P. copriniforme* (see Reumaux 2004 and notes above).

Pseudosperma spurium (Jacobsson & E. Larss.) Matheny & Esteve-Rav., described from Northern Europe and reported from western North America (Cripps 1997, as *Inocybe squamata*, see Kropp et al. 2013) differs in e.g. larger and stouter basidiomata and on average much smaller spores (Jacobsson & Larsson 2009).

Pseudosperma pakistanense differs from *P. napaeum* in e.g. missing velipellis, different form of spores, not (sub)capitate cheilocystidia and habitat with *Quercus* (Ullah et al. 2018).

Pseudosperma neoumbrinellum is to be distinguished from *P. napaeum* by e.g. an acute umbo, chocolate to dark brown pileus colour and missing velipellis (Bau & Fan 2018).

Pseudosperma keralense differs in e.g. a more reddish brown pileus colour, larger spores and tropical habitat (Pradeep et al. 2016, Latha & Manimohan 2017), and *P. brunneosquamulosum* (K.P.D. Latha & Manim.) Matheny & Esteve-Rav. and *P. luteobrunneum* (K.P.D. Latha & Manim.) Matheny & Esteve-Rav., two species also described from Kerala (Tibpromma et al. 2017, Latha & Manimohan 2017), have smaller spores and grow in tropical habitats as well. This holds true also for *P. notodryinum* (Singer, I.J. Araujo & Ivory) Matheny & Esteve-Rav., a species known from Costa Rica (Singer et al. 1983). *Pseudosperma araneosum* differs in a missing velipellis, smaller spores and lacking (sub)capitate cheilocystidia as well as in a different habitat tropical or warm temperate forests in Australia (Matheny & Bougher 2017). *Pseudosperma gracilissimum* differs by a missing velipellis and smaller spores and tropical habitat (Matheny & Bougher 2017), and finally *P. avellaneum* has much smaller spores (Kobayasi 1952, Kobayashi 2002).

The genetically most closely related species is an unclarified species from Australia and Papua New Guinea (KJ729879, see above in the results, not shown in Fig. 1) with 97% congruence in the ITS, followed by *P. umbrinellum* with 96% congruence (GenBank HM209796, holotype), see Fig. 1.

Additional type specimens

Fig. 5

***Pseudosperma aureocitrinum* (Esteve-Rav.) Matheny & Esteve-Rav.**

Basionym: *Inocybe aureocitrina* Esteve-Rav. 2014

Isotype: Spain, Balearic Islands, Mallorca, Sierra de Tramontana, Bunyola Sa Comuna, *Quercus ilex* subsp. *ilex* on calcareous soil, 21 Nov 2012, leg. F. Esteve-Raventós, J. Llistosella, J.C. Salom & J.L. Siquier (DB21-11-12-Esteve-Raventós, STU, BAN2903, GenBank MW010047).

Spores 9.2–11.6 μm (av. 10.2 μm , SD 0.7 μm) \times 5.6–7.3 μm (av. 6.4 μm , SD 0.4 μm); Q = 1.4–1.9 (av. 1.6, SD 0.1), smooth, broadly ellipsoid to (sub)ovoid, also (sub)amygdaloid, with obtuse apex. Basidia 4-spored. Cheilocystidia 33–47 μm (av. 39 μm , SD 4 μm) \times 8–18 μm (av. 12 μm , SD 3 μm); Q = 2.6–4.4 (av. 3.3, SD 0.5), (sub)cylindrical to (sub)clavate or (sub)utriform, sometimes subcapitate, thin-walled. Paracystidia not observed. Caulocystidia at the apex of the stipe, subclavate, often somewhat larger than cheilocystidia, also with segmented hyphoid elements.

***Pseudosperma copriniforme* (Reumaux) Matheny & Esteve-Rav.**

Basionym: *Inocybe copriniformis* Reumaux 2004

Isotype: France, Île de France, forêt de Compègne, *Salix*, *Betula pendula*, *Alnus incana*, leg. Bruneau, 20 Oct 1982 (XC no. 82101001, DB20-10-82-Reumaux, BAN2800, GenBank MW010046).

Spores 9.3–12.5 μm (av. 10.8 μm , SD 0.8 μm) \times 5.0–7.0 μm (av. 6.3 μm , SD 0.4 μm); Q = 1.5–2.0 (av. 1.7, SD 0.1), smooth, (sub)cylindrical to (sub)amygdaloid, mostly without, seldom with faint suprahilar depression, with obtuse apex. Basidia 4-spored. Cheilocystidia 15–48 μm (av. 30 μm , SD 8 μm) \times 7–20 μm (av. 11 μm , SD 3 μm); Q = 1.7–2.0 (av. 1.7, SD 0.1), (sub)cylindrical, (sub)utriform to (sub)clavate, often catenate with longer apical element (up to 15 μm). Paracystidia not observed. Caulocystidia not studied because stipe not present.

***Pseudosperma flavellum* (P. Karst.) Matheny & Esteve-Rav.**

Basionym: *Inocybe flavella* P. Karst. 1890

Holotype: Finland, lake Särkjärvi, Aug 1889, Pinetum, leg. E. Karsten (H6050800).

Spores 9.6–11.7 μm (av. 10.6 μm , SD 0.5 μm) \times 4.0–5.6 μm (av. 4.9 μm , SD 0.3 μm); Q = 1.8–2.7 (av. 2.2, SD 0.2), smooth, oblong, (sub)cylindrical, (sub)phaseoliform, with (sub)obtuse to (sub)acute apex. Basidia 4-spored. Cheilocystidia 32–55 μm (av. 42 μm , SD 5 μm) \times 8–14 μm (av. 10 μm , SD 1.8 μm); Q = 3.1–5.5 (av. 4.3, SD 0.8), mostly (sub)cylindrical to subutriform, also subclavate, thin-walled. Paracystidia not observed. Caulocystidia not studied (to preserve the material).

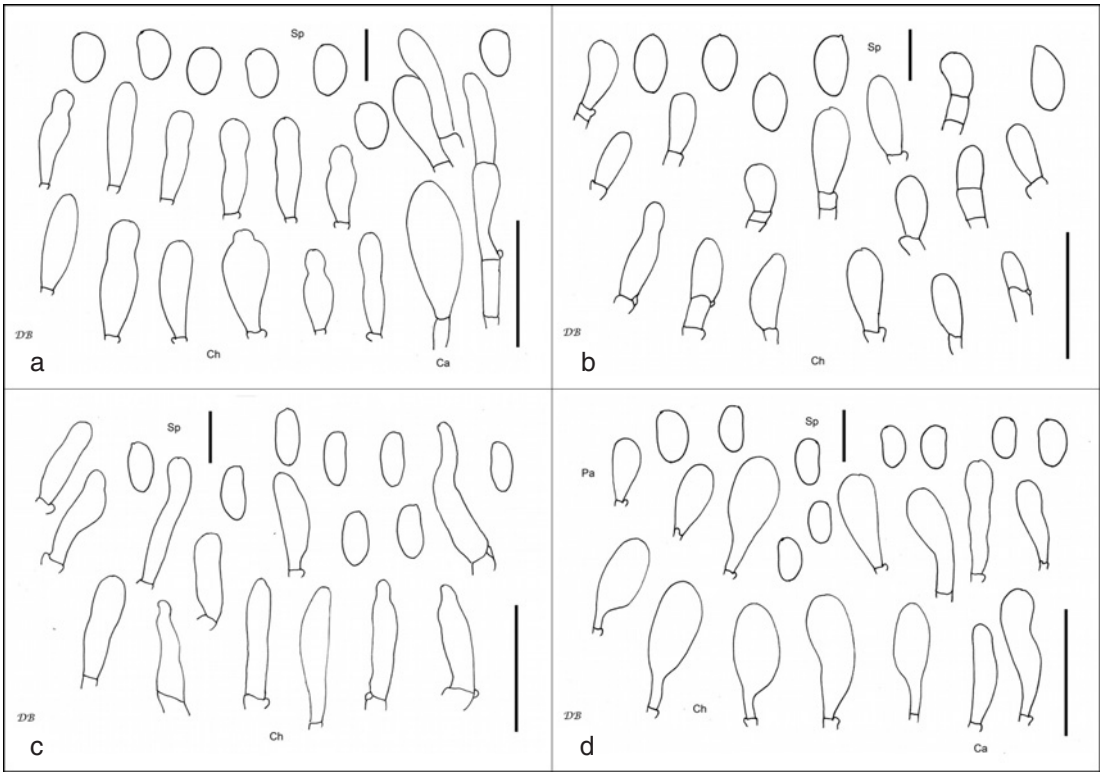


Fig. 5. Microscopic characters of type collections. **a** – *Pseudosperma aureocitrinum* (isotype; DB21-11-12-Esteve-Raventós). **b** – *P. copriniforme* (isotype; XC no. 82101001). **c** – *P. flavellum* (holotype; H6050800). **d** – *P. spurium* (isoparatype; DB14-7-87-Vauras-JV2607). Ca = caulocystidia, Ch = cheilocystidia, Pa = paracystidia, Sp = spores; scale bar spores = 10 µm, scale bar cystidia = 50 µm. Drawings D. Bandini.

Pseudosperma spurium (Jacobsson & E. Larss.) Matheny & Esteve-Rav.

Basionym: *Inocybe spuria* Jacobsson & E. Larss. 2009

Isoparatype: Finland, Varsinais-Suomi, Turku, Ilpoinen, 14 Jul 1987, leg. J. Vauras (TUR-A-175730, DB-14-7-87-Vauras-JV2607, STU; paratype: GenBank AM882785.2).

Spores 8.0–10.7 µm (av. 8.9 µm, SD 0.7 µm) × 4.5–6.0 µm (av. 5.0 µm, SD 0.4 µm); Q = 1.6–2.0 (av. 1.8, SD 0.1), smooth, subellipsoid to broadly ellipsoid, (sub)phaseoliform, often with suprahilar depression, with (sub)cylindrical, obtuse apex. Basidia 4-spored. Cheilocystidia 35–60 µm (av. 44 µm, SD 7 µm) × 15–31 µm (av. 19 µm, SD 4 µm); Q = 1.8–2.8 (av. 2.4, SD 0.3), mostly (sub)clavate. Paracystidia not observed. Caulocystidia only near the apex, slender (sub)cylindrical to subclavate.

DISCUSSION

All three species described here were found on calcareous soil. *Pseudosperma amoris* seems to grow preferably close to frondose trees in low-altitude parks and woods, while *P. napae anum* is so far known only from the banks of the river Isar – a rather special, rare habitat – with *Pinus* and *Dryas octopetala*. *Pseudosperma amabile* grows both with conifers and frondose trees, apparently preferably not in low-altitude terrain, since all collections are from an altitude of several hundred metres. While the colour of pileus of *P. amoris* is yellow(ish), the pileus of *P. napae anum* is brownish and the pileus of *P. amabile* brown to dark brown. As is the case with most species of the genus *Pseudosperma*, the spores of all three species have an obtuse apex and the cheilocystidia are mostly (sub)cylindrical, (sub)clavate to (sub)capitate. This is why we had to compare the three species with many other species – several of which have been described from non-European countries only recently.

It is not too far-fetched to compare even species described from Costa Rica, Pakistan, India, China, Japan, Australia and other foreign countries, since – to mention only two examples – *Inocybe involuta* Kuyper, described originally from the Netherlands, is also known from China, and *I. vestalis* Bandini, Weholt & B. Oertel, recently described from Germany, is documented as ectomycorrhiza from Japan (for both species see Bandini et al. 2020).

Naturally, we concentrated on somehow similar species, for instance leaving out those which are much paler in colour, as e.g. *P. obsoletum* (Romagn.) Matheny & Esteve-Rav. The types of most species mentioned above for comparison have been sequenced (see Fig. 1). The genetic differences in combination with the morphological differences enumerated and/or with entirely different climatic environments, exclude identity with any of the three species described here newly. The types of some species have not yet been sequenced, but in those cases the original description was always detailed enough to exclude identity with our species.

No species genetically closely related to *P. amabile* and *P. amoris* are known, whereas *P. napae anum* is rather closely related to *P. umbrinellum*, a species well known from coastal dunes, growing there in the sand with *Salix repens*. It is, however, to be found also in other habitats. Because of the morphological similarities, however, it is possible that *P. napae anum* has so far been mistaken for this species or also for *P. rimosum* – as is the case with *P. amoris*, while *P. amabile* could be mistaken for *Inosperma maculatum*.

ACKNOWLEDGEMENTS

We are grateful to the curators Otto Miettinen (H), F. Javier Rejos (AH), Jukka Vauras (TUR-A), as well as to Xavier Carteret (Chaville, France), Fernando Esteve-Raventós (Alcalá de Henares, Spain) and Patrick Reumaux (Paris, France) for the loan or gifts of specimens from their herbaria. We also thank Martin Bemann (Heidelberg) for his help with technical matters.

REFERENCES

- ALTSCHUL S.F., GISH W., MILLER W., MYERS E.W., LIPMAN D.J. (1990): Basic local alignment search. – *Journal of Molecular Biology* 215: 403–410. DOI: [https://doi.org/10.1016/S0022-2836\(05\)80360-2](https://doi.org/10.1016/S0022-2836(05)80360-2)
- BANDINI D., OERTEL B., SCHÜSSLER C., EBERHARDT U. (2020): Noch mehr Risspilze: Fünfzehn neue und zwei wenig bekannte Arten von *Inocybe*, Untergattung *Inocybe*. – *Mycologia Bavarica* 20: 13–101.
- BAU T., FAN Y.-G. (2018): Three new species of *Inocybe* sect. *Rimosae* from China. – *Mycosystema* 37(6): 693–702. DOI: <https://doi.org/10.13346/j.mycosystema.180033>
- BON M. (1997a): Clé monographique du genre *Inocybe* (Fr.) Fr. (1^{ère} partie). – *Documents Mycologiques* 27(105): 1–51.
- BON M. (1997b): Clé monographique du genre *Inocybe* (Fr.) Fr. (2^{ème} partie). – *Documents Mycologiques* 27(108): 1–77.
- BON M. (1998): Clé monographique du genre *Inocybe* (Fr.) Fr. (3^{ème} partie). – *Documents Mycologiques* 28(111): 1–45.
- BRESADOLA G. (1905): Hymenomycetes novi vel minus cogniti. – *Annales Mycologici* 3(2): 159–164.
- BULLIARD P. (1789): *Histoire des Champignons de la France*, Vol. 9. – Leblanc Imprimeur, Paris.
- CARTERET X., REUMAUX P. (2017) [2015]: Miettes sur les inocybes (8^e série). – *Bulletin de la Société mycologique de France* 131(1–2): 1–96.
- COOKE M.C. (1886): *New British Fungi*. – *Grevillea* 15(74): 39–43.
- CRIPPS C.L. (1997) The genus *Inocybe* in Montana aspen stands. – *Mycologia* 89: 670–688. DOI: <https://doi.org/10.2307/3761005>
- DERMEK A., VESELSKÝ J. (1977): *Inocybe fastigiata* (Schaeff. ex Fr.) Quéł. and its subspecific taxonomy. – *Česká Mykologie* 31(4): 189–192.
- ESTEVE-RAVENTÓS F. (2014): *Inocybe aureocitrina* (*Inocybaceae*), a new species of section *Rimosae* from Mediterranean evergreen oak forests. – *Plant Biosystems* 148: 377–383. DOI: <https://doi.org/10.1080/11263504.2013.877532>
- GRUND D.W., STUNTZ D.E. (1975): Nova Scotian *Inocybes* III. – *Mycologia* 67: 19–31. DOI: <https://doi.org/10.1080/00275514.1975.12019717>
- GRUND D.W., STUNTZ D.E. (1981): Nova Scotian *Inocybes* VI. – *Mycologia* 73: 655–674. DOI: <https://doi.org/10.1080/00275514.1981.12021393>
- GRUND D.W., STUNTZ D.E. (1983): Nova Scotian *Inocybes* VII. – *Mycologia* 75: 257–270. DOI: <https://doi.org/10.1080/00275514.1983.12021663>
- HOLMGREN P.K., HOLMGREN N.H., BARNETT L.C. (1990): *Index Herbariorum*, 8th ed. – 693 p., Botanic Garden, New York.
- JACOBSSON S., LARSSON E. (2009): *Inocybe spuria*, a new species in section *Rimosae* from boreal coniferous forests. – *Mycotaxon* 109: 201–207. DOI: <https://doi.org/10.5248/109.201>
- JACOBSSON S., LARSSON E. (2012): *Inocybe* (Fr.) Fr. – In: Knudsen H., Vesterholt J., eds., *Funga Nordica. Agaricoid, boletoid, clavarioid, cyphelloid and gastroid genera*, 2nd ed. – pp. 981–1021 & 1028, Nordsvamp, Copenhagen.

- KARSTEN P.A. (1889): Symbolae ad mycologiam Fennicam. XXIX. – Meddelanden af Societas pro Fauna et Flora Fennica 16: 84–106.
- KATOH K., ROZEWICKI J., YAMADA K.D. (2019): MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. – Briefings in Bioinformatics 20: 1160–1166.
- KAUFFMAN C.H. (1924): *Inocybe* (Fries) Quél. – North American Flora 10(4): 227–260.
- KOBAYASHI T. (2002): The taxonomic studies of the genus *Inocybe*. – Nova Hedwigia, Beiheft 124, 246 p., Cramer, Vaduz.
- KOBAYASHI Y. (1952): On the genus *Inocybe* from Japan. – Nagaoa 2: 76–115.
- KROPP B.R., MATHENY P.B., HUTCHISON L.J. (2013): *Inocybe* section *Rimosae* in Utah: phylogenetic affinities and new species. – Mycologia 105(3): 728–747. DOI: <https://doi.org/10.3852/12-185>
- KÜHNER R. (1956): Compléments à la 'Flore analytique'. VI. *Inocybe* goniosporés et *Inocybe* acystidiés. Espèces nouvelles ou critique. – Bulletin de la Société mycologique de France 71(3): 169–201.
- KÜHNER R. (1988): Diagnoses de quelques nouveaux *Inocybes* récoltés en zone alpine de la Vanoise (Alpes françaises). – Documents Mycologiques 19(74): 1–27.
- KUYPER T.W. (1986): A revision of the genus *Inocybe* in Europe. I. Subgenus *Inosperma* and the smooth-spored species of subgenus *Inocybe*. – Persoonia Supplement 3(1): 1–247.
- LANGE J.E. (1917): Studies in the Agarics of Denmark. Part III. *Pluteus*, *Collybia*, *Inocybe*. – Dansk Botanisk Arkiv 2(7): 1–50.
- LARSSON E., RYBERG M., MOREAU P.-A., MATHIESEN Å.D., 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. DOI: <https://doi.org/10.3767/003158509X475913>
- LATHA K.P.D., MANIMOHAN P., MATHENY P.B. (2016): A new species of *Inocybe* representing the *Nothocybe* lineage. – Phytotaxa 267(1): 50. DOI: <https://doi.org/10.11646/phytotaxa.267.1.4>
- LATHA K.P.D., MANIMOHAN P. (2017): *Inocybes* of Kerala. – 181 p., SporePrint Books, Calicut, India.
- MALENÇON G., BERTAULT R. (1970): Flore des champignons supérieurs du Maroc, Vol. 1. – 601 p., Faculté des Sciences, Rabat.
- MATHENY P.B., BOUGHER N.L. (2017): Fungi of Australia. *Inocybaceae*. – 582 p., ABRS, Canberra & CSIRO Publishing, Melbourne.
- MATHENY P.B., HOBBS A.M., ESTEVE-RAVENTÓS F. (2020): Genera of *Inocybaceae*: New skin for the old ceremony. – Mycologia 112: 83–120. DOI: <https://doi.org/10.1080/00275514.2019.1668906>
- MATHENY P.B., KUDZMA L.V. (2019): New species of *Inocybe* (*Inocybaceae*) from eastern North America 1. – The Journal of the Torrey Botanical Society 146(3): 213–235. DOI: <https://doi.org/10.3159/TORREY-D-18-00060.1>
- MILLER M.A., PFEIFFER W., SCHWARTZ T. (2010): Creating the CIPRES science gateway for inference of large phylogenetic trees. – In: Xavier J., ed., Gateway Computing Environments Workshop (GCE). Proceedings of a meeting held 14 Nov 2010, New Orleans, Louisiana, USA, pp. 1–8. Institute of Electrical and Electronics Engineers (IEEE), Piscataway, New Jersey.
- MUNSELL (2009): Soil color charts. – X-Rite, Grand Rapids.
- PRADDEEP C.K., VRINDA K.B., VARGHESE S.P., KOROTKIN H.B., MATHENY P.B. (2016): New and noteworthy species of *Inocybe* (*Agaricales*) from tropical India. – Mycological Progress 15(3/24): 1–25. DOI: <https://doi.org/10.1007/s11557-016-1174-z>
- REUMAUX P. (2004): Fantômes à suivre. – Bulletin de la Société mycologique de France 120(1–4): 105–117.
- SINGER R., ARAUJO I., IVORY M.H. (1983): The ectotrophically mycorrhizal fungi of the neotropical lowlands, especially Central Amazonia. – Nova Hedwigia, Beiheft 77, 352 p., Cramer, Vaduz.
- SOOP K., DIMA B., COOPER J.A., PARK D., OERTEL B. (2019): A phylogenetic approach to a global supraspecific taxonomy of *Cortinarius* (*Agaricales*) with an emphasis on the southern mycota. – Persoonia 42: 261–290. DOI: <https://doi.org/10.3767/persoonia.2019.42.10>
- STAMATAKIS A. (2014): RAXML Version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. – Bioinformatics 30: 1312–1313. DOI: <https://doi.org/10.1093/bioinformatics/btu033>
- STANGL J. (1989): Die Gattung *Inocybe* in Bayern. – Hoppea 46: 5–388.

- STUNTZ D.E. (1947): Studies in the genus *Inocybe*. I. New and noteworthy species from Washington. – *Mycologia* 39: 21–55. DOI: <https://doi.org/10.1080/00275514.1947.12017588>
- TAMURA K., STECHER G., PETERSON D., FILIPSKI A., KUMAR S. (2013): MEGA6: molecular evolutionary genetics analysis version 6.0. – *Molecular Biology and Evolution* 30: 2725–2729.
DOI: <https://doi.org/10.1093/molbev/mst197>
- TIBPROMMA S. et al. (2017): Fungal Diversity notes 491–602: taxonomic and phylogenetic contributions to fungal taxa. – *Fungal Diversity* 83: 1–261. DOI: <https://doi.org/10.1007/s13225-017-0378-0>
- ULLAH Z., JABEEN S., AHMAD H., KHALID A.N. (2018): *Inocybe pakistanensis*, a new species in section *Rimosae* s.str. from Pakistan. – *Phytotaxa* 348(4): 279–288.
DOI: <https://doi.org/10.11646/phytotaxa.348.4.4>