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Morphology and phylogeny reveal *Inosperma sorongense* sp. nov. (Agaricales: Inocybaceae), from Sorong, Southwest Papua, Indonesia

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Abstract

Inosperma sorongense Retn. & W.H.Lu, a novel species from Sorong, Southwest Papua, is described based on a suite of unique morphological characteristics and unique phylogenetic placement based on analysis of combined ITS and LSU loci. The morphological features of the novel taxon include medium-sized basidiomata with a reddish-orange convex, umbonate pileus, a reddish-orange stipe with a bulbous base, and large basidiospores. Phylogenetically, *Is. sorongense* sister to *Is. misakaense* (Matheny & Watling) Matheny & Esteve-Rav. with well support (MLB = 99%, BPP = 1.0). This study provides a full description of the new species, including field photographs of the basidiomata, micrographs, phylogenetic analysis results, and a comparison with similar taxa.

Introduction

Inocybaceae Jülich is an ectomycorrhizal fungal family associated with many kinds of higher plant families (Matheny *et al.* 2020). The family comprises about 1,050 species distributed worldwide (Matheny *et al.* 2020). The revision of the family revealed seven genera, namely *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).

Inosperma was historically erected as a subgenus of *Inocybe* by Kühner (1980) and is now treated at genus rank. The genus is characterized by small to medium-sized basidiomata, a rimose to scaly pileus, an often rubescent context, phaseoliform to subglobose basidiospores, thin-walled cheilocystidia with cyanophilous contents, absence of pleurocystidia, and distinctive odours (Deng *et al.* 2021). *Inosperma* comprises approximately 55 species distributed in Africa, Australasia, Asia, Europe, and North America (Matheny *et al.* 2020). Phylogenetically, the genus is monophyletic

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with six major clades: the Cervicolores clade, Maculatum clade (Inosperma section Inosperma), *Is. misakaense* (Matheny & Watling) Matheny & Esteve-Rav. lineage, *Is. africanum* Aïgnon, Yorou & Ryberg lineage, and two Old World tropical clades (Matheny *et al*. 2020, Deng *et al*. 2021, Li *et al*. 2022, Zhou *et al*. 2023, Crous *et al*. 2024).

Southwest Papua is a province of Indonesia located in the northwestern tip of the island of New Guinea and is well known as the biodiversity center for most organisms. Administratively, the province consists of 6 regencies: namely Sorong, Sorong City as a capitol city, South Sorong, Maybrat, Tambrauw, and Raja Ampat (https://papuabaratdayaprov.go.id/, accessed on 29 March 2026). The ecosystem of Southwest Papua has various ecosystem types (Lense *et al*. 2024), from coastal to alpine, with tropical forests dominating and providing the most favourable habitat for ectomycorrhizal fungi. The earliest documented evidence of ectomycorrhizal fungi was provided by Nugroho *et al*. (2010), who identified *Scleroderma* sp. in association with *Intsia bijuga* (Colebr.) Kuntze (Fabaceae).

During the ectomycorrhizal fungal survey in Sorong, Southwest Papua, in July 2022, some interesting ectomycorrhizal fungal samples were collected, one of which was identified as a potentially new species. Morphological and molecular phylogenetic analyses based on two genes (ITS and LSU) revealed that the taxon is a distinct species. Thus, the present study describes the new species *Inosperma sorongense*, providing a detailed description, illustrations, and the results of the phylogenetic analysis.

Materials & Methods

Morphological study

Inosperma sorongense was collected in July 2022 from a primary forest in the Nature Tourism Park of Sorong, Southwest Papua, Indonesia (Figure 1), and the relevant collection information was noted (Rathnayaka *et al*. 2024). The colour of fresh basidiomes was related to the codes of Kornerup & Wanscher (1967). Macro-morphological characteristics of the basidiomata were recorded before drying process, which was carried out using an electronic food dryer at 40°C (Hu *et al*. 2022).

Microscopic characteristics were described from dried materials rehydrated in KOH (5% aqueous solution) and stained with Congo Red (5%) or Melzer's reagent. The microscopic study was conducted with a light microscope. A total of 25 basidiospores were measured for the examined material. Furthermore, the basidiospores' length (L) and width (W) were measured, and the ratio was calculated using Q = L/W. The shape of basidiospores and cystidia was observed using a Thermo Scientific Quattro S Scanning Electron Microscope (SEM) at the Integrated Laboratory of Bioproduct (i-lab), National Research and Innovation Agency of Indonesia (BRIN). The specimens described in this study were deposited in the Herbarium Bogoriense (BO), BRIN.

DNA Extraction, PCR, and Sequencing

The genomic DNA was extracted from dried basidiomata using Geneaid Plant Genomic DNA Mini Kit (Geneaid Biotech, Taiwan, China) according to the procedure mentioned in the extraction kit. ITS4-ITS5 primer pair was used to amplify the Internal Transcribed Spacer (ITS) region of the nuclear ribosomal DNA (White *et al*. 1990), while the Large Subunit (LSU) region was amplified using LR0R and LR6 primer pair (Vilgalys & Hester 1990, Rehner & Samuels 1995). All PCR products were purified and sequenced at the manufacturing of 1st BASE (Selangor, Malaysia, https://base-asia.com/).

Sequence alignments and phylogenetic analyses

The newly generated sequences in this study were checked and edited in BioEdit (Hall 1999) and subjected to a blastn search available at NCBI to search for the homologous sequences (https://blast.ncbi.nlm.nih.gov/Blast.cgi). Sequences of *Inosperma* and related genera of Inocybaceae obtained from previous studies (Matheny *et al*. 2020, Crous *et al*. 2024, Esteve-Raventós *et al*. 2024) were downloaded from GenBank for phylogenetic analyses (Table 1). Seven taxa of *Crepidotus* (Fr.) Staude, *Simocybe* P.Karst. and *Pleuroflammula* Singer in the family Crepidotaceae Fr. were selected as outgroups following Matheny *et al*. (2020).

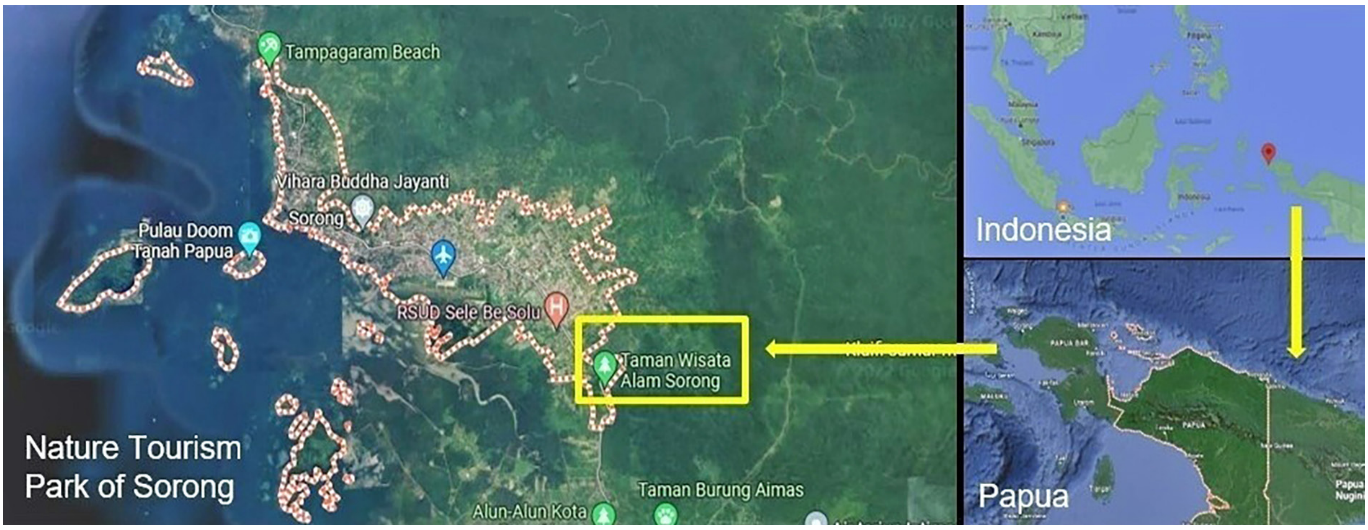

Figure 1. Collection site of *Inosperma sorongense* (Google Maps accessed on 29 December 2022).

The individual datasets of ITS and LSU were aligned in the MAFFT v. 7 online server (https://mafft.cbrc.jp/alignment/server/) (Katoh *et al*. 2019). The datasets were trimmed in TrimAl v.1.3 using the gt 0.6 option for both datasets (Capella-Gutiérrez *et al*. 2009). The finalized datasets of each gene were concatenated into a combined dataset using SequenceMatrix 1.7.8. (Vaidya *et al*. 2011) in the order ITS-LSU. The final alignment contained 1445 characters, including gaps from 118 sequences (ITS+LSU), representing ten genera in two families (Figure 2). The alignments and phylogenetic tree(s) are deposited in Figshare: https://doi.org/10.6084/m9.figshare.28031999.v1.

Maximum likelihood (ML) analysis was conducted using RAxML-HPC2 on XSEDE (8.2.12) (Stamatakis *et al*. 2008, Stamatakis 2014) in the CIPRES Science Gateway platform (https://www.phylo.org/portal2/login!input.action) with 1000 rapid bootstrap replicates and GTRGAMMA as the substitution model (Miller et al. 2010). Bayesian analysis (BI) was performed using MrBayes on XSEDE (3.2.7a) (Ronquist *et al*. 2012) in the above platform with the best-fit model (GTR+I+G) that was tested by MrModeltest v. 2.2 for each gene locus (Nylander *et al*. 2004). Four simultaneous Markov Chains were run for 2,000,000 generations, with tree sampling occurring every 200th generation (resulting in 20,000 total trees).

Table 1. Names, voucher numbers, and corresponding GenBank accession numbers of taxa used in the phylogenetic analysis.

Taxa	Voucher	GenBank accession numbers	
		ITS	LSU
Inosperma africanum	MR00387	MN096189	MN097881
Inosperma africanum	HLA0383 (T)	MT534298	MT560733
Inosperma africanum	HLA0353	MT534299	-
Inosperma akirnum	CAL1358(T)	KY440085	NG_057279
Inosperma bicoloratum	ZT12187	GQ892984	GQ892938
Inosperma bongardii	JV7450F	-	EU555448
Inosperma bulbomarginatum	MR00357 (T)	MN096190	MN097882
Inosperma calamistratoides	ZT9630	JQ801392	JQ815413
Inosperma calamistratum	EL1904	AM882938	AM882938
Inosperma carnosibulbosum	TBGT12047	KT329448	KT329454
Inosperma cervicolor	TURA:4761	JQ801395	JQ815417
Inosperma changbaiense	HMJAU25861(T)	NR_160610	NG_066407
Inosperma chlorochroum	GC06090501(T)	MK508903	-
Inosperma cyanotrichium	TENN065728(T)	NR_153127	JN975033
Inosperma dodonae	STU: SMNS-STU-F-0901253(T)	NR_173967	-
Inosperma erubescens	JV9070F	-	EU569846
Inosperma aff. *fastigiellum*	PBM3325	JQ801399	JQ815419
Inosperma flavobrunneum	HLA0372	MT534290	MT536756
Inosperma flavobrunneum	HLA0367 (T)	MN096199	MT536754
Inosperma geminum	EL 63-06	OR823936	OR823936
Inosperma geminum	JV 31497 (T)	OR823937	OR823937
Inosperma geraniodorum	EL10606	FN550945	FN550945
Inosperma gracilentum	EL 8519 (T)	OR817726	OR817726
Inosperma gracilentum	J. Favre Z.A.82a	PP431544	-
Inosperma gregarium	CAL1309(T)	NR_153174	KX852306
Inosperma hainanense	Zeng4937 (T)	MZ374070	MZ374761
Inosperma ismeneanum	STU: SMNS-STU-F-0901561	MW647625	-
Inosperma lanatodiscum	PBM2451	JQ408759	JQ319690
Inosperma latericium	PDD:92382	GU233367	GU233413
Inosperma longisporum	MHNNU32337(T)	OP135509	OP135495
Inosperma longisporum	MHNNU33070	OP135504	OP133999
Inosperma macrocarpa	HLAO787	OQ300390	OQ286290
Inosperma macrocarpa	HLA0791 T	OQ300373	OQ300370
Inosperma maculatum	EL12604	AM882964	AM882964
Inosperma maximum	PBM 2222	-	EU569854
Inosperma maximum	MTS2732	JQ801400	JQ815420

Taxa	Voucher	GenBank accession numbers	
		ITS	LSU
Inosperma misakaense	PC96234	JQ801409	EU569874
Inosperma monastichum	STU: SMNS-STU-F-0901533	NR_173977	-
Inosperma mucidiolens	DG1824(T)	HQ201339	HQ201340
Inosperma muscarium	FYG6091 (T)	MZ373982	MZ373991
Inosperma mutatum	PBM3020	JQ801385	JN975021
Inosperma aff. *mutatum*	PBM2953	JQ801410	JQ994476
Inosperma neobrunnescens	PBM2452	-	EU569868
Inosperma neobrunnescens var. *leucothelotum*	SAT0427406	JQ801411	JN975025
Inosperma neohirsutum	AH 26947(T)	PP431510	PP431532
Inosperma neohirsutum	AH 48235	PP431512	PP431533
Inosperma nivalellum	MHNNU31689(T)	OP135502	OP134006
Inosperma nivalellum	MHNNU31689-1	OP389161	OP389202
Inosperma pavithrum	DKP-SERB65	PP350421	PP192110
Inosperma praetermissum	P.A. Karsten 2497 (H)	PP431551	-
Inosperma praetermissum	ACAD:10206	MH024863	MH539758
Inosperma praetermissum	PBM1105	JQ801386	JQ815409
Inosperma proximum	ZT13015	EU600839	EU600840
Inosperma quietiodor	EL115_04	AM882960	AM882960
Inosperma cf. *reisneri*	MCA 646	-	EU555463
Inosperma rhodiolum	EL223_06	FJ904175	FJ904175
Inosperma rimosoides	PBM2459	DQ404391	AY702014
Inosperma rosellicaulare	ACAD:11618(T)	MT237482	-
Inosperma rubricosum	PBM3784(T)	NR_152369	NG_057260
Inosperma saragum	CAL1360(T)	KY440103	NG_057285
Inosperma shawarense	ASSW79A	KY616964	KY616966
Inosperma sorongense	**BO24735 (T)**	**PQ687483**	**PQ687484**
Inosperma sp.	BB3233	JQ801415	EU600885
Inosperma sp.	PC:96013	JQ801383	EU600883
Inosperma sp.	PC96073	JQ801417	EU600870
Inosperma sphaerobulbosum	MHHNU 32266(T)	OP135501	OP134001
Inosperma sphaerobulbosum	MHHNU 32266-1	OP389166	OP389205
Inosperma squamulosobrunneum	FYG2869	OP389200	OP389211
Inosperma squamulosobrunneum	MHNNU32162	OP135508	OP134005
Inosperma squamulosobrunneum	MHHNU 32351	OP135507	OP134003
Inosperma squamulosobrunneum	MHHNU 32359(T)	OP135499	OP134000
Inosperma squamulosohinnuleum	FYG2015388	OP389199	OP389209
Inosperma squamulosohinnuleum	MHHNU 32195(T)	OP135500	OP134002
Inosperma squamulosohinnuleum	MHHNU 32362	OP135503	OP134004
Inosperma subhirsutum	EL7612	OR817729	OR817729
Inosperma subhirsutum	AH 46825	PP431508	-
Inosperma subhirsutum	AH 56195	PP431507	PP431530
Inosperma subhirsutum	JV11950	-	EU555452
Inosperma subsphaerosproum	FHMU3153 (T)	MW403825	MW397171
Inosperma turietoense	AH 47710 T	PP431526	PP431541
Inosperma turietoense	AH 47669	PP431525	PP431540
Inosperma veliferum	AH 56198	PP431519	PP431539
Inosperma vinaceobrunneum	PBM2951	-	HQ201353
Inosperma vinaceum	AMB 18747 (T)	MW561108	NG_075430

Taxa	Voucher	GenBank accession numbers	
		ITS	LSU
Inosperma viridipes	TENN 066999(T)	NR_153168	KP171094
Inosperma virosum	TBGT:753(T)	KT329452	KT329458
Inosperma zonativeliferum	FYG6441	OL850878	OM845772
Inosperma adaequatum	JV 16501F	-	AY380364
Crepidotus applanatus	PBM 717	DQ202273	AY380406
Crepidotus prostratus	PBM3463	HQ728537	HQ728538
Pleuroflammula flammea	MCA339	DQ494685	AF367962
Pleuroflammula praestans	PBM3461	HQ832450	HQ832464
Pleuroflammula tuberculosa	PAM02072903	HQ832452	HQ832465
Simocybe phlebophora	PBM3089	MK421963	MK421967
Simocybe serrulata	AFTOL-ID 970	DQ494696	AY745706
Auritella brunnescens	PBM3174	KJ702344	JQ313571
Auritella dolichocystis	T24844	-	AY380371
Inocybe cacaocolor	PBM3790	KJ778845	KJ756464
Inocybe pileosulcata	TBGT:10742	KP308810	KP170979
Inocybe magnifolia	MCA2441	NR_119996	JN642244
Inocybe humidicola	PBM3719	KP171126	KJ801181
Inocybe lanuginosa	TENN:062780	HQ232480	KP170923
Inocybe thailandica	DED8049	GQ893013	GQ892968
Inocybe fuscicothurnata	PBM3980	MF487844	KY990485
Inocybe pallidicremea	PBM2744	KY990553	AY380385
Inocybe luteifolia	PBM2642 T	NR_119719	EU307814
Inocybe corydalina	EIU:AM10687	MH216083	MH220259
Inocybe melanopus	PBM3975	-	MH220276
Inocybe relicina	JV 10258 T	AF325664	AY038324
Nothocybe distincta	CAL 1310 T	NR_173156	NG_057278
Pseudosperma sororia	PBM3901 T	JQ408772	JQ319700
Pseudosperma bulbosissima	DBG19916	MH024849	MH024885
Pseudosperma notodryina	CO4463	MH578028	MK421970
Mallocybe myriadophylla	AFTOL-ID 482	DQ221106	AY700196
Mallocybe terrigena	JV16431 T	AM882864	AY380401
Mallocybe tomentosa	PBM4138	MG773814	MK421969
Tubariomyces inexpectatus	AH20390 T	GU907095	EU569855
Tubariomyces sp.	BB6018	MK421965	EU600887

Newly generated sequences are indicated in black bold. “-” indicates no data available in GenBank.

Results

Phylogenetic analyses

The topologies of the resulting tree from ML analysis are similar to those of BI analysis and consistent with previous research results (Matheny *et al.* 2020, Crous *et al.* 2024, Esteve-Raventós *et al.* 2024). The ML tree is shown in Figure 2 with Maximum Likelihood Bootstrap (MLB) and Bayesian Posterior Probabilities (BPP) equal to or more than 60% and 0.90, respectively.

The phylogenetic tree showed that *Inosperma* species formed a monophyletic lineage with maximum support (MLB= 100%, BPP = 1.0) and were classified into six major lineages: *Inosperma* section *Inosperma*, Maculatum clade, *Is. misakaense* lineage, *Is. africanum* lineage, and two Old World tropical clades. The new taxon, *Is. sorongense* clustered with *Is. misakaense* within *Is. misakaense* lineage. Our phylogenetic results align with previous studies, which have also indicated a sister relationship between the species of the *Is.* sect. *Inosperma* and the *Is. misakaense* lineage (Deng *et al.* 2021, Crous *et al.* 2024). Additionally, two other clades, Maculatum and Old World Tropical clades, also formed monophyletic lineage groups.

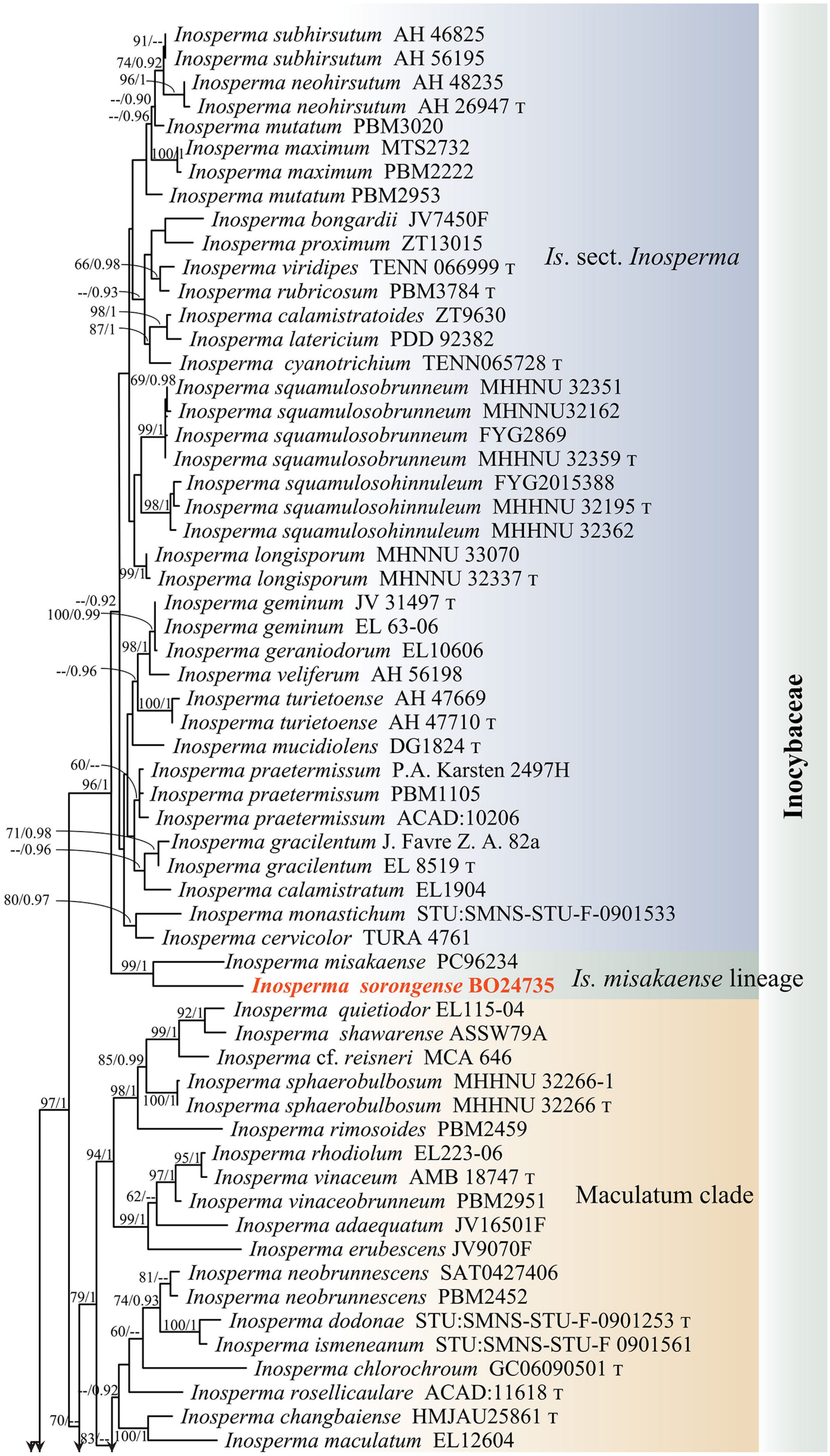

Figure 2. Part A – see caption below.

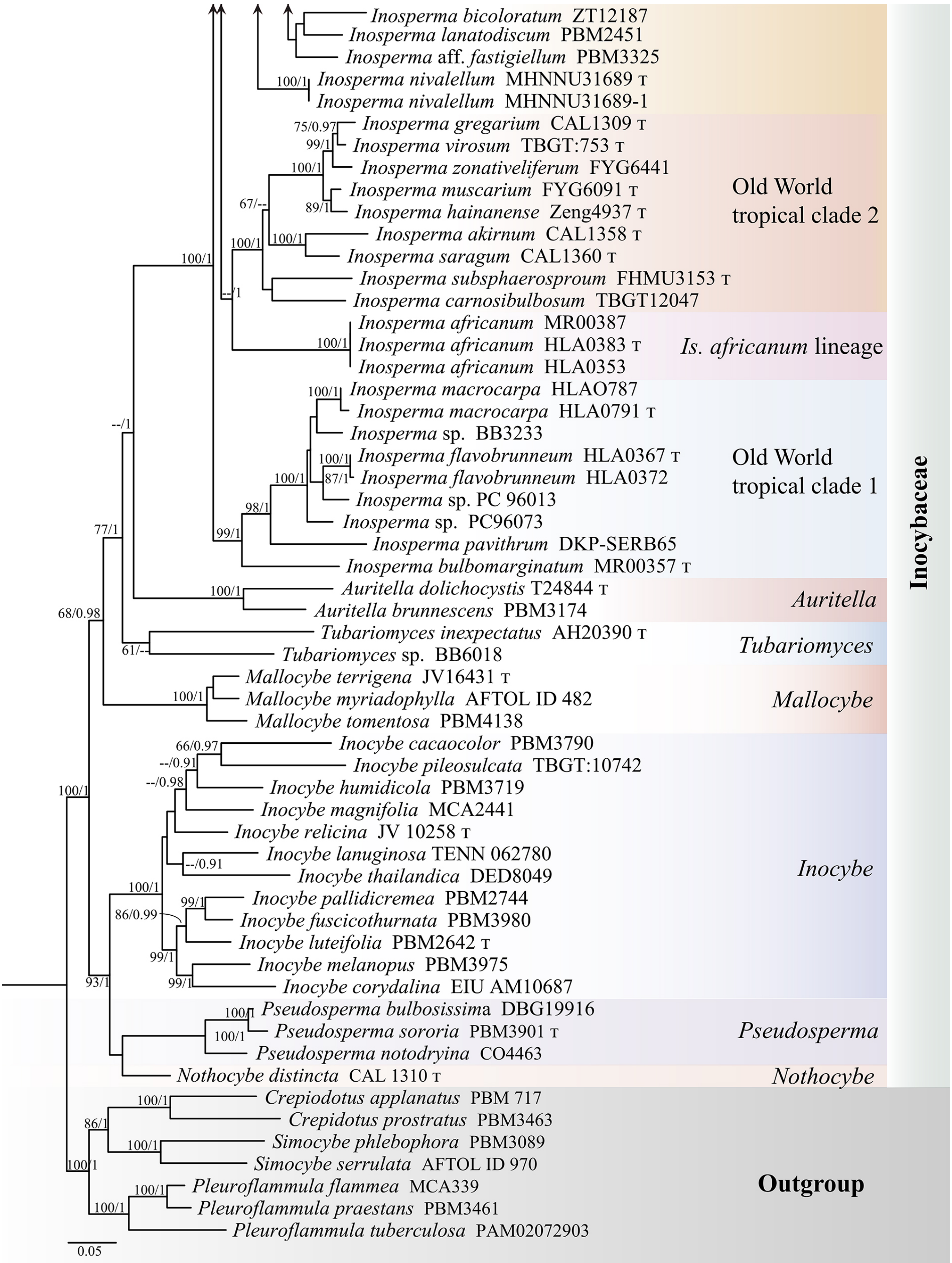

Figure 2. Phylogenetic tree generated from ML analysis based on a combined ITS + LSU sequence dataset. ML bootstrap values equal to or greater than 60% and BPP values of BI equal to or greater than 0.90 are given above the branches as MLB/BPP. The new taxa is in red. "T" indicates the sequences are from the type specimen.

Taxonomy

Inosperma sorongense Retn. & W.H. Lu, *sp. nov.*

MycoBank – MB 856851.

Type: Indonesia: Papua New Guinea: West Papua, Sorong, Nature Tourism Park, 0°54'S, 131°51'E, soil within a lowland natural vegetation dominated by *Vatica papuana* (Dipterocarpaceae) and *Syzygium* sp. (Myrtaceae), at an elevation of approximately 35 m asl, 15 July 2022, A. *Retnowati 1271* (holotype: BO 24735!). GenBank accession number – ITS = PQ687483, nrLSU = PQ687484).

Diagnosis: *Inosperma sorongense* resembles *Is. misakaense* in basidiomata size, white marginate of lamellae, and shape of cheilocystidia. Key physical traits and genetic placement distinguish them. Unlike *Is. sorongense*, *Is. Inosperma misakaense* features a cinnamon-buff, light yellowish brown to clay colour, (light brown) or clay colour, at times with fulvous center, a white to light brown stipe without a bulbous base; smaller basidiospores with bigger Q index, necro-pigmented basidia and smaller cheilocystidia. Both species inhabit different environments. *Inosperma misakaense* was collected in seasonally burnt woodlands characterized by *Brachystegia*, *Gilbertiodendron*, *Isoberlinia*, and *Julbernardia* (caesalpinioid genera of the Fabaceae family), as well as *Uapaca* (Phyllanthaceae). In contrast, *Is. sorongense* was sampled from a natural plant community primarily composed of *Vatica papuana* and *Syzygium* sp.

Figure 3. a–d Basidiomata of *Inosperma sorongense* (*A. Retnowati 1271*, holotype). Scale bars = 1 cm.

Pileus 2–2.7 cm in diameter, convex when young, then becoming plano-convex with a broadly umbo in age; margin decurved; surface dry, entirely squarrose at first, then becoming squamose towards the margin in age, with white underneath; reddish-orange (7A7). Lamellae adnate, crowded, with 14 attached, two series of lamellulae, thin (1–1.6 mm), white serrulate edge, concolorous to the pileus. Stipe 2.2–2.6 × 0.3–0.6 cm, cylindrical, central, solid, surface concolorous with the pileus on the upper part of the stipe, white underneath, subsquarrose along the entire length, with a swollen bulbous base. Veil remnants absent. Context white, up to 0.6 cm thick. Odour and taste not distinctive. Basidiospores (10.5)11–12.4 (13.3) × 7–9.5 µm (x_m = 11.90 ± 0.77 × 8.16 ± 0.51, Q = 1.31–1.82, Q_m = 1.46 ± 0.12 (25 basidiospores per specimen), smooth, ellipsoid, thick-walled, brown. Basidia 30.3–42.5 × 9–11 µm, clavate, 4-spored, not necro-pigmented, hyaline. Pleurocystidia absent. Cheilocystidia 42.5–70.8 × 12–14.3 µm, subcylindrical to cylindrical, clavate, or turbinate, thin-walled, forming a sterile edge, thin-walled, hyaline. Hymenophoral trama regular arranged; hyphae 3-8 µm, thin-walled, hyaline to pale yellow. Pileipellis a cutis with cylindrical, smooth, thin-walled, incrusted hyphae; 5–6.1 µm wide, containing brown pigment, hyaline. Pileal trama composed of cylindrical hyphae, 3.3–8.4 µm, smooth, thin-walled, hyaline to pale yellow in KOH. Stipitipellis a cutis radially arranged, hyphae 5.2–7.7 µm wide, parallel, cylindrical, hyaline. Caulocystidia absent. Oleiferous hyphae present, 1.9–5.7 µm, scattered, thick-walled, smooth, and bright yellow. Clamp connections present. Figures 3–6.

Habit, habitat, and distribution: Occurring as solitary or scattered on soil in a lowland natural habitat where *Vatica papuana* and *Syzygium sp.* are the dominant species. The species is distributed only in Sorong (Papua).

Etymology: The species epithet *sorongense* refers to the location “Sorong” from where the holotype was collected.

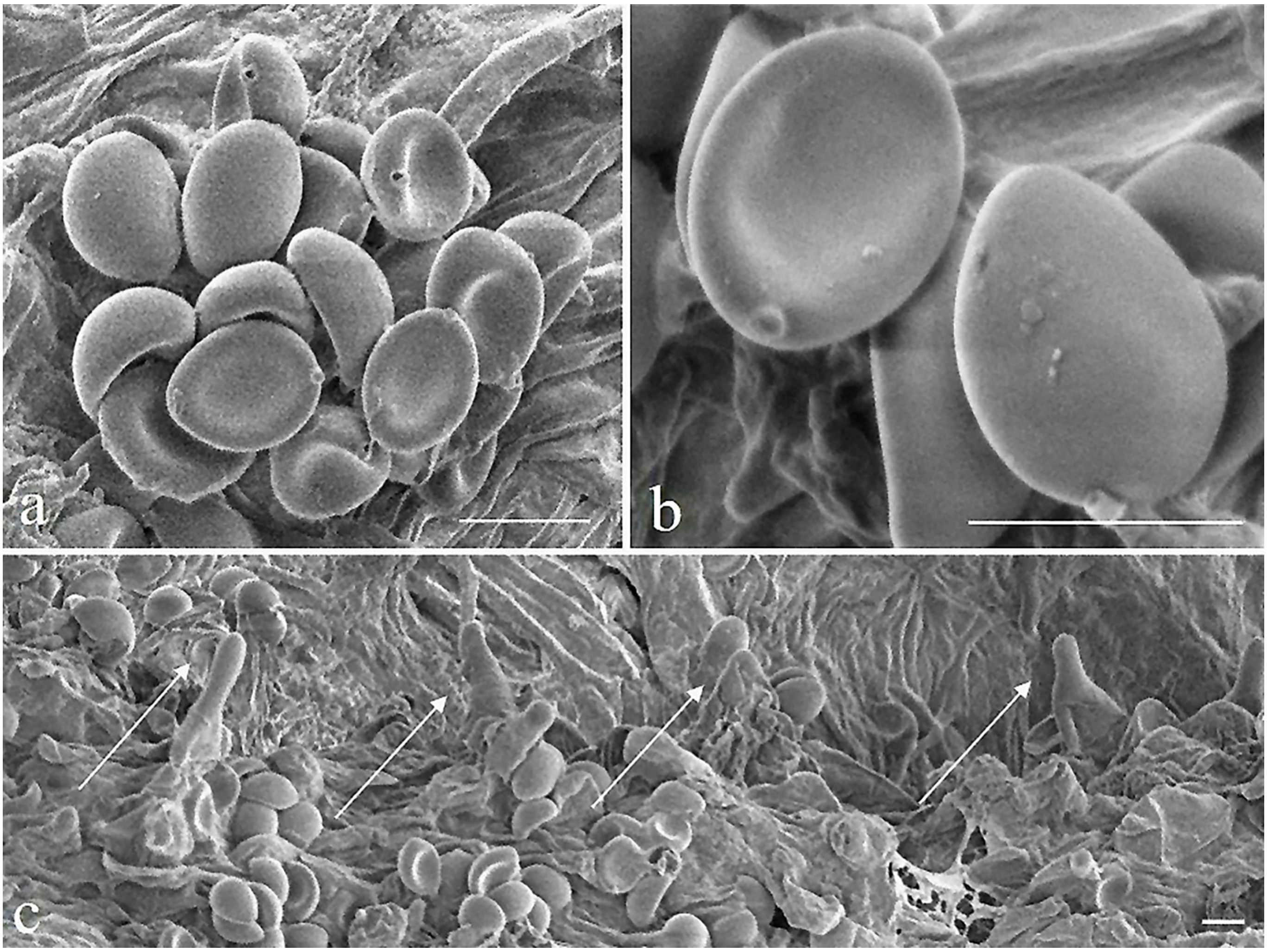

Figure 4. Microscopic characteristics of *Inosperma sorongense* (*A. Retnowati 1271*, holotype) under SEM. a–b, basidiospores; c, cheilocystidia. The arrow shows cheilocystidia. Scale bar: a–b = 10 µm; and c = 20 µm.

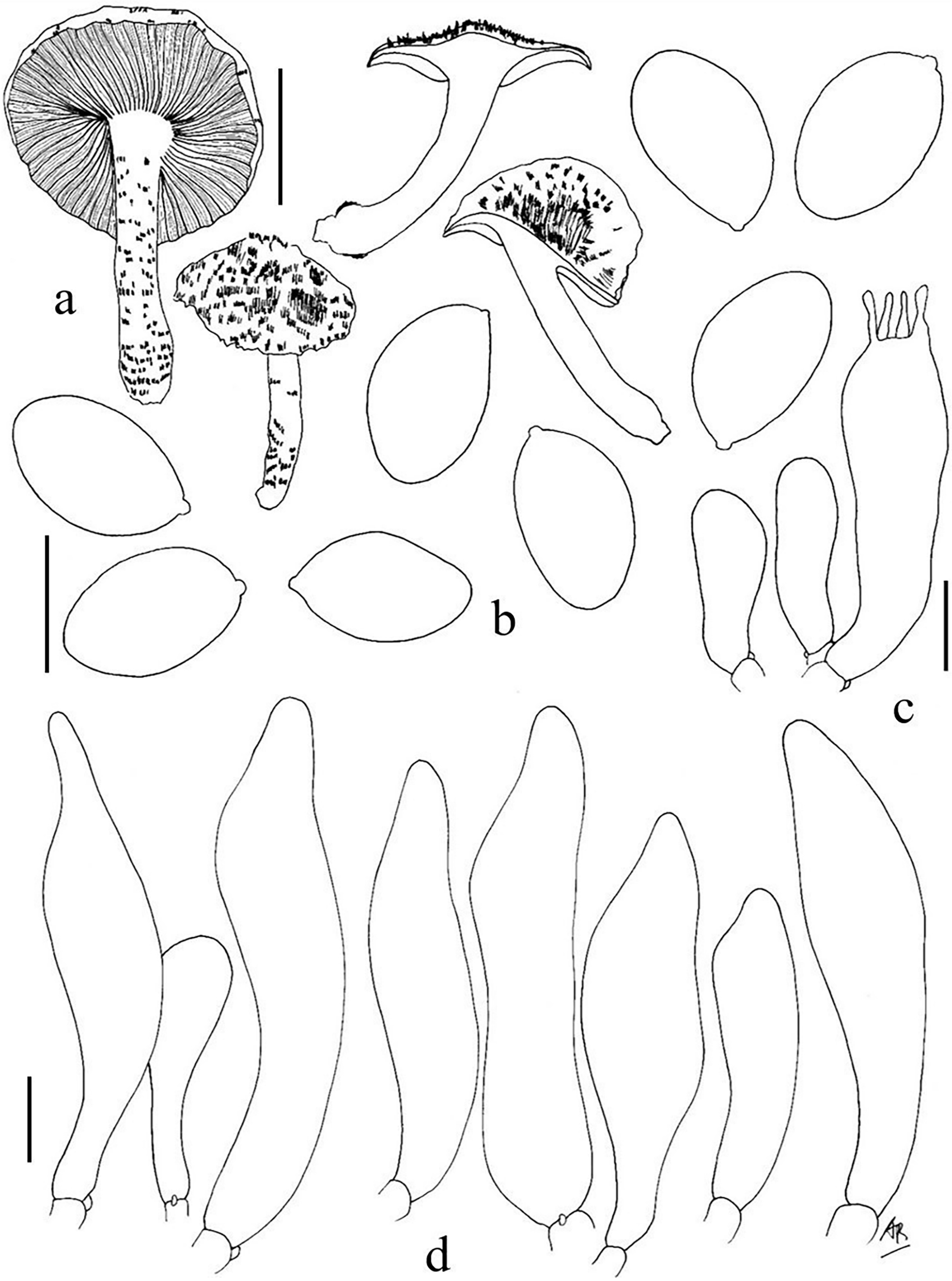

Figure 5. Line drawings of morphological characteristics of *Inosperma sorongense* (from *A. Retnowati 1271*, holotype). a, basidiomata; b, basidiospores; c, basidium and basidioles; d, cheilocystidia. Scales bar: a = 1.5 cm; b–d = 10 µm.

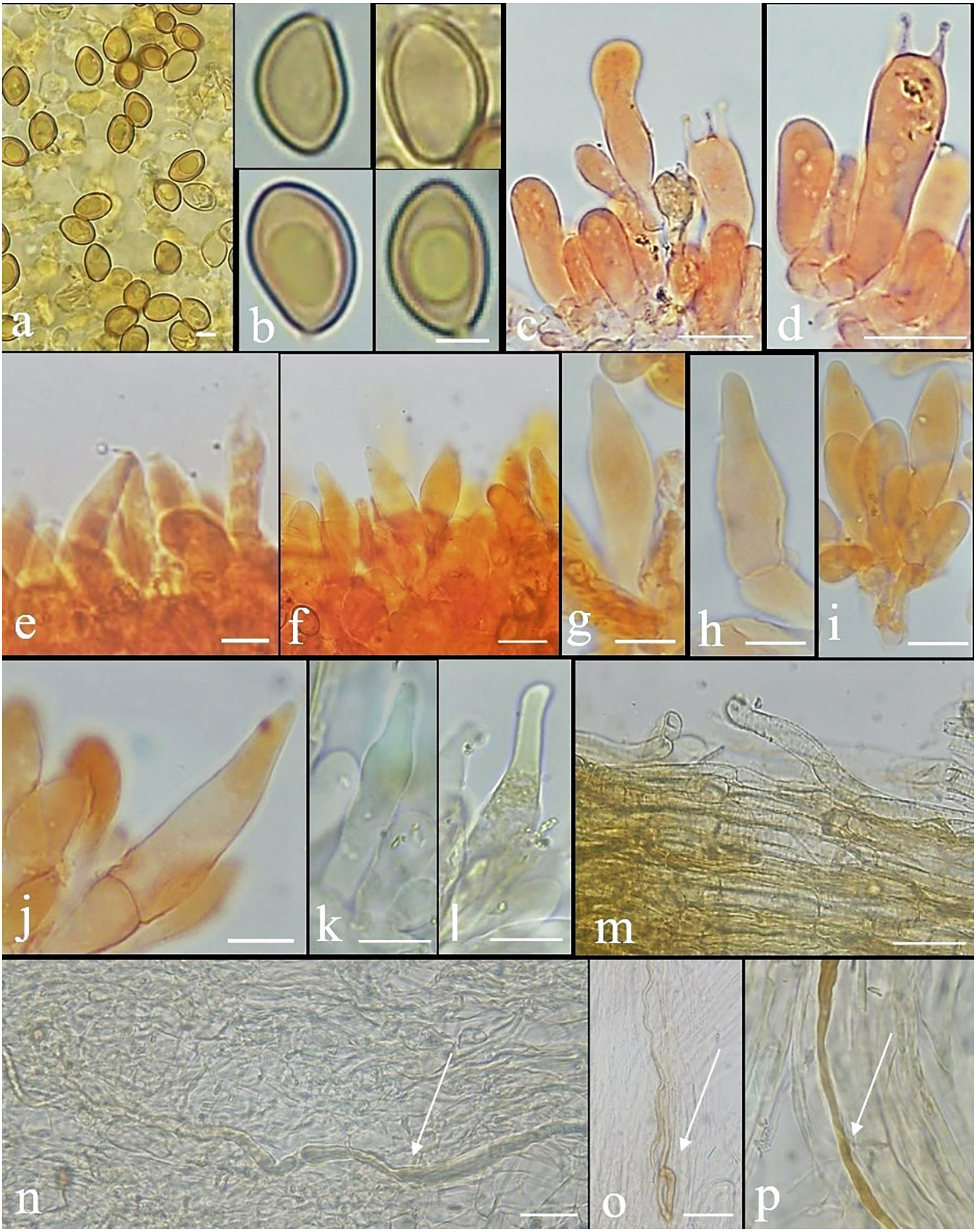

Figure 6. Micro-morphological characteristics of *Inosperma sorongense* (from *A. Retnowati 1271*, holotype). a–b, basidiospores; c–d, basidia and basidioles; e–l, cheilocystidia; m, pileipellis; n, oleiferous hypha at the pileus context; o–p, oleiferous hypha at the stipe context. Scale bar: a–b = 5 µm; c–p = 20 µm.

Notes: The new species *Inosperma sorongense* can be distinguished from other known *Inosperma* species by having medium-sized basidiomata, a convex, reddish-orange, umbonate pileus with a squarrose centre and squamose towards the margin; crowded and white edge lamellae, subsquarrose stipe with a bulbous base, large basidiospores, the presence of cheilocystidia, and the absence of pleuro- and caulocystidia (Figure 3–6).

Phylogenetically, *Is. sorongense* sister to *Is. misakaense* with strong statistical support (MLB = 99%, BPP = 1.0), forming a distinct lineage separate from other members of *Inosperma*. *Inosperma misakaense* (synonym: *Inocybe misakaensis*) was first described in Zambia, Africa, within the *Inosperma* clade of the genus *Inocybe* sensu lato. At the time of its proposal, phylogenetic analyses placed it as a sister lineage to the *Is.* sect. *Cervicolores* within the *Inosperma* clade (Matheny & Watling 2004). Subsequently, Matheny *et al*. (2020) elevated the *Inosperma* section to the genus level, *Is. misakaense* was transferred to Inosperma.

The position of *Is. sorongense* in the phylogenetic tree confirmed *Is. sorongense* as a new species based on a combined ITS + LSU sequence dataset with strong MLB and BPP support. This molecular evidence reinforces the morphological distinctions of *Is. sorongense* from other described species of *Inosperma*. Thus, the morphological and molecular data provide strong evidence supporting the novelty of the present species described in this study.

Discussion

The phylogenetic position of *Inosperma africanum* in our analysis differs from most previous studies. In our phylogenetic tree, it is recovered as sister to the Old World tropical clade 2; however, this relationship is weakly supported and should be interpreted with caution. In contrast, the original description and subsequent studies consistently place *Is. africanum* as sister to the rest of *Inosperma*, with strong statistical support (Aïgnon *et al*. 2021, 2023; Deng *et al*. 2022; Crous *et al*. 2024). Interestingly, a similar placement to ours has been reported in one previous study (Li *et al*. 2022), suggesting that its phylogenetic placement remains unresolved and may be affected by differences in taxon sampling and gene selection, especially given the absence of the protein-coding *rpb*2 gene in our dataset, which is known to improve phylogenetic resolution in *Inosperma*.

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