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First record of *Inosperma subsphaerosporum* (Inocybaceae) in Indonesia

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Summary. *Inosperma* (Inocybaceae) was originally described as a subgenus of *Inocybe*. Some species of *Inosperma* are considered edible mushrooms, but this genus also includes a few toxic species with high levels of muscarine. To date, the knowledge of this genus in Indonesia remains poor. During a mushroom hunting in Central Kalimantan (Indonesia) by the Indonesian mushroom hunter community, some fruiting bodies of inocyboid fungi which consumed and traded by the local people were collected. At glance, the specimens resembled *Inosperma* or *Pseudosperma* by the macromorphological characters in the field. Our goal was to justify the taxonomical position of our inocyboid specimens based on morphological and molecular evidence. The fresh fruiting bodies were used for the analysis. The basidiomata was described based on the macro- and micromorphological characters. The molecular analysis and phylogenetic tree construction were performed based on ITS 1–2 sequences. The combination of morphological and molecular analyses confirmed our collection as *Inosperma subsphaerosporum*. Morphologically, our specimens can be determined by the conical applanate cap with umbo, incurved to decurved margin, dry pileus with fibrillose to rimulose surface, lamellae adnexed to sinuate, cylindrical stipe, subglobose to globose smooth basidiospores, and abundant cheilocystidia in clusters. The yellow intracellular contents of cheilocystidia distinguished our specimen from *Pseudosperma*, while the outline of basidiospores differed our specimens to closely morphological species of *I. carnosibulbosum*, *I. akirnum*, and *I. saragum*. The BLAST result revealed that our specimen exhibits 96 % similarity to *I. subsphaerosporum* as the top hit. The phylogenetic tree (RAxML) nested our specimens in the *I. subsphaerosporum* clade from type material. The current study provides the first information on the occurrence of *I. subsphaerosporum* in Indonesia. Future study should be done to analyze both nutritional and muscarine content of this Indonesian *Inosperma*.

Первая находка *Inosperma subsphaerosporum* (Inocybaceae) в Индонезии

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Ключевые слова: Борнео, дикорастущие грибы, морфология, филогенез, Basidiomycota.

Аннотация. *Inosperma* – род грибов семейства Inocybaceae, первоначально описанный в качестве подрода рода *Inocybe*. Некоторые виды рода *Inosperma* считаются съедобными грибами, но этот род также включает несколько токсичных видов с высоким содержанием мускарина. На сегодняшний день изученность этого рода в Индонезии остается фрагментарной. Во время сбора грибов в Центральном Калимантане (Индонезия) индонезийским обществом грибников-любителей было собрано несколько плодовых тел иноцибоидных грибов, которые местные жители употребляли в пищу и продавали. По макроморфологическим признакам в поле образцы напоминали *Inosperma* или *Pseudosperma*. Нашей целью было установить видовую принадлежность собранных иноцибоидных образцов на основе морфологических и молекулярных данных. Для анализа использовали свежие плодовые тела (базидиомы). Базидиомы описаны по макро- и микроморфологическим признакам. Молекулярный анализ и построение филогенетического дерева проводили на основе последовательностей ITS 1–2. Сочетание морфологического и молекулярного анализов подтвердило нашу находку как *Inosperma subsphaerosporum*. Морфологически наши образцы можно определить по конической уплощенной шляпке с вершиной, вогнутой к неизогнутому краю, сухим ворсинкам с волокнистой или слегка ребристой поверхностью, пластинкам, прикрепленным выемкой, цилиндрической ножке, гладким полушаровидным до шаровидных базидиоспорам и многочисленным скоплениям хейлоцистид. Желтое внутриклеточное содержимое хейлоцистид отличало наш образец от *Pseudosperma*, а очертание базидиоспор отличало наши образцы от близких по морфологии видов *I. carnosibulbosum*, *I. akirnum* и *I. saragum*. Результат BLAST показал, что наш образец имеет 96%-е сходство с *I. subsphaerosporum*. Филогенетический анализ (RAxML) подтвердил принадлежность наших образцов к кладе *I. subsphaerosporum* из типового материала. Настоящее сообщение представляет информацию о первой находке *I. subsphaerosporum* в Индонезии. Для анализа содержания питательных веществ и мускарина в этой индонезийской иносперме необходимы дополнительные исследования.

Introduction

The genus *Inosperma* (Kühner) Matheny et Esteve-Rav. (typified by *I. calamistratum*) was initially conceived as a subgenus of *Inocybe* by Kühner (1980). Currently, *Inosperma* is recognized as a genus rank in Inocybaceae Jülich (Matheny et al., 2019). Members of this genus are characterized by small to medium-fruited bodies (basidiomata), rimose to scaly cap, reddening context when bruised, hyaline basidia, phaseoliform basidiospores, thin-walled cheilocystidia, lack of pleurocystidia, and often with distinctive odors (Matheny et al., 2019). The genus *Inosperma* accommodates species which were previously distributed to *Inocybe* sect. *Cervicolores* Singer (1975), Maculata clade (Larsson et al., 2009), and Old-World tropical clades (Kropp et al., 2013; Pradeep et al., 2016). A total of 80 taxa have been recorded in this genus worldwide (Index Fungorum, 2023). Currently, *Inosperma* is comprised of about 55 species in Africa, Australasia, Asia, Europe, and North America (Matheny et al., 2019). The number will increase as several recently described species of *Inosperma* have been reported (Aignon et al., 2021; Deng et al., 2021; Li et al., 2022), including *I. subsphaerosporum*.

Inosperma subsphaerosporum, a new species of *Inosperma* was recently reported from Hainan Tropical Rainforest National Park China (Deng et al., 2021). The specific epithet “*subsphaerosporum*” refers to the shape of its basidiospores. Morphologi-

cally, this species can be determined by the brown to yellowish, scaly-fibrillose cap, grayish to brownish dense lamellae, a cylindrical longitudinally fibrillose stipe with recurved fibrils at the apex, and a salty or musty smell (Deng et al., 2021). To date, the distribution of this species was only known from the type locality in Hainan Province (China), grow on soil and associated with Fagaceae (Deng et al., 2021). Previously, *I. subsphaerosporum* was phylogenetically placed in an Old-World tropical clade, in which all members are described from South Asia. However, knowledge of this species in Southeast Asia has yet to be found.

The information on wild Indonesian inocyboid mushroom is scarce, and species of *Inosperma* are poorly known. No information provided regarding the *I. subsphaerosporum* strain history, nor herbarium collection number that deposited in Indonesia. In 2022 and 2023, our field examination on the distribution of Inocybaceae in Central Kalimantan (Borneo) in Indonesia has revealed the consumption of wild inocyboid mushroom by the local community. The foraging and consuming of wild inocyboid mushrooms have been done for decades. During the fungus foray held by the Indonesian mushroom hunter community (KPJI), we obtained some basidiomata of wild edible inocyboid mushroom. The goal of this study was aimed to reveal the taxonomical position of our inocyboid specimens based on morphological and molecular evidence.

Material and Methods

The specimens were obtained at Buntok, Dusun Selatan, Barito Selatan, Central Kalimantan, Indonesia (1°42'30.3"S, 114°49'25.8"E), in 2022 and 2023 during a mushroom hunting carried by the KPJI. The fruiting bodies were photographed *in situ* and ecological information (coordinate, substrate, vegetations) were noted. Some of the specimens were deposited to Herbarium Bandungense Indonesia with the collection number FIPIA-DEP59. The morphological characteristics were examined from fresh basidiomata *in situ* and in Mycology Laboratory, Department of Biology, Faculty of Mathematics and Natural Sciences, IPB University, Indonesia and in the Integrated Laboratory of Bioproducts (iLaB), BRIN, Bogor, Indonesia. The macromorphological features including color, size, pileus and stipe ornamentation, margin, and lamellae were observed directly and by a loupe. The micromorphological characters of basidium, cystidia, spores (shape, size, color, ornamentation), and clamp connection were observed using light microscope. Specimens were also subjected to examination via scanning electron microscopy (SEM), which was prepared following the methods of Goldstein et al. (1992). Lamellae were cut into small pieces (5 × 5 mm), pre-fixed in 2.5 % glutaraldehyde of a cacodylate buffer with a pH of 8.4 at 27 °C for two days. Next, they were pre-fixed in 2 % tannic acid for six hours and washed with four different cacodylate buffers. The samples were dehydrated in 50–100 % ethanol series, infiltrated with t-butanol twice for 10 minutes, and freeze dried. Freeze dried samples were mounted on an aluminum stub with double-sided carbon tape and coated with gold. Samples observed using the JSM IT 200 SEM system (JEOL, Tokyo, Japan). The specimens were identified using related identification references (Matheny et al., 2019; Deng et al., 2021; Li et al., 2022).

Fresh basidiomata were used to isolate DNA. DNA was extracted using a Qiagen DNeasy Plant Mini Kit according to the manufacturer's instructions. A Thermo Scientific Arktik Thermal Cycler was used for DNA amplification (ThermoFisher-Scientific). The amplification reaction was carried out using the primer pairs ITS 5 (5'-GGA AGT AAA AGT CGT AAC AAG G-3') and ITS 4 (5'-TCC TCC GCT TAT TGA TAT GC-3') (White et al., 1990). The PCR amplification was performed in 50 µL total reaction containing 9 µL ddH₂O, 1.5 µL of 10 pmol of each primer, 25 µL PCR mix from 2× PCR buffer for KOD FX Neo (Toyobo), and 2 µL 100 ng template DNA. The PCR condition was set as follows: initial denaturation at 94 °C for 5 minutes, followed by 30 cycles of denaturation at 94 °C for 30 seconds, annealing at 56 °C for 45 seconds, and extension at 72 °C for 1 minute. The final extension was set at 72 °C for 10 minutes. PCR product was analyzed using 1.5 % agarose gel electrophoresis run with TAE buffer (40 mM Tris-acetate, pH 8.0 1 mM EDTA), stained with FloroSafe DNA stain and visualized by the Gel Doc EZ Gel Documentation System (Bio-rad). PCR products were sent to the 1st Base Malaysia for sequencing.

The sequences were assembled using ChromasPro software. The final aligned sequences were deposited in GenBank (<https://www.ncbi.nlm.nih.gov/>) to obtain the accession number. The sequence was subjected to Basic Local Alignment Search Tool (BLAST) in NCBI to compare the homology with previous data. Selected published sequences based on BLAST results (Table) were used for phylogenetic tree analyses with *Auritella hispida* as the outgroup. The phylogenetic tree of Randomized Axelerated Maximum Likelihood (RaxML) Black Box was generated on CIPRES (Stamatakis, 2014). All trees were then edited using TreeGraph Software version 2.9.2-622 beta. The Bootstrap value (BS) ≥ 70 % was shown on the branch of the phylogenetic tree.

Table

Species, outgroup, herbarium voucher, and GenBank accession numbers used in this study

Species	Collection Code	ITS Accession Number
<i>Auritella hispida</i>	Strain TH1009	KT378203
<i>Inosperma</i> aff. <i>calamistratum</i>	Strain REH8420	JQ801390
<i>I.</i> aff. <i>calamistratum</i>	DED8134	GQ892983
<i>I.</i> aff. <i>fastigiellum</i>	Strain PBM3325	JQ801399
<i>I.</i> aff. <i>latericum</i>	Strain TR109-02	JQ801405
<i>I.</i> aff. <i>maculatum</i>	Isolate AFTOL-ID-476	DQ241778
<i>I. africanum</i>	Voucher MR00387	MN096189
<i>I. africanum</i>	Voucher HLA0383	MT534298
<i>I. akirnum</i>	Voucher CAL1358	KY440085

Table (continued)

Species	Collection Code	ITS Accession Number
<i>I. apiosmotum</i>	Strain PBM3020	JQ801385
<i>I. bicoloratum</i>	Voucher ZT12187	GQ892984
<i>I. bulbomarginatum</i>	Voucher HLA0417	MT534300
<i>I. bulbomarginatum</i>	Voucher MR00357	MN096190
<i>I. calamistratoides</i>	Strain PBM3384	JQ801393
<i>I. calamistratum</i>	Strain PBM1105	JQ801386
<i>I. carnosibulbosum</i>	TBGT12047	KT329448
<i>I. cervicolor</i>	Voucher TURA-4761	JQ801395
<i>I. cf. lanatodiiscum</i>	Voucher TURA1812	JQ408763
<i>I. changbaiense</i>	Voucher HMJAU25861	MH047251
<i>I. cyanotrichium</i>	Strain I37	JQ801396
<i>I. dodonae</i>	Voucher STU-SMNS-STU-F-0901253	MW647615
<i>I. flavobrunneum</i>	Voucher HLA0372	MT534290
<i>I. gregarium</i>	Voucher CAL1309	KX852305
<i>I. hainanense</i>	Voucher Zeng4937	MZ374070
<i>I. hainanense</i>	Voucher Zeng4936	MZ374069
<i>I. ismeneanum</i>	Voucher STU-SMNS-STU-F-0901561	MW647625
<i>I. latericium</i>	Voucher PDD-92382	GU233367
<i>I. misakaense</i>	Strain PC96234	JQ801409
<i>I. monastichum</i>	Voucher STU-SMNS-STU-F-0901533	MW647631
<i>I. mucidiolens</i>	Voucher WTU: DG1824	HQ201339
<i>I. muscarium</i>	Voucher Zeng4720	MZ373978
<i>I. muscarium</i>	Voucher Zeng4736	MZ373979
<i>I. neobrunnescens</i>	Strain SAT0427406	JQ801411
<i>I. rimosoides</i>	Isolate AFTOL-ID-520	DQ404391
<i>I. rubricosum</i>	Strain PBM3784	KP308817
<i>I. saragum</i>	Voucher CAL1360	KY440103
<i>I. subsphaerosporum</i>	Voucher FHMU3154	MW403826
<i>I. subsphaerosporum</i>	Voucher FHMU3153	MW403825
<i>I. subsphaerosporum</i>	Voucher FIPIA-DEP59	OP880257
<i>I. subsphaerosporum</i>	Voucher FHMU3155	MW403827
<i>I. vinaceum</i>	Voucher AMB-18747	MW561108
<i>I. viridipes</i>	Voucher HO-562693	KP641646
<i>I. virosum</i>	TBGT753	KT329452

Results

Taxonomy

Inosperma subsphaerosporum Y. G. Fan, L. S. Deng, W. J. Yu et L. Y. Liu, 2021, in Deng, Yu, Zeng, Liu and Fan, *Phytotaxa* 502(2): 172. (Figs 1–5)

Fruiting bodies medium in size. Cap 4–7 mm, conical in young basidiomata, plano-convex to applanate in mature stages with an obtuse umbo, margin incurved at first and then slightly decurved in time, surface moist to dry, pileus radially fibrillose to rimulose with patches, scales of veil remnants, margin rough to split in in time, yellowish brown to brown around umbo, yellowish white with paler col-

or compared to the central region towards the margin, golden yellow in very mature stages. Lamellae adnexed to sinuate, dense, with series of lamellula, 20–40 mm length, brownish to white, edge slightly serrate. Stipe 40–100 × 8–11 mm, cylindrical, hollow, equal from apex to base with a slightly swollen base, squamulose at the apex, fibrillose downwards, white to cream. Context solid, fleshy, white to cream. Basidiospores subglobose to globose, 5–7 × 4–6 μm, smooth, yellowish to tan, with a prominent lipid body and an indentation in the center region when observed using SEM. Basidia clavate, notable oil inclusion, 26–31 × 7–8 μm in dimension, hyaline, 4-spored, sterigmata 3–4.5 μm in length. Pleurocystidia absent. Cheilocystidia abundant, 21–41 × 8–11

μm , in clusters, mostly club-shaped, septate, primarily thin-walled and some with thick-walled, hyaline, with yellow intracellular cytoplasm. Hyphal trama composed of cylindrical to inflated hyphae, 12–15 μm in diameter, hyaline. Pileipellis is a cutis, golden yellow, with thin-walled, cylindrical hyphae, 7–10 μm

in diameter. Oleiferous hyphae prominent, 3–4 μm wide, pale to yellow brown, smooth, occasionally dichotomously branched. Hymenial and stipe trama with dense interwoven hyphae, thin-walled, yellowish, 5–10 μm wide. Clamp connections are present in all tissues.



Fig. 1. Field photograph of *Inosperma subsphaerosporum* FIPIA-DEP59: A, B – upper side of pileus; C – lamellae. Bars = 5 cm.

Habitat: gregarious near surrounding Euphorbiaceae and Arecaceae trees.

Distribution: To date, known only from Hainan Province, China.

Specimen examined: “Buntok, Dusun Selatan, Barito Selatan, Central Kalimantan, Indonesia, 1°42'30.3"S, 114°49'25.8"E, 12 m. a. s. l., on soil mixed with leaves litter, XII 2022, V 2023, collected by Andi B and Agnes I Toemon, FIPIA-DEP59”.

Molecular Analyses

The aligned nucleotide sequence was deposited to GenBank with the accession number ITS OP880257.

The BLAST result revealed that our specimens had high similarity to *Inosperma subsphaerosporum* from type material (96 %) as the top hits. The phylogenetic tree (Fig. 6) constructed from ITS sequences resolved specimen FIPIA-DEP59 was in the same clade of *I. subsphaerosporum* from type material with 93 % BS value. The phylogenetic tree displayed that *I. subsphaerosporum* FIPIA-DEP59 was a sister clade to *I. flavobrunneum*. *Inosperma subsphaerosporum* FIPIA-DEP59 was in the different clade to morphologically similar species *I. carnosibulbosum*, *I. akirnum*, and *I. saragum*.



Fig. 2. Field collection and consumption of *Inosperma subsphaerosporum* FIPIA-DEP59: A, B – fresh basidiomata collection of *I. subsphaerosporum* from field; C – consumption of *I. subsphaerosporum* by the local people. Bars = 5 cm.

Discussion

Currently, there are only eighty taxa of *Inosperma* (Inocybaceae) documented worldwide (Index Fungorum, 2023). *Inosperma sphaerobulbosum* was recently introduced as a new species from China by Deng et al. (2021). The current study reports for the first time the distribution of this species aside from the type locality (Hainan Province, China) and contributes a new information to Indonesian macrofungi. Our work revealed the extension of geographical distribution of *I. sphaerobulbosum* in Kalimantan (Indonesia), which approximately 2474 km away from the type locality. Previously, Putra and Hafazallah (2020) reported the unidentified edible mushroom from Central Java (Indonesia) with the local name “jamur lengkuas” morphologically similar to *I. sphaerobulbosum* FIPIA-DEP59 which therefore warrants a further examination. In the sampling site, our specimens were collected from soil mixed

with leaves litter. Larsson et al. (2009) emphasized that many *Inocybe* species in the section *Rimosae* (currently genus *Inosperma*) are known to occur on more nutrient rich soil. In addition, *I. sphaerobulbosum* FIPIA-DEP59 grows near Euphorbiaceae and Arecaceae which dominate the surrounding area and in contrast to Deng et al. (2021) reported the specimens were collected near fagaceous trees. The Inocybaceae is known as family of ectomycorrhizal mushroom-forming fungi (Matheny et al., 2019), however the host plant of *I. sphaerobulbosum* FIPIA-DEP59 remains unclear.

In the field, *I. sphaerobulbosum* FIPIA-DEP59 can be recognized by its gregarious habit, medium-sized basidioma, having scaly-fibrillose pileus, and a fibrillose stipe. *Inosperma sphaerobulbosum* FIPIA-DEP59 has approximately similar of pileus dimension to *I. carnosibulbosum* (Pradeep et al., 2016) but larger in size when compared to *I. akirnum*, and *I. saragum* Latha and Manimohan (2017). Some ba-

sidiomata of *I. sphaerobulbosum* FIPIA-DEP59 displays pileus with layer of universal veil. Deng et al. (2021) emphasized that this feature is non persistent character and is influenced easily by the weather. The lamellar edge of *I. sphaerobulbosum* FIPIA-DEP59 was fimbriate and slightly serrate which in contrast to the related morphological similar species in having only fimbriate edge. Microscopically, the outline of basidiospores of *I. sphaerobulbosum* FIPIA-DEP59 differs it to the closely morphological species of *I. carnosibulbosum*, *I. akirnum*, and *I. saragum*. The spore dimension of our specimen was slightly lower than the three closely related species. However, in line with those species, *I. sphaerobulbosum* FIPIA-DEP59 has abundant cheilocystidia in clusters. In addition, the yellow intracellular contents of cheilocystidia distinguished our specimen from the genus *Pseudosperma*.

A comparison of the ITS sequence of specimen FIPIA-DEP59 derived from Central Kalimantan with the available taxa information from GenBank

indicated that BLAST queries led to *I. sphaerobulbosum* from type material as the top hits. Accordingly with BLAST result, the phylogenetic tree committed that our *Inosperma* was identified as *I. sphaerobulbosum*. The phylogenetic placement of our specimen in the same clade as *I. sphaerobulbosum* from Hainan, China with 93 % BS value. In the phylogenetic tree, the position of clade of *I. sphaerobulbosum* FIPIA-DEP59 was mixed between Old World tropical clade 1 and Old World tropical clade 2 (Pradeep et al., 2016; Latha, Manimohan, 2017; Matheny et al., 2019; Aïgnon et al., 2021) due to only single gene used in this study. Previous study confirmed that Old World tropical clade 2 was composed of *Inosperma* species from India, Thailand, Papua New Guinea, and China (Matheny et al., 2019; Deng et al., 2021). *Inosperma sphaerobulbosum* is reported for the first time for Indonesia and enriches the knowledge of the distribution of Old World tropical clade 2. Our study provides the available morphological and molecular information of *I. sphaerobulbosum* in Indonesia.

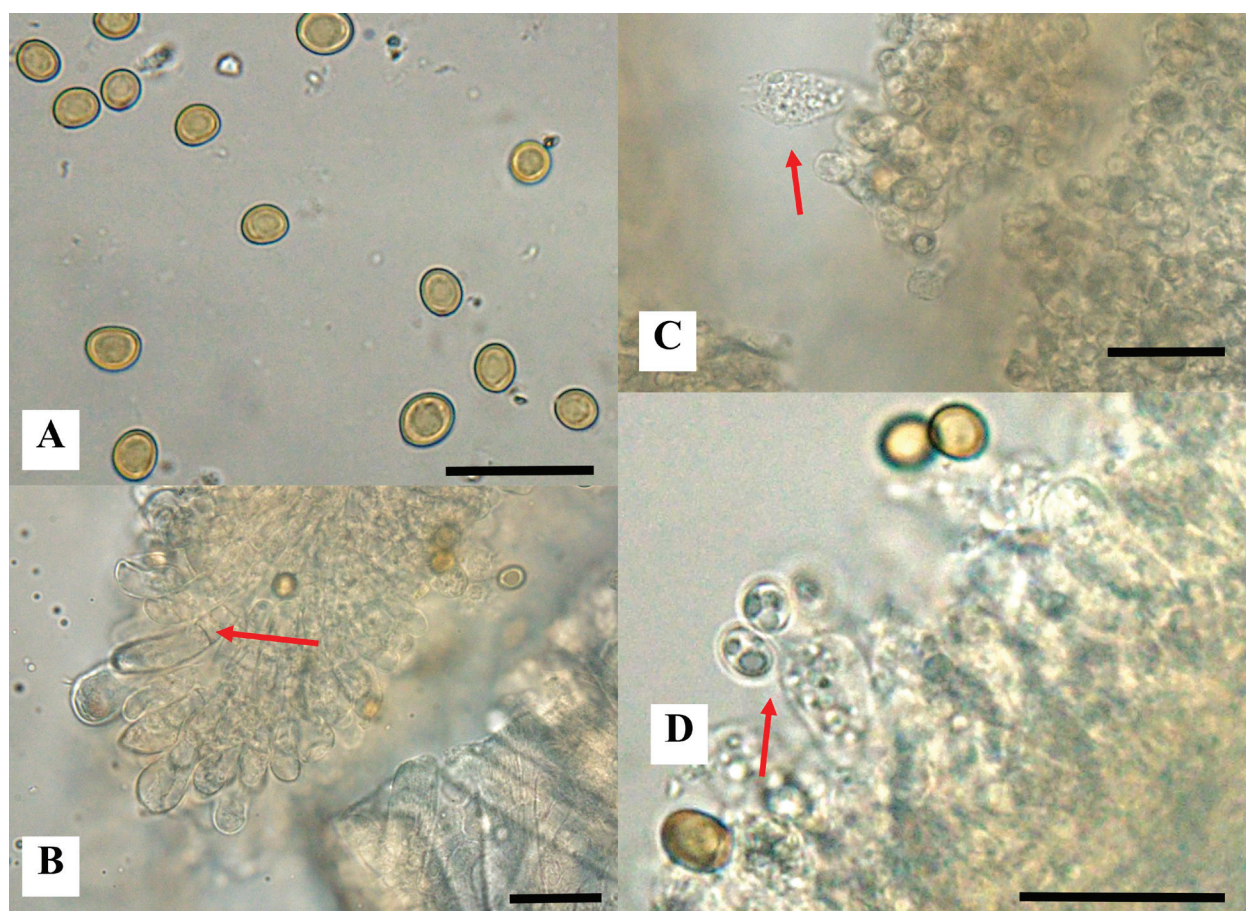


Fig. 3. Microscopic characters of *Inosperma subsphaerosporum* FIPIA-DEP59: A – globose to subglobose basidiospores; B – cheilocystidia in clusters; C – basidia; D – basidia with basidiospores. Bars = 20 μ m.

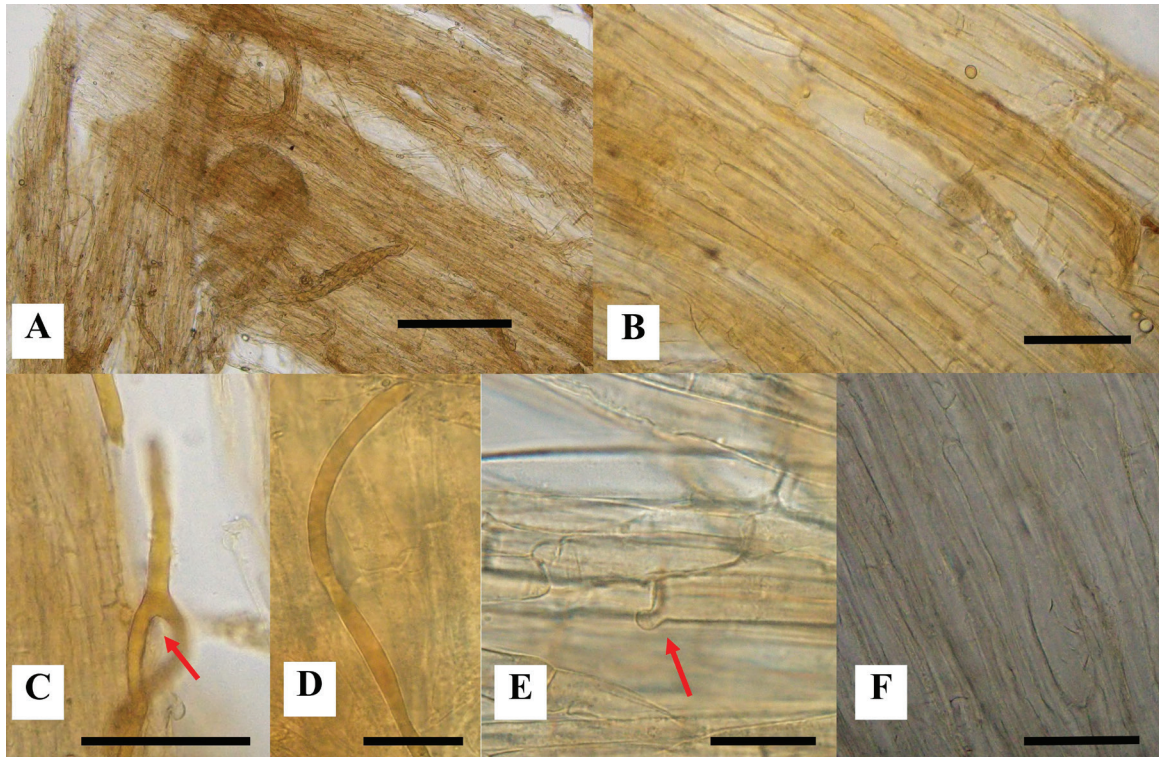


Fig. 5. Microscopic characters of *Inosperma subsphaerosporum* FIPIA-DEP59: A – pileipellis; B – pileal trama; C, D – oleiferous hyphae; E – clamp connection; F – stipe trama. Bars A = 200 μ m, B, C, F = 50 μ m, D, E = 20 μ m.

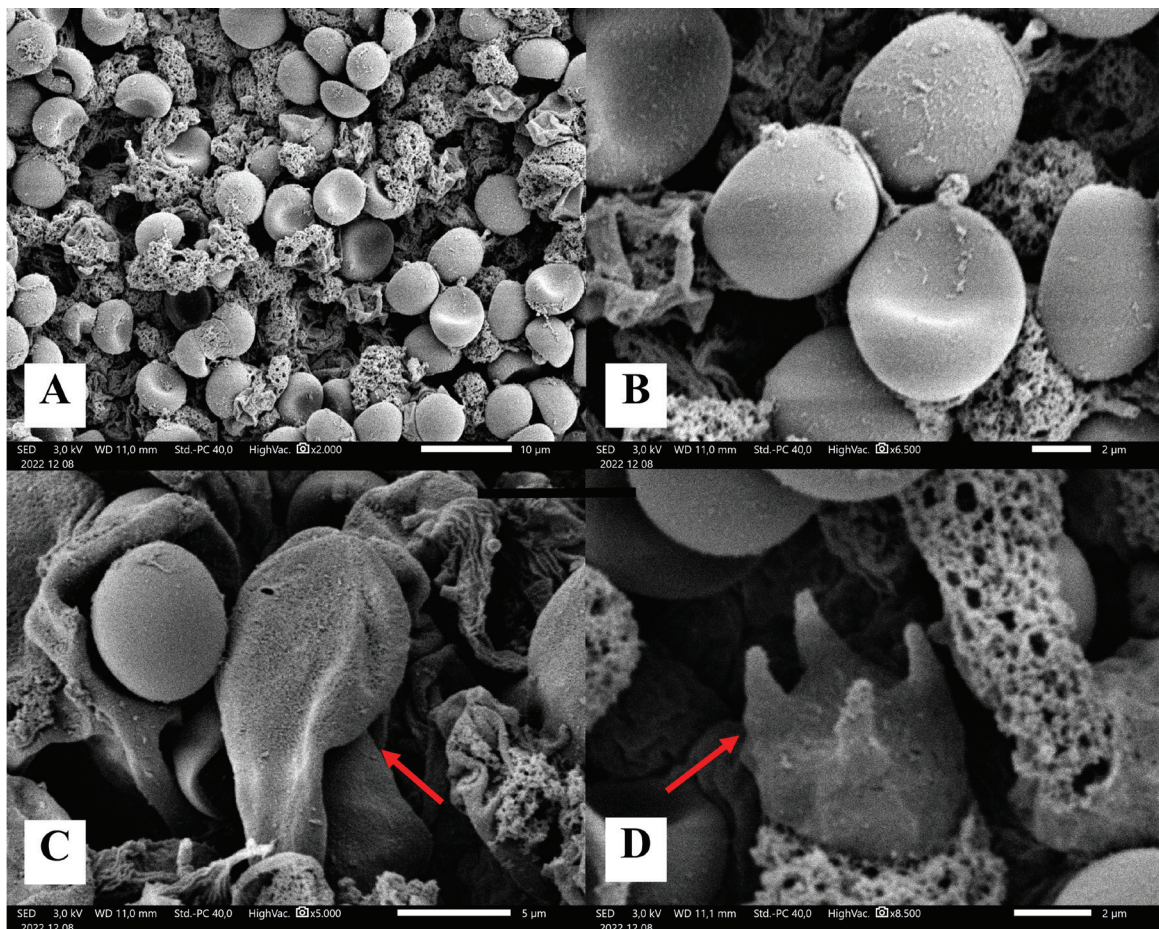


Fig. 4. Scanning electron microscope image of *Inosperma subsphaerosporum* FIPIA-DEP59: A, B – basidiospores with an indentation; C – cystidium; D – basidium with four sterigmata.

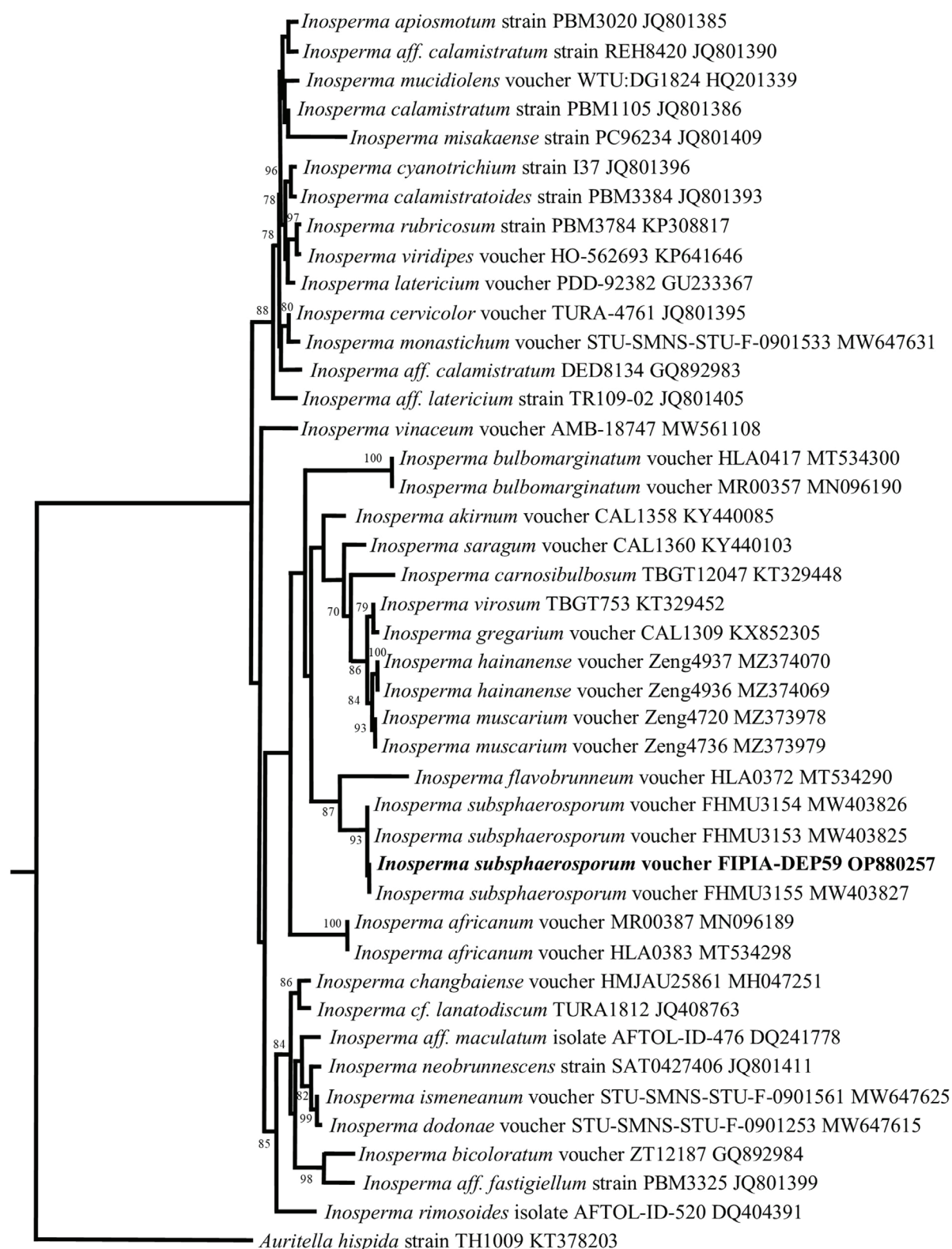


Fig. 6. *Inosperma subsphaerosporum* FIPIA-DEP59 phylogenetic tree based on ITS1–2 region using Randomized Accelerated Maximum Likelihood method and 1000 Bootstrap Analysis. Our specimen is bold on the phylogenetic tree.

In the research site, *I. sphaerobulbosum* is considered as delicacy mushroom and traded at local market as well as by using the social media. The mushroom is prized Rp. 18000/kg or US\$1.15/kg.

The indigenous people usually forage this species around September to December, and sometimes March to April when the rain and relative humidity are high. Considering the edibility of this species, we

suggest that the nutritional analysis and cultivation efforts of *I. sphaerobulbosum* needs a warrant in Indonesia, as many wild mushrooms are recognized as source of secondary metabolite and medicinal properties (Bukharova et al., 2020). However, many species of *Inosperma* were reported to cause neurotoxic poisoning in humans after consumption worldwide (Bijeesh et al., 2020; Parnmen et al., 2021; Deng et al., 2022; Li et al., 2022). For example, *I. erubescens* caused mass poisoning in Germany (Lurie et al., 2009), 10 cases of poisoning caused by *Inosperma* species in Thailand from 2010 to 2018 (Parnmen et al., 2021), and recently *I. zonativeliferum* caused poisoning in 10 people in China (Deng et al., 2022). Li et al. (2022) reported that *I. sphaerobulbosum* contains none of the tested neurotoxins. Although no report indicates the poisoning case by consumption of this mushroom from type locality as well as in our sampling site, we expect to determine the four main mushroom neurotoxins (muscarine, psilocybin, ibotenic acid, and muscimol) contents of *I. sphaerobulbosum* FIPIA-DEP59 and closely related species in the near future.

Conclusion

The current study reports the first distribution of *Inosperma subsphaerosporum* in Indonesia and new information aside from type locality (China).

Morphologically, *I. sphaerobulbosum* FIPIA-DEP59 can be determined by the conical applanate cap with umbo, incurved to decurved margin, dry pileus with fibrillose to rimulose surface, lamellae adnexed to sinuate, cylindrical stipe, subglobose to globose smooth basidiospores, and abundant cheilocystidia in clusters. The BLAST result and the phylogenetic tree confirmed our specimens as *I. subsphaerosporum*. Future study should be done to analyze both nutritional and mushroom neurotoxins content of this Indonesian *Inosperma*.

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