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A Morphological and Molecular Study of *Phallus multicolor* in Indonesia

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Abstract

Phallus is known as stinkhorn mushroom. Previous reports have shown that this genus is recognized by the size and color of the basidioma, which is a highly plastic morphological character that can potentially lead to misidentification. In Indonesia, no study has combined morphological and molecular analyses to identify *Phallus*. This study aimed to determine the identity of *Phallus* that has the orange color of an indusium found in Bekasi, West Java, Indonesia. The morphological characteristics were described by observing the macroscopic and microscopic features of fresh specimens. Molecular analyses were performed based on the internal transcribed spacer 4/5 region sequence. The results showed that specimen BO24430 was identified as *Phallus multicolor* with 100% similarity in the BLAST results and a 98% bootstrap value on the phylogenetic tree. This taxonomic placement was supported by morphological features, such as a campanulate pileus, yellowish to white pseudostipe, brown to whitish eggs, and ellipsoid spores. This study is the only record of *P. multicolor* in Indonesia with a herbarium voucher since Boedijn in 1932. In addition, the current study assessed the diversity of *Phallus* in Indonesia using morphological and molecular evidence.

Keywords: Indonesia, macrofungi, phallus, phylogenetic tree, taxonomy

Introduction

Stinkhorn is a cosmopolitan group of macrofungi with an unusual horn-shaped slimy cap. This group is recognized as the basis of Phallales [1]. Stinkhorn contains many genera, including *Aseroe*, *Blumenavia*, *Clathrus*, *Colus*, *Laternea*, *Lysurus*, *Mutinus*, *Phallus*, *Pseudocolus*, and *Staheliomyces* [2]. Then, some genera have been added as Phallales members, including *Anthurus*, *Claustula*, *Dictyophora*, *Ileodictyon*, *Kjeldsenia*, *Kobayasia*, *Phlebogaster*, *Protubera*, *Trappea* [3], and *Itajahya* [4]. *Phallus* is the most frequently studied genus in Phallales [5–8].

Phallus (Phallaceae) is more similar to Lysuraceae than other families in Phallales [3]. In addition, *Phallus* is closely related to Geastrales (earthstar mushroom) and Gomphales (coral and club fungi) based on morphological, molecular, and evolutionary studies [3]. *Phallus* has 181 taxa [9]. However, a taxonomic study of *Phallus* described only 13 species (excluding forms and varieties) based on the molecular data in GenBank [6], including *P. atrovolvatus*, *P. cinnabarinus*, *P. echinovolvatus*, *P. hadriani*, *P. haitangensis*, *P. impudicus*, *P. indusiatus*, *P. mengsongensis*, *P. multicolor*, *P. rubrovolvata*, *P. rugulosus*, *P. serrata*, and *P. ultraduplicatus*.

Phallus studies in Indonesia have focused on the morphological features of *P. indusiatus* [10–12]. The majority of studies also lack the documentation, description, and key characters of *Phallus.* Boedijn provided the first comprehensive report of *P. multicolor* in 1932 without fresh samples [13]. However, he still used the taxonomic name *Dictyophora multicolor* based on the morphological data. The genus *Phallus* is complex, and the morphological features are highly plastic [14]. Hence, there is a need to reveal the taxonomic position of *Phallus* in Indonesia. This study aimed to assess *P. multicolor* in Indonesia based on morphological and molecular evidence.

Materials and Methods

Mushroom collection. The specimens were collected in August 2020 at Bekasi, West Java, Indonesia. All stages of the fruiting bodies were collected and documented *in situ*. The specimens were deposited at Herbarium Bogoriense, Indonesia, with voucher number BO24430.

Morphological identification. The fresh materials were characterized at the Mycology Laboratory, Department of Biology, Faculty of Mathematics and Natural Sciences, IPB University. The basic morphological characteristics of the fruiting bodies were observed including, shape, size, ornamentation, type of indusium, and spores. The characterization and morphological identification followed Kuo [2], Hosaka [5], and Kreisel & Hausknecht [15].

DNA extraction, polymerase chain reaction, and sequencing. Genomic DNA was extracted from the fresh material. The sterile part of the egg stage was used as the DNA source. The protocol followed Hermawan [16]. DNA quality and quantity were verified using a Nanodrop spectrophotometer. The internal transcribed spacer (ITS) 5 (5′-GGAAGT AAA AGT CGT AAC AAG G-3′) and reverse ITS 4 (5′-TCC TCC GCT TAT TGA TATGC-3′) primers were amplified following a previous protocol [17]. Polymerase chain reaction (PCR) amplification was performed in a 40 µL total reaction volume containing 20 µL of PCR mix from 2× Kappa Fast 2G, 2 µL (10 pmol) of each primer, 4 µL (100 ng) of template DNA, and 12 µL of ddH_2O. The PCR conditions were initial denaturation at 94 °C for 2 min, followed by 30 cycles of denaturation at 94 °C for 30 s, annealing at 55 °C for 30 s, and extension at 72 °C for 1 min. The final extension was 72 °C for 10 min. The amplicons were checked by 1% agarose gel electrophoresis and visualized with the Gel Doc™ XRsystem. The PCR products were sent to First Base Malaysia for sequencing.

Phylogenetic analyses. The obtained sequence was deposited in GenBank (ITS MT916293). The homologous sequence was analyzed using BLAST. In addition, the sequences from selected BLAST results of this study (bold), 34 *Phallus* sequences from [7,14,18-24], and selected BLAST results were used to reconstruct the phylogenetic tree (Table 1). *Mutinus caninus* was used as the outgroup. The sequences were aligned using MEGA Ver. X software [25]. The phylogenetic tree was constructed using Randomized Axelerated Maximum Likelihood (RAxML) HPC2 of XSEDE on CIPRES RAxML [26] with 1000 bootstrap (BS) replicates. Bootstrap (BS) values ≥ 70 were displayed on the phylogenetic tree branches.

Results and Discussion

Taxonomy. *Phallus multicolor* **(**Berk. & Broome) Cooke Grevillea 11(58): 57 (1882). Basionym: *Dictyophora multicolor* Berk. & Broome 1883 Trans. Linn. Soc. London, Bot. 2(3): 65 (1883).

Immature fruiting bodies 1.5–2.4 cm in diam, blackish with minor whitish color on the surface, gregarious on humic soil, pseudoepigeous, resembling egg shape, with a striking rhizomorph (Figures 1b and c). Rhizomorph (length 2.5–4.3 cm) occasionally branched on the apex, developed well, and long into the ground. The inside structure of the immature basidioma consists of five layers (Figures 1d and e). The first layer (Figure 1e1) is brown and slim and develops the volva during the mature stage. The second layer (Figure 1e2) contains the basidiospores with the darkest color and a gelatinous immature gleba. The third layer (Figure 1e3) is the initial indusium, which is cream-colored. The fourth layer (Figure 1e4), yellow to orange, becomes the cap of the mature basidioma. The fifth layer (Figure 1e5) is pale cream-yellow and is the initial structure of the receptaculum. Mature basidiomata expanded up to 7.5–9.1 cm high, unbranched, with indusium emerging from the base of the receptacle, spongy pesudostipe (Figures 1a and f). Receptacle 2.5–2.8 cm high, 3.1–3.3 cm wide, conical to bell-shaped (campanulate), pale pinkish, reticulated surface, blackish sticky gleba, slightly uplifted (Figures 1g, i, and j). Pseudostipe 5.7–6.7 cm high, creamy to yellowish-white, spongy, cylindrical to slightly tapering downward, hollow, and 3.9–4.2 cm in diam (Figures 1f, h, i, and l). Indusium (length 4.2–4.6 cm) not extended to the ground, pale to light orange, polygonal to rounded mesh, 10–20 mm in diam (Figures 1f and h). Volva epigeous to nearly hypogeous, pale blackish with a creamy surface, attached to the substrate with yellowish creamy rhizomorph (Figures 1c, f, and i). The basidiospores are finely ellipsoid, 3.5–4.2 × 1.3–1.7 µm, and free of ornamentation (Figure 1o). The indusium with globose to subglobose cells is a yellowish color with a smooth surface (Figure 1n).

Specimen examined: Indonesia, West Java, Bekasi, potted plant, August 26, 2020, collected by Gunawan MRW, Amelya MP, BO24430.

Phylogenetic analyses. The sequence was submitted to GenBank (https://www.ncbi.nlm.nih.gov/) with Accession number MT916293. The BLAST results showed that the sequence had 100% similarity with *P. multicolor* (KP012762) from Australia. In addition, the phylogenetic tree confirmed the taxonomic position of BO 204430 as *P. multicolor* with a 98% BS value (Figure 2). The specimen was placed in different clades with morphologically similar species (*P. luteus* and *P. cinnabarinus)*.

Most of the studies that have described *Phallus* in Indonesia focused on *P. indusiatus* [11–12, 27]. Those records were based on morphological characters, which often lacked documentation, preserved specimens, and descriptions. Among the *Phallus* species, *P. indusiatus* is the most often studied, so it has complete morphological data. Information on other *Phallus* species is scarce, and *P. multicolor* is no exception. A recent study demonstrated that the genus *Phallus* has highly plastic morphological features [14]. Hence, our study combined the macro and micromorphological features with

phylogenetic analyses to assess *P. multicolor* from Indonesia.

According to a previous study [7], the LSU region has a substantial BS value compared to the ITS region to distinguish *P. multicolor* from *P. fuscoechinovolvatus*. However, the BS value based on the ITS region in the present study used to clarify our specimens was 98%. This BS value is reliable at the clade level. To our knowledge, complete reports on the genus *Phallus* are limited in Indonesia. Most publications that have considered *Phallus* are based on morphological characters and lack specimen descriptions. In addition, morphological plasticity is common in the genus *Phallus* [14]. In line with previous studies [3, 14], we suggest that molecular analyses should be considered in taxonomic studies of *Phallus*.

Table 1. Species, Collection Code, and GenBank Accession Numbers used in this Study

Species	Collection code (Voucher/Strain)	ITS GenBank acc. no
Mutinus zenkeri	MA-2013 Isolate JD781	KC128650
Phallus atrovolvatus	MEL 2382962	KP012823
Phallus atrovolvatus	MEL 2382871	KP012745
Phallus cinnabarinus	INPA 255835	KJ764821
Phallus cremeo-ochraceus	GDGM 80070	MZ890332
Phallus cremeo-ochraceus	GDGM 85857	MZ890333
Phallus echinovolvata	ASI 32008	AF324166
Phallus echinovolvata	ASI 32010	AF324167
Phallus fuscoechinovolvatus	GDGM 43465	MF039580
Phallus fuscoechinovolvatus	GDGM 48589	MF039581
Phallus hadriani	TNS-F-61696	KP222542
Phallus hadriani	TNS-F-70036	KU516100
Phallus haitangensis	HKAS 88197	KU705383
Phallus impudicus	TNS-F-70035	KU516099
Phallus impudicus	TNS-F-70037	KU516101
Phallus indusiatus	Mushroom Observer 181359	MF428417
Phallus luteus	TNS-F-61695	KP222543
Phallus mengsongensis	HKAS 78342	KF052627
Phallus mengsongensis	HKAS 78344	KF052626
Phallus multicolor	MEL 2382891	KP012762
Phallus multicolor	**BO 24430**	**MT916293**
Phallus rigidiindusiatus	GDGM 81196	MZ890337
Phallus rigidiindusiatus	GDGM 85470	MZ890338
Phallus rubrovolvatus	YZS045	KF939505
Phallus rubrovolvatus	YZS046	KF939506
Phallus rugulosus	ASI 25007	AF324170
Phallus rugulosus	ASI 32004	AF324169
Phallus serratus	HKAS 78341	KF052623
Phallus ultraduplicatus	HMAS 253050	KJ591584
Phallus ultraduplicatus	HMAS 253051	KJ591585

Figure 1. Morphology of *Phallus multicolor* BO 24430. (a) Fruiting Bodies on Humic Soil; (b) Eggs of *P. multicolor*; (c) Eggs with Rhizomorph; (d) Transverse Section of Mature Egg; (e) Egg Layers; (f) Mature Fruiting Body in the Field; (g) Head of a Fresh Fruiting Body; (h) Indusium of a Fresh Fruiting Body; (i) Mature Fruiting Body after Washing with Sterile Aquadest; (j) Head of the Fruiting Body; (k) Indusium of the Fruiting Body; (l) Surface of the Pseudostipe of a Mature Fruiting Body; (m) Transverse Slice of the Pseudostipe (n) Indusium Cells; (o) Basidiospores. Scale Bars: (c) 1 cm; (d) 0.5 cm; (e) 2 cm; (f, i) 5 cm; (l, m) 4 cm; (n) 10; (o) 5 µm

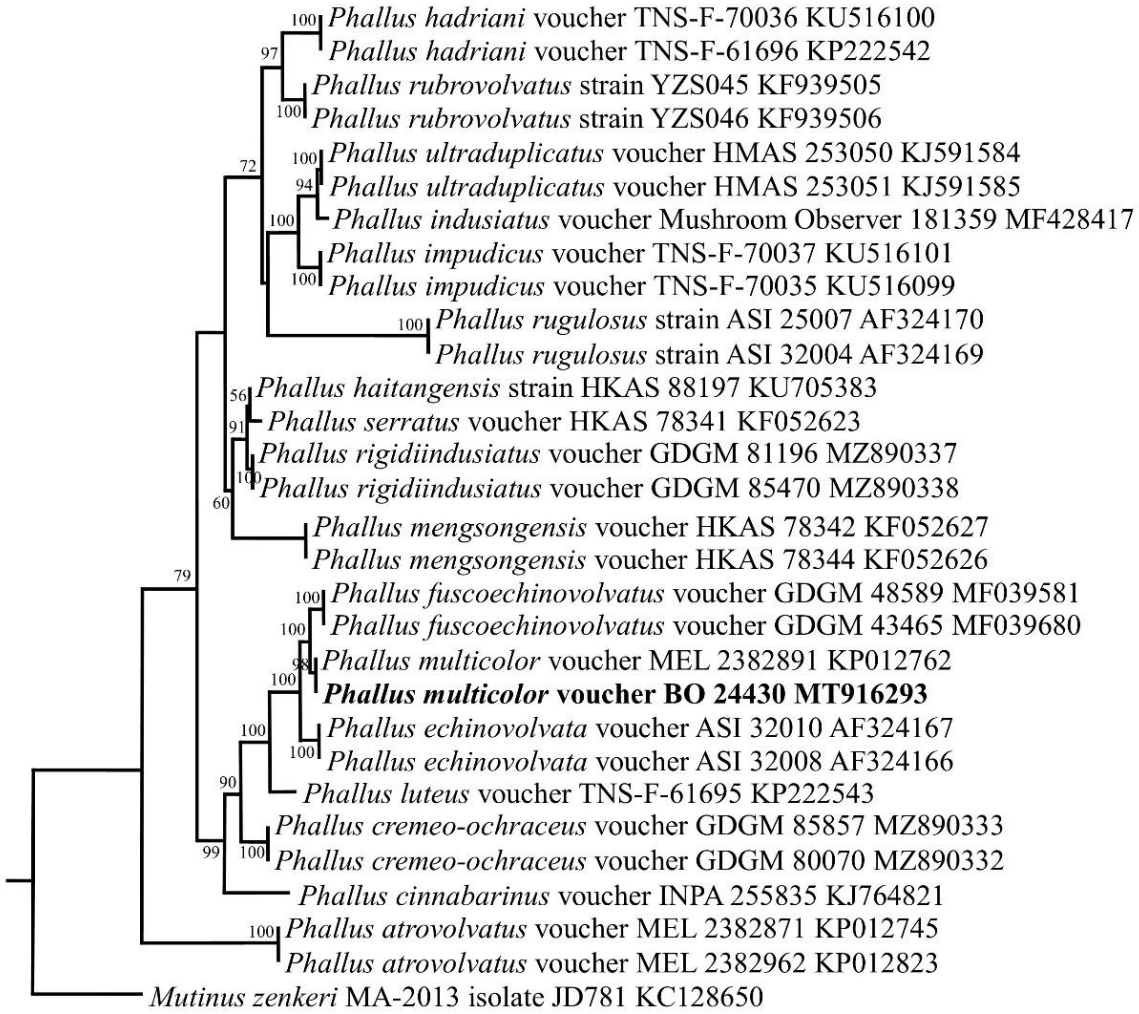

Figure 2. ***Phallus Multicolor*** **BO24430 Phylogenetic Tree Inferred using the RAxMLBlack Box. The Recorded Species are Indicated in Bold. Bootstrap (BS) Values ≥70 are Presented on the Branches**

The current phylogenetic tree revealed that the *P. multicolor* clade is closely related to *P. fuscoechinovolvatus* and *P. echinovolvata*. Based on the morphological features, *P. fuscoechinovolvatus* and *P. echinovolvata* produce immature basidiomata with spiny ornamentation on the surface, which are absent in *P. multicolor* [6, 15]. Furthermore, the color of the *P. multicolor* indusium differs from that of those two species. *Phallus fuscoechinovolvatus* and *P. echinovolvata* have white indusia, while *P. multicolor* possesses a yellowish-orange indusium [6, 15, 29]. According to the morphology of the mature basidioma, our samples were identical to *P. luteus* and *P. cinnabarinus*. *Phallus luteus* has a yellowish-orange indusium [28] and *P. cinnabarinus* has a red-orange indusium [15], which was highly similar to our specimen. *Phallus luteus* has a whitish pseudostipe and a pale pink to the reddish-purple egg surface. *P. multicolor* has a yellowish-white pseudostipe and a brown to whitish egg stage.

The pseudostipe and the color of immature basidioma are traditional distinct character differences between *P. multicolor* and *P. cinnabarinus* [16]. *Phallus cinnabarinus* has "cinnabar" or salmon-colored indusium and pileus. The volva is grayish-white to brownish, with pinkish mycelial cords. *Phallus multicolor* has a purplish volva and mycelial cords [15]. In addition, the basidioma of *P. cinnabarinus* is less stinky [29]. However, these characters are frequently difficult to distinguish and can lead to misidentification. Characters, such as shape, color, and size, can be affected by environmental factors. A key for *P. cinnabarinus* has been published [29] but was later revised, as another *P. cinnabarinus* specimen with different morphological characters was identified [15]. Those studies demonstrate that there is a need to support the morphological data with molecular analyses to obtain more accurate results in the genus *Phallus* [6].

The previous *Dictyophora multicolor* (current name *P. multicolor*) records in Indonesia were provided by

Boedjin [13] from Sumatra, Java, and Kalimantan (Borneo). Since then, no additional reports of *P. multicolor* have been published with comprehensive data and Indonesian herbarium specimens. To the best of our knowledge, this is the first study to contribute *P. multicolor* molecular data from Indonesia. Until recently, most of the studies on *Phallus* taxonomy worldwide relied on morphological features, and only a few conducted molecular analyses. Our sequencing data are available in GenBank and can be used for future studies of *Phallus* taxonomy in Indonesia.

Conclusion

The current study reports the only collection with herbarium specimens of *Phallus multicolor* after Boedjin in 1932 in Indonesia. *Phallus multicolor* BO24430 was collected from Bekasi, West Java, Indonesia and identified based on morphological and molecular data. The campanulate pileus, yellowish to white pseudostipe, brown to whitish eggs, and ellipsoid spores distinguished our specimen from other species of *Phallus*. The BLAST result revealed that our specimens have 100% similarity with *P. multicolor*. In addition, the phylogenetic tree inferred by ITS 4/5 nested our specimens in the clade of *P. multicolor* with 98% bootstrap value.

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