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An Introduction to Indonesian Wild Shiitake

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ABSTRACT

Pegler suggested that shiitake comprises three morphological species: *Lentinula edodes* (continental and northeast Asia), *L. lateritia* (tropical Asia and Australasia), and *L. novae-zelandiae* (New Zealand). The current study reported for the first time the occurrence of *L. lateritia* (Berk.) Pegler in Indonesia. During a fungus foray in Kerinci (Jambi, Sumatra, Indonesia) in 2022 and 2023 by the Indonesian mushroom hunter community, some basidiomata of *Lentinula* were obtained. At a glance, our specimens resembled *L. edodes*. The current study aims to justify the taxonomical position of our specimens based on morphological and molecular data. The fresh basidiomata were used for morphological and molecular analyses. The molecular work was done using ITS 4/5 Primers for phylogenetic analysis of rDNA-ITS region. Morphologically, the uniformly reddish brown, smooth, and glabrous of pileus confirmed our specimens as *L. lateritia*. In addition, the absence of a range of colors and squamules pileus distinguished *L. lateritia* BO24628 form *L. edodes*, while the formation of florets cheilocystidia in *L. madagasikarensis* was the distinctive character of our specimens. The BLAST result revealed that our specimen has high similarity (99-100%) with *L. lateritia* and *L. edodes* as the top hits. The phylogenetic tree (RAxML) nested our specimens in the *L. lateria* clade and is closely related to one specimen from Papua New Guenia (PNG) (BS 98%). In addition, *L. lateritia* BO24628 has a sister clade of the specimen from PNG and Australia. Moreover, we provide the herbarium collection of wild *L. lateritia* in Indonesia.

1. Introduction

Lentinula is a small group of lignicolous agarics that is well known and represented by the cultivated shiitake mushrooms worldwide (Kobayashi *et al.* 2020). This genus was erected by Earle (1909) and typified by *Lentinus cubensis* Berk. and M.A. Curtis (*Lentinula boryana* Berk. and Mont. Pegler). In a monograph described by Pegler (1983), *L. boryana* and *L. edodes* were the early species to be placed in this genus. Prior works (Wilson and Desjardin 2005; He *et al.* 2019) have proved that *Lentinula* is monophyletic and placed within the Omphalotaceae (Agaricales). There are nine species of *Lentinula* from Asia-Australasia, the Americas, and Madagascar noted by previous authors (Pegler 1983; Hibbett 2001; Mata *et al.* 2001; Kirk *et al.* 2008; Looney *et al.* 2021). In addition, Menoli Jr *et al.* (2022) recognized 15 lineages of *Lentinula* worldwide based on morphology, mating criteria, and geographic distribution. To date, Index Fungorum (2023) accepted 15 taxa of *Lentinula* including *L. aciculospora, L. boryana, L. cubensis, L. detonsa, L. edodes, L. guarapiensis, L. lateritia, L. madagasikarensis, L. novae-zelandiae, L. platinedodes, L. raphanica, L. reticeps, L. sajor-caju, L. squarrosulus*, and *L. tigrinus.* Pegler (1983) suggested that *L. edodes* and *L. lateritia* were distributed in Asia or Australasia. However, *L. edodes* is frequently growing throughout Japan-China and does not extend to more tropical areas, favoring an optimal temperature of 24°C (Pegler 1983).

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L. lateritia occurs in tropical Asia such as Southeast Asia (Pegler 1983). This species was first described as *Lentinus lateritius* by Berkeley (1881) in Australia (the precise locality is unclear; habitat details were provided other than growing on wood). Then, *L. lateritius* was moved to genus *Lentinula* by Pegler (1983) from observation of the specimens in Sabah (Mt. Kinabalu), Malaysia. Recently, the GBIF (2023) records 34 occurrences of this species (32 from Australia and 2 from Papua New Guinea). *L. lateritia* can be recognized by glabrous stipe or with a few appressed squamules towards the base, pileus 2-5 cm in diam., uniformly reddish brown, smooth and glabrous, context thin, stipe slender, 3-9 mm diam., and can be found in Southeast Asia (Pegler 1983).

Lentinula is a saprobic mushroom commonly found in Asia and grows naturally in warm and humid climates (Chiu *et al.* 1999). Wild populations of *Lentinula* were reported to be distributed in Asia, Australasia, and the Americas (Hibbett *et al.* 1998). *L. lateritia* has an Asian-Australasian (Old World) distribution (Pegler 1983; Hibbett *et al.* 1998). However, after described by Pegler in 1983 in Sabah, Malaysia (Borneo), there was no further report of *L. lateritia* in Indonesia. The information on wild Indonesian *Lentinula* is scarce. Previously, Jomura *et al.* (2020) employed a strain of *L. edodes* obtained from Cibodas (West Java, Indonesia) in their research. However, no information was provided regarding the strain history nor herbarium collection number that deposited in Indonesia. During a fungus foray held by the Indonesian mushroom hunter community (KPJI) in highland area of Mount Kerinci (Jambi, Indonesia), we obtained some *Lentinula's* fruiting bodies resembling *L. edodes* or *L. lateritia*. The goal of this study was aimed to ensure the taxonomical position of our *Lentinula* specimens based on morphological and molecular evidence.

2. Materials and Methods

2.1. Specimen Collection

The basidiomata were obtained at Jernih River, Sungai Penuh, Sungai Penuh City, Jambi, Indonesia, in 2022 and 2023 during a fungal foray carried by the KPJI. The fruiting bodies were documented in situ and ecological information (coordinate, temperature, substrate, vegetations) were noted. Some of the specimens were deposited to Herbarium Bogoriense, BRIN, Indonesia with the collection number BO24628.

2.2. Morphological Identification

The morphological characteristics were investigated from fresh specimens in situ and in Mycology Laboratory, Department of Biology, Faculty of Mathematics and Natural Sciences, IPB University, Indonesia. The macromorphological features including color, size, pileus and stipe ornamentation, margin, and lamellae were observed using loupe. The micromorphological characters of basidium, cystidia, spores (shape, size, color, ornamentation), and clamp connections were observed using light microscope. The features were observed using binocular microscopes (1,000×). The samples were mounted in distilled water. The specimens were identified using related identification references (Berkeley 1881; Pegler 1983; Mata and Petersen 2000; Mata *et al.* 2001; Looney *et al.* 2021).

2.3. Molecular Analyses

The fresh fruiting body was used for genomic DNA isolation. DNA extraction followed by PCR were performed in the Research Center for Applied Microbiology, National Research and Innovation Agency (BRIN), Indonesia. The fruiting body was extracted using hexadecyltrimethylammonium bromide (Hermawan *et al.* 2020). The amplification was performed to Internal Transcribed Spacer (ITS) region ITS 5 (5'-GGA AGT AAA AGT CGT AAC AAG G-3') and ITS 4 (5'-TCC TCC GCT TAT TGA TAT GC-3') primers (White *et al.* 1990). The PCR amplification was performed in 40 µL total reaction containing 12 µL ddH_2O, 2 µL of 10 pmol of each primer, 20 µL PCR mix from 2× Kappa Fast 2G, and 4 µL 100 ng template DNA. The PCR condition was set as follows: initial denaturation at 94°C for 2 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. The amplicons were checked on 1% agarose gels and visualized by the Gel Doc™ XR system. 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 1) were used for phylogenetic tree analyses with *Lentinus squarrosulus* 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 Tree Graph Software version 2.9.2-622 beta. The Bootstrap value (BS) ≥70% was shown on the branch on the phylogenetic trees.

3. Results

3.1. Taxonomy

Lentinula lateritia (Berk.) Pegler, Sydowia 36: 232 (1983) (Figure 1 and 2).

Synonym: *Lentinus lateritius* Berk., Botanical Journal of the Linnean Society 18: 384 (1881).

Pocillaria lateritia (Berk.) Kuntze, Revisio generum plantarum 2: 866 (1891).

Pileus up to 4 cm in diam, fleshy, convex when young, applanate to broadly depressed at mature stage, uniformly reddish brown, darker at margin, smooth and glabrous, with long crack on few specimens, not squamose, margin incurved, not straight, with cream velar remnants in young fruiting bodies. Lamellae adnexed-notched to the stipe, white, cream, to ivory, crowded, with lamellulae, edge entire and blade like shape. Stipe 2-4 cm × 4-10 mm, concolorous with pileus, with purplish brown tints in some areas, paler near pileus/concolorous with lamellae, fine scattered fibrils near the base can be observed. Stipe central to excentric, straight to curved, slender, approximately cylindrical, with solid interior. Cortinoid veil poorly developed, leaving traces of a ring-zone on stipe. Context thin, up to 5 mm, white to cream, constructed by interwoven hyphae, 4-8 µm diam. Clamp connection present. Basidia 14-22 µm × 3.8-4.6 µm, clavate, 4-spored. Spores 3.9-4.5 µm × 2.8-3.2 µm, ovoid to ellipsoid, hyaline, thin walled. Cheilocystidia scarce, 17-25 µm × 10-11 µm, pyriform to inflated clavate, hyaline, thin walled.

Specimen examined: Indonesia, Jambi, Kerinci, Jernih River, 2°06'33.0"S 101°22'16.0"E, 1580 m.a.s.l., 22°C, on unidentified wood, 2023, collected by Hidayat N, Sihotang S, BO24628.

Table 1. Species, outgroup, herbarium voucher, and GenBank accession numbers used in this study

Species	Collection code (country)	GenBank acc. number of ITS
Lentinula aciculospora	TFB9447 (CRI)	AY016443
Lentinula aciculospora	TFB10418 (CRI)	AY016444
Lentinula aciculospora	PPNag001 (EQU)	JQ247977
Lentinula boryana	wc794 (MEX)	AF079576
Lentinula boryana	TFB10292 (MEX)	KY026657
Lentinula boryana	IE154R50 (MEX)	AF031177
Lentinula edodes	LeBIN0899 (RUS)	MG735346
Lentinula edodes	OE2 (IND)	AY636052
Lentinula edodes	UASWS0311 (POL)	EF174451
Lentinula edodes	B2SN033 (NPL)	LC149603
Lentinula edodes	TMI1546 (NPL)	AF031191
Lentinula edodes	B2SN037 (NPL)	LC149606
Lentinula lateritia	BO 24628 (ID)	OP051103
Lentinula lateritia	TMI1502 (PNG)	U33086
Lentinula lateritia	TMI1499 (PNG)	U33085
Lentinula lateritia	DSH92147 (PNG)	U33072
Lentinula lateritia	RV95378 (AUS)	AF031181
Lentinula lateritia	wc800 (PNG)	AF079573
Lentinula madagasikarensis	BB06.007 (MAD)	MW810301
Lentinula madagasikarensis	BB08.120 (MAD)	MW810302
Lentinula novaezelandiae	TMI1449 (NZL)	U33082
Lentinula novaezelandiae	RHP7563 (NZL)	U33079
Lentinula raphanica	TENN56663 (CRI)	AY256687
Lentinula raphanica	HN2002 (USA)	AF031178
Lentinula raphanica	Sp834 (BRA)	AF079579
Lentinus squarrosulus	BO 24427 (ID)	MT815446

Figure 1. Field photograph of *Lentinula lateritia* BO24628. (A) Upper side of pileus, (B) stipe, (C) lamellae, (D) crack on pileus. Bars = 1 cm

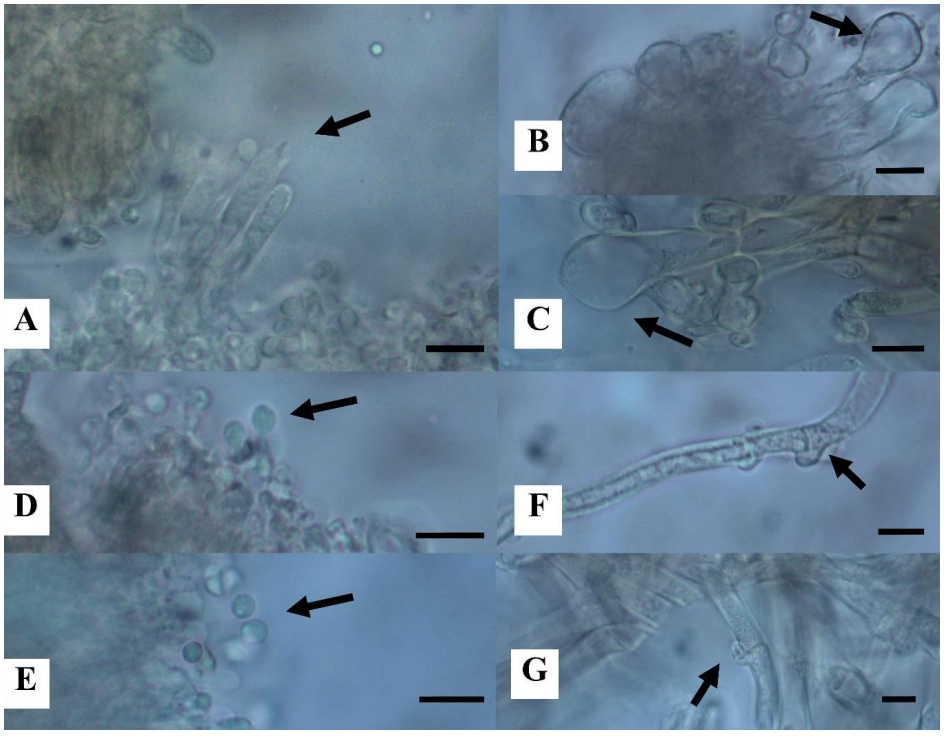

Figure 2. Microscopic characteristics of *Lentinula lateritia* BO24628. (A) Clavate basidia, (B and C) cheilocystidia, (D and E) Basidiospores, (F and G) clamp connections. Bars = 10 µm

3.2. Molecular Analyses

The aligned sequence was submitted to GenBank with ITS number OP051103. The BLAST result displayed that our specimens had the high similarity to *L. lateritia* and *L. edodes* (98-100%) as the top hits. The phylogenetic tree based on ITS sequence resolved three major clades: American, Madagascar, and Asia-Australasian species. The tree (Figure 3) showed that specimen BO24628 was closely related to *L. lateritia* DSH92147 from Papua New Guinea (PNG) with 98% BS value. The phylogenetic tree displayed that *L. lateritia* BO24628 was a sister clade to *L. lateritia* from Australia and another specimen form PNG. In addition, our specimens were in the different clade with similar morphological species (*L. edodes*).

4. Discussion

Lentinula lateritia was suggested to be the tropical form of shiitake (Pegler 1983) as it is distributed in tropical Asia and Australia. In contrast to the true shiitake (*L. edodes*) which is reported to grow throughout East Asia, especially Japan and China, but does not extend to the tropical zones (Pegler 1983). The current study introduces additional information on the occurrence and record of *L. lateritia* from the Old World (new to Indonesia). Previously, this species was reported from New South Wales, Australia (Pegler 1983), Sabah, Malaysia (Kobayasi 1966; Pegler 1983), Papua New Guinea (Kobayasi *et al.* 1973 as *L. edodes*), Bhutan

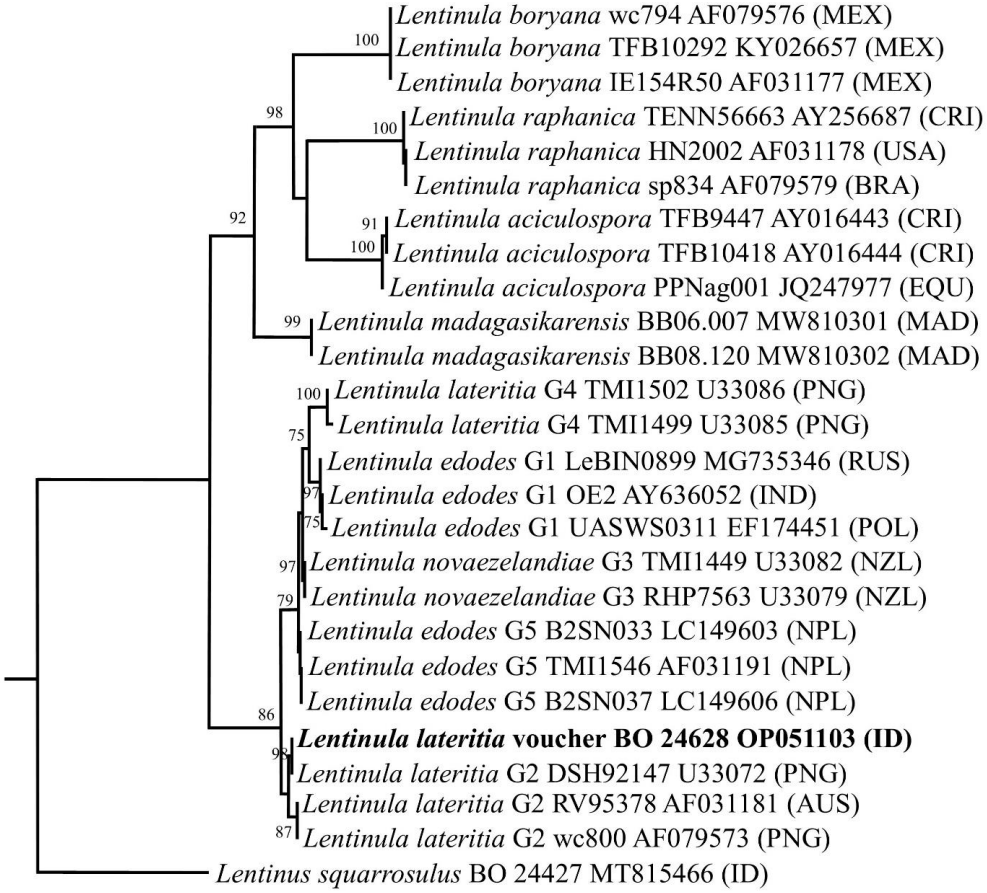

Figure 3. *Lentinula lateritia* BO24628 phylogenetic tree based on rDNA-ITS1/2 region using MEGA Version X with Maximum Likelihood method and 1,000 Bootstrap Analysis. *L. lateritia* BO24628 is bold on the phylogenetic tree

(Pegler 1983), India (Pegler 1983), and Vietnam (Tham *et al.* 2012). In line with our specimens, those collections of fruiting bodies were obtained from the highland areas. In addition, our study revealed evidence of an extension geographical distribution of *L. lateritia*, approximately 1,500 km away from Sabah (Borneo), located in Jambi (Sumatra Island). Hibbett *et al.* (1998) suggested that *Lentinula* poses a complex biogeography, with distribution on some continents.

To date, the GBIF (2023) has registered some occurrences of this species mostly from Australia and few from Papua New Guinea. A series of historical biogeographic scrutiny proposed the Neotropics (Guzman *et al.* 1997; Nicholson *et al.* 1997; Menoli Jr *et al.* 2022) as the most feasible ancestral origin of *Lentinula*, including the Asian-Australasian lineages which probably reached Oceania through long-distance dispersal (Menoli Jr *et al.* 2022). *L. leteritia* was first described by Berkeley (1881) from Australia as *Lentinus lateritius*. However, no locality or habitat details were provided other than growing on wood (Berkeley 1881). In this study, the fruiting bodies of *L. lateritia* BO24628 were found on decaying unidentified wood covered by mosses. The species of *Lentinula* usually grow on Fagaceae or Nothofagaceae (Pegler 1983), *Quercus* spp. (Mata *et al.* 2001), and *Eucalyptus* (Looney *et al.* 2021). In addition, Menoli Jr *et al.* (2022) suggested that *Lentinula* had the Fagaceae (*Quercus, Castanopsis*, and *Nothofagus*) as their ancestral hosts.

Some parameters, including morphological characters, mating compatibility, and molecular analyses had been used in the delimitation of *Lentinula* (Menoli Jr *et al.* 2022). Morphologically, *L. lateritia* BO24628 resembled *L. edodes* in pileus shape, pileus pigmentation, and ornamentation of the stipe. However, our specimens posed the persistent uniform reddish-brown pileus in fruiting bodies and did not produce squamules or fissures on pileus, which distinguished it from *L. edodes* (Pegler 1983). The absence of florets cheilocystidia in our specimens distinguished it from *L. madagasikarensis* described by Looney *et al.* (2021). The size of fruiting bodies of *L. lateritia* BO24628 was smaller compared to *L. edodes* (Pegler 1983) and *L. lateritia* (Pegler 1983). In addition, the basidiospores of our specimens were smaller compared to those reported by Pegler (1983). *L. lateritia* usually form smaller basidiomata with thinner context and more elongated stipe in comparison to *L. edodes* (Pegler 1983). Moreover, Pegler (1983) suggested that *L. lateritia* may be no more than a tropical form of *L. edodes*. However, the morphological appearance of the fruiting bodies in Southeast Asia and Australasia was remained different.

The BLAST search using our ITS sequence (OP051103) retrieved *L. lateritia* and *L. edodes* as the top hits. In line with BLAST result, the phylogenetic tree confirmed that specimen BO24628 was identified as *L. lateritia*. The phylogenetic tree placed *L. lateritia* BO24628 in the same clade as *L. lateritia* DSH92147 from PNG, revealing the geographic extension of this species, which approximately 4.5 million km away. *L. lateritia* BO24628 is reported for the first time in Indonesia, as well as the similar morphological species *L edodes*. Prior work of the phylogenetic study (Hibbet *et al.* 1998) using ITS sequence suggests that *L. laterita* and *L. edodes* may each contain multiple species-level lineages. Recently, Menoli Jr *et al.* (2022) recognized fifteen lineages of *Lentinula* based on sequences of ITS, LSU, and tef1-α from 24 countries in the Americas, Africa (Madagascar), and Asia-Australasia. They resolve some putative species including *L. lateritia* (Group 2), and *L.* aff. *lateritia* (Group 4). For the time being, we are not sure that our specimen represents which group in their report. Finally, our study provides the available morphological and molecular information on wild *L. lateritia* in Indonesia.

Conflict of Interest

The authors declare no conflict of interest.

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