




A recent collection of *Polyporus udus* from type locality (Indonesia)

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ABSTRACT. *Polyporus udus* (*Bresadolia uda*) was initially described as originating from Indonesia. Few recent studies showed that *P. udus* was placed in doubtful taxonomical treatment in *Polyporus*. There is no recent collection of this genus accessible from type locality after approximately two centuries. Therefore, this study aimed to update the current data and show the taxonomic position of *P. udus* to previous reports globally. During the wild mushroom survey 2023, the stipitate basidiomata of *Polyporus* was obtained. The morphology of the basidiomata was described based on the macroscopic and microscopic features. The molecular analysis and phylogenetic tree construction were performed using the ITS 1/2 sequence. The results showed that the combination of morphological and molecular analyses confirmed the taxonomical position of the specimens as *B. uda* (Jungh.). *Bresadolia uda* BO24625 grew in solitary to caespitose, basidia clavate, basidiospores cylindrical to sub-ellipsoid. Based on the phylogenetic tree, our specimens were in the same clade as those from Lao and China but different compared to the United States of America (USA) and India. In conclusion, this study provided the first morphological dimension of basidiospores and molecular information on *P. udus* from type locality and could be used for future investigation of *Polyporus*.

Keywords: *Bresadolia uda*; Indonesia; morphology; phylogeny; taxonomy.

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Introduction

Polyporus [P. Micheli ex Adans.] was described in 1821 with *P. tuberaster* (Jacq. ex Pers.) Fr. as the type species (Ryvarden, 1991; Sotome et al., 2008). This genus accommodates polypore fungi with stipitate basidioma, poroid hymenophore, wood-rotting or rarely terrestrial (sclerotium), dimitic hyphal system, skeleton-binding hyphae, cylindrical, and smooth basidiospores (Ryvarden, 1991; Núñez & Ryvarden, 1995). Núñez and Ryvarden (1995) accepted 32 species of *Polyporus* with six infrageneric groups based on macro-morphological features, namely *Admirabilis*, *Dendropolyporus* [= *Dendropolyporus* (Pouzar) Jülich], *Favolus* (= *Favolus* Fr.), *Polyporellus* (= *Polyporellus* P. Karst.), *Melanopus* (= *Melanopus* Pat.), and *Polyporus* s.s. Additionally, He et al. (2019) accounted for 35 species of *Polyporus* and Index Fungorum recorded 3467 taxa. Several *Polyporus* species are known for edible or medicinal use (Lindequist et al., 2005; Teplyakova et al., 2012; Bandara et al., 2015; Bulam et al., 2018). This genus has a global distribution and gained significant attention, particularly for taxonomic studies (Krüger & Gargas, 2004).

Recent reports have shown that *Polyporus* is not monophyletic based on molecular and morphological results, with several new taxonomic descriptions, reposition, and restoration (Ko & Jung, 2002; Sotome et al., 2008, 2013; Binder et al., 2013; Seelan et al., 2015; Palacio et al., 2017). Sotome et al. (2008) considered six well-supported clades within *Polyporus* using multigene analyses. The results showed that *Polyporus* and its allied genera share similar microscopic characters, but did not completely equate to the morphological groups. Furthermore, there is a need for a taxonomic revision of *Polyporus* and its allied genera for future studies (Sotome et al., 2008). Although the combination of morphological and molecular analyses has resolved several taxonomical problems, there are still unresolved questions about many species (Sotome et al., 2008; Motato et al., 2018). *Polyporus udus* is a *Polyporus* species whose phylogenetic position is considered highly uncertain, due to its less recent sampling (Krüger, & Gargas, 2004; Sotome et al., 2008).

Polyporus udus was constructed by Junghuhn in 1840 and originally described from Indonesia (Mount Pangrango, Java). The following collections have been reported from many areas globally, including Asia (Núñez & Ryvarden, 1995), Africa (Ryvarden & Johansen, 1980), and Neotropics region (Corner, 1984; Silveira & Wright, 2005; Ryvarden & Meijer, 2002; Louza & Gugliotta, 2007; Robledo & Rajchenberg, 2007; Coelho & Silveira, 2014). Recently, there has been limited knowledge about *P. udus* in type locality (Indonesia), as only one document has been reported to the country. Recently, the GBIF recorded 113 occurrences of *P. udus* worldwide, with only two being from Indonesia in 1996 and preserved in the Fungarium Oslo (University of Oslo, 2022). Putra (2021) suggested that more field sampling and results from type locality should be conducted to deepen the current knowledge of Indonesian mushrooms, and *P. udus* is no exception. More specimens should be preserved in Indonesia and easily accessible for mycologists.

Few studies of *Polyporus* showed that *P. udus* was placed in an uncertain position (Sotome et al. 2008; Dai et al., 2014; Motato-Vásquez et al., 2018). It is suggested the need for re-evaluation by phylogenetic study with more members in *Polyporaceae*. Based on recent morphological characters, *P. udus* was regarded as the type species of the new genus *Bresadolia* (Audet, 2017), namely *B. uda* (Index Fungorum, 2023a). Previous reports from morphological and molecular analysis recognized *B. uda* as a species complex (Corner, 1984; Silveira & Wright, 2005; Motato-Vásquez et al., 2018). Motato-Vásquez et al. (2018) suggested that the recognition as species complex was due to the limited taxonomic sampling and scarce molecular reports, particularly from Indonesia. The morphological and molecular data of *P. udus* from type locality will show the taxonomic position and its relation to similar collections worldwide (Motato-Vásquez et al., 2018). Therefore, this study aimed to update the recent collection of *P. udus* from type locality to enhance the understanding of taxonomic placement.

Material and methods

Specimen collection

Specimens of mushrooms were collected two times in 2023 and 2024 from Purworejo, Central Java, Indonesia. Some of the specimens were preserved in 70% ethanol for further analysis and herbarium. Photographs of the mushrooms were taken *in situ*, along with descriptions of the surrounding vegetation. In this study, voucher samples were deposited in the Herbarium Bogoriense, Research Center for Biology, National Research and Innovation Agency (BRIN), Indonesia.

Morphological identification

The macroscopic characteristics of the mushroom basidiocarp were observed immediately. These included habitat, growth pattern, fruiting body texture, pileus characters such as shape, surface, wetness, color, and margin. Lamellae characters included color, attachment to the stipe, density, margin, and lamellulae. Meanwhile, stipe characters were shape, color, diameter, surface, attachment to the pileus and substrate, texture, as well as interior. Microscopic studies of pileipellis, clamp connection, basidia, basidiospores, and cystidia were performed using a digital bright field microscope Olympus BX-63, Japan at the Integrated Laboratory of Bioproducts (iLaB), National Research and Innovation Agency (BRIN), Bogor, Indonesia. Identification of the specimens was based on several references, including Junghuhn (1840), Núñez and Ryvarden (1995), and Motato-Vásquez et al. (2018). Scanning Electron Microscopy (SEM) was also performed using JSM IT 200 SEM system (JEOL, Tokyo, Japan). Specimen preparation followed Goldstein et al. (1992) methods before being observed using SEM. The lamellae part of the basidiocarps were cut into small pieces (5x5 mm), and soaked in 2.5% glutaraldehyde of caccodylate buffer pH 8.4 at 27 °C for two days. This was followed by fixing in 2% tannic acid for a few days and washing with four caccodylate buffer changes. Specimens were dehydrated in 50-100% ethanol series, infiltrated with t-butanol for 10 minutes twice, and freeze-dried. Subsequently, freeze-dried specimens were mounted on an aluminum stub with double-sided carbon tape and coated with gold using an Ib2 ION COATER (Eiko Engineering, Tokyo, Japan).

Molecular analyses

DNA extraction followed by PCR was conducted in Integrated Laboratory of Bioproducts (iLaB), National Research and Innovation Agency (BRIN), Bogor, Indonesia. Fresh materials were extracted using hexadecyltrimethylammonium bromide following the protocol from Putra et al. (2024). The PCR amplification was used Internal Transcribed Spacer (ITS) region of ITS 5 (5'-GGA AGT AAA AGT CGT AAC

AAG G-3') and reverse ITS 4 (5'-TCC TCC GCT TAT TGA TAT GC-3') primers (White et al., 1990). PCR amplification was performed in a 40 µL total reaction containing 12 µL ddH₂O, 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 two 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 sequence was assembled using ChromasPro Software, deposited in GenBank (<https://www.ncbi.nlm.nih.gov/>), and used for nucleotide Basic Local Alignment Search Tool (BLAST). The phylogenetic tree was constructed from the sequence of this study (bold), selected BLAST result, *Bresadolia* species from a previous report (Motato-Vásquez et al., 2018), and *Lentinus squarrosulus* (Hermawan, 2020) as the outgroup, as shown in Table 1. The arrangement of the sequences used Clustal X Ver. 2.1 software (Larkin et al., 2007). The phylogenetic tree was generated based on maximum likelihood (ML) method with MEGA X software. The phylogenetic tree used 1000 replicates of Bootstrap. Bootstrap (BS) ≥ 80 was shown on the branch (Figure 2).

Table 1. Selected species, voucher information, origin, and GenBank accession of sequences used in this study.

Species	Collection Code	Origin	GenBank Accession Number of ITS region
<i>Bresadolia craterella</i>	Isolate CR001	The United States of America (USA)	MT196970
<i>Bresadolia cuticulata</i>	Voucher Yuan 5397	China (CN)	KX851618
<i>Bresadolia cuticulata</i>	Dai 13101	China (CN)	KP297863
<i>Bresadolia paradoxa</i>	Voucher FCOS45	Argentina (AR)	KY777234
<i>Bresadolia paradoxa</i>	Voucher SP445579	Brazil (BR)	KY777231
<i>Bresadolia paradoxa</i>	Voucher SP445678	Brazil (BR)	KY777232
<i>Bresadolia paradoxa</i>	Voucher FCOS44	Argentina (AR)	KY777233
<i>Bresadolia paradoxa</i>	Voucher SP445677	Brazil (BR)	KY777230
<i>Bresadolia uda</i>	Voucher BO24625	Indonesia (ID)	ON015648
<i>Bresadolia uda</i>	Voucher WA0000072214	Lao (LA)	MT252560
<i>Bresadolia uda</i>	Voucher Cui 11045	China (CN)	KX851643
<i>Bresadolia uda</i>	Voucher Yuan 356	China (CN)	KX851644
<i>Bresadolia uda</i>	Voucher Vui 11071	China (CN)	KX851642
<i>Bresadolia uda</i>	H6518	India (IN)	AF518756
<i>Bresadolia uda</i>	Voucher FLAS-F-60005	The United States of America (USA)	KY654718
<i>Lentinus squarrosulus</i>	Voucher BO 24427	Indonesia (ID)	MT815466

Results

Taxonomy

Bresadolia uda (Jungh.) Audet Index Fungorum 311: 1 (2016)

Basionym: Polyporus udus Jungh., Tijdschr. Nat. Gesch. Physiol. 7: 289 (1940)

= *Polyporus fuscomaculatus* Bres. & Pat. Mycological Writings 1(6): 49 (1901)

Basidiomata (Figure 1A-B) annual, solitary to cespitose, central to eccentric stipitate, two basidiomata united at base, fleshy to rigid, and brittle when dry. Cap flabelliform to circular, flattened to concave, with approximately 6–15 cm long, 5–11 cm wide, and 4 cm thick at the base. Pilear surface papery, glabrous, smooth, wrinkled cuticle, beige, and some specimens with chestnut color. Margin entire, smooth, thin, hyalin to cream, inrolled when dry. Hymenial surface poroid (Figure 1C), angular to hexagonal, cream when fresh, darkening/buff-yellow upon drying, pores regular to irregular, decurrent on the stipe, concolorous tubes to the hymenial surface, thin, whole to lacerated dissections at maturity. In some specimens, daedaloid pores can be observed near the stipe. Context (Figure 1D) fleshy when fresh to leathery upon drying, homogeneous, white to cream. Stipe cylindrical, fleshy, rigid to hard upon drying, expanded at base, light to dark brown, fibrillose, with tufts of hairs, 1.9–3 × 1.2–5 cm. Homogeneous context, white, spongy. Pileipellis (Figure 2A) a cutis with incrusting pigment. Hyphal system dimitic with generative (Figure 2B) and skeleton-binding hyphae (Figure 2C). Generative hyphae with clamp connections, non-inflated hyphae 2.5–4 µm diam, and inflated hyphae 7.8–9.8 µm diam. Skeletal hyphae, branched, 3.4–4.8 µm wide. Cystidia absent. Fusoid cystidioles present (Figure 3C,D). Crystals near basidioles are common (Figure 4), 5–10 × 1–2 µm. Basidia and basidioles clavate. Basidia hyaline, tetraspores, 13–17 × 5–9 µm. Basidiospores (Figure 3A,B) hyaline to yellowish, cylindrical to sub-ellipsoid, thin walled, smooth, 7.5–11.5 × 3–5 µm.

Specimen examined: On decayed wood, Baledono, Purworejo, Central Java (Indonesia), 7°42'10.6"S 110°01'41.1"E 100 m a.s.l, KPJI May 2023,2024, *Bresadolia uda* BO24625.

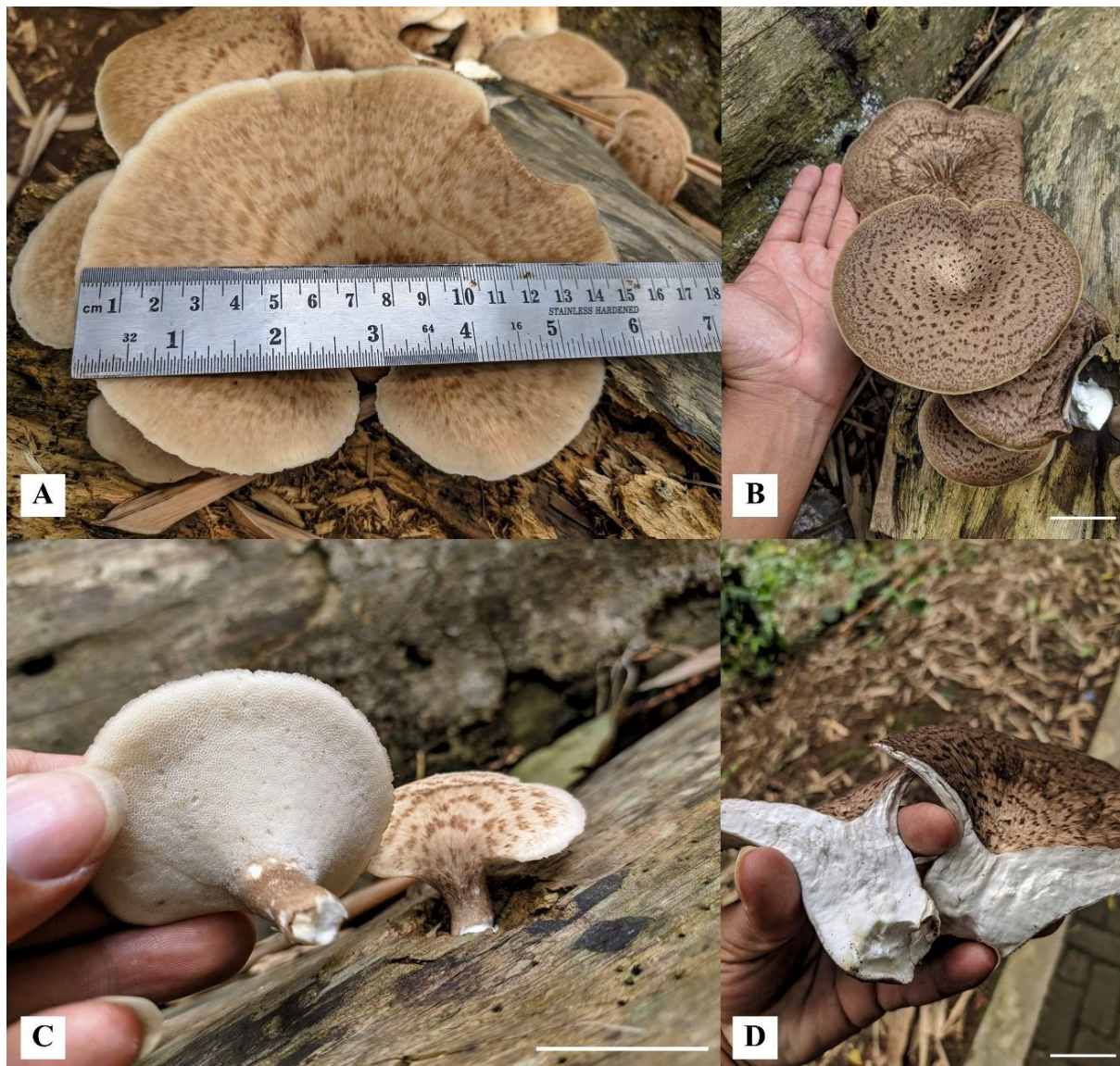


Figure 1. Macroscopic characteristics of *Bresadolia uda* BO24625. A–B. Basidioma showing surface features of pileus. C. Pore surface detail. D. Context detail. Bars B–C= 5 cm, D= 3cm.

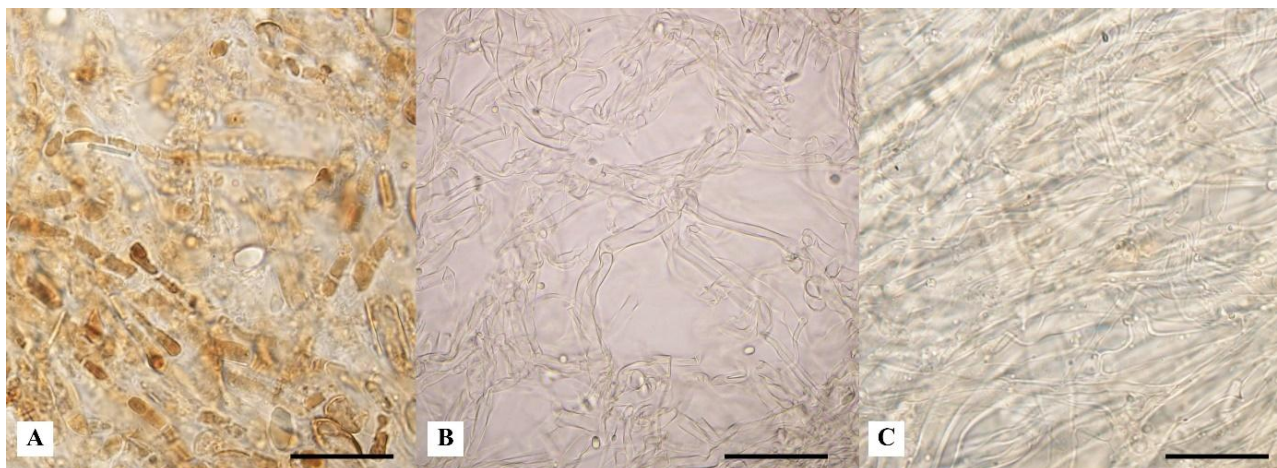


Figure 2. The characteristics of pileipellis and hyphae of *Bresadolia uda* BO24625. A. Cutis pileipellis. B. Generative hyphae. C. Generative and skeleton-binding hyphae from the context. Bar= 20 μ m.

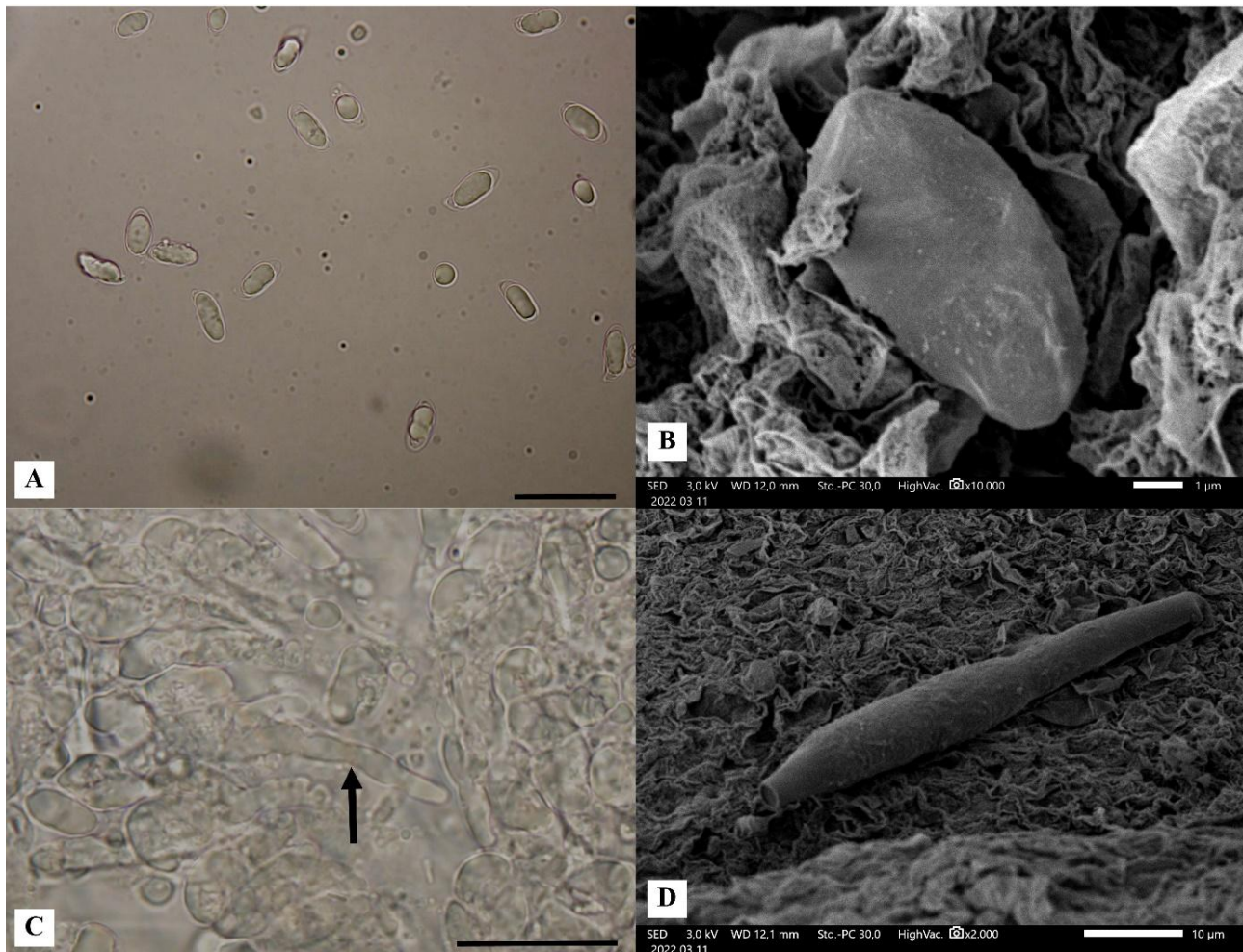


Figure 3. The characteristics of basidiospores and fusoid cystidiole of *Bresadolia uda* BO24625. A. Basidiospores with cylindrical to sub-ellipsoid shape. B. Scanning electron microscope (SEM) observation of basidiospore. C. Fusoid cystidiole. D. SEM observation of fusoid cystidiole. Bar A&C = 20 µm, B = 1µm, D = 10 µm.

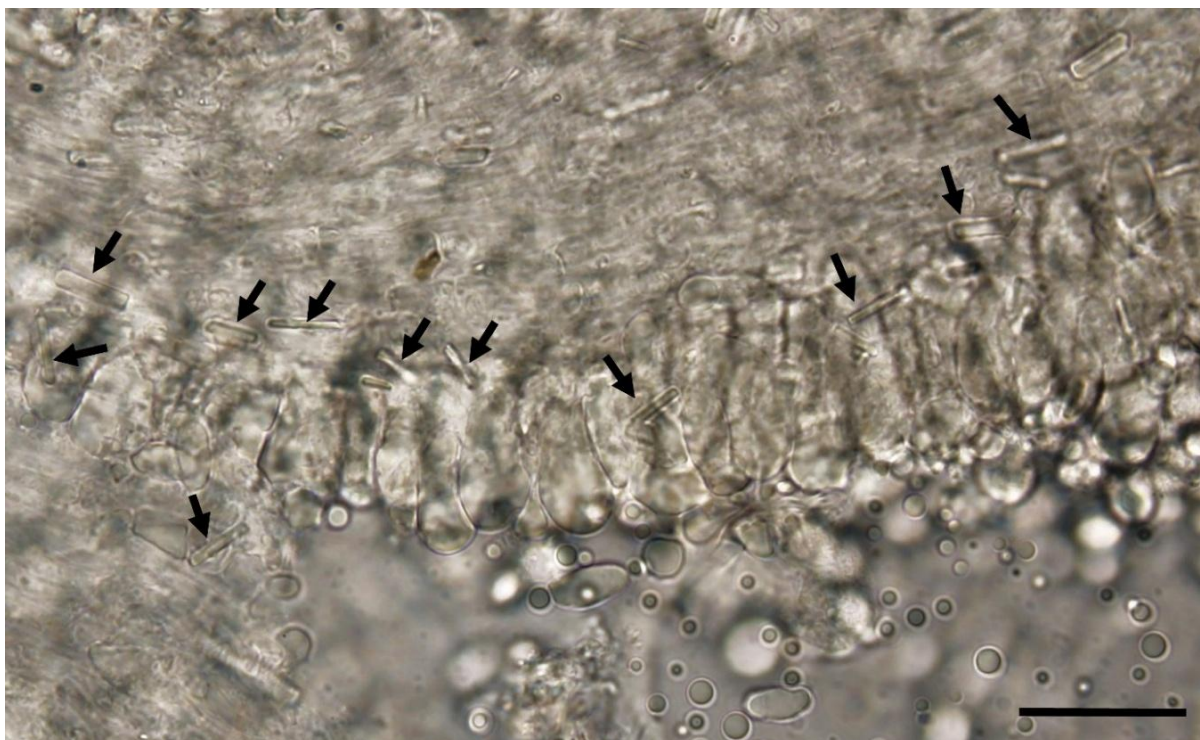


Figure 4. The abundant crystals near basidioles of *Bresadolia uda* BO24625. Bar= 20 µm.

Molecular analysis

The obtained and arranged sequence was registered with the ITS ON015648 reference number at GenBank. The BLAST search result showed that *B. uda* BO24625 had the high query cover with *B. uda* / *P. udus* (91–96%) as the first four top hits. Additionally, *B. uda* BO24625 had 91% query cover with *P. cuticulatus*. The percentage identity showed that *P. udus* had the highest results. The phylogenetic tree in Figure 5 was constructed from four species of *Bresadolia* with available ITS sequences. The phylogenetic tree showed that *B. uda* BO24625 was in the same clade as *B. uda* collected from Laos and China with 100% BS values. Furthermore, *B. uda* BO24625 was in a different clade with specimens from India and the USA.

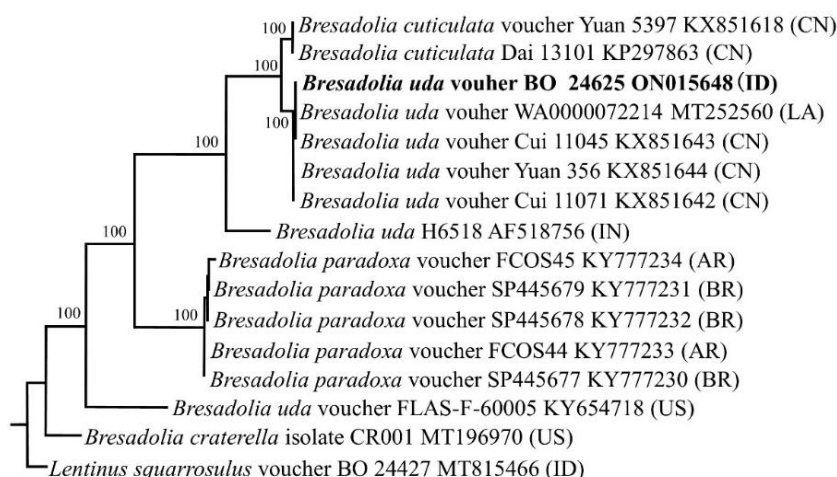


Figure 5. The phylogenetic tree of *Bresadolia uda* BO24625 based on ITS1/2 region using MEGA Version X with Maximum Likelihood method and 1000 Bootstrap Analysis.

Discussion

Currently, there are eight species of *Bresadolia* accepted by Index Fungorum (2023b). Among these species, only *B. uda* was originally described from Indonesia. It was previously noted as *P. udus*, now synonymized with *B. paradoxa* (Audet, 2017). The current study provided the latest information on *P. udus* from type locality after approximately 200 years of hiatus. *B.uda* (*P. udus*) was first described by Junghuhn in 1840 and originally found on Mount Pangrango, West Java, in Indonesia. Subsequently, there have been reports about collections from Asian and African countries, including the Neotropics. Few additional recent studies have been conducted on *B. uda*, with the majority being carried out in Brazil (Louza & Gugliotta, 2007; Coelho & Silveira, 2014).

The limited study of the locality type of *B. uda* placed this species in an uncertain position, in the major phylogenetic clades of *Polyporus* s.l (Sotome et al., 2008). The Indonesian *Bresadolia* and related genus is not fully understood particularly on the number of species and zonal distribution. Therefore, this study provides the morphological and molecular data of *B. uda* from Central Java, Indonesia (type locality). The results showed that specimen BO24625 had the common characteristics of *Bresadolia* such as being fleshy to rigid, brittle when dry, pilear surface was papery, glabrous, smooth, wrinkled cuticle, and daedaloid pore could be observed near the stipe. Other morphological characteristics included context fleshy when fresh to leathery upon drying, cylindrical stipe, skeleton-binding hyphae cystidia absent, fusoid cystidioles, basidia and basidioles clavate, basidiospores with smooth surface hyaline to yellowish, cylindrical to sub-ellipsoid, thin-walled (Motato-Vásquez et al., 2018). However, the abundant crystals near basidioles were first reported from *B. uda* BO24625.

The basidiome of our specimen was slightly smaller compared to *P. udus* reported by Coelho and da Silveira (2014) from Santa Maria, Southern Brazil (15 mm and 18.5 mm, respectively). Previous studies suggested that *B. uda* is a complex species by range variation of morphological characteristics (Corner, 1984; Silveira & Wright, 2005). Sotome et al. (2008) reported that *P. udus* posed the unique basidiomata and were considered to be a phylogenetically distinct lineage from other species in *Polyporus*. Morphologically, *B. uda* BO24625 was identical to *B. cuticulata* due to the presence of thick context, papery cuticle on upper pileus, and monomitic tramal hyphae (Si & Dai, 2016). However, *B. uda* BO24625 has bigger pores (1–2 per mm) and larger basidiospores (Núñez & Ryvarden, 1995).

Bresadolia uda BO24625 has a slightly smaller dimension of basidiospores compared to *B. uda* from the description of Núñez and Ryvarden (1995) ($7.5\text{--}11.5 \times 3\text{--}5 \mu\text{m}$ and $10\text{--}15 \times 4\text{--}6 \mu\text{m}$, respectively). The current study provided the actual dimension of basidiospores of *B. uda* from type locality, which was not reported by Junghuhn in 1840. Additionally, the abundance of crystals near the basidium and basidioles was encountered. The micromorphological features of *B. uda* are similar to *P. squamosus*, but the former has sessile basidiomata and prominent wrinkled pileus surface when dried (Ryvarden & Johansen, 1980). Based on morphological analysis, Motato-Vásquez et al. (2018) re-identified some neotropical specimens as *B. paradoxa*. This showed that the recent collection of *B. uda* worldwide, including Asia, Africa, and Neotropics region should be reinvestigated. The morphological data of *B. uda* from type locality would contribute to confirming the taxonomical re-examination of this species worldwide.

Previous studies showed that *B. uda* was placed in an uncertain position, unrelated to any of the major phylogenetic clades recognized in *Polyporus* (Sotome et al., 2008; Motato Vasquez et al., 2018). A homological test based on nucleotide BLAST result showed that our specimen has a high similarity to *B. uda*, *P. udus*, and *P. cuticulatus*. The phylogenetic tree based on ITS sequences confirmed specimen BO24625 as *B. uda* (*P. udus*) and formed sister clade with *B. cuticulata* (*P. cuticulatus*). Dai et al. (2014) and Motato-Vasquez et al. (2018) suggested that the monophyly of group *Polyporus* should be reevaluated by phylogenetic study of more members including *P. udus* from type locality due to the lack of its DNA sequences. For example, Ji et al. (2022) could not include *P. udus* in their phylogenetic analyses of *Polyporus* and related genera as lacked sufficient DNA sequences.

This study was the first to provide information on DNA sequence of *B. uda* from type locality. Based on the phylogenetic tree, *B. uda* BO24625 was not retrieved as a monophyletic clade. The result was in line with the report by Motato-Vasquez et al. (2018), where ITS and LSU genes were used. *B. uda* BO24625 was in the same clade as *B. uda* from Lao and China but placed separately from specimens collected in the USA and India. The *B. uda* specimens from India and the USA were placed in different clades to each other when compared to collection from Japan (LSU sequence) in the phylogenetic tree made by Motato-Vasquez et al. (2018). This raises concern about whether there is a variety or subspecies in *B. uda*. To confirm the hypothesis, more taxonomic sampling and a higher number of molecular reports should be provided, as stated by Rosenberg and Kumar (2001, 2003) and Oliveira et al. (2020). For the time being, the molecular data of this study confirmed the taxonomical position of *B. uda* from type locality in relation to the same specimens recorded worldwide. For further studies, the use of multiple genes was recommended to assess *B. uda* type locality and provide more information on the phylogenetic position.

Conclusion

In conclusion, this study reported *Bresadolia* specimens with solitary to cespitose, flattened to concave, poroid hymenophore, white to cream context, cylindrical stipe, dimitic hyphal system, cystidia absent, fusoid cystidioles present, prominent crystals common, basidia clavate, and cylindrical to sub-ellipsoid basidiospores. Morphological and molecular analyses confirmed this specimen as *B. uda*, which was previously described as *P. udus* from type locality (Indonesia). The results provided the recent collection of *B. uda* (with herbarium deposited in Indonesia) from type locality after approximately 200 years of hiatus. Based on the analysis, this study provided the first information on DNA sequence of *B. uda* from type locality. the ITS sequence of the specimen (ON015648) was deposited at GenBank and could be used for future studies of *Polyporus*.

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