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SYSTEMATICS OF *Heimioporus retisporus* (PAT. & C.F. BAKER) E. HORAK (AGARICOMYCETES: BOLETACEAE), AN EDIBLE WILD MUSHROOM FROM SOUTHEAST SULAWESI, INDONESIA

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Abstract
The genus *Heimioporus* was previously proposed as *Heimiella* by Boedijn from Indonesian specimens. Currently, the knowledge of Indonesian *Heimioporus* is limited due to a lack of field sampling. The only notable *Heimioporus* from Indonesia is *jamur pelawan* (local name), a wild edible mushroom from Bangka-Belitung Province, for which the taxonomical identity remains unclear. During a mushroom collecting field trip near Kendari (Indonesia) in 2024, a wild edible bright red bolete mushroom resembling *Heimioporus* was encountered, and specimens were collected. The current study confirms the taxonomical identity of our specimens. Fresh fruiting bodies were evaluated for morphological and molecular evidence. The basidiomata were described based on the macro- and micromorphological characteristics. Molecular analysis and phylogenetic tree construction were performed using the ITS (Internal Transcribed Spacer) locus. The combination of morphological and molecular analyses confirmed our collection as *H. retisporus*. Our study proves that the previous Indonesian *Heimioporus* collection from Bangka-Belitung Province was not *H. retisporus*. The indigenous people in the area where *H retisporus* was collected consume this wild edible mushroom and sell it at local markets.

***Keywords*:** Basidiomycota, Fungi, *Hemioporus*, *Heimiella*, morphology, phylogeny, taxonomy

Introduction

Heimioporus belongs to the family Boletaceae, within the order Boletales. *Heimioporus* E. Horak (Boletales, Boletaceae) represented by *H. retisporus* (Pat. & C.F. Baker) E. Horak as the type species, was proposed by Horak (2004) to substitute a previous invalid genus name (*Heimiella*, not Lohmann) erected by Boedjin (1951). Taxa of *Heimioporus* are primarily identified by their vibrant colored fruiting bodies, reticulated stipe, and basidiospores that have a reticulate or pitted appearance (Boedijn 1951, Corner 1972, Horak 2004, Halling *et al*. 2015, Zeng *et al*. 2018). Halling *et al*. (2015) have confirmed that *Heimioporus* is a monophyletic group within the subfamily Xerocomoideae. Currently, Index Fungorum (2024) registered 25 epithets of *Heimioporus* globally with 19 species: *H. alveolatus*, *H. anguiformis*, *H. australis*, *H. conicus*, *H. cooloolae*, *H. fruticicola*, *H. gaojiaocong*, *H. ivoryi*, *H. japonicus*, *H. kinabaluensis*, *H. mandarinus*, *H. punctisporus*, *H. retisporus*, *H. ridleyi*, *H. rubropunctus*, *H. sinensis*, *H. subcostatus*, *H. subretisporus*, and *H. xerampelinus*.

Heimioporus species are ectomycorrhizal (ECM) fungi and are known to have a wide range of host trees. They are commonly found in association with various tree genera, such as *Eucalyptus*, *Casuarina*, and *Acacia* (Fuhrer 2005). Helbert *et al*. (2019) reported that *Heimioporus* is associated with *Tristaniopsis* and could function as refugia for ECM fungi that inhabit primary mixed dipterocarp forests in Southeast Asia. Of many species of *Heimioporus*, *H. retrisporus* has gained attention as a delicacy and medicinal wild edible mushroom. Zeng *et al*. (2018) reported that this species is sold in markets in Yunnan Province, southwest China. In addition, *Heimioporus retisporus* Polysaccharide (HRP), a new type of polysaccharide, was obtained from *H. retisporus* (Feng *et al*. 2022). *Heimioporus* is primarily found in Asia, Australia, New Zealand, and America (Horak 2004, Halling and Fechner 2011, Halling *et al*. 2015). However, to date, no comprehensive records are available on the distribution of *Heimioporus* in Indonesia.

Wild edible mushrooms are a valuable natural resource frequently sought by local communities and have become an integral part of the daily life of various ethnic groups in Indonesia. This collective knowledge, transmitted through generations, constitutes a crucial component of traditional wisdom. It is imperative to document and preserve this information to ensure its availability for future generations. In Indonesia, previous studies have reported the utilization of *Heimioporus* sp. (local name: *jamur pelawan*), recognized as a delicacy by local people in Bangka Belitung Province (Tasuruni 2012, Putra 2020). To date, this species is considered to be closely related to *H. retrisporus* based on morphological data. In addition, *H. retrisporus* has been discussed for years as the taxonomic name of the popular Indonesian wild edible *Heimioporus*, but with insufficient evidence. During our mushroom survey in Kendari (Southeast Sulawesi, Indonesia) in 2024, some basidiomata of red bolete (local name: *taliku eha*), which resemble *jamur pelawan* were collected. Upon first observation, we recognized it as *Heimioporus* due to its macromorphological characteristics in its natural habitat. Furthermore, after discussing with the local community, we discovered that they typically consume and trade this mushroom. The main objective of this study was to establish the taxonomic classification of our samples using both morphological and molecular data.

Materials and methods

***Specimen collection*.** In our mycobiota survey of 2024, basidiomata of red bolete were gathered from Konda, South Konawe, Southeast Sulawesi, Indonesia. During this process, the mushrooms were photographed in their natural setting, and ecological details were recorded. Some specimens were preserved in 70% ethanol for further analysis, and others were deposited at the Herbarium Bogoriense, housed within the Research Center for Biology under the National Research and Innovation Agency (BRIN), Indonesia. Information on the use of this mushroom, which included the foraging time and the price of the mushrooms, was acquired through conversations with the local inhabitants.

***Morphological identification*.** We examined the macromorphological and micromorphological features of the basidiomata in their natural habitat. Observations included habitat, growth pattern, texture, pileus features, hymenophore attributes, and stipe characteristics. The color classifications adhere to Kornerup & Wanscher (1978). A digital bright field microscope and scanning electron microscopy were used to analyse micromorphological features, including pileipellis, clamp connections, basidia, basidiospores, and cystidia. Measurement and notations of basidiospores followed Vadthanarat

et al. (2020). Samples were prepared according to Goldstein *et al*. (1992) before being observed under a scanning electron microscope. The lamellae were first cut into 5 × 5 mm pieces and immersed in a 2.5% glutaraldehyde solution mixed with cacodylate buffer (pH 8.4) at 27 °C for two days. Next, the samples were fixed in a 2% tannic acid solution for a few days and rinsed with the cacodylate buffer four times. The samples underwent dehydration using a gradual ethanol series (50-100%), followed by infiltration with t-butanol for two 10-minute intervals. After freeze-drying, the samples were secured on an aluminium base using double-sided carbon tape and coated with gold using an IB2 ION COATER from Eiko Engineering in Tokyo, Japan. Morphological description and identification were made by referring to related references, including Boedjin (1951), Corner (1972), Horak (2004), Tasuruni (2012), Putra (2020), and Zheng *et al*. (2018).

DNA extraction, PCR, Sequencing, and phylogenetic analyses. DNA extraction followed by PCR was done in the Research Center for Applied Microbiology at the National Research and Innovation Agency (BRIN), Indonesia. Fresh basidiomata were extracted using hexadecyltrimethylammonium bromide (CTAB). The Internal Transcribed Spacer (ITS) region was amplified using ITS 5 and reverse ITS 4 primers (White *et al*. 1990). The PCR reaction consisted of 40 µL, 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 process involved 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. Amplicons were analyzed on 1% agarose gels and visualized using the Gel Doc™ XR system. PCR products were sent to 1st Base Malaysia (Axil Scientific Pte Ltd) for sequencing.

The sequence was assembled using ChromasPro Software. The obtained sequence was deposited in GenBank and analyzed using a nucleotide Basic Local Alignment Search Tool (BLAST). In addition, the sequences (Sup. Table 1) from selected BLAST results of this study, sequences from Hosen *et al*. (2013), and sequences from the current study were used to reconstruct the phylogenetic tree. *Chalciporus piperatus* was used as the outgroup. The Clustal X Ver. 2.1 software (Larkin *et al*. 2007) was employed for sequence alignment. The phylogenetic tree was constructed with the maximum likelihood (ML) method using MEGA X software (Kumar *et al*. 2018) with 1000 Bootstrap (BS) replications. Other parameters used in the ML analysis were selected according to the default standard in MEGA X software. Bootstrap values of 50% or higher were shown.

Results

Molecular Analyses. Our ITS sequence, which was matched and recorded under GenBank's reference number ITS PQ220248, revealed that *Heimioporus* BO24642 had a significant query coverage (100%) with *H. retisporus* as the leading match. A phylogenetic tree (Fig. 1), created using closely related *Heimiosporus* species that had accessible ITS sequences, demonstrated that *H. retisporus* BO24642 and *H. retisporus* voucher SL2141 from the Singapore collection shared the same clade with 99% bootstrap support values. Furthermore, *H. retisporus* BO24642 was found in a different clade alongside the previous Indonesian collection of *Heimioporus* sp. (*jamur pelawan*).

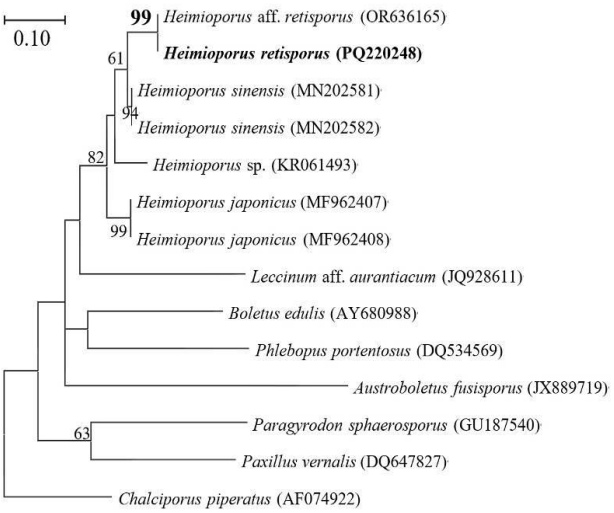

Figure 1. *Heimioporus retisporus* BO24642 phylogenetic tree based on ITS1–2 region using Maximum Likelihood method and 1,000 Bootstrap Analysis. The specimen used in this study is in bold.

Taxonomy

Heimioporus retisporus (Pat. & C.F. Baker) E. Horak, 2004 (Figs. 2–3)

Basidiomata medium, solitary to gregarious, bright red (8A8) to pinkish red (8A5) when young, reddish brown (8E8) in maturity, 6–9 cm diameter. Pileus slightly convex at first,

Plate 6

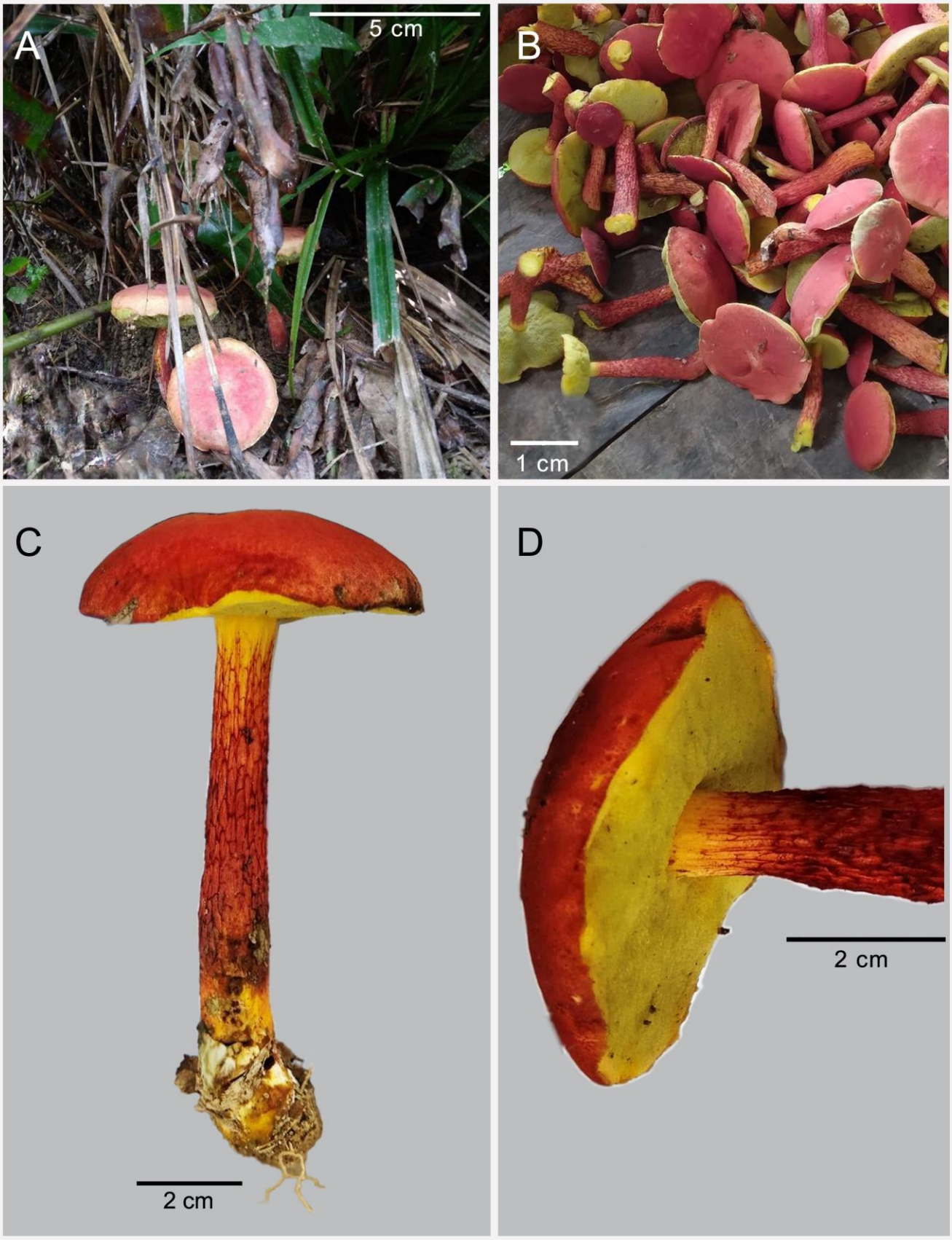

Figure 2. *Heimioporus retisporus* BO24642 in-situ **(A)** Basidiomata solitary to gregarious, **(B)** Basidiomata at the market, **(C)** Pileus, stipe, and mycelium base characters, **(D)** Poroid hymenophore

afterwards expanding to applanate, sometimes depressed at centre, margin flat to slightly incurved. Surface dry, smooth to nearly glabrous, cracking in some areas. Context thick, yellowish, unchanging in colour when sliced. Hymenophore poroid, flat at surface, sometimes wavy, free form stipe, pores angular, pale yellow, dull yellow to brownish yellow, unchanging in colour when injured, tube detachable. Stipe cylindric, slightly enlarged at base, 9–13 × 1–1.4 cm, solid, central, dry, concolorous with pileus paler at upward regions, stipe with reticulations, darker than stipe colour, without ring, basal mycelium white to cream. Basidiospores somewhat ovoid, 10–12 × 6–8 µm, pale brown, completely reticulate and irregular. Basidia club-shaped, 29–37 × 11–15 µm, 4 sterigmata, thin-walled, hyaline, sometimes with prominent lipid bodies, sterigmata 3–4 µm in length. Cheilocystidia thin-walled, flask-shaped, hyaline, and without encrustation. Clamp connection absent. Pileipellis trichoderm, 7–12 µm in diam, nearly vertical in arrangement, often branched, slightly thick-walled, pale brownish. Stipe trama composed of parallel hyphae.

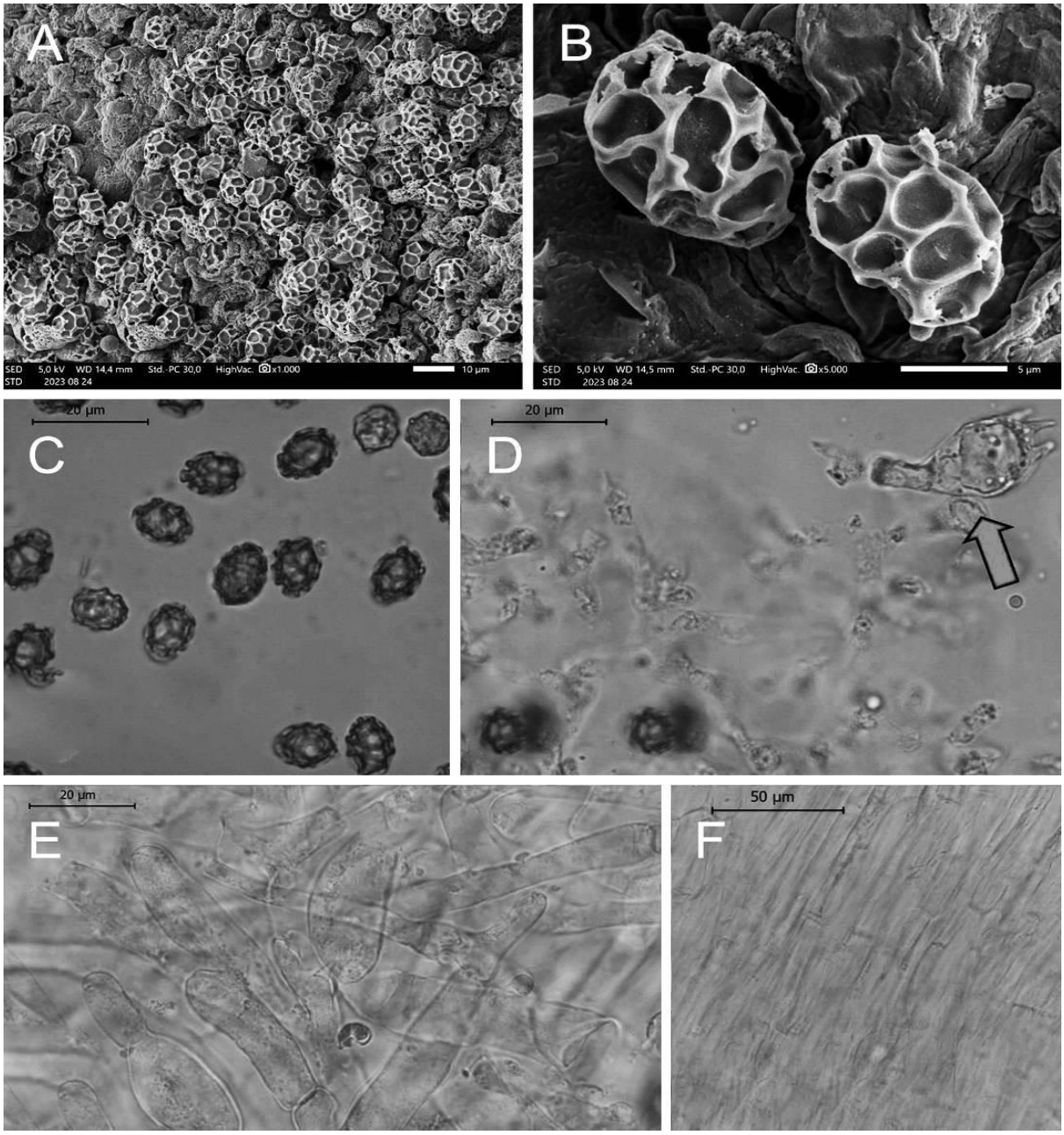

Figure 3. Microscopic characters of *Heimioporus retisporus* BO24642: **(A, B)** reticulate basidiospores under SEM microscope, **(C)** reticulate basidiospores under light microscope, **(D)** basidium with four-spored sterigmata (pointing arrow), **(E)** trichoderm type of pileipellis, **(F)** stipe trama.

Specimen examined. Ambololi, Konda, South Konawe, Southeast Sulawesi, Indonesia, 4° 7' 16.9932" S 122° 27' 40.4676" E, 56 m a.s.l, near *Castanopsis buruana* Miq., collected by SAAT 2024, *Heimioporus retisporus* BO24642.

Discussion

Heimioporus retisporus is a rare species of bolete mushroom, with only 23 occurrences recognized worldwide. These occurrences have been reported in Thailand, Japan, Malaysia, Indonesia, China, Mexico, and Singapore (GBIF 2024). The only record from Indonesia was documented by Halling in 2001 at Haurbentes, West Java, Indonesia (Halling *et al*. 2015). However, no herbarium specimen was deposited in Indonesia. The current study updated and provided the herbarium collection for the country, which is now deposited with Herbarium Bogoriense, Indonesia, for future reference. Additionally, this study reveals a geographical extension of the range of *H. retisporus* to Kendari, Southeast Sulawesi, Indonesia, which is more than 2,000 km away from previously recorded locations, and indicates that more field sampling should be done to correctly determine the true range of this species. Tasuruni (2012) reported an edible red bolete from Bangka Belitung (Indonesia), suggesting it to be *Heimioporus* sp. and closely related to *H. retisporus*. Imanuddin *et al*. (2020) concluded that the edible mushroom from Bangka Belitung was *H. retisporus*, but with insufficient evidence. The present study reveals that the mushroom from Bangka Belitung is a distinct species or might be a subspecies of *H. retisporus*. Currently, there is limited information available about *H. retisporus* in Indonesia. More research and data are needed to better understand its distribution, ecology, and potential uses. Further studies are necessary to determine its conservation status and any potential economic or medicinal properties.

Heimioporus retisporus BO24642 can be recognized by its conical to flat cap, which is reddish-brown and has a slightly velvety texture with a net-like pattern on its stem. This specimen has a crimson stipe and smaller basidiospores compared to *H. gaojiaocong*. Unlike *Heimiella retispora* reported from Indonesia by Boedijn (1951), our specimen lacked an umbo. *Heimioporus retisporus* BO24642 differs from *H. sinensis* and *H. japonicus* due to its crimson pores and comparatively fewer cracker-like pits and thicker ridges (Wu *et al*. 2016, Zeng *et al*. 2018). *Heimioporus retisporus* BO24642 and *H. subretisporus* share yellow to olive pores under the pileus, but the latter species has no reticulations on the stipe (Corner 1972) or yellow to orange reticulations and comparatively larger basidiospores (Wu *et al*. 2016). In addition, our specimen had larger diameter spore reticulations. *Heimioporus retisporus* BO24642 has a smaller pileus diameter compared to the Indonesian *Heimioporus* reported by Tasuruni (2012), but a slightly larger dimension compared to the specimen reported as *H. retispora* by Boedijn (1951) from Bogor Botanical Garden, West Java, Indonesia. The basidiospores of our specimen exhibit similar characters and dimensions to *H. retisporus* reported from the type locality (Singapore) (Corner 1972) and a specimen described from Sarawak (Malaysia) by Watling and Hollands (1990). Our future work should compare our specimens to those collected by Halling from Haurbentes, West Java, Indonesia.

The taxonomy and classification of *Heimioporus* have been studied in detail, with several species recognized based on the combination of morphological and molecular analyses (Wu *et al*. 2016). For example, in China, *H. japonicus* was misidentified as *H. retisporus* (Wu *et al*. 2016). Therefore, we combined the morphological data with molecular evidence in the current study. The BLAST result revealed that our specimen has a high similarity to *H. retisporus* from the Singapore collection. In line with the BLAST result, our phylogenetic tree confirmed that specimen BO24642 is *H. retisporus* (99% BS value) and closely related to the *H. retisporus* voucher SL2141 from its type locality and distant from other closely related species by morphology. In addition, our specimen formed a different clade from an edible *Heimioporus* sp. from a previous study (Tasuruni 2012), and was confirmed as a different taxon. There have been limited molecular studies conducted on *H. retisporus* in Indonesia. Further molecular studies may provide more insights into the genetic diversity, evolution, and taxonomic relationships of *H. retisporus* and other related species. These studies could help improve our understanding of the evolutionary history of *H. retisporus* as well as aid in conservation efforts for this mushroom species, as it is acknowledged as an ectomycorrhizal-forming fungus.

Heimioporus species are commonly found in tropical and subtropical regions (Halling *et al*. 2015, Ayala-Vásquez *et al*. 2018, Zeng *et al*. 2018), often growing in association with various tree species. In our study site, *H. retisporus*

BO24642 usually grows on the ground under *Castanopsis buruana* Miq. surrounded by herbs. Previously, Tasuruni (2012) reported that *Heimioporus* sp. from Sumatra were collected near *Tristaniopsis merguensis*. Wu *et al*. (2016) noted that *H. retisporus* was usually scattered on soil in subtropical forests mixed with Pinus and fagaceous plants (*Quercus* spp., *Castanopsis* spp., and *Lithocarpus* spp.), or in subtropical to tropical forests dominated by Fagaceae (*Castanopsis* spp.). In addition, other reports indicate that this mushroom was also usually found on the ground near old stumps or attached to decaying wood (Boedjin 1951, Corner 1972, Watling and Hollands 1990). *Heimioporus* species exist in Indonesia, particularly in the rainforests of Sumatra (Tasuruni 2012, Imanuddin *et al*. 2020, Java Boedjin 1951), and Kalimantan (personal communication). Corner (1972) indicated that *H. retisporus* was common in the lowlands and mountains to 1,300 m a.s.l while Wu *et al*. (2016) obtained the fruiting bodies at 2000 m.a.s.l of alt. The current study is in line with Tasuruni (2012), in which the basidiomata were found in the lowlands (8 and 56 m.a.s.l, respectively).

Earlier studies identified *H. retisporus* as a poisonous mushroom (Chen *et al*. 2014, Tolgor *et al*. 2014), but Zeng *et al*. (2018) found that this species is still being sold as an edible item in Yunnan Province, southwest China. At our study site, *H. retisporus* BO24642 is appreciated for its culinary attributes and gathered by local communities for consumption and trade. The indigenous people of Kendari (Southeast Sulawesi) typically collect this species in February. In the study site, the locals refer to this mushroom as the 'taliku eha-eha' mushroom, which signifies its host plant (*taliku* plant). In the Kendari area, the mushroom is valued at Rp. 40,000/kg or US$ 2.58/kg. The biocultural significance of *H. retisporus* is deeply rooted in the traditions and practices of the *Tolaki* tribe. In Kendari, these mushrooms are not only a source of nutrition but also a part of the cultural heritage, often featured in traditional dishes and local markets. Previous studies have suggested that *Heimioporus*, be cultivated, particularly in the Bangka Belitung region (Putra 2020). However, these efforts have not been successful. Considering the nutritional composition, taste, price, and biotrophic style of this species, the cultivation of *H. retisporus* requires further study and justification in Indonesia.

Author contributions

All the authors contributed equally

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Research permits

No research permit required

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Supplemental data

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