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Five new species of Phylloporus (Boletales: Boletaceae) from dipterocarp forest in East Kalimantan, indonesia

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Five new species of *Phylloporus* (Boletales: Boletaceae) from dipterocarp forest in East Kalimantan, indonesia

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Abstract

Five species of *Phylloporus* from East Kalimantan, Indonesia, are proposed as new species: *P. bangkiraiensis*, *P. fusoidiclavatus*, *P. wainensis*, *P. squamulosus*, and *P. parvicorticola*. Identification was based on morphological characteristics and molecular phylogenetic analyses of DNA sequences from the internal transcribed spacer (ITS) and large subunit (LSU) regions. Phylogenetic analyses of both regions support the placement of these five species within the genus *Phylloporus*. Descriptions, macro- and micro-morphological illustrations, phylogenetic analysis results, and comparisons with closely related species are presented.

Keywords Bangkirai, Basidiomycota, ectomycorrhiza, Samboja, Sungai Wain, taxonomy.

Running head: *Phylloporus* of Indonesia

Introduction

As one of the megadiverse countries, Indonesia is predicted to host 30–35 thousand species of higher plants. This high number of plant species enables the ectomycorrhizal (ECM) fungi to establish mutualistic symbioses with these plants, particularly those in the Dipterocarpaceae, Fagaceae, and Myrtaceae families (Wu et al., 2018; Sato et al., 2024). Fungi involved in ECM associations include a diverse range of species, primarily in Ascomycota and Basidiomycota (Smith & Read, 1997; Ryberg et al., 2022). During the ectomycorrhizal survey in August 2024,

we documented the diversity of ectomycorrhizal fungi and lichens, including the genus *Phylloporus*

Phylloporus Quél. belongs to the family *Boletaceae* and was typified by *P. pelletieri* (Lév.) Quél. The genus is morphologically characterized by its fleshy texture and lamellate hymenophore beneath the cap, rather than pores. This genus is widely distributed globally, especially in tropical and subtropical regions (Neves & Halling, 2010; Chuankid et al., 2019; Montoya et al., 2019). Wijayawardene et al. (2022) estimated that the genus *Phylloporus* contains approximately 90 species; however, subsequent research has reported several additional taxa (Wang et al., 2023; Xue et al., 2023). Corner (1970) recorded 15 *Phylloporus* species from Malaya and Borneo. Meanwhile, Index Fungorum recorded 138 species of *Phylloporus* (https://www.indexfungorum.org, accessed on 15 October 2026).

Neves et al. (2012) and Zeng et al. (2013) considered *Phylloporus* monophyletic, yet it still encompassed both poroid and lamellate taxa. Several studies on the systematics of *Phylloporus* have revealed that some species previously classified under this genus are more closely related to other groups. Therefore, several taxa were proposed to accommodate different genera, such as *Hourangia* (Zhu et al., 2015), *Phylloporopsis* (Farid et al., 2018), and *Erythrophylloporus* (Zhang & Li, 2018).

Two species of Indonesian *Phylloporus*, *P. pumilus* and *P. bogoriensis*, have previously been reported from Java (Neves et al., 2012). *Phylloporus pumilus* was described as a new species based on specimens collected from Haurbentes Park in Java, whereas *P. bogoriensis* was originally described from Bogor Botanical Garden, West Java. The latter species has also been recorded in Selangor, Malaysia. In this study, we identified five additional *Phylloporus* species in East Kalimantan, specifically in Bukit Bangkirai, Sungai Wain, and Samboja. These species were characterized using both morphological and molecular approaches. The findings contribute to a broader understanding of ectomycorrhizal (ECM) biodiversity in Indonesia.

Materials and Methods

Collection sites

The study was conducted at three lowland forest sites in East Kalimantan, Indonesia: Bukit Bangkirai, Sungai Wain Protection Forest, and Samboja Research Forest (Fig. 1). These sites represent a gradient of forest conditions, ranging from relatively intact ecosystems to managed systems. Bukit Bangkirai consists of secondary dipterocarp forest on undulating terrain with well-drained sandy-to-loamy soils, supporting a semi-closed canopy dominated by *Shorea*, *Dipterocarpus*, and *Dryobalanops*. In contrast, Sungai Wain Protection Forest comprises primary and mature secondary stands with minimal disturbance. This site is characterized by highly stratified vegetation, loamy-to-clay-rich soils with high organic matter, and a dipterocarp-dominated canopy with a dense understory under stable humid conditions. Samboja Research Forest exhibits greater structural and compositional heterogeneity, featuring secondary forests, reforested areas, and experimental plots on similar terrain. Its soils range from sandy loam to clay loam, while the vegetation varies from open, pioneer-dominated stands to semi-closed canopies with regenerating and planted tree species.

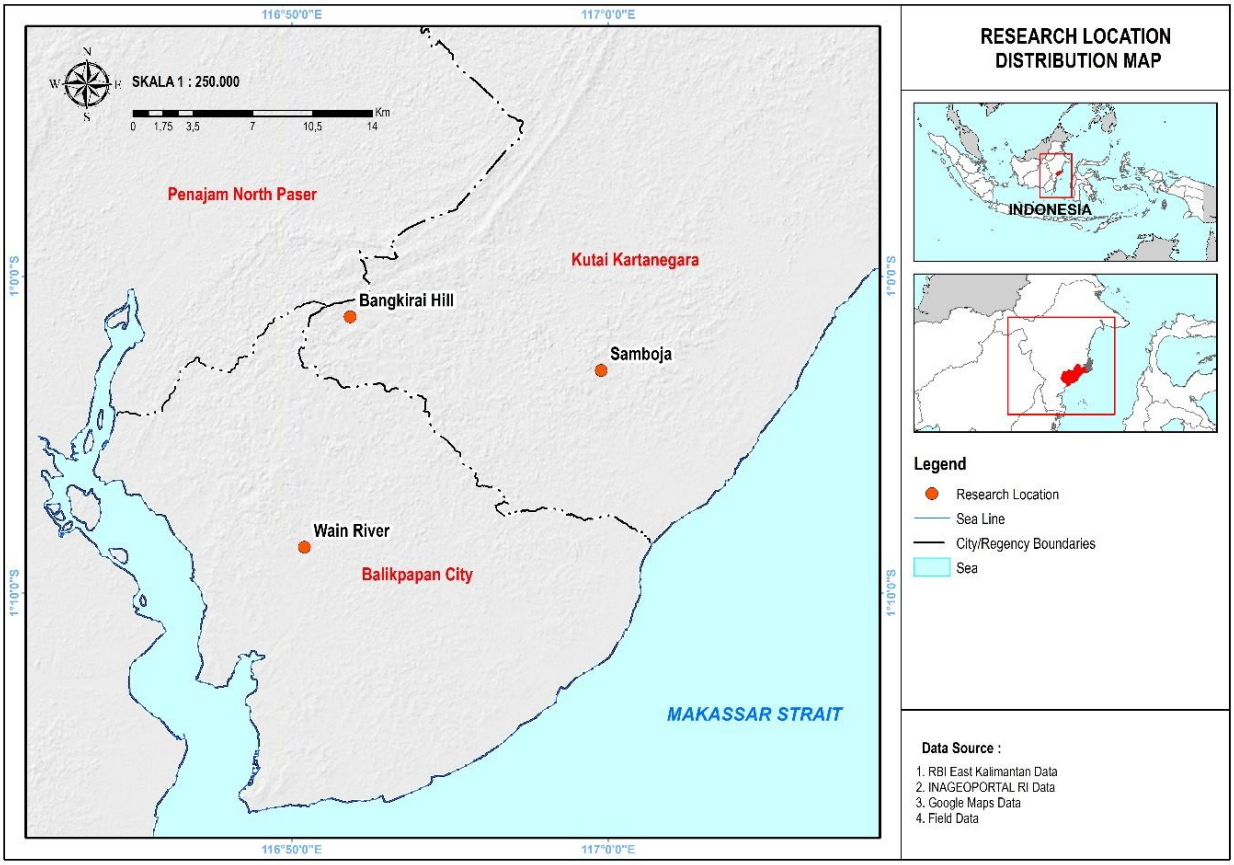


Fig. 1 Map of collection sites where five new species of *Phylloporus* were collected

Morphological study

Phylloporus specimens were photographed in situ in August 2024 at Bukit Bangkirai, East Kalimantan, using a Nikon Coolpix P530 camera. Collection details and macro-morphological features were recorded (Rathnayaka et al., 2025), and specimens were taken to the laboratory in plastic mushroom collection boxes. The specimens were dried in an electric food dehydrator at 40 °C and deposited in the Herbarium Bogoriense (BO), National Research and Innovation Agency of Indonesia (BRIN). Colour codes are from Kornerup and Wanscher (1967). Basidiospores, basidia, basidioles, hymenial cystidia, pileipellis, and caulocystidia were described from dried materials saturated in KOH (5% aqueous solution), Congo Red (5%), or Melzer's reagent. The microscopic study was done using an Olympus CX22LED connected to a computer. The 25 mature basidiospores were measured to obtain the spore range. Basidiospore statistics include: the arithmetic mean of the spore length by spore width (± standard deviation) for n spores measured in a single specimen (x_m); the range of spore means (x_{mr}), and the mean of spore means (± SD) when more than one specimen is available (x_{mm}); the quotient of basidiospore length and basidiospore width in any one basidiospore, indicated as a range of variation in n basidiospores measured (Q); the mean of Q-values in a single specimen (Q_m); the range of Q_m-values where more than one specimen is available (Q_{mr}); and the mean of Q_m-values where more than one

specimen is available (Q_{mm}). Basidiospore and cystidia shapes were observed using a JEOL (JSM-IT200) Scanning Electron Microscope (SEM), National Research and Innovation Agency of Indonesia (BRIN).

Molecular analyses

DNA extraction, PCR amplification, and sequencing

DNA was extracted from voucher specimens using the Geneaid Plant Genomic DNA Extraction Kit, following the manufacturer's protocol. The internal transcribed spacer (ITS) region and the large subunit (LSU) of the ribosomal DNA were amplified using the primer pairs ITS1F/ITS4B (White et al., 1990) and LR0R/LR7 (Gardes & Bruns, 1993), respectively. PCR was performed in a total volume of 35 µL, containing 3 µL of template DNA, 1.5 µL of each primer, and 29 µL of KOD FX Neo (Toyobo).

The PCR thermal cycling conditions for ITS and LSU consisted of an initial denaturation at 95°C for 3 minutes, followed by 35 cycles of denaturation at 95°C for 30 seconds, annealing at 55°C for 30 seconds, and extension at 72°C for 60–90 seconds; a final extension was performed at 72°C for 7 minutes. The resulting PCR products were purified and sequenced at the manufacturing facility of 1st BASE (Selangor, Malaysia, https://base-asia.com/) via PT Genetika Science Indonesia.

Sequence alignment and phylogenetic analyses

A concatenated dataset consisting of ITS and LSU gene regions was assembled for phylogenetic analyses. Raw sequence chromatograms were first examined and edited using BioEdit v.7.0.5.3 (Hall 1990) and were spliced by aligning forward and reverse reads in Geneious 9.1.8 (Kearse et al. 2012). Newly generated sequences were searched in the NCBI GenBank database (http://blast.ncbi.nlm.nih.gov/) using BLAST to determine their closest relatives and confirm preliminary taxonomic placement. Additional reference sequences were selected based on previously published studies and downloaded from GenBank to represent closely related taxa and appropriate outgroups (Das et al. 2024; Gutiérrez-Domínguez et al. 2024) (Table 1). Sequence alignments were compiled in FASTA format and subsequently used for phylogenetic inference. The FASTA alignment was converted into PHYLIP and NEXUS formats using ALTER for Maximum Likelihood (ML) and Bayesian Inference (BI) analyses, respectively (Glez-Peña et al. 2010). Phylogenetic trees were performed through the CIPRES Science Gateway platform. The ML analysis was conducted with RAxML-HPC2 on XSEDE (v.8.2.12) under the GTR+I+G substitution model with 1,000 bootstrap replicates to evaluate branch support (Stamatakis et al. 2008; Stamatakis 2014). The BI analyses were performed with MrBayes on XSEDE (v.3.2.7a) using a Markov Chain Monte Carlo (MCMC) approach to estimate posterior probabilities (Richard and Lippmann 1991). The most appropriate nucleotide substitution model, GTR+G, for ITS and LSU was determined using MrModelTest 2.3 according to the Akaike information criterion (AIC) (Nylander Citation2004). Six independent Markov chains were run simultaneously for 2,000,000 generations, with trees sampled every 100th generation. Convergence of the MCMC chains was assessed based on standard diagnostics, and the first 25% of the sampled trees were discarded as burn-in. The resulting phylogenetic trees were visualized in FigTree v.1.4.2 and further refined using Adobe Illustrator 2019. All sequences newly generated in this study were deposited in the GenBank database. The newly proposed taxa were registered in MycoBank.

Table 1 *Phylloporus* taxa included in this study: voucher, GenBank accession number, and location

Taxa	Voucher	Country	ITS	LSU
Phylloporus alboinfuscatus	FHMU:3276 T	China	MW588663	MW588626
P. alborufus	MAN022 T	Costa Rica	JQ003624	JQ003678
P. attenuatus	HKAS:76168 T	Bangladesh	NR_155651	NG_059569
P. bangkiraiensis	**AR 1782 T**	**Indonesia**	**PZ579742**	**PZ579752**
P. bellus	HKAS:42850	China	JQ967240	JQ967197
P. bellus	HKAS:56763	China	JQ967239	JQ967196
P. bellus	FHMU:3285	China	MW588655	MW588589
P. biyangensis	HMJAU:60058	China	OP391534	OP377733
P. biyangensis	HMJAU:60059 T	China	OP391535	N/A
P. bogoriensis	DED7785	Indonesia	JQ003625	JQ003680
P. bogoriensis	REH8691	Malaysia	JQ003619	N/A
P. brunneiceps	HKAS:56903 T	China	NR_120120	NG_042664
P. caballeroi	REH7906	Panama	JQ003638	JQ003662
P. castanopsidis	NY:1491225 T	Thailand	NR_120024	NG_060095
P. catenulatus	HKAS:76157 T	Bangladesh	NR_155650	NG_059568
P. centroamericanus	MAN043	Costa Rica	JQ003633	N/A
P. centroamericanus	MAN057	Costa Rica	JQ003632	N/A
P. centroamericanus	MAN059	Costa Rica	JQ003631	N/A
P. cyanescens	REH8681	Australia	JQ003621	JQ003684
P. dimorphus	NY:1491201 T	Thailand	NR_120026	NG_060097
P. foliiporus	JLM1677	USA	JQ003641	JQ003687
P. foliiporus	iNAT:86166978	USA	MZ955971	N/A
P. fusoidiclavatus	**AR1878**	**Indonesia**	**PZ579744**	**PZ579754**
P. fusoidiclavatus	**AR1917 T**	**Indonesia**	**PZ579748**	**PZ579758**
P. gajari	AG 20-003	India	OP550185	OP550198
P. gajari	HKAS:81585 T	Bangladesh	NR_155649	NG_059562
P. grossus	FHMU:3277 T	China	MW588662	MW588625
P. hainanensis	FHMU:1718	China	MW588632	MW588581
P. himalayanus	KD 23-046 T	India	OR665532	OR663998
P. himalayanus	KD 23-047	India	OR665533	OR663999
P. imbricatus	HKAS:54647 T	China	JQ967245	NG_059475
P. infuscatus	MAN123 T	Thailand	N/A	JQ003695
P. leucomycelinus	CNV80	USA	MT345256	N/A
P. leucomycelinus	MB00-43	USA	JQ003628	JQ003677
P. leucomycelinus	MB05-007	USA	JQ003653	JQ003666
P. luxiensis	HKAS:57036	China	JQ967250	JQ967207
P. luxiensis	HKAS:57037	China	JQ967251	JQ967208
P. luxiensis	HKAS:57048	China	JQ967252	JQ967209
P. maculatus	HKAS:56683 T	China	NR_120121	NG_042665
P. microsquamus	FHMU:1678 T	China	MW588648	NG_088206
P. montanus	Gutiérrez62	Mexico	PP359574	PP731536
P. montanus	Gutiérrez88	Mexico	PP359572	PP354877
P. montanus	Gutiérrez94 T	Mexico	PP359573	PP354878
P. nigrisquamus	FHMU:3271 T	China	N/A	NG_088205
P. nigrobrunneus	FHMU:3268 T	China	MW588638	NG_088207
P. orientalis	REH8755	Australia	JQ003651	JQ003701

P. orientalis	REH8756	Australia	JQ003652	JQ003709
P. pachycystidiatus	HKAS:54540 T	China	NR_120122	NG_042666
P. parvicorticola	**AR1907 T**	**Indonesia**	**PZ579746**	**PZ579756**
P. parvicorticola	**AR1908**	**Indonesia**	**PZ579750**	**PZ579759**
P. parvicorticola	**AR1909**	**Indonesia**	**PZ579747**	**PZ579757**
P. parvisporus	HKAS:54768	China	JQ967257	JQ967214
P. parvisporus	HKAS:59725	China	JQ967256	JQ967213
P. pelletieri	K(M)191952	United Kingdom	MZ159513	N/A
P. pelletieri	K(M)128205	United Kingdom	JQ967258	KC215221
P. pelletieri	Pp1	Germany	DQ534566	AF456818
P. pruinatus	HKAS:101929 T	China	MH624124	MH624125
P. purpurellus	MAN050	Costa Rica	JQ003630	JQ003672
P. pusillus	CMUB: OR1310 T	Thailand	NR_173794	N/A
P. quercophilus	Montoya 5239 T	Mexico	MK226550	NG_068866
P. rhodoxanthus	BD374	USA	JN021070	HQ161851
P. rhodoxanthus	JLM1808	USA	JQ003654	JQ003688
P. rhodoxanthus	REH8714	USA	JQ003629	JQ003675
P. rimosus	XAL Montoya 4834 T	Mexico	NR_164045	NG_068865
P. rimosus	ECM-DREC130B	Mexico	OP555737	OR413509
P. rubeolus	HKAS:52573 T	China	NR_120123	NG_042667
P. rubiginosus	NY:1491248 T	Thailand	NR_120025	NG_060096
P. rubrosquamosus	HKAS:54559 T	China	NR_120124	NG_042668
P. rufescens	HKAS:59722	China	JQ967263	JQ967220
P. rufescens	HKAS:59723	China	JQ967264	JQ967221
P. rufescens	FHMU:1227	China	MW588645	
P. scabripes	CfMR:BZ-3252 TJB-9709 T	Belize	MN250204	NG_078679
P. septocystidiatus	TBGT:14204 No. K(M) T	India	KP789659	N/A
P. smithii	KD 23-012 T	India	OR656501	OR656502
P. smithii	KD 23-022	India	OR656500	OR656503
Phylloporus sp.	ECM-DREC117F	Mexico	OP555738	OR413510
P. squamulosus	**AR1773 T**	**Indonesia**	**PZ579741**	**PZ579751**
P. squamulosus	**AR1861**	**Indonesia**	**PZ579743**	**PZ579753**
P. squamulosus	**AR1900**	**Indonesia**	**PZ579745**	**PZ579755**
P. subbacillisporus	HMAS:279879 T	China	NR_173793	N/A
P. subrubeolus	FHMU:3274	China	MW588661	MW588623
P. subrubeolus	FHMU:3273	China	MW588664	MW588627
P. subrubeolus	OR0612	Thailand	MH686276	N/A
P. tenuissimus	FHMU:2964 T	China	MW588646	MW588593
P. wainensis	**AR1891 T**	**Indonesia**	**PZ579749**	**N/A**
P. xalapensis	Gutiérrez49	Mexico	PP359576	PP354880
P. xalapensis	Gutiérrez46	Mexico	PP359575	PP354879
P. xalapensis	Gutiérrez84 T	Mexico	PP359581	PP354885
P. yunnanensis	HKAS:56999 T	China	JQ967267	NG_059476

Xerocomus magniporus	HKAS:59820	China	JQ678697	JQ678699
X. perplexus	MB00-005	USA	JQ003657	JQ003702

Note: Information about the *Phylloporus* specimens and published *Phylloporus* sequences used in phylogenetic analysis. Vouchers with a "T" are those from holotype material; sequences newly produced in this study are presented in bold, and N/A refers to data unavailability.

Results

Phylogenetic analyses

The topologies inferred from Maximum Likelihood and Bayesian Inference analyses were largely congruent, and therefore only the ML tree is presented (Fig. 2). The combined ITS and LSU alignment included 60 taxa and contained a total of 1,764 aligned nucleotide positions, including gaps (ITS: 719 and LSU: 1045). Our newly collected specimens, *Phylloporus bangkiraiensis* (AR1782, holotype), formed a well-supported clade that is clearly distinct from *P. novae-zelandiae* (JAC13406 and JAC13407) and several undescribed *Phylloporus* species, with strong statistical support (100% BS/1 PP). *Phylloporus parvicorticola* (AR1907 holotype, AR1908, and AR1909) resolved as an independent lineage closely related to *P. attenuates* (HKAS:76168, holotype), supported by 95% BS/0.98 PP. In addition, the specimens representing *P. fusoidiclavatus* (AR1917, holotype, and AR1878) clustered together and formed a distinct monophyletic lineage with strong statistical support (100% BS / 1.00 PP). This clade was resolved as an independent lineage within the *Phylloporus* clade and was clearly separated from the closely related species, including *P. tenuissimus* (FHMU:2964 holotype) and *P. gajari* (AG 20-003 and HKAS:81585 holotype). *Phylloporus wainensis* (AR1891, holotype) was recovered as a separate lineage sister to the *P. squamulosus* (AR1900 holotype, AR1773, and AR1861) clade with strong support (100% BS / 1.00 PP), and together they formed a lineage sister to *P. fusoidiclavatus* with strong support (96% BS). These phylogenetic results clearly indicate that *P. fusoidiclavatus*, *Phylloporus wainensis*, and *P. squamulosus* represent three distinct species within *Phylloporus*.

Taxonomic treatment

Phylloporus bangkiraiensis Retn. & W.H. Lu, sp. nov.
MycoBank no.: 864496.
Figures 3, 4, 14A–B

Etymology: *bangkiraiensis* refers to the type locality, Bukit Bangkirai.

Diagnosis: The new species is distinguished by a combination of features, including a convex to plano-convex, light brown pileus, absence of blue staining when bruised, a thin white basal tomentum, oblong or ovoid basidiospores, ventricose-rostrate to digitate cheilocystidia and pleurocystidia, and a trichoderm pileipellis composed of chains of cylindrical elements. *Phylloporus bangkiraiensis* is closely related to *P. novae-zelandicae;* both species share similar pleurocystidia morphology and size, pileipellis type, absence of clamp connections, and comparable growth habits. However, the species differ in pileus diameter and basidiospore size.

Holotype: INDONESIA, East Kalimantan, Bukit Bangkirai, 13 August 2024, A. Retnowati 1782 (Holotype, BO-2006087), collected by the Ectomycorrhizal research team. GenBank: ITS-PZ579742, LSU-PZ579752.

Description: Pileus 1.8–4.2 cm diam., convex to plano-convex in age, dry, pruinose, light brown (7D4) with slightly darker at center, staining absent. Context ochraceous brown, thick. Hymenophore lamellate, lamellae decurrent, subdistant, 2–3 lamellulae, greyish yellow (2B4) at

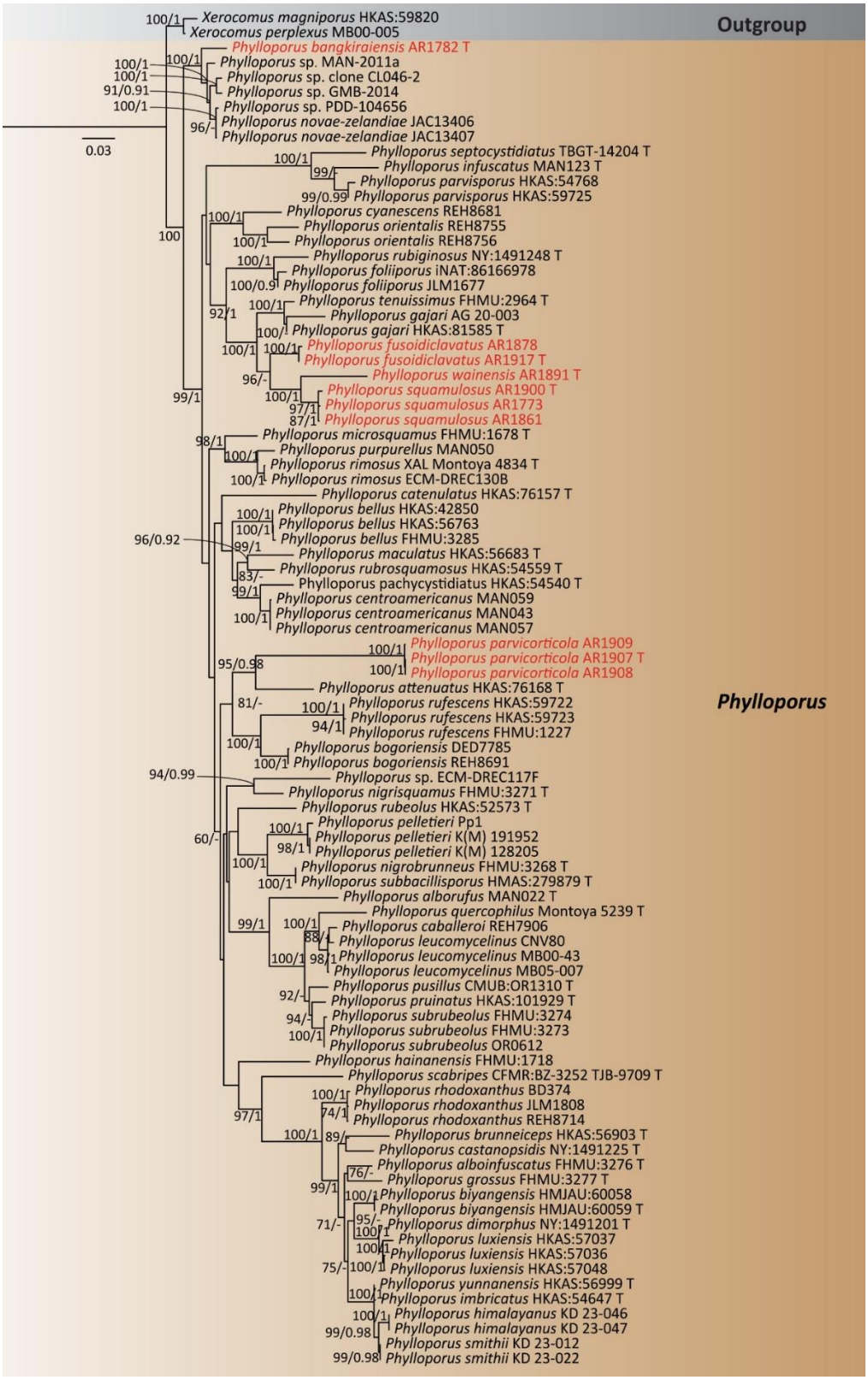


Fig. 2 The maximum likelihood (ML) of the combined data set of ITS and LSU of *Phylloporus* species was used to build the phylogenetic tree. At each node, there are values for the maximum-likelihood bootstrap support (BS)⩾60% and the Bayesian posterior probability (PP)≥0.90. The newly discovered strains are displayed in red on the tree, which was rooted to *Xerocomus magniporus* (HKAS:59820) and *X. perplexus* (MB00-005). Holotypes are denoted by T.

first, then paler in age, staining light blue absent. Stipe 2.1–3.2 cm, equal, dry, pruinose, reddish-brown at the top, paler at the base, white, thin, basal tomentose absent.

Basidiospores x = 7–10.7 × 4–4.9(–5.8) µm (x_m = 8.2 ± 1 × 4.4 ± 0.4; Q = 1.6–2.3; Q_m = 1.9 ± 0.2; 25 spores per specimen), oblong or ovoid, smooth, inamyloid, ochraceous/olive in KOH in mass. Basidia 30.3–33 × 7.68–9.30 µm, clavate, 4-spored. Cheilocystidia 42.4–69.8 × 10–19 µm, common, ventricose-rostrate to digitate, pigment absent. Pleurocystidia common, 53–66.5 × 10–18.9 µm, hyaline to yellowish-brown, slightly thick-walled, ventricose-rostrate to digitate, pigment absent. Pileipellis a trichoderm type, composed of chains of cylindrical elements, 19.9–39 µm, inamyloid, yellowish in KOH. Pileus trama interwoven; hyphae 4.3–10.5 µm broad, cylindrical, thin-walled, hyaline. Stipe hyphae monomitic, 4.5–10 µm; cylindrical, parallel, hyaline. Caulocystidia uncommon, 15–53 × 6.7–16 µm, cylindrical to clavate, thin-walled, hyaline. Clamp connection absent.

Distribution: Indonesia (Bukit Bangkirai, East Kalimantan)

Habit and habitat: Gregarious or caespitose on soil

Mycorrhizal host: *Shorea* sp.

Notes. Phylloporus bangkiraiensis can be identified by its convex to plano-convex, light brown pileus, lack of blue staining when bruised, sub-lageniform cheilocystidia and pleurocystidia, and a trichoderm pileipellis consisting of chains of cylindrical elements.

Phylogenetic analysis places this species in a clade with *P. novae-zelandicae* and several undescribed *Phylloporus* species (MAN 2011a, CL046-2, GMB 2014, and PDD 104656). Although *Phylloporus novae-zelandiae,* which is native to New Zealand, is morphologically similar to *P. bangkiraiensis,* it can be distinguished by its larger pileus (2.5–9.5 cm in diameter) and larger basidiospores (9–13 × 3.8–4.5 µm). *Phylloporus bangkiraiensis* occurs in forests dominated by *Shorea* species, while *P. novae-zelandicae* is associated with *Nothofagus* trees (McNabb, 1971).

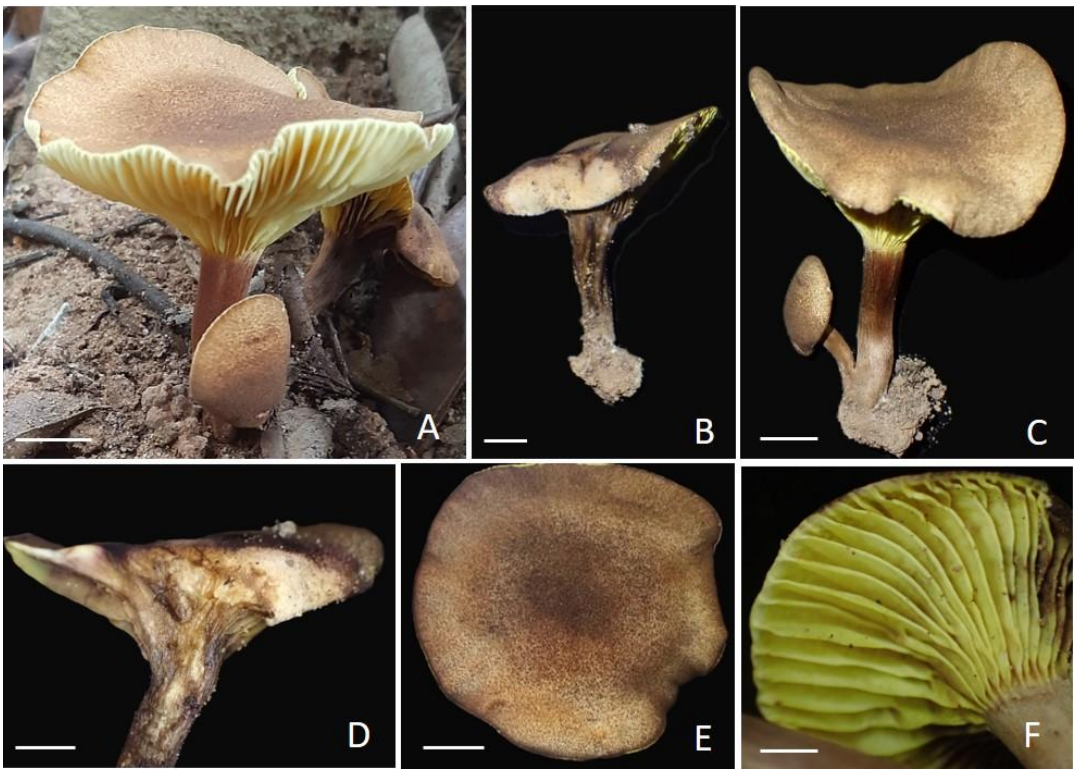


Fig. 3 Fresh basidiomata of *Phylloporus bangkiraiensis* (holotype, A. Retnowati 1782). **A–C** Pileus on immature and mature basidiomata. **D** Context. **E** Surface of the pileus. **E** Greyish-yellow lamellae. Scale bars: **A – F** = 1 cm.

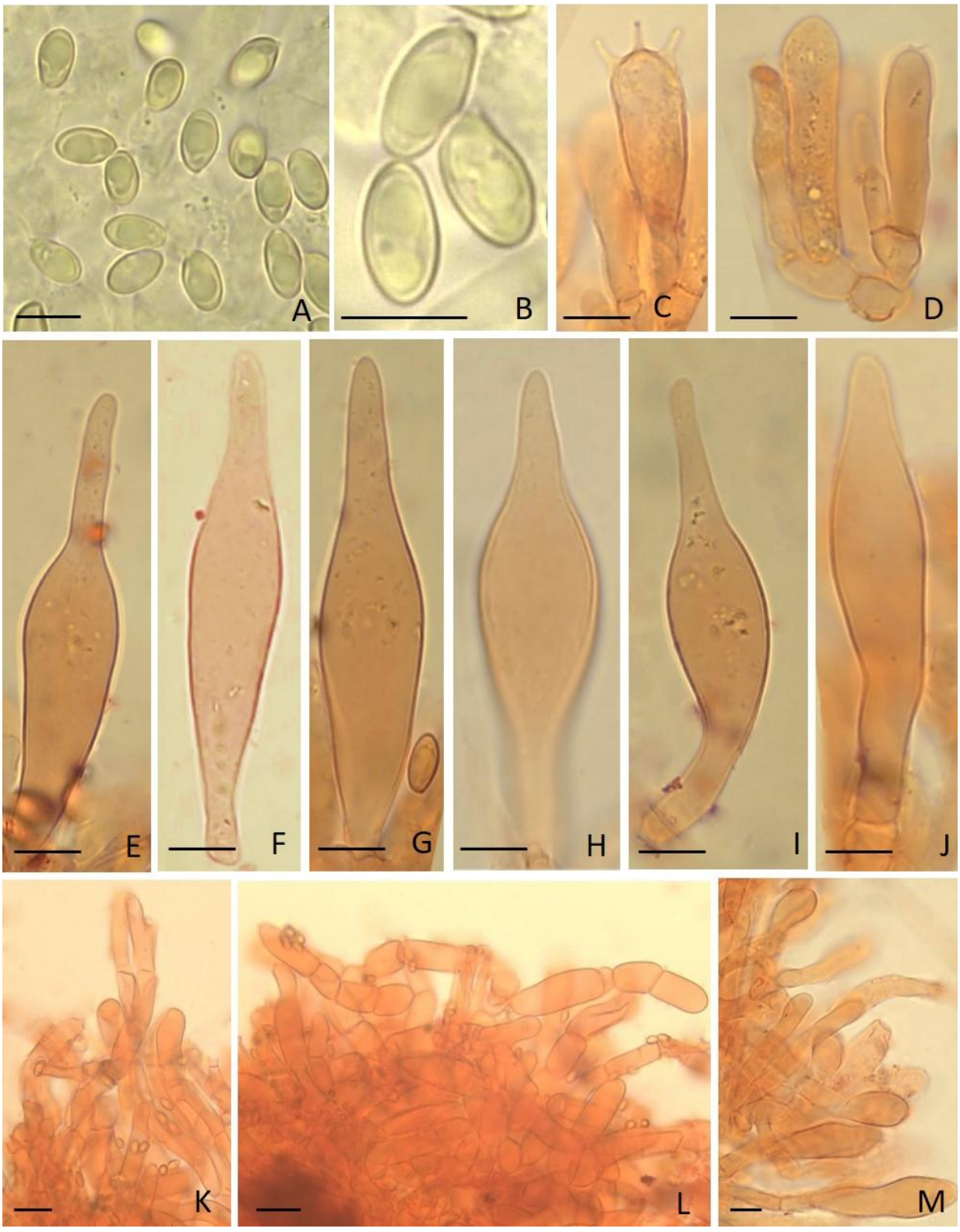


Fig. 4 Microscopic characteristics of *Phylloporus bangkiraiensis* (holotype A. Retnowati 1782). **A–B** Basidiospores. **C** Basidium. **D** Basidioles. **E–G** Cheilocystidia. **H–J** Pleurocystidia. **K–L** Pileipellis. **M** Caulocystidia. Scale bars: **A–M** = 10 µm.

Phylloporus fusoidiclavatus Retn. & W.H. Lu, sp. nov.
MycoBank no.: 864497.
Figs. 5, 6, 14C–D.

Etymology: *fusoidiclavatus* refers to the distinct shapes of the cheilocystidia, ranging from fusoid to clavate.

Diagnosis: The species can be distinguished from other *Phylloporus* species by its initial brownish-grey coloration (5E2), which gradually transitions to yellowish brown (5E5) and eventually to light brown (5D5), as well as by its closed lamellae, larger basidiospores, and smaller cheilocystidia and pleurocystidia. *Phylloporus gajari* and *P. tenuissimus* are closely related to the new species, sharing similar pileus coloration, bluish tissue upon injury, a hairy stipe, and the presence of cheilocystidia, pleurocystidia, and caulocystidia. However, these species differ in lamellar spacing, basidiospore size, and growth habit.

Holotype: Indonesia, East Kalimantan, Sungai Wain, Medium Track, 19 January 2025, A. Retnowati 1917 (Holotype: BO-2006095), GenBank: ITS-PZ579748, LSU-PZ579758.

Description: Basidiomata small to large–sized. Pileus 0.5–4.5 cm diam., convex to plane–convex at first, then depressed at center or even infundibuliform in age; surface dry, velvety; margin inrolled, at first brownish grey (5F2), gradually becomes yellowish brown (5E5), eventually light brown (5D5). Context thick, white, weakly bluish when bruised. Lamellae decurrent at first, then decurrent in age, closed (32–40 attached) with 2 series of lamellulae, not intervenose, bluish when bruised, olive yellow (3C8). Stipe 1–4 × 0.4–0.9 cm, central, cylindrical, solid; surface dull, dry, covered by thin fibrillose hair, greyish yellow (3B5), thin, white tomentose.

Basidiospores x = 10.22–13.1 × 4.33–5.79 µm (x_{mr}= 11.3–11.7 × 5.3–6.3–8.0, x_{mm}= 12.73 ± 0.3 × 7.69 ±0.3, Q= 1.9–2.7, Q_{mr}= 2.12–2.14, Q_{mm}= 2.13±0.02, 25 spores per specimen), lacrymoid to subfusoid, smooth, inamyloid, golden yellow in KOH. Basidia unobserved. Basidioles 21.05–25.07 × 5.97–7.66 µm, clavate. Cheilocystidia common, 70.92–111.30 × 12.80–26.66 µm, broadly fusoid to clavate, thin-walled, yellowish white. Pleurocystidia common, 68.37–91.71 × 11.5–14.39 µm, fusoid to clavate, slightly thick-walled, yellowish white. Pileipellis a trichoderm element, vertically arranged, 2–3 cells; terminal cells 33.74–51.45 × 12.01–15.86 µm, clavate to broadly clavate, thin-walled, some granular content present, no cell wall incrustation, yellowish white. Pileal trama interwoven, hyphae 4.8–7.2 µm, thin-walled, cylindrical, hyaline to yellowish brown. Caulocystidia common, 22.50–39.90 × 10.93–12.42 µm, clavate to broadly clavate, thin-walled, hyaline to pale yellowish brown. Stipe hyphae monomitic; hyphae 4.7–8.32 µm, cylindrical, parallel, yellowish brown. Clamp connection rare; 2 clamps observed in stipe tissue.

Distribution: Indonesia (Samboja and Sungai Wain, East Kalimantan)

Habit and habitat: Gregarious or caespitose on soil

Mycorrhizal host: *Shorea* sp.

Material examined: Indonesia, East Kalimantan, primary forest at Samboja, 17 January 2025, A. Retnowati 1878 (BO-2006089); GenBank: ITS-PZ579744; LSU-PZ579754.

Notes: Phylogenetic analysis indicates that *P. fusoidiclavatus* is closely related to *P. gajari* and *P. tenussimus*. *Phylloporus gajari,* originally described from Bangladesh (Hosen & Li 2015), can be distinguished by its brownish red to reddish brown pileus in immature specimens, which transitions to yellowish brown or pale yellow-brown with age, as well as a brownish red to reddish brown stipe and comparatively smaller basidiospores, cheilocystidia, and pleurocystidia. In contrast, *Phylloporus tenussimus* has small basidiomata (23 cm in diameter), a pileus covered with pale brown to brown (5C6) squamules, anastomosing lamellae, small cheilocystidia and pleurocystidia, and notably large caulocystidia.



Fig. 5 Basidiomata of *Phylloporus fusoidiclavatus* (holotype, A. Retnowati 1917). **A** Basidiomata in situ habitat. **B–C** Morphological features. **D–E** Olive-yellow lamellae with a bluish color. Scale bars: **A–F** = 1 cm

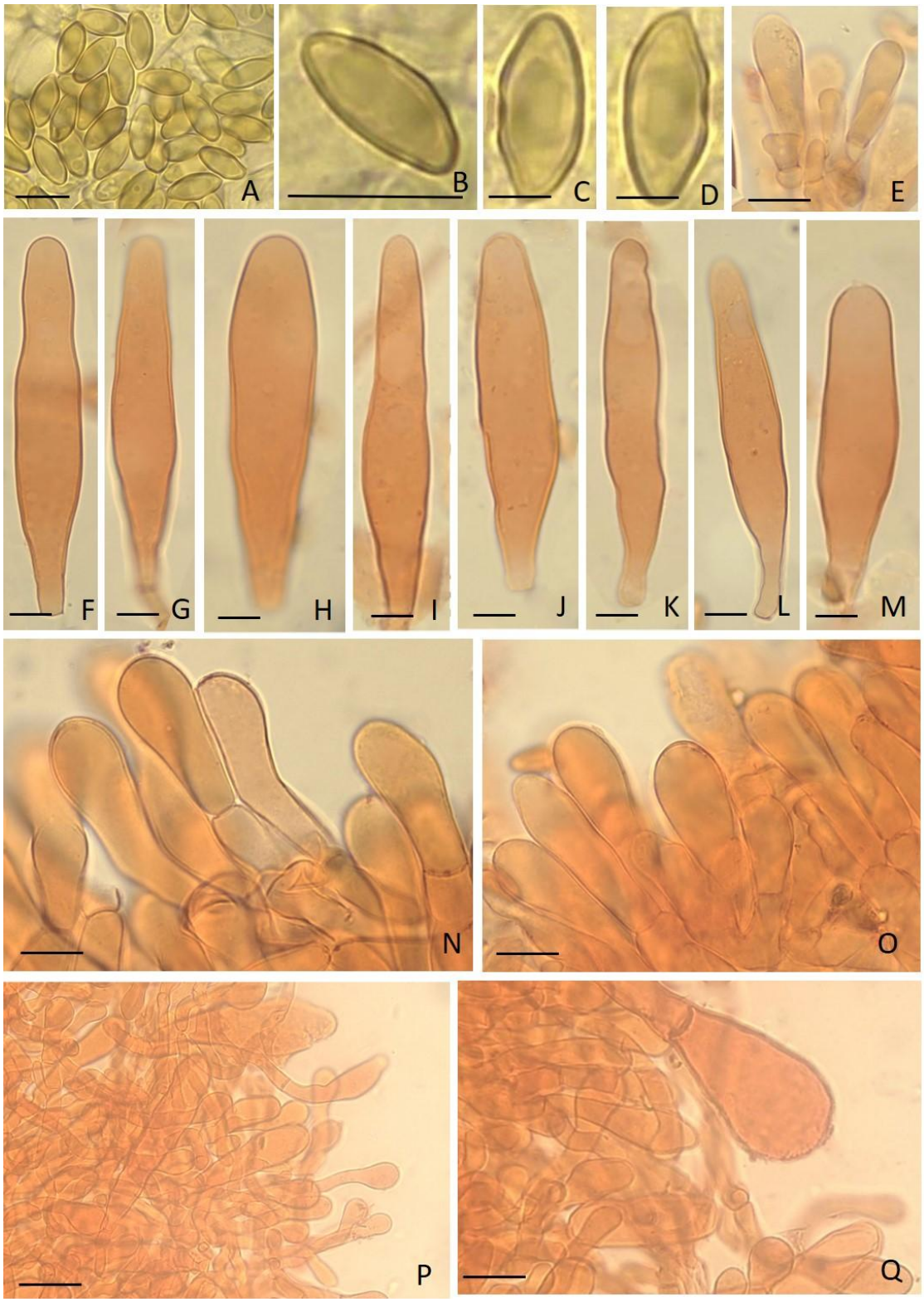


Fig. 6 Microscopic characteristics of *Phylloporus fusoidiclavatus* (holotype, A. Retnowati 1917): **A–D** Basidiospores. **E** Basidioles. **F–I** Cheilocystidia. **J–M** Pleurocystidia. **N–O** Pileipellis. **P–Q.** Caulocystidia. Scale bars: **A–B** = 10 µm, **C–D** = 4 µm, **E–Q** = 10 µm

Phylloporus wainensis Retn. & W.H. Lu, sp. nov.
MycoBank no.: 864498.
Figures 7, 8, 14E–F.

Etymology: *wainensis* refers to the type locality Sungai Wain.

Diagnosis: *Phylloporus wainensis* differs from other *Phylloporus* by sub-decurrent lamellae with 1–3 series of lamellulae, a slightly eccentric to central stipe, smaller basidiospores, the presence of cheilocystidia, pleurocystidia, and caulocystidia, a trichoderm pileipellis with 2–3 cells, and cylindrical terminal cells. Phylogenetically, *P. wainensis* is closely related to *P. squamulosus*, which is also described in this paper. However, morphologically these species differ in pileus size and shape, basidiospore size, the number of chains in the pileipellis, and caulocystidia shape.

Holotype: Indonesia, East Kalimantan, forest at Sungai Wain, second track, ecotourism trail, 18 January 2025, A. Retnowati 1891 (Holotype: BO-2006090). GenBank: ITS-PZ579749.

Description: Basidiomata medium-sized. Pileus 1.3–5 cm diam., cup-shaped pileus at first, then becoming plano-convex with depressed center in age; surface dry, sub-tomentose; margin straight when young, then slightly uplifted in age; dark brown (6F8) at first, then a reddish grey (7B2), covered by thin dark brown scales (6F8) in age. Context thick, white, slightly turning blue when cut. Lamellae sub-decurrent, distant (20–24 attached), 1–3 series of lamellulae, not intervenose, bluish when injured, yellow (3B8). Stipe 1.3–3.4 × 0.5–1 cm, slightly eccentric to central, cylindrical; surface dry, concolorous to pileus. Base tomentose, thin-white.

Basidiospores 11.6–13.8 × 4.2–5.2 µm (x_m = 12.74 ± 0.53 × 4.59 ± 0.26; Q = 2.38–3.08; Q_m = 2.78 ± 0.18, 25 spores per specimen), fusoid to subfusoid, smooth, inamyloid, golden yellow in KOH. Basidia 25.4–36.4 × 8.5–9.7 µm, 4-spored, clavate; Basidioles 22.6–26.8 × 6–9.6 µm, clavate. Cheilocystidia common, 69.3–94 × 14.9–18.4 µm, broadly fusoid to sub-clavate, or clavate, thin-walled, yellowish-white. Pleurocystidia common, 54.5–100.1 × 8.8–15.4 µm, narrowly fusoid to clavate, slightly thick-walled, yellowish white. Pileipellis a trichoderm element, vertically arranged of 2–3 cells; terminal cells 39.9–72.8 × 8.2–14.7 µm, cylindrical, thin-walled, no cell wall incrustation, smooth, yellowish white. Pileal trama interwoven, hyphae 8.7–14.3 µm, thin-walled, cylindrical, hyaline to yellowish brown. Stipe tissue monomitic; hyphae 5.2–15 µm, parallel, cylindrical, thin-walled, hyaline to greyish brown. Caulocystidia common; 29.5-60.6 × 9.8-13.5 µm, cylindrical, clavate to broadly clavate, thin-walled, yellowish brown. Clamp connection absent.

Habit and habitat: Gregarious or caespitose on soil.

Distribution: Indonesia (East Kalimantan).

Mycorrhizal host: Dipterocarpaceae forest.

Notes: *Phyloporus wainensis* is distinguished by a medium-sized, cup-shaped pileus that flattens and develops a depressed center with maturity. The cap exhibits a color transition from dark brown to reddish-grey and is covered with thin scales. The thick white flesh and yellow gills characteristically turn blue when cut or injured. The cylindrical stem, similar in color to the cap, has a white, fuzzy base. Microscopically, this species is identified by smooth, spindle-shaped spores that appear golden yellow in potassium hydroxide (KOH) and by thin-walled, yellowish-white cystidia. The hyphae lack clamp connections.



Fig. 7 *Phylloporus wainensis* (holotype, A. Retnowati 1891). **A–D** Basidiomata. Scale bars: **A** = 10 cm, **B–D** = 8 cm

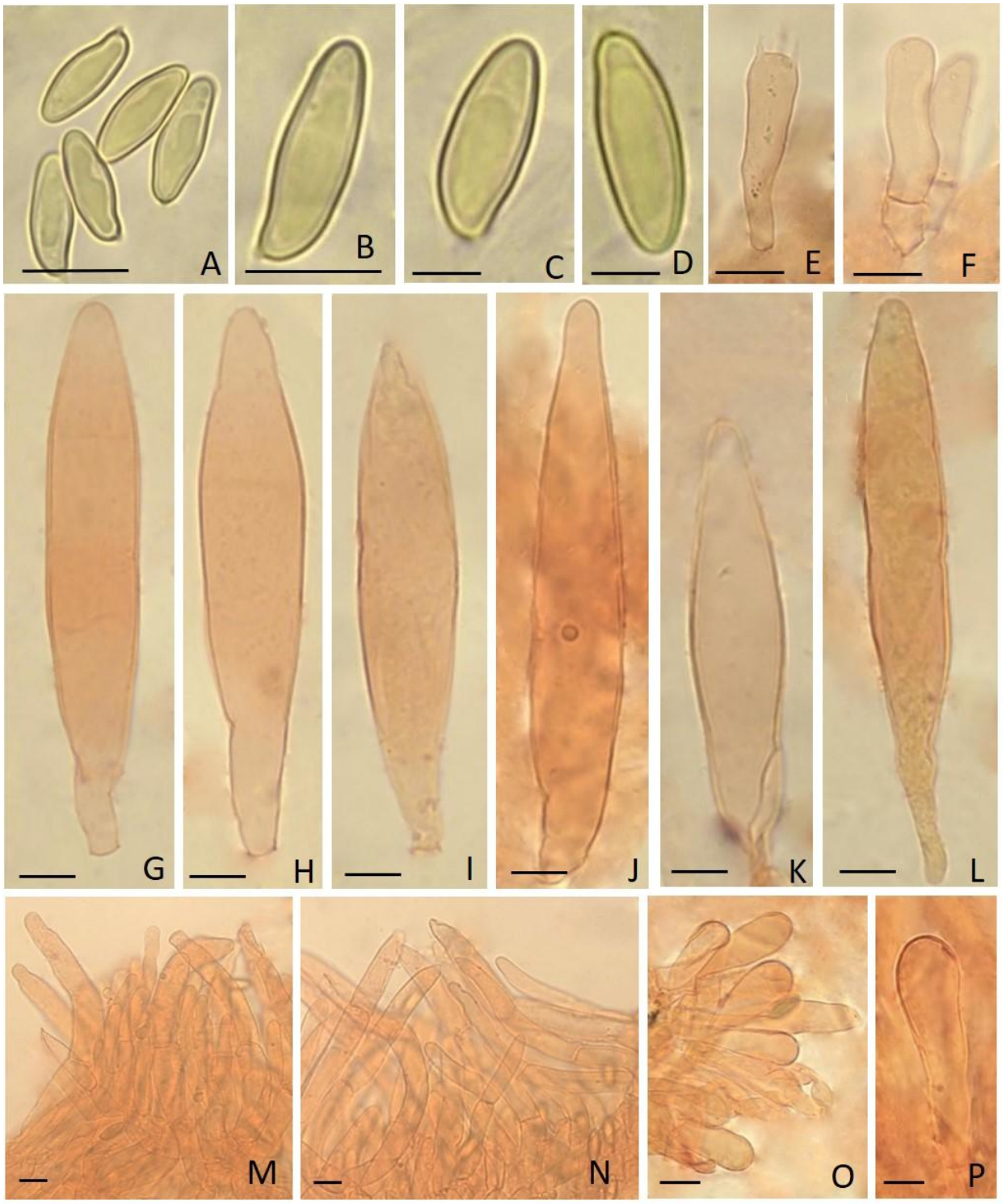


Fig. 8 Microscopic characteristics of *Phylloporus wainensis* (holotype, A. Retnowati 1891). **A–D** Basidiospores. **E** Basidia. **F** Basidioles. **G–I** Cheilocystidia. **J–L** Pleurocystidia. **M–N** Pileipellis. **O–P** Caulocystidia. Scale bars: **A–L** = 10 µm, **M–N** = 20 µm, **O–P** = 10 µm.

Phylloporus squamulosus Retn. & W.H. Lu, sp. nov.
MycoBank no.: 864499.
Figures 9, 10, 14G–H.

Etymology: *squamulosus* refers to the description of the pileus surface texture that is covered with very small scales (= squamulose).

Diagnosis: *Phylloporus squamulosus* is distinguished from other *Phylloporus* by having a medium-sized, dark brown pileus that forms a flat-convex shape to a deep, funnel-like form as it matures. Lamellae are yellow and stain blue when injured. The pileipellis is composed of vertical chains of cells that are encrusted and colorless to yellowish-brown.

Holotype: Indonesia, East Kalimantan, Bukit Bangkirai, on soil, 13 August 2024, A. Retnowati 1773 (Holotype: BO-2006086). GenBank*:* ITS PZ579741, LSU PZ579751.

Basidiomata medium-sized. Pileus 2.6–4.6 cm in diameter, plano-convex with slightly depressed centre when young, becomes depressed to an infundibulum; surface dry, velvety, distinctly cracked, sub-tomentose to squamulose, dark brown with white underneath. Lamellae subdecurrent, subdistant (20–24 attached), 2–3 series of lamellulae, anastomosing absent or present, staining blue when injured, broad, thick, yellow. Stipe 2.1–3.5 × 0.4–0.6 cm, central, cylindrical, curved, glabrous with some pruinose at the apex, dark brown. Basal tomentose white, thin.

Basidiospores 12.01–16.77(17.06) × 3.55–5.66 µm (x_m = 14 ± 1.53 × 4.75± 0.53, Q = 2.25–3.74, Q_m = 2.98 ± 0.40, 25 spores per specimen), subfusoid, smooth, in KOH greenish. Basidia 31.5–42 × 8.4–9.3 µm, clavate, 4-spored, long sterigmata up to 6.5 µm. Basidioles 31.1–33.8 × 7.1–8.4 µm, clavate. Cheilocystidia 53.20–59.1 × 10.1–15.3 µm, subclavate to fusiform, thin–walled, hyaline. Pleurocystidia common, 51.5–79 × 12.5–16.2 µm, subclavate to fusiform, slightly thick-walled, hyaline. Pileipellis composed of trichoderm, some intercalary terminal cells, composed of short chains of 3–5 cells; terminal cells 31.3–48.3 × 7.2–12.5 µm, subcylindrical, clavate, ventricose-rostate to digitate, thin–walled to some thick-walled, incrusted, hyaline to yellowish brown. Pileal tramal interwoven; hyphae 3.1–8.6 µm, thin–walled, hyaline to pale yellowish brown. Stipe monomitic, hyphae 3.9–14.6 µm diam., parallel, cylindrical, hyaline. Caulocystidia uncommon, 39.9–47.2 × 10.2–12.8 µm, clavate, thin-walled. Clamp connection absent.

Habit and habitat. Gregarious on soil.

Distribution. Indonesia (East Kalimantan).

Host. Dipterocarpaceae forest.

Material examined. Samboja, primary forest, 17 January 2025, A. Retnowati 1861 (BO-2006088); Sungai Wain, eco-tourism trail, 18 January 2025, A. Retnowati 1900 (BO-2006091). GenBank: AR 1861: ITS-PZ579743, LSU-PZ579753; AR 1900: ITS-PZ579745, LSU-PZ579755

Notes: Specimens of *Phylloporus squamulosus* were collected from three locations in East Kalimantan: Bukit Bangkirai, Samboja, and Sungai Wain. Although all collections fall within the same clade, they show distinct morphological differences. The Bukit Bangkirai collection (AR 1773) is characterized by immature, dark brown fruiting bodies that are sub-tomentose to squamulose, with a white context that turns bluish when bruised. In contrast, the collections from Samboja and Sungai Wain do not exhibit this bluish reaction but display clearly anastomosing lamellae, or interconnected gills.

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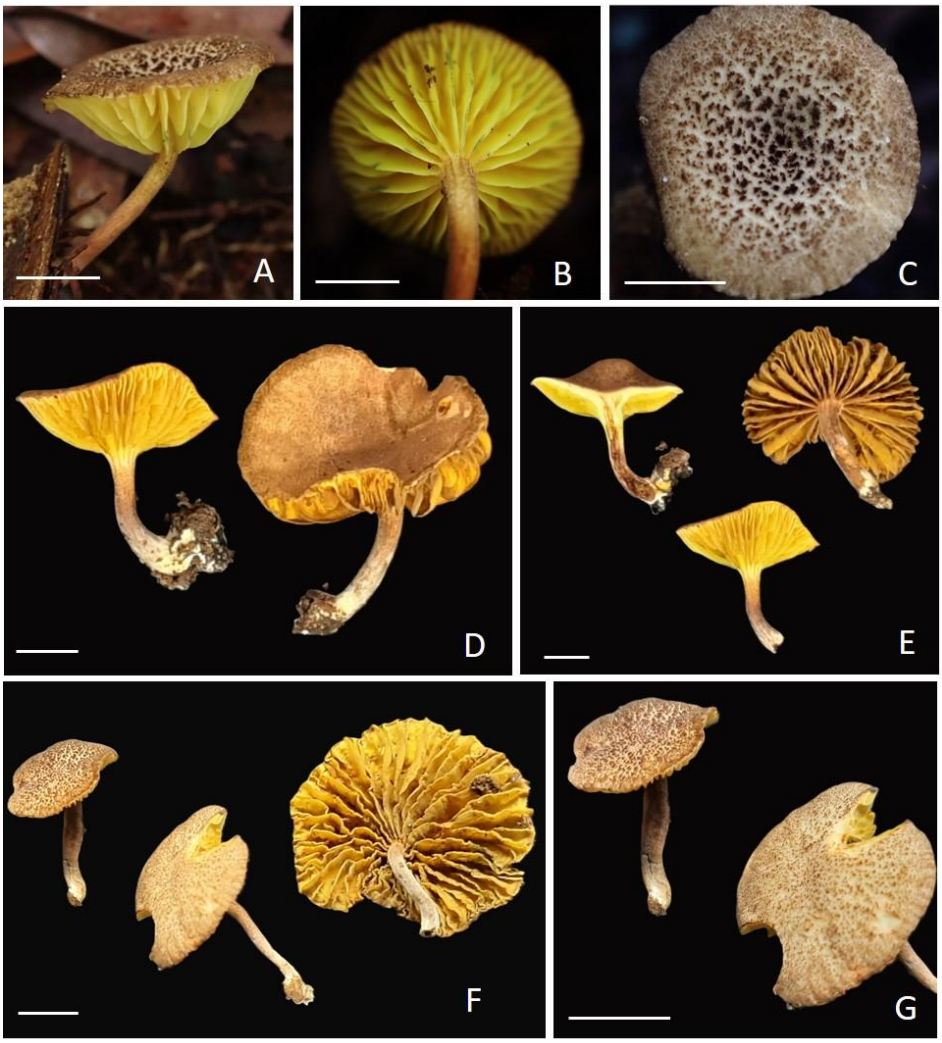


Fig. 9 Basidiomata of *Phylloporus squamulosus*. **A–C** Collection AR 1773. **D–E** Collection AR 1861. **F–G** Collection AR 1900. Scale bars: **A–G** = 1 cm.

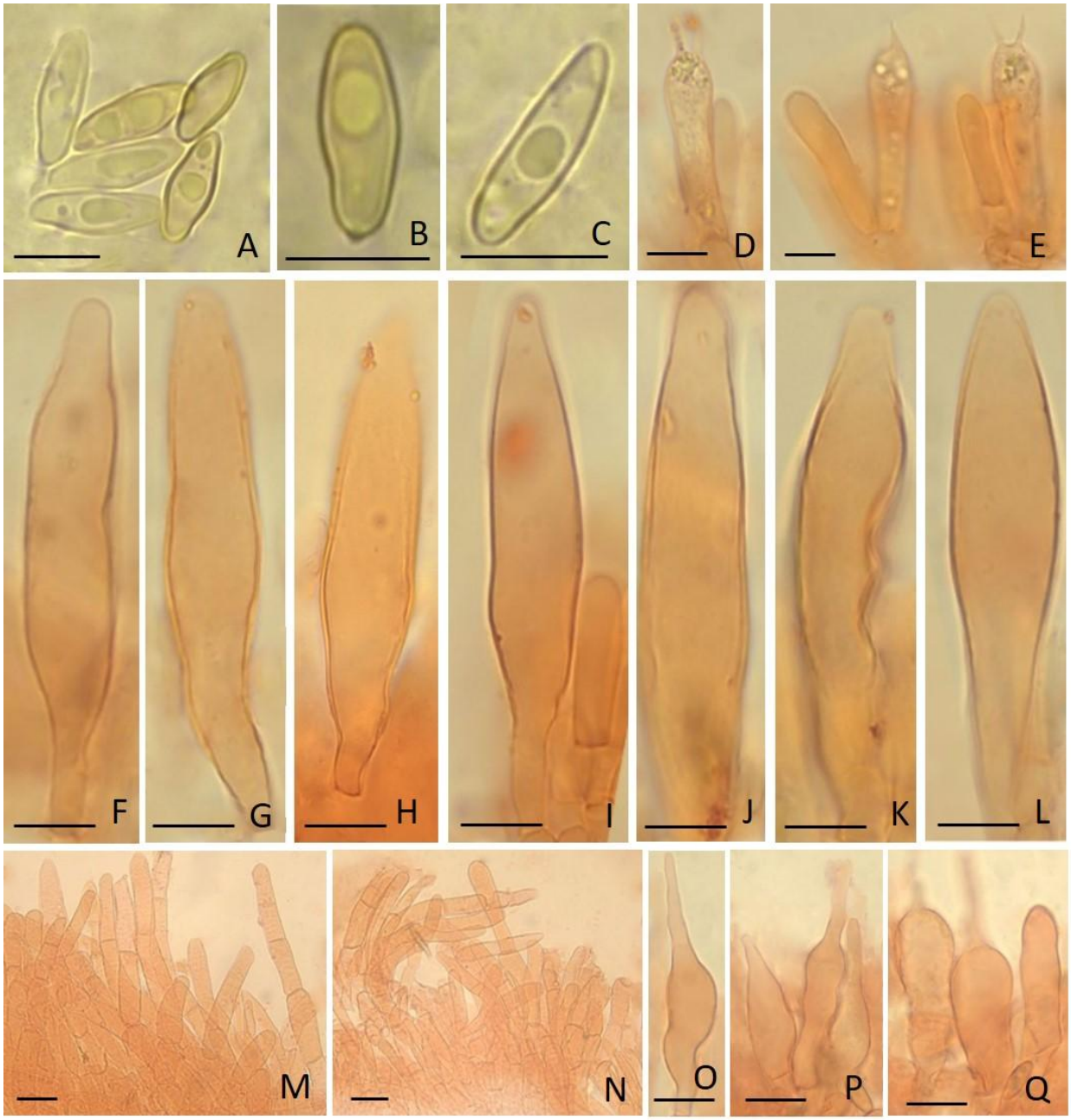


Fig. 10 Microscopic characteristics of *Phylloporus squamulosus* (holotype, A. Retnowati 1773): **A–C** Basidiospores. **D–E** Basidia-basidioles. **F–I** Cheilocystidia. **J–L** Pleurocystidia. **M–N** Pileipellis. **O–Q** Caulocystidia. Scale bars: **A–L** = 10 µm, **M–N** = 20 µm, and **O–Q** = 10 µm.

Phylloporus parvicorticola Retn. & W.H. Lu, sp. nov.
MycoBank 864500.
Figures 11, 12, 13, 14I–K

Etymology: *parvicorticola* refers to a small fruiting body that grows on the bark of a tree; parvus = small, corticola = bark-dwelling.

Diagnosis: *Phylloporus parvicorticola* is characterized by a small fruiting body, brownish-orange (7C4), paler at the center, white beneath the pileus, staining blue when bruised, the presence of cheilocystidia and pleurocystidia, arising from a volva-like, trichodermal pileipellis, the presence of caulocystidia, and gregarious growth on wood. The new species is closely related to *P. attenuatus*, *P. rufescens*, and *P. bogoriensis,* which differ in basidiomata size, pileus color, cheilocystidia, pleurocystidia, and caulocystidia.

Holotype: Indonesia, East Kalimantan, Sungai Wain, Ecotourism trail, on wood, 18 January 2025, A. Retnowati 1907 (Holotype: BO-2006092). GenBank: ITS-PZ579746, LSU-PZ579756.

Description: Basidiomata small. Pileus 0.4–1.8 cm diam., convex with flattened or slightly depressed center; surface dry, tomentose to subsquamulose; margin incurved; brownish orange (7C4), paler at center, white underneath. Lamellae subdecurrent, crowded (16-20 attached), with 2–3 series of lamellulae, changing blue when bruised, pale yellow marginate, yellow (2A6). Stipe 0.7–1.6 × 0.15–0.3 cm, central, cylindrical, tomentose, brownish orange (7C4), unchanging color when bruised. Basal tomentose, thin, white.

Basidiospores 9.52–12.22 × 3.45–4.58 µm (x_{mr}= 10.4–11.4 × 4.0–4.2–8.0, x_{mm}= 10.85 ± 0.5 × 4.12 ±0.1, Q= 2.1–3.3, Q_{mr}= 2.53–2.80, Q_{mm}= 1.67±0.1, 25 spores each collection), subfusiform to ellipsoid, smooth, olive brown in KOH. Basidia 24.3–28.6 × 8.8–9.1 µm, 2–4-spored. Basidioles 16.5–20.6 × 5.1–6.8 µm, clavate. Cheilocystidia common; 63.7–95.4 × 10.2–15.2 µm, cylindrical and fusiform, thick-walled up to 3 µm, obtuse apex, thick-walled, slightly incrusted, colorless to yellowish in KOH; swollen base 7–9 µm in diam., subglobose to globose, thin-walled, hyaline. Pleurocystidia common, 81.4–130.7 × 10.2–15.3 µm, cylindrical to subclavate, thick-walled up to 2.6 µm, yellowish in KOH, no encrustations; swollen base 5.5–8.4 µm in diam., subglobose to globose, thin-walled, hyaline. Pileipellis composed of cutis with a trichoderm apex, composed of chains of 2–5 cells; terminal cells 30.9–46 × 11.9–13.2 µm, clavate to cylindrical, hyaline; hyphae 9–14.7 µm, cylindrical, thin–walled, no incrustation, hyaline. Pileal trama interwoven; hyphae 5.5–13.5 µm, thin–walled, hyaline to pale yellowish brown. Stipe monomitic, hyphae 9.3–18.9 µm, cylindrical, parallel, thin–walled, hyaline. Caulocystidia common, composed of two types cells: 1) clavate, 17.3–24.1 × 5.5–10.2 µm, clavate, thin to thick-walled up to 1.9 µm, pale yellow; 2) long cylindrical cells, 36.6–209 × 3–12.3 µm, thick-walled up to 1.8 µm, to golden yellow; swollen apex, 5–15 µm in diam, thin-walled, pale yellow to yellow. Clamp connection absent.

Habit and habitat: Gregarious on wood.
Distribution: Indonesia (East Kalimantan).
Host: Dipterocarpaceae forest.
Material examined: Indonesia, East Kalimantan, Sungai Wain, Ecotourism trail, on wood, 18 January 2025, A. Retnowati 1908 (BO-2006093); same location and date, A. Retnowati 1909 (BO-2006094). GenBank: AR1907 (ITS: PZ579746; LSU: PZ579756); AR1908 (ITS: PZ579750; LSU: PZ579759); AR1909 (ITS: PZ579747; LSU: PZ579757).

Notes: *Phylloporus parvicorticola* is characterized by a small fruiting body that displays bluish discoloration upon bruising. The species possesses both cheilocystidia and pleurocystidia with swollen bases. Unlike other *Phylloporus* species, it typically grows in clusters on the bark of living trees. Molecular phylogenetic analyses demonstrate that this species belongs to the same clade as *P. attenuatus* Iqbal Hosen, which is closely related to the clade containing *P. rufescens* Corner and *P. bogoriensis* Hoehn. *Phylloporus attenuatus,* described from Bangladesh (Hosen & Li, 2017), differs from *P. parvicorticola* by its larger basidiomata, wine-red or brownish-violet to brownish-red pileus, smaller basidiospores, and terrestrial growth in forests dominated by *S. robusta*. *Phylloporus rufescens,* originally described from Singapore by Corner (1970), is distinguished by its large basidiomata, smaller basidiospores, and larger cystidia. *Phylloporus*

bogoriensis is defined by an umber brown or chestnut brown pileus, context that turns dull red, and lamellae that become pale cyanescent when bruised.

Morphologically, *P. parvicorticola* closely resembles *P. tunicatus*. *Phylloporus tunicatus* was described by Corner (1970) from a type collection at Gunong Panti (Johore, Malaya; Corner s.n., 16 April 1931, CGE) and has also been collected from Mt. Kinabalu. According to the Global Biodiversity Information Facility (GBIF), eight occurrences of this species have been recorded across Costa Rica, Malaysia, Brunei Darussalam, and Indonesia. Although the record lists Mt. Kinabalu as being in Indonesia, it is actually located in Malaysia. *Phylloporus tunicatus* can be distinguished from *P. parvicorticola* by its larger basidiomata, larger basidiospores, wider pleurocystidia with a more pronounced swollen base, larger caulocystidia, and a distinct habitat.



Fig. 11 Basidiomata of *Phylloporus parvicorticola* (holotype, A. Retnowati 1907). **A–E** Fresh fruiting bodies. **F–H** White marginate on the dried collections. Scale bars: **A–F** = 1 cm.



Fig. 12 Morphological variation in *Phylloporus parvicorticola*: **A**. Collection A. Retnowati 1908. **B**. Collection A. Retnowati 1909. Scale bars: **A–B** = 1 cm.

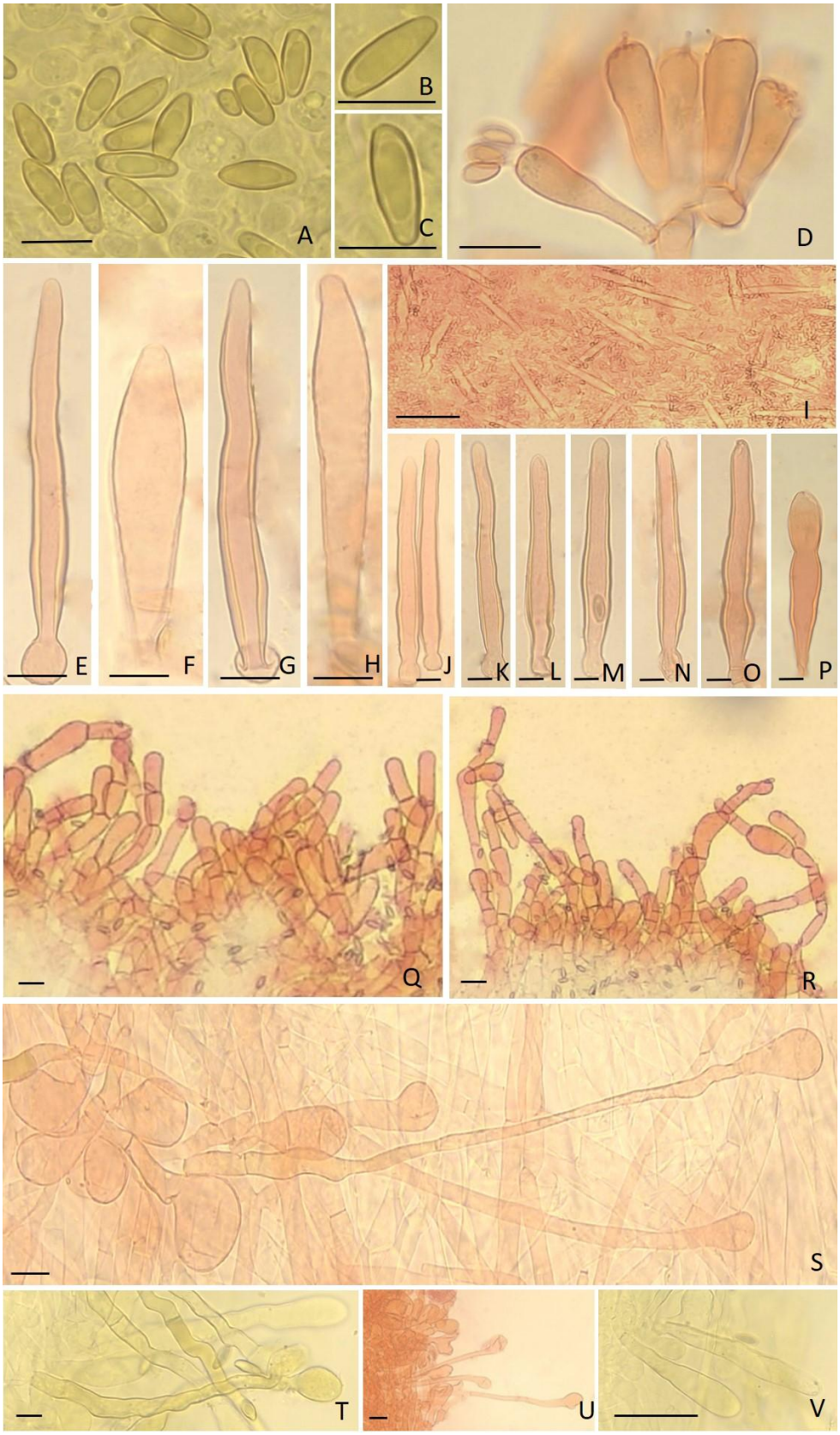


Fig. 13 Microscopic characteristics of *Phylloporus parvicorticola* (holotype, A. Retnowati 1907). **A–C** Basidiospores. **D** Basidia-basidioles. **E–H** Cheilocystidia. **I.** Pleurocystidia at the surface of lamellae. **J–P** Pleurocystidia. **Q–R** Pileipellis. **S–V** Caulocystidia. Scale bars: **A–V**= 10 µm.

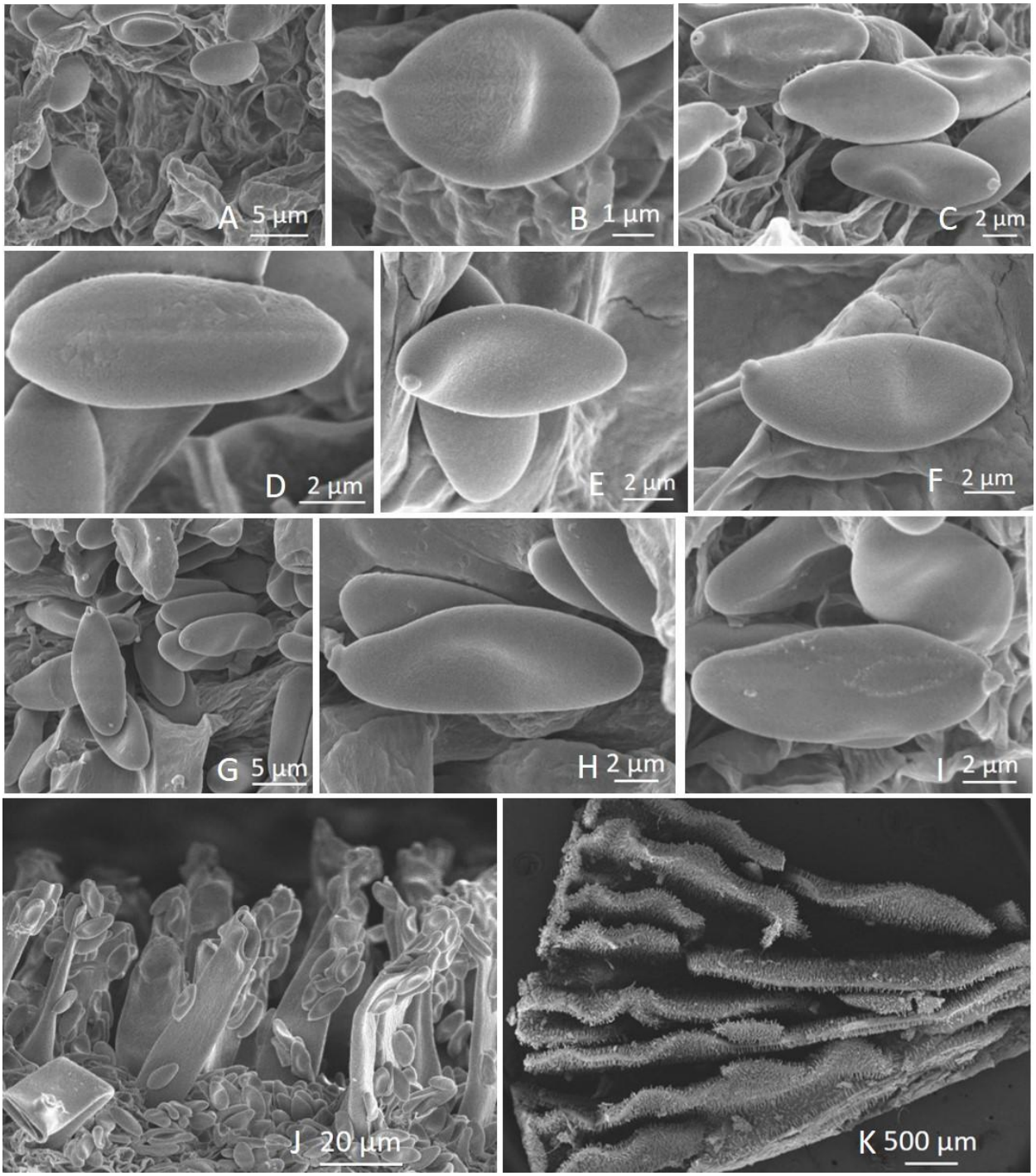


Fig. 14 *Phylloporus* from East Kalimantan under SEM. **A–B** Basidiospores of *Phylloporus bangkiraensis* (A. Retnowati 1782). **C–D** Basidiospores of *Phylloporus fusoidiclavatus* **(**A. Retnowati 1878). **E–F** Basidiospores of *Phylloporus wainensis* (A. Retnowati 1891). **G–H** Basidiospores of *Phylloporus squamulosus* (A. Retnowati 1773). **I–K** Basidiospores and cheilocystidia of *Phylloporus parvicorticola* (A. Retnowati 1907).

Discussion

This study identified five new species of *Phylloporus* from the lowland dipterocarp forests of East Kalimantan: *P. bangkiraiensis*, *P. fusoidiclavatus*, *P. wainensis*, *P. squamulosus*, and *P.*

parvicorticola. These additions substantially increase the documented diversity of the genus in Indonesia, which previously included only two species from Java, *P. pumilus* and *P. bogoriensis*. By integrating morphological characteristics with ITS and LSU molecular data, the study shows that the newly discovered species form distinct lineages within the genus. This outcome highlights the considerable, largely unexplored ectomycorrhizal diversity in Indonesia.

From both morphological and ecological perspectives, *P. parvicorticola* represents the most notable discovery of this study. This species is characterized by small basidiomata and a lignicolous habit, whereas most *Phylloporus* species are terrestrial ectomycorrhizal fungi that grow in soil. Microscopically, *P. parvicorticola* is distinguished by thick-walled cheilocystidia and pleurocystidia with distinctly swollen, subglobose to globose bases. These features are absent in its closest relatives, *P. rufescens* and *P. bogoriensis*. Phylogenetic analysis indicates that *P. parvicorticola* forms an independent lineage closely related to *P. attenuatus* from Bangladesh.

The discovery of these five new *Phylloporus* species enhances our knowledge of fungal diversity in Indonesia, especially ectomycorrhizal fungi in the region. These findings also emphasize the urgent need to conduct mycological surveys of the Dipterocarp forests in other parts of Kalimantan.

Key to *Phylloporus* Species from Indonesia

1. Growing on wood (Lignicolous); cystidia thick-walled with distinctly swollen, globose-to-subglobose bases ..... ***P. parvicorticola***

1. Growing on soil; cystidia thin-walled without swollen bases …….... 2

2. Context or lamellae tissue distinctly turning blue/cyanescent when bruised……..……... 3

2. Context and lamellae tissue unchanging blue/cyanescent absent 6

3. Pileus small (up to 1.1 cm diam); basidiospores small (mature spore up to 10.4 µm in length)……. ***P. pumilus***

3. Pileus (mostly exceeding 1.5 cm diam, ranging up to 5 cm); basidiospores larger (mature spores averaged >11 µm in length) 4

4. Pileus surface cracked and covered with squamulose scales; terminal cells of pileipellis heavily incrusted ..... ***P. squamulosus***

4. Pileus surface even, sub-tomentose, or velvety; terminal cells of pileipellis smooth, lacking cell wall incrustations 5

5. Pileus cup-shaped when young, dark brown scales with age; lamellae distant (20–24 attached); terminal cells of the pileipellis cylindrical ..... ***P. wainensis***

5. Pileus convex to plano-convex, brownish-grey to light brown, velvety; lamellae closed/crowded (32–40 attached); terminal cells of pileipellis clavate to broadly clavate……..... ***P. fusoidiclavatus***

6. Context turning dull red upon cutting; lamellae pale yellow, cyanescent present; pileus umber brown to chestnut brown……..... ***P. bogoriensis***

6. Context ochraceous brown, lamellae greyish-yellow to pale; cyanescent absent; pileus light brown …….……..... ***P. bangkiraiensis***

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Author contribution Atik Retnowati project managed, collected, designed, and wrote. Wenhua Lu designed and wrote. Fandri S. Fastanti collected and wrote. Desimaria Panjaitan collected and wrote. Samantha C. Karunarathna designed and wrote. Helbert collected and wrote. Roland Putra Pribadi Ahmad collected and wrote.

Data availability Material of *Phylloporus* are available in Herbarium Bogoriense (BO), and available datasets were submitted to GenBank (https://www.ncbi.nlm.nih.gov).

Declarations
Conflict of interest The authors declare that they have no competing interests.

Consent for publication Authors have given a consent to this submitted paper.

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