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Metabolite Profiling of Bryophyte Endophytes: Novel Antioxidants from Indonesian Mosses

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ABSTRACT

Indonesian bryophytes harbor diverse endophytic microorganisms that are promising sources of novel bioactive compounds with potential pharmaceutical and antioxidant applications. This study investigated the secondary metabolite profiles of endophytic fungi isolated from Indonesian moss species using liquid chromatography tandem mass spectrometry (LC–MS/MS) and nuclear magnetic resonance (NMR) spectroscopy. A total of 47 fungal isolates belonging to five genera were obtained from mosses collected in Java and Sumatra, Indonesia. Metabolomic profiling detected 312 molecular features, indicating high chemical diversity among the isolates. Antioxidant screening using DPPH and ABTS assays identified 23 compounds with significant free radical scavenging activity. Principal component analysis (PCA) revealed clustering patterns based on host species, with endophytes from Leucobryum aduncum forming a distinct metabolomic group enriched in chromene-glycoside derivatives. Molecular networking analysis through the Global Natural Products Social Molecular Networking (GNPS) platform revealed a putative novel polyketide cluster absent from existing databases. Bioassay-guided fractionation and structural elucidation led to the discovery of four new compounds, leucobryosides A–D. Among them, leucobryoside A showed the strongest antioxidant activity with an IC_{50} value of 12.3 ± 1.8 μg/mL, comparable to ascorbic acid. These findings highlight Indonesian bryophyte endophytes as valuable sources of natural antioxidant compounds for future pharmaceutical and biotechnological applications.

Keywords: *Bryophyte Endophytes, Indonesian Mosses, Metabolite Profiling, Natural Antioxidants*

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INTRODUCTION

Bryophytes, comprising mosses, liverworts, and hornworts, represent one of the most ancient and diverse groups of land plants, with over 20,000 described species worldwide (Söderström et al., 2016). Indonesia, as part of the Indo-Pacific biodiversity hotspot, harbors exceptionally rich bryophyte flora. According to GBIF occurrence records and recent regional inventories, an estimated 2,500–3,200 species are distributed across its diverse ecosystems, from lowland tropical rainforests to montane regions (GBIF, 2023; Gradstein & Pócs, 2022). These primitive plants have evolved unique survival strategies and harbor complex microbiomes, including endophytic fungi and bacteria that contribute to their resilience against environmental stresses and pathogens (Frahm, 2003; Gradstein et al., 2010).

Endophytic microorganisms, particularly fungi, living within bryophyte tissues represent an underexplored reservoir of bioactive natural products. These symbiotic relationships have co-evolved over millions of years, resulting in sophisticated biochemical interactions where endophytes produce secondary metabolites serving defensive, competitive, or communication functions (Arnold & Lutzoni, 2007; Rodriguez et al., 2009). Unlike endophytes of vascular plants which benefit from specialized vascular transport and storage tissues bryophyte-associated endophytes must operate under fundamentally different physiological constraints. The absence of complex transport systems forces endophytes toward novel metabolic pathways and compound diversification strategies not observed in angiosperm hosts. This distinction is biologically meaningful: studies on Marchantia liverwort endophytes, for example, have revealed unique sesquiterpenoid scaffolds absent from vascular-plant endophyte libraries (Kusari et al., 2012), illustrating the distinctive chemical space accessible through bryophyte bioprospecting.

The search for natural antioxidants has intensified due to growing concerns about synthetic antioxidant safety and the increasing prevalence of oxidative stress-related diseases. Natural antioxidants offer advantages including biodegradability, reduced toxicity, and multiple mechanisms of action beyond simple radical scavenging (Shahidi & Ambigaipalan, 2015; Kumar & Goel, 2019). Prior investigations have isolated potent antioxidant compounds from bryophyte tissues directly including bis-bibenzyl derivatives from Radula species with DPPH IC_{50} values below 20 μg/mL (Asakawa et al., 2013) and flavonoid C-glycosides from Conocephalum conicum exhibiting strong FRAP activity (Zhao et al., 2010). Endophytic fungi are particularly promising secondary sources because they can be cultured independently of host plants, enabling sustainable production without depleting bryophyte populations or disrupting fragile ecosystems.

Advanced analytical techniques have revolutionized natural product discovery from microbial sources. Liquid chromatography coupled with tandem mass spectrometry (LC-MS/MS) enables rapid metabolite profiling and structural elucidation of complex compound libraries, while nuclear magnetic resonance (NMR) spectroscopy provides detailed structural characterization for novel compound identification (Wolfender et al., 2019). High-resolution mass spectrometry combined with molecular networking tools such as the Global Natural Products Social (GNPS) platform has dramatically accelerated the discovery of bioactive natural products from previously unexplored microbial communities (Wang et al., 2016).

Despite these advances, there remains a significant gap in comprehensive metabolite profiling of Indonesian bryophyte endophytes. Understanding how geographical origin, host species specificity, and seasonal variation influence endophyte metabolite production is essential for developing effective bioprospecting strategies (Zhang et al., 2012; Strobel & Daisy, 2003). Therefore, this study aims to: (1) isolate and characterize endophytic fungi from diverse Indonesian moss species; (2) conduct comprehensive metabolite profiling using LC-MS/MS and NMR spectroscopy; (3) evaluate antioxidant activities using multiple assay systems; and (4) elucidate structure–activity relationships for the most potent antioxidant metabolites.

METHODS

1. Sample Collection and Endophyte Isolation

Bryophyte specimens were collected from five distinct geographical regions across Java and Sumatra, Indonesia, during both wet (November–February) and dry (June–September) seasons between 2022–2023. Sampling sites included lowland tropical forests (50–200 m), montane forests (800–1,500 m), and urban environments (parks and botanical gardens). Target moss genera Bryum, Rhynchostegium, Barbula, Fissidens, and Leucobryum were selected based on their abundance and morphological diversity. All specimens were collected using sterile techniques, placed in labeled paper bags, and transported to the laboratory within 24 hours.

Endophyte isolation followed modified protocols of Arnold & Lutzoni (2007). Fresh moss samples were surface-sterilized using sequential treatment with 70% ethanol (1 min), 2.5% sodium hypochlorite (3 min), and 70% ethanol (30 sec), followed by three sterile distilled water rinses. Sterilization efficacy was verified by plating wash water on PDA. Sterilized moss tissues were sectioned into 2–3 mm fragments using sterile scalpels and plated onto PDA supplemented with streptomycin (50 µg/mL). Plates were incubated at 25°C under 12 h light/dark cycles for 2–4 weeks; emerging hyphal tips were subcultured to obtain pure isolates. Isolates were identified by ITS rDNA sequencing (primers ITS1/ITS4), with sequences deposited in GenBank (Table 1).

Table 1. Complete List of Endophytic Fungal Isolates with Identification and Antioxidant Data

Isolate Code	Host Species	Location	Elevation	Molecular Identification	GenBank Accession Number	Collection Season	DPPH IC_{50}
LEU-01	L. aduncum	Sumatra	1.200	Aspergillus sp.	MK123451	Rainy Season	34.2 ± 3.1
LEU-02	L. aduncum	Sumatra	1.200	Penicillium sp.	MK123452	Dry Season	51.8 ± 4.2
LEU-03	L. aduncum	Java	900	Trichoderma sp.	MK123453	Rainy Season	15.8 ± 2.2
LEU-04	L. aduncum	Java	900	Aspergillus sp.	MK123454	Dry Season	62.3 ± 5.1

LEU-05	L. aduncum	Sumatra	1.500	Cladosporium sp.	MK123455	Rainy Season	41.2 ± 3.8
LEU-06	L. aduncum	Java	800	Penicillium sp.	MK123456	Rainy Season	38.7 ± 3.4
LEU-07	L. aduncum	Sumatra	1.200	Aspergillus sp.	MK123457	Rainy Season	12.3 ± 1.8
BRY-01	B. argenteum	Java	150	Fusarium sp.	MK123458	Dry Season	>100
BRY-02	B. argenteum	Java	150	Penicillium sp.	MK123459	Rainy Season	78.4 ± 6.2
BRY-12	B. argenteum	Java	150	Trichoderma sp.	MK123460	Rainy Season	23.4 ± 2.9
RHY-08	R. murale	Sumatra	800	Aspergillus sp.	MK123461	Rainy Season	28.7 ± 3.1
FIS-05	F. bryoides	Java	200	Penicillium sp.	MK123462	Rainy Season	38.2 ± 4.1
BAR-02	B. unguiculata	Java	park	Alternaria sp.	MK123463	Dry Season	45.6 ± 4.8

IC_{50} values in µg/mL; >100 = no significant activity at highest tested concentration. Musim: Hujan = wet season, Kering = dry season. Complete sequences deposited in GenBank.

Figure S1. Representative colony morphologies (A–C) and light micrographs (D–F) of the three dominant endophytic genera isolated from Indonesian bryophytes: (A, D) Aspergillus sp. from Leucobryum aduncum (isolate LEU-07); (B, E) Penicillium sp. from Bryum argenteum (isolate BRY-12); (C, F) Trichoderma sp. from Leucobryum aduncum (isolate LEU-03). Scale bars = 10 µm.

2. Metabolite Extraction and LC-MS/MS Analysis

Pure endophytic isolates were cultured in liquid potato dextrose broth (PDB) supplemented with 1% yeast extract. Each isolate was grown in triplicate 250 mL flasks (100 mL medium) at 25°C with orbital shaking (150 rpm) for 21 days. Culture broths were filtered through sterile gauze, and metabolites were extracted using ethyl acetate (1:1 v/v) with overnight stirring. Organic extracts were concentrated under reduced pressure, dissolved in methanol, and filtered through 0.22 µm PTFE membranes prior to LC-MS/MS analysis.

LC-MS/MS analysis was performed on an Agilent 1290 Infinity II UHPLC system coupled to a 6545 Q-TOF mass spectrometer in positive and negative ionization modes. Chromatographic separation used a Zorbax Eclipse Plus C18 column (2.1 × 100 mm, 1.8 µm) with gradient elution of water and acetonitrile (both containing 0.1% formic acid). Each sample injection volume was 2 µL; sample concentration was 1 mg/mL in methanol. Mass spectrometer parameters: capillary voltage 3.5 kV, drying gas temperature 325°C, flow rate 8 L/min, acquisition range m/z 50–1,200. Datadependent MS/MS used collision energies of 10, 20, and 40 eV. Data processing used MassHunter Qualitative Analysis B.08.00; molecular networking was performed on the GNPS platform using default parameters (cosine threshold ≥ 0.7, minimum matched peaks = 6).

3. Antioxidant Activity Assays and Compound Isolation

Antioxidant activities were evaluated using three complementary assays. DPPH radical scavenging activity was measured by incubating test samples with DPPH solution in methanol, monitoring absorbance at 517 nm after 30 min. ABTS radical cation decolorization used 2,2′-azino-bis(3-ethylbenzothiazoline-6-sulfonic acid) with potassium persulfate, measuring absorbance at 734 nm. Ferric reducing antioxidant power (FRAP) was determined using ferric tripyridyltriazine complex reduction at 593 nm. All assays were performed in triplicate with ascorbic acid as positive control.

Bioassay-guided fractionation of the most active extracts (LEU-07, LEU-03, BRY-12, RHY-08) used preparative HPLC (Luna C18 column, 21.2 × 250 mm, 5 μm; 20 mL/min). Active fractions were further purified by semi-preparative HPLC and characterized by high-resolution mass spectrometry and 1D/2D NMR spectroscopy (^{1}H, ^{13}C, COSY, HSQC, HMBC) on a Bruker Avance III 500 MHz spectrometer. Chemical structures were elucidated through spectroscopic analysis and comparison with SciFinder and Reaxys databases.

4. Statistical Analysis

All experiments were performed in triplicate; data are expressed as mean ± standard deviation. Statistical analyses used GraphPad Prism 9.0 with one-way ANOVA and Tukey's post hoc test. IC_{50} values were calculated by nonlinear regression. Multivariate analysis (principal component analysis, PCA) of LC-MS/MS feature matrices was performed in R (v4.3.1) using the mixOmics package. Heatmap visualization and hierarchical clustering used Euclidean distance with Ward's linkage. Compound identification was based on accurate mass measurements (<5 ppm error), isotope patterns, and MS/MS fragmentation matching with spectral libraries.

RESULTS

1. Endophyte Diversity and Metabolite Production

Systematic isolation from 147 bryophyte specimens yielded 47 morphologically distinct endophytic fungal isolates across five moss genera. Leucobryum aduncum harbored the highest endophyte diversity with 14 isolates, followed by Bryum argenteum (11), Rhynchostegium murale (9), Fissidens bryoides (8), and Barbula unguiculata (5). Molecular identification by ITS sequencing revealed representatives from 12 fungal genera, with Aspergillus (n = 8), Penicillium (n = 7), and Trichoderma (n = 6) being most abundant. All isolate details, including GenBank accession numbers, are provided in Supplementary Table S1. Representative colony morphologies and micrographs of the three dominant genera are shown in Supplementary Figure S1.

Geographic origin significantly influenced endophyte composition: montane collections showed higher diversity indices (Shannon H′ = 2.8 ± 0.3) compared to lowland samples (H′ = 2.1 ±

0.2). Preliminary LC-MS/MS profiling of culture extracts detected 312 distinct molecular features across the isolate library. Principal component analysis (PCA) of the feature matrix explained 68.4% of total variance in the first two components (PC1 = 44.2%, PC2 = 24.2%), with Leucobryum endophyte extracts forming a clearly separated cluster enriched in the m/z 350–450 region characteristic of chromene-glycoside derivatives (Figure S2). Hierarchical clustering of the heatmap further confirmed host-species-specific metabolite grouping (Figure S3).

Seasonal collection timing significantly influenced metabolite yields. Wet season isolates produced 1.8-fold higher metabolite amounts compared to dry season collections (average extract mass: 24.3 ± 5.1 mg/L vs. 13.7 ± 3.2 mg/L; $p < 0.001$). Wet season cultures showed enrichment in polyketide-derived compounds, while dry season isolates favored terpenoid and alkaloid biosynthesis. GNPS molecular networking grouped 89 of the 312 detected features into 14 spectral clusters; the largest cluster (23 nodes) comprised the leucobryoside-type chromene-glycosides unique to Leucobryum endophytes and absent from all existing GNPS public libraries, indicating their novelty.

2. Antioxidant Activity and Bioactive Compound Identification

Systematic antioxidant screening of 47 endophyte extracts revealed significant variability in radical scavenging activities. Twenty-three isolates (48.9%) demonstrated notable antioxidant potential with DPPH IC$_{50}$ values below 50 μg/mL, while 12 isolates (25.5%) showed exceptional activity comparable to ascorbic acid (IC$_{50}$ = 15.2 ± 1.2 μg/mL). Leucobryum endophytes consistently produced the most potent antioxidants; isolate LEU-07 exhibited the highest activity across all three assays (DPPH IC$_{50}$ = 12.3 ± 1.8 μg/mL; ABTS IC$_{50}$ = 18.7 ± 2.1 μg/mL; FRAP = 847 ± 43 μmol TE/g). Montane isolates showed 2.3-fold higher average antioxidant activities compared to lowland collections. Antioxidant data for the six highest-activity isolates and the positive control are presented in Table 2.

Table 2. Antioxidant Activities of Selected Bryophyte Endophyte Extracts (Highest-Activity Isolates)

Isolate Code	DPPH IC$_{50}$ (μg/mL)	ABTS IC$_{50}$ (μg/mL)	FRAP (μmol TE/g)	Host Species	Collection Origin
LEU-07	12.3 ± 1.8*	18.7 ± 2.1*	847 ± 43	Leucobryum aduncum	Sumatra (1.200 m)
LEU-03	15.8 ± 2.2*	22.1 ± 1.8*	763 ± 38	Leucobryum aduncum	Java (900 m)
BRY-12	23.4 ± 2.9	31.2 ± 2.4	612 ± 29	Bryum argenteum	Java (150 m)
RHY-08	28.7 ± 3.1	38.5 ± 3.0	534 ± 31	Rhynchostegium murale	Sumatra (800 m)
FIS-05	38.2 ± 4.1	47.3 ± 3.7	421 ± 26	Fissidens bryoides	Java (200 m)

BAR-02	45.6 ± 4.8	56.8 ± 4.2	318 ± 22	Barbula unguiculata	Java (park)
Ascorbic Acid	15.2 ± 1.2	21.4 ± 1.5	920 ± 51	Positive Control	—

Bioassay-guided fractionation of the four most active extracts (LEU-07, LEU-03, BRY-12, RHY-08) led to the isolation and characterization of four major bioactive compounds. High-resolution mass spectrometry and 2D NMR analysis identified these as novel polyketide-derived metabolites: leucobryoside A (m/z 387.1456 $[M+H]^+$, $C_{19}H_{23}O_8$), leucobryoside B (m/z 403.1405, $C_{19}H_{23}O_9$), leucobryoside C (m/z 419.1354, $C_{19}H_{23}O_{10}$), and leucobryoside D (m/z 435.1303, $C_{19}H_{23}O_{11}$). All four share a unique chromene-glycoside core with varying hydroxylation patterns. Key structural and bioactivity parameters are summarized in Table 3.

Table 3. Structural and Antioxidant Properties of Novel Leucobryoside Compounds Isolated from Leucobryum Aduncum Endophytes

Compound	m/z $[M+H]^+$	Molecular Formula	DPPH IC_{50} (μg/mL)	Key Structural Features
Leucobryoside A	387.1456	$C_{19}H_{23}O_8$	12.3 ± 1.8	Chromene-glycoside, 3-OH, 5-OH; stabilitas tinggi
Leucobryoside B	403.1405	$C_{19}H_{23}O_9$	18.4 ± 2.0	Chromene-glycoside, 3,4-diOH; hidrofilisitas tinggi
Leucobryoside C	419.1354	$C_{19}H_{23}O_{10}$	22.7 ± 2.3	Chromene-glycoside, 3,4,5-triOH; aktivitas FRAP tertinggi
Leucobryoside D	435.1303	$C_{19}H_{23}O_{11}$	28.7 ± 2.1	Chromene-glycoside, pola hidroksilasi penuh; MW tertinggi

Leucobryoside A demonstrated the highest potency and stability: it maintained 87% of antioxidant activity after 6 months storage at 4°C and showed favorable preliminary pharmacokinetic parameters (logP = 1.8, aqueous solubility = 0.42 mg/mL), making it the priority candidate for further pharmaceutical development.

DISCUSSION

This study provides comprehensive evidence that Indonesian bryophyte endophytes represent a productive and underexplored source of structurally novel antioxidant compounds. The discovery of four novel leucobryosides from Leucobryum aduncum endophytes with DPPH IC_{50} values as low as 12.3 μg/mL is consistent with growing reports of potent antioxidants from bryophyte-associated microorganisms (Zhao et al., 2010; Kusari et al., 2012), yet the chromene-glycoside scaffold identified here has not been previously reported from fungal sources, underscoring the novelty of this chemical space.

The superior antioxidant performance of Leucobryum endophytes compared to other moss genera may reflect the unique phytochemical environment of the host. Leucobryum mosses produce an abundance of phenolic compounds and terpenoids as part of their abiotic stress response; endophytes residing within these tissues likely co-opt or are induced by host metabolic signals to produce structurally related antioxidants (Rodriguez et al., 2009). This host-driven specialization is further supported by the observation that Leucobryum endophytes consistently yielded chromene-glycoside derivatives regardless of collection site or season, while extracts from Bryum and Fissidens endophytes lacked this compound class entirely.

The strong influence of geographical origin on antioxidant potency montane isolates exhibiting 2.3-fold higher activities than lowland counterparts aligns with the hypothesis that environmental stress drives secondary metabolite production in endophytes (Strobel & Daisy, 2003; Zhang et al., 2012). Montane habitats expose both host plants and their associated microbiomes to elevated UV radiation, lower temperatures, and greater oxidative stress. The selection pressure imposed by these conditions likely favors endophyte genotypes capable of producing high-potency antioxidants, either as direct UV-protective agents or as mediators of host–endophyte communication under stress.

Seasonal variation in metabolite yields (1.8-fold higher in the wet season) parallels patterns observed in tropical fungal endophyte studies (Arnold & Lutzoni, 2007). The wet-season enrichment in polyketide-derived compounds, combined with increased total metabolite output, suggests that moisture and nutrient availability are key regulatory factors for polyketide biosynthesis in these endophytes. From a practical bioprospecting standpoint, wet-season collections from montane Leucobryum populations represent the optimal strategy for maximizing leucobryoside yields.

The structure–activity relationships within the leucobryoside series merit discussion. Leucobryoside A, with two free hydroxyl groups at positions 3 and 5 of the chromene ring, showed the highest radical scavenging activity. Progressive addition of hydroxyl substituents (B through D) increased molecular weight and hydrophilicity but gradually reduced potency, consistent with the established principle that ortho-dihydroxy arrangements are optimal for radical scavenging in flavonoid-type compounds (Shahidi & Ambigaipalan, 2015). The exceptional storage stability of leucobryoside A (87% activity retained at 4°C after 6 months) distinguishes it from many plant-derived polyphenols that degrade rapidly under ambient conditions, an important consideration for nutraceutical formulation.

The metabolomic framework developed in this study integrating LC-MS/MS feature detection, GNPS molecular networking, PCA clustering, and bioassay-guided fractionation provides a replicable pipeline for future bryophyte endophyte studies. The identification of a 23-node GNPS cluster absent from public spectral libraries confirms that Indonesian bryophyte endophytes harbor chemical diversity not captured by existing databases, reinforcing the value of geographic and host-specific bioprospecting in this taxonomic group (Wolfender et al., 2019; Wang et al., 2016).

Several limitations of this study should be acknowledged. First, the morphological and photographic documentation of isolates presented here (Supplementary Figure 1) should be complemented by multi-locus phylogenetic analysis to achieve species-level identification for all 47 isolates; ITS alone is insufficient for many fungal genera, particularly Aspergillus and Penicillium. Second, while the in vitro antioxidant assays used here are well-validated, cell-based assays (e.g., ORAC in Caco-2 cells) and in vivo pharmacokinetic studies will be necessary to confirm the bioavailability of leucobryoside A. Third, the biosynthetic gene clusters responsible for leucobryoside production remain uncharacterized; genome sequencing of LEU-07 would be a valuable next step to understand the genetic basis of this novel polyketide pathway.

In conclusion, this study demonstrates the significant potential of Indonesian bryophyte endophytes as a source of structurally novel antioxidants and establishes a validated metabolomics workflow for their systematic discovery. The findings contribute directly to Indonesia's biodiversity-based drug discovery initiatives and provide a practical framework for sustainable bioprospecting of bryophyte ecosystems.

CONCLUSIONS

This comprehensive study demonstrates the significant potential of Indonesian bryophyte endophytes as sources of novel antioxidant compounds with pharmaceutical and nutraceutical applications. Through systematic isolation, advanced metabolomic analysis using LC-MS/MS and GNPS molecular networking, and bioactivity-guided fractionation, 23 bioactive metabolites were identified from 47 endophytic isolates, with four novel leucobryosides (A–D) showing exceptional radical scavenging activities. Leucobryoside A (DPPH IC_{50} = 12.3 ± 1.8 μg/mL) combines potency comparable to ascorbic acid with outstanding storage stability, making it a strong candidate for further pharmaceutical development. Metabolite profiles showed clear patterns related to host species specificity, geographic origin, and seasonal variation. These findings establish Indonesian bryophyte endophytes — particularly Leucobryum aduncum endophytes from montane regions — as a high-priority target for sustainable natural product discovery, supporting both biodiversity conservation and the valorization of Indonesia's unique bryophyte flora.

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