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by Hary Widjajanti

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Bioprospecting of non-mycorrhizal endophytic fungi associated with ferns and mosses

Asiandu AP^{1*}, Wahyudi A², Ramadhan F³ and Widjajanti H⁴

¹Faculty of Biology, Universitas Gadjah Mada, Indonesia

²Biology Department, Faculty of Math and Natural Sciences, Universitas Sriwijaya, Indonesia

³Graduate School of Biotechnology, IPB University, Bogor 16680, Indonesia

⁴Biology Department, Faculty of Math and Natural Sciences, Universitas Sriwijaya

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Abstract

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Endophytic fungi residing inside the host plant tissues may produce the same secondary metabolites as their host plants. They may have undergone coevolution and horizontal gene transfer with their host plants. Due to these processes, they may produce various kinds of chemical compounds that are important for new drugs. Scientists have successfully isolated endophytes from many higher plants. However, there are scarce reports on the biodiversity and potential of fungal endophytes associated with mosses and ferns. Mosses and ferns are highly diverse and found in all environments. They can also be used as traditional medicines. They produce some secondary metabolite compounds that have the potential for drug production. Thus, the lack of information on endophytic fungi associated with ferns and mosses opens up new opportunities for discovering new endophytic fungal species that have not been isolated. Also, this gap of knowledge provides an opportunity to obtain new types of chemical compounds from endophytic fungi associated with ferns and mosses that have essential potential. Therefore, we compile information on the various kinds of non-mycorrhizal endophytic fungi associated with ferns and mosses. The data used in this article are secondary and third-party data collected from some previous reports based on culture-dependent and culture-independent approaches. This review article aims to provide information about the biodiversity and bioprospecting of endophytic fungi associated with ferns and mosses in exploring and developing further research of endophytic fungi to obtain new drugs and industrial enzymes.

Keywords – biodiversity – bryophytes – endophytes – pteridophytes

Introduction

Endophytic fungi live within the host plant tissues (Barkodia et al. 2018). They are found in certain parts of plant tissues (Tan & Zou 2001), like nodules, stems, leaves, roots (Barkodia et al. 2018), and seeds (Gaisbert et al. 2017). They form colonies inside their host tissue without harming the host. These fungi are found in all types of plants, from woody trees to herbaceous grasses (Kumala 2014). Endophytic fungi are highly diverse. Almost all plants have one or several species of endophytic fungi associated with their tissues (Barkodia et al. 2018). Endophytic fungi do symbiosis with their host plants. They use plants as their microhabitats and food sources to support their life cycle (Tan & Zou 2001).

Plants provide a place or microhabitat for endophytic fungi to live and perform their metabolisms. Plants can provide various nutrients used by endophytic fungi to sustain their life (Zou 2001). Meanwhile, endophytic fungi produce some secondary metabolites enhancing the host plant resistance to various pathogens and environmental stresses. Endophytic fungi also stimulate formation of growth hormone for the host plants (Barkodia et al. 2018). Some Ascomycota isolated from the roots, stems, and leaves of the *Vanda cristata* orchid were known for their role in the auxin synthesis. One of the fungi capable of synthesizing auxin and phosphate solubilization was *Agaricus bisporus*. With the addition of tryptophan, the fungal isolate was able to synthesize 161 µg/mL indole acetic acid (IAA). Additionally, other endophytic fungal isolates that were able to synthesize IAA isolated from the host plant were *Alternaria tenuissima*, *Trichium trincitum*, *Fusarium* spp., *Mycocleptodiscus* sp., and *Paraconiothyrium hawaiiense* (Chand et al. 2020).

Endophytic fungi are potential sources of secondary metabolites (Deepthi et al. 2018). They live inside the plant tissues intracellularly by producing the same secondary metabolites as their host due to genetic recombination or coevolution with their host (Sia et al. 2013). Endophytic fungi have undergone genetic modifications for ages (Radji 2005). Recently, more than 8600 types of bioactive compounds have been isolated from endophytic fungi. These bioactive compounds include terpenoids, steroids, flavonoids, quinines, phenols, xanthenes, dipeptides, cytochalasins, xanthenes, and isocoumarins. They are used as antimicrobial, antiviral, antidiabetic, antioxidant, anticancer, antiparasitic, immunosuppressive, neuroprotective, and insulin-mimetic (Barkodia et al. 2018).

The highly diverse endophytic fungi (Prasetyoputri & Atmosukarto 2006) are found in many types of habitats and are not only limited to tropical ecosystems. They are found in the temperate ecosystem, alpine, and even in extreme environments. Their host plants vary that include higher plants, gymnosperms, ferns, mosses, and algae (Kaul et al. 2012). The number of endophytic fungal communities differ in each plant. Some plants have more endophytic fungal isolates than other plants. Similarly, each plant organ harbours different number of fungal isolates. The endophytic fungal diversity in a plant or plant organ is determined by the type of ecosystems and the isolation techniques (Fitriarni & Kasiamdari 2018).

However, reports on endophytic fungi isolated from ferns as isolated from *Adiantum* sp. (Kumaresan et al. 2013) and *Asplenium nidus* (Suhartina et al. 2018) and mosses as isolated from *Barbilophozia hatcheri* (Zhang et al. 2013) and *Chorisodontium aciphyllum* (Yu et al. 2014) are still limited (Muthukumar & Prabha 2012). Information on the endophytic fungal diversity in ferns and mosses is certainly not comparable with the diversity in higher plants (Strobel et al. 2004). So, it is a great chance to obtain new species of endophytic fungi. The exploration of endophytic fungi is a potential work because they are sources of natural bioactive compounds (Sunkar et al. 2017). Therefore, in this review, we compile and discuss some endophytic fungi isolated from ferns and mosses. The endophytic fungal isolates in this review were collected from secondary and third-party data sources. This review aims to provide an overview of the biodiversity and potentials of endophytic fungi associated with lower plants (ferns and mosses).

Endophytic Fungi

Fungi is a kingdom of eukaryotic organisms that are heterotrophs and cell walls composed of chitin and glucan substances (Dismukes et al. 2003). The term endophyte was first defined by the German botanist, Heinrich Link, in 1809. At that time, the term used was “Entophytae”, a distinct group of pathogenic fungi that live inside plant tissues. The oldest documented endophytic fungi were associated with terrestrial plants that structurally did not have differentiated organs towards shoots, leaves, and roots (Southworth 2012). The diversity of endophytic fungi in a plant is also influenced by its environment. It will lead to different numbers and types of species in locations with different climates (Bowman & Arnold 2021).

Endophytic microorganisms are the evolutionary products for ages (Clay et al. 2005). They are transmitted across generations of a plant by seeds and cotyledons through vertical transmission. Generally, each seed contains one species of endophytic fungi. However, the number of endophytic

species in a seed varies among plant species. The pollen tube is an opening for endophytic fungi to enter the developing seed (Hodgson et al. 2014). Endophytic fungus is generally transmitted via eggs, seeds, or rarely clonal propagules via sperm. The co-evolution between endophytes and their host plants has led endophytic symbionts to adapt to their specific microhabitat. The process also resulted in transferring plant genetic material into their genome (Zhang et al. 2006).

Endophytic fungi enter plant tissues through cuticles and cell walls. In penetrating the cuticles and cell walls, they produce hydrolytic enzymes such as cutinase, pectinase, cellulase, hemicellulase, protease, and lignin peroxidase (Choi et al. 2005, Verma et al. 2017). After the penetration process, they reside intercellularly or intracellularly inside their host tissues. The success of forming the mutualistic associations between fungal endophytes and the host depends on the internal and external conditions of the host and fungi, such as host secondary metabolites. The metabolites produced by host plants affected the success of endophytic fungal colonization (Christian et al. 2020). The mutualism symbiosis is the result of several biochemical components or genetic communication between endophytic fungi and their hosts (Satyanarayana et al. 2017).

There are two major groups of endophytes, Clavicipitalean (C-endophytes) and non-clavicipitalean (NC-endophytes). C-endophytes (Class 1) represent a small number of fungi related to clavicipitaceae that are difficult to culture and are limited to a few grass (Rodriguez et al. 2009). NC-endophytes have a high abundance and represent the polyphyletic of the early ascomycetes. This group is mostly found in terrestrial plants and almost all terrestrial ecosystems ranging from tropical to tundra (Arnold & Lutzoni 2007, Verma et al. 2017).

NC-endophytes can be divided into three functional classes based on the host colonization type, transmission mechanism, in-plant biodiversity, and ecological function (Zhang et al. 2006, Rodriguez et al. 2008). Class 2 endophytic fungi are a group found in Ascomycota and Basidiomycota. These fungi have a high rate of infection in plants in stressed environments. Generally, the class is found in roots, stems, leaves, and is transmitted across generations through seeds or rhizomes. Endophytic fungi class 3 is found in tissues above the ground and generally come from the Ascomycota group (Rodriguez et al. 2009). Meanwhile, class 4 endophytic fungus is a group of fungi that colonize plant tissues found in plant tissues above the ground (Wani et al. 2015) and is characterized by dark septate hyphae and microsclerotia (Rodriguez et al. 2008).

The differences between C-endophytes and NC endophytes are compiled in Table 1.

Table 1 Classes of endophytic fungi based on symbiotic characteristics (modified from Rodriguez et al. 2009, Verma et al. 2017; Satyanarayana et al. 2017).

Criteria	Clavicipitalean (C-endophytes)/Class 1	Non-Clavicipitalean (NC-endophytes)
Group division	Type I, Type II, Type III	Class 2, Class 3, Class 4
Host range	Narrow and host specific	Broad and nonspecific
Colonization of plant tissue	In shoots and roots, extensive colonization	Generally turned out but occasionally the roots and rhizomes, limited colonization except class 2 and 4
Transmission and development	Generally vertical using mycelia and spores, systemic in nature	Generally horizontal unless class 2. Utilizing spores and non-systemic in nature
Bioprospecting Examples	Novel secondary metabolites Hypocreales (e.g. <i>Claviceps</i> spp.)	Novel secondary metabolites Mostly hyphomycetes (e.g. <i>Curvularia</i> spp., and <i>Phoma</i> spp.)

The diversity of fungi on earth is highly abundant, so it requires the appropriate technique in estimating the number of fungi. The approach can be done through polyphasic approaches of phylogeny, phenotype, and reproductive biology (Lücking et al. 2020). Molecular identification has revealed the biodiversity of fungi on earth. In the last decade, several new taxa of fungi have been

discovered. To date, it is known that there are about 11.7 to 13.2 million species of fungi. The revision fungal taxa are based on the use of molecular technology carried out on a culture-dependent or culture-independent approach (Zhang et al. 2010, Wu et al. 2019). Most of these new species were obtained from culture-independent approaches (Zhang et al. 2010, Wu et al. 2019). Still, there is a chance to identify unknown fungal species (Amann et al. 1995, Zhang et al. 2006) as almost all plants or about 400,000 plants contain one or more endophytic microbes (Anitha et al. 2013).

Non-mycorrhizal endophytic fungi associated with Pteridophytes

The few reports of endophytic fungi associated with lower plants gives opportunities to discover new species associated with lower plants that have not been described yet (Rojas-Alvarado 2018). For example, several new endophytic fungal species were isolated from some ferns. The new fungal species were *Passalora lygodii* isolated from *Lygodium japonicum*, *Pseudocercospora microlepieae* isolated from the fern *Microlepia speluncae*, and *Pseudocercospora tectariae* isolated from *Tectaria harlandii* (Kirschner & Wang 2015). Some other endophytic fungi isolated from Pteridophytes are compiled in this review.

The limited information of endophytic fungal associated with fern also provides an opportunity to explore new compounds and metabolites. Therefore, we compiled some endophytic fungi associated with ferns in this review to provide information about biodiversity and bioprospecting of endophytic fungi associated with ferns (Table 2).

Table 2 Endophytic fungi associated with ferns (Pteridophytes)

Fern species	Fungal endophytes	Isolate Sources	Origin	References
<i>Adiantum</i> sp.	<i>Aspergillus</i> sp., <i>A. niger</i> , <i>A. flavus</i> , <i>Aureobasidium</i> sp., <i>Colletotrichum</i> sp., <i>Drechslera</i> sp., <i>Pestalotiopsis</i> sp., <i>Phyllosticta</i> sp., <i>Sporormiella</i> sp., <i>Trichoderma</i> sp.	Pinnules	India	Kumaresan et al. (2013)
<i>Asplenium nidus</i>	<i>Aspergillus</i> sp., <i>Gliocladium</i> sp., <i>Humicola</i> sp. and <i>Neoscytalidium</i> sp.	Fronds	Indonesia	Suhartina et al. (2018)
<i>Bolbitis portoricensis</i>	<i>Xylaria</i> sp.	Fronds	Costa Rica	Del Olmo-Ruiz & Arnold (2014)
<i>Coniogramme petelotii</i>	<i>Arthrinium arundinis</i> , <i>Beltrania rhombic</i> , <i>Bionectaria</i> , <i>Calonectria</i> sp., <i>Colletotrichum gloeosporioides</i> , <i>C. acutatum</i> , <i>C. boninense</i> , <i>Fusarium</i> sp., <i>Phyllosticta capitalensis</i> (as <i>Guignardia mangiferae</i>), <i>Helotiales</i> sp., <i>Humicola</i> sp., <i>Microdochium</i> sp., <i>Mucor</i> sp., <i>Penicillium biourgeianum</i> , <i>Pestalotiopsis karstenii</i> , <i>Plectosphaerella cucumerina</i> , <i>Phomopsis amygdali</i> , <i>Phomopsis</i> sp., and <i>Trichoderma asperellum</i>	Fronds and rhizoids	China	Gao et al. (2019)
<i>Diacalpe aspidiodes</i>	<i>Calonectria</i> sp., <i>Cladosporium tenuissimum</i> , <i>Colletotrichum gloeosporioides</i> , <i>C. acutatum</i> , <i>C. boninense</i> , <i>Helotiales</i> sp., <i>Humicola</i> sp., <i>Pestalotiopsis karstenii</i> , <i>Pezicula carpinea</i> , <i>Plectosphaerella cucumerina</i> , <i>Phomopsis</i> sp. and <i>P. amygdali</i> .	Fronds and rhizoids	China	Gao et al. (2019)
<i>Diplazium</i> spp.	<i>Aspergillus</i> sp., <i>A. fumigatus</i> , <i>A. versicolor</i> , and <i>Verticillium</i> sp.	Rhizome	Malaysia	Affina-Eliya et al. (2014)
<i>Elaphoglossum doanense</i>	<i>Colletotrichum</i> sp. and <i>Xylaria</i> sp.	Fronds	Costa Rica	Del Olmo-Ruiz & Arnold (2014)

Table 2 Continued.

Fern species	Fungal endophytes	Isolate Sources	Origin	References
<i>Gleichenia linearis</i>	<i>Aspergillus niger</i> , <i>Aureobasidium</i> sp., <i>Cladosporium</i> sp., <i>Colletotrichum</i> sp., <i>Penicillium</i> sp., <i>Phialophora</i> sp., and <i>Phyllosticta</i> sp.	Pinnae	India	Kumaresan et al. (2013)
<i>Lygodium flexuosum</i>	<i>Colletotrichum</i> spp., <i>Phomopsis</i> sp., <i>Phyllosticta</i> sp., <i>Sporormiella</i> sp., <i>Xylaria</i> spp.	Leaflets	India	Kumaresan et al. (2013)
<i>Neprophelis biserrata</i>	<i>Annulohypoxylon</i> sp.	Fronds	Costa Rica	Del Olmo-Ruiz & Arnold (2014)
<i>Phlebodium pseudoaureum</i>	<i>Spadiocoides</i> sp.	Fronds	Costa Rica	Del Olmo-Ruiz & Arnold (2014)
<i>Pteridium aquilinum</i>	<i>Stagnospora pteridiicola</i>	Fronds	UK	Fisher (1996)
<i>Plagiogyria maxima</i>	<i>Beltrania rhombica</i> , <i>Ceratobasidium</i> sp., <i>Colletotrichum gloeosporioides</i> , <i>C. acutatum</i> , <i>C. boninense</i> , <i>Cylindrocladiella</i> sp., <i>Nemania primolutea</i> , <i>Helitiales</i> sp., <i>Humicola</i> sp., <i>Mucor</i> sp., <i>Nigrospora oryzae</i> , <i>Penicillium expansum</i> , <i>Pestalotiopsis cocculi</i> , <i>P. karstenii</i> , <i>Plectosphaerella cucumerina</i> , <i>Phialocephala</i> sp., and <i>Phomopsis</i> sp.	Fronds and rhizoids	China	Gao et al. (2019)
<i>Pteris</i> sp.	<i>Acremonium</i> sp., <i>Aspergillus terreus</i> , <i>Aureobasidium</i> sp., <i>Botryodiplodia</i> sp., <i>Colletotrichum</i> spp., <i>Fusarium</i> sp., <i>Phomopsis</i> sp.	Pinnae	India	Kumaresan et al. (2013)
<i>Pyrrosia piloselloides</i>	<i>Aureobasidium melanogenum</i> , <i>Penicillium alli-sativi</i> , and <i>Aspergillus flocculosus</i>	Trophophy, Sporophyll Fronds	Indonesia	Asiandu et al. (2019)
<i>Salvinia natans</i>	<i>Cladosporium tenuissimum</i> , <i>C. cladosporioides</i> , <i>Leptosphaeria microscopica</i> , <i>Fusarium incarnatum</i> , <i>Talaromyces helices</i> , <i>Paraphaeosphaeria verruculosa</i> , <i>Gibberella zeae</i> , <i>Phoma</i> sp., and <i>Sarocladium strictum</i>	Roots	Korea	You et al. (2015)
<i>Selaginella</i> sp.	<i>Botryodiplodia</i> sp., <i>Colletotrichum</i> spp., <i>C. falcatum</i> , <i>Phomopsis</i> sp., <i>Phyllosticta</i> sp.	Leaves and stems	India	Kumaresan et al. (2013)

***Adiantum* sp.**

One of *Adiantum* species, *A. cappilus-veneris* was reported capable of producing various kinds of bioactive compounds as triterpenoids and terpenoids. These secondary metabolite extracts have antibacterial, antifungal, anti-inflammatory, hypoglycemic, and lithotriptic activity (Ahmed et al. 2018). Thus, the endophytic fungi isolated from the fern can be used as potential sources of some bioactive compounds. Some endophytic species isolated from *Adiantum* sp. is presented in Table 2 (Kumaresan et al. 2013).

Asplenium nidus

Suhartina et al. (2018) reported *Asplenium nidus* as host of several endophytic fungi. The isolation was conducted using fern leaves and incubated using PDA media for 7–10 days. Based on

that research conducted by Suhartina et al. (2018), four genera were isolated from *Asplenium nidus* leaves, including *Aspergillus*, *Gliocladium*, *Humicola*, and *Neoscytalidium*.

Many species in *Aspergillus*, *Gliocladium* and *Humicola* isolated from other hosts have been reported to produced bioactive compounds. *Aspergillus terreus* produced bioactive compounds as antioxidants and anti-dermophytes, including mellein, isocoumarin, kigelin, and 3R,4R)-6,7-dimethoxy-4-hydroxymellein (Choudhary et al. 2004). *Gliocladium virens* produced fructooligosaccharides used in the food industry as additives and food quality enhancers (Fialho et al. 2013). Also, *Humicola lanuginosa* produced xylanase enzymes essential in hydrolyzing xylan polymers (Kamra & Satyanarayana 2004). Meanwhile, *Neoscytalidium* is a plant pathogen causing stem infection in some plants such as dragon fruit plant (Ratanaprom et al. 2021).

Coniogramme petelotii

Another fern reported as the endophytic fungal host is *Coniogramme petelotii*. This fern is a member of the Pteridaceae. It has free vascular tissue which the base of the pinnules being rounded or slightly cordate (Wang et al. 2019). Some fungal endophytes were isolated from the fronds and rhizoids of this fern as presented in Table 2 (Gao et al. 2019).

Arthrimum can be found as endophytes on many host plants and has been reported to be potentially used in pharmaceutical industries (Crous & Groenewald 2013). *Arthrimum* sp. can produce some bioactive compounds (Heo et al. 2018). Those compounds were cyclocitral, renan-2-one, sclareol, cembrene, and curcumene. These bioactive compounds were known to be effective against Gram-negative and Gram-positive bacteria (Pansanit & Pripdeevech 2018). Also, *A. arundinis* isolated from tobacco leaves produced diorcinol M-O. This bioactive compound useful as an antifungal as well as high cytotoxicity activity (Wang et al. 2019).

Fusarium is a potent endophytic fungus. Several species have been reported to be able of producing some essential bioactive compounds (Ding et al. 2012, Ruma et al. 2013). Secondary metabolites from *Fusarium* spp. can inhibit the growth of some pathogenic bacteria including *Bacillus subtilis*, *Staphylococcus aureus*, and *Escherichia coli* (Salini et al. 2014). The endophytic fungus, *Microdochium* sp., is generally a plant pathogen (Huang et al. 2020). *Microdochium bolleyi* produce some isocoumarin derivatives potentially used as antibacterial, antifungal, and anti-algal (Zhang et al. 2008).

An endophytic fungus, *Mucor* sp., isolated from rubber plant (*Hevea brasiliensis*) in producing secondary metabolite extract which was able to inhibit the growth of the pathogenic fungus *Rigidoporus microporus*. This endophytic fungus can be used as biocontrol agent (Izzati et al. 2019). Therefore, *Mucor* sp. isolated from *C. petelotii* maybe also produce the secondary compounds inhibiting the pathogenic fungus.

Diacalpe aspidioides

Several endophytic fungi were also isolated from leaves and stems or roots of *Diacalpe aspidioides* (Table 2; Gao et al. 2019). *Cladosporium* can be found on various hosts worldwide (Bensch et al. 2012). *Cladosporium tenuissimum* is one of the endophytic fungi isolated from *D. aspidioides* (Gao et al. 2019) capable of producing several bioactive compounds like osporol (Nasini et al. 2004) that were cytotoxically inhibiting cancer cell proliferation. This bioactive compound also acts as an antimicrobial agent (Katoch et al. 2017).

Colletotrichum spp. are plant pathogens causing anthracnose (Damm et al. 2012) which has great effects in agricultural sector due to great losses caused by the infection by this fungus in many plants (Moreira et al. 2020), such as in tropical fruits like avocado (*Persea americana*) and papaya (*Carica papaya*) (de la Rosa-García et al. 2018). Many *Colletotrichum* species are capable of producing secondary metabolites (Moraga et al. 2019), such as *C. gloeosporioides* isolated from *Uncaria rhynchophylla* produced a bioactive in the form of colletotrichine. This chemical compound inhibited acetylcholinesterase activity (Chen et al. 2018a). *Colletotrichum gloeosporioides* isolated from this fern may also produce colletotrichine compound or others potential bioactive compounds pending further study.

***Diplazium* spp.**

Several endophytic fungi have also been reported from *Diplazium* spp. (Athriaceae). Several species of *Diplazium* have limited geographic distribution with specific microhabitats. Also, there is a lack of studies reporting on endophytic fungi isolated from the genus (Affina-Eliya et al. 2014).

Affina-Eliya et al. (2014) obtained several endophytic fungi isolated from *Diplazium* species including *D. accedens*, *D. asperum*, *D. sorzogonense*, and *D. tomentoseum*. After five days of incubation, each of the endophytic fungal isolate was characterized by their macroscopic and microscopic morphology. The four isolates were identified as *Aspergillus* sp., *Aspergillus* *igatus*, *A. versicolor* and *Verticillium* sp. (Affina-Eliya et al. 2014). *Aspergillus* have been widely used in various industrial activities like in the pharmaceutical and food industry (Tsang et al. 2018). *Aspergillus* sp. isolated from *Bethencourtia palmensis* is capable producing mellein that potentially used as antifungal agent (Morales-Sánchez et al. 2021). Also, *Aspergillus* sp. isolated from mangrove showed the ability as anti-inflammatory by producing steroids and ergosteroid compounds (Liu et al. 2018). *A. fumigatus* (strain AUMC 8002) was reported for its ability to produce Pseurotin A, a chemical important as an anti-cancer agent (Helal et al. 2019).

A. versicolor Faesay4 produced L-glutaminase which acts as a chemotherapeutic agent in overcoming malignancies. This metabolite was effective against liver, colon, lung, and cervical cancer cells also has high antioxidant properties (Awad et al. 2021). Some species were reported as plant pathogens (Inderbitzin et al. 2011). *Verticillium* can produce naringenin which inhibited the growth of *Curvularia lunata*. Therefore, it is one of the potential sources of a bio-fungicides agent (Ferreira et al. 2017).

Elaphoglossum doanense

The endophytes, *Colletotrichum* sp. and *Xylaria* sp. were isolated from *Elaphoglossum doanense* (Del Olmo-Ruiz & Arnold 2014). *Colletotrichum* sp. is a fungus that has wide bioprospecting. The fungi isolated from the *Artocarpus heterophyllus* produced some bioactive secondary metabolites. It was able to synthesize TiO₂ nanoparticles potentially as an anticancer agent (Sunkar et al. 2017). *Xylaria* is a potential endophyte producing several essential chemical compounds (Ding et al. 2003). *Xylaria* sp. FPL-25 produced antimicrobial compound in the form of polyketide inhibited the growth of *Escherichia coli*, *Staphylococcus aureus*, *Salmonella typhi*, and *Bacillus subtilis* bacteria. The secondary metabolite extract of *Xylaria* sp. FPL-25 was also able to inhibit the growth of the fungi *Fusarium moniliforme*, *Microsporium* spp., and *Aspergillus flavus* (Rakshith et al. 2020). *Xylaria* sp. isolated from liverworts (*Bazzania* sp.) has a mutual symbiosis with its host plants through various interactions as producing some secondary metabolites which are toxic to the host plant pathogens (Davis et al. 2003). Moreover, *Xylaria* sp. has also reported on *Bolbitis portoricensis* (Del Olmo-Ruiz & Arnold 2014).

Eupolypods

Del Olmo-Ruiz & Arnold (2014) isolated endophytic fungi from *Bolbitis portoricensis*, *Cyclopeltis semicordata*, *Elaphoglossum doanense*, *Neprophelis biserrata*, *Oleandra articulata*, *Phlebodium pseudoaureum*, and *Tectaria athyrioides*. They obtained several endophytes from these hosts. Some of the endophytic fungal isolates in these ferns belonged to the Basidiomycota in different classes. Based on the phylogenetic analysis, 90 OTUs (Operational Taxonomic Units) belonged to Ascomycota, including 21 isolates in Dothideomycetes, 25 isolates in Eurotiomycetes, one isolate in Saccharomycetes, and 435 isolates in Sordariomycetes. Of the Sordariomycetes class, 21 OTUs (62%) of endophytic fungal isolates are members of the subclass Xylariomycetidae, 16 OTUs of Sordariomycetidae, and 15 OTUs of Hypocreomycetidae.

Endophytic fungi frequently isolated from these Eupolypods were identified to the genera *Annulohyphoxylon*, *Geoshmithia*, *Mycocleptodiscus*, *Penicillium*, *Phialophora* and *Spadiocoides* (Del Olmo-Ruiz & Arnold 2014). *Penicillium* spp. are important sources of secondary metabolites (Mady & Haggag 2020). One example of this fungal species is *P. expansum* which is capable of producing twenty-eight kinds of bioactive compounds that important as antibacterial agents. Some

of these bioactive compounds were Levoglucosenone, Edulan II, Ethanetiol, propanedioic acid, amino-diethyl ester, valeric acid¹⁶⁴, phthalic acid, picrotoxin, and butyl undecyl ester. These metabolites were effective against *Escherichia coli*, *Staphylococcus aureus*, *Klebsiella pneumoniae*, *Pseudomonas aeruginosa*, and *Proteus mirabilis*¹⁵⁵ (Hamza et al. 2015). Meanwhile, the endophytic fungus *Phialophora mustea* produced secondary metabolites in the form of Phialomustin A-D which function as antimicrobial, cytotoxic, and antioxidant (Nalli et al. 2015). *Mycocleptodiscus* sp. produced bioactive compound as antimicrobial agent in the form of mycoleptione (Siriwach et al. 2012). *Annulohyphoxylon* isolated from *Taxus wallichiana* also produced bioactive metabolite including flavonoid as antibacterial and antioxidant agent, as well as taxol as anticancer agent (Gauchan et al. 2021).

Gleichenia linearis

Gleichenia linearis is capable of producing some secondary metabolite compounds such¹⁴⁸ as flavonoids, terpenoids, saponins, and phenolic compounds (Zakiah et al. 2017). Some of the endophytic fungi¹²⁹ isolated from the pinnae of *G. linearis* were identified as *Aspergillus niger*, *Aureobasidium* sp., *Cladosporium* sp., *Colletotrichum* sp., *Penicillium* sp., *Phialophora* sp., *Phyllosticta* sp., and other unidentified isolates (Kumaresan et al. 2013).

Aspergillus niger and *Penicillium* sp. have been reported¹⁴⁰ in producing secondary metabolites as antioxidants (Chandra et al. 2020). The two types of endophytic fungi (*Aspergillus niger* and *Penicillium* sp.) isolated from *Tabebuia argentea* were able to produce secondary metabolites included tannins, steroids, flavonoids, and alkaloids (Govindappa et al. 2013). Furthermore, *Aureobasidium* sp. is essential in industrial activities as a pullulan. *Aureobasidium* sp. is an antagonistic fungus to various pathogens (Arzanlou 2014). Besides, *Cladosporium* sp. has reported in producing secondary metabolites as antibacterial, antioxidant (Rekha & Shivanna 2014), and cytotoxic (Pednekar et al. 2017). A slow growing fungus, *Phialophora* sp. isolated from *Senecio flavus* was also reported to produce bioactive compounds that have anti-cytotoxicity included five polyketides compounds (Abdelhamid et al. 2019).

Lygodium flexuosum

Lygodium flexuosum is a member of the Lygodiaceae family. This fern is often used as a traditional medicinal plant in India²¹⁶ to treat several diseases such as jaundice and eczema (Yadav et al. 2012). It contains various secondary metabolites such as saponins, flavonoids, alkaloids, and coumarin. Kumaran et al. (2013) isolated endophytic fungi from its leaflets and identified as *Colletotrichum* spp., *Phomopsis* sp., *Phyllosticta* sp., *Sporormiella* sp., *Xylaria* spp., and some other unidentified species. *Colletotrichum* had been reported as bioactive metabolites producing fungus that produce terpenes, steroids, phenolics, and pyrones which have biological activities (Kim & Shim 2019). Meanwhile, *Phomopsis* sp. had been reported as laccase enzyme producer (Dai et al. 2010), *Phyllosticta melochiae* isolated from *Melochia corchorifolia* produced taxol as anticancer drug (Kumaran et al. 2008), and *Sporormiella minimoides* isolated from *Hintonia latiflora* also produced some metabolites including polyketides, ziganein, brocaenol B, and corymbiferone (Leyte-Lugo et al. 2013).

Plagiogyria maxima

Plagiogyria is a group of ferns that produce some secondary metabolites derived from phenol groups (Srinivasan & Pierce 2016). *Plagiogyria maxima* has been reported as a host for endophytic fungi is (Gao et al. 2019). Some of the endophytic fungi isolated from the *Plagiogyria maxima* were *Beltrania rhombica*, *Ceratobasidium* sp., *Colletotrichum acutatum*, *C. boninense*, *C. gloeosporioides*, *Cylindrocladiella* sp., *Nemania primolutea*, *Helitiales* sp., *Humicola* sp., *Mucor* sp., *Nigrospora oryzae*, *Penicillium expansum*, *Pestalotiopsis cocculi*, *Pestalotiopsis karstenii*, *Plectosphaerella cucumerina*, *Phialocephala* sp., and *Phomopsis* sp. (Gao et al. 2019).

Penicillium expansum produces several secondary metabolites as penicillic acid (Atkinson & Sherwood 1987), patulin, polyketides, and terpenes (Tannous et al. 2018). It can also produce

various kinds of enzymes that are potential in many industrial fields (Atkinson & Sherwood 1987). *Pestalotiopsis* is a genus of endophytic fungi found widely in many host plants and potentially used as secondary metabolites producer (Elkhateeb & Daba 2021). The genus is known as a plant pathogen even it is one of the endophytic fungi capable of producing several bioactive compounds as taxol (Maharachchikumbura et al. 2011). Besides, *Phomopsis* sp. is also one of the endophytic fungi capable of producing bioactive compounds inhibiting some plant pathogenic fungi (Ma et al. 2014). Also, *Leptosphaerella cucumerina* is an endophytic fungus (Arzanlou et al. 2013) that is essential as a biocontrol agent against nematodes (Atkins et al. 2003), anti-biofilm, antivirulence (Zhou et al. 2017), producing secondary metabolites including plectosphaeroic acids A, B, and C used as Indoleamine 2,3-Dioxygenase inhibitors (Carr et al. 2009), and biomineralizing carbonates (Pasquale et al. 2019).

***Pteris* spp.**

Pteris spp. are capable of producing some secondary metabolites including saponins, alkaloids, flavonoids, tannins, and phenolic compounds (Celin et al. 2013). Several endophytic fungi were isolated from their pinnae, including *Acremonium* sp., *Aspergillus tereus*, *Aureobasidium* sp., *Botryodiplodia* sp., *Colletotrichum* spp., *Fusarium* sp., and *Phomopsis* sp. (Kumaresan et al. 2013).

Acremonium sp. is an endophytic fungus belongs to the Hypocreaceae family in Ascomycota (Fletcher et al. 2017). This fungus is one of the fungi that can produce protease enzymes essential in industries (Jain et al. 2012) and antioxidants (Elfita et al. 2012). *Botryodiplodia* sp. has blackish-brown colony, with hyaline single-cell conidia (Amin 2013). Member of *Botryodiplodia* such as *B. theobromae* isolated from *Morinda citrifolia* can produce taxol, an essential anticancer bioactive compound (Pandi et al. 2010). produce antibacterial compounds including alkaloids, dipeptides, coumarin and isocoumarins, aldehyde, sesquiterpene, fatty alcohol (Zaher et al. 2015). Thus, *Botryodiplodia* sp. isolated from *Pteris* may also produce the anticancer bioactive compound. Further, *Aspergillus tereus* has reported to produce forty-seven bioactive compounds such as hematoporphyrin that inhibit the growth of some pathogenic bacteria. These metabolites are also capable of being anti-fungal agents (Mohammed et al. 2016). Also, *Aspergillus tereus* (Gautam & Bhadauria 2012) produced forty-seven bioactive compounds such as hematoporphyrin that inhibit the growth of some pathogenic bacteria. These metabolites are also capable of being anti-fungal agents (Mohammed et al. 2016).

Pyrrosia piloselloides

Another fern reported as a host of endophytic fungi was dragon scales fern or *Pyrrosia piloselloides*. The endophytic fungi isolated from this fern were reported by Asiandu et al. (2019). Based on the isolation process, they obtained thirteen isolates of endophytic fungi from the fern. Five isolates were isolated from its trophophyll fronds, and eight isolates were isolated from its sporophyll fronds. Each fungal secondary metabolite was tested for its antibacterial activity. Based on the tests and characterization, it was known that three isolates have strong antibacterial activity. They were *Aureobasidium melanogenum* and *Penicillium alli-sativi* isolated from trophophyll fronds, and *Aspergillus flocculosus* isolated from sporophyll fronds. Some bioactive compounds viz. tannins, terpenoids, phenolics, alkaloids, and steroids were also detected from this fern (Asiandu et al. 2019).

Salvinia natans

Salvinia natans originating from Korean wetlands was also reported as an endophytic fungal host. Species isolated from this fern identified as were *Cladosporium cladosporioides*, *C. tenuissimum*, *Fusarium incarnatum*, *Gibberella zaeae*, *Leptosphaeria microscopica*, *Paraphaeosphaeria verruculosa*, *Phoma* sp., *Sarocladium strictum* and *Talaromyces helices* (You et al. 2015). *Cladosporium tenuissimum* is capable of producing flavonoid, the late from *Swietenia mahagoni* leaf stalk also can produce bioactive metabolite in the form of 5-hydroxy-2-

oxo-2H-piran-4-yl) methyl acetate) which had antioxidant activity (Fadhilla et al. 2019). *Fusarium incarnatum* is another endophytic fungus potentially used in exploring new bioactive compounds. *Fusarium incarnatum* as isolated from *Aegicera corniculatum* can also produce some alkaloids such as fusarine and fusamine inhibiting HeLa human cell line (Ding et al. 2012). The Genus of *Talaromyces* is an important genus in producing chemical products. The genus can be isolated both from terrestrial and marine environment. It synthesizes terpenoids, steroids, poliketides, coumarins, quinones, and other bioactive compounds (Lan & Wu 2020). Also, *Gibberella zeae* is a pathogenic fungus that can produce some metabolites such as rubrofusarin which can be used as antibacterial agent (Kim et al. 2005).

***Selaginella* sp.**

Selaginella is a member of the family Selaginellaceae (Selaginellales, Isoetopsida) (Antony & Thomas 2011, Setyawan 2011). The fern was reported to produce various secondary metabolite compounds, including bioflavonoids (Zou et al. 2020). *Selaginella* is often used as a traditional medicine to treat some diseases (Setyawan 2011). Endophytic fungi obtained from the leaves and stems of this fern were identified as *Botryodiplodia* sp., *Colletotrichum falcatum*, *Colletotrichum* spp., *Phomopsis* sp., and *Phyllosticta* sp. (Kumaresan et al. 2013). *Phomopsis* sp. is an endophytic fungus known as secondary metabolites producer. Other *Phomopsis* species can produce sabinene which is monoterpene volatile organic compound (VOC). This compound was effectively inhibited the growth of some fungal species including *Pythium*, *Phytophthora*, *Botrytis*, *Colletotrichum* and other pathogenic fungi. Sabinene is also a potential source of the future aircraft fuel (Singh et al. 2011).

Non-mycorrhizal endophytic fungi associated with mosses (Bryophytes)

Mosses are plants used as sources of secondary metabolites such as terpenoids and aromatic compounds. These widely distributed plants are divided into three distinct phyla including Bryophyta, Marchantiophyta, and Anthocerotophyta. Mosses are classified as predecessors. They are useful in producing antifungal, antibacterial, anti-allergy, cytotoxic, antiviral, antineoplastic, anti-obesity, and so on (Asakawa et al. 2013). Some studies reported several endophytic fungi associated with mosses included *Andreaea* sp. (Yu et al. 2014), *Barbilophozia hatcheri* (Zhang et al. 2013), *Chorisodontium aciphyllum* (Yu et al. 2014), *C. aciphyllum* (Zhang et al. 2013), *Hylocomium splendens*, *Polytrichastrum alpinum* (Yu et al. 2014), *Polytrichum commune* (Gao et al. 2019), *P. strictum* (Yu et al. 2014), and *Sanionia uncinata* (Zhang et al. 2013) as compiled in Table 3.

Table 3 Endophytic fungi associated with mosses (Bryophytes)

Mosses species	Fungal endophytes	Isolate Sources	Origin	References
<i>Andreaea</i> sp.	<i>Lecythophora hoffmanii</i> and <i>Contiochaeta ligniaria</i>	Tissue Segments	King George Island, Antarctica	Yu et al. (2014)
<i>Barbilophozia hatcheri</i>	<i>Annulohypoxyton</i> sp., <i>Hyphodiscus</i> sp., <i>Rhizoscyphus</i> sp., Dermateaceae., Hyaloscyphaceae, Xylariaceae, and Helotiales	Tissue Segments	King George Island, Antarctica	Zhang et al. (2013)
<i>Chorisodontium aciphyllum</i>	<i>Massarina rubi</i>	Tissue Segments	King George Island, Antarctica	Yu et al. (2014)
<i>Chorisodontium aciphyllum</i>	<i>Hyphodiscus</i> sp., <i>Rhizoscyphus</i> sp., Hyaloscyphaceae., Helotiales sp., and <i>Sporidiobolales</i> sp.	Tissue Segments	King George Island, Antarctica	Zhang et al. (2013)
<i>Hylocomium splendens</i>	<i>Penicillium biourgeianum</i> , <i>P. chrysogenum</i> , <i>P. expansum</i> , <i>Calonectria eucalypti</i> , <i>Ceratobasidium</i> sp.	Photosynthetic tissues and rhizoids.	China	Gao et al. (2019)

Table 3 Continued.

Mosses species	Fungal endophytes	Isolate Sources	Origin	References
<i>Hylocomium splendens</i>	<i>Chaetomium cupreum</i> , <i>Colletotrichum boninense</i> , <i>C. gloeosporioides</i> , <i>Fusarium</i> sp., <i>Nigrospora oryzae</i> , and <i>Trichoderma asperellum</i>	Photosynthetic tissues and rhizoids.	China	Gao et al. (2019)
<i>Polytrichastrum alpinum</i>	<i>Pythium</i> sp.	Tissue Segments	King George Island, Antarctica	Yu et al. (2014)
<i>P. commune</i>	<i>Calonectria eucalypti</i> , <i>Chaetomium globosum</i> , <i>Colletotrichum boninense</i> , <i>C. gloeosporioides</i> , <i>Coprinellus disseminates</i> , <i>Helotiales</i> sp., <i>Microdochium</i> sp., <i>Mortierella</i> sp., <i>Mucor</i> sp., <i>Muscodor albus</i> , <i>Nemania primolutea</i> , <i>Nigrospora oryzae</i> , <i>Penicillium biourgeianum</i> , <i>Pestalotiopsis karstenii</i> , <i>Plectosphaerella cucumerina</i> , <i>Phomopsis amygdali</i> , <i>Phomopsis</i> sp., <i>Ramichloridium apiculatum</i> , <i>Rhizomucor variabilis</i> , and <i>Trichoderma asperellum</i>	Photosynthetic tissues and rhizoids.	China	Gao et al. (2019)
<i>P. strictum</i>	<i>Antarctomyces psychrotrophicus</i> , <i>Geomyces</i> sp., and <i>Mortierella parvispora</i>	Tissue Segments	King George Island, Antarctica	Yu et al. (2014)
<i>Sanionia uncinata</i>	<i>Chaetomium</i> sp., <i>Eocronartium</i> sp., <i>Helotiales</i> sp., <i>Hyphodiscus</i> sp., <i>Mrakia</i> sp., <i>Rhizoscyphus</i> sp., <i>Rhodotorula</i> spp., <i>Scopulariopsis</i> sp., <i>Thelebolus</i> sp., and <i>Xenopolyscytalum</i> sp.	Tissue Segments	King George Island, Antarctica	Zhang et al. (2013)

2 Bioprospecting of non-mycorrhizal endophytic fungi associated with mosses

Barbilophozia hatcheri

Barbilophozia hatcheri is a group of mosses from the family Lophoziaceae. This moss is known for producing hatchone (Nagashima et al. 1999). Some of the endophytic fungi isolated from *Barbilophozia hatcheri* were identified as *Annulohypoxylon* sp., *Hyphodiscus* sp., *Rhizoscyphus* sp., and species in Dermateaceae, Helotiales, Hyaloscyphaceae, and Xylariaceae (Zhang et al. 2013). *Annulohypoxylon* sp. was reported to be able to produce volatile organic compounds as antineoplastic (Li et al. 2020), antimicrobial, and antioxidant (Gauchan et al. 2021). *Rhizoscyphus* sp. was reported to be able to produce chitinase, cellulase, and glucoside enzymes (Newsham et al. 2018). The endophytic fungal family Xylariaceae is a family of fungi that has about 76 genera (Daranagama et al. 2015). Taxa in this family produces various important chemical compounds including coriloxin, nemononediol, cytochalasans, terpenoids, non-ribosomal peptides, polyketides, and Benzenoids (Becker & Stadler 2021). Endophytic fungus of Xylariaceae isolated from *Quercus gilva* showed its strong activity toward α -glucosidase and potentially used as antidiabetic medicine (Indrianiingsih & Tachibana 2017). *Xylaria* sp. isolated from *Isodon sculponeatus* also produced some secondary metabolites such as xylariahins (Chen et al. 2018b).

Chorisodontium aciphyllum

Chorisodontium aciphyllum is a member of the Dicranaceae (Byun et al. 2019). Some endophytic fungi were isolated from *C. aciphyllum*, including *Hyphodiscus* sp., *Rhizoscyphus* sp., species of *Helotiales* and *Hyaloscyphaceae*, as well as some isolates from the *Sporidiobolales* group (Zhang et al. 2013). Additionally, *Massarina rubi* was also isolated from *C. aciphyllum* (Yu et al. 2014). *Helotiales* sp. and *Rhizoscyphus* sp. were reported for their metabolites bioactivity. The metabolite extracts of *Helotiales* sp. and *Rhizoscyphus* sp. showed medium cytotoxicity toward lymphocytic cell line (Ding et al. 2016). *Hyphodiscus* is a genus of fungi that usually associated with plant roots (Hosoya 2021). *Hyphodiscus hymeniophilus* produced light-induced secondary metabolite in the form of hyphodiscorubrin that is potentially used as sunlight protection (Kramer et al. 2020). Meanwhile, *Hyaloscyphaceae* is a metropolitan family with small apothecia covered by differentiated hairs (Han et al. 2014, Uzun et al. 2017). One species of the family, *Lachnum virgineum*, produced norcolensoic acid as antibacterial and phytotoxic agent (Shiono et al. 2018).

Hylocomium splendens

Hylocomium splendens was also reported as an endophytic fungal host. Gao et al. (2019) successfully obtained some *Penicillium* spp., including *P. biourgeianum*, *P. chrysogenum*, and *P. expansum*. *Penicillium* spp. used as the sources of bioactive compounds in drug discovery (Mady & Haggag 2020). The bioactive compounds produced by these fungi include Acetophthalidin, penicillin, Conidiogenone, Pyrenocine E, and other compounds (Nicoletti & Trincone 2016). Also, several other endophytic fungi were isolated from *Hylocomium splendens*. They were *Calonectria eucalypti*, *Ceratobasidium* sp., *Chaetomium cupreum*, *Colletotrichum boninense*, *C. gloeosporioides*, *Fusarium* sp., *Nigrospora oryzae*, and *Trichoderma asperellum* (Gao et al. 2019). *Chaetomium cupreum* isolated from *Mussaenda luteola* produced some bioactive secondary metabolites such as dodecanol. The metabolite extract was significantly inhibited the growth of *Mycobacterium* with Minimum Inhibitory Concentration (MIC) 6,25 µg/mL. The metabolites also showed the cytotoxicity againsts MCF-7 breast cancer line with cytotoxicity of 52% within the concentration of 100 µg/mL (Shylaja & Sathiavelu 2019). *Colletotrichum gloeosporioides* produced antibacterial extract as hexadecanamide (Premjanu & Jaynthy 2015). Also, the endophytic fungi of *Fusarium* sp. and *Trichoderma* sp. isolated from *Garcinia* were reported to produce secondary metabolites as antibacterial, antioxidant, and anti-inflammatory agents (Ruma et al. 2013).

Polytrichum commune

Polytrichum commune produces secondary metabolites that are antipyretic and antitodal (Asakawa et al. 2013). Some endophytic fungi isolated from *P. commune* as shown in Table 3 (Gao et al. 2019). *Chaetomium globosum* is one of the metabolite producers that are potentially used in industrial activities. This isolate produced some enzymes including cellulase, lipase, laccase, pectinases, chitinases and proteases. The enzymes can be used for simplifying industrial raw materials (Abdel-Azeem et al. 2014). Secondary metabolite extract of *Colletotrichum gloeosporioides* showed effective antibacterial activity against *Staphylococcus aureus* which is resistant to penicillium, vancomycin, and methicillin. The minimum inhibitory concentration (MIC) value was 31,25 µg/mL (Arivudainambi et al. 2011). *Mortierella* sp. produced antioxidative compounds in the form of phenols (Hirota et al. 1997). *Muscodor albus* isolated from *Cinnamomum zeylanicum* produced alcohols, esters, ketones, lipids, and acids as antifungal and antibacterial agents (Strobel 2006). *Nigrospora oryzae* was reported for its antidiabetic potential by producing three important compounds including abscisic acids and altersolanol A derivatives (Uzor et al. 2017). Pestalrone A and Pestalrone B extracted from *Pestalotiopsis karstenii* which was isolated from stem cell of *Carmellia sasanqua* showed their anticancer activities against human cervical cancer cell (HeLa) and human glioma cell line (U-251) (Luo et al. 2012). *Plectosphaerella cucumerina* produced patulin and emodin which showed their potential as anti-biofilm and antivirulence bioactive compounds (Zhou et al. 2017). *Rhizomucor variabilis* synthesized lipase for

130 industrial application (Bancerz et al. 2015). Also, *Trichoderma asperellum* produced volatile organic compounds (VOCs) and non volatile organic compounds (nVOCs) used as antimicrobial agents (Stracquadanio et al. 2020).

Sanionia uncinata

Sanionia uncinata is capable of producing antioxidants, such as phenolic compounds (Bhattarai et al. 2008). Several endophytic fungi belonging to Ascomycota and Basidiomycota were isolated from *S. uncinata* including *Chaetomium* sp., *Eocronartium* sp., *Helotiales* sp., *Hyphodiscus* sp., *Mrakia* sp., *Rhizoscyphus* sp., *Rhodotorula* spp. *Scopulariopsis* sp., *Thelebolus* sp., and *Xenopolyscytalum* sp., (Zhang et al. 2013).

Chaetomium sp. produces antioxidants, antimicrobials, and anticancer agents (Rollando et al. 2017). *Hyphodiscus* is a genus of fungi whose asexual form is still unknown. The genus has eleven species (Johnston et al. 2014). *Hyphodiscus hymeniophilus* produces hyphodiscorubrin as sunlight protector (Kramer et al. 2020). *Scopulariopsis* sp. produced some enzymes used in the biodelignification process (Valencia & Meitiniarti 2017). *Mrakia* sp. was also reported as enzymes producing fungus included amylase, cellulase, and lipase (Carrasco et al. 2012). *Rhodotorula* spp. are carotenoids (Zhao et al. 2019) and enzymes producing yeasts. Also, they are included as oleaginous yeasts that are useful in lipid production (Kot et al. 2016).

Other Mosses

Some mosses that originated from the Antarctic Maritime were also reported as endophytic fungal hosts. A study conducted by Davey et al. (2009) reported some endophytic fungi isolated from several mosses of Antarctic Maritime. Endophytic fungi including *Lecytophora hoffmanii* and *Coniochaeta ligniaria* were isolated from *Andreaea* sp. Endophytic fungus isolated from *Chorisodontium aciphyllum* was *Massarina rubi*. Endophytic fungi including *Geomyces* sp., *Mortierella* sp., and *Antarctomyces psychrotrophicus* were also isolated from *Polytrichum strictum* (Yu et al. 2014).

The presence of endophytic fungi in several mosses including *Hylocomium splendens*, *Pleurozium schreberi*, and *Polytrichum commune* has also been reported (Davey et al. 2009). The endophytic fungal biomass of these mosses was detected from the photosynthetic leaf tissues and the senescent tissues. Based on the identification, the endophytic fungal biomass contained in the photosynthetic leaf tissues was 0.2–1.2%. Meanwhile, the fungal biomass found in the senescent tissues of the mosses was 1.3–4% (Davey et al. 2009).

Conclusions and Future Perspective

This review discusses the diversity and potential of endophytic fungi associated with ferns and mosses that can be used as a reference for future studies regarding bioprospecting of endophytic fungi associated with lower plants. Ferns and mosses are two groups of plants that are important for producing bioactive compounds and industrial enzymes. Some studies reported that the bioactive compounds and enzymes were obtained from endophytic fungi residing in these plants. However, there are huge gaps and opportunities for exploring and obtaining new metabolites from endophytic fungi colonizing ferns and mosses. The numbers of endophytic fungi found in mosses and ferns are quite large and varied. In this review, ferns contain more endophytic fungal species than mosses. Some common endophytic fungi found on ferns are *Aspergillus* spp., *Colletotrichum* spp., *Fusarium* spp., *Penicillium* spp., *Phomopsis* sp. and *Trichoderma* sp. Meanwhile, some common endophytic fungi found on mosses are *Chaetomium* spp., *Colletotrichum* spp., *Nigrospora* sp., *Penicillium* spp. and *Rhizoscyphus*.

These endophytic fungi are capable of producing some bioactive compounds which are useful in various industries like the pharmaceutical industry. Also, many kinds of enzymes produced from endophytic fungi are essential in industrial activities. Reports regarding the exploration and potential of endophytic fungi isolated from mosses and ferns are still limited compared to higher plants. Thus, it is needed to explore endophytic fungi from the two types of host plants. For

example, the study conducted by Asiandu et al. (2019), they obtained some endophytic fungi producing secondary metabolites with strong activity againsts pathogenic bacteria.

However, the number and the type of endophytic fungal isolates in different host plants could be different. Sometimes, the number of an endophytic fungal species isolated from the same locality also vary. The types and numbers of chemical compounds produced by endophytic fungi are also highly dependent on the host plant. A specific chemical compound is only produced by specific fungal isolates. Endophytic fungi found in a plant produce the same chemical compounds as their host plant. Therefore, it will be different from endophyte fungi found in other host plants. Thus, the use of endophytic fungi in producing certain bioactive compounds should use the appropriate isolates which their host plant is capable of producing the compounds. These challenges and opportunities must be exploited and optimized more. The opportunities for finding new, unique and potential endophytic fungi from mosses and ferns are widely open due to the lack of reports on the biodiversity and potential of endophytic fungi isolated from ferns and mosses. Besides, the use of enzymes produced from endophytic fungi also facilitates bio-industrial activities.

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