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CASSIANE FURLAN LOPES

CONTRIBUIÇÕES AO ESTUDO DOS FUNGOS AGARICOMYCETES BRIÓFILOS NO RIO GRANDE DO SUL, BRASIL

São Gabriel, 2025

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Tese apresentada ao Programa de PósGraduação em Ciências Biológicas stricto sensu da Universidade Federal do Pampa, como requisito parcial para a obtenção do Título de Doutora em Ciências Biológicas.

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Sonhe com aquilo que você quer ser, porque você possui apenas uma vida, e nela só se tem uma chance, de fazer aquilo que quer. Tenha felicidade bastante para fazê-la doce. Dificuldades para fazê-la forte. Tristeza para fazê-la humana e esperança suficiente para fazê-la feliz. As pessoas mais felizes não têm as melhores coisas, elas sabem fazer o melhor das oportunidades que aparecem em seus caminhos. A felicidade aparece para aqueles que choram, para aqueles que se machucam, para aqueles que buscam e tentam sempre. E para aqueles que reconhecem a importância das pessoas que passaram por suas vidas.

Clarice Lispector.

RESUMO

A ordem Basidiomycota é a segunda mais diversa em espécies entre os fungos, sendo que apenas a classe dos Agaricomycetes possui mais de 30.000 espécies descritas, dentre elas espécies comestíveis, tóxicas e com diversas relações ecológicas (saprófitas, liquenizadas, briofílicas, parasitas entre outros). Os fungos briófilos, que apresentam crescimento associado à briófitas ainda são pouco estudados, sendo que no Brasil são escassos os estudos que realizam análises sobre a ecologia destes organismos com as suas associações, assim como aqueles que analisam sua taxonomia. Para tanto, este estudo busca estimar a diversidade de fungos Agaricomycetes, principalmente os da Ordem Agaricales em associação com Briófitas (Bryophyta e Marchantiophyta), na mata ripária do Rio dos Sinos, localizada na Floresta Nacional em São Francisco de Paula, no estado do Rio Grande do Sul - Brasil, contribuindo para compreender suas associações ecológicas. Dessa forma, conduzimos revisões bibliográficas com base em buscas nas platafromas Google Schoolar, Scielo, NCBI, dentre outros bancos de dados. As coletas utilizaram o método de caminhamento ao longo das trilhas da Floresta Nacional de São Francisco de Paula, onde os basidiomas que apresentavam crescimento associado a briófitas eram coletados. Esse material era posteriormente analizado via microscopia óptica, fotografado e seco em estufa para armazenamento. Assim, regiões taxonômicas dos fungos e das briófitas, além das evidências de associação entre esses organismos, como hifas na periferia ou no interior da camada celular das briófitas eram analisadas. Para análise de dados moleculares, extração, amplificação e sequênciamento da região LSU foi realizado e para a análise filogenética, foram usados os métodos de inferência bayesiana, máxima verossimilhança e inferência de parcimônia. No primeiro capítulo, a primeira revisão tratou apenas sobre os Agaricales briófilos do Brasil, e foram encontradas 19 espécies e foi elaborada uma chave de identificação, dentre estas, nove são reconhecidas como parasitas de musgos. Para o segundo capítulo, houve expansão da revisão bibliográfica para toda a classe dos Agaricomycetes, onde catalogamos 33 espécies, pertencentes a Agaricales, Boletales, Hymenochaetales e Polyporales. No terceiro capítulo, foram descritas microscopicamente associações inéditas entre fungos e briófitas, como: *Gerronema stuckertii* com *Campylopus pilifer*,

Galerina stylifera com *Campylopus julicaulis* e *Chlorella sp.*, *Oudemansiella platensis* com *Metzgeria consanguinea* e *Psathyrella murrilli* com *Brachythecium sp.*. No quarto capítulo foi descrita a associação de *Rimbachia bryophila*, que é um novo registro para o Brasil, com *Dicranella riograndensis*, *Neesioscyphus argillaceus* e *Jungermannia decolor*. No quinto capítulo descrevemos morfologicamente e via filogenia com caracteres moleculares *Cora simasi* Furlan-Lopes & Putzke, associada com *Neesioscyphus argillaceus*, *Campylopus uleanus* e *Dicranella riograndensis* A análise filogenética posicionou *C. simasi* no subclado *Applanata*, próxima a *C. applanata*, e revelou uma relação de grupo-irmão entre as linhagens *Ciferrii* e *Aspera*. Todas espécies de fungos briófilos foram evidenciadas por hifas distribuídas nas briófitas estudadas sem estruturas parasitárias evidentes, sugerindo relação não prejudicial. Observou-se que a diversificação de *Cora* é influenciada por isolamento geográfico e ambiental, com adaptações a micro-habitats úmidos e de alta altitude.
Palavras-Chave: Associações, ecologia, nova espécie, fungos, briófitas.

ABSTRACT

The order Basidiomycota is the second most species-rich among fungi, with the class Agaricomycetes alone comprising more than 30,000 described species, including edible, toxic, and ecologically diverse species (saprophytic, lichenized, bryophilous, parasitic, among others). Bryophilous fungi, which grow in association with bryophytes, are still poorly studied, and in Brazil, studies addressing the ecology of these organisms and their associations, as well as those analyzing their taxonomy, are scarce. Therefore, this study aims to estimate the diversity of Agaricomycetes fungi, especially those of the order Agaricales in association with bryophytes (Bryophyta and Marchantiophyta), in the riparian forest of the Rio dos Sinos, located in the Floresta Nacional de São Francisco de Paula, in the state of Rio Grande do Sul, Brazil, contributing to the understanding of their ecological associations. To this end, bibliographic reviews were conducted based on searches in platforms such as Google Scholar, Scielo, NCBI, among other databases. Field collections employed the walking method along the trails of the Floresta Nacional de São Francisco de Paula, where basidiomata exhibiting growth associated with bryophytes were collected. This material was subsequently analyzed by optical microscopy, photographed, and oven-dried for storage. Taxonomic regions of the fungi and bryophytes, as well as evidence of associations between these organisms, such as hyphae at the periphery or within the cellular layer of the bryophytes, were analyzed. For molecular data analysis, extraction, amplification, and sequencing of the LSU region were performed, and for phylogenetic analysis, Bayesian inference, maximum likelihood, and maximum parsimony methods were used. In the first chapter, the review addressed only bryophilous Agaricales from Brazil, identifying 19 species and producing an identification key, of which nine are recognized as moss parasites. In the second chapter, the bibliographic review was expanded to the entire class Agaricomycetes, where 33 species were catalogued, belonging to Agaricales, Boletales, Hymenochaetales, and Polyporales. In the third chapter, novel microscopic associations between fungi and bryophytes were described, such as *Gerronema stuckertii* with *Campylopus pilifer, Galerina stylifera* with *Campylopus julicaulis* and *Chlorella sp., Oudemansiella platensis* with *Metzgeria consanguinea*, and *Psathyrella murrilli* with *Brachythecium sp.* In the fourth chapter, the association of *Rimbachia bryophila*, which is a new record for Brazil, with *Dicranella riograndensis, Neesioscyphus argillaceus*, and *Jungermannia decolor* was described. In the fifth chapter, we described morphologically and phylogenetically, with molecular characters, *Cora simasi* Furlan-Lopes & Putzke, associated with *Neesioscyphus argillaceus, Campylopus uleanus,* and *Dicranella riograndensis*. The phylogenetic analysis placed *C. simasi* in the subclade *Applanata*, close to *C. applanata*, and revealed a sister-group relationship between the *Ciferrii* and Aspera lineages. All bryophilous fungal species were evidenced by hyphae distributed in the bryophytes studied without evident parasitic structures, suggesting a non-harmful relationship. It was observed that the diversification of *Cora* is influenced by geographical and environmental isolation, with adaptations to humid, high-altitude microhabitats.

Keywords: associations, ecology, new species, fungi, bryophytes.

LISTA DE FIGURAS

Capítulo V -

A new species of Cora (Basidiomycota: Agaricales: Hygrophoraceae) associated with Bryophytes in Southern Brazil

LISTA DE ABREVIATURAS E SIGLAS

APP – Area de Preservação Permanente

μm – Micrometro.

cm – Centímetro.

FLONA – Floresta Nacional de São Francisco de Paula.

GPS - Sistema de Posicionamento Global.

IB – Inferência Bayesiana.

ICMBio – Instituto Chico Mendes de Conservação da Biodiversidade

IP – Inferência de Parcimônia.

KOH – Hidróxido de Potássio.

m – metros

ML – Máxima Verossimilhança.

mm – Milímetros.

mM - micromol

MP – Máxima Parcimônia.

NCBI – National Center for Biotechnology of Information

PCR – Reação em cadeia de Polimerase

SISBIO - Sistema de Autorização e Informação em Biodiversidade

SUMÁRIO

1. INTRODUÇÃO

Os fungos são organismos heterotróficos fundamentais para o meio ambiente, sendo essenciais no ciclo de nutrientes no solo e na decomposição dos organismos (DIGHTON, 2016). Com milhares de espécies descritas atualmente, ainda se estima que esse número seja substimado (WIJAYAWARDENE et al., 2020; HAWKSWORTH & LÜCKING, 2017; WU et al., 2020; HE et al., 2022; HYDE et al., 2024). Dentro de Basidiomycota, a classe Agaricomycetes, possuem mais de 30.000 espécies descritas, além de apresentar uma ampla gama de comportamentos ecológicos (KIRK et al., 2008; DIGHTON, 2016; DIEDERICH et al., 2018; PUTZKE et al., 2017; HE et al., 2019; WIJAYAWARDENE et al., 2020).

Dentre estes, o comportamento briófilo, quando o fungo apresenta alguma fase da sua vida associada com briófitas ainda é um campo promissor com poucos estudos para os Agaricomycetes (REDHEAD, 1989; GRZESIAK et al., 2015). No Brasil, os estudos sobre fungos briófilos se limitam a descrições de associações realizadas com base em observações a campo (FURLAN-LOPES et al., 2023). As briófitas, são compostas por musgos (divisão Bryophyta), hepáticas (divisão Marchantiophyta) e antóceros (divisão Anthocerophyta) e representam o segundo maior grupo de plantas em diversidade, atrás apenas das Angiospermas (COSTA; PERALTA, 2015; CAMELO et al., 2024; SPECIESLINK, 2025). Sendo um grupo de organismos que tem sido encontrado em diversos tipos de associações com diversos organismos (DAVEY & CURRAH, 2006; DAVEY et al., 2013a, b).

Locais como a Floresta Nacional de São Francisco de Paula (FLONA), localizada no nordeste do Rio Grande do Sul, em região de Mata Atlântica, são ambientes que propiciam a ocorrência de fungos e briófitas (KOMONEN et al., 2008; WIERZCHOLSKA et al., 2018). Com extensas áreas de vegetação ripária oriunda da alta bacia do Rio dos Sinos, a FLONA abriga grande diversidade ecológica, e é um local propício para o estudo das interações entre fungos e briófitas. Além disso, metodologias clássicas bem aplicadas, como a microscopia óptica e a biologia molecular, incluindo a amplificação e mapeamento de regiões ITS por PCR, permitem realizar avanços significativos na taxonomia e interações entre esses organismos (LUCKING et al., 2017; KOROTKIN et al., 2018). Assim, o uso dessas técnicas é essencial para contribuir para a conservação da biodiversidade de fungos Agaricomycetes briófilos e briófitas nos ecossistemas de vegetação ripária no Brasil.

2. REVISÃO DA LITERATURA

2.1 Características do Reino Fungi

Os fungos são organismos heterotróficos, utilizando a energia armazenada na biomassa vegetal e animal para crescer, sendo um grupo chave na regulação dos processos do ecossistema por sua interação com o ambiente abiótico e com outros organismos (DIGHTON, 2016). Seu crescimento apical nas formas miceliais, ocorre por meio das hifas, que são filamentos microscópicos com crescimento apical formadoras do micélio, permitindo penetração de substratos e colonização de espaços pela busca nutricional (RAGHUKUMAR et al., 2017).

Atualmente, os fungos compreendem 19 filos, 83 classes, 1.220 famílias, 10.685 gêneros e cerca de 140.000 espécies (HYDE et al., 2024). Para os fungos do Filo Basidiomycota se estima que até 2030 haverão mais de 54.000 espécies descritas, cerca de um terço das 144.000 espécies conhecidas (He et al., 2022). Quanto a diversidade global de Basidiomycota, se estima existir um total que varie entre 1,4 a 4,2 milhões de espécies, valores menores do que os sugeridos anteriormente (HE et al., 2019; WIJAYAWARDENE et al., 2020; HAWKSWORTH & LÜCKING, 2017; WU et al., 2020).

O filo Basidiomycota é formado principalmente por formas miceliais, embora também apresente leveduras unicelulares, sendo formado majoritariamente por espécies terrestres sapróbicas ou simbióticas (RAGHUKUMAR et al., 2017). Dentro de Basidiomycota, a classe dos Agaricomycetes possui cerca de 128 famílias, divididas em 1.434 gêneros e mais de 30.000 espécies descritas mundialmente, sendo um número que cresce ao longo dos anos (HE et al., 2019; WIJAYAWARDENE et al., 2020; HYDE et al., 2024). Os Agaricomycetes possuem grande importância ecológica, e apresentam inúmeras espécies de comportamento saprófito, formador de ectomicorrizas, liquênico, parasita, briófilo, dentre outros (KIRK et al., 2008; DIGHTON, 2016; DIEDERICH et al., 2018; PUTZKE et al., 2017; HE et al., 2022).

2.2 Comportamento briófilo e os estudos no Brasil

O comportamento briófilo ocorre quando o fungo tem pelo menos uma fase da sua vida em associação com briófitas (REDHEAD, 1989; GRZESIAK et al., 2015), destacando a importância ecológica desse grupo de plantas. As briófitas tradicionalmente incluem três grandes grupos: os musgos (divisão Bryophyta), hepáticas (divisão Marchantiophyta) e antóceros (divisão Anthocerophyta), constituindo o segundo grupo de plantas mais diversificado depois das Angiospermas (SHAW et al., 2011; HERNÁNDEZ-HERNÁNDEZ & WIENS, 2020; CAMELO et al., 2024; WFO, 2025).

No Brasil a flora de briófitas compreendia até 2015 1.524 espécies, com 880 espécies de musgos, 633 de hepáticas e 11 de antóceros (COSTA; PERALTA, 2015). Entretanto, dados atualizados indicam que atualmente existem cerca de 1.789 espécies catalogadas, com espécimes preservados em herbário (SPECIESLINK, 2025). A maioria dos estudos sobre interações entre fungos e plantas, tanto a nível morfológico quanto molecular é feito entre fungos e plantas vasculares com sementes, enquanto os que envolvem as plantas avasculares são escassos (NELSON; SHAW, 2019). Briófitas podem associar-se a diversos organismos como fungos, líquens, algas, invertebrados e vertebrados, ocorrendo até mesmo em regiões extremas como na Antártica, demonstrando a sua importância ecológica (PUTZKE, 2020).

Embora as briófitas não produzam estruturas ricas em nutrientes ou tecidos de transporte especializados ricos em produtos fotossintéticos encontrados em plantas vasculares, a patogênese fúngica dos musgos está sendo relatada com frequência crescente (DAVEY & CURRAH, 2006; PRESSEL et al., 2021). Sendo que diversos grupos de fungos têm sido encontrados associados a briófitas como sapróbios, patógenos, parasitas e comensais (DAVEY et al., 2013a, b; KOROTKIN et al., 2018).

O desenvolvimento de apressórios costuma ser incomum entre os fungos briófilos, entretanto, outra estratégia de conquista do hospedeiro é a digestão enzimática. Esta, facilita a entrada das hifas no tecido vegetal e a formação de hifas especializadas em invasão tecidual, como já caracterizado em *Tephrocybe palustris* (REDHEAD 1981, DURING AND VAN TOOREN, 1990) e *Arrhenia retiruga* (Agaricales: Tricholomataceae) (HASSEL & KOST 1998). Há muito foi demonstrado que os patógenos briófilos podem explorar diferentes micronichos nutricionais dentro do gametófito, sendo que alguns fungos que aproveitam os derivados fotossintéticos facilmente assimiláveis degradam a parede celular da briófita de forma menos intensa comparado aos que, obtêm nutrição de componentes estruturais e de armazenamento da célula (DAVEY & CURRAH, 2006; DIGHTON, 2016).

Evolutivamente, Moncalvo et al. (2002) afirmam que a transição para o modo de nutrição briófilo ocorreu várias vezes de forma independente, e sempre teve um ancestral saprófito, pois geralmente a madeira comumente degradada por estes organismos apresenta composição similar à das briófitas parasitadas, facilitando o salto evolutivo (DAVEY & CURRAH, 2006). Entretanto os autores sugerem que este modo não parece ter sido muito bem sucedido, devido à radiação limitada de clados, ocorrendo apenas quatro vezes: em *Psilocybe*, *Ompalina* e *Rimbachia*, *Arrhenia* e em todos os fungos lamelados de Himenochaetales.

Entretanto, estudos mais recentes têm demonstrado que essa relação pode ser bem sucedida, como o estudo de Seitzman et al. (2011), que sugere por meio de análises de isótopos estáveis e de filogenia, que os gêneros de Hygrophoraceae (Basidiomycota: Agaricales) *Hygrophorus, Hygrocybe, Humidicutis, Cuphophyllus* e *Gliophorus* desenvolveram um modo de nutrição propriamente briófilo. Assim como Korotkin et al. (2018), que por meio de um conjunto de análises, como de isótopos estáveis, ensaios de PCR, experimentos *in* vitro e genômica, constataram uma assinatura de isótopos única para espécies de *Rickenella*, que também foi suportada filogeneticamente para o modo trófico de alimentação briofílica neste grupo, corroborando em parte Moncalvo et al. (2002). Também Korotkin et al. (2018) afirmaram que os gametófitos de musgos infectados previamente com *Rickenella fibula* se desenvolveram sem dificuldades, como se não houvesse infecção. Isto demonstra a necessidade de uma melhor compreensão das relações ecológicas entre briófitas e fungos, que indicam ser diversas e ter diferentes mecanismos ainda desconhecidos envolvidos.

No Brasil, trabalhos sobre fungos briófilos Agaricomycetes são escassos, sendo realizados de forma mais aprofundada alguns trabalhos com fungos conidiais pertencentes à Ascomycota (GRANDI et al., 2008; LEÃO-FERREIRA et al., 2024). Para Agaricales, o trabalho pioneiro foi o de Singer (1953a) que apenas cita fungos ocorrendo entre musgos ou associado com *Sphagnum*, sem realizar análises de microscopia ou fazer a identificação das espécies de briófitas parasitadas. Da mesma forma, trabalhos que relatam a ocorrência de briófitas em fungos como o de Vital et al. (2000) que apenas apresentam uma lista das espécies coletadas em basidiomycetes, sem realizar análises. A falta de cooperação entre briologistas e micologistas, ou a falta de treinamento de taxonomistas em ambas áreas pode ser uma das razões, que inclusive é relatada em outras partes do mundo (DÖBBELER,2021).

2.3 Floresta Nacional de São Francisco de Paula e zonas ripárias

O bioma Mata Atlântica é composto por formações florestais nativas, como a Floresta Ombrófila Densa; Ombrófila Mista, composta por Araucárias; Ombrófila Aberta, dentre outros, além de ecossistemas únicos como manguezais, vegetações de restingas, campos de altitude e brejos (BRASIL, 2025). Porém, devido às atividades humanas na região, hoje restam cerca de 24% de sua cobertura original (SOS MATA ATLÂNTICA, 2024). A Mata Atlântica é a segunda maior biodiversidade das Américas, atrás apenas da Amazônia (MORELLATO; HADDAD, 2000; ARRUDA et al., 2025).

A FLONA - Floresta Nacional de São Francisco de Paula (Figura 1) se localiza na região nordeste do Rio Grande do Sul, apresentando altitude de 647 a 940 m acima do nível do mar, possui clima subtropical com verões brandos e invernos frios e úmidos, se enquadrando dentro do bioma Mata Atlântica (ICMBIo, 2020). Com 1.606,70 ha de extensão, a FLONA é constituída por cerca de 56% de vegetação nativa, com solos rasos e ricos em matéria orgânica (BONATTI et al., 2006). A FLONA possui quatro trilhas para visitação e utilização por pesquisadores, a Trilha das Araucárias Centenárias (4.490m) Trilha Cascata Bolo de Noiva (4.744m), Trilha Mirante Cascata da Usina (3.740m) e Trilha Equestre Ciclística (6.400m) (ICMBio, 2020). Com grande riqueza de espécies, a vegetação que predomina é a Floresta Ombrófila Mista (com araucárias cultivadas), banhados, campos e áreas cultivadas pelo homem com grandes extensões de *Pinus sp*., *Eucalyptus sp*., *Cryptomeria japonica* (Xaxim) e *Araucaria angustifolia* (ICMBio, 2020). O conceito de Floresta Ombrófila Mista se refere às formações vegetais que contém a mistura de floras de diferentes origens, definindo padrões fisionômicos típicos em zona climática pluvial (RIBEIRO et al., 2007).

Por fazer parte da alta da bacia hidrográfica do Rio dos Sinos, a FLONA é constituída por grandes áreas de vegetação ripária, constituindo Area de Preservação Permanente (APP) (ICMBIo, 2020). As vegetações de zona ripária são áreas de grande umidade e são consideradas APPs, devendo apresentar faixas que variam de 30 a 500 metros de distância dos cursos de água, sejam eles lóticos ou lênticos (BRASIL, 2012). A diversidade fúngica nas zonas ripárias é geralmente associada à grande quantidade de matéria orgânica e madeira em decomposição (KOMONEN et al., 2008). Por outro lado, as briófitas são organismos extretamente sensíveis à mudanças no ambiente, fazendo com que estudar sua diversidade em ambientes de zonas ribeirinhas seja fator chave na conservação de sua biodiversidade (WIERZCHOLSKA et al., 2018).

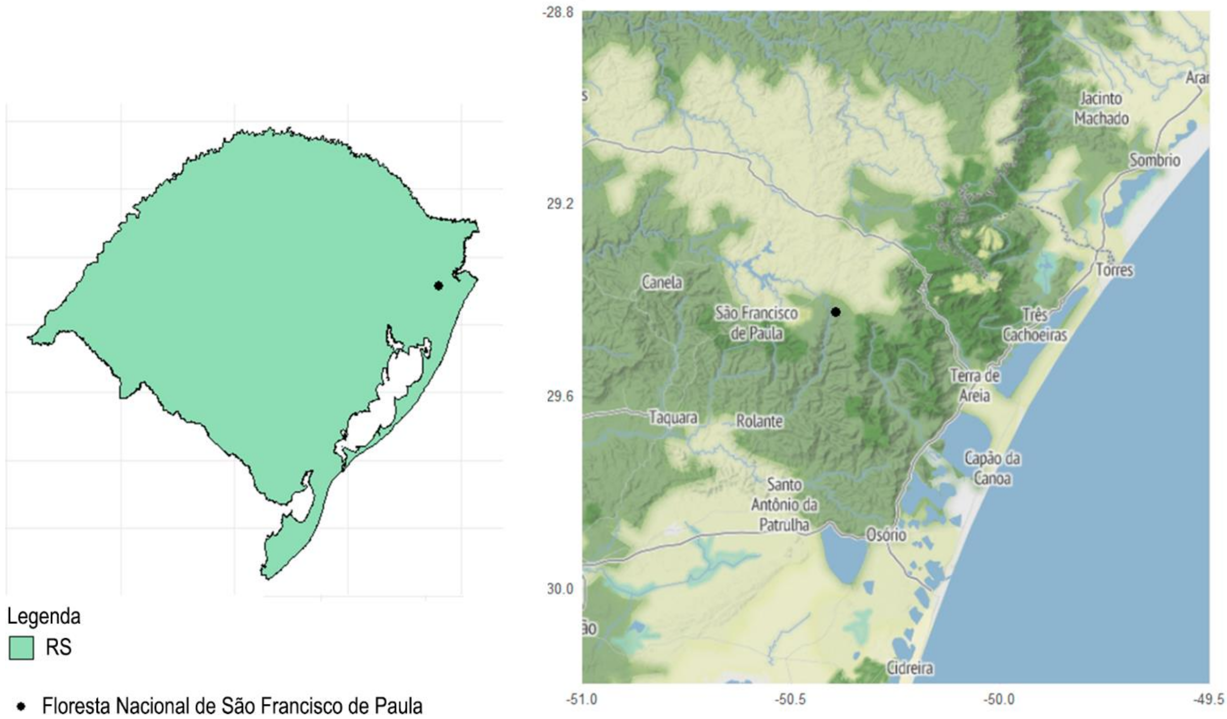

Figura 1. Mapa da área de estudo. RS - Rio Grande do Sul.

2.4 Técnicas empregadas no estudo dos fungos briófilos

Dentre os principais metodos utilizados no estudo tanto de taxonomia clássica, quanto ne detecção de estruturas envolvidas em associações entre fungos briófilos e briófitas, está a microcopia óptica (GREIFF, 2021). Esta permite a observação direta da morfologia e das estruturas envolvidas nessas associações ecológicas (DAVEY & CURRAH, 2006). Por outro lado, ferramentas como a extração de ácidos nucleicos e a PCR, que permitem amplificar regiões específicas do DNA, permitindo uma avaliação taxonômica mais robusta (LUCKING et al., 2017).

A análise da região ITS (Espaçador Transcrito Interno) do complexo de genes rRNA têm sido amplamente usada para a identificação e separação de novos taxons, entretanto, estudos demonstram que a região 28S – LSU mostra resultados tão bons quanto a região ITS (BROWN et al., 2014). Assim, o uso de primers que delimitem a região do DNA para amplificação, com resolução na diferenciação genotípica de espécies, auxiliam na taxonomia e identificação de diferentes genomas de fungos associados a briófitas (HACQUARD et al., 2010; DAVEY et al., 2013a, b; KOROTKIN et al., 2018). Em conjunto com técnicas de sistemática filogenética, como inferência bayesiana, máxima verossimilhança e inferência de parcimônia, podem auxiliar a compreender os caminhos evolutivos percorridos por fungos associados a briófitas.

3 OBJETIVOS

3.1 Objetivo Geral

Estimar a diversidade de fungos Agaricomycetes, principalmente entre os Agaricales em associação com musgos (divisão Bryophyta) e hepáticas (divisão Marchantiophyta), na mata ripária do Rio dos Sinos, buscando compreender melhor sua ecologia no estado do Rio Grande do Sul.

3.2 Objetivos Específicos

- Fazer uma revisão bibliográfica sobre os fungos Agaricales briófilos registrados no Brasil, com foco em suas interações com briófitas, taxonomia e distribuição.

- Estimar a diversidade de Briófitas e de Agaricomycetes associados na mata ripária do Rio dos Sinos na Floresta Nacional de São Francisco de Paula, localizada na região sul do Brasil.

- Descrever morfologicamente a associação entre Agaricomycetes e briófitas, identificando evidências estruturais por meio de análises macroscópicas e de microscopia óptica.

- Catalogar as espécies conhecidas de Agaricales associadas a briófitas, que ocorrem na Floresta Nacional de São Francisco de Paula incluindo dados de ocorrência, hábitos ecológicos e tipos de associação.

- Descrever novas ocorrências de fungos briófilos, associações e espécies.

- Discutir os padrões evolutivos e ecológicos observados nas interações entre Agaricales e briófitas.

4 APRESENTAÇÃO DA PESQUISA E ANÁLISE DOS RESULTADOS

Os resultados obtidos nesse trabalho serão apresentados em capítulos, conforme descrição abaixo.

Capítulo I: “Muscicolous Agaricales (Basidiomycota: Agaricomycetes) found in Brazil”, publicado em 2022, vol. 137, n. 4, no periódico Mycotaxon, ISSN: 0093-4666. DOI: https://doi.org/10.5248/137.1015.

Capítulo II: “Bryophilous Agaricomycetes (Fungi, Basidiomycota): A Review to Brazil”, publicado como capítulo do livro “Bryophytes - The State of Knowledge in a Changing World”, editado por Jair Putzke, publicado em 2023, pela Intech Open. ISSN: 978-1-80356-938-3. DOI: 10.5772/intechopen.102134.

Capítulo III: “Bryophilous Agaricales in Southern Brazil”, publicado em 2023, vol. 10, n. 4, no periódico Acta Biológica Catarinense, ISSN: 2358-3363. DOI: https://doi.org/10.21726/abc.v10i4.2197.

Capítulo IV: “*Rimbachia bryophila* (Pers.) Redhead associada a briófitas na Floresta Nacional de São Francisco de Paula”, publicado em 2024, vol. 16, n.4, no periódico Revista Ambientale (Revista da Universidade Estadual de Alagoas/UNEAL), e-ISSN: 2318-454X, DOI: https://doi.org/10.48180/ambientale.v16i4.601

Capítulo V: “A new species of *Cora* (Basidiomycota: Agaricales: Hygrophoraceae) associated with Bryophytes in Southern Brazil”, submetido em maio de 2025 ao periódico Turkish Journal of Botany (TUBIKAT), ISSN: 1300-008X.

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5 RESULTADOS E DISCUSSÃO

Muscicolous *Agaricales (Basidiomycota: Agaricomycetes)* found in Brazil

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ABSTRACT— *Agaricomycetes* muscicolous fungi have been little studied in Brazil, both in their taxonomy and in ecology. Thus, here we present a compendium of species of muscicolous Agaricales found in Brazil based on a bibliographic review. To assist the taxonomic identification of the group, a dichotomous identification key is also proposed. Based on the literature review, 19 species of muscicolous *Agaricales* were cataloged as occurring in Brazil. Among the species dealt with here, nine are identified as moss parasites. This demonstrates a great gap in the scientific knowledge of this subject in Brazil, which needs a broad deepening to better understand the diversity of these interactions and their ecology.

Keywords — *Bryophilous fungi*, *Bryophyta*, parasitic associations.

Introduction

Among all fungi, there is a group that was little studied by science: fungi associated with mosses. There is a very striking characteristic in this group: they only complete their life cycle in association with mosses (Korotkin 2018). Among the fungi that develop macroscopic reproductive structures, the most frequently cited are the members of *Basidiomycota* in particular, mostly the ones belonging to the class *Agaricomycetes* (Davey & Currah 2006). The *Agaricomycetes* (*Basidiomycota*) comprises twenty-two orders, with more than 20,000 described species, of which *Agaricales*, *Amylocorticiales, Atheliales, Boletales* and *Jaapiales* form the subclass *Agaricomycetidae* (Kirk & al. 2008, Hibbett & al. 2014).

Studies such as Davey & Currah (2006) reviewed the existing interactions between bryophilic fungi (including *Agaricales*) and mosses (*Bryophyta*), such as parasitism, pathogenesis, and saprophytism. Other works as Davey & al. (2013), Korotkin & al. (2018), and Raudabaugh & al. (2021), indicated that the relationships between mosses and fungi are not always harmful or parasitic.

A particular group of *Agaricomycetes* is found among bryophytes. The members of the genera *Leptoglossum* Karst., *Mniopetalum* Donk & Singer, and *Cyphellostereum* D.A. Reid, for example, which use that substrate exclusively for growth and development (Høiland 1976, Segedin 1994). Some species in *Galerina* Earle (*Hymenogastraceae*), may parasitize mosses (Putzke & Putzke, 2018), and others such as *Lichenomphalia* Redhead, Lutzoni, Moncalvo & Vilgalys and *Cora* Fr. (*Hygrophoraceae*) are associated with algae forming basidiolichens (Lawrey & al. 2009). Some relationships between mushrooms and mosses are unique, as observed by Redhead (1981) who described, among his results, a specimen of *Lyophyllum palustre* (Peck) Singer (*Lyophyllaceae*) as an effective *Sphagnum* L. (*Sphagnaceae*) parasite. Later, Redhead & al. (2002) proposed two new genera, *Loreleia* Redhead, Moncalvo, Vilgalys & Lutzoni and *Sphagnomphalia* Redhead, Moncalvo, Vilgalys & Lutzoni, based in ecology, molecular and morphological characters, that were seemingly obligatory when associated with living bryophytes.

One of the pioneering works to taxonomically study the muscicolous representatives in Brazil was Singer (1953a), who found 10 putative *Agaricales* parasitizing species in mosses. Another one was the Vital & al. (2000) study, who found diverse species of *Himenochaetales* growing associated with mosses and liverworts. Since then, there have been no studies focusing on this type of association in Brazil, demonstrating the importance of a bibliographic survey containing all species already cited in the Brazilian territory. Even so, we aimed to review all literatures about occurrence of putative muscicolous fungi belonging to *Agaricales* in Brazil, and present a key to identify the occurring species, contributing to a better understanding on taxonomy, ecology, and distribution of the group.

Material and Methods

Data Collect

A bibliographical review was carried out on muscicolous *Agaricales* specimens growing on mosses found in Brazil, based on 30 published works, including articles and books. Identifications of Agaricales at the genus level were also considered. The taxonomic classification was based in He & al. (2019) and Wijayawardene & al. (2020) and a species nomenclature check-up was made on the websites: IndexFungorum (http://www.indexfungorum.org/names/names.asp) and MycoBank (https://www.mycobank.org/). The review spanned from the years 1953 to 2021, and used the following digital platforms: GoogleScholar (https://scholar.google.com.br/), Scientific Electronic Library Online (Scielo) (https://scielo.org/), Elselvier (https://www.elsevier.com/pt-br), ScienceDirect (https://www.sciencedirect.com/) and Periódico Capes (https://www-periodicos-capes-gov-br.ezl.periodicos.capes.gov.br/). The keywords used in the searches were: '*Agaricales* with moss Brazil'; '*Agaricales* with moss'; 'Bryophilous *Agaricales'*; 'Bryophilous Agaricales in Brazil". A distribution map involving the species was prepared in the Adobe Photoshop software, based on bibliographic data collected from georeferencing in the revised works.

Results and Discussion

Checklist of Agaricales species parasitically associated with mosses in Brazil

Citations about Agaricales growing on mosses in Brazil were found for 10 families, 13 genus (two genus *incertae sedis*) and 19 species and are presented in the list.

Agaricales Underw.
Agaricales incertae sedis

- ***Collybia dryophila* var. *oedipus*** Quél., Flore mycologique de la France et des pays limitrophes: **226**, 1888.
Bas.: *Agaricus dryophilus* Bull. ex Fr., *Herb. Fr. (Paris)*, **10**: 434, 1790.
Grows in a humid open environment away from trees, associated with *Sphagnum*, found in Rio Grande do Sul state (Singer 1953a, Putzke & Putzke, *in press*).

- ***Rimbachia arachnoidea*** (Peck) Redhead, Can. J. Bot. 62(5): 878, 1984.≡ *Mniopetalum bisporum* Singer, *Darwiniana*, **14**: 10, 1966.
Gregarious growth on mosses, found in Rio Grande do Sul state (Singer 1986, Putzke & Putzke in press).

Chromocyphellaceae **Knudsen**

- ***Chromocyphella muscicola*** (Fr.) Donk, *Persoonia* **1**(1): 95, 1959.
≡ *Arrhenia muscicola* (Fr.) Quél., *Fl. mycol. France (Paris)* 33, 1888.
Grow among mosses and in lichens, found in Minas Gerais state (Albuquerque & al. 2007, De Oliveira & al. 2019).

Clavariaceae **Chevall.**

- ***Clavaria fragilis*** Holmsk., *Beata Ruris Otia Fungis Danicis*, **1**: 7, 1790.
Sanctioned by Fries (1821), found in Rio Grande do Sul, Santa Catarina and Paraná states growing in the ground with mosses (Furtado & al. 2016).

Hymenogastraceae **Vittad**

- ***Galerina montivaga*** Singer, *Nova Hedwigia,* **29**: 306, 1969.
Growing gregarious in moss fields and on humus, found in Paraná state (Singer 1969, De Meijer 2008, Putzke & Putzke 2018).

- ***Galerina semiglobata*** Singer, *Lilloa*, **26**: 147, ('1953'), 1954.
Forming dense groups on *Sphagnum* that is burned in some points, found in Rio Grande do Sul state (Singer 1953a, Putzke & Putzke 2018).

- ***Galerina sphagnorum*** (Pers.) Kühner, *Encyclop. Mycol.,* **7**: 179, 1935.
Sanctioned by Fries.
Grows gregarious in *Sphagnum*, found in Rio Grande do Sul state (Singer 1953a, Putzke & Putzke 2018).

- ***Galerina subtibiicystis*** Singer, *Lilloa*, **26**: 146 ('1953'), 1954.

They grow scarcely among the peat bogs of *Sphagnum* moss in Rio Grande do Sul state (Singer 1953a, Putzke & Putzke 2018).

- Galerina taimbesinhoensis Singer, *Lilloa*, 26: 148 ('1953'), 1954.
Growing exclusively on *Sphagnum* moss, found in Rio Grande do Sul state (Singer 1953a, Putzke & Putzke 2018).

- Psilocybe paupera Singer, Sydowia, 9 (1-6): 404, 1955.
Grows gregarious, attached to the stalks of the moss *Sphagnum*, found in Rio Grande do Sul state (Guzmán 1983, Coimbra 2015, Putzke & Putzke 2018).

- Psilocybe sp. (Fr.) P. Kummer
Growing among *Sphagnum* in open marshes, found in Rio Grande do Sul state (Singer 1953a).

***Hygrophoraceae* Lotsy**

- Hygrocybe helobia (Arnolds) Bon, Doc. Mycol. 6(no. 24): 43, 1976. ≡ *Hygrocybe miniata* (Fr.) P. Kumm., *Der Führer in die Pilzkunde*: **112**, 1871.
Grows in soil, often between mosses and generally gregarious, found in Rio Grande do Sul and São Paulo states (Pegler 1983b, Putzke & Putzke 2017).

***Omphalotaceae* Bresinsky**

- ***Gymnopus aquosus*** (Bull.) Antonín & Noordel., in Antonín, Halling & Noordeloo*s,* Mycotaxon **63**: 363 1997 ≡ *Collybia dryophila* (Bull. ex Fr.) Kummer var. *oedipus* Quél., *Fl. mycol. France (Paris)*: **226**, 1888.
Bas.: *Agaricus dryophilus* Bull. ex Fr., *Herb. Fr. (Paris)*, **10**: 434, 1790.
= *Marasmius dryophilus* (Bull. ex Fr.) Karsten, *Finl. Nat. Folk*, **48**: 103, 1889.
Grows in a humid open environment away from trees, associated with *Sphagnum*, found in Rio Grande do Sul state (Singer 1953a, Putzke & Putzke *in press*).

***Psathyrellaceae* Vilgalys, Moncalvo & Redhead**

***-Psathyrella* sp**. - Found in mountain woods among mosses, found in Rio Grande do Sul state (Singer 1953a).

***Strophariaceae* Singer & Smith**

- Hypholoma elongatum (Pers.) Ricken, Die Blätterpilze 1: 250, 1915. ≡ *Psilocybe uda* (Pers. ex Fr.) Gillet, *Hyménomycètes (Alençon)*: **586**, 1878.
Growing attached to the stalk of *Sphagnum*, away from trees, found in Rio Grande do Sul state (Singer 1953a).

- ***Hypholoma ericaeum*** (Pers.: Fr.) Kühner, *Bull. Trimest. Soc. mycol. Fr.*, **52**: 23, 1936.
Growing in wet and sandy soil among mosses and grasses, found in Rio Grande do Sul and São Paulo states (Da Silva & al. 2006, Cortez & Silveira 2007).

- ***Deconica inquilina*** (Fr.) Pat. ex Romagn., Revue Mycol., Paris 2(6): 244, 1937.
≡ *Psilocybe muscorum* (P.D. Orton) M.M. Moser, in Gams, Kl. Krypt.-Fl., *Ed.* 3 (Stuttgart) 2b/2: 239, 1967.
Growing among mosses in sandy soil, found in Rio Grande do Sul state (Da Silva & al. 2006).

***Biannulariaceae* Jülich**

- Callistosporium luteo-olivaceum (Berk. & M.A. Curtis) Singer, Lloydia 89: 117, 1946.
= *Callistosporium luteofuscum* Singer, *Lilloa*, **26**: 115 ('1953'), 1954.
They are found growing on decaying wood and between *Sphagnum* in Rio Grande do Sul and Paraná states (Singer 1953a, De Meijer 2008, Putzke & Putzke, *in press*).

***Mycenaceae* Overeem**

- Atheniella amabillissima (Peck) Redhead, Moncalvo, Vilgalys, Desjardin & B.A. Perry, Index Fungorum 14: 1, 2012. ≡ *Mycena amabilissima* (Peck) Sacc., *Syll. Fungorum*, **9**: 37. 1891.
≡ *Agaricus amabillissimus* Peck, *Rep. (Annual) Trustees State Mus. Nat. Hist.*, New York, **39**: 39 ('1886'), 1887.
≡ *Mycena amabillissima* (Peck) Sacc., Sylloge Fungorum **9**: 37. 1891.
Growing among mosses, found in Rio Grande do Sul state (Putzke & Putzke, *in press*; Raithelhuber 1991).

***Macrocystidiaceae* Kühner**
- ***Macrocystidia sp.*** Joss.
Growing associated with mosses, found in Amazônia state (Souza & Aguiar 2004).

Identification key for the muscicolous Agaricomycetes species from Brazil

1a. Coralloid basidiomes, cylindrical or clavate form (Furtado & al. 2016)..***Clavaria fragilis***
1b. Lamellate basidiome………...**2**

2a. Spores with plage, sometimes indistinct; lamellae adnate to decurrent, stipe central, rusty brown spored……………………..**3**
2b. Spores without plage; lamellae free, adnexed, adnate or decurrent; stipe lateral, central or absent, hyaline spore or strongly pigmented…….......................................**7**

3a. Conical to bell-shaped pileus up to 35 mm in diameter, pale yellowish to ochreous brown, stipe concolor with the pileus, cylindrical or nearly so, sometimes flexuous…...……….....……………………………………………………………...**4**
3b. Pileus as above or different, with a diameter of less than 15 mm, different colors, cylindrical stipe……………...…………...**5**

4a. Grow gregarious in *Sphagnum* and have fibulae present (Putzke & Putzke 2018)……………………………………………………….**...*Galerina sphagnorum***
4b. Grow solitary in *Sphagnum* and fibulae absent (Putzke & Putzke 2018)...………**..*Galerina subtibiicystis***

5a. Fibulae absent, thick-walled ellipsoid spores (Putzke & Putzke 2018)………………………………………………….…….........***Galerina montivaga***
5b. Fibulae present, spores as above or different, without distinct plage....................**6**

6a. Spores smooth and fusoid (Putzke & Putzke, 2018)............***Galerina semiglobata***
6b. Spores ornamented and elongated (Putzke & Putzke 2018)...***Galerina taimbenhoensis***

7a. Stipe always absent, spores globose and smooth, pileus between 3–3.5 mm, white color (Putzke & Putzke, *in press*)................................***Rimbachia arachnoidea***
7b. Stipe always present, usually central, smooth or ornamented spores, pileus of different size and coloration………………..……..…………………...………..…....**8**

8a. Dark spores....………………………………………………………….……...**9**
8b. Pale spores....………………………………………………..……......…....**13**

9a. Dusky black spores, paling when treated with sulfuric acid (Putzke & Putzke, 2018)....……….……………………………......…..............…...……..***Psathyrella* sp.**
9b. Dark lilac to cinnamon brown, dark cinnamon-brown spores, paling when treated with sulfuric acid (Putzke & Putzke, 2018)..**10**

10a. Pileus up to 15 mm in diameter, if the lamellae are adnate, subdistant, yellowish-brown with regular and whitish edges (Da Silva & al. 2006)..***Deconica inquilina***
10b. Pileus with different diameter, lamellae of varying shapes and colors……………………………………………………………………………..**11**

11a. Pileus 9-34 mm in diameter, yellowish brown, adnexed lamellae, dark violet with the ripening of the spores with a white line in the margin (Putzke & Putzke 2018; Cortez & Silveira 2007)..…***Hypholoma ericaeum***
11b. Pileus with 20–25 mm in diameter, variable color of lamellae…………..…...**12**

12a. Pileus yellow to orange, adnate lamellae, yellow to yellowish-brown, pleurocystidia absent (Singer 1953a)......................................***Hypholoma elongatum***
12b. Pileus yellow to brownish, adnexed lamellae, yellowish to pale, pleurocystidia present (Putzke & Putzke 2018)...***Psilocybe paupera***

13a. Yellowish-orange to reddish-orange pileus, 10-40 mm in diameter, always white spores, the cortical layer of the thricodermal pileus with subcylindrical terminal elements and fusoid (Putzke & Putzke 2017).................. ***Hygrocybe helobia***
13b. Pileus variable in colors, of different sizes, spores varying from white to cream, which can be pink or light green...**14**

14a. Pileus up to 5 cm in diameter, sometimes larger, abundant clavate-inflated or cylindrical cheilocystidia, convex to flattened pileus, then finally depressed, hygrophanous surface, whitish to luteous, rare darker (Putzke & Putzke, *in press*)……………………...................…………………...…....***Gymnopus aquosus***
14b. Pileus with up to 2 cm in diameter, as above or different, cheilocystidia absent, if cheilocystidia and pleurocystidia present are similar and numerous…..……….....**15**

15a. Cheilocystidia and pleurocystidia numerous and similar, reddish pileus in the primordium and turning white or pale cream to pink (Putzke & Putzke, *in press*)...***Atheniella amabillissima***
15b. Cystidia absent and dusky pileus, hygrophanous, ocher when dry, when mature slightly pellucid-striate, convex, umbilicated or subumbilicated, the cortical layer of pileus formed by prostrate hyphae (Putzke & Putzke, *in press*)...***Callistosporium luteo-olivaceum***

Number of Agaricomycetes and Bryophytes parasitized in Brazil

In this survey, 19 species and 10 families of *Agaricales* growing in the same ambient of mosses in Brazil were found, although there is no evidence that these mosses are effectively parasitized by fungi. Among the families, *Hymenogastraceae* is the most represented and rich, with seven species belonging to the genera *Galerina* and *Psilocybe* (Fr.) Kumm. Strophariaceae was the second most representative family, with three species belonging to *Hypholoma* (Fr.) Kumm and *Deconica* (W.G. Sm.) P. Karst. Finally, *Mycenaceae*, *Chromocyphellaceae*, *Clavariaceae*, *Hygrophoraceae*, *Psathyrellaceae*, *Biannularicaea*, *Macrocystidiaceae*, and *Rimbachia* Pat. (*Incertae sedis genus*) contain one species associated with mosses.

In Boreal Forest regions in Europe, it has been reported that about 11% of the fungi detected by DNA sequencing endophytically associated with photosynthetic regions of *Hylocomium splendens* (Hedw.) Schimp., *Pleurozium schreberi* Mitten and *Polytrichum commune* L. ex Hedw. belonged to *Agaricales* (Kauserud & al. 2008). *Rimbachia* and *Galerina* are generally not associated with limited niches as plant tissues, however, studies such as Davey & al. (2013), conducted in Norway, indicate mycelial colonization in photosynthetic and senescent tissues in several bryophyte species, including the genera *Pleurozium* (Brid.) Mitt., *Polytrichum* Hedw., and *Hilochomium* (Hedw.) Schimp. In North America, the work of Raudabaugh & al. (2021) indicates that *Pholiota carbonaria* (Fr.) Singer (Strophariaceae) is capable of forming appressoria and penetration pins associated with live spores in the germination of the moss *Polytrichum commune* and protonema, colonizing mature rhizoids in vitro with asymptomatic infection.

For other *Agaricomycetes* orders, some studies such as Korotkin & al. (2018), for *Hymenochaetales*, indicate, for example, that *Rickenella fibula* (Bull.) Raithelh. (*Hymenochaetalles*: Agaricomycetes) has developed a new trophic mode associated with mosses (Bryophyta), but without harming the development and reproduction of moss. Through radioactive tracking, Carleton & Read (1991) demonstrated the transfer of phosphate and carbon from the moss *Pleurozium schreberi* to *Pinus contorta* Douglas ex Loudon through the ectomycorrhizal fungus *Suillus bovinus* (L.) Kuntze (*Suillaceae, Boletales*), with mycelium associated to senescent regions of gametophytes.

Regarding the geographical distribution of muscicolous *Agaricales* species in Brazil, the state of Rio Grande do Sul had the highest number of species cited (16), followed by Paraná with four, São Paulo with two and Santa Catarina, Minas Gerais and Amazonas with one species each (Figure 1). This shows that, although Brazil is a vast country, few studies have been carried out on the subject. According to BFG (2021), studies on fungi demand many taxonomists, as many new species to science are discovered each year and there are still large areas in Brazil that have never been visited by specialists and that lack collections to have their biodiversity known. In addition, among the studies that cited mushrooms associated with mosses (*Bryophyta* and *Marchantiophyta*) in Brazil, most did not identify the parasitized moss species. Only nine parasitized mosses have been identified at the genus level, and all belong to *Sphagnum*. The agaricoid genus *Galerina* (Cortinariaceae) presented four species directly associated with *Sphagnum*, as well as *Psilocybe* (*Strophariaceae*) that presented two species; *Callistosporium* Singer (*Biannulariaceae*), *Hypholoma* and *Gymnopus* (*Agaricales incertae sedis*) have one species each.

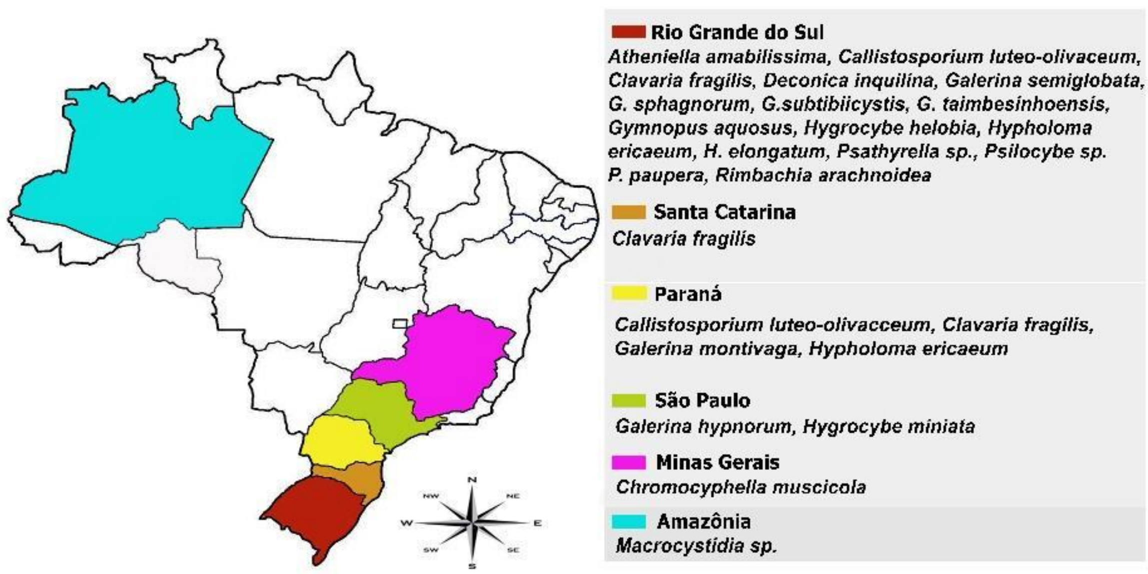

Figure 1 - Distribution of species of muscicolous Agaricales in Brazil. The Brazilian states are followed by the color corresponding to the place of occurrence of each species. (This study).

There are several mentions about the importance of associations between *Agaricomycetes* fungi and bryophytes around the world. Among them we can consider, for example, the development of differentiated trophic modes (Korotkin & al. 2018); formation of associations after forest fires, aiding in the recolonization in burnt areas (Raudabaugh & al. 2021); among other associations that still are unknown (Davey & al. 2013; Kauserud & al. 2008). Unfortunately, no specific studies addressing this interaction were made in Brazil, but only regarding taxonomy and only mentioning the interaction and sometimes identifying the moss putative host. This demonstrates that studies on *Agaricales* fungi associated with bryophytes in Brazil require more attention in order to understand the importance and diversity of those interactions.

Author contributions

CFL, JP, ALC, MAH and KRF conceived the study, CFL and JP conducted the literature review, CFL and JP were the main author of the paper, MAH and KRF commented on the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Chapter

Bryophilous Agaricomycetes (Fungi, Basidiomycota): A Review to Brazil

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Abstract

Bryophilous fungi have at least one stage of its life cycle linked to Bryophytes. There are few studies in relation to their taxonomy and ecology all around the world, includ- ing Brazil. The Agaricomycetes (Basidiomycota) have gained prominence worldwide and contained several species of economic interest. Based on a bibliographic review and discussion about identification methods and experimental models on this association a species list of bryophilous/Agaricomycetes found in Brazil was elaborated. In the works found among the techniques used to identify effective fungi/Bryophytes associations it can be cited: phylogenetics analysis, optical and electron microscopy, and cultivation experiments. In Brazil, four orders of Agaricomycetes (Basidiomycota), belonging to Agaricales, Boletales, Hymenochaetales, and Polyporales, with 33 species were found associated to Bryophytes in the literature. Information of the worldwide distribution of Brazilian muscicolous species and application of these groups were realized associating edibility, toxicity, and others. It was noted that in this country there is a scarcity of scientific knowledge of this subject, that needs to be better understood in terms of ecology and taxonomy.

Keywords: bryophytes, mosses, liverworts, Agaricales, Hymenochaetales, Polyporales

1. Introduction

Bryophylous or muscicolous fungi can be defined as those that have at least one stage of its life cycle linked to Bryophytes (mosses, liverworts and hornworts). Bryo- phytes do not produce nutrient-rich storage structures or specialized transport tissues rich in photosynthetic products as vascular plants, but fungal pathogenesis of mosses is being reported with increasing frequency [1].

The relationship between these two groups is indicated as important to the land colonization by plants [2–4]. Studies of bryophyte/fungal symbioses have also provided powerful insights into the origin and evolution of mycorrhizal associations in land plants [4]. Palaeontologic researchers found fungal structures of Glomeromycota associated with young bryophytes in Ordovician sediments 460 and 400 million years old [5, 6].

Mycorrhizal fungi that inhabit symbiotically healthy tissues of terrestrial plants using organs of absorption [7] inhabiting the rhizoids and/or thalli of liverworts and hornworts were reported associated to different fungi phylla, as Ascomycota, Glomeromycota, and Basidiomycota [4, 8, 9]. Ascomycota has been better studied in this field of knowledge than Basidiomycota [8–11]. Among the Basidiomycota, Agaricomycetes present a total of 19 known orders: Agaricales, Amylocorticiales, Atheliales, Auriculariales, Boletales, Cantharellales, Corticiales, Geastrales, Gloeophyllales, Gomphales, Hymenochaetales, Hysterangiales, Jaapiales, Phallales, Polyporales, Russulales, Sebacinales, Thelephorales, and Trechisporales [12]. With a worldwide distribution, the Agaricomycetes have gained prominence since the class contain several species of economic interest [13–15].

Many of the Agaricomycetes orders are mentioned in different studies about Bryophilous fungi, such as Agaricales, Hymenochaetales, and Polyporales [16–18]. Different structures were developed by fungi to parasite the Bryophytes [1]. Morphological, molecular, and in vitro experiments have shown that mosses such as *Sphagnum*, *Polytrichum* and *Hylochomium* are often associated with Agaricomycetes [16, 17, 19]. A biotrophic trophic mode, in which the fungi species can degrade plant cell walls and lignin, cleaving sucrose to glucose, was recently suggested to occur on 15 species of Hymenochaetales [18].

In Brazil, the are few studies citing the association between Agaricomycetes and Bryophytes [16, 20]. This "gap" in these subjects to science often occurs due to a lack of cooperation between Bryologists and Mycologists [1]. This almost absence of scientific knowledge on this subject is considered as a barrier to better understanding this relation in terms of ecology and taxonomy.

This study as a revision of the knowledge generated up to date to Brazil in this area is an outline of the main employed methods used to identify the interactions of bryophilic mushrooms, as well as a revision of the data of occurrence in the world, and perform a list of Brazilian bryophilous Agaricomycetes. The data presented here are proposed as a starting point to call for more mycologists and bryologists to join the efforts to better understand the Fungi-Bryophyte relationship.

1. Materials and methods

The main employed methods used to identify the interactions of bryophilic mushrooms were illustrated, also, studies in the world with bryophilous Agaricomycetes among 1980 to 2022 were revised. A list of bryophilous Agaricomycetes found in Brazil, with their distribution was made, using bibliographic research available in: Google Scholar, Scopus and Scielo. The nomenclature follows according to the Index Fungorum [12]. The distribution also was obtained from Global Biodiversity Information Facility (GBIF) platform, with the filter "Preserved Specimen" and "Reflora" (Flora e Funga do Brasil). The states of Brazil were named with their respective acronyms: Acre - AC, Alagoas - AL, Amapá - AP, Amazonas - AM, Bahia - BA, Ceará

- CE, Distrito Federal - DF, Espírito Santo - ES, Goiás - GO, Maranhão - MA, Mato Grosso - MT, Mato Grosso do Sul - MS, Minas Gerais - MG, Pará - PA, Paraíba - PB, Paraná - PR, Pernambuco - PE, Piauí - PI, Roraima - RR, Rondônia - RO, Rio de Janeiro - RJ, Rio Grande do Norte - RN, Rio Grande do Sul - RS, Santa Catarina - SC, São Paulo - SP, Sergipe - SE, Tocantins - TO.

2. Methods used to identify the interactions of bryophilic mushrooms

The most used methods for the identification of bryophyta/Agaricomycetes asso- ciations are: optical and electronic microscopy, molecular and phylogenetic analyses, and *in vitro* culture experiments (**Figure 1**). Initially, it is necessary to identify the site of mushroom/bryophyte association, such as non-photosynthetic regions like rhi- zoids, or photosynthetic regions like the thalli or leaf structures. As for example, an optical microscopy analysis was used to identify the fungi *Chromocyphella muscicola* (Fr.) Donk in association with bryophytes, reporting this species usually known from the Northern Hemisphere in Brazil for the first time [21].

With the preparation of slides with KOH (5%), it is possible to visualize the structures of the mushrooms, especially the hyphae which are sometimes linked to the bryophyte cells. In the scanning electron microscope, slides were prepared as usually with reagents that can also be used to identify the association between Bryophytes and Agaricomycetes fungi [1]. As a differential, when analyzing the species *Sphagnum fuscum* Klinggräff with this methodology, it was possible to visualize the rudimentary appressoria that mechanically facilitated the entry into the cells of photosynthetic structures, belonging to the bryophilic species *Glomus mosseae* (T.H. Nicolson & Gerd.) Gerd. & Trappe [1]. An illustrative schematic of the step-by-step of these techniques is shown in **Figure 1A**.

The phylogenetic analyses can be made to detect the feeding and ecological habits using gene portions (ITS 1–2 and 5.8S rRNA) DNA extractions, sequencing and with subsequent bioinformatic analysis [19]. Analysis performed with *Mycena* sp. and *Galerina* sp. showed close evolutionary relationships with *Dicranum* sp. and *Hylocomium* sp. [19]. Key findings include that *Galerina* sp. showed a preference to associate with senescent, rather than photosynthetic tissues, and thus ancestral saprotrophic habit. On the other hand, *Mycena* sp. showed colonization in both tis- sues, and therefore ancestral parasitic habit [19]. In general, phylogenetics is performed in several steps: (I) Material preparation; (II) DNA extraction; (III) Sequencing; and (IV) Sequence analysis by bioinformatics [22]. This results in four advantages: an independent framework for clade construction; a well-supported sta- tistical basis, as the sites of an alignment integrate matrices of different sizes; a low incidence of putative homeoplasies compared to morphological characters; and the implementation of evolutionary models applied independently to each base [23]. An illustrative schematization of these main steps is shown in **Figure 1B**.

In vitro culture experiments are performed to analyze the ecology of interactions and resistance of bryophytes. The bryophytic fungi are part of a diffuse group, often only detected by molecular analyses [24]. The basidioma emerges at specific periods, temperature and humidity, which can make it difficult to visualize between the photosynthesizing or non-photosynthesizing structures of bryophytes [25]. The mycelial phase is the most predominant fungal phase, and this structure can be visualized under microscope when associated to bryophytes. When growing the species *Atrichum androgynum* (Müll. Hal.) A. Jaeger in culture medium, an association with the fungi *Arthrobotrys oligospora* Fresen., was visualized which is known to capture nematodes [24]. This was only possible due to the growth of the fungi in

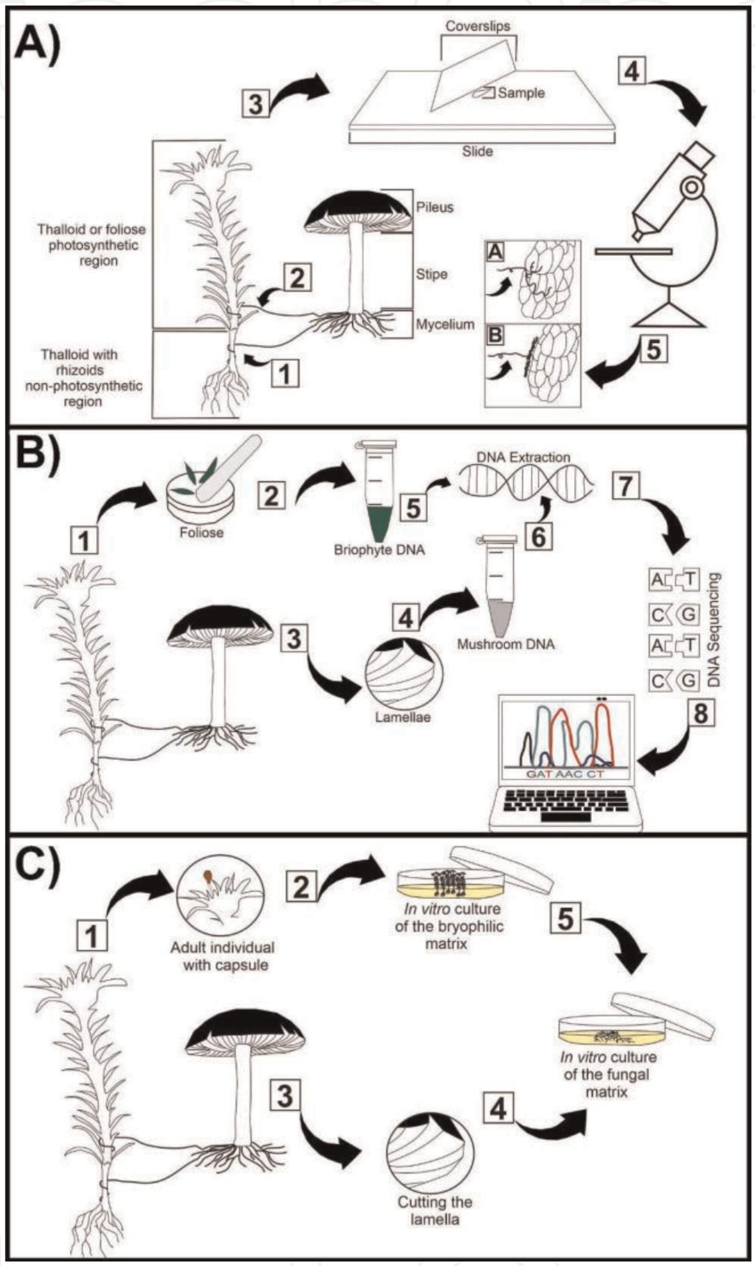

Figure 1. *Methodology frequently used for detection of Fungi-bryophyte associations (FBA). (A) Optical microscopy: association site, non-photosynthetic (1) or photosynthetic (2); slide cuts and use of reagents with cover by coverslip (3); microscope observation (4); FBA endophilic (5-A) or exophytic (5-B) structures. (B) Steps of molecular analyses of FBA: preparation of material for DNA extraction in bryophytes (1 and 2); preparation of material for DNA extraction in mushrooms (3 and 4); use of reagents for DNA extraction (5 and 6); sequencing of gene portions of interest (7); analysis of the sequences by bioinformatics techniques (8). (C) Visualization of FBA in culture medium: a mature bryophyte containing the capsule is isolated (1), and disposed in culture medium (2); the basidiomata (3), when lamellar region is cut and the structure is placed in culture medium (4); when the fungi is not visible, the hyphae grow in the culture medium starting from the bryophytes and can be isolated and cultured separately for species identification (5).*

culture medium, since it was not visible among the collected bryophytes [24]. Sometimes the structures of the fungi can be detected so that with the aid of microscopy, tweezers, and accessories the fungi can be isolated and grown separately in usual culture medium (like PDA). An illustration of the methodological steps mentioned above is shown in **Figure 1C**.

3. Studies about bryophilic mushrooms

Bryophilic mushrooms have been known for a long time, their habitats are well known (swamps, moss-covered tree trunks and mounds). In the 1980's the works about bryophilous fungi around the world include optical microscopy observations, in both Ascomycota and Basidiomycota. In 1981, the fungal species *Lyophyllum palustre* (Peck) Singer was found in mosses and it was constantly associated with necrotic areas of the species, and relationships with bryophytes discussed. Apparently less aggressive species of associated mushrooms were obtained from pure cultures made of *Sphagnum capillaceurn* (Weiss) Schrank, isolating *Lyophyllum palustre* and *Galerina paludosa* (Fr.) Kühner [26]. Research was carried out in 1987 on bryophilic fungi found in samples from the main herbaria in central and northern Europe, identifying ascomycetes associated with the bryophyte *Polytrichum sexangulare*: *Bryochiton heliotropicus* Döbb., *Bryochiton perpusillus* Döbb., *Lizonia sexangularis* Döbb. & Poelt., *Protothelenella polytrichi* Döbb. & Mayrh., *Gloeopeziza interlamellaris* Döbb. and *Hymenoscyphus norvegularis* Döbb [27].

Bryophytes are involved in a variety of competitive, parasitic, symbiotic, mutual- istic and not yet specified interactions with fungi [28]. Some of Bryophilous species have very specific substrates such as *Galerina paludosa* found only in *Sphagnum* swamps, *Cyphellostereum laeve* was found on polytrichoid mosses in coastal regions, in addition to *Rickenella fibula* (Bull.) Raithelh. and *Rickenella setipes* which descriptions reported that a mound formed by *Alnus glutinosa* roots, covered by bryophytes served as substrate for the development of the species [29, 30]. In the 1990s, the main genera of bryophytic fungi were well known: *Galerina*, *Omphalina*, *Rickenella*, *Hypholoma*, *Mycenella* and *Psilocybe*, whose collection area was more widespread, knowing that their nature is more delicate they must be collected with a considerable amount of their substrate of origin [30]. Some islands were targets of ecological studies, such as South Georgia (Southern South America) and Iceland where the bryophyte substrate used by some Agaricomycetes was reported. Collections focused further south of the island of South Georgia were found to have species of the genus *Galerina*, *Gerronema*, *Phaeogalera* and *Hypholoma* [31]. Experiments about growth symbiosis using *Laccaria* spp. on different substrates, including *Sphagnum*, showed that when *Sphagnum* was mixed with vermiculite it was beneficial for the development of the *Laccaria* species and its symbiotic effects [32]. Another research reports that *Sphagnum* and other bryophytes can increase the presence of macrofungi in the substrate [33]. Studies of capture and evasion of nitrogen in soils with suspension of mosses verified that rhizomes of bryophytes have covering links with hyphae of Basidiomycetes fungi, forming a sheath around the rhizoids. This is important since the soil alone cannot handle nitrogen excess, nor accumulating without moss [34].

Research related to Agaricomycetes fungi and mosses among the years 2000 to

2010 cover mainly themes involved in the taxonomy, phylogeny, distribution, diver- sity, and classification of these organisms. Based on morphological characteristics and phylogenetic analysis, it was proposed that the *Omphalina giovanellae* Bres. systematic position is better maintained in another genus, making the mushroom that grows between mosses and low grass belonging to the genus *Clitopilus* (Fr. ex Rabenh.) P. Kumm [35]. *Multiclavula ichthyiformis* Nelsen, Lücking, L. Umaña, Trest & Will- Wolf, was identified as a new basidiolichen from Costa Rica with terricolous habits that grows with bryophytes [36]. *Psathyrella laurentiana* A.H. Sm and *Omphalina philonotis* (Lasch) Quél. (currently classified as *Arrhenia philonotis* (Lasch) Redhead, Lutzoni, Moncalvo & Vilgalys) had their occurrence linked to bryophytes and/or peatlands, suggesting a more specialized niche for some basidiomycetes [37]. The occurrence of decomposing species of the genus *Galerina* Earle and *Coprinus* Pers. in bryophyte swamps including *Polytrichum alpestre* Hoppe in South Georgia Island [38], previously reported [32] can suggest a niche specialization in some species of these genera. *Chromocyphella muscicola* (Fr.) Donk was reported for the first time in Turkey [39], a species that grows near or on mosses, or even parasitizes them while alive [40]. The occurrence in association with mosses is used as identifying character for *Maireina callostoma* (Pilát) W.B. Cooke when using an identification key of this genus [41], showing that associations between Bryophytes and Fungi is an important char- acter also to the taxonomy of Fungi.

Phylogenetic analysis helped to understand the bryophilic habits and high concen-tration of basidiolichens in Hygrophoraceae (Basidiomycota, Agaricales), suggesting a predisposition of these fungi to change their mutualist nutrition associated with photobionts to saprotrophic [42]. The occurrence of *Marasmius epidryas* Kühner, currently classified as *Rhizomarasmius epidryas* (Kühner ex A. Ronikier) A. Ronikier & Ronikier, among mosses was recorded in cold areas of Canada, Denmark and Russia highlights the occurrence of this relationships in cold and harshest areas [43].

Among 2015–2022 most analyses focused on more complex analyses about bryophilic mushrooms. Association among *Sphagnum* mosses and 26 species of Aga-rics and Boleti (Agaricomycetes, Basidiomycota) were found in Ukraine, whereas *Galerina cerina*, *G. paludosa*, *G. sphagnicola*, *Hypholoma elongatum*, *H. udum,* and *Tephrocybe palustris* could be considered as closely associated by substrate links [44]. In 2018, it was demonstrated that many bryophilous Hymenochaetales have values of stable isotope indicating ectomycorrhizal habits or a biotrophic cluster indicative of parasitism or an endophytic lifestyle [18].

The mycorrhizal-like associations, diversity and distribution of fungal associations in bryophytes, as between liverworts of the Jungermaniidae and Marchantiidae with Basidiomycota clades were explored by bibliographic review [4]. Although several works have been published reporting the occurrence of Agaricomycetes fungi growing among mosses, the importance of more specialized studies on the subject is highlighted. Part of these works did not perform microscopic and phylogenetic anal-ysis in order to prove the relationship between Fungi and Bryophytes, but only reported the growth of certain species among mosses. The use of microscopic and phylogenetic analysis will contribute not only to prove the association, but also to understand the phylogeny and evolution of these organisms.

5. Brazilian Agarycomycetes growing with Bryophytes

In Brazil, a total of 33 species from four orders of Agaricomycetes were reported growing with mosses and/or liverworts. Agaricales was the most representative order, with 10 families and 14 genera divided into 20 species. Hymenogastraceae shows a greater number of species associated with *Sphagnum*, although many of the other species of mosses associated with Agaricomycetes have not been identified in the literature. Hymenochaetales presented three families and seven genera, divided into nine species. This order stands out by the diversity mosses and liverworts associated with fungi, including *Rickenella fibula*, which has a feeding habit specialized in bryophytes [18]. Polyporales presented three families and three genera, with several species of mosses and liverworts. Boletales presented only one species growing next to mosses.

List of Agaricomycetes fungi reported to Brazil:

Agaricales Underw.

Agaricales incertae sedis

Rimbachia arachnoidea (Peck) Redhead, Can. J. Bot. 62(5): 878, 1984. = *Mniopetalum bisporum* Singer, Darwiniana, 14: 10, 1966.

Ecology and importance: Growing gregarious on unidentified mosses [45, 46]. *R. arachnoidea* could also be confused with *Rimbachia bryophila* (Pers.) Redhead. Both species are parasitic on mosses and differ in not having venose hymenophore [47].

Distribution: In Brazil it is found in RS (**Figure 2**) [46]. It is found also in Spain, Germany, Switzerland, Norway, Finland, Sweden, Austria, Estonia, Netherlands, Denmark, Belgium, Canada, Argentina, New Zealand, United States of America, Turkey, Poland, among others [47–49].

Chromocyphellaceae Knudsen.

Chromocyphella muscicola (Fr.) Donk, *Persoonia* 1(1): 95, 1959.

= *Arrhenia muscicola* (Fr.) Quél., *Fl. mycol. France* (Paris) 33, 1888.

Ecology and importance: Grow among unidentified mosses and in lichens [21, 50]. Distribution: In Brazil it is found in MG (**Figure 2**) [21, 50]. It is also found in Switzerland, Germany, Spain, Portugal, Australia, Austria, Norway, New Zealand, Netherlands, Cuba, Turkey, among others [39, 48].

Clavariaceae Chevall.

Clavaria fragilis Holmsk., Beata Ruris Otia Fungis Danicis, 1: 7, 1790.

Ecology and importance: Growing in the ground with unidentified mosses [51]. This species is edible [14], showing antioxidant activity [52].

Distribution: In Brazil it is found in RS, SC, and PR (**Figure 2**) [51]. It is also found in Russian Federation, United States of America, Norway, Finland, Sweden, Italy, Switzerland, Spain, Japan, Germany, Canada, Netherlands, Puerto Rico, Australia, South Africa, among other [48, 53–55].

Hymenogastraceae Vittad.

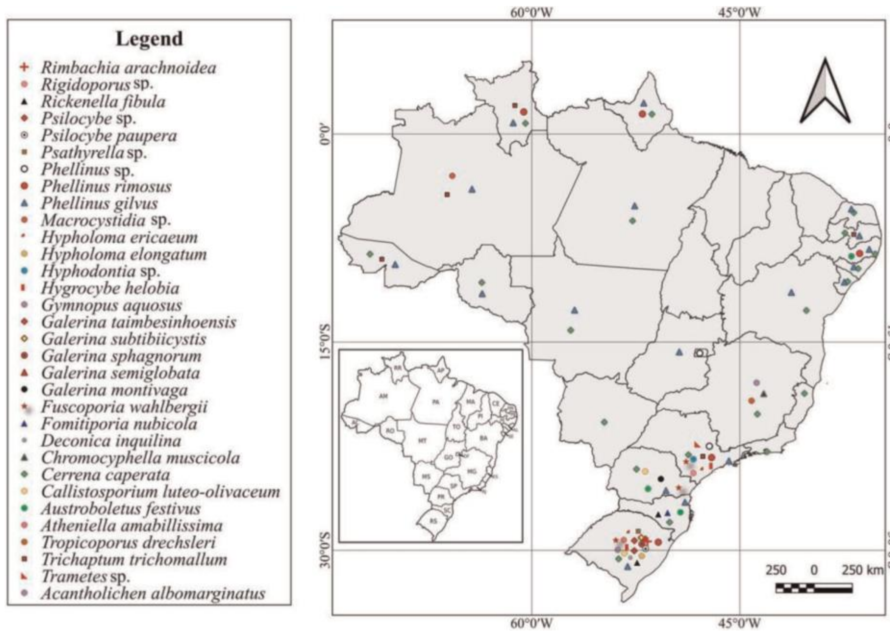

Figure 2. *Distribution of bryophilous species in Brazilian states/regions.*

Galerina montivaga Singer, *Nova Hedwigia,* 29: 306, 1969.

Ecology and importance: Growing gregarious in unidentified moss fields and on humus [56–58].

Distribution: In Brazil it is found in PR (**Figure 2**) [56–58]. It is found also in the United States of America, Slovakia and Argentina [48].

Galerina semiglobata Singer, *Lilloa*, 26: 147, ('1953'), 1954.

Ecology and importance: Forming dense groups on *Sphagnum* that, in some points, are burned. In Brazil it was found in RS (**Figure 2**) [20, 58].

Distribution: This species is endemic to Brazil and is found in Rio Grande do Sul state [20, 58].

Galerina sphagnorum (Pers.) Kühner, *Encyclop. Mycol*., 7: 179, 1935. Sanctioned by Fries.

Ecology and importance: Grow gregarious in *Sphagnum* [20, 58]. In Romania, this species is in the red list in the category "near threatened" [59]. In Poland, *G. sphagnorum* was found associated with eight different species of mosses, *Polytrichum commune, S. centrale, S. fallax, S. cuspidatum, S. flexuosum, Sphagnum magellanicum, S. palustre and S. papillosum* [60].

Distribution: In Brazil it is found in RS (**Figure 2**) [20, 58]. It is also found in Russian Federation, Finland, United States of America, Estonia, Sweden, Austria, Switzerland, Japan, Belgium, Spain, Canada, among others [48, 59].

Galerina subtibiicystis Singer, *Lilloa*, 26: 146 ('1953'), 1954.

Ecology and importance: They grow scarcely among the peat bogs of *Sphagnum* moss [20, 58].

Distribution: This species is endemic to Brazil and is found in RS (**Figure 2**) [20, 58].

Galerina taimbesinhoensis Singer, *Lilloa*, 26: 148 ('1953'), 1954.

Ecology and importance: Growing exclusively on *Sphagnum* moss [20, 58].

Distribution: This species is found in RS (**Figure 2**) [20, 58]. *G. uchumachiensis* Singer is considered a synonym of *G. taimbesinhoensis* [61]. It is also found in the Hawaiian Islands [62].

Psilocybe paupera Singer, Sydowia, 9 (1–6): 404, 1955.

Ecology and importance: Growing gregarious, attached to the stalks of the moss *Sphagnum* [58, 63, 64]. Belongs to the Red List of Macrofungi of China [65].

Distribution: In Brazil, it is found in RS (**Figure 2**) [58, 63, 64]. It is found also in Germany, Costa Rica and China [48, 65].

Psilocybe sp. (Fr.) P. Kummer.

Ecology and importance: Growing among *Sphagnum* in open marshes [20]. This genus can be found in diverse substrates such as soil, dung, wood, and mosses [66].

Distribution: In Brazil the bryophyte associated specimen was found in RS (**Figure 2**) [20]. The genus contains over 150 species distributed worldwide [67]. Occurs worldwide in Mexico, Australia, Canada, Sweden, Germany, United Kingdom, Spain, Netherlands, Costa Rica, Iceland, France, Argentina, New Zealand, Colombia, Russian Federation, Japan, among other countries [48].

Hygrophoraceae Lotsy.

Hygrocybe helobia (Arnolds) Bon, Docums Mycol. 6(no. 24): 43, 1976. = *Hygrocybe miniata* (Fr.) P. Kumm., *Der Führer in die Pilzkunde*: 112, 1871.

Ecology and importance: It was found growing on soil, often between unidentified mosses, and are generally gregarious [25, 68].

Distribution: In Brazil it is found in RS and SP (**Figure 2**) [25, 68]. It was also recorded in Finland, Russian Federation, Switzerland, Sweden, Spain, Austria, Germany, Colombia, Costa Rica, Canada, among other countries [48].

Acantholichen albomarginatus Dal-Forno, Marcelli & Lücking, Mycologia 108(1): 43, 2016.

Ecology and importance: found on the edge of Nebular forest, by the road, on dense vegetation on road side banks, growing on unidentified mosses and liverworts [69].

Distribution: Endemic to Brazil, found in MG (**Figure 2**) [69].

Psathyrellaceae Vilgalys, Moncalvo & Redhead.

Psathyrella sp.

Ecology and importance: Growing in woods at mountains and among unidentified mosses [20]. *Psathyrella* has about 400–600 species, and molecular studies suggest its separation into several others [58]. This genus presents species that have antibacterial diterpenoids [70].

Distribution: In Brazil the bryophyte associated specimen was found in RS (**Figure 2**) [20]. In the world it is reported to the United States of America, Norway, Finland, Congo, Australia, Germany, Russian Federation, Estonia, Spain, New Zealand, Austria, Sweden, Denmark, Poland, Japan [48].

Strophariaceae Singer & Smith.

Hypholoma elongatum (Pers.) Ricken, Die Blätterpilze 1: 250, 1915. = *Psilocybe uda* (Pers. ex Fr.) Gillet, Hyménomycètes (Alençon): 586, 1878.

Ecology and importance: it was found growing attached to the stalk of *Sphagnum* moss, away from trees [20].

Distribution: In Brazil it is found in the RS (**Figure 2**) [20]. It is a cosmopolitan species and is reported to the United States of America, Sweden, Norway, Australia, Russian Federation, Mexico, Japan, Switzerland, Spain, Colombia, New Zealand, Ger- many, South Africa, Poland, Costa Rica, Argentina, France, Iceland, Bolivia, Indone- sia, China, Ukraine, Cameroon, Portugal, Republic of Korea, Peru, Paraguay, among other countries [48].

Hypholoma ericaeum (Pers.: Fr.) Kühner, Bull. Trimest. Soc. mycol. Fr., 52: 23, 1936.

Ecology and importance: Growing in wet and sandy soils among unidentified mosses and grasses [71, 72]. Found in peat bogs among or near peat mosses, but also in wet meadows [73].

Distribution: In Brazil it is found in RS and SP (**Figure 2**) [71, 72]. It is also reported to Spain, United States of America, Poland, Belgium, Norway, Netherlands, Denmark, Russian Federation, Australia, Austria, France, and Greenland [48].

Deconica inquilina (Fr.) Pat. ex Romagn., Revue Mycol., Paris 2(6): 244, 1937. = *Psilocybe muscorum* (P.D. Orton) M.M. Moser, in Gams, Kl. Krypt.-Fl., *Ed.* 3 (Stuttgart) 2b/2: 239, 1967.

Ecology and importance: Growing among an unidentified moss in sandy soil [71]. Distribution: In Brazil it is found in RS (**Figure 2**) [71]. It is also reported to Poland, Estonia, Spain, Iceland, United States of America, Austria, Colombia, Italy, Mexico, Portugal, Russian Federation, Denmark, Norway, Sweden, Finland, Canada, Switzer- land, Belgium, Germany, among other countries [48].

Biannulariaceae Jülich.

Callistosporium luteo-olivaceum (Berk. & M.A. Curtis) Singer, *Lloydia* 89: 117, 1946. = *Callistosporium luteofuscum* Singer, *Lilloa*, 26: 115 ('1953'), 1954.

Ecology and importance: It grow on decaying wood and between the moss *Sphagnum* [20, 46, 57]. It was also reported with saprotrophic habits, on angiosperm wood and growing naturally on rich, deep and moist soils [74].

Distribution: In Brazil it is found in RS and PR (**Figure 2**) [20, 46, 57]. It is reported also to the United States of America, Japan, Canada, Switzerland, Spain, Austria, Costa Rica, Netherlands, Sweden, Australia, Norway, Bolivia, China, Colombia, Czechia, among other countries [48, 72].

Omphalotaceae Bresinsky.

Gymnopus aquosus (Bull.) Antonín & Noordel., in Antonín, Halling & Noordeloos, Mycotaxon 63: 363, 1997 = *Collybia dryophila* (Bull. ex Fr.) Kummer var. *oedipus* Quél., *Fl. mycol. France (Paris)*: 226, 1888. Bas.: *Agaricus dryophilus* Bull. ex Fr., *Herb. Fr. (Paris)*, 10: 434, 1790. = *Marasmius dryophilus* (Bull. ex Fr.) Karsten, *Finl. Nat. Folk*, 48: 103, 1889.

Ecology and importance: It grow in a humid open environment away from trees, associated with *Sphagnum* [20, 46]. It presents β-glucan with antioxidant activity [75].

Distribution: In Brazil it is found in RS (**Figure 2**) [20, 46]. It is also reported to Denmark, France, Germany, Sweden, Finland, Spain, Austria, Russian Federation, Switzerland, Norway, United Kingdon of Great Britain, Netherlands, Estonia, among other countries [48, 75, 76].

Mycenaceae Overeem.

Atheniella amabillissima (Peck) Redhead, Moncalvo, Vilgalys, Desjardin & B.A. Perry, Index Fungorum 14: 1, 2012. = *Mycena amabilissima* (Peck) Sacc., *Syll. Fungorum*, 9: 37. 1891. Bas.: *Agaricus amabilissimus* Peck, *Rep. (Annual) Trustees State Mus. Nat. Hist.*, New York, 39: 39 ('1886'), 1887. = *Prunulus amabilissimus* Murrill, *North Am. Flora*, 9: 324, 1916.

Ecology and importance: Growing among unidentified mosses [46, 77].

Distribution: In Brazil it is found in RS (**Figure 2**). In the world it is reported to the United States of America, Canada, Finland and Argentina [46, 48, 77, 78].

Macrocystidiaceae Kühner.

Macrocystidia sp.

Ecology and importance: Associated with an unidentified moss species [79].

Distribution: In Brazil the bryophyte associated specimen was found in AM (**Figure 2**) [79]. The genus is reported also to Sweden, Denmark, Norway, Spain, Germany, Switzerland, New Zealand, Finland, Austria, United States of America, Japan, Belgium, Canada, Poland, Estonia, Iceland, Mexico, France, Italy, Netherlands, Australia, Republic Democratic of Congo, Czechia, United Kingdom of Great Britain and Northern Ireland, among other countries [48].

Boletales.

Boletaceae

Chevall.

Austroboletus festivus (Singer) Wolfe, *Biblthca Mycol*., 69: 92, 1980 ('1979').

= *Porphyrellus festivus* Singer, *VI. Lilloa*, 26:57–159, 1953.

Ecology and importance: Growing among unidentified mosses in Restinga Forest [80–82].

Distribution: In Brazil it is found in PE, PR, and SC (**Figure 2**) [80–82]. It is also reported to Guyana [48, 83].

Hymenochaetales.

Hymenochaetales *incertae sedis.*

Trichaptum trichomallum (Berk. & Mont.) Murrill, *Bull. Torrey bot. Club* 31(11): 608, 1904.

Ecology and importance: Growing associated with the moss *Entodon beyrichii* (Schwaegr.) C. Muell. Int the Cerrado biome [16]. It is an edible species [13].

Distribution: In Brazil it is found in SP, RO, PB, AC, and AM (**Figure 2**) [16, 48]. It is reported also to Mexico, Peru, Costa Rica and United States of America [48].

Hyphodontiaceae.

Hyphodontia sp.

Ecology and importance: Growing in Atlantic Forest associated with the mosses - *Fabronia ciliaris* (Brid.) Brid. *var. polycarpa* (Hook.) Buck, *Isopterygium tenerum* (Sw.) Mitt., *Sematophyllum subpinnatum* (Brid.) Britt., *Syrrhopodon africanus* (Mitt.) Par. *subsp. graminicola* (Williams) Reese [16]. It has been found also associated with liverworts - *Chonecolea doellingeri* (Nees) Grolle, *Harpalejeunea molleri* (Steph.) Grolle, *Lejeunea flava* (Sw.) Nees, *Metzgeria cf. dichotoma* (Sw.) Nees [16].

Distribution: In Brazil the bryophyte associated specimen was found in SP [16]. This genus occurs also in PA, RO, MG, RJ, PR, RS and SC (**Figure 2**) [84]. In the world, is reported to Sweden, Spain, Denmark, Norway, Estonia, Switzerland, Ger- many, Australia, United States of America, New Zealand, Finland, Poland, Austria, Ukraine, Belgium, Russian Federation, France, Canada, Portugal, India, Costa Rica, Italy, Romania, Islamic Republic of Iran, Réunion, Turkey, Ethiopia, United Republic of Tanzania, Japan, Argentina, Colombia, French Guiana, among other countries [48].

Hymenochaetaceae Donk.

Fomitiporia nubicola Alves-Silva, Bittencourt & Drechsler-Santos, *Mycological Progress*, 19(8): 769–790, 2020.

Ecology and importance: Growing on the living tree of *Drimys angustifolia*, among unidentified mosses [85].

Distribution: Described from Brazil, found in SC [85].

Fuscoporia wahlbergii (Fr.) T. Wagner & M. Fisch., Mycol. Res. 105(7): 780, 2001.

= *Phellinus wahlbergii* (Fr.) D.A. Reid, Contr. Bolus Herb. 7: 97, 1975.

Ecology and importance: Growing between mosses - *Octoblepharum pulvinatum*

(Dozy & Molk.) Mitt., *Syrrhopodon prolifer* Schwaegr. var. *acanthoneuros* (C. Muell.) C. Muell., *Trichosteleum papillosum* (Hornsch.) Jaeg. [16]. It can be fuond growing also with liverworts: *Calypogeia peruviana* Nees & Mont., *Cephalozia crassifolia* (Lindenb. & Gott.) Fulf., *Cyclolejeunea luteola* (Spruce) Grolle, *Kurzia capillaris* (Sw.) Grolle, *Monodactylopsis minima* (Schust.) Schust., *Riccardia chamaedryfolia* (With.) Grolle, *Telaranea nematodes* (Gott. ex Aust.) Howe, *Zoopsis antillana* Steph. [16]. Antioxidant activity [86].

Distribution: In Brazil it is found in BA, RJ, SP, PR, RS, and SC (**Figure 2**) [16, 87]. It is also reported to New Zealand, Japan, Democratic Republic of Congo, Spain, United States of America [48].

Phellinus rimosus (Berk.) Pilát, *Annls mycol.* 38(1): 80, 1940. = *Fulvifomes rimosus* (Berk.) Fiasson & Niemelä, Karstenia 24(1): 26, 1984.

Ecology and importance: Growing between mosses - *Erythrodontium squarrosum* (C. Muell.) Par., *Racopilum tomentosum* (Hedw.) Brid., *Trichostomum weisioides* C. Muell., *Campylopus cryptopodioides* Broth., *I. tenerum* (Sw.) Mitt., *Syrrhopodon gaudichaudii* Mont., *Thamniopsis incurva* (Hornsch.) Buck., *R. tomentosum* (Hedw.) Brid. [16]. Also, can be growing between liverworts - *Anoplolejeunea conferta* (Meissn.) Evans, *Aphanolejeunea* sp., *Bazzania heterostipa* (Steph.) Fulf., *Cephaloziella stellulifera* (Tayl.) Schiffn., *Drepanolejeunea mosenii* (Steph.) Bischl. *L. flava* (Sw.) Nees, *Plagiochila bunburii* Taylat. [16]. Presents cytotoxic, antitumor and antimalarial activity [15, 88].

Distribution: In Brazil it is found in "Cerrado" vegetation and secondary Atlantic Forest in SP, PE, RS, AP, and RR (**Figure 2**) [16, 89–91]. It is also reported to Australia, United States of America, Mexico, Japan, Senegal, Democratic Republic of Congo, Tanzania, Zimbabwe, Canada, Rwanda, Bahamas, Costa Rica, France, Kenya, Bangladesh, Belize, Ecuador, Spain, Gambia, India, among other countries [48].

Phellinus gilvus (Schwein.) Pat., Essai Tax. Hyménomyc. (Lons-le-Saunier): 82, 1900.

Ecology and importance: Growing between mosses - *Pyrrhobryum spiniforme* (Hedw.) Mitt., *I. tenerum* (Sw.) Mitt [16]. It can be also found growing with liverworts - *T. nematodes* (Gott. ex Aust.) Howe, *L. flava* (Sw.) Nees [16]. This is a medicinal mushroom showing antitumor activities, anti-oxidative, anti-fungal, healing, to treat stomach ache and various inflammations [92, 93].

Distribution: In Brazil it is found in SP, AC, AM, BA, GO, MT, PA, PB, PR, PE, RN, RS, RO, RR, SC, SP, and SE (**Figure 2**) [16, 94]. It is also reported to the United States of America, Mexico, Australia, Japan, Costa Rica, Democratic Republic of Congo, New Zealand, Jamaica, French Guiana, Peru, Zimbabwe, Burundi, Puerto Rico, Uganda, Argentina, Canada, Rwanda, Ecuador, among other countries [48].

Phellinus sp.

Ecology and importance - Growing between mosses - *I. tenerum* (Sw.) Mitt., *P. spiniforme* (Hedw.) Mitt., *Thamniopsis incurva* (Hornsch) Buck, *Sematophyllum galipense* (C. Muell.) Mitt, *S. subpinnatum* (Brid.) Britt., *Campylopus cryptopodioides* Broth., *C. cryptopodioides* Broth., *F. ciliaris* (Brid.) Brid. var. *polycarpa* (Hook.) Buck, *Thamniopsis incurva* (Hornsch.) Buckand [16]. It can be also found in liverworts - *Cheilolejeunea trifaria* (Reinw. et al.) Mizut., *Frullania ericoides* (Nees) Mont., *Lophocolea bidentata* (L.) Dum., *L. martiana* Nees, *Radula angulata*, Steph. *Riccardia chamaedryfolia* (With.) Grolle, *T. nematodes* (Gott. ex Aust.) Howe Steph., *D. mosenii* (Steph.) Bischl., *Microlejeunea globosa* (Spruce) Steph., *Aphanolejeunea subdiaphana*

(Jovet Ast) Pócs var. *cristulata* (Schust.) Pócs, *C. doellingeri* (Nees) Grolle, *L. flava* (Sw.) Nees, *Lejeunea ulicina* subsp. *bullata* (Taylor) Schust., *L. glaucescens* Gott., *L. martiana* Nees, *L. muricata* (Lehm.) Nees [16].

Distribution: In Brazil, the bryophyte associated specimens are found in DF and SP [16], but this genus also occurs in AC, AL, AM, BA, CE, ES, MA, MT, MS, PA, PR, PB, PE, PI, RJ, RN, RS, RO, RR, SC, SP, SE (**Figure 2**) [16, 95]. The genus *Phellinus* is reported to the United States of America, Brazil, Sweden, Norway, Finland, Estonia, Australia, Russian Federation, Canada, Mexico, Costa Rica, Germany, Switzerland, Spain, Austria, Japan, New Zealand, Czech Republic, China, Argentina, Democratic Republic of Congo, Denmark, India, among other countries [48].

Tropicoporus drechsleri Salvador-Montoya & Popoff, in Salvador-Montoya, Costa-Rezende, Ferreira-Lopes, Borba-Silva & Popoff, Phytotaxa 338(1): 80. 2018.

Ecology and importance: Frequently among unidentified mosses growing on it (Pagin-Claudio et al., 2022).

Distribution: In Brazil it is found in MG (**Figure 2**) [96]. It is also reported to Argentina [48].

Rickenellaceae Vizzini

Rickenella fibula (Bull.) Raithelh., *Metrodiana* 4: 67, 1973.

Ecology and importance: Growing solitary to gregarious, inhabiting moss beds in high altitude areas (700 and 1500 m above sea level), found inhabiting humid moss beds of *Polytrichium* Hedw. and *Schizymenium* Harv. [97]. Presence of psilocybin [98].

Distribution: In Brazil, it is found in RS and SC (**Figure 2**) [46, 97]. It is also reported to United States of America, Norway, Denmark, Switzerland, Germany, Sweden, Finland, Poland, Spain, Australia, Russian Federation, Canada, New Zealand, Japan, Austria, Belgium, Iceland, Netherlands, China, Democratic Republic of Congo, Italy, among other countries [48].

Polyporales Gäum 1926

Polyporaceae Fr. ex Corda 1839

Trametes sp.

Ecology and importance: Growing between mosses - *Donnellia commutata* (C. Muell.) Buck, also can be found grown with the liverworts *D. mosenii* (Steph.) Bischl. [16].

Distribution: In Brazil, the bryophyte associated specimen is found in SP [16], but this genus also occurs in AC, AM, AP, PA, RO, RR, TO, AL, BA, PA, PB, SE, MS, MT, MG, RJ, SP, PR, RS and SC (**Figure 2**) [99]. The genus *Trametes* is reported also to the United States of America, Mexico, Australia, Norway, Japan, Sweden, Germany, Switzerland, Spain, Costa Rica, Canada, Russian Federation, Estonia, Finland, Den- mark, Austria, Argentina, Jamaica, among others countries [48].

Cerrenaceae Miettinen, Justo & Hibbett 2017

Cerrena caperata (Berk.) Zmitr., Mycena 1(1): 91, 2001. = *Datronia caperata* (Berk.) Ryvarden, Mycotaxon 23: 172, 1985.

Ecology and importance: Growing between mosses - *I. tenerum* (Sw.) Mitt., *Thamniopsis langsdorffii* (Hook.) Buck, also can be found grown with the liverworts - *D. mosenii* (Steph.) Bischl., *Lejeunea glaucescens* Gott. and *L. martiana* Nees. [16]. Present cytotoxic and immunomodulatory activity [87].

Distribution: In Brazil, it is found in AC, AL, AP, BA, ES, MT, MG, PA, PB, PR, PE, RJ, RN, RS, RO, RR, MS, SC, SP and SE (**Figure 2**) [16, 100]. Around the world it is found in Brazil, Costa Rica, Mexico, Panama, Democratic Republic of Congo, Cuba, Guyana, Venezuela, Trinidad and Tobago, Puerto Rico, Kenya, Cameroon, Colombia, French Guiana, Peru, Bolivia, Belize, Guatemala, Nicaragua, Argentina, United States of America, Ghana, Suriname, Tanzania, Sri Lanka, among other countries [48].

Meripilaceae Jülich 1982

Rigidoporus sp.

Ecology and importance: Growing between mosses - *I. tenerum* (Sw.) Mitt., *Thamniopsis langsdorffii* (Hook.) Buck, also can be found grown with the liverworts - *Lejeunea caespitosa* Lindenb., *L. martiana* Nees,*T. nematodes* (Gott. ex Aust.) Howe [16].

Distribution: In Brazil, the bryophyte associated specimen is found in SP [16], this genus also occurs in AC, AM, AP, PA, RO, RR, AL, BA, CE, MA, PB, PE, SE, MT, PR,
RS and SC (**Figure 2**) [101]. The genus *Rigidoporus* is reported to Costa Rica, Mexico, United States of America, Australia, Germany, Estonia, Denmark, Sweden, Puerto Rico, Switzerland, Norway, Japan, New Zealand, Democratic Republic of Congo, French Guiana, Panama, Canada, among other countries [48].

2. Discussion

The bryophilous Agaricomycetes have been analyzed by optical and electron microscopy, *in vitro* cultures, DNA sequencing and phylogenetic analysis in the articles published up to now. Some works highlighted other relevant characteristics, such as edibility, toxicity, and antioxidant properties. Thirty-three species from four orders of Agaricomycetes were reported growing with mosses and liverworts in Brazil. In general, the diversity of possible associations between bryophytes and Agaricomycetes of woody basidioma stands out in small species of lamellate fungi. Moreover, most studies including Brazilian bryophilic species do not approach this interaction satisfactorily, and usually the associated bryophytes are not identified, or when they are identified, it is not described how the association is really occurring.

Bryophyte-Fungi associations sometimes present mutually beneficial symbiosis with bidirectional exchange of resources between partners, i.e., to be mycorrhizal-like even in the absence of true roots in bryophytes [4]. Also, it has not been investigated whether opportunistic parasitism of damaged or stressed bryophytes occurs [1]. In Brazil, about 1524 species of bryophytes were recorded, distributed in 117 families, divided into 11 species of hornworts, 633 liverworts, and 880 mosses [102]. These plants display a higher diversity and a greater number of species in areas of higher elevations and with less anthropic activity [102]. However, bryophytes may grow on different substrates, such as corrugated iron roofs, invertebrates, among others [16]. Among the types of substrates colonized by bryophytes there is a predominance of corticolous, followed by terricolous, rupicolous, and epixilous [102], without the mention of Fungicolous Bryophyte lifestyle.

In our study, the majority of mosses/liverworts and fungi growing together shows occurrences from high and damp places, in the Atlantic Forest, Amazonia, Caatinga, and Pampa biomes. Some species found in our revision, such as, *Rickenella fibula* and *Gerronema sphagnorum*, among others, occurs only on mosses [18, 20, 58]. Many of the identified bryophytes occur on identified fungi [16], such as of *Phellinus*, *Fuscoporia,* and *Hyphodontia.* Also, the mosses usually grew abundantly on the dead trunks on which the fungi were found [16]. Although bryophytes can colonize different environments, studies reveal that the majority of bryophyte species must havea preference for a single type of substrate [103]. The appearance of bryophytes must be influenced by several abiotic factors, as light availability, moisture, and water [102]. The fungi also need moist environments to complete their life cycle but light is not needed by all species [25].

The abiotic conditions are usually found in mountainous tropical areas, as humid climate with rains distributed throughout the year, ample variation of temperatures from the lowland to the high mountains, high rainfall, and topography, all factor enabling greater number of microhabitats [102]. Despite bryophytes can produce defense mechanisms, in response to fungi attack, with the host plant in the process of evolving mechanisms to stop the pathogen's advance [26], some studies show that some bryophyte species do not have their reproduction affected by parasitic fungi [18]. Also, associations between bryophytes and fungi can function in different ways, such as mycorrhizal, parasitic, and commensal [1]. Furthermore, they can have several benefits, both for fungi and for bryophytes, such as improvement in obtaining and cycling nitrogen, carbon (and other nutrients) and in the maintenance of more humid and protected environments [3, 4, 9, 34]. Many species of fungi associated to bryophytes are also found also in extreme environments, such as Antarctica, for example, probably indicating a symbiotic more than parasitic relationship [31, 38].

However, in Brazil these relationships Bryophyte/Agaricomycetes have not been characterized and studied and it is not known whether the occurrence of bryophytes was casual or whether a fungal association really occurred. This demonstrate the importance of more studies in this area in Brazil, what will make it possible to elucidate the ecological and physiological nature of these associations, among other issues, such as the influence of the environment on these associations.

3. Conclusions

Relationships involving bryophilous Agaricomycetes fungi and mosses are not yet well known. These associations are being studied around the world by optical and scanning electron microscopy, *in vitro* culture, sequencing of DNA, and phylogenetics analysis. In Brazil, a total of 33 species from four orders of Agaricomycetes were reported on bryophytes. Although much has been discovered about these interactions around the world, in Brazil these relationships are still not well characterized, either for lack of cooperation between mycologists and bryologists or for other reasons. Most of the Agaricomycetes species reported growing with mosses in Brazil occur in environments with high humidity and high altitude. However, the real influence of the environment on these associations has not yet been identified. Thus, it emphasizes the need for further studies on the interactions between bryophytes and Agaricomycetes, making it possible to better understand their ecology and taxonomy.

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Bryophilous Agaricales in Southern Brazil

Agaricales briófilos no Sul do Brasil

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ABSTRACT
Bryophytes colonize different substrates, while fungi, such as basidiomycetes, can occur on the same substrate as these plants and sometimes associate with them. In Brazil, there are few studies with bryophilous Agarycomycetes and they rarely identify the mosses or the liverworts involved in this association. Taxonomic studies involving bryophyte fungi and the bryophytes involved could demonstrate the ecological relationship and help in the conservation efforts of these groups. This study aimed to investigate the biodiversity and associations of Agaricales (Fungi, Agaricomycetes) and bryophytes in a portion of the Atlantic Forest biome in the state of Rio Grande Sul, southern Brazil. The São Francisco de Paula National Forest (FLONA - SFP) is a preserved high and humid environment and was selected to carry out the collections. Our study described for the first time the true association with microscopic evidence between *Gerronema stuckertii* and *Campylopus pilifer*, *Galerina stylifera*, *Campylopus julicaulis* and *Chlorella* sp., *Oudemansiella platensis* and *Metzgeria consanguinea*, *Psathyrella murrilli* and *Brachythecium* sp. With regard to biological diversity in Brazil, this study improves the understanding of associations between mosses and fungi.
Keywords: Agaricomycetes; bryophytes; ecology; liverworts; mosses.

RESUMO
As briófitas colonizam diferentes substratos, enquanto os fungos, como os basidiomicetos, podem ocorrer no mesmo substrato dessas plantas e, às vezes, se associar a elas. No Brasil, existem poucos estudos com Agarycomycetes briófilos e raramente identificam os musgos ou as hepáticas envolvidas nessa associação. Estudos taxonômicos abrangendo fungos briófilos e as briófitas envolvidas poderiam demonstrar a relação ecológica e auxiliar nos esforços de conservação desses grupos. Este estudo teve como objetivo investigar a biodiversidade e as associações de Agaricales (Fungos, Agaricomycetes) e briófitas em uma porção do bioma mata atlântica no estado do Rio Grande Sul, Sul do Brasil. A Floresta Nacional de São Francisco de Paula (FLONA – SFP), um ambiente alto e úmido preservado, foi selecionada para realizar as coletas. Nosso estudo descreveu pela primeira vez a verdadeira associação com evidência microscópica entre *Gerronema stuckertii* e *Campylopus pilifer*, *Galerina stylifera*, *Campylopus julicaulis* e *Chlorella* sp., *Oudemansiella platensis* e *Metzgeria consanguinea*, *Psathyrella murrilli* e *Brachythecium* sp. No que diz respeito à diversidade biológica no Brasil, este estudo melhora o entendimento sobre as associações entre musgos e fungos.
Palavras-chave: Agaricomycetes; briófitas; ecologia; hepáticas; musgos.

INTRODUCTION

Bryophytes colonize different substrates, such as rocks, soil, and trees, moreover, actively playing in the process of photosynthesis, microhabitat creation, nutrient cycling, and pedogenesis (GRZESIAK & WOLSKI, 2015). Several fungal species growing in association with mosses, including ascomycetes, discomycetes, glomeromycetes, and basidiomycetes, have evolved in a so-called

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bryophilous lifestyle (FELIX, 1988; DÖBBELER, 2002; DAVEY & CURRAH, 2006; STENROOS *et al*., 2010; KOROTKIN *et al*., 2018; GREIFF, 2019). Pressel *et al.* (2021) highlight the vast diversity of fungal symbionts forming mycorrhizal of Glomeromycota, Ascomycota, and Basidiomycota in the tissues of mosses and liverworts from different orders.

Taxa of bryophilous Agaricomycetes (Basidiomycota) fungi remain little known in Brazil and studies that reference this association uncommonly identify mosses or liverworts involved (FURLAN-LOPES *et al*., 2022). Taxonomic studies involving bryophilous fungi and the bryophytes involved may demonstrate the ecological relationship and aid in the conservation efforts of these groups (DAVEY *et al*., 2013). Works as Davey & Currah (2006) and Döbbeler (2021) assert that this gap is due to the lack of cooperation between mycologists and bryologists. Also, Döbbeler (2021) affirms that general neglect of the bryophilous fungi in research may be explained by the fact that nowadays mycologists are often unfamiliar with mosses and liverworts and, likewise, bryologists are unfamiliar with fungi. To Davey & Currah (2006), the moss specimens in herbaria are collected with a bias for healthy plants and many minute parasitic fungi remain unnoticed by the few visible symptoms in their hosts.

Many species of Agaricales of genus *Galerina* Earle, *Psilocybe* (Fr.) P. Kumm., *Omphalina* Quél. were found repeatedly in moss beds (FELIX, 1988). Studies elaborated by Redhead (1981), Redhead (2002), described and classified the bryophilous taxa. The fungal pathogens of bryophytes can be detected by the macroscopic, black, brown, or yellow necrotic and chlorotic patches they cause in otherwise healthy stands of moss gametophytes (DAVEY & CURRAH, 2006). In Brazil, pioneer studies, such as Singer (1953), identified many Agaricales growing with bryophytes, however few Bryophytes were identified to genus level. Vital *et al.* (2000) approached the environment in which the bryophyte species were found. Also, Putzke & Putzke (2017), Putzke & Putzke (2022) catalogued many species of *Agaricales* fungi from different families growing with unidentified mosses.

Optical microscopy analyses provide essential evidence regarding bryophyte-fungal associations (DAVEY & CURRAH, 2006). The microscopy evidence of the hyphae association describes the first record of the possible association involving *Gerronema stuckertii* (Speg.) Singer (Agaricales genera *incertae sedis*) and *Campylopus pilifer* Bridel (Dricanales, Dicranaceae); *Galerina stylifera* (G.F. Atk.) Smith & Singer(Agaricales, Hymenogastraceae) with *Campylopus julicaulis* Brotherus (Dricanales,Dicranaceae) and *Chlorella* sp. (Chlorophyta, Oocystaceae); *Oudemansiella platensis*(Speg.) Spegazzini (Agaricales, Physalacriaceae) and *Metzgeria consanguinea* Schiffner (Metzgeriales, Metzgeriaceae); *Psathyrella murrilli* Smith (Agaricales, Psathyrellaceae) and *Brachythecium* sp. (Hypnales, Brachiteciaceae). Also, the first occurrence citation of *G. stylifera* and *P. murrilli* species were made to the Rio Grande do Sul state. Thus, due to the importance of taxonomic studies related to bryophilous fungi, their characterization and a better understanding of interactions of bryophilous Agaricales fungi, this study aimed to investigate the biodiversity and associations of Agaricales (Fungi, Agaricomycetes) and bryophytes in a portion of the Atlantic Forest biome in Rio Grande do Sul state, southern Brazil.

MATERIAL AND METHODS

Bryophytes (Bryophyta) and Liverworts (Marchantiophyta) from different families associated with Agaricales (Badidiomycota: Agaricomycetes) basidiomata fungi were collected along with the riparian vegetation of the Rio dos Sinos, in the municipality of São Francisco de Paula, in the Floresta Nacional de São Francisco de Paula (FLONA-SFP) (figure 1), Rio Grande do Sul, Brazil, according to SISBIO license (n. 80711-1). The (FLONA-SFP) is located in the Atlantic Forest biome with an altitude between 647 and 940 m, with a temperate, subtropical climate, with humid summers and winters (ICMBio, 2020). The method used to determine the location of the collections was adapted to the rapid survey (WALTER & GUARINO, 2006) and the basidiomes collection, following Putzke & Putzke (2017), with the preservation of the substrate. The collection locations were georeferenced using the MapsMe application and the specimens of fungi and bryophytes were dried in an oven at 40°C. To identify the bryophyte species, the Reflora – Flora e Funga do Brasil (http://floradobrasil.jbrj.gov.br/) site and the identification keys by Gradstein *et al.* (2001), Gradstein & Costa (2003) and Carmo & Peralta (2020) were used. The Agaricomycetes were identified using Putzke & Putzke (2017; 2018; 2022). The macro and micro analysis of the bryophytes and Agaricomycetes were realized at the Laboratório de Taxonomia de Fungos (LATAF) and the deposits of specimens were made in Herbário Bruno Edgar Irgang (HBEI), both at the Universidade Federal do Pampa, in São Gabriel municipality, Rio Grande do Sul, Brazil. The microstructures and the presence of the fungal hyphae in the analyzed bryophytes were examined with a Zeiss Axio microscope at 100 to 1000x magnification. The macrostructures were analyzed with a stereo microscope Olympus SZ51.

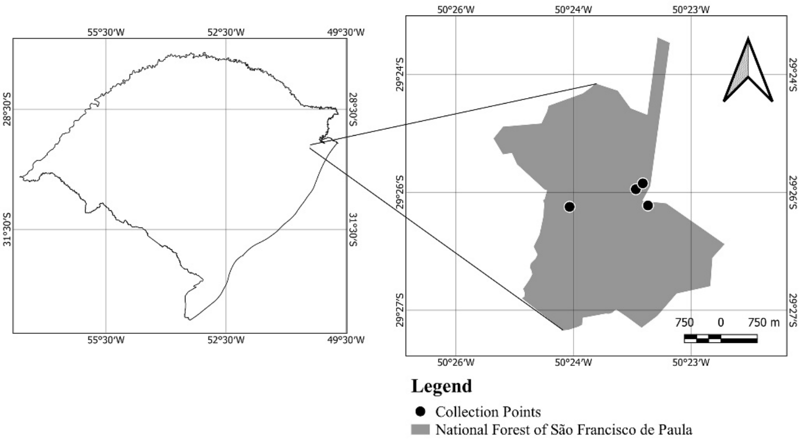

Figure 1 – Collection points of the Agaricomycetes and bryophytes in São Francisco de Paula in the Rio Grande do Sul state, Brazil. Source: primary.

RESULTS

Gerronema stuckertii **(Speg.) Singer, 1959 and** ***Campylopus pilifer*** **Bridel 1819**

Examined material – Brazil, Rio Grande do Sul, São Francisco de Paula, Floresta Nacional de São Francisco de Paula, 29°25'26.1"S 50°23'19.8"W and 29°25'27.4"S 50°23'12.4"W, C. Furlan-Lopes, 12/09/2021 (in this study). Deposited in Herbário Bruno Edgar Irgang (HBEI): HBEI_69 at Universidade Federal do Pampa (Unipampa).

Ecology – *G. stuckertii* was found associated with *C. pilifer* (figure 2) on the soil next to *Araucaria angustifolia* (Bertol.) Kuntze.

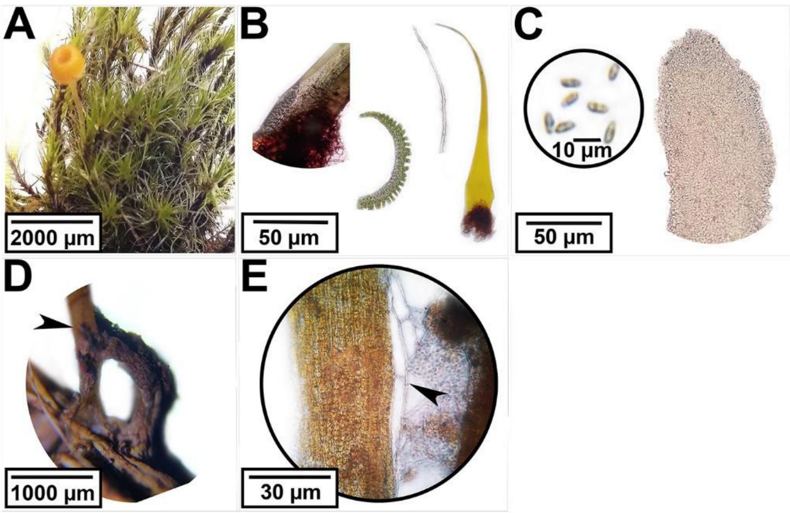

Figure 2 – A) *G. stuckertii* basidiome associated with *C. pilifer*; B) leave, cross section, apical detail, and elongated quadratic cells of leaves of *C. pilifer*; C) spores and hymenophore lamellae woof of *G. stuckertii*; D) detail of performed structure between *G. stuckertii* stipe and *C. pilifer* rhizoids; the arrow head indicate the binding site; E) hyphae of the *G. stuckertii* linked to cells of *C. pilifer*; the arrow head indicate the hyphae binding to the foliar tissue. Source: primary.

G. stuckertii (figure 2)
Description – Presents an umbilicate to infundibuliform pileus, 4-14 mm, orange. Decurrent lamellae of colour cinnamon-yellow. Stipe greyish-yellow, almost white at the base, not cylindrical, 4-29 x 1-1.7 mm in diameter. White basidiospores 6-6.5 x 3.5-4.2 µm in diameter, smooth, thin-walled, hyaline and inamyloid. Tetrasporous basidia. Versiform cheilocystidia, pleurocystidia absent and fibulae present. The cortical layer of pileus with sparse elements, interlaced or free, hyaline, with brown intracellular pigments.
Distribution – Is related in central Argentina (SINGER, 1970), and in Brazil is registered to Rio Grande do Sul state (RICK, 1961; PUTZKE & PUTZKE, 2022).

C. pilifer (figure 2)
Description – Presents leaves evenly distributed along the stem, imbricated with curved margins and an oval base. Also, the leaves have a long acuminate and hyaline apex, with serrated margins at the apex and incurved at the median portion. The stems have a distal portion with deciduous leaves or no shoots. Percurrent and thick costa. Dorsal lamellae show three layers of ventral and central hyalocytes. The cells of the leaf blade are long rectangular, while the basal cells are hyaline. Plants with leafy tufts, light green to yellowish, large.
Distribution – This species have been seen in Brazil in Amazonas, Pará, Roraima Bahia, Ceará, Espírito Santo, Minas Gerais, Mato Grosso, Distrito Federal, Alagoas, Pernambuco, Paraná, Santa Catarina, Rio de Janeiro, Rio Grande do Sul, and São Paulo (MEDINA *et al.*, 2006; SILVA *et al.*, 2014; OLIVEIRA-DA-SILVA & ILKIU-BORGES, 2018; CARMO *et al.*, 2022). This species is cosmopolitan with pantropical distribution, occurring in India, Africa, Occidental Europa, Netherlands and North America (GRADSTEIN & SIPMAN, 1978; OLIVEIRA-DA-SILVA & ILKIU-BORGES, 2018).

***Galerina stylifera* (G.F. Atk.) Smith and Singer, 1958 and *Campylopus julicaulis* Brotherus, 1924**
Examined material – Brazil, Rio Grande do Sul, São Francisco de Paula, Floresta Nacional de São Francisco de Paula, 29°25’26.1”S 50°23’19.8”W and 29°25’27.4”S 50°23’12.4”W, C. Furlan-Lopes, 12/09/2021 (in this study). Deposited in Herbário Bruno Edgar Irgang (HBEI): HBEI_68 at Universidade Federal do Pampa (Unipampa).
Ecology – *G. stylifera* was found associated with *C. julicaulis* (figure 3) on the soil next to *Pinus* sp. L.

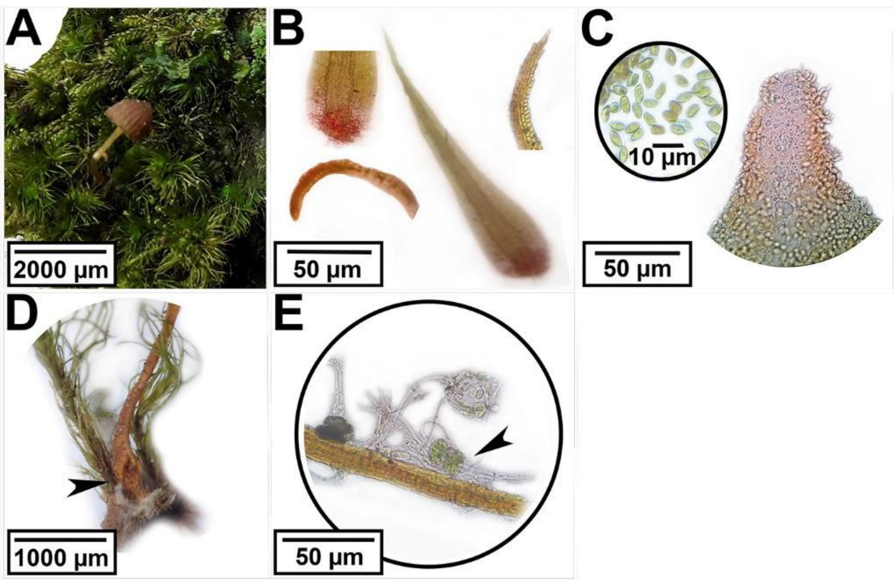

Figure 3 – A) *G. stylifera* basidiome associated with *C. julicaulis*; B) leave, cross section, apical detail, and quadratic cells of leaves of *C. julicaulis*; C) spores and hymenophore lamellae woof of *G. stylifera*; D) detail of performed structure between *G. stylifera* stipe and *C. julicaulis*; the arrow head indicate the binding site. E) hyphae of the *G. stylifera* linked to cells of *C. julicaulis* with *Chlorella* sp.; the arrow head indicate the hyphae binding to the foliar tissue. Source: primary.

G. stylifera
Description – Presents a pileus with 15-50 mm diameter, convex without a pronounced umbo, glabrous and viscid, with a flat margin at maturity, colour ochraceous to cinnamon, pallid when mature with a sometimes-yellowish margin. The lamellae are adnate, ochraceous brown when mature, and have two to three intermediate lamellae. The stipe presents 40-60 x 3-6 mm in diameter, brownish and cylindrical darker at the apex, and spores with 6.3-8.7 x 4-5 µm of diameter, ochre brown, smooth ellipsoidal shape, with a discreet plage. The fibulas are present, and cheilocystidia have 23-28 x 3.5-8 µm, and are subcapitate and hyaline in KOH. Pleurocystidia are absent.
Distribution – Has been seen in Brazil in Paraná state (SMITH & SINGER, 1958; MEIJER, 2008), Rio Grande do Sul (this work). This species has been recorded in several parts of the world, in Spain, Peru, Holanda, China, United States of America, Canada, Italy, Albany, Finland, Sweden (GARCÍA-MANJÓN & MORENO, 1980; DE VRIES & KUYPER, 1988; IBARGUREN, 2001; LAGANÀ *et al.*, 2002; LINDHE *et al.*, 2004; KOKKONEN, 2005; ALLI, 2011; YUTING, 2017; LANDRY, 2019).

C. julicaulis
Description – Presents leaves evenly distributed throughout the stem, which have their distal portion with deciduous leaves or without buds. The leaves have a long acuminate apex concolor to the median and basal parts, and the base of the leaves is oval with curved margins. Percurrent and thick costa. The cells of the leaf blade are quadrangular and the basal cells are hyaline, a little differentiated from the others. The transverse section of the leaves shows a layer of ventral hyalocytes. These plants have leafy tufts, light green to yellowish.
Distribution – *C. julicaulis* is a Brazilian endemic species and have been recorded in Amazônia, Bahia, Rio de Janeiro, São Paulo, Minas Gerais, Paraná, Santa Catarina and Rio Grande do Sul (PEÑALOZA-BOJACÁ *et al.*, 2016; INÁCIO-SILVA *et al.*, 2017; CARMO *et al.*, 2022).

***Oudemansiella platensis* Spegazzini, 1881 and *Metzgeria consanguinea* Schiffner**
Examined material – Brazil, Rio Grande do Sul, São Francisco de Paula, Floresta Nacional de São Francisco de Paula, 29°25’26.1”S 50°23’19.8”W and 29°25’27.4”S 50°23’12.4”W, C. Furlan-Lopes, 12/09/2021 (in this study). Deposited in Herbário Bruno Edgar Irgang (HBEI): HBEI_71 at Universidade Federal do Pampa (Unipampa).
Ecology – *O. platensis* was found associated with *M. consanguinea* (figure 4) on the soil next to *Araucaria angustifolia* Linnaeus.

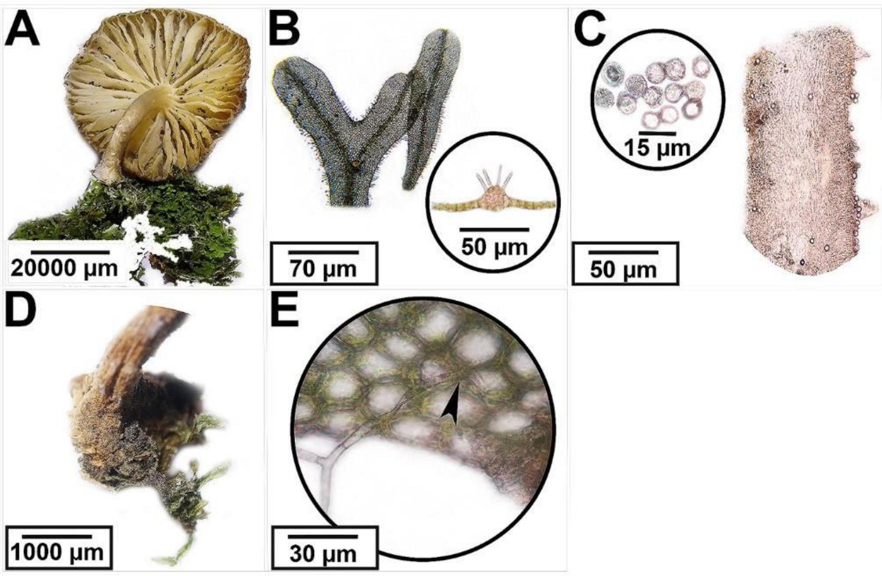

Figure 4 – A) *O. platensis* basidiome associated with *M. consanguinea*; B) leave and cross section of gametophyte with marrow;C) spores and hymenophore lamellae woof of *O. platensis*; D) detail of gametophyte growing on stipe of *O. platensis*; E) hyphae of the *O. platensis* linked to cells of *M. consanguinea*. Source: primary.

O. platensis
Description – Presents a shallowly convex pileus with 35-62 mm of diameter, viscid, gray to beige with margin white. Stipe white, central, without veil. Lamellae adnate, subventricose, distant. Stipe central, folded, expanded base. Spores are white, globose, and smooth, up to 25 µm in diameter, inamyloid. Pileus surface presented scattered patches, with proximal cells relatively narrow and long, terminal cells are subglobose to globose. The cortical layer of the pileus is a trichoderm composed of gelatinized hyphae, with elongated elements and subclavate terminal cells.
Distribution – In Brazil, this species has been found from north to south, in Rio Grande do Sul, São Paulo, Amazônia (RICK, 1937, 1961 (as *Armillaria mucida* Schrad.); SINGER, 1950, 1953, 1955, 1964 (as *Agaricus radiculosus* Cooke); BONONI *et al.*, 1981; PUTZKE & PEREIRA, 1988; GUERRERO & HOMRICH, 1983, PUTZKE & PUTZKE, 2022; REFLORA, 2022). In the world, this species has tropical and subtropical to south-temperate regions distribution in Colombia, Argentina, Costa Rica, Cuba, Dominican Republic, Ecuador, Panamá (BARONI & ORTIZ, 2002; PETERSEN *et al.*, 2008; PIEPENBRING, 2008; YANG *et al.*, 2009).

M. consanguinea
Description – Presents a gametophyte with medium size, dark green. Flat to convex thallus with sparse hairs and irregular dichotomies. Cross-section showing unistratified lamina, up to 24 cells wide, with thick-walled nipple cells, costa shows two rows of cells darker than the others. Marrow with thickened wall cells, with 4 to 5 layers, with 19 to 24 cells (figure 4 B).
Distribution – Has been recorded, in Brazil, to Rio Grande do Sul, Pernambuco, Goiás, Mato Grosso, Paraná, Rio de Janeiro and São Paulo states (COSTA, 2008; BORDIN *et al.,* 2020). Was recorded to Switzerland, Spain, Portugal, Bhutan, China, India, Indonesia, Japan, Nepal, Philippines, Vietnam, Burundi, Cameroon, Democratic Republic of Congo, Ethiopia, Kenya, Lesotho, Madagascar, Malawi, Réunion, Rwanda, South Africa, Tanzania, Uganda, Zimbabwe (SO, 2003, 2004; INFANTE & BRUGUÉS, 2019; SÉRGIO *et al.*, 2021; URMI & HOFMANN, 2021).

***Psathyrella murrillii* Smith, 1972 and *Brachytecium* sp.**
Examined material – Brazil, Rio Grande do Sul, São Francisco de Paula, Floresta Nacional de São Francisco de Paula, 29°25'40.0"S 50°23'03.0"W, C. Furlan-Lopes, 13/09/2021 (in this study). Deposited in Herbário Bruno Edgar Irgang (HBEI): HBEI_70 at Universidade Federal do Pampa (Unipampa).
Ecology – *P. murrilli* was found associated with *Brachythecium* sp. on the soil next to *A. angustifolia* (figure 5).

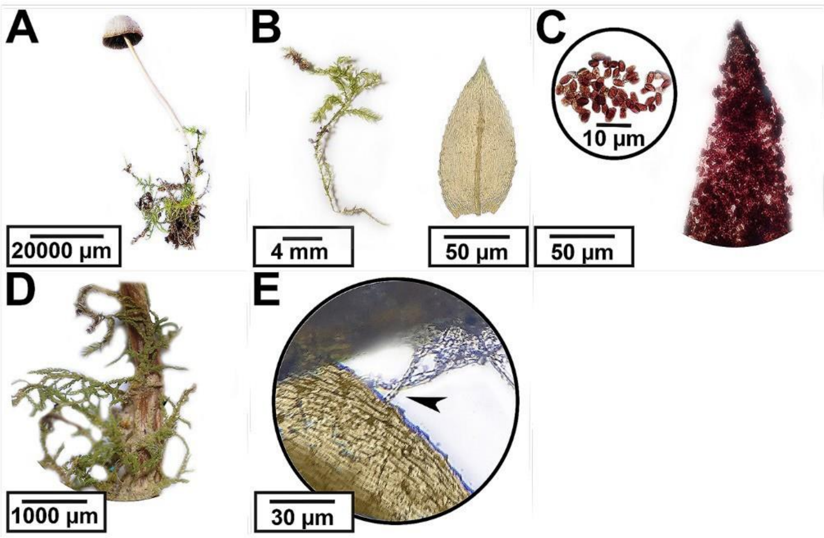

Figure 5 – A) *P. murrillii* basidiome associated with *Brachythecium* sp; B) leave and detais of basal; C) spores and hymenophore lamellae woof of *P. murrillii*; D) detail of *Brachythecium* sp. growing on stipe of *P. murrillii*; E) hyphae of the *P. murrillii* linked to cells of *Brachythecium* sp. Source: primary.

P. murrillii
Description – Presents a smooth pileus, conical with a slight umbo, up to 2.5 cm in diameter, with colour ranging from light brown to ochraceous, with adnexa lamellae, close and brown. Stipe white and smooth, 2.5 – 6 x 0.2 – 0.3 cm in diameter. Dusky brown spores with a thick germinal pore, ellipsoid in shape, measuring up to 7.5 x 4.5 µm in diameter. Basidia with four sterigma. Hyaline cheilocystidia, thin-walled, ellipsoid-shaped, pleurocystidia absent, and fibulae present. The cortical layer of the pileus is formed by cellular epithelium, with hyaline and thin-walled elements and a globose shape.
Distribution – Has been recorded in Brazil to São, Mato Grosso Paulo (PEGLER, 1997; BONONI *et al.*, 2008) and Rio Grande do Sul (this work). This species also was registered in Cuba, Martinica, Colombia, India (PEGLER, 1983; PALACIO *et al.*, 2015; KAUR, 2020; GÓMEZ-MONTOYA *et al.*, 2022).

Brachythecium sp.
Description – Pleurocarpic plant, with leaves evenly distributed on the stem. Green stems of unplanned branches. Primary stems without coma tufts. Leaves are generally oval- elliptical, with acute apex and serrulate edge. Costa extends beyond half of the branch, formed by double layers of cells. Alar cells are barely differentiable, thin-walled, rectangular and smooth. Cells in the middle region of the leaflet are hexagonal and elongated. This genus is usually considered problematic to identify (KHAN *et al.*, 2021). In Brazil, it is possible to find the species *Brachythecium occidentale* (Hampe) A.Jaeger, *B. plumosum* (Hedw.) Schimp., *B. poadelphus* Müll. Hal., *B. ruderale* (Brid.) W.R.Buck (BÔAS-BASTOS & PERALTA, 2022). The *Brachythecium* sp. collected has conflicting characteristics concerning other Brazilian species of *Brachythecium* because it does not present acuminate apex as *B. ruderale* and does not present costa to the middle of leaf lamina as *B. plumosum* but more enormous. These plants are bigger than 2 mm but differ from *B. occidentale* and *B. poadelphus* because they do not present lanceolate leaves.
Distribution – The *Brachythecium* genus is cosmopolitan, including about 150 described species (FREY & STECH, 2009).

DISCUSSION

Studies about bryophilous Agaricales in Brazil primarily focus on fungi, not doing a bryophyte interaction analysis. Four species of possible bryophilous Agaricomycetes associated with four bryophytes species were collected in different places in Floresta Nacional de São Francisco de Paula (figures 2, 3, 4, 5). In Brazil, relationships among Bryophyte/Agaricomycetes have not been characterized and studied, and it is not known whether the occurrence of bryophytes was casual or whether a fungal association occurred (FURLAN-LOPES *et al.*, 2023). Döbbeler (2021) says that, crucially in the field of bryomycology, the basic bryological knowledge provides host identifications, which is of particular relevance for the study of fungal parasites with narrow host spectra. Microscopy evidence through analysis of bryophytes tissue demonstrates possible hyphae association among *G. stuckertii* with *C. pilifer* (figure 2) next to *Araucaria angustifolia* (Bertol.) Kuntze, *G. stylifera* with *C. julicaulis* (figure 3) next to *Pinus* sp. L., *O. platensis* with *M. consanguinea* (figure 4) next to *A. angustifolia*, and *P. murrili* with *Brachythecium* sp. next to *A. angustifolia* (figure 5). for the first time. Also, the first citation of the occurrence of *G. stylifera* and *P. murrillii* was made to Rio Grande do Sul state (figure 1).

G. stuckertii was already found growing on roots (PUTZKE & PUTZKE, 2022). Besides, *C. pilifer* was reported in rocky places, presenting rhizoids for rock attachment (MEDINA *et al.*, 2006). In warm-temperature regions, these species occur at low elevations, whereas in tropical regions, they are mainly found in higher altitudes, 3,500m above the sea level in Central Africa, Andes and northern South America (GRADSTEIN & SIPMAN, 1978). On the other hand, *Campylopus introflexus* Bridel, that is an invasive moss, was found growing with diverse fungal groups, such as the Zygomycota's *Mortierella* Coemans genus and anamorphic fungi belonging to *Acremonium*, among others (REPEČKIENĖ *et al.*, 2015).

Among the bryophilous Agaricomycetes, *Campylopus* Bridel was found associated with *Rickenella indica* Latha & Manimohan, belonging to Himenochaetales (LATHA *et al.*, 2015). Also, *Gerronema fibula* (Bull.) Singer was reported in close relation with *Pleurozium schreberi* Mitten (REDHEAD, 1981; FELIX, 1988). The connection between *G. stuckertii* stipe with rhizoids of the *C. pilifer* (figure 2 D) and the hyphae connection of *G. stuckertii* with the cells of *C. pilifer* (figure 2 E) suggests that the species are genuinely associated. The cosmopolitan distribution pattern of *C. pilifer* contrasts with the restricted distribution of *G. stuckertii* in southern South America (RICK, 1961; SINGER, 1970; PUTZKE & PUTZKE 2022) suggesting that these associations are probably not species-specific. *G. stylifera* was reported ecologically on *Pinus sylvestris* Linnaeus debris at 905m of altitude (GARCÍA-MANJÓN *et al.*, 1980; ALLI, 2011). Putzke & Putzke (2018) have said these species grow up on roots and can be gregarious on wood. This species was also reported to grow in *Pinus* sp. Plantation, in the upper montane mixed rain forest at 950m of altitude (MEIJER, 2008). Laganà *et al.* (2002) have found this species as litter and saprotrophic on wood. Kokkonen (2005) found it in areas affected by the fire. *C. julicaulis* is a Brazilian endemic species, having great plasticity to the amount of needed water, occurring from humid to drier areas (INÁCIO-SILVA *et al.*, 2017). Many species of *Galerina* Earle may colonize bryophyte substrates to some degree, but a relatively small number do so with considerable success (DAVEY *et al.*, 2013).

Moreover, other species of *Galerina*, such as *G. indica,* grew on the moss bed of *Leucobryum* (LATHA *et al.*, 2015) and also *G. paludosa* presents a close association with the host *Sphagnum capillaceum* Schrank (REDHEAD, 1981; FELIX, 1988). *G. stylifera* was found growing with rhizoids of *C. julicaulis* linked to its stipe base (figure 3 D) and with hyphae of *G. stylifera* and a species of *Chlorella* sp. (algae) linked to the cells of *C. julicaulis* (figure 3 E). Sanders & Masumoto (2021) reviewed the role of algae in lichens, stating that they are essential in providing nitrogen and carbohydrates. It is not yet known if the fungus provides anything for the algae besides protection from desiccation. Bryophytes could coexist with algae, fungi or bacterial, playing an irreplaceable role in the restoration of degraded ecosystems (CAO *et al.*, 2020).

O. platensis is found on hardwood trunks (PETERSEN *et al.*, 2008), although Piepenbring (2008) observed the growth of this species on dead branches and trunks, both on the ground and suspended in the air. This species inhabits also the interior of forests next to isolated trees but does not have a specific substrate, which in the Rio Grande do Sul is usually found in dead wood (PUTZKE & PUTZKE, 2022). *M. consanguinea* is usually found on trunks of living trees that are not above sea level, with clustered trees, rarely on branches or shrubs or dead trees, and sometimes found in limestone rock (URMI & HOFMANN, 2021). This species also has already been found on slopes, on rocks and epiphytes on *Castanea sativa* Linnaeus (SÉRGIO *et al.*, 2021). The association occurs between the stipe base of *O. platensis* and the gametophyte leaves of *M. consanguinea* (figure 4 D) and hyphae were also observed in the cells (figure 4 E), suggesting a relationship. Pressel *et al.* (2021) discovered that associations between Metzgeriaceae and Fungi improved the atmosphere as this family increase CO_2 concentration, similarly to the Palaeozoic times when land plants originated, amplifying the net benefits of the association.

P. murrillii grows in the soil inside forests in a gregarious manner (PUTZKE & PUTZKE, 2017). Palacio *et al.* (2015) also observed the gregarious habit but found the species growing in a very exposed place, on the road. The association with bryophytes occurs in other species of the genus, such as *Psathyrella* sp. found with *Sphagnum linnaeus* in Rio Grande do Sul (SINGER, 1953) and *Psathyrella paludosa* Smith reported to Europe as an occasional association to *Sphagnum* sp. (FELIX, 1988). *Scleropodium obtusifolium* (Mitten) Kindberg, an aquatic moss that was emerging from the water, was also reported as an effective host of *Psathyrella aquatica* (FRANK *et al.*, 2010). *Brachythecium* sp. was found on soil associated with the stipe of *P. murrillii*, and hyphae were also found in the cells of *Brachythecium* sp. (figure 5 D and E).

Based exclusively on cytological evidence, bryophyte-fungal associations were assumed to represent, like their counterparts in vascular plants, mutually beneficial symbioses with a bidirectional exchange of resources between partners, i.e., to be mycorrhizal-like given the absence of true roots in bryophytes (PRESSEL *et al.*, 2021). Moss and fungus could also live together because they require similar environmental conditions, and intracellular mycelium is an indication of parasitism (FELIX, 1988). Bryophilous fungi have diverse modes of nutrition, and saprotrophs live on decaying organic matter; most of those that may colonize bryophytes are very poorly known, partly because some may be able to decompose vascular plants as well (GREIFF, 2019).

In species that inhabit wood, the mycorrhizal habit involving bryophytes can be found as a tool for bryo-nutrition. Bryopathogenic species such as the agarics *Arrhenia* Fries and *Rimbachia* Pat. are thought to have arisen from soil and wood-degrading species (DAVEY & CURRAH, 2006). The transfer of phosphate and carbon from *Pleurozium schreberi* to *Pinus contorta* Douglas via the ectomycorrhizal *Suillus bovinus* (Suillaceae, Boletales) was demonstrated through radioactive tracing experiments, with mycelium invasion of gametophytes (CARLETON & READ, 1991). Also, bryophilous species have come from clades with saprotrophic feeding habits, such as *Rickenella fibula* (Bull.) Raithelhulber (Himenochaetales) (KOROTKIN *et al.*, 2018). The phylogenetic analysis of Moncalvo *et al.* (2002) demonstrates that the transition to a facultative or an obligatory bryophilous habit has occurred several times independently, apparently always from a saprophyte ancestor. Bryophytes are organisms adapted to extreme environments and the association between bryophytes and fungi allows them to occur in places where they would not usually occur, because Bryophytes are capable of supporting fungal growth by providing a suitable microenvironment (FELIX, 1988). This shows that fungal mechanisms involved in the successful colonization of bryophytes still need to be understood, demonstrating the importance of realizing more studies with ecological bias.

CONCLUSION

Many taxa of bryophilous fungi remain unknown. On the other hand, studies have yet to be made in Brazil. Even with the ease of use of microscopy in Brazil, the description of bryophilous Agaricales associations employing this analysis had yet to be carried out. Our study described for the first time the true association, with microscopy evidence, between *G. stuckertii* and *C. pilifer*, *G. stylifera* and *C. julicaulis,* and *Chlorella* sp., *O. platensis* and *M. consanguinea*, *P. murrilli* with *Bracthecium* sp. Regarding the biological diversity in Brazil, data shown in this study helps us understand the associations between mosses and fungi. However, more studies are needed to carry on the morphological description and to describe the main characteristics of the ecology of these interactions.

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Rimbachia bryophila (Pers.) Redhead associada a briófitas na Floresta Nacional de São Francisco de Paula

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RESUMO - Fungos briófilos são conhecidos por exibirem pelo menos uma fase de seu ciclo de vida associada a briófitas. Esses organismos desempenham um papel crucial em ecossistemas tropicais na ciclagem de nutrientes. Entretanto ainda existem poucos estudos sobre as suas interações parasitárias e de outros tipos com briófitas. Além disso, no Brasil, estudos utilizando microscopia para evidenciar como ocorre a associação e mecanismos envolvidos entre esses organismos são praticamente inexistentes. Desta maneira descrevemos, por meio de análises macroscópicas e microscópicas, a associação entre o fungo *Rimbachia bryophila* (Fungi, Basidiomycota) e *Dicranella riograndensis*, *Neesioscyphus argillaceus* e *Jungermannia decolor* (Bryophyta). Além disso, fornecemos registro de nova ocorrência de *R. bryophila* registrada para o Brasil. A coleta dos espécimes ocorreu na Floresta Nacional de São Francisco de Paula, no estado do Rio Grande do Sul, sul do Brasil. As análises macro e microscópicas revelaram poucos sinais de necrose, mas não evidenciaram a presença de haustórios ou apressórios nas espécies de briófitas estudadas, como frequentemente relatado em relações parasitárias. No entanto, hifas de *R. bryophila* foram amplamente observadas nos tecidos vegetativos das três espécies de briófitas, sugerindo um tipo de relação não prejudicial. Assim, este trabalho contribui para o entendimento da ecologia dessas espécies e suas associações, destacando a importância desses estudos emergentes no Brasil.

Palavras-chave: Fungos briófilos. Agaricales. Ecologia.

ABSTRACT - Bryophilous fungi are known to exhibit at least one stage of their life cycle in association with bryophytes. These organisms play a crucial role in nutrient cycling within tropical ecosystems. However, there are still few studies on their parasitic and other interactions with bryophytes. Moreover, in Brazil, studies utilizing microscopy to elucidate the associations and mechanisms involved between these organisms are virtually nonexistent. In this study, we describe, through macroscopic and microscopic analyses, the association between the fungus *Rimbachia bryophila* (Fungi, Basidiomycota) and *Dicranella riograndensis*, *Neesioscyphus argillaceus*, and *Jungermannia decolor* (Bryophyta). Additionally, we provide a new record of *R. bryophila* for Brazil. Specimens were collected in the São Francisco de Paula National Forest, located in the state of Rio Grande do Sul, southern Brazil. The macro and microscopic analyses revealed few signs of necrosis but did not show evidence of haustoria or appressoria in the studied bryophyte species, as often reported in parasitic relationships. However, hyphae of *R. bryophila* were widely observed in the vegetative tissues of the three bryophyte species, suggesting a non-detrimental relationship. Thus, this work contributes to the understanding of the ecology of these species and their associations, highlighting the importance of these emerging studies in Brazil.

Keywords: Bryophilous fungi. Agaricales. Ecology.

INTRODUÇÃO

Fungos briófilos são conhecidos por exibirem uma relação simbiótica com briófitas em alguma fase de seu ciclo de vida (Davey e Currah, 2006; Furlan-Lopes et al., 2023). O gênero *Rimbachia* (Basidiomycota: Agaricales: *Incertae sedis*) se distingue morfologicamente por sua forma em taça, caracterizada por veias radiais em vez de lamelas, às vezes acompanhadas de pilosidade, além de um pseudoestipe com fímbrias e uma estrutura ramificada diferenciada (Singer, 1986). Ecologicamente, *Rimbachia* é reconhecido como um gênero briófilo bem estabelecido, amplamente distribuído em ambientes tropicais (Redhead, 1984; Kirk et al., 2008). No Brasil, há uma escassez de estudos referenciados sobre fungos Agaricales briófilos, resultando em uma lacuna significativa de pesquisa que não fornece evidências substanciais corroborando essa associação (Furlan-Lopes et al., 2023). Sinais de decomposição no tecido das briófitas, induzidos por pequenos fungos, como manchas marrons nos filídios e haustórios, são facilmente observáveis por microscopia óptica (Davey et al., 2006; Davey et al., 2013; Greiff, 2019; Greiff, 2021).

Entretanto, muitas briófitas em relações simbióticas com fungos não exibem essas indicações de infecção prejudicial, ou mesmo que exibam alguma destas não manifestam sinais de interferência no desenvolvimento vegetal, mesmo após infecções deliberadas *in vitro* (Korotkin et al., 2018). Desta forma, se fazem importantes estudos que caracterizem a relação entre fungos e briófitas, mesmo que apenas as encontradas ambiente natural, sem ensaios específicos. Portanto, o objetivo deste estudo é descrever macro e microscopicamente o modo de associação entre o fungo briófilo *Rimbachia bryophila* (Pers.) Redhead e as briófitas *Dicranella riograndensis* Broth, *Neesioscyphus argillaceus* (Nees) Grolle e *Jungermannia decolor* Schiffner.

MATERIAL E MÉTODO

Coleta e Identificação do Material

Espécimes examinados. BRASIL. Rio Grande do Sul, Floresta Nacional de São Francisco de Paula, -29°25′22″S, -50°23′11″W, sob licença SISBIO (nº 80711-1), no solo, 26 de mar. de 2023, Jair Putzke (Laboratório de Taxonomia de Fungos, Universidade Federal do Pampa). As amostras de *Rimbachia bryophila, Dicranella riograndensis, Neesioscyphus argillaceus* e *Jungermannia decolor* foram coletadas em conjunto e utilizadas neste estudo.
O material foi depositado no Laboratório de Taxonomia de Fungos da Universidade Federal do Pampa (UNIPAMPA).

A Floresta Nacional de São Francisco de Paula (FLONA-SFP) oferece um ambiente favorável para a biodiversidade de espécies, caracterizado por alta umidade ao longo do ano, invernos frios, verões amenos e altitude média variando de 600 a mais de 900m (ICMBIO, 2020). Os métodos de coleta e armazenamento seguiram Putzke e Putzke (2017) e Gradstein et al. (2001). Para a identificação das espécies de briófitas, foram utilizadas as chaves de identificação de Gradstein et al. (2001), Gradstein e Costa (2003) e Carmo e Peralta (2020). Além disso, o site REFLORA - Flora e Fungos do Brasil (http://floradobrasil.jbrj.gov.br/) foi utilizado como ferramenta de apoio. *R. bryophila* foi identificada usando a chave de Redead (1984).

As análises macro e microscópicas das briófitas e *R. bryophila*, bem como as observações da associação entre esses organismos, foram realizadas utilizando um estereomicroscópio Olympus SZ51 e um microscópio Zeiss Axio com ampliações de 100 a 1000x. As análises foram realizadas no Laboratório de Taxonomia de Fungos (LATAF), e os espécimes foram depositados no Herbario Bruno Edgar Irgang (HBEI), sob número HEBEI-140, na Universidade Federal do Pampa, São Gabriel, Rio Grande do Sul, Brasil.

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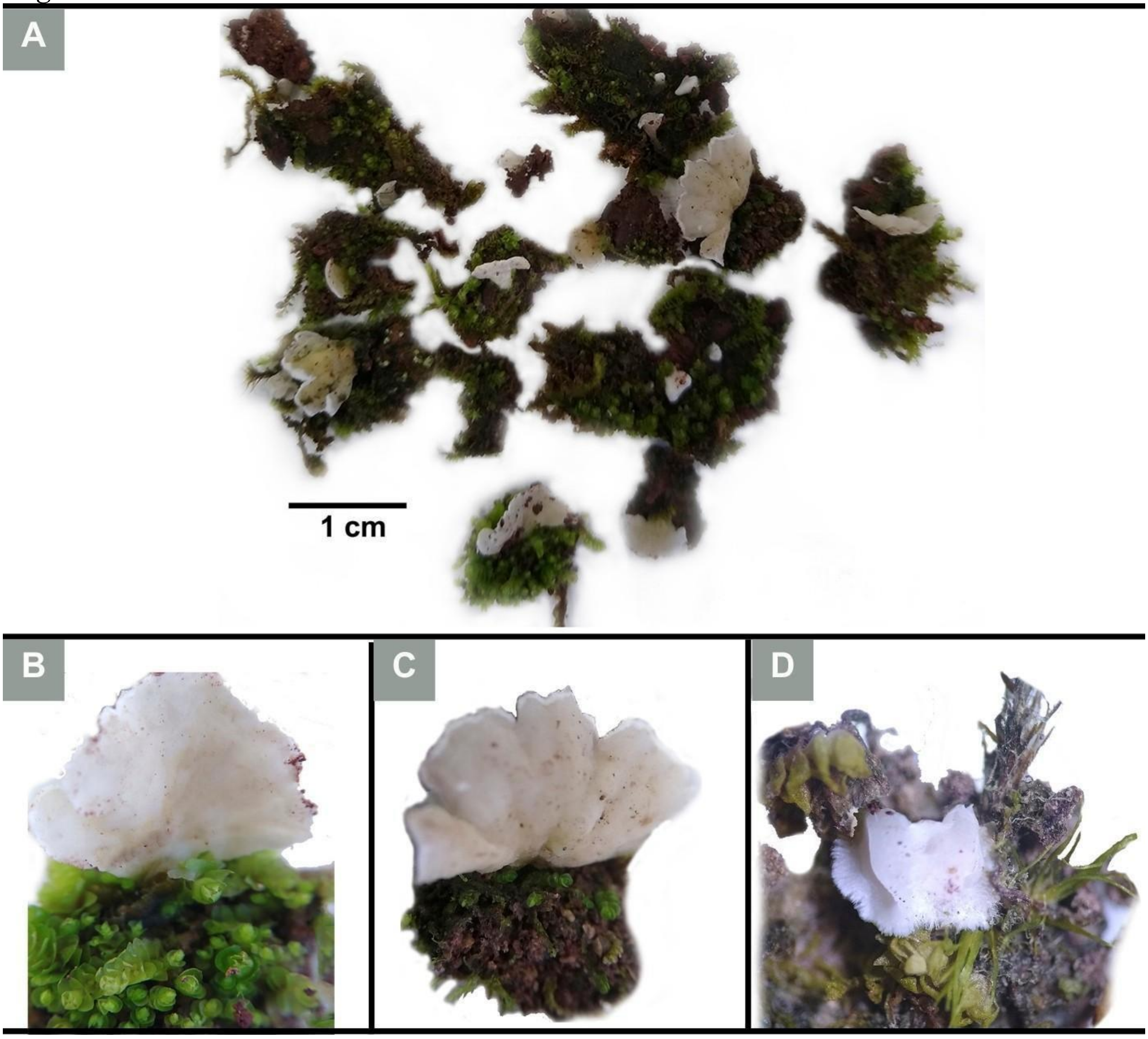
RESULTADOS E DISCUSSÃO

A espécie *Rimbachia bryophila* foi encontrada crescendo no solo associado a *, N. argillaceus, J. decolor* e *D. riograndensis* (Figura 1 A, B, C, D). Não foram observadas estruturas de apressórios ou haustórios. Entretanto, foram visualizadas algumas manchas necróticas nas folhas analisadas macro e microscopicamente.

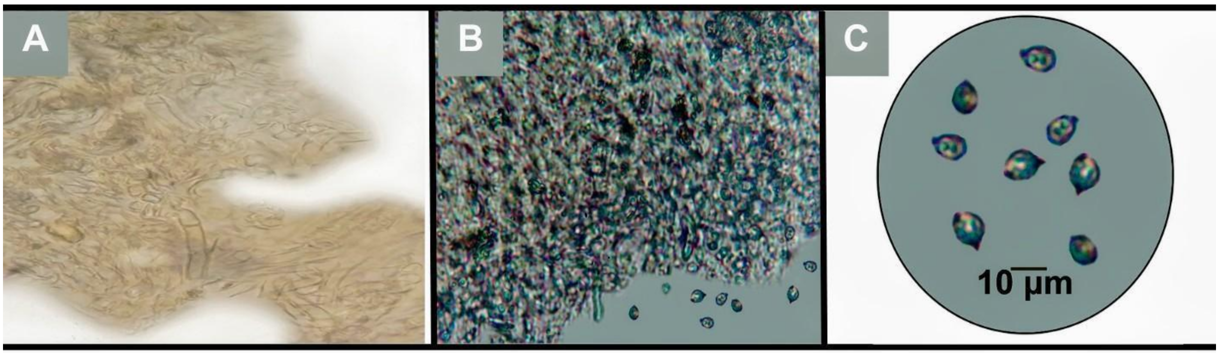
Figura 1. Morfologia de *R. bryophila* e espécies de briófitas. A – Visão geral de *R. bryophila* junto a briófitas; B – Basidioma de *R. bryophila* crescendo com *N. argillaceus*; C – Basidioma de *R. bryophila* crescendo com *J. decolor*; D – Basidioma de *R. bryophila* crescendo com *D. riograndensis*.



Fonte: Autores

Nas análises realizadas conseguimos verificar que a espécie *R. bryophila* (Figura 1 A, B, C, D) é caracterizada por seus basidiomas pequenos e brancos, de até 7 mm de diâmetro, em forma de taça, sésseis ou com um curto pseudo estipe, himenóforo liso em basidiomas jovens, com dobras semelhantes a lâminas e bifurcadas em basidiomas maduros. A trama da lamela é característica e os esporos são elipsoides, hialinos, lisos e com ápice pontiagudo (Figura 2 A, B, C).

Figura 2. Morfologia microscópica de *Rimbachia bryophila*. A – Himenóforo de *R. bryophila.* seta indica os esporos de *R. bryophila*; B – Hifas e esporos de *R. bryophila.* C – Esporos ampliaados de *R. bryophila.*

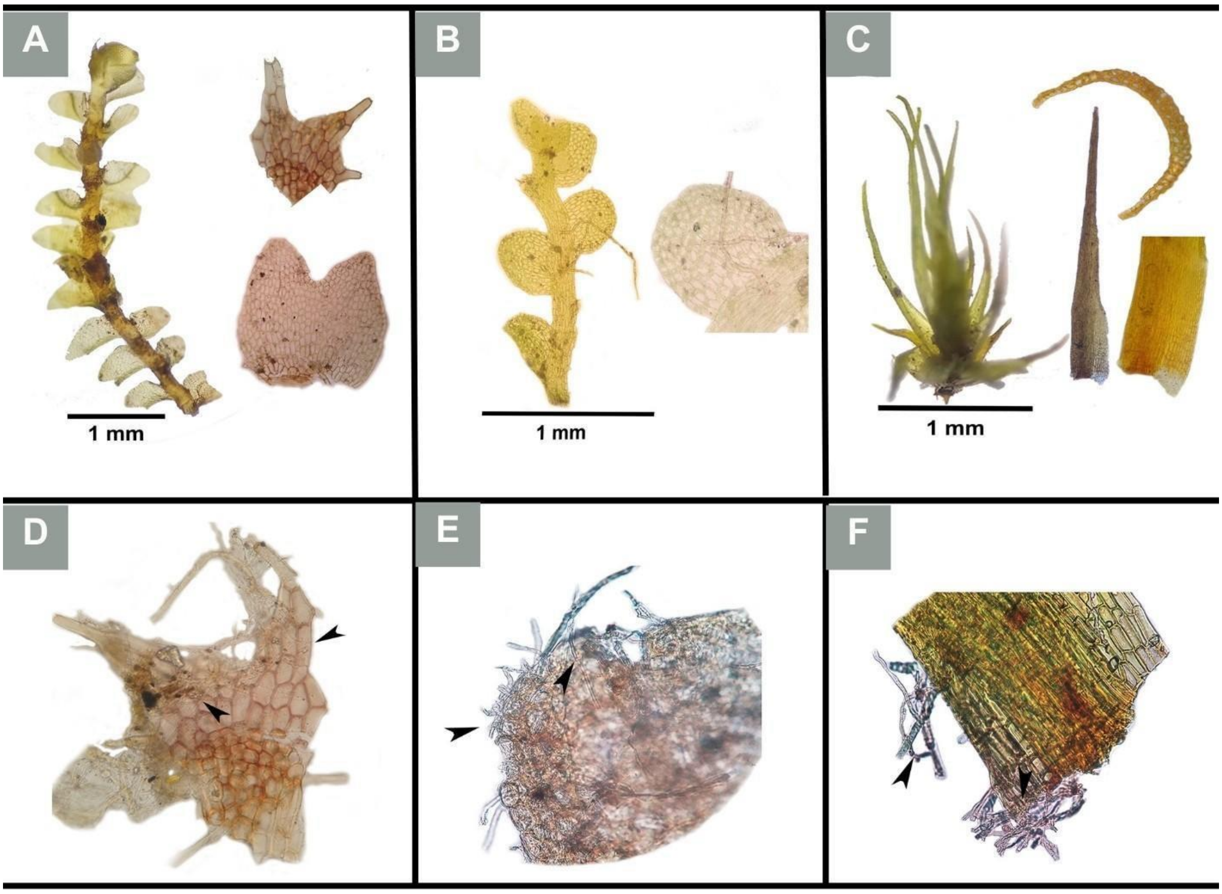


Fonte: Autores.

N. argillaceus (Figura 3 A, D) é caracterizado por coloração verde-clara com filídios bifurcados subcumbentes e anfigastros assimétricos bifurcado, consistente com a descrição de Bordin e Yano (2009). A espécie *J. decolor* (Figura 3 B, E) é caracterizada por folhas arredondadas e inteiras, com fixação sucuba ao caulículo, coloração verde-clara, rizoides marrons, plantas com até 3 mm de altura, ausência de anfigastros e células de parede fina e não diferenciadas ao longo do filoide, que são quadradas. Descrições estas, para *J. decolor,* que são corroboradas por VÁŇA (1974).

D. riograndensis (Figura 3 C, F) apresenta folhas lanceoladas com ápices acuminados e subulados, bases em cunha ou ligeiramente dilatadas, células-guia em secção transversal, e a costa se estendendo aproximadamente 1/3 do comprimento da folha. Em um indivíduo jovem foram observadas bases de algumas folhas com células hialinas. A descrição de *D. riograndensis* está em conformidade com o relato de Carmo e Peralta (2019), que também discute o peristômio dicranoide, sem anel, com esporos marrons e papilosos.

Figura 3. Morfologia e microscopia das espécies de *N. argillaceus, J. decollor* e *D. riograndensis*. A – Morfologia de *N. argillaceus*, com detalhes do filídio e dos anfigastros; B – Morfologia de *J. decolor*, com detalhes do filídio; C – Morfologia de *D. riograndensis*, com detalhes do filídio, secção transversal, células alares, laterais e da região mediana da folha; D – Folhas inferiores de *N. argillaceus* mostrando hifas de *R. bryophila* associadas às suas células; E – Folha de *J. decolor* apresentando hifas de *R. bryophila* associadas às suas células; F – Filídio de *D. riograndensis* apresentando hifas de *R. bryophila* associadas às suas células.



Fonte: Autores.

Morfologia dos espécimes

As descrições dos fungos estão alinhadas com às realizadas por Redhead (1984). *R. bryop*hila possui hifas largas dispostas de forma frouxa e estruturas ramificadas diferenciadas (Singer, 1986). Entretanto, observou-se leve pilosidade sobre o himenóforo de *R. bryophila*.

Comportamento e ecologia das briófitas estudadas

Em relação ao comportamento e ecologia das briófitas envolvidas nas associações estudadas, *N. argillaceus* é uma espécie comumente encontrada à beira de estradas, em solo

(Gradstein e Costa, 2003), ocorrendo sobre rochas e muros de alvenaria, sendo considerada generalista quanto à adesão ao substrato, formando tapetes (Visnadi, 2013). A espécie *N. argillaceus* não é endêmica do Brasil, ocorrendo em regiões neotropicais como Chile e Peru (Grolle, 1964).

No Brasil, é encontrada nos estados do Distrito Federal, Espírito Santo, Goiás, Mato Grosso, Rio de Janeiro, Rio Grande do Sul e São Paulo (Bordin e Yano, 2009). A espécie *J. decolor* ocorre em locais próximos a rios e em altitudes elevadas, como formações montanhosas (Gradstein et al., 2001). Também foi relatada em florestas ombrófilas densas e abertas (Costa et al., 2009). Esta espécie não é endêmica do Brasil, sendo registrada em Minas Gerais (Costa et al., 2013), Ceará e Maranhão. Considerada neotropical (Oliveira, 2023), é uma espécie rara na América do Sul (Costa et al., 2013). Por outro lado, a espécie *D. riograndensis* é encontrada na Mata Atlântica, crescendo em ambientes com solos e rochas frequentemente úmidos, a altitudes de 200 a 1.200 metros. É endêmica do Brasil, registrada nos estados do Espírito Santo, Paraná, Rio de Janeiro, Rio Grande do Sul e Santa Catarina (Carmo e Peralta, 2020).

Comportamento briófilo de *Rimbachia bryophila*

A espécie *R. bryophila* é comumente encontrada crescendo ao lado de campos de musgos (Kaya et al., 2013; Palfner et al., 2020). Esta espécie foi relatada em algumas regiões crescendo com *Sanionia uncinata* (Hedw) Loeske na Tundra Antártica, como parasita (Palfner et al., 2020). Também foi citada crescendo com musgos pleurocárpicos em serrapilheira (Senn- Irlet e Moreau, 2003), e como uma espécie liquenícola, crescendo sobre *Collema undulatum var. granulos* Degel. (Svane e Alstrup, 2004). Em relação à distribuição, embora *R. bryophila* seja relatada como espécie rara, possui uma distribuição em regiões temperadas e polares em ambos os hemisférios (Palfner et al., 2020). Foi relatada na Espanha (Rocabruna e Tabarés, 2005), Turquia (Kaya et al., 2013), Islândia (Svane e Alstrup, 2004), Canadá, Estados Unidos (Redhead, 1984; 1997), Áustria (Hausknecht e Klofac, 2011), Dinamarca (Læssøe, 2012), Nova Zelândia (Segedin, 1994), Suíça, França (Senn-Irlet e Moreau, 2003), e Ilha Rei George - Antártica (Palfner et al., 2020). No Brasil essa espécie está sendo relatada pela primeira vez neste estudo para o estado do Rio Grande do Sul .

Os fungos briófilos são pouco estudados no Brasil, e as descrições morfológicas das estruturas envolvidas nessas associações com Agaricales, embora cruciais para caracterizar essas relações, ainda são inexistentes (Furlan-Lopes et al., 2023). Em nosso estudo, encontramos, por meio de microscopia óptica, hifas de *R. bryophila* associadas às folhas de *D. riograndensis, N. argillaceus* e *J. decolor* (Figura 3 - D, E, F). Entretanto, as observações microscópicas realizadas para com as espécies envolvidas não revelaram a presença de apressórios ou haustórios. E, embora tenham sido observados sinais de necrose foliar, não existem evidências suficientes para indicar que *R. bryhophila* esteja prejudicando o desenvolvimento das briófitas que estavam crescendo sobre ele. Assim, estudos envolvendo o comportamento briófilo em espécies de Agaricales no Brasil citam essas ocorrências apenas com base em observações de campo e evidências macroscópicas (Furlan-Lopes et al., 2023).

O parasitismo fúngico em plantas vasculares frequentemente resulta em sintomas conhecidos, como necrose foliar (Taiz et al., 2021). Os fungos podem ser categorizados em três tipos: necrotróficos, onde o fungo mata o tecido vegetal e se alimenta do tecido morto; biotróficos, onde eles evitam as defesas da planta para consumir recursos sem matar o hospedeiro; e hemibiotróficos, utilizando ambas as estratégias em diferentes estágios de vida (Naranjo-Ortiz e Gabaldón, 2019). Em briófitas, o parasitismo é comumente indicado por manchas marrons nos filídios (necrose) e pela presença de estruturas especializadas como apressórios e haustórios (Davey e Currah, 2006). Além disso, fungos parasitas em briófitas podem atuar de forma oportunista, explorando partes senescentes dos musgos ao se desenvolverem a partir de esporos armazenados no solo (Davey et al., 2012).

É especialmente importante caracterizar os Agaricomycetes briófilos, já que a maioria dos fungos briófilos conhecidos são ascomicetos (Greiff, 2021). Também, deve-se ressaltar que os fungos associados a briófitas podem formar sistemas dinâmicos e complexos (Davey et al., 2012). Assim, a relação do fungo *R. bryophila* com as briófitas *D. riograndensis, N. argillaceus* e *J. decolor* descrita neste estudo auxilia na compreensão de como as estruturas fúngicas se associam a essas briófitas.

CONCLUSÕES

A relação encontrada entre *R. bryophila* e *D. riograndensis*, *N. argillaceus* e *J. decolor* no Sul do Brasil é nova para a ciência. No entanto, essa associação foi observada apenas na natureza, sem a realização do cultivo dessas espécies em laboratório. Desta forma, tornam-se necessários estudos adicionais envolvendo o cultivo e a inoculação proposital de *R. bryophila* nessas briófitas para elucidar o mecanismo dessa associação e o impacto desta para os organismos envolvidos. Além disso, a nova ocorrência de *R. bryophila* no Brasil demonstra a plasticidade da espécie em colonizar diferentes nichos.

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CONFLITOS DE INTERESSE

Os autores declaram que o trabalho não possui conflito de interesses.

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A new species of *Cora* (Basidiomycota: Agaricales: Hygrophoraceae) associated with Bryophytes in Southern Brazil

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Abstract: The genus *Cora* (Agaricales: Hygrophoraceae) is a diverse group of lichenized fungi primarily found in the Neotropics. Despite its wide distribution, the taxonomy of *Cora* remains unclear, and many species have yet to be discovered, especially in Brazil, where bryophilous fungi have been under-researched. This study describes the species *Cora simasi* Furlan-Lopes & Putzke spec. nov. and examines his interaction with bryophytes in the Floresta Nacional de São Francisco de Paula, Southern Brazil. Microscopic analyses revealed hyphal structures and photobionts, indicating a bryophilous association that likely benefits the fungus. Phylogenetic analyses placed *Cora simasi* within the Applanata subclade, closely related to *Cora applanata*, and revealed a sister relationship between the *Ciferrii* and *Aspera* lineages. The phylogenetic analysis showed a close relationship between *Ciferrii* and *Aspera*, with *Cora applanata* and *Cora simasi* Furlan-Lopes & Putzke spec. nov. identified as the most derived species within the *Applanata* subclade. Adapted to high-altitude, humid environments, *Applanata* species exhibit unique microhabitat specialization. The broad ecological diversification of *Aspera* suggests a paraphyletic clade. Speciation within *Cora* appears driven by geographic and environmental isolation. Future research should further explore the ecological and evolutionary processes underlying the diversification of this genus.

Key words:, Bryophilous fungi, ITS, ecology, new taxa.

1. Introduction

The lichens are an active part of cryptogamic communities. Lichens are, by definition, “A self-sustaining ecosystem formed by the interaction of an exhibiting fungus and an extracellular arrangement of one or more photosynthetic partners and an indeterminate number of other microscopic organisms” (Hawksworth and Grube, 2020). While most lichen-forming fungi belong to the phylum *Ascomycota* (about 99%), only a small fraction (<1%) are found within *Basidiomycota* (Lawrey et al., 2007; Lücking et al., 2017).

Among basidiolichens, the genus *Cora sensu strictu* (Basidiomycota: Agaricales: Hygrophoraceae) represents a prevalent group of lichenized fungi. It is a parte of a clade that includes the genera *Acantholichen, Cora, Corella, Cyphellostereum,* and *Cora* s.str, with new species continuing to be discovered as research on the group advances (Dal-Forno et al., 2021; Lücking et al., 2013). In basidiolichens, only the Agaricomycetes present lichenized fungi and are obligatorily associated with cyanobacteria or green algae (Lucking et al., 2016)

Cora s.stric. is commonly found growing in association with bryophytes (Lawrey et al., 2009). However, the bryophilous lifestyle could be more successful due to its limited clade radiation. Also, the transition to a facultative or obligatory bryophilous habit has occurred several times independently, apparently always from a saprophytic ancestor (Moncalvo et al., 2002). Additionally, many Hygrophoraceae fungi are associated directly with bryophytes or with photosynthetic microbial biofilms containing a mixture of green algae, cyanobacteria, and moss protonema on peat or well-decayed wood (Lawrey et al., 2009).

In Brazil, the study of bryophilous fungi is still underdeveloped, and there is a lack of research providing microscopic evidence of the association between bryophytes and fungi. Furthermore, molecular data used in phylogenetic reconstruction analyses provide valuable insights into the evolution of species. In the state of Rio Grande do Sul, few species of fungi have been reported with a bryophilous habit. Thus, this study aimed to identify and describe *Cora simasi* Furlan-Lopes & Putzke, reconstruct their phylogenetic relationships, and contribute to a deeper understanding of their ecological roles and evolutionary history.

2. MATERIAL AND METHODS

2.1 Material collection, macroscope and microscopic analyses

The collections were done in Floresta Nacional de São Francisco de Paula (FLONA-SFP), Rio Grande do Sul state, Brazil (24º29'35.00"S and 47º50'33.00"W) (Figure 1). FLONA-SFP is a region with a subtropical climate, cold and humid winters, and an altitude of up to 940 m above sea level, featuring mostly native vegetation and shallow soil rich in organic matter (ICMBio, 2020). The collections were made under SISBIO, n° 80711-1 (Biodiversity Information and Authorization System) regulated by Chico Mendes Institute for Biodiversity Conservation (ICMBio) in 2022 March in Spring. The method used to collect material was walking, and the fungi basidiomes were collected together to subtract portions (Putzke and Putzke, 2017).

For the morphological description of the macroscopic and microscopic structures of the basidiomes and bryophytes, slides were prepared with fragments of the studied specimens in 3% potassium hydroxide. After, the slides were visualized in the Optical Microscope Zeiss model Axio Scope. A1 and Estereoscope Microscope Olympus Sz 51. The material was deposited in Herbarium Bruno Edgar Irgand HEBEI 141. To determine the color code of the fungi the site RGB color codes chart[1] was used. To identify the Hepaticae and Bryophyta filo specimens, were used the Flora e Funga do Brasil (REFLORA)[2] database and identification keys written by Carmo and Peralta (2020), Gradstein et al. (2001), and Grandstein and Da Costa (2003).

2.2 rDNA Extraction, PCR, and Similarity Analysis

[1] RGB Color Codes Chart (2024). Online Calculators and Tools - RapidTables.com. [online]. Website https://www.rapidtables.com/web/color/RGB_Color.html.[accessed 10 October 2024].

[2] REFLORA, Flora e Funga do Brasil (2020). Data biodiversity of plants and fungi Brasil. [online]. Website:https://reflora.jbrj.gov.br/reflora/listaBrasil/ConsultaPublicaUC/ConsultaPublicaUC.do#CondicaoTaxonCP. [accessed 17 April 2024].

Fungal DNA extraction was performed using desiccated tissue obtained from *Cora simasi* The E.Z.N.A.® Fungal DNA Mini Kit (Omega Bio-tek) was employed and DNA sequences of the 28S nuclear ribosomal DNA (LSU) was conducted using LR0R (ACCCGCTGAACTTAAGC) and LR5 (ATCCTGAGGGAAACTTC) (Vilgalys and Hester 1990) were obtained using primers ITS1 (5'-CTTGGTCATTTAGAGGAAGTAA-3') and ITS4 (5'-TCCTCCGCTTATTGATATGC-3'). PCR was conducted in a final volume of 25 µl containing: 25 ng of genomic DNA (1 µl), 20 mM of each primer (0.25 µl), 10 mM of dNTP mix (2 µl), 50 mM of MgCl2 (0.75 µl), 10× PCR buffer (2.5 µl), Taq polymerase at 5 U/µl (0.25 µl) (Ludwig Biotecnologia), and Milli-Q water to complete the reaction volume. The PCR conditions were as follows: an initial denaturation at 94°C for 2 min, followed by 35 cycles of 94°C for 30 s, 55°C for 40 s, and 72°C for 1 min, with a final extension at 72°C for 1 min (White et al., 1990). The PCR product was purified using a PCR Product Purification Kit (Ludwig Biotecnologia) and sequenced automatically on an ABI 3500 XL sequencer (Applied Biosystems).

2.3 Phylogenetic analysis

For the phylogenetic relationship reconstructions of the genus *Cora*, 59 species were used, which already included portions of the LSU (large subunit 28S) sequences. The study employed a comparative method with external groups of the following species: *Corella tomentosa* and *Corella zahlbruckneri*, both selected due to their ancestral proximity to the group of interest (Lucking et al., 2017). The sequences were obtained during a BLAST search on the National Center for Biotechnology Information (NCBI) GenBank platform (Sayers et al., 2020). All sequences, including the one from the species sequenced in this study, were aligned using CodonCode Aligner v.3.7 (Aligner, 2016) with the MUSCLE option (Edgar, 2004) and gap opening: default extension cost parameters.

Maximum Parsimony (MP) analyses were performed using TNT v.1.5 (Goloboff et al., 2008), applying equal weighting for all bases (Equal Weighting – EW). Traditional searches for the most parsimonious trees were conducted with 1,000 replications using the TBR algorithm, retaining 100 cladograms at each step of the heuristic search (option "hold = 100"). Maximum Likelihood (ML) analyses were performed in RAxML-GUI v.1.5 (Silvestro and Michalak, 2012). Parameters were estimated with 200 rounds calculated using 1,000 repetitions. For the most likely reconstruction, the New Rapid Hill Climbing algorithm was used with the "ML search" option activated. Bayesian Inference (BI) was performed in MrBayes v.3.2 (Ronquist et al., 2012) with four independent Markov chains and Monte Carlo (MCMC) generations, running for 10,000 generations, sampling topologies every 1,000 generations. For the matrix, topology was sampled every 1,000 generations. Both MP and ML analyses included a test of relative node reliability of the resulting cladograms, known as bootstrap (Kitching et al., 1998), based on 1,000 replicates.

3. Results

3.1 Morphological description of the species

3.1.1 *Cora simasi* Furlan-Lopes & Putzke spec. nov.

Mycobank:859439; Figure 2A-1I

Etymology: The epithet honours the mycologist Maria Francisca Simas Teixeira, in honour of her significate contributions to Brazilian mycology.

Holotype: HEBEI141, deposited in Herbário Bruno Edgar Irgang (HBEI). Jair Putzke collected the specimen on 28 march 2022, at Floresta Nacional de São Francisco de Paula, Rio Grande do Sul, Brazil (24°29′35.00″S, 47°50′33.00″W).

Diagnosis: This species is characterised by the flattened nature of the basidiospores, medium lobes 1- 4cm), growing adnate to the ground, and the presence of clamp connections, which are absent in the sister species, *Cora applanata*. Also, *Cora simasi* shows globose basidiospores and is lichen-associated with bryophyte species.

Morphology description: *Cora simasi* shows small to medium 2-4 cm with up to 0,5 mm in thickness (Figure 2A). The thallus of the observed species is terricolous and grows on slopes with bare soil in association with bryophyte species (see description). The *Cora simasi* presents a morphology with a blue-green basidiome (415c67, 487578 and a1b7b5) when fresh (Figure 2A, 1B, 1C), without stipe, with a smooth surface, applanate and projecting horizontally upon to substrate and forming semicircular lobes (concentrically zonate). The organisation of the hymenium presents hyaline hyphae and an abundance of algae (in groups of three to four) in semicircles inside the thallus (Figure 2 - D). Hymenophore in section 70–90 µm, elongate to irregular, creamy colour hyphae, without papillae. The clamp-connections (fibulae) are present and numerous. The basidiospores are globose (5–7 × 5–7.5 µm) (Figure 2 - E). Hymenium is composed of numerous basidioles and scattered borne basidia to 40–45 X 5–6 µm, 4–sterigmate (Figure 2 - F). The cortical layer is composed of globose, hyaline cells 20–25 µm (Figure 2 - G). Pleurocystidia 31–35 X 6–7 µm (Figure 1 - H) and cheilocystidia 30–42 X 8–9 µm (Figure 2 - D) are present.

Material examined: Holotype collected in the Floresta Nacional de São Francisco de Paula, municipality of São Francisco de Paula, state of Rio Grande do Sul, Brazil (24°29′35.00″S, 47°50′33.00″W), under permit SISBIO no. 80711-1 (Biodiversity Information and Authorization System, Brazil).

Ecology and Distribution: The species inhabits shaded, humid forest slopes with exposed soil in subtropical highland forests (Mixed Ombrophilous Forest). It was observed growing in association with bryophyte. Known only from the type locality in southern Brazil.

3.1.2 *Campylopus uleanus* (Müll.Hal.) Broth. (Dicranales: Dicranaceae) (Figure 2A)

The plants form tussocks with a light green coloration (Figure 3A: 1, 2, 3). The stems have a distal portion without buds. At the same time, the leaves are grouped distally on the stem, imbricate, subulate with an ovate to lanceolate base, and a long, pointed, concolourous apex with slightly incurved margins (Figure 3A: 3, 4, 5). The cells of the blade and basal portions are rectangular to elongate rectangular (Figure 3A: 5). The costa extends to the leaf apex, and the cross-section of the leaf blade has ventral and central hyalocysts (Figure 3A: 6).

3.1.3 *Dicranella riograndensis* Broth. (Dicranales: Dicranaceae) (Figure 2B)

Small plants, reaching an average of up to 0.5 cm, with a greenish to yellowish colour (Figure 3 – B: A, B). Branches imbricated and spiralled, with a spiky appearance and lanceolate shape (Gradstein et al., 2001, Carmo and Peralta, 2020). They present slightly amplectant to cuneate, apex acuminate and gradual, concolor with the leaf, presenting a subula, basal and apical cells of rectangular shape, dichranoid peristome, and brown spores (Figure 3B: 3, 4, 5, 6).

3.1.4 *Neesioscyphus argillaceus* (Ness) Grolle (Jungermanniales: Balantiopsidaceae) (Figure 2C).

Small plants, with threads of light green colour, succubus insertion, distant from each other, concave, always bifid with one side larger than the other, providing an irregular aspect, reduced underleaves, usually trifid and with one in each pair of leaves (Bordin and Yano, 2009). Laminate cells are smooth and similar to the leaf edge.

3.2 Phylogenetic reconstructions

The data used in this study compiled 59 species of the genus *Cora*, including the species from this study (*Cora simasi* – PV643873), where evolutionary analyses using Maximum Parsimony (MP), Maximum Likelihood (ML), and Bayesian Inference (BI) were based on the relationships of 1,470 base pairs from ribosomal gene portions LSU (Large subunit 28S). The Bayesian topology expressed the relationships with bootstrap support >60% as described in the order for the analyses (MP/ML/BI), alongside the branches of the master tree. The model that best represented the relationships within the genus was the Tamura-Nei model (Tamura and Nei, 1993), with branch lengths expressed in descending order in log (-8924.37). A discrete Gamma distribution was used for the reference rate of substitution sites, with 0.05 for every 10 categories in the +G parameter = 0.6231 (Figure 4).

In the parsimony analysis, the phylogenetic relationships maintained most of the relationships consistent with those of the other analyses, particularly involving the *Ciferrii* and *Aspera* clades, as well as the *Applanata* (containing the species of this study), *Bovei*, and *Elephas* subclades. The likelihood and Bayesian analyses displayed similar topologies, maintaining previously described relationships, as well as relationships between adjacent internal subclades. The phylogenetic reconstructions resulted in a monophyletic clade for the genus *Cora*, with bootstrap support of (94/73/61). For the species described in this study, *Cora simasi*, the reconstructed relationship indicated a phylogenetic proximity within the *Applanata* subclade and sister to *Cora applanata*, with bootstrap support of (76/81/64). The subclade behaved as sister to the *Ciferrii* clade with bootstrap support of (91/90/-), and to *Aspera* with bootstrap support of (81/63/70). Internally, both the clades and the subclade maintained bootstrap support of (97/89/67). Among the other reconstructed relationships, the *Bovei* subclade exhibited bootstrap support of (77/98/81), and the *Elephas* subclade showed bootstrap support of (87/76/89). These subclades remained paraphyletic sisters to *Aspera*, *Applanata*, and

Ciferrii, with bootstrap support of (-/98/87).

3.1 Associations found

We found three bryophyte species associated with seventeen individuals of *Cora simasi* (Figure 2 and Figure 3). These species are *Neesioscyphus argillaceus* (Ness) Grolle (Marchantiophyta: Jungermanniales: Balantiopsidaceae) with twelve specimens, *Campylopus uleanus* (Müll.Hal.) Broth. with seven and *Dicranella riograndensis* Broth. (Bryophyta: Dicranales: Dicranaceae) with six. Evidence of the bryophilous association between these species is the presence of hyphae and chlorosis in bryophyte leaves, caused by *Cora simasi.*

4. Discussion

Cora genus is widely distributed throughout the Neotropical region and new species of this genus are being discovered every year (Dal-Forno et al., 2013; Käffer et al., 2010; Lücking et al., 2013). Taxonomically, *Cora simasi* shares several morphological features with other species in the genus *Cora*, such as the blue-green coloration of the lobes, concentric arrangement, and terricolous habit traits also observed in *C. gigantea*, *C. hafecesweorthensis*, and *C. imi* (Lücking et al., 2017). However, *C. simasi* is distinguished by its globose and slightly flattened basidiospores (5–7 × 5–7.5 µm), and more notably, by the presence of clamp connections (fibulae), which are absent in species such as *Cora applanata*. This latter species also differs in the structure of the medulla, since the cortical layer in *C. simasi* is composed of globose, hyaline cells (20–25 µm in diameter). In contrast, most species in *Cora* exhibit a viaduct-type or collapsed cortex.

The thallus of *C. simasi*, which grows adnate to bare soil on slopes and in constant association with bryophytes, represents a restricted ecological niche, differentiating it from species such as *C. parabovei* and *C. pichinchensis*, which occur on more compact soils in montane forest environments (Lücking et al., 2017). The hymenophore in *C. simasi* is smooth and cream-colored, lacking papillae—a condition contrasting with the subcyphelloid hymenophore of *C. gigantea* or the cyphelloid structures observed in *C. arachnodavidea* and *C. gomeziana* (Lücking et al., 2017). Other terricolous species such as *C. dulcis* and *C. caliginosa* may exhibit a similar external morphology and coloration but differ in the presence of papillae and hymenophore architecture. Notably, *C. simasi* also lacks soredia and trichomes, features commonly found in species like *C. squamiformis*, *C. quillacinga*, *C. arcabucana*, *C. accipiter*, and *C. dewisanti* (Lücking et al., 2017).

The absence of papillae, the fresh blue-green pigmentation, and the hymenophore organisation further distinguish *C. simasi* from species such as *C. fuscodavidiana*, *C. strigosa*, *C. campestris*, *C. ciferrii*, *C. terricoleslia*, and *C. urceolata*, all of which present brownish colouration and hyphae bearing papillae (Lücking et al., 2017). Thus, the unique combination of morphological traits (semicircular lobes, smooth and applanate surface, absence of papillae), anatomical features (flattened basidiospores, presence of clamp connections and well-developed cystidia), ecological preferences (terricolous, on bare soil, and associated with bryophytes), and phylogenetic distinction (from *C. applanata* and clustering in divergent morphological clades), supports the recognition of *Cora simasi* as a well-defined new species within the genus *Cora*. As with our findings regarding the evolutionary phylogenetic relationships of the genus *Cora*, Dal Forno et al. (2021) also reported the proximity between the *Ciferrii* and *Aspera* clades. In the analysis by Lücking et al. (2017), the description of the *Applanata* subclade took into account both evolutionary and ecological relationships, such as adaptations to humid and high-altitude environments. The subclade within the *Ciferrii* clade, sister to the *Aspera* clade, remains in our analyses and also includes the species from this study. Regarding ancestry, based on branch length, the species in this study exhibited less internal divergence within the subclade, with *Cora applanata* being the most derived. In this context, it is important to emphasise that the *Ciferrii* clade encompasses species derived from independent radiative evolutionary events, primarily involving the diversification of photobiont symbionts, which may have resulted in the recent divergences of the group. Collectively, these clades and the subclade present more recent divergence axes, as proposed by Oset et al. (2024) regarding the phylogenetic cohesion of the group.

The *Applanata* subclade was grouped based on genomic similarity and the flattened morphology of the thalli, which was inferred as an adaptive feature in specific microhabitat conditions, reinforcing its phylogeny as a related subgroup but ecologically differentiated due to extreme environmental pressures (Dal Forno et al., 2021). In the study by Lücking et al. (2017), as well as in our results, the phylogenetic relationship supported by distinct molecular analyses using ribosomal gene portions is considered close. The *Ciferrii* clade is particularly noted for its colonization of humid habitats and soils, while *Applanata*, like *Ciferrii*, also occurs in soils, as well as in mountainous or high-altitude habitats. On the other hand, *Aspera* exhibits extensive ecological diversification, which may suggest its behaviour as a paraphyletic clade, sister to both. This aligns with our findings, inferring that, hypothetically, the genus' speciation was guided by distinct ecological geographic isolations.

In the analyses of Dal Forno et al. (2022) related to the genus’s adaptations, species of the *Bovei* subclade showed close relationships throughout their evolutionary history, with a recent common ancestor. However, their divergence may be related to changes in microhabitats, as these species share morphological characteristics, indicating a possible apomorphy. For the *Elephas* subclade, the evolutionary proximity and recent divergence may be related to a synapomorphy of ecological radiation, as the subclade encompasses species from both humid environments and high altitudes (Dal Forno et al., 2022).

The Atlantic Forest is the second most biodiverse region in the Americas, surpassed only by the Amazon (Morellato and Haddad, 2000; Arruda et al., 2025). However, due to human activities in the region, only about 24% of its original cover remains today (Sos Mata Atlântica, 2022). *Cora simasi* was found in a preserved Atlantic Forest in high-altitude region, and the results of phylogenetic reconstructions suggest that it may represent a new species. Furthermore, the bryophilous associations of *Cora simasi* with *C. uleanus, D. riograndensis* and *N. argillaceus* represent ecologically significant novelties of scientific interest. The mosses *C. uleanus* and *D. riograndensis* are endemic to Brazil (Carmo and Peralta, 2020; Inácio-Silva et al., 2017). However, *C. uleanus* has occurrence from the wettest to the driest zones in elevated altitude, occurring in Bahia, Goiás, Rio de Janeiro, São Paulo, and Santa Catarina states (Costa and Peralta, 2015; Inácio-Silva et al., 2017). *D. riograndensis* is found growing on terrestrial and rocky substrates, often wet soils and rocks, at altitudes between 200 and 1200 m in the Atlantic Forest, occurring in the Brazilian states of Espírito Santo, Paraná, Rio De Janeiro, Rio Grande do Sul, and Santa Catarina (Carmo and Peralta, 2020; Costa and Peralta, 2015). However, the niche modelling indicates that *C. uleanus* has a potential reduction in the territory of distribution soon (Inácio-Silva et al., 2017). *N. argillaceus* is not an endemic species, and Bordin and Yano (2009) confirmed that this species is quite common but little collected. This species can be found on steep lands, along roadsides, or in ravines in the forest, up to 1000 m (Bordin and Yano, 2000; Gradstein and Da Costa, 2003). It occurs in the Brazilian states of Espírito Santo, Goiás, Minas Gerais, Mato Grosso, Rio de Janeiro, Rio Grande do Sul, and São Paulo and in the Distrito Federal (Bordin and Yano, 2009; Costa and Peralta, 2015). *C. simasi* was found in association both with bryophyte species of restricted distribution and high niche specificity, such as *J. decollor* and *D. riograndensis*, and with *N. argillaceus*, a widely distributed species occurring across diverse environments. This highlights the remarkable plasticity of *C. simasi* in colonizing different habitats where its symbionts are present.

The microscopic analyses corroborated the bryophilous lifestyle, revealing chlorosis in the leafy bryophyte and hyphae connections of the type wall-to-wall between the lichenized fungi *Cora simasi* and *C. uleanus*, *D. riograndensis*, and *N. argillaceus* bryophytes' species. These associations among these species are described in this work for the first time, providing new insights into their ecology. The bryophilous symbiosis with fungi can maintain plant nutrition, health, and quality, but it also enhances microfungus-induced carbon sequestration, ecosystem functioning, and nutrient cycling (Bais and Sherrier, 2015). Collective association in lichens considers lichen-forming fungi and other species with different biologies, with many fungi being facultatively lichenized depending on ecological conditions, making it essential to view lichens as self-sustaining and adaptable partnership systems (Hawksworth and Grube, 2020).

Stable isotope values analyzed in many Hygrophoraceae genera, differing considerably from those found for saprotrophic or ectomycorrhizal organisms, suggest a biotrophic bryophilous lifestyle on either bryophyte or with another bryophyte-associated organism (Seitzman et al., 2011). Also, the frequency of lichen-formers in the Hygrophoraceae and its allies suggests a predisposition to switching from a saprotrophic to a photobiont-associated mutualistic mode of nutrition (Lawrey et al., 2009). Our results showed that these hyphae structures act in the influential association between the lichen talus structure of *Cora simasi* and bryophytes. Also, the diversity of communities of bryophytes found suggests that *Cora simasi* has no specificity to a bryophyte substrate. Also, inside Hygrophoraceae, some genera with unknown nutritional strategies may get part of their carbon from mosses, algae or cyanobacteria as mutualists, parasites, or perhaps as saprotrophs (Seitzman et al., 2011). The lichen mycobiont forms a protective thallus over the algal components, shielding symbionts from desiccation, while bryophytes linked to thallus algae provide energy and carbon that benefit associated fungi and enhance nitrogen fixation. In this context, the newly identified bryophilous associations of *Cora simasi* with *C. uleanus*, *D. riograndensis*, and *N. argillaceus* represent ecologically significant interactions, requiring further investigation.

CONCLUSIONS

In this work, we describe the species *Cora simasi*, and provide important insights into its ecology, reporting its association with the bryophyte species *C. uleanus*, *D. riograndensis* and *N. argillaceus* in the Floresta Nacional de São Francisco de Paula, Brazil. Other species to *Cora* present a relationship with bryophytes, furthermore, these associations are poorly studied. The observed associations with bryophytes its an important novel to the ecology of these species. Also, the facultative bryophilous relationship between *C. simasi, C. uleanus*, *D. riograndensis* and *N. argillaceus* is characterized by the absence of specificity towards any particular bryophyte partner. The hyphal structures observed in the association between the lichen thallus of *Cora simasi* show that the species involved do not appear to show specificity towards any particular bryophyte partner. This association likely contributes to nitrogen fixation for the bryophytes, facilitated by cyanobacteria and algae present in the mycobiont, thus offering a stable environment for bryophilous growth. In return, bryophytes may provide essential nutritional support to the fungi. However, further research is required to explore the nitrogenase activity in these associated lichen species, which would validate and refine the observed interactions.

The genus *Cora* presents exponential diversity when it comes to discovering new species. Combining molecular biology tools and morphological data is the way for more and more species to be described around the tropics. The results also contribute to a deeper understanding of the phylogenetic relationships within the *Cora* genus, particularly concerning its clades' evolutionary connections. Our analysis demonstrated that species within the *Ciferrii* clade, including those identified in this study, exhibit minimal internal divergence, with *Cora applanata* being the most derived species. This finding supports the notion of distinct evolutionary events within the genus, likely driven by the diversification of photobionts. The *Applanata* subclade, with its unique morphological traits, appears to have evolved specific adaptations to high-altitude and humid environments, further underlining the ecological pressures that have shaped the genus' diversification. These findings suggest that ecological factors, such as habitat specificity and geographic isolation, played significant roles in the evolutionary history and speciation of *Cora simasi* species. This work describes *Cora simasi* but also underscores the importance of bryophyte associations in its ecology, while contributing to the broader understanding of phylogenetic and evolutionary processes driving diversity within the *Cora* genus.

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Conflict of interests

The authors declare that they have no conflict of interest.

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Figures

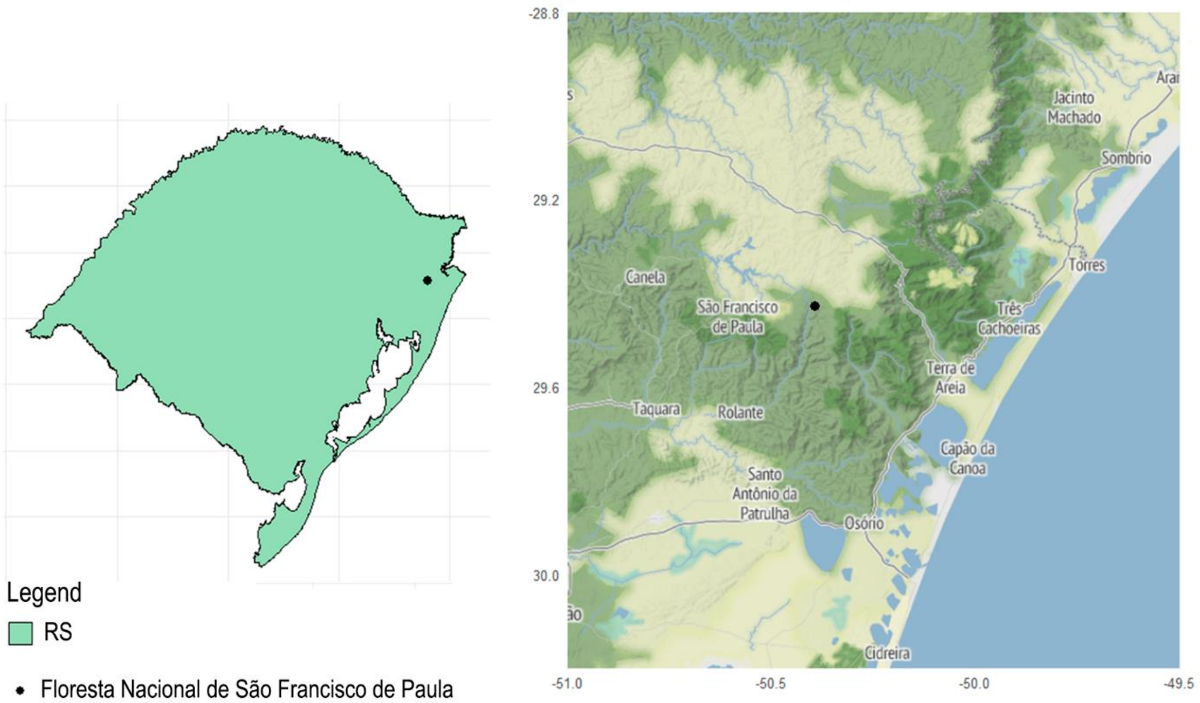

Figure 1. Collect point map. RS: Rio Grande do Sul State.

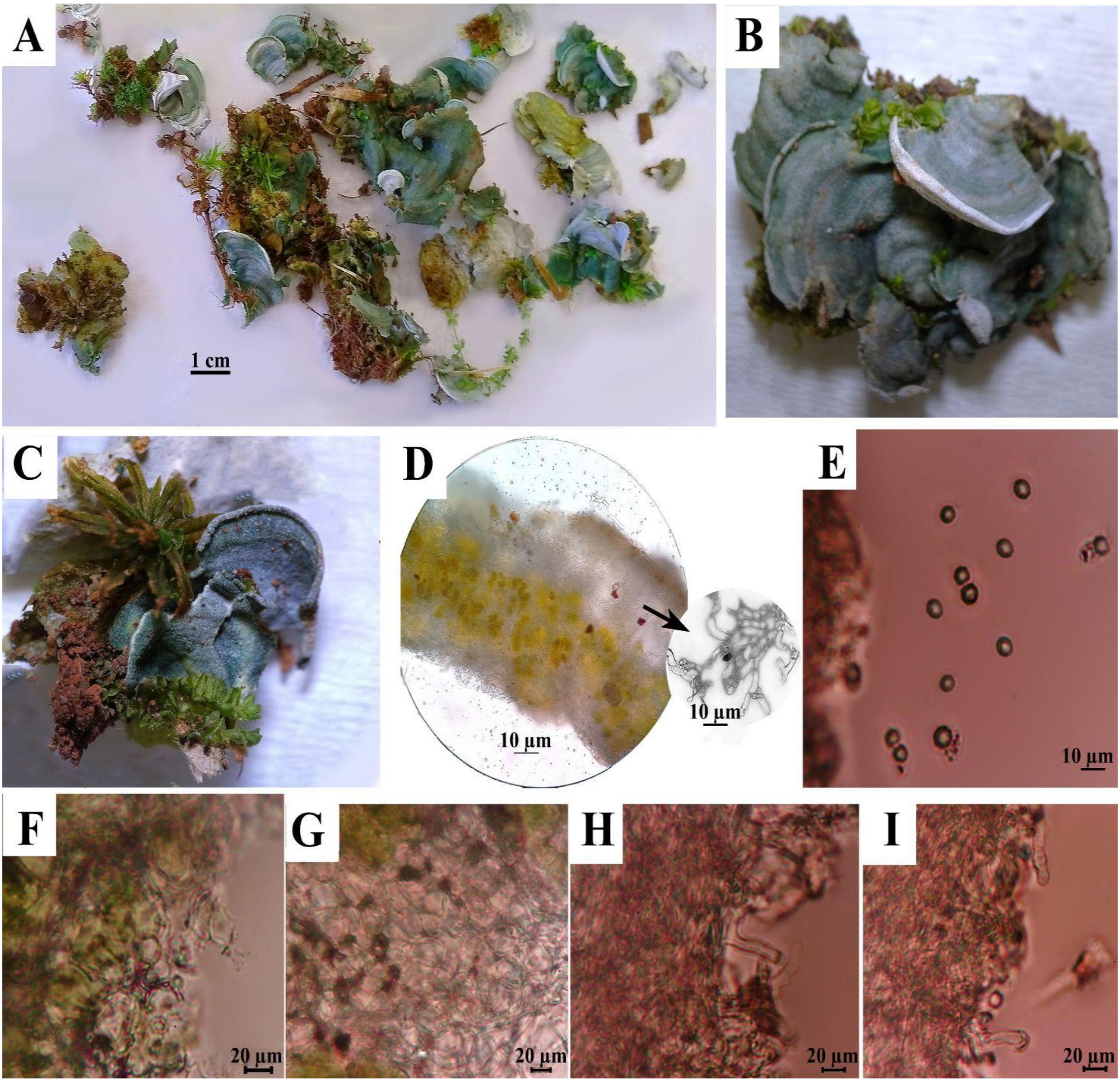

Figure 2. General morphology of *Cora simasi* A) *Cora simasi*, basidiome with diverse bryophytes morphotypes. B and C) *Cora simasi* basidiome detail. D) Lamellae with algae disposition, hyphae detail zoom. E) Basidiospores. F) Basidia. G) Cortical layer cells. H) Pleurocystidia. I) Cheilocystidia.

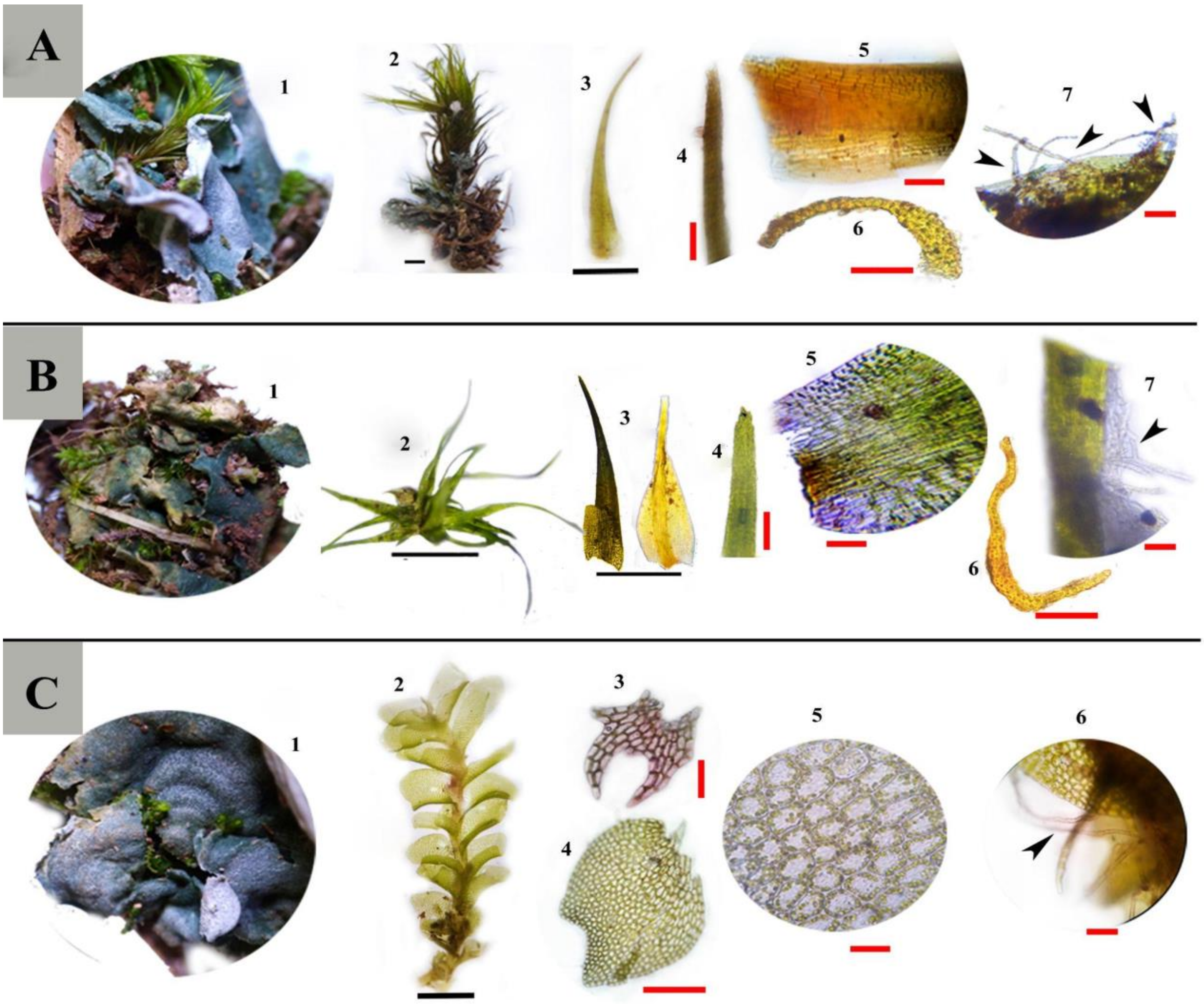

Figure 3. A) *C. uleanus*. 1 – *Cora simasi* together with *C. uleanus*. 2 – Gametophyte of *C. uleanus*. 3 – Leafy. 4 – Apical leafy with hyphae to *Cora simasi* structure. 5 – basal and laminal cells with black points indicating chlorosis. 6 – Transversal leaf section. 7 – *Cora simasi* hyphae connections in *C. uleanus* leafy. C) *D. riograndensis* 1 – *Cora simasi* together to *D. riograndensis*. 2 – Gametophyte of *D. riograndensis* with black points indicating chlorosis. 3 – Leaf with black points indicating chlorosis. 4 – Apical part of leaf. 5 – basal and laminal cells with one black point indicating chlorosis. 6 – Transversal leaf section. 7 – *Cora simasi* hyphae connections in *D. riograndensis* leaf. D) *N. argillaceus* 1 – *Cora simasi* together to *N. argillaceus*. 2 – Gametophyte of *N. argillaceus* with black points indicating chlorosis. 3 – underleaves. 4 – irregular bifid leaves. 5 – laminal cells. 6 – *Cora simasi* hyphae connections in *N. argillaceus* leaf. Scale bar – black line: 1mm, red line: 50µm.

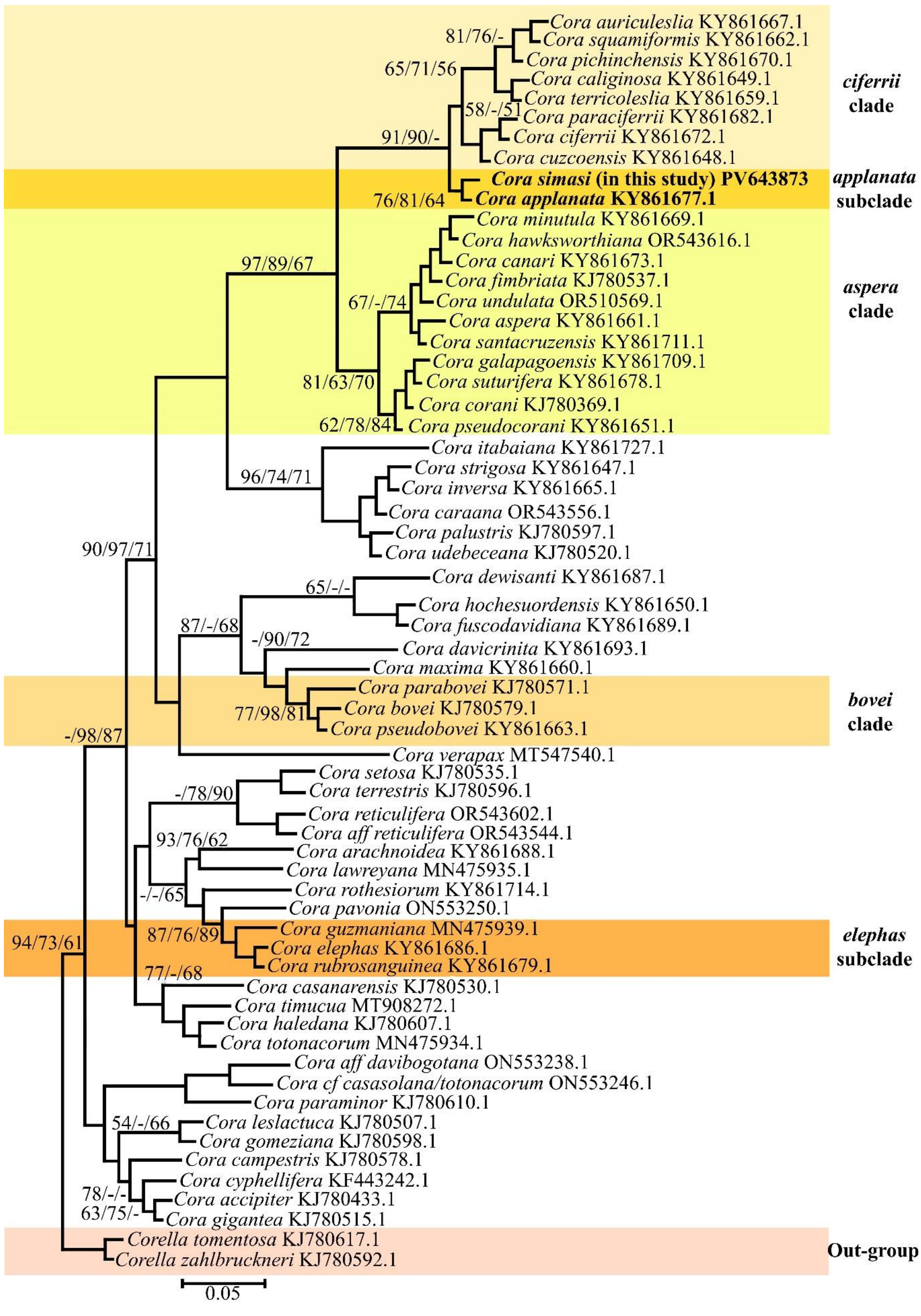

Figure 4. Bayesian master tree with the dataset. The topology of the branches is arranged in

descending order, from the longest (least divergence) to the shortest (greatest divergence). Bootstrap support >50% is provided in the order of Maximum Parsimony, Maximum Likelihood, and Bayesian Inference (MP/ML/BI) alongside the branches, with (-) indicating missing values in the topology or values greater than 60%.

Supplementary Data

Sequence ITS to *Cora simasi* spec. nov. Furlan-Lopes & Putzke :

<CATAGCGAGAAAGRACTAMCAGRATYCCYCTARKWACTGCGAGTGAAGCGGG

AAAAGCTCAAATTTAAAATCTGGCGGTCCCCCGCGGCCGCCCGAGTTGTAATCTA

GAGAAGCGCCATCCGCGCCAGCCCGCGTACAAGTCTCTTGGAACAGAGCGTCAT

AGAGGGTGAGAATCCCGTCTCTGACGCGGACTGCTGGCGCGTTGCGATGCGCTCT

CGACGAGTCGAGTTGTTTGGGAATGCAGCTCAAAATGGGTGGTAAATTCCATCTA

AAGCTAAATATTGGCGAGAGACCGATAGCGAACAAGTACCGTGAGGGAAAGATG

AAAAGAACTTTGGAAAGAGAGTCAAACAGTACGTGAAATTGTTGAAAGGGAAAC

GCTTGAAGTCAGTCGCGTGCGCCGGGAATCAACCTTCTCTCGAGTCGGTGTACTT

TCCGTCGAACGGGTCGGCATCAATTTCATCTGCCGGAGAAAGATGGGAGGAATGT

GGCATCTTCGGATGTGTTATAGCCTCCCGTCGCATGCCGCCGACGGGATTGAGGA

TCTCAGCACGCCGCAAGGCCGGGGTTCGCCCACGTTACGTGCTTAGGATGCCGAC

ATAATGGCTTTAATCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCTC

GCGAGTGTTTGGGTGTCAAACCCATGCGCGAAACGAAAGTGAAAGTTGAGATCT

CTGTCATGGAGAGCATCGACGCCCAGACCAGACCTTCTGCGACGGATCTGCGGTC

GAGCGCGTATGTTGGGACCCGAAAGATGGTGAACTATGCCTGAATAGGGCGAAG

CCAGAGGAAACTCTGGTGGAGGCTCGTAGCGATTCTGACGTGCAAATCGATCGTC

GAATTTGGGTATAGGGGCGAARRCTATCGACATCTAGTARCTRRTCGAACY

6 CONSIDERAÇÕES FINAIS

Neste trabalho realizaram-se inferências sobre fungos Agaricomycetes associados a briófitas no Brasil (TABELA 1). Dessa forma, se analisou por meio de revisão bibliográfica os fungos briófilos das ordens Agaricales, Boletales, Hymenochaetales e Polyporales. E de maneira mais aprofundada, foi realizado levantamento taxonômico e estudos a campo, de espécies pertencentes à diferentes famílias dentro da ordem Agaricales. Essas análises utilizaram de ferramentas como microscopia óptica, biologia molecular e análises filogenéticas, revelando aspectos pouco estudados sobre a ecologia e biodiversidade dos fungos briófilos no Brasil.

A primeira revisão da literatura, apresentada no Capítulo I, evidenciou a escassez de estudos aprofundados sobre fungos Agaricales briófilos no Brasil. Mostrando apenas 19 espécies registrados até o momento da publicação. Sendo que aproximadamente 50% das espécies apresentaram caráter parasítico sobre musgos nos trabalhos analisados.

Durante o Capítulo II, com a ampliação dessa análise de literatura, englobando os Agaricomycetes, o número de espécies com algum tipo de associação ou relato de crescimento junto às briófitas sobe para 33. Estas, distribuídas nas ordens Agaricales, Boletales, Hymenochaetales e Polyporales. Esses dados culminam em uma lacuna conhecimento micológico nacional, em relação às interações ecológicas com briófitas, ainda subestimadas.

As coletas realizadas na Floresta Nacional de São Francisco de Paula possibilitaram identificar e descrever associações ecológicas inéditas entre diferentes espécies de fungos e briófitas. Dessa forma, durante o Capítulo III, apresentam-se as associações entre *Gerronema stuckertii* e *Campylopus pilifer*, *Galerina stylifera* e *Campylopus julicaulis*, e *Psathyrella murrilli* com *Brachythecium* sp.. Estas associações foram analisadas com técnicas de microscopia óptica, aliadas à taxonomia clássica. Destacamos o estudo sobre *Rimbachia bryophila*, no Capítulo IV, que além de apresentar associações não parasíticas inéditas com as espécies *Dicranella riograndensis, Neesioscyphus argillaceus e Jungermannia decolor*, relatou *R. bryophila* como novo registro para o Brasil.

No Capítulo V, descrevemos a espécie nova *Cora simasi* Furlan-Lopes & Putzke, aliando técnicas de biologia molecular e taxonomia clássica. *C. simasi*, espécie liquenizada, pertencente à família Hygrophoraceae, apresentou hábitos briófilos, se associando à *Neesioscyphus argillaceus*, *Campylopus uleanus, Dicranella riograndensis* e endemismo para o sul do Brasil. As análises filogenéticas de IP, ML e IB posicionaram essa espécie no subclado *Applanata*, enfatizando o papel da especialização de nicho e do isolamento geográfico na diversificação do gênero *Cora*. Reforçando o potencial do bioma Mata Atlântica como hotspot para espécies de fungos briófilos e liquenizados.

Enfatizamos nesse trabalho, que não foram demonstrados prejuízos à vitalidade das espécies de briófitas observadas em associação com nenhumas das espécies de fungos estudadas. Além disso, foram destacadas as estruturas envolvidas nessas associações, contribuindo para melhor compreensão das relações entre fungos e briófitas. Com advento das drásticas mudanças climáticas, cresce a necessidade de melhorar os esforços para conservação de habitats úmidos de altitude na Mata Atlântica, principalmente quando se pensa sobre os fungos briófilos. Uma vez que os mesmos possuem alta afinidade por ambientes conservados em altitude, uma vez que são ainda mais escassos no bioma Pampa, onde houveram tentativas de coletar e catalogar esses organismos, entretanto com pouco sucesso. Além disso, a elaboração de mais estudos sobre a taxonomia, evolução e ecologia de fungos briófilos se faz necessária, uma vez que essa é uma área ascendente dentro da micologia. Sendo que a quantidade limitada de estudos nessa área, reportando dados específicos sobre essas associações impacta na compreensão da biodiversidade fúngica brasileira. Nossos resultados contribuem para ocupar parte dessa lacuna de conhecimento para que possam ser realizadas investigações futuras sobre a complexidade envolvida nas relações briófilas.

Tabela 1 – Fungos briófilos registrados no Brasil, briófitas associadas, tipo de evidência e referências.

Fungos briófilos	**Espécie de briófita envolvida em associação**	**Tipo de evidência de associação**	**Referências**
Acantholichen albomarginatus	Musgos e hepáticas não identificados	Crescimento sobre musgos e hepáticas em vegetação densa de borda de floresta nebular	DAL-FORNO, M. et al. (2016)
Atheniella amabillissima	Musgos não identificados	Crescimento entre musgos	PUTZKE & PUTZKE (no prelo); RAITHELHUBER (1991)
Austroboletus festivus	Musgos não identificados	Crescimento entre musgos em floresta de Restinga	MAGNAGO, A.C.; NEVES, M.A. (2014); SINGER, R. (1961); WATLING, R.; DE MEIJER, A.R. (1997)
Callistosporium luteo-olivaceum	*Sphagnum sp.*	Crescimento entre musgos e madeira em decomposição	SINGER (1953a); DE MEIJER (2008); PUTZKE & PUTZKE (no prelo)
Cerrena caperata	*Isopterygium tenerum, Thamniopsis langsdorffii, Lejeunea glaucescens, L. martiana, Drepanolejeunea mosenii*	Crescimento entre musgos e hepáticas	VITAL, D.M. et al. (2000)
Chromocyphella muscicola	Musgos e líquens não identificados	Crescimento entre briófitas	ALBUQUERQUE et al. (2007); DE OLIVEIRA et al. (2019)
Clavaria fragilis	Musgos não identificados	Crescimento em solo com briófitas	FURTADO et al. (2016)
Collybia dryophila var. Oedipus	Sphagnum sp.	Observação de campo em ambiente úmido	SINGER (1953a); PUTZKE & PUTZKE (no prelo)
Deconica inquilina	Musgos não identificados	Crescimento em solo arenoso com musgos	DA SILVA et al. (2006)
Fomitiporia nubicola	Musgos não identificados	Crescimento entre musgos sobre *Drimys angustifolia*	VITAL, D.M. et al. (2000)
Fuscoporia wahlbergii	*Octoblepharum pulvinatum, Syrrhopodon prolifer var. acanthoneuros, Trichosteleum papillosum*, diversas hepáticas	Crescimento entre musgos e hepáticas	VITAL, D.M. et al. (2000)
Galerina montivaga	Musgos não identificados	Crescimento gregário em campo de musgos e húmus	SINGER (1969); DE MEIJER (2008); PUTZKE & PUTZKE (2018)
Galerina semiglobata	*Sphagnum sp.*	Crescimento denso sobre musgos queimados	SINGER (1953a); PUTZKE & PUTZKE (2018)
Galerina sphagnorum	*Sphagnum sp.; Polytrichum commune*	Crescimento gregário sobre musgos	SINGER (1953a); PUTZKE & PUTZKE (2018)

Fungos briófilos	Espécie de briófita envolvida em associação	Tipo de evidência de associação	Referências
Galerina subtibiicystis	*Sphagnum sp.*	Crescimento esparso em turfeiras	SINGER (1953a); PUTZKE & PUTZKE (2018)
Galerina taimbesinhoensis	*Sphagnum sp.*	Crescimento exclusivo em musgo	SINGER (1953a); PUTZKE & PUTZKE (2018)
Gymnopus aquosus	*Sphagnum sp*.	Crescimento em área úmida longe de árvores	SINGER (1953a); PUTZKE & PUTZKE (no prelo)
Hygrocybe helobia	Musgos não identificados	Crescimento entre musgos, solo úmido	PEGLER (1983b); PUTZKE & PUTZKE (2017)
Hyphodontia sp.	*Fabronia ciliaris, Isopterygium tenerum, Sematophyllum subpinnatum, Syrrhopodon africanus*, diversas hepaticas	Crescimento sobre musgos e hepáticas em Floresta Atlântica	VITAL, D.M. et al. (2000)
Hypholoma elongatum	*Sphagnum sp.*	Crescimento em caules de musgos	SINGER (1953a)
Hypholoma ericaeum	Musgos não identificados	Crescimento em solo úmido com musgos e gramíneas	DA SILVA et al. (2006); CORTEZ & SILVEIRA (2007)
Macrocystidia sp.	Musgos não identificados	Crescimento entre musgos	SOUZA & AGUIAR (2004)
Phellinus gilvus	*Pyrrhobryum spiniforme, Isopterygium tenerum, Telaranea nematodes, Lejeunea flava*	Crescimento entre musgos e hepáticas	VITAL, D.M. et al. (2000)
Phellinus rimosus	*Erythrodontium squarrosum, Racopilum tomentosum, Trichostomum weisioides, Campylopus cryptopodioides, Syrrhopodon gaudichaudii, Thamniopsis incurva*, diversas hepaticas	Crescimento entre musgos e hepáticas em vegetação de Cerrado e Floresta Atlântica	VITAL, D.M. et al. (2000)
Phellinus sp.	Diversos musgos e hepaticas	Crescimento entre musgos e hepáticas	VITAL, D.M. et al. (2000)
Psathyrella sp.	Musgos de floresta montana	Crescimento entre musgos	SINGER (1953a)
Psilocybe paupera	*Sphagnum sp.*	Crescimento nos caules de musgos	GUZMÁN (1983); COIMBRA (2015); PUTZKE & PUTZKE (2018)
Psilocybe sp.	*Sphagnum sp.*	Crescimento entre musgos em brejo aberto	SINGER (1953a)
Rickenella fibula	*Polytrichium, Schizymenium*	Crescimento em leitos úmidos de musgos em áreas de altitude	VITAL, D.M. et al. (2000)
Rigidoporus sp.	*Isopterygium tenerum, Thamniopsis langsdorffii, Lejeunea caespitosa, L. martiana, Telaranea nematodes*	Crescimento entre musgos e hepáticas	VITAL, D.M. et al. (2000)
Rimbachia arachnoidea	Musgos não identificados	Crescimento gregário sobre musgos	SINGER (1986); PUTZKE & PUTZKE (no prelo)
Trametes sp.	*Donnellia commutata, Drepanolejeunea mosenii*	Crescimento entre musgos e hepáticas	VITAL, D.M. et al. (2000)

Fungos briófilos	Espécie de briófita envolvida em associação	Tipo de evidência de associação	Referências
Trichaptum trichomallum	*Entodon beyrichii*	Crescimento associado à espécie em bioma Cerrado	VITAL, D.M. et al. (2000)
Tropicoporus drechsleri	Musgos não identificados	Crescimento frequente entre musgos	PAGIN-CLAUDIO, E.R. et al. (2022)
Cora simasi	*Neesioscyphus argillaceus, Campylopus uleanus, Dicranella riograndensis*	Evidência microscópica de conexão de hifas com os filídios e clorose nas briófitas	FURLAN-LOPES et al., dados não publicados
Galerina stylifera	*Campylopus julicaulis*	Evidência microscópica de conexão de hifas com os filídios	FURLAN-LOPES et al. (2023)
Gerronema stuckertii	*Campylopus pilifer*	Evidência microscópica de conexão de hifas com os filídios	FURLAN-LOPES et al. (2023)
Oudemansiella platensis	*Metzgeria consanguinea*	Evidência microscópica de conexão de hifas com os filídios	FURLAN-LOPES et al. (2023)
Psathyrella murrillii	*Brachythecium sp.*	Evidência microscópica de conexão de hifas com os filídios	FURLAN-LOPES et al. (2023)
Rimbachia bryophila	*Dicranella riograndensis, Neesioscyphus argillaceus, Jungermannia decolor*	Evidência microscópica de conexão de hifas com os filídios	FURLAN-LOPES et al. (2024)

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