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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.

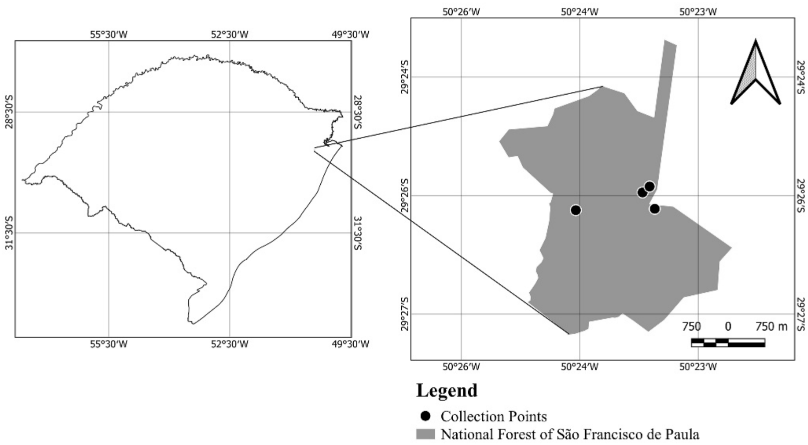

Figure 1 – Collection points of the Agaricomycetes and bryophytes in São Francisco de Paula in the Rio Grande do Sul state, Brazil. Source: primary.

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.

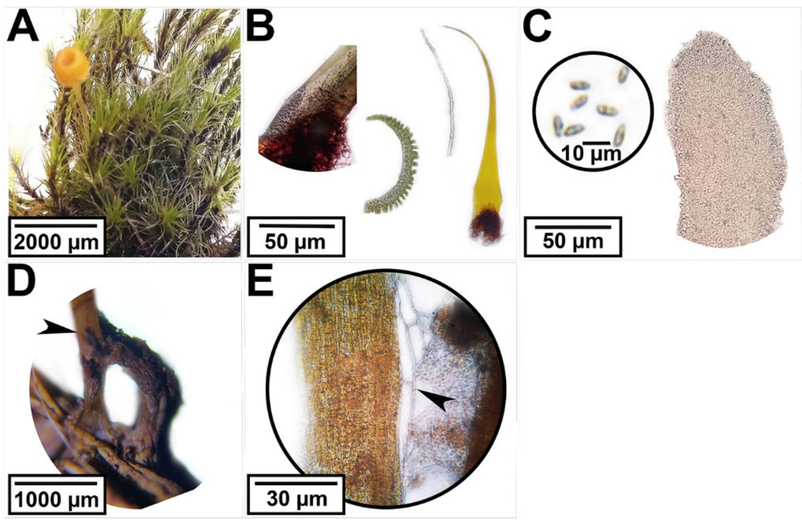

Figure 2 – A) *G. stuckertii* basidiome associated with *C. pilifer*; B) leave, cross section, apical detail, and elongated quadratic cells of leaves of *C. pilifer*; C) spores and hymenophore lamellae woof of *G. stuckertii*; D) detail of performed structure between *G. stuckertii* stipe and *C. pilifer* 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.

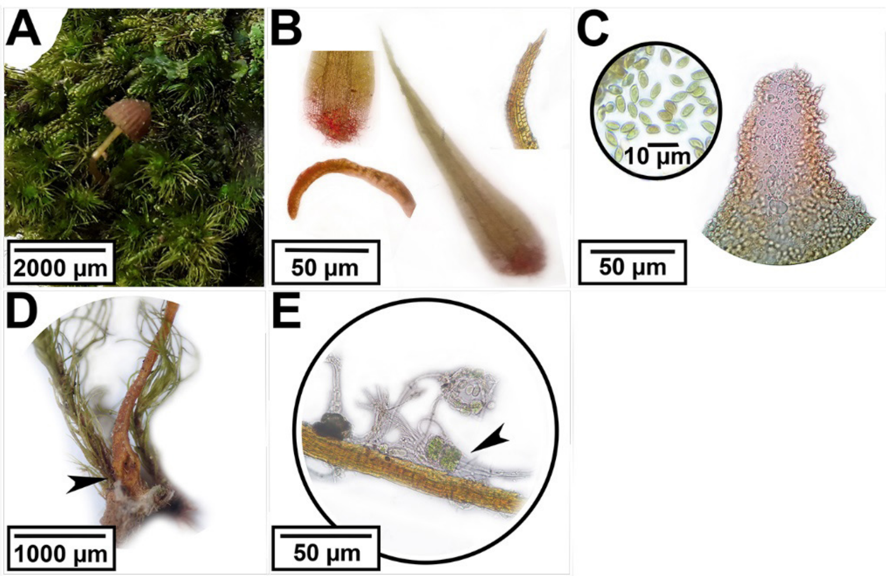

Figure 3 – A) *G. stylifera* basidiome associated with *C. julicaulis*; B) leave, cross section, apical detail, and quadratic cells of leaves of *C. julicaulis*; C) spores and hymenophore lamellae woof of *G. stylifera*; D) detail of performed structure between *G. stylifera* stipe and *C. julicaulis*; 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.

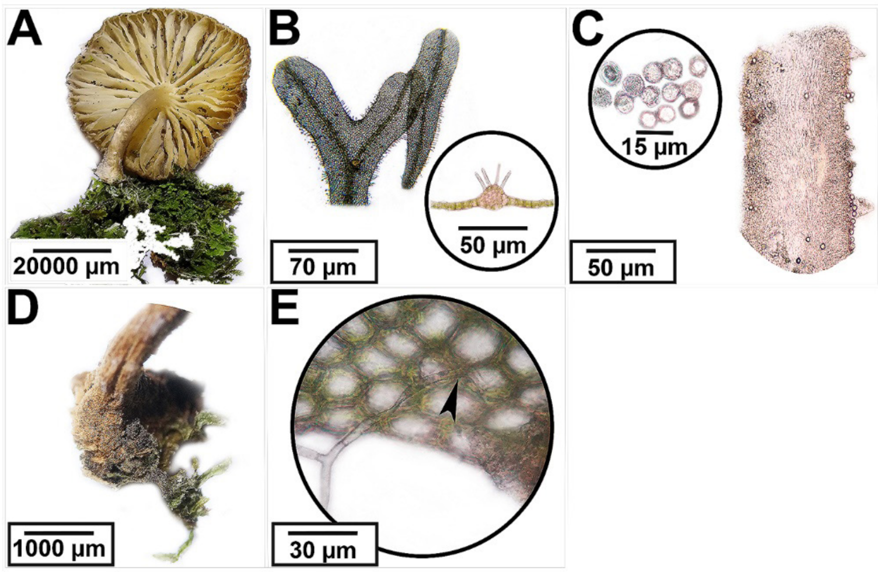

Figure 4 – A) *O. platensis* basidiome associated with *M. consanguinea*; B) leave and cross section of gametophyte with marrow;C) spores and hymenophore lamellae woof of *O. platensis*; D) detail of gametophyte growing on stipe of *O. platensis*; E) hyphae of the *O. platensis* linked to cells of *M.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

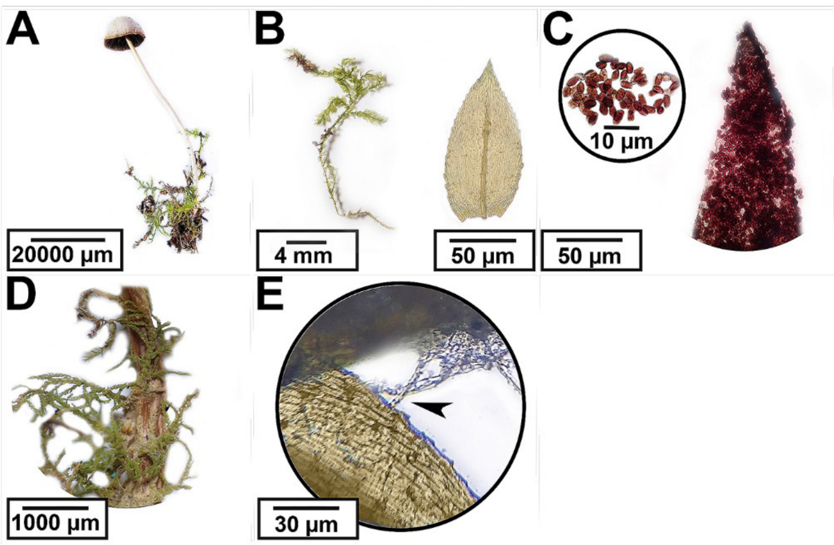

Figure 5 – A) *P. murrillii* basidiome associated with *Brachythecium* sp; B) leave and detais of basal; C) spores and hymenophore lamellae woof of *P. murrillii*; D) detail of *Brachythecium* sp. growing on stipe of *P. murrillii*; E) hyphae of the *P. murrillii* linked to cells of *Brachythecium* sp. 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 CO2 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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