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, including 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). Bryophytes 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.

2. 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.

3. Methods used to identify the interactions of bryophilic mushrooms

The most used methods for the identification of bryophyta/Agaricomycetes associations 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 rhizoids, 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 tissues, 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 statistical 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

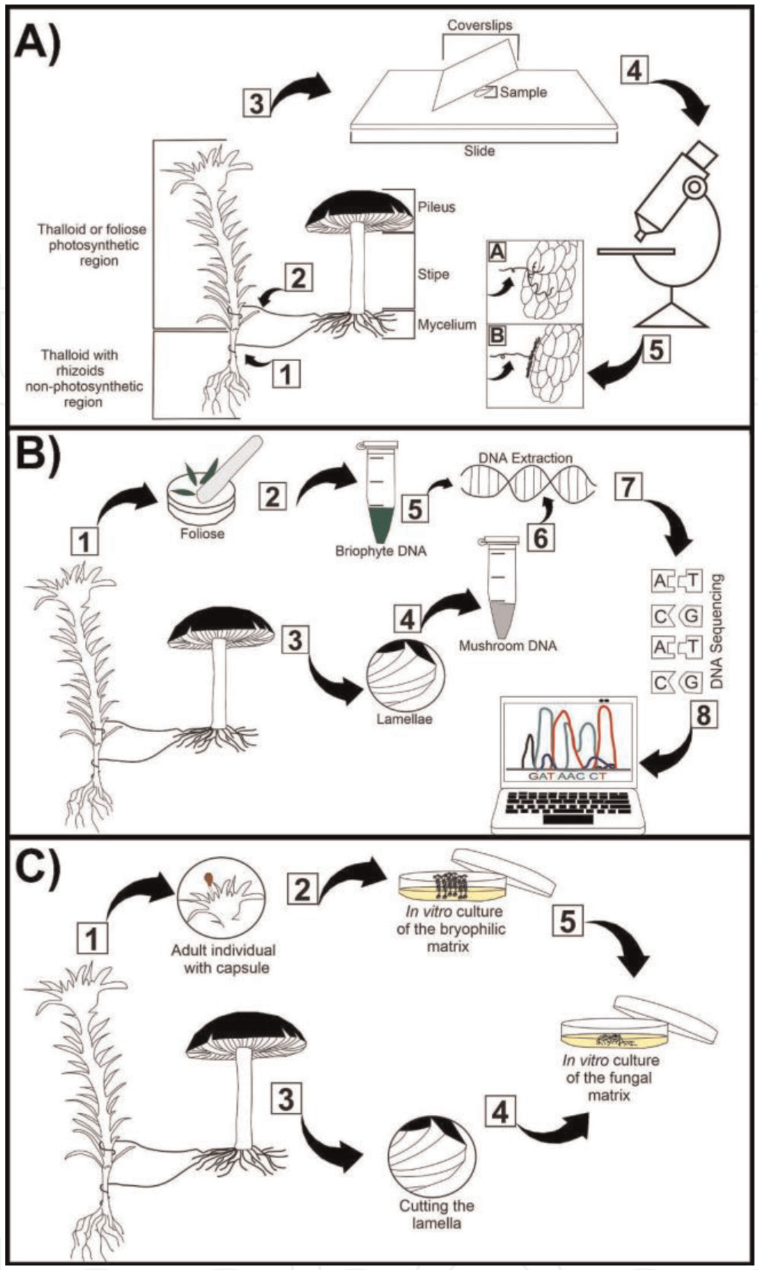

Figure 1.
Methodology frequently used for detection of Fungi-bryophyte associations (FBA). (A) Optical microscopy: association site, non-photosynthetic (1) or photosynthetic (2); slide cuts and use of reagents with cover by coverslip (3); microscope observation (4); FBA endophilic (5-A) or exophytic (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**.

4. 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, mutualistic 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, diversity, 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 character also to the taxonomy of Fungi.

Phylogenetic analysis helped to understand the bryophilic habits and high concentration 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 Agarics 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 analysis 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.

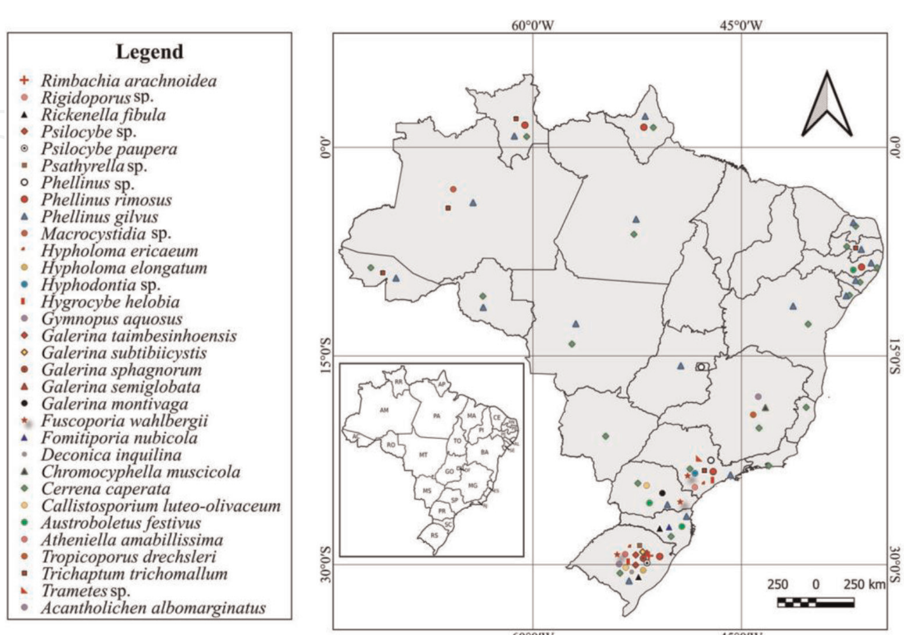

Figure 2.
Distribution of bryophilous species in Brazilian states/regions.

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. taimbesinhoensi*s [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, Germany, South Africa, Poland, Costa Rica, Argentina, France, Iceland, Bolivia, Indonesia, 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, Switzerland, 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 & 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.

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, Germany, 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, Denmark, 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].

6. 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 have a 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.

7. 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.

Acknowledgements

We would like to thank to the team of LATAF (Laboratório de Taxonomia de Fungos), of Universidade Federal do Pampa (UNIPAMPA) for the support to this research. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001.

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