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.

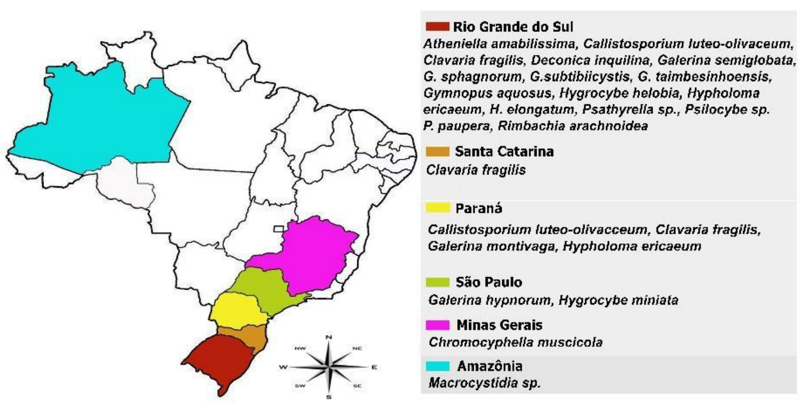

Figure 1 - Distribution of species of muscicolous Agaricales in Brazil. The Brazilian states are followed by the color corresponding to the place of occurrence of each species (This study).

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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