

Mycophagy of Attini Ants (Hymenoptera, Formicidae, Myrmicinae) with Agaricales Mushrooms (Basidiomycota, Agaricomycetes) at Riparian Zone in Southern Brazil

Micofagia de Formigas Attini (Hymenoptera, Formicidae, Myrmicinae) com Cogumelos Agaricales (Basidiomycota, Agaricomycetes) em Zonas Ripárias no Sul do Brasil

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ABSTRACT

Attini ants (Hymenoptera, Formicidae, Myrmicinae) have great diversity in exploiting food resources. However, little is known about the mycophagy involving Agaricales fungi (Basidiomycota, Agaricomycetes). Moreover, these associations are of paramount importance in riparian zones, as the interaction among soil, fauna and flora is fundamental to the maintenance of these environments. Thus, the aim of this study was to describe cases of mycophagy between ants and fungi in order to understand how these associations occur in riparian zones. To this, collections were made between 2021-2022 in the valleys of the Rio Vacacaí, Rio dos Sinos and Rio Pardo in the state of Rio Grande do Sul, Brazil. The samples were analyzed for characters macro and microscopic and identified taxonomically. Mycophagy activities of six species of ants worker were cataloged, among them *Acromyrmex niger*, *Acromyrmex versicolor*, *Tranopelta gilva*, *Tranopelta subterranea*, *Pheidole flavens* and *Mycetosoritis hartmanni*, which included in their diet the mushrooms *Agaricus rufoaurantiacus*, *Macrocybe titans*, *Agrocybe underwoodii*, *Dactylosporina steffenii*, *Lepiota micropholis* and *Neopaxillus echinospermus*, respectively. The observed interactions demonstrate the dispersal of fungal spores through ant body structures, such as legs, antennae, thorax and abdomen; basidiomata as aliment source, such as pileus, lamellae and stipe; and generalized and specialized levels of predation on various fungi structures. Our results demonstrate unprecedented mycophagous relationships and show that Agaricales fungi can be considered a food source for Attini in riparian zones in Brazil south.

Keywords: Food resource, spore dispersing agents, ecological interactions.

RESUMO

As formigas Attini (Hymenoptera, Formicidae, Myrmicinae) apresentam grande diversidade na exploração de recursos alimentares. No entanto, pouco se sabe sobre a micofagia envolvendo fungos Agaricales (Basidiomycota, Agaricomycetes). Além disso, essas associações são de suma importância em zonas ripárias, pois a interação entre solo, fauna e flora é fundamental para a manutenção desses ambientes. Assim, o objetivo deste estudo foi descrever casos de micofagia entre formigas e fungos a fim de entender como essas associações ocorrem em zonas ripárias. Para isso, foram feitas coletas entre 2021-2022 nos vales do Rio Vacacaí, Rio dos Sinos e Rio Pardo no estado do Rio Grande do Sul, Brasil. As amostras foram analisadas quanto aos caracteres macro e microscópicos, e identificadas taxonomicamente. Foram catalogadas as atividades de micofagia de seis espécies de formigas operárias, dentre elas *Acromyrmex niger*, *Acromyrmex versicolor*, *Tranopelta gilva*, *Tranopelta subterranea*, *Pheidole flavens* e *Mycetosoritis hartmanni*, que incluíam em sua dieta os cogumelos *Agaricus rufoaurantiacus*, *Macrocybe titans*, *Agrocybe underwoodii*, *Dactylosporina steffenii*, *Lepiota micropholis* e *Neopaxillus echinospermus*, respectivamente. As interações observadas demonstram a dispersão de esporos dos fungos através

das estruturas do corpo das formigas, tais como pernas, antenas, tórax e abdômen; estruturas dos basidiomas como fonte alimentar, tais como pileo, lamelas e estipe; e níveis generalizados e especializados de predação em várias estruturas dos cogumelos. Nossos resultados demonstram relações micofágicas inéditas, e mostram que os fungos Agaricales podem ser considerados como fonte de alimento para Attini em zonas ripárias no sul do Brasil.

Palavras-chave: Recurso alimentar, agentes de dispersão de esporos, interações ecológicas.

1 INTRODUCTION

The ant species Attini (Hymenoptera, Formicidae, Myrmicinae) is one of the most successful groups of Arthropods, both in terms of diversity and abundance. The group has a high social complexity and a great exploration ability in a variety of food niches (Houadria and Menzel, 2020). Food from various parts of plants, such as leaves, seeds, fruits, and roots; also multiple kinds, such as carrion, manure, and others, are part of a wide variety of dietary habits of this group (Lanan, 2014). Many nutritional forms are used to some extent by ants, and consequently, some become specialists and others generalists in terms of their diet (Csata and Dussutour, 2019).

Little is known about the inclusion of fungi in ant diet, nor about the types of mycophagy habit involving the ants with Agaricales Fungi (Basidiomycota, Agaricomycetes) (Epps and Penick, 2018). Except for *Euprenolepis* ants, with reports of mycophagy in the Old World (Claridge and Trappe, 2005; Witte and Maschwitz, 2008; Von-Beeren *et al.* 2014), in addition to a select group of Attini endemic to the New World and known to cultivate fungi (de Fine *et al.* 2014). For these fungiculture ants, five types of agricultural systems are cataloged: lower agriculture, coral-fungus agriculture, yeast agriculture, generalized higher agriculture, and leafcutter agriculture (Branstetter *et al.* 2017).

In terms of fungal structures associated with ant feeding, gongylidia (swollen hyphae), hyphae tissues in general (pileus and stipe), spores, and mycelium are the most commonly reported (Epps and Penick, 2018). However, even with few studies on mycophagy in Hymenoptera, other Arthropod orders such as Acari, Coleoptera, Collembola, Diptera, Lepidoptera, and Orthoptera have already had important inferences regarding the inclusion of fungi in their diet (Schigel, 2012; Dash *et al.*, 2018; Innocenti and Sabatini, 2018; Pollierer *et al.*, 2020; Tozlu *et al.*, 2022; Wakil *et al.*, 2022). As nutritional importance of fungi, regarding the benefits of their consumption by arthropods, mainly minerals, vitamins and fats are listed (Biedermann and Vega, 2020).

In contrast, there are several reports of ants visiting the basidiomata of various fungi, mainly in relation to foraging and predation of larvae attached to the fungal tissues (Branstetter *et al.* 2017; Epps and Penick, 2018; Pereira *et al.* 2020). However, it is unclear whether the visit is limited to hunting larvae, or whether mycophagy also occurs. It is believed that many ants spread fungal spores

even when there is no mycophagy because the spores can attach to the ants' body structures and travel with them short and long distances (Witte and Maschwitz, 2008; Von-Beeren *et al.* 2014; Epps and Penick, 2018).

Riparian zones are permanent protected areas where the presence of vegetation, mycota, and fauna play unique ecological interactions related to their conservation (Brasil, 2012). In this respect, little is known about the activity of ants in these areas, as well as the fungal community. Nevertheless, nutrient cycling for fungi is an important process that takes place in all environments (White *et al.* 2018). The benefits cited for ants include supporting plant reproduction, improving the nutrient quality of the soil, and aerating the soil, among others (Tuma *et al.* 2020).

In this form, to better understand the mycophagy associations that occur in different riparian zones in southern Brazil, this study aimed to describe unique cases of mycophagy involving *Acromyrmex niger* (Smith, 1858), *Acromyrmex versicolor* (Pergande, 1893), *Tranopelta gilva* (Mayr, 1866), *Tranopelta subterranea* (Mann, 1916), *Pheidole flavens* (Roger, 1863) and *Mycetosoritis hartmanni* (Wheeler, 1907), who have included in their diet *Agaricus rufoaurantiacus*, *Macrocybe titans*, *Agrocybe underwoodii*, *Dactylosporina steffenii*, *Lepiota micropholis* and *Neopaxillus echinospermus*, respectively. Also, to analyze how these interactions occur and the levels of mycophagy performed by the group, in order to aid in their understanding.

2 MATERIAL AND METHODS

Sample location

In the period 2021-2022, visits were realized to riparian zones in Rio Vacacaí, locality of São Gabriel (Point A, latitude -30°21'56"S and longitude -54°18'48"W); Rio dos Sinos, locality of São Francisco de Paula (Point B, latitude -29°25'22"S and longitude -50°23'1"W); and in the Vale do Rio Pardo, locality of Vera Cruz (Point C, latitude -29°42'53 "S and longitude -52°30'20 "W). All points located in Rio Grande do Sul state, southern Brazil.

Collection and taxonomic identification of specimens

The Rapid Survey method used for tree vegetation (Walter and Guarino, 2006) was adapted to collect basidiomata with signs of mycophagy. The fungal material with the ants was collected under license from SISBIO n°78538-1. For the mushrooms, collections were performed according to Putzke and Putzke (2017), where each specimen was collected with the substrate. The basidiomata were stored individually in plastic containers and dehydrated at 40°C. Identification of Agaricales mushrooms was performed according to the key for Agaricales Fungi of Brazil available

in Putzke and Putzke (2017) and data available on the Index Fungorum platform (<http://www.indexfungorum.org/>).

The ants found in basidiomata were stored in tubes with 70% alcohol. The keys of Fisher and Cover (2007) and Baccaro *et al.* (2015) were used for identification, as well as the data available on the AntWiki platform (<http://www.antwiki.org/>). Specimens were analyzed according to their macromorphological and micromorphological characteristics using the Olympus CH-2 optical microscope. All collected specimens (mushrooms and ants) were stored in the Laboratório de Taxonomia de Fungos of Universidade Federal do Pampa, São Gabriel campus, Rio Grande do Sul state, Brazil.

Statistical analyzes of the data

ANOVA test was conducted under the model of variables with the "predation location" factor and predation levels for the "amount" factor, conducted in the form of data percentage (Sabin and Stafford, 1990). Comparisons among the means of spore quantity, as well as of each individual were conducted under the LSMeans model (Lenth and Lenth, 2018), applying the Test-Tukey at 5% significance using the Estat v.2.0 program (Estat, 1994).

3 RESULTS AND DISCUSSION

For the Attini six species of workers ants were cataloged involved in mycophagy activities: *Acromyrmex niger*, *Acromyrmex versicolor*, *Tranopelta gilva*, *Tranopelta subterranea*, *Pheidole flavens* and *Mycetosoritis hartmanni*. The ants were associated with six species of Agaricales: *Agaricus rufoaurantiacus*, *Macrocybe titans*, *Agrocybe underwoodii*, *Dactylosporina steffenii*, *Lepiota micropholis* and *Neopaxillus echinospermus* respectively. After the identification of the specimens, two taxonomic keys were prepared, one for the identification of the mushrooms and the other for identifying the ants, both involved in mycophagy.

Key of identification of Agaricales Fungi involved in mycophagy

1a. Hymenophore with free or adnate lamellae, context not gelatinized. Spores amyloid or inamyloid, smooth or angular, without hilar appendage, globose to ellipsoid, nodose-subangular or subangular. Annulus often present. Cortical layer of pileus formed by a palisadoderm or hymenoderm, sometimes epithelial with prostrate hyphae.....2

1b. Hymenophore with adnate or decurrent lamellae, gelatinized context. Spores inamyloid, globose equinate with hilar appendage, smooth thin-walled. Annulus absent. Cortical layer himeniform or

sub-hymeniform, with smooth elements
(Physalacriaceae).....*Dactylosporina steffenii*

2a. Spores varying from yellow to fuscous-brown, tobacco-brown or clay-brown. Germinative pore present or absent**3**

2b. Spores white to cream colored, inamyloid subglobose to ovoid, thin-walled. Germinative pore absent (Callistosporiaceae).....*Macrocybe titans*

3a. Cortical layer of the pileus formed by a palisadoderm or hymenioderm, which may also be epithelial, or formed by spherocysts with prostrate hyphae. Hymenophore trama regular to irregular, never bilateral or inverse (Agaricaceae).....**4**

3b. Cortical layer of pileus formed by a cellular epithelium or by subsodiametric spherocysts, hymenophore trama regular (Strophariaceae) or inverse (Paxillaceae).....**5**

4a. Basidiome does not change color in KOH. Spores inamyloid dark-toned, brown, thick-walled ovoid, germinative pore absent. Absent clamp connections. Pileus 2 - 5 cm in diameter, with recurved orange-brown scales.....*Agaricus rufoaurantiacus*

4b. Basidiome does not change color when bruised. Spores pseudoamyloid light-toned, white, ovoid not truncate at base, thin-walled, germinative pore absent. Absent clamp connections. White pileus up to 1.5 cm in diameter containing white scales.....*Lepiota micropholis*

5a. Pileus up to 20 mm in diameter, ochraceous brown. Cystidia usually more than 55 µm long. Spores ellipsoid thick-walled and smooth, containing a truncated germinative pore.....*Agrocybe underwoodii*

5b. Pileus up to 40 mm in diameter, yellowish brown or orange-gold. Annulus imperceptible to absent. Spores subglobose to globose, thick-walled inamyloid, germinative pore absent.....*Neopaxillus echinospermus*

Key of identification of Attini worker ants involved in mycophagy

1a. Mesosoma covered with non-flexible, mostly homogeneous spines, hairs or bristles.....**2**

1b. Mesosoma covered with short, widely spaced hairs; long hairs may occur, but then flexible and largely heterogeneous.....**4**

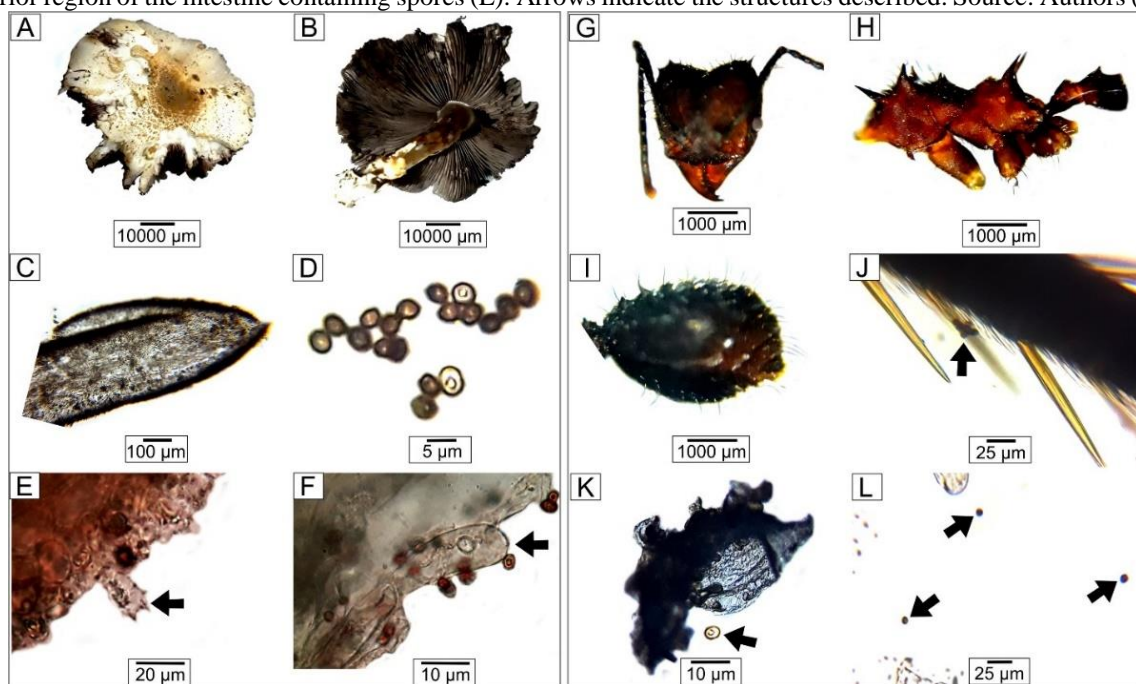
- 2a.** Body and head with rigid, incised, erect spines. Head usually containing a pair of dorsal tubercles. Frontal lobes well developed, partially or completely covering the insertion of the antennae, clearly separated by the posterior median portion of the clypeus (*Acromyrmex*).....**3**
- 2b.** Body and head with conspicuous erect bristles, often stiff and curled. Head without the presence of dorsal tubercles. Frontal lobes poorly developed and not expanded laterally to cover sides of head, but then enlarged and reaching anterior margin of clypeus in full-face view (*Mycetosoritis*).....***Mycetosoritis hartmanni***
- 3a.** Eyes and mandibles covered by a uniform opaque integument. Mandible subtly prolonged. Tubercles on back of gaster grouped in four longitudinal and sometimes imperceptible series, containing varying thicknesses that are shorter or of some size like that of the spines.....***Acromyrmex niger***
- 3b.** Eyes and apical edge of mandibles more blackish than integument. Mandible prolonged and robust. Tubercles on the back of the gaster randomly distributed, median and short, of varying thickness, but shortened on each side of the anterior margin.....***Acromyrmex versicolor***
- 4a.** Mandibles with 4 or more teeth that gradually increase in size toward the apex. Propodeum with projections and spines (*Pheidole*).....***Pheidole flavens***
- 4b.** Mandibles with 4 to 5 teeth, not increasing toward the apex, but may contain differentiated preapical tooth. Propodeum without projections or spines (*Tranopelta*).....**5**
- 5a.** Promesonotum and propodeum slightly convex, continuous in lateral view. Scap of antennae not extending beyond vertexal border. Eyes equidistant between ocelli and clypeal margin, small and faceted.....***Tranopelta gilva***
- 5b.** Promesonotum and propodeum strongly convex in lateral view. Scap of antennae surpassing vertexal edge. Eyes closer to posterior margin of clypeus than to ocellus, amphagi and prominent.....***Tranopelta subterranea***

Taxonomic description of species involved in mycophagy

Agaricus rufoaurantiacus Heinem and *Acromyrmex niger* (Smith, 1858)

The fungus has a pileus 2 - 3 cm in diameter, convex and umbonate. Pileus pale cream with orange-brown scales (Figure 1 A). Lamellae free and membranous, proximal and brown (Figure 1 B). Stipe 2.5 - 4 cm in diameter, central, cylindrical and inflated at base with recurved squamules (Figure 1 B). Hymenophoreal trama regular (Figure 1 C). Annulus present, membranous, superior and near the pileus. Spores 4 - 5 x 2.5 - 3.7 μm , ellipsoid to ovoid, brown, smooth, thick-walled (Figure 1 D). Basidia 12.5 - 18 x 5 - 6.5 μm , clavate to sub-fusoid with 2 to 4 sterigmata (Figure 1 E). Pleurocistidia absent. Cheilocystidia 13.5 - 20 x 5 - 7.5 μm , inflated-clavate, with thin wall (Figure 1 F). Cortical layer trichodermal, with narrow and parallel terminal hyphae. Absent clamp connections. Grows on soil. Distribution in Brazil: the occurrence in Rio Grande do Sul in the Pampa biome is unprecedented, being mentioned for Brazil by Pegler (1997) only for the states of São Paulo and Pernambuco in the Atlantic Forest biome.

Figure 1 - *Agaricus rufoaurantiacus* (A-F) and *Acromyrmex niger* (G-L). Pileus top view (A). Basidiome with lamellae (B). Lamellar trama (C). Spores (D). Basidium (E). Cheilocystidium (F). Frontal view of head (G). Lateral view of thorax (H). Side view of gaster (I). Spores attached to leg (J). Posterior region of intestine with spore (K). Cut of the posterior region of the intestine containing spores (L). Arrows indicate the structures described. Source: Authors (2022).



The ant has a supraocular spine present, a pair of defined dorsal spines, small eyes, and a short extension on the mandible (Figure 1 G). Tegument opaque with uniform coloration. Postpetiole articulated, first segment of gaster rigid, does not flex over mesosoma. Thorax with 3 or 4 pairs of smooth spines (Figure 1 H). Tubercles on dorsum of gaster grouped in four longitudinal and sometimes imperceptible series (Figure 1 I). Spores of the fungus were found in external body

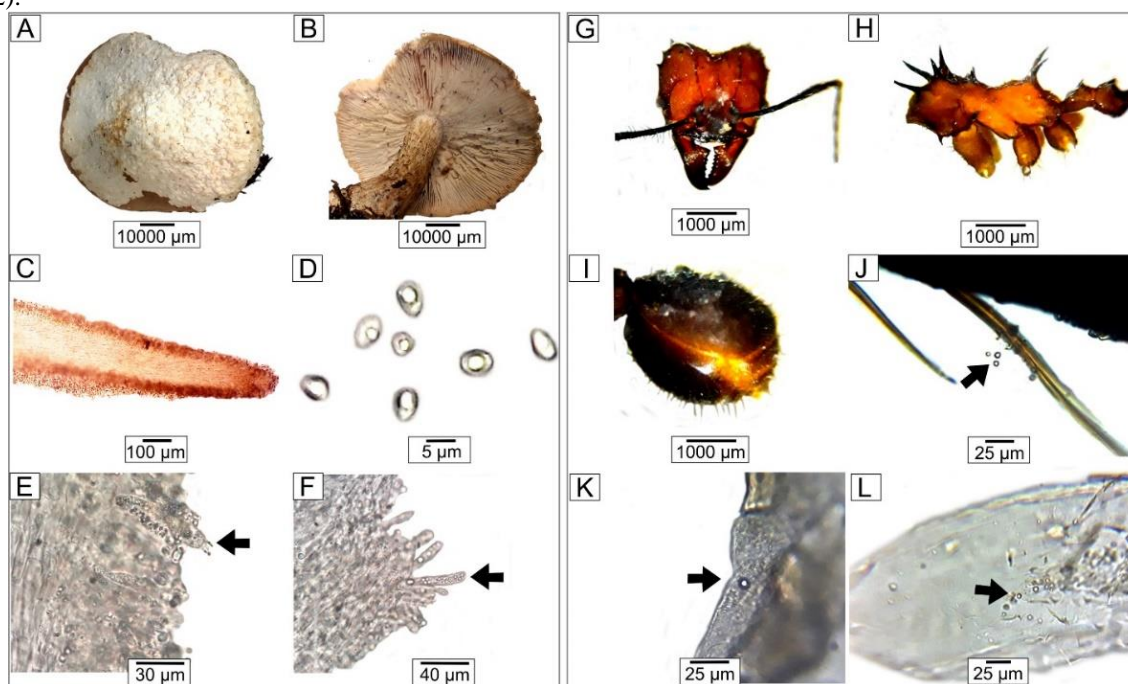
structures of the ants, arranged in the head, thorax and abdomen region, also among spines, antennae and legs (Figure 1 J). Internally, spores were found in the gut (Figure 1 K and L). Distribution in Brazil: in the Rio Grande do Sul, in the Pampa biome, *A. ninger* has already been described (Loeck *et al.* 2003). Also, in the Atlantic Forest (Garcia *et al.* 2011), Cerrado (Vaz-de-Mello *et al.* 1998), Pantanal and Amazon (Gonçalves, 1961), being considered a native species of the Neotropical region.

***Macrocybe titans* (H.E. Bigelow & Kimbr.) Pegler, Lodge & Nakasone and *Acromyrmex versicolor* (Pergande, 1893)**

The fungi present pileus 8 - 50 cm in diameter, convex to flat. Pileus surface ochraceous, with grayish margin (Figure 2 A). Lamellae strongly sinuate, grayish white and proximal (Figure 2 B). Stipe 6 - 15 cm of diameter, cylindrical to subclavate, containing small squamules (Figure 2 B). Hymenophoreal trama regular (Figure 2 C). Annulus absent. Spores 5.5 - 7.0 × 4.0 - 5.0 μm, subglobose to ovoid with thin walls (Figure 2 D). Basidia 25 - 38 × 6.5 - 10 μm, narrowly clavate containing 4 sterigmata (Figure 2 E). Pseudocystidia scattered 35 - 50 × 7 - 10 μm, fusoid with narrow, filiform apex, with thin walls (Figure 2 F). Cortical layer of the pileus subhymenial, not gelatinized, narrow, interwoven thin-walled hyphae with conspicuous clamp connections. Grows directly on soil. Distribution in Brazil: in Rio Grande do Sul the species already has a record of occurrence in the Atlantic Forest biome (Singer, 1990). Occur in the states of Paraná, Atlantic Forest biome (Battistin and Picciola, 2015).

The ant has an absent supraocular spine, a wide and shallow frontal canal, eyes and apical border of the mandible black, large and triangular mandible (Figure 4 G). Tegument opaque, postpetiole articulated, first segment of gaster rigid, does not flex over mesosoma, thorax with 3 or 4 pairs of smooth long spines (Figure 2 H). Tubercles on the dorsum of the gaster grouped in lateral series, arranged in irregular rows (Figure 2 I). Spores of fungi were found in the region of the head, thorax and legs (Figure 2 J). In the gut spores were found (Figure 2 K and L). Distribution in Brazil: in the Atlantic Forest biome, the species has no cataloged occurrence, as well as for Brazil. There are only records of occurrence for North and Central America (Fowler, 1988; Julian and Fewell, 2004), and a single occurrence in South America for Guyana (Fernández and Sendoya, 2004), being considered a species native to the Neo-Arctic region.

Figure 2 - *Macrocybe titans* (A-F) and *Acromyrmex versicolor* (G-L). Pileus top view (A). Basidiome with lamellae (B). Hymenophoral trama (C). Spores (D). Basidium (E). Pseudocystidia (F). Frontal front view of head (G). Lateral view of thorax (H). Side view of gaster (I). Spores attached to leg (J). Posterior region of intestine with spore (K). Cut of the posterior region of the intestine containing spores (L). Arrows indicate the structures described. Source: Authors (2022).



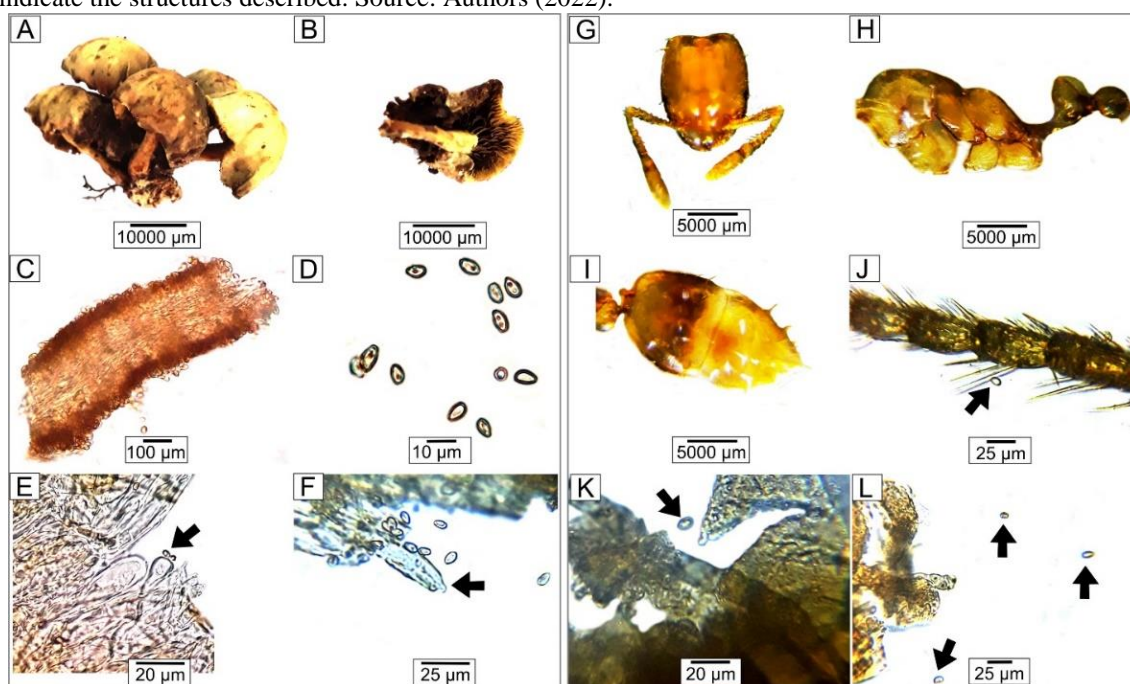
Agrocybe underwoodii (Murrill) Singer and *Tranopelta gilva* (Mayr, 1866)

The pileus of fungi with up to 20 mm in diameter, convex to flattened shape with an ochraceous brown hue (Figure 3 A). Lamellae adnate, close, broad with yellowish tones. Stipe 25 - 30 x 2 - 3 mm, central with slightly enlarged base. Annulus absent or hardly noticeable (Figure 3 B). Hymenophoreal trama regular (Figure 3 C). Spores 8 - 11.5 × 6 - 7 µm, ellipsoid thick-walled and smooth, with truncated germinal pore (Figure 3 D). Basidia 18 - 20 × 3 - 5 µm, smooth, thick-walled with 2 - 4 sterigmate. Pleurocystidia 55 - 70 × 15 - 23 µm, broad, thin-walled, hyaline, clavate (Figure 3 E). Cheilocystidia 25 - 55 x 9 - 18 µm of diameter, ventricose at base and narrowed apex up to 8 µm in diameter (Figure 3 F). Cortical layer of the pileus formed by a cellular epithelium containing subglobose to pyriform elements with 22 - 30 x 12 - 18 µm. Clamp connections present. Specimens were found growing on substrate of *Araucaria angustifolia* (Bertol.) Kuntze, 1898. Distribution in Brazil: in Rio Grande do Sul the description is unprecedented. However, in Atlantic Forest biome the species already has occurrence for the state of Paraná (Watling, 1992; Meijer, 2008; Coimbra, 2015).

The ant contains a rectangular head, diminutive faceted, equidistant eyes. Antennal scrobes absent. Mandibles small, smooth with sheen and longitudinal striations (Figure 3 G). Propodeum and promesonotum continuous in lateral view, weakly convex and interrupted by a metanotal groove (Figure 3 H). Gaster ranging from translucent to white, containing fine, short, shiny, whitish and

flexible pilosity (Figure 3 I). Mushroom spores were found in the region of the antennae and legs (Figure 3 J). Internally, spores were also found in the gut (Figure 3 K and L). Distribution in Brazil: in the Atlantic Forest biome the species already has a cataloged occurrence (Fernandez, 2003), as well as for the Pantanal and Cerrado (Demétrio *et al.* 2017), Amazonia (Ryder *et al.* 2007) and Caatinga (Prado *et al.* 2019), being considered native to the Neotropical region.

Figure 3 - *Agrocybe underwoodii* (A-F) and *Tranopelta gilva* (G-L). Pileus top view (A). Basidiome with lamellae (B). Hymenophoral trama (C). Spores (D). Basidium and pseudocystidia (E). Cheilocystidia (F). Front view of head (G). Lateral view of thorax (H). Lateral view of gaster (I). Spore attached to the leg (J). Section of the gut with spore (K-L). Arrows indicate the structures described. Source: Authors (2022).

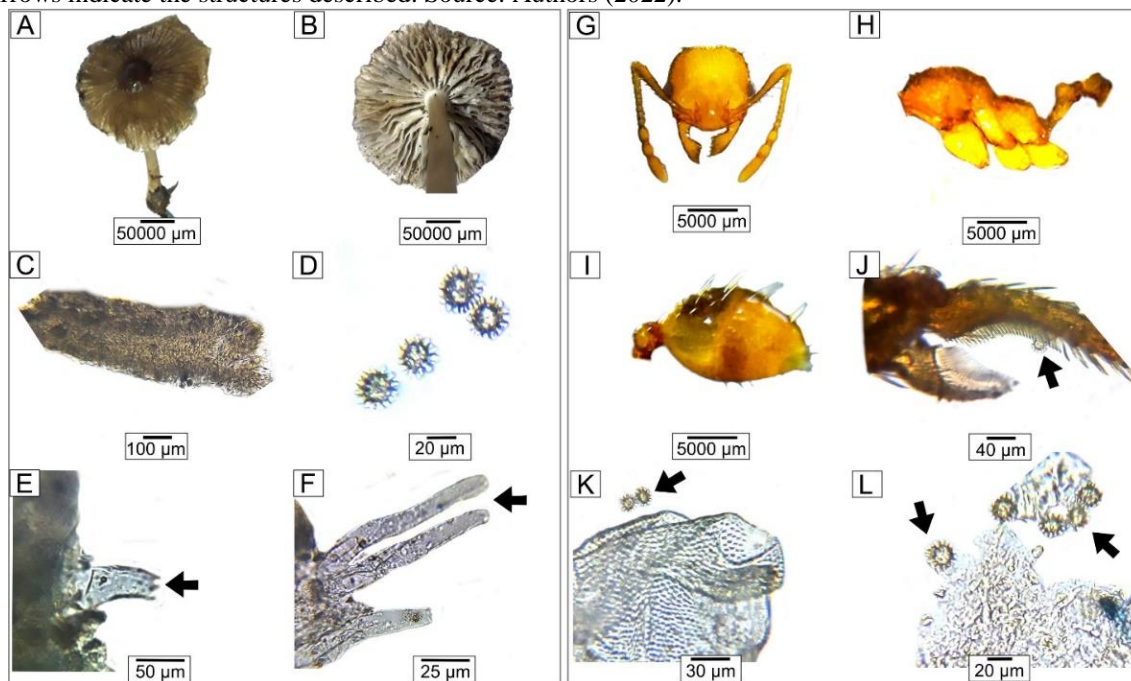


Dactylosporina steffenii (Rick) Dörfelt and *Tranopelta subterranea* (Mann, 1916)

The fungi exhibit pileus 3.5 - 10 cm in diameter, umbrinous, dark gray or grayish in color, convex to flattened in shape (Figure 4 A). Lamellae adnate, white, sub-close to distant. Stipe clear, broad at base showing pseudorriza (Figure 4 B). Hymenophoreal trama regular with filamentous and septate hyphae (Figure 4 C). Spores 15 - 23 x 14 - 21 µm (including spines), globose, equinate with large hilar appendage. Spines 1.5 - 3.5 µm long, inamyloid (Figure 4 D). Basidia 40 - 60 x 10 - 20 µm, hyaline, usually containing four sterigma (Figure 4 E). Thin-walled hyaline cheilocystidia 30 - 40 x 15 - 22 µm, thin-walled, hyaline, vesicular to filamentous or nearly clavate. Pleurocystidia 80 - 160 x 15 - 50 µm, ampulaceous, mucronate to subcapitate, thin-walled, sometimes with resinous incrustations at the apex (Figure 4 F). Cortical layer of the pileus formed by globose cells 15 - 30 x 8 - 10 µm, with palisade hymeniodermal terminal cells. Present clamp connections. Grow in soil and its pseudorriza extends more than 10 cm deep into the soil. Distribution in Brazil: the species has been described for all state of Rio Grande do Sul (Atlantic Forest and Pampa biome) (Putzke and

Pereira, 1988), Pantanal, Cerrado and Caatinga (Valões-Araújo and Wartchow, 2021), and for the Amazon (Wartchow *et al.* 2010).

Figure 4 - *Dactylosporina steffenii* (A-F) and *Tranopelta subterranea* (G-L). Pileus top view (A). Basidiome with lamellae (B). Lamellar trama (C). Spores (D). Basidium (E). Pleurocystidia (F). Front view of head (G). Lateral view of thorax (H). Lateral view of gaster (I). Spore attached to the leg (J). Posterior region of intestine with spores (K and L). Arrows indicate the structures described. Source: Authors (2022).



The ant has wider than long head, moderate and faceted eyes. Antennal scrobes absent. Mandibles smooth, shiny and longitudinally carinae. Five robust teeth with apical and subapical ones larger than the rest (Figure 4 G). Propodeum and promesonotum strongly convex in lateral view, containing deep metanotal sulcus (Figure 4 H). Gaster translucent, containing almost imperceptible striations in the posterior region, long and flexible erect hairs of whitish color (Figure 4 I). Spores were found in the region of the antennae and legs (Figure 4 J). In the gut, mushroom spores were also found (Figure 4 K and L). Distribution in Brazil: in the Pampa biome the occurrence record is unpublished, containing records only for the Pantanal (Demétrio *et al.* 2017) and Amazonia (Mertl *et al.* 2012), where it is considered native.

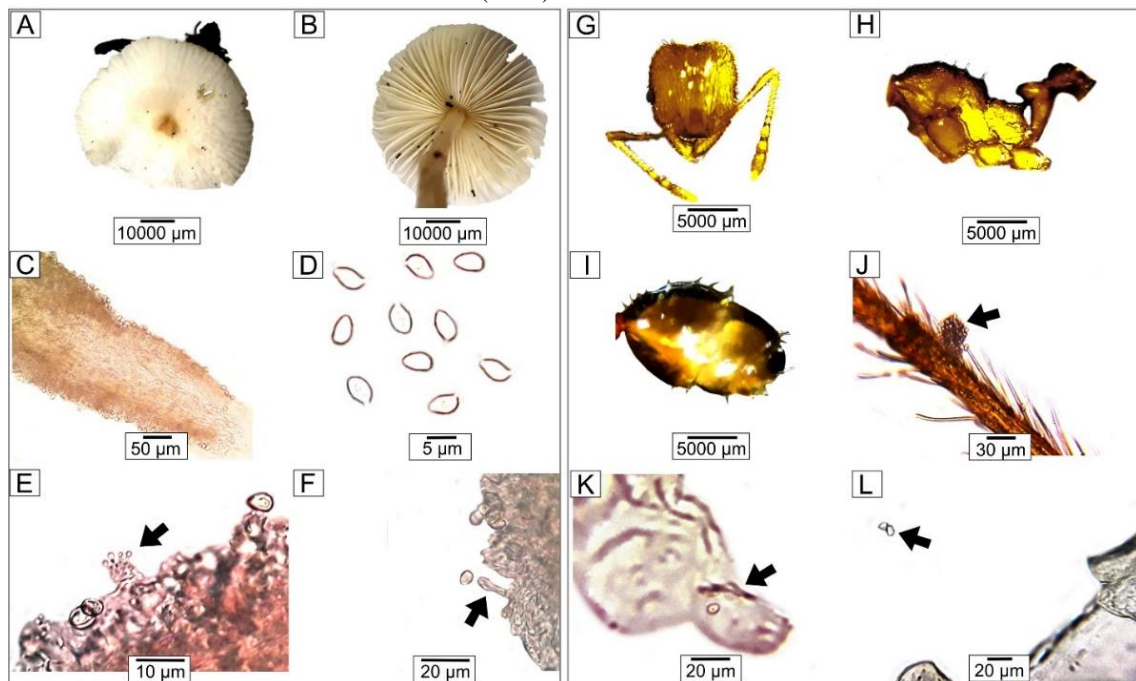
***Lepiota micropholis* (Berk. & Broome) Sacc. and *Pheidole flavens* (Roger, 1863)**

The fungi has a pileus up to 1.5 cm in diameter, convex and slightly umbonate, white in color, slightly squamous near the striated margin (Figure 5 A). Lamellae close free, white in color. Stipe 3.8 - 4 x 0.2 - 0.5 µm, white and thin near apex. Annulus present and evanescent (Figure 9 B). Hymenophoreal trama regular (Figure 5 C). Spores 4.9 - 6.5 x 4 - 5 µm, pseudoamyloid, ovoid, smooth, thin-walled and hyaline, without germinal pore (Figure 5 D). Basidia 20 - 30 x 8 - 12 µm,

clavate and tetrasporate (Figure 5 E). Cheilocystidia 30 - 40 x 10 - 15 μm , clavate, thin-walled hyaline (Figure 5 F). Pileus cortical layer trichodermal. Grows on soil. Distribution in Brazil: in the state of Rio Grande do Sul, in Pampa biome the description is unprecedented. It has been described for Brazil only for the Atlantic Forest biome in São Paulo by Pegler (1997).

The ant has a rectangular head longer than wide and a rugoreticulum between the eyes and the antennal fossa, eyes moderate and faceted. Antennal scrobes absent. Mandibles with four teeth or more that gradually increase in size toward apex (Figure 5 G). Propodeum and promesonotum with projections and short spines, propodeal spine well developed (Figure 5 H). Gaster shiny, smooth, containing flexible whitish hairs (Figure 5 I). Spores were found in the region of the antennae, legs and abdomen (Figure 5 J). Internally, in the gut mushroom spores were found (Figure 5 K and L). Distribution in Brazil: it has distribution in American continent, considered native to the Neotropical region. Its distribution is cataloged for the Pampa biome by Casadei-Ferreira *et al.* (2020), Atlantic Forest (Sarnat *et al.* 2014), Pantanal (Silva, 2018), Cerrado and Caatinga (Moreira *et al.* 2020).

Figure 5 - *Lepiota micropholis* (A-F) and *Pheidole flavens* (G-L). Pileus top view (A). Basidiome with lamellae (B). Trama lamellar (C). Spores (D). Basidium (E). Cheilocystidia (F). Front view of head (G). Lateral view of thorax (H). Lateral view of gaster (I). Spores attached to the leg (J). Posterior region of intestine with spore (K and L). Arrows indicate the structures described. Source: Authors (2022).

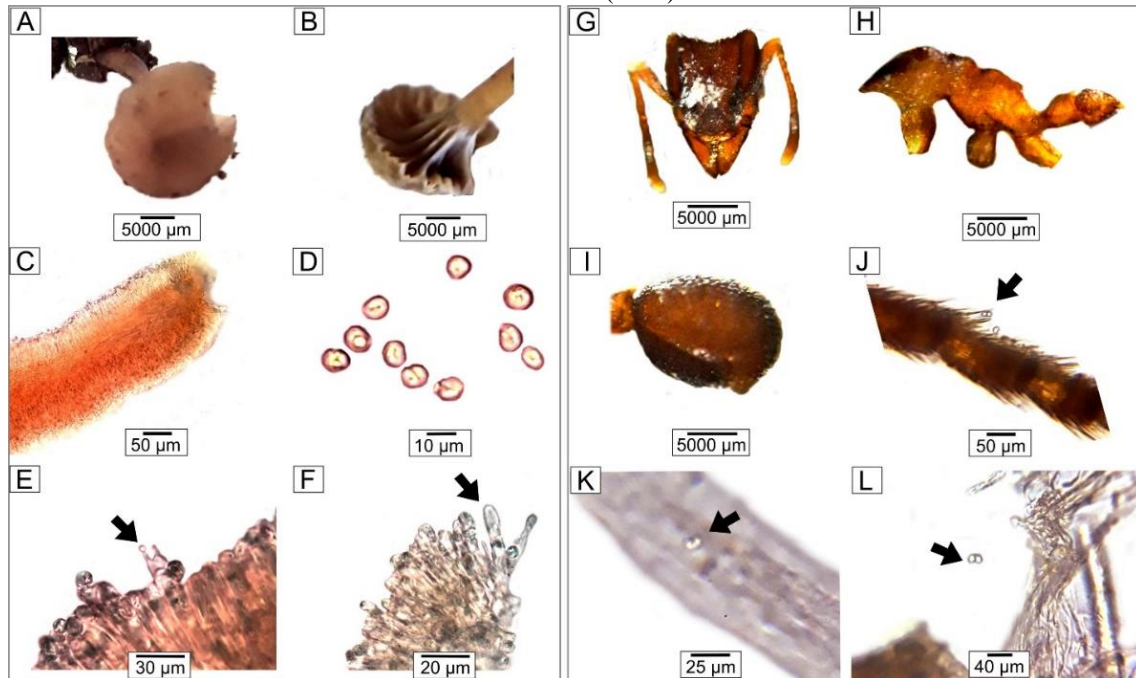


***Neopaxillus echinospermus* (Speg.) Singer and *Mycetosoritis hartmanni* (Wheeler, W.M., 1907)**

The fungi has pileus up to 40 mm in diameter, flattened or flattened to infundibuliform, dark yellow brown or reddish orange in color, with lobed to wavy margins (Figure 5 A). Lamellae decurrent, distant to subdistant with brown coloration and concolorous border. Stipe 20 - 40 x 2 - 3.5 μm , cylindrical, keeled at apex region, bulbous base pale yellowish-brown and smooth. Ring absent (Figure 5 B). Hymenophoreal trama subregular (Figure 5 C). Spores 6.5 - 9 x 6.5 - 8.5 μm , subglobose to globose, thick walled. pale brown, inamyloid in coloration (Figure 5 D). Basidia tetrasporate and rarely bisporate of 28 - 40 x 8 - 15 μm (Figure 5 E). Cheilocystidia 18.5 - 32 x 6.5 - 16 μm , vesiform thin-walled hyaline and pale (Figure 5 F). Pleurocystidia absent. Cortical layer of the hymenophoreal pileus subregular. Present clamp connections. Grows on soil. Distribution in Brazil: in the state of Rio Grande do Sul Pampa biome this description is unpublished. However, the species has records for the Atlantic Forest biome in the states of Rio Grande do Sul, Paraná and São Paulo (Singer and Digilio, 1951; Singer, 1964; Watling and Meijer, 1997; Silva-Filho *et al.* 2018).

The ant has a broad, rectangular head, without the presence of tubercles and with poorly developed frontal lobes. Eyes moderate and faceted. Mandibles sclerotized, robust with attenuated, slightly curved apical portion and slender apical tooth (Figure 5 G). Bristles along dorsum diminutive, conspicuous erect, often stiff and curled, propodeal spine poorly developed (Figure 5 H). Gaster blackened, covered with short, distant, almost imperceptible bristles distributed in transverse rows (Figure 5 I). Mushroom spores were found on the legs (Figure 5 J). Internally, spores were found in the gut (Figure 5 K and L). Distribution in Brazil: this is the first record of occurrence of the species for the Pampa biome. However, for the Cerrado (Sosa-Calvo *et al.* 2009) and Atlantic Forest (Sosa-Calvo *et al.* 2017) biomes the species already has occurrence records.

Figure 6 - *Neopaxillus echinospermus* (A-F) and *Mycetosoritis hartmanni* (G-L). Pileus top view (A). Basidiome with lamellae (B). Trama lamellar (C). Spores (D). Basidium (E). Cheilocystidia (F). Front view of head (G). Lateral view of thorax (H). Lateral view of gaster (I). Spores attached to the leg (J). Posterior region of intestine with spore (K and L). Arrows indicate the structures described. Source: Authors (2022).



Mycophagic associations between ants and mushrooms

About 70 individuals of *Acromyrmex niger* showed associations with *Agaricus rufoaurantiacus* on the soil surface during the daytime at point A. At the site, 7 basidiomata were found in the area and 4 contained signs of mycophagy. The main parts of the basidiomata involved in predation were the pileus surface, lamellae and stipe. Mycophagous associations have already been described for *Acromyrmex niger* with other Agaricales fungi, including *Leucoagaricus gongylophorus*, where besides preying on all parts of the basidiome, it is also associated with its cultivation as a fungiculture (Aylward *et al.* 2013). For *Agaricus rufoaurantiacus*, this is the first record of association with this ant species. However, in the study by Wartchow *et al.* (2008), unidentified nests of leafcutter ants were found near basidiomata of this mushroom in the Atlantic Forest biome in Pernambuco.

About 20 individuals of *Acromyrmex versicolor* showed mycophagy associations with *Macrocybe titans* on the soil surface at point C at night. In the area, two basidiomata of *Macrocybe titans* were found there, and only 1 showed signs of predation. In the mushroom, only the surface of the pileus showed signs of mycophagy, including a small portion of the lamellar margin region. For *Acromyrmex versicolor*, the title of fungiculture is frequent and connected to the survival of their nests (Clark and Fewell, 2014). Also, *Leucocoprinus* sp. has already been reported in fungiculture association with this ant species (Bizarria *et al.* 2022). For the *Macrocybe titans*, there are already records of occurring near nests of unidentified leafcutter ants in Costa Rica (Pegler *et*

al. 1998; Mueller and Mata, 2001). Nevertheless, this is the first report of mycophagy between the two species of this study.

Approximately 7 individuals of *Tranopelta gilva* were found during the day at point B in mycophagy activity with *Agrocybe underwoodii* on the soil surface. A total of 5 basidiomata of *Agrocybe underwoodii* were found in the region and 3 specimens showed signs of mycophagy, only the bordon of the lamellae showed signs of predation. Although *Tranopelta gilva* is cited as a fungiculture ant (Fernandez, 2003), there are no known cases in the literature with Agaricales fungi. For *Agrocybe underwoodii*, this is the first report of mycophagy associated with ants. However, there are citations for the genus from Russia (Rayner *et al.* 1985) and Malaysia (Fung and Tan, 2022) with unidentified fire ants.

About 16 individuals of *Tranopelta subterranea* showed associations with *Dactylosporina steffanii* at point A on the soil surface during the day. In the area, 3 basidiomata of *Dactylosporina steffanii* were found and 2 showed signs of mycophagy. Of the parts of the basidiomata involved in predation, only the lamellar region was affected. Although there is evidence in the literature of possible interaction with filamentous fungi (Delabie *et al.* 2000), there are no records of mycophagic interactions of *Tranopelta subterranea* with Agaricales fungi, which is a novelty for both the ant and the fungi. However, for *Oudemansiella*, a taxonomic classification that precedes *Dactylosporina*, there are records of unidentified ants collecting their basidiomata in Manaus in Amazon biome (Amaringo-Cortegano *et al.* 2013).

Only 3 individuals of *Pheidole flavens* showed mycophagous activity with *Lepiota micropholis* at point A on the soil surface during the day. In the area, 4 basidiomata of *Lepiota micropholis* were found, but only 1 showed signs of mycophagy. Basidiome structures showing signs of predation included the surface of pileus and lamellae portions. For both species, the association of mycophagy is unprecedented. However, for *Pheidole*, there is evidence in the literature of association with filamentous fungi (Wilson, 2003). For *Lepiota*, associations with fungal gardens of leafcutter ant species of *Acromyrmex*, *Atta*, *Apterostigma*, *Cyphomyrmex*, and *Trachymyrmex* are known (Hervey *et al.* 1977).

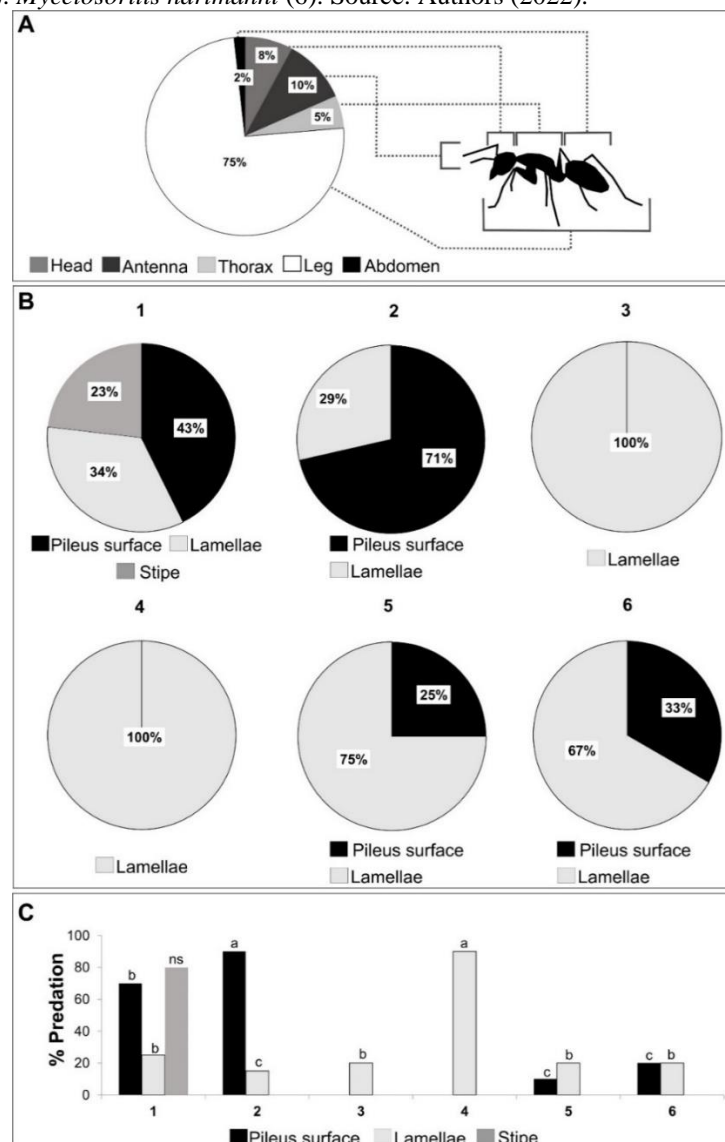
Approximately 2 individuals of *Mycetosoritis hartmanni* showed mycophagous activity with *Neopaxillus echinospermus* on the soil surface at point A during the day. In the area, 3 basidiomata of *Neopaxillus echinospermus* were found and 1 showed signs of mycophagy. The surface part of the pileus and a small part of the lamellar margin showed signs of predation. For *Mycetosoritis hartmanni*, mycophagy associations with fungal gardens are recorded in the literature, including *Escovopsis* and *Trichoderma* (Sanchez-Peña, 2010; Solomon *et al.* 2011), but both belong to the Ascomycota. For Agaricales fungi, the ant has a description of association with *Lepiota* (Batra and

Batra, 1967). For *Neopaxillus echinospermus*, the report of mycophagous association is unpublished.

Levels of interaction and predation of ants with the mushrooms

The present study reports the interaction of six ant species in mycophagous activities with six Agaricales fungi. Our results describe novel associations with ants already cited in literature as fungiculture and not cited. For the ants, the report is similar once that of the activities mycophagy involved fungi with and without a description of the application in Attini fungiculture. The interactions involving these associations are summarized in Figure 7.

Figure 7 - Potential of spore dispersal, mycophagy, and predation activity of ants associated with mushrooms. Percentage of ants body structures that contained the fungi spores (A). Percentage of structures of basidiomata that were eaten by the ants (B). Comparison of the level of predation among the ants in relation to the structures of mushroom. Divergent letters in the graphs indicate significant differences with a *P*-value of 0.05% (C). Note: ns indicates non-significant value. *Acromyrmex niger* (1). *Acromyrmex versicolor* (2). *Tranopelta gilva* (3). *Tranopelta subterranean* (4). *Pheidole flavens* (5). *Mycetosoritis hartmanni* (6). Source: Authors (2022).



In general, it could be seen that the ants not only eat but also carry parts of the fungi to their nests. Several parts of the basidiomata were associated with predatory activities, such as the surface of the pileus, the lamellae, and the stipe. According to Von-Beeren *et al.* (2014), ant harvesting performed directly on basidiomata affects spore dispersal and has a significant positive impact on the local fungal community, as does ant harvesting of seeds, which affects the plant community (Nelsen *et al.* 2018). Under this premise, the ant structures that contained the most fungal spores followed in descending order: legs, antennae, head, thorax, and abdomen (Figure 7 A).

Several ant genera have been described in the literature as fungal spore dispersers, including the members of this study: *Acromyrmex* (Aylward *et al.* 2013; Clark and Fewell, 2014), *Tranopelta* (Delabie *et al.* 2000; Fernandez, 2003), *Pheidole* (Wilson, 2003), and *Mycetosoritis* (Sanchez-Peña, 2010; Solomon *et al.* 2011). However, little is known about the forms of interaction and mycophagy. Thus, the data presented help in questions relevant to the known Attini mycophagy, describing predation standards and reported forms of association.

Studies show that certain ants visit the basidiomata to capture larvae of arthropods in general and that many are predatory in the basidiome itself (Witte and Maschwitz, 2008). Ants are also known to collect fungi to grow them in their nests (Epps and Penick, 2018). However, the main point of contention is whether or not ants benefit nutritionally from fungal structures, such as the surface of the pileus, lamellae and stipe. According to de Moura and Okura (2022), basidiomata are rich in proteins, carbohydrates and dietary fiber, which can vary of 9 - 40%, 23 - 70%, and 12 - 40%, respectively, depending of specimen. Thus, our study demonstrates optimization of the Attini-Mycophagous interaction, because the cataloged ants not only collected parts of the fungi but also disseminated their spores and fed on them as shown in Figures 1-7.

All structures of the basidiomata were eaten by ants in descending order: lamellae, pileus surface, and stipe (Figure 7 B). Each species studied exhibited specific characteristics. *Acromyrmex niger* showed generalist mycophagy preying on all parts of the basidiome, while *Acromyrmex versicolor* showed a preference for the lamellae and also surface pileus part. *Tranopelta gilva* and *Tranopelta subterranea* showed a preference only the lamellar portions of the basidiomata. *Pheidole flavens* and *Mycetosoritis hartmanni* showed more interest in the lamellae and later in the surface pileus portion.

Acromyrmex niger and *Acromyrmex versicolor* had a high percentage of predation compared to the other species of this study (Figure 7 C). According to Clark and Fewell (2014), *Acromyrmex* has a collective foraging pattern that is fast and efficient. This is evidence of optimization of mycophagous strategy, as they were also the species that benefited most from the diverse structures of basidiomata. According to Wartchow *et al.* (2008), the species of this genus tend to be generalists

in terms of feeding, which would explain the diversity of structures integrated into mycophagy. Therefore, it can be concluded that mycophagy is generalized in these species.

For *Tranopelta gilva* and *Tranopelta subterranea* there are descriptions of generalist dietary habits (Rayner *et al.* 1985), particularly in relation to the diversity of decomposing organic matter (Fernandez, 2003). For the samples of this study, specifications related to mycophagy were cataloged, the mycophagy occurred preferably in lamellae region of the basidiomata (Figure 7 C). These data are consistent with the reports of Fung and Tan (2022), in which more than 20 species of edible mushroom were implicated in predation by fire ants in lamellae region, including individuals of *Tranopeltra*. Thus, is possible to infer that occur a specialization of mycophagy on the lamellae regions involving these ants.

Pheidole flavens has a diet that is classified as generalist (Wilson, 2003), while *Mycetosoritis hartmanni* is considered a fungiculture (Sanchez-Peña, 2010; Solomon *et al.* 2011). Regarding the mycogaphy of Agaricales fungi, both showed a percentage of predation in the lamellae region and on the pileus surface (Figure 7 C). In this case, it is possible to infer a generalist pattern with respect to the parts of the fungi that were used in their diet. Corroborated with the theory of Branstetter *et al.* (2017), who inferred the generalist feeding success for both genera from the fact that they do not only use photosynthetic food as a food source.

Attini ants are known for their generalist diet (Lanan, 2014). However, few data are available on the diet of fungi, and these data refer only to a selected group of fungiculture ants (Witte and Maschwitz, 2008). In a controlled laboratory study with individuals of *Aphaenogaster*, a generalist ant group known for its carnivorous habits, Epps and Penick (2018) infer that not only was prey (larvae) collected in basidiomata, but that workers also collected pieces of mushroom free of prey, chewed the same, and deposited them in their nests. In the nest, the workers continued the process of macerating the basidiome pieces and distributing them all over the colony. In our study, only worker ants were identified, but our observations and sampling were limited to the soil surface. Further studies could elucidate the mycophagous associations of these species and their internal interactions within the colony, as well as possible cultivator groups that have not yet been described.

The species this study inhabit a very important ecosystem, there are many unknown interactions in riparian zones (Vidon *et al.* 2019). As previously described in the literature, fungi in mycorrhizal associations integrate a nutritional mycelial network, and among the species studied, *Dactylosporina steffenii* forms pseudorriza (Putzke and Putzke, 2017). In this sense, the diversity of ants active in these zones is underestimated, and they could play an important role in the interaction plants-fungi-soil. Another important point to study is the spread and maintenance of the fungal network that plays an active role in the nutrient cycling of these environments. In this case, the

dispersal of spores over short or long distances by ants could be an important issue for the local fungal community.

4 CONCLUSION

From the findings related to the ants, it can be deduced that mycophagous Attini is an underestimated group that contradicts the idea that they use basidiomata only as hunting grounds or act only as disseminators of fungal spores. Each ant showed peculiarities in relation to the associated fungi, preferences structures and the levels of predation in basidiomata. In the case of Agaricales fungi, our results revealed new interactions that will serve as a basis for further studies, especially in relation to nest dynamics associated with mycophagy and fungiculture.

However, it is possible to conclude that these interactions in the riparian zones studied may favor either the predator or the fungus grower, the prey or the culture. In addition, the ability of ants to exploit a temporally limited resource such as basidiomata may be related to their success in food diversity. Our study reveals a diverse social potential of mycophagous, as specificities related to food resource exploitation were cataloged. It can be concluded that Attini-Mycophagous integrate an important group in the riparian zones of southern Brazil.

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