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# FIRST RECORDS OF MYXOMYCETES IN BRAZILIAN CAVES

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**RESUMO**: O objetivo deste artigo é relatar os primeiros registros de mixomicetos em cavernas brasileiras, com base em três espécimes coletados na área cárstica do município de Pains, localizado no estado de Minas Gerais, sudeste do Brasil. Os espécimes, todos pertencentes à família Trichiaceae (Trichiales, Myxogastromycetidae), foram identificados como *Arcyria denudata* (L.) Wettst., *Hemitrichia calyculata* (Speg.) M.L. Farr e *Metatrichia vesparia* (Batsch) Nann.-Bremek. ex G.W. Martin & Alexop Notavelmente, *Hemitrichia* Rostaf. e *Metatrichia* Ing não haviam sido anteriormente documentados em ambientes de cavernas ao redor do mundo. Embora todas as três espécies sejam cosmopolitas, não haviam sido registradas na região centro-oeste de Minas Gerais ou em ambientes de cavernas globalmente.
**Palavras-chave**: Amoebozoa, Mixomicetos, Cavernas, Carste, Trichiaceae

**ABSTRACT**: The aim of this article is to report the first records of myxomycetes in Brazilian caves, based on three specimens collected in the karst area of the municipality of Pains, located in the state of Minas Gerais, southeastern Brazil. The specimens, all belonging to the Trichiaceae family (Trichiales, Myxogastromycetidae), were identified as *Arcyria denudata* (L.) Wettst., *Hemitrichia calyculata* (Speg.) M.L. Farr and *Metatrichia vesparia* (Batsch) Nann.-Bremek. ex G.W. Martin & Alexop. Notably, *Hemitrichia* Rostaf. and *Metatrichia* Ing have not previously been documented in cave environments around the world. While all three species are cosmopolitan, they had not been recorded in the central-west region of Minas Gerais or in cave environments globally.
**Key-words**: Amoebozoa, Myxomycetes, Caves, Karst, Trichiaceae

## INTRODUCTION

For many years, myxomycetes were classified into different groups based on newly discovered characteristics, being included in the Animal Kingdom, the Plant Kingdom, and even the Fungi Kingdom (Lado & Eliasson, 2022). Molecular evidence indicates that

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myxomycetes are an evolutionarily ancient group, belonging to the "crown" clade of eukaryotes, and that the group Mycetozoa, to which they belong, is monophyletic (Rollins & Stephenson, 2011). Currently, myxomycetes are classified in the Kingdom Protist (Amoebozoa) and are considered amoeboid, unicellular, and heterotrophic organisms. They have a complex life cycle, which includes an amoeboflagellate, uninucleate, and haploid phase that functions as isogametes, giving rise to the zygote and, subsequently, the multinucleate plasmodial mass. This plasmodium exhibits motility and actively seeks out food sources such as bacteria, fungi, and other organic matter (Novozhilov et al., 2022; Schnittler, 2001).

Depending on environmental conditions and the stage of maturation, the plasmodium, initially negative phototropic, moves to brighter locations and undergoes intense physiological and morphological changes. During this process, all its biomass is directed towards the formation of one or more sporocarps, where the only living part is the spores. In the fruiting body stage, myxomycetes become fixed to the substrate and acquire an appearance quite similar to some ascomycetes and basidiomycetes (Keller et al., 2022). These sporocarps produce resilient spores that, upon release and dispersion, typically by wind or animal vectors (Schnittler, 2001), encounter favorable conditions for germination. This germination process leads to the formation of new amoeboflagellates and subsequently, the zygote and plasmodium thereby initiating a new life cycle.

The class Myxomycetes is widely distributed, with 1100 species (Lado, 2005-2024) often exhibiting preferences for specific environmental factors such as temperature, humidity, and nutrient availability. These organisms have been found in all terrestrial ecosystems, across different climates and vegetation zones, including dryland or restrictive ecosystems, as the Brazilian Caatinga and Mangroves, being particularly abundant in warm-temperate and tropical forests (Vaz et al., 2017; Cavalcanti & Agra, 2019; Hosokawa et al., 2019).

Myxomycetes occupy a variety of microhabitats (Keller et al., 2022), and can be found on aerial or ground litter, leaves (foliicolous), decaying wood (lignicolous), the bark of living trees (corticicolous), succulent plants (succulenticolous), inflorescences (floricolous), mosses (muscicolous), basidiomes (myceticolous), lichens (lichenicolous) snow banks (nivicolous), and herbivore dung (fimicolous). In addition to performing a variety of important ecological functions, such as nutrient mineralization, myxomycetes play a crucial role as regulators of bacterial populations (Coûteaux & Darbyshire, 1998).

The unique microclimatic conditions and types of substrates found in subterranean environments, which usually differ from those in surrounding external environments, are likely the primary factors driving the formation of exclusively cave-dwelling communities (Mammola, 2019). These communities are primarily composed of detritivorous species, with the organic resources available in these environments being predominantly allochthonous, originating from the external environment. These resources play a crucial role in determining the diversity within the ecosystem (Ferreira et al., 2000).

Both bacteria and protozoa, including myxomycetes, play fundamental roles in the dynamics of cave ecosystems. They actively contribute to the production and decomposition of organic matter, making these resources available to other species within the cave invertebrate communities (Galán, 2015). Furthermore, air currents in subterranean environments can transport spores from the external environment, serving as a crucial mechanism for the dispersal and establishment of microorganisms such as fungi and slime molds (Vanderwolf et al., 2013).

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Few studies highlight the presence of myxomycetes in subterranean environments. The documentation of Mycetozoa species in caves of the Iberian Peninsula was first reported through research conducted in northern Spain (Galán & Nieto, 2010, 2022; Galán et al., 2010, 2011, 2018, 2021a, 2021b, 2022; Galán & Rivas, 2019). Apart from the material found in the Urdallue cave in Artikutza, where plasmodia and aethalia of *Fuligo septica* (L.) F.H. Wigg. were recorded (Galán, 2015), other specimens were not identified and are considered potential new cave-dwelling species, possibly belonging to the orders Trichiales and Physarales. These bright yellow microorganisms were found on rocks and speleothems. They are macroscopic and cosmopolitan protozoa commonly found on rocks, soils, and decaying wood in temperate and humid forests. They were also discovered in leaf litter near cave entrances, on speleothems, and on walls in aphotic zones.

These studies emphasize the presence of these "giant amoebae" in subterranean environments, particularly due to the type of substrate they inhabit and their ecological role. Most were found on speleothems rich in chemoautotrophic bacteria, making this habitat conducive to completing their subterranean life cycle without relying on surface nutrients. As Mycetozoa are known bacterivores, Galán & Nieto (2022) suggested that they can be considered bioindicators of bacteria involved in rock corrosion and the creation or destruction of secondary mineral deposits in caves.

In a study conducted by Nieves-Rivera (2003) in the Rio Camuy cave system in Puerto Rico, the presence of protozoa from the phylum Myxomycota was documented. Sporangia of *Arcyria* sp., *Comatricha* sp., and *Stemonitis* cf. *herbatica* Peck. were found on various substrates, including bat bones, decomposing wood, and leaf litter.

Another group of amoebae closely related to myxomycetes, the dictyostelids, have been discovered in caves throughout North America, as well as in Puerto Rico and Bahamas. Researchers have identified a total of 14 species of dictyostelids and 4 species of *Protostelium* of thriving on various substrates within these cave systems (Waddell 1982; Reeves et al., 2000; Landolt et al., 2006). Similar to myxomycetes, these organisms form fruiting bodies, but their spores are enclosed in a mucilaginous mass, which restricts their dispersal; bats, amphibians, and some invertebrates facilitate the dispersal of dictyostelid spores through ingestion and defecation (Landolt et al., 2006). These findings underscore caves as environments that provide conducive conditions for these protozoa to thrive and complete their life cycles.

Protozoa in general, and myxomycetes in particular, have been underrepresented in studies of cave environments; nevertheless, they may play an important role as intermediaries in the food chain of subterranean ecosystems. By consuming bacteria, these organisms provide a vital food source for invertebrates inhabiting caves, particularly troglobitic species that depend on diets rich in bacteria and fungi (Galán et al., 2010; Galán & Nieto, 2010; Galán, 2011).

The aim of this article is to document the first observations of myxomycetes in caves in Brazil, using specimens collected from the karst region of Pains municipality. This study forms part of a larger project investigating the ecology of macrofungi in the karst areas of Pains, Minas Gerais. The primary objective of this project is to explore how environmental filters influence species distribution in subterranean habitats, emphasizing the crucial role of these organisms in ecosystem dynamics and their importance for the conservation of karst areas.

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## METHODOLOGY

### Study area

Specimens were documented on pieces of wood and tree trunks within two caves in the karst region of Pains, situated in central-western Minas Gerais (Meyer et al., 2022). The climate in this area is humid subtropical, characterized by a dry season from May to August and a rainy season from September to March. The region lies within the São Miguel River Basin and the Ribeirão dos Patos Basin, both significant tributaries of the São Francisco River (Figure 1).

The regional landscape showcases diverse karst formations, featuring carbonate rock outcrops that create distinct features such as sinkholes, caves, residual massifs, lapiaz, cliffs, crevices, and joints (Lucon et al., 2020). Vegetation cover forms a mosaic of phytophysiognomies, encompassing forested areas and open spaces, with Seasonal Semideciduous Forest prevalent at lower elevations and among the outcrops (Melo et al., 2013). In more eroded zones, an additional open phytophysiognomy known as open karst formation is evident. Presently, the region boasts 3,000 registered caves, representing the highest concentration of caves in Latin America (CANIE, 2024).


*Figure 1. Map of the karst area of Pains, including the location of the Brega and Angá dos Negros II caves.*

The two caves where myxomycetes were recorded are Brega and Angá dos Negros II (Figure 2). Brega cave stretches linearly for approximately 1,208 meters with entrances located at opposite ends of the main cavity passage. While most of this cave is dry, there is a lower

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level where the water table is accessible, maintaining water year-round with fluctuations during the rainy season. This section also accumulates significant organic matter of plant origin, transported by runoff and deposited in the cave's lower regions.

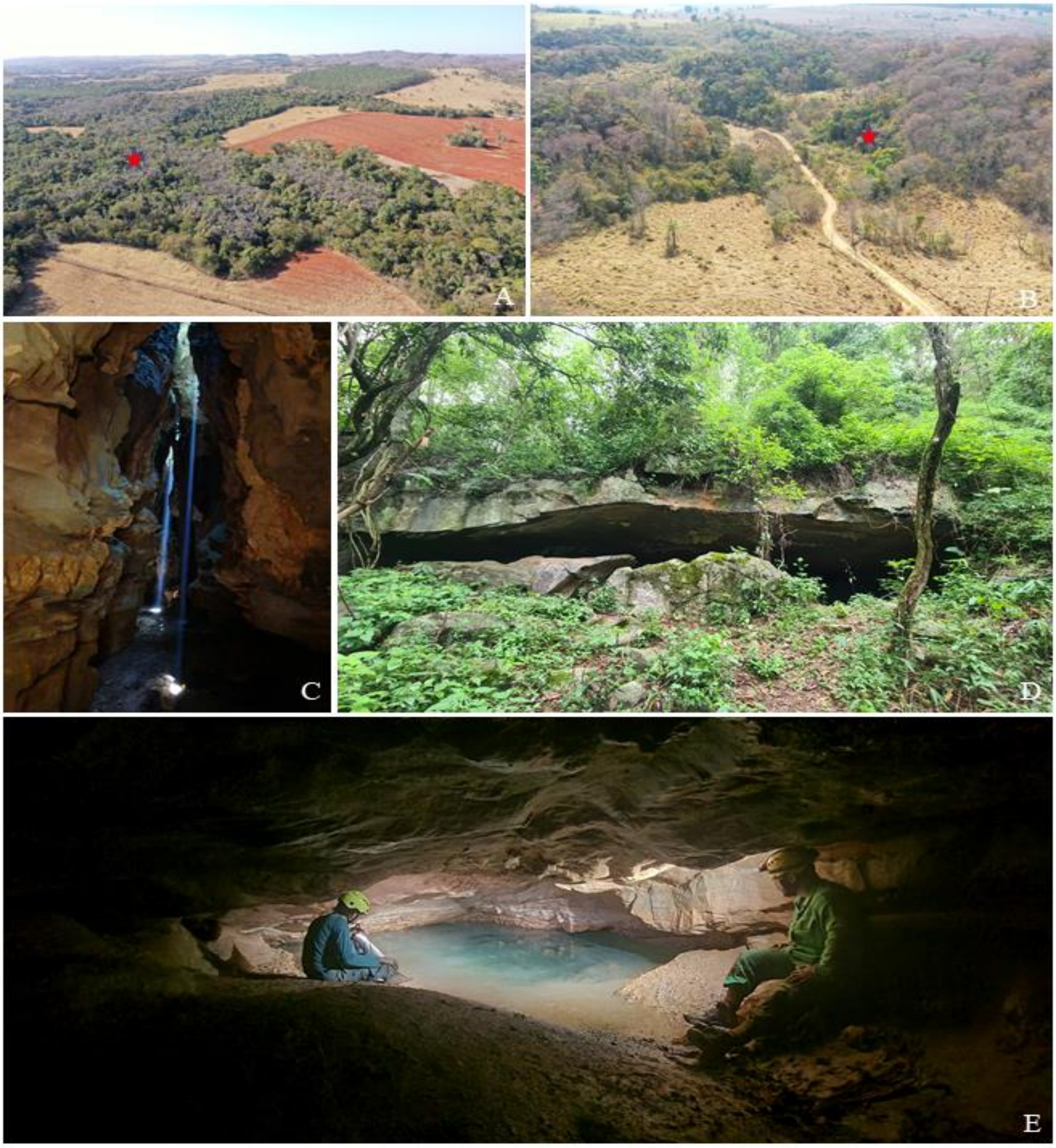

*Figure 2. A. Location of the Angá dos Negros II Cave area, B. Location of the Brega Cave area, C. Entrance of the Angá dos Negros II Cave, D-E. Entrance and conduit of the Brega Cave. Photos by Rodrigo L. Ferreira and Marconi Souza Silva.*

In contrast, Angá dos Negros II cave is much smaller, measuring about 100 meters in length. It features three entrances: two horizontal and one vertical (skylight), facilitating the entry of plant materials into the cave through gravitational forces.

**Sampling, analysis, identification and herborization**

The collected specimens were placed in cardboard boxes along with data sheets specifying substrate type, coloration, collection date, temperature, light exposure, and

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humidity at the collection site. Subsequently, they were transported to the laboratory where they underwent dehydration in an oven at temperatures ranging from 40 to 50°C. This process prepared them for macroscopic and microscopic analysis of the sporocarps to facilitate their identification.

The macroscopic and microscopic characteristics of the sporangia were analised following the methodology described by Parentes & Cavalcanti (2023). The specimens were identified using keys, illustrations, and descriptions provided by Farr (1976) and Poulain et al. (2011). Exsiccates were deposited in the ESAL Herbarium at the Federal University of Lavras under the numbers: ESAL33567, ESAL33568 and ESAL33569.

Taxonomic nomenclature adheres to Lado (2005-2024), and distribution within Brazil is referenced from BFG (2022) and Cavalcanti & Agra (2024). State acronyms follow the standards established by IBGE (2021). Color codes for sporocarps are based on the Kornerup & Wanscher color chart (1978).

## RESULTS AND DISCUSSION

The specimens of myxomycetes discovered in the Brega and Angá dos Negros II caves in Pains belong to the genera *Arcyria* F.H. Wigg., *Hemitrichia* Rostaf., and *Metatrichia* Ing, all classified under the family Trichiaceae, order Trichiales (Figures 3-5). These genera are known to occur in diverse Brazilian biomes.

### ***Arcyria denudata*** **(L.) Wettst.**

Wood fragments were found near a skylight in Angá dos Negros II Cave, suggesting they originated from the upper part of the limestone outcrop and were likely introduced into the cave by gravitational forces. However, the site was shielded from direct light and rainfall and numerous recently sporulated sporocarps of *Arcyria denudata* were found on the decomposing wood.

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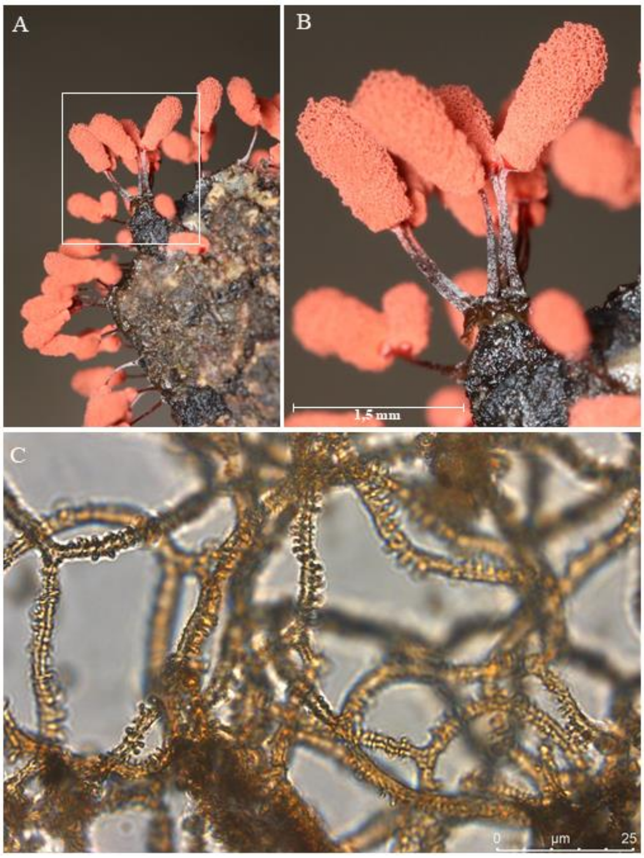


*Figure 3. A. Red sporangia of Arcyria denudata. B. Microscopy showing capillitium and spores. Photos by Rodrigo L. Ferreira and Laise de Holanda Cavalcanti.*

The sporangia displayed typical characteristics of the species (Farr, 1976): red sporotheca (B8), cylindrical stalks pedicels that were dark and about half the total height of the sporocarp, containing subglobose cysts measuring 10-17 µm in diameter; the capillitium was abundant, elastic, and firmly attached to the calyculus (Figure 3). The distinguishing feature was a shallow calyculus instead of the funnel-shaped one more commonly observed in the species, which still fits within the description by Martin & Alexopoulos (1969).

This species has a cosmopolitan distribution (Martin & Alexopoulos, 1969), documented across Brazil's North (AM, AP, PA, RO, RR), Northeast (AL, BA, CE, MA, PB, PE, PI, RN, SE), Midwest (DF, GO, MS, MT), Southeast (MG, RJ, SP), and South (PR, RS, SC) regions, encompassing all of the country's phytogeographical domains (Agra et al., 2024a). It is commonly found on decomposing logs and branches in humid forests, as well as on live tree trunks, aerial litter, and basidiomes (Costa et al., 2014). There are no documented occurrences of *A. denudata* in caves in the global literature, and only Nieves-Rivera (2003) reports the presence of an unidentified species of the genus in Puerto Rico.

***Hemitrichia calyculata* (Speg.) M.L. Farr.**

Few sporocarps, indicating relatively older sporulation, were found on decomposing wood in Brega Cave. These fragments were located near the water table observed in the lower passage of the cave, where a significant accumulation of decomposing plant material occurs during rainy periods. Various filamentous fungi were also observed, some growing diffusely on the plant fragments.

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The sporangia, yellow in color (A8), exhibited typical morphological characteristics of the species, including a deep calyculus, a stalk about half the total height, elastic capillitium completely detached from the edges of the calyculus, and filaments adorned with spirals (Figure 4).

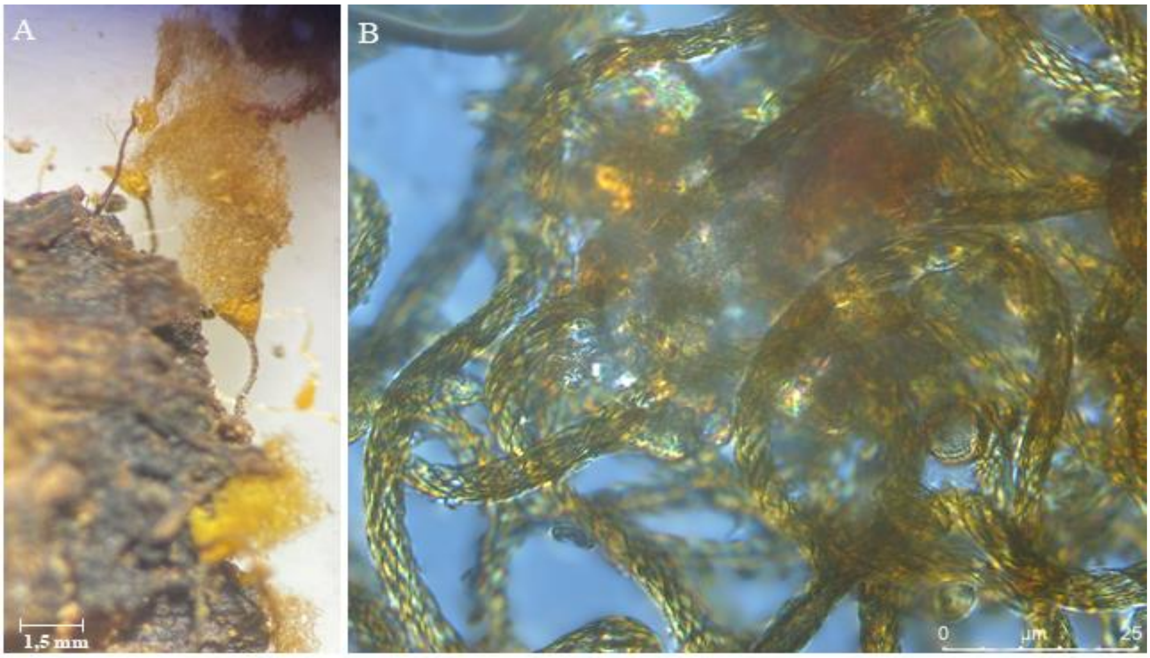


*Figure 4. A. Yellow sporangia of Hemitrichia calyculata, showing the membranous calyculus and elastic capillitium, B. Microscopy of capillitium and spores. Photos by Mariana A. Moreira and Laise de Holanda Cavalcanti.*

This species has a cosmopolitan distribution, with a high frequency in tropical regions (Farr, 1976; Poulain et al., 2011). Agra et al. (2024b) documented its occurrence across the North (AM, RR), Northeast (AL, BA, CE, MA, PB, PE, PI, RN, SE), Midwest (DF, GO, MS, MT), Southeast (RJ, SP), and South (RS, SC) regions of Brazil, spanning all biomes. Cavalcanti & Agra (2024) listed *H. calyculata* among the species found in Minas Gerais without specifying exact locations. It inhabits various microhabitats within different Brazilian phytophysiognomies, sporulating on forest floor litter, aerial litter, dead logs and branches, live tree bark, and basidiomes (Costa et al., 2014). No records were found in the global literature of *Hemitrichia* species occurring in caves.

***Metatrichia vesparia*** **(Batsch) Nann.-Bremek. ex G.W. Martin & Alexop.**

Small clusters of sporangia were collected on decomposing wood within Brega Cave, where *H. calyculata* also sporulated, in similar habitat conditions: located near the observed water table in the cave's lower passage, with a notable accumulation of decomposing plant material. The sporangia observed were aged, short- stalked, obovate, grouped closely together, and dark reddish-brown (E8), with a ruptured cartilaginous peridium facilitating expansion of the elastic capillitium (Figure 5). Filaments were adorned with spirals and characteristic spines of the species (Farr, 1976; Poulain et al., 2011).

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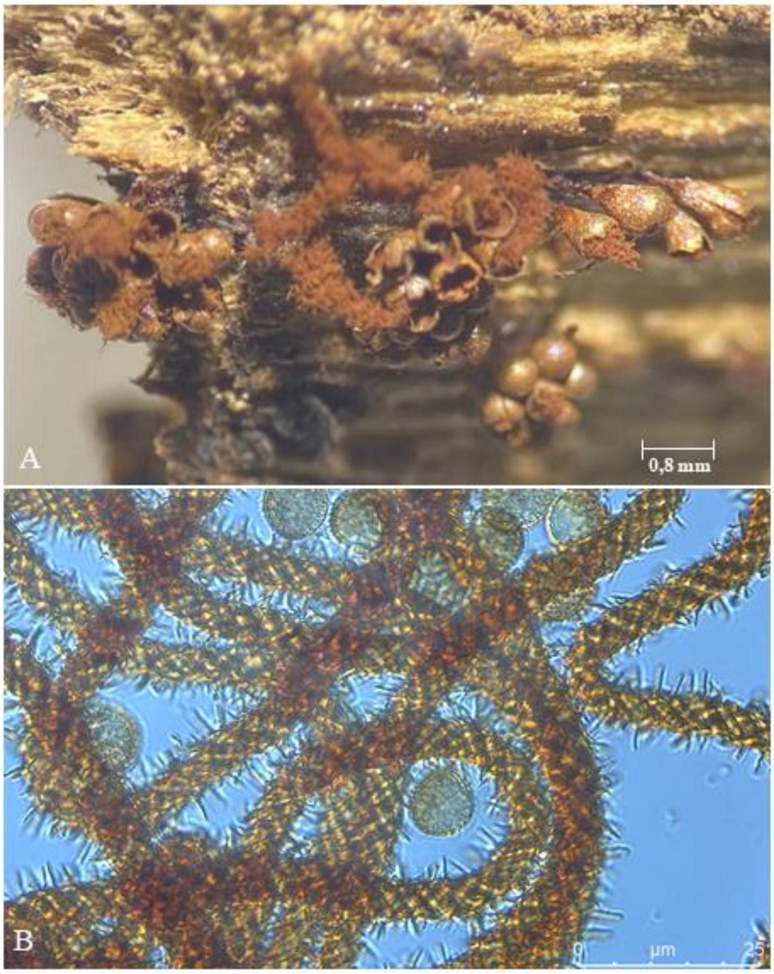


*Figure 5. A. Gregarious clusters of sporangia of Metatrichia vesparia, some of them showing the strongly elastic capillitium. B. Microscopy of capillitium and spores. Photos by Mariana A. Moreira and Laise de Holanda Cavalcanti.*

This species exhibits a broad distribution in temperate regions, appearing less common in tropical and Southern Hemisphere climates, likely cosmopolitan (Martin & Alexopoulos, 1969; Farr, 1976). In Brazil, it has been recorded in the North (AM, RO, RR), Northeast (AL, BA, PB, PE, PI, RN, SE), Midwest (DF, MS), Southeast (RJ, SP), and South (PR, RS, SC) regions, across all biomes (Lima & Cavalcanti, 2017; Agra et al., 2024c). Agra's unpublished thesis (2017) includes occurrences in Cerrado areas of Mato Grosso, Barra do Garças, and Santo Antônio do Monte, Minas Gerais.

The genus *Metatrichia* encompasses six species, three of which are found in Brazil (Lado, 2005-2024; Agra et al., 2024c). Despite its extensive distribution within Brazilian territory, *M. vesparia* is not typically among the most common species, sporulating on dead logs, branches, forest litter, and dung of the wild rabbit *Sylvilagus brasiliensis* L. (Bezerra et al., 2008; Costa et al., 2014). No publications were found in the global literature regarding the presence of *Metatrichia* species in cave environments.

Additionally, sporangia of *Arcyria cinerea* (Bull.) Pers., and an unidentified species from the order Physarales were documented on tree trunks in the forested area near Angá dos Negros II cave through photographs (Figure 6). Species of both orders are frequently found

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in the various ecosystems of Brazil and in other countries of the Neotropics (Lado & Basanta, 2008; BFG, 2022).


*Figure 6. Photographic record of two species of Myxomycetes, sporulated on tree trunks in the forested area near Angá dos Negros II Cave A-B. Arcyria cinerea . C. Sporangia of unidentified specie of Physarales. Photos by Rodrigo Lopes Ferreira.*

**Myxomycetes in caves**

Minas Gerais stands out as one of Brazil's most taxonomically diverse states, boasting a rich variety of taxa ranging from seed plants (11,432 species) to lycophytes, ferns (728 species), hornworts, mosses, and liverworts (785 species), as reported by BFG (2022). However, the Flora and Funga of Brazil (2024) lists only seven families, 12 genera, and 15 species of myxomycetes recorded in the state, notably excluding genera like *Hemitrichia* and *Metatrichia*. A thorough review by Cavalcanti & Agra (2024) expanded this count to 48 species, encompassing 15 genera and three families. This included records from Agra's thesis (2017), which documented *A. denudata*, *H. calyculata*, and *M. vesparia* in Cerrado areas near Santo Antônio do Monte, approximately 200 km from Pains.

The presence of Trichiaceae representatives in caves was first documented by Nieves-Rivera (2003), who found sporangia of an unidentified *Arcyria* species on bat bones and decomposing wood in Puerto Rico's Rio Camuy Cave Park (Table 1). More recently, Galan & Nieto (2022) observed unidentified specimens, probably belonging to the order Trichiales, in Gipuzkoa caves.

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The specimens discovered in the Brega and Angá dos Negros II caves mark the first global published records of *A. denudata*, *H. calyculata*, and *M. vesparia* in cave environments, providing initial insights into the presence of myxomycetes in Brazilian cave ecosystems.

Reports of Mycetozoa taxa in caves are notably rare, likely due to the significant scarcity or complete absence of organic matter in the deeper parts of these subterranean environments. These organisms are found more frequently and abundantly in temperate forests, but they can also inhabit arid environments, such as cold or hot deserts like the Atacama, semi-arid regions like the Caatinga, and seasonally dry areas like the Cerrado. It is crucial to recognize that the references cited in Table 1 likely do not encompass all publications mentioning myxomycetes in caves, given the diverse array of specialists and the various journals where their findings may appear. Moreover, due to their lesser-known status, these organisms are sometimes only mentioned at higher taxonomic levels in publications. In some instances, such as Landolt et al. (1992), even the title, keywords, or abstract may not explicitly indicate a new record of myxomycetes occurring in cave environments.

| TAXON | SUBSTRATE* | COUNTRY | SOURCE** |
|---|---|---|---|
| Trichiales<br>Trichiaceae<br>*Arcyria* cf | B; W | Puerto Rico: Camuy, Camuy River Caves National Park. La Catedral, Clara de Empalma and Sumidouro Caves. | 3 |
| Trichiales<br>Trichiaceae<br>*Arcyria denudata* | W | Brazil: Minas Gerais, Pains. Angá dos Negros Cave. | 15 |
| Trichiales<br>Trichiaceae<br>*Hemitrichia calyculata* | W | Brazil: Minas Gerais, Pains. Brega Cave. | 15 |
| Trichiales<br>Trichiaceae<br>*Metatrichia vesparia* | W | Brazil: Minas Gerais, Pains. Brega Cave. | 15 |
| Physarales<br>Physaraceae<br>*Fuligo séptica* | R, L | Spain: Navarra, Goizueta, Artikutza, Urdallue Caves. | 7 |
| Physarales<br>Didymiaceae<br>*Didymium trachysporum* | SMC | USA: Maryland, Belstsville. Whitings Neck Cave. | 2 |
| Stemonitales<br>Stemonitaceae<br>*Comatricha* cf | L | Puerto Rico: Camuy, Camuy River Caves National Park. La Catedral, Clara de Empalma and Sumidouro Caves. | 3 |
| Stemonitales<br>Stemonitaceae<br>*Stemonitis* cf *herbatica* | W | Puerto Rico: Camuy, Camuy River Caves National Park. La Catedral, Clara de Empalma and Sumidouro Caves. | 3 |
| Myxomycetes | S | Mexico: Morelos, Emiliano Zapata. Salitre Cave. | 1 |

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| | | | |
|---|---|---|---|
| Mycetozoa<br>Myxomycetes<br>? Trichiales | R | Spain: Basque Country, Gipuzkoa.<br>Caves:.Leizarãn; Aixa, Igitegi, Montxon, Tortuga; Urkita 2, Meru 4., Akaitz txiki 1 and 2; Txispiri and Ibarrondo. | 4,5,6,8 |
| Mycetozoa | R | Spain: San Sebastian, Errera. Txoritokieta 1 and 2 Caves. | 10 |
| Mycetozoa<br>Trichiales and Physarales | R | Spain: Navarra, Serra de Urbasa. Lezeaundi Cave. | 9 |
| Mycetozoa<br>Trichiales | R | Spain: Navarra, Aralar. Kolosobarne Cave.. | 12 |
| Mycetozoa | R | Spain: Basque Country, Gipuzkoa. Aitzelarko; Burnigurutze 1 and 2 Caves. | 11,13 |
| ?Mycetozoa | R | Spain: Andaluzia, Malaga, Hoyo Conique de Archidona system caves. | 14 |
| Unidentified plasmodium. | SG | Puerto Rico: Mayagüez, Mona Island, beach of Pájaros. El Cabalo/Pájaros and Uvero Caves. | 3 |

*Table 1. Records of Mycetozoa in underground environments around the world.*
*Substrate: W – Decomposing wood. L – Leaf litter. B – Bat bones. S – Soil. SG – Soil enriched with bat guano. SMC – Soil in a moist chamber. R – Rock and speleothems.
**Source: 1 – Hoffman et al. 1986. 2 – Landolt et al. 1992. 3 – Nieves-Rivera 2003. 4– Galán et al. 2010. 5 – Galán & Nieto 2010. 6 – Galán 2011. 7– Galán 2015. 8 – Galán et al .2018. 9 – Galán & Rivas 2019. 10 – Galán et al. 2021a. 11 – Galán et al. 2021b. 12 – Galán & Nieto 2022. 13 – Galán et al. 2022.14 – Martinez Rodríguez et al. 2023. 15 – This work.

It is important to emphasize that the karst region of Pains represents one of Brazil's most significant conflicts between the preservation of speleological heritage and the environmental impacts of mining. The caves in this region are under considerable threat from limestone extraction and improper land use, resulting in irreversible environmental damage and endangering the high diversity of cave-restricted species, many of which are endemic to single caves (Ferreira et al., 2022; Galvão & Costa, 2022).

This study is the first to explore the occurrence of myxomycetes in karst areas in Brazil. These pioneering efforts provide a foundation for future research in this area, contributing to the monitoring of these organisms in specific environments such as caves.

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