

ORIGINAL ARTICLE

Checklist of Amazonian gasteroid fungi (Agaricomycetidae, Phallomycetidae, Basidiomycota)

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ABSTRACT

The Amazon rainforest is the largest tropical rainforest in the world, with high biodiversity of organisms. Despite the increasing knowledge about fungal diversity in the last few years, many fungal taxa, including gasteroid clades, are still poorly known. Gasteroid fungi are recognized by the maturation of basidiospores inside the basidiomata and by the passive release of spores. We conducted a detailed survey of published data on the species that occur in Amazon forests. We confirmed the occurrence of 83 species distributed in 22 genera, eight families and four orders. The most representative genera was *Geastrum*, followed by *Cyathus*, *Lycoperdon* and *Phallus*. We present an identification key for Amazonian gasteroid genera and a map of record distribution. This review is expected to contribute to identify distribution gaps for further research on gasteroid fungi and to subsidize policies for the conservation of fungi in the Amazon region.

KEYWORDS: Neotropics, biodiversity, taxonomy, Gasteromycetes, rainforest

Checklist de fungos gasteróides da Amazônia (Agaricomycetidae, Phallomycetidae, Basidiomycota)

RESUMO

A floresta amazônica é a maior floresta tropical do mundo, com alta biodiversidade de organismos. Apesar do crescente aumento sobre o conhecimento da diversidade fúngica nos últimos anos, muitos táxons de fungos, especialmente clados gasteróides, ainda são pouco conhecidos. Os fungos gasteróides são reconhecidos pela maturação dos basidiósporos no interior do basidioma e pela liberação passiva de esporos. Baseado em dados publicados, realizamos um levantamento detalhado das espécies que ocorrem na floresta amazônica. Nós confirmamos a ocorrência de 83 espécies distribuídas em 22 gêneros, 8 famílias e 4 ordens. Os gêneros mais representativos foram *Geastrum*, seguido por *Cyathus*, *Lycoperdon* e *Phallus*. Apresentamos uma chave de identificação para gêneros de gasteróides amazônicos e um mapa de distribuição de registros. Espera-se que esta revisão contribua para identificar lacunas de distribuição para futuras pesquisas sobre fungos gasteróides e para subsidiar políticas de conservação de fungos na região amazônica.

PALAVRAS-CHAVE: Neotrópicos, biodiversidade, taxonomia, Gasteromycetes, floresta tropical

INTRODUCTION

The Amazon rainforest is a mosaic of different phytophysiognomies that form one of the largest and most diverse rainforests in the world (Coutinho 2006; MMA 2007). The region faces important conservation challenges, with increasingly high rates of deforestation and biodiversity loss (Oliveira-Filho and Metzger 2006; Giam 2017). In this context, the knowledge about the fungal community is essential for the conservation and restoration of these areas

(Fink *et al.* 2021) since fungi act directly in nutrient cycling in the soil (Kirk *et al.* 2008).

Estimates indicate that 90% of the species of fungi are unknown to science (Antonelli *et al.* 2020). The Neotropical region, especially in extensive forests such as Amazonia, probably harbors many undiscovered species, mainly due to the high rate of endemic species per area (Hawswork and Lücking 2017). Recent studies reported the occurrence of about 1000 species of macrofungi for the Brazilian Amazon

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forest (Maia *et al.* 2015). Despite being relatively better known than other groups, publications on gasteroid fungi, a group characterized by passive spore dispersion, are also scarce and widely dispersed throughout the Amazon domain, concentrating mainly around few research poles in the region (Maia *et al.* 2015).

Gasteroid fungi have various morphotypes and grow on different types of substrates, such as soil, wood, manure, and leaves, acting directly in nutrient cycling, as well as decomposition of organic matter and mycorrhizal symbiosis (Miller and Miller 1988; Alexopoulos *et al.* 1996). Some groups have medical and pharmacological importance. For example, *Cyathus* Haller species have compounds capable of reducing neurodegenerative effects (Yin *et al.* 2019). *Geastrum* Pers. has species with bactericidal efficacy and biotechnological potential for waste degradation through enzymatic activities (Kuhar *et al.* 2016; Sevindik *et al.* 2017).

The first records of gasteroid fungi cited for the Amazon were made by Montagne (1839), who recorded *Geastrum ambiguum* Mont. and *Phallus indusiatus* Vent.: Pers. in the Bolivian Amazon forest. Since then, most records of new Amazonian genera and species were from Brazil, especially in recent years (e.g., Trierveiler-Pereira *et al.* 2009; Henkel *et al.* 2010; Alfredo *et al.* 2012a; Alfredo *et al.* 2012b; Silva *et al.* 2013; Cabral *et al.* 2014a; Smith *et al.* 2015; Baseia *et al.* 2016; Crous *et al.* 2016; Cabral *et al.* 2017; Crous *et al.* 2017; Accioly *et al.* 2018; Crous *et al.* 2018; Accioly *et al.* 2019; Assis *et al.* 2019; Cabral *et al.* 2019).

In this study, we carried out a compilation of published records of gasteroid fungi in Amazonian forests and provide an identification key for Amazonian genera.

MATERIAL AND METHODS

In this study, the geographical delimitation for the Amazon domain presented by Tejada *et al.* (2020), which comprises the Amazon Basin, was used. Data for this checklist were obtained through an extensive search in literature records published for the Amazon domain in Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, Surinam, and Venezuela until March 2021. Electronic databases such as Google Scholar, Biodiversity Heritage Library, and Web of Science were used in the research. Regarding habitat, the search terms were rainforest, moist forest, flooded forest, tropical lowland rainforest, forest of pre-Andean slopes, floodplain forest (*várzea*), forested stream swamps (*igapó*), and upland or non-flooded forest (*terra firme*). The search concerned mostly indexed journals, however, for older publications, we also used thesis, books and short communications that contained records of gasteroid fungi for Amazonia. Records with doubtful identification or that did not indicate any specific data about locality were not considered.

The author names and basionym of each species were obtained from Mycobank (<http://www.mycobank.org/>) and Index Fungorum (<http://www.indexfungorum.org/>), and taxonomical treatment followed Kirk *et al.* (2008). Records without identification at the species level were not considered. When the original manuscript did not provide geographical coordinates, points from nearby localities were used as proxies. In cases where only the country was reported, no geographic coordinates were informed, and the record was not included in the distribution map. QGIS software was used to produce a map of record distribution. Species were listed in alphabetical order.

RESULTS

The survey returned 54 publications resulting in 83 species of gasteroid fungi recorded for the Amazonian domain (Table 1), of which 26 have been originally described for this region, comprising 22 genera. Figure 1 shows the records of gasteroid fungi species that were observed in the Amazon domain. The most representative are *Geastrum* (30 species), *Cyathus* (10), *Lycoperdon* Pers. (8) and *Phallus* Junius ex L. (7), which represented about 65% of all records published until March 2021. All genera recorded are distributed in eight families (Agaricaceae Chevall., Boletaceae Chevall., Diplocystaceae Kreisel, Geastraceae Corda, Nidulariaceae Dumort., Phallaceae Corda, Physalacriaceae Corner, Sclerodermataceae Corda) and four orders (Agaricales Underw., Phallales E. Fisch., Geastrales K. Hosaka & Castellano and Boletales E.-J. Gilbert).

Most records were from the Brazilian Amazon (64 species), followed by Bolivia and French Guiana (10 species each),



Figure 1. Records of gasteroid fungi species (red circles) in the Amazon domain. Each dot represents a species record, and there may be more than one dot for the same species. Records for which it was not possible to estimate the geographic coordinates are not shown on the map. The green line represents the limits of the Amazon biome. AC = Acre state; AM = Amazonas state; AP = Amapá state; PA = Pará state; RO = Rondônia state; RR = Roraima state; MT = Mato Grosso state. This figure is in color in the electronic version.

Table 1. Species of gasteroid fungi recorded for the Amazon rainforest. Asterisks (*) represent species originally described based on types from the Amazon. (–) indicates that the location indicated by the authors was too vague to approximate geographical coordinates.

Family/Species	Country (state/province)	Coordinates	Reference
Agaricomycetidae Parmastto.			
<i>Arachnion album</i> Schwein.	Bolivia (Concepción)	16°07'41.4"S, 62°02'23.1"W	Calonge <i>et al.</i> (2000)
<i>Castellanea pakaraimophila</i> T.W. Henkel & M.E. Smith*	Guiana (Cuyuni-Mazaruni)	5°26'21.3"N, 60°04'43.1"W	Smith <i>et al.</i> (2015)
<i>Calvatia oblongispora</i> V.L. Suárez, J.E. Wright & Calonge	Brazil (Amazonas)	3°04'45.4"S, 60°05'18.1"W	Suárez <i>et al.</i> (2009)
<i>Calvatia cyathiformis</i> (Bose) Morgan	Brazil (Pará)	1°47'37.0"S, 51°26'03.8"W	Sotão <i>et al.</i> (2009)
<i>Costatisporus cyanescens</i> T.W. Henkel & M.E. Smith*	Guiana (Potaro-Siparuni)	5°18'04.8"N, 59°54'40.4"W	Smith <i>et al.</i> (2015)
<i>Cyathus amazonicus</i> Trierv.-Per. & Baseia*	Brazil (Rondônia)	8°07'39.1"S, 63°21'52.9"W	Trierveiller-Pereira <i>et al.</i> (2009)
	Brazil (Amazonas)	3°14'09.0"S, 60°53'10.0"W	Accioli <i>et al.</i> (2018)
	Brazil (Mato Grosso)	13°05'60.0"S, 54°25'55.3"W	Assis <i>et al.</i> (2021)
<i>Cyathus albinus</i> Accioli, R. Cruz & Baseia*	Brazil (Amazonas)	3°14'09.0"S, 60°53'10.0"W	Accioli <i>et al.</i> (2018)
<i>Cyathus berkeleyanus</i> (Tul. & C. Tul.) Lloyd	Brazil (Pará)	1°47'37.0"S, 51°26'03.8"W	Sotão <i>et al.</i> (2009)
<i>Cyathus earlei</i> Lloyd	Brazil (Amazonas)	3°14'09.0"S, 60°53'10.0"W	Accioli <i>et al.</i> (2018)
	Brazil (Amazonas)	3°05'31.0"S, 59°59'39.0"W	
<i>Cyathus helenae</i> H.J. Brodie	Brazil (Pará)	1°47'37.0"S, 51°26'03.8"W	Sotão <i>et al.</i> (2009)
	Brazil (Amazonas)	0°18'43.1"N, 68°39'09.3"W	Berkeley and Cooke (1876)
	Brazil (Amazonas)	2°57'47.5"S, 59°55'23.2"W	Accioli <i>et al.</i> (2018)
<i>Cyathus limbatus</i> Tul. & C. Tul. = <i>Cyathodes limbatum</i>	Brazil (Rondônia)	10°48'45.0"S, 61°54'51.7"W	Capelari and Maziero (1988) Trierveiller-Pereira <i>et al.</i> (2011b)
	Guiana	–	Brodie and Dennis (1954)
<i>Cyathus morelensis</i> C.L. Gómez & Pérez-Silva	Brazil (Amazonas)	2°57'47.5"S, 59°55'23.2"W	Cruz <i>et al.</i> (2012)
<i>Cyathus stercoreus</i> (Schwein.) De Toni ≡ <i>Nidularia stercorea</i> Schwein.	Brazil (Pará)	1°47'37.0"S, 51°26'03.8"W	Sotão <i>et al.</i> (2009)
<i>Cyathus striatus</i> (Huds.) Wild	Brazil (Pará)	1°47'37.0"S, 51°26'03.8"W	Sotão <i>et al.</i> (2009)
	Colombia (Amazonas)	1°32'00.1"S, 71°21'56.6"W	Vasco-Palacios <i>et al.</i> (2005)
<i>Cyathus triplex</i> Lloyd	Brazil (Amazonas)	3°14'09.0"S, 60°53'10.0"W	Accioli <i>et al.</i> (2018)
	Brazil (Pará)	1°47'37.0"S, 51°26'03.8"W	Sotão <i>et al.</i> (2009)
	Guiana (Potaro-Siparuni)	4°58'07.2"N, 59°35'00.9"W	Brodie and Dennis (1954)
<i>Disciseda verrucosa</i> G. Cunn.	Bolivia (Concepción)	16°07'41.4"S, 62°02'23.1"W	Calonge <i>et al.</i> 2000
<i>Guyanagaster necrorhiza</i> , M.E. Sm & Aime*	Guiana (Potaro-Siparuni)	5°18'04.8"N, 59°54'40.4"W	Henkel <i>et al.</i> (2010)
<i>Jimtrappea guyanensis</i> T.W. Henkel, M.E. Sm. & Aime*	Guiana (Potaro-Siparuni)	5°18'04.8"N, 59°54'40.4"W	Smith <i>et al.</i> (2015)
	Brazil (Amazonas)	2°45'27.4"S, 66°45'35.7"W	Dennis (1953)
<i>Lycogalopsis solmsii</i> E. Fisch. as <i>Morganella rimosa</i> Baseia & Alfredo in (Alfredo et al 2012)	Brazil (Amazonas)	2°57'47.5"S, 59°55'23.2"W	Alfredo <i>et al.</i> (2012a)
	Brazil (Pará)	1°47'37.0"S, 51°26'03.8"W	Sotão <i>et al.</i> (2009)
<i>Lycoperdon albstipitatum</i> (Baseia & Alfredo) Baseia, Alfredo & M.P. Martín* ≡ <i>Morganella albstipitata</i> Baseia & Alfredo	Brazil (Amazonas)	2°57'47.5"S, 59°55'23.2"W	Alfredo <i>et al.</i> (2012a)
<i>Lycoperdon arenicola</i> (Alfredo & Baseia) Baseia, Alfredo & M.P. Martín* ≡ <i>Morganella arenicola</i> Alfredo & Baseia	Brazil (Amazonas)	3°05'51.4"S, 60°01'02.8"W	Alfredo <i>et al.</i> (2014)
<i>Lycoperdon costaricense</i> (M.I. Morales) Baseia, Alfredo & M.P. Martín ≡ <i>Morganella costaricensis</i> M.I. Morales	Bolivia (Vaca Diez)	11°00'46.2"S, 66°00'42.0"W	Suarez and Wright (1996)
<i>Lycoperdon juruense</i> Henn.	Brazil (Amazonas)	5°05'04.4"S, 64°47'25.8"W	Hennings (1904)
<i>Lycoperdon fuligineum</i> Berk. & M.A. Curtis ≡ <i>Morganella fuliginea</i> (Berk. & M.A. Curtis) Kreisel & Dring	Brazil (Amazonas)	2°58'45.3"S, 59°57'09.9"W	Cabral <i>et al.</i> (2014a)
	Brazil (Pará)	1°47'37.0"S, 51°26'03.8"W	Sotão <i>et al.</i> (2009)

Table 1. Continued

Family/Species	Country (state/province)	Coordinates	Reference
Agaricomycetidae Parmastto.			
<i>Lycoperdon fuliginum</i> Berk. & M.A. Curtis ≡ <i>Morganella fuliginea</i> (Berk. & M.A. Curtis) Kreisel & Dring	Brazil (Rondônia)	10°56'25.3"S, 63°11'08.5"W	Capelari and Maziero (1988)
	Brazil (Mato Grosso)	13°06'44.3"S, 54°28'35.5"W	Rodrigues <i>et al.</i> (2021)
	Bolivia (Manuripi)	11°17'52.6"S, 67°11'09.4"W	Suarez and Wright (1996)
	Venezuela (Aragua)	4°24'25.8"N, 65°49'25.3"W	Dennis (1953)
<i>Lycoperdon oblongatum</i> Accioly, Baseia & M.P. Martín*	Brazil (Amazonas)	2°58'45.3"S, 59°57'09.9"W	Alfredo <i>et al.</i> (2017)
<i>Lycoperdon pyriforme</i> (Schaeff.) Kreisel & D. Krüger ≡ <i>Morganella pyriformis</i> (Schaeff.) Kreisel & D. Krüger	Bolivia (Santa Cruz de la Sierra)	11°31'41.5"S, 65°18'38.4"W	Rocabado <i>et al.</i> (2007)
<i>Lycoperdon epixylon</i> Berk. & M.A. Curtis	Brazil (Amazonas)	4°56'32.3"S, 64°56'29.5"W	Hennings (1904)
<i>Sclerangium braziliense</i> Henn	Brazil (Amazonas)	0°47'35.5"S, 67°15'48.3"W	Hennings (1904)
<i>Scleroderma anomalosporum</i> Baseia, B.D.B. Silva & M.P. Martín*	Brazil (Pará)	5°13'24.2"S, 55°28'01.3"W	Baseia <i>et al.</i> (2016)
<i>Scleroderma camassuense</i> M.P. Martín, Baseia & B.D.B. Silva*	Brazil (Pará)	5°13'24.2"S, 55°28'01.3"W	Baseia <i>et al.</i> (2016)
<i>Scleroderma duckei</i> B.D.B. Silva, M.P. Martín & Baseia*	Brazil (Amazonas)	2°58'45.3"S, 59°57'09.9"W	Baseia <i>et al.</i> (2016)
<i>Scleroderma minutisporum</i> Baseia, Alfredo & Cortez*	Brazil (Amazonas)	2°55'12.9"S, 59°54'15.0"W	Alfredo <i>et al.</i> (2012b)
<i>Scleroderma sinnamariense</i> Mont.	Brazil (Amazonas)	4°10'44.1"S, 67°13'45.0"W	Singer and Araújo (1979)
	Guiana (Potaro-Siparuni)	4°41'53.1"N, 59°13'01.3"W	Henkel <i>et al.</i> (2012)
<i>Scleroderma stellatum</i> Berk.	Brazil (Amazonas)	4°56'32.3"S, 64°56'29.5"W	Berkeley and Cooke (1876)
	Brazil (Pará)	1°48'13.5"S, 51°26'29.9"W	Sotão <i>et al.</i> (2009)
	Surinam	–	Linder (1930)
<i>Tremellogaster surinamensis</i> E. Fisch. *	Guiana (Bartica)	6°23'25.0"N, 58°37'55.9"W	Linder (1930)
	Guiana (Potaro-Siparuni)	4°42'23.0"N, 59°22'12.2"W	Henkel <i>et al.</i> (2012)
	Colombia (Amazonas)	1°23'42.6"S, 72°47'45.0"W	Vasco-Palacios <i>et al.</i> (2005)
<i>Tulostoma exasperatum</i> Mont. = <i>Schizostoma exasperatum</i>	Brazil (Rondônia)	11°18'09.4"S, 61°03'11.0"W	Trierveiler-Pereira <i>et al.</i> (2011b)
<i>Vascellum pampeanum</i> (Speg.) Homrich as <i>Lycoperdon pampeanum</i> Speg.	Bolivia (Entre Rios)	17°42'57.5"S, 63°52'41.8"W	Rocabado <i>et al.</i> (2007)
Phallomycetidae K. Hosaka, Castellano & Spatafora			
<i>Clathrus crispus</i> Turpin ≡ <i>Clathrella crispa</i> (Turpin) E. Fischer	French Guiana (Roura)	4°36'25.2"N, 52°17'07.1"W	Cheype (2010)
<i>Geastrum albonigrum</i> Calonge & M. Mata	Brazil (Mato Grosso)	10°49'31.8"S, 61°27'31.7"W	Trierveiler-Pereira <i>et al.</i> (2011b)
	Brazil (Mato Grosso)	13°06'19.4"S, 54°27'33.3"W	Rodrigues <i>et al.</i> (2021)
<i>Geastrum ambiguum</i> Mont.	Bolivia (Santa Cruz)	18°00'48.3"S, 59°37'39.1"W	Montagne (1839)
<i>Geastrum baculicrystallum</i> J.O. Sousa, Accioly, Baseia & M.P. Martín*	French Guiana (Saint-Laurent-du-Maroni)	4°12'25.8"N, 53°29'15.6"W	Accioly <i>et al.</i> (2019)
<i>Geastrum echinulatum</i> B.D.B. Silva & Baseia*	Brazil (Amazonas)	2°56'34.2"S, 60°01'08.3"W	Silva <i>et al.</i> (2013)
<i>Geastrum englerianum</i> Henn	Brazil (Amazonas)	3°07'09.7"S, 60°01'19.1"W	Hennings (1904)
	Brazil (Pará)	1°56'53.3"S, 51°40'09.6"W	Leite <i>et al.</i> (2011)
<i>Geastrum entomophilum</i> Fazolino, Calonge & Baseia	Brazil (Mato Grosso)	12°51'11.0"S, 54°28'47.3"W	Rodrigues <i>et al.</i> (2021)
	Brazil (Pará)	1°56'53.3"S, 51°40'09.6"W	Leite <i>et al.</i> (2011)
<i>Geastrum fimbriatum</i> Fr.	Brazil (Rondônia)	8°05'57.6"S, 63°23'08.4"W	Trierveiler-Pereira <i>et al.</i> (2009)
	Brazil (Pará)	1°27'39.1"S, 48°26'24.2"W	Trierveiler-Pereira <i>et al.</i> (2011a)
	Bolivia (Concepción)	16°07'52.1"S, 62°02'29.6"W	Calonge <i>et al.</i> (2000)
	Brazil (Mato Grosso)	13°06'44.3"S, 54°28'35.5"W	Rodrigues <i>et al.</i> (2021)
<i>Geastrum hariotii</i> Lloyd	Brazil (Pará)	1°47'52.9"S, 51°26'24.6"W	Sotão <i>et al.</i> (2009)
	Surinam (?) as <i>Geaster hariotii</i>	–	Coker and Couch (1928)

Table 1. Continued

Family/Species	Country (state/province)	Coordinates	Reference
Phallomycetidae K. Hosaka, Castellano & Spatafora			
<i>Geastrum hyalinum</i> Freitas-Neto, N.M. Assis, J.O. Sousa & Baseia*	Brazil (Mato Grosso)	13°02'28.6"S, 54°33'31.6"W	Assis <i>et al.</i> (2019)
<i>Geastrum hirsutum</i> Baseia & Calonge	Brazil (Pará)	1°47'32.2"S, 51°29'39.8"W	Sotão <i>et al.</i> (2009)
<i>Geastrum inpaense</i> T.S. Cabral, B.D.B. Silva & I.G. Baseia*	Brazil (Amazonas)	3°05'46.6"S, 59°58'44.0"W	Cabral <i>et al.</i> (2014a)
<i>Geastrum ishikawae</i> Accioly, J.O. Sousa, Baseia & M.P. Martín*	Brazil (Amazonas)	3°05'46.6"S, 59°58'44.0"W	Crous <i>et al.</i> (2016)
<i>Geastrum javanicum</i> Lév.	Brazil (Pará)	1°42'09.6"S, 50°59'39.9"W	Sotão <i>et al.</i> (2009)
	Brazil (Mato Grosso)	13°06'44.3"S, 54°28'35.5"W	Rodrigues <i>et al.</i> (2021)
<i>Geastrum juruense</i> Henn. (as <i>Geaster juruensis</i>)	Brazil (Amazonas)	2°42'52.9"S, 60°09'09.3"W	Hennings (1904)
<i>Geastrum lageniforme</i> Vittad.	Brazil (Amazonas)	3°05'31.0"S, 59°59'39.0"W	Cabral <i>et al.</i> (2014a)
	Brazil (Pará)	1°56'53.3"S, 51°40'09.6"W	Leite <i>et al.</i> (2011)
	Brazil (Mato Grosso)	10°50'31.3"S, 61°27'37.0"W	Trierveiler-Pereira <i>et al.</i> (2011b)
	Bolivia (Concepción)	16°07'52.3"S, 62°02'29.9"W	Calonge <i>et al.</i> (2000)
<i>Geastrum lilloi</i> L.S. Domínguez	Brazil (Pará)	1°56'53.3"S, 51°40'09.6"W	Leite <i>et al.</i> (2011)
<i>Geastrum lloydianum</i> Rick	Brazil (Amazonas)	3°05'46.6"S, 59°58'44.0"W	Cabral <i>et al.</i> (2014a)
<i>Geastrum mirabile</i> Mont.	Guiana (Upper Demerara-Berbice)	5°26'12.8"N, 58°15'39.1"W	Dennis (1953)
<i>Geastrum neoamericanum</i> J.O. Sousa, Accioly, M.P. Martín & Baseia	Brazil (Rondônia)	9°34'53.4"S, 65°23'06.3"W	Accioly <i>et al.</i> (2019)
	French Guiana	4°56'13.92"N, 52°19'33.60"W	Accioly <i>et al.</i> (2019)
<i>Geastrum ovalisporum</i> Calonge & Mor.-Arr.	Bolivia (Concepción)	16°07'52.1"S, 62°02'29.6"W	Calonge <i>et al.</i> (2000)
<i>Geastrum pusillipilosum</i> J.O. Sousa, Alfredo, R.J. Ferreira, M.P. Martín & Baseia	Brazil (Mato Grosso)	12°59'52.8"S, 54°38'28.6"W	Rodrigues <i>et al.</i> (2021)
<i>Geastrum rubellum</i> P.-A. Moreau & C. Lécure*	Brazil (Acre)	9°56'39.1"S, 69°40'04.1"W	Accioly <i>et al.</i> (2019)
<i>Geastrum rusticum</i> Baseia, B.D.B. Silva & T.S. Cabral	Brazil (Mato Grosso)	12°57'29.2"S, 54°35'38.7"W	Rodrigues <i>et al.</i> (2021)
	Brazil (Amazonas)	3°05'46.6"S, 59°58'44.0"W	Cabral <i>et al.</i> (2014a)
<i>Geastrum saccatum</i> Fr.	Brazil (Amazonas)	3°07'09.7"S, 60°01'19.1"W	Hennings (1904)
	Brazil (Pará)	1°56'53.3"S, 51°40'09.6"W	Leite <i>et al.</i> (2011)
	Bolivia (Concepción)	16°07'52.1"S, 62°02'29.6"W	Calonge <i>et al.</i> (2000)
	Colombia (Caquetá)	0°34'15.7"N, 73°49'07.1"W	Vasco-Palacios <i>et al.</i> (2005)
<i>Geastrum schweinitzii</i> (Berk. & M.A. Curtis) Zeller	Brazil (Amazonas)	3°05'46.6"S, 59°58'44.0"W	Cabral <i>et al.</i> (2014a)
	Brazil (Pará)	1°42'09.6"S, 50°59'39.9"W	Sotão <i>et al.</i> (2009)
	Brazil (Mato Grosso)	13°04'38.9"S, 54°32'35.7"W	Rodrigues <i>et al.</i> (2021)
	Surinam (Paramaribo)	5°50'00.0"N, 55°10'00.0"W	Zeller (1948)
<i>Geastrum scleroderma</i> Mont.	Brazil (Amazonas)	3°07'09.7"S, 60°01'19.1"W	Hennings (1904)
<i>Geastrum triplex</i> Jungh.	Brazil (Amazonas)	3°05'46.6"S, 59°58'44.0"W	Cabral <i>et al.</i> (2014a)
	Brazil (Mato Grosso)	13°21'24.6"S, 54°35'01.2"W	Rodrigues <i>et al.</i> (2021)
	Venezuela	10°28'23.0"N, 66°59'44.0"W	Coker and Couch (1928)
<i>Geastrum trichifer</i> Rick	Guiana (Cuyuni-Mazaruni)	7°04'00.0"N, 59°51'00.0"W	Dennis (1953)
<i>Geastrum velutinum</i> Morgan	Brazil (Pará)	1°42'09.6"S, 50°59'39.9"W	Sotão <i>et al.</i> (2009)
<i>Geastrum verrucoramulosum</i> T.S. Cabral, J. O. Sousa & Baseia*	Brazil (Amazonas)	3°07'09.9"S, 60°01'40.4"W	Cabral <i>et al.</i> (2017)
	Brazil (Acre)	7°56'14.6"S, 72°47'23.2"W	Cabral <i>et al.</i> (2017)
<i>Lysurus arachnoideus</i> (E. Fisch.) Trierv.-Per. & Hosaka ≡ <i>Aseroe arachnoidea</i> E. Fisch.	Brazil (Amazonas)	3°23'00.8"S, 59°45'23.2"W	Cabral <i>et al.</i> (2015)
<i>Mutinus bambusinus</i> (Zoll.) E. Fisch.	Bolivia (Vaca Díez)	10°49'26.7"S, 65°22'19.2"W	Wright (1960)

Table 1. Continued

Family/Species	Country (state/province)	Coordinates	Reference
Phallomycetidae K. Hosaka, Castellano & Spatafora			
<i>Mutinus fleischeri</i> Penz.	Brazil (Amazonas)	3°05'31.0"S, 59°59'39.0"W	Cabral <i>et al.</i> (2014a)
<i>Mutinus verrucosus</i> T.S. Cabral, B.D.B. Silva, K. Hosaka, M.P. Martín & Baseia *	Brazil (Pará)	3°55'43.8"S, 54°37'22.8"W	Crous <i>et al.</i> (2017)
<i>Mutinus caninus</i> (Huds.) Fr.	Brazil (Rondônia)	11°00'13.4"S, 61°11'15.7"W	Trierveiler-Pereira <i>et al.</i> (2011b)
<i>Phallus aff. multicolor</i> (Berk. & Broome) Cooke ≡ <i>Dictyophora multicolor</i> Berk. & Broome	French Guiana (Cayenne)	4°53'57.4"N, 52°19'12.2"W	Cheype (2010)
<i>Phallus atrovolvatus</i> Kreisel & Calonge	Brazil (Amazonas)	2°58'19.6"S, 60°03'35.0"W	Cabral <i>et al.</i> (2014a)
	French Guiana (Cayenne)	4°52'17.0"N, 52°14'51.6"W	Cheype (2010)
<i>Phallus cinnabarinus</i> (W.S. Lee) Kreisel ≡ <i>Dictyophora cinnabarina</i> W.S. Lee	Brazil (Pará)	1°25'50.8"S, 48°27'26.8"W	Cabral <i>et al.</i> (2015)
	Brazil (Pará)	1°27'07.8"S, 48°28'37.7"W	
	French Guiana (Cayenne)	4°56'41.7"N, 52°19'00.9"W	Cabral <i>et al.</i> (2015)
<i>Phallus denigricans</i> T.S. Cabral, B.D.B. Silva & Baseia*	Brazil (Amazonas)	2°01'39.8"S, 64°58'53.0"W	Cabral <i>et al.</i> (2019)
	Brazil (Amazonas)	0°02'18.9"N, 66°12'25.8"W	
	Brazil (Amazonas)	3°46'54.9"S, 62°06'56.7"W	Cabral <i>et al.</i> (2019)
	Brazil (Pará)	1°47'54.5"S, 51°29'13.7"W	Sotão <i>et al.</i> (2009)
	Brazil (Pará)	2°48'60.0"S, 55°01'48.7"W	Cabral <i>et al.</i> (2019)
	Brazil (Rondônia)	8°06'27.5"S, 63°24'56.4"W	Trierveiler-Pereira <i>et al.</i> (2009)
	Brazil (Rondônia)	8°41'09.0"S, 63°52'04.7"W	
<i>Phallus indusiatus</i> Vent.: Pers. ≡ <i>Dictyophora indusiata</i> (Vent.) Desv.	Brazil (Mato Grosso)	13°14'41.1"S, 54°30'29.7"W	Rodrigues <i>et al.</i> (2021)
	Colombia (Amazonas)	0°01'20.8"S, 74°12'55.9"W	Vasco-Palacios <i>et al.</i> (2005)
	Colombia (Caquetá)	0°20'57.9"S, 72°17'18.8"W	
	French Guiana (Cayenne)	4°33'48.2"N, 52°12'23.5"W	Cheype (2010)
	French Guiana (Cayenne)	4°37'54.0"N, 52°20'14.4"W	
	Bolivia (Vaca Díez)	10°49'26.7"S, 65°22'19.2"W	Wright (1960)
	Bolivia	–	Montagne (1839)
<i>Phallus merulinus</i> (Berk.) Cooke ≡ <i>Dictyophora merulina</i> Berk.	Brazil (Amazonas)	3°05'31.6"S, 59°59'42.2"W	Cabral <i>et al.</i> (2014a)
	Brazil (Amazonas)	3°05'31.0"S, 59°59'39.0"W	
	Brazil (Amazonas)	3°01'52.4"S, 59°50'35.7"W	
	Brazil (Amazonas)	3°01'52.4"S, 59°50'35.7"W	
	French Guiana (Cayenne)	4°52'28.6"N, 52°15'37.8"W	Cheype (2010)
	French Guiana (Cayenne)	4°56'46.1"N, 52°18'28.5"W	
	French Guiana (Tonnégrande)	4°49'50.4"N, 52°26'42.4"W	Cheype (2010)
<i>Phallus purpurascens</i> T.S. Cabral, B.D.B. Silva & Baseia*	Brazil (Amazonas)	3°05'31.0"S, 59°59'39.0"W	Cabral <i>et al.</i> (2019)
	Brazil (Mato Grosso)	11°50'02.7"S, 55°30'02.3"W	
<i>Staheliomyces cinctus</i> E. Fisch., Mitt.	Brazil (Amazonas)	3°47'29.5"S, 62°10'28.9"W	Cabral <i>et al.</i> (2014a)
	French Guiana (Cayenne)	4°33'04.6"N, 52°21'49.2"W	Cheype (2010)
	Bolivia (Madre de Dios)	11°19'56.8"S, 66°10'22.6"W	Wright (1960)
	Ecuador (Rio Napo)	2°14'07.4"S, 76°36'05.0"W	Burr <i>et al.</i> (1996)
	Surinam	–	Dennis (1970)
	French Guiana (Cayenne)	4°52'17.0"N, 52°14'51.6"W	Cheype (2010)
<i>Xylophallus xylogenus</i> (Mont.) E. Fisch	French Guiana (Cayenne)	4°56'39.0"N, 52°19'25.6"W	
	Peru (Madre de Dios)	12°21'50.6"S, 70°24'60.0"W	Gómez and Gazis (2006)

Table 1. Continued

Family/Species	Country (state/province)	Coordinates	Reference
Phallomycetidae K. Hosaka, Castellano & Spatafora			
<i>Xylophallus xylogenus</i> (Mont.) E. Fisch	Ecuador (Sucumbíos/Orellana)	0°18'53.3"S, 75°42'22.7"W	
	Brazil (Mato Grosso)	13°06'44.3"S, 54°28'35.5"W	Rodrigues et al. (2021)
<i>Xylophallus clavatus</i> T.S. Cabral, M.P. Martín, C.R. Clement, K. Hosaka & Baseia*	Brazil (Amazonas)	0°02'18.9"N, 66°12'25.8"W	Crous et al. (2018)
	Brazil (Amazonas)	2°38'04.2"S, 56°42'29.6"W	
	Brazil (Pará)	2°57'11.0"S, 54°58'27.7"W	

Guiana (7 species), Surinam (4 species), Colombia (3 species), Venezuela and Ecuador (2 species each) and Peru (1 species). All species are listed in Table 1.

Among the 83 species present in the Amazon, 26 have been originally described for this region in recent years, showing a huge potential occurrence of new taxa (Table 1). Among the 22 genera, *Stabeliomyces* E. Fisch. had the highest number of records in all Amazonian countries, being absent only from Colombia, Peru, and Venezuela. In Brazil, most genera and species were recorded in the states of Amazonas and Pará, followed by Rondônia and Mato Grosso, while no records were found for the states of Amapá, Tocantins and Maranhão. An identification key for the genera reported from the Amazon domain is presented below.

Identification key to Amazon genera of gasteroid fungi

- 1 – Presence of stipe or pseudostipe.....2
- 1' – Absence of stipe.....3
- 2 – Pulverulent gleba.....4
- 2' – Mucilaginous gleba.....5
- 3 – Gleba stored in peridioles.....*Cyathus*
- 3' – Mucilaginous, pulverulent or spongy gleba, not stored in peridioles.....10
- 4 – Dehiscence of the peridium through the formation of an apical pore.....*Tulostoma*
- 4' – Irregular dehiscence of the peridium.....21
- 5 – Pseudostipe with arms or gleba.....6
- 5' – Pseudostipe without arms.....7
- 6 – Basidiomata vertical; Arms triangular-shaped without any connections.....*Lysurus*
- 6' – Basidiomata in a form of a cage, with connected arms.....*Clathrus*
- 7 – Receptacle conical and campanulate, located in the apical portion of the pseudostipe; Pseudostipe reticulate.....8
- 7' – Void pseudoestipe; Gleba located at the apex of the basidiomata on the pseudostipe or forming a constriction above the center and below the apex on the pseudostipe.....9

- 8 – Gleba on a receptacle fixed on the apical portion of the pseudostipe; Pseudostipe cylindrical and reticulate.....*Phallus*
- 8' – Small basidiomata (up to 15 mm); Receptacle smooth with umbilicated apex and attached to the pseudostipe... *Xylophallus*
- 9 – Gleba located at the apex of the basidiomata, directly on the pseudostipe.....*Mutinus*
- 9' – Gleba forming a constriction above the center and below the apex on the pseudostipe.....*Stabeliomyces*
- 10 – Pulverulent gleba.....11
- 10' – Mucilaginous or spongy gleba.....12
- 11 – Dehiscence through the formation of a pore.....16
- 11' – Dehiscence through irregular peridium disruption.....19
- 12 – Epigeous habit; Subglobose basidiomata.....13
- 12' – Hypogeous or semi-hypogeous habitat; Subglobose to ovoid basidiomata.....14
- 13 – Exoperidium black and verrucous; Gleba reddish orange; Spores ornamented.....*Guyanagaster*
- 13' – Exoperidium white and with a little ornamentation; Spores smooth.....*Lycogalopsis*
- 14 – Peridium glabrous to subtomentose; Columella absent.....*Costatisporus*
- 14' – Peridium glabrous to subglabrous; Columella present...15
- 15 – Gleba brown in color; Basidiospores subfusiform, yellowish brown, often dextrinoid; Basidia subclavate and cystidia absent..... *Castellanea*
- 15' – Gleba pink in color; Basidiospores subfusiform, pink to reddish brown and inamyloid; Basidia clavate and cystida present.....*Jimtrappea*
- 16 – Dehiscence through the exoperidium, shattering into rays, star-shaped basidiomata; Subgleba absent.....*Geastrum*
- 16' – Dehiscence does not result in a star-shaped basidiomata; Subgleba present or absent.17
- 17 – Subgleba absent.....*Disciseda*
- 17' – Subgleba present.....18
- 18 – Presence of a membrane separating the gleba from the subgleba (diaphragm).....*Vascelum*

18 ² – Absence of diaphragm.....	<i>Lycoperdon</i>
19 – Capillitium absent.....	20
19 ² – Capillitium present.....	<i>Calvatia</i>
20 – Peridium three-layered.....	<i>Tremellogaster</i>
20 ² – Peridium one-layered.....	<i>Arachnion</i>
21 – Basidiospores with reticulate or spiny ornamentation	<i>Scleroderma</i>
21 ² – Basidiospores with subreticulate ornamentation	<i>Sclerangium</i>

DISCUSSION

Throughout the twentieth century, publications on gasteroid fungi in the Amazon were scarce and scattered among the domain countries. However, in the 21st century, publications have undergone a significant increase, and most are concentrated in the Brazilian Amazon. Despite the significant increase in data on the gasteroid mycota, knowledge about these organisms in the Amazon domain is still scarce relative to the extent and large biodiversity in this region. Although Amazonian centers of endemism are widely known for animals and plants (Silva *et al.* 2005), for fungi there are no studies with quantitative data on endemism rates, even with some species being found in the same regions, e.g. *Scleroderma* species (Baseia *et al.* 2016).

Studies carried out in the Neotropical region involving integrative taxonomy have revealed a great diversity of species hidden within cosmopolitan taxa and contributed to the description of new species and new genera (Alfredo *et al.* 2017; Sousa, *et al.* 2017; Accioly *et al.* 2018; Accioly *et al.* 2019; Cabral *et al.* 2019; Sousa, *et al.* 2019). These works, besides solving taxonomic conflicts, show the great diversity of species that remain undetected, especially in poorly sampled areas. Some species found in the Amazon have morphological features that suggest possible adaptations to the region, such as *Geastrum verrucoramulosum* T.S. Cabral, J.O. Sousa & Baseia and *Cyathus albinus* Accioly, R. Cruz & Baseia (Cabral *et al.* 2017; Accioly *et al.* 2018).

Genera such as *Arachnion* Schwein., *Castellanea* T.W. Henkel & M.E. Smith, *Costatisporus* T.W. Henkel & M.E. Smith, *Clathrus* P. Micheli ex L., *Disciseda* Czern., *Guyanagaster* T.W. Henkel, M.E. Smith & Aime, *Jimtrappea* T.W. Henkel, M.E. Smith & Aime, *Lysurus* Fr., *Sclerangium* Lév., *Tulostoma* Pers., and *Vascellum* F. Šmarda have been recorded only once, which reflects sampling effort rather than restricted distribution. Some records, especially the older ones, lack detailed information on the collection site and other aspects, such as habitat. *Geastrum hariotii* Lloyd was recorded for South Guiana (currently Guiana, French Guiana, and Surinam), but the authors did not mention the specific collection locality of the species (Coker and Couch 1928). Likewise, *Geastrum schweinitzii* (Berk. & M.A. Curtis) Zeller

is only mentioned for Surinam (Zeller 1948), and *Geastrum triplex* Jungh. only for Venezuela (Coker and Couch 1928).

The analysis of species distributions is frequently complicated by taxonomic problems, mainly in groups where interspecific differences are inconspicuous, as in species complexes and cryptic species (Vizzini *et al.* 2013). This is a recurrent problem for gasteroid fungi, and recent studies merging classical taxonomy with molecular techniques (e.g., barcoding) have shown that there is a high diversity of hidden species for groups that were considered as well known (Accioly *et al.* 2019). This is the case for *Geastrum hirsutum* Baseia & Calonge, *G. schweinitzii* and *G. triplex*, which have already been proven to be species complexes (Kasuya *et al.* 2012; Accioly *et al.* 2019). Likewise, the genus *Myriostoma* Desv. was thought to be monospecific, but more recent revisions revealed a diversity of five species for the genus (Sousa *et al.* 2017; Sousa *et al.* 2019). *Lycoperdon* is another genus that had recent changes in its classification. Due to the high morphological similarity between *Lycoperdon* and closely related genera, such as *Morganella* Zeller and *Vascellum*, many species were incorrectly identified, showing the need for molecular data to delimit species with higher reliability (Larsson and Jeppson 2008; Phosri *et al.* 2014; Rusevska *et al.* 2014; Alfredo *et al.* 2017). Using molecular and morphological data, Alfredo *et al.* (2017) also demonstrated the existence of new species and new combinations of previously identified materials, evidencing that there was a hidden diversity of *Lycoperdon* species under the name *Morganella*. Most records for these groups occur in the Amazon, highlighting that low geographical coverage of fungal surveys and taxonomic uncertainty allow the assumption that the diversity and distribution of gasteroid fungi in Amazonian forests is still widely underestimated.

The need for more studies to increase the knowledge of gasteroid diversity is made more urgent by the accelerating anthropic impacts on the region. For example, Baseia *et al.* (2016) identified three new species of *Scleroderma* Pers. and classified them as endangered. Two of these species were found in areas that are now flooded by hydroelectric dams. Greater knowledge on the Amazonian funga is necessary to better evaluate its diversity, ecosystemic roles and conservation strategies.

CONCLUSIONS

This checklist contributes to the expansion and summarization of the current knowledge of gasteroid fungi in the Amazon region. The data presented here highlight the necessity to expand collection efforts, especially in little or unexplored areas, to improve the representativeness of gasteroid fungi in herbaria and reduce the unknown component of Amazonian fungi. However, an increase in publications on Amazonian gasteroid fungi over the past two decades provided data on unexplored areas and revealed

taxonomic novelties. In this context, continuing biodiversity surveys are the foundation for an increase of the knowledge on these fungi and the design of more effective conservation strategies for the promotion of forest preservation.

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