

Neotropical distribution of *Leocarpus* (Physaraceae, Myxomycetes) and rediscovery of *L. fragilis* in Brazil

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Abstract: The known distribution of *Leocarpus* Link in the Neotropics, with special attention to Brazil, is presented herein, enhancing our understanding of the worldwide distribution of the genus. Field collections, herbarium documentation, supplemented with a literature review (1863-2024), showed that *L. fragilis* (Dicks.) Rostaf., the single species of the genus, is very rare in Brazil, with only five records in over 100 years. Geographic distribution, climate types, elevation ranges, vegetational environments, microhabitats, and substrates where this species has been recorded are commented upon.

Keywords: amoebozoa, chorology, brazilian myxobiota, Physarales.

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Introduction

The genus *Leocarpus* Link belongs to the class Myxomycetes (Amoebozoa) and is included in the order Physarales, family Physaraceae, because it has dark spores and deposits of non-crystalline calcium in the sporocarps (Poulain et al. 2011; Lado and Eliasson 2022). With an extensive synonymy (Lado 2005-2024), it is considered monotypic, both in older publications such as Lister (1925), Macbride and Martin (1932), and Martin and Alexopoulos (1969) as well as in recent ones such as Poulain et al (2011) and Lado and Eliasson (2022). The four species proposed by Fries in 1849, *L. cyanescens* (Fr.) Fr., *L. granulatus* (Schumach.) Fr., *L. minutus* (Schumach.) Fr., and *L. nitens* Fr., as well as *L. melaleucus* Mont., proposed by Montagne (1855), are considered invalid or doubtful according to Lado (2005-2024).

The phaneroplasmodium of the only species in the genus, *L. fragilis* (Dicks.) Rostaf., commonly occupies large areas of different microhabitats, such as fallen dead trunks, soil litter, bark of living trees (Lado et al 2014; Schnittler et al 2016; Rojas et al 2018), developing and sporulating more rarely on living herbs, succulents, mosses, lichens and herbivore dung (Amrani and Abdel-Azeem 2018; Moreno et al 2018; Calaçã et al 2020). The reddish-brown to ochre-yellow sporocarps, densely packed and numerous

in each sporulation, are very typical and conspicuous and according to Farr (1976), *L. fragilis* can be considered as one of the easiest myxomycete species to recognize in the field.

With a worldwide distribution, *L. fragilis* was considered cosmopolitan by several authors, such as Teixeira (1971) and Martin et al. (1983), being common in temperate regions (Lister 1925). However, after reviewing the distribution patterns of the species, Stephenson et al. (2008) questioned whether it should actually be considered cosmopolitan.

Farr (1976) included *Leocarpus* in her Flora Neotropica monograph citing it for Brazil, Colombia, Chile, Mexico and the USA (Florida), but commented that, despite being very common and widely distributed, she had never encountered *L. fragilis* in tropical or even subtropical environments. In the synthesis of knowledge accumulated between 1828 and 2008 about the species of myxomycetes that occur in the Neotropics, Lado and Wrigley de Basanta (2008) added records for Argentina and Costa Rica, but the occurrence of *Leocarpus* was indicated for only 20% of the countries listed in the review.

After analyzing the worldwide distribution pattern of *L. fragilis*, Stephenson et al. (2008) concluded that it seems to have a clear preference for the temperate regions of the planet, being rarely found in arctic regions, absent or scarce in arid regions and in the humid tropics, reappearing in the temperate regions of the southern hemisphere in Argentina, South Africa, and South Australia. Novozhilov et al. (2017) recorded the presence of *L. fragilis* in typical environmental conditions for nivicolous myxomycetes in the Kamchatka Peninsula, Russia, and commented that the specimen found could represent an unknown nivicolous form of this morphospecies.

The expansion of knowledge about the geographic distribution of myxomycete species in the Neotropical region can complement databases, allowing the development of more in-depth ecological studies and contributing to the biological monitoring of the effects of climate change on the diversity of the myxobiota (Rojas et al. 2012, 2017). Thus, in the present work, the knowledge on the occurrence of the genus *Leocarpus* in Brazil is updated and the geographic distribution, types of macroclimates, elevations, vegetational environments, microhabitats, and substrates of sporulation of *L. fragilis* in countries located in the Neotropics are commented upon.

Materials and methods

The data presented below were obtained through collections of sporocarps in the field, consulting Brazilian and foreign herbaria through Species Link and the Global Biodiversity Information Facility (GBIF), complemented by bibliographical research (1863-2024) on collections of specimens of *Leocarpus* in Brazil and other Neotropical countries. When consulting the collections, all data associated with the specimen, such as place and date of collection, collector, determinator, identification, ecological data, such as type and species of substrate, were tabulated and analyzed. Herbarium acronyms are in line with Thiers (2024).

The geographic area covered in the queries corresponds to the same criteria adopted by Lado and Wrigley de Basanta (2008) for delimiting the countries included in the Neotropics, covering all territories between Mexico, as the northern limit, and Tierra del Fuego, as the southern limit. The files in shapefile format were downloaded from the IBGE database, and the map was assembled using QGIS Desktop 3.16.0 with GRASS 7.8.4 software. Graphs were made using the GGPlot2 package (Wickham 2016) in the Rstudio software.

The analysis of the specimens collected in Rio Grande do Sul followed the LABMIX-UFPE protocol and the identification was based on the keys, description, and illustration by Poulain et al. (2011). Based on the specimens analyzed, a description of the species was elaborated, followed by comments on the history of records and distribution in Brazil. Such tasks were complemented with information on climate types, altitude, microhabitats, and substrates of the places where *L. fragilis* was found in South America (Argentina, Chile, and Colombia), Middle Americas (Bahamas and Costa Rica) and North America (Mexico).

Results and discussion

Field and laboratory work complemented by literature reviews and analyses herbarium collections indicated the occurrence of the genus *Leocarpus* in seven countries, with the first record for the Neotropics obtained at the end of the 19th century (Figs. 1 and 2). The map in Figure 1 illustrates the currently known distribution of *L. fragilis* in the Neotropics and Tables 1 and 2 show the type of climate, the altitude of the locations and the type of substrate where the species has been recorded.

According to Chardon and Toro (1930) and Uribe-Meléndez (1995), the first record of myxomycete species in South America was carried out in Colombia, with the publication of the article by Lévillé (1863), where *L. fragilis* is cited as *L. vernicosus* (Pers.) Link ex Nees constituting the first record of the genus *Leocarpus* published for the Neotropics. Exsiccate data provided by GBIF (Lado Rodriguez 2018) inform that the sporocarps were collected in the Municipality of Tequendama, Department of Cundinamarca, at high altitude, on mosses and wet roots, and can be classified as muscicolous (Tables 1 and 2).

When estimating what is known so far about the Colombian myxobiota, one of the difficulties reported by Ortiz-Moreno et al. (2022) was locating the specimens deposited in national and foreign collections. When located, most of the time they were poorly preserved or with important data missing from the labels. The authors reported that, among the 234 officially recognized biological collections for Colombia, only 66 have fungi in their collections, the majority without digitized databases. In the table that lists the national collections, only the HUA herbarium, from the University of Antioquia, has a clear indication of the inclusion of myxomycetes, and in the foreign ones there are some specimens in the BPI and UARK herbaria, both based in the United States (Ortiz-Moreno et al. 2022). The survey of the literature and biological collections available online carried out in the present work indicate that the material collected 160 years ago constitutes the only known record of *L. fragilis* for the Colombian myxobiota.

In Brazil, the first collection of a representative of the genus *Leocarpus* was made in Serra da Mantiqueira, in March 1894, by Ernst Heinrich Georg Ule, during the period that he worked at the National Museum, headquartered in Rio de Janeiro. The material received the collection number 2075 and specimens were deposited in the fungal collection of the Herbarium of the National Museum (R-Fungi), in Rio de Janeiro, and in the Herbarium Hamburgense (HBG), of the University of Hamburg, Germany (Paszchke 1896; Friederichsen 1973).

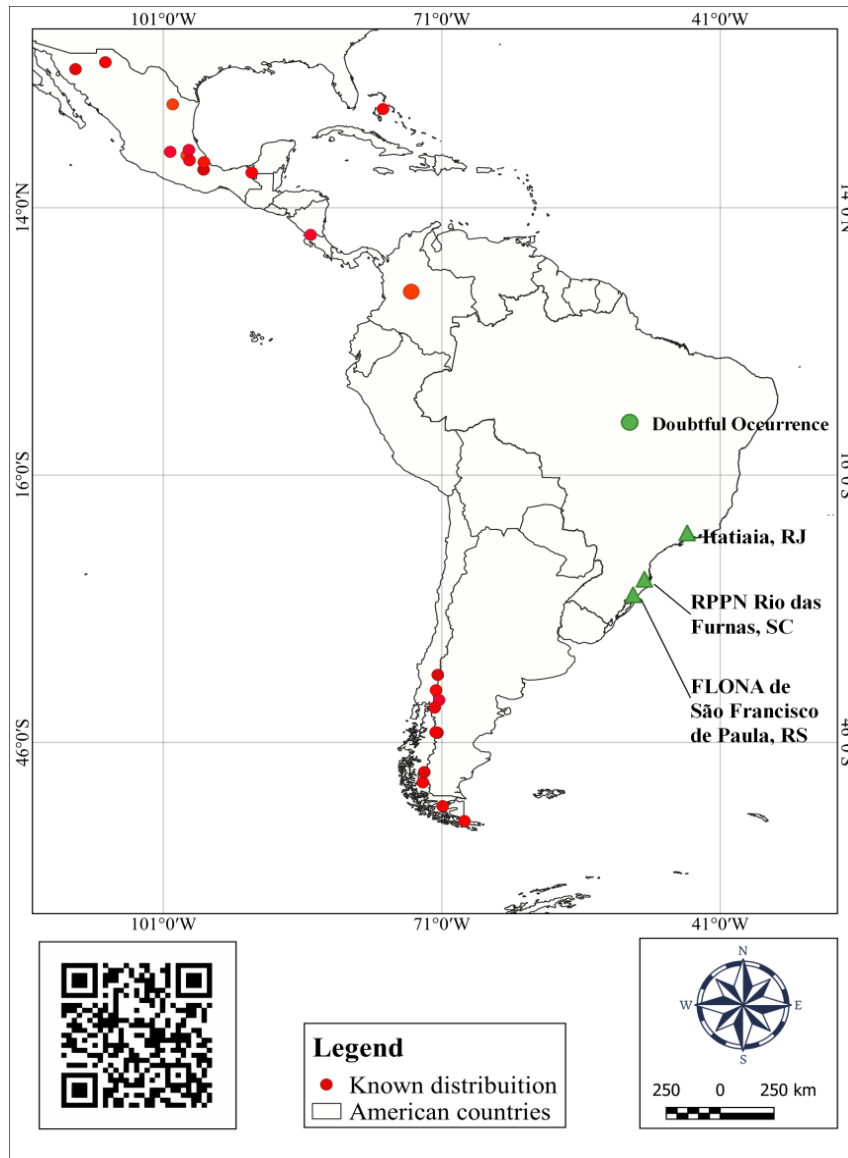


Figure 1. Distribution of *Leocarpus fragilis* in the Neotropics, with emphasis on Brazil. The QR Code directs to the promotional page of Brazilian Myxomycetes on Instagram.

When mentioning *L. fragilis* on page 55 of his article on fungi collected in Brazil by E. Ule, Pazschke (1896) reported that the specimen Ule 2075 was found in a forest located in the Municipality of Itatiaia, state of Rio de Janeiro, at an altitude of 2000 m. In the list published by Friederichsen (1973), with about 3300 specimens of fungi deposited in the HBG Herbarium collected by E. Ule between 1883-1903 in Brazil, *L. fragilis* is cited under the same collection number. In the two publications, as well as on the label of the R-Fungi 84407 specimen, there is no information about the sporulation substrate.

The Municipality of Itatiaia, where the species was found, is currently part of the area of Itatiaia National Park, created in 1937. This Atlantic Forest conservation unit is located in the southwest of Rio de Janeiro and south of the State of Minas Gerais, where the altitude varies from 500 m, in the southern part, with hillside forests, to 2789 m, in the more rugged parts of the relief, such as Agulhas Negras (Martinelli et al. 1989; Ribeiro and Medina 2002) The vegetation is classified as Dense Ombrophylous

Forest and comprises two phytogeographies: Montana Forest (500-1500 m) and Alto-Montana Forest or cloud forest (above 1500 m), including highland grasslands, which are generally found above 2200 m (Martinelli et al. 1989; Velloso et al. 1991). According to the Köppen classification, the local climate is Cwa type. At lower altitudes, around 1000 m, the average annual rainfall varies between 1500 and 1800 mm. In Campos de Altitude, the average annual precipitation varies from 2000 to 3000 mm, with an average temperature in the range of 9°C to 13°C, in the highest parts, and 17°C to 23°C, in the lowest parts (Safford 1999).

The collection n. 2075 by E. Ule was used in citations of the occurrence of *L. fragilis* in Brazil, both in old publications, such as Pazschke (1896), Friederichsen (1973), Farr (1976), Putzke (1996), and more recent ones, such as Maimoni-Rodella (2002), Lado and Wrigley de Basanta (2008), Cavalcanti and Trierveiler-Pereira (2010), Cavalcanti et al. (2020) and BFG (2024). However, the map that illustrates the worldwide distribution of the species, constructed from 1474 records, in the paper published by Stephenson et al. (2008), does not indicate the occurrence of *Leocarpus* in Brazil.

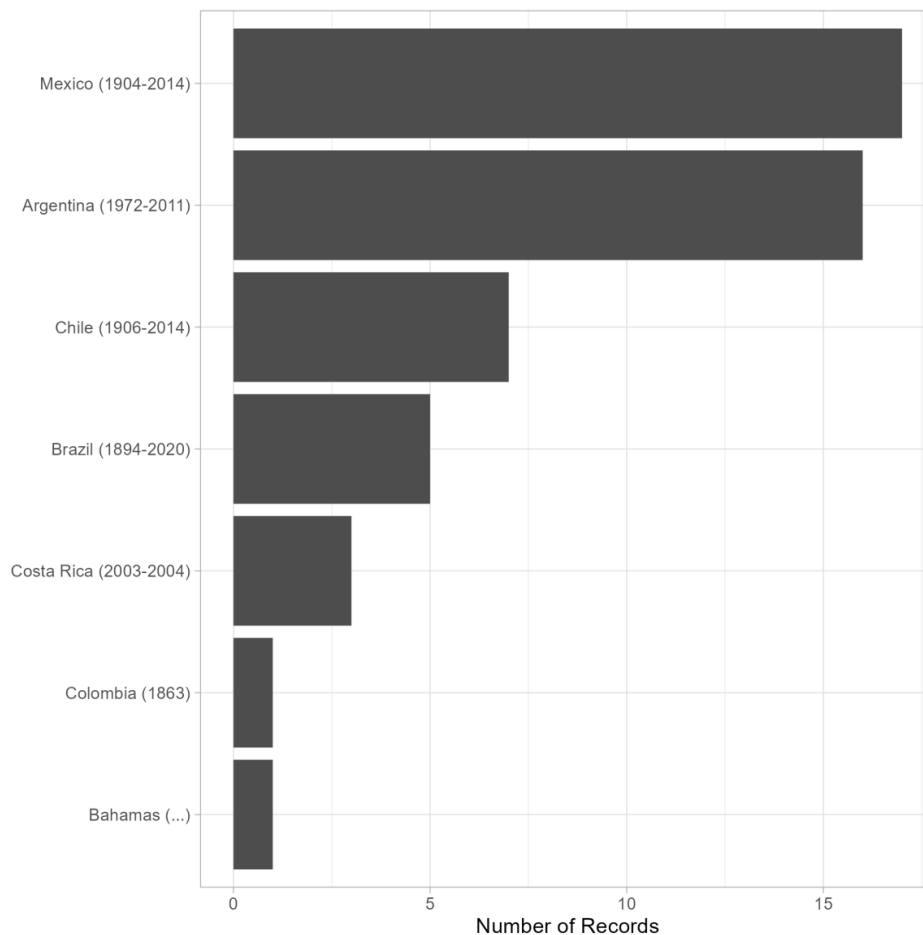


Figure 2. Number of occurrence records of *Leocarpus fragilis* found between 1863 and 2020 in countries located in the Neotropics.

In the present work, a second record of occurrence of the species in Brazil was located, documented as exsiccate BPI 722654, collected in 1914, identified as *L. vernicosus* (Pers.) Link ex Nees, currently included in the synonymy of *L. fragilis*. The label on the specimen indicates the French priest Louis-Joseph Grelét, botanist and mycologist, as collector, and C.G. Lloyd, American mycologist as determinator. Lloyd's collection, originally housed at the Mycological Collection of the Smithsonian Institute, was transferred to the BPI herbarium, where the specimen now resides. The original label does not contain information about the sporulation substrate or the environment and place of collection. The geographic coordinates 9.9°S and 50.913°W contained in GBIF (2024) place the collection site in the State of Mato Grosso (Brazilian Midwest), 11 km from the border with Pará and 25 km from the municipality of Vila Rica, Mato Grosso, where the altitude is around 200 m, and the climate is type Am. No reference was found to the material collected by Grelét in Lloyd's publications up to 1926, nor articles that cite collections carried out by the mycologist in the Midwest and North regions of Brazil, making the origin of the specimen doubtful. Considering the date of collection, the material preserved in the BPI herbarium corresponds to a second occurrence record of *L. fragilis* in Brazil, but the location, state and region of the country where it was found, as well as the vegetational environment and substrate remain uncertain (Fig. 1, Table 1).

In the IPA Herbarium collection, four specimens collected in July 1951 in the Municipality of Recife, Pernambuco (Northeast Brazil), on leaves of *Persea gratissima* L. (IPA 38098), soil (IPA 38485), *Carica papaya* L. (IPA 38486) and unidentified palm tree (IPA 38997) were considered as a new species of *Leocarpus* by A.C. Batista. Analyzing the production of the renowned mycologist (Silva and Minter 1995) it was found that *L. candida* Batista was neither described nor published, but two of the specimens are catalogued with the binomial in the GBIF database (GBIF 2024) and Species Link (Pereira 2022). The four specimens, all relatively well preserved, were studied by one of the authors of the present work (LHC) and redetermined as *Physarum didermoides* (Pers.) Rostaf.

In April 2001, sporocarps of *L. fragilis* were found in the National Forest of São Francisco de Paula, in the Municipality of Campos de Cima da Serra, Rio Grande do Sul, indicating for the first time the occurrence of the genus in the southern region of Brazil (Table 1). The specimen was collected on decomposing wood by Janaína Velede and determined by one of the authors of the present work (LHC), with specimen deposited in the HCB herbarium, at the University of Santa Cruz do Sul (Velede et al. 2005). The São Francisco de Paula FLONA is in the northeast of the state, in the Campos de Cima da Serra region, in Rincão dos Kröeff, in the Municipality of São Francisco de Paula, between coordinates 29°23' and 29°27'S and 50°23' and 50°25'W, in the State of Rio Grande do Sul, with an altitude of 930 m (Ribeiro et al. 2007).

The Serra Gaúcha is one of the wettest regions of the state, with rainfall exceeding 2000 mm and an average annual temperature of approximately 14.5°C. According to the Köppen classification, the climate is Cfb, subtropical humid (Alvares et al. 2013). The total area is of 1606.69 hectares and is located in the transition zone between the Dense Ombrophylous Forest and the Mixed Ombrophylous Forest, of which 901.9 ha are native forest, covering about 56% of the unit's total area, in which there are also reforestations from *Araucaria angustifolia* (Bertol.) Kuntze, *Eucalyptus* spp. and *Pinus* spp. (Kanieski 2017). According to Dobrovolski et al. (2006) the relief is predominantly undulating, with 7.1% of the total area having a slope greater than 30 degrees. The soil is of the typical Aluminic Humic Cambisol type (Streck 2002) and the average annual values of temperature and precipitation are, respectively, less than 18.5° C and 2468 mm (Moreno 1961), with a medium mesothermal climate, Cfb in the classification of

Köppen (Alvares et al. 2013), dominated by altitudes between 1000 and 1100 m in the north of the State of Rio Grande do Sul (Longhi et al. 2010).

Table 1. Location, climate and elevations where *Leocarpus fragilis* has been recorded in the Neotropics. Abbreviations follow Lado and Wrigley de Basanta (2008): AGA- Argentina. BAH- Bahamas. BZL- Brazil. CHI- Chile. COL- Colombia. COS- Costa Rica. MEX-Mexico.

Country*	Locality	Coordinates	Climate	Elevation (m)	Source*
AGA	Pq. Nac. Tierra del Fuego, Ushuaia, La Roca.	54°49'29"S 68°33'52"W	ET	~	1
	Prov. de Santa Cruz, El Calafate, Pq. Nac. Los Glaciares	50°29'12"S 73°02'26"W	BWk	~200	1
	Prov. de Santa Cruz, Lago Argentino, El Chaltén, Salto del Anillo.	49°19'47.6"S	BW	471	3
		72°53.1'63"W			3
	Prov. de Neuquen, Lacar, San Martín de los Andes, Pq Nac. Lanín.	40°08'35"S	Cfa	168	1
		71°37'21"W			
	Prov. de Río Negro, San Carlos de Bariloche, Pq. e National Reserve Nahuel Huapi.	41°15'36"S	BS	~1143	1
		71°17'30"W			
	Prov. de Chubut, Río Sengue, Lago Fontana.	44°55'59.88"S	BS	975	3
		71°29'3.84" W			3
	Prov. Chubut, Río Sengue, Lago Fontana.	44°53'58.2"S	BS	975	3
		71°28' 36.0"W			3
	Prov. Chubut, Río Sengue, Lago Fontana.	44°51'20.1"S	BS	938	3
		71°39' 35.3"W			3
Prov. Chubut, Cushamen, Nat. Park Lago Puelo.	42°05'57.8"S	BS	292	3	
	71°86' 18.4"W			3	
BAH	New Providence Island, Nassau.	25° 4' 1" N 77° 19' 59" W	Aw	8	5
BZL	Mun. de Itatiaia, Rio de Janeiro.	22° 29' 29" S	Cwa	2000	2
		44° 33' 33" W			
	Not informed	9,9°S 50,913 ° W	Am	?200	10
	Mun. S. Francisco de Paula, Rio Grande do Sul, FLONA de São Francisco de Paula, Brazil	29°25'36,58" S 50°23'09,50" W	Cfb	980	8;12
RPPN Rio das Furnas, Alfredo Wagner,,Santa Catarina, Brazil	27°40'53,61" S	Cfb	916	12	
	49°10'10,70" W				
CHI	Prov. Magallanes-Antártica, mun. Punta Arenas	53°09'17" S	Cfc	~75	10
		70°54'40" W			
Araucania Region, Malleco, Los Arenales.	38°25'37"S	Csb	1548	10	
	71°26'13"W				
CLM	Tequendama	4°34'29.5" N 74°17'36.2" W	Cfb, Am	~ 2500	4

COS	Prov. de San Jose.	10°57'06" N 85°08'09" W	Am	2300-3820	11
MEX	Prov. de Sonora	19°06'43" N 96°38'07" W	BSh	~50	7
	Prov. Chihuahua	28°38'07" N 106°05'20" W	BSk	~2100	7
	State of Mexico	23°38'4.2" N 102°33.167' W	Cwb	~2600	7
	State of Hidalgo	19°52'0" N, 98°29'0" W	BSh	~2400	7
	Prov. de Jalisco	17°55'53 N 91°28'45.98" W	Csa	~1800	7
	Prov. Nuevo Leon	30° 49' - 23° 11' N	BSh	~400	7
	State of Queretaro	20°16'04" N 100°16'05' W	Cwb	~2200	7;9
	Prov. de Tlaxcala	19°19'8.6" N 98°11.989' W	Cwb	~2300	7
	State of Veracruz de Ignacio de la Llave	18° 42'56" N 95° 58'20" W	Aw, Am	~300	6;7
	State of Veracruz de Ignacio de la Llave, Mun. Xico	19° 22' 19 ° 33' N 96° 54' - 97° 09' W	ET	700 – 4200	6

*Source: 1. Wrigley de Basanta *et al.* 2010; 2. Pazschke 1896; 3. CSIC-Real Jardín Botánico-Colección de Hongos (MA-Fungi); 4. Léveillé 1863; 5. United States National Fungus Collections (BPI); 6. Villarreal 1983; 7. Lizárraga *et al.* 2008; 8. Veleza *et al.* 2005; 9. Tapia *et al.* 2008; 10. GBIF. 11. Rojas and Stephenson 2008; 12. This work.

After almost two decades, in January 2021, a new collection was obtained at São Francisco de Paula FLONA by one of the authors of the present work (JRPV). The specimen, described below, presents the typical characteristics of the species and was deposited at the Bruno Edgar Irgang Herbarium (HBEI0069, HBEI0070), at the Universidade Federal do Pampa, São Gabriel campus (Tables 1 and 2).

Leocarpus fragilis (Dickson) Rostafinski, Sluzowce Monogr. 132. 1874 (Fig. 3)

Sporangia short-pedicellate to almost sessile, densely clustered, about 2-4 mm in total height. Sporotheca subglobose to ellipsoid, 0.5-1.5 mm diam. Peridium glossy, cartilaginous, consisting of three layers, the outer reddish-brown to ochre-yellowish, the median white, calcareous and the innermost membranous, colorless, with dehiscence by lobes, persisting at the base. Hypothallus well-developed, ochraceous, common to several sporangia. Stalk flattened, orange to ochre. Capillitium abundant, consisting of a network of hyaline filaments, thin and large yellow nodules filled with calcium granules. Pseudocolumella absent. Spore print brown to blackish-brown. Spores brown under transmitted light, lighter on one hemisphere, verrucous, 12-18 µm diam.

Material examined: BRASIL. RIO GRANDE DO SUL: Municipality of Campos de Cima da Serra, Floresta Nacional São Francisco de Paula, on decomposing trunk and leaves of *Araucaria angustifolia* (Bertol.) Kuntze, JRPVelloso1208, JRPVelloso1209.

Table 2. Ecological groups based on substrate associated with the occurrences of *Leocarpus* in Neotropical countries. Abbreviations follow Lado and Wrigley de Basanta (2008): AGA- Argentina. BAH- Bahamas. BZL- Brazil. CHI- Chile. COL- Colombia. COS- Costa Rica. MEX-Mexico

Group	Country	Locality	Substrate /Source*
Lignicolous	AGA	Tierra del Fuego; Chubut.	<i>Nothofagus pumilio</i> ^{1;2}
		Santa Cruz.	<i>Nothofagus alpina</i> ²
		Neuquén; Rio Negro.	<i>Nothofagus betuloides</i> ²
	BZL	Chubut.	Wood not identified
		Itatiaia, Rio de Janeiro.	Wood not identified ^{3;4;5}
		São Francisco de Paula, Rio Grande do Sul.	Dead trunk, not identified ¹³
CHI	Malleco, Araucania.	<i>Nothofagus pumilio</i> ⁶	
COS	San Jose.	Trunk and branchlets, <i>Quercus costaricensis</i> ⁷	
Foliicolous	MEX	Veracruz.	Wood in decomposition, not identified and branches of <i>Pinus</i> sp. ⁸
		Sonora.	Wood not identified ⁹
		Veracruz; Sonora.	Leaf litter ⁸ ; leaves of <i>Quercus</i> sp. ⁹
	COS	San Jose.	Leaf litter in soil ⁷
	BZL	São Francisco de Paula, Rio Grande do Sul.	Dead leaves of <i>Araucaria angustifolia</i> (Bertol.) Kuntze ¹³
	Herbicolous	BZL	Alfredo Wagner, Santa Catarina.
Corticicolous	NI	Not informed	Live trunks ¹⁰
Muscicolous	COL	Tequendama.	A moss not identified ¹¹
	MEX	Sonora.	A moss not identified ⁹
Lichenicolous	MEX	Veracruz.	Lichen <i>Peltigera</i> sp. ⁸
Myceticolous	MEX	Guerrero.	Fungi <i>Daedalea</i> sp. ¹²

*Source: 1. Crespo and Lugo 2003; 2. Wrigley de Basanta et al. 2010; 3. Pазschke 1896; 4. Friederichsen 1973; 5. Maia et al. 2015; 6. CSIC-Real Jardín Botánico-Colección de Hongos (MA-Fungi); 7. Rojas et al. 2018; 8. Villarreal 1983; 9. Lizárraga et al. 2008; 10. Farr 1976; 11. L veillé 1863; 12. S nchez-Cordero D vila 2020. 13. This work.

In July 2020, sporocarps of *L. fragilis* were found in the State of Santa Catarina, also located in southern Brazil, approximately 230 km away in a straight line from the S o Francisco de Paula FLONA, in Rio Grande do Sul (Fig. 1). Covering only 96400 km², the state has an extensive coastal region, with a rich marine biodiversity, mangroves, sandbanks, and forested areas of the Serra do Mar, where the dense rainforest and the subtropical humid climate of the Cfa and Cwa type of K ppen predominate (Alvares et al. 2013). In addition to the vegetation of the coastal region, areas with dense rainforest, mixed rainforest, seasonal deciduous forest, and highland grasslands are found in other regions of the state (Northeast, South, Midwest, West, Itaja  Valley, North Plateau and Plateau Serrano).

The State of Santa Catarina has 76 Private Natural Heritage Reserves (RPPN), which together preserve approximately 30000 ha (ICMBio 2023), corresponding to about 70% of the existing phytogeographic formations. The species was found in the RPPN Rio das Furnas (27 40'53.61" S and -49 10'10.70"W), located in the Municipality of Alfredo Wagner, within the Alto Vale do Itaja  region, between Serra da Boa Vista (to the east) and Serra Geral (to the west), in the mountain plateau region,

with altitudes in the range of 750-900 m. Serra Geral, Serra da Boa Vista and Serra dos Faxinais stand out in the relief and the municipality's climate fits into the Köppen Cfb type, with an average annual temperature of 16.3°C and average annual rainfall of 1911 mm. The relative humidity of the air is always high, around 83% in the driest month (September). In winter, frost, hail and, in some years, snow are registered sometimes. In the RPPN, several indicator species of Dense and Mixed Ombrophylous Forest are found, such as *Rapanea ferruginea* (Ruiz & Pav.) Mez., *Cupania vernalis* Cambess, *Piptocarpha angustifolia* Dusén ex Malme and *Alchornea triplinervia* (Spreng.) Müll. Arg. (CONAMA 1994).

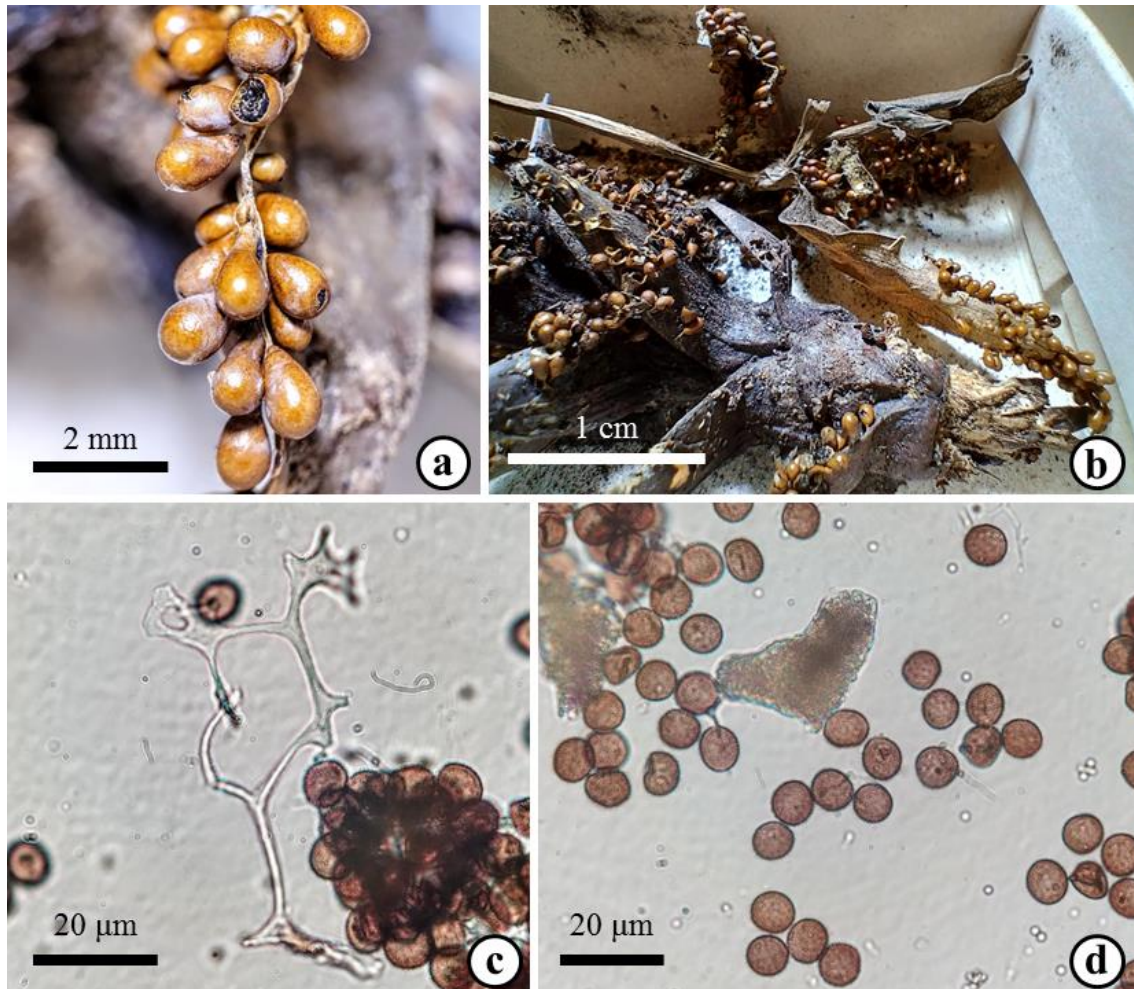


Figure 3. *Leocarpus fragilis*. **a.** Sporangia. **b.** Sporangia with substrate in detail. **c.** Capillitium. **d.** Spores and calcium nodes.

Inserted at the top of the first canyon of the Itajaí Basin, in Serra da Boa Vista, in a place of difficult access, the RPPN has as main objective to protect the macro and microorganisms that live in the 53.5 ha covered by transitional vegetation of an ombrophylous forest of lowlands, mixed *Araucaria* forest and highland grasslands. The sporocarps of *L. fragilis* were found by one of the owners, Dr. Maria Alice Neves, specialist in fungi, in the coldest and driest period of the year, sporulating on live herbaceous plants and represent the first record of occurrence of the species in the State of Santa Catarina (Fig. 4).



Figure 4. *Leocarpus fragilis* specimen sporulating on alive plant in the RPPN Rio das Furnas, Santa Catarina, southern Brazil. Photo: Maria Alice Neves, July 2020.

Surveys carried out in the literature and in national and foreign herbaria collections, complemented by field collections, showed that, in Brazil, over a period of 129 years, *L. fragilis* was found only in the southeast (Rio de Janeiro, 1 record) and southern (Santa Catarina, 1 record; Rio Grande do Sul, 2 records) regions. The geographic coordinates of the specimen BPI 722654, identified as *L. fragilis*, which belongs to the U.S. National Fungus Collections, indicate that it was collected in the central region of the country, but they probably do not correspond to the place of origin and the information must have been added later, procedure adopted for specimens whose collection location was not specified on the label.

In Chile, the occurrence of *Leocarpus* has been known since the beginning of the 20th century, when Sturgis (1916) presented a list of 47 species of myxomycetes collected by Roland Thaxter in Punta Arenas, Magallanes region in Southern South America, between 1905-1906, with specimens deposited in the FH Herbarium, University of Harvard. Located on the eastern slope of the Andes Mountain range, in southern Chile, the Magallanes region is the southernmost and most extensive in the country, characterized by a low biodiversity caused by the rigorous climate, with very low temperatures and strong winds during all seasons of the year (Pérez 2018).

Like Brazil, occurrence records of *Leocarpus* in Chile are scarce and carried out with long intervals, in forested areas and places with a cold climate and altitudes above 800 m. In addition to the three specimens, collected on unidentified substrate at the beginning of the last century, two specimens were located in the MA-Fungi herbarium, collected by Carlos Lado, Arturo Estrada-Torres and Diana

Wrigley de Basanta in Malleco, Lonquimay (38°25'37" S and 71°26'13" W), at an altitude of 1532.5± 7 m, with an average annual temperature of 8.4°C and rainfall of 1851 mm (Table 1).

The area studied by Lado et al. (2013) is in the central part of Chile, where a Mediterranean climate dominates, with dry summers and rainy winters and the specimens were found in the Araucanía Region in March 2006, in a mixed forest, sporulating on wood in decomposition of *Nothofagus pumilio* (Poepp. & Endl.) Krasser (Nothofagaceae, Fagales). In May 2014, Bernardo S. Silva (iNaturalist 2024) recorded the presence of *L. fragilis* in Arauco (37°33'00.76" S, 73°28'59.61" W), in the province of Biobio, where the altitude varies between 800–1300 m, included in the sites explored by Lado et al. (2013) but without any collection of the species.

Argentina gathers the largest number of occurrence records of *L. fragilis* in South America (Fig. 2). A specimen of *Leocarpus* found in Buenos Aires on leaves, stems, live and dead bark of plants, in humid places was identified by Spegazzini (1921) as *L. melaleucus* Montag. described by Montagne (1855), with type collected in Cayenne (4°56'5" N, 52°19'49" W), in French Guiana, on living leaves of *Musa paradisiaca* L. In the catalog where he listed the 25 genera and out of 67 known species for the Argentine myxobiota until the first half of the 20th century, Digilio (1946) included *Leocarpus*, based on the citation of *L. melaleucus*, but this is considered invalid by Lado (2005-2024).

The publications by Arambarri (1975) and Deschamps (1976) refer the occurrence of *Leocarpus* to Tierra del Fuego, based on specimens collected in 1972 by I. Gamundi and A. M. Arambarri, on trunks and leaf litter, in Ushuaia, Lapataia. Between 2005-2011, specimens were again found in surveys carried out in the provinces of Chubut, Neuquén, Rio Negro, Santa Cruz, and Tierra del Fuego (Tables 1 and 2).

Wrigley de Basanta et al. (2010) explored areas of subantarctic or Andean-Patagonian vegetation, distributed in a south-north gradient (39° to 55°S and 67° to 73°W) of summer temperatures (9°C-18°C) and *L. fragilis* was found only in four of the 50 sites explored, established in National Parks, both in lowland forests (ca. 12 m, 9°C, Tierra del Fuego; ca 200 m, 13°C, Santa Cruz), as well as altitude (680–1430 m, 18°C, Neuquén), sporulating on the wood of three tree species native to the Andean Patagonian biomes of the extreme south of Argentina and Chile: *Nothofagus pumilio* (Poepp. & Endl.) Krasser (MA-Fungi 78813;78814), *N. betuloides* (Mirb.) Oerst. (MA-Fungi 78810; 78811; 78812) and *N. alpina* Popp. & Endl. (MA-Fungi 78815).

Ecuador was not included in the distribution area of *Leocarpus* in the Flora Neotropica monograph published by Farr (1976), as well as in the literature review carried out by Lado and Wrigley de Basanta (2008). The occurrence found in GBIF that indicates the presence of *L. fragilis* in the myxobiota of Ecuador is based on human observation (Lado 2018); however, in the paper indicated as a source (Stephenson et al. 2008) the authors commented that "...in fairly well studied tropical regions (e.g. Central America, **Ecuador**, Tanzania and Taiwan), *L. fragilis* **has not yet been found** (emphasis added), except for a single record from the paramo region of Costa Rica". Literature surveys and herbarium collections did not confirm the presence of *L. fragilis* in the Ecuadorian myxobiota.

Costa Rica was the country where the first record of occurrence of *Leocarpus* in Central America was obtained, carried out at the beginning of the 21st century by Rojas and Stephenson (2007), based on a specimen collected from decomposing wood (UARKM 30753), in San Jose. The research, carried out in an altitude forest (9°56'39" N 83°59'56" W), revealed a myxobiota different from that found in lowland tropical forests, being taxonomically and ecologically similar to those of temperate forests. The sporocarps were obtained directly in the field, 30 cm above the ground, in a woody substrate with a diameter of 9.50

cm, and the species was classified as occasional in the myxobiota of Cerro Bellavista (3700 m; climate type Af). In the same article, Rojas and Stephenson (2007) cited another specimen, found by M. Schnittler and C. Rojas in the Cerro Chirripó paramo (3820 m; climate Af), also in the province of San Jose, Talamanca region, and suggest that the species could be restricted to areas located at high elevations (Tables 1 and 2).

In the list of myxomycete species that occur in Costa Rica, based on an examination of herbarium specimens and a review of the literature, Rojas et al. (2018) reported the occurrence of *L. fragilis* in only one of the seven Provinces of the country (San Jose), sporulating in high-altitude locations, on bark and trunks of dead trees, twigs and soil litter, in low-mountain and montane humid forest environments and humid subalpine paramos (Fig. 1, Tables 1 and 2).

The Bahamas archipelago is located in the Caribbean Bioregion and comprises more than 700 islands, most of which are uninhabited. In the analysis of the world distribution of *L. fragilis* carried out by Stephenson et al. (2008), as well as in the review carried out by Lado and Wrigley de Basanta (2008), no records of occurrence of the species were found for the archipelago. Farr (1976) cited Florida as an area of occurrence for *Leocarpus* in the Neotropics and, considering that the distance between Nassau, on New Providence Island, and Miami, in that North American state, corresponds to about 300 km, it is possible that, dispersed by the winds, spores of *L. fragilis* can reach the islands of the archipelago. The climate is tropical, with types Aw (savannah), Am (monsoons) and Af (forest), with a predominance of the former; the annual precipitation is in the range of 1100 – 1500 mm and the temperature shows little variation in the different seasons of the year, with minimums in the range of 17-24°C and average maximums between 25-32°C. Nassau, the country's capital, is located on the island of New Providence, with an average altitude of 34 m, Aw climate, average temperature ranging from 17-25°C and maximums reaching between 25.6-32°C.

The research carried out in the present work revealed the existence of the specimen BPI 813034 (USDA-ARS US National Fungus Collection 2024) whose coordinates indicates its occurrence in Nassau (25°4'1" N, 77°19'59" W). It is worth highlighting the low altitude of the location where the collection was carried out, which differs from the records obtained for Brazil, Chile, Colombia, and Costa Rica, always above 800 m (Table 1). The known distribution area for *L. fragilis* in the Mesoamerican and Caribbean Bioregions only included Colombia, Costa Rica, and Mexico (Rojas et al. 2018). The inclusion of the Bahamas enhances knowledge of the range of *Leocarpus* in the Caribbean and Neotropics.

Mexico has the highest number of records of *L. fragilis* in the Neotropics (Fig. 2). Villarreal (1983) cited its occurrence on decaying wood, fallen branches of *Pinus* and lichens of the genus *Peltigera*, in Veracruz, located in the southeast of the country. In the State of Queretaro, specimens of *L. fragilis* were collected in oak forest, on decomposing wood in the Municipality of Arealco (2281 m alt.) and in Cerro El Zemorano, Municipality of Colón, in the pine forest litter (3170 m alt), directly in the field (Tapia et al 2008). Lizárraga et al (2008) provided the distribution of the species in the Mexican territory, citing its occurrence in the provinces of Sonora, on decomposing wood, dead leaves of *Quercus* sp. and mosses, in Chihuahua, Estado de Mexico, Hidalgo, Jalisco, Nuevo Leon, Queretaro, Tlaxcala and Veracruz.

The survey carried out in the literature and herbarium collections showed that, in addition to Brazil, *L. fragilis* occurs in six more Neotropical countries, distributed from the southern part of North America (Mexico) to the south of Chile, in South America, apparently with a preference for high altitude sites and milder climate (Fig. 1; Table 1). In the occurrences for the species and its synonyms available in GBIF, it

was observed that the oldest collections were carried out in South America, in the late 19th and early 20th centuries (Colombia, 1862; Brazil 1894; Chile, 1906) and in North America (Mexico, 1904), while in Central America it was only found in 2003, at the beginning of the 21st century, in Costa Rica (Fig. 5). The records obtained for the seven countries showed that *L. fragilis* can develop and sporulate in different substrates, with a predominance of dead trunks and branches (lignicolous), and can also be classified as foliicolous, corticolous, herbicolous, lichenicolous, myceticolous and muscicolous (Table 2). In other biogeographical regions, the species also has records sporulating on herbivore excrement (fimicolous), as recorded in Sweden on cow dung (Eliasson and Lundqvist 1979) and succulent plants, developing on cacti, as reported by Moreno et al. (2018), who collected sporocarps on *Opuntia ficus-indica* (L.) Mill. cladodes in Badajoz-Azuaga, Spain.

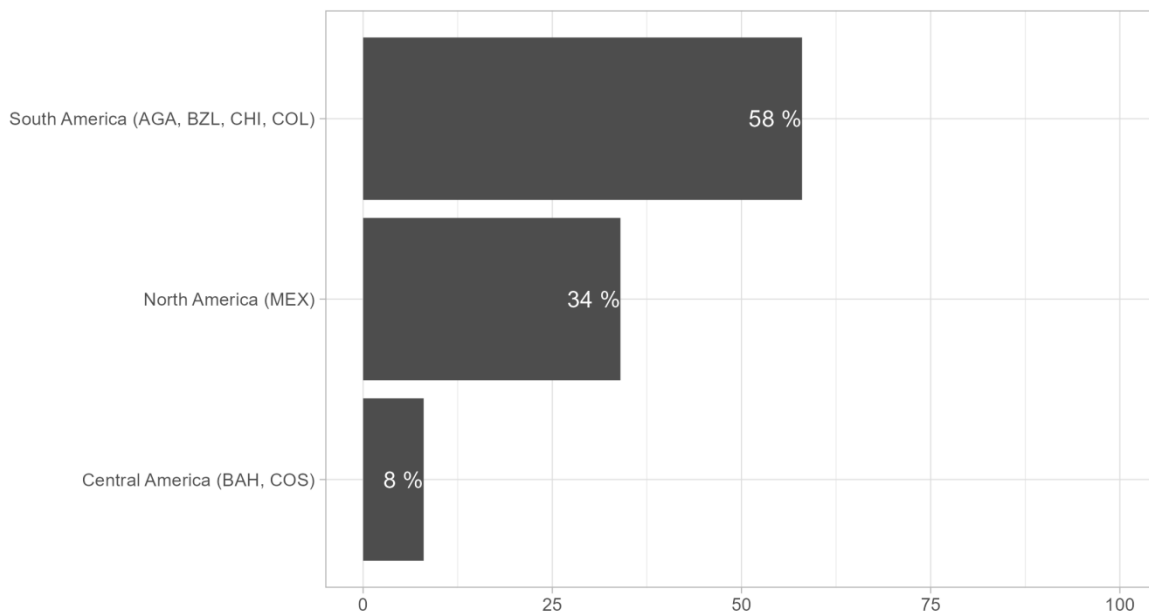


Figure 5. *Leocarpus fragilis* registered in the Neotropics documented in Herbaria and in the literature (1863- 2024). AGA = Argentina. BAH = Bahamas. BZL = Brazil. CHI = Chile. COL = Colombia. COS = Costa Rica. MEX = Mexico.

According to Stephenson et al. (2008), the geographic distribution of *L. fragilis* would be conditioned more by the climate than by the availability of microhabitats or other environmental factors, and the species would be absent in extremely arid regions and in the humid tropics. In Brazil, it has so far been found in the Atlantic Forest domain, in fragments of Atlantic Forest located at altitudes above 600 m, in the Southeast and South of the country, under humid subtropical climates of types Cwa (dry winter, hot summer) and Cfb (oceanic, without dry season). The first, typical of southeastern Brazil, covers 2.5% of the national territory, while the second, observed in 2.6%, covers a good part of the territory of the States of Rio Grande do Sul and Santa Catarina, the coldest regions of all the national territory (Alvarez et al. 2013).

With the data obtained in the present work, it can be concluded that, despite being very common in the USA and in several countries in Europe and Asia, *L. fragilis* is a rare species in the Neotropics, with

about 50 records between 1863-2024, carried out in only seven countries, most of the time with occurrences located at high altitudes and mild climate.

The analysis of specimens collected in the field and the consultation of national and foreign herbaria confirmed that, although rare, the genus *Leocarpus* and *L. fragilis*, its only species, are part of the Brazilian myxobiota, sporulating on decomposing trunks and leaf litter branches, rarely on live herbs. The records obtained so far indicate its presence only in the Southeast and South regions of the country, in the Atlantic Forest domain, in places with altitudes above 900 m, high rainfall and mild temperatures in the different seasons of the year.

There are few collections of myxomycetes in Brazilian herbaria, not differing much from the panorama of countries located in the Neotropics. The difficulties found in this research to locate specimens, combined with the current reality of official institutions no longer accepting the deposit of myxomycete specimens in collections, such as the URM, one of the largest mycological herbaria in Latin America, point to the need for support for the maintenance of myxomycete collections that allow studies based on well-preserved specimens, as well as the documentation of myxobiota inventories and ecological studies.

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