New records of myxomycetes for the state of Veracruz from Cofre de Perote National Park

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Received: 19 August 2021 Accepted for publication: 5 September 2021 Published: 20 September 2021 Corresponding editor: Steven L. Stephenson

Abstract: Most of the species of myxomycetes from Mexico are well documented, but their patchy geographical and temporal distribution responds to the individual efforts carried out in different areas of the territory over time. As such, even for well-studied areas, new projects can substantially increase biodiversity-based information. The present study constitutes an update of the myxomycete catalog of the state of Veracruz, carried out from an intensive study in a section of *Abies religiosa* at the Cofre de Perote National Park. The methodology consisted in field collections, complemented with a laboratory isolation process using diverse substrates from different locations. The study was carried out in two years (2018-2019) and in two seasons (dry and rainy). A total of 30 taxa were identified, out of which, 21 species were not previously known for the state of Veracruz, increasing the number of myxomycetes known in such state to 168 species, making it one of the most diverse states in Mexico, with approximately 45% of the known species in the country.

Keywords: fir forest, microbial diversity, myxogastrids, slime molds

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Introduction

Myxomycetes are amoeboid organisms with different stages in their life cycle that facilitate dispersal and colonization of new environments (Schnittler et al. 2017). There are about 1000 recognized species (Lado 2005-2020), from which, 369 have been reported in Mexico (A. Estrada-Torres, pers. comm. 2020). The states of Tlaxcala and Veracruz are prominently rich in species, but it is also in these states where efforts have been concentrated (see Hernández-Cuevas et al. 1991; Rodríguez-Palma and Estrada-Torres 1996; Hernández-Cuevas and Estrada-Torres 1997, Rodríguez-Palma 1998; Mosquera et al. 2000; Rodríguez-Palma et al. 2002; Estrada-Torres et al. 2003; Mosquera et al. 2003; Rodríguez-Palma et al. 2010). In Veracruz, the highest species richness is associated with montane cloud forests (Braun and Keller 1986; Villarreal 1990; Welden and Guzmán 1978) and tropical rain forests (Welden and Guzmán 1978; Villarreal, 1990; Lado et al. 2003). Conifer-dominated forests, located in

different life zones are important habitats for myxomycetes in Veracruz as well (Guzmán and Villarreal 1984; Rojas et al. 2010, 2011; Villarreal 1983, 1985, 1990).

Despite the latter, in Veracruz, forests dominated by conifers have not been studied with the same intensity as broadleaf systems and it is likely that the diversity of myxomycetes for the former type has been underestimated. Due to the human effect on conifers in some areas of the state (Pineda-López et al. 2017), such as the threats on the *Abies religiosa* (Kunth) Schltdl. and Cham. populations in the Cofre de Perote National Park (Aguilar Sánchez and Ortiz Escamilla 2011; Arriola-Padilla et al. 2015), it is important to perform the biological documentation of these environments. Such relevant task, which is also embodied in the objective 15 of the Sustainable Development Goals (https://sdgs.un.org/goals), has the potential of increasing governmental efforts for the conservation of biological resources and ecosystem services as well. For modelling of myxomycetes, and microbial species distribution, higher density of presence/absence data of morphological species in association with particular habitats also allows for a higher resolution of analyses (see Stephenson et al. 2020a)

Given the restricted character (i.e. intense effort but in a short and limited time) of the most recent myxomycete surveys in conifer areas of Veracruz, but with the support a documentation of previous studies in the Cofre de Perote National Park area (e.g. Villarreal 1983; Guzmán and Villarreal 1984; Villarreal 1985; Rojas et al. 2010, 2011), this area is an excellent reference for research intended to document the completeness of previous efforts. For myxomycetes, this type of integrated analyses has recently revealed that even in intensely studied areas of the world, classical surveys that are designed to document assemblages during non-studied seasons or substrates tend to reveal important associations (Stephenson et al. 2020a, b). These are relevant contributions that allow researchers adjust survey techniques and temporal resolutions according with research objectives.

In this sense, the 39 species of myxomycetes previously recorded in the Cofre de Perote National Park (Villarreal 1983; Guzmán and Villarreal 1984; Villarreal 1985, 1990; Rojas et al. 2010, 2011) serve as a basis for an effort/results comparison since a total of 171 species of myxomycetes have been recorded in La Malinche National Park (see Rodríguez-Palma et al. 2005), an area with equivalent habitats. These values suggest that the former has been understudied, which likely has had an impact on the number of species known for the State of Veracruz. As such, the main objectives of this study have been the recording of myxomycetes in a section of the *Abies* forest in Cofre de Perote National Park using a more extended (temporally and geographically) sampling methodology than previous efforts to 1) assess the impact of a different recording design on data acquisition and 2) update the list of myxomycetes for the state of Veracruz.

Materials and methods

This study was carried out during 2018 and 2019 in a forest section dominated by *Abies religiosa* at the Cofre de Perote National Park in Veracruz, Mexico (Figure 1). The general climate in this area is subhumid temperate, with an average temperature between 10 and 12 °C and an annual precipitation between 1200 and 1500 mm. Open paramo-like zones and forest patches dominated by *Pinus hartwegii* Lindl are also present in the area (Narave-Flores 1985).

Myxomycetes were recorded both directly in the field and in laboratory conditions. For the first approach, field work was conducted in 12 surveys within a period of 11 months between August 2018 and June 2019, from which six surveys took place in the dry season and six in the rainy season. All field collecting was carried out in an elevational range between 3200 and 3600 m asl. During each visit, sporocarps of myxomycetes were surveyed on substrates such as coarse woody debris and decomposing twigs or leaves on the ground using the methods of Wrigley de Basanta and Estrada-Torres (2017). Sporocarps were collected, glued to pasteboard boxes, dried out in natural conditions, and set aside for posterior identification.

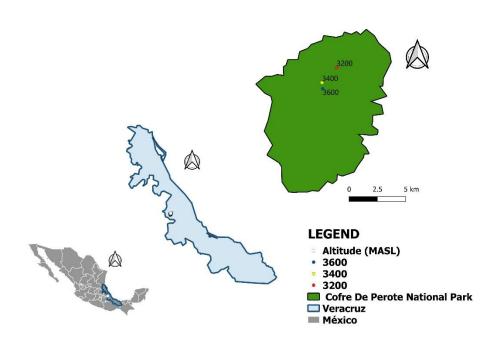


Figure 1. General location of the study sites within the Cofre de Perote National Park (green), the state of Veracruz (light blue) and Mexico (gray).

For laboratory isolation, a series of ground leaves, bark of living trees, twigs and decayed wood, all from *Abies religiosa*, were collected and taken to the Laboratorio de Organismos Simbióticos at the Instituto de Biotecnología y Ecología Aplicada (INBIOTECA) of the Universidad Veracruzana in Xalapa, Veracruz. Substrate samples were used to set up 576 moist chamber cultures, as described by Gilbert and Martin (1933), and were checked weekly for myxomycetes growth and presence of sporocarps, this for a period of four months. During the complete period of myxomycete isolation, the temperature of the laboratory oscillated around 25°C. Myxomycete sporocarps growing in the moist chambers were extracted and treated in similar manner to field collections, for posterior identification.

All collected specimens of myxomycetes, from both the field and the laboratory methods, were identified using appropriate monographs and literature (e.g. Martin and Alexopoulos 1969; Pando 1999; Poulain et al. 2011), as well as online platforms (https://www.discoverlife.org, https://www.gbif.org and https://eumycetozoa.com) for verification of nomenclatural status and reported geographical extent.

Microscopical features were examined using both a stereoscope (Eakins, SZM7045B) and a compound light microscope (Iroscope MG-11TF). A series of photographs were taken using a Canon EOS Rebel T6 camera. Upon identification, all specimens were catalogued and curated to deposit them at the mycological collection of the Instituto de Biotecnología y Ecología Aplicada (INBIOTECA) in Xalapa, Veracruz.

Results

A total of 30 species were identified, out of which 21 represented new records for the state of Veracruz (see Table 1). Of the latter, 16 species were recorded only in the field, three were observed only in moist chamber cultures (7.5 % of productivity in 576 established moist chambers) and two were recorded using both methods. Similarly, 11 of those new records were observed only during the dry season, three only during the rainy season and seven in both. Only those species considered to be new records are described

Descriptions

Arcyria ferruginea Saut., Flora, Regensburg 24: 316 (1841). Figure 2A

Aggregated sporocarps. Stipe 0.2-0.6 mm long; yellowish brown to black; extended calyculus; globose, pyriform or cylindric sporotheca, 1-2 mm long x 0.5-1 mm wide, ferruginous to reddish to brownish orange; capillitium with rings, half rings, spines and reticulations, pale yellow on transmitted light; smooth spores, 9-11 μ m in diameter, pale yellow under the microscope.

Habitat. On logs directly in the field, at 3200 m asl (19°32'02.7"; 97°08'50.4") and 3400 m asl (19°31'17.1"; 97°09'34.5").

Studied specimens. Mexico. Veracruz. Perote municipality. Parque Nacional Cofre de Perote, August 14, 2018, Salazar-Hernández 1; April 5, 2019, Salazar-Hernández 2.

Taxonomic comments: the ornamented and thick capillitium, large spores and orange-like color are all characteristic of this species of *Arcyria* (Farr 1976). The studied specimens showed ferruginous sporocarps and the capillitium easily separated from the calyculus.

The species has been previously recorded on *Pinus, Quercus* and *Nothofagus* (Keller and Braun 1977; Lado and Moreno 1980; Castillo et al. 2009; Wrigley de Basanta et al. 2010; Lado et al. 2014; Yatsiuk et al. 2017).

Badhamia utricularis (Bull.) Berk., Proc. Linn. Soc. London 2: 199 (1852). Figure 2B

Aggregated sporocarps, in bunches; long stipes, thin, membranous, pale yellow; globose to pyriform sporotheca, 0.7-1.0 mm in diameter; changing color from pale orange when young to cinereous bluish iridescent when mature; peridium simple, hyaline, ornamented with fine lime veins resembling stretch marks; capillitium thin, badhamioid, white; clustered spores, dark under transmitted light, in groups of 7-10, globose, 9-14 μ m in diameter, uniformly spiny; yellow to orange plasmodium.

Habitat. On logs directly in the field, at 3400 m asl (19°31'17.1"; 97°09'34.5").

Studied specimen. Mexico. Veracruz. Perote municipality. Parque Nacional Cofre de Perote, June 7, 2019, Salazar-Hernández 3.

Taxonomic comments: the sporocarps of this species have long, branched stipes, often hanging from an upper surface, in which case the sporothecas are located below. The iridescent peridium is also characteristic of this species. Spores have been documented to disintegrate easily (Farr 1976). The studied specimen showed all previous characters. During the maturation of sporocarps, we observed the presence of a fine white reticulum over the peridium that disappeared at the end.

The species has been recorded on *Betula, Stereum, Pinus, Fagus, Quercus, Acer, Yucca, Larix, Abies, Acacia, Jumellia* and *Fraxinus* (Lado and Moreno 1980; Ing 1982; Portela and Lado 1989; Ing and Ivancevic 2000; Oran and Ergül 2004; Stojanowska and Panek 2004; Oltra 2006; Castillo et al. 2009; Estrada-Torres et al. 2009; Ergül and Akgül 2011; Lawrynowicz et al. 2011; Lado et al. 2014; Thomas 2016).

Comatricha laxa Rostaf., Śluzowce monogr. (Paryz): 201 (1875) [1874]. Figure 2C

Aggregated sporocarps, 0.9-1.5 mm tall; thin, cylindrical stipes, with broader base, reaching half or more of the total height, shiny black, forming a columella that reaches almost the top of the sporotheca; subglobose or ovoid sporotheca; peridium fugacious; lax capillitium with large loops, reddish brown, with many free and short tips; globose spores, 7-11 μ m in diameter; finely verrucose.

Habitat. On branches at the ground level, at 3200 m asl (19°32'02.7"; 97°08'50.4").

Studied specimen. Mexico. Veracruz. Perote municipality. Parque Nacional Cofre de Perote, September 7, 2018, Salazar-Hernández 4.

Taxonomic comments: this species has ovoid sporocarps, red to reddish brown in color, and an open network with primary branching in a horizontal manner (Farr 1976). The studied specimen showed the same characteristics.

The species has been recorded on *Quercus, Pinus, Yucca, Echynocactus, Opuntia, Ferocactus, Neobuxbaumia, Acacia, Prosopis, Nothofagus, Atriplex, Ephedra, Schinus, Larrea, Montea* and *Chuquiraga* (Wrigley de Basanta 2004; Demirel et al. 2006; Castillo et al. 2009; Estrada-Torres et al. 2009; Wrigley de Basanta, 2010; Lado et al. 2011; Yatsiuk et al. 2017).

Craterium minutum (Leers) Fr., Syst. mycol. (Lundae) 3(1): 151 (1829). Figure 2D

Dispersed sporocarps; grooved stipe, orange to brown in color; cup-shaped sporotheca, showing circular dehiscence that creates an operculum; double peridium, cartilaginous external layer, with lime or not in the internal layer; capillitium with irregular lime nodes, white or pale yellow, clustering to form a pseudocolumella; pale brown spores, $7.5-9 \mu m$ in diameter, finely spinose.

Habitat. On branches and Abies leaves on the ground, at 3400 m asl (19°31'17.1"; 97°09'34.5").

Studied specimens. Mexico. Veracruz. Perote municipality. Parque Nacional Cofre de Perote, March 21, 2019, Salazar-Hernández 5, 6; April 5, 2019, Salazar-Hernández 7, 8, 9.

Taxonomic comments: this species has stiped sporocarps with an ochraceous yellow, orange, or brown color. Also, the deep cup-shaped sporotheca with operculate dehiscense and capillitium with large lime nodes clustering to form a pseudocollumela are characteristic (Farr, 1976). Reported spore size ranges between 8-10 μ m in diameter, and the material studied herein showed slightly smaller spores.

The species has been recorded on *Rubus, Fraxinus, Brachypodium, Olea, Quercus, Viburnum, Populus, Galium, Eucalyptus, Betula* and *Cistus* (Oltra 2004; Castillo et al. 2009; Thomas 2016).

Cribraria lepida Meyl., Bull. Soc. Vaud. Sci. Nat. 56: 326 (1927). Figure 2E

Dispersed sporocarps; with long stipe, reddish-brown or orange, sometimes translucent, turning dark violet close to the top; globose or prolate sporotheca, violet; peridium remains as a deep cup measuring up to half the total height of the sporotheca; peridial net with open mesh, numerous, well differentiated and irregular, no nodes; violet spores, 6-8 µm diameter, finely vertucose.

Habitat. On rotten log, at 3200 m asl (19°32'02.7"; 97°08'50.4").

Studied specimens. Mexico. Veracruz. Perote municipality. Parque Nacional Cofre de Perote, March 28, 2019, Salazar-Hernández 10, 11.

Taxonomic comments: The violet color of the sporocarp, with a deep calyculus, open peridial network with irregular nodes and spores between 6-7 μ m diameter (Ramírez-Ortega et al. 2017). The examined material showed slightly larger spores, similar to the observations of Martin and Alexopoulos (1969).

The species has been recorded on Hechtia and Puya (Estrada-Torres et al. 2009; Lado et al. 2011).

Cribraria oregana H.C. Gilbert, in Peck & Gilbert, Am. J. Bot. 19: 142 (1932). Figure 2F

Solitary to aggregated sporocarps; 0.4-0.7 mm tall, with stipe measuring up to three times the height of the sporotheca; yellowish orange to brown sporotheca; peridial net thin, with nodes filled with granules measuring 2-3 μ m; polygonal spores, 8-9 μ m in diameter, reddish brown under transmitted light, slightly vertucose.

Habitat. On logs, at 3200 m asl (19°32'02.7"; 97°08'50.4") and 3600 m asl (19°30'58.7"; 97°09'32.4").

Studied specimens. Mexico. Veracruz. Perote municipality. Parque Nacional Cofre de Perote, October 26, 2018, Salazar-Hernández 12, 13; March 28, 2019, Salazar-Hernández 14, 15, 16.

Taxonomic comments: The rusted brown to hazelnut color, a calyculus measuring about half of the height of the sporotheca and dictydine granules forming thin lines on it are characteristic of this species.

The spores have been reported 6.5-8 µm diameter, with prominent but sparse warts (Yatsiuk et al. 2017). The examined material has larger spores, similarly to the observations of Martin and Alexopoulos (1969).

This species has been recorded on *Pinus* (Eliasson and Gilert 2007; Rojas et al. 2010; Yatsiuk et al. 2017).

Cribraria vulgaris Schrad., nov. gen. pl. (Lipsiae): 5 (1797). Figure 2G

Aggregated sporocarps; 0.8-2 mm tall, with a stipe measuring 2-4 times the diameter of the sporotheca; orange-brown sporotheca, 0.5-0.7 mm in diameter; calyculus without longitudinal lines of dictydine granules; peridial net pale yellow, with flat and wide nodes, sometimes angular and irregular; light brown spores, 6-7.5 μ m in diameter, finely vertucose.

Habitat. On log, at 3400 m asl (19°31′17.1″; 97°09′34.5″).

Studied specimen. Mexico. Veracruz. Perote municipality. Parque Nacional Cofre de Perote, April 5, 2019, Salazar-Hernández 17.

Taxonomic comments The flat pale nodes inserted in a yellow to light brown peridial net and the spores finely vertucose, with diameters between 5-6 μ m (Farr 1976) are distintive characters of this species. The studied material showed larger spores.

The species has been recorded on *Pinus* and *Hesperomeles* (Oltra 2004; Demirel et al. 2006; Rojas et al. 2010; Yatsiuk et al. 2017; Treviño-Zevallos and Lado Rodríguez 2020).

Diderma asteroides (Lister & G. Lister) G. Lister, Monogr. Mycetozoa, Edn 2 (London): 113 (1911). Figure 2H

Gregarious to dispersed sporocarps; sessile; globose sporotheca; peridium with three layers, the external one cartilaginous and brown in color, firmly attached to the medium layer made of calcium carbonate, the internal one membranous; with floriform dehiscence, forming stellate white figures on the substrates; with a pulvinate columella, beige; capillitium thin, dark brown except on the simple or anastomosed tips where is pale; dark brown spores, 10-11 μ m in diameter, verruculose.

Habitat. On logs, branches and *Abies* leaves on the ground, at 3200 m asl (19°32'02.7"; 97°08'50.4"), 3400 m asl (19°31'17.1"; 97°09'34.5") and 3600 m asl (19°30'58.7"; 97°09'32.4").

Studied specimens. Mexico. Veracruz. Perote municipality. Parque Nacional Cofre de Perote, October 26, 2018, Salazar-Hernández 18; March 21, 2019, Salazar-Hernández 19, 20, 21; April 5, 2019, Salazar-Hernández 22, 23, 24; June 4, 2019, Salazar-Hernández 25.

Taxonomic comments: The sessile sporocarp that sometimes has a very short stipe, the sporotheca is usually subglobose or prolate, reddish-brown or hazelnut in color, with holes or longitudinal stripes on the peridium and a typical stellate dehiscence. Nannenga-Bremekamp (1991) communicated branched

capillitium in some specimens of the species. The studied specimens match general descriptions and branching in the capillitium was not observed.

The species has been recorded on *Pinus, Fagus, Abies, Picea, Quercus, Eucalyptus, Arbutus, Betula, Puya* and *Ilex* (Schnittler and Novozhilov et al. 1998; Moreno et al. 2003; Castillo et al. 2009; Oltra and Gracia 2009; Lado et al. 2013; Amrani and Abdel-Azeem 2018).

Table 1. Species of myxomycete taxa recorded in the present study showing the previous status of the species in the state of Veracruz (R: Recorded previously, N: New record) the origin of the record (F: Field collections, M:moisture chamber, B. both), and the season (rainy (R) and/or dry (D) or both (B) when the observation was made.

Таха	Status in Veracruz	Origin	Season
Arcyria ferruginea	Ν	F	R
Badhamia utricularis	Ν	F	D
Comatricha laxa	Ν	F	R
Craterium minutum	Ν	F	D
Cribraria lepida	Ν	F	D
Cribraria oregana	Ν	F	В
Cribraria vulgaris	Ν	F	D
Diderma asteroides	Ν	F	В
Diderma umbilicatum	Ν	F	D
Didymium serpula	Ν	F	D
Hemitrichia intorta	Ν	F	D
Licea castanea	Ν	Μ	D
Licea pygmaea	Ν	М	В
Metatrichia floriformis	Ν	F	D
Mucilago crustacea	Ν	В	В
Paradiacheopsis solitaria	Ν	Μ	D
Physarum newtonii	Ν	F	D
Prototrichia metallica	Ν	F	В
Trichia decipiens	Ν	F	В
Trichia lutescens	Ν	В	В
Trichia subfusca	Ν	F	R
Arcyria cinerea	R	В	В
Arcyria incarnata	R	F	D
Arcyria pomiformis	R	F	D
Badhamia sp.	R	F	R
Calomyxa metallica	R	F	D
Comatricha nigra	R	F	В
Comatricha pulchella	R	F	В
Cribraria microcarpa	R	М	В
Dianema sp.	R	F	R

Diderma umbilicatum Pers., Syn. meth. fung. (Göttingen) 1: 165 (1801). Figure 2I

Gregarious sporocarps; 1.5 mm tall; subglobose sporothecas, umbilicate below, 0.5-1.3 mm in diameter, white or pearl gray, slightly shiny; calcareous peridium, with irregular dehiscence, leaving a cup

with a shaggy edge; subglobose prominent columella (1/2 to 3/4 the size of the sporotheca), white or pale brown; thin capillitium, with dispersed anastomosed warts, brown; globose spores, $9-12 \mu m$ in diameter, dark brown, vertuculose.

Habitat. On logs, at 3400 m asl (19°31'17.1"; 97°09'34.5").

Studied specimen. Mexico. Veracruz. Perote municipality. Parque Nacional Cofre de Perote, March 21, 2019, Salazar-Hernández 26.

Taxonomic comments: The subglobose, oblate and umbilicate sporcarps, white or gray with lime or brown without it, the stipe is short and thick, and the columella is large and reddish in color (Nannenga-Bremekamp 1991) distinguish this species. The studied material was similar to such description, except for the reddish color of the columella.

This species has been recorded on *Eucalyptus, Metasequoia, Populus, Quercus, Brachytecium, Pinus* and *Agave* (Critchfield and Demaree 1991; Ukkola et al. 2001McHugh et al. 2003; Novozhilov et al. 2003; Oltra 2004, Stojanocwzka and Panek 2004; Oltra 2006; Oran and Ergül 2015).

Didymium serpula Fr., Syst. mycol. (Lundae) 3(1): 126 (1829). Figure 2J

Flat, thin plasmodiocarp, lilaceous with iridescent tints; membranous peridium, lilaceous, covered with stellate or irregularly shaped lime crystals; capillitium thin, branched, yellowish, broader in the section connected to vesicles; vesicles of 30-50 μ m of diameter, with minute warts, filled with granular yellowish-brown material; globose spores, 7.5-9 μ m in diameter, pale brown under transmitted light, minutely vertucose.

Habitat. On a branch at the ground level, at 3400 m asl (19°31'17.1"; 97°09'34.5").

Studied specimen. Mexico. Veracruz. Perote municipality. Parque Nacional Cofre de Perote, March 21, 2019, Salazar-Hernández 27.

Taxonomic comments: *Didymium serpula* forms plasmodiocarps shaped like a net, white to gray in color; with membranous peridium, pale purple, covered with lime crystals. This species also has large vesicles and spores between 8-10 μ m in diameter (Nannenga-Bremekamp 1991). The studied specimen corresponds to such description, but the spores were slightly smaller.

The species has been recorded on *Ilex, Laurus, Rubus, Parasitaxus, Opuntia* and *Artocarpus* (Beltrán et al. 2004; Bridge Cooke 1971; Stojanowska and Panek 2004; Oltra 2006; Kylin et al. 2013; Amrani and Abdel-Azeem 2018; Youssouf and Ergül 2018).

Hemitrichia intorta (Lister) Lister, Monogr. Mycetozoa (London): 176 (1894). Figure 2K

Gregarious sporocarps; robust stipe, brown or violaceous brown, 0.5-0.7 mm tall; subglobose or pyriform sporotheca, 0.4-0.6 mm wide, ochraceous yellow changing to dark brown or violaceous brown at the base; persistent peridium, thin and shiny, with brown spots resembling plates, remaining as a

calyculus when open; capillitium tangled, in the shape of spiral bands with long and discontinuous spines, with few free ends; globose spores, 8-10 µm in diameter, yellow under transmitted light, spinulose.

Habitat. On fallen branches, at 3200 m asl (19°32'02.7"; 97°08'50.4") and 3400 m asl (19°31'17.1"; 97°09'34.5").

Studied specimens. Mexico. Veracruz. Perote municipality. Parque Nacional Cofre de Perote, March 21, 2019, Salazar-Hernández 28; April 5, 2019, Salazar-Hernández 29.

Taxonomic comments: this species has reddish brown stiped sporocarps, with a turbinate to pyriform sporotheca. When the peridium breaks, it forms a deep calyculus showing the orange-yellow capillitium, coiled and spiny, with spirals (Farr 1976). The specimens studied showed robust stipes and long, discontinuous spines in the capillitium similarly to the observations of Martin and Alexopoulos (1969).

The species has been recorded on ground litter and wood (Keller and Braun 1977; Novozhilov et al. 2006).

Licea castanea G. Lister, J. Bot., Lond. 49: 61 (1911). Figure 2L

Dispersed to aggregated spororcaps; pulvinate, with angular dehiscence plates, 0.1-1 mm x 0.1-0.3 mm in size; peridium with yellowish dehiscence lines, hazelnut brown to dark brown, coriaceous, covered in waste material, with papillae decorating the internal margin; no capillitium; globose spores, olivaceous brown; 11-13 μ m in diameter, with thick walls, smooth.

Habitat. On moist chamber set up with material from a fallen branch, at 3400 m asl (19°31'17.1"; 97°09'34.5").

Studied specimen. Mexico. Veracruz. Perote municipality. Parque Nacional Cofre de Perote, March 21, 2019, Salazar-Hernández 30.

Taxonomic comments: this species has sessile, pulvinate, angular sporocarps, yellowish brown to hazelnut in color; with pale dehiscence lines on the surface and smooth spores between 9-12.5 μ m in diameter (Ronikier et al. 2017). The spores have been reported to have thick walls and a thinner (paler) area covering about half of the sphere. The specimen examined corresponded to the descriptions provided.

The species has been recorded on *Quercus, Pinus* and *Abies* (Wrigley de Basanta 2004; Ergül and Akgül 2011).

Licea pygmaea (Meyl.) Ing, Trans. Br. mycol. Soc. 78(3): 443 (1982). Figure 3A

Dispersed or gregarious sporocarps; angular, subglobose or pulvinate, dark gray or black; coriaceous peridium, dark olive color, with dehiscence lines adorned with dense warts or crests, papillate internal surface; globose spores, 12-14 μ m in diameter, olive color, with thin walls, vertucose.

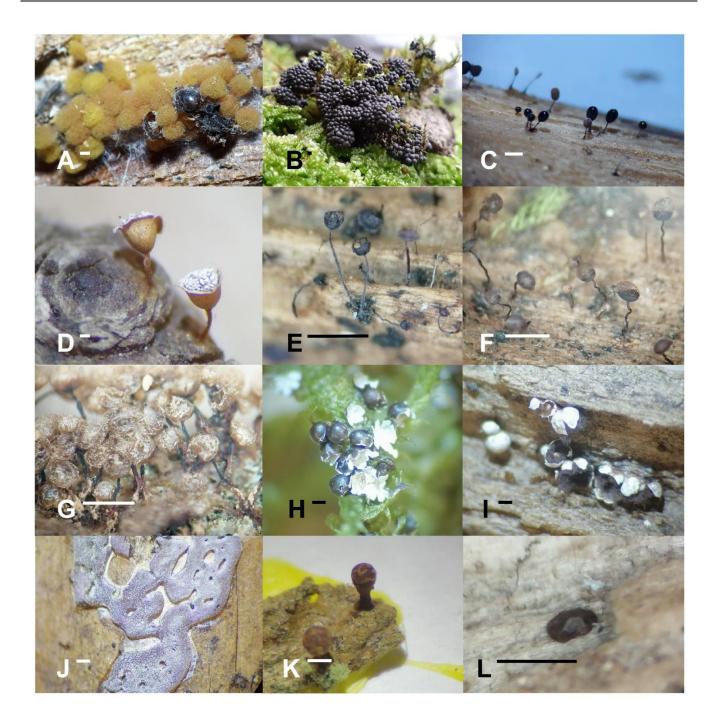


Figure 2. Macroscopic images of the new records for the state of Veracruz reported in the present study. A. *Arcyria ferruginea*, B. *Badhamia utricularis*, C. *Comatricha laxa*, D. *Craterium minutum*, E. *Cribraria lepida*, F. *Cribraria oregana*, G. *Cribraria vulgaris*, H. *Diderma asteroides*, I. *Diderma umbilicatum*, J. *Didymium serpula*, K. *Hemitrichia intorta*, L. *Licea castanea*. Scale bar 2 mm.

Habitat. On moist chambers set up with material from decayed logs and branches, at 3200 m asl $(19^{\circ}32'02.7''; 97^{\circ}08'50.4'')$, 3400 m asl $(19^{\circ}31'17.1''; 97^{\circ}09'34.5'')$ and 3600 m asl $(19^{\circ}30'58.7''; 97^{\circ}09'32.4'')$.

Studied specimens. Mexico. Veracruz. Perote municipality. Parque Nacional Cofre de Perote, October 23, 2018, Salazar-Hernández 31; October 26, 2018, Salazar-Hernández 32, 33, 34, 35; March 21, 2019, Salazar-Hernández 36, 37.

Taxonomic comments: The sessile, pulvinate, angular sporocarps, dark brown to black, opaque, with dehiscence lines and papillae covering the peridial plates are characteristic of this species (Ronikier et al. 2017). The spores are usually between 11-15 μ m in diameter and have a olivaceous brown color, with a thicker and a thinner half. The studied material has papillae that looked like warts.

The species has been recorded on *Prosopsis* and *Stipa* (Lado et al. 2011)

Metatrichia floriformis (Schwein.) Nann.-Bremek., Proc. K. Ned. Akad. Wet., Ser. C, Biol. Med. Sci.85(4): 557 (1982). Figure 3B

Dispersed sporocarps; 1-3 mm tall; stipe between 0.5-1.6 mm long, dark red, without amorphous particles; subglobose to pyriform sporotheca, reddish brown to black; peridium of two layers, the outer one cartilaginous, the internal one membranous, united; petaloid dehiscence (5/6 lobes); elastic capillitium, decorated with 4-6 spiral bands, smooth, no branching; globose spores, 11.5-12 μ m in diameter, red to orange under transmitted light, densely spinose.

Habitat. On log, at 3600 m asl (19°30'58.7"; 97°09'32.4").

Studied specimen. Mexico. Veracruz. Perote municipality. Parque Nacional Cofre de Perote, June 4, 2019, Salazar-Hernández 38.

Taxonomic comments: this species is normally found in numerous colonies and the sporocarps show rugose, red sporocarps with two peridial layers and orange red capillitium with 5-6 smooth spirals (Farr 1976). The specimen studied shows those characteristics but the peridium was more cartilaginous than normally described (see Martin and Alexopoulos 1969).

The species has been recorded on *Nothofagus, Fagus, Populus* and *Fraxinus* (Wrigley de Basanta et al. 2010; Dudka and Leontyev 2011; Lado et al. 2014; Thomas 2016).

Mucilago crustacea P. Micheli ex F.H. Wigg., Prim. fl. holsat. (Kiliae): 112 (1780). Figure 3C

Irregularly shaped aethalia; 1-3 cm x 1-8 cm x 1-5 cm in size, grayish white, covered with lime scales that give the appearance of a disintegrating sponge; membranous pseudocapillitium, translucent, calcareous, thick and branched; globose spores, 11-14 μ m in diameter, echinulate, dark brown under transmitted light; beige plasmodia.

Habitat. On fallen branches and *Abies* leaves on the ground, also in moist chamber set up with branch material, at 3200 m asl (19°32'02.7"; 97°08'50.4") and 3400 m asl (19°31'17.1"; 97°09'34.5").

Studied specimens. Mexico. Veracruz. Perote municipality. Parque Nacional Cofre de Perote, September 22, 2018, Salazar-Hernández 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55; October 23, 2018, Salazar-Hernández 56; March, 21, 2019, Salazar-Hernández 57.

Taxonomic comments: this species is characterized by the white or grayish aethalia, covered in lime crystals giving the appearance of scales, the thin and hyaline pseudocapillitium and the echinulate spores, between 9-14 µm diameter (Farr 1976). The examined material matches such description.

The species has been recorded on *Quercus, Brachypodium, Cynodon, Pinus, Salix, Juniperus, Cercocarpus, Betula, Corylus, Picea, Populus* and *Fraxinus* (Castillo et al. 2009; Gabel et al. 2010; Oltra 2004; Thomas 2016).

Paradiacheopsis solitaria (Nann. -Bremek.) Nann. -Bremek., Proc. K. Ned. Akad. Wet., Ser. C, Biol. Med. Sci. 70: 209 (1967). Figure 3D

Solitary to dispersed sporocarps; 0.4-0.7 mm tall; black stipe, with reticulated fibers at the base, measuring half of the total height; globose sporotheca, dark brown to black; columella splitting at the center of the sporotheca, generating the main capillitial branches; capillitium branching 2/3 times, with free and thick ends but without visible swollen sections; globose spores, 12.5-13 µm in diameter; dark brown, finely vertucose.

Habitat. On moist chambers made with bark, at 3200 m asl (19°32'02.7"; 97°08'50.4") and 3400 m asl (19°31'17.1"; 97°09'34.5").

Studied specimens. Mexico. Veracruz. Perote municipality. Parque Nacional Cofre de Perote, March 21, 2019, Salazar-Hernández 58, 59; April 22, 2019, Salazar-Hernández 60; June 13, 2019, Salazar-Hernández 61, 62.

Taxonomic comments: this species is known for the solitary dark brown sporocarps, with fibers at the base of the stipe and branching columella at about half of the height of the sporotheca (Nannenga-Bremekamp 1991). The vertucose spores have been reported to have diameters between 12-19 μ m. The studied material has a similar morphology to previous reports, including the thicker base tapering toward the sporotheca.

The species has been reported on *Sassafras, Larix, Ailanthus, Quercus, Pinus, Malus, Alnus, Juniperus, Abies* and *Fraxinus* (Ukkola et al. 2001; Wrigley de Basanta 2004; Eliasson and Gilert 2007; Rojas et al. 2010; Ergül and Akgül 2011; Thomas 2016).

Physarum newtonii T. Macbr., Bull. Iowa Lab. Nat. Hist. 2: 390 (1893). Figure 3E

Aggregated to dispersed sporocarps; short stipe, with a violaceous red base; subglobose sporotheca, with irregular dehiscence leaving a pinkish purple to violet calyculus; dual capillitium, made of translucent filaments connecting lime nodes, the latter large, irregular and angular, white; globose spores, 8-10 µm diameter, dark brown, verrucose.

Habitat. On decayed wood and branch, at 3200 m asl (19°32'02.7"; 97°08'50.4") and 3400 m asl (19°31'17.1"; 97°09'34.5").

Studied specimens. Mexico. Veracruz. Perote municipality. Parque Nacional Cofre de Perote, March 21, 2019, Salazar-Hernández 63; June 13, 2019, Salazar-Hernández 64.

Taxonomic comments: The characteristic solitary to clustered sporocarps, with limy violaceous peridium and a short dark red stipe are tipical of this sprecies. The capillitium has been reported to have violet angular nodes and Lizárraga et al. (2005) reported the vertucose spores to have diameters between 10-13 μ m. The studied material had a pinkish purple calyculus and smaller spores, coinciding with Martin and Alexopoulos (1969).

The species has been reported on *Quercus, Pinus, Puya, Nothofagus* and *Festuca* (Castillo et al. 2002; Lizárraga et al. 2005; Lado et al. 2013, 2014).

Prototrichia metallica (Berk.) Massee, J. Roy. Microscop. Soc.: 350 (1889). Figure 3F

Aggregated sporocarps; sessile, orange-brown to pinkish-brown; subglobose to pulvinate sporotheca, shiny, with iridescence; simple peridium, membranaceous, smooth, marked in the inner surface with numerous points of capillitial insertion; elastic capillitium, thick walled and united to the peridium, branching, with penicillate tips; globose spores, 10-14 µm in diameter, pinkish brown, spinose.

Habitat. On logs, at 3200 m asl (19°32'02.7"; 97°08'50.4"), 3600 m asl (19°30'58.7"; 97°09'32.4").

Studied specimens. Mexico. Veracruz. Perote municipality. Parque Nacional Cofre de Perote, August 14, 2018, Salazar-Hernández 65, 66; October 23, 2018, Salazar-Hernández 67, 68, 69; March 28, 2019, Salazar-Hernández 70, 71; June 4, 2019, Salazar-Hernández 72.

Taxonomic comments: the sessile sporocarps, with translucent but slightly iridescent peridium, capillitium with penicillate tips and spinose spores (Baba et al. 2008), are diagnostic characters of the species. The specimens studied showed all mentioned characteristics, but the pinkish brown color of the spores coincided with the observations of Lister and Hagelstein in Martin and Alexopoulos (1969).

The species has been recorded on *Larix, Pinus* and *Cedrus* (Novozhilov et al. 1999; Sánchez et al. 2002; Lado and Ronikier 2008; Amrani y Abdel-Azeem 2018).

Trichia decipiens (Pers.) T. Macbr., N. Amer. Slime-moulds, ed. 1, 218 (1899). Figure 3G

Aggregated sporocarps; stiped; 0.5-1 mm tall, olivaceous to dark brown; pyriform to subglobose sporotheca, olivaceous; simple peridium, membranaceous, with irregular to circular dehiscence; smooth capillitium, elastic, olivaceous yellow, with 3-5 spiral bands and sharp tips; globose spores, 12-14 μ m in diameter; yellow under transmitted light, reticulated.

Habitat. On logs, at 3600 m asl (19°30'58.7"; 97°09'32.4").

Studied specimens. Mexico. Veracruz. Perote municipality. Parque Nacional Cofre de Perote, October 23, 2018, Salazar-Hernández 73, 74, 75, 76; June 4, 2019, Salazar-Hernández 77.

Taxonomic comments: this species is characterized by the olivaceous colour of the sporocarps and the reticulate spores (Martin and Alexopoulos 1969). Also, the presence of circular dehiscence is important (Nannenga-Bremekamp 1991). The examined material showed the characteristics previously reported in the literature.

The species has been recorded on *Betula, Eucalyptus, Quercus, Pinus, Abies, Fagus, Fraxinus* and *Picea* (Castillo et al. 2009; Dudka and Leontyev 2011; Ergül and Akgül 2011; Ribes et al. 2016; Dudka and Leontyev 2017).

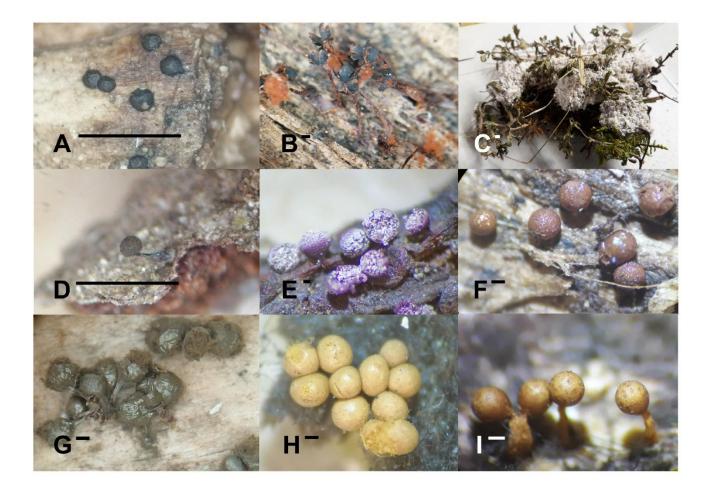


Figure 3. Macroscopic images of the new records for the state of Veracruz reported in the present study. A. *Licea pygmaea*, B. *Metatrichia floriformis*, C. *Mucilago crustacea*, D. *Paradiacheopsis solitaria*, E. *Physarum newtonii*, F. *Prototrichia metallica*, G. *Trichia decipiens*, H. *Trichia lutescens*, I. *Trichia subfusca*. Scale bar 2 mm.

Trichia lutescens (Lister) Lister, J. Bot., Lond. 35: 216 (1897). Figure 3H

Aggregated sporocarps; in small groups, subglobose or oblate, shiny yellow; simple peridium, membranous, translucent; elastic capillitium, smooth, with 5-6 spiral bands, with blunt or tapering tips; globose spores, $9-14 \mu m$, yellow, spinulose.

Habitat. On logs and in moist chambers set up with decayed wood, at 3200 m asl $(19^{\circ}32'02.7''; 97^{\circ}08'50.4'')$ and 3600 m asl $(19^{\circ}30'58.7''; 97^{\circ}09'32.4'')$.

Studied specimens. Mexico. Veracruz. Perote municipality. Parque Nacional Cofre de Perote, October 26, 2018, Salazar-Hernández 78, 79, 80, 81, 82, 83, 84, 85, 86; March 28, 2019, Salazar-Hernández 87, 88; May 20, 2019, Salazar-Hernández 89.

Taxonomic comments: this species is sessile, with a characteristic pulvinate to globose shape and yellow in color. The smooth capillitium with 5-6 spiral bands with blunt or tapering tips is also characteristic (Farr 1976). The spinulose spores have been reported between 10-14 μ m, the studied specimens have the same characteristics reported in the literature (Martin and Alexopoulus, 1969).

The species has been recorded on *Nothofagus dombeyi*, *N. pumilio*, *Pinus nigra*, *P. sylvestris*, *Populus nigra*, *Quercus ilex*, *Quercus petraea* and *Quercus* sp. (Lado and Moreno 1980; Wrigley de Basanta 2004; Demirel et al. 2006; Lizárraga et al. 2008; Wrigley de Basanta et al. 2010).

Trichia subfusca Rex, Proc. Acad. Nat. Sci. Philad. 42: 192 (1890). Figure 3I

Dispersed to slightly aggregated sporocarps; 0.8-1.2 mm tall, sometimes in pairs; globose to slightly ovoid sporotheca, ochraceous with light brown areolae; dark brown stipe, 0.5 mm tall; smooth capillitium, with 4 uneven spirals, smooth, with blunt or curved tips; globose spores, 12-14.5 μ m in diameter; straw yellow, vertuculose.

Habitat. On logs, at 3200 m asl (19°32'02.7"; 97°08'50.4") and 3600 m asl (19°30'58.7"; 97°09'32.4").

Studied specimens. Mexico. Veracruz. Perote municipality. Parque Nacional Cofre de Perote, October 26, 2018, Salazar-Hernández 90, 91, 92, 93.

Taxonomic comments: this species has gregarious sporocarps, with globose or ovoid sporothecas, reddish brown peridium and vertuculose spores between 10-15 μ m in diameter (Martin and Alexopoulos 1969). The examined material showed these characteristics.

The species has been recorded on *Quercus, Carpinus, Juniperus, Pinus, Nothofagus* and *Betula* (Ukkola et al. 2001; Oran and Ergül 2004; Rojas et al. 2010; Lado et al. 2014; Yatsiuk et al. 2017).

Discussion

Before the present study, the last research on myxomycetes in Cofre de Perote was conducted by Rojas et al. (2010, 2011). In such studies, carried out exclusively with the moist chamber technique,

researchers recorded 40 species of myxomycetes in the *Abies religiosa* forest and calculated a ratio of species to genera of approximately 2.66. Interestingly, the overlap of the recorded species between results of that study and the present investigation is extremely low, with only two species in common, *Comatricha nigra* and *C. pulchella*. With those values, only 7% of the species recorded herein had been observed the last time myxomycetes were investigated in the same area.

The remarkable aspect of the comparison is that such study was carried out in June/July of 2006 and 2007 with a high sampling effort of 384 substrate samples. As such, even though the sampling effort was robust, the temporal range of field surveys was limited to one season, which directly constrained the structure of the observed species assemblage. As contrast, results from the present study showed a ratio of species to genera of approximately 1.76 (not shown before), indicating that intraspecific richness was lower. This result does not imply that the complexity of the observed data is lower, but rather that more heterogeneity of myxomycete forms (i.e. different genera) was recorded in the present study using an experimental design in which the sampling effort was less intense per visit, but more spread across several months. Rare long-term phenological data available seems to suggest that fruiting patterns of myxomycetes can be determined by seasonal environmental fluctuations (Novozhilov et al. 2017) and that harsher climates induce more pronounced patterns (Stephenson et al. 2004). In this manner, results from the present study support the idea that temporality should be considered in the design of biodiversity-based research on myxomycetes.

The same way temporal variability has the potential of increasing the number of niches for myxomycetes to occur, geographical or topographical variability has a similar capacity (see Lado et al. 2011, 2013). As such, recent studies have shown that temperate-like climates with mountainous landscapes have an increased capacity to generate opportunities for myxomycete fructifications to occur than more homogeneous tropical environments do (Rojas and Stephenson 2020). Based on these observations it is not surprising that Cofre de Perote National Park shows such a high diversity of myxomycete species and that the state of Veracruz does so as well (Williams-Linera et al. 2013 for a discussion on the effect of environmental heterogeneity and plant diversity in Veracruz). As mentioned earlier, extensive work in La Malinche National Park (Rodríguez-Palma et al. 2005) demonstrated that conifer forests in the Central part of Mexico are rich in myxomycete species. However, with the greater variety of environments present in Veracruz, in comparison with Tlaxcala (the other well studied state in Mexico for myxomycetes), it would be expected for the former to have a more contrasting myxobiota than the latter.

Even though one aspect to consider in such comparison is the different effort invested in different localities or states, results from previous studies and the present investigation point to the fact that the myxomycetes from Veracruz are still very undocumented. The present investigation was geographically limited and still yielded more than 20 new records for the state, a particularly good result. If a species accumulation curve were to be constructed with all data from Veracruz, the pattern would show a high number of new species still recorded in each unit of effort. In this sense, the present investigation has supported such documentation, but provided a relevant result for methodological considerations.

In a situation where anthropogenic pressures on natural environments are decreasing biological complexity, such as the case of the state of Veracruz (Castillo-Campos et al. 2011) and Cofre de Perote National Park (Arriola-Padilla et al. 2015), it is imperative to continue the process of documentation of their biodiversity. It is true that biological assemblages naturally change over time, since they represent

dynamic systems, but the poor documentation of some groups of organisms for some geographical areas makes it very hard to determine the extent of such natural oscillations. In this manner, basic biodiversity research is still highly valuable for monitoring and management of natural systems. The present study has been a contribution to the knowledge of myxomycete biodiversity in one of those rapidly changing systems over time.

Acknowledgements

This project was funded by CONACYT grant number 812944 to the first author, to carry out his master's studies in biological sciences at the Faculty of Biology of the Universidad Veracruzana, Thanks to the members of Laboratorio de Organismos Simbióticos from the Instituto de Biotecnología y Ecología Aplicada and the Laboratorio de Micología Integral of Centro de Investigación en Micología Aplicada, both from the Universidad Veracruzana. Additional support for the identification of species was received from Universidad de Costa Rica (VINV 570-B9-B74) for the promotion of myxomycete studies in Latin America. To Leonel Zayas for the elaboration of the map.

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