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Myxomycetes associated with *Dicymbe corymbosa* in Guyana

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Myxomycetes are ubiquitous in terrestrial ecosystems and have two trophic (feeding) stages—myxamoebae and plasmodia. When conditions are suitable, the trophic stages give rise to the reproductive stage, a macroscopic sporophore. Although the myxamoebae and plasmodia of myxomycetes can appear saprotrophic, they are not decomposers but feed on microscopic organisms. In the first of the two feeding stages, they have the morphology of an amoeba or can be flagellated. While myxomycetes are in the amoeboflagellate feeding stage, bacteria represent their primary food; when they transition to their plasmodial stage, they are more omnivorous and can feed upon algae, spores, protozoans, fungal fruiting bodies, and possibly even lichens (Stephenson 1988; Stephenson & Stempen 1994; Rollins & Stephenson 2011). Their ingestion of bacteria is vital to liberating nutrients from bacterial biomass (Crotty *et al.* 2012). The amoeboflagellate stage eventually becomes a plasmodium, which ultimately produces the sporophore. Sporophores can be found in the field or triggered to fruit in moist chamber cultures (Stephenson & Stempen 1994). This study reviews and expands what is known about myxomycete diversity in Guyana and characterizes myxomycete assemblages associated with substrates produced by *Dicymbe corymbosa* Spruce ex Benth. (Fabaceae subfam. Detarioideae). This tree species is endemic to the Guiana Shield of northeastern South America and can form monodominant stands (Henkel 2003). The reiterative physiognomy and mast fruiting of *D. corymbosa* provides copious amounts of litter from foliar, reproductive, and woody materials that are suitable substrata for myxomycetes (Woolley *et al*. 2008; Henkel & Mayor 2019).

In January 2024 a survey for myxomycetes was carried out in a lowland rainforest dominated by *D. corymbosa* along the Ireng River in western Guyana (5°04’36.0”N 59°58’25.0”W). Myxomycetes sporophores were collected when found fruiting from *D. corymbosa* substrates (Figure 1) and these were dried for later identification. Moist chamber cultures were prepared from non-living substrates produced by *D. corymbosa*. Substrates included: mixed ground litter (mostly dead leaves), aerial litter (dead leaves still attached to the tree), aerial woody twigs (the tips of small dead branches above the ground), decaying pods of *D. corymbosa* on the forest floor, and old fruits of *D. corymbosa* on the forest floor. These samples were used to prepare 36 moist chamber cultures in the manner described by Stephenson and Stempen (1994). Numbers of cultures for the various substrate types were: ground litter (10), pods (9), aerial litter (7), aerial twigs (7), and fruits (3). Over a 3 month period when myxomycete sporophores were detected, they were removed, dried, and placed in small pasteboard boxes for identification and storage.

Specimens collected in the field (a total of 10) under the TH number series are housed at the University of Guyana Herbarium (BRG) with duplicates at Cal Poly Humboldt (HSC-F) and moist chamber specimens (a total of 30) are housed at the Stephenson herbarium (SLS). One or more voucher specimens are given for each species. Nomenclature follows Lado (2005-2025). Collection numbers are those of Terry W. Henkel (TH) and Steven L. Stephenson (SLS). Twenty-seven (75%) of the 36 moist chamber cultures prepared in the present study were positive for myxomycetes, and 14 (40%) of the cultures produced sporophores. In some instances, more than a single species was recorded from one culture. Thirteen cultures (36%) produced plasmodia and no sporophores. We recorded 14 species in nine genera from our study (Annotated Species List) and we combine this with previous Guyanese myxomycete research to compile a list of all myxomycetes currently known to occur in Guyana (Table 1).

Many species of myxomycetes are widely distributed both geographically and over a wide range of different substrates. However, some species are more substrate-specific. For example, certain species of myxomycetes are found only in association with dead parts of succulent plants in their native region, but these myxomycete taxa can be found over a much broader geographic area when the associated succulent plant has been introduced to a different continent (Lado *et al.* 2007,

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García-Martín *et al.* 2018, Stephenson & Elliott 2022). Other species are dung associated (coprophilous) (Bezerra *et al.* 2008, Eliasson 2013, Stephenson *et al.* 2023a). Some species are mostly substrate generalists but have a preference for particular environmental conditions (Liu *et al.* 2015, Stephenson *et. al.* 2025). There are some myxomycete taxa that prefer arid habitats (Novozhilov *et al.* 2006, Stephenson *et al.* 2020a), grasslands (Rollins & Stephenson 2013, Carascal *et al.* 2017), or rainforests (Rojas *et al.* 2014, Novozhilov *et al.* 2018). Certain species are also known from specific substratum types such as aerial litter, ground litter, bryophytes, inflorescences of large tropical herbs, and decaying logs (Liu *et al.* 2015, Stephenson *et al.* 2020b, Stephenson *et al.* 2023b). Three of the species recorded in this study (*Ceratiomyxa fruticulosa*, *Comatricha nigra*, and *Physarum viride*) are known to be associated with decaying wood. All of the other species we recorded are more broadly associated with various types of litter and woody fruit parts.

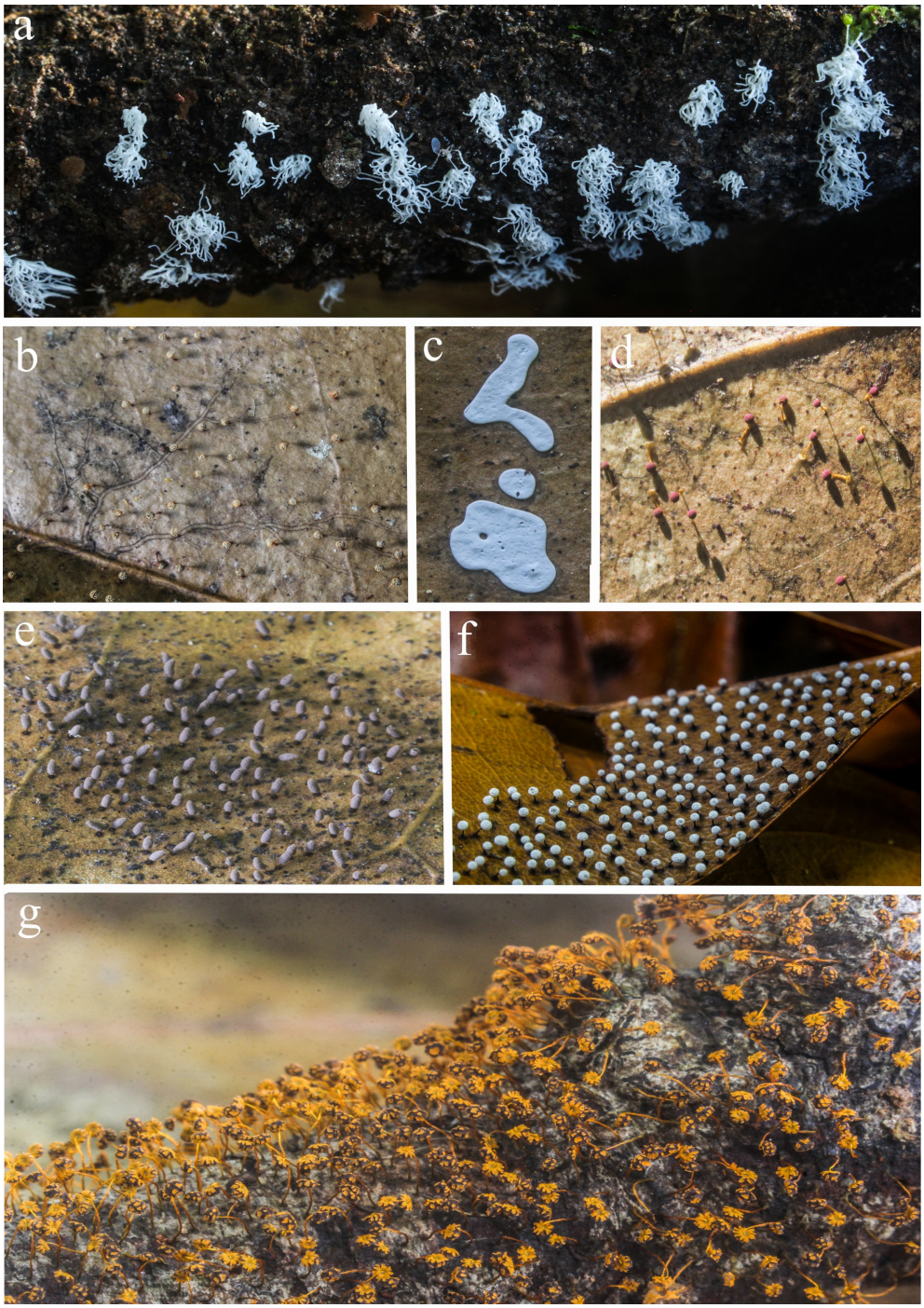

FIGURE 1. Seven species of myxomycetes found producing sporophores naturally at the field site. **a.** *Ceratiomyxa fruticulosa* (Collection # TH 11345). **b.** *Craterium leucocephalum* (Collection # TH 11365). Note the gray feeding trails of the plasmodium winding between the sporophores. **c.** *Diderma effusum* (Collection # TH 11369). **d.** *Craterium roseum* (Collection # TH 11367). **e.** *Comatricha pulchella* (Collection # TH 11366). **f.** *Didymium nigripes* (Collection # TH 11330). **g.** *Physarum viride* (Collection # TH 11344). Photo © Todd F. Elliott

TABLE 1. List of the 22 myxomycetes reported to occur in Guyana.

Arcyria afroalpina	This study
Arcyria cinerea	This study; Lado & Wrigley de Basanta 2008
Arcyria denudata	This study; Lado & Wrigley de Basanta 2008
Ceratiomyxa fruticulosa	This study; Lado & Wrigley de Basanta 2008
Ceratiomyxa sphaerosperma	Lado & Wrigley de Basanta 2008
Comatricha nigra	This study
Comatricha cf. tenerrima	This study
Comatrica pulchella	This study
Craterium leucocephalum	This study
Craterium roseum	This study
Cribraria microcarpa	This study
Diderma effusum	This study
Didymium nigripes	This study; Lado & Wrigley de Basanta 2008
Echinostelium minutum	This study
Lycogala exiguum	Lado & Wrigley de Basanta 2008
Perichaena chrysosperma	Lado & Wrigley de Basanta 2008
Physarella oblonga	Lado & Wrigley de Basanta 2008
Physarum bogoriense	Lado & Wrigley de Basanta 2008
Physarum polycephalum	Lado & Wrigley de Basanta 2008
Physarum tenerum	Lado & Wrigley de Basanta 2008
Physarum viride	This study
Stemonitopsis typhina	Lado & Wrigley de Basanta 2008

This study significantly expands what is known about the neotropical myxomycete diversity and distribution (Farr 1976). In the Neotropics, and in Guyana in particular, very few studies have examined myxomycete diversity (Wakefield 1934, Rojas & Doss 2013). This study contributes towards developing a comprehensive picture of global patterns of biodiversity of this group of organisms and provides novel data on the assemblage of myxomycetes associated with various substrata from a single tree species, *Dicymbe corymbosa*.

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Annotated species list

Arcyria afroalpina Rammeloo

Represented by five specimens (including SLS-03, SLS-04, and SLS-06) arising from ground litter and pods in moist chamber cultures. This species differs from *A. cinerea* in the very long (and usually curved) stipe and the ovoid sporotheca. This is the first record of this species from Guyana (Table 1).

Arcyria cinerea (Bull.) Pers.

Represented by 13 specimens (including SLS-02 and SLS-09) arising from ground litter, fruits, aerial twigs, and pods in moist chamber cultures. *Arcyria cinerea* is one of the most common of all myxomycetes and has been recorded from virtually all surveys of these organisms ever carried out, including previous studies in Guyana (Table 1).

Arcyria denudata (L.) Wettst.

Represented by one specimen (SLS-07) appearing on pods in a moist chamber culture. This species has been previously recorded from Guyana as well as other countries in the region (Table 1).

Ceratiomyxa fruticulosa (O.F. Mull.) T. Macbr.

Collected by TWH and TFE on 8 Jan 2024 from woody twigs (TH 11345) (Figure 1a). This species has been previously recorded from Guyana as well as other countries in the region (Table 1). *Ceratiomyxa fruticulosa*, traditionally considered as a myxomycete, is now known to be a member of another group of amoebozoans.

Comatricha nigra (Pers. ex J.F. Gmel.) J. Schröt.

Represented by one specimen (SLS-11) appearing on aerial twigs in a moist chamber culture. This is the first record of this species from Guyana (Table 1). *Comatricha nigra* can be recognized by its very long stalk, globose sporotheca, intricately branched capillitium, and black, faintly warted or almost smooth spores.

Comatricha pulchella (C. Bab.) Rostaf.

Collected by TWH and TFE on 8 Jan 2024 from ground litter (TH 11366) (Figure 1e). This is the first record of this species from Guyana (Table 1). Ground litter is the usual habitat for *Comatricha pulchella*, the short-stalked, ovoid, pinkish brown fruiting bodies occur in small groups.

Comatricha cf. ***tenerrima*** (M.A. Curtis) G. Lister

Represented by one specimen (SLS-10) appearing on pods in a moist chamber culture. This is the first record of this species from Guyana (Table 1). This species is characterized by its long stipe, spindle-shaped sporotheca, and somewhat pinkish brown spores. The apex of the stipe sometimes projects beyond the spore mass, as was the case of this specimen. This specimen is listed as "cf." because it was represented by only a single specimen and the fact that in the experience of the second coauthor, the appearance of *Comatricha tenerrima* in a moist chamber culture is unusual.

Craterium leucocephalum (Pers. ex J.F. Gmel.) Ditmar

Collected by TWH and TFE on 8 Jan 2024 from ground litter (TH 11364,TH 11365, and TH 11368) (Figure 1b). We also collected one specimen of this species on the spiny pods of a species of *Sloanea* within a forest that was otherwise dominated by *Dicymbe corymbosa* (See: TH 11370). This is the first record of this species from Guyana (Table 1). The taxon considered as the *C. leucocephalum* morphospecies is variable, and a number of varieties have been recognized. Typical specimens have a stalked, top-shaped or cylindrical sporotheca that is orange or brown below and white above. All specimens collected in the present study were old and weathered but did possess the features mentioned above.

Craterium roseum (Berk. & Broome) J.M. Garcia-Martin, J.C. Zamora & Lado
Collected by TWH and TFE on 8 Jan 2024 from ground litter (TH 11367) (Figure 1d). This is the first record of this species from Guyana (Table 1). Earlier treatments of myxomycetes list this species as *Physarum roseum* Berk. & Broome. The bright red peridium of this species is distinctive.

Cribraria microcarpa (Schrad.) Pers.
Represented by three specimens (including SLS-06) appearing on pods in a moist chamber culture. This is the first record of this species from Guyana (Table 1). No other species of *Cribraria* has an exceeding long stipe and a peridial net with small, dark nodes.

Diderma effusum (Schwein.) Morgan
Collected by TWH and TFE on 8 Jan 2024 from ground litter (TH 11369) (Figure 1c). This is the first record of this species from Guyana (Table 1). *Diderma effusum* is distinguished by its thin, broadly effused plasmodiocarps.

Didymium nigripes (Link) Fr.
Collected by TWH and TFE on 8 Jan 2024 from ground litter (TH 11330) (Figure 1f). This species has been previously recorded from Guyana (Table 1). The single specimen was checked against authentic material to verify the identification.

Echinostelium minutum de Bary
Represented by three specimens (including SLS-01) appearing on ground litter and aerial twigs in moist chamber cultures. This is the first record of this species from Guyana (Table 1). *Echinostelium minutum* is exceedingly common in temperate regions of the world but uncommon in the tropics. It is easily identified by its large size (for a species of *Echinostelium*) and branched (albeit sparse) capillitium.

Physarum viride (Bull.) Pers.
Collected by TWH and TFE on 8 Jan 2024 from woody twigs (TH 11344) (Figure 1g). This is the first record of this species from Guyana (Table 1). The lens-shaped, nodding sporotheca, and yellow peridium allow this species to be easily identified.