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Author(s): Steven L. Stephenson, Martin Schnittler, Carlos Lado, Arturo Estrada-Torres, Diana Wrigley de Basanta, John C. Landolt, Yuri K. Novozhilov, Jim Clark, Donna L. Moore, Frederick W. Spiegel

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Studies of neotropical mycetozoans

Steven L. Stephenson^{a,*}, Martin Schnittler^b, Carlos Lado^c, Arturo Estrada-Torres^d,
Diana Wrigley de Basanta^e, John C. Landolt^f, Yuri K. Novozhilov^g,
Jim Clark^h, Donna L. Mooreⁱ & Frederick W. Spiegel^j

^a Dept. of Biological Sciences, University of Arkansas, Fayetteville, Arkansas 72701, USA

^b Botanical Institute and Botanical Garden, Ernst-Moritz-Arndt University Greifswald,
Grimmer Str. 88, D-17487 Greifswald, Germany

^c Real Jardín Botánico de Madrid, Plaza de Murillo 2, 28014 Madrid, Spain

^d Universidad Autónoma de Tlaxcala, Apdo. Postal 183, Tlaxcala C.P. 90000, Tlaxcala, Mexico

^e The American School of Madrid, Apartado 80, 28080 Madrid, Spain

^f Department of Biology, Shepherd College, Shepherdstown, West Virginia 25443, USA

^g V. L. Komarov Botanical Institute of the Russian Academy of Sciences, St. Petersburg, Russia

^h T. H. Morgan School of Biological Sciences, University of Kentucky, Lexington, Kentucky 40506, USA

ⁱ Division of Biology & Chemistry, Corning Community College, Corning, New York 14830, USA

^j Department of Biological Sciences, University of Arkansas, Fayetteville, Arkansas 72701, USA

* author for correspondence [slsteph@uark.edu]

Abstract. – During the period of 1995 to 2002, biotic surveys for mycetozoans (slime moulds) were carried out in a number of study areas in Central and South America to document more completely the species associated with tropical forests and other ecosystems in this region of the world. Primary emphasis of these surveys was on myxomycetes; more limited data were obtained for dictyostelids and protostelids, two other groups of mycetozoans that share some of the same microhabitats as myxomycetes. The body of data represented by the more than 8,000 field and moist chamber collections of myxomycetes accumulated during these surveys have provided evidence for a number of ecological patterns not previously reported for myxomycetes. The most important of these are that (1) both overall abundance and species richness of myxomycetes appear to be lower in tropical forests than in temperate forests, (2) species richness and [especially] relative abundance increase with decreasing moisture conditions, and (3) in tropical forests, distinct assemblages of myxomycetes are associated with microhabitats that have no counterparts in temperate forests. The most extensive of the latter is the aerial litter (dead but still attached plant parts) microhabitat, where myxomycetes appear to be especially abundant and diverse. Most of the dictyostelids recovered from samples collected in the various study areas are cosmopolitan forms or species known to have tropical or subtropical affinities. However, one new species (*Acytostelium minutissimum*), several other forms that possibly represent undescribed species, and a number of species not previously known from the Neotropics also were recorded. For the most part, the species of protostelids associated with Neotropical forests are the same as those found in temperate regions of the world, and species richness in this group appears to be highest in mesic but not wet habitats. Microhabitat trends of particular species of protostelids appear to vary with habitat. Overall in

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tropical montane habitats, protostelids are more abundant in aerial microhabitats than in ground microhabitats while in mesic habitats they are present in both types of microhabitats, but with some species displaying a preference for one or the other.

Key words: *Neotropics, myxomycetes, forests, ecology, dictyostelids, protostelids.*

1 Introduction

The myxomycetes (plasmodial slime moulds) are a small group of fungus-like organisms, with approximately 875 species described worldwide (Lado 2001). The majority of species are probably cosmopolitan, but a few species appear to be confined to the tropics or subtropics and some others have been collected only in temperate regions of the world (Alexopoulos 1963, Farr 1976, Martin & al. 1983). Myxomycetes appear to be particularly abundant in temperate forests, but at least some species apparently occur in any terrestrial ecosystem with plants (and thus plant detritus) present (Stephenson & Stempen 1994). For example, they have been reported from deserts (e.g., Blackwell & Gilbertson 1980) and high-latitude tundra (Stephenson & Laursen 1993), where harsh environmental conditions place severe constraints on the occurrence of living organisms.

Most of what is known about the assemblages of myxomycetes associated with particular types of terrestrial ecosystems has been derived from studies carried out in temperate regions of the Northern Hemisphere; few studies have been conducted in tropical/subtropical regions of the world. The primary objective of the project reported herein was to carry out biotic surveys for myxomycetes in a number of study areas in the Neotropics of Central and South America to document more completely the species associated with tropical forests and other ecosystems in this region of the world (Stephenson & Schnittler 2002). More limited data were obtained for dictyostelids and protostelids, two other groups of mycetozoans that share some of the same microhabitats as myxomycetes.

2 Study areas

Most studies of myxomycetes in the Neotropics have been based on short-term, often cursory visits to particular localities (Farr 1976). In many instances, myxomycetes were collected only in the context of a project in which primary emphasis was directed towards some group of the true fungi. For the project described herein, an effort was made to spend longer periods of time (usually a minimum of 5-7 days) in a limited number of primary study areas. Moreover, whenever possible, a particular study area was visited on more than a single occasion. At the beginning of the project, four primary study areas were selected. These were (1) the Luquillo Experimental Forest, located in the Luquillo Mountains in northeastern Puerto Rico [at approximately 18° N latitude], (2) the Area de Conservación Guanacaste, located in northwestern Costa Rica [at approximately 10° N latitude], (3) the El Edén Ecological Reserve, located on the Yucatan peninsula of Mexico [at approximately 10° N latitude], and (4) the Maquipucuna Cloud Forest Reserve, located on the western slopes of the Andes in Ecuador [and situated almost on the equator at 0° N latitude]. The four study areas were selected to encompass a range of tropical forests types (from lowland tropical dry forests near sea level to tropical cloud forests located at elevations > 2,700 m) and a geographic area that

extends from the equator to near the northern astronomic limit (i.e., the Tropical of Cancer at 23° 30' N latitude) of the Neotropics. One of the study areas is located on an island (Puerto Rico), whereas the others are on the mainland of northern South America (Ecuador), middle Central America (Costa Rica), and northern Central America (Mexico). As the project developed, other study areas were added to these original four (fig. 1). For the most part, these other study areas were selected to include additional vegetation types and/or geographic areas of particular interest or relevance to the overall project.



Figure 1. Location of study areas in the Neotropics.

3 Materials and methods

In temperate forests, myxomycetes are known to be associated with a number of different microhabitats. These include the bark surface of living trees, forest floor leaf litter, soil, the dung of herbivorous animals, and aerial portions of dead but still standing herbaceous plants. Each of these microhabitats tends to be characterized by a distinct assemblage of myxomycetes (Stephenson 1989). Similar microhabitats in tropical forests had not, prior to the present study, been subjected to intensive study, but preliminary data (e.g., Edmunds & Stephenson 1996) obtained from studies of the myxomycetes associated with litter microhabitats at several sites in Puerto Rico and Costa Rica suggested that the same situation was true in the tropics. As such, all microhabitats known to support myxomycetes were examined in the various study areas. Moreover, as it became apparent that other microhabitats, either specific to one of the non-forest vegetation types investigated or that have no counterparts in temperate forests, also support myxomycetes, these were included in the survey.

The basic methods used for carrying out surveys for myxomycetes in the various study areas were essentially the same as those described by Stephenson (1988, 1989) for a similar project that involved five study areas located in upland forests in temperate eastern North America. In addition to collecting specimens that had fruited under natural conditions in the field, the moist chamber culture technique (*sensu* Gilbert & Martin 1933) was used to examine the species associated with the

microhabitats represented by (1) forest floor litter, (2) aerial litter [dead but still attached plant parts above the ground], and (3) the bark surface of living trees. During the course of the project, this component was expanded to include a number of additional microhabitats, including inflorescences of large tropical herbs, living leaves of understory plants with a cover of leafy liverworts present, and dead lianas.

The moist chamber cultures used throughout the project consisted of disposable plastic Petri dishes (10 cm diam) lined with filter paper. Samples were moistened with distilled water adjusted to pH 7.0 with KOH. After a period of approximately 24 hours, the pH of each culture was determined using a flat plate electrode and a pH meter. After pH had been determined, excess water in each dish was poured off or removed with a pipette. Cultures were maintained at room temperature (ca. 22 to 25°C) in diffuse daylight and examined with a stereomicroscope at regular intervals for a period of up to several months to detect the presence of plasmodia and/or fruiting bodies of myxomycetes. Isolation procedures used for dictyostelids were those described by Cavender & Raper (1965), whereas protostelids were isolated using a modification of the technique described by Olive (1975).

Identifications of specimens were made using the descriptions and keys provided by Martin & Alexopoulos (1969), Farr (1976), Mitchell (1980), and Lado & Pando (1997) or by means of direct comparisons with authentic material of a particular species obtained on loan from the National Fungus Collections (BPI) in Beltsville, Maryland. All field and moist chamber culture collections of myxomycetes made during the project were dried at room temperature and then glued in small boxes for permanent storage. Voucher specimens of all species reported herein are deposited in the herbaria of University of Arkansas (UARK), the Royal Botanical Garden, Madrid (MA-Fungi), Universidad Autónoma de Tlaxcala, or the personal collection of Martin Schnittler, which is stored at the Botanische Staatssammlung München (M). Nomenclature used herein follows Lado (2001) for myxomycetes (except for the genus *Ceratiomyxa* and *Tubifera*, where the more traditional names are retained), Raper (1984) for dictyostelids, and Olive (1975) for protostelids.

Comparisons of data sets for different assemblages of myxomycetes were carried out using coefficient of community (CC) and percentage similarity (PS) indices (Mueller-Dombois & Ellenberg 1974). The equation for the former, which is based solely on presence or absence of species, is $CC = 2c/(a + b)$, where a is the total number of species in the first data set being compared, b is the total number in the second data set, and c is the number of species common to both data sets. The value of CC ranges from 0 (when the data sets being compared have no species in common) to 1.0 (when all species are present in both data sets). The equation for percentage similarity, which considers relative abundance of species and not just their presence, is $PS = \sum \min(a, b, \dots, x)$ where \min is the lesser of two percentage compositions of species a, b, \dots, x in the two data sets. The value for PS ranges from 0 for assemblages with no species in common to 1.0 for assemblages identical both in species composition and in quantitative values for the species.

4 Results and discussion

Some of the more important results obtained from the surveys carried out thus far are outlined in the sections that follow. Information is provided for all four primary study areas and also for one additional major study area and one of the countries (Mexico) for which a considerable body of data now exists. Although emphasis is placed upon the data that these surveys have yielded for myxomycetes, the more limited results obtained for dictyostelids and protostelids also are discussed.

In addition to the surveys described herein, very preliminary data are available for one study site near Iquitos in eastern Peru, and it is anticipated that future surveys will be carried out in Brazil. Moreover, in June of 2000 and late June/early July of 2001, samples of aerial litter and ground litter were collected from tropical forests in northern Queensland, Australia (Black & al. 2002). Ultimately, the myxomycete data obtained from these samples will be compared with data for litter microhabitats in the Neotropics, in order to determine whether or not similar assemblages of species are associated with a particular type of microhabitat in tropical forests in very different regions of the world.

4.1 Luquillo Experimental Forest

The first major survey related directly to the overall project described in this paper was carried out during March 1996 in the Luquillo Experimental Forest, which is located in the Luquillo Mountains in northeastern Puerto Rico (18°20' N, 65°49' W). The primary objective of this survey was to investigate the quantitative ecology and distributional relationships of all three groups of slime

moulds (myxomycetes, dictyostelids and protostelids) in the forest floor litter microhabitat. A secondary objective was to obtain baseline data on the assemblages of protostelids associated with aerial litter microhabitats in the same study sites from which samples of forest floor litter were collected (Stephenson & Moore 1998).

Samples for isolation of the three groups of slime moulds were collected from five primary study sites within the Luquillo Experimental Forest. Each of these study sites (tabonuco forest, secondary tabonuco forest, palo colorado forest, palm forest, and elfin forest) represents a different type of forest community and the five types are stratified roughly by elevation (Brown & al. 1983). Tabonuco forest is found below 600 m, palo colorado forest generally occurs between 600 and 750 m, and elfin forest is located above 750 m. Palm forest occurs on sites characterized by steeper slopes, poor drainage and saturated soils within the range of elevations usually occupied by palo colorado and elfin forests. In each study site, samples were collected from 100 different microsites, with microsites located approximately 2.0 m apart along three or more transects extending through the particular study area. Petri dishes already lined with filter paper were transported into the field, where samples of litter were added individually to each dish. These were brought back to the laboratory and processed in the usual manner. In order to assess patterns of occurrence for dictyostelids and protostelids, which apparently coexist with myxomycetes in the forest floor litter microhabitat, additional samples for isolation of these two groups of slime moulds were collected from 50 of the same microsites (ten in each study site) used for litter samples collected for myxomycetes.

At least twenty-four species of myxomycetes representing twelve genera were isolated from the 500 moist chamber cultures prepared with samples of forest floor litter. These figures were lower than those (34 species in 16 genera) obtained for a comparable series of samples collected in upland forests of eastern North America (Stephenson 1989). Consequently, the Puerto Rican data suggested that species richness of the assemblages of myxomycetes associated with the forest floor litter microhabitat is somewhat lower in tropical forests than in temperate forests. Percentages of positive cultures (39 to 79 % versus 70 to 87 %) also were lower for samples of tropical forest litter.

Only three species of myxomycetes (*Arcyria cinerea*, *Cribraria microcarpa*, and *Stemonitis fusca* var. *nigrescens*) were recorded from all five study sites. However, each was common to abundant in one or more study sites but uncommon in the others. Other species recorded from at least two study sites were *Clastoderma debaryanum*, *Cribraria violacea*, *Diderma effusum*, *Didymium iridis*, *Physarum compressum*, and *P. album*. Thirteen species of dictyostelids were recovered from the 50 litter samples, with the number of species (10) recorded from the secondary tabonuco forest more than twice that for any other study site. The most consistently abundant species was *Polysphondylium pallidum* (probably best regarded as a species complex rather than a single taxonomic entity), which represented 36 % of all clones isolated. Forest floor litter samples collected for protostelids yielded at least thirteen species, with *Schizoplasmodiopsis pseudoendospora* the single most common example. Representatives of all three groups of slime moulds were recovered from 32 % (16 of 50) of all microsites examined in this aspect of the study. Only three microsites (6 %) did not yield positive cultures for at least one group. Protostelids were isolated from 94 % of all microsites, dictyostelids from 54 %, and myxomycetes from 44 %. These data indicate that slime moulds are nearly ubiquitous components of the microflora associated with forest floor litter microhabitats in the Neotropical forests investigated, although differences in relative abundance existed from one forest type to another. Myxomycetes, dictyostelids, and protostelids all displayed their highest levels of abundance in the two forest types (tabonuco and secondary tabonuco) located at the low end of the elevation gradient. In contrast, species richness and abundance were lowest for each of the three groups in the elfin forest, located at the high end of the gradient. As such,

the general pattern observed was that of decreasing diversity with increasing elevation. This pattern, although not reported previously, appears to be especially apparent for myxomycetes and, as will be noted later in this paper, has been supported by the results obtained in other regions of the Neotropics as a result of subsequent studies.

The data obtained in this initial survey were supplemented by additional data from a number of other surveys (e.g., Novozhilov & al. 2000) carried out during the period of 1997 to 2002. These studies considered both the Luquillo Experimental Forest and other vegetation types throughout Puerto Rico (Nieves-Rivera & Darrah 2002).

4.2 Guanacaste Conservation Area

The Area de Conservación Guanacaste (ACG) encompasses about 120,000 ha in the northwestern corner of Costa Rica [10° 51' N, 85° 36' W]. Elevations within the ACG extend from sea level to more than 1,500 m, and forest types present range from tropical dry forest to cloud forest (Schnittler & Stephenson 2000). ACG was selected as a primary study area because, at the time the grant proposal seeking funding for the overall Neotropical project was submitted, plans were underway to carry out an All Taxa Biodiversity Inventory (ATBI) in this region of Costa Rica (Rossman & al. 1998). Surveys for slime moulds would represent one component of this much larger and more comprehensive project. Although the ATBI did not materialize, a considerable body of data was obtained for slime moulds from study sites located in four different forest types at ACG. These were (1) tropical dry forest, located in Santa Rosa National Park and on the Santa Elena Peninsula; (2) tropical moist forest, located near the Mariza Biological Station; (3) tropical wet forest, located on the lower slopes of Volcano Cacao near the Cacao Biological Station; and (4) cloud forest, located on the upper slopes of Volcano Cacao. These are described in more detail by Schnittler & Stephenson (2000).

The region of Costa Rica in which the ACG is located includes not only the driest part of the country but also a moisture/vegetation gradient that extends from tropical dry forests near the coast to cloud forests at higher elevations on three volcanoes. The primary study sites for the surveys carried out at ACG were located along a gradient that extended from dry forest on the coast of the Santa Elena Peninsula to cloud forest on the summit of the Volcano Cacao (1759 m). The dry forest type has an annual precipitation less than 2000 mm and a long and well-pronounced dry season that extends from November to May. A considerable proportion of the trees shed their leaves entirely or partially during the dry season, thus allowing the litter layer to dry out completely. Trees are often completely free of epiphytes or have only a few patches of small lichens or liverworts. Tropical moist forests have a less severe dry season and a higher annual precipitation (2000 to 3000 mm). Most trees are evergreen; as a result, the litter layer does not dry out completely. The epiphyte cover on the bark of trees is appreciable, with average values ranging from 10 to 65 %. Tree diversity is high; only locally does a single tree species become dominant. The tropical wet forest type, which covers the middle slopes of the volcanoes, is characterized by high precipitation (ranging from 3000-4000 mm per year). Canopy trees are evergreen, up to 55 m tall, with mostly closed but still thin covers of epiphytes, predominantly liverworts and with average cover values of 75-100 %. The litter layer stays moist the year around. Cloud forests, occurring at the summits of the volcanoes, have a very high annual precipitation (> 4000 mm) and are characterized by almost daily cloud exposure. Trees are almost completely covered with a thick (> 2 cm) layer of mosses and liverworts interwoven with the rhizomes of Hymenophyllaceous ferns. The litter layer is permanently wet and often covered by a film of water.

For each study site, the sampling protocols followed consisted of (1) studying a limited unit of vegetation very thoroughly, examining all microhabitats potentially suitable for myxomycetes;

(2) recording all fruitings encountered and then estimating the numbers of sporocarps in each fruiting; (3) classifying the particular microhabitat (defined as a small space presumably homogeneous for both substrate and microclimate) within which each fruiting occurred; and (4) complementing field collections by extensive use of the moist chamber culture technique to examine the myxomycetes associated with such substrates as the bark surface of living trees and leaf litter. This type of study involves a much greater effort than simple field collecting but yields the data required to address a number of fundamental questions relating to myxomycetes. Among these are such things as: How complete is the species inventory obtained? What are the most common species associated with the various microhabitats? Are there distinct assemblages of species of myxomycetes associated with a particular microhabitat? To what extent are the species found in a particular microhabitat specialised for that microhabitat?

Three surveys were carried out in at ACG, one in January 1998, another in June 1999, and the third in April 2001. The results obtained from the first two surveys were described by Schnittler & Stephenson (2000). Data from the third survey, which essentially expanded the data set for the various forest types and added an additional study site on the coast of the Santa Elena Peninsula that represents the very driest forest in found in the region, confirmed the pattern of decreasing myxomycete diversity with increasing elevation and precipitation as reported in the latter paper. Altogether, 596 myxomycete records, with 295 of these originating from 444 moist chamber cultures, were considered. However, from the 86 species encountered (including two undescribed forms of *Arcyria* and one of *Perichaena*), only fourteen were represented by at least ten records and 21 were collected only once. When the intensity of the survey is taken into account (a total of four weeks of fieldwork), these data seem to confirm the relative rarity of myxomycetes in most tropical forests.

The distribution of species in the different forest types investigated reflected the pattern of decreasing species richness with decreasing elevation: tropical dry forest (51 species), tropical moist forest (51 species), tropical wet forest (41 species) and cloud forest (six species). Although the two forest types at the low end of the elevation gradient had the same number of species present, the distribution of these species with respect to microhabitat differed significantly. The tropical dry forest type had by far the richest flora of corticolous (bank-inhabiting) myxomycetes; fifteen of the 51 species occurred exclusively in this microhabitat. The most common species in this forest type were *Cribraria violacea* (a corticolous species), *Hyporhamma serpula* (associated with succulent litter and wood), *Macbrideola martinii*, *M. scintillans* and *Perichaena vermicularis* (all corticolous). The species richness of the tropical moist forest originated mostly from field collections of wood-inhabiting species, and 27 species were found only on decaying wood. The most commonly encountered species were *Arcyria cinerea*, *A. denudata*, *Ceratiomyxa fruticulosa*, *C. morchella*, *Cribraria intricata*, *C. languescens*, *Hyporhamma calyculata*, *Lycogala exiguum*, *Stemonitis axifera* and *Tubifera microcarpa* (all wood-inhabiting). In contrast to tropical dry forest and tropical moist forest, the cloud forest was almost devoid of myxomycetes, with *Arcyria cinerea* accounting for three of the six records. However, all forest types were investigated with equal intensity using the moist chamber culture technique (Schnittler & Stephenson 2000). As a general observation, representatives of myxomycete taxa known to form protoplasmodia, as is the case for the genus *Perichaena* (with seven species recorded), were much more common at the dry end of the moisture gradient. Species known to form phaneroplasmodia, a group represented by such examples as members of the genera *Physarum* (fourteen species), *Diderma* (5) and *Didymium* (6) were equally common in the tropical dry and the tropical moist forests, but they represented only fifteen of the 41 species recorded from the tropical wet forest.

4.3 El Edén Ecological Reserve

An intensive survey of the myxomycetes associated with semideciduous tropical dry forests in the El Edén Ecological Reserve (21°12' N, 87°12' W) on the Yucatán Peninsula of Mexico was carried out during November of 1999 (Stephenson & al. 2003). Field studies over a period of five days by seven researchers yielded four hundred and sixty-two collections of material that had fruited in the field under natural conditions. As a result of subsequent laboratory studies, 226 collections were obtained from 171 moist chamber cultures prepared with samples of bark or litter from El Edén. At least 74 species in 27 genera were identified from the entire series of collections, which increased the totals known for the general study area to at least 94 species in 29 genera. Based on these data, forests of the Yucatán Peninsula have a moderate to high myxomycete biodiversity when compared to other regions of the Neotropics for which comparable data exist. However, overall biodiversity appears to be somewhat lower than has been reported for temperate forests (e.g., Stephenson 1988, 1989).

The majority of field collections at El Edén were associated with coarse woody debris on the forest floor, where a few species were exceedingly common; prominent examples were *Arcyria cinerea*, *A. denudata*, *Hyporhamma calyculata*, and *H. serpula* (fig. 2). In addition to coarse woody debris (i.e., such things as dead stumps, decaying logs on the forest floor, dead branches that had fallen from trees, and fragments of wood), other substrates from which specimens of myxomycetes were collected in the field included decaying palm fronds and dead leaves on the forest floor. At least 56 different species in 23 genera were identified from field collections. This total included representatives of all six taxonomic orders recognized for myxomycetes (Martin & Alexopoulos 1969), although the majority (74 %) of the specimens collected belong to just two orders – the Physarales and the Trichiales. Members of the Trichiales alone accounted for almost 42 % of all

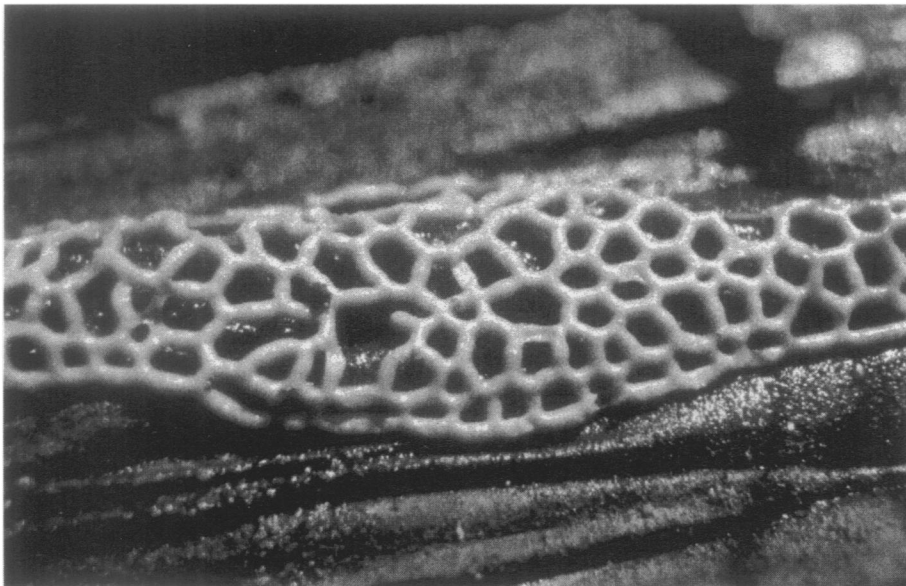


Figure 2. *Hyporhamma serpula*, a myxomycete that is often common on ground substrates in Neotropical forests.

collections. This is due in part to the fact that four of the five most common species collected belong to the Trichiales. The predominance of the Trichiales was less apparent when numbers of species and not number of collections were considered, since more than half (52 %) of all species recorded as field collections are members of the Physarales. Members of the Trichiales (16 % of all species), Stemonitales (16 %), and Liceales (12 %) also were fairly common, whereas the Ceratiomyxales and Echinosteliales were each represented by a single species. The relative importance of the Physarales and Trichiales in the assemblages of myxomycetes associated with tropical forests in southern India was noted by Stephenson & al. (1993) and also appears to be a consistent feature of Neotropical forests.

Moist chamber cultures prepared with bark samples from El Edén yielded at least nineteen species of myxomycetes in fourteen genera. *Physarum* cf. *crateriforme* was represented by the largest number of collections (16), with *Macbrideola martinii* (7 collections), *M. scintillans* (4), *Cribraria violacea* (4), and *Perichaena vermicularis* (4) the only other species represented by more than three collections. Members of the Stemonitales and Trichiales each made up 32 % of the assemblage of species recorded from bark, whereas the Physarales (35 %) and Stemonitales (31 %) were represented by the greatest numbers of collections. Values of pH recorded for these moist chamber cultures ranged from 7.7 to 8.3, with a mean value of 8.0. These values are generally higher than those reported for bark samples from temperate trees (Stephenson 1989).

Nineteen species in eleven genera were collected from moist chamber cultures prepared with samples of forest floor litter, and seventeen species in ten genera were recorded from cultures prepared with samples of aerial litter. The most common species of myxomycetes on forest floor litter were *Perichaena chrysosperma* (15 collections), *Arcyria cinerea* (14), *Hyporhamma minor* (13), *Hyporhamma serpula* (11), and *Diderma hemisphaericum* (9). The four most common species all belong to the Trichiales, which was clearly the predominant order (with > 60 % of all collections) in this microhabitat. The Trichiales and the Physarales were represented by the most species. For aerial litter, *Cribraria microcarpa* (12), *Collaria arcyronema* (10), *Arcyria cinerea* (7), and *Physarum pusillum* (5) were the only species represented by at least five collections. Members of the Liceales, Stemonitales, Trichiales, and Physarales were all relatively common in the aerial litter microhabitat, where their respective contributions to the total numbers of collections and species ranged from 19 % to 30 % and 18 % to 29 %, respectively. Values of pH (5.5 to 7.3) recorded for these two sets of moist chamber cultures were remarkably similar, and the percentage of positive cultures (87 %) was the same for both types of litter.

Coefficient of community and percentage similarity indices calculated from all possible combinations of the data sets from the four different microhabitats, yielded mean values of 0.36 and 0.21, respectively. Consequently, the differences among the microhabitats resulted more from differences in abundances for species shared in common than from differences in actual species composition. The comparison of field collections and collections from bark yielded the very lowest values for both indices. A comparison of field collections with a data set obtained from combining the records of species obtained from all 171 moist chamber cultures produced a CC value of just 0.34. This would indicate that the assemblage of species fruiting in the field under natural conditions is distinctly different from the assemblage appearing in moist chamber cultures. Indeed, only 16 species were recorded both as field and moist chamber culture collections, and only a few of these (e.g., *Arcyria cinerea*, *Hyporhamma serpula*, and *Collaria arcyronema*) were fairly common in the two different situations. The data set for aerial litter had the highest overall CC value (mean = 0.45) when compared to those for the other microhabitats, and a comparison of the two types of litter microhabitats yielded the very highest value (0.61). However, the PS value calculated for these two microhabitats was much lower (0.35).

4.4 Mexico

The El Edén Ecological Reserve represents only one of a number of study areas that have been investigated in Mexico, and major emphasis of the project was directed towards this country during the period of 2000 to 2002. Mexico stands out among the Neotropical countries because of its geographic location between the Neotropical and the Nearctic realms, a situation that results in the overlap of plants and animals from more northern (temperate and boreal) and southern (subtropical and tropical) regions. In addition, other geographic and historical factors such as Mexico's varied topography, the oceanic influence that affects the climate of some portions of the country, and the geographic isolation of some areas have contributed to the high biodiversity of this country (Rzedowski 1978). More than 22,000 species of vascular plants occur in Mexico, many of them Neotropical in origin or endemics with their origin and diversification in Mexico (Rzedowski 1991). In contrast to its high plant biodiversity, only 265 species of Myxomycetes have been recorded from Mexico (Illana & al. 2000), although in the last few years the advances in knowledge for this group have been remarkable.

On three separate occasions during the period of 1999-2001, as part of the project described herein, intensive field sampling was carried out by a group of researchers in a particular region of Mexico, and samples of such substrates as the bark of living trees, lianas and shrubs for preparation of moist chamber cultures were collected from nine different vegetation types. The study areas were chosen to encompass different ecological zones, from semiarid to humid tropical, and a range of elevations that extended from lowland tropical dry forests near sea level to montane tropical cloud forests. The sampling effort produced approximately 1000 field collections and more than 500 specimens from moist chamber cultures. More than 130 species were collected, many of which represented new records for either a particular region of Mexico or for the entire country. In addition, 14 rare or apparently undescribed species are currently under investigation. Some of the latter were found in microenvironments widely occupied by myxomycetes, but others appear to be restricted to particular ecological situations. As a result of these studies, at least 25 species have been added to the total previously reported from Mexico (Illana & al. 2000, Estrada-Torres & al. 2001).

The data obtained from moist chamber cultures indicated that a major proportion of all specimens are associated with substrates characterised by a circumneutral pH, which appears to be optimal for many species of myxomycetes (Wrigley de Basanta & al. 2002). This is significant in so far as the substrates were collected from a wide range of habitats over an extensive area and entirely at random with respect to pH. Water retention of the substrates also was found to be correlated with the relative number of specimens collected. Moreover, there was a high degree of specificity with respect to ecological conditions, since only five species could be regarded as "generalists" as a result of being common to all of major vegetation types sampled (i.e., humid tropical, semi-humid temperate and arid). Bark samples from arid and semiarid areas were very productive, as were certain aerial substrates in the humid tropics. Our results suggest that the apparent low level of abundance for myxomycetes in humid tropical regions is possibly due, at least in part, to the fact that the life cycles or specific ecological niches of myxomycetes in these regions are different from those of temperate regions. Some of the other data obtained during the project point to this conclusion. The number of species that appeared exclusively in moist chamber cultures confirms the value of using this technique in any effort to assess myxomycete biodiversity.

In Mexico, myxomycetes were collected in ecosystems as varied as evergreen and semi-evergreen tropical forests, "tintales" (tropical flooded forests), cloud and coniferous forests, and several kinds of xerophytic shrublands. As a consequence of this very broad spectrum of substrates and microenvironments that is associated with the exceedingly high plant diversity of Mexico, it seems possible that the myxomycetes have been presented with a unique opportunity for ecological

specialization and speciation. Three previously unknown ecological groups have been described from the Neotropics. These are the succulenticolous myxomycetes (Lado & al. 1999), the floricolous myxomycetes (Schnittler & Stephenson 2002), and the species found on the substrate represented by covers of foliicolous liverworts on the leaves of understory shrubs (Schnittler 2001). A number of other ecological groups, such as those associated with tropical dry fruits (a group that includes *Ceratiomyxa sphaerosperma*), moss beds on rocks in the tropics (for which *Physarum alvoradianum* and *Diderma* aff. *rugosum* are examples), or dead lianas are still under study. Although many Mexican myxomycetes (e.g., *Craterium paraguayense*, *Diachea silvaepluvialis*, *Metatrachia horrida*, and *Physarum javanicum*) have a pantropical distribution or apparently occur only in the Neotropics (a group represented by *Diderma miniatum*, *Diderma rimosum*, and *Physarum alvoradianum*), more new species known only from Mexico or neighbouring countries are being described. Examples of the latter include *Cribraria fragilis*, *Didymium mexicanum*, *Physarum tropicale*, *Diderma acanthosporum*, and *D. yucatanensis* (Lado & al. 1999, Estrada-Torres & al. 2001, Lado & al. 2003). Some others of Mexican origin but with distributions known to extend to other continents, apparently are associated only with introduced Mexican plants. One example of such a species is the recently described *Cribraria zonatispora* (Lado & al., 1999).

All these data seem to indicate that, as has been demonstrated for other groups, the myxomycetes may be undergoing a rapid speciation process, facilitated by the ecological conditions created in diverse Mexican environments. The simple morphology of the myxomycetes is perhaps masking the effect of these processes, which we will understand only when much more intensive fieldwork has been carried out and more powerful analytical techniques have been applied to systematic, ecological and biogeographical studies of this group (Estrada-Torres & al. 2002).

4.5 Maquipucuna Cloud Forest Reserve

The Maquipucuna Cloud Forest Reserve encompasses about 4500 ha of tropical moist forest, tropical premontane wet forest, and tropical lower montane rain forest on the northwestern slopes of the Andes approximately 40 km west of Quito, Ecuador (Pichincha Province, 00°07' N, 78°38' W). In a manner similar to the surveys carried out in the ACG of northwestern Costa Rica, three study sites (located at elevations of 1300, 1900 and 2700 m) were selected, with each representing one of the three forest types mentioned above. The myxomycetes associated with these forest types were studied by means of field surveys and the moist chamber culture technique (Schnittler & al. 2002). During a period of three weeks (involving two researchers for the entire time and two others for the first week), 475 samples were collected from all types of microhabitats known to support myxomycetes. These samples, when placed in moist chamber cultures, produced 443 records representing 35 taxa. Moist chamber culture data were supplemented by 590 field collections representing 67 taxa, which yielded a final total of 77 taxa. An effort to estimate the completeness of the survey with the use of statistical methods indicated that for both the field (92 %) and the moist chamber component of the survey (67-92 %), a high proportion of the entire species assemblage should have been recorded. In terms of sampling intensity, the results from this survey appear to be comparable with the studies carried out in the GCA, and essentially the same pattern of decreasing species richness with increasing elevation was observed. As was the case in northwestern Costa Rica, the highest study site was almost devoid of myxomycetes, and more than 95 % of the field and 50 % of the moist chamber records were obtained from the lowest study site. For the moist chamber studies, the pattern observed differed from that observed in northwestern Costa Rica by virtue of the fact that only eight species of corticolous myxomycetes (representing just ten records) were obtained from the 76 cultures prepared with samples of bark. One obvious explanation for these results is the lack of a study site located in tropical dry forest, which accounted for more than two thirds of all records

of corticolous myxomycetes in the ACG. On the other hand, covers of foliicolous liverworts on living leaves of understory plants were investigated as a new habitat for myxomycetes. For this microhabitat, which can dry out within a few hours when exposed to sunshine, the pattern of decreasing myxomycete abundance with increasing elevation (with 52, 51 and 33 records from 21, 20 and 20 moist chamber cultures) was less pronounced.

For the entire survey carried in the Maquipucuna Cloud Forest Reserve, a considerable body of ecological data was recorded. It is anticipated that these data, when analyzed completely, will provide insights into distributional patterns and niche relationships of myxomycetes to a greater extent than possible for any other study area investigated in the overall project (Stephenson & al., in prep.).

4.6 Yasuní National Park and Biosphere Reserve

In addition to the four primary study areas, an intensive survey was carried out in the Yasuní National Park and Biosphere Reserve (0° 40' S, 76° 23' W), in Ecuador (Lado & al. 2002). The reserve is located on the right bank of the Tiputini River, a tributary of the Napo River. With a total extent of 980,000 hectares of pristine tropical rain forest, it is one of the largest protected areas in Ecuador. Moreover, Yasuní is adjacent to the Huaorani Indian Reserve, which encompasses an additional 680,000 hectares. Elevations in the Reserve range from 200 to 350 meters above sea level, and evergreen lowland forests and evergreen flooded palm forests are the predominate vegetation types. These forests are rather diverse, with more than 300 species of trees per hectare recorded in a study by Romoleroux & al. (1997). The climate of the region is typically tropical, with a mean annual temperature of 25-28°C and a mean annual precipitation of 2500-2700 mm.

In April of 2000, three researchers spent three weeks carrying out a rapid biodiversity assessment of the myxomycetes at Yasuni. The rapid biodiversity assessment, which also was used for an earlier study (carried out in 1998) of the myxomycetes associated with cloud forests in Maquipucuna Cloud Forest Reserve in Ecuador (Schnittler & al. 2002), is a method used to determine, with a reasonable sampling effort, the myxobiota of relatively undisturbed regions in the tropics that are rich in species but largely unexplored. The period of time spent at Yasuni was relatively short, considering the size of the area to be studied. However, because the climatic conditions of tropical forests in the region are very constant and there are no marked seasons, the problem of sporulation phenology (i.e., fruitings being present at the time of the visit) was minimized.

Fieldwork in Yasuní National Park was centered at a Scientific Station that the Catholic Pontificia University of Ecuador has in the Reserve. The most pristine areas of the surrounding forests as well as some areas that had been degraded by the presence of the field station were investigated. All potential substrates were examined in the field and samples of plant litter, bark, fruits, and inflorescences were collected. Later, these samples were used to prepare a large series (a total of 215) of moist chamber cultures.

For all field collections, a collection number and the type of substrate was noted along with a number of ecological parameters that characterized the substrate (i.e., diameter or extent, stage of decomposition, etc.) and the conditions (e.g., estimated humidity conditions, sun or shade, etc.) under which the particular specimen developed. The exact methods used are described by Schnittler & al. (2002) and have been used in other study areas such as El Edén (Mexico) and Maquipucuna (Ecuador), where they have yielded large amounts of data over relatively short periods of time. These data can be used to characterize the distributional patterns to a greater extent than has been possible in most previous studies of the myxomycetes. Because Yasuni is a protected area, not all fruitings were collected, only the most representative or interesting. However, data were recorded for every fruiting observed in the field.

The entire survey yielded 550 collections of myxomycetes, 300 from the field and 250 from the moist chamber cultures. Eighty-nine taxa representing 25 genera were identified, considerably increasing number of species of myxomycetes known from of this region of the world. Of the 89 taxa identified, 28 were new records for Ecuador and four were known previously in the country only from the Galápagos islands. In addition, eight species (representing the genera *Arcyria*, *Hyporhamma*, *Didymium*, *Paradiacheopsis* and *Physarum*) are possibly new to science, but additional specimens are needed to confirm their identity and the stability of their characters.

The most diverse genus at Yasuni was *Physarum*, with 21 species. Other more important genera were *Cribraria* (seven species), a genus long considered primarily boreal in its distribution, *Arcyria* and *Didymium* (six species), *Ceratiomyxa*, *Perichaena* and *Stemonitis* (five species each), and *Comatricha*, *Diderma* and *Hyporhamma* (four species each). All the species described for the genus *Ceratiomyxa* were recorded, which confirms its predominantly tropical distribution. There were also a surprisingly large number of species from the order Trichiales, especially representatives of such genera as *Arcyria*, *Perichaena* and *Hyporhamma*. Interestingly, only a single species of *Trichia* was recorded. *Arcyria afroalpina* was confirmed as tropical and not restricted to Africa, where the species was described originally. *Arcyria cinerea* was common, but the forms collected certainly included the various biotypes have been recognized for this species. Species reported for the first time for the Neotropics were *A. major* and *Badhamia gigantospora*. Among the other more interesting results was the occurrence of *Lycogala conicum* and *L. exiguum* but not the more common *L. epidendrum*, which perhaps raises some question as to whether the latter species is truly cosmopolitan. *Physarum compressum* was also found growing on inflorescences of *Heliconia* and *Calathea*, one of the new microhabitats (fig. 3) noted for myxomycetes in the Neotropics (Schnittler & Stephenson 2002). Among the most productive other substrates at Yasuni were palm fronds.

The quantity and variety of results obtained at Yasuni demonstrated the richness of species in these tropical forests and the effectiveness of a rapid biodiversity assessment for myxomycetes. It is anticipated that method could serve as a model for further investigations of the myxobiota of regions and vegetation types for which data are lacking.

4.7 Myxomycete biosystematics

Specimens collected during the project have provided the basis for laboratory studies on the biosystematics of selected species of myxomycetes. Data reported from other studies indicate that morphologically defined species are in most cases species complexes composed of a number of allopatric and/or sympatric, genetically isolated biological species and numerous small apomictic clones (Clark 2000). These morphospecies also contain morphotypes, controlled by a few genes, that are often recognized as separate species, and biotypes, such as the forms with dwarf sporangia found in some types of aerial microhabitats.

The largest numbers of Neotropical isolates investigated are in the genus *Didymium* (Clark & Mires 1999, Clark & al. 2001, Clark & Stephenson 2002). In *Didymium iridis*, a cosmopolitan species, 40 Neotropical isolates have been examined and found to contain representatives of four of the nine known biological species of this taxon, as well as 30 apomictic isolates. *Didymium anellus* and *D. megasporum* are cosmopolitan species displaying similar patterns, although fewer isolates have been cultured and studied in these taxa (Clark & Landolt 2001). *Didymium squamulosum* is more of a tropical species and is well represented in the 38 studied Neotropical isolates, with representatives in five of the known biological species and also having many of the known apomictic isolates having been identified thus far (El Hage & al. 2000). Only a few Neotropical isolates of *Didymium ovoideum* and *D. saturnus* have been studied, and to date they are all apomictic clones.



Figure 3. Fruiting of *Physarum didermoides* on the bract of large tropical herb, a newly described microhabitat for myxomycetes.

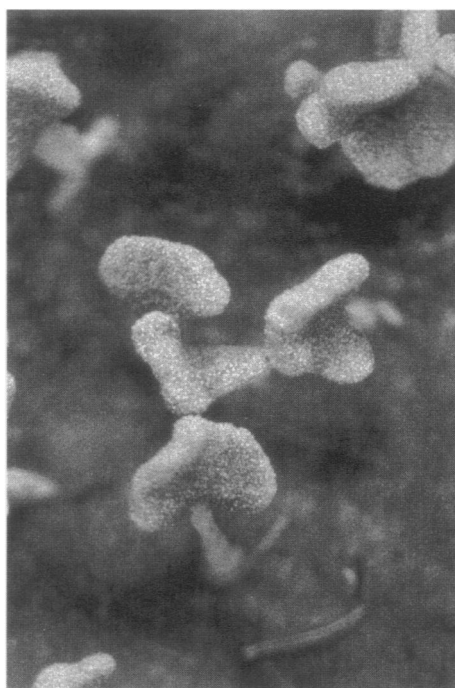


Figure 4. *Physarum compressum*, a very common morphospecies throughout the Neotropics, appears to be represented in nature almost exclusively by apomictic clones.

Similar patterns are found in the genus *Physarum*, although the species that have been studied to date generally have fewer sexual isolates. *Physarum compressum* (fig. 4) and *P. melleum*, which are mainly tropical in their distribution, have yielded only one of 35 and zero of 20 isolates that are heterothallic (Clark & Stephenson 2000, Irawan & al. 2000). The related *Badhamia gracilis*, a species apparently adapted to arid regions, also has been found to contain only apomictic lines in the 39 Neotropical isolates that have been investigated to date (Clark & al. 2003). On the other hand, *P. pusillum* has yielded three sexual isolates, each in a different biological species, from the eight known Neotropical isolates. This taxon is also highly variable morphologically, with a yellow sporangia variant and a dwarf form apparently adapted to epiphytic microhabitats.

The only species, outside of the Physarales, in which a number of Neotropical isolates has been studied, is *Arcyria cinerea*. Of the thirteen Neotropical isolates investigated, only three, in two biological species, have been found to be sexual and the other ten are apomictic (Clark & al. 2002). This is another morphologically variable taxon, with both an ochraceous colour variant and a small epiphytic form being present. Single apomictic Neotropical isolates of *Collaria arcyrionema* and *Ceratiomyxa fruticulosa* also have been cultured and studied.

Except for the somewhat higher rate of apomictic clones in the species of *Physarum*, Neotropical myxomycetes do not appear to differ significantly, in terms of reproductive population structure, from the myxomycetes found in other regions of the world. The morphologically defined species are species complexes consisting of several biological sibling species and numerous apomictic clonal lines that often display morphotype and biotype variations.

4.8 Dictyostelids

Dictyostelid cellular slime moulds (dictyostelids) are single-celled, eukaryotic, phagotrophic bacterivores usually present and often abundant in terrestrial ecosystems. These organisms represent a normal component of the microflora in soils and apparently play a role in maintaining the natural balance that exists between bacteria and other microorganisms in the soil environment. For most of their life cycle, dictyostelids exist as independent, amoeboid cells (myxamoebae) that feed upon bacteria, grow, and multiply by binary fission. When the available food supply within a given microsite becomes depleted, numerous myxamoebae aggregate to form a structure called a pseudoplasmodium, within which each cell maintains its integrity. The pseudoplasmodium then produces one or more fruiting bodies (sorocarps) bearing spores. Dictyostelid fruiting bodies are microscopic and rarely observed except in laboratory culture. Under favorable conditions, the spores germinate to release myxamoebae, and the life cycle begins anew. Dictyostelids are most abundant in the surface humus layer of forest soils, where populations of bacteria are the highest and microenvironmental conditions appear to be the most suitable for dictyostelid growth and development (Raper 1984). Approximately 100 species of dictyostelids are known to science. Some of these appear to be cosmopolitan, whereas others have a more restricted distribution (Swanson & al. 1999).

Previous reports of dictyostelids from the Neotropics include those of Cavender (1973), Cavender & Raper (1968), Vadell & al. (1995), and Cavender & Vadell (2000). In addition, a considerable body of data relating to the distribution and ecology of these organisms in Belize and (particularly) the vicinity of Tikal in Guatemala is available in the unpublished MS theses of Holmes (1991), Swanson (1992), and Vadell (1993).

In the context of this project, samples for isolation of dictyostelids have been collected from a number of localities in the Neotropics, particularly Costa Rica, Mexico, Ecuador and the Caribbean island of Puerto Rico, including the five study sites in the Luquillo Experimental Forest that were described earlier in this paper. In Costa Rica, several different vegetation types, ranging from semi-deciduous tropical dry forests to lowland rain forests and montane cloud forests, have been sampled. A total of about 25 described species and a large number of as yet unassigned forms have been recovered. Species richness varied between 5-12 species at any given locality, with the exception of a high elevation paramo study site and one elfin cloud forest, where only a few isolates of single species were recovered from one in ten samples. The greatest values (10-12 different species) for species richness were associated with the montane forests of the Monteverde region, the forests along the slopes of Volcano Cacao in the northwestern part of the country, the lowland rainforest on the Caribbean slope in the vicinity of La Selva, and the forests along the Caribbean coast near Cahuita in the southeast. The following are the most common or widespread species that have been isolated from four or more localities: *Dictyostelium purpureum*, *D. mucoroides* complex, *Polysphondylium pallidum* complex, *D. vinaceofuscum* *P. violaceum*, *D. aureostipes*, *D. macrocephalum*, and *D. monochasioides*. Most of these apparently common and widespread species were reported previously from Costa Rica by Cavender (1973). In addition, the following species are noteworthy: *Acytostelium ellipticum*, *D. deminutivum* (rare tropical forms), *A. minutissimum* (the type specimen for this recently described species), *D. aureum*, *D. coeruleostipes*, *D. citrinum*, *D. granulophorum* (relatively rare Neotropical forms), *D. mexicanum*, *D. lavandulum* and *D. rhizopodium* (typical Neotropical forms), *D. discoideum* (possible new record for the Neotropics as a previous record for this species in Costa Rica was similar morphologically but different genetically), *D. minutum* (possible new record for Costa Rica), and *D. polycephalum* (globally widespread but rare). With the exception of *D. aureostipes*, *D. minutum*, and *D. discoideum*, all of the species of dictyostelids recovered from samples collected in Costa Rica during the project reported herein

are generally considered to be cosmopolitan, Neotropical or pantropical in distribution (Swanson & al. 1999) and have been reported previously from the country or might have been expected, based on results from other studies.

Sampling carried out in central and southern Mexico has encompassed vegetation types ranging from cactus communities to hardwood and coniferous forests at higher elevations. About 25 described forms have been collected, with the lowland forests of the Yucatan Peninsula (e.g., El Edén) having the greatest species richness (17 species) of any locality sampled. Species richness in deciduous and semi-deciduous tropical forests was usually about 7-8 forms, with most of the arid cactus- or yucca/agave vegetation types having only single species of dictyostelid present. The most common and widespread species were: *D. purpureum*, *D. mucoroides*, *P. pallidum*, *D. vinaceofuscum* (Yucatan), *D. macrocephalum*, and *P. violaceum*. All of these are cosmopolitan or tropical forms (Swanson & al. 1999). Among the more notable dictyostelids recovered from Mexican samples was *D. polycarpum*, recorded from a fir forest near the summit of an old volcano in southern Mexico. This species was described originally from subalpine coniferous forests of Switzerland by Traub & al. (1981) and has since been reported from deciduous forests of Germany (Cavender & al. (1995), from warm evergreen and cool temperate deciduous forests of Japan (Cavender & Kawabe 1989), and once from North America (Cavender, unpubl. data). Other interesting forms from Mexico include *D. polycephalum* (rare but widespread worldwide, usually occurring in lowlands), *D. rosarium* (very disjunct distribution worldwide, usually reported from dry, saline and alkaline soils [Raper 1984] and in caves), *P. candidum* (type specimen from Japan and isolated occasionally in Europe and the United States), *P. colligatum* or *P. asymmetricum* (both described recently from Tikal in Guatemala [Vadell & Cavender 1998]), *P. pseudocandidum* (type specimen from Japan, also isolated in the United States), and *P. tenuissimum* (type specimen from Japan, but some isolates of *P. pallidum* from here or elsewhere are likely to fit this taxon). The temperate deciduous forest species *Dictyostelium discoideum* was isolated from a few samples collected, as reported previously by Cavender & Raper (1968).

The total number of different forms recovered from samples collected in Ecuador was at least twelve and perhaps as high as fifteen. Sampling was carried out in vegetation types ranging from a coastal forest near Guayaquil (5 species), montane cloud forests at several elevations in the highlands at Maquipucuna (8-11 species), and a tropical moist forest at the Yasuni Biological station near Orellana (6-7 species). The most commonly isolated species were members of the *D. mucoroides* complex, *D. vinaceofuscum*, *D. purpureum*, *P. pallidum* complex, and *P. violaceum*. All of these are species considered to be cosmopolitan or predominantly tropical in distribution (Swanson & al. 1999). The most noteworthy aspect of these collections is the fact that in the Maquipucuna cloud forests, dictyostelids recovered from epiphytic soils were more diverse and abundant than those isolated from ground soil samples. Myxomycete plasmodia commonly appeared in isolation plates prepared with samples of epiphytic soil and litter.

Soil and litter samples from Puerto Rico have been collected from a variety of vegetation types, including tropical dry forests, moist forests, montane forests, and cloud forests. Particular attention has been directed towards the forests of the Luquillo Mountains on the eastern end of the island, as reported by Stephenson & Landolt (1998) and Stephenson & al. (1999). Cavender & Vadell (2000) recently have described a new species of *Acytostelium* from Puerto Rico. Thus far, about 15 described species of dictyostelids have been recovered, together with as many as another five or six forms that do not seem to conform closely to any described species. Greatest species richness seems to be associated with the tropical moist and wet forests of the Luquillo Mountains, with as many as 10-12 species present. Elfyn forests at the highest elevations of the Luquillo Mountains and the very dry forest in the southeast portion of the country have yielded very few species (2-4), and these

occur at very low densities. The moist and wet forests of northwestern Puerto Rico that are associated with limestone karst substrates are characterized by relatively high species richness (8-9 species) and particularly high levels of density, the highest recorded for any locality sampled on the island. The most common species are *D. mucroides* complex, *D. purpureum*, *P. pallidum* complex, and *D. giganteum*. These and other isolates that can be assigned with some certainty to described species (*A. leptosomum*, *D. monochasioides*, *D. rhizopodium*, and *D. tenue*) are either cosmopolitan or considered to have subtropical and tropical affinities (Swanson & al. 1999). One exception to this general pattern may be several isolates that seem to conform to the description of *D. minutum*. This species has been rarely if ever isolated from tropical regions (Swanson & al. 1999). Unlike the situation in the highlands of Ecuador, species richness and densities of dictyostelids recovered from samples of epiphytic soil and litter in Puerto Rico were found to be lower than comparable values recorded for samples of ground soil/litter substrates (Stephenson & Landolt 1998).

Based upon the data obtained thus far, dictyostelids are common to abundant in the Neotropics, and the large number of forms recovered that can not, as yet, be assigned to any described species suggests that some of the species present are not known to occur in any other region of the world. Moreover, the recovery, sometimes in appreciate numbers, of dictyostelids from microhabitats located well above the forest floor would indicate that these organisms are found within a wider range of ecological situations than revealed by previous studies, which have focused almost exclusively on the soil/litter layer of ground sites (Stephenson & Landolt 1998).

4.9 Protostelids

The protostelids (the unicellular slime moulds) are a group of slime moulds characterized as having small fruiting bodies comprised of a single acellular stalk with one to a few spores, amoeboid feeding cells with a centrally located nucleus, and mitochondria with tubular cristae. Protostelids appear to be present and abundant in most terrestrial ecosystems, but because they are microscopic, they can be sampled only by collecting the substrates on which they occur (e.g., dead, attached plant parts, leaf litter, bark, dung, and soil) and then isolating these organisms in the laboratory. Ecological research suggests that assemblages of protostelids vary greatly based on habitat. Within a given habitat, microhabitat trends may exist, but these trends may not hold in another habitat type. Species richness of protostelids in the Neotropics appears to be highest in mesic but not wet habitats. Moreover, the species present in mesic habitats exhibit microhabitat trends, with some species preferring ground microhabitats (e.g., leaf litter lying on the ground) as opposed to aerial microhabitats (e.g., dead, but still attached plant parts above the ground). As research on Neotropical protostelids continues, our knowledge of the biogeography of protostelids is gradually unfolding.

Since 1995, research on protostelid ecology in the Neotropics has included study areas in Costa Rica and Puerto Rico. In addition, some comparative ecological data have been obtained from one other tropical region of the world (Hawaii). Collections of native substrates from primary and secondary tropical moist, tropical wet, and tropical montane wet forests in Costa Rica yielded seventeen species of protostelids, thirteen species on aerial litter and twelve species from samples of ground litter (Stephenson & Moore 1998). Species richness was highest for aerial litter samples from a secondary tropical moist forest and ground litter samples from a primary tropical moist forest. Protostelid diversity appeared to be lowest in the forest type located at highest elevation. Only eight species were recovered from samples collected in a cloud forest (3440 m), whereas ten species were recovered from samples collected in a secondary tropical moist forest near sea level (ca. 5 m). Overall, most of the species sampled were equally abundant on aerial and ground litter samples.

A follow-up study in Costa Rica by Moore & Stephenson (2003) used a standardized technique (Moore & Spiegel 1995) to compare the assemblages of protostelids on native substrates with those on sterile substrates introduced into a particular microhabitat (aerial litter or ground litter) in a tropical wet forest at the La Selva Biological Station in northeastern Costa Rica. Introduced substrates were recollected after 3, 4, 5 and 6 weeks and the number of colonies per species determined. Only nine species were recovered from native and introduced substrates. Again, most species were equally abundant in aerial and ground litter microhabitats. Common species included *Schizoplasmodiopsis pseudoendospora*, *Echinostelium bisporum*, and *Cavostelium apophysatum*, while uncommon or rare species (at least in Costa Rica for this study) included *Nematostelium gracile*, *Protostelium mycophaga*, *Echinosteliopsis oligospora*, *Protostelium arachisprorum*, *Nematostelium ovatum*, and *Schizoplasmodiopsis vulgare*.

Similar studies were carried out in moist, montane, and cloud forests of the Luquillo Mountains of Puerto Rico by Moore & Spiegel (2000a) as an extension of a pilot study that took place in 1996 (Stephenson & al. 1999). This study also involved the introduction of sterile substrates into four forest types along an elevation gradient. Species richness ranged from 4-10 on introduced substrates and 1-6 on native substrates. Overall, species diversity was greater for the aerial litter microhabitat than for the ground litter microhabitat. However, particular species did not clearly show increased abundance in either aerial or the ground litter. In general, protostelids were more abundant and colonized substrates faster in aerial microhabitats than in ground litter microhabitats. In this study, comparisons of forests at varying elevations did not conform to the trends noted for Costa Rica (i.e., species diversity did not clearly decrease as elevation increased). Data obtained recently for lowland dry, mesic, wet, and montane wet forests in several localities in Puerto Rico suggest that species richness and colonization is highest for lowland mesic, wet and dry forests lowest for moist montane forests (Spiegel, unpublished data). In general, species from mesic forests of Puerto Rico exhibited microhabitat preferences comparable to those reported for temperate forests. Common species include *P. mycophaga*, *S. cavostelioides*, *N. gracile*, and *S. pseudoendospora*.

On a collecting trip to Puerto Rico in November of 2001, 116 samples of native substrates were collected. Most of these consisted of dead primary plant tissues such as leaves, herbaceous stems, and old inflorescences. Five collections consisted of segments of lianas and six were of tree bark. Fifty-nine percent of all samples collected were aerial, that is, substrates suspended above the ground, and 47 % were of ground litter. Approximately 25 % of the samples were collected from each of the following four general habitat types: lowland wet forests (3 different sites), montane wet forests (2 sites), lowland mesic forests (2 sites), and lowland dry forests (2 sites). The samples collected from the mesic and dry sites were the first surveys carried out for protostelids in these types of habitats in Puerto Rico.

All samples were air-dried and transported to the lab, where they were plated and observed using standard techniques for protostelids (Spiegel 1990). At least one species of protostelid was recovered from 87 % of the samples. One sample from a lowland mesic forest yielded thirteen species. Over 90 % of all samples from each of the lowland forest types contained at least one species of protostelid. Only 63 % of the samples from montane wet forests contained protostelids. In both types of wet forests, significantly more aerial samples contained protostelids than ground litter collections, while the number of samples with protostelids was approximately equal between aerial and ground litter samples from mesic and dry forests. The average number of species per sample was highest in lowland mesic forests (5 species/sample), slightly lower in lowland wet forests and lowland dry forests (4.7 and 4.5 species/sample, respectively), and lowest in montane wet forests (1.5 species/sample).

Twenty-five of the 32 described species of microscopic protostelids were observed fruiting in cultures prepared from the Puerto Rican samples. The 32 described species include the very small myxomycete *Echinostelium bisporum* and exclude the macroscopic species of *Ceratiomyxa*. In addition, as many as seven possibly undescribed species were observed. The lowland forests were all about equal in species richness, with 19-20 describes species each, while the montane wet forests had much lower species richness, with only twelve described species. The abundant species, recorded from more than 40 % of the samples, were *Protostelium mycophaga*, *Schizoplasmodiopsis amoeboidea*, *Nematostelium gracile*, and *Schizoplasmodiopsis pseudoendospora*. Common species, 10-40 % of all samples, were *Cavostelium apophysatum*, *Protostelium arachisporum*, *Soliformovum irregularis*, *So. expulsus*, *N. ovatum*, *E. bisporum*, and *P. nocturnum*. Of the abundant and common species, the *Nematostelium* spp. were the only ones equally common in all habitat types. Most of the rest were either less common in the montane wet forest or both the wet forest types. *Protostelium mycophaga* clearly preferred lowland mesic forests.

The number of described species observed is consistent with what has been found for a similar collecting effort on the island of Hawaii (Spiegel, unpublished data), another region of the tropics. However, the number of potentially undescribed species is considerably less than that found in Hawaii. The patterns of species richness and frequency are very similar to Hawaii except for lowland dry forests. In both Hawaii and Puerto Rico, the average number of species per sample was highest in lowland mesic forests, slightly lower in lowland wet forests and very low in montane wet forests (Spiegel & al. 2002). However, lowland dry forests in Hawaii are very species poor, while those in Puerto Rico have a level of species richness that is similar to that of lowland wet forests.

In a study of the colonization of introduced sterile substrates by protostelids in the wet forests of Puerto Rico, Moore & Spiegel (2000a) reported that species richness and frequency decreased with increasing elevation. This study of protostelids on natural substrates is consistent with those results. Moore & Spiegel (2000a) also reported that protostelids such as *Nematostelium* spp. that are most common in the ground litter in temperate habitats are more commonly found on aerial substrates in Puerto Rican wet forests. This is true for natural substrates as well.

With respect to particular species of protostelids, *Protostelium mycophaga* is the most commonly encountered species in Puerto Rico as is also the case world wide (Olive 1975; Spiegel 1990, unpublished data; Best & Spiegel 1984, Moore & Spiegel 2000b, Spiegel & Stephenson 2000). As in Hawaii, this species is less common in wet forests than in drier habitats (Spiegel, unpublished data). *Nematostelium gracile* is much more common in Puerto Rico than in any other place that has been quantitatively sampled (Moore & Spiegel 2000b; Best & Spiegel 1984; Spiegel, unpublished data). *Cavostelium apophysatum* is common in Puerto Rico as it is in Hawaii (Spiegel, unpublished data). This species is much less common in temperate regions (Moore & Spiegel 2000b; Best & Spiegel 1984), which suggests that it may be primarily a tropical protostelid. With the inclusion of information on protostelids for other regions of the Neotropics, it may be possible to determine how typical the protostelid biota of Puerto Rico is of the Neotropics in particular and the tropics in general.

In summary, results obtained from ecological studies of protostelids in the Neotropics suggest that protostelid assemblages vary considerably from one type of habitat to another. Lowland mesic areas seem to be the "best" places for protostelids, since they tend to exhibit the highest levels of both abundance and species diversity. Studies involving montane moist and wet forests may not accurately reveal the diversity of protostelids. Microhabitat trends of protostelids species also appear to vary with habitat. In more mesic situations, microhabitat trends appear, while in dry or tropical montane habitats, trends do not seem as obvious. Further research on protostelid ecology will provide a more complete picture of their biogeography.

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