
Dictyostelid cellular slime moulds of Mexico

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Surveys for dictyostelid cellular slime moulds (dictyostelids) carried out in various areas of Mexico over the past half century have yielded considerable data on the distribution of these organisms in one region of the Neotropics. The species recovered in these surveys include several forms later described as new to science. The present paper provides a comprehensive overview of what is known about the taxonomy, ecology and distribution of the dictyostelids of Mexico.

Key words – *Acytostelium* – *Dictyostelium* – distribution – Neotropics – *Polysphondylium*

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Introduction

Mexico is a large country geographically, with a diverse topography consisting of high plateaus, mountain ranges that run from north to south and east to west, numerous volcanoes and an extensive coastal plain, wet on the east side but drier on the west. The country extends from the warm temperate zone to well into the subtropics, with a temperate climate at high elevations. A network of good roads provides access to a wide variety of different habitats. In the early 1960's, there were still appreciable areas of forest remaining that could be accessed without going very far off road. At that time, there were no published studies of the cellular slime moulds (dictyostelids) of Mexico. Subsequently, samples for the isolation of these organisms in Mexico have been collected by Cavender in 1961-1963, 1967 and 2011, by Hannah Suthers in 1983-1984 and by Landolt and Stephenson in 1990, 1999, 2000 and 2001.

Methods

In 1960, Cavender began a survey of the dictyostelids associated with various forest types in eastern North America (Cavender & Raper 1965b). The nine species isolated during this survey were described by Raper and others (Raper 1984). However, collecting in southern Florida at Lake Okeechobee and in the Everglades produced two new species that were later described as *Dictyostelium coeruleo-stipes* and *D. rhizopodium*. This suggested that collecting at lower latitudes would produce other new species not occurring in temperate forests. After reading various published works by such ornithologists as Peterson & Fisher (1955), Sutton (1951) and Beebe (1905) for ideas on possible collecting sites in Mexico (bird biologists have a good knowledge of biodiversity), three expeditions were carried out in December 1961, 1962 and 1963. The objective was to collect soils from a wide variety of different forest types, including

montane, cloud and temperate forests in the Sierra Madre Oriental, seasonal evergreen forests on the Atlantic coastal plain, forests of premontane areas and desert, thorn forests and tropical deciduous forests on the west coast from Sinaloa to Oaxaca. The first series of collections, which included a subtropical montane site at Xilitla, San Luis Potosi in the Sierra and a seasonal evergreen forest site near Poza Rica, Veracruz, in the coastal foothills produced a number of new species, including those later described as *Dictyostelium mexicanum*, *D. deminutivum*, *D. tenue*, *D. vinaceo-fuscum*, *D. rhizopodium* and *D. coeruleo-stipes*. Another new species, *D. rosarium* was isolated from a desert area near the base of Volcan Orizaba. These collections confirmed the fact that Mexico was a rich environment for dictyostelids. The 1962 expedition involved collecting samples down the west coast of Mexico in areas of desert, thorn forest and tropical deciduous forest. Collecting sites for the 1963 expedition included more areas of seasonal evergreen forest, cloud forests and tropical deciduous forests in Veracruz, Puebla and Oaxaca. Some of the results of these expeditions were published by Cavender & Raper (1968). A fourth expedition in June 1967 included Veracruz, Jalisco, Oaxaca and Nayarit. By this time, many of the forests near the roads where samples had been collected previously were gone. Recently (June 2011) soil samples from a montane forest on Nevado de Colima were collected by Jeannine Cavender, and these samples produced additional undescribed species. This certainly suggests that Mexico has even more species of dictyostelids yet to be discovered

Each expedition extended over a period of about two weeks. Soil samples were kept protected in a cooler until returned to the laboratory, where they were processed with the method described by Cavender & Raper (1965a). When the earliest expeditions were carried out, many species of dictyostelids had not yet been described or defined well morphologically (e.g., the relatively common *Dictyostelium giganteum*, *D. aureo-stipes*, and *D. implicatum*). Therefore, these do not appear in the data set compiled by Cavender except for the Colima site.

As a professional research assistant to John T. Bonner at Princeton University, Hannah B. Suthers (an avocational bird bander studying songbird ecology), combined birds and dictyostelids in an independent research project that demonstrated the fact that these organisms could be dispersed by migratory songbirds (Suthers 1985). She collected soil samples and samples of bird fecal material along an elevation gradient in Mexico during January 1983 and 1984 while serving as a volunteer bird bander in Princeton University's graduate tropical ecology courses. Samples of soil taken from just beneath the leaf litter to a depth of about 1 cm were scraped into the mouths of wide-mouthed vials of 20 ml (1983) or 40 ml (1984) capacity, with each sample representing about 20-30 g. In the laboratory, dictyostelids were isolated with the method of Cavender & Raper (1965a). Timothy hay, 2-3 years old, was used in the preparation of hay-infusion agar. Incubation was at 21° C under continuous light. Plates were read on the 4th, 5th, 7th, and 14th days. After two weeks, a second series of plates were prepared with the remaining soil. A small amount of each soil sample was dried at room temperature for one week and weighed again to determine moisture content. Clones per gram, absolute density, relative density and frequencies were calculated for each species of dictyostelid isolated at a particular locality. In addition, the species were subcultured and lyophilized for storage.

In July 1990, Landolt visited the Yucatan Peninsula and collected a total of 30 soil samples from tropical deciduous forests in the states of Quintana Roo and Yucatan, 10 samples each from two coastal woodlands south of Cancun and 10 samples from the forest surrounding the site of Chichen Itza. In November 1999, Stephenson collected 25 soil samples, five each from two primary seasonal rain forest sites, two secondary forests and one "swamp" primary forest site within the El Eden Ecological Reserve in the State of Quintana Roo. Also in late 1999, Landolt processed five samples of soil collected by Diana Wrigley de Basanta and Carlos Lado during their collecting visit to a tropical rainforest site at the Tuxtlas Biological Reserve in the State of Veracruz. Landolt and Stephenson traveled to Central Mexico in October 2000, collecting

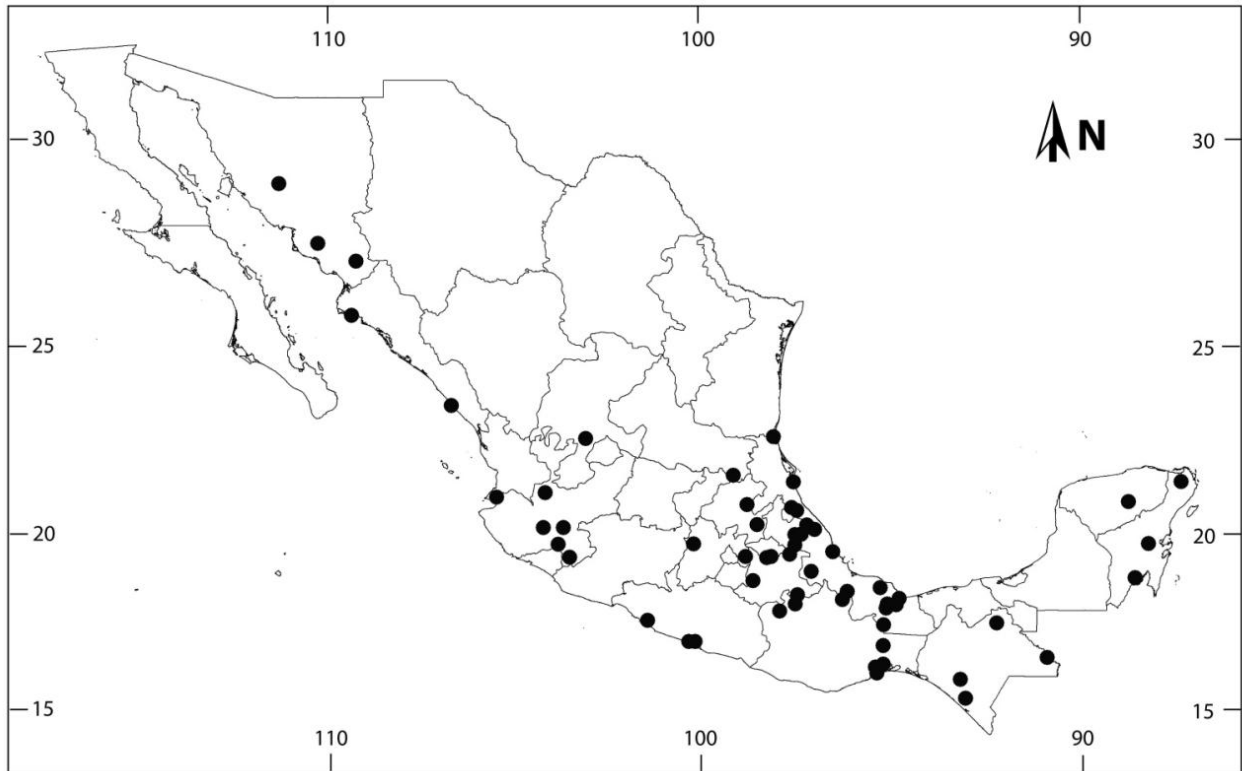


Fig.1 – Outline map of Mexico showing locations of sites sampled for dictyostelids

samples in several different vegetation types in the states of Tlaxcala, Veracruz and Puebla. Ten samples each were obtained from one montane fir forest and one oak (*Quercus laurina*) forest in La Malinche National Park, a cloud forest site near Atzalan, and a tropical deciduous forest near Misantla. A few samples were collected from a stand of pines growing on almost bare volcanic lava at El Esquilon and from an alpine grassland near the top of Cofre de Perote in the State of Veracruz. In July 2001, Stephenson collected five samples each from a montane oak-pine forest near Huayacocotla and a desert shrubland in the Tehuacán-Cuicatlán Biosphere Reserve as well as 10 samples from an *Opuntia*/desert palm community in the same reserve. All samples consisted of 25-50 g of soil/litter placed in individual plastic bags, and all were processed as soon as possible following collection, using the Cavender & Raper (1965a) method.

Results and Discussion

The samples considered in this paper were collected over a period of 50 years by four individuals. Samples were obtained from 14 different states in Mexico, with the total

area extending from Sonora and Tamaulipas in the north to Zacatecas and San Luis Potosi in the central part of the country, to Chiapas, Oaxaca and Guerrero in the south and Quintana Roo and Yucatan on the Yucatan Peninsula (Fig. 1). Types of habitats represented among these samples included everything from coastal plain and lowland swamp forest to oak, pine and alder scrub at 3300 m in the Sierra Mountains. The sample data are divided among five habitat types—desert, thorn forest, tropical deciduous forest, seasonal evergreen rainforest and montane/cloud forest (Table 1).

The majority (417) of the 595 samples collected were from rainforests and montane/cloud forests. At least 33 species of dictyostelids were isolated, with several of these yet to be described, and the average number of clones/g was 229. Information on the species recovered, including data on the relative number of clones for each of the five habitat types as well as the mean values is provided in Tables 2-7. We have arbitrarily divided the list of species into five groups on the basis of their numbers. These groups are (1) very common, (2) common, (3) rare, (4) very rare and (5) extremely rare. *Dictyostelium*

Table 1 Information on collecting sites in Mexico

Abb.	Vegetation type	Place name	State	Latitude/longitude
HE	Desert	Hermosillo	Sonora	29° 04' 00"N; 110° 58'00"W
VN	Desert	Villa Nueva	Zacatecas	22° 21'12"N; 102° 52'59"W
CH	Scrub	Ciudad Hidalgo	Michoacan	19° 34' 00"N; 100° 28'00"W
JL	Desert	Magdalena	Jalisco	20° 55' 00"N; 103° 57'00"W
ODP	Desert	T-CBR*	Oaxaca	17° 59' 04"N; 97° 21'09" W
YAG	Desert	Emilio Portes Gil	Puebla	19° 17' 40"N; 97° 30' 22" W
DSH	Desert	T-CBR*	Puebla	18° 14' 10"N; 97° 17' 58"W
AL	Thorn Forest	Alamos	Sonora	27° 01' 39"N; 108°56'24"W
Ob	Thorn Forest	Ciudad Obregon	Sonora	27° 29' 38"N; 109°56'20"W
CU	Thorn Forest	Culiacan	Sonora	25° 36' 00"N; 109°03'00"W
TP	Thorn Forest	Tehuantepec	Oaxaca	16° 10' 00"N; 95° 12'00"W
AC	Tropical Rain Forest	Acayucan	Veracruz	17° 56' 32"N; 94° 54' 37"W
MT	Tropical Rain Forest	Martinez de Torre	Veracruz	20° 04' 00"N; 97° 03'00"W
AZ	Tropical Semi-evergreen	Alazan	Veracruz	21° 12' 00"N; 97° 24' 00"W
PA	Tropical Rain Forest	Papantla	Veracruz	20° 26' 52"N; 97°19'12"W
CA	Tropical Rain Forest	Sayula de Aleman	Veracruz	17° 52' 52"N; 94°57'39"W
CO	Tropical Rain Forest	Cordoba	Veracruz	18° 51' 30"N; 96°55'51"W
JP	Tropical Rain Forest	Jaltipan de Morelos	Veracruz	17° 58' 00"N; 94° 42'00"W
JC	Tropical Rain Forest	Jesus Carranza	Veracruz	17° 26' 07" N; 95° 01'58"W
LC	Tropical Rain Forest	Las Choapas	Veracruz	17° 59' 00"N; 94° 56'00"W
PR	Tropical Rain Forest	Poza Rica	Veracruz	20° 32' 00"N; 97° 27'00"W
PRA	Tropical Rain Forest	Poza Rica	Veracruz	20° 32' 00"N; 97° 27' 00"W
ST	Tropical Rain Forest	San Andres Tuxtlas	Veracruz	18° 25' 00"N; 95° 07' 00"W
TB	Semi-evergreen Forest	Tierra Blanca	Veracruz	18° 19' 00"N; 95° 59' 00"W

Table 1 Continued. Information on collecting sites in Mexico

Abb.	Vegetation type	Place name	State	Latitude/longitude
TX	Semi-evergreen Forest	Tuxpan/Alazan	Veracruz	21° 12' 00''N; 97° 24' 00''W
TUX	Semi-evergreen Forest	Tuxtepec	Oaxaca	18° 06'00''N; 96° 07'00''W
EIE	Semi-evergreen Forest	El Eden Ecol.Reserve	Quintana Roo	21° 13' 00''N; 87° 11'00''W
MTX	Tropical Rain Forest	Los Tuxtlas Reserve	Veracruz	18° 08'00''N; 94° 37'00''W
BL	Semi-evergreen Forest	Boca Lacantun	Chiapas	16° 34'50''N; 90° 42'50''W
RI	Semi-evergreen Forest	Zihuatanejo	Guerrero	17° 33'18''N; 101°15'10''W
RIX	Semi-evergreen Forest	Zihuantanejo	Guerrero	17° 33'18''N; 101°15'10''W
FCP	Semi-evergreen Forest	Felipe Carrillo Puerto	Quintana Roo	19° 34'43'' N; 88° 02' 43''W
SF	Semi-evergreen Forest	San Felipe	Quintana Roo	18° 40' 37''N; 88° 23'43''W
PAL	Tropical Rain Forest	Palenque	Chiapas	17° 29'33''N; 92° 02'47''W
GP	Semi-evergreen Forest	Victoria	Chiapas	15° 30 '00''N; 92° 52' 00''W
HJ	Tropical Deciduous Forest	Huajuapán de León	Oaxaca	17°48' 00''N; 97° 46' 00''W
MM	Tropical Deciduous Forest	Matamoros	Puebla	18° 36' 00''N; 98° 28' 00''W
MR	Tropical Deciduous Forest	Matias Romero	Oaxaca	16° 52'95''N; 95° 02' 00''W
MZ	Tropical Deciduous Forest	Mazatlan	Sinaloa	23° 13'12''N; 106°25'12''W
PV	Tropical Deciduous Forest	Puerto Vallarta	Nayarit	20° 48' 00''N; 105°14' 00''W
TA	Tropical Deciduous Forest	Tampico	Tamaulipas	22° 23'46''N; 97° 56'13''W
TC	Tropical Deciduous Forest	Tehuantepec	Oaxaca	16° 24'24''N; 95° 02' 00''W
TT	Tropical Deciduous Forest	Tehuantepec	Oaxaca	16° 19'28''N; 95° 14'20''W
VA	Tropical Deciduous Forest	Las Vallas	Jalisco	19° 13'11''N; 103°18'17''W
VC	Tropical Deciduous Forest	Veracruz	Veracruz	19° 22'00''N; 96° 22' 00''W
TF	Tropical Deciduous Forest	Misantla	Veracruz	19° 57' 20''N; 96° 50' 51'' W
QR	Tropical Deciduous Forest	Chichen Itza	Yucatan	20° 40' 58''N; 88° 34' 07'' W
AT	Montane Forest	Altotongo	Veracruz	19° 48'00''N; 97° 18' 00''W
XI	Montane Forest	Xilitla	San Luis Potosi	21° 23'02''N; 98° 59'24'' W
TO	Cloud Forest	Huachinango	Puebla	20°05' 00''N; 98° 22' 00''W

Table 1 Continued. Information on collecting sites in Mexico

Abb.	Vegetation type	Place name	State	Latitude/longitude
MX	Montane (Pine) Forest	P.N. Izta/Popo	Mexico	19° 14' 10'' N; 98° 39' 48'' W
TZ	Cloud Forest	Tezuitlan	Puebla	19° 49' 04'' N; 97° 22' 00'' W
Clma	Montane Forest	Nevado de Colima	Jalisco	19° 33' 48'' N; 103° 36' 30'' W
VM	Montane Forest	Volcan Malintzi	Tlaxcala	19° 14' 29'' N; 97° 59' 38'' W
OT	Montane (Oak) Forest	Malinche Nat. Pk.	Tlaxcala	19° 12' 51'' N; 98° 06' 38'' W
CF	Cloud Forest	Atzalan	Veracruz	19° 49' 41'' N; 97° 12' 05'' W
MID	Montane Forest	Cofe de Perote	Veracruz	19° 32' 22'' N; 97° 21' 59'' W
MOP	Montane Forest	Huayacocotla	Veracruz	20° 36' 29'' N; 98° 37' 32'' W
OAK	Montane (Oak) Forest	El Triunfo Nat. Pk.	Chiapas	16° 00' 00'' N; 93° 00' 00'' W
PC	Montane Forest	El Triunfo Nat. Pk.	Chiapas	16° 00' 00'' N; 93° 00' 00'' W
CH	Montane Forest	El Triunfo Nat. Pk.	Chiapas	16° 00' 00'' N; 93° 00' 00'' W
EJ	Cloud Forest	El Triunfo Nat. Pk.	Chiapas	16° 00' 00'' N; 93° 00' 00'' W
TR	Montane Forest	El Triunfo Nat. Pk.	Chiapas	16° 00' 00'' N; 93° 00' 00'' W
SM	Montane Forest	Puerto de Gallo	Guerrero	17° 00' 00'' N; 100° 10' 00'' W
CG	Montane Forest	Ciudad Guzman	Jalisco	20° 00' 00'' N; 103° 28' 00'' W
PG	Montane Forest	Puerto de Gallo	Guerrero	17° 00' 00'' N; 100° 10' 00'' W
COL	Montane Forest	Nevado de Colima	Jalisco	20° 00' 00'' N; 104° 00' 00'' W
PNN	Montane Forest	Nevado de Colima	Jalisco	20° 00' 00'' N; 104° 00' 00'' W

Table 2 Numbers of clones for species of dictyostelids isolated from soil/litter samples collected from desert sites in Mexico. Relative density (Rel. Dens.) = number of clones of a particular species/total number of clones. Site abbreviations are given in Table 1.

	Sites							Totals	Rel. Dens.
	HE	VN	CH	JL	ODP	YAG	DSH		
Number of samples	5	5	5	5	10	5	5	40	
<i>Polysphondylium violaceum</i>	88							88	0.484
<i>Dictyostelium mucoroides</i>			34	2				36	0.198
<i>Dictyostelium</i> spp.			3		19			22	0.121
<i>Polysphondylium pallidum</i>	13			8				21	0.115
<i>Dictyostelium purpureum</i>	13							13	0.071
<i>Dictyostelium implicatum</i>						1		1	0.005
<i>Dictyostelium rosarium</i>					1			1	0.005
Number of species	3	0	2	2	2	1	0	7	Avg. 1.7
Total clones	114	0	37	10	20	1	0	182	Avg. 26
Clones/gram	317	0	123	33	50	3	0		Avg. 75

Table 3 Numbers of clones for species of dictyostelids isolated from soil/litter samples collected from thorn forest sites in Mexico. Relative density (Rel. Dens.) = number of clones of a particular species/total number of clones. Site abbreviations are given in Table 1.

	Sites				Totals	Rel. Dens.
	AI	Ob	CU	TP		
	8	6	6	5	25	
<i>Polysphondylium violaceum</i>	216	4	17		237	0.545
<i>Polysphondylium pallidum</i>	92	3	6	3	104	0.240
<i>Dictyostelium purpureum</i>	25		16	8	49	0.113
<i>Dictyostelium mucoroides</i>	8		13		21	0.048
<i>Dictyostelium polycephalum</i>	16		1	1	18	0.041
<i>Dictyostelium mexicanum</i>	1	3	1		5	0.011
<i>Dictyostelium</i> spp.			1		1	0.002
Number of species	6	3	7	3	7	Avg. 4.75
Total clones	358	10	55	12	435	Avg. 109.8
Clones/ gram	746	28	156	40		Avg. 243

mucoroides ranks at the top of the list of very common species, a position it has occupied in most surveys carried out worldwide, including Patagonia (Vadell et al. 2011) and Japan (Cavender & Kawabe (1989). In some regions such as Arkansas (Landolt et al. 2009) and India (Cavender & Lakhanpal 1986), *Polysphondylium pallidum* has been reported as the single most abundant species. However, the totals compiled for *D. mucoroides* do include some clones of *D. leptosomum*, *D. giganteum*, *D. implicatum* and *D. aureostipes*, all of which were not well differentiated species when the surveys began in the early 1960's. *Polysphondylium violaceum* is a close second in overall abundance, with *P. pallidum* and *D. purpureum* the third and fourth most abundant species. These same species are very common in the temperate forests of the eastern United States, along with *D. minutum*, as reported by Cavender & Vadell (2006) for Ohio, Landolt & Stephenson (1989) for West Virginia and Landolt et al. (2006) for the Great Smoky Mountains National Park. Common species in Mexico are *D. minutum*, *D. tenue*, *D. polycephalum* and several unidentified species of *Dictyostelium*, most of which were probably small species belonging to phylogenetic group III (Schaap et al. 2006). Ten small species in this same group have been described recently from isolates collected in Belize and Guatemala (Cavender et al. unpublished). Rare species are *Dictyostelium vinaceo-fuscum*, *D. discoideum*, *Polysphondylium* spp. (either unidentified or possibly undescribed) and what has been considered as *D. macrocephalum*. The latter actually may turn out to be *D. sphaerocephalum* on the basis of genetic studies carried out by Romeralo et al (2007). A number of the light-spored species of *Polysphondylium* may be the same as those described from Tikal, Guatemala (Vadell & Cavender 1998). Most other species recovered (a total of 21) are either very rare or extremely rare. These include several species (e.g., *Dictyostelium deminutivum*, *D. rhizopodium* and *D. granulophorum*) restricted to rainforests as well as several others that appear to be confined to specialized habitats. Prominent examples are *D. rosarium*, which occurs in drier,

saltier soils, and *D. polycarpum* or *D. menorah*, found only at high elevations in montane/cloud forest habitats. *Guttulina*, listed for the rainforest habitat, is an acrasid cellular slime mould and not a dictyostelid. It is associated with rainforests inhabited by howler monkeys and spider monkeys. The extremely rare species *D. lacteum* is common in the deciduous forests of Ohio and West Virginia, as is also the case for the rare Mexican species, *D. giganteum*. Some species appear to be restricted to tropical or subtropical forests. These include *D. citrinum*, *D. coeruleostipes* and *D. mucoroides* var. *stoloniferum*. However *D. aureo-stipes* and *D. giganteum* are perhaps not as rare as their position in the table indicates, because they were not recognized as such in early surveys by Cavender.

Deserts and thorn forests are very dry environments but contained nine species. Thorn forests can be productive after a period of rain, as was the case during the present study. The average number of clones/g (243) recorded was actually higher than the overall average (229) for the entire study. The numbers for *Polysphondylium violaceum* are higher than is generally the case for the other habitats. This is possibly because drier soils are more alkaline, a condition favored by *P. violaceum* in Ohio (Cavender & Hopka 1986). Thorn forests are distinguished by the presence of the very rare *D. mexicanum*.

Tropical deciduous forests had 14 species, which is twice the number recorded for thorn forests. *Dictyostelium mucoroides* is extraordinarily abundant, with almost as many clones as all of the other very common species combined. Of the latter, *D. purpureum* is the most abundant, and is better represented here than in any other habitat. However, while *D. minutum*, a common species in Mexican montane forests is absent from the tropical deciduous collections, *Dictyostelium tenue*, *D. macrocephalum* (probably *D. sphaerocephalum*, Romeralo et al, 2007) and *D. vinaceo-fuscum* (a crampon-based species) are common. This is the only forest type where *P. tenuissimum* was found. Tropical deciduous forests had the most species per collecting site but lack many of the very rare and extremely rare species.

Table 4 Numbers of clones of species of dictyostelids isolated from soil/litter samples collected from tropical deciduous forest sites in Mexico. Relative density (Rel. Dens.) = number of clones of a particular species/total number of clones. Site abbreviations given in Table 1.

Site	Sites												Totals	Rel. Dens.
	HJ	MM	MR	MZ	PV	TA	TC	TT	VA	VC	TF	QR		
Number of samples	5	10	5	8	5	10	10	5	5	10	10	30	113	
<i>Dictyostelium mucoroides</i>	56	116	44	173	49	22		5	53	38			556	0.320
<i>Dictyostelium purpureum</i>			4	41	2	11	24	2	2	16	161	61	324	0.187
<i>Polysphondylium pallidum</i>	2	54	8	40	3	25		9	3	56			200	0.115
<i>Polysphondylium violaceum</i>	10	75	7	33	3	20	1	6	9	2	4	13	183	0.105
<i>Dictyostelium vinaceo-fuscum</i>			10									67	77	0.044
<i>Dictyostelium cf. tenue</i>		15	15	5	8	19	1		3			5	71	0.041
<i>Dictyostelium macrocephalum</i>											1	67	68	0.039
<i>Polysphondylium cf. tenuissimum</i>												64	64	0.037
<i>Polysphondylium</i> spp.											1	58	59	0.034
<i>Acytostelium leptosomum</i>	1	7	4		1	2				24		1	40	0.023
<i>Dictyostelium mexicanum</i>							4					23	27	0.016
<i>Dictyostelium polycephalum</i>	8	6				1		5	1	1		4	26	0.015
<i>Dictyostelium monochasioides</i>												25	25	0.014
<i>Dictyostelium</i> spp.									3		2	10	15	0.009
Number of species	5	6	7	5	6	7	4	5	7	6	8	9	14	Avg. 6.25
Total clones	77	273	92	292	66	100	30	27	74	137	222	345	1735	Avg. 145
Clones/ gram	255	544	305	811	217	165	50	90	247	230	555	309		Avg. 315

Table 5 Numbers of clones of species of dictyostelids isolated from samples collected from seasonal rain and semi-evergreen forest sites. Relative density (Rel. Dens.) = number of clones of a particular species/total number of clones. Site abbreviations given in Table 1.

	Site												
	AC	MT	AZ	PA	CA	CO	JP	JC	LC	PR	PRA	ST	TB
Number of samples	5	5	5	10	5	6	10	5	16	7	10	10	5
<i>Dictyostelium mucoroides</i>	83	12	18	40	48	63	186	51	58	23	38	143	49
<i>Polysphondylium pallidum</i>	254	10	6	7	1	4	29	29	31	14	13	314	2
<i>Dictyostelium cf. tenue</i>	14	2	3	13	1		107	1			121		1
<i>Dictyostelium purpureum</i>	1	7	34	19		2	5	4	8	4	27	6	4
<i>Polysphondylium violaceum</i>	98				1		8	4		9	25	9	1
<i>Dictyostelium vinaceo-fuscum</i>		4		1						100	55		
<i>Dictyostelium polycephalum</i>			48	25		1				7	11	4	1
<i>Dictyostelium</i> spp.			1										
<i>Polysphondylium</i> spp.													
<i>Dictyostelium minutum</i>				33					5	2	12		
<i>Dictyostelium rhizopodium</i>							12	2			27	1	
<i>Dictyostelium aureo-stipes</i>													
<i>Dictyostelium sphaerocephalum</i>													
<i>Dictyostelium deminutivum</i>				3							3		
<i>Dictyostelium giganteum</i>											2		
<i>Guttulinopsis nivea</i>													
<i>Dictyostelium granulophorum</i>													
<i>Dictyostelium discoideum</i>	2												
<i>Acytostelium leptosomum</i>				1			2						
<i>Dictyostelium mexicanum</i>											4		
<i>Dictyostelium mucoroides</i> var. <i>stoloniferum</i>													
<i>Dictyostelium citrinum</i>													
<i>Dictyostelium coeruleo-stipes</i>												1	
<i>Dictyostelium macrocephalum</i>													
Number of species	6	5	6	9	4	4	7	6	4	7	12	7	6
Total clones	452	35	110	142	51	70	349	91	102	159	338	478	58
Clones/ gram	1505	117	375	233	170	194	585	305	105	379	565	951	193

Table 5 Continued. Numbers of clones of species of dictyostelids isolated from samples collected from seasonal rain and semi-evergreen forest sites. Relative density (Rel. Dens.) = number of clones of a particular species/total number of clones. Site abbreviations given in Table 1.

	Site											Totals	Rel. Dens.
	TX	TUX	EIE	MTX	BL	RI	RIX	FCP	SF	PAL	GP		
Number of samples	10	8	25	5	10	10	10	10	10	10	10	217	
<i>Dictyostelium mucoroides</i>	166	33	2	6	26	6		2	4	2		1059	0.330
<i>Polysphondylium pallidum</i>	8	3	8		26	1		6	5	3		774	0.241
<i>Dictyostelium cf. tenue</i>	4											267	0.083
<i>Dictyostelium purpureum</i>	10		46	1	29	2	1	9	1	1		221	0.067
<i>Polysphondylium violaceum</i>	36		7		5	3		1	2			209	0.065
<i>Dictyostelium vinaceo-fuscum</i>		3	4									167	0.052
<i>Dictyostelium polycephalum</i>	11	1	14					11	3	4		141	0.044
<i>Dictyostelium</i> spp.			5		92	8						106	0.033
<i>Polysphondylium</i> spp.			20	40	1							61	0.019
<i>Dictyostelium minutum</i>					4					1		57	0.018
<i>Dictyostelium rhizopodium</i>	1											43	0.013
<i>Dictyostelium aureo-stipes</i>			32		1	1	1		2			37	0.012
<i>Dictyostelium sphaerocephalum</i>					1	15						16	0.005
<i>Dictyostelium deminutivum</i>			2		4				1			13	0.004
<i>Dictyostelium giganteum</i>					7					2		11	0.003
<i>Guttulinopsis nivea</i>								3		7		10	0.003
<i>Dictyostelium granulophorum</i>			7									7	0.002
<i>Dictyostelium discoideum</i>	2							1				5	0.002
<i>Acytostelium leptosomum</i>			1									4	0.001
<i>Dictyostelium mexicanum</i>												4	0.001
<i>Dictyostelium mucoroides</i> var. <i>stoloniferum</i>					2							2	0.001
<i>Dictyostelium citrinum</i>			1									1	<0.001
<i>Dictyostelium coeruleo-stipes</i>												1	<0.001
<i>Dictyostelium macrocephalum</i>				1								1	<0.001
Number of species	8	4	13	4	12	7	2	7	7	7	0		Avg. 6.4
Total clones	238	40	149	48	198	36	2	33	18	20	0		Avg. 134
Clones/ gram	370	167	149	240	158	90	10	83	18	20	0		Avg. 291

Table 6 Numbers of clones of dictyostelid species isolated from soil/litter samples collected from montane and cloud forest sites. Relative density (Rel. Dens.) = number of clones of a particular species/total number of clones. Site abbreviations given in Table 1.

	Sites												
	AT	XI	TO	MX	TZ	Clma	VM	OT	CF	MID	MOP	OAK	PC
Number of samples	5	20	10	5	10	14	10	10	10	1	5	10	10
<i>Dictyostelium mucoroides</i>	2	35	144	65	21	49	256	22		91	12	2	28
<i>Dictyostelium minutum</i>			70			140	80						
<i>Dictyostelium discoideum</i>	13	8	28		17	7		2	6			5	10
<i>Dictyostelium polycephalum</i>		58	2			1						1	
<i>Polysphondylium pallidum</i>		36	1	2			1				2	1	3
<i>Polysphondylium violaceum</i>		6	1		19	14							6
<i>Dictyostelium cf. tenue</i>		44											
<i>Dictyostelium giganteum</i>						9			19			5	
<i>Dictyostelium menorah</i>						16							
<i>Dictyostelium purpureum</i>		4	1									8	
<i>Dictyostelium</i> spp.		1					14						
<i>Polysphondylium candidum</i>						5		1					
<i>Dictyostelium sphaerocephalum</i>													
<i>Polysphondylium</i> spp.						2			1				
<i>Acytostelium leptosomum</i>			2										
<i>Acytostelium</i> spp.						1							
<i>Dictyostelium aureo-stipes</i>						1						1	
<i>Dictyostelium lacteum</i>											1		
<i>Dictyostelium cf. polycarpum</i>							2						
Number of species	2	8	8	2	3	11	5	3	3	1	3	7	4
Total clones	15	193	249	67	57	245	353	28	26	91	15	23	47
Clones/ gram	50	483	415	233	95	292	473	70	65	1517	75	58	51

Table 6 Continued. Numbers of clones of dictyostelid species isolated from soil/litter samples collected from montane and cloud forest sites. Relative density (Rel. Dens.) = number of clones of a particular species/total number of clones. Site abbreviations given in Table 1.

	CH	EJ	TR	SM	CG	PG	COL	PNN	Totals	Rel. Dens.
Number of samples	10	10	10	10	10	10	10	10	200	
<i>Dictyostelium mucoroides</i>	16	86	169	4	4	1	4		1011	0.590
<i>Dictyostelium minutum</i>				1			3		294	0.172
<i>Dictyostelium discoideum</i>					1				97	0.057
<i>Dictyostelium polycephalum</i>									62	0.036
<i>Polysphondylium pallidum</i>									46	0.027
<i>Polysphondylium violaceum</i>						1			47	0.027
<i>Dictyostelium cf. tenue</i>									44	0.026
<i>Dictyostelium giganteum</i>	10								43	0.025
<i>Dictyostelium menorah</i>									16	0.009
<i>Dictyostelium purpureum</i>				2					15	0.009
<i>Dictyostelium</i> spp.									15	0.009
<i>Polysphondylium candidum</i>									6	0.004
<i>Dictyostelium sphaerocephalum</i>						3			3	0.002
<i>Polysphondylium</i> spp.									3	0.002
<i>Acytostelium leptosomum</i>									2	0.001
<i>Acytostelium</i> spp.									1	0.001
<i>Dictyostelium aureo-stipes</i>									2	0.001
<i>Dictyostelium lacteum</i>									1	0.001
<i>Dictyostelium cf. polycarpum</i>									2	0.001
Number of species	2	1	1	3	4	1	2	0	19	Avg. 3.5
Total clones	26	86	169	7	9	1	7	0	1714	Avg. 82
Clones/ gram	65	214	423	18	22	3	18	0		Avg. 221

Table 7 Species of dictyostelids isolated from five vegetation types ranked on the basis of relative density.

Vegetation Types	DST	THN	SR/SE	TD	MC	Totals	Avg. RD
Number of samples	40	25	217	113	200	595	(Tot RD/5000)
<i>Dictyostelium mucoroides</i>	198	48	330	320	590	1486	0.297
<i>Polysphondylium violaceum</i>	484	545	65	105	27	1226	0.245
<i>Polysphondylium pallidum</i>	115	240	241	115	27	738	0.148
<i>Dictyostelium purpureum</i>	71	113	67	187	9	447	0.089
<i>Dictyostelium minutum</i>			18		172	190	0.038
<i>Dictyostelium</i> spp.	121	2	33	9	9	174	0.035
<i>Dictyostelium</i> cf. <i>tenue</i>			83	41	26	150	0.030
<i>Dictyostelium polycephalum</i>		41	44	15	36	136	0.027
<i>Dictyostelium vinaceo-fuscum</i>			52	44		96	0.019
<i>Dictyostelium discoideum</i>			2		57	59	0.012
<i>Polysphondylium</i> spp.			19	34	2	55	0.011
<i>Dictyostelium macrocephalum</i>			1	39		40	0.008
<i>Polysphondylium</i> cf. <i>tenuissimum</i>				37		37	0.007
<i>Dictyostelium giganteum</i>			3		25	28	0.006
<i>Dictyostelium mexicanum</i>		11	1	16		28	0.006
<i>Acytostelium leptosomum</i>			1	23	1	25	0.005
<i>Dictyostelium monochasioides</i>				14		14	0.003
<i>Dictyostelium aureo-stipes</i>			12		1	13	0.003
<i>Dictyostelium rhizopodium</i>			13			13	0.003
<i>Dictyostelium menorah</i>					9	9	0.002
<i>Dictyostelium sphaerocephalum</i>			5		2	7	0.001
<i>Dictyostelium implicatum</i>	5					5	0.001
<i>Dictyostelium rosarium</i>	5					5	0.001
<i>Dictyostelium deminutivum</i>			4			4	0.001
<i>Polysphondylium candidum</i>					4	4	0.001
<i>Guttulinopsis nivea</i>			3			3	0.001
<i>Dictyostelium granulophorum</i>			2			2	< 0.001
<i>Acytostelium</i> spp.					1	1	< 0.001
<i>Dictyostelium citrinum</i>			1			1	< 0.001
<i>Dictyostelium coeruleo-stipes</i>			1			1	< 0.001
<i>Dictyostelium lacteum</i>					1	1	< 0.001
<i>Dictyostelium mucoroides</i> var. <i>stoloniferum</i>			1			1	< 0.001
<i>Dictyostelium</i> cf. <i>polycarpum</i>					1	1	< 0.001
Total number of species	7	7	24	14	19		
Avg. No. species/ collection site	1.7	4.75	6.4	6.25	3.5		
Avg. No. clones/ collection site	26	109.8	135	144	82		
Avg. c/g per collection site	75	243	291	315	221		

The seasonal rain and semievergreen rainforests had the highest biodiversity of dictyostelids with 24+ species. This is among the highest diversities recorded for a tropical forest and can be compared to the 35 species reported by Vadell et al. (1995) for Tikal in Guatemala, 27 for the Amazon (Cavender 1996) or Iguazu in Argentina, where Vadell &

Cavender (2007) listed 27 species. The Tikal and Iguazu sites are characterized by the highest numbers of species known for any single, localized collections sampled worldwide. The 33+ species for Mexico as a whole can be compared to the 26 species known for Japan (Cavender & Kawabe 1989). The number of clones/g (291) in seasonal rain

and semievergreen forests is not high when compared to Ohio (437) and is lower than the total recorded for tropical deciduous forests (315). The number of species per sample site (6.4) is also lower than in Ohio (8.7). These data suggest that there are more species of dictyostelids to be found in Mexican rain forests, but they are extremely rare. The leading species in the group of very common species are *Dictyostelium mucoroides* and *Polysphondylium pallidum*, in the common group it is *D. tenue*, and in the rare group *D. vinaceo-fuscum*. Two other crampon-based species occur very rarely—*D. rhizopodium* and, extremely rarely, *D. coeruleo-stipes*. *Dictyostelium aureo-stipes*—not recorded in the 1960's, is definitely more common than indicated in the tables. A single isolate of *D. discoideum* (AC4) was collected in rainforest. The occurrence of *D. minutum* is doubtful because the small rainforest group 3 isolates could belong to any one of a number of other small species which are currently being described (Cavender, unpublished data).

Rainforest dictyostelid biodiversity in Mexico is distinguished by the high number (12) of very rare and extremely rare species. Montane/cloud forest had the next highest biodiversity (19 species), although *Dictyostelium mucoroides* was the most prominent species, followed by *D. minutum*. This is the same order of abundance found in the Great Smoky Mountains National Park, where 17 of the 26 sites sampled were mid- to high-elevation (Landolt et al. 2006). *Dictyostelium discoideum* was also common in both areas. However, the Mexican sites also commonly had *Dictyostelium polycephalum* and *D. tenue*. *Dictyostelium giganteum* was more abundant than in other forest types, while *P. candidum*, *D. lacteum* and *D. menorah* were found only there. Numbers of clones/g (221) and species per collecting site (3.5) were next to lowest. A low number for average clones/g (143) was also the case in the Great Smoky Mountains.

There is little doubt that Mexico will produce other species of dictyostelids if more collecting is carried out in rainforest, tropical deciduous and montane/cloud forests. In addition, there will be a number of new species to be described from these collections in the future.

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