

Myxomycetes associated with dryland ecosystems of the Tehuacán-Cuicatlán Valley Biosphere Reserve, Mexico

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Estrada-Torres, A., Wrigley de Basanta, D., Conde, E. and Lado, C. (2009). Myxomycetes associated with dryland ecosystems of the Tehuacán-Cuicatlán Valley Biosphere Reserve, Mexico. *Fungal Diversity* 36: 17-56.

The results of a biodiversity survey of a xeric Mexican Biosphere Reserve are presented. This survey represents the first intensive study of cacti and succulent plants ever carried out for myxomycetes. The results include 104 species and one variety, identified from 1200 records from field and moist chamber culture collections. Two new species (*Didymium tehuacanense* and *Perichaena stipitata*), found on decayed remains of succulent plants, are described. Eleven species (*Comatricha reticulospora*, *Cribraria lepida*, *Didymium clavodecus*, *D. eremophilum*, *D. orthonemata*, *D. sturgisii*, *D. subreticulosporum*, *Licea belmontiana*, *Macbrideola oblonga*, *M. synsporos* and *Perichaena quadrata*) are new records for the Neotropics, and seven others taxa have not been recorded previously from Mexico. Taxonomic comments, data on distribution and SM, LM and SEM micrographs of selected species are included. An analysis of the relationships that exist between myxomycetes and the substrates on which they develop confirms the presence of a distinct assemblage of myxomycetes associated with specific plants from arid environments. Hypotheses are proposed for the patterns of species distribution and the ecological requirements of this specialised myxobiota.

Key words: Agavaceae, arid zones, Cactaceae, distribution, ecology, Eumycetozoa, microhabitat, succulent plants, xerophyllous scrubland.

Article Information

Received 16 January 2008

Accepted 2 March 2009

Published online 31 May 2009

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Introduction

The myxomycetes are a group of holotrophic eukaryotic organisms that have a motile amoeboid phase in their life cycle, and a spore-forming reproductive phase similar to the fungi (Stephenson and Stempen, 1994; Everhart and Keller, 2008). They are found in almost all terrestrial ecosystems and are particularly abundant in temperate and tropical forests (Ing, 1994; Rojas and Stephenson, 2008; Kosheleva *et al.*, 2008). Although some species are known to be present in warm dryland ecosystems (Ing, 1994), few studies have been carried out to characterize the myxomycete assemblages from these areas. Evenson (1961) reported 22 species from the desert and semi-desert areas of Arizona. Later, Blackwell and Gilbertson (1980b) indicated that 46 species were known from the Sonoran desert, the most common

substrates for field collections being cacti and the dung of herbivores. Novozhilov *et al.* (2003) reported a great richness and variety of myxomycetes from the dry and semi-desert region of the Colorado Plateau, finding 93 species and one variety. Lado *et al.* (2007a) reported the presence of 24 species and 11 genera of myxomycetes in the Atacama desert (Chile), probably the driest region of the world. Novozhilov and Schnittler (2008) in winter cold-deserts and steppes of western Mongolia also reported 36 species and 13 genera. An ecological group of species developing on decaying succulent plants was recently identified by Lado *et al.* (1999), among which several previously unknown species were described. These included *Didymium eremophilum* (Blackwell and Gilbertson, 1980a), *D. subreticulosporum* (Moreno *et al.*, 1996; Lizárraga *et al.*, 1998), *D. mexicanum* (Moreno

et al., 1997), *Cribraria zonatispora* (Lado *et al.*, 1999), *Trichia agaves* (Moreno *et al.*, 2000; Mosquera *et al.*, 2000b), *C. fragilis* (Estrada-Torres *et al.*, 2001), *Licea succulenticola* (Mosquera *et al.*, 2003), *D. wildpretii* (Lado *et al.*, 2007b) and *D. umbilicatum* (Wrigley de Basanta *et al.*, 2008b) The presence of these species indicated that a special myxobiota, adapted to arid conditions, and much more numerous and varied than previously imagined, may develop in these environments. An exhaustive study of an arid area of Mexico was undertaken to investigate the relationships that exist between myxomycetes and the plants that live in these warm dryland ecosystems.

Study area

The Tehuacán-Cuicatlán Valley, the most southern of the North American arid zones, was declared a Biosphere Reserve in 1998. It lies between 17°48' and 18°58' North latitude and 97°03' and 97°43' West longitude, in the states of Puebla and Oaxaca (Mexico) (Jaramillo-Luque and González-Medrano, 1983) and covers an area of approximately 10,000 km² (Fig. 14). It is geographically part of the Mixteca-Oaxaqueña Province (Villaseñor *et al.*, 1990) and is made up of broad dry valleys with more humid mountain ranges along each flank. The elevational gradient extends from 600-2,950 m. The annual rainfall ranges from 300 mm in the valleys to 1,000 mm in the mountains, and the mean temperature is 16-30°C.

The climate and topography have promoted the development of numerous plant communities with very high diversity and many endemic species. Twenty-nine different vegetation types have been recognized in this reserve (Valiente-Banuet *et al.*, 2000), and large columnar and candelabra cacti such as species of *Cephalocereus*, *Neobuxbaumia*, *Stenocereus*, *Pachycereus*, *Pilosocereus* and *Myrtillocactus* dominate over extensive areas of the valleys. These xerophyllous scrublands include a number of characteristic types of vegetation that are named after the most dominant plants growing in them. Examples include “tetechera” with *Neobuxbaumia tetetzo* (Weber) Backeb. (Fig. 1), “cardonal” with *Pachycereus weberi* (Coul.) Buxb. (Fig. 2) and

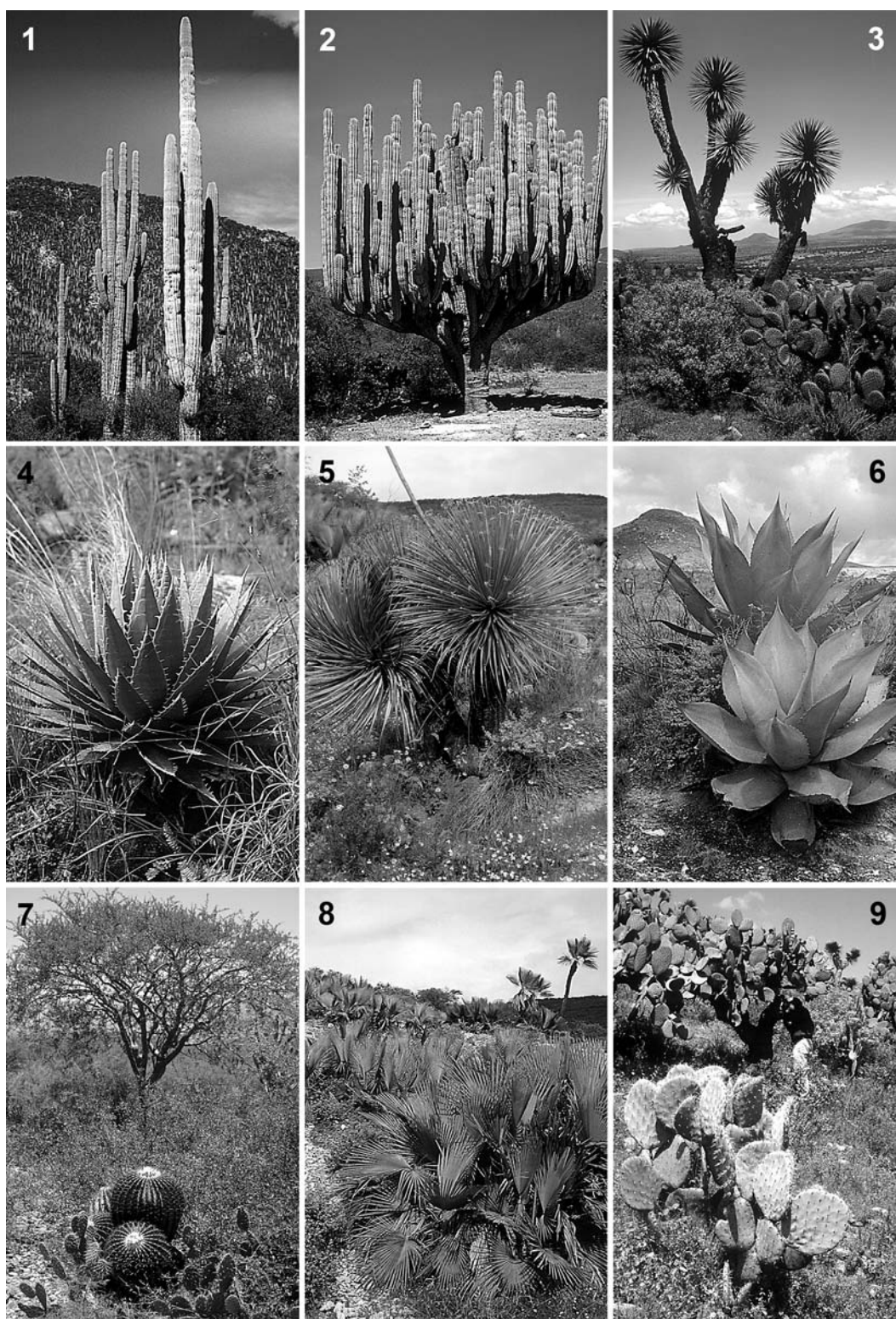
“izotal” with *Yucca periculosa* Baker (Fig. 3) or *Beaucarnea gracilis* Lem. There are spiny scrublands with species of *Dasyllirion*, *Agave*, *Hechtia*, *Echinocactus* or *Opuntia* (Figs. 4-7, 10-12), tropical dry forests with elements of the genera *Bursera* and *Mimosa*, and thorn forest with species of *Prosopis* (Fig. 7) and *Fouquieria*. There are also trees such as the palm *Brahea dulcis* (Kunth) Mart. (Fig. 8), and *Opuntia streptacantha* Lem. (Fig. 9). We have followed the terminology of Valiente-Banuet *et al.* (2000) for these types of vegetation, and have given their equivalents in English, as closely as possible, in the list of localities.

The variety of vegetation in the Tehuacán-Cuicatlán Valley is a result of the elevational gradients and consequent variable climatic conditions. It is influenced also by the heterogeneous rocks and soils which favour a mosaic of plant communities of high species turnover, giving rise to high diversity (Osorio-Beristain *et al.*, 1996). The valley is at the interface of the arid North and the tropical South of Mexico (Rzedowsky, 1973), and is among the drylands with the greatest floristic richness, in spite of its small size (Villaseñor *et al.*, 1990). An estimated 2,700 species from 900 genera of vascular plants grow there, of which about 30% are endemic, and it is considered to be an important centre of diversity for the Cactaceae and the Agavaceae (Arias-Montes, 2000).

The characteristics of this important geographical region, coupled with the fact that the Myxomycete communities of the arid areas of Mexico were little known, afforded a unique opportunity to achieve the principal objective of the present study, to inventory the myxobiota of dryland areas dominated by succulent plants.

Materials and methods

Sampling was done mostly in the arid and sub-arid scrublands, and the tropical deciduous forests of the valley of Tehuacán-Cuicatlán. Other vegetation was also investigated, but this paper only includes results from arid areas generally between 750 and 2,450 m elevation, with an annual precipitation of up to 500 mm, and not those from the more humid zones of the mountains.



Figs 1-9. Some typical plants of the Tehuacán-Cuicatlán Valley. **1.** Desert scrub dominates by *Neobuxbaumia tetetzo* (tetechera). **2.** *Pachycereus weberi*. **3.** *Yucca periculosa*. **4.** *Agave* sp., one of the rosette-leaved plants (rosulifolios). **5.** *Dasyliirion acrotriche*. **6.** *Agave* sp. **7.** *Prosopis* sp. (background) and *Echinocactus platyacanthus* (foreground). **8.** Area dominated by the palm *Brahea dulcis*. **9.** *Opuntia streptacantha* trees (background).

Fieldwork was done in four collecting forays of up to 5 days each, from 1999 to 2003. In total, 36 localities along the length and breadth of the valley were sampled (Fig. 14). In each locality, the microhabitats in which myxomycetes are

known or suspected to occur (Fig. 13), with the exception of the dung of herbivores, were subjected to an intensive survey. Dung was not collected because of the scarcity of large herbivores in the area under study. All

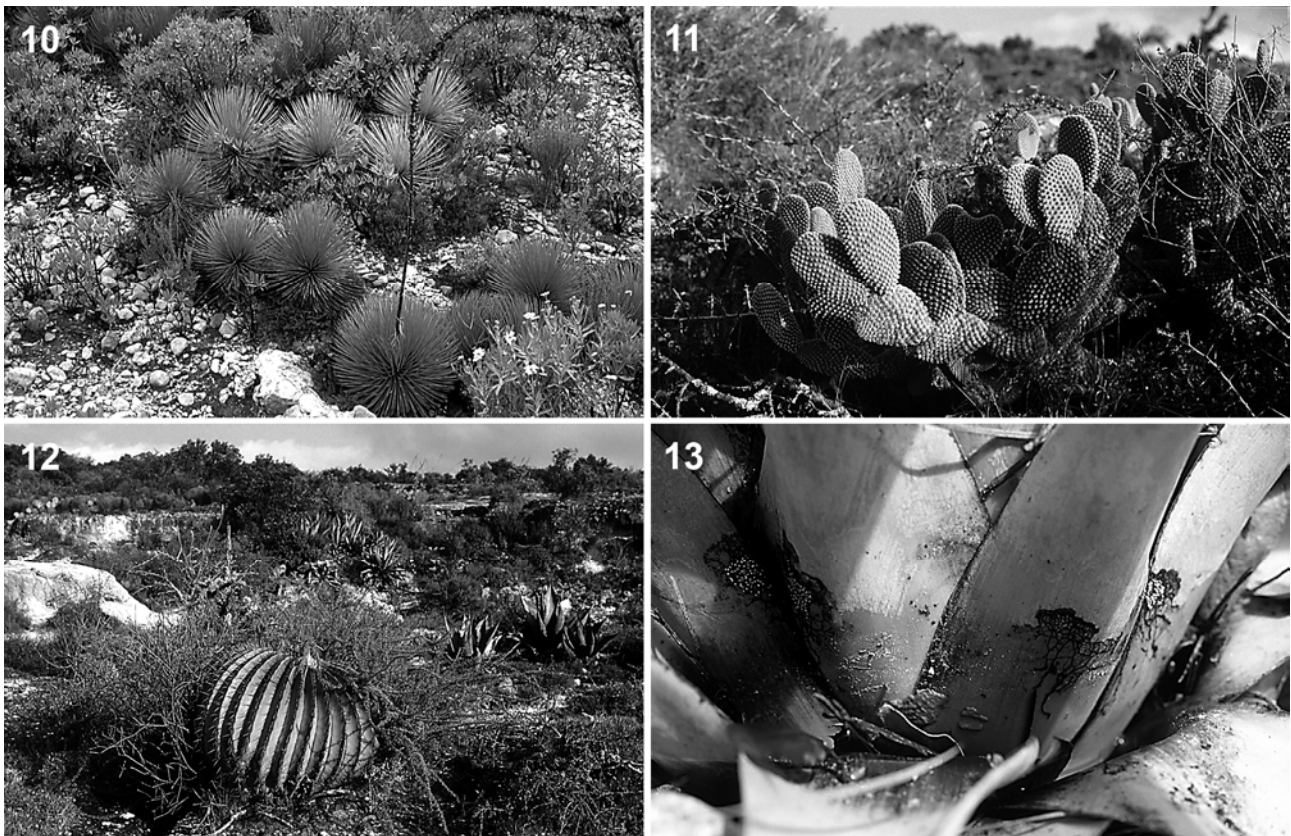


Fig. 10. *Agave stricta* showing the tall inflorescence peduncle. **Fig. 11.** *Opuntia* sp. **Fig. 12.** *Echinocactus platyacanthus* in the foreground of a view of spiny scrubland. **Fig. 13.** A typical microhabitat for desert myxomycetes among the leaf bases of a rosette-leaved plant, showing plasmodia and some fruiting bodies.

localities were georeferenced with a GPS (Garmin 12 model, Datum NAD27) and with topographic maps (1:50,000 series of the Instituto Nacional de Estadística, Geografía e Informática de México, INEGI) for named places. Collection methods were those described by Stephenson (1989), Rossman *et al.* (1998), and Schnittler *et al.* (2002), and included removal of plant material at each site for subsequent laboratory culture.

Moist chamber (mc) cultures were prepared with 145 samples of the various substrates, in the manner described by Mitchell (1977). These substrates included the bark, which forms from the persistent layered epidermal tissue, at the base of the stems of arborescent cacti (Figs. 1-2, 9). Water was added every few days as required, to maintain the humidity for the entire observation period of up to three months. In addition, serial cultures of dead remains of 10 representative species of Cactaceae were done. For each species of cactus, 25 moist chambers were set up, each from a different individual plant of the same species. The species used were *Cephalocereus columna-trajani*, *Echinocactus*

platyacanthus, *Ferocactus latispinus*, *Mammillaria carnea*, *Myrtillocactus geometrizans*, *Opuntia depressa*, *O. pilifera*, *O. tomentosa*, *Pachycereus hollianus* and *P. weberi*. The type of substrate and the pH of each moist chamber culture (taken at 24 hours) were recorded in all instances. Details of the methods used can be found in Stephenson *et al.* (2003). Cultures were examined every day for the first two weeks, and subsequently every 2-3 days for the full culture period of three months. A species recorded from one moist chamber culture was regarded as a single collection, irrespective of the number of sporophores appearing, or the days separating their appearance.

To examine community similarity, the Sørensen coefficient of community (CC) index was used, which considers the presence or absence of species in the study areas compared. Taxonomic diversity was examined using the mean number of species per genus (S/G), which has been used in other studies of myxomycetes (Stephenson *et al.*, 1993) and species richness of the moist chamber cultures was calculated as the number species appearing divided by the number of moist chamber

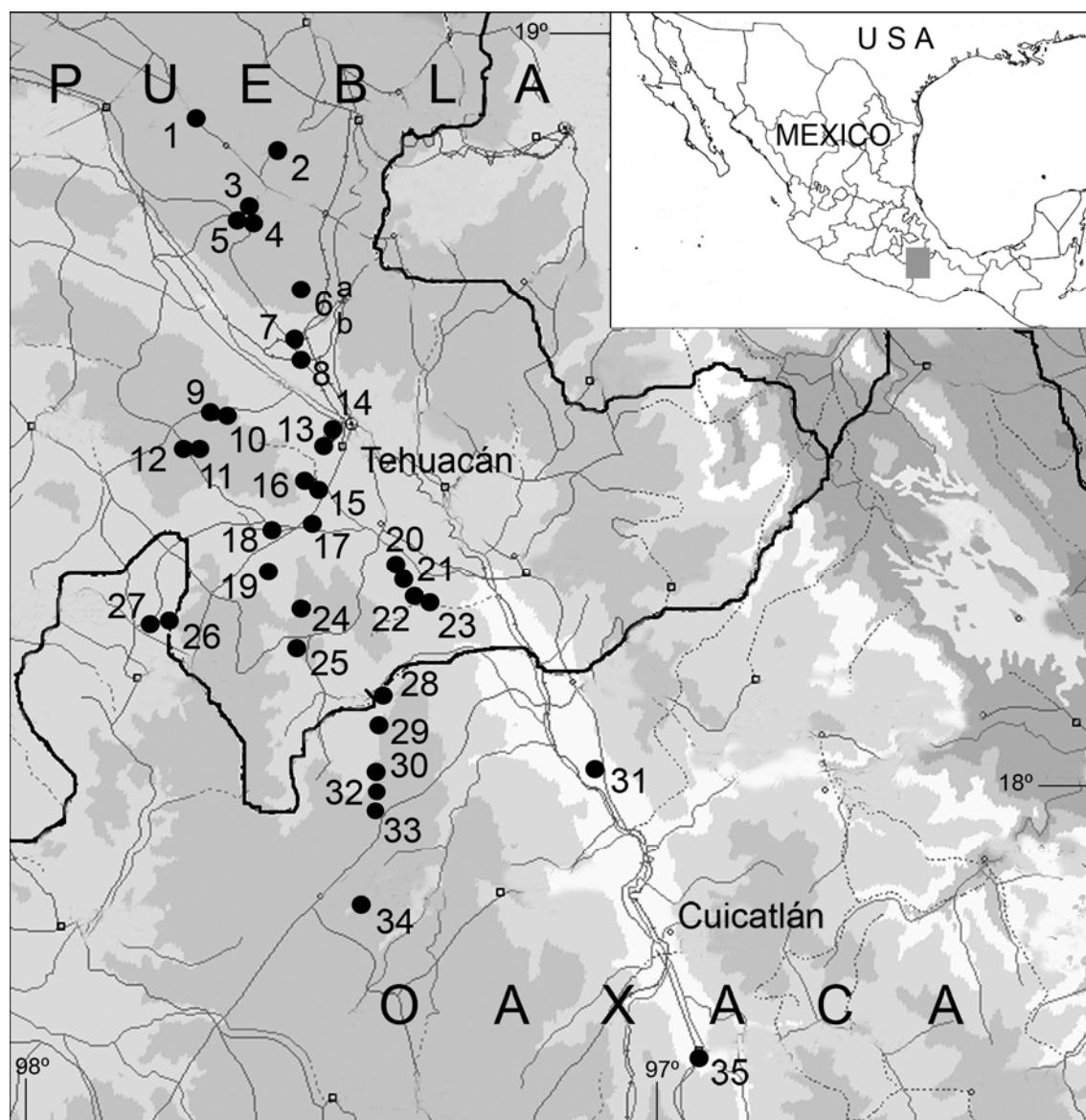


Fig. 14. Map of the Tehuacán-Cuicatlán Valley showing the sampling localities (numbers).

cultures made. The tripartite similarity index (TSI: Tulloss, 1997), and the UPGMA clustering method using the program NTSYS v.2.1 (Rohlf, 2000), were used to analyse similarities between the serial moist chamber cultures of cacti. All the numbers cited for field or moist chamber collections, refer to specimens deposited in the respective herbaria TLXM sub AET (Arturo Estrada-Torres), sub MAFR (Marco A. Flores) or sub ECC (Enrique Conde Cano), with duplicates of the field collections (AET) in MA-Fungi (sub Lado), or private collection of Diana Wrigley de Basanta (dwb).

All microscopic measurements and observations were made with material mounted directly in Hoyer's medium or polyvinyl alcohol (PVA). Differential interference microscopy was used to obtain descriptive data. Specimens were examined at 10-15 kV, with a Hitachi S-3000N scanning electron microscope (SEM), in the Real Jardín Botánico, CSIC. For all SEM-photographs the critical point dried material technique was employed. Colour notations in parenthesis are from the ISCC-NBS Color Name Charts Illustrated with Centroid Colors (Anonymous, 1976). The nomenclature follows Lado (2001,

2008) and Hernández-Crespo and Lado (2005).

List of sampling localities (Fig. 14).

- Loc. 1: Puebla: San Miguel Xaltepec, 18°51'43"N 97°36'18"W, 2,248 m, 8-VII-2003, desert scrub with rosette-leaved succulent plants (matorral rosulifolio) with species of *Hechtia*, *Agave* and *Opuntia*.
- Loc. 2: Puebla: Palmar de Bravo, junction of Puebla-Orizaba highway and Cuacnopalan-Oaxaca highway (Mex-135) km 1, 18°49'10"N 97°29'27"W, 2,400 m, 5-X-1999, desert scrub with rosette-leaved succulent plants (matorral rosulifolio) with species of *Agave*, *Hechtia* and *Opuntia*.
- Loc. 3: Puebla: San Martín Esperilla, 18°44'45"N 97°31'44"W, 2,389 m, 8-VII-2003, desert scrub with rosette-leaved succulent plants (matorral rosulifolio) with species of *Dasyllirion*, *Agave*, and *Opuntia*.
- Loc. 4: Puebla: San Martín Esperilla, 18°43'59"N 97°31'48"W, 2,412 m, 8-VII-2003, desert scrub with rosette-leaved succulent plants (matorral rosulifolio) with species of *Dasyllirion*, *Agave*, *Hechtia*, *Opuntia*, *Ferocactus* and *Echinocactus*.
- Loc. 5: Puebla: San Martín Esperilla, 18°43'59"N 97°32'40"W, 2,440 m, 8-VII-2003, cultivated land with species of *Agave*, *Juniperus* and *Opuntia*.
- Loc. 6: Puebla: Chapulco, Cuacnopalan-Oaxaca (Mex-135) highway, km 22, 18°38'23"N 97°27'33"W, 2,220 m, 8-X-1999, xerophyllous perennial scrub (Matorral esclerófilo perennifolio) with species of *Quercus*, *Yucca*, *Dasyllirion*, *Agave* and *Hechtia*.
- Loc. 6a: Puebla: Santiago Miahuatlán, Cuacnopalan-Oaxaca (Mex-135) highway, km 26, 18°36'25"N 97°28'29"W, 1,980 m, 5-X-1999, desert scrub dominated by *Yucca periculosa* (Izotal de *Yucca periculosa*) with species of *Agave* and *Mimosa*.
- Loc. 7: Puebla: Tehuacán, Cuacnopalan-Oaxaca (Mex-135) highway, km 30, 18°34'12"N 97°27'52"W, 1,860 m, 21-X-2000, desert scrub dominated by *Yucca periculosa* (Izotal de *Yucca periculosa*) with *Dasyllirion acrotriche*, and species of *Agave*, *Acacia* and *Opuntia*.
- Loc. 8: Puebla: Tehuacán, Cuacnopalan-Oaxaca (Mex-135) highway, km 32, 18°32'58"N 97°27'42"W, 1,770 m, 5-X-1999, desert scrub dominated by *Yucca periculosa* (Izotal de *Yucca periculosa*) with *Stenocereus marginatus*, *Polaskia chichipe*, *Stenocereus stellatus*, *Pilosocereus chrysacanthus* and species of *Opuntia* and *Mimosa*.
- Loc. 9: Puebla: San Bartolo Teontepec, road to Santiago Nopala, km 37, 18°28'31"N 97°34'36"W, 1,967 m, 9-VII-2003, desert scrub dominated by *Yucca periculosa* (Izotal de *Yucca periculosa*) with *Brahea dulcis* and *Echinocactus platyacanthus*.
- Loc. 10: Puebla: San Bartolo Teontepec, road to Santiago Nopala, km 38, 18°28'31"N 97°33'48"W, 1,922 m, 9-VII-2003, thorn forest (selva baja espinosa perennifolia) with *Prosopis laevigata* and *Yucca periculosa*.
- Loc. 11: Puebla: Santiago Nopala, road to San Bartolo Teontepec, km 30, 18°25'57"N 97°36'46"W, 2,158 m, 9-VII-2003, area dominated by the palm *Brahea dulcis* (palmar).
- Loc. 12: Puebla: San Bartolo Teontepec, road to Santiago Nopala, km 32, 18°26'04"N 97°36'17"W, 2,145 m, 9-VII-2003, area dominated by the palm *Brahea dulcis* (palmar), with *Dasyllirion acrotriche* and species of *Agave*.
- Loc. 13: Puebla: San José Miahuatlán, Cuacnopalan-Oaxaca (Mex-135) highway, km 46, 18°26'28"N 97°25'30"W, 1,650 m, 21-X-2000, thorn forest (selva baja espinosa perennifolia) with *Yucca periculosa*, and species of *Acacia* and *Opuntia*.
- Loc. 14: Puebla: San José Miahuatlán, Cuacnopalan-Oaxaca (Mex-135) highway, km 47, 18°25'55"N 97°25'07"W, 1,689 m, 26-VII-2002, thorn forest (selva baja espinosa perennifolia) with *Prosopis laevigata* and *Opuntia tomentosa*.
- Loc. 15: Puebla: Zapotitlán de las Salinas, San Antonio Texcala, Tehuacán-Santiago Chazumba (Mex-125) road, km 17, 18°23'18"N 97°26'41"W, 1,623 m, 10-VII-2003, desert scrub dominated by *Cephalocereus columna-trajani* (Cardonal de *Cephalocereus columna-trajani*) with *Echinocactus platyacanthus*, *Yucca periculosa*, *Beaucarnea gracilis* and *Neobuxbaumia tetetzo*.
- Loc. 16: Puebla: Zapotitlán de las Salinas, Zapotitlán de las Salinas, 18°22'42"N 97°26'09"W, 1,511 m, 10-VII-2003, desert scrub dominated by *Neobuxbaumia tetetzo* (Tetechera de *Neobuxbaumia tetetzo*) with *Beaucarnea gracilis* and *Mimosa* sp.
- Loc. 17: Puebla: Zapotitlán de las Salinas, Zapotitlán Botanic Garden, 18°20'00"N 97°27'45"W, 1,504 m, 10-VII-2003, desert scrub dominated by *Cephalocereus columna-trajani* (Cardonal de *Cephalocereus columna-trajani*) with *Neobuxbaumia tetetzo*.
- Loc. 18: Puebla: Zapotitlán de las Salinas, Zapotitlán de las Salinas, Tehuacán-Santiago Chazumba (Mex-125) road, km 30, 18°19'31"N 97°29'58"W, 1,511 m, 10-VII-2003, desert scrub dominated by *Beaucarnea gracilis* (Izotal de *Beaucarnea gracilis*) with *Cercidium praecox*, *Yucca periculosa* and *Pachycereus hollianus*.

- Loc. 19: Puebla: Los Reyes Mexontla, Los Viveros, 18°16'27"N 97°30'11"W, 1,670 m, 10-VII-2003, desert scrub dominated by *Neobuxbaumia tetetzo* (Tetechera de *Neobuxbaumia tetetzo*) with *Bursera* spp.
- Loc. 20: Puebla: San José Miahuatlán, San Gabriel Chilac, Cuacnopalan-Oaxaca (Mex-135) highway, km 69, 18°16'40"N 97°19'40"W, 1,230 m, 8-X-1999, 21-X-2000, 8-VII-2001, 9-II-2002, desert scrub dominated by *Cephalocereus columna-trajani* (Cardonal de *Cephalocereus columna-trajani*) with *Echinocactus platyacanthus*, *Pachycereus hollianus*, and *Opuntia* spp.
- Loc. 21: Puebla: San José Miahuatlán, Cuacnopalan-Oaxaca (Mex-135) highway, km 70, 18°16'06"N 97°19'06"W, 1,200 m, 21-X-2000, desert scrubland (matorral crasicaule) with *Neobuxbaumia tetetzo*, *Myrtillocactus geometrizans*, *Ipomoea arborea* and species of *Opuntia*.
- Loc. 22: Puebla: San José Miahuatlán, Cuacnopalan-Oaxaca (Mex-135) highway, km 73, 18°14'29"N 97°18'02"W, 1,380 m, 5-X-1999, desert scrubland (matorral crasicaule) with *Echinocactus platyacanthus* and species of *Agave*.
- Loc. 23: Puebla: San José Miahuatlán, Cuacnopalan-Oaxaca (Mex-135) highway, km 74, 18°14'04"N 97°17'05"W, 1,200 m, 21-X-2000, 8-VII-2001, desert scrub dominated by *Pachycereus weberi* (Cardonal de *Pachycereus weberi*) with *Neobuxbaumia tetetzo*, *Myrtillocactus geometrizans*, *Ipomoea arborea*, and species of *Fouquieria* and *Opuntia*.
- Loc. 24: Puebla: San Francisco Xochiltepec, 18°13'28"N 97°27'18"W, 1,934 m, 10-VII-2003, desert scrub dominated by *Escontria chiotilla* (Jilotillal de *Escontria chiotilla*) with *Opuntia* spp.
- Loc. 25: Puebla: San José Tilapa, 18°10'22"N 97°27'45"W, 910 m, 11-VII-2003, tropical dry forest (selva baja caducifolia) with *Pachycereus weberi*, *Myrtillocactus geometrizans*, *Isolatocereus dumortierii*, *Cercidium praecox* and species of *Bursera* and *Fouquieria*.
- Loc. 26: Oaxaca: Santiago Chazumba, road Tehuacán-Huajuapán de León (Mex-125), border of Oaxaca-Puebla states, 18°12'32"N 97°38'28"W, 1,950 m, 9-VII-2001, area dominated by the palm *Brahea dulcis* (palmar) with *Dasyllirion acrotriche* and *Echinocactus platyacanthus*.
- Loc. 27: Oaxaca: Santiago Chazumba, road Tehuacán-Huajuapán de León (Mex-125), Km 60, 18°12'11"N 97°39'38"W, 1,950 m, 9-VII-2001, thorn forest (selva baja espinosa perennifolia) with species of *Yucca*, *Mimosa* and *Opuntia*.
- Loc. 28: Oaxaca: El Rodeo, Cuacnopalan-Oaxaca (Mex-135) highway, Km 96, before El Escorial, 18°06'25"N 97°20'41"W, 1,650 m, 8-VII-2001, 12-VII-2003, desert scrub dominated by *Beaucarnea gracilis* (Izotal de *Beaucarnea gracilis*) with *Yucca periculosa*, *Dasyllirion acrotriche*, *Myrtillocactus geometrizans* and *Opuntia* spp.
- Loc. 29: Oaxaca: El Rodeo, Cuacnopalan-Oaxaca (Mex-135) highway, km 97, 18°04'23"N 97°21'08"W, 2,200 m, 7-X-1999, desert scrub dominated by *Yucca periculosa* (Izotal de *Yucca periculosa*) with *Agave* spp.
- Loc. 30: Oaxaca: Tepelmeme, La Unión, Cuacnopalan-Oaxaca (Mex-135) highway, km 109, 18°00'35"N 97°21'19"W, 2,096 m, 12-VII-2003, tropical dry forest (selva baja caducifolia) with *Yucca periculosa*.
- Loc. 31: Oaxaca: San Juan de los Cues, Barranca Chile, road Cuacnopalan-Oaxaca (Mex-135), km 79, 18°00'58"N 97°03'23"W, 751 m, 11-VII-2003, thorn forest (selva baja espinosa perennifolia) with *Pachycereus weberi*, *Myrtillocactus geometrizans*, *Isolatocereus dumortierii* *Cercidium praecox* and *Mimosa* sp.
- Loc. 32: Oaxaca: El Rodeo, El Escorial, Cuacnopalan-Oaxaca (Mex-135) highway, km 113, 17°59'00"N 97°21'10"W, 2,010 m, 7-X-1999, 8-VII-2001, area dominated by the palm *Brahea dulcis* (palmar) with *Dasyllirion acrotriche*.
- Loc. 33: Oaxaca: Tepelmeme, La Unión, Cuacnopalan-Oaxaca (Mex-135) highway, km 115, 17°57'38"N 97°21'26"W, 2,107 m, 12-VII-2003, desert scrub with rosette-leaved succulent plants (matorral rosulifolio) with *Dasyllirion acrotriche* and *Agave* spp.
- Loc. 34: Oaxaca: Tepelmeme, Cuacnopalan-Oaxaca (Mex-135) highway, km 130, 17°50'15"N 97°22'32"W, 2,130 m, 7-X-1999, gypsum soil grassland (pastizal yipsófilo).
- Loc. 35: Oaxaca: San José del Chilar, 17°38'15"N 96°55'01"W, 830 m, 11-VII-2003, thorn forest (selva baja espinosa perennifolia) with *Pachycereus weberi*, *Myrtillocactus geometrizans*, *Isolatocereus dumortierii*, *Cercidium praecox* and species of *Mimosa*.

Results

This is the first comprehensive study of myxomycetes from arid areas in the Neotropics. The five year research produced 104 species and one variety from 27 different genera. The 1200 collections included 454 samples from the field and 746 from moist chamber culture, of which 477 were obtained

from the serial cultures of representative cacti. Two species are described below as new to science. Eleven species are new records for the Neotropics, and six more and a variety are reported for the first time from Mexico. In addition, 41 and 56 taxa are new records for Oaxaca and Puebla respectively.

Annotated list of species

For the sake of brevity, only collections on different substrates or in different localities have been fully listed for each species, although the total number of collections has been included after the species name. The first number in parenthesis refers to the field collections and the second to collections from moist chamber cultures. The names of the substrate species have been abbreviated as follows: **Ac** - *Acacia* sp., **A** - *Agave* sp., **Bg** - *Beaucarnea gracilis*, **Bd** - *Brahea dulcis*, **B** - *Buddleia* sp., **Bs** - *Bursera simaruba*, **Bu** - *Bursera* sp., **Cct** - *Cephalocereus columna-trajani*, **Da** - *Dasyllirion acrotriche*, **Ep** - *Echinocactus platyacanthus*, **Fl** - *Ferocatus latispinus*, **F** - *Fouquieria* sp., **H** - *Hechtia* sp., **Jd** - *Juniperus deppeana*, **Mc** - *Mammillaria carnea*, **M** - *Mamillaria* sp., **Mg** - *Myrtillocactus geometrizans*, **Nm** - *Neobuxbaumia mezcalensis*, **N** - *Neobuxbaumia* sp., **Nt** - *Neobuxbaumia tetetzo*, **Ng** - *Nicotiana glauca*, **Od** - *Opuntia depressa*, **Op** - *Opuntia pilifera*, **O** - *Opuntia* sp., **Os** - *Opuntia streptacantha*, **Ot** - *Opuntia tomentosa*, **Ph** - *Pachycereus hollianus*, **Pw** - *Pachycereus weberi*, **Pl** - *Prosopis laevigata*, **Q** - *Quercus* sp., **Yp** - *Yucca periculosa*, **Y** - *Yucca* sp.

Arcyria cinerea (Bull.) Pers. [11, 14]

Loc. 2: On leaves of *H*, AET5553. **Loc. 6:** On inflorescence peduncle of *A*, AET5537; on *A* leaf, AET5512; on *A* stem, AET5547. **Loc. 8:** On leaves of *Yp*, AET5370. **Loc. 18:** On bark of *Bg*, dwb2137 (mc; pH = 6.5); on leaves of *A*, AET9306. **Loc. 20:** On inflorescence peduncle of *A*, AET5506; on stem of *A*, AET7485 (mc); on decayed *Ep*, ECC3 (mc, pH = 8.3). **Loc. 23:** On *O* cladodes, MAFR51b (mc); on *Od* cladodes, ECC1a (mc, pH = 8.7); on *Op* cladodes, ECC5 (mc, pH = 8.3); on decayed *Mc*, ECC11 (mc, pH = 8.4); on decayed *Pw*, ECC6 (mc, pH = 8.2). **Loc. 32:** On leaves of *Bd*, AET5467. **Loc. 33:** On leaves of *Da*, AET9448. **Loc. 35:** On angiosperm wood, AET9396.

Previously recorded from Oaxaca by Welden and Guzmán (1978) and from Puebla by Villarreal (1990), but widely distributed in the rest of the country (Moreno *et al.*, 2007). We found it almost exclusively in the field on rosette-leaved succulent plants, but in culture it also appeared on cacti.

Arcyria denudata (L.) Wettst. [20, 2]

Loc. 1: On leaves of *H*, AET9123. **Loc. 6:** On stem of *A*, AET5543. **Loc. 6a:** On leaves of *A*, AET5375, AET5389. **Loc. 9:** On leaves of *Da*, AET9225; on stem of *Bd*, AET9221. **Loc. 10:** On leaves of *A*, AET9207. **Loc. 11:** On stem of *Bd*, AET9247. **Loc. 15:** On decayed *Ep*, AET9283. **Loc. 17:** On decayed *Cct*, AET9295; on decayed *Nt*, AET9292. **Loc. 18:** On leaves of *A*, AET9305. **Loc. 19:** On decayed *Nt*, AET9357. **Loc. 20:** On decayed *Ep*, AET7332; on decayed *Cct*, AET8300. **Loc. 32:** On twigs, AET5483. **Loc. 33:** On angiosperm wood, AET9430. **Loc. 34:** On leaves of *A*, AET5456. **Loc. 35:** On angiosperm wood, AET9403.

This species is frequently found on angiosperm wood (Ing, 1994) and is relatively common in the tropical forests of Mexico (Lado *et al.*, 2003). In the Tehuacán-Cuicatlán Valley it is common but appears more often on succulents such as *Agave* and *Dasyllirion*, and different cacti such as species of *Cephalocereus*, *Echinocactus* or *Neobuxbaumia*. It has been previously recorded from Puebla by Martínez-Alfaro *et al.* (1983).

Arcyria insignis Kalchbr. & Cooke [10, 0]

Loc. 1: On leaves of *H*, AET9131. **Loc. 11:** On wood, AET9241; on twigs, AET9261. **Loc. 12:** On *Yp* stem, AET9229. **Loc. 23:** On inflorescence peduncle of *A*, AET7328. **Loc. 34:** On stem of *Ng*, AET5444. **Loc. 33:** On inflorescence peduncle of *A*, AET9433; on angiosperm wood, AET9441. **Loc. 35:** On angiosperm wood, AET9397.

Badhamia affinis Rostaf. [2, 2]

Loc. 4: On leaves of *Yp*, AET9142. **Loc. 8:** On leaves of *Yp*, AET5369. **Loc. 28:** On bark of *Yp*, dwb2069 (mc; pH = 7.0). **Loc. 33:** On bark of *Yp*, dwb2336 (mc; pH = 7.0).

This species was only found on *Yucca periculosa* both in the field and in moist chamber culture.

Badhamia cf. goniospora Meyl. [1, 0]

Loc. 4: On leaves of *A*, AET9150.

The macroscopic characters of the Tehuacán-Cuicatlán material agree with the description and photographs of *Badhamia goniospora* (Kowalski, 1975; Neubert *et al.*, 1995), except for the capillitium which is densely limy and sometimes massed in the center. The spores are larger than those cited by Kowalski (1975) (14.9-18.7 µm diam. vs. 12-13 µm) although the spore size increases up to 16 µm with the inclusion of *B. dearnessi* Hagelst., as a synonym of this species. The spores are globose to sub-globose, not oval nor ellipsoid, with a pale band, which is poorly defined.

Badhamia melanospora Speg. [80, 149]

Loc. 1: On *O* cladodes, AET9104; on leaves of *A*, AET9110; On decayed *Fl*, AET9107; On decayed *M*, AET9118. **Loc. 2:** On *O* cladodes, AET5555. **Loc. 4:** On *O* cladodes, AET9167; on decayed *Fl*, AET9164. **Loc. 5:** On leaves of *A*, AET9138, AET9141. **Loc. 6:** On leaf of *A*, AET5546a, AET7342; on stem of *Yp*, AET5514. **Loc. 6a:** On leaves of *A*, AET5384. **Loc. 8:** On *O* cladodes, AET5371, AET5372. **Loc. 9:** On leaves of *Bd*, AET9211. **Loc. 10:** *O* cladodes, AET9209. **Loc. 13:** On stem of *Yp*, AET7337, AET7338. **Loc. 14:** On *Ot* cladodes, ECC207b (mc, pH = 7.9). **Loc. 15:** On *O* cladodes, AET9286; on decayed *Cct*, AET9287; on decayed *Ph*, AET9288. **Loc. 17:** On decayed *Cct*, AET9300; on decayed *Nt*, AET9299. **Loc. 18:** On decayed *Mg*, AET9301. **Loc. 19:** On decayed *Nt*, AET9354. **Loc. 20:** On leaves of *A*, AET5501; on *O* cladodes, AET5507; on *Od* cladodes, ECC296 (mc, pH = 8.7); on decayed unidentified columnar cactus, AET5504; on decayed *Cct*, ECC297 (mc, pH = 8.7); on decayed *Ep*, ECC302 (mc, pH = 8.3); on decayed *Fl*, ECC320 (mc, pH = 8.2); on decayed *Ph*, AET7623. **Loc. 21:** On *O* cladodes, AET7331; on decayed *Mg*, AET7436 (mc). **Loc. 22:** on bark of *Ep*, AET5397; on decayed *Ep*, AET5398. **Loc. 23:** On *O* cladodes., MAFR40b (mc); on *Od* cladodes, ECC313 (mc, pH = 8.3), ECC323 (mc, pH = 9.1); on *Op* cladodes, ECC295 (mc, pH = 8.5); on decayed *Fl*, ECC294 (mc, pH = 8.6); on decayed *Mc*, ECC300 (mc, pH = 8.5); on decayed *Mg*, AET7564 (mc); on decayed *N*, MAFR22 (mc); on decayed *Ph*, ECC303 (mc, pH = 9.4); on decayed *Pw*, AET7612, ECC301 (mc, pH = 9.6). **Loc. 24:** On *O* cladodes, AET9310; on decayed unidentified columnar cactus, AET9308; on decayed *M*, AET9317. **Loc. 29:** On stem of *Yp*, AET5490. **Loc. 31:** On decayed unidentified cactus, AET7621. **Loc. 34:** On leaves of *A*, AET5458; on decayed *M*, AET5574. **Loc. 35:** On *O* cladodes, AET9407; on decayed unidentified columnar cactus, AET9406; on decayed *Mg*, AET9378; on decayed *Pw*, AET9382.

Badhamia melanospora is the commonest and most widely distributed species in arid or semi-arid zones of the Tehuacán-Cuicatlán Valley, and constitutes a new record for Oaxaca and Puebla. It is most frequently found on decayed cacti, but has also been found on leaves of *Agave*, *Yucca* and palms of the genus *Brahea*. In other arid zones it is also very common in cacti (Lado *et al.*, 2007a).

Badhamia nitens Berk. [3, 0]

Loc. 3: On leaves of *Yp*, AET9190. **Loc. 4:** On leaves of *Yp*, AET9143. **Loc. 8:** On leaves of *Yp*, AET5367.

This species was also found exclusively on *Yucca periculosa*.

Badhamia utricularis (Bull.) Berk. [0, 1]

Loc. 28: On bark of *Yp*, dwb2338 (mc; pH = 6.5).

This was a large collection with clear taxonomic characters of the species, although it only appeared once.

Badhamia versicolor Lister [0, 2]

Loc. 28: On bark of *Pl*, dwb2346 (mc; pH = 6.6). **Loc. 33:** On bark of *Ac*, dwb2492 (mc; pH = 5.9).

The sessile sporocarps have a capillitium with a pale apricot tinge and the spores are clustered, minutely warted to the outside of the cluster and smooth inside. The clusters are hollow. Our specimens have almost no lime on the peridium which is thin and iridescent. This is a new record for Mexico.

Badhamiopsis ainoae (Yamash.) T.E. Brooks & H.W. Keller [1, 0]

Loc. 6: On stem of *Yp*, AET5516.

In the Neotropics it has also been reported from Brazil (Putzke, 1996).

Calomyxa metallica (Berk.) Nieuwl. [1, 1]

Loc. 6a: On leaves of *A*, AET5386b. **Loc. 18:** On bark of *Bg*, dwb2341 (mc; pH = 7.2).

This species is more frequent in other environments, such as the conifer forest of the Malinche National Park, Tlaxcala, Mexico, a neighbouring state, where it made up almost 0.5% of the specimens collected (Rodríguez-Palma, 2002), but is rarely found in arid areas.

Ceratiomyxa fruticulosa (O.F. Müll.) T. Macbr. [3, 1]

Loc. 20: On decayed *Ep*, ECC13 (mc, pH = 8.0). **Loc. 23:** On decayed unidentified columnar cactus, AET7611. **Loc. 24:** On leaves of *A*, AET9322. **Loc. 27:** On stem of *Yp*, AET7630.

This species has been included, as it has traditionally been listed among myxomycetes, although it is more closely related to another group of Eumycetozoa, the Protostelids (Olive, 1975). It has been previously recorded from Oaxaca by Welden and Guzmán (1978) and from Puebla by Welden and Lemke (1961) and Martínez-Alfaro *et al.* (1983). We use the conserved name for this species as proposed by Lado *et al.* (2005) and accepted by the IAPT (Gams, 2005).

Clastoderma debaryanum var. *imperatorium* Emoto [0, 1]

Loc. 28: On bark of *Yp*, dwb2086 (mc; pH = 6.8).

The tiny protoplasmodia are visible against the dark surface of this bark, looking like drops of water. This material by LM (Fig. 15) has the distinct nets on the polygonal peridial plates as described by Emoto (1929) and illustrated by Eliasson and Keller (1996). The plates are smooth on the outer surface as visible by SEM (Fig. 16). The coarse warts on the spore surface are irregularly distributed by SEM (Fig. 17). It is the first record of this variety for Mexico.

Collaria arcyronema (Rost.) Nann.-Bremek. ex Lado [0, 2]

Loc. 20: On decayed *Ep*, ECC8 (mc, pH = 8.2).

The single specimen obtained is a small form of the species. The sporocarps are 0.6-1.1 mm in height and the sporothecae are 0.18-0.45 mm in diam., where Martin and Alexopoulos (1969) report a height of 1-2.5 mm, and sporotheca diam. 0.25-0.75 mm. They enter however in the range given by Neubert *et al.* (2000) of a height of 0.5-3 mm and sporotheca diam. 0.2-0.8 mm. The peridium of the sporotheca is bronze by reflected light and purple brown by transmitted light, and persists at the base as a collar around the stipe. The columella reaches the middle of the sporotheca, where it branches into two or three main branches, which divide further to form a dense flexuose capillitium with dark tips. The spores are globose, 6.7-7.2 μm diam., and warted with groups of darker warts. The spore size is within the lower limits of the range reported by the above authors.

Comatriza laxa Rostaf. [3, 3]

Loc. 6a: On leaves of *Yp*, AET5390. **Loc. 20:** On decayed *Ep*, ECC23 (mc, pH = 8.1). **Loc. 23:** On *O* cladodes, MAFR49 (mc); on decayed *Fl*, MAFR34 (mc); on decayed *Nm*, AET7617. **Loc. 34:** On leaves of *A*, AET5433.

All specimens are typical of this species, except specimen ECC23, which is scant material and seems to be poorly developed. However, its macroscopic and microscopic characters as well as its spore size are typical of *C. laxa*. This species appeared in both rosette-leaved succulent plants and cacti.

Comatriza pulchella (C. Bab.) Rostaf. [1, 0]

Loc. 35: On leaf litter, AET9410.

This species only appeared on its typical

substrate, not on the multiple cacti examined. It as cited more than a hundred years ago from Oaxaca by Macbride and Smith (1896), and had not been found in the state since.

Comatriza reticulospora Ing & Holland [0, 1]

Loc. 20: On *Od* cladodes, ECC10 (mc, pH = 8.1).

Only one collection was made of this species from moist chamber culture. The characters of this material are the same as the original description of Ing and Holland (1967), except that the sporocarps are slightly smaller. The sporocarps measure 1.4-1.6 mm in height with sub-cylindrical sporothecae of 0.6-0.8 x 0.2 mm, and stalks up to 0.8 mm long. The spores are globose, from 8-8.6 μm diam., and are warted-reticulate. This ornamentation is similar to the spores of *Stemonitis fusca* Roth and *S. virginensis* Rex, from which it can be distinguished by its capillitium with numerous free ends and not a superficial net. This material represents the first record for the Neotropics and for Mexico.

Comatriza tenerrima (M. A. Curtis) G. Lister [2, 2]

Loc. 6: On inflorescence peduncle of *A*, AET5532. **Loc. 11:** On angiosperm wood, AET9253. **Loc. 23:** On decayed *N*, MAFR179 (mc). **Loc. 25:** On bark of *Pw*, dwb2451 (mc, pH = 7.1).

The specimens from Tehuacán-Cuicatlán have pink-beige sporocarps and the sporotheca pointed at the apex. The columella also ends at the apex of the sporotheca and the spores are warted with groups of more conspicuous warts.

Craterium leucocephalum (Pers. ex J.F. Gmel.) Ditmar [1, 0]

Loc. 35: On angiosperm twigs, AET9393.

Cribraria cancellata (Batsch) Nann.-Bremek. [1, 0]

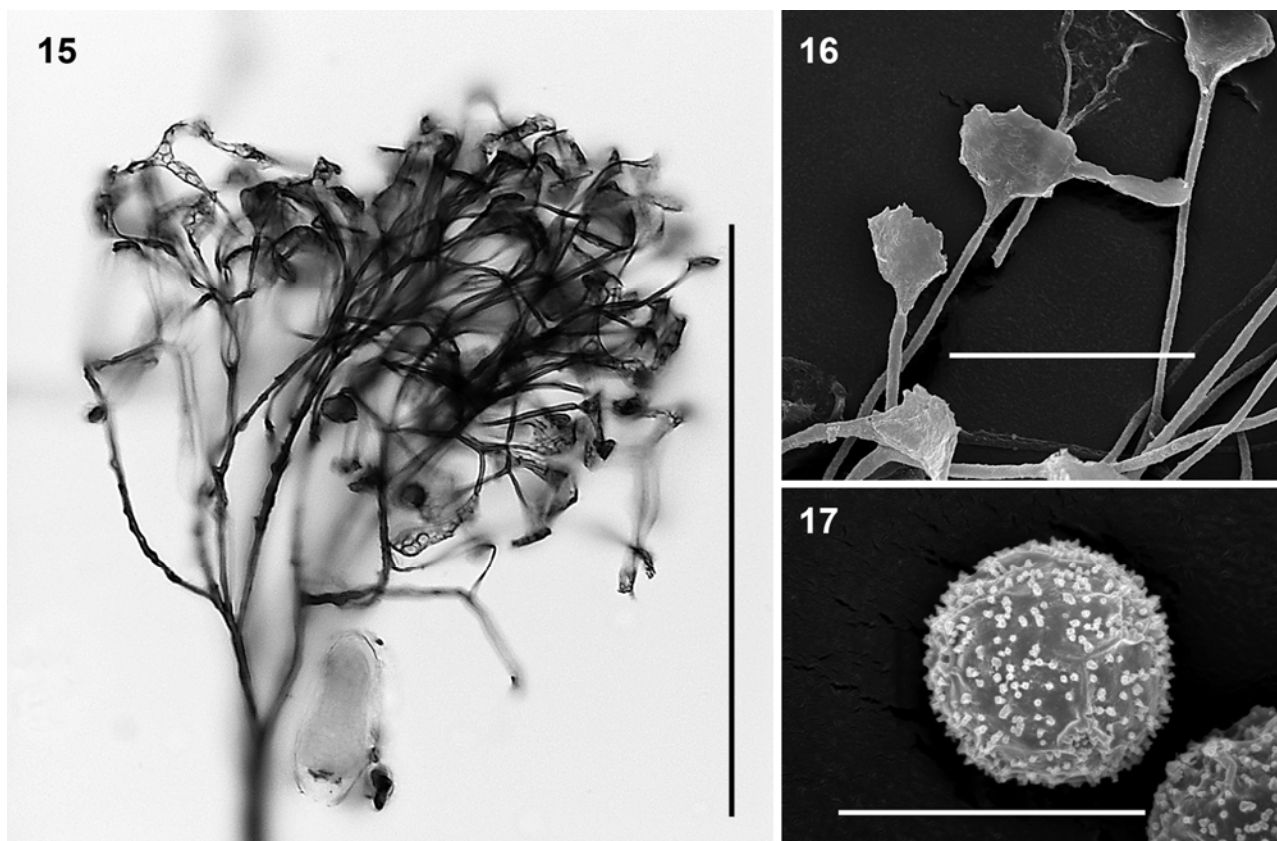
Loc. 11: On wood of a Leguminosae, AET9246.

Common in other environments, but rare in this area.

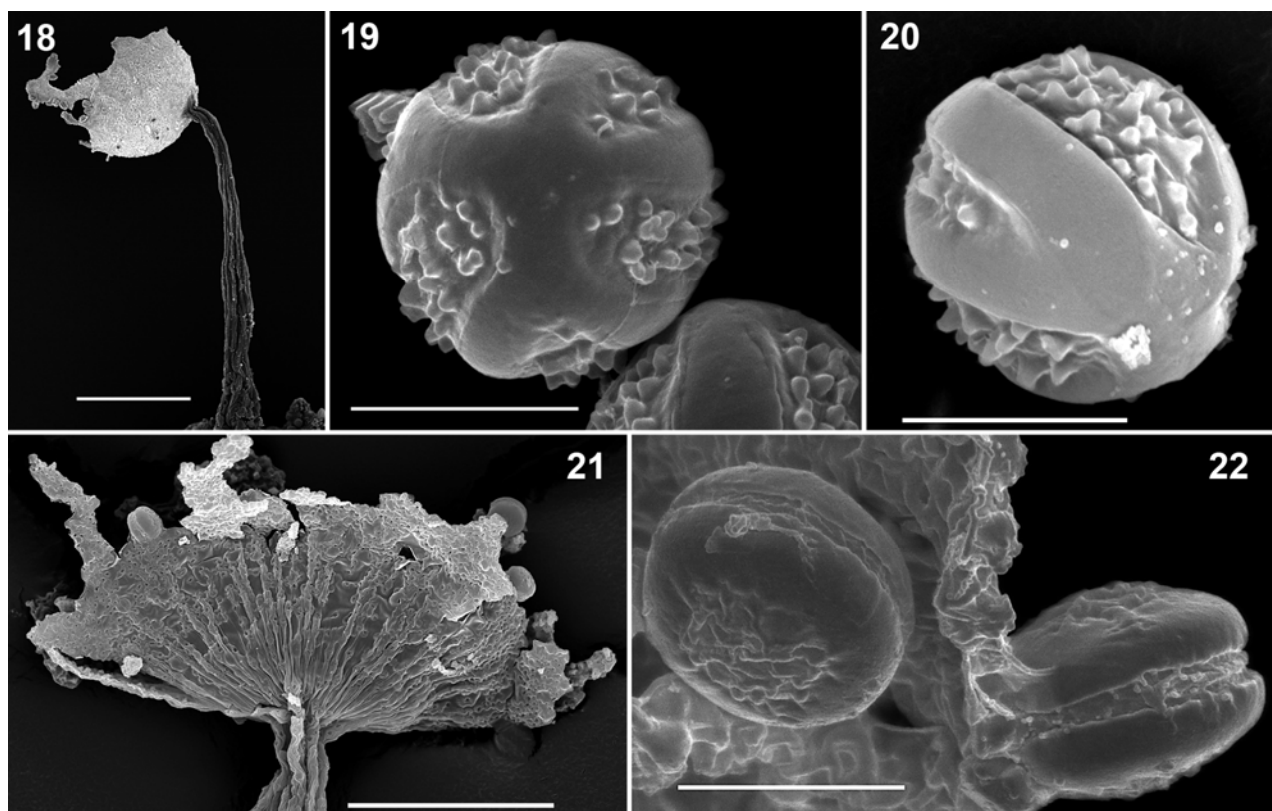
Cribraria fragilis Lado & Estrada [0, 2]

Loc. 23: On decayed *Fl*, AET7550 (mc); on decayed *Pw*, ECC21 (mc, pH = 9.3).

This is the third record in the world of this species. It is known previously from the type locality in Morelos, Mexico (Estrada-Torres *et al.*, 2001), and from Sierra de Álamos-Río Cuchujaqui Biosphere Reserva,



Figs 15-17. *Clastoderma debaryanum* var. *imperatorium* (dwb2086). **15.** Dehiscent sporotheca showing the peridial plates with a reticulum by LM (bar = 100 µm). **16.** Detail of the outer surface of the peridial plates by SEM (bar = 20 µm). **17.** Detail of spore ornamentation by SEM (bar = 10 µm).



Figs 18-20. *Cribraria fragilis* (ECC21) by SEM. **18.** Whole sporocarp (bar = 100 µm). **19-20.** Spores with the unusual bands (bar = 5 µm). **Figs 21-22.** *Cribraria zonatispora* (ECC107) by SEM. **21.** Detail of the calyculus in a dehiscent sporotheca (bar = 30 µm). **22.** Spores (bar = 5 µm).

in the state of Sonora (Lizárraga *et al.*, 2008). These specimens confirm all the described characters, including the unique spores (Figs 18-20), and also its succulent habit, which appears to be exclusive to the Cactaceae (Estrada-Torres *et al.*, 2001). Spores of specimen AET7550 have less pronounced bands.

Cribraria lepida Meyl. [1, 0]

Loc. 1: On leaves of *H*, AET9127a.

Only one collection was obtained of this rare species, which is cited for the first time for the Neotropics and for Mexico. It differs from *Cribraria violacea* in that it has a much shallower calyculus and has numerous thickened nodes, not a few flat nodes on the peridial net. It has otherwise only been found in the type locality which was Switzerland (Meylan, 1927), Germany (Neubert *et al.*, 1993), and questionably in the USA (Martin and Alexopoulos, 1969).

Cribraria violacea Rex [4, 10]

Loc. 6: On stem of *A*, AET5531b. **Loc. 11:** On stem of *Bd*, AET9230b. **Loc. 20:** On stem of *A*, AET7462 (mc); on decayed *Ep*, ECC22 (mc, pH = 7.5). **Loc. 23:** On *Od* cladodes, ECC118 (mc, pH = 8.2); on *Op* cladodes, ECC372 (mc, pH = 8.2); on decayed *Fl*, ECC15 (mc, pH = 8.2). **Loc. 34:** On stem of *A*, AET5564a.

Previously cited from Puebla by Keller and Braun (1977).

Cribraria zonatispora Lado, Mosquera & Beltrán-Tej. [0, 1]

Loc. 23: On decayed *Pw*, ECC107 (mc, pH = 9.2).

This is the second record for Mexico. This species, originally described from the state of Hidalgo, Mexico, is also known from mainland Spain and the Canary Islands (Lado *et al.*, 1999). These specimens confirm the unique spores and the reduced calyculous of the species (Figs 21-22), and also its succulent habit. This is the first time it has been found on columnar cacti.

Dictydiaethalium plumbeum (Schumach.) Rostaf. [1, 0]

Loc. 34: On stem of *Ng*, AET5439.

The Tehuacán-Cuicatlán Valley collection agrees with the original description of *D. ferrugineum* Nann.-Bremek., in the reddish peridium, the ornamentation and size of the

spores (warted from 11-12 µm diam.) and the bands of the pseudocapillitium which are almost smooth (Nannenga-Bremekamp, 1966). However, Martin and Alexopoulos (1969) and Lado and Pando (1997) have pointed out that the latter is only a form of *D. plumbeum*.

Diderma acanthosporum Estrada & Lado [2, 0]

Loc. 35: On angiosperm wood, AET9405. **Loc. 33:** On angiosperm wood, AET9415.

It was originally described by Estrada-Torres *et al.* (2001) from the states of Mexico and Morelos. These collections confirm the characters and substrate of this species, and extend its area of distribution. The spores of the Tehuacán-Cuicatlán specimens have large spines with open tips and one paler hemisphere, typical of the species.

Diderma effusum (Schwein.) Morgan [1, 1]

Loc. 23: On decayed *Pw*, ECC436 (mc, pH = 8.5). **Loc. 34:** On twigs, AET5461.

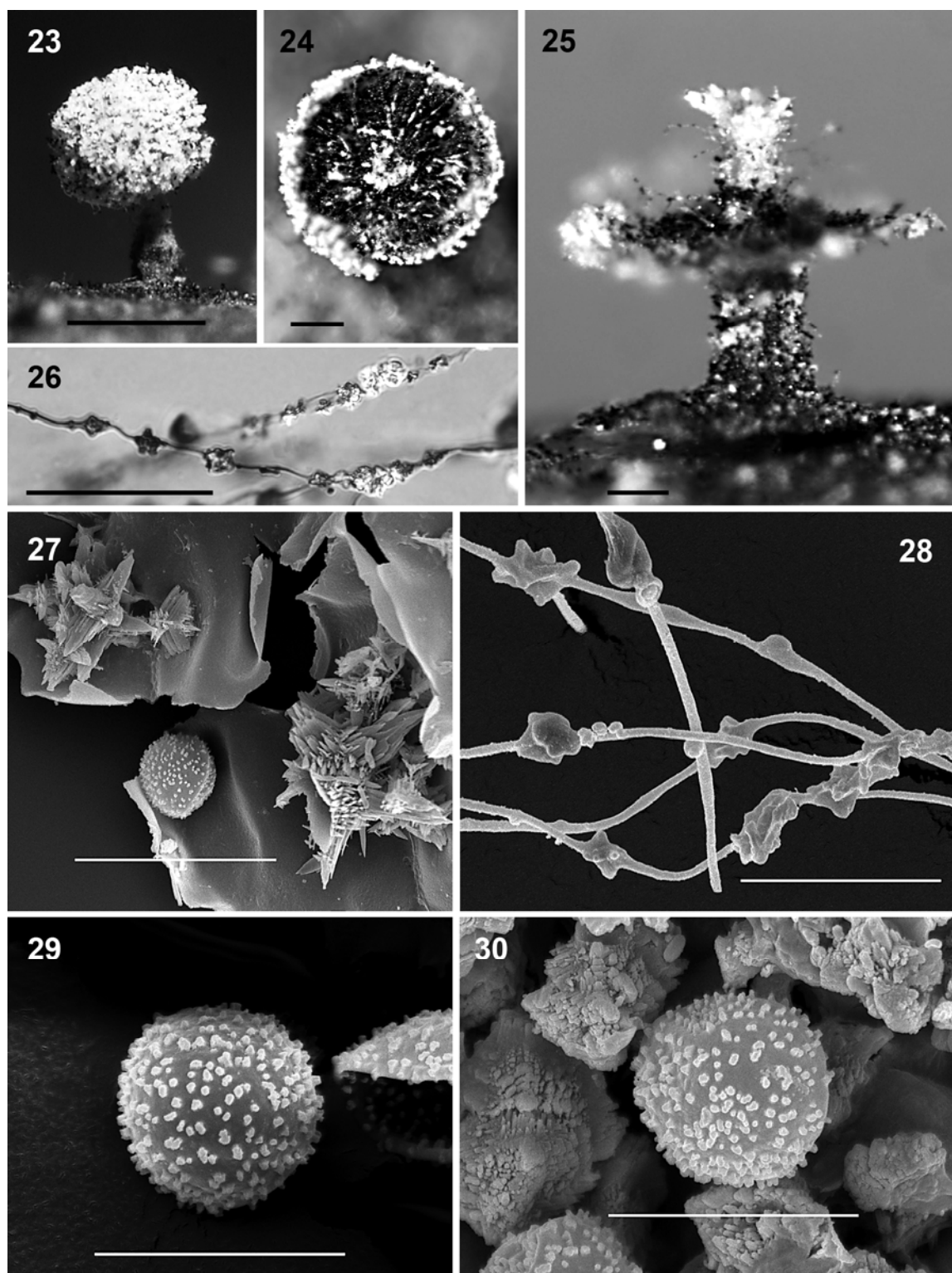
Diderma hemisphaericum (Bull.) Hornem. [10, 0]

Loc. 11: On leaf litter, AET9250b; on leaves of *Bd*, AET9267a; on twigs, AET9258. **Loc. 33:** On living herbaceous plants, AET9416; on leaf litter, AET9424. **Loc. 34:** On stem and twigs of an Asteraceae, AET5440. **Loc. 35:** On wood, AET9400; on twigs, AET9392.

Didymium anellus Morgan [2, 9]

Loc. 6: On leaves of *A*, AET5538. **Loc. 10:** On leaf litter, AET9191b. **Loc. 14:** On *Ot* cladodes, ECC472 (mc, pH = 7.6). **Loc. 20:** On decayed *Cct*, ECC440b (mc, pH = 7.9). **Loc. 23:** on decayed *Mg*, ECC427 (mc, pH = 8.2), MAFR50 (mc), MAFR191 (mc); on decayed *N*, MAFR205 (mc); on decayed *Pw*, AET7444 (mc), AET7451, (mc), MAFR6 (mc).

Specimens MAFR50, MAFR191 and MAFR 205, obtained from moist chamber cultures, have effuse perforated plasmodiocarps, reminiscent of the fructifications of *D. perforatum*. The microscopic characters however, agree with those described by Martin and Alexopoulos (1969) for *D. anellus*. Under this taxon we have included all material with sessile sporocarps to short flat plasmodiocarps, dark capillitium with many anastomoses and free ends, and spores from 8-10 µm with homogeneous warted ornamentation.



Figs 23-30. *Didymium tehuacanense*. **23.** Stipitate sporocarp by SM (Lado 14784) (bar = 0.5 mm). **24.** Open sporotheca showing calcareous capillitium radiating from the columella by SM (AET9158) (bar = 100 μm). **25.** Detail of the cylindrical columella with an expanded apex in a dehisced sporocarp by SM (AET9158) (bar = 100 μm). **26.** Capillitium with enlargements filled with crystals by LM (AET9159) (bar = 50 μm). **27.** Smooth peridium with crystals by SEM (AET9163) (bar = 20 μm). **28.** Detail of the capillitium showing irregular enlargements by SEM (AET9163) (bar = 20 μm). **29.** Spore by SEM with warty ornamentation (Lado 14784) (bar = 10 μm). **30.** Spore by SEM (AET9163) (bar = 10 μm).

Didymium applanatum Nann.-Bremek. [0, 2]

Loc. 23: On decayed *Mg*, ECC430 (mc, pH = 9.0).

This specimen is the first record of this species for Mexico and the second record for the Neotropics, as it was reported by McHugh (2005) from Ecuador. The species is similar in appearance to *D. clavus* (Alb. & Schwein.) Rabenh., but the stalk is calcareous. In this it is similar to *D. squamulosum* (Alb. & Schwein.) Fr., but the sporotheca of *D. applanatum* is wider and flattened and it lacks a columella (Nannenga-Bremekamp, 1972).

Didymium bahiense Gottsb. [1, 0]

Loc. 19: On decayed *Nt*, AET9359.

This is a new substrate for this species, since it is usually found on the leaves and twigs of angiosperms.

Didymium clavodecus K.D. Whitney [1, 0]

Loc. 34: On leaves of *A*, AET5434b.

This is the first record of this species for the Neotropics, although it has been cited previously from the Nearctic region of Mexico by Lizárraga *et al.* (1997, 2004).

Didymium clavus (Alb. & Schwein.) Rabenh. [1, 0]

Loc. 1: On leaves of *H*, AET9113.

This species was found only once on a rosette-leaved succulent plant. In other types of angiosperm leaf litter it is very common.

Didymium difforme (Pers.) Gray [1, 0]

Loc. 8: On *O* cladodes, AET5356.

As with the previous species, this single collection on cacti represents a new substrate and contrasts with its normally frequent appearance on angiosperm litter.

Didymium dubium Rostaf. [0, 4]

Loc. 20: On decayed *Ep*, ECC247 (mc, pH = 8.1). **Loc. 23:** On decayed *Mg*, MAFR92 (mc); on decayed *N*, MAFR175 (mc).

Didymium eremophilum M. Blackw. & Gilb. [0, 3]

Loc. 23: On decayed *Pw*, AET7441 (mc), ECC272 (mc, pH = 9.5).

These specimens are the first record of this species for the Neotropics and Mexico. It was only previously known on *Carnegiea gigantea* from the localities of its description in Arizona, USA (Blackwell and Gilbertson, 1980a). Its presence on *Pachycereus weberi*

confirms a succulent habit for this species on columnar cacti.

Our material has small sporocarps, up to 0.15 mm in total height (Fig. 57), with a hyaline peridium with crystals deposited on the surface (Fig. 58). The capillitium is absent and the spores have a paler, spinulose area, and the rest of the spore is darker and spiny-reticulate which agrees with the original description of this species (Blackwell and Gilbertson, 1980a). The specimen AET7441 has spores with less marked ornamentation but the paler area is present.

Didymium* cf. *floccosum G.W. Martin & K.G. Mukerji [1, 0]

Loc. 20: On leaves of *A*, AET5510.

This single collection was poorly developed and did not allow us to confirm all the characters of this species not previously reported from Mexico.

Didymium iridis (Ditmar) Fr. [1, 0]

Loc. 10: On leaf litter, AET9191a.

Didymium nigripes (Link) Fr. [5, 0]

Loc. 24: On *O* cladodes, AET9337; on leaf litter of an unidentified bush, AET9313. **Loc. 33:** On living herbaceous plants, AET9432; on leaf litter, AET9431.

The presence of this species on cacti represents a new substrate for this common foliicolous species.

Didymium ochroideum G. Lister [0, 5]

Loc. 23: On decayed *Mg*, MAFR160 (mc); on decayed *N*, MAFR89 (mc).

These specimens are the second record of the species for Mexico. It was previously cited from Quintana Roo by Lado *et al.* (2003). The Tehuacán-Cuicatlán specimens all appeared on columnar cacti in moist chamber culture.

Didymium orthonemata H.W. Keller & T.E. Brooks [0, 4]

Loc. 3: On leaves of *Y*, dwb2342 (mc; pH = 7.6). **Loc. 28:** On bark of a Leguminosae, dwb2068 (mc; pH = 6.6). **Loc. 29:** On bark of *Pl*, dwb2352 (mc; pH = 6.8).

These specimens are the first record of this species for the Neotropics and Mexico. It is only previously known from the type locality in Florida (Keller and Brooks, 1973). This species is very similar to *D. anellus* Morgan, except for the darker colour and larger size of the spores, which are 12-15 μm versus less than 11 μm in *D. anellus*.

Didymium squamulosum (Alb. & Schwein.) Fr. [26, 1]

Loc. 6: On leaves of *A*, AET5533d. **Loc. 10:** On leaf litter, AET9192; on leaves of *Yp*, AET9193. **Loc. 11:** On leaf litter, AET9233; on *B* leaf litter, AET9271; on angiosperm wood, AET9243; on twigs, AET9237; on stem of *Bd*, AET9240; on stem of *Yp*, AET9236a. **Loc. 20:** On decayed *Cct*, ECC440a (mc, pH = 7.9). **Loc. 33:** On leaf litter, AET9413; on twigs, AET9414. **Loc. 35:** On angiosperm wood, AET9399; on twigs, AET9394.

Didymium sturgisii Hagelst. [1, 0]

Loc. 6: On stem of *Yp*, AET-5514b.

The most distinctive character of this rather rare species is the vertical lime-filled pillars between the base and the upper peridium. This is a new record for the Neotropics although cited previously from the Nearctic region of Mexico by Moreno *et al.* (2001).

Didymium subreticulosporum Oltra, G. Moreno & Illana [1, 2]

Loc. 23: On decayed *Mg*, MAFR74 (mc); on decayed *Pw*, ECC370 (mc, pH = 8.5). **Loc. 24:** On *O* cladodes, AET9333.

Specimens from the Tehuacán-Cuicatlán Valley developed in moist chamber cultures on columnar cacti and their characters are the same as the description by Mosquera *et al.* (2000a). The continuous membranous structure inside the sporothecae, filled with calcareous crystals, and the reticulate spores, with the reticulum less marked and often broken on the paler side, are the most distinctive features of this species. This is the first record of this species for the Neotropics, although in Mexico it has been previously recorded from Baja California. Outside Mexico it is only known from Spain on introduced cacti (Oltra *et al.*, 1997; Lizárraga *et al.*, 1998; Mosquera *et al.*, 2000a).

Didymium tehuacanense Estrada, D. Wrigley & Lado, **sp. nov.** [7, 0] Figs 23-30.

Sporophora sporocarpica, potius albida, 0.5-1.3 mm alta, aggregata, stipitata. Stipes calcareus, distaliter saltem albidus, 0.2-0.7 × 0.1-0.15 mm altus latusque. Peridium unicum, membranaceum, crystallis albis, calcareis, coopertum. Columella cylindrica, distaliter expansa et/aut ramificata, crystallis impleta. Capillitium tubulare, tubulis 0.6-1.9 µm diametro — aliquibus,

crystallis impletis—. Sporae liberae, griseo-brunneae, 8-10 µm diametro, verrucosae.

Sporophores sporocarpic, grouped, rarely plamodiocarpic by fusion of several sporocarps. Sporocarps stalked, rarely sessile, 0.5-1.3 mm in total height. Plasmodiocarps from 1-1.5 mm in extension. Sporotheca sub-globose to sub-hemispheric, sometimes flattened below, 0.4-0.9 mm diam, 0.2-0.5 mm height, whitish (263. White – 264. l. Gray) when almost completely covered with calcium carbonate crystals, the crystals stelliform, usually larger than the spores, from 5.5-23.6 x 5.3-21.1 µm, iridescent when the crystals are sparse. Hypothallus inconspicuous, membranaceous, individualized to each sporophore and discoid, brownish orange, sometimes covered with calcium carbonate crystals and then almost white. Stalk cylindrical, 0.2-0.7 mm in height, 0.1-0.15 mm wide, completely calcareous or at least the apical half to two-thirds, filled with lime crystals and with refuse matter at the base, sometimes slightly striated, whitish when calcium carbonate is present, blackish when absent. Peridium single, iridescent, brownish grey to yellowish brown (63. l. br Gy – 80. gy. y Br), sometimes with darker to almost colourless areas by transmitted light, membranous, covered by white, stellate lime crystals; crystals forming an almost continuous roughened layer, sometimes showing the iridescent peridium; dehiscence irregular leaving a basal disc. Columella cylindrical, up to 0.2 mm in height, and 0.1 mm wide, expanded and/or branched at the apex up to 0.2 mm diam, white to yellowish, usually with spiny projections, filled with lime crystals. Capillitium arising radially from the columella, filiform, straight, threads 0.6-1.9 µm diam., branched, forming a net, joined to the peridium, brownish grey (63. l. br Gy – 60. l. gy. Br), turning pale to colourless through the ends, with dark, irregular enlargements of 1.3-7.9 µm long, some threads filled with crystals that macroscopically resemble fusiform calcareous nodes, of the same colour as the projections of the columella. Spores free, brown black in mass, light greyish brown (63. l. br Gy – 61. gy. Br) by LM, subglobose, 8-10 µm diam., uniformly warted, even by SEM.

HOLOTYPE. MEXICO. Puebla: San Martín Esperilla, 18°43'59"N 97°31'48"W, 2,412 m, on dead leaves of *Agave* sp., 8-VII-2003, A. Estrada-Torres, C. Lado, D. Wrigley de Basanta, Lado 14784 (MA-Fungi 73605). Isotype TLXM (AET9159).

The epithet *tehuacanense* refers to the Tehuacán-Cuicatlán Valley where the species was found.

Habitat: Dead leaves of *Agave* spp.

Known distribution: Puebla and Oaxaca, Mexico

Other specimens examined.

Loc. 4: On leaves of *Agave* sp., AET9158, AET9163, AET9169. **Loc. 6:** On leaves of *Agave* sp., AET5539, AET5546c. **Loc. 32:** On leaves of *Agave* sp., AET5474.

The most obvious characters of this new species are the distinct long cylindrical columella with an expanded apex and spiny projections (Figs 24-25), the capillitium which has irregular enlargements filled with crystals (Figs 26, 28), which are smaller and morphologically distinct from those on the peridium (Fig. 27). *Didymium tubicrystallinum* Nann.-Bremek. & R.L. Critchf. described on dead branches from California (Nannenga-Bremekamp and Critchfield, 1988), also has large widenings of the capillitium filled with lime, but this species is sessile and plasmodiocarpic, not stipitate and sporocarpic (Fig. 23) and has larger spores (12-13 µm in diam. vs. 8-10 µm in *D. tehuacanense*). *Didymium annulisporum* H.W. Keller & Schokn. is another species with lime in the capillitium, but its sessile habit and spores with an equatorial ring (Keller & Schoknecht, 1989) clearly differentiate it from *D. tehuacanense*. Other sporocarpic and stipitate species are *D. squamulosum* and *D. subreticulosporum*. The first is different in its rounded columella and its capillitium without crystals. *Didymium tehuacanense* differs from *D. subreticulosporum* in the uniformly warted spores (Figs 29-30), not in a sub-reticulate pattern, and its calcareous stalk. The capillitium in the new species is formed by filiform straight threads, filled with crystals, and lacks the unique crystalline membranous elements inside the sporotheca of *D. subreticulosporum*, interpreted as a functional capillitium and illustrated by Mosquera *et al.* (2000a).

Didymium umbilicatum D. Wrigley, Lado & Estrada [2, 1]

Loc. 4: on bark of *Yp*, dwb2339 (mc, pH = 7.4). **Loc. 20:** on dead A, AET5502. **Loc. 34:** on dead A, AET5561.

The material of this taxon from the Tehuacán-Cuicatlán Valley, is included in Wrigley de Basanta *et al.* (2008b) where it is described as a new species.

Didymium vaccinum (Durieu & Mont.) Buchet [26, 0]

Loc. 1: On leaves of A, AET9119; on leaves of *H*, AET9114. **Loc. 3:** On leaves of *Da*, AET9178. **Loc. 4:** On leaves of A, AET9148. **Loc. 5:** On leaves of A, AET9139. **Loc. 6:** On leaves of A, AET5533a; on stem of A, AET5542a. **Loc. 9:** On leaves of *H*, AET9216. **Loc. 20:** On decayed *Nt*, AET5500. **Loc. 24:** On *O* cladodes, AET9335. **Loc. 27:** On leaves of A, AET7626. **Loc. 32:** On leaves of A, AET5482. **Loc. 33:** On leaves of A, AET9455. **Loc. 34:** On leaves of A, AET5457.

This species seems to have a marked preference for the leaves of rosette-leaved succulent plants of the families Agavaceae, Bromeliaceae and Liliaceae.

Didymium wildpretii Mosquera, Estrada, Beltrán-Tej., D. Wrigley & Lado [0, 100]

Loc. 14: on decayed *Ot*, ECC 208a (mc, pH = 8.6). **Loc. 20:** on decayed *Ep*, ECC 445 (mc, pH = 7.8); on decayed *Fl*, ECC 444 (mc, pH = 9.1); on decayed *Mc*, ECC 441 (mc, pH = 8.4); on decayed *Mg*, ECC 492 (mc, pH = 8.5); on decayed *Ph*, ECC 412 (mc, pH = 9.2). **Loc. 21:** on decayed *Mg*, AET 7523 (mc). **Loc. 23:** on decayed *Fl*, MAFR 139 (mc); ECC 424 (mc, pH = 9.0); on decayed *Mc*, ECC 419 (mc, pH = 8.7); on decayed *Od* cladodes, ECC 462 (mc, pH = 8.4); on decayed *Op* cladodes, ECC 327b (mc, pH = 8.5), ECC 420 (mc, pH = 9.2); on decayed *O* cladodes, MAFR 42 (mc); on decayed *Mg*, ECC 422 (mc, pH = 9.0); on decayed *N*, MAFR 112 (mc); on decayed *Ph*, ECC 415 (mc, pH = 9.2); on decayed *Pw*, ECC 414 (mc, pH = 8.6).

The material of this taxon from the Tehuacán-Cuicatlán Reserve is included in Lado *et al.* (2007b) where it is described as a new species.

Echinostelium apitectum K.D. Whitney [0, 7]

Loc. 25: On bark of *Bs*, dwb2475 (mc, pH = 6.5); on bark of unidentified tree, dwb2476 (mc, pH = 6.3). **Loc. 28:** On bark of a leguminosae, dwb2056 (mc, pH = 5.6); on bark of *Pl*, dwb2312 (mc, pH = 6.8), dwb2313 (mc, pH = 6.6). **Loc. 33:** On bark of *Ac*, dwb2482 (mc, pH = 6.4).

These are the first records for Oaxaca of this obligate corticole. Its characteristic variable columella enclosed in a spore-like body is sometimes very reduced (Figs 31-33) but the peridium persisting as a collar and

roughened spores which are prominently warted by SEM, (Fig. 33) distinguish this species. *Echinostelium apitectum* usually develops best on bark with a lower pH value than the substrates from Tehuacán-Cuicatlán (Wrigley de Basanta, 2004) but has been found before in Spain on bark with values up to pH 6.5 (Pando, 1989). It only appeared on tree bark, not on any of the other bark studied.

Echinostelium arboreum H.W. Keller & T.E. Brooks [0, 8]

Loc. 20: On decayed *Cct*, ECC24 (mc, pH = 8.7). **Loc. 23:** On decayed *Fl*, AET7576 (mc); on *O* cladodes, MAFR53 (mc).

Originally described from the Yucatan Peninsula, Mexico (Keller and Brooks, 1976) and also cited from Baja California (Illana *et al.*, 2000). It is an easily recognised species with a peridium which remains as a wide collar, produced during the circumcissile dehiscence at the base of the sporotheca. It has a robust cylindrical columella. It was originally described from bark of tropical (*Psycotria*) and temperate (*Quercus* and *Ulmus*) trees (Keller and Brooks, 1976), but in arid areas it appears on decayed *Yucca* (Novozhilov *et al.*, 2003) and cacti (*Cephalocereus*, *Ferocactus* and *Opuntia*).

Echinostelium colliculosum K.D. Whitney & H.W. Keller [0, 11]

Loc. 3: On bark of *Yp*, dwb2324 (mc; pH = 7.2), dwb2328 (mc; pH = 7.3). **Loc. 4:** On bark of *Yp*, dwb2327 (mc; pH = 7.4); on bark of *Jd*, dwb2477, dwb2498 (mc; pH = 7.0). **Loc. 15:** On bark of *Nt*, dwb2462 (mc; pH = 7.1). **Loc. 16:** On bark of *Bg*, dwb2057 (mc; pH = 7.2). **Loc. 18:** On bark of *Bg*, dwb2333 (mc; pH = 7.0). **Loc. 25:** On bark of *Pw*, dwb2438 (mc; pH = 7.1). **Loc. 28:** On bark of *Yp*, dwb2315 (mc; pH = 7.0). **Loc. 33:** On bark of *Os*, dwb2436 (mc; pH = 7.1).

The holotype of this species was found on *Yucca brevifolia* bark from Nevada USA, in moist chamber (Whitney, 1980). In the description of the species (Whitney and Keller, 1980), specimens from Colorado and Arizona of H.W. Keller, previously listed as *Echinostelium* sp. (Keller and Brooks, 1976) were included. One of the specimens illustrated in that paper (Figs 18 and 20, page 1218) is very similar to our specimens above. The height of the white sporocarps of our collections ranges from 80 to 130 μm , the

spore-like structure at the stipe apex is not globose, but looks slightly collapsed and indented to a shape like a clover leaf (Figs 34-36), and the spores are similarly shaped (Fig. 35) and (8-)9-13 μm diam. at the base. The morphology of the sporelike structure and spores are constant in all these specimens, and also in specimens later found on the bark of cacti and succulent plants in other arid areas of Mexico, Chile and Argentina (unpublished data). The collapsed shape of the spore-like body is seen by SEM also (Figs 37-38) and the spores show flattened warts, only clearly distinguishable at high magnification (Fig. 38) and unlike the marked baculate ornamentation visible in other SEM micrographs of this species (Schnittler and Novozhilov, 2000; Moreno *et al.*, 2001; Adamonyte, 2006). At lower magnification and by transmitted light, even with good optics and Nomarski, the spores appear to be smooth (Fig. 35). The spore size and other characters however agree perfectly with *Echinostelium colliculosum*, and we feel the minor differences described are not enough to separate our specimens from this taxon. The variations may represent a different ecotype, showing a response of this species to developing rapidly in arid environments. Attempts to culture spores from our specimens on agar have been unsuccessful.

This species was previously cited from Baja California Sur (Moreno *et al.*, 2001) and Chihuahua (Lizárraga *et al.*, 2003). It is also known in the Neotropics from Belize (Ing and Haynes, 1999), and Brazil (Cavalcanti, 2002), and according to Novozhilov *et al.* (2006) it is common in Eurasian arid areas.

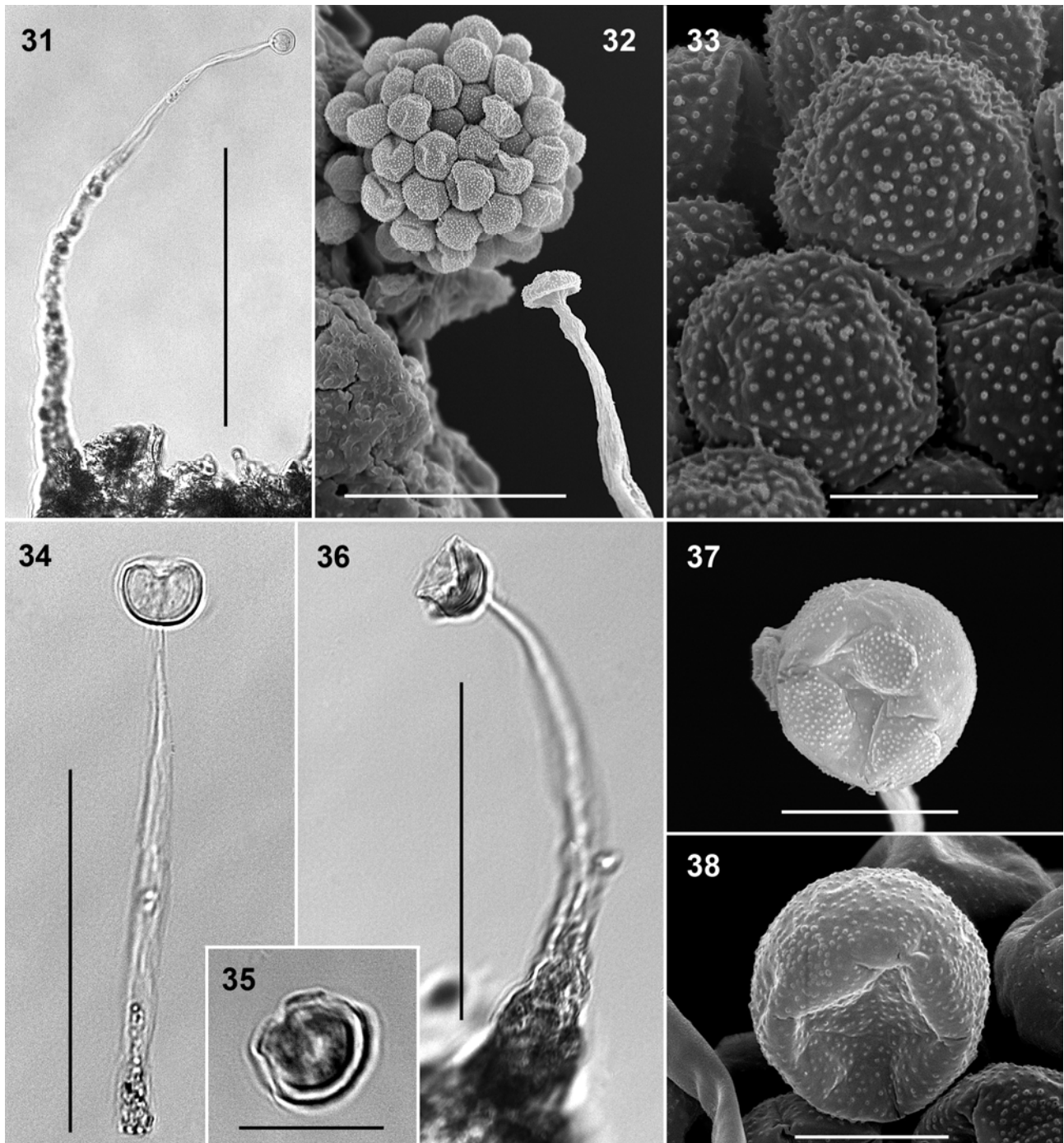
Echinostelium fragile Nann.-Bremek. [0, 1]

Loc. 12: On bark of *Bd*, dwb2369 (mc, pH = 5.3).

This is the second record of this tiny species for the Neotropics. It recently has been reported on *Oxalis gigantea* from arid areas of Chile (Lado *et al.*, 2007a). It is easily recognised by its fusiform slightly pigmented columella. The pigmentation is not always apparent, and hyaline specimens are best viewed with Nomarski optics.

Echinostelium minutum de Bary [0, 7]

Loc. 12: On bark of *Bd*, dwb2405 (mc, pH = 5.9). **Loc. 19:** On bark of *Bu*, dwb2486 (mc; pH = 6.1). **Loc. 27:**



Figs 31-33. *Echinostelium apitectum* (dwb2482). **31.** Whole sporocarp by LM (bar = 100 μ m). **32.** Spore mass separating from the warted spore-like body, which retains a disc of the peridium below by SEM (bar = 30 μ m). **33.** Spore surface covered with evenly dispersed warts by SEM (bar = 5 μ m). **Figs 34-38.** *Echinostelium colliculosum* (dwb2328). **34, 36.** Whole sporocarps by LM showing spore-like body with indented shape (bar = 50 μ m). **35.** Spore by LM with indented shape (bar = 10 μ m). **37.** Spore-like body by SEM with inconspicuous warts and indentation (bar = 10 μ m). **38.** Spores by SEM with indentation and flattened inconspicuous warts (bar = 5 μ m).

On bark of *O*, dwb2176 (mc; pH = 6.7). **Loc. 28:** On bark of *Yp*, dwb2065 (mc; pH = 6.8). **Loc. 33:** On bark of *Ac*, dwb2484 (mc; pH = 5.9).

Reported from Puebla by Keller and Braun (1977).

Enerthenema papillatum (Pers.) Rostaf. [0, 2]
Loc. 16: On bark of *Bg*, dwb2062 (mc; pH = 7.2). **Loc.**

18: On bark of *Bg*, dwb2318 (mc; pH = 7.0).

The pH of *Beaucarnea gracilis* is more circa neutral than the normal substrates of this acid-tolerant species (Stephenson, 1989; Ing, 1997; Wrigley de Basanta, 2004).

Fuligo septica (L.) F.H Wigg. [2, 0]

Loc. 11: On a log of *Bd*, AET9232. **Loc. 19:** On decayed *Nt*, AET9353.

Reported previously from Puebla by Martínez-Alfaro *et al.* (1983).

Hemitrichia calyculata Speg. [11, 0]

Loc. 6: On stem of *A*, AET5531a. **Loc. 6a:** On leaves of *A*, AET5383. **Loc. 7:** On leaves of *A*, AET7339. **Loc. 10:** On leaves of *A*, AET9185. **Loc. 11:** On stem of *Bd*, AET9230a. **Loc. 32:** On leaves of *A*, AET5475. **Loc. 34:** On leaves of *A*, AET5451; on stem of *A*, AET5455.

Hemitrichia calyculata is basically a lignicolous species in forested areas, but in the Tehuacán-Cuicatlán Valley it was consistently found on decayed *Agave* spp., mainly between the dried leaves. This species was previously cited from Oaxaca by Welden and Guzmán (1978).

Hemitrichia minor G. Lister [6, 5]

Loc. 1: On *O* cladodes, AET9112. **Loc. 6:** On leaves of *Q*, AET7492 (mc). **Loc. 8:** On *O* cladodes, AET5351. **Loc. 23:** On decayed *Mg*, ECC32 (mc, pH = 9.0); on decayed *Pw*, ECC37a (mc, pH = 7.7). **Loc. 24:** On *O* cladodes, AET9332.

Specimen AET7492 has capillitium with spines that reach 5.0 µm in length, reminiscent of the capillitium of *Perichaena chryso sperma* (Curr.) Lister. The spirals present however leave no doubt as to the identity of the sample.

Hemitrichia pardina (Minakata) Ing [3, 3]

Loc. 6: On leaves of *A*, AET5518; on leaves of *Q*, AET7549 (mc). **Loc. 23:** On decayed *Pw*, ECC119 (mc, pH = 8.5). **Loc. 33:** On bark of *Yp*, dwb2347 (mc; pH = 6.9). **Loc. 34:** On inflorescence peduncle of *A*, AET5564b.

For this species we follow the species concept of Ing (1999). In our collections both stipitate and sessile sporocarps appeared, but all had the characteristic dark raised warts on the outer surface of the peridium. This species was reported from Quintana Roo and Veracruz by Lado *et al.* (2003).

Licea belmontiana Nann.-Bremek. [1, 0]

Loc. 6a: On leaves of *A*, AET5386c.

The characteristics of the totally smooth spore as well as the absence of ornamentation on the borders of the peridial platelets make it an easy species to recognise. It can be distinguished from *Licea deplanata* Kowalski by the absence of fused papillae on the very edge of the platelet margins. First record for the Neotropics and Mexico.

Licea biforis Morgan [0, 2]

Loc. 20: On leaves of *A*, AET7539 (mc); on decayed *Ep*, ECC388 (mc, pH = 8.1).

This species is similar to *L. succulenticola* Mosquera, Lado, Estrada & Beltrán-Tej., but was clearly separated from this species by Mosquera *et al.* (2003).

Licea denudescens H.W. Keller & T.E. Brooks [0, 1]

Loc. 18: On bark of *Bg*, dwb2320 (mc; pH = 7.1).

This is the first record of this species for Mexico. In the Neotropics it is also known from Belize (Ing and Haynes, 1999) and Brazil (Cavalcanti, 2002).

Licea kleistobolus G.W. Martin [0, 2]

Loc. 12: On bark of *Bd*, dwb2412 (mc; pH = 5.9). **Loc. 30:** On bark of an unidentified tree, dwb2473 (mc; pH = 6.9).

Schnittler and Novozhilov (2000) found it abundantly on the bark of desert shrubs in Kazakhstan.

Licea minima Fr. [0, 1]

Loc. 33: On bark of *Ac*, dwb2500 (mc; pH = 6.4).

Licea nannengae Pando & Lado [0, 3]

Loc. 4: On bark of *Jd*, dwb2469; dwb2488; dwb2489 (mc; pH = 6.9; 7.0).

This species has been recorded from Tlaxcala by Rodríguez-Palma *et al.* (2002).

Licea rugosa Nann.-Bremek. & Y. Yamam. var. *rugosa* [0, 4]

Loc. 11: On bark of *Yp*, dwb2332 (mc; pH = 7.3); on bark of *Bg*, dwb2335 (mc; pH = 7.1). **Loc. 17:** On bark of *Bg*, dwb2311 (mc; pH = 6.8).

This material formed part of the study of stipitate species of *Licea* carried out by Wrigley de Basanta and Lado (2005), and represents the first records of this species from the Neotropics. Illustrations and comments on the species can be found in this publication.

Licea rugosa var. *fujio kana* (Y. Yamam.) D. Wrigley & Lado [0, 7]

Loc. 3: On bark of *Yp*, dwb2344 (mc; pH = 7.2). On bark of *Yp* dwb2348 (mc; pH = 7.3). **Loc. 15:** On bark of *Ac*, dwb2471 (mc; pH = 6.9). **Loc. 18:** On bark of *Bg*, dwb2077 (mc; pH = 6.5). **Loc. 28:** On bark of *Pl*, dwb2316 (mc; pH = 6.3). **Loc. 30:** On bark of *Yp*, dwb2349 (mc; pH = 6.9); On bark of unidentified tree, dwb2474 (mc; pH = 6.9).

All the specimens above, except dwb2471 and dwb2474, formed part of the study of stipitate *Licea* spp. by Wrigley de Basanta and Lado (2005), and represent the first records of this variety from the Neotropics. Illustrations and comments on the species can be found in this publication.

Licea succulenticola Mosquera, Lado, Estrada & Beltrán-Tej. [0, 40]

Loc. 5: On bark of *Yp*, dwb2356 (mc; pH = 7.4). **Loc. 14:** On *Ot* cladodes, ECC70 (mc, pH = 8.7). **Loc. 18:** On bark of *Bg*, dwb2073 (mc; pH = 6.5). **Loc. 20:** On *Od* cladodes, ECC61 (mc, pH = 9.1); on decayed *Ep*, ECC71 (mc, pH = 8.1). **Loc. 21:** On decayed *Mg*, AET7509 (mc). **Loc. 23:** On *O* cladodes, MAFR65b (mc); on *Od* cladodes, ECC57 (mc, pH = 8.3); on *Op* cladodes, ECC68 (mc, pH = 8.6); on decayed *Mc*, ECC19 (mc, pH = 8.6); on decayed *Mg*, ECC30 (mc, pH = 8.7); on decayed *N*, MAFR90 (mc); on decayed *Pw*, ECC18 (mc, pH = 8.5), ECC79 (mc, pH = 8.5).

Licea succulenticola was originally described from Spain, the United States and the states of Hidalgo, Morelos, Puebla and Tlaxcala in Mexico (Mosquera *et al.*, 2003). These specimens are the first record for the Tehuacán-Cuicatlán Valley and extend the distribution of the species in the arid areas of Mexico, where it appears to be common.

Lycogala epidendrum (L.) Fr. [2, 0]

Loc. 17: On decayed *Cct*, AET 9296. **Loc. 34:** On leaves of *A*, AET5436.

Previously recorded from Oaxaca by Macbride and Smith (1896) and Welden and Guzmán (1978), and from Puebla by Welden and Lemke (1961) and Martínez-Alfaro *et al.* (1983).

Macbrideola martinii (Alexop. & Beneke) Alexop. [0, 1]

Loc. 17: On bark of *Bg*, dwb2334 (mc, pH = 7.2).

Previously recorded in Mexico from Quitana Roo and Veracruz (Lado *et al.*, 2003). The clusters of warts on the spores and the long primary branches of the capillitium (Fig. 39) are characteristics of this species.

Macbrideola oblonga Pando & Lado [0, 2]

Loc. 25: On bark of *Pw*, dwb2437 (mc, pH = 7.1). **Loc. 31:** On bark of *Pw*, dwb2434 (mc, pH = 7.1).

This is the first record for the Neotropics and Mexico. Our collections extend the distribution of this species, described from Europe by Pando and Lado (1988) on

Juniperus thurifera bark, and represent a different substrate, as they developed on the bark of cacti. The oblong shape of the sporotheca and the presence of free spores (Figs 40, 42) differentiate this species.

Macbrideola synsporos (Alexop.) Alexop. [0, 1]
Loc. 15: On bark of *Ac*, dwb2491 (mc, pH = 6.9).

This is the first record for the Neotropics. Lizárraga *et al.* (2005) and Moreno *et al.* (2006) reported it from Chihuahua and Sonora in the Nearctic region of Mexico. This species, easily identified by its clustered spores (Fig 41), is common on the bark of *Quercus ilex* in Mediterranean woodlands (Wrigley de Basanta, 1998) and here only appeared on *Acacia* bark and not on the bark of cacti or of any other plant in the Tehuacán-Cuicatlán Valley.

Paradiachaeopsis cf. ***erythropodia*** (Ing) Nann.-Bremek. [0, 2]

Loc. 4: On bark of *Jd*, dwb2487 (mc, pH = 7), dwb2479 (mc, pH = 6.9).

The scattered brown sporocarps have a slender stalk with a characteristic red-brown fibrous base (Fig. 43), and the greyish brown spores of 9-11 µm diam. which are minutely warty. The capillitium branches from the top of the stalk (Fig. 44) and has dichotomously branched ends. All these characters fit the description of the species above (Nannenga-Bremekamp, 1967), but the specimens differ in that some of the capillitium anastomoses into a very open net. This species was described from Nigeria, and if the identity of the specimens is confirmed it will be the only report other than the type material, extending its distribution to another continent and from the Palearctic to the Neotropics.

Perichaena chrysosperma (Curr.) Lister [13, 12]

Loc. 3: On leaves of *Da*, AET9176, AET9184. **Loc. 4:** On leaves of *A*, AET9149b. **Loc. 6:** On leaves of *Q*, AET7490 (mc). **Loc. 14:** *Ot* cladodes, ECC17. **Loc. 20:** On stems of *A*, AET7334 (mc). **Loc. 23:** On stems of *A*, AET7418 (mc). **Loc. 32:** On leaves of *A*, AET5472; on stem of *Bd*, AET5481. **Loc. 34:** On leaves of *A*, AET5443; on stem of *A*, AET5563a. **Loc. 12:** On bracts of *Bd*, AET 9228; on leaves of *Da*, AET 9224. **Loc. 24:** On leaves of *A*, AET9320.

The capillitium of specimen AET7490, which developed in moist chamber culture on

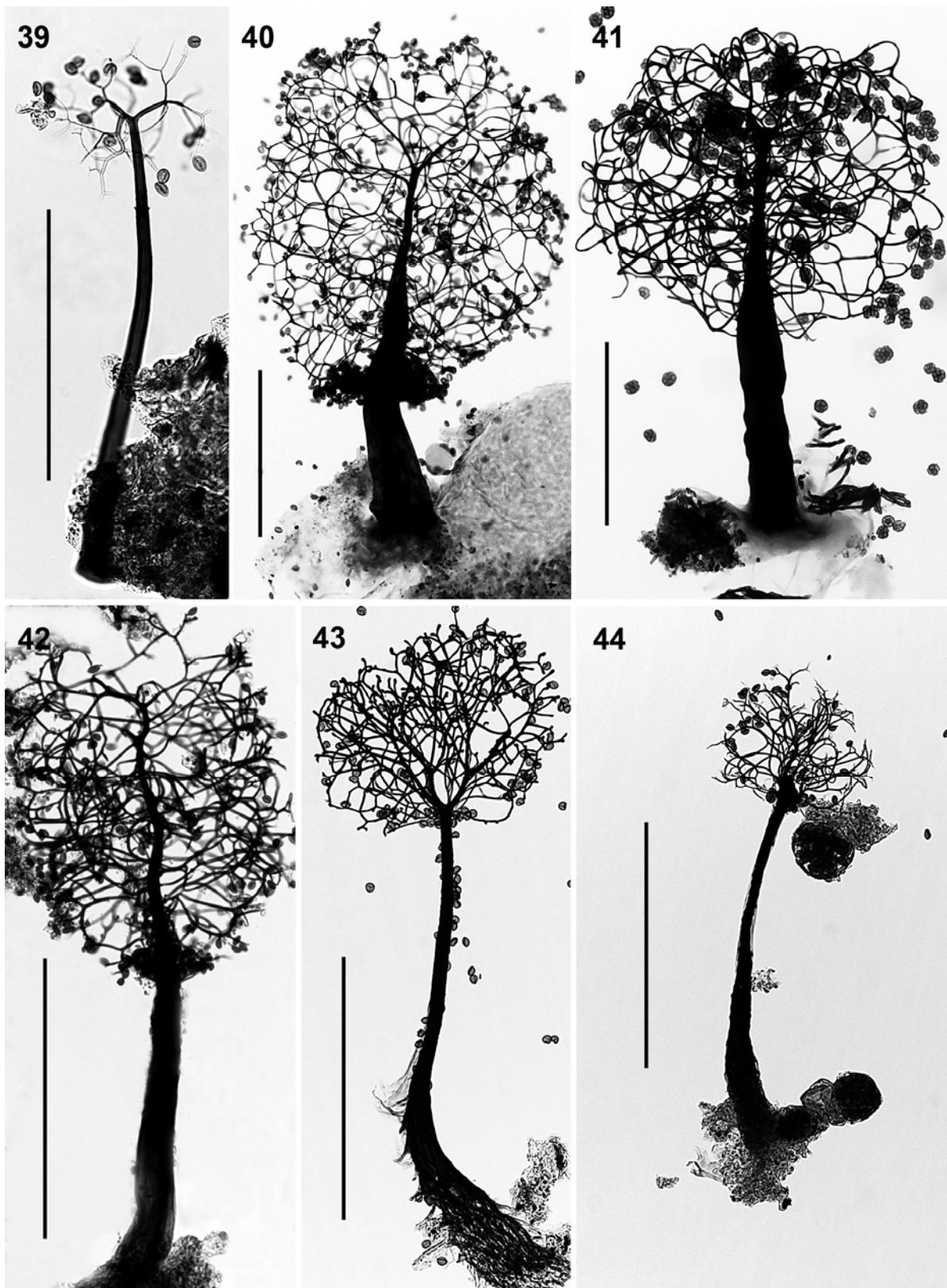


Fig. 39. *Macbrideola martinii* (dwb2334a). Sporocarp by LM (bar = 200 μ m). **Fig. 40.** *Macbrideola oblonga* (dwb3434). Sporocarp by LM (bar = 200 μ m). **Fig. 41.** *Macbrideola synsporos* (dwb2491). Sporocarp by LM (bar = 200 μ m). **Fig. 42.** *Macbrideola oblonga* (dwb2437). Sporocarp by LM (bar = 300 μ m). **Figs 43-44.** *Paradiacheopsis* cf. *erythropodia* (dwb2487). Sporocarps by LM (bar = 300 μ m).

oak leaves, has relatively small spines compared to the specimens which developed on *Agave* spp.

Perichaena corticalis (Batsch.) Rostaf. [4, 25]

Loc. 6: On inflorescence peduncle of *A*, AET5526; on leaves of *A*, AET5538b; on stem of *A*, AET5577. **Loc. 15:** On decayed *Cct*, AET9290. **Loc. 20:** On *Op* cladodes, ECC166a (mc, pH = 8.3); on *Op* cladodes, ECC179 (mc, pH = 8.4); on decayed *Ep*, ECC141 (mc, pH = 8.3); on decayed *Cct*, ECC387 (mc, pH = 8.6). **Loc. 23:** On decayed *Mc*, ECC20 (mc, pH = 7.8); on decayed *Fl*, ECC129 (mc, pH = 8.6); on decayed *Mg*, ECC403 (mc, pH = 8.1); on decayed *Pw*, ECC42 (mc, pH = 9.2); on stems of *A*, AET7419 (mc).

Perichaena depressa Lib. [16, 9]

Loc. 6: On stem of *Yp*, AET5521, AET5513b. **Loc. 6a:** On leaves of *A*, AET5400b. **Loc. 10:** On leaves of *A*, AET9195; on leaves of *Da*, AET9205. **Loc. 11:** On stem of *Bd*, AET9234. **Loc. 12:** On stem of *Bd*, AET9220. **Loc. 20:** On stem of *A*, AET5498, AET7486 (mc). **Loc. 22:** On leaves of *A*, AET5399. **Loc. 23:** On *Op* cladodes, ECC199a (mc, pH = 8.2); on decayed *Mc*, ECC20b (mc, pH = 7.8); on stem of *A*, AET7329. **Loc. 32:** On stem of *Bd*, AET5485.

The distinction between *Perichaena depressa* and *P. quadrata* T. Macbr. is complex as their most characteristic differences are best seen by SEM. Following Keller and Eliasson (1992), we have placed in this species all material with grouped, markedly flattened sporocarps with warted or spinulose ornamentation on the capillitium and no sign of reticulation even under oil immersion. In *P. quadrata* we included the specimen with more rounded pulvinate sporocarps with capillitium which was more uniform in diameter and ornamented with a reticulum observable by LM at high magnification. This species was previously cited from Puebla by Keller and Braun (1977).

Perichaena luteola (Kowalski) Gilert [8, 65]

Loc. 6a: On *O* cladodes, AET5388. **Loc. 14:** On *Ot* cladodes, ECC126 (mc, pH = 8.4). **Loc. 17:** On decayed *Nt*, AET9294. **Loc. 20:** On *O* cladodes, AET5508; on *Od* cladodes, ECC36 (mc, pH = 8.6); on *Op* cladodes, ECC40 (mc, pH = 8.6); on decayed *Cct*, ECC34 (mc, pH = 8.5); on decayed *Fl*, ECC136 (mc, pH = 9.1); on decayed *Mc*, ECC187 (mc, pH = 8.5). **Loc. 23:** On *O* on cladodes, MAFR129 (mc); on *Od* cladodes, ECC1b (mc, pH = 8.7); on *Op* cladodes, ECC51 (mc, pH = 8.2); on decayed *Fl*, ECC197 (mc, pH = 8.5); on decayed *Mc*, ECC50 (mc, pH = 8.2); on decayed *Ph*, ECC205 (mc, pH = 9.4); on decayed *Pw*, ECC124 (mc, pH = 8.4). **Loc. 24:** On *O* cladodes, AET9345. **Loc. 27:** On *O* cladodes, AET7636. **Loc. 29:** On leaves of *A*, AET5494b; on stem

of *Yp*, AET5496. **Loc. 31:** On *O* cladodes, AET9373.

The spore size of these specimens was slightly smaller (10-12.5 µm diam.) than the material described by Kowalski (1969) as *Calonema luteolum* Kowalski (12-13 µm diam.). The sporocarps are 0.1-0.5 mm diam., scattered or in small groups, the peridium single, thin, membranous, iridescent, transparent and with the spore mass clearly visible through the peridium. These characters, as well as the spinulose spores agree with the original description. Before this study, the species was only known to appear on herbivorous dung or leaf litter (Kowalski, 1969; Braun & Keller, 1976), so these specimens represent an entirely new substrate for the species, and they are from numerous localities and developed on many varieties of cacti.

Perichaena pedata (Lister & G. Lister) G. Lister [0, 1]

Loc. 6: On leaves of *Q*, AET7491 (mc).

This collection has only three stipitate fruit bodies which are sporocarpic and yellowish brown (77. m. y Br), with a black cylindrical stalk, and a double peridium, with the inner membranous layer covered by granular material. There is little capillitium forming a net and covered with warts. According to Rammeloo (1984c), *P. pedata* was described as a variety of *P. variabilis* Rostaf., which in turn was considered to be conspecific with *P. chrysosperma* (Curr.) Lister by Martin and Alexopoulos (1969). However, Rammeloo (1981), Nannenga-Bremekamp (1991) and Ing (1999) have considered it a separate species because of its usually foliicolous habit, the presence of stalks and the absence of long spines on the capillitium characteristic of *P. chrysosperma*. Ing (1999) points out that it is frequently confused with other *Perichaena* species, and is close to *Hemitrichia minor* G. Lister, from which it is separated by the lack of spiral bands on the capillitium. McHugh (2005) discussed these differences also. This is the first record for Mexico. In the Neotropics, previously reported from Costa Rica and Ecuador (Lado and Wrigley de Basanta, 2008).

Perichaena quadrata T. Macbr. [0, 1]

Loc. 16: On bark of *Bg*, dwb2124 (mc; pH = 7.3).

See comments under *P. depressa*. First record of this species for the Neotropics and Mexico.

Perichaena stipitata Lado, Estrada & D. Wrigley, **sp. nov.** [0, 3] Figs 45-56

Sporophora sporocarpica, dispersa vel aggregata, stipitata, sub-globosa vel sub-hemisphaerica, 0.1-0.5 mm diam., flavo-aurantiaca. Stipes calcareus, albus, cylindricus aut conicus, 0.08-0.38 × 0.05-0.38 µm altus latusque. Peridium unicum, membranaceum, intus ocellatum. Capillitium exiguum, flavum, tubulare, tubulis 1.4-6.8 µm diam., ramificatis, extus valde irregularibus atque praeditis cavitatibus 3.8-6.8 µm diam. Sporae liberae, flavae, 12-15 µm diam., verrucosae.

Sporophores sporocarpic, scattered or in small groups of 2-4 sporocarps, stalked. Sporotheca sub-globose to sub-hemispheric, occasionally pyriform, 0.1- 0.5 mm diam, orange yellow (67. brill. OY - 72. d. OY) above, sometimes dark brown (78. d. y Br) to blackish below; slightly immature sporocarps have a darker ring at the apex and base of the sporotheca or darker patches. Hypothallus inconspicuous. Stalk cylindrical to conical, often with a sharply reduced apex, 0.08-0.38 mm in height, 0.05-0.38 mm wide, calcareous and white or without obvious calcium deposits, and then brown (81. d. gy. y Br) to black, filled with crystalline deposits and refuse matter, sometimes slightly striated. Peridium single, yellow (89. p. Y- 86. l. Y) by transmitted light, membranous, inner surface ocellate and faintly wrinkled with oil immersion and by SEM; dehiscence irregular in the top half of the peridium leaving a small basal cup-like calyculus. Columella absent. Capillitium scanty, tubular, brilliant yellow (83. brill. Y), concolorous with the spores by transmitted light, threads of 1.4-3.6 µm diam., branched, sometimes with loops, with few free ends, surface irregular, with large holes, 3.8-6.8 µm diam. at high magnification or by SEM. Spores free, orange yellow (67. brill. OY) in mass, brilliant yellow (83. brill. Y) by LM, sub-globose, 12-15 µm diam., warted, with flat warts by SEM.

HOLOTYPE. MEXICO. Puebla, San José Miahuatlán, Cuacnopalan-Oaxaca (Mex-135) highway, km 75, 18°14'04"N 97°17'05"W, 1200 m, 8-VII-2001, on decayed

Myrtillocactus geometrizans in moist chamber, *E. Conde*, ECC 16 (TLXM). Isotype MA-Fungi 73606.

Etymology: From the Latin *stipitatus*, provided with a stalk.

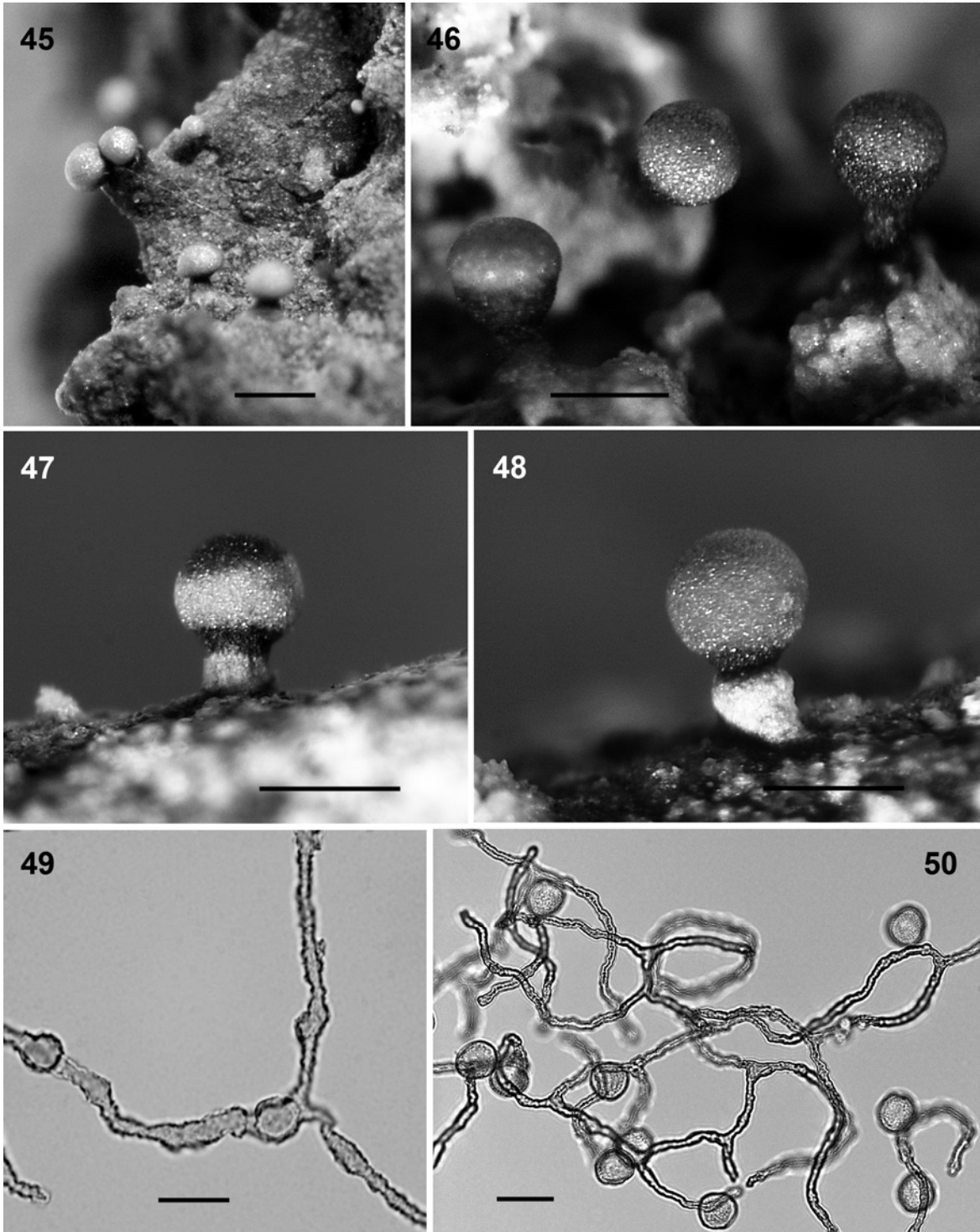
Habitat: Decaying remains of cacti

Known distribution: Puebla and Querétaro, Mexico

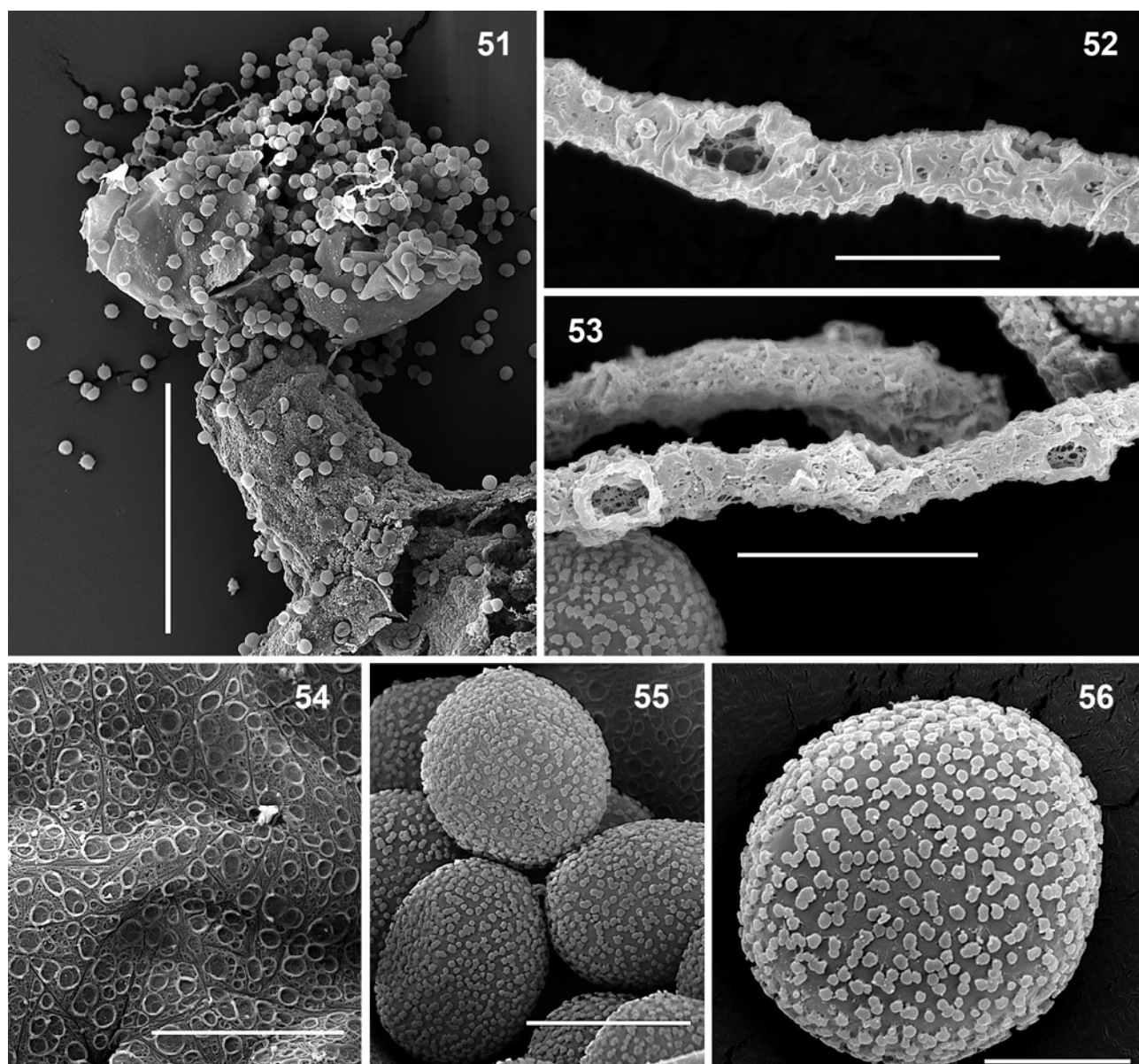
Other specimens examined

Loc. 23: On decayed *Myrtillocactus geometrizans*, ECC386 (mc, pH = 9.1), ECC395 (mc, pH = 8.5). MÉXICO: Querétaro, Tolimán, Panales, 20°52'22"N 99°59'34"W, 1664 m, 16-VII-2003, on decayed *Stenocereus* sp. in mc, Lado15712. Jalpan de Serra, Tancoyol, road to San Antonio Tancoyol, km 16, 21°25'26"N 99°19'58"W, 629 m, 18-VII-2003, on decayed *Pachycereus* sp. in mc, Lado 15723, Lado 15729.

In addition to the 3 collections from the Tehuacán-Cuicatlán Valley, three moist chamber culture collections of this same myxomycete were made from substrates collected in the Sierra Gorda Biosphere Reserve (Querétaro, Mexico) growing also on columnar cacti. The most obvious character of this new *Perichaena* is the stalk (Figs 45-48, 51), which is usually white, with calcium deposits, giving the appearance of a tiny *Physarum melleum* (Berk. & Broome) Masee. Some specimens with dark stalks (Fig. 46) are somewhat similar to *Perichaena pedata* (Lister & G. Lister) G. Lister, another stipitate species in this genus, but the spores are larger, (12-15 µm diam. vs. 9.3-11.6 µm) and the ornamentation of the interior of the peridium and the capillitium are different. The interior of the peridium of *Perichaena pedata* is ornamented with short rounded low ridges in an incomplete network and with numerous verrucate elements by SEM, not ocellate and wrinkled. The capillitium of *P. pedata* has none of the large holes present in *P. stipitata* (Figs 49-50, 52-53) and has papilla-like excrescences (Rammeloo, 1984c) which are absent in *P. stipitata*. The spores by SEM (Figs 55-56) are somewhat similar to those of *Perichena chrysosperma* (Curr.) Lister (Rammeloo, 1984b) but it is different from that species in the capillitium, which does not bear the long spines. *Perichaena stipitata* has ocellate markings and fine wrinkles on the inside of the peridium (Fig. 54) which is



Figs 45-50. *Perichaena stipitata* (Lado 15723). **45.** Sporocarps by SM (bar = 0.5 mm). **46.** Three stipitate sporocarps by SM (bar = 0.2 mm). **47.** Sporocarp with dark ring at the apex and the base of the sporotheca by SM (bar = 0.3 mm). **48.** Sporotheca showing calcareous stalk with reduced apex by SM (bar = 0.3 mm). **49.** Capillitium with irregular surface and large holes by LM (ECC 16) (bar = 10 μ m). **50.** Branched capillitium with loops and few free ends by LM (bar = 20 μ m).



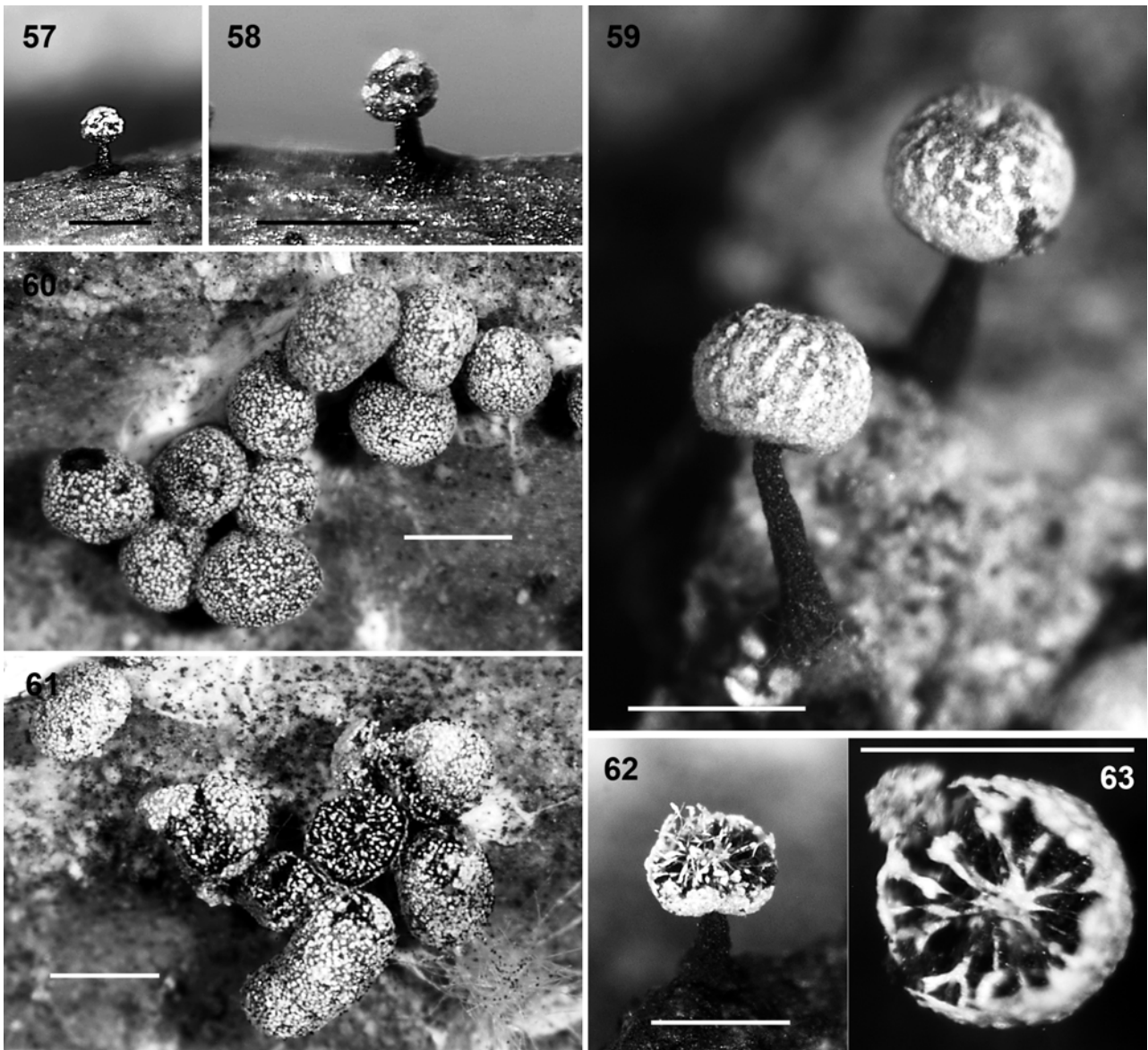
Figs 51-56. *Perichaena stipitata* (ECC16) by SEM. **51.** Whole dehisced sporocarp (bar = 200 µm). **52.** Capillitium showing irregular surface and holes (bar = 5 µm). **53.** Pitted capillitium typical of the genus, with large holes (bar = 10 µm). **54.** Ocellate inner surface of peridium with wrinkles (lines) (bar = 10 µm). **55.** Group of spores (bar = 10 µm). **56.** Detail of spore surface showing ornamentation with flattened warts (bar = 5 µm).

regularly and densely verrucose in *P. chrysosperma*.

Other *Perichaena* species with stalks are *P. areolata* Rammeloo, and *P. reticulospora* H.W. Keller & D.R. Reynolds, but both have short non-calcareous stalks. In addition *P. areolata* has a double peridium with dense regular papillate ornamentation on the inner surface by SEM (Rammeloo, 1984a). *Perichaena reticulospora* has a banded-reticulate ornamentation on the spores (Keller and Reynolds, 1971), not warted.

Perichaena vermicularis (Schwein.) Rostaf. [7, 26]

Loc. 5: On bark of *Yp*, dwb2354 (mc; pH = 7.1). **Loc. 6:** On stem of *Yp*, AET5513. **Loc. 6a:** On leaves of *A*, AET5387a. **Loc. 8:** On *O* cladodes, AET 5374. **Loc. 11:** On a log of *Bd*, AET9231. **Loc. 20:** On *Od* cladodes, ECC43 (mc, pH = 8.6), ECC80 (mc, pH = 8.1), ECC116 (mc, pH = 9.1); on decayed *Ep*, ECC83 (mc, pH = 8.0); on decayed *Cct*, ECC81 (mc, pH = 8.8). **Loc. 23:** On *O* cladodes, MAFR38 (mc); on *Op* cladodes, ECC39 (mc, pH = 8.4); on decayed *Mc*, ECC44 (mc, pH = 8.7); on decayed *Pw*, ECC35 (mc, pH = 8.5). **Loc. 25:** On bark of *Bs*, dwb2490 (mc, pH = 6.4); on bark of unidentified tree, dwb2481 (mc, pH = 6.3). **Loc. 30:** On bark of



Figs 57-58. *Didymium eremophilum* (AET7441). **57.** Minute stipitate sporocarp by SM (bar = 200 μ m). **58.** Detail of stipitate sporocarp by SM (bar = 200 μ m). **Fig. 59.** *Physarum crateriforme* (dwb2435). Sporocarps with a long stalk by SM (bar = 0.5 mm). **Figs 60-61.** *Physarum spectabile* (AET9186). **60.** Group of sporocarps and short plasmodiocarps by SM (bar = 0.5 mm). **61.** Dehiscent sporocarps and short plasmodiocarps by SM (bar = 0.5 mm). **Figs 62-63.** *Physarum crateriforme* (dwb2447) by SM. **62.** Open sporocarp with strongly calcareous capillitium (bar = 0.5 mm). **63.** Open sporocarp showing the columella with massed nodes of the capillitium (bar = 0.5 mm).

unidentified tree, dwb2470 (mc, pH =6.9). **Loc. 34:** On leaves of *A.*, AET5442, AET5572; on stem of *A.*, AET5568.

Physarella oblonga (Berk. & M.A. Curtis) Morgan [2, 0]

Loc. 18: On leaves of *A.*, AET9304. **Loc. 24:** On leaves of *A.*, AET9339.

This is a common tropical (Lado and Wrigley de Basanta, 2008) and lignicolous species, but it was found exclusively on *Agave* leaves in the Tehuacán-Cuicatlán Valley.

Physarum album (Bull.) Chevall. [18, 0]

Loc. 1: On leaves of *H.*, AET9133. **Loc. 3:** On leaves of *Yp.*, AET9183 (Esporas 9-10). **Loc. 6:** On leaves of *A.*, AET5548. **Loc. 8:** On leaves of *Yp.*, AET5359. **Loc. 11:** On leaves of *Bd.*, AET9256; on stem of leguminosae, AET9245. **Loc. 24:** On leaves of *A.*, AET9321. **Loc. 32:** On leaves of *Bd.*, AET5471. **Loc. 33:** On angiosperm wood, AET9425; twigs, AET9429. **Loc. 34:** On inflorescence peduncle of *A.*, AET5560; on leaves of *A.*, AET5453. **Loc. 35:** On bark of *Acacia*, AET9387.

Physarum bitectum G. Lister [3, 4]

Loc. 6: On leaves of *Q.*, AET7515 (mc). **Loc. 11:** On twigs, AET9260. **Loc. 33:** On leaf litter, AET9421; on twigs, AET9422.

Physarum brunneolum (W. Phillips) Masee [2, 0]

Loc. 34: On leaves of *A*, AET5434b.

First record from the Neotropical area of Mexico. Previously cited from Baja California by Lizárraga *et al.* (1997, 2004). This is a new substrate for the species, which is frequently found in sclerophyllous forests (Lado, 1993)

Physarum cinereum (Batsch) Pers. [7, 0]

Loc. 6a: On leaves of *A*, AET5386a. **Loc. 11:** On bracts of *Bd*, AET9248; twigs, AET9269a, AET9279b. **Loc. 35:** On bark of *Mg*, AET9384.

Physarum compressum Alb. & Schwein. [3, 11]

Loc. 1: On leaves of *H*, AET9121. **Loc. 4:** On bark of *Jd*, dwb2499 (mc, pH = 7.0). **Loc. 23:** On decayed *Fl*, ECC232 (mc, pH = 9.1); on *Mg*, MAFR15b (mc); on decayed *Pw*, AET7446 (mc). **Loc. 34:** On leaves of *Yp*, AET5465.

Physarum crateriforme Petch [0, 5]

Loc. 11: On bark of *Yp*, dwb2340 (mc; pH = 7.3). **Loc. 18:** On bark of *Bg*, dwb2321 (mc; pH = 7.1). **Loc. 25:** On bark of *Pw*, dwb2435 (mc; pH = 7.1). **Loc. 31:** On bark of *Pw*, dwb2446; dwb2447 (mc; pH = 7.0; 7.1). **Loc. 35:** On bark of *Mg*, AET9385.

This species has been reported previously in Mexico from Quintana Roo and Veracruz by Lado *et al.* (2003). The depressed top of the sporotheca, the large columella, the opaque black stalk (Fig. 59), and the strongly calcareous capillitium (Fig. 62), with nodes massed around the columella (Fig. 63) are characteristics of this tropical species, which appears to be an obligate corticole both in the field and in moist chamber cultures.

Physarum decipiens M.A Curtis [2, 8]

Loc. 15: On bark of *Ac*, dwb2502 (mc; pH = 6.9). **Loc. 16:** On bark of *Bg*, dwb2185 (mc; pH = 7.1). **Loc. 20:** On decayed *Cct*, ECC264 (mc, pH = 8.7). **Loc. 23:** On decayed *N*, MAFR24 (mc). **Loc. 28:** On bark of Leguminosae tree, dwb2072; dwb2075 (mc; pH = 6.4; 6.6). **Loc. 29:** On stem of *Yp*, AET5495b. **Loc. 32:** On leaves of *Bd*, AET5480. **Loc. 33:** On bark of *Ac*, dwb2495 (mc; pH = 6.4).

Some of the moist chamber samples (dwb2502, dwb2495) and the field samples have plasmodiocarps and spore characters that also fit the description of *Physarum serpula* Morgan, but Farr (1961), after studying more than 100 specimens, was of the opinion that the latter is just an environmental variant of

Physarum decipiens.

Physarum didermoides (Pers.) Rostaf. [4, 4]

Loc. 4: On leaves of *A*, AET9170b. **Loc. 6:** On leaves of *A*, AET5534. **Loc. 7:** On leaves of *A*, AET7341. **Loc. 13:** On leaves of *Yp*, AET7335. **Loc. 14:** On *Ot* cladodes, ECC221 (mc, pH = 8.6). **Loc. 23:** On decayed *Mg*, ECC398 (mc, pH = 8.5).

The field collections were all on rosette-leaved succulent plants, but the species also appeared on cacti in moist chamber cultures.

Physarum megalosporum T. Macbr. [6, 0]

Loc. 1: On leaves of *H*, AET9111. **Loc. 3:** On leaves of *A*, AET9179. **Loc. 6a:** On leaves of *A*, AET5377. **Loc. 34:** On leaves of *A*, AET5464.

Second record for Mexico. This species was previously recorded from Tlaxcala where it was found on wood and moss in *Juniperus* forests and secondary scrub (Hernández-Cuevas, 1993; Rodríguez-Palma, 1998), but in the four localities of the Tehuacán-Cuicatlán Valley it was always on rosette-leaved plants (*Hechtia* and *Agave*). From the Neotropics it is also previously known from Brazil (Cavalcanti, 2002), and from the Atacama desert of Chile (Lado *et al.*, 2007a), where it was found on dead tissues of different species of cacti (*Eulychnia*, *Copiapoa* and *Opuntia*).

Physarum melleum (Berk. & Broome) Masee [1, 0]

Loc. 9: On leaves of *Bd*, AET 9213.

Physarum notabile T. Macbr. [0, 7]

Loc. 11: On bark of *Yp*, dwb2350 (mc; pH = 7.3). **Loc. 15:** On bark of *Ac*, dwb2480; dwb2496 (mc; pH = 6.8; 6.9). **Loc. 16:** On bark of *Bg*, dwb2165 (mc; pH = 7.1). **Loc. 23:** On leaves of *A*, AET7417 (mc). **Loc. 25:** On bark of *F*, dwb2485 (mc; pH = 6.5). **Loc. 31:** On bark of *Pw*, dwb2445; dwb2448 (mc; pH = 7.0; 7.1).

The samples in moist chamber had spores 11-13 μm diam., which in some samples appeared to have a lighter area in the middle of the spore looking like a band at low magnification. The dark stipe and limeless circle at the base of the sporotheca and spore size and colour agree with the description of *Physarum notabile*. One sample, dwb2463, has been left as uncertain (cf) since it has more sessile sporocarps with a rudimentary pseudocolumella. It appeared in mc on *Cephalocereus columna-trajanii* collected at locality 15 which had a pH of 7.1. This species

was common in cold deserts of Eurasia and its variability has been observed in these areas (Novozhilov *et al.*, 2006).

Physarum oblatum T. Macbr. [4, 4]

Loc. 6: On stem of *Yp*, AET5515, on leaves of *A*, AET5536; on stem of *A*, AET5524. **Loc. 20:** On decayed *Ep*, ECC253a (mc, pH = 8.1). **Loc. 23:** On decayed *Mc*, ECC396 (mc, pH = 8.6); on decayed *Mg*, ECC292 (mc, pH = 8.5). **Loc. 32:** On leaves of *Da*, AET5477.

Physarum cf. ovisporum G. Lister [1, 0]

Loc. 6: On leaves of *A*, AET5544.

The scant material did not permit a firm identification of this sample.

Physarum pusillum (Berk. & M.A. Curtis) G. Lister [28, 27]

Loc. 1: On leaves of *H*, AET9117. **Loc. 3:** On leaves of *Da*, AET9177. **Loc. 4:** On leaves of *A*, AET9153. **Loc. 8:** On leaves of *Yp*, AET5353. **Loc. 6:** On leaves of *A*, AET5545; on a log of *Yp*, AET5530. **Loc. 11:** On twigs, AET9269b. **Loc. 17:** On decayed *Nt*, AET9297. **Loc. 18:** On leaves of *A*, AET9303. **Loc. 20:** On decayed *Ep*, ECC248 (mc, pH = 8.2); on *Cct*, ECC394 (mc, pH = 8.6). **Loc. 23:** On *O. cladodes*, MAFR36 (mc); on *Od* cladodes, ECC238 (mc, pH = 8.3); on *Op* cladodes, ECC257 (mc, pH = 7.9); on decayed *Fl*, ECC252 (mc, pH = 8.2); on decayed *Mc*, ECC219 (mc, pH = 8.3); on decayed *Mg*, AET7563 (mc). **Loc. 24:** On leaves of *A*, AET9331. **Loc. 32:** On leaves of *Da*, AET5479; on leaves of *Bd*, AET7619. **Loc. 33:** On leaves of *Da*, AET9461. **Loc. 34:** On leaves of *A*, AET5430; on stems and twigs of an *Asteraceae*, AET5445. **Loc. 35:** On bark of *Pw*, AET9377.

This is a common species in arid areas and appears on many substrates (Novozhilov *et al.*, 2006; Lado *et al.*, 2007a), but is more frequently found here on rosette-leaved succulent plants.

Physarum rubiginosum Fr. [4, 0]

Loc. 11: On *Bd* bract, AET9249; on twigs, AET9270.

This is the second record of this species for Mexico. It was reported previously from Tlaxcala (Hernández-Cuevas *et al.*, 1991).

Physarum spectabile Nann.-Bremek., Lado & G. Moreno [23, 92]

Loc. 1: On leaves of *A*, AET9126; on leaves of *H*, AET9132b. **Loc. 4:** On leaves of *A*, AET9175. **Loc. 6a:** On leaves of *A*, AET5380. **Loc. 10:** On leaves of *Yp*, AET9186, AET9189. **Loc. 6b:** On leaves of *A*, AET5546b; on stem of *A*, AET5519. **Loc. 15:** On decayed *Cct*, AET9284, AET9285. **Loc. 17:** On decayed *Nt*, AET9293. **Loc. 20:** On decayed *Cct*, ECC229 (mc, pH = 8.8). **Loc. 13:** On leaves of *Yp*, AET7336. **Loc. 14:** On *Ot* cladodes, ECC206 (mc, pH = 8.4). **Loc. 23:** On

Op cladodes, ECC210 (mc, pH = 9.1); on decayed *Fl*, AET7529; on decayed *Mc*, ECC271 (mc, pH = 8.7); on decayed *Mg*, AET7564b (mc); on decayed *N*, MAFR26 (mc); on decayed *Pw*, AET7479 (mc). **Loc. 24:** On *O* cladodes, AET9309. **Loc. 27:** On leaves of *A*, AET7633. **Loc. 28:** On decayed *Mg*, AET7622. **Loc. 31:** On decayed *Pw*, AET9372. **Loc. 35:** On decayed *Pw*, AET9386.

This is one of the most common species on cacti and succulent plants. It has very variable characters, and can be sessile or with a well defined calcareous stalk. It can be confused with *Physarum straminipes* Lister, but the latter has a non-calcareous membranous extension of the hypothallus and not a stalk. Even when *Ph. spectabile* is sessile, the narrow pale bands on the usually angular spore separate these species (Nannenga-Bremekamp *et al.* 1984). The first light micrographs of the habit of this species are presented here (Figs 60-61). Its distribution may be wider than reported in arid areas on account of this confusion. This is the second record of this species for the Neotropics, recently has been reported on the cacti *Opuntia*, *Eulychnia* and *Copiapoa*, from the Atacama desert and other arid lands of Chile (Lado *et al.*, 2007a).

Physarum viride (Bull.) Pers. [1, 0]

Loc. 1: On leaves of *H*, AET9128.

Stemonitis axifera (Bull.) T. Macbr. [1, 0]

Loc. 11: On stem of *Bd*, AET9244.

Our material could be included in *S. smithii* T. Macbr., but this species is now considered synonymous with *S. axifera* (Moreno *et al.*, 2004).

Stemonitis fusca Roth [6, 3]

Loc. 6: On inflorescence peduncle of *A*, AET5522; on stem of *Yp*, AET5520. **Loc. 11:** On stem of *Yp*, AET9238. **Loc. 19:** On decayed *Nt*, AET9355. **Loc. 20:** On decayed *Cct*, ECC14 (mc, pH = 8.8). **Loc. 23:** On *O* cladodes, MAFR88 (mc); on leaves of *A*, AET7610. **Loc. 34:** On angiosperm wood, AET5446.

Previously recorded from Puebla by Martínez-Alfaro *et al.* (1983).

Stemonitis cf. mussooriensis G.W. Martin, K.S. Thind & Sohi [1, 0]

Loc. 32: On leaves of *Bd*, AET5487.

The specimen has spores smaller than in the original description and one hemisphere is also conspicuously paler. Yamamoto (1998) considered *S. emotoi* Nann-Brem. &

Y. Yamam. to be a variety of *S. mussooriensis*, and it has spores similar to the Tehuacán-Cuicatlán material.

Trichia agaves (G. Moreno, Lizárraga & Illana) Mosquera, Lado, Estrada & Beltrán-Tej. [22, 2]

Loc. 1: On leaves of *H.*, AET9127a. **Loc. 2:** On leaves of *A.*, AET5549. **Loc. 6:** On leaves of *A.*, AET5511. **Loc. 6a:** On leaves of *A.*, AET5379. **Loc. 8:** On leaves of *Yp.*, AET5368. **Loc. 9:** On leaves of *H.*, AET 9215. **Loc. 10:** On leaves of *A.*, AET9199; on leaves of *Yp.*, AET9204. **Loc. 20:** On leaves of *A.*, AET5505. **Loc. 23:** On decayed *Mg.*, ECC145 (mc, pH = 9.0); on decayed *N.*, MAFR94 (mc). **Loc. 29:** On leaves of *A.*, AET5494a.

Trichia agaves was described, as *Trichia perichaenoides* Mosquera, Lado, Estrada & Beltrán-Tej. by Mosquera *et al.* (2000b) from Spain and the States of Hidalgo, Oaxaca, Puebla and Tlaxcala (Mexico), simultaneously it was published as *Hemitrichia agaves* by Moreno *et al.* (2000) from Spain and Baja California (Mexico). Lado (2001) proposed the new combination *T. agaves* based on the presence of capillitium in the form of short elaters, not like the long capillitial threads forming a net as it does in the genus *Hemitrichia*. Some of the specimens cited from Oaxaca and Puebla in the description of the species by Mosquera *et al.* (2000b) are from the Tehuacán-Cuicatlán Valley, and four of these are included above. It is a species frequently found on decayed rosette-leaved succulent plants like *Yucca periculosa* and different species of *Agave* and *Hechtia*, although in moist chamber culture it has developed also on columnar cacti.

Trichia contorta (Ditmar) Rostaf. [3, 1]

Loc. 6: On stem of *A.*, AET5527. **Loc. 33:** On bark of *Yp.*, dwb2326 (mc; pH = 6.9). **Loc. 34:** On leaves of *A.*, AET5434a.

Specimen AET5434a has less conspicuous more widely spaced spirals on the capillitium, and the spores have a paler hemisphere, which differ from the description of this species. It has been assigned to this taxon however, as the characters match it the closest.

Trichia varia (Pers. ex J. M. Gmel.) Pers. [3, 0]

Loc. 4: On leaves of *A.*, AET9144. **Loc. 34:** On stem of *A.*, AET5463b.

Willkommlangea reticulata (Alb. & Schwein.) Kuntze [1, 0]

Loc. 35: On angiosperm wood, AET9404.

This species is normally characteristic of more humid areas, but one collection appeared in these arid areas. It was reported previously from arid areas of the Colorado Plateau (Novozhilov *et al.*, 2003) on *Pinus edulis* bark.

Discussion

This study of the myxomycetes from the Tehuacán-Cuicatlán Valley has produced 1200 records, 454 field collections and 746 collections from moist chamber culture. The total number of species recorded was 104 and one variety from 27 genera, of which 38 were from the field collections only, 36 were from moist chamber culture only and 31 from both. The results include 2 species which are described as new to science, and another two, *Didymium wildpretii* and *Didymium umbilicatum*, which were described recently with specimens from this area (Lado *et al.*, 2007b; Wrigley de Basanta *et al.*, 2008b), as was *Trichia perichaenoides* (= *T. agaves*) Mosquera *et al.* (2000b). The total of 105 taxa includes eleven species which are new records for the Neotropics (Lado and Wrigley de Basanta, 2008): *Comatracha reticulospora*, *Cribraria lepida*, *Didymium clavodecus*, *D. eremophilum*, *D. orthonemata*, *D. sturgisii*, *D. subreticulosporum*, *Licea belmontiana*, *Macbrideola oblonga*, *M. synsporos* and *Perichaena quadrata*; apart from which, six species are new for Mexico: *Badhamia versicolor*, *Didymium applanatum*, *Echinostelium fragile*, *Licea denudescens*, *Perichaena pedata* and *Physarum spectabile*.

Among the species recorded from the country for the second time are records of *Cribraria zonatispora* and *Diderma acanthosporum*, which extend the known distribution of these recently described species (Lado *et al.*, 1999; Estrada-Torres *et al.*, 2001). There are in addition several taxa under study as possible new species, but the material we have collected so far is insufficient for formal descriptions.

The ten most common species are listed in table 1 and together represented over half of the collections studied. *Didymium wildpretii* and *Licea succulenticola* were only recorded

Table 1. Summary data on the ten most common species in the Tehuacán-Cuicatlán Valley.

Species	Field collections	Moist chamber	Total	% of records	Localities found (%)
<i>Badhamia melanospora</i>	80	149	229	19.1	66.8
<i>Physarum spectabile</i>	23	92	115	9.6	45.7
<i>Didymium wildpretii</i>	0	100	100	8.3	11.1
<i>Perichaena luteola</i>	8	65	73	6.1	25.7
<i>Physarum pusillum</i>	28	27	55	4.6	42.9
<i>Licea succulenticola</i>	0	40	40	3.3	16.7
<i>Perichaena vermicularis</i>	7	26	33	2.8	28.6
<i>Didymium squamulosum</i>	26	1	27	2.3	16.7
<i>Didymium vaccinum</i>	26	0	26	2.2	34.3
<i>Trichia agaves</i>	22	2	24	2.0	30.5

here from moist chamber cultures, but the others were found both in the field and in moist chamber culture. These ten species made up almost half of the field specimens collected and 67% of the moist chamber culture collections, and as such are the most characteristic of these arid areas.

Badhamia melanospora and *Physarum spectabile* were among the most frequently found species in both the field and moist chamber cultures. *Perichaena luteola* was less abundant in the field and *Licea succulenticola* was not found in the field, probably due to its small size. One third of the field collections, 24 species, were only collected once. Of the 68 species obtained from moist chamber culture, 16 were obtained only once. These are some of the rarer species such as *Echinostelium fragile* or *Licea belmontiana*, but also the variety of substrates cultured could account for the variety obtained, although a minimum of three different samples of each substrate were cultured and so more than one collection of all but the rarest species would be expected.

The most common species were also predictably the most widespread in distribution in the Reserve. *Badhamia melanospora*, *Physarum spectabile*, *Physarum pusillum*, *Didymium vaccinum*, *Trichia agaves* and *Perichaena vermicularis*, were found in the greatest number of localities (see Table 1), whereas the rest of the species were found in ten or fewer localities, and 41% of these were only encountered at one sampling site in the arid Tehuacán-Cuicatlán Valley. *Badhamia melanospora* was found in 24 of the 36 localities sampled and on almost all of the succulent substrata. Novozhilov *et al.* (2003) in

their study of the Colorado Plateau also found this species to be one of the most common on litter, in which they included remains of cacti. *Physarum spectabile* and *Ph. pusillum* are other species with a broad geographic distribution appearing in over 40% of the localities. Since many of the species found in one locality were also represented by only one collection (see above), these results indicate that some myxomycetes have a high degree of specificity to microhabitat, and emphasize the importance of sampling as broad and varied an area as possible to better survey its biodiversity.

It has been noted before for arid areas, that species with larger, lime-covered sporocarps and phaneroplasmodia seem to be the most successful (Blackwell and Gilbertson, 1980b, 1984; Novozhilov *et al.*, 2003, 2006; Lado *et al.*, 2007a) in terms of the large numbers produced. This was certainly the case in the Tehuacán-Cuicatlán Valley, where the most common genera also belonged to the order Physariales, which made up almost 50% of the results (Fig. 64). Among them, there were 20 species of *Didymium* and 17 species of *Physarum*. These results are very similar to those obtained in the arid areas of Chile in the southern hemisphere, where *Didymium* species made up 21% of the species found vs 19% in Tehuacán-Cuicatlán and *Physarum* 16% in both places, in spite of the great differences in the substrate species (Lado *et al.*, 2007a). The species within these genera however, differed in Chile and Mexico, and only a few of the more common species were shared. This seems to indicate that individual species have different microhabitat requirements but that the

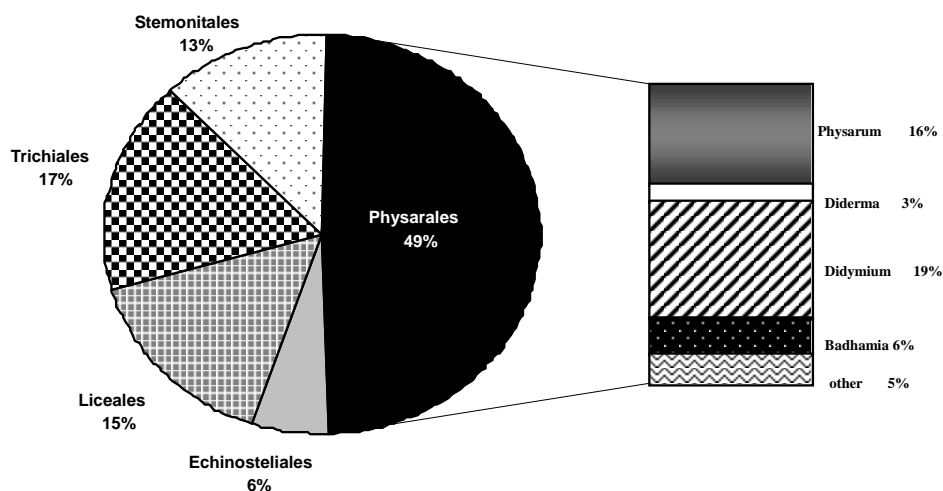


Fig. 64. Number of species in different orders of Myxomycetes found in the Tehuacán-Cuicatlán Valley (Physarales split into genera).

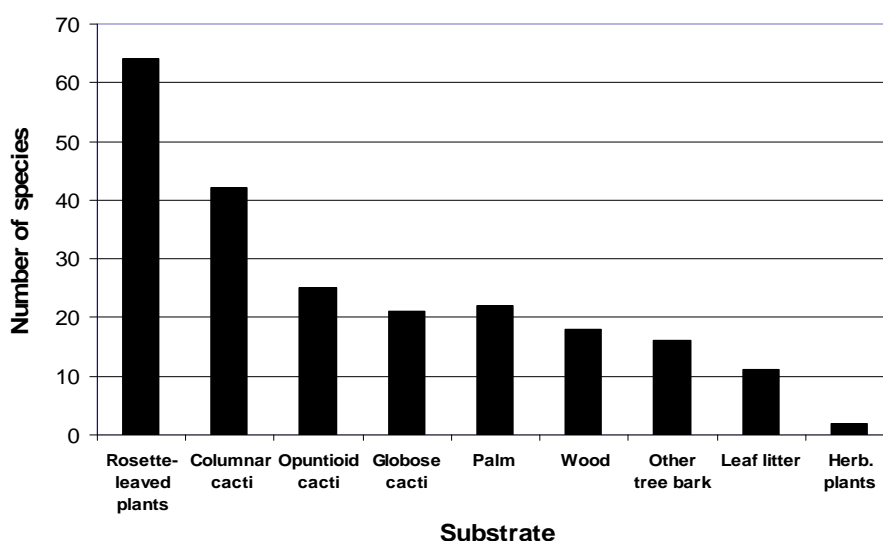


Fig. 65. Species distribution on different groups of substrata.

characteristics of the genus determine the relative success in the extremes of the particular environment, in this case the desert. In a recent study done in the arid regions of the Volga basin (Novozhilov *et al.*, 2006), the authors also found that the microhabitat features of bark were the most important in determining the distribution of corticolous myxomycete species there.

Looking at the different groups of substrata (Fig. 65), the rosette-leaved succulent plants (genera *Agave*, *Beaucarnea*, *Dasyilirion*, *Hechtia* and *Yucca*), had the greatest richness of myxomycete species with almost 61% (64 species), if the bark, stems and leaves of the rosette-leaved trees are included. The relationship of myxomycete species to specific substrates showed that 42 species were found

on *Agave* alone, followed by *Yucca* with 35 species. It is interesting to note that except *Arcyria insignis*, *Comatricha tenerrima* and *Cribraria violacea*, all the species found on other parts of *Agave* (stems or inflorescence peduncles) were also found on the leaves. Various species that commonly develop on wood in other environments, developed on the tough fibrous *Agave* leaves in the arid scrub of Tehuacán-Cuicatlán. Among these normally lignicolous species were *Arcyria cinerea*, *A. denudata*, *Calomyxa metallica*, *Ceratiomyxa fruticulosa*, *Comatricha laxa*, *C. tenerrima*, *Hemitrichia calyculata*, *Lycogala epidendrum*, *Physarella oblonga*, *Physarum album*, *Trichia contorta* and *Trichia varia*. Some of them were only found once, and some may be considered generalists, developing on a variety of substrates, such as *L. epidendrum*. However *A. cinerea*, *A. denudata* and *H. calyculata*, were found so frequently on *Agave* leaves, that it indicates an adjustment strategy to a new substrate in these arid environments where wood is scarcer, or restricted by the low humidity, high insolation and high temperatures, which impede the development of favourable moist conditions in the wood for myxomycete growth.

Apart from the rosette-leaved succulent plants, the next most productive group of substrates was that made up of different types of cacti, including columnar, opuntoid and globose cacti and the bark of tree cacti like *Pachycereus* spp. or *Myrtillocactus* spp., with 51 different myxomycete taxa appearing on them. However, many of them were obtained from the intensive study done by serial moist chamber culture of 10 representative species of cacti. Even so, in spite of the large number of collections that resulted from this serial study, the species richness was still less than that of the rosette-leaved succulent plants. In an analysis of the different types of cacti, the columnar cacti (genera *Cephalocereus*, *Isolatocereus*, *Myrtillocactus*, *Neobuxbaumia* and *Pachycereus*) were the most productive as 42 species were found on these, whereas opuntoid cacti (*Opuntia* spp.) produced 25 species and globose cacti (genera *Echinocactus*, *Ferocactus* and *Mammillaria*) 21 species. Some species were common to all types of cacti. Perhaps the large size and

different anatomy and morphology of the columnar cacti, which produced almost twice the number of species, provide more microhabitats and available water for the development of different species of myxomycete.

The tree palm *Brahea dulcis* was also a productive substrate with 22 species. Palms in other temperate and tropical areas have been shown to be productive substrates. In two tropical forests in Mexico over one third of the species (36) reported were found on palms (Lado *et al.*, 2003), and in New Zealand, 37 species were recorded on the nikau palm, mostly from field collections (Stephenson, 2003).

Bark of different living plants produced 37 different taxa. The bark of tree columnar and opuntoid cacti produced 9 species, 21 taxa were on bark of trees with rosette leaves like *Yucca* and *Beaucarnea*, 3 on bark of the palm *Brahea dulcis*, and 16 on bark of other trees like species of *Prosopis*, *Acacia*, *Bursera* or *Juniperus* (Fig. 65). Of all these species, 21 were exclusive to bark and the others were found on bark as well as other substrates. Only *Echinostelium minutum* appeared on bark of these four different types of trees, while *Echinostelium colliculosum* and *Physarum notabile* appeared on all except the palm. In the Tehuacán-Cuicatlán Valley, the usual corticolous species were found, such as species of *Echinostelium*, *Licea* and *Macbrideola*, but also some species not usually found on bark appeared, like *Badhamia melanospora*. A number of bark species also appeared on rosette-leaved plants.

The scarcity of leaf litter in these desert scrublands, caused by the frequent drying winds, which prevent litter accumulating, and lack of moisture, reduced a normally very productive microhabitat for myxomycetes. Only 12 species were found here on leaf litter. This indicates differences between this study area and the arid areas of the Volga basin where leaf litter was found to be an important habitat for myxomycetes (Novozhilov *et al.*, 2006). Some species, usually common on litter, such as *D. effusum*, *D. bahiense*, *D. iridis*, *D. squamulosum*, *Ph. brunneolum* and *Ph. cinereum*, appear to be able to make use of an alternative, and were found instead by us

Table 2. Summary data on serial cultures of ten representative cacti.

	Nc	Cp	%+	pH	Ncol	Gen	Sp	S/G
<i>Cephalocereus columna-trajani</i>	25	21	84	8.58	23	7	12	1.71
<i>Echinocactus platyacanthus</i>	25	14	56	8.13	19	10	14	1.40
<i>Ferocactus latispinus</i>	25	9	36	8.41	13	5	7	1.40
<i>Mammillaria carnea</i>	25	18	72	8.41	34	6	11	1.83
<i>Myrtillocactus geometrizans</i>	25	19	76	8.68	35	7	13	1.86
<i>Opuntia depressa</i>	25	24	96	8.42	44	8	10	1.25
<i>Opuntia pilifera</i>	25	21	84	8.62	46	7	11	1.57
<i>Opuntia tomentosa</i>	25	25	100	8.59	43	5	8	1.60
<i>Pachycereus hollianus</i>	25	17	68	9.03	16	3	3	1.00
<i>Pachycereus weberi</i>	25	24	96	8.93	50	9	16	1.78
TOTAL	250	192	76.8	8.58	323	15	37	2.47

Abbreviations: Nc = number of cultures; Cp = cultures positive for myxomycetes; %+ = percent of cultures positive; pH = mean pH of each group of 25 cultures; Ncol = number of collections made; Gen = number of genera found; Sp = number of species found; S/G = species to genus ratio.

among the decaying remains of cacti, and among the decaying leaf rosettes of succulent plants. This apparent change of microhabitat preference may be another example of an adjustment strategy to a new substrate in arid areas, in the absence of sufficient angiosperm leaf litter, or simply that they are greater generalists than previous work has shown. Novozilov *et al.* (2003) found that *Physarum decipiens* moved microhabitat to leafy litter of sagebrush in desert conditions.

The results of the 250 moist chamber cultures of ten representative cacti are summarised in table 2. In this part of the study, 323 collections of 37 species of myxomycete from 15 different genera were obtained. The remains of *Opuntia tomentosa* were the most productive cultures, followed by *O. depressa* and *Pachycereus weberi*. The latter has very broad stem ramifications and retains a large amount of water, whereas cultures of the remains of another cactus of the same genus, *Pachycereus hollianus*, which has narrower ramifications, were only 64% positive (Table 2). This cactus lacks the mucilage, characteristic of many other species (Gibson and Horak, 1978), and used to retain water, which will affect the optimum conditions for myxomycete development. The cultures of the remains of the two globose cacti, *Echinocactus platyacanthus* and *Ferocactus latispinus*, were the least productive (< 60%) and decreased the overall productivity of these cultures.

Substrate pH has been shown to be an important factor in the distribution of myxomycetes (Wrigley de Basanta, 2000,

2004), and there are different pH optima for different species. The high pH of the internal tissue of cacti, ranged from pH 7.5 to 10.0, with a mean pH value for these cultures of 8.6. The basic pH of the internal tissue contrasts with the neutral pH of cactus bark from Tehuacán-Cuicatlán, which ranged from 6.7-7.2. The predominance of the order Physarales in these arid areas is probably closely linked to the microhabitat factor of high pH. Certainly, the more characteristic species like *Badhamia melanospora*, various *Didymium* species and *Physarum spectabile*, were abundant in the basic moist chambers made with decaying inner tissue of cacti. The high pH may selectively control the food organisms, and consequently the myxomycete species.

The mean number of species per genus (S/G), a measure of taxonomic diversity used in other studies of myxomycetes (Stephenson *et al.*, 1993), shows overall higher diversity the lower the value. The values for the same number of cultures of each of the representative cacti varied from 1 to 1.9 with a ratio of 2.5 for all the cultures of cactus remains.

In the dendrogram comparing the indices of similarity between the consortia of myxomycete species (Fig. 66), the four most similar groups (TSI > 0.65) were found on two species of *Opuntia* (*O. pilifera* and *O. depressa*) and two globose cacti (*Mammillaria carnea* and *Echinocactus platyacanthus*) since these have eight species in common. Another pair of consortia with relative similarity (TSI = 0.6) are those produced by *Ferocactus latispinus* and *Pachycereus hollianus* which

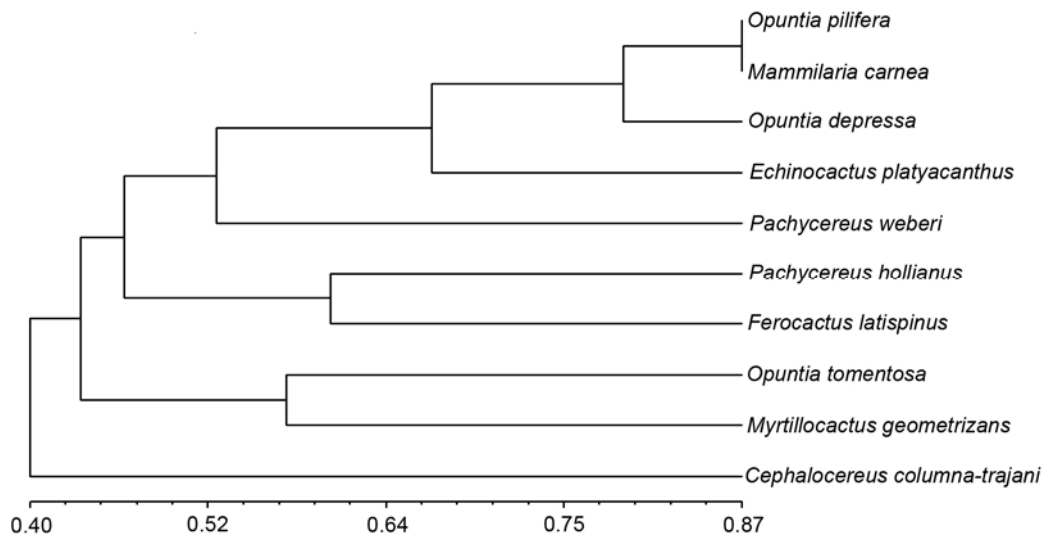


Fig. 66. Dendrogram showing the similarity coefficients between consortia of species produced in moist chamber cultures by the remains of ten species of cacti.

had the fewest species. Three species were common to both these substrata, and also common to most of the other cacti. The remaining consortia give lower indices (TSI < 0.6) since they share only the most common species but have other different ones. These low similarity coefficients indicate the existence of a degree of substrate specificity, with groups of myxomycetes associated with only a particular species of cactus. The results obtained can perhaps be explained by the morpho-structural and chemical differences between the species of cacti, considered of great taxonomic and phylogenetic importance by authors such as Gibson and Horak (1978). For example, *Pachycereus weberi* is a columnar cactus with a large number of alkaloids, but *Myrtillocactus geometrizans* another columnar cactus has abundant triterpenes and the genus *Cephalocereus*, has cortical ground tissue and epidermis with numerous calcium oxalate crystals. These differences will create varying microhabitat conditions for the development and survival of the microbial flora of the plant, which include the food organisms of the myxomycetes.

Species richness, as measured by the number of species divided by the number of cultures, of all the moist chamber cultures prepared in this study was high (0.17), with 68 species from the 395 cultures, and similar to that obtained for other arid regions (0.15) (Novozhilov *et al.*, 2006). That of only the 250

cultures of cacti in this study was also 0.15. Productivity was also high with 86% of the moist chambers producing myxomycetes. The bark cultures, while not the richest substrate for myxomycetes (Fig. 65), were 93% positive for myxomycete fruiting bodies or plasmodia, which is similar to results in sagebrush desert in the Colorado Plateau (Novozhilov *et al.*, 2003). The average pH of all (84) bark cultures was circa neutral at pH 6.8. Some bark species like *Echinostelium apitectum* and *Enerthenema papillatum* have been able to develop on bark in this pH range in these cultures, but they are acid-tolerant species frequently found on bark with a much lower pH. The bark of tree cacti normally absorbs little water, and retains it poorly in comparison to other substrates (Wrigley de Basanta *et al.*, 2008a), but in moist chamber cultures it is artificially maintained moist, which may have improved its productivity. This bark is waxy in appearance in culture, and on the plant protects the interior reservoir of water and minimises evaporation in dry surroundings, providing a succulent microhabitat for myxomycetes in the internal tissue, as is evident from the number of moist chamber collections on cacti. Field observations by Blackwell and Gilbertson (1980b) showed that cacti were able to retain moisture in their internal tissue, when everything else had dried up, even a month after the last rains. Our field observations support this, and we have observed moisture

Table 3. Comparison of results between different arid areas and the Tehuacán-Cuicatlán Valley.

Study area	Species richness (mc only)	Number mc cultures	Records	Species	S/G ratio	CC
Tehuacán-Cuicatlán Valley, Mexico	0.17	395	1214	105	3.9	—
Atacama desert, Chile (Lado <i>et al.</i> , 2007a)	0.14	85	164	24	2.2	0.28
Volga basin, Russia (Novozhilov <i>et al.</i> , 2006)	0.15	1470	3227	158	4.5	0.39
Colorado plateau, USA (Novozhilov <i>et al.</i> , 2003)	0.18	433	1165	78	3.6	0.48
Sonoran desert Arizona, USA (Blackwell and Gilbertson, 1980b)	NA	NA	NA	33	3.7	0.26

(NA = data not available, S/G = mean number of species per genus, CC = coefficient of community)

retained inside cacti even after many months without rain in the Atacama Desert.

The mean number of days of incubation for bark cultures was 19, versus 39 days for a similar number of cultures of lianas and liana bark (Wrigley de Basanta *et al.*, 2008a). Some of these rapidly appearing myxomycetes may have been on the bark when it was put into culture as sclerotia or microcysts. *Didymium wildpretii* showed rapid incubation in moist chamber, compared to its life cycle on agar, which we presumed was for this reason (Lado *et al.*, 2007b). In the cultures from the Tehuacán-Cuicatlán Reserve there were often plasmodia which produced sclerotia, returned to plasmodia when moisture was increased, and then produced sclerotia again. Some of these never produced fruiting bodies in the three-month culture period. Blackwell and Gilbertson (1980b) also maintained that the rapid production of sclerotia (they found many, especially small ones, near fruiting bodies and plasmodia) is a favourable attribute in desert environments enabling the myxomycetes to quickly produce plasmodia and fruit bodies. We frequently found sclerotia in the field, so some desert myxomycetes probably spend a large part of their life cycle in this alternation of states between feeding plasmodia and resistant sclerotia, and form fruiting bodies only rarely.

The results of this biodiversity survey of the Tehuacán-Cuicatlán Valley were compared with other data on arid areas in the literature (Table 3). The species/genus ratio for this study is 3.9, similar to the 3.6 for the whole study area of the Colorado Plateau, which was a similar sized study with both moist chamber and field collections (Novozhilov *et al.*, 2003),

but apparently less diverse than Chile 2.2, which had fewer collections (Lado *et al.*, 2007a). In the Volga Basin study, mainly moist chamber collections were made, and their S/G ratio was 4.5 (Novozhilov *et al.*, 2006). In the present study, taking only the 250 moist chamber cultures of cacti, the S/G ratio was 2.5 (Table 2) indicating a more diverse myxomycete assemblage.

When community similarity between the myxobiota of the Tehuacán-Cuicatlán Reserve and other arid areas in the literature was examined, using the Sørensen coefficient of community (CC) index, the myxomycete assemblage of the Colorado Plateau (Novozhilov *et al.*, 2003) showed the greatest similarity to that of the Tehuacán-Cuicatlán Valley CC = 0.48 (Table 3). Had herbivore and other dung been available for inclusion as substrates in the Tehuacán-Cuicatlán survey, as they have in some other studies (Blackwell and Gilbertson, 1980b; Novozhilov *et al.*, 2003), the number of species found in this area would certainly be increased, and the coefficient of community indexes probably even more similar. The study done in Arizona by Blackwell and Gilbertson (1980b) was the least similar to Tehuacán-Cuicatlán (CC = 0.26) and those done in the Volga Basin (Novozhilov *et al.*, 2006) CC = 0.39 and in Northern Chile (Lado *et al.*, 2007a) CC = 0.275 were between the two. This index, like the one above, is influenced greatly by the size and type of study, and whether both moist chamber and field collections were included, apart from the real community differences. For example in the Atacama desert in Chile, a similar region to Mexico in terms of temperature and vegetation types, 75% of the species collected were also

found in Tehuacán-Cuicatlán, but the large difference in number of species between each study gives the impression of a lack of similarity using this index. In five upland forests of southwestern Virginia (Stephenson, 1988), the species composition was much more similar (average CC = 0.675), as would be expected due to the proximity of the study areas and the uniformity of the method.

Patterns in these results suggest that combined microhabitat factors appear to permit the development of a large number and variety of myxomycetes in and on plants in arid environments. These factors include a higher pH than other environments studied, and a high level of retained moisture, particularly in the cacti and other succulent plants. There are obviously other precise unknown attributes of the substrate plants, since there is a degree of substrate-group specificity seen for example with *Cribraria fragilis*, *C. zonatispora*, *Didymium tehuacanense*, *Physarum megalosporum*, *Physarum spectabile* or *Trichia agaves*. In addition, quite a number of myxomycetes moved from the microhabitat where they are normally found in other ecosystems, to the cacti and succulents of these drylands. What is more, it has been shown above that groups of species are associated with certain species of cacti. Further investigation into this combination of microhabitat factors and patterns of species distribution is currently in progress in the southern hemisphere deserts of Northern Chile and Argentina.

The recently described *D. wildpretii*, *D. umbilicatum* and *Licea succulenticola* as well as *D. tehuacanense* and *Perichaena stipitata* described here, are so far exclusive to plants in xeric environments. *Badhamia melanospora* is the most representative species of the desert scrublands of the Tehuacán-Cuicatlán Valley, as it was in the desert areas of Northern Chile, where it appeared in practically all the sites sampled (Lado *et al.*, 2007a). It almost always develops on plants in arid environments, although it is a generalist on *Cactaceae*. Predictably, it was not collected from arid areas in the Volga basin (Novozhilov *et al.*, 2006), where there were no cacti. *Physarum pusillum*, *Didymium vaccinum*, *Perichaena luteola*, *Physarum spectabile* and *Trichia agaves*, are

also important components of the distinctive myxobiota associated with plants of the xerophyllous scrublands of Tehuacán-Cuicatlán Reserve. The last two of these species, along with *Badhamia melanospora*, *Cribraria fragilis*, *C. zonatispora*, *Didymium eremophilum*, *D. subreticulosporum*, *D. umbilicatum*, *D. wildpretii* and *Licea succulenticola* make a total of ten of the twelve myxomycete species previously described from substrates in arid areas of the world (Lado *et al.*, 2007b, Wrigley de Basanta *et al.*, 2008b), which have been found again here. Finding such a high percentage (> 80%) of these species together in this area confirms their association with the cacti and succulent plants of American drylands, and is evidence for the existence of a distinct succulenticolous group of myxomycetes. This group, along with the species that appear to have different ecotypes in arid areas, seems to have evolved and diversified rapidly to exploit the unique ecological conditions only present in plants of the desert biome.

Acknowledgements

This research has been supported by the Ministry of Science and Innovation of Spain (projects REN 2002-00445/GLO and CGL2005-00320/BOS) and the National Council of Science and Technology of Mexico (CONACyT project SEP-2003-02-44621-Q). We are very grateful to Dr M. Laínz, S.J. for the Latin descriptions.

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