Myxomycetes collected in the first phase of a north-south transect of Chile

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The results of the first sampling of myxomycetes from the North of Chile are reported in this paper. The survey forms part of the project Global Biodiversity of Eumycetozoans and is the first of a three phase north-south (more than 5,000 km), transect of the country. This phase was between 18º and 30º South latitudes and encompassed the arid and semi-arid regions known as the Atacama Desert. A total of 24 species of Myxomycetes from 11 genera have been identified from these extreme environments, 14 are new records for Chile and 4 (*Badhamia dubia*, *Didymium synsporon*, *Echinostelium fragile* and *Physarum spectabile*) are previously unknown for South America. Comments are provided on morphology, distribution and ecology.

Key words: Atacama Desert, distribution, endemic plants, Eumycetozoa, plasmodial slime moulds, species inventory.

Introduction

Our knowledge of the myxomycetes of South America is scant, and large areas of the continent such as the Andes, the Amazon Basin and Patagonia still remain virtually unexplored. A number of different ecosystems, including mangrove swamps, various types of xerophytic vegetation, and certain types of tropical forests have never been systematically investigated. To address this lack of information, the National Science Foundation (NSF), through the program Planetary Biodiversity Inventories, has supported several expeditions to this rich and varied biogeographical region (http://slimemold.uark.-edu/eventsframe.htm), to obtain a body of information on the distribution and ecology of the myxomycetes associated with these understudied ecosystems (Novozhilov *et al*., 2006; Tran *et al*., 2006).

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In the project described herein, a north-south transect of Chile, a country barely explored for myxomycetes, is being carried out. The interesting features of Chile are that the country represents a linear series of different vegetation types that extend for more than 5,000 km along the Pacific coast, from latitude 18ºS to latitude 56ºS, with an elevational gradient of 0 m to 5,000 m. The vegetation in this part of the world changes from the desert zones of the north, on the border of Peru, through the Mediterranean type of woodlands of the central part of the country, to the Valdivian and *Araucaria* forests of the south, and subantarctic forests (*Nothofagus* spp.) of the Patagonian region and Tierra del Fuego (Fig. 1). The “Andean puna”, a characteristic alpine grassland, is also very distinctive and dominates along the Andean range above 4,000 m. This zonation provides an opportunity to sample the myxobiota of many of the vegetation types found in South America within a single country.

There is little previous information available on the myxomycetes of Chile, and the few records that do exist are from Central and Southern Chile. Bertero (1828) published the first reports of myxomycetes from Chile, but Spegazzini (1887, 1917, 1921), in a series of papers at the beginning of the nineteenth century, was the first to make a more intensive study of these organisms. A number of other important authors such as Montagne (1852), Massee (1892), Torrend (1909), Sturgis (1916), Macbride (1922), Lister (1925) or Hagelstein (1944) also contributed some records from this country. However, Lazo (1966) published the first catalogue of myxomycetes, with 77 species. Most of these were new records for Chile, and some (*Hemitrichia calyculata*, *Stemonitis axifera* and *Stemonitopsis typhina*) were the first collections from Fray Jorge Forest National Park, the only records known from the area covered by this study. After this date no additional myxomycete information from Chile has been published (Farr, 1976). The North of the country has never been sampled for these organisms.

Study area

Due to the size of the country, which extends more than 5,000 km from north to south, we divided the survey effort along the transect into three phases. The north was covered in the first phase, the central region in the second phase (which took place in the early part of 2006, see Wrigley de Basanta *et al*., 2006 and http://slimemold.uark.edu/eventsframe.htm), and the Patagonian region of the country will be visited in the third. In this paper we report the results of the first phase of this survey, limited to the north zone, between the latitudes 18º and 30ºS (Figs 1-2). This area, called “Norte Grande” and “Norte Chico”, is probably the most arid region of the world, with enormous areas

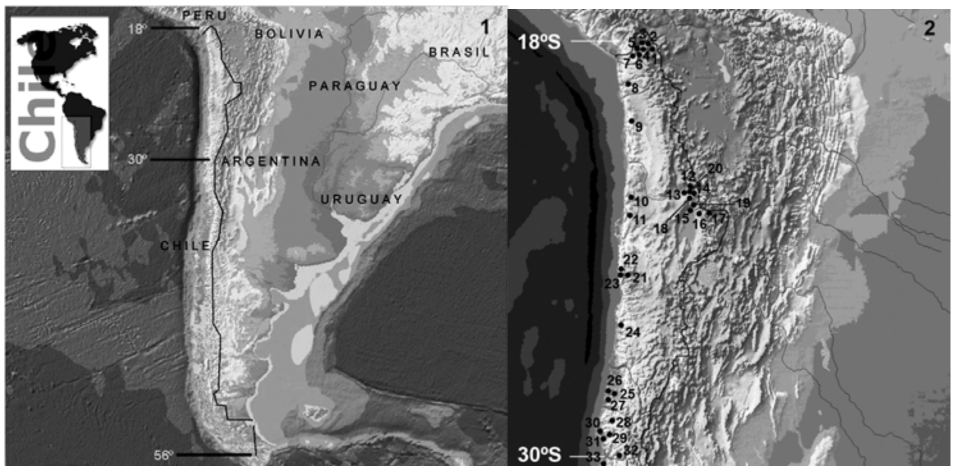


Fig. 1. Map of the portion of South America that includes the country of Chile. **Fig. 2.** Sampling localities in Chile.

devoid of any type of vegetation, dominated by salt flats (salares) and the desert of Atacama.

The climate of the region is extremely arid. The mean temperature is between 17-25°C all year long. This is due to the influence of the Humboldt current, a cold stream that bathes the coast and even permits penguins to live as close as 1 km from the desert. The annual precipitation is practically 0 mm in the north and at sea level, and it slowly increases toward the south. In the Andes, the precipitation increases, but practically all of it occurs in the form of snow due to the elevation, with a period of maximum precipitation during the months of December to February, the middle of the Southern summer, due to what is called the Bolivian winter phenomenon.

In all the western coasts of the world, between latitudes 10º and 25ºS there are deserts. This is because of high pressure areas, close to the coast of each ocean, which impede the passage of low pressure fronts carrying rain. What is more, in Chile, a coastal mountain range reaching 3,000 m represents an impassable barrier to the moist marine winds. Here also the dryness of the desert is aggravated by the absence of rivers running down from the Andes, which are blocked by a third mountain range, called the Domeyko Range, located between the Andes and the coastal range. This retains the water in inner lagoons which, because of the high evaporation rate, dry out as salt flats.

Along the coast, due to the Humboldt current, a dense and cold fog (called the "camanchaca") develops in the mornings but disappears by midday. It results from high evaporation from the sea retained by high pressure in low lying strata which, neither releases precipitation nor rises over the mountains. The camanchaca is very important for the survival of many coastal plants, since it is the only moisture they get, and in places gives rise to fairly dense ground cover (Fig. 3). The endemic cacti (Fig. 8) are able to develop due to this minimum humidity. In this area it was not unusual to see cacti covered with thick layers of lichens (Fig. 9).

Sampling was carried out along a strip of land between the Pacific Ocean and the Andean mountain range, which over a distance of less than 100 km rises from sea level to more than 5,000 m above sea level. This large gradient in elevation causes an altitudinal zonation of vegetation, from the coastal desert to the Andean puna.

Access to many of these areas was very difficult, as there are no roads, no human settlements and no vegetation. To explore the zone, we developed a sampling strategy based on a north-south transect along the coast, with three short west-east transects from the coast to the Andes, at latitudes 18ºS between Arica and Putre (Lauca National Park), 23ºS between Antofagasta and San Pedro de Atacama, and 30ºS between La Serena and Vicuña (Fig. 2). There were very few trees, and even close to the mountains, only cacti, shrubs or grasslands occurred over large areas.

Localities where the native vegetation was well preserved were selected for sampling. In many cases, due to the extreme aridity, the vegetation was very scanty (Fig. 4), but the plants present are well adapted to these extreme environments and many of them are endemic. In many areas cacti and succulent plants dominated, and these were the productive substrates for myxomycetes in the field, especially in areas of the coast, between 0-1,000 m elevation. South of latitude 23ºS the vegetation increased gradually and dense populations of globular cacti (*Copiapoa* spp.) and shrubs dominated (Fig. 3), especially at sea level. At latitude 30ºS the vegetation became denser and candelabra cacti of the genus *Eulychnia*, *Echinopsis* and *Eriosyce* covered large areas (Fig. 8).

In the west-east transects, from the coast to the Andes, at latitude 18ºS, there was virtually no vegetation between 0-2,500 m elevation. At about 2,500 m the endemic cacti *Browningia candelaris* and some species of *Haageocereus* appeared. Between 3,000-4,000 m, the cover of vegetation increased and cacti of the genus *Oreocereus*, *Eulychnia*, *Miquelopuntia* and *Opuntia* dominated, with shrubs of the genus *Parastrephia* also very common. Above 4,000 m the Andean puna, a grassland consisting largely of *Stipa atacamensis* dominated,

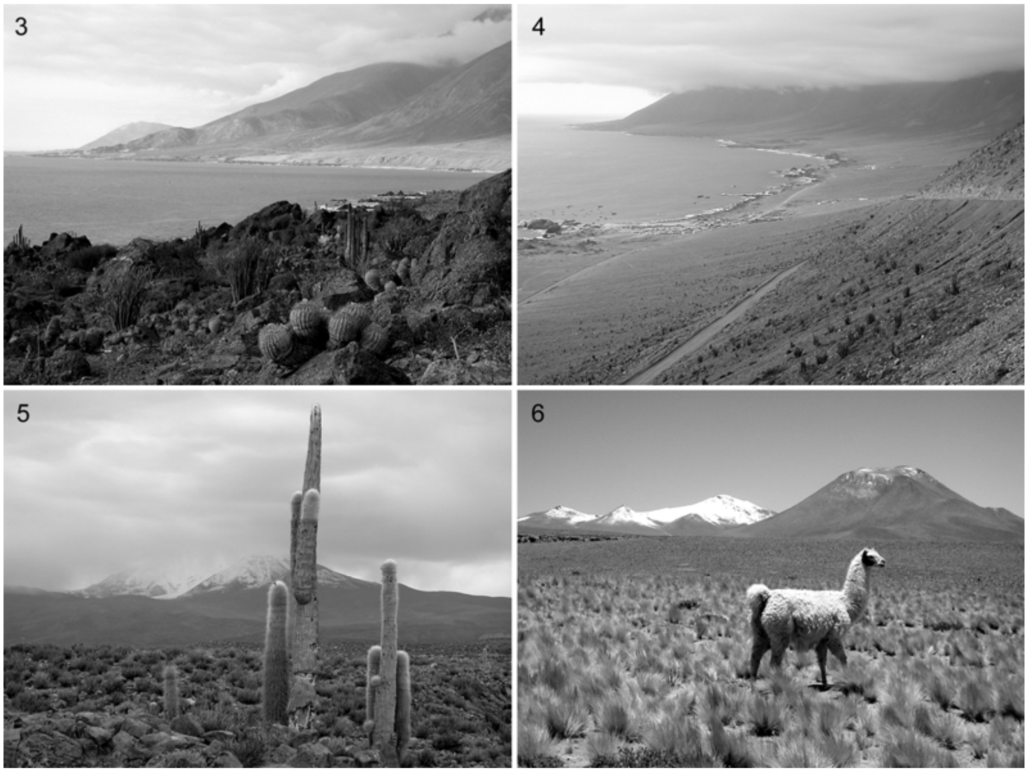


Fig. 3. Xerophytic shrubland in Paposo National Reserve. **Fig. 4.** Xerophytic shrubland influenced by the "camanchaca" in Paposo National Reserve (Loc. 21). **Fig. 5.** Xerophytic shrubland with *Echinopsis atacamensis* in San Pedro de Atacama area. **Fig. 6.** Andean puna, near to Licancabur volcano.

but some endemic plants such as *Azorella compacta*, or *Polylepis besseri* (Fig. 7), a unique tree that grows at the highest altitude in the world (around 4,500 m), were very characteristic. Another unique tree *Prosopis tamarugo*, an halophyllic endemic tree, was found growing on the crust of salt in the salt flats (Fig. 10).

The xerophytic shrublands with globular cacti (*Copiapoa* spp.), well represented at sea level (Fig. 3), gradually disappeared with increasing elevation at latitude 23º S. From 600-3,000 m there was no vegetation, only desert. Between 3,000-4,000 m, xerophytic shrublands (Fig. 11), with some columnar cacti such as the endemic *Echinopsis atacamensis* (Fig. 5), dominated. Around 4,000-5,000 m the Andean puna covered large areas, and these were home to the llamas (Fig. 6).

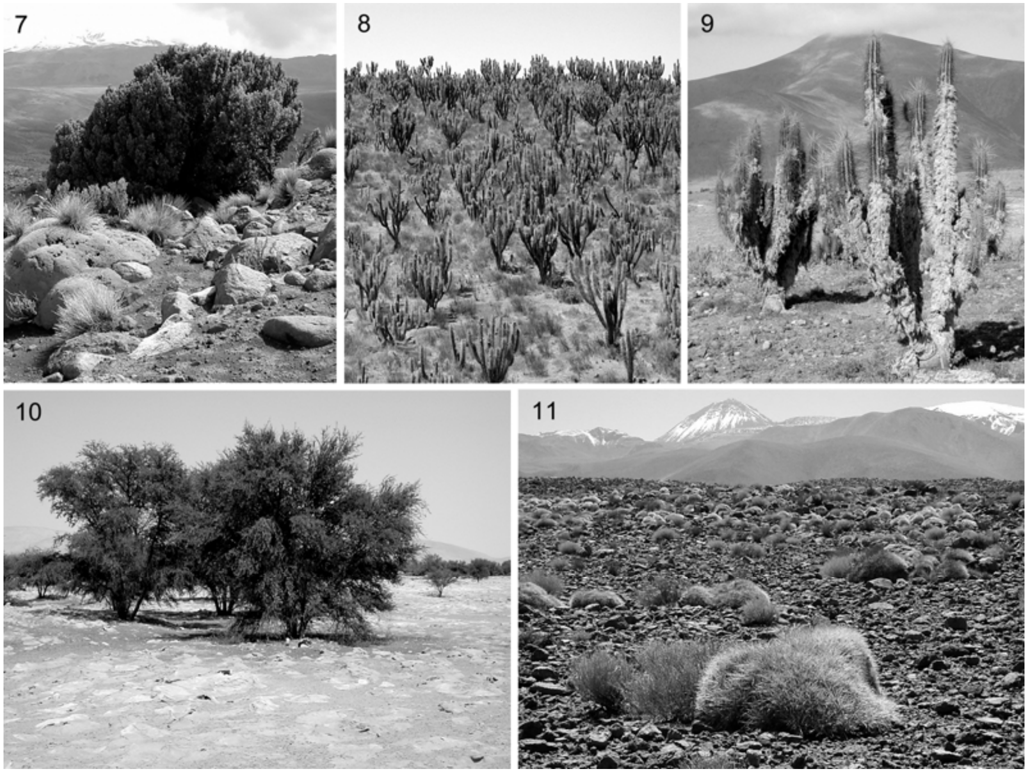


Fig. 7. Alpine grassland with *Azorella compacta* and some trees of *Polylepis besser*, near to Chungara Lake in Lauca National Park. **Fig. 8.** Xerophytic shrubland with *Eulychnia* sp., *Echinopsis chiloensis* and *Eriosyce* sp. near Fray Jorge National Park. **Fig. 9.** Xerophytic shrubland with *Eulychnia iquiquensis* covered by lichens in the Paposo National Reserve. **Fig. 10.** Forest of *Prosopis tamarugo* growing on the salar in the Pampa del Tamarugal National Reserve. **Fig. 11.** Xerophytic shrubland with *Opuntia* spp. near San Pedro de Atacama.

There was more humidity and vegetation at latitude 30ºS. In this area, especially in the valleys, Mediterranean vegetation appeared, and overlapped with the arid lands. From 0 m to 2,500 m elevation, were large areas of xerophytic shrubland with candelabra cacti. This mosaic of vegetation, and apparently desolate landscape, provides great challenges for the survival of myxomycetes.

List of sampling localities

A total of 33 localities were sampled during this survey (Fig. 2). Geographical data, geo-references, as well as vegetation type are given below.

Loc. 1: CHILE, Región de Tarapacá, Provincia de Parinacota, Comuna de Putre, Chungara Lake, km 176 of the road Ch-11, 18°13'40"S 69°11'04"W, 4,665 m, 13-I-2004, alpine grassland with *Azorella compacta* and some trees of *Polylepis besseri* (fig. 7).

Loc. 2: CHILE, Región de Tarapacá, Provincia de Parinacota, Comuna de Putre, Quebrada Taipicahue, km 135 of the road Ch-11, 18°10'38"S 69°30'53"W, 4,100 m, 13-I-2004, alpine shrubland of *Parastrephia* sp. (Asteraceae) and Andean puna.

Loc. 3: CHILE, Región de Tarapacá, Provincia de Parinacota, Comuna de Putre, Putre, 18°11'46"S 69°32'47"W, 3,640 m, 13-I-2004, xerophytic shrubland with *Oreocereus* sp.

Loc. 4: CHILE, Región de Tarapacá, Provincia de Parinacota, Comuna de Putre, km 101 of the road Ch-11, 18°19'38"S 69°34'55"W, 3,415 m, 12-I-2004, xerophytic shrubland with *Oreocereus* sp. and other columnar cacti.

Loc. 5: CHILE, Región de Tarapacá, Provincia de Parinacota, Comuna de Putre, Zapahuira, 18°20'35"S 69°30'53"W, 3,322 m, 14-I-2004, km 95 road Ch-11, xerophytic shrubland with *Eulychnia iquiquensis*.

Loc. 6: CHILE, Región de Tarapacá, Provincia de Parinacota, Comuna de Putre, Pukara Copaquilla, km 90 of the road Ch-11, 18°23'33"S 69°38'32"W, 3,116 m, 12-I-2004, xerophytic shrubland with rests of columnar cacti.

Loc. 7: CHILE, Región de Tarapacá, Provincia de Arica, Comuna de Arica, km 67 of the road Ch-11, 18°27'59"S 69°48'14"W, 2,200 m, 12-I-2004, xerophytic shrubland with *Browningia candelaris* and *Haageocereus* sp.

Loc. 8: CHILE, Región de Tarapacá, Provincia de Iquique, Comuna de Huara, Zapiga, km 1882 of the road Ch-5, 19°38'48"S 69°56'28"W, 1,140 m, 14-I-2004, tamarugal (forest of *Prosopis tamarugo*) (fig. 10).

Loc. 9: CHILE, Región de Tarapacá, Provincia de Iquique, Comuna de Pozo Almonte, Pintados, km 1790 of the road Ch-5, 20°24'41"S 69°42'47"W, 990 m, 15-I-2004, tamarugal (forest of *Prosopis tamarugo*).

Loc. 10: CHILE, Región de Antofagasta, Provincia de Tocopilla, Comuna de Tocopilla, Mina Horacio, km 148 of the road Ch-1, 22°22'15"S 70°13'41"W, 280 m, 16-I-2004, xerophytic shrubland with *Eulycnhnia iquiquensis*.

Loc. 11: CHILE, Región de Antofagasta, Provincia de Tocopilla, Comuna de Tocopilla, Cobija, km 122 of the road Ch-1, 22°35'26"S 70°15'34"W, 370 m, 16-I-2004, xerophytic shrubland with *Eulycnhnia iquiquensis*.

Loc. 12: CHILE, Región de Antofagasta, Provincia de El Loa, Comuna de Calama, Toconce, km 81 of the road Ch-169, 22°15'34"S 68°10'11"W, 3,320 m, 17-I-2004, xerophytic shrubland with *Echinopsis atacamensis*, *Opuntia* spp., *Euphorbia* sp. and *Ephedra* sp.

Loc. 13: CHILE, Región de Antofagasta, Provincia de El Loa, Comuna de Calama, Toconce, km 78 of the road Ch-169, 22°15'29"S 68°12'00"W, 3,268 m, 17-I-2004, xerophytic shrubland with *Echinopsis atacamensis* and *Ephedra* sp. (fig. 5).

Loc. 14: CHILE, Región de Antofagasta, Provincia de El Loa, Comuna de Calama, Caspana, km 16 of the road Ch-B159, 22°20'42"S 68°17'29"W, 3,300 m, 20-I-2004, xerophytic shrubland with *Oreocereus leucotrichus*.

Loc. 15: CHILE, Región de Antofagasta, Provincia de El Loa, Comuna de San Pedro Atacama, Licancabur volcano, km 24 of the road Ch-23, 22°54'31"S 67°57'43"W, 3,380 m, 18-I-2004, xerophytic shrubland with *Opuntia* spp.

Loc. 16: CHILE, Región de Antofagasta, Provincia de El Loa, Comuna de San Pedro Atacama, Licancabur volcano, km 40 of the road Ch-23, 22°55'27"S 67°49'03"W, 4,595 m, 18-I-2004, Andean puna, alpine grassland with *Stipa atacamensis* (fig. 6).

Loc. 17: CHILE, Región de Antofagasta, Provincia de El Loa, Comuna de San Pedro Atacama, Volcán Licancabur, km 50 of the road Ch-23, 22°54’17”S 67°45’46”W, 4,767 m, 18-I-2004, Andean puna, alpine grassland with *Stipa atacamensis*.

Loc. 18: CHILE, Región de Antofagasta, Provincia de El Loa, Comuna de San Pedro Atacama, Cuesta del Diablo, road Ch-B245, Km 32, 22°42’50”S 68°00’51”W, 3,788 m, 19-I-2004, xerophytic shrubland with *Opuntia* spp. (fig. 11).

Loc. 19: CHILE, Región de Antofagasta, Provincia de El Loa, Comuna de San Pedro Atacama, Termas de Puritama, km 27 of the road Ch-B245, 22°43’39”S 68°02’33”W, 3,580 m, 19-I-2004, xerophytic shrubland with *Echinopsis atacamensis* and *Opuntia* spp.

Loc. 20: CHILE, Región de Antofagasta, Provincia de El Loa, Comuna de Calama, road km 24 of the road Ch-B159, 22°23’41”S 68°13’13”W, 3,477 m, 20-I-2004, xerophytic shrubland.

Loc. 21: CHILE, Región de Antofagasta, Provincia de Antofagasta, Comuna de Taltal, Mina Liverpool, km 103 of the road Ch-B710, 25°00’19”S 70°24’23”W, 935 m, 21-I-2004, xerophytic shrubland with *Copiapoa cinerea* (fig. 4).

Loc. 22: CHILE, Región de Antofagasta, Provincia de Antofagasta, Comuna de Taltal, Paposo, km 89 of the coastal road, 24°53’45”S 70°31’29”W, 60 m, 21-I-2004, xerophytic shrubland with *Eulychnia iquiquensis*, *Copiapoa* spp. and *Euphorbia* sp. (fig. 3)

Loc. 23: CHILE, Región de Antofagasta, Provincia de Antofagasta, Comuna de Taltal, Paposo, km 80 of the coastal road, 24°57’26”S 70°28’41”W, 65 m, 22-I-2004, xerophytic shrubland with *Eulychnia iquiquensis*, *Copiapoa* spp. and *Euphorbia* sp. (fig. 9)

Loc. 24: CHILE, Región de Atacama, Provincia de Chañaral, Comuna de Chañaral, Pan de Azucar National Park, 26°09’21”S 70°38’59”W, 80 m, 18-I-2004, xerophytic shrubland with *Copiapoa* spp.

Loc. 25: CHILE, Región de Atacama, Provincia de Huasco, Comuna de Huasco, Llanos de Challe, km 55 of the road Ch-C410, 28°08’48”S 71°03’50”W, 125 m, 24-I-2004, xerophytic shrubland with *Eulychnia breviflora* and *Miquelopuntia miquelli*.

Loc. 26: CHILE, Región de Atacama, Provincia de Huasco, Comuna de Huasco, Llanos de Challe, km 60 of the road Ch-C410, 28°07’10”S 71°05’46”W, 75 m, 24-I-2004, xerophytic shrubland with *Copiapoa* spp.

Loc. 27: CHILE, Región de Atacama, Provincia de Huasco, Comuna de Huasco, Caleta Angosta, km 29 of the road Huasco to Carrizal Bajo, 28°15’03”S 71°09’29”W, 45 m, 24-I-2004, xerophytic shrubland with *Copiapoa* spp. and *Eulychnia* sp.

Loc. 28: CHILE, Región de Atacama, Provincia de Huasco, Comuna de Vallenar, km 651 of the road Ch-5, 28°40’14”S 71°46’16”W, 620 m, 25-I-2004, xerophytic shrubland with *Eulychnia* sp. and *Opuntia* sp.

Loc. 29: CHILE, Región de Coquimbo, Provincia de Elqui, Comuna de La Higuera, Incahuasi, km 556 of the road Ch-5, 29°21’38”S 71°03’40”W, 370 m, 25-I-2004, xerophytic shrubland with *Eulychnia* sp. and *Neoporteria* sp.

Loc. 30: CHILE, Región de Coquimbo, Provincia de Elqui, Comuna de La Higuera, road to Choros Bajos, 29°19’18”S 71°14’10”W, 204 m, 25-I-2004, xerophytic shrubland with *Eulychnia* sp. and *Opuntia* sp.

Loc. 31: CHILE, Región de Coquimbo, Provincia de Elqui, Comuna de La Higuera, San José de los Choros Bajos, 29°18’25”S 71°16’47”W, 165 m, 25-I-2004, xerophytic shrubland with *Eulychnia* sp., *Miquelopuntia miquelii* and *Copiapoa* spp.

Loc. 32: CHILE, Región de Coquimbo, Provincia de Elqui, Comuna de Vicuña, quebrada Chumí, 30°04’51”S 70°36’43”W, 1,305 m, 28-I-2004, xerophytic shrubland with *Echinopsis chiloensis*, *Eriosyce aurata* and *Flourencia sp*.

Loc. 33: CHILE, Región de Coquimbo, Provincia de Limari, Comuna de Ovalle, road to Fray Jorge National Park, 30°36'51"S 71°33'19"W, 275 m, 27-I-2004, xerophytic shrubland with *Eulychnia* sp., *Echinopsis chiloensis* and *Eriosyce* sp. (fig. 8).

Material and Methods

Field work along the transect was carried out by the first two authors, in the 33 localities listed above, over a period of three weeks in January of 2004, a relatively humid period in northern Chile due to the Bolivian winter. All potential substrates were examined in the field and samples of plant litter or bark were removed for preparation of moist chambers and laboratory cultures of myxomycetes. The predominant substrates examined can be classified as cacti, which in other areas of the world are productive substrates for myxomycetes (Lado *et al*. 1999, Mosquera *et al*. 2000, 2003). Many of the cacti from which we collected samples are endemic, including such examples as *Browningia candelaris*, *Echinopsis atacamensis*, *Copiapoa dealbata*, and *Eulychnia iquiquensis*. In addition, two endemics trees, *Prosopis tamarugo* (Fig. 10) and *Polylepis besseri* (Fig. 7), were sampled. In these cases, pieces of bark were taken for cultures. Samples of shrubs (*Parastrephia* sp., *Oxalis gigantea*), and of *Stipa atacamensis* from the Andean puna (Fig. 6), were also taken for moist chamber cultures.

Descriptions of the sampling methods and preparation of moist chamber (mc) cultures of myxomycetes can be found in Schnittler *et al*. (2002) and Stephenson *et al*. (2004). The observation period for cultures was up to three months. The type of substrate and the pH of each moist chamber culture (determined at 24 hours) were recorded in each instance and these data provided in the annotated species list that follows.

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, as in previous work (Lado *et al*. 2003). All the numbers cited herein (for field or moist chamber collections) refer to specimens deposited in the herbarium MA-Fungi (sub Lado) or the mycological herbarium (UARKM) of the University of Arkansas (SLS), with duplicates in TLXM (sub AET). All microscope measurements and observations were made with material mounted directly in Hoyer's medium and polyvinyl alcohol. Differential interference contrast microscopy was used to obtain descriptive data.

Results

As a result of this survey, 135 collections of myxomycetes that had developed in the field under natural conditions were obtained. From the 85 samples used for preparing moist chamber cultures 29 additional collections were obtained. A total of 24 taxa representing 11 genera of myxomycetes have been identified as living in these extreme environments.

Annotated species list

Arcyria cinerea (Bull.) Pers.

Loc. 2, on litter of *Parastrephia* sp. in mc, pH 5.1, SLS 19571.

Only one record obtained in moist chamber. The species is cosmopolitan and very common in other regions of South America and the Neotropics (Farr 1976), especially in tropical humid forests, but it seems rare in arid regions.

Badhamia dubia Nann.-Bremek. (Figs 12-14)

Loc. 18, on dead tissue of *Opuntia* sp., Lado15583 (AET9821).

Loc. 19, on dead tissue of *Opuntia* sp., Lado15594 (AET9832).

Our two collections have the same features. The spores occur in persistent and solid clusters of 4-8 spores (Fig. 14), the individual spores are slightly turbinate, of 9-11 µm diam., and have a cap of warts or spines which is denser on the outside of the spore cluster. This species has been reported from temperate regions as usually corticolous, but in our case it appeared on dead tissue of *Opuntia*. These collections are the first known from South America.

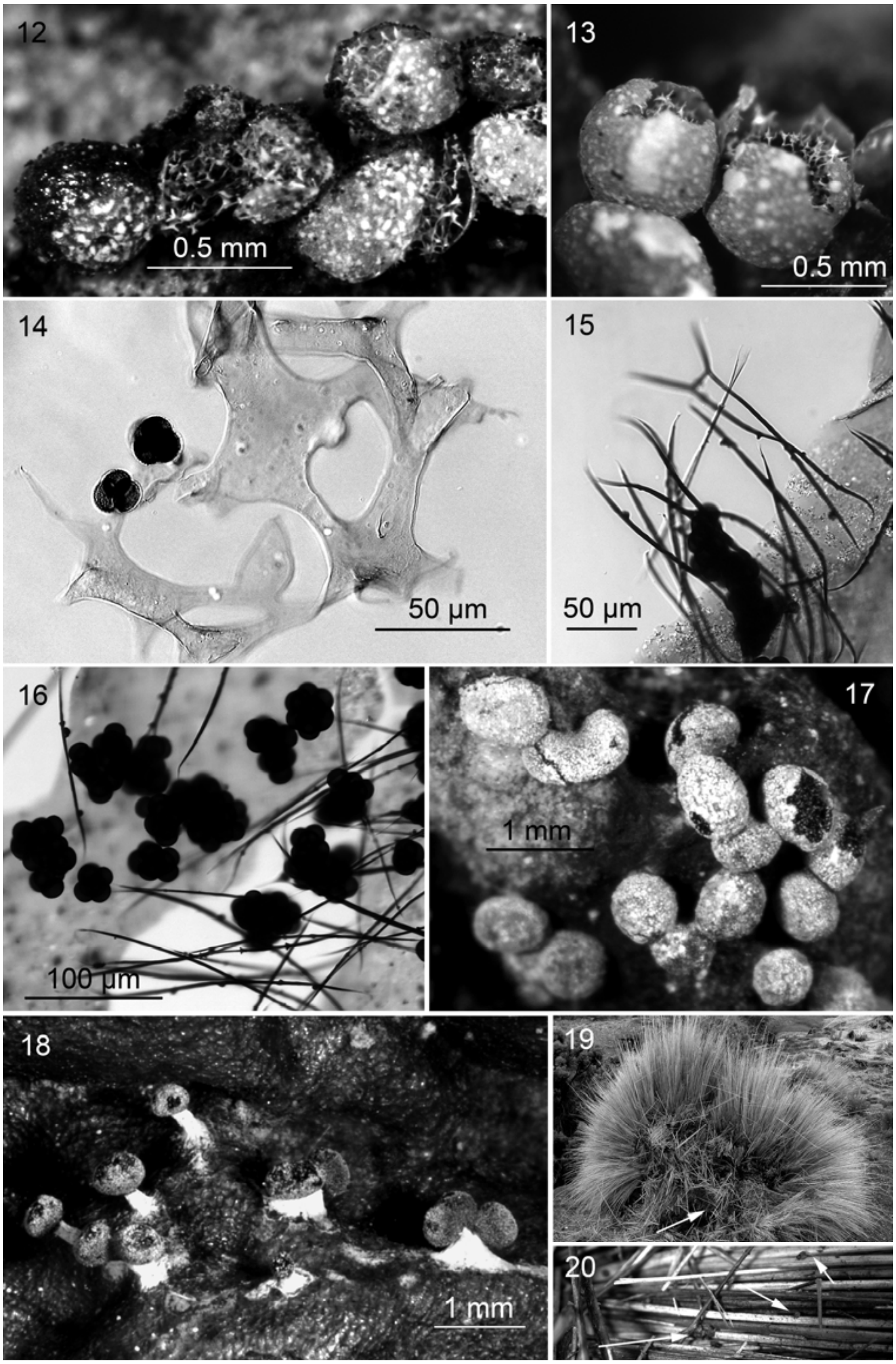
Badhamia melanospora Speg. [= *B. gracilis* (T. Macbr.) T. Macbr.]

Loc. 2, on litter of *Parastrephia* sp. in mc, pH 4.9-8.2, SLS 19392.

Loc. 3, on dead tissue of *Oreocereus* sp., Lado15552 (AET9790), Lado15553 (AET9791).

Loc. 4, on dead tissue of *Oreocereus* sp., Lado15537 (AET9775), Lado15540 (AET9778), on dead tissue of columnar cacti, Lado15541 (AET9779), Lado15544 (AET9782).

Figs 12-14. *Badhamia dubia*. **12.** Sporocarps (Lado15583). **13.** Two sporocarps with the peridium broken showing the capillitium (Lado15594). **14.** Capillitium and two clusters of spores (Lado15583). Figs. 15-16. *Didymium synsporon* (Lado15661). **15.** Capillitial threads. **16.** Clusters of spores and capillitial threads. **Figs 17-18.** *Physarum spectabile*. **17.** Group of sessile sporocarps and short plasmodiocarps (Lado15590). **18.** Stipitate sporocarps (Lado15685). **Fig. 19.** *Stipa atacamensis* (Andean puna), arrow indicates the area of the plant where the myxomycetes develop. **Fig. 20.** Detail of the grass *Stipa atacamensis*, arrows show fructifications of the myxomycete *Trichia affinis* (Lado15549).


12
0.5 mm
13
0.5 mm
14
50 µm
15
50 µm
16
100 µm
17
1 mm
18
1 mm
19
20

Loc. 5, on dead tissue of *Eulychnia iquiquensis*, Lado15555 (AET9793), Lado15558 (AET9796), Lado15560 (AET9798), Lado15562 (AET9800), Lado15565 (AET9803).

Loc. 6, on dead tissue of columnar cacti, Lado15535 (AET9773).

Loc. 7, on dead tissue of *Haageocereus* sp., Lado15528 (AET9766), Lado15531 (AET9769), Lado15532 (AET9770), Lado15533 (AET9771), on dead tissue of *Browningia candelaris*, Lado 15529 (AET 9767), Lado15530 (AET9768).

Loc. 8, on bark of *Prosopis tamarugo* in mc, pH 4.9-8.2, SLS 19392.

Loc. 9, on bark of *Prosopis tamarugo* in mc, pH 4.9-8.2, SLS 19392.

Loc. 10, on dead tissue of *Eulycnhia iquiquensis* in mc, pH 4.9-8.2, SLS 19392.

Loc. 11, on dead tissue of *Eulycnhia iquiquensis* in mc, pH 4.9-8.2, SLS 19392.

Loc. 12, on dead tissue of *Echinopsis atacamensis*, Lado15567 (AET9805), Lado15569 (AET9807). On dead tissue of *Opuntia* sp., Lado15572 (AET9810), Lado15574 (AET9812). On bark of *Echinopsis atacamensis* in mc, pH 4.9-8.2, SLS 19392.

Loc. 13, on dead tissue of *Opuntia* sp., Lado15579 (AET9817).

Loc. 14, on dead tissue of *Oreocereus leucotrichus*, Lado15598 (AET9836), Lado15600 (AET9838), Lado15601 (AET9839).

Loc. 15, on dead tissue of *Opuntia* sp., Lado15580 (AET9818), Lado15582 (AET9820).

Loc. 18, on dead tissue of *Opuntia* sp., Lado15584 (AET9822), Lado15586 (AET9824), Lado15587 (AET9825), Lado15588 (AET9826), Lado15589 (AET9827), Lado15592 (AET9830).

Loc. 19, on dead tissue of *Opuntia* sp., Lado15595 (AET9833), also in mc, pH 4.9-8.2, SLS 19392.

Loc. 20, on bark of *Echinopsis atacamensis* in mc, pH 4.9-8.2, SLS 19392.

Loc. 21, on dead tissue of *Copiapoa* sp., Lado15605 (AET9843), Lado15613 (AET9851)

Loc. 22, on dead tissue of *Copiapoa* sp., Lado15615 (AET9853).

Loc. 23, on dead tissue of *Eulychnia iquiquensis*, Lado15623 (AET9861), Lado15626 (AET9864), Lado15628 (AET9866), Lado15629 (AET9867), Lado15631 (AET9869).

Loc. 24, on dead tissue of *Copiapoa* sp., Lado15620 (AET9858), Lado15622 (AET9860).

Loc. 25, on dead tissue of *Eulychnia* sp., Lado15635 (AET9873), Lado15636 (AET9874), Lado15639 (AET9877), Lado15640 (AET9878), Lado15641 (AET9879), Lado15643 (AET9881). On dead tissue of *Opuntia* sp., Lado15638 (AET9876). On bark and dead tissue of *Miquelopuntia miquelli* in mc, pH 4.9-8.2, SLS 19392.

Loc. 26, on dead tissue of *Copiapoa* sp., Lado15644 (AET9882).

Loc. 27, on dead tissue of *Copiapoa* sp., Lado15647 (AET9885), Lado15657 (AET9895). On dead tissue of *Eulychnia* sp., Lado15652 (AET9890).

Loc. 28, On dead tissue of *Opuntia* sp., Lado15659 (AET9897), Lado15660 (AET9898), Lado15662 (AET9900), Lado15663 (AET9901). On dead tissue of *Eulychnia* sp., Lado15664 (AET9902), Lado15665 (AET9903), Lado15666 (AET9904), Lado15667 (AET9905), Lado15668 (AET9906), Lado15669 (AET9907).

Loc. 29, on dead tissue of *Eulychnia* sp., Lado15670 (AET9908), Lado15671 (AET9909), Lado15672 (AET9910), Lado15673 (AET9911), Lado15674 (AET9912), Lado15675 (AET9913), Lado15676 (AET9914).

Loc. 30, on dead tissue of *Eulychnia* sp., Lado15677 (AET9915).

Loc. 31, on dead tissue of *Eulychnia* sp., Lado15679 (AET9917), Lado15680 (AET9918), Lado15681 (AET9919), Lado15682 (AET9920), Lado15688 (AET9926), Lado15690 (AET9928). On dead tissue of *Copiapoa* sp., Lado15684 (AET9922).

Loc. 32, on dead tissue of *Eriosyce aurata*, Lado15695 (AET9933). On dead tissue of *Echinopsis chiloensis*, Lado15696 (AET9934), Lado15702 (AET9940).

Loc. 33, on dead tissue of *Echinopsis chiloensis*, Lado15691 (AET9929), on dead tissue of *Eulychnia acida*, Lado15694 (AET9932).

This is the most common and most widely distributed species in the region we surveyed. It appeared in all localities where myxomycetes were found in the field, except locality 1 where there were no cactaceae as it was at 4,600 m elevation. It is typically succulenticolous and has been found on all of the substrates studied, even the endemic cacti, such as *Browningia candelaris* or *Echinopsis atacamensis*, with a very restricted distribution. It also appeared in moist chamber cultures, on the bark of *Prosopis tamarugo*, from localities 8 and 9, where this was practically the only possible substrate. It was one of the two species found in these places.

The species was described by Spegazzini (1880) on *Cereus peruvianus* from Argentina, and recently (Castillo *et al*. 1996) analyzed its similarity to *B. gracilis*. Lado (2001) considered that they are synonyms. The small difference in spore size is not sufficient to maintain them as two taxa. In the material from Chile, the variability of the species was confirmed. It varies in the shape and size of the sporocarps, the presence or absence of stalk, and spore size. In addition, in numerous collections (Lado15647, 15652, 15657, 15659, 15660, 15662, 15664-15671, 15673-15674, 15676-15677, 15679-15682, 15688, 15695-15696, 15702), spores appear in loose clusters, a character mentioned by Spegazzini (1880) in the original description of the species, as well as by Massee (1892) and Lister (1925) but not by Castillo *et al*. (1996). As Clark *et al*. (2003) indicated in a study of *B. gracilis*, this species is probably a widespread species complex consisting of a number of local sexual populations and numerous asexual clones that are adapted to arid conditions.

Clastoderma debaryanum A. Blytt

Loc. 21, on dead tissue of *Copiapoa* sp., Lado15603 (AET9841)

Only one collection found, where it was associated with *Licea succulenticola*, *Badhamia melanospora* and *Didymium* sp.

Comatricha elegans (Racib.) G. Lister

Loc. 26, on litter of *Oxalis gigantea* in mc, pH 4.4-4.8, SLS 19440.

Only one collection obtained in moist chamber.

Comatricha laxa Rostaf.

Loc. 4, on dead tissues of columnar cacti, Lado15566 (AET9804).

Loc. 5, on dead tissue of *Eulychnia iquiquensis*, Lado15557 (AET9795).

Loc. 25, on bark and dead tissue of *Miquelopuntia miquelli* in mc, pH 7.3-8.0, SLS 19432.

Loc. 30, on bark and dead tissue of *Miquelopuntia miquelli* and *Eulychnia acida* in mc, pH 7.3-8.0, SLS 19432.

This species has been found in the field and in moist chamber cultures. These collections are the first known from Chile.

Didymium anellus Morgan

Loc. 2, on litter of *Parastrephia* sp. in mc, pH 5.1-8.2, SLS 19391.

Loc. 25, on bark and dead tissue of *Miquelopuntia miquelli* in mc, pH 5.1-8.2, SLS 19391.

Loc. 31, on bark and dead tissue of *Miquelopuntia miquelli* and *Eulychnia acida* in mc, pH 5.1-8.2, SLS 19391.

This species is a new record for Chile. Previously known in the Neotropics (Farr, 1976), and also from temperate areas of the world.

Didymium melanospermum (Pers.) T. Macbr.

Loc. 4, on dead tissue of columnar cacti, Lado15542 (AET9780), Lado15545 (AET9783).

Loc. 5, on dead tissue of *Eulychnia iquiquensis*, Lado15564 (AET9802).

The three collections found have the same characters, plasmodiocarpic fruit bodies with a large, flat and orange columella and an areolate peridium. The material could represent the variety *bicolor* G. Lister (cf. Nannenga-Bremekamp and Lado, 1985).

Didymium squamulosum (Alb. & Schwein.) Fr

Loc. 2, on litter of *Parastrephia* sp. in mc, pH 6.3-7.3, SLS 19506.

Loc. 26, on litter of *Oxalis gigantea* in mc, pH 6.3-7.3, SLS 19506.

This species has been reported from every region of the world investigated to date (Martin and Alexopoulos, 1969) and is particularly common on litter substrates in tropical forests (Stephenson *et al*., 2004). However, our collections only appeared in moist chamber cultures on shrubs and not on cacti.

Didymium synsporon T.E. Brooks & H.W. Keller (Figs 15-16)

Loc. 28, on dead tissue of *Opuntia* sp., Lado15661 (AET9899),

This collection is the first known from South America. We include our material in this species because of the distinctive clustered spores (figs. 16), unique in this genus. The shape of the plasmodiocarps and short sporocarps and the shape, dimensions and color of the spores are the same as the species described by Keller and Brooks (1973) from Arkansas (USA), but the capillitium, in our case, is composed of dark, typical *Didymium* filaments (Figs 15-16), with sharp, very slender and pale ends. In our material we have not observed the capillitial threads attached to the basal portion of the peridial wall, nor the upper extremities of sharply expanded and forming a broad attachment.

Didymium vaccinum (Durieu & Mont.) Buchet

Loc. 12, on dead tissue of *Echinopsis atacamensis*, Lado15568 (AET9806), on dead tissue of *Opuntia* sp., Lado15575 (AET9813), Lado15577 (AET9815).

Loc. 15, on dead tissue of *Opuntia* sp., Lado15581 (AET9819), also in mc, pH 7.0-7.8, SLS 19503.

Loc. 19, on dead tissue of *Opuntia* sp., Lado15596 (AET9834), also in mc, pH 7.0-7.8, SLS 19503.

Loc. 21, on dead tissue of *Copiapoa* sp., Lado15604 (AET9842), Lado15612 (AET9850), Lado15614 (AET9852)

Loc. 23, on dead tissue of *Copiapoa* sp., Lado15627 (AET9865).

Loc. 24, on dead tissue of *Copiapoa* sp., Lado15618 (AET9856), Lado15621 (AET9859).

Loc. 26, on dead tissue of *Copiapoa* sp., Lado15645 (AET9883). On litter of *Oxalis gigantea* in mc, pH 7.0-7.8, SLS 19503.

Loc. 27, on dead tissue of *Copiapoa* sp., Lado15650 (AET9888), Lado15651 (AET9889), Lado15655 (AET9893).

Loc. 31, on dead tissue of *Copiapoa* sp., Lado15683 (AET9921), Lado15685 (AET9923).

These collections are the first of this species known from Chile. *Didymium vaccinum* appears to be a species more commonly associated with dead tissue of succulent plants than any other type of substrate. It appeared more frequently in the Southern parts of the study area associated principally with *Copiapoa* spp. This may be because in these areas the effect of the Camanchaca increases the ambient humidity.

Echinostelium fragile Nann.-Bremek.

Loc. 26, on litter of *Oxalis gigantea* in mc, pH 5.6, SLS 19574.

Only one collection obtained in moist chamber culture. This is a new record for South America.

Hemitrichia minor G. Lister

Loc. 27, on dead tissue of *Copiapoa* sp., Lado15646 (AET9884).

This species is very common in arid regions of North America but seems rare in the South (Farr, 1976). We found only one collection, which represents the first known from Chile.

Licea biforis Morgan

Loc. 6, on dead tissue of columnar cacti, Lado15535 (AET9773).

This is a new record for Chile.

Licea succulenticola Mosquera, Lado, Estrada & Beltrán-Tej.

Loc. 21, on dead tissue of *Copiapoa* sp., Lado15603 (AET9841).

This collection is the second known from South America. This typically succulenticolous species is known only from the Canary Islands, Mexico, USA (Mosquera *et al*., 2003) and Ecuador (McHugh, 2005).

Perichaena chrysosperma (Curr.) Lister

Loc. 26, on litter of *Oxalis gigantea* in mc, pH 7.8, SLS 19713.

This is a new record for Chile although the species has been reported previously from numerous localities in the Neotropics and the adjacent country of Argentina (Farr, 1976)

Perichaena depressa Lib.

Loc. 2, on litter of *Parastrephia* sp. in mc, pH 4.7-8.0, SLS 19555.

Loc. 12, on dead tissue of *Opuntia* sp., Lado15578 (AET9816). On bark of *Echinopsis atacamensis* in mc, pH 4.7-8.0, SLS 19555.

Loc. 15, on dead tissue of *Opuntia* sp. in mc, pH 4.7-8.0, SLS 19555.

Loc. 26, on litter of *Oxalis gigantea* in mc, pH 4.7-8.0, SLS 19555.

Reported previously from the Galapagos Islands and neighbouring countries of Chile such as Argentina and Bolivia (Farr, 1976).

Perichaena vermicularis (Schwein.) Rostaf.

Loc. 5, on dead tissue of *Eulychnia iquiquensis*, Lado15561 (AET9799).

Loc. 29, on dead tissue of *Eulychnia* sp., Lado15676 (AET9914).

Loc. 31, on dead tissue of *Eulychnia* sp., Lado15678 (AET9916), Lado15679 (AET9917), Lado15681 (AET9919).

Loc. 33, on dead tissue of *Eulychnia acida*, Lado15694 (AET9932).

Physarum echinosporum Lister

Loc. 1, on bark and litter of *Polylepis besseri* in mc, pH 4.1-5.0, SLS 19564.

This is a new record for Chile. This apparently rare species resembles *Physarum bivalve* in general aspect but can be distinguished rather easily on the basis of having spores with conspicuous spines. *Physarum echinosporum* appears to have a distribution centred in the tropics (Martin and Alexopoulos, 1969: 300; Farr, 1976: 136). This sample from moist chamber of bark and litter from 4,665 m, probably represents the highest elevation from which a substrate for culture of myxomycetes has ever been collected.

Physarum megalosporum T.Macbr.

Loc. 5, on dead tissue of *Eulychnia iquiquensis*, Lado15555 (AET9793), Lado15556 (AET9794).

Loc. 31, on dead tissue of *Copiapoa* sp., Lado15685 (AET9923), Lado15686 (AET9924). On dead tissue of *Opuntia* sp., Lado15687 (AET9925).

These collections are the first known from Chile. The strongly limy capillitium, approaching a badhamioid condition, and the spores which are dark brown by transmitted light, with a paler area of dehiscence, and densely verrucose, 12-14 µm diam., are the distinctive features of this species that seems to be not uncommon on cacti.

Physarum pusillum (Berk. & M.A.Curtis) G.Lister

Loc. 4, on dead tissue of *Oreocereus* sp., Lado15548 (AET9786).

Loc. 9, on bark of *Prosopis tamarugo* in mc, pH 4.8-6.2, SLS 19547.

Loc. 26, on litter of *Oxalis gigantea* in mc, pH 4.8-6.2, SLS 19547.

This is a new record for Chile but the species has been reported previously from the neighbouring countries of Bolivia and Argentina (Farr, 1976).

Physarum spectabile Nann.-Bremek., Lado & G. Moreno (Figs 17-18)

Loc. 18, on dead tissue of *Opuntia* sp., Lado15590 (AET9828).

Loc. 25, on dead tissue of *Eulychnia* sp., Lado15637 (AET9875), Lado15642 (AET9880).

Loc. 27, on dead tissue of *Eulychnia* sp., Lado15653 (AET9891), Lado15654 (AET9892). On dead tissue of *Copiapoa* sp., Lado15656 (AET9894).

Loc. 31, on dead tissue of *Copiapoa* sp., Lado15685 (AET9923),

These collections are the first known from South America. Our specimens expand considerably the distribution of this succulenticolous species described from the Canary Islands by Nannenga-Bremekamp *et al*. (1984). In the Chilean collections, the sporophores are variable. In some samples (Lado15990) the normal sessile sporocarps and short plasmodiocarps are mixed (Fig. 17), whereas in others (Lado15685), stipitate sporocarps dominate (Fig. 18). This character was not mentioned in the original description. In all the collections, the spores and capillitium are similar and constant. It resembles *Badhamia melanospora*, especially in the ornamentation and shape of the spores, but the angles of the spores are pale and the capillitium is typically physaroid, with white nodes and hyaline connecting threads.

Trichia affinis de Bary (Fig. 20)

Loc. 2, on *Stipa atacamensis*, Lado15549 (AET9787).

Only one collection, with a very dispersed habit, which is unusual for this species. It was found in the tufts of the grassland puna (Figs 19-20), at 4,100 m probably one of the highest elevations from which a collection of a myxomycete has ever been recorded anywhere in the world.

Trichia contorta (Ditmar) Rostaf.

Loc. 4, on dead tissue of *Oreocereus* sp., Lado15539 (AET9776), on dead tissue of columnar cactus, Lado15547 (AET9785).

This very variable species, for which a number of varieties have been described, appears to be most common in temperate regions of the Northern Hemisphere (Martin and Alexopoulos 1969) but often occurs in small fruitings which are likely to be overlooked in many instances.

Discussion

From the results presented in this paper, it is apparent that even under some of the most extreme conditions of drought, elevation and salinity, myxomycetes not only survive but are varied and surprisingly numerous. From the list of 164 collections representing 24 species, 14 species are new records for Chile, and four (*Badhamia dubia*, *Didymium synsporon*, *Echinostelium fragile* and *Physarum spectabile*) are new records for South America. The total number of myxomycetes from this area would almost certainly be increased by doing a more intense survey, and repeating it under various conditions of humidity, although these are virtually impossible to predict for northern Chile.

As has been reported from other arid zones of the world (Blackwell and Gilbertson 1980, 1984; Novozhilov & Goluleva 1986; Schnittler & Novozhilov 2000; Novozhilov *et al*., 2006), the species of myxomycetes with lime, members of the order *Physarales*, predominated in the areas surveyed in the present study, and *Didymium*, *Physarum* and *Badhamia* were the genera represented by the most species. *Badhamia melanospora* (= *B. gracilis*) was the single most abundant species and was recorded from, 30 of the 33 sampling localities. In two of the remaining three localities no myxomycetes were collected in the field nor in the moist chamber cultures. It is unusual that only one species of *Arcyria* (*A. cinerea*, a very common species in most regions of the world) was encountered only once and then in moist chamber culture. Moreover, only two species in the order Stemonitales were collected. Moist chamber cultures yielded a total of 12 species. Most were common species such as *A. cinerea*, *B. melanospora*, *C. elegans*, *D. squamulosum* or *D. vaccinum*, but two rare species (*E. fragile* and *Ph. echinosporum*) also appeared. The substrates for moist chamber cultures that produced positive results were *Prosopis tamarugo*, *Polylepis besseri*, *Parastrephia* sp., *Eulychnia iquiquensis*, *Echinopsis atacamensis*, *Miquelopuntia miquelli*, *Oxalis gigantea* and *Eulychnia acida*. Practically all of these are endemic plants to this part of the world. This shows the adaptation of myxomycetes to substrates that are very restrictive in their distribution.

When the type of substrate was considered for both field and moist chamber collections, cacti were the most productive. Of the field collections 99% were on *Cactaceae* and many of the same species previously found on these substrata in Mexico (unpublished data) appeared again in this survey (*Badhamia melanospora*, *Didymium vaccinum*, *Hemitrichia minor*, *Licea succulenticola*, *Physarum pusillum*, *Ph. spectabile*) and were also especially frequent on the under side of the plants close to the ground.

The most decisive factor determining the abundance of myxomycetes in these adverse climatic conditions was the presence or absence of water. At 18ºS latitude, in the areas influenced by the Bolivian winter, we obtained the greatest diversity of myxomycetes (13 species), followed (9 species) by at 30ºS in semi-arid areas of the south, and the least (7 species) at 23ºS which is the most arid area of the Atacama desert and salt flats. It seems likely that they obtain water directly from the tissues of the plants on which they occur. Only where there were plants present, were myxomycetes found. There were large areas where there was no vegetation, and no humus. Even where plants such as *Prosopis tamarugo*, produced enough leaf litter to generate humus, which collects in small depressions around the base of the plant, it did not decompose. This is probably due to lack of water, aggravated by the crust of salt on the ground, and in this litter not even plasmodial tracks, common in other litter, were found. The litter of *Oxalis gigantea*, however, did produce 6 myxomycetes in moist chamber culture, but this plant grows in the zones influenced by the Camanchaca, and in the absence of salt flats. Many of the collections were associated with the more favourable microclimate surrounding the base of plants where a little moisture was conserved. This was particularly noticeable in the puna, where the tussocks of *Stipa atacamensis* could be opened to reveal fructifications in situations where neither sun nor wind can dry them out. The Andean puna is a typical alpine grassland, and the myxomycetes that obtain refuge inside the tufts of grass (Figs 19-20), can grow and develop there at more than 4,000 m elevation. Shrubs such as *Parastrephia* sp., located at 4,100 m, were less productive, and we did not observe any fructifications in the field. However, these shrubs did provide good substrates for moist chambers.

A comparison between species appearing in the coastal section of the transverse transects (0-1,000 m), with those appearing at the highest altitudes (3,000-4,700 m), showed the same number of species. The two elevations had almost 60% of the 24 species in common. However, with the other 40% of the species there was no pattern of association of species to elevation. The intermediate altitude coincided with the driest desert where only *Badhamia melanospora* was found.

Opuntia and Miquelopuntia spp. were the substrates which produced the greatest diversity of species (8 species), followed by *Copiapoa* spp. (7 species), *Oxalis gigantea*, *Eulychnia sp*., and (6 species), and *Parastrephia* sp. (5 species).

It would seem unlikely to predict that any myxomycetes would be found in this, one of the driest places on earth. The 24 species representing 11 different genera found in this study reflect not only a presence, but a surprisingly high diversity of these organisms in such an extreme environment, and are evidence that myxomycetes are well adapted to survive, even under the conditions of the exceedingly limited water available in the desert.

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