Biodiversity studies of myxomycetes in Madagascar

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Received: 30 April 2012 / Accepted: 12 June 2012 / Published online: 6 September 2012 Mushroom Research Foundation 2012

Abstract The results of the first comprehensive study of myxomycetes from the island of Madagascar, a world biodiversity hotspot, are reported in this paper. The island is of continental origin, the fourth largest in the world, and has been geographically isolated for more than 160 million years, since its separation from Gondwanaland. The isolation, size and topography of Madagascar have triggered the development of a great variety of different habitats and favoured multiple evolutionary pathways, resulting in many animals and plants that exist nowhere else on earth. Fieldwork for the biodiversity survey of the central and southern parts of the island took place in May 2009, to coincide with the end of the rainy season. Tropical moist forest, sclerophyll forest and dry forest were selected for sampling in Ranomafana, Andringitra, Andohahela and L'Isalo National Parks. Some unique vegetation was sampled in the spiny dry forest and succulent scrub with plants from the genera Alluaudia, Euphorbia, Kalanchoe and Pachypodium. The survey produced 124 species from 22 different genera in more than 750 myxomycete collections. In this paper one species, Perichaena madagascariensis, is described as new to science, 21 species are new records for Africa, and 106 are reported for the first time from Madagascar. Some

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unusual collections included *Physarum lakhanpalii* that appeared on *Ravenala madagascariensis*, *Fuligo intermedia* and *Licea nannengae* found on *Adansonia grandidieri*, *Perichaena pulcherrima*, *Physarum dictyosporum*, and *P. echinosporum* on *Euphorbia* and *Licea rufocuprea* on bark. The scope, methods and results of this survey are included in this paper, and comments are made on the ecology, distribution and substrate association of the myxomycetes of these areas of Madagascar. Macrographs, micrographs and SEM images of interesting species are included. The results indicate that the island of Madagascar has a unique assemblage of species of myxomycetes, different from neighbouring islands and from similar but distant environments.

Keywords Amoebozoa · Biogeography · Endemism · Myxogastria · SEM · Spiny forest

Introduction

Madagascar, situated in the Indian Ocean between 12° and 25° S latitude and 43° – 51° E longitude, is the fourth largest island in the world, following Greenland, Papua New Guinea and Borneo (Ingram and Dawson 2005). It has been geographically isolated for more than 160 million years, following its separation from the continent of Africa at the break up of Gondwana (Wells 2003). It is recognised as a global biodiversity hotspot with a remarkable number of endemisms at various taxonomic levels, and its endemic plants (11 endemic families and 310 endemic genera of plants) make up over 3 % of the plant species worldwide (Myers et al. 2000). It has been estimated that as many as 90 % of the organisms that are unique to Madagascar live in forests, and yet only a small fraction of the original forests remain (Dufils 2003).

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The vegetation of Madagascar is distributed around a 1200 m high central mountain range that runs from North to South along the length of the island, with massifs above 2600 m (Jury 2003). It ranges from humid dense forest on the eastern slopes to southern and western dry forests, with degraded central grasslands of fire-adapted grasses between. It has been suggested that slash and burn agricultural practice has resulted in the clearing of native forest in these areas to plant crops, however recent work on C₄ grasses (Bond et al. 2008; Willis et al. 2008), suggests that these may be ancient grasslands and not anthropogenically derived.

The climate of Madagascar, caused by its geographic location and relief, is alternately influenced by dry trade winds in the winter from May to September, and tropical storms from monsoon winds in the summer from December to March (Jury 2003). The eastern humid forests have no significant dry season and receive from1500 to 4000 mm annual precipitation, whereas the southern spiny thicket may have under 300 mm a year (Wells 2003). In general, the climate is one of unpredictable frequency and amount of precipitation, and the variability affects the flowering and fruiting patterns of plants (Dewar and Richard 2007).

The survey described in this paper was designed to assess the biodiversity and ecology of the myxomycetes associated with various types of plant communities in Madagascar, as one component of the planetary biodiversity inventory for eumycetozoans project, supported by the National Science Foundation of the United States. The myxomycetes are eumycetozoans, traditionally considered to be fungi, but now molecular data and an increasing amount of data accumulated over the last few decades, indicate that they are amoebozoans (Stephenson 2011). The only myxomycetes previously published from Madagascar are 10 species cited by Patouillard (1928), almost a hundred years ago. The 21species recorded from the island according to a checklist of African Myxomycetes (Ndiritu et al. 2009), include these and otherwise unpublished records by Locquin from the UARK database. There are also collections of 4 species from Madagascar recently published by Poulain et al. (2011).

Study area

The area of the survey covered the central to southern part of the island from latitudes $19^{\circ}-25^{\circ}$ S (Fig. 1). As far as possible National parks with undisturbed natural vegetation were selected for sampling, and these were Ranomafana NP, Andringitra NP, Andohahela NP, l'Isalo NP and the environs of the Berenty Reserve. In addition, sampling was done en route from Antananarivo to Fianarantsoa, en route from Ihosy to Fort Dauphin (Tôlanaro) and on the road from Antananarivo to Moromanga, near Majakandriana. The vegetation selected (Figs. 2-10) included primary tropical moist forest (Fig. 2), with the tree that is used as the National emblem, Ravenala madagascariensis (Fig. 10), ravines with gallery forest and Pandanus stands and sclerophyll "tapia" forest with Uapaca bojerii (Fig. 3). Among the dry forests of the South, there is a very characteristic ecosystem of spiny thicket (Fig. 6) that may represent the oldest remaining biome on the island (Wells 2003), and includes the endemic family Didiereaceae with four genera including Alluaudia (Fig. 6), with species of Adansonia, the baobabs (Fig. 8), and members of the Euphorbiaceae (Fig. 9). The rocky outcrops in the central grasslands (Fig. 4), or inselbergs (Barthlott and Porembski 1996), have another very characteristic biota, the succulents, that include Pachypodium spp. (Fig. 7), and species of Aloe (Fig. 5) and Kalanchoe. Sampling was also carried out in the central grassland and degraded areas with introduced Agave and Opuntia spp. Data on the areas sampled is given in Table 1.

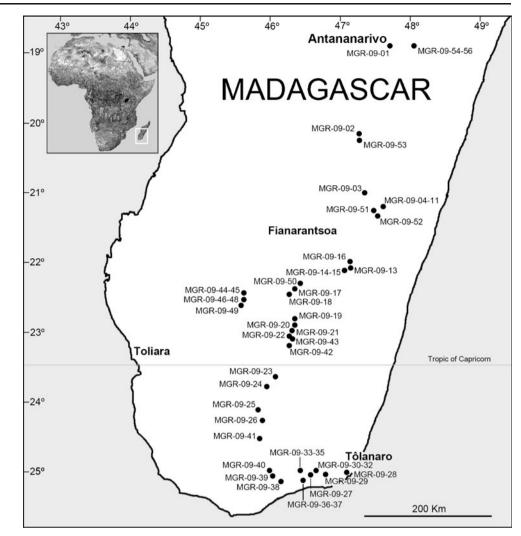
The country had six administrative provinces until 2009 when they were dissolved leaving their 22 regions as the first level divisions. In Table 2, our data on the collecting localities list both the former provinces, still shown in many literature resources, and the regions (in brackets) for each site.

Materials and methods

The fieldwork of the survey took place over 3 weeks in May 2009, to coincide with the end of the rainy season, at the 56 localities listed in Table 2. Specimens and samples of substrates to be examined for the presence of eumycetozoans were obtained from two rainforests, two mesic forests and two dry forests across the central and southern parts of the island. Collections were made of myxomycete fruitings in the field and samples of various substrates, such as dead parts of standing plants (aerial litter), ground litter, bark, and coarse woody debris for subsequent moist chamber cultures. The fieldwork was carried out by: Arturo Estrada-Torres, Carlos Lado, Martin Schnittler, Estelle Razanatzoa and Diana Wrigley de Basanta. Moist chamber (mc) cultures were prepared with 195 samples of the various substrates, in the manner described by Wrigley de Basanta et al. (2009). Water was added every few days as required, to maintain the humidity for the entire observation period of up to 3 months. The type of substrate and the pH of each moist chamber culture (taken at 24 h) were recorded in all instances. Cultures were examined every day for the first 2 weeks, and subsequently every 2-3 days for the full culture period. A species recorded from one moist chamber culture was regarded as a single collection, irrespective of the number of sporophores appearing, or the number of days separating their appearance.

Fig. 1 Map of the study area

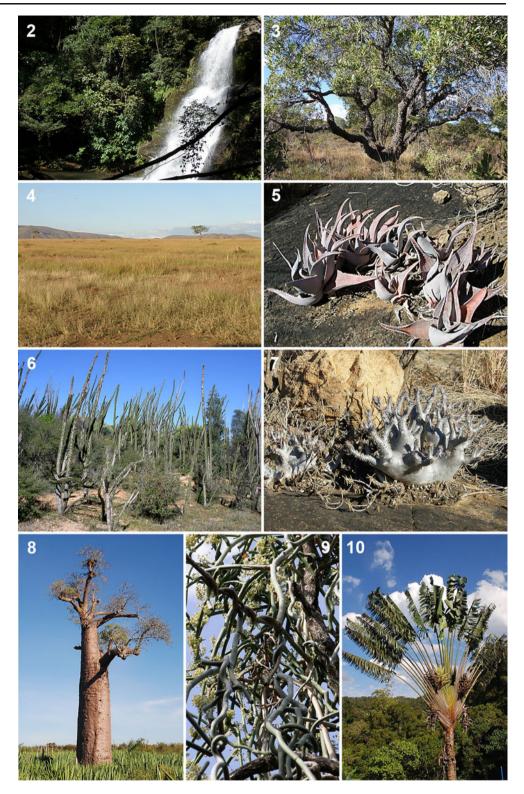
and localities sampled



Geographical data, geo-references, as well as vegetation type are given in Table 2. For the geo-references a GPS model Magellan 600 (datum WGS84) and a Garmin eTrex Vista HCx (datum WGS84) were used. All collection numbers cited refer to specimens deposited in the herbaria MA-Fungi (sub Lado), UARKM (sub sls), TLXM (sub aet) or the private collection of Diana Wrigley de Basanta (dwb), All microscopic measurements and observations were made with material mounted in Hoyer's medium or polyvinyl alcohol. Differential interference contrast (DIC) microscopy was used to obtain descriptive data. The light photomicrographs were obtained using a Nikon AZ100 microscope. Some specimens were examined at 10-15 kV, with a Hitachi S-3000 N scanning electron microscope (SEM), at the Real Jardín Botánico, CSIC. For the SEM photographs, the critical point dried material technique was employed. Where color notations are made in parenthesis, they are from the ISCC-NBS Color Name Charts Illustrated with Centroid Colors (Anonymous 1976).

Data analysis In this paper, 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). 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 using the formula CC=2z / (x+y), where x and y equal the number of species in communities A and B, respectively, and where z is the number of species in common to both communities.

The completeness of the sampling effort was evaluated using the ACE and CHAO1 abundance indices (Colwell and Coddington 1994; Colwell et al. 2004) and the species accumulation curve adjusted according to Clench, where $S_n = (a*n)/[1+(b*n)]$, and S_n is the number of species accumulated for a unit of collecting effort (Jiménez-Valverde and Hortal 2003). Each collecting site was considered to be a unit of collecting effort, using the total number of species found with the programme EstimateS v. 7.5.2 (http:://viceroy.eeb.uconn.edu/estimates). The adjustment according to Clench was carried out with the programme Statistica v. 10, using the Simplex and Quasi-Newton adjustment (JiménezFig. 2–10 Tropical moist forest at Ranomafana National Park. 3 *Uapaca bojerii* in tapia forest, L'Isalo National Park. 4 Central grassland. 5 *Aloe* sp. 6 Spiny thicket with *Alluaudia* sp., Andohahela National Park. 7 *Pachypodium* sp. on an inselberg. 8 *Adansonia* grandidieri, a baobab. 9 *Euphorbia* sp. in tropical dry forest 10 *Ravenala* madagascariensis at Ranomafana National Park



Valverde and Hortal 2003). To calculate the completeness of sampling the 124 identified species plus 10 species identified to genus and *Physarum viride* var. *aurantium* and *Stemonitis fusca* var. *rufescens* were considered as separate entities.

Results

This is the first comprehensive study of myxomycetes from the island of Madagascar. The research produced 124 species from 22 different genera. The 761 collections included

Table 1	Summary	data on	vegetation	types	surveyed
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Vegetation type	% of Forest formations 1	National parks visited	Location ⁴	Annual temp mean	Annual precipitation
Humid forest	44	Ranomafana	21°02′–22°25′S 47°18′–47°37′E	14–24 ° C	1500–4000 mm ³
		Andringitra	22°07′–22°21′S 46°47′–47°02′E	14–24 ° C	1400 mm ⁵
Gallery forest	1	L'Isalo	22°22′–22°40′S 45°11′–45°23′ E	17–25 ° C	966 mm ⁶
Tapia sclerophyll forest	2	L'Isalo	22°22′–22°40′S 45°11′–45°23′ E	17–25 ° C	966 mm ⁶
Grasslands/inselbergs	NA	NA	22°03′S–23°38′S 45°50′E–46°56′E	16–20 ° C ²	200–500 mm ⁷
Southern dry forest and spiny thicket	18	Andohahela	24°30′–25°02′S 46°32′–46°54′E	19–30 ° C	>300 ³ -532 mm ⁶

¹ Dufils 2003; ² Natural Environment Research Council (2002); ³ Wells 2003; ⁴ Madagascar National 2003; ⁵ World Meteorological Organization; ⁶ Dewar and Richard 2007; ⁷ Jury 2003

one species described below as new to science, 21 species as new records for all of Africa, and 106 are reported for the first time from Madagascar.

Annotated list of species

All the collections of myxomycetes recorded in our survey are listed below by genus and species in alphabetical order. To save space, in species with a large number of collections, only a few are listed and the totals are abbreviated beside the species name as follows: field collections (fc), moist chamber collections (mc), number of localities (loc), number of different substrates (subs). Moist chamber culture collections (mc) are followed by the pH of the culture in which the particular species was obtained. Comments are included on specimens of particular interest or species new for Africa or Madagascar. The former are indicated with a cross ([†]) and the latter with an asterisk (^{*}). Nomenclature follows Lado (2005-2012). Although species of Ceratiomyxa do not belong to the myxomycetes, they have been traditionally included in this type of survey and thus are reported here. The abbreviation 'cf.' in the name of a taxon indicates that the specimen representing the source of the record could not be identified with certainty. Unless otherwise stated the distribution comments are based on Ndiritu et al. (2009).

Arcyria cinerea (Bull.) Pers. 19 fc, 20 mc, 24 loc, 13 subs MGR-09-08: wood, MA-Fungi 81462 (Lado 19731). MGR-09-31: *Euphorbia* sp. litter, (mc, pH 5.6), dwb 3374. MGR-09-32: *Alluaudia procera*, MA-Fungi 81666 (Lado19944). MGR-09-46: *Dypsis isaloensis* leaf litter, MA-Fungi 81744 (Lado 20039). MGR-09-50: *Kalanchoe* sp. litter, (mc, pH 6.9), dwb 3240.

In Africa, this species is widely distributed and has been reported previously in Madagascar from Maromandia (Patouillard 1928), and from Aldabra (Ing and Hnatiuk 1981) and La Réunion (Adamonyte et al. 2011).

Arcyria denudata (L) Wettst. 9 fc, 0 mc, 7 loc, 3 subs MGR-09-05: wood, MA-Fungi 81438 (Lado19706). MGR-09-10: small twig, MA-Fungi 81523 (Lado19794). MGR-09-53: *Pinus patula* wood, MA-Fungi 81821 (Lado 20123). MGR-09-54: bark of a dead liana, MA-Fungi 81859 (Lado 20164). MGR-09-55: bark of a dead liana, MA-Fungi 81864 (Lado 20171).

In Africa, this species has been reported previously from 16 different countries, including Madagascar from Beraty near Maromandia and Antananarivo (Patouillard 1928) as *Arcyria punicea* Pers.

*Arcyria incarnata (Pers. ex J.F. Gmel.) Pers.

MGR-09-20: small savannah tree bark, (mc, pH 4.1), dwb 3315.

**Arcyria insignis* Kalchbr. & Cooke MGR-09-52: liana bark, (mc, pH 5.1), dwb 3332.

Arcyria minuta Buchet

MGR-09-30: wood, MA-Fungi 81651 (Lado 19928), MA-Fungi 81648 (Lado 19925). MGR-09-31: *Euphorbia* sp. twigs MA-Fungi 81660 (Lado 19938). MGR-09-47: wood of a liana, MA-Fungi 81768 (Lado 20059); wood, MA-Fungi 81780 (Lado 20071). MGR-09-49: wood, MA-Fungi 81791 (Lado 20083). MGR-09-52: wood, MA-Fungi 81811 (Lado 20111).

This species was described by Buchet, based on a specimen on wood from Maromandia, Madagascar (Patouillard 1928).

Table 2 Summary data on collecting localities

MGR-09-01: Antananarivo (Analamanga), Antananarivo city, University campus, city limits, western Hills, 18°54'50"S 47°33'13"E, 1339±3 m, gardens, 7-V-2009. MGR-09-02: Fianarantsoa (Amoron'i Mania). Ambositra, RN-7 road from Antananarivo to Fianarantsoa, km 212. Col de Tapia, ca. 5 km S of Ambohimanjaka, 20°14'11"S 47°05'58"E, 1448±4 m, sclerophyllous "Tapia" forest, 9-V-2009. MGR-09-03: Fianarantsoa (Amoron'i Mania), Ambositra, RN-7 road from Antananarivo to Fianarantsoa, km 336, S of Talata, 21°02'23"S 47°10'27"E, 1293±3 m, secondary Eucalyptus forest, planted, 9-V-2009. MGR-09-04: Fianarantsoa (Haute Matsiatra), Ranomafana, Ranomafana NP, near the park entrance ca. 5 km W of the village Ambatolahy, 21°15′22″S 47°25′18″E, 943±3 m, forest fringe with plantations, 10-V-2009, 11-V-2009. MGR-09-05: Fianarantsoa (Haute Matsiatra), Ranomafana, Ranomafana NP, near the park entrance ca. 5 km W of the village Ambatolahy, trail along the river, 21°15′31″S 47°25′15″E, 914±6 m, primary tropical moist forest, 10-V-2009. MGR-09-06: Fianarantsoa (Haute Matsiatra), Ranomafana, Ranomafana NP, near the park entrance ca. 5 km W of the village Ambatolahy, junction between BF350 and B1200 trails, 21°15′44″S 47° 25'16"E, 1001±6 m, primary tropical moist forest, 10-V-2009. MGR-09-07: Fianarantsoa (Haute Matsiatra), Ranomafana, Ranomafana NP, near the park entrance ca. 5 km W of the village Ambatolahy, hill "Belle Vue", 21°15'42"S 47°25'27"E, 1017±3 m, primary tropical moist forest, 10-V-2009. MGR-09-08: Fianarantsoa (Haute Matsiatra), Ranomafana, Ranomafana NP, near the park entrance ca. 5 km W of the village Ambatolahy, NW-exp. slope in a small side valley, 21°15′50″S 47°25′22″E, 1010±7 m, primary tropical moist forest, 10-V-2009. MGR-09-09: Fianarantsoa (Haute Matsiatra), Ranomafana, Ranomafana town, garden of the Ihary hotel in the river valley, 21°15'41"S 47°27'22"E, 627±3 m, gardens and planted trees, 11-V-2009. MGR-09-10: Fianarantsoa (Haute Matsiatra), Ranomafana, Ranomafana NP, ca. 6 km W of the village Ambatolahy, trail to the waterfall, around the falls, 21°15′46″S 47°24′47″E, 989±10 m, primary tropical moist forest, 11-V-2009. MGR-09-11: Fianarantsoa (Haute Matsiatra), Ranomafana, Ranomafana NP, ca. 6 km W of the village Ambatolahy, trail to the waterfall, near the last bridge, 21°15'39"S 47°24'51"E, 934±13 m, primary tropical moist forest, 11-V-2009. MGR-09-12: Fianarantsoa (Haute Matsiatra), Ranomafana, Ranomafana NP, ca. 6 km W of the village Ambatolahy, trail to the waterfall, around first bridge, 21°15'36"S 47°25'08"E, 922±3 m, primary tropical moist forest, 11-V-2009. MGR-09-13: Fianarantsoa (Haute Matsiatra), Ambalavao, Andringitra NP, near the entrance of the National Park, around the village Antanifotsy, 22°05'42"S 46°55'42"E, 1442±3 m, fallow grassland overgrown with Asteraceae shrubs, 12-V-2009. MGR-09-14: Fianarantsoa (Haute Matsiatra), Ambalavao, Andringitra NP, edge of the park, northern fringe of the Andringitra ridge, 22°07'36"S 46°53'35"E, 1622±3 m, fallow grassland overgrown with Asteraceae shrubs, 12-V-2009. MGR-09-15: Fianarantsoa (Haute Matsiatra), Ambalavao, Andringitra NP, edge of the park, northern fringe of the Andringitra ridge, 22°08′07″S 46°53′27″E, 1625±4 m, primary montane moist forest, slopes above a river valley, 12-V-2009. MGR-09-16: Fianarantsoa (Haute Matsiatra), Ambalavao, Andringitra NP, gravel road to the park entrance, 22°03'42"S 46°56'13"E, 1255±25 m, anthropogenic grassland, 12-V-2009. MGR-09-17: Toliara (Ihorombe), Ihosy, RN-7 road from Ihosy to Toilara, city limits of Ihosy, 22°23'48"S 46°07'09"E, 735±3 m, gardens and planted succulents, 13-V-2009. MGR-09-18: Toliara (Ihorombe), Ihosy, RN-13 road from Ihosy to Betroka, 28 km S of Ihosy, grassland plains near Ampandrabe, 22°29'25"S 46°02'55"E, 1117±3 m, grassland with some Eucalyptus trees, 13-V-2009. MGR-09-19: Toliara (Ihorombe), Ihosy, RN-13 road from Ihosy to Betroka, 50 km S of Ihosy, S of village Andrera, 22°51'31"S 46°08'41"E, 1000±3 m, gallery tropical dry forest along a river, 13-V-2009. MGR-09-20: Toliara (Anosy), Betroka, RN-13 road from Ihosy to Betroka, south of Ilanana, 22°53'11"S 46°08'46"E, 1017±3 m, anthropogenic grassland, with a few remnant trees, 13-V-2009. MGR-09-21: Toliara (Anosy), Betroka, RN-13 road from Ihosy to Betroka, ca. 2.5 km N of village Androtsa, 22°59'03"S 46° 07'39"E, 1077±3 m, small rivulet with Pandanus stands, 13-V-2009. MGR-09-22: Toliara (Anosy), Betroka, RN-13 road from Ihosy to Betroka, between Androtsa and Iritsoka, 23°03'06"S 46°05'51"E, 1018±3 m, succulent scrub on rock a flat rock outcrop, 13-V-2009. MGR-09-23: Toliara (Anosy), Betroka, RN-13 road from Betroka to Ambovombe, km 169, near Soatana, 23°38'01"S 45°50'46"E, 758±3 m, succulent scrub on rock a flat rock outcrop, 14-V-2009. MGR-09-24: Toliara (Anosy), Betroka, RN-13 road from Betroka to Ambovombe, N of village Manankotiva, 23° 46'27"S 45°45'02"E, 697±3 m, slightly degraded tropical dry forest, many shrubs, 14-V-2009. MGR-09-25: Toliara (Anosy), Betroka, RN-13 road from Betroka to Ambovombe, between Isoanala and Beraketa, 10 km N of Beraketa, near village Meba, 24°06'42"S 45°36'54"E, 544±3 m, very open tropical dry forest, 14-V-2009. MGR-09-26: Toliara (Anosy), Betroka, RN-13 road from Betroka to Ambovombe, between Beraketa and Antanimora, 10 km S of Beraketa, SE of village Andamoty, 24°15′26″S 45°39′12″E, 509±3 m, very open tropical dry forest, 14-V-2009. MGR-09-27: Toliara (Anosy), Amboasary, RN-13 road from Ambovombe to Fort Dauphin (Tôlanaro), near Sampona, 25°01'31"S 46°25'45"E, 97±3 m, spiny Didiereaceae forest, 15-V-2009. MGR-09-28: Toliara (Anosy), Fort Dauphin (Tôlanaro), city limits, 25°01'34"S 46°59'15"E, 17 ±4 m, gardens with planted coconut palms, 15-V-2009. MGR-09-29: Toliara (Anosy), Fort Dauphin (Tôlanaro), RN-13 road from Tôlanaro to Ambovombe, within Andohahela NP sector 3, W of Analamatsaky, 25°01'25"S 46°38'38"E, 123±3 m, spiny Didiereaceae forest, 16-V-2009. MGR-09-30: Toliara (Anosy), Fort Dauphin (Tôlanaro), RN-13 road from Tôlanaro to Ambovombe, 21 km E of Amboasary, within Andohahela NP sector Manihari, W of Bevilany, 25°59'51"S 46°33'46"E, 72±3 m, spiny Didiereaceae forest, 16-V-2009. MGR-09-31: Toliara (Anosy), Fort Dauphin (Tôlanaro), RN-13 road from Tôlanaro to Ambovombe, 16 km E of Amboasary, within Andohahela NP, W of Bevilany, 24°59'42"S 46° 31/23"E, 43±3 m, spiny Didiereaceae forest, 16-V-2009. MGR-09-32: Toliara (Anosy), Fort Dauphin (Tôlanaro), RN-13 road from Tôlanaro to Ambovombe, 12 km E of Amboasary, within Andohahela NP, W of Bevilany, 25°00'05"S 46°28'55"E, 30±3 m, dense spiny Didiereaceae forest, 16-V-2009. MGR-09-33: Toliara (Anosy), Amboasary, environs of Berenty NP, road from Amboasary to Ifotaka, S of Tsilebo, 24°58'15"S 46°13' 58"E, 43±3 m, transition tropical dry to spiny Didiereaceae forest, 17-V-2009. MGR-09-34: Toliara (Anosy), Amboasary, environs of Berenty NP, road from Ambosary to Ifotaka, 16 km N of RN-13, S of Tsilebo, 24°58'35"S 46°14'00"E, 43±3 m, transition tropical dry to spiny Didiereaceae forest, 17-V-2009. MGR-09-35: Toliara (Anosy), Amboasary, environs of Berenty NP, road from Ambosary to Ifotaka, 12 km N of RN-13, S of Berenty, $24^{\circ}59'25''S 46^{\circ}16'08''E$, 37 ± 3 m, tropical dry forest, 17-V-2009. MGR-09-36: Toliara (Anosy), Amboasary, environs of Berenty NP, road from Ambosary to Ifotaka, 2 km N of RN-13, S of Berenty, 25°02'59"S 46°19'58"E, 48±3 m, sisal plantation with an old baobab tree, 17-V-2009. MGR-09-37: Toliara (Anosy), Amboasary, RN-13 road from branch to Berenty NP to Ambovombe, 10 km W of Amboasary, W of village Ankitry, 25°05'30"S 46°17'53"E, 234±3 m, tropical dry forest on hills with coral reef limestone, 17-V-2009. MGR-09-38: Toliara (Anosy), Ambovombe, Ampamalora, RN-13 road from Ambovombe to Betroka, 9 km N of Ambovombe, near Ampamalora, 25°06' 33"S 45°58'12"E, 164±3 m, sisal plantation with old baobab trees, 18-V-2009. MGR-09-39: Toliara (Anosy), Ambovombe, RN-13 road from Ambovombe to Betroka, 39 km N of Ambovombe, SE of village Ambaliandra, 25°01'46"S 45°49'37"E, 154±3 m, tropical dry forest with succulents, 18-V-2009. MGR-09-40: Toliara (Androy), Ambovombe, RN-13 road from Ambovombe to Betroka, S of village Manave, 24°58'25" S 45°46'28"E, 180±3 m, tropical dry forest with succulents, 18-V-2009. MGR-09-41: Toliara (Androy), Beraketa, RN-13 road from Ambovombe to Betroka, 42 Km S of Beraketa, ca. 5 km S of branch to Imanombo, 24°31′03″S 45°37′29″E, 445±3 m, savannah cleared for corn and maniok fields, 18-V-2009. MGR-09-42: Toliara (Anosy), Betroka, RN-13 road from Betroka to Ihosy, 11 km N of Betroka, ca. 5 km NW of

Table 2 (continued)

Naninora, 23°10'55"S 46°03'12"E, 870±3 m, succulent scrub on a flat rock outcrop, 19-V-2009. MGR-09-43: Toliara (Anosy), Betroka, RN-13 road from Betroka to Ihosy, around Iritsoka, 23°04'45"S 46°05'05"E, 973±3 m, grassland with a small rivulet with Pandanus stands, 19-V-2009. MGR-09-44: Toliara (Ihorombe), Ranohira, l'Isalo NP, Andranokova, canyon of a tributary of the Menamaty river from the Isalo ridge, 22°29' 13"S 45°22'42"E, 720±6 m, ravine with gallery forest, 20-V-2009. MGR-09-45: Toliara (Anosy), Betroka, l'Isalo NP, canyon of a tributary of the Menamaty river from the Isalo ridge, 22°29'24"S 45°23'03E, 722±3 m, ravine with gallery forest and Pandanus stands, 20-V-2009. MGR-09-46: Toliara (Ihorombe), Ranohira, I'Isalo NP, Canyon of the Namaza river, 22°32'19"S 45°22'32"E, 774±5 m, ravine with gallery forest and Pandanus stands, division of the ravine ca. 600 m from its mouth, 21-V-2009. MGR-09-47: Toliara (Ihorombe), Ranohira, l'Isalo NP, Canvon of the Namaza river, 22°32′23″S 45°22′41″E, 782±6 m, ravine with gallery forest and Pandanus stands, ca. 400 m from its mouth, 21-V-2009. MGR-09-48: Toliara (Ihorombe), Ranohira, l'Isalo NP, Canyon of the Namaza river, 22°32'23"S 45°22'53"E, 740±4 m, ravine with gallery forest and Pandanus stands, ca. 200 m from its mouth, 21-V-2009. MGR-09-49: Toliara (Ihorombe), Ranohira, l'Isalo NP, N of RN-7 road, NE of summit Vonandraka and 18 km W of Ranohira, 22°37/26″S 45°20′34″E, 867±3 m, scerophyllous "Tapia" forest, 21-V-2009. MGR-09-50: Toliara (Ihorombe), Ihosy, RN-7 road from Ihosy to Fianarantsoa, km 586,15 km NE of Ihosy, near the village Ambararata, 22°19'29"S 46°14' 33"E, 695±3 m, succulent scrub on rock a flat rock outcrop, 22-V-2009. MGR-09-51: Fianarantsoa (Haute Matsiatra), near Ranomafana NP, NS-45 road from Fianarantsoa to Ranomafana, km 11, 11 km E of Alakanisy Ambohimaha and 12 km W of Vohiparara, N of village Ambatovaky, 21°17′06″S 47°18′49″E, 1266±3 m, montane tropical wet forest in a steep river valley, 22-V-2009. MGR-09-52: Fianarantsoa (Haute Matsiatra), near Ranomafana NP, road NS-45 from Fianarantsoa to Ranomafana, km 12, 12 km E of Alakanisy Ambohimaha and 11 km W of Vohiparara, N of village Ambatovaky, 21°17'11"S 47°19'09"E, 1222±3 m, montane tropical wet forest in a steep river valley, 22-V-2009. MGR-09-53: Fianarantsoa (Amoron'i Mania), Ambositra, RN-7 road from Fianarantsoa to Antananarivo, km 215, ca. 5 km N of Mahatsanda, col de Tapia, 20° 15'46"S 47°06'45"E, 1490±3 m, secondary Pinus patula forest replacing "Tapia" sclerophyllous woodland, 23-V-2009. MGR-09-54: Antananarivo (Analamanga), Manjakandriana, Mandraka, RN-2 road from Antananarivo to Moramanga, km 65, W-exp. slopes of the Hantsamba Tonangavo ridge, 18°54'42"S 47°55'09"E, 1203±3 m, primary montane tropical wet forest on a steep slope, 24-V-2009. MGR-09-55: Antananarivo (Analamanga), Manjakandriana, Mandraka, RN-2 road from Antananarivo to Moramanga, km 68, W-exp. slopes of the Hantsamba Tonangavo ridge, 18°55'30"S 47°55'52"E, 1112±3 m, primary montane tropical wet forest at a steep N-exp. slope, 24-V-2009. MGR-09-56: Antananarivo (Analamanga), Manjakandriana, Mandraka, RN-2 road from Antananarivo to Moramanga, km 67, W-exp. slopes of the Hantsamba Tonangavo ridge, 18°55'25"S 47°55'44"E, 1153±3 m, stands of Hedychium in the river valley, open areas cleared for fields, 24-V-2009.

In Africa it is also known from Angola, Democratic Republic of Congo, Rwanda, South Africa, Tanzania and Zambia.

*Arcyria obvelata (Oeder) Onsberg

MGR-09-49: wood, MA-Fungi 81792 (Lado 20085), MA-Fungi 81794 (Lado 20087); decayed termite nest MA-Fungi 81795 (Lado 20088); bark of a living tree, MA-Fungi 81793 (mLado 20086).

*Arcyria pomiformis (Leers) Rostaf.

MGR-09-10: litter and twigs, MA-Fungi 81465 (Lado 19734). MGR-09-28: *Cocos nucifera* leaves, MA-Fungi 81608 (Lado 19883).

*Badhamia macrocarpa cf (Ces.) Rostaf

MGR-09-25: wood, MA-Fungi 81589 (Lado 19862).

This one collection has blackish to greyish robust stalks, but the spores are somewhat angular, 14–15 μ m resembling those of *B. melanospora*.

*Badhamia melanospora Speg. 37 fc, 3 mc, 17 loc, 8 subs MGR-09-18: Agave victoria-reginae remains MA-Fungi 81569 (Lado 19843). MGR-09-22: Aloe sp. litter, (mc, pH 6.7), dwb 3319. MGR-09-27: Kalanchoe sp. bark, dwb 3285. MGR-09-31: Alluaudia procera remains, MA-Fungi 81654 (Lado 19931). MGR-09-42: Pachypodium rosulatum var. gracilis remains, MA-Fungi 81701 (Lado 19990).

This species is common on succulent substrates in the Americas. In Madagascar it apparently has been able to move from the Cactaceae and Agavaceae to other families. It was found on species of the genera *Alluaudia*, *Aloe*, *Pachypodium*, *Euphorbia* and *Kalanchoe* as well as introduced *Opuntia* sp. and *Agave* sp. The three moist chamber collections on *Aloe* sp., (dwb 3319, dwb 3320, dwb 3325) have been left as "cf." *B. melanospora* since the spores are paler and smaller than typical specimens (12–14 μ m instead of 15–18 μ m), although the range of spore size for this species is from 12 to 18 μ m if we consider *B. gracilis* (T. Macbr.) T. Macbr. as a synonym.

*Badhamia nitens Berk.

MGR-09-42: Ground litter, sls 23203.

This collection consists of the basal portion of a single sporocarp but the features that can be observed of clustered spores and yellowish peridium suggest this species, which would be the first record for Africa.

†Badhamia obovata (Peck) S.J. Sm.

MGR-09-55: Leaf litter and twigs, MA-Fungi 81893 (Lado 20202).

The collection belongs to the variety *dictyospora* (Rostaf.) Lister ex Nann.-Bremek. It is easily distinguished by the stalked sporocarps, dense lime capillitial net, and the ornamentation of the spores as an incomplete reticulum of rather low ridges and warts. This is the first record of this species for Africa.

*Badhamia viridescens Meyl.

MGR-09-31: *Euphorbia* sp. twigs, MA-Fungi 81894 (Lado 19933).

This collection has 11 subglobose sporocarps with darker bases. They are reminiscent of *P. pusillum* but with larger spores $(12-14 \ \mu m)$ and a clearly badhamioid capillitium.

Ceratiomyxa fruticulosa (O.F. Müll.) T. Macbr. 10 fc, 0 mc, 7 loc, 3 subs

MGR-09-05: wood, MA-Fungi 81925 (Lado 19692). MGR-09-12: bamboo shoots, MA-Fungi 81506 (Lado 19776). MGR-09-14: wood, MA-Fungi 81540 (Lado 19811). MGR-09-32: *Alluaudia procera* remains, MA-Fungi 81664 (Lado 19942). MGR-09-55: wood, MA-Fungi 81867 (Lado 20174).

†Ceratiomyxa morchella A.L. Welden

MGR-09-11: wood, MA-Fungi 81491 (Lado 19761).

The collection is typical of the species looking like a diminutive *Morchella*. This is the first record of this tropical species for Africa. This suggests its probable pantropical distribution since it is well known from the tropical rainforests of the Neotropics (Rojas et al. 2008).

*Ceratiomyxa sphaerosperma Boedijn

MGR-09-08: wood, MA-Fungi 81460 (Lado 19729).

This species has been reported previously in Africa from Tanzania.

*Clastoderma debaryanum A. Blytt

MGR-09-15: wood, MA-Fungi 81550 (Lado 19823). MGR-09-52: wood, MA-Fungi 81803 (Lado 20102).

This species has been reported previously from Egypt and the Seychelles and also from La Réunion (Adamonyte et al. 2011) and Equatorial Guinea (Lado and Teyssiere 1998).

**Collaria arcyrionema* (Rostaf.) Nann.-Bremek. ex Lado 3 fc, 12 mc, 5 loc, 4 subs

MGR-09-11: wood, MA-Fungi 81649 (Lado 19926). MGR-09-27: twigs, (mc, pH 6.4), aet 12045. MGR-09-30: *Euphorbia* sp. twigs, MA-Fungi 81486 (Lado 19756). MGR-09-39: *Euphorbia* sp. ground litter, (mc, pH 8.6), aet 12057. MGR-09-46: wood, MA-Fungi 81735 (Lado 20027).

**Comatricha elegans* (Racib.) G. Lister MGR-09-31: *Euphorbia* sp. litter, (mc, pH 5.1), dwb 3352.

**Comatricha nigra* (Pers. ex J.F. Gmel.) J. Schröt. MGR-09-27: aerial litter, (mc, pH 6.37), sls 23255.

**Comatricha pulchella* (C. Bab.) Rostaf. 4 fc, 15 mc, 10 loc, 6 subs

MGR-09-05: wood, MA-Fungi 81442 (Lado 19710). MGR-09-10: leaf litter, MA-Fungi 81519 (Lado 19790). MGR-09-27: aerial litter, (mc, pH 6.37), sls 23255. MGR-09-42:

ground litter, (mc, pH 4.83), sls 23258. MGR-09-53: *Pinus patula* needles, MA-Fungi 81826 (Lado 20128).

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

MGR-09-31: wood, MA-Fungi 81661 (Lado 19939); *Euphorbia* sp. litter, (mc, pH 5.6), dwb 3378. MGR-09-55: wood, MA-Fungi 81870 (Lado 20178); twigs, MA-Fungi 81873 (Lado 20181).

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

MGR-09-39: *Euphorbia* sp. twigs, MA-Fungi 81698 (Lado 19987). MGR-09-50: leaf litter, MA-Fungi 81796 (Lado 20090).

Material of this species from Madagascar, is cited by Ndiritu et al. (2009) from the UARK database.

*Craterium cf. minutum (Leers) Fr.

MGR-09-15: living grass, MA-Fungi 81552 (Lado 19824).

The doubt on the identity of this collection stems from the fact that the sporocarps are old and weathered and it was not possible to confirm some characters. However this is a common species and is probably present in Madagascar.

*Cribraria cancellata (Batsch) Nann.-Bremek.

MGR-09-47: wood, MA-Fungi 81759 (Lado 20053). MGR-09-53: wood of *Pinus patula*, MA-Fungi 81823 (Lado 20125), MA-Fungi 81825 (Lado 20127), MA-Fungi 81827 (Lado 20129), MA-Fungi 81829 (Lado 20131).

*Cribraria microcarpa (Schrad.) Pers.

MGR-09-05: liana bark, (mc, pH 5.7), dwb 3180. MGR-09-14: aerial litter, (mc, pH 5.1), sls 23255. MGR-09-25: ground litter, (mc, pH 6.5), sls 23496. MGR-09-12: twig, MA-Fungi 81535 (Lado 19806). MGR-09-54: liana wood, MA-Fungi 81843 (Lado 20144b). MGR-09-55: wood, MA-Fungi 81890 (Lado 20199b).

*Cribraria minutissima Schwein. Figures 11-13.

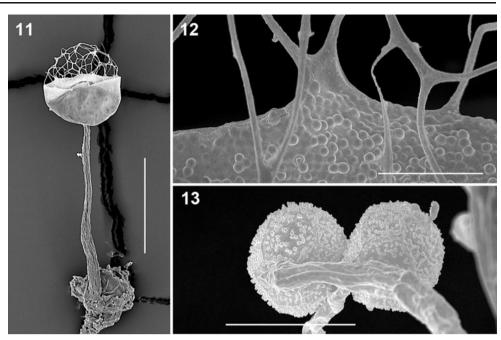
MGR-09-20: liana bark, (mc, pH 4.6), dwb 3305. MGR-09-22: twigs, (mc, pH 5.22), aet 12049, (mc, pH 5.13), aet 12051 (mc, pH 5.58), aet 12069.

Specimen dwb 3305 showed the typical peridial net (Figs. 11, 12) of this species with no granular inclusions or thickened nodes, and small spores (Fig. 13). The samples from locality 22 had larger spores than usual (8.5–11.0 μ m vs. 6.5–8 μ m diam), but in every other respect the characters coincide with the description given in Keller et al. (1988).

* Cribraria violacea Rex

MGR-09-15: liana bark, (mc, pH 6.7), dwb 3185. MGR-09-22: *Pachypodium* sp. remains, MA-Fungi 81580 (Lado 19854). MGR-09-27: ground litter, (mc, pH 6.37), sls 23527. MGR-09-33: ground litter, (mc, pH 7.3), sls 23528. MGR-09-34: *Euphorbia* sp. litter, (mc, pH 7.7), dwb 3345.

Fig. 11–13 *Cribraria minutissima* (dwb 3305) by SEM 11. Whole sporocarp showing the peridial net without thickened nodes 12. Detail of inner surface of calyculus with granules 13. Spores. Bar: $11=300 \mu m$; $12=20 \mu m$; $13=10 \mu m$



*Diachea bulbillosa (Berk. & Broome) Lister

MGR-09-25: ground litter, (mc, pH 7.03), sls 23251. MGR-09-42: ground litter, (mc, pH 6.14), sls 23243.

In Africa previously reported from Liberia and the Seychelles.

*Diachea leucopodia (Bull.) Rostaf.

MGR-09-11: leaf litter, (mc, pH 5.3), dwb 3331. MGR-09-18: *Eucalyptus* sp. litter, MA-Fungi 81574 (Lado 19849).

**Diderma deplanatum* Fr. 18 fc, 0 mc, 4 loc, 4 subs MGR-09-05: leaves, MA-Fungi 81534 (Lado 19805). MGR-09-08: leaf litter, MA-Fungi 81450 (Lado 19719). MGR-09-10: leaf litter, MA-Fungi 81466 (Lado 19735). MGR-09-11: wood, MA-Fungi 81487 (Lado 19757); living herbs, MA-Fungi 81495 (Lado 19764).

In Africa, this species has only been reported previously from Equatorial Guinea (Lado and Teyssiere 1998) and from Tanzania.

Diderma effusum (Schwein.) Morgan 10 fc, 8 mc, 11 loc, 7 subs

MGR-09-06: ground litter, (mc, pH 5.6), sls 23254. MGR-09-12: leaf litter, MA-Fungi 81502 (Lado 19772). MGR-09-28: *Cocos nucifera* leaves, MA-Fungi 81613 (Lado 19888). MGR-09-37: *Aloe* sp. remains, MA-Fungi 81691 (Lado 19975). MGR-09-44: ground litter, (mc, pH 5.4), sls 23235.

Material of this species from Madagascar is cited by Ndiritu et al. (2009) from the UARK database.

Diderma hemisphaericum (Bull.) Hornem. 3 fc, 4 mc, 6 loc, 5 subs

MGR-09-08: leaf litter, MA-Fungi 81459 (Lado 19728). MGR-09-14: ground litter, (mc, pH 6.4), sls 23225. MGR-09-37: *Kalanchoe* sp. litter (mc, pH 7.0), dwb 3231. MGR-09-50: ground litter, (mc, pH 6.1), sls 23245. MGR-09-53: *Pinus patula* needles, MA-Fungi 81830 (Lado 20132).

Material of this species from Madagascar, is cited by Ndiritu et al. (2009) from the UARK database.

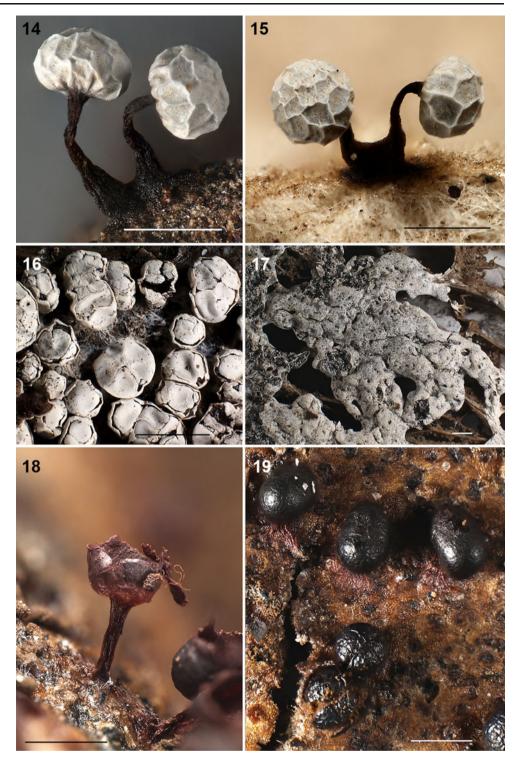
†Diderma rimosum Eliasson & Nann.-Bremek. Figures 16, 20, 22

MGR-09-08: leaf litter, MA-Fungi 81452 (Lado 19721).

The large, typical collection of this unusual species, originally described from the Galápagos Islands, has crowded sessile sporocarps on a calcareous white hypothallus, with a wrinkled ridged peridium that falls apart into polygonal plates (Fig. 16). The peridium is impregnated with amorphous lime granules (Fig. 20) and the spores are $10-11 \mu m$ diam. and irregularly ornamented with short pila by SEM (Fig. 22). It has also been previously reported from Mexico (Lado et al. 2003). This is the first record of the species for Africa and considerably extends its distribution.

**Diderma rugosum* (Rex) T. Macbr. Figures 14, 15, 21, 23. MGR-09-50: *Kalanchoe* sp. litter, (mc, pH 6.9), dwb 3259.

This collection of typical specimens with stalked sporocarps, the sporotheca giving a polygonal appearance due to preformed ridges (Figs. 14, 15) where dehiscence occurs, and black stalks. By SEM the spores are regularly warted (Fig. 23) and the peridial plates are covered with amorphous lime granules (Fig. 21). In Africa reported previously from Tanzania. Fig. 14–15 Diderma rugosum (dwb 3259) Sporocarps showing the black noncalcareous stipe and ridged sporotheca. 16. Diderma rimosum (Lado 19721) sporocarps from above. 17. Fuligo intermedia (Lado 19831) aethalia. 18–19 Perichaena pulcherrima (Lado 19927) 18. Sporocarp lateral view. 19. Sporocarps from above. Bar: 14–15, 18– 19=0.5 mm; 16–17=1 mm



*Diderma testaceum (Schrad.) Pers.

MGR-09-08: leaf litter, MA-Fungi 81453 (Lado 19722).

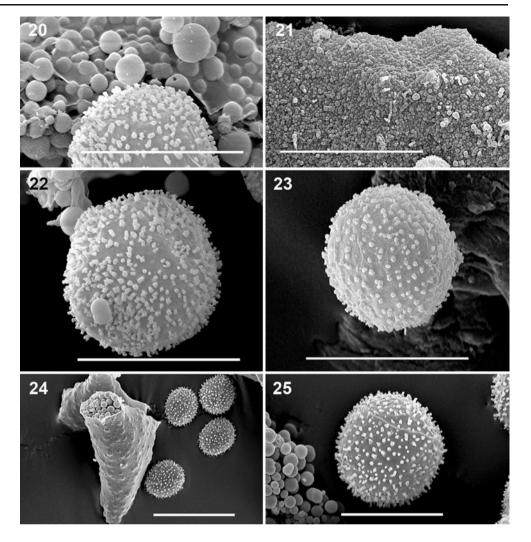
In Africa this species has only been reported previously from the North in Algeria and Morocco.

*Didymium cf. anellus Morgan

MGR-09-10: leaf litter, MA-Fungi 81467 (Lado 19736).

Macroscopically this collection fits the concept of the species except for the presence of areolae on the peridium, a character not previously mentioned in the literature.

*Didymium bahiense Gottsb. 13 fc, 0 mc, 6 loc, 2 subs MGR-09-04: *Hedychium coronarium* inflorescence, MA-Fungi 81420 (Lado 19689). MGR-09-07: *Hedychium* Fig. 20-25 SEM images 20. Diderma rimosum (Lado 19721) Detail of lime granules in peridium. 21. Diderma rugosum (dwb 3259) Peridium covered with amorphous lime granules. 22. Diderma rimosum (Lado 19721) Spore. 23. Diderma rugosum (dwb 3259) Spore. 24. Fuligo intermedia (Lado 19831) node of capillitium containing lime granules 25. Fuligo intermedia (Lado 19831) Spore. Bar: 20, 22-23, 25=10 µm; 21=30 µm; 24=20 µm



coronarium inflorescence, MA-Fungi 81445 (Lado 19714). MGR-09-10: leaf litter, MA-Fungi 81529 (Lado 19800). MGR-09-44: leaf litter, MA-Fungi 81708 (Lado 19996). MGR-09-56: *Hedychium coronarium* inflorescence, MA-Fungi 81882 (Lado 20192).

*Didymium clavus (Alb. & Schwein.) Rabenh.

MGR-09-28: leaf litter, MA-Fungi 81616 (Lado 19891), MA-Fungi 81622 (Lado 19897), MA-Fungi 81623 (Lado 19898), MA-Fungi 81626 (Lado 19901).

*Didymium difforme (Pers.) Gray

MGR-09-14: aerial litter, (mc, pH 6.76), sls 23217, (mc, pH 6.25), sls 23218, (mc, pH 7.1), sls 23219, (mc, pH 6.38), sls 23228, (mc, pH 6.05), sls 23233.

*Didymium intermedium J. Schröt.

MGR-09-15: leaf litter, MA-Fungi 81548 (Lado 19820).

This poorly developed collection with calcareous stipes and spiny to sub-reticulate spores agrees with the description given in Martin and Alexopoulos (1969: 387). Only previously reported in Africa from the Seychelles.

*Didymium iridis (Ditmar) Fr.

MGR-09-01: Aloe sp. leaf litter, MA-Fungi 81407 (Lado 19674).

This collection has sporocarps with a clavate columella, and so would fall under what Nannenga-Bremekamp (1972) maintained as *Didymium proximum* Berk. & M.A. Curtis.

Didymium leoninum Berk. & Broome

MGR-09-08: leaf litter, MA-Fungi 81456 (Lado 19725). MGR-09-10: twigs, MA-Fungi 81463 (Lado 19732); leaf litter MA-Fungi 81522 (Lado 19793); leaves, MA-Fungi 81524 (Lado 19795), MA-Fungi 81526 (Lado 19797), MA-Fungi 81528 (Lado 19799).

A collection from Andasibe, Madagascar that is conserved at PC (97614) was published in Poulain et al. (2011).

†Didymium listeri Massee

MGR-09-16: *Hedychium coronarium* inflorescence, MA-Fungi 82089 (Lado 19830). MGR-09-50: *Aloe* sp.

leaf litter, (mc, pH 6.7), dwb 3237, (mc, pH 6.6), dwb 3241.

The material is of small collections composed of short plasmodiocarps with a shell-like outer peridium made of closely aggregated crystals. The capillitium is pale and not elastic. The spores are $8-11 \mu m$ diam. covered with very fine warts, smaller and paler than in *D. dubium*, which this species resembles. First records for Africa.

*Didymium nigripes (Link) Fr. 12 fc, 0 mc, 10 loc, 5 subs MGR-09-02: leaf litter, MA-Fungi 81411 (Lado 19680). MGR-09-04: *Musa paradisiaca* leaves, MA-Fungi 81507 (Lado 19777). MGR-09-11: living herbs, MA-Fungi 81494 (Lado 19764). MGR-09-47: woody fruits, MA-Fungi 81773 (Lado 20064). MGR-09-53: *Eucalyptus* sp. twigs and leaves, MA-Fungi 81824 (Lado 20126).

**Didymium ochroideum* G. Lister 3 fc, 11 mc, 7 loc, 7 subs MGR-09-27: twigs, (mc, pH 6.4), aet 12066. MGR-09-34: *Agave* sp. remains, MA-Fungi 81685 (Lado 19968). MGR-09-36: *Adansonia grandidieri* bark, (mc, pH 6.8), dwb 3386. MGR-09-37: *Euphorbia* sp. litter, (mc, pH 7.4), dwb 3372. MGR-09-50: ground litter, (mc, pH 6.1), sls 23246.

In Africa, only previously reported from Kenya.

*Didymium pertusum Berk.

MGR-09-14: ground litter, (mc, pH 6.99), sls 23210. MGR-09-37: *Kalanchoe* sp. litter, (mc, pH 7.0), dwb 3232. MGR-09-42: ground litter, (mc, pH 5.4), sls 23213. MGR-09-50: ground litter, (mc, pH 6.25), sls 23221.

In Africa this species has only been reported previously from La Réunion (Adamonyte et al. 2011).

*Didymium squamulosum (Alb. & Schwein.) Fr.

MGR-09-15: leaf litter, MA-Fungi 81542 (Lado 19813). MGR-09-25: ground litter, (mc, pH 6.68), sls 23234; aerial litter, (mc, pH 5.98), sls 23253.

*Didymium trachysporum G. Lister

MGR-09-34: *Euphorbia* sp. twigs, MA-Fungi 81679 (Lado 19959). MGR-09-38: *Agave* sp. remains, MA-Fungi 81694 (Lado 19978).

The collections have spores $9-10 \ \mu m$ diam. with dispersed but prominent spinules with a broad base that are pyramid–shaped in optical section. These represent the first records of this species for Africa.

*Didymium verrucosporum A.L. Welden

MGR-09-05: leaf litter, MA-Fungi 81429 (Lado 19696).

This collection has a delicate colorless peridium, a white pseudocolumella and spores that are dark violaceous brown and densely ornamented with warts and groups of darker warts. In the stipe and shape of the sporocarps it is similar to *D. nigripes*. In Africa previously reported from Malawi and the Seychelles.

†Echinostelium apitectum K.D. Whitney

MGR-09-29: liana bark, (mc, pH 6.8), dwb 3193. MGR-09-33: *Euphorbia* sp. bark, (mc, pH 5.8), dwb 3226, (mc, pH 6.0), dwb 3229.

Small collections of dispersed, erect, greyish pink sporocarps with the typical spore-like body and collar. These represent the first records of this species for Africa.

†*Echinostelium arboreum* H.W. Keller & T.E. Brooks MGR-09-33: *Adansonia grandidieri* bark, (mc, pH 7.0), dwb 3194. MGR-09-36: *Adansonia grandidieri* bark, (mc, pH 6.7), dwb 3358.

The plentiful collections have a shiny persistent peridium and are yellow when fresh, fading to a pink-white when dried. These features and the wide collar make it an easily recognised species. These represent the first records of this species for Africa.

**Echinostelium colliculosum* K.D. Whitney & H.W. Keller 0 fc, 6 mc, 5 loc, 3 subs

MGR-09-18: *Aloe* sp. dead leaves, (mc, pH 7.1), dwb 3329. MGR-09-27: *Euphorbia stenoclada* bark, (mc, pH 7.1), dwb 3198. MGR-09-33: *Adansonia grandidieri* bark, (mc, pH 6.9), dwb 3203. MGR-09-36: *Adansonia grandidieri* bark, (mc, pH 6.8), dwb 3355. MGR-09-38: *Adansonia grandidieri* bark, (mc, pH 7.1), dwb 3234.

Only previously reported in Africa from Tunisia and Tanzania.

**Echinostelium minutum* de Bary 0 fc, 8 mc, 5 loc, 6 subs MGR-09-18: *Aloe* sp. dead leaves, (mc, pH 7.1), dwb 3329. MGR-09-20: small savannah tree bark, (mc, pH 4.6), dwb 3288. MGR-09-27: *Euphorbia stenoclada* bark, (mc, pH 7.2), dwb 3195; twigs, (mc, 6.2), aet 12047. MGR-09-49: *Uapaca bojerii* leaf litter, (mc, pH 4.5), dwb 3263.

**Fuligo intermedia* T. Macbr. 3 fc, 9 mc, 4 loc, 2 subs Figs. 17, 24, 25.

MGR-09-17: *Opuntia* sp. remains, MA-Fungi 81557 (Lado 19831), MA-Fungi 81559 (Lado 19833). MGR-09-33: *Adansonia grandidieri* wood, (mc, pH 8.5), aet 12059. MGR-09-36: *Adansonia grandidieri* bark, (mc, pH 6.7), dwb 3385. MGR-09-38: *Adansonia grandidieri* bark, (mc, pH 7.1), dwb 3264.

All the aethalia in these collections were covered with varying thicknesses of crusted lime (Fig. 17). The capillitium is of large angular lime nodes packed with granules (Fig. 24), and the spores by SEM are globose to slightly ovate and spinulose (Fig. 25). In Africa previously reported from Sierra Leone.

*Fuligo megaspora Sturgis

MGR-09-44: leaf litter, MA-Fungi 81707 (Lado 19996), MA-Fungi 81733 (Lado 20025).

In Africa previously reported from Morocco.

Fuligo septica (L.) F.H. Wigg.

MGR-09-18: *Aloe* sp. remains, MA-Fungi 81565 (Lado 19839). MGR-09-47: leaf litter, MA-Fungi 81752 (Lado 20047). MGR-09-53: *Pinus patula* wood, MA-Fungi 81828 (Lado 20130).

Previously reported in Madagascar from Maromandia (Patouillard 1928).

**Hemitrichia calyculata* (Speg.) M.L. Farr 32 fc, 0 mc, 11 loc, 6 subs

MGR-09-02: *Pinus patula* bark, MA-Fungi 81414 (Lado 19683). MGR-09-03: *Eucalyptus* sp. wood, MA-Fungi 81416 (Lado 19685). MGR-09-15: wood, MA-Fungi 81544 (Lado 19815). MGR-09-44: *Dypsis isaloensis* leaf litter, MA-Fungi 81723 (Lado 20012). MGR-09-54: dead liana bark, MA-Fungi 81850 (Lado 20153).

Hemitrichia serpula (Scop.) Rostaf. ex Lister 30 fc, 0 mc, 6 loc, 4 subs

MGR-09-05: *Ravenala madagascariensis* leaf litter, MA-Fungi 81427 (Lado 19694). MGR-09-44: *Dypsis isaloensis* palm leaf, MA-Fungi 81724 (Lado 20013). MGR-09-46: wood, MA-Fungi 81739 (Lado 20031). MGR-09-47: liana, MA-Fungi 81761 (Lado 20055). MGR-09-52: wood, MA-Fungi 81816 (Lado 20118).

This species has been reported previously in Madagascar from Mayotte (Patouillard 1928).

†Lamproderma collinsii T.N. Lakh. & K.G. Mukerji

MGR-09-44: wood, MA-Fungi 81734 (Lado 20026).

The collection has the remains of the peridium as a collar around the stalk and the columella reaches half of the sporotheca diameter, ending abruptly in the primary capillitial branches. The capillitium is undulate, branched and anastomosed. Although the collection is not in perfect condition these characters suggest this species. This collection is the first record for Africa.

*Lamproderma scintillans (Berk. & Broome) Morgan MGR-09-25: Kalanchoe leaves, MA-Fungi 81590 (Lado 19863); aerial litter, (mc, pH 6.9), sls 23236. MGR-09-33: Euphorbia sp. twigs, MA-Fungi 81674 (Lado 19952). MGR-09-44: Tamarindus indica litter, (mc, pH 7.3), dwb 3248. MGR-09-50: ground litter, (mc, pH 6.1), sls 23244.

*Licea biforis Morgan

MGR-09-39: *Euphorbia* sp. litter, (mc, pH 8.6), aet 12038, (mc, pH 8.4), aet 12039, (mc, pH 8.6), aet 12063.

†Licea eleanorae Ing

MGR-09-20: small savannah tree bark, (mc, pH 5.1), dwb 3289.

This very characteristic species has solitary stipitate sporocarps with a cap of birefringent crystals on the upper third of the sporotheca. Described from Switzerland (Ing 1999), it has been found in other European countries but this collection is the first record of the species for Africa.

*Licea kleistobolus G.W. Martin

MGR-09-20: small savannah tree bark, (mc, pH 4.6), dwb 3290, (mc, pH 5.1), dwb 3311, dwb 3313.

†Licea minima Fr.

MGR-09-47: liana, MA-Fungi 81764 (Lado 20057).

This is the first record for Africa, although it has previously been reported from the Canary Islands.

*Licea nannengae Pando & Lado Figs. 26-30.

MGR-09-36: *Adansonia grandidieri* bark, (mc, pH 6.8), dwb 3357. MGR-09-38: *Adansonia grandidieri* bark, (mc, pH 7.1), dwb 3225, (mc, pH 7.0), dwb 3233.

These collections represent the second record of this minute species for Africa. It has been reported from Tanzania. Described originally from Spain (Pando and Lado 1988) as having smooth spores, SEM analysis has shown the spores of the type specimen to be ornamented with evenly distributed pila (Fig. 29), obvious even at low magnification by SEM (Fig. 26). The spores appear smooth by LM, however, and even with Nomarski optics the ornamentation is only just discernable. SEM images show that the moist chamber specimens from baobab bark have the same ornamentation on the spores as the type specimen (Fig. 30), and a smooth surface to the inner peridium by LM, as in the original description. However the inner peridium by SEM is seen to be very finely warted and the peridium is double, both in the type specimen (Fig. 27) and the Malagash specimen (Fig. 28).

*Licea pseudoconica T.E. Brooks & H.W. Keller

MGR-09-33: *Adansonia grandidieri* bark, (mc, pH 7.0), dwb 3196. MGR-09-38: *Adansonia grandidieri* bark, (mc, pH 7.0), dwb 3235.

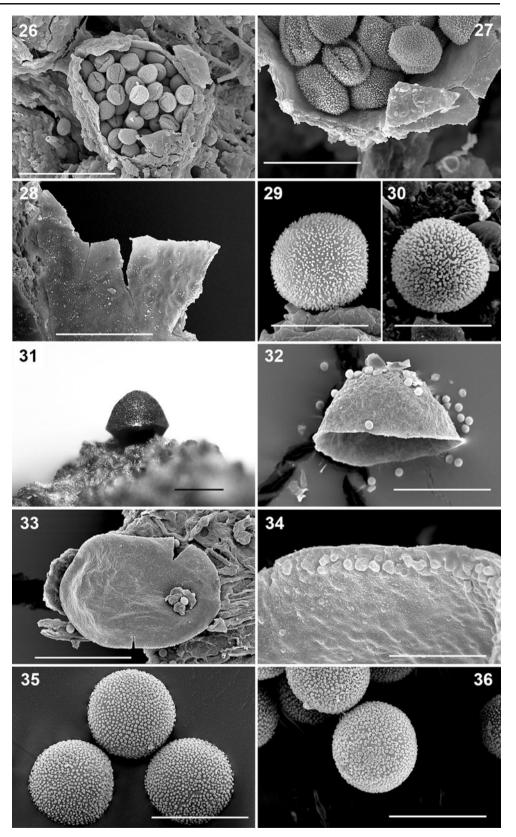
Only previously reported in Africa from Tanzania.

†Licea rufocuprea Nann.-Bremek. & Y. Yamam. Figures 31–36.

MGR-09-14: Eucalyptus sp. bark, (mc, pH 5.2), dwb 3291.

This is a rare species described originally from Japan on bark (Nannenga-Bremekamp and Yamamoto 1987). The chestnut-brown, shiny, sessile sporocarps are subconical on a wider base (Fig. 31) with a translucent margin to the area of dehiscence. The dehiscence of the

Fig. 26–30 Licea nannengae SEM images. 26. Whole sporocarp showing dehiscence into platelets (Holotype, MA-Fungi 16056). 27. Detail of open sporocarp showing inner surface of double peridium (Holotype MA-Fungi 16056). 28. Detail of inner surface of double peridium (dwb 3225). 29. Spore (Holotype MA-Fungi 16056). 30. Spore (dwb 3225). 31-36. Licea rufocuprea (dwb 3291). 31. Whole sporocarp with shiny circumscissile ring. 32. Upper peridium dehisced whole as a conical cap. 33. Shallow concave base of peridium. 34. Detail of lightly warted inner surface of the peridium with prominent peg-like warts close to the edge of dehiscence. 35–36. Spores with flattened warts. Bar: 26=50 µm; 27-28= 20 µm; 29–30, 34–36=10 µm; 31=100 µm; 32-33=100 µm



double peridium is circumscissile near the base of the sporotheca, the whole upper part lifting off like a small conical cap (Fig. 32) with a slightly revolute margin.

This leaves a shallow concave base (Fig. 33). The inner edge of the peridium at the point of dehiscence on both the cap and the base is ornamented on the inner surface

with peg-like warts (Fig. 34), and the rest of the inner surface is minutely warted by SEM. The spores are dark brown in mass, pale rosy brown by transmitted light and 10–11.5 μ m diam., appearing slightly roughened by LM with Nomarski, but warted with flattened warts by SEM (Figs. 35–36). Adamonyte et al. (2011) reported an unconfirmed collection from La Réunion, but this collection from Madagascar represents the first confirmed record of the species for Africa.

†*Licea succulenticola* Mosquera, Lado, Estrada & Beltrán-Tej. MGR-09-18: *Aloe* sp. dead leaves, (mc, pH 7.1), dwb 3402. MGR-09-22: *Aloe* sp. dead leaves, (mc, pH 6.7), dwb 3344. MGR-09-30: *Euphorbia* sp. ground litter, (mc, pH 8.1), aet 12089b. MGR-09-39: *Euphorbia* sp. ground litter, (mc, pH 8.6), aet 12098, (mc, pH 8.4), aet 12099, (mc, pH 8.6), aet 12101.

This is the first record of this species for Africa, although it was described from the Canary Islands and Mexico (Mosquera et al. 2003). These endemic substrates confirm the preference of this species for succulent plants.

†Macbrideola argentea Nann.-Bremek. & Y. Yamam.

MGR-09-14: *Eucalyptus* sp. bark, (mc, pH 5.2), dwb 3308. MGR-09-20: Small savannah tree bark, (mc, pH 4.6), dwb 3306. MGR-09-45: *Pandanus amoagensis* bark, (mc, pH 6.8), dwb 3202.

The silver iridescent persistent peridium of this small species makes it easy to identify. It looks like a miniature *Lamproderma*, but differs in its hollow base to the stalk and the capillitium with very few anastomoses. It has been reported previously from the type locality in Japan (Nannenga-Bremekamp and Yamamoto 1983). These are the first records of this species for Africa.

*Metatrichia horrida Ing 17 fc, 0 mc, 4 loc, 3 subs

MGR-09-44: *Dypsis isaloensis* palm leaf, MA-Fungi 81722 (Lado 20011). MGR-09-47: wood, MA-Fungi 81748 (Lado 20043), MA-Fungi 81754 (Lado 20049). MGR-09-54: liana, MA-Fungi 81832(Lado 20135). MGR-09-46: wood, MA-Fungi 81738 (Lado 20030).

**Perichaena chrysosperma* (Curr.) Lister 11 fc, 3 mc, 6 loc, 7 subs

MGR-09-27: *Euphorbia* sp. twigs, MA-Fungi 81600 (Lado 19875). MGR-09-28: *Cocos nucifera* leaves, MA-Fungi 81621 (Lado 19896). MGR-09-32: *Aluaudia procera* remains, MA-Fungi 81669 (Lado 19948). MGR-09-44: wood, MA-Fungi 81718 (Lado 20006). MGR-09-50: *Kalanchoe* sp. litter, (mc, pH 6.9), dwb 3238.

*Perichaena corticalis (Batsch) Rostaf.

MGR-09-30: *Euphorbia* sp. ground litter, (mc, pH 8.1), aet 12090.

**Perichaena depressa* Lib. 9 fc, 4 mc, 10 loc, 10 subs MGR-09-22: *Pachypodium* sp. remains, MA-Fungi 81581 (Lado 19854). MGR-09-23: *Aloe* sp. remains, MA-Fungi 81583 (Lado 19856). MGR-09-27: ground litter, (mc, pH 6.4), sls 23248, twigs, (mc, pH 6.2), aet 12140. MGR-09-44: liana bark, MA-Fungi 81712 (Lado 20000). MGR-09-55: liana bark, MA-Fungi 82093 (Lado 20169).

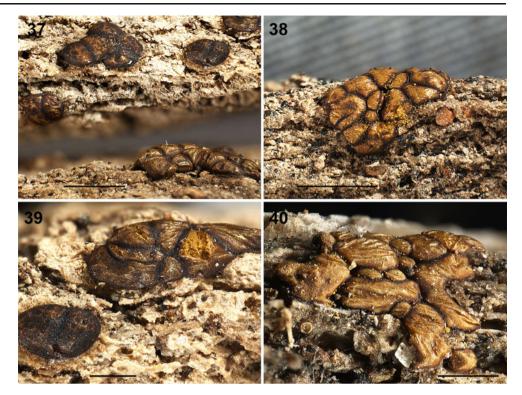
†Perichaena luteola (Kowalski) Gilert

MGR-09-26: *Opuntia* sp. remains, MA-Fungi 82094 (Lado 19865). MGR-09-29: *Opuntia* sp. remains, MA-Fungi 81730 (Lado 19905), MA-Fungi 81733 (Lado 19909).

This species was described originally as *Calonema luteolum* Kowalski from California (USA) on cow dung. It is recognizable by the golden yellow color of the heaped sporocarps, the iridescent and translucent peridium, the capillitium in the form of a reticulum and the spinulose spores of 12–13 μ m diam. (Kowalski 1969). Gilert (1995) clarified the taxonomic identity of the species and ascribed it to the genus *Perichaena* based on the perforate capillitial threads. We agree with this decision. This is the first record of this species for Africa.

Perichaena madagascariensis D. Wrigley, Lado, Estrada & S.L. Stephenson, **sp. nov.** Figures 37–40, 41–51 Mycobank: MB 800244

Sporophores sporocarpic, crowded, polygonal from mutual contact, in groups of 4-50 sporocarps, occasionally single or in pairs, sessile. Sporotheca pulvinate, 0.1-0.8 mm diam., 0-02-0.05 mm tall, yellow (88. d. y - 95. m. OL Br) to deep yellow brown (77. m. y. Br - 78. d. y Br), sometimes with darker areas on the surface (Fig. 37) and often with dark lines of thicker refuse material marking the junction of the upper peridium to the lower around the area of dehiscence (Figs. 37-39), and at the points of contact between sporocarps. Hypothallus inconspicuous, common to a group of sporocarps. Peridium double, outer layer wrinkled, with very little granular material, translucent, vellow (74. s. y Br), to yellowish brown (77. m. y Br) by transmitted light on the upper surface, usually darker below; inner layer membranous, translucent, yellowish (89. p. y -86. l. Y), strongly adhered to the external layer, with the inner surface finely warted and crossed with narrow furrows by SEM (Figs. 41, 42), sometimes marked with spore impressions; dehiscing along a preformed darker line around the circumference (Figs. 38, 39), the upper portion of the peridium breaking up irregularly, leaving a shallow cup-like base (Fig. xx). Columella absent. Capillitium tubular, tubules of irregular diameter, 2-3 (-5) μ m diam., pale yellow (86. l. Y - 84. s. Y) by LM, sparse, simple or branched, usually perforated by SEM, ornamentation very irregular, from massed nodules in (younger) tubules attached to the peridium (Figs. 42-43), to warted with furrows Fig. 37–40 Perichaena madagascariensis 37. Three groups of sporocarps on *Euphorbia* sp. showing the peridium with dark inclusions (dwb 3333). 38. Group of sporocarps with few inclusions on the peridium showing shiny surface (dwb 3333). 39. Detail of open sporocarp and dark lines at point of contact between the sporocarps (dwb 3333). 40. Group of flattened sporocarps (Holotype, MA-Fungi 82091)



(Figs. 45–46), or very perforate with irregular larger warts on the surface (Figs. 44, 47). Spores free, vivid yellow (82. v. Y- 88. d. Y) in mass, mid yellow (87. m. Y) to deep yellow (88. d. Y) by LM, sub-globose, 10-12.5 (-13) µm diam., densely warted, with prominent pila by SEM, up to 0.5 µm tall (Figs. 48–51). Plasmodium yellow.

HOLOTYPE. MADAGASCAR. Toliará (Androy): Ambovombe, RN-13 road from Ambovombe to Betroka, 39 km N of Ambovombe, SE of village Ambaliandra, 25° 01'46"S 45°49'37"E, 154±3 m, tropical dry forest with succulents, on twigs of *Euphorbia* sp., leg. 18-V-2009, *C. Lado, A. Estrada* and *D. Wrigley de Basanta*, Lado 19981 (MA-Fungi 82091)

Etymology: The epithet *madagascariensis* refers to the geographic area where the species was found.

Habitat: Twigs, stem and litter of *Euphorbia* spp. Known distribution: Southern Madagascar dry forests.

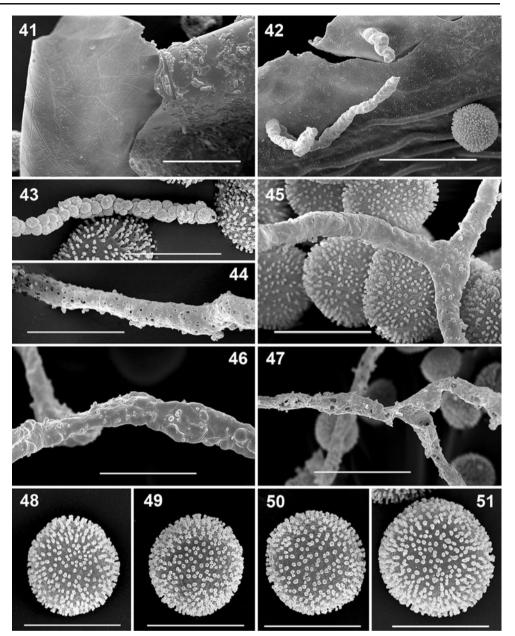
Other specimens examined:

MGR-09-33: Ground litter, (mc, pH 7.6), sls 23205, (mc, pH 7.3), sls 23207. MGR-09-34: *Euphorbia* sp. litter, (mc, pH 7.8), dwb 3333, (mc, pH 7.6), dwb 3337, (mc, pH 7.7), dwb 3340; *Euphorbia* sp. stem, MA-Fungi 82090 (Lado 19964), MA-Fungi 61682 (Lado 19963). MGR-09-35: *Euphorbia* sp. ground litter, (mc, pH 8.1), aet 12080, (mc, pH 8.2), aet 12139. MGR-09-37: *Euphorbia* sp. litter, (mc, pH 7.1), dwb 3362, (mc, pH 7.4), dwb 3365, (mc, pH 7.0), dwb 3368. MGR-09-39: *Euphorbia* sp. ground litter, (mc, pH 6.8), aet

12076, (mc, pH 7.3), aet 12077, (mc, pH 7.4), aet 12078, (mc, pH 8.6), aet 12100.

The characters that distinguish this species from others in the genus are the combination of closely packed sporocarps with a circumscissile dehiscence and sparse uniquely ornamented capillitium. It is most like Perichaena liceoides Rostaf., a synonym of Perichaena corticalis (Batsch) Rostaf., because of the scant capillitium, but P. madagascariensis differs in that it does have some fully formed capillitium (Figs 43–47), it has a circumscisile dehiscence and slightly larger spores (10-13 µm vs. 9.2-10 µm diam.) with an ornamentation by SEM of prominent pila. The new species also differs in the substrate since P. liceoides is predominently coprophilous (Gilert 1990). The new species seems to fall between Perichaena liceoides and P. luteola (Kowalski) Gilert, another coprophilous myxomycete, frequently found on succulent plants in arid areas of Mexico (Estrada-Torres et al. 2009), from which it differs in the absence of capillitium in the form of a distinct network arising from the base, in having a double peridium, not a membranous transparent single peridium like P. luteola, and spores with denser different ornamentation by SEM. In addition, the capillitial tubules of the new species are covered with irregular warts, not smooth as in P. luteola and the sporocarps are crowded but not heaped as in P. luteola.

Perichaena madagascariensis has some fully developed capillitium, and so it differs from the two new species of Perichaena without capillitium, P. heterospinispora Novozh., Zemly., Schnittler & S. L. Stephenson and P. Fig. 41–51 Perichaena madagascariensis by SEM 41. Inner surface of the peridium (dwb 3333). 42. Inner surface of the peridium (Lado 19981). 43. Hollow capillitial tubules with massed nodules (Lado 19983). 44. Perforate capillitium with minutely warted surface (dwb 3337). 45. Warted branched capillitium (dwb 3365). 46. Warted branched capillitium (dwb 3337). 47. Perforate branched capillitium of hollow tubules (dwb 3337). 48. Spore with prominent pila (dwb 3365). 49-50. Spore (Holotype, MA-Fungi 82091). 51. Spore (Lado 19983). Bar: 41-42, 47= 20 µm; 43-46, 48-51=10 µm



polygonyspora Novozh., Zemly., Schnittler & S. L. Stephenson, described by Novozhilov et al. (2008) from Russia and Kazakstan. In addition, the sporocarps of the two latter species are dispersed, sessile to stalked and have a totally unique ornamentation of the spores. The new species also differs from *Perichaena quadrata* Macbr. because of its more depressed habit, the type and irregular ornamentation of the capillitium, not marked with a reticulum of low bands (Figs 58–59), and the ornamentation of the inner peridium (Figs. 41–42, 56–57).

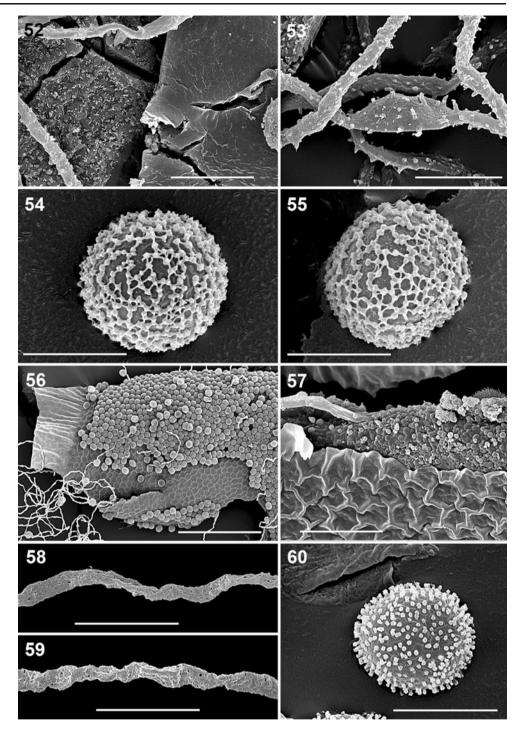
Perichaena madagascariensis was found in natural fruitings in the field, and also isolated from moist chamber cultures in a total of 18 collections from 5 different localities. Spore to spore culture of this species was unsuccessful, but a small collection (dwb 3216) was isolated from sclerotia, found on the substrate of collection Lado 19963, and placed on 2 % water agar in the dark. The orange sclerotium became activated in 24 h forming yellow veins of plasmodium. Fine sterile oat flour and water were added to the culture at intervals, and the plasmodium grew and formed 4 sporocarps over a month later. It is interesting to note that to date the new species has been found only on species of *Euphorbia* growing in the dry forests of southern Madagascar.

Perichaena pulcherrima Petch Figs. 18-19, 52-55

MGR-09-30: *Euphorbia* sp. twigs, MA-Fungi 81750 (Lado 19927).

These purple-red sporocarps with red-brown furrowed stalks are unmistakable (Figs. 18–19). The peridium is thick and double (Fig. 52). The capillitium by SEM is covered with spines (Fig. 53), and the spores are ornamented with a clear

Fig. 52–55 *Perichaena pulcherrima* (Lado 19927) SEM images **52.** Peridium. **53.** Capillitium. **54.** Spore. **55.** Spore. **56–60** *Perichaena quadrata* SEM images **56.** Peridium (Lado 20095). **57.** Peridium (Lado 20095). **57.** Peridium (Lado 20095). **57.** Capillitium (Lado 20095). **60.** Spore (Lado 20095). Bar: 52– 53, 57=20 μm; 56=100 μm; 54–55, 58–60=10 μm



reticulum (Figs. 54–55). This species was described from Sri Lanka (Petch 1909). A collection from Tsimbazaza, Madagascar, that is conserved at PC (97208) was published in Poulain et al. (2011). In Africa also reported from the Seychelles.

*Perichaena quadrata T. Macbr. Figs. 56-60

MGR-09-13: *Aloe* sp. remains, MA-Fungi 81537 (Lado 19808). MGR-09-33: *Adansonia grandidieri* bark, (mc, pH 7.0), dwb 3211. MGR-09-35: *Euphorbia* sp. ground litter,

(mc, pH 8.2), aet 12079. MGR-09-50: *Aloe* sp. remains, MA-Fungi 82095 Lado 20092. MGR-09-52: liana bark, MA-Fungi 82096 Lado 20114.

Some of the capillitium of these collections was not as strongly marked with a reticulum as shown and described by Keller and Eliasson (1992), possibly due to irregularities during the maturation of the specimen, but otherwise the spores, peridium and capillitium are typical of this species (Figs. 56–60), that has been commonly found in dry areas of the Americas (Estrada-Torres et al. 2009; Lado et al. 2011). In Africa only previously known from Tanzania.

*Perichaena vermicularis (Schwein.) Rostaf.

MGR-09-06: ground litter, (mc, pH 4.8), sls 23539. MGR-09-56: *Hedychium coronarium* inflorescence, MA-Fungi 81880 (Lado 20190b).

*Physarum album (Bull.) Chevall.

MGR-09-04: *Musa* sp. leaf litter, MA-Fungi 81419 (Lado 19688). MGR-09-05: bamboo shoots, MA-Fungi 81443 (Lado 19712). MGR-09-15: wood, MA-Fungi 81546 (Lado 19817). MGR-09-44: wood, MA-Fungi 81716 (Lado 20004). MGR-09-47: wood, MA-Fungi 81755 (Lado 20050).

*Physarum bivalve Pers.

MGR-09-15: leaf litter, MA-Fungi 81553 (Lado 19825). MGR-09-18: *Aloe* sp. remains, MA-Fungi 82097 (Lado 19838).

Physarum cinereum (Batsch) Pers.

MGR-09-04: *Hedychium coronarium* inflorescence, MA-Fungi 81421 (Lado 19689), MA-Fungi 81510 (Lado 19779). MGR-09-10: leaf litter, MA-Fungi 81531 (Lado 19802). MGR-09-39: liana ground litter, (mc, pH 7.8), aet 12088. MGR-09-50: leaf litter, MA-Fungi 81796 (Lado 20089), ground litter, (mc, pH 6.3), sls 23240.

Material of this species from Madagascar is cited by Ndiritu et al. (2009) from the UARK database.

**Physarum compressum* Alb. & Schwein. 12 fc, 7 mc, 13 loc, 9 subs

MGR-09-09: *Ravenala madagascariensis* inflorescence, MA-Fungi 81516 (Lado 19784). MGR-09-21: *Pandanus* sp. leaves, MA-Fungi 81578 (Lado 19853). MGR-09-33: aerial litter, (mc, pH 7.7), sls 23227. MGR-09-49: *Uapaca bojerii* leaf litter, (mc, pH 5.0), dwb 3274. MGR-09-46: *Dypsis isaloensis* leaves, MA-Fungi 81643 (Lado 20038).

†Physarum conglomeratum (Fr.) Rostaf.

MGR-09-10: *Pandanus* sp. leaves, MA-Fungi 81532 (Lado 19803). MGR-09-15: leaf litter, MA-Fungi 81554 (Lado 19827).

These collections are typical with sessile yellowish sporocarps on a broad base are in dense groups and often angular by mutual pressure. Normally found on leaves, one of these collections was on a species of *Pandanus*, a characteristic plant from Madagascar of probable ancient origin (Callmander and Laivao 2003). These represent the first records for Africa, although it has been reported from the Canary Islands.

*Physarum crateriforme Petch

MGR-09-33: liana, (mc, pH 6.9), dwb 3200; *Euphorbia* sp. bark (mc, pH 6.0), dwb 3230.

*Physarum decipiens M.A. Curtis

MGR-09-08: leaf litter, MA-Fungi 81515 (Lado 19783), MA-Fungi 81457 (Lado 19726). MGR-09-11: leaves, MA-Fungi 81485 (Lado 19755).

In Africa, it has been reported previously from Morocco, and is also known from the Canary Islands.

*Physarum dictyosporum G.W. Martin Figs. 71-75

MGR-09-39: *Euphorbia* sp. ground litter, (mc, pH 7.3), aet 12091, (mc, pH 7.4), aet 12094.

This species is macroscopically very similar to *P. echinosporum*, also found here, with a white double peridium (Fig. 71) packed with lime. The difference is that the latter species has spiny spores and *P. dictyosporum* on the other hand has a clearly reticulate ornamentation on the spores by LM, and this can be seen by SEM (Figs. 73) to be a network of connected pila with the expanded caput of several pila joined together. The capillitial nodes are large and packed with lime granules (Fig. 72). This species has only previously been reported in Africa from the Aldabra atoll (Ing and Hnatiuk 1981).

*Physarum didermoides (Pers.) Rostaf.

MGR-09-25: ground litter, (mc, pH 6.7), sls 23749. MGR-09-33: aerial litter, (mc, pH 7.9), sls 23262.

One collection (sls 23262) is typical for this species, whereas the other (sls 23749) consists of very limited material and is more problematic.

*Physarum echinosporum Lister 13 fc, 1 mc, 4 loc, 3 subs Figs. 61–62, 67–70

MGR-09-32: *Euphorbia stenoclada* remains, MA-Fungi 81665 (Lado 19943). MGR-09-33: *Euphorbia* sp. twigs, MA-Fungi 81671 (Lado 19950). MGR-09-34: *Euphorbia* sp. stem, MA-Fungi 61683 (Lado 19964), *Euphorbia* sp. ground litter (mc, pH 7.8) dwb 3334. MGR-09-39: *Euphorbia* sp. twigs, MA-Fungi 81695 (Lado 19982).

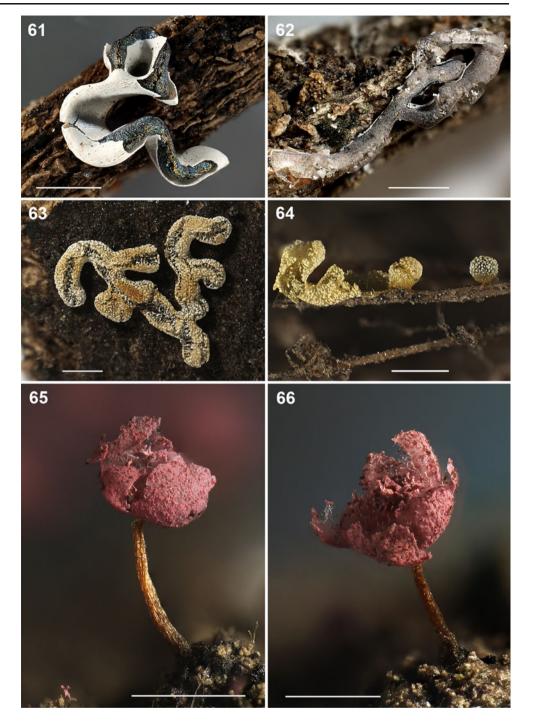
This unusual species (Figs. 61–62) with laterally compressed sinuous plasmodiocarps and a double peridium, the outher peridium white and packed with lime and the inner membranous and iridescent (Fig. 67), is very similar to *Physarum dictyosporum* (see comments above). Its spores, however, by SEM have separate pila without the tips joining together (Figs. 69–70) giving a spinulous appearance by LM, not an irregular reticulum like in *P. dictyosporum. Physarum echinosporum* has been reported previously from eastern and central Africa, and from the Aldabra atoll (Ing and Hnatiuk 1981).

*Physarum flavicomum Berk.

MGR-09-15: wood, MA-Fungi 81543 (Lado 19814).

In Africa, it has been reported previously from Angola, South Africa, Sierra Leone and is also known from Equatorial Guinea (Lado and Teyssiere 1998). Fig. 61 Physarum echinosporum plasmodiocarp (Lado 19950). 62. Physarum echinosporum plasmodiocarp (Lado 19964). 63. Physarum lakhanpalii plasmodiocarp (Lado 19890). 64. Physarum lakhanpalii plasmodiocarp and sporocarp (Lado 19894). 65–66. Physarum roseum open

sporocarps (Lado 20201). Bar: 61–64=1 mm; 65–66=0.5 mm



†Physarum galbeum Wingate

MGR-09-46: leaf litter, MA-Fungi 81740 (Lado 20032).

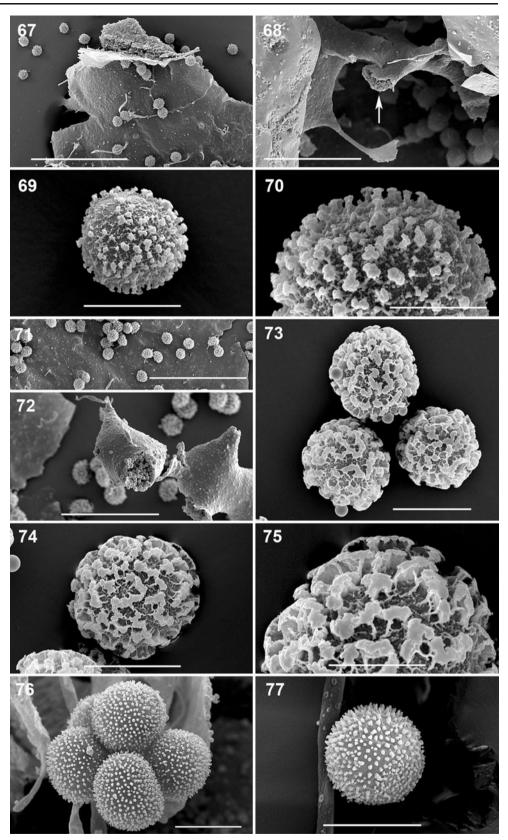
The collection has only four sporocarps of this species, characterized by the small, globose sporotheca of yellow to chrome color and the concolorous longitudinally furrowed stalk. The spores are 7–9 μ m diam. This is the first record of the species for Africa.

**Physarum* cf. *globuliferum* (Bull.) Pers. MGR-09-10: leaf litter, MA-Fungi 81481 (Lado 19751).

The doubt as to the identity of this collection is because the material is of a dozen weathered sporocarps, but the calcareous stalk and columella, the type of substrate and the small (5–6 μ m diam) spores suggest this species.

*Physarum hongkongense Chao H. Chung

MGR-09-02: leaf litter, MA-Fungi 81409 (Lado 19677). MGR-09-10: leaf litter, MA-Fungi 81477 (Lado 19746). MGR-09-18: twigs, MA-Fungi 81573 (Lado 19848). MGR- Fig. 67–70 Physarum echinosporum (Lado 19964) 67. Peridium filled with lime granules. 68. Detail of the capillitium showing the node filled with lime granules (arrow). 69. Spore. 70. Detail of ornamentation on the spore. 71–75. Physarum dictyosporum (aet 12094) 71. Peridium. 72. Detail of the capillitium showing nodes filled with lime granules. 73. Group of spores. 74. Spore 75. Detail of spore ornamentation showing fused expanded tips of the pila forming a subreticulum. 76–77. Physarum lakhanpalii (Lado 19884) 76. Clustered spores. 77. Spore separated from a cluster. Bar: 67, 71=100 µm; 68,72=50 µm; 69-70,73-77=10 μm



09-50: *Aloe* sp. remains, MA-Fungi 81798 (Lado 20091). MGR-09-54: wood, MA-Fungi 81860 (Lado 20165).

Reported from La Réunion by Adamonyte et al. (2011), but otherwise unknown from Africa.

Physarum javanicum Racib.

MGR-09-11: wood, MA-Fungi 81490 (Lado 19760), liana bark, MA-Fungi 81493 (Lado 19763).

A previous collection from Andasibe, Madagascar is conserved at PC (97681) and is published in Poulain et al. (2011) and it was also recorded from South Africa and Tanzania.

**Physarum lakhanpalii* Nann.-Bremek. & Y.Yamam. 11 fc, 3 mc, 4 loc, 4 subs Figs. 63–64, 76–77.

MGR-09-05: Ravenala madagascariensis leaf litter, MA-Fungi 81432 (Lado 19699). MGR-09-23: Aloe sp. dead leaves, (mc, pH 6.0), dwb 3379. MGR-09-28: Cocos nucifera leaves, MA-Fungi 81607 (Lado 19882), MA-Fungi 81609 (Lado 19884). MGR-09-33: Euphorbia sp. bark, (mc, pH 6.0), dwb 3251.

The yellow plasmodiocarps (Figs. 63–64) with a dense physaroid capillitium, and clustered spores (Fig. 76) are the differentiating characters of this species. Other than these collections, reported only from Tanzania in Africa.

*Physarum cf. leucophaeum Fr.

MGR-09-11: leaf litter, MA-Fungi 81497 (Lado 19766).

This differs from typical material by the completely black stalk and rudimentary columella, with spores of 10-12 μ m diam., but Nannenga-Bremekamp (1991:195) observed a form of this species, that is not rare in the Netherlands, with these characters.

*Physarum leucopus Link

MGR-09-39: *Euphorbia* sp. ground litter, (mc, pH 6.0), aet 12084.

**Physarum licheniforme* (Schwein.) Lado 5 fc, 2 mc, 5 loc, 6 subs

MGR-09-13: leaf litter, MA-Fungi 81536 (Lado 19807). MGR-09-15: *Aloe* sp. remains, MA-Fungi 81555 (Lado 19828). MGR-09-29: *Opuntia* sp. remains, MA-Fungi 81527 (Lado 19902). MGR-09-37: *Kalanchoe* sp. litter, (mc, pH 7.0), dwb 3266. MGR-09-40: *Xerosicyos* sp. leaf litter, (mc, pH 6.8), dwb 3276.

This is a species usually associated with succulent substrates and is not rare in arid areas of the Neotropics (Lado et al. 2011, 2012). Previously reported from La Réunion (Adamonyte et al. 2011) for Africa, and also reported from the Canary Islands.

*Physarum luteolum Peck

MGR-09-23: Adansonia grandidieri bark, (mc, pH 7.0), dwb 3249.

In Africa reported previously from Mozambique and Angola.

Physarum melleum (Berk. & Broome) Massee

MGR-09-10: leaf litter, MA-Fungi 81471 (Lado 19740), MA-Fungi 81473 (Lado 19742), MA-Fungi 81474 (Lado 19743), MA-Fungi 81478 (Lado 19747), MA-Fungi 81482 (Lado 19752). MGR-09-28: *Cocos nucifera* leaves, MA-Fungi 81612 (Lado 19887).

Material of this species from Madagascar, is cited by Ndiritu et al. (2009) from the UARK database.

*Physarum mutabile (Rostaf.) G. Lister

MGR-09-30: wood, MA-Fungi 81644 (Lado 19921). MGR-09-34: wood, MA-Fungi 81686 (Lado 19969). MGR-09-35: *Agave* sp. remains, MA-Fungi 81688 (Lado 19972).

*Physarum nucleatum Rex

MGR-09-11: leaf litter, MA-Fungi 81489 (Lado 19759). MGR-09-55: wood, MA-Fungi 81891 (Lado 20200).

*Physarum notabile T. Macbr.

MGR-09-39: *Euphorbia* sp. twigs, MA-Fungi 82098 (Lado 19984).

In Africa reported previously from Tanzania and South Africa.

**Physarum oblatum* T. Macbr. 4 fc, 4 mc, 6 loc, 5 subs MGR-09-22: *Pachypodium* sp. remains, MA-Fungi 81579 (Lado 19854). MGR-09-29: *Opuntia* sp. remains, MA-Fungi 81628 (Lado 19903). MGR-09-30: *Euphorbia* sp. aerial litter, (mc, pH 7.96), aet 12082. MGR-09-36: *Adansonia grandidieri* bark, (mc, pH 6.7), dwb 3384. MGR-09-38: *Adansonia grandidieri* bark, (mc, pH 7.1), dwb 3244.

In Africa reported previously from Tanzania, Nigeria and the Seychelles.

†Physarum pulcherrimum Berk. & Ravenel

MGR-09-02: leaf litter, MA-Fungi 81410 (Lado 19679), MA-Fungi 81415 (Lado 19684). MGR-09-29: *Dypsis decaryi* leaves, MA-Fungi 81642 (Lado 19918). MGR-09-53: *Pinus patula* wood, MA-Fungi 81820 (Lado 20122); *Pinus patula* needles, MA-Fungi 81822 (Lado 20124). MGR-09-55: wood, MA-Fungi 81868 (Lado 20176).

The purplish to deep brown sporocarps and nodes of the capillitium make this species easy to recognize. It resembles *P. roseum* Berk. & Broome, also found in Madgascar (Figs. 65–66) but differs in the darker color of the sporocarps and dense and persistent capillitium. We consider their conspecificity a possibility, as do Martin and Alexopoulos (1969: 324). These collections represent the first records of this species for Africa.

**Physarum pusillum* (Berk. & M.A. Curtis) G. Lister 30 fc, 12 mc, 21 loc, 12 subs

MGR-09-07: *Hedychium coronarium* inflorescence, MA-Fungi 81514 (Lado 19782). MGR-09-28: *Cocos nucifera* leaves, MA-Fungi 81615 (Lado 19890). MGR-09-33: aerial litter, (mc, pH 7.7), sls 23220. MGR-09-40: *Xerosicyos* sp. leaf litter, (mc, pH 6.8), dwb 3236. MGR-09-42: *Pachypodium rosulatum* remains, MA-Fungi 81702 (Lado 19991).

*Physarum roseum Berk. & Broome Figs. 65-66

MGR-09-55: liana bark, MA-Fungi 81892 (Lado 20201).

These pink-purple sporocarps are typical of the species (Figs. 65–66). The species is similar to *P. pulcherrimum* Berk. & Ravenel (see comment above). Reported previously from La Réunion and the Seychelles.

†Physarum rubiginosum Fr.

MGR-09-27: wood, MA-Fungi 82099 (Lado 19868).

The collection has sessile sporocarps and short plasmodiocarps with a brownish peridium with purple patches. The dense capillitium is of large orange nodes, paler on the outside and joined by hyaline threads. The spores are $10-12 \mu m$ diam. and minutely spinulose. This is the first record of this species for Africa.

*Physarum cf. sessile Brândza

MGR-09-10: leaf litter, MA-Fungi 81518 (Lado 19788).

Our material has the short plasmodiocarps with a white calcareous hypothallus that is well illustrated by Lister (1925: pl. 22) and Emoto (1977: pl. 96). In Africa reported previously from La Réunion (Adamonyte et al. 2011), Morocco, Angola and Mozambique.

**Physarum spectabile* Nann.-Bremek., Lado & G. Moreno MGR-09-22: *Aloe* sp. dead leaves, (mc, pH 7.5), dwb 3343. MGR-09-34: *Euphorbia* sp. ground litter, (mc, pH 7.6), dwb 3341. MGR-09-29: *Opuntia* sp. litter, MA-Fungi 81640 (Lado 19915).

Typical succulenticolous species common in arid lands of the Neotropics (Estrada-Torres et al. 2009; Lado et al. 2007, 2011) but not previously recorded in the Paleotropics except for an unconfirmed collection from La Réunion (Adamonyte et al. 2011).

Physarum stellatum (Massee) G.W. Martin

MGR-09-11: bark, MA-Fungi 81500 (Lado 19769). MGR-09-44: *Dypsis isaloensis* litter, MA-Fungi 81721 (Lado 20010). MGR-09-55: wood, MA-Fungi 81871 (Lado 20179).

A previous collection from Foulpoint, Madagascar is conserved at PC (97353) and is illustrated in Poulain et al. (2011).

*Physarum sulphureum Alb. & Schwein.

MGR-09-10: wood, MA-Fungi 81521 (Lado 19792).

In Africa reported previously from Morocco, Angola and the Seychelles.

*Physarum superbum Hagelst.

MGR-09-18: *Aloe* sp. remains, MA-Fungi 81564 (Lado 19837), MA-Fungi 81571 (Lado 19846); *Aloe* sp. dead leaves (mc, pH 6.8), dwb 3382, (mc, pH 7.1), dwb 3403; *Agave victoriae-reginae* remains, MA-Fungi 81575 (Lado 19850).

We prefer to leave the field collections as cf. since the peridium appears to be single and the sporocarps are not very compressed laterally. They have orange-yellow flakes on the peridium and the nodes of the capillitium are also orange-yellow. In Africa, only reported previously from La Réunion (Adamonyte et al. 2011) and Tanzania.

*Physarum tenerum Rex

MGR-09-15: wood, MA-Fungi 81551 (Lado 19823). MGR-09-54: dead liana, (mc, pH 5.6), dwb 3209.

Reported previously from the neighbouring islands of La Réunion and the Seychelles.

*Physarum vernum Sommerf.

MGR-09-33: dead liana, (mc, pH 6.9), dwb 3205.

Physarum viride (Bull.) Pers. 26 fc, 0 mc, 8 loc, 4 subs

MGR-09-05: bamboo shoots, MA-Fungi 81440 (Lado 19708). MGR-09-44: liana, MA-Fungi 81709 (Lado 19997). MGR-09-54: wood, MA-Fungi 81831 (Lado 20133), bark, MA-Fungi 81851 (Lado 20154). MGR-09-55: wood, MA-Fungi 81866 (Lado 20173).

Nine of these collections belong to the variety *aurantium* (Bull.) Lister. A collection from Maromandia in Madagascar was cited by Patouillard (1928).

Stemonitis axifera (Bull.) T. Macbr.

MGR-09-31: *Euphorbia* sp. litter, (mc, pH 5.1), dwb 3376, dwb 3377.

This species was cited from Maromandia and Antananarivo, Madagascar, as *S. ferruginea* Ehrenb. by Patouillard (1928).

*Stemonitis flavogenita E. Jahn

MGR-09-27: *Agave* sp. remains, MA-Fungi 81606 (Lado 19881). MGR-09-50: *Aloe* sp. litter, (mc, pH 6.6), dwb 3245, (mc, pH 6.7), dwb 3254.

*Stemonitis fusca Roth

MGR-09-47: liana, MA-Fungi 81766 (Lado 20058). MGR-09-52: wood, MA-Fungi 81810 (Lado 20110) MGR-09-54: liana, MA-Fungi 81852 (Lado 20155).

One of these collections (MA-Fungi 81810) belongs to the variety *rufescens* Lister. Material of this species from Madagascar, is cited by Ndiritu et al. (2009) from the UARK database.

†Stemonitis cf. *mussooriensis* G.W. Martin, K.S. Thind & Sohi

MGR-09-25: wood, MA-Fungi 81588 (Lado 19861).

Since this single collection had some weathered sporocarps 6-9 mm tall rather than 1.5-2.5(-3) mm we could not confirm its identity. The sporocarps were in large groups, with warted spores (not spiny-warted), $10-11 \mu m$ diam., and had a lax capillitium with membranous expansions at the junctions of the primary branches. If confirmed this would be the first record for Africa.

*Stemonitis splendens Rostaf.

MGR-09-02: *Pinus patula* wood, MA-Fungi 81413 (Lado 19682). MGR-09-47: wood, MA-Fungi 81756 (Lado 20051), MA-Fungi 81757 (Lado 20052), MA-Fungi 81774 (Lado 20065). MGR-09-46: wood, MA-Fungi 81741 (Lado 20034).

†Stemonitis virginiensis Rex

MGR-09-12: *Pandanus* sp. leaves, MA-Fungi 81501 (Lado 19771). MGR-09-39: *Euphorbia* sp. ground litter, (mc, pH 6.8), aet 12095, (mc, pH 7.3), aet 12093.

This species is normally found on wood and is common in the United States (Martin and Alexopoulos 1969) but not on leaves and litter. This is the first record of this species for Africa.

*Trichia affinis de Bary

MGR-09-52: wood, MA-Fungi 81814 (Lado 20116), MA-Fungi 81815 (Lado 20117). MGR-09-54: liana bark, MA-Fungi 81855 (Lado 20160).

†Trichia crateriformis G.W.Martin

MGR-09-39: *Euphorbia* sp. ground litter, (mc, pH 6.8), aet 12095.

This collection has brown obpyriform sporothecae. They dehisce by an operculum or sometimes areolae, and the peridium in the area of dehiscence is thinner, showing the spores. The sporocarps have short black opaque stipes filled with refuse material and the elaters are long and yellow with pointed apices. They give the impression macroscopically of a short-stemmed *T. botrytis.* This is the first record for Africa of this species.

*Trichia favoginea (Batsch) Pers.

MGR-09-06: wood, MA-Fungi 81444 (Lado 19713).

Discussion

As a result of this first survey for myxomycetes of Madagascar, an island representing less than 0.4 % of land surface area of the earth, it has been possible to identify 761 collections of myxomycetes, which include 124 species from 22 genera. Among these results, 106 species have not been recorded previously from Madagascar, and 21 of the species are new records for the whole of Africa, which increases the number reported so far for the continent by Ndiritu et al. (2009), by more than 7 % and brings the total catalogue to 315 species. One species, Perichaena madagascariensis, is described here as new to science, and in addition, among the specimens examined from this survey, at least 10 other species from the genera Comatricha, Diderma, Didymium, Licea, Physarum and Stemonitis do not fit any species in the literature, and are probably undescribed species, but all are represented by too few collections to describe them here. A total of eight of the ten species recorded almost a hundred years ago by Patouillard (1928) have been found again in this survey. These are Arcyria cinerea, A. denudata, A. minuta, Ceratiomyxa fruticulosa, Fuligo septica, Hemitrichia serpula, Physarum viride, and Stemonitis axifera. Not included in the results of the present survey, but cited by Patouillard were Cribraria intricata and Tubifera microsperma. All of the other records compiled by Ndiritu et al. (2009) were also found again, except Fuligo cinerea. The results include older species such as Badhamia obovata, Diderma rugosum, Didymium listeri, Physarum galbeum and P. luteolum described over a century ago, and some quite rare species such as Diderma rimosum, Fuligo intermedia, Licea rufocuprea, Perichaena pulcherrima, Physarum dictyosporum, P. echinosporum and P. lakhanpalii. The species that were represented by the largest number of collections were Physarum pusillum and Badhamia melanospora. These are typically found in arid areas and were also the dominant species in Chile, and the Tehuacán-Cuicatlán valley in Mexico (Lado et al. 2007; Estrada-Torres et al. 2009). However, certain species that were commonly found in arid areas of America were not among the species found in the dry areas here. These include Didymium vaccinum, Didymium squamulosum and Perichaena vermicularis, and also the recently described species Licea eremophila and the species of the genus Didymium (Wrigley de Basanta et al. 2009, 2010, 2011). In the humid forests the most abundantly appearing myxomycetes were Hemitrichia calyculata and H. serpula, which also occur in other tropical

Vegetation type	Localities	Collections	Species	Genera	S/G ratio
Humid forest	13	211	66	17	3.88
Gallery forest	5	95	30	15	2.0
Tapia sclerophyll forest	3	32	16	10	1.6
Grassland and inselbergs	13	115	42	17	2.47
Southern dry/spiny forest	17	260	59	19	3.1
Secondary vegetation	5	49	15	7	2.1

Table 3 Summary of data fromdifferent vegetation types

	Madagascar (present paper)	La Reunion (Adamonyte et al.2011)	Aldabra atoll (Ing and Hnatiuk1981)	All Africa (Ndiritu et al. 2009)
Genera	22	25	16	49
Species	124	92	55	294
S/G ratio	5.6	3.7	3.4	6.0
Species shared w/ Madagascar	124	50	42	97
CC with Madagascar	**	0.45	0.47	0.46

forests of the world. Many other species with a tropical distribution like *Metatrichia horrida*, *Physarum javanicum* and *P. stellatum* (Lado et al. 2003) were found in these areas, and notably *Ceratiomyxa morchella*, *C. sphaerosperma* and *Diderma rimosum* frequently cited from moist forests of the Neotropics (Lado et al. 2003; Stephenson et al. 2008; Rojas et al. 2008). Of the total 124 species, 34 species were represented by only a single collection. The most widespread species was *Arcyria cinerea*, collected at 24 of the 56 collecting localities, followed by *P. pusillum* at 21 sites. The genus *Physarum* was the most frequently represented genus with 37 species followed by *Didymium* with 14 species. In total, the order Physarales accounted for 54 % of the species recovered in the survey.

All but two of the localities sampled (MGR-24 and MGR-43), produced identifiable collections of myxomycetes, showing widespread occurrence of these organisms in the areas of the island sampled. Table 3 shows a summary of the results from the different vegetation types. The ratio of the number of species per genus (S/G) can be used to compare taxonomic diversity (Stephenson et al. 1993), and a lower number is an indication of a greater diversity. It can be seen from the table that individual vegetation types show diversity comparable to other temperate and tropical forests (2.2–4.6, Stephenson et al. 1993), but the whole survey shows apparently less diversity (S/G=5.6) than the arid

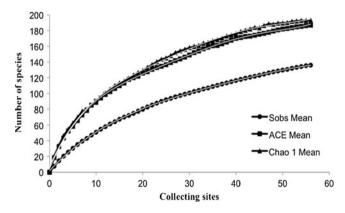
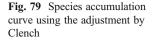
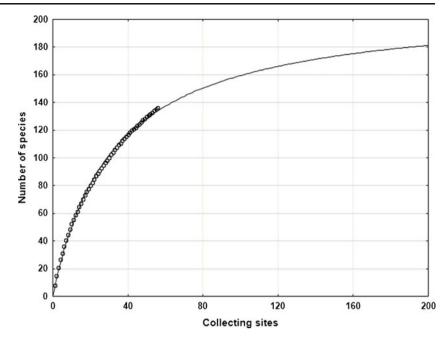


Fig. 78 Curves of abundance (ACE and CHAO1 estimators) compared to the species observed curves (Sobs) of this survey. White lines indicate the polinomial best-fit curve

areas of the Monte Desert in Argentina (S/G=3.3, see Lado et al. 2011), or the drylands of the Tehuacán valley in Mexico (S/G=3.9, see Estrada-Torres et al. 2009). However, in the present survey there are different vegetation types, not only arid vegetation. The greatest number of collections (260), were made in the dry forests (Table 3), followed by the humid forests that represent up to 44 % of the main forest cover of the island (Table 1). Slightly fewer species were identified in the dry forests (59) but from more different genera (19 vs. 17 from the humid forests), and so the dry areas showed more taxonomic diversity than the humid forests, with a S/G ratio of 3.1. This result is comparable to and shows slightly more diversity in the dry areas of Madagascar than the dryland areas of America cited above. The diversity of the grasslands (Table 3) with the rocky outcrops or inselbergs, another dry area with a characteristic succulent plant biota, was surprisingly high, given the low annual precipitation (Table 1). The same number of genera of myxomycetes were recorded here from the same number of collecting sites as the humid forests, although there were fewer different species and fewer collections, showing a more specialised myxobiota.

One of the closest islands to Madagascar is the much smaller, volcanic island of La Réunion, 780 km to the East. In a recent paper on the myxomycete biodiversity of that island, Adamonyte et al. (2011) reported 92 species with the Physarales making up a similar proportion of the results (52 %) to that in this survey. A comparison of the myxobiota of the two islands shows that surprisingly only 40 % of the species found in Madagascar also appeared in La Réunion. Ing and Hnatiuk (1981) studied the myxomycetes of the Aldabra atoll, a group of coral islands in the Indian Ocean to the North of Madagascar. Their research shows 42 species in common with those reported here on Madagascar or 34 % of the Malagash biota. Table 4 shows comparative data between these areas. The coefficient of community between these islands however, shows less than 50 % similarity between the myxobiota, despite their geographic proximity. Perhaps like the phytogeographic connections reported for plants (Schatz 1996), they are more similar to Indian and Malasian communities than African. Five of the unusual species collected in Madagascar, Diachea bulbillosa,





Didymium leoninum, Perichaena pulcherrima, Physarum crateriforme and *P. roseum* were originally described from Sri Lanka.

The total number of collections made during this survey included 511 field collections, with the largest number found on wood and leaf litter, and 250 collections isolated from moist chamber cultures. The cultures were made using 18 different substrates of the principal endemic plants from the most prominent vegetation types, with the Euphorbia spp. producing the largest number of moist chamber culture collections in addition to 40 field collections. The cultures were 79 % positive for myxomycetes, either producing plasmodia, sclerotia or fruiting bodies. In La Réunion (Adamonyte et al. 2011) the 124 cultures made with 35 different substrates were 67 % positive. The moist chamber cultures from dry areas of America were from 65 % to 82 % positive (Lado et al. 2011, 2012; Estrada-Torres et al. 2009). The range of pH of the positive cultures was from pH 4.1 to 8.6 with a mean pH of 5.4, but a large number of the substrates were circa-neutral (mode 7.1). This may have had a favourable influence on the productivity (Wrigley de Basanta 2000, 2004). The pH range is narrower than in central Chile or the Argentinian Monte Desert, in spite of the variety of vegetation sampled (Lado et al. 2011, 2012).

According to the estimators ACE and CHAO1, if the sampling effort were exhaustive, the number of species expected is calculated at 187 and 193 respectively (Fig 78), and the estimate based on the Clench function is 210 species.

This means that the sampling effort of this survey was 70–73 % according to the former ACE and CHAO1 estimators, or 65 % according to the Clench function (Fig. 79). If the results of the field collections and collections from moist chamber culture are assessed separately, the former recovered 63–54 % of the expected species by ACE and CHAO1 estimators and 81–85 % respectively were isolated in the moist chamber cultures. These results show that the survey recovered a large proportion of the assemblage of myxomycetes to be expected in the studied area. The results of the moist chamber culture component of the survey particulary, shows that most of the species that develop in these cultures have been recovered. The figures are very similar to those returned by the same indices for moist chamber cultures in the study of the Monte Desert of Argentina, which were 81–

 Table 5
 Community similarity between myxobiota of arid areas using the coefficient of community index. Coefficient top right bold, species in common bottom left

	Madagascar dry areas	Monte Desert	Tehuacán-Cuicatlán drylands	Atacama Desert
Madagascar dry areas (present paper)	**	0.31	0.42	0.28
Monte Desert Argentina (Lado et al. 2011)	22	**	0.46	0.49
Tehuacán-Cuicatlán drylands Mexico (Estrada-Torres et al. 2009)	37	41	**	0.40
Atacama Desert Chile (Lado et al. 2007, 2012)	16	30	29	**

84 % (Lado et al. 2011). The field results alone from Madagascar are lower and suggest that more species potentially exist than were found in this survey, but any field collecting is more subject to the fruiting phenology of the myxomycetes and climatic conditions, at the moment of the visit to an area, than laboratory cultures. Considering the amount of time used in the fieldwork, to find over half of the expected species indicates a high yield and a very effective survey. The overall values are comparable to values obtained in a survey of the central area of Chile (Lado et al. 2012). When the results of all the dry areas were processed, ACE and CHAO1 estimate 107 and 103 species, respectively, and using the Clench function 142 species are calculated. Since 82 taxa were observed, the completeness of survey for these areas was 77-80 % complete for the first two estimates and 58 % using the third.

In order to assess the similarity of the myxomycete communities of just the dry areas in both hemispheres of America with the dry areas of Madagascar the coefficient of community was calculated for each (Table 5). The surveys are comparable since they were done by the same team, using the same methods, in both the dry areas of Madagascar and of America. The myxomycete community similarity from Madagascar is closest to that of the Tehuacán-Cuicatlán Valley in Mexico (0.42), according to this coefficient, although the areas with the most similar assemblage of species are the Monte Desert in North Argentina and the Atacama Desert and its environs in northern Chile (0.49). Even so, all these areas have less than half their species in common. As would be expected, the assemblage of the total number of myxomycetes from all areas of Madagascar are slightly more similar (CC 0.45-0.47) to those of nearby areas (Table 4) than the assemblage from the dry areas of Madagascar to other dry areas in America, although still less than 50 % as mentioned above.

One of the most surprising results of this research is that in the first intensive survey for these organisms on Madagascar, there appear to be few undescribed species and no apparent endemisms. This is particularly surprising since many of the substrates have never been previously examined for myxomycetes. Unlike higher animals and plants present on the island, that show an unusually high level of endemism and high speciation, it would appear from the results so far that the myxomycetes do not follow the trend, which is usually put down to evolution during geographical isolation. However, apart from the new species Perichaena madagascariensis described above, there are at least ten species among the results that are clearly different from currently described species, but represented by too little material to describe them yet, and there may be cryptic species among the variations commented upon above. Following the argument of Foissner (2008), abundant species are found often and they are usually recognized in samples

from many places globally, while rare species, many of which have not yet been discovered or may be endemics, are not recognized in ordinary surveys, mainly due to undersampling. This could be the case for these ten unidentified species, and maybe some others among the almost 30 % of the species not detected in this survey according to the estimators discussed above. Only the central and southern parts of Madagascar were included in the present survey, so the northern areas, such as the transition zone from the dry forests to the rainforests, the Sambirano region, may hold new, endemic or different species.

The question is, are the species that have been detected on Madagascar ancestral mainland species evolved after the separation of Gondwana? Were they introduced with plant substrates? Have they simply been distributed by southern trade winds? Or are all of the above true for different species? To support the first hypothesis a number of the species listed are older species that may have been already associated with the ancestors of the endemic plants before their diversification. Thus one explanation for the apparent different pattern of distribution in the myxomycetes could be that they are much more ancient lineages and had already diversified before the breakup of Gondwana. More recent introduction with host plants, such as Opuntia spp. introduced for fodder in the 18th century (Binggeli 2003), is another possibility and almost certainly the method of dispersal in the case of Badhamia melanospora as has been suggested before (Estrada-Torres et al. 2009) and Licea succulenticola may have arrived in the same manner, although it appeared in this survey only on the native plants Aloe and Euphorbia spp.

It could be argued, following the third hypothesis, that the myxomycetes arrived many times on Madagascar, using mainly wind dispersal and following a distribution pattern consistent with the ubiquity hypothesis (Baas Becking 1934). But this would have lead to us finding largely the most common species that are widely distributed throughout the world, and this was not the case. There were some common and cosmopolitan species, but also rare or unusual species as mentioned above. The fact that there is little similarity between the myxobiota of the selected studies from neighbouring areas, even though it is greater than from similar environments in America, also contradicts this idea. Other studies have suggested that a moderate endemicity model proposed by Foissner (2006) is probably closer to the manner of distribution in these microorganisms (Stephenson et al. 2008; Wrigley de Basanta et al. 2009, 2010, 2011; Lado et al. 2011). The latter papers highlighted specific assemblages of myxomycetes with restricted distribution developing on plants in areas of the Americas. Obviously much further research using molecular and other data is necessary to support or contradict these hypotheses, but these results give an indication of lines of investigation to pursue.

The results of this survey indicate that although, as yet, a large number of new or endemic species have not been recognised, the island of Madagascar does have a unique assemblage of species of myxomycetes, different from neighbouring islands and from similar but distant environments. They also indicate a very high myxomycete biodiversity. The completeness of survey indices suggest that there are probably even more species in the areas of the island sampled, than have been identified in this first survey, apart from the number of undescribed different species and probable cryptic species included in the research. There is evidence that much more fieldwork in Madagascar is necessary, and this is of some urgency, given that the natural vegetation is rapidly disappearing and with it, its unknown and possibly unique microbial inhabitants like the myxomycetes.

Acknowledgements This research was supported by the National Science Foundation, of the United States (grant DEB-03316284 for a project entitled "PBI: Global Biodiversity of Eumycetozoans") and the Spanish government (grant CGL 2008 00720/BOS and CGL2011-22684). We are grateful to Dr. Patricia Wright (Stony Brook University, New York), the Madagascar Institut pour la Conservation des Ecosystèmes Tropicaux, the National Parks of Madagascar and the University of Antananarivo for their assistance in setting up and then carrying out fieldwork in Madagascar, Yolanda Ruiz for her technical assistance with SEM and Carlos de Mier for his help with the light micrographs.

References

- Adamonyte G, Stephenson SL, Michaud A, Seraoui E-H, Meyer M, Novozhilov YK, Krivomaz T (2011) Myxomycete species diversity on the island of La Réunion (Indian Ocean). Nov Hedwig 92:523–549
- Anonymous (1976) ISCC-NBS color-name charts illustrated with centroid colors. Inter-Society Color Council, National Bureau of Standards. Washington
- Baas Becking LGM (1934) Geobiologie of inleiding tot de milieukunde. Van Stockum and Zoon, The Hague
- Barthlott W, Porembski S (1996) Biodiversity of arid islands in tropical Africa the succulents of inselbergs. In: Van der Maesen LJG, Van der Burgt XM, Van Medenbach De Rooy JM (eds) The biodiversity of African plants proceedings, XIVth AETFAT Congress, 22– 27 August 1994. Wageningen, The Netherlands, pp 49–57
- Binggeli P (2003) Cactaceae, Opuntia spp. prickly pear, raiketa, rakaita, raketa. In: Goodman S and Banstead J (eds), The natural history of Madagascar, pp. 335-339. University of Chicago Press
- Bond WJ, Silander JA, Ranaivonasy J, Ratsirarson J (2008) The antiquity of Madagascar's grasslands and the rise of C4 grassy biomes. J Biogeogr 35:1743–1758
- Callmander MW, Laivao MO (2003) New findings on *Pandanus* sect. *Imerinenses* and sect. *Rykiella* (Pandanaceae) from Madagascar. Adansonia sér, 3 25(1):53–63
- Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. Philos Trans R Soc (Ser B) 345:101–118
- Colwell RK, Mao CX, Chang J (2004) Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecol 85:2717–2727

- Dewar RE, Richard AF (2007) Evolution in the hypervariable environment of Madagascar. The National Academy of Sciences of the USA. PNAS 104(34):13723–13727
- Dufils JM (2003) Remaining forest cover. In: Goodman S and Banstead J (eds), The natural history of Madagascar, pp. 16–34. University of Chicago Press
- Emoto Y (1977) The Myxomycetes of Japan. Sangyo Tosho Publishing Co., Ltd. Tokio
- Estrada-Torres A, Wrigley de Basanta D, Conde E, Lado C (2009) Myxomycetes associated with dryland ecosystems of the Tehuacán-Cuicatlán Valley Biosphere Reserve, Mexico. Fungal Divers 36:17–56
- Foissner W (2006) Biogeography and dispersal of micro-organisms: a review emphasizing protists. Acta Protozool 45:111–136
- Foissner W (2008) Protists diversity and distribution: Some basic considerations. Biodivers Conserv 17(2):235–242
- Gilert E (1990) On the Identity of *Perichaena liceoides* (Myxomycetes). Mycol Res 94(5):698–704
- Gilert E (1995) Taxonomic evaluation of the myxomycete *Calonema luteolum*. Mycol Res 99(3):698–704
- Ing B (1999) The Myxomycetes of Britain and Ireland. An identification handbook. The Richmond Publishing Co. Ltd, Slough, England
- Ing B, Hnatiuk RJ (1981) Myxomycetes of Aldabra Atoll. Atoll Research Bulletin No. 249. The Smithsonian Institution. Washighton. USA
- Ingram JC, Dawson TP (2005) Climate change impacts and vegetation response on the island of Madagascar. Phil Trans R Soc A 363:55–59
- Jiménez-Valverde J, Hortal J (2003) Las curvas de acumulación de especies y la necesidad de evaluar la calidad de los inventarios biológicos. Rev Ibér Aracnol 8:151–161
- Jury MR (2003) The climate of Madagascar. In: Goodman S, Banstead J (eds) The natural history of Madagascar. The University of Chicago, Chicago, pp 75–87
- Keller HW, Eliasson UH, Braun KL, Buben-Zurey MJ (1988) Corticolous Myxomycetes X: ultrastructure and taxonomic ttatus of Cribraria minutissima and C. confusa. Mycol 80(4):36–545
- Keller HW, Eliasson UH (1992) Taxonomic evaluation of *Perichaena depressa* and *P. quadrata* based on controlled cultivation, with additional observations on the genus. Mycol Res 96(12):1085–1097
- Kowalski DT (1969) A new coprophilous species of *Calonema* (Myxomycetes). Madrono 20(4):229–231
- Lado C (2005–2012) An online nomenclatural information system of Eumycetozoa. http://www.nomen.eumycetozoa.com (23 April 2012)
- Lado C, Teyssiere M (1998) Myxomycetes from Equatorial Guinea. Nov Hedwig 67(3–4):421–441
- Lado C, Estrada-Torres A, Stephenson SL, Wrigley de Basanta D, Schnittler M (2003) Biodiversity assessment of myxomycetes from two tropical forest reserves in Mexico. Fungal Divers 12:67–110
- Lado C, Estrada-Torres A, Stephenson SL (2007) Myxomycetes collected in the first phase of a north–south transect of Chile. Fungal Divers 25:81–101
- Lado C, Wrigley de Basanta D, Estrada-Torres A (2011) Biodiversity of myxomycetes from the Monte Desert of Argentina. An Jard Bot Madr 68(1):61–95
- Lado C, Wrigley de Basanta D, Estrada-Torres A, Stephenson SL (2012) The Biodiversity of myxomycetes in Central Chile. Fungal Divers. doi:10.1007/s13225-012-0159-8
- Lister A (1925) A monograph of the Mycetozoa, 3^a ed., revised by G. Lister. Printed by order of the Trustees. London
- Madagascar National Parks (2003) Magascar protected area system management plan 2001 – 2006. Ministère de l'Environnement, des Eaux et Forêts

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- Martin GW, Alexopoulos CJ (1969) The Myxomycetes. Univ. of Iowa Press, Iowa
- Mosquera J, Lado C, Estrada-Torres A, Beltrán-Tejera E, Wrigley de Basanta D (2003) Description and culture of a new Myxomycete, *Licea succulenticola*. An Jard Bot Madr 60(1):3–10
- Myers N, Mittermeier RA, Mittermeier CG, da Gustavo AB, Fonseca GAB, Jennifer Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858
- Nannenga-Bremekamp NE (1972) Notes on myxomycetes XVIII. A new Didymium and some comments on the *Didymium* species with longstalked sporangia. Proc Kon Ned Akad Wet C 75(4):352–363
- Nannenga-Bremekamp NE (1991) A guide to temperate myxomycetes. Biopress Limited, Bristol
- Nannenga-Bremekamp NE, Yamamoto Y (1983) Additions to the myxomycetes of Japan. I Proc Kon Ned Akad Wet C 86 (2):207–241
- Nannenga-Bremekamp NE, Yamamoto Y (1987) Additions to the myxomycetes of Japan. III Proc Kon Ned Akad Wet C 90 (3):311–349
- Natural Environment Research Council (2002) Groundwater Quality: Madagascar. British Geological Survey
- Ndiritu GG, Winsett KE, Spiegel FW, Stephenson SL (2009) A checklist of African myxomycetes. Mycotaxon 107:353–356
- Novozhilov YK, Zemlyanskaya IV, Schnittler M, Stephenson SL (2008) Two new species of *Perichaena* (Myxomycetes) from arid areas of Russia and Kazakhstan. Mycol 100(5):816–822
- Pando F, Lado C (1988) Two new species of corticolous myxomycetes from Spain. Mycotaxon 31:299–303
- Patouillard N (1928) Contribution a l'étude des champignons de Madagascar. Mém Acad Malagache 6:1–49
- Petch T (1909) New Ceylon Fungi. Ann Roy Bot Gard (Peradeniya) 4 (5):299–307
- Poulain M, Meyer M, Bozonnet J (2011) Les Myxomycètes. Fédération mycologique et botanique Dauphiné-Savoie, Sevrier
- Rojas C, Schnittler M, Biffi D, Stephenson SL (2008) Microhabitat and niche separation in species of *Ceratiomyxa*. Mycol 100(6):843–850

- Schatz GE (1996) Malagasy/Indo-Australo-Malesian phytogeographic connections. In: Lourenço WR (ed) Biogeography of Madagascar. Editions Orstom, Paris
- Stephenson SL (2011) From morphological to molecular: studies of myxomycetes since the publication of the Martin and Alexopoulos (1969) monograph. Fungal Divers 50:21–34. doi:10.1007/ s13225-011-0113-1
- Stephenson SL, Kalyanasundaram I, Lakhanpal TN (1993) A comparative biogeographical study of myxomycetes in the mid-Appalachian of eastern North America and two regions of India. J Biogeogr 20:645–657
- Stephenson SL, Schnittler M, Novozhilov YK (2008) Myxomycete diversity and distribution from the fossil record to the present. Biodivers Conserv 17(2):285–301
- Wells NA (2003) Some hypotheses on the Mesozoic and Cenozoic paleoenvironmental history of Madagascar. In: Goodman S and Banstead J (eds), The natural history of Madagascar, pp. 16–34. University of Chicago Press
- Willis KJ, Gillson L, Virah-Sawmy M (2008) Nature or nurture: the ambiguity of C4 grasslands in Madagascar. J Biogeogr 35:1741– 1742
- World Meteorological Organization (WMO) Online at http:// www.worldweather.org/004/m004.htm, consulted 18 June 2011
- Wrigley de Basanta D (2000) Acid deposition in Madrid and corticolous myxomycetes. Stapfia 73:113–120
- Wrigley de Basanta D (2004) The effect of simulated acid rain on corticolous myxomycetes. Syst Geogr Plant 74:175–181
- Wrigley de Basanta D, Lado C, Estrada-Torres A, Stephenson SL (2009) Description and life cycle of a new *Didymium* (Myxomycetes) from arid areas of Argentina and Chile. Mycol 101(5):707–716
- Wrigley de Basanta D, Lado C, Estrada-Torres A (2010) Licea eremophila, a new myxomycete from arid areas of South America. Mycol 102(5):1185–1192
- Wrigley de Basanta D, Lado C, Estrada-Torres A (2011) Spore to spore culture of *Didymium operculatum*, a new myxomycete from the Atacama Desert of Chile. Mycol 103(4):895–903