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Licea eremophila, a new myxomycete from arid areas of South America

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Abstract: A new stipitate species of myxomycete of the genus *Licea* is described based on material from arid areas in Argentina and Chile. It was isolated from moist chamber cultures and found fruiting on field collections, usually on the same substrate, *Puya* sp. (Bromeliaceae). It differs from all described species in the genus in that it has stipitate sporocarps with dehiscence by defined preformed platelets and a smooth inner peridial surface. The new species has polyhedral, yellow spores with a uniform thick spore wall and dense warts except on irregularly dispersed raised bands with fewer warts, visible by SEM, an ornamentation not previously observed in the genus. Life-cycle events are described and illustrated, from germination to sporulation, based on moist chamber and agar cultures. The morphology of the myxomycete specimens was examined with scanning electron microscopy and light microscopy, and both light and SEM micrographs of relevant details are included.

Key words: Andes, deserts, ecology, life cycle, Mycetozoa, *Puya*, succulenticolous species, taxonomy

INTRODUCTION

Assessing the biodiversity of myxomycetes associated with arid areas has been the focus of a study in the deserts of Argentina and Chile for more than 4 y (Lado et al. 2008; Wrigley de Basanta et al. 2008, 2009). During these surveys most types of native vegetation were examined in the field for myxomycetes and samples of the same vegetation returned to the laboratory for moist chamber culture. One productive substrate in the field and subsequently in culture was the dead leaf bases of the bromeliad *Puya* spp. This genus has almost 200 species distributed from northern Argentina and Chile to Central America. *Puya* is a large genus with plants particularly well adapted to dry areas, growing on rocky slopes, and some species have the water-saving crassulacean acid mechanism (CAM) type of photosynthesis (Crayn et al. 2004). It has produced many small myxomycetes to date, among which are two recently described species, *Didymium infundibuliforme* (Wrigley de Basanta et al. 2009) and *Perichaena calongei* (Lado et al. 2009). The same substrate also has produced a minute myxomycete of genus *Licea*, which we describe here as new to science. This tiny species appeared on examination of substrata before they were placed in moist chamber culture. It subsequently was obtained in several moist chamber cultures of the same and other substrates, and close examination of all field collections of *Puya* spp. from the same areas revealed several further collections of this stipitate *Licea*.

The genus *Licea* (order Liceales) was described at the end of the 18th century by Schrader (1797:16). It now includes more than 65 species worldwide (Lado 2008). It is probably a polyphyletic genus (Gilert 1994) and is defined principally by the lack of capillitium, an informative taxonomic character in most other genera of myxomycetes, and usually the presence of a protoplasmodium. A taxonomic study of all stipitate *Licea* species (Wrigley de Basanta and Lado 2005) highlighted the importance of additional characters to be used in distinguishing among species of this genus. These were the type of dehiscence of the peridium, the ornamentation of the peridium and the details of the spore ornamentation by SEM. Where agar or moist chamber culture have enabled the observation of a plasmodium, the presence of a protoplasmodium is also a useful character. Other families of order Liceales, such as Cribrariaceae and Reticulariaceae, also are noted for their lack of, or reduced, capillitium, but other characters, such as the dictydine granules or a peridial net in the first case and the aethaliod fructifications and pseudocapillitium in the second, readily separate them from genus *Licea*. A few members of genus *Perichaena* (*P. corticalis* var. *liceoides*) also have been described as having a reduced or absent capillitium, and the authors of three described species with no capillitium, *P. taimyriensis* (Novozhilov and Schnittler 2000), *P. heterospinispora* and *P. polygonospora* (Novozhilov et al. 2008), comment on the fact that they may represent intermediates between genera *Licea* and *Perichaena*. The plasmodium was not observed in these cases. We hope that molecular data will help to

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resolve the phylogenetic relationships and taxonomic status of these species.

MATERIALS AND METHODS

Collecting sites of the substrates producing this myxomycete were 26–31°S and 67–70°W, in northwestern Argentina and northern Chile. The vegetation sampled was predominantly xerophyllous scrubland with rosette-leaf succulent plants such as *Puya* spp. and desert scrubland dominated by cacti such as *Trichocereus* spp. This paper is based on material obtained from field collections (fc) and moist chamber cultures (mc) prepared with leaf bases of *Puya* spp. and epidermal remains of two cacti, *Trichocereus* sp. and *Miqueliopuntia miqueli*, that were collected in three provinces of Argentina (Catamarca, La Rioja and San Juan) and Atacama (III Region) in Chile. Field collections and the substrate material for moist chamber cultures were obtained on three different occasions Nov 2006–Mar 2008. Field collections were glued into herbarium boxes and dried in situ. Material for preparation of moist chamber cultures was air-dried in situ and transported to the laboratory in sealed paper bags. All localities were geo-referenced with GPS (Magellan eXplorist 600 5.1, Datum WGS84).

Agar cultures and moist chamber cultures were set up in the manner described by Wrigley de Basanta et al. (2009). Germination slide cultures were set up as described by Spiegel et al. (2005). A sterile substrate extract was made with 25 g *Puya* sp. leaf base in 1 L sterile water boiled then filtered and the filtrate autoclaved. This was used as a nutrient solution added to the surface of agar cultures. Details of other media and specific agar culture techniques can be found in Haskins and Wrigley de Basanta (2008). In moist chamber cultures all sporocarps of the same species in one culture were regarded as representing one collection. The dates for moist chamber (mc) collections in *Specimens examined* are the dates that specimens were obtained in culture. All specimens are deposited in the herbaria MA-Fungi (sub Lado) and the private collection of the first author (dwb). All microscope measurements and observations were made with material mounted directly in polyvinyl alcohol medium. Spore measurements were made of at least 10 spores from each collection. A microscope with differential interference contrast (DIC) was used to obtain descriptive data and light micrographs. Critical-point drying was used for scanning electron microscope (SEM) preparations, and the SEM analyses and photomicrographs of specimens were made by the Scanning Electron Microscopy Department of the Royal Botanic Garden of Madrid, employing a Hitachi S-3000N scanning electron microscope, at 10–15 kV. Color notations in parentheses are from the ISCC-NBS color-name charts illustrated with centroid colors (Anon. 1976).

RESULTS

Thirteen collections of this new myxomycete have been obtained, nine from moist chamber culture and four from field collections. They are from three provinces in Argentina and one region in Chile, obtained during three different years of collecting. The morphogenesis of the sporocarps has been observed in moist chamber culture, and stages of the life cycle of this species have been observed in agar culture. The combination of characters of this myxomycete is unique in the genus and thus we describe it here as a new species.

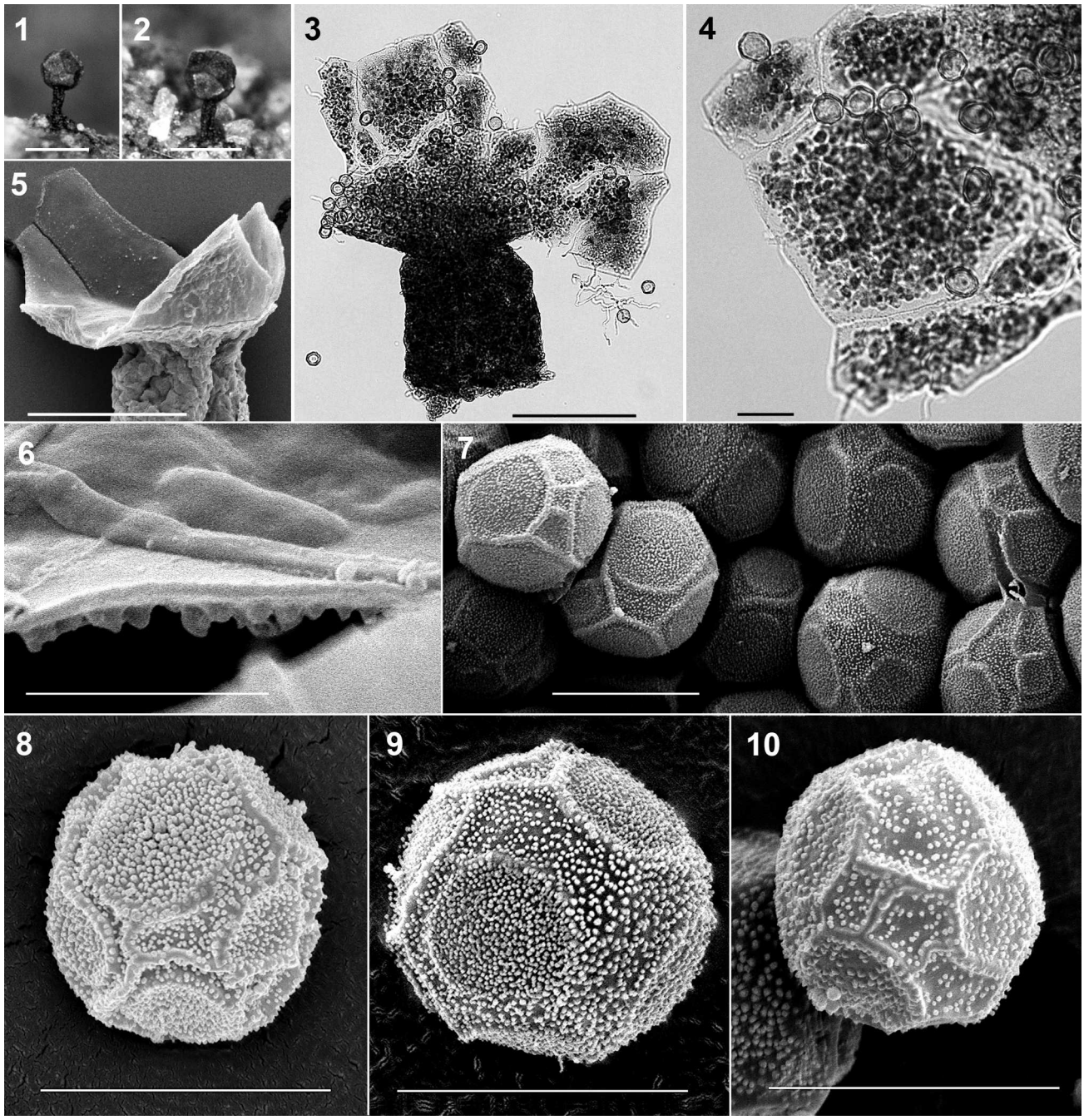
Licea eremophila D.Wrigley, Lado et Estrada sp. nov. FIGS. 1–22

MycoBank MB516047

Sporophora sporocarpica dispersa usque aggregata, stipitata, interdum subsessila, altitudine tota 0.10–0.35 mm. Sporotheca subglobosa, 0.07–0.20 mm diam, luteo fusca. Stipes cylindricus, fuscus vel atratus. Peridium unicum, membranaceum, materia granulata deposita tectum; faciebus polygonalis dehiscentibus desinenti. Capillitium nullum. Sporae liberae, massa flavo aurantiacae, luce transmissa flavae, polyedricae, verrucosae, (9–)10–12(–13) μm diam.

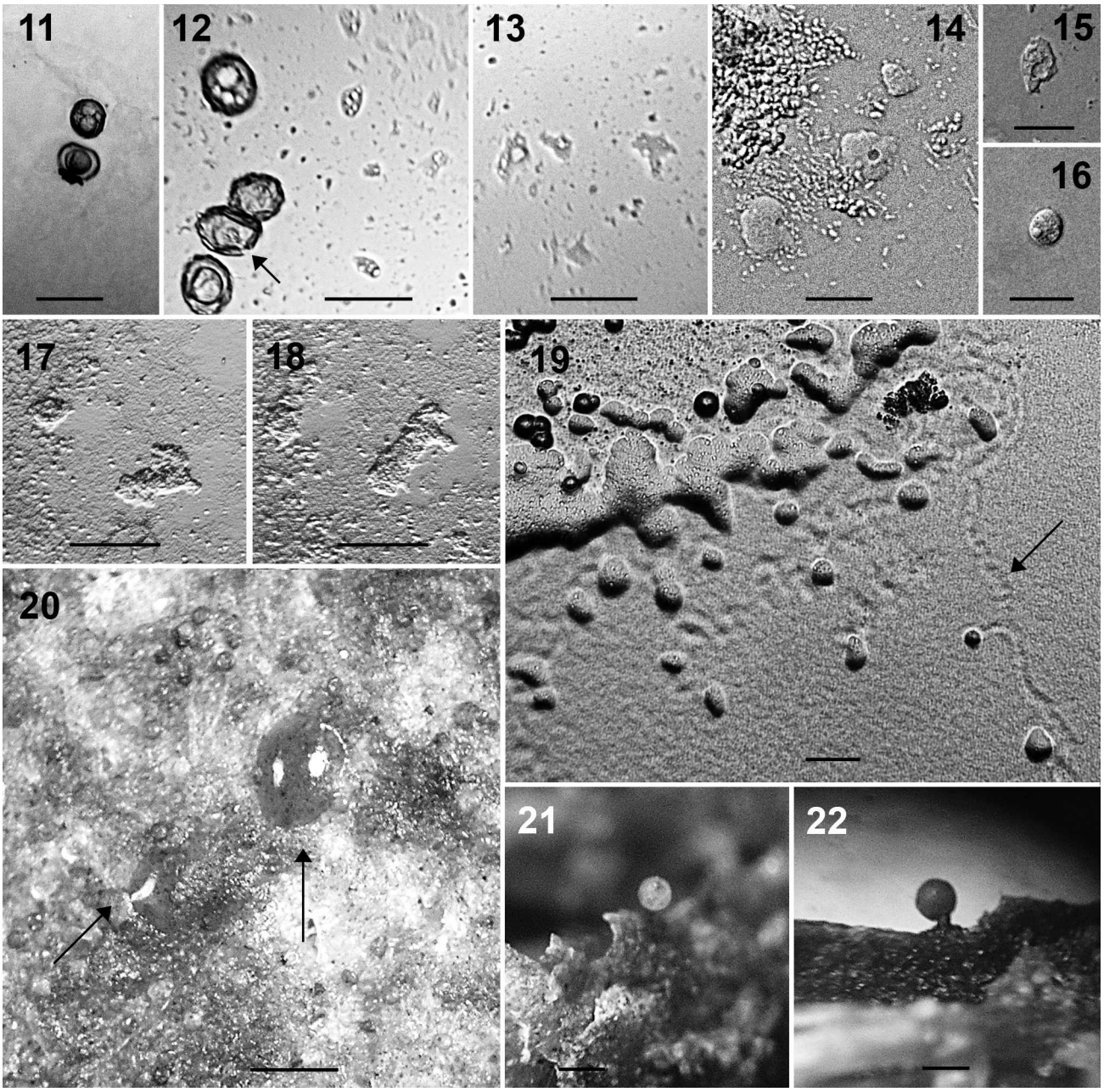
Sporophores sporocarpic, dispersed or grouped, stipitate, occasionally subsessile, 0.10–0.35 mm high. Sporotheca strong yellowish brown (74. s. y Br–95. m. Ol Br), subglobose, 0.07–0.2 mm diam, angular where peridial platelets meet (FIGS. 1, 2). Hypothallus membranous, inconspicuous. Stalk dark brown to blackish, by LM brown (55. s. Br–56. deep Br), cylindrical, filled with refuse material, 0.03–0.18 mm high, mid-width approximately one-quarter stalk height. Peridium single, entirely composed of platelets, light brown (57. l. Br–76. l. y Br) to almost colorless by LM; membranous, covered with a layer of embedded refuse material sometimes forming darker thick deposits appearing as spots on the surface (FIG. 2); the inner surface smooth (FIG. 5) except for a few dispersed warts and a line of warts along the margins of the platelets only visible by SEM (FIGS. 5, 6); dehiscence by platelets (FIGS. 3, 4) sometimes leaving only a thin collar-like base attached to the stalk, 10–15 platelets per sporotheca; platelets polygonal with well defined margins. Capillitium absent. Columella absent. Spores free, strong yellow in mass, yellow (86. l. Y) by LM, polyhedral, (9–)10–12(–13) μm diam, roughened by LM, minutely and densely warted except on raised bands with fewer warts by SEM, bands sometimes interconnected or forming rings (FIGS. 7–10); spore wall uniformly thick. Protoplasmodium (FIGS. 19, 20) colorless, becoming milky and then turning pale yellow.

HOLOTYPE. ARGENTINA, La Rioja: Independencia, Talampaya National Park, km 99 RN-26, 30°07′42″S 67°44′19″W, 1378 m, 12-III-2007, on dead leaf bases of *Puya* sp. in moist chamber culture (pH 6.9), *D. Wrigley de Basanta*, dwb 2826 (MA-Fungi 79158).



FIGS. 1–10. 1–5. *Licea eremophila* (Holotype dwb 2826, MA-Fungi 79158). 1. Habit. Bar = 0.2 mm. 2. Sporocarp showing peridial platelets, with spots of thicker refuse material on the peridial surface. Bar = 0.2 mm. 3. Dehisced sporocarp by transmitted light. Bar = 100 µm. 4. Detail of peridial platelets by transmitted light. Bar = 20 µm. 5. Dehisced sporocarp showing smooth inner surface of peridial platelets with warted edges by SEM. Bar = 50 µm. 6. *Licea eremophila* (dwb 3151). Detail of the edge of a peridial platelet showing ornamentation on the inside edge by SEM. Bar = 5 µm. 7. *Licea eremophila* (dwb 3151). Group of spores inside the base of the sporotheca by SEM. Bar = 10 µm. 8. *Licea eremophila* (Holotype dwb 2826, MA-Fungi 79158). Spore by SEM showing ornamentation with densely warted areas and less densely warted irregularly dispersed raised bands. Bar = 10 µm. 9. *Licea eremophila* (dwb 3151). Spore by SEM. Bar = 10 µm. 10. *Licea eremophila* (dwb 3002). Spore by SEM. Bar = 10 µm.

Specimens examined. ARGENTINA, La Rioja: Independencia, Talampaya National Park, km 99 RN-26, 30°07′42″S 67°44′19″W, 1378 m, 6-V-2007, on dead leaf base of *Puya* sp., (mc, pH 7.2), dwb 2885; 15-XI-2008, (mc, pH 6.9), dwb 3151; 30-XI-2006, (fc) Lado 18420 (MA-Fungi 79160), (fc) Lado 18422 (MA-Fungi 79161). Catamarca: Tinogasta, La Puntilla, 28°06′13″S 67°30′52″W, 1184 m, 12-III-2007, on dead leaf base of *Puya* sp. (fc) dwb 2837; 29-V-2007, (mc,



FIGS. 11–22. *Licea eremophila*. Stages in the life cycle. 11. Spore with multiple protoplasts (dwb 3002). Bar = 20 µm. 12. Spores showing germination pore (arrow) and early amoebae (dwb 2826). Bar = 20 µm. 13. Amoebae (dwb 2826). Bar = 20 µm. 14. Detail of older amoebae feeding on bacteria (dwb 3002). Bar = 20 µm. 15. Amoeba showing contractile vacuole (dwb 3002). Bar = 20 µm. 16. Amoeba rounding up to form a microcyst. (dwb 3002). Bar = 20 µm. 17–18. Two protoplasmodia on agar in a 10 min sequence (dwb 3092). Bar = 200 µm. 19. Protoplasmodia making tracks on agar (arrow) (dwb 3092). Bar = 100 µm. 20. Two protoplasmodia on the filter paper of a moist chamber culture (dwb 3002). Bar = 100 µm. 21–22. Sporocarps maturing on filter paper of moist chamber culture (dwb 3002). Bar = 0.2 mm.

pH 6.9), dwb 2888; 29-XI-2006, (fc) Lado 18359 (MA-Fungi 79159). Tinogasta, Costa de Reyes, road RN-3, 28°16′18″S 67°38′51″W, 1437 m, 7-XII-2007, on dead leaf base of *Puya* sp. (mc, pH 7.4), dwb 2982. Tinogasta, Costa de Reyes, road RN-3, 34 km from Tinogasta, 28°23′12″S 67°39′44″W, 1647 m, 15-I-2008, on epidermis and internal tissue of *Trichocereus* sp. (mc, pH 7.4), dwb 3002. San Juan: Ullum, Quebrada de las Burras, 31°00′46″S 68°45′58″W, 1370 m, 10-VII-2007, on dead leaf base of *Puya* sp. (mc, pH 6.7), dwb 2920.

CHILE. III Region, Atacama: Chañaral, Pan de Azúcar National Park, mirador Pan de Azúcar, 26°06′40″S 70°38′54″W, 313 m, 6-VIII-2008, on dead leaf base of *Puya* sp., (mc, pH 7.4) dwb 3092. Copiapó, Canto del Agua, road

RN-5, km 713, 28°08′42″S 70°38′06″W, 446 m, 8-XI-2008, on *Miqueliopuntia miqueli* epidermis, (mc, pH 6.9), dwb 3113.

Etymology. From the Greek *erem* (desert) + *philus* (loving), from its desert habitat.

Substrate. On dead leaf bases of the bromeliad *Puya* spp. and on dead remains of the cacti *Trichocereus* sp. and *Miqueliopuntia miqueli*.

Distribution. Known from northwestern Argentina (provinces of La Rioja, Catamarca and San Juan) and northern Chile (Atacama region). Possibly occurring in other areas of South America, following the distribution of species of the plant genus *Puya* or certain cacti.

Life-cycle events.—Spores were seen to contain four protoplasts (FIG. 11) and germinated by a pore in the spore wall (FIG. 12). Germination took 3 d both on 0.75% water agar (WA) and in germination slide cultures. Fewer than 30% of the germination attempts were successful. The spores produced four small (10–20 μm long) myxamoebae (FIGS. 12–16) that in slide cultures quickly converted to microcysts (FIG. 16). Myxamoebae on 0.75% WA plates grew and multiplied rapidly, forming vigorous feeding fronts. Swarm cells were observed when sterile water was added to the amoebal mass. On several occasions after weeks to several months of growth in the thick bacterial and yeast mélange isolated with spores from the original substrate, polynucleate early protoplasmodia were observed. These fed vigorously and showed many food vacuoles and active contractile vacuoles. As the protoplasmodia grew (50 μm) they formed in a massed feeding front but then moved out on the agar as individuals, leaving tracks on the agar surface (FIG. 19). The protoplasmodia fed, grew, moved around the same area of the dish and changed shape (FIGS. 17, 18). These protoplasmodia never formed sporocarps on agar. Protoplasmodia in moist chamber cultures (FIG. 20) at first were hyaline, 0.15 mm diam, becoming milky and turning pale yellow before sporocarp morphogenesis. Sporothecae at first were hyaline, but with patches of refuse material visible on the surface (FIG. 21). As the spores matured the peridium became darker and thicker (FIG. 22).

DISCUSSION

Taxonomy.—*Licea eremophila* differs from all described species in the genus in that it has yellowish brown sporotheca on a dark brown stalk, with dehiscence by defined preformed platelets with a covering of refuse material leaving a clear band around the edge by LM (FIGS. 3, 4). In addition this *Licea* has a smooth inner peridial surface, with ornamented platelet edges (FIG. 5), and polyhedral spores, angular in optical section (FIGS. 4, 12), with unique ornamentation under SEM (FIGS. 7–10). Dehiscence by platelets is common among sessile members of the genus, but none of the 21 stipitate *Licea* species examined in Wrigley de Basanta and Lado (2005) dehisced by this method. The most similar dehiscence was that of *Licea verrucospora* (T.N. Lakh., Nann-Bremek., & R.K.Chopra) D. Wrigley & Lado, with a ridged peridium that fragments into irregular platelets that do not follow the peridial ridges, and it does not have defined preformed platelets with ornamented edges like *L. eremophila*. We have examined the paratype material of this species (NENB 13.877 in BR as *Licea scyphoides* var. *reticulata*), and the sporothecae are dark brown with a concolorous stalk, not yellowish brown on a dark brown stalk. *Licea verrucospora* differs also in having a peridium that is densely and prominently warted on the inner surface, not smooth with warts only on the edges of the platelets. A further difference is in the spores that are globose and minutely warted, with warts in irregular patches, and the spore wall has a thinner paler area by LM in *L. verrucospora* vs. angular to polyhedral spores, roughened and with a uniformly thick spore wall by LM in *L. eremophila*. Another species of *Licea* with a stalk and a smooth inner peridium is *L. bulbosa* Nann.-Bremek. & Y. Yamam., but this is easily distinguished from *L. eremophila* by the circumscissile dehiscence of the sporotheca, the absence of peridial plates, the transparent base of the sporotheca and the almost hyaline, smooth spores. *Licea parvicapitata* Y. Yamam. has stipitate sporocarps with large warts on the outer surface of the sporotheca, but it also has circumscissile dehiscence, a single peridium strongly warted on the inner surface and small spores (7–8 μm diam vs. 10–12 μm diam in *L. eremophila*).

The occasional subsessile sporocarps, always accompanied by stipitate fruiting bodies in our collections, can be readily distinguished from any other sessile member of the genus with platelets by the strong yellowish brown sporotheca and the yellow, polyhedral, thick-walled spores. A newly described species of another genus, *Perichaena polygonospora* Novozh., Zeml., Schnittler & S.L. Stephenson, has polygonal spores, but *Licea eremophila* can be readily distinguished from this species by the presence of a protoplasmodium and the dehiscence of the sporotheca by means of defined platelets. In addition the inner surface of the peridium of *Licea eremophila* is smooth, unlike that of *Perichaena polygonospora*.

Agar culture.—The reason that germination occurred in fewer than 30% of trials is unknown, but germination might be inhibited by factors on the

spores themselves, as suggested by Ashworth and Dee (1975) for *Physarum polycephalum*, or stimulated by food organisms taken into the cultures on the surface of the spores. The thick spore walls in this species are probably an additional adaptation against rapid germination, which would have a selective advantage in such arid environments. Spores sown on sterile soft water agar, either 0.5% or 0.75%, took 3 d to germinate. In trials repeated from the same collection the addition of a drop of a 72 h substrate infusion made from 1 g substrate in 20 mL sterile water to stimulate germination did not alter the germination time. In one trial where germination had not taken place after 3 d the substrate infusion was added and the spores germinated a few days later (7–11 d dwb 3002 isolate 0821 on 0.5% WA), but repetition of the method in other cultures failed to stimulate germination.

Some spores in the slide cultures began to germinate, extruding cytoplasm through the pore but later retracting it. These spores died and the protoplasts shriveled inside them. The reason is not known, but it might have been due to lack of moisture. Amoebae were grown on various media including 0.5–2% water agar (WA), weak malt yeast agar (wMY) and half strength cornmeal agar (CM/2). The mélange of bacteria isolated with the spores grew on these media, but growth was stimulated by the addition of the nutrient solution of sterile substrate extract. This also stimulated the growth of amoeba culture. Addition of other food supplements included *Cryptococcus laurentii* streaked on the agar surface before transfer of an agar block containing amoebae. Amoebae grew well on these plates, but cultures were not as vigorous as on the natural bacteria with nutrient solution. Finely powdered sterile Quaker oat flour sprinkled on the agar surface also sustained cultures of amoebae once they had established feeding fronts on the natural mélange. Cultures with *Escherichia coli* showed poor growth.

The conditions under which protoplasmodia were formed were on CM/2 agar with an inoculating loop full of sterile nutrient solution, bacterial mélange transferred with the amoebae and enriched later with Quaker oat flour. Addition of 1–2 mL sterile water to the agar surface was necessary for protoplasmodia to develop. This was noted by Mock and Kowalski (1976) in the culture of *Licea alexopouli* M. Blackw. but was not necessary in the cultures of *Didymium umbilicatum* D. Wrigley, Lado & Estrada or *Didymium infundibuliforme* D. Wrigley, Lado & Estrada (Wrigley de Basanta et al. 2008, 2009). In cultures of *Licea eremophila*, even with this addition of water, small protoplasmodia (50 μm), never progressed, whether left in the original plates or transferred to new agar plates with more moisture and food. They either lysed or formed cysts. Encystment also occurred in cultures with ambient temperature variations up to 5 C. When transfers were made to encourage excystment protoplasmodia never developed on agar. However reverse transfers of protoplasmodia from moist chamber cultures to 2% water agar formed normal fruiting bodies. The reason for this discrepancy is unknown.

The life cycle on agar was naturally affected by the specific culture conditions and particularly by the necessity to constantly subculture the amoebae as they ran out of food and space during their log phase of growth. Many subcultures went into resting stages as microcysts or macrocysts. However in moist chamber cultures on natural substrates this species showed incubation of up to 106 d (av. 44 d) except one collection (dwb 2826) that took only 3 d, where the myxomycete was almost certainly in the form of undetected sclerotia at the time of initiating the culture. *Licea succulenticola* Mosquera, Lado, Estrada & Beltrán-Tej., a myxomycete isolated from decaying succulent plants from arid areas of Mexico and Spain, took only 6 d for its life cycle from spore to spore in culture (Mosquera et al. 2003). Another species from the genus, the coprophilous myxomycete *Licea alexopouli*, had a life cycle in culture from spore to spore of 30 d (Mock and Kowalski 1976).

Ecology.—The formation of protoplasmodia by myxomycete genera seems to be an adaptation to a habitat with high exposure to desiccation (Lado et al. 1999). Myxomycetes from genus *Licea* occur frequently on the bark of living trees (Keller and Brooks 1977), a habitat that fits into that category. In addition *L. eremophila* also appears to have a long life cycle with the ability to encyst rapidly at almost any stage, providing survival advantage in arid areas. The uniformly thick-walled spores are probably an additional adaptation against drying. Observations of moist chamber culture development of this *Licea* suggest that all initial stages of the life cycle happen inside the leaf bases of *Puya* spp., which retain a considerable amount of water through the culture period. Mature protoplasmodia emerge on the surface of leaf bases only to sporulate. At the time of collection of the leaf bases of *Puya* sp., both for culture and collections of myxomycetes in the field, underneath other dead dried leaves at the base of the plant rosettes, they were frequently still moist, even in the extremely arid conditions associated with the areas where they were collected. It is possible that morning dew, or sea mist in some cases, is condensed and accumulates at the base of the leaf rosettes of these plants, providing a source of water. Over 24 h the substrates in moist chamber culture were pH 6.7–

7.4 (mean 7.1). This differs from the basic mean pH of the succulent plant remains producing *Licea succulenticola*, although this myxomycete also completed its life cycle on agar at a neutral pH (Mosquera et al. 2003).

Licea eremophila appears not to be a common species because only nine collections developed in moist chambers from 98 cultures (42 cultures of *Puya* sp., six cultures of the species of cactus producing the *Licea* and 50 cultures of the remains of other species of cactus from the same area). In total *Puya* spp. have produced more than 25 species and 130 collections of myxomycetes in moist chamber culture and 155 collections of myxomycetes in the field (unpubl data), and among the latter only four collections of this tiny *Licea* were made, further suggesting that this is a rare species. Other myxomycete species obtained from the same cultures as *Licea eremophila* included *L. succulenticola*, *Perichaena calongei* Lado, D. Wrigley & Estrada, *Perichaena vermicularis* (Schwein.) Rostaf., *Didymium infundibuliforme*, *Didmium vaccinum* (Durieu & Mont.) Buchet and *Physarum pusillum* (Berk. & M.A.Curtis) G.Lister. Some of the species that developed on *Puya* spp. (*Perichaena vermicularis*, *D. vaccinum* and *Physarum pusillum*) also have developed on species of *Hechtia*, another bromeliad genus abundant in a dry area of central Mexico (Estrada-Torres et al. 2009). The two bromeliad genera have similar morphology, with their leaves in a rosette and the internal tissues specialized for water storage, producing similar microhabitats for myxomycetes in distinct geographical regions. However, in spite of an intensive survey of the Valle de Tehuacán-Cuicatlán, central Mexico (Estrada-Torres et al. 2009), other species of myxomycetes that developed on *Puya* spp. were not found on *Hechtia*. These two genera adapted to arid areas arose independently with morphological and physiological characters originating by convergent evolution in response to extreme aridity (Givnish et al. 2007). It is possible that the different distribution and independent phylogenetic origin of *Hechtia* and *Puya* species produced conditions for the specialization of a distinct myxobiota in the latter genus, which has a relatively recent origin and mainly Andean distribution (Crayn et al. 2004). Among this myxobiota are *D. infundibuliforme* (Wrigley de Basanta et al. 2009), *P. calongei* (Lado et al. 2009) and *Licea eremophila* described here, which seems to indicate the importance of the microhabitat for these myxomycetes.

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