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Morphology and life cycle of a new species of *Didymium* (Myxomycetes) from arid areas of Mexico

D. Wrigley de Basanta[1]
C. Lado
Real Jardín Botánico, CSIC, Plaza de Murillo 2, 28014 Madrid, Spain

A. Estrada-Torres[2]
Centro de Investigación en Ciencias Biológicas, Universidad Autónoma de Tlaxcala, km 10.5 carretera Texmelucan-Tlaxcala, Ixtacuixtla, 90122, Tlaxcala, México

Abstract: A new species of myxomycete, *Didymium umbilicatum*, isolated from the bark of Agavaceae, is described from arid zones of Mexico. This species was obtained from moist chamber cultures of *Yucca* spp. bark, collected in four different years from two states (Puebla and Querétaro) in central Mexico and found in the field from Hidalgo, Oaxaca and Puebla on the dead remains of *Agave* sp. The new species has small, flat, white sporocarps or short plasmodiocarps, 0.2–1.3 mm diam, and 0.15–0.4 mm tall. They are sessile on a reduced base or have a short, calcareous pale stalk and warted spores, warts fused in an irregular subreticulum by SEM. It is the sixth species of *Didymium* recently described from arid areas. The stability of the taxonomic characters of the species was confirmed by spore-to-spore culture on agar. Life cycle events are described from germination to sporulation. The morphology of the myxomycete specimens was examined with scanning electron microscopy and light microscopy, and micrographs of relevant details are included.

Key words: agar culture, *Agave*, moist chamber culture, morphogenesis, *Nolina*, taxonomy, *Yucca*

INTRODUCTION

The myxomycete genus *Didymium* has sporophores with a peridium covered with stellate crystals of calcium carbonate, sometimes forming a crust of aggregated crystals. It originally was described by Schrader (1797), and Lister (1925) divided the genus into two subgenera, the *Eudidymium* with a membranous sporangial wall and the *Lepidodermopsis* with a cartilaginous sporangial wall. These divisions were maintained by Martin and Alexopoulos (1969: 377), as *Didymium* and *Lepidodermopsis*, but the separation is no longer considered by these authors (Martin et al 1983), who include the single species of *Lepidodermopsis* in *Didymium*. The genus now includes more than 70 species (Lado 2001, Hernández-Crespo and Lado 2005), of which about 10% have been described in the past 15 y.

During studies of the biodiversity of myxomycetes associated with the microhabitats and dominant vegetation types in the arid zones in Mexico, a small *Didymium* appeared in moist chamber cultures of the bark of species of *Yucca*. The sporocarps had an umbilical depression on the upper surface, and examination of the spores showed a distinctive type of ornamentation suggesting an undescribed species. The characters were constant in specimens from different zones of Mexico and in five different years of fieldwork. Because of its small size and the variability of some *Didymium* species (Clark and Mires 1999, ElHage et al 2000, Clark and Landolt 2001) the new species also was cultured from spore-to-spore on agar to verify the stability of its taxonomic characters.

MATERIALS AND METHODS

The study areas were in Mexico, which has a variety of natural habitats and one of the richest floras in the world, including a large number of endemic plants (Rzedowski 1986). Among these areas are two biosphere reserves, which are of considerable biogeographic importance. The first, Sierra Gorda Biosphere Reserve, is in the north of the state of Querétaro 20°50′–21°45′N and 98°50′–100°10′W, and the Tehuacán-Cuicatlán Biosphere Reserve is in the states of Puebla and Oaxaca, 17°48′–18°58′N and 96°55′–97°43′W. In the driest areas of these reserves the annual rainfall is only about 350 mm and deciduous tropical forests and xerophyllous scrublands predominate. These are a vestige of Chihuahuan Desert, at the southern limit of the deserts of North America, and an important center of endemism and speciation of cacti (Valiente-Banuet et al 2000).

The studies of biodiversity of myxomycetes in these areas involved sampling all microhabitats in which myxomycetes are known or expected to occur, and included collection in the field and also removal of substrates for laboratory culture. This paper is based on material obtained from moist chamber culture of bark collected in xerophyllous scrubland in the states of Puebla and Querétaro, field collections from xerophyllous scrubland in Hidalgo, Oaxaca and Puebla, and also material obtained from spore-to-spore cultures on agar. The substrate material for moist chamber cultures was collected on four different occasions, between

Accepted for publication 14 August 2008.
[1] E-mail: dwb@eresmas.net, lado@rjb.csic.es
[2] E-mail: arturomixo@hotmail.com

Jul 2001 and Aug 2005. The bark was air-dried in situ and transported in sealed paper bags. All localities were georeferenced with a GPS (Garmin 12 model, Datum WGS84).

The isolate (dwb 0725) used for spore-to-spore culture was from mature sporocarps from collection dwb 2665. The spores were sown on 0.75% water agar at pH 7.0. The sporocarps were crushed and touched over the agar in four quadrants of sterile 9 cm plastic Petri dishes. Cultures were kept at room temperature (21 C–23 C) with an approximate 12 h light-dark regime. Details of media and techniques can be found in Haskins and Wrigley de Basanta (in press). In addition slide cultures (Spiegel et al 2005) were made for the light micrographs of germinating spores and amoebae. For the moist chamber technique used see Lado et al (1999). All the 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 Hoyer's medium. A microscopy with differential interference contrast (DIC) was used to obtain descriptive data and light micrographs. The critical-point drying technique was used for scanning electron microscopy (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 Jeol T 330 A 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

Didymium umbilicatum D. Wrigley, Lado et Estrada, sp. nov. FIGS. 1–14, 16–28

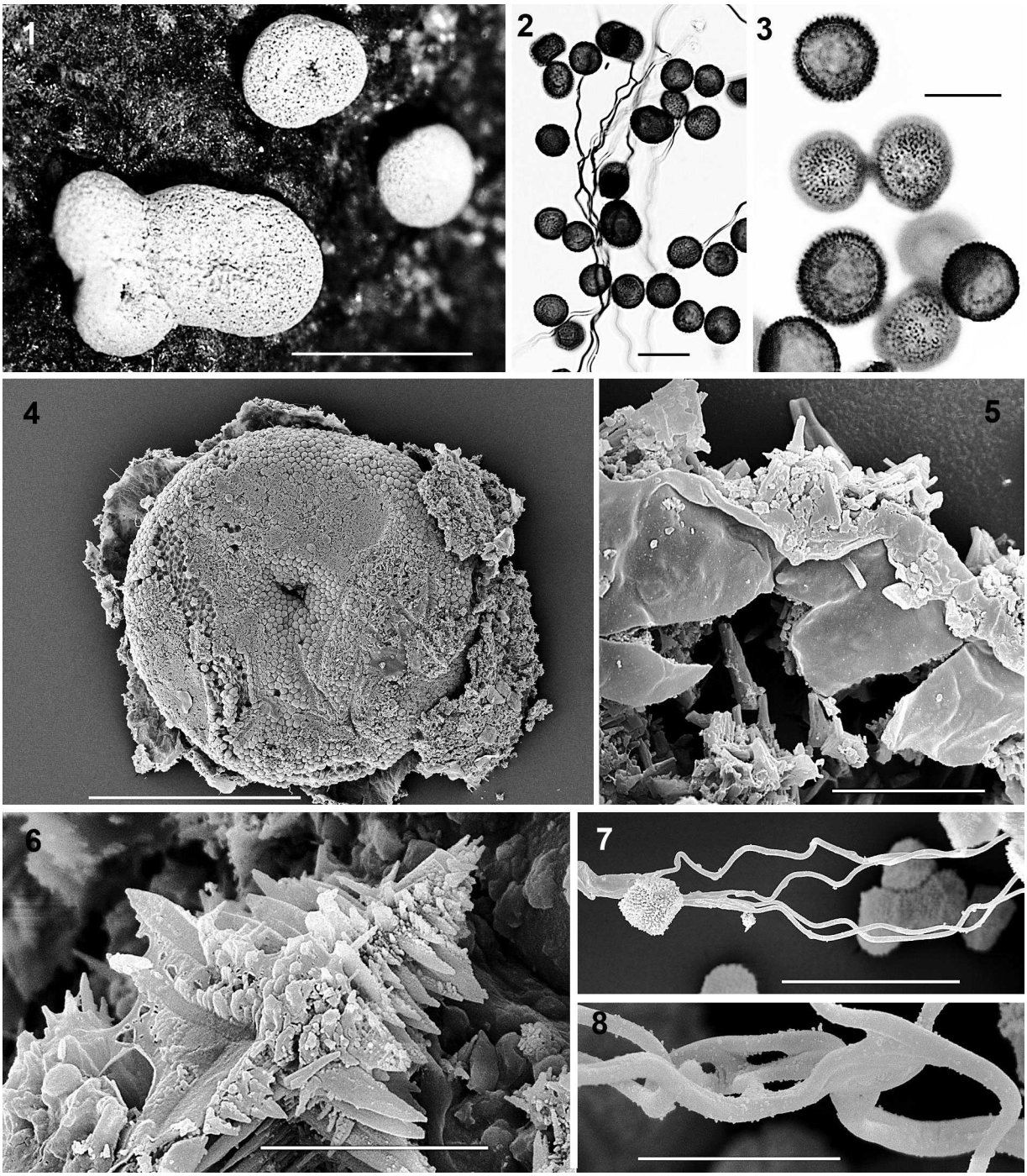
Sporophora sporocarpica, nonnumquam ita concrescentia ut brevia plasmodiocarpa efforment, pallidissime grisea vel prorsus alba, 0.15–0.4 mm alta, dispersa vel aggregata, plana, supra umbilicata, brevissime stipitata vel sessilia. Sporocarpia discoidea, 0.2–0.7 mm diam. Plasmodiocarpia discoidea vel irregularia, 0.6–1.3 mm longa. Stipes calcareus, 0.1–0.2 mm altus, 0.05–0.1 mm latus. Peridium unicum, membranaceum, crystallis albis, calcareis, coopertum. Capillitium filamentosum, filamentis 0.8–2 μm diam, parce ramificatis, undulatis. Sporae liberae, griseo-brunneae, 11–14(–15) μm diam, verrucosae, verrucis autem ± coalescentibus in irregulare subreticulum.

Sporophores sporocarpic, occasionally fused to make short plasmodiocarps, pale gray to white, 0.15–0.4 mm high, dispersed or grouped, flattened, umbilicate above (FIG. 4), with short stalks to sessile. Sporocarps discoid, 0.2–0.7 mm diam. Plasmodiocarps discoid to irregular, 0.6–1.3 mm long. Sporotheca covered with calcium carbonate crystals, pale gray to white, blackish and iridescent when the crystals are sparse or absent. Hypothallus insconspicuous, membranaceous, individualized to each sporophore. Stalk short, 0.1–0.2 mm tall, 0.05–0.1 mm wide, calcareous, with lime crystals on the surface, often only a restricted base of the sporotheca, light yellow-brown (76. l. y Br) to brownish pink (33. br Pink) by LM. Peridium single, membranous, light yellow-brown (76. l. y Br) to brownish pink (33. br Pink) by LM., its inner surface smooth, also by SEM (FIG. 5), covered by white, elongated lime crystals (FIG. 6); crystals forming an almost continuous roughened layer (FIG. 1), sometimes scattered showing the iridescent peridium, dehiscence irregular. Columella absent or reduced to a thickened funnel at the base of the sporotheca. Capillitium filiform (FIGS. 2, 7), threads 0.8–2 μm diam, scarcely branched, undulating, with a few cross connections, light grayish brown (45. l. gy. r Br), smooth but with a granular surface by SEM (FIG. 8). Spores free, black in mass, grayish brown (45. l. gy. r Br-60. l. gy. Br) to brown (58. m. Br-43. m. r Br) by LM, subglobose, 11–14(–15) μm diam, warted, warts fused in an irregular subreticulum (FIG. 3) by oil immersion and SEM (FIGS. 9–13). Phaneroplasmodium hyaline to pinkish white (9. pk White).

HOLOTYPE. MEXICO. Querétaro, Peñamiller, Plazuela, 21°03′24″N 99°42′35″W, 1395 m, on bark of *Yucca* sp. in moist chamber culture, 19-III-2005, *D. Wrigley de Basanta, C. Lado & A. Estrada-Torres*, dwb 2554 (MA-Fungi 73566).

Specimens examined. MEXICO. Puebla: Azumbilla, road to Nicolas Bravo, 18°37′39″N 97°22′15″W, 2176 m, on bark of *Yucca periculosa* in moist chamber culture, 7-XI-2005, dwb 2665. Tepeyahualco, Cantona arqueological zone, 19°33′07″N 97°30′09″W, 2520 m, on *Nolina parviflora* leaf bases in moist chamber culture,12-III-2002, dwb2166. San Martín Esperilla, 18°43′58″N 97°31′47″W, 2412 m, on bark of *Yucca periculosa* in moist chamber culture, 21-XI-2003, dwb 2339. San Luis Temalacayuca, 18°36′54″N 97°32′39″W, 1961 m, on bark of *Yucca* sp. in moist chamber culture, 31-I-2007, dwb 2808. San José Miahuatlán, Tehuacán-Cuicatlán Biosphere Reserve, San Gabriel Chilac, Cuacnopalan-Oaxaca (Mex-135) highway, km 69, 18°16′40″N 97°19′40″W, 1,230 m, on dead *Agave* sp., 8-X-1999, Lado 10922 (MA-Fungi 64464). Oaxaca: Tepelmeme, Cuacnopalan-Oaxaca (Mex-135) highway, km 130, 17°50′15″N 97°22′32″W, 2,130 m, on dead *Agave* sp., 7-X-1999, Lado 10981 (MA-Fungi 64522). Querétaro: Peñamiller, Plazuela, 21°03′24″N 99°42′35″W, 1395 m, on the bark of *Yucca* sp., in moist chamber culture, 19-III-2005, dwb 2554 (MA-Fungi 73566) (Holotypus); *ibidem*, 19-III-2005, dwb 2552; *ibidem*, 31-III-2005, dwb 2553. Hidalgo: Cardonal, San Cristobal, 20°36′53″N 98°59′12″W, 1,830 m, on dead *Agave* sp. leaf, 14-X-1999, Lado 11206 (MA-Fungi 64629). Cardonal, El Arenal, Cerro Xistha, 20°36′16″N 98°06′18″W, 1770 m, on dead *Agave* sp., 14-X-1999, Lado 11256 (MA-Fungi 64652).

Other material examined: *Didymium mexicanum* G. Moreno, Lizárraga et Illana MEXICO. Baja California, Cataviña-Bahia de los Angeles highway (near Cataviña), on decayed stalk of *Agave schawii*, 14-II-1993, G. Moreno, M. Lizárraga and C. Illana (Holotype AH 18481). Road to Valle

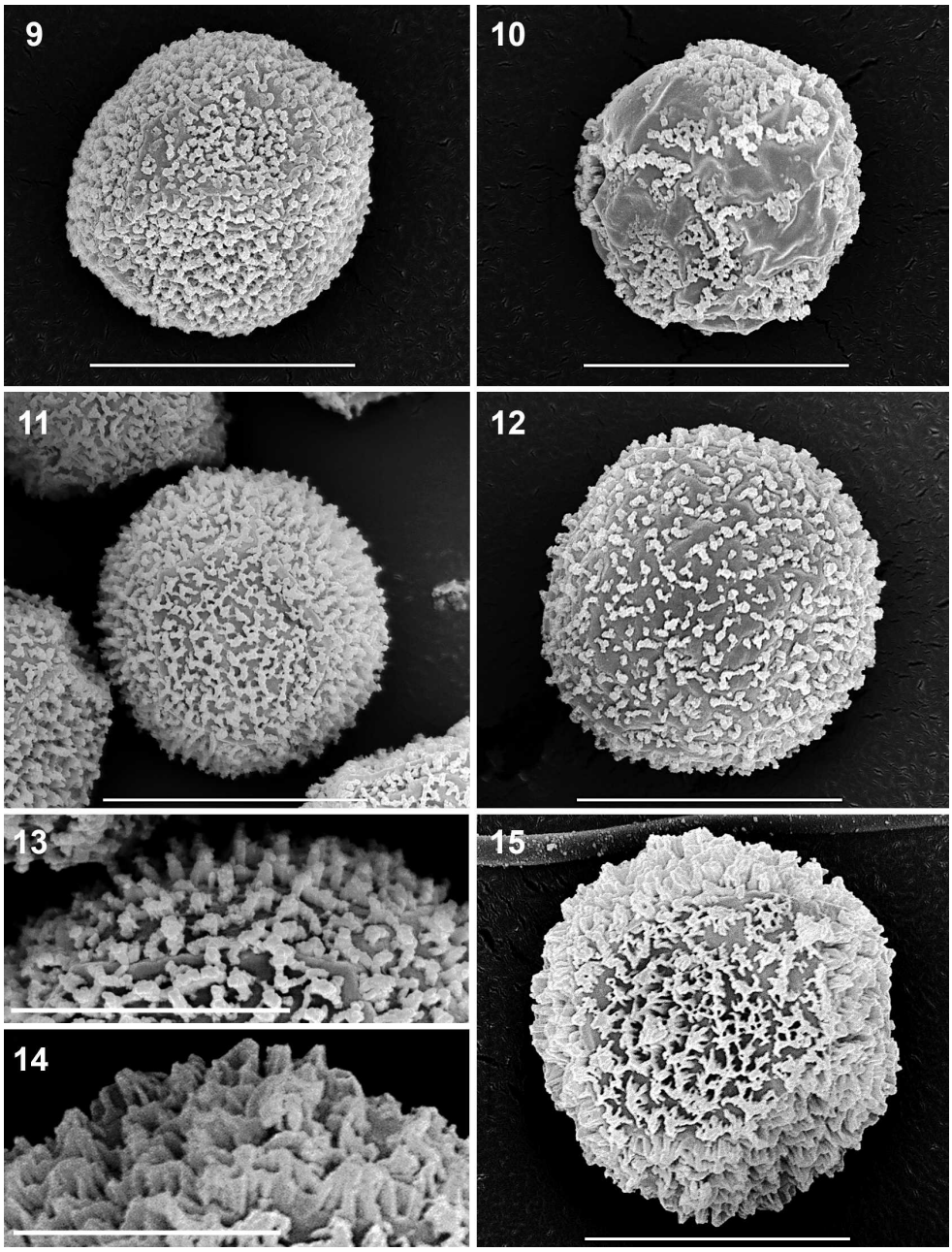


FIGS. 1–8. *Didymium umbilicatum*. 1. Sporocarps (dwb 2554). Bar = 1 mm. 2. Capillitium and spores (dwb 2554). Bar = 20 µm. 3. Spores LM (dwb 2554). Bar = 10 µm. 4. Top view of a partially dehisced sporocarp showing the central hollow by SEM (Lado 11206). Bar = 300 µm. 5. Peridium showing smooth inner surface by SEM (dwb 2554). Bar = 10 µm. 6. Crystals (dwb 2665). Bar = 10 µm. 7. Undulating capillitium (dwb 2554). Bar = 30 µm. 8. Detail of capillitium by SEM (dwb 2665). Bar = 10 µm.

Las Palmas, Rancho Los Alisos, Tijuana, on decayed stalk of *Yucca* sp., 13-XI-1994, M. Lizárraga & E.J. Torres (AH 17100).

Etymology. From the Latin: *umbilicatus-a-um*, navel-like, having a small central depression or hollow, referring to the shape of the sporotheca.

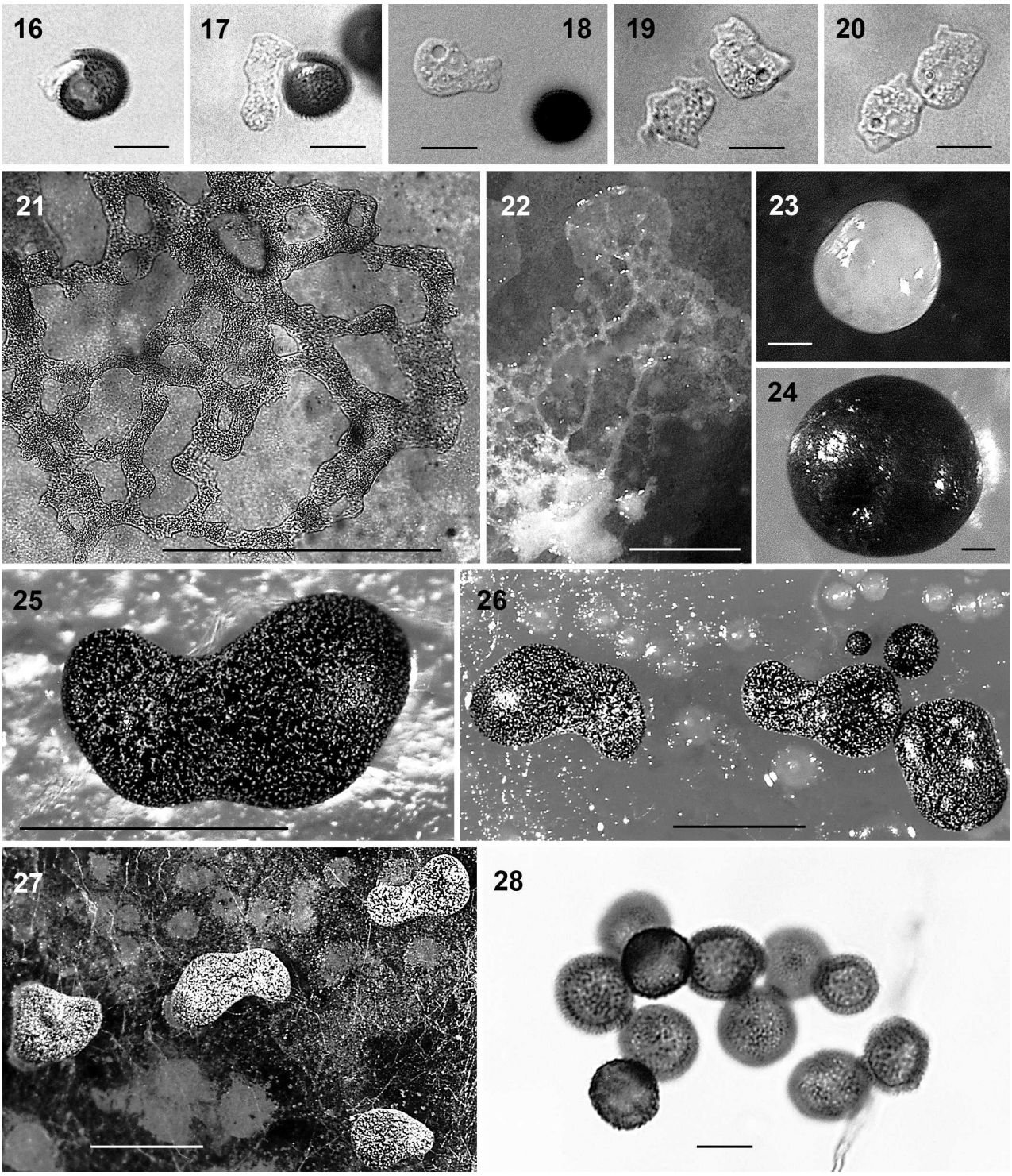
Habitat. On the bark of *Yucca* spp., dead leaf bases of *Nolina parviflora* and dead remains of *Agave* spp.



FIGS. 9–15. *Didymium umbilicatum* by SEM. Spores from different collections showing variable subreticulum patterns. 9. (Lado 10922). Bar = 10 μm. 10. (dwb 2665). Bar = 10 μm. 11. (dwb 2554). Bar = 10 μm. 12. (Lado 11206). Bar = 10 μm. 13. Detail of spore ornamentation (dwb2554). Bar = 5 μm. 14–15. *Didymium mexicanum* (AH 18481) by SEM. 14. Detail of spore ornamentation. Bar = 5 μm. 15. Spore. Bar = 10 μm.

Distribution. Known from central Mexico (states of Hidalgo, Oaxaca, Puebla, Querétaro). Possibly occurring in other arid regions of the world.

Agar culture.—Germination was by a V-shaped split in the spore wall, starting in the thinner area of the spore wall (FIGS. 16–17). Some spores germinated after 3 h, but most took 20–48 h after sowing the spores on agar. In three quadrants the spores produced myxamoebae about 12–15 μm long (FIGS. 18–20) some of which began to retract pseudopodia and differentiate into microcysts almost immediately. Swarm cells were not observed, possibly due to lack of a film of surface water necessary for some species to make these (Haskins and Wrigley de Basanta in press). Small agar blocks, containing myxamoebae and some spores and spore cases, were transferred from the germination plate to fresh plates with 1.5%



FIGS. 16–28. *Didymium umbilicatum*. Agar culture. 16–20 (dwb 2554). Bar = 10 μm. 16–17. Germinating spores. 18–20. Myxamoebae. 21–28 (dwb 2665, isolate 0725). 21. Early reticulate plasmodium. Bar = 100 μm. 22. Phaneroplasmodium. Bar = 2 mm. 23–24. Developing sporocarps. Bar = 0.1 mm. 25–26. Maturing sporocarps and short plasmodiocarps showing lime crystal deposits. Bar = 1 mm. 27. Mature sporocarps on dried agar film. Bar = 1 mm. 28. Spores from a new generation sporocarp. Bar = 10 μm.

water agar (WA) with the bacterial melange isolated incidentally with the spores. After 18 d small hyaline phaneroplasmodia were observed in the rich bacterial melange. Sterile Quaker oat flour was added and the plasmodia grew, from pinkish reticulate forms (FIG. 21) to larger white phaneroplasmodia (FIG. 22) over a further 8–12 d. On day 51 from sowing the spores, the first fruiting bodies were observed, pale at first (FIG. 23) then darkening as the spores matured to become black and shiny (FIG. 24). Small pieces of agar with the forming sporocarps were transferred to sterile 2% WA to mature and be dried slowly with the lid unsealed over several days. On drying, lime crystals became visible over the surface (FIGS. 25–27). Material from agar culture had identical sporocarps, capillitium and spores to the moist chamber collection from which it was isolated (FIGS. 3, 28).

DISCUSSION

The most distinctive characters of *Didymium umbilicatum* are the flat sporophores, 0.15–0.4 mm total height, the umbilicate shape of the sporotheca, the uniform undulating capillitium and the warted spores with the warts fused in an irregular subreticulum. The combination of these characters makes this species unique in the genus.

Other species of this genus, which are close to *Didymium umbilicatum*, have been described from arid areas, but all have distinguishable characters (TABLE I). The closest species is *Didymium mexicanum* G. Moreno, Lizárraga et Illana which was described by Lizáraga et al (1996) based on specimens collected on decaying desert vegetation (*Agave shawii* and *Yucca* sp.) in Baja California, Mexico. A more detailed description, including illustrations and a third specimen, was given by Moreno et al (1997). The holotype collection was on dead wood (''in ligno mortuo'' [Lizáraga et al 1996]). Examination of this holotype material and the paratype showed that *Didymium mexicanum* has mainly pulvinate sporocarps or plasmodiocarps, not flattened sporocarps, and they lack the characteristic umbilicus, a hollow that penetrates the sporotheca (FIGS. 1, 4), that gives *D. umbilicatum* its name. *Didymium mexicanum* also has darker spores (44. d. r Br-59. d. Br versus 45. l. gy. r Br-60. l. gy. Br to 58. m. Br-43. m. r Br in *D. umbilicatum*) with paler areas (Moreno et al 1997 FIG. 5), absent in *D. umbilicatum* (FIGS. 3, 28), and the spores are generally larger than the species described here (14–16[–18] μm diam vs. 11–14[–15] μm diam in *D. umbilicatum*). In addition the spores of *D. umbilicatum* are subglobose, whereas in *D. mexicanum* they are somewhat polygonal in optical section ''with strong ridges, bearing warts united laterally in a reticulum'' and ''with vertical processes that interconnect'' by SEM (Moreno et al 1997:328). This spore ornamentation forms distinct muri (FIGS. 14, 15) according to the terminology used by Rammeloo (1974, 1975) and is different from the warts or bacula of *D. umbilicatum* some of which are fused in an irregular and discontinuous subreticulum by SEM (FIGS. 9–13). (FIGURES 9–12 show the irregularity of the subreticulum on the spores from different collections of *D. umbilicatum*, but none of them have the vertical interconnecting processes seen in *D. mexicanum* spores.) A high magnification section of the spore of each is included, which clearly illustrates the different ornamentation (FIGS. 13, 14). The bacula of *D. umbilicatum* spores have spaces between them where individual bacula are not fused, and the vertical processes of *D. mexicanum* spores are linked by a thinner continuous structure without free space underneath. The spore (FIG. 10) is typical of a slightly immature sporophore, with large smooth areas lacking the subreticulum. A further difference between these two species is the capillitium, which in *D. umbilicatum* is undulating (FIGS. 2, 7–8) but is straight in *D. mexicanum*, and the threads have dark, rounded and funnel shaped swellings, absent in *D. umbilicatum*.

Didymium subreticulosporum Oltra, G. Moreno & Illana was described from *Opuntia* in Spain (Moreno et al 1996:57) and also found in Mexico (Lizáraga et al 1998), but the spore ornamentation of *Didymium umbilicatum* is different from *D. subreticulosporum* in that the reticulum of the latter species is even, smooth and continuous, except for the paler side (Mosquera et al 2000:980), whereas in *D. umbilicatum* it is discontinuous, and formed by the fusion of warts or bacula that project above the bands of the subreticulum (FIG. 11–13). The reduced or absent stalk, umbilicate shape of the sporotheca and the presence of true capillitium also differentiate it from *D. subreticulosporum*, and the spores of the latter are smaller (8.4–11.6 μm). *Didymium reticulosporum* Novozh. & Zeml. was described from a dry steppe community in the watershed of the Volga River and has large-mesh banded reticulate spores with 3–4 meshes across the hemisphere (Novozhilov and Zemlyanskaya 2006), not subreticulate like *D. umbilicatum*, and has subglobose to pulvinate sporocarps and no capillitium.

Another *Didymium* from arid areas that has a reduced or absent columella is *D. wildpretii* Mosquera, Estrada, Beltrán-Tej., D. Wrigley & Lado, but the yellow sporotheca and the small spores, 7.5–9.5 μm diam, covered with warts that are dense, flat and uniform (Lado et al 2007), not subreticulate, differentiate it from *D. umbilicatum*. Blackwell and

TABLE I. Morphological characters differentiating some similar *Didymium* species

Species	Sporophores	Capillitium	Spore size	Spore ornamentation
D. umbilicatum	Sessile to short stalked, flattened, umbilicate, 0.15–0.4 mm tall. Pale gray to white.	Undulating, of uniform diameter	11–14(–15) µm	Warts or bacula fused in a discontinuous sub-reticulum.
D. mexicanum	Sessile to short stalked, pulvinate or discoid to elongate depressed, 0.2–0.8 mm tall. White.	Straight, with dark funnel-shaped enlargements	14–6(–18) µm	Reticulum of vertical processes interconnected by lower muri.
D. subreticulosporum	Stalked, globose to reniform, 1–2 mm tall. White to gray.	No true capillitium but with an enlarged columella.	8.4–11.6 µm	Subreticulum, broken on one side.
D. reticulosporum	Sessile, subglobose or pulvinate, 0.5–1.5 mm diam. Snow-white to ash gray.	none	13–16 µm	Reticulum of uniform bands.

Gilbertson (1980) described *Didymium eremophilum* from the Sonoran Desert in Arizona, but this species also lacks capillitium and has erect tall stalked sporocarps and smaller echinulate spores, 9–11 µm diam.

In the moist chamber cultures of bark producing *Didymium umbilicatum*, the substrate pH was 6.2–7.3 (average pH 6.8). This range was similar to the circumneutral pH of the agar media on which it completed its life cycle from spore to spore. There is an apparent association of many species of myxomycetes with substrates that have a circumneutral pH, and experience has shown that moist chamber cultures with substrate pH at each extreme tend to be less productive (Wrigley de Basanta 2000, 2004; Wrigley de Basanta et al in press). There are however some species that appear to be selected to grow in other pH values. In arid areas other species have developed in very basic media, for example *Didymium wildpretii* which grows on substrata with basic pH values of 7.8–10.0, and an optimum of 8.5–9.4 (Lado et al 2007) or *Licea succulenticola* (Mosquera et al 2003) on substrata with pH 10. The differences in pH selection might reflect different food organism availability during a succession in substrate decay, instead of a direct effect on the myxomycete. Both bacteria and yeasts have been shown to have high levels of specialization in host plant use, and different species even grow on the same plant according to tissue types, and in yeasts species composition is thought to vary according to the stage of plant rot (Foster et al 1993, Starmer et al 1991).

In moist chamber cultures myxomycetes show a wide range of incubation times, even within one species (Wrigley de Basanta 1998). The incubation times in moist chamber culture of *D. umbilicatum* were 12–49 d with a mode of 30 d. *Didymium wildpretii* also had a shorter development time in moist chamber than in agar culture, but with these cultures it is never possible to know whether the bark had the initiate in the form of spores, microcysts or sclerotia (Lado et al 2007). The shorter times seem to indicate one of the latter resistant forms. In moist chamber culture the sporocarps developed between the layers of bark, not on the surface, and sometimes were flattened by this environment. Culture times on agar and in moist chamber of *Didymium eremophilum* (Blackwell and Gilbertson 1980) were reported to be similar.

The germination of *D. umbilicatum*, within 48 h is about the same as the time taken another recently described succulenticolous species of the same genus. *Didymium wildpretii* (Lado et al 2007) took under 48 h to germinate; *D. annulisporum*, a species described from bovine dung, took about 19 h to

germinate (Keller and Schoknecht 1989) and also had a much shorter life cycle than either of the succulenticolous species, completing its cycle on agar in 6 d. The life cycle on agar of *D. eremophilum* was completed in 5 d but that of *D. umbilicatum* on agar was at least 51 d and that of *Didymium wildpretii* was 28–56 d (Lado et al 2007). It may seem that a shorter life cycle would be more adaptive in the extreme desert conditions, as suggested by Blackwell and Gilbertson (1980), but the ability and tendency of these species to rapidly produce microcysts and sclerotia would be a surer survival mechanism to resist sudden environmental change, and these dormant periods would lengthen the cycle. The precise conditions of agar culture in the laboratory also might alter the natural life cycle length. In agar culture, a closed system with constant moisture, the formation of microcysts was not a response to drying but might be due to an excess of or lack of food organisms. In some plates when amoebae and cysts in an abundant growth of bacterial melange were subcultured to new agar plates microcysts excysted. Similarly when plates with little bacterial film were sprinkled with oat flour, microcysts excysted and amoebal populations increased.

Among other observations made while culturing this *Didymium* was that tiny rounded reticulate plasmodia, only twice the spore diameter, formed in one remaining quadrant of the 0.75% WA germination plate. Whether the size means that, at least on 0.75% water agar medium, the amoebae quickly formed minute plasmodia instead of remaining as amoebae is unknown. Even mature plasmodia in agar culture were small and gave rise to a single, or only a few, sporocarps each. This might account for the dispersed habit of this species and is probably another strategy for success in arid areas that Blackwell and Gilbertson (1980) found with *D. eremophilum*, which also produced tiny young plasmodia after 72 h and then small phaneroplasmodia.

Didymium umbilicatum seems to be a rare species because only six cultures from 60 (10%) of *Yucca* bark produced this myxomycete, and apart from one very small collection from the leaf bases of *Nolina parviflora* so far no other substrate in more than 500 cultures from arid areas have produced it. Its appearance in the field on the decayed tissue of *Agave* spp. confirms its presence on succulents, where its flat shape against or between the layers of the substrate might have caused it to be overlooked in the field.

The material for moist chamber cultures, which produced *D. umbilicatum*, has been collected from two different states in central Mexico and in four different years, and the myxomycete also was found in the field on the inner remains of dead *Agave* spp. from a further two Mexican states. It has completed its cycle from spore to spore on agar and the stability of its morphotaxonomic features has been confirmed. It therefore is described here as a new species and increases the number of *Didymium* species recently described from arid areas to six (*D. eremophilum*, *D. mexicanum*, *D. subreticulosporum*, *D. wildpretii*, *D. reticulosporum*, *D. umbilicatum*). The presence of the species on three genera of succulent plants from the same family, but from states almost 1000 km apart, supports the idea that the appearance of this myxomycete is influenced by the microhabitat conditions associated with the substrate more directly than the macrohabitat or biogeographical factors.

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