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ADDENDA TO "THE MEROSPORANGIFEROUS MUCORALES" III DIMARGARIS

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In my summary of the genus *Dimargaris* published nearly six years ago (Benjamin, 1959, pp. 365–380) three species, *D. cristalligena* Van Tieghem, *D. verticillata* Benjamin, and *D. bacillispora* Benjamin, were described and illustrated. Since that time, three more taxa have been characterized by Mehrotra & Baijal from dung and soil collected in India: *Dimargaris oblongispora* Mehrotra & Baijal (1963), *D. verticillata* Benjamin var. *xerosporica* Mehrotra & Baijal (1964), and *D. simplex* Mehrotra & Baijal (1964).

Both *D. oblongispora* and *D. simplex* resemble *D. bacillispora* in that the sporiferous branchlets composing the fertile head are few in number (2–3 or 4) and borne directly on the apex of the fertile branch, not on a vesicular enlargement of the latter as in other known species of *Dimargaris*. It may be noted that the fungus referred by Boedijn (1958, p. 355) to *D. cristalligena* is of this type, but its specific identity is uncertain. Unfortunately, living cultures of the type collections of *D. oblongispora* and *D. simplex* were not preserved, and material representing these species has not been available for study by the writer.

An unusual feature of *D. verticillata* var. *xerosporica* is that the fertile heads remain dry at maturity. This is in contrast to the production of spore-drops by all other described species of the genus. The dry-spored condition is characteristic of the known species of *Dispira* and *Tieghemiomyces* also of the Dimargaritaceae (Benjamin, 1959, 1961, 1963).

A living culture of the type collection of *Dimargaris verticillata* var. *xerosporica* was obtained through the courtesy of Dr. C. W. Hesseltine, Northern Utilization Research and Development Division, United States Department of Agriculture, Peoria, Ill. This fungus has been grown in culture on *Cokeromyces recurvatus* and compared with several isolates, including the type, of *D. verticillata*. The two taxa are quite distinct specifically. In addition, a second dry-spored species of *Dimargaris* has been obtained from soil collected near Brownsville, Texas. The latter fungus was isolated by the writer from a dry agar culture of soil received from Dr. Constantine J. Alexopoulos, Department of Botany, University of Texas, Austin.

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Fig. 1. *Dimargaris xerosporica*.—a. Habit sketches of sporophores. $\times 30$.—b. Typical sporophore showing characteristic cymose branching pattern. The lowermost fertile head is the oldest; the one at the tip of the apparent main axis (upper right) is the youngest. $\times 145$.—c. Haustorium. $\times 1080$.—d-f. Three successive stages in the development of the sporiferous branchlets and merosporangia. $\times 1360$.—g. Three mature merosporangia prior to disappearance of the sporangial wall and four sporangiospores. $\times 1360$.

It is the purpose of this paper to describe and compare the above dry-spored taxa of *Dimargaris*.

***Dimargaris xerosporica* (Mehrotra & Baijal) comb. nov.**

Dimargaris verticillata Benjamin var. *xerosporica* Mehrotra & Baijal. Zentralbl. Bakt., Parasitenk., Infektionskr. und Hygiene, Abt. 2. 118: 171. 1964.

(Fig. 1 and 2 b-e)

Colonies on *Cokeromyces recurvatus* on YpSs agar white, near "Cartridge Buff" (Ridgway, 1912) in age; vegetative hyphae colorless, septate, 2-4 μ in diam.; haustoria at first simple, then ramose, the branches mostly 1-1.5 μ wide, up to 15-20 μ long; sporophores erect, septate, colorless, at first simple and producing white fertile heads terminally when about 0.5-1.5 mm high, becoming cymosely branched by the successive development of fertile branches, each of which arises as a divergent outgrowth from a point immediately below a septum in the upper part of the preceding branch; sporophores, in age, 1.5-3(-4) mm high, 6-10 μ in diam., composed of cells that vary in length from about 50-350 μ ; fertile branches 1-6, usually 40-300(-750) μ long, slightly tapered, 5-10 μ in diam. at the base, terminated by single fertile heads; fertile heads globoid, 35-100 μ in diam., producing, over their entire surface, numerous sporiferous branchlets consisting usually of three slender, clavate, superposed cells about 9-20 μ long $\times$ 3.9-5.2 μ in diam. at the widest point, 2.2-3.1 μ in diam. at the base; the basal cell of each sporiferous branchlet typically giving rise to a single, divergent, subequal cell distally; all cells of the sporiferous branchlets bearing distal whorls of merosporangia containing two spores each; the terminal portion of the merosporangium developing by budding from the basal; spores elongate-ovoid, 3.7-7 μ $\times$ 2.6-3.1 (mean: 5.3 μ $\times$ 2.9 μ); most cells of the sporiferous branchlets disarticulating at maturity; fertile heads remaining dry; zygospores not observed.

Holotype.—INDIA. Isolated from snail excreta by B. S. Mehrotra and Usha Baijal (M-76). A transfer of the type culture received from the Northern Utilization Research and Development Division, Peoria, Ill. (NRRL A-12,037) has been examined. Dry specimens of this culture (RSA Culture 1266) have been deposited in the Mycological Collections of the Rancho Santa Ana Botanic Garden, Claremont, Calif., and transfers of the living culture have been sent to the ATCC, CBS, and CMI.

***Dimargaris arida* sp. nov.**

(Fig. 3-5)

Coloniae in *Cokeromycete recurvato* in agaro YpSs albae, in aetate "Cartridge Buff"; hyphis vegetantibus hyalinis, septatis, ramosis, 2-4 μ diam.; sporophoris rectis, septatis, levibus, in juvenitate simplicibus, in aetate pseudoverticillatis, 1-4 ramos divaricatos infra 1-5 septa in partibus superioribus fertilibus gerentibus; ramis plerumque 2-cellulis, 40-160 μ $\times$ 5-10 μ ; axibus principalibus 1-2 axes secundarios gerentibus; sporophoris in aetate 0.5-3(-4) mm altis; cellulis in stipitibus principalibus 40-260 μ $\times$ 6-11 μ ; caputibus fertilibus terminalibus, globosis, 30-80(-100) μ diam., in vesiculis globosis, 8-20

Fig. 2. a. *Dimargaris verticillata*.—Fertile head showing compact appearance. $\times 325$.—b-e. *Dimargaris xerosporica*.—b. Fertile head showing more open arrangement of the sporiferous branchlets. $\times 325$.—c. The same. $\times 600$.—d. Several sporiferous branchlets. $\times 1000$.—e. Typical cross-wall $\times 1300$.

Fig. 3. *Dimargaris arida*.—a. Habit sketches of sporophores. $\times 30$.—b. Typical sporophore showing characteristic pseudovericillate branching pattern. $\times 145$.—c. Haustorium, $\times 1080$.—d-f. Three successive stages in the development of the sporiferous branchlets and merosporangia. $\times 1360$.—g. Three mature merosporangia prior to disappearance of the sporangial wall and five sporangiospores. $\times 1360$.—h-o. Successive stages in the development of the zygospore. $\times 600$.

FIGURE 3

μ diam., et ramusculis sporogenis consistentibus; ramusculis sporogenis in 3 cellulis clavatis $7.5-18 \mu \times 3.5-5 \mu$, per gemmascentem gestis, consistentibus; cellulis sporogenis merosporangia de 2 sporis gerentibus; merosporangiis per gemmascentem gestis; sporis elongato-ovoideis, $3.5-4.8 \mu \times 2.2-2.6 \mu$; ramusculis sporogenis et sporis in maturitate disarticulatis et siccis, zygosporis hyalinis, levibus, de muris crassis, globosis vel plerumque subglobosis, $31-42 \mu \times 30-37 \mu$, globulos singulos excentricos, $9-17 \mu$ diam., continentibus; muro $4-7 \mu$ crasso.

Colonies on *Cokeromyces recurvatus* on YpSs agar white, near "Cartridge Buff" (Ridgway, 1912) in age; vegetative hyphae colorless, septate, $2-4 \mu$ in diam.; haustoria at first simple, then ramose, the branches mostly $1-1.5 \mu$ wide, $10-20 \mu$ long; sporophores erect, septate, colorless, at first simple and producing single fertile heads terminally when about $0.5-3$ mm high, becoming pseudoverticillately branched by the successive formation of $1-4$ divergent fertile branches immediately below $1-5$ of the distal septa of the main stalk; one or more secondary fertile axes often arising from the primary axis in the same manner as the fertile branches; fertile branches usually 2-celled including the terminal vesicle, about $40-160 \mu$ long, slightly tapered, $5-10 \mu$ in diam. at the base, terminated by single fertile heads; sporophores, in age, $0.5-3$ (-4) mm high, $6-11 \mu$ in diam., composed of cells that vary in length from about $40-260 \mu$; fertile heads globoid, mostly $30-80$ (-100) μ in diam., composed of nearly globose vesicles $8-20 \mu$ in diameter, producing, over their entire surface, numerous sporiferous branchlets consisting usually of three slender, clavate, superposed cells about $7.5-18 \mu$ long $\times 3.5-5 \mu$ in diam. at the widest point, $1.8-2.6 \mu$ in diam. at the base; the basal cell of each sporiferous branchlet typically giving rise to a single, divergent, subequal cell distally; all cells of the sporiferous branchlets bearing distal whorls of merosporangia containing two spores each; the terminal portion of the merosporangium developing by budding from the basal; spores elongate-ovoid, $3.5-4.8 \mu \times 2.2-2.6 \mu$ (mean: $4.1 \mu \times 2.3 \mu$); most cells of the sporiferous branchlets disarticulating at maturity; fertile heads remaining dry; zygosporos developed from the conjugation of an undifferentiated hyphal branch with a vegetative hypha and formed by the enlargement of a cell developed in the sexual branch, colorless, thick-walled, globose but mostly subglobose, $31-42 \mu \times 30-37 \mu$ (mean: $36 \mu \times 33 \mu$), wall $4-7 \mu$ thick, containing, when mature, single eccentric globules $9-17 \mu$ in diam.

Holotype.—TEXAS, Cameron County: 2 miles east of Brownsville, November, 1963, soil under *Prosopis* sp. Collector unknown; the original soil culture from which the fungus was isolated was prepared by Mary R. Henney, Department of Botany, University of Texas, Austin, and was sent to the writer by Dr. Constantine J. Alexopoulos. Dry specimens of the holotype (RSA Culture 1355) have been deposited in the Mycological Collections of the Rancho Santa Ana Botanic Garden, Claremont, Calif., and transfers of the living culture have been sent to the ATCC, CBS, and CMI.

When *Dimargaris xerosporica* and *D. arida* are grown in pure two-membered culture on *Cokeromyces recurvatus* on YpSs agar they are very similar macroscopically. However, a careful study of the development of the sporophore of these species reveals a fundamental difference by which they may be readily

Fig. 4. *Dimargaris arida*.—a. Two fertile heads. $\times 325$.—b. One fertile head showing open arrangement of the sporiferous branchlets. $\times 600$.—c. Sporiferous branchlets. $\times 1000$.—d. Typical cross-wall. $\times 1300$.

distinguished. *Dimargaris xerosporica* is characterized by a cymose branching pattern (both helicoid and scorpioid) in which the apparent main axis of the sporophore is formed by a succession of fertile branches each of which arises as a divergent outgrowth immediately below a distal septum of the preceding branch (Fig. 1 a-b). Thus, the oldest fertile head typically terminates the lowermost branch of the apparent main axis of the sporophore and the youngest fertile head is positioned at the apex. Pseudovercillate branching may

occur occasionally in *D. xerosporica* in which case two or more fertile branches arise at a single node. Also, one or more secondary axes may develop from the primary axis in the same manner as the fertile branches.

Unlike *D. xerosporica*, the branching pattern of the sporophore of *D. arida* is strictly pseudoverticillate (Fig. 3 a-b) and in this regard *D. arida* resembles *D. verticillata* more closely than does *D. xerosporica*. In the fully mature sporophore of *D. arida* the first formed, and oldest, fertile head terminates the primary axis. One to four secondary fertile branches usually arise, successively, immediately below several of the septa in the upper part of the primary sporophore. Secondary fertile axes often arise as divergent outgrowths from the primary axis (Fig. 3 a).

Branches of the substrate mycelium of both *D. xerosporica* and *D. arida* penetrate the host hyphae by means of small appressoria and form haustoria typical of the family (Fig. 1 c; Fig. 3 c). Like all Dimargaritaceae, each septum in the vegetative and fruiting hyphae possesses a median disciform cavity containing a biconvex plug bearing a small globose enlargement at each pole (Fig. 2 e; Fig. 4 d).

In the fertile head of *D. xerosporica*, *D. arida*, and *D. verticillata*, the dimensions of the vesicle subtending the sporiferous branchlets vary within approximately the same limits. The cells composing the sporiferous branchlets of *D. verticillata* (Benjamin, 1959, Pl. 17 h-j) are shorter and wider than those of the other two species. This results in a rather compact head in *D. verticillata* (Fig. 2 a) whereas in *D. xerosporica* (Fig. 2 b-c) and *D. arida* (Fig. 4 a-b) the head is more open in appearance.

The sporiferous branchlets in *D. xerosporica* (Fig. 1 d-f; Fig. 2 d) and *D. arida* (Fig. 3 d-f; Fig. 4 c) are very similar both in size and shape. Those of *D. xerosporica* are, however, slightly larger than those of *D. arida*. Also, the spores of this species (Fig. 1 g) average about $5.3 \mu \times 2.9 \mu$ and are a bit larger than those of *D. arida* (Fig. 3 g) which average about $4.1 \mu \times 2.3 \mu$. Unlike *D. verticillata* and other known species of *Dimargaris*, the fertile heads of *D. xerosporica* and *D. arida* remain dry when mature. The cells of the sporiferous branchlets disarticulate as in other species of the family, and the powdery spores fall away at the slightest disturbance.

Zygospores have not been observed in *D. xerosporica* under the conditions of culture employed. They are produced abundantly by *D. arida*, and, as in other species of the family, develop within the substratum following conjugation of undifferentiated vegetative hyphae. The pattern of development of the zygospore in *D. arida* resembles that observed in *Coemansia mojavnensis* (Benjamin, 1958, Pl. 5 a-e). The zygosporangium is formed as an enlargement of a usually short sexual branch near the point of fusion of the branch with another hypha (Fig. 3 h-o; Fig. 5 a-f). The maturation process is like that described previously for other members of the family (Benjamin, 1959, pp. 373-374). When the zygosporangium reaches its maximum diameter, the wall of the zygospore proper begins to thicken and the dense protoplasm filling the young spore is charged with numerous small refractive globules of varying sizes (Fig. 5 c). Narrow channels through the gradually thickening spore wall maintain continuity between the contents of the developing spore and the supporting hyphae throughout the maturation process (Fig. 3 n; Fig. 5 c-d, f).

Fig. 5. *Dimargaris arida*—a-f. Several successive stages in the development of the zygospore. Note the narrow channels through the thickened wall that lead from the supporting hyphae to the interior of the spore (d and f, on right). $\times 600$.

Only when the spore is nearly mature do these channels become closed completely (Fig. 3 o). When mature, the zygosporangial membrane is thin and inconspicuous; the thick-walled zygospore is smooth and contains usually only one large eccentric globule (Fig. 5 e-f).

On the basis of the published descriptions of *D. oblongispora* and *D. simplex* and my own study of the other species, the known species of *Dimargaris* may be separated as follows:

- A. Sporiferous branchlets many, subtended by vesicles..... B.
- AA. Sporiferous branchlets few, not subtended by vesicles..... E.
- B. Sporophores typically cymosely branched..... C.
- BB. Sporophores typically pseudoverticillately branched..... D.
- C. Sporophores large, reaching 1-2 cm high; fertile heads forming spore-drops..... *D. cristalligena*
- CC. Sporophores small, reaching 3-4 mm high; fertile heads remaining dry..... *D. xerosporica*
- D. Fertile heads forming spore-drops; zygospores punctate..... *D. verticillata*
- DD. Fertile heads remaining dry; zygospores smooth..... *D. arida*
- E. Upper part of the merosporangium formed by budding from the lower part; sporiferous branchlets 2-3..... *D. simplex*
- EE. Merosporangium elongating uniformly and forming spores simultaneously..... F.
- F. Sporophores reaching 3.5 mm high; zygospores pedicellate..... *D. oblongispora*
- FF. Sporophores reaching 5-8 mm high; zygospores not pedicellate..... *D. bacillispora*

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