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ADDENDA TO "THE MEROSPORANGIFEROUS MUCORALES"

R. K. BENJAMIN¹

Tieghemiomyces parasiticus sp. nov.

Coloniae in *Cokeromyces recurvatus* in agar YpSs albae vel in aetate "Pinkish Buff"; hyphis vegetantibus 2–5 μ diam.; sporophoris rectis, levibus, in juventate simplicibus, ramos singulos fertiles divaricatos septatos infra 3 septa in partibus superioribus gerentibus; ramis fertilibus subverticillatis; ramis ultimis fertilibus; extentionibus sterilibus absentibus; sporophoris in aetate ad 3 mm. altis; stipitibus principalibus 325–825 μ altis, 7–10 μ diam.; in cellulis 100–200 μ longis consistentibus; ramusculis sporogenis in 1–3 vel 4 cellulis consistentibus; cellulis sporogenis merosporangia de 2 sporis gerentibus; merosporangiis per gemmascentem gestis; sporis globosis vel nonnihil ovoideis, 3–4 $\mu \times$ 2.5–3 μ , in aetate siccis; zygosporis globosis, hyalinis, de muris crassis, punctatis, 43–58 μ (med. 51 μ) diam., globulos singulos excentricos, 22–31 μ diam., continentibus; muro 5–9 μ (med. 7.4 μ) crasso.

Colonies on *Cokeromyces recurvatus* on YpSs white, becoming "Pinkish Buff" (Ridgway, 1912) in age; vegetative hyphae colorless, septate, branched 2–5 μ in diameter; haustoria at first simple, becoming more or less lobate, developing numerous branchlets about 1.5–3 μ wide and up to 25 μ long; sporophores erect, septate, at first simple, forming single, septate, divergent fertile branch systems immediately below usually three of the distal septa; fertile branches subverticillately branched, without sterile projections, the main axes consisting of 1 to 3 or 4 superposed cells constricted at their septa, the ultimate sporiferous branchlets consisting of 1–3 superposed cells bearing distal whorls of merosporangia; sporophores, in age, up to 3 mm. high, including simple sterile prolongations of the stipes above the fertile regions; stipes below the fertile regions about 325–825 μ long, 7–10 μ wide, composed of cells about 100–200 μ long; merosporangia containing two spores each; the terminal parts of the merosporangia developing by apical budding from the basal; spores globose to slightly ovoid 3–4 $\mu \times$ 2.5–3 μ , remaining dry at maturity; zygosporos developed from the conjugation of short undifferentiated hyphal branches with similar vegetative hyphae, globose, colorless, thick-walled, (35–)43–58 μ (aver. 51 μ) in diameter, uniformly sculptured with small circular pits, containing, when mature, usually single, large, eccentric, refractive globules (17–)22–31 μ (aver. 27 μ) in diameter; walls 5–9 μ (aver. 7.4 μ) thick.

Holotype.—ILLINOIS. Champaign County: Champaign, 26 March, 1959, isolated from mouse dung collected by Mrs. Ethel Dickens (RSA Culture 861). Transfers of the holotype have been deposited in the ATCC, CBS, and CMI.

Like *Tieghemiomyces californicus*, *T. parasiticus* parasitizes other Mucorales; the vegetative hyphae of the parasite penetrate the walls of the substrate hyphae of the host and form branched haustoria (Pl. 1c; Pl. 2c) characteristic of the Dimargaritaceae (Benjamin, 1959: p. 364). When grown on ME-YE, *T. parasiticus*, like its congener, develops slowly but apparently normally without a host. Known members of other genera of the family that have been studied in culture require a host for vigorous growth and sporulation on ordinary

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agar media although some may develop slowly, albeit aberrantly, in pure culture.

Tieghemiomyces parasiticus and *T. californicus* are distinguished readily—even when examined at low magnification with a dissecting microscope—by the nature of their fertile branches, for in the former species these structures are less highly ramified than in the latter

PLATE 1. *Tieghemiomyces parasiticus* Benjamin.—a. Habit sketch showing general characteristics of fruiting structures. $\times 30$.—b. Immature sporophore showing early stages of development of lateral branches. $\times 300$.—c. Mature haustorium. $\times 1080$.—d. Terminal portion of young sporophore showing conformation of developing fertile branches. $\times 780$.—e. Young sporiferous branchlet showing origin of merosporangia from fertile cells. $\times 1360$.—f. Nearly mature fertile branch showing disposition of sporiferous branchlets and merosporangia. $\times 660$.—g. Mature spores. $\times 1360$.

and lack the free terminations so characteristic of *T. californicus* (compare: Benjamin, 1959, Pl. 25a, f–g, and Pl. 26e–f, with Pl. 1a, b, d, and f; Pl. 2a and b). In the type species three, but often four, tiers of fertile branches are formed and two or even three branches may be developed immediately below one or more of the septa in the fertile region (Benjamin, 1959: Pl. 26d–e). In no instance have more than three tiers of single fertile branches been observed in *T. parasiticus* and these, with rare exceptions, are borne one above the other on the same side of the sporophore (Pl. 1b, d; Pl. 2b).

When the sporophore of *T. parasiticus* matures, the stipe, like that of *T. californicus* (Benjamin, 1959: Pl. 26c), separates by circumscissile rupture immediately below the proximal fertile branch system, and, because of intertwined stipe prolongations, a large portion of a given colony of the parasite may be swept away *in toto*.

The zygospores of *T. parasiticus* (Pl. 2e–f), although averaging about 10% larger, are similar to those of *T. californicus*.

Because of the nature of the fertile branches of *T. parasiticus*, the description of *Tieghemomyces* given originally (Benjamin, 1959: p. 390) must be emended to included forms with fertile branches lacking free terminations.

The two known species of *Tieghemomyces* may be separated as follows:

- A. Main axes of the fertile branches and often their laterals with sterile prolongations *T. californicus*
- AA. Main axes of the fertile branches and their laterals without sterile prolongations *T. parasiticus*

DISPIRA SIMPLEX Benjamin

At the time *Dispira simplex* was described (Benjamin, 1959: p. 387) it had not been grown in two-membered culture on agar media. Repeated attempts to cultivate the species in association with *Cokeromyces recurvatus*, *Mucor hiemalis*, and *Mycotypha microspora*—species readily parasitized by other members of the Dimargaritaceae thus far cultured—failed, and the fungus was described from material growing in association with miscellaneous fungi on the original dung substrata. In the fall of 1959, Geoffrey F. Orr, University of California, Los Angeles, succeeded in growing *D. simplex* in mixed culture with a species of *Chaetomium*. Subsequently, the writer has isolated several additional strains of this parasite together with *Chaetomium* associates and has demonstrated that it is, indeed, parasitic on at least one representative of this genus of Ascomycetes. *Dispira simplex* thus joins *Piptocephalis xenophila* (Dobbs and English, 1954) and *Syncephalis wynneae* (Thaxter, 1897) of the Piptocephalidaceae as one of the few members of the merosporangiferous Mucorales known to parasitize non-mucoralean hosts.

No effort has been made as yet to examine the host range of *D. simplex* on *Chaetomium*. Using the keys of Skolko and Groves (1953), I have placed the four strains of *Chaetomium* so far isolated with and used as hosts for the parasite near *C. bostrychodes* Zopf.

Media such as YpSs, PDA, and ME-YE (Benjamin, 1959: p. 322), are very satisfactory for obtaining apparently normal development of *D. simplex* on *Chaetomium*, but all attempts to culture the parasite alone and with the mucor hosts listed above have been negative. No significant changes in the original description of *D. simplex* are necessitated, but it now is possible to describe its zygospores.

In my previous work on merosporangiferous Mucorales (Benjamin, 1959: pp. 386–387), I interpreted the zygospore-like bodies of *D. cornuta*, first described by Ayers (1935), as true zygospores although they are borne terminally on lateral outgrowths of vegetative hyphae. Zygospore-like bodies resembling those of *D. cornuta* are formed readily in cultures of *D. simplex*. In the latter species, these too are borne on robust stalks that vary greatly in length, often reaching a length nearly equal to the diameter of the spore. With

PLATE 2

great frequency the spore stalk arises from the point of anastomosis of the tip of one vegetative hypha to the lateral wall of another so that it is subtended by the apparent juncture of three hyphae. Conjugation of undifferentiated vegetative hyphae is the typical method of initiation of zygospores in both the Dimargaritaceae (Benjamin, 1959) and the related Kickxellaceae (Benjamin, 1958). The zygospore-like bodies of *D. simplex*, like those of *D. cornuta*, are regarded here as true zygospores.

Zygospores of *D. simplex* (Pl. 2g-h) grown on YpSs are colorless, measure about 20–38 μ (aver. 29 μ) in diameter, and have walls (3–)4–6 μ thick. When mature, each spore contains one or rarely two or three refractive globules about 9–16 μ in diameter. The mean diameter of the zygospores of this species is about 25% less than in *D. cornuta*. Whereas the exospore of *D. cornuta* appears minutely punctate (Benjamin, 1959: Pl. 22d), the exospore of *D. simplex* is marked by relatively large nearly circular depressions measuring 2.5–3 μ in diameter (Pl. 2h).

Cultures of the following isolates of *Dispira simplex* have been deposited in the ATCC, CBS, and CMI:

RSA Culture 946.—CALIFORNIA. San Bernardino County: Lake View, August 19, 1959, isolated from rat dung.

RSA Culture 952.—CALIFORNIA. Riverside County: 3 miles east of Earp, fall, 1959, isolated from rabbit dung by G. F. Orr.

RSA Culture 1000.—CALIFORNIA. San Bernardino County: 2 miles east of Wheaton Springs, April 22, 1960, isolated from rat dung.

Dipsacomyces gen. nov.

Hyphis fertilibus septatis; sporocladis lateralibus stipitatis septatis attenuatis, cellulis intercalaribus plerumque ordines transversos vesicularum sporigerarum in superficie una gerentibus; vesiculis sporigeris elongatis ad apices repente attenuatibus; sporangiolis singulis ellipsoideis-fusiformis, in apices attenuatibus, ad maturitatem in liquido involutis.

Sporocladia pleurogenous, arising as lateral outgrowths of branched, septate aerial hyphae, stalked, septate, with narrowed apices, the intercalary cells producing pseudophialides arranged in more or less transverse rows on one side; pseudophialides elongate, with narrowed apices bearing single sporangiola; sporangiola elliptic-fusiform with elongate, acuminate apices, immersed in liquid at maturity.

(Etyim.: *δίστακος*, the teasel plant + *μύκης*, fungus)

Type species:

Dipsacomyces acuminosporus sp. nov.

Coloniae albae; hyphis vegetantibus septatis, ramosis, 2–6 μ diam.; hyphis aeriis levibus, ramosis, (1.3–)2.2–4.4(–5.7) μ diam.; stipitibus sporocladiorum levibus, 25–150 (–200) μ longis $\times$ 3–5 μ diam., 2–4(–6) cellulis; sporocladis minute asperulatis, non-nihil curvatis, 25–55 μ longis $\times$ 5–7 μ diam., in 6–13 (med. 9) cellulis consistentibus; cellulis intercalaribus 2 ordines plerumque transversos vesicularum sporigerarum in superficie una gerentibus; cellulis terminalibus plerumque sterilibus, attenuatis, 12–30 μ longis;

PLATE 2. a. *Tieghemiomyces californicus* Benjamin.—Fertile region of a sporophore in late stage of development. Note the sterile prolongations of several branches of the fertile branch systems. $\times 235$.—b-f. *Tieghemiomyces parasiticus* Benjamin.—b. Fertile region of a sporophore at a stage of development comparable to that of the individual of *T. californicus* shown in the previous figure. Note absence of sterile prolongations. $\times 235$.—c. Haustorium in hypha of host. $\times 1300$.—d. Typical cross-wall. $\times 1300$.—e. Optical section of mature zygospore. $\times 740$.—f. Zygospore as seen in surface view. $\times 740$.—g-h. *Dispira simplex* Benjamin.—g. Optical section of zygospore. $\times 740$.—h. Zygospore as seen in surface view. $\times 740$.

vesiculis sporigeris elongato-ovalis vel subcylindricis, $4.4\text{--}6.6\ \mu \times 2\ \mu$ sporangiosporis hyalinis, levibus, ellipsoideis-fusiformis, $19\text{--}34\ \mu$ (med. $27\ \mu$) longis, $3\text{--}4.5\ \mu$ diam.; apicibus $11\text{--}20\ \mu$ (med. $15\ \mu$) longis; zygosporis ignotis.

Colonies developing rapidly on natural substrata, white; vegetative hyphae colorless, septate, branched $2\text{--}6\ \mu$ wide, producing irregularly branched, septate aerial hyphae that form a more or less dense turf up to 4 mm. high; aerial hyphae delicate, smooth, $(1.3\text{--})\ 2.2\text{--}4.4\text{--}(5.7)\ \mu$ in diameter, giving rise to more or less divergent, irregularly disposed sporocladia; sporocladial stipe smooth, $2\text{--}4\text{--}(6)\text{--}celled$, $25\text{--}150\text{--}(200)\ \mu$ long $\times\ 3\text{--}5\ \mu$ wide, often proliferating and producing one or rarely more additional sporocladia; sporocladia minutely asperulate, slightly curved, $25\text{--}55\ \mu$ long $\times\ 5\text{--}7\ \mu$ wide, composed of about 6–13 cells (aver. 9) excluding the stipe, the usually sterile terminal cells, $12\text{--}20\ \mu$ long attenuated, slightly rounded apically; pseudophialides elongate-oval to subcylindric, $4.4\text{--}6.6\ \mu \times 2\ \mu$, arranged on one side of the sporocladium in two more or less transverse rows per cell. Sporangiola colorless, smooth, elliptic-fusiform, with elongate-acuminate apices; total length $19\text{--}34\ \mu$ (aver. $27\ \mu$), greatest width $3\text{--}4.5\ \mu$, apices $11\text{--}21\ \mu$ (aver. $15\ \mu$) long; sporangial wall everywhere adnate to the spore, readily sloughed away at maturity. Zygosporangia unknown.

Holotype.—HONDURAS. Vicinity of La Lima, February, 1960, isolated in a soil immersion tube (RSA Culture 1012). Transfers of the holotype have been deposited in the ATCC, CBS, and CMI.

I am indebted to Dr. Roger D. Goos who kindly sent this unusual representative of the Kickxellaceae to me for study.

Bearing a terminal spinous protuberance as long as or longer than the body of the spore (Pl. 3f–h; Pl. 4c–d), the sporangiospore of *Dipsacomyces acuminosporus* has no counterpart in other known members of the family although certain species of *Coemansia*, as *C. mojavensis* (Benjamin, 1958: Pl. 4j), have spores with rudimentary apical spines. When implanted upon media such as YpSs, PDA, CM, or ME-YE (Benjamin, 1959: p. 322), spores of *D. acuminosporus* germinate readily and growth is relatively rapid under conditions ordinarily prevailing in the laboratory. Production of basal germ tubes by spores of this species (Pl. 3h) recalls *Linderina pennispora* and *Martensiomycetes pterosporus* rather than *Kickxella alabastrina*, *Spirodactylon aureum*, species of *Coemansia*, and presumably species of *Martensella*, where germ tubes arise near the middle of the spores. Only meager vegetative growth occurs on SMA (Standard Mucor Agar, Hesseltine, 1954: p. 362—prepared with 1% rather than 4% dextrose), and *D. acuminosporus* fails to produce aerial hyphae or to sporulate on this synthetic medium.

Colonies of *D. acuminosporus* remain white and may reach diameters of 2–3 cm. in five days. The aerial hyphae branch freely and by intertwining soon form a more or less dense turf. Sporulation may begin within 4–5 days or be delayed for a week or more. Also, fruiting may take place abundantly in one portion of a colony and be absent in another. Production of sporocladia usually is initiated in the lower portion of a colony and progresses upward.

As far as structure and development are concerned, the sporocladium of *Dipsacomyces acuminosporus* (Pl. 3b–e; Pl. 4a–b) is similar to that of species of *Coemansia*, *Martensella*, *Martensiomycetes*, and *Spirodactylon*. The apparently random development of sporocladia on the fruiting hyphae in *D. acuminosporus* (Pl. 3a) is quite distinct, however, from the acrogenous development of these structures in *Coemansia*, *Martensella*, and *Spirodactylon*, where the sporocladia become arranged pleurogenously as the fertile axes elongate. The sporocladia of *Martensiomycetes*, although produced successively, typically are borne in terminal umbels.

When the sporangiolium of *D. acuminosporus* matures, the delicate sporangial membrane separates readily from the spore, and this phenomenon may be demonstrated easily in

PLATE 3. *Dipsacomyces acuminosporus* Benjamin.—a. Habit sketch showing general characteristics of fruiting structures. $\times 50$.—b-d. Three immature sporocladia; the stipe of the one shown in fig. d has proliferated and produced a second sporocladium. $\times 660$.—e. Mature sporocladium; the fertile region of the sporocladium has been rotated toward the observer by 90° relative to its position in the previous three figures. $\times 660$.—f. Mature sporangium showing separation of the sporangial membrane at a point near the juncture of the body of the spore and its apical projection. $\times 1360$.—g. Mature spore. $\times 1360$.—h. Two germinating spores. $\times 1360$.

liquid mounts. The wall appears always to rupture circumscissilely at a point near the juncture of the body of the spore and its spinous protuberance (Pl. 3f). Upper and lower portions of sporangial walls are illustrated photographically in Plate 4c-d.

The teasel-like appearance of the mature sporocladium when this is observed in face view (Pl. 3e; Pl. 4b) suggested the generic name applied to this singular genus of the Kickxellaceae.

PLATE 4. *Dipsacomyces acuminosporus* Benjamin.—a. Young sporocladium. $\times 620$.—b. Nearly mature sporocladium. $\times 620$.—c. Three detached sporangiola (below) and several remnants of the terminal portions of sporangial membranes (above). $\times 1300$.—d. Five detached sporangiola; note the distinct sporangial membranes separated slightly from the basal portions of the four spores shown at the left. This is especially clear in the one marked by the arrow. $\times 1300$.

The key to the known genera of the family presented in an earlier paper (Benjamin, 1959: p. 399) may be revised as follows:

- A. Sporocladia globoid, nonseptate. *Linderina*
- AA. Sporocladia elongate, usually attenuated distally, septate. B.
 - B. Spores ellipsoidal, only slightly longer than broad; fertile region of the sporophore coiled. *Spirodactylon*
 - BB. Spores elongated, more than twice as long as broad; fertile region of the sporophore not coiled. C.
- C. Sporocladia verticillate or umbellate. D.
- CC. Sporocladia pleurogenous. E.
 - D. Sporocladia verticillate, formed simultaneously. *Kickxella*
 - DD. Sporocladia umbellate, formed successively. *Martensiomycetes*
- E. Sporocladia not formed acrogenously. *Dipsacomycetes*
- EE. Sporocladia formed acrogenously. F.
 - F. Sporangiola borne on the upper surfaces of the sporocladia. *Martensella*
 - FF. Sporangiola borne on the lower surfaces of the sporocladia. *Coemansia*

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NOTE

In my earlier paper, "The merosporangiferous Mucorales," *Aliso* 4(2), 1959, the magnifications listed for the following figures should be $\times 1360$, not $\times 1860$: Plate 18, fig. j; Plate 20, fig. c-k; Plate 23, fig. c-i,k; Plate 25, fig. h-l.