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ADDENDA TO "THE MEROSPORANGIFEROUS MUCORALES" II

RICHARD K. BEN JAMIN¹

Spiromyces gen. nov.

Sporophoris rectis vel ascendentibus, septatis, simplicibus vel ramosis, spiralibus; sporocladis laterale gestis, sessilibus, nonseptatis, subterminaliter constrictis, parte terminale sporangiolam unisporiam deinceps gerente; sporangiolis per gemmascentem gestis, in aetate siccis; zygosporis globosis vel subglobosis de muris crassis.

Sporophores erect or ascending, septate, simple or branched, coiled; sporocladia pleurogenous, sessile, nonseptate, constricted subterminally, the terminal part forming unisporous sporangiola successively by budding; sporangiola remaining dry; zygosporous globoid, thick-walled.

(Etym.: *σπειρα*, that which is coiled + *μύκης*, fungus)

Type species:

Spiromyces minutus sp. nov.

Coloniae in agaro ME-YE lente crescentes, in aetate prope "Maize Yellow" vel "Chamois"; hyphis vegetantibus hyalinis, septatis, ramosis, 1.7–3.5 μ diam.; sporophoris levibus, simplicibus vel ramosis, rectis vel ascendentibus, laxe spiralibus, 350–550 μ altis, 2.6–4.8 μ diam., in cellulis 12–20 μ longis consistentibus, juxta basem sterilibus; 2–3 sporocladia in parte superiore cellulae fertilis gerentibus; partibus basalibus sporocladiorum, 4.8–7.5 $\mu \times$ 3.9–4.4 μ , uno latere valde convexo, partibus terminalibus sporocladiorum globosis, 2.6–3.6 μ diam., 8–9 sporangiolas, 2.6–3.3(–3.5) $\mu \times$ 2.4–2.6(–3.1) μ , deinceps producentibus; zygosporis pallide aurantiaco-fuscis, globosis, (26–)30–37 μ diam., vel ovoideis, 32–40 $\mu \times$ 30–37 μ , punctatis, globulos singulos vel plures continentibus; muro 4–7 μ (med. 5.5 μ) crasso.

Colonies on ME-YE agar developing slowly, restricted, in age "Maize Yellow" (Ridgway, 1912, Pl. IV) to "Chamois" (op. cit., Pl. XXX); vegetative hyphae colorless, septate, branched, about 1.7–3.5 μ in diam; sporophores smooth-walled, simple or branched, erect or ascending, loosely coiled, mostly 350–550 μ high, 2.6–4.8 μ diam, composed of cell-segments 12–20 μ long, fertile except near the base; sporocladia 2–3 per cell-segment, usually arising near the distal septum; sporocladium at first subovoid, becoming strongly convex on one side and forming a slightly recurved cell, 4.8–7.5 $\mu \times$ 3.9–4.4 μ , that gives rise by budding to a terminal globose enlargement 2.6–3.6 μ in diam; terminal enlargement of sporocladium bearing up to 8–9 slightly ovoid sporangiola, 2.6–3.3(–3.5) $\mu \times$ 2.4–2.6(–3.1) μ , in succession; zygosporous pale orange-brown by transmitted light, thick-walled, globose, (26–)30–37 μ in diam, or ovoid, 32–40 $\mu \times$ 30–37 μ uniformly sculptured with nearly circular shallow depressions about 2–4 μ in diam, containing, when mature, single

¹This work was supported, in part, by a National Science Foundation grant, NSF-G14273.

refractive globules 10–20 μ in diam, or several smaller globules; wall 4–7 μ (aver. 5.5 μ) thick.

Holotype.—CALIFORNIA. Madera County: 13 miles south of Coarsegold on State Highway 41, April 3, 1962, R. K. Benjamin; isolated from mouse dung (RSA Culture 1198). Cultures have been sent to the ATCC, CBS, and CMI.

Excellent development of this fungus—comparable with that observed when the species first was encountered growing on dung—takes place on ME-YE² agar under ordinary laboratory conditions, although it is relatively slow and colonies initiated by single spores usually reach diameters of only 1–2 mm in 3–4 weeks. Growth is less satisfactory on YpSs and CM agars and is practically nil on SMA agar.

The vegetative and fruiting hyphae of *Spiromyces minutus* are uniformly septate and each cross-wall is provided with the median disciform expansion or plug (Fig. 2 k) that is characteristic of all members of the Kickxellaceae. The small hyphal dimensions of this fungus, however, render this structure less conspicuous than in many other species of the family.

Zygospores of *S. minutus* (Fig. 2 l) were formed in abundance in the original mixed culture on dung. They also are produced in pure culture on ME-YE but are less numerous and are erratic in their appearance—often developing in one culture and not in another. Structurally, they are like the zygospores of other members of the Kickxellaceae in which such spores are known (Benjamin, 1958, 1959). Their surface sculpturing resembles that of the zygospores of several species of the closely related Dimargaritaceae (Benjamin, 1959, 1961).

Sporophores of *S. minutus* arise directly from substrate hyphae and usually, but not always, are unbranched. As it describes a loose but uniform spiral in its upward development (Fig. 1 a–b and 2 a), the sporophore delimits uninucleate cell-segments (Fig. 2 b), each of which gives rise to usually two or three lateral sporocladia (Fig. 1 b). It may be noted that the sporocladia are not formed acrogenously as in several other genera of Kickxellaceae, i.e., *Linderina* Raper & Fennell (1952), *Martensella* Coemans (Jackson & Dearden, 1948; Benjamin, 1959), *Coemansia* Van Tieghem & Le Monnier (Linder, 1943; Benjamin, 1958), and *Spirodactylon* Benjamin (1959), but pleurogenously as in *Dipsacomyces* Benjamin (1961). As a sporocladium is initiated, the nucleus in the subtending cell-segment divides and one of the resulting daughter nuclei migrates into the young sporocladium (Fig. 2 c) which then is delimited by a basal septum (Fig. 1 c and 2 d). The initially ovoid sporocladium becomes strongly convex on one side and only slightly convex to slightly concave on the other and gives rise to a terminal globose enlargement from which the subglobose sporangiola arise successively by budding (Fig. 1 d–h). As each sporangiola develops from the terminal enlargement of the sporocladium, the single nucleus in the sporocladium divides (Fig. 2 e); one daughter nucleus migrates into the young sporangiola which is cut off by a basal septum and the other daughter nucleus remains in the sporocladium only to divide again as the next sporangiola is initiated (Fig. 2 f–g). Eight or nine sporangiola may be formed by a sporocladium. Each initially is borne on a relatively broad base (Fig. 1 f and 2 h) but, as it matures, it is elevated slightly by the formation of a basal constriction (Fig. 1 g and 2 i) which remains behind when the sporangiola falls away (Fig. 1 h and 2 j). Like *Spirodactylon aureum*, the sporangiola of *Spiromyces minutus* remain dry when mature and may be detached by the slightest disturbance.

When compared with other genera of the Kickxellaceae, the sporocladium of *Spiromyces*

²For constitution of media cited in this paper see Benjamin (1959, p. 322; 1961, p. 16).

minutus is unique. In all other known genera, the sporangiole is subtended by a small phialide-like cell that I previously have termed a pseudophialide (Benjamin, 1958, p. 150). This cell is separated from the sporocladium proper by a cross-wall during formation of the single sporangiole produced by it. In 1959, the nuclear phenomena accompanying sporo-

Fig. 1. *Spiromyces minutus*.—a. Habit sketch showing general characteristics of the fruiting structures. $\times 120$.—b. Terminal part of a sporophore showing origin and arrangement of sporocladia. Note that the sporangiole readily fall away when mature. $\times 900$.—c—g. Successive stages of development of a sporocladium. The terminal enlargement of the sporocladium is just beginning to form in c and in d the first sporangiole is developing from this enlargement. In e two sporangioles have been delimited and a third is being produced. A nearly mature sporocladium is shown in f and in g and h some or all of the mature sporangioles have become detached. $\times 1360$.

cladium development in *Coemansia mojavensis* were illustrated (Benjamin, 1959, Pl. 28). In that species the sporocladium at first is uninucleate; it becomes multicellular basifugally and each cell is uninucleate. Except for the basal stalk-cell and usually the terminal cell, each cell of the sporocladium gives rise, unilaterally, to successive pseudophialides each of which receives a single nucleus following division of the nucleus in the subtending cell. The nucleus in the pseudophialide divides; one daughter nucleus migrates into the developing sporangiole and one remains behind. The development of the sporocladium of *Spiromyces minutus* would seem to represent only a simplification of that observed in *Coemansia mojavensis*. As each sporangiole develops on the terminal enlargement of the sporocladium it receives one of the daughter nuclei resulting from the division of the nucleus in the sporocladium. The terminal enlargement of the sporocladium, then, may be homologized with the pseudophialide of other genera of the family. Unlike the pseudophialides of the latter, in *Spiromyces* the corresponding structure—the terminal enlargement—gives rise directly to all of the sporangiole produced by a sporocladium and remains functional throughout sporocladial development. The nucleus remaining in the sporocladium retains its stainability by orcein after the sporangiole have matured and fallen away (Fig. 2 j). A similar phenomenon has been observed in the sporocladia of other Kickxellaceae (see Benjamin, 1959, Pl. 28 m).

The key to the known genera of Kickxellaceae presented earlier (Benjamin, 1961, p. 19) may be revised as follows:

- A. Sporocladia nonseptate B.
- AA. Sporocladia septate, elongate, usually attenuated distally C.
 - B. Sporocladium arising acrogenously, globoid, bearing numerous elongate sporangiole singly on pseudophialides *Linderina*
 - BB. Sporocladium arising pleurogenously, ovoid, bearing a small number of globose or subglobose sporangiole on a single terminal enlargement *Spiromyces*
- C. Spores ellipsoidal, only slightly longer than broad; fertile region of the sporophore coiled *Spirodactylon*
- CC. Spores elongate, more than twice as long as broad; fertile region of the sporophore not coiled D.
 - D. Sporocladia verticillate or umbellate E.
 - DD. Sporocladia pleurogenous F.
 - E. Sporocladia verticillate, formed simultaneously *Kickxella*
 - EE. Sporocladia umbellate, formed successively *Martensiomycetes*
 - F. Sporocladia not formed acrogenously *Dipsacomycetes*
 - FF. Sporocladia formed acrogenously G.
 - G. Sporangiole borne on the upper surface of the sporocladium *Martensella*
 - GG. Sporangiole borne on the lower surface of the sporocladium *Coemansia*

Fig. 2. *Spiromyces minutus*.—a. Terminal portion of a sporophore. $\times 350$.—b. Terminus of a sporophore showing two uninucleate cells; a sporocladium is arising laterally from the lower cell. $\times 2110$.—c. Two young sporocladia; the one at the right is receiving a nucleus from the subtending cell. $\times 2110$.—d. Immature sporocladium showing single nucleus and formation of the apical enlargement. $\times 2110$.—e. Sporocladium at same stage of development shown in Fig. 1 d. Note single dividing nucleus. $\times 2110$.—f—g. Later stages in the development of a sporocladium showing uninucleate sporangiole and the single sporocladial nucleus. $\times 2110$.—h. Immature sporangiole prior to formation of basal constrictions. $\times 2110$.—i. Mature sporangiole showing subtending apiculi. $\times 2110$.—j. Mature sporocladium with only one sporangiole still attached. $\times 2110$.—k. Cross-wall showing median disciform cavity. $\times 2110$.—l. Mature zygospores. $\times 620$. (Specimens shown in a and k mounted in KOH-Phloxine; those in b—j mounted in aceto-orcein; those in l mounted in Hoyer's medium.)

FIGURE 2

HEIMIODORA VERTICILLATA Nicot & Parguey

Ann. Sci. Nat., Botan., Sér. 12. 1: 384. 1960.

Heimiadora verticillata was isolated from soil collected near Bangkok, Thailand, and designated as the type of a new genus of Kickxellaceae by its authors. A study of the holotype, kindly supplied by the Centraalbureau voor Schimmelcultures, Baarn, Netherlands, has convinced the author that this fungus is not a member of this family but is a hyphomycete referable to the Dematiaceae.

According to the description and illustrations given by Nicot and Parguey, the typical sporophore of *H. verticillata* is pale brown or reddish-brown, 250–350 μ high, and consists of a primary and often several divergent secondary axes bearing terminal verticils of elongate sterile branchlets. One or two, sometimes three, claviform vesicles bearing several cylindrical conidia terminally are produced proximally on the primary and secondary axes. Except for the one or two basal cells of the main stalk the sporophore and fertile vesicles become coarsely roughened. The formation of terminal sporiferous vesicles is said to be exceptional.

My study of *H. verticillata* has been conducted using ME-YE agar on which the fungus grows rapidly—colonies often reaching 5–6 cm in five days—and sporulates abundantly. Colony color, both surface and reverse, is near "Vinaceous-Rufous" or "Ferruginous" (Ridgway, 1912, Pl. XIV). Conidiophores arise directly from the richly branched, septate vegetative hyphae and usually are 3–6 μ in diameter, simple or branched, and vary greatly in height, often reaching 1 mm. Each usually produces a terminal claviform vesicle bearing several, usually 3–6, oblong-elliptical conidia (Fig. 3 a–e), 10–18 $\mu \times$ 3–6 μ . The terminal vesicle often, but not always, is subtended by a divergent fertile vesicle arising from the upper end of the cell below (Fig. 3 b, d, e). Spore drops are formed. The conidiophores initially are hyaline and smooth, but become variably roughened and reddish-brown in age. Conidiophores bearing sterile branches resembling those described by Nicot and Parguey are found only in older regions of the colonies.

Raper and Fennell (1952) were the first to suggest the taxonomic significance of the characteristic type of cross-wall in the Kickxellaceae. The septum in members of this family is distinguished by a well-defined disciform or biumbonate median enlargement that is readily observed both in living and stained vegetative and fruiting hyphae (for examples see Raper & Fennell, 1952, fig. 17; Benjamin, 1958, Pl. 8 g, and 1959, Pl. 28 a, 29 c, and 33 d). The author has examined over 100 isolates representing the eight known genera of Kickxellaceae and this distinctive type septum is a constant feature of all of them. In no instance has such a septum been observed in *Heimiadora verticillata* (Fig. 2 f–h) and its absence is regarded as conclusive evidence against classifying this fungus in the Kickxellaceae.

Globose, ovoid, or elongate chlamydospores, formed singly and more commonly in chains, are produced in abundance in the vegetative hyphae of *H. verticillata* (Fig. 3 i–k). Because these may resemble the zygospores of the Kickxellaceae, Nicot and Parguey treat their presence as strong evidence of the kickxellaceous affinity of *Heimiadora*. Anastomoses

Fig. 3. *Heimiadora verticillata*.—a. Upper part of a simple conidiophore showing slightly clavate distal cell bearing conidia in an apical whorl. $\times$ 250.—b. Similar conidiophore with single conidiiferous vesicle formed distally by the subterminal cell. $\times$ 250.—c. Upper cell of a conidiophore bearing three conidia. $\times$ 600.—d. Upper end of a conidiophore; note single conidium formed at base of the terminal cell. $\times$ 600.—e. Two-celled conidiophore arising from vegetative hypha. $\times$ 600.—f–h. Cross-walls of vegetative hyphae as seen in optical section: mounted in water (f), lacto-phenol + aniline blue (g), and KOH-Phloxine (h). $\times$ 1300.—i–k. Typical chlamydospores formed in vegetative hyphae. i, $\times$ 350; j–k, $\times$ 600.

FIGURE 3

are common between hyphae in *H. verticillata*. The above authors occasionally encountered configurations (their Plate VI, fig. 1–2) resembling the two distinctive types of conjugation associated with zygospor formation in *Coemansia aciculifera* and *C. mojavenis* (Benjamin, 1958). They do not, however, trace the development of chlamydospores from such anastomoses and they state that these spores usually are formed within the vegetative hyphae in the absence of any distinctive type of conjugation. Because of their interpretation of its chlamydospores, they suggest the possibility of the simultaneous occurrence in *H. verticillata* of agamic cysts or azygospores—the abundant chlamydospores—and zygosporos resulting from fusion of gametangia. My study of *H. verticillata* has convinced me that spores homologous with the zygosporos of the Kickxellaceae are absent in this species and that the spores produced in its vegetative hyphae are typical chlamydospores of the type encountered in many unrelated groups of fungi.

In the absence of cytological verification, Nicot and Parguey reserve judgement on the sexual nature of what I consider, on morphological grounds, to be true zygosporos in the Kickxellaceae. The skepticism of these authors is understandable, for the zygosporos of members of the Kickxellaceae, and the Dimargaritaceae as well, may resemble somewhat chlamydospores observed in fungi of various groups. Although the zygosporos thus far found in the Dimargaritaceae (Benjamin, 1959, 1961) are distinctively sculptured, most of those described in the Kickxellaceae are smooth (except *Spiromyces minutus* described above). Also, the zygosporos in these families are formed following union of hyphae that retain the appearance of ordinary vegetative hyphae, and the zygosporangial membrane remains thin and inconspicuous. It may be recalled that similar features also characterize unquestioned zygosporos of many Entomophthorales and Zoopagales.

Interpretation of the reality of a zygospor founded on purely morphological evidence depends more on the presence of a uniform and readily recognizable conjugation mechanism leading to spore formation than on the gross appearance of the resulting spore. Likewise, an azygospor can be designated only if it results from the obvious failure of sexual organs to react normally or if it has other morphological features that mark it as azygosporic in character. When the above conditions can not be satisfied, as in the case of *Martensella corticii* (Benjamin, 1959), a zygospor-like body must be considered as a chlamydospore until proven otherwise. In the zygosporos of typical examples of the Mucoraceae, such as *Mucor hiemalis*, *Rhizopus stolonifer*, and *Phycomyces blakesleeana*, not only do the well-defined copulatory organs become conspicuously differentiated from the vegetative hyphae from which they arise but also the mature zygosporangial membrane, derived from the gametangia, becomes highly modified. The zygospor proper, however, usually is smooth-walled and may be readily displaced from the outer wall (see Benjamin, 1959, Pl. 4 j). The latter phenomenon is equally conspicuous in the kickxellaceous zygospor (Benjamin, 1958, Pl. 5 h) in which the zygosporangial membrane does not become noticeably modified. When stripped of its outer, often very distinctive, membrane, or when this membrane is thin and inconspicuous as in *Radiomyces* (Embree, 1959; Benjamin, 1960), the typical mucoralean zygospor may be very chlamydospore-like in appearance. However, its consistent origin from the copulation of distinctive hyphae arising from the same or different thalli marks the mucoraceous zygospor as sexual in nature.

During my studies of zygospor formation in *Coemansia aciculifera* and *C. mojavenis* (Benjamin, 1958) the ontogeny of innumerable spores was observed. The spores are formed singly, never in chains, and the developmental sequence described and illustrated for the zygosporos of each of these species always is the same. Although the hyphae associated with zygospor formation in the Kickxellaceae, and in the Dimargaritaceae, are not distinctly modified at maturity like those of most Mucorales, the conjugation mechanism

leading to zygospore formation in these families is just as uniform in a given species as it is in various species of other families of the order.

Dispira parvispora sp. nov.

Coloniae in *Cokeromyces recurvatus* in agar YpSs albae, in aetate "Light Buff"; sporophoris rectis, septatis, simplicibus vel ramosis, ad 6 mm altis, 5–10 μ diam, in cellulis (70–)90–170 μ longis consistentibus, 20–30 (vel in sporophoris ramosis plures) ramos fertiles gerentibus; 1–2 ramis fertilibus sub septam distantem cellulae gestis; ramis fertilibus sympodialibus, axes angulares gerentibus, axibus ad 4–5 ramusculos fertiles recurvos, 12–38 μ longos, ferentibus, ramusculis fertilibus 2–3 ramusculos sporogenos terminales, deinceps per gemmascentem gestis, gerentibus; ramusculis fertilibus per ramusculos steriles, singulos, attenuatos, 12–38 μ (med. 25 μ) longos, subtentis; ramusculis sporogenis, 8–11 $\mu \times 3.5$ –4.8 μ , per gemmascentem gestis, in 2 cellulis sporogenis subaequalibus consistentibus; cellulis sporogenis merosporangia de 2 sporis gerentibus; merosporangiis per gemmascentem gestis; sporis globosis vel subglobosis, 2.2–3.9 μ (med. 2.9 μ) diam, in aetate siccis; zygosporis ignotis.

Colonies on *Cokeromyces recurvatus* on YpSs agar white, becoming "Light Buff" (Ridgway, 1912, Pl. XV) in age; sporophores erect, septate, simple or branched, up to 6 mm high, 5–10 μ in diam, smooth-walled, composed of cells (70–)90–170 μ long, giving rise laterally to 20–30 (or more in branched sporophores) fertile branches; fertile branches arising singly, rarely in pairs, immediately below the septa delimiting the succeeding cell-segments of the sporophore; fertile branch consisting of a recurved central axis terminated by 2, rarely 3, sporiferous branchlets and usually two pairs of lateral branches that may be 4–5 times successively trichotomously branched, one branch of each trichotomy forming terminal sporiferous branchlets, one branchlet remaining sterile, and one branchlet continuing the axis, or all branchlets remaining sterile; sterile branchlets slender, acuminate, 12–38 μ (aver. 25 μ) long; fertile branchlets about equal in length to the sterile branchlets, terminated by usually 2, sometimes 3, sporiferous branchlets; sporiferous branchlets formed by apical budding, 8–11 $\mu \times 3.5$ –4.8 μ , composed of two subequal, slightly ovoid cells bearing distal whorls of merosporangia containing two spores each; the terminal part of the merosporangium developed by apical budding from the basal; spores globose or slightly ovoid, 2.2–3.9 μ (aver. 2.9 μ) in diam, remaining dry at maturity; zygosporos not observed.

Holotype.—CALIFORNIA. Kern County: 10 miles north-northeast of Oildale at the junction of road to Woody and Poso Creek Road, April 4, 1962, R. K. Benjamin; isolated from rodent dung (RSA Culture 1196). Cultures have been sent to the ATCC, CBS, and CMI.

When *Dispira parvispora* first was encountered growing in moist chamber culture on the substratum listed above, it was thought to represent only another strain of *D. simplex* (Benjamin, 1959) which it resembles in many respects. Accordingly, efforts were made to isolate it in two-membered culture on *Chaetomium bostrychodes*, the host for *D. simplex* (Benjamin, 1961). Attempts to isolate *D. parvispora* on the *Chaetomium* were unsuccessful. Finally, *Cokeromyces recurvatus*, which I use routinely for culturing other mucor parasites, was used as host and it grew readily. Subsequent efforts to parasitize *Chaetomium bostrychodes* with *D. parvispora* also failed.

When *Dispira simplex* and *D. parvispora* are grown in pure two-membered culture on their respective hosts, i.e., *Chaetomium bostrychodes* and *Cokeromyces recurvatus*, their colonies are easily distinguished macroscopically. Those of *D. parvispora* are relatively open and are composed of sporophores that often reach heights of 6 mm and give rise to a suc-

Fig. 4. *Dispira parvispora*.—a. Habit sketch of sporophores. $\times 20$.—b-f. Successive stages in the development of sporiferous branchlets and merosporangia from the apices of fertile branchlets. $\times 1360$.—g. Early stage in the development of a fertile branch showing young sporiferous branchlets arising at the apex of the primary axis and young lateral secondary axes. $\times 660$.—h. Later stage showing trichotomous branching pattern of lateral axis (above). $\times 660$.—i. Mature fertile branch. $\times 485$.—j. Mature spores. $\times 1360$.

Fig. 5. a. *Dispira simplex*.—One secondary axis of a fertile branch showing about 20 successive trichotomies. Compare sterile branchlets with those of *D. parvispora* shown in b and c. $\times 285$.—b-f. *Dispira parvispora*.—b. Portion of sporophore showing two fertile branches. $\times 285$.—c. The same showing one fertile branch. $\times 285$.—d. Young sporiferous branchlets arising at the apex of a fertile branchlet. $\times 1300$.—e. Cluster of sporiferous branchlets, some showing merosporangia *in situ*. $\times 1300$.—f. Typical cross-wall. $\times 1300$.

cession of up to 30 or more relatively compact fertile branches (Fig. 4 a). The fruiting structures of *D. simplex* rarely reach heights of more than 2 mm and they give rise to relatively few, usually 2–4, fertile branches in which the lateral axes are more elongate (Fig. 5 a) and usually become so entangled with the branches of adjacent sporophores that the colony completely obscures the host. The low-growing, dense colony of *D. simplex* contrasts sharply with the elevated, rather lax colony of *D. parvispora*.

Like *D. simplex*, the fertile branch of *D. parvispora* develops by a branching process in which the primary axis gives rise to a small number of lateral secondary axes that may be several times trichotomously branched. In *D. parvispora*, one branch of the trichotomy forms 2–3 terminal sporiferous branchlets (Fig. 4 b–f and 5 d), one branch remains sterile and the other continues the axis (Fig. 4 h), or all three branches may remain sterile and terminate development of the axis (Fig. 4 i). Fertile branches of *D. parvispora* usually are not successively branched more than 4–5 times (Fig. 4 i and 5 b), whereas those of *D. simplex* may form 20 or more successive trichotomies (Fig. 5 a).

The sporiferous branchlets, sterile branchlets, and sporangiola of *D. parvispora* have significantly smaller dimensions than those of *D. simplex*. These structures may be compared by examining the drawings of *D. parvispora* given here (Fig. 4) and those of *D. simplex* presented earlier (Benjamin, 1959, Pl. 23) in which all figures except the habit sketches of the sporophores are reproduced at the same magnifications. The sterile branchlets of *D. simplex* (Fig. 5 a) average about twice the length of those of *D. parvispora* (Fig. 5 b–c). The sporangiola of *D. simplex* average about 4.3 μ in diameter (based on five strains), whereas those of *D. parvispora* average about 2.9 μ in diameter. This represents a volume difference of about 325%.

The three known species of *Dispira* may be separated as follows:

- A. Fertile head composed of many sporiferous branchlets subtended by a nearly globose vesicle *D. cornuta*
- AA. Fertile head composed of few sporiferous branchlets not subtended by a globose vesicle B.
- B. Sterile branchlets averaging about 55 μ long; sporangiola about 3.5–4.8 μ in diam. *D. simplex*
- BB. Sterile branchlets averaging about 25 μ long; sporangiola about 2.2–3.9 μ in diam. *D. parvispora*

Piptocephalis benjaminii (Embree) comb. nov.

Chaetocladium benjaminii Embree. Mycologia 54: 305. 1962.

Colonies on *Cokeromyces recurvatus* on YpSs agar near "Deep Olive Buff" (Ridgway, 1912, Pl. XL) in age, forming a lax to dense turf up to 1 cm deep consisting of erect, ascending, or prostrate branched hyphae that form upright dichotomous fertile branch systems or sterile free terminations; sporophores at first non-septate, septate in age, slender below, nearly hyaline, about 3–6 μ in diam, the distal portion of the main stalk wider, 5–12 μ in diam, smooth, becoming striate, 8–10 times dichotomously branched; branches of the primary dichotomies 80–650 $\mu \times$ 4–10 μ , successive branches progressively shorter and narrower, the ultimate branches about 3–7 $\mu \times$ 1.5–3.5 μ giving rise to 2–3 unisporeous sporangiola borne on slender projections 1.5–3 μ long; sporangiospores ovate or obovate, 4.4–10.5 $\mu \times$ 2.4–5.2 μ , remaining dry; homothallic; zygospores globose, orange-brown, 43–75 μ in diam, with prominent gametangial remnants; progametangia apposed; suspensors smooth, often inflated distally; exospore wall delicately reticulate; endospore wall smooth, 3–6 μ thick.

Fig. 6—*Piptocephalis benjaminii*.—a. Habit sketch showing conformation of fertile and sterile branches. $\times 60$.—b. Terminal branches of sporophore showing sporangiole initials. $\times 900$.—c. Terminal branches of a sporophore showing immature sporangiola. $\times 600$.—d. The same showing nearly mature sporangiola. $\times 900$.—e. The same after the sporangiola have fallen away. Note disposition of cross-walls. $\times 600$.—f-g. Outline sketches of sporangiola. Note the two-spored sporangiola shown in f. $\times 1360$. (f, RSA 1206; g, RSA 1205).—h. A germinating spore and one ungerminated spore. $\times 500$.

Type.—CALIFORNIA. Sonoma County: Green Valley. On carnivorous animal dung collected by Robert W. Embree, February, 1961. Herbarium, University of California, Berkeley, No. 1,206,512.³

³I wish to thank Dr. H. L. Mason, Director of the Herbarium, for the loan of the type specimen.

Other specimens examined—CALIFORNIA. Madera County: 13 miles south of Coarsegold on State Highway 41, April 3, 1962, R. K. Benjamin, isolated from mouse dung (RSA Culture 1205); San Bernardino County; 8 miles southeast of junction of Interstate 15 and road to Cima, April 15, 1962, R. K. Benjamin, isolated from dung (RSA Culture 1206).

While this section was being completed, the description of *Chaetocladium benjaminii* was published (Embree, 1962). Because Dr. Embree did not succeed in his efforts to study its development in culture, his classification of this fungus in *Chaetocladium* is readily understandable. Unlike all other described species of *Piptocephalis*, this one does not have deciduous head cells⁴ (Fig. 6 e) and its merosporangia typically are monosporous (Fig. 6 d, f-g and 7 e-f).

In 1899, Mangin briefly characterized a species, *Piptocephalis monospora*, bearing presumably single-spored sporangiola on small globoid terminal vesicles. His description was based on material of questionable maturity preserved in alcohol, and the illustration given resembles what could have been the immature stage of any of several sphaerocephalous species of *Piptocephalis*. Recognition of *P. monospora* as a valid taxon must await its rediscovery. In any event, the fungus described by Mangin can not be confused with *P. benjaminii*.

Like other members of the genus, the latter readily parasitizes various Mucorales. Its development has been studied using YpSs agar and *Cokeromyces recurvatus* as host. The two isolates cited above show several marked morphological differences. Strain 1205 produces a relatively dense turf, has sporangiospores averaging about $7.2 \mu \times 4 \mu$, and zygospores averaging about 54μ in diameter, whereas strain 1206 produces a lax turf, has smaller sporangiospores averaging about $5.7 \mu \times 2.8 \mu$ and larger zygospores averaging about 63μ in diameter. Also, zygospores are formed in relatively small numbers by strain 1205, whereas they are produced in abundance by strain 1206. The conspicuous difference in the development of aerial mycelium by these two strains may be correlated with their pronounced difference in sexual vigour.

Septa usually are not delimited in the stalk and branches of the sporophore until after the sporangiola are mature and have been shed (Fig. 6 e and 7 a). Cross-walls frequently are formed at the base of each dichotomy but they may be randomly distributed. Although a terminal group of fertile branchlets may be subtended by a septum it never separates from the sporophore (Fig. 6 e). The exterior surface of the sporophore wall is smooth, but, as in several other species of *Piptocephalis* (Benjamin, 1959, Pl. 4 f, 6 k, and 7 c), it may become striate in age (Fig. 7 b).

The sporangiola are borne on the apices of the minute ultimate branches of the sporophore (Fig. 6 b-d and 7 c-d) and usually are ovate or obovate but occasionally may be cordate (Fig. 6 f-g). Although rare, two-spored merosporangia may occur (Fig. 6 f) and their formation is considered good evidence that the monosporous sporangiole in this species represents the final step in the reduction of a multisporous merosporangium. With respect

⁴Another acephalous species of *Piptocephalis* is known (Benjamin, 1959, p. 338) which will be described soon by G. Leadbeater and W. Morris, Dept. of Science, Nottingham & District Technical College, Nottingham, England.

Fig. 7. *Piptocephalis benjaminii*.—a. Upper region of a sporophore showing branching pattern and disposition of sporangiola. $\times 235$.—b. Portion of sporophore stipe showing cross-wall and longitudinal striae. $\times 1000$.—c. Terminal branches of a sporophore showing sporangiole initials. $\times 800$.—d. The same with immature sporangiola. $\times 600$.—e. Two mature sporangiola still attached to their subtending branchlets. $\times 1930$.—f. Five mature sporangiola. $\times 1300$.—g. Mature zygospore showing conformation of suspensors and gametangial remnants. $\times 295$.—h. Crushed zygospore showing reticulate zygosporangial wall. $\times 560$. (a-b, e-f, RSA 1205; c-d, g-h, RSA 1206.)

FIGURE 7

to the base of the spore, germination is lateral (Fig. 6 h) and from two to as many as 16 germ tubes have been observed arising from a single spore.

As in other species of *Piptocephalis*, the zygosporé develops following fusion of gametangia delimited by apposed progametangia (Fig. 7 g) and the bases of the gametangia form conspicuous ramnants projecting from the surface of the spore. At maturity, the orange-brown zygosporangial membrane is finely reticulate (Fig. 7 h), and the cytoplasm of the zygosporé proper includes a conspicuous peripheral layer of globules that measure about 2–5 μ in diameter.

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