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R. K. Benjamin

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THE MEROSPORANGIFEROUS MUCORALES

R. K. BENJAMIN

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INTRODUCTION

The Mucorales comprises a group of terrestrial Phycomyceteae characterized in general by: (1), extensive, branched, usually submerged vegetative mycelia composed of hyphae which are multinucleate and initially nonseptate or, in several derived forms, septate from the beginning; septa typically are formed to delimit reproductive structures or in age; (2), asexual reproduction by means of nonmotile, one- or several-nucleated unicellular spores produced singly or in small or large numbers within rod-like or sac-like sporangia borne on more or less specialized aerial hyphae (sporangiophores); chlamydospores often are formed in the vegetative or fruiting hyphae; and (3), sexual reproduction by means of thick-walled zygosporangia produced in zygosporangia formed from the fusion of similar, or more rarely dissimilar, gametangia. Most representatives of the order are saprobic, but a few species typically are parasitic on higher plants or on other fungi—mostly other Mucorales.

In his recent synopses of the Mucorales, Hesseltine (1952, 1955) reviewed briefly the history of the development of the modern approach to the taxonomy of the order and presented (Hesseltine, 1955) a comprehensive key to the families and genera together with notes on synonymy. Hesseltine (1955) recognizes nine families of Mucorales, Choanephoraceae, Cunninghamellaceae, Endogonaceae, Kickxellaceae, Mortierellaceae, Mucoraceae, Pilobolaceae, Piptocephalidaceae, and Thamnidaceae.

During the past five years the writer has made a special effort to collect living representatives of Mucorales which, in the past, usually have been classified in the Piptocephalidaceae (Cephalidaceae) and Kickxellaceae, and he has had the good fortune to be able to study not only asexual but also sexual reproduction of species representing most of the genera belonging to these and related families. The purpose of this paper is to summarize the characteristics of the families and genera of mucors characterized by the production of sporangiospores in rod-like sporangia (merosporangia) and to discuss their presumed natural relationships.

MATERIALS AND METHODS

With few exceptions, the fungi discussed in this paper may be grown in pure culture or, in the case of the parasitic forms, in pure mixed culture on any of several natural or defined media. The following substrata have been used routinely in the course of this study:

CM (*Corn meal agar*).—Corn meal, 20 g., cooked for 10 min. in 700 cc. water, strained through porous cloth; dextrose, 10 g.; agar, 20 g.; enough water to bring the total volume to 1 liter.

PDA (*Potato dextrose agar*).—Potatoes, 200 g., without skins and diced, cooked for 10 min. in 700 cc. water, strained through porous cloth; dextrose, 20 g.; agar, 15 g.; enough water to bring the total volume to 1 liter.

PAB (*Pablum agar*).—Pablum (Mead Johnson Co.), 50 g., cooked for 10 min. in 700 cc. water, strained through porous cloth; agar, 15 g.; enough water to bring the total volume to 1 liter.

PAB-DEX (*Pablum dextrose agar*).—PAB plus 10 g. dextrose per liter.

YpSs (*Yeast extract soluble starch agar*).—Yeast extract, 4 g.; soluble starch, 15 g.; K_2HPO_4 , 1 g.; $MgSO_4 \cdot 7 H_2O$, 0.5 g.; agar, 20 g.; water, 1 liter.

ME-YE (*Malt extract yeast extract agar*).—Malt extract, 3 g.; yeast extract, 3 g.; peptone, 5 g.; dextrose, 10 g.; agar, 20 g.; water, 1 liter.

Unless otherwise indicated in the text, strains of species studied in the course of the present work were isolated by the writer from soil or the dung of small wild animals—rats and mice especially. Samples of dung taken in the field were placed

directly into small cellophane bags or glass vials for transport to the laboratory. The materials then were dispensed into aseptic damp chambers prepared by moistening several thicknesses of filter paper discs in Petri dishes having depths of two centimeters. These cultures were incubated under the conditions of light and temperature prevailing in the laboratory and observed frequently for a period of two to three weeks or longer for the development of desired fungi. Isolation of the latter usually was effected by direct transfer of spores to suitable media by means of alcohol flamed watch-maker's tweezers or small needles mounted in match sticks. Often, for dry-spored species, spores were simply scattered onto the surfaces of sterile microscope slides using fine tweezers for handling sporophores, and spores thus desposited were transferred to culture media. Soil was plated on CM or PAB, and isolations were carried out as above.

In order to study such phenomena as spore germination, the haustoria of parasitic species, the development of zygospores in species where the sexual spores normally are produced by a completely submerged vegetative mycelium, etc., frequent use was made of the well-known cellophane membrane culture technique. Young colonies grown on small sterile squares of dialysis membrane placed on the surface of agar media in Petri dishes or culture tubes may be prepared for microscopic observation with minimum effort.

The writer selected *Cokeromyces recurvatus* Poitras (Shanor *et al*, 1950) as the standard host for culturing members of the Piptocephalidaceae and other parasitic species. *Cokeromyces recurvatus* forms a colony which normally does not exceed a height of more than 1 mm., and this characteristic facilitates observation of the developing sporophores of the parasite and also provides a means of obtaining abundant pure spores of the latter for transfer to other hosts. The fact that *C. recurvatus* is homothallic did not detract from its usefulness as a host for the study of zygospore development in the parasitic forms studied here, for the zygospores of *C. recurvatus* may be distinguished readily from those of the latter fungi. For studying zygospores of *Piptocephalis* and *Syncephalis* species, *Mucor hiemalis* also was employed as host.

Whenever possible, all microscopical observations were carried out using living specimens mounted in water. In order to prevent Brownian movement, spores and other small structures such as the head-cells of species of *Piptocephalis* were mounted on thin agar films prepared by dipping microscope slides in melted 1.5 percent water agar. For studying haustoria of parasitic species and especially for obtaining better contrast for photomicrography, preparations in KOH-Phloxine (Martin, 1952) proved very useful. Lacto-fuchsin preparations (Carmichael, 1955) also were used occasionally. Hoyer's solution (Alexopoulos and Beneke, 1952) was found to be an excellent mounting medium for studying and photographing the architecture of the zygospore exospore. Aceto-orcin was used for cytological studies. Measurements given in the diagnoses are based on from 25-100 or more observations depending on the variability of the structure in question. Colors cited with quotation marks are those listed by Ridgway (1912).

Transfers of cultures referred to in the text which have been deposited in the collections of the following institutions, American Type Culture Collection, Washington, D. C., Centraalbureau voor Schimmelcultures, Baarn, Netherlands, and Commonwealth Mycological Institute, Kew, Surrey, England, are indicated by the abbreviations ATCC, CBS, and CMI respectively. Dried specimens have been placed in the Mycological Collections of the Rancho Santa Ana Botanic Garden, Claremont, California.

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I wish to express my gratitude to Dr. I. Mackenzie Lamb for the loan of the Thaxter and Linder collection of Kickxellaceae and Thaxter's type of *Dispira americana* on deposit in the Farlow Herbarium and to Drs. C. W. Hesseltine and G. Leadbeater for their contribution of numerous isolates of fungi examined during the course of this study. Dr. Leadbeater kindly sent the writer cultures of several species of *Piptocephalis* while these still were under investigation by him or his students. Others who have contributed specimens, cultures, or substrata from which pertinent fungi subsequently have been isolated include the following: H. E. Ahles, G. L. Barron, H. L. Barnett, Roy F. Cain, J. W. Carmichael, Robert W. Embree, D. H. Ford, Sally E. Gochenaur, Curtis R. Jackson, T. W. Johnson, Jr., G. F. Orr, K. B. Raper, Elizabeth Sprague, J. H. Warcup, H. A. Dade, and Miss A. L. van Beverwijk. Thanks also are due to my colleagues, Drs. Verne Grant and Sherwin Carlquist, for welcome criticisms during the preparation of the manuscript. Dr. Philip A. Munz kindly assisted in the preparation of the Latin diagnoses.

SYNCEPHALASTRACEAE AND PIPTOCEPHALIDACEAE

INTRODUCTION

Ever since the original description of *Piptocephalis* by de Bary (1865), *Syncephalis* by Van Tieghem and Le Monnier (1873), and *Syncephalastrum* by Schroeter (1886), there has been much speculation concerning the relationships of this group of fungi. Zygosporangia were described for *Piptocephalis* by Brefeld in 1872 and for *Syncephalis* by Van Tieghem and Le Monnier in 1873, and thus the position of these genera in the Zygomycetes never has been questioned. Although definitive knowledge of the sexual nature of *Syncephalastrum* was not presented until much later (Blakeslee, 1920; Vuillemin, 1922), this genus generally was classified in the Zygomycetes along with the above genera on the basis of its general morphology. Interpretation of the distinctive asexual reproductive structures of these fungi, however, has been the subject of considerable debate. The spores typically are formed uniseriately in cylindrical outgrowths from the usually swollen tips of simple or branched sporophores. Two conflicting philosophies developed regarding the nature of these sporogenous structures: (1) Van Tieghem and Le Monnier (1873) believed that the spores have an endogenous origin comparable to that of typical mucors, and this point of view subsequently has been supported by many students of the fungi including Schroeter (1886), Berlese and de Toni (1888), Marchal (1892), Leger (1896), Thaxter (1897), Mangin (1899), Vuillemin (1902, 1922), Bainier (1907), Moreau (1913, 1953), Gäumann (Gäumann and Dodge, 1928; Gäumann and Wynd, 1952), Fitzpatrick (1930), Naumov (1935, 1939), Zycha (1935), Martin (1940), and Hesseltine (1955). Among these investigators, however, there have been several points of view as to the homologies of the "sporangia": Van Tieghem and Le Monnier (1873) were of the opinion that each spore-row is homologous to a typical mucor sporangium; Mangin (1899) believed that each spore (of *Piptocephalis arrhiza*) possesses two distinct walls and that each spore chain, therefore, consists of several unispored sporangia; Gäumann (Gäumann and Wynd, 1952) regards the vesicle subtending the sporangia of a species like *Syncephalastrum racemosum* as a nonfunctional sporangium which gives rise to "extramatrix partial sporangia"; perhaps the most novel interpretation was that of Moreau (1913)—he later, however, apparently abandoned the idea (Moreau, 1953)—who believed that the sporogenous rod of *Syncephalastrum* was derived from a primitive conidium which produced spores internally.

(2) Brefeld (1872), studying *Piptocephalis*, believed that the spores represent fragments of a disarticulated multinucleate conidium of exogenous origin. The conidial idea has been supported by several other prominent students of the fungi including de Bary (1866, 1887), Fischer (1892), Schroeter (1897), Lendner (1908), and Migula (1910).

As will be seen from the discussion of *Syncephalastrum* presented below, except for the production of asexual spores in cylindrical outgrowths from terminal vesicles, the vegetative and sexual characteristics of this genus are nearly identical to those of a typical member of the Mucoraceae such as *Mucor*. Early studies by Marchal (1892), Thaxter (1897), and Moreau (1913) demonstrated that delimitation of spores within the merosporangium (Martin, 1940) of *Syncephalastrum* takes place essentially as in *Mucor*. Both Vuillemin (1887 b) and Marchal (1892) stressed the probable intermediary position of *Syncephalastrum* between the Mucoraceae and *Syncephalis*. Vuillemin later (1922) actually proposed that *Syncephalastrum* should be classified in the Mucoraceae in close alliance with *Absidia*; this concept also was adopted by Thouvenin (1924), one of Vuillemin's students.

In the absence of convincing evidence to the contrary, the writer is inclined to interpret the spore-bearing structures of *Syncephalastrum* as sporangiola which, except for the usually uniseriate spores, are not fundamentally different from those of other genera of Mucorales like *Cokeromyces* and *Radiomyces* (Embree, 1959). Although numerous modifications of vegetative and reproductive structures have been effected during the evolution of the more highly derived merosporangiferous genera such as *Piptocephalis*, *Syncephalis*, *Dispira*, and *Coemansia*, the alliance of these and related genera with *Syncephalastrum* in a single phylogenetic complex seems to me to be most natural. It is hoped that the discussions to be presented in this paper will lend additional support to this notion which, of course, also has been held by many other mycologists including Thaxter (1895), Fitzpatrick (1930), Zycha (1935), Linder (1943), and Hesselstine (1952, 1955).

At the conclusion of his classic paper on *Mucor mucedo*, *Chaetocladium jonesii* (= *C. brefeldii* Van Tieghem and Le Monnier, according to Hesselstine and Anderson, 1957), and *Piptocephalis freseniana*, Brefeld (1872, p. 53) erected the family Piptocephalidaceae (as Piptocephalideen) for the last named species of presumably conidial zygomycetes. The following year Van Tieghem and Le Monnier described the genus *Syncephalis* and referred it also to the family proposed by Brefeld (Van Tieghem and Le Monnier, 1873, pp. 383-384). In 1875, however, Van Tieghem abandoned Brefeld's name and classified *Piptocephalis* and *Syncephalis* in the tribe Syncéphalidéés—one of four in his all-inclusive family, Mucorinéés. Schroeter retained the name Piptocephalidaceae (as Piptocephalidei) when he described *Syncephalastrum* in 1886. Fischer treated these genera under a different family name, Cephalidaceae, in 1892. The latter name subsequently has been used by Vuillemin (1902), Lendner (1908), Ling-Yong (1930), Naumov (1935), Zycha (1935), and others, whereas the name Piptocephalidaceae has been favored by Schroeter (1897), Migula (1910), Fitzpatrick (1930), Martin (1940), and Hesselstine¹ (1955). As Hesselstine points out, the latter name should be retained not only because it is most appropriate but also because it has priority.

Although the zygomycetous affinities of *Piptocephalis*, *Syncephalis*, and *Syncephalastrum* have not been seriously questioned in the past, the status of several other

¹Hesselstine (1955) attributes the family name to Brefeld, 1881 (p. 161); Brefeld, however, used the name in 1872 (p. 53) in exactly the same sense as he did in 1881.

genera, *Kickxella* Coemans (1862), *Martensella* Coemans (1863), *Coemansia* Van Tieghem and Le Monnier (1873), *Dimargaris* Van Tieghem (1875), *Dispira* (1875), and *Spinalia* Vuillemin (1904), has been open to doubt. Because of the phycomycetous habit of the vegetative mycelia and fruiting structures of their known species the latter genera have been variously classified in the Mucorales in general or the Piptocephalidaceae in particular (de Bary, 1866, 1887; Istvánffi, 1895; Thaxter, 1895, 1897; Vuillemin, 1904; Lendner, 1908; Fitzpatrick, 1930; Naumov, 1935; Zycha, 1935; and Hesseltine, 1955). In the absence of definitive knowledge of sexuality, these fungi also have been placed in the Fungi Imperfecti (Hyphomycetes) as probable imperfect stages of Ascomyceteae (Coemans, 1862, 1863; Crouan and Crouan, 1867; Roumeguere, 1870; Van Tieghem and Le Monnier, 1873; Van Tieghem, 1875; Saccardo, 1883, 1886; Costantin, 1888; Lambotte, 1890; Lindau, 1900, 1907; Beer, 1902; Oudemans, 1886, 1905; Bainier, 1906 a, b; Torrey, 1921; and Migula, 1934). Linder (1943) discovered what appeared to be an immature zygosporangium in one of Thaxter's slide mounts of a species of *Coemansia*, and he erected a new family, Kickxellaceae, for the genera *Kickxella*, *Martensella*, and *Coemansia*. More recently the writer was able to confirm and extend the findings of Linder regarding the sexual nature of the Kickxellaceae (Benjamin, 1958). In addition to a detailed discussion of *Dimargaris* and its allies, a summary of the genera of Kickxellaceae will be presented in subsequent portions of this paper.

SYNCEPHALASTRACEAE

In 1892, Fischer, expressing his notions regarding the nature of the asexual fruiting structures of members of the order, classified the Mucorales in two suborders, Sporangiphoreae (including the Mucoraceae and Mortierellaceae) and Conidiophoreae (including the Chaetocladiaceae and Cephalidaceae). Fischer's subordinal categories, with various degrees of modification, were adopted subsequently by Lendner (1908), Naumov (1935), and Zycha (1935). Naumov (1924) extended Fischer's system by transferring the Cephalidaceae (in which, following Lendner (1908), he included *Dispira*) to a separate suborder, the Pseudoconidiophoreae, and in 1935 he proposed a fourth suborder, Choanephoreae, for the Choanephoraceae (*Choanephora* and *Blakeslea*).

An innovation in Naumov's treatment of the Pseudoconidiophoreae in 1935 was the transfer of *Syncephalastrum* to a new family, Syncephalastraceae. Although the writer believes that *Syncephalastrum* should, indeed, be distinguished from *Piptocephalis*, *Syncephalis*, and *Dispira* at the family level, it is for a reason other than the one presented by Naumov. In parentheses following the name Syncephalastraceae, Naumov (1935, p. 16) also listed the name Acephalae—undoubtedly to emphasize the character which he stressed in separating this family from the Cephalidaceae. Naumov interpreted as "sterigmata" the deciduous fertile vesicles, or head-cells (Dobbs and English, 1954), of *Piptocephalis*, the basal spores of branched merosporangia found in several species of *Syncephalis*², and the secondary branches inter-

²When Van Tieghem and Le Monnier described *Syncephalis* in 1873, the small, deciduous, more or less triangular bodies subtending the spore chains of several species (*S. cordata* and *S. asymmetrica*) were likened to the deciduous head-cells ("têtes") of *Piptocephalis*, and it was this interpretation that led these authors to coin the name *Syncephalis*. In 1875, however, Van Tieghem found that these small bodies are nothing more than spores formed in the basal portions of branched merosporangia. Van Tieghem (1875, p. 148) concluded, therefore, that "le véritable analogue de la tête caduque des *Piptocephalis*, c'est le renflement terminal lui-même du tube des *Syncephalis*."

posed between the merosporangia and the subtending vesicles of a few species of *Syncephalis* (Thaxter, 1897) and *Dispira* (Van Tieghem, 1875; Thaxter, 1897). The merosporangia of *Syncephalastrum* are borne directly on the terminal vesicles of the sporophores and, therefore, by Naumov's interpretation, are not subtended by "sterigmata," i.e., are acephalous. The fact that in several species of *Syncephalis* the merosporangia arise from the subtending vesicles in a manner exactly comparable to that found in *Syncephalastrum* was recognized by Naumov (1935, p. 16), but in his brief characterization of the Cephalidaceae he passed this over as being merely an exception to the rule. Naumov's "sterigmata," then, include such fundamentally different structures as the deciduous fertile vesicles of *Piptocephalis*, secondary branchlets produced by the vesicles of *Dispira* and several species of *Syncephalis*, and what actually were shown by Van Tieghem as early as 1875 to be basal spores of ramified merosporangia.

Although the vegetative and asexual characters of *Syncephalastrum* are considerably more generalized than those of *Piptocephalis* and *Syncephalis*, these factors alone probably would not warrant the exclusion of the former genus from the Piptocephalidaceae, but on the basis of sexual reproduction such a separation seems to be justified.

When he established the Pseudoconidiophoreae in 1924, Naumov stated only that the fungi "ayant des mérisporocystes" corresponded to "la tribu des Syncéphalidées de Van Tieghem (1875)," and he apparently did not formally recognize the Syncephalastraceae as a family until 1935. The latter name was not accompanied by a Latin diagnosis or by a reference to a previously and effectively published Latin diagnosis. Thus, according to the Article 34 of the International Code of Botanical Nomenclature (Lanjouw *et al.*, 1956) the name Syncephalastraceae as used by Naumov in 1935 was not validly published, and it was not validated by Buchet and Mouraviev in their well-known translation of Naumov's work, *Clés des Mucoriniées* (Naumov, 1939). Accordingly, the following diagnosis is presented here:

Syncephalastraceae Naumov fam. nov.

SYNCEPHALASTRACEAE Naumov, Oprelidelit Mukorovykh (Mucorales),
p. 16. 1935. (nomen nudum)

Hyphis vegetantibus hyalinis, expansis, ramosis, nonseptatis vel in aetate septatis; sporangiophoris rectis, ascendentibus vel recumbentibus et rhizoideis adventiticis gerentibus, in aetate septatis, ramosis; ramis apice in vesiculas inflatis; vesiculis globosis vel ovoideis merosporangia gerentibus; sporis globosis vel ovoideis plerumque uniseriatis, hyalinis; zygosporis globosis, episporio scabri; hyphis sexualibus approximate aequalibus, oppositis.

Vegetative hyphae hyaline, wide-spreading, branched, nonseptate, septate in age; sporangiophores erect, ascending, or recumbent and stolon-like, often producing adventitious rhizoids, becoming irregularly branched, septate in age; septa unmodified, imperforate; the main stalks of the sporangiophores and their branches forming terminal globose or ovoid vesicles bearing merosporangia directly over their entire surfaces; merosporangial wall evanescent at maturity; sporangiospores globose or ovoid, formed simultaneously by simple cleavage, usually uniseriate; zygosporis globose, dark-colored, rough, formed by the fusion of nearly equal gametangia borne on opposed suspensors.

Type genus: *Syncephalastrum* Schroeter (1886, p. 217).

With a single genus.

SYNCEPHALASTRUM Schroeter.

in Cohn's Kryptogamen-Flora von Schlesien. 3(2): 217. 1886.

With the characters of the family.

Type species: *Syncephalastrum racemosum* Cohn ex Schroeter (1886, p. 217).

In addition to the type species, the following species or varieties of *Syncephalastrum* have been proposed: *S. nigricans* Vuillemin (1887 b, p. 336), *S. elegans* Marchal (1892, p. 124), *S. cinerum* (Bainier 1907, p. 222), *S. fuliginosum* Bainier (1907, p. 223), *S. javanicum* Raciborski (1909, p. 347), *S. rhizopi* Vuillemin (1922, p. 986), and *S. racemosum* var. *paucisporum* Moreau (1949, p. 146; without a Latin diagnosis).

Members of this genus typically are saprobic³ and commonly are encountered in dung and soil. *Syncephalastrum rhizopi* was said by Vuillemin (1922) to be parasitic on *Rhizopus*; on the basis of Vuillemin's brief description, it would appear, as suggested by Zycha (1935), that this species undoubtedly should be referred to *Syncephalis*.

There has been no comprehensive taxonomic treatment of *Syncephalastrum* based on a study of a large series of living strains, and there has been little agreement among the more recent students of the Mucorales regarding the validity of all of the species listed above. Naumov (1935, 1939) accepted all of them at face value; Zycha (1935) recognized only three species, and one of these with reservation; Hesseltine (1955) expressed the opinion that one or perhaps as many as three species might be accepted as valid; Moreau (1949) suggested that *S. racemosum* might represent a polymorphic species with several stable varieties.

Among the criteria which in the past have been stressed in the delimitation of species of *Syncephalastrum* (Bainier, 1907; Lendner, 1912) are the following: (1) pattern of sporophore branching, (2) colony color, (3) presence or absence of septa in the sporophore, (4) presence or absence of "stolons," (5) dimensions of the vesicles subtending the merosporangia, (6) dimensions of the merosporangia, and (7) number, shape, and size of the spores.

In his brief, unillustrated description of the type species of *Syncephalastrum*, Schroeter (1886) stated that the sporophore was umbellately branched, yet he named the species *S. racemosum*. This descriptive specific epithet most certainly could not apply to any characteristic of the species other than the branching pattern of the fruiting structure. This fact, however, apparently was not taken into account by Schroeter's contemporaries, for the production of a racemose sporophore was listed by Vuillemin (1887 b), Marchal (1892), and Bainier (1907) as a character of prime importance in distinguishing *S. nigricans*, *S. elegans*, and *S. cinereum*, respectively, from the "umbellately branched" *S. racemosum*.

The writer has obtained over thirty isolates of *Syncephalastrum* from various localities, and a study of these has shown that characters such as vesicle diameter, number of spores per merosporangium, and spore size and shape—whether globose or ovoid—are of very little use as taxonomic criteria. A single isolate may exhibit such extreme variation in the above characters that it could be assigned to any of several of the named species.

Colony color has been stressed as an important species character: nearly white for *S. racemosum* and *S. elegans*; gray to nearly black for *S. nigricans*, *S. cinereum*, *S.*

³Thouvenin (1924), in his doctoral dissertation, reported the results of studies of the pathogenicity of *Syncephalastrum* on animals. His results were negative.

fuliginosum, and *S. javanicum*. The taxonomic value of this character, however, also is very questionable. Although the aerial hyphae may become slightly pigmented with age, the colony of a given isolate of *Syncephalastrum* derives most of its grayish or brownish color from the usually deeply pigmented sporiferous heads, especially the vesicles subtending the merosporangia. The writer has observed considerable variation among strains in the number of spore heads produced. Even among sexually compatible strains, one isolate producing few spore heads and, as a result, having a nearly colorless colony may mate with another isolate producing abundant spore heads and having a darkly pigmented colony.

During early stages of development, both vegetative and fruiting hyphae of *Syncephalastrum* are nonseptate. However, as in most of the more generalized members of the Mucorales, simple imperforate septa commonly are delimited in aging hyphae, and in old cultures septa may be present in abundance. When the sporiferous head has matured, a cross-wall typically is formed immediately below the terminal vesicle.

In the humid environment of tube or plate cultures, stolons may be produced when young sporophores touch the walls of the container or when recumbent sporophores contact the surface of the culture medium and give rise to adventitious rhizoids. As pointed out by Lendner (1912), the presence or absence of stolons and rhizoids is not, contrary to the opinion of Bainier (1907), a reliable taxonomic character in *Syncephalastrum*.

A perusal of the literature has convinced me that all of the species of *Syncephalastrum* characterized subsequent to the description of the type species, *S. racemosum*, have been segregated from the latter on the basis of characters which, in the light of an examination of a relatively large series of living isolates, are not reliable taxonomic criteria for the delimitation of species in this genus. Zycha (1935) included in his monograph only three species of *Syncephalastrum*: *S. racemosum*, *S. fuliginosum*, and *S. javanicum*; he relegated *S. nigricans* and *S. cinereum* to synonymy with the first, and he distinguished *S. javanicum* from *S. fuliginosum* by the much larger size of the fertile head of the former. Zycha stated, however, that if the dimensions of the fertile head of *S. javanicum* given by Raciborski included both vesicle and merosporangia, then this species probably should be considered as a synonym of *S. fuliginosum*. The status of *S. fuliginosum*, however, certainly is open to question. Bainier (1907) encountered this species along with *S. cinereum* on germinating seeds of *Delphinium staphisagria* L., and he stated that only *S. cinereum* was studied in culture. He separated *S. fuliginosum* from *S. cinereum* on the basis of the darker color, slightly ovoid spores, and presumably nonseptate sporophores of the former.

For the present, I am inclined to recognize only the following widespread and variable species of *Syncephalastrum*:

SYNCEPHALASTRUM RACEMOSUM Cohn ex Schroeter.

in Cohn's Kryptogamen-Flora von Schlesien 3(2): 217. 1886.

(Plates 1-2)

Syncephalastrum nigricans Vuillemin, Jour. Bot., Paris 1(21): 336. 1887.

Syncephalastrum elegans Marchal, Bull. Soc. Belge Microscopie 18: 124. 1892.

Syncephalastrum cinereum Bainier, Bull. Soc. Mycol. France 23: 222. 1907.

Syncephalastrum fuliginosum Bainier, Bull. Soc. Mycol. France 23: 223. 1907.

Syncephalastrum javanicum Raciborski, Bull. Internat. l'Acad. Sci. Cracovie, Cl. Sci. Mat. et Nat. 1909: 347. 1909.

Syncephalastrum racemosum var. *paucisporum* Moreau, Bull. Soc. Mycol. France 65: 146. 1949. (nomen nudum)

Colonies on YpSs or PDA remaining nearly white or becoming "Drab" to "Deep Neutral Gray," 0.5-1.5 cm. high; vegetative hyphae growing rapidly at 21°C, color-

less, becoming highly branched, 4-8 μ in diam., nonseptate at first, irregularly septate in age; septa simple, without median perforations; sporangiophores arising directly from the vegetative hyphae, at first simple, nonseptate, erect, ascending, or recumbent, often stolon-like and producing adventitious rhizoids, becoming irregularly racemously or cymosely branched and forming a densely intertwined aerial myelium; primary axes of the sporophores, 10-25 μ in diam., producing terminal globose or ovoid enlargements, 30-80 μ in diam.; lateral branches straight or sharply recurved, highly variable, 20-300 μ or more in length, 5-15 μ in diam., producing terminal vesicles about 10-40 μ in diam.; vesicles, at maturity, usually subtended by simple septa; numerous septa also formed at irregular intervals in the sporophores; terminal enlargements of the sporophores fertile, giving rise, by budding, usually over their entire surfaces, to rod-like merosporangia and forming pale to dark gray or brownish spore-heads about 40-150 μ in diam.; vesicles becoming pale gray or brownish in color and contrasting sharply with the hyaline or only slightly pigmented sporophores; merosporangia slender, normally containing a single row of (3-)5-10(-18) smooth sporangiospores; a second usually incomplete file of spores not uncommon; sporangiospores globose or ovoid, about 3-5 μ in diam.; more rarely oblong or cylindrical; merosporangial wall evanescent; heads not forming spore-drops at maturity; heterothallic; zygospores globose, 50-90 μ (aver. 70 μ) in diam., black at maturity, roughened with broad, shallow, tooth-like projections, formed above the substratum on hyaline aerial hyphae; suspensors opposed, hyaline, smooth-walled, nearly equal.

Specimens examined.—CALIFORNIA. Kern County: Inyokern, isolated from soil by G. F. Orr, 1958 (RSA Culture 702, +). Los Angeles County: San Antonio Canyon, San Gabriel Mts., 4.5 miles northeast of Claremont, isolated from coyote dung collected by D. H. Ford, January 8, 1954 (RSA Culture 229; NRRL A-5989, —); 3 miles northwest of San Dimas, isolated from soil collected by D. H. Ford, December 19, 1953 (RSA Culture 230; NRRL A-5990, +). Riverside County: near Blythe, isolated from soil by G. F. Orr, 1958 (RSA Culture 697, —). San Bernardino County: 1 mile north of Cucamonga, isolated from soil collected by D. H. Ford, December 29, 1953 (RSA Culture 236, +). Transfers of all of the above cultures have been distributed to ATCC, CBS, and CMI.

Sporangiospores of *Syncephalastrum racemosum* usually begin to germinate within 6-8 hours when placed on nutrient media such as YpSs or PDA. The germinating spore swells to about 2-3 times its original diameter and gives rise to one or more germ hyphae which elongate rapidly, branch more or less at right angles, and soon give rise to a richly branched and vigorous mycelium. Simple undifferentiated septa are delimited in hyphae of the older portions of the mycelium usually after the onset of sporangiophore development. Sporangiophores begin to appear in about 24 hours, elongate rapidly, and may attain lengths of a centimeter or more before the terminal sporiferous enlargements begin to form. The young sporophore is without septa and its colorless protoplasm contains an abundance of small nuclei. As the usually slightly

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PLATE 1. *Syncephalastrum racemosum* Cohn ex Schroeter.—*a.* Multinucleate terminal enlargement of sporophore prior to the appearance of merosporangial primordia. $\times 1300$. *b.* Same showing mostly uninucleate merosporangial primordia. $\times 1300$. *c.* Multinucleate merosporangia prior to delimitation of spores. $\times 1300$. *d.* Terminal part of merosporangium showing apparently discrete chromosomes of dividing nuclei. $\times 2100$. *e.* Mature fertile head showing merosporangia before distarticulation. $\times 560$. *f.* Immature merosporangium showing cleavage of protoplasmic contents into spore primordia. $\times 2100$. *g.* Nearly mature merosporangia showing single files of spores and discrete sporangial walls. $\times 2100$. *h.* Merosporangium from which spores have been removed by means of gentle pressure exerted on the cover glass. $\times 2100$. *i.* Merosporangium containing five spores. One spore is lateral in position. $\times 2100$. *j.* Six spores still in their original positions after the sporangial wall has nearly disappeared. $\times 2100$. *k.* Sporangiospores. $\times 2100$.

PLATE 1

ovoid terminal vesicle enlarges, it becomes filled with a densely granular protoplasm which may contain several hundred nuclei (Pl. 1 *a*). The merosporangial initials are formed by budding directly over the entire surface of this enlargement (Pl. 1 *b*) and into each primordium one or perhaps several nuclei migrate from the subtending vesicle (Moreau, 1913). Although a detailed cytological study has not been undertaken, apparently typical mitoses have been observed in a few instances in the developing merosporangia (Pl. 1 *c-c'*). As Marchal (1892) and Thaxter (1897) showed, the protoplasmic contents of each merosporangium forms, by simple cleavage, several distinct portions (Pl. 1 *e*). These are the presumptive spores, each of which includes one or sometimes two or three nuclei (Moreau, 1913). Each spore becomes surrounded by a wall of uniform thickness, and the resulting spore is easily distinguished from the merosporangial wall (Pl. 1 *f-g*). By exertion of gentle pressure on the cover glass of a slide mount, a merosporangium can be emptied of its spores (Pl. 1 *b*). One may occasionally find instances in which the spores are formed irregularly (Pl. 1 *i*) rather than in a single row, and, like Marchal (1892), the writer has observed merosporangia with as many as 25 or more spores disposed in two nearly complete files. The spores are freed by the eventual fragmentation of the sporangial wall (Pl. 1 *j-k*), portions of which may remain attached to the spores for some time after they have been liberated. Unlike certain species of *Piptocephalis* and *Syncephalis*, the mature spore heads (Pl. 1 *d*) remain dry rather than forming viscous drops.

While the terminal, or primary, sporiferous head is developing, the sporophore typically gives rise to a succession of lateral branches, each of which produces a terminal head similar in all respects to the primary head but usually somewhat smaller. Continued branching results in a sporophore of considerable complexity. Lateral branches arise without the prior formation of septa immediately above their points of origin. Septa produced later, however, appear definitely to be correlated with the state of maturity of that portion of the sporophore above their point of origin. After a spore head has matured, the vesicle subtending the merosporangia becomes separated from the sporangiophore by a cross-wall. The position of this septum is rather variable and it may be located as much as half a vesicle diameter below the base of the vesicle itself. Septa delimited in the sporophore proper usually are spaced at very irregular intervals and they appear to be formed progressively backward from mature portions of the sporangiophore.

Blakeslee apparently observed zygospores in *Syncephalastrum* as early as 1906 (Vuillemin, 1922) and he later carried out an extensive series of tests on sexual dimorphism in the genus (Blakeslee, 1920). Vuillemin (1922) indicated that the zygospores of his *S. nigricans* were similar to those found in typical species of *Mucoraceae*, but he, like Blakeslee, did not illustrate them. Thus, the question of the true nature of the zygospore in *Syncephalastrum* has remained rather vague.

During the course of the present study, zygospores of the type reported by Vuillemin have been obtained on numerous occasions by mating various strains of *S. racemosum*. Zygospores begin to appear in about 5-7 days when compatible strains are contrasted on YpSs and incubated under ordinary laboratory conditions. The sexual spores of *S. racemosum* are produced above the substratum by the fusion of nearly equal gametangia formed apically by opposed progametangia (Pl. 2 *a-c*). When mature, the nearly globose, *Mucor*-like zygospores measure about 50-90 μ in diameter and have blackish walls roughened with shallow, conical, tooth-like projections.

Inclusion of *Syncephalastrum* in a distinct family intermediate between the *Mucoraceae* and *Piptocephalidaceae* appears to be the most natural disposition of the genus. The unspecialized coenocytic vegetative mycelium, the undifferentiated fertile hyphae

PLATE 2. *Syncephalastrum racemosum* Cohn ex Schroeter.—*a*. Early stage of zygospore formation showing opposed sexual hyphae and nearly equal gametangia which have fused. $\times 340$. *b*. Mature zygospore. $\times 340$. *c*. Several zygospores. $\times 170$. (all RSA Culture 229 $\times$ RSA Culture 230)

which become irregularly septate in age, the *Mucor*-like manner in which the asexual spores are formed, and especially the typically mucoraceous zygosporangia would seem to indicate a close relationship of the genus to the Mucoraceae. The development of cylindrical sporangia containing usually a single file of spores is, however, a character of sufficient importance to warrant the exclusion of *Syncephalastrum* from the Mucoraceae where it actually was placed by Vuillemin in 1922.

PIPTOCEPHALIDACEAE Brefeld.

Botan. Untersuch. über Schimmelpilze I: 53. 1872.

Vegetative hyphae hyaline, delicate, branched nonseptate or septate; sporangiophores simple or branched, septate or nonseptate, bearing merosporangia on terminal deciduous or nondeciduous enlargements; sporangiospores usually uniseriate; merosporangial wall evanescent at maturity or persistent and separating along with the spores by circumscissile rupture; zygosporangia formed from the union of gametangia produced terminally by apposed or coiled progametangia; species typically obligate parasites of other fungi—mostly other Mucorales.

Type genus: *Piptocephalis* de Bary (1865, p. 356).

A KEY TO THE GENERA

- A. Sporangiophores branched; merosporangiferous vesicles usually deciduous..... *Piptocephalis* (p. 334)
- AA. Sporangiophores not branched; merosporangiferous vesicles not deciduous..... *Syncephalis* (p. 352)

PIPTOCEPHALIS de Bary.

Abh. Senckenb. Natf. Ges. 5: 356. 1865.

Mucoricola Nieuwland, Amer. Mid. Nat. 4: 82. 1916. (nomen nudum)

Vegetative hyphae slender, becoming septate, highly branched, running over the host hyphae and forming small appressoria which penetrate the host wall and give rise to restricted, delicate, branched haustoria; sporangiophores erect, ascending, or recumbent, septate, smooth or appearing longitudinally striate, giving rise to two or more repeatedly dichotomous branch systems, the ultimate branches producing relatively small enlargements bearing few to many merosporangia containing two or more uniseriate, globose, ellipsoid, cylindrical, or fusiform sporangiospores; terminal enlargements usually deciduous at maturity; merosporangial wall delicate, evanescent; spore heads remaining dry or forming viscous drops; zygosporangia globose, usually light-colored, rough, formed as bud-like enlargements above the point of fusion of slightly unequal gametangia delimited apically by apposed progametangia.

Type species: *Piptocephalis freseniana* de Bary (1865, p. 356).

Observed first by Fresenius in 1864 and described and illustrated very briefly by de Bary the following year, *Piptocephalis freseniana* was studied in detail in 1872 by Brefeld who discovered its zygosporangia. Subsequently, some eighteen species and varieties of the genus have been named: *Piptocephalis repens* Van Tieghem and Le Monnier (1873, p. 364), *P. arrhiza* Van Tieghem and Le Monnier (1873, p. 366), *P. sphaerospora* Van Tieghem (1875, p. 150), *P. fusispora* Van Tieghem (1875, p. 146), *P. microcephala* Van Tieghem (1875, p. 147), *P. cruciata* Van Tieghem (1875, p. 149), *P. cylindrospora* Bainier (1882, p. 111), *P. corymbifer* Vuillemin (1887 a, p. 111), *P. fusispora* Van Tieghem var. *lepidula* Marchal (1891, p. 136), *P. monospora* Mangin (1899, p. 377), *P. sphaerocephala* Mangin (1899, p. 376), *P. tieghemiana* Matruchot (1900, p. 58), *P. lemonnieriana* Vuillemin (1902, p. 47), *P. macrospora* Beyma (1944, p. 42), *P. xenophila* Dobbs and English (1954, p. 375),

P. dichotomica Krzemieniewska and Badura (1954, p. 733), and *P. virginiana* Leadbeater and Mercer (1957, p. 461). Schroeter (1886, p. 215) listed Van Tieghem's *P. cruciata* as a variety of *P. freseniana*.

In 1860, Schultz-Bipontinus proposed the name *Piptocephalum* for a genus of Compositae. This name later was relegated to synonymy with *Catananche* L. (see Index Kewensis II: 543. 1895). Subsequently, Nieuwland (1916) treated *Piptocephalis* as a later homonym of *Piptocephalum*, and he disposed of the former name with a single statement, "*Mucoricola* may be used for the fungus." Nieuwland did not transfer any species of *Piptocephalis* to *Mucoricola*. There is no possibility of confusing *Piptocephalis* and *Piptocephalum* and in the sense of Article 75 of the International Code of Botanical Nomenclature (Lanjouw *et al.*, 1956) Nieuwland's action was unwarranted. Also, *Mucoricola* was not validly published, for, technically, Nieuwland did not accept the name (Article 33(1) of the Code).

In nature, all known species of *Piptocephalis* appear always to be obligate parasites of other fungi and, with the exception of *P. xenophila*, are known to develop only on other members of the Mucorales (Brefeld, 1872; Van Tieghem and Le Monnier, 1873; Van Tieghem, 1875; Matruchot, 1900; Bainier, 1907; Berry and Barnett, 1957; Leadbeater and Mercer, 1957 b). In addition to species of several families of Mucorales, *Piptocephalis xenophila* readily attacks various Ascomyceteae and Fungi Imperfecti (Dobbs and English, 1954). As yet, however, the host range of only a limited number of species of *Piptocephalis* has been tested.

As a result of his own collecting activities and the cooperation of numerous colleagues, the writer has obtained over sixty living isolates representing at least fourteen species of *Piptocephalis*. Included in this collection are the recently described *P. xenophila* and *P. virginiana* as well as *P. arrhiza*, *P. cylindrospora*, *P. microcephala*, and *P. repens*.

The more recent keys of Naumov (1935, 1939) and Zycha (1935) serve to mirror the present taxonomic status of *Piptocephalis*. Of the thirteen species and one variety of the genus described prior to 1935, Zycha, who considered twelve of these taxa, recognized only seven species as valid, whereas Naumov accepted all of the species but one. It is the writer's opinion that until a revision of the genus is based on standardized cultural techniques, accurate identification of any species of *Piptocephalis* except those possessing certain unique characteristics will be difficult and uncertain, and in the discussion presented below, the question of the validity of several doubtful species is avoided for the most part. A taxonomic treatment of the species of *Piptocephalis* is deferred at this time; however, a summary of the general characteristics of the genus and a number of personal observations, based on a study of the literature and the material at hand, are given.

When sowed upon a suitable medium, sporangiospores of *Piptocephalis* species swell greatly, often reaching 5-6 times their original diameter, become nearly spherical (Pl. 6 a), and give rise laterally to one or usually several slender germ hyphae. The thickened, more or less inextensible terminal end-walls often are a quite conspicuous feature of the germinating spores (Pl. 3 m; Pl. 7 b). Origin of the germ hyphae from the lateral extensible wall of the sporangiospore was recorded originally by Brefeld (1872) for *P. freseniana* and described subsequently for other species of *Piptocephalis* by Van Tieghem (1875), Dobbs and English (1954), and Leadbeater and Mercer (1957 b). The spores of all species of the genus studied by the writer germinate in the manner described above.

Spore germination usually will take place on ordinary media such as PDA or YpSs in the absence of a host, and in the case of *P. virginiana* it has been shown that a

limited mycelium will develop and produce depauperate or dwarf sporophores (Berry and Barnett, 1957; Leadbeater and Mercer, 1957 b). The spores produced by such dwarf sporophores were found by Leadbeater and Mercer (1957 b) not to germinate in the continued absence of a host, but they are capable of infecting a suitable host. Several other species of *Piptocephalis* studied by the writer likewise produce dwarf sporophores in pure culture, but, as in the case of *P. virginiana*, normal development in the absence of a proper host never has been observed. Leadbeater and Mercer (1957 b) reported that the spores of *P. xenophila* will germinate on certain media but will not give rise to dwarf sporophores; this observation has been confirmed by the writer.

When spore germination takes place in the presence of a susceptible host, the delicate germ hyphae of the parasite soon contact the hyphae of the latter and produce small, slightly enlarged, terminal appressoria which penetrate the host wall by means of minute tubes and give rise to restricted, delicate, simple or branched haustoria (Pl. 3 p; see also Van Tieghem, 1875; Dobbs and English, 1954; Berry and Barnett, 1957; Leadbeater and Mercer, 1957 b). The development of several penetration tubes from a single appressorium, as was shown by Brefeld (1872, Pl. V, fig. 17) and Van Tieghem and Le Monnier (1873, Pl. 25, fig. 117; incorrectly referred to an undetermined species of *Syncephalis* according to Van Tieghem, 1875, p. 116), have never been observed by the writer in any species of *Piptocephalis* studied. After establishing direct union with the host protoplasm, the vegetative mycelium of the parasite develops rapidly and soon envelops the host hyphae with an often very extensive overgrowth. The parasitic hyphae branch freely, usually are about 2-4 μ in diameter for most species studied, and with age delimit numerous simple, imperforate septa, the primary function of which appears to be the separation of living from apparently dead segments of hyphae.

The vegetative mycelium of species of *Piptocephalis* usually develops most abundantly within or upon the surface of the substratum (agar, dung, etc.) in close contact with the vegetative mycelium of the host; some species, however, especially in culture, may develop a more or less extensive aerial vegetative mycelium in addition to fruiting hyphae. The latter, in pure mixed culture, may develop in profusion and form, by their intermingling, a relatively dense turf. With a single known exception, the aerial mycelium of species of *Piptocephalis* does not, as in *Syncephalis* species, vigorously attack the aerial growth of the host. Dobbs and English (1954) observed a single case in which *P. xenophila* formed haustoria in the stalk of a conidiophore of a species of *Aspergillus*. *Piptocephalis* species may, however, attack aerial hyphae of their hosts, especially in the humid atmosphere of tube or plate cultures, and spores produced by sporophores of parasites growing in company with such species as *Mucor hiemalis* and *Rhizopus stolonifer* readily germinate in water droplets adhering to host sporophores and may produce appressoria and haustoria in abundance.

When grown in culture on a fungus such as *Mucor hiemalis*, most species of *Piptocephalis* studied here appear to reduce only slightly the capacity of the host to reproduce itself, and the latter usually produces an abundance of fruiting structures. This is in marked contrast to the pathological effect of species of *Syncephalis*, for members of the latter genus often suppress almost completely the formation of sporangioophores by the host.

When characterized originally, *P. repens* (Van Tieghem and Le Monnier, 1873), *P. fusispora*, and *P. microcephala* (Van Tieghem, 1875) were described as stoloniferous and the sporangioophores of these species were said to arise from well-defined systems of branched rhizoids. In the figures given by Van Tieghem for *P. fusispora*

and *P. microcephala* (Van Tieghem, 1875, Pl. 4, fig. 137 and 146 respectively) distinct stolons and rhizoids are shown. Van Tieghem (1875) classified the species of *Piptocephalis* known to him into two series on the basis of the presence or absence of stolons and rhizoids, and these characters were used similarly in the systems of Fischer (1892) and Zycha (1935).

Several strains of *P. microcephala* have been isolated by the writer and a culture of a strain of *P. repens* on deposit at the Centraalbureau voor Schimmelcultures has been sent to the author by Dr. Leadbeater. When cultivated on *Cokeromyces recurvatus*, these species, like several other members of the genus, may give rise not only to wide spreading aerial vegetative hyphae but also to numerous long, slender fertile hyphae which may remain nearly erect, or, lacking the support of neighboring hyphae, may become more or less recumbent. Thus, potentially fertile hyphae may extend horizontally over the surface of the substrate for some distance before forming fertile dichotomous branch systems. Under these conditions it is not unusual for several branches of the dichotomous system in contact with the surface of the substrate or culture dish to abort and give rise to rhizoid-like structures while the remainder of the branches produce normal sporiferous heads. Sporophores like those shown in Plate 5 *j-k* frequently are encountered in dung cultures where the parasite is growing in company with other fungi on a substrate of limited surface area; these fruiting structures are very similar to those described and figured by Van Tieghem and Le Monnier for *P. repens* (1873, Pl. 25, fig. 107) and by Van Tieghem for *P. fusispora* and *P. microcephala*. In pure mixed culture on *Cokeromyces recurvatus*, recumbent sporophores of *Piptocephalis* in contact with the moist surface of the agar substrate or the walls of the culture dish often produce rhizoidal sporophores, whereas fertile hyphae which remain more or less erect usually form nearly symmetrical dichotomous branch systems (Pl. 3 *q-r*; Pl. 4 *a-b*; Pl. 6 *b*; Pl. 7 *b*). In connection with his original characterization of *P. corymbifer*, Vuillemin (1887 a) described the formation of adventitious rhizoid-like structures by potentially fertile branches of recumbent sporophores. It is apparent, then, that under certain conditions of culture some of the branches of the sporophore may remain sterile and function as rhizoids while others, often only one, project upward and give rise to sporogenous branchlets. The writer is convinced that this phenomenon accounts for the so-called stoloniferous habit described for several species of *Piptocephalis*. Under the usual conditions of culture, a few species of the genus, such as *P. xenophila* and *P. arrhiza* (Pl. 7), typically produce nearly erect sporophores which normally do not give rise to pseudostoloniferous fruiting structures. The taxonomic value of the latter character in *Piptocephalis* needs further critical study.

Longitudinally striate sporophores are very characteristic of many species of *Piptocephalis*. The striae appear to result from the formation of secondary thickenings on the inner face of the sporophore wall (Pl. 4 *f*), especially in the upper reaches of the main stalk and in the branches of the dichotomous system, and the striations usually become increasingly conspicuous as the sporophore ages. Mangin (1899) reported cellulose in the striae of *P. arrhiza*. Striate sporophores were described first by Van Tieghem and Le Monnier (1873) for *P. repens* and *P. arrhiza*, and the phenomenon later was reported for *P. cruciata*, *P. fusispora*, *P. microcephala* (Van Tieghem, 1875), *P. corymbifer* (Vuillemin, 1887 a), *P. sphaerocephala* (Mangin, 1899), *P. lemonnieriana* (Vuillemin, 1902), *P. freseniana* (Bainier, 1907), *P. macrospora* (Beyma, 1944), *P. cylindrospora* (Leadbeater and Mercer, 1957 a), and *P. virginiana* (Berry and Barnett, 1957; Leadbeater and Mercer, 1957 b). The sporophore of *P. xenophila* was described originally as non-striate (Dobbs and English, 1954), but

the writer has found that aged sporophores of this species may be very faintly striate (Pl. 6 *i*). Striae have not been reported in the other described species of *Piptocephalis*. Sporophore striations, then, are characteristic of many species of *Piptocephalis*, and further study may show that, to a degree, they are common to most species of the genus. In some species, longitudinal striae are one of the most outstanding features of sporophore morphology (Pl. 4 *f*; Pl. 7 *c*), whereas in others they are not apparent except in age and even then are very inconspicuous.

The ultimate branches of the sporophores of *Piptocephalis* species produce small, often inconspicuous, terminal enlargements bearing the usually rod-like merosporangia. As the spores are delimited, these terminal enlargements become indurated and in all but one known species separate, at maturity, from their supporting branches (Pl. 6 *b*; see Leadbeater and Mercer, 1957 *b*). Dobbs and English (1954) proposed a purely descriptive term, head-cell, for the terminal vesicle of *Piptocephalis* and this term is used in the present work. The branch subtending the head-cell is here called the head-cell branch. In a unique and as yet undescribed species of *Piptocephalis* being studied by W. Morris and G. Leadbeater in Dr. Leadbeater's laboratory, the terminal enlargement is nondeciduous at maturity. This species also produces a very extensive aerial mycelium which, like species of *Syncephalis*, attacks and decimates the host.

Three basic types of head-cells are found in the genus *Piptocephalis*, the conical or trigonal type, the globoid type, and the lobed type. The first type is found in the so-called microcephalous species such as *P. microcephala* (Pl. 6 *l-m*) and *P. xenophila* in which the head-cell is a small somewhat turbinate structure about 2-4 μ in diameter bearing a small number of merosporangia, usually about 4-6, distally. The second type is characteristic of what are termed the sphaerocephalous species. In these the head-cells usually are about 5-10 μ in diameter, often are slightly broader than tall, and bear greater numbers of merosporangia than the head-cells of the microcephalous forms—in some species as many as 30 or more spore chains may be produced on each vesicle. Except for the area adjacent to its point of attachment to its supporting branch, this type head-cell typically bears merosporangia over its entire surface (Pl. 3 *i, k*; Pl. 6 *g*). The third type of head-cell is characteristic of the macrocephalous species such as *P. freseniana* and its allies, including *P. repens*, *P. arrhiza*, *P. cruciata*, *P. corymbifer*, and *P. dichotomica*. In these species the fertile vesicle may be as much as 14-20 μ in diameter, usually is somewhat cupulate and deeply incised (Pl. 7 *f-g*), and bears few to many merosporangia distally on each lobe (see de Bary, 1865, Pl. V, fig. 18; Van Tieghem, 1875, Pl. 5, fig. 157; Mangin, 1899, fig. 4-5; Krzemieniewska and Badura, 1954, fig. 1).

The sporangiospore is round in *P. sphaerospora*, fusiform in *P. fusispora*, ovoid or

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PLATE 3. *Piptocephalis lepidula* (Marchal) Benjamin.—*a*. Terminal enlargements of sporophores, the one at the right showing initial stages of development of merosporangia. $\times 1700$. *b-b*. Successive stages in the acropetal development of a merosporangium. $\times 1700$. *i*. Terminal enlargement of sporophore showing arrangement of nearly mature merosporangia. $\times 1700$. *j*. Mature spores. $\times 1700$. *k*. Head-cell showing wart-like prominences marking the original positions of merosporangia. $\times 1700$. *l*. Terminal portion of typical sporophore showing conformation of successive branches; each ultimate branchlet bears a fertile head. $\times 180$. *m*. Germinating spores; note lateral origin of germ hyphae. $\times 1080$. *n*. Head-cell branches. $\times 780$. *o*. Typical cross-wall from the lower reaches of fertile hyphae; note the conspicuous tubular projection formed upwardly from the median perforation in the septum. $\times 1700$. *p*. Vegetative hyphae of the parasite showing minute, branched haustoria inside a host hypha. $\times 1080$. *q*. Habit sketch showing general characteristics of fruiting structures and the formation of pseudostolons and rhizoids by recumbent sporophores. The lengths of the stipes are not drawn to scale. $\times 15$. *r*. Habit sketches showing variation in the branching pattern of sporophores $\times 40$.

PLATE 3

ellipsoidal in *P. fusispora* var. *lepidula*, *P. monospora*, and *P. lemonnieriana*, and more or less short-cylindrical in all other described species. Spore shape alone, therefore, has only limited value as a taxonomic criterion. Spore size, too, would appear to be useful only when it is considered in connection with other criteria. In all of the known species of *Piptocephalis*, the spore is smooth walled and rather small, ranging from a mean of about $2\ \mu \times 5\ \mu$ in *P. virginiana* (Leadbeater and Mercer, 1957 b) to $4\ \mu \times 8\ \mu$ for the relatively large spored *P. arrhiza* (Pl. 7 f, b-j).

With few exceptions, variable numbers of spores are produced in the merosporangia of most species of *Piptocephalis*. Mangin (1899) described a species with single-spored merosporangia, *P. monospora*, from specimens which he encountered in company with preserved material of another fungus used previously in his studies of the cell wall. He did not indicate the quantity of material available to him for study, and he expressed doubt as to the state of maturity of the specimens at the time they had been preserved in alcohol. It is not possible, on the basis of Mangin's very incomplete description, to contrast *P. monospora* with other members of the genus, and only the rediscovery of this doubtful species will establish its validity. His only figure of *P. monospora* (Mangin, 1899, fig. 7) very well could represent the immature head of any of several sphaerocephalous species. *Piptocephalis microcephala*, *P. fusispora* var. *lepidula*, and *P. lemonnieriana* were characterized as typically two-spored. Although two-spored merosporangia are the rule in *P. microcephala* (Pl. 6 l), the production of three spores (Pl. 6 m) is not infrequent; I have never observed more than three spores in the spore chain of this species. *Piptocephalis fusispora* var. *lepidula* is invariably two-spored (Pl. 3 g-i; Pl. 5 g-b): this form is considered here as a distinct species and will be discussed in detail below.

Vuillemin recorded three-spored merosporangia for *P. corymbifer*, and he did not indicate a deviation from this number. According to Matruchot (1900), *P. tieghemiana* produces one to three, usually two, spores in each chain, and Beyma (1944) reported chains of two to three spores for *P. macrospora*. The writer has found two to three spores per merosporangium to be usual in the several isolates of *P. arrhiza* obtained in southern California. An average of more than three spores per merosporangium apparently is typical of the other described species of *Piptocephalis*. Dobbs and English (1954) found the number of spores in the merosporangia of *P. xenophila* to range from four to eleven with a mean of about six. Leadbeater and Mercer (1957 a) note that variability in the number of spores per chain may limit the use of this character as a taxonomic criterion.

Processes leading to the production of sporangiospores in *Piptocephalis* differ only slightly from those found in *Syncephalastrum*. Mangin (1899), studying *Piptocephalis arrhiza*, demonstrated what he believed were two distinct walls surrounding each spore. Thus he interpreted the spore chain as a series of one-spored sporangia. As shown clearly in Plate 7 i-j, however, the spores of this species are borne within

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PLATE 4. *Piptocephalis lepidula* (Marchal) Benjamin.—a-b. Terminal portions of upright sporophores showing characteristic branching patterns; preparations from cultures grown on *Cokeromyces recurvatus*. $\times 75$. c. Detail of distal dichotomous branch system of one primary branch of a sporophore. $\times 310$. d. Same; head-cells and spores have fallen away. $\times 310$. e. Typical septum in lower region of sporophore showing tubular perforation. $\times 1180$. f. Portion of striate sporophore stipe showing irregularity of the secondary thickenings forming the striae. $\times 1180$. g. Early stage in the development of a zygosporangium showing tongs-like sexual hyphae. $\times 415$. h. Immature zygosporangium. $\times 415$. i. Mature zygosporangium showing smooth-walled gametangial remnants and suspensors. $\times 415$. j. Mature zygosporangium crushed in order to show the smooth endospore (right) and the rough-walled exospore (zygosporangium). $\times 425$. k. Crushed zygosporangium showing the reticulate zygosporangial wall. $\times 910$.

PLATE 4

the merosporangium in a manner comparable to that observed in *Syncephalastrum* (Pl. 1 *e-g*). Although branched merosporangia may occur occasionally in some species of *Piptocephalis* (Pl. 7 *j*), the spores apparently always are formed uniseriately. Spore formation has been admirably described for *P. virginiana* by Leadbeater and Mercer (1957 *b*), and the process outlined for this species probably is typical of most members of the genus.

The ultimate branches of the dichotomous system swell distally and several nuclei pass into each of the resulting vesicles (Pl. 5 *d-e*). The latter soon develop small bud-like outgrowths (Pl. 3 *a*; Pl. 5 *e*) which in most species soon elongate into nearly cylindrical rods (Pl. 5 *a-c*). Although the nuclear cycle of the sporing rod has not been followed in all of the species studied here, the sequence shown in Plate 5 *a-c* (for an unidentified species producing usually two- to three-spored merosporangia) probably is representative of most species producing elongate multispored merosporangia. Here a single nucleus in the young merosporangium divides once (Pl. 5 *a-b*) and two spores are delimited (Pl. 5 *c*) or one of the above nuclei may divide again and three spores are formed (Pl. 5 *c*).

Following nuclear division, the first visible stage of spore formation (Leadbeater and Mercer, 1957 *b*) is the appearance of narrow transverse hyaline zones separating the contents of the merosporangium into distinct regions which will become spores. Walls are laid down on either side of each interstitial zone; these, the end-walls of the spores, increase in thickness as the lateral walls are formed, and, as stated earlier, are in evidence as nearly inextensible polar caps on the germinating spores (Pl. 7 *b*). While the spores are developing, the thin merosporangial membrane remains intact (Pl. 7 *i-j*), but as soon as the spores reach maturity, the interstitial material breaks down (Leadbeater and Mercer, 1957 *b*) and the merosporangial wall separates by circumscissile rupture in the region opposite the interstitial zones (Pl. 6 *g*; Pl. 7 *f, i-j*).

During the course of the present study, numerous isolates of a species of *Piptocephalis* possessing a unique type of merosporangial development have been obtained. In this species, each bud-like outgrowth of the young vesicle (Pl. 3 *a-f*) does not elongate to form a cylindrical structure as in other known species of the genus but, concurrently with the division of its single nucleus (Pl. 5 *f*), gives rise, also by budding, to a terminal enlargement into which one of the daughter nuclei of the first division migrates (Pl. 5 *g*). The basal and terminal portions of the resulting merosporangium delimit single spores (Pl. 3 *g-i*; Pl. 5 *h*). Each spore contains one nucleus or, as a result of a mitotic division, two nuclei (Pl. 5 *h-i*). As described below, acro-

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PLATE 5. *a-c*. *Piptocephalis* sp. indet. (RSA Culture 642).—*a-b*. Nearly cylindrical, immature merosporangia, most of which are uninucleate; in a few instances single nuclear divisions have occurred (arrows). $\times 2100$. *c*. Nearly mature two- or three-spored merosporangia showing uninucleate spores. $\times 2100$. *d-j*. *Piptocephalis lepidula* (Marchal) Benjamin.—*d*. Early stage of development of fertile vesicular enlargement showing multinucleate supporting (head-cell) branch. $\times 2100$. *e*. Multinucleate vesicular enlargements showing very early stage in the development of merosporangia. $\times 2100$. *f*. Young merosporangia; all but one, shown at the upper left, are uninucleate. The terminal part of each merosporangium is developing as a bud-like outgrowth from the basal part. $\times 2100$. *g*. Later stage in the development of merosporangia. One nucleus of a pair resulting from a nuclear division in the basal portion of a merosporangium is shown migrating into the terminal portion of the merosporangium (arrow). $\times 2100$. *h*. Nearly mature merosporangia showing mostly uninucleate spores. $\times 2100$. *i*. Seven spores; in two of these the nucleus has divided once. $\times 2100$. *j*. Small sporophore from gross culture on dung; note basal rhizoids and stolon. Further discussion is in the text. $\times 80$. *k-l*. *Piptocephalis microcephala* Van Tieghem.—*k*. Small sporophore from gross culture on dung; note basal rhizoids and aborted fertile hyphae. Further discussion is in the text. $\times 60$. *l*. Mature zygospore. The zygospores of this species (RSA Culture 628) were found to measure 43-60 μ (aver. 52 μ) in diameter. $\times 310$.

PLATE 5

petal development of the merosporangium also is characteristic of at least one known species of *Syncephalis* and all but one of the known species of *Dimargaris* and its allies.

Among the described sphaerocephalous members of *Piptocephalis*, only *P. lemonnieriana* (Vuillemin, 1902) and *P. fusispora* var. *lepidula* (Marchal, 1891) have been reported to produce merosporangia containing two more or less ovoid spores. For reasons to be given later, the species being considered here can not be identified with *P. lemonnieriana*.

Marchal's unillustrated description of *P. fusispora* var. *lepidula* is very brief, and he established his fungus as a variety of *P. fusispora* on the basis of its branching pattern, its small size, and its two-spored rather than many- (five-) spored merosporangia (Van Tieghem, 1875, Pl. 4, fig. 142). In *P. fusispora*, according to Van Tieghem (1875), the first few dichotomies of the fruiting structures are alternately very short and very long; thus, the secondary and quaternary bifurcations are associated two by two and appear, at first glance, to be associated four by four. The arrangement of the primary branches of *P. fusispora* var. *lepidula* was said by Marchal to resemble the above species very closely. Also *P. fusispora* var. *lepidula* was described as rhizoidal and the sporophore presumably attained a height of 140-280 μ —about one-fifth the dimensions of *P. fusispora*. In his description of *P. fusispora*, Van Tieghem did not state the dimensions of the fruiting structures. The sporophore shown in figure 137 of plate 4 of Van Tieghem's work is stated to be five times natural size (Van Tieghem, 1875, p. 172); this would indicate that the original sporophore measured about 2 mm. high. It is from this figure only that Marchal could have derived the dimensions of the fruiting structures of *P. fusispora* from Van Tieghem's description. The dimensions of the rhizoidal sporophore shown in Pl. 5 *j* are of the same order of magnitude as those given by Marchal for *P. fusispora* var. *lepidula*. Marchal did not mention that his fungus possessed striate sporophores and he did not discuss the process of spore formation. He stated that a comparison of *P. fusispora* var. *lepidula* with Van Tieghem's species might warrant establishment of the former as a distinct species.

Eleven strains of the species illustrated in Plates 3, 4, and 5 *d-j* have been obtained from dung collected in California and two more isolates from England, on deposit at Kew, have been sent to the writer by Dr. Leadbeater. The latter informs me that he also has collected several additional strains of this species from materials collected in England. These collections, from widely separated localities, indicate that the species is common both in America and in Europe. On the basis of Marchal's brief description and discussion of *P. fusispora* var. *lepidula*, I am inclined to consider that his fungus and the above isolates represent the same species. Marchal described *P. fusispora* var. *lepidula* from specimens parasitizing *Mucor racemosus* growing on a culture of kangaroo dung collected in the Gandavens Zoological Gardens. As has been demonstrated earlier, the production of small rhizoidal sporophores is common in many species of *Piptocephalis* growing in culture on dung. A comparison of the fruiting structures shown in Plate 5 *j* (from dung) with those shown in Plate 4 *a-b* (from pure mixed cultures on *Cokeromyces recurvatus*; see also Pl. 3 *a*) illustrates the influence of cultural conditions on the dimensions and character of the sporophores, and this may very well account for the small sporophores described by Marchal. As suspected by Marchal, *P. fusispora* var. *lepidula* undoubtedly should be recognized as a distinct species:

***Piptocephalis lepidula* (Marchal) comb nov.**

(Plates 3, 4, 5 d-j)

Piptocephalis fusispora var. *lepidula* Marchal, Bull. Soc. Royale Bot. Belgique, Deuxieme Partie. 30: 136. 1891.

Colonies on *Cokeromyces recurvatus* on YpSs after 14 days near "Warm Buff," forming a turf up to 10 mm. or more deep; vegetative hyphae colorless, becoming septate, highly branched, mostly 2-3 μ in diameter; sporophores erect or ascending, often becoming prostrate and stolon-like; the lower portion of the main stalk slender, 5-6 μ in diameter, nearly hyaline, smooth, septate; septa perforate, the apertures with tubular projections; the distal portions of the main stalks robust, 8-12 μ in diameter, these and the branches of the fertile regions non-septate, becoming distinctly longitudinally striate; the fertile branch systems consisting of two, three, or four primary branches of varying lengths, about 180-550 μ long; these or shorter secondary branches giving rise to whorls of 2-4 branches which, in turn, are followed by three or four successive dichotomies as shown in Pl. 4 c-d; the ultimate or head-cell branches tapered, (5-)10-20(-30) μ long by 2.2-3.0 μ wide at the base; head-cells depressed-globose, 4.8-7.0 μ (aver. 5.8 μ) in diameter, bearing 18-34 (aver. 25) merosporangia, each containing two ellipsoidal spores; sporangiospores 3.9-6.6 μ (aver. 5.2 μ) by 2.2-2.6 μ , the terminal spore slightly smaller than the basal; merosporangia developing acropetally. Spore heads remaining dry. Homothallic; zygo-spores globose, yellow-orange, 40-65 μ (aver. 53 μ) in diameter, formed as bud-like enlargements from the fused apices of slightly unequal gametangia borne terminally on apposed progametangia; suspensors smooth, becoming tongs-like; exospore wall delicately reticulate; endospore wall smooth, about 3-5 μ thick.

Neotype.—CALIFORNIA. Mono County: Harvey Monroe Hall Natural Area, Slate Creek Valley, Tioga Pass region, Sierra Nevada, August 1, 1957, isolated from mouse dung collected by Elizabeth Sprague (RSA Culture 591). Transfers of this culture have been deposited in the ATCC, CBS, and CMI.

Other specimens examined.—CALIFORNIA. Los Angeles County: Evey Canyon, San Gabriel Mts., 4.5 miles northeast of Claremont, March 28, 1954, on *Mucor* sp. on rotting agaric collected by D. H. Ford (RSA Culture 292); from same locality, all isolated from mouse dung, December 24, 1957 (RSA Cultures 630 and 631), March 26, 1958 (RSA Culture 660), January 23, 1959 (RSA Culture 785). Plumas County: Belden, June 19, 1958, isolated from mouse dung (RSA Culture 691). San Bernardino County: near Cajon, November 20, 1953, isolated from rabbit dung collected by D. H. Ford (RSA Culture 218); southeast slope of Mt. San Antonio, San Gabriel Mts., November 1, 1953, isolated from rat dung collected by D. H. Ford (RSA Culture 275); near Lytle Creek Ranger Station, Lytle Creek Canyon, San Gabriel Mts., January 1, 1954, isolated from rat dung collected by D. H. Ford (RSA Culture 276). Shasta County: 2 miles west of Fall River Mills, June 20, 1958, isolated from dung (RSA Culture 695). ENGLAND. Derbyshire, isolated from soil by A. Brown (RSA Cultures 662 and 663; communicated by G. Leadbeater). Transfers of Cultures 275, 292, 691, and 695 have been deposited in the ATCC, CBS, and CMI.

In several of its characteristics, *P. lemonnieriana* (Vuillemin, 1902) resembles *P. lepidula*. Both species have in common: (1) striate sporophores with tubular perforations in the septa of the lower portions of the main stalks, (2) an absence of septa in the distal portions of the main stalks and the branches of the dichotomies, and (3) similar head-cells and head-cell branches. These species differ fundamentally, however, in the development of their merosporangia. The latter, in *P. lemonnieriana*, prior to spore formation, are more or less uniformly cylindrical and the distal portions are not formed by budding from the proximal portions as in *P. lepidula*. Another character which readily distinguishes *P. lepidula* from *P. lemonnieriana* is the formation of spore drops by the mature fertile heads of the latter species; in *P. lepidula* the spore heads remain dry.

In the foregoing account, several criteria which have been stressed in the keys of Van Tieghem (1875), Fischer (1892), Zycha (1935), and Naumov (1935, 1939) have been discussed, namely (1) presence or absence of stolons and rhizoids, (2) presence or absence of sporophore striations, (3) nature of the head-cell, (4) size and shape of the spore, and (5) number of spores per merosporangium. In addition to these, several other characters which have received little attention in the past may prove to be useful taxonomically and should receive further study.

The presence or absence of septa in the stipe and branches of the fruiting structure and the nature of these septa, if present, may be of specific importance. Septa reportedly are absent in the sporophore of *P. dichotomica* (Krzemienievska and Badura, 1954) and in the branches of the successive dichotomies of the fruiting structures of *P. fusispora* (Van Tieghem, 1875) and *P. lemonnieriana* (Vuillemin, 1902). In *P. lepidula*, as we have seen, septa normally are not present in the upper reaches of the mature sporophore (Pl. 4 *d*), whereas in some species, such as *P. arrhiza* (Pl. 7 *d*), cross-walls may be formed in abundance in the dichotomies of the mature fruiting structure.

Septation normally proceeds from the base towards the apex of the sporophore in species of *Piptocephalis* and the septa develop centripetally (Pl. 6 *j*; Leadbeater and Mercer, 1957 *b*). Apparently there is a correlation between the state of maturity of the sporangiophore and the formation and characteristics of the septa. Cross-walls appear first in the lower part of the stipe of the developing sporophore and have median perforations which apparently permit the ready movement of protoplasm into the developing extremities. These septa may be unmodified (Pl. 6 *e*; Pl. 7 *a*) or, in several species such as *P. microcephala*, *P. fusispora*, *P. lemonnieriana*, and *P. lepidula*, they may possess tubular perforations which project upward (Pl. 3 *o*; Pl. 4 *e*). After the fertile heads have matured, the apertures of the septal perforations often become completely closed (Pl. 6 *i, k*; Pl. 7 *c*) by the deposition of wall-material (?). The obstructions formed in the septa of mature sporophores of *Piptocephalis* often resemble, superficially, the median thickenings produced in the cross-walls of members of the Kickxellaceae (Pl. 29 *c*; Pl. 31 *c*; Pl. 33 *d*) and *Dimargaris* and its allies (Pl. 15 *c*; Pl. 19 *a, e*; Pl. 21 *c*; Pl. 24 *e*; Pl. 26 *g*), but these structures, in the latter forms, are quite different from those formed in *Piptocephalis* both in origin and presumably in function.

In many species of *Piptocephalis*, the branches subtending the head-cells appear to be less variable than those formed at lower levels in the dichotomous system, and the characteristics and dimensions of the head-cell branches (Pl. 3 *n*; Pl. 6 *f*; Pl. 7 *e*) may prove to be useful criteria for the separation of species or groups of species.

Another well-known phenomenon in the Mucorales and many of the Fungi Imperfecti is the tendency of the mature sporiferous heads to form liquid drops. In *Mucor*

PLATE 6. *a-b. Piptocephalis cylindrospora* Bainier.—*a*. Germinating spores. $\times 340$. *b*. Terminal portion of upright sporophore showing characteristic branching pattern. $\times 110$. *c-d*. Detail of distal dichotomous branch systems of sporophores. $\times 340$. *e*. Typical septum in lower region of sporophore. $\times 1300$. *f*. Head-cell branches. $\times 560$. *g*. Head-cell showing three mature merosporangia which have not yet fallen away. $\times 1300$. *h*. Head-cell which has not fallen away from the head-cell branch. $\times 1300$. *i. Piptocephalis xenophila* Dobbs and English.—Cross-wall in aged sporophore showing occlusion of the median perforation by deposition of wall-material. $\times 1300$. *j-m. Piptocephalis microcephala* Van Tieghem.—*j*. Perforate septum in sporophore showing its formation by annular ingrowth from the lateral wall. $\times 1300$. *k*. Cross-wall in aged sporophore showing occlusion of the median perforation by deposition of wall-material. Note longitudinal striae. $\times 1300$. *l-m*. Head-cells with attached merosporangia. $\times 1300$.

PLATE 6

and other genera some species always are what may be termed wet-spored whereas other species always are dry-spored. This character is not due merely to the condensation of water on the sporangium or conidial head of a fungus growing in a humid environment, but is inherent in the species and appears to result, at least in part, from exudation of liquid by the fungus itself (Vuillemin, 1902). The phenomenon is especially conspicuous in species of *Syncephalis* and *Dimargaris*, and may represent an adaptation for spore dispersal by small animals such as insects and mites. Several species of *Piptocephalis* typically are wet-spored (*P. freseniana*, Brefeld, 1872; *P. repens*, Van Tieghem and Le Monnier, 1873; *P. corymbifer*, Vuillemin, 1887 a; and *P. lemonnieriana*, Vuillemin, 1902). Van Tieghem and Le Monnier (1873) reported spore drops in *P. arrhiza*, but four strains of this species (Pl. 7) collected by the writer show that it actually is dry-spored. Dobbs and English (1954) described a slight tendency for the formation of spore drops by *P. xenophila*, but when this species is grown under the same conditions as a truly wet-spored species it readily may be classified as dry-spored. The writer has two isolates of *P. xenophila*, one received from Dr. H. L. Barnett and another collected in California.

Finally, the studies of Leadbeater and Mercer (1956, 1957 a, b) have brought attention to the probable significance of the zygosporangium as a useful taxonomic character in *Piptocephalis*. Zygosporangia have been described or reported for *P. freseniana* (Brefeld, 1872; Morini, 1905; Bainier, 1907), *P. arrhiza* (Spegazzini, 1891), *P. tieghemiana* (Matruchot, 1899 b, 1900), *P. fusispora* (Morini, 1905), *P. cylindrospora* (Leadbeater and Mercer, 1956), *P. xenophila* (Leadbeater and Mercer, 1957 a), and *P. virginiana* (Leadbeater and Mercer, 1957 b).

Brefeld discovered the zygosporangia of *P. freseniana* in 1872 and showed that these are produced in bud-like enlargements which develop above the point of fusion of gametangia borne on tongs-like suspensors. According to Brefeld, the zygosporangium exospore of this species is roughened with conical tooth-like projections. Measurements were not given in the text, but, on the basis of the magnification indicated by Brefeld for his Figure 18 of Plate VI (Brefeld, 1872), the zygosporangium shown in Figure 18 f would have measured about 28 μ . In 1907, Bainier described zygosporangia of a species referred to *P. freseniana*, but comparison of Bainier's figures with those of Brefeld leads me to suspect that different species may have been involved in the two studies. Sexual structures having configurations like those shown in Bainier's illustrations (Bainier, 1907, Pl. 24, fig. 13-16) never have been observed in any of the species of *Piptocephalis* studied by the writer. Bainier states that the zygosporangia produced by his fungus measured about 40 μ in diameter and possessed an exospore covered with small echinulations. A zygosporangium having an exospore bearing coarse tooth-like prominences was figured by Morini (1905) and referred to *P. freseniana*; spore dimensions were not given. In the same work, Morini also described and illustrated zygosporangia of a species identified as *P. fusispora*. These spores were said to be blackish-brown,

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PLATE 7. *Piptocephalis arrhiza* Van Tieghem and Le Monnier.—a. Segment of stipe from lower region of a sporophore showing septa. $\times 340$. b. Terminal portion of upright sporophore showing branching pattern. $\times 70$. c. Segment of stipe from upper region of a sporophore showing characteristic punctae; note longitudinal striae and median occlusion in the cross-wall. $\times 1300$. d. Detail of the dichotomous branch system of one of the secondary branches of an aged sporophore showing extreme septation. $\times 110$. e. Head-cell branches. $\times 1300$. f. Typical head-cell in lateral view showing disarticulating merosporangia. $\times 1300$. g. Head-cell as seen from below. $\times 1300$. h. Spores; the one above is beginning to germinate; note inextensible polar caps representing the end-walls of the spore. $\times 1300$. i-j. Nearly mature merosporangia showing spores surrounded by discrete sporangial walls. $\times 1970$. k. Mature zygosporangium showing characteristic smooth, slightly inflated gametangial remnants. $\times 465$.

PLATE 7

to measure 42-50 μ in diameter, and to have an exospore provided with large, somewhat widely-spaced papillae—a type of exospore sculpture unique in the genus. Morini's illustrations (Morini, 1905, fig. 5-6) indicate that the zygosporangia of the species referred to *P. fusispora* develop above the point of fusion of the gametangia as in *P. freseniana*, and Morini states that the zygosporangia of his strain of *P. fusispora* were larger than those produced by his isolate of *P. freseniana*. Spegazzini (1891) reported, but did not illustrate, small, echinulate zygosporangia measuring about 15-20 μ for a species referred to *P. arrhiza*. Blakeslee (1904 b) believed that Spegazzini actually had studied *P. freseniana*. In the four isolates of *P. arrhiza* studied by the writer, the zygosporangia (Pl. 7 k) have been found to measure about 25-45 μ (aver. 35 μ). With the exception of Brefeld's work, these early descriptions of zygosporangia in *Piptocephalis* were vague and poorly illustrated.

Recent studies by Leadbeater and Mercer (1956, 1957 a, b) have shown that zygosporangium formation in *P. cylindrospora*, *P. xenophila*, and *P. virginiana* takes place in a manner essentially like that described originally by Brefeld for *P. freseniana*. Leadbeater and Mercer give a detailed account of zygosporangium morphology and show that the mature spore typically consists of a stratified, more or less highly sculptured exospore (the zygosporangium) bearing remnants of the gametangia (Pl. 4 i-k; Pl. 7 k; Pl. 8 e-f, h-i, k-l) and a stratified nearly smooth endospore (the zygosporangium proper; Pl. 4 j).

Of the fourteen species of *Piptocephalis* in the writer's collection, only four have not been induced to produce zygosporangia in culture. Nine of the sexual species regularly form zygosporangia when grown on YpSs or PDA in company with *Cokeromyces recurvatus* or *Mucor hiemalis* and, although single-spore cultures have not been tested, are presumed to be homothallic. Homothallism has been demonstrated for three of these species, *P. cylindrospora*, *P. xenophila*, and *P. virginiana*, by Leadbeater and Mercer (1956, 1957 a, b). Five strains of one species studied here have never formed zygosporangia when grown separately, but each of four of these isolates always gives rise to zygosporangia when crossed with the fifth, and the species apparently is heterothallic.

With only minor variations, the pattern of zygosporangium formation in all of the species of *Piptocephalis* studied by the writer is essentially like that found in *P. cylindrospora*⁴ (Pl. 8 a-e). Closely apposed progametangia give rise to terminal gametangia

⁴Bainier's description of this species is very brief and the illustration provided is not at all diagnostic (Bainier, 1882, p. 111, Pl. X, fig. 8). In Bainier's characterization, the branches of the sporophore of *P. cylindrospora* supposedly have nearly the same diameter [which is most unlikely] and are successively shorter and shorter. The final branches produced spherical heads bearing elongate sporangia measuring about 25.2 μ long and containing spores 4.2 $\mu \times$ 2.1 μ . These are the only measurements given by Bainier, and, if they represent mean values, the microsporangia contained about six spores on the average. The writer has six similar isolates which are here referred to *P. cylindrospora*. The species may be characterized as follows:

PIPTOCEPHALIS CYLINDROSPORA Bainier.

Étude sur les Mucorinées. Thèse. p. 111. 1882.

(Plates 6 a-b and 8 a-g)

Colonies on *Cokeromyces recurvatus* on YpSs after 14 days near "Light Buff" or "Cartridge Buff," forming a turf up to 15 mm. deep; sporophores erect or ascending, often becoming prostrate and stolon-like; the lower portion of the main stalk slender, 5-7 μ in diameter, nearly hyaline, smooth, septate; septa perforate, the median apertures without tubular extensions; the distal portion of the main stalk more robust, 7-9 μ in diameter, septate, faintly striate in age; the primary dichotomy of the fertile branch system consisting usually of two relatively short branches, 30-130 μ or more long, each of which gives rise to two long branches, 200 μ to as much as 950 μ in length (Pl. 6 b); short tertiary branches followed by long quaternary branches may or may not be produced; the branches of the second and fourth dichotomies, if the latter are produced, are

which usually differ somewhat in size, especially in length (Pl. 8 *a-b*). Although *P. cylindrospora* is homothallic, sexual hyphae commonly arise from different hyphae (Pl. 8 *a*), and the origin of progametangia from a single hypha in the manner shown by Bainier (1907, Pl. 24, fig. 13) has never been observed in any species of *Piptocephalis* studied by the writer. The slightly heterogametangial nature of *Piptocephalis* species was stressed by Leadbeater and Mercer (1956, 1957 *a, b*). This character also was described and illustrated by Van Tieghem as early as 1875 for *Syncephalis cornu* (Van Tieghem, 1875, pp. 123-124, Pl. 3, fig. 88-90) in which the early stages of zygospor development are very similar to those found in *Piptocephalis*. The young copulation branches may remain nearly parallel (Pl. 8 *a-b, j*); however, they often become more or less sharply curved outward at maturity and are tongs-like in appearance (Pl. 4 *i*; Pl. 7 *k*; Pl. 8 *e, g-b*). The degree of curvature of the suspensors may be quite variable, even in a single species. When fully developed, the gametangia fuse at their apices and the young zygospor normally develops as a bud-like outgrowth which typically enlarges more rapidly above than below the point of fusion (Pl. 4 *b*; Pl. 8 *b-d*).

In conjunction with his characterization of *P. tieghemiana*, Matruchot (1899 *b*, 1900) described a mechanism of zygospor formation which he regarded as fundamentally distinct from that observed by Brefeld in *P. freseniana*. The zygospor of *P. tieghemiana* appeared to form *between* rather than *above* the point of fusion of the gametangia and thus was thought to originate in a manner comparable to that found in such genera as *Mucor* and *Syzygites*. Matruchot's figures (Matruchot, 1900, fig. 1-2) indicate, however, that the gametangia in this species are borne on tongs-like suspensors as in other members of the genus. The writer has found that the final position of the gametangial remnants on the exospor may be quite variable in a given species of *Piptocephalis* (Pl. 8 *g*), and he is convinced that the distinction which Matruchot made between the formation of zygospor in *P. tieghemiana* and *P. freseniana* is more apparent than real.

As the zygospor enlarges, the layered exospor becomes unevenly thickened and, at maturity, appears more or less coarsely reticulate or pitted in surface view (Pl. 4 *k*; Pl. 8 *f, i, l*). Although fundamentally alike in all of the species of *Piptocephalis* studied, the fine structure of exospor architecture may vary considerably from species to species. The proximal portion of each gametangium usually becomes void of cytoplasm and is attached to the exospor. These gametangial remnants normally remain smooth and usually are progressively thickened toward their points of attachment to the exospor (Pl. 4 *i*; Pl. 8 *e, b, k*). The endospor, or zygospor proper, typically is smooth-walled or bears a delicate replica of the exospor architecture (Leadbeater and

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followed by three or four successive dichotomies as shown in Pl. 6 *b-d*; head-cell branches 15-35 μ (aver. 25 μ) long by 2.6-3.1 μ wide, or these furcate and correspondingly shorter, 5-20 μ (aver. 12 μ) long (Pl. 6 *f*); head-cells subglobose 5.2-8.7 μ (aver. 7.3 μ) in diameter (Pl. 6 *g-h*), bearing 22-37 (aver. 30) slender merosporangia; the latter forming 2-11 (aver. 5) cylindrical spores 3.5-7.4 μ (aver. 5.6 μ) $\times$ 2.2 μ ; spore heads remaining dry; homothallic; zygospor globose, orange to orange-brown, 30-42 μ (aver. 37 μ) in diameter, formed as bud-like enlargements of the fused apices of slightly unequal apposed gametangia borne on tongs-like suspensors (Pl. 8 *a-e*); exospor coarsely reticulate (Pl. 8 *f*); endospor smooth, wall about 3 μ thick.

Specimens examined.—CALIFORNIA. Los Angeles County: Roadside, Angeles Crest Highway, San Gabriel Mts., November 20, 1953, isolated from dung collected by D. H. Ford (RSA Culture 158); 2 miles south of La Verne, January 1, 1954, isolated from horse dung collected by D. H. Ford (RSA Culture 209); 3 miles northeast of Glendora, November 24, 1953, isolated from soil collected by D. H. Ford (RSA Culture 223); Evey Canyon, San Gabriel Mts., 4.5 miles northeast of Claremont, February 13, 1957, isolated from *Mucor* sp. on rotting basidiomycete (RSA Culture 525); same locality, January 23, 1959, isolated from mouse dung (RSA Culture 786). Siskiyou County: Lava Beds National Monument, June 21, 1958, isolated from rat dung (RSA Culture 696). Transfers of RSA Culture 209 have been deposited in the ATCC, CBS, and CMI.

Mercer, 1956), is nearly globose, and often is slightly bulged into the gametangial remnants (Pl. 4 *j*). The zygospore of *P. microcephala*, however, normally fills each gametangial remnant almost completely and characteristically is dome-like in appearance (Pl. 5 *l*).

In most species of *Piptocephalis*, the formation of zygospores often takes place most abundantly beneath the surface of the substratum. Often, however, zygospores may be produced in more or less large numbers on aerial hyphae, and in tube cultures of *P. cylindrospora*, sexual spores typically are delimited in abundance where aerial hyphae contact the surface of the container. The exospores of zygospores formed on aerial hyphae often are much darker colored than are the walls of spores developed within the agar medium.

Double or single azygospores often are encountered in species of *Piptocephalis* (Leadbeater and Mercer, 1956, 1957 a, b), and in their description of zygospores in *P. xenophila*, Leadbeater and Mercer (1957 a) reported a 99.8% frequency of azygospores. In this laboratory, cultures of *P. xenophila* grown on YpSs agar in company with *Mucor hiemalis* have produced mostly normal zygospores (Pl. 8 *k*), and in a random sample of 560 zygospores only 4, or 0.7%, were atypical. The results obtained by Leadbeater and Mercer must somehow have been influenced by cultural conditions.

As suspected by Leadbeater and Mercer, the nature of the zygospore of *Piptocephalis* species should prove to be very useful taxonomically. As shown in the accompanying illustrations (Pl. 4 *k*; Pl. 8 *f*, *i*, *l*), the character of the exospore architecture, especially, may vary considerably from species to species.

In addition to collections of *Piptocephalis cylindrospora* and *P. lepidula* cited above, cultures of the following named species have been deposited in the collections of the ATCC, CBS, and CMI:

Piptocephalis arrhiza Van Tieghem and Le Monnier.—CALIFORNIA. Los Angeles County: Cobel Canyon, San Gabriel Mts., 3.5 miles northeast of Claremont, December 24, 1957, isolated from mouse dung (RSA Culture 629).

Piptocephalis microcephala Van Tieghem.—CALIFORNIA. Los Angeles County: Evey Canyon, San Gabriel Mts., 4.5 miles northeast of Claremont, December 24, 1957, isolated from mouse dung (RSA Culture 628).

Piptocephalis xenophila Dobbs and English.—CALIFORNIA. Plumas County: Belden, June 19, 1958, isolated from mouse dung (RSA Culture 694).

SYNCEPHALIS Van Tieghem and Le Monnier.

Ann. Sci. Nat., Bot., Sér. 5. 17: 372. 1873.

Monocephalis Bainier, étude sur les Mucorinées. Thèse. Paris. p. 114. 1882. (nomen provisorium)

Calvocephalis Bainier, étude sur les Mucorinées. Thèse. Paris. p. 120. 1882. (nomen provisorium)

Microcephalis Bainier, étude sur les Mucorinées. Thèse. Paris. p. 123. 1882. (nomen provisorium)

Extramatrinal vegetative hyphae arachnoid, delicate, nonseptate except in age,

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PLATE 8. *a-g. Piptocephalis cylindrospora* Bainier.—*a*. Apposed progametangia; slightly unequal gametangia, their lower limits marked by indentations on the outer margins of the sexual hyphae, are being delimited terminally. $\times 620$. *b-d*. Initial stages of development of the zygosporangium as a bud-like enlargement above the point of fusion of the gametangia. $\times 620$. *e*. Mature zygospore. $\times 620$. *f*. Crushed zygospore showing coarsely reticulate zygosporangial wall. $\times 1000$. *g*. Three mature zygospores. $\times 250$. *h-i. Piptocephalis* sp. indet. (RSA Culture 196; NRRL 1462).—*h*. Mature zygospore. $\times 560$. *i*. Crushed zygospore showing finely pitted zygosporangial architecture. $\times 1000$. *j-l. Piptocephalis xenophila* Dobbs and English.—*j*. Apposed sexual hyphae. $\times 1000$. *k*. Mature zygospore. $\times 560$. *l*. Crushed zygospore showing zygosporangium in surface view. $\times 1000$.

PLATE 8

highly branched with nodose anastomoses, running over the host hyphae and giving rise to appressoria or sporangiophores; appressoria relatively large, penetrating the host wall and producing often extensive, branched, rather robust, nonseptate haustoria; sporangiophores smooth, simple, erect, straight, slightly curved or uncinatate, nonseptate or septate near the bases which are provided with prominent, usually septate, rhizoids; septa unmodified; sporangiophores dilated apically, forming clavate or globoid vesicles which give rise to merosporangia directly or to short branchlets bearing merosporangia distally; merosporangia rod-like, simple or branched near the base, containing two or more uniseriate, spherical, ellipsoid, fusiform, or cylindrical sporangiospores; merosporangial wall evanescent or persistent and separating with the spores by circumscissile rupture; fertile heads forming liquid drops; stylospores reported in a few species; zygosporangia globose, light-colored, rough, formed as in *Piptocephalis* or in bud-like outgrowths arising from one of the paired gametangia delimited apically on coiled undifferentiated progametangia.

Type species: *Syncephalis cordata* Van Tieghem and Le Monnier (1873, p. 374).

In addition to the type species, the following species or varieties of *Syncephalis* have been described: *S. asymmetrica* Van Tieghem and Le Monnier (1873, p. 375), *S. depressa* Van Tieghem and Le Monnier (1873, p. 375), *S. cornu* Van Tieghem and Le Monnier (1873, p. 376), *S. minima* Van Tieghem and Le Monnier (1873, p. 376), *S. sphaerica* Van Tieghem (1875, p. 125), *S. intermedia* Van Tieghem (1875, p. 127), *S. ramosa* Van Tieghem (1875, p. 129), *S. fasciculata* Van Tieghem (1875, p. 130), *S. nodosa* Van Tieghem (1875, p. 131), *S. ventricosa* Van Tieghem (1875, p. 133), *S. tetrathela* Van Tieghem (1875, p. 134), *S. reflexa* Van Tieghem (1875, p. 134), *S. furcata* Van Tieghem (1876, p. 386), *S. nigricans* Van Tieghem (1876, p. 387), *S. pendula* Van Tieghem (1876, p. 388), *S. curvata* Bainier (1882, p. 114), *S. fusiger* Bainier (1882, p. 123), *S. wynneae* Thaxter (1897, p. 11), *S. pycnosperma* Thaxter (1897, p. 11), *S. tenuis* Thaxter (1897, p. 12), *S. cordata* Van Tieghem and Le Monnier var. *minor* Schroeter (1886, p. 216), *S. glabra* Morini (1902, p. 233), *S. aurantiaca* Vuillemin (1902, p. 36), *S. adunca* Vuillemin (1903, p. 423), *S. bispora* Raciborski (1909, p. 347), *S. tranzschelii* Naumov (1935, p. 104; without Latin diagnosis), *S. nana* Dade (1937, p. 21), *S. tengi* Ou (1940, p. 48), and *S. ubatubensis* Viegas and Teixeira (1943, p. 243).

Subordinate to his description of *Syncephalis curvata*, Bainier (1882, p. 114) proposed the new genus *Monocephalis* for this and other species of *Syncephalis* bearing simple merosporangia directly on the surfaces of the vesicles of the sporophores. Bainier similarly erected two other genera, *Calvocephalis* and *Microcephalis* (Bainier, 1882, p. 120 and p. 123 respectively). *Calvocephalis* was proposed for *Syncephalis nodosa* Van Tieghem (1875) because of the unique method of zygosporangium formation found in this species, and *Microcephalis* was proposed for *Syncephalis fusiger* because in this species small, sterile, unicellular branchlets are interposed between the merosporangia and the subtending vesicles. In 1883, Bainier published a summary of his thesis in *Annales des Sciences Naturelles* and he did not mention the generic names which he had proposed the year before. Because they were not accepted by their author, *Monocephalis*, *Calvocephalis*, and *Microcephalis* are not valid according to Article 33 of the International Code of Botanical Nomenclature.

In 1899, Matruchot described a new genus, *Gliocephalis*, based on *G. hyalina*, characterized by short unbranched sporophores producing terminal enlargements bearing double series of phialides very similar to those found in several groups of the genus *Aspergillus* (Thom and Raper, 1945). According to Matruchot the small ovoid conidia of *G. hyalina* are produced successively from the tips of the secondary phia-

lides, become detached as soon as they are formed, and are enveloped in a mucilaginous drop as in *Gliocladium*. Superficially, the sporophore of Matruchot's species is very similar in appearance to that of members of the genus *Syncephalis*, and in 1902 von Höhnelt transferred *G. hyalina* to the latter genus. If the spores of *Gliocephalis* are produced in the manner described by Matruchot, then the genus undoubtedly belongs in the Fungi Imperfecti and von Höhnelt's action was unwarranted. Matruchot was very familiar with *Syncephalis*, and he contrasted his new genus with the latter, believing that *Gliocephalis* and *Gliocladium*, *Aspergillus* (*Sterigmatocys-*

PLATE 9. *a-i. Syncephalis nodosa* Van Tieghem.—*a*. Nearly mature sporophore before disarticulation of the merosporangia. $\times 660$. *b-d*. Early and intermediate stages in the development of the merosporangia; note circular disposition of these on the upper, outer surface of the vesicle. $\times 1080$. *e*. Mature zygospore showing configuration of the sexual hyphae and the lobate outgrowths from the suspensor bearing the larger of the two gametangia. The zygosporangium arises as a bud-like outgrowth near the base of the largest gametangium. $\times 660$. *f*. Nearly mature merosporangium; the separation rings are only faintly visible. $\times 1080$. *g-h*. Mature spores showing wrinkled merosporangial membrane, a portion of which remains attached to each spore. $\times 1080$. *i*. Appressorium and haustorium of parasite attacking sporophore of *Mucor* sp. $\times 1080$. *j. Syncephalis cornu* Van Tieghem and Le Monnier.—Mature zygospore showing configuration of the sexual hyphae; note lobate outgrowths arising from only one of the suspenders. $\times 660$.

tis) and *Penicillium*, and *Syncephalis* and *Piptocephalis* represented parallel series in unrelated groups of fungi. Until better evidence to the contrary is available, the writer prefers to exclude *Gliocephalis* from synonymy with *Syncephalis*.

Species of *Syncephalis* appear commonly in cultures of soil and dung and typically are parasitic on other Mucorales. *Syncephalis wynneae* (Thaxter, 1897) was described from material found growing on *Wynnea macrotus* Berkeley, and, according to Thaxter, "it seemed to be truly parasitic, growing not very densely and inducing a rapid decay in the large spoon-shaped apothecia." This appears to be the only instance in which a species of *Syncephalis* has been reported parasitizing fungi other than members of the Mucorales. In their classic studies of the Mucorales, Van Tieghem and Le Monnier (1873) and Van Tieghem (1875) reported the growth of *S. cordata*, *S. nodosa*, and *S. reflexa* in pure culture, and these workers made the generalization that species of *Syncephalis* are facultative rather than obligate parasites. Of the few species of *Syncephalis*, including *S. nodosa*, which the writer has studied in culture, none ever has developed normally in the absence of a host; scant growth may occur on ordinary media, however, and in the case of *S. cornu* a few atypical sporangio-phores were produced after about ten days on PDA. Nevertheless, it is the writer's opinion that most if not all members of the genus *Syncephalis*, like those of *Piptocephalis*, require a host for normal growth and reproduction.

During the course of the present investigation, six or seven species of *Syncephalis* have been examined and several of these have been maintained in culture for several years. Of these, only the very common *S. nodosa* and *S. cornu* and the type strain of *S. nana*, kindly supplied by Dr. Dade, have been identified. A lack of sufficient first-hand information precludes any attempt to treat the systematics of *Syncephalis* at this time, and the reader is referred to the works of Zycha (1935) and Naumov (1935, 1939) for the most recent taxonomic resumes of the genus. A brief summary of the general characteristics of *Syncephalis* follows.

Details of spore germination previously have been described for only a few species of *Syncephalis* (*S. cordata* and *S. cornu*, Van Tieghem and Le Monnier, 1873; *S. fasciculata*, *S. intermedia*, *S. sphaerica*, and *S. ventricosa*, Van Tieghem, 1875). Van Tieghem (1875, Pl. 3, fig. 135 b) figured four germ tubes arising from the germinating spore of *S. ventricosa*, one of the few sphaerosporus species, but in the other species the germ hyphae were found to arise only from the polar extremities of the spore, and only polar germination has been observed in the species studied by the writer (Pl. 10 a, e). As was shown in the previous section, germinating spores of *Piptocephalis* species typically become spherical, often reach several times their original diameter, and give rise to one or several lateral germ hyphae. Polar germination never has been observed in *Piptocephalis*.

Spore germination apparently reflects a fundamental difference in the mechanism of spore formation in these genera. The method by which spores are delimited in the merosporangium of *Piptocephalis virginiana* (Leadbeater and Mercer, 1957 b) appears to be typical for most species of this genus. As already has been described, this mechanism results in spores with rather thick inextensible terminal walls and rela-

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PLATE 10. *a-d. Syncephalis nodosa* Van Tieghem.—*a.* Germinating spores showing polar origin of germ tubes. The triangular spore at the upper right (arrow) is typical of those spores formed at the base of the branched merosporangia characteristic of this species; these spores always produce three germ hyphae. $\times 560$. *b.* Early stage of development of fruiting structure showing formation of rhizoid system on host hypha. $\times 340$. *c.* Later stage of development of fruiting structures showing origin of sporophore stipes from basal rhizoid systems. $\times 340$. *d.* Nearly mature sporophore. $\times 480$. *e. Syncephalis* sp. (RSA 523).—Four sporangiospores. The two

shown above have not started to germinate and the wrinkled sporangial membrane surrounding the spores laterally is in evidence; the germinating spores show the polar origin of the germ hyphae, and evidence of the taut sporangial membrane may be detected on the left extremity of the upper germinating spore. $\times 1300$. *f. Syncephalis nana* Dade.—Immature merosporangium showing the formation of spore primordia by a process of constriction; note the conformation of the intermediary zone and the pronounced terminal and basal constrictions. Further discussion is in the text. $\times 1670$.

tively thin extensible lateral walls from which the germ hyphae arise at the time of spore germination. Thaxter (1897) described a distinctly different process of spore formation in *S. pycnosperma* and an unnamed species of *Syncephalis*. In these, the protoplasm of the young merosporangium is divided by gradually narrowing isthmuses (Thaxter, 1897, Pl. II, fig. 39-41) into smaller portions which eventually are separated, invested with walls, and become spores. The portion of the sporangial filament separating each spore, termed the "intermediary zone" by Thaxter, becomes deliquescent in whole or in part almost as soon as the spore wall is formed (Thaxter, 1897, Pl. II, fig. 42), and in *S. pycnosperma* (Pl. 12 d-f) this zone consists of two parts, one of which (Pl. 12 f a) is persistent and remains united with the spore wall proper, whereas the other (Pl. 12 f b) becomes converted into an oily substance which functions in the separation of the spores (Pl. 12 e). The latter structure was termed a "separation disc" by Thaxter, but, being perforate, it more logically should be termed a separation ring. In the apex of each merosporangium is delimited a small cell-like structure which, like the separation ring, disappears when the spores mature (Pl. 12 d, f).

Spore formation preceded by a process of constriction of the protoplasm within the merosporangium also has been observed in other species of *Syncephalis* (*S. fusiger*, Bainier, 1882, 1883; *S. cordata*, Thaxter, 1897, and Vuillemin, 1902; and *S. nodosa*, Thaxter, 1897). Whether a similar mechanism of spore formation is common to all species of *Syncephalis* remains to be determined. The formation of spores in a manner comparable to that described above may account for the peculiar type of polar germination observed in many species of *Syncephalis*, for this mechanism apparently gives rise to spores having lateral walls which are somewhat thicker than those at the polar extremities.

In his characterization of *Syncephalis tenuis*, Thaxter (1897) described a type of acropetal merosporangial development (Pl. 12 a-c) very similar to that reported above for *Piptocephalis lepidula*. Krzemieniewska and Badura (1954) reported *S. tenuis* (as *Spinalia tenuis* (Thaxter) Zycha, 1935) from Poland, but, unfortunately, did not describe details of spore formation or spore germination. In his illustrations of the developing sporophore of *Syncephalis nana*, Dade (1937, fig. 2A) showed what appears to be a type of acropetal merosporangium formation in this species, but the writer's study of this species shows that the merosporangium develops in a manner exactly like that described by Thaxter for *S. pycnosperma* (Pl. 10 f).

Unlike *Piptocephalis*, germinating spores of species of *Syncephalis* usually do not swell to more than twice their original linear dimensions (Pl. 10 e; see also Van Tieghem, 1875). When sowed on an ordinary medium (YpSs or PDA) the spores of species of *Syncephalis* such as *S. nodosa* or *S. cornu* germinate quite readily. In the presence of a suitable host, the characteristic arachnoid vegetative mycelium of the parasite develops rapidly and soon envelops the host hyphae with an often very dense overgrowth. The parasitized colony may be so decimated by the parasite that the production of sporangiophores by the host fungus may be reduced to only a fraction of normal. The mycelium of *Syncephalis* consists of extremely delicate, highly branched, nonseptate hyphae which often are less than 1 μ in diameter (Pl. 11 b-c), and, as in *Piptocephalis*, these hyphae become septate in age. On contacting host hyphae, the

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PLATE 11. a-b. *Syncephalis* sp. (RSA 526).—Note erect stipe forming nearly globose terminal enlargements bearing merosporangia over their entire surfaces. a, $\times 120$; b, $\times 620$. c. *Syncephalis cornu* Van Tieghem and Le Monnier.—Mature fruiting structure showing recurved stipe. $\times 475$. d-e. *Syncephalis* sp. (RSA 544).—Note merosporangia over the upper surface only of the terminal enlargement of the sporophore. d, $\times 340$; e, $\times 1300$.

PLATE 11

vegetative hyphae of *Syncephalis* species give rise to appressoria or sporophore initials. The former are relatively very large in comparison with the hyphae from which they arise (Pl. 9 *i*; see also Van Tieghem and Le Monnier, 1873, Pl. 24, fig. 118-119—incorrectly interpreted as sexual structures according to Van Tieghem, 1875, p. 117; Van Tieghem, 1875, Pl. 3, fig. 136), and after penetrating the host membrane usually produce bulbous expansions from which an often very extensive haustorium develops. The hyphae comprising the haustoria usually have somewhat greater diameters than those of the vegetative mycelium. Sporophore initials (Pl. 10 *b*) form in abundance and may develop not only on the host hyphae but also on the walls of the culture chamber and on the hyphae of the parasite itself. The initials at first resemble young appressoria but soon give rise to several short, robust branchlets, one of which, rarely more in a few species, develops into the sporophore proper (Pl. 10 *c-d*) while the remainder form usually septate rhizoids which attach the fruiting structure to the substratum (Pl. 9 *a*; Pl. 10 *d*; Pl. 11 *c*; Pl. 12 *a, g*).

The erect sporophore normally is simple (reportedly once branched in *S. furcata*, Van Tieghem, 1876), nearly straight, slightly curved (Pl. 9 *a*; Pl. 10 *d*; Pl. 11 *a, d*; Pl. 12 *a, g*), or in a few species uncinately or reflexed (Pl. 11 *c*) and its height is a millimeter or less in most described species, although *S. cordata* may reach as much as 2-3 mm. (Van Tieghem and Le Monnier, 1873). Septa, if present, are formed only at the base of the main stalk (Pl. 9 *a*; Pl. 11 *d*; Pl. 12 *a, g*).

The terminal vesicular enlargements of the sporophores may be nearly globose in a few species of *Syncephalis* (Pl. 11 *a, b*), but in most species they are somewhat depressed-globose or clavate (Pl. 9 *a-d*; Pl. 12 *e, k*). Merosporangia may be borne over the entire surface of the vesicle (Pl. 11 *a-b*) or, more commonly, on the upper hemisphere only (Pl. 11 *d-e*); in *S. nodosa* (Pl. 9 *b-d*) and *S. tetrathela* (Van Tieghem, 1875) the sporiferous elements are disposed in a circle on the upper surface of the vesicle.

In most species of *Syncephalis*, the merosporangium is sessile, and, as in *Piptocephalis*, its position on the vesicle is marked only by a small tooth-like or wart-like prominence after the spores have matured and fallen away. A few species, however, develop small (*S. fusiger*, Bainier, 1882, Pl. X, fig. 13) or sometimes relatively large non-deciduous branchlets (*S. wynneae* and *S. pycnosperma*, Thaxter, 1897) on which the merosporangia are borne (Pl. 12 *e, k*). The merosporangia may be simple (Pl. 11 *e*) or branched near the base as in *S. nodosa* (Pl. 9 *a-d, f*) where the basal portion of the merosporangium produces a functional spore differing from those formed above it only in size and shape (Pl. 9 *f-g*; Pl. 10 *a*). The merosporangial membrane reportedly is quite evanescent in some species of *Syncephalis* (Van Tieghem, 1875, p. 124), whereas in others, such as *S. cordata* (Van Tieghem and Le Monnier, 1873) and *S. nodosa* (Pl. 9 *g-b*) the sporangial wall ruptures (gelatinizes?) in a circumscissile manner so that each spore is partially enclosed in a portion of the persistent

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PLATE 12. *a-c. Syncephalis tenuis* Thaxter.—*a*. Mature fruiting structure. *b-c*. Successive stages in the acropetal development of the merosporangium. *d-f. Syncephalis pycnosperma* Thaxter.—*d*. Mature merosporangia prior to disarticulation of spores. *e*. Mature head as seen in optical section showing secondary branchlets, three of which still bear a few spores. *f*. Portion of immature merosporangium showing two intermediary zones, the lower not completely formed; *a*—portion of zone later incorporated into spore wall; *b*—separation ring. Note the small terminal cell; this structure, like the separation ring, disappears when the spores mature. *g-k. Syncephalis wynneae* Thaxter.—*g*. Mature fruiting structure. *h*. Secondary branchlet of sporophore bearing immature merosporangia. *i*. Similar branchlet bearing nearly mature merosporangia. *j*. Nearly mature merosporangium. *k*. Optical section of fertile head showing secondary branchlets from which all spores have fallen away. (All figures after Thaxter, Bot. Gaz. 24: 1-15, Pl. I-II, 1897. Redrawn without change of magnification.)

PLATE 12

membrane. The number of spores produced in each merosporangium may be relatively constant for a given species, varying from two in *S. fusiger*, *S. tenuis*, *S. bispora*, and *S. nana* to as many as ten in *S. cordata*. The mature heads of many species of *Syncephalis* typically form spore drops; whether or not this is true for all described species of the genus is not known, for in many of the original descriptions this character was not mentioned. All species of *Syncephalis* studied by the writer are wet-spored.

Stylospores resembling those found in several species of *Mortierella* have been reported for *S. reflexa* and *S. nodosa* by Van Tieghem (1875, Pl. 3, fig. 99-100, 130-131) and *S. curvata* by Bainier (1882, Pl. XI, fig. 6). These small, roundish, rough, deciduous spores, reportedly are produced in large numbers on slightly swollen segments of the aerial mycelium and are borne singly on short perpendicular pedicels. The writer never has encountered such spores in any of his cultures of *S. nodosa*.

Zygospores first were described in *Syncephalis* by Van Tieghem who discovered them in cultures of *S. cornu* (Van Tieghem, 1875, Pl. 3, fig. 88-93). In this species, apposed progametangia delimit slightly unequal gametangia terminally; these fuse apically and give rise to zygospores (Pl. 9 j) in a manner exactly comparable to that found in species of *Piptocephalis*. Van Tieghem (1875, pp. 123-124) noted the slightly heterogametangial nature of this species and expressed the following opinion regarding the possible significance of the phenomenon: "La différence sexuelle y est nettement accusée au dehors par la constante différence de longueur des deux cellules conjuguées, la plus petite devant être regardée comme mâle, la plus grande comme femelle." The very similar heterogametangial nature of *Piptocephalis* was first noted by Leadbeater and Mercer in 1956. The zygospores of *S. curvata* (= *S. cornu* according to Berlese and De Toni, 1888) were studied in 1882 by Bainier who was the first to describe the formation of curious vesicular outgrowths on the suspensors of this species. Similar outgrowths are associated with the sexual structures of several other species of *Syncephalis* for which zygospore formation is known, i.e., *S. nodosa* (Bainier, 1882, 1883; Thaxter, 1897), *S. reflexa* (Thaxter, 1897), and *S. depressa* (Christenberry, 1940). Leadbeater and Mercer (1956, 1957 a, b) described "basal hypertrophies" associated with the suspensors of several species of *Piptocephalis*, and the author has observed similar structures in species of *Piptocephalis* studied here. Although less pronounced in members of the latter genus, these outgrowths probably are homologous with those formed by the suspensors of species of *Syncephalis*.

The mechanism of zygospore formation in *S. reflexa* and *S. depressa* apparently is similar to that found in *S. cornu*, i.e., the zygospores are formed in bud-like enlargements between and above the fused apices of gametangia delimited by apposed progametangia as in *Piptocephalis*. In *S. nodosa*, however, Bainier (1882, 1883) and Thaxter (1897) described a distinctly different pattern of zygospore development. In this species, the gametangia are delimited apically by two relatively undifferentiated hyphae, one of which is spirally twisted around the other (Pl. 9 e). The gametangium produced by the enveloping hypha is somewhat larger than the one cut off by the other and gives rise to the zygospore in a short-stalked, bud-like enlargement formed some distance from the point of fusion of the gametangia. The suspensor bearing the largest gametangium forms lobate outgrowths similar to those found in the species listed above; these outgrowths often become irregularly septate with age (Pl. 9 e).

Morini (1902) described and illustrated zygospores in his *S. glabra*. These appear to be formed as in *Piptocephalis*, but Morini's figures (Morini, 1902, fig. 5-6) lack sufficient detail to be diagnostic.

Cultures of the following species of *Syncephalis* have been deposited in the ATCC, CBS, and CMI:

Syncephalis cornu Van Tieghem and Le Monnier.—CALIFORNIA. Los Angeles County: 1.5 miles north of Claremont, November 23, 1958, isolated from rat dung (RSA Culture 793). NEW YORK. Dutchess County: Hyde Park, December, 1958, isolated from rat dung collected by H. E. Ahles (RSA Culture 756).

Syncephalis nodosa Van Tieghem.—CALIFORNIA. Los Angeles County: 1.5 miles north of Claremont, November 23, 1958, isolated from rat dung (RSA Culture 794).

DIMARGARITACEAE

INTRODUCTION

In an addendum to his second major contribution to the Mucorales, Van Tieghem (1875) described two very unusual monotypic genera of fungi, *Dimargaris* and *Dispira*, which along with *Coemansia*, *Kickxella*, and *Martensella*, he referred provisionally to the Hyphomycetes. He believed that representatives of these genera possibly represented the imperfect stages of Ascomycetae. Van Tieghem probably included his discussion of *Dimargaris cristalligena* and *Dispira cornuta* in his work on the mucors because, like species of *Piptocephalis*, *Syncephalis*, and *Chaetocladium*, they were found to be parasites and apparently attacked only members of the Zygomycetes.

Using hanging drop cultures and boiled horse dung, Van Tieghem studied spore germination, the development of the vegetative mycelium, and the formation and characteristics of the fruiting structures of both *Dimargaris cristalligena* and *Dispira cornuta*. These representatives of obviously closely related genera were characterized as having erect, branched, white, septate sporophores arising from delicate, colorless, septate vegetative hyphae. The latter formed small, swollen appressoria which penetrated the host membrane and developed branched haustoria of rather limited extent. In both of the above species, the septa of the vegetative and fruiting hyphae were found to possess median lenticular thickenings very similar in appearance to those of *Kickxella* and *Coemansia* except that they had, in addition, a more or less conspicuous knob-like or bead-like projection at each pole. Because of the invariable presence of the latter structures Van Tieghem coined the generic name *Dimargaris* (Gr.: *di-* < *dis*; two; *margaris*, pearl).

Dimargaris cristalligena (the specific epithet was derived from the crystalloids normally present in the cytoplasm of the sporophore) was described as producing relatively large, simple or cymosely branched fruiting structures with large terminal spore heads consisting of vesicular enlargements bearing numerous cellular branches giving rise terminally and laterally to chains of smallish spores; the latter were said to develop acropetally. At maturity, the fertile head formed a spore-drop. This species apparently has not been reported again since its original description, and the status of the genus has been questioned in recent years; Zycha (1935) relegated *Dimargaris* to synonymy with *Dispira*.

Dispira cornuta, as described by Van Tieghem, differed from *Dimargaris cristalligena* in having much smaller and presumably dichotomously branched sporophores. The diverse branches of the fertile region produced loose spirals bearing terminal spore heads subtended by short, horn-like, sterile branchlets. Like those of *Dimargaris*, the fertile heads were said to consist of vesicular enlargements producing cellular branchlets bearing spores in chains. *Dispira cornuta* has been reported several times since it was described (Thaxter, 1895; Bainier, 1906 a; Elliott, 1926; Ayers, 1933, 1935; Ou, 1940) and, because of certain inaccuracies in Van Tieghem's original characterization, the species subsequently has been described under two other names, *D. americana* (Thaxter, 1895) and *D. circinata* (Elliott, 1926). Ayers (1933, 1935) succeeded in growing *D. cornuta* in pure culture and conducted extensive tests of its host range.

From a study of preserved material, Vuillemin (1904) described a fungus which appeared to have been growing as a parasite in company with *Piptocephalis lemonnieriana* on *Mucor fragilis*. This species, *Spinalia radians*, the type of a new genus, was characterized as possessing lax, creeping, nonseptate, stolon-like hyphae from which arose usually simple, sparingly septate sporophores producing terminal spore heads. The latter consisted simply of vesicular enlargements bearing chains of spore-like bodies directly over their entire surfaces. These chains were composed of but two elements, presumably spores, developed acropetally. Vuillemin allied *Spinalia* with *Dimargaris*, *Dispira*, and *Syncephalastrum* in a separate series, *Dispirées*, of the Mucorales. Zycha (1935) included *Spinalia*, along with *Dispira*, in the Piptocephalidaceae (as Cephalidaceae), whereas Naumov (1935, 1939) placed Vuillemin's genus in a separate family, Spinaliaceae, allied to the Cunninghamellaceae. I shall follow Vuillemin's disposition of *Spinalia* and classify it with *Dimargaris* and *Dispira*.

In April, 1956, I found and isolated a singular mold which, following a cursory examination, was passed on to C. W. Hesseltine as possibly representing an unusual species of *Syncephalis*. Dr. Hesseltine later informed me that the fungus undoubtedly belonged to *Dimargaris* which, to his knowledge, had not been rediscovered since Van Tieghem described the genus originally. The new isolate fits Van Tieghem's characterization of *D. cristalligena* in all respects except that, as indicated in Van Tieghem's illustrations of the species (Van Tieghem, 1875, Pl 4, fig. 169), two rather than five to seven spores are produced in each spore chain. However, for reasons which will be considered subsequently, the above isolate and a subsequent collection have been referred to *D. cristalligena*. In addition, two more very distinct species of *Dimargaris*, two species of *Dispira*, including *D. cornuta*, and a species representing an allied new genus have been collected. All of these species are parasites or facultative parasites of other Mucorales and, with the exception of an undescribed species of *Dispira*, may be grown without difficulty in pure mixed culture on *Cokeromyces recurvatus* or other mucoraceous hosts. Descriptions of the genera and species presented below will show that these fungi form a natural and relatively highly derived group of Mucorales paralleling the Kickxellaceae. The writer is convinced that these forms cannot logically be included in the latter family or in the Piptocephalidaceae, and, therefore, the following new family is proposed:

Dimargaritaceae fam. nov.

Hyphis vegetantibus tenuibus, hyalinis, ramosis, septatis; hyphis appressoria parva et haustoria gerentibus; hyphis hausteriorum brevibus nonseptatis; sporangiophoris albis vel pallidis, rectis, septatis, simplicibus vel ramosis, merosporangia de 2 sporis in vesiculis terminalibus vel in ramisculis cellularibus terminalibus vel lateralibus gerentibus; sporangiosporis hyalinis, subglobosis, ellipsoideis vel bacilliformibus; sporis ad maturitatem in liquido involutis vel siccis; septis cavernulas medianas discoideas gerentibus; cavernulis obturacula hyalina discoidea continentibus; obturaculis plerumque tubercula globosa polariaque gerentibus; zygosporis globosis, de muris crassis, globulos 1- plures continentibus; hyphis sexualibus simplicibus, hyphis vegetantibus persimilibus.

Vegetative hyphae delicate, hyaline, branched, regularly septate, giving rise to numerous small, slightly swollen appressoria producing restricted, more or less ramified, aseptate haustoria; sporangiophores white or light colored, erect, septate, simple or branched, forming two-spored merosporangia directly on the surfaces of terminal enlargements or on cellular branchlets produced laterally or terminally; sporangiospores hyaline, subglobose, ellipsoid, or bacilliform; spores at maturity remaining dry or immersed in liquid; septa of both the vegetative and fruiting hyphae

characteristically with median disciform cavities containing solid, colorless, more or less biconvex plugs bearing small, usually globose enlargements at their poles; zygo-spores globose, thick-walled, hyaline, formed from the fusion of similar undifferentiated hyphae, usually containing one or more refractive globules at maturity. Parasites or facultative parasites of other Mucorales.

Type genus: *Dimargaris* Van Tieghem (1875, p. 154).

A KEY TO THE GENERA

- A. Merosporangia produced directly on the surfaces of terminal vesicular enlargements of the sporophores. . . . . *Spinalia* (p. 394)
- AA. Merosporangia not produced directly on the surfaces of vesicular enlargements. . . . . B.
- B. Sporangiophores without sterile branches; spores immersed in liquid at maturity. . . . . *Dimargaris* (p. 365)
- BB. Sporangiophores with numerous sterile branches; spores remaining dry at maturity. . . . . C.
- C. Sporiferous branchlets two-celled, borne in terminal clusters of few to many elements. . . . . *Dispira* (p. 380)
- CC. Sporiferous branchlets one- to three-celled, borne laterally, formed singly or in whorls. . . . . *Tieghemiomyces* (p. 390)

DIMARGARIS Van Tieghem.

Ann. Sci. Nat., Bot., Sér. 6. 1: 154. 1875.

Sporangiophores erect, septate, at first simple, becoming irregularly cymosely or verticillately branched and producing fertile heads terminally; sterile branches absent; spore-heads composed of few or many sporiferous branchlets subtended or not subtended by vesicular enlargements; sporiferous branchlets simple or ramiform, consisting of several superposed cells produced by apical and lateral budding, each cell giving rise to distal whorls of two-spored merosporangia; spores smooth, ellipsoidal or bacilliform, immersed in liquid at maturity; zygosporangia thick-walled, hyaline, smooth or delicately punctate.

Type species: *Dimargaris cristalligena* Van Tieghem (1875, p. 154).

A KEY TO THE SPECIES

- A. Sporophores becoming cymosely branched. . . . . *D. cristalligena* (p. 365)
- AA. Sporophores becoming verticillately branched. . . . . B.
- B. Sporiferous branchlets subtended by vesicles. . . . . *D. verticillata* (p. 374)
- BB. Sporiferous branchlets not subtended by vesicles. . . . . *D. bacillispora* (p. 376)

DIMARGARIS CRISTALLIGENA Van Tieghem.

Ann. Sci. Nat., Bot., Sér. 6. 1: 154. 1875.

(Plates 13, 14, 15, 16)

Colonies on *Cokeromyces recurvatus* on YpSs white, becoming "Pinkish Buff" in age; vegetative hyphae colorless, septate, branched, 2.5-6 μ in diameter; haustoria at first simple, often somewhat clavate, becoming more or less lobate and developing numerous short, irregular branches about 2-3 μ wide, up to 20 μ or more long; sporophores erect, septate, at first simple and producing white fertile heads terminally when about 3-6 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 the distal septum of the preceding branch; sporophores, in age, 0.5-2(-3.5) cm. high; the cells bearing the fertile heads about 400-1200 μ long $\times$

20-45 μ wide; the other cells about 300-600 $\mu \times$ 20-45 μ , except the proximal ones which usually are somewhat shorter, 180-300 μ long; the attenuated basal cells producing, below their upper septa, whorls of hyphal branches slightly swollen at their bases; fertile heads globose, 250-325 μ in diameter, composed of slightly ovoid vesicles 25-65 μ in diameter, producing, over their entire surfaces, numerous slender, elongate branches which become somewhat constricted and septate at several points along their distal one-half to two-thirds and consist of about 3-6 superposed cells; the basal cell long and nearly uniform in diameter, 40-75 $\mu \times$ 5-8 μ , the other cells progressively shorter and more or less clavate or ovoid; all cells giving rise distally, by budding, to shorter divergent branchlets of usually 1-3 superposed, smallish, clavate or ovoid cells produced by apical budding; the cells of the main axis and its branches bearing distal whorls of merosporangia containing two spores each; the terminal portions of the merosporangia developing by apical budding from the basal; spores ellipsoidal or slightly reniform, 3.9-8.7 μ (aver. 5.6 μ) $\times$ 2.6-3.9 μ (aver. 3.2 μ); most cells of the sporiferous branchlets disarticulating at maturity and, with the spores, immersed in drops of liquid which form glistening white spheres about 165-290 μ in diameter; zygospores developed from the conjugation of similar undifferentiated hyphae, colorless, thick-walled, minutely punctate, 55-100 μ (aver. 75 μ) in diameter, containing, when mature, one or several large, usually eccentric, refractive globules 15-35 μ in diameter; wall 6-12 μ (aver. 9 μ) thick.

Neotype.—CALIFORNIA. Los Angeles County: Evey Canyon, San Gabriel Mts., 4.5 miles northeast of Claremont, April 24, 1956, isolated from mouse dung (RSA Culture 468).

Other specimen examined.—CALIFORNIA. Los Angeles County: Sunset Peak, San Gabriel Mts., 8 miles north of Claremont, July 10, 1957, isolated from mouse dung (RSA Culture 585). Transfers of RSA Cultures 468 and 585 have been deposited in the ATCC, CBS, and CMI.

In his original descriptions of *Dimargaris cristalligena* and *Dispira cornuta* Van Tieghem (1875) did not comment verbally on the number of spores comprising the spore chains of either of these species. His figures (Van Tieghem, 1875, Pl. 4, fig. 169 and 175 respectively) show chains of five to seven spores formed terminally and laterally on the several cells of the sporiferous branchlets of *D. cristalligena* and single chains of six spores formed terminally on the upper cells only of the two-celled sporiferous branchlets of *D. cornuta*. In 1895, Thaxter studied a *Dispira*, obtained from rat dung collected in Ohio, which was very similar to Van Tieghem's *D. cornuta* except that it produced distal whorls of two-spored merosporangia on the upper angles of both cells of the sporiferous branchlets as well as a single two-spored chain terminally on the upper cell. Because of the apparent differences between the fungus from Ohio and the one described by Van Tieghem, Thaxter treated the former as new and called it *D. americana*. A few years later Bainier (1906 a) reported that the fertile heads of collections of *Dispira* obtained in the vicinity of Paris showed essentially the same developmental pattern and characteristics as those described by Thaxter

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PLATE 13. *Dimargaris cristalligena* Van Tieghem.—*a*. Habit sketch of sporophore showing branching pattern and septation. $\times$ 20. *b*. Typical haustorium inside host hypha. $\times$ 1080. *c*. Base of sporophore stipe showing whorls of lateral branchlets. $\times$ 180. *d*. Habit sketch showing general characteristics of fruiting structures. $\times$ 8. *e-i*. Successive stages in the development of the sporiferous branchlets showing the origin, by budding, of lateral branchlets and merosporangia. $\times$ 780. *j*. Terminal portion of a sporiferous branchlet showing distal whorls of young merosporangia. $\times$ 1360. *k*. Single fertile cell of sporiferous branchlet bearing distal whorl of mature merosporangia. $\times$ 1360. *l*. Five mature spores showing variation in size. $\times$ 1360. *m*. Terminal vesicular enlargement of sporophore after distarticulation of all but a few of the elongate basal cells of the sporiferous branchlets. $\times$ 400.

PLATE 13

for *D. americana*, and he concluded that Van Tieghem somehow had erred in his interpretation of *D. cornuta*. Accordingly, Bainier reduced *D. americana* to synonymy with *D. cornuta*; Thaxter later concurred with this opinion (Ayers, 1935).

The two collections here referred to *Dimargaris cristalligena* fit Van Tieghem's original description of the species in every respect except that all spore-chains of the new world isolates are composed of but two spores. Because two-spored merosporangia are typical of the six species representing the three genera of Dimargaritaceae studied here, two-spored chains very likely are a fundamental characteristic of the family. Thus, pending rediscovery of a fungus producing spore-chains like those illustrated by Van Tieghem, the writer has preferred not to create another name but has instead emended the description of *D. cristalligena* with regard to the number of spores per merosporangium. Should this admittedly arbitrary action eventually be proved wrong, its remedy will not be difficult for some enterprising taxonomist.

Dimargaris cristalligena and the other species of the genus described below will grow weakly as saprobes on ordinary media such as PAB-DEX, YpSs, PDA, and especially ME-YE, and in about two or three weeks these species will give rise to fruiting structures. Spores produced in pure culture are capable of infecting susceptible hosts and will germinate in the absence of a host. In the period September 23, 1957, to November 24, 1958, *D. cristalligena*, *D. verticillata*, and *D. bacillispora* survived five successive transfers on ME-YE and had showed no indication of having lost their capacity to grow alone. Although growth and development in pure culture are relatively slow and less vigorous than on a mucoraceous host, these species will grow and sporulate, and in the case of *D. bacillispora* not only asexual but also sexual spores are produced. When grown on any of the above media in the presence of a fungus such as *Cokeromyces recurvatus*, species of *Dimargaris* are vigorous parasites and sporophores usually begin to appear in about four to six days.

Germinating spores of *D. cristalligena* swell to about two or three times the size of the original spores, become nearly spherical, and give rise to two or more, often four or five, slender germ hyphae (Pl. 14 *a*) which soon produce the peculiar septa characteristic of the family (Pl. 14 *b*). Germ hyphae and branches of the vegetative mycelium contact the host hyphae, form small swollen appressoria, and penetrate the host membrane by means of minute tubes. Upon reaching the host cytoplasm, the latter usually become somewhat dilated and form more or less lobate haustoria bearing numerous short radiating branchlets (Pl. 13 *b*; Pl. 14 *c*). There may be considerable variation, of course, in the complexity of the haustorium depending upon its age. The mycelium of the parasite develops rapidly and has been found to attack only the vegetative hyphae of the host. Sporophore initials usually begin to form in about four days in cultures maintained at 21°C. Fruiting structures are simple at first and when about three to six millimeters high they produce fertile heads terminally. One, two, or sometimes more proximal cells of the sporophore stipe characteristically develop whorls of slender hyphal branches (Pl. 13 *c*), often swollen at their bases, which, as pointed out by Van Tieghem (1875), recall the prop-roots of many higher

PLATE 14. *Dimargaris cristalligena* Van Tieghem.—*a*. Germinating spores; note early formation of septa. $\times 560$. *b*. Germ hypha showing characteristic cross-wall. $\times 1300$. *c*. Haustorium. $\times 1300$. *d*. Terminal enlargement of sporophore bearing sporiferous branchlets in early stage of development. $\times 170$. *e*. Mature fertile head prior to disarticulation of merosporangia and sporiferous branchlets. $\times 170$. *f*. Portion of terminal vesicular enlargement after disarticulation of sporiferous branchlets showing characteristic basal scars in surface view and in optical section. $\times 1300$. *g-i*. Several successive stages in the development of sporiferous branchlets. $\times 620$. *j*. Terminal part of a sporiferous branchlet showing distal whorls of nearly mature merosporangia. $\times 1300$.

PLATE 14

plants. Similar outgrowths have not been observed on the sporophores of other members of the Dimargaritaceae.

The fruiting hyphae of *D. cristalligena* often reach 45 μ in diameter, and the relatively large size of the septa in these hyphae has permitted more detailed study of the nature of the cross-wall than is possible in other known species of the family. Septa are formed during very early stages of development of the vegetative and fruiting hyphae in members of the Dimargaritaceae, and the structure of these cross-walls is one of the most interesting and outstanding characteristics of the family. The mature sporophore wall consists of two distinct layers: (1) a thicker inner layer which divides the sporophore into elongate cellular compartments and takes part directly in the formation of septa, and (2) a thinner outer layer which is continuous throughout the length of the sporophore. The septa consist of the apposed end-walls of adjacent cells, and the double character of a septum may be demonstrated easily by causing the sporophore to be broken transversely through a cross-wall (Pl. 15 *g-i*) or by plasmolysis (Pl. 15 *e*). The two apposed elements of a cross-wall possess median perforations and are slightly separated in the central region of the septum. Thus, there is formed a more or less lenticular cavity with an opening at each pole (Pl. 15 *d*). This cavity contains a solid, brittle, biconvex, colorless plug having polar protuberances which project through the openings in the septum (Pl. 15 *c*). In the sporophore septa of *D. cristalligena*, the upper protuberance is globose whereas the lower one is obconic (Pl. 15 *b-c*). In all other species of the family studied here, both protuberances are globose (Pl. 19 *a, e*; Pl. 21 *c*; Pl. 24 *e*; Pl. 26 *g*). By careful manipulation a nearly intact plug may be liberated from the retaining walls of a septum (Pl. 15 *f*). In members of the Dimargaritaceae the plug is readily dissolved by dilute alkali (2-3% KOH) and by acidic solutions such as Carnoy's fixative and Lacto-phenol or Lacto-fuchsin mounting media, whereas in representatives of the Kickxellaceae the septal plug is more or less persistent in alkaline or acidic solutions and may be rather deeply stained by Carmine, Aniline blue, and Acid fuchsin. When microscopic examination of living sporophores of members of the Dimargaritaceae and Kickxellaceae is carried out using relatively low magnifications, one observes that the protoplasm immediately below each septum is much more dense and less highly vacuolate than in the rest of the cell. It would seem that the very remarkable and highly complex septa of members of the Dimargaritaceae and the Kickxellaceae as well (Raper and Fennell, 1952, p. 85) may somehow be actively associated with the movement of protoplasm through the vegetative and fruiting hyphae and that the plugs formed in the median concavities of these septa may function as valves which in some way regulate such movement. A study of the way in which these structures effect such control, if any, should prove most interesting.

The fertile heads of *D. cristalligena* are composed of numerous sporiferous branchlets borne on the dilated apices of the primary sporophores and their branches (Pl. 13 *a, d*; Pl. 14 *e*). A sporiferous branchlet at first consists of a simple slender outgrowth arising directly from the subtending vesicle (Pl. 13 *e*; Pl. 14 *d*) and contains a single nucleus (Pl. 16 *a*). This primary branch becomes slightly constricted at intervals along its length and normally gives rise by budding to several slightly divergent outgrowths (Pl. 13 *f*; Pl. 14 *g*). Septa are formed in the region of the constrictions of the primary branch and its laterals so that each sporiferous branchlet consists finally of a rather long basal cell and several shorter superposed slightly inflated cells often bearing, at their upper angles, one or more short cellular branchlets (Pl. 13 *g-i*; Pl. 14 *b*). At this stage of development, each cell of a sporiferous branchlet contains a single nucleus. Merosporangia arise by a process of terminal and lateral budding from the upper part of each fertile cell (Pl. 13 *g-j*; Pl. 14 *b-j*). While the mero-

PLATE 15. *Dimargaris cristalligena* Van Tieghem.—*a*. Segment of sporophore stipe showing single cell. $\times 245$. *b*. Upper part of stipe cell showing accumulation of densely granular protoplasm below septum. $\times 500$. *c*. Cross-wall in optical section showing lenticular plug with conical protuberance below and knob-like protuberance above. $\times 1000$. *d*. Lacto-fuchsin mount of cross-wall as seen in optical section showing median cavity with circular openings above and below. $\times 1000$. *e*. Chlor-iodide of zinc preparation showing double character of cross-wall. $\times 1000$. *f*. Nearly intact plug which has been separated from its cross-wall and is floating free in lumen of stipe cell. $\times 1000$. *g-i*. Sporophore broken transversely through a cross-wall; one segment has rotated slightly on its longitudinal axis with regard to the other segment. The photographs, taken at three levels of focus, clearly show the double nature of the cross-wall and the inner and outer membranes of the stipe. $\times 560$.

sporangial initial is in the process of formation, the nucleus of the cell from which it arises divides (Pl. 16 *b-c*); one daughter nucleus migrates into the young merosporangium and the other remains in the fertile cell (Pl. 16 *d*). The same nuclear cycle accompanies the formation of succeeding merosporangial initials. Following migration of a nucleus into the young merosporangium, the latter is separated from its supporting cell by a cross-wall (Pl. 16 *e*). Further development of the merosporangium involves the formation of a second cell through apical budding by the basal cell. While this terminal cell is forming, the nucleus in the basal cell divides once (Pl. 16 *e-f*) and one of the daughter nuclei of this division migrates into the upper cell (Pl. 16 *g*). The resulting uninucleate portions of the merosporangium each delimits a usually ellipsoidal sporangiospore (Pl. 13 *k*; Pl. 16 *h-i*). It may be noted that this type of merosporangial development is exactly like that described earlier in *Piptocephalis lepidula* (Pl. 5 *f-h*).

The nearly mature spore head of *Dimargaris cristalligena* is pure white and often reaches as much as 325 μ in diameter (Pl. 14 *e*). Following maturation, the merosporangia and the cells composing the fertile branches disarticulate and become enveloped in liquid, and the heads form glistening white spheres about 160-290 μ in diameter. A few of the basal cells of the fertile branches may remain attached to the vesicle (Pl. 13 *m*), but most of these also become detached near their bases and their former positions on the vesicle are marked by small circular scars (Pl. 13 *m*; Pl. 14 *f*).

When grown on *Cokeromyces recurvatus* on YpSs at 21°C. in Petri dishes 2 cm. deep or 18 mm. test tubes (slants), *Dimargaris cristalligena* normally gives rise to sporophores which eventually reach the upper surfaces of the containers and become highly distorted. This factor interferes with accurate observation of ultimate sporophore dimensions. To overcome this difficulty, the species may be grown—other conditions remaining the same—in Petri dishes having depths of 7 cm., and under these circumstances the sporophores of *D. cristalligena* attain heights of as much as 3.5 cm. In order to allow for extended vertical clearance in tube cultures, agar media may be allowed to solidify in test tubes stored in a vertical position. However, when *D. cristalligena* is grown on such unslanted agar surfaces of relatively limited area, using the same host, medium, and incubation temperature as listed above, the sporophores of the parasite typically reach heights of only 5-8 mm.—heights comparable to the 3-5 mm. reported originally by Van Tieghem (1875). Further, under these conditions of culture, zygospores of *D. cristalligena* are produced in abundance after about three or four weeks, whereas in Petri dish or slanted tube cultures, sexual spores of this species are formed in very small numbers. The physiological phenomena responsible for the reduced size of the sporophores and the increased sexual activity of *D. cristalligena* in unslanted tube cultures have not been studied here.

Zygospores of the Dimargaritaceae are very similar in structure and manner of formation to those of the Kickxellaceae (Benjamin, 1958), and usually develop within the substratum. Sexual spores have been found in cultures of five of the six

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PLATE 16. *Dimargaris cristalligena* Van Tieghem.—*a*. First nuclear division in a sporiferous branchlet. $\times 2100$. *b-d*. Nuclear divisions in the cells of the sporiferous branchlets. *b*. Early stage of division of the single nucleus in each of three fertile cells. Each cell is forming a single merosporangium initial. $\times 2100$. *c*. Telophase (lower left) and late anaphase (upper right) of nuclear divisions in fertile cells. $\times 2100$. *d*. In the two fertile cells shown on the right, daughter nuclei resulting from previous nuclear divisions are migrating into merosporangial initials. Migration of a single nucleus into the young merosporangium shown at the lower left already has occurred. $\times 2100$. *e-h*. Nuclear cycle in developing merosporangia. *e*. Early stages of division of nuclei in the lower cells of immature merosporangia. Terminal cells, formed by budding from the basal, have reached nearly definitive size. Additional merosporangia are beginning to

form. $\times 2100$. *f*. Late telophase of nuclear division in basal cell of young merosporangium. $\times 2100$. *g*. Migration of one daughter nucleus into terminal cell of merosporangium. $\times 2100$. *b*. Nearly mature merosporangium showing uninucleate spores. $\times 2100$. *i*. Fertile cells showing distal whorls of merosporangia prior to disarticulation. $\times 1300$. *j*. Optical section of mature zygospore. $\times 410$. *k*. Zygospore as seen in surface view. $\times 665$.

species of the former family studied in connection with the present work. In most species of *Dimargaritaceae*, the apex of a short undifferentiated hyphal branch fuses with another hypha or the one from which the first branch arose, and the zygosporangium develops as a nearly globose swelling around the point of fusion (Pl. 18 *n-p*; Pl. 19 *b*). In one species, *Dispira cornuta*, the zygosporangium develops terminally on a lateral outgrowth of a vegetative hypha (Pl. 22 *a-c*). During early stages of development, the protoplasm within the zygosporangium consists of a thin peripheral layer of cytoplasm surrounding a large central vacuole (Pl. 18 *n*; Pl. 19 *b*). As the zygosporangium enlarges and the zygosporangium develops, the protoplasm becomes increasingly dense and less highly vacuolate and finally condenses and forms numerous small globules (Pl. 19 *i-k*) which decrease in number and increase in size (Pl. 19 *l*) until at maturity the zygosporangium contains one or several relatively large refractive globules surrounded by a nearly homogenous cytoplasm (Pl. 16 *j*; Pl. 18 *p*; Pl. 19 *m*; Pl. 22 *a-c*, *e-f*; Pl. 25 *m*; Pl. 26 *i*). The mature thick-walled zygosporangium may be smooth (Pl. 18 *p*; Pl. 19 *m*) or delicately punctate or pitted (Pl. 16 *k*; Pl. 22 *d*; Pl. 26 *j*).

***Dimargaris verticillata* sp. nov.**

(Plates 17, 19 *a*, 22 *e-f*)

Coloniae in *Cokeromyces recurvatus* in agar YpSs albae vel in aetate "Cream Color"; hyphis vegetantibus 2-4 μ diam.; sporophoris rectis, in juventute simplicibus, in aetate verticillatis, 1-18 ramos divaricatos infra 2-4 septa in partibus superioribus fertilibus gerentibus; ramis plerumque 2-cellulis, 35-100 $\mu \times$ 6-10 μ ; axibus principalibus axes secundarios gerentibus; sporophoris in aetate 1-3 mm. altis; cellulis in partibus superioribus stipitium principalium 125-260 $\mu \times$ 6-13 μ ; capitibus fertilibus terminalibus, globosis, 40-80 μ diam., in vesiculis globosis, 8-22 μ diam., et ramusculis sporogenis consistentibus; ramusculis sporogenis in cellulis basalibus, 6-12 $\mu \times$ 4-6 μ , et plerumque 2 ramusculis 1-3 cellulis terminalibus consistentibus; cellulis sporogenis merosporangia de 2 sporis gerentibus; merosporangiis per gemmascentem gestis; sporis oblongis-ellipsoideis, 4.4-6.6 $\mu \times$ 2.2-3.1 μ ; ramusculis sporogenis et sporis in maturitate disarticulatis et globulos liquideos, 30-65 μ diam., gerentibus; zygosporis globosis, hyalinis, de muris crassis, plerumque levibus vel minute punctatis, 22-45 μ (med. 35 μ) diam., 1-plures globulos, 9-18 μ diam., continentibus; muro 3-8 μ (med. 5.2 μ) crasso.

Colonies on *Cokeromyces recurvatus* on YpSs white, becoming "Cream Color" in age; vegetative hyphae colorless, septate, branched, 2-4 μ in diameter; haustoria at first simple, becoming more or less ramose; sporophores erect, septate, colorless, at first simple and producing white fertile heads terminally when about 0.5-2 mm. high, becoming irregularly verticillately branched by the successive development of 1 to as many as 18 divergent, usually 2-celled, slightly tapered fertile branches, 35-100 μ long $\times$ 6-10 μ wide (at the base); fertile branches formed immediately below each of the distal 2-4 septa of the main stalk; the basal cells of the fertile branches usually about twice as long as the distal cells; one or more secondary fertile axes often arising from the primary axes in the same manner as the fertile branches;

PLATE 17. *Dimargaris verticillata* Benjamin.—*a*. Habit sketch showing general characteristics of fruiting structures. $\times$ 30. *b*. Upper portion of sporophore showing arrangement and characteristics of fertile branches. $\times$ 300. *c*. Haustorium. $\times$ 1080. *d*. Vesicular enlargement of fertile branch showing origin, by budding, of sporiferous branchlet initials. $\times$ 1360. *e-f*. Successive stages in the development of the sporiferous branchlets and merosporangia. $\times$ 1360. *k*. Mature spores. $\times$ 1360. *l*. Terminal vesicular enlargement of sporophore branch after disarticulation of all but a few of the clavate basal cells of sporiferous branchlets. $\times$ 1360.

PLATE 17

sporophores, in age, about 1-3 mm. high; the distal cells of the main stalk 125-260 μ long $\times$ 6-13 μ wide; the basal cells slightly shorter and more slender, about 5-10 μ in diameter; fertile heads globose, 40-80 μ in diameter, composed of nearly globose vesicles, 8-22 μ in diameter, producing, over their entire surfaces, numerous sporiferous branchlets consisting of clavate cells, 6-12 $\mu \times$ 4-6 μ , each of which bears usually two distal branches of 1-3 smaller superposed ovoid cells produced by budding; the cells of the sporiferous branchlets bearing distal whorls of merosporangia containing two spores each; the terminal portions of the merosporangia developing by apical budding from the basal; spores short oblong-ellipsoidal, 4.4-6.6 $\mu \times$ 2.2-3.1 μ ; all but a few of the basal cells of the sporiferous branchlets disarticulating at maturity and, with the spores, immersed in drops of liquid which form glistening white spheres about 30-65 μ in diameter; zygospores developed from the conjugation of similar undifferentiated hyphae, colorless, thick-walled, nearly smooth or minutely punctate, 22-45 μ (aver. 35 μ) in diameter, containing, when mature, one or rarely more, usually eccentric, refractive globules 9-18 μ in diameter; wall 3-8 μ (aver. 5.2 μ) thick.

Holotype.—CALIFORNIA. Los Angeles County: Rancho Santa Ana Botanic Garden, Claremont, February 26, 1957, isolated from mouse dung (RSA Culture 527).

Other specimens examined.—Several additional strains (RSA Cultures 565, 566, 567) were isolated from frog dung collected at the type locality April 16, 1957. Transfers of RSA Culture 527 have been deposited in the ATCC, CBS, and CMI.

As in *Dimargaris cristalligena*, the sporiferous branchlets of *D. verticillata* arise by budding from the surfaces of vesicular enlargements (Pl. 17 *d*) produced apically on the primary axes and the secondary branches of the sporophores (Pl. 17 *a-b*). The sporiferous branchlets develop by apical and lateral budding (Pl. 17 *d-g*) and differ from those of *D. cristalligena* only in being shorter, in having fewer branches, and in being composed of fewer cells. As in *D. cristalligena*, the merosporangia of *D. verticillata* develop acropetally (Pl. 17 *g-i*) and are arranged in distal whorls on the cells of the fertile branchlets (Pl. 17 *j*). The spores of the latter species (Pl. 17 *k*) average about 5.2 $\mu \times$ 2.6 μ , and are much more uniform in size and shape than those of the former species. The irregularly verticillately branched sporophores of *D. verticillata* (Pl. 17 *a-b*), which usually attain heights of only 1-3 mm., readily distinguish this species from the relatively very large, cymosely branched *D. cristalligena* (Pl. 13 *a, d*).

Dimargaris bacillispora sp. nov.

(Plates 18, 19 *b-m*)

Coloniae in *Cokeromyces recurvatus* in agar YpSs albae vel in aetate "Smoke Gray"; hyphis vegetantibus 1.5-3.5 μ diam.; sporophoris rectis, in juventate simplicibus, in aetate verticillatis; 1-6 ramos divaricatos infra 3-4 septa in partibus superioribus fertilibus gerentibus; ramis plerumque 1-cellulis, 100-210 $\mu \times$ 7-10 μ ; axibus

PLATE 18. *Dimargaris bacillispora* Benjamin. —*a*. Habit sketch showing general characteristics of fruiting structures. $\times$ 30. *b-e*. Successive stages in the development of the sporiferous branchlets. Fig. *e* shows origin of merosporangia from tips of apical cells and upper angles of intercalary cells. $\times$ 890. *f-h*. Successive stages in the development of the sporiferous branchlets and merosporangia. $\times$ 1360. *i*. Fertile head after disarticulation of all but a few cells of the sporiferous branchlets. $\times$ 600. *j*. Five mature spores (above) and one germinating spore. $\times$ 1860. *k*. Haustorium. $\times$ 1080. *l*. Upper portion of sporophore showing arrangement and characteristics of fertile branches. $\times$ 225. *m*. Base of sporophore stipe. $\times$ 600. *n-o*. Early stages in the development of the zygospore showing origin of the zygosporangium around the point of fusion of an undifferentiated sexual branch with the hypha from which the branch arose. *n*, $\times$ 600; *o*, $\times$ 660. *p*. Optical section of a mature zygospore. $\times$ 485.

PLATE 18

principalibus axes secundarios gerentibus; sporophoris in aetate 5-8 mm. altis; cellulis in partibus superioribus stiptitum principalium $225-385\ \mu \times 10-15\ \mu$; caputibus fertilibus terminalibus turbinatis, $50-65\ \mu$ diam., in 3-4 ramusculis sporogenis nonnihil divaricatis consistentibus; ramusculis sporogenis in 3-6 cellulis clavatis vel ovoideis, per gemmascentem gestis, consistentibus; ramusculis principalibus ramusculis 1-3 cellularum gerentibus; cellulis basalibus ramusculorum principalium $12-20\ \mu \times 7-10\ \mu$; cellulis sporogenis merosporangia cylindratas de 2 sporis gerentibus; sporis bacilliformibus nonnihil curvatis, $4-4.8\ \mu \times 1.3\ \mu$; ramusculis sporogenis et sporis in maturitate disarticulatis et globulos liquidos, $35-50\ \mu$ diam., gerentibus; zygosporis globosis, hyalinis, levibus, de muris crassis, $43-63\ \mu$ (med. $53\ \mu$) diam., globulos singulos excentricos, $19-33\ \mu$ diam., continentibus; muro $3-9\ \mu$ (med. $6.6\ \mu$) crasso.

Colonies on *Cokeromyces recurvatus* on YpSs white, becoming "Smoke Gray" in age; vegetative hyphae colorless, septate, highly branched, $1.5-3.5\ \mu$ in diameter; haustoria at first simple, becoming more or less ramose, the branches mostly $1-2.5\ \mu$ wide, up to $20\ \mu$ or more long; sporophores erect, septate, colorless, at first simple and producing white fertile heads terminally when about $1.5-3.5$ mm. high, becoming irregularly verticillately branched by the development of 1 to as many as 6 divergent, usually 1-celled, slightly tapered fertile branches, $100-210\ \mu$ long $\times 7-12\ \mu$ wide (at the base); fertile branches formed immediately below each of the distal 3 or 4 septa of the main stalks; 2-celled fertile branches, mostly less than twice the length of the 1-celled branches, not uncommon; one or more secondary fertile axes usually arising from the primary axes in the same manner as the fertile branches; sporophores, in age, about 5-8 mm. high; the distal cells of the main stalks $225-385\ \mu$ long $\times 10-15\ \mu$ wide; the basal cells slightly shorter and more slender, about $7-10\ \mu$ in diameter; fertile heads somewhat turbinate, $50-65\ \mu$ in diameter, composed of 3-4 slightly divergent sporiferous branchlets composed of 3-6 superposed clavate to ovoid cells formed successively by budding; the basal cells largest, about $12-20\ \mu \times 7-10\ \mu$; the cells of the primary branches producing similar divergent cellular branches of 1-3 cells which, in turn, may give rise to 1- or 2-celled branchlets; the cells of these branch systems bearing distal whorls of merosporangia; merosporangia at first uniformly cylindrical, forming, simultaneously, two bacilliform slightly curved sporangiospores, $4-4.8\ \mu \times 1.3\ \mu$; all cells of the sporiferous heads, except a few of the proximal cells of the primary and secondary branches, disarticulating at maturity and, with the spores, immersed in drops of liquid which form glistening white spheres about $35-50\ \mu$ in diameter; zygosporos developed in the substratum from the conjugation of short undifferentiated hyphal branches with similar vegetative hyphae, globose, colorless, smooth, thick-walled, $43-63\ \mu$ (aver. $53\ \mu$) in diameter, containing, when mature, usually single, large, eccentric, refractive globules $19-33\ \mu$ in diameter; wall $3-9\ \mu$ (aver. $6.6\ \mu$) thick.

Holotype.—CALIFORNIA. San Bernardino County: Jenk's Lake, San Bernardino Mts., about 10 miles east of Camp Angelus, July 26, 1957, isolated from mouse dung (RSA Culture 592). Transfers of this culture have been deposited in the ATCC, CBS, and CMI.

Macroscopically, the branching pattern of the sporophores of *D. bacillispora* resembles that of *D. verticillata* very closely; however, the height of the fruiting structures of the former species normally exceeds that of the latter by a factor of 2-3

PLATE 19. *a. Dimargaris verticillata* Benjamin.—Typical cross-wall. $\times 1300$. *b-m. Dimargaris bacillispora* Benjamin.—*b-d.* Early and intermediate stages in the development of the fertile head. $\times 560$. *e.* Typical cross-wall. $\times 1300$. *f.* Haustoria. $\times 1300$. *g.* Mature head before disarticulation. $\times 560$. *h-m.* Successive stages in the development of the zygosporos. $\times 560$.

PLATE 19

(Pl. 17 *a*; Pl. 18 *a*). As shown in Plates 17-19, these species are quite distinct microscopically. Unlike both *D. cristalligena* and *D. verticillata*, the sporiferous branchlets of *D. bacillispora* are not subtended by vesicular enlargements. In the latter species, the sporophore branches give rise by budding to relatively small numbers of divergent sporiferous branchlets arranged in terminal clusters (Pl. 18 *b-e*, *l*; Pl. 19 *b-d*, *g*). The merosporangia of *D. bacillispora* are disposed in distal whorls on the cells of the sporiferous branchlets as in the other species of the genus, but, unlike *D. cristalligena* and *D. verticillata*, the merosporangia of *D. bacillispora* do not develop acropetally (Pl. 18 *f-b*). Instead, the young merosporangia of the latter species are at first uniformly cylindrical as in most species of *Piptocephalis*, and the spores of *D. bacillispora* appear to be delimited in a manner comparable to that found in many species of the latter genus (see Pl. 5 *a-c*).

Zygosporangia of *D. bacillispora* are usually produced in abundance by the fungus growing not only parasitically but also saprobically. The formation and characteristics of these zygosporangia (Pl. 18 *n-p*; Pl. 19 *h-m*) already have been described above in connection with the discussion of *D. cristalligena*.

DISPIRA Van Tieghem.

Ann. Sci. Nat., Bot., Sér. 6. 1: 160. 1875.

Sporangiophores erect, septate, giving rise above to fertile branch systems; branches irregularly sympodially branched, forming one or more somewhat coiled or angular main axes bearing sterile and/or fertile branchlets, these often coiled or recurved; sterile branchlets usually narrowly attenuated and longer than the fertile ones; fertile branchlets with or without sterile laterals, terminated by few or many two-celled sporiferous branchlets subtended or not subtended by nearly globose vesicles; merosporangia two-spored, borne in distal whorls on the cells of the sporiferous branchlets; sporangiospores smooth, ellipsoid or ovoid, remaining dry at maturity; zygosporangia thick-walled, hyaline, minutely punctate.

Type species: *Dispira cornuta* Van Tieghem (1875, p. 160).

A KEY TO THE SPECIES

- A. Fertile heads composed of many sporiferous branchlets subtended by nearly globose vesicles..... *D. cornuta* (p. 380)
- AA. Fertile heads composed of few sporiferous branchlets not subtended by vesicles..... *D. simplex* (p. 387)

DISPIRA CORNUTA Van Tieghem.

Ann. Sci. Nat., Bot., Sér. 6. 1: 160. 1875.

(Plates 20, 21, 22 *a-d*)

Dispira americana Thaxter, Bot. Gaz. 20: 517. 1895.

Dispira circinata Elliott, Jour. Bot. 64: 105. 1926.

Colonies on *Cokeromyces recurvatus* on YpSs remaining white; vegetative hyphae colorless, septate, branched, 2-6 μ in diameter; haustoria at first simple, often slightly inflated and developing numerous short irregular branchlets 1-2 μ wide; sporophores erect, septate, giving rise above to 2-6 simple or ramose fertile branches, the latter sympodially branched, forming usually spirally coiled main axes each bearing up to 15 or more recurved fertile branchlets terminated by fertile heads; main axes of the fertile branches finally narrowly attenuated and forming sterile prolongations about 2-4 μ wide, up to 3.5 mm. long; fertile branchlets bearing 1-2, rarely 3, narrowly attenuated, usually once or twice septate, recurved or slightly coiled, sterile branchlets, 50-150 μ long; sporophores, in age, up to 5 mm. high including the sterile prolonga-

tions of the main axes of the fertile branches; stipes below the fertile regions 1.5-3 mm. long, 10-12 μ wide, composed of cells 175-300 μ long; fertile heads nearly globose, 35-45 μ in diameter, composed of nearly globose vesicles, 9-13 μ in diameter, bearing, over their entire surfaces, about 25-30 two-celled sporiferous branchlets formed by budding; sporiferous branchlets 7.5-9 $\mu \times$ 3.5-4.5 μ , composed of two subequal cells bearing distal whorls of merosporangia containing two spores each; the terminal portions of the merosporangia developing by apical budding from the basal; spores elongate-ovoid, 3-4.8 $\mu \times$ 1.8-2.2 μ ; spore heads remaining dry at maturity; zygospores developed terminally in lateral outgrowths of vegetative hyphae, colorless, thick-walled, minutely punctate, 30-50 μ (aver. 40 μ) in diameter, containing, when mature, one or several large refractive globules 5-15 μ in diameter; wall 5-10 μ (aver. 7.3 μ) thick.

Specimens examined.—OHIO. Darke County: Greenville, 1895, on rat dung collected by W. H. Rush (Farlow Herbarium: *R. Thaxter Acc. No. 352*; Type.—*Dispira americana*). CALIFORNIA. San Bernardino County: Cajon, January 5, 1958, isolated from mouse dung (RSA Culture 632); 3.5 miles south of Lytle Creek, September 7, 1958, isolated from dung (RSA Culture 712); 4 miles north of Cajon Pass, Mojave Desert, December 12, 1958, isolated from mouse dung (RSA Culture 757). Tulare County: 4.8 miles east of Springville, June 18, 1958, isolated from dung (RSA Culture 670). Transfers of RSA Cultures 632 and 670 have been deposited in the ATCC, CBS, and CMI.

Earlier in the present section, mention was made of the confusion surrounding the identity of *D. cornuta* subsequent to the description of this species by Van Tieghem (1875). Ayers (1933, 1935) has discussed the taxonomic history of the species in some detail and this will be summarized only briefly here.

Van Tieghem (1875) originally described the sporophore of *D. cornuta* as consisting of an erect stipe dichotomously divided above into two nearly equal spiral branches bearing numerous fertile branches terminated by spore heads. The fertile branchlets were said to bear usually one or two horn-like sterile branchlets and the spore heads presumably consisted of small globose vesicles subtending numerous two-celled sporiferous branchlets. Van Tieghem did not verbally describe spore formation or give the number of spores per spore chain, but in his illustration of the fertile head (Van Tieghem, 1875, Pl. 4, fig. 175) he depicted a single chain of about six spores produced terminally on the upper cell of each sporiferous branchlet. *Dispira* was not encountered again until 1895 when Thaxter, studying material obtained from rat dung which had been collected in Ohio, described *D. americana*. The latter species presumably differed from *D. cornuta* in that its sporophore branched with a false dichotomy and often gave rise to more than two fertile branches. Also, the two-celled sporiferous branchlets of the fertile heads of *D. americana* produced two-spored rather than six-spored chains not only on the apex of the upper cell but also in whorls of several chains on the upper angles of both cells. Bainier (1906 a) reported that he had studied a *Dispira* collected in the vicinity of Paris which did not differ essentially from the species described by Thaxter. As a result of his studies, Bainier concluded that Van Tieghem had erred in his interpretation of the fruiting head of *D. cornuta* and that the latter species and *D. americana* are conspecific.

In 1926, Elliott, without reference to the work of Thaxter or Bainier, described another species of *Dispira*, *D. circinata*, from England. The sporophores of this species were said to differ from those of *D. cornuta* by producing up to five or six rather than two fertile branches and several spore chains instead of only one on the cells of the sporiferous branchlets. In her illustration of the spore head of *D. circinata*, Elliott (1926, Fig. 1 b) shows sporiferous branchlets composed of only one cell. Elliott did not discuss the developmental morphology of her species, and she gave no indication as to whether or not her description was based on a study of living material

or dried herbarium specimens (she states that the species appeared on a sheep dung culture in the zoological laboratory at Birmingham in June, 1922—nearly three years prior to the publication of the description of *D. circinata* in April, 1926).

From his rather detailed cultural study of *Dispira*, Ayers (1933, 1935) demonstrated a range of structural variability in his material that led him to conclude that the above three species, *D. cornuta*, *D. americana*, and *D. circinata*, represent, in reality, a single species which must be recognized under the original name, *D. cornuta*. The present writer is in complete accord with Ayers. A *Dispira* corresponding to the one described and figured by Bainier (1906 a, Pl. XII, fig. 1-5) from the environs of Paris (presumably the locality of Van Tieghem's original collection of *D. cornuta*) has been reported from Ohio (Thaxter, 1895), Massachusetts (Ayers, 1933, 1935), and China (Ou, 1940); the writer also has found the same species in California. Thus, it is evident that this species is very widely distributed. The difference in the number of fertile branches stressed by Van Tieghem (1875) for *D. cornuta* and by Elliott (1926) for *D. circinata* is of no taxonomic value, for when *D. cornuta* is grown in culture, the number of branches produced by the sporophores is quite variable and commonly ranges from as few as two to as many as five or six. The discrepancy in the number of spores per merosporangium reported in the literature—several by Van Tieghem (1875) and Elliott (1926), only two by Thaxter (1895), Bainier (1906 a), Ayers (1933, 1935), and Ou (1940)—can not be explained directly. However, the writer has studied living material of five other species of Dimargaritaceae in addition to *Dispira cornuta*, and two-spored merosporangia are characteristic of all of these. My work has shown that one must study early developmental stages of the fertile head in order to interpret properly the true nature of the merosporangia in members of this family. In *Dimargaris* species, as we have seen, the branches and spores of the mature fertile heads disarticulate and form spore drops; in *Dispira*, however, the heads remain dry and the mature spores readily fall away when the fruiting structures are disturbed. Also, in the latter genus the cells of the sporiferous branchlets become more or less collapsed after they mature (Pl. 20 l), especially if the sporangiophores become desiccated. The illustration of the anomalous spore head of *D. circinata* published by Elliott very well may have been based on a study of preparations of material which had matured fully prior to storage in the herbarium for an extended period of time.

Ayers (1933) succeeded in growing *Dispira cornuta* in pure culture. He found that ordinary nutrient agar media were unsuitable for normal development of this fungus but that proteinaceous materials such as swordfish, meat, and especially egg yolk would support normal growth and sporulation in the absence of a host. Ayers found that several of the many agar media which he tested would support limited vegetative growth of *D. cornuta*, but only on a special synthetic Malt agar did even a trace of sporulation occur. The writer has not carried out a detailed program of testing like that of Ayers, but he has obtained essentially the same results with regard to the use of nutrient agar substrata. However, in a test carried out over the period January 12, 1958, to November 24, 1958, *Dispira cornuta* was grown in pure culture on

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PLATE 20. *Dispira cornuta* Van Tieghem.—a. Habit sketch showing general characteristics of fruiting structures. $\times 30$. b. Upper portion of young sporophore showing three fertile branches and the configuration of fertile and sterile branchlets. $\times 400$. c-e. Early stages in the development of fertile heads showing formation of sporiferous branchlets. $\times 1860$. f-j. Successive stages in the development of the sporiferous branchlets and merosporangia. $\times 1860$. k. Mature spores; note spore-pairs held together by the persistent sporangial wall. $\times 1860$. l. Portion of fertile branch showing fertile branchlets bearing sterile branchlets and terminal heads; the latter are seen in optical section after spores have fallen away. $\times 400$. m. Haustorium. $\times 1080$.

PLATE 20

ME-YE through four successive transfers; sporangiophores produced in these cultures were rather aberrant and spore production was meager, but spores produced under these cultural conditions retained their capacity to infect a susceptible host.

In 1935, Ayers reported the results of an extensive study of the host range of *Dispira cornuta* and he demonstrated that the species apparently is limited in its parasitism to members of the Mucorales.

All studies of the general morphology and development of *D. cornuta* carried out by the writer were made using cultures of the parasite grown on *Cokeromyces recurvatus* on YpSs or PDA. When cultivated on the above substrata at 21°C., *D. cornuta* usually begins to produce sporophores within 4-5 days. Germination of sporangiospores and development of the vegetative mycelium of *D. cornuta* takes place exactly as has been described above for *Dimargaris cristalligena*. The young sporophores at first are simple but give rise progressively to from two to as many as six fertile branches of which all but the last formed assume a lateral position with respect to the sporophore stipe (Pl. 20 *b*; Pl. 21 *a*). The fertile branches develop by a process of scorpioid sympodial branching in which the apparent main axes become more or less spirally twisted and bear short lateral recurved fertile branchlets bearing terminal spore heads (Pl. 20 *b*, *l*; Pl. 21 *a-b*). One or usually two sterile, eventually septate, lateral branchlets typically are produced by the fertile branchlets, and a septum is formed in the fertile branchlet immediately above the point of origin of each of the sterile branchlets (Pl. 20 *l*). Each fertile branch of the sporophore may give rise to as many as fifteen or more fertile branchlets before the former finally becomes greatly elongated and forms a slender, septate, sterile prolongation (Pl. 20 *a*).

The fertile heads of *Dispira cornuta* are composed of numerous two-celled sporiferous branchlets developed by budding over the entire surfaces of the swollen apices of the fertile branchlets (Pl. 20 *c-e*; Pl. 21 *e-f*). The upper cells of the sporiferous branchlets develop by budding from the basal and are soon separated from the latter by septa having the peculiar structure characteristic of members of the family. Merosporangia arise by budding from the tips of the upper cells and the upper angles of both cells of the sporiferous branchlets (Pl. 20 *g-i*; Pl. 21 *g-i*). In his original characterization of *D. americana*, Thaxter described the formation of a uniformly cylindrical merosporangium which became divided into two parts each of which formed a spore (Thaxter, 1895, Pl. 34, fig. 6-9). Through the kindness of Dr. I. Mackenzie Lamb, I have been permitted to study the type of *D. americana* on deposit in the Farlow Herbarium. Fortunately, this collection was dried before all the sporophores had matured fully and a study of immature spore heads present in this material has shown that the merosporangia of Thaxter's fungus actually developed acropetally in a manner exactly like that of the merosporangia of isolates of *D. cornuta* studied here (Pl. 20 *g-i*; Pl. 21 *g-i*).

At maturity, each sporiferous branchlet of *D. cornuta* bears distal whorls of several merosporangia (Pl. 20 *j*). The white spore heads (Pl. 20 *b*; Pl. 21 *j*) remain dry and the mature spores fall away at the slightest disturbance. The walls of detached mero-

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PLATE 21. *Dispira cornuta* Van Tieghem.—*a*. Upper portion of young sporophore. $\times 170$. *b*. Upper portion of nearly mature sporophore. $\times 115$. *c*. Typical cross-wall. $\times 1300$. *d*. Haustorium. $\times 1300$. *e-f*. Early stages in the development of sporiferous branchlets from terminal vesicular enlargements of fertile branchlets. $\times 1300$. *g*. Initial stage in the formation of a merosporangium. $\times 1300$. *h*. Slightly later stage of merosporangial formation showing acropetal development of the upper cell from the lower cell. $\times 1300$. *i*. Immature fertile head showing merosporangia in various stages of development. $\times 1300$. *j*. Mature fertile head before spores have fallen away. $\times 1300$. *k*. Two spores held together by the persistent sporangial membrane. $\times 1300$.

PLATE 21

PLATE 22. *a-d*. *Dispira cornuta* Van Tieghem.—*a-c*. Mature zygospores. *a*, $\times 310$; *b-c*, $\times 475$. *d*. Crushed zygospore showing punctate surface architecture. $\times 750$. *e-f*. *Dimargaris verticillata* Benjamin.—Mature zygospores. $\times 540$.

sporangia usually are somewhat persistent so that sporangiospores may remain associated in pairs for some time—even in liquid mounts (Pl. 20 *k*; Pl. 21 *k*).

In 1895, Thaxter also described and illustrated peculiar zygospore-like bodies formed following the fusion of the presumed vegetative hyphae of his *D. americana* with the sporangiophores of a species of *Mucor* (Thaxter, 1895, Pl. 34, fig. 10-13). Later, however, Thaxter (Blakeslee, 1904 b, p. 245) recognized that these presumed zygospores were, in reality, highly differentiated gall-like structures formed by the vegetative hyphae of the recently discovered mucoraceous parasite of other mucors, *Parasitella* (Bainier, 1903). Thaxter's original error, however, later was perpetuated by Fitzpatrick (1930) and Ou (1940); Zycha (1935) regarded the structures described by Thaxter as parasitic cells formed by the vegetative mycelium of *Dispira*.

Ayers described and figured zygospore-like bodies formed in many of his cultures of *D. cornuta* (Ayers, 1935, fig. 2 *c-j*) but was hesitant actually to regard these structures as true zygospores because he could not discover conjugation stages. In aging cultures of *D. cornuta* studied here, the writer also has found zygospore-like bodies like those described by Ayers (Pl. 22 *a-d*), and, like Ayers, he has not observed the direct formation of these structures from conjugating hyphae. In all instances, the large thick-walled spores are formed in terminal enlargements of lateral branches of

the vegetative hyphae so that the mature spores are borne on stalks having lengths which often may equal or exceed the diameters of the spores themselves. In view of the fact that these thick-walled bodies are formed in relatively specialized branches arising from a richly anastomosed vegetative mycelium and have a structure identical with that of the zygosporangia of other members of the Dimargaritaceae and Kickxellaceae, the writer considers that they probably are of sexual origin and they are here regarded as true zygosporangia.

Dispira simplex sp. nov.

(Plates 23, 24)

Coloniae in fimo albae vel in aetate "Pinkish Buff"; sporophoris rectis, 2-4 ramos fertiles in partibus superioribus gerentibus; ramis fertilibus sympodialibus, axes angulares gerentibus; axibus ad 10 vel plures ramusculos fertiles recurvos, 30-50 μ longos, ferentibus; ramusculis fertilibus 2-3 ramusculos sporogenos terminales, deinceps per gemmascentem gestis, gerentibus; ramusculis fertilibus per ramusculos steriles, singulos, attenuatos, simplices vel septatos, 35-85 μ longos, subtentis; sporophoris in aetate circa 3 mm. altis; stipitibus principalibus 0.5-1 mm. altis, 7-10 μ diam., in cellulis 100-200 μ longis consistentibus; ramusculis sporogenis, 11-13 $\mu \times 4.5$ -5.7 μ , per gemmascentem gestis, in 2 cellulis sporogenis subaequalibus consistentibus; cellulis sporogenis merosporangia de 2 sporis gerentibus; merosporangiis per gemmascentem gestis; sporis subglobosis vel ovoideis, 3-4 $\mu \times 2.8$ -3.5 μ , in aetate siccis; zygosporis ignotis.

Colonies on natural substrata (dung) white, becoming "Pinkish Buff" in age; sporophores erect, septate, giving rise above to 2-4 fertile branches, the latter at first often several times branched, each division more or less regularly sympodially branched, forming angular axes each bearing up to 10 or more recurved fertile branchlets, 30-50 μ long, terminated by usually three sporiferous branchlets formed successively by budding; fertile branchlets subtended by single narrowly attenuated, simple or septate, sterile branchlets 35-85 μ long; sporophores, in age, up to 3 mm. high, including sterile distal prolongations of the main axes; stipes below the fertile regions, 0.5-1 mm. long, 7-10 μ wide, composed of cells about 100-200 μ long, sporiferous branchlets formed by apical budding, 11-13 $\mu \times 4.5$ -5.7 μ , composed of two subequal cells bearing distal whorls of merosporangia containing two spores each; the terminal parts of the merosporangia developing by apical budding from the basal; spores subglobose to ovoid, 3-4 $\mu \times 2.8$ -3.5 μ , remaining dry at maturity; zygosporangia unknown.

Holotype.—CALIFORNIA. Los Angeles County: Evey Canyon, San Gabriel Mts., 4.5 miles northeast of Claremont, November 5, 1956, on mouse dung (RSA 6).

Other specimens examined.—CALIFORNIA. Los Angeles County: from the type locality—April 30, 1957, on mouse dung (RSA 8 and 9), May 10, 1957, on mouse dung (RSA 10); Dalton Canyon Camp Ground, San Gabriel Mts., 3 miles northeast of Glendora, March 26, 1957, on mouse dung (RSA 7); Claremont, May 29, 1958, on rat dung (RSA 11). Riverside County: Joshua Tree National Monument, about 10 miles southeast of Twentynine Palms, November 29, 1958, on rodent dung (RSA 13). All specimens have been deposited in the Mycological Collections of the Rancho Santa Ana Botanic Garden, Claremont, California.

This very distinct species has been collected several times and abundant material in all stages of development has been available for study. Unfortunately, the writer has not yet succeeded in growing the species in pure mixed culture.

As may be seen from the accompanying illustrations (Pl. 20, 21, 23, 24), the general habit of the sporophore of *D. simplex* is quite different from that of *D. cornuta*; the fertile branches of the latter species form more or less elongate, divergent, spirally coiled structures (Pl. 20 *a-b*; Pl. 21 *a-b*) whereas the angular fertile branches of *D.*

PLATE 23. *Dispira simplex* Benjamin.—*a.* Habit sketch showing general characteristics of fruiting structures. $\times 40$. *b.* Initial stages of development of a fertile branch showing origin of fertile and sterile branchlets. $\times 660$. *c-i.* Successive stages in the development of sporiferous branchlets and merosporangia from the apices of fertile branchlets. $\times 1860$. *j.* Portion of sporophore showing conformation of the branches of a fertile branch system. $\times 485$. *k.* Five mature spores. $\times 1860$.

simplex tend to be arranged in rather dense aggregates borne on branches which often project nearly at right angles from the main stipe (Pl. 23 *a, j*; Pl. 24 *a-b*).

The fertile branch of *D. simplex* develops by a process of sympodial branching in which the several branches of the first few divisions usually appear to be trichoto-

PLATE 24. *Dispira simplex* Benjamin.—*a*. Portion of fruiting structure showing three fertile branch systems. $\times 220$. *b*. The same showing a fertile branch system. $\times 560$. *c*. Sporiferous branchlets after the spores have fallen away. $\times 1300$. *d*. Merosporangia *in situ* on cells of sporiferous branchlets. $\times 1300$. *e*. Typical cross-wall. $\times 1300$. *f*. Sporophore stipe broken transversely through a cross-wall. $\times 1300$.

mously branched, forming, at each node, a fertile branchlet, a sterile branchlet, and a branch which continues the development of the axis (Pl. 23 *b, j*).

Unlike *D. cornuta*, each fertile branchlet of *D. simplex*, at maturity, is terminated by usually only three, rarely two, sporiferous branchlets. The first of these is formed terminally by budding (Pl. 23 *c-d*) and while still in early stages of development is separated from the fertile branchlet by a septum below which the second and third sporiferous branchlets arise laterally (Pl. 23 *e-g*). The cells of the sporiferous branchlets of *D. simplex* give rise, by budding, to distal whorls of merosporangia each of which delimits two subglobose to slightly ovoid sporangiospores (Pl. 23 *f-i, k*).

Tieghemiomyces gen. nov.

Sporangiophoris rectis, septatis, infra simplicibus, ramos fertiles in partibus superioribus gerentibus; ramis fertilibus septatis, deinceps inaequaliter subverticillatis, multas extentiones steriles gerentibus; ramis ultimis fertilibus, in paucis cellulis uniseriatis fertilibus consistentibus; cellulis fertilibus merosporangia de 2 sporis in verticillis distalibus gerentibus; sporangiosporis subglobosis vel ovoideis, levibus, in aetate siccis; zygosporis de muris crassis, hyalinis, punctatis.

Sporangiophores erect, septate, simple below, giving rise above to fertile branch systems; branches septate, several times irregularly subverticillately branched, with many free terminations, the ultimate branches consisting of small numbers of superposed fertile cells, each cell giving rise distally to whorls of two-spored merosporangia; sporangiospores smooth, subglobose to ovoid, remaining dry at maturity; zygosporis thick-walled, hyaline, punctate.

Type species:

Tieghemiomyces californicus sp. nov.

(Plates 25, 26)

Coloniae in *Cokeromyces recurvatus* in agaro YpSs albae vel in aetate "Pinkish Buff"; hyphis vegetantibus 2-4.5 μ diam.; sporophoris rectis, in juvenate simplicibus, 1-2 ramos fertiles divaricatos septatos infra 3-4 septa in partibus superioribus gerentibus; ramis fertilibus; sporophoris in aetate ad 3 mm. altis; stipitibus principalibus 325-625 μ altis, 7-10 μ diam., in cellulis 60-150 μ longis consistentibus; ramusculis sporogenesis in 1-3 vel 4 cellulis consistentibus; cellulis sporogenesis merosporangia de 2 sporis gerentibus; merosporangia per gemmascentem gestis; sporis globosis vel nonnihil ovoideis, 3-3.5 $\mu \times$ 3.5-4 μ , in aetate siccis; zygosporis globosis, hyalinis, de muris crassis, punctatis, 35-57 μ (med. 45 μ) diam., globulos singulos excentricos, 18-30 μ diam., continentibus; muro 5-8 μ (med. 6.7 μ) crasso.

Colonies on *Cokeromyces recurvatus* on YpSs white, becoming "Pinkish Buff" in age; vegetative hyphae colorless, septate, branched, 2-4.5 μ in diameter; haustoria at first simple, often somewhat clavate, becoming more or less lobate and developing numerous short branchlets about 1.5-3 μ wide, up to 20 μ long; sporophores erect, septate, at first simple, forming, immediately below each of the distal 3-4 septa, 1-2

PLATE 25. *Tieghemiomyces californicus* Benjamin. — *a*. Habit sketch showing general characteristics of fruiting structures. $\times$ 30. *b-c*. Immature and mature haustoria respectively. $\times$ 1080. *d*. Base of sporophore stipe. $\times$ 495. *e*. Terminal portion of young sporophore showing origin of lateral branches. $\times$ 300. *f*. Terminal portion of sporophore showing conformation of developing fertile branch systems. $\times$ 485. *g*. Single fertile branch system showing origin and arrangement of sporiferous branchlets. $\times$ 750. *h*. Young sporiferous branchlet showing origin of merosporangia from fertile cells. $\times$ 1860. *i-k*. Three mature sporiferous branchlets showing disposition of merosporangia. $\times$ 1860. *l*. Mature spores. $\times$ 1860. *m*. Mature zygosporis as seen in optical section showing origin of zygosporangium around the point of fusion of an undifferentiated sexual branch with the hypha from which the branch arose. $\times$ 400.

PLATE 25

divergent, septate, fertile branches, the latter 2-5 times irregularly subverticillately branched, the ultimate or sporiferous branchlets consisting of 1-3, rarely 4, superposed cells bearing distal whorls of merosporangia; sporophores, in age, up to 3 mm. or more high, including simple, sterile, septate prolongations of the stipes and often the main axes of the fertile branches; stipes, below the fertile regions, about 325-625 μ long, 7-10 μ wide, composed of cells about 60-150 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, 3-3.5 $\mu \times$ 3.5-4 μ , remaining dry at maturity; zygospores developed from the conjugation of short undifferentiated hyphal branches with similar vegetative hyphae, globose, colorless, thick-walled, 35-57 μ (aver. 45 μ) in diameter, uniformly sculptured with small circular pits, containing, when mature, usually single, large, eccentric, refractive globules 18-30 μ in diameter; wall 5-8 μ (aver. 6.7 μ) thick.

Holotype.—CALIFORNIA. Los Angeles County: Evey Canyon, San Gabriel Mts., 4.5 miles northeast of Claremont, April 28, 1956, isolated from mouse dung (RSA Culture 467).

Other specimens examined.—CALIFORNIA. Los Angeles County: from the type locality—April 28, 1956, on mouse dung (RSA Culture 469), February 13, 1957, on mouse dung (RSA Culture 524), March 5, 1957, on mouse dung (RSA Cultures 534 and 535). Riverside County: Joshua Tree National Monument, about 10 miles southwest of Twentynine Palms, November 29, 1958, on mouse dung (RSA Culture 748). San Bernardino County: Jenk's Lake, San Bernardino Mts., about 10 miles east of Camp Angelus, July 26, 1957, on mouse dung (RSA Culture 584); same locality—September 27, 1958, on dung (RSA Culture 728). Transfers of RSA Cultures 467, 584, and 748 have been deposited in the ATCC, CBS, and CMI.

This species, like the other known members of the Dimargaritaceae studied here, is a vigorous parasite of other Mucorales, but it also grows saprobically and reproduces, sexually and asexually, in a nearly normal manner on an ordinary medium such as ME-YE.

In its general vegetative and reproductive characters, *Tieghemiomyces* obviously is closely allied to *Dimargaris* and *Dispira*. *Tieghemiomyces californicus* has been separated generically from *Dimargaris* and *Dispira* because of the very distinct branching pattern of its sporophores. The fruiting hyphae of *Dimargaris* become cymosely (Pl. 13 a, d) or irregularly verticillately (Pl. 17 a-b; Pl. 18 a, l) branched and the branches are terminated by few or many sporiferous branchlets which may or may not be subtended by vesicles; sporophores of known members of this genus lack sterile branchlets. The fertile branches of *Dispira* develop by a process of sympodial branching which gives rise to one or more apparent main axes bearing numerous fertile branches terminated by spore heads (Pl. 20 a-b, l; Pl. 21 a-b; Pl. 23 a-b, j); in this genus, sterile branchlets may arise from the fertile branchlets themselves or from the main axes of the fertile branches. As in *Dimargaris*, the sporiferous branchlets of known species of *Dispira* may or may not be subtended by vesicles. In *Tieghemiomyces californicus*, one or sometimes two divergent branches arise immediately below several of the distal septa of the young sporophore; these lateral branches elongate, become septate, and give rise in turn to irregular whorls of shorter branchlets (Pl.

PLATE 26. *Tieghemiomyces californicus* Benjamin.—a. Germinating spores $\times$ 560. b. Germ hypha showing characteristic cross-wall. $\times$ 1300. c. Photograph showing separation of the fertile region of the sporophore following the dissolution of the stipe along a line of dehiscence formed immediately below the lowest fertile branch system. $\times$ 1000. d-f. Early, intermediate, and late stages in the development of the fertile region of the sporophore. $\times$ 235. g. Typical cross-wall. $\times$ 1300. h. Portion of fertile branch system showing sporiferous branchlets and merosporangia. $\times$ 1300. i. Optical section of mature zygospore. $\times$ 740. j. Zygospore as seen in surface view. $\times$ 740.

PLATE 26

25 *e*; Pl. 26 *d*). This process of subverticillate branching continues and finally each of the original lateral branches of the young sporophore is transformed into a more or less arborescent fertile branch system (Pl. 25 *g-f*; Pl. 26 *e-f*) in which the ultimate branches produce merosporangia and correspond to the sporiferous branchlets of *Dimargaris* and *Dispira*. As a rule, the proximal branches of each fertile branch system are more highly ramified than the distal and the latter often may function directly as sporiferous branchlets. The usually simple sporiferous branchlets consist of from one to as many as three or four superposed cells each giving rise, by budding, to distal whorls of two-spored merosporangia (Pl. 25 *b-k*; Pl. 26 *b*).

As the fruiting structures of *T. californicus* mature, the main axes of the sporophores elongate distally and form slender, septate prolongations which may become 2-3 times longer than the stipes subtending the fertile regions; occasionally the main axes of the fertile branch systems become similarly prolonged (Pl. 25 *a*).

When the sporangiophore of *T. californicus* matures, the stipe separates by circumscissile rupture at a point immediately below the proximal fertile branch (Pl. 26 *c*). This separation is preceded by the formation, in the wall of the sporophore, of a distinct line of dehiscence which is in no way associated with a cross-wall. As a result of the above phenomenon, which has not been observed in other members of the Dimargaritaceae, the fertile branch systems of an entire mature colony of *T. californicus*, held together by the intertwined sterile prolongations of the sporophores, may be swept away in mass leaving only a stubble composed of the sporophore stipes. In nature, this unusual characteristic may be a factor in spore dispersal.

SPINALIA Vuillemin.

Bull. Soc. Mycol. France. 20: 32. 1904.

Sporangiophores erect or ascending, at first continuous, septate in age, simple or rarely branched, developing terminal vesicular enlargements bearing two-spored merosporangia (?) directly over their entire surfaces; spores smooth, ellipsoidal.

Type species: *Spinalia radians* Vuillemin (1904, p. 32).

SPINALIA RADIANs Vuillemin.

Bull. Soc. Mycol. France. 20: 32. 1904.

(Plate 27)

With the characters of the genus; sporangiophores yellowish; fertile vesicular enlargements of the sporophores nearly globose, 4-30 μ in diameter; terminal part of the merosporangium developing by apical budding from the basal; spores elongate-ellipsoidal, sub-equal, 4.4-6.8 $\mu \times$ 1.8-3 μ .

The above brief characterizations and the accompanying illustrations of *Spinalia radians* have been adapted from Vuillemin's original description. The species was described from material encountered in old preparations of *Mucor fragilis* parasitized by *Piptocephalis lemonnieriana*, and, like the latter species, *Spinalia radians* appeared also to have been parasitizing the mucor. All three of these fungi had been collected originally at Epinal, Vosges, France, April 17, 1900, growing together on sap flowing from the stump of a recently felled birch tree.

It is evident from the original account of *S. radians* that Vuillemin did not actually observe the mechanism, if any, by which the vegetative hyphae of this species penetrated the hyphae of its presumed host. Vuillemin states only that a scarcely evident thallus produces long, creeping, nonseptate stolons which eventually grow upward and form simple sporangiophores terminated by fertile heads. The mean diameter of the stolon ranges from about 1.5 μ at its origin to 4 μ at the fruiting extremity. The

diameter of the fertile vesicular enlargement of the sporophore does not exceed about $30\ \mu$. The presumed sporiferous elements arise nearly simultaneously by budding over the entire surface of the terminal swelling (Pl. 27 *a-c*). Each of these elongate-ovoid outgrowths, which measure about $4.4\text{--}5.6\ \mu \times 1.8\text{--}2.8\ \mu$, then gives rise, by apical budding (Pl. 27 *d*), to a second outgrowth which eventually attains a size nearly equal to that of the first (Pl. 27 *e*). Both parts of these bicellular outgrowths then become invested with walls; the terminal member of each pair is essentially indistin-

PLATE 27. *Spinalia radians* Vuillemin.—*a*. Early stage of development of fertile vesicular enlargement of sporophore. *b-e*. Successive stages in the development of the merosporangia on the terminal enlargements as seen in optical section. *f*. Portion of mature fertile head as seen in optical section; most of the terminal spores have fallen away. *g*. Aged fertile head after the spores have fallen away; note cross-wall with median lenticular cavity. (All figures after Vuillemin, Bull. Soc. Mycol. France 20: 26-33, Pl. II, 1904. Redrawn without change of magnification.)

guishable morphologically from the basal and becomes detached from the latter as soon as it is mature (Pl. 27 *f*). Finally, the basal member also falls away and its original position on the fertile vesicle is marked only by a small prominence. On the basis of their structure and manner of formation, the above deciduous bodies were thought by Vuillemin to be spores although their germination was not observed. Until *Spinalia radians* is rediscovered and the true nature of these spore-like bodies determined from a study of living material, it seems best to interpret these structures as spores.

Vuillemin found that secondary branches sometimes were formed by the stolon,

stipe, and even the fertile head of *S. radians*, and these branches occasionally produced heads similar to those formed by the primary sporophores. Cross walls "rarement renflées au milieu" were said to form in the fruiting hyphae of *S. radians* only after the fertile heads had fully matured.

In a rather extended discussion of interrelationships, Vuillemin concluded that *Spinalia* undoubtedly is a phycomycete and he allied the genus with *Dispira*, *Dimargaris*, and *Syncephalastrum*. Vuillemin went on to propose that all of the above genera and "sans doute" the genera *Martensella*, *Coemansia*, and *Coemansiella* (= *Kickxella*), be included in a separate series, *Dispirées*, of the Mucorales until their true family relationships within the order could be determined. Lendner (1908) and Fitzpatrick (1930) listed *Spinalia* as doubtfully belonging to the Piptocephalidaceae, whereas Zycha (1935) accorded the genus full status as a member of this family, Zycha, however, interpreted the bicellular elements of the fertile head of *Spinalia* as consisting of sterile "basalzellen" bearing single spores terminally. Naumov (1935, 1939), who accepted a bisporous interpretation of the outgrowths of the fertile heads of *Spinalia*, placed the genus in a separate family, the Spinaliaceae⁵, allied to the Cunninghamellaceae. Hesseltine listed *Spinalia* only as a probable member of the Mucorales with unknown affinities.

As Hesseltine (1955) points out, until *S. radians* is rediscovered and the true nature of the vegetative and fruiting structures determined, this species can not be classified precisely. The conflicting opinions of Zycha and Naumov, cited above, regarding the sporiferous elements of *Spinalia* illustrate very clearly the need for a clarification of the nature of the spore bearing structures in the genus. I have included *S. radians* in the Dimargaritaceae because the ontogeny of the presumed sporiferous elements of this species resembles that of the merosporangia of most species of this family, and, also, like all known members of the Dimargaritaceae, both elements of these bicellular structures are finally deciduous. However, early development of the latter structures is very similar to that of the sporiferous elements borne on the sporocladia of members of the Kickxellaceae (Benjamin, 1958). In all known species of the latter family, however, the terminal parts of the bicellular outgrowths of the sporocladia are transformed into sporangiola containing single spores, whereas the basal parts are sterile and nondeciduous.

According to Vuillemin's description, the fruiting hyphae of *S. radians* would appear to be considerably more generalized than in other members of the Dimargaritaceae and in the Kickxellaceae. Septa presumably are absent in the young fruiting hyphae of *Spinalia* and, reminiscent of *Syncephalastrum* and many members of the Mucoraceae, form only after the spore bearing heads have matured. Vuillemin stated that occasionally the septa are swollen in the middle and one of his figures (see Pl. 27 g) shows a cross wall—subtending an old fertile vesicle—with a median lenticular cavity very similar in appearance to the type found in the septa of all members of the Dimargaritaceae and Kickxellaceae.

Although *Spinalia radians* was based on preserved and apparently scanty material, Vuillemin's description of the fungus seems to me to be sufficiently detailed so that the species may reasonably be allied provisionally with the Dimargaritaceae, especially in the light of more complete knowledge of the several genera of fungi to which Vuillemin himself related the species.

⁵Characterized as new by Naumov (1935) but without a Latin diagnosis and, therefore, not published validly according to Article 34 of the International Code of Botanical Nomenclature (Lanjouw *et al.*, 1956).

KICKXELLACEAE

INTRODUCTION

As mentioned earlier, for many years the relationships of several genera of mucor-like fungi, *Kickxella* Coemans (1862), *Martensella* Coemans (1863), *Coemansia* Van Tieghem and Le Monnier (1873), *Dimargaris* Van Tieghem (1875), *Dispira* Van Tieghem (1875), and *Spinalia* Vuillemin (1904), were in doubt. Although in many respects phycomycetous in habit, most representatives of the above genera are characterized by regularly septate hyphae and erect sporophores which have a growth form very similar to that of many Fungi Imperfecti. Also, the number of spores per merosporangium is reduced to one or two, and the merosporangia usually develop by a process of apical budding analogous to conidial formation in some Hyphomycetes. Thus, in the absence of a definitive knowledge of sexuality, the above genera were for many years variously classified either in the Hyphomycetes or Zygomycetes (see p. 326 for references). In 1943, however, Linder presented direct evidence of zygospore formation in *Coemansia* and placed this genus together with *Kickxella* and *Martensella* in a new family, the Kickxellaceae. A discussion of sexuality in this family was the subject of a recent paper by the writer (Benjamin, 1958). The characteristics of *Dimargaris* and its allies were considered in the previous section of this paper; the characteristics of the Kickxellaceae and its included genera are reviewed briefly below.

Whereas most of the known species of the Dimargaritaceae are vigorous parasites of other Mucorales or only weakly saprobic, nearly all of the known species of the Kickxellaceae appear to be typically saprobic and commonly occur in dung, humus, or other organic materials. *Martensella pectinata* Coemans (1863), known only from its original description, was thought by Coemans to be growing parasitically on species of Mucoraceae and Saprolegniaceae. *Martensella corticii* Thaxter ex Linder (1943) never has been grown in culture and, although not yet proven, parasitism of this species on another fungus is suspected, for *M. corticii* has been found in nature growing only on the hymenium of a single species of Basidiomyceteae, *Corticium radiosum* Fries (Jackson and Dearden, 1948). *Coemansia reversa* Van Tieghem and Le Monnier (1873) frequently has been encountered, presumably growing parasitically, on the synnemata of coprophilous isarioid fungi (Bainier, 1906 b; Linder, 1943), and all specimens of *C. reversa* in the Thaxter Herbarium at Harvard are represented by material which had developed on the white synnemata of fungi listed as species of *Isaria* by Linder (1943). The writer has isolated an unidentified isarioid fungus (RSA Culture 752) very similar to the ones represented in Thaxter's collections, and this species has been grown in pure mixed culture with *C. reversa*. Although the latter species develops sporophores in profusion in company with the former, I have not been able to demonstrate that the hyphae of *C. reversa* actually penetrate the hyphae of the hyphomycete. *Coemansia reversa*, like all other members of the Kickxellaceae—except *Martensella corticii*—studied by the writer, readily grows and sporulates in pure culture, and the author has maintained two strains of this species on ordinary media such as YpSs and PAB-DEX for several years (see also Thaxter, 1895, p. 517; Farrow, 1954; Agnihothrudu, 1957). Parasitism of any species of Kickxellaceae on other fungi has not yet been proven.

Germinating sporangiospores of *Coemansia* (Benjamin, 1958, Pl. 1 *m-n* and Pl. 4 *k-l*), *Kickxella* (l.c., Pl. 8 *d-f*), and *Spirodactylon* typically give rise to one or two germ hyphae produced laterally near the central part of the spore, whereas the germ tubes of *Linderina* (Pl. 29 *b*) and *Martensiomyces*, although lateral, arise near the base of the spore. Spore germination in *Martensella* has not been observed, but it probably proceeds as in *Coemansia*.

The hyphae of all known members of the Kickxellaceae become septate very early in their development, and all septa of both vegetative and fruiting hyphae possess median plugs (Pl. 28 *a*; Pl. 29 *c*; Pl. 31 *c*; Pl. 33 *d*) very similar to those formed in the septa of species of the Dimargaritaceae. As in the latter family, the sporophore wall of members of the Kickxellaceae is double, consisting of a thicker inner layer which divides the sporophore into elongate cells and a thinner outer layer which is continuous throughout the length of the sporophore; the septa are compounded of the apposed end walls of adjacent cells (Pl. 28 *b*). Although they often may be somewhat biumbonate, the septal plugs of representatives of the Kickxellaceae never have the conspicuous bead-like polar protuberances characteristic of all known species of the Dimargaritaceae. As stated earlier, in members of the Kickxellaceae the plugs are more or less persistent in solutions of acid or base and may be rather deeply stained by such dyes as Aniline blue, Carmine, and Phloxine (Pl. 28 *a*). In all species of the Dimargaritaceae studied, the plugs are dissolved completely in 2-3% KOH or in acidic fixatives or mounting media.

The hyaline or light colored, usually yellowish, often minutely asperulate, simple or branched fruiting structures of members of the Kickxellaceae give rise to highly specialized sporiferous branchlets (sporocladia) bearing numerous one-spored sporangia produced singly by apical budding on small ovoid or flask-shaped cells (pseudophialides). The sporocladia of *Coemansia* (Pl. 28 *l*; Benjamin, 1958, Pl. 1 *c* and Pl. 4 *c*), *Kickxella* (l.c., P. 7 *b-i*), *Martensella* (Pl. 29 *g*), *Martensiomycetes* (Pl. 31 *f*), and *Spirodactylon* (Pl. 32 *d*) are more or less elongate, finger-like, septate structures which produce pseudophialides and sporangia laterally on one surface. The sporocladia of *Linderina* (Pl. 29 *e*; Pl. 30 *b*) are nonseptate, subglobose, and bear pseudophialides crowded on their upper, or outer, surfaces. In *Coemansia*, *Linderina*, *Martensella*, and *Spirodactylon*, the sporocladia arise acrogenously, but, by the continued growth of the fertile axes, become diffusely arranged along the fertile branches and appear pleurogenous; the sporocladia of *Kickxella* (Benjamin, 1958, Pl. 7 *c-i*) are formed simultaneously and are arranged in verticils on the apices of the sporophore branches; the sporocladia of *Martensiomycetes* are produced successively, as in *Coemansia*, but the fertile axes usually do not elongate and the sporocladia are arranged in terminal umbels (Pl. 31 *b, d-e*).

Zygospores have been observed in three genera of the Kickxellaceae, *Coemansia*, *Kickxella*, and *Spirodactylon*, and are nearly identical in structure and manner of formation to those of representatives of the Dimargaritaceae. In both families, differentiated sexual hyphae are absent, and the zygosporangium develops from the conjugation of hyphae which can not be distinguished morphologically from branches of the vegetative mycelium. Zygosporangium formation in *Coemansia* and *Kickxella* was described and illustrated in detail in my earlier paper (Benjamin, 1958).

KICKXELLACEAE Linder.

Farlowia 1 (1): 56. 1943.

Vegetative mycelium submerged, consisting of delicate, hyaline, branched, thin-walled, regularly septate hyphae; fruiting structures white or light-colored, erect or ascending, simple or branched, septate, relatively thick-walled, forming sessile or stalked, septate or nonseptate sporiferous branchlets (sporocladia) bearing deciduous unispored sporangia acrogenously on small, hyaline, ovoid or elongate-ellipsoid, nondeciduous cells (pseudophialides); sporangiole wall delicate, persistent; sporangiospores simple, hyaline or yellowish, ovoid, elongate-ellipsoid, or fusoid, enveloped in liquid at maturity or remaining dry; septa of both the vegetative and fruiting hyphae characteristically with median disciform cavities containing colorless biconvex

or biumbonate plugs; zygospores formed from the fusion of similar hyphae, thick-walled, hyaline or yellowish, usually containing several refractive globules.

Type genus: *Kickxella* Coemans (1862, p. 155).

A KEY TO THE GENERA

- A. Sporocladia globoid, nonseptate.....*Linderina* (p. 405)
- AA. Sporocladia elongate, usually attenuated distally, septate..... B.
  - B. Spores ellipsoidal, only slightly longer than broad; fertile region of the sporangiophore coiled.....*Spirodactylon* (p. 408)
- BB. Spores elongate, more than twice as long as broad; fertile region of the sporangiophore not coiled..... C.
- C. Sporocladia pleurogenous..... D.
- CC. Sporocladia verticillate or umbellate..... E.
  - D. Sporangiola borne on the upper surfaces of the sporocladia.....*Martensella* (p. 402)
- DD. Sporangiola borne on the lower surfaces of the sporocladia.....*Coemansia* (p. 399)
- E. Sporocladia verticillate, formed simultaneously.....*Kickxella* (p. 399)
- EE. Sporocladia umbellate, formed successively.....*Martensiomycetes* (p. 406)

KICKXELLA Coemans.

Bull. Soc. Royale Bot. Belgique, 1: 155.⁶ 1862.

Coronella Crouan and Crouan, Florule du Finistère, p. 12, 1867.

Coemansiella Saccardo, Sylloge Fungorum, 2: 815. 1883.

Sporangiophores erect or ascending, septate, at first simple, becoming irregularly cymosely branched and forming apical whorls of sporocladia; the latter elongate, arcuate, septate, producing numerous pseudophialides arranged in more or less transverse rows on their upper surfaces; pseudophialides ellipsoidal to elongate-ovoid, bearing single sporangiola terminally; sporangiospores fusiform, smooth, immersed in liquid at maturity; zygospores smooth, thick-walled, hyaline.

Type species: *Kickxella alabastrina* Coemans (1862, p. 155).

The reader is referred to my earlier paper on the Kickxellaceae (Benjamin, 1958) for illustrations and a discussion of the history and characteristics of the type and only known species of *Kickxella*.

COEMANSIA Van Tieghem and Le Monnier.

Ann. Sci. Nat. Bot., Sér. 5, 17: 392. 1873.

(Plate 28)

Sporangiophores erect or ascending, septate, simple or regularly or irregularly branched; branches forming sporocladia acrogenously; sporocladia becoming laterally disposed by the continued growth of the fertile axes and appearing pleurogenous, stalked, elongate, nearly straight, arcuate, or slightly sigmoid, septate, producing pseudophialides arranged in more or less transverse rows on their lower surfaces; pseudophialides ellipsoidal to elongate-ovoid, bearing single sporangiola terminally; sporangiospores elongate-elliptical to fusiform, smooth, immersed in liquid at maturity; zygospores smooth, thick-walled, hyaline or yellowish.

Type species: *Coemansia reversa* Van Tieghem and Le Monnier (1873, p. 392).

Subsequent to the description of *Coemansia reversa* by Van Tieghem and Le Monnier and prior to the publication of Linder's monograph in 1943, three additional

⁶Citation of p. 153 in my earlier paper (Benjamin, 1958, p. 160) was an error.

species of *Coemansia* were described, i.e., *C. spiralis* Eidam (1888), *C. pectinata* Bainier (1906 b), and *C. erecta* Bainier (1906 b). Bainier had reported *C. spiralis* in 1879, but he described the species under the name *Martensella* (*Coemansia*) *spiralis*. Thus, Eidam, apparently independently, was the first to use the binomial, *C. spiralis*, and he must be credited with authorship of the species (Linder, 1943). For many years, Dr. Thaxter collected and often cultured species of *Coemansia* and related genera, and, at the time of his death, his herbarium, deposited in the Farlow Herbarium, contained material representing several species which had not been characterized. From a study of Thaxter's specimens, Linder (1943) described nine new species of *Coemansia*: *C. aciculifera*, *C. braziliensis* Thaxter, *C. breviramosa*, *C. ceylonensis*, *C. guatemalensis* Thaxter, *C. interrupta*, *C. kamerunensis* Thaxter, *C. scorpioidea*, and *C. thaxteri*. The writer's collection of Kickxellaceae presently includes over seventy isolates of *Coemansia* representing about fifteen species; one of these, *C. mojavenensis*, recently was described as new (Benjamin, 1958). Detailed study of all of the available material has not been completed, and the taxonomy of *Coemansia* will not be discussed at this time. The reader may consult Linder's monograph for the most recent treatment of the genus.

In *Coemansia mojavenensis*, the young sporocladium is initially uninucleate (Pl. 28 c). The first division of this nucleus takes place near the base of the young sporocladium with the spindle oriented approximately along the long axis of the sporocladium (Pl. 28 d). A cross-wall then is formed which separates the sporocladium into a small uninucleate basal cell and an elongate terminal cell (Pl. 28 e). The nucleus of the latter cell divides as shown in Pl. 28 f and a second cross-wall separates the proximal from the distal nucleus. A succession of similar nuclear divisions followed by the formation of cross-walls results in a sporocladium composed of a series of several superposed uninucleate cells (Pl. 28 g). The basal (stalk) and terminal cells of the sporocladium typically are sterile although the latter occasionally may form single pseudophialides and sporangiola terminally. All of the intercalary cells are fertile and each gives rise, on its lower surface, to a succession of small, ovoid, uninucleate cells, the pseudophialides. Preceding the formation of each pseudophialide, the nucleus in the fertile cell divides (Pl. 28 h-i); one nucleus remains in the fertile cell and the other migrates into the young pseudophialide (Pl. 28 j) which then is separated from the fertile cell by a septum. Each pseudophialide gives rise, by budding, to a terminal cell, the sporangiole initial (Pl. 28 k). The pseudophialide nucleus divides and one of the daughter nuclei migrates into the young sporangiole. Just as the cells of the sporocladia are formed acropetally, so, too, are the pseudophialides and sporangiola, and sporangiola may be in various stages of development on the proximal fertile cells of the young sporocladium while pseudophialides are still in early stages of development on the distal cells (Pl. 28 k). When mature, the sporangiola containing uninucleate sporangiospores (Pl. 28 l) are deciduous and are soon enveloped in a drop of liquid; the pseudophialides, as in all known species of Kickxellaceae, are non-deciduous (Pl. 28 m).

Sporocladium development in *Kickxella alabastrina* is essentially like that found in *Coemansia mojavenensis*. In the former species, however, each of the usually two

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PLATE 28. a-b. *Coemansia* sp. (RSA Culture 371).—a. Typical cross-wall showing persistent median plug. (Treated with KOH-Phloxine and then washed with dilute acetic acid.) $\times 1300$. b. Preparation in chlor-iodide of zinc showing double nature of the septum and sporophore wall. $\times 1300$. c-m. *Coemansia mojavenensis* Benjamin.—Nuclear cycle accompanying the development of sporocladia, pseudophialides, and sporangiola. Explanation is in the text. c-j, $\times 2100$; k-m, $\times 1300$.

PLATE 28

fertile cells of the sporocladium contains several nuclei. The nuclear cytology of sporocladial development in *Martensella*, *Martensomyces*, and *Spirodactylon* has not yet been studied; it is very probable, however, that the nuclear cycle in representatives of these genera will prove to be like that found in members of the closely related *Coemansia*.

Two distinct patterns of zygospore development have been found in *Coemansia* (Benjamin, 1958). In *C. aciculifera*, the zygospore is initiated by the fusion of small gametangia delimited apically by two usually relatively short undifferentiated sexual branches. The zygosporangium enlarges as a more or less lateral bud-like outgrowth within which the thick-walled zygospore is differentiated (Benjamin, 1958, Pl. 2-3). In contrast with the above mechanism of zygospore formation, the zygosporangium of *C. mojavensis* and *C. braziliensis* develops from an intercalary cell delimited in an undifferentiated sexual branch near the point of fusion of the branch with an ordinary vegetative hypha (Benjamin, 1958, Pl. 5 and Pl. 6 a-c).

MARTENSELLA Coemans.

Bull. Acad. Royale Sci., Lett., et Beaux-Arts Belgique, Sér. 2. 15: 540. 1863.

(Plate 29 f-i).

Sporangiophores erect or ascending, septate, simple or irregularly branched above; sporocladia formed acrogenously, becoming laterally disposed by the continued growth of the main axis of the sporangiophore and appearing pleurogenous, stalked, elongate, arcuate, septate, producing pseudophialides arranged in more or less transverse rows on their upper surfaces; pseudophialides ellipsoidal, bearing single elongate-ovoid or fusiform sporangiola at their apices.

Type species: *Martensella pectinata* Coemans (1863, p. 540).

The type species of this genus is known only from Coemans' original description of material presumably growing parasitically on the hyphae of members of the Mucoraceae and Saprolegniaceae. The generic name commemorates M. M. Martens, Professor in the University of Louvain, and the specific epithet describes the character of the fertile hyphae. On the basis of the description given by Coemans, *M. pectinata* may be characterized briefly as follows:

Vegetative hyphae scanty, colorless, septate, anastomosed, attached to the host by short rhizoids; sporophores gray to yellow or greenish, erect or ascending, subflexuous, sparingly branched, rarely simple, septate, 0.5-1 mm. tall, 7-9 μ in diameter; sporocladia divaricate, distant, arranged in loose spirals on the sporophores, usually one per cell-segment, stalked, navicular, arcuate, attenuated distally, composed of (6-) 10-12 cells excluding the stipe; pseudophialides paired on the upper surfaces of the sporocladia, ovoid, bearing single fusiform spores 8-9 μ long, or, more rarely, on some sporocladia, chains of small oval spores 2-3 μ long.

Rediscovery of this species is highly desirable, for the production of two kinds of sporocladia, one bearing single elongate spores and the other chains of smaller spores, has not been observed in any other member of the family. According to Coemans, the chains of spores appeared to be formed by segmentation of the fusiform spores.

The only other species referred to the genus *Martensella* is the anomalous *M. cor-*

PLATE 29. a-e. *Linderina pennispora* Raper and Fennell.—a. Two detached sporangiola. $\times 1300$. b. Germinating spore showing lateral origin of germ hypha from basal part of spore; note septum. $\times 1000$. c. Typical cross-wall. $\times 1300$. d. Terminal portion of sporophore showing acropetal development of sporocladium. $\times 320$. e. Mature sporocladium. $\times 790$. f-i. *Martensella corticii* Thaxter ex Linder.—f. Sporophores on hymenium of host, *Corticium radiosum* Fries. $\times 310$. g. Terminal portion of sporophore; the oldest sporocladium is at the right. $\times 1000$. h. Detached sporangiolium. $\times 1300$. i. Presumed chlamydospores. $\times 1300$.

PLATE 29

ticii Thaxter ex Linder (1943; Pl. 29 *f-i*), which recently was the subject of detailed study by Jackson and Dearden (1948) who showed that it is widely distributed throughout North America on *Corticium radiosum* Fries. The fungus appears to be an obligate parasite growing on the hymenium of this common basidiomycete, a species which typically produces its corticioid fructifications on the lower surface of its substrate. Jackson and Dearden reasoned that the pendent habit of growth of *M. corticii* on its resupinate host accounts for the apparent position of the pseudophialides on the upper surface of the sporocladia, and they concluded that the species probably should be considered a *Coemansia*. They questioned whether or not *Coemansia* and *Martensella* should be maintained as distinct genera, but they did not make nomenclatural changes.

The status of *Martensella* as a genus depends on the validity of the type species, *M. pectinata*, and, pending the rediscovery of this species, the description and illustrations of it given by Coemans will have to serve as the basis for the acceptance of the genus. As pointed out by Linder (1943, p. 51), subsequent studies have shown that Coemans' description of *Kickxella alabastrina* is acceptable, and as yet there is no real evidence against the acceptance of his *Martensella pectinata*. *Martensella corticii* may, with further study, prove to be a *Coemansia* which has evolved an altered morphology due to its development on a resupinate host, but no such anomalous habitat was given for *M. pectinata*. The latter species was said to have an erect or ascending growth habit with the spores definitely borne on the upper surface of the sporocladia. Jackson and Dearden state that the separation of *Martensella* and *Coemansia* as distinct genera simply on the basis of the position of the pseudophialides on the upper or lower surface of the sporocladia may be artificial and may be conditioned by the position of the fungus on its substrate. The writer twice has found *Coemansia scorpideae* Linder growing on dead insects affixed to the lower surfaces of dead logs, and no alteration in the typical coemansoid pattern of sporocladial development was observed in this species growing under such conditions. In addition, the author has studied numerous species of *Coemansia* growing in pure culture and, contrary to the suggestion of Jackson and Dearden (1948, p. 175), the random orientation of pseudophialides in any direction as a result of the diffuse arrangement of the sporocladia has not been observed. The spores of species of *Coemansia* are produced on the lower surfaces of the sporocladia with respect to the development of the latter on the branches of the sporangiophores. In several species of *Coemansia*, the writer has observed an occasional anomalous sporocladium in which the pseudophialides and spores of a single fertile cell are produced on the upper surface as in *Martensella*. Van Tieghem and Le Monnier (1873, p. 389, Pl. 25, fig. 133) described similar anomalies in *Kickxella*. The segregation of species of Kickxellaceae with pleurogenous sporocladia into separate genera on the basis of the uniform production of pseudophialides and spores on the upper or lower surfaces of the sporocladia is, in my opinion, justified, and until good evidence to the contrary is found, I believe that *Martensella*, based on *M. pectinata*, should be retained.

Jackson and Dearden (1948) described smooth, thick-walled, subglobose bodies about 10-20 μ in diameter associated with the vegetative hyphae of all of the more than thirty strains of *Martensella corticii* which they studied. Because these structures often occurred in chains of 2-5 and because there was no evidence of a union of hyphal branches prior to their formation, Jackson and Dearden interpreted these bodies as chlamydospores of asexual origin. This would seem not to be the only possible interpretation, however. An alternative explanation, which thus far has not been ruled out by any observational evidence, is that these so-called chlamydospores are actually the products of fusion of compatible nuclei within coenocytic segments of a

hypha. In this connection it is significant that structures very similar to those termed chlamydospores in *Martensella corticii* by Jackson and Dearden (Pl. 29 *i*) have been shown, on morphological grounds, to be zygospores in *Coemansia* (Benjamin, 1958, Pl. 3 *d* and Pl. 5 *g*), *Kickxella* (l.c., Pl. 8 *m*), and members of the Dimargaritaceae.

PLATE 30. *Linderina pennispora* Raper and Fennell.—*a*. Habit sketch showing general characteristics of the fruiting structures. $\times 4$. *b*. Upper portion of fruiting branch showing acrogenous formation of a sporocladium and the ultimate disposition of the sporocladia on the fertile axis. $\times 400$. *c-d*. Early stages in the development of the sporocladium. $\times 900$. *e*. Immature sporocladium with all but three young sporangia and pseudophialides removed. Note variation in shape and size of the lateral and terminal pseudophialides. $\times 900$. *f-l*. Successive stages in the acrogenous development of the unispored sporangium. $\times 1360$. *m*. Pseudophialide after the sporangium has been shed; note the apical collar-like projection representing the basal part of the sporangial wall. $\times 1360$.

LINDERINA Raper and Fennell.

Amer. Jour. Bot. 39(1): 81. 1952.

Colonies effuse, mucoroid; sporangiophores erect, simple or irregularly branched above in the fertile area; sporocladia sessile, formed acrogenously, becoming lateral by the continued growth of the fertile axes and appearing pleurogenous, nonseptate, ovoid or dome-shaped, producing pseudophialides crowded over their upper surfaces; pseudophialides ellipsoidal, bearing single elongate-obclavate sporangia at their apices; sporangia enveloped in liquid at maturity; zygospores unknown.

Type species: *Linderina pennispora* Raper and Fennell (1952, p. 83).
With a single species.

LINDERINA PENNISPORA Raper and Fennell.

Amer. Jour. Bot. 39 (1): 83. 1952.

(Plates 29 *a-e* and 30)

Colonies on YpSs or PDA near "Maize Yellow" or "Apricot Yellow"; vegetative hyphae colorless, septate, about 5-8 μ wide; sporangiophores yellowish, more or less erect, septate, delicately asperulate, up to 1 cm. or more high, irregularly branched above with the branches mostly fertile or a few sterile and often stoloniferous; sporangiophore segments of the main stalk below the fertile region 130-230 μ long $\times$ 10-15 μ wide; sporocladia usually alternate, typically arranged in a zigzag pattern on the fertile axes, usually one per cell-segment; intersporocladial distance 30-70 μ ; sporocladia sessile, asperulate, nonseptate, ovoid or dome-shaped, 15-30 μ wide $\times$ 12-25 μ high, bearing pseudophialides crowded over their upper surfaces; pseudophialides ellipsoidal, 6-8 μ $\times$ 2-2.8 μ ; sporangiola nearly hyaline, elongate-obclavate, 17.5-21.5 μ (aver. 19.5 μ) long $\times$ 3.5-4.5 μ wide near the base; sporangial wall projecting about 2 μ beyond the apex of the spore as a hyaline enlargement having a diameter about equal to the greatest diameter of the spore; sporangiospores 15.5-19.5 μ (aver. 17.5 μ) long $\times$ 3.5-4.5 μ wide near the base, uniformly tapered to the acute apices, rounded and abruptly truncate below.

Specimen examined.—LIBERIA. Vicinity of Monrovia, isolated from forest soil, March, 1950 (NRRL 2237—*Type*).

The unique sporocladium of *Linderina pennispora* readily distinguishes this species from all other known members of the Kickxellaceae. As in species of *Coemansia*, *Martensella*, and *Spirodactylon*, the sporocladium of *L. pennispora* is formed acrogenously, but it soon becomes lateral as the main axis of the sporophore grows out immediately below it and continues to elongate and produce additional sporocladia (Pl. 29 *d*; Pl. 30 *b*). Each successive sporocladium usually is slightly smaller than the one preceding it. Prior to pseudophialide formation, the young sporocladium of *L. pennispora* contains several nuclei (I have not yet succeeded in demonstrating a uninucleate stage in the development of the young sporocladium of this species). The nuclear cycle accompanying the development of pseudophialides and sporangiola in *L. pennispora* is exactly like that described above for *Coemansia mojaviensis*.

MARTENSIOMYCES Meyer.

Bull. Soc. Myc. France 73 (2): 189. 1957.

Colonies effuse; sporangiophores arising from submerged vegetative hyphae, erect or ascending, becoming irregularly cymosely branched with many free ends; sporocladia stalked, formed successively, borne in umbels on recurved branchlets, nearly straight or slightly curved, producing pseudophialides arranged in more or less transverse rows on the lower surfaces; pseudophialides ellipsoidal, bearing single elongate-obclavate sporangiola distally, the latter enveloped in liquid at maturity; zygospores unknown.

Type species: *Martensiomycetes pterosporus* Meyer (1957, p. 190).
With a single species.

MARTENSIOMYCES PTEROSPORUS Meyer.

Bull. Soc. Mycol. France 73 (2): 190. 1957.

(Plate 31)

Colonies on YpSs near "Yellow Chrome"; vegetative hyphae colorless, septate,

irregularly branched, about $4.5\ \mu$ wide, producing a bright yellow pigment which diffuses into the substrate; sporangiophores erect or ascending, becoming cymosely branched, septate, smooth, up to 2 mm. high, with the cells of the lower portion of the main stalk about $30\text{--}80\ \mu$ long $\times$ $7\text{--}10\ \mu$ wide; sporangiophore branches usually alternately sterile and fertile; sterile branches elongate, septate, usually more slender than the main axes, those arising from the lower portion of the sporophore often becoming spirally wound around neighboring hyphae; fertile branches short, $40\text{--}80\ \mu$ long, recurved, usually 1- or 2-celled, bearing terminal umbels of about 6-12 (aver. 9) stalked sporocladia produced successively; sporocladial stipe slightly tapered, $18\text{--}35\ \mu$ (aver. $25\ \mu$) long $\times$ $3.5\text{--}5\ \mu$ wide at the middle; sporocladia smooth, tapered, composed of 4-5 cells, usually 4, excluding the stipe, $16\text{--}25\ \mu$ (aver. $20\ \mu$) long $\times$ $6\text{--}8\ \mu$ wide at the base, turned back sharply on the stipe, nearly straight, the sterile apical cell slightly recurved; pseudophialides ovoid, $3\text{--}4\ \mu \times 2\ \mu$, arranged on the fertile cells in usually two more or less transverse rows of 3-7 pseudophialides each; sporangiola pale yellow, elongate-obclavate, $12.5\text{--}17\ \mu$ (aver. $15.5\ \mu$) long $\times$ $3\text{--}3.5\ \mu$ wide near the base; sporangiole wall projecting $1\text{--}1.5\ \mu$ beyond the apex of the spore as a hyaline enlargement having a diameter about equal to the greatest diameter of the spore; sporangiospores $12\text{--}16\ \mu$ (aver. $14\ \mu$) long $\times$ $3\text{--}3.5\ \mu$ wide near the base, uniformly tapered to the acute apices, rounded and abruptly truncate below.

Specimen examined.—BELGIAN CONGO. Yangambi, isolated from forest soil, October, 1954, J. Meyer, isolate 3863 (*Type*). Subcultures of the type, on deposit at CBS and CMI, were obtained for study.

In age, the fruiting structures of *Martensiomycetes pterosporus* may become rather highly branched, and the aerial portion of the colony consists of a densely interwoven turf up to 2 mm. deep. Many of the sterile branches produced by the sporophores, especially immediately above the surface of the substrate, become tightly coiled in a tendril-like manner around neighboring hyphae. Although there are many irregularities, the branching of the sporophore follows a more or less regular pattern so that the main axis typically bears, alternately, long sterile branches followed closely by shorter fertile branches (Pl. 31 *a*) which in turn produce the distal umbels of sporocladia (Pl. 31 *a-b, e*).

In his description of this very distinct and unusual species, Meyer interpreted the sporocladia as giving rise to the pseudophialides and spores on the upper surface as in *Kickxella* and *Martensella*. In reality, the spores are borne on what morphologically is the lower surface of the sporocladium as in *Coemansia*. This fact is obscured in *Martensiomycetes* because, unlike *Coemansia*, the fertile axis does not normally continue to elongate as sporocladia are produced, and the successively formed sporocladia (Pl. 31 *d*) remain closely associated on the slightly swollen extremity of the fertile branch (Pl. 31 *e*). The coemansoid nature of the sporocladium of *Martensiomycetes* is readily discerned, however, in sporocladia which occasionally are borne singly or in pairs on the lower cells of fertile branches (Pl. 31 *b*, lower branch). Here the development and orientation of the sporocladia with respect to the axis of the sporophore are exactly as in *Coemansia*.

The sporangiola of *M. pterosporus* (Pl. 31 *g*) are nearly identical in appearance to those of *Linderina pennisporea* (Pl. 29 *a*; Pl. 30 *l*), and the spores of both species germinate in the same manner, i.e., the germ hyphae arise near the base of the spore (Pl. 29 *b*) rather than near the middle as in *Kickxella*, *Coemansia*, and *Spirodactylon*.

Spirodactylon gen. nov.

Sporangiophoris rectis vel ascendentibus, septatis, simplicibus vel ramosis, ramos spirales fertiles in partibus superioribus gerentibus; sporocladia acropetale gestis et deinceps in superficiebus inferioribus spirarum latis; sporocladia stipitatis, septatis, attenuatis, cellulis intercalaribus plerumque ordines transversos vesicularum sporigerarum in superficiebus interioribus gerentibus; vesiculis sporigeris ovoideis ad apices repente attenuatibus; sporangiolis singulis, brevis-ellipsoideis, in aetate siccis; zygosporis globosis, de muris crassis, globulos parvos continentibus.

Sporangiophores erect or ascending, septate, simple or branched, giving rise distally to coiled fertile branches of few to many turns; sporocladia formed acrogenously, becoming pleurogenous by the continued growth of the main axes and borne successively on the lower surfaces of the coils; sporocladia stalked, septate, with narrowed apices, the intercalary cells producing pseudophialides arranged in more or less transverse rows on their inner faces; pseudophialides ovoid, with narrowed apices bearing single short-ellipsoidal sporangiola, the latter not enveloped in liquid at maturity; zygosporis globose, thick-walled, containing small globules.

(Etym.: *σπειρα*, that which is coiled + *δάκτυλος*, a finger)

Type species:

Spirodactylon aureum sp. nov.

(Plates 32 and 33)

Coloniae in agar CM in temperatura aeris lente crescentes, in aetate prope "Pinard Yellow"; hyphis vegetantibus 2-8 μ diam.; sporangiophoris sparsis vel gregariis, rectis vel ascendentibus, septatis, minute asperulatis, simplicibus vel di- vel trichotomis in partibus superioribus; stipitibus ad 2 mm. altis, in cellulis 100-250 $\mu \times 7-14 \mu$ consistentibus; axibus principalibus vel ramis in partibus superioribus trichotomis, in 1 ramo minuto inconspicuo et 2 ramis elongatis consistentibus; ramis elongatis plerumque 2 raro 3-4 ramos fertiles spirales gerentibus, ramis in 3-25 vel pluribus gyris consistentibus; spiris 35-320 μ longis $\times$ 30-45 μ diam. in hyphis septatis asperulatis, 4-6 μ diam., consistentibus; hyphis sporocladias in superficiebus inferioribus gerentibus; sporocladia circa 15-25 μ (med. 20 μ) distantibus, in cellula vulgo 3-4 (in gyro circa 4); 1-2 spiris fertilibus secundariis vulgo in extensionibus spirarum fertilium gestis; extensionibus ad 1.5-2 mm. longis; spiris fertilibus tertiariis raro in extensionibus spirarum secundariarum gestis; sporocladia asperulatis, saepe rectis, 15-25 $\mu \times$ 4.4-5.2 μ , in 4 cellulis consistentibus; cellulis basalibus sterilibus, 2-3 $\mu \times$ 3-4 μ ; cellulis terminalibus plerumque sterilibus, attenuatis, 7-12 μ longis; cellulis intercalaribus subaequalibus, 2 ordines plerumque transversos 2-3 vel 4 vesicularum sporigerarum in superficiebus interioribus gerentibus; vesiculis sporigeris 3.5 $\mu \times$ 2.4 μ , sporangiola singula terminalia ferentibus; sporangiolis ellipsoideis, levibus, 4.6 $\mu \times$ 3.3 μ ; zygosporis globosis, hyalinis, levibus, 20-45 μ (med. 33 μ) diam., 2-8 globulis 2-16 μ diam. continentibus; muro 3-9 μ (med. 6.8 μ) crasso.

Colonies on CM developing slowly at room temperature, near "Pinard Yellow"; vegetative hyphae colorless, septate, irregularly branched, about 2-8 μ wide; spor-

PLATE 31. *Martensiomycetes pterosporus* Meyer. — a. Habit sketch showing general characteristics of the fruiting structures. $\times 60$. b. Upper portion of fruiting branch showing configuration of branches and sporocladia; note coemansoid habit of the sporocladium borne on the basal cell of the lower fertile branch. $\times 450$. c. Cross-wall. $\times 2720$. d. Terminal portion of fertile branch showing successive formation of sporocladia. $\times 1200$. e. Terminal portion of mature fertile branch showing umbellate arrangement of sporocladia. $\times 800$. f. Terminal portion of a sporocladium showing slightly immature sporangiola borne singly on small flask-shaped pseudophialides. $\times 1325$. g. Mature sporangium. $\times 2720$.

PLATE 31

angioophores scattered or gregarious, erect or ascending, septate, minutely asperulate, simple or once or twice di- or trichotomously branched above; stalk up to 2 mm. high, composed of cells $100-250\ \mu$ long $\times$ $7-10\ \mu$ wide; the main axis of the sporangio-phore or its branches trichotomous distally, one arm of each trichotomy reduced to an inconspicuous protuberance, the others giving rise immediately to two, rarely three or four, regularly coiled fertile branches of 3-25 or more turns each; coils about $35-320\ \mu$ long $\times$ $30-45\ \mu$ wide; hyphae composing fertile coils septate, asperulate, $4-6\ \mu$ wide, bearing sporocladia on their lower surfaces; sporocladia more or less evenly spaced, about $15-25\ \mu$ (aver. $20\ \mu$) apart, about 3-4 per cell-segment (usually four per gyre); one, rarely two, secondary fertile coils usually produced distally by prolongations of primary coils; prolongations variable in length to as much as 1.5-2 mm.; tertiary fertile coils rarely produced by prolongations of secondary coils; sporocladia asperulate, nearly straight, $15-25\ \mu \times 4.4-5.2\ \mu$, consisting of four cells; the basal cells sterile, slightly more broad than long, $2-3\ \mu \times 3-4\ \mu$; the terminal cells usually sterile, $7-12\ \mu$ long, the distal two-thirds abruptly attenuated; the two subequal intercalary cells each bearing on their inner faces, 5-8 pseudophialides disposed in two nearly transverse rows of 2-3 or 4 pseudophialides each; pseudophialides $3.5\ \mu \times 2.4\ \mu$, abruptly narrowed and bearing single sporangiola terminally; sporangiola short-ellipsoidal, smooth, mostly $4.6\ \mu \times 3.3\ \mu$, the sporangial wall everywhere adnate to the spore; zygospores nearly hyaline, smooth, thick-walled, globoid, $20-45\ \mu$ (aver. $33\ \mu$) in diameter, containing 2-8 refractive globules $2-16\ \mu$ in diameter; wall $3-9\ \mu$ (aver. $6.8\ \mu$) thick.

Holotype.—CALIFORNIA. San Bernardino County: Mojave Desert, 4 miles northeast of Cajon Pass, December 12, 1958, isolated from mouse dung (RSA Culture 791).

Other specimens examined.—CALIFORNIA. Los Angeles County: 5 miles west of Camp Baldy, January 1, 1954, isolated from rat dung collected by D. H. Ford (RSA Culture 273). San Bernardino County: southeast slope of Mt. San Antonio, San Gabriel Mts., September 22, 1955, isolated from dung (RSA Culture 458); near Cajon, January 5, 1958, isolated from mouse dung (RSA Culture 648); from the type locality, December 12, 1958, isolated from mouse dung (RSA Culture 792). Transfers of the holotype have been deposited in the ATCC, CBS, and CMI.

In the structure and development of its sporocladia, *Spirodactylon aureum* is very similar to species of *Coemansia* and *Martensella*; however, in the opinion of the writer, the unique habit of the fertile branches of *S. aureum* warrants generic status in the Kickxellaceae. Typically, the coiled fertile branches are associated in groups of four (Pl. 32 *a-b*), each group consisting of two pairs of dichotomies produced by two arms of a trichotomous branch system. One arm of the latter seems always to abort and is represented only by a small protuberance subtending the other two (Pl. 32 *b*). Each member of a pair of coils is a mirror image of the other, and both coils develop at the same rate. Likewise, each pair of coils is a mirror image of the pair opposite it (Pl. 32 *b*). Whereas the pattern of development described above is the one most commonly encountered, there are variations, and, occasionally, three or even four coils are produced by one or both of the subtending branches.

Successive sporocladia are produced acrogenously by the fertile hyphae as the latter advance in their spiral courses (Pl. 33 *c*). Each young sporocladium soon becomes pendent from the lower surface of the parent hypha with its long axis directed slightly

PLATE 32. *Spirodactylon aureum* Benjamin. —*a*. Habit sketch showing general characteristics of the fruiting structures. $\times 20$. *b*. Upper portion of a sporophore showing configuration of the fertile branches. $\times 200$. *c*. Coiled fertile branch showing arrangement of the sporocladia. $\times 580$. *d*. Sporocladium showing pseudophialides and sporangiola. $\times 2100$.

PLATE 32

forward and inward with respect to the gyre of the coil. Sporocladia mature progressively as in *Coemansia*. A basal septum separates the young sporocladium from the main axis, and successive septa, laid down acropetally, delimit the short stipe and the cells of the fertile region (Pl. 32 *d*). With regard to their orientation on the hypha of a fertile branch, the sporocladia give rise to the pseudophialides on their inner faces so that the sporangiola are borne within the coil (Pl. 32 *c*; Pl. 33 *a-b*).

Unlike other known members of the family, the spores of *S. aureum* are not immersed in liquid at maturity. After producing coils of as few as three to as many as twenty-five or more gyres, all of which are fertile, the branches may abruptly cease producing sporocladia and become extended into prolongations which often reach lengths of as much as 2 mm. These hyphal extensions usually give rise to single shorter secondary fertile coils exactly like the primary coils from which the prolongations arise, even with regard to the direction of coiling (Pl. 32 *c-d*). When, occasionally, a prolongation dichotomizes and gives rise to a pair of fertile coils (Pl. 32 *b*, center above), one coil is dextrorse and the other sinistrorse.

Early stages of zygospore formation have not been observed in *Spirodactylon aureum*; the mature zygospores (Pl. 33 *e*) are similar in appearance to those produced by species of *Coemansia*.

DISCUSSION

INTRODUCTION

One of the primary objectives of this investigation has been to extend our knowledge of the natural relationships not only of the merosporangiferous Mucorales but also of this group with the Mucorales as a whole. It is difficult to separate this objective from the elaboration of a hypothetical phylogeny of the order, for the pattern of relationships between living species presumably is an expression of the evolutionary history of the group. The comparative morphological data gained during the course of this study, however, provide evidence which can be used much more reliably for devising a natural system of classification of the merosporangiferous group than for tracing its phylogeny.

To know the phylogeny of the Mucorales we would require, in addition to the evidence of comparative morphology, a fossil record and perhaps genetic and cytogenetic data on relationships at the species level. The fossil record would be needed to fill in the gaps caused by extinction. Cytogenetic evidence might reveal the extent to which the phylogenetic pattern is reticulate due to the hybrid origin of some phylogenetic lines. However, we have neither type of evidence in the Mucorales at present.

From a study of comparative morphology it is possible to draw conclusions regarding the possible primitiveness or advancement of various morphological characters, and, although such conclusions often may be rather arbitrary, these do provide a basis for speculation on probable phylogenetic relationships.

In trying to make as much use as possible of the comparative morphological evidence that is available, the writer, like other students of the fungi, has been involved inevitably in considerations of phylogeny. He has attempted, however, to keep the speculations about phylogeny to a minimum, while utilizing the available evidence to block out as natural a system as possible of the modern groups.

In the Mucorales our present systems of classification (Zycha, 1935; Naumov, 1935, 1939; Hesseltine, 1955) are based almost entirely upon the characteristics of sexual and asexual reproductive structures. To a lesser extent, use has been made of physiological and ecological phenomena; cytological and genetical data are almost

entirely lacking and are still of little value in determining interrelationships within the order (see Cutter, 1942 a, b; Sjöwall, 1945). Hesseltine (1952) suggested that the known genera of Mucorales probably represent at least six more or less distinct lines of evolution; in the opinion of the writer the scheme outlined by Hesseltine (1952, p. 212), which is essentially like that of Gäumann (Gäumann and Wynd, 1952), Naumov (1935), and others, best represents the natural relationships of the Mucorales on the basis of present knowledge and his arrangement is adopted here.

PLATE 33. *Spirodactylon aureum* Benjamin.—*a-b*. Coiled fertile branch as seen in surface view (*a*) and in optical section (*b*). $\times 340$. *c*. Upper portions of three fertile branches showing configurations of developing sporocladia. $\times 560$. *d*. Typical cross-wall. $\times 1300$. *e*. Zygospore. $\times 1300$.

LINES OF EVOLUTION IN THE MUCORALES

THE MUCOR LINE

The Mucoraceae, with some thirteen genera (Hesseltine, 1955), is the largest family in the Mucorales, and its members are, for the most part, relatively unspecialized both morphologically and physiologically. The wide-spreading, rapidly-growing vegetative mycelium usually consists of robust hyphae which typically are nonseptate during early stages of development. Simple imperforate septa are formed to delimit reproductive structures and to wall off senescent portions of the mycelium as the bulk of physiologically active protoplasm flows out of mature into growing hyphae (Buller, 1933, pp. 150-158). Sporangiphores are simple or branched and, like the vegetative hyphae, are nonseptate during early stages of development; septa, often irregularly disposed, may be laid down in the fruiting hyphae as the latter age. Stolons and rhizoids are formed by members of several genera. In most species, nondeciduous, columellate, more or less globose or ovoid sporangia delimit relatively large numbers of spores; sporangiola typically are absent. The usually delicate sporangial wall may be fugacious or persistent, but it usually is not strongly cutinized. The mature spores may remain dry or become immersed in liquid. Zygospores of members of the family typically are relatively large, thick-walled, rough, and dark-colored at maturity and they usually are formed between nearly equal, morphologically differentiated, opposed suspensors developed above the substratum on aerial hyphae. Most species of Mucoraceae are saprobic and grow on a wide variety of organic substrata; a few species are facultative parasites of other fungi.

THE THAMNIDIUM-CUNNINGHAMELLA LINE

This line of evolution includes two families, Thamniaceae and Cunninghamellaceae. In all members of these families (Hesseltine, 1955) the characteristics of the vegetative mycelium and structure and manner of formation of the zygospores are essentially like those in the Mucoraceae. Representatives of this group differ from those of the latter family primarily in the production of more highly specialized sporangiphores which bear sporangiola of various kinds with or without an accompanying *Mucor*-type sporangium.

In the Thamniaceae, terminal, columellate, *Mucor*-like sporangia may or may not be present on the simple or branched sporangiphores of species of *Thamnidium*, *Helicostylum*, and *Chaetostylum*, whereas terminal multispored sporangia are absent in *Cokeromyces*, *Chaetocladium*, and *Radiomyces* (Embree, 1959). However, members of this family always give rise to sporangiola produced on simple or ramiform branchlets borne singly or in clusters, laterally or terminally, on the main axes of the sporangiphores. Some of the branches associated with sporangiola in *Chaetostylum* and *Chaetocladium* are sterile and form spine-like prolongations; in the other genera of the family sterile sporophore branchlets are absent. In all of the above genera except *Chaetocladium* the sporangiola delimit several spores; the sporangium of *Chaetocladium* always contains but one spore and the sporangial wall may be readily distinguished from the spore proper. *Chaetocladium* species are facultative parasites of other Mucorales; the other known species of the family are saprobes.

The Cunninghamellaceae⁷ includes at least three genera, *Cunninghamella*, *Tham-*

⁷When Naumov (1935, p. 16) proposed this family he did not provide a Latin diagnosis. According to Article 34 of the International Code of Botanical Nomenclature (Lanjouw *et al*, 1956), the name was not validly published, and the name has not been validated in subsequent treatments of the family (Naumov, 1939; Cutter, 1945; Hesseltine, 1955). On the basis of present knowledge, the inclusion of *Cunninghamella*, *Thamnocephalis*, and *Mycotypha* in a sepa-

nocephalis, and *Mycotypha* (Hesseltine, 1955), all species of which are saprobic. Here multispored sporangia and sporangiola are unknown, and only one-spored sporangiola borne on the surfaces of globose or elongate terminal vesicles are produced. The wall of the sporangium can not be (or at least has not been) distinguished from that of the spore, but there is little doubt that the sporangium of members of the Cunninghamellaceae is the homologue of the unispored sporangium of genera such as *Chaetocladium* and *Choanephora*. The sexual stage of *Thamnocephalis* and *Mycotypha* still is unknown, and recently Wolf (1957) concluded that the only known species of the latter genus, *M. microspora* Fenner (1932), may not be a phycomycete but possibly should be classified with the Dematiaceae. The writer questions this opinion in view of the fact that *M. microspora* is readily attacked by many species of Piptocephalidaceae and Dimargaritaceae.

THE CHOANEPHORA LINE

The Choanephoraceae^s includes a single genus, *Choanephora*, with several species (Hesseltine, 1953; Poitras, 1955; Hesseltine and C. R. Benjamin, 1957) that may be weakly parasitic on higher plants although they also are saprobic and occur in soil. Vegetatively, *Choanephora* resembles members of the Mucoraceae. The genus is characterized, however, by the production of not only columellate many-spored sporangia but also one- or few spored sporangiola. Sporangia and sporangiola always are borne on separate stalks. The ovoid, usually brownish sporangiospores characteristically are longitudinally striate and bear long, stiff, hyaline appendages at their apices. Zygospores of *Choanephora* are formed in or at the surface of the substrate and arise from the fusion of nearly equal gametangia developed by closely appressed tongs-like suspensors borne at the tips of more or less entwined hyphal branches. The thick-walled, dark-colored zygospores are nearly smooth in outline but possess delicate striations similar to those found on the walls of the sporangiospores; the zygosporangium is thin-walled, smooth, and nearly colorless.

THE PILOBOLUS LINE

The Pilobolaceae includes two coprophilous genera, *Pilobolus* and *Pilaira* (Buller, 1934; Hesseltine, 1955), which lack sporangiola and have somewhat flattened multi-spored sporangia with thin hyaline lower walls and thick, black, highly cutinized upper walls. In both genera, the sporangium possesses a well-defined columella, and in *Pilobolus* the sporangium is subtended by a hyaline turgid swelling which eventually ruptures violently and may propel the sporangium a distance of several feet (Buller, 1934, p. 63). Although highly modified, the sporangium of *Pilobolus* and *Pilaira* is fundamentally like that of members of the Mucoraceae.

rate family seems entirely justified. Accordingly, the following diagnosis is presented in order to validate the family name:

Cunninghamellaceae Naumov fam. nov.

CUNNINGHAMELLACEAE Naumov, Opređelitel' Mukorovykh (Mucorales), p. 16. 1935 (nomen nudum)

Hyphis vegetantibus expansis, ramosis, nonseptatis vel in aetate septatis; sporangiophoris rectis vel ascendentibus, simplicibus vel ramosis, sporangiolis de 1 sporis in terminalibus vesiculis globosis vel elongatis gestis; sporangiolis levibus vel echinulatis; zygosporis globosis, episporio scabri; hyphis sexualibus approximate aequalibus, oppositis.

Type genus: *Cunninghamella* Matruchot, Ann. Mycol. 1: 46. 1903.

^sHesseltine (1955, p. 360) attributes this family to Fitzpatrick (1930) emended by Naumov (1939). Authorship of the family undoubtedly should be credited to Brefeld (1881, p. 161) who used the Choanephoreen (as well as Thamnidieen, which Hesseltine, 1955, p. 352, accepts) as one of his five families of Zygomycetes. The family Choanephoraceae also was included by Schroeter (1897, p. 131) in his treatment of the Mucorineae in Engler and Prantl, Die natürlichen Pflanzenfamilien.

Zygospores of the Pilobolaceae (Buller, 1934; Lyr, 1954) are nearly globose, smooth or slightly roughened, pale or brownish in color, and are formed between apposed, tongs-like suspensors which initially may be coiled around one another; the zygospores are produced in or near the surface of the substrate. In early stages of development, the pilobolaceous zygospore resembles that of species of *Phycomyces*, *Choanephora*, and *Piptocephalis*, and, as in the first two genera, it is formed in the entire space occupied by both of the fused gametangia rather than in a bud-like outgrowth of the fused gametangia as in *Piptocephalis*. The suspensors of *Pilobolus* and *Pilaira* lack appendages, and the wall of the zygospore proper is not striate.

THE MORTIERELLA-ENDOGONE LINE

The degree of affinity between the two families, Mortierellaceae and Endogonaceae, tentatively included in this evolutionary series is by no means certain. In both groups the vegetative mycelium is initially coenocytic but may become more or less septate in age and is mucoraceous in character; the mycelium of most members of the Mortierellaceae consists usually of very slender and delicate hyphae which produce a creeping, highly anastomosed aerial mycelium which, in culture, often develops an extensive, compact turf. In representatives of the latter family, the delicate, thin-walled sporangium, which may contain one, two, or few to many spores, usually lacks a well-defined columella, and of the three or four genera included in the Mortierellaceae (Hesseltine, 1955), *Mortierella* is the best known (Linnemann, 1941). The zygospores which have been reported in a few species of this genus are smooth-walled, yellowish or brownish in age, borne between tongs-like suspensors, and enveloped, at maturity, by dense mycelial overgrowths. In addition to sporangia, several species of *Mortierella* produce highly modified acrogenous chlamydospores (stylospores) on short branches of the vegetative hyphae. Species of Mortierellaceae are mostly saprobic and commonly are found in soil; some may be weakly parasitic on other fungi. Van Tieghem (1875, p. 97, Pl. 2, fig. 82) reported the parasitism of *Mortierella polycephala* Coemans on species of *Pilobolus*, and he described appressoria and intramatrix haustoria very similar to those characteristic of *Syncephalis* species.

The Endogonaceae (Thaxter, 1922) as presently understood may include only a heterogenous assemblage of apparently saprobic species, many of which are hypogaeous. The best known genus of the family, *Endogone*, may be more closely related to *Mortierella* than to other members of the Mucorales. However, both columellate and noncolumellate sporangia have been reported in species included in *Endogone*. Only sporangia lacking columellae have been found in *Endogone malleola* Harkness and *E. reniformis* Bresadola (Thaxter, 1922; Walker, 1923), whereas Kanouse (1936) reported *Mucor*-like, columellate sporangia in cultures of *E. sphagnophila*. Because of the above differences, Miss Kanouse proposed that *E. malleola* and *E. reniformis* be transferred to a new genus, *Modicella*, and placed in the Mortierellaceae. Kanouse believed that the *Mucor*-like sporangia associated with her presumed pure cultures of *E. sphagnophila* indicated a close affinity of the Endogonaceae with the Mucoraceae. The highly derived character of the zygospore in *Endogone* would seem to argue against this point of view, however. Like *Mortierella*, many species of Endogonaceae produce large, thick-walled, highly specialized acrogenous chlamydospores. Zygospores have been described for several species of *Endogone* and are formed in a manner recalling that found in *Piptocephalis* and *Syncephalis*, with apposed suspensors and the zygosporangium arising as a bud-like enlargement from one of the fused gametangia or between and above the fused gametangia. Like *Piptocephalis*, gametangial remnants may be present on the mature zygospore of species of *Endogone*. The three types of spores—sporangiospores, chlamydospores, and zygospores—en-

countered in the Endogonaceae are produced, usually in scattered masses, inside loosely or tightly interwoven aggregates of hyphae termed sporocarps. No species is yet known to form the three types of spores in one sporocarp, and only a few species are known to produce both chlamydospores and zygospores in a common fruiting structure.

Although certain vegetative and reproductive characters of members of the above evolutionary series resemble those of representatives of the Piptocephalidaceae especially, the writer believes that these similarities are the result of parallel evolution.

THE PIPTOCEPHALIS-KICKXELLA LINE

The final line of evolution discussed by Hesseltine (1952) included the Piptocephalidaceae with four genera, *Dispira*, *Piptocephalis*, *Syncephalis*, and *Syncephalastrum*, and the Kickxellaceae, also with four genera, *Coemansia*, *Kickxella*, *Linderina*, and *Martensella*. The history and characteristics of the above and several other related genera have been discussed in some detail in the main text of this paper. During the course of this study additional information regarding the characteristics of several previously poorly known or even unknown members of this group of fungi has led the writer to recognize four rather than two families which seem better to represent the true natural relationships of these fungi.

MORPHOLOGICAL CHARACTERS

In most treatments of the Mucorales, the forms presently included in the Mucoraceae are considered to be the most generalized and, thus, are thought probably to represent the most primitive living representatives of the order. The rate of evolution of various morphological characters has varied greatly in the different evolutionary lines and, as a result, only a few families display a predominance of primitive or advanced characters. Morphological characters in the Mucorales may be discussed under the following major headings:

MYCELIUM

In most species of Mucorales, the germinating sporangiospore gives rise to one or several germ hyphae which soon produce an extensive, nonseptate, multinucleate mycelium ramified throughout the substratum. Septa typically are formed only to delimit reproductive structures—chlamydospores, sporangia, gametangia—or to seal off segments of hyphae which have suffered mechanical injury or have otherwise evacuated the main mass of their protoplasm due to the formation of reproductive structures or aging (Buller, 1933). Asexual fruiting structures may arise directly from submerged or aerial hyphae; the latter often may be differentiated into well-defined stolons and rhizoids. Production of stolons and rhizoids appears inherent in species of several genera, including *Absisia*, *Rhizopus*, and a few species of *Helicostylum*, whereas in some forms, such as *Cunninghamella* and *Syncephalastrum*, the formation of these structures apparently is influenced mostly by cultural conditions. The immature sporangiophore usually is continuous but often becomes more or less highly septate after the formation of the sporangium or sporangia. Septa formed in aging sporophores, as in vegetative hyphae, usually are irregularly spaced throughout the length of the stipe; outstanding examples of extreme septation in age are seen in the sporophores of such species as *Syncephalastrum racemosum*, *Thamnidium anomalum*, *Mycotypha microspora*, and *Syzygites megalocarpus*. In many species with racemosely or cymosely branched sporophores a septum commonly is formed in the main axis immediately above the point of origin of successive laterals. Septum formation in the Mucorales has received very little study. Early investigations by Harper on three species of *Pilobolus* (1899) and Swingle on *Rhizopus stolonifer* and *Phyco-*

myces nitens (1903) showed that the columella in these species is formed in place by the deposition of wall-substance in the cleavage plane between the mass of protoplasm destined to form spores in the sporangium proper and the protoplasm of the sporophore apex. The same phenomenon subsequently has been observed in other members of the order (Moreau, 1913; Cutter, 1942 a). Thus, the columella is not the result of the bulging upward of a simple cross-wall into the sporangium. Buller and Neufeld (Buller, 1933) showed that septa in the mycelium of *Rhizopus stolonifer* are delimited by a process of annular ingrowth from the lateral wall and become completely closed at maturity; the whole process of septum formation required about 20-25 minutes. Cutter (1942 a) states that the developing progametangia of *Absidia spinosa* are separated into gametangia and suspensors by the delimitation of transverse walls formed by a similar process of annular ingrowth. Whether or not the *Rhizopus*-type septum is characteristic of the vegetative and fruiting hyphae of all Mucorales having relatively undifferentiated thalli has yet to be determined.

In the first five evolutionary lines listed earlier, the pattern of development and characteristics of the vegetative and fruiting hyphae appear to be essentially like those described in the preceding paragraph, i.e., they are what may be termed mucoraceous. Such hyphae, which are initially continuous and form mostly adventitious, simple, imperforate septa in age undoubtedly represent the primitive condition in the order. The vegetative and especially the fertile hyphae of representatives of the sixth line of evolution, the merosporangiferous forms, exhibit remarkable transitional stages in specialization if, as the writer believes, the nature of the septum is a reliable indicator of specialization. The vegetative and fertile hyphae of *Syncephalastrum* are entirely mucoraceous in character. In the *Piptocephalidaceae*, where the vegetative hyphae of *Piptocephalis* and *Syncephalis* species have become highly modified because of the parasitic habit of members of these genera, the substrate mycelium, which is extensive only in the first genus, often becomes septate during early stages of development and the septa are of the simple, imperforate, generalized type. Septa have not been discerned in the haustoria of either genus. The usually unbranched sporophores of *Syncephalis* species typically are continuous except for the formation of simple septa at the base of the upright stalks and in the branches of the basal rhizoid systems. The arachnoid extramatrical hyphae of members of this genus become septate in age. In many species of *Piptocephalis*, perforate septa formed by annular ingrowth from the lateral walls typically are formed in the young fruiting hyphae and in several species these septa develop tubular extensions that project toward the growing tips of the sporophores—in the direction of flow of protoplasm moving into the region of spore formation. As far as the writer is aware, septa of this type are not known in other members of the Mucorales. These perforate septa undoubtedly offer some resistance to the flow of protoplasm through the hyphae, but their regulatory function, if any, must be very slight. When the fertile heads have matured, these septa become completely plugged with wall-material (?)

Septa are formed in the vegetative and fruiting hyphae of all known species of *Dimargaritaceae* and *Kickxellaceae*. These septa appear during early stages of spore germination and their nature has been discussed in some detail in earlier sections of this paper. The highly developed septa of members of the above families, with their median cavities, perforate above and below, containing valve-like plugs are without parallel in other members of the order. Whatever influence these unique septa may have on the movement of protoplasm through the hyphae is unknown, but their effect undoubtedly is more than just passive.

SPORANGIA AND SPORANGIOLA

In the Mucoraceae, the characteristic asexual reproductive structures are large columellate sporangia borne terminally on simple or branched sporangiophores. The usually conspicuous columella persists after the shedding of the spores and typically is more or less globose, ovoid, or pear shaped. The number of spores produced in a single sporangium of members of this family may be extremely great—as many as 70,000 according to Blakeslee (1920). As mentioned earlier, the columella does not represent the bulging upward of an ordinary transverse septum, but is formed in place during sporangial development (Harper, 1899; Swingle, 1903). The entire multinuclear contents of the sporangium proper are divided by cleavage planes into naked uni- or multinucleate more or less polyhedral cells which round up, are invested with walls, and function as spores. Spore germination evidences no apparent correlation with the manner of spore formation. In *Pilobolus* and *Pilaira*, of the Pilobolaceae, the essentially mucoraceous sporangium has become highly modified as a result of adaptation for spore dispersal by browsing animals. *Mucor*-type sporangia are found also in members of the Choanephoraceae and Thamniaceae.

The relatively large sporangia of most Mucoraceae, with their well-developed columellae, are in contrast with the usually much smaller, few-spored sporangiola characteristic of several other families of Mucorales. As many as fifty or more spores may be delimited in the sporangiola of some of the *piriforme*-type species of *Helicostylum*, although the number of spores per sporangium usually is considerably less in most sporangioliferous species. In *Chaetocladium* and *Cunninghamella* and some species of *Choanephora* the sporangium is unisporous.

Sporangiola probably have arisen independently of the *Mucor*-type sporangium in several evolutionary lines of Mucorales. In his studies of *Blakeslea trispora* (= *Choanephora trispora*) (Thaxter) Sinha, according to Sinha, 1940), Thaxter (1914) described the development, under certain cultural conditions, of progressively depauperate sporangia in which reduction in sporangium size was accompanied not only by a reduction in the number of spores produced but also by a diminution in the size of the columella. In extremely small sporangia the columellae were found to be no more than small hemispherical enlargements projecting into the sporiferous region (Thaxter, 1914, Pl. 27, fig. 14). Although this phenomenon is suggestive of the possible mode of origin of the sporangium from a typical *Mucor*-type sporangium in this genus (Fitzpatrick, 1930, p. 235), it does not necessarily offer a satisfactory explanation of the origin of the sporangium in such genera as *Thamnidium* and *Helicostylum* of the Thamniaceae. Even in *Choanephora*, it is difficult to conceive of the origin of the polycephalous sporangiophore from a presumably derived and highly reduced *Mucor*-type sporangiophore. Implications of Thaxter's observation, however, are the possible correlation between sporangial size and the nature of the columella and the possibility that the *Mortierella*-type sporangium, which usually lacks a well-defined columella, has evolved from a *Mucor*-type sporangium by reduction. Although there are exceptions, many of the modern species of *Mortierella* are characterized by relatively small sporangia; the sporangia of the known species of *Dissophora* and *Haplosporangium* contain greatly reduced numbers of spores—only one or two in the latter genus—and are essentially sporangiola. Several species of *Mortierella* do, in fact, have rudimentary columellae (Linnemann, 1941). In *Syzygites megalocarpus*, usually placed in the Mucoraceae, the sporangium typically contains a relatively small number of rather large spores and the columella is only slightly enlarged above the attachment of the sporangial wall (Hesseltine, 1957); this species, of course, is characterized by a typical mucoraceous zygospor. Very recently Lythgoe

(1958) demonstrated that the larger sporangiola of *Helicostylum elegans* may possess well-marked hemispherical columellae which are laid down in their final positions during sporangiolium development and are not bulged septa. The author has observed similar hemispherical columellae in the sporangiola of *Helicostylum piriforme* and its allies. The presence or absence of a columella as an absolute character in distinguishing sporangia and sporangiola is more apparent than real.

The most outstanding feature of the THAMNIDIUM-CUNNINGHAMELLA line of evolution is the great diversity in the nature of the sporangiolium and the manner in which it is borne on the sporangiophore. In their vegetative and sexual characters, all members of this group are essentially mucoraceous, and the sporophores of several species of *Thamnidium*, *Helicostylum*, and *Chaetostylum*, of the Thamnidiaceae, bear terminal sporangia exactly like those produced by such genera as *Mucor* and *Rhizopus* of the Mucoraceae, whereas *Mucor*-type sporangia are unknown in *Chaetocladium*, *Cokeromyces*, and *Radiomyces*, also placed in the Thamnidiaceae, and in all known representatives of the Cunninghamellaceae.

The sporophores of *Thamnidium elegans*, *Helicostylum elegans*, and *Chaetostylum fresenii* (for recent discussions of these and other species of these genera see Hesseltine and Anderson, 1956, 1957; Lythgoe, 1958) give rise to large, deliquescent *Mucor*-like sporangia terminally and to lateral whorls of relatively short, racemose, dichotomous or verticillate branchlets which bear small, nondeliquescent, few-spored, often deciduous sporangiola terminally on straight or curved pedicels. In all known members of the Thamnidiaceae producing both sporangiola and sporangia, the walls of the latter are deliquescent at maturity whereas the walls of the former typically are relatively persistent and nondeliquescent.

Very recently the writer isolated several strains of an unidentified fungus which are characterized by erect sporophores bearing large, deliquescent, *Mucor*-like sporangia terminally and great numbers of pedicellate sporangiola produced progressively along nearly the entire lengths of the main axes of the stipes. The sporangiola have spinose, persistent walls and contain a usually small number of relatively large smooth spores; the sporangioliar pedicel is nearly straight. This species recalls *Helicostylum elegans* and *H. venustellum* except that the sporangiola are not borne in more or less compact clusters on the sporophores and it would seem to represent a form transitional between a typical *Mucor* and species of *Helicostylum* like those listed above. The characteristics of these species lend support to the notion, held here, that the thamnidiaceous sporangiolium has originated independently of the *Mucor*-type sporangium. *Thamnidium simplex* Brefeld (1881; syn: *Mucor agglomeratus* Schostakowitsch according to Hesseltine and Anderson, 1956), bearing clusters of short-pedicellate sporangiola on small swellings of the axes of simple or branched *Mucor*-like sporangiophores, also suggests a rather primitive condition in the Thamnidiaceae. This species in some respects resembles *Helicostylum piriforme* more than a species of *Thamnidium*.

Chaetostylum has been distinguished from *Helicostylum* and *Thamnidium* because the main axes of the branchlets bearing sporangiola often are prolonged as sterile spine-like processes. Branches of *Thamnidium* species are not known to form free ends. Lythgoe (1958) demonstrated that the main stalks of sporangioliferous branchlets of *Helicostylum venustellum* may occasionally be sterile terminally and he transferred *Chaetostylum fresenii*, the only recognized species of the genus (Hesseltine and Anderson, 1957) to *Helicostylum*. Whether or not *Chaetostylum* should be retained as a distinct genus I shall not debate here. However, the nature of the sporangioliferous branchlets of *Chaetostylum fresenii* suggests for this species a position

transitional between a primitive *Helicostylum* of the type represented by *H. elegans* and the well-defined genus *Chaetocladium* in which *Mucor*-type sporangia are unknown and only unisporous sporangiola, borne in lateral whorls on short spine-like branchlets, are produced (Hesseltine and Anderson, 1957).

Helicostylum piriforme Bainier (1882) represents the most advanced type in the genus. In this species, usually large numbers of stalked sporangiola are borne in pairs or small clusters on extremely short dichotomous branchlets crowded over the surfaces of often well-defined interclary swellings of the sporangiophores. One or several aggregates of sporangiola may be formed along the length of a given sporangiophore. The sporangiola of *H. piriforme* are pyriform and sharply recurved on the slender pedicels. *Mucor*-type sporangia may or may not be formed terminally on the simple or branched main axes of the sporangiophores; often the axis is reduced to nothing more than a short blunt process projecting beyond the enlargement bearing sporangiola. In the writer's collection of over forty isolates of *Helicostylum*, there are several species allied to *H. piriforme*; in one of these, typical sporangia never have appeared in culture. Mucoraceous zygospores have been demonstrated in several species, all of which have proved to be heterothallic.

Two unusual and highly derived monotypic genera of Thamniaceae are represented by *Cokeromyces recurvatus* Poitras (Shanor *et al.*, 1950) and *Radiomyces spectabilis* Embree (1959). Both species are strongly homothallic and neither is known to produce *Mucor*-type sporangia. In *Cokeromyces recurvatus*, small globose sporangiola are borne terminally on irregularly recurved or twisted unbranched pedicels arising from the surfaces of terminal vesicular enlargements of simple sporophores. The smooth sporangiola contain about 12-20 ovoid spores. Like those of *Cokeromyces recurvatus*, the sporophores of *Radiomyces spectabilis* usually are simple and sporangiola are formed on outgrowths of terminal vesicular enlargements. In the latter species, however, the branchlets arising from the primary vesicles are nearly straight and produce, in turn, smaller secondary vesicles over the surfaces of which small, nearly sessile, subglobose or ovoid sporangiola are borne. The sporangiola contain only 5-12 elongate-reniform spores and the sporangiolum wall is adorned with tiny spine-like processes having rounded apices.

In all known members of the Cunninghamellaceae (Hesseltine, 1955), only monosporous sporangiola are known. These are borne directly over the surfaces of more or less globose or elongate vesicles formed terminally on simple or branched sporophores. Although the sporangiolar wall can not be readily demonstrated, the cunninghamellaceous sporangiolum is generally considered to be the homologue of the unispored sporangiolum of such genera as *Chaetocladium* and *Choanephora* (Bessey, 1950; Fitzpatrick, 1930). In their vegetative and sexual characters (zygospores thus far are known only in *Cunninghamella*) members of the Cunninghamellaceae and Thamniaceae are very similar. Although the sporiferous heads of members of the former family bear some resemblance to those of *Cokeromyces* and *Radiomyces*, the latter genera probably are not closely related to any of the known representatives of the Cunninghamellaceae.

The above summary shows that sporophores producing nearly sessile or pedicellate sporangiola directly from the surfaces of terminal vesicular enlargements have evolved several times in the Mucorales (*Choanephora*, *Cokeromyces*, *Radiomyces*, members of the Cunninghamellaceae). This type of sporophore probably represents a highly derived type within the order. In the PIPTOCEPHALIS-KICKXELLA line of evolution such a sporophore is characteristic of several genera of which *Syncephalas-trum* undoubtedly is the most primitive. In the latter genus, large numbers of cylindri-

cal sporangiola (merosporangia) arise by budding from the surfaces of terminal enlargements and the spores appear to be delimited as in members of the Mucoraceae. Usually only a single file of spores is produced in each merosporangium, but not infrequently a second, often incomplete, file is formed. Spore germination in *Syncephalastrum* is mucoraceous in that there is no apparent correlation between the origin of the germ hyphae and the manner in which the spores are delimited within the sporangia. In both *Piptocephalis* and *Syncephalis*, the merosporangia arise from terminal enlargements also; only occasionally, as in a few species of *Syncephalis*, are the merosporangia borne on stalk-like outgrowths from the vesicles. The pattern of spore formation in *Piptocephalis* and *Syncephalis*, however, shows certain more specialized tendencies than in *Syncephalastrum*. Spore formation has been studied in only a few species of *Syncephalis*. Thaxter (1897) demonstrated a unique type of spore development in *S. pycnosperma* and an unidentified species of the genus wherein spore formation is preceded by a process of constriction of the protoplasm within the merosporangium. This mechanism, which also has been observed in several other species of the genus (see p. 358), apparently results in spores having walls which are thicker laterally than terminally. Thus, in *Syncephalis* the germ hyphae appear always to arise from the spore apices; only polar germination has been observed in those species of the genus in which spore germination has been studied.

The process of spore formation in *Piptocephalis* is different from that observed thus far in *Syncephalis* and is more nearly like that found in *Syncephalastrum*. In all but one described species of *Piptocephalis* which have been studied in any detail, the protoplasm in the nearly cylindrical immature merosporangium becomes divided into discrete units by the formation of transverse hyaline zones (see p. 342), and on either side of these hyaline zones walls are laid down (Leadbeater and Mercer, 1957 b); these, the apposed end-walls of adjacent spores, ultimately are somewhat thicker than the lateral walls and usually are in evidence as nearly inextensible polar caps on the germinating spores. Spore germination in *Piptocephalis* is lateral.

In one known species of *Piptocephalis*, *P. lepidula*, a type of merosporangial development very different from that described above has been observed in the course of the present study. In this species, each ovoid bud-like outgrowth from the subtending vesicle does not elongate to form a cylindrical structure as in other described species of the genus but gives rise, by budding, to a terminal enlargement into which a nucleus migrates from the basal cell. Both cells then delimit single spores. The same process of merosporangial formation characterizes all but one of the known species of Dimargaritaceae; in the one known exception, *Dimargaris bacillispora*, the merosporangium develops in a manner comparable to that found in the majority of species of *Piptocephalis*. In their vegetative and sexual characters, however, members of the Dimargaritaceae appear to be considerably more advanced than those of the genus *Piptocephalis*, and the writer believes that the modern representatives of these groups represent separate lines of evolution within the merosporangiferous Mucorales. Representing the most highly derived type in the merosporangiferous mucors, the sporangiolium of members of the Kickxellaceae is reduced to one spore borne terminally on a sterile nondeciduous cell, or pseudophialide (Benjamin, 1958). The presumed homology of the latter structure will be discussed below.

ZYGOSPORES

Sexual reproduction has been observed in members of about three-fourths of the recognized genera of Mucorales. The classical discovery of Blakeslee (1904 a, b) regarding the nature of sexual compatibility, whether homothallic or heterothallic, in members of the order is well-known (Blakeslee, 1920; Fitzpatrick, 1930; Bessey,

1950) and will not be discussed here. In most species of Mucorales the sexual process begins when two compatible hyphae come in contact and are stimulated to develop a pair of opposed lateral branchlets each of which grows outward nearly at right angles to its parent hypha. These branches, or progametangia, remain in contact at their apices, swell somewhat, becoming more or less clavate, and delimit single gametangia terminally by the formation of transverse walls. That portion of the original progametangium remaining after the separation of the gametangium is termed the suspensor. The walls separating the usually nearly equal gametangia break down centrifugally, and the multinucleate contents of both gametangia then occupy the common cavities of the fused gametangia. Thus there is formed a relatively thin-walled zygosporangium which enlarges rapidly and becomes more or less thickened by the deposition of often several concentric layers of wall-material. In many species the outer layer may become irregularly thickened so that the zygosporangium, at maturity, is conspicuously roughened with more or less elevated tooth-like projections. Also, the exospore (zygosporangium) often becomes highly pigmented, usually orange, brownish, or wholly black. Within the zygosporangium the usually smooth, thick-walled endospore, or zygosporangium proper, is delimited. The combination of zygosporangium and zygosporangium is usually termed the zygosporangium.

The above pattern of zygosporangium formation is characteristic of most species of Mucoraceae, Thamniaceae, and Syncephalastraceae (Pl. 2) in which sexuality has been observed. Several members of the order, however, show marked deviations from this pattern. Thus, in species of *Zygorhynchus* and *Dicranophora*—the latter is included in the Mucoraceae by Naumov (1935, 1939) and Hesseltine (1955), in the Thamniaceae by others (Fitzpatrick, 1930; Bessey, 1950)—the gametangia and suspensors are very unequal in size and the zygosporangium is formed almost entirely from the larger gametangium. In several species of other families, including *Endogone fasciculata* Thaxter and *E. lactiflua* Berkeley (Thaxter, 1922) and *Syncephalis nodosa* Van Tieghem (Bainier, 1882, 1883; Thaxter, 1897), the zygosporangium arises as a bud-like outgrowth from the larger of two fused gametangia (Pl. 9 e). In species of *Choanephora*, *Mortierella*, *Phycomyces*, *Pilaria*, *Pilobolus*, *Piptocephalis*, and some species of *Syncephalis* and *Endogone*, the progametangia initially are apposed, often arising from intertwined hyphae and later becoming curved outward and tongs-like in appearance. In *Piptocephalis* and certain species of *Syncephalis* and *Endogone*, the zygosporangia arise as bud-like outgrowths above and slightly between the point of fusion of the gametangia and the basal portions of the gametangia remain as often widely separated, cylindrical appendages attached to the exospore (Pl. 4 g-i; Pl. 8 a-e; Pl. 9 j). In species of *Absidia*, *Phycomyces*, and *Radiomyces*, one or both suspensors may give rise to simple or branched appendages which surround the mature zygosporangium; in *Mortierella*, a dense overgrowth of vegetative hyphae envelops the zygosporangium; the zygosporangia of some species of *Endogone* are enclosed in definite mycelial sporocarps. The exospore of most species of Mucorales may be extremely thick, rough, and pigmented; in *Choanephora*, *Mortierella*, *Radiomyces*, and all known sexual species of the Dimargaritaceae, Kickxellaceae, and Endogonaceae, the exospore usually is relatively thin and smooth and often may be nearly hyaline. In the families just named, sexual hyphae usually are relatively undifferentiated and often can not be distinguished from ordinary vegetative hyphae until zygosporangium begin to form.

With the exception of the Thamniaceae, Cunninghamellaceae, and Syncephalastraceae, extreme modifications of the basic pattern of zygosporangium formation in the Mucorales, as exemplified by the Mucoraceae, appear to be more or less correlated with the evolution of derived types of asexual reproductive structures. This is espe-

cially well-marked in the merosporangiferous forms. Thus, the production of opposed, morphologically differentiated sexual hyphae giving rise to nearly equal gametangia which fuse and delimit zygospores within relatively large, thick, roughened, highly pigmented zygosporangia probably represents the primitive condition within the order. Advanced characters are thought here to include (1) apposed progametangia, (2) undifferentiated sexual hyphae, (3) heterogametangy, (4) suspensor appendages, (5) thin, smooth, nearly hyaline zygosporangia, and (6) the formation of the zygosporangium from a bud-like enlargement which incorporates only a part of each of the fused gametangia or from a vesicular outgrowth developed from only one of a pair of fused gametangia. By their promiscuous occurrence in several groups, most of the presumably advanced characters listed above probably have arisen independently in the various lines in which they are found at present.

ORIGIN OF THE MUCORALES

The problem of the origin of the Mucorales has, of course, intrigued many mycologists. What phylogenetic significance, if any, may be attached to many characteristics of the mucoralean asexual and sexual reproductive structures is difficult to ascertain, for whether or not in a given species, genus, or family a given morphological character represents the retention of an ancestral characteristic or something which has arisen independently can not be determined. As Bessey (1950, p. 634) points out, as far as the asexual mode of reproduction is concerned, there appears to be basis for the assumption that the Mucorales may have evolved from some aplanosporous saprolegniaceous ancestor, whereas it is more difficult to homologize the typical sexual reproductive structures of these groups. Several students, including Gäumann (Gäumann and Dodge, 1928; Gäumann and Wynd, 1952) and Jaczewski (1929-1930), have suggested the origin of the mucors from chytrid-like ancestors.

Sexual apparatuses like those found in known representatives of the Saprolegniales have no counterparts in the Mucorales. Extreme heterogametangy such as is found in species of *Zygorhynchus* and *Dicranophora* undoubtedly is only a modification of the typical more or less isogamous condition of most Mucoraceae and probably has no phylogenetic significance. Vague parallels between the marked oogamy of the Saprolegniales and the heterogamy of some Mucorales are found primarily in the more derived members of the latter order as well as in other highly specialized Zygomycetes, Entomophthorales and Zoopagales. Here one often encounters gametangia borne on relatively undifferentiated hyphae and a type of heterogametangy, often only slight, wherein the zygospore is formed wholly within one gametangium or in a bud-like outgrowth from one, usually the largest, gametangium. There is no evidence to indicate, however, that the various modifications in the pattern of zygospore formation—heterogametangy and the formation of the zygospore in the concavity of one rather than both fused gametangia—in the more specialized Zygomycetes have arisen from anything other than typical mucoraceous sexual structures. Indeed, Ling-Yong (1930, 1931) points out that in many heterothallic Mucoraceae the suspensors and gametangia produced by one strain (termed ♀) often are slightly larger than those produced by the opposite strain (♂), and in *Mucor hiemalis* this author claims that the contents of the smaller gametangium pass into the larger gametangium which then delimits the zygospore.

In considering the possible origin of the Mucorales from chytrid-like ancestors, one anomalous member of the Chytridiales, *Zygochytium aurantiacum* (Sorokin, 1874), is of especial interest. Sparrow (1943), who tentatively includes this genus in the Megachytriaceae, points out that the existence of this organism generally has

been discounted by most mycologists because the fungus has not again been encountered. Sparrow further states, however, that Sorokin's description and illustrations of this organism are exceptionally detailed and clear and that there probably is no good reason for doubting them. In this I concur. As a case in point, the status of *Dimargaris cristalligena* long was questioned simply because no one reported the species again after Van Tieghem described it in 1875, and Zycha (1935) arbitrarily relegated the genus to synonymy with *Dispira*. In the present work not only the validity of *Dimargaris* but also the distinctness of the genus from *Dispira* has been, I think, adequately demonstrated. Van Tieghem's description of *Dimargaris* and Sorokin's description of *Zygochytrium* are quite lucid when compared with the characterizations prepared by many of these workers' contemporaries. Undoubtedly there are many other instances in which failure to rediscover an unusual organism has led students, many years later, to conclude that the person who originally described the entity had overly exercised his imagination. This points up, it would seem, the importance not only of adequately describing but also of illustrating organisms, especially ephemeral microfungi, in which preservation of specimens often is difficult if not impossible.

In *Zygochytrium aurantiacum*, Sorokin described and illustrated a type of zygospore which in its gross morphology and manner of formation appears to be exactly comparable to that of a typical member of the Mucoraceae. Sparrow reasons that the nearly identical mechanisms of sexual reproduction in *Zygochytrium* and the Mucoraceae may represent only a case of parallel evolution. This very well may be the case, but it is interesting, nevertheless, to note that no truly zygomycetous type of sexual reproduction has yet been discovered in any member of the Saprolegniales.

RELATIONSHIPS WITHIN THE MUCORALES

Regardless of their origin, the Mucorales appear to constitute a well-defined and natural group of Phycomycetaceae. As stated earlier, the six lines of evolution suggested by Hesseltine (1952) seem best to represent natural subgroups within the order. Admittedly, members of the MORTIERELLA-ENDOGONE line need much additional study before their status as a truly natural group can be accepted without reservation. *Choanephora*, with its striate sporangiospores—often bearing peculiar appendages at their apices—and dark-colored, striate zygospores borne within relatively thin-walled, smooth, nearly hyaline zygosporangia, clearly is not closely allied to members of the Cunninghamellaceae. Representatives of the latter family together with members of the Thamniaceae are essentially mucoraceous in character with regard to their vegetative and sexual characters, and they are distinguished from the Mucoraceae primarily on the basis of their more specialized sporophores. *Pilobolus* and *Pilaira* are very close to the Mucoraceae, but their highly modified sporangia and specialized sexual structures justify their inclusion in a separate family.

In the merosporangiferous mucors, the genus *Syncephalastrum*, being mucoraceous in its vegetative and sexual characters, is believed to represent the most primitive member of this line of evolution. The cylindrical sporangiola, or merosporangia, of *Syncephalastrum*, borne directly on terminal enlargements of the sporophores, are thought to be homologous with the sporangiola of other mucors like *Choanephora*, *Cokeromyces*, and *Radiomyces*. The sporangiospores of *Syncephalastrum* are formed and germinate as in the Mucoraceae. On the basis of the zygospore, especially, *Syncephalastrum* is here, following Naumov, retained in a separate family, Syncephalastraceae.

The vegetative mycelia of species of Piptocephalidaceae have undergone extreme modifications as a result of the parasitic habit of members of this family. In repre-

sentatives of both *Piptocephalis* and *Syncephalis*, however, the merosporangia usually are borne directly on terminal enlargements of the sporophores as in *Syncephalastrum*. Distinctive specialized tendencies in the pattern of spore formation within the merosporangium have appeared in the former genera, especially in *Syncephalis*. In the character of their zygosporangia, *Piptocephalis* and *Syncephalis* show marked affinity, and in both genera well-defined apposed progametangia typically delimit slightly unequal gametangia which form zygosporangia within bud-like enlargements developed more above than between the points of fusion of the gametangia. The basal portion of the wall of each gametangium usually remains unchanged during the development of the zygosporangium and is attached to the mature exospore as a conspicuous so-called gametangial remnant. The sexual apparatus of *Syncephalis nodosa* shows further modification, for in this species the zygosporangium develops as a vesicular outgrowth of the larger of two gametangia delimited terminally on intertwined, relatively undifferentiated sexual hyphae. More or less conspicuous vesicular hypertrophies often are formed on the suspensors of members of both *Piptocephalis* and *Syncephalis*; these may be especially well-marked in the latter genus. In all described species of *Piptocephalis*, the fertile vesicles are relatively small and deciduous at maturity; this character probably has evolved in the genus as an adaptation for spore dispersal. In one as yet undescribed species of *Piptocephalis*, the head-cell is not deciduous; in the nature of its vegetative growth and parasitism this species also displays marked *Syncephalis*-like tendencies not exhibited by other known species of *Piptocephalis*. In their vegetative and asexual characters, species of *Piptocephalis* and *Syncephalis* would seem to constitute two well-defined and rather divergent lines within the Piptocephalidaceae.

The most highly evolved forms not only in the merosporangiferous line but in the Mucorales as a whole probably occur in two apparently very closely related yet well-defined family groups: (1) *Dimargaris* and its allies; (2) *Kickxella* and its allies. The vegetative and fruiting hyphae, with their unique cross-walls, and the mode of sexual reproduction of members of both the Dimargaritaceae and Kickxellaceae are very similar; the two families differ primarily in the nature of their merosporangia. In all known members of the Dimargaritaceae the merosporangium delimits two spores, whereas in the Kickxellaceae the merosporangium is reduced to a single spore borne on a small nondiciduous cell, or pseudophialide.

Among the Dimargaritaceae, only *Spinalia* has merosporangia which arise directly from terminal enlargements. This genus, unfortunately, is known only from the original description of the type species, *S. radians*, and until this species is rediscovered we will not be able to judge its relationships accurately. If both elements of the presumed merosporangium are functional spores, then placement of this species in the Dimargaritaceae will be more secure. Conversely, if the basal element remains sterile, the inclusion of the genus in the Kickxellaceae would be indicated. In all other known members of the Dimargaritaceae, the merosporangia arise from cellular branches, here termed sporiferous branchlets, which may or may not arise from terminal enlargements of the sporophores. The nuclear cycle and process of septation accompanying the development of the sporiferous branchlets of *Dimargaris*, *Dispira*, and *Tieghemiomycetes* parallels that encountered in the development of the highly specialized sporiferous branchlets, termed sporocladia, of most known representatives of the Kickxellaceae, and the sporiferous branchlets and sporocladia of these groups appear to be homologous structures. The vesicular, nonseptate sporocladia of *Linderina*, however, are quite distinct from those of other genera of Kickxellaceae and would seem to represent a primitive condition in the family; actually they resemble some-

what the fertile heads of *Spinalia*. However, merosporangial development in *Linderina* is exactly like that in the other genera of the family. Morphologically and cytologically, early stages of merosporangial formation in the Dimargaritaceae are very similar to those encountered in the development of the unisporous sporangiola and pseudophialides in the Kickxellaceae, and the writer believes that the sporangiola and pseudophialides of the latter family have evolved directly from a bisporous merosporangium like that found at present in *Piptocephalis lepidula* and most members of the Dimargaritaceae. Thus the sterile, nondeciduous pseudophialide in the Kickxellaceae is thought to be derived from the fertile, deciduous, basal portion of a presumably more primitive merosporangium of the type found in the above forms. Linder (1943) suggested that the sporocladium of members of the Kickxellaceae has evolved from fertile heads of fungi like those characterizing certain species of *Syncephalis*. The writer believes, however, that the genus *Syncephalis*, with its unique type merosporangium, represents an isolated group within the merosporangiferous Mucorales that, along with *Piptocephalis*, diverged from the line of evolution leading to the Dimargaritaceae and Kickxellaceae. Spore germination in the Kickxellaceae and Dimargaritaceae is lateral—reflecting a type of spore formation more nearly like that in the genus *Piptocephalis*. Acropetal development of the merosporangium has been evolved in *Piptocephalis* and is characteristic of all known species of Dimargaritaceae except *Dimargaris bacillispora*, where the merosporangium develops as in most species of *Piptocephalis*. The writer, however, believes that the latter genus represents a separate phyletic line within modern groups of merosporangiferous forms, but that the characteristics of the Dimargaritaceae and Kickxellaceae reflect closer affinity of the members of these families to the genus *Piptocephalis* than to *Syncephalis*.

In the diagram presented in Plate 34, the areas, A, B, and C, bounded by dotted lines, are intended to represent levels of advancement of morphological characters which may be summarized, in general, as follows:

A. *Primitive.*

1. Vegetative and fruiting hyphae generalized, initially nonseptate; simple imperforate septa formed to delimit reproductive structures or laid down adventitiously in aging hyphae.
2. Sporangia relatively large, multispored, columellate.
3. Progametangia opposed, highly differentiated morphologically; zygospores usually formed on aerial hyphae; zygosporangium thick-walled, rough, often highly pigmented.

B. *Intermediate.*

1. Vegetative and fruiting hyphae essentially as in A; perforate septa sometimes formed in fruiting structures.
2. Sporangiola containing relatively small numbers of spores; columellae absent or rudimentary.
3. Progametangia apposed, more or less differentiated; zygospores often as in A, sometimes formed in or at the surface of the substrate; zygosporangium sometimes thin-walled, hyaline, nearly smooth.

C. *Advanced.*

1. Vegetative and fruiting hyphae septate from the beginning; septa highly modified.
2. Sporangiola containing only one or two spores.
3. Sexual hyphae relatively undifferentiated; zygospores usually formed in or near the surface of the substrate; zygosporangium thin-walled, hyaline, nearly smooth.

Because the rate of evolution of given morphological characters has varied greatly in the different families or even in various representatives of a given family, this scheme is intended only to indicate the range of primitiveness or advancement ex-

hibited by a family as a whole. For example, in the Cunninghamellaceae, as presently understood, the vegetative and sexual characters fall within area A, whereas the nature of the sporangiola falls within area C.

PLATE 34. Relationships of the families of Mucorales. Explanation is in the text.

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