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OBLIGATE AZYGOSPORE FORMATION IN TWO SPECIES OF MUCOR (MUCORALES)

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In the course of sexual reproduction in many Mucorales, gametangial copulation occasionally fails to take place normally and one or both of the gametangia involved in the sexual act may give rise to a parthenospore or azygospore. Azygospores typically are morphologically like the true zygospores of the species in which they occur, although they may be somewhat smaller. They may be single or double depending on whether or not one or both of the opposed gametangia develop parthenogenetically (for typical examples see Leadbeater & Mercer, 1957a, Pl. 5, fig. 7–9, and 1957b, fig. 4 g–h). In many instances, according to Ling-Young (1930), presumed double azygospores may be only true zygospores in which the exospore [zygosporangium] differentiates prior to complete fusion of the gametangia.

As Ling-Young states in the discussion of the azygospore included in his classic work on sexuality in the Mucorales (Ling-Young, 1930, pp. 351–361, 681–692), the story of the azygospore is as old as that of the zygospore. As early as 1825 Fries established the genus *Azygites* based, apparently, on azygosporic material of *Syzygites megalocarpus* (Fisher, 1892; Hesseltine, 1957). Subsequently, azygospores have been reported in many species of Mucorales including the following:

Absidia cylindrospora Hagem: Ling-Young, 1930, p. 357. *(het.)*[3]
A. capillata Van Tieghem: Van Tieghem, 1876, p. 362. *(?hom.)*
A. caerulea Bainier: Vuillemin, 1903, p. 116 (as *Proabsidia saccardoi*). *(het.)*
A. glauca Hagem: Ling-Young, 1930, p. 356. *(het.)*
A. scabra Cocconi: Cocconi, 1900 (Kniep, 1928, p. 333). *(?hom.)*
A. septata Van Tieghem: Van Tieghem, 1876, p. 362. *(?hom.)*
A. spinosa Lendner: Blakeslee, 1915, p. 94. *(hom.)*
A. spinosa var. *azygospora* Boedijn: Boedijn, 1958, p. 334. *(az.)*
Choanephora simsoni Cunningham: Cunningham, 1895 (Kniep, 1928, p. 333). *(?hom.)*
Cunninghamella bertholletiae Stadel: Blakeslee, et al., 1921, p. 214. *(het.)*
Mucor erectus Bainier: Bainier, 1884, p. 208. *(?hom.)*
M. fragilis Bainier: Zopf, 1890 (Kniep, 1928, p. 333); Dangeard, 1903, p. 232. *(het)*.
M. genevensis Lendner: Lendner, 1908, p. 81; Blakeslee, 1915, p. 91. *(hom.)*
M. hiemalis Wehmer: Ling-Young, 1930, p. 355. *(het.)*
M. mucedo L. ex Fresenius: Brefeld, 1872 (Kniep, 1928, p. 333); Ling-Young, 1930, p. 360. *(het.)*
M. neglectus Bainier: Bainier, 1903, p. 160 (not. *M. neglectus* Vuill., 1887, or *M. neglectus* Hansen, 1902). *(az.)*
M. parvisporus Kanouse: Kanouse, 1924 (Hesseltine, 1954). *(hom.)*
M. plumbeus Bonorden: Zikes, 1924 (Kniep, 1928, p. 333). *(het.)*
M. racemosus Fresenius: Bainier, 1883, p. 352; Lendner, 1908, p. 77 *(het.)*
M. silvaticus Hagem: Hagem, 1908, p. 32; Linnemann, 1935, p. 193. *(het.)*
M. tenuis Bainier: Bainier, 1883, p. 353; Burgeff, 1924, p. 41. *(az.)*
M. vicinus Bainier: Bainier, 1903, p. 159. *(az.)*
Phycomyces blakesleeanus Burgeff: Orban, 1919, p. 49 (as *P. nitens*). *(het.)*
P. nitens Kunze: Blakeslee, 1906, p. 23, *(het.)*

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[3]*hom.*=homothallic species; *het.*=heterothallic species; *az.*=species in which only azygospores are known.

Pilobolus nanus Van Tieghem: Van Tieghem, 1876, p. 341. *(?az.)*
Piptocephalis virginiana Leadbeater & Mercer: Leadbeater & Mercer, 1957b, p. 468. *(hom.)*
P. xenophila Dobbs & English: Leadbeater & Mercer, 1957a, p. 112; Benjamin, 1959, p. 352. *(hom.)*
Rhizopus sexualis (Smith) Callen: Callen, 1940, p. 801. *(hom.)*
R. stolonifer (Ehrenb. ex Fries) Vuill.: Zopf, 1890 (Kniep, 1928, p. 333); Namyslowski, 1907 (Namyslowski, 1920, p. 207). *(het.)*
Spinellus fusiger (Link) Van Tieghem: Van Tieghem, 1875, p. 72; Bainier, 1882, p. 57; Vuillemin, p. 492 (as *Spinellus rhombosporus*). *(hom.)*
Syzygites megalocarpus Ehrenb. ex Fries: Ehrenberg, 1829 (Hesseltine, 1957); Fries, 1832, p. 330 (as *Azygites mougeotii* Fr. ex Fr.); Corda, 1839, p. 49; De Bary, 1864, p. 217. As *Sporodinia grandis* Link: Van Tieghem, 1875, p. 9; Bainier, 1882, p. 63; Tavel, 1892, p. 30; Leger, 1896, p. 51; Vuillemin, 1904, p. 490; Blakeslee, 1906, p. 4; Keene, 1914; Ling-Young, 1930 ,p. 356. *(hom.)*
Zygorhynchus heterogamus (Vuill.) Vuill.: Vuillemin, 1887, as *Mucor neglectus* Vuill. (Vuillemin, 1907, p. 29). *(hom.)*
Z. macrocarpus Ling-Young: Ling-Young, 1930, p. 356. *(hom.)*
Z. moelleri Vuill.: Vuillemin, 1907, p. 29; Lendner, 1908, p. 73 (as *Mucor moelleri)*; Namyslowski, 1910, p. 477 (as *Z. vuilleminii)*; Moreau, 1913, p. 258 (as *Z. bernardi)*; Blakeslee, 1915, p. 95. *(hom.)*

In 29 of the 34 taxa listed above, azygospores may occur more or less sporadically, and true zygospores formed in the usual way, i.e., by union of gametangia delimited by opposed or apposed progametangia, are the rule. Of this group of species, 14 are known to be heterothallic, 10 homothallic, and the status of five still is uncertain (Naumov, 1939; Kniep, 1928).

Formation of azygospores in the complete absence of true zygospores has been reported only a few times, and the phenomenon has received little or no attention by students interested in sexuality of the Mucorales. In his description of *Pilobolus nanus,* Van Tieghem (1876, pp. 341–342, Pl. 10, fig. 22) described and illustrated zygospore-like bodies borne terminally on short, recurved branches arising from the submerged vegetative hyphae. These bodies later were interpreted as azygospores by Fischer (1892). Unfortunately, this species apparently has not been observed again (Grove, 1934).

Bainier described three azygosporic species of *Mucor, M. tenuis* (1883), *M. vicinus* (1903), and *M. neglectus* (1903). Of these *M. vicinus* and *M. neglectus* were so poorly described, neither measurements nor illustrations being provided, that both Lendner (1908) and Zycha (1935) rejected them as inadequately described. The description of *Mucor tenuis* was somewhat better, and Bainier did include several good illustrations. He stated that the species was similar to *M. racemosus* from which it differed in forming minutely asperulate chlamydospores in the vegetative and fruiting hyphae as well as in producing only azygospores. Along with his accompanying description of the zygospores of *M. racemosus,* Bainier illustrated an erect filament bearing azygospores which he stated were like those of *M. tenuis.* From his discussion of this phenomenon (Bainier, 1883, p. 352–353), which he observed only two or three times, it is apparent that one can not rule out completely the possibility that his cultures of *M. racemosus* occasionally had become contaminated by *M. tenuis.* Lendner (1908) recognized *M. tenuis* on the basis of Bainier's description, whereas Zycha (1935) placed it in synonymy with *M. racemosus.* As will be seen below, there is little reason to doubt that Bainier actually did observe truly azygosporic species of *Mucor.*

In 1958, Boedijn described an azygosporic *Absidia* which he had isolated from soil collected in a coffee garden in Malang, Java. This fungus, which he called *Absidia spinosa* var. *azygospora,* was characterized by the formation of one or more azygospores on simple or branched suspensor-like outgrowths of the aerial hyphae. The azygospores were subtended by slender, straight or curved outgrowths like those formed on one or both suspensors in several species of *Absidia.* We have not had an opportunity to examine this fungus, and it apparently was not distributed to any of the major culture collections.

The purpose of this paper is to describe two species of *Mucor* that produce abundant azygospores in the complete absence of true zygospores.

Mucor bainieri Mehrotra & Baijal sp. nov.

Coloniae in agaro SMA (20°C) albae, in aetate pallide cinereae; sporangiophoris hyalinis, levibus, rectis vel ascendentibus, ramosis, ad 2 cm altis, 5–13 μ diam; sporangiis pallide cinereis, globosis, (10–)40–110(–135) μ diam (med. 80 μ); tunicis sporangiorum minute asperulatis, liquentibus; columellis globosis, subglobosis, ovoideis, vel pyriformibus, hyalinis, levibus, (5–)15–60 μ diam (med. 35 μ); collari manifesto; sporangiosporis hyalinis, levibus, ovoideis, ellipsoideis, vel nonnihil reniformibus, (3.5–)4.4–11.4(–15) μ × (2.2–)2.6–5.7(–10) μ (med. 7.2 μ × 4 μ); chlamydosporis in sporangiophoris et hyphis aeriis raris, intercalaribus vel terminalibus, subglobosis vel cylindricis, de muris crassis, 10–25 μ × 8–20 μ; chlamydosporis in hyphis vegetantibus numerosis, singulis vel in catenis gestis, globosis vel subglobosis, de muris tenuibus, 10–35 μ diam; zygosporis absentibus; azygosporis terminalibus vel subterminalibus in azygophoris simplicibus vel ramosis 0.1–1.5 cm altis gestis; azygosporis globosis vel subglobosis, aurantio-fuscis vel fusco-nigris, 30–120 μ (med. 75 μ) diam.

Colonies on SMA (20°C) at first white, becoming "Pale Smoke Gray" (Ridgway, 1912, Pl. XLVI) in age; turf dense, composed of sporangiophores and azygophores; sporangiophores hyaline, smooth, erect or ascending, becoming cymosely branched, up to 2 cm in heighth, the primary stalk 5–13 μ in diam; sporangia grayish, wall minutely asperulate, rapidly deliquescent, globose, (10–)40–110(–135) μ in diam (aver. 80 μ); columella usually globose or subglobose, sometimes ovoid or pyriform, hyaline, smooth, (5–)15–60 μ in diam (aver. 35 μ); collar well-defined; sporangiospores hyaline, smooth, ovoid, ellipsoid, or slightly reniform, (3.5–)4.4–11.4(–15) μ × (2.2–)2.6–5.7(–10) μ (aver. 7.2 μ × 4 μ); chlamydospores rare in aging sporophores and aerial hyphae, intercalary or terminal, subglobose to cylindric, thick-walled, 10–25 μ × 8–20 μ, more common in substrate hyphae, single or in chains, mostly globose or subglobose, thin-walled, 10–35 μ in diam; zygospores never formed; azygospores abundant, produced terminally and subterminally on simple or branched azygophores 0.1–1.5 cm in height; azygospores globose or subglobose, orange-brown to brownish-black, 30–120 μ in diam (aver. 75 μ), including the coarse, conical exospore projections up to 12 μ in height.

Holotype.—INDIA. Uttar Pradesh. Near Ranikhet, B. S. Mehrotra and Usha Baijal; isolated from forest soil (RSA 1210; NRRL A-11,496). Cultures of the type have been sent to ATCC, CBS, and CMI.

A second isolate of this species was obtained recently from forest soil collected near Gorakhpur, Uttar Pradesh, but it had been studied by only one of us (BSM) at the time this paper went to press.

We have named this species for G. Bainier who was a pioneer student of the mucoraceous zygospore and the first to describe azygosporic species of the genus.

Mucor bainieri grows rapidly on SMA, YpSs, and ME-YE[4] agars under ordinary laboratory conditions. Its sporangiophores soon become irregularly cymosely branched with the successive branches and the sporangia they bear having smaller and smaller dimensions. As a result, there is great variation in the size of sporangia and columellae (Fig. 1 a–d) in any given study slide. Chlamydospores are formed only rarely in aerial hyphae (Fig. 1 g–i). They are common in the substrate hyphae, have thin walls, and are oidia-like in appearance (Fig. 1 f).

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[4]For constitution of media cited in this paper see Benjamin (Aliso 4: 322. 1959; Aliso 5: 16. 1961).

Twenty single-spore cultures derived from the original isolate of *M. bainieri* produced azygospores freely. Simple or branched azygophores arise directly from the substrate mycelium and vary in length from a millimeter to a centimeter or more. In mature cultures, azygospores are found at all levels within the colony. Although azygospores are numerous at room temperature (22–25°C), they are produced in great abundance when cultures are maintained at about 16–18°C. Growth is relatively slow at 6°C, but colonies often reach diameters of 6–8 cm after one month and sporangia and azygospores are produced in relatively great numbers at this temperature.

Azygospores are initiated by the formation of a small terminal or lateral cell delimited by the azygophore (Fig. 2 a). One to several spores may be formed by each azygophore

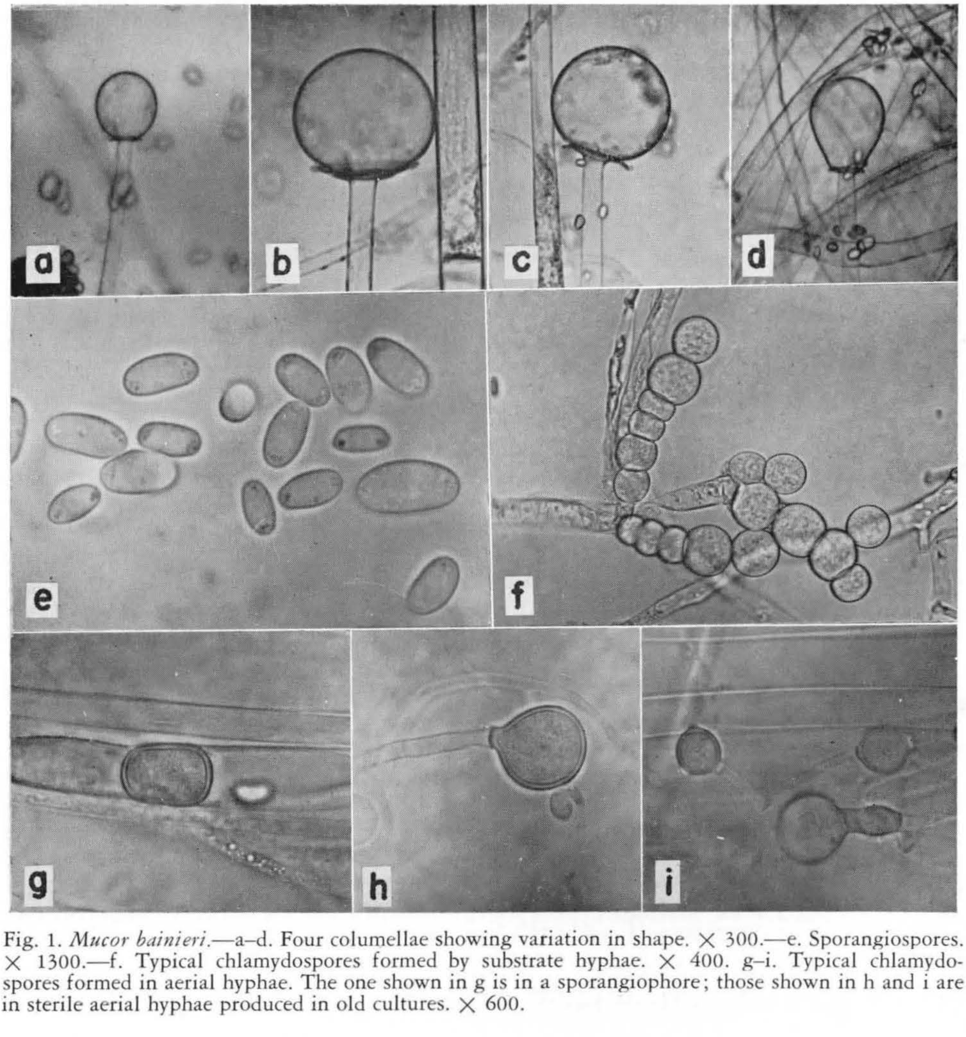

Fig. 1. *Mucor bainieri*.—a–d. Four columellae showing variation in shape. × 300.—e. Sporangiospores. × 1300.—f. Typical chlamydospores formed by substrate hyphae. × 400. g–i. Typical chlamydospores formed in aerial hyphae. The one shown in g is in a sporangiophore; those shown in h and i are in sterile aerial hyphae produced in old cultures. × 600.

(Fig. 2 b–f), and not infrequently one or more short branches may proliferate from the slightly swollen enlargement subtending an azygospore. These branches often give rise, in turn, to azygospores. Structurally, the azygospore of *M. bainieri* is like that of a typical zygospore of other species of *Mucor*. It has a smooth, hyaline, thick-walled endospore that may be readily displaced from the coarse, orange-brown to brownish-black exospore. The conical projections of the latter are very pronounced, often reaching 12 μ in height.

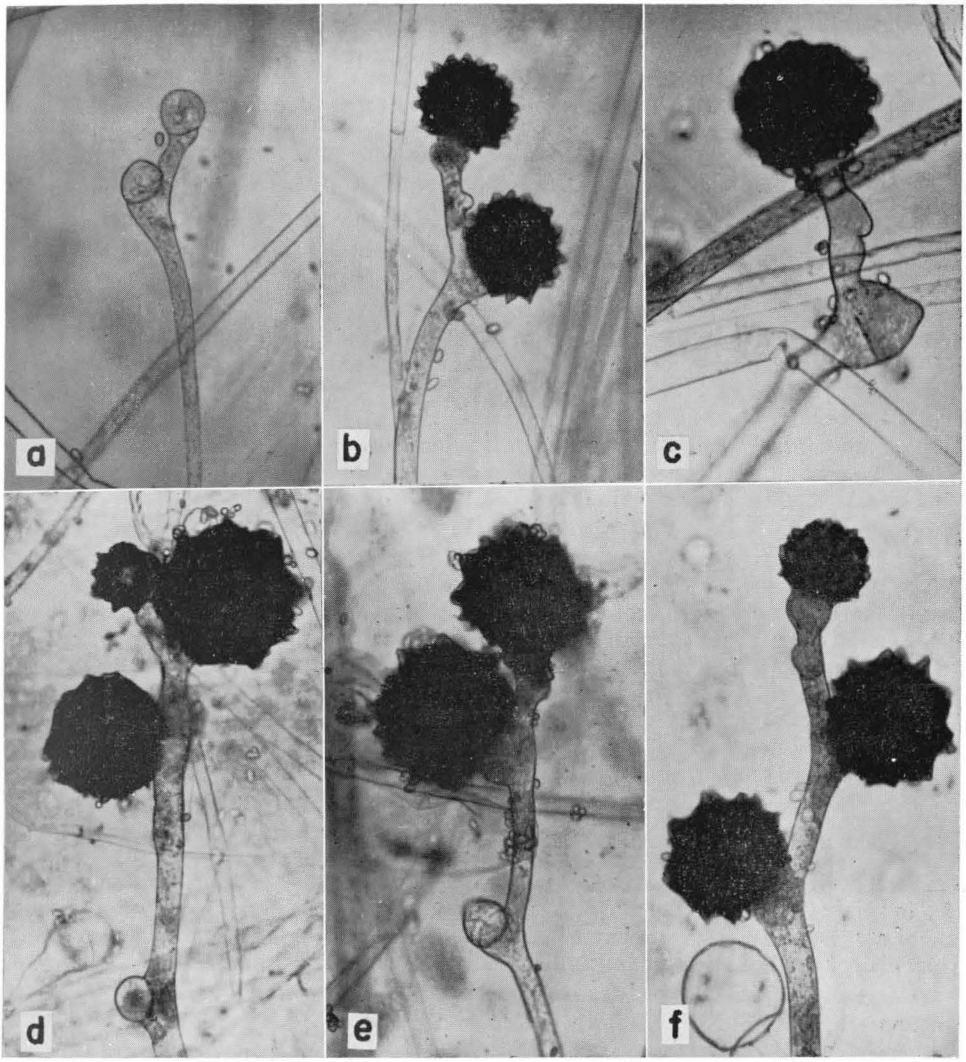

Fig. 2. *Mucor bainieri*—a. Terminus of an azygophore showing early stage of development of two azygospores. × 250.—b–f. Typical azygospores showing their arrangement on the azygophore. × 250.

In his original description of *Mucor tenuis,* Bainier (1883) stressed its similarity to *M. racemosus*. His Plate 19, fig. 3, shows numerous chlamydospores in its sporophores, a well-marked characteristic of species belonging to section *Racemosus* of the genus *Mucor* (Hesseltine, 1954). The chlamydospores of *M. tenuis* were shown to be minutely asperulate (Bainier, 1883, Pl. 19, fig. 4–6) and its azygospores were depicted as being formed by cells cut off by simple or branched suspensor-like outgrowths of the azygophores (Bainier, 1883, Pl. 19, fig. 10–12). *Mucor bainieri* would seem to resemble *M. tenuis* in some respects. However, the rarity of chlamydospores in the aerial hyphae and their smooth walls when present, the diffluent sporangia, and the more or less sessile azygospores should render *M. bainieri* quite distinct from *M. tenuis.*

The azygosporic *Mucor* described briefly and illustrated by Burgeff (1924, pp. 41–43, fig. 15) may have been the same as the one described here as *M. bainieri.* Burgeff called his isolate *Mucor racemosus* var. *tenuis*—*M. tenuis* in the legend to his figure—and regarded it as an example of a homothallic species of Mucoraceae.

Because *M. vicinus* and *M. neglectus* (Bainier, 1903) were inadequately described, it is not possible to compare them with *M. bainieri.*

Mucor azygospora Benjamin sp. nov.

Coloniae aurantiae; sporangiophoris simplicibus, rectis vel ascendentibus, ad 2 cm altis, 8–14 μ diam; sporangiis globosis, aurantiis, 35–175 μ diam (med. 110 μ); tunicis sporangiorum minute asperulatis, liquentibus; columellis aurantiis, nonnihil applanatis, 30–100 μ diam × 25–95 μ altis; collari manifesto; sporangisporis levibus, aurantiis, ellipsoideis, 5–13(–19) μ × 4–12 μ (med. 8.8 μ × 6.9 μ); chlamydosporis in sporangiophoris absentibus; oidiis in hyphis vegetantibus gestis, globosis vel subglobosis, 8–30 μ diam; zygosporis absentibus; azygosporis terminalibus, in azygophoris simplicibus vel ramosis 0.4–2 mm altis gestis; azygosporis nigris, nonnihil applanatis, 85–180 μ diam × 65–145 μ altis (med. 120 μ × 96 μ).

Colonies on SMA becoming "Orange" to "Orange Buff" (Ridgway, 1912, Pl. III), reverse concolorous; vegetative mycelium branched, becoming septate in age, consisting of robust primary hyphae, 10–25 μ in diam, giving rise to tapered lateral branches ranging from about 10–15 μ to 3–4 μ in diam, these branches, in turn, forming numerous laterals 2–5 μ in diam; turf lax, composed of sporangiophores, azygophores, and, in age, sterile irregularly branched hyphae; sporangiophores erect or ascending, unbranched, up to 2 cm long, 8–14 μ in diam, phototrophic; sporangia nearly globose, orange, 35–175 μ in diam (aver. 110 μ), wall minutely asperulate, rapidly deliquescent; columellae orange, subglobose, slightly flattened, 30–100 μ in diam × 25–95 μ in height, collar well-defined; sporangiospores smooth, orange, mostly ellipsoidal, 5–13(–19) μ × 4–12 μ (aver. 8.8 μ × 6.9 μ); chlamydospores absent in sporangiophores; oidia formed by subtrate hyphae, globose or ovoid, 8–30 μ in diam; zygospores never formed; azygospores abundant, formed terminally on simple or branched azygophores, black subglobose, slightly flattened, 85–180 μ in diam × 65–145 μ in height (aver. 120 μ × 96 μ) including exospore projections up to 12 μ in height; azygophores erect, phototrophic, 0.4–2 mm in height, 30–60 μ wide at juncture of azygospore, tapering downward abruptly and then 8–20 μ in diam, often becoming sympodially branched and forming 1–2 additional terminal azygospores.

Holotype.—OKLAHOMA. Blaine County. 8.8 miles west of Okeene, on Highway 51, September 1, 1960, R. K. Benjamin; isolated from lizard (?) dung (RSA Culture 1014). Cultures have been sent to the ATCC, CBS, and CMI.

This species develops rather slowly at room temperature, and colonies on SMA often reach diameters of only 7–8 cm after three weeks. Unlike *M. bainieri,* it fails to grow at 6°C.

The vegetative and fruiting hyphae as well as the sporangiospores are bright orange, and the color tends to fade noticeably as a culture ages. The materials responsible for this pigmentation do not diffuse into the substrate. When mycelium is homogenized and extracted with petroleum ether, at least three substances—two orange and one red—may be separated readily by paper chromatography using a 50 : 50 mixture of benzene and petroleum ether as the solvent system. These substances, one undoubtedly a carotene, have not been examined further.

The distinctive, more or less open growth habit of the vegetative mycelium of *M. azygospora* is shown in Fig. 4 a. Sporangiophores and azygophores develop concurrently, and the latter usually outnumber the former during early development of a colony. Both are phototrophic.

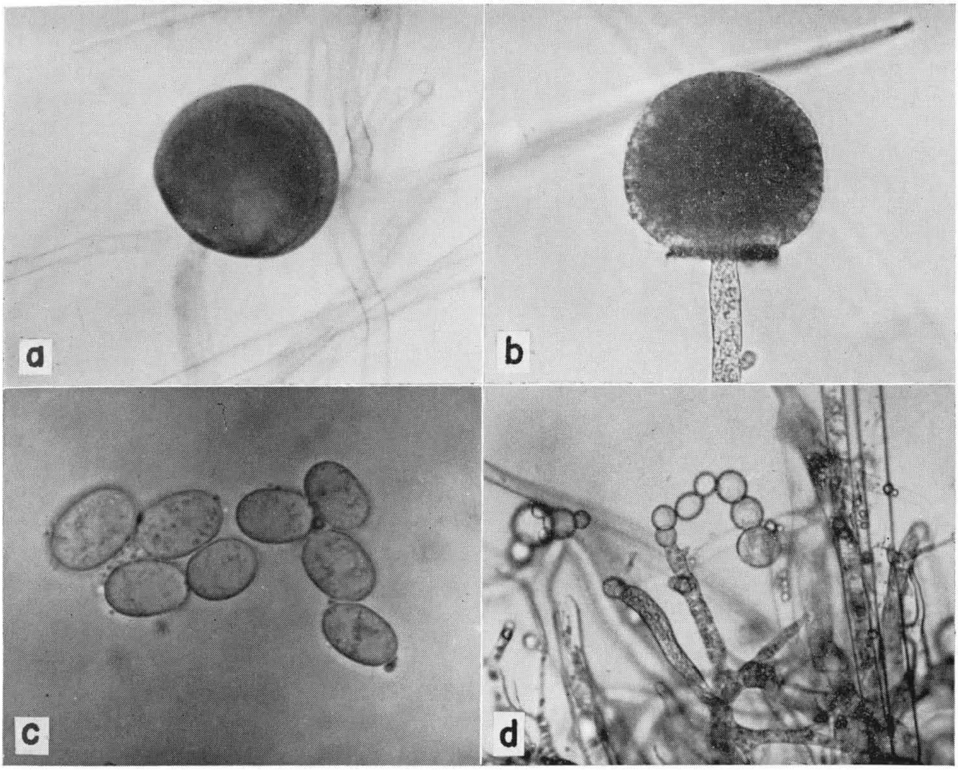

Fig. 3. *Mucor azygospora.*—a. Immature sporangium showing columella and intact sporangial wall. × 250.—b. Typical columella showing basal collar. × 400.—c. Sporangiospores. × 1300.—d. Oidia formed by substrate hyphae. Note budding in those at left. × 250.

Sporangiophores are unbranched and without chlamydospores. The columella is intensely pigmented, and it has a well-defined basal collar that usually is reflexed at its margin (Fig. 3 b). The sporangial wall (Fig. 3 a) rapidly deliquesces and the orange spores (Fig. 3 c) are retained in a drop of liquid. Oidia, that may bud yeast-like, are formed by the submerged vegetative hyphae (Fig. 3 d).

As in *M. bainieri,* azygospore formation is a stable characteristic of *M. azygospora.* Ten single-spore cultures derived from the original collection of the latter have produced such spores without exception. The erect azygophore becomes clavate distally and delimits a small terminal cell (Fig. 4 c) that enlarges rapidly and forms a slightly flattened azygospore (Fig. 4 d–e). Although usually simple (Fig. 4 f), azygophores occasionally may branch sympodially (Fig. 4 b).

* * *

In his paper on sexuality in the Mucorales, Ling-Young (1930) summarized various factors found to influence azygospore formation in many well-known homothallic and heterothallic species. Adverse cultural conditions were shown, as had been suspected for many years, to have a decided affect. Thus, high concentrations of asparagine, glucose, and peptone were found to increase greatly the number of azygospores formed by *Absidia glauca, Zygorhynchus macrocarpus,* and *Syzygites megalocarpus (Sporodinia grandis)* respectively. Also, azygospore formation was stimulated in such species as *Absidia glauca* and *Mucor mucedo* when opposite strains—one growing in a favorable medium (bread agar) and one growing in an unfavorable medium (2–3% urea in 5% gelatine)—were allowed to make contact (Ling-Young, 1930, pp. 356, 358). Blakeslee (1906, p. 4) obtained azygospores in *Syzygites megalocarpus* when young zygosporic cultures were subjected to the effects of drying and reduced atmospheric pressure. Imperfect sexual reactions, either between different species or races of the same species, may result in azygospores. These have been found in crosses of *Absidia cylindrospora* with *A. glauca* and, more rarely, with *Mucor hiemalis* (Ling-Young, 1930, p. 356) ; *Cunninghamella bertholletiae* with *C. echinata* (Blakeslee, et. al., 1921, p. 214) ; and *Mucor genevensis* with *Mucor V (=M. hiemalis), Absidia spinosa* with several species of Mucoraceae, *Zygorhynchus moelleri* with *Mucor* V, and *Z. vuilleminii* var. *agamus* with *Z. vuilleminii* (Blakeslee, 1915, pp. 91–95). Ling-Young (1930, p. 357) demonstrated that crosses of certain strains of *Mucor hiemalis* gave rise to more or less numerous azygospores. Azygospores of *Rhizopus sexualis* were obtained by Callen (1940, p. 801–802) in crosses of this species with *Mucor hiemalis* and *Absidia glauca,* and he found a definite stimulation of azygospore production in *R. sexualis* in his hybridization experiments. Orban (1919, p. 59) stated that azygospores were formed in *Phycomyces blakesleeanus* (as *P. nitens*) only when a homothallic mycelium was crossed with a heterothallic mycelium.

Ling-Young (1930, p. 361) concluded that parthenogenesis in the Mucorales is only an accidental phenomenon and is without real significance. He also believed that it is not necessarily indicative of a loss of sexuality or of a tendency for a shift from heterothallism to homothallism, or the reverse, as had been postulated by various authors (Van Tieghem, 1875; Hagem, 1908; Vuillemin, 1907; Namyslowski, 1920).

Elucidation of the biological significance, if any, of obligate azygospore formation—as observed in *Mucor bainieri, M. azygospora,* and *Absidia spinosa* var. *azygospora* in contrast to the apparently fortuitous occurrence of such spores in other Mucorales—must await further study. These fungi may represent, as Burgeff (1924) apparently believed in the case of the fungus he called *Mucor racemosus* var. *tenuis,* only a special case of homothallism (homomixis, fide Burnett, 1956). They may, however, be truly amictic (Burnett, 1956) as has been suggested for *Syzygites megalocarpus* (Cutter, 1942). Knowledge of the nuclear behavior of their azygospores as well as the reactions of these fungi when mated with typical homothallic and heterothallic species should give precise information of their sexual nature.

LITERATURE CITED

Bainier, G. 1882. Étude sur les Mucorinées. Thèse. F. Pichon et A. Cotillon, Paris. 136 p.

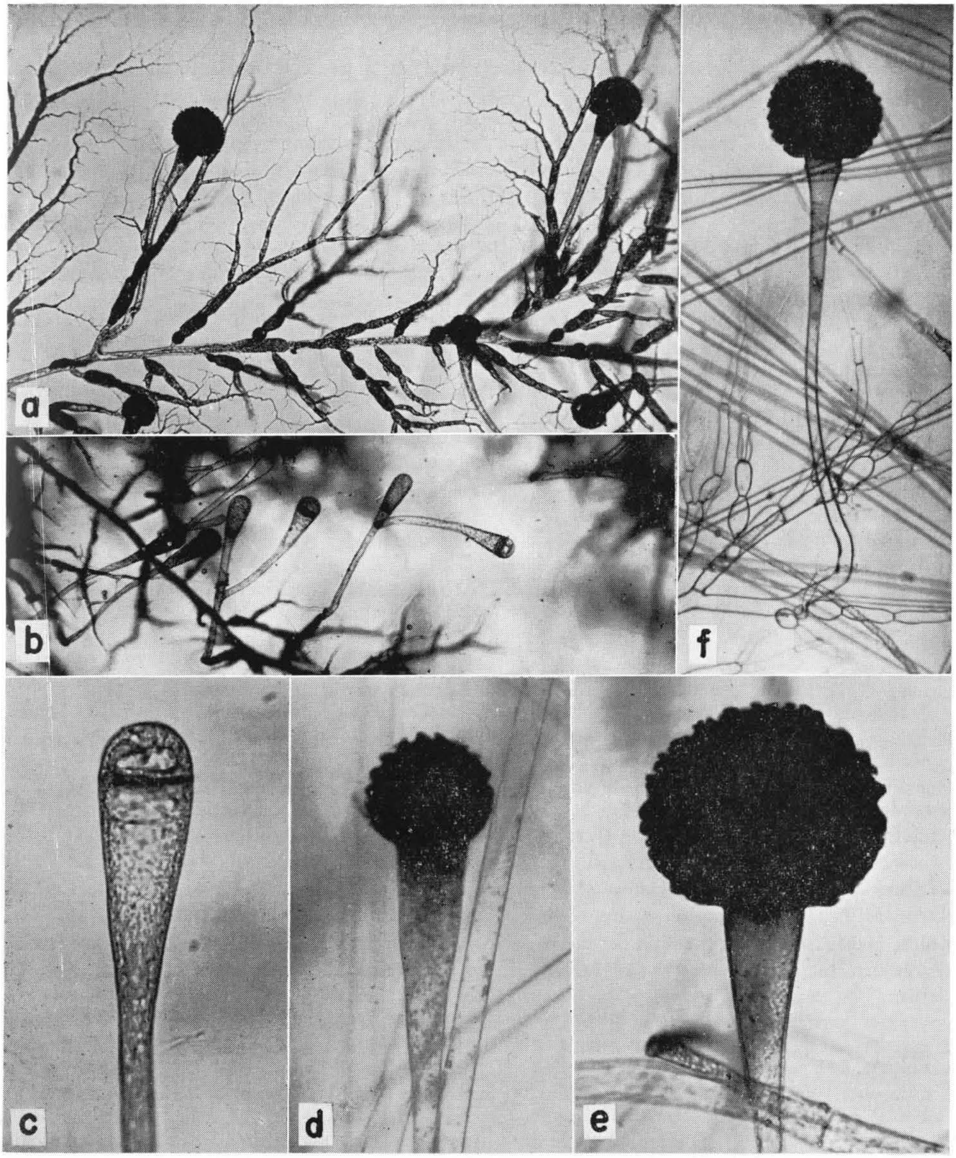

Fig. 4. *Mucor azygospora.*—a. Typical substrate hyphae giving rise to azygophores. × 60.—b. Two immature azygophores that are sympodially branched. × 50.—c. Terminus of an azygophore showing initial stage in the development of a terminal azygospore. × 250.—c. Later stage of development of an azygospore. × 250.—e. Mature azygospore. × 250.—f. Mature azygospore showing its terminal position and the relationship of the azygophore to the substrate hyphae. × 100.

———. 1883. Sur les zygospores des Mucorinées. Ann. Sci. Nat., Botan., Sér. 6. 15: 342–356.

———. 1884. Nouvelles observations sur les zygospores des Mucorinées. Ann. Sci. Nat., Botan., Sér. 6. 19: 200–216.

———. 1903. Sur quelques espèces de Mucorinées nouvelles ou peu connues. Bull. Soc. Mycol. France 19: 153–172.

Benjamin, R. K. 1959. The merosporangiferous Mucorales. Aliso 4: 321–433.

Blakeslee, A. F. 1906. Zygospore germinations in the Mucorineae. Ann. Mycol. 4: 1–28.

———. 1915. Sexual reactions between hermaphroditic and dioecious Mucors. Biol. Bull. 29: 87–103.

———., J. L. Cartledge, and D. S. Welch. 1921. Sexual dimorphism in *Cunninghamella*. Bot. Gaz. 72: 185–219.

Boedijn, K. B. 1958. Notes on the Mucorales of Indonesia. Sydowia, Ann. Mycol., Ser. II. 12: 321–362.

Burgeff, H. 1924. Untersuchungen über Sexualität und Parasitismus bei Mucorineen. I. Botan. Abhandlungen 4: 1–135.

Burnett, J. H. 1956. The mating systems of fungi. I. New Phytol. 55: 50–90.

Callen, E. O. 1940. The morphology, cytology, and sexuality of the homothallic *Rhizopus sexualis* (Smith) Callan. Ann. Bot., N. S. 4: 791–818.

Corda, A. C. J. 1839. Pracht-Flora Europaeischer Schimmelbildungen. Gerhard Fleischer, Leipzig und Dresden. 55 p.

Cutter, Victor M., Jr. 1942. Nuclear behavior in the Mucorales—II. The *Rhizopus, Phycomyces* and *Sporodinia* patterns. Bull. Torrey Botan. Club. 69: 592–616.

Dangeard, P. A. 1903. Recherches sur le developpement du périthèce chez les Ascomycetès. Le Botaniste 9: 57–303.

De Bary, A. 1864. Beiträge zur Morphologie und Physiologie der Pilze. IV. *Syzygites megalocarpus.* Abhand. Senckenb. nat. Ges. 5: 210–224, 230–232.

Fischer, A. 1892. Phycomycetes, *in* Rabenhorst, L., Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz, Zweite Auflage. 1(4): 1–505.

Fries, E. 1825. Syst. Orb. Veg., Part 1, p. 365.

———. 1829-1832. Syst. Mycol. 3: 1–524.

Grove, W. B. 1934. A systematic account and arrangement of the Pilobolidae. *In* A. H. R. Buller. Researches on fungi. Vol. 6, pp. 190–224. Longmans, Green & Co., New York.

Hagem, O. 1908. Untersuchungen über Norwegische Mucorineen. I. Videnskabs-Selskabets Skrifter. I. Math.-Naturv. Klasse., Christiana. No. 7. 1907. 50 p.

Hansen, E. C. 1902. Recherches sur le physiologiè et la morphologie des ferments alcooliques. Comptes rendus Lab. Carlsberg. 5: 95–107.

Hesseltine, C. W. 1954. The section *Genevensis* of the genus *Mucor*. Mycologia 46: 358–366.

———. 1957. The genus *Syzygites* (Mucoraceae). Lloydia 20: 228–237.

Kanouse, B. B. 1924. The life history of a new homothallic *Mucor*. Pap. Mich. Acad. Sci. 3: 123–130.

Keene, M. L. 1914. Cytological studies of the zygospore of *Sporodinia grandis*. Ann. Bot. 28: 455–470.

Kniep, Hans. 1928. Die Sexualität der niederen Pflanzen. Verlag von Gustav Fischer, Jena. 544 p.

Leadbeater, G., and C. Mercer. 1957a. Zygospores in *Piptocephalis*. Trans. Brit. Mycol. Soc. 40: 109–116.

——— and ———. 1957b. *Piptocephalis virginiana* sp. nov. Trans. Brit. Mycol. Soc. 40: 461–471.

Léger, Maurice. 1896. Recherches sur la structure des Mucorinées. E. Druinaud, Libraire-Éditeur, Poitiers. 153 p.

Lendner, A. 1908. Les Mucorinées de la Suisse, *in* Beiträge zur Kryptogamenflora der Schweiz. 3(1): 1–180. K.-J. Wyss, Libraire-Éditeur, Berne.

Ling-Young. 1930, 1931. Étude biologique des phénomenès de la sexualitié chez les Mucorinées. Rev. Gén. Botan. 42: 144–158, 205–218, 283–296, 348–365, 409–428, 491–504, 535–552, 618–639, 681–704, 722–752; 43: 30–43.

Linnemann, G. 1935. Beitrag zu einer Flora der Mucorineae Marburgs. Flora, Neue Folge 30: 176–217.

Moreau, F. 1913. Une nouvelle Mucorinée du sol, *Zygorhynchus Bernardi* nov. sp. Bull. Soc. Botan. France 60: 256–258.

Namyslowski, Boleslaw. 1910. Studien über Mucorineen. Bull. Acad. Sci. Cracovie. Cl. Sci. Math. et Nat., Sér. B: Sci. Nat.: 477–520.

———. 1920. État actuel des recherches sur les phénomènes de la sexualité des Mucorinées. Rev. Gén. Botan. 32: 193–215.

Naumov, N. A. 1939. Clés des Mucorinées (Mucorales). Encyclopédie Mycologique 9: 1–137.

Orban, Grete. 1919. Untersuchungen über die Sexualität von *Phycomyces nitens*. Beih. z. Botan. Centralb., Erste Abteil. 36: 1–59.

Ridgway, R. 1912. Color standards and color nomenclature. Publ. by the author. Washington, D. C.

Tavel, F. von. 1892. Vergleichende Morphologie der pilze. Verlag von Gustav Fischer, Jena. 208 p.

Van Tieghem, Ph. 1875. Nouvelles recherches sur les Mucorinées. Ann. Sci. Nat., Botan., Sér. 6. 1: 5–175.

———. 1876. Troisième mémoire sur les Mucorinées. Ann. Sci. Nat., Botan., Sér. 6. 4: 312–398.

Vuillemin, Paul. 1887. Études biologiques sur les Champignons. Bull. Soc. Sci. Nancy, II. 8(22): 33–161.

———. 1903. Importance taxinomique de l'appareil zygosporé des Mucorinées. Bull. Soc. Mycol. France 19: 106–118.

———. 1904. Recherches morphologiques et morphogéniques sur la membrane des zygospores. Ann. Mycol. 2: 483–506.

———. 1907. Les bases actuelles de la systématique en Mycologie. Progressus Rei Botan. 2(1): 1–170.

Zycha, H. 1935. Mucorineae, *in* Kryptogamenflora der Mark Brandenburg. 6a: 1–264.