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OBSERVATIONS ON THAMNIDIACEAE (MUCORALES).
 II. *CHAETOCLADIUM*, *COKEROMYCES*, *MYCOTYPHA*,
 AND *PHASCOLOMYCES*^{1,2}

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SUMMARY

Four previously established genera of Thamnidiaceae and their recognized species are described and illustrated. Seven species are treated as follows: *Chaetocladium jonesii*, *C. brefeldii*, *Cokeromyces recurvatus*, *Mycotypha africana*, *M. microspora*, *M. poitrasii* (a new combination based on *Cokeromyces poitrasii*), and *Phascolomyces articulatus*.

Phascolomyces articulatus, the type species of *Phascolomyces*, was described in 1959 without the preservation of a nomenclatural type as required by the *International Code of Botanical Nomenclature*, and original material is unknown. A neotype specimen is designated (preserved in RSA) for validation of the genus and species.

INTRODUCTION

In our first contribution on the Thamnidiaceae (Benny and Benjamin, 1975),³ we characterized the family, briefly reviewed its taxonomic history, and discussed six of the 13 genera we include in it, *Thamnostylum* von Arx & Upadhyay (von Arx, 1970), *Backusella* Hesseltine & Ellis (Ellis and Hesseltine, 1969), *Fennellomyces* Benny & Benjamin (1975), *Ellisomyces* Benny & Benjamin (1975), *Zychaea* Benny & Benjamin (1975), and *Dichotomocladium* Benny & Benjamin (1975).

Our purpose here shall be to provide descriptions and illustrations of the members of four additional genera of Thamnidiaceae, *Chaetocladium* Fresenius (1863), *Cokeromyces* Shanor (Shanor, Poitras, and Benjamin, 1950), *Mycotypha* Fenner (1932), and *Phascolomyces* Boedijn (1958 [1959]). Like

¹ Based on a portion of a thesis by the senior author presented in partial fulfillment of the requirements for the Ph.D. degree in Botany at the Claremont Graduate School, Claremont, California 91711, 1973.

² Florida Agricultural Experiment Station Journal Series 9082.

³ Errata found in part I:

p. 301, l. 13 of Introduction—delete Zycha et al., 1969.

p. 310, l. 2 of *Specimens examined*—IMI 86838 not 86383.

p. 339, l. 26, should read: . . . at 7 C, and *C. jonesii* develops poorly at. . .

p. 345, last line of legend—(RSA 1081+ × 1346-) not (RSA 1081- × 1346+).

p. 349, l. 8 from bottom—Corda, A. C. J. not A. C. I.

species of *Dichotomocladium*, all representatives of these genera lack terminal, columellate, multispored sporangia; they produce only unispored or multispored sporangiola.

In a concluding work, to appear later, the remaining thamnidiaceous genera, *Helicostylum* Corda (1842), *Thamnidium* Link ex Gray (1821), and *Pirella* Bainier (1882), will be treated.

Procedures for procuring, culturing, studying, and disposing of cultures or specimens were given in our previous paper (Benny and Benjamin, 1975: 303-304).

DESCRIPTIONS AND COMMENTARY

CHAETOCADIUM Fresenius, Beitr. Mykol., p. 97. 1863.

Sporophores arising directly from the substrate mycelium, from stolons, or from galls formed on the hyphae of parasitized mucoralean hosts; erect, ascending, or repent; simple or branched; the primary axis and its branches forming sterile terminations and giving rise laterally to fertile branches. Fertile branches several times successively verticillately branched, the ultimate branches forming small terminal or intercalary vesicular enlargements bearing short-stalked unispored sporangiola. Vesicles globose to subglobose or angular in outline. Sporangiole pedicels short, tapered. Sporangiole globose to subglobose, columellate; wall thin, persistent, nearly smooth to spinulose; columella flattened to slightly convex above. Sporangiospores like the sporangiola in size and shape, smooth. Zygosporangia globose to subglobose; wall pigmented, ornamented with coarse projections; suspensors opposed.

Type species: Botrytis jonesii Berkeley & Broome.

The history and taxonomy of *Chaetocladium* and its two known species, *C. brefeldii* van Tiegh. & Le Monn. (1873b) and *C. jonesii* (Berk. & Br.) Fres. (1863), were reviewed by Hesseltine and Anderson in 1957 and we can add little to their treatment. Because of their unispored sporangiola, *Chaetocladium* spp. have been regarded by many students of Mucorales as constituting a separate family, Chaetocladaceae (Brefeld, 1872, 1881b; Schröter, 1886, 1893; Engler, 1898; Fischer, 1892; Migula, 1910; Lendner, 1908; Lindau, 1922; and Fitzpatrick, 1930). Milko and Beljakova (1967) and Milko (1967, 1974) treated *Chaetocladium* as a genus of Cunninghamellaceae rather than Thamnidiaceae; in 1971 Pidoplichko and Milko placed all Mucorales having unispored sporangiola—regardless of characteristics suggesting other relationships—together in the Cunninghamellaceae. Because, in our view (Benny and Benjamin, 1975: 302), the unispored sporangiole should not be overemphasized in classifying Mucorales at the family level, we follow several other students of these fungi, including Christenberry (1940), Hesseltine (1955), Hesseltine and Ellis (1973), Zycha (1935), and Zycha, Siepmann, and Linneman (1969), and retain *Chaetocladium* in the Thamnidiaceae.

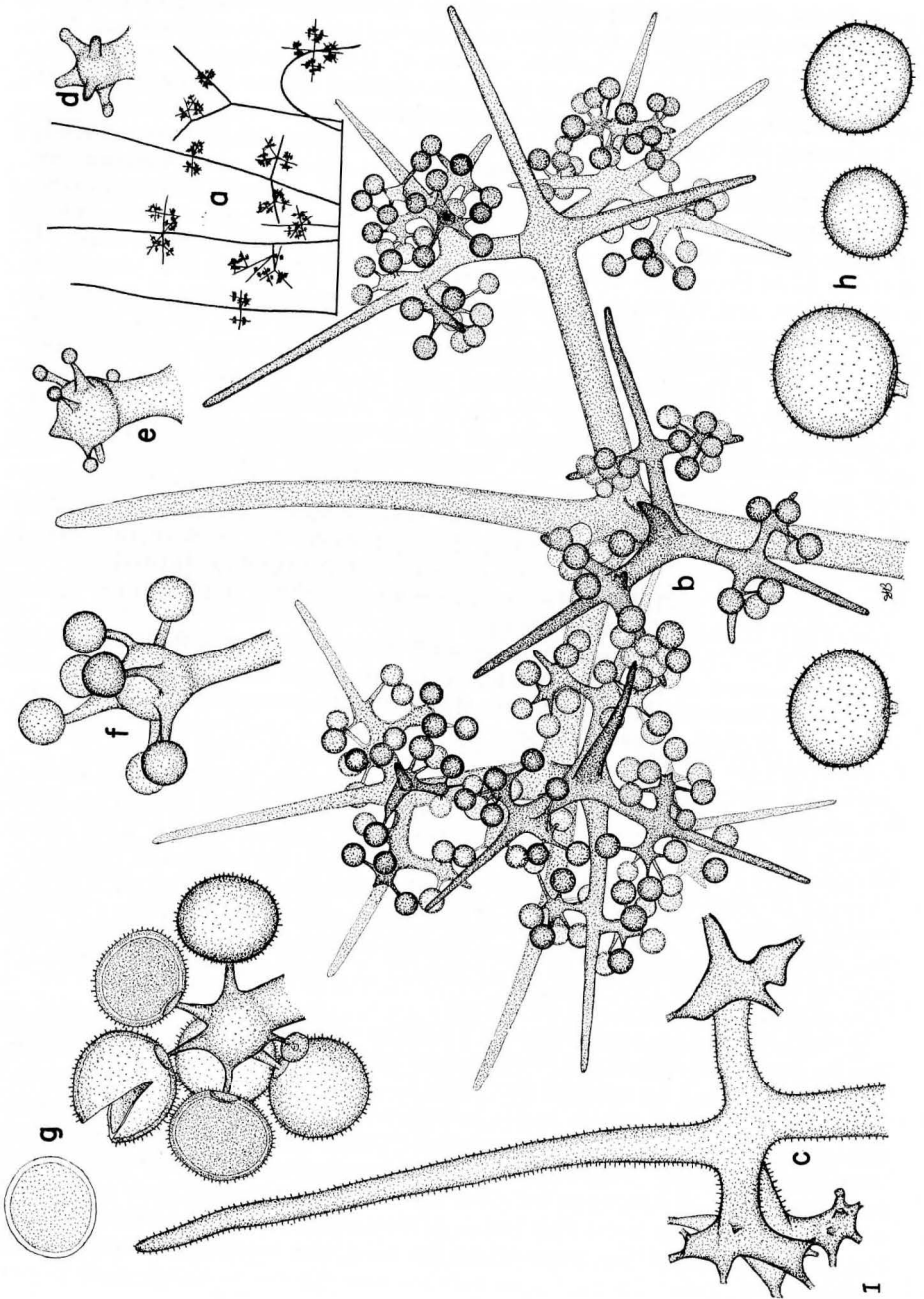
In our earlier paper (Benny and Benjamin, 1975: 338-339) we compared *Chaetocladium* with the newly described *Dichotomocladium*. Representatives of these genera resemble one another in gross aspect but differ funda-

mentally in the branching pattern of the sporangiole-bearing elements—dichotomous in *Dichotomocladium* and verticillate in *Chaetocladium*. Unlike species of *Dichotomocladium*, species of *Chaetocladium* may occur in nature as gall-forming facultative parasites of other Mucorales and will grow and sporulate readily at reduced temperatures (as low as 7 C).

Following Fresenius's (1863) transfer of Berkeley and Broome's (1854) *Botrytis jonesii* to a new genus, *Chaetocladium*, de Bary and Woronin (de Bary, 1865, 1866) regarded both *Botrytis jonesii* (i.e., *Chaetocladium jonesii*) and *Thamnidium elegans* Link ex Gray as states of a presumably pleomorphic species of *Mucor*—identified by them as possibly representing *M. mucedo* L. ex Fres. Van Tieghem and Le Monnier (1872) at first concurred with de Bary and Woronin and attributed a remarkable number of spore and sporangial types to *M. mucedo*—the result of working with mixed cultures. However, their further studies employing pure cultures (van Tieghem and Le Monnier, 1873a,b) soon convinced them that *C. jonesii* and other taxa (i.e., species of *Circinella* van Tiegh. & Le Monn. [1873b], *Helicostylum*, *Thamnidium*) were distinct members of the Mucorinées [Mucorales] and that *C. jonesii* possessed a true, albeit unispored, sporangium with an endogenously formed spore and should not be regarded as a conidial state of *Mucor mucedo* comparable to the relationship between "*Aspergillus glaucus*" and *Eurotium herbariorum* [Pers.] Link ex Fr. or *Botrytis cinerea* Pers. ex Fr. and *Peziza fuckeliana* de Bary [= *Botryotinia fuckeliana* (de Bary) Whetz. (1945)] of the ascomycetes in which the asexual spore (conidium) is developed exogenously.

Brefeld (1872), in a carefully controlled study, gave a detailed account of the development of the asexual and sexual states of *Mucor mucedo* and a species of *Chaetocladium* which he showed to be parasitic on *M. mucedo*. However, Brefeld actually studied an undescribed small-spored species of *Chaetocladium* which he identified with *C. jonesii*. This oversight was clarified a year later by van Tieghem and Le Monnier (1873b) who named the small-spored form *C. brefeldii* and conducted extensive studies on both species of *Chaetocladium* in pure culture and mixed culture with other Mucorales in fruit juices and dung decoction. They demonstrated that parasitism of *C. jonesii* and *C. brefeldii* on other Mucorales is facultative rather than obligate. The classic studies of van Tieghem and Le Monnier (1873b) and van Tieghem (1875, 1876) established a generic concept not only for *Chaetocladium* but for many other genera of Mucorales that has changed little during the succeeding 100 years.

Brefeld refused to recognize van Tieghem and Le Monnier's *C. brefeldii* and he continued to call the small-spored species *C. jonesii* (Brefeld, 1881a, 1891); in 1881(a) he applied the name *C. fresenianum* to the large-spored form, recognized by others as *C. jonesii*, and described and illustrated its zygospore and its parasitism on several species of Mucorales. Ten years later Brefeld (1891: 65), undoubtedly in error, used the name *C. fresenii* Bref. for his *C. fresenianum*; he cited the former name only once in his text where otherwise he used the latter. Unfortunately, Tavel (1892: 26 and Fig. 8) perpetuated the error when he used the name *C. fresenii* in his textbook.



Brefeld (1891: 64-65) believed that the two species of *Chaetocladium* demonstrated the transition from a unispored sporangium like that occasionally found in *Thamnidium elegans* and his *T. chaetocladioides* [= *Helicostylum pulchrum* (Preuss) Pidoplichko & Milko (1971)], where only one spore, rather than several, is free-formed within a previously delimited sporangium and its wall clearly separated from the sporangial wall, to an entirely new structure in which the sporangium and single spore are presumably formed simultaneously and have their walls fused from the beginning of their development. The term conidium already had come into general use for a variety of asexual spores having different ontogenetic and phylogenetic origins (de Bary, 1866), and Brefeld adopted it for the *Chaetocladium*-type spore. He (Brefeld, 1872) subdivided his "Zygomyceten" into two subdivisions, one sporangial (Mucorinen) and the other conidial (Chaetocladiaceen and Piptocephaliden). We (Benny and Benjamin, 1975; Benjamin, 1966) already have noted the influence of Brefeld's philosophy on subsequent classifications of the Mucorales.

KEY TO THE SPECIES OF *CHAETOCLADIUM*

- A. Sporangia mostly 7-10 μ m in diam; wall strongly spinulose 1. *C. jonesii*
 AA. Sporangia mostly 4-6 μ m in diam; wall nearly smooth to minutely roughened
 2. *C. brefeldii*

1. *CHAETOCLADIUM JONESII* (Berkeley & Broome) Fresenius, Beitr. Mykol. p. 98. 1863. FIGS. 1, 3a-c
 = *Botrytis jonesii* Berk. & Br., Ann. Mag. Nat. Hist., Ser. II 13: 462. 1854.
 = *Chaetocladium fresenianum* Bref., Bot. Untersuch. Schimmelpilze 4: 55. 1881.
 = *Chaetocladium fresenii* Bref., Untersuch. Gesamtgebiete Mykol. 9: 65. 1891. (nomen superfl.)

Colonies on MEYE to ca. 8.5 cm in diam in 7-10 days at 17 C; turf dense, reaching lid of Petri dish (2 cm), soon collapsing, white at first, in 10 days near Pale Neutral Gray, becoming near Olive-Gray on drying. Sporophores simple or branched, rough, hyaline to pale yellow, arising directly from the substrate hyphae or from stolons; in nature often arising directly from galls

Fig. 1. *Chaetocladium jonesii*.—a. Habit sketches of sporophores. $\times 15$.—b. Distal part of a sporophore showing typical verticillate branching pattern. $\times 435$.—c. Portion of a secondary branch showing verticillate ultimate branchlets terminated by the fertile enlargements from which the sporangia have fallen leaving the pedicellar bases. $\times 1,670$.—d-f. Three stages of development of sporangia from fertile vesicles. $\times 1,670$.—g. Mature pedicellate sporangia still attached to subtending vesicle; two sporangia are shown in optical section; one sporangiospore has been dislodged from the persistent sporangial wall. Note small, discoid columellae. $\times 1,670$.—h. Representative detached sporangia, two with part of pedicel still attached. $\times 1,670$.

on parasitized mucoralean hosts; erect, ascending, or repent with stolons and rhizoids; 3–20 mm or more high, 5–30 μm in diam; often ending in a blunt, sterile prolongation; producing up to 3 successive verticils of branches that often are irregularly septate and rough in age; the ultimate branches bearing sporangiola. Branches comprising each succeeding verticil smaller than the branch from which they arise; typically consisting of a stalk subtending the next order of more or less perpendicular branches and a sterile, spinose prolongation. Primary branches of fertile branch system nearly perpendicular or slightly divergent from the main axis; borne singly, in pairs, or in verticils of 3–7 branches; straight or slightly curved, tapered, variable in length, 275 μm or more including spinose prolongation, 10–25 μm in diam at base. Secondary and tertiary branches arising singly, in pairs, or in verticils of usually 3–4 branches, tapered, variable in length from about 25 μm to 175 μm or more; the ultimate branches 25–100 μm long, 3–6 μm in diam at base. Ultimate branches bearing pedicellate sporangiola on small terminal or intercalary enlargements or giving rise to whorls of short branchlets, 5–15 μm long, terminated by small vesicles bearing sporangiola; fertile branchlets often with spinose prolongations. Vesicles globoid, clavate, or irregular in shape, up to 12 μm in diam; smooth or minutely roughened. Sporangiolar pedicels smooth, tapered, 2–8 μm long, 1–2 μm in diam at base, ca. 1 μm in diam at apex. Sporangiola grayish, slightly subglobose in lateral view, (6–)7–10(–14) μm in diam; wall thin, grayish, spinulose, readily rupturing under pressure and releasing the sporangiospore; columella discoid, flattened to slightly convex above, 2–3 μm in diam. Sporangiospores like the sporangiola in size and shape, grayish, smooth, thin walled. Zygospores (after Brefeld, 1881a, Pl. II, Fig. 4a–b) globose to subglobose, est. ca. 100 μm in diam, ornamented with blunt, more or less conical projections; suspensors slightly swollen, more or less equal, est. ca. 40–55 \times 35–50 μm . Heterothallic.

Distribution.—Belgium, England, France, Germany, Japan, The Netherlands, U.S.A. (Zycha et al., 1969).

Illustrations.—As *Botrytis jonesii* state of *Mucor mucedo*: de Bary and Woronin (1866 [see de Bary, 1865]), Taf. VI, Figs. 11–22; de Bary (1866), Fig. 72.—As *Chaetocladium fresenianum*: Brefeld (1881a), Pl. 2, Figs. 1–4; (1891), Pl. II, Figs. 22–23.—As *Chaetocladium fresenii*: Tavel (1892), Fig. 16(8).—As *Chaetocladium jonesii*: Fischer (1892), Fig. 47d; Fresenius (1863), Pl. XII, Figs. 5–12 (see pp. 97–98); Fitzpatrick (1930), Fig. 91d; Léger (1896), Pl. XII, Figs. 75–78; Lindau (1922), p. 67, Fig. 111; Naumov (1954), Fig. 76; van Tieghem and Le Monnier (1873b), Pl. 23, Figs. 64–70; Zycha (1935), Fig. 75b; Zycha et al. (1969), Fig. 50b.

Specimen examined.—U.S.A. WISCONSIN. Sauk Co.: Ferry Bluff, nr. Sauk City, hardwood forest soil, 1946, C. W. Hesseltine (RSA 772; = NRRL 2343; = CBS 161.48).

2. *CHAETOCLADIUM BREFELDII* van Tieghem & Le Monnier, Ann. Sci. Nat. Bot., Sér. 5, 17: 342. 1873. Figs. 2, 3d–g
 = *Chaetocladium jonesii* Bref., Bot. Untersuch. Schimmelpilze 1: 29. 1872. [non *C. jonesii* (Berk. & Br.) Fres.]
 = *Chaetocladium brefeldii* van Tiegh. & Le Monn. var. *macrosporum* Burgeff, Bot. Abh. 1(4): 109. 1924.

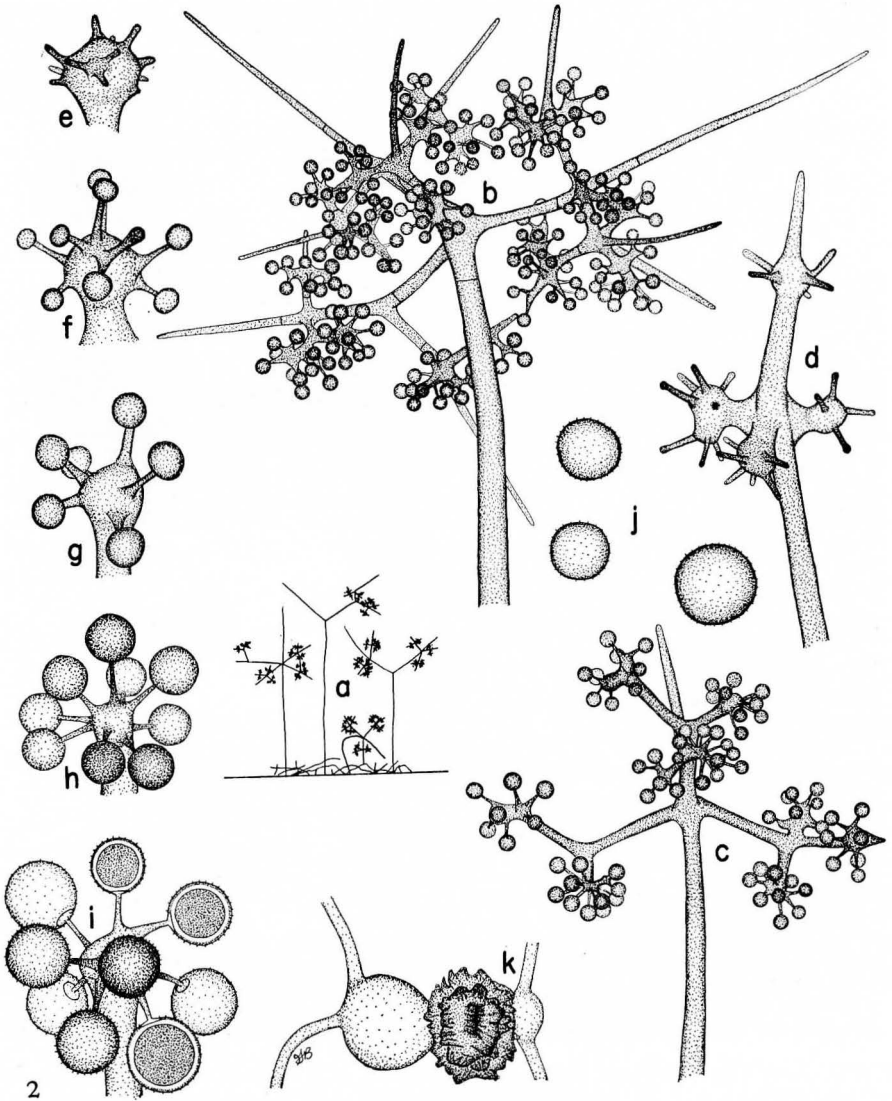


Fig. 2. *Chaetocladium brefeldii*.—a. Habit sketches of sporophores. $\times 15$.—b-c. Distal parts of two sporophores showing verticillate branching pattern of sporangiole-bearing and sterile branchlets. $\times 435$.—d. Secondary branch showing fertile vesicles being formed by main axis and lateral branchlets; sporangial initials are developing. $\times 1,210$.—e-h. Four stages of development of sporangia from fertile vesicles. $\times 1,670$.—i. Mature pedicellate sporangia still attached to the subtending vesicle; three sporangia are shown in optical section. Note small, discoid columellae. $\times 1,670$.—j. Representative detached sporangia. $\times 1,670$.—k. Typical zygospore and its suspensors (RSA 1119- \times RSA 1137+). $\times 320$.

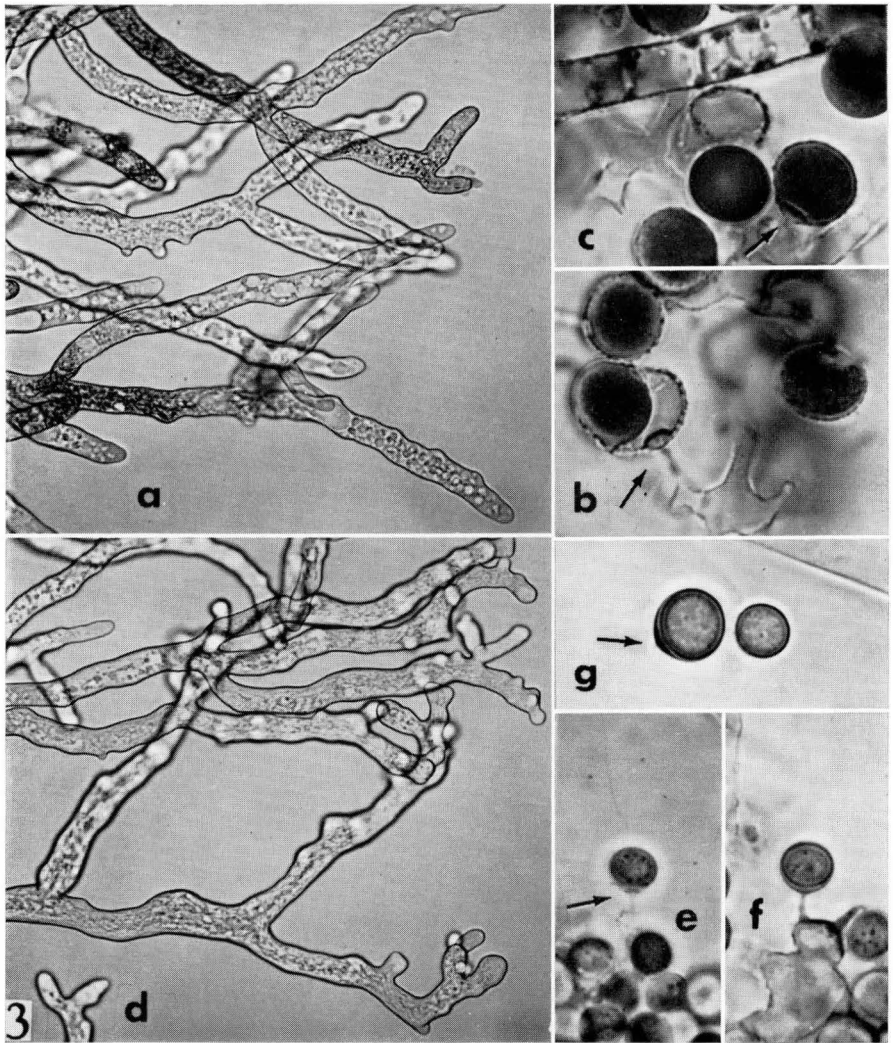


Fig. 3. a-c. *Chaetocladium jonesii*.—a. Vegetative hyphae from margin of 2-day-old colony on MEYE (17 C). $\times 250$.—b-c. Sporangia showing columellae (arrows) and persistent, rough sporangial wall. The smooth-walled sporangiospore has been dislodged from two of the sporangia (KOH-phloxine mount). $\times 1,300$.—d-g. *Chaetocladium brefeldii*.—d. Vegetative hyphae from margin of 2-day-old colony on MEYE (21 C). $\times 250$.—e. Nearly mature sporangiole showing columella (arrow) (KOH-phloxine mount). $\times 1,300$.—f. Mature sporangiole still attached by pedicel to subtending vesicle showing lower part of sporangial wall slightly separated from sporangiospore (KOH-phloxine mount). $\times 1,300$.—g. Two detached sporangia; one shows sporangial wall slightly separated from spore and its greater refractivity in the region of columella (arrow). $\times 1,300$.

Colonies on MEYE to ca. 8.5 cm in diam in 7–10 days at 21 C; turf lax to relatively dense, 3 mm–2 cm high, soon collapsing, white at first, in 10 days near Pale Mouse Gray to Olive-Gray, becoming near Pale Olive-Gray, Grayish Olive, or Drab on drying. Sporophores simple or irregularly branched, rough, hyaline to pale yellow, arising directly from the substrate hyphae or from stolons; in nature often arising from galls on parasitized mucoralean hosts; erect, ascending, or repent with stolons and rhizoids; 3–5 mm or more high, 5–35 μm in diam; often ending in a blunt, sterile prolongation; producing 3–4, rarely more, successive verticils of branches that often are irregularly septate and rough in age; the ultimate branches bearing sporangiola. Branches comprising each succeeding verticil smaller than the branch from which they arise; typically consisting of a stalk subtending the next order of more or less perpendicular branches and a sterile, spinose prolongation. Primary branches of fertile branch system nearly perpendicular to the main axis; borne singly, in pairs or in verticils of 3–7 branches; straight or slightly curved, tapered, variable in length to 300 μm or more including spinose prolongation, 10–25 μm in diam at base; sometimes furcate above the base or irregularly branched. Secondary, tertiary, and, if formed, quaternary branches arising singly, in pairs, or in verticils of usually 3–4 branches, tapered, variable in length from about 25 μm to as much as 200 μm or more; the ultimate branchlets 25–100 μm long, 3–6 μm in diam at the base. Ultimate branches bearing pedicellate sporangiola on small terminal or intercalary enlargements or giving rise to whorls of short branchlets, 2–15 μm long, terminated by small vesicles bearing sporangiola; fertile branchlets sometimes with a short, spinose prolongation. Vesicles globoid, clavate, or irregular in shape, up to 12 μm in diam; smooth or minutely roughened. Sporangiolar pedicels smooth, tapered, 1–4.5 μm long, 1–2 μm in diam at base, ca. 0.5–1 μm in diam at apex. Sporangiola grayish, slightly subglobose in lateral view, (3.4–)4–6.5(–9.5) μm in diam; wall thin, grayish, minutely roughened; columella discoid, flattened, 1–2.5 μm in diam. Sporangiospores like the sporangiola in size and shape, grayish, smooth, thin walled. Zygospores formed by aerial hyphae near surface of substrate, (38–)40–50(–55) μm in diam; wall yellow to pale yellow-brown, translucent, ornamented with undulating projections up to 4 μm high; suspensors opposed, hyaline to pale brown, smooth, unequal; one suspensor globose to subglobose, nearly as large as the zygospore, usually retaining its original shape in age; the other suspensor smaller, ovoid to ellipsoid, often collapsing in age. Heterothallic.

Distribution.—Canada, China, France, Germany, India (Zycha et al., 1969); Mexico, U.S.A. (Christenberry, 1940); U.S.S.R. (Naumov, 1954).

Illustrations.—As *Chaetocladium jonesii*: Brefeld (1872), Pl. III: Figs. 1–15, Pl. IV: Figs. 16–31; (1891), Pl. II: Figs. 20–21; Moreau (1953), Figs. 620, 636; Tavel (1892), Fig. 16(9–10); Zycha (1935), Fig. 75a; Zycha et al. (1969), Fig. 50a.—As *Chaetocladium brefeldii* var. *macrosporum*: Burgeff (1920), Figs. 1–23, 27, Pl. I: Figs. 24–26; (1924), Figs. 35f–k, 37a–c, 38a–i; Christenberry (1940), Pl. 17: Figs. 155–156; Ou (1940), Pl. III: Fig. 13.—As *Chaetocladium brefeldii*: Bainier (1882), opp. p. 97, Figs. 1–4; (1884), Pl. 9: Figs. 1–10; Chadefaud (1960), Fig. 593(11); Clements and Shear (1931), Pl. 2: Fig. 6; Fischer (1892), Fig. 47a–c.e; Fitzpatrick (1930), Fig. 91a–c; Cäumann (1926), Figs. 56f–i,k, 64(9–10); (1949), Figs. 67(3–4), 74(2); (1964),

Figs. 80(3-4), 85(2); Greis (1943), Fig. 42B; Grove (1884), Pl. 245: Fig. 10a-c; Hesseltine and Anderson (1957), Figs. 4-8; Ingold (1965), Fig. 24F-G; Ingold and Zoberi (1963), Fig. 12F-G; Langeron, Vanbreuseghem, and Wilkinson (1965), Fig. 29; Léger (1896), Pl. XII: Figs. 79-80; Migula (1910), Pl. 3H: Figs. 4-5; Müller and Loeffler (1968), Fig. 80b; Pidoplichko and Milko (1971), Fig. 147a-b; Schröter (1893), Fig. 117; Singh (1966 [1968]), Figs. 1-4; Srivastava (1962), Fig. 43D iii-iv; Verona and Benedek (1963), Pl. B66.

Specimens examined.—GREAT BRITAIN. ENGLAND. Sussex: Bignor Hill, rabbit dung, 1960, S. Scott (RSA 1119-; = IMI 80480); on *Mucor* sp. from rat dung, 1937, J. T. Duncan (RSA 1136-; = IMI 89258; = NRRL 2508). U.S.A. ARIZONA. Pima Co.: Sta. Catalina Mts., 6,400 ft, rodent dung, 18 Apr., 1962, R. K. Benjamin (RSA 1336+). CALIFORNIA. Los Angeles Co.: Evey Canyon, San Gabriel Mts., ca. 4.5 mi NE of Claremont, mouse dung, 5 Nov., 1956, R. K. Benjamin (RSA 503+), 18 Jan., 1957, R. K. Benjamin (RSA 516+), pack rat dung, 5 Mar., 1957, R. K. Benjamin (RSA 541+); Claremont, pack rat dung, 3 Apr., 1957, R. K. Benjamin (RSA 554+; RSA 555+), 27 Mar., 1959, R. K. Benjamin (RSA 864-), 7 Feb., 1963, R. K. Benjamin (RSA 1337+); Cobel Canyon, San Gabriel Mts., ca. 3.5 mi N of Claremont, rodent dung, 30 Apr., 1960, R. K. Benjamin (RSA 1087+; RSA 1088+); Dalton Canyon, N of Glendora, pack rat dung, 26 Mar., 1957, R. K. Benjamin (RSA 558-).—Orange Co.: Holy Jim Canyon, 5 mi NE of Tustin, mouse dung coll. by C. J. Anastasiou, 13 Feb., 1961, R. K. Benjamin isol. (RSA 1097-; RSA 1098+; RSA 1099+; RSA 1100-).—San Bernardino Co.: Ice House Canyon, San Gabriel Mts., mouse dung, 5 July, 1965, R. K. Benjamin (RSA 1632-); Barton Flats, San Bernardino Mts., mouse dung, 16 Mar., 1969, R. K. Benjamin (RSA 1780). OREGON. Linn Co.: House Rock Camp Gd., Willamette Nat. Forest, rodent dung, 25 Aug., 1962, R. K. Benjamin (RSA 1338+).—Collection data unknown: Burgeff (RSA 1137+; = CBS 116.24; = NRRL 1350. Possibly Burgeff's type strain of *Chaetocladium brefeldii* var. *macrosporum* isolated from horse dung, Geisenheim, Germany, Feb., 1919); Blakeslee (RSA 1138-; = CBS 137.28); Blakeslee (RSA 1139+; = CBS 136.28).

Notes.—The larger sporangiola and spores of *Chaetocladium jonesii* (Figs. 1g-h; 3b-c) serve most readily to distinguish this species from the smaller-spored *C. brefeldii* (Figs. 2i-j; 3e-g). The spore diameter of 1.8-3.3 μm given by Brefeld (1872) for *C. brefeldii* (his *C. jonesii*) has not been observed by others working with this fungus. Sporangiar size in *C. brefeldii* may vary slightly from strain to strain, but in all of the isolates studied by us it fell within the limits given in our description (3.4-9.5 μm ; usually about 4-6.5 μm) which correlates well with the dimensions cited by van Tieghem and Le Monnier (1873b) (3-5 μm) and Burgeff (1920; 1924) (4.5-6.2 μm). Burgeff based his *C. brefeldii* var. *macrosporum* on the discrepancy between the dimensions of spores as observed by him and those given by Brefeld.

The sporangiar wall is more strongly spinulose and more readily separable from the spore, and the columella more conspicuous, in *C. jonesii* (Figs. 1g-h; 3b-c) than in *C. brefeldii* (Figs. 2i-j; 3e-g). However, except for size and surface ornamentation, there is no apparent fundamental morphological difference in the sporangiola of these species as suspected by Brefeld.

Chaetocladium jonesii and *C. brefeldii* grow about equally well on MEYE and YpSs, the former developing best at temperatures slightly below 20 C (down to at least 7 C), the latter likewise is psychrophilic but will grow well at 20-25 C. Juvenile vegetative hyphae are similar in both species (Fig. 3a, d), being rather irregular in diameter with frequent rounded, lateral protuberances. In age, the hyphae are richly branched and possess numerous

short, simple or branched laterals [i.e., "peg-like" cells (Hesseltine and Anderson (1957))] and do not give rise to accessory structures such as chlamydospores or oidia, although Hesseltine and Anderson (1957) reported giant cells in *C. brefeldii*. The latter have not been observed by us and must be infrequent or absent in most strains.

Our only available isolate of *Chaetocladium jonesii* (RSA 772) grew and sporulated well on MSMA at 17 C, whereas all isolates of *C. brefeldii* tested on this medium made very limited growth (colonies reaching only a few mm to about a cm in diam in 3 wk) and sporulation was sparse or none.

Both species of *Chaetocladium* are similar in appearance when observed under low magnification (Figs. 1a; 2a). A relatively dense colony with abundant substrate hyphae and erect or ascending sporophores develops radially from the point of inoculation, and beyond the central region of the colony a more or less lax turf consisting mostly of stolons spreads rapidly over the agar surface. The stolons develop rhizoids where they contact the agar and give rise at varying intervals to the characteristic verticils of fertile branches (Figs. 1b; 2c-d). The pattern of sporangiole development on the fertile ultimate branchlets is alike in both species (Figs. 1d-g; 2d-i).

The radiating, spinose prolongations of the branches comprising the fertile branch systems (Figs. 1b-g; 2b) are a conspicuous feature of the spore-bearing structures. However, in *C. brefeldii*, where we had a number of isolates available for examination, we found considerable variability in the dimensions of these prolongations in different strains. In the absence of the prolongations, the branches may appear more dichotomous than verticillate (Fig. 2c).

Testers for determining the mating types of all isolates of *C. brefeldii* were RSA 555(+) and RSA 1138(-). MEYÉ and YpSs serve about equally well for obtaining zygospores (Fig. 2k).

EXCLUDED SPECIES

1. *CHAETOCLADIUM BENJAMINII* Embree, *Mycologia* 54: 305. 1962.
 = *Piptocephalis benjaminii* (Embree) Benjamin, *Aliso* 5: 284. 1963.
2. *CHAETOCLADIUM ELEGANS* Zopf, *Die Pilze, in Schenk's Handbuch der Botanik* 4: 373. 1890. *Nomen nudum*: no description or illustrations (see Hesseltine and Anderson, 1957).
3. *CHAETOCLADIUM HESSELTINII* Mehrotra & Sarbhoy, *Mycologia* 42: 797. 1960.
 = *Dichotomocladium hesseltinii* (Mehrotra & Sarbhoy) Benny & Benjamin, *Aliso* 8: 345. 1975.
4. *CHAETOCLADIUM OVALISPORUM* (Mehrotra & Mehrotra) Milko & Beljakova, in Milko, *Identification of mucoralean fungi*, p. 229. 1974 (first complete citation of place of publication of basionym).
 = *Thamnocephalis ovalispora* Mehrotra & Mehrotra, *Zentralbl. Bakteriol. Parasitenk. Infektionskr. Hyg.*, 2 Abt. 117: 425. 1963 [1964].

Milko and Beljakova first proposed the new combination in 1967 but failed to give full reference to the place of publication of the basionym in accordance with Art. 33 of the then-current *International Code of Botanical Nomenclature* (Lanjouw, 1966).

5. CHAETOCADIUM QUADRUPEDATUM (Blakeslee) Milko & Beljakova, in Milko, Identification of mucoralean fungi, p. 229. 1974 (first complete citation of place of publication of basionym).

≡ *Thamnocephalis quadrupedata* Blakeslee, Bot. Gaz. (Crawfordsville) 40: 165. 1905.

As for previous taxon, Milko and Beljakova (1967) failed to give reference to place of publication of the basionym when they proposed the new combination.

MYCOTYPHA Fenner, Mycologia 24: 196. 1932.

≡ *Benjaminia* Pidoplichko & Milko, Atlas of mucoralean fungi, Acad. Sci. Ukrain. S.S.R., Kiev, p. 96. 1971 (non *Benjaminia* Ahmad, Biologia 13: 21. 1967).

Sporophores arising from the substrate mycelium, erect, simple or branched; producing globose to cylindrical terminal enlargements bearing pedicellate, unispored, monomorphic or dimorphic sporangiola. Sporangiola freed from the subtending vesicle by circumscissile, subbasal rupture of the pedicel. Sporangiospores like the sporangiola in size and shape. Zygosporangia globose to subglobose; wall dark, ornamented with more or less conical projections; suspensors opposed.

Type species: Mycotypha microspora Fenner.

Although *Mycotypha microspora* has sporophores that outwardly resemble a hyphomycete, Fenner (1932) classified it in the tribe Cephalideae of the Mucoraceae according to the system of Gäumann (in Gäumann and Dodge, 1928) because of its coenocytic thallus and its susceptibility to parasitism by a species of *Piptocephalis* de Bary (1865). Bessey (1950) assigned *Mycotypha* to the Choanephoraceae along with *Blakeslea* Thaxter (1914), *Choanephora* Currey (1873), *Cunninghamella* Matruchot (1903), *Sigmoideomyces* Thaxter (1891), and *Thamnocephalis* Blakeslee (1905). Hesseltine (1952, 1955) placed *Mycotypha* in the Cunninghamellaceae with *Cunninghamella* and *Thamnocephalis*; his opinion subsequently was followed by several other mycologists (Benjamin, 1959; Milko, 1967, 1974; Pidoplichko and Milko, 1971), but Zycha et al. (1969) included *Mycotypha* in their relatively broad concept of the Choanephoraceae which comprised, in addition, *Blakeslea*, *Choanephora*, *Rhopalomyces* Corda (1839), *Cunninghamella*, *Radiomyces* Embree (1959), *Thamnocephalis*, and *Sigmoideomyces*. Young (1969) was the first to suggest a thamnidiaceous relationship for *Mycotypha* when he demonstrated that the sporangial wall of *M. africana* Novak & Backus (1963) is clearly separable from the sporangiospore.

In 1955, Wolf described what he believed to be a second species of *Mycotypha*, *M. dichotoma*, which he placed in the Mucoraceae. He soon

(Wolf, 1957) concluded that the fungus probably was the imperfect state of an ascomycete, *Plicaria fulva* Schneider (1954), which Korf (1960 [1961]) later assigned to *Peziza* as *P. ostracoderma* Korf. Recently, Hennebert and Korf (1975) have confirmed the synonymy of *Mycotypha dichotoma* with *Chromelosporium fulvum* (Link) McGinty, Hennebert & Korf, the conidial state of *Peziza ostracoderma*.

Concomitant with his revised opinion on the status of *Mycotypha dichotoma*, Wolf (1957) also questioned the phycomycetous affinity of *M. microspora*—an opinion shared by Boedijn (1958 [1959])—and suggested that it might be congeneric with *Microtypha* Spegazzini (1910). The type and only species of this genus of dematiaceous hyphomycetes, *Microtypha saccharicola*, was found by Spegazzini in Argentina on decaying culms of *Saccharum officinarum* L. The type specimen of *M. saccharicola* later was studied by Subramanian (1956) who concluded that it represented a species of *Arthriniium* Kunze ex Fr. (Cooke, 1954) and gave it a new name, *A. spegazzinii* Subram. Monte, Oddo, and Tonolo (1968), apparently unaware of Subramanian's study, decided, on the basis of Spegazzini's description and illustrations of *Microtypha saccharicola*, that *Mycotypha* should be relegated to synonymy with *Microtypha* and retained in the Phycomycetes; accordingly, they transferred both *Mycotypha microspora* and *M. africana* to *Microtypha*.

The description by Novak and Backus (1963) of the homothallic *Mycotypha africana* dispelled all doubts regarding the mucoralean affinities of the genus in the absence of a demonstrated sexual state for the morphologically similar *M. microspora*.

Recently, Matsushima (*in* Kobayasi, 1971) described a fourth species of *Mycotypha*, *M. guadacanalensis*, but Matsushima's description and illustrations as well as our examination of the type culture of this species show clearly that it is not a true *Mycotypha* but an unidentified hyphomycete.

We have reevaluated the status of *Cokeromyces poitrasii* Benjamin (1960) and are convinced that it should be treated as a species of *Mycotypha*.

KEY TO THE SPECIES OF *MYCOTYPHA*

- A. Sporangia dimorphic, borne on clavate to cylindrical vesicles; pedicels subtending sporangia very short, much less than length of sporangia B
- AA. Sporangia monomorphic, borne on globoid vesicles; pedicels subtending sporangia variable in length, mostly many times the length of the sporangia 3. *M. poitrasii*
 - B. Larger sporangia ovoid to obovoid; zygospores not observed; presumably heterothallic 1. *M. microspora*
 - BB. Larger sporangia oblong; zygospores always formed; homothallic 2. *M. africana*

1. *MYCOTYPHA MICROSPORA* Fenner, *Mycologia* 24: 196. 1932.

Figs. 4h-y; 5f-j

≡ *Microtypha microspora* (Fenner) Monte, Oddo & Tonolo, *Ann. Ist. Super. Sanità* 3: 737. 1967.

Colonies on MEYE 4-5 cm in diam in 12-14 days at 26 C; turf dense, more or less zonate, Deep Purplish Gray to Dark Purplish Gray, becoming Drab,

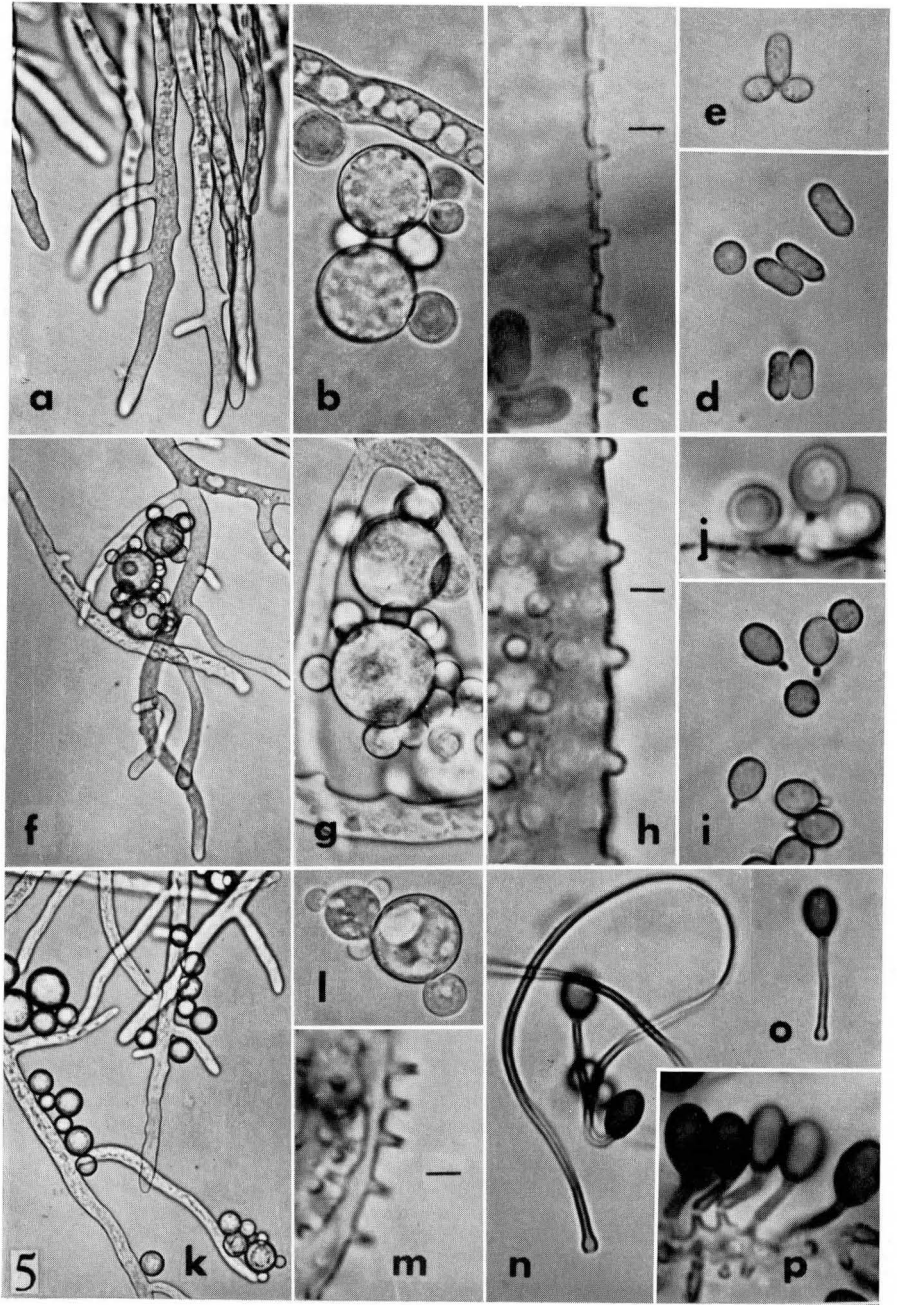
Hair Brown, or Deep Grayish Olive in age. Sporophores simple at first, often secondarily branched; more or less erect, up to 3–4 mm high, (3–)5–10(–13) μm in diam; hyaline at first, becoming pale bluish gray; grayish brown in age; becoming irregularly multiseptate, especially distally below vesicle; wall minutely roughened, especially distally, thicker proximally. Terminal vesicles variable in length, ovoid to clavate, but mostly short- to long-cylindrical; minutely roughened; (10–)100–300(–500) μm long, (8–)12–18(–25) μm in diam without sporangiola; rounded at apex; bearing sporangiola over entire surface except at extreme tip. Sporangiola dimorphic, forming two distinct layers over surface of vesicle: (1) Sporangiola comprising outer layer ovoid to obovoid, 4–6 \times 3–4 μm , pale bluish gray, smooth, borne on more or less conical pedicels ca. 2 μm long, 1.5 μm wide at base, ca. 0.5 μm wide above; after dehiscence, sporangiole bearing remnant of pedicel ca. 1 μm long; pedicellar base forming a conical, truncate to rounded denticle ca. 1 μm high on the subtending vesicle. (2) Sporangiola comprising inner layer globose to subglobose, 3–4 μm in diam, pale bluish gray, smooth, borne on short, conical pedicels ca. 1 μm or less high, ca. 1 μm wide at base; after dehiscence, sporangiole bearing remnant of pedicel ca. < 0.5 μm long; pedicellar base forming an inconspicuous, truncate denticle ca. < 0.5 μm high on the subtending vesicle. Sporangiospores like the sporangiola in size and shape. Substrate hyphae branched, nonseptate at first, becoming irregularly septate; giving rise to hyaline, globose, yeastlike budding cells up to 40 μm in diam; in age, occasional cell segments forming relatively thin-walled chlamydospores. Zygosporos not observed.

Distribution.—England (Cat. Cult. Coll. CMI, 7th ed., 1975), India (Rai and Mukerji, 1961), Nigeria (Cat. Cult. Coll. CMI, 7th ed., 1975), U.S.A.

Illustrations.—von Arx (1970), Fig. 22c; Fenner (1932), Fig. 1, Pl. 2–3; Hall and Kolankaya (1974), Figs. 3b, 4; Ingold (1965), Fig. 24A–C; Ingold and Zoberi (1963), Fig. 12A–C; Kahn and Talbot (1975), Fig. 1, Pl. 4(4–11), Pl. 5(12–16); Novak and Backus (1963), Figs. 1–3; Price, Storck, and Gleason (1973), Fig. 3; Schulz, Kraepelin,

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Fig. 4. a–g. *Mycotypha africana*.—a. Habit sketches of sporophores and zygosporos. $\times 40$.—b. Typical zygosporos and its suspensors. $\times 435$.—c. Septate basal portion of sporophore. $\times 435$.—d. Aseptate upper part of sporophore and elongate fertile vesicle bearing sporangiola. $\times 435$.—e. Lateral view of two oblong sporangiola borne on slightly conical pedicels and a nearly sessile, subglobose sporangiole. $\times 1,670$.—f. Sporangiola viewed from above showing outer, oblong sporangiola (darkly stippled) and inner, subglobose sporangiola (lightly stippled). $\times 1,670$.—g. Group of detached, adherent, oblong and subglobose sporangiola; two shown in optical section. $\times 1,670$.—h–y. *Mycotypha microspora*.—h. Habit sketches of sporophores. $\times 40$.—i. Aseptate basal part of sporophore. $\times 435$.—j. Septate upper part of sporophore and elongate fertile vesicle bearing sporangiola. $\times 435$.—k–v. Semidiagrammatic representation of comparative stages of development of sporangiola as viewed laterally (k, m, o, q, s, u) and from above (l, n, p, r, t, v). $\times 1,670$.—w. Segment of fertile vesicle showing prominent pedicellar denticles, remaining after dehiscence of obovoid sporangiola, alternating with less prominent denticles that subtended the smaller subglobose sporangiola. $\times 1,670$.—x. Subglobose and obovoid sporangiola; two shown in optical section. $\times 1,670$.—y. Diagrammatic representation of surface of fertile vesicle showing relationship of long (*) and short (•) pedicellar denticles alternating with one another transversely and vertically.



and Hinkelmann (1974), Fig. 5a,b; Verona and Benedek (1971), Pl. B125; Young (1969), Fig. 1e-l, Pl. 1(4, 8, 10), Pl. 2(12-17); Zycha et al. (1969), Fig. 56.

Specimens examined.—U.S.A. ARIZONA. Yuma Co.: bark of saguaro (*Carnegie gigantea* Britton & Rose), 1960, R. K. Benjamin (RSA 1559). CALIFORNIA. Kern Co.: Shark Tooth Hill, nr. Bakersfield, soil coll. by O. A. Plunkett, Nov., 1961, G. F. Orr 1078 (RSA 1185).—Los Angeles Co.: Cobel Canyon, San Gabriel Mts., ca. 3.5 mi N of Claremont, lizard dung, 22 Apr., 1965, R. K. Benjamin (RSA 1522).—Monterey Co.: 1 mi S of King City, soil, 27 Jan., 1958, E. E. Butler Mt 101 (RSA 774).—Riverside Co.: Andreas Canyon, ca. 3 mi S of Palm Springs, rodent dung coll. by G. L. Benny, 11 Dec., 1969, R. K. Benjamin isol. (RSA 1841).—San Bernardino Co.: 9 mi SE of Daggett, mouse dung, 11 Nov., 1960, R. K. Benjamin (RSA 1183); Calico Mts., pack rat dung coll. by V. E. Grant, 13 Nov., 1960, R. K. Benjamin isol. (RSA 1184).—Solano Co.: Rio Vista, soil, 27 Jan., 1958, E. E. Butler Mt 102 (RSA 775). DISTRICT OF COLUMBIA. Washington, cultural contaminant, before 1932, E. A. Fenner (type culture: RSA 776; = ATCC 8982; = CBS 230.32; = IMI 139109). IOWA. Dubuque Co.: Pine Hollow, pine wood, Oct., 1938, G. W. Martin (RSA 710; = NRRL 684; = QM 6745). KANSAS. Riley Co.: Manhattan, air contaminant, 5 June, 1953, C. T. Rogerson (RSA 708).—Collection data incomplete: received 15 Oct., 1958, from G. M. Luedemann, Schering Corp., Bloomfield, N.J., isol. from paper mill (RSA 716).

2. *MYCOTYPHA AFRICANA* Novak & Backus, *Mycologia* 55: 793. 1963.

FIGS. 4a-g; 5a-e

= *Microtypha africana* (Novak & Backus) Monte, Oddo & Tonolo, *Ann. Ist. Super. Sanità* 3: 737. 1967.

Colonies on MEYE 3-4 cm in diam in 12-14 days at 26 C; turf dense, more or less zonate, Mouse Gray to Deep Quaker Drab, becoming Drab to

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Fig. 5. a-e. *Mycotypha africana*.—a. Vegetative hyphae from margin of 2-day-old colony; surface growth. $\times 250$.—b. Globose, yeastlike budding cells from subsurface of 2-day-old colony below point of original inoculation. $\times 600$.—c. Optical section of margin of fertile vesicle following dehiscence of sporangiola. Pedicellar denticles remaining after separation of the oblong sporangiola project ca. 1 μ m or less above surface of the vesicle; those which subtended the subglobose sporangiola are barely perceptible, slightly elevated scars alternating with the first. $\times 2,100$ (line = ca. 2 μ m).—d. Detached subglobose and oblong sporangiola. $\times 1,300$.—e. One oblong and two subglobose sporangiola adhering to one another following dehiscence from their subtending pedicels. $\times 1,300$.—f-j. *Mycotypha microspora*.—f. Vegetative hyphae and associated budding cells from margin of 2-day-old colony; surface growth. $\times 250$.—g. The globose, yeastlike budding cells shown in the previous figure. $\times 600$.—h. Optical section of margin of fertile vesicle following dehiscence of sporangiola. The broad-based, conical pedicellar denticles remaining after separation of the obovoid sporangiola project ca. 1 μ m above surface of vesicle; those which subtended the subglobose sporangiola are barely perceptible elevations of the vesicular wall alternating with the conical denticles. $\times 2,100$ (line = ca. 2 μ m).—i. Detached subglobose and obovoid sporangiola. $\times 1,300$.—j. Two subglobose and one obovoid sporangiola in situ on fertile vesicle. $\times 2,100$.—k-p. *Mycotypha poitrasii*.—k. Vegetative hyphae and associated budding cells from margin of 2-day-old colony; surface growth. $\times 250$.—l. Globose, yeastlike budding cells from surface colony. $\times 600$.—m. Optical section of margin of fertile vesicle following dehiscence of sporangiola showing pedicellar denticles of uniform size. $\times 2,100$ (line = ca. 2 μ m).—n-o. Detached sporangiola showing great variability in length of pedicel; note slight enlargement of pedicellar base above point of detachment $\times 1,300$.—p. Several sporangiola still attached to fertile vesicle but showing line of dehiscence near base of pedicel. $\times 2,100$. (All cultures on MEYE; 25 C.)

Light Grayish Olive in age. Sporophores simple at first, often secondarily branched; more or less erect, up to 3–4 mm high, (3–)5–10(–13) μm in diam; hyaline at first, becoming pale grayish or grayish green; grayish brown in age; nonseptate distally below vesicle; becoming irregularly multiseptate proximally; wall minutely roughened, especially distally, thicker proximally. Terminal vesicles variable in length, ovoid to clavate, but mostly short- to long-cylindrical, minutely roughened; (25–)150–300(–500) μm long, (13–)18–25(–35) μm in diam; usually truncate or slightly concave at apex; bearing sporangiola over entire surface except at extreme tip. Sporangiola dimorphic, forming two distinct layers over surface of vesicle: (1) Sporangiola comprising outer layer cylindrical with rounded ends, often with slight median constriction, 4–7 \times 2–3.5 μm , pale grayish or grayish green, smooth, borne on a slightly conical to cylindrical pedicel ca. 1.5 μm long, ca. 1 μm wide; after dehiscence, sporangiola bearing remnant of pedicel ca. < 0.5 μm long; pedicellar base forming a slightly conical to cylindrical, truncate denticle ca. 1 μm high on the subtending vesicle. (2) Sporangiola comprising inner layer globose to subglobose, 2–3.5 μm in diam, pale grayish or grayish green, smooth, borne on a pedicel ca. < 1 μm long, ca. < 1 μm wide at base; after dehiscence, sporangiola bearing remnant of pedicel ca. < 0.5 μm long; pedicellar base forming an inconspicuous, truncate denticle ca. < 0.5 μm high on the subtending vesicle. Sporangiospores like the sporangiola in size and shape. Substrate hyphae branched, nonseptate at first, becoming irregularly septate; giving rise to hyaline, globose, yeastlike budding cells up to 55 μm in diam; in age, occasional cell segments forming relatively thin-walled chlamydospores. Zygosporangia abundant, formed on aerial hyphae near surface of substrate; globose to subglobose, (25–)30–50 (–55) μm in diam including projections; wall brownish black to black, covered with coarse, conical projections up to 7 μm or more high; suspensors opposed, more or less equal, smooth, hyaline to pale gray or brownish black. Homothallic.

Distribution.—Africa (Southern Rhodesia); known only from the type collection.

Illustrations.—Hall and Kolankaya (1974), Figs. 1, 3a; Novak and Backus (1963), Figs. 3–7; Pidoplichko and Milko (1971), Fig. 139a–d; Schulz et al. (1974), Fig. 5c; Verona and Benedek (1971), Pl. B125(2); Young (1969), Figs. 1a–d, 2, Pl. 1(1–3, 5–7, 9), Pl. 2(11, 18, 19), Pl. 3.

Specimen examined.—AFRICA. SOUTHERN RHODESIA. Sabi River valley S of Umtali, soil coll. by Martha Christensen, 11 Oct., 1961, R. O. Novak isol. (type culture: RSA 1193; = ATCC 15344; = CBS 122.64; = IMI 139108; = NRRL 2978).

Notes.—Although *Mycotypha africana* and *M. microspora* are similar in gross morphology (Fig. 4a,c,h,i), they are readily distinguished by the larger of their dimorphic sporangiola (Figs. 4e,g,x; 5d,e,i,j). In both species, the smaller sporangiola are more or less transversely ovoid in lateral view and lie below the level of the elongate, long-pedicellate sporangiola which mature first (Figs. 4e–f, k–v; 5e,j) and alternate with the small sporangiola both transversely and longitudinally on the vesicle (Fig. 4w,y). The larger sporangiola of *M. microspora* always are ovoid to obovoid and bear, in line with the long axis, a conspicuous remnant of the pedicel (Figs. 4x; 5i),

whereas the larger sporangiola of *M. africana* are cylindric and bear an inconspicuous pedicellar remnant (Figs. 4g; 5d,e). The sporangiola of *M. africana* often remain attached to one another after abscission and form chains of few to many sporangiola (Figs. 4g; 5e). From his electron microscopic studies, Young (1969) described and illustrated small circular elevations on the walls of the sporangiola of *M. africana*, apparently formed where the walls are in contact during sporangial development. He suggested that these surface elevations might be involved in the temporary union of the sporangiola following abscission. Sporangiola of *M. microspora* are not adherent and their walls lack elevated circular marks.

Like the sporangiola, the vesicular denticles formed by the pedicellar bases that remain after sporangial dehiscence are dimorphic in *M. africana* (Fig. 5c) and *M. microspora* (Fig. 5h). Denticular organization and structure have been described and illustrated for these species by Young (1969) and Khan and Talbot (1975) both of whom used the light and electron microscope in their studies.

With maturation, the sporophore of *Mycotypha africana* typically becomes irregularly multiseptate in its lower extremity (Fig. 4k) and is nonseptate distally, whereas that of *M. microspora* becomes often abundantly septate distally (4i) and has only a few scattered septa below. Another apparently consistent difference between these species is the tendency for the vesicle of *M. africana* to be more or less flattened or even slightly concave at its tip, whereas the vesicle of *M. microspora* is rounded at the apex.

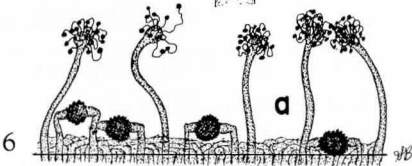
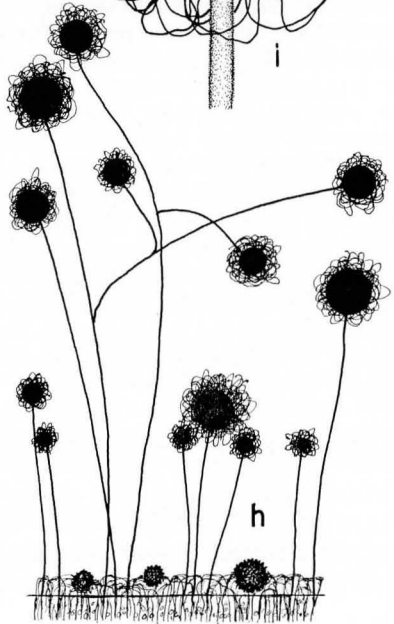
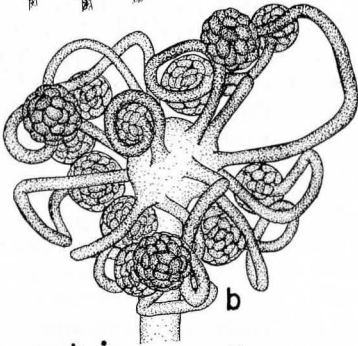
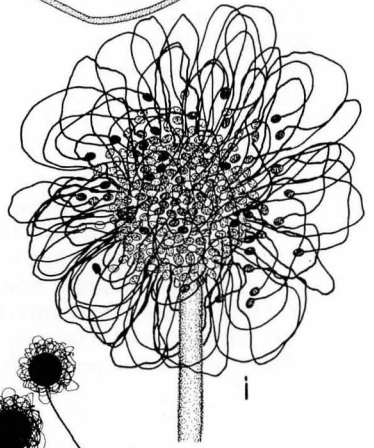
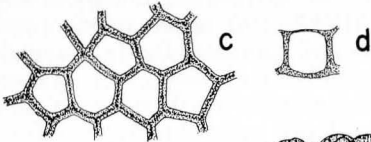
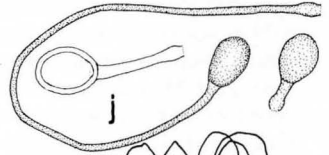
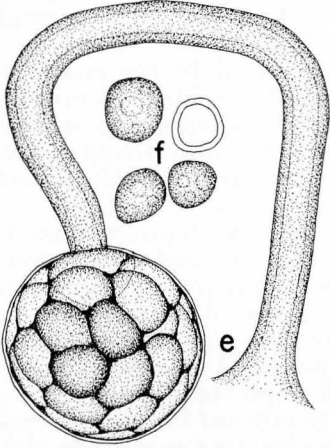
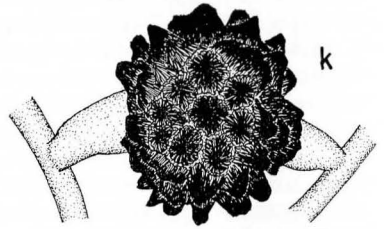
Mycotypha africana and *M. microspora* grow poorly on MSMA. Although they may develop a colony one to several cm in diam on this medium, they form an extremely lax substrate mycelium that gives rise to only a few scattered, depauperate sporophores. On MEYE and other nutrient-rich media like YpSs both species develop rapidly and sporulate freely. Juvenile vegetative hyphae are similar in both species (Fig. 5a,f), being at first more or less uniform in diameter and giving rise to frequent nearly perpendicular or strongly divergent laterals. As the mycelium ages, the hyphae form numerous simple septa that delimit cell segments, variable in length and diameter, some of which may develop into relatively thin-walled chlamydospores. A regular feature of the substrate mycelium of both species when growing on rich media like MEYE is the formation of globose budding cells (Fig. 5b,g). These yeastlike cells regularly develop along the filamentous hyphae on the agar surface but usually are formed in greater abundance within the substrate. Physiological and ecological factors influencing yeast/mold dimorphism in species of *Mycotypha* have been the subject of several recent investigations (Price, Storck, and Gleason, 1973; Hall and Kolankaya, 1974; Schulz et al., 1974).

3. *Mycotypha poitrasii* (Benjamin) Benny & Benjamin, comb. nov.

FIGS. 5k-p; 6h-k

≡ *Cokeromyces poitrasii* Benjamin, Aliso 4: 523. 1960 (basionym).

≡ *Benjaminia poitrasii* (Benjamin) Pidopl. & Milko, Atlas of mucoralean fungi, Acad. Sci. Ukrain. S.S.R., p. 96. 1971.



Colonies on MEYE to 6–7 cm in diam in 12–14 days at 26 C; turf dense, more or less zonate, near Deep Mouse Gray, becoming Hair Brown in age. Sporophores simple at first, often secondarily branched; more or less erect, 1–3 mm high, 5–10 μm in diam; hyaline at first, becoming pale gray; few septate in age; wall roughened; apical enlargements and sporangiola forming more or less globoid heads 50–150 μm in diam. Terminal vesicles smooth, 25–75 μm in diam; bearing pedicellate sporangiola over entire surface. Sporangiolar pedicels variable in length, 2–100(–150) μm long, 0.5–1 μm wide, straight to strongly recurved or twisted; deciduous; with a slight basal enlargement, ca. 1–1.5 \times 1–1.5 μm , immediately above point of ascission; pedicellar base forming a more or less conical to cylindrical, truncate denticle 1.5–2 μm high, ca. 1 μm wide at the base, on the subtending vesicle. Sporangiola ovoid to obovoid, 3.5–6(–8) \times 2.5–4 μm ,⁴ pale gray, smooth, readily separating from pedicel. Sporangiospores like the sporangiola in size and shape. Substrate hyphae at first nonseptate, becoming irregularly septate; giving rise to hyaline, globose, yeastlike budding cells up to 30 μm in diam; in age, some cell segments forming thin-walled chlamyospores variable in size and shape. Zygosporangia abundant; formed on aerial hyphae near the surface of the substrate; globose to subglobose, (30–)40–60(–70) μm in diam including projections; wall black, covered with coarse, conical projections 5–10 μm high; suspensors opposed, nearly equal, smooth, hyaline to pale gray or brownish black. Homothallic.

Distribution.—Mexico, U.S.A.

Illustrations.—Benjamin (1960), Pls. 1–2; Ingold (1965), Fig. 19G; Ingold and Zoberi (1963), Fig. 7G, Pl. 9(14); Pidoplichko and Milko (1971), Fig. 141a–d; Price et al. (1973), Figs. 1A–D, 2; Young (1968), Fig. 1a. (All as *Cokeromyces poitrasii*.)

Specimens examined.—MEXICO. BAJA CALIFORNIA DEL NORTE. Between El Terminal and San Juan Valley, ca. 20 mi SW of Bahía de los Angeles, rodent dung, 27 Feb., 1963, R. K. Benjamin (RSA 1245; RSA 1264); La Suerte, lizard dung, 4 June 1963, R. K. Benjamin (RSA 1267). U.S.A. CALIFORNIA. Riverside Co.: San Jacinto Mts., ca.

⁴ Sporangiolar measurements given in the original description [“8–14(–19) \times 6–9 μ ”] (Benjamin, 1960: 523–524) are erroneous, resulting from the author’s failure to convert ocular micrometer values to μm .

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Fig. 6. a–g. *Cokeromyces recurvatus*.—a. Habit sketches of sporophores (stalk length not to scale) and zygosporangia. $\times 75$.—b. Fertile head terminating sporophore showing arrangement of multispored sporangiola on elongate, twisted, contorted pedicels. $\times 435$.—c–d. Surface and lateral views of dark, netlike deposit formed around spores immediately below surface of sporangiolar wall. $\times 1,670$.—e. Sporangiole showing pedicel, columella (stippled line), and sporangiospores. $\times 1,670$.—f. Sporangiospores; one in optical section showing relative thickness of wall. $\times 1,670$.—g. Typical zygosporangium and its suspensors. $\times 435$.—h–k. *Mycotypha poitrasii*.—h. Habit sketches of sporophores (stalk length not to scale) and zygosporangia. $\times 75$.—i. Fertile head terminating sporophore showing numerous sporangiola borne on slender, twisted, contorted pedicels. $\times 435$.—j. Three sporangiola; one showing relative thickness of spore wall. Note variable length of pedicels which are slightly swollen at base above point of detachment from subtending vesicle. $\times 1,670$.—k. Typical zygosporangium and its suspensors. $\times 435$.

15 mi SW of Palm Desert, pack rat dung, 2 Sept., 1959, *R. K. Benjamin* (type culture: RSA 903; = ATCC 13844; = CBS 158.60; = IMI 81585; = NRRL 2845); Hidden Valley, Joshua Tree National Monument, pack rat dung, 22 Feb., 1961, *R. K. Benjamin* (RSA 1096).—San Bernardino Co.: Deep Creek Canyon, San Bernardino Mts., rodent dung, 25 Nov., 1960, *R. K. Benjamin* (RSA 1095).

Notes.—In 1960, the junior author placed this species in *Cokeromyces* primarily because its sporophore—an upright stalk terminated by a globose enlargement bearing mostly long-pedicellate sporangiola (Fig. 6h-i)—resembled the type species of *Cokeromyces*, *C. recurvatus* (Fig. 6a-b); also, its dense, low-growing colony resembled that of the type and, like *C. recurvatus*, it was homothallic. However, in the light of subsequent studies it seems clear that the fungus is less closely allied to *Cokeromyces* than to *Mycotypha* and we have here effected its transfer to the latter genus. The robust, nondeciduous pedicels of more or less uniform length bearing distinctive, columellate, multispored sporangiola in *C. recurvatus* (Figs. 6b; 8b-d) are wholly different from the slender, deciduous pedicels of variable length bearing easily detached, unispored, noncolumellate sporangiola in *M. poitrasii* (Figs. 5n-p; 6j). Except for pedicellar length, the sporangiola of *M. poitrasii* are similar in all respects to those of *M. africana* and *M. microspora* (Figs. 4g,x; 5d,e,i,j). Vegetative and colonial characteristics of *M. poitrasii* also are more like those of *M. africana* and *M. microspora* than *C. recurvatus*.

Unlike *M. africana* and *M. microspora*, *M. poitrasii* grows about as well on MSMA as on MEYE and YpSs, producing abundant sporophores and zygosporangia. Juvenile vegetative hyphae of *M. poitrasii* (Fig. 5k) are similar in morphology to those of the other two species (Fig. 5a,f), and in age form a highly branched, irregularly septate mycelium which commonly forms relatively thin-walled chlamydoconidia conforming in size and shape to the cell segments from which they develop. Like *M. africana* and *M. microspora*, the vegetative hyphae of *M. poitrasii* regularly give rise to globose, yeastlike budding cells (Fig. 5l). These may arise in great numbers from hyphae growing within the agar medium and commonly develop on the surface of the agar, especially in young colonies (Fig. 5k). Spores of *M. poitrasii* scattered on MEYE plates often develop exclusively yeastlike colonies several mm in diam before giving rise to filamentous hyphae and sporophores. Some physiological aspects of yeast/mold dimorphism in *M. poitrasii* (as *Cokeromyces poitrasii*) have been described by Price et al. (1973).

Morphologically, the zygosporangia of *M. poitrasii* and *M. africana* are nearly identical (Figs. 4b; 6k).

Because of its unispored sporangiola, *Cokeromyces poitrasii* was transferred by Pidoplichko and Milko in 1971 to a new genus, *Benjaminia* [a name anticipated by Ahmad (1967) for a genus of Sphaeropsidaceae], and removed to the Cunninghamellaceae in company with *Cunninghamella*, *Chaetocladium*, *Mycotypha*, *Phascolomyces*, and *Radiomyces*. The latter genus also was established by Pidoplichko and Milko at this time to accommodate *Radiomyces embreei* Benjamin (1960) which differs from *R. spectabilis* Embree (1959) primarily in having unispored sporangiola

formed on elongate, stalked, secondary vesicles (Benjamin, 1960: Pls. 3c-j; 4c-d) rather than multispored sporangiola borne on globose, stalked, secondary vesicles (Embree, 1959: Figs. 1c-d; 6-7). These two homothallic species form nearly identical zygospores and clearly are congeneric. We believe that it is not taxonomically realistic to separate them generically and place them in separate families solely on the basis of the number of spores in their sporangiola; we reject the genus *Radiomyopsis*. We do concur with Ellis and Hesselstine (1974) in their alliance of *Radiomyces* and *Hesseltinella* Upadhyay (1970) and their removal of these genera from the Thamniaceae into a family of their own, Radiomycetaceae.

One can speculate that sporangiar and pedicellar dimorphism may have evolved in *M. africana* and *M. microspora* as a means of fully utilizing the available space on the vesicle for spore production (Young, 1969) with the concomitant elimination of any adverse effects of crowding. In the same vein, one can speculate that sporangiar dimorphism has not developed in *M. poitrasii* because the evolution of pedicels highly variable in length has allowed maximum capacity for spore production per unit area of the subtending vesicle and also has essentially eliminated crowding as a factor affecting sporangial development. Sporangiar size is of the same order of magnitude in the three species (Fig. 5e,d,i,o,n) as is the distance between the vesicular denticles formed by the pedicellar bases remaining after sporangiar dehiscence (Fig. 5c,h,n). The number of sporangiola produced per unit surface area of the vesicle is approximately the same in the three species, ca. 35-40/200 μm^2 .

Capacity for sporangiar production by the vesicles of *M. africana* and *M. microspora* is increased primarily by vesicular elongation rather than by an increase in vesicular diameter as in *M. poitrasii*. In the latter, the surface area of the more or less globose vesicle quadruples with a twofold increase in diameter. If one regards the vesicle of *M. africana* and *M. microspora* as a simple cylinder then a similar increase in surface area requires not only a doubling of the diameter but also a doubling of the height. This does not occur, for the vesicle of these species typically is much longer than wide. If the height of the cylindrical vesicle increases greatly with little or no increase in diameter, the surface area is correspondingly greatly increased. Thus, a globose vesicle 60 μm in diam in *M. poitrasii* has a surface area of approximately 11,300 μm^2 . A cylindrical vesicle 15 μm in diam in *M. africana* and *M. microspora* would have about the same surface area available for sporangiar production if its height were about 240 μm ; at a diameter of 20 μm the height would need to be about 180 μm . Such dimensions are commensurate with those actually observed in these fungi.

EXCLUDED SPECIES

1. MYCOTYPHA DICHOTOMA Wolf, J. Elisha Mitchell Sci. Soc. 71: 217. 1955.
= *Chromelosporium fulvum* (Link) McGinty, Hennebert & Korf, in Hennebert and Korf, Mycologia 67: 216. 1975 (see Hennebert and Korf [1975] for a full account of their need to seek the counsel of

Prof. Aloysius T. McGinty, long-time collaborator of the late G. C. Lloyd, in their resolution of the nomenclatural problems involving this taxon).

Imperfect state of *Peziza ostracoderma* Korf (1960 [1961]).

2. MYCOTYPHA GUADACANALENSIS Matsushima, in Kobayasi, Bull. Nat. Sci. Mus. 14(3): 469. 1971.

This taxon is an unidentified hyphomycete.

COKEROMYCES SHANOR, in Shanor, Poitras, and Benjamin, Mycologia 42: 272. 1950.

Sporophores arising directly from the substrate mycelium, erect, simple, terminated by a globoid enlargement producing pedicellate sporangiola. Sporangiar pedicels elongate, nondeciduous, producing single, columellate sporangiola apically. Sporangiola multispored, globoid; wall persistent, smooth; columella well defined. Sporangiospores globose, ovoid, or irregular in shape; smooth. Zygosporangia globose to subglobose; wall dark, ornamented with rounded or conical projections; suspensors opposed.

Type species: Cokeromyces recurvatus Poitras.

Shanor et al. (1950) originally classified *Cokeromyces recurvatus* in the Choanephoraceae, as defined by Zycha (1935), because of its pedicellate, multispored sporangiola borne on the inflated tips of erect sporophores (Fig. 6a,b). Poitras (1950) soon decided that the species should be regarded as thamnidiaceous and his opinion was accepted by Hesselatine (1952, 1955) and others (Benjamin, 1959; Boedijn, 1958 [1959]; Milko, 1967; Zycha et al., 1969).

With our transfer of *Cokeromyces poitrasii* to *Mycotypha*, *Cokeromyces* again is monotypic.

COKEROMYCES RECURVATUS Poitras, in Shanor, Poitras, and Benjamin, Mycologia 42: 272. 1950.

Colonies on MEYE to 5–7 cm in diam in 10–12 days at 26 C; margin more or less irregular; turf dense, zonate, soon becoming near Benzo Brown to Chaetura Black. Sporophores simple, rough, at first hyaline, becoming pale brown to brown, 0.5–1 mm high, 6–12 μm wide; producing more or less globose terminal enlargements bearing (5–)20–22(–30) pedicellate sporangiola that form a lax, globoid head 50–100 μm in diam. Sporangiar pedicels 50–120 μm long (1.5–)2–4 μm wide, recurved or irregularly contorted, smooth, wall slightly thicker (0.5–1 μm) and darker than wall of subtending vesicle. Sporangiola usually containing 10–25 sporangiospores, purplish brown, globose to subglobose, 8–14 μm in diam; outer surface of wall smooth; inner surface of wall appearing reticulate from the formation of a dark-colored deposit around the outer layer of spores; columella dome shaped, slightly compressed, 5–7 μm in diam. Sporangiospores hyaline to pale brown, containing several small, conspicuous, globose vacuoles; smooth;

globose, 3–6 μm in diam, or ovoid to irregular and slightly angular in outline, 3–6 \times 3–6 μm . Substrate hyphae at first nonseptate; freely branched; soon becoming irregularly septate and forming numerous globoid to ovoid or elongate vesiculose cells. Zygosporangia abundant, globose to subglobose, formed by aerial hyphae immediately above the surface of the substrate and by the submerged vegetative hyphae; (30–)35–45(–55) μm in diam including projections; wall brown, translucent, ornamented with undulating, rounded or more or less conical projections up to 4 μm high; suspensors roughened, nearly equal. Homothallic.

Distribution.—Mexico, U.S.A.

Illustrations.—Gilman, Tiffany, and Lichtwardt (1957), Figs. 3–4; Ingold (1965), Fig. 19F; Ingold and Zoberi (1963), Fig. 7F, Pl. 9(12); Pidoplichko and Milko (1971), Fig. 132a–c; Poitras (1954), Figs. 1–9; Shanor et al. (1950), Figs. 1–12; Verona and Benedek (1963), Pl. B67; Young (1968), Figs. 1b–d, 8, 9, 12; Zycha et al. (1969), Fig. 49.

Specimens examined.—MEXICO. BAJA CALIFORNIA DEL NORTE. La Suerte, rodent dung, 4 June, 1963, R. K. Benjamin (RSA 1274). U.S.A. ARIZONA. Pima Co.: ca. 4.5 mi W of Sells, pack rat dung, 18 Apr., 1962, R. K. Benjamin (RSA 1232). CALIFORNIA. El Dorado Co.: Near Grass Lake, ground squirrel dung coll. by G. L. Benny, R. K. Benjamin isol. (RSA 2141).—Kern Co.: El Paso Mts., ca. 11 mi S of Inyokern, rodent dung, 24 Aug., 1975, G. L. Benny (RSA 2160).—Los Angeles Co.: 3 mi SW of Palos Verdes Estates, lizard dung, no date, G. F. Orr 494 (RSA 942).—Mono Co.: N margin of Mono Lake, rodent dung, 16 Aug., 1975, R. K. Benjamin (RSA 2142).—Riverside Co.: ca. 10 mi N of Desert Center, pack rat dung, 12 Oct., 1959, R. K. Benjamin (RSA 917); 3 mi E of Indio, lizard dung, 1959, G. F. Orr 490 (RSA 918).—San Bernardino Co.: Twentynine Palms, pack rat dung coll. by W. Egbert Schenck, 27 Mar., 1955, R. K. Benjamin isol. (RSA 345; = ATCC 13568; = CBS 168.59; = IMI 77585); Lytle Creek Canyon, San Gabriel Mts., pack rat dung, 7 Sept., 1958, R. K. Benjamin (RSA 714); Ice House Canyon, San Gabriel Mts., mouse dung, 5 July, 1965, R. K. Benjamin (RSA 2162). FLORIDA. Lake Co.: Eustis, rodent dung, 6 Mar., 1976, G. L. Benny (RSA 2166). ILLINOIS. Champaign Co.: Urbana, Brownfield Woods, rabbit dung, 17 Mar., 1949, A. W. Poitras (type culture: RSA 1; = CBS 158.50). MICHIGAN. Emmet Co.: Pellston, Univ. of Mich. Biol. Sta., rodent dung, Aug., 1958, R. W. Embree 58–32 (RSA 1231). TEXAS. Comal Co.: Rebecca Creek, soil, Nov., 1963, Mary Henney (RSA 1357).

Notes.—Except for the Texas isolate (RSA 1357), all other collections of *Cokeromyces recurvatus* known to us have come from the dung of small animals, where the fungus forms a dense, feltlike, brownish or blackish turf over the substrate. Its appearance is the same when growing on rich agar media like MEYE or YpSs. On MSMA, its growth is sparse, with a thin, restricted, nearly colorless colony giving rise to a few scattered sporophores and no zygosporangia. Strains that give rise to abundant sporophores form blackish to brownish black colonies due primarily to the dark color of the sporangiola (Figs. 6e; 8b). Colonies of less heavily sporulating strains owe their color more to zygosporangia and pigmented hyphae than to sporangiola and are yellowish or brownish orange. White, sterile aerial hyphae are sparse in some strains, more or less abundant in others.

Juvenile substrate hyphae of *C. recurvatus* are nonseptate at first but quickly form simple septa and more or less globoid to ovoid vesiculose cell segments (Fig. 8a). These comprise much of the subsurface colony and give rise to feeder hyphae below and more or less vertically oriented hyphae that

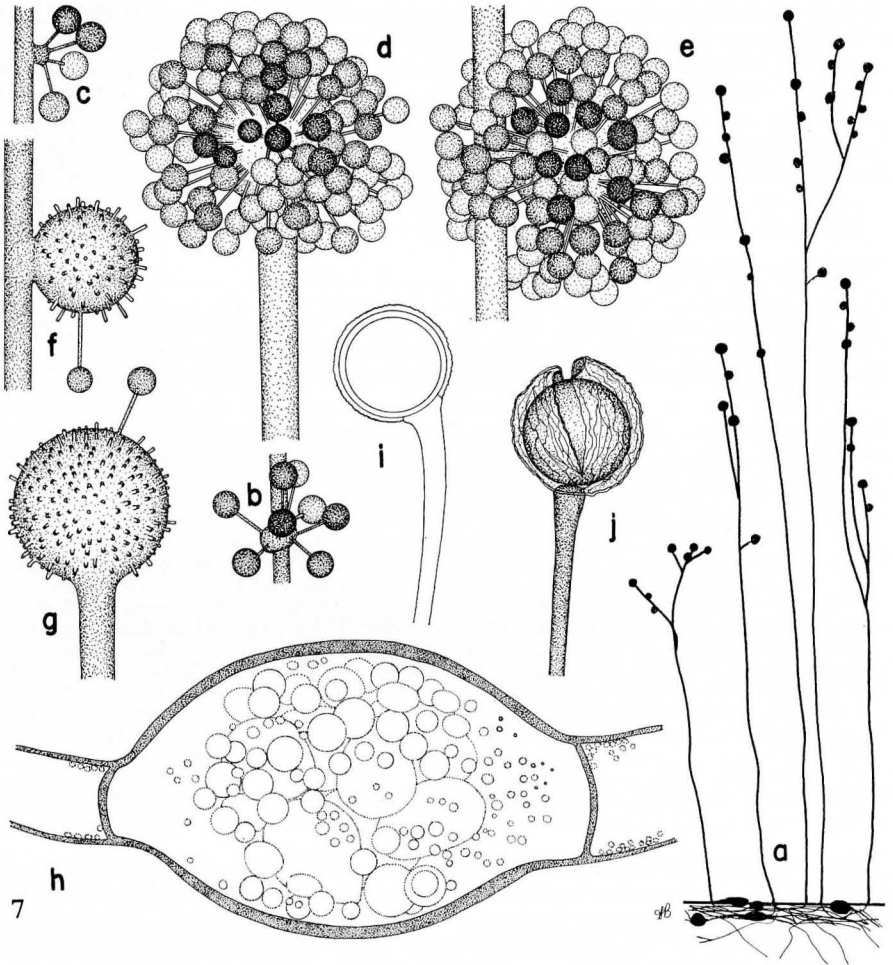


Fig. 7. *Phascolomyces articulatus*.—a. Habit sketches of sporophores and giant cells formed by substrate hyphae. $\times 15$.—b–e. Terminal and lateral fertile heads of few to many sporangiole. $\times 435$.—f–g. Lateral and terminal fertile vesicles showing stubble of pedicellar bases following dehiscence of sporangiole along with part of subtending pedicel. $\times 435$.—h. Giant cell showing numerous variable-sized globules in cytoplasm. $\times 435$.—i. Optical section showing, in outline, a mature sporangiole with compressed columella. $\times 1,670$.—j. Sporangiole as it appears mounted in KOH-phloxine with ruptured sporangiole wall; note small, rounded columella and slight apophysis. $\times 1,670$.

emerge from the substrate and develop the asexual and sexual reproductive structures (Fig. 6a).

The distinctive, darkly pigmented substance deposited around the outer layer of sporangiospores is hardly noticed in the intact, purplish black

sporangiole of *C. recurvatus* (Figs. 6b,e; 8b), but when the sporangiole is crushed in water the material may be freed or partly freed from the pale spores (Figs. 6f; 8c,d) and sporangiolar wall and its reticulate structure is readily apparent (Figs. 6c,d; 8c,d). The nature and origin of this substance is unknown.

Zygosporos (Fig. 6g) of *C. recurvatus* characteristically develop in great numbers in the region just above the surface of the substrate. They also, especially in tube cultures, are formed abundantly by the submerged vegetative mycelium where they are most numerous in the region 1–2 mm below the agar surface.

PHASCOLOMYCES Boedijn, Sydowia 12: 349. 1958 [1959].

Sporophores erect or ascending, simple or branched, producing terminal and lateral vesicular enlargements bearing pedicellate unispored sporangiola. Sporangiolar pedicels slender, elongate, straight or curved. Sporangiola globose to subglobose, with rudimentary columella, slightly apophysate; wall thin, persistent. Substrate hyphae forming dark-colored giant cells.

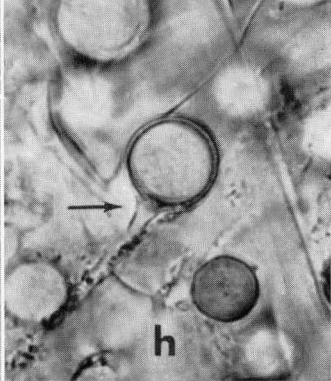
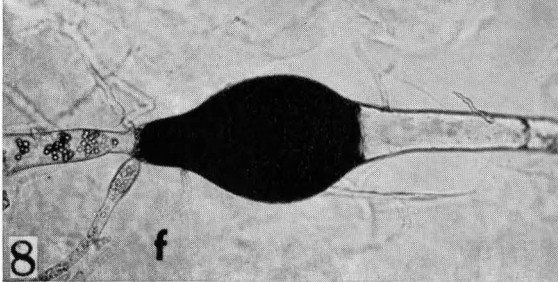
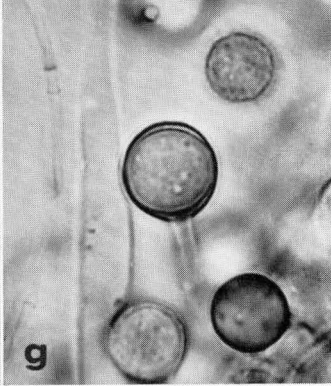
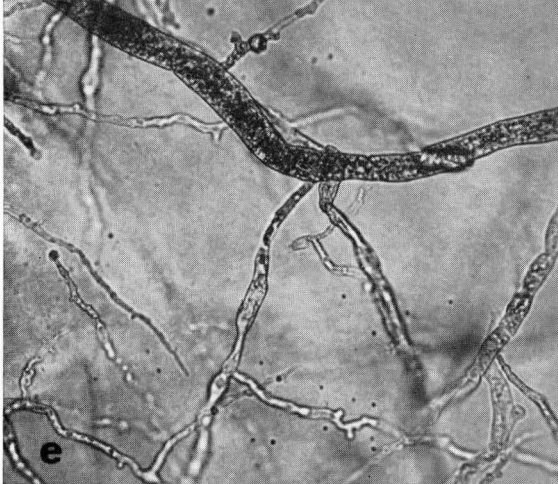
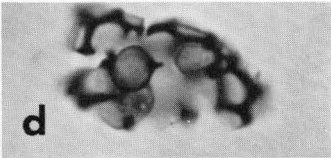
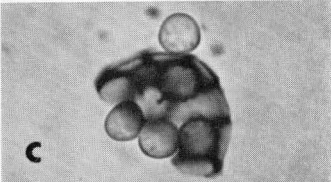
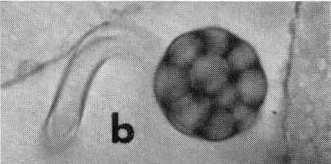
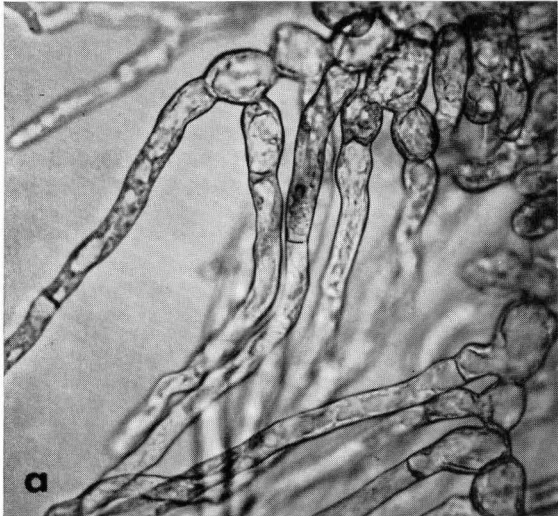
Type species: *Phascolomyces articulatus* Boedijn.

PHASCOLOMYCES ARTICULOSUS Boedijn, Sydowia 12: 349. 1958 [1959].

Figs. 7; 8e–h

Colonies on MSMA to 8.5 cm in diam in 7–10 days at 26 C; turf lax to relatively dense, consisting almost entirely of sporophores; white at first, then off-white to pale grayish, becoming pale yellowish brown in age. Substrate hyphae branched, variable in diam to ca. 15 μm , smooth, hyaline to pale yellow; forming a compact, often more or less raised and furrowed colony; giving rise to large numbers of nearly globose, subglobose, ovoid, clavate, pyriform, or irregularly shaped intercalary giant cells, 50–175 \times 75–350 μm , that become dark brown to nearly black in age. Sporophores erect or ascending, 0.5–1.5 cm high, 10–12(–20) μm wide, hyaline to pale brown; wall smooth to rough, sometimes faintly striate; simple or sympodially branched; branches often septate near base, as small as 3.5 μm wide; producing fertile vesicles terminally or laterally. Terminal vesicles globose to subglobose, rarely obpyriform or obovate, 18–90 μm in diam; laterally formed vesicles variable in size and shape, usually globoid, 4–50 μm in diam, sessile or subtended by short stalks up to 20 μm long. Sporangiolar pedicels nearly straight, 6–25 μm long, 0.5–1.5 μm wide, smooth, fragile, readily breaking at maturity, with distal part remaining attached to sporangiole, proximal part remaining on vesicle as a variably elongate stub. Sporangiola globose to subglobose, 6–10(–12) μm in diam; wall hyaline, smooth to wrinkled; columella smooth, compressed, becoming convex with spore release. Sporangiospores smooth, like the sporangiola in size and shape. Zygosporos not observed.

Neotype.—INDONESIA. JAVA. Bogor, substrate unknown, ?1960, J. H. B. Garner (RSA 1941; =NRRL 2880). A dried culture has been deposited in



the herbarium of RSA. In addition, living cultures have been transmitted to ATCC, CBS, and IMI.

Illustrations.—Boedijn (1958 [1959]), Fig. 10.

Other specimens examined.—REPUBLIC OF CHINA. TAIWAN. Tainan, dung of *Rattus losea* Swinhow coll. by Chin-chyu Tu, Jan., 1976, G. L. Benny isol. (RSA 2164A; RSA 2164B). PANAMA. Isol. from ?bat dung, June, 1940, W. H. Weston (RSA 658; =IMI 81613(A); =NRRL 1593; =QM 6802).

Notes.—When Boedijn (1958 [1959]) described *Phascolomyces articulatus* he failed to designate a nomenclatural type in accordance with Article 35 of the then-current *International Code of Botanical Nomenclature* (Lanjouw, 1956), although he did provide adequate diagnostic figures. Boedijn apparently did not preserve specimens or cultures of this fungus according to Dr. M. A. A. Schipper of CBS (personal communication). It would have been possible to preserve a type specimen (Art. 10, Note, of the 1956 Code); therefore, in accordance with Articles 7–9 of the 1972 Code (Stafleu, 1972), we are here validating Boedijn's genus and species by designating a neotype specimen of *P. articulatus* derived from an isolate collected in the vicinity of Bogor. The culture was forwarded to the NRRL by J. H. B. Garner in 1960.

Phascolomyces articulatus grows readily and rapidly on MEYE, YpSs, and MSMA. The vegetative mycelium from the beginning (Fig. 8e) consists mostly of a system of robust hyphae of relatively large diameter that give rise to branching laterals of much smaller diameter. The hyphae are at first non-septate but become irregularly septate as they mature. The large-diameter hyphae very soon begin to develop the distinctive, intercalary giant cells (chlamydospores) (Figs. 7a,h; 8f). These often are nearly globose, commonly being more or less ovoid, clavate, or pear shaped, sometimes irregularly shaped, always considerably larger in diameter than the hyphae in which they arise. The chlamydospores at first are nearly hyaline but gradually darken, finally becoming black or nearly so. Three of our four isolates (RSA 1941, 2164A, 2164B) consistently produce abundant chlamydospores and a relatively lax turf of sporophores that usually does not obscure the substrate. The other strain (RSA 658) typically gives rise to fewer chlamydospores and a dense turf that wholly obscures the colonial surface.

The first-formed sporangiole-bearing vesicles of *P. articulatus* arise terminally on the main axis of the sporophore and on the secondary branches

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Fig. 8. a–d. *Cokeromyces recurvatus*.—a. Vegetative hyphae from near margin of 2-day-old colony on MEYE (25 C) showing characteristic rapid formation of short, ovoid cell segments. $\times 250$.—b. Intact sporangiole; only part of subtending pedicel is in focus. $\times 1,300$.—c–d. Portions of two crushed sporangiola showing opaque, blackish deposits formed around spores lying immediately below surface of sporangiole wall. $\times 1,300$.—e–h. *Phascolomyces articulatus*.—e. Vegetative hyphae (submerged) from 2-day-old colony on MEYE (25 C) showing primary hyphae of relatively large width from which secondary hyphae of highly variable but smaller width arise. $\times 250$.—f. Typical thick-walled, dark giant cell formed in substrate hyphae (MEYE; 6 wk; 22–25 C). $\times 175$.—g–h. Typical sporangiola showing separable outer wall; note small columella and apophysis (arrow). $\times 1,300$.

(Fig. 7d,g). The primary vesicles are followed by secondary, lateral, sessile to short-stalked fertile vesicles that continue to arise along the distal reaches of the main axis and its branches as the sporophore ages (Fig. 7a). Secondary fertile vesicles vary greatly in size and in the number of sporangiola they produce, some being very small and bearing only a few sporangiola (Fig. 7b-c) whereas others may be nearly as large as the terminal vesicles (Fig. 7e-f). The stalks subtending the sporangiola are fragile and break readily when mature, the distal part often remaining attached to the sporangiole (Fig. 7j), the lower part remaining on the vesicle which typically bears a stubble of pedicellar bases over its surfae after sporangiole dehiscence (Fig. 7f,g).

Phascolomyces articulatus apparently has no inherent stoloniferous tendency, but its sporophore may form rhizoidal tufts if it chanced to contact the agar surface or the moist surface of the container in tube or plate cultures.

Boedijn (1958 [1959]) included *Phascolomyces articulatus* in the Cunninghamellaceae along with *Cunninghamella* and *Thamnocephalis*, and it was retained in this family by Milko (1967, 1974) and Pidoplichko and Milko (1971). Zycha et al. (1969) regarded it as insufficiently described and appended it to their treatment of *Cunninghamella*. We are including it in the Thamniaceae because its persistent sporangiole wall is readily separable from the sporangiospore (Figs. 7j; 8g,h). Unfortunately, zygosporidia have not been observed in *P. articulatus*, and crosses of our four isolates in all possible combinations on a variety of media have not given evidence of a mating reaction.

Attempts to infect *P. articulatus* (on YpSs) with five species of *Piptocephalis* [*P. arrhiza* van Tiegh. & Le Monn. (1873b), *P. cylindrospora* Bainier (1882), *P. freseniana* de Bary (1865), *P. lepidula* (Marchal) Benjamin (1959), and *P. tieghemiana* Matruchot (1899)] have been negative, but it readily serves as host for another mucoralean parasite, *Dimargaris cristalligena* van Tiegh. (1875).

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