Aliso: A Journal of Systematic and Evolutionary Botany

Volume 8 | Issue 3 Article 10

1975

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ALISO

VOL. 8, No. 3, pp. 301–351 SEPTEMBER 22, 1975

OBSERVATIONS ON THAMNIDIACEAE (MUCORALES). NEW TAXA, NEW COMBINATIONS, AND NOTES ON SELECTED SPECIES[1,2]

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SUMMARY

The Thamnidiaceae is defined and six of the 13 genera included in the family by the authors are discussed. Thirteen species are described and illustrated as follows (basionyms given for new combinations): Previously established genera.–(1) *Thamnostylum piriforme*, *T. lucknowense*, *T. nigricans* (≡ *Helicostylum nigricans*), and *T. repens*; (2) *Backusella circina*, *B. lamprospora* (≡ *Mucor lamprosporus*), and *B. ctenidia*. New genera.–(1) *Fennellomyces linderi* (≡ *Circinella linderi*); (2) *Ellisomyces anomalus* (≡ *Thamnidium anomalum*); (3) *Zychaea mexicana*; and (4) *Dichotomocladium elegans*, *D. robustum*, and *D. hesseltinii* (≡ *Chaetocladium hesseltinii*).

INTRODUCTION

Lendner, in 1908, characterized his Thamnidiacées [i.e., Thamnidiaceae Brefeld (1881b: as Thamnidiaceen)] to include those Mucorales (his Mucorinées) in which the sporophore produces sporangia of two types: (1) a large, terminal, columellate, multispored (i.e., *Mucor*-like) sporangium having a *deliquescent* wall; and (2) a small, few-spored, caducous sporangiole that sometimes lacks a columella and has a distinct but *persistent* wall. This delimitation of the Thamnidiaceae is still the basis of most modern concepts of the family (Zycha et al., 1969; Hesseltine and Ellis, 1973).

Lendner, like most students writing before the appearance of his work (Brefeld, 1872, 1881a; Schröter, 1886, 1893; Berlese and DeToni, 1888; Fischer, 1892; Engler, 1898) and many after (Migula, 1910; Fitzpatrick, 1930; Zycha et al., 1969; Pidoplichko and Milko, 1971), placed special emphasis on the production of unispored sporangiola—with little or no distinction being made between this and the conidium verum—by repre-

[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.

[2] Florida Agricultural Experiment Station Journal Series 5893.

sentatives of several genera of Mucorales, and he retained *Chaetocladium* Fres. (1863) in a separate family, Chaetocladiacées [i.e., Chaetocladiaceae Brefeld (1872: as Chaetocladiaceen)]. Lendner also followed Fischer (1892) in recognizing a separate suborder of Mucorales, Conidiophorées (Fischer's Conidiophoreae), for presumably "conidial" taxa and included the Chaetocladiaceae in this group.

In 1935, both Naumov and Zycha classified *Chaetocladium* with *Thamnidium* Link ex Gray (1821), *Helicostylum* Corda (1842), and *Chaetostylum* van Tiegh. & Le Monn. (1873) which had been included in all concepts of the Thamnidiaceae appearing after the classical studies of these genera by van Tieghem in 1875. In 1958, Lythgoe transferred *Chaetostylum* to *Helicostylum*, a disposition of the former genus that has been accepted by Pidoplichko and Milko (1971), Upadhyay (1973), and by us. In 1970, von Arx and Upadhyay (von Arx, 1970) segregated two species of *Helicostylum*, *H. piriforme* Bainier (1880) and *H. lucknowense* Rai, Tewari & Mukerji (1961), into a new genus, *Thamnostylum* von Arx & Upadhyay. *Cokeromyces* Shanor, based on *C. recurvatus* Poitras (Shanor, Poitras, and Benjamin, 1950), originally was classified in the Choanephoraceae (Brefeld, 1881b) but soon was shifted to the Thamnidiaceae (Poitras, 1950; Hesseltine, 1952). Young (1969), on the basis of his studies demonstrating a clearly separable sporangiolar wall enclosing the spore of *Mycotypha africana* Novak & Backus (1963), suggested that *Mycotypha* Fenner (1932) also should be classified in the Thamnidiaceae. *Backusella* Ellis & Hesseltine (1969) was included in the Mucoraceae Bonorden (1851) by its authors, but they commented on its possible alliance with the Thamnidiaceae and in 1971 Pidoplichko and Milko transferred the genus to this family.

Dicranophora Schröt., based on *D. fulva* Schröt. (1886), also has been placed in the Thamnidiaceae (Lendner, 1908; Fitzpatrick, 1930; Zycha, 1935; Zycha et al., 1969) and in 1968 Milko transferred *D. fulva* to *Thamnidium*. Hesseltine and Ellis (1973) include the genus in the family with reservation, and they indicate their uncertainty by keying it out in both the Mucoraceae and Thamnidiaceae. We agree with Dobbs (1938) who suggested that the genus is allied to *Syzygites* Ehrenb. ex Fr. (1832) and *Spinellus* van Tiegh. (1875) which at present are classified in the Mucoraceae (Hesseltine and Ellis, 1973). Lendner (1908) placed *Actinomucor* Schost. (1898) in the Thamnidiaceae, but this notion has not been supported by later students of the Mucorales (C. Benjamin and Hesseltine, 1957; Hesseltine and Ellis, 1973) and this genus, too, is retained in the Mucoraceae.

Our concept of the Thamnidiaceae is not fundamentally different from that of Lendner (1908) and others. Like Naumov (1935, 1939), Zycha (1935), Hesseltine (1955), Zycha et al. (1969), and Hesseltine and Ellis (1973) and unlike Pidoplichko and Milko (1971) we reject overemphasis—in the absence of other criteria—of the importance of the unispored sporangiole in classifying Mucorales at the family level. Accordingly, we characterize the family as follows:

Sporophore erect or ascending, rarely repent, simple or branched, arising directly from the substrate mycelium or from stolons; producing large, terminal, columellate, multispored sporangia having a deliquescent wall, or sporangia absent; always producing pedicellate, uni- or multispored sporangiola having a persistent but separable wall. Sporangia and sporangiola apophysate or nonapophysate. Sporangiospores thin walled, smooth as viewed with the light microscope. Zygospores roughened, usually dark colored, borne between opposed, equal or unequal suspensors that lack appendages.

This definition of the family distinguishes a sizeable number of species of Mucorales from other species of the order that have similar vegetative characteristics and that also may produce sporangia and/or sporangiola. In addition to four new genera described in this paper, we also include the following genera in the Thamnidiaceae: *Backusella, Chaetocladium, Cokeromyces, Helicostylum, Mycotypha, Phascolomyces* Boedijn (1958), *Pirella* Bainier (1882), *Thamnidium*, and *Thamnostylum*.

Our purpose in this paper is to describe a number of new taxa of the Thamnidiaceae and to update information on several others. Genera not treated here will be discussed in forthcoming works.

MATERIALS AND METHODS

The source of specimens examined is given in the text. Institutional designations are those of Holmgren and Keuken (1974) except BKMF (Department of Type Cultures, Institute of Microbiology, U.S.S.R. Academy of Sciences, Moscow), IFO (Institute for Fermentation, Osaka, Japan), and NRRL (Northern Regional Research Laboratory, U.S.D.A., Peoria, Illinois 61604). The collection formerly located at the U.S. Army Natick Laboratories, Natick, Mass. (QM) is now housed at the Department of Botany, Univ. of Mass., Amherst 01002.

Dried cultures of all specimens cited have been deposited in the Mycological Collections of the Rancho Santa Ana Botanic Garden (RSA). Type cultures of all taxa described as new will be forwarded to ATCC, CBS, IMI, and NRRL.

Descriptions of colonial characteristics and vegetative and asexual reproductive structures of all taxa discussed are based on pure cultures of the fungi grown on a modification of the Synthetic Mucor Agar of Hesseltine (1954) formulated as follows: MSMA (modified synthetic mucor agar)—dextrose, 10 g; $NaNO_3$, 4 g; K_2HPO_4, 0.5 g; $MgSO_4 \cdot 7H_2O$, 0.5 g; thiamine hydrochloride, 0.5 mg; agar, 15 g; and water, 1 liter. Other media (as noted in the text) employed in the study included the following: YpSs (yeast extract-soluble starch agar)—yeast extract, 4 g; soluble starch, 15 g; K_2HPO_4, 1 g; $MgSO_4 \cdot 7H_2O$, 0.5 g; agar, 15 g; water, 1 liter. 2% ME (2% malt extract agar)—malt extract, 20 g; agar, 20 g; water, 1 liter. MEYE (malt extract-yeast extract agar)—malt extract, 3 g; yeast extract, 3 g; peptone, 5 g; dextrose, 10 g; agar, 15 g; water, 1 liter. LYE (Leonian's agar + yeast extract)—malt extract, 6 g; yeast extract, 1 g; peptone, 0.6 g; maltose, 6 g; KH_2PO_4, 1.2 g; $MgSO_4 \cdot 7H_2O$, 1.2 g; agar, 15 g; water, 1 liter. YpD—YpSs agar supplemented with 5 g of dextrose. Wort + 3.5—wort agar, 50 g; dextrose, 35 g; water, 1 liter. Except for the chemicals, Difco products were used in preparing all of the above media. TPO (tomato paste-oatmeal agar; Hesseltine, 1960)—tomato paste, 20 g; baby oatmeal (instant), 20 g; agar, 15 g; water, 1 liter.

Measurements given in the descriptions were determined by use of water mounts of living fungi. Spores and sporangiola were mounted on agar films on glass slides to prevent Brownian movement. Size ranges are based on 25–100 measurements; when a mean value is given, the range is based on 50–100 measurements. Drawings were prepared from specimens mounted in water or KOH-phloxine (Martin, 1952), and all drawings were executed with the aid of a camera lucida. Capitalized color names are those designating color chips in Ridgway (1912).

The mating type indicated for cited strains of each species is based on crosses of the strain with strongly mating tester strains of the species that had been arbitrarily designated + and –, either by us or someone else in the case of testers received from other institutions.

DESCRIPTIONS AND COMMENTARY

THAMNOSTYLUM von Arx & Upadhyay, *in* von Arx, The genera of fungi sporulating in pure culture, p. 247. 1970.

Sporophores arising from the substrate mycelium or from stolons, erect, simple or branched, producing large terminal sporangia and more or less compact clusters of few or many pedicellate sporangiola borne in terminal fascicles or on vesicular enlargements arising laterally from the sporophoral axis. Terminal sporangia columellate, multispored, subglobose to broadly clavate, apophysate; wall encrusted, deliquescent; columellae hemispherical, obovoid, or elongate, smooth. Fertile vesicles, if present, subterminal or intercalary, sessile on a broad base or subtended by a more or less narrowed stalklike base. Sporangiolar pedicels elongate, usually abruptly recurved distally immediately below the sporangiole, smooth or encrusted. Sporangiola columellate, few or many spored, globose, subglobose, or obpyriform, apophysate; wall persistent, smooth. Sporangiospores alike from sporangia and sporangiola, subglobose to ovoid, smooth. Zygospores globose to subglobose; wall dark, roughened, ornamented with more or less prominent projections; gametangial remnants often present, smooth, dark; suspensors opposed, smooth or roughened, equal or slightly unequal.

Type species: Helicostylum piriforme Bainier.

Von Arx and Upadhyay (von Arx, 1970) established *Thamnostylum* for *Helicostylum piriforme* and *H. lucknowense* because these species differed from the type of the genus, *H. elegans* Corda (1842), in being stoloniferous, in having apophysate primary (i.e., terminal) sporangia, and in producing usually pyriform sporangiola on more or less strongly reflexed pedicels arising in clusters from nodose enlargements of the sporangiophore. The sporophore of true *Helicostylum* spp. is more or less constricted immediately below the primary sporangium, and the sporangiola of species of this genus are always globose to subglobose and nonapophysate.

Upadhyay (1973) transferred *Helicostylum repens* van Tiegh. (1876) to *Thamnostylum* on the basis of its original, brief, unillustrated description, and we are able to confirm this action from a study of numerous isolates of the fungus. We also have obtained several strains of what we regard as being *H. nigricans* van Tiegh. (1876) and are transferring this species to *Thamnostylum.*

KEY TO THE SPECIES OF *THAMNOSTYLUM*

A. Sporangiola including apophysis globose to subglobose .... 3. *T. nigricans*
AA. Sporangiola including apophysis obpyriform, rarely subglobose .... B
B. Sporangiola not arising from vesicles; produced in fascicles terminating the main axis of the sporophore or its branches .... 4. *T. repens*
BB. Sporangiola arising from vesicles; these sessile on a broad base or short stalked .. C
C. Colony becoming olivaceous or blackish; vesicles typically stalked, arising singly or, more commonly, in whorls encircling a more or less nodose enlargement of the sporophore; sporangiola arising in pairs or small fascicles, their pedicels dichotomously branched at the base .... 1. *T. piriforme*
CC. Colony becoming pale brownish yellow; vesicles usually arising singly, often more or less lobate, on a broad base or short stakled; sporangiola arising singly .... 2. *T. lucknowense*

1. THAMNOSTYLUM PIRIFORME (Bain.) von Arx & Upadhyay, *in* von Arx, The genera of fungi sporulating in pure culture, p. 247. 1970. FIG. 1

≡ *Helicostylum piriforme* Bain., Bull. Soc. Bot. France 27: 227. 1880.

≡ *Thamnidium piriforme* (Bain.) Migula, Kryptogamen-Fl. Deutsch., Deutsch-Österr., Schweiz 3(1): 207. 1910.

Colonies developing moderately rapidly on MSMA, to ca. 8.5 cm in diam in 7 days at 26 C; turf dense, colorless at first, Pale Smoke-Gray to Smoke-Gray in age (Dark Olive to Olivaceous Black on YpSs); strongly stoloniferous. Stolons arising from the substrate mycelium, 7–20 μm in diam, hyaline at first, pale olivaceous to brownish in age, smooth or roughened, septate or nonseptate, simple, becoming branched; forming clumps of rhizoids upon contacting the substratum or walls of the culture chamber and giving rise to erect sporophores; often bearing clusters of sporangiola at irregular intervals. Rhizoids 2–10 μm in diam, hyaline, becoming olivaceous to brown, septate, branched. Sporophores arising directly from substrate mycelium or from stolons, (12–)15–20(–33) μm in diam, simple or sympodially branched, rarely dichotomously or umbellately branched distally, hyaline at first, olivaceous to brownish in age; the primary axis and its branches bearing a sporangium terminally (rare on MSMA; common on YpSs) or ending in a sterile spine subtended by a more or less globoid cluster of sporangiola arising from fertile vesicles; axis usually giving rise to one or more additional clusters of few to many sporangiola. Primary sporangia subglobose, (50–)115–130(–200) μm in diam, dark olive to dark brown; wall hyaline, encrusted, diffluent; columellae ovoid to short cylindrical, 30–115 × 25–75 μm, hyaline to olivaceous, with basal collar; apophysis well defined. Fertile vesicles sessile on a broad base or short stalked, arising singly or, more commonly, in a whorl surrounding a nodose enlargement of the sporophoral axis; producing small fascicles of pedicellate sporangiola over their entire surface. Heads of sporangiola 80–400 μm in diam. Sporangiolar pedicels 20–100 μm long, 2–4.5 μm wide below the apophysis, usually strongly recurved distally, dichotomously branched near the base, smooth, hyaline to subhyaline. Sporangiola subglobose to obpyriform, 11–22(–33) μm in diam, light gray to steel blue, olivaceous to brownish in age; wall hyaline, smooth; columella hemispherical, up to 14 μm in diam; apophysis well defined. Sporangiospores alike in sporangia and sporangiola, ovoid to ellipsoid, (4–)5.2–7.2(–9.2) × (3.2–)4–5.6(–6) μm (av. 6.5 × 4.5 μm); 5–32 per sporangiole. Zygospores on MEYE globose to subglobose, 70–175 μm (av. 115 μm) in diam; wall dark brown to nearly black, opaque, verrucose, becoming scaly; suspensors 40–100 μm long, 20–45 μm wide near zygospore, hyaline to olivaceous, smooth to roughened. Heterothallic.

Distribution.—Cosmopolitan.

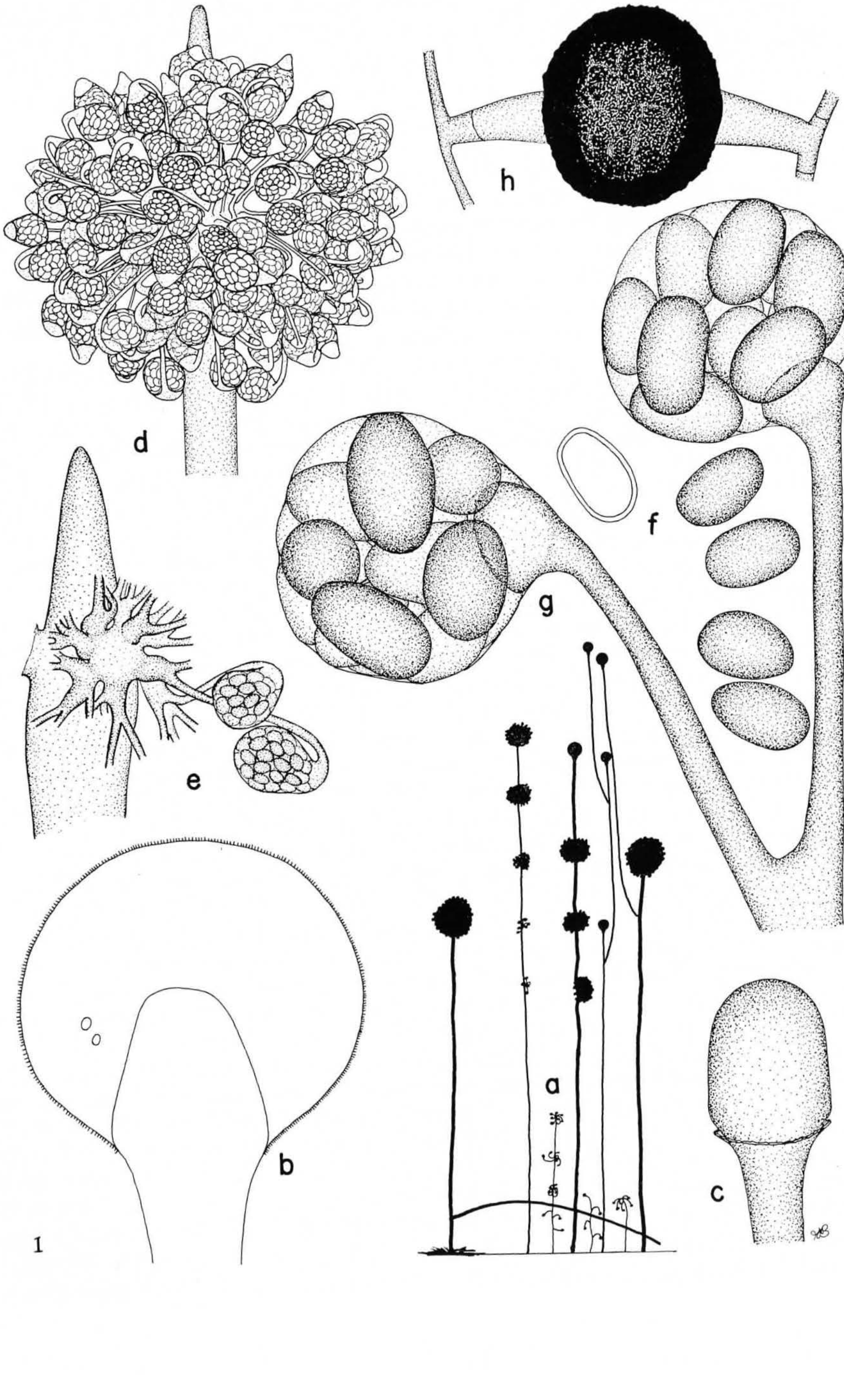
Illustrations.—As *Helicostylum piriforme*: Bainier (1880), Pl. 5, Figs. 5–11; (1882), facing p. 69, Figs. 5–11; (1883), Pl. 4, Figs. 5–11; Christenberry (1940), Pl. 17, Figs. 158–168; Grehn (1932), Fig. 14a–d; Ingold (1965), Fig. 18F–G; Ingold and Zoberi (1963), Fig. 6F–G, Pl. 9, Fig. 9; Lythgoe (1958), Fig. 2; Massee and Salmon (1902), Pl. V, Figs. 105–108; Mehrotra and Mehrotra (1962), Figs. 1–14; Ou (1940), Pl. III, Fig. 12; Pidoplichko and Milko (1971), Fig. 122a–e; Verona and Benedek (1963), Pl. B69, Fig. 1a–c; Zycha (1935), Fig. 76a–d; Zycha et al. (1969), Fig. 48.—As *Thamnostylum piriforme:* Upadhyay (1973), Figs. 8–13.

Specimens examined.—AFRICA. Sierra Leone. Njala, insect larva, 1954, *F. C. Deighton* (RSA 1026+; =IMI 57466a). Sudan. Soil, isol. at Commonwealth Mycological Inst., 1953, *M. A. Nour* (RSA 1025+; =IMI 52123). "West Africa." Fermented cacao beans, 1949, *W. C. Moore* (RSA 1024; =IMI 34453). INDIA. Madras. Coimbatore, sugar cane leaf, 1960, *J. N. Rai* (RSA 1115–; =IMI 80552). JAPAN. Exact localities unknown. Received by the NRRL in Dec., 1953, from the Nagao Institute, Tokyo (RSA 506A+; =NRRL 2530; =CBS 206.55.—RSA 506B–; =NRRL 2529; =CBS 205.55). MEXICO. Baja California del Norte. Mission San Borja, ca. 15 mi WSW of Bahía de los Angeles, pack rat dung, Feb. 25, 1963, *R. K. Benjamin* (RSA 1311); Cedros Island, pack rat dung coll. by R. Moran, Apr. 17, 1963, *R. K. Benjamin* isol. (RSA 1339). Tamaulipas. Cuesta de la Seja, ca. 3 mi W of Jaumave, rodent dung coll. by T. Anderson, Jan. 25, 1961, *R. K. Benjamin* isol. (RSA 1330+). PAKISTAN. Multar. Pirawal nr. Khanewal, domestic rat dung coll. by S. Mahmood, Dec., 1974, *R. K. Benjamin* isol. (RSA 2107+); Lyallapur, domestic rat dung coll. by J. Ahmad, Nov., 1974, *R. K. Benjamin* isol. (RSA 2108+). U.S.A. Arizona. Coconino Co.: 3 mi N of Meter Crater, pack rat dung, Sept. 2, 1960, *R. K. Benjamin* (RSA 1056–).—Maricopa Co.: 8.5 mi E of Tortilla Flats, dung, Apr. 17, 1962, *R. K. Benjamin* (RSA 1302–).—Pima Co.: 1 mi N of entrance to Oregon Pipe National Monument, pack rat dung, Sept. 3, 1960, *R. K. Benjamin* (RSA 1057+).—Yavapai Co.: 3 mi N of Bumble Bee, pack rat dung, Sept. 2, 1960, *R. K. Benjamin* (RSA 1056–). California. Butte Co.: 10 mi N of Oroville, dung, June 19, 1958, *R. K. Benjamin* (RSA 732+).—Inyo Co.: Deep Springs, pack rat dung coll. by R. M. Straw, 1955, *R. K. Benjamin* isol. (RSA 511+).—Kern Co.: Tupman, rabbit dung, no date, *G. F. Orr 504* (RSA 954–).—Los Angeles Co.: Evey Canyon, San Gabriel Mts., ca. 4.5 mi NE of Claremont, pack rat dung, Apr. 28, 1955, *R. K. Benjamin* (RSA 507–).—Mono Co.: June Lake, ca. 12 mi S of Mono Lake, soil and leaf mold coll. by D. H. Ford, June 10, 1953, *R. K. Benjamin* isol. (RSA 107–).—Monterey Co.: Santa Lucia Mts., 1 mi W of China Camp, deer dung coll. by E. K. Balls, Oct. 7, 1953, *R. K. Benjamin* isol. (RSA 171).—Riverside Co.: Joshua Tree National Monument nr. Split Rock, pack rat dung, Nov. 29, 1958, *R. K. Benjamin* (RSA 841+).—San Bernardino Co.: Cucamonga, pack rat dung coll. by D. H. Ford, Jan. 1, 1954, *R. K. Benjamin* isol. (RSA 251–); S of Needles, nr. Colorado River, pack rat dung coll. by D. H. Wiens, Dec. 21, 1958, *R. K. Benjamin* isol. (RSA 847–); Victorville, mouse dung, Nov. 4, 1969, *G. L. Benny* (RSA 2025).—San Diego Co.: 7 mi E of Jamul, mouse dung, Oct. 16, 1960, *R. K. Benjamin* (RSA 1058–); San Clemente Island, fox(?) dung coll. by P. H. Raven, Apr. 11, 1962, *R. K. Benjamin* isol. (RSA 1298–).—Shasta Co.: O'Brien Mt., raccoon dung coll. by O. A. Plunkett, July, 1960, *G. F. Orr 834* isol. (RSA 1010–). ILLINOIS. Champaign Co.: Champaign, mouse dung coll. by Ethel Dickens, Dec. 1958, *R. K. Benjamin* isol. (RSA 848). LOUISIANA. Orleans Parish. New Orleans, snake dung, Mar., 1960, *A. L. Welden* (RSA 1013). NEBRASKA. Lincoln Co.: Lincoln, Univ. of Nebraska campus, mouse dung, Jan., 1971, *W. Gauger* (RSA 2039).

Notes.—*Thamnostylum piriforme* is one of the most common species in the genus and in the family. The specimens cited above represent only a few of the over 100 isolates in the collection of the Rancho Santa Ana Botanic Garden, and during recent years we have not routinely isolated the fungus when it has been encountered on substrata collected in southern California. It was most recently described and illustrated by Upadhyay (1973) and has been reported and illustrated (as *Helicostylum piriforme*) numerous times in the past (see under Illustrations).

Thamnostylum piriforme occurs most commonly on dung but is occasionally found in soil or other organic debris. It grows and sporulates readily in culture; the substrate mycelium giving rise to sporophores bearing sporangia or sporangiola or both (Fig. 1a) followed by stolons that contact the walls of the growth chamber, develop tufts of rhizoids, and form sporophores. The sporophoral axis typically arises from the stolon a short distance from the rhizoidal complex (Fig. 1a). When one encounters this and other species of *Thamnostylum* in moist-chamber cultures of dung or other debris, it is often an isolated sporophore with its subtending rhizoids developing some distance from the point of origin of a stolon that attracts one's attention to the fungus (Fig. 1a). Isolates vary greatly in the production of primary sporangia, some forming these in abundance, others only rarely. Strains also show much variation in sexual vigor, and in matings of compatible strains on YpSs or MEYE at room temperature (20–24 C) the number of zygospores may vary from a few scattered spores to many hundreds in the contact zone. Zygospores (Fig. 1h) develop in crosses on a variety of media including MSMA, YpSs, MEYE, YpD, and TPO. Many strains in our collection never have formed zygospores with testers.

Thamnostylum piriforme is readily distinguished from other species of the genus. Like *T. repens* (Fig. 4) it is strongly stoloniferous and both species, especially on media like YpSs, MEYE, and TPO, form colonies that become Dark Olive to Olivaceous Black from the production of abundant sporangiola and the hyphal wall pigments. The heads of sporangiola of *T. piriforme* (Fig. 1a,d) and *T. repens* (Fig. 4a,d) are relatively much larger than those of *T. lucknowense* (Fig. 2a,f) and *T. nigricans* (Fig. 3a,f,g) so that the glomerulate nature of the sporophore is a much more conspicuous feature of the former species than of the latter when their colonies are viewed with the unaided eye. The sporangiola of *T. repens* do not arise from vesicles formed laterally on the sporophore, but in small, often more or less lax clusters developed on the irregularly branched terminus of the sporophore or its branches (Fig. 4d,e). In *T. lucknowense* each sporangiolar pedicel arises directly from the subtending vesicle and is rarely branched (Fig. 2f) whereas in *T. piriforme* the pedicels are regularly two or more times branched near the base so that the sporangiola are grouped in small fascicles on the subtending vesicle (Fig. 1d,e,g). Sporangiospores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of *T. piriforme* are on the average larger than those of *T. lucknowense*, 6.5 × 4.5 μm vs. 5.5 × 3.3 μm. In age, the colony of *T. lucknowense* becomes buff to honey colored, never the dark olivaceous to blackish shades of the other species.

2. THAMNOSTYLUM LUCKNOWENSE (Rai, Tewari & Mukerji) von Arx & Upadhyay, *in* von Arx, The genera of fungi sporulating in pure culture, p. 247. 1970. FIG. 2

≡ *Helicostylum lucknowense* Rai, Tewari & Mukerji, Canad. J. Bot. 39: 1282. 1961.

Colonies on MSMA to ca. 8.5 cm in diam in 8 days at 26 C; turf dense, white at first, Ivory-Yellow to Dark Olive-Buff in age. Odor fruity. Stolons arising from the substrate mycelium, 4–7.5 μm in diam, hyaline, becoming buff to olivaceous, smooth or roughened, coenocytic, rarely septate in age; forming clumps of rhizoids upon contacting the substratum or walls of the culture chamber. Rhizoids 2.5–5 μm in diam, highly branched, nonseptate, hyaline. Sporophores arising directly from substrate mycelium or from stolons, (5–)8.5–12.5(–21) μm in diam, simple or sympodially branched, often dichotomously or umbellately branched distally, hyaline at first, becoming brownish yellow; the main axis and each branch bearing a terminal sporangium or sterile and spinelike; axis forming one or more intercalary fertile vesicles. Primary sporangia subglobose to obpyriform, 30–85(–110) × 22–65(–75) μm; wall hyaline, diffluent; columellae hemispherical to obovoid, 13–37 × 8–30 μm, subtended by a slightly developed apophysis, hyaline to subhyaline, basal collar usually present. Fertile vesicles arising laterally, usually singly; more or less bilobate, elongate; the long axis perpendicular to the axis of the sporophore; nearly sessile on a broad base or with a rudimentary, slightly narrowed stalk; 1–8 or more per sporophore; bearing pedicellate sporangiola over their entire surface. Sporangiolar pedicels 25–65(–90) × 1.5–3 μm, strongly recurved distally, hyaline to subhyaline, smooth. Sporangiola obpyriform, rarely subglobose, 7–18 μm in diam, brownish yellow, deciduous; wall hyaline; columellae dome shaped to hemispherical, up to 8 μm in diam, smooth; apophysis abruptly tapered below, well developed. Sporangiospores alike in sporangia and sporangiola,

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Fig. 1. *Thamnostylum piriforme*.—a. Habit sketches of sporophores. × 10.—b. Optical section through a primary sporangium showing columella and apophysis; two sporangiospores are included for comparison. × 235.—c. Columella of a primary sporangium showing basal collar and apophysis. × 235.—d. Distal portion of a typical sporophore showing sterile apex projecting above the pedicellate sporangiola forming a globoid head that almost completely obscures the subtending vesicles. × 235.—e. Distal portion of a similar sporophore showing a nodose enlargement and only one of several stalked fertile vesicles as seen from above. Two pedicellate sporangiola are shown in their entirety. The others have been omitted to show their origin from the vesicle in pairs or small fascicles. × 460.—f. Sporangiospores, one showing relative thickness of wall. Spores are similar in both primary sporangia and sporangiola. × 1,690.—g. Two nearly globose sporangiola showing spores, columella, and apophysis. × 1,690.—h. Typical zygospore and its suspensors (RSA 251– × RSA 511+). × 235.

ovoid to ellipsoid, 3–7 × 2–4 μm (av. 5.5 × 3.3 μm); 3–22 per sporangiole; pale brownish yellow. Zygospores on YpSs globose to subglobose, (42–)52–78(–105) μm in diam including surface projections; wall reddish brown, translucent, covered with flat-topped pyramidal projections up to 5 μm high; gametangial remnants dark brown, to 7.5 μm long; suspensors (12–)15–30(–50) μm long, (12–)15–20(–25) μm wide, hyaline to light yellow, smooth. Heterothallic.

Distribution.—India, Mexico, U.S.A.

Illustrations.—As *Helicostylum lucknowense*: Rai et al. (1961), Figs. 1–17; Upadhyay (1973), Figs. 14–17; Verona and Benedek (1963), Pl. B69, Fig. 3; (1972), Pl. B130; Zycha et al. (1969), Pl. 47.

Specimens examined.—INDIA. UTTAR PRADESH. Lucknow, soil, 1959, *J. N. Rai* (type culture: RSA 1015+; =NRRL 2892; =ATCC 14746; =CBS 576.69; =IMI 86383). MEXICO. CHIHUAHUA. Ca. 22 km N of Moctezuma, lizard dung coll. by J. Henrickson, July 4, 1964, *R. K. Benjamin* isol. (RSA 1402–); ca. 45 km N of Villa Ahumada, lizard dung coll. by J. Henrickson, July 4, 1964, *R. K. Benjamin* isol. (RSA 1473). SINALOA. Ca. 3 mi E of Topolobampo and ca. 15 mi SW of Los Mochis, mouse dung coll. by J. Henrickson, June 19, 1964, *R. K. Benjamin* isol. (RSA 1420–; RSA 1499). TAMAULIPAS. Ca. 3 mi W of Jaumave, rat dung coll. by T. Anderson, Jan. 25, 1961, *R. K. Benjamin* isol. (RSA 1094–). U.S.A. CALIFORNIA. Inyo Co.: Deep Spring Lake, ca. 8 mi SW of Deep Springs, dung coll. by D. Webb, Feb. 27, 1956, *R. K. Benjamin* isol. (RSA 480–).—Riverside Co.: ca. 25 mi E of Indio, rodent dung, Apr. 12, 1964, *R. K. Benjamin* (RSA 1371+).—San Bernardino Co.: Lake View, ca. 10 mi W of Nipton, pack rat dung, Aug. 19, 1959, *R. K. Benjamin* (RSA 894–; =CBS 874.69); 5 mi SE of Dagett, mouse dung, Nov. 11, 1960, *R. K. Benjamin* (RSA 1093–; =CBS 879.69). COLORADO. Moctezuma Co.: Highway 40, 3 mi E of New Mexico-Colorado border, pack rat dung, Aug. 28, 1964, *R. K. Benjamin* (RSA 1500; RSA 1523+).

Notes.—Although *Thamnostylum lucknowense* was described from India, the several isolates from the United States and Mexico reported here suggest that it is widely distributed. The species was discussed most recently by Upadhyay (1973). It grows readily on a variety of media and at temperatures of 25–30 C forms a dense turf that within 2–3 wk fills the interior of a 2 × 8.5-cm Petri dish. It is stoloniferous, but, like *T. nigricans*, this habit of growth is not as conspicuous as in *T. piriforme* and *T. repens* where the aerial mycelium spreads rapidly by this means.

Thamnostylum lucknowense is easily separated from *T. piriforme* by (1) its more or less bilobate, nearly sessile, transversely oriented fertile vesicles bearing sporangiola on simple, rarely branched pedicels (Fig. 2f–h), (2) its smaller sporangiospores, and (3) the color and gross appearance of its colony. The fertile vesicles of *T. nigricans* resemble those of *T. lucknowense*, but the globose sporangiola of the former (Fig. 3k) vs. the typically obpyriform sporangiola of the former (Fig. 2i) distinguish the two species.

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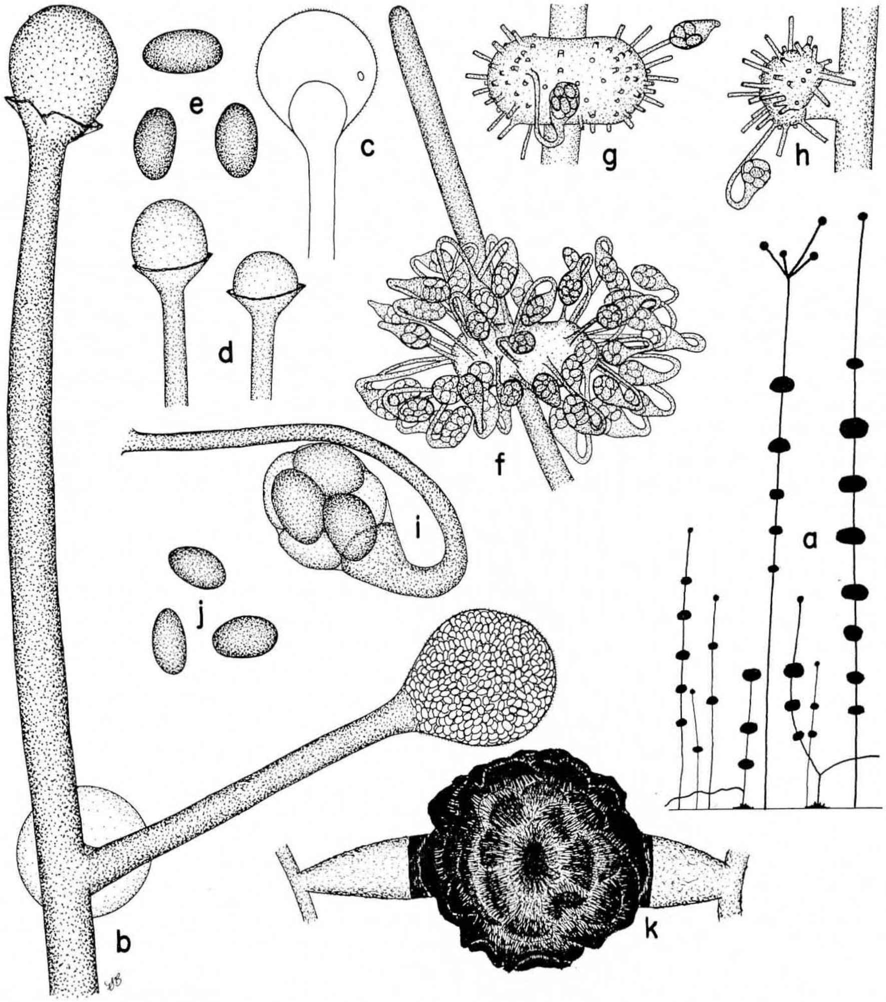
Fig. 2. *Thamnostylum lucknowense*.—a. Habit sketches of sporophores. × 10.—b. Distal part of a sporophore showing the columella of a primary sporangium at its apex and intact primary sporangia at the apices of two lateral branches (one projecting away from the viewer at right angles). × 350.—c. Optical section through a primary sporangium showing shape of columella and relative size of a sporangiospore. × 350.—d. Two columellae from primary sporangia; note collar and broad apophysis. × 350.—e.



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Sporangiospores from a primary sporangium. × 1,715.—f. Portion of a sporophore with sterile termination and a sporangiolar head consisting of a transversely oriented fertile vesicle bearing pedicellate sporangiola over its entire surface. × 350.—g. Frontal view of a fertile vesicle with two pedicellate sporangiola still attached; note stubble formed by remnants of sporangiolar pedicels and the characteristic transverse orientation of the somewhat bilobed vesicle. × 350.—h. Vesicle as seen in lateral view with a single intact sporangiole; note short stalk subtending the vesicle. × 350.—i. A sporangiole showing strongly reflexed pedicel; note the rounded columella and the broad, abruptly tapered apophysis. × 1,715.—j. Sporangiospores from a sporangiole. × 1,715.—k. Typical zygospore and its suspensors (RSA 480– × RSA 1015+). × 350.

3. **Thamnostylum nigricans** (van Tiegh.) Benny & Benjamin, comb. nov. Fig. 3

≡ *Helicostylum nigricans* van Tiegh., Ann. Sci. Nat. Bot., Sér. 6, 4: 374. 1876 (basionym).

≡ *Thamnidium nigricans* (van Tiegh.) Migula, Kryptogamen-Fl. Deutsch., Deutsch-Österr., Schweiz 3(1): 207. 1910.

Colonies on MSMA to ca. 8.5 cm in 9 days at 26 C; turf dense, white at first, Deep Olive-Buff in center to Light Brownish Olive at margin in age. Stolons arising from the substrate mycelium, 5–10 μm in diam, hyaline, becoming brownish olive in age, smooth or slightly roughened; forming clumps of rhizoids upon contacting the substratum or walls of the culture chamber. Rhizoids 2–5 μm in diam, hyaline, branched, nonseptate. Sporophores arising directly from the substrate mycelium or from stolons, to ca. 1.5 cm high, smooth, sometimes becoming roughened in age, light yellow to olivaceous brown, simple or dichotomously or umbellately branched distally, (6–)8–12(–15) μm in diam; the main axis and its branches bearing terminal sporangia and one or more intercalary fertile vesicles. Primary sporangia broadly clavate, (35–)45–60(–70) μm long, (30–)45–55(–60) μm in diam, light gray; wall hyaline, diffluent; columellae obovoid to short cylindrical, (25–)40–60(–67) μm long including apophysis, (15–)25–45 μm in diam, hyaline to light yellow, with more or less prominent basal collar. Fertile vesicles arising laterally, rounded to transversely elongate, often more or less lobed; the long axis perpendicular to the axis of the sporophore; sessile on a broad base or with a slightly narrowed short stalk, smooth, light yellow to olivaceous brown; 1–8 or more per sporophore; bearing pedicellate sporangiola from their expanded extremities. Sporangiolar pedicels usually recurved distally, rarely twisted and contorted, (40–)50–60(–65) × (1.2–)1.8–2.2(–2.8) μm, aseptate, roughened. Sporangiola globose, rarely subglobose, 9–16 μm in diam, pale gray to light brown; wall hyaline, smooth; columellae small, obovoid to subglobose, 2–2.4 μm in diam, with only slightly developed apophysis. Sporangiola often separating intact from tip of pedicel. Sporangiospores alike in sporangia and sporangiola, ovoid to ellipsoid, (3.6–)4.8–6.4(–6.8) × (2–)2.4–3.2 μm (av. 5.6 × 2.8 μm), pale yellow, 7–13(–25) per sporangiole. Zygospores on YpD (50–)55–75(–85) μm in diam including surface projections; wall brown to blackish, opaque, covered with conical projections to ca. 8.5 μm high; gametangial remnants often visible, light to dark brown, to 8 μm long; suspensors (8–)15–33(–42) μm long, 15–25 μm wide, hyaline to pale yellow. Heterothallic.

Neotype.—MEXICO. Chihuahua. Ca. 22 km N of Moctezuma, lizard dung coll. by J. Henrickson, July 4, 1964, *R. K. Benjamin* isol. (RSA 1406+). A dried culture has been deposited in the herbarium of RSA. In addition, living cultures have been transmitted to ATCC, CBS, IMI, and NRRL.

Distribution.—France, Mexico, U.S.A.

Illustrations.—van Tieghem (1876), Pl. 13, Figs. 79–83 (as *Helicostylum nigricans*).

Other specimens examined.—MEXICO. Chihuahua. Ca. 22 km N of Moctezuma, lizard dung coll. by J. Henrickson, July 4, 1964, *R. K. Benjamin* isol. (RSA 1404–;

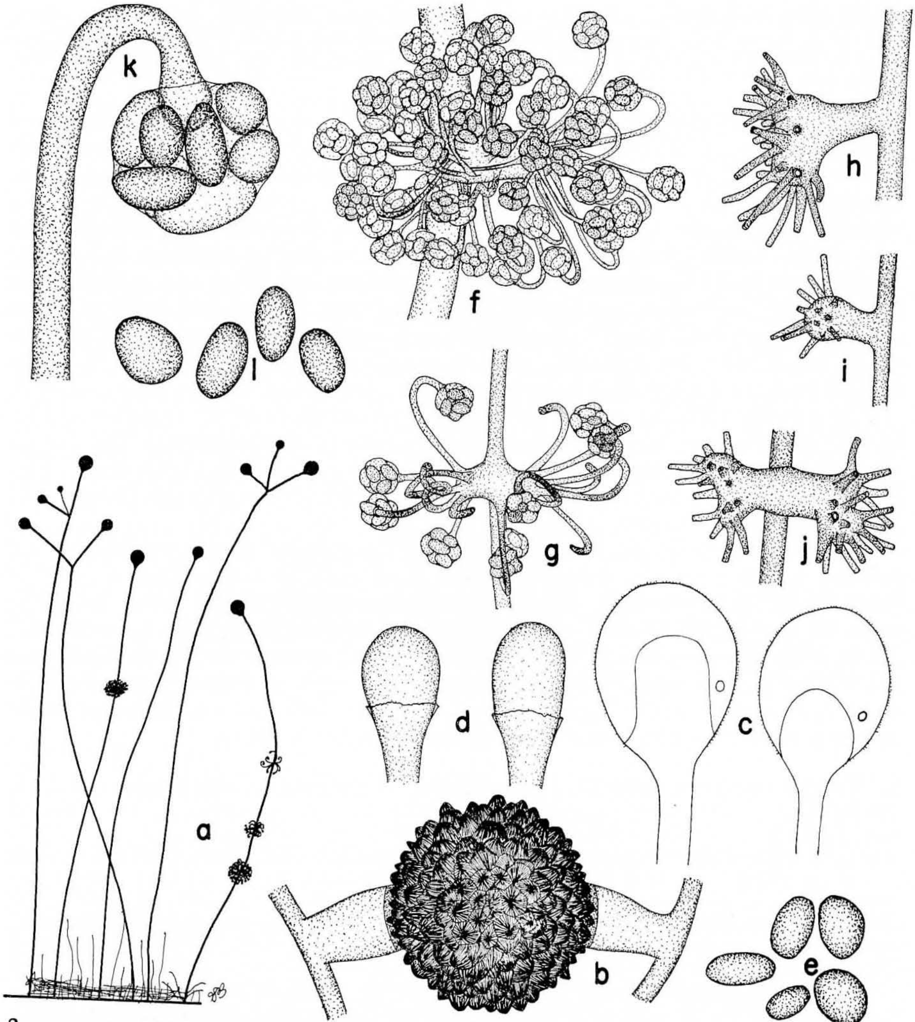

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Fig. 3. *Thamnostylum nigricans*.—a. Habit sketches of sporophores. × 30.—b. Typical zygospore and its suspensors (RSA 1404– × RSA 1406+). × 440.—c. Optical sections through two primary sporangia showing variation in shape of columellae and relative size of sporangiospores. × 440.—d. Columellae of two primary sporangia showing basal collars and apophyses. × 440.—e. Sporangiospores from a primary sporangium. × 1,690.—f–g. Portions of two sporophores showing variation in number of sporangiola in heads; note the subtending vesicles and their relationship to the sporophore; some sporangiola have fallen away. × 440.—h–j. Portions of three sporophores showing remains of sporangiolar pedicels on the enlarged, more or less lobate, stalked, fertile vesicles. × 440.—k. A sporangiole and the distal portion of its reflexed pedicel; note columella and only slightly developed apophysis. × 1,690.—l. Sporangiospores from a sporangiole. × 1,690.

RSA 1405–; RSA 1407–). DURANGO. Ca. 10 mi N of Tlahualilo de Zaragoza, dung coll. by J. Henrickson, June 29, 1964, *R. K. Benjamin* isol. (RSA 1408–). U.S.A. CALIFORNIA. Riverside Co.: ca. 3 mi E of Indio, lizard dung, no date, *G. F. Orr 492* (RSA 953–).

Notes.—Thamnostylum nigricans was originally described and illustrated by van Tieghem (1876) as a species of *Helicostylum* with essentially the following characteristics: (1) an encrusted, deliquescent, apophysate sporangium with an ovoid columella; (2) globose sporangiola with a small, slightly apophysate columella; (3) sporangiolar pedicels recurved distally; (4) sessile fertile vesicles; and (5) the wall of the sporophore below the sporangium and the columella becoming light to dark brown in age. Stolons and rhizoids were not mentioned. The characteristics of our isolates agree closely with van Tieghem's description and somewhat diagrammatic figures of *H. nigricans*. Accordingly, we are transferring his species to *Thamnostylum* and are designating a neotype in the absence of known type material.

The usually globose, never obpyriform, sporangiola of *T. nigricans* (Fig. 3f,g,k) set the species apart from other members of the genus. The fertile vesicles of *T. nigricans* (Fig. 3h–j) resemble those of *T. lucknowense* (Fig. 2f–h) but are less bulbous and, when pedicellate, the stalks are longer and more constricted below.

Like other species of *Thamnostylum*, *T. nigricans* grows readily on all culture media routinely employed and does well at temperatures ranging from 18 to 30 C or more. However, zygospores (Fig. 3b) were found to form best at 21–22 C and were not observed in cultures grown at 18 and 26 C. This species, like *T. lucknowense*, is less conspicuously stoloniferous than *T. piriforme* and *T. repens*, but stolons with well-developed rhizoids do develop when aerial hyphae become repent and contact the substratum or when they encounter the walls of the growth chamber.

4. THAMNOSTYLUM REPENS (van Tiegh.) Upadhyay, Mycologia 65: 747. 1973. FIG. 4

≡ *Helicostylum repens* van Tiegh., Ann. Sci. Nat. Bot., Sér. 6, 4: 398. 1876.

≡ *Thamnidium repens* (van Tiegh.) Migula, Kryptogamen-Fl. Deutsch., Deutsch-Österr., Schweiz 3(1): 208. 1910.

Colony on MSMA to ca. 8.5 cm in diam in 10 days at 26 C; turf dense, low growing, light brown at first, Light Brownish Olive to Brownish Olive (Dark Olive to Olivaceous Black on YpSs) in age; strongly stoloniferous. Stolons arising from the substrate mycelium, 8–32 μm in diam, smooth or roughened, light to dark brown, irregularly septate in age, simple, becoming branched; forming rhizoids upon contacting the substratum or walls of the culture chamber and giving rise to erect sporophores; forming numerous short lateral branchlets bearing terminal fascicles of sporangiola. Rhizoids 1.5–5 μm in diam, smooth, simple or branched, becoming olivaceous brown. Sporophores smooth to roughened, light to dark brown; those arising from the substrate mycelium to ca. 1 cm high, 15–25 μm wide, simple or sympodially branched, the main axis and each branch terminating in a sporangium (rare on MSMA; common on Wort +3.5) or a head of pedicellate sporangiola; those arising from stolons varying greatly in length, from 40 μm to ca. 2 mm, 5–30 μm wide, constricted slightly at the base where attached to stolon, distally branched 3–8 times and producing only pedicellate sporangiola in dense fascicles. Primary sporangia subglobose, 75–105 μm in diam, white to olive-gray; wall hyaline, encrusted, diffluent; columellae obovoid to cylindrical, 45–65 μm high, 40–65 μm wide, with a conspicuous basal collar; apophysis small, inconspicuous; sporophore immediately below sporangium becoming dark olivaceous. Sporangiolar heads compact to lax, subglobose to irregular in outline, highly variable in size, 60–560 μm wide. Sporangiolar pedicels (14–)20–35(–47) μm long, 1.8–2.2 μm wide; wall encrusted, light to dark brown. Sporangiola obpyriform, 10–18 μm in diam, bluish becoming olivaceous brown; columellae hemispherical to dome shaped, 5–10 μm in diam, smooth; apophysis well developed, encrusted below. Sporangiospores alike in sporangia and sporangiola, ovoid to ellipsoidal, (4.4–)4.8–7.2(–7.6) × (3.6–)4–5.2(–6) μm (av. 6 × 4.6 μm), pale yellow; 7–28 per sporangiole. Zygospores (50–)70–100(–125) μm in diam; wall dark brown, translucent to opaque, covered with irregularly shaped, rounded projections 2–5 μm high, becoming more or less scaly; gametangial remnants dark brown, to ca. 7 μm long; suspensors 50–105 μm long, 23–38 μm wide, roughened, hyaline to olivaceous. Heterothallic.

Neotype.—U.S.A. CALIFORNIA. Los Angeles Co.: Sunset Peak, San Gabriel Mts., ca. 8 mi NNE of Claremont, mouse dung, Mar. 26, 1956, *R. K. Benjamin* (RSA 459+). A dried culture has been deposited in the herbarium of RSA. In addition, living cultures have been transmitted to ATCC, CBS, IMI, and NRRL.

Distribution.—France, U.S.A.

Other specimens examined.—U.S.A. CALIFORNIA. Los Angeles Co.: ca. 5 mi W of Mount Baldy, mouse dung, Mar. 26, 1957, *R. K. Benjamin* (RSA 546+); ca. 3 mi NE of Glendora, mouse dung, Mar. 26, 1957, *R. K. Benjamin* (RSA 542+); Sunset Peak, San Gabriel Mts., ca. 8 mi NNE of Claremont, mouse dung, July 10, 1957, *R. K. Benjamin* (RSA 583+); Evey Canyon, San Gabriel Mts., ca. 4.5 mi NNE of Claremont, mouse dung, Nov. 18, 1969, *G. L. Benny* (RSA 1991+).—San Bernardino Co.: Ice House Canyon, San Gabriel Mts., ca. 1.5 mi NE of Mount Baldy, mouse dung, Oct. 11, 1959, *R. K. Benjamin* (RSA 908+), mouse dung, July 5, 1965, *R. K. Benjamin* (RSA 1577+; RSA 1578+), dung, Nov. 4, 1969, *G. L. Benny* (RSA 1990–), mouse dung, Mar. 29, 1971, *G. L. Benny* (RSA 2089), mouse dung, Sept. 2, 1974, *R. K. Benjamin* (RSA 2090); Camp Angelus, San Bernardino Mts., mouse dung, Sept. 27, 1958, *R. K. Benjamin* (RSA 834+); Forest Plantation View, San Bernardino Mts., dung, Sept. 15, 1962, *R. K. Benjamin* (RSA 1294–); Indian Cove, Joshua Tree National Monument, mouse dung, Oct. 17, 1965, *R. K. Benjamin* (RSA 1628).—San Diego Co.: ca. 3 mi E of Julian, mouse dung, Sept. 17, 1958, *R. K. Benjamin* (RSA 909).

Notes.—Upadhyay, in 1973, transferred *Helicostylum repens* to *Thamnostylum* on the basis of van Tieghem's (1876) unillustrated description of it in an appendix to his third and last memoir on the Mucorales. Van Tieghem, who found the fungus on wine dregs, gave as its salient features the following: (1) vegetative mycelium giving rise to creeping, sympodially branched stolons forming clumps of rhizoids where in contact with the substratum and producing erect, encrusted sporophores bearing terminal sporangia or "umbels" of sporangiola; (2) terminal sporangia large, globoid, columellate, apophysate, deliquescent, containing spores averaging about 12×10 μm [the only measurements given by van Tieghem]; (3) sporangiola borne on curved, encrusted pedicels, nondeliquescent, with well-defined apophysis, and a columella so large that it often limited the spores to a single layer within the sporangiole; and (4) stolons, sporophores, columellae, and sporangiolar pedicels becoming dark colored in age. Although there is a discrepancy between the size of the sporangiospores as observed by us and as reported by van Tieghem, we believe that our isolates can otherwise be identified with van Tieghem's brief verbal description of *Helicostylum repens*. Accordingly, we accept Upadhyay's transfer of it to *Thamnostylum* and are designating a neotype in the absence of a known type. The species has not, apparently, been reported again since its original description.

The specific epithet aptly describes the creeping habit of *Thamnostylum repens* in culture (Fig. 4a). Sporophores bearing primary sporangia (Fig. 4b) were rarely produced by any of our strains on media other than Wort +3.5 where they developed in abundance. Zygospores (Fig. 4h) formed readily on MEYE, YpSs, and TPO at room temperature (22–26 C) but the number produced varied greatly in pairings of compatible strains. The suspensors usually are equal to or longer than the diameter of the zygospore (Fig. 4h).

BACKUSELLA Hesseltine & Ellis, *in* Ellis and Hesseltine, Mycologia 61: 863. 1969.

Sporophores arising directly from the substrate mycelium, erect or ascending, simple or branched, smooth or roughened, usually producing large terminal sporangia and few to many lateral, pedicellate sporangiola. Terminal sporangia columellate, multispored, globose to subglobose, nonapophysate, subtended by a slight constriction of the sporophore; wall encrusted, deliquescent; columellae subglobose, obovate, or oblong, smooth. Sporangiolar pedicels straight, curved, or recurved, simple or branched, smooth or encrusted. Sporangiola columellate, multispored or unispored; wall verrucose or spinulose or both, persistent. Sporangiospores from sporangia and multispored sporangia alike, globose to ovoid or reniform,

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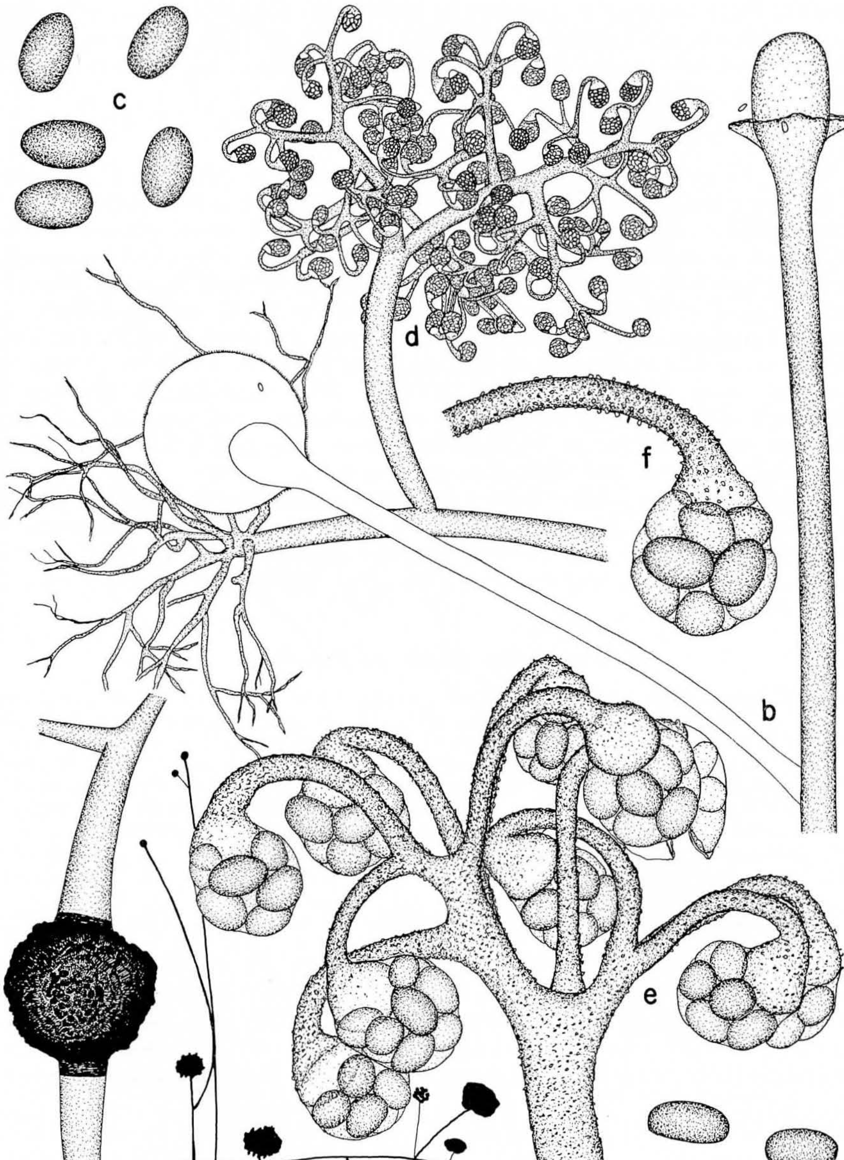
Fig. 4. *Thamnostylum repens*.—a. Habit sketches of sporophores. × 10.—b. Distal portion of a branched sporophore showing columella of a primary sporangium that terminated the main axis, and optical section of an intact sporangium terminating a lateral branch; sporangiospores are shown for size comparison. × 235.—c. Sporangiospores from a primary sporangium. × 1,670.—d. Terminus of a stolon showing extensive rhizoidal system and a short lateral sporophore bearing a terminal head of sporangiola; note branching pattern of sporophore in fertile region and relationship of sporangiola to the subtending branchlets. × 235.—e. Portion of a fertile branch system showing arrangement of the sporangiola, curvature of the sporangiolar pedicels, and degree and extent of encrustation. × 1,200.—f. A single sporangiole; note columella and encrusted apophysis. × 1,670.—g. Sporangiospores from a sporangiole. × 1,670.—h. Typical zygospore and its suspensors (RSA 459+ × RSA 1990–).



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smooth; from unispored sporangiola globose to subglobose, smooth. Zygospores globose to subglobose; wall dark, opaque or translucent, ornamented with conical or rounded projections; suspensors opposed, smooth or roughened, equal or unequal.

Type species: Backusella circina Ellis & Hesseltine.

When Hesseltine and Ellis described *Backusella* (Ellis and Hesseltine, 1969) they noted in the type species, *B. circina*, a combination of characteristics, i.e., terminal *Mucor*-like, diffluent-walled sporangia and laterally produced, pedicellate, persistent-walled uni- and multispored sporangiola, that suggested an alliance of the genus with the Thamnidiaceae. However, they retained it in the Mucoraceae. Von Arx, in 1970, included *Backusella* in a group of genera whose members then were classified in either the Thamnidiaceae or Choanephoraceae (Hesseltine, 1955; Zycha et al., 1969), and the next year Pidoplichko and Milko (1971) transferred Durrell and Fleming's *Thamnidium ctenidium* to *Backusella* and included both *B. ctenidia* and *B. circina* in the Thamnidiaceae. We prefer this disposition of *Backusella*, and we are adding another species.

Backusella species differ from other sporangiate members of the Thamnidiaceae not only in their *Mucor*-like habit but also in the simultaneous production of both uni- and multispored sporangiola singly or in clusters on the main axis of the sporophore or on short sporophores formed near the substrate.

KEY TO THE SPECIES OF *BACKUSELLA*

A. Sporophore below terminal, primary sporangium not recurved during initial stages of development; colonies becoming olivaceous brown to brown; sporangiola abundant, usually arising unilaterally along the median one half or more of the sporophore; sporangiospores usually subglobose to ovoid .... 3. *B. ctenidia*

AA. Sporophore at first strongly recurved immediately below the terminal sporangium, soon becoming erect; colonies becoming grayish or pale yellowish; sporangiola few to many, not clustered; sporangiospores mostly globose to subglobose .... B

B. Sporangiola mostly unispored .... 1. *B. circina*

BB. Sporangiola mostly multispored .... 2. *B. lamprospora*

1. BACKUSELLA CIRCINA Ellis & Hesseltine, Mycologia 61: 863. 1969. FIG. 5

Colonies developing rapidly on MSMA, to ca. 8.5 cm in diam in 3 days at 26 C; turf dense, white at first, near Light Olive-Gray in age. Sporophores erect or ascending, soon reaching the lid of a Petri dish (2 cm), 9–16 μm in diam, sharply recurved distally when young, erect at maturity, simple or sympodially branched; the main axis and its branches bearing terminal

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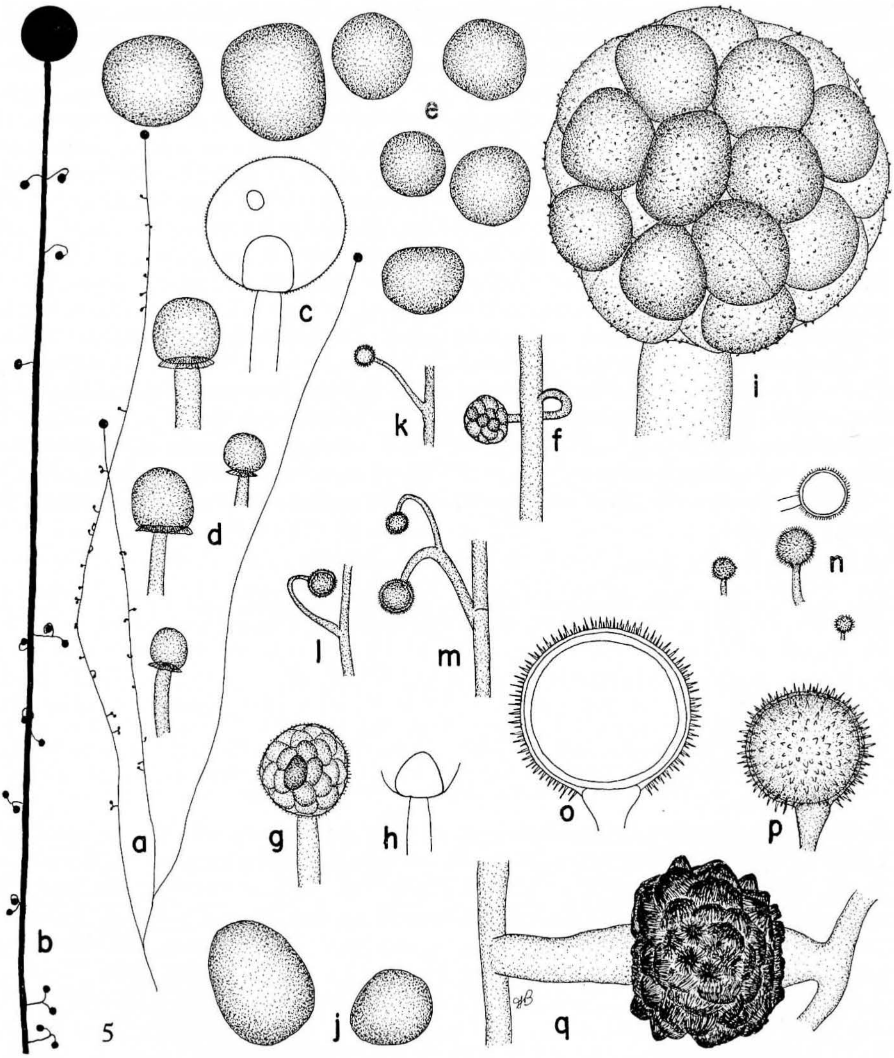
Fig. 5. *Backusella circina*.—a. Habit sketch of distal portion of sympodially branched sporophore showing terminal sporangia and relative size and arrangement of pedicellate sporangiola. × 20.—b. The same. × 75.—c. Optical section of a primary sporangium showing columella and sporangiospore. Note slight constriction of sporophore immediately below columella. × 320.—d. Four columellae of terminal sporangia showing basal collars. × 320.—e. Sporangiospores from primary sporangium. × 1,670.—f–g.



Two pedicellate, multispored sporangiola. × 320.—h. Columella of a multispored sporangiole. × 320.—i. Multispored sporangiole showing spinulose wall, and arrangement and relative size of sporangiospores; dotted line outlines columella. × 1,670.—j. Two sporangiospores from a multispored sporangiole. × 1,670.—k–m. Segments of sporophores showing unispored sporangiola; note, in m, smaller pedicellate spore that has arisen from pedicel of previously formed spore. × 320.—n. Four unispored sporangiola showing size range; one is shown in optical section. × 320.—o–p. Two unispored sporangiola, one in optical section, the other in surface view, showing their spinulose walls, columellae, and slight apophyses. × 1,670.—q. Typical zygospore and its suspensors (RSA 1770+ × 1771–). × 320.

sporangia and giving rise laterally at varying intervals to numerous pedicellate sporangiola. Primary sporangia globose to subglobose, 35–110 μm in diam, gray; wall hyaline, minutely spinulose, diffluent; columellae subglobose to oblong, 11–35 × 11–30 μm, hyaline, with basal collar. Sporangiolar pedicels slightly to strongly recurved, up to 50 μm long, to ca. 4 μm in diam at base, tapering to ca. 2.5 μm in diam at apex, simple or sympodially branched and forming 1–2(–3) stalked secondary sporangiola. Multispored sporangiola globose to subglobose, 10–50 μm in diam; wall spinulose, hyaline, persistent; columellae broadly obovate, to ca. 18 μm in diam. Unispored sporangiola abundant, globose to subglobose, (4.5–)6–16(–26) μm in diam, brown; wall spinulose, with spines to ca. 2 μm long; columella compressed when spore is present, to ca. 5.5 μm in diam. Sporangiospores in terminal sporangia and multispored sporangiola alike, subglobose to ovoid, (6.4–)7.2–10(–12.8) × (5.6–)6.4–9.2(–10) μm (av. 8.4 × 7.8 μm), hyaline to pale yellow, 2–14 per multispored sporangiole. Zygospores globose to subglobose, (35–)40–70(–80) μm in diam (av. 55 μm) including projections; wall brownish black, opaque, covered with more or less conical projections to ca. 7 μm high; suspensors 5–40 μm long, 15–30 μm wide, hyaline to pale brown, smooth or roughened, equal or unequal. Heterothallic.

Distribution.—India, Japan, U.S.A.

Illustrations.—Ellis and Hesseltine (1969), Figs. 1–8; Verona and Benedek (1971), Pl. B129.—As *Mucor lamprosporus*: Baijal and Mehrotra (1965), Pl. XXXIX, Figs. 7–17, Pl. XL, Fig. 7.

Specimens examined.—INDIA. "Shantiniketan," soil, *B.S. Mehrotra Mx-61* (RSA 2033–; =NRRL 6007; =IMI 146487). U.S.A. Florida. Soil, 1955, isolated at the Northern Regional Research Laboratory (type culture: RSA 1770+; =NRRL 2246; ATCC 18878; CBS 128.70; IMI 146484).—New Jersey. Soil, 1957, isolated in the laboratories of the Department of Botany, Univ. of Mass., Amherst (RSA 1771+; =NRRL 3293; =ATCC 18879; =CBS 129.70; =IMI 146485).

Notes.—*Backusella circina* develops rapidly in culture on media such as MSMA, YpSs, and MEYE and its intertwined sporophores will, within a week, completely fill a 2 × 8.5-cm Petri dish with a densely compacted, grayish-white turf. Zygospores form readily in the contact zone of opposed mating types at 26 C on a variety of media including MSMA. Of the three isolates we studied, RSA 1770(+) reacted more strongly with RSA 1771(–) than with RSA 2033(–), but in all instances well-formed zygospores were produced within a week. The species also has been reported from Japan and its identity confirmed by J. J. Ellis at the NRRL, Peoria (Tubaki, 1973). Additional comments on *B. circina* appear below in notes on *B. lamprospora.*

2. **Backusella lamprospora** (Lendner) Benny & Benjamin, comb. nov. Fig. 6

≡ *Mucor lamprosporus* Lendner, Beitr. Kryptogamenfl. Schweiz 3(1): 92. 1908 (basionym).

= *Mucor dispersus* Hagem, Ann. Mycol. 8: 271. 1910.

= ? *Mucor dispersus* var. *megalosporus* Linnemann, Flora 130: 184. 1936.

Colonies on MSMA developing rapidly, to ca. 8.5 cm in diam in 5 days at 26 C; turf dense, white at first, near Pale Olive-Buff in age. Sporophores erect or ascending, soon reaching the lid of a Petri dish (2 cm), 4–23 μm in diam, sharply recurved distally when young, erect at maturity, simple or sympodially branched; the main axis and its branches bearing terminal sporangia, giving rise laterally to pedicellate sporangiola. Short, sympodially branched sporophores bearing only sporangiola formed near the substrate. Primary sporangia globose to subglobose, 50–90 μm in diam, pale brown; wall hyaline, diffluent; columellae hemispherical to globose or ovoid, 15–50 × 18–48 μm, with small but prominent basal collar. Sporangiolar pedicels curved or recurved distally, smooth or slightly roughened, up to 90 μm long, to ca. 4 μm in diam, simple or sympodially branched and forming 1–2(–3) stalked, secondary sporangiola. Multispored sporangiola abundant, globose to subglobose, 12–50 μm in diam; wall verrucose, spinulose, or both, hyaline, persistent; columellae compressed to convex, 12–20 μm in diam, smooth. Unispored sporangiola infrequent, globose to subglobose, 6.5–16 μm in diam; wall verrucose, spinulose, or both, hyaline, persistent; columellae compressed to convex, 3–7 μm in diam, smooth. Sporangiospores in terminal sporangia and multispored sporangiola alike, mostly subglobose, (6.8–)8–13(–14.5) × (6.4–)7.6–13(–14) μm (av. 10.7 × 10.2 μm), hyaline to pale yellow, 2–8(–18) per multispored sporangiole. Gemmae in substrate hyphae present or absent. Zygospores globose to subglobose, (35–)40–70(–85) μm in diam (av. 60 μm) including projections; wall blackish brown, opaque, covered with conical projections to ca. 7 μm high; suspensors 10–30 μm long, 10–23 μm wide, pale brown, smooth or slightly roughened, equal or unequal. Heterothallic.

Distribution.—Belgium, Canada, Czechoslovakia, China, England, France, Germany, Norway, Poland, Switzerland, U.S.A. (Zycha et al., 1969); U.S.S.R. (Naumov, 1954); Argentina, Hong Kong, India, Japan.

Illustrations.—As *Mucor lamprosporus*: Lendner (1908), Fig. 33; Kominami et al. (1953), Fig. 16; Pidoplichko and Milko (1971), Fig. 81a–d; Schipper (1969), Figs. 2f–g, 3g; Mehrotra et al. (1972 [1974]), Text fig. II, 1–11, Pl. I, Figs. 6–8.—As *M. dispersus*: Christenberry (1940), Pl. 15, Figs. 74–79; Hagem (1910), Fig. 4; Mehrotra et al. (1972 [1974]), Text fig. I, 14–21, Pl. I, Figs. 3–4; Yang and Liu (1972), Pl. II, Figs. 3–6.

Specimens examined.—ARGENTINA. Buenos Aires, Parque Pereya, Feb., 1968, *J. E. Wright 167* (RSA 2116+; =NRRL 6047). FRANCE. SAVOIE. Mt. Vnache, forest soil, 1907, *A. Lendner* (type culture of *Mucor lamprosporus* fide Schipper, 1969: RSA 2060+; =NRRL 3300; =ATCC 18469; =CBS 118.08; =IMI 116943; =BKMF 1319). HONG KONG. NEW TERRITORIES. Soil, ?1962, *Ma Liu Shiu* (RSA 2114+; =NRRL 6045). INDIA. UTTAR PRADESH. Allahabad, ?1957, *B. B. S. Raezada* (RSA 2111–; =NRRL 6038). JAPAN. HONSHU. Mt. Fuji, soil, ?1969, *K. Tubaki* (RSA 2123+; =NRRL 6052; =IFO 6747); received by NRRL in July, 1969, without data (RSA 2124–; =NRRL 6053; =IFO 6748). U.S.A. OREGON. Benton Co.: Berry Creek, Sept. 4, 1961, *Wm. B. Cooke* (RSA 2115+; =NRRL 6046); Berry Creek, soil, Sept. 4, 1961, *Wm. B. Cooke* (RSA 2113+; =NRRL 6044). OHIO. Franklin Co.: Columbus, T. J. Long (RSA 2120+; =NRRL 6041).—The following strains received with incomplete data or without collection data: *Blakeslee*, "fr. fallen leaves" (RSA 2061–; =NRRL 3619; =CBS 196.28); *Blakeslee* (RSA 2062+; =NRRL 3618; CBS 195.28); soil at base of chestnut tree, Feb., 1919, *Blakeslee C576* (RSA 2109–; =NRRL 1401); Feb., 1919, *Blakeslee C586* (RSA 2110+; =NRRL 1402); *Milko 3136* (RSA 2057–; =BKMF 1377); *Milko 2* (RSA 2058+; =BKMF 944); *Milko 3063* (RSA 2059–; =BKMF 1378); (RSA 2112–; =NRRL 6039; =QM 4384).

Notes.—Similarities and differences between *Backusella circina* and *Mucor lamprosporus* and *M. dispersus* were discussed by Ellis and Hesseltine (1969) when they described *B. circina.* Schipper (1969), in a comprehensive study of the zygosporic state of several heterothallic species of *Mucor*, concluded from a study of their type strains that *M. dispersus* and *M. lamprosporus* are synonymous. Mehrotra, Singh, and Baijal (1972 [1974]), on the other hand, recognized both *M. lamprosporus* and *M. dispersus*, as well as a presumed large-spored variety of the latter, *M. dispersus* var. *megalosporus* Linnemann, and separated these from other sphaerosporus taxa of *Mucor* because of their production of sporangiola. *Mucor dispersus* has been distinguished from *M. lamprosporus* primarily by its production of enlarged, thick-walled gemmae (i.e., giant cells [GC]) in its substrate hyphae and by slightly larger sporangiospores (Zycha, 1935; Zycha et al., 1969). Of the 17 strains listed above under specimens examined, 10 lack GC and would be identified with *M. lamprosporus*, whereas seven form GC and produce slightly larger sporangiospores on the average. The latter would be called *M. dispersus* on the basis of these criteria.

Using the type strain of *Mucor lamprosporus* (RSA 2060+) as the initial tester, followed by crosses of unknowns with other strains as their mating types were determined, we were able to characterize the mating type of all 17 of our isolates. These were then crossed on 2% ME and YpSs agars at 26 C with the results shown in Table 1. Under the conditions employed, only four combinations failed to give an observable sexual reaction, and these involved only RSA 2109(–). In the other 66 matings, there was a strong sexual reaction in the contact zone between contrasted colonies. In 36 of these the reaction was imperfect (Blakeslee, 1904, 1915, 1920; Satina and Blakeslee, 1930); progametangia developed, gametes often were formed, but zygospores were not observed. Thirty matings resulted in production of well-formed, full-sized zygospores borne between fully developed suspensors (Fig. 61). Fourteen combinations gave rise to a more or less large number of zygospores that formed a dark line visible to the unaided eye, whereas 16 combinations produced few spores, readily observed with a dissecting microscope or in slide mounts.

As shown in Table 1, crosses between strains with GC (i.e., *Mucor dispersus*) and strains without GC (i.e., *M. lamprosporus*) resulted in the formation of zygospores. Strain RSA 2114(+), which lacks GC, formed zygospores in combination with all of the (–) strains available, and RSA 2061(–), which has GC, formed zygospores with all of the (+) strains except RSA 2123. The latter readily developed zygospores when mated with RSA 2112(–) and 2124(–).

It is well known that sexual potency can vary greatly in different strains of a given species of Mucorales (Blakeslee, Cartledge, Welch, and Bergner, 1927). Imperfect reactions are common in interspecific crosses (Blakeslee and Cartledge, 1927; Burgeff, 1924), but such reactions should also be expected in intraspecific crosses between strains if one or both partners

TABLE 1. *Mating reactions of seventeen strains of* Backusella lamprospora.

RSA No.	2058+ (GC)	2062+ (GC)	2110+ (GC)	2113+ (GC)	2115+ (GC)	2060+	2114+	2116+	2120+	2123+
2061– (GC)	Z +++	Z +	Z +	Z +++	Z +++	Z +	Z +	Z +	Z +	R*
2109– (GC)	Z +++	O	Z +	O	Z +	O	Z +	R	Z +	O
2057–	Z +++	R	Z +	Z +	Z +	Z +++	Z +++	R	R	R*
2059–	Z +++	R	R	Z +	Z +	Z +++	Z +++	R	R	R*
2111–	R	R	R	R	R	R	Z +++	R	R	R*
2112–	R	R	R	R	R	R	Z +++	R	R	Z +++
2124–	R	R	R	R	R	R	Z +	R	R	Z +++

GC = Giant cells (gemmae) formed in substrate hyphae.
Z = Zygospores produced; + = few; +++ = many to abundant.
R = Strong sexual reaction but no zygospores observed; progametangia abundant, gametes differentiated by some progametangia. * = occasional azygospore observed.
O = No sexual reaction observed.
(*Media*: 2% ME and YpSs agars. *Temperature*: 26 C. *Time*: 14 days.)

were of extremely low sexual vigor. We are inclined to place greater emphasis on zygospore production than on differences in sporangiospore size or vegetative characteristics such as presence or absence of gemmae—characteristics that may reflect only minor genetic differences between strains. Accordingly, we support Schipper (1960) in treating *Mucor dispersus* and *M. lamprosporus* as synonyms.

Our transfer of *Mucor lamprosporus* to *Backusella* is effected on the basis of the simultaneous production in this species of terminal, diffluent sporangia and lateral, nondiffluent sporangiola.

Backusella lamprospora and *B. circina* resemble one another superficially in the gross aspects of their colonies. In plate cultures, both form a dense turf that soon reaches the lid of the Petri dish. In both species, the colony is initially white, eventually becoming pale grayish or yellowish depending on the strain. Sporangiola of *B. lamprospora* are borne mostly on short sporophores that may or may not form prolongations bearing terminal, diffluent sporangia (Fig. 6a), whereas in *B. circina* sporangiola are more numerous on the elongate primary sporangiophores (Fig. 5a,b). In both species, the terminal, primary sporangium is at first strongly reflexed, becoming erect as the sporophore elongates. Pedicels bearing sporangiola usually remain more or less recurved in both species (Fig. 5l,m; Fig. 6e,i).

Sporangiospores from the primary sporangia and multispored sporangiola of *B. circina* and *B. lamprospora* are similar, being mostly subglobose; those of *B. lamprospora* are consistently slightly larger (Fig. 6d,h), on the average, than those of *B. circina* (Fig. 5e,i). *Backusella circina* differs from *B. lamprospora* in its production of large numbers of spiny-walled, brown, uni-

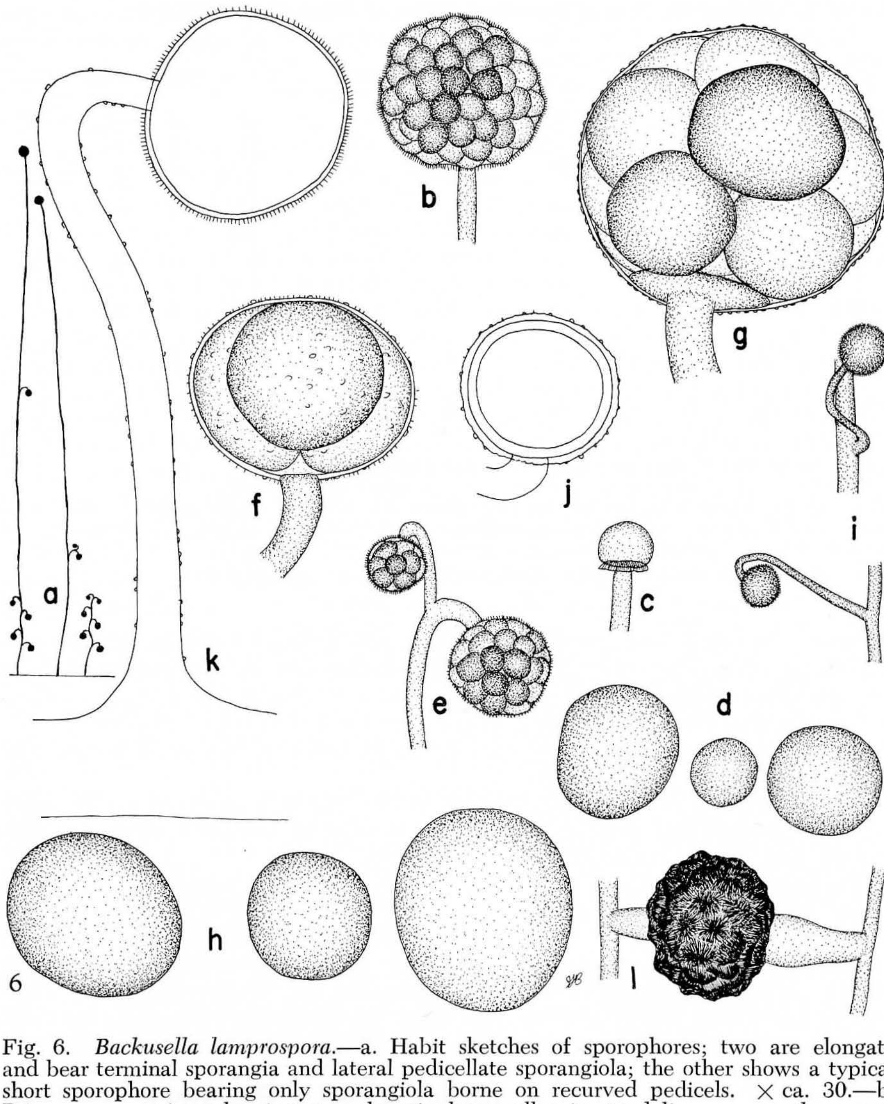


Fig. 6. *Backusella lamprospora*.—a. Habit sketches of sporophores; two are elongate and bear terminal sporangia and lateral pedicellate sporangiola; the other shows a typical short sporophore bearing only sporangiola borne on recurved pedicels. × ca. 30.—b. Primary sporangium showing strongly spinulose wall prior to deliquescence; the sporophore is slightly constricted immediately below the sporangium. × 320.—c. Columella of terminal sporangium showing basal collar. × 320.—d. Sporangiospores from primary sporangium. × 1,670.—e. Distal end of a short sporophore showing two sporangiola. × 320.—f. A three-spored sporangiole with a verrucose and spinulose wall. × 1,670.—g. Multispored sporangiole with a verrucose wall showing compressed columella. × 1,670.—h. Sporangiospores from a sporangiole. × 1,670.—i. Segments of sporophores showing two unispored sporangiola. × 320.—j. Optical section of a unispored sporangiole with verrucose wall; shows thickness of sporangiospore wall. × 1,670.—k. Segment of sporophore bearing pedicellate unispored sporangiole as seen in optical section. × 1,670.—l. Typical zygospore and its suspensors (RSA 2059– × RSA 2060+). × 320.

spored sporangiola (Fig. 5k–p); these readily detach by rupture of the subtending pedicel, a portion of which remains attached to the persistent wall surrounding the spore (Fig. 5n–p). Unispored sporangiola are much less common in *B. lamprospora* and are nearly hyaline (Fig. 6i,j).

Zygospores of *B. lamprospora* (Fig. 6l) are nearly identical in size and shape to those of *B. circina* (Fig. 5q).

3. BACKUSELLA CTENIDIA (Durrell & Fleming) Pidoplichko & Milko, Atlas of mucoralean fungi, p. 85. 1971. FIG. 7

≡ *Thamnidium cteniidum* Durrell & Fleming, Mycologia 58: 797. 1966.

Colonies on MSMA developing rapidly, to ca. 8.5 cm in 6 days at 26 C; turf sparse to moderately dense, white at first, soon near Tawny-Olive to Brownish Olive, becoming Isabella Color in age. Sporophores more or less erect, 3–10 mm high, up to 11 μm in diam, simple or branched; the main axis and its branches bearing terminal sporangia and numerous lateral pedicellate sporangiola or more or less elongate branchlets bearing terminal and lateral sporangiola. Primary sporangia globose to subglobose, 50–70 μm in diam, brown; wall hyaline, encrusted, diffluent; columellae obpyriform, obovoid, to subglobose, 45–60 × 35–45 μm, with basal collar; sporangiospores subglobose, ovoid, or slightly reniform, 4–8 × 3.2–6.4 μm (av. 6 × 4.5 μm). Sporangiolar pedicels usually simple, less commonly bearing pedicellate sporangiola laterally, 11–75 μm long, 2–5 μm wide, straight or slightly curved, usually uniseptate and encrusted. Multispored sporangiola globose to subglobose, 12–30 μm in diam; wall tuberculate to spinulose, hyaline, persistent; columellae strongly to slightly compressed in presence of spores, up to 11 μm in diam, smooth; sporangiospores subglobose, ovoid, or reniform, variable in size, 4–17.5 × 3.5–13 μm (av. 9. × 7.5 μm), pale yellow to brown, 2–18 or more per sporangiole. Unispored sporangiola globose to subglobose, 7–16(–22) μm in diam; wall spinulose, hyaline, persistent; columellae compressed, subglobose after spore release. Zygospores globose to subglobose, 35–55 μm in diam (av. 45 μm); wall reddish brown, translucent, covered with small tuberculate projections; suspensors 12–30 μm long, 10–21 μm wide, hyaline, equal or slightly unequal. Heterothallic.

Distribution.—Mexico, U.S.A.

Illustrations.—Durrell and Fleming (1966), Figs. 1–8 (as *Thamnidium ctenidium*).

Specimens examined.—MEXICO. BAJA CALIFORNIA DEL NORTE. Agua Amarga, ca. 20 mi NW of Bahía de los Angeles, pack rat dung coll. by R. Hanamin, Mar. 1, 1963, *R. K. Benjamin* isol. (RSA 2040); San Luis, pack rat dung coll. by R. Hanamin, Mar. 1, 1963, *R. K. Benjamin* isol. (RSA 2095); La Suerte, ca. 50 mi E of San Quintín, dung, June 4, 1963, *R. K. Benjamin* (RSA 2096). CHIHUAHUA. Ca. 18 mi S of Chihuahua, lizard dung coll. by J. Henrickson, July 3, 1964, *R. K. Benjamin* isol. (RSA 1409–). TAMAULIPAS. Ca. 3 mi W of Jaumave, dung coll. by T. Anderson, Jan. 26, 1961, *R. K. Benjamin* isol. (RSA 1178). U.S.A. ARIZONA. Coconino Co.: ca. 3–4 mi SW of Marsh Pass, Highway 64, pack rat dung, Aug. 28, 1964, *R. K. Benjamin* (RSA 1501).—Maricopa Co.: ca. 5 mi N of Mesa, margin of Salt River, rabbit dung, Apr. 29, 1970, *G. Benny* (RSA 2094). CALIFORNIA. Inyo Co.: Death Valley National Monument, soil, 1966, *L. W. Durrell & M. Fleming* (type culture: RSA 1180+; =ATCC 16377; =CBS 293.66);

4 mi E of Shoshone, pack rat dung, Apr. 22, 1960, *R. K. Benjamin* (RSA 1168).—Riverside Co.: ca. 2 mi SW of Palm Springs, in Andreas Canyon, pack rat dung, Dec. 19, 1969, *G. Benny* (RSA 2093).—San Bernardino Co.: Whipple Mts., 6 mi NW of Cross Roads, pack rat dung, Apr. 20, 1960, *R. K. Benjamin* (RSA 1155–); Needles, bank of Colorado River, pack rat dung, Dec. 21, 1958, *R. K. Benjamin* (RSA 761).—San Diego Co.: 6 mi NW of Agua Caliente Hot Springs, pack rat dung, Apr. 5, 1960, *R. K. Benjamin* (RSA 1148); ca. 5 mi E of Banner, pack rat dung, Sept. 17, 1959, *R. K. Benjamin* (RSA 907). NEVADA. Clark Co.: 10 mi NW of Goodsprings, pack rat dung, Apr. 22, 1960, *R. K. Benjamin* (RSA 1166–).

Notes.—Backusella ctenidia is, along with *Thamnidium elegans* and *Thamnostylum piriforme*, one of the most common species of Thamnidiaceae in southern California. The specimens cited represent only a few of the more than 50 strains of *B. ctenidia* obtained from the southwestern United States and northern and central Mexico. Durrell and Fleming (1966) found the type strain (RSA 1180) in desert soil, but all of our isolates have come from dung. Interestingly, the fungus has been encountered only on substrata collected in extremely arid, desert habitats. The species, however, grows readily in culture and usually begins to sporulate in 36–48 hr.

Although Durrell and Fleming described *Backusella ctenidia* as a species of *Thamnidium*, it actually resembles *Helicostylum elegans* more than *T. elegans*, and it was tentatively assigned to *Helicostylum* by the junior author when he first isolated it in 1958. However, as recognized by Pidoplichko and Milko (1971), it clearly is best placed in *Backusella* as defined by Hesseltine and Ellis (Ellis and Hesseltine, 1969) on the basis of its simultaneous production of uni- and multispored sporangiola.

Culturally, *Backusella ctenidia* cannot be confused with *B. circina* or *B. lamprospora*. Its colony soon becomes dark olivaceous then brownish, more so on natural media like YpSs and MEYE than on MSMA; although it forms a dense turf, its sporophores rarely exceed 1 cm in height. *Backusella ctenidia* also differs markedly from the other two species by its production of great numbers of sporangiola in large, more or less compact clusters that occur at irregular intervals or in more or less continuous series—often arising unilaterally—along the length of the sporophore or its branches (Fig. 7a,f,g). Like *B. circina*, *B. ctenidia* forms large numbers of unispored sporangiola (Fig. 7l–n); these as well as the multispored sporangiola (Fig. 7h–i) readily separate from the usually once-septate pedicel, a portion of which typically remains attached to the persistent sporangiolar wall.

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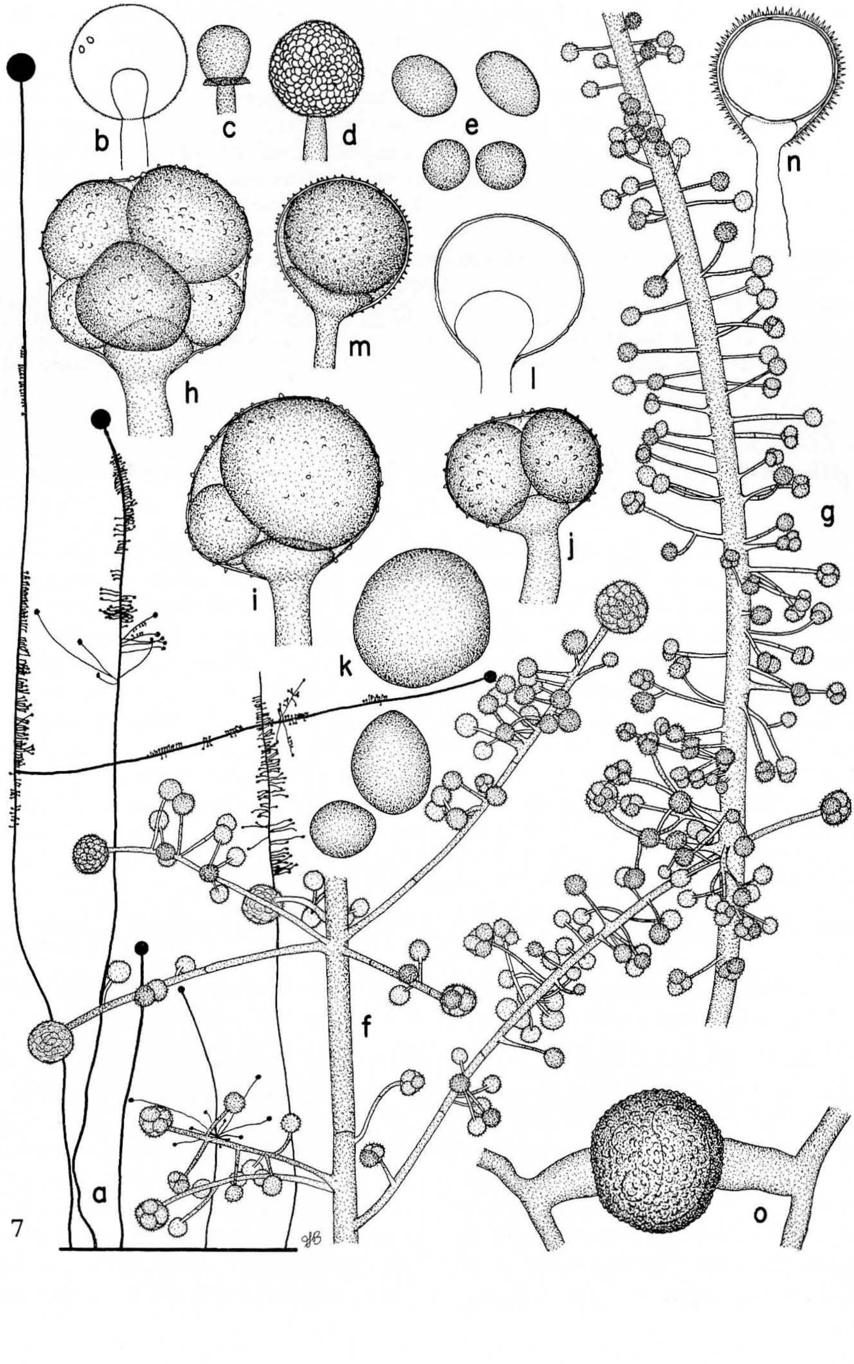
Fig. 7. *Backusella ctenidia.*—a. Habit sketches of sporophores. × 30.—b. Primary sporangium in optical section showing columella and spores. × 230.—c. Columella of terminal sporangium with basal collar. × 230.—d. Primary sporangium prior to deliquescence; note slight constriction of sporophore immediately below sporangium (also see *b*). × 230.—e. Sporangiospores from a primary sporangium. × 1,300.—f–g. Segments of sporophores showing arrangement of secondary branches and uni- and multispored sporangiola. × 230.—h–j. Multispored sporangiola showing verrucose walls and compressed columellae. × 1,660.—k. Sporangiospores from sporangiola. × 1,660.—l. Empty sporangiole showing columella. × 1,660.—m–n. Unispored sporangiola in surface view and optical section showing spinulose walls and compressed columellae. × 1,660.—o. Typical zygospore and its suspensors (RSA 1166– × RSA 1180+). × 315.



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Zygospores of *Backusella ctenidia* (Fig. 7o) were observed in crosses made only on Leonian's + YE medium, whereas those of *B. circina* (Fig. 5q) and *B. lamprospora* (Fig. 6l) formed readily on a vairety of media including 2% ME, YpSs, MEYE, and MSMA. Unlike the zygospores of *B. circina* and *B. lamprospora*, which are blackish brown, opaque, and covered with relatively large, conical projections, the zygospore of *B. ctenidia* is pale brown to brown, translucent, and marked by numerous, small, tuberculate projections.

Fennellomyces Benny & Benjamin, gen. nov.

Sporophora nascentia recta via e substrato mycelio vel, minus plerumque, e stolonibus, recta vel ascendentia, simplica vel ramosa, distale tumida juxta subter magno terminali sporangio, a latere proferentia pauca vel multa sporangiola pedicellata. Sporangia columelliformia, multispora, globosa vel subglobosa; parietes lenes, deliquescentes; columellae hemisphericae vel oblongae, lenes. Pedicelli subconflexi vel torti contortique, simplices vel ramosi, lenes vel spinulosi. Sporangiola columelliformia, multispora, parce unispora, subglobosa vel obpyriformia, parietes asperi, persistantes. Sporangiosporae enatae similia sporangiorum et multispororum sporangiolorum, ovoidea vel ellipsoidea, lenia, et enatae similia unispororum sporangiolorum, globosa vel subglobosa, lenia.

Species typica: *Circinella linderi* Hesseltine & Fennell

Sporophores arising directly from the substrate mycelium, less commonly from stolons, erect or ascending, simple or branched, swollen distally immediately below a large terminal sporangium; producing few to many pedicellate sporangiola laterally. Terminal sporangia columellate, multispored, globose to subglobose; wall smooth, deliquescent; columellae hemispherical to oblong, smooth. Sporangiolar pedicels slightly curved to twisted and contorted, simple or branched, smooth or spinulose. Sporangiola columellate, apophysate, multispored, rarely unispored, subglobose to obpyriform; wall roughened, persistent. Sporangiospores alike from primary sporangia and multispored sporangiola, ovoid to ellipsoid, smooth; from unispored sporangiola globose to subglobose, smooth.

Etymology.—Named for Dorothy I. Fennell, mycologist.

Fennellomyces linderi (Hesseltine & Fennell) Benny & Benjamin, comb. nov.
FIG. 8

≡ *Circinella linderi* Hesseltine & Fennell, Mycologia 47: 205. 1955 (basionym).

Colonies on MSMA to ca. 8.5 cm in 10 days at 26 C; turf lax to dense, white at first, near Light Grayish Olive in age. Sporangiospores simple or sympodially branched, arising directly from the substrate mycelium, rarely from stolons, erect or ascending, of two kinds: (1) tall sporophores reaching 1.5 cm or more in height, 6–18 μm in diam, producing only large terminal sporangia or terminal sporangia and lateral sporangiola borne on circinate pedicels; and (2) short sporophores up to 2 mm in height lacking terminal sporangia and bearing only pedicellate sporangiola. Primary sporangia globose to subglobose, 30–120 μm in diam, olive-gray to pale yellow; wall hyaline, smooth, deliquescent; columellae hemispherical, ovoid, or oblong, sometimes with a slight median constriction, 8–40 μm wide, 20–65 μm high above an inconspicuous basal collar, pale brown to olivaceous brown. Subsporangial swelling clavate to ovoid, 10–40 μm in diam, pale brown to olivaceous brown, the color fading below. Sporangiolar pedicels variable in length to 200 μm or more, 3–10 μm in diam, recurved to twisted and contorted, rigid, roughened, simple or sympodially branched 1–7 times and forming secondary pedicellate sporangiola. Multispored sporangiola olive-gray, globose, subglobose, to obpyriform, variable in size, 10–80 μm in diam, apophysate, without subsporangial swelling; wall hyaline, smooth to minutely indented, membranous, rupturing under pressure, then more or less rugose; columellae subglobose to hemispherical, (4.5–)15–25(–30) μm in diam, smooth, brownish olivaceous, the color extending downward to the upper part of the pedicel. Unispored sporangiola rare, globose to subglobose, to 10 μm in diam, slightly apophysate; wall roughened, hyaline; columellae emarginate, concave, to 5 μm in diam. Sporangiospores from sporangia and multispored sporangiola alike, ovoid to ellipsoid, (5–)6–10(–12.5) × (4–)5–7.5 μm, smooth, hyaline to pale grayish. Zygospores unknown.

Distribution.—U.S.A. (known only from type collection).

Illustrations.—As *Circinella linderi*: Hesseltine and Fennell (1955), Fig. 2; Pidoplichko and Milko (1971), Fig. 56a–c; Zycha et al. (1969), Fig. 23.

Specimen examined.—U.S.A. FLORIDA. Isolated from poplin, *D. H. Linder* (type culture: RSA 1016; =NRRL 2342; =ATCC 11744; =CBS 158.54; =QM 672).

Notes.—In their commentary following its description, Hesseltine and Fennell (1955) noted the thamnidiaceous characteristics of *Circinella linderi*, but they classified it in *Circinella* because its sporangiola were borne on more or less circinate branchlets and the persistent sporangiolar wall ruptured in a manner resembling that of the sporangia of members of that genus.

The fungus is an anomaly in an otherwise well-defined genus of Mucoraceae, for the sporophore of all other species assigned to *Circinella* (Hesseltine and Fennell, 1955; Zycha et al., 1969) lacks a terminal *Mucor*-type sporangium distinct from the circinately borne sporangia which are formed singly, in umbels, or in sympodia, with or without accompanying sterile spines. The sporangiola of *C. linderi* are distinctly apophysate—the apophysis more conspicuous the larger the sporangiole—whereas in true species of *Circinella* the sporangium is nonapophysate, the subtending stalk being of nearly uniform diameter up to its juncture with the sporangium. Accordingly, we have transferred *C. linderi* to a new genus, there being none other in the Thamnidiaceae to accommodate it.

The conspicuous enlargement of the sporophore immediately below the terminal sporangium (Fig. 8b,c) readily distinguishes *Fennellomyces linderi* from other Thamnidiaceae, where we classify it because of its simultaneous production of both deliquescent-walled primary sporangia and persistent-walled sporangiola. Unlike the fragile but persistent sporangiolar wall of other Thamnidiaceae, that of *F. linderi* is tough and membranous.

Hesseltine and Fennell (1955) described and illustrated stolons and rhizoids, reminiscent of many Thamnidiaceae, in *F. linderi* growing on Czapek's solution agar but not on synthetic mucor agar (SMA), the medium they used for descriptive purposes. We have not observed stolons and rhizoids in the species growing on MSMA or natural media such as YpSs and MEYE.

Ellisomyces Benny & Benjamin, gen. nov.

Sporophora nascentia recta via e substrato mycelio, recta vel ascendentia, ramosa; principalis axis ramique pluries ramosi distale, extremi rami cum pedicellatis sporangiolis. Pedicelli attenuati, simplices. Sporangiola columelliformia, multispora, globosa vel subglobosa; parietes lenes, persistentes. Sporangiosporae subglobosae vel ovoideae vel subcylindricae, lenes. Zygosporae globosae vel subglobosae; parietes atri, ornati a processibus crassis; suspensores oppositi, lenes, plus minusve aequi.

Species typica: *Thamnidium anomalum* Hesseltine & Anderson

Sporophores arising directly from the substrate mycelium, erect or ascending, branched; main axis and its branches several times successively bi- or trifurcate distally; the ultimate branches bearing pedicellate sporangiola terminally or laterally. Sporangiola columellate, multispored; wall persistent. Sporangiospores subglobose, ovoid, or subcylindrical, smooth, Zygospores globose to subglobose; wall pigmented, ornamented with coarse projections; suspensors opposed, more or less equal.

Etymology.—Named for John J. Ellis, mycologist.

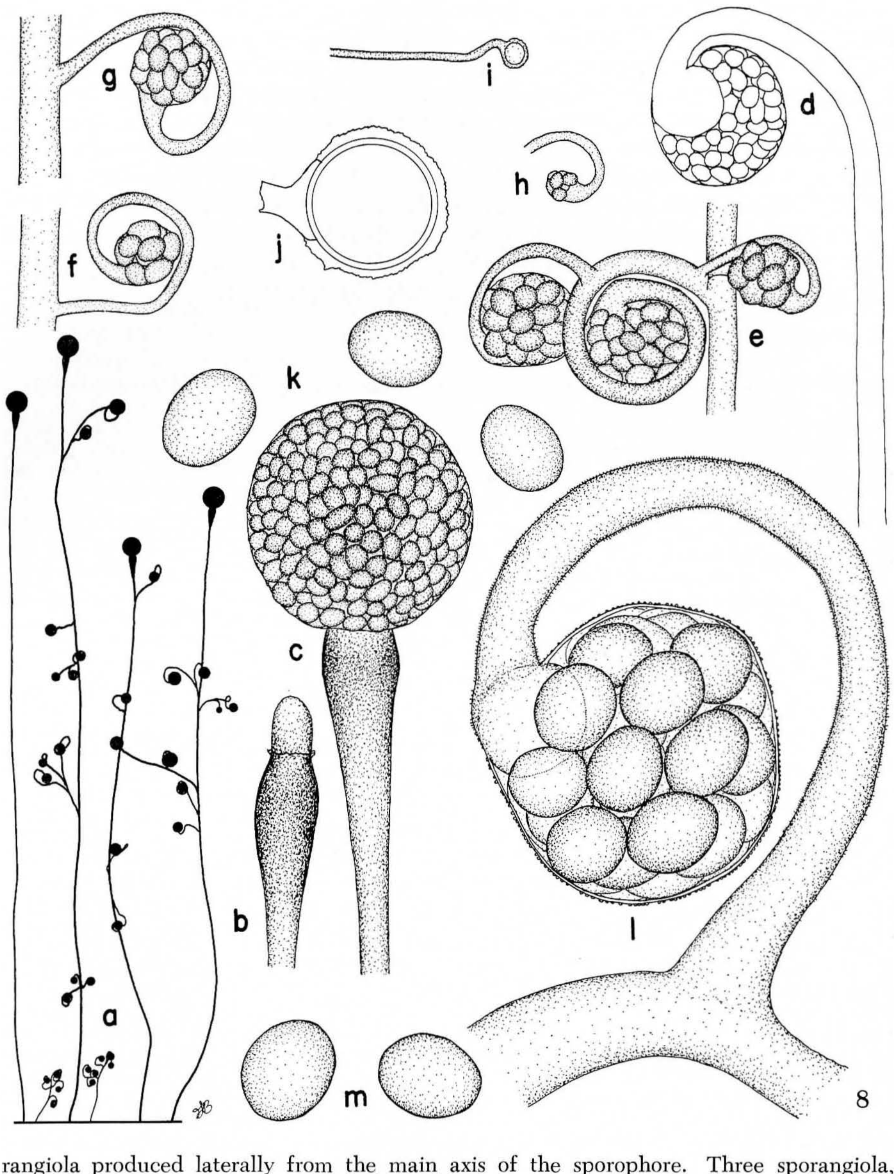
Ellisomyces anomalus (Hesseltine & Anderson) Benny & Benjamin, comb. nov. FIG. 9

≡ *Thamnidium anomalum* Hesseltine & Anderson, Amer. J. Bot. 43: 699. 1956 (basionym).

Colonies on MSMA to ca. 8.5 cm in diam in 10 days at 26 C; turf dense, white at first, soon becoming Light Olive-Gray to Deep Olive-Gray, then Light Grayish Olive in age. Sporophores hyaline to pale yellow, to ca. 1 cm in height, (7–)10–15(–20) μm in diam, septate in age, irregularly to sympodially branched, smooth walled below terminal branches; each branch 4–5 times bi- or trifurcate distally; branches encrusted, variable in length, usually successively shorter; lowermost branches 40–250 μm in length, 3.5–8.5 μm in diam; ultimate branches 3.2–18 μm in length, 3.2–4.5 μm in diam, bearing 1–7 pedicellate, multispored sporangiola apically and laterally. Sporangiolar pedicels smooth, 2–4.5 μm long, ca. 1 μm wide apically, tapered. Sporangiola globose to subglobose, 8–13(–17) μm in diam; wall smooth,

→

Fig. 8. *Fennellomyces linderi.*—a. Habit sketches of sporophores. × 25.—b. Columella from a primary sporangium showing subsporangial swelling. × 435.—c. Smooth-walled primary sporangium prior to deliquescence; note subsporangial swelling. × 435.—d. Optical section of large sporangiole produced directly from surface of substratum showing recurved pedicel, columella, and sporangiospores. × 435.—e–h. Multispored spo-



rangiola produced laterally from the main axis of the sporophore. Three sporangiola, two of which have arisen secondarily from the primary pedicel, are shown in *e*. × 435.—i. Unispored sporangiole borne on a long, slender pedicel. × 435.—j. Enlargement of sporangiole depicted in *i* showing the columella, the thin-walled sporangiospore, and the roughened sporangiolar wall. × 1,670.—k. Sporangiospores from a primary sporangium. × 1,670.—l. Multispored sporangiole showing columella and sporangiospores. × 1,670.—m. Sporangiospores from a multispored sporangiole. × 1,670.

hyaline; columellae subglobose to dome shaped, smooth, 2–5 μm in diam. Sporangiola usually separating intact with or without columella and portion of pedicel. Sporangiospores subglobose, ovoid, angular ovoid, or slightly cylindrical, 3.2–9 × 2.5–6.5 μm, hyaline, grayish in mass, contents granular with small globules; 12 or fewer spores per sporangiole. Chlamydospores abundant in both submerged and emergent vegetative hyphae, thin walled, globose, ovoid, or cylindrical, solitary or in chains, highly variable in size, mostly 4–20 × 4–30 μm. Zygospores globose to subglobose, (35–)40–55(–60) μm in diam including projections; wall reddish brown, translucent, covered with undulating projections up to 6 μm high; suspensors hyaline to pale yellow, 5–20(–26) μm long, 11–17 μm wide. Heterothallic.

Distribution.—U.S.A. (California).

Illustrations.—Hesseltine and Anderson (1956), Figs. 4–6 (as *Thamnidium anomalum*).

Specimens examined.—U.S.A. CALIFORNIA. Fresno Co.: Coalinga, soil, May, 1957, *G. F. Orr 177* (RSA 668+).—Imperial Co.: ca. 1 mi N of Westmorland, lizard dung, Apr. 19, 1962, *R. K. Benjamin* (RSA 2098).—Los Angeles Co.: Crystal Lake, San Gabriel Mts., ca. 30 mi N of Azusa, dung, June 30, 1953, *R. K. Benjamin* (type culture: RSA 88+; =NRRL 2465; =CBS 243.57); Palmar Canyon, ca. 3 mi N of Claremont, leaf mold and soil coll. by D. H. Ford, May 15, 1953, *R. K. Benjamin* isol. (RSA 80; 109–); Glendora Mountain Road, W of Mount Baldy, soil coll. by D. H. Ford, Nov. 10, 1953, *R. K. Benjamin* isol. (RSA 367); Pearblossom, leaf mold coll. by D. H. Ford, Nov. 20, 1953, *R. K. Benjamin* isol. (RSA 169); 15 mi S of Crystal Lake, San Gabriel Mts., soil coll. by D. H. Ford, Dec. 6, 1953, *R. K. Benjamin* isol. (RSA 364); Covina, soil coll. by D. H. Ford, Dec. 13, 1953, *R. K. Benjamin* isol. (RSA 365); Glendora Mountain Road, ca. 5 mi W of Mount Baldy, pack rat dung coll. by D. H. Ford, Jan. 1, 1954, *R. K. Benjamin* isol. (RSA 359–); Sunset Peak, San Gabriel Mts., ca. 7 mi N of Claremont, mouse dung, July 10, 1957, *R. K. Benjamin* (RSA 581–); San Antonio Canyon, San Gabriel Mts., dung, Nov. 3, 1958, *R. K. Benjamin* (RSA 804); Evey Canyon, ca. 4.5 mi NE of Claremont, mouse dung, May 7, 1970, *G. L. Benny* (RSA 2100).—Madera Co.: ca. 1.5 mi NE of Raymond, dung, Apr. 3, 1962, *R. K. Benjamin* (RSA 2097).—Marin Co.: ca. 1 mi NE of light house on Point Reyes, mouse dung, June 6, 1962, *R. K. Benjamin* (RSA 2099).—San Bernardino Co.: Cajon Pass, soil coll. by D. H. Ford, June 21, 1953, *R. K. Benjamin* isol. (RSA 110+); Stoddard Canyon, San Gabriel Mts., ca. 5 mi NNE of Claremont, soil coll. by D. H. Ford, Nov. 2, 1953, *R. K. Benjamin* isol. (RSA 360); E slope of Mt. San Antonio, San Gabriel Mts., soil coll. by D. H. Ford, Nov. 2, 1953, *R. K. Benjamin* isol. (RSA 361); Mount Baldy, soil coll. by D. H. Ford, Nov. 2, 1953, *R. K. Benjamin* isol. (RSA 362); ca. 5 mi S of Ontario, pack rat dung coll. by D. H. Ford, Dec. 28, 1953, *R. K. Benjamin* isol. (RSA 356–); ca. 8 mi N of San Bernardino, soil coll. by D. H. Ford, Dec. 29, 1953, *R. K. Benjamin* isol. (RSA 366); Cucamonga, pack rat dung coll. by D. H. Ford, Jan. 1, 1954, *R. K. Benjamin* isol. (RSA 358–); S slope of Mt. San Antonio, San Gabriel Mts., soil, Sept. 21, 1955, *R. K. Benjamin* (RSA 377); Telegraph Peak, San Gabriel Mts., mouse dung, Sept. 13, 1958, *R. K. Benjamin* (RSA 803); Jenk's Lake, San Bernardino Mts., dung, July 13, 1961, *R. K. Benjamin* (RSA 1182); ca. 6 mi N of Cajon Pass, pack rat dung, Feb. 15, 1970, *G. L. Benny* (RSA 2101–); Ice House Canyon, San Gabriel Mts., bark of *Quercus agrifolia* Neé, Oct. 2, 1973, *R. K. Benjamin* (RSA 2102).—San Diego Co.: ca. 7 mi N of Mt. Laguna, Laguna Mts., soil, Apr., 1960, *R. K. Benjamin* (RSA 1036).—Siskiyou Co.: Lava Beds National Monument, mouse dung, June 21, 1958, *R. K. Benjamin* (RSA 669–).—Ventura Co.: Pine Mt. Summit, Highway 399, soil, Apr. 3, 1961, *R. K. Benjamin* (RSA 1116).

Notes.—We believe that Hesseltine and Anderson's *Thamnidium anomalum* differs in so many ways from the type species of *Thamnidium*, *T. elegans* Link ex Gray, that it merits generic status; accordingly, we have renamed it *Ellisomyces anomalus*. As Hesseltine and Anderson (1956) intimated when they described *T. anomalum*, the fungus had little in common with the other three species of *Thamnidium* they recognized except for the production of small, mostly globose to subglobose sporangiola. Actually, the very common *Thamnidium elegans* is the only well-known species of the genus, for *T. simplex* Brefeld (1881a) and *T. verticillatum* van Tiegh. (1876) still are known only from their original descriptions and until they are rediscovered and studied critically their status as good species must remain in doubt.

The typical sporangiophore of *Thamnidium elegans* is robust, erect, only occasionally branched, rarely becomes repent except in age, and is terminated by a large, *Mucor*-like, deliquescent sporangium. The sporangiola terminate the ultimate branchlets of nearly dichotomous branch systems developing from short branches arising laterally from the main axis of the sporophore. The sporangiole itself is readily deciduous at maturity, falling away intact from the often only slightly enlarged apex of its relatively thick-walled subtending branchlet, i.e., pedicel. The latter never fractures below the sporangiole or remains attached to the caducous sporangiole. A sporangiolar columella is nearly absent or at the most very poorly developed. *Thamnidium elegans* is a facultative psychrophil, growing and sporulating almost equally as well at 6–7 C as at 20 C but with little or no growth at 32 C (Hesseltine and Anderson, 1956). Its zygospores will form only when compatible strains are mated on a suitable medium at low temperatures, i.e., 6–7 C.

In contrast to *Thamnidium elegans*, the sporophore of *Ellisomyces anomalus* typically is delicate, becomes sympodially branched (Fig. 9a) and highly septate at maturity, and never forms columellate primary sporangia. Its sporangiola are borne on short, thin-walled pedicels that arise terminally and laterally from the distal branchlets of a more or less dichotomous system of branchlets terminating the sporophore and its branches (Fig. 9b,c). Unlike *T. elegans*, the sporangiole of *E. anomalus* has a well-developed columella (Fig. 9c,f,g) that usually falls away with the sporangiole following rupture of the pedicel below the sporangiole (Fig. 9g), although under the pressure of a cover slip in slide mounts the sporangiole not uncommonly separates leaving the pedicel and columella intact (Fig. 9f). *Ellisomyces anomalus* will develop at reduced temperatures, but, unlike *T. elegans*, grows and sporulates well at temperatures up to 32 C, and compatible strains of *E. anomalus* form zygospores (Fig. 9e) readily at room temperature (i.e., 22–26 C) on a variety of media including YpSs and MSMA.

Ellisomyces anomalus differs from all other species of Thamnidiaceae that we have studied in its production of abundant chlamydospores in both submerged and emergent vegetative hyphae from even the earliest stages of development of the colony, not just in age as often occurs in many species of Mucorales. These spores develop singly or in chains and may be apical or intercalary (Fig. 9h); they are very distinct from the gemmae formed in the substrate hyphae of some strains of *Backusella lamprospora*.

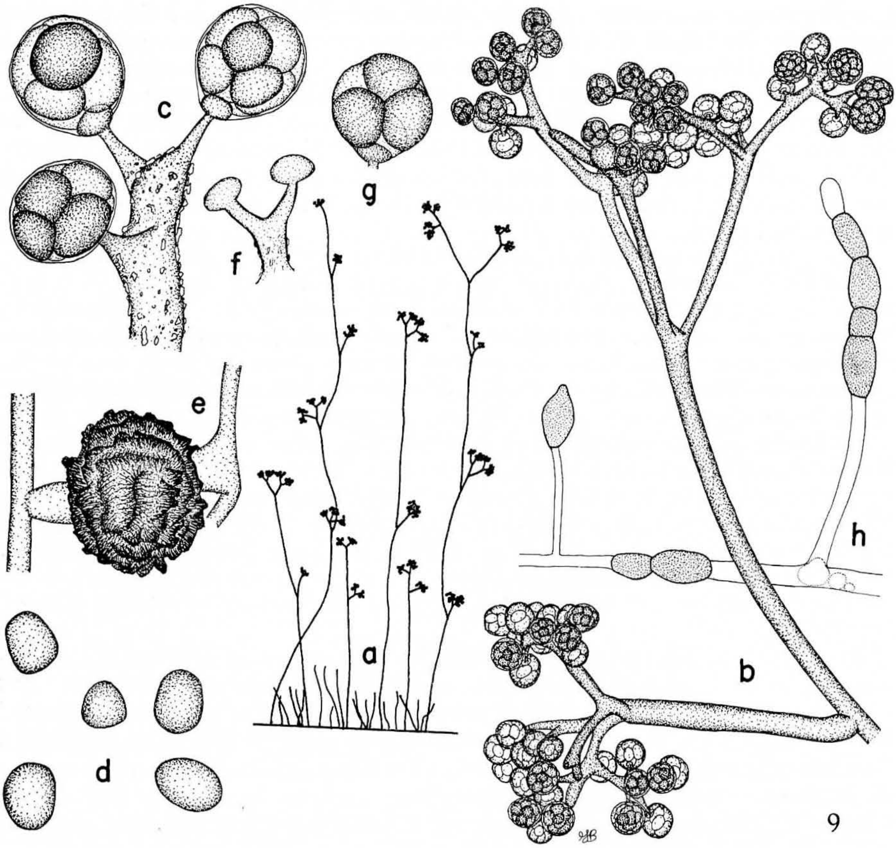


Fig. 9. *Ellisomyces anomalus*.—a. Habit sketches of sporophores. × 30.—b. Distal portion of a sporophore showing branching pattern and arrangement of sporangiola. × 450.—c. Distal portion of encrusted, ultimate branchlet of sporophore bearing three pedicellate, multispored, columellate sporangiola. × 1,715.—d. Sporangiospores from a sporangiole. × 1,715.—e. Typical zygospore and its suspensors (RSA 668+ × RSA 669–). × 450.—f. Two sporangiolar pedicels with intact columellae from which the sporangiola have become detached. × 1,715.—g. Typical detached sporangiole showing columella and remnant of subtending pedicel. × 1,715.—h. Chlamydospores formed in vegetative hyphae showing terminal and intercalary origin. × 1,240.

Thus far, *E. anomalus* has been found only in California where it is widely distributed. It occurs on a variety of substrata including dung, soil, and bark.

Zychaea Benny & Benjamin, gen. nov.

Sporophora nascentia recta via e substrato mycelio vel e stolone aereo, recta vel ascendentia, lenia vel aspera, parientia pauca vel multa pedicellata sporangiola in pedunculatis vesicis. Fecundae ramosae vesicae consistentes e lobatis segmentis inaequalibus in magnitudine figuraque, cum sporangiolis in dispansis extremis. Pedicelli recti vel conflexi, lenes. Sporangiola globosa vel subglobosa, multispora, parce unispora; parietes lenes, persistantes. Columellae convexae vel hemisphaericae, lenes. Sporangiosporae ovoideae vel ellipsoideae, lenes.

Species typica: *Zychaea mexicana* Benny & Benjamin

Sporophores erect or ascending, arising directly from the substrate mycelium or from stolons, producing few to many pedicellate sporangiola on stalked vesicles terminating the sporophore and its branches. Vesicles branched, consisting of lobate segments irregular in size and shape, bearing sporangiola on their extremities. Sporangiolar pedicels straight or curved, smooth. Sporangiola globose to subglobose, multispored, rarely unispored; wall persistent; columellae convex to hemispherical, smooth. Sporangiospores ovoid to ellipsoid.

Etymology.—Named for H. Zycha, mycologist.

Zychaea mexicana Benny & Benjamin, sp. nov. FIG. 10

Coloniae in MSMA 8.5 cm in diametro in 10 dies (26 C); primum albae, paene bubalinae vel pallide subbruneola olivacea in atatem. Sporophora recta vel ascendentia, 0.2–2 cm alta, 7–40 μm in diametro, simplica vel simpodice ramosa, aut distale simplica aut dichotome vel umbellate ramosa, hyalina cum immatura sunt, pallida vel fusca cum vetusta sunt, crassitunicata, irregulariter septata cum vestuta sunt, procreantia irregulariter conformata densa capita, 30–200 μm in diametro, terminaliter vel a latere, consistentia e paucis ad multis pedicellatis sporangiolis latis in fecundis vesicis. Fecundae vesicae brevipedunculatae, usque ad 50 μm in diametro, hyalinae vel pallidae flavae, lenes, consistentes e subglobosis, ovoideis vel productis, vel lobatis, irregulariter colligatis segmentis, uniseptatae statim infra fecundam partem. Pedicelli recti vel subcurvati, plerumque distale abrupte curvi, (25–)45–60(–70) μm longi, 2.8–3.5 μm in diametro distale, 1–1.5 μm in diametro proximale, hyalini vel pallide flavi. Sporangiola globosa vel subglobosa, 10–15 μm in diametro; hyalini parietes; columellae 3–6.8 μm in diametro, convexae vel hemisphaericae, cum parva apophyse. Sporangiosporae ovoideae vel ellipsoideae, (4.8–)6–7(–13.5) × (3.2–)4–5.5(–10) μm, hyalinae vel pallide flavae, lenes; (1–)4–8(–10) sporae in singula sporangiola. Zygosporae non animadversae.

Holotypus: RSA 1403.

Colonies on MSMA to ca. 8.5 cm in 10 days at 26 C; turf becoming moderately dense, white at first, near Cartridge Buff to Light Brownish Olive in age. Sporophores erect or ascending, arising directly from the substrate mycelium or from sprawling stoloniferous aerial hyphae, simple or sympodially branched, hyaline, light to dark brown in age, 0.2–2 cm high, soon reaching the lid of a Petri dish (2 cm), 7–40 μm in diam, thick walled, smooth or slightly roughened, irregularly septate in age, producing heads of sporangiola terminally or on short lateral branchlets. Heads irregular in shape, globoid or dorsiventrally flattened, 35–200 μm in diam, becoming dark gray to brown, consisting of few to many pedicellate sporangiola borne on 1–3 or more short-stalked vesicles up to 50 μm in diam. Vesicles hyaline to pale yellow, smooth, consisting of subglobose, ovoid to elongate, or lobate, irregularly constricted segments that become uniseptate immediately below the fertile portion. Sporangiolar pedicels straight or somewhat curved, usually slightly but abruptly bent distally, (25–)45–60(–70) μm long, 2.8–3.5 μm wide distally, 1–1.5 μm wide proximally, hyaline to pale yellow. Sporangiola globose to subglobose, 10–15 μm in diam; wall hyaline, smooth; columellae 3–6.8 μm in diam, convex to hemispherical, with slight apophysis. Sporangiospores ovoid to ellipsoid, (4.8–)6–7(–13.5) × (3.2–)4–5.5(–10) μm, hyaline to pale yellow, smooth; (1–)4–8(–10) spores per sporangiole. Zygospores not observed.

Holotype.—MEXICO. SINALOA. Fifteen mi SW of Los Moches and ca. 3 mi E of Topolobampo Bay, on mouse dung coll. by J. Henrickson, June 19, 1964, *R. K. Benjamin* isol. (RSA 1403). A dried culture has been deposited in the herbarium of RSA. In addition, living cultures have been transmitted to ATCC, CBS, IMI, and NRRL.

Etymology.—Named for the country of origin of the holotype.

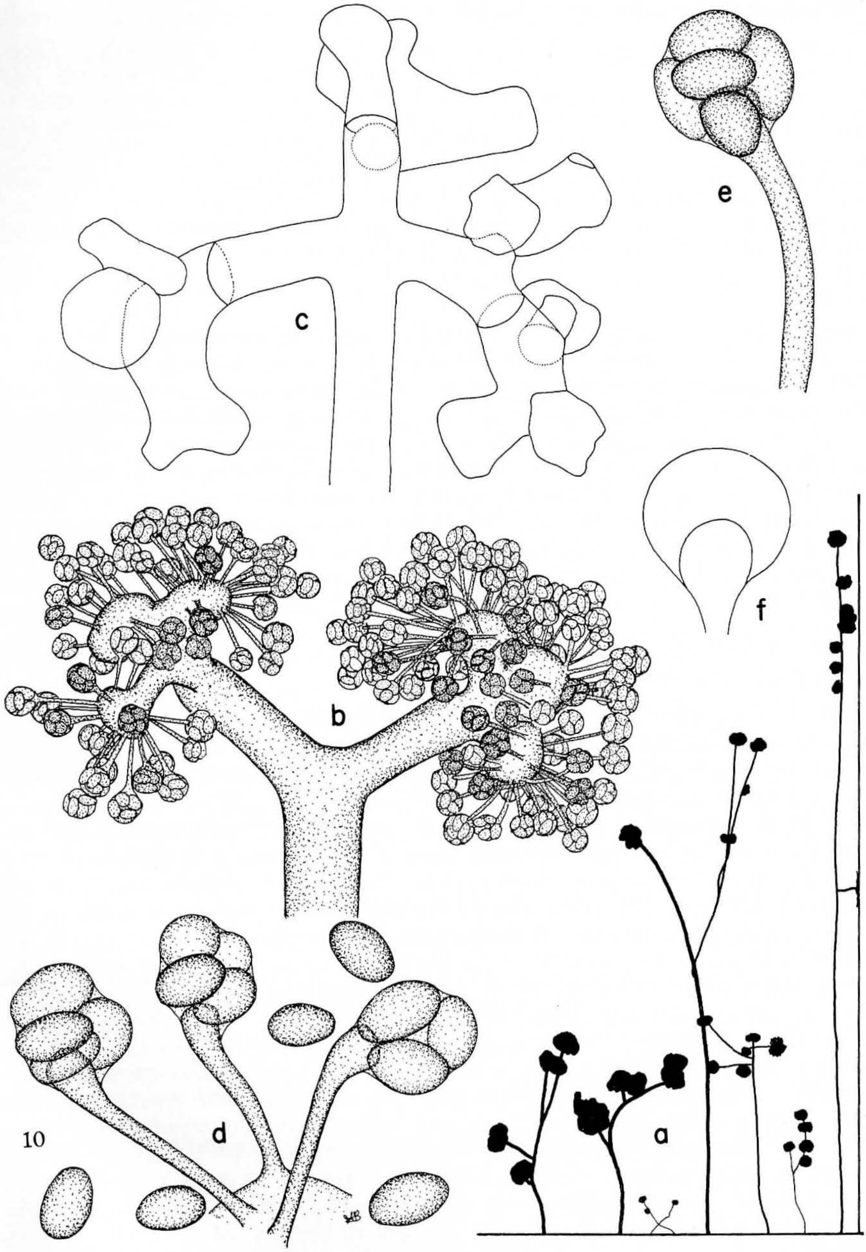
Notes.—The above-cited isolate was long carried in the culture collection of RSA as a tentative new species of *Helicostylum*, but our comparison of it with established species of this genus and the recently segregated *Thamnostylum* has convinced us that, while obviously allied to these genera, especially *Thamnostylum*, it should be separated generically. Under no conditions of culture has *Z. mexicana* been induced to form *Mucor*-like sporangia as in species of *Helicostylum* and *Thamnostylum*.

The young sporophore of *Z. mexicana* typically becomes bi- or trifurcate apically (Fig. 10b,c) with each branch elongating only slightly before again giving rise to two, three, or sometimes more shorter branches that become inflated distally and produce more or less globoid enlargements from which the pedicellate sporangiola all develop simultaneously (Fig. 10b). After the sporangiola mature, the subtending vesicles usually are cut off by septa (Fig. 10c). The sporangiophore continues to branch, forming elongate or often very short branchlets each of which develops a head of sporangiola like that formed initially (Fig. 10a).

Sporangiola of *Z. mexicana* resemble those of *Thamnostylum* spp. but their pedicels are only slightly, though abruptly, bent distally (Fig. 10b,d,e), never strongly reflexed as in members of the latter genus (Figs. 1d,e; 2f–i; 3f,g,k; 4d,e). Pedicellate, multispored sporangiola arising from vesicles terminating the sporophore are also found in *Cokeromyces recurvatus* Poitras (Shanor et al., 1950), but the habit of the latter species is otherwise wholly unlike that of *Z. mexicana.*

→

Fig. 10. *Zychaea mexicana.*—a. Habit sketches of sporophores. × 12.—b. Apical portion of sporophore showing arrangement of pedicellate sporangiola on irregularly shaped vesicles borne on short branchlets. × 445.—c. Sporophore apex without sporangiola showing short branchlets subtending fertile vesicles; note irregular conformation of the latter, each of which is separated from its subtending branch by a septum. × 445.—d. Portion of a fertile vesicle showing three pedicellate sporangiola; note slightly bent pedicels and position of columellae. Five free spores also shown. × 1,690.—e. Sporangiole with slightly curved pedicel. × 1,690.—f. Optical section of sporangiole with spores omitted to show globoid columella. × 1,690.



10

Dichotomocladium Benny & Benjamin, gen. nov.

Sporophora nascentia recta via e substrato mycelio, recta vel ascendentia, simplica vel ramosa, gignentia fecunda capita terminaliter vel subterminaliter. Fecunda capita consistentia e pluries dichotomo ramorum systemate, alii rami steriles spineique, alii gignentes pedicellata, unispora sporangiola super terminalibus, subamplificatis, angularibus vel rotundatis vesicis. Steriles spinae rectae vel subcurvatae, attenuatae. Pedicelli tenues, cylindracei vel attenuati. Sporangiola columelliformia, obovoidea vel ellipsoidea; parietes spinulosi, tenues, persistentes; columellae emarginatae, concavae. Sporangiosporae similes sporangioli in magnitudine formaque. Zygosporae globosae vel subglobosae; parietes fusci, ornati ab irregulariter conformatis processibus; gametangialia residua conspicua, fusca, lenia vel aspera; suspensores oppositi.

Species typica: *Dichotomocladium elegans* Benny & Benjamin

Sporophores arising directly from the substrate mycelium, erect or ascending, simple or branched, producing fertile heads laterally or terminally. Fertile head consisting of a several times dichotomous branch system, some branches sterile and spinelike, others terminating in slightly enlarged, angular or rounded vesicles bearing pedicellate sporangiola. Sterile spines straight or curved, acuminate. Sporangiolar pedicels slender, cylindrical or tapered. Sporangiola unispored, minutely columellate, globoid to ellipsoid; wall spinulose, thin, persistent; columellae emarginate, concave. Sporangiospores like the sporangiola in size and shape. Zygospores globose to subglobose; wall dark, ornamented with coarse projections; gametangial remnants prominent, dark, smooth to roughened; suspensors opposed.

Etymology.—From *dichotomus* (Gr.: διχοτόμος), cutting in two + *cladodes* (Gr.: κλαδώδης), branchlike.

Macroscopically, species of *Dichotomocladium* superficially resemble those of *Chaetocladium* which also produce only unispored sporangiola. However, development of the spore-bearing structures is fundamentally very different in representatives of the two genera and in our opinion justifies their separation generically. In members of both genera the sporangiola arise from small enlargements of the ultimate branches of a repeatedly branched system of branches. The branch systems arise laterally or terminally from the main axis of the sporophore and form more or less compact clusters composed of both sterile and fertile elements.

In *Chaetocladium* spp. the branching pattern of the fertile branch system is verticillate (Brefeld, 1872, 1881a; Hesseltine and Anderson, 1957). Two or more spinelike branches arise in a whorl from the sporophore axis. These branches, in turn, give rise to intercalary whorls of a few smaller branches, followed by a third or even fourth order of yet smaller branches. The ultimate branchlets give rise to pedicellate sporangiola from their slightly enlarged tips or from just below spinelike terminations.

In *Dichotomocladium* spp. the branching pattern of the fertile branch system is dichotomous. A branch arising laterally or terminally from the main axis of the sporophore may dichotomize 10–15 or more times. Successive branches may continue to branch uniformly (Fig. 13d) or some branches may cease development and form spines (Figs. 11b,d; 12b,d; 13d,e). Arrested development of one or both branches of successive dichotomies can result in a marked curvature of the developing axis so that the several branches comprising the fertile branch system form a more or less globoid head with outwardly projecting spines and inwardly projecting spore-bearing branches (Figs. 11b; 12b). Few or many of the ultimate branchlets enlarge distally and give rise to pedicellate sporangiola (Fig. 14).

Zygospores have been reported in both species of *Chaetocladium*, *C. brefeldii* and *C. jonesii*, but those of the latter species are known only from Brefeld's account published in 1881 (as *C. fresenianum* Bref.) where a somewhat diagrammatic rendition shows a zygospore borne between two nearly equal but small, globoid suspensors. Zygospores of *C. brefeldii*, which is heterothallic, are well known (Brefeld, 1872 [as *C. jonesii*]; Hesseltine and Anderson, 1957) and are very distinctive. When mature, they are yellow to yellow-brown and covered by coarse, ridgelike projections. They develop between suspensors that at first are nearly equal, but as the zygospore matures, one suspensor enlarges, becomes nearly globose, and approaches the size of the mature spore itself, whereas the other suspensor remains relatively small, rarely reaching half the size of the first. The zygospore lacks evident gametangial remnants.

The two species of *Dichotomocladium* described as new in this study are heterothallic and several compatible strains of each have been isolated. Zygospores of both species are darkly pigmented, coarsely roughened, borne between nearly equal, opposed suspensors, and have more or less prominent gametangial remnants (Figs. 11e,f; 12e).

Characteristics other than those morphological also distinguish members of *Chaetocladium* and *Dichotomocladium*. Both species of *Chaetocladium* are psychrophilic, growing and sporulating well at 7 C and poorly at temperatures much above 20 C (Hesseltine and Anderson, 1957). *Dichotomocladium* spp. show little development at 7 C but make excellent growth at all temperatures from 18 to 31 C, and above in the case of *D. hesseltinii*. *Chaetocladium brefeldii* and *C. jonesii* are facultative parasites of other Mucorales on which they produce gall-like structures. We never have observed parasitic tendencies in the three known species of *Dichotomocladium*.

KEY TO THE SPECIES OF *DICHOTOMOCLADIUM*

A. Fertile branches forming lax, *Piptocephalis*-like heads; sterile spines few; vesicles subtending sporangiola more or less angular in outline .... 3. *D. hesseltinii*

AA. Fertile branches forming compact, globoid heads; sterile spines many; vesicles subtending sporangiola globose to subglobose .... B

B. Diameter of largest fertile heads 250–300 μm; many heads per sporophore; zygospore diameter greater than length of suspensors .... 1. *D. elegans*

BB. Diameter of largest fertile heads 400–550 μm; few heads per sporophore; zygospore diameter less than length of suspensors .... 2. *D. robustum*

Dichotomocladium elegans Benny & Benjamin, sp. nov. FIGS. 11, 14k–o

Coloniae plus minusvae restrictae, in MSMA 3 cm in diametro in 6 dies (26 C), intense olivaceae-luteae vel atro-olivaceae in aetatem. Sporophora recta vel ascendentia, 1–2 cm alta, (3–)5–8(–9.5) μm in diametro, simplica vel sympodice ramosa, gignentia 2–18(–29) (av. 8) fecunda capita paribus intervallis in brevibus lateralibus ramis. Latarales rami (15–)25–45(–60) × 4.2–8.4 μm. Fecunda capita irregularia vel subglobosa, (110–)160–225(–300) μm in diametro; composita e 10–15 dichotomis ramulis divisis in primas, medias et fecundas partes. Steriles spinae 6–32 μm longae. Fecundae vesicae globosae vel late clavatae (2.5–)4–6(–7) μm in diametro; gignentes (2–)6–8(–9) sporangiola per totam superficiem. Sporangiola obovoidea vel ellipsoidea, (3.5–)5–6(–6.8) × (3–)3.5–4.5(–5) μm (av. 5.5 × 4 μm); tenuis spinulosus paries. Zygosporae globosae vel subglobosae, (35–)40–60(–80) μm in diametro (av. 53 μm) comprehensis processibus; paries brunneus, diaphanus; suspensores recti, (10–)15–25(–30) μm longi, (15–)18–25(–27) μm lati. Heterothallicus.

Holotypus: RSA 601.

Colonies more or less restricted on MSMA, to ca. 3 cm in diam in 6 days at 26 C; turf relatively dense, white at first, Deep Olive-Buff to Dark Olive in age. Sporophores erect or ascending, hyaline to pale yellow, irregularly septate in age, 1–2 cm high, (3–)5–8(–9.5) μm in diam, simple or sympodially branched; wall thick, roughened; the main axis and its branches producing 2–18(–29) (av. 8) fertile heads, these arising singly, in pairs, or in verticles at more or less regular intervals on short, straight or slightly curved, echinulate, 1(–3)-septate lateral branches, (15–)25–45(–60) × 4–8.5 μm, that become 10–15 times regularly or helicoidally dichotomously branched and form the fertile heads. Fertile heads gray to tan when mature, irregular in outline to subglobose, (110–)160–255(–300) μm in diam; successive branchlets echinulate, subequal, usually uniseptate, only the ultimate 2–4(–5) branchlets fertile, the intermediate branches or their dichotomies forming elongate, acuminate, echinulate spines 6–32 μm long by 1–3 μm wide at the base. Penultimate branches of the fertile branch system 3–6 × 1–3 μm, usually uniseptate; ultimate branches 1–3 × 3 μm, producing globose to broadly clavate, echinulate vesicles, (2.5–)4–6(–7) μm in diam, bearing (2–)6–8(–9) pedicellate sporangiola. Pedicels tapered, 1–2 μm long. Sporangiola ovoid to ellipsoid, (3.5–)5–6(–6.8) × (3–)3.5–4.5(–5) μm (av. 5.5 × 4 μm), hyaline to pale yellow; wall thin, echinulate; columellae emarginate, ca. 2 μm in diam. Sporangiospores like the sporangiola in size and shape; wall thin, smooth. Zygospores globose to subglobose, (35–)40–60(–80) μm in diam (av. 53 μm) including surface projections; outer wall brown, translucent, with irregularly shaped projections 2–5 μm high; gametangial remnants dark brown, (1–)2–5(–7) μm long; suspensors straight, smooth or roughened, hyaline to pale yellow, (10–)15–25(–30) μm long, (15–)18–25(–27) μm wide, slightly constricted where joining the gametangial remnants. Heterothallic.

Holotype.—U.S.A. CALIFORNIA. Los Angeles Co.: San Antonio Canyon, San Gabriel Mts., mouse dung, Sept., 1957, *R. K. Benjamin* (RSA 601+; =NRRL 2664). A dried culture has been deposited in the herbarium of RSA. In addition, living cultures have been transmitted to ATCC, CBS, IMI, and NRRL.

Etymology.—From *elegans* (L.), choice, fine, neat.

Other specimens examined.—MEXICO. BAJA CALIFORNIA DEL NORTE. Ca. 5 mi S of San Quintín, mouse dung coll. by D. Gregory, Nov. 28, 1957, *R. K. Benjamin* isol. (RSA 620–); ca. 1 mi W of El Aguajito, mouse dung, Feb. 23, 1963, *R. K. Benjamin* (RSA 1349–); ca. 2 mi S of Santa Inés, pack rat dung, Feb. 24, 1963, *R. K. Benjamin* (RSA 1350–); ca. 12 mi S of Laguna Chapala, mouse dung, Feb. 25, 1963, *R. K. Benjamin*

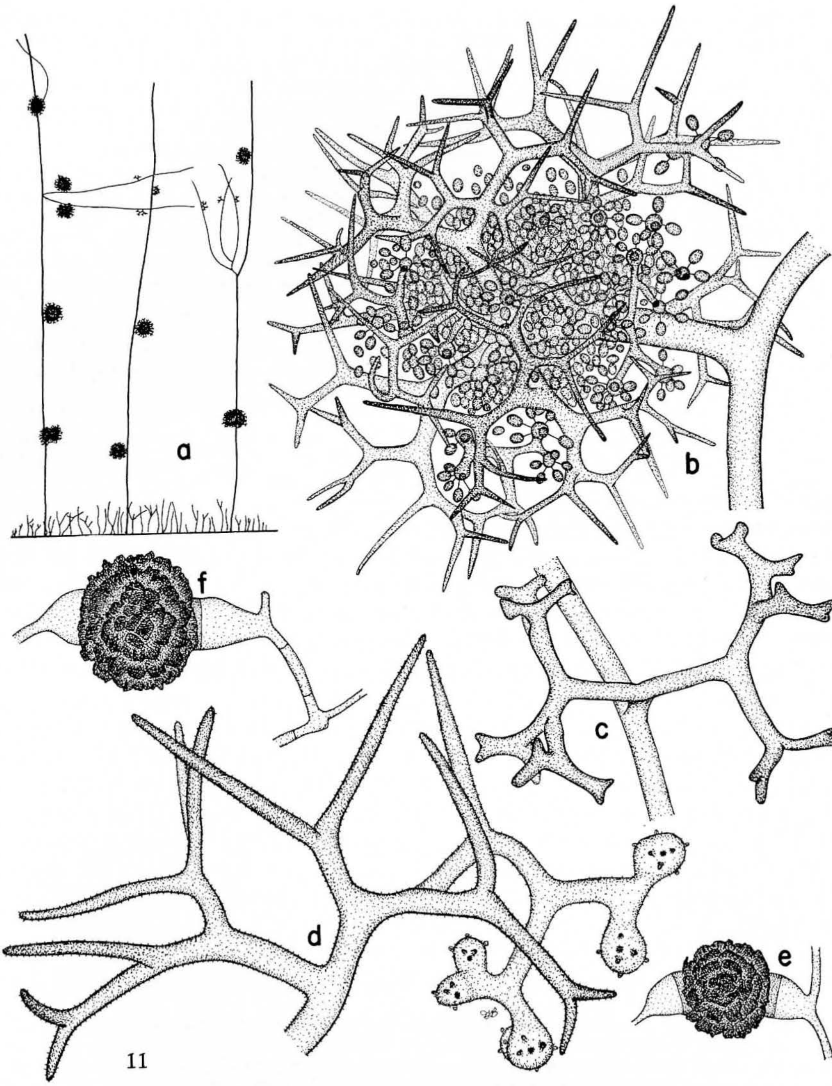


Fig. 11. *Dichotomocladium elegans.*—a. Habit sketches of sporophores. $\times$ 5.—b. Fruiting head showing its subtending stalk arising from the sporophore and the relationship of the sterile, spinose branchlets and fertile ultimate branchlets bearing sporangiola. $\times$ 480.—c. Early stage in development of a fertile branch system; note dichotomous branching pattern. $\times$ 1,200.—d. Part of a dichotomous fertile branch system. Most of the branchlets are sterile and spinose; several, shown at the right, formed small terminal vesicles bearing sporangiola that have fallen away leaving only the subtending pedicellar remnants. $\times$ 1,200.—e–f. Typical zygospores and their short, basally constricted suspensors; note the prominent gametangial remnants (RSA 601+ $\times$ RSA 1092–). $\times$ 315.

(RSA 1351+); nr. Calamujué, pack rat dung coll. by R. Hanamin, Mar. 1, 1963, *R. K. Benjamin* isol. (RSA 1352+; RSA 1353+); La Suerte, ca. 70 mi W of San Quintín, dung, June 4, 1963, *R. K. Benjamin* (RSA 1354–). U.S.A. CALIFORNIA. Fresno Co.: 5 mi W of Coalinga, dung, Apr. 3, 1962, *R. K. Benjamin* (RSA 1343).—Los Angeles Co.: Claremont, pack rat dung, Oct. 14, 1958, *R. K. Benjamin* (RSA 738–); San Antonio Canyon, San Gabriel Mts., mouse dung, Nov. 3, 1958, *R. K. Benjamin* (RSA 730–; RSA 739+).—Riverside Co.: "Split Rock," Joshua Tree National Monument, pack rat dung, Nov. 29, 1958, *R. K. Benjamin* (RSA 762–); ca. 15 mi W of Desert Center, mouse dung, Oct. 12, 1959, *R. K. Benjamin* (RSA 920–); Andreas Canyon, ca. 3 mi S of Palm Springs, pack rat dung, Nov. 24, 1960, *R. K. Benjamin* (RSA 1091–), May 3, 1961 (RSA 1132–; RSA 1133+; RSA 1134), mouse dung, Nov. 22, 1962 (RSA 1758).—San Bernardino Co.: nr. Cajon, mouse dung, Jan. 5, 1958; *R. K. Benjamin* (RSA 634–); Ivanpah Mts., ca. 10 mi N of Cima, pack rat dung, Aug. 19, 1959, *R. K. Benjamin* (RSA 904–); ca. 3 mi E of Earp, rabbit dung, fall, 1959, *G. F. Orr 491* (RSA 919–); ca. 12 mi SW of Running Springs, San Bernardino Mts., mouse dung, Mar. 31, 1960, *R. K. Benjamin* (RSA 1090–); Deep Creek Canyon, San Bernardino Mts., dung, Nov. 26, 1960, *R. K. Benjamin* (RSA 1092–); Victorville, mouse dung, Dec. 16, 1969, *G. L. Benny* (RSA 2103–).—San Diego Co.: ca. 7 mi E of Jamul, mouse dung, Oct. 16, 1960, *R. K. Benjamin* (RSA 1083–).

Notes.—Dichotomocladium elegans resembles *D. robustum* in habit, but it always forms fertile heads (Fig. 11a,b) whose maximum size is much less than in the latter species (Fig. 12a,b). Sporophores of *D. elegans* are more or less uniform in length and typically give rise to a succession of fertile heads (Fig. 11a), whereas the sporophores of *D. robustum* tend to vary greatly in length and usually form only one fertile head (Fig. 12a). As cultures age, however, and secondary branching takes place followed by continued production of fertile heads, the number of heads per sporophore serves less to distinguish the species on the basis of gross appearance than does head size.

Although mating strains of *D. elegans* and *D. robustum* are required for obtaining zygospores, the characteristics of the sexual structures readily distinguish the two species. In *D. robustum* the length of each suspensor is always greater than—sometimes nearly double—the diameter of the zygospore (Fig. 12e). Conversely, the zygospore of *D. elegans* always is greater than the length of its suspensors which usually are somewhat bell shaped and often slightly constricted where they meet the gametangial remnants (Fig. 11e,f).

Dichotomocladium robustum Benny & Benjamin, sp. nov. FIGS. 12, 14f–j

Coloniae in MSMA 7.5–8 cm in diametro in 6 dies (26 C), ochraceae vel stramineae in aetatem. Sporophora recta vel ascendentia, 0.5–20 mm alta, (4–)6–9.5(–10.5) µm in diametro, saepe sympodice ramosa super fecunda capita; 1(–3) fecunda capita pariuntur in sporophori lateralibus ramis. Laterales rami (20–)25–35(–50) × (6–)8–10(–12.5) µm. Fecunda capita irregularia vel subglobosa; ea quae sunt juxta substratum (85–)100–175(–200) µm in diametro; et ea quae sunt super substratum (190–)250–450(–550) µm in diametro; constituta e 11–16 dichotomis ramulis divisis in primas, medias, et fecundas partes. Steriles spinae 10–80 µm longae. Fecundae vesicae globosae vel late clavatae, (3.5–)4.5–6(–7.5) µm in diametro; gignentes (4–)7–9(–11) sporangiola per totam superficiem. Sporangiola obovoidea vel ellipsoidea (5–)6–7(–8.5) × (4–)5–7(–8.5) µm; tenuis spinulosus paries. Zygosporae globosae vel subglobosae, (40–)50–70(–85) µm in diametro (av. 60 µm) comprehensis processibus; paries brunneus, diaphanus; suspensores parce vel valde curvati, (45–)60–100(–135) µm longi, (10–)15–20(–25) µm lati. Heterothallicus.

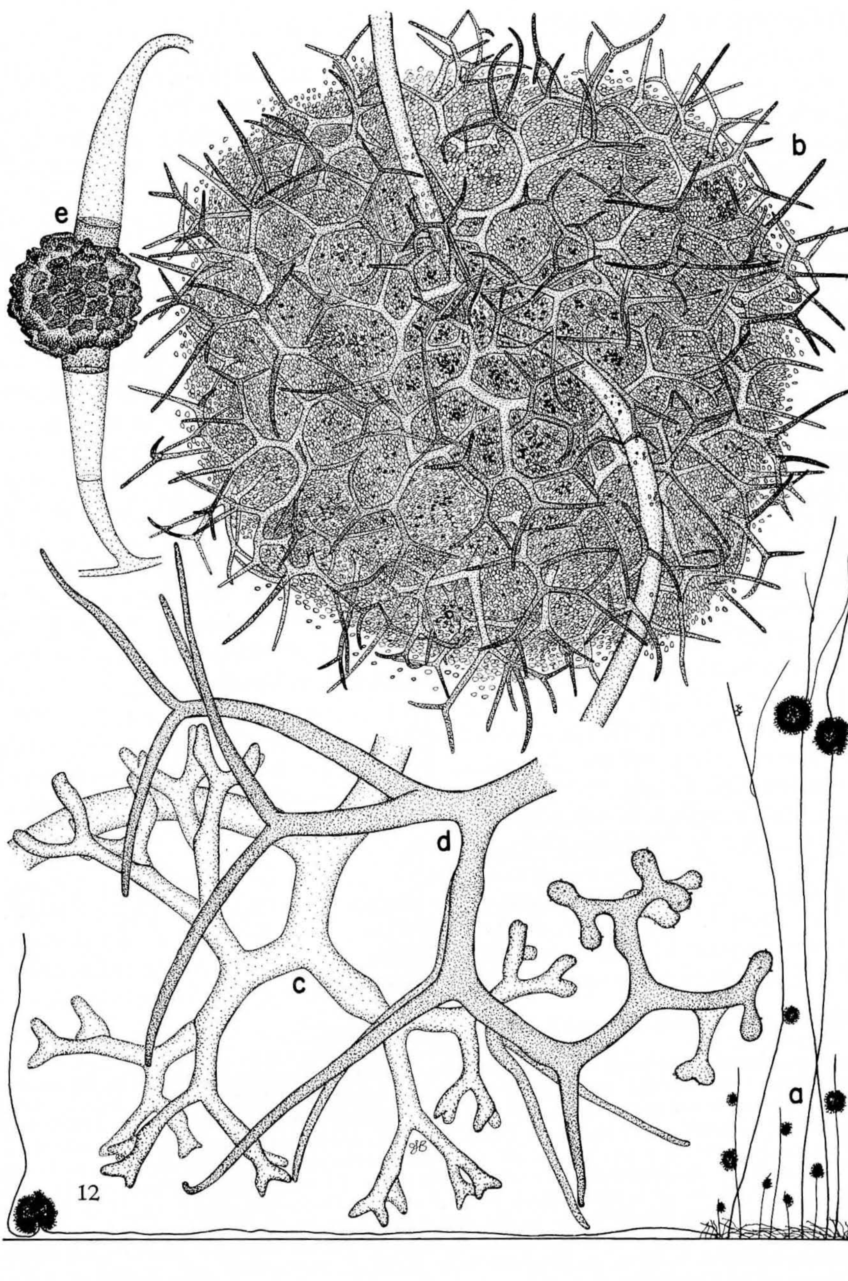
Holotypus: RSA 1081.

Colonies developing rapidly on MSMA, to ca. 7.5–8 cm in diam in 6 days at 26 C; turf dense, white at first, Chamois or Cream-Buff in age. Sporophores erect or ascending, rarely recumbent, irregularly septate in age, 0.5–20 mm high, (4–)6–9.5(–10.5) μm in diam, simple or sympodially branched above the fertile heads; wall thick, roughened; the main axis producing 1, rarely 2–3, fertile heads, these arising singly, in pairs, or in verticles on short, straight or slightly curved, echinulate, 1(–3)-septate lateral branches, (20–)25–35(–50) × (6–)8–10(–12.5) μm, that become 11–16 times regularly or helicoidally dichotomously branched and form the fertile heads. Fertile heads gray or tan when mature, irregular in outline to subglobose; heads on short sporophores near the substrate (85–)100–175(–200) μm in diam, those on more elongate sporophores (190–)250–450(–550) μm in diam; successive branchlets echinulate, subequal, usually uniseptate, only the ultimate (2–)3–4(–5) branchlets fertile, the intermediate branches or their dichotomies forming elongate, acuminate, echinulate spines 10–80 μm long by 2–3 μm wide at the base. Penultimate branches of the fertile branch system 3–6 × 2–3 μm, usually uniseptate; ultimate branches 1–2 × 2–3 μm, producing globose to broadly clavate, echinulate vesicles, (3.5–)4.5–6(–7.5) μm in diam, bearing (4–)7–9(–11) pedicellate sporangiola. Pedicels tapered, 1–2 μm long. Sporangiola ovoid to ellipsoid, (5–)6–7(–8.5) × (4–)5–7(–8.5) μm (av. 6.5 × 5.8 μm), hyaline to pale yellow; wall thin, echinulate; columellae emarginate, ca. 2 μm in diam. Sporangiospores like the sporangiola in size and shape; wall thin, smooth. Zygospores globose to subglobose, (40–)50–70 (–85) μm in diam (av. 60 μm) including surface projections; outer wall brown, translucent, with irregularly shaped projections 2–5 μm high; gametangial remnants dark brown, 5–15 μm long; suspensors slightly to strongly curved, smooth or roughened, hyaline to pale yellow, (45–)60–100(–135) μm long, (10–)15–20(–25) μm wide. Heterothallic.

Holotype.—U.S.A. CALIFORNIA. San Diego Co.: ca. 5 mi E of Dalzura, mouse dung, Oct. 16, 1960, *R. K. Benjamin* (RSA 1081+). A dried culture has been deposited in the herbarium of RSA. In addition, living cultures have been transmitted to ATCC, CBS, IMI, and NRRL.

Etymology.—From *robustus* (L.), hard, strong.

Other specimens examined.—MEXICO. BAJA CALIFORNIA DEL NORTE. Ca. 12 mi S of Maneadero, mouse dung, Feb. 22, 1963, *R. K. Benjamin* (RSA 1346–). U.S.A. CALIFORNIA. Kern Co.: Poso Creek, ca. 10 mi N of Oildale, lizard dung, Apr. 4, 1962, *R. K. Benjamin* (RSA 1344+); just S of Bodfish, dung, May 6, 1962, *R. K. Benjamin* (RSA 1345+).—Madera Co.: ca. 2.5 mi W of Coarsegold, pack rat dung coll. by A. Diboll, May 10, 1959, *R. K. Benjamin* isol. (RSA 898–); ca. 13 mi S of Coarsegold, mouse dung, Apr. 3, 1962, *R. K. Benjamin* (RSA 1342–).—San Diego Co.: ca. 5 mi E of Dalzura, pack rat dung, Oct. 16, 1960, *R. K. Benjamin* (RSA 1080–); ca. 2 mi W of Pala, dung coll. by G. Wallace, Feb. 2, 1972, *G. L. Benny* isol. (RSA 2104–).—Shasta Co.: Obrien Mt., mouse dung coll. by O. A. Plunkett, July, 1960, *G. F. Orr 833* (RSA 1009+; =NRRL 3029).—Tulare Co.: Sequoia National Forest, ca. 17 mi E of Springville, dung coll. by R. E. Benny, Dec. 28, 1969, *G. L. Benny* isol. (RSA 2036+).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Notes.—Primary characteristics by which *Dichotomocladium robustum* and *D. elegans* can readily be distinguished have been given following the description of the latter.

Dichotomocladium robustum has not been isolated as frequently as *D. elegans,* but neither species appears to be uncommon in California and adjacent Mexico. All isolates of both species have been obtained from dung.

Dichotomocladium hesseltinii (Mehrotra & Sarbhoy) Benny & Benjamin, comb. nov. FIGS. 13, 14a–e

≡ *Chaetocladium hesseltinii* Mehrotra & Sarbhoy, Mycologia 52: 797. 1960 (basionym).

Colonies developing rapidly on MSMA, to ca. 8.5 cm in diam in 5 days at 26 C; turf dense, white at first, Buffy Olive to Ivory Yellow in age. Sporophores erect or ascending, hyaline to pale yellow, height variable, 1 mm to 5 cm, (9.5–)11–17(–31) μm in diam; wall roughened; the main axis simple, often sympodially branched above the fertile heads. Fertile heads arising singly, in pairs, or in verticles, gray to tan when mature, irregular to subglobose in outline, those close to the substrate (60–)175–400(–500) μm in diam, those terminating the elongate sporophores (0.45–)0.7–1.5(–2) mm in diam; each head consisting of a 9–15-times regularly dichotomous branch system. The initial branch straight or slightly curved, (10–)35–210(–390) × (9.5–) 11–16(–35) μm, 1(–3) septate, roughened; successive branchlets progressively shorter, roughened, usually uniseptate, the ultimate branchlets mostly fertile; some intermediate and ultimate branchlets forming elongate, acuminate, echinulate spines 10–60 μm long by 2–7 μm wide at the base. Penultimate branchlets of the fertile branch system 2–20 × 2–5 μm, usually uniseptate; ultimate branches 1–5 × 1–5 μm, rarely uniseptate, producing subglobose to angular, echinulate vesicles (3.3–)3.5–5(–6) μm in diam bearing (1–)2–5(–7) pedicellate sporangiola. Pedicels tapered, 1–2(–4.5) μm long. Sporangiola globose, 4.8–6.6 μm in diam, or ovoid to ellipsoid, 5–10 × 3.5–8.5 μm, hyaline to pale yellow; wall thin, echinulate; columellae emarginate, concave, ca. 2.2 μm in diam. Sporangiospores like the sporangiola in size and shape; wall thin, smooth. Zygospores not observed.

Distribution.—India.

Illustrations.—As *Chaetocladium hesseltinii*: Mehrotra and Sarbhoy (1960), Figs. 1–8; Mukerji (1969), Figs. 2–3.

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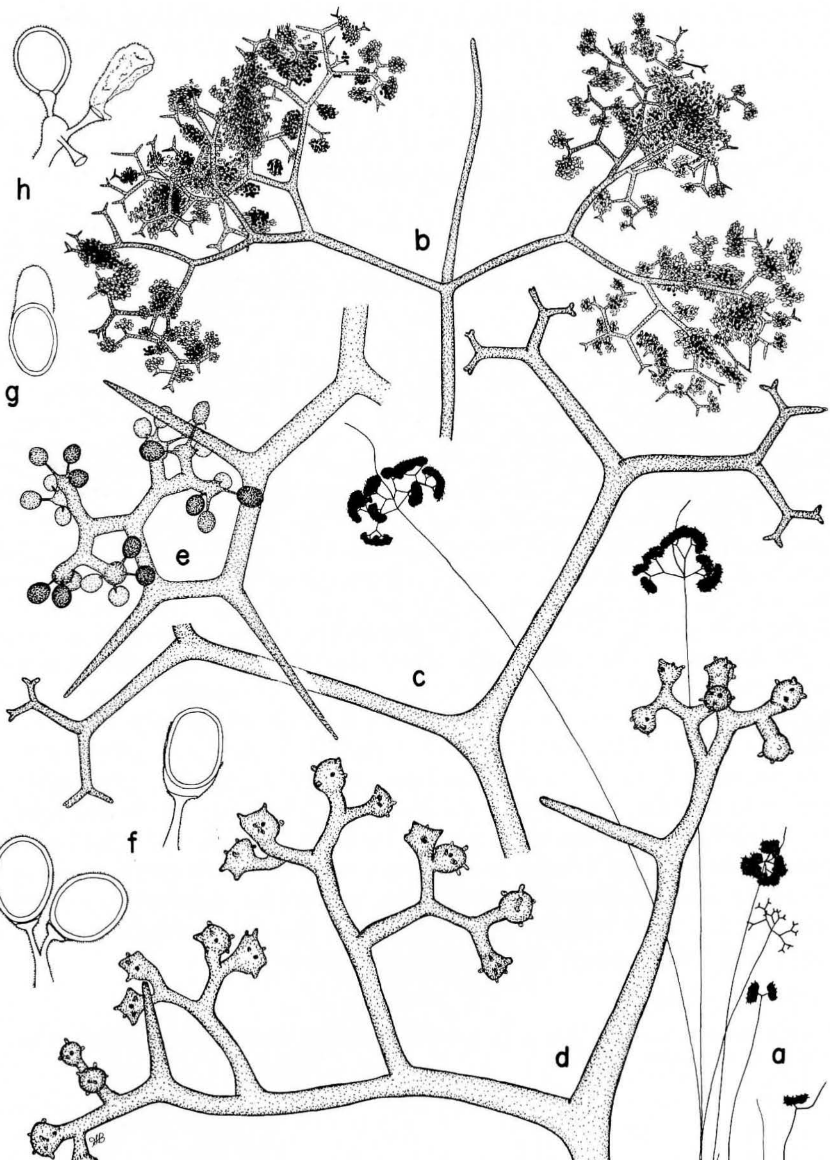
Fig. 12. *Dichotomocladium robustum.*—a. Habit sketches of sporophores. × 5.—b. Large fruiting head showing projecting spinose branchlets and abundant sporangiola. × 230.—c. Initial branchlets of a fertile head showing three-dimensional dichotomy. × 315.—d. Part of a dichotomous fertile branch showing sterile spines and fertile branchlets (right) ending in vesicles from which the sporangiola have become detached. × 1,200.—e. Typical zygospore and its elongate, slightly curved suspensors; note prominent gametangial remnants (RSA 1081– × 1346+). × 315.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Specimens examined.—INDIA. UTTAR PRADESH. Allahabad, soil, no date, 1960 or earlier, *B. S. Mehrotra & A. K. Sarbhoy* (type culture: RSA 1089; =NRRL 2912; =IMI 115181; =CBS 164.61). DELHI. Delhi, rabbit dung, June 15, 1965, *K. G. Mukerji* (RSA 1729).

Notes.—When Mehrotra and Sarbhoy (1960) described *Chaetocladium hesseltinii* they did not recognize the distinctly different branching pattern of its sporebearing branches in comparison with those of *C. brefeldii* and *C. jonesii*, i.e., dichotomous vs. verticillate. They listed two characteristics which they regarded as major differences between their species and the other two: (1) the absence of spines; and (2) the absence of growth at 7 C and poor growth at 20 C. In their illustrations, however, these authors did picture the spinose branches that result from arrested development of one or both arms of a dichotomy (their figs. 6–7). Mukerji recognized the spinose nature of some branchlets of the fruiting head when he reported his isolate of *C. hesseltinii* (Mukerji, 1969, figs. 2–3). The Mukerji isolate, in our experience, does tend to produce more sterile spines (Fig. 13e) than the type isolate of Mehrotra and Sarbhoy (Fig. 13b,d). We already have given our reasons for transferring *C. hesseltinii* to *Dichotomocladium.*

Dichotomocladium hesseltinii is readily distinguished from *D. elegans* and *D. robustum* by its large, *Piptocephalis*-like fertile heads (Fig. 13a,b). Except for the slightly angular fertile vesicles, the spore-bearing branchlets of *D. hesseltinii* are nearly identical to those of *D. elegans* and *D. robustum* (Fig. 14).

Our isolates of *D. hesseltinii* apparently are of the same mating type, for zygospores never have been induced on any of the media we have tried at temperatures ranging from 18 to 31 C.

ACKNOWLEDGMENTS

We thank all those persons who kindly collected and transmitted to us substrata from which many of the specimens cited in this work were obtained or who sent cultures or specimens of fungi. We also express our gratitude to the curators and other staff members of institutions from which cultures or specimens were obtained. Special thanks are due the following individuals for assistance rendered or information given while we were carrying out our

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Fig. 13. *Dichotomocladium hesseltinii.*—a. Habit sketches of sporophores. × 8.—b. Distal portion of a sporophore showing a sterile prolongation of the main axis and two fertile branch systems forming the fertile head. × 75.—c. Initial branches of a fertile branch system showing three-dimensional dichotomy. × 230.—d. Last several dichotomies of a fertile branch system. Only two branchlets have formed sterile spines; the others end in fertile vesicles which are in an early stage of sporangiole formation. × 1,210.—e. Last several branchlets of a fertile branch system (RSA 1729) showing sterile spines and fertile branchlets each giving rise distally to several sporangiola. × 900.—f–h. Sporangiola. Three still are attached to their subtending pedicels; two are in the process of being liberated from the delicate sporangiolar membrane. Note the small, broadly flattened columellae (*f*) and the remnant of a sporangiolar wall still attached to a pedicel after spore release (*h*) (drawn from KOH-phloxine preparation). × 1,360.

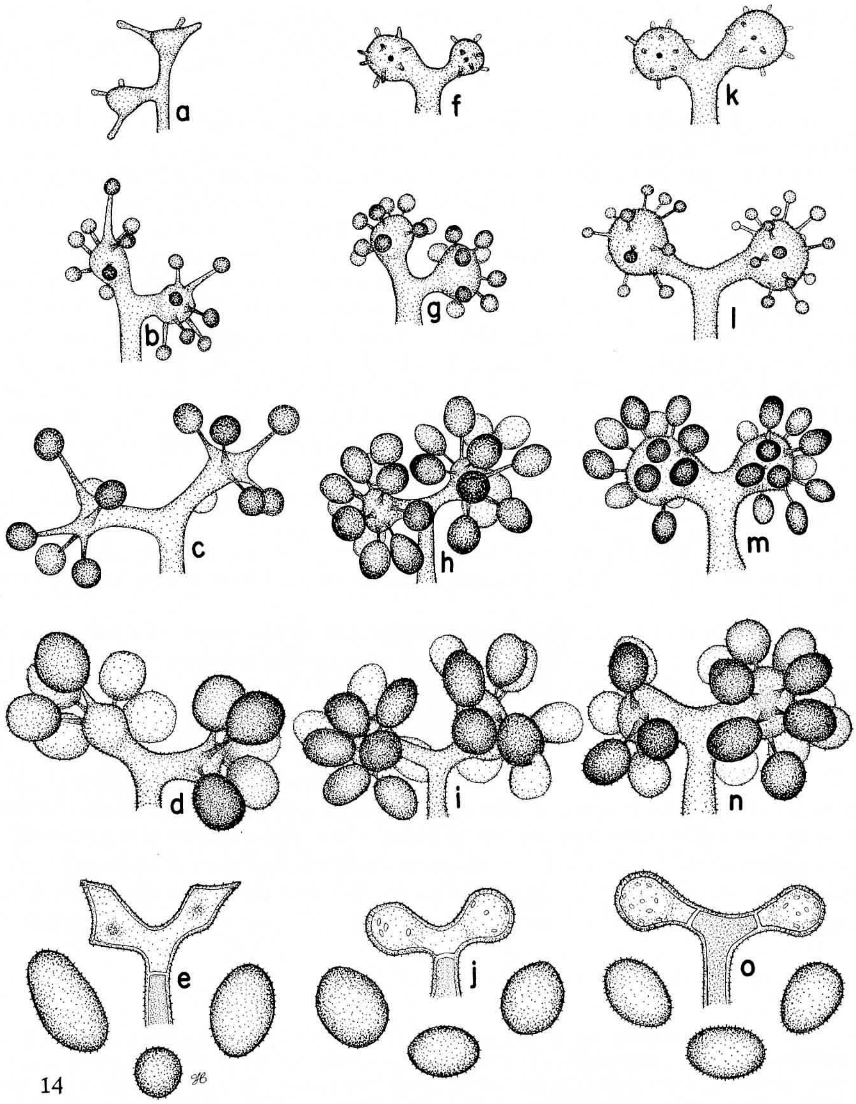

Fig. 14. *Dichotomocladium.* Several stages of development of sporangiola from fertile vesicles.—a–e. *D. hesseltinii.*—f–j. *D. robustum.*—k–o. *D. elegans.*—The final drawings in each series show mature sporangiola and shape of mature fertile vesicles, angular in *D. hesseltinii* (e), globoid in *D. robustum* (j) and *D. elegans* (o). (All × 1,670.)

investigations: L. A. Beljakova, K. P. Dumont, J. J. Ellis, L. Faurel, W. Gauger, C. W. Hesseltine, S. J. Hughes, A. A. Milko, M. Orsengio, W. Rau, H. Riedhl, M. A. A. Schipper, R. Siepman, E. G. Simmons, and H. P. Upadhyay.

The senior author acknowledges with thanks financial aid from traineeships provided by the Claremont Graduate School and the National Science Foundation. The junior author thanks the National Science Foundation for a grant (G-14273) that supported much of the preliminary work on which this study was based.

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