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LABOULBENIALES ON SEMIAQUATIC HEMIPTERA. III.
RHIZOPODOMYCES

Richard K. Benjamin

Abstract.—Thaxter's original description of *Rhizopodomyces* is emended to reflect new information gained from a study of not only the type species, *R. merragatae*, but also of six additional species described as new, *R. basifurcatus*, *R. californicus*, *R. erectus*, *R. geniculatus*, *R. mexicanus*, and *R. polhemusii*. All of the species have been found on semiaquatic bugs of the family Hebridae (Hemiptera). The female thallus of *Rhizopodomyces* spp. consists of a simple, two-celled receptacle, the suprabasal cell bearing a one-celled primary appendage and giving rise usually to a single, long-stalked perithecium. The male thallus initially consists of three cells, a two-celled receptacle and a terminal cell which may form a simple antheridium directly or remain sterile and form a simple appendage, in which case the suprabasal cell of the receptacle divides and forms one or two simple antheridia directly. *Rhizopodomyces* is compared with several other dioecious genera of Laboulbeniales of similar morphology, *Amorphomyces*, *Dioicomyces*, *Dicrandromyces*, *Triandromyces*, and *Tetrandromyces*. Speculations regarding the possible relationship of *Rhizopodomyces* to these genera are presented.

In the first of my earlier papers on Laboulbeniales parasitizing semiaquatic Hemiptera (Benjamin 1967, 1970), my treatment of the classification of Hemiptera followed that outlined by Brues, Melander, and Carpenter (1954) in which the order is divided into two suborders, Homoptera and Heteroptera. I am now following a system preferred by many entomologists which recognizes two orders, Homoptera and Hemiptera (=Heteroptera) (Comstock 1947; Borror, DeLong, and Tripelhorn 1976). In the latter treatment, the Hemiptera are divided into three suborders: (1) Hydrocorizae, long-horned bugs (Cryptocerata of authors) which are mostly aquatic or semiaquatic; (2) Amphibicorizae, short-horned bugs (Gymnocerata, in part, of authors) which are primarily semiaquatic or shore inhabiting; and (3) Geocorizae, short-horned bugs (Gymnocerata, in part, of authors) which are usually terrestrial. With regard to Laboulbeniales, no representative has as yet been found on any of the Homoptera, whereas several have been described on Hemiptera.

Coreomyces Thaxter (1902), with 19 described species, is restricted to Corixidae (water boatmen), and members of this genus are the only Laboulbeniales known on Hydrocorizae, which includes also the backswim-

mers (Notonectidae), pleid water bugs (Pleidae), creeping water bugs (Naucoridae), giant water bugs (Belostomatidae), waterscorpions (Nepidae), toad bugs (Gelastocoridae), and velvety shore bugs (Ochteridae). Only three of a large number of families included in the Geocorizae are known to harbor Laboulbeniales: *Hesperomyces lasiochili* (Thaxt.) Thaxt. (1931) occurs on *Lasiochilus pallidus* Reuter (Anthocoridae); *Corethromyces myodochae* Thaxt. (1931) has been described on *Myodocha unispinosa* Stal (Lygaeidae); and species of *Polyandromyces* Thaxt. (1931) are peculiar to *Coptosoma* spp. (Plataspidae). On the other hand, 16 species of Laboulbeniales have been characterized thus far on members of the Amphibicorizae: 10 species of *Laboulbenia* Mont. & Robin (Robin 1853), eight on Veliidae (broad-shouldered water striders or ripple bugs) and two on Macroveliidae (macrovelioid shore bugs) (Thaxter 1912; Benjamin 1967); two species of *Autophagomyces* Thaxt. (1912), one on Veliidae and one on Mesoveeliidae (water treaders) (Thaxter 1931; Benjamin 1970); one species of *Dioicomyces* Thaxt. (1901) on Mesoveeliidae (Benjamin 1970); two species of *Prolixandromyces* Benjamin (1970) on Veliidae; and one species of *Rhizopodomyces* Thaxt. (1931) on Hebridae (velvet water bugs). Laboulbeniales still have not been reported on the other families of Amphibicorizae: Gerridae (water striders), Hydrometridae (watermeasurers), Saldidae (shore bugs), and Sep-topodidae (spiny shore bugs).

My collection of Laboulbeniales includes a sizeable number of undescribed species on semiaquatic Hemiptera (Amphibicorizae). Many of these came to me through the courtesy of a number of people, several of whom were thanked in my earlier papers. Most of the material described in the present work was provided by two friends, Hugh B. Leech, formerly of the California Academy of Sciences, San Francisco, and John Polhemus, Englewood, Colorado, and The University of Colorado Museum, Boulder. As a guest in the home of Mr. and Mrs. Polhemus for a week during August, 1973, I was permitted to examine Mr. Polhemus's large holdings of aquatic and semiaquatic bugs for Laboulbeniales, and many of these fungi were obtained for study. The account of *Rhizopodomyces* presented here is based, for the most part, on specimens taken from various Hebridae received from Mr. Polhemus at that time or earlier. I also thank Dr. Donald H. Pfister, the Farlow Herbarium, Harvard University, for lending me Thaxter's collection of *R. merragatae*.

Descriptions and Commentary

Rhizopodomyces Thaxt., Mem. Amer. Acad. Arts Sci. 16: 60, 1931, emend.

Dioecious.

Male: Consisting initially of three superposed cells, the terminal cell forming a single, simple, flask-shaped antheridium; or the terminal cell function-

ing as a sterile primary appendage, the suprabasal cell dividing and forming one or two simple, flask-shaped antheridia and a subtending sterile cell.

Female: Consisting initially of three superposed cells; the terminal cell forming a simple primary appendage; the basal and suprabasal cells constituting the receptacle; the suprabasal cell giving rise distally to a divergent branch bearing a terminal perithecium; the basal cell, above the point of attachment to the host, often forming laterally divergent, lobate or rhizoid-like, nonseptate outgrowths. Perithecium with well-developed stalk cells and basal cells; basal cells persistent; outer wall consisting of three vertical rows of four cells each and one vertical row of five cells. Spores once septate.

Type species: *Rhizopodomyces merragatae* Thaxt.

The thalli of species of *Rhizopodomyces* typically develop on the upper surface of the host, mostly on the pronotum or hemelytra, although thalli may occasionally be found on the head, lower surface, or legs. The foot, i.e., the modified part of the basal cell (I) by which the fungus is attached to the host, is more or less appressed to the insect cuticle and may or may not become somewhat blackened (Fig. 1D; 2J; 4A, C-J; 5A-C, G-M; 6B, C, D, I, H, L-O). Host penetration appears to be effected by a simple haustorium which is easily broken at the juncture of fungus and host when a parasite is removed. In whole mounts, haustoria could not be detected in the more or less transparent hemelytra at the point of attachment of a fungus although a small, circular region centrally located at the base of the foot marks the point of entry of the haustorium into the host cuticle (Fig. 2D-I, K).

Ascospores, where these could be observed *in situ* on the host, appeared always to have been discharged in pairs as is usual in most monoecious and dioecious Laboulbeniales. Mature ascospores observed inside perithecia (Fig. 1F, I; 2L; 4B, M, N; 5F, N) did not exhibit marked dimorphism as has been observed in some dioecious species (Benjamin 1970: Fig. 3D). The spore destined to become the female individual enlarges more rapidly as it develops than does the one forming the male (Fig. 2A-D). Paired males and females remain closely associated throughout their development, and the two sexes often adhere to one another at the base when removed for study (Fig. 1A, D; 2J-K; 4A, C, E, H; 5A, G, I, L; 6I).

Maturation begins when the thalli reach the three-cell stage, which involves simply a single transverse division of the lower spore segment into the basal cell (I) and suprabasal cell (II) of the receptacle (Fig. 2E; 6B). In the male of five of the species studied, the terminal cell, i.e., the upper spore segment, is transformed into a single flask-shaped antheridium (Fig. 1C; 2E-J; 4I; 5B, H, J, M). In the other three taxa where males were observed, it functions as a sterile appendage which becomes more or less shriveled but persistent (Fig. 4D, F; 6B, C, D, I); the suprabasal cell then

Fig. 1. *Rhizopodomycetes merragatae*.—A–C. Lectotype specimen from Guatemala (Thaxter 1542).—A. Mature female individual and its associated male. The receptacle of the female consists of two cells: the basal cell (I) bearing elongate, rhizoidlike prolongations; and the suprabasal cell (II) supporting the elongate primary stalk cell (VI) of the perithecium $\times 400$.—B. Perithecium showing relationship of primary stalk cell (VI), secondary stalk cell (VII), and basal cells (m , n , n') to the four rows of outer wall cells. Note protrudent fifth cell of the five-celled row. Other details of perithecial cellular structure omitted. $\times 895$.—C. Male individual adherent to female at base near point of attachment of fungus to host. $\times 660$.—D–F. Costa Rican specimen (RKB 2698).—D. Mature female and associated male (broken distally). $\times 400$.—E. Perithecium in lateral view showing terminus of primary stalk cell (VI), secondary stalk cell (VII), basal cell m from which has arisen the posterior row of four wall cells, and basal cell n from which have arisen one lateral row of four wall cells and the anterior row of five wall cells (w^1 – w^5). Cell five of the anterior row (w^5) protrudes well beyond the apices of the terminal wall cells. $\times 895$.—G. Mature female and associated male (broken distally). $\times 400$.—H. Perithecium showing relationship of primary stalk cell (VI), secondary stalk cell (VII), and basal cells (m , n , n') to the four rows of outer wall cells. Note protrudent fifth cell of the five-celled row. Other details of perithecial cellular structure omitted. $\times 895$.—I. Male individual adherent to female at base near point of attachment of fungus to host. $\times 660$.—app. Appendix.

divides transversely and forms one or occasionally two distal antheridia having divergent efferent tubes (Fig. 4D, F; 6C, D, H, I, M). The primary appendage of the female has been observed in seven of the eight species studied, and it is always simple, more or less elongate, and somewhat clavate. It may be missing (Fig. 1A, D; 2J; 4A, G; 5A, C; 6D, H), be more or less persistent (Fig. 2K; 5G, L) although sometimes shriveled (Fig. 1G; 4J), or the distal part may slough away and only the basal part remain (Fig. 4C, E; 6I, O).

Material adequate for a study of the salient features of perithecial development was available only for *R. californicus*. The perithecial primordium arises from the upper end of cell II immediately below the primary appendage (Fig. 2F) which is shifted laterally and diverges from the upper end of the receptacle during maturation of the perithecium (Fig. 2F–H, K). The perithecial branch divides distally (Fig. 2F; 3A), forming a small terminal cell (*i*), the primordial cell of the procarp from which will be derived the female sexual organ, and an elongate cell (*h*), the primordial cell of the perithecium from which will arise the stalk cells and basal cells of the perithecium. Cell *i* divides transversely and forms the trichophoric cell (*tc*) above and the carpogenic cell (*cp*) below (Fig. 2G; 3B). The trichophoric cell elongates distally and cuts off a slender, more or less recurved, simple trichogyne (*tr*) (Fig. 2H; 3C, D). Subsequently, the inner and outer wall cells of the perithecium will grow upward and around the carpogenic cell (Fig. 3G–I) which constitutes the carpogonium and from which the asci will derive (Fig. 3J).

Development of the perithecial wall begins with the delimitation of a small cell (*j*) which is cut off diagonally from the upper end of cell *h* (Fig. 2G; 3B). Cell *h* then cuts off a second small cell (*m*) which lies more or less adjacent to cell *j* (Fig. 2H; 3D). Cell *h* now is termed the primary stalk cell of the perithecium (VI). Cell *j* then delimits two smallish cells (*n*, *n'*) which are displaced upwardly to the right and left so that they lie more or less side by side (Fig. 2I–K; 3E). Cell *j* now is termed the secondary stalk cell of the perithecium (VII). Cells *m*, *n*, and *n'* constitute the basal cells of the perithecium.

Perithecial wall development continues with the delimitation by cells *m*, *n*, and *n'* of the primary wall cells (*o*) (Fig. 3E). In *R. californicus* these

←

cells of the adjacent rows. $\times 895$.—F. Ascospores. $\times 1,360$.—G–I. Mexican specimen (RKB 2705A).—G. Mature female showing shriveled appendage (*app*). $\times 400$.—H. Perithecium, somewhat flattened, showing relationship of primary stalk cell (VI), secondary stalk cell (VII), basal cells *m* and *n'*, and outer rows of wall cells; cell *n* and its two associated rows of wall cells are on the opposite side of the perithecium as shown. $\times 895$.—I. Ascospores. $\times 1,360$. (Further details are given in the text.)

cells elongate considerably during which time the trichogyne shrivels and is carried downward on the posterior side of the perithecium, the carpogenic cell (*cp*) elongates and the first parietal or inner wall cells (*pc*), which also arise from the basal cells, are formed between the carpogenic cell and the primary wall cells (Fig. 3F–G). No attempt was made in this study to trace the further development of the inner wall cells or the ascogenous system. As the perithecium elongates, additional outer wall cells (w^1 – w^5) are delimited (Fig. 3H–J) until finally there are three vertical rows of four cells and one of five cells (Fig. 3K–M). Cell *m* gives rise to a single posterior row of four cells which always lies adjacent to the remnant of the trichogyne borne on the surface of the perithecium (Fig. 2K; 3I, K); cell *n* gives rise to two rows of cells, a lateral row of four and an anterior row of five (Fig. 3K–M); and cell *n'* gives rise to the other lateral row of four cells (Fig. 3K–M). The position of cells *n* and *n'* relative to cell *m* may vary, *n* being dextral and *n'* sinistral in one individual and vice versa in another individual.

In maturing females of all the species of *Rhizopodomycetes* studied, the lower cell of the receptacle produces two or three basal protrusions that may elongate and become more or less rhizoidlike (Fig. 1A, D, G; 2J, K; 4A, C, E, G, H, J; 5A, C, G, I, L; 6H, I, L, N, O). These outwardly extending structures appear to maintain close contact with the host surface but nowhere penetrate the integument. They most likely serve as buffer organs or props that help maintain the thallus in an erect posture.

Key to the species of *Rhizopodomycetes*

- A. Basal cell *m* of perithecium growing upward distally and forming a conspicuous free appendage 8. *Rhizopodomycetes* sp.
- Basal cell *m* not forming a free appendage B
- B. Primary stalk cell of perithecium one half to two or more times longer than perithecium and its included basal cells C
- Primary stalk cell of perithecium usually shorter than perithecium and its basal cells E

Fig. 2. *Rhizopodomycetes californicus* (RKB 1991).—A–D. Paired male and female individuals showing development of attachment organ (foot) prior to first division of basal cell. Note more rapid enlargement of the female as development begins. $\times 1,080$.—E–I. Early and intermediate stages of development of the female. Note that the associated male is fully developed at about the time the female sexual organ presumably is mature (H). Further details and terminology are given in the text. E–H, $\times 1,080$; I, $\times 660$.—J. Paired mature male and female individuals. The primary appendage of the female is missing. The perithecium is shown in surface view. $\times 895$.—K. Paired mature male and female individuals. The perithecium is shown in optical section. The primary appendage (*app*) still is attached to the suprabasal cell (II) of the receptacle. $\times 660$.—L. Ascospores. $\times 1,360$.

- C. Stalk cell usually 2–3 times longer than perithecium; cell 5 of anterior row of outer wall cells of perithecium forming a fingerlike projection at perithecial apex 1. *R. merragatae*
- Stalk cell less than 2 times longer than perithecium; cell 5 of anterior row of wall cells not conspicuously protrudent D
- D. Perithecium geniculate; basal cell *m* of perithecium conspicuously enlarged and rounded externally; receptacular rhizoids poorly developed 3. *R. geniculatus*
- Perithecium not geniculate, cell *m* not enlarged; receptacular rhizoids two, well developed, projecting at an acute angle from one another 7. *R. basifurcatus*
- E. Perithecium not geniculate, its long axis continuous with that of its primary stalk cell, its posterior and anterior margins about equally convex 2. *R. californicus*
- Perithecium more or less geniculate, posterior margin more strongly convex than anterior margin which may be nearly straight or slightly concave F
- F. Basal cells of perithecium prominent, relatively large and externally rounded, especially cells *m* and *n* 5. *R. mexicanus*
- Basal cells of perithecium not conspicuously rounded externally G
- G. Receptacle and primary stalk cell of perithecium forming a nearly straight axis; basal cell of receptacle two times longer than wide 4. *R. erectus*
- Receptacle and primary stalk cell of perithecium more or less geniculate; basal cell of receptacle no longer than wide 6. *R. polhemusii*

1. *Rhizopodomyces merragatae* Thaxt., Mem. Amer. Acad. Arts Sci. 16: 60, 1931, emend. FIG. 1

Male: Hyaline, faintly yellowish; receptacle nearly uniform in diam, attenuated near base; basal cell curved, about twice as long as the suprabasal cell; antheridium terminal, only slightly shorter than the basal cell. Total length 38–43 μm ; ca. 4–5 μm wide.

Female: Hyaline, faintly yellowish, usually somewhat curved, especially below; basal cell only slightly longer than wide, 15–25 $\times$ 10–18 μm , with 2–3 basal rhizoidlike prolongations radiating irregularly, these 30–50 μm long, 9–12 μm wide at the base, 5–8 μm wide near the tip; suprabasal cell up to three or more times longer than the basal cell, 35–95 $\times$ 10–25 μm , bearing distally the laterally divergent, simple primary appendage; well-developed appendages not observed; primary stalk cell of the perithecium elongate, two times or more as long as the suprabasal cell, with which its long axis is continuous, 107–165 $\times$ 10–18 μm ; perithecium in line with the long axis of the primary stalk cell, its basal cells well defined and usually somewhat rounded externally, its posterior and anterior margins about equally convex, tapered distally, 48–77 $\times$ 16–30 μm , including basal cells;

Fig. 3. *Rhizopodomycetes californicus* (RKB 1991).—A–J. Early and intermediate stages of development of the perithecium. Details and terminology are given in the text. A–H, J, $\times 1,080$; I, $\times 895$.—K–M. Three more or less flattened perithecia as observed in three different positions and showing relationship of stalk cells (VI, VII) and basal cells (m, n, n') to the four rows of outer wall cells. Other details are given in the text. $\times 895$.

outer rows of wall cells straight or somewhat spirally arranged; posterior and lateral rows consisting of four cells each; anterior row consisting of five cells, the terminal cell protruding as a fingerlike projection. Total length 225–330 μm . Ascospores $18\text{--}25 \times 3\text{--}3.5 \mu\text{m}$.

Specimens examined.—GUATEMALA; Izabal: Los Amates (*Thaxter* 1542, Acc. No. 3819, lectotype, FH), on hemelytra of *Merragata brevis* Champion.—COSTA RICA: Boca de Barranca, 7 Jan. 1970, J. T. Polhemus coll. (CL 1303); on hemelytra of *Hebrus* sp.; RKB 2698; slide in RSA.—MEXICO; Chiapas: San Cristóbal las Casas, 2 May 1965, J. T. Polhemus coll. (CL 1078); on pronotum of *Hebrus bilineatus* Champion; RKB 2705A; slides in RSA.

Thaxter's description of this species was based on two mature females and their accompanying males. Both specimens were figured by Thaxter (1931, Pl. XIV, Figs. 17–18) and, according to records accompanying the Thaxter Collection at the Farlow Herbarium, the individual shown in his Fig. 18 represents the holotype. The slide bearing this specimen (Acc. No. 3818) has been lost according to Dr. Pfister. The other specimen (Acc. No. 3819), here designated the lectotype, is represented in Thaxter's Fig. 17 and my Fig. 1A–C.

The type collection of *R. merragatae* was found on *Merragata brevis*, whereas the other two collections cited above were found on species of *Hebrus*. These two genera of small, shore-inhabiting bugs are differentiated primarily on antennal characteristics. They are otherwise similar and their separation may be for no other good reason than taxonomic convenience (Usinger 1956). Of two mature specimens from the Costa Rican collection, only one was intact and is shown in Fig. 1D–F (RKB 2698). Except for having two rather than three basal rhizoidlike prolongations and straight rather than slightly spiraled rows of outer wall cells this specimen seems hardly separable from the type. Three mature females make up the Mexican collection (RKB 2705A), and of these only one (Fig. 1G–I) is in good condition. Except for being somewhat larger, these specimens seem sufficiently like the type to be identified with it.

Rhizopodomyces merragatae most closely resembles *R. californicus* in the shape of its perithecium and the protrudent terminal cell of the 5-celled row of wall cells. It is readily distinguished from this and the other species of the genus by its relatively very long perithecial stalk cell and from all but *R. californicus* by the conformation of its perithecium.

2. *Rhizopodomyces californicus* Benjamin, sp. nov.

FIG. 2–3

Mas: Hyalinus, albidus, 25–37 μm in tota longitudine, 4.5–6 μm in diametro; diametrum receptaculi prope uniforme; cellula basilaris receptaculi plus minusve curvata, 8–16(–18) μm longa; cellula suprabasilaris receptaculi 5–7(–8) μm longa; antheridium terminale 10–14(–18) μm longum.

Femina: Hyalina, albida, 132–200 μm in tota longitudine; axis aliquantum curvatus; cellula basilaris receptaculi 12–30 $\times$ 8–16 μm 2–3 rhizoideos basilaria 6–22 $\times$ 5–8 μm gignens; cellula suprabasilaris receptaculi 30–50 $\times$ 9–16 μm ; appendix primaria simplex recta vel leniter curvata clavata 20–30 $\times$ 5–10 μm ; stipes perithecii 35–60 $\times$ 9–13(–16) μm ; perithecium 45–60(–70) $\times$ 18–25(–30) μm attenuatum ad apicem, marginibus anticis et posticis prope aequae convexis, cellulis basilaribus leniter extra rotundatis; series cellulosa posticae et laterales parietis ex 4 cellulis constantes; series cellulosa antica parietis ex 5 cellulis constans, cellula terminali processum digitiformem facienti. Ascosporae 15–20 $\times$ 3–4 μm . Typus *RKB 1991* (RSA).

Male: Hyaline, whitish, receptacle nearly uniform in diam, slightly constricted at septa; basal cell more or less curved, about two times longer than the suprabasal cell; antheridium terminal, typically longer than the suprabasal cell, often equalling the basal cell. Total length 25–37 μm ; ca. 4.5–6 μm wide.

Female: Hyaline, whitish; usually somewhat curved, basal cell about two times longer than wide, 12–30 $\times$ 8–16 μm , with two to three basal lobate or more or less elongate projections radiating irregularly, these 6–22 μm long, ca. 5–8 μm wide; suprabasal cell usually two times as long as the basal cell, 30–50 $\times$ 9–16 μm , bearing distally the laterally divergent, simple, straight or slightly curved, clavate primary appendage, 20–30 $\times$ 5–10 μm ; primary stalk cell of the perithecium usually only slightly longer than the suprabasal cell, with which its long axis is continuous, 35–60 $\times$ 9–13(–16) μm ; perithecium in line with the long axis of the primary stalk cell, its basal cells well defined and barely rounded externally, its posterior and anterior margins about equally convex, tapered distally, 45–60(–70) $\times$ 18–25(–30) μm including basal cells; outer rows of wall cells nearly straight; posterior and lateral rows consisting of four cells each; anterior row consisting of five cells, the terminal cell protruding as a fingerlike projection. Total length 132–200 μm . Ascospores 15–20 $\times$ 3–4 μm .

Holotype.—U.S.A.; California; San Bernardino Co. Mojave River nr. Victorville, 12 Feb. 1956, R. K. Benjamin coll.; on pronotum and hemelytra of *Merragata hebroides* White; *RKB 1991* (holotype, Fig. 2K); slide in RSA.

Other specimens examined.—U.S.A.; California. Data as for the holotype, *RKB 1991* (isotypes); slides in RSA.—San Louis Obispo Co., Oso Flaco Lake, 5 Feb. 1953, J. D. Lattin coll.; on pronotum and hemelytra of *Merragata hebroides*; *RKB 2672*; slide in RSA.

Rhizopodomycetes californicus is the only species discussed in this paper for which an adequate sample of specimens was available for determining the probable true range of variation of thallus dimensions (31 females from the type locality were measured) and for observing early stages of development as discussed above. This species most closely resembles *R. merragatae* in the conformation of its perithecium. In both species the posterior and anterior perithecial margins are about equally convex and cell five of

Fig. 4. A–F. *Rhizopodomycetes geniculatus* (RKB 2695).—A, C, E. Mature females with associated males. $\times 400$.—B. Perithecium of female shown in A (optical section); note relatively large basal cell *m*. $\times 895$.—D, F. Mature males associated with females figured in C and A respectively. Note somewhat shriveled primary appendages (*app*) derived from the terminal spore segment and the formation of one or two antheridia (*an*) from the suprabasal cell of the receptacle. $\times 915$.—G. Mature female (Arizona collection: RKB 2704). $\times 400$.—H–N. *Rhizopodomycetes erectus* (RKB 2696B).—H. Mature female and associated male; the upper part of the primary appendage of the female is missing. $\times 400$.—I. Male individual from H showing

the anterior row of wall cells is conspicuously protrudent (Fig. 1B, E, H; 2J, K; 3K–M). The primary perithecial stalk cell of *R. merragatae* is two or more times as long as either its perithecium or the suprabasal cell of its receptacle, whereas in *R. californicus* the stalk cell and suprabasal cell are about equal in length. In the latter species the perithecium commonly is longer than its primary stalk cell (Fig. 2J, K). On the basis of material at hand for study, the prolongations arising from the basal cell of *R. merragatae* (Fig. 1A, D, G) are more elongate and rhizoidlike than those of *R. californicus* (Fig. 2I–K).

3. *Rhizopodomycetes geniculatus* Benjamin, sp. nov.

FIG. 4A–F

Mas: Hyalinus, albidus, 31–36 μm in tota longitudine; diametrum thalli prope uniforme, cellulis leniter extra rotundatis; cellula terminalis sterilis appendicem simplicem elongatam plus minusve clavatam ca. $8\text{--}9 \times 4.5 \mu\text{m}$ formans; cellula suprabasilaris receptaculi 1–2 antheridia et cellulam suprabasilem secundariam formans; cellula basilaris receptaculi $13\text{--}15 \times 5.5\text{--}6.5 \mu\text{m}$.

Femina: Hyalina, albida, 175–215 μm in tota longitudine; axis uniformiter moderate curvatus; cellula basilaris receptaculi $20\text{--}30 \times 12\text{--}18 \mu\text{m}$, 1–2 projecturam basilem $8\text{--}10 \times 6\text{--}7 \mu\text{m}$ formans; cellula suprabasilaris receptaculi $40\text{--}55 \times 10\text{--}13 \mu\text{m}$; appendix primaria non observata; stipes perithecii $65\text{--}75 \times 9\text{--}14 \mu\text{m}$; perithecium fortiter geniculatum $44\text{--}57 \times 14\text{--}25 \mu\text{m}$ attenuatum ad apicem, margine postico fortiter convexo, margine antico concavo; cellula basilaris *m* perithecii grandis elongatis, margine externo fortiter convexo; series cellulosa posticae et laterales parietis ex 4 cellulis constantes; series cellulosa antica parietis ex 5 cellulis constans, cellula terminali non fere protrudenti. Ascospores ca. $17 \times 3 \mu\text{m}$. Typus *RKB 2695* (RSA).

Male: Hyaline, whitish, nearly uniform in diameter, cells slightly rounded externally between septa; terminal cell sterile, forming a simple, elongate, more or less clavate appendage ca. $8\text{--}9 \times 4.5 \mu\text{m}$; suprabasal cell dividing distally and forming one or two superposed antheridia having divergent efferent tubes; the resulting suprabasal cell and the basal cell subequal. Total length to tip of antheridium 31–36 μm ; ca. $5.5\text{--}6.5 \mu\text{m}$ wide.

Female: Hyaline, whitish, uniformly curved from foot to base of perithecium; basal cell about two times longer than wide, $20\text{--}30 \times 12\text{--}18 \mu\text{m}$, with one or two basal projections, these hardly longer than wide, $8\text{--}10 \times 6\text{--}7$

←

terminal antheridium (*an*). $\times 915$.—J. Mature female showing intact though somewhat shriveled primary appendage (*app*). $\times 400$.—K–L. Perithecium of specimen shown in H as seen in optical section and surface view. Figure 5L shows the relationship of the wall cells ($w^1\text{--}w^3$) to the basal cells (*m*, *n*, *n'*) and stalk cells (VI, VII). $\times 895$.—M–N. Ascospores. $\times 1,360$.

μm ; suprabasal cell about two times longer than the basal cell, $40\text{--}55 \times 10\text{--}13 \mu\text{m}$, with a more or less conspicuous subapical, posterior protrusion subtending the primary appendage; intact appendages not observed; primary stalk cell of the perithecium about 1.5 times longer than the suprabasal cell, with which its long axis is continuous, $65\text{--}75 \times 9\text{--}14 \mu\text{m}$; perithecium geniculate, its posterior margin strongly convex, its anterior margin concave, its basal cells well defined, cell *m* strongly convex externally and ca. 2–2.5 times longer than the secondary stalk cell, tapered distally, the apical $\frac{1}{2}$ to $\frac{1}{3}$ bent downward slightly, $44\text{--}57 \times 14\text{--}25 \mu\text{m}$ including basal cells; outer rows of wall cells nearly straight; posterior and lateral rows consisting of four cells each; anterior row consisting of five cells, the terminal cell hardly projecting beyond the terminal cells of the other rows. Total length 175–215 μm . Ascospores ca. $17 \times 13 \mu\text{m}$.

Holotype.—COSTA RICA; Guanacaste: 4 mi N of La Cruz, 8 Jan. 1970, J. T. Polhemus coll. (CL 1307); on right hemelytron of *Hebrus* sp.; RKB 2695 (holotype, Fig. 4C, D; isotypes, Fig. 4A, E, F); slide in RSA.

Other specimen examined.—U.S.A.; Arizona; Yavapa Co.: Castle Hot Springs, 1 Oct. 1954, J. T. Polhemus coll.; on right hemelytron of *Hebrus* sp.; RKB 2704; slide in RSA.

Three mature females with their accompanying males from the type locality (Fig. 4A, C, E) and one mature female from Arizona (Fig. 4G) constitute the material upon which the description of *R. geniculatus* is based. The strongly geniculate perithecium with its prominent, externally rounded basal cell *m* (Fig. 4B) readily distinguishes the species from its congeners. Each of the three males observed bore a somewhat shriveled appendage (Fig. 4D, F) undoubtedly derived from the terminal segment of the spore. In one male, two antheridia (Fig. 4A, F) rather than one (Fig. 4C, D) had developed from the suprabasal cell of the receptacle.

4. *Rhizopodomycetes erectus* Benjamin, sp. nov.

FIG. 4H–N

Mas: Hyalinus, luteolus, ca. 39 μm in tota longitudine; cellula basilaris receptaculi $16 \times 7 \mu\text{m}$ infra attenuata; cellula suprabasilaris receptaculi $10 \times 7 \mu\text{m}$ externe rotundata; antheridium terminale $13 \times 6 \mu\text{m}$.

Femina: Hyalina, luteola, 157–171 μm in tota longitudine; axis prope rectus; cellula basilaris receptaculi $28 \times 13\text{--}15 \mu\text{m}$ 3 rhizoideos basilaria $22\text{--}28 \times 5\text{--}8 \mu\text{m}$ gignens; cellula suprabasilaris receptaculi $34\text{--}42 \times 18 \mu\text{m}$; appendix primaria simplex erecta elongata $31 \times 7 \mu\text{m}$; stipes perithecii $40\text{--}43 \times 15\text{--}17 \mu\text{m}$; perithecium leniter geniculatum $55\text{--}58 \times 21\text{--}22 \mu\text{m}$ attenuatum ad apicem, margine postico fortiter convexo, margine antico leniter convexo vel paene plano, cellulis basilaribus non fere externe rotundatis; series cellulosa posticae et laterales parietis ex 4 cellulis constantes; series cellulosa antica parietis ex 5 cellulis constans, cellula terminali fortiter protudenti. Ascosporae $21\text{--}25 \times 4\text{--}4.5 \mu\text{m}$. Typus RKB 2696B (RSA).

Male: Hyaline, pale yellowish, basal cell attenuated below, somewhat longer than the suprabasal cell, which is wider and slightly rounded externally; antheridium terminal, only slightly longer than the suprabasal cell. Total length $39\text{ }\mu\text{m}$; ca. $6\text{--}7\text{ }\mu\text{m}$ wide.

Female: Hyaline, pale yellowish, receptacle and primary stalk cell forming a nearly straight axis; basal cell about two times longer than wide, $28 \times 13\text{--}15\text{ }\mu\text{m}$, with three basal rhizoidlike prolongations, $22\text{--}28 \times 5\text{--}8\text{ }\mu\text{m}$, radiating at nearly equal angles from one another; suprabasal cell slightly longer than the basal cell, $34\text{--}42 \times 18\text{ }\mu\text{m}$, bearing distally the elongate primary appendage, ca. $31 \times 7\text{ }\mu\text{m}$, which projects upwardly and nearly parallels the stalk cell; primary stalk cell of the perithecium only slightly longer than the suprabasal cell, $40\text{--}43 \times 15\text{--}17\text{ }\mu\text{m}$; perithecium very slightly geniculate, its basal cells well defined and barely rounded externally, its posterior margin strongly convex, its anterior margin slightly convex to nearly plane, tapered distally, $55\text{--}58 \times 21\text{--}22\text{ }\mu\text{m}$ including basal cells; outer rows of wall cells nearly straight; posterior and lateral rows consisting of four cells each; anterior row consisting of five cells, the terminal cell projecting well beyond the apices of the terminal cells of the other rows. Total length $157\text{--}171\text{ }\mu\text{m}$. Ascospores $21\text{--}25 \times 4\text{--}4.5\text{ }\mu\text{m}$.

Holotype.—COSTA RICA; Puntarenas: 31 mi S of San Isidro del General, 6 Jan. 1970, J. T. Polhemus coll. (CL 1302); on upper surface of head and pronotum of *Hebrus* sp.; RKB 2696B (holotype, Fig. 4H, I); RKB 2696A (isotype, Fig. 4J); slides in RSA.

One immature and two mature females and one male of *R. erectus* have been studied. The species is readily distinguished from the other three species of *Rhizopodomyces* in which the length of the perithecium equals or exceeds that of either the primary stalk cell of the perithecium or the suprabasal cell of the receptacle (*R. californicus*, *R. mexicanus*, and *R. polhemusii*) by its erect, nearly straight thallus and the conformation of its perithecium. Like *R. californicus*, cell five of the anterior row of outer wall cells in *R. erectus* is conspicuously protrudent but the perithecium is less symmetrical and is very slightly geniculate (Fig. 2J, K; 4J, H). The perithecia of both *R. mexicanus* and *R. polhemusii* are considerably more geniculate than those of *R. erectus* and their length-to-width ratio is somewhat less (2:1 compared to about 2.5:1). The basal cells and secondary stalk cell of the perithecium of *R. mexicanus* are relatively large and more prominently rounded externally (Fig. 5D, E) than in either *R. erectus* (Fig. 4K, L) or *R. polhemusii* (Fig. 5K).

5. *Rhizopodomyces mexicanus* Benjamin, sp. nov.

FIG. 5A–F

Mas: Hyalinus, $44\text{--}46\text{ }\mu\text{m}$ in tota longitudine; diametrum receptaculi prope uniforme; cellula basilaris receptaculi ca. $19 \times 6\text{ }\mu\text{m}$; cellula suprabasilaris receptaculi $9\text{--}11 \times 6\text{ }\mu\text{m}$; antheridium terminale ca. $16 \times 5.5\text{--}6\text{ }\mu\text{m}$.

Fig. 5. A–F. *Rhizopodomyces mexicanus* (RKB 2705B).—A. Mature female and associated male. $\times 400$.—B. Male individual from A showing terminal antheridium (an). $\times 895$.—C. Mature female. $\times 400$.—D–E. Perithecium of specimen shown in C as seen in optical section and surface view. Although cell *m* and its associated lateral row of four cells and anterior row of five cells are depicted in solid rather than stippled outline, they actually are positioned on the opposite side of the perithecium as shown. In all other figures, cells shown in solid outline are nearest the viewer. $\times 895$.—F. Ascospores. $\times 1,360$.—G–N. *Rhizopodomyces polhemusii* (RKB 2703).—G, H, I, J, L, M. Three mature females and their accompanying males shown together and the males separately. The distinctive, broadly clavate primary appendages still are attached to the suprabasal cells of the females in G and L. G, I, L, $\times 400$; H, J, M, $\times 895$.—K. Perithecium of specimen shown in G as seen in optical section. $\times 895$.—N. Ascospores. $\times 1,360$.

Femina: Hyalina, luteola, 128–131 μm in tota longitudine; axis leniter curvatus; cellula basilaris receptaculi supra aliquantum amplificata 2 rhizoideos basilaria 50–72 μm longa, 7–8 μm in diametro ad basin, 4 μm in diametro ad apicem, gignens; cellula suprabasilaris receptaculi 30–32 $\times$ 10–13 μm ; appendix primaria non observata; stipes perithecii 27–32 $\times$ 10–12

μm ; perithecium moderate geniculatum $42\text{--}44 \times 20\text{--}23 \mu\text{m}$ attenuatum ad apicem, margine postico fortiter convexo, margine antico leniter concavo, cellulis basilaribus, apprime cellula *m*, externe bene rotundatis; series cellulosa posticae et laterales parietis ex 4 cellulis constantes; series cellulosa antica parietis ex 5 cellulis constans, cellula terminali non protrudenti. Ascosporae $25\text{--}27 \times 3.5\text{--}4 \mu\text{m}$. Typus *RKB 2705B* (RSA).

Male: Hyaline, receptacle nearly uniform in diam; slightly constricted at the septa; basal cell about two times longer than the suprabasal cell, antheridium terminal, about half again as long as the suprabasal cell. Total length $44\text{--}46 \mu\text{m}$; ca. $5.5\text{--}6 \mu\text{m}$ wide.

Female: Hyaline, pale yellowish, axis formed by the receptacle and primary stalk cell curved slightly; basal cell about two times longer than wide, slightly inflated above, $22\text{--}25 \times 13 \mu\text{m}$, with two basal rhizoidlike lateral prolongations $50\text{--}72 \mu\text{m}$ long, $7\text{--}8 \mu\text{m}$ wide at the base, $4 \mu\text{m}$ wide near the tip; suprabasal cell about one-third longer than the basal cell, $30\text{--}32 \times 10\text{--}13 \mu\text{m}$; primary appendage not observed; primary stalk cell of the perithecium about as long as the suprabasal cell, $27\text{--}32 \times 10\text{--}12 \mu\text{m}$; perithecium moderately geniculate, its basal cells well defined and prominently rounded externally, especially cell *m*, its posterior margin strongly convex, its anterior margin slightly concave, tapered to its unmodified apex, $42\text{--}44 \times 20\text{--}23 \mu\text{m}$ including basal cells; outer rows of wall cells nearly straight; posterior and lateral rows consisting of four cells each; anterior row consisting of five cells, the terminal cell not protruding beyond the apices of the terminal cells of the other rows. Total length $128\text{--}131 \mu\text{m}$. Ascospores ca. $25\text{--}27 \times 3.5\text{--}4 \mu\text{m}$.

Holotype.—MEXICO; Chiapas: San Cristóbal las Casas, 2 May 1964, J. T. Polhemus coll. (*CL 1078*); on right hemelytron of *Hebrus bilineatus* Champion; *RKB 2705B* (holotype Fig. 5A, B; isotype, Fig. 5C); slide in RSA.

Five females, four mature and one immature, and three males (*RKB 2705B*) of this species were found on the same host that bore specimens here identified as *R. merragatae* (*RKB 2705A*; Fig. 1G–I). Two of the mature females were in poor condition, one having the basal part missing. The male of *R. mexicanus* is relatively very large, nearly equaling the length of the receptacle of the female (Fig. 5A). Although the two females illustrated (Fig. 5A, C) bear only one intact or broken rhizoidal prolongation, they have scars on the basal cells marking the location of second rhizoids broken off, probably, when the specimens were being removed from the host for mounting. The immature female, not figured, clearly has two basal rhizoids. The perithecium with its strongly convex posterior margin, slightly concave anterior margin, and especially the prominent basal cells (Fig. 5D–E) distinguish *R. mexicanus* from the other species. Unfortunately, the primary appendage was absent from all females.

6. *Rhizopodomyces polhemusii* Benjamin, sp. nov.

FIG. 5G-N

Mas: Hyalinus, 23–30 μm in tota longitudine; cellulae receptaculi subaequales externe rotundatae, cellula basilari 7–9 $\times$ 7–8 μm , cellula suprabasilaris 6–9 $\times$ 6–7 μm ; antheridium terminale 10–13 $\times$ 5–8 μm .

Femina: Hyalina, luteola, 105–115 μm in tota longitudine; axis plus minusve geniculatus; cellula basilaris receptaculi 7–10 $\times$ 10 μm 2 rhizoideos basilaria 44–55 μm longa, ca. 7 μm in diametro ad basin, ca. 5 μm in diametro ad apicem, gignens; cellula suprabasilaris receptaculi 20–22 $\times$ 13–17 μm ; appendix primaria late clavata vel obovata 18 $\times$ 12–13 μm in latere postico cellulae suprabasilaris genita; stipes perithecii 33–40 $\times$ 12–17 μm ; perithecium moderate geniculatum 40–45 $\times$ 20–24 μm attenuatum ad apicem, paginis posticis et lateralibus brunneo-aurantiacus, margine postico fortiter convexo, margine antico paene plano vel ad basin leniter convexo; cellulae apicales consimiles. Ascosporae 16–19 $\times$ 2.5 μm . Typus *RKB 2703* (RSA).

Male: Hyaline, basal and suprabasal cells subequal, externally convex; antheridium terminal, somewhat longer than either cell of the receptacle. Total length 23–30 μm ; ca. 5–8 μm wide.

Female: Hyaline, pale yellowish, the posterior and lateral median surfaces of the perithecium with a brownish-orange suffusion; axis formed by the receptacle and primary stalk cell more or less geniculate; basal cell no longer than wide, 7–10 $\times$ 10 μm , with two nearly opposite, basal, rhizoidlike prolongations 44–55 μm long, ca. 7 μm wide at the base, ca. 5 μm wide near the tip; suprabasal cell slightly wider than and two times longer than the basal cell, 20–22 $\times$ 13–17 μm ; primary appendage broadly clavate to obovate, 18 $\times$ 12–13 μm , borne near the middle of the posterior side of the suprabasal cell from which it projects nearly at right angles; primary stalk cell of the perithecium 1.5 to 2 times longer than the suprabasal cell, 33–40 $\times$ 12–17 μm ; perithecium moderately geniculate, its basal cells well defined but inconspicuous, its posterior margin strongly convex, its anterior margin nearly straight or very slightly rounded below, tapered to the relatively unmodified apex, 40–45 $\times$ 20–24 μm including basal cells. Total length 105–115 μm . Ascospores 16–19 $\times$ 2.5 μm .

Holotype.—MEXICO; Sinaloa: 103 mi W of Durango, 1964, J. T. Polhemus coll. (*CL 1017*); on upper surface of left hemelytron near base of *Hebrus* sp.; *RKB 2703* (holotype, Fig. 5G, H: isotypes, Fig. 5I–L); slide in RSA.

Three females and their accompanying males (Fig. 5G–M) constitute the material upon which this species is based. *Rhizopodomyces polhemusii* is somewhat smaller than the other species and is the only one displaying any marked pigmentation other than around the foot. The brownish-orange suffusion involving the posterior and lateral surfaces of the perithecium is uni-

formly present on all three females. The primary appendage is present on two of the females and is unlike that observed on other species in being broadly clavate to obovate and in projecting almost at right angles from near the middle of the suprabasal cell (Fig. 5G, L). I was unable to determine the exact number and arrangement of the outer wall cells, but it is doubtful that they deviate from the pattern established in the other species.

7. *Rhizopodomycetes basifurcatus* Benjamin, sp. nov.

FIG. 6K–O

Mas: Individua matura non observata.

Femina: Luteola, 275–295 μm in tota longitudine; axis uniformiter moderate curvatus; cellula basilaris receptaculi $18\text{--}20 \times 22\text{--}27 \mu\text{m}$ 2 rhizoideas basilaria ex latere antico producens; rhizoidea 45–55 μm longa, 12–15 μm in diametro ad basin, 4–5 μm in diametro ad apicem; cellula suprabasilaris receptaculi $60\text{--}70 \times 18\text{--}25 \mu\text{m}$ abrupte contracta ad apicem appendici primaria recta paene cylindrica $35\text{--}37 \times 9\text{--}10 \mu\text{m}$ gignens; stipes perithecii $100\text{--}130 \times 22\text{--}25 \mu\text{m}$; perithecium $63\text{--}75 \times 30\text{--}40 \mu\text{m}$ attenuatum ad apicem, margine postico fortiter convexo, margine antico moderate convexo, cellulis basilaribus aliquantum extra rotundatis; series cellulosa posticae et laterales parietis ex 4 cellulis constantes; series cellulosa antica parietis ex 5 cellulis constans, cellula terminali leniter protrudenti. Ascosporae non observatae. Typus *RKB 1813A* (RSA).

Male: Mature individuals not seen.

Female: Pale yellowish, uniformly curved from foot to tip of perithecium; basal cell slightly shorter than wide, $18\text{--}20 \times 22\text{--}27 \mu\text{m}$, with two broad-based rhizoidlike prolongations diverging laterally on the anterior side at an acute angle from one another, these 45–55 μm long, 12–15 μm wide at the base, 4–5 μm wide near the tip; suprabasal cell ca. three times longer than the basal cell, $60\text{--}70 \times 18\text{--}25 \mu\text{m}$, abruptly narrowed distally at the point of attachment of the nearly erect primary appendage; appendage nearly cylindrical with a rounded apex, $35\text{--}37 \times 9\text{--}10 \mu\text{m}$; primary stalk cell of the perithecium about two times longer than the suprabasal cell, with which its long axis is continuous, $100\text{--}130 \times 22\text{--}25 \mu\text{m}$; perithecium with well-defined basal cells which are somewhat rounded externally, its posterior margin more strongly convex than its anterior margin, uniformly tapered to its apex, $63\text{--}75 \times 30\text{--}40 \mu\text{m}$; outer rows of wall cells nearly straight; posterior and lateral rows consisting of four cells each; anterior row consisting of five cells, the terminal cell projecting slightly beyond the apices of the terminal cells of the other rows. Total length 275–295 μm . Ascospores not observed.

Holotype.—MEXICO; Jalisco: 30 mi NE of Colima, 4 Dec. 1948, H. B. Leech coll.; on upper surface of the left hemelytron near the base of *Hebrus* sp.; *RKB 1813A* (Fig. 6O); slide in RSA.

The material upon which this species is based is not in the best condition. It consists of three mature and three immature females and several paired

immature males and females in various stages of development (Fig. 6K–N). Nevertheless, the fungus clearly is distinct from the other species and I have given it a name although I suspect that when more material becomes available for study its description, like that perhaps of several other taxa included in this paper, will need some emendation. The receptacle of *R. basifurcatus* is distinguished especially by its very short and wide basal cell bearing two broad-based, attenuated prolongations that diverge from one another at a rather close angle (Fig. 6L, N, O). In one immature pair, the suprabasal cell of the male is growing upward immediately below the terminal cell (Fig. 6M), and it is likely that in this species, as in *R. geniculatus*, the terminal cell of the original spore forms a sterile appendage, the antheridium being derived from the suprabasal cell. This cannot be verified until mature males are discovered.

One of the females bore two perithecia, the stalk cell of the second having

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Fig. 6. A–J. *Rhizopodomycetes* sp. (RKB 1813C).—A. Paired male and female individuals prior to first division of basal spore segment. $\times 1,080$.—B. Paired male and female individuals in early stage of development. The basal segment of the female spore (left) has divided and formed the basal and suprabasal cells of the receptacle, whereas the upper spore segment remains undivided and constitutes the primary appendage. The basal segment of the male spore (right) has divided once and formed the two cells of the receptacle; the upper of these cells has divided and formed two smaller cells. The upper segment of the spore has collapsed somewhat and constitutes the primary appendage. $\times 895$.—C. Paired immature female (left) and apparently mature male (right). The primary appendage (*app*) of the female has assumed a lateral position on the suprabasal cell of the receptacle following the upgrowth of the perithecial primordium. In the male, the upper of the two cells derived from the suprabasal cell (see B) has been converted into an antheridium (*an*) having an upwardly directed efferent tube; the still-persistent appendage (*app*) has been diverted on one side. $\times 895$.—D. Immature female and accompanying male. The perithecium is in an early stage of development, but cell *m* is beginning to elongate. $\times 660$.—E–G. Three sequential stages of development of the perithecium. In E, cell *m* has not yet cut off its primary wall cell. In F the upward development of *m* has begun, and in G it is beginning to elongate. E, $\times 1,080$; F, G, $\times 1,360$.—H. Immature female and accompanying male. The perithecium still is in an early stage of development, but the upward growth of cell *m* is well advanced. $\times 660$.—I. Immature female and accompanying male. The outer walls of the perithecium have reached the four-cell stage, but the perithecium still is immature. The appendage derived from cell *m* probably has reached maximum size. Its base is adnate to the lower surface of the perithecium on the side away from the viewer. $\times 1,210$.—J. Near view of surface of perithecium shown in I. $\times 1,210$.—K–O. *Rhizopodomycetes basifurcatus* (RKB 1813A).—K. Paired male and female individuals prior to first division of basal spore segment. $\times 895$.—L. Paired male and female individuals at three-cell stage of development; the basal cell of the female already has developed the two divergent, broad-based outgrowths characteristic of this species. $\times 895$.—M. Immature paired male and female individuals; the female has not yet formed basal outgrowths; the suprabasal cell of the male is growing upward past the terminal cell, suggesting that the antheridium forms from the suprabasal cell. $\times 895$.—N. Immature female showing well-developed basal outgrowths and intact primary appendage. $\times 485$.—O. Mature female; only a remnant of the primary appendage remains. $\times 400$.

arisen immediately below that of the first. Whether or not the secondary perithecium had arisen following abortion or damage to the primary could not be determined. This is a phenomenon often observed in Laboulbeniales. In another collection of *Rhizopodomyces* in my collection (*RKB 2701*) specimens of female individuals that could not be positively identified (? nr. *R. merragatae*) bore the remnants of the stalk cells of several successive perithecia that had arisen from the suprabasal cell. The production of two or more successive perithecia in some species of *Rhizopodomyces* may prove to be of regular occurrence but additional observations are needed to resolve this question.

8. *Rhizopodomyces* sp.

FIG. 6A-J

Near the base of the right hemelytron of the specimen of *Hebrus* sp. bearing *R. basifurcatus* there occurred a number of specimens in various stages of early and intermediate development of a species of *Rhizopodomyces* (*RKB 1813C*) obviously very distinct from the others. There were no mature females, so the species cannot be given a name at this time. A unique feature of this taxon is the upward growth of basal cell *m* soon after perithecial development has begun (Fig. 6D-H). By the time the perithecium has reached the stage where four tiers of outer wall cells have formed, cell *m* has developed an elongate, nonseptate appendage (85-100 × 11-16 μm in the immature specimens observed) which is longer than and nearly as wide as the receptacle (Fig. 6I-J).

Like *R. geniculatus* and perhaps *R. basifurcatus*, the terminal spore segment of the male of *Rhizopodomyces* sp. forms a sterile appendage, the antheridium developing from the upper of two cells derived from the suprabasal cell of the receptacle (Fig. 6B, C). A shriveled but persistent appendage was still attached to males accompanying their respective females in several other of the specimens studied (Fig. 6D, H, I). The only intact female primary appendage observed is shown in Fig. 6C attached laterally to the suprabasal cell of the receptacle of an immature individual from which the perithecial upgrowth is arising.

Discussion

When he described *Rhizopodomyces*, Thaxter (1931) did not have immature specimens of the type species, *R. merragatae*, available for study. The two mature females he observed lacked any vestige of an appendage and Thaxter believed that the perithecium of this species had a strictly terminal origin from the upper cell of a two-celled receptacle. The account presented here, which includes results of a study of juveniles of several species, shows that the perithecium of *Rhizopodomyces* spp. actually has an intercalary origin, arising laterally from the suprabasal cell of a two-

celled receptacle that is derived from the lower cell of the bicellular spore. A simple, unicellular appendage, derived from the upper cell of the spore, is present during early stages of development of the female but it may more or less disintegrate or apparently be easily detached prior to or soon after maturation of the thallus. Enlargement of the suprabasal cell of the receptacle and the primary stalk cell of the perithecium coupled with their realignment into a more or less straight axis masks the original lateral origin of the perithecial primordium.

Thaxter (1931) suggested that *Rhizopodomycetes* resembles the dioecious *Amorphomyces* Thaxter (1893) most closely "in producing a strictly terminal perithecium and in the two-celled receptacle of the male individual." He also thought that *Dioicomycetes* and three apparently allied dioecious genera, *Dicrandromycetes* Thaxter (1931), *Triandromycetes* Thaxter (1931), and *Tetrandromycetes* Thaxter (1931) are related to *Amorphomyces*, although their females, unlike those of *Amorphomyces* bear a well-defined appendage. The females of *Dicrandromycetes*, *Triandromycetes*, and *Tetrandromycetes* are nearly identical in basic design to those of *Dioicomycetes*, and these genera were separated from one another by Thaxter on the basis of their males as will be discussed below.

Eleven species of *Amorphomyces* have been described, all from Staphylinidae (Coleoptera), and mostly on members of subfamily Aleocharinae. Twenty-six of the 32 described taxa of *Dioicomycetes* occur on beetles of the family Anthicidae (Coleoptera), and the same group of insects provides the hosts for the known species of *Dicrandromycetes* (1 species) and *Triandromycetes* (3 species). Four species of *Dioicomycetes* have been reported on members of other families of Coleoptera: *D. endogaeus* Picard (1912) on Carabidae; *D. floridanus* (Thaxt.) Thaxt. (1901) and *D. obliqueseptatus* (Thaxt.) Thaxt. (1901) on Staphylinidae, also the host family for the single described species of *Tetrandromycetes*, *T. brachidae* Thaxt. (1931); and *D. myrmecophilus* Majewski (1973) on Colydiidae. Benjamin (1970) described *D. mesoveliae*, an anomalous species on a true bug of the family Mesoveliidae, and Balazuc (1971, 1975) described *D. bournieri* on Phlaeothripidae (Thysanoptera), the only known laboulbenialean parasite of thrips. The eight taxa of *Rhizopodomycetes* discussed in this paper parasitize Hebridae (Hemiptera), but it cannot be presumed that other species will not be discovered on members of other groups of insects that coinhabit the same environment as the hebrids. Although many genera of Laboulbeniales have apparently very limited host ranges, others have become adapted to a broad spectrum of insect groups and other arthropods (Benjamin 1967, 1971). Host range can be an uncertain guide in assessing relationships or in making taxonomic judgements in the Laboulbeniales.

Except for *Dioicomycetes mesoveliae* in which the appendage of the female is two celled, the appendage of the female of all other species of *Dioico-*

myces and of those of *Dicrandromyces*, *Triandromyces*, and *Tetrandromyces* is one celled as in *Rhizopodomyces* species. The appendage of all species of *Dioicomyces* and its presumed allies is persistent whereas in those of *Rhizopodomyces* it often deteriorates or apparently is readily broken off. Species of *Amorphomyces* differ from all others in the Laboulbeniales in that the mature thallus shows no evidence of having borne an appendage. The apparent lack of this structure in members of this genus was easily explained earlier (Thaxter 1931) because of a misconception regarding the nature of the spore. Thaxter always maintained that the spore of *Amorphomyces* spp. was unique in the Laboulbeniales in being nonseptate, and this idea was accepted without question until Tavares (1970) demonstrated that it is indeed two celled. She also described not only the lateral origin of the perithecium in this genus but also the development of a distinctive type of rudimentary two-celled appendage on the female individuals. This appendage can be easily detected only on very immature stained specimens. Its remnant is incorporated into the wall of the perithecium and cannot be readily observed on individuals in late stages of development and at maturity. The spore of *Amorphomyces* spp. differs from that of other genera in that its upper segment is very small compared to the lower segment. It might be mentioned in passing that Thaxter undoubtedly observed the spore septum in a species of *Amorphomyces* when he described *A. obliqueseptatus* in 1900. He later transferred the species to *Dioicomyces* as *D. obliqueseptatus* because of its septate spores. The species had been based on a few female specimens lacking intact receptacles. There was no evidence of an appendage on the females, and males were missing. Thaxter illustrated *D. obliqueseptatus* in the 1908 segment of his monograph (Pl. XLII, Figs. 16–17). His figure 17 shows a spore having an oblique septum—exactly the kind of spore now known to occur in *Amorphomyces* spp.

The receptacle of the perithecium-bearing individual in many genera of Laboulbeniales, both monoecious and dioecious, may appear to be two celled, but a true two-celled receptacle is rare in the order and appears to be constant only in the females of *Rhizopodomyces* and *Amorphomyces* (Tavares 1970). Other genera with simple receptacles, like *Dioicomyces*, *Dicrandromyces*, *Triandromyces*, and *Tetrandromyces*, always have a third receptacular cell (III) lying more or less above cells I and II. In these genera cell III subtends the primary appendage, i.e., the modified upper spore segment, and all three cells of the receptacle, although often small, are well defined and clearly distinguished from the often elongate stalk cell of the perithecium which diverges from the suprabasal cell, i.e., cell II. In *Amorphomyces* the basal cell of the receptacle appears to comprise the whole of the receptacle proper, and it often is separated from the cells above by a slight constriction that may become more or less suffused. The small suprabasal cell of the receptacle, which subtends the rudimentary appendage,

is intimately associated with the stalk cells and basal cells of the perithecium and is not at all conspicuous in mature individuals. The two-celled receptacle of the female of *Rhizopodomycetes* is very different from that of *Amorphomyces* in being separated from the body of the perithecium and its basal cells by the elongate primary stalk cell. The suprabasal cell usually comprises the greater part of the receptacle of *Rhizopodomycetes* spp. and bears a free, well-developed, unicellular appendage—at least during development of the thallus. Unlike *Rhizopodomycetes*, the basal cell of the receptacle of species of *Amorphomyces* and *Dioicomyces* and its allies never develops rhizoidlike outgrowths and typically forms a blackened, indurated foot like that of most Laboulbeniales.

The males of the taxa here being discussed, although simple in structure and resembling one another superficially, display distinct differences from genus to genus. The lower cell of the male spore of species of *Dioicomyces* and *Tetrandromycetes* remains undivided and forms a one-celled receptacle (Benjamin, unpublished). The upper spore segment typically becomes divided into three smallish cells by the formation of two cross walls. In *Dioicomyces* the terminal cell is converted directly into a single antheridium having either a terminal or subterminal discharge tube. A second antheridium forms only if the first aborts (Thaxter 1931). In *Tetrandromycetes* the terminal cell of the four-celled thallus gives rise to two small cells disposed side by side each of which gives rise in turn to a pair of antheridia; the four antheridia thus formed are adnate at the base with only their discharge tubes free. The male of *Tetrandromycetes* seems sufficiently distinct from that of *Dioicomyces* to warrant recognition of the genus.

In *Triandromycetes* and *Dicrandromycetes* the lower cell of the male spore divides and forms a two-celled receptacle (Thaxter 1931), the original spore septum being more or less oblique. The upper spore segment of *Triandromycetes* typically divides and forms two cells; occasionally it remains undivided or sometimes may form three cells. The terminal cell of four-celled thalli usually gives rise to two free antheridia and the subterminal cell to one free antheridium; three- or five-celled thalli may give rise to only two or as many as five antheridia (Thaxter 1931). In *Dicrandromycetes* the upper spore segment produces a pair of divergent cells from each of which arise two free antheridia. In their two-celled receptacles and the production of free antheridia, the males of *Dicrandromycetes* and *Triandromycetes* are distinctly different from those of *Dioicomyces* and *Tetrandromycetes*. Because so few species of *Dicrandromycetes*, *Triandromycetes*, and *Tetrandromycetes* are known it is perhaps premature, as suggested by Thaxter (1931), to stress the taxonomic significance of the male thallus at the generic level, but the question should be kept open.

The lower segment of the male spore of *Amorphomyces* spp. also becomes once septate and forms a simple two-celled receptacle while the

initially small upper segment enlarges and is converted directly into a flask-shaped antheridium with an elongate, terminal or slightly eccentrically placed discharge tube (Tavares 1970; Thaxter 1931).

Like members of *Dicrandromyces*, *Triandromyces*, and *Amorphomyces*, the lower segment of the male spore of *Rhizopodomycetes* spp. becomes once septate and forms a two-celled receptacle. The upper spore segment of some species, as in all species of *Amorphomyces*, forms a simple antheridium directly; however, in other species it becomes a simple, sterile appendage resembling that of the female individuals. In the latter species, the supra-basal cell of the receptacle divides and forms one or two antheridia directly and what amounts to a secondary suprabasal cell. Sterile appendages are unknown on the males of *Amorphomyces*, *Dioicomycetes*, *Dicrandromyces*, *Triandromyces*, and *Tetrandromyces*, and in no instance has the male of any of these genera been found to form antheridia from a cell derived from its receptacle.

Perithecial ontogeny in *Rhizopodomycetes* spp. is basically like that described by Thaxter in 1896 for *Stigmatomyces baeri* (Knoch) Peyritsch, *Peyritschella geminata* Thaxt., and *Laboulbenia flagellata* Peyritsch. Thaxter subsequently often referred to such perithecia as having "normal development," and the sequence of cell divisions accompanying formation of such perithecia is the one most commonly encountered in the Laboulbeniales (Benjamin 1971: 43). Briefly, in this pattern of development a branch arising from the receptacle becomes divided near the tip. The upper cell ultimately forms the female organ which gives rise to asci, and the lower cell gives rise to the enveloping perithecium consisting of two stalk cells, three basal cells, and four inner and outer vertical rows of wall cells. The number of cells in each row of outer wall cells may vary, being three to many, but most commonly it is four or five or a combination of these numbers. The number of cells may be constant in the species of some genera in which the number is relatively small according to Tavares and Majewski (1976). This has proved to be the case in the species of *Rhizopodomycetes* observed thus far where there are four cells in three rows and five cells in the fourth row. Thaxter stated that there were five cells in each row of outer wall cells in *Amorphomyces* and *Dioicomycetes* and implied that this was true also for *Dicrandromyces*, *Triandromyces*, and *Tetrandromyces* (Thaxter 1931), although he did admit to some doubt that this was true for all the rows.

Tavares (1970) demonstrated the so-called "normal" pattern of early perithecial development in *Amorphomyces falagriae* Thaxt., the type species of the genus, but did not comment on the number of cells in each row of wall cells in the mature perithecium. I have examined immature and mature perithecia of *A. falagriae* and several species of *Dioicomycetes*. In all instances where early development could be followed, I have found the

"normal" sequence of cell divisions leading to wall cell formation in *Dioicomycetes*. Outer and inner wall cell configurations in mature females of *Amorphomyces* and *Dioicomycetes* are difficult to interpret, especially near the perithecial tip. Here, cellular boundaries often are obscured by mature spores and the persistent inner wall cells. The problem is compounded in *Dioicomycetes* spp. where the spores usually begin to germinate prior to discharge as evidenced by differentiation and suffusion of the foot. In no instance, however, have I found five cells in all rows of outer wall cells in *A. falagriae* or in the species of *Dioicomycetes* studied. In *A. falagriae*, where the rows of cells are somewhat spirally arranged, each row appears to consist of three elongate cells until maturation when the terminal cell of one row cuts off a fourth small cell. In all species of *Dioicomycetes* examined, each row of outer wall cells consists of four cells until perithecia approach maturity. In *D. mesoveliae* there is no evidence of further division of any of the terminal cells, whereas in the other species the terminal cell of one row appears always to cut off a fifth cell. In a few instances I found what appears to be a fifth extremely small cell cut off terminally by the wall cell row opposite the five-celled row.

Structural changes in perithecia of Laboulbeniales by supplementary divisions of wall cells at or near the apices, formation of specialized outgrowths by wall cells, and alterations in perithecial shape undoubtedly are in some way correlated with ascospore discharge. Such modifications may affect opening and closing of the ostiole when perithecia contact a host. There possibly may be differences in the number of cells formed at the tip of the perithecium in different species of a given genus depending on adaptations relating to spore dispersal. *Dioicomycetes*, a relatively large genus, exhibits considerable variation in perithecial structure, or at least conformation, from species to species. In some, the perithecium is little modified, being nearly straight or only slightly curved and with a relatively undistinguished tip (i.e., *D. anthici*, *D. trinitatis* Thaxt., *D. formicellae* Thaxt., *D. mesoveliae*, etc.). In a few species the perithecium itself may become greatly altered in shape as in *D. umbonatus* Thaxt., *D. falcatus* Spegazzini, and especially *D. malleolaris* Thaxt. where the long axis of the ascus-containing part becomes oriented nearly at right angles to the primary stalk cell. In still other species, wall cells at or near the tip of the perithecium produce thickened projections which presumably function as trigger organs (i.e., *D. spiniger* Thaxt., *D. glossophorus* Speg., *D. myrmecophilus*, *D. onchophorus* Thaxt., *D. prominens* Thaxt., *D. rostellatus* Speg.). Comparative studies of perithecial development in this genus are needed to determine what effect, if any, marked structural modifications may have on wall cell number, especially near the tip.

Only one species of *Amorphomyces*, *A. biformis* Thaxt., forms any kind of specialized perithecial outgrowth. In this species Thaxter (1931) described

two types or forms (*a* and *b*) of females, both more or less crescent shaped; in form *a* the perithecium develops a conspicuous, elongate, median outgrowth projecting nearly at right angles to the long axis of the perithecium; form *b* develops no such outgrowth. Other species of *Amorphomyces* typically have perithecia that are nearly straight or only slightly curved.

Four species of *Rhizopodomyces*, *R. merragatae*, *R. californicus*, *R. erectus*, and *R. basifurcatus*, have perithecia in which the long axis is nearly in line with that of the primary stalk cell. It may be significant that in these species the terminal cell of the five-celled row of wall cells is more or less protrudent, which is not the case in the geniculate species, *R. geniculatus*, *R. mexicanus*, and *R. polhemusii*. One can speculate that in these two groups of species perithecial shape and the nature of the apical wall cells are correlated with spore discharge. It is unfortunate that mature perithecia are unknown in *Rhizopodomyces* sp. where extreme modification of one of the basal cells gives rise to an appendage of remarkable size but unknown function.

From the above considerations, it can be seen that species of *Rhizopodomyces*, *Amorphomyces*, *Dioicomyces*, *Dicrandromyces*, *Triandromyces*, and *Tetrandromyces* resemble one another in several ways: (1) All are dioecious and have simple males consisting of only a few cells. The male typically lacks an appendage and produces one or a small number of antheridia that are derived from the upper, smaller segment of the two-celled spore; the only exception is *Rhizopodomyces* where in a few species the upper spore segment forms a sterile appendage like that of the female and the antheridia arise from the suprabasal cell of the receptacle. (2) The receptacle of the male thallus consists of only one or two cells; that of the female thallus consists of only two or three cells. (3) A simple primary appendage derived from the upper spore segment is borne by the female receptacle and consists of one, sometimes two, cells. (4) Except for *Rhizopodomyces*, in which there is some evidence in a few species that more than one perithecium may be produced, the female thallus typically gives rise to only one perithecium which always arises from the suprabasal cell of the receptacle. And except for *Amorphomyces*, the primary stalk cell of the perithecium usually is relatively large and frequently forms an elongate perithecial stipe. (5) The sequence of cellular divisions involved in perithecial formation is the same in all of the species and follows what is termed the "normal pattern of development" in the Laboulbeniales. The number of cells in each vertical row of wall cells is small, most commonly four or five, but as few as three in *Amorphomyces*.

In comparative morphological studies like the one presented here, one is tempted to speculate on possible interrelationships of the organisms examined. In the Laboulbeniales, as in most fungi where there is no fossil record, such speculations must be based on characteristics of extant species.

In the absence of physiological data, the primary characteristics available are similarities and differences in structure.

Laboulbeniales probably are monophyletic (Benjamin 1973; Denison and Carroll 1966). The group, however, must be of ancient origin, its evolution coinciding with that of its arthropod hosts, and the great diversity of generic types suggests that many divergent phylogenetic lines have developed at different times throughout its long evolutionary history, an evolution that undoubtedly is progressing rapidly in present time. It is to be expected that similarities in thallus structure reflect close relationship within some groups of genera as a result of parallel evolution from a common ancestor. An example of this would seem to be especially evident in a number of genera centered around *Stigmatomyces* Karsten (Benjamin 1970; Tavares 1973). However, similarities in structure also may result from convergent evolution and this phenomenon would lead to superficial resemblances of genera having distantly related ancestral types. I believe that *Rhizopodomyces* resembles *Amorphomyces* and *Dioicomyces* as a result of convergence and that the former genus is not closely related to the latter genera.

Despite the fact that the perithecium-bearing individual in *Amorphomyces* and *Rhizopodomyces* has a two-celled receptacle—a characteristic known only in these two genera of Laboulbeniales—the genera are very distinct. The lack of cell III in the receptacle of *Amorphomyces* may be the result of reduction of a formerly three-celled receptacle, as is found in *Dioicomyces*, *Dicrandromyces*, *Triandromyces*, and *Tetrandromyces*, coupled with the incorporation of the suprabasal cell, appendage, and stalk cells along with the true basal cells into the functional base of the perithecium. *Amorphomyces* appears to be one of the most specialized genera of Laboulbeniales having simple receptacles. The two-celled receptacle bearing a well-defined, though somewhat ephemeral, simple appendage of *Rhizopodomyces* suggests that this genus may be relatively primitive and less specialized than *Amorphomyces* and also *Dioicomyces*, etc., in which the appendage is persistent, often thick walled. I suspect that the receptacle of *Rhizopodomyces* is primitively two celled and that its precursor lacked a cell III. The foot of *Rhizopodomyces* spp. is less highly modified than in the latter genera and in the female part of the function of support if not attachment is assumed by lobate or rhizoidlike outgrowths of the basal cell.

Another possibly primitive characteristic of *Rhizopodomyces* is found in the males where a tendency for antheridia to be derived from the upper segment only of the spore has not become stabilized, as apparently it has in *Amorphomyces* and *Dioicomyces* and its allies. In some species of *Rhizopodomyces*, the suprabasal cell of the receptacle of the male, like that of the female, gives rise to the functional sexual organ, and the original terminal segment of the spore forms a sterile appendage. In this way the male of these species of *Rhizopodomyces* resembles the female, except for its

sexual structures, as in *Dimeromyces* Thaxt. (1896) and its allies, *Dimorphomyces* Thaxt. (1893), *Nycteromyces* Thaxt. (1917), and *Trenomycetes* Chatton & Picard (1908, 1909), and especially *Laboulbenia formicarum* Thaxt. (1902; Benjamin and Shanor 1950) which is perhaps one of the most primitively dioecious of all Laboulbeniales except possibly *Herpomyces* Thaxt. (1902). All species of *Herpomyces*, which occur on cockroaches, are dioecious, but sexual dimorphism may not be obligate in the genus. In her studies of *H. paranensis* Thaxt., Tavares (1965) confirmed an earlier observation of Thaxter (1908) that perithecial abortion on the female thallus of this species often leads to the formation of functional antheridia identical to those on the male thallus. Whether or not this is true of other species of *Herpomyces* still is unknown.

The male and female ascospores of some dioecious Laboulbeniales are conspicuously different in size, the female often much larger than the male, and spore dimorphism undoubtedly is a derived characteristic in the order. Ascospore dimorphism is much more pronounced in *Amorphomyces* and *Dioicomyces* than in *Rhizopodomycetes*—where the male and female spores are nearly of equal size—and most dioecious Laboulbeniales with a few exceptions which will be discussed in a future paper.

In conclusion, I believe that *Rhizopodomycetes* is not closely related to *Amorphomyces* or *Dioicomyces* and, like so many genera of Laboulbeniales, cannot be allied directly with any other of the known genera. *Dioicomyces*, *Dicrandromycetes*, *Triandromycetes*, and *Tetrandromycetes* appear to be very closely related on the basis of the female thallus. If distinct differences in their male thalli prove to be stable as additional species, especially of the latter three genera, are discovered, then these genera should continue to be recognized as distinct. *Amorphomyces* appears to be related to *Dioicomyces* and its allies, but may represent the most highly specialized member of this complex of dioecious genera.

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Rancho Santa Ana Botanic Garden, Claremont, California 91711.