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LABOULBENIALES ON SEMI-AQUATIC HEMIPTERA. *LABOULBENIA.*

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INTRODUCTION

The Hemiptera, or true bugs, a large and diverse assemblage of insects, are characterized by (1) mouth-parts articulated into an often elongate tubular beak adapted for feeding on plants or animals by piercing and sucking, (2) gradual metamorphosis, and (3) overlapping front wings having a hardened basal part, the *corium*, and a thin, transparent apex, the *membrane*. The order commonly is divided into two suborders, the Homoptera and the Heteroptera (Brues, Melander & Carpenter, 1954; Ross, 1956). At present no member of the Homoptera (which includes such well-known bugs as the cicadas, tree hoppers, plant lice, etc.) is known to be parasitized by Laboulbeniales. These fungi occur on insects classified in the Heteroptera, but only 26 species have been described.

Entomologists subdivide the Heteroptera into two major groups based, in part, on the length of the antennae. These are the Cryptocerata (short-horned bugs) in which the antennae are short and are concealed beneath the head and the Gymnocerata (long-horned bugs) in which the antennae typically are longer than the head and are exposed.

The Cryptocerata include many aquatic or semi-aquatic insects belonging to the following families: Belostomatidae (giant water bugs); Corixidae (water boatmen); Naucoridae (creeping water bugs); Nepidae (water scorpions); Gelas-tocoridae (toad-bugs); Notonectidae (back swimmers); Ochteridae (Ochterids); and Pleidae, thought to be closely related to the back swimmers (Usinger, 1956). The termitophilous Termitaphididae also are placed in the Cryptocerata (Brues, Melander & Carpenter, 1954). Of these groups, Laboulbeniales have been found only on the Corixidae, and all of the nineteen species discovered thus far may be classified in the genus *Coreomyces* Thaxter (1902) which is known only on this family. The discovery of Laboulbeniales on other families of Cryptocerata is greatly to be desired.

The Gymnocerata is a more complex and diverse group of insects than the Cryptocerata, and its members may be classified in no less than eleven superfamilies (see Brues, Melander & Carpenter, 1954, pp. 19-20, 167-181). Laboulbeniales are unknown on six of these: Coreoidea, Dipsocoroidea (a few members of the

family Dipsocoridae are semi-aquatic), Helotrephoidea, Polycenoidea, Reduvioidea, and Tingioidea. Seven species of Laboulbeniales have been described from members of the other five superfamilies as follows:

ARADOIDEA.—In the system of classification of Brues, Melander & Carpenter (1954) this superfamily encompasses ten families of insects of which four (Hebridae, Hydrometridae, Mesoveliidae, and Saldidae) are primarily semi-aquatic, the adults living on or near water. In 1931, Thaxter described an unusual genus of Laboulbeniales, *Rhizopodomycetes*, from one of the Hebridae. The type and only known species, *R. merragatae*, was found on a species of *Merragata* from Guatemala. I subsequently have obtained what appears to be the same species on *Merragata hebrioides* White from near Victorville, California, as well as on a species of *Hebrus* from near Palm Springs, California.

CIMICOIDEA.—This group, named for the Bedbug family, Cimicidae, is comprised of eight families of which only one, the Anthocoridae (minute pirate bugs), includes a known host of a laboulbeniaceus parasite. In 1917, Thaxter described *Stigmatomyces lasiochili* from an insect collected in Grenada, West Indies, and identified as *Lasiochilus pallidus* Reuter. Later, Thaxter (1931) transferred the fungus to the genus *Hesperomyces*.

GERROIDEA.—Two families, Gerridae and Veliidae, are included here; their members commonly are referred to as water striders. Several Laboulbeniales are known on Veliidae. In 1912, Thaxter described two species of *Laboulbenia*, *L. hemipteralis* and *L. veliae*, on *Velia platensis* Berg. collected in the vicinity of Buenos Aires, Argentina, and later (1931) he characterized *Autophagomyces microveliae* on *Microvelia albolineolata* Bueno from Fort de Kock, Sumatra.

LYGAEOIDEA.—This superfamily, named for the Lygaeidae (chinch bugs; plant bugs), includes six families. One species of Laboulbeniales, *Corethromyces myodochoae* Thaxter (1931) on *Myodocha unispinosa* Stal, a member of the Lygaeidae, has been described. The host was collected in Guatemala.

SCUTELLEROIDEA.—Seven families of bugs are included in this group by Brues, Melander & Carpenter. A singular dioecious genus of Laboulbeniales, *Polyandromyces*, has been described by Thaxter (1931) on members of the family Plataspidae. *Polyandromyces coptosomalis* was found on *Coptosoma* spp. from Madagascar, Fiji, and the Solomon Islands, and a variety of this species, *minor*, on a *Coptosoma* taken in the Cameroons, West Africa. *Polyandromyces* apparently is widely distributed; what may be the same species as the one described by Thaxter is in my own collection from an undetermined member of the Plataspidae from Ecuador.

During the many years that I have been examining insects in search of Laboulbeniales only a few additional representatives of these fungi have been found on Hemiptera. With the exception of the species of *Polyandromyces* from Ecuador mentioned above and several species of *Coreomyces* on various Corixidae, all of the species that I have encountered were found on semi-aquatic bugs of the families Hebridae, Mesoveliidae, Veliidae, and Macroveliidae. In this paper only species of *Laboulbenia* that are known on semi-aquatic Hemiptera will be described. Representatives of other genera of Laboulbeniales parasitizing these insects will be treated later.

ACKNOWLEDGMENTS

Many of the specimens discussed in this paper were obtained from insects gathered by persons other than myself. To the collectors, known and unknown, cited following the descriptions given below I express my sincere thanks. Collections of insects belonging to several institutions have been examined from time to time and permission to retain parasitized hosts for future study always has been given freely. In this connection I wish to express my gratitude to Drs. Harlow B. Mills, Herbert H. Ross, and Milton W. Sanderson, Illinois Natural History Survey, Urbana, Ill.; Dr. Edward S. Ross and Mr. Hugh B. Leech, California Academy of Sciences, Golden Gate Park, San Francisco, Calif.; Dr. Paul D. Hurd, University of California, Berkeley, Calif., and Dr. Fred S. Truxal, Los Angeles County Museum of Natural History, Exposition Park, Los Angeles, Calif. Finally, I am indebted to Dr. I. Mackenzie Lamb, Director, Farlow Herbarium, Harvard University, Cambridge, Mass., for loan of the type specimens of *Laboulbenia hemipteralis* and *L. veliae*.

DESCRIPTIONS

Laboulbenia (Robin, 1853; Thaxter, 1896, 1908) is the largest in number of known species of the more than 100 genera of Laboulbeniales, and its representatives have been found on seven orders of insects and one order of arachnids. Most of the over 400 described species of *Laboulbenia* parasitize various Coleoptera; fewer than 20 species are known on Diptera, three on Hymenoptera, two on Hemiptera, two on Orthoptera, and one each on Blattaria and Isoptera. Two species have been described on mites (Acarina).

The two species on Hemiptera, *Laboulbenia hemipteralis* and *L. veliae*, described by Thaxter in 1912 were never illustrated. As stated in the introduction, both of these species were found on a member of the family Veliidae, *Velia platensis* Berg., from Argentina. Subsequently, I have obtained six additional species on members of the same family collected in various parts of North and Central America and two species on a representative of the Macroveliidae, *Macrovelia hornii* Uhler, from California.

Species of *Laboulbenia*, the large size of the genus notwithstanding, are readily distinguished from other members of the order. The vegetative body, or receptacle, is relatively simple and consists of a two-celled stalk that subtends and appendage and a single perithecium. The relationship of the basal cells of what may be termed the primary appendage and those of the stalk and lower perithecium is so precise and the number of the cells so constant that Thaxter (1896) found it convenient to number the successive cells from I to VI for descriptive purposes. Cells I and II are the basal- and subbasal cells of the stalk (Fig. 1e). Cell III is the lowermost cell of the primary appendage and is followed immediately above by cells IV and V (Fig. 1f). The latter is in reality two cells placed side by side. The cell subtending the perithecium is termed the stalk-cell (VI) and may be relatively small and inconspicuous or more or less elongate depending on the species. This cell and the basal part of the perithecium usually are variably adnate to cells III-V. Rarely, cells III and IV are replaced by a single cell. Cells IV and V subtend a usually broadly flattened cell, the insertion

cell (Fig. 1f), that often becomes more or less opaque externally. This cell supports two or more small cells that in turn bear the secondary appendages—referred to simply as the appendages in descriptions of *Laboulbenia*. The outer appendage typically is sterile, whereas the inner appendage, in many species, gives rise to the presumed male reproductive structures, the simple flask-shaped antheridia. The latter may be sessile or stalked and are persistent in some species, deciduous in others; they commonly are replaced or displaced by sterile branches like those comprising the outer appendage. The perithecium consists of four usually small basal cells, one cell immediately above cell VI is more or less surrounded distally by three cells from which is developed the wall proper of the perithecium. In *Laboulbenia*, as in many other genera of Laboulbeniales, the wall of the mature perithecium consists of four paired inner and outer longitudinal rows of four cells each. The terminal cells of the outer series are termed the lip-cells; these together with the upper cells of the corresponding inner rows of wall-cells form the exit pore or ostiole of the perithecium. The lip-cells often become more or less opaque and modified structurally.

In the descriptions that follow, the side of the receptacle and the appendages away from the perithecium are termed outer. Likewise the side of the perithecium away from the appendages is termed outer.

Specimens cited are in the author's collection of Laboulbeniales on deposit at the Rancho Santa Ana Botanic Garden (RSA) and, where indicated, duplicates also have been forwarded to the Farlow Herbarium, Harvard University (FH).

SPECIES ON *Velia* (VELIIDAE).

LABOULBENIA HEMIPTERALIS Thaxter.

Proc. Amer. Acad. Arts & Sci. 48(8): 194. 1912.

(Fig. 1 a-d)

Receptacle: More or less olivaceous, delicately punctate above; basal and subbasal cells (I-II) nearly equal in length, forming a stout stalk 40–70 μ long $\times$ 17–20 μ in greatest width; cells III–IV well-defined, subequal; cell V smaller; cell VI small, inconspicuous.

Appendages: Insertion cell compressed, relatively broad, nearly opaque externally, lying slightly above the middle of the perithecium. Basal cell of the

Fig. 1. a–d. *Laboulbenia hemipteralis* Thaxter.—a. Immature individual showing early stages of development of the perithecium; note the trichogyne (tr.). The inner appendage bears three antheridia (anth.) and the outer appendage shows several secondary branchlets in early stages of development. $\times 970$.—b–c. Two mature individuals. In both, the posterior antheridium has been displaced by a sterile appendage. Note the highly developed outer appendages. $\times 600$.—d. Perithecium showing conformation of the tip. $\times 1210$.—e–f. *Laboulbenia veliae* Thaxter.—e. Mature individual. The basal and subbasal cells of the receptacle are designated by Roman numerals I and II. $\times 600$.—f. Early stage of development of perithecium and upper cells of receptacle; the latter cells are designated by Roman numerals III–VI in accordance with the usual practice employed in describing the receptacle of species of *Laboulbenia*. Note insertion cell (in. c.). $\times 1210$.

outer appendage usually strongly rounded externally, bearing a single robust branch, bent inward slightly, producing four or five successive branchlets externally; the lowest branchlet distinguished by a thin darkened septum and bearing up to four secondary simple branchlets, the lowest of which is externally suffused at its base and projects subhorizontally; branchlets nearly hyaline, simple or furcate, often spirally twisted, the longest about 100μ . Basal cell of the inner appendage subtending usually three small subequal cells, an inner and two outer, that bear single flask-shaped antheridia, $12-15\mu \times 6-7\mu$, having darkened basal septa; antheridia persistent, the inner one usually displaced laterally by the development of a branched appendage like those above the base of the outer appendage; the two outer antheridia usually unmodified, rarely displaced by a branched appendage.

Perithecium: Olivaceous, tapering, $55-70\mu$ long $\times$ $20-27\mu$ wide, the distal $\frac{1}{2}$ free; the tip more or less opaque and bent inward slightly, bluntly rounded or slightly pointed; pore directed inward; spores about $25-30\mu \times 3\mu$.

Total length from base of foot to tip of perithecium, $100-135\mu$ (mean, 115μ ; based on 20 mature individuals).

Holotype.—ARGENTINA. Parque 3-de-Febrero, between Palermo and Belgano, Buenos Aires, October, 1905; on legs and inferior surface of *Velia platensis* Berg.; *Thaxter 1951 in part*; slides 9931-9935 in the Thaxter Collection of Laboulbeniales, Farlow Herbarium.

LABOULBENIA VELIAE Thaxter.

Proc. Amer. Acad. Arts & Sci. 48(7): 195. 1912.

(Fig. 1 e-f)

Receptacle: Olivaceous; cells I-II forming an elongate, slightly curved stalk, $200-210\mu$ long $\times$ $12-18\mu$ wide, about five times the length of the distal part; cell II nearly two times the length of cell I; cells III-V well-defined, small, adnate to the posterior lower one-third or less of the perithecium; stalk-cell (VI) relatively large, about equal in size to cells II and IV.

Appendages: Insertion cell broad, thick, the lower part externally nearly opaque; the basal cells of the outer and inner appendages small, subequal. The outer appendage consisting of an outer and inner branch each of which bears several divergent branchlets, the shorter lower cells distinguished by darkened septa; the longest branches up to 200μ in length. The basal cell of the inner appendage subtending two small, subequal cells that bear single flask-shaped antheridia; antheridia persistent, displaced laterally by the development of branches similar to those of the outer appendage.

Perithecium: Olivaceous, paler near the tip, about $\frac{2}{3}$ free, narrow, $115-125\mu$ long $\times$ $22-26\mu$ wide, slightly and inwardly geniculate below the tip; the inner lip-cells greatly enlarged, extending beyond the hyaline outer lip-cells and forming a conspicuous, bluntly rounded, externally suffused prominence; pore directed outward slightly; spores $50\mu \times 7\mu$.

Total length from base of foot to tip of perithecium, 350μ (one unbroken mature individual).

Holotype.—ARGENTINA. Parque 3-de-Febrero, between Palermo and Belgano, Buenos Aires, October, 1905; on superior surface of *Velia platensis* Berg.; Thaxter 1951 in part; slides 9936–9938 in the Thaxter Collection of Laboulbeniales, Farlow Herbarium.

SPECIES ON *Microvelia* (VELIIDAE).

Laboulbenia microveliae sp. nov.

(Fig. 2 a–b)

Receptaculum: Cellula basilaris (I) fere hyalina, $35\text{--}50\mu$ longa $\times$ $15\text{--}20\mu$ lata prope septum supernum, frequenter plus minusve arcuata. Cellulae II–V olivaceae paene opacae cum tunicis minute punctatis; cellulis III–IV in cellulam unam grandem $25\text{--}33\mu \times 15\text{--}37\mu$ unitis. Cellula V parvula. Cellula VI perparva et inconspicua.

Appendices: Insertionis cellula complanata nonopaca praeter septa inferiora appendicium. Cellula basilaris appendicis externae parva fere isodiametra 1 ramum primum sterilem gerens; cellula basilaris rami primi ramum secundarium gignenti; ramis primis et secundariis saepe ramulos gerentibus; appendice longissima $50\text{--}80\mu$. Cellula basilaris appendicis internae 2 cellulas antheridiiferas gignens; antheridiis 1, 2 vel raro 3 simplicibus persistentibus $10\text{--}15\mu \times 5\mu$ in aetate ramis sterilibus appendicibus externis similibus substitutis; appendicibus longissimis $50\text{--}70\mu$.

Perithecium: Olivaceum divergente triangulare $\frac{1}{2}$ liberum $50\text{--}70\mu$ longum $\times$ $20\text{--}25\mu$ latum infra et lateraliter receptaculo adnatum; apice abrupte constricto extrinsecus nigro; sporis $35\mu \times 5\mu$.

Totus fungus (85--) $100\text{--}125\mu$ longus.

Receptacle: Basal cell (I) nearly hyaline, $35\text{--}50\mu$ long $\times$ $15\text{--}20\mu$ wide near the upper septum, usually more or less recurved at maturity; cells II–V deep olivaceous, often nearly opaque, marked externally by numerous, short, transverse punctae; cell II somewhat compressed, the upper anterior face broadly and obliquely attached to the base of the perithecium; cells III–IV replaced by a single large cell, $25\text{--}33\mu \times 15\text{--}27\mu$, that is about twice the size of cell V, these cells broadly and obliquely adnate to the posterior lower $\frac{1}{2}$ of the perithecium; cell VI small, hardly distinguishable except in early stages of development.

Appendages: Insertion cell compressed, relatively broad, widest in the middle, not becoming opaque except immediately below the basal cells of the appendages. Basal cell of the outer appendage nearly isodiametric, often strongly rounded posteriorly, bearing a single branch that produces a secondary branchlet internally from its basal cell; both branches often forming additional branchlets, these slightly bent to strongly recurved distally, the longest reaching $50\text{--}80\mu$. Basal cell of the inner appendage subtending two small cells each of which bears one, two or rarely three flask-shaped antheridia about $10\text{--}15\mu \times 5\mu$; antheridia persis-

tent, displaced laterally by the development of usually single ramified branchlets, 50–70 μ long, similar to the outer appendages.

Perithecium: Deep olivaceous, divergent 50–70 μ long $\times$ 20–35 μ wide, the free portion subtriangular, forming an oblique angle with the upper surface of cell V of the receptacle; the tip not or scarcely exceeding the level of the insertion cell; outer lip-cells completely opaque and blackened externally below the hyaline tip; pore directed upward or slightly inward; spores about 35 μ $\times$ 5 μ .

Total length from base of foot to tip of perithecium, (85–)100–125 μ (mean, 110 μ ; based on 25 mature individuals).

Etym.—Named for the host genus, *Microvelia*.

Holotype.—CALIFORNIA. Orange County: 2 miles west of the Riverside County-Orange County line, Highway 74, Cleveland National Forest, Santa Ana Mts., 17 May, 1955, R. K. Benjamin; on all parts of *Microvelia beameri* McKinstry; RKB 1912; slides in RSA, FH.

Other specimens examined.—ARIZONA. Mohave County: Willow Springs, 19 miles northwest of Kingman, 25 March, 1958, F. S. Truxal; on legs of *Microvelia* sp.; RKB 2410; slides in RSA.—CALIFORNIA. Los Angeles County: San Dimas Canyon, San Gabriel Mts., 20 June, 1956, Arnold Menke; on all parts of *Microvelia beameri* McKinstry; RKB 2407; slides in RSA.—Soledad Canyon, San Gabriel Mts., 15 Aug., 1956, coll. unknown; on all parts of *Microvelia beameri* McKinstry; RKB 2408; slides in RSA.—Marin County: Muir Beach, 14 March, 1954, H. B. Leech; on legs and abdomen of *Microvelia* sp.; RKB 1974; slides in RSA.—Riverside County: In a palm canyon, 14 April, 1952, R. L. Usinger; on legs of *Microvelia beameri* McKinstry; RKB 2022; slides in RSA.—San Bernardino County: 2 miles south of Tres Pinos, 21 June, 1957, coll. unknown; on legs of *Microvelia* sp.; RKB 2411; slides in RSA.—San Diego County: 8 miles west of Boulevard, 8 April, 1954, R. M. Straw; on legs and antennae of *Microvelia* sp.; RKB 1973; slides in RSA.—Tulare County: near Porterville, 5 March, 1934, R. P. Allen; on legs of *Microvelia* sp.; RKB 2020; slides in RSA.—ILLINOIS. Fayette County: near St. Elmo, 11 Oct., 1932, H. H. Ross; on all parts of *Microvelia* sp.; RKB 1688; slides in RSA.—Kane County: Elgin Botanical Garden, Elgin, 6 June, 1950, R. K. Benjamin; on legs of *Microvelia* sp.; RKB 529; slides in RSA.—NEW YORK. Suffolk County: Cold Spring Harbor, Long Island, 11 July, 1928, H. M. Parshley; on legs of *Microvelia* sp.; RKB 2018; slides in RSA.—TEXAS. Frio County: Pearsall, 16 June, 1957, David Lauck; on legs of *Microvelia* sp.; RKB 2111; slides in RSA.—Jeff Davis County: Limpia Creek Canyon, Davis Mts., 9 Aug., 1959, coll. unknown; on legs and lower surface of *Microvelia* sp.; RKB 2409; slides in RSA.—MEXICO. Durango: Las Conchas, 1 Aug., 1952, J. D. Lattin;

Fig. 2. a–b. *Laboulbenia microveliae* Benjamin.—a. Immature individual. The outer appendage already has developed two secondary branchlets one of which has, in turn, formed a branchlet. The inner appendage bears two antheridia. $\times 520$.—b. Mature individual. The antheridia persist but have been displaced by sterile appendages. Note single large cell in place of cells III and IV. $\times 400$ (Note: Because of slight compression of the specimen by the cover glass, the perithecium shown in this drawing is somewhat broader and externally more convex than in undisturbed specimens).—c–d. *Laboulbenia macroveliae* Benjamin.—c. Immature individual. The outer appendage consists of several branchlets and the inner appendage bears two antheridia. $\times 530$.—d. Mature individual; the antheridia have been displaced by simple sterile branchlets. Note conformation of lip-cells of perithecium. $\times 400$.—e–f. *Laboulbenia lechii* Benjamin.—e. Immature individual showing early stage of development of the perithecium and appendages. Secondary branchlets are forming on the outer appendage; the inner appendage bears two antheridia. $\times 530$.—f. Mature individual. Note displacement of one antheridium by a sterile appendage and the prolongation of the outer lip-cells of the perithecium. $\times 400$.—g–h. *Laboulbenia uhlerii* Benjamin.—g. Immature individual showing perithecium, young outer appendage, and inner appendage bearing two antheridia. $\times 530$.—h. Mature individual showing intact outer appendage and displacement of one antheridium by a sterile branch. Note conformation of tip of perithecium with the pore directed inward slightly. $\times 400$.

on legs and head of *Microvelia* sp.; RKB 2405; slides in RSA.—Nayarit: Maria Magdalena, Tres Marias Is., 24–26 March, 1964, R. R. Snelling; on legs of *Microvelia* sp.; RKB 2415, 2416;

slides in RSA.—Nuevo Leon: Cienega de Flores, 18 June, 1957, David Lauck; on legs of *Microvelia* sp.; RKB 2110; slides in RSA.—Puebla: Chignaulingo, 16 Aug., 1959, coll. unknown; on legs of *Microvelia* sp.; RKB 2412; slides in RSA.

This species of *Laboulbenia* is the one most commonly encountered on Veliidae, and its known range extends from Long Island, N. Y., across the United States to California and south into Mexico as far as the state of Puebla. It is readily distinguished from *L. leechii*, also found on *Microvelia*, by the relatively large size of the upper cells of the receptacle in which cells III–IV are not differentiated and by the strongly divergent perithecium in which the upturned tip lacks an external protuberance.

Laboulbenia leechii sp. nov.

(Fig. 2 e–f)

Receptaculum: Cellula basilaris (I) prope hyalina $35\text{--}40\mu$ longa $\times$ $15\text{--}17\mu$ lata. Cellula II brevior infra paene hyalina supra olivacea et minute punctata. Cellulae III–IV subaequantes olivaceae minute punctatae. Cellula V concolora parvula triangula minute punctata. Cellula VI perparva complanata.

Appendices: Insertionis cellula complanata paene opaca. Cellula basilaris appendicis externae parva fere isodiametria extra rotundata ramulos primos et secundarios gerens; cellula basilari rami primi ramulos gignenti; ramulis hyalinis rectis vel curvatis longissimis $60\text{--}70\mu$. Cellula basilaris appendicis internae 2 cellulas antheridiiferas gignens; antheridiis singulis simplicibus persistentibus $10\text{--}12\mu \times 4\text{--}5\mu$ in aetate saepe ramis sterilibus appendicibus externis similibus substitutis.

Perithecium: Olivaceum punctatum ad apicem attenuatum $\frac{1}{2}$ liberum $55\text{--}75\mu$ longum $\times$ $16\text{--}22\mu$ latum; apice prope hyalino processum externum gracilem $10\text{--}12\mu \times 3\text{--}4\mu$ gerenti; processu et apice extrinsecus opacis.

Totus fungus $105\text{--}160\mu$ longus.

Receptacle: Basal cell (I) nearly hyaline, $35\text{--}40\mu$ long $\times$ $15\text{--}17\mu$ wide, about two times as long as the subbasal cell (II); the latter slightly longer than wide, narrower and hyaline below, becoming olivaceous above; cells III, IV, and V well-defined, dark olivaceous; these cells together with the upper part of cell II and the base of the perithecium marked externally by numerous, minute, darkened punctae; cells III–V subequal, the latter nearly triangular in lateral view, adnate to the posterior lower $\frac{1}{2}$ of the perithecium; cell VI well-defined, small, flattened.

Appendages: Insertion cell compressed, oblique, lying at or slightly below the level of the middle of the perithecium, becoming more or less opaque below. Basal cell of the outer appendage nearly isodiametric, strongly rounded externally, bearing a single branch, the outer branchlet of which is darkened externally below and bears one or more inner branchlets successively; the basal cell of the outer branch giving rise to an inner branch that bears several successive branchlets, these nearly straight or slightly curved, hyaline, the longest reaching $60\text{--}70\mu$. Basal cell of the inner appendage small, subtending subequal outer and inner cells that bear flask-shaped antheridia having darkened basal septa; antheridia $10\text{--}12\mu$

× 4–5 μ , persistent, displaced laterally by the development of sterile branchlets similar to those of the outer appendage; the outer antheridium often remaining unmodified.

Perithecium: Deep olivaceous below, paler above, 55–75 μ long × 16–22 μ wide including the terminal prominence, tapering, the distal $\frac{1}{2}$ free; the tip bearing anteriorly a slightly curved, blunt prominence, 10–12 μ × 3–4 μ , that is deeply suffused and opaque along the outer margin, the opacity extending 10–12 μ below the otherwise hyaline tip of the lip-cells; pore directed upward or slightly inward.

Total length from base of foot to tip of prominence, 105–160 μ (mean, 133 μ ; based on 28 mature individuals).

Etym.—Named for Hugh B. Leech, California Academy of Sciences, entomologist, student of aquatic insects, especially Coleoptera.

Holotype.—MEXICO. Jalisco: 7 miles south of Mazamitla, 1 Dec., 1948, H. B. Leech; on various parts, especially the legs and antennae, of *Microvelia* sp.; RKB 1902; slides in RSA, FH.

Other specimens examined.—ARIZONA. Cochise County: Sunnyside Canyon, 6000 ft, west side of Huachuca Mts., 4 Aug., 1952, H. B. Leech; on various part of *Microvelia* sp.; RKB 1970; slides in RSA.—NEW MEXICO. Valencia County: Grants, 16 Feb., 1945, H. P. Chandler; on legs of *Microvelia* sp.; RKB 2019; slides in RSA.—MEXICO. Michoacán: 14 miles northwest of Zitácuaro, 24 Aug., 1959, coll. unknown; on legs and head of *Microvelia* sp.; RKB 2417; slides in RSA.

The known distribution of this very distinct species thus far is limited to Arizona and New Mexico in the United States and to central Mexico. It doubtless is widely distributed throughout this range. *Laboulbenia leechii* never has been found in company with *L. microveliae* on the same host.

SPECIES ON *Rhagovelia* (VELIIDAE).

Laboulbenia usingerii sp. nov.

(Fig. 3 a–b)

Receptaculum: Cellulae I–II stipitem elongatum aliquantum geniculatum 315–400 μ longum × 18–21 μ latum gerentes. Cellula I prope hyalina. Cellula II plus minusve olivacea. Cellulae III–IV parvae subaequales atroolivaceae punctatae. Cellula VI parva inconspicua.

Appendices: Insertionis cellula complanata obliqua inferne opaca. Cellula basilaris appendicis externae parva 1 ramum simplicem sterilem fortiter reflexum gerens; ramo ex cellula parva basilare et cellula elongata apicale constante. Cellula basilaris appendicis internae 2 cellulas parvas antheridiiferas gignens; antheridiis singulis simplicibus persistentibus 10–13 μ × 6–7 μ in aetate ramis singulis sterilibus appendicibus externis similibus substitutis.

Perithecium: Atroolivaceum $\frac{1}{2}$ liberum 65–75 μ longum × 15–22 μ latum lateraliter receptaculo adnatum; apice interne nigro.

Totus fungus 365–470 μ longus.

Receptacle: Cells I–II forming an elongate, slightly geniculate stalk, 315–400 μ

long $\times$ $18\text{--}21\mu$ wide, often 5–6 times the length of the slightly narrower distal part; cell I nearly hyaline; cell II about $1\frac{1}{2}$ –2 times the length of cell I, pale olivaceous; cells III–V small, subequal, dark olivaceous brown, often delicately punctate, especially cell V, adnate to the posterior lower $\frac{3}{4}$ of the perithecium; stalk-cell (VI) small, inconspicuous.

Appendages: Insertion cell compressed, oblique, lying mostly above the middle of the perithecium, becoming completely opaque below. Basal cell of the outer appendage small, bearing a single strongly reflexed appendage consisting of a small basal cell and an elongate terminal cell. Basal cell of the inner appendage subtending two subequal inner and outer cells that bear single flask-shaped antheridia, $10\text{--}13\mu \times 6\text{--}7\mu$, having darkened basal septa; antheridia persistent, displaced laterally by the development of simple elongate branchlets; inner and outer branches approximately equal, about $100\text{--}125\mu$ long.

Perithecium: Dark olivaceous brown except near the slightly out-turned tip, $65\text{--}75\mu$ long $\times$ $15\text{--}22\mu$ wide, the distal $\frac{1}{4}$ free; apex deeply suffused and opaque internally below the hyaline tips of the lip-cells; pore directed slightly outward.

Total length from foot to tip of perithecium, $365\text{--}470\mu$ (5 individuals).

Etym.—Named for Robert L. Usinger, University of California, Berkeley, entomologist, student of aquatic Hemiptera.

Holotype.—CANAL ZONE. Gatun, March, 1930, T. O. Zschokke; on eyes of *Rhagovelia uncinata* Champion; RKB 1901A; slides in RSA, FH.

Other specimens examined.—CANAL ZONE. Fort Clayton, Feb., 1945, K. E. Frick; on right eye of *Rhagovelia* sp.; RKB 2117B; slide in RSA.

Five mature and six immature individuals of *L. usingerii*, from two localities in the Canal Zone, have been examined. The elongate, slightly geniculate stalk and the strongly reflexed simple outer appendage distinguish this species from others on *Rhagovelia*.

Laboulbenia drakei sp. nov.

(Fig. 3 c–d)

Receptaculum: Cellulae I–II subaequales stipitem subolivaceum elongatum plus minusve rectum $130\text{--}200\mu$ longum $\times$ $17\text{--}23\mu$ latum gerentes; septo medio aliquantum obscuro. Cellulae III–V parvae olivaceae infra minute punctatae supra grosse punctatae; cellulis III–IV in cellulam unam $20\text{--}25\mu \times 16\text{--}22\mu$ unitis. Cellula V $20\text{--}25\mu \times 8\text{--}10\mu$. Cellula VI perparva fere isodiametria.

Appendices: Insertionis cellula complanata obliqua opaca. Cellula basilaris appendicis externae parva pauxillum elongata 1 ramum primum sterilem rectum vel curvatum extrinsecus obscurum gerens; cellula basilaris primi ramum secundarium curtum ad apicem deminutum gignenti; ramo primo ramulos gerenti; appendice longissima $45\text{--}70\mu$. Cellula basilaris appendicis internae 3 cellulas parvas antheridiiferas gignens; antheridiis singulis simplicibus persistentibus $12\text{--}15\mu \times 5\text{--}6\mu$ in aetate ramis singulis simplicibus $20\text{--}45\mu$ longis appendicibus externis similibus substitutis.

Perithecium: Olivaceum pauxillum divergente $\frac{1}{2}$ liberum $65\text{--}85\mu$ longum $\times$

20–32 μ latum; apice extrinsecus subapicali aliquantum constricto intrinsecus et lateraliter nigro.

Totus fungus 200–300 μ longus.

Receptacle: Cells I–II subequal in length, forming an elongate, nearly straight stalk, 130–200 μ $\times$ 17–23 μ , that often is 3½–4½ times the length of the distal part, pale olivaceous, somewhat darker around the septum; cells III–V olivaceous, minutely punctate below, coarsely punctate above, obliquely adnate to the lower posterior ½ or less of the perithecium; cells III–IV replaced by a single cell, 20–25 μ $\times$ 16–22 μ ; cell V about two times longer than broad, 20–25 μ $\times$ 8–10 μ , its free upper surface slightly convex; cell VI well-defined, small, nearly isodiametric.

Appendages: Insertion cell compressed, oblique, opaque externally, lying below the level of the middle of the perithecium. Basal cell of the outer appendage slightly longer than broad, bearing, at first, a single straight or curved branch that may bear several simple branchlets successively internally; the basal cell of the outer branch giving rise usually to a single short tapered inner branchlet; the outer inferior surface of the outer appendage becoming dark brownish-red and nearly opaque; the longest outer appendages 45–70 μ . Basal cell of the inner appendage subtending usually three subequal cells that bear single flask-shaped antheridia, 12–15 μ $\times$ 5–6 μ , having darkened basal septa; antheridia persistent, displaced laterally by the development of simple branchlets 30–45 μ long.

Perithecium: Olivaceous, paler near the slightly out-turned tip, 65–85 μ long $\times$ 20–32 μ wide, the distal ½ free; apex suffused and opaque internally and laterally below the hyaline tips of the lip-cells; the opacity extending upward along the lateral margin of the inner lip-cells; pore directed slightly outward.

Total length from foot to tip of perithecium, 200–300 μ (mean, 245 μ ; based on 8 mature individuals).

Etym.—Named for the late Carl J. Drake, U. S. National Museum, Washington, D.C., entomologist, student of aquatic Hemiptera.

Holotype.—CANAL ZONE. Fort Clayton, Feb., 1945, K. E. Frick; on posterior legs of *Rhagovelia* sp.; RKB 2017C; slides in RSA, FH.

This species was found in company with *L. rhagoveliae* and *L. usingerii* on a single individual of a species of *Rhagovelia*. It is readily distinguished from *L. usingerii* by its upright, branched outer appendage and by the production of usually three antheridia. The two anterior antheridia are displaced by simple branches that tend to become laterally divergent. Also, the distal one-half or more of the perithecium of *L. drakei* is free.

Laboulbenia rhagoveliae sp. nov.

(Fig. 3 e–f)

Receptaculum: Cellulae I–II fere hyalinae stipitem plus minusve rectum 80–200 μ longum $\times$ 12–23 μ latum gerentes; stipite 1½plo longior quam pars supernus. Cellulae III–V atroolivaceae minute vel grosse punctatae. Cellula VI parva inconspicua.

Appendices: Insertionis cellula complanata obliqua opaca. Cellula basilaris

appendicis externae parva paene isodiametria 1 ramum primum parvum simplicem sterilem gerens; ramo primo in aetate per ramum singulum simplicem internum robustum $75-95\mu$ longum substituto. Cellula basilaris appendicis internae 2 cellulas parvas antheridiiferas gignens; antheridiis singulis simplicibus persistentibus $10-11\mu \times 7\mu$ in aetate ramis singulis sterilibus $35-90\mu$ longis appendicibus externis similibus substitutis.

Perithecium: Atroolivaceum inferne punctatum sursum ad apicem pallescens $50-75\mu$ longum $\times 16-25\mu$ latum infra et lateraliter receptaculo adnatum; apice solum libero intrinsecus nigro.

Totus fungus $130-265\mu$ longus.

Receptacle: Cells I-II nearly hyaline, forming a more or less straight stalk, $80-200\mu$ long $\times 13-23\mu$ wide, often $1\frac{1}{2}-2$ times the length of the distal portion, the basal cell slightly longer than the subbasal; cells III-V well-defined, dark olivaceous, delicately to coarsely punctate, adnate to the posterior $4/5$ of the perithecium; stalk-cell (VI) small, inconspicuous.

Appendages: Insertion cell broad, compressed, oblique, lying above the level of the middle of the perithecium, becoming almost completely opaque externally. Basal cell of the outer appendage slightly longer than broad, bearing at first a single, usually smallish branch that is displaced outward by the formation, internally, of a usually simple, robust, tapered branchlet $75-90\mu$ long. Basal cell of the inner appendage subtending two subequal inner and outer cells that bear flask-shaped antheridia having blackened basal septa; antheridia, $10-11\mu \times 7\mu$, persistent, displaced laterally by the development of usually single, elongate, tapered sterile branchlets $35-90\mu$ long.

Perithecium: Dark olivaceous, paler near the tip, $50-75\mu$ long $\times 16-25\mu$ wide, the distal $1/5$ free, the lower $2/3$ delicately punctate; apex deeply suffused and opaque internally below the hyaline tips of the lip-cells; pore directed slightly outward.

Total length from foot to tip of perithecium, $130-265\mu$ (mean, 205μ ; based on 20 mature individuals).

Fig. 3. a-b. *Laboulbenia usingerii* Benjamin.—a. Immature individual showing greatly elongated basal and subbasal cells of receptacle and strongly reflexed, simple outer appendage. The inner appendage bears two antheridia. $\times 530$.—b. Mature individual. The antheridia have been displaced laterally by development of simple sterile branches. $\times 400$.—c-d. *Laboulbenia drakei* Benjamin.—c. Immature individual showing branching pattern of outer appendage and the formation of three antheridia by the inner appendage. $\times 530$.—d. Mature individual. Each antheridium has been displaced laterally by development of simple sterile branches; those displacing the two inner antheridia are laterally divergent. A single cell replaces cells III-V of upper receptacle. $\times 400$ (Note: Because of some distortion in the mounted specimen, the inner margin of the perithecium depicted in this drawing appears slightly concave; in undisturbed specimens it is slightly convex).—e-f. *Laboulbenia rhagoveliae* Benjamin.—e. Immature individual. The inner of the two antheridia is already being displaced by development of a branchlet. The elongate outer branchlet of the outer appendage is more strongly developed in this individual than in any other of the many specimens examined. Usually this branch is greatly reduced as shown in the next figure. $\times 530$.—f. Mature individual. Note the small, spur-like primary branch of the outer appendage that is characteristic of most individuals of this species. Both antheridia have been displaced by sterile branches. Note degree of adnation of perithecium to cells of upper receptacle. $\times 400$.

Etym.—Named for the host genus, *Rhagovelia*.

Holotype.—CANAL ZONE. Fort Clayton, Feb., 1945, K. E. Frick; on lower surface of abdomen, antennae and anterior legs of *Rhagovelia* sp.; RKB 2017A; slides in RSA, FH.

Other specimens examined.—CANAL ZONE. Gatun, March, 1930, T. O. Zschokke; on trochanter of right anterior leg of *Rhagovelia uncinata* Champion; RKB 1901B; slides in RSA.—MEXICO. Puebla: Chignaulingo, 16 Aug., 1959, coll. unknown; on anterior leg of *Rhagovelia* sp.; RKB 2413; slide in RSA.

The outer appendage of this species typically consists of a tiny, divergent, primary branchlet situated externally at the base of the large, simple, secondary branchlet. In mature individuals the spur-like outer branchlet usually has been destroyed in whole or in part. The outer appendage is more or less erect rather than reflexed as in *L. usingerii*. Like the latter, the inner appendages of *L. rhagoveliae* are simple. The degree of adnation of the perithecium of *L. rhagoveliae* to the upper receptacle is more complete than in any other species on Veliidae.

Laboulbenia truxalii sp. nov.

(Fig. 4 a-c)

Receptaculum: Cellulae I-II subaequales paene hyalinae stipitem aliquantum sigmoideum $95-110_{\mu}$ longum $\times$ $12-20_{\mu}$ latum gerentes; stipite $\frac{1}{2}$ toti longitudinis fungi aequanti. Cellulae II-V atroolivaceae minute punctatae; cellulis III-IV in cellulam unam grandem $20-27_{\mu}$ $\times$ $17-20_{\mu}$ unitis. Cellula V obliqua $20-25_{\mu}$ $\times$ $8-10_{\mu}$. Cellula VI parva paene isodiametria conspicua.

Appendices: Insertionis cellula complanata lata aliquantum obliqua opaca. Cellula basilaris appendicis externae pauxillum longior quam lata extrinsecus nigra 1 ramum primum sterilem gerens; cellula basilaris rami primi ramum secundarium gignenti; ramis primis et secundariis saepe ramulos gerentibus; appendice longissima $50-75_{\mu}$. Cellula basilaris appendicis internae 2 cellulas antheridiiferas gignens; antheridiis singulis simplicibus persistentibus $13-15_{\mu}$ $\times$ $7-9_{\mu}$ in aetate saepe ramis sterilibus $40-50_{\mu}$ longis appendicibus externis similibus substitutis.

Perithecium: Inferne olivaceum divergente ad apicem attenuatum et pallescens $\frac{1}{2}$ liberum $80-100_{\mu}$ longum $\times$ 25_{μ} latum; cellulis labiis internis processum hyalinum in apicem rotundatum 7_{μ} latum $\times$ 10_{μ} longum gerentibus.

Totus fungus circa 200_{μ} longus.

Receptacle: The basal and subbasal cells subequal, nearly hyaline, forming a slightly sigmoid stalk, $95-110_{\mu}$ long $\times$ $13-20_{\mu}$ wide, that is about $\frac{1}{2}$ the total length of the individual; cells II-V becoming dark olivaceous at maturity and marked externally by numerous minute, conspicuous punctae; cells III-IV replaced by a single large cell, $20-25_{\mu}$ $\times$ $17-20_{\mu}$; cell V about two times longer than broad, $20-25_{\mu}$ $\times$ $8-10_{\mu}$, oblique, its free upper surface slightly convex; cell VI small, nearly isodiametric, well-defined.

Appendages: Insertion cell compressed, broad, slightly oblique, becoming opaque externally, lying slightly below the level of the middle of the perithecium.

Basal cell of the outer appendage slightly longer than broad, forming, at first, a single branch that bears usually three successive branchlets internally, the last often bearing a single branchlet externally; the basal cell of the outer appendage giving rise to a single simple or branched branchlet; the outer inferior surface of the outer appendage becoming dark reddish brown and nearly opaque; the longest branches, 50–75 μ . Basal cell of the inner appendage subtending two

Fig. 4. a–c. *Laboulbenia truxalii* Benjamin.—a. Immature individual showing sterile, branched outer appendage and two antheridia borne on the inner appendage. $\times 530$.—b. Individual in intermediate stage of development showing developing perithecium and appendages. The antheridia are being displaced laterally by sterile branches. $\times 400$.—c. Nearly mature individual showing paired, rounded projections of inner lip-cells of perithecium. Note single cell in place of cells III–IV in upper receptacle. $\times 400$.

subequal cells that bear single flask-shaped antheridia, 13–15 μ $\times$ 7–9 μ , having darkened basal septa; antheridia persistent, displaced laterally by the development of simple or once-branched branchlets; the longest branchlets 40–50 μ .

Perithecium: Divergent, tapered, olivaceous below, paler above, 80–100 μ long $\times$ 25 μ wide, the distal $\frac{1}{2}$ free; the two inner lip-cells each forming a hyaline

rounded protuberance about 7μ wide $\times$ 10μ long; pore directed slightly outward.

Total length from foot to tip of perithecium about 200μ .

Etym.—Named for Fred S. Truxal, Los Angeles County Museum of Natural History, entomologist, student of aquatic Hemiptera.

Holotype.—MEXICO. Puebla: Chignaulingo, 16 Aug., 1959, coll. unknown; on middle and anterior legs of *Rhagovelia* sp.; RKB 2414; slides in RSA.

Laboulbenia truxalii is distinguished by its slightly sigmoid habit and relatively elongate perithecium the inner lip-cells of which bear separate bluntly rounded protuberances. The fungus depicted in Fig. 4c is the most mature of 13 specimens studied. I doubt that it represents a fully mature individual. Thus, when additional material is available the description may require slight modification, especially with regard to pigmentation.

SPECIES ON *Macrovelia* (MACROVELIIDAE).

Laboulbenia macroveliae sp. nov.

(Fig. 2 c-d)

Receptaculum. Cellula basilaris (I) prope hyalina $30-60\mu$ longa $\times$ $16-22\mu$ lata. Cellula subbasilaris (II) subpentagona olivacea $17-25\mu$ longa $\times$ $24-35\mu$ lata supra minute punctata. Cellulae III-IV conspicuae atroolivaceae subaequales punctatae. Cellula V concolora parvula triangularis minute punctata. Cellula VI complanata parva conspicua.

Appendices. Insertionis cellula complanata obliqua opaca. Cellula basilaris appendicis externae parva isodiametrica 1 ramum primum sterilem prope basem extrinsecus obscurum gerens; ramo primo ramulos plures internos successive gerenti; cellula basilaris rami primi ramum simplicem vel ramosum gignenti; appendice longissima $60-80\mu$. Cellula basilaris appendicis internae 2 cellulas parvae isodiametricae antheridiiferas gignens; antheridiis singulis simplicibus persistentibus $10-15\mu$ $\times$ $6-8\mu$ in aetate saepe ramis simplicibus sterilibus usque ad 80μ longis substitutis.

Perithecium. Atroolivaceum inferne punctatum sursum ad apicem attenuatum et pallescens $\frac{1}{2}$ liberum $65-85\mu$ longum $\times$ $25-35\mu$ latum; cellulis labiis internis processum extrinsecus denigratum $7-9\mu$ longum $\times$ $6-7\mu$ latum in apicem rotundatum gerentibus; sporis $35-40\mu$ $\times$ 4μ .

Totus fungus $120-170\mu$ longus.

Receptacle. Basal cell (I) hyaline, two to three times as long as broad, $30-60\mu$ $\times$ $16-22\mu$, the rest of the receptacle more or less deep olivaceous and delicately punctate; cell II subpentagonal in lateral view, $17-25\mu$ long $\times$ $24-35\mu$ wide, separated from cell I by a more or less constricted septum; cells III-IV well-defined, subequal; cell V smaller, its upper margin free, convex; cells III-V obliquely adnate to the posterior lower $1/3-1/2$ of the perithecium; stalk-cell (VI) small, compressed, well-defined.

Appendages. Insertion cell compressed, oblique, lying well below the level of the middle of the perithecium, becoming nearly opaque. Basal cell of the outer appendage rounded externally, bearing, at first, a single branch the outer

branchlet of which is sharply recurved and blackened externally below and bears usually several inner branchlets successively; the basal cell of the outer branch giving rise to a short branch that may, in turn, form one or more branchlets; the longest outer branchlets reaching $60\text{--}80\mu$. Basal cell of the inner appendage small, subtending subequal inner and outer cells that bear single flask-shaped antheridia having blackened basal septa; antheridia persistent, $10\text{--}15\mu \times 6\text{--}8\mu$, usually displaced laterally by the development of often simple branchlets up to 80μ long.

Perithecium: Deep olivaceous and punctate below, paler above, $65\text{--}85\mu$ long $\times$ $25\text{--}35\mu$ wide, the distal $\frac{1}{2}$ or more free, tapering to the slightly outcurved tip; the inner lip-cells extending beyond the outer lip-cells and forming a conspicuous broad prominence, $7\text{--}9\mu$ long $\times$ $6\text{--}7\mu$ wide, that is deeply suffused and opaque externally below its hyaline apex, the opacity extending $10\text{--}15\mu$ below the hyaline outer lip-cells; pore directed upward and outward. Spores about $35\text{--}40\mu \times 4\mu$.

Total length from base of foot to tip of prominence of perithecium, $120\text{--}170\mu$ (mean, 150μ ; based on 31 mature individuals).

Etym.—Named for the host genus, *Macrovelia*.

Holotype.—CALIFORNIA. San Bernardino County: Ice House Canyon, San Gabriel Mts., 4 June, 1954, R. K. Benjamin; on legs of *Macrovelia hornii* Uhler; RKB 1904A; slides in RSA, FH.

Other specimens examined.—CALIFORNIA. San Bernardino County: type locality, 8 Oct., 1953, 11 Aug., 1954, R. K. Benjamin; on legs of *Macrovelia hornii*; RKB 1681A, 1903A; slides in RSA.—Riverside County: Lake Fulmor Recreation Area, San Jacinto Mts., 10 miles north of Idyllwild, 4 Aug., 1955, R. K. Benjamin; on legs of *Macrovelia hornii*; RKB 2023A; slides in RSA.—Ventura County: Mt. Pinos, 5 miles west of Frazier Peak, 17 Oct., 1956, R. K. Benjamin; on legs of *Macrovelia hornii*; RKB 2406; slides in RSA.

This species and *Laboulbenia uhlerii* are the only Laboulbeniales known on the Macroveliidae. Although they have been collected only in southern California, they probably occur on their host, *Macrovelia hornii*, throughout its range. *Laboulbenia macroveliae* is distinguished from *L. uhlerii* by the conformation of its perithecium, especially. The prolonged, internally blackened inner lip-cells of *L. macroveliae* (Fig. 2d) contrast sharply with the bluntly rounded, externally blackened, slightly protruding outer lip-cells of *L. uhlerii* (Fig. 2h).

Laboulbenia uhlerii sp. nov.

(Fig. 2 g-h)

Receptaculum: Cellula basilaris (I) hyalina a latere convexa $40\text{--}55\mu$ longa $\times$ $20\text{--}25\mu$ lata; septo superno constricto. Cellula subbasilaris (II) $\frac{1}{2}$ longa quam cellula I fere isodiametria infra paene hyalina supra olivacea et minute punctata. Cellula III-IV subaequales atroolivaceae punctatae distinctae vel in cellulam unam unitae. Cellula V parva triangula. Cellula VI parva indistincta.

Appendices: Insertionis cellula complanata obliqua opaca. Cellula basilaris appendicis externae paxillum longior quam lata 1 ramum primum sterilem ad basem externe nigrum gerens; cellula basilari rami primi ramum secundarium gignentem; ramis primis et secundariis ramulos tertiarios gerentibus; appendice

longissima 175μ . Cellula basilaris appendicis internae 2 cellulas parvas antheridiiferas gignens; antheridiis singulis simplicibus persistentibus $14-16\mu \times 6-7\mu$ in aetate saepe ramis simplicibus sterilibus usque ad 100μ longos substitutis.

Perithecium: Inferne olivaceum et minute punctatum ad apicem aliquantum attenuatum et pallescens $\frac{1}{2}$ liberum $65-75\mu$ longum $\times$ $25-35\mu$ latum; apice late rotundato; cellulis labiis externe nigris.

Totus fungus $115-158\mu$ longus.

Receptacle: Basal cell (I) hyaline, about twice as long as broad, $40-55\mu$ long $\times$ $20-25\mu$ wide, separated from cell II by a markedly constricted septum; cell II nearly isodiametric, about $\frac{1}{2}$ the length of cell I, slightly broader than long, pale below, becoming olivaceous above; the rest of the receptacle olivaceous, minutely punctate; cells III-IV subequal, well-defined or replaced by a single large cell; cell V smaller, its upper margin free, externally convex between the insertion cell and the posterior margin of the perithecium.

Appendages: Insertion cell relatively broad, compressed, oblique, lying below the level of the middle of the perithecium, becoming almost wholly opaque. Basal cell of the outer appendage slightly longer than broad, rounded externally, bearing, at first, a single branch the outer branchlet of which is sharply recurved and blackened externally below and bears usually several inner branchlets successively, these often forming branchlets; the basal cell of the outer branch giving rise to an inner branch that forms several successive branchlets internally; branchlets straight or slightly curved, the longest often reaching 175μ . Basal cell of the inner appendage small, subtending subequal inner and outer cells that bear single flask-shaped antheridia having blackened basal septa; antheridia $14-16\mu \times 6-7\mu$, persistent, unmodified at maturity or displaced laterally by the development of an often simple sterile branch up to 100μ long.

Perithecium: Olivaceous, paler above, $65-75\mu$ long $\times$ $25-35\mu$ wide, the distal $\frac{1}{2}$ free, tapering to the bluntly rounded or slightly truncate hyaline apex which is turned slightly inward; outer lip-cells relatively large, extending beyond the smaller inner lip-cells, externally suffused and opaque; pore directed slightly inward. Spores about $35-40\mu \times 4\mu$.

Total length from base of foot to tip of perithecium, $115-158\mu$ (mean, 139μ ; based on 21 mature individuals).

Etym.—Named for the late Philip R. Uhler, entomologist and geologist.

Holotype.—CALIFORNIA. San Bernardino County: Ice House Canyon, San Gabriel Mts., 8 Oct., 1953, R. K. Benjamin; on the upper and lower surface of the abdomen of *Macrovelia hornii* Uhler; *RKB 1681B*; slides in RSA, FH.

Other specimens examined.—CALIFORNIA. San Bernardino County: the type locality, 4 June and 11 Aug., 1954, R. K. Benjamin; on the abdomen and legs of *Macrovelia hornii*; *RKB 1903B, 1904B*; slides in RSA.—Riverside County: Lake Fulmor Recreation Area, San Jacinto Mts., 10 miles north of Idyllwild, 4 Aug., 1955, R. K. Benjamin; on upper and lower surface of the abdomen of *Macrovelia hornii*; *RKB 2023B*; slides in RSA.

This species was contrasted with *Laboulbenia macroveliae*, its congener on *Macrovelia hornii*, under the description of the latter given above.

DISCUSSION

Among the more interesting aspects of the biology of the Laboulbeniales are

the specificity phenomena and patterns of distribution of these parasites on their arthropod hosts. With few exceptions a given species of fungus is limited to a given host species, to closely related species of a genus, or to species of closely related genera. All species of many genera of Laboulbeniales apparently are confined to certain narrowly limited groups of insects. Among those genera for which a sufficient number of species have been discovered to suggest the existence of definite host preferences are *Amorphomyces* (Thaxter, 1893, 1931) and *Dichomyces* (Thaxter, 1893, 1908, 1931) on Staphylinidae, *Eucantharomyces* (Thaxter, 1895, 1908, 1926) on Carabidae, *Autoicomycetes* (Thaxter, 1908, 1931) on Hydrophilidae and many others. Remarkable examples of position specificity and sex-of-host specificity also are well known in these fungi (Benjamin & Shanor, 1952; Benjamin, 1965; Thaxter monographs, numerous references).

The Coleoptera are parasitized by the majority of the described species of Laboulbeniales. On the basis of my present knowledge of them I recognize some 113 genera of these parasites. All known species of 90 genera occur only on members of the Coleoptera; seven genera occur not only on Coleoptera but also on one or more other orders of insects or on mites; and 16 genera are found on insect orders other than Coleoptera. The monotypic genus, *Trogloomyces* Colla (1932), is the only member of the order known on the Diplopoda.

A few genera of Laboulbeniales apparently have been more successful in exploiting new host groups than have other genera. The occurrence of species of *Laboulbenia* on seven orders of true insects and one order of arachnids was mentioned above. *Dimeromyces* (Thaxter, 1896, 1908, 1924, 1926) also is a large genus with species known on at least five orders of insects as well as a few mites. *Corethromyces* species (Thaxter, 1892, 1896, 1908, 1931) are numerous on Coleoptera, especially families of the superfamily Staphylinoidea, but one species has been reported on an earwig (Dermaptera) and one species on a true bug (Hemiptera). *Autophagomyces* (Thaxter, 1912, 1931), *Hesperomyces* (Thaxter, 1891, 1896, 1931), *Stigmatomyces* (Thaxter, 1896, 1908, 1931), and *Rickia* (Thaxter, 1926) are other genera having species on hosts belonging to more than one order. With the exception of *Stigmatomyces* and *Rickia*, the majority of species belonging to genera having a more or less wide host range are found on Coleoptera with a relatively small number of species occurring on other orders. Species of *Stigmatomyces* predominate on various families of Diptera, but several are known on Staphylinidae and Scydmaenidae of Coleoptera. *Rickia*, with over 100 known species, is only slightly more abundant on Coleoptera than on mites—mostly species associated with beetles—and has one species on Orthoptera and one on Hymenoptera.

Among the 15 genera of Laboulbeniales infecting insects other than members of the Coleoptera, there are several that do not appear to be closely related to other known forms. *Herpomyces* (Thaxter, 1902, 1908, 1931; Richards & Smith, 1954) on several families of cockroaches (Blattaria) and *Tettigomyces* (Thaxter, 1915, 1926) on Mole crickets (Orthoptera: Gryllotalpidae) are notable examples. Some genera appear certainly to have evolved from forms clearly related to other known genera. *Arthrorhynchus* (Thaxter, 1896, 1908) on Nycteribiidae and *Gloeandromyces* (Thaxter, 1931) on Streblidae have characteristics that indicate a direct relationship with *Stigmatomyces*, a genus common on free-living

flies. The Nycteribiidae and Streblidae are families of parasitic flies restricted to bats. *Rhizomyces* (Thaxter, 1896, 1908, 1931), with species known only on flies of the family Diopsidae, and *Ilytheomyces* (Thaxter, 1917, 1931), in which all species are limited to a single genus of flies, *Ilythea* (Ephydriidae), resemble *Corethromyces* in many respects. *Trenomyces* (Chatton & Picard, 1909; Thaxter, 1926), a dioecious genus that appears related to the widespread *Dimeromyces*, includes the only Laboulbeniales found on Mallophaga. These insects are all specialized parasites of birds and mammals. It is perhaps significant that several as yet undescribed species of *Trenomyces* are known on Hippoboscidae, a family of ectoparasitic flies that also are found only on birds and mammals. The phoretic association of Mallophaga and Hippoboscidae is well known (Bequaert, 1953, p. 163).

The Laboulbeniales, then, as presently known are predominately parasites of Coleoptera. Several genera have exploited other orders of insects, even a few representatives of two other classes of arthropods. Many genera are restricted to single closely related taxa of hosts, and the characteristics of some of these do not offer clues to their possible alliance with other genera of Laboulbeniales. Several taxa, however, do appear to be derived from forms resembling other known genera, and some of these probably evolved from an ancestral fungus that was present on an ancestral host that invaded a new habitat as in the case of insects now parasitic on other animals. Conversely, new types undoubtedly have evolved following the ecological invasion of a new type host by an ancestral fungus. Among genera of Laboulbeniales having a wide host range, it is not uncommon that only one or a very few species of a given genus are on insects completely unrelated to the group providing hosts for the majority of the species. Many examples of such disjunct distribution almost certainly illustrate cases of fortuitous colonization of new host groups. Such colonization—probably a rare event in nature—and the resulting isolation of the colonizer and its progeny undoubtedly has led to the development of several genera known today as well as to many of the obviously closely related species groups in such large genera as *Laboulbenia*.

All of the Laboulbeniales that had been described earlier on Hemiptera were summarized in the introduction. *Coreomyces*, known only on the Corixidae, has a type of perithecial development that is unique among the Laboulbeniales, and the genus does not appear to be closely related to any other genus in the order. *Polyandromyces*, a dioecious genus in which the receptacle of the male produces a large terminal compound antheridium and the female a single lateral perithecium, probably is a derivative of a *Dimeromyces*-like ancestor. The monotypic *Rhizopodomycus* on Hebridae also is dioecious, but here the male has a simple two-celled receptacle terminated by a simple antheridium. The female likewise has a two-celled receptacle terminated by a single perithecium in which the greatly elongated stalk-cell forms part of the apparent stalk of the receptacle. This genus may be distantly related to other dioecious genera such as *Amorphomyces* and *Dioicomycus* (Thaxter, 1896, 1901, 1908, 1931) but the single known species on *Merragata* and *Hebrus* does not bear much resemblance to known species of these genera. A very distinct species of *Dioicomycus*, as yet undescribed, taken from one of the Mesoveliidae is in my collection. With the exception

of two species on Staphylinidae, all other known species of *Dioicomyces* occur on species of Anthicidae (Coleoptera). The Mesoveliidae, according to Brues, Melander & Carpenter (1954) are allied with the Hebridae in the superfamily Aradoidea of the Hemiptera. Thus, the past association of a *Dioicomyces*-like precursor of *Rhizopodomycetes* on this group of bugs is a possibility.

The occurrence of a species of *Corethromyces* on a member of the Lygaeidae, *Autophagomyces* on one of the Veliidae, and *Hesperomyces* on one of the Anthocoridae may be only examples of what I call fortuitous colonization resulting from close association of unrelated insects sharing the same environment. *Corethromyces* is a large genus that is especially abundant on beetles of the superfamily Staphylinoidea. These insects abound in habitats similar to those of the chinch bugs and their relatives (Lygaeidae). *Hesperomyces*, although not a large genus as presently known, does have four species on Coccinellidae (Coleoptera) which commonly live on plants where they would be associated with the pirate bugs or flower bugs (Anthocoridae). *Autophagomyces* has at least 15 known species on Coleoptera belonging to the families Pselaphidae, Anthicidae, Orthoperidae, and Phalacridae (all Coleoptera), many species of which live in moist debris and litter bordering pools and streams frequented by Veliidae.

More than half of the known species of *Laboulbenia* occur on Carabidae—the well-known ground beetles. Many species of this family of insects share the shore environment of the semi-aquatic bugs. Thus, transfer in the past of a *Laboulbenia* from a carabid beetle to one of the Veliidae is highly probable.

Except for *Coreomyces* on Corixidae and *Laboulbenia* on Veliidae and Macroveliidae, too few species of the genera parasitizing Hemiptera are known for one to visualize adaptive radiation of a parasite following its successful colonization of a new host group. As was stated earlier, *Coreomyces* is a unique generic type among known Laboulbeniales, and its affinities with other members of the order are obscure. *Laboulbenia*, on the other hand, is a large genus parasitizing many diverse groups of arthropods. Within the genus there are many complexes in which the included species obviously are more closely related to one another than to other members of the genus. Some 40 species of *Laboulbenia*—some as yet undescribed—are known on Gyrinidae (Coleoptera) throughout the world. Although each species may be more or less limited to certain hosts and thus have a restricted range, all of the species on this family of beetles have more features in common with one another—especially appendage characteristics—than they have with other *Laboulbenia* species on other families of beetles. The evolution of this particular line from a common ancestor along with the divergence of the Gyrinidae is a logical explanation of this group similarity. There are numerous other examples of unique species complexes on specific groups of insects not only in *Laboulbenia* but in other large widely distributed genera of Laboulbeniales as well. Thaxter (1896, 1908, 1924, 1926, 1931) alluded to many of these in his writings on these fungi.

The discovery of eight additional species of *Laboulbenia* on Veliidae and Macroveliidae brings to ten the number now known on Hemiptera—all from the Western Hemisphere. An examination of the accompanying illustrations reveals that the development and gross morphology of these species have many char-

acteristics in common. The greatest similarity is found in the immature individuals, especially in the appendages. Immature specimens of Thaxter's *Laboulbenia veliae* were not present in his slide mounts of this species, but in his preparations of *L. hemipteralis* several were found so that comparisons of the latter with the other species are possible. In all of the species, a relatively broad insertion cell is followed immediately above by a single posterior and a single anterior cell. The former bears a simple, or more often, a branched sterile appendage, whereas the latter gives rise to two, rarely three, cells that in turn bear usually single simple antheridia. The antheridia, in all species, persist on the mature individual, but they commonly are displaced laterally by development of simple or branched sterile appendages similar to those subtended by the posterior basal cell. When mature, the species differ more or less greatly in the elongation of cells I and II, the degree of adnation of the perithecium with the upper cells of the receptacle, and the modification of the lip-cells. In all, however, the upper cells of the receptacle tend to become deeply pigmented and more or less conspicuously punctate. The perithecium, too, usually is concolorous with the upper receptacle and likewise may be variably punctate.

Although all of these species appear related, a degree of divergence is evidenced by the parasites. The four species on *Rhagovelia* comprise two somewhat distinct groups, i.e. *Laboulbenia usingerii*-*L. rhagoveliae* and *L. drakeii*-*L. truxalii*. In both of the latter species, cells III-IV of the receptacle are replaced by a single cell. This feature also is common to *L. microveliae* on *Microvelia*. This characteristic is not unique to these fungi, however, for a similar tendency toward reduction in the number of cells in the upper part of the receptacle is found in species of *Laboulbenia* infecting other unrelated groups of insects, i.e. species on Diptera and some Coleoptera (Chrysomelidae). When more species are known, the patterns of divergence of the parasites of Veliidae should become more apparent.

Although the Veliidae and Macroveliidae occur in similar habitats and resemble one another superficially, they are not regarded as very closely related (Usinger, 1956). The two families are placed in separate superfamilies by Brues, Melander & Carpenter (1954). The Veliidae, like the closely related Gerridae, have preapical tarsal claws and thus are able to skate over water without breaking the surface film. The Macroveliidae, however, have apical claws and are unable to walk on the surface film; they do, however, live very near water in a perpetually moist environment. Details of the life history of the Macroveliidae apparently still are unknown. As yet, *Laboulbeniales* are not known on Gerridae. I have examined many representatives of this family during the past 18 years without success. Discovery of these fungi, especially *Laboulbenia*, on the gerrids would be most desirable in view of the occurrence of eight species of the latter on Veliidae. The occurrence on Macroveliidae of two species of *Laboulbenia* that appear to be related to those on Veliidae may be only the result of the close association of these insects in a similar habitat. It may, however, indicate a closer relationship between these insects than is suspected at present.

SUMMARY

All *Laboulbeniales* previously described on insects of the order Hemiptera

are summarized briefly, and the distribution of the 26 known species of these fungi on the various taxa comprising the order is noted. Only the species of *Laboulbenia* occurring on semi-aquatic insects of the families Veliidae and Macroveliidae are described in detail. In addition to *Laboulbenia veliae* and *L. hemipteralis* described on *Velia platensis* by Thaxter in 1912, six new species on Veliidae are characterized as follows: *Laboulbenia microveliae* and *L. leechii*, on *Microvelia*; and *L. drakei*, *L. rhagoveliae*, *L. truxalii*, and *L. usingerii* on *Rhagovelia*. Two species, *L. macroveliae* and *L. uhlerii*, are described on *Macrovelia hornii*, a member of the Macroveliidae, and represent the first Laboulbeniales found on this family of semi-aquatic bugs.

The general distribution of Laboulbeniales on arthropods is discussed. Members of the Coleoptera among the true insects serve as hosts for the majority of the species of these fungi. The disjunct occurrence on an unrelated host of a species of a genus in which most species are otherwise found on a narrowly circumscribed taxon is perhaps due to fortuitous colonization—the transfer and successful development of a parasite on a new host. The existence of apparently closely related groups of species of various genera of Laboulbeniales on definitive host taxa is viewed as the result of adaptive radiation following successful transfer of a species of parasite to a new host group. A few, perhaps many, genera of Laboulbeniales undoubtedly have evolved following invasion of a new type host by an ancestral fungus. Similarly, ecological isolation of a parasitized ancestral host surely has led to development of new fungus types. For example, the Nycteribiidae and Streblidae are families of parasitic flies narrowly restricted to bats. The first is infected by species of *Arthrorhynchus* and the second by species of *Gloeandromyces*. These genera of Laboulbeniales are distinct from but obviously related to *Stigmatomyces* which is widely distributed on free-living flies.

Morphological similarities of the thallus, especially immature stages, of the ten known species of *Laboulbenia* on the semi-aquatic Veliidae and Macroveliidae suggest a common ancestry for these fungi. Although the Veliidae, which are true water-striders, and the Macroveliidae, which are unable to walk on water, resemble one another superficially, they are not regarded as very closely related by entomologists who place them in separate superfamilies, the Gerroidea and Aradoidea respectively. The insects, however, always are closely associated in the perpetually moist environment of pools, lakes and streams. The occurrence of apparently related laboulbeniaceae parasites on these two families of semi-aquatic bugs may be the result only of the close association of the insects in their environment, or the insects themselves may be more nearly related than is evidenced by present knowledge.

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