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TAXONOMY AND MORPHOLOGY OF *APOROMYCES* (LABOULBENIALES)

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ABSTRACT

Thaxter's original circumscription of *Aporomyces* (Laboulbeniales) is emended in this study of the eight known species of the genus, three of them new: *A. byrrhini*, *A. lutrochi*, and *A. physemi*. The new species, as well as *A. subulatus*, *A. szaboi*, *A. trinitatis*, and *A. uniflagellatus* (type), are dioecious and occur on beetles belonging to the Limnichidae (Coleoptera: Dryopoidea). The eighth species, *A. perpusillus*, appears to be monoecious and occurs on Staphylinidae (Coleoptera: Staphylinoidea). All taxa are described and illustrated with line drawings and/or photographs. Aspects of thalloid structure and development are summarized. *Aporomyces* is removed from tribe Euphoriomyceteae (as subtribe Aporomycetinae) and elevated to the rank of tribe, Aporomyceteae.

Key words: *Aporomyces*, Byrrhidae, Coleoptera, fungi, insects, Laboulbeniales, Limnichidae, morphology, taxonomy.

INTRODUCTION

The genus *Aporomyces* was described by Thaxter (1931) to accommodate three new taxa, *A. subulatus*, *A. trinitatis*, and *A. uniflagellatus*, found on beetles then included in the family Byrrhidae (Coleoptera). The first two species, on hosts identified simply as species of *Limnichus* Latreille, were clearly dioecious; each perithecial individual was accompanied by a diminutive male consisting of three superposed cells terminated by a single antheridium. Antheridia were not found on any of the similar small individuals associated with the perithecium-bearing thalli of *A. subulatus*, on *Byrrhinus punctatus* Pic, so the dioecious nature of this fungus, although indicated, could not be firmly established.

Bánhegyi (1944) added a fourth species of *Aporomyces*, *A. szaboi* Bánhegyi, found on *Pelochares versicolor* Walzl, also referred at the time to the Byrrhidae, in several localities in the vicinity of Lake Balaton, Hungary. This species bears some resemblance to *A. uniflagellatus* in the nature of both the female and male thalli.

Tavares (1981), who examined several type collections of Laboulbeniales described by Spegazzini, determined that *Ecteinomyces perpusillus* Speg. (Spegazzini 1917), found on a myrmecophilous species of Staphylinidae (Coleoptera), *Rhopalophorus gestroi* Bernhauer, belonged instead to *Aporomyces*. *Aporomyces perpusillus* (Speg.) Tavares differs from other members of the genus in its apparent monoecy; antheridia have not been observed, however. Like many monoecious Laboulbeniales, perithecium-bearing thalli of *A. perpusillus* often are associated in pairs; diminutive thalli resembling the male or presumed male of the other species of *Aporomyces* are unknown in *A. perpusillus*.

With the exception of the staphylinid host of *Aporomyces perpusillus*, the host genera given for the other four species of *Aporomyces*, i.e., *Limnichus*, *Byrrhinus*

Motschulski, and *Pelochares* Mulsant & Rey, belong to the Limnichidae rather than the Byrrhidae as given by Thaxter (1931) and Bánhegyi (1944). The placement of the limnichids with the byrrhids, based primarily on certain superficial resemblances of the adults of these insects, has a long history (Hinton 1939a, b). The Limnichidae began as a tribe of the Byrrhidae (Erichson 1847) but was elevated to the rank of family and placed near the Dryopidae by Thomson (1860). However, subsequent students usually recognized the group only as a tribe or subfamily of Byrrhidae (Dalla Torre 1911; Leng 1920:192) until Hinton (1939a, b) carried out detailed studies of external and internal anatomy of members of these taxa and resurrected the family Limnichidae, which he removed from the superfamily Byrrhoidea and placed in the superfamily Dryopoidea near the family Dryopidae, in line with Thomson's earlier opinion. Recognition of the Limnichidae as a family of Dryopoidea now seems well established (Arnett 1962, 1985; Blackwelder 1944; Crowson 1955; Leech and Chandler 1956; Wooldridge 1986).

Limnichid beetles are very small (1–3 mm in length), oval or convex, brownish to blackish, sometimes metallic, and may be invested with dense, fine, golden or grayish hairs. They are mostly riparian and commonly occur in and around debris, among rocks, or on mudflats near the waterline. They may be taken in blacklight traps placed near suitable habitats.

The only other member of the Laboulbeniales described from Limnichidae is *Cantharomyces bordei* Picard (1912), found on *Limnichus sericeus* (Duft.) in Algeria. This species also has been reported from Italy on *L. incanus* Kiesenw. by Rossi and Cesari Rossi (1980).

During my many years of accumulating Laboulbeniales, I have obtained a number of forms representing several genera infesting Limnichidae. It is intended that this material be the subject of several separate studies. My purpose here is to present a taxonomic survey of *Aporomyces* and to give an account of the morphology and development of representative species. The work includes an emendation of Thaxter's original circumscription of the genus, a key to the species, and descriptions and illustrations of eight taxa, three of them new.

MATERIALS AND METHODS

The hosts bearing *Aporomyces* were originally received preserved in 50–70% ethyl alcohol, or in the case of those from T. E. Brooks, dry and layered on soft tissue paper in pill boxes. The dried insects were relaxed in 0.3% NaCl in H₂O and transferred to 70% ethyl alcohol for ease of manipulation. Collection data are given following the descriptions in the taxonomic section.

Using techniques given previously (Benjamin 1971:101, 1986:247), I mounted the fungi on slides in glycerine containing a trace of cotton blue or acid fuchsin.

Through the cooperation of the curator of the Farlow Herbarium, Dr. Donald H. Pfister, I received for study Thaxter's type and other collections of the species of *Aporomyces* he described. Dra. Irma J. Gamundi de Amos, Instituto de Botanica "Spegazzini," La Plata, Argentina, kindly arranged for me to receive and study Spegazzini's type collection of *Ecteinomyces perpusillus*, which had been on loan to Dr. Isabelle Tavares at the University of California, Berkeley.

Hosts were kindly identified by Dr. David P. Wooldridge, Department of Biology, The Pennsylvania State University, Ogotz Campus, Abington.

Direct observations and the preparation of drawings and photomicrographs

were carried out with the aid of a Leitz Dialux microscope equipped with differential interference contrast optics. Kodak Technical Pan Film #2415, 4 in. $\times$ 5 in., was used. The camera was a WILD MPS 15/11 Semiphotomat with ASA settings of 80 or 125. Film was developed for 8 min in Kodak HC-110, Dilution D or F, at 20 C. Prints were made on Kodak Polyfiber FS paper.

Where applicable, terminology and abbreviations used to describe and discuss the fungal thallus are those of Tavares (1985:431–434). Some modifications in terminology were necessitated because of deviations in the development of the perithecium of *Aporomyces*.

TAXONOMY

APOROMYCES Thaxter. Mem. Amer. Acad. Arts 16:74. 1931, emended R. K. Benjamin.

Diocious (or monoecious[?]). *Male individual*: Consisting of two or three superposed cells terminated by a single simple antheridium; sometimes consisting of a small number of superposed cells without an identifiable antheridium. *Female individual*: Receptacle at first consisting of three superposed cells, I, II, and III; subsequently consisting of a uniseriate row of few to many cells corresponding to the true basal cell (I), a variable number of cells derived from cell II, and cell III, which subtends a simple or branched, few-celled primary appendage. Simple or branched secondary appendages, if present, arising from cell III and/or cell-II derived cells of the receptacular axis above the perithecium. Perithecium developed from a single terminal or intercalary cell (the perithecial initial) of the receptacular axis derived from cell II; often appearing terminal at maturity; bearing near its base or on its outer, posterior surface the upper part of the receptacular axis and the associated appendages. The lower part of the ascigerous cavity of the mature perithecium bounded below by the adjacent cell of the receptacle and laterally by the lower part of the greatly enlarged perithecial initial. Primary stalk cell (VI) absorbed; secondary stalk cell (VII) persisting in some species and displaced upward posteriorly along with the perithecial basal cells and wall cells. The upper part of the perithecium, enclosed by the distal part of the perithecial initial, consisting of five basal cells and five vertical rows of inner and outer wall cells of two or three cells each. Walls of upper outer wall cells persistent; walls of basal cells and one or more cells of the lower tier of outer wall cells persistent or not. In some species, one upper outer wall cell giving rise to a unicellular prolongation the tip of which protrudes from the open tip of the perithecial initial, which functions as the ostiole. Ascospores 2-celled, elongate fusiform, typically dimorphic.

Type species: Aporomyces uniflagellatus Thaxter.

The number of receptacular cells of *Aporomyces* varies according to species. Thaxter (1931:74) noted that the receptacle elongates secondarily by intercalary division. Although proof was not obtained in my study, I have followed Tavares (1985:60) in her assumption that the lower segment of most laboulbenialean ascospores initially divides and produces a primary receptacle consisting of a basal cell (I), a subbasal cell (II), and a terminal cell (III). Cell I forms the foot. Cell III subtends the primary appendage derived from the upper spore segment.

In some genera cell III may subdivide and contribute to the ultimate shape and size of the receptacle, including the formation of secondary appendages, or it may, as in members of the Stigmatomycetinae, undergo no change save for increase in size. Cell II may give rise directly to the perithecial initial, as in Stigmatomycetinae, or it too may divide or subdivide. The resulting receptacle may be bulky and three dimensional, due to both longitudinal and transverse divisions, or it may be uniseriate as in *Aporomyces* and several other genera (for examples see Tavares 1985:61). In such genera, including *Aporomyces*, one or more cell II-derived cells may give rise to perithecia or secondary appendages.

A KEY TO THE SPECIES OF *APOROMYCES*

- A. Receptacle below the perithecium consisting of a uniseriate row of several cells (more than two) above the basal cell B
 - Receptacle below the perithecium consisting invariably of only two superposed cells above the basal cell F
- B. Receptacle above the perithecium consisting of an elongate cellular axis of many cells (9–20) terminated by the primary appendage and bearing along its length a number of branched secondary appendages (on *Lutrochus*: Limnichidae) 5. *A. lutrochi*
 - Receptacle above the perithecium consisting of an axis of only a few cells (2–5) terminated by the primary appendage; secondary appendages few or absent C
- C. Perithecial apex attenuate, prolonged some distance beyond the level of the tips of the upper outer wall cells, one of which forms a slender cellular upgrowth which protrudes beyond the apical opening (on *Physemus*: Limnichidae) 4. *A. physemi*
 - Perithecial apex blunt; tips of upper outer wall cells nearly level with the apical opening or slightly protrudent D
- D. Secondary appendages not formed; primary appendages simple, often elongate, soon deciduous; mature perithecium usually with a single cell of the upper receptacle more or less imbedded in its upper, posterior surface (on *Pelochares*: Limnichidae) 1. *A. uniflagellatus*
 - Secondary appendages formed, few in number, arising from cell III or from the distal cell or cells of the upper receptacular axis E
- E. Upper receptacle consisting of 3–4 large, more or less flattened cells below cell III (on *Pelochares*: Limnichidae) 2. *A. szaboi*
 - Upper receptacle consisting of only one cell below cell III (on *Limnichoderus*: Limnichidae) 3. *A. trinitatis*
- F. Thallus small, well under 100 μm in length; paired perithecial individuals (presumably mon-oecious) (on *Rhopalophorus*: Staphylinidae) 8. *A. perpusillus*
 - Thallus larger, exceeding 100 μm in length; perithecial individuals paired with a simple, reduced thallus (?male); presumably dioecious (on *Byrrhinus*: Limnichidae) G
- G. Thallus somewhat geniculate; long axis of the perithecium diverging nearly at a 45° angle from that of the lower receptacle; cell III curved 6. *A. subulatus*
 - Thallus nearly straight; long axis of the perithecium in line with that of the lower receptacle; cell III straight 7. *A. byrrhini*

1. *APOROMYCES UNIFLAGELLATUS* Thaxter. Mem. Amer. Acad. Arts 16:75. 1931.

Fig. 1–10

Male individual. — Nearly hyaline; consisting of a 3-celled receptacle and a terminal antheridium; usually more or less curved; basal cell of receptacle elongate, 10–16 $\times$ 4–6 μm distally; median and upper cells often slightly rounded externally, subequal, or the upper cell slightly longer than the median cell, 3–5(–7) $\times$ 4–7 μm ; antheridium 8–13 $\times$ 4–6 μm . Total length 22–38 μm .

Female individual. — Receptacle below the perithecium 27–150(–195) μm long, nearly hyaline or pale yellowish, consisting of the basal cell (I) and 4–19 (average

10) somewhat flattened or squarish cells derived from cell II, forming a nearly straight or slightly curved perithecial stalk 11–21(–24) μm wide distally, tapering downward gradually to the elongate basal cell; the latter usually reddish brown, with nearly parallel outer margins, 13–25(–27) $\times$ 7–11 μm ; the foot broader, opaque, flat below; receptacle above the perithecium terminated by cell III, which is only slightly longer than broad, 6–10 $\times$ 4–9 μm , and usually two cells derived from cell II. *Primary appendage* rarely persistent on mature individuals; simple, variable in length, 30–140 $\times$ 6–9 μm ; consisting of a variable number (6–9 observed) of elongate cells. *Secondary appendages* not observed. *Perithecium* reddish brown, slightly more than twice as long as broad, nearly symmetrical, 30–35 $\times$ 14–26 μm , the lower margins parallel or slightly convex, abruptly tapered to the blunt apex; posterior margin bearing usually only one persistent receptacular cell which is more or less imbedded in the perithecial wall above the middle of the perithecium; walls of secondary stalk cell (VII), basal cells, and the three tiers of outer wall cells inconspicuous but persistent; walls of upper two tiers of inner wall cells persistent. Female ascospores 25–30 $\times$ 3 μm ; male ascospores 15–20 $\times$ 2 μm .

Total length from base of foot to tip of perithecium: 65–195(–245) μm .

Specimens examined.—AFRICA. CAMEROONS: Gross Batanga, 1911, on ?*Pelochares* sp. (as *Limnichus* sp.), George Schwab coll., *Thaxter* 2267 (Acc. No. 3451 [TYPE], 3452, 3454, 3455; FH).—JAPAN. OKINAWA: Shana Wan, Sep 1945, on *Pelochares ryukyuensis* Sato, G. E. Bohart coll., *RKB* 3095 (RSA).—PHILIPPINE ISLANDS. LEYTE: locality not given, 16 Apr, 3, 12, 17 Jun 1945, on *P. diversus* (Pic), C. L. Remington coll., *RKB* 2783, 2784, 2786, 2787 (RSA); Tarraghoa, 10 Sep 1945, on *P. diversus* and *P. philippinensis* Deleve, C. L. Remington coll.; *RKB* 2785 (RSA).—LUZON: Los Baños, May 1924, on ?*Pelochares* (as ?*Limnichus* sp.), C. F. Baker coll., *Thaxter* 3225 (Acc. No. 3453, 3460; FH).—MINDANAO: Cotabato Prov., Liguasan marsh, 21 Dec 1946, on *P. diversus*, F. G. Werner coll., *RKB* 395 (RSA).—MINDORO: San Jose, Nov 1945, on *P. diversus*, E. S. Ross coll., *RKB* 3108 (RSA).—SUMATRA. Ft. de Kock, date ?, on ?*Pelochares* sp. (as ?*Limnichus* sp.), E. Jacobson coll., *Thaxter* 3163 (Acc. No. 3459; FH); Jan 1923, on ?*Pelochares* sp. (as ?*Limnichus* sp.), E. Jacobson coll., *Thaxter* 3181 (Acc. No. 3456, 3457, 3458; FH).

Thaxter's collections of *Aporomyces uniflagellatus* from the Cameroons, Philippine Islands, and Sumatra, comprise some 23 mature or nearly mature females, 9 immature females, and 15 males. The type collection from the Cameroons includes about half the mature females, 10 males, and all but one of the immature females. My specimens, which compare in all respects with the type, include over 90 mature or nearly mature females, 49 immature females, and 71 males.

Although the number of receptacular cells may vary greatly, the receptacle of *A. uniflagellatus* usually is long, rather slender, and relatively uniform in width above the narrow, elongate basal cell (Fig. 2, 3, 9). It becomes only moderately widened distally where it joins the perithecium. The mature, nearly symmetrical perithecium, with its long axis in line with that of the receptacle (Fig. 2, 3, 9), typically bears only one large cell on its upper outer surface (Fig. 5–8)—all that remains of the upper part of the young receptacle and the simple, elongate primary appendage (Fig. 1, 9). *Aporomyces szaboi*, which also occurs on *Pelochares*, is readily distinguished from *A. uniflagellatus* by its more inflated perithecium and the several-celled remnant of the upper part of the receptacle, which often bears the broken remains of secondary appendages and the branched primary appendage (Fig. 12; see also Bánhegyi 1944, Pl. I, fig. 1, 3–4, and Pl. II, fig. 1, 3).

The presently known distribution of *A. uniflagellatus*, from Okinawa south

Fig. 1-8. *Aporomyces uniflagellatus* (Fig. 1, 5-8: RKB 2784; Fig. 2, 3: RKB 2786; Fig. 4: RKB 2783).—1. Young female showing the receptacle consisting of a basal cell (I), a terminal cell (III) (separated from the primary appendage [pa] by the original spore septum [a]), and a uniseriate row

through the Philippines and Sumatra west into Africa, indicates that the species probably is widespread throughout the warmer regions of the Old World.

Dr. Wooldridge's determination of my hosts to *Pelochares* spp. suggests that the hosts of Thaxter's collections of *A. uniflagellatus* may have belonged to *Pelochares* rather than *Limnichus*.

2. *APOROMYCES SZABOI* Bánhegyi. Bot. Kozlem. 41:51. 1944. Fig. 11-12

Male individual.—Hyaline to pale yellow, 25–28 μm long, 5–6 μm wide; consisting of a 3-celled, slightly curved receptacle and a terminal antheridium; basal cell of receptacle 5–6 μm long, with a blackened foot; median and upper cells quadrangular, 3.5–4 μm long; antheridium 12 μm long, venter cylindrical, neck attenuate.

Female individual.—*Receptacle* below the perithecium 80–110 $\times$ 18–29 μm , pale yellow, consisting of 4–14 quadrangular or somewhat flattened cells; basal cell about twice as long as broad; foot opaque; receptacle above the perithecium consisting of 3–4 slightly flattened cells terminated by cell III, which is longer than broad, and the primary and often several secondary appendages, the combination of upper receptacle and appendages 110–140 μm long. *Primary appendage* simple or branched, composed of more or less elongate cells. *Secondary appendages* arising from cell III and one or more of the distal cells of the upper receptacle, consisting of variably elongate cells, usually more or less broken or missing on mature individuals. *Perithecium* dark reddish brown, broadest below, asymmetrical, 50–58 $\times$ 29–34 μm ; apex nearly hyaline, flat; anterior margin very slightly convex; posterior margin strongly convex, bearing the persistent upper receptacle and appendages above the middle of the perithecium. Female ascospores 34–35 $\times$ 3 μm ; male ascospores 24–25 $\times$ 2.5 μm .

Total length of fungus from base of foot to tip of perithecium: (80–)130–185 μm .

Records.—HUNGARY. Vicinity of Lake Balaton: Balatonszemes, 24 Jul 1940, 3–4 Aug 1943; Fonyód, 20 Jul 1939; Keszthely, 5 Aug 1943; Tihany, 6 Aug 1943; on *Pelochares versicolor* Waltl; J. Bánhegyi coll.

I have seen no specimens of *Aporomyces szaboi* and have had to depend on Bánhegyi's original description and illustrations for my interpretation of the species. Bánhegyi presented photographs of six mature and one immature individuals, and I have constructed drawings based on two of these (Fig. 11, 12). *Aporomyces szaboi* appears on the basis of its morphology to be more like *A. uniflagellatus* than any other species of the genus. It differs most noticeably from *A. uniflagellatus* in the shape of its perithecium and especially in the larger number of upper receptacular cells, which, along with the branched primary appendage and an

←

of cell II-derived cells. A distal cell of the receptacle is forming a perithecium (*per*) bearing a trichogyne (*tr*).—2, 3. Mature females with males at their base.—4. Male showing terminal antheridium (*an*).—5–8. Perithecium shown at four levels of focus: near, near median, far median, and far, respectively. The tips of the five terminal outer wall cells are indicated by arrowheads. The five terminal inner wall cells are shown between the arrows in Fig. 6 and 7. (Fig. 1, 4: bar with Fig. 4 = 10 μm ; Fig. 2, 3: bar with Fig. 3 = 50 μm ; Fig. 5–8: bar with Fig. 8 = 10 μm .)

Fig. 9–12. —9–10. *Aporomyces uniflagellatus* (Fig. 9: RKB 2783; Fig. 10: RKB 3095). —9. Mature female showing primary appendage (*pa*) (bar = 20 μ m). —10. Female in which the primary perithecium has aborted. A two-celled upgrowth has developed into the perithecial cavity from the subtending receptacular cell. A secondary perithecium is beginning to develop from another cell of the receptacular axis (arrow) (bar = 10 μ m). —Fig. 11–12. *Aporomyces szaboi* (drawn from photographs in Bánhegyi 1944, Pl. I, fig. 2 and 4 respectively). —11. Immature female (bar = 20 μ m). —12. Mature female with associated male (bar = 20 μ m).

occasional secondary appendage (Fig. 11), surmount the upper posterior surface of the perithecium (Fig. 12; see also Bánhegyi 1944, Pl. I, fig. 1, and Pl. II, fig. 1, 3).

3. APOROMYCES TRINITATIS Thaxter. Mem. Amer. Acad. Arts 16:75. 1931.

Fig. 13–20, 67–80

Male individual. — Nearly hyaline; consisting of a 3-celled receptacle and a terminal antheridium; often strongly curved, especially the basal cell; basal cell of receptacle, including foot, 8–15 $\times$ 4–5 μ m distally; median and upper cells externally nearly straight or slightly rounded, subequal, or the upper cell slightly longer than the median cell, 4–7 $\times$ 4–5 μ m; antheridium 18–35 $\times$ 3–4 μ m, the neck somewhat longer than the venter. Total length 33–48 μ m.

Female individual. — *Receptacle* below the perithecium (60–)70–90 μ m long, consisting of the basal cell (I) and 8–10 squarish to more or less flattened cells derived from cell II, broadest distally, 24–31 μ m wide, rather abruptly narrowed downward, 6–10 μ m wide above the basal cell, which is dark yellowish brown, 10–21 $\times$ 6–10 μ m distally; the foot broad, flat, marginally opaque, often with a spinose

lateral projection; the 3–4 cells above the basal cell dark yellowish brown to reddish brown, often nearly opaque, especially the septa; the remaining cells pale yellowish brown to nearly hyaline; receptacle above the peritheciium terminated by cell III, which is only slightly longer than broad, $5-7(-10) \times 4-6(-7) \mu\text{m}$, and a single cell derived from cell II. *Primary appendage* rarely persistent on mature individuals, hyaline, simple, up to $120 \mu\text{m}$ long, $4-5 \mu\text{m}$ wide near the base, consisting of a small number (2–4 observed) of elongate cells. *Secondary appendages* few, arising from cell III or the subtending receptacular cell derived from cell II; simple or branched, straight or slightly curved, consisting of 1–4 elongate cells, the longest up to $100 \mu\text{m}$, $3-5 \mu\text{m}$ wide. *Peritheciium* uniformly reddish brown except for the hyaline tip; broadly rounded below, somewhat asymmetrical; posterior margin more strongly convex than the anterior margin, $40-60 \times 30-45 \mu\text{m}$; tapered to the blunt apex; bearing on the posterior margin the persistent upper receptacular cell, which is more or less imbedded in the perithecial wall at or slightly below the middle of the peritheciium, and usually cell III and the remnants of the primary and secondary appendages; walls of secondary stalk cell (VII), basal cells, the three tiers of outer wall cells, and upper two tiers of inner wall cells persistent. Female ascospores $30-40 \times 3 \mu\text{m}$; male ascospores $25-30 \times 2 \mu\text{m}$.

Total length from base of foot to tip of peritheciium: $(105-120-145 \mu\text{m})$.

Specimens examined. — COSTA RICA. Picuare, Rio General, 1 Jul 1967, on *Limnichoderus lutrochinus* (Le Conte), P. J. Spangler coll., RKB 3098 (RSA). — HONDURAS. Olanchito, 21 Jun 1949, on *L. naviculatus* (Casey), E. C. Becker coll., RKB 2781 (RSA). — MEXICO. CHIAPAS: Las Nubes, Volcan de Tacana, 6 Aug 1950, on *L. lutrochinus*, C. & M. Goodnight coll., RKB 1576 (RSA). — COLIMA. San Antonio, 26 Mar 1970, on *L. lutrochinus*, H. P. Brown coll., RKB 3096 (RSA). — SAN LUIS POTOSÍ: El Banito, nr. Ciudad Valles, 17 Jul 1970, on *L. naviculatus*, A. Newton coll., RKB 3115 (RSA). — PUERTO RICO. Rio Cañas, 24–27 Apr 1965, on *L. barberi* Wooldg., H. P. Brown coll., RKB 3097 (RSA). — TRINIDAD. ST. GEORGE: brook, Maraval Valley, Port of Spain, date ?, on ?*Limnichoderus* sp. (as *Limnichus* sp.), coll. ?, Thaxter 2882 (Acc. No. 3447 [TYPE], 3448, 3449, 3450; FH). — U.S.A. ARKANSAS: Washington Co., 2 Apr 1941, on *Limnichoderus naviculatus*, M. W. Sanderson coll., RKB 2788 (RSA). — CALIFORNIA: Riverside Co., 10 mi W of Indio, 1 Apr 1955, on *L. naviculatus*, R. K. Benjamin coll., RKB 1891 (RSA); Mesa de Colorado, Santa Ana Mts., 6 Jun 1969, on *L. naviculatus*, R. K. Benjamin coll., RKB 2627 (RSA). — OKLAHOMA: Marshall Co., campus of Univ. of Okla. Biol. Sta., 10, 18, 23 Jun 1971, on *L. lutrochinus*, T. E. Brooks coll., RKB 2770, 2771, 2779, 3117 (RSA). — TEXAS: Gonzales Co., Palmetto State Park, 14 Jun 1969, on *L. naviculatus*, M. W. Sanderson coll., RKB 2790 (RSA). — VENEZUELA. D. F.: Rio Las Carácas, 20 Jun 1968, on *L. vicinus* Pic. H. P. Brown coll., RKB 3099 (RSA); Rio Chiquito, 20 Jun 1968, on *L. vicinus*, H. P. Brown coll., RKB 3105 (RSA).

Thaxter's four slide mounts of *Aporomyces trinitatis* from Trinidad include 17 mature or nearly mature females, 14 immature females, and 8 males. In all of the female specimens the contents of the immature and mature perithecia are more or less disorganized, a condition I suspect was true when Thaxter studied the material. This would account for his not being able to discern aspects of early stages of perithecial development (Thaxter 1931:74). Thaxter attributed the host of *A. trinitatis* to *Limnichus*; however, this genus of Limnichidae does not occur in the New World (Wooldridge, pers. comm.). Like the hosts of my collections of *A. trinitatis* from North, Central, and South America, the host of Thaxter's collection doubtless belonged to *Limnichoderus*, which resembles the Old World *Limnichus* (Wooldridge 1981). The range of the collections of *A. trinitatis* cited above suggest that the species is widely distributed on *Limnichoderus* in the New World.

Fig. 13–20. *Aporomyces trinitatis* (Fig. 13–15, 19: RKB 2771; Fig. 16, 20: RKB 2770; Fig. 17–18: RKB 3117).—13–15. Female with immature perithecium shown at three levels of focus: near, median, and far, respectively. Shows relationship of the five basal cells (*m*, *m'*, *mac*, *n*, and *n'*) to cells VI and VII. The perithecium is at the two-outer-wall-cell stage of development and the first inner wall cells (*p*) have formed. For a drawing of this perithecium see Fig. 75. Further details are in the text.—16. Mature female with associated male (out of focus).—17, 18. Two nearly mature perithecia shown in optical section. The positions of the three tiers of inner (*p*) and outer wall cells (*w*¹, *w*², *w*³), basal cells

My specimens of *Aporomyces trinitatis* include nearly 100 mature or nearly mature females, about 160 immature females, and some 30 males. Not all of the material is in the best condition, but many specimens, both immature and mature, are well-preserved and give a good over-all picture of thalloid and perithecial development (Fig. 13–15, 17, 18, 67–79) as will be described in this paper.

The reddish-brown pigmentation of the lower three to four cells of the lower receptacle of *Aporomyces trinitatis* is perhaps the one characteristic that most readily distinguishes the species from *A. uniflagellatus* and *A. physemi*, the only other taxa with which it might be confused. The basal cell of the receptacle may or may not be deeply pigmented. Like *A. physemi*, the upper cells of the receptacle of *A. trinitatis* are relatively broad compared to the proximal cells (cf. Fig. 16, 24). The basally inflated, asymmetric, reddish-brown perithecia are similar in the two species, but that of *A. trinitatis* lacks the narrow, elongate, hyaline termination and slender cellular upgrowth of one terminal outer wall cell of *A. physemi* (Fig. 24, 32).

4. *Aporomyces physemi* Benjamin, sp. nov.

Fig. 21–33

Mas.—Hyalinus. *Receptaculum* cellularum 2 constans; cellula basilaris elongata $11\text{--}15 \times 4\text{--}5 \mu\text{m}$; cellula superna isodiametra $4\text{--}5 \times 4\text{--}5 \mu\text{m}$. *Antheridium* $10\text{--}13 \times 4\text{--}5 \mu\text{m}$. *Thallus* totus $25\text{--}30 \mu\text{m}$ longus.

Femina.—*Receptaculum* infra perithecium rectum prope hyalinum, $45\text{--}60\text{--}(75) \mu\text{m}$ longum, cellulae basilaris (I) et cellularum $6\text{--}10\text{--}(12)$ ($\bar{x} = 8$) superpositorum applanatarum ex cellula II constans, ad apicem $13\text{--}22 \mu\text{m}$ latum; cellula basilaris (I) hyalina $14\text{--}21 \times 6\text{--}8 \mu\text{m}$; pes latus denigratus prope opacus. *Receptaculum* supra perithecium cellulae III et cellularum 2 superpositorum applanatarum ex cellula II constans; cellula III $4 \times 5\text{--}7 \mu\text{m}$. *Appendix primaria* recta vel arcuata, $20\text{--}40 \times 3\text{--}5 \mu\text{m}$, cellularum elongatarum 2–3 constans. *Appendices secundariae* ex cellula III et cellula subtenenti receptaculi oriundae, simplices, plerumque fortiter arcuatae, usque ad $55 \mu\text{m}$ longae, $3\text{--}5 \mu\text{m}$ latae, cellularum 1–3 elongatarum constantes. *Perithecium* atroporphyreum praeter apicem attenuatum elongatum hyalinum. *Corpus perithecii* asymmetricum, $34\text{--}50 \times 19\text{--}30 \mu\text{m}$; margo antica leniter convexa; margo postica fortiter convexa receptaculo supra perithecium et appendicibus in mediano affixa. Cellula VII, cellulae basales, et cellulae terminales et subterminales parietium interiora et exteriora persistentes. *Appendix gracilis unicellularis* $10\text{--}14 \mu\text{m}$ longa, ex cellula superna parietis enata. *Ascosporae femineae* c. $25 \times 2.5 \mu\text{m}$; *ascosporae masculae* c. $20 \times 2 \mu\text{m}$. *Thallus* totus $(80\text{--})85\text{--}100\text{--}(125) \mu\text{m}$ longus ad apicem perithecii. Typus RKB 2754 (RSA).

Male individual.—Hyaline; consisting of a 2-celled receptacle and a terminal antheridium; nearly straight or somewhat curved; basal cell of receptacle, including foot, elongate, $11\text{--}15 \times 4\text{--}5 \mu\text{m}$ distally; upper cell isodiametric, $4\text{--}5 \mu\text{m}$ wide and high; antheridium $10\text{--}13 \times 4\text{--}5 \mu\text{m}$. Total length $25\text{--}30 \mu\text{m}$.

Female individual.—*Receptacle* below the perithecium $45\text{--}60\text{--}(75) \mu\text{m}$ long, nearly hyaline; consisting of the basal cell (I) and $6\text{--}10\text{--}(12)$ (average 8) superposed somewhat flattened cells derived from cell II; forming a nearly straight, multi-

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(bc), and the secondary stalk cell (VII) are indicated in Fig. 18. These cells also can be seen clearly in Fig. 17. Note the extent of the ascigerous cavity, most of which has resulted from enlargement of cell VI and the basal part of the original perithecial initial.—19. Paired female (left) and male (right) ascospores.—20. Paired very immature male (left) and female (right) individuals in which the foot is differentiating from the lower end of the basal cell. The original spore septum (a) is indicated. (Fig. 13–15, 17–20: bar with Fig. 18 = $10 \mu\text{m}$; Fig. 16: bar = $20 \mu\text{m}$.)

Fig. 21–25. *Aporomyces physemi* (Fig. 21: RKB 2789; Fig. 22: RKB 2775; Fig. 23, 25: RKB 2772; Fig. 24: RKB 2754).—21. Immature female with associated male (mostly out of focus) at base. The receptacle consists of a basal cell (I), a series of superposed cells derived from cell II, and cell III, which subtends the primary appendage (*pa*).—22. Immature female with associated male (out of

cellular perithecial stalk 13–22 μm wide distally, which tapers downward gradually and is somewhat abruptly narrowed immediately below its juncture with the basal cell; basal cell hyaline, with nearly parallel margins, $14\text{--}21 \times 6\text{--}8 \mu\text{m}$; the foot broader, black, more or less opaque, flat below; receptacle above the perithecium terminated by cell III, which is broader than long, $4 \times 5\text{--}7 \mu\text{m}$ at maturity, and usually two superposed, somewhat flattened cells derived from cell II. *Primary appendage* rarely persistent on mature individuals; straight or curved, 20–40 μm long, 3–5 μm wide; consisting of 2–3 elongate cells. *Secondary appendages* arising from cell III and the subtending receptacular cell; simple, usually strongly curved; the longest up to 55 μm long, 3–5 μm wide; consisting of 1–3 elongate cells. *Perithecium* dark reddish brown except for the hyaline, somewhat elongate, narrow tip; broadest below, asymmetrical, $34\text{--}50 \times 19\text{--}30 \mu\text{m}$; anterior margin only slightly convex; posterior margin strongly convex, bearing the persistent upper receptacular cells and appendages near the middle of the perithecium; walls of secondary stalk cell (VII), basal cells, the two tiers of outer and inner wall cells persistent; one posterior, upper, outer wall cell giving rise to an elongate, slender, unicellular upgrowth, 10–14 μm long, which may project slightly beyond the terminal opening. Female ascospores about $25 \times 2.5 \mu\text{m}$; male ascospores about $20 \times 2 \mu\text{m}$.

Total length from base of foot to tip of perithecium: (80–)85–100(–125) μm .

Etymology.—Named for the host genus, *Physemus*.

Holotype.—U.S.A. TEXAS: Aransas Co., Aransas National Wildlife Refuge, 15 Jun 1969, on *Physemus minutus* Le Conte, M. W. Sanderson coll., RKB 2754 (RSA).

Other specimens examined.—HONDURAS. Twelve km W of Olanchito, 8 Sep 1949, on *Physemus excavatus* Wooldg., E. C. Becker coll., RKB 2791 (RSA).—MEXICO. JALISCO: Thirteen mi NW of Bana de Navidad, 18 Sep 1971, on *P. ?excavatus*, A. Newton coll., RKB 3114 (RSA).—U.S.A. OKLAHOMA: Marshall Co., campus of Univ. of Okla. Biol. Sta., 10, 23 Jun 1971, on *P. minutus*, T. E. Brooks coll., RKB 2773, 2775 (RSA); Lake Texoma, Buncombe Recreation Area, 15 Jun and 8 Jul 1971, T. E. Brooks coll., RKB 2772, 2774 (RSA).—TEXAS: Gonzales Co., Palmetto State Park, 14 Jun 1969, on *P. minutus*, M. W. Sanderson coll., RKB 2789 (RSA).

The above description of *Aporomyces physemi* is based on 25 mature (Fig. 24, 25, 32) or nearly mature females and 18 males (Fig. 33) in the cited collections. Seventeen immature females provided material sufficient to study several pertinent stages of development of the thallus and perithecium (Fig. 21–23, 26–31). Details of these observations will be given later.

Aporomyces physemi resembles *A. trinitatis* more closely than any of the other species of the genus but is readily distinguished by its smaller size and differences in perithecial structure, i.e., the attenuate tip and the cellular upgrowth from one upper outer wall cell (compare Fig. 24 with Fig. 16–18).

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focus). The perithecium and female organ are at very early stages of development. For drawings see Fig. 29 and 30. See text for terminology.—23. Female with perithecium at the two-outer-wall-cell stage of development as seen in optical section. For individual at about the same stage of development see Fig. 31.—24. Mature female with associated male at base. See Fig. 32 for drawing.—25. Mature female showing development of secondary perithecium after abortion of the terminal primary perithecium. (All figures: bar with Fig. 25 = 10 μm .)

Fig. 26-35.—26-33. *Aporomyces physemi* (Fig. 26-31: RKB 2775; Fig. 32: RKB 2754; Fig. 33: RKB 2774).—26-31. Several stages of development of female and male individuals; see text for details and terminology. The young male shown in Fig. 30 was drawn separated slightly from its position at the base of the female (see Fig. 22); the terminal cell is intact, not yet having differentiated—into an antheridium as in the individual shown in Fig. 33.—32. Mature female with associated male (see Fig. 24).—33. Mature male showing two-celled receptacle separated from the terminal antheridium by the original spore septum (*a*).—34-35. *Aporomyces lutrochi* (RKB

Members of the host genus of *Aporomyces physemi*, *Physemus*, are minute beetles which are mostly 1 mm or slightly less in length (Wooldridge 1976, 1984).

5. *Aporomyces lutrochi* Benjamin, sp. nov.

Fig. 34-40

Mas.—Hyalinus. *Receptaculum* cellularum 2 constans; cellula basilaris $18-21 \times 4-7 \mu\text{m}$; cellula superna $5-8 \times 6-9 \mu\text{m}$. *Antheridium* $10-14 \times 6-8 \mu\text{m}$. *Thallus* totus $34-40 \mu\text{m}$ longus.

Femina.—*Receptaculum* infra perithecium prope hyalinum, interdum curvatum infra mediano, $115-145 \mu\text{m}$ longum, cellulae basilaris (I) et cellularum 9-13 superpositorum aliquanto applanatarum ex cellula II constans, ad apicem $31-39 \mu\text{m}$ latum; cellula basilaris (I) hyalina $21-30 \times 11-15 \mu\text{m}$; pes denigratus opacus. *Receptaculum* supra perithecium $105-225 \times 19-28 \mu\text{m}$ cellulae III et cellularum 9-20 superpositorum isodiametrarum vel applanatarum ex cellula II constans; cellula III $12-14 \times 8-9 \mu\text{m}$. *Appendix primaria* erecta, simplex vel ramosa, usque ad $50 \mu\text{m}$ longa, $5-6 \mu\text{m}$ lata, cellularum 2-3 elongatarum constans. *Appendices secundariae* ex cellula III et superficie superna cellularum plurium receptaculi superni oriundae; appendices ramosae, rami usque ad $100 \mu\text{m}$ longa, $4-6 \mu\text{m}$ lata, cum cellulis basilaribus $8-14 \times 6-8 \mu\text{m}$. *Perithecium* plus minusve hyalinum ad basin, porphyreum in parte superna praeter apicem hyalinum. *Corpus perithecii* symmetricum $59-81 \mu\text{m}$ longum, $43-58 \mu\text{m}$ latum ad basin; apex obtusus vix rotundatus; margo postica receptaculo supra perithecium et appendicibus ad basin affixa. Cellula VII et cellulae basiliares nondistinguibiles; cellulae parietium interiora et exteriora persistentes. *Ascospores* femineae $38-43 \times 5 \mu\text{m}$; *ascospores* masculae $17-21 \times 3 \mu\text{m}$. *Thallus* totus $180-225 \mu\text{m}$ longus ad apicem perithecii. Typus RKB 2364 (RSA).

Male individual.—Hyaline; rather stout, consisting of a 2-celled receptacle and a terminal antheridium; basal cell of receptacle, including foot, broadest distally, $18-21 \times 4-7 \mu\text{m}$, upper cell slightly broader than long, $5-8 \times 6-9 \mu\text{m}$, externally rounded; antheridium $10-14 \times 6-8 \mu\text{m}$, the neck short, divergent. Total length $34-40 \mu\text{m}$.

Female individual.—*Receptacle* below the perithecium $115-145 \mu\text{m}$ long, nearly hyaline; consisting of the basal cell (I) and 9-13 superposed somewhat flattened cells derived from cell II; forming a perithecial stalk $31-39 \mu\text{m}$ wide distally, which tapers downward gradually and often is more or less strongly curved below the middle; basal cell hyaline, broadest distally, otherwise the sides nearly parallel, $23-30 \times 11-15 \mu\text{m}$; the foot broader, blackish brown, flat below; receptacle above the perithecium terminated by cell III; consisting of 9-20 superposed isodiametric or slightly flattened cells derived from cell II and functioning as an elongate, simple appendage $105-225 \times 19-28 \mu\text{m}$ that diverges posteriorly from the base of the perithecium nearly at a right angle to the long axis of the lower receptacle; cell III $12-14 \times 8-9 \mu\text{m}$. *Primary appendage* hyaline, rarely persistent on mature individuals; simple or branched; up to $50 \mu\text{m}$ long, $5-6 \mu\text{m}$ wide; consisting of 2-3 elongate cells. *Secondary appendages* hyaline, arising from cell III and from the upper surface of several (4-7 observed) cells of the upper receptacle; consisting of a basal cell $8-14 \times 6-8 \mu\text{m}$ and several branches up to $100 \mu\text{m}$ long and $4-6 \mu\text{m}$ wide, these consisting of up to six elongate cells and bearing one or several shorter lateral branchlets. *Perithecium* more or less hyaline near the base, reddish

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2634).—34. Mature male showing two-celled receptacle separated from the terminal antheridium by the original spore septum (a).—35. Mature female and associated male (see Fig. 34 and 38). Note origin of secondary appendages (sa) from upper surface of cells of the upper part of the receptacle. (Fig. 26-31, 33: bar with Fig. 33 = $10 \mu\text{m}$; Fig. 32: bar = $10 \mu\text{m}$; Fig. 34: bar = $10 \mu\text{m}$; Fig. 35: bar = $20 \mu\text{m}$.)

Fig. 36–40. *Aporomyces lutrochi* (RKB 2634).—36. Immature female showing intercalary origin of the perithecium, which is at an early stage of development. The female organ consists of the carpogenic cell (*cp*), trichophoric cell (*tc*), and trichogyne (*tr*). Arrows indicate dividing receptacular cells.—37. Female and its associated male; the perithecium is at an intermediate stage of development.—38. Mature female with male at base (see Fig. 35).—39. Cluster of small male and large female ascospores. Note extreme spore dimorphism.—40. Upper end of receptacle showing cell III and the primary appendage (*pa*). Apices of secondary appendages project upward from the lower left. (Fig. 36, 39, 40: bar with Fig. 40 = 10 μ m; Fig. 37, 38: bar with Fig. 38 = 50 μ m.)

brown in the upper two thirds, except the hyaline tip; broadest below, symmetrical, $59-81 \times 43-58 \mu\text{m}$, tapered abruptly to the blunt, barely rounded apex; walls of secondary stalk cell (VII) and basal cells not clearly defined at maturity; walls of the three tiers of outer wall cells and the upper two tiers of inner wall cells persistent. Female ascospores $38-43 \times 5 \mu\text{m}$; male ascospores $17-21 \times 3 \mu\text{m}$.

Total length from base of foot to tip of perithecium: $180-225 \mu\text{m}$.

Etymology.—Named for the host genus, *Lutrochus*.

Holotype.—MEXICO. NUEVO LEON: Zaragoza, 3 Jul 1969, on *Lutrochus* sp., J. Mathieu and M. W. Sanderson coll., RKB 2634 (RSA).

Ten mature females, 14 immature females, and 13 males of *Aporomyces lutrochi* were found on the upper surface of four of 10 individuals of the host, a relatively large, unidentified species of *Lutrochus* measuring between 2 and 3 mm in length.

The elongate, multicellular receptacle of *A. lutrochi* is nearly straight before perithecial development begins. Unlike other species of the genus, the perithecium of *A. lutrochi* always arises from a receptacular cell remote from the upper end of the uniseriate axis (Fig. 36), which is terminated by cell III and the primary appendage (Fig. 40). As the perithecium develops and matures, the upper part of the receptacle is deflected laterally so that it becomes nearly perpendicular to or is at an acute angle to the lower part (Fig. 35, 37, 38). Secondary appendages arise from the upper, never the lower, surface of a variable number of cells of the upper receptacle (Fig. 35, 37, 38). As in *A. szabo*i (Fig. 11, 12), the apparent appendage of *A. lutrochi* consists largely of receptacular cells along with the variably persistent primary and secondary appendages.

The relatively tiny male ascospore always is closely associated with the base of a female ascospore (Fig. 39), and all of the 13 males recovered were still firmly attached to the foot of mature or nearly mature females (Fig. 35, 37, 38).

6. APOROMYCES SUBULATUS Thaxter. Mem. Amer. Acad. Arts 16:76. 1931.

Fig. 41-48, 54-60

Male individual.—Hyaline; consisting of a 3-celled, slightly curved receptacle and a terminal simple or once-branched, 2-3-celled appendage up to $50 \mu\text{m}$ long; differentiated antheridia not observed; basal cell of receptacle, including foot, $18-25 \times 4-5 \mu\text{m}$ distally; median and upper cells subequal, $6-8 \times 6-8 \mu\text{m}$. Total length $55-90 \mu\text{m}$.

Female individual.—Hyaline or very pale yellowish. *Receptacle* below the perithecium $35-50 \mu\text{m}$ long; consisting of the basal cell (I) and two superposed cells derived from cell II; broadest immediately below the base of the perithecium, $20-28 \mu\text{m}$ wide; tapered downward and abruptly narrowed near the middle of cell I; $7-9 \mu\text{m}$ wide above the broad, hyaline foot, which has a usually conspicuous anterior spinose projection; basal cell (I) $16-21 \mu\text{m}$ long, $14-18 \mu\text{m}$ wide distally; the succeeding two cells subequal, slightly broader than long, externally rounded; receptacle above the perithecium consisting only of cell III, which is elongate and slightly curved outward, $16-23 \times 6-8 \mu\text{m}$. *Primary appendage* simple, up to $225 \mu\text{m}$ long, $5-6 \mu\text{m}$ wide at the base; consisting of up to six elongate cells; often broken near the base of the subbasal cell and renewed by proliferation. *Secondary*

Fig. 41-53. —41-48. *Aporomyces subulatus* (Thaxter 2433). —41-46. Several stages of development of the female thallus. Pertinent details and terminology are given in the text. —47-48. Two presumptive males; antheridia not differentiated. —49-53. *Aporomyces perpusillus* (LPS 38636). —49-50. Two immature individuals showing origin of the perithecial initial (*d*) from the upper cell of the three cells derived from cell II of the receptacle. —51-53. Three mature individuals. (Fig. 41-48: bar with Fig. 46 = 10 μ m; Fig. 49-53: bar with Fig. 53 = 10 μ m.)

appendages not observed. *Perithecium* relatively slender, elongate, its axis divergent to nearly 45° from that of the receptacle; broadest near the base, $25\text{--}30\text{ }\mu\text{m}$ wide; gradually tapered, $85\text{--}100\text{ }\mu\text{m}$ long; with an elongate, attenuate termination extending $33\text{--}43\text{ }\mu\text{m}$ beyond the tips of the upper, outer wall cells; secondary stalk cell (VII) persistent, subtending cell III; only the walls of the upper one or two tiers of outer and inner wall cells persistent; one anterior upper, outer wall cell giving rise to an elongate, slender, unicellular upgrowth, $50\text{--}65\text{ }\mu\text{m}$ long, which projects up to $18\text{ }\mu\text{m}$ beyond the apical opening. Ascospores not precisely measurable within the perithecium; the longest ca. $40\text{--}45 \times 3\text{ }\mu\text{m}$.

Total length from base of foot to tip of perithecium: $120\text{--}145\text{ }\mu\text{m}$.

Specimens examined.—PHILIPPINE ISLANDS. LUZON: Manila, Dec 1911, on *Byrrhinus punctatus* Pic, coll. ?, Thaxter 2423 (Acc. No. 3439 [TYPE], 3440, 3441, 3442, 3443, 3444, 3445; FH).

Thaxter's type material is in excellent condition, and, if one may judge by comparing them with his drawings, the specimens appear to have remained unchanged during the nearly 60 years since Thaxter prepared his illustrations and description. The material consists of 25 mature females (Fig. 59, 60), 1 nearly mature female, 13 immature females in various stages of development (Fig. 41–46, 54–58), and 9 males (Fig. 47–48), none possessing an identifiable, clearly differentiated antheridium.

Aporomyces subulatus and *A. byrrhini* are morphologically very different from the species of *Aporomyces* discussed to this point. In both, the perithecium with its greatly prolonged beak terminates that part of the short receptacle derived from cell II of the young receptacle. The secondary stalk cell (VII) of the perithecium persists in the lower posterior part of the ascigerous cavity where it subtends cell III. The latter cell never is subtended by one or more receptacular cells derived from cell II as in the other species on Limnichidae.

The perithecial apex of *Aporomyces physemi* bears some resemblance to that of *A. subulatus* and *A. byrrhini* in extending well beyond the tips of the upper outer wall cells, although to a lesser degree. Like these species, one upper outer wall cell of *A. physemi* forms a cellular prolongation that projects through the ostiole (Fig. 24, 32).

7. *Aporomyces byrrhini* Benjamin, sp. nov.

Fig. 61–64

Mas.—Hyalinus. *Receptaculum* curvatum cellularum 3 constans; cellula basilaris $20 \times 5\text{ }\mu\text{m}$; cellulae medianae et terminales subaequales $9\text{--}11 \times 4\text{ }\mu\text{m}$. *Appendix* simplex cellularum plurium constans. *Antheridia* non visa.

Femina.—Hyalina. *Receptaculum* infra perithecium rectum, $52\text{--}60\text{ }\mu\text{m}$ longum, cellulae basilaris (I) et cellularum 2 superpositorum subaequalium cylindricarum $10\text{--}15 \times 16\text{--}19\text{ }\mu\text{m}$ ex cellula II constans, ad apicem $18\text{--}20\text{ }\mu\text{m}$ latum; cellula basilaris (I) constricta ad basin, $25\text{--}35\text{ }\mu\text{m}$ longa, $15\text{--}20\text{ }\mu\text{m}$ lata; pes denigratus prope opacus processu spiniformi laterali. *Receptaculum* supra perithecium cellulae III constans; cellula III elongata recta $17\text{--}26 \times 5\text{--}7\text{ }\mu\text{m}$. *Appendix primaria* simplex erecta $150\text{ }\mu\text{m}$ longa excedens (exempla observata effracta), cellularum plurium elongatorum gracilium c. $5\text{ }\mu\text{m}$ latarum ad basin constans. *Appendices secundariae* nullae. *Perithecium* gracile elongatum rectum uniformiter decrescens ad apicem, $85\text{--}90\text{ }\mu\text{m}$ longum, $18\text{--}19\text{ }\mu\text{m}$ latum ad basin; cellula VII persistens; solum cellulae terminales et subterminales parietum interiora et exteriora persistentes. *Appendix* gracilis unicellularis ex cellula superna parietis enata. Ascosporae c. $35\text{--}40 \times 2\text{ }\mu\text{m}$. *Thallus* totus $145\text{--}150\text{ }\mu\text{m}$ longus ad apicem perithecii. Typus *RKB 3107* (RSA).

Fig. 54-59. *Aporomyces subulatus* (Thaxter 2423).—54-56. Perithecial initial at median stage of development shown at three levels of focus: near, median, and far, respectively. Note relationship of wall cells to the wall of the perithecial initial, which projects upward and forms an elongate termination open at the tip. The tips of the five terminal outer wall cells are indicated by arrowheads.—57. Part

Male individual.—Hyaline; consisting of a 3-celled, curved receptacle and a terminal, simple appendage of several elongate cells; differentiated antheridia not observed; basal cell of receptacle, including foot, $20 \times 5 \mu\text{m}$; median and upper cells elongate, subequal, $9\text{--}11 \times 4 \mu\text{m}$.

Female individual.—Hyaline. *Receptacle* below the perithecium $52\text{--}60 \mu\text{m}$ long, straight; consisting of the basal cell (I) and two superposed cells derived from cell II; $18\text{--}20 \mu\text{m}$ wide immediately below the perithecium; tapered gradually downward to the base, which is somewhat constricted, ca. $9 \mu\text{m}$ wide immediately above the blackish, nearly opaque foot; the latter with a conspicuous posterior spinose projection; basal cell (I) $25\text{--}35 \mu\text{m}$ long, $15\text{--}20 \mu\text{m}$ wide distally; the succeeding two cells subequal, cylindrical, $10\text{--}15 \mu\text{m}$ long, $16\text{--}19 \mu\text{m}$ wide; receptacle above the perithecium consisting only of cell III, which is elongate, straight, $17\text{--}26 \times 5\text{--}7 \mu\text{m}$. *Primary appendage* subtended by cell III, simple, in excess of $150 \mu\text{m}$ long (observed examples with tip missing); composed of several elongate, slender cells, ca. $5 \mu\text{m}$ wide near the base. *Secondary appendages* not observed. *Perithecium* slender, elongate, its axis in line with that of the receptacle; broadest near the base, $18\text{--}19 \mu\text{m}$ wide, straight; gradually tapered to the tip, $85\text{--}90 \mu\text{m}$ long; with an elongate, attenuate termination extending ca. $25 \mu\text{m}$ beyond the tips of the upper, outer wall cells; secondary stalk cell (VII) small, persistent, subtending cell III; only the walls of the upper one or two tiers of outer and inner wall cells persistent; one distal outer wall cell giving rise to an elongate, slender, unicellular upgrowth which reaches the apical opening. Ascospores not precisely measurable within the perithecium; the longest ca. $35\text{--}40 \times 2 \mu\text{m}$.

Total length from base of foot to tip of perithecium: $145\text{--}150 \mu\text{m}$.

Etymology.—Named for the host genus, *Byrrhinus*.

Holotype.—MEXICO. COLIMA: El Cobano, 25 Mar 1970, on *Byrrhinus vestitus* (Sharp), H. P. Brown coll., RKB 3107 (RSA).

I have described *Aporomyces byrrhini* on the basis of only five specimens: one mature with numerous ascospores in the perithecium (Fig. 61); four in several stages of perithecial immaturity. The receptacles of three of the immature specimens are mature in that their dimensions are comparable to those of the mature individual. Additional collections of this taxon are needed to establish better its dimensions.

Aporomyces byrrhini resembles *A. subulatus* but differs markedly in overall habit, especially in the shape of the receptacle and cell III. The attenuated perithecial termination in *A. subulatus* is more abruptly narrowed near its base than it is in *A. byrrhini* (compare Fig. 60 and 61).

The host genus, *Byrrhinus*, is one of only two genera of Limnichidae known to occur in both the Old World and New World (Wooldridge 1987), the other being *Paralimnichus* Delève (Wooldridge 1983).

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of female individual depicted in Fig. 46 showing relationship of the trichogyne (*tr*) and trichophoric cell (*tc*) to ruptured apex of perithecial initial.—58. Early stage of formation of upgrowth from one anterior, outer wall cell (arrow).—59. Mature cellular upgrowth from outer wall cell projecting through open tip of perithecial initial (arrow). (All figures: bar with Fig. 59 = $10 \mu\text{m}$.)

Fig. 60–64.—60. *Aporomyces subulatus* (Thaxter 2423). Mature female showing curved cell III and divergent perithecium with elongate apex abruptly narrowed at base.—61–64. *Aporomyces byrrhini* (RKB 3107).—61. Mature female and presumptive male (mostly out of focus). Note nearly straight cell III and perithecium in line with the axis of the receptacle. The perithecium narrows uniformly from its base.—62–64. Perithecium at median stage of development shown at three levels of focus: near, median, and far, respectively. The tips of the five terminal outer wall cell primordia are indicated by arrowheads. (Fig. 60: bar = 20 μ m; Fig. 61: bar = 20 μ m; Fig. 62–64: bar with Fig. 64 = 10 μ m.)

Fig. 65–66. *Aporomyces perpusillus* (LPS 38636).—65. Immature individual showing perithecial initial (d) (see Fig. 50).—66. Mature individual. (Both figures: bars = 10 μm .)

8. *APOROMYCES PERPUSILLUS* (Spegazzini) Tavares. *Mycotaxon* 12:440. 1981.

Fig. 49–53, 65–66

=*Ecteinomyces perpusillus* Spegazzini. *Anales Mus. Nac. Hist. Nat. Buenos Aires* 29:543. 1917.

Presumably monoecious, but antheridia not observed. Hyaline. *Receptacle* below the perithecium 18–20 μm long; consisting of the basal cell (I) and two superposed, somewhat flattened, externally rounded cells derived from cell II; broadest below the perithecium, 10–11 μm wide; abruptly tapered downward to the blackened foot; basal cell longer than wide, about as long as the combined lengths of the two receptacular cells above; receptacle above the perithecium consisting of two superposed cells, a single cell derived from cell II, and cell III, the latter about twice as long as broad, 6–8 $\times$ 3–4 μm . *Primary appendage* up to 25 μm long, 2 μm wide; consisting of a small number (?–3) of elongate cells, usually broken near the base of a proximal cell and renewed by proliferation. *Secondary appendages* not observed. *Perithecium* stout, elongate, its long axis strongly divergent; broadest near the base, 12–13 μm wide; nearly symmetrical, about 30 μm long, its lower margins convex, tapered distally and forming an attenuated termination extending 8–10 μm beyond the tips of the upper, outer wall cells; only the walls of the upper two or three tiers of outer and inner wall cells persistent; one anterior upper, outer wall cell giving rise to an elongate, slightly curved, acuminate, unicellular upgrowth 13–15 μm long, which projects slightly beyond the apical opening. Ascospores not precisely measurable.

Total length from base of foot to tip of perithecium 35–40 μm .

Specimens examined.—ARGENTINA. Buenos Aires (Escuela Regional de Santa Catalina), Florencio Varela, and La Plata, 1913–1916, on *Rhopalophorus gestroi* Bernh. (as *rhopalophorus*) (Staphylinidae; Oxytelinae) in nests of the ant *Acromyrmex lundi* (Guérin-Méneville) (as *Atta lundi*), C. Spegazzini coll. (38635 [TYPE], 38636; LPS).

Spegazzini's specimens are mounted in diaphane. The high refractive index of this substance made it difficult to resolve details of thallus structure except for thickened cell walls (Fig. 49–53, 65–66). Aspects of cellular structure in immature perithecia could not be determined.

Although *Aporomyces perpusillus* parasitizes a host taxonomically far removed from those bearing all other known species of *Aporomyces*, Tavares's transfer of Spegazzini's taxon to this genus appears correct. Paired perithecial thalli of *A. perpusillus* indicate that the species may be monoecious although no indication of an antheridium on any of the thalli studied, immature or mature, was found. In the 3-celled receptacle and cellular extension of one upper, outer wall cell, the mature thallus of *A. perpusillus* (Fig. 51–53) bears closer resemblance to the female thalli of *Aporomyces* spp. on *Byrrhinus* (Fig. 60–61) than to those on other genera of Limnichidae.

There is a discrepancy between the dimensions given for *A. perpusillus* by Spegazzini and those obtained by me from an examination of his specimens. Spegazzini's figures for the total height of the thallus (60–65 μm) and the size of the perithecium (45–48 $\times$ 17–18 μm) are considerably larger than mine.

I have in my collection one mature and two immature specimens (RKB 1965, 1966) in rather poor condition of an *Aporomyces* that is nearly identical to *A. perpusillus* in its general morphology, although it is somewhat larger. The mature individual has a total length of 78 μm and a perithecium measuring 48 μm long and 25 μm wide. These specimens were found on the club of the left antenna of an unidentified beetle belonging to the Histeridae (Coleoptera: Histeroidea) collected by Hugh B. Leech (California Academy of Sciences, Golden Gate Park, San Francisco) near "Potrero," Mexico, 17 Dec 1948. The exact locality of "Potrero" is unknown, for the state in which this site is located was not given on the field-collection label. Further collections of this fungus and its host are to be desired, for the histerid beetle may, like the staphylinid host of *A. perpusillus*, be myrmecophilous. It is possible that *A. perpusillus* can infect hosts of at least two distinct families of beetles that share the same restricted habitat. Such a relationship of a species of Laboulbeniales, *Laboulbenia ecitonis* Blum (= *L. adinventa* Blum) with staphylinid and histerid hosts is known (Blum 1924; Rossi 1980).

MORPHOLOGY AND DEVELOPMENT

Ascospores

The ascospores of *Aporomyces* species are hyaline, elongate, more or less fusiform, and two-celled. Except for *A. trinitatis* (Fig. 19) and *A. lutrochi* (Fig. 39) measurements were made of ascospores inside perithecia. This was necessitated by a desire not to break specimens of limited material for the purpose of liberating spores. The cross wall of the ascospore is nearly median in the female ascospore of *A. lutrochi* (Fig. 39). In the male spore of this species (Fig. 39) and in both female and male spores of *A. uniflagellatus* (Fig. 6), *A. trinitatis* (Fig. 19), and *A. physemi* the longest cell, which is uppermost in the perithecium prior to discharge, is ca. 60% of the total length of the spore. Bánhegyi (1944) did not give the proportions of the two cells of the ascospore in *A. szaboi* and I could not determine this statistic for *A. subulatus*, *A. byrrhini*, and *A. perpusillus*.

The ascospores of *A. uniflagellatus*, *A. szaboi*, *A. trinitatis*, and *A. lutrochi* are

dimorphic. The spore giving rise to female individuals always is larger than that giving rise to males and ranges from about 20% greater in length in *A. physemi* and *A. trinitatis* (Fig. 17–19), 30% in *A. szaboi*, 35% in *A. uniflagellatus* (Fig. 6), to slightly over 50% in *A. lutrochi* (Fig. 39). In the last species, the relatively tiny male ascospore appears to be embedded in the gelatinous envelope surrounding the female spore (Fig. 39). Ascospore dimorphism, if it exists, could not be determined for *A. subulatus*, *A. byrrhini*, and *A. perpusillus*.

Thallus of Aporomyces perpusillus

Spegazzini's specimens of *Aporomyces perpusillus* included a number of pairs of perithecium-bearing individuals in several stages of development. There was no evidence of males like those of other species of the genus, and nothing resembling an antheridium was observed on any thallus. The receptacle invariably consisted of three cells subtending the perithecium which, in turn, subtended the relatively large cell III bearing a simple, several-celled appendage (usually broken) (Fig. 49–53, 66). There was a hint of structural organization (Fig. 65) inside the perithecium of many of the immature individuals, but details of development could not be inferred.

Because of their thickened walls, the upper outer and inner wall cells of *A. perpusillus* could be observed without difficulty in mature individuals, as well as the single, elongate, cellular projection of one of the outer wall cells (Fig. 51–53). Ascospores and gross aspects of the centrum could be seen in vague outline (Fig. 66).

Thallus of dioecious taxa

Male individual.—In five of the species of *Aporomyces* [including *A. szaboi*, as reported by Bánhegyi (1944)], found on Limnichidae, a diminutive male was frequently observed in close association with the foot of the perithecium-bearing individual (*A. uniflagellatus*: Fig. 2, 3; *A. szaboi*: Fig. 12; *A. trinitatis*: Fig. 16; *A. physemi*: Fig. 24, 25, 32; *A. lutrochi*: Fig. 35, 37, 38). A very early stage in the development of a pair of male and female individuals of *A. trinitatis* is shown in Fig. 20. The male thallus consisted of a few superposed cells in which two or three cells derived from the lower cell of the ascospore constitute the receptacle (Fig. 4, 33, 34, 47, 48, 54–56, 80). The upper cell of the spore, separated from the basal part by the original spore septum (*a*), became more or less elongate (Fig. 28, 30, 47, 48, 61) and eventually differentiated a single, simple antheridium in *A. uniflagellatus* (Fig. 2–4), *A. szaboi* (Fig. 12; Bánhegyi 1944, Pl. I, fig. 3, 4, Pl. II, fig. 2, 3), *A. trinitatis* (Fig. 80), *A. physemi* (Fig. 32, 33), and *A. lutrochi* (Fig. 34, 35, 37, 38). Spermatia were present in the antheridial neck in many instances.

An identifiable antheridium was not found on any of the presumed males of *A. subulatus* (Fig. 47, 48, 54–56) or *A. byrrhini* (Fig. 61). The upper part of the presumptive male thallus of these species, which corresponds to the primary appendage of the female individual, consists of a small number of elongate cells; this is simple in *A. byrrhini* but is occasionally once-branched in *A. subulatus*. The upper part of this appendage was missing in the presumably mature individuals observed, but the remnant of the distal cell showed no evidence of differentiation into an antheridium.

Female individual. — Receptacle: The foot of the receptacle begins differentiating prior to any division of the basal cell of the young individual derived from the ascospore (Fig. 20). The next-youngest individuals found among all the material studied were represented by germlings of *A. physemi* (Fig. 26) and *A. subulatus* (Fig. 41) showing an immature receptacle already composed of several superposed cells: the foot-forming basal cell (I); an upper cell (III) subtending the primary appendage (*pa*); and several intercalary cells resulting from the multiplication of cell II. Elongation of the receptacle varied according to the species and took place by intercalary division of cell II-derived cells (arrows: Fig. 27, 36).

Division of cell II did not go beyond the formation of three cells in *Aporomyces subulatus* (Fig. 41, 42) and *A. byrrhini* (Fig. 61) where the receptacle proper consisted only of the basal cell (I) and the two cell II-derived cells subtending the perithecium (Fig. 43–46, 60, 61). The perithecium subtended cell III directly in these species. Continued division of cell II-derived cells in the other species resulted in a more or less elongate receptacle consisting of a variable but relatively large number of cells (*A. uniflagellatus*: Fig. 1–3, 9; *A. szaboi*: Fig. 11, 12; *A. trinitatis*: Fig. 16; *A. physemi*: Fig. 21–25, 27–29, 31, 32; *A. lutrochi*: Fig. 35–38). The number of receptacular cells distal to the perithecium and subtending cell III varied from one or two (*A. uniflagellatus*: Fig. 1, 9; *A. trinitatis*: Fig. 13–15; *A. physemi*: Fig. 28, 29, 31, 32) to several (*A. szaboi*: Fig. 11, 12) or many (*A. lutrochi*: Fig. 35, 37, 38).

Primary appendage: The upper segment of the ascospore of *Aporomyces* develops into a primary appendage (*pa*) that typically consists of only a few superposed, elongate cells. Branching of this appendage was seen only in *A. szaboi* (Fig. 11; Bánhegyi 1944, Pl. I, fig. 2) and *A. lutrochi*, in which, however, it usually is simple and nearly straight (Fig. 40). The primary appendage is simple, relatively long, and straight or somewhat curved in *A. uniflagellatus* (Fig. 1, 9), *A. trinitatis*, and *A. subulatus* (Fig. 44), whereas it usually is considerably shorter and often strongly curved in *A. physemi* (Fig. 21, 28–31).

Secondary appendages: Secondary appendages were not found in *Aporomyces byrrhini*, *A. perpusillus*, *A. subulatus*, and *A. uniflagellatus*, but were observed in the other species. Bánhegyi (1944, Pl. II, fig. 1) illustrated a mature specimen of *A. szaboi* with secondary appendages arising from all but the lowermost cell of the receptacular axis surmounting the perithecium, but in his photographs of other mature specimens (Bánhegyi 1944, Pl. I, fig. 3, 4, Pl. II, fig. 3) secondary appendages were absent from all but the uppermost cells of this part of the receptacle. Secondary appendages (*sa*) also arose not only from cell III but also from one or more cell II-derived cells of the axis distal to the perithecium in *A. trinitatis*, *A. physemi*, and *A. lutrochi*. These appendages were simple or sparingly branched, composed of only one to three or four cells, and were straight, flexuous, or strongly curved in *A. trinitatis* (Fig. 13–15; Thaxter 1931, Pl. 14, fig. 4–8) and *A. physemi* (Fig. 22–25, 28, 29, 31, 32). They were somewhat longer and more highly branched in *A. lutrochi* where single appendages arose from the upper surface of four to seven cells of the laterally projecting axis (Fig. 35, 37, 38).

Perithecium: The perithecial initial (*d*) (Fig. 28, 43, 65, 67, 68) develops from a single cell of the receptacular axis derived from cell II. It may terminate this part of the axis as in *A. byrrhini* and *A. subulatus* (Fig. 42, 43), be subterminal

Fig. 67-80. *Aporomyces trinitatis* (RKB 2771).—67-76. Stages of development of the perithecium. Details and terminology are given in the text.—77-78. Relationship of the five vertical rows of outer wall cells to the five basal cells (*m*, *m'*, *mac*, *n*, *n'*), cell VII, and cell VI, which has contributed to most of the lumen of the perithecial cavity. See text.—79. Tip of perithecium showing relationship of the upper two tiers of the five rows of inner and outer wall cells.—80. Male individual. (Fig. 67-76, 79, 80: bar with Fig. 79 = 10 μ m; Fig. 77-78: bar with Fig. 78 = 10 μ m.)

as in *A. physemi* (Fig. 22, 23, 28, 29, 31), *A. trinitatis* (Fig. 13–15), *A. perpusillus* (Fig. 49, 50, 65), and *A. uniflagellatus* (Fig. 1), or arise from a cell more or less remote from the apex as in *A. lutrochi* (Fig. 36, 37) and *A. szabo*i (Fig. 11). When the first-formed perithecium has for some reason aborted, another receptacular cell may be transformed into a perithecial initial and give rise to a secondary perithecium. This phenomenon was observed in *A. lutrochi*, *A. physemi* (Fig. 25), and *A. uniflagellatus* (Fig. 10).

As cell *d* enlarges, its divergent or upwardly growing, rounded or acute apex may become more or less elongate before the first division of its protoplast takes place (Fig. 28, 43, 65, 68). The cell increases in size as perithecial development proceeds and its outer wall eventually encloses the true stalk cells, basal cells, and wall cells of the perithecium as they develop from the original protoplast, which often was more or less withdrawn from the cell wall (Fig. 28, 43, 67, 68), undoubtedly due to inadequate fixation of material studied.

Division of the protoplast of cell *d* gives rise to the primordial cell of the perithecium (*h*) and the primordial cell of the procarp (*i*) (Fig. 69). Cell *i* divides and forms the carpogonial cell (*cp*) below and the trichogyne initial (*e*) above (Fig. 44, 70). Cell *h* divides by the formation of a diagonal cross wall and forms a lower cell *k* and an upper cell *j* (Fig. 71). Cell *k* cuts off two anterolateral cells (basal cells *m* and *m'*), one on each side, and becomes the primary stalk cell (VI) (Fig. 72). Cell *j* also cuts off two anterolateral cells (basal cells *n* and *n'*), one on each side, and becomes the secondary stalk cell (VII) (Fig. 29, 72, 73). Cell *m* delimits a small cell, the auxiliary basal cell (*mac*), that lies between cells *m* and *m'* (Fig. 44, 73). The relationship of the five basal cells to one another and to cells VI and VII in a mature perithecium is shown in posterior and anterior views, respectively, in Figure 77 and 78 where septal pores between VII and cells *n* and *n'* and between cells *m* and *mac* are indicated (upper arrowheads). It is possible in some mature perithecia to detect the remnants of the septal pores between the lumen of what was once cell VI, which has enlarged and formed the greater part of the venter, and cells *m* and *m'* (Fig. 78, lower arrowheads).

Cell *e*, the trichogyne initial, grows upward, penetrates the wall at the tip of the perithecial initial (Fig. 72, 73) and becomes the trichophoric cell (*tc*) after giving rise to the trichogyne (*tr*) above (Fig. 1, 36, 45, 46, 57, 74). The latter may consist of several elongate cells and form one to several branches. The trichogyne of immature individuals of *A. uniflagellatus* was seen to bend sharply near the tip of the young perithecium and extend downward in the direction of the foot. In the specimen shown in Figure 1, the trichogyne doubtless was displaced upward when the specimen was mounted (see Thaxter 1931, Pl. 14, fig. 15).

Each of the five basal cells (*m*, *m'*, *mac*, *n*, *n'*) surrounding the lower end of the carpogenic cell (*cp*) (Fig. 44, 73) cuts off the first inner and outer wall cells (*o*) (Fig. 74). Development of the perithecium involves the upward growth of the five inner and outer rows of wall cells around the maturing female apparatus (Fig. 13–15, 23, 31, 45, 46, 54–56, 62–64, 75, 76). The trichogyne persists to at least the two-outer-wall-cell stage in *A. subulatus* (Fig. 45, 46). The degree of persistence of this structure in the other species could not be determined.

Development of the centrum could not be studied precisely, but a possible re-formed trichophoric cell (*tc'*) (combination of the trichophoric cell and carpogenic cell [see Tavares 1985]) was observed in *A. physemi* (Fig. 31) and *A. trinitatis*

(Fig. 14, 75). As formation of the perithecial walls and centrum proceeds inside the outer wall of the expanding perithecial initial (Fig. 76), the region occupied by the original cell VI enlarges and eventually forms the major portion of the perithecial venter enclosing the ascogenous cells and developing and maturing asci (Fig. 5-8, 17-18, 24, 25, 32, 35, 38, 60, 61). Cell VII and the basal and wall cells are displaced upward. All but the lowermost inner wall cells may persist in their entirety in *A. trinitatis* (Fig. 17-18), *A. physemi* (Fig. 32), *A. uniflagellatus* (Fig. 5-8), and possibly *A. lutrochi*, whereas only cell VII and the upper inner and outer wall cells appear to persist in *A. byrrhini* and *A. subulatus*. Only the upper two or three tiers of outer and inner wall cells appear to persist in *A. perpusillus* (Fig. 51-53).

One upper outer wall cell of the perithecia of *Aporomyces physemi*, *A. subulatus*, *A. byrrhini*, and *A. perpusillus* forms a slender cellular extension that grows upward through the ruptured tip of the perithecial initial, the greatly enlarged wall of which now encloses the true walls of the perithecium (Fig. 24, 32, 51-53, 59, 60). This apical opening, which sometimes has a jagged or uneven margin, functions as the ostiole in these species where the true ostiole formed by the upper true wall cells lies some distance below. In the other species the true ostiole is emergent or nearly so, e.g., *A. uniflagellatus* (Fig. 5-8), *A. trinitatis* (Fig. 16-18, 77-79), *A. lutrochi* (Fig. 35-38), and possibly *A. szabo*i (Fig. 12). An early stage of development of the cellular upgrowth in *A. subulatus* is shown in Figure 58. The fully developed upgrowth in this species after its separation from the mother cell by a cross wall is shown in Figures 59 and 60.

There are only two tiers of outer wall cells in the mature perithecium of *A. physemi*; cells of the upper tier are nearly twice as long as those of the lower tier (Fig. 32). There are three tiers of outer wall cells in *A. uniflagellatus* (Fig. 5-8), *A. trinitatis* (Fig. 17-18), and *A. lutrochi* (Fig. 35, 38); cells of the upper tier are about equal in length to those of the subterminal tier. There may be only two tiers in *A. byrrhini*, *A. subulatus* (Fig. 59, 60), and *A. perpusillus* (Fig. 51-53), but this could not be firmly established due to the ephemeral nature of the basal cells and perhaps the cells above.

DISCUSSION

Dioecious species of Laboulbeniales having dimorphic ascospores first were reported in *Dioicomyces* Thaxter (1908:293, Pl. XLII, fig. 24, 25, 29) where the female spore may be considerably larger than the male (see also Benjamin 1970, fig. 3D). Thaxter did not comment on this phenomenon in connection with other dioecious taxa including the species of *Aporomyces* he described (Thaxter 1931), but Bánhegyi (1944:51) noted a marked difference in the size of the ascospores of *A. szabo*i. As shown in this study, spore dimorphism is a feature of other species of the genus as well, reaching its greatest extreme in *A. lutrochi*. Except for *Dioicomyces*, I have not seen dimorphic ascospores in any other of the dioecious Laboulbeniales I have studied including *Laboulbenia formicarum* Thaxter, (Benjamin and Shanor 1950), *Rhizopodomyces* Thaxter (Benjamin 1979), *Triceromyces* Majewski p. p. (Benjamin 1986), and others in my collection for which I have unpublished observations. Ascosporic dimorphism is perhaps a derived condition in *Aporomyces* and *Dioicomyces*, but when one considers other aspects

of thalloid morphology it probably is a feature having little or no bearing on a close phylogenetic relationship of these genera.

Perithecial development, as it takes place in *Laboulbenia* (Thaxter 1896; Benjamin and Shanor 1950; Tavares 1985) and many other genera of Laboulbeniaceae (e.g., *Acallomyces* Thaxter [Tavares 1973], *Filariomyces* Shanor [1952], *Idiomyces* Thaxter [Benjamin 1983], *Microsomyces* Thaxter [Benjamin 1985], *Prolixandromyces* Benjamin [1981], *Rhizopodomyces* Thaxter [Benjamin 1979], *Stigmatomyces* Karsten [Thaxter 1896], *Synandromyces* Thaxter [Benjamin 1984], *Triceromyces* [Benjamin 1986]), involves the formation of only three basal cells: *m* from cell VI, and *n* and *n'* from cell VII. These three basal cells give rise to four rows of wall cells: *m* forms one row, *n'* forms one row, and *n* forms two rows. In a few genera of Ceratomycetaceae an extra stalk cell or basal cell may be formed (see discussion in Tavares, 1985:67–68), but the number of complete rows of wall cells has been regarded as fixed at four in all members of the order up to now.

In two genera, *Hydrophilomyces* Thaxter (1908) and *Kyphomyces* Tavares (1985), an accessory cell, similar to that in *Aporomyces*, is formed along with the three basal cells that give rise to the four vertical rows of inner and outer wall cells. This accessory cell, however, grows upward and forms only an elongate, uninucleate cell separating the two anterior cells of the lowermost tier of outer wall cells and often the lower ends of the neighboring cells of the subbasal tier (Tavares 1985; Benjamin, unpubl. obs.). The accessory cell in *Hydrophilomyces* and *Kyphomyces* does not function as an extra basal cell giving rise to an additional row of inner and outer wall cells as in *Aporomyces*.

The trichogyne of *Aporomyces* emerges through the tip of the perithecial initial during an early stage of perithecial development. The ruptured tip later serves as the ostiole in several species of the genus, such as *A. subulatus* for example, where the true ostiole formed by the distal perithecial wall cells does not reach the level of this opening as it does in other species, such as *A. trinitatis*.

In *Aporomyces* there is no trichogynic scar, which represents the persistent base of the degenerated trichogyne, on the upper, outer wall below the mature perithecial apex. Such a trichogynic remnant is found on the surface of the perithecium in many genera of Laboulbeniales in which the trichogyne is deflected laterally from its initial, more or less terminal position as the perithecium develops and forms an ostiole some distance removed from the original trichogynic orifice, as in *Synandromyces* (Benjamin 1984) and *Triceromyces* (Benjamin 1986).

Thaxter (1931:74) believed that the prolonged tip of the perithecium of *Aporomyces*, as in *A. subulatus*, represented the base of the trichogyne. However, young specimens of this species clearly show that the juncture between the true base of the trichogyne and the upper end of the trichophoric cell may lie some distance below the open tip, which shows no evidence of having been continuous with the wall of the basal cell of the trichogyne.

The venter of the perithecium of *Aporomyces* was thought by Thaxter (1931:74) to derive from the absorption not only of the walls of the basal cells of the perithecium but also the walls of one or more of the adjacent receptacular cells. As shown in this study, the basal cells do disappear in *A. subulatus*, *A. byrrhini*, *A. perpusillus*, and possibly *A. lutrochi*, but they persist in other species, including *A. uniflagellatus*, *A. trinitatis*, and *A. physemi*. The greater part of the ascigerous cavity appears to develop from enlargement of the portion of the perithecial initial

occupied originally by cell VI (the primary stalk cell), at least the upper part of which breaks down. The developing centrum intrudes into the space formerly occupied by cell VI. I found no evidence that any cell of the receptacle other than the lower part of the perithecial initial contributed to the formation of the perithecial venter.

In the upgrowth of the perithecial wall cells around the carpogonium, *Aporomyces* clearly is a member of suborder Laboulbeniineae according to the classification of Tavares (1985). Also, the formation of simple antheridia (phialides) places the genus in her subfamily Laboulbenioideae. However, perithecial development in *Aporomyces* is unique among all other genera in the suborder, as far as is known, in having five complete rows of inner and outer wall cells derived from five basal cells.

Thaxter (1931:74) thought *Aporomyces* bore little resemblance to other dioecious genera of Laboulbeniales and stated that it seemed unrelated to any of them. Tavares (1985) agreed with Thaxter but suggested that, because of the apparent disappearance of the basal cells and presumably the secondary stalk cell (VII) (which actually persists in all but one species [*A. perpusillus*]) the genus might somehow be related to *Euphoriomyces* Thaxter (1931) and certain other genera she allied with *Euphoriomyces* (*Carpophoromyces* Thaxter [1931], *Meionomyces* Thaxter [1931]), *Phaulomyces* Thaxter [1931], and *Siemaszkoa* Tavares & Majewski [1976]) in a subtribe Euphoriomycetinae of her tribe Euphoriomyceteae. However, she separated *Aporomyces* into her monotypic subtribe Aporomycetinae, within this tribe. In view of differences in perithecial structure (i.e., five vertical rows of inner and outer wall cells in *Aporomyces* [Aporomycetinae] vs. four rows in members of Euphoriomycetinae), I here propose that *Aporomyces* be removed from the Euphoriomyceteae and placed in a separate tribe **Aporomyceteae** (Tavares) Benjamin, stat. nov. (basonym: Aporomycetinae Tavares, Mycol. Mem., No. 9:98, 1985).

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