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CORYLOPHOMYCES, A NEW DIOECIOUS GENUS OF LABOULBENIALES ON CORYLOPHIDAE (COLEOPTERA)

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ABSTRACT

A new dioecious genus of Laboulbeniaceae (Laboulbeniales), *Corylophomyces*, was established to accommodate five species parasitizing Corylophidae (Coleoptera; Cucujoidea): *C. peyerimhoffii* (= *Cryptandromyces peyerimhoffii*); *C. sericoderi* (= *Autophagomyces sericoderi*); *C. sarawakensis* (= *A. sarawakensis*); and two new species, *C. reflexus* and *C. weirii*. A key to the taxa was given and all were illustrated with line drawings. *Corylophomyces* was placed in Amorphomycetinae sensu Tavares. The other genera included in this subtribe by Tavares in 1985, i.e., *Amorphomyces*, *Dioicomycetes*, *Nanomyces*, *Rhizopodomycetes*, and *Tetrandromyces*, were compared with one another and with the new genus.

Key words: *Autophagomyces*, Coleoptera, Corylophidae, *Corylophomyces*, fungi, insect parasites, Laboulbeniales, morphology, taxonomy.

INTRODUCTION

Autophagomyces Thaxter (1912) is based on *A. plattensis* Thaxt., a species found on *Tomoderus forticornis* Pic (Coleoptera: Cucujiformia; Tenebrionoidea; Anthicidae) collected in Argentina. Thaxter coined the name *Autophagomyces* because he considered the type, as well as another species, *A. nigripes* Thaxt., found on the same host, to be dioecious, with a simple, antheridium-bearing male growing parasitically near the base of the receptacle of the female. Thaxter did, however, express some doubt regarding this idea in suggesting that the presumed male might be simply an antheridial branch arising from an improbable location near the base of the receptacle of a hermaphrodite. When, in 1931, he revised *Autophagomyces* he had long since realized the truth of the latter interpretation, and he amended the generic diagnosis to include only fungi considered to be monoecious. His treatment of *Autophagomyces* (Thaxter 1931) encompasses 16 taxa that include not only four additional species found on members of Anthicidae but also several others parasitizing beetles assigned to three families of Cucujoidea, i.e., Phalacridae (three species), Pselaphidae (five species), and Corylophidae (one species), as well as a species on a semiaquatic bug (Heteroptera; Veliidae).

As characterized by Thaxter (1931), *Autophagomyces* includes Laboulbeniales having a simple, two-celled receptacle with the suprabasal cell bearing a stalked perithegium and a usually simple, sometimes furcate, appendage consisting of usually three or four superposed cells terminated by an antheridial phialide. It should be noted that the terminal cell of a primary three-celled receptacle derived from the lower cell of

a two-celled spore was termed the basal cell of the appendage by Thaxter. Thus, in Thaxter's descriptions of *Autophagomyces* spp., as well as other related genera, the lowermost cell of the appendage is in reality the terminal cell of the receptacle, i.e., cell III as it now is defined (Tavares 1985: 433). The genus is classified in subtribe Stigmatomycetinae (Laboulbeniaceae; Laboulbeniales) by Tavares (1985).

Several species have been added to *Autophagomyces* since 1931, i.e., *A. poissonii* R. K. Benj. (Benjamin 1970) (= the monoecious morph of *Triceromyces poissonii* [R. K. Benj.] R. K. Benj. [Benjamin 1986]) on Mesoveliidae (Heteroptera); *A. falcatus* T. Majewski (1973) on Cryptophagidae (Coleoptera; Cucujoidea); *A. castellinii* W. Rossi (1982) on Pselaphidae; *A. tiwaiensis* W. Rossi (1990) on Pselaphidae; and *A. sericoderi* Santam. (Santamaría 1993) on Corylophidae.

Three of the species that have been placed in *Autophagomyces*, namely *A. peyerimhoffii* (Maire) Maire in Thaxt. (1931: 366) (syn. *Cryptandromyces peyerimhoffii* Maire [1920: 138]), *A. sarawakensis* Thaxt. (1931: 94), and *A. sericoderi* (Santamaría 1993: 412), which parasitize members of Corylophidae, prove not only to be dioecious but also to have other characteristics that clearly separate them from *Autophagomyces* sensu Thaxter (1931) and Tavares (1985). Accordingly, because these taxa cannot be accommodated in an existing genus, they are here assigned to a new genus to which are added two new species, one found on the host bearing *A. sarawakensis*. In addition, my purposes shall be to (1) illustrate the species with line drawings, (2) provide a key to the species, (3) comment briefly on morphology and development, and (4) compare the

genus with other possibly allied genera of Laboulbeniales.

MATERIALS AND METHODS

While at Harvard University as a National Research Council Fellow many years ago (1951–1952), where I studied the Thaxter collection of Laboulbeniales at the Farlow Herbarium (FH), I was fortunate in locating, both at the Farlow and the Museum of Comparative Zoology (MCZ), duplicates of a few of the insect hosts from which Thaxter had removed Laboulbeniales he later described. These insects originally had been preserved in small, cork-stoppered, glass vials containing alcohol and a small amount of glycerine; only the glycerine remained because of the evaporation of the alcohol. Thaxter had included in each vial a label with minimal data, often only the country of origin of the collection, but in many instances he included the accession number of the host as cited in his published works along with the description of a given taxon. The late Drs. W. Lawrence White, (Director, FH), and P. J. Darlington, Jr., (Curator of Insects, MCZ), permitted me to retain on permanent loan many of these insects and to keep for future reference any specimens of Laboulbeniales removed from them that duplicated species described by Thaxter. Through the years, several of the fungi recovered, supplemented in some instances by specimens borrowed from the Thaxter collection, have provided me with valuable information pertaining to my studies of Laboulbeniales. In connection with the present investigation, specimens of *A. sarawakensis*, as well as a related new species not detected by Thaxter, were found on individuals in two small lots of hosts among the above insects, including duplicates of the same lot from which *A. sarawakensis* had been taken. Dr. Michael C. Thomas, Florida State Collection of Arthropods, Gainesville, who has examined these insects, found that they belong to the family Corylophidae, not Phalacridae as given by Thaxter.

Through the courtesy of Dr. Donald H. Pfister, Curator of the Farlow Herbarium, I have received on loan Thaxter's slide mounts of *A. sarawakensis*, including the type. Dr. Sergio Santamaría, Universitat Autònoma de Barcelona, Bellaterra, Spain, kindly has provided me with a loan of mounted specimens of *A. sericoderi*, including the holotype, and two collections of *A. peyerimhoffii* from Spain. Finally, Mr. Alex Weir, Stockton-on-Tees, Cleveland, and The Natural History Museum, London, U. K., sent me an undescribed species, congeneric with the others being treated here, which was found on undetermined Corylophidae collected in Sulawesi, Indonesia.

All of these fungi were mounted on slides either in glycerine (Thaxter's original specimens and those I re-

covered from his duplicate hosts) or Amann's fluid (Santamaría's and Weir's specimens).

A Leitz Dialux microscope equipped with differential interference contrast optics was used for making microscopic observations, and, with the aid of a camera lucida, for preparing drawings.

Terms and abbreviations as defined in the text are essentially those of Tavares (1985: 431–434). The female ascomata of these fungi typically are positioned so that they can be observed only in lateral view; thus, the drawings and descriptions of these are based, for the most part, on observations of specimens as seen from one side or the other. With reference to the perithecium and receptacle of female individuals, anterior (outward) is in the direction away from the appendage whereas posterior (inward) is in the direction towards the appendage. With reference to cells of the receptacle, stalk and basal cells of the perithecium, and cells of the appendage, inner is in the direction of the axis of the ascoma, outer is in the direction away from the axis. Unless indicated otherwise, height precedes width in the measurements given in the descriptions.

TAXONOMY

Corylophomyces R. K. Benj., gen nov.

Dioecius. Mas.—Receptaculum cellularum duarum superpositarum constans; antheridio uno simplici terminali. *Femina.*—Receptaculum cellularum trium constans; cellulo basali (I) et cellulo suprabasali (II) oblique separatis; cellulo terminali (III) et cellulo I unitis; basi cellulae VI perithecii et cellula III plus minusve unitis. Appendix primaria cellularum duarum vel trium constans; apice rotundato vel acuto. Perithecium cellulis basilaribus tribus persistentibus et cellulis parietis externis in quatuor ordinibus longitudinalibus numusquique quatuor vel quinque cellularum. Trichogyna valde deflexa cellularum duarum constans; basi constricta; ramulo terminali. Ascosporeae 1-septatae.

Dioecious. Male.—Receptacle consisting of two superposed cells; with a single, simple, terminal antheridium. *Female.*—Receptacle consisting of three cells; the basal cell (I) obliquely separated distally from the suprabasal cell (II); the terminal cell (III) united below with cell I and more or less united on the inside below with cell II and above with the base of the primary stalk cell (VI) of the perithecium. Primary appendage, subtended by cell III of the receptacle, consisting of two or three superposed sterile cells, apically rounded or acute. Perithecium, subtended by cell II of the receptacle, with well-defined stalk and basal cells, and four vertical rows of outer wall cells of four or five cells each; trichogyne strongly deflexed, consisting of two cells separated by a transverse cross wall, the proximal cell more or less basally constricted, the distal cell forming slender branchlets terminally. Ascospores 1-septate.

Type species.—*Corylophomyces sericoderi* (Santam.) R.K. Benj.

Etymology.—From the name of the host family, Corylophidae, + *myces*, fungus.

KEY TO THE SPECIES OF *CORYLOPHOMYCES*

- A. Appendage of female consisting of two cells B
- Appendage of female consisting of three cells C
- B. Perithecial apex broadly rounded; terminal outer wall cells hardly protrudent, one with a barely perceptible upgrowth on one side (1) *C. peyerimhoffii*
- Perithecial apex attenuate; terminal outer wall cells \pm protrudent, one with a distally rounded, curved prolongation (2) *C. sericoderi*
- C. Female ascoma nearly straight; perithecial apex asymmetric, bearing distally two pairs of short, rounded prominences (3) *C. sarawakensis*
- Female ascoma sharply inclined or recurved; perithecial apex \pm symmetric D
- D. Female ascoma strongly reflexed; perithecium curved, asymmetric, apex abruptly narrowed, bearing a single blunt subterminal prominence on one side (4) *C. reflexus*
- Female ascoma strongly inclined; perithecium straight, symmetric; apex broadly rounded (5) *C. weirii*

1. *Corylophomyces peyerimhoffii* (Maire) R. K. Benj., comb. nov. Fig. 1–9

=*Cryptandromyces peyerimhoffii* Maire. *Bull. Soc. Hist. Nat. Afrique N.* 11: 38, 1920.

=*Autophagomyces peyerimhoffii* (Maire) Maire in Thaxt. *Mem. Amer. Acad. Arts* 16: 366, 1931.

Male.—Hyaline except for a partially opaque foot, elongate, slender; basal cell of receptacle, including foot, ca. $25 \times 4 \mu\text{m}$, ca. five times longer than the suprabasal cell, which is quadrangular, nearly isodiametric, $4 \times 4 \mu\text{m}$; antheridium \pm abruptly attenuate distally, $10\text{--}13 \times 4 \mu\text{m}$. Total length ca. $40 \mu\text{m}$.

Female.—Ascoma nearly straight or slightly curved; pale yellowish brown. Total length from tip of foot to tip of perithecium $140\text{--}160 \mu\text{m}$. *Receptacle:* Triangular, $35\text{--}40 \mu\text{m}$ high, $14\text{--}18 \mu\text{m}$ wide distally, tapered downward to the acute hyaline tip of the otherwise opaque foot; the basal cell (I) $27\text{--}35 \times 7\text{--}13 \mu\text{m}$, subtending the terminal cell (III) and suprabasal cell (II), from which it is separated by a strongly diagonal cross wall; cells II and III \pm trapezoidal, united, in part, on the inside and \pm parallel to one another; cell II up to twice as high as wide, $14\text{--}20 \times 6\text{--}10 \mu\text{m}$, subtending the primary stalk cell of the perithecium; cell III $10\text{--}15 \times 6\text{--}10 \mu\text{m}$, subtending the primary appendage. *Appendage:* Suffused with brown, consisting of two superposed cells in line with cells I and III of the receptacle, $18\text{--}20 \mu\text{m}$ long; basal cell quadrangular, wider than high, $5\text{--}6 \times 10\text{--}11 \mu\text{m}$; terminal cell nearly twice as high as wide, $13\text{--}15 \times 9\text{--}11 \mu\text{m}$, apically rounded to somewhat acute, separated from the basal cell by a transverse cross wall that becomes darkly

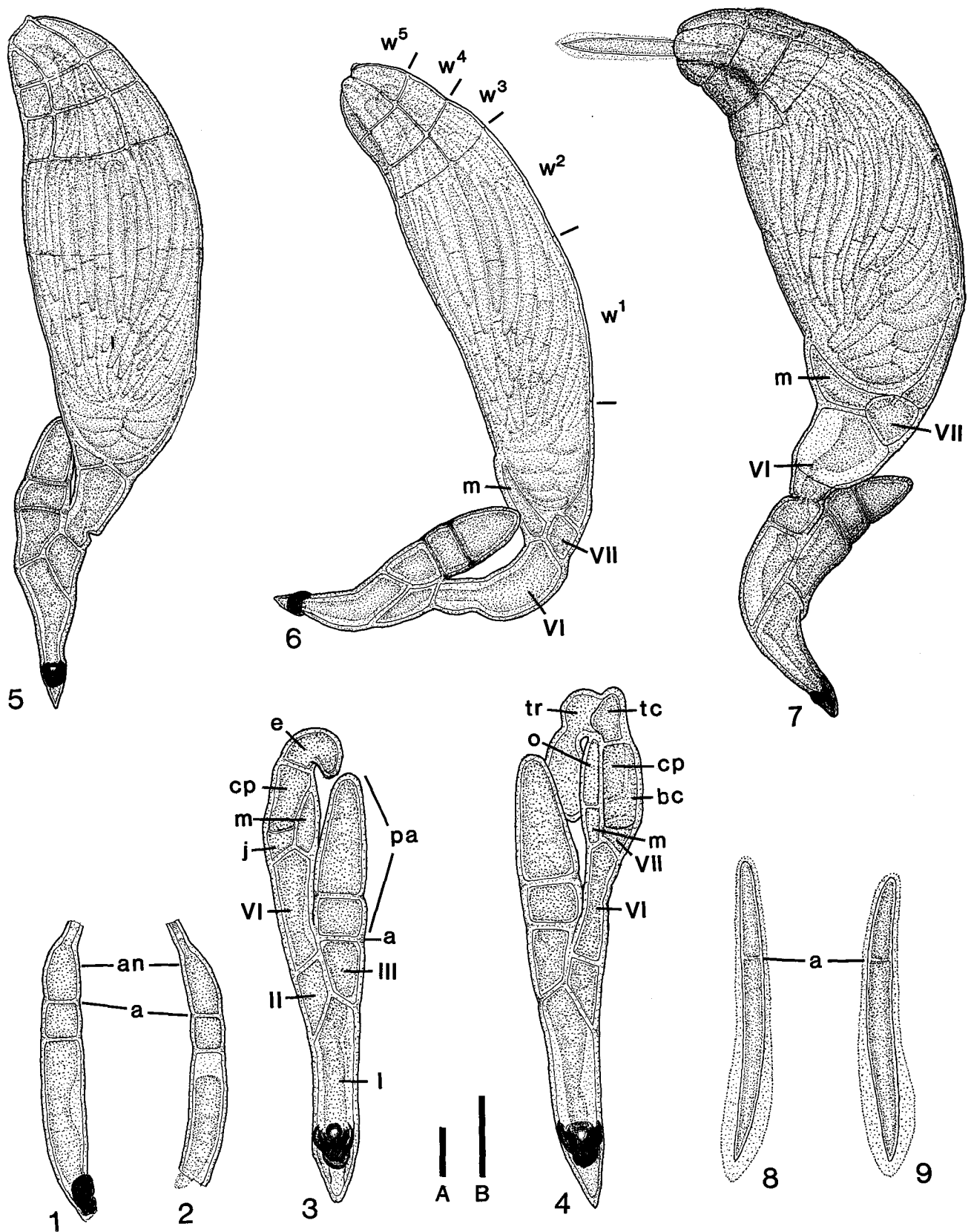
suffused with brown. *Perithecium:* Primary stalk cell (VI) elongate, $15\text{--}30 \times 10\text{--}15 \mu\text{m}$, widest distally, \pm constricted immediately above the base, nearly free, slightly incurved; secondary stalk cell (VII) small, nearly isodiametric, lying above cell VI on the outside, partially enclosed distally by the basal cells (*m*, *n*, *n'*), which, along with cell VII, constitute ca. 25% of the total length of the body of the perithecium above cell VI and envelop the base of the ascigerous cavity; body, including basal cells, $93\text{--}105 \mu\text{m}$ long, slightly inflated, median width $30\text{--}40 \mu\text{m}$, the outer margin more strongly convex than the inner, abruptly narrowed distally, the apex bluntly rounded, bent slightly inward, more darkly suffused with brown on the outside and inside than laterally, with a narrow, dark, longitudinal subterminal, postero-lateral band on each side, one terminal outer wall cell forming a \pm inconspicuous projection ca. $2.5 \times 2 \mu\text{m}$. Ascospores hyaline, $34\text{--}41 \times 3.5\text{--}4 \mu\text{m}$.

Specimens examined.—SPAIN. Zaragoza: Pina de Ebro, Retuerta de Pina, 30 July 1990, J. Blasco coll., on elytra and legs of *Sacium aequale* Woll. (Coleoptera: Corylophidae), *S. Santamaría 1623a* (BCB-ss-1623a).—Girona: Riells i Viabrea, Junior Parc, 2 Aug 1993, on inferior surface of *S. aequale*, *S. Santamaría 1713* (BCB-ss-1713).

Notes.—My description and drawings of are based on specimens received from Dr. Santamaría. This material includes one nearly mature and two fully mature females, two immature females with early stages of development of the trichogyne, and three males. In addition there are two immature, but aberrant, females, and a mature receptacle and perithecium, which are widely separated from one another. The mature females, however, match closely Maire's (1920) description and somewhat diagrammatic illustration of *Cryptandromyces peyerimhoffii*, found on *Arthrolips obscurus* J. Sahlb. var. *sancta-balmae* Abeille (Corylophidae). Maire's description was based on five perithecium-bearing individuals, and certain of the dimensions he cites differ somewhat from those given above, i.e., total length, $125\text{--}135 \mu\text{m}$; perithecial stalk, $20\text{--}23 \mu\text{m}$; perithecium $85\text{--}95 \times 33\text{--}35 \mu\text{m}$; and ascospores, $33\text{--}36 \times 4 \mu\text{m}$.

Balazuc (1974) records a collection of four specimens of *Corylophomyces peyerimhoffii* (as *Autophagomyces peyerimhoffii*) taken from the elytra of *Sacium nanum* (Muls.) from France. Dr. Tavares kindly sent me a photograph of one of Balazuc's specimens, which shows an ascoma corresponding closely to the taxon as illustrated by Maire in having an acute appendage with a similarly pigmented cross wall separating its two cells. Santamaría (1993) reports a single specimen, also as *A. peyerimhoffii*, on the elytron of *Arthrolips* sp. from Spain.

In the course of my studies of Laboulbeniales as a graduate student at the University of Illinois, 1947–



Key to labeling of the figures: *a*, original septum of spore and its position in a developing thallus; *an*, antheridium; *bc*, an undefined cell cut off from cell VII that has not yet divided and formed a true basal cell (*n* or *n'*) and a primordial outer wall cell (*o*); *cp*, carpogonial cell, subterminal cell of young perithecium, gives rise to ascogonium; *d*, perithecial initial; *e*, terminal cell of young perithecium, gives rise to trichophoric cell and trichogyne; *k*, lowermost cell of young perithecium, gives rise to cells VI and *m*; *j*, suprabasal cell of young

1951, I found single male and female individuals of a dioecious fungus congeneric with but specifically different from the taxa described in this paper. They parasitized a specimen of *Molamba fasciata* Say (Corylophidae) collected in Arkansas. When I studied the fungus, I suspected that it might be related to Maire's *Cryptandromyces peyerimhoffii*. Unfortunately, the mounted specimens are now in very poor condition and not suitable for description, and the fungus has not been encountered again. When it is rediscovered and can be properly described, characteristics of the male as given in the generic diagnosis of *Corylophomyces* will need emendation, for, in addition to a terminal antheridium, two lateral, secondary antheridia arise from cells cut off distally by the receptacle.

It was during my tenure at the Farlow Herbarium, where I first studied *Autophagomyces sarawakensis* and determined its dioecious character, that I suspected that this taxon and very likely *A. peyerimhoffii* were misplaced generically (Benjamin 1970). Santamaría's description of *A. sericoderi* and his report of new collections of *A. peyerimhoffii* revived my interest in Laboulbeniales parasitizing Corylophidae, and his willingness to share his material with me enabled me to complete a study I started so long ago.

2. *Corylophomyces sericoderi* (Santam.) R. K. Benj.,
comb. nov. Fig. 10–19

=*Autophagomyces sericoderi* Santam. *Nova Hedwigia* 56: 412, 1993.

Male.—Hyaline except for a partially opaque foot, elongate, slender; basal cell of receptacle, including foot, $23\text{--}25 \times 4.5\text{--}5 \mu\text{m}$, ca. five times longer than the suprabasal cell, which is slightly higher than wide, $5\text{--}6 \times 4.5\text{--}5 \mu\text{m}$; antheridium gradually attenuate distally, $12\text{--}14 \times 4\text{--}5 \mu\text{m}$. Total length $40\text{--}45 \mu\text{m}$.

Female.—Ascoma elongate, nearly straight; hyaline to pale yellow. Total length from tip of foot to tip of perithecium $143\text{--}170 \mu\text{m}$. **Receptacle:** Triangular, $31\text{--}39 \mu\text{m}$ high, $10\text{--}13 \mu\text{m}$ wide distally, tapered downward to the acute, hyaline tip of the otherwise opaque foot; basal cell (I) ca. three times longer than wide, nearly cylindrical, only slightly wider above than be-

low, $23\text{--}31 \times 6\text{--}9 \mu\text{m}$, subtending the terminal cell (III) and suprabasal cell (II), from which it is separated by a strongly diagonal cross wall; cells II and III \pm trapezoidal, united, in part, on the inside and \pm parallel to one another; slightly longer than wide; cell II $9\text{--}11 \times 5\text{--}7 \mu\text{m}$, subtending the primary stalk cell of the perithecium; cell III $7\text{--}9 \times 6\text{--}8 \mu\text{m}$, subtending the primary appendage. **Appendage:** Consisting of two superposed cells in line with cells I and III of the receptacle, $20\text{--}24 \mu\text{m}$ long; basal cell quadrangular, with slightly concave margins, nearly isodiametric, $8\text{--}11 \times 7\text{--}10 \mu\text{m}$; terminal cell elongate, \pm acute, $12\text{--}15 \mu\text{m}$ high, $6\text{--}9 \mu\text{m}$ wide at the base, separated from the basal cell by a transverse cross wall. **Perithecium:** Primary stalk cell (VI) elongate, $25\text{--}40 \times 10\text{--}12 \mu\text{m}$, incurved, widest distally, nearly free, slightly constricted at the base; secondary stalk cell (VII) small, \pm triangular in lateral view, lying above cell VI on the outside, partially enclosed distally by the basal cells (*m*, *n*, and *n'*), which, along with cell VII, constitute ca. 20 % of the total length of the body of the perithecium above cell VI; basal cells barely enveloping the base of the ascigerous cavity; basal cell *m* externally \pm strongly convex, as are the outer wall cells of the first three tiers; body, including basal cells, $85\text{--}105 \mu\text{m}$ long, slightly inflated, broadest medianly, $24\text{--}28 \mu\text{m}$ wide, outer margin nearly straight, inner margin convex, gradually narrowed toward the apex; the terminal outer wall cell of the antero-lateral row formed by basal cell *n* forming an elongate, slightly curved protuberance $5\text{--}7 \times 3 \mu\text{m}$. Ascospores hyaline, $20\text{--}22 \times 3 \mu\text{m}$.

Specimens examined.—SPAIN. Barcelona: Gualba, Gualba de baix, Riera de Gualba, 10 Aug 1990, on elytra of *Sericoderus lateralis* (Gyll.) (Coleoptera: Corylophidae), *S. Santamaría* 991 (HOLOTYPE; BCB-SS-991).—Barcelona: Gualba, Torrent de Can Dansa, 31 July 1993, on elytra of *S. lateralis*, *S. Santamaría* 1707 (BCB-SS-1707).

Notes.—The slide bearing the holotype, BCB-SS-991, includes three mature females (one lacking the foot), one nearly mature female, one mature perithecium separated from its receptacle, four receptacles with appendages, and six males (one broken); slide BCB-SS-1707 includes five immature females, six males (two broken), and one receptacle with appendage. The fe-

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perithecium, gives rise to cells VII, *n*, and *n'*; *m*, perithecial basal cell derived from cell VI, gives rise to one vertical row of wall cells; *n*, one of two perithecial basal cells derived from cell VII, gives rise to two vertical rows of wall cells; *n'*, the other perithecial basal cell derived from cell VII, gives rise to one vertical row of wall cells; *o*, a primordial outer wall cell; *pa*, primary appendage; *tc*, trichophoric cell, lies between carpogenic cell and trichogyne; *tr*, trichogyne (also trichogynic remnant); *w*¹⁻⁵, outer wall cell tiers 1 (basal) to 5 (terminal); I, basal cell of receptacle; II, suprabasal cell of receptacle; III, terminal cell of receptacle; VI, primary stalk cell of perithecium; VII, secondary stalk cell of perithecium.

Fig. 1–9. *Corylophomyces peyerimhoffii* (Fig. 1, 6–9: BCB-SS-1623a; Fig. 2–5: BCB-SS-1713).—1–2. Two males, the one on the right with the foot missing.—3–4. Two juvenile females showing early stages of development of the perithecium.—5–7. Three mature females. Cell VI of the perithecium of the ascoma shown in Fig. 7 was twisted and the perithecial body rotated 180° when the specimen was mounted; thus, the positions of cells VII and *m* in this individual are reversed in comparison to the same cells in the individual shown in Fig. 6.—8–9. Two ascospores. (Bars = 10 μm : A, Fig. 5–7; B, Fig. 1–4, 8–9.)

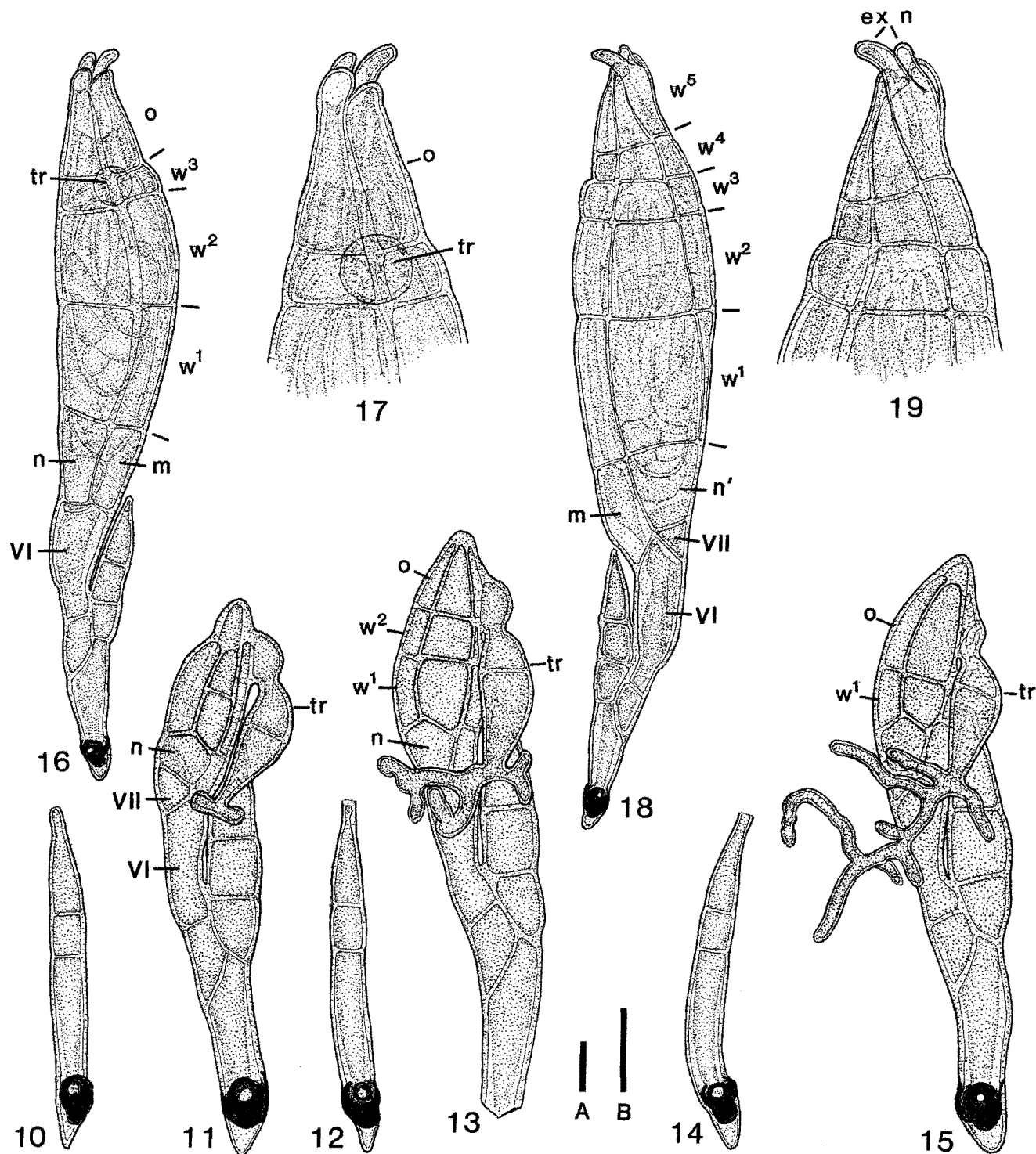


Fig. 10–19. *Corylophomyces sericoderi* (Fig. 10–15: BCB–SS–1707; Fig. 16–19: BCB–SS–991).—10, 12, 14. Three males; the one shown in Fig. 10 not yet mature.—11, 13, 15. Three juvenile females showing early stages of development of the perithecium and trichogyne. In the individual shown in Fig. 13, development of the trichogyne was slightly less advanced than that of the individual shown in Fig. 15; conversely, the outer wall of the perithecium of the former was slightly more advanced than in the latter, already having two rather than one permanent tiers of outer wall cells.—16. Nearly mature female.—17. Slightly enlarged tip of the perithecium shown in Fig. 16.—18. Fully mature female.—19. Slightly enlarged apex of the perithecium shown in Fig. 18; the pair of distal prominences (here designated *ex n*) are formed at the apex of the row of outer wall cells derived from basal cell *n* adjacent to the row of cells derived from basal cell *n'*. (Bars = 10 μ m: A, 16, 18; B, 10–15, 17, 19.)

male of *Corylophomyces sericoderi* is readily distinguished from that of *C. peyerimhoffii*, which also has a two-celled appendage, by its nearly straight habit, by its relatively slender acute appendage lacking a pigmented cross wall, and especially by its perithecial apex with its two short prominences, the longer of which is somewhat curved.

3. *Corylophomyces sarawakensis* (Thaxt.) R. K. Benj., comb. nov. Fig. 20–35

= *Autophagomyces sarawakensis* Thaxt., *Mem. Amer. Acad. Arts.* 16: 94, 1931.

Male.—Hyaline except for a partially opaque foot, elongate, slender, straight or slightly curved, 43–55 μm long, \pm gradually attenuate from near the base to the tip of the antheridium; basal cell of receptacle, 24–27 \times 5–6 μm , ca. five times longer than the suprabasal cell, which is nearly isodiametric, 5 \times 5 μm ; antheridium \pm uniformly narrowed toward the apex, 13–23 μm long, 4–5 μm wide at the base.

Female.—Ascoma elongate, erect, pale brownish yellow. Total length from tip of foot to tip of perithecium 135–156 μm . **Receptacle:** Triangular, 33–40 μm high, 10–15(–20) μm wide distally, tapered downward to the acute, hyaline tip of the otherwise opaque foot; basal cell (I) 22–31 \times 8–10(–15) μm , in contact above with the terminal cell (III) and suprabasal cell (II), from which it is separated by an oblique cross wall; cells II and III \pm trapezoidal, united with each other, in part, on the inside; suprabasal cell slightly higher than wide, 6–12 \times 6–8(–10) μm , subtending the primary stalk cell (VI) of the perithecium; cell III nearly isodiametric, 7–12 \times 7–12 μm , subtending the primary appendage. **Appendage:** Hyaline, consisting of three superposed cells in line with cells I and III of the receptacle, 24–38 μm long; basal cell quadrangular, slightly wider than high, 9–15 \times 6–9 μm ; median cell about half again as high as wide, \pm convex externally, narrowed distally, 12–18(–21) \times 9–13(–15) μm ; terminal cell small, triangular, only slightly higher than wide, 6–11 μm high, 5–7 μm wide at the base, separated from the median cell by a transverse cross wall. **Perithecium:** Primary stalk cell (VI) 20–27 μm long, 8–14 μm wide distally; secondary stalk cell (VII) small, \pm triangular in lateral view, lying above cell VI on the outside, partially enclosed distally by the basal cells (*m*, *n*, *n'*), which, along with cell VII constitute ca. 20% of the total length of the body of the perithecium above cell VI; basal cells barely enclosing the base of the ascigerous cavity; body, including basal cells, 65–100 μm long, nearly straight, narrowest at the base, inflated distally, 25–29 μm wide; the apex broad, asymmetrical, with a pair of short, fingerlike protuberances, 5–8 \times 3–5 μm , distally on the inside opposite a broad-

based, divergent, pointed prominence on the outside; and with a second pair of short, distally rounded protuberances, 5–8 \times 6–8 μm , borne laterally at the level of the median tier of outer wall cells. Ascospores hyaline, 33–35 \times 3–4 μm .

Specimens examined.—MALAYSIA. Sarawak: Kuching, 1912, J. C. Moulton coll., on the base of the left elytron of a minute unidentified species of Corylophidae ("Phalacrid allied to *Olibrus*" fide Thaxter [1931]), *Thaxter* 2374 (HOLOTYPE: FH, Acc. No. 4037; ISOTYPES: FH, Acc. Nos. 4038, 4039); on the base of the left elytron of duplicates of the host that bore the holotype, i.e., *Thaxter* 2374, *RKB* 1331B (RSA); "Sarawak": the only data other than Thaxter's accession number, i.e., *Thaxter* 1820, accompanying the hosts (undoubtedly received from J. C. Moulton to whom Thaxter attributed insects collected in Sarawak [Thaxter 1931: 6]); on the base of the left elytron of an unidentified species of Corylophidae, *RKB* 1438B (RSA).

Notes.—The three slides from the Thaxter collection (Acc. Nos. 4037–4039) include a total of eight mature and six immature females, one receptacle, and one male. Specimens found on the other hosts from Sarawak (*RKB* 1331B, 1438B) include four mature females (two in very poor condition), two nearly mature females, 13 immature females, 20 males, and four appendages. This material has been ample for preparing the above revised description of Thaxter's taxon, and for illustrating the male as well as several stages of early development of the ascoma of the female.

4. *Corylophomyces reflexus* R. K. Benj., sp. nov.

Fig. 36–42

Mas.—Hyalinus praeter pedem opacum, elongatus, gracilis, prope rectus, 35–37 μm longus; cellula basalis receptaculi elongata, 17–20 \times 5–6 μm ; cellula suprabasalis prope isodiametra, 5 \times 5 μm ; antheridium attenuatum, 12–13 μm longum, basi 5 μm . **Femina.**—Ascoma valde intro recurvatum, aurantiaco-brunneum praeter corpus perithecii fuscum infra apicem. Thallus 104–136 μm pede ad marginem antica perithecii. **Receptaculum:** Plus minusve triangulare, 17–35 μm altum, latitudine distali 12–20 μm ; cellula basalis (I) 23–28 \times 9–12 μm , externe convexa, interne concava; cellula suprabasalis (II) plus minusve trapezoidea, 6–11 μm alta, 9–13 μm lata; cellula terminalis (III) prope isodiametra, 6–7 \times 8–10 μm , paulo divergens, margine externa valde convexa. **Appendix:** Leniter curvata, 18–24 μm longa; cellula basalis externe convexa, 6–8 μm alta, 12–17 μm lata; cellula media valde externe convexa, 9–13 μm alta, 12–17 μm lata; cellula terminalis parva, triangularis, 4–5 μm alta, basi 5–8 μm lata. **Perithecium:** Cellula VI 51–65 μm longa, ad medium ca. 20 μm lata, \pm intro arcuata; cellula VII relative parva, 14–18 \times 11–15 μm , margine externa valde convexa; corpus, cum cellulis basilaribus, ca. 110–116 \times 46–53 μm , margine antica valde convexa, margine postica prope stricta; cellulae apicis rotundatae leniter protrudentes, prominentia parva laterali 9–11 \times 6–8 μm . Ascospores hyalinae, 31–36 \times 4–5 μm . Typus *RKB* 1331C: FH.

Male.—Hyaline except for a partially opaque foot, elongate, slender, nearly straight, 35–37 μm long, \pm attenuate from near the base of the foot to the tip of the antheridium; basal cell of receptacle 17–20 \times 5–6 μm , ca. five times longer than the suprabasal cell, which is nearly isodiametric, 5 \times 5 μm ; antheridium

gradually attenuate, \pm abruptly constricted apically, 12–13 μm long, 5 μm wide at the base.

Female.—Ascoma strongly recurved inwardly, the perithecial tip reaching nearly to the level of the basal cell of the receptacle, brownish orange, the body of the perithecium darker below the tip and above the primary stalk cell (VI). Total distance from the tip of the foot to the most distant point on the anterior margin of the perithecial body 104–136 μm . **Receptacle:** More or less triangular, 27–35 μm high, 12–20 μm wide distally, tapered downward to the rounded hyaline tip of the otherwise opaque foot; basal cell (I) more than twice as high as wide, 23–28 \times 9–12 μm , the inner margin convex, the outer margin \pm concave; suprabasal cell \pm trapezoidal, slightly less high than wide, 6–11 \times 9–13 μm , subtending the primary stalk cell (VI) of the perithecium, from which it is separated by a transverse septum; cell III nearly isodiametric, 6–7 \times 8–10 μm , somewhat divergent, the free outer margin strongly convex, united on the inside with cells I, II, and the base of cell VI, broadly united above with the basal cell of the appendage. **Appendage:** Consisting of three superposed cells, curved outward slightly, 18–24 μm long; basal cell 6–8 μm high, 10–12 μm wide, outer and inner margins strongly convex; median cell 9–13 μm high, 12–17 μm wide, outer and inner margins very strongly convex; terminal cell small, triangular, 4–5 μm high, 5–8 μm wide at the base, separated from the median cell by a transverse cross wall. **Perithecium:** Primary stalk cell (VI) 51–65 μm long, broadest distally, median width ca. 20 μm , \pm inwardly curved; secondary stalk cell relatively small, slightly longer than broad, 14–18 \times 11–15 μm , outer margin strongly convex; basal cells (*m*, *n*, *n'*) enclosing only the base of the ascigerous cavity, constituting ca. 20% of the total length of the body of the perithecium above cell VI; basal cell *n* strongly externally rounded below; body, including basal cells strongly curved, ca. 110–116 \times 46–53 μm ; the basal and suprabasal outer wall cells derived from basal cell *m* much shorter than the relatively greatly elongated and somewhat thickened basal and suprabasal cells of the basal-cell-*n*-derived row of outer wall cells that constitute the prominent anterior margin of the perithecial body; the apex distinguished by the \pm protrudent, rounded terminal outer wall cells and a short, divergent, subapical, lateral prominence, 9–11 \times 6–8 μm , near the juncture of the

upper two outer wall cells of the lateral row of wall cells derived from basal cell *n*. Ascospores hyaline, 31–36 \times 4–5 μm .

Etymology.—From *reflexus* (L.), reflexed.

Holotype.—MALAYSIA. Sarawak: Kuching, 1912, J. C. Moulton coll., on the anterior margin of the left metasternal episternum of a minute unidentified species of Corylophidae ("Phalacrid allied to *Olibrus*" fide Thaxter [1931]) (duplicate hosts of *Thaxter* 2347), *RKB* 1331C (HOLOTYPE: FH; ISOTYPES: RSA).

Other specimens examined.—"Sarawak": the only data other than Thaxter's accession number (i.e., *Thaxter* 1820) accompanying the hosts (probably received from J. C. Moulton [Thaxter 1931]); on the anterior margin of the left metasternal episternum of a minute unidentified species of Corylophidae, *RKB* 1437A, 1438A (RSA).

Notes.—The material upon which the description and illustrations of *C. reflexus* are based consists of six mature or nearly mature females (one in very poor condition) and six males. When I originally examined the few available hosts, I was indeed fortunate in encountering these specimens, which were attached in a very obscure position on the underside of what is an extremely small insect. The female of this taxon resembles those of *C. sarawakensis* and *C. weirii* in having a three-celled appendage. It is wholly distinct from that of *C. sarawakewnsis* in the conformation of its appendage and perithecium. It differs from that of *C. weirii* most noticeably in its asymmetrical, strongly reflexed perithecium.

Corylophomyces weirii R.K. Benj., sp. nov.

Fig. 43–45.

Mas.—Non observatum.

Femina.—Ascoma valde intro inclinatam, praeter receptaculum, cellulam VI, et apicem perithecii dilutum flavo-brunneolum; distantia 140–160 μm apice pedis ad apicem perithecii. **Receptaculum:** Atrobrunneum, triangulare, 40–44 μm altum, latitudine distali 24–26 μm ; cellula basalis (I) triangularis, 33–38 μm alta, latitudine distali 17–23 μm , pede opaco, a latere visus striis dendroideis lateralibus usque ca. 10 μm longis; cellula II et III \pm trapezoideis, intra uniti; cellula II 7–9 \times 12–14 μm ; cellula III 8–9 \times 15–19 μm . **Appendix:** Prope recta, 25–26 μm longa; cellula basalis \pm quadrangularis, 6–8 \times 16–19 μm ; cellula media tholiformis, 10–12 μm alta, basi 15–16 μm lata; cellula terminalis parvula, acuta, 7–8 μm alta, basi 4–6 μm lata. **Perithecium:** Cellula VI liberum, basi abrupte constricta, inflata, extra fortiter convexa, intra prope recta vel leniter concava, in dimidio superno vel plus atrobrunneo, 30–36 μm longa, latitudine distali 23–28 μm ; corpus, cum cellulis basilaribus et cellula VII,

←
Fig. 20–35. *Corylophomyces sarawakensis* (Fig. 23, 28, 30–35: *Thaxter* 2374; Fig. 20–22, 24–27, 29: *RKB* 1438B).—20–22, 29. Four males.—23–28. Six juvenile females showing several stages of development of the perithecium and trichogyne. Details are given in the text.—30–31. Two females in intermediate and late stages of development, respectively. Note position of the trichogynic remnant, and, in Fig. 31, the development of the two distal prominences, characteristic of the species, from primordial outer wall cell (*o*) of the row of outer wall cells derived from basal cell *n* adjacent to the row of cells derived from basal cell *m*.—32. Mature female. Division into two cells of the distal cell of the row of outer wall cells derived from basal cell *n*, which gave rise to the terminal prominences, could not be determined and the cell is here designated *w*⁴⁻⁵.—33–35. Three ascospores. (Bars = 10 μm : A, 20–31, 33–35; B, 32.)

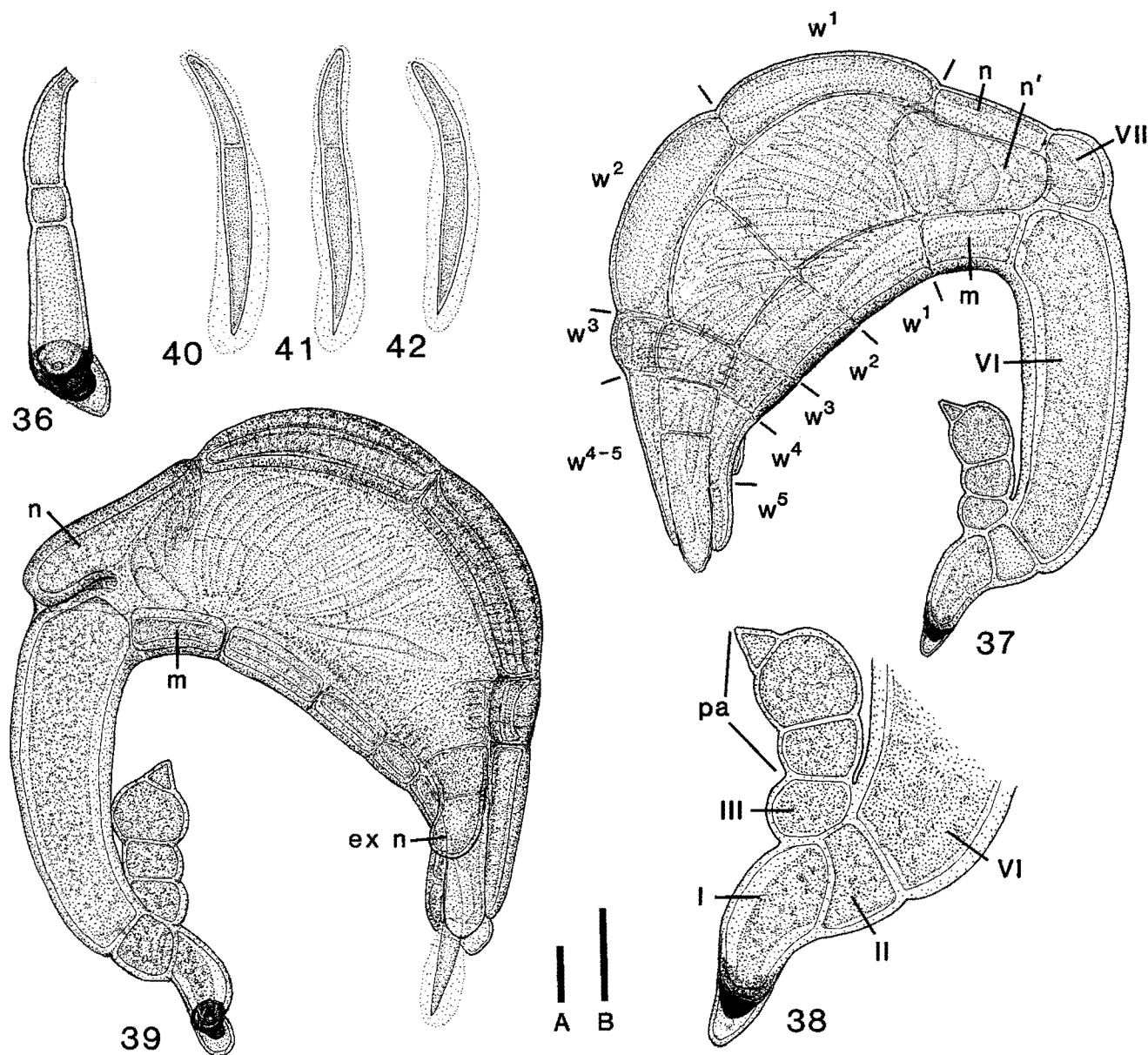


Fig. 36-42. *Corylophomyces reflexus* (Fig. 36, 39, 40-42: RKB 1331C; Fig. 37, 38: RKB 1438A).—36. Mature male.—37. Nearly mature female.—38. Slightly enlarged receptacle and appendage of the individual illustrated in Fig. 37.—39. Mature female (holotype) viewed from the side opposite that of the individual shown in Fig. 37. Note the subterminal perithecial prominence (designated *ex n*) near the juncture of the fourth and fifth cells of the basal-cell-*n*-derived row of outer wall cells adjacent to the row of cells derived from basal cell *m*.—40-42. Three ascospores. (Bars = 10 μ m: A, 37, 39; B, 36, 38, 40-42.)

114-153 μ m longum, prope uniformiter inflatum, latitudine media 45-60 μ m; apex gradatim angustatus, rotundatus, atrobrunneus; cellulae terminales leniter protrudentes. Ascospores hyalinae, ca. 45-50 \times 3.5-4 μ m. Typus Weir 0053: κ .

Male.—Not observed.

Female.—Ascoma strongly inclined inwardly, \pm pale yellow brown; distance from tip of foot to tip of perithecialium 140-160 μ m. *Receptacle*: Dark brown, triangular, 40-44 μ m high, 24-26 μ m wide distally, tapered downward to the hyaline tip of the otherwise opaque foot; basal cell (I) triangular, 33-38 μ m high,

17-23 μ m wide distally, with opaque, dendriform striae as much as 10 μ m long extending upward from the foot on the surface opposite the haustorial opening; cells II and III \pm trapezoidal, united on the inside; cell II wider than high, 7-9 \times 12-14 μ m, subtending the primary stalk cell of the perithecialium; cell III about twice as wide as high 8-9 \times 15-19 μ m, broadly separated from the basal cell of the appendage by a transverse cross wall. *Appendage*: Nearly straight, consisting of three superposed cells in line with cells I and III of the receptacle, 25-26 μ m long; basal cell \pm

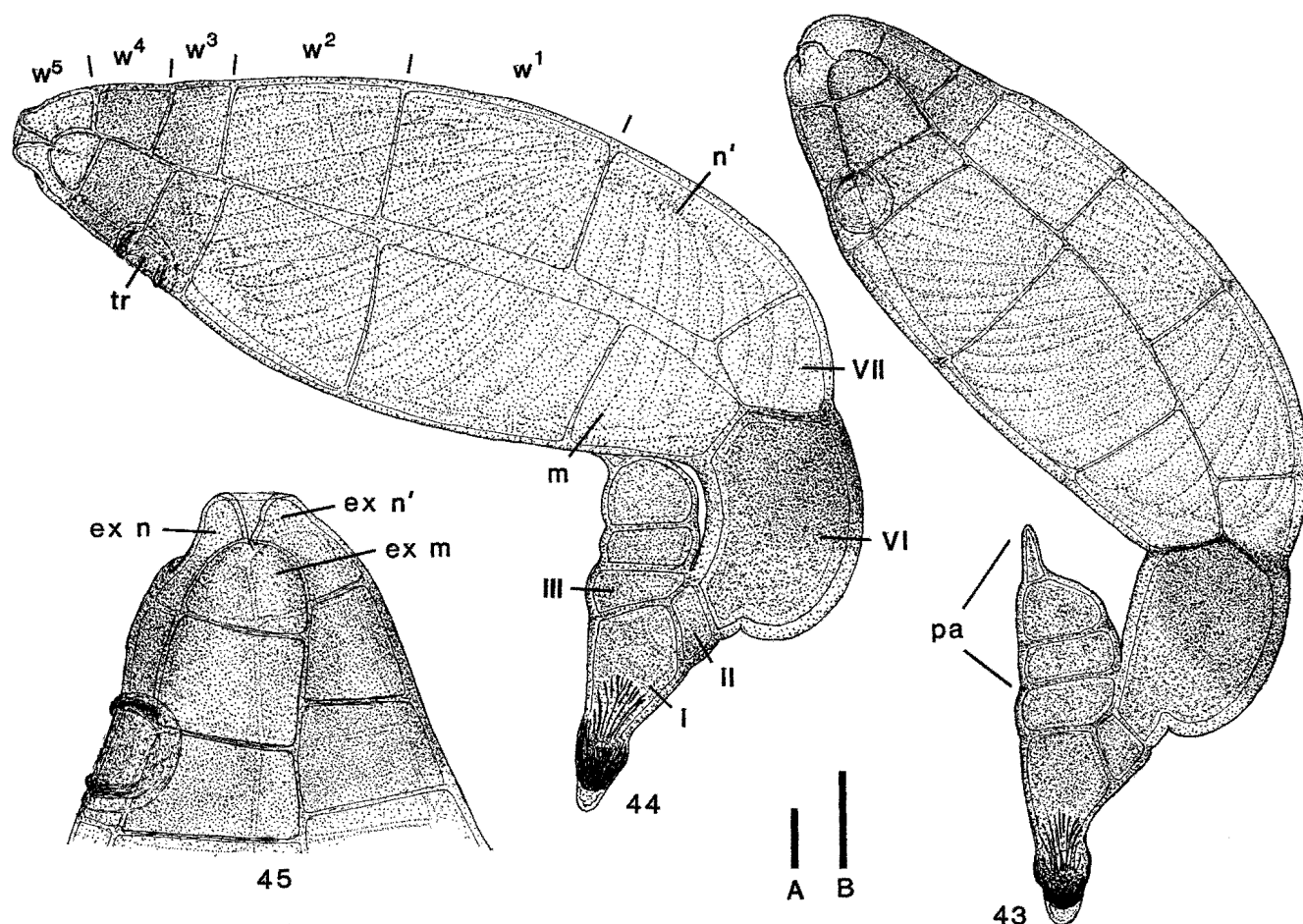


Fig. 43–45. *Corylophomyces weirii* (Weir 491).—43–44. Two mature females (holotype: Fig. 43). When mounted, the individual shown in Fig. 44 was compressed slightly, causing a slight longitudinal separation of some of the cells of the perithecial body, which was pushed downward against the upper end of the appendage.—45. Sketch, slightly enlarged, of the tip of the perithecium depicted in Fig. 44. The relationship of three of the four terminal outer wall cells to the vertical rows of outer wall cells derived from basal cells *m*, *n'*, and *n* is indicated. The fourth terminal outer wall derived from basal cell *n* is out of view on the opposite side of the perithecial tip. The apex of the terminal basal-cell-*n*-derived outer wall cell (*ex n*) adjacent to the terminal cell derived from basal cell *m* (*ex m*) forms a pair of terminal prominences, one much more pronounced than the other. (Bars = 10 μ m: A, 43, 44; B, 45.)

quadrangular, about half as high as wide, $6\text{--}8 \times 16\text{--}19\text{ }\mu\text{m}$; median cell dome shaped, $10\text{--}12\text{ }\mu\text{m}$ high, $15\text{--}16\text{ }\mu\text{m}$ wide at the base; terminal cell relatively small, acute, $7\text{--}8\text{ }\mu\text{m}$ high, $4\text{--}6\text{ }\mu\text{m}$ wide at the base. *Perithecium*: Primary stalk cell (VI), free, abruptly constricted near the base where it joins cell II of the receptacle, inflated above, strongly convex on the outside, nearly straight or slightly concave on the inside, upper one half or more dark brown, $30\text{--}36\text{ }\mu\text{m}$ long, $23\text{--}28\text{ }\mu\text{m}$ wide distally; secondary stalk cell (VII) lying above cell VI on the outside, together with the basal cells (*m*, *n*, *n'*) enveloping the base of the ascigerous cavity and constituting ca. one third the total length of the body of the perithecium above cell VI; body, including basal cells, $114\text{--}153\text{ }\mu\text{m}$ long, nearly uniformly inflated, median width $45\text{--}60\text{ }\mu\text{m}$, abruptly and uniformly narrowed distally, the apex gradually narrowed, rounded, with the terminal outer wall cells

projecting only slightly. Ascospores hyaline, ca. $45\text{--}50 \times 3.5\text{--}4\text{ }\mu\text{m}$.

Etymology.—Named for Alex Weir, British student of Laboulbeniales.

Holotype.—INDONESIA. Sulawesi: Sulawesi Utara Prov.; Dumoga Bone National Park; Plot A; lowland forest, el. ca. 200 m, July 1985, P. M. Hammond coll.; on elytra and pronotum of Corylophidae, gen. et. sp. indet. (British Museum Code 94.5) Weir 491 (HOLOTYPE: K; ISOTYPE: RSA).

Other specimens examined.—INDONESIA. Sulawesi, Sulawesi Utara Prov.; Dumoga Bone National Park; Plot B; lowland forest, el. ca. 300 m, Apr 1985, P. M. Hammond coll.; on elytra and pronotum of Corylophidae, gen. et. sp. indet. (British Museum Code 94.5), Weir 490 (K).

Notes.—The specimens of *Corylophomyces weirii* received from Weir were mounted on four slides and

included six mature, one nearly mature, and three immature females as well as three female receptacles with appendages. Weir also forwarded two of the hosts from which he had removed some of the fungi, and from these insects I recovered three more immature females, but no males. None of the immature females examined was at a stage of development showing the nature of the trichogyne, being either too young or too old. The host insects appear, according to Weir, to belong to a single species, and they await identification. They currently are referenced under the British Museum code number given above.

The female of *Corylophomyces weirii*, like that of *C. sarawakensis* and *C. reflexus* has a three-celled appendage. However, as can be seen from an examination of the accompanying figures of these species, they differ greatly from one another in the morphology of their perithecia. The distinctive dendritic striae radiating upward from the opaque foot along the surface of the basal cell of the receptacle of *C. weirii* appear very early in the development of the receptacle.

OBSERVATIONS

Ascospore

Spores did not appear to differ enough in size in any of the species of *Corylophomyces*, when observed inside or outside the perithecium, to suggest male-female ascospore dimorphism. The body of the ascospore was divided by a single, transverse cross wall (*a*) into long and short segments having a ratio to one another of ca. 2:1 (Fig. 8, 9, 33–35, 40–42), with the longest segment uppermost in the perithecium prior to discharge (Fig. 5–7, 18, 32, 37, 39, 44, 45).

Male

In all instances, the male consisted of a receptacle of but two cells, in which the basal cell was uniformly about five times longer than the suprabasal cell. The latter was nearly isodiametric and subtended a single, elongate, more or less flask-shaped or attenuate antheridial phialide (*an*) (Fig. 1, 2, 10, 12, 14, 20–22, 29, 36). When viewed face-on, the opaque part of the otherwise hyaline foot, which had been in direct contact with the host, was distinguished by a small, circular, more or less median, clear opening that coincided with the proximal end of the contents (plasmolyzed) of the basal cell (Fig. 10, 12, 14, 22, 36). In all instances but one, males and females had been dispersed when mounted. However, in one preparation of *C. reflexus* where single male and female individuals still were attached to a fragment of host integument, the feet of the two sexes were in contact.

Female

Receptacle.—Early stages of development of the receptacle of females from the two-celled ascospore were not found. In the juveniles encountered, the receptacle already consisted of three cells (Fig. 3, 4, 11, 13, 23–28) in which the relatively elongate basal cell (I) was separated from the suprabasal and terminal cells (II and III) by more or less oblique cross walls. Cells II and III were nearly transversely arranged, with III positioned slightly above the level of II (Fig. 3, 4, 11, 13, 15, 23–28), and the relationship of these cells remained essentially unchanged as the ascoma matured (Fig. 5–7, 16, 18, 30–32).

Appendage.—In all instances but one, the primary appendage (*pa*) of the juvenile individuals examined consisted of two or three cells and, depending on the species, was morphologically nearly like that of the mature ascoma (Fig. 3–7, 11, 13, 15, 16, 18, 24–28, 30–32). In a single individual of *C. sarawakensis*, the appendage consisted of a single, relatively large, dome-shaped cell, presumably representing the initial stage of development of the appendage from the upper cell of the original ascospore (Fig. 23, *pa*).

Perithecium.—The earliest stage of perithecial development was found only in two immature specimens of *C. sarawakensis* (Fig. 23, 24) where the perithecial initial (*d*) had arisen from the suprabasal cell (II) of the receptacle. As seen in the individual depicted in Fig. 24, the primary appendage (*pa*) already had reached its three-cell limit before further development of the perithecium from cell *d* had begun. In the next earliest stage of perithecial development encountered (Fig. 25), four cells, *k*, *j*, *cp* (the carpogonial cell), and *e*, had arisen from cell *d*. In the individuals shown in Fig. 3 and 26, cell *m*, the first of three perithecial basal cells, had arisen distally on the inside from cell *k*, which had become the primary stalk cell (VI) of the perithecium. As shown in Fig. 3, 25, and 26, the distal part of cell *e* had begun to recurve posteriorly. In the young perithecium pictured in Fig. 4, cell *j* had divided and formed the secondary stalk cell of the perithecium (VII), which in turn had cut off an elongate cell (here termed *bc*) that had grown upward around the base of the carpogonic cell (*cp*); cell *m* had divided and formed a primordial wall cell (*o*) distally on the inside; and cell *e* had given rise terminally, to the reflexed trichogyne initial (*tr*), which had become constricted above its base, and the trichophoric cell (*tc*), which had begun to grow upward. A somewhat later stage of perithecial development is shown in Fig. 27 where the other two perithecial basal cells *n* and *n'*, derived from what was now cell VII, had formed. From these and basal cell *m*, the first permanent tier of outer wall cells (*w*¹) had developed, the cells of

which had, in turn, given rise to a tier of primordial wall cells (*o*); the enlarged distal part of the reflexed trichogyne (*tr*), now strongly constricted near its base, had been divided into two parts by a transverse cross wall.

A few stages of trichogynic development beyond the level of that shown in Fig. 27 were found in juveniles of *C. sericoderi* and *C. sarawakensis*. In *C. sericoderi*, the relatively elongate, strongly reflexed, two-celled trichogyne extended downwardly and inwardly alongside the body of the immature perithecium (Fig. 11, 13, 15). The lower part of the constricted basal cell formed a lateral, bulbous enlargement broadly attached to the perithecium below the tip. The upper cell gradually narrowed toward the apex where it ramified and formed a complex of slender, coenocytic branchlets (Fig. 11, 13, 15). A mature trichogyne of *C. sarawakensis* (Fig. 28), which was in poor condition and may have begun to degenerate at the time the specimen bearing it was mounted, appeared to have the same basic structure as that of *C. sericoderi*. As development of the perithecium progressed, the trichogyne had disappeared except for a portion of its base, which remained in the form of a slightly elevated scar on the surface of the perithecium (Fig. 16, 17, 30–32, 43–45). This relatively large, persistent remnant was located at the juncture between the third and fourth outer wall cells of the vertical rows of cells derived from basal cell *m* and the adjacent row of the two rows derived from basal cell *n*.

The outer wall of the mature perithecium consisted of four vertical rows of cells derived from the three basal cells, one row each from cells *m* and *n'*, and two rows from cell *n*, one row adjacent to the basal-cell-*m*-derived row, the other adjacent to the basal-cell-*n'*-derived row (Fig. 30, 31). Only the upper two tiers of inner wall cells could be discerned with any certainty in mature perithecia, those lower down having been compressed and rendered \pm unrecognizable as ascospores matured within the ascigerous cavity. In fully mature individuals of *C. peyerimhoffii* (Fig. 6), *C. sericoderi* (Fig. 18), and *C. weirii* (Fig. 43, 44) the outer wall appeared comprised of five tiers of cells (w^{1-5}); however, in *C. sarawakensis* (Fig. 32) and *C. reflexus* (Fig. 37, 39) I could not detect a fifth cell in the basal-cell-*n*-derived row adjacent to the basal-cell-*n'*-derived row.

In *C. peyerimhoffii*, *C. sericoderi*, *C. sarawakensis*, and *C. weirii* (Fig. 5–7, 16, 18, 32, 43, 44), the longest outer wall cells were those comprising the basal tier, with those of the suprabasal tier being only slightly shorter. Together, these cells comprised one half or more of the total length of the perithecial body. In these species and *C. reflexus* as well (Fig. 37, 38), the shortest cells were those of the third and fourth tiers, which were often subequal. In the recurved body of

C. reflexus, the basal and suprabasal cells of the basal-cell-*m*-derived row were relatively short compared to those of the other three rows (derived from basal cells *n* and *n'*), with those of the row comprising the outside of the arc being about twice as long as those comprising the inside of the arc (Fig. 37, 38).

DISCUSSION

When Thaxter studied the fungus he described as *Autophagomyces sarawakensis* he must not have found the single male individual, which would have suggested dioecism, located some distance from three mature, perithecium-bearing individuals closely associated on one of his slides (Acc. No. 4038), otherwise he undoubtedly would have mentioned it—he was careful about such details. Thus, he did not recognize that the fungus possibly was dioecious and that the appendage of the ascoma might be sterile. The apices of the terminal cell of several (four) appendages in Thaxter's preparations contain fragments of cytoplasm resembling spermatia, and the malformed tip of one appendage is perforated much like that of a simple antheridium (Thaxter 1931: Pl. XVII, fig. 20). Thaxter's observation of these features, which resemble the antheridium of *Autophagomyces* as he defined the genus (Thaxter 1931: 94), especially species on Pselaphidae, apparently is what led him to assign the taxon to *Autophagomyces*. However, from my studies, it is clear that Thaxter's interpretation of the distal cell of the appendage of *A. sarawakensis* as a simple, spermatium-forming antheridium was based on artifacts.

Thaxter's handwritten notations (in black ink) on the labels of his slides of *A. sarawakensis* suggest his early assessment of the fungus prior to its placement in *Autophagomyces* (Thaxter 1931). When Thaxter actually mounted the specimens after he received the hosts from his correspondent in Sumatra (i.e., Moulton) is unknown to me. On the upper margin of each label is written "n. g.," indicating that initially he thought the fungus might represent a new genus. However, immediately below is written the binomial "*Bordea sarawakensis*," showing that he considered assigning it to *Bordea* Maire (Maire 1916), a genus he later transferred to *Autophagomyces* (Thaxter 1931). There follows "on base left el. minute ~~Nitidulid~~ Phalacridae." Thus, the host first was thought to belong to the Nitidulidae, but "Nitidulid" subsequently was struck through and Phalacridae added. Finally, at the bottom of each label is listed the locality and date, "Kuching, Sarawak, 1912." On one slide (Acc. No. 4039) is noted, in pencil, "near Olibrus," the genus he named as being allied to the host of *A. sarawakensis*. The name he actually gave to the fungus was not added to the labels.

In his discussion of *Cryptandromyces peyerimhoffii*,

Maire (1920) states that he hesitated to classify the fungus in the genus *Cryptandromyces* as defined by Thaxter (1912: 173), and he stresses the fact that in no instance did the appendage of any of the specimens he studied bear antheridia. He also notes the resemblance of the reduced appendage to that of certain dioecious species. His collection did include a single pair of individuals, which he figures (Maire 1920, Pl. 1, fig. 11), in which one is well developed, the other aborted but with the same type of appendage. The male of this taxon, here referred to *Corylophomyces*, proves, like that of *C. sarawakensis*, to be small and inconspicuous, so it is not surprising that Maire, who doubtless was not looking for males, did not detect them when he mounted his specimens. The associated pair he illustrates must have consisted of juxtaposed females from which the males had become separated, as often happens when one mounts dioecious species of Laboulbeniales. Later, in correspondence with Thaxter, Maire agreed that the species be transferred to *Autophagomyces* (Thaxter 1931: 366).

Perithecial ontogeny in *Corylophomyces* is like that of the perithecia of most genera of subfamily Laboulbenioideae (Laboulbeniaceae) (Tavares 1985) whose morphological development has been described in some detail, e. g., *Acallomyces* Thaxt. (Tavares 1973), *Acompsomyces* Thaxt. (Benjamin 1989), *Amorphomyces* Thaxt. (Tavares 1970), *Cupulomyces* R. K. Benj. (Benjamin 1992a), *Filariomyces* Shanor (Shanor 1952), *Idiomyces* Thaxt. (Benjamin 1983), *Laboulbenia* Thaxt. (Thaxter 1896; Tavares 1985), *Microsomyces* Thaxt. (Benjamin 1985), *Phalacrichomyces* R.K. Benj. (Benjamin 1992b), *Prolixandromyces* R. K. Benj. (Benjamin 1981), *Rhizopodomyces* Thaxt. (Benjamin 1979), *Stigmatomyces* Karsten (Thaxter 1896), *Synandromyces* Thaxt. (Benjamin 1984), *Tavaresiella* Majewski (Benjamin 1993), and *Triceromyces* Majewski (Benjamin 1986), in that two stalk cells form three basal cells (*n*, *n'*, and *m*) that give rise to four vertical rows of outer wall cells: two rows from cell *n*, and one row each from cells *n'* and *m*. Thaxter considered this a feature of what he termed the "normal" type of perithecial development in Laboulbeniales, for it is the one most often encountered in the order.

Within the Laboulbenieae, Tavares (1985) recognizes a subtribe, Amorphomycetinae, that includes four clearly dioecious genera, *Amorphomyces*, *Dioicomycetes* Thaxt., *Rhizopodomyces*, and *Tetrandromyces* Thaxt. (1912), and one genus, *Nanomyces* Thaxt. (1931) that may include both monoecious and dioecious taxa. In the context of Tavares's system of classification, *Corylophomyces* can be placed in Amorphomycetinae.

The receptacle of the female of *Amorphomyces* and *Rhizopodomyces* consists of but two cells, whereas that of the other four genera consists of three cells. Species

of *Rhizopodomyces* parasitize Hebridae (Heteroptera) (Benjamin 1979; Thaxter 1931); those of *Amorphomyces* parasitize Staphylinidae (Coleoptera), where they are known only on species of subfamilies Aleocharinae and Oxytelinae (Tavares 1985; Thaxter 1931).

Eleven species of *Amorphomyces* have been characterized (Tavares 1985; Thaxter 1931). Tavares describes in detail the development of the receptacle and appendage of the female of *Amorphomyces falagriae* Thaxt. (Tavares 1970, Fig. 8–12), which undoubtedly is representative of the genus as a whole. The basal cell of the receptacle proper comprises the apparent receptacle. The suprabasal cell, termed cell II–III by Tavares, represents a combination of cells II and III of the three-celled receptacle as found in *Dioicomycetes* and *Tetrandromyces*. Cell II–III gives rise to the perithecium on one side and a very small, rudimentary, bicellular primary appendage on the other side, and it is closely associated, at the same level, with the true stalk cells and basal cells of the perithecium. Early in the development of the perithecium, the primary appendage becomes embedded in the perithecial wall and is virtually undetectable. The lower segment of the male spore divides and forms a two-celled receptacle; the small, inconspicuous terminal segment, which is separated from the lower segment by a diagonal cross wall and was not detected by Thaxter (1908, 1931), gives rise to a single, simple antheridium in line with the receptacle (e. g., Tavares 1970, Fig. 1–3).

Rhizopodomyces includes seven described species (Benjamin 1979; Tavares 1985). In the female, the two-celled receptacle is well separated from the body of the perithecium by the usually greatly elongate primary stalk cell (VI) (e. g., Benjamin 1979, Fig. 1 A, 2 K). The suprabasal cell, II (actually a II–III cell), typically forms much of the receptacle proper and bears, in addition to the perithecium, a free, well-developed, unicellular appendage, which may or may not persist as the ascoma ages (e. g., Benjamin 1979, Fig. 2 E–K). The basal cell, I, usually forms one or more laterally directed, rhizoidlike outgrowths (e. g., Benjamin 1979, Fig. 1 A, 2 E–K, 4 H). The male consists of three or sometimes four superposed cells in which the basal cell, derived from the lower segment of the spore, constitutes the receptacle. The terminal cell forms a simple antheridium directly (e. g., Benjamin 1979, Fig. 2J, 4I) or a sterile appendage, which is subtended by one or two divergent antheridia (e. g., Benjamin 1979, Fig. 4D F, 6C).

Nanomyces is represented by three relatively small species that parasitize Labiidae (Dermoptera). Thaxter (1931) characterizes the presumed females as resembling depauperate forms of *Dimeromyces* Thaxter (1896). However, as Tavares (1985) points out, unlike the female of *Dimeromyces*, the perithecium has a greater number of wall cells and well-defined basal

and stalk cells. The primary stalk cell forms an elongate perithecial stipe (e. g., Tavares 1985, Pl. 56h; Thaxter, 1931, Pl. XXXVIII, fig. 24, 27, 28, 30, 31). Thaxter describes the male as consisting of an axis of a variable number of superposed cells ranging from three to six cells, depending on the species, in which the third cell of the axis bears one or more simple antheridia, these sometimes associated with a sterile branchlet (e. g., Thaxter 1931, Pl. XXXVIII, fig. 24–26, 29). Tavares (1985: 263) has studied in detail the Thaxter collections of *Nanomyces* at the Farlow Herbarium and concludes that the genus appears definitely to include both monoecious and dioecious taxa.

Dioicomycetes currently encompasses perhaps 31 taxa: 25 species, one variety, and one form on Anthicidae (Coleoptera) (Majewski and Sugiyama 1987; Rossi 1993; Tavares 1985; Thaxter 1931); one species, *D. myrmecophilus* Majewski, on Colydiidae (Coleoptera) (Majewski 1973); one species, *D. floridanus* (Thaxt.) Thaxt., on *Bledius* spp. (Staphylinidae) (Thaxter 1901, 1908), and two species needing further study to establish their validity within the genus. One of the latter, *D. bournieri* Balazuc, on Phlaeothripidae (Thysanoptera) (Balazuc 1972, 1975), is the only member of the Laboulbeniales known on thrips. Balazuc's sketch of the female receptacle (Balazuc 1972, Fig. 7–8), which is depicted as having a two-celled appendage, suggests that the taxon does not belong in *Dioicomycetes*. The other, *D. obliqueseptatus* (Thaxt.) Thaxt. (Thaxter 1901, 1908), on Staphylinidae, was described as *Amorphomyces obliqueseptatus* Thaxt. (Thaxter 1900) and is known only from broken females lacking receptacles. Thaxter later found that the fungus has obliquely septate spores (Thaxter 1908, Pl. XIII, Fig. 17) and transferred it to *Dioicomycetes*. The small size of the terminal cell of the spore suggests that Thaxter's original disposition of the taxon was correct (Benjamin 1979).

Dioicomycetes mesoveliae R. K. Benj., on a species of Mesoveliidae (Heteroptera), was misplaced generically when described (Benjamin 1970: 172) and was later transferred to *Triceromyces* as the dioecious morph of *T. poissonii* (Benjamin 1986: 163). Likewise, *D. verruculosus* T. Majewski and *D. yongboi* T. Majewski, also described from Mesoveliidae (Majewski 1988: 156, 157), are synonyms of species of *Triceromyces*, representing the dioecious morphs of *T. biformis* R. K. Benj. and *T. bullatus* R. K. Benj. (Benjamin 1986: 256, 261), respectively.

The appendage of the female of *Dioicomycetes* always is one celled. In many species it is more strongly convex on the outer margin than on the inner (e. g., Thaxter 1908, Pl. XLII, Fig. 18–20, 22, 30, 31), although in a few it is nearly symmetrical (e. g., Thaxter 1931, Pl. XII, Fig. 1, 2, and Pl. XIII, Fig. 26, 27). The primary stalk cell of the perithecium forms an elongate

perithecial stipe, whereas the secondary stalk cell typically is small, relatively inconspicuous, and closely associated with the basal cells. Ascospores are more or less obliquely septate and often strongly dimorphic (e. g., Benjamin 1970, Fig. 3 D; Thaxter 1908, Pl. XLII, Fig. 24, 25, 29). The lower cell of the male spore remains undivided and forms the receptacle; the upper cell forms three superposed cells, with the distal cell being converted into a simple antheridium having a terminal or subterminal discharge tube (e. g., Rossi 1993, Fig. 5; Thaxter 1908, Pl. XLII, Fig. 23, 28, 33, 36; 1931, Pl. XII, Fig. 6, 7).

Thaxter (1912: 168) based *Tetrandromyces* on a single species, *T. brachidae* Thaxter found on one of the Staphylinidae, *Brachida reyi* Sharp, from Argentina. The female of this species (Thaxter 1931, Pl. XIII, Fig. 21, 22) is nearly identical in structure to that of species of *Dioicomycetes* having symmetrical appendages. The male (Thaxter 1931, Pl. XIII, Fig. 23, 24), however, resembles that of *Dioicomycetes* only in having an undivided receptacle. The upper spore segment forms three superposed cells followed above by a pair of cells, united on the inside, bearing four adnate antheridia with only the discharge tubes free. I have in my collection single male and female individuals of an unnamed *Tetrandromyces* (RKB 396), which is nearly identical to *T. brachidae*, taken from an unidentified staphylinid from Mindanao, Philippine Islands.

In addition to *Dioicomycetes*, Thaxter named two other dioecious genera from Anthicidae, *Dicrandromyces* (Thaxter 1931: 72), with one species from the Philippine Islands (Thaxter 1931, Pl. XIII, Fig. 16–20), and *Triandromyces* (Thaxter 1931: 69), with three species from Africa (Thaxter 1931, Pl. XIII, Fig. 1–15), which, also like *Tetrandromyces*, have females closely resembling those of *Dioicomycetes* with symmetrical appendages. The male spore of *Triandromyces* resembles that of *Dioicomycetes* and *Tetrandromyces* in having a more or less oblique septum (Thaxter 1931: 61, 69), whereas in *Dicrandromyces* the septum is nearly transverse (Thaxter 1931: 72). The mature male of *Dicrandromyces* and *Triandromyces* differs from that of *Dioicomycetes* and *Tetrandromyces* in having a two-celled rather than a one-celled receptacle. Unlike *Dioicomycetes* and like *Tetrandromyces*, the male in these genera characteristically forms more than one antheridium. In *Dicrandromyces*, the upper spore segment produces a single cell that subtends a pair of free cells each of which bears a pair of free antheridia. Thus, the male of this genus superficially resembles that of *Tetrandromyces*, but differs in its two-celled receptacle and free antheridia borne on free supporting cells. In *Triandromyces*, the upper spore segment forms two or three, but usually two, superposed cells; the distal cell bearing a pair of free antheridia, the subtending cell or cells forming single free antheridia.

Tavares (1985), in her treatise on Laboulbeniales, relegated *Dicrandromyces* and *Triandromyces* to synonymy with *Tetrandromyces*, acting, in part, on an earlier query by Thaxter (1931) as to whether these genera and *Dioicomycetes* should be united under a single name. At this time I agree, on the basis of its distinctive male, that *Tetrandromyces* sensu Thaxter should be retained as a genus separate from *Dioicomycetes*; however, also on the basis of the male, I regard as uncertain the synonymy of *Dicrandromyces* and *Triandromyces* with *Tetrandromyces*. The males and females of *Dioicomycetes italicus* Spg. (= *D. formicomi* Thaxt., fide Rossi [Rossi 1993]) (Thaxter 1931, Pl. XII, Fig. 1, 2, 6, 7) and *D. indentatus* Thaxt. (Thaxter 1931, Pl. XIII, Fig. 26–29) resemble those of *Dicrandromyces* and *Triandromyces* except for the male having only one antheridium and a single-celled receptacle. The discovery and study of additional taxa fitting Thaxter's concepts of *Dicrandromyces* and *Triandromyces* could provide a better understanding of the taxonomic significance of the male in these genera. It may be that *Dicrandromyces* and *Triandromyces* should be united with *Dioicomycetes* or placed in a single genus distinct from either *Dioicomycetes* or *Tetrandromyces*.

In consideration of the characteristics, briefly summarized above, of the genera Tavares included in her *Amorphomycetinae*, it is my opinion that *Nanomyces* and *Rhizopodomycetes* are not closely related to the other three genera or to one another. *Dioicomycetes* and *Tetrandromyces* (including *Dicrandromyces* and *Triandromyces*) probably are closely related in view of the marked similarity of their males and especially their females. *Amorphomyces*, with its diagonally septate spores, which is a feature common to many species of *Dioicomycetes* and *Tetrandromyces*, suggests its relationship to the latter genera, especially *Dioicomycetes* (Tavares 1970; Thaxter 1931). However, the modified receptacle and two-celled, albeit vestigial, appendage of the female of *Amorphomyces*, clearly distinguish the genus from other *Amorphomycetinae*.

Corylophomyces is here included in *Amorphomycetinae* because of features it has in common with *Dioicomycetes* and its presumed allies, e. g., a simple male, a female having a three-celled receptacle, and a small, determinate appendage. Its ascoma has a similar peritheciium with four or five cells in each row of outer wall cells, a relatively elongate primary stalk cell, and a smallish secondary stalk cell closely associated with the basal cells. The trichogyne of *C. sarawakensis* and *C. sericoderi* resembles that of *D. anthici* Thaxter (Thaxter 1908, Pl. XLII, Fig. 23) and other species of *Dioicomycetes* (unpublished observations) in consisting of two relatively large cells separated by a transverse cross wall and ending in a receptive branch. Downward growth of the trichogyne toward the male, as seen in these taxa, probably should not in itself be

viewed as an indication of close relationship, for this phenomenon appears to be characteristic of other dioecious Laboulbeniales as well, e. g., *Aporomyces uniflagellatus* Thaxt. (Benjamin 1989, Fig. 1); *Rhizopodomycetes californicus* Benjamin (Benjamin 1979, Fig. 2 H, Fig. 3 C–E); and the female of the dioecious morph of *Triceromyces biformis* Benjamin (Benjamin 1986, Fig. 50, 51).

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