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CUPULOMYCES, A NEW GENUS OF LABOULBENIALES (ASCOMYCETES) BASED ON *STIGMATOMYCES LASIOCHILI*

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ABSTRACT

A new genus of Laboulbeniales, *Cupulomyces*, is described. Its type species, *C. lasiochili*, is based on *Stigmatomyces lasiochili*, originally described by Roland Thaxter in 1917. This taxon subsequently has been classified in two other genera, *Hesperomyces* and *Acompsomyces*. Structure and development of the thallus of *C. lasiochili* are described and illustrated with photographs and line drawings. Distinctive features of the receptacle, appendage, and perithecium warrant recognition of a new genus.

Key words: *Acompsomyces*, Ascomycetes, *Cupulomyces*, fungi, *Hesperomyces*, Heteroptera, insect parasites, Laboulbeniales, morphology, *Stigmatomyces*, taxonomy.

INTRODUCTION

Stigmatomyces lasiochili Thaxter was found on a terrestrial bug, *Lasiochilus pallidulus* Reut. (order: Heteroptera; suborder: Cimicomorpha; superfamily: Cimicoidea; family: Anthocoridae [Henry 1988]), collected in Grenada, West Indies (Thaxter 1917). This fungus is one of the relatively few Laboulbeniales known on Heteroptera (see summary in Benjamin [1986]) and the only one that has been found on a member of the Anthocoridae. These insects, termed Minute Pirate Bugs, are found commonly in flowers, on living vegetation, in ground debris, in fungi, under bark, and even in the nests of mammals and birds.

Thaxter transferred *S. lasiochili* to *Hesperomyces* Thaxt. (Thaxter 1891) as *H. lasiochili* (Thaxt.) Thaxt. (Thaxter 1931), and later Tavares transferred the taxon again, placing it in *Acompsomyces* Thaxt. (Thaxter 1901, 1908) as *A. lasiochili* (Thaxt.) Tavares (Tavares 1985).

Stigmatomyces lasiochili falls within the concept of Tavares's subtribe Stigmatomycetinae, a taxon of some 38 currently recognized genera (Tavares 1985; Tavares and Balazuc 1989), all of which are distinguished by having a simple receptacle composed of three superposed cells with usually a single perithecium arising from the subbasal cell (possibly from the terminal cell in *Sugiyamaemyces* Tavares & Balazuc [1989]). The upper cell of the receptacle subtends a determinant or indeterminant primary appendage bearing antheridia (still unknown in some genera). Secondary appendages arising from the upper cell of the receptacle are known for only a few genera of the subtribe. Genera of Stigmatomycetinae are each defined within rather narrow limits based on a combination of characteristics relating to the form and structure of the receptacle, primary appendage, and perithecium.

On the basis of evidence presented in my recent study of *Acompsomyces* (Benjamin 1989), I argued that features of the structure of the receptacle, appendage, and perithecium of *S. lasiochili* preclude its placement not only in *Stigmatomyces* but also in *Hesperomyces* and *Acompsomyces*. It is my purpose in this paper to

present a more detailed account of the development and morphology of *S. lasiochili* than the one given in the 1989 study and to place the taxon in a new genus.

MATERIALS AND METHODS

All of the specimens of *Stigmatomyces lasiochili* examined in the course of this study were removed from duplicate infected hosts representing the same lot of *Lasiochilus pallidulus* from which Thaxter had obtained his type collection. These insects were among material that had been transferred from the Farlow Herbarium to the Entomology Department of the Museum of Comparative Zoology, Harvard University, sometime after Thaxter's death in 1932. They had been preserved in glycerine in a small vial and were kindly made available to me by the late Philip J. Darlington.

The parasites were removed from the host and mounted on glass slides in glycerine containing trace amounts of cotton blue or acid fuchsin by methods given previously (Benjamin 1971:101; 1986:247).

Direct observations, drawings, and photomicrographs were made using a Leitz Dialux microscope equipped with differential interference contrast optics. Drawings were made with the aid of a camera lucida. Photographs were taken on 4 in. × 5 in. Kodak Technical Pan Film #2415. The camera employed was a WILD 15/11 Semiphotomat with ASA settings of 80 or 125. The film was developed for 8 minutes in Kodak HC-110, Dilution F, at 20 C. All prints were made on Kodak Polyfiber FS paper.

Terminology and abbreviations used in the text to describe or discuss the fungal thallus are, with a few exceptions, those of Tavares (1985:431–434).

TAXONOMY

Cupulomyces Benjamin, gen. nov.

Receptaculum cellularum trium superpositorum constans appendicem liberum et perithecium gignens. Cellulae basilaris (I) et subbasilaris (II) receptaculi fortiter oblique superpositae; cellula I cellulam VII perithecii subtenens; cellula II cellulae VI perithecii et III receptaculi subtenens. Cellulae III, VI, et VII transverse dispositae et parallelae. Appendix cellularum trium superpositarum constans; cellula basalis elongatis sterilis; cellula terminalis antheridia duo simplicia gignens; cellula mediana antheridium unum gignens. Antheridia prope libera antheridio terminali spinifero. Trichogyne non ramosa cellularum trium superpositum constans; cellula terminalis prominentis brevibus rotundatis apicalibus. Perithecium cellulis basilaribus tribus persistentibus et cellulis parietis externis in quatuor ordinibus longitudinalibus numusquique quinque cellularium; basis cellularum parietibus externarum terminalium prominentiam divergentes gignens; cellula ascogena unica; ascosporae 1-septatae.

Receptacle consisting of three superposed cells bearing on one side a free appendage and on the other side a perithecium. The basal cell (I) and subbasal cell (II) of the receptacle are very strongly obliquely superposed; the upper end of cell I is in contact with the base of the secondary stalk cell (VII) of the perithecium; cell II is posterior to cell I and in contact distally with the base of the upper cell (III) of the receptacle and the primary stalk cell (VI) of the perithecium. Cells III, VI, and VII are transversely arranged and parallel to one another. The appendage is subtended by cell III of the receptacle and consists of three superposed cells; the lower cell elongate, sterile; the middle and upper cells short, bearing, respectively, one and two simple, nearly free antheridia; the terminal antheridium externally spinose. Trichogyne unbranched, consisting of three superposed cells, the

upper cell terminated by short, rounded prominences. Perithecium with three persistent basal cells and four vertical rows of outer wall cells of five cells each; the base of each terminal outer wall cell with a divergent, terminally rounded outgrowth; ascogenic cell single; ascospores 1-septate.

Type species.—*Cupulomyces lasiochili* (Thaxter) Benjamin.

Etymology.—From *cupula* (L.), a little cup + *myces,* fungus. Refers to the cupolaed shape of the perithecial apex.

Cupulomyces lasiochili (Thaxter) Benjamin, comb. nov. Fig. 1–21

=*Stigmatomyces lasiochili* Thaxter, Proc. Amer. Acad. Arts 54:703. 1917.
=*Hesperomyces lasiochili* (Thaxter) Thaxter, Mem. Amer. Acad. Arts 16:111. 1931.
=*Acompsomyces lasiochili* (Thaxter) Tavares, Mycol. Mem. No. 9, p. 131. 1985.

Thallus: Faintly tinged with greenish yellow; the basal cell of the receptacle and the appendage grayish or purplish brown. *Receptacle:* Cells I and II obliquely superposed, forming a triangular stalk, 35–43 × 15–20 μm, tapered to the blackened foot; cell I, 35–43 × 9–12 μm, in contact distally with the base of the secondary stalk cell (VII) of the perithecium, with two thirds to three fourths of its posterior margin overlapped by cell II, which measures 16–23 × 8–10 μm and subtends the primary stalk cell (VI) of the perithecium and cell III of the receptacle; the latter slightly longer than broad, subtriangular to subrectangular, 10–14 × 7–10 μm, slightly prominent distally. *Appendage:* Relatively slender, 50–65 μm long to tip of outer antheridium, 8–11 μm in greatest width; the axis consisting of usually three cells and terminated by three antheridia; the basal cell pale brownish, sterile, elongate, slightly inflated or nearly cylindrical, 20–30 × 8–11 μm, about as long as the upper part of the appendage from which it is separated by a horizontal, dark septum; the rest of the appendage, including the antheridia, more deeply colored than the basal cell; the median cell and terminal cell obliquely superposed; the former 9–11 × 7–9 μm, bearing a single antheridium from its upper, inner angle; the latter, 10–14 × 5–7 μm, bearing an inner and an outer antheridium distally; the latter externally spinose; antheridia nearly free, 15–20 × 3.5–4.5 μm, the necks long, 2 × 8–10 μm, slightly divergent, nearly straight, directed inward or sideways. *Perithecium:* Primary stalk cell (VI) lying between and parallel to the secondary stalk cell (VII) and cell III of the receptacle; cell VII externally concave, 16–20 × 7–10 μm, extending well above the top of cell VI, which measures 11–14 × 6–7 μm and reaches the level of the base of the appendage; the basal cells (*m, n, n'*) constituting only ca. 10–15% of the total height of the perithecium above the stalk cells, slightly if at all enveloping the base of the ascigerous cavity; body relatively large, nearly straight or very slightly curved, 110–170 × 30–45 μm, the venter slightly inflated, the juncture between the first and second and second and third tiers of wall cells externally prominent; the basal tier of outer wall cells ca. twice the height of the subbasal tier, the two tiers constituting ca. two thirds of the total height of the body above the basal cells; the median and subterminal tiers subequal, their combined heights slightly less than that of the subbasal tier; the terminal tier about as high as the two subtending tiers, forming a minaret-shaped apex, the base of each cell with a median, terminally rounded, divergent outgrowth 5–7 × 3.5–4 μm; the tip proper consisting

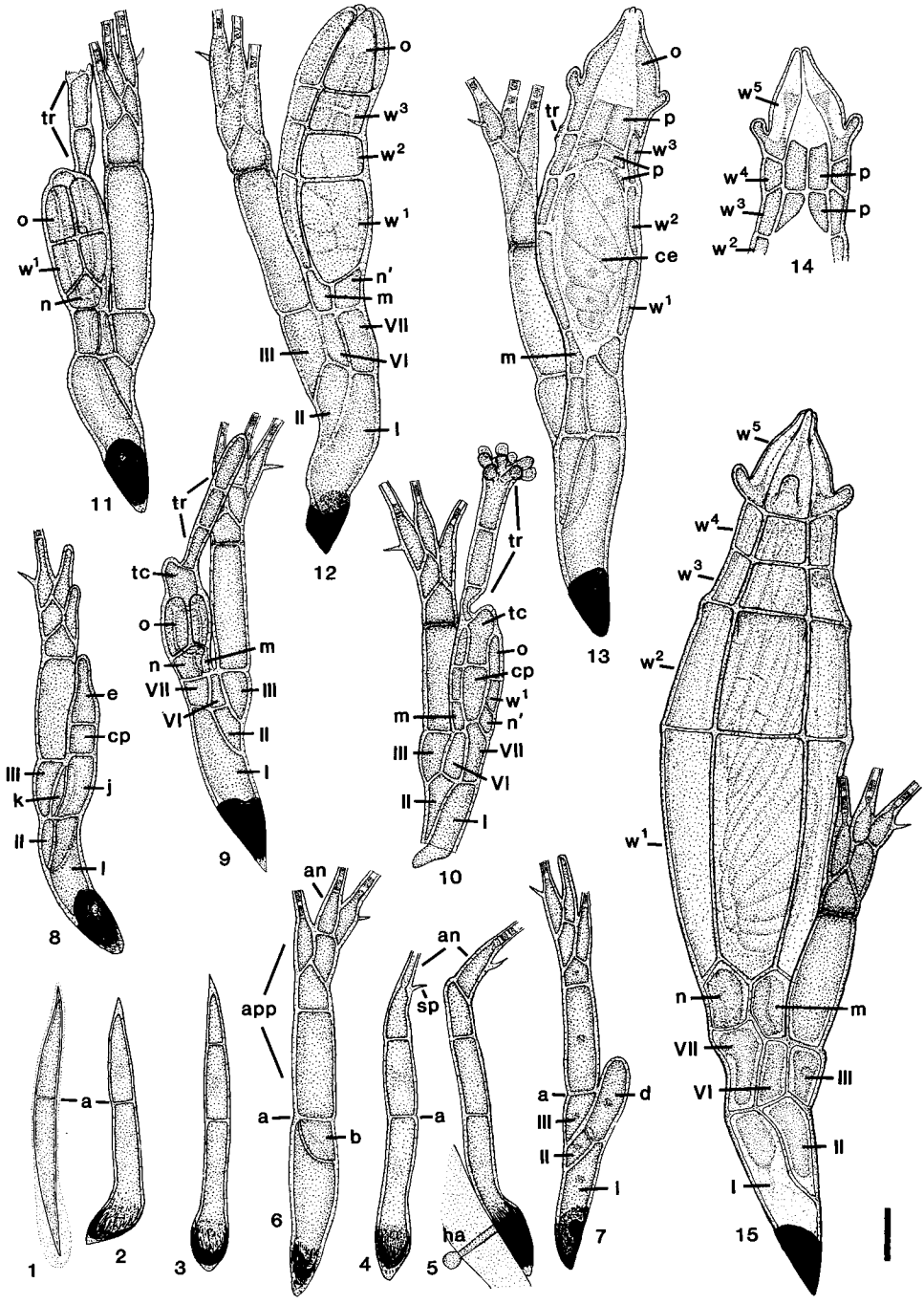

Fig. 1–15. *Cupulomyces lasiochili* (*RKB 1334*).—1–14. Stages of development of the receptacle, appendage, and perithecium. Details and terminology are given in the text.—15. A mature individual showing the relationship of the three cells of the receptacle (I, II, III), the perithecial stalk cells (VI, VII), the perithecial basal cells (*n, n'* [far side], *m*), and the five tiers of outer wall cells (w^{1-5}). (All figures, bar at lower right = 10 μm.)

of four slender, closely appressed, free, lobate terminations 7–8 μm long. Ascospores 40–50 × 3.5–4 μm.

Total height from tip of foot to tip of ostiole 150–230 μm.

Specimens examined.—*Stigmatomyces lasiochili*: GRENADA. GRAND ETANG: On various parts of *Lasiochilus pallidulus*, date of collection unknown, *R. Thaxter 2771* (Acc. No. 4991 [type]; FH) (*RKB 1334*; RSA).

OBSERVATIONS

Ascospores

The ascospore of *Cupulomyces lasiochili* is acicular, two celled, and surrounded by a hyaline envelope, which is increasingly thickened around the lower approximately one third of the spore (Fig. 1). The submedian cross wall (*a*) divides the spore into a basal cell (originally uppermost in the perithecium) and a slightly shorter upper cell. As development proceeds, the tip of the upper cell persists as an indurated spine (*sp*) attached to the outer surface of the uppermost of the antheridia formed distally on the appendage (Fig. 4–13, 15, 16). The earliest visible stage of spore germination is the formation of a blackened foot at the base of the lower cell (Fig. 2). The foot attaches the germinating spore firmly to the host (Fig. 5) and always possesses a smallish, circular, opening on its lower surface. This opening is visible as a hyaline spot clearly visible when the foot is viewed at various angles and marks the point of egress of a simple haustorium (*ha*) (Fig. 5) passing through the host cuticle. The haustorium forms a small globoid enlargement once it reaches the region of the hemolymph (Fig. 5). Haustoria like that shown in Figure 5 also were found emanating from the foot of several mature individuals in situ.

Receptacle

The youngest individual encountered in the study (Fig. 2) has the foot already differentiated at the base of the lowermost cell of the spore. (The original spore septum [*a*] is indicated in the next several figures.) Development of the appendage from the upper spore segment (Fig. 3–6), often with apparently functional antheridia, takes place before the first of the divisions leading to formation of the receptacle (Fig. 6) from the lower spore segment. In the individual shown in Figure 6 a small cell (*b*) has been cut off distally from the basal cell by a diagonal cross wall. In the individual shown in Figure 7, the three cells comprising the receptacle proper (I, II, and III) and the perithecial initial (*d*) have been delimited. A sequence of divisions of either cell *b* or the basal cell leading to the stage of receptacular development shown in Figure 7 was not found among the juvenile thalli recovered for study. As the thallus matures, the three cells of the receptacle enlarge considerably but do not divide. Cells I and II become progressively more obliquely superposed (Fig. 8–13, 15) than when first delimited (Fig. 7). Cell II is posterior to cell I and subtends cells III and VI (the primary stalk cell of the perithecium). Cell I subtends cell VII (the secondary stalk cell of the perithecium).

Appendage

The appendage of *Cupulomyces lasiochili* develops from the upper cell of the ascospore. This cell initially divides into two cells (Fig. 3) the uppermost of which

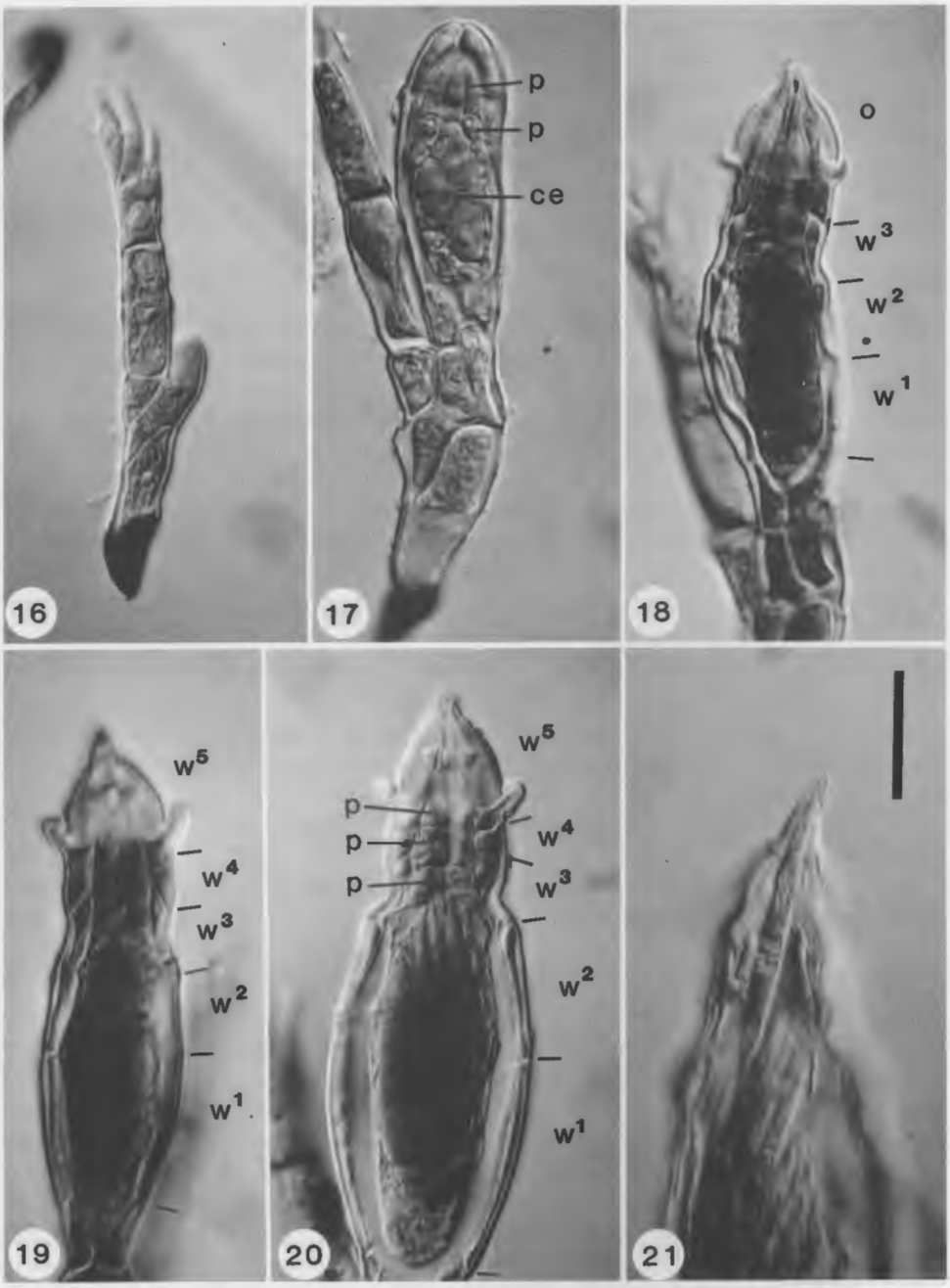

Fig. 16–21. *Cupulomyces lasiochili* (*RKB 1334*).—16. Photograph of the immature individual shown in Figure 7. The small globoid bodies visible in several of the cells presumably are the nucleoli of poorly fixed nuclei.—17. Juvenile individual showing early development of the centrum (*ce*) and its relationship to upper inner wall cells (*p*).—18. Photograph of the individual depicted in Figure 13. The small bars indicate the juncture of wall-cell tiers in this and the next two figures.—19. Nearly

is transformed into a simple antheridium bearing the indurated spore apex as a lateral spinose projection (Fig. 4). The cell subtending this antheridium divides (Fig. 5) and the upper cell apparently gives rise to a second antheridium distally, although this stage was not observed. If one may judge from the structure of a mature appendage (*app*: Fig. 6), this antheridiiferous cell divides again and the resulting proximal cell, which is subtended by the elongate stalk cell, gives rise distally to a third antheridium (Fig. 6–13, 15, 16). No appendage was found bearing more than three antheridia. The venters of the antheridia and their subtending cells darken slightly with age contrasting with the paler stalk (Fig. 15).

Perithecium

The perithecial initial (*d*: Fig. 7, 16), presumably derived from the same cell that gave rise to the subbasal cell (II) of the receptacle, grows upward alongside the appendage adjacent to the anterior side of the young thallus. Figure 8 shows a stage of development in which the immature perithecium consists of four cells: 1) a distal cell *e*; 2) a median cell *cp*, the carpogenic cell; and 3) two proximal cells *j* and *k* adjacent to cell III and parallel to one another. Cell *j* grows upward and, on opposite sides of the young perithecium, gives rise to two of the three perithecial basal cells (*n* and *n'*) and becomes the secondary stalk cell (VII) of the perithecium (Fig. 9). Cell *k* divides and gives rise to the primary stalk cell (VI) of the perithecium and the third of the perithecial basal cells (*m*) (Fig. 9). Cell *e* (Fig. 8) divides and gives rise below to the trichophoric cell (*tc*) and above to the trichogyne (*tr*) (Fig. 9, 10). Figure 9 shows a young perithecium bearing an immature trichogyne consisting of three superposed cells and two of four outer perithecial wall-cell primordia (*o*) derived from the basal cells (*m*, *n*, and *n'*). These wall-cell primordia have surrounded the carpogenic cell (*cp*) and the base of the trichophoric cell (*tc*). The inner perithecial wall cells also are derived from the basal cells, but early stages of their development could not be detected in the material studied. The perithecium shown in optical section in Figure 10 is slightly older than the one depicted in Figure 9. It has reached the two-outer-wall-cell stage of development and the trichogyne (*tr*) apparently is mature. The first tier of permanent outer wall cells (w^1) has been formed by division of the first tier of wall-cell primordia (Fig. 9) and now subtends another tier of outer wall-cell primordia (*o*), which surrounds the lower part of the trichophoric cell (*tc*). The specimen depicted in Figure 11 is only slightly older than the one shown in Figure 10; fertilization presumably has occurred and the trichogyne has begun to deteriorate.

←

mature individual in optical section showing the five tiers of outer wall cells (w^{1-5}); note divergent prominences at bases of terminal wall cells.—20. Mature individual showing the five tiers of outer wall cells and the three tiers of inner wall cells (*p*) above the centrum.—21. Upper part of a mature perithecium in optical section showing an ascospore beginning to emerge through the ostiole at the time of fixation. (All figures, bar at upper right in Figure 21 = 20 μm.)

The perithecium of the individual shown in Figure 12 has reached the four-outer-wall-cell stage. It has three tiers of permanent outer wall cells (w^1, w^2, w^3) and a distal tier of outer wall-cell primordia (*o*). The vertical row of wall cells in nearest view has arisen from basal cell *n'*; the row nearest the appendage has arisen from basal cell *m*; the two rows mostly out of view on the other side of the perithecium arose from basal cell *n*. The specimen shown in optical section in Figure 17 is at nearly the same stage of development as the one in Figure 12; the centrum (*ce*), which could not be studied in detail, has begun to develop.

In Figure 13, the perithecium (optical section) also is at the four-outer-wall-cell stage, but a small outgrowth, characteristic of *C. lasiochili,* is growing outward and upward from each of the outer wall-cell primordia (*o*), only two of which are shown. The upper two tiers of inner wall cells (*p*) are well defined above the young centrum (*ce*), which is compressing the next lowest tier of inner wall cells against the adjacent outer wall cells. A small remnant of the base of the trichogyne (*tr*) is present on the posterior surface of the perithecium near the junction of the terminal primordial and tier-three wall cells derived from basal cell *m*. Figure 18 is a photograph of the same thallus as the one shown in Figure 13.

Figure 14 is a drawing of the perithecial apex shown in Figure 19. Division of the wall-cell primordia, immediately below the lateral prominences, has resulted in the fourth and fifth tiers of outer wall cells (w^4 and w^5). In a mature thallus (Fig. 15) the prominences appear to have arisen at the base of the terminal wall cells (w^5).

By the time ascospores begin to mature, the cells of the upper tier of inner wall cells shown in Figure 14 have divided (Fig. 20). The resulting three tiers of upper inner wall cells (*p*) line the neck of the perithecium above the centrum and form a channel through which each ascospore passes on its way to being discharged (Fig. 21).

DISCUSSION

The description of *Cupulomyces* given in this paper, based as it is on a single species, *C. lasiochili,* may require emendation in the future when and if additional species are found. Other Anthocoridae should be examined for the presence of Laboulbeniales. The simple outgrowth at the base of each upper outer wall cell as well as the number of antheridia developed on the appendage could be specific rather than generic characteristics. Specific variation as regards perithecial prominences and the proliferation of antheridia-bearing cells is known in many genera of Laboulbeniales, e.g., *Triceromyces* Majewski (1981; Benjamin 1986).

Transverse arrangement of cell III of the receptacle and the perithecial stalk cells VI and VII, as seen in *C. lasiochili,* is found sometimes in *Stigmatomyces* Karsten (1869), but in all species of this genus, which occur on Diptera, cells I and II of the receptacle are vertically superposed and separated by a transverse septum. Anterior positioning in *C. lasiochili* of cell I relative to cell II is not found in any species of *Stigmatomyces, Acompsomyces,* or *Hesperomyces.* It is characteristic of *Acrogynomyces* Thaxter (1931) and *Prolixandromyces* Benjamin (1970, 1981), which differ from *C. lasiochili* in characteristics of the appendage and perithecium. In *Acompsomyces* and *Hesperomyces* the cross wall separating cells I and II may be transverse, but more often is diagonal; however, in these genera the primary perithecial stalk cell (VI) forms a distinctive, nearly free, often elongate

pedicel, which subtends the closely associated secondary stalk cell (VII) and perithecial basal cells (*m, n, n'*).

The appendage of *C. lasiochili* is similar to that of *Hesperomyces* in having a sterile basal cell. In *Hesperomyces,* the appendage displays considerable variability among the species in the number of superposed sterile or fertile cells, as well as in the position of a spinose antheridium (Benjamin 1989). The basal cell of the appendage of *Acompsomyces* and *Stigmatomyces* typically forms one or more sessile antheridia. Lack of additional species of *Cupulomyces,* however, precludes at this time further comparison of the appendage of this genus with these and other genera.

The perithecium of *Cupulomyces lasiochili* and all species of *Acompsomyces* has five cells in each of the four vertical rows of outer wall cells. This contrasts with the perithecium of *Stigmatomyces* and *Hesperomyces,* in which there are only four cells in each vertical row (Tavares 1985). The structure of the perithecial apex in *Hesperomyces* (Benjamin 1989) further distinguishes this genus from *Cupulomyces* and *Acompsomyces* (Benjamin 1989).

In conclusion, when considered in combination, distinctive features of the receptacle, appendage, and perithecium of *Cupulomyces lasiochili* preclude the placement of this genus in *Stigmatomyces, Hesperomyces,* or *Acompsomyces.*

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