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BALAZUCIA, A NEW GENUS OF LABOULBENIALES ALLIED TO CUCUJOMYCES SPEGAZZINI

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Balazucia gen. nov.

Receptaculum primum bicellulare; cellula subbasilaris perithecium primum et appendicem primam sterilem simplicem et cellulas secundarias dextrorsum et sinistrorsum gerens; cellulae secundariae receptacula secundaria recta gignentis; receptacula secundaria antheridia simplicia terminalia et quoque perithecia lateralia gerentes; perithecium cum cellula stipiti et cellulis basilaribus persistentibus; ascosporae 1-septatae.

Primary receptacle consisting of a basal and subbasal cell, the latter bearing a primary appendage and a primary perithecium and proliferating right and left and forming cellular upgrowths bearing secondary perithecia laterally and/or simple flask-shaped antheridia distally. Perithecia with well-developed and persistent basal- and stalk-cells and four rows of wall-cells of four cells each. Ascospores 1-septate.

Etym.—Named for Jean Balazuc, M.D., Eaubonne, France, long-time student of the Laboulbeniales who has favored me with many specimens as well as much data from his unpublished studies of these fungi and their hosts.

Type species.—*Balazucia bilateralis* Benjamin.

Balazucia bilateralis sp. nov.

(Fig. 1-2)

Cellula basilaris receptaculi 20-25 μ \times 8-10 μ cum pede nigro; appendix prima hyalina sterilis 20-60 μ longa simplex vel ramosa; basis perithecii nigra et quoque opaca; corpus perithecii supra basin extrinsecus $\frac{2}{3}$ paene opacum; corpus perithecii aspectu frontali symmetricum ovoideum 50-70 μ longum \times 20-30 μ latum; corpus perithecii a latere visum asymmetricum extrinsecus pulvinatum intrinsecus parum convexum; axes secundarii receptaculi hyalini plerumque in quoque latere 2; axes interiores a cellulis binatis 12-14 compositi; axes interiores 1-2 antheridia terminalia 10-12 μ \times 3-4 μ et quoque 1-2 perithecia proximalia gerentes; axes externi simplices a 5-7 cellulas superpositas compositi et quoque antheridia singula terminalia gerentes; axes interiores et

externi in aetate ramos steriles terminales 20–60 μ longos gignentes. Totus fungus a basi ad apicem perithecii primi 80–115 μ longus. Ascosporis hyalinis 32–35 μ longis \times 3–4 μ latis.

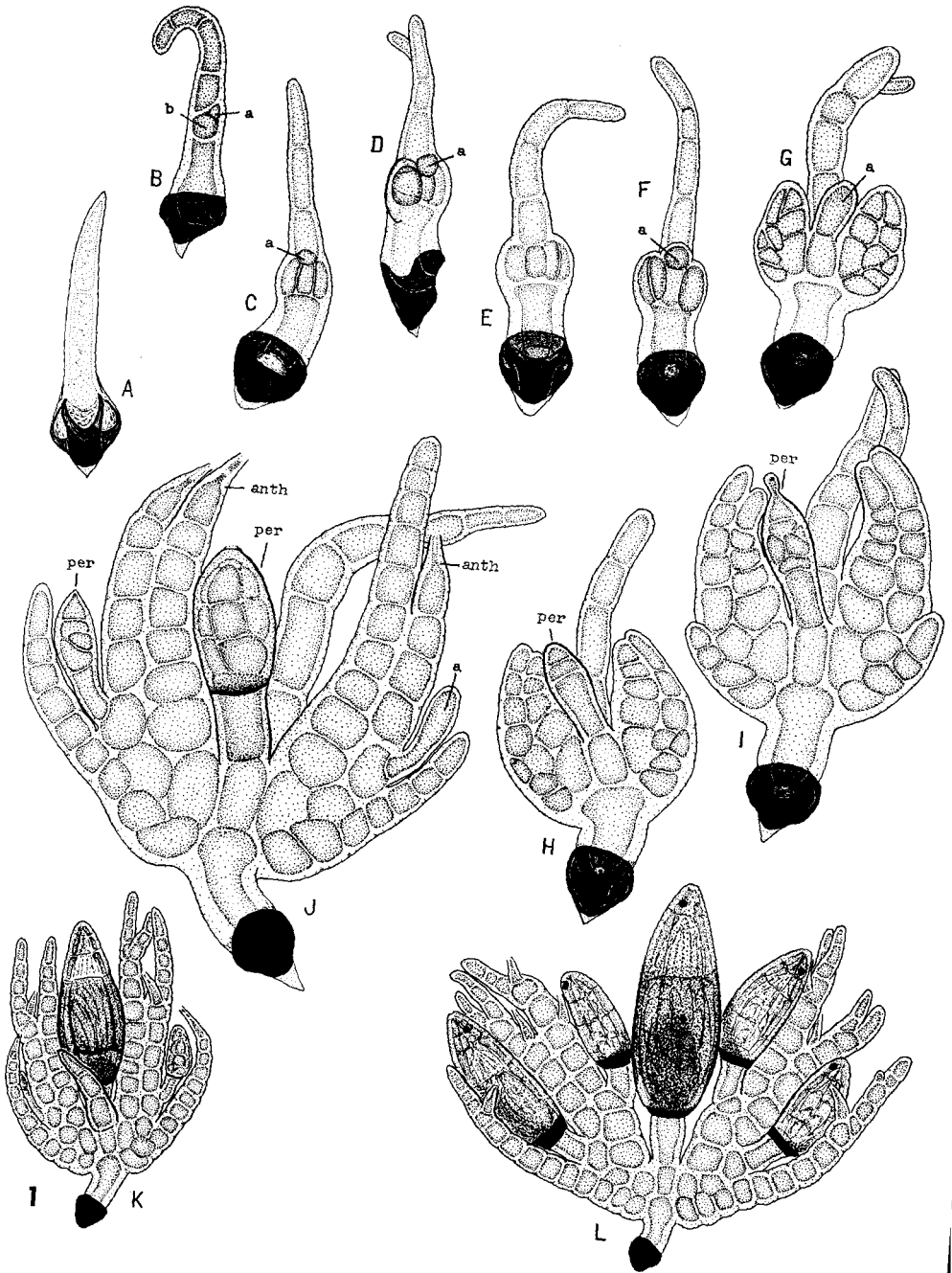
Basal cell of the receptacle about two times as long as broad, 20–25 μ \times 8–10 μ , its base differentiated into a blackened foot. Primary appendage nearly hyaline, sterile, 20–60 μ long, consisting of 3–7 elongate cells, simple or forming one or more short divergent branches distally. Primary perithecium short-stalked; the stalk nearly hyaline, 10–20 μ \times 8–12 μ ; basal region of perithecium black and opaque, the opacity extending upward externally and laterally and obscuring more or less completely the outer 2/3 of the body; the latter nearly symmetrical in dorsal or ventral view, ovoid, 50–70 μ long \times 20–30 μ wide, tapering to the nearly hyaline unmodified apex; body of perithecium asymmetrical in lateral view, strongly convex and dark brownish-red externally, only slightly convex and paler internally. Secondary axes of receptacle hyaline, usually two on each side of the median cell; the inner upgrowths consisting of 4–6 tiers of paired cells bearing simple flask-shaped antheridia, 10–12 μ \times 3–4 μ , distally, these later displaced laterally by simple or branched cellular appendages 20–60 μ long; a single secondary perithecium, like the primary perithecium in structure, arising from the outer basal cell of each inner upgrowth and these usually followed by the formation of similar single perithecia by a proximal inner cell of each upgrowth; the outer upgrowths consisting of a single series of 5–7 superposed cells bearing single terminal antheridia, these usually displaced laterally in age by the continued growth of the axis; the outer upgrowths only rarely giving rise to single perithecia internally from a proximal cell. Total length to tip of the primary perithecium 80–115 μ . Ascospores hyaline, 32–35 μ long \times 3–4 μ wide.

Etym.—Named for the usually bilaterally symmetrical receptacle.

Holotype.—MEXICO. Chiapas: Finca Guauhtemoc, 4,000 ft. elevation, August, 1950, Clarence and Marie Goodnight coll.; on all parts of *Phloeonomus* sp. (*Order*: Coleoptera; *Superfamily*: Staphylinioidea; *Family*: Staphylinidae; *Subfamily*: Omaliinae); *RKB 1522*; slides in RSA, FH.

The host of *Balazucia bilateralis* is a small beetle that was found associated with an unidentified member of the Araceae, probably on the flowers although this was not stated on the label accompanying the preserved insects. Many members of the Omaliinae occur on flowers or decaying fruit. A relatively large number of parasitized insects was collected by the Goodnights so that specimens of the fungus in many stages of development were available for study. Perithecial

Fig. 1. *Balazucia bilateralis* Benjamin.—A. Germinating spore showing advanced development of the basal foot prior to differentiation of the body of the spore.—B–J. Early and late stages of development of the individual; for discussion see text.—K. Posterior view of individual showing short median primary appendage subtending base of nearly mature primary perithecium. The inner secondary upgrowths of the receptacle show terminal appendages subtending simple antheridia and young secondary perithecia arising from outer basal cells. The outer uniseriate cellular upgrowths are terminated by single simple antheridia.—L. Anterior view of individual showing mature median primary perithecium and immature outer secondary and inner tertiary perithecia arising from the inner upgrowths of the receptacle. Note outer upgrowths in which the originally terminal antheridia have been displaced laterally by continued growth of the axes. (A–J, $\times 1080$; K–L, $\times 485$.)



ontogeny is basically like that described for *Stigmatomyces baeri* by Thaxter in 1896 and again summarized by Gäumann & Dodge in 1928. The characteristics of the receptacle distinguish *Balazucia* generically from other Laboulbeniales, but they resemble somewhat those of *Cucujomyces* Spegazzini (1917) to which genus *Balazucia* appears to be most closely allied.

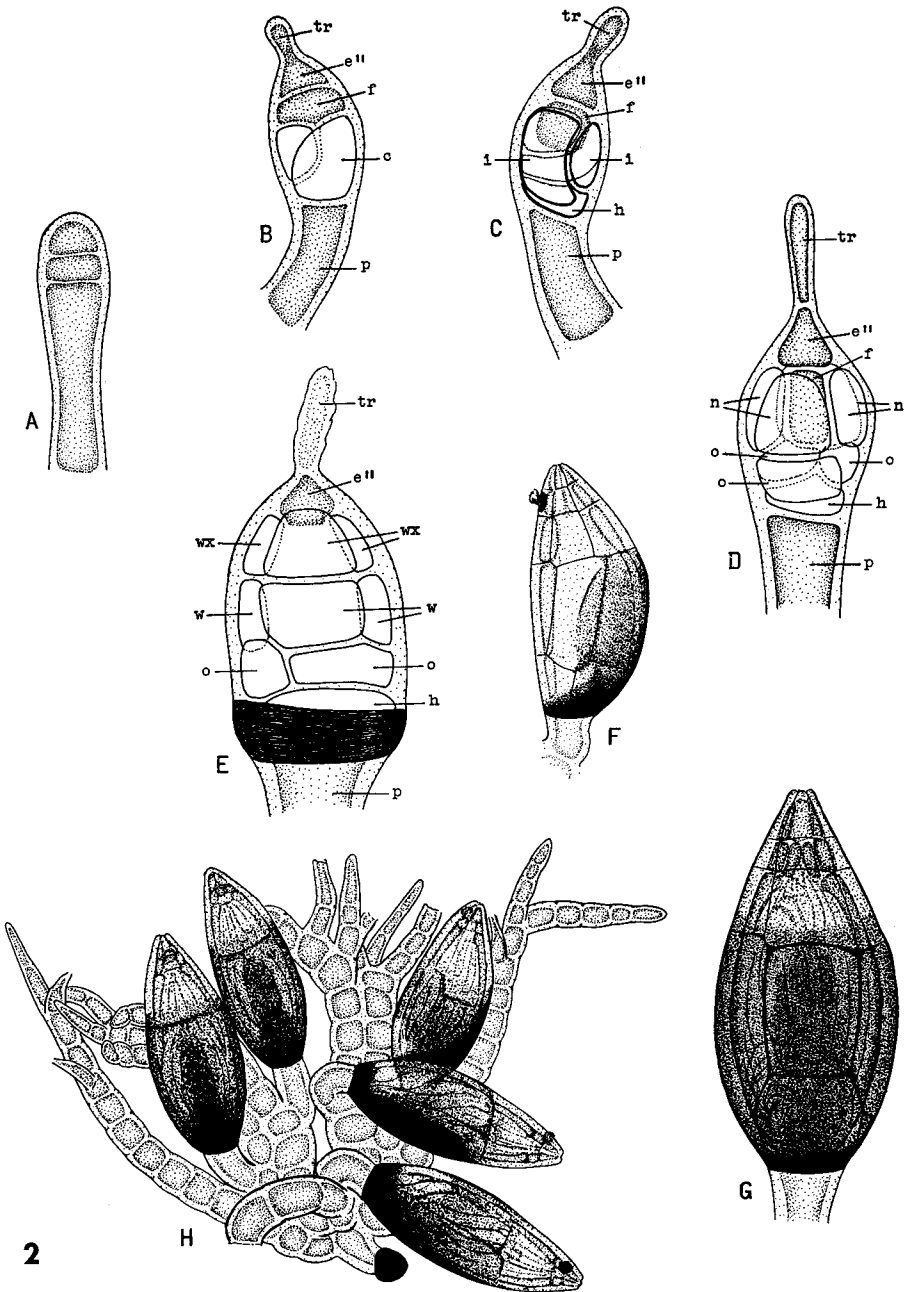
The ascospore consists of two unequal cells the longer of which is uppermost in the perithecium so that it exits first when the spore is discharged. Like the spores of other Laboulbeniales, a sheath of hyaline material surrounds the spore of *B. bilateralis* and is thickest around the apex of the longest cell. Spore germination consists initially of the differentiation of the foot—the organelle of attachment of the fungus to the host insect—and this is well-developed before further differentiation of the spore takes place (Fig. 1 A). The upper, shorter cell of the germinating spore subsequently forms a short, simple or once-branched primary appendage consisting of several superposed cells (Fig. 2 B–J). This appendage remains sterile. The basal cell of the spore becomes divided into three superposed cells (Fig. 1 B). The lowermost cell constitutes the stalk of the primary receptacle; the upper cell forms the base of the primary appendage; and the median cell gives rise not only to the primary perithecium but also to the initials from which the secondary cells of the receptacle arise (Fig. 1 B–J). The latter give rise to simple flask-shaped antheridia and secondary perithecia as shown in Fig. 1 J.

When the spore of *B. bilateralis* becomes affixed to the host integument it is nearly appressed throughout its length. Although the exact nature of the haustorial apparatus was not determined, the connection between the haustorium and the lumen of the basal cell of the receptacle is easily observed (Fig. 1 B, D), and the foot of the detached fungus shows a distinct circular opening marking the location of the point of exit of the connection between the foot and the haustorium (Fig. 1 F–G). The primary perithecium arises from the side of the primary receptacle nearest the host integument. As the fungus develops, the receptacle becomes more or less erect or ascending.

Early stages of development of the primary perithecium and receptacle are shown in Fig. 1 B–H. The subbasal cell of the young individual separates a small bud-like cell (a) distally on one side (Fig. 1 B) that grows upward and outward (Fig. 1 C–D, F–G) and a larger lower cell (b) that develops additional cells laterally to the right and left (Fig. 1 C–F). Cell (a) eventually gives rise to the primary perithecium and its stalk (Fig. 1 H–I).

Longitudinal divisions of cell (b) and its progeny result in a transverse series of usually only five elongate cells. The median cell subtends the primary perithecium and appendage and undergoes no further change except for slight enlargement (Fig. 1 E–F). From each cell bordering the median cell to the right and left there develops an upwardly directed series of 4–6 tiers of more or less

Fig. 2. *Balazucia bilateralis* Benjamin.—A–E. Early stages of development of the perithecium; for discussion see text. $\times 2015$.—F. Lateral view of slightly immature perithecium showing strongly convex outer margin and only slightly convex inner margin. Note remnant of trichogyne on upper inner margin. $\times 660$.—G. Posterior view of mature perithecium. $\times 1080$.—H. Mature individual showing five mature perithecia. The lowermost primary perithecium is bent downward around the base of the broken primary appendage. Note proliferation of upper cells of the upgrowths of the receptacle. $\times 485$.



paired cells that gives rise distally to simple flask-shaped antheridia and proximally to secondary perithecia (Fig. 1 J). Each of the outer cells of the original series of five transverse cells arising from cell (b) produces a divergent branch-like upgrowth consisting of a series of 5-7 superposed cells ending in a simple antheridium (Fig. 1 J-K).

In many instances only the primary perithecium matures. Often, however, the primary upgrowths of the receptacle give rise not only to single secondary perithecia externally (Fig. 1 J) but also to additional single perithecia that arise internally from cells lying slightly above the level of those forming the outer perithecia (Fig. 1 L, 2 H). In two very large individuals I observed young perithecia arising from inner proximal cells of the outer uniseriate upgrowths. This appears to be of rare occurrence in this species, however.

The mature receptacle of *Balazucia bilateralis* is more or less flattened and bilaterally symmetrical. One to five, very rarely seven, perithecia may be present depending on whether or not all of the secondary perithecia mature. The primary and secondary upgrowths of the receptacle often continue to proliferate in age and form not only additional antheridia but also sterile branchlets distally (Fig. 1 L, 2 H).

The perithecial bud (Fig. 1 B-a) elongates rapidly. A single cell is cut off terminally, and this cell soon divides once more as shown in Fig. 1 H and 2 A. The resulting terminal cell elongates apically (Fig. 2 B-C) and finally is separated into two cells, the elongate simple trichogyne (tr) above and the conical trichophoric cell (e'') below. In this discussion, the various cells are designated by the same letters employed by Thaxter (1896) in his descriptions of the development of the perithecia of *Stigmatomyces baeri*, *Peyritschiella geminata*, *Laboulbenia flagellata* (as *L. elongata*), and *Enarthromyces indicus*. The sub-basal cell shown in Fig. 2 A remains unchanged for a time and constitutes the carpogenic cell (f) from which the ascogonium eventually is derived (Fig. 2 B-D). The elongate basal cell shown in Fig. 2 A again divides and produces a lower primary stalk-cell (p) that remains unchanged during later development and an upper cell (c), the primordial cell of the perithecium, from which the basal cells and the walls of the perithecium eventually are derived. The first division of cell (c) already has taken place in the young perithecium shown in Fig. 2 B. Subsequent divisions of the products of cell (c) result in the formation of a small flattened cell (h), the secondary stalk-cell, situated just above the primary stalk-cell (p), and three primordial cells of the perithecial wall-cells (i) that are growing upward around the carpogenic cell (Fig. 2 C). One of the primordial cells (i) gives rise to two tiers of wall-cells, whereas each of the other primordial cells (i) gives rise to a single tier of wall-cells (Fig. 2 D-n). The three lower cells remaining after formation of the first, or primordial wall-cells (n) are termed the basal cells (o) of the perithecium (Fig. 2 D). The basal cells actually initiate two series of cells, an outer series of four rows that persist in their entirety and comprise the wall-cells proper and a corresponding inner series termed the parietal cells (lower) and the canal cells (upper). The parietal cells are destroyed by the subsequent development of the ascogonia and asci whereas the canal cells may remain apparently to function in spore discharge (see Benjamin, 1968, Fig. 6). Only the outer series of wall-cells are depicted in the accompanying figures. It was not possible to trace accurately the develop-

ment of the inner cells or the fate of the carpogenic cell in the material at hand.

Figure 2 D shows a young perithecium at the time the female sexual organ presumably is mature. The stalk-cell (p) is surmounted by the secondary stalk-cell (h) which in turn subtends the three basal cells (o). The latter are followed above by four primordial wall-cells (n) that completely surround the carpogenic cell (f). The trichophoric cell (e") is interposed between the trichogyne (tr) and the carpogenic cell. If the sexual organs are functional in this species, it might be presumed that fertilization would take place at about this stage of development of the perithecium. Observations of perithecia in later stages of development show that the trichogyne rapidly breaks down (Fig. 2 E).

Figure 2 E shows a young perithecium in which a second tier of wall-cells (wx) have been derived from the primordial wall-cells (n) shown in the previous figure. The lower wall-cells now may be designated as the basal wall-cells (w) for they will only enlarge without dividing further. The trichophoric cell (e") is still in evidence, but it becomes disorganized and disappears as the perithecium matures. A nearly mature perithecium is shown in lateral view in Fig. 2 F. It may be noted that the perithecium is markedly asymmetrical. The side facing away from the position of the primary appendage is noticeably more convex than the side adjacent to the appendage. The base of the perithecium becomes black and completely opaque. A brownish-red opacity extends upward over the outer surface and more or less completely obscures from view the interior of the lower two-thirds of the perithecium (Fig. 2 G). The outer wall of the mature perithecium is composed of the three basal cells followed above by four longitudinal rows of wall-cells of four cells each. The terminal wall-cells, or lip-cells, form a simple ostiole that remains unmodified. The base of the trichogyne becomes blackened and persists on the inner surface of the perithecium at the level of the sub-terminal tier of wall-cells (Fig. 2 F).

As stated above, the characteristics of *Balazucia bilateralis* suggest a closer relationship of the genus to *Cucujomyces* than to any other known genus of Laboulbeniales. For purposes of comparison, I offer drawings of three species of the latter genus including the type species, *C. cylindrocarpus* Speg. (Fig. 3 A-B), as well as *C. elegans* Speg. (Fig. 3 C-D) and *C. diplocoeli* Thax. (Fig. 3 E-G).

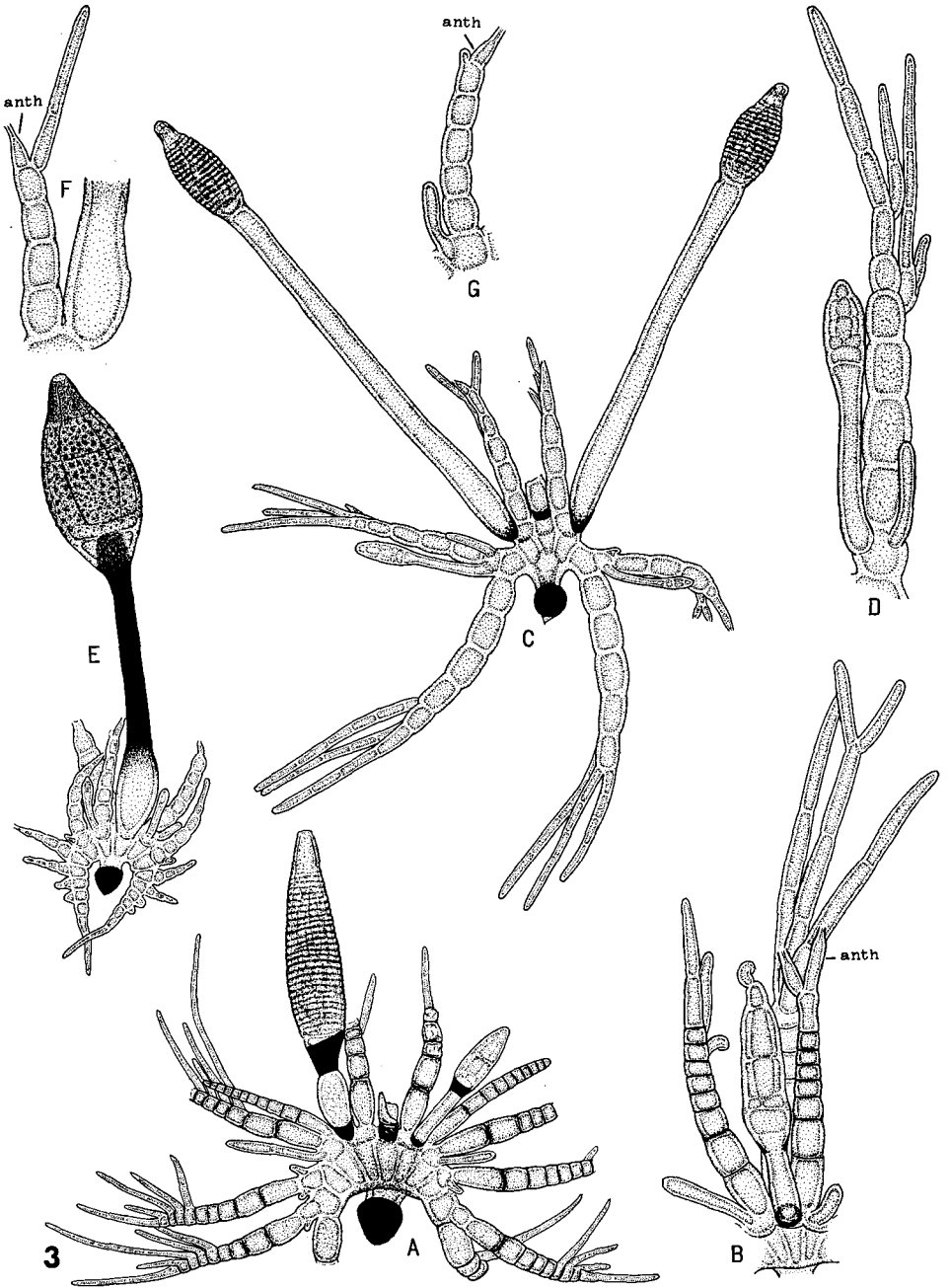
The primary receptacle of *Cucujomyces* consists of two superposed cells. The basal cell forms the foot and may remain unchanged or become enlarged distally and more or less overlap the subbasal cell. The upper cell, like that of *Balazucia*, supports a primary appendage subtended by a primary perithecium and forms secondary axes to the right and left. The latter may extend more or less horizontally and become strongly recurved with appendage-like terminations as in the species illustrated here, or they may remain somewhat compacted as in *C. stipitatus* Thax. (1918, 1931) or *C. elegantissimus* (Speg.) Thax. (1931). Variable numbers of cells of the secondary axes give rise from their upper face to erect, simple or branched, uniseriate cellular appendages bearing terminal simple antheridia (Fig. 3 B, F, G) that may persist or be displaced by one or more secondary branchlets. Perithecia arise from the basal cell of the appendages. Although the basal cell of a given appendage may form the rudiments of two perithecia (Fig. 3 B), one of these appears always to abort, and in the species of *Cucujomyces* known at present an individual typically bears only one or two

mature perithecia. In some species, secondary perithecia appear to develop only when the primary perithecium is damaged or otherwise fails to develop.

At present there are eleven described species of *Cucujomyces*. Eight of these infest beetles belonging to the superfamily Cucujoidea. Five species, *C. cylindrocarpus* Speg. (1917), *C. elegans* Speg. (1917), *C. melanopus* Speg. (1917), *C. intermedius* Thax. (1918), and *C. stipitatus* Thax. (1918), have been found only on *Brontes chilensis* Blanch. (= *Uleiota chilensis* Blanch.¹) of the Cucujidae in Argentina and Chile; a single species, *C. diplocoeli* Thax. (1918), also from Chile, occurs on *Diplocoelus* sp. of the Biphylidae, a family closely related to the Cucujidae; another species, *C. bilobatus* Thax. (1918), was described from New Zealand on an undetermined genus of Cryptophagidae; and *C. elegantissimus* (Speg.) Thax. (1931), placed originally by Spegazzini (1917) in a separate genus, *Stephanomyces*, was found in Argentina on a member of the Mycetophagidae, listed as *Typhaea fumata* L. (= *T. stercorea* L.) by Spegazzini. Thaxter (1931) described two species from Trinidad, *C. goniocoeli* and *C. reynoldsii*, on *Goniocloeus* sp. [incorrectly spelled *Gonicoelus* by Thaxter] of the family Anthribidae (Superfamily: Curculionoidea). Finally, a single Chilean species, *C. curtipes*, was described by Thaxter (1918) from a species of *Anisotoma* of the family Leiodidae (Superfamily: Staphylinoidea). Although the hosts of the known species of *Cucujomyces* belong to three different superfamilies of Coleoptera (Arnett, 1960–1962), it is interesting and perhaps significant that these beetles occupy similar habitats and usually feed on fungi in association with dead bark or moldy vegetable debris. The occurrence of species of this very distinct genus of Laboulbeniales on more or less unrelated hosts that share a similar environment would seem to offer additional support to the idea expressed elsewhere (Benjamin, 1967) that fortuitous parasite transfer may account for disjunct distribution in many genera of Laboulbeniales.

¹The name *Hylliota* given by Thaxter (1931) apparently is an erroneous spelling, for I can find no such name listed in the works of Arnett (1960–62) or Blackwelder (1945).

Fig. 3. A–B. *Cucujomyces cylindrocarpus* Spegazzini.—A. Anterior view of mature individual showing one mature secondary perithecium and several immature perithecia in various stages of development arising from the basal cell of secondary appendages. The median primary perithecium and appendage have been broken away. $\times 400$.—B. Portion of receptacle showing immature primary perithecium subtending the primary appendage the base of which is hidden from view. Note secondary appendages to the right and left with perithecial initials arising from their bases. The appendage on the right is terminated by two simple, flask-shaped antheridia (anth). $\times 660$.—C–D. *Cucujomyces elegans* Spegazzini.—C. Individual showing two mature secondary perithecia. The primary perithecium and appendage have been broken away. Note the elongate appendiculate terminations of the receptacle and the young perithecia that have arisen from the basal cells of the secondary appendages immediately below the mature perithecia. $\times 300$.—D. Appendage showing two perithecial rudiments arising from the basal cell; only one perithecium is developing. $\times 610$.—E–G. *Cucujomyces diplocoeli* Thaxter.—E. Individual with mature primary perithecium. Note progressive development of secondary appendages from the successive cells of the receptacle the extremities of which are strongly recurved. $\times 300$.—F. Secondary appendage with single terminal antheridium (anth) and young branchlet; the base of a perithecial stalk-cell is at the right. $\times 660$.—G. A similar appendage showing perithecial initial arising from basal cell and early stage of development of a branchlet from the cell subtending the terminal antheridium (anth). $\times 660$.



SUMMARY

A new genus and species of Laboulbeniales, *Balazucia bilateralis*, parasitic on an unidentified species of *Phloeonomus* of the subfamily Omaliinae (Coleoptera: Staphylinidae) from Mexico is described and illustrated. Among the known genera, *Cucujomyces* Spegazzini appears to be most closely related to *Balazucia*. Three species of *Cucujomyces* including the type species *C. cylindrocarpus* Speg. as well as *C. elegans* Speg. and *C. diplocoeli* Thax. are illustrated for comparison with *Balazucia bilateralis*.

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