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COMPARATIVE MORPHOLOGY OF *IDIOMYCES* AND ITS
POSSIBLE ALLIES *DIPLOMYCES*, *SANDERSONIOMYCES*,
SYMPLECTROMYCES, AND *TERATOMYCES*
(ASCOMYCETES: LABOULBENIALES)

Richard K. Benjamin

Abstract.—Pertinent stages of development of the receptacle, primary and secondary appendages, and perithecium of *Idiomyces peyritschii* are described and illustrated and comparison is made between this species and the type species of *Diplomyces*, *Sandersoniomyces*, *Symplectromyces*, and *Teratomyces* for which early stages of receptacular and appendage development also are described and illustrated. Possible close relationship of these genera with one another is examined in the light not only of morphological similarities and differences but also of host range. It is concluded that *Diplomyces*, *Sandersoniomyces*, *Symplectromyces*, and *Teratomyces* do indeed constitute a closely allied group of genera. However, the gap between this alliance and *Idiomyces* is deemed great enough to warrant their separation into separate tribes within the Laboulbeniales, proposed by Thaxter in 1908, i.e., Idiomyceteae for *Idiomyces* and Teratomyceae for the other four genera.

INTRODUCTION

Idiomyces peyritschii was described by Thaxter (1893) as the type of a new genus of Laboulbeniales parasitizing a staphylinid beetle, *Deleaster dichrous* (Grav.), collected in Germany. Thaxter named the species for the pioneer student of Laboulbeniales, J. Peyritsch, who, perhaps in error, listed *D. dichrous* as one of the hosts for his newly described *Laboulbenia vulgaris* Peyr. (1873:249). Peyritsch later (1875:385) claimed also to have observed on *D. dichrous* a second species of *Laboulbenia* Mont. & Robin (Robin 1853), i.e., *L. gracilis* (non *L. gracilis* Speg. [1915]), which, however, he never described. *Laboulbenia vulgaris* occurs on various Carabidae, especially species of *Bembidion* Latreille, several of which were cited as hosts by Peyritsch. No species of *Laboulbenia* has subsequently been found on *Deleaster* Erichson spp., and Peyritsch may have misinterpreted the true nature of immature specimens of *I. peyritschii* which vaguely resemble *Laboulbenia* and as a result may have assigned them to the common *L. vulgaris*.

Idiomyces peyritschii apparently is of widespread occurrence in Europe and has been reported as follows: On *Deleaster adustus* Küst. (= *D. dichrous* fide Balazuc 1974); England (Thaxter 1908).—On *D. dichrous*: England

(Thaxter 1908); France (Picard 1913; Balazuc 1974); Germany (Thaxter 1908); Holland (Middelhoek 1943, 1947); Hungary (Bánhegyi 1940); Italy (Rossi and Cesari-Rossi 1978); Poland (Siemaszko and Siemaszko 1932); Scotland (Thaxter 1908); Switzerland (Thaxter 1908); Yugoslavia (Bánhegyi 1960; Balazuc 1974).—On *D. dichrous* (Grav.) var. *leachi* Curt.: Poland (Siemaszko and Siemaszko 1932).—On *D. erichsoni* Hochh.: Caucasus, USSR (Siemaszko and Siemaszko 1932). The species recently has been found on *D. yokoyamai* Adachi in Japan (Hokkaido) by Terada (1977). The study of *I. peyritschii* presented in this paper is based on specimens found on *D. concolor* LeC. from California. These collections are the first reported from the Western Hemisphere.

Based on the arrangement of antheridia on fertile appendages, Thaxter (1893, 1896) suggested that *Idiomyces* might be most nearly allied to *Stigmatomyces* Karsten (1869) despite the marked differences between these genera in the structure of their receptacles and in the manner of origin of their appendages and perithecia. In 1908, however, he noted the resemblance of *Idiomyces* to “the group of genera immediately associated with *Teratomyces* [Thaxt.],” i.e., *Diplomyces* Thaxt. (1895) and *Symplectromyces* Thaxt. (1908). However, lack of information regarding early stages of development of these genera prevented a critical comparison of *I. peyritschii* with them for indications of close relationship, at least on morphological grounds.

In 1968, I described *Sandersoniomyces divaricatus*, type of a new genus, and compared it with *Diplomyces actobianus* Thaxt. (1895), *Symplectromyces vulgaris* (Thaxt.) Thaxt. (1908; syn. *Teratomyces vulgaris* Thaxt. [1900]), and *T. mirificus* Thaxt. (1893), the type species of their respective genera. *Sandersoniomyces* is morphologically most like *Diplomyces*, but all four genera share similarities that suggest their close relationship. My study did not include *Idiomyces*, and my purpose here is to describe and compare the development of *I. peyritschii* with that of the above species and, hopefully, determine whether or not *Idiomyces* should be closely allied with this group of genera.

MATERIALS AND METHODS

For this and my previous study (Benjamin 1968a), observations were made on and illustrations were prepared from among the following collections, all of which along with their hosts originally had been preserved in 50–70% alcohol. All of the fungi are mounted in glycerine containing a trace of cotton blue or acid fuchsin dyes. The slides are in RSA.

Idiomyces peyritschii: CALIFORNIA. Marin County: S. P. Taylor State Park, 8 Nov. 1953, R. O. Schuster coll. (*RKB 1801*); Mt. Tamalpais, date unknown (1940's), H. B. Leech coll. (*RKB 2031*); Lagunitas Creek at To-

caloma, 4 May and 17 June 1969, H. B. Leech coll. (RKB 2528, 3384). All on *Deleaster concolor* LeC.

Symplectomyces vulgaris: ALABAMA. Madison County: Spook Cave, 21 Mar. 1966, Stewart Peck coll. (RKB 2449); Marshall County: Merrill Cave, 16 Mar. 1966, Stewart Peck coll. (RKB 2454).—ARKANSAS. Washington County: locality not given, 20 Jan. 1940, M. W. Sanderson coll. (RKB 2355).—CALIFORNIA. Amador County: 2 mi NE of Jackson, 16 Apr. 1957, L. M. Smith and R. O. Schuster coll. (RKB 2353); Modoc County: Joseph Creek, 15 mi N of Alturas, 17 June 1954, R. O. Schuster coll. (RKB 2354); Tehama County: Mineral, 8 June 1954, R. K. Benjamin coll. (RKB 1739).—COLORADO. Eagle County: 5 mi N of Walcott, 2 Sept. 1958, 7700 ft, C. C. Hoff coll. (RKB 2356).—ILLINOIS. Henderson County: Goose Hollow Cave, 2.5 mi E of Oquawka, 13 Nov. 1965, Stewart Peck coll. (RKB 2450); Jo Daviess County: Hitchings Mine, 5 mi E of Galena, 31 Oct. 1965, Stewart Peck coll. (RKB 2456); Monroe County: Furth's Spider Cave, 11 and 26 June 1965, Stewart Peck coll. (RKB 2448 [incorrectly cited 2458 in Benjamin 1968a:8], 2453).—KENTUCKY. Woodford County: Clifton Cave, 8 Sept. 1964, Stewart Peck coll. (RKB 2455).—MISSOURI. Jefferson County: Pleasant Valley Cave, 24 June 1965, Stewart Peck coll. (RKB 2451).—SOUTH DAKOTA. Pennington County: 6 mi E of Hill City, 14 July 1959, C. C. Hoff coll. (RKB 2452).—UTAH. Cache County: Blacksmith Fork Canyon, 27 Oct. 1959, G. F. Knowlton coll. (RKB 2348), Logan Canyon, 1 Nov. 1959, G. F. Knowlton coll. (RKB 2347). All on *Quedius* spp.

Teratomyces mirificus: FLORIDA. Columbia County: O'Leno State Park, 25 Oct. 1981, J. H. Frank coll. (RKB 3416), on *Acylophorus zdenae* Smetana (new Florida record for this host fide J. H. Frank); Holmes County: Choc-tawhatchee River at hwy 2, 30 Apr. 1980, J. H. Frank coll. (RKB 3417), on *A. lecontei* Duvivier.—ILLINOIS. Carroll Co.: Thomson, 12 Aug. 1944, Sanderson and Leighton coll. (RKB 206, 207), on *Acylophorus* sp.; Champaign County: Mahomet, 19 July 1952, M. W. Sanderson coll. (RKB 2457), on *A. flavicollis* Sachse, Urbana, 3 June 1949, R. K. Benjamin coll. (RKB 161, 162, 163), on *Acylophorus* sp.; Christian County: Palmer, 24 Sept. 1943, H. H. Ross and M. W. Sanderson coll. (RKB 2447), on *A. flavicollis*; Lake County: Wauconda, 24 Aug. 1944, T. Frison and H. H. Ross coll. (RKB 1103), on *Acylophorus* sp.; La Salle County: Starved Rock State Park, 12 July 1944, T. Frison and M. W. Sanderson coll. (RKB 405), on *Acylophorus* sp.; McHenry County: Cary, 11 July 1946, Mohr and Sanderson coll. (RKB 1093), on *Acylophorus* sp.; Vermilion County: Muncie, 22 Sept. 1943, Sanderson and Sommermann coll. (RKB 2338), on *A. filius* Smetana.—LOUISIANA. Jefferson Parish: Harahan, 2 Sept. 1944, C. L. Remington coll. (RKB 1002, 2459) on *Acylophorus* sp.—MAINE. York County, Kittery Point, 1911, R. Thaxter coll. (RKB 2458), on *Acylophorus* sp.

Sandersoniomyces divaricatus: See Benjamin 1968a, p. 2, for citation of specimens *RKB* 1737, 1826, 1883, 2026, and 2051 from California. Additional collection: CALIFORNIA. San Bernardino County: Jenk's Lake, San Bernardino Mountains, 18 July 1957, R. K. Benjamin coll. (*RKB* 2331), on *Quedius* (*Raphirus*) sp.

Diplomyces actobianus: ILLINOIS. Jackson County: Giant City State Park, 13 July 1948, M. W. Sanderson and L. J. Stannard coll. (*RKB* 402, 1104B), on *Erichsonius* sp.; Johnson County: Vienna, 25 Jan. 1947, Burks et al. coll. (*RKB* 366C, 1070C), on *Erichsonius* sp.; Marshall County: Sparland, 15 Mar. 1947, H. Mills and H. H. Ross coll. (*RKB* 363, 364A), on *Erichsonius* sp.; Pope County: Hays Creek Canyon, near Eddyville, 23 Oct. 1957, M. W. Sanderson coll. (*RKB* 2343C, 2344B, 2345B, 2346B), on *E. patella* (Horn); Putnam County: Magnolia, 23 Mar. 1944, H. H. Ross coll. (*RKB* 1832C), on *E. patella*; Sangamon County: New Salem State Park, 3 Apr. 1956, L. J. Stannard coll. (*RKB* 2358C), on *E. patella*. — VIRGINIA. Carroll County: Fancy Gap, 23 Oct. 1960, J. S. Ayars coll. (*RKB* 2359B), on *E. patella*.

All drawings were prepared with the aid of a camera lucida mounted on a Leitz Dialux microscope equipped with interference contrast optics. Kodak Tri-X Pan Professional Film 4164 (ASA 320) was used for making the photographic illustrations.

Perithecial terminology is based on the system originally proposed by Thaxter (1896:217–234, Pl. I), modifications of which have most recently been summarized by Benjamin (1979:383–385, Fig. 3) and Tavares (1979:241–244; 1980:489).

OBSERVATIONS

A. Development of Idiomycetes peyritschii

The ascospore of *Idiomycetes peyritschii* is two celled like that of all Laboulbeniales. The hyaline sheath surrounding the body of the spore is conspicuously enlarged distally around the longer of the two cells (Fig. 1, 25). The longer cell, originally oriented towards the perithecial ostiole prior to spore discharge (Fig. 17), forms the foot (Fig. 2) and eventually gives rise to all cells of the receptacle, numerous secondary appendages, and perithecia (Fig. 3–11, 18–21). The tip of the lower cell is separated as a hyaline, enucleate, homogeneous end-piece that contrasts sharply with the granular contents of the adjacent cell (Fig. 1, 25) and appears somewhat sheathlike in character.

Among the 178 preperithecial juvenile individuals available for study, the earliest stage in thallus development that I could find is shown in Fig. 2 where the foot is differentiating but divisions of the lower and upper cells, separated by the original spore cross wall (a), have not begun.

In the stage of development shown in Fig. 3, divisions of the upper spore segment have resulted in three superposed cells. This is the young primary appendage (*pa*) and for purposes of further reference the lower two cells are designated by the letters *b* and *c*; the upper cell is terminated by a spine (*sp*) representing the indurated spore apex. This spine typically persists as the primary appendage matures (Fig. 4–11, 18).

The lower spore segment (Fig. 3) divides and forms the primary receptacle consisting of three superimposed cells, I, II, and III (Fig. 4). Cell II of the young receptacle soon is divided into two cells, IIa and IIb, by an oblique cross wall (Fig. 5). Cell IIa then is separated by a transverse cross wall into two cells, IIa and IIa' (Fig. 6–7), the latter cell more or less paralleling cell

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Fig. 1–17. *Idiomyces peyritschii*.—1. Ascospore showing conformation of hyaline adhesive sheath, cross wall (*a*), and hyaline basal end-piece.—2–10. Pertinent stages of development of the receptacle, primary appendage (*pa*), and primary and secondary receptacular upgrowths (*pru*, *sru*). Details and terminology are given in the text.—11. Young individual prior to appearance of first perithecial initial. Note relationship of primary appendage (*pa*) and primary and secondary receptacular upgrowths (*pru*, *sru*) to cells of the primary receptacle (I, IIa, IIa', IIb). Both receptacular upgrowths are forming secondary appendages.—12. Young secondary appendage.—13. Secondary appendage showing basal and terminal sterile branchlets and two tiers of antheridia.—14. Young perithecial initial (see Fig. 18, inset). Basal cell *m* has been formed by the primary stalk cell, VI; the secondary stalk cell, VII, already has cut off basal cell *n* and is growing upward around the near face of cell *n* and will eventually cut off basal cell *n'*. Also shown are the carpogenic (*cp*) and trichophoric (*tc*) cells of the young female organ.—15. Young perithecium showing well-developed trichogyne (*tr*) (see Fig. 19). The secondary stalk cell, VII, and basal cell *m* are beginning to elongate. The first two cells (*o*, *w*) of the outer rows of wall cells have been formed (those derived from basal cells *m* and *n'* are shown) and are growing upward around the female sexual organ and the first-formed inner wall cells.—16. Still later stage of perithecial development as viewed from the side opposite that shown in Fig. 15. Three wall cells (*o*, *w*, *w'*) have now been delimited in each row of outer wall cells. Basal cell *n* has given rise to two of these wall cell rows. Cells VII and *m* are continuing to elongate. The trichogyne has disappeared except for a small basal remnant.—17. Mature perithecium less most of the primary stalk cell. There are four tiers of outer wall cells (*w*¹–*w*⁴). Basal cell *n'* is relatively small compared to the greatly elongate cells VII and *m*. (Fig. 1–10, 15–16, $\times 495$: bar B = 20 μ m; Fig. 11, 17, $\times 305$: bar A = 40 μ m; Fig. 12, $\times 880$: bar C = 10 μ m; Fig. 14, $\times 745$: bar D = 10 μ m.)

Fig. 18–21. *Idiomyces peyritschii*.—18. Young individual showing first-formed perithecial initial (see inset and Fig. 14) arising from the secondary receptacular upgrowth (*sru*). The spine-bearing outer branch of the primary appendage (*pa*) is visible on the right side of the primary receptacular upgrowth (*pru*), $\times 375$ (bar = 50 μ m); inset, $\times 800$ (bar = 10 μ m).—19. Slightly older individual showing perithecium with well-developed trichogyne (*tr*) (see Fig. 15 for drawing), $\times 300$ (bar = 50 μ m).—20. Still older individual showing first-formed perithecium (upper left) with elongating secondary stalk cell (VII) and basal cell (*m*) and a second younger perithecium with trichogyne (*tr*). Note numerous secondary appendages with seriate antheridia borne on the primary and secondary receptacular upgrowths (*pru*, *sru*), $\times 300$ (bar = 50 μ m).—21. Mature individual with one perithecium, $\times 250$ (bar = 50 μ m).

IIb (Fig. 7) which is regarded as posterior in position. As the receptacle continues to grow and mature, cells I, IIa, and IIb typically remain undivided (Fig. 8–11, 18–22), although adventitious septa occasionally are formed in one or more of these cells.

Development of the primary appendage is illustrated in Fig. 5–10. As shown in Fig. 5–6, the original spore septum (*a*) and the septum separating cell *b* from cell *c* become blackened. The terminal spinose cell elongates and divides and eventually forms a simple branch consisting of several cells; the lower of which bears the divaricate, indurated spore apex (Fig. 5–11). A second sterile branch subtending the spinose cell arises from cell *c* (Fig. 6–11). Finally, development of the primary appendage is completed by the formation of a simple or divaricate, sterile, cellular branchlet from cell *b* (Fig. 7–11).

Continued development of the receptacle involves the formation of a progression of cells, the primary receptacular upgrowth (*pru*) from cell III (Fig. 8–9). The earliest stage of formation of these cells is seen in Fig. 8 where a cell cut off by cell III already is forming an upright branch. In the young individual shown in Fig. 9 three nearly vertical cells have been delimited from cell III. The basal cell of the secondary appendage arising from the outer cell, as in most appendages formed by *I. peyritschii*, is delimited above and below by black septa.

As growth and enlargement of the thallus proceeds, the primary receptacular upgrowth assumes a nearly vertical position concomitant with the development of what can be termed the secondary receptacular upgrowth (*sru*) from cell IIa' opposite cell IIb (Fig. 11, 18–19, 21–23). The primary appendage gradually is deflected aside and projects laterally from the base of the primary receptacular upgrowth (Fig. 11, 18) where it usually is obscured by antheridial branches and commonly is broken or missing in older thalli (Fig. 20–22).

The several cells of the primary receptacular upgrowth cut off smaller cells to the right and left, and each of these cells may form additional cells. As they appear, each cell gives rise to a simple or branched, sometimes sterile but mostly fertile, several-celled secondary appendage (Fig. 11, 18–20). Cells comprising sterile appendages or sterile branchlets of fertile appendages typically are two to many times longer than broad; fertile cells destined to delimit antheridia are nearly isodiametric or slightly wider than high (Fig. 12–13).

Secondary appendages vary in number of fertile cells and in the number of branchlets they may form. The basal cell, as already mentioned, typically is delimited above and below by blackened septa. This cell may occasionally give rise to antheridia or a sterile branchlet (Fig. 13). The axis of a fertile appendage above the basal cell may be 8–10 cells in length. The terminal

cell and frequently the preceding one or two cells may develop short or elongate, several-celled prolongations (Fig. 13). Each fertile cell cuts off a single cell from its inner face which forms a simple, sessile, broad-based antheridium having a free efferent tube; the fertile cells then commonly delimit another antheridium on one or both sides. Sometimes a fertile cell, especially one near the base of the appendage, gives rise not only to an antheridium but also to another cellular sterile or fertile branchlet.

By the time perithecial production begins (Fig. 18), the primary receptacular upgrowth, subtended by the enlarged and protruding cell IIb, consists of a relatively massive, more or less vertical assemblage of about five progressively smaller cells and numerous small lateral cells. This complex of cells bears a relatively large number of sterile or antheridial appendages on its posterior surface (Fig. 18–19).

Soon after the primary receptacular upgrowth begins to develop, cell IIa' initiates the formation of the secondary receptacular upgrowth (*srw*) mentioned above. This cell has divided once in the individual shown in Fig. 10 and a small cell has been cut off distally on the outside. The first-formed cell then divides and forms a second cell (Fig. 11) and so on until 4–5 cells have been produced; each of these cells may cut off one or more cells to the right or left. The secondary upgrowth does not become vertically oriented as does the primary upgrowth. Instead, it is a more or less transverse group of cells subtended by the relatively large cell IIa' (Fig. 18–19). As soon as they are delimited, cells of the secondary upgrowth give rise distally to usually fertile secondary appendages identical to those formed by cells of the primary upgrowth (Fig. 11, 18–20). A young secondary appendage is shown in Fig. 12, and several mature or nearly mature appendages bearing successive ranks of antheridia are shown in Fig. 11, 18–20.

At about the stage of development shown in Fig. 18, perithecial formation begins. The first perithecial initial appears to arise always from the upper end, either on the right or left side, of the original cell IIa' (Fig. 18–19). The side of the receptacle opposite the first perithecial initial bears secondary appendages. Additional perithecia usually arise from inner cells of the secondary upgrowth where they are flanked by secondary appendages. Though uncommon, perithecia also may arise from the primary receptacular upgrowth, especially from distal cells of the median row of cells (Fig. 22–24). The formation of perithecial initials always is progressive, never simultaneous.

Of 213 individuals bearing one or more mature or immature perithecia, 186 had perithecia arising only from the secondary upgrowth. Only one individual bore a perithecium on the primary upgrowth without any evidence of a perithecium having been initiated on the secondary upgrowth; 26 individuals bore immature or mature perithecia on both the primary and

secondary upgrowths. Fourteen of the latter thalli bore one or more damaged or aborted perithecia on the secondary upgrowth—often the first-formed perithecium.

The number of perithecia initiated by a thallus varied from one to seven in the 213 individuals mentioned above; however, those bearing only one or two mature perithecia were most common. One hundred and seven individuals bore mature perithecia as follows: 82 with one; 19 with two; 3 with three; 1 with four; and 1 with seven. In the latter individual (Fig. 24) two of the perithecia arose from the primary receptacular upgrowth.

Soon after perithecial development begins (Fig. 14, 18), the stalk cell (VI), secondary stalk cell (VII), and basal cell *m* begin to elongate (Fig. 15, 16, 19) and rapidly carry the body of the perithecium together with the other two basal cells, *n* and *n'*, upward and away from the level of the appendages (Fig. 20). At maturity, the greatly elongated cells VII and *m* constitute at least one third or more often one half of the total length of the perithecial stalk (Fig. 21, 22, 24). Basal cell *m* typically is slightly longer than the body of the perithecium proper (Fig. 17).

The trichogyne (*tr*) first appears as a budlike upgrowth from the tip of the trichophoric cell (*tc*) at a stage of development slightly later than that shown in Fig. 14. One to three simple or two- to three-times divaricate, septate branchlets then grow out from the more or less ovoid upgrowth, and each branchlet becomes bi- or trilobate at its apex (Fig. 15, 19). None of the trichogynic septa become externally blackened. The trichogyne often persists at the apex of the young perithecium through at least the two wall-cell stage (Fig. 20). When it disappears, it leaves an inconspicuous basal remnant that persists on the surface of the perithecial wall near the distal end of the third wall cell of the row of wall cells derived from basal cell *m*.

The mature perithecial body is relatively short compared to the elongate stalk (Fig. 21–22); it is broadest near the middle, nearly symmetrical, and

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Fig. 22–25. *Idiomycetes peyritschii*.—22. Individual showing two mature perithecia, one developed from the primary receptacular upgrowth, the other from the secondary receptacular upgrowth. This individual also bears, from the secondary upgrowth, an immature perithecium (projecting upward to the left [*per*]) and the broken base of the first-formed perithecium which had arisen from cell IIa' (see next figure), $\times 160$ (bar = 100 μm).—23. Enlargement of individual shown in Fig. 22 showing more clearly the origin of the two mature perithecia from the primary and secondary receptacular upgrowths (*pru*, *sru*). The upper end of the broken primary stalk cell of the primary perithecium formed on the secondary receptacular upgrowth is indicated by an arrow, $\times 300$ (bar = 50 μm).—24. Aged individual showing seven mature perithecia. The two at the left have arisen from the primary receptacular upgrowth; the five at the right (two with damaged or aborted perithecia [top]) have arisen from the secondary upgrowth, $\times 125$ (bar = 100 μm).—25. Ascospores showing the hyaline adhesive sheath and the hyaline end-piece terminating the longer of the two cells of the spores, $\times 850$ (bar = 20 μm).

uniformly tapered to the blunt apex which is distinguished only by an inconspicuous median protuberance on the upper margin of each terminal cell (Fig. 17). There are four progressively smaller cells in each vertical row of outer wall cells. Cells of the lowermost tier are largest and up to 40% longer than those of the subbasal tier; cells of the terminal tier are smallest and slightly less than one half the length of those of the subterminal tier (Fig. 17). There are four ascogenic cells.

The mature thallus is nearly uniformly yellow brown or orange brown, except for the basal cells of the appendages, the junctions between septa of the receptacle, and the posterior surface of cell IIb which usually are darker. Likewise, the transverse septa separating cell VI from cells VII and *m* and those near the base of the perithecium as well as the surface of the third tier of outer wall cells are more deeply pigmented than adjacent cell surfaces.

B. Supplemental Observations on Development of Presumably Allied Taxa

In the commentaries on *Symplectomyces*, *Teratomyces*, *Sandersoniomyces*, and *Diplomyces* to follow in this section, all references to my earlier study (Benjamin 1968a) on representatives of these genera will be indicated simply by the year date 1968a and the appropriate page number and/or figure number.

1. *Symplectomyces vulgaris*

Several stages of early development of *S. vulgaris* were described and illustrated in my earlier account of the species (1968a:8–10, Fig. 5A–F); however, there were certain errors in this treatment which need to be corrected together with some addenda.

The terminus of the ascospore (Fig. 26), like that of *Idiomyces peyritschii*, persists as a conspicuous, divergent, indurated spine on the outermost branch of the primary appendage (Fig. 27–31; 1968a:Fig. 5E–F). The tip of the lower cell (Fig. 26) is without any special modification.

My account of early stages of development of the receptacle and primary appendage given previously (1968a:8, 10, Fig. 5B–C) contains several errors of interpretation. In the stage of development shown in Fig. 27, the primary receptacle consists of three cells, I, II, and III, separated from the young three-celled primary appendage by the original spore septum (*a*) which in 1968 I wrongly interpreted as being the darkened septum above cell *b*. Contrary to my earlier thoughts (1968a:8, Fig. 5C), it is cell II, not cell III, that is divided by a more or less oblique cross wall into two cells, IIa and IIb (Fig. 28), resulting in a primary receptacle of four superimposed cells.

The terminal cell of the three-celled primary appendage shown in Fig. 27 grows outward and upward past the spinose process which diverges near its base, forming a simple sterile prolongation which becomes septate in age.

Fig. 26–47.—Ascospores and early stages of development of the receptacle and primary and secondary appendages of the following species: 26–31. *Symplectomyces vulgaris*; 32–38. *Teratomyces mirificus*; 39–44. *Sandersoniomyces divaricatus*; and 45–47. *Diplomyces actobianus*. Details and terminology are given in the text. All $\times 620$ (bar opposite Fig. 47 = 20 μm).

The cells immediately below also may give rise to short sterile branchlets (Fig. 28–31; 1968a:Fig. 5C, E–F). Two or three additional branchlets usually arise from basal cell *b* of the young primary appendage and the septa separating each of these branchlets from cell *b* become blackened (Fig. 2–31; 1968a:Fig. 5E–F). Most intercalary cells of these branchlets are converted into simple antheridia (Fig. 30–31; 1968a:Fig. 5E–F).

While the primary appendage still is in early stages of development, cell III of the young receptacle begins to divide and cut off small cells around its periphery (Fig. 30–31; 1968a:Fig. 5D–E). As the receptacle enlarges, cells I, IIa, and IIb remain undivided, but the number of cells surrounding cell III continues to increase and from them are developed numerous simple or branched, sterile or antheridial, secondary appendages and one or more perithecial initials (1968a:Fig. 5H). Secondary appendages typically have blackened septa separating the basal cell from the branch or branches above (1968a:Fig. 5G): in age, proximal and distal cells tend to elongate and the antheridial cells may proliferate and give rise to short, divergent, sterile branchlets (1968a:Fig. 5I).

Several stages of development of the perithecium of *S. vulgaris* were described and illustrated earlier (1968a:11–12, Fig. 6). The trichogyne usually becomes several times branched as it matures, but only the septum separating the lowermost cell from the trichophoric cell becomes externally blackened (1968a:Fig. 5H, 6C). This septum forms a remnant on the perithecial wall that appears always to lie near the lower margin of the terminal outer wall cell of the row of wall cells derived from basal cell *n* adjacent to the basal cell *n'*-derived row of outer wall cells. This remnant may even straddle the vertical septum separating these cells. The mature perithecial body together with the relatively large basal cells *n* and *n'* usually is nearly equal in length to the perithecial stalk (1968a:Fig. 5I). As in *I. peyritschii*, basal cell *m* is much longer than basal cells *n* and *n'* and its lower one half or more parallels the secondary stalk cell (VII) which subtends cells *n* and *n'*. Cells VII and *m* often contribute nearly one half of the total length of the stalk (1968a:Fig. 5I) although the primary stalk cell (VI) may be longer in some individuals. Unlike *I. peyritschii*, however, basal cell *m* always is much shorter than the body of the perithecium. There are four or eight ascogenic cells.

Each vertical row of outer wall cells of the mature perithecium consists of four cells (1968a:Fig. 5I). Cells of the lowermost tier may be up to 20% longer than those of the subbasal tier and together these tiers constitute about four fifths of the total length of the body of the perithecium. Cells of the terminal tier are relatively small and inconspicuous, being one half to one third the length of cells of the subterminal tier.

Perithecia arise progressively, never simultaneously, on the receptacle. In his description of *S. vulgaris*, Thaxter (1908) reported one to three perithecia per individual, although in one of his figures (Thaxter 1908, Pl. L, Fig. 15)

he depicted a specimen with four. I have observed up to four immature perithecia on developing specimens, but I have found that most commonly only one or two perithecia mature. In a sample of 203 adult specimens, the count of mature perithecia per thallus was as follows: 1 on 131 thalli; 2 on 69 thalli; and 3 on three thalli.

2. *Teratomyces mirificus*

The illustrations accompanying my brief discussion of *T. mirificus* in 1968 did not include thalli in early stages of development. I have reexamined hosts from which material was taken earlier and have found a number of immature specimens several of which are figured here. Although these have not given as clear a picture of the earliest stages of growth of juvenile thalli as could be desired, they do suggest that development of this species is similar to that of *S. vulgaris*.

There is no evidence that the spore apex forms a persistent spine as in *I. peyritschii* and *S. vulgaris*. However, it proved difficult to remove very young individuals of *T. mirificus* intact, and the primary appendages of specimens observed were often more or less broken (Fig. 34–37). The lower cell of the ascospore consistently displays a distinct subterminal constriction (Fig. 32; 1968a:Fig. 4G).

I could not find a stage of development earlier than the one shown in Fig. 33 where the young receptacle consists of four superimposed cells separated from a four-celled primary appendage by a cross wall, *a*, believed on the basis of later development of the thallus, to represent the original cross wall of the ascospore. Even at this stage, the lower two cells of the young receptacle above and below the cross wall separating them have in part become nearly obscured by darkening and thickening of their outer walls; this is characteristic of most thalli of this species. Although the origin of the middle two cells of the receptacle shown in Fig. 33 from the division of a previously formed cell II, as in *S. vulgaris*, could not be determined, I have designated the four cells I, IIa, IIb, and III at this stage of development for sake of consistency.

In the young individual shown in Fig. 34, the tip of the primary appendage is missing, but a single branchlet is developing from its basal cell. Figure 35 shows another young thallus in a slightly more advanced stage of development. The primary appendage (*pa*) is broken and consists only of the original basal cell and a single three-celled branchlet with a pointed tip. Cell III has been divided into two cells by a vertical cross wall, and the daughter cell has given rise to the first secondary appendage. Further proliferation of cell III and its progeny and the continued formation of secondary appendages are shown in Fig. 36–38. Cells I, IIa, and IIb of the receptacle do not divide further, but there is rapid enlargement and elongation of the receptacle,

especially cell IIb, along with an increasing number of appendiculate cells and secondary appendages (1968a:Fig. 4A–B).

Secondary appendages, depending on their age, vary from simple to highly branched (1968a:Fig. 4B–F). They may consist only of two or three small superimposed cells, with the terminal cell more or less curved and beaklike. Or, more commonly, they consist of a relatively large elongate basal cell bearing a unilateral series of free, elongate, sessile phialides and several lateral or terminal sterile or fertile branchlets bearing phialides or beaklike cells. Cross walls typically are blackened externally.

Perithecia arise successively from inner cells of the complex of cells arising from cell III of the receptacle (1968a:Fig. 4A). As the receptacle enlarges and the number of appendiculate cells increases, a relatively large conical cell may be evident in the center of this mass of cells and probably represents the original cell III (1968a:Fig. 4B). Whether or not perithecial initials arise from this cell could not be determined for sure; if not, they certainly arise from cells closely associated with it. The trichogyne of *T. mirificus* is more or less highly branched and septate (1968a:Fig. 4H; Thaxter 1896, Pl. II, Fig. 1) with the basal septum and those of the lowermost branches externally blackened. The basal septum remains as a conspicuous trichogynic remnant on the outer wall of the perithecium, usually near the upper end of the juncture between the subterminal outer wall cells of the *m*- and *n*-basal cell-derived rows of wall cells. There are two ascogenic cells.

Each vertical row of outer wall cells of the mature perithecium of *T. mirificus* consists of four cells (1968a:Fig. 4C). The basal and subbasal tiers are nearly equal in length and together they constitute about 85% of the total length of the body of the perithecium. The very small terminal outer wall cells are about one half the length of the subterminal cells. Basal cell *m* and the secondary stalk cell (VII) usually form a relatively small part of the perithecial stalk, and their combined length together with basal cells *n* and *n'* is about equal to that of a basal outer wall cell (1968a:Fig. 4C). The primary stalk cell (VI) may vary greatly in length, commonly being two times and often three to four times the length of the perithecium (1968a:Fig. 4C; Thaxter 1896:Pl. X, Fig. 4, 1931:Pl. XLIII, Fig. 4).

Like Thaxter (1896), I have observed only one to three mature perithecia on adult specimens of *T. mirificus*, although I have seen as many as four mature and immature perithecia on some thalli. The number of mature perithecia per individual in a sample of 94 specimens examined was as follows: 1 on 75 thalli; 2 on 17 thalli; and 3 on two thalli.

In 1968, I reported a taxon thought to be a *Symplectromyces* found on *Philonthus* Curtis spp. collected in Colorado (RKB 2334), New Mexico (RKB 2339), and California (RKB 2351, 2352). Further study of these collections shows that the taxon has ascospores with a subterminal constriction like that

of *T. mirificus*. Also, its perithecium has only two ascogenic cells, and its secondary appendages resemble those of other *Teratomyces* species in having relatively large basal cells with blackened, stepwise septa delimiting the lateral branchlets. However, beaklike cells are lacking, and its antheridia are formed like those of *S. vulgaris*, i.e., they are formed directly from intercalary cells of fertile branchlets. This taxon may be distinct, but it is tentatively being referred to *T. philonthi* Thaxt. (1900). These observations support Balazuc's (1974) contention that Thaxter's (1908) report of *S. vulgaris* on a *Philonthus* from Hungary probably was based on an erroneous host determination.

3. *Sandersoniomyces divaricatus*

Several additional drawings of immature specimens of *S. divaricatus* are added here to supplement those accompanying my description of the species in 1968. The tip of the lower cell of the ascospore is without special modification (Fig. 39). Reexamination of the youngest individual illustrated earlier (1968a:Fig. 1B) has revealed what appears to be the spinose remnant of the spore apex on the upper cell of the right branchlet of the primary appendage (*pa*) (Fig. 41). However, this branchlet apparently is easily broken or is readily deciduous, and the consistent presence of a spinose appendage cell could not be determined. No stage of receptacular development earlier than that shown in Fig. 40 has been encountered. As in the other species being discussed in this paper, the four cells of the young primary receptacle are numbered I, IIa, IIb, and III from the base.

The primary appendage (*pa*) of the individual shown in Fig. 40 is broken and only the basal cell and part of the next cell are intact above what is believed to be the original spore septum (*a*). The primary appendage of the specimen shown in Fig. 41 is intact and a three-celled branchlet already has arisen from the basal cell next to the spinose primary branchlet. The secondary branchlet is terminated by a beaklike cell with a minutely rounded apex which is characteristic of the pointed terminal cells of sterile branchlets in this species (Fig. 43–44; 1968a:Fig. 1B–F; 2C–G). As thalli mature, primary appendages were not observed on any maturing individuals studied. Some branches may be deciduous, for basal cells of primary appendages usually bear one or more circular scars left by the basal septa of detached branchlets (Fig. 43; 1968a:Fig. 1E; 2B).

As the receptacle enlarges, cell III gives rise to a pair of one-celled outgrowths on one side below the primary appendage, and from these cells axes of superposed cells develop which give rise to secondary appendages and perithecia (1968a:Fig. 1E–F, 2A–B). Figure 42 shows a young individual in which the first of these outgrowths has developed. A slightly later stage is

shown in Fig. 43. This individual is seen from the rear and shows the median primary appendage and, on the far side, the first secondary appendages arising from the pair of cells formed by cell III. A somewhat older individual as seen from the front is shown in Fig. 44 where the third cells of the succession of cells forming the fertile cellular axes are arising from the second, already appendiculate, cells. Stages of development comparable to those shown in Fig. 43 and 44, but viewed from opposite sides, are shown in Fig. 1C and 1D, respectively, in my 1968 study.

Each cell of a fertile axis bears one secondary appendage distally on its posterior side (1968a:Fig. 2A–B). Secondary appendages are more or less uniform in structure, consisting of a relatively large basal cell subtending externally a three-celled, sterile branchlet with a terminal beaklike cell having a minutely rounded tip and internally a several times branched branchlet the distal cells of which are converted into antheridial cells (1968a:Fig. 2G).

Proximal cells of primary cellular axes may give rise to additional axes or to perithecial initials (1968a:Fig. 1F, 2A–B). Axis cells distal to the one giving rise to the first perithecial initial may give rise to one or more initials; however, unless the first-formed perithecium on an axis is damaged or aborts the others apparently do not develop. Whether or not this is the usual situation in this species remains to be determined, for only 12 of the 95 individuals examined thus far bore mature perithecia. Of these, 11 bore one perithecium, the other bore two.

The mature trichogyne of *S. divaricatus* is more or less highly branched and septa separating its lower cells are externally blackened (1968a:Fig. 1G). Its lower part may remain attached at or near the perithecial tip until at least the first three outer wall cells have been delimited. When it finally sloughs away, its basal septum forms a subterminal scar on the perithecial wall at or near the juncture of the two terminal outer wall cells of the *m*- and adjacent *n*-basal cell-derived rows of wall cells. There are two ascogenic cells.

Outer wall cells of the perithecium are disposed in four vertical rows of four cells each (1968a:Fig. 1A–B). Cells of the basal tier are only slightly longer than those of the subbasal tier on the average, and together these tiers constitute 85% or slightly more of the total length of the body of the perithecium. Cells of the terminal tier are only slightly shorter than those of the subterminal tier. The combined length of the basal cells and secondary stalk cell is considerably less than that of cells of the lower tier of outer wall cells (1968a:Fig. 2A–B). The primary stalk cell in all but one of the 12 mature individuals examined was about equal in length to the combination of basal cells and secondary stalk cell (1968a:Fig. 1A–B). In the one exception, this cell was about twice as long as any of the others, and only with a larger sample of mature specimens could one determine the degree of variability in the dimensions of this cell which in species of many genera of Laboulbeniales often ranges most widely in length.

4. *Diplomyces actobianus*

Early stages of development of *D. actobianus* prior to perithecial initiation were not included in my 1968 paper. Two are added here, but the earliest stages of growth following spore germination still have not been encountered in the material available for study. Ascospores are relatively slender (Fig. 45) but are not otherwise different from those usually found in Laboulbeniales. Thaxter (1896:Pl. X, Fig. 20) figured an immature individual younger than any found by me. He shows a four-celled receptacle in which the cross wall separating the middle two cells is oblique, suggesting that the subbasal cell of the young receptacle divides and forms two cells in a manner similar to that found in *I. peyritschii* and *Symplectromyces vulgaris* (Fig. 5, 28). Again, I have numbered the cells of the young receptacle I, IIa, IIb, and III.

I have not observed a young primary appendage of *D. actobianus* at a stage of development comparable to that shown for *Sandersoniomyces divaricatus* in Fig. 41. The two terminal branches on the young individual figured by Thaxter (1896:Pl. X, Fig. 20) appear to be attached to cell III of the receptacle which is shown undivided. One of these branches surely is the primary appendage. The other could be a branch of this appendage, incorrectly depicted, or it could be the first branch of a secondary appendage arising from a cell cut off on the far side of cell III. The primary appendage of *D. actobianus* soon is obscured by development of the two posterior upgrowths characteristic of this species and by secondary appendages and perithecia (Fig. 47; 1968a:Fig. 3A–C). However, observations on some 30 immature specimens indicates that the primary appendage of *D. actobianus* is similar to that of *S. divaricatus* and consists of a relatively large basal cell bearing several branchlets, some of which form beaklike terminal cells. Whether or not cells of some branchlets form antheridia still is undetermined.

As in *S. divaricatus*, cell III of the young receptacle of *D. actobianus* forms a pair of anterior cellular upgrowths on one side below the primary appendage. These cellular upgrowths give rise first on the outside to single, secondary, antheridia-bearing appendages (Fig. 46; 1968a:Fig. 3D) followed soon on the inside by cellular upgrowths (Fig. 47) the successive cells of which bear single antheridial secondary appendages (1968a:Fig. 3E) and, later, secondary perithecial initials (1968a:Fig. 3F). Lastly, the paired cells give rise, anteriorly and distally, to single primary perithecial initials (1968a:Fig. 3A). Soon after the paired anterior cells begin forming the structures listed above, cell III also initiates formation, posteriorly and distally, of the pair of sterile, two-celled upgrowths characteristic of the species (Fig. 47; 1968a:Fig. 3B).

The first-formed secondary appendages arising on the outside of the paired anterior cells of the receptacle consist of relatively large basal cells bearing

one or more three-celled, beaked, sterile branchlets and several fertile branchlets the cells of which are converted into antheridia (1968a:Fig. 3A, D). In age, the appendage may become distally more or less sympodially branched, each branch bearing several sterile and fertile branchlets, and the basal cell may become somewhat elongate with a unilateral series of sterile or fertile branchlets. These appendages never approach the inner cellular axes in length or number of branches and they do not give rise to perithecial initials. The secondary appendages formed on the elongate inner branches are comparatively simple, most commonly consisting of a basal cell bearing externally a beaked three-celled branchlet and one or several antheridial branchlets (1968a:Fig. 3B, C, E). Cross walls separating cells of appendages typically are blackened.

Despite the more or less symmetrical development of the receptacle and its appendages and sterile upgrowths, the perithecia of *D. actobianus* develop and mature progressively. The first-formed or primary perithecia arise from first one then the other of the anterior cellular outgrowths of cell III (1968a:Fig. 3A). Both primary perithecia may eventually mature and the result is a symmetrical thallus like the one shown in Fig. 3C of my 1968 paper. Or as shown in Fig. 3B of the same work only one perithecium may mature. Additional perithecial initials arise not from the paired anterior cells of the receptacle but from the basal and later succeeding cells of the inner cellular upgrowths formed by the paired cells (1968a:Fig. 3F). This occasionally results in a thallus bearing more than two mature perithecia, i.e., two primary and one or perhaps two secondary perithecia. I have not seen mature secondary perithecia on cells other than the basal cells of the cellular upgrowths. Only 23 of about 50 specimens studied bore mature perithecia. Eight had only one primary perithecium; 13 had two primary perithecia; and 2 had three perithecia, two primary and one secondary. One of the latter specimens bore an additional immature secondary perithecium that appeared normal and probably would have matured eventually.

The trichogyne of *D. actobianus* is at first simple (1968a:Fig. 3A) but becomes more or less branched with the proximal cells slightly constricted at their blackened septa. The basal cell and often several cells of the lowermost branch or branches of the trichogyne usually remain broadly attached to the outer surface of the perithecium near or across the junction of the two terminal outer wall cells of the rows of wall cells derived from basal cell *n* (1968a:Fig. 3C). There are two ascogenic cells.

Perithecial outer wall cells are disposed in four vertical rows of four cells each, with those of the lower two tiers nearly equal in length and together comprising ca. 80% of the length of the body of the perithecium (1968a:Fig. 3B, C). Cells of the subterminal tier are only slightly longer than those of the terminal tier. The primary stalk cell appears never to elongate greatly and typically is equal to or only slightly longer than the combined lengths

of the secondary stalk cell and basal cells. The stalk cells and basal cells together constitute about one third of the total length of the perithecium.

DISCUSSION

A. *Hosts*

Species of *Diplomyces*, *Sandersoniomyces*, *Symplectromyces*, *Teratomyces*, and *Idiomyces* are known only on beetles belonging to the Staphylinidae. This huge family of insects, on a worldwide basis, was divided into 18 subfamilies by Blackwelder (1952) and of these eight have been confirmed as including hosts of one or more species of perhaps 53 genera of Laboulbeniales (55 with the addition of two segregate genera of *Misgomyces* Thaxt. [1900] to be recognized by Tavares in an as yet unpublished major revision of these fungi). Modifications of Blackwelder's treatment of the subfamilies Oxytelinae (Arnett 1961; Frank 1982) and Staphylininae (Frank 1982) increase the number of host subfamilies to 12. Frank's (1982) definitive survey of staphylinid hosts of Laboulbeniales serves as the basis of the following summary of the genera of Laboulbeniales occurring on Staphylinidae.

All species of 34 genera of Laboulbeniales are known only on Staphylinidae, whereas 19 genera are known not only on Staphylinidae but also on other families of arthropods, mostly true insects. Of the genera found only on Staphylinidae, one or more species of 29 are limited to insects belonging to only one of nine subfamilies: Omaliinae: *Balazucia* Benjamin (1968b); Osoriinae: *Osoriomyces* Terada (1981) and *Scelephoromyces* Thaxt. (1912a); Oxytelinae: *Euhaplomyces* Thaxt. (1901), *Eumonoicomycetes* Thaxt. (1901); *Haplomyces* Thaxt. (1893), and *Idiomyces*; Steninae: *Ilyomyces* Picard (1917); Paederinae: *Camptomyces* Thaxt. (1894), *Chaetomyces* Thaxt. (1893), *Clematomyces* Thaxt. (1900), *Euceratomyces* Thaxt. (1931), *Moschomyces* Thaxt. (1894), *Neohaplomyces* Benjamin (1955), *Rhadinomyces* Thaxt. (1893), *Sphaleromyces* Thaxt. (1894), and *Zeugandromyces* Thaxt. (1912a); Staphylininae: *Diplomyces*, *Sandersoniomyces*, *Symplectromyces*, and *Teratomyces*; Trichophyinae: *Polyascomyces* Thaxt. (1900); Tachyporinae: *Clonophoromyces* Thaxt. (1931), *Smeringomyces* Thaxt. (1908), and *Stichomyces* Thaxt. (1901); Aleocharinae: *Acallomyces* Thaxt. (1902), *Diandromyces* Thaxt. (1918), *Kleidiomyces* Thaxt. (1903), and *Tetrandromyces* Thaxt. (1912a). Species of three genera parasitize insects of two subfamilies, i.e., *Amorphomyces* Thaxt. (1893) on Aleocharinae and Oxytelinae; *Compso-*
myces Thaxt. (1894) on Omaliinae and Paederinae; and *Mimeomyces* Thaxt. (1912a) on Paederinae and Staphylininae. One genus, *Dichomyces* Thaxt. (1894), is found on three subfamilies, i.e., Aleocharinae (1 of 34 species), Staphylininae, and Xantholininae. *Monoicomycetes* Thaxt. (1900) has been found on members of five subfamilies, i.e., Aleocharinae, Oxytelinae, Osoriinae, Tachyporinae, and Xantholininae. There is an apparent high degree

of specificity among genera and species of Laboulbeniales parasitizing Staphylinidae and Frank's (1982) study should be consulted in this regard.

Members of subfamily Staphylininae sensu Frank (1982) serve as hosts for all species of *Diplomyces*, *Sandersoniomyces*, *Symplectomyces*, and *Teratomyces*. Blackwelder's (1952) Staphylininae included three tribes, Xantholinini, Staphylinini, and Quediini. Arnett (1961) retained only the Xantholinini and Staphylinini and placed the Quediini in the latter tribe as one of five subtribes, only three of which, Staphylinina, Oxygina, and Quediina, occur in the United States. Frank (1982) narrowed the concept of Staphylininae by recognizing a separate subfamily, Xantholininae, for the Xantholinini. His concept is the one adopted here. Insects of only two of the five subtribes of Staphylinini, Oxygina and Quediina, host all of the above genera of Laboulbeniales. Among the Oxygina two genera are hosts: *Erichsonius* Fauvel (*Teratomyces actobii* Thaxt. [1894], *T. brevicaulis* Thaxt. [1894], *Diplomyces actobianus*, and *D. clavifer* Rossi & Cesari-Rossi [1978]) and *Gabrieus* Curtis (as *Philonthus*) (*T. philonthi*). Among the Quediina three genera are hosts: *Acylophorus* Nordmann (*T. mirificus*); *Atanygnathus* Jacobson (*D. atanygnathi* Thaxt. [1931] and *T. atanygnathi* Thaxt. [1931]); and *Quedius* Stephens (*Sandersoniomyces divaricatus*, *Symplectomyces vulgaris*, *T. insignis* Thaxt. [1901], *T. petiolatus* Thaxt. [1901], *T. quedianus* Thaxt. [1896], and *T. zealandicus* Thaxt. [1901]).

Idiomyces peyritschii is found only on species of *Deleaster*. This genus is included by Arnett (1961) in subtribe Coprophilina of the Oxytelini, one of eight tribes of the subfamily Oxytelinae. The concept of this subfamily as treated by Arnett and Frank (1982) is more restricted than that of Blackwelder (1952) in that the latter's Oxytelinae is divided into five subfamilies of which four, Oxytelinae, Piestinae, Omaliinae, and Osoriinae, are known to include hosts of Laboulbeniales. This system essentially follows that of Crowson (1955) who places *Deleaster* in a separate tribe, Deleasterini, as does Hatch (1957). The Coprophilina of Blackwelder and Arnett includes 12 genera of which, in addition to *Deleaster*, only *Manda* Blackwelder (syn. *Acrognathus* Erichson) has a species, *M. mandibularis* (Gyllenhal), known to be a host of one of the Laboulbeniales, *Peyritschella protea* Thaxt. (1900), which also has been reported on species of *Anotylus* Thomson, *Bledius* Leach, *Oxytelus* Grav., and *Planeustomus* Jac. de Val of subtribe Oxytelina of the Oxytelini. As a genus, *Peyritschella* Thaxt. (1890) infects a broader spectrum of hosts than *Idiomyces*, and its species are known not only on other groups of Staphylinidae (suborder Polyphaga) but on Carabidae (suborder Adephaga) as well.

Among the Staphylinidae, Crowson (1955) regards the Staphylininae (including the Xantholininae as a tribe, Xantholinini) together with another subfamily, Paederinae, to be phylogenetically the most highly evolved groups in the family and not closely connected by transitional forms with the oth

er subfamilies. The larvae of Oxytelinae appear to be closely related to those of Aleocharinae and bear no special resemblance to those of Staphylininae s. l. (Böving and Craighead 1931). Paederinae and Staphylininae host 13 genera of Laboulbeniales, listed above, not found on any other group of insects, and the Oxytelinae are host to four such genera. Of 19 genera known not only on Staphylinidae but also on other families of insects as well, only two, *Laboulbenia* and *Peyritsiella*, have been confirmed on both Oxytelinae and Staphylininae. With regard to their laboulbeniaceus parasites, Oxytelinae and Staphylininae appear to have little in common, reflecting perhaps early divergence in the evolutionary history of these insect subfamilies and their parasites.

One must be cautious, however, in making taxonomic judgments based on host range in the Laboulbeniales. There are some genera, perhaps representing the most ancient lineages, that have developed a remarkable capacity for exploiting different host groups, e.g., *Dimeromyces* Thaxt. (1896), known on Acarina, Coleoptera, Dermaptera, Diptera, Hymenoptera, Isoptera, and Orthoptera; *Laboulbenia*, known on Acarina, Blattaria, Coleoptera, Diptera, Hemiptera, Hymenoptera, Isoptera, and Orthoptera; and *Rickia* Cava (1899), known on Acarina, Blattaria, Coleoptera, Diplopoda, Hymenoptera, and Orthoptera. One also must be aware of the possible spread of these parasites to unrelated host groups which happen to be closely associated in a very restricted environment. This undoubtedly has led to the occurrence of *Trenomyces* Chatton & Picard (1908) on such diverse insects as members of the Haematopinidae (Anoplura) (Benjamin unpubl.), Hippoboscidae (Diptera) (Bequaert 1953, 1957), and Laemobothriidae, Menoponidae, and Philopteridae (Mallophaga) (Chatton and Picard 1908; Eichler 1939, 1942, 1951; Thaxter 1912b, 1924) which are specialized ectoparasites of birds and mammals. Finally, survival and subsequent development of a fungus following its fortuitous transfer from one host to a wholly unrelated host in any environment must account for marked disjunctions in host range occasionally observed (Benjamin 1967), and this kind of dispersal probably has played a major role in the diversification of Laboulbeniales, at both the genus and species levels, on related as well as unrelated host groups. However, as in the Staphylinidae, most genera of Laboulbeniales are restricted to a single taxon or a few related taxa of hosts, e.g., *Coreomyces* Thaxt. (1902) on Corixidae (Hemiptera), *Herpomyces* Thaxt. (1902) on Blattaria, *Tettigomyces* Thaxt. (1915) on Gryllotalpidae (Orthoptera), and *Eucantharomyces* Thaxt. (1895) on Carabidae (Coleoptera); one genus, *Ilytheomyces* Thaxt. (1917), is found only on a single genus, *Ilythea* Curtis, of the Ephydriidae (Diptera). All of these genera are large enough in number of known species and are sufficiently widespread throughout the world to indicate that they do, indeed, have fixed host requirements.

The high degree of host specificity exhibited by so many genera of La-

boulbeniales occurring on Staphylinidae suggests that closely related genera may be expected to occur on closely related rather than on distantly related hosts, even within the same host family. With 14 taxa restricted to five allied genera of insects, *Diplomyces*, *Sandersoniomyces*, *Symplectromyces*, and *Teratomyces* exhibit a degree of host specificity suggesting that their presumed near relatives would also be found on similar hosts.

B. Ascospores

Ascospores of Laboulbeniales display a remarkable uniformity in shape and structure, being in all instances colorless, elongate, narrow, sometimes slightly rounded but mostly acute at both ends, and once septate. All are surrounded by a hyaline adhesive sheath that usually is more or less expanded at the foot-forming end of the spore. The position of the cross wall usually is off center with the longer cell directed towards the perithecial ostiole prior to spore discharge. In a few genera, i.e., *Ceratomyces* Thaxt. (1892), *Coreomyces*, *Rhynchophoromyces* Thaxt. (1908), and *Zodiomyces* Thaxt. (1891), the shorter of the two cells is uppermost prior to spore discharge (Thaxter 1896, 1908) and eventually forms the foot. The cross wall typically is transverse, although in some genera it may be slightly oblique, e.g., *Dioicomycetes* Thaxt. (1901, 1908, 1931). The adhesive sheath, except where enlarged distally at one end, usually is continuous around the spore, although in species of *Autoicomycetes* Thaxt. (1908) it may be constricted at the spore septum where it appears to be attached to the spore wall (Thaxter 1896, 1908). In some dioecious genera, e.g., *Dioicomycetes*, there is a marked difference in size of male and female spores, the latter being much the larger (Thaxter 1908; Benjamin 1970). In the first two parts of his monograph, Thaxter (1896, 1908) often figured ascospores and pointed out deviations from the norm as mentioned above. However, in the last three parts of his illustrated work (Thaxter 1924, 1926, 1931) ascospores rarely were figured separately and minor ascospore anomalies, if such existed, beyond those he had pointed out earlier were not discussed. Because in most genera of Laboulbeniales there is so little variation in the morphology of ascospores, other than size, spores have been little emphasized in the taxonomy of these fungi above the species level.

Ascospores of *Diplomyces*, *Sandersoniomyces*, and *Symplectromyces* (Fig. 26, 39, 45) lack any special modifications to set them apart from the spores of most other Laboulbeniales, at least as they have been described in the literature. In species of these genera the foot-forming cell is the longer of the two cells comprising the spore body; the spore septum is transverse; the cellular apices are acute; and the thin hyaline sheath is more or less expanded around the lower one fourth to one third of the spore. Ascospores of the known species of *Diplomyces*, *D. actobianus*, *D. atanygnathus*, and *D. clavifer*, based on study of specimens in my collection, differ from those of species

of the other genera being considered here in their slenderness, being about one half as wide.

The distinctive modifications of the tip of the foot-forming cell of the ascospores of *I. peyritschii* (Fig. 1, 25) and *T. mirificus* (Fig. 32) have not, as far as I am aware, been reported for any other genera of Laboulbeniales. A conspicuous subterminal constriction of the basal cell like that of *T. mirificus* also is characteristic of the taxon on *Philonthus* spp. earlier identified with *T. philonthi*. I have a number of collections referable to *T. actobii* and *T. brevicaulis* and have not found a similar obvious constriction of the lower cell of their ascospores. This phenomenon and its possible significance in the taxonomy of *Teratomyces* should be taken into account in future studies of the genus.

The hyaline end-piece terminating the truncate foot-forming cell of the ascospore of *I. peyritschii* apparently is unique in the Laboulbeniales. If this structure were correlated with early stages of spore germination, then similar structures surely would have been reported in other species. For the same reason, it probably is not associated with the formation of the often-observed more or less hyaline tip of the foot (Fig. 2–6, 27–29) in juvenile and adult individuals of other species (Benjamin 1968b, 1973, and unpublished).

C. Receptacle

Divisions of the lower segment of the ascospore give rise to the receptacle comprised, depending on the taxon, of a small, fixed number of cells, i.e., a determinate receptacle, or of a variable, often large number of cells, i.e., an indeterminate receptacle (Thaxter 1908). In the simplest type of determinate receptacle, the primary receptacle derived from the lower spore segment remains three celled; the lower cell (I) forms the foot, the suprabasal cell (II) gives rise to the perithecial branch, and the upper cell (III) subtends the primary appendage derived from the upper spore segment, e.g., *Stigmatomyces* (Thaxter 1908, 1931), *Haplomyces* (Thaxter 1896) and their allies. Exceptions are found in *Amorphomyces* and *Rhizopodomycetes* Thaxt. (1931) in which a cell III is not separated from cell II (Tavares 1970; Benjamin 1979). Determinate receptacles having more than three cells are not common. Thaxter (1908) made a case of *Ceratomyces* and *Autoicomyces* in which the primary receptacle consists of only three or four cells below the perithecium and appendage. The receptacle of most species of *Laboulbenia* (Thaxter 1896, 1908) consists of only five cells, designated by Thaxter with Roman numerals I to V. Cells I, II, and III correspond to those of the simple determinate receptacle as defined above; extra divisions of cell III give rise to cells IV and V which commonly parallel or are attached to the stalk cells of the perithecium derived from cell II. Thaxter used numerals VI and VII to designate the primary stalk cell and secondary stalk cells of the perithecium

of *Laboulbenia* and these numbers now are used, following Tavares (1970, 1973), for describing these perithecial cells in all members of the Laboulbeniales. In many species of *Laboulbenia*, especially some of those on Chrysomelidae (Coleoptera) and Diptera, cell III does not divide and the receptacle is like that of the simplest determinate type. In other species, however, e.g., *L. proliferans* Thaxt. (1908), *L. variabilis* Thaxt. (1908), etc., cells IV and/or V divide and form several additional cells and the receptacle becomes more or less indeterminate.

There are many kinds of indeterminate receptacles. In some, the perithecia and often secondary appendages arise directly from cells of a more or less elongate uniseriate axis, e.g., *Enarthromyces* Thaxt. (1896), *Filariomyces* Shanor (1952), *Hydrophilomyces* Thaxt. (1908); or multiseriate axis, e.g., *Euzodiomyces* (Thaxter 1900, 1908), *Zodiomyces* (Thaxter 1891, 1896). In others, an often small, sterile primary receptacle gives rise laterally to fertile secondary axes or receptacles, e.g., *Dimorphomyces* Thaxt. (1893, 1896, 1908, 1924), *Rhachomyces* Thaxt. (1895, 1896, 1908, 1931), *Herpomyces* (Thaxter 1908, 1931; Tavares 1965, 1966), *Monoicomycetes* (Thaxter 1908, 1931), and *Sympodomyces* Benjamin (1973). In still others, both the primary and secondary receptacles or axes give rise to perithecia, e.g., *Balazucia* (Benjamin 1968b) and *Cucujomyces* Speg. (1917; Thaxter 1931).

Receptacles of *Diplomyces*, *Sandersoniomyces*, *Symplectromyces*, and *Teratomyces* are indeterminate, but secondary development, including formation of perithecia and secondary appendages, is confined to a complex of cells derived from what can be interpreted as cell III of the primary receptacle, the lower cells being determinate in number and retaining their identity in the mature thallus. A fourth cell is added to the young primary receptacle by division of cell II (Fig. 28), but in none of these genera does a perithecium arise from either cell derived from cell II. Perithecial development from cell II is the rule in all genera having simple, determinate, two- or three-celled receptacles.

Thaxter (1908, 1931) regarded *Symplectromyces* as very closely related to *Teratomyces*. He originally had placed *S. vulgaris* in that genus (Thaxter 1900) but later (Thaxter 1908) separated it from *Teratomyces* because of its intercalary antheridia (compare Benjamin 1968a:Fig. 4D–F and 5G). The origin and arrangement of secondary appendages are similar in both genera, but, as noted by Thaxter (1896), the arrangement of appendages of *Teratomyces* spp. does not have the same appearance from all sides (Benjamin 1968a:Fig. 4A–C) as it does in *S. vulgaris* (Benjamin 1968a:Fig. 5H–I; Thaxter 1908:Pl. L, Fig. 14–16). There is in *Teratomyces* a hint of the kind of asymmetrical development of the upper receptacle that is so pronounced in *Diplomyces* (Fig. 46, 47) and *Sandersoniomyces* (Fig. 42–44).

Receptacular development is similar in *Diplomyces* and *Sandersoniomyces*. In species of both genera, cell III of the primary receptacle cuts off

a pair of anterior cells which in *Diplomyces* may give rise to perithecia, secondary appendages, and secondary cellular axes bearing both perithecia and secondary appendages (Benjamin 1968a:Fig. 3A-C); in *S. divaricatus* these cells give rise only to secondary cellular axes bearing perithecia and secondary appendages (Benjamin 1968a:Fig. 2A-B). In both genera the posterior cell subtends a small, sterile primary appendage. In *Sandersoniomyces* this cell undergoes no further development other than enlargement (Benjamin 1968a:Fig. 2B). In *D. actobianus* (Benjamin 1968a:Fig. 3B) and *D. atanygnathus* (Thaxter 1931:Pl. XLIII, Fig. 1) the cell gives rise to a pair of sterile upgrowths, whereas *D. clavifer* (Rossi and Cesari-Rossi 1978:Fig. 3-4) develops only one such upgrowth. The basal cell of *D. clavifer* also is distinguished by the formation of a single, large, clavate, externally blackened upgrowth, of specific importance only, similar to those found on a few species of several other genera, e.g., *Corethromyces* (Thaxter 1908, 1931), *Meionomyces* Thaxt. (1931), and *Misgomyces* (Thaxter 1931).

The receptacle of *Idiomyces peyritschii* is different in several ways from that of *Diplomyces*, *Sandersoniomyces*, *Symplectromyces*, and *Teratomyces* although in the three- and four-celled stages of development of the young receptacle there are similarities (compare Fig. 4-5, 27-28, and Thaxter 1896: Pl. X, Fig. 20) which suggest that these genera may be related. The primary receptacle of *I. peyritschii* consists of five rather than four cells, with three cells (Fig. 4, 5, 7) rather than two being derived from cell II (Fig. 27, 28). In *I. peyritschii* as in the other four genera, cell III proliferates (Fig. 8-11) and forms a cellular complex that gives rise to secondary appendages (Fig. 18-24). Although perithecia occasionally arise from these cells in *I. peyritschii* (Fig. 22-23), their production appears to be suppressed in favor of their development, along with secondary appendages, from cells of a second complex of fertile cells derived from cell II of the receptacle (Fig. 10, 11, 18-21). This might be interpreted as suggesting that phylogenetically *I. peyritschii* is more closely linked to an ancestor having a determinate receptacle with cell II-derived perithecia than are species of *Diplomyces*, *Sandersoniomyces*, *Symplectromyces*, and *Teratomyces*.

The occasional formation of perithecia by cells of the primary receptacular upgrowth in *I. peyritschii* may be in response to damage to or abortion of perithecia arising normally from cells of the secondary receptacular upgrowth. As noted earlier, 14 of 26 thalli bearing perithecia on the primary upgrowth showed clear evidence of damaged or aborted perithecia—often the first-formed—on the secondary upgrowth (Fig. 22, 23). In the specimen shown in Fig. 24, the two functional perithecia borne on the primary upgrowth are accompanied by two aborted perithecia on the secondary upgrowth. This may be only coincidental; on the other hand it may be a teratological phenomenon similar to others frequently encountered in the Laboulbeniales (see Balazuc 1976 and references therein).

D. Appendages and Antheridia

One or several appendages are found on all Laboulbeniales, although these structures may not be apparent on all mature specimens, and especially on the males of some dioecious species. In his general discussion of appendages, Thaxter (1896, 1908) distinguished two kinds, primary and secondary. The first is defined as having its origin from the upper spore segment of the ascospore, whereas the latter has some other origin, i.e., from cells of the receptacle or, in a few genera, from the perithecium.

Primary appendages may be sterile, as on females of dioecious species, or, as on monoecious species, be associated with the formation of antheridia. They may be one celled, e.g., *Rhizopodomycetes* (♀'s and ♂'s) (Benjamin 1979) and *Amorphomyces* (♂'s) (Thaxter 1908, 1931); two celled, e.g., *Dioicomyces* (♀'s) (Thaxter 1908, 1931) and *Nycteromyces* Thaxt. (1917) (♀'s and ♂'s) (Thaxter 1924); or several to many celled. Among the latter kinds are those lacking sterile outgrowths, other than the occasional spinose remnant of the spore apex, or branchlets and in which most cells above the basal cell produce antheridia, e.g., *Stigmatomyces* (Thaxter 1908, 1931), *Synandromyces* Thaxt. (1931), *Eucantharomyces* (Thaxter 1908, 1926), and *Haplomyces* (Thaxter 1896). This type of appendage is more or less determinate as regards a given species. Finally, there are more or less indeterminate, simple or branched, few- to many-celled primary appendages some cells or branches of which may give rise to antheridia, e.g., *Laboulbenia* (Thaxter 1896, 1908), *Corethromyces* Thaxt. (1892, 1908, 1931), and *Rhizomyces* Thaxt. (1896, 1908, 1931).

Secondary appendages are most commonly associated with the receptacle. They also may be sterile or fertile, one to many celled, and simple or branched. Simple, one-celled, sterile appendages are the rule in species of several genera including *Rickia* (Thaxter 1926), *Peyritschella* (Thaxter 1896), *Limnaiomycetes* Thaxt. (1900, 1908), *Chitonomyces* Peyritsch (1873; Thaxter 1896, 1924), and *Diaphoromyces* Thaxt. (1926). Genera with several- or multi-celled, simple or branched, sterile or antheridial secondary appendages include *Compsomyces* (Thaxter 1896), *Coreomyces* (Thaxter 1908, 1931), *Cucujomyces* (Thaxter 1931), *Dimeromyces* (Thaxter 1924), *Histeridomyces* Thaxt. (1931), *Rhachomyces* (Thaxter 1896, 1908, 1931), *Sympodomycetes* (Benjamin 1973), *Trochoideomyces* Thaxt. (1931), and several others. In genera of Euceratomycetaceae (Tavares 1980), i.e., *Cochliomyces* Speg. (1912; Thaxter 1931), *Colonomyces* Benjamin (1955), *Eucratomyces* (Thaxter 1931; Tavares 1980), *Euzodiomyces* (Benjamin and Shanor 1951; Thaxter 1908), and *Pseudoecteinomyces* Rossi (1977), the stalk cells of the perithecium are intercalary cells of secondary appendages.

Secondary appendages on perithecia always are sterile and may serve as trigger organs involved in spore discharge. They may be unicellular, e.g.,

Zodiomyces (Thaxter 1896) and *Eusynaptomyces* Thaxt. (1931), or multicellular and branched or unbranched, e.g., *Autoicomyces* (Thaxter 1896 [as *Ceratomyces* in part], 1908, 1931), *Ceratomyces* (Thaxter 1896, 1908, 1931), and *Synaptomyces* Thaxt. (1931).

Primary appendages of *Diplomyces*, *Sandersoniomyces*, *Symplectromyces*, *Teratomyces*, and *Idiomyces* all are more or less branched and multicellular. Some branches of the primary appendage of *Symplectromyces vulgaris* definitely form seriate antheridia (Fig. 30–31) like those of the secondary appendages of this species (Benjamin 1968a:Fig. 5G). Antheridia were not observed on primary appendages of species of the other genera, and I suspect that they are sterile. However, this still must be confirmed or denied for species of *Diplomyces*, *Sandersoniomyces*, and *Teratomyces*. The absence of antheridia on primary appendages of any of the intact juveniles of *I. peyritschii* that I studied (Fig. 8–11) indicates that this appendage in this species is indeed sterile.

Well-developed, multicellular, usually branched, fertile secondary appendages are characteristic of the above five genera. The relationship of these appendages to the primary appendage and/or secondary receptacles or secondary cellular axes of these taxa already has been discussed. A close relationship between *D. actobianus*, *D. clavifer*, and *S. divaricatus* is indicated by the similarity of their secondary appendages (compare Fig. 2D–F and 3D in Benjamin 1968a and Rossi and Cesari-Rossi 1978, Fig. 3–4) and receptacles. In all these species, this appendage consists of a single basal cell bearing, externally, a usually three-celled, sterile, beaked branchlet and, internally, several branchlets forming series of intercalary antheridia resembling those of the appendages of *Symplectromyces vulgaris* (Benjamin 1968a: Fig. 5G). The elongate, simple or branched appendages of *S. vulgaris*, however, never bear beaked sterile branchlets (Benjamin 1968a:Fig. 5H–I). In this connection it should be noted that the secondary appendages of *D. atanygnathus*, as described by Thaxter (1931:173, Pl. XLIII, Fig. 1), are not like those of the other two species of this genus and would seem to resemble more closely those of *Symplectromyces*. This also is suggested by specimens referable to *D. atanygnathi* from the Philippines in my collection (RKB 799). In its perithecial and ascospore characteristics and furcillate receptacular upgrowths, however, *D. atanygnathi* more closely resembles the other species of *Diplomyces*.

Secondary appendages of *T. mirificus* (Benjamin 1968a:Fig. 4D–F) become sympodially branched and bear both free antheridia (phialides) and sterile branchlets with beaked terminal cells. Secondary appendages of all other species of *Teratomyces* (Thaxter 1896, 1908, 1931) are similar in their construction except perhaps for *T. philonthi* (Thaxter 1908). Thaxter's description of this species does not mention and his figures of it do not show phialidelike antheridia, nor does the photograph of it published recently by

Rossi and Cesari-Rossi (1978:Fig. 9). Instead, the appendages as Thaxter depicts them and as they are shown by the Rossi photograph appear to be separated into short cells many of which are separated by diagonal, darkened septa. This construction is like that of the appendages of specimens in the series of collections on *Philonthus* in my collection which in a previous section of this paper was tentatively referred to *T. philonthi*. This taxon lacks free phialides; instead the antheridia develop directly from intercalary cells as in *Symplectromyces*. *Teratomyces philonthi* may represent a form linking *Symplectromyces* and other *Teratomyces* spp. Likewise, *D. atanygnathi* may be a link between *Symplectromyces* and other species of *Diplomyces*.

Secondary appendages of *I. peyritschii* may be branched or unbranched. They often have one or more elongate, cellular branchlets arising from basal and distal cells with each cell in between delimiting two or three simple, sessile, adnate antheridia placed side by side and separated from the mother cell by broad septa. The manner in which antheridia are formed in this species recalls that of *Stigmatomyces* (Thaxter 1908, 1931), and on this basis alone Thaxter (1896) suggested near relationship between *Idiomyces* and *Stigmatomyces* despite the marked differences in their receptacles and the origin of their appendages, i.e., primary in *Stigmatomyces* vs. secondary in *Idiomyces*. In 1908, Thaxter speculated that *Idiomyces* might be a transitional type between *Stigmatomyces* and *Teratomyces* and its allies. On the basis of some similarities in their receptacles and the positioning of secondary appendages and perithecia, *Idiomyces* may be distantly related to *Teratomyces*, *Symplectromyces*, *Diplomyces*, and *Sandersoniomyces*, but a relationship between these five genera and *Stigmatomyces* must at best be remote.

E. *Perithecia*

Perithecial development in the five genera discussed in this paper is like that of all members of suborder Laboulbeniineae (Thaxter 1908) in which the walls of the perithecium grow up and around the carpogonium which is derived from a preexisting initial (Tavares 1977, 1980) in contrast to members of suborder Herpomycetinae (Tavares 1981) in which the first wall cells are developed prior to formation of the carpogonial initial which grows upward between the surrounding wall cell rows. Perithecial development has been described for a number of genera of Laboulbeniineae, e.g., *Balazucia* (Benjamin 1968b), *Eucratomyces* (Tavares 1980), *Filariomyces* (Shanor 1952), *Laboulbenia* (Benjamin and Shanor 1950; Thaxter 1896), *Peyritschella* (Thaxter 1896), *Rhizopodomycetes* (Benjamin 1979), *Stigmatomyces* (Thaxter 1896), and *Symplectromyces* (Benjamin 1968a).

Despite their often varying length and spatial separation from the asciger-

ous part, i.e., body of the perithecium, the primary and secondary stalk cells, VI and VII respectively, are regarded as integral parts of the perithecium as a whole (Thaxter 1896). The length of these cells may vary depending on the species and even within a given species. In many Laboulbeniales the stalk cells are small and relatively inconspicuous, whereas in others they—especially cell VI—may elongate and form a well-defined pedicel which elevates the body some distance above the level of the receptacle.

The three perithecial basal cells, *m*, *n*, and *n'*, give rise to the four rows of perithecial wall cells and typically enclose the lower part of the ascigerous cavity in most Laboulbeniales. In a few genera the basal cells and stalk cells become disorganized, in part, as the perithecium matures, and the ascigerous cavity becomes continuous with that of the primary stalk cell, e.g., *Dimeromyces* (Thaxter 1896, 1924, 1926), *Euphoriomyces* Thaxt. (1931), and *Trenomycetes* (Thaxter 1924). Basal cell *m* arises from the primary stalk cell, whereas cells *n* and *n'* arise from the secondary stalk cell. Thus, the lower part of cell *m* may more or less parallel cell VII and in species having well-defined perithecial stalks may contribute significantly to the overall length of the pedicel, as in *I. peyritschii* (Fig. 17, 22) and *S. vulgaris* (Benjamin 1968a:Fig. 51).

The stalk and basal cells of *Diplomyces*, *Sandersoniomyces*, *Symplectromyces*, *Teratomyces*, and *Idiomyces* persist and are well defined in age, and the perithecia of all species of these genera are pedicellate. Perithecial stalks of *Diplomyces* spp., *Sandersoniomyces divaricatus*, and six species of *Teratomyces* are relatively short compared to the total length of the perithecium. Short pedicels may prove to be characteristic of the perithecia of *Diplomyces* and *Sandersoniomyces*, but too few species of these genera are known to make one really confident of such a generalization in view of the variation in length of the primary stalk cell of three species of *Teratomyces*, i.e., *T. mirificus* (Benjamin 1968a; Thaxter 1896), *T. petiolatus* (Thaxter 1908), and *T. insignis* (Thaxter 1908). Of the known *Teratomyces* species, only *T. petiolatus* has enlarged basal and secondary stalk cells that approach those of *Symplectromyces vulgaris* in size compared to the perithecial body. In both of these species the combined length of these cells may equal one half or more of the length of the latter, and in the case of *S. vulgaris* one half or more of the length of the pedicel may consist of the combination of cells *m* and VII. *Idiomyces peyritschii* appears to be unique among known Laboulbeniales in regard to the length of basal cell *m* relative to the rest of the perithecium. The length of the entire perithecial body including basal cells *n* and *n'* often is less than that of cell *m* (Fig. 17), and like *S. vulgaris* up to one half of the length of the perithecial stalk of *I. peyritschii* may consist of the combination of cells *m* and VII (Fig. 21, 22, 24).

The outer walls of the perithecial body of all taxa belonging to *Diplomyces*, *Sandersoniomyces*, *Symplectromyces*, *Teratomyces*, and *Idiomyces* consist

of four nearly vertical rows of four cells each. Except for *I. peyritschii* and *Symplectromyces vulgaris*, cells comprising the basal and subbasal tiers of wall cells in species of these genera are subequal in length and typically constitute from 80 to 85 percent of the total length of the ascigerous cavity. This proportion of the total length of the perithecial body also is characteristic of *S. vulgaris*, but the basal tier of wall cells in this species is about 20% longer than the subbasal. Cells of the subterminal tier range from two times to only slightly longer than those of the upper tier which always are very small and surround a strictly terminal ostiole in all cases. There are no perithecial appendages, but the upper margins of the terminal cells usually bear a small, rounded, divergent median protrusion. The trichogyne scar always lies slightly below the perithecial apex either near the base of a terminal cell or near the upper end of a subterminal cell, and it sometimes straddles the juncture between neighboring cells. Its position appears always to be the same for perithecia of a given species based on those I have studied.

The complement of ascogenic cells in the several species examined was determined by counting the number of well-developed and separated centers of ascus production (see Thaxter 1896, Pl. I, Fig. 38–39) visible in several mature perithecia. Large perithecia of *Symplectromyces vulgaris* contained eight ascogenous cells whereas small perithecia contained only four; perithecia of this species with six ascogenous cells were not found. Perithecia of *T. mirificus*, *T. cf. philonthi*, *Diplomyces actobianus*, and *Sandersoniomyces divaricatus* had only two ascogenous cells, a condition common to species of many genera of Laboulbeniales (Thaxter 1896). Whether or not any phylogenetic significance can be attached to ascogenic cell number is uncertain; the number of these cells in the perithecium of a given species may be influenced simply by constraints imposed by size or even by age (Tavares 1973).

Unlike the usually elongate, slender perithecia of *Teratomyces* and its allies, the perithecia of *I. peyritschii* are comparatively short and stout. Cells of the lowermost tier of wall cells are considerably larger and often 30 to 40 percent longer than those of the subbasal tier (Fig. 17). However, the upper two tiers are relatively short, and the lower two tiers constitute at least three fourths of the total length of the perithecial body. The subterminal tier of cells is about twice as long as the terminal tier, and apparently the subterminal cell of the row of wall cells derived from basal cell *m* always subtends the trichogyne scar. Four ascogenic cells appear to be the usual number formed in perithecia of this species as earlier noted by Thaxter (1896).

CONCLUSIONS

1. Previous speculations allying *Symplectromyces*, *Teratomyces*, *Sandersoniomyces*, and *Diplomyces* (Benjamin 1968a; Thaxter 1908) remain un-

altered. All members of these genera have in common (1) a similar type of indeterminate receptacle consisting initially of four superposed cells in which only the upper cell, corresponding to cell III of a simple determinate receptacle, becomes further divided and gives rise to secondary appendages and perithecia, (2) similar perithecia formed in progression, and (3) closely related hosts.

2. Of these genera, *Symplectromyces* is perhaps the most primitive in having (1) secondary appendages lacking specialized sterile branchlets, (2) antheridia formed by direct transformation of appendage cells and developed by both primary and secondary appendages, and (3) cells of the lower tier of outer wall cells somewhat longer (ca. 20%) than those of the subterminal tier.

3. *Teratomyces* is near *Symplectromyces* in the structure of its receptacle and the manner of origin of its secondary appendages and perithecia. In the formation of free phialides by most species, *Teratomyces* appears to represent a well-defined and divergent line of evolution away from the other genera. However, a connection with *Symplectromyces* is suggested in that at least one species of *Teratomyces* may intergrade with that genus in its antheridial characteristics.

4. *Sandersoniomyces* and *Diplomyces* are probably the most highly evolved and the most closely allied of the four genera in view of their similar appendages and the precise manner in which the upper cells of the receptacle give rise to a reduced number of cells bearing perithecia, secondary appendages, and secondary fertile axes. Both genera have retained antheridial characteristics like those of *Symplectromyces*.

5. The gap between *Idiomyces* and the other four genera listed above probably is great enough to preclude near relationship between them. The distinctive hosts of *I. peyritschii* are not closely related to those of the other genera. Early divergence of these genera from a common ancestor is suggested, however, by similarities in early stages of receptacular development, especially as observed in *I. peyritschii* and *S. vulgaris*, but the mature receptacle of *I. peyritschii* is distinct in its type of asymmetrical development and in the origin of secondary appendages from both cells II and III of the primary receptacle. Perithecia of *I. peyritschii* typically arise progressively from progeny of cell II rather than cell III of the primary receptacle as in *Symplectromyces* and its allies; those perithecia that do develop on cells derived from cell III appear to be the result only of a teratological phenomenon.

6. Although Thaxter (1908) misinterpreted the structure of the receptacle and primary appendage of *I. peyritschii*, his placement of the genus in a tribe, Idiomycetaceae, separate from the Teratomycetaceae (for *Symplectromyces*, *Teratomyces*, and *Diplomyces*) is supported by my observations.

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