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LABOULBENIALES ON SEMIAQUATIC HETEROPTERA. VI. THE GENUS *TAVARESIELLA*

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ABSTRACT

Majewski's original circumscriptions of *Tavaresiella* (Laboulbeniales; Laboulbeniaceae; Stigmatomycetinae) and its type species, *T. hebri,* were emended in this study of the genus. In addition, three new species were described, *T. majewskii, T. polhemi,* and *T. santamariae.* These, like the type species, occurred on true bugs of the family Hebridae (Heteroptera). A key to the species was provided, and all were described and illustrated with line drawings and photographs. Aspects of ascomatic structure and development were summarized, and the genus was compared with other genera of the subtribe having similar characteristics.

Key words: Ascomycetes, fungi, Hebridae, *Hebrus,* Heteroptera, insects, Laboulbeniales, morphology, *Tavaresiella,* taxonomy, *Timasius.*

INTRODUCTION

Tavaresiella, named for the well-known student of Laboulbeniales, Isabelle Tavares, was established by Majewski (1981). The type species, *T. hebri* Majewski, was collected in Poland and is said to parasitize both *Hebrus ruficeps* Thomson and *H. pusillus* (Fallén) (Heteroptera: Hebridae). Majewski (1981) suggested that the genus appears most closely related to *Sphaleromyces* Thaxt. (1894). In her book on the Laboulbeniales, Tavares (1985), while noting distinct differences in the structure of their appendages, also allies *Tavaresiella* with *Sphaleromyces* on the basis of antheridial characteristics and similarities in perithecial structure. She includes *Tavaresiella* in subtribe Stigmatomycetinae (Laboulbeniaceae; Laboulbenieae). Santamaria (1993) also reports *Tavaresiella hebri* on collections of *H. pusillus* in Spain. Neither Majewski (1981) nor Santamaria (1993) provided information on early development of the ascoma in *Tavaresiella,* especially the nature of the appendage.

I have acquired several unidentified Tavaresiellas on Hebridae collected in Indonesia and Madagascar by Drs. J. T. and D. A. Polhemus. In addition, Dr. Majewski sent me specimens of *T. hebri* on *H. ruficeps* from Poland, and Dr. Santamaria contributed specimens of his collections identified as *T. hebri* on *H. pusillus* from Spain. Based on my study of these collections of *Tavaresiella,* my purposes here shall be the following: (1) to present emended descriptions of the genus and the type species, *T. hebri*; (2) to describe three new species; (3) to illustrate all of the taxa with line drawings and photographs; (4) to provide a key for their identification; and (5) to comment on aspects of morphology and development.

MATERIALS AND METHODS

Material received from Drs. Majewski and Santamaria already had been mounted on microscope slides. All other specimens studied in this work were found on

insects that had been stored in 70–80% ethyl alcohol. The fungi were carefully removed from their hosts and mounted in glycerine on slides by a technique given previously (Benjamin 1986:247 [modified by substituting PERMOUNT® (Fisher Scientific, Fair Lawn, N.J. 07410), for COVERBOND® as the sealant and ringing the cover glass with clear plastic nail protector]).

A Leitz Dialux microscope equipped with differential interference contrast optics was used for making all observations and, with the aid of a camera lucida, for preparing drawings. Photographs were taken on 4 in. × 5 in. Kodak Technical Pan Film #4415. The camera was a WILD 15/11 Semiphotomat with an ASA setting of 100. The film was developed for 6 minutes in Kodak HC-110, Dilution B, at 20 C.

Terminology and abbreviations used in describing the ascomata are defined in the text, and with few exceptions are those of Tavares (1985:431–434). Because of their bilateral symmetry, the ascomata of these fungi typically are oriented in slide mounts so that they can only be viewed laterally; thus, the descriptions are based on observations of ascomata as seen from one side or the other. With reference to the perithecium and receptacle, anterior is in the direction away from the appendage whereas posterior is in the direction towards the appendage. With reference to cells of the receptacle, stalk and basal cells of the perithecium, and cells of the appendage, inner is in the direction of the mid axis of the ascoma, outer is in the direction away from the mid axis.

TAXONOMY

TAVARESIELLA Majewski, Acta Mycol. 16:147, 1981, emend. R. K. Benj.

Receptacle consisting of three cells; the basal cell (I) posteriorly and obliquely separated from the suprabasal cell (II); the terminal cell (III), which may or may not be in contact at its base with cell I, united internally, at least in part, with cell II, with which it is more or less parallel, and often in contact distally on the inside with the base of the primary stalk cell (VI) of the perithecium. Primary appendage, subtended by cell III, consisting of a short appendage, which bends outward and produces on the inner side of its basal cell an erect branch that forms many short lateral branchlets; the outer branch simple, composed of a small number of superposed cells, one proximal cell often spinose; the inner branch consisting of a single cell or a series of superposed cells, which give rise externally to a succession of simple or branched branchlets in which the terminal cell or one or more intercalary cells may form simple antheridial phialides. Perithecium, subtended by cell II, with well-defined stalk and basal cells, and four vertical rows of outer wall cells of five cells each.

Type species.—*Tavaresiella hebri* Majewski.

A KEY TO THE SPECIES OF *TAVARESIELLA*

A. Basal cell of receptacle forming a prominent, elongate, more or less opaque spur that extends upward beyond the base of the appendage ..... B
– Basal cell of receptacle without a spur (on *Timasius*) ..... (4) *T. polhemi*
B. Axis of inner branch of appendage consisting of several superposed cells that are of nearly the same length; each cell bearing (1–)2(–3) branchlets on the outside; perithecial stalk cell elongate, free except near the base on the inside (on *Hebrus*) ..... (2) *T. santamariae*

- Axis of inner branch of appendage consisting of a single cell bearing a succession of ± divergent branchlets on the outside C

C. Perithecial stalk cell (VI) barely free distally, otherwise adnate internally to basal cell of appendage (on *Hebrus*) ..... (1) *T. hebri*

- Perithecial stalk cell (VI) wholly adnate on the inside to the upper nearly one half of cell III of the receptacle and enclosed on the outside by the secondary stalk cell (VII) (on *Timasius*) ..... (3) *T. majewskii*

(1) TAVARESIELLA HEBRI Majewski, Acta Mycol. 16:148, 1981, emend. R. K. Benj. Fig. 1–8, 30

Ascoma: Nearly straight; hyaline, except for the pale brown-orange perithecial venter, in which the posterior surface becomes more deeply suffused than the anterior, and except for the small, opaque foot and the ± opaque projection arising from the basal cell of the receptacle. Total length from tip of foot to tip of perithecium 70–105 μm. *Receptacle*: Triangular, 19–25(–28) μm high, broadest above, 11–15(–19) μm wide, tapered downward to the acute tip of the foot; the basal cell (I) small, 9–11 × 5–7 μm, subtending the suprabasal cell (II), from which it is separated by an oblique septum, and the terminal cell (III), and bearing a free, elongate, nearly straight, apically rounded, externally opaque projection 16–30 × 2–3 μm, which extends upward alongside cell III beyond the basal cell of the primary appendage; cells II and III parallel to one another; cell II oblong, usually slightly more than twice as long as wide, 10–16(–18) × 5–7(–8) μm, subtending the stalk cell of the perithecium; cell III triangular, 10–16 μm long, 6–11 μm wide distally, separated above from the basal cell of the appendage by a transverse or ± oblique septum and, on the inside, barely contacting the base of the perithecial stalk cell. *Appendage*: Basal cell about as long as wide, 7–9 × 6–10 μm, ± pentagonal, separated from the persistent, somewhat smaller lowermost cell of the outer branch by a diagonal cross wall; inner branch consisting of a single elongate cell, 11–18 × 3.5–4 μm, giving rise on the outside to a succession of 5–8 branchlets consisting of single elongate cells forming simple antheridia directly or 2–3(–4) superposed cells in which the terminal cell often forms an antheridium; the distal branch usually in line with the proximal cell and slightly curved inward towards the perithecium; proximal cell together with the terminal branch forming an axis 25–50 μm long; antheridia straight or slightly curved, 7–10 × 2.5–3 μm. *Perithecium*: Primary stalk cell (VI) relatively short, only slightly longer than broad, 10–15(–17) × 8–12(–15) μm, its inner margin ± adnate to the basal cell of the appendage, its outer margin slightly rounded; secondary stalk cell (VII) somewhat smaller than and lying above cell VI on the outside, isodiametric, 6–10(–12) × 7–10(–12) μm, enclosed on the inside and above by the perithecial basal cells (*m, n, n'*), which, along with cell VII, constitute only ca. 20–22% of the total length of the body of the perithecium above cell VI; basal cells only slightly enveloping the base of the ascigerous cavity; body, including basal cells, 43–60(–68) μm long, ± uniformly inflated, broadest near the middle, 15–22(–28) μm wide, tapered to the undistinguished narrow apex, which is defined by the rounded tips of the terminal wall cells. Ascospores hyaline, 17–18 × 2 μm.

Specimens examined.—POLAND. Włocławek Prov.; Długie, near Izbica Kujawska, 22 May 1976, on *Hebrus ruficeps*, leg. Tomasz Majewski (isotype: *Ma-*

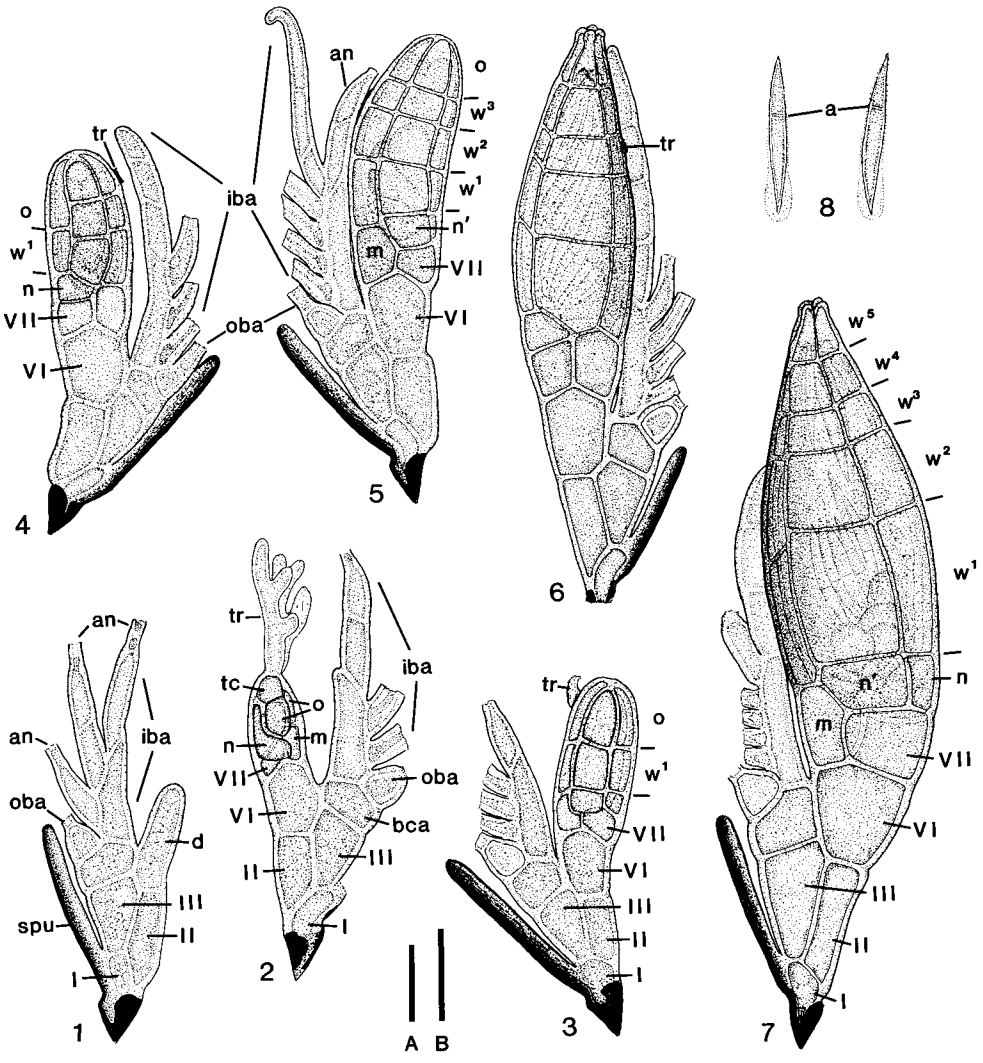

Fig. 1–8. *Tavaresiella hebri* (Fig. 1, 4, 5: *Majewski 4929*; Fig. 2, 3, 6–8: *Majewski 4929a*).—1–5. Juvenile individuals showing several stages of development of the appendage and perithecium. Details and terminology are given in the text.—6–7. Two mature individuals (see also Fig. 30). The position of the trichogynic remnant (*tr*) is shown in Figure 6. Figure 7 shows the relationship of the cells of the receptacle (I, II, III), the perithecial stalk cells (VI, VII), the perithecial basal cells (*m, n, n'*), and the five tiers of outer wall cells (w^{1-5}).—8. Two ascospores. (Fig. 4–7: bar A = 10 μm; Fig. 1–3, 8: bar B = 10 μm.)

jewski 1594; Majewski collection); Leszno Prov.; Turew, 26 Jun 1990, on *H. ruficeps*, leg. Tomasz Majewski (*Majewski 4929, 4929a*).

My emended characterization of *T. hebri* is based on the specimens, mounted on two slides, which were received from Dr. Majewski (*4929, 4929a*) in 1991. This material, taken from the same host, *H. ruficeps*, as the type specimen (Majewski 1981, Fig. 3*a*), included 24 mature, two nearly mature, and 10 immature individuals. Majewski (1981, Fig. 3*e*) provides a sketch of only one mature individual of the form on *H. pusillus*. Dr. Santamaria sent me two slides bearing

the fungus he collected on *H. pusillus* in Spain, which he identified as *T. hebri* (Santamaria 1993). There were 13 mature, two nearly mature, and one immature individuals. These appear to be identical to the form found by Majewski in Poland on *H. pusillus.*

My comparison of the *Tavaresiella* specimens from *H. ruficeps* with those on *H. pusillus* (cf. Fig. 30 and 33) convinces me that they are not conspecific; accordingly, I am restricting the concept of *T. hebri* to the form on *H. ruficeps.* The form on *H. pusillus,* which Majewski included in his protolog of *T. hebri,* is regarded as conspecific with Santamaria's collections from Spain (Fig. 33) and those on other *Hebrus* spp. from Indonesia (Fig. 31) and Madagascar (Fig. 32) described below as *T. santamariae.*

The inner branch of the appendage of *T. hebri* differs significantly from that of *T. santamariae* in consisting of a relatively greatly elongate cell, which may bear, in succession, as many as eight branchlets. In a mature individual of *T. hebri* the distal branchlet of the series of branchlets formed by the elongate cell does not deflect outward but remains more or less in line with the elongate cell (Fig. 6, 7). Thus, the terminal branchlet together with the elongate cell resembles the axis of the inner branch of *T. santamariae.* However, in *T. santamariae,* the axis of the inner branch of the appendage may consist of a series of up to at least 10 superposed cells all of which, including the proximal, are only about twice as long as wide and each cell bears usually only one or two, rarely three, branchlets (Fig. 13, 14). The primary stalk cell of the perithecium of *T. hebri* is relatively short and adnate to the basal cell of the appendage except distally where it may be more or less free (Fig. 6, 7), whereas in *T. santamariae* the stalk cell is more or less elongate and free from the basal cell of the appendage except near the base (Fig. 13, 14). Also, in *T. hebri* the perithecium below the tip and above the basal cells is much more darkly pigmented on the posterior surface than the anterior, whereas in *T. santamariae* the perithecium below the pale, nearly hyaline tip is more or less uniformly pigmented above the basal cells.

(2) **Tavaresiella santamariae** R.K. Benj., sp. nov. Fig. 9–15, 31–33

Ascoma prope rectum vel paulo geniculatum, tota 80–110 μm longum ad apicem perithecii. *Receptaculum* triangulare 18–24 μm altum latitudine distali 11–14 μm; cellula I parva 10–13 × 5–7 μm, pede opaco et appendici postica plus minusve opaca recta vel paulo curvata 18–25 × 2.5–3 μm; cellula II elongata 11–16 × 5–7 μm; cellula III triangularis vel quadrangularis 7–11 × 6–8 μm. *Appendix*: Cellula basalis plus minusve pentagona 5–7 × 7–10 μm; ramus externus simplex curtus saepe effractus supra cellulam infimum; ramus internus simplex vel ramosus in parte distalem 40–85 μm longus; axis rami interioris cellulae 5–10 superpositae 7–11 × 5–6 μm constans; cellulae axis (1–)2(–3) ramulos gignentes; ramuli 15–35 × 3–4 μm cellularum (1–)2–3(–4) constantes; antheridia liberum vel intercalarium 8–14 × 3–4 μm. *Perithecium* uniformiter inflatum externe convexum 61–93 μm longum; cellula VI prope libera 13–26 × 6–7 μm; cellula VII 9–15 × 7–12 μm; corpus 50–65 μm longum 15–23 μm latum in mediano attenuatum, supra cellulam basale praeter apicem hyalinum dilutum aurantiacum-luteum. *Ascosporae* hyalinae 17–22 × 2 μm. Typus *RKB 3567B*; RSA.

Ascoma: Hyaline except for the body of the perithecium, which is uniformly pale orange-yellow from above the basal cells to near the hyaline tip, and except for the small opaque foot and the ± opaque projection arising from the basal cell of the receptacle; nearly straight or slightly geniculate. Total length from tip of foot to tip of perithecium 80–110 μm. *Receptacle*: Triangular, 18–24 μm high, broadest above, 11–14 μm wide, tapered downward to the acute tip of the foot; the basal cell (I) small, 10–13 × 5–7 μm, subtending the suprabasal cell (II), from

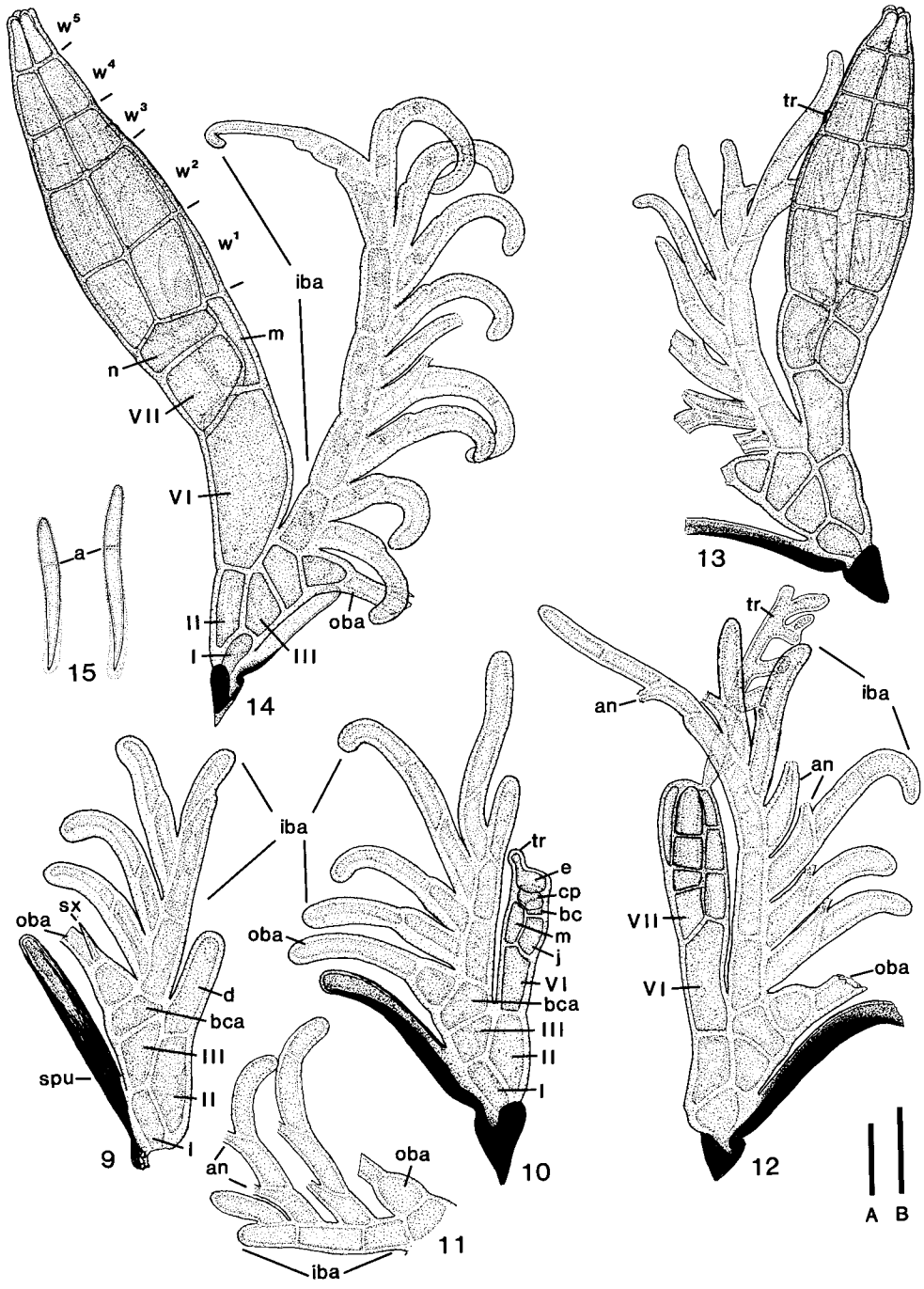

Fig. 9–15. *Tavaresiella santamariae* (Fig. 9: *RKB 3568C* [Madagascar]; Fig. 10–13, 15 [left] *RKB 3567B* [Madagascar]; Fig. 14, 15 [right]: *RKB 3561* [Flores Island]).—9, 10, 12. Juvenile individuals showing several stages of development of the appendage and perithecium. Details and terminology are given in the text.—11. Young appendage showing the persistent lowermost cell of the broken outer branch (*oba*) and four intercalary antheridia formed by cells of branchlets of the inner branch (*iba*).—13–14. Two mature individuals (see also Fig. 31–33). The position of the trichogynic remnant (*tr*) is

which it is separated by an oblique septum, and the terminal cell (III), and bearing a free, elongate, straight or slightly curved, apically rounded, ± externally opaque projection 18–25 × 2.5–3 μm, which extends upward alongside cell III well beyond the level of the basal cell of the primary appendage; cells II and III parallel to one another; cell II elongate, oblong, usually slightly more than twice as long as wide, 11–16 × 5–7 μm, subtending the stalk cell of the perithecium; cell III triangular or ± quadrangular, 7–11 × 6–8 μm, separated above from the basal cell of the appendage by a transverse or ± oblique septum and, on the inside, not or barely contacting the base of the perithecial stalk cell. *Appendage*: Basal cell slightly shorter than wide, ± pentagonal, 5–7 × 7–10 μm, separated from the persistent, somewhat smaller lowermost cell of the outer branch by a diagonal cross wall; inner branch usually ± curved, 40–85 μm long, simple or branched distally, consisting of an axis of 5–10 superposed, subequal cells, which are about twice as long as wide, 7–11 × 5–6 μm, each cell of the axis bearing externally (1–)2(–3) ± recurved branchlets, 15–35 × 3–4 μm, consisting of (1–)2–3(–4) cells, the lowermost one or two cells of which may develop into simple antheridia with short, upwardly directed efferent tubes; antheridia 8–14 × 3–4 μm. *Perithecium*: Primary stalk cell (VI) about twice as long as wide, 13–26 μm long, 6–7 μm wide at the base, 8–14 μm wide distally, free except near the base where it is adnate to the basal cell of the appendage and the base of the lowermost cell of the inner branch of the appendage; secondary stalk cell (VII) smaller than and lying above cell VI on the outside, nearly isodiametric, 9–15 × 7–12 μm, enclosed on the inside and above by the perithecial basal cells (*m, n, n'*), which, along with cell VII, constitute only ca. 25% of the total length of the body of the perithecium above cell VI; basal cells only slightly enveloping the base of the ascigerous cavity; body, including basal cells, 50–65 μm long, ± uniformly inflated, broadest near the middle, 15–23 μm wide, tapered to the undistinguished narrow apex, which is defined by the rounded tips of the terminal outer wall cells. Ascospores hyaline, 17–22 × 2 μm.

Etymology.—Named for Sergio Santamaria, Spanish student of Laboulbeniales.

Type.—MADAGASCAR. Majunga Prov.; 113 km E of Majunga, Ampijora Forest Station, 76 m, 21 Nov 1986, J. T. & D. A. Polhemus (CL 2283), on legs of *Hebrus isaloi* Poisson (holotype: *RKB 3567B*; RSA [designated slide]; isotype: RSA).

Other specimens examined.—MADAGASCAR. Data as for the holotype (*RKB 3568C*; RSA).—INDONESIA. FLORES ISLAND: Nusa Tenggara River, 6 km W of Tuteng, 1100 m, 24 Oct 1985, J. T. & D. A. Polhemus (CL 2179), on femora of right anterior and middle legs of *Hebrus* sp. (*RKB 3561*; RSA).—SPAIN. Mura (Barcelona), 19 Jun 1991, S. Santamaria coll., on abdomen of *Hebrus pusillus* (*BCB-SS-1051*); Sant Sebastià de Montmajor (Barcelona), 4 Nov 1992, S. Santamaria coll., on abdomen of *H. pusillus* (*BCB-SS-1556*).

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shown on Figure 13. Figure 14 shows the relationship of the cells of the receptacle (I, II, III), the perithecial stalk cells (VI, VII), the perithecial basal cells (*n* and *m* [*n'* is on the far side]), and the five tiers of outer wall cells (w^{1-5}).—Fig. 15. Two ascospores. (Fig. 13–14: bar A = 10 μm; Fig. 9–12, 15: bar B = 10 μm.)

As indicated above under *T. hebri,* features that readily separate *T. santamariae* from the former include the more or less elongate, nearly free perithecial stalk cell, perithecial pigmentation, and especially the structure of the inner branch of the appendage. In *T. santamariae,* the cells composing the axis of the inner branch, including the proximal, are of nearly the same length, and each of these cells bears one to three, usually only two, lateral branchlets. Also, in *T. hebri* the elongate cell bearing up to at least eight branchlets is terminated by a branchlet that does not become deflected outward, but forms an in-line extension of the elongate cell. In *T. santamariae,* antheridia may be single and sessile or, more commonly, they develop from the basal cell, and sometimes the suprabasal cell, of the lateral branchlets and have upwardly directed tips (Fig. 11–14). In *T. hebri,* antheridia have been observed in only a few instances. They, too, may be single and sessile (Fig. 1), but appear usually to form terminally on the lateral branchlets (Fig. 1, 2, 5).

As can be seen from the accompanying illustrations (Fig. 13, 14, 33), there is, as would be expected, some difference in the habitus of the ascomata of *T. santamariae* as described here over its known range, but such variations would not seem, in my opinion, to warrant recognition of anything other than a single species exhibiting minor geographical variation.

(3) **Tavaresiella majewskii** R. K. Benj., sp. nov. Fig. 16–23, 34

Ascoma (pede opaco excepto et calcare receptaculi opaco excepto) hyalinum, tota 80–84 μm longum ad apicem perithecii. *Receptaculum* relative grande 34–38 μm altum latitudine distali 16–19 μm; cellula I parva 12–13 × 5 μm, pede opaco et appendici postica plus minusve curvata prope opaca 30–50 × 2.5 μm; cellula II elongata 19–21 × 7–9 μm; cellulae II et III in parte parallelae; cellula III elongata 20–23 × 9–10 μm, dimidio distali cellulae III cum cellula VI perithecii adnato. *Appendix*: Cellula basalis lata 5–7 × 12–18 μm; ramus externus 20–35 × 3 μm cellulae 3–4 superpositae constans, cellula subbasalem spinuloso; axis rami interioris cellulae singulis 11–14 × 5–9 μm constans; cellula axis usque ad ramulos 12 simplices elongatos plus minusve curvatus 23–35 × 4 μm gignens; ramuli cellulae 3–4 elongatarum constans; antheridia non observata. *Perithecium* (cum cellulis basilaribus) 45–49 μm longum, basi 17–19 μm latum, versus apicem gradiatim contractum; cellula VI 10–12 × 7–8 μm et cellula VII 6–9 × 8 μm plus minusve parallele, cellula VI interjecta cellulae III et VII. *Ascosporae* hyalinae 22–23 × 2 μm. Typus *RKB 3565B*; RSA.

Ascoma: Hyaline except for the opaque foot and the nearly opaque projection arising from the basal cell of the receptacle. Total length from tip of foot to tip of perithecium 81–84 μm. *Receptacle*: Relatively large, broadest distally, 34–38 × 16–19 μm; the basal cell (I) small, 12–13 × 5 μm, subtending the suprabasal cell (II), from which it is separated by an oblique septum, and the terminal cell (III), the base of which it barely contacts distally, and bearing a free, elongate ± strongly recurved, apically rounded, nearly opaque projection 30–50 × 2.5 μm, which extends upward alongside cell III well beyond the level of the basal cell of the primary appendage; cell II elongate, 19–21 × 7–9 μm, its mid outer margin slightly concave, its upper, inner margin parallel to the lower half of cell III; cell III elongate, only slightly larger than cell II, 20–23 × 9–10 μm, its upper half adnate on the inside to the primary stalk cell (VI) of the perithecium up to the level of perithecial basal cell *m,* separated from the basal cell of the appendage by a ± oblique septum. *Appendage*: Basal cell shorter than wide, 5–7 × 12–18 μm, extending upward beyond its contact with the upper end of cell III and adnate to the posterior margin of perithecial basal cell *m*; outer branch, 20–35 × 3 μm,

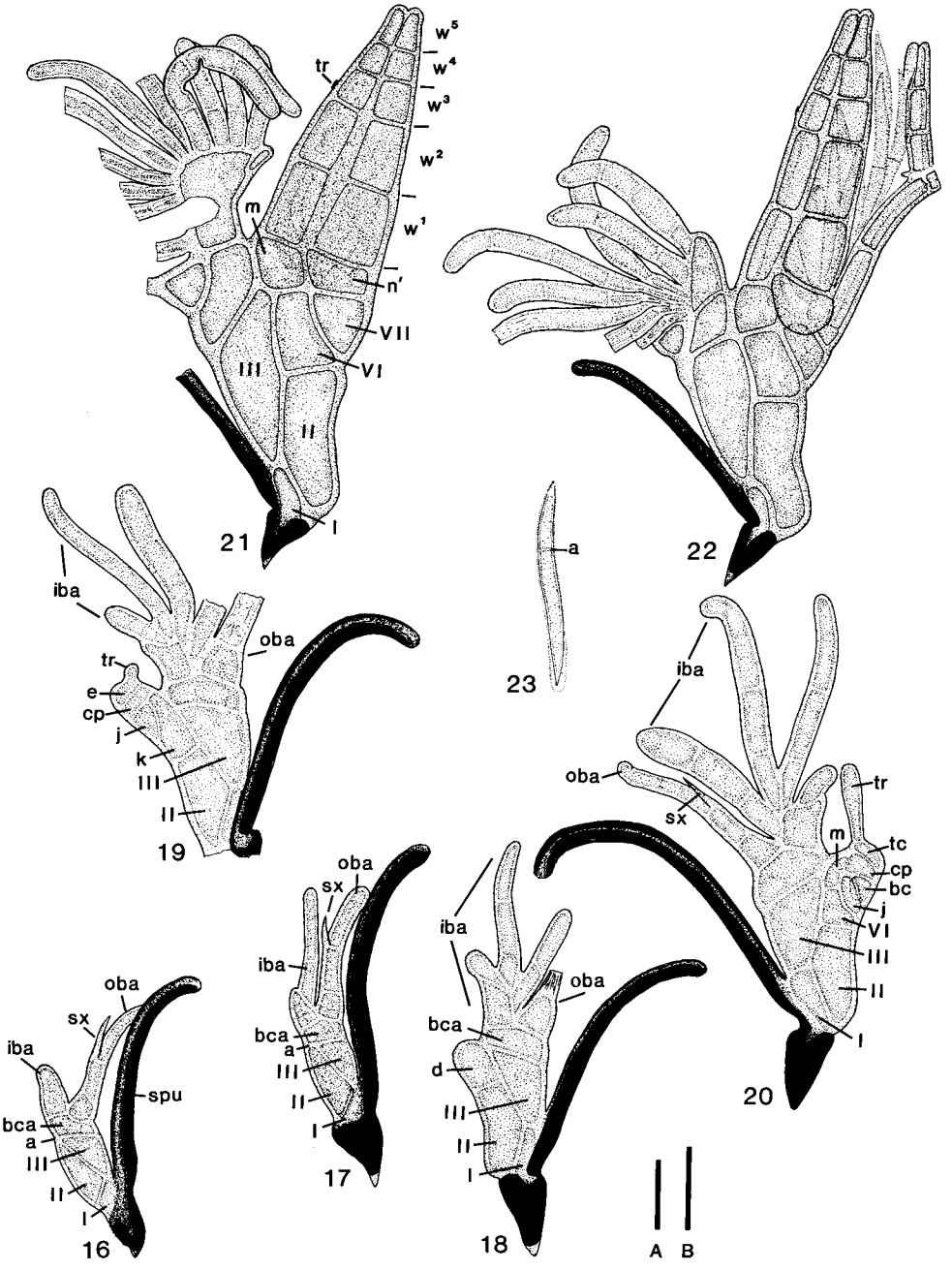

Fig. 16–23. *Tavaresiella majewskii* (*RKB 3565B*).—16–20. Five juvenile individuals showing several stages of development of the perithecium and appendage. Details and terminology are given in the text.—21–22. Two mature individuals. The ascoma depicted in Figure 21 (see also Fig. 34) shows the position of the trichogynic remnant (*tr*) and the relationship of the cells of the receptacle (I, II, III), the stalk cells of the perithecium (VI, VII), the perithecial basal cells (*n'* and *m* [*n* is on the far side]), and the five tiers of outer wall cells (w^{1-5}).—23. Ascospore. (Fig. 21–22: bar A = 10 μm; Fig. 16–20, 23: bar B = 10 μm.)

consisting of 3–4 superposed cells, the subbasal cell bearing a spine; inner branch consisting of a single elongate cell 11–14 × 5–9 μm, which gives rise on the outside to a succession of up to 12 (? or more) simple, elongate, ± curved branchlets, 23–35 × 4 μm, consisting of 3–4 elongate cells; (antheridia not observed). *Perithecium*: Primary stalk cell (VI) quadrangular, slightly longer than broad, 10–12 × 7–8 μm, lying between the upper half of cell III and the slightly smaller secondary stalk cell (VII), from which it is separated by a ± oblique septum; cell VII 6–9 × 8 μm, together with cell VI lying ± below the level of the perithecial basal cells (*m, n, n'*), which constitute only ca. 17% of the total length of the perithecium above the stalk cells; basal cells only slightly enveloping the base of the ascigerous cavity; body, including basal cells, 45–49 μm long, broadest at the base, 17–19 μm wide, gradually tapered to the undistinguished, narrow apex, which is defined by the rounded tips of the terminal outer wall cells. Ascospores hyaline, about 22–23 × 2 μm.

Etymology.—Named for Tomasz Majewski, Polish student of Laboulbeniales.

Type.—INDONESIA. SUMATRA: Sumatra Utara Prov.; river 18 km E of Prapat, 1000 m, 8 Nov 1985, J. T. & D. A. Polhemus (CL 2189), on femora and tibiae of left middle and anterior legs of *Timasius chinai* Anderson (holotype: *RKB 3565B*; RSA).

Other specimens examined.—Locality near that of type; river 14 km NE of Prapat, 1000 m, 12 Nov 1985, J. T. & D. A. Polhemus (CL 2196), on femur and tibia of left middle leg of *T. chinai* (*RKB 3566C*; RSA).

Only two mature and nine immature specimens of *T. majewskii* were recovered. Both of the mature individuals (Fig. 21–22) were slightly broken in the process of removing them from the host and mounting them on slides. When additional mature specimens are found, the dimensions given in the description doubtless will need modification. However, the distinctive appendage and the relationship of the cells of the receptacle and the basal cell of the appendage to the stalk and basal cells of the perithecium readily distinguish *T. majewskii* from the other taxa having a receptacular spur. It should be easily recognizable when again encountered. Several of the juvenile individuals (Fig. 16–20) provided valuable information on the early development of the receptacle and appendage of *Tavaresiella* as will be discussed later. Antheridia were not observed.

(4) **Tavaresiella polhemi** R. K. Benj., sp. nov. Fig. 24–29, 35

Ascoma (pede plus minusve opaco excepto) hyalinum, tota 75–95 μm longum ad apicem perithecii. *Receptaculum*: Cellula basalis (I) relative grandis 16–21 × 9–11 μm; cellula II plus minusve curvata 15–19 × 10–12 μm; cellula III 15–19 × 12–15 μm leviter divergens parte distali libera. *Appendix*: Cellula basalis relative grandis 7–10 × 10–13 μm extra rotundata infra constricta; cellula basalis rami externi persistentis (rami intactes non observati); axis rami interioris cellulae singulis 8–10 × 6–11 μm constans; cellula axis ramulos 4–7 simplices elongatos rectos vel paulo curvatos usque ad cellularum 6 gignens; ramuli cylindrici vel plus minusve clavati; antheridia non observata. *Perithecium*: Cellula VI prope isodiametra 11–15 × 12–14 μm extra rotundata supra liberam; cellula VII parva 6–7 × 9–12 μm extra rotundata; cellula *m* 13–18 × 10–12 μm fortiter extra convexa; cellula *n* et 2 cellulae successivae perithecii extra rotundatae porcam prominentem longitudinalem formantes; cellula muri supra cellulam *m* prominentiam divergentem elongatem 26–33 × 13–17 μm formans; corpus (cum cellulis basilaribus) 48–55 μm longum 18–25 μm latum apice abrupte attenuato et fortiter recurvato. *Ascosporae* hyalinae 23–26 × 2.5 μm. Typus *RKB 3566A*; RSA.

Ascoma: Hyaline except for the small opaque foot. Total length (as measured along median axis) from tip of foot to tip of perithecium 75–95 μm. *Receptacle*: Basal cell (I) and suprabasal cell (II) obliquely superposed; cell I, including the opaque foot, which has a ± acute, hyaline tip, broadest distally, 16–21 × 9–11 μm; suprabasal cell (II) about half again as long as broad, 15–19 × 10–12 μm, ± curved; the terminal cell (III), 15–19 × 12–15 μm, somewhat divergent from cell II, externally rounded, ± free distally on the inside where it is proximally adnate to the lower posterior margin of the primary perithecial stalk cell (VI). *Appendage*: Basal cell slightly shorter than wide, 7–10 × 10–13 μm, externally rounded, its juncture with cell III moderately constricted, subtending on the outside the persistent, smaller, proximal cell of the outer branch (intact branches not observed) and subtending on the inside the inner branch, which is composed of a single cell, 8–10 × 6–11 μm, that gives rise to a succession of 4–7 simple, elongate, straight or slightly curved, cylindrical or ± clavate branchlets consisting of up to six variably elongate cells; (antheridia not observed). *Perithecium*: Primary stalk cell (VI) nearly isodiametric, 11–15 × 12–14 μm, externally rounded, free above, adnate below to the lower ca. one half of cell III of the receptacle; secondary stalk cell (VII) smaller than and lying above cell VI on the outside, externally rounded, 6–7 × 9–12 μm, enclosed on the inside and above by the perithecial basal cells (*m, n, n'*), which, along with cell VII, constitute ca. 25% of the total height of the body of the perithecium above cell VI; basal cells only slightly enveloping the base of the ascigerous cavity; cell *m* strongly externally convex, slightly longer than broad, 13–18 × 10–12 μm; cell *n'* externally convex as are the first two cell *n'*-derived outer wall cells, these three cells forming a prominent longitudinal ridge on the outer wall of the perithecium; the lowermost cell of the cell *m*-derived row of outer wall cells giving rise to a broad, divergent, apically rounded prominence 26–33 × 13–17 μm; body, including basal cells, 48–55 μm long, inflated, broadest near the middle, 18–25 μm wide, abruptly tapered and strongly recurved near the apex in the direction of the perithecial prominence; the tip defined by the two distally rounded terminal cells of the rows of outer wall cells derived from basal cells *m* and *n'*, which project beyond the tips of the two terminal outer wall cells derived from basal cell *n*. Ascospores hyaline, 23–26 × 2.5 μm.

Etymology.—Named for entomologist John T. Polhemus, student of Heteroptera.

Type.—INDONESIA. SUMATRA: Sumatra Utara Prov.; 14 km NE of Prapat, 1000 m, 12 Nov. 1985, J. T. & D. A. Polhemus (CL 2196), on the lower, left, lateral, anterior surface of the abdomen of *Timasius chinai* (holotype: *RKB 3566A* [designated slide]: RSA; isotypes: RSA).

Tavaresiella polhemi is based on five mature individuals. Juvenile specimens were not encountered, and antheridia were not observed. This species was found growing on the same host as *T. majewskii,* albeit in different positions on the integument; however, the two taxa are readily distinguished from one another by marked differences in the conformation of the cells of the receptacle and perithecium. The appendage of both species is similar in that the axis of the inner branch, like *T. hebri,* consists of but one cell that gives rise to a succession of mostly outwardly deflected branchlets. The perithecium of *T. polhemi,* with its pronounced, robust appendage and conspicuous longitudinal ridge (Fig. 24–28, 35) is very unlike the relatively unmodified perithecia of other species of the genus.

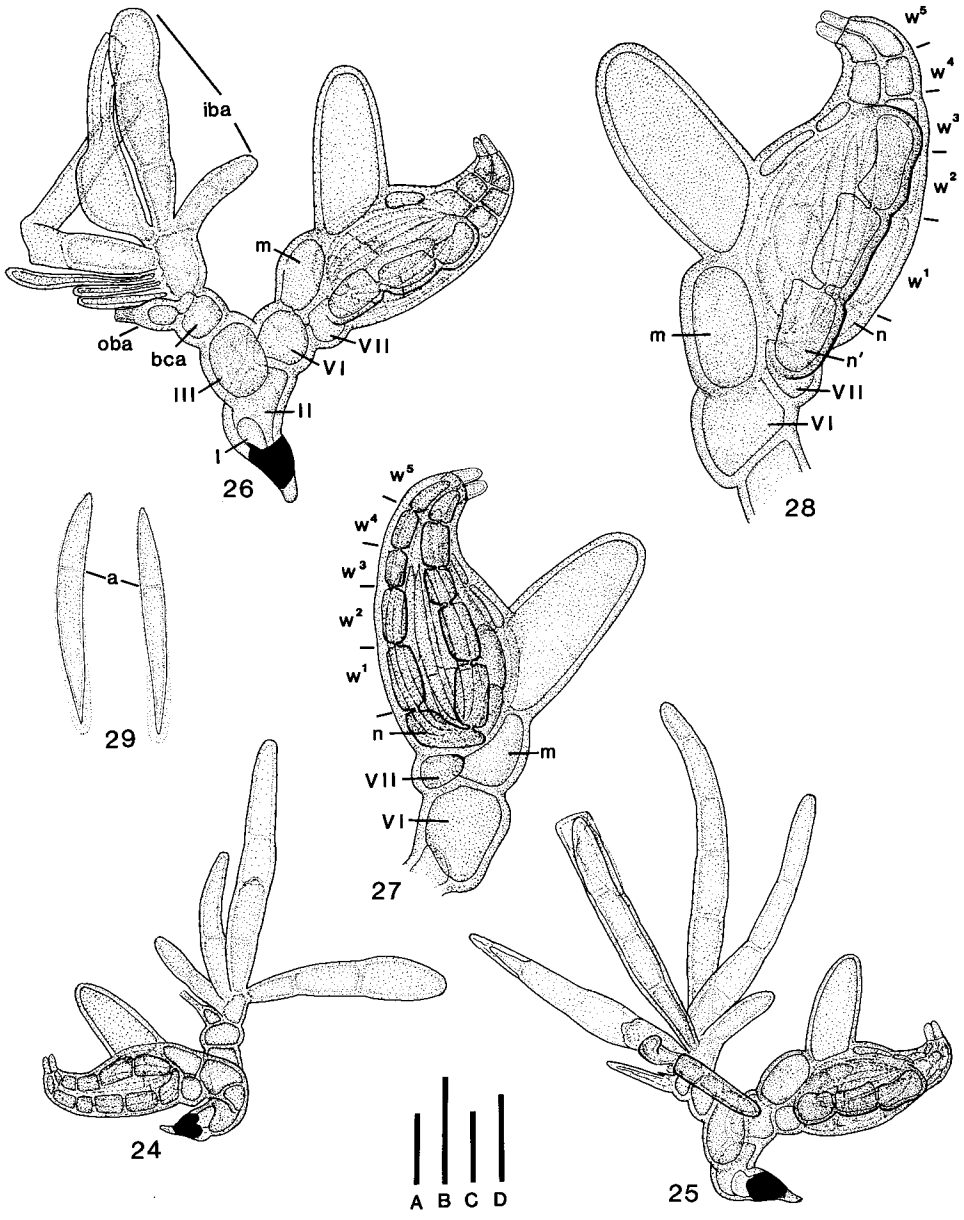

Fig. 24–29. *Tavaresiella polhemi* (*RKB 3566B*).—24–26. Three mature individuals. The relationship of the cells of the receptacle (I, II, III), the perithecial stalk cells (VI, VII), basal cell *m*, the basal cell of the appendage (*bca*), the persistent lowermost cell of the outer branch of the appendage (*oba*), and a nearly intact inner branch of the appendage (*iba*) is shown in Figure 26 (see also Fig. 35).—27. An enlarged view of the perithecium of the individual depicted in Figure 24 showing the conformation of the stalk cells (VI, VII), two of the three basal cells (*n* and *m*), and the five tiers of outer wall cells (w^{1-5}). Note the relationship of the terminal cells of the two vertical rows of wall cells derived from cell *n* to those (far side) of the rows derived from basal cells *n'* and *m* (see Fig. 28).—28. An enlarged view of the perithecium of the individual in Figure 25 showing the stalk cells (VI, VII), the basal cells (*m*, *n'*, *n*), and the five tiers of outer wall cells (w^{1-5}); note the posterior perithecial prominence and the vertical ridge composed of basal cell *n'* and the first two cells of the row of outer wall cells derived from *n'*.—29. Two ascospores. (Fig. 24–25: bar A = 20 μm; Fig. 26: bar B = 20 μm; Fig. 27–28: bar C = 10 μm; Fig. 29: bar D = 10 μm.)

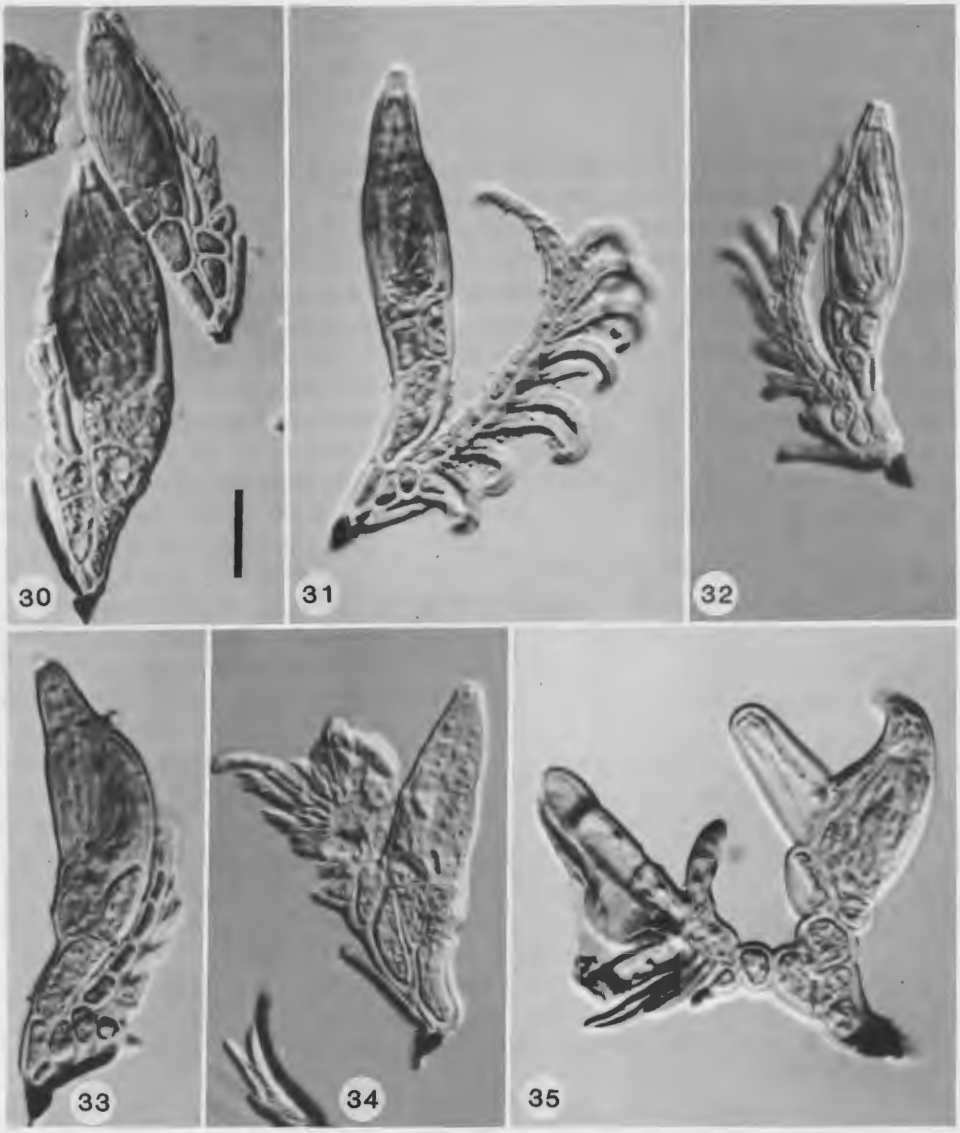

Fig. 30–35. Mature individuals of *Tavaresiella* species.—30. *T. hebri* from Poland (*Majewski 4929a*); see also Figures 6 and 7.—31–33. *T. santamariae.*—31. From Flores Island, Indonesia (*RKB 3561*); see also Figure 14.—32. From Madagascar (*RKB 3567B*); see also Figure 13.—33. From Spain (*Santamaria BCB-SS-1051*).—34. *T. majewskii* from Sumatra, Indonesia (*RKB 3565B*); see also Figure 21.—35. *T. polhemi* from Sumatra, Indonesia (*RKB 3566A*); see also Figure 26. (All figures: bar = 20 μm.)

OBSERVATIONS

Ascospore

As in other Laboulbeniales the ascospore of *Tavaresiella* spp. is hyaline and two celled. The cross wall (*a*) divides the spore into long and short segments, which have a ratio to one another of about 2:1. Inside the perithecium, the spores are oriented so that the longer segment is uppermost (Fig. 6–7, 13–14, 22, 27,

28), and the sheath surrounding the spore is more or less abruptly expanded near the tip of the long segment (Fig. 8, 15, 23, 29).

Ascoma

Receptacle.—Spores showing the earliest stages of germination were not found. In the youngest of the juvenile individuals observed (Fig. 1, 9, 16), the young receptacle already consisted of three cells, which is typical of the mature receptacle of members of Stigmatomycetinae. Even in immature individuals where development of the ascoma had progressed to a point where the appendage was just beginning to differentiate from the upper cell of the ascospore (Fig. 16), the outgrowth of the basal cell, i.e., the receptacular spur (*spu*), appeared already to have reached nearly definitive size (Fig. 1, 9, 16). Cell I was separated from the suprabasal cell (II) by an oblique cross wall and was in contact distally with the upper cell (III), which, in turn, was separated from cell II by a more or less oblique septum. As the ascoma matured, the receptacular cells enlarged but did not divide again (Fig. 2–7, 10, 12–14, 17–22).

Appendage.—The earliest stage of development of the appendage observed in this study was found in *Tavaresiella majewskii* (Fig. 16). The basal cell of the appendage (*bca*), which was separated from cell III of the receptacle by the enlarged original spore septum (*a*), bore on its upper outer angle what is here termed the outer branch of the appendage (*oba*), which, in the example shown (Fig. 16), consisted of three superposed cells. The median cell of this branch bore a distinct spine (*sx*), the indurate original spore apex. Arising from the upper, inner angle of the basal cell (*bca*) was the first or primary cell of the axis of the inner branch of the appendage (*iba*).

Figures 17–20 depict several stages of the further development of the appendage in *T. majewskii.* The outer branch (*oba*) had undergone little change (Fig. 17, 20); it commonly was broken off above the persistent lowermost cell (Fig. 18, 19), and this was true also in the other species (Fig. 1–5, 9, 11–14, 18–21, 26). The primary cell of the *iba* gave rise on the outside to the first of the several branchlets it formed (Fig. 17). As it enlarged it delimited a succession of branchlets (Fig. 18–20), which deflected outward above and over the outer branch (*oba*) (Fig. 20). Thus, in *T. majewskii* the axis of the inner branch of the appendage above the basal cell was a single cell bearing an external series of branchlets; the youngest at the tip and the oldest at the base. In mature individuals, the distal part of the lower branchlets usually had been broken off leaving more or less disorganized basal remnants (Fig. 21, 22).

Although juvenile individuals of *T. polhemi* were not observed, it appeared, on the basis of the structure of mature specimens, that development of the appendage in this species was essentially the same as in *T. majewskii.* Although the basal cell (*bca*) was wholly free in *T. polhemi,* rather than being adnate to the base of the perithecium as in *T. majewskii,* the axis of the inner branch consisted of but one cell that, as in *T. majewskii,* gave rise to an external series of branchlets (Fig. 24–26).

In *T. hebri,* early development of the appendage resembled that of *T. majewskii*; however, the primary cell of the inner branch (*iba*) continued to elongate to a much greater degree as successive lateral branchlets formed (Fig. 1–5); these

branchlets consisted of a single cell forming a simple antheridial phialide directly or of a small number of superposed cells in which the terminal cell formed an antheridium (Fig. 1, 2, 5). As the ascoma matured, the final branch arising from the primary cell elongated more or less and formed a several-celled continuation in line with this cell (Fig. 6, 7). In none of the mature or nearly mature individuals I studied did I find a lateral branchlet on any but the primary cell. In *T. hebri,* as in *T. majewskii* and *T. polhemi,* the older lateral branchlets of the *iba* broke off readily above the base as did the distal part of the *oba* (Fig. 2–7).

In *T. santamariae,* the primary cell of the inner branch of the appendage (*iba*) divided after having given rise to one or more often two, rarely three, branchlets externally, and division of each successive terminal cell of the axis continued as new branchlets appeared (Fig. 9–12). This resulted in a multicellular axis of up to ten cells, and each cell bore a small number of branchlets (Fig. 13, 14, 31–33). In some instances the axis of the *iba* branched once or twice and gave rise to shorter distal axes bearing branchlets like those on the main axis. Antheridia developed directly from lateral branchlets before they divided or, more commonly, they developed from the basal one or two cells; the short discharge tubes of intercalary antheridia always were directed upward (Fig. 11–14).

Perithecium.—The number of young specimens of *Tavaresiella* spp. bearing perithecia in early stages of development was limited. However, study of several juveniles of *T. hebri, T. majewskii,* and *T. santamariae* provided information pertinent to understanding perithecial ontogeny in the genus.

The perithecial initial (*d*) arose from the distal end of the suprabasal cell of the receptacle (II), and in the young ascomata studied it had not appeared until development of the appendage was well under way (Fig. 1, 9, 18). In *T. hebri,* antheridial phialides already were forming on the appendage (Fig. 1). In the next earliest stage of perithecial development found (Fig. 19), cell *d* had given rise to four cells, *k, j, cp* (the carpogonial cell), and *e,* arranged one above the other. The lower cell (*k*) divided and formed the primary stalk cell of the perithecium (VI) below and perithecial basal cell *m* above on the inside (Fig. 10, 20). Cell *j* gave rise distally, first on one side and then the other, to perithecial basal cells *n* and *n'* (Fig. 10, 20 [where only one of these cells had been delimited and is designated simply as *bc*]). Cell *e* formed a small bud distally (Fig. 10, 19), which elongated and developed into the trichogyne (*tr*; Fig. 20). The latter was separated by a basal septum from what became the trichophoric cell (*tc*). In the young perithecium shown in Figure 2, the first of the primordial outer wall cells (*o*) had developed or had begun to develop from the basal cells, two of which (*n* and *m*) are illustrated.

Stages of trichogynic development more advanced than that shown in Figure 20 are depicted in Figures 2 and 12. As the trichogyne elongated it developed short, lateral, more or less divergent branchlets. It is possible that the trichogyne in *Tavaresiella* may become more highly branched than the one shown for *T. santamariae* (Fig. 12), but this can be determined only with discovery of additional specimens. The young perithecium of *T. hebri* shown in Figure 2 bore two similar trichogynes having a common origin from the apex; however, one of these (far side) lacked stainable cytoplasm and appeared to have aborted.

As development of the perithecium proceeded (Fig. 3–5, 12), four rows of inner and outer wall cells, derived from the three basal cells (one row each from cells *m* and *n'*, and two rows from cell *n*), grew upward around the developing centrum.

The outer wall of the mature perithecium comprised five tiers of cells (w^1–w^5) (Fig. 6, 7, 13, 14, 21, 22, 27, 28). Cells of the basal tier (w^1) usually were slightly longer than or subequal to those of the subbasal tier (w^2), and together these two tiers constituted about one half the total length of the body of the perithecium above the basal cells. The cells of the median tier (w^3) were shorter than or subequal to those of the subterminal tier (w^4). In *T. hebri, T. santamariae,* and *T. majewskii,* all four cells of the terminal tier (w^5) were of equal length and were subequal to or slightly longer than those of the subterminal tier (Fig. 6, 7, 13, 14, 21, 22), whereas in *T. polhemi* the two terminal cells of the vertical rows derived from basal cells *m* and *n'* were longer than and projected well beyond those of the rows derived from basal cell *n* (Fig. 27, 28). A trichogynic remnant often was present on the posterior surface of the mature perithecium at the level of the third tier of outer wall cells (Fig. 6, 13, 21).

DISCUSSION

My study of the development of the ascoma in *Tavaresiella* was based on a limited number of immature specimens. However, perithecial ontogeny in the genus does not differ fundamentally from the pattern usually found in other Laboulbeniaceae that have been examined in greater detail, e.g., *Laboulbenia* Mont. & Robin (DeKesel 1989; Tavares 1985), *Stigmatomyces* Karsten (Thaxter 1896) *Triceromyces* Majewski (Benjamin 1986), and *Acompsomyces* Thaxt. (Benjamin 1989). The four vertical rows of perithecial wall cells develop from but three basal cells, which are derived from two stalk cells subtended by cell II of the receptacle. The receptacle, consisting as it does of three cells, is typical of members of Stigmatomycetinae as defined by Tavares (1985).

Comparison of young and mature individuals of *T. hebri* shows that the lateral branchlets arising from the elongate primary cell of the inner branch of the appendage commonly break off near the base. Thus, in *T. hebri* the status of such branch remnants, i.e., as having been the base of an antheridial phialide or the base of a sterile several-celled branchlet, cannot be determined with certainty from an examination of mature specimens. To a lesser extent, the same is true for *T. santamariae* except that the antheridial nature of the basal cell of a lateral branchlet can be known if the upper part of the branchlet happened to break off above the lateral opening of an antheridial cell when a series of at least two antheridia had formed from successive cells of the branchlet. In *T. majewskii* and *T. polhemi,* where antheridia were not observed, the first-formed branchlets may break off or at least degenerate to some degree as the ascoma matures.

The distinctiveness of *Tavaresiella* has been reinforced with the description of three additional species. All species of the genus have a uniformity in the basic structure of receptacle and appendage, which, in combination, distinguishes them from other Stigmatomycetinae. In addition to *Tavaresiella,* six other genera currently included in the subtribe have taxa with cells II and III of the receptacle arranged side-by-side or nearly so, i.e., *Cryptandromyces* Thaxt. (Thaxter 1912; Tavares 1985), *Sphaleromyces* (Tavares 1985), *Distolomyces* Thaxt. (Thaxter 1931; Tavares 1985), *Triceromyces* (Majewski 1981; Benjamin 1986), *Aphanandromyces* Rossi (Rossi 1982; Tavares 1985), and *Autophagomyces* Thaxt. (Thaxter 1912, 1931; Tavares 1985). In the latter four genera, however, the appendage lacks sterile branchlets and usually consists of a simple series of only a few super-

posed cells bearing a single terminal antheridium or several antheridia terminally and laterally.

In *Cryptandromyces* and *Sphaleromyces,* cell I of the receptacle is relatively large compared to cells II and III, from which it is separated by a transverse or only slightly oblique cross wall. In *Tavaresiella,* cell I is relatively much smaller than cells II and III and is separated from cell II by a strongly oblique cross wall. Unlike *Tavaresiella,* the basal cell of the appendage of *Cryptandromyces* and *Sphaleromyces* does not bear distinct inner and outer branchlets. Instead, the appendage consists of a simple series of superposed cells with or without lateral branchlets. In some species of *Cryptandromyces,* free or intercalary antheridia are known to form directly on the axis of the appendage or its branches; two of the 13 or 14 species recognized by Tavares (1985) appear to be dioecious. In *Sphaleromyces,* branchlets bearing a terminal and sometimes a subtending series of intercalary antheridia arise from the upper end of successive cells of the appendage, but the branchlets develop on the inside of the axis. This is in sharp contrast to the condition in *Tavaresiella* where the lateral branchlets arising from the inner branch of the appendage develop on the outside of the axis.

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