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LABOULBENIALES ON SEMIAQUATIC HETEROPTERA. VII. ADDENDA TO
SPECIES OF *TRICEROMYCES* ON HYDROMETRIDAE AND
FURTHER OBSERVATIONS ON DIOECISM IN THE ORDER

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ABSTRACT

Four new species of *Triceromyces* (Laboulbeniales) parasitic on *Hydrometra* (Heteroptera: Hydrometridae) were described and aspects of their morphology and development were discussed and illustrated with line drawings. Two of the species, *T. floridanus* and *T. elongatus*, are monoecious; *T. floridanus*, known only from Florida, U.S.A., has features allying it with *T. elongatus*, which ranges from Madagascar and Kenya in Africa to India, Indonesia, and Sri Lanka in Asia. The other two undoubtedly closely related species, *T. lithophilus* and *T. terrestris*, are dioecious and parasitize two closely related endemic species of *Hydrometra* thriving in a small region in northwestern Madagascar. *Hydrometra cavernicola*, the host of *T. lithophilus*, is semiterrestrial, living on damp rock faces or in small caves near water. The host of *T. terrestris*, *H. phytophila*, lives on terrestrial vegetation often far removed from the nearest stream or other source of free water. The male of *T. lithophilus* and *T. terrestris* consists of a few superposed cells bearing a terminal antheridium whereas the female has a primary appendage bearing only sterile, antheridialike branchlets instead of functional antheridia as in a presumed closely related monoecious species *T. hydrometrae*. New records for *T. hydrometrae* were presented showing that it is widely distributed in both the New World and Old World. Circumscription of *Triceromyces* was emended and a key to all known species of the genus was given. Dioecy and its occurrence throughout the Laboulbeniales was reviewed and its morphological diversity summarized. It was concluded that the phenomenon has arisen independently several times in the order.

Key words: dioecism, fungi, Heteroptera, *Hydrometra*, Hydrometridae, insect parasites, Laboulbeniales, morphology, taxonomy, *Triceromyces*.

INTRODUCTION

Triceromyces was characterized by Majewski (1981: 150) to accommodate a single species, *T. balazucii* T. Majewski, parasitizing a velvet water bug, *Hebrus ruficeps* (Thomson) (Heteroptera: Hebridae), collected in Poland in 1976 in the vicinity of Długie (Voiv. Włocławek); Majewski (1994: 148) found the species again in 1990 on the same host near Turew (Voiv. Leszno). Subsequent to Majewski's description of *T. balazucii*, I offered (Benjamin 1986) a revision of the genus based not only on a study of this species, specimens of which were kindly provided by Dr. Majewski, but also on several congeners that had been accessioned during my years of accumulating Laboulbeniales. In this work, four additional taxa, all parasitic on Heteroptera (see Henry and Froeschner 1988: xii) were described: *Triceromyces hebri* R. K. Benj. (on *Hebrus* sp. [Hebridae] from Jalisco, Mexico); *T. hydrometrae* R. K. Benj. (on *Hydrometra australis* Say [= *H. martini* Kirkaldy] [Hydrometridae] from Arizona, U.S.A.); and *T. biformis* R. K. Benj. and *T. bullatus* R. K. Benj. (on *Mesovelvia vittigera* Horváth [Mesoveliidae] from Luzon, Philippine Islands). Also discussed was *T. poissonii* (R. K. Benj.) R. K. Benj. (on

Mesovelvia mulsanti White from Arizona and Texas, U.S.A.; Durango, Jalisco, Oaxaca, and Michoacan, Mexico; and Nicaragua). *Triceromyces biformis*, *T. bullatus*, and *T. poissonii* were distinguished from all other known Laboulbeniales in being both monoecious and dioecious, producing hermaphroditic and unisexual morphs that may develop together on the same host insect.

Previously, I had failed to recognize the trioecious nature of *Triceromyces poissonii*, describing the monoecious morph (i.e., male and female sexual organs on the same individual) as a species of *Autophagomyces* Thaxt. (i.e., *A. poissonii* R. K. Benj.) and the dioecious morph (i.e., male and female organs on separate individuals) as a species of *Dioicomyces* Thaxt. (i.e., *Dioicomyces mesoveliae* R. K. Benj.) (Benjamin 1970). The existence of trioecy, which is not uncommon in the diploid sporophytic states of some embryophytes, i.e., bryophytes, pteridophytes, and angiosperms (Cruden and Lloyd 1995), in the Laboulbeniales, which are haploid, became apparent later only with the discovery of *T. biformis* and *T. bullatus*. Majewski (1988b) described the dioecious morphs of both *T. biformis* and *T. bullatus* as *Dioicomyces verrucu-*

losus T. Majewski and *D. yongboi* T. Majewski, respectively, on *Mesovelgia vittigera* collected on Iriomote Island (Okinawa Prefecture, Japan). Majewski (1988b), with reservation, also recorded *A. poissonii* on Iriomote Island from the same locality and host as his *D. yongboi*. The fungus he identified with *A. poissonii* doubtless is the monoecious morph of *T. bifor-mis*.

Subsequent to its description, *Triceromyces hydrometrae* has been reported on *Hydrometra stagnorum* (L.) from Spain (Santamaria 1989a, 1996a) and Portugal (Santamaria 1992), and on *H. albolineolata* Reuter from Sierra Leone (Rossi 1994).

During three visits to Dr. John T. Polhemus's laboratory at the Colorado Entomological Museum, Englewood, in June 1990, April 1991, and May 1993, I obtained, among others, a number of specimens of *Hydrometra* spp. parasitized with *Triceromyces* spp. This material, collected in the wild by John and/or his son Dr. Dan A. Polhemus, included not only insects bearing *T. hydrometrae* from heretofore unrecorded localities but also several previously unrecognized species of *Triceromyces*. The purpose of this paper is to (1) update the known range of *T. hydrometrae*; (2) describe and illustrate four new species, two of which are dioecious, having a male consisting of a simple series of superposed cells bearing a terminal antheridium and a female with an appendage bearing antheridialike branchlets that are sterile, a condition not found before in dioecious members of the genus; and (3) review the occurrence of dioecy (and trioecy) in the Laboulbeniales.

MATERIALS AND METHODS

Hydrometra spp. bearing fungi were found among miscellaneous bugs preserved in vials in 70% ethyl alcohol or on dry, pinned (affixed to paper points) specimens in museum boxes. Pinned insects were relaxed before any attempt was made to remove parasites. Labels and insects were carefully separated from the pin. The former were placed in vials and set aside for their eventual reunion with the insect. The latter were placed directly into 0.2% saline or a relaxing fluid consisting of benzene (5%), ethyl alcohol (45%), water (35%), and ethyl acetate (15%) for a few hours or overnight after which they were removed to 70% ethyl alcohol for storage.

By means of methods described previously (Benjamin 1971: 101–102 [up to step e], 1986: 247, 1993: 560), fungi were carefully removed from the hosts and mounted on slides in glycerine. All observations related to the descriptions and illustrations were made using a Leitz Dialux microscope having differential interference contrast optics. In the citation of specimens collected by John and/or Dan Polhemus, CL

numbers—detailed descriptions of *collection localities* as recorded in their field note books—are given.

Terminology and abbreviations used in describing the ascoma (i.e., the entire perithecium-bearing thallus) are defined in the text or in the legends for figures and, in general, are those outlined by Tavares (1985: 431–434). Ascomata of *Triceromyces* spp. are bilaterally symmetrical and, as in other similar fungi, usually are oriented on slides so that they can be viewed only laterally. Thus, with few exceptions, descriptions and measurements of thalli were based on study of specimens viewed 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 toward the appendage. In referring to cells of the receptacle, stalk and basal cells of the perithecium, and cells of the appendage, inner is in the direction of the longitudinal axis of the ascoma, outer is in the direction away from the axis.

TAXONOMY

TRICEROMYCES T. Majewski, *Acta Mycol.* **16**: 149, (1980) 1981, emended R. K. Benj.

Monoecious, dioecious, or trioecious. Males of dioecious and trioecious morphs consisting of a one-celled receptacle subtending several superposed cells terminated by a single, simple, sometimes spinose antheridium. Receptacle in monoecious morphs and females of dioecious and trioecious morphs consisting of three cells; basal cell (I) small, subtending the relatively elongate suprabasal cell (II) and terminal cell (III), which are laterally adnate and parallel to one another. Cell III becoming secondarily divided into an upper, nucleate cell and a lower, empty segment. Primary appendage, subtended by cell III, free; in ascomata of monoecious or dioecious morphs consisting of a stalk comprising three superposed sterile cells subtending two or more superposed cells that give rise internally to one, rarely two, simple antheridia (monoecious morphs) or antheridialike sterile cells (dioecious morphs) or one or more of the distal cells forming elongate sterile branches; in ascomata of trioecious morphs consisting of two, rarely three, superposed sterile cells. Perithecium, subtended by cell II, with well-defined stalk and basal cells, four vertical rows of outer wall cells of four or five cells each, and a single ascogenic cell; with or without a prominent outgrowth from one or more outer wall cells. Trichogyne consisting of four superposed cells; the suprabasal cell forming a single-celled divergent branch distally; tip of main axis and the branch with or without a terminal crown of short, digitiform prominences. Ascospores 1-septate.

Type species.—*Triceromyces balazucii* T. Majewski.

Two features shared by all members of *Triceromyces* distinguish the genus from other Stigmatomycetinae (Benjamin 1986), namely (1) an appendage, in the ascumata of monoecious and dioecious morphs, having a three-celled stipe supporting few or many cells bearing antheridia or antheridialike sterile branchlets, and (2) in all perithecia-bearing morphs the eventual partition of cell III of the receptacle, by the formation of an adventitious cross wall, into an upper nucleate cell and a lower enucleate cell. It is likely that the trichogynic structure given in the above description will prove to be typical of all members of the genus. Mature trichogynes having these characteristics have been observed in five of the ten taxa described, including those treated in this paper, and immature trichogynes suggesting a similar morphology have been observed in three of the others.

Coevolution of *Triceromyces* on members of three families of Gerroidea (Heteroptera), i.e., Hebridae, Hydrometridae, and Mesoveliidae, has been accompanied by considerable morphological and sexual diversification among the species. Thus, the discovery of additional taxa has here required further emendation of the generic description given previously (Benjamin 1986: 248).

A KEY TO THE SPECIES OF *TRICEROMYCES*

- A. Appendage above the 3-celled stalk consisting of 2, rarely 3, cells with or without antheridia, sterile branchlets absent B
- Appendage above the stalk consisting of 4 or more cells with or without antheridia; sterile branchlets often present (on Hydrometridae) H
- B. Perithecium with distinctive \pm elongate outgrowths C
- Perithecium lacking distinctive outgrowths D
- C. Perithecium with 1 short and 2 elongate outgrowths (on Hebridae) *T. balazucii*
- Perithecium with only 1 elongate outgrowth (on Hebridae) *T. hebrici*
- D. Perithecial wall of monoecious morph and female of dioecious morph bullate in part; trioecious (on Mesoveliidae) *T. bullatus*
- Perithecial wall of monoecious morph and female of dioecious morph smooth; trioecious (on Mesoveliidae) E
- E. Dioecious F
- Monoecious (morphs nearly indistinguishable) G
- F. Primary appendage of female slender, elongate, 35–51 μ m long, 6–9 μ m wide at the base (Old World) *T. biformis*
- Primary appendage of female shorter and broader, 26–34 μ m long, 9–13 μ m wide at the base (New World) *T. poissonii*
- G. On *Mesovelina* in Old World *T. biformis*
- On *Mesovelina* in New World *T. poissonii*
- H. Monoecious I
- Dioecious K
- I. Outer margin of appendage above the stalk nearly uniform or only weakly undulate 1 *T. hydrometrae*
- Outer margin of appendage above the stalk strongly undulate J
- J. Distal cell of primary appendage terminated by a single elongate, relatively wide, \pm circinate sterile appendage 2. *Triceromyces floridanus*
- Distal 1–2(–3) cells of primary appendage bearing 1(–2) elongate, slender, \pm straight, sterile appendages 3. *Triceromyces elongatus*
- K. Terminal outer wall cell of perithecium derived from basal cell *m* weakly protrudent in lateral view; male consisting of 4 superposed cells including antheridium, darkly pigmented below the basal septum 4. *Triceromyces lithophilus*
- Terminal outer wall cell of the perithecium derived from basal cell *m* strongly protrudent in lateral view; male consisting of 5(–6) superposed cells including antheridium, darkly pigmented above and below the basal septum 5. *Triceromyces terrestris*

1. *TRICEROMYCES HYDROMETRAE* R. K. Benj., *Aliso* 11: 253, fig. 14–31, 81–82, 1986.

Triceromyces hydrometrae first was found on *Hydrometra australis* (as *H. martini*) collected in Arizona (Benjamin 1986), and, as mentioned above, the species has since been reported from Spain (Santamaria 1989a, 1996a), Portugal (Santamaria 1992), and Sierra Leone (Rossi 1994). Based on additional finds in the Polhemus collections, it probably is widely distributed in both the New World and Old World. Aside from differences in thalloid dimensions, degree of pigmentation of the receptacle and the outer margin of the appendage, and number of cells comprising the antheridiiferous part of the primary appendage, which may range from as few as three or four up to as many as 12 or 13 (primarily in some of the specimens from Indonesia), all of the collections cited below compare well with the holotype from *H. australis*.

With one exception where a few specimens were found at the base of the proboscis, *T. hydrometrae* was found in scattered positions only on the legs and antennae of both male and female host insects.

Additional specimens examined.—NEW WORLD.—**North America.** U.S.A.: Florida; Collier Co.; Turner River Canal at Hwy. 41; 2 July 1988; D. A. Polhemus; on the legs and antennae of *Hydrometra australis*; RKB 3546A (RSA).—**South America.** PERU: Dept. Loreto; forest stream 80 km NE of Iquitos, 106 m, nr. Explorara Lodge; 14 Aug 1989; D. A. & J. T. Polhemus (CL2457); on the legs and antennae of *H. williamsi* Hungerford; RKB 3787 (RSA).—OLD WORLD.—**Europe.** SPAIN: Gerona; Riells i Vibreana; 2 Sept 1989; S. Santamaria; on the legs and antennae of *H. stagnorum*; RKB 3768 (RSA).—**Africa.** KENYA: Masai Mara, Mara River; 5 Feb 1980; J. T. Polhemus (CL1669); on the legs and antennae of *H. marani* Hoberlandt; RKB 3684A (RSA).—MADAGASCAR: Tulare Prov.; river 10 km N of Betsimba drill site, 105 km SE of Morondava, 107 m; 25 Nov 1986; J. T. & D. A. Polhemus (CL2287); on the left anterior leg of *H. fanjahira* Hungerford & Evans; RKB 3548 (RSA); and on the legs and antennae of *H. isaka* Hungerford & Evans; RKB 3549A (RSA); and on the antennae of *H. bifurcata* Hungerford & Evans; RKB 3550A (RKB).—Majunga Prov.; Ampijoroa Forest Station; 113 km E of Majunga, 76 m; damp forest floor; 21 Nov 1986; J. T. & D. A. Polhemus (CL2283); on the legs and antennae of *H. bifurcata*; RKB 3552A (RSA).—TANZANIA: Mkwaja; Msangazi River; 10 Mar 1979; J. T. Polhemus coll. (CL995); on the legs and antennae of *Hydrometra* sp.; RKB 3685 (RSA).—**Asia.** INDONESIA: Timor; Nusa Tenggara Timur Prov.; spring and stream at Oe Hala, 10 km N of Soe, 685 m; 11 Sept 1991; D. A. & J. T. Polhemus (CL2593); on

the legs, antennae, and base of the proboscis of *H. lombok* Polhemus & Polhemus; *RKB 3784A, 3785A* (RSA); spring and stream at Oe Noah nr. Polen, 24 km NE of Soe, 840 m; 12 Sept 1991; D. A. & J. T. Polhemus (CL2594); on the leg, antennae, and proboscis (3784A) of *H. lombok*; *RKB 3786A* (RSA).—MALAYSIA: Johor; swamp-forest stream 15 km W of Sedili Besar, 20 m; 16 Oct 1986; J. T. & D. A. Polhemus (CL2218); on the femur of the right mid leg of *H. cracens* Polhemus & Polhemus; *RKB 3547* (RSA).—Australia. Northern Territory; Alligator Creek, on Daly River Road; 11 Dec 1977; J. T. Polhemus (CL909); on the tibia of the left anterior leg of *H. halei* Hungerford & Evans; *RKB 3681* (RSA); stream at Robin Falls; 12 Dec 1977; J. T. Polhemus (CL910); on the legs and antennae of *H. halei*; *RKB 3683* (RSA).—Norfolk Island; meadow near Gaoli; 28 Dec 1977; J. T. & M. S. Polhemus (CL1423); on the legs of *H. strigosa* (Skuse); *RKB 3682* (RSA).

2. *Triceromyces floridanus* R. K. Benj., n. sp. Fig. 1–8

Ascoma prope rectum, luteolum ad plus minusve hyalinum supra pedem denigratum, praeter receptaculum brunneolum et paginam posticum appendicis plus minusve brunneolum; 254–263 μm longum ad apicem peritheci. *Receptaculum* triangulare, 45–59 μm longum, 18–19 μm latum in parte distalibus; cellula I (cum pede) 19–23 μm longa, 8–9 μm lata in parte distalibus; cellula II 30–38 μm longa; cellula III 31–36 μm longa, pars supra cellulae cellulam 20–25 μm longam formans. *Appendix* 93–106 μm longa. Stipes 48–61 μm longus; cellulae subaequales, paene cylindricae, 17–21 \times 9–11 μm ; septum superum fuscum. Pars antheridiifera ex 5–6 cellulis superpositis constans; margines externae cellularum valde convexae; cellulae basales vel suprabasales saepe spinosi; spina circa 2.5 μm longa; cellulis antheridia singula prope liberis facientibus; cellula terminalis prolongationem 90–100 μm longam, basi 5–7 μm , relative crassam valde recurvatam ad circinatam productens. Antheridia elongata attenuata 30–40 \times 4.5–5 μm . *Perithecium* elongatum, externe valde convexum, 194–205 μm longum (cum stipite et cellulis basilaribus), in medio 35–40 μm latum; pars terminalis basi constrictae, collum 56–60 μm longum prope apicem 19 μm latum faciens; apex rotundatus, processibus duo curtis lateralibus, 10 μm longis, 5 μm latis ad basin. Cellulae basales (*n*, *n'*, *m*) prope 0.18 corporis peritheci in tota longitudine. Cellula VI 12–15 \times 30 μm . Cellula VII 18–19 μm longa. Ascospores hyalinae 39–43 \times 3.5–4 μm .

Ascoma: Nearly straight; pale yellow to \pm hyaline above blackened foot, except for receptacle and posterior surface of appendage, which become \pm suffused with brown. Total length from tip of foot to tip of perithecium 254–263 μm . *Receptacle*: Triangular, 45–59 μm long by 18–19 μm wide distally, tapered down-

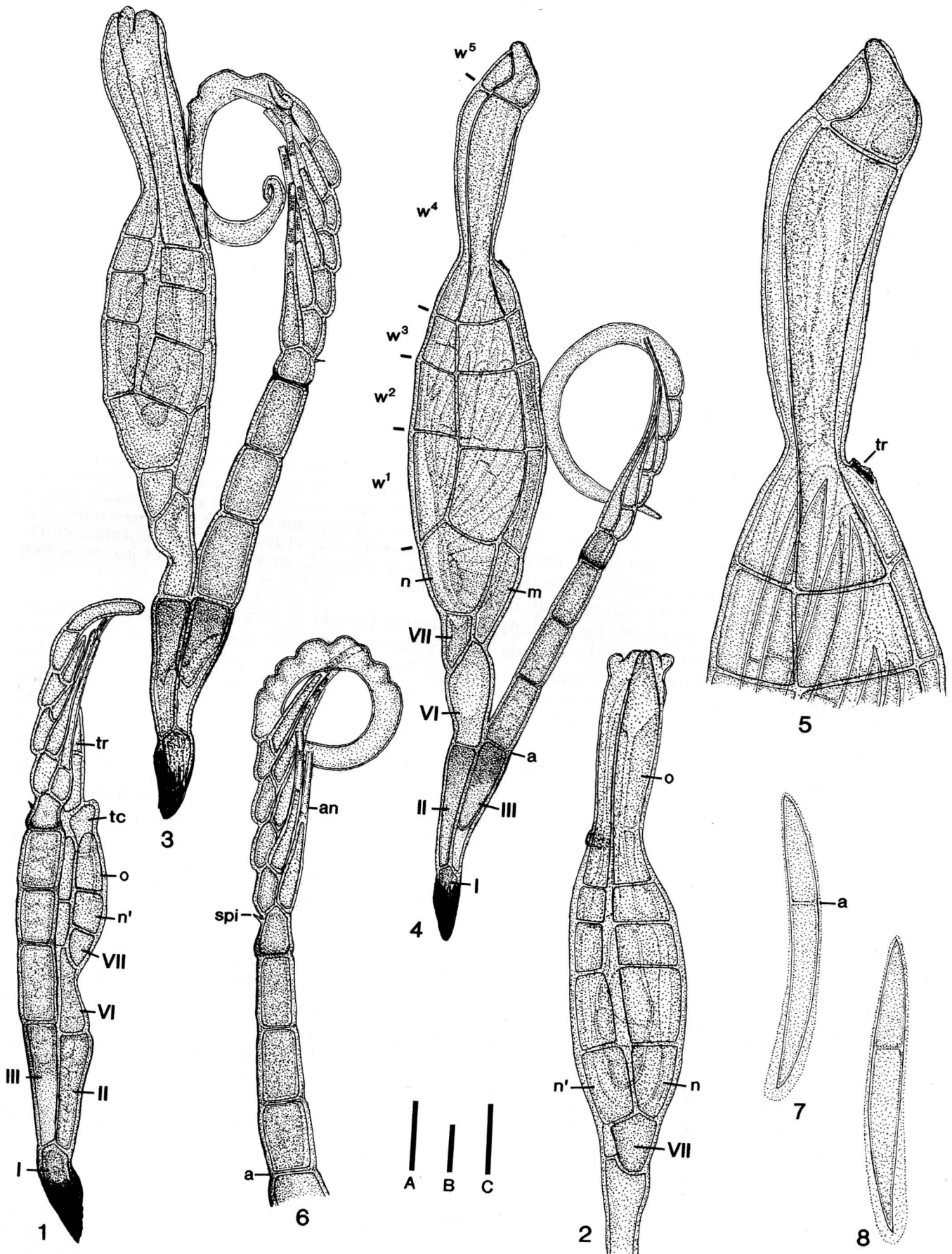
ward to acute tip of foot; basal cell (I), including foot, relatively small, 19–23 μm long by 8–9 μm wide immediately below cells II and III, which are elongate and subequal; cell II 30–38 μm long; cell III 31–36 μm long, divided submedianly by a \pm convex secondary cross wall and forming a basal, empty segment and an upper, elongate cell 20–25 μm long. *Appendage*: The three-celled stalk 48–61 μm long; cells subequal, longer than broad, nearly cylindrical, 17–21 \times 9–11 μm ; distal antheridiiferous part consisting of 5–6 superposed, externally strongly convex cells separated from upper cell of stalk by a slightly darkened septum; basal or suprabasal cell often bearing, externally, a spine ca. 2.5 μm long; cells each bearing internally a single upwardly directed, nearly free antheridium; terminal cell subtending a relatively thick, elongate, strongly recurved to circinate appendage, 90–110 μm long by 5–7 μm wide near base; antheridia elongate, uniformly tapered upward, widest at base, 30–40 \times 4.5–5.5 μm . Total length to base of terminal appendage 93–106 μm . *Perithecium*: Stalk cell (VI) ca. two times longer than broad, 12–15 \times 30 μm ; secondary stalk cell (VII) relatively small, slightly longer than broad as viewed laterally, 18–19 μm long; basal cells (*m*, *n*, *n'*) constituting ca. 18% of total length of body above stalk cells; body elongate, 194–205 μm long, including stalk and basal cells, externally strongly convex, broadest near middle, 35–40 μm wide; terminal part abruptly constricted at level of trichogynic remnant and forming a neck 56–60 μm long, 18 μm wide distally; apex rounded, recurved slightly, with short, anteriorly directed lateral outgrowths, ca. 10 μm long by 5 μm wide at base, arising from posterolateral rows of outer wall cells derived from basal cells *n* and *n'*; trichogynic remnant positioned near base of subterminal cell of vertical row of outer wall cells derived from basal cell *m*. Ascospores 39–43 \times 3.5–4 μm .

Etymology.—Named for the state of Florida, where the holotype was collected.

Holotype.—U.S.A.: Florida; Collier Co.; Turner River Canal at Hwy. 41; 2 July 1988; D. A. Polhemus coll.;

Fig. 1–8. *Triceromyces floridanus* (All *RKB 3546* [Florida]).—1. Juvenile individual with immature perithecium and primary appendage.—2. Immature perithecium at four-outer-wall-cell stage of development rotated slightly and showing conformation of perithecial tip; note elongate primordial outer wall cell (*o*).—3. Immature individual in lateral view with perithecium at nearly the same stage of development as perithecium shown in Figure 2.—4. Mature individual (the holotype) showing the five tiers of outer wall cells; note the relatively great length of cells comprising tier four as compared with cells of tiers three and five.—5. Distal part of perithecium shown in Figure 4.—6. Mature primary appendage showing spinose basal cell of antheridiiferous part and robust, circinate, terminal sterile appendage.—7, 8. Two ascospores. (Bars. A=20 μm , Fig. 4; B=10 μm , Fig. 1–3, 6; C=10 μm , Fig. 5, 7, 8.)

Key to labeling of the figures: I, basal cell of receptacle; II, suprabasal cell of receptacle; III, terminal cell of receptacle; VI, primary stalk cell of perithecium; VII, secondary stalk cell of perithecium; *a*, original septum of spore and its position in a developing thallus; *alb*, antheridiumlike branchlet; *an*, antheridium; *m*, perithecial basal cell derived from cell VI, gives rise to one vertical row of wall cells; *n*, one of two perithecial basal cells derived from cell VII, gives rise to two vertical rows of wall cells; *n'*, the other perithecial basal cell derived from cell VII, gives rise to one vertical row of wall cells; *o*, a primordial outer wall cell; *pa*, primary appendage; *spi*, spine, indurate tip of spore; *tc*, trichophoric cell, lies between carpogenic cell and trichogyne; *tr*, trichogyne (also trichogynic remnant); *w*^{1–5}, tiers of outer wall cells, 1 (basal) to 5 (terminal).



on the head at the base of the antennae of a male of *H. australis*; *RKB 3546B* (designated slide; RSA).

Isotypes.—Locality and host data as for the holotype; on the upper and lateral surfaces of the abdomen near the tip of two males; *RKB 3546B* (designated slides; RSA).

Notes and observations.—The material on which *Triceromyces floridanus* is based was growing on the upper surface of the head and on the abdomen nr. the tip of a host insect that also bore *T. hydrometrae* on its antennae and legs. Several immature individuals of the latter were mixed with the former on one of the slide mounts. However, the two species, even when immature, are readily distinguished from one another. Specimens of *T. floridanus* available for study included two mature individuals (e.g., Fig. 4); six immature individuals in \pm advanced stages of development (e.g., Fig 2, 3) (one with a young trichogyne [Fig. 1]), and one broken individual consisting of an intact receptacle with a mature appendage. Though fewer in number than might be desired, the specimens available provided ample opportunity to study the taxon and compare it with the other species parasitic on Hydrometridae.

The appendage, even in juvenile specimens, readily distinguishes *T. floridanus* from *T. hydrometrae* (see Benjamin 1986: 253, Fig. 14–31, 81, 82) not only in the stout, \pm circinate terminal branchlet (Fig. 3, 4, 6) but also in the externally convex antheridia-bearing cells, which lends the outer margin of the antheridiiferous region, in lateral view, a distinctive wavelike appearance (Fig. 1, 3, 6), a feature shared with *T. elongatus* (Fig. 9–12, 16), described below. It is likely that the crenate margins observed on some of the terminal branchlets of the appendage of *T. floridanus* (Fig. 3, 4, 6) are artifactual, the result of earlier desiccation or poor fixation of the specimens.

The perithecium of *T. floridanus*, like that of *T. hydrometrae*, is abruptly constricted just above the trichogynic remnant that persists on the posterior surface of the perithecium (Fig. 4, 5). Unlike *T. hydrometrae*, in which the distal end of the third cell of the outer row of wall cells derived from basal cell *m* forms a distinctive terminally rounded or acute, divergent projection (Benjamin 1986, Fig. 30, 81), the perithecium of *T. floridanus* is unmodified in this regard (Fig. 4, 5). The short, lateral outgrowths arising from the perithecial apex of *T. hydrometrae* are posteriorly directed (Benjamin 1986, Fig. 30, 81) whereas those of *T. floridanus* are anteriorly directed (Fig. 4, 5).

The drawings of ascospores of *T. floridanus* (Fig. 7, 8) were based on spores still inside the perithecium.

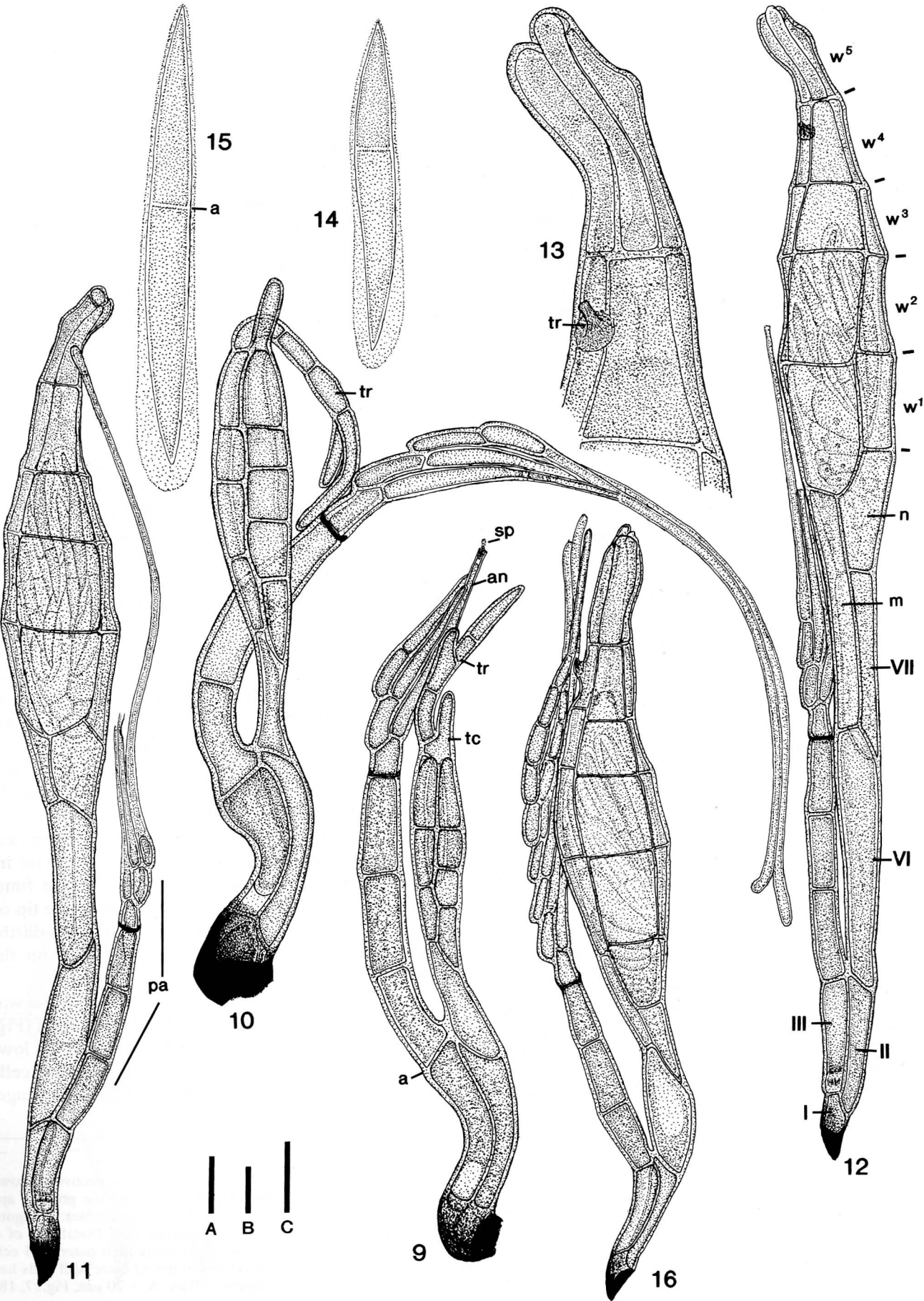
3. *Triceromyces elongatus* R. K. Benj., sp. nov. Fig. 9–16

Ascoma gracile, rectum vel leniter sigmoideum, luteolum ad plus minusve hyalinum supra pedem denigratum; 175–440 μm longum ad apicem perithecii. *Receptaculum* plus minusve curvatum, 41–62 μm longum, (13–)15–21 μm latum in parte distalibus; cellula I (cum pede) (13–)16–21 μm longa, 9–13 μm lata in parte distalibus; cellula II (27–)31–46 μm longa; cellulae III 26–40(–46) μm longa, pars supra cellulae cellulam 24–31 μm longam formans. *Appendix* 85–190 μm longa. Stipes 49–91 \times 9–11(–13) μm ; cellulae subaequales, paene cylindricae, (13–)16–33 \times 9–11(–13) μm ; septum superum leniter fuscum. Pars antheridiifera ex 3–8 cellulis superpositis constans; cellula basalis parva; margines externae cellularum intermediarum valde convexae; cellulis intermediis antheridia singula prope liberis facientibus; 1–2(–3) cellulae terminales 1(–2) prolongationes usque ad 175 μm longas 2–3.5 μm latas productentes. Antheridia elongatae, attenuatae, 40–60 \times 4–6 μm . *Perithecium* elongatum, externe valde convexum, 130–390 μm longum (cum stipite et cellulis basilaribus), in medio 26–49 μm latum. Cellulae VI, VII et *m* variabiles stipitem perithecii 25–190 μm longum facientes. Apex rectus vel plus minusve acute flexus, ad apicem obtusatus. Cellulae basilares *n* et *n'* et *m* in parte prope 0.18–0.2 corporis perithecii in tota longitudine. Cellula VI 28–132 \times 12–23 μm . Cellula VII 12–93 μm longa. Ascospores 40–60(–68) \times 5–6.5 μm . Typus *RKB 3552B* (RSA).

Ascoma: Straight to very slightly sigmoid, slender; pale yellow to \pm hyaline above blackened foot. Total length from tip of foot to tip of perithecium 175–440 μm . *Receptacle*: More or less curved, anteriorly convex, posteriorly concave, 41–62 μm long by (13–)15–21 μm wide distally, tapered downward to acute or rounded tip of foot; basal cell (I), including foot, relatively small, (13–)16–26 μm long by 9–13 μm wide immediately below cells II and III, which are elongate and subequal; cell II (27–)31–46 μm long; cell III 26–40(–46) μm long, divided near the base by a nearly transverse cross wall and forming an inconspicuous, small, empty, basal segment and an upper, elongate cell 24–31 μm long. *Appendage*: The three-celled stalk 49–91 \times 9–11(–13) μm ; cells longer than broad, subequal, nearly cylindrical (13–)16–33 \times 9–11(–13) μm ; distal antheridiiferous part, separated from upper cell of stalk by a slightly darkened septum, consisting of 3–8 superposed cells, lowermost cell small, slightly longer than broad, those above externally strongly convex, proximal cells each bearing internally a single upwardly directed, nearly free antheridium; terminal 1–2(–3) cells each subtending 1(–2) elongate, slender,

→

Fig. 9–16. *Triceromyces elongatus*. (Fig. 9–15: *RKB 3552* [Madagascar]; Fig. 16: *RKB 3545* [Sri Lanka]).—9. Juvenile individual with immature perithecium and appendage; note proximity of developing trichogyne and antheridium-producing spermatia.—10. Juvenile individual at slightly later stage of development; note elongate sterile branchlets formed by distal cells of the primary appendage.—11, 12. Two mature individuals (holotype, Fig. 12).—13. Distal part of perithecium shown in Figure 12.—14, 15. Two ascospores.—16. Mature individual. (Bars. A = 20 μm , Fig. 11, 12, 16; B = 10 μm , Fig. 9, 10, 13; C = 10 μm , Fig. 14, 15.)



sterile branchlets of varying length up to 175 μm long by 2–3.5 μm wide; antheridia elongate, uniformly tapered upward to tip, widest at base, 40–60 \times 4–6 μm . Total length to base of terminal appendage 85–190 μm . *Perithecium*: Stalk cells (VI, VII) and basal cell *m* variable in length, often comprising nearly one half total length of perithecium; primary stalk cell (VI) 28–132 \times 12–23 μm ; secondary stalk cell (VII) 12–93 μm long, often united in part throughout its length with basal cell *m*, which ranges in length from 20 to 85 μm ; basal cells *n*, *n'*; and upper part of basal cell *m* constituting ca. 18–20% of total length of body above stalk cells; body elongate, 130–390 μm long, including stalk and basal cells, intervals between successive tiers of wall cells often slightly concave, broadest near middle, 26–49 μm wide; apex nearly straight or \pm sharply bent with a slight external hump below \pm bluntly rounded tip; trichogynic remnant located about midway up from base of fourth cell of row of outer cells derived from basal cell *m*. Ascospores 40–60(–68) \times 5–6.5 μm .

Etymology.—From *elongatus* (L.), pertaining to the elongate, slender branchlets terminating the appendage.

Holotype.—**Africa**. MADAGASCAR: Majunga Prov.; Ampijoroa Forest Station; 113 km E of Majunga, 76 m; damp forest floor; 21 Nov 1986; J. T. & D. A. Polhemus (CL2283); clustered on the coxa and trochanter of the right rear leg of a male of *H. bifurcata*; *RKB 3552B* (designated slide; RSA).

Isotypes.—Locality and host data as for holotype; scattered or clustered on the lower surface of the head and clustered at the base of the rear legs of males; scattered before and after the eyes on the upper surface of the head of females; *RKB 3552B* (designated slides; RSA).

Paratypes.—**Africa**. KENYA: Masai Mara, Mara River; 5 Feb 1980; J. T. Polhemus coll. (CL1669); on left side of the abdomen near the tip of a male of *H. marani*; *RKB 3684B* (RSA).—MADAGASCAR: Tuléar Prov.; river 10 km N of Betsimba drill site, 105 km SE of Morondava, 107 m; 25 Nov 1986; J. T. & D. A. Polhemus (CL2287); on the tip of the abdomen on right side of a female of *H. isaka*; *RKB 3549B* (RSA); on the lower surface of the head between the eyes at the base of the proboscis and at the base of the left antenna of males of *H. bifurcata*; *RKB 3550B* (RSA).—Diego Suarez Prov.; small forest stream 5 km N of Joffreyville, 488 m; 16 Nov 1986; J. T. & D. A. Polhemus (CL2281); on the upper surface of the head between the eyes of a female of *H. bifurcata*; *RKB 3551* (RSA).—**Asia**. INDIA: Anamalai Hills; Cinchona, 3500 ft; 1959; P. S. Nathan

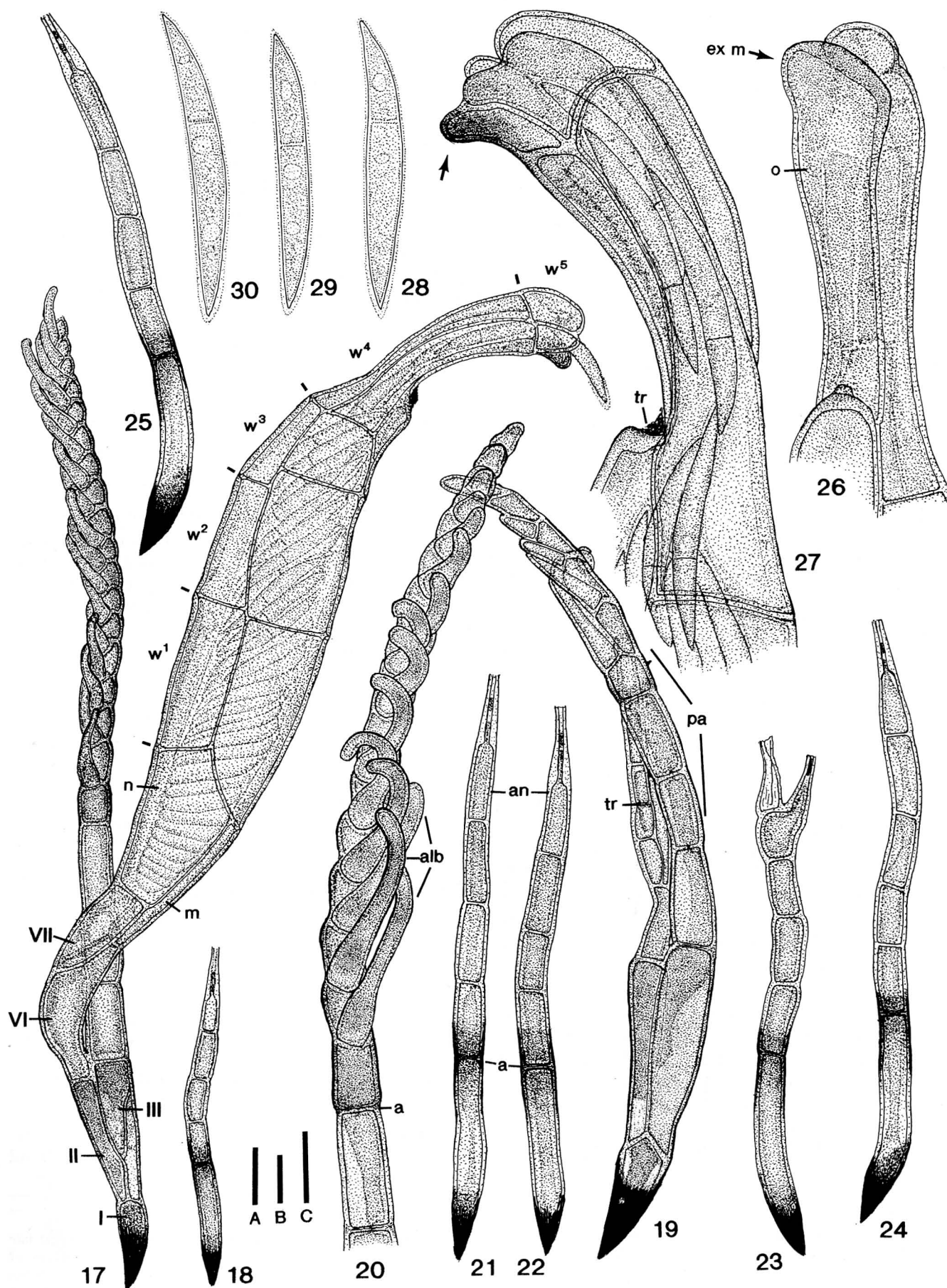
coll.; on upper surface of the abdomen nr. the tip of *H. greeni* Kirkaldy; *RKB 3680* (RSA).—INDONESIA: Timor; Nusa Tenggara Prov.; spring and stream at Oe Hala, 10 km N of Soe, 685 m; 11 Sept 1991; D. A. & J. T. Polhemus (CL2593); on the upper surface of the abdomen nr. the tip of two winged females of *H. lombok*; *RKB 3784B* (RSA) and on the lower surface of the abdomen nr. the tip of a winged male of *H. lombok*; *RKB 3785B* (RSA); spring and stream at Oe Noah nr. Polen; 24 km NE of Soe, 840 m; 12 Sept 1991; D. A. & J. T. Polhemus (CL2594); on the lower surface of the abdomen near tip of two males of *H. lombok*; *RKB 3786B* (RSA).—SRI LANKA: Colombo Dist.; Nausinna; 4 Oct 1964; K. L. A. Perera coll.; on the upper surface of the abdomen near the tip of *H. greeni*; *RKB 3543* (RSA); Gampha Dist., Yakkalamulla; 4 Feb 1964; K. L. A. Perera coll.; on the lateral surface of the abdomen nr. the tip on both sides of *H. greeni*; *RKB 3544* (RSA); Polonnaruwa; 13 Feb 1964; K. L. A. Perera coll.; on the lower surface of the abdomen nr. the tip of *H. greeni*; *RKB 3545* (RSA); Nuwara Eliya Dist.; Dambuwa Estate; 17 June 1965; K. L. A. Perera coll.; on the lower surface of the abdomen nr. the tip of a male of *H. greeni*; *RKB 3679* (RSA).

Notes and observations.—With a known range extending from eastern Africa to India, Sri Lanka, and Indonesia, *Triceromyces elongatus* probably is widely distributed on *Hydrometra* throughout the Old World tropics and perhaps beyond. Abundant material was available for study: 138 mature and 55 immature individuals (42 with mature or immature trichogynes [Fig. 9, 10]). Of these 104 mature and 39 immature specimens came from the hosts collected in Madagascar.

Triceromyces elongatus and *T. hydrometrae* shared the same host individuals in seven accessions among insects from Madagascar, Indonesia, and Kenya. In all collections of the two species, *T. hydrometrae* always was scattered randomly on either the legs or antennae of the host. *Triceromyces elongatus*, on the other hand, appeared \pm restricted in its position of growth to the upper or lower surface of the head near the eyes, or the upper, lateral or lower surface of the abdomen near the tip. Parasites often grew in clumps of several individuals. Except in those instances where the fungi developed on the sides of the abdomen near the tip on either sex, females were found to be infected on the upper surface, whereas males were infected on the lower surface.

Variability in thalloid structure of *T. elongatus* was found mostly in the length of the perithecial stalk (Fig. 11, 12, 16), which involves cells VI, VII, and the lower part of basal cell *m*, and in the number of cells comprising the antheridiiferous part of the appendage.

Fig. 17–30. *Triceromyces lithophilus*. (All *RKB 3554* [Madagascar]).—17, 18. Mature female and male individuals, respectively, showing relative size.—19. Juvenile individual with immature perithecium; the young trichogyne is partially hidden behind the primary appendage.—20. Upper part of a primary appendage showing arrangement of antheridialike branches.—21–25. Five mature males; in Figure 23 note secondary development of an antheridium from cell immediately below an aborted primary antheridium.—26. Distal part of a perithecium that is rotated slightly toward the viewer; note divergent, liplike outgrowth (arrow) of the upper primordial outer wall cell derived from basal cell *m*.—27. Distal part of a mature perithecium viewed laterally in which the short, distal tier of outer wall cells has been delimited; note extent of darkened extremity of liplike outgrowth (arrow).—28–30. Three ascospores. (Bars. A = 20 μm , Fig. 17, 18; B = 10 μm , Fig. 19–25; C = 10 μm , Fig. 26–30.)



The terminus of the main axis and the branch of the mature trichogyne lack distal prominences (Fig. 10).

4. *Triceromyces lithophilus* R. K. Benj., sp. nov.

Fig. 17–30

Dioecious. *Mas.*—Elongatus, gracilis, ex 4(–5) cellulis superpositis constans, antheridium terminale gignens, prope hyalinus praeter pedem denigratum et aream circa septum basale atrobrunneum, 110–125 μm longus; receptaculum (cum pede) 40–50 \times 6.5–8 μm ; 3(–4) cellulae aliae subaequales, cylindricae, 13–18 \times 6–8 μm ; antheridium attenuatum, 25–33 \times 5–7 μm . *Femina.*—*Ascoma* elongatum, luteolum vel luteobrunneum supra pedem denigratum; receptaculum atrobrunneum et cellulae appendicis supra stipitem atroluteobrunneae; (346–)370–430 μm longum ad apicem peritheci. *Receptaculum* triangulare, gracile, 73–85 μm altum, 23–25 μm latum in parte distalibus; cellula I (cum pede) 26–31 μm longa, 10–11 μm lata in parte distalibus; cellula II 41–54 μm longa; cellula III 45–50 μm longa, pars superum cellulae cellulam 34–40 μm longa formans. *Appendix* 229–271 μm longa. *Stipes* 73–84 μm longus; cellulae subaequales, paene cylindricae, (20–)23–31 \times 13–16 μm ; septum superum fuscum. Pars supra stipitem ex 13–18 cellulis parvis, superpositis, externe aliquantulum convexae constans; cellulis ramulos, sterilis, singulos, liberos, plus minusve curvatos, 20–45 \times 4–5 μm , basi 6–7 μm latos, gignentibus. *Perithecium* elongatum, externe leniter convexum, 289–396 μm longum (cum stipite et cellulis basilaribus), in medio 45–63 μm latum; pars terminalis basi paulo contractae, collum 59–70 μm longum, basi 12–21 μm latum, faciens; apex rotundatus, 21–29 μm latus. Cellula terminalis seriei cellulosa ex *m*-cellula basilaris oriundae prominentiam atrobrunneolam 5–6 μm longam a latere visus faciens. Cellulae basiliares (*n*, *n'*, *m*) prope 0.18 corporis peritheci in tota longitudinae. Cellula VI 38–50 \times 14–24 μm . Cellula VII 29–50 μm longa. Ascospores 34–41 \times 4.5–5 μm . Typus *RKB 3554* (RSA).

Dioecious. *Male.*—Elongate, slender, consisting of a series of 4(–5) superposed cells bearing a terminal antheridium; nearly hyaline except for blackened foot and blackish brown suffusion of area immediately above and below septum separating lowermost cell (receptacle) from those above; receptacle, including foot, 40–45 \times 6.5–8 μm ; succeeding 3(–4) cells subequal, cylindrical, 13–18 \times 6–8 μm ; antheridium 25–33 \times 5–7 μm , tapered distally, venter \pm cylindrical. Total length 110–125 μm . *Female.*—*Ascoma* elongate, yellowish to yellowish brown above blackened foot; receptacle and cells comprising appendage above stalk dark yellowish brown. Total length from tip of foot to tip of perithecium (346–)370–430 μm . *Receptacle:* Triangular, elongate, slender, 73–85 μm long by 23–25 μm wide distally, tapered downward to acute tip of foot; basal cell, including foot, relatively small, 26–31 μm long by 10–11 μm wide immediately below cells II and III, which are elongate and subequal; cell II 41–54 μm long; cell III 45–50 μm long, divided \pm me-

dianly by a strongly diagonal secondary wall and forming an elongate, empty, basal segment and an upper, elongate cell 34–40 μm long. *Appendage:* The three-celled stalk 73–84 μm long; cells subequal, longer than broad, nearly cylindrical, (20–)23–31 \times 13–16 μm ; distal part, separated from stalk by a slightly darkened septum, consisting of 13–18 small, superposed, externally slightly convex cells; each cell bearing internally a single, tapered, upwardly directed, free, \pm curved sterile branchlet; branchlets 20–45 \times 4–5 μm , 6–7 μm wide at base. Total length, including stalk, 229–271 μm . *Perithecium:* Primary stalk cell (VI) 38–50 \times 14–24 μm ; secondary stalk cell (VII) 29–50 μm long; basal cell region (i.e., cells *n*, *n'*, and *m*) 43–58 μm high, constituting ca. 18 % of total length of body above stalk cells; body, including stalk and basal cells, 289–396 μm long, \pm abruptly expanded above stalk cells, then externally slightly convex, widest near middle, 45–63 μm wide, narrowing distally, terminal part forming a slightly curved neck 59–70 μm long, by 12–21 μm wide above trichogynic remnant, which is positioned near base of fourth cell of *m* row of outer wall cells at bottom of a slight declivity formed by a distally rounded upgrowth of third outer wall cell of the *m* row; apex rounded, 21–29 μm wide, with a short, dark brownish, rounded protrusion, ca. 5–6 μm long in lateral view, formed by an extension of fifth cell of the *m* row of outer wall cells. Ascospores 34–41 \times 4.5–5 μm .

Etymology.—From *lithophilus* (in Gk. comp.), loving stones; growing or living in stony places, i. e., pertaining to the habitat of the host.

Holotype.—**Africa.** MADAGASCAR: Diego Suarez Prov.; Montagne d'Ambre Forest Reserve; Petite Cascade, cave alongside plunge pool, ca. 990 m; 16 Nov 1986; J. T. & D. A. Polhemus (CL2280); on the legs of one male and four females of *H. cavernicola* J. T. & D. A. Polhemus; *RKB 3554* (designated slide, RSA).

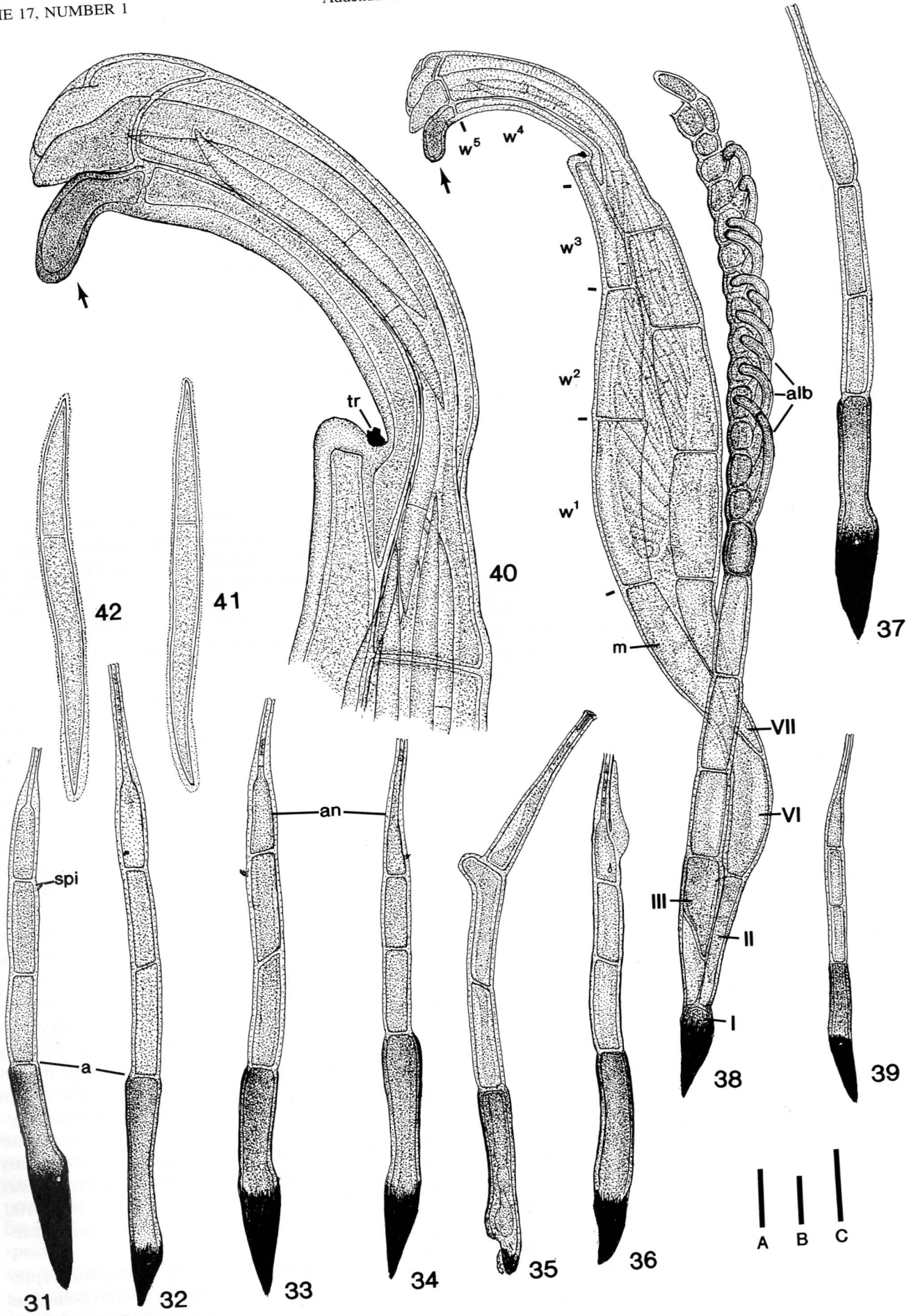
Isotypes.—Data as for holotype (designated slides, RSA).

Paratypes.—**Africa.** MADAGASCAR: Diego Suarez Prov.; Montagne d'Ambre Forest Reserve; Petite Cascade; stream, 991 m; 15 Nov 1986; J. T. & D. A. Polhemus coll. (CL2280); on the legs of a female of *H. cavernicola*; *RKB 3553* (designated slides, RSA).

Notes and observations.—See under next species.

5. *Triceromyces terrestris* R. K. Benj., sp. nov. Fig. 31–42

Fig. 31–42. *Triceromyces terrestris*. (All *RKB 3555* [Madagascar]).—31–37. Seven mature males; note (Fig. 35, 36) early and late stages of development of secondary antheridium from cells subtending primary antheridia, which may have been in early stages of abortion.—38, 39. Mature female and male individuals, respectively, showing relative size.—40. Distal part of mature perithecium shown in Figure 38 viewed laterally; note relatively long liplike extension of terminal outer wall cell (arrow).—41, 42. Two ascospores. (Bars. A = 20 μm , Fig. 38, 39; B = 10 μm , Fig. 31–37; C = 10 μm , Fig. 40–42.)



Dioecious. *Mas.*—Elongatus, gracilis, ex 3 cellulis superpositis constans, antheridium terminale gignens, prope hyalinus praeter pedem denigratum et aream infra septum basale atrobrunneum, 106–138 μm longus; *Femina.*—*Ascoma* elongatum, luteolum vel luteobrunneum supra pedem denigratum; receptaculum atrobrunneum et cellulae appendicis supra stipitem atroluteobrunneae; 338–430 μm longum ad apicem peritheci. *Receptaculum* triangulare, gracile, 80–91 μm altum, 20–24 μm latum in parte distalibus; cellula I (cum pede) 34–40 μm longa, 10–13 μm lata in parte distalibus; cellula II 41–50 μm longa; cellula III 49–56 μm longa, pars superum cellulae cellulam 31–40 μm longa formans. *Appendix* 250–294 μm longa. Stipes 88–105 μm longus; cellulae subaequales, paene cylindricae, 28–38 \times 11–16 μm ; septum superum leniter fuscum. Pars supra stipitem ex 14–21 cellulis parvis, superpositis, externe aliquantum convexae constans; cellulis ramulos, steriles, singulos, libero, plus minusve curvatos, 35–56 \times 3–5 μm , basi 5–7 μm latos, gigentibus. *Perithecium* elongatum, externe leniter convexum, 211–275 μm longum (cum stipite et cellulis basilaribus), in medio 43–53 μm latum; pars terminalis basi paulo constrictae, collum 59–69 μm longum, basi 13–16 μm latum, faciens; apex rotundatus, (18–) 21–25 μm latus. Cellula terminalis seriei cellulosa ex *m*-cellula basilari oriundae prominentiam agrobunneolam 11–15 μm longam a latere visus faciens. Cellulae basillares (*n*, *n'*, *m*) prope 0.16 corporis peritheci in tota longitudine. Cellula VI 40–55 \times 15–19 μm . Cellula VII 25–31(–40) μm longa. Ascospores 51–56 \times 3.5–4 μm . Typus RKB 3555 (RSA).

Dioecious. *Male.*—Elongate, slender, consisting of a series of 3 superposed cells bearing a terminal antheridium; nearly hyaline except for blackened foot and blackish brown suffusion of basal cell (receptacle) below septum separating it from cells above; receptacle, including the foot, (25–)40–51 \times 6–9 μm ; succeeding 2 cells subequal, cylindrical, 16–28 \times 6–7.5 μm ; antheridium 29–47 \times 5–7 μm , tapered distally, venter \pm cylindrical. Total length 106–138 μm . *Female.*—*Ascoma* elongate, yellowish to yellowish brown above blackened foot; receptacle and cells comprising appendage above stalk dark yellowish brown. Total length from tip of foot to tip of perithecium 338–430 μm . *Receptacle:* Triangular, elongate, slender, 80–91 μm high by 20–24 μm wide distally, tapered downward to acute tip of foot; basal cell, including foot, relatively small, 34–40 μm long by 10–13 μm wide immediately below cells II and III, which are elongate and subequal; cell II 41–50 μm long; cell III 49–56 μm long, divided \pm medianly by a diagonal secondary wall and forming an elongate, empty, basal segment and an upper, elongate cell 31–40 μm long. *Appendage:* The three-celled stalk 88–105 μm long; cells subequal, longer than broad, nearly cylindrical, 28–38 \times 11–16 μm ; distal part, separated from stalk by a slightly darkened septum, consisting of 14–21 small, superposed, externally slightly convex cells; each cell bearing internally a single, tapered, upwardly directed, free, sterile branchlet; branchlets 35–56 \times 3–5 μm , 5–7 μm wide at base. Total length, including stalk, 250–294 μm . *Perithecium:* Primary stalk cell (VI) 40–55 \times 15–19 μm ; secondary stalk cell (VII) 25–31(–40) μm long; basal cell region (i.e., cells *n*, *n'*, and *m*) 31–

48 μm high, constituting ca. 16 % of total length of body above stalk cells; body, including stalk and basal cells, 211–275 μm long, \pm abruptly expanded above stalk cells, then externally convex, widest near middle, 43–53 μm wide, narrowing distally, terminal part forming a slightly curved neck 59–69 μm long by 13–16 μm wide above trichogynic remnant, which is positioned near base of fourth cell of *m* row of outer wall cells at bottom of a declivity formed by a distal, rounded upgrowth of third outer wall cell of *m* row; apex rounded, (18–)21–25 μm wide, with a relatively long, dark brownish, distally rounded protrusion, ca. 11–15 μm long in lateral view, formed by an extension of fifth cell of the *m* row of outer wall cells. Ascospores 51–56 \times 3.5–4 μm .

Etymology.—From *terrestris* (L.), terrestrial, i.e., pertaining to the habitat of the host.

Holotype.—**Africa.** MADAGASCAR: Diego Suarez Prov.; Montagne d'Ambre Forest Reserve; Petite Cascade trail S of Diego Suarez, 990 m; 16 Nov 1986; J. T. & D. A. Polhemus (CL2280); on the legs and antennae of *H. phytophila* J. T. & D. A. Polhemus; RKB 3555 (designated slide; RSA).

Isotypes.—Data as for holotype (designated slides; RSA).

Paratypes.—Data as for the holotype; RKB 3556 (designated slides; RSA).

Notes and observations.—*Triceromyces lithophilus* and *T. terrestris* are unique among the species of *Triceromyces* parasitizing Hydrometridae in being dioecious. Their closely related hosts, *Hydrometra cavernicola* and *H. phytophila*, respectively, were collected in moist montane forests at the extreme northwestern end of Madagascar (Polhemus and Polhemus 1987).

The hosts live in an essentially terrestrial rather than a truly riparian to semiaquatic environment typical of other Hydrometras (Smith 1988; Polhemus and Chapman 1979). *Hydrometra cavernicola* was taken from the damp walls of a small basaltic cave and from pockets in \pm vertical rock walls near a waterfall. *Hydrometra phytophila* initially was captured by Dan Polhemus while sweeping for insects in understory vegetation, e.g., ferns and soft-stemmed plants, growing ca. 25 m below the forest canopy. Although it later was found on plants to within about 1 m of the stream at Petite Cascade, *H. phytophila* was taken from vegetation up to several km from any obvious water source. In these species, Polhemus and Polhemus (1987) postulate that a transition from the typical subaquatic environment of Hydrometras to a terrestrial habitat may have occurred locally in this forested region of Madagascar.

Hydrometra cavernicola and *H. phytophila* represent a monophyletic subgroup of the genus (Polhemus and Polhemus 1987) and are but two of some six spe-

Table 1. A contrast of morphological characteristics of males and females that distinguish *Triceromyces lithophilus* from *T. terrestris*.

	<i>T. lithophilus</i>	<i>T. terrestris</i>
Female		
Stalk of appendage	73–85 μm long	88–105 μm long
Darkened extension of lip cell as viewed laterally	5–6 μm long	11–15 μm long
Ascospores	34–41 \times 4.5–5 μm	51–56 \times 3.5–4 μm
Basal cell (I) of receptacle	26–31 \times 10–11 μm	34–40 \times 10–13 μm
Male		
Number of superposed cells including antheridium	5 (–6)	4
Brownish black suffusion of basal and suprabasal the cells above foot	Extends above and below the basal septum	Confined to region below the basal septum

cies of *Hydrometra* endemic to Madagascar. The others are *H. bifurcata*, *H. fanjahira*, and *H. isaka*, which are riparian and widespread on the island, and the rare *H. madagascarensis* Hungerford & Evans, which possibly may be terrestrial (Polhemus and Polhemus 1987); the latter was described from the island's eastern rain forests. *Triceromyces elongatus*, described above, was found on *H. bifurcata* and *H. isaka* as was the apparently cosmopolitan *T. hydrometrae*, which also was taken from *H. fanjahira*.

According to the Polhemuses, *Hydrometra cavernicola* and *H. phytophila* (see Polhemus and Polhemus [1987] for characteristics that distinguish these taxa) appear to be most closely allied to *H. madagascarensis*, *H. zeylanica* Gunawardane & Karunaratne from Sri Lanka, and *H. longicapitis* Torre-Bueno and *H. aberrans* Hungerford & Matsuda from southeast Asia. Discovery of *Triceromyces* on any of the latter species for comparison with *T. lithophilus* and *T. terrestris* could prove interesting.

Scattered thalli of *Triceromyces lithophilus* and *T. terrestris* grew in random positions on the legs or antennae of their hosts. Material of the two species recovered for study included for *T. lithophilus*: 16 mature females, 11 immature females (two with mature and one with immature trichogynes), one receptacle + appendage, and seven males; and for *T. terrestris*: 14 females, one nearly mature female, nine immature females (three with immature trichogynes), 15 receptacles + appendages, and 12 males. Comparison of these taxa suggests that *T. lithophilus* (Fig. 17–30) and *T. terrestris* (Fig. 31–42) are closely related and provide an example of the coevolution of parasites and their hosts from common ancestors, in this case possibly a riparian *Hydrometra* parasitized by a *Triceromyces* resembling—based on perithecial and trichogynic morphology—*T. hydrometrae*. To stress this presumed divergence of the parasites, I have opted to treat the fungi on *H. cavernicola* and *H. phytophila* as distinct species—they could just as well be regarded as subspecies. Several morphological characteristics serving to distinguish *T. lithophilus* and *T. terrestris* from one another are given Table 1.

The appendage of the female ascomata of both *T. lithophilus* and *T. terrestris* (Fig. 17, 20, 38) resembles that of the hermaphroditic ascomata of *T. hydrometrae* (Benjamin 1986, Fig. 29–30), *T. floridanus* (Fig. 3, 4, 6), and *T. elongatus* (Fig. 11, 12, 16) in having a three-celled stalk subtending a series of superposed cells some or all of which may give rise to single divergent branchlets. In the latter three species, as in other hermaphroditic species of *Triceromyces* (Benjamin 1986), these branchlets are transformed into simple antheridia which form spermatia exiting through often relatively elongate discharge tubes that early on are positioned near trichogynes (Benjamin 1986, Fig. 23, 26; Fig. 1, 6, 9, 10). In *T. lithophilus* and *T. terrestris* trichogynes develop on juvenile individuals; however, the branchlets formed by the upper cells of the appendage, though antheridialike in appearance, are sterile (Fig. 17, 19, 20, 38). On appendages of aged females, some branchlets may break off distally, undoubtedly the result of external forces, and have the appearance of antheridia, but there is no evidence of their ever producing spermatia. Instead, antheridia are developed terminally on the cellular axes of simple males, which differ subtly in dimension and pigmentation in the two species as shown in Figures 18, 21, 22, 23–25, 31–37, 39 and as contrasted in Table 1. As in hermaphrodites, the trichogyne terminating the young perithecium of a juvenile female ascoma in *T. lithophilus* and *T. terrestris* would be at about the same level as the antheridium terminating a male with which it is paired on the host (cf. Fig. 19, 21, 22, which are depicted at the same magnification).

REVIEW OF DIOECISM IN THE LABOULBENIALES

Since publication of my previous study of *Triceromyces* (Benjamin 1986), seven genera have been added to the 132 recognized at the time by Tavares in her treatise on Laboulbeniales (Tavares 1985): *Majewskia* Y. B. Lee & K. Sugiy. (Lee and Sugiyama 1986), *Sugiyamaemyces* I. I. Tav. & Balazuc (Tavares and Balazuc 1989); *Cupulomyces* R. K. Benj. (Benjamin 1992a), *Phalacrichomyces* R. K. Benj. (Benjamin

Table 2. Currently known occurrence of dioecy and trioecy in the Laboulbeniales. Suprageneric hierarchies are those of Tavares (1985) except for Aporomycetaceae (Benjamin 1989: 365).

Tavares's classification (in part)	Only dioecious taxa known	Dioecious and monoecious taxa known	Monoecious, dioecious, and trioecious taxa known
Herpomycetinae			
Herpomycetaceae	<i>Herpomyces</i> Thaxt. (1902)		
Laboulbeniineae			
Laboulbeniaceae			
Laboulbenioideae			
Laboulbenieae			
Laboulbeniinae		<i>Laboulbenia</i> Mont. & Robin (in Robin 1853)	
Stigmatomycetinae	<i>Apatomyces</i> Thaxt. (1931) <i>Parvomyces</i> Santam. (1995) <i>Picardella</i> I. I. Tav. (1985)	<i>Cryptandromyces</i> Thaxt. (1912)	<i>Triceromyces</i> T. Majewski (1981)
Amorphomycetinae	<i>Amorphomyces</i> Thaxt. (1893) <i>Corylophomyces</i> R. K. Benj. (1995) <i>Dioicomyces</i> Thaxt. (1901) <i>Rhizopodomyces</i> Thaxt. (1931) <i>Tetrandromyces</i> Thaxt. (1912)	<i>Nanomyces</i> Thaxt. (1931) <i>Aporomyces</i> Thaxt. (1931)	
Aporomycetaceae			
Euphoriomycetaceae			
Euphoriomycetinae		<i>Euphoriomyces</i> Thaxt. (1931)	
Peyritschelloideae			
Dimorphomycetaceae	<i>Dimeromyces</i> Thaxt. (1896) <i>Dimorphomyces</i> Thaxt. (1893) <i>Nycteromyces</i> Thaxt. (1917) <i>Polyandromyces</i> Thaxt. (1920) <i>Trenomyces</i> Chatton & F. Picard (1908)		

1992b), *Corylophomyces* R. K. Benj. (Benjamin 1995), *Parvomyces* Santam. (Santamaria 1995), and *Triainomyces* W. Rossi & A. Weir (Rossi and Weir 1998). The species comprising *Corylophomyces* and *Parvomyces* are dioecious, bringing the number of genera from 18 to 20 in which dioecism has been demonstrated or strongly suspected in some or all included species. For ease of comparison, the distribution of dioecy and trioecy among genera included in the several suprageneric taxa of those recognized by Tavares (1985: 93–99) is listed in Table 2.

Suborder Herpomycetinae has but one monogeneric family, Herpomycetaceae. *Herpomyces* (Table 2), which includes some 25 dioecious species, occurs only on cockroaches (Blattaria) (Tavares 1985; Thaxter 1908, 1931). Spores producing males and females usually become attached at each end to host spines or setae where they germinate and form a primary receptacle consisting of several (usually four) superposed cells. The basal attachment persists and is incorporated into a relatively small blackened foot, whereas the upper end of the receptacle frequently separates from the seta or spine. In the male of some species, one or more distal cells of the primary receptacle forms short branchlets bearing elongate, flask-shaped antheridia; in

other species the suprabasal cell gives rise to a fertile branch that forms a secondary receptacle, which becomes attached to the host and bears antheridial branchlets. In females, the terminal and subterminal cells of the germinated spore typically do not divide, whereas the suprabasal cell may give rise directly to a fertile branch or it may divide and form a series of superposed cells each of which may form fertile branches. Fertile branches become attached to the host, giving rise to secondary receptacles that may form one or more perithecia. Tavares (1965) reported the formation of functional antheridia on aborted females of *H. paranensis* Thaxt., demonstrating the potential for maleness in stressed or damaged female thalli in members of this genus.

In Laboulbeniineae, dioecious taxa have been reported in two of the four subfamilies, Laboulbenioideae and Peyritschelloideae, of the Laboulbeniaceae, one of the three families recognized in the suborder by Tavares (1985).

Some or all taxa belonging to 14 genera of Laboulbenioideae are dioecious (Table 2).

The receptacle of *Laboulbenia* (tribe Laboulbenieae; subtribe Laboulbeniinae) typically comprises five cells disposed in four tiers: the basal cell (I), which includes

the foot; the suprabasal cell (II) surmounted by cell III; and finally two cells placed \pm side by side, an outer cell IV and an inner cell V. Cell II subtends the perithecium and its stalk cells (VI and VII), which may be free or, more often, united with the upper receptacular cells (III–V). Thaxter's (1896) use of Roman numerals I–VII to designate the receptacular cells and perithecial stalk cells of *Laboulbenia* has, by convention, been adopted (with modifications here and there because of lack of divisions, especially of cell III, or of secondary divisions of some of the cells) by later students in describing other Laboulbeniales. In *Laboulbenia*, cells IV and V subtend a broad, usually flattened cell, the insertion cell, which is the basal cell of the usually multicellular primary appendage. The appendage typically consists of an outer simple or ramified branch and an inner, often smaller, branch bearing antheridia. Each vertical row of outer wall cells of the perithecium consists of four cells of unequal height.

Laboulbenia is a large, diverse genus with many hundreds of species; however, it has but few confirmed dioecious taxa. In *Laboulbenia formicarum* Thaxt. males and females are nearly identical morphologically, differing only in the lack of antheridia on females and perithecia on males (Benjamin and Shanor 1950). Three presumed dioecious species of *Laboulbenia*, *L. vignae* W. Rossi (1978), and *L. inflata* Thaxt. and *L. marina* F. Picard (Santamaria 1996b), have ascomata that lack antheridia-bearing appendages but are paired with small presumptive males consisting of a few superposed cells terminated by an apparent simple antheridium. In *L. inflata*, Santamaria (1996b) describes and illustrates minute, sawtoothlike organelles formed along the inner margins near the base of juxtaposed spores. These organelles, which fit tightly into one another, appear to strengthen the union not only of a pair of spores during and after discharge but also of thalli developing on the host, for remnants of them persist and can be found on the blackened feet of thalli separated in slide mounts (Santamaria 1996b). From my own unpublished observations, and as noted by Santamaria (1996b), questions regarding the variation in and the extent of dioecism in *Laboulbenia* need much additional study.

Currently there are five genera of subtribe Stigmatomycetinae (tribe Laboulbenieae) in which dioecy has been described (Table 2). All known species of three genera, *Apatomyces*, *Parvomyces*, and *Picardella* are dioecious. *Apatomyces*, with one species, *A. laboulbenioides* Thaxt. (1931), resembles a *Laboulbenia* superficially but has only a three-celled receptacle (a characteristic of all Stigmatomycetinae) in which cell III is united with cell VI. The perithecium above cell VI is free of the primary appendage, the latter consisting of two small superposed cells the upper of

which bears two to three slender branchlets. The male comprises four superposed cells subtending a single terminal antheridium. *Parvomyces*, also with but one species, *P. merophysiae* Santam. (Santamaria 1995), is one of the smallest known members of the Laboulbeniales. Cells I and II of the receptacle are laterally adnate to one another; cell III bears an elongate unbranched appendage; cell II subtends a perithecium in which the two vertical rows of outer wall cells derived from basal cell *n* have fewer cells than the two rows derived from basal cells *m* and *n'*. The male consists of but three superposed cells bearing a terminal, spinose antheridium. In *Picardella*, with two species, *P. catalaunica* Santam. (Santamaria 1989b) and *P. endogaea* (F. Picard) I. I. Tav. (Tavares 1985), cells I, II, and III are superposed. In *P. catalaunica* cells II and III may divide secondarily, so that the receptacle may consist of more than three cells. In *Picardella*, unlike *Apatomyces*, cell III is free from cell VI and the primary appendage is simple and unbranched. The male of *P. endogaea* consists of three superposed cells bearing a single, relatively large antheridium; the male is unknown in *P. catalaunica*.

Cryptandromyces, as revised by Tavares (1985), includes some 13 species on Scydmaenidae and Pselaphidae (Coleoptera) and one species on a wholly unrelated host, an unidentified species of Dermaptera. The receptacle of *Cryptandromyces* consists of three cells in which cells II and III are side by side or diagonally placed. The multicellular primary appendage is unbranched or only slightly branched. Antheridia may be formed directly from intercalary cells of the appendage and have lateral, divergent discharge tubes, or in some instances they are free phialides. Each vertical row of outer perithecial wall cells consists of five cells of \pm equal height. Based on her studies of the genus, Tavares concluded that only *Cryptandromyces batrisoceni* (Thaxt.) I. I. Tav., on a pselaphid (Thaxter 1931, Pl. 35, fig. 19–31), and *C. sarawakensis* (Thaxt.) I. I. Tav., on a scymaenid (Tavares 1985, Pl. 46, fig. i, j) are dioecious, the small male consisting of some four cells terminated by simple antheridia.

In the final genus of Stigmatomycetinae to be summarized here, *Triceromyces*, the subject of this paper, we find the greatest degree of sexual diversification yet found in the Laboulbeniales (Table 2). Two of the new species described, *T. floridanus* and *T. elongatus*, bring to five the number of apparently strictly monoecious taxa, two on Hebridae and three on Hydro-metridae. *Triceromyces bullatus*, *T. biformis*, and *T. poissonii* are the only known trioecious species in the order, having both monoecious (i.e., hermaphroditic) morphs and dioecious morphs in which a small, few-celled male is accompanied by a female having a simple, few-celled primary appendage lacking branchlets. Finally, in the two apparently strictly dioecious taxa,

T. lithophilus and *T. terrestris*, a simple male is paired with a female having a primary appendage resembling that of a hermaphrodite in which sterile, antheridialike branchlets have replaced functional antheridia.

Subtribe Amorphomycetinae (tribe Laboulbenieae) includes six genera (Tavares 1985). In five of these all known species are dioecious, i.e., *Amorphomyces*, *Corylophomyces*, *Dioicomycetes*, *Rhizopodomycetes*, and *Tetrandromycetes*. The other genus, *Nanomyces*, with three presumably dioecious species according to Thaxter (1931), was studied by Tavares (1985) who concluded that this may be true for only two. In my studies of *Corylophomyces* (Benjamin 1995) and *Rhizopodomycetes* (Benjamin 1979), I discussed the above genera in some detail; thus, I shall mention their characteristics only briefly here. The receptacle of the male of *Amorphomyces* and *Corylophomyces* is two-celled and bears a single terminal antheridium. The female receptacle of *Corylophomyces* is three celled, with cell II subtending a stalked perithecium and cell III subtending a free, two- or three-celled appendage. In *Amorphomyces* the female receptacle is two celled; the suprabasal cell, termed a II-III cell by Tavares (1970), bears on one side a short-stalked perithecium and on the other side a rudimentary, inconspicuous, two-celled appendage that is completely fused with the base of the perithecium (Tavares 1970). The receptacle of the male of *Rhizopodomycetes* also is two celled. In some species the terminal cell is transformed into an antheridium. In others it is sterile and forms a simple, one-celled, sometimes nonpersistent appendage; in such cases, the suprabasal cell of the receptacle divides and one or two of the resultant cells form antheridia directly. The female of *Rhizopodomycetes*, like that of *Amorphomyces*, is two celled and the suprabasal cell, a II-III cell, initially subtends a simple, one-celled appendage (which may or may not persist) that is deflected aside as the long-stalked perithecium develops from cell II-III (Benjamin 1979). In the male of *Dioicomycetes* and *Tetrandromycetes* the receptacle is one-celled, subtending two or several cells that form one or several antheridia respectively. The female is nearly identical in both of these genera, having a three-celled receptacle bearing a stalked perithecium on one side and a single-celled appendage on the other (Thaxter 1931; Tavares 1985). In the presumably dioecious species of *Nanomyces*, *N. appendiculatus* Thaxt. and *N. fijianus* Thaxt. (Tavares 1985), the males consist of a small but variable number of superposed cells. Tavares (1985) observed distinct dimorphism in a pair of germinating spores of *N. fijianus*, a feature of some species of *Dioicomycetes* and *Aporomyces*. Thaxter observed simple, sterile branchlets accompanying the 1–3 antheridia on males of *N. fijianus* (Thaxter 1931: Pl. XXXVIII, fig. 24–26). Having observed several presumptive males of *N. perpendicularis* Thaxt., Thaxter

(1931) believed the species to be dioecious; however, Tavares (1985) found a female bearing an antheridium in Thaxter's collections and disputes the dioecious status of this species. The females (or hermaphrodites) of *Nanomyces* have a short, three-celled receptacle with cells II and III side by side; the primary appendage consists of 3–5 superposed cells; the long-stalked perithecium has small, well-defined basal cells and, according to Tavares (1985), five to six unequal cells in each row of outer wall cells. Among Amorphomycetinae, *Amorphomyces*, *Corylophomyces*, *Dioicomycetes*, and *Tetrandromycetes* probably are closely related based on morphological similarities; however, *Nanomyces* and *Rhizopodomycetes* appear not closely related to these genera or to one another (Benjamin 1995).

Species of *Aporomyces*, the only genus in tribe Aporomyceteae, stand apart from those of other genera of Laboulbeniales in the development and structure of the perithecium, which has five, rather than the usual four, vertical rows of inner and outer wall cells. These five rows, which in mature species consist of only two or three cells each depending on the species, arise from five rather than three basal cells as in other Laboulbeniinae (i.e., *n*, *n'*, and *m*) as follows: Each of basal cells *n* and *n'*, derived from cell VII, gives rise to a single row of wall cells. Cell VI gives rise early on to two basal cells, *m* and *m'*, and, indirectly via cell *m*, to an auxiliary basal cell *mac* lying between *m* and *m'*; each of these cells forms a single row of wall cells (for details and illustrations see Benjamin 1989). The perithecium of *Aporomyces*, reminiscent of *Coreomyces* Thaxt. (Benjamin 1971; Thaxter 1908; Tavares 1985), comprises the perithecial wall cells, stalk cells, basal cells, and centrum that have developed inside of and are bounded above and laterally by the ever-expanding wall of the original perithecial primordial cell and below by the subtending cell of the receptacle. As the perithecium matures, cell VI gradually enlarges, its wall appears to become disorganized, and the resultant cavity forms much of the perithecial venter within which the centrum with its complement of ascospores matures.

Five of the eight known species of *Aporomyces*, *A. uniflagellatus* Thaxt., *A. szaboi* Bánhegyi, *A. trinitatis* Thaxt., *A. physemi* R. K. Benj., and *A. lutrochi* R. K. Benj., are demonstrably dioecious with a large female individual always being accompanied by a small male consisting of two or three superposed cells terminated by a simple antheridium. Two species, *A. subulatus* Thaxt. and *A. byrrhini* R. K. Benj., have ascomata (?females) accompanied by reduced, presumably male thalli in which antheridia have not been demonstrated. All of the above taxa parasitize species of Limnichidae (Coleoptera). One poorly known species, *A. perpusillus* (Speg.) I. I. Tav., on a myrmecophilous species of Staphylinidae (Coleoptera) may be monoecious; how-

ever, ascomata bearing antheridia or reduced malelike thalli have not been observed.

The female receptacle in *Aporomyces* consists initially of a basal cell (I), a suprabasal cell (II), and a terminal cell (III), which subtends a primary appendage of few to many cells. Secondary appendages often arise from cell III or cells resulting from the division of III. Cell II may undergo a variable number of transverse divisions leading to a receptacle consisting of few or, in the dioecious species especially, many superposed cells. The perithecial initial arises from an intercalary cell of the receptacle. When mature, the thallus consists of a perithecium subtended by a multicellular stalk and a few- or many-celled extension of the receptacle attached near the base of the perithecium or distally on the perithecial wall. In all five species of *Aporomyces* having apparently functional males, the male ascospore is much smaller than that of the female. Dimorphic ascospores also are a well-known feature of some species of *Dioicomyces* (Thaxter 1908; Benjamin 1970).

With the removal of *Aporomyces* from Euphoriomyceteae (Benjamin 1989), the tribe, as treated by Tavares (1985), includes five genera, of which *Euphoriomyces*, with 14 currently recognized species (Tavares 1985; Majewski 1988a; Santamaria 1991; Rossi and Santamaria 1992), has two species, *E. aglyptonoti* Thaxt. and *E. cioideus* Thaxt., that are dioecious (Tavares 1985). Basically, the thallus of *Euphoriomyces* consists of an axis of superposed cells terminating in a simple or branched primary appendage. Cells of the axis may not divide or those above the basal two or three cells may divide longitudinally and form tiers of two or more cells. Stalked perithecia or secondary appendages arise laterally from marginal cells of the axis on one or both sides. At maturity, the perithecial body is subtended only by the cell of the axis from which it arose, the true stalk and basal cells having become disorganized. The outer wall of the perithecium consists of three vertical rows of three cells each and one row of four cells. The cells comprising the basal tier are much longer than those of the upper tiers. Simple terminal or intercalary antheridia may develop on branches of the primary or secondary appendages. *Euphoriomyces aglyptonoti* and *E. cioideus* do not appear to be closely related (Tavares 1985). Both have simple males consisting of several superposed cells; that of *E. cioideus* may form an antheridium from each of several distal cells (personal observation).

All known dioecious members of subfamily Peyrischielloideae are classified in five genera of tribe Dimorphomyceteae (Tavares 1985) (Table 2). *Dimorphomyces* currently includes some 29 species, 27 on members of two orders of insects (Hexapoda), i.e., Coleoptera (26), mostly Staphylinidae, and Hymenoptera (one), and two on one order of arachnids (Arachno-

idea), i.e., Acarina. The female receptacle consists of three superposed cells. The upper cell (III) subtends a usually simple, few-celled primary appendage; cell I grows outward on one side (rarely on both sides) to a varying degree depending on the species and cuts off a succession of few to many cells that become \pm parallel to one another and to the suprabasal cell (II). The cells of this lateral, \pm divergent secondary axis may give rise above, usually alternately, to single perithecia and single sterile appendages. The male of *Dimorphomyces* is like the female but lacks sterile appendages and forms only one (rarely more) compound antheridium. *Dimeromyces*, which resembles *Dimorphomyces*, is one of the larger genera of Laboulbeniales with at least 108 currently recognized species. Hosts are diverse, being found in five orders of insects, i.e., Coleoptera, Dermaptera, Diptera, Isoptera, and Orthoptera, and one order of arachnids, i.e., Acarina. The female receptacle of *Dimeromyces* differs from that of *Dimorphomyces* in that products of division of cell I are interposed between cells I and II, forming a vertical axis in which the basal and suprabasal cell of the primary receptacle become \pm distantly separated from one another. Cells of the resulting secondary axis, as in *Dimorphomyces*, give rise to perithecia and sterile secondary appendages, often on both sides, the latter often outnumbering the former. The male of *Dimeromyces* often forms several compound antheridia, and it may, in addition, bear sterile secondary appendages. In mature perithecia of both genera, the walls between the stalk-cells and basal cells disappear so that the perithecial cavity is continuous to its point of attachment to the cell of the secondary axis from which it arose.

Nycteromyces and *Trenomyces* appear to be related to *Dimeromyces* especially, but their included taxa have a much more limited host range. The type and only described species of *Nycteromyces*, *N. streblidinus* Thaxt. (1917) is parasitic on one of the Streblidae (Diptera), a family of flies ectoparasitic on bats. The receptacles of males and females of this taxon are similar in being three-celled; they are terminated by nearly identical, single-celled, slightly apiculate, domelike appendages, which represent the distal cell of the original ascospore. In the male, cells I and III become separated from one another by the proliferation of the suprabasal cell (II), which forms a series of as many as five superposed cells, each giving rise to single compound antheridia, which are arranged unilaterally. In the female, the suprabasal cell gives rise to a perithecium in which, from early development, the stalk cells and basal cells lose their identity and the perithecial cavity is continuous from base to apex. In as yet undescribed representatives of *Nycteromyces* in my collection from both hemispheres, cell II of the receptacle of females in material from Australia, India, The Philippines, and Africa, all on Streblidae, proliferates

as in males, each cell often giving rise to a perithecium. Sterile secondary appendages have not been observed in the genus.

All of the eleven described species of *Trenomyces* are parasitic on biting lice, i.e., Mallophaga, wingless ectoparasites of birds and mammals (Tavares 1985); however, a number of as yet undescribed forms are known on Hippoboscidae (Diptera), also from birds and mammals, and on sucking lice, i.e., Anoplura (Tavares 1985; Benjamin, unpubl.). The primary receptacle of males and females in this genus is two celled and, depending on the species, bears distally a one- or two-celled primary appendage derived from the distal segment of the ascospore. The upper cell of the receptacle in both sexes cuts off few or many smallish cells that \pm corticate the upper surface of cell I. These cells give rise to stalked compound antheridia in males and stalked perithecia in females. Sterile secondary appendages are unknown in the genus. Like other Dimorphomycetaceae, the cavity of the perithecium is continuous throughout at maturity.

The final member of the tribe to be considered here, *Polyandromyces*, with one species, *P. coptosomalis* Thaxt., and one variety, *P. coptosomalis* var *minor* Thaxt., found on *Coptosoma* (Heteroptera; Pentatomidea; Plataspidae [Henry and Froeschner 1988: xiv]) resembles *Nycteromyces* and *Dimeromyces* somewhat in the characteristics of the female, but differs greatly in the characteristics of the male (Thaxter 1924: 316; Benjamin 1971: 49). In the female, the upper spore segment forms a short, distally rounded, two-celled, sterile appendage whereas divisions of the lower segment produce a superposed series of four short cells above the more elongate basal cell. The supra-basal cell separates a small cell laterally that eventually is united with the base of the perithecium, which arises from the median cell (Thaxter 1924). The perithecium lacks discernable stalk and basal cells. The distinctive male, when mature, consists of a two-celled receptacle, derived from the basal spore segment, and a large, terminal compound antheridium subtended by two small superposed cells derived from the distal spore segment (Thaxter 1924).

DISCUSSION

Triceromyces on *Hydrometridae*

Although similar in many respects, the five species of *Triceromyces* on *Hydrometridae* treated in this paper appear to fall into two distinct groups based on morphology of the ascoma and position of growth on the host. One group comprises *T. floridanus* and *T. elongatus*, the other *T. hydrometrae*, *T. terrestris*, and *T. lithophilus*.

Triceromyces floridanus and *T. elongatus* are more closely comparable to one another than to the other

three species in the nature of the antheridiiferous part of their primary appendages, where, in lateral view, the cells have strongly convex outer margins, with each cell in the upward series above the stalk—excepting the lowermost cell—appearing \pm offset from the preceding cell. Both differ noticeably, however, in the character of the elongate sterile terminations of the appendage. In *T. floridanus* there is a single, robust, strongly recurved branchlet, whereas in *T. elongatus* there may be several slender, elongate, \pm straight branchlets. The abrupt constriction of the perithecial neck at the level of the trichogynic remnant in *T. floridanus* recalls that of *T. hydrometrae*, but in the former, unlike the latter, there is no pronounced upgrowth of cell three of the outer row of perithecial wall cells arising from basal cell *m* (Benjamin 1986).

Aside from bearing sterile antheridialike branchlets rather than functional antheridia, the cells comprising the appendage above the stalk in ascomata of *T. lithophilus* and *T. terrestris* resemble those of *T. hydrometrae* in being hardly or only moderately externally convex and superposed \pm in line. These species also are similar in that the perithecial neck is \pm constricted at the level of the trichogynic remnant, which in all three taxa is located at the base of a \pm pronounced recess between the perithecial body and a distally rounded upgrowth of the third cell of the *m*-cell-derived row of outer wall cells.

The position of growth on the host reflects an apparent distinct difference in the mode of transmission of the species comprising the two groups proposed above. Thalli of *T. elongatus* typically develop on the host—often in clusters—on either the head or the abdomen near the tip. Females typically are infected on the upper surface, males on the lower surface. In some instances thalli are found on the lateral surface of the abdomen near the tip of both male and female hosts. Too few specimens of *T. floridanus* were observed to note a trend; however, the few thalli recovered were on males, and, unlike those on most males of *T. elongatus*, grew on the upper surface of the head of one host and on the upper and lateral surfaces of the abdomen of two hosts. Nevertheless, growth of these parasites on relatively restricted areas on the abdomen or head of the host suggests that transmission of these fungi may be related to contact between the bodies of female and male insects at the time of mating. The apparently anomalous position of growth of *T. floridanus* on males could be the result of attempted copulations between males as was observed by Whisler (1968) in *Stigmatomyces ceratophorus* Whisler on *Fannia canicularis* (L.). On the other hand, in *T. hydrometrae*, *T. lithophilus*, and *T. terrestris*, fungal thalli typically are scattered randomly on legs and antennae of male and female hosts. Thus, a different behavior pattern involving only contact of legs and/or

antennae between interacting insects may be involved in transmission of these fungi from host to host.

Sexuality in Laboulbeniales

There is scant direct evidence of fertilization in Laboulbeniales. Tavares (1985) demonstrates diakinesis in the young ascus of the dioecious species *Herpomyces periplanetae* Thaxt., indicating meiosis and suggesting that one nucleus in the dikaryon came from an antheridium on a male thallus. However, there is much indirect evidence based on morphology of the reality of sexual interactions in both monoecious and dioecious Laboulbeniales (Benjamin 1971: 51–52, 1979, 1986, 1989, 1995; Tavares 1985: 83–88). Throughout the order where early stages of ascomatal development have been studied, the young perithecium bears a trichogyne that typically matures close to one or more antheridia that are actively producing spermatia. Also spermatia often are found attached to trichogynes. Soon after a perithecium begins to enlarge and mature, the trichogyne typically degenerates and disappears except, in many species, for a \pm conspicuous basal remnant affixed to the perithecial surface. In taxa producing only one perithecium, antheridia may become nonfunctional as a thallus ages; falling away (e.g., *Mimeomyces* Thaxt., 1931); becoming disorganized (e.g., *Gloeandromyces* Thaxt., 1931); or withering and giving way to sterile branchlets (e.g., *Laboulbenia* spp. [Benjamin 1967]). In taxa having \pm indeterminate growth, where several successive perithecia may develop, each young perithecium may be accompanied by its own antheridia-bearing branch (e.g., *Balazucia* R. K. Benj., 1968; *Cucujomyces* Thaxt., 1931; *Histeridomyces* Thaxt., 1931; *Scaphidiomyces* Thaxt., 1931).

Dioecism in Laboulbeniales

The existence of morphologically distinct male and female thalli, i.e., dioecism, in Laboulbeniales first was recognized by Thaxter when he described *Amorphomyces* and *Dimorphomyces* in 1893. Subsequently, as reviewed in the previous section and summarized in Table 2, the phenomenon proved to be a feature of some or all members of disparate genera in the order. However, in the near absence of definitive knowledge of functional sexuality in Laboulbeniales (see above), the role, if any, of dioecism in the reproductive biology of those taxa in which it occurs is unknown.

Based on morphology, the many differences in the degree of thalloid modification of males and females suggest that dioecism has evolved independently several times in the Laboulbeniales (Benjamin, 1971, 1979, 1986, 1989, 1995; Tavares 1985). With some exceptions, it is common in Laboulbeniales for ascospores to be discharged from the perithecium in pairs and to be thus affixed to the integument of the host

(Thaxter 1896). Instead of two similar hermaphroditic thalli developing from a pair of spores, common in monoecious Laboulbeniales, one occasionally encounters an antheridium-bearing, i.e., male, thallus growing with a hermaphrodite. Examples of this phenomenon include *Stigmatomyces sarcophagae* Thaxt. (Thaxter 1908: Pl. XLIX, fig. 16–17), *Hydrophilomyces rhynchophorus* (Thaxt.) Thaxt. (Tavares 1985: Pl. 51f), and *Stigmatomyces ceratophorus* (Whisler 1968: Fig. 5f). Such males, growing alongside typical bisexual thalli, probably result from anomalous development of one member of a spore pair, and their occurrence may have nothing to do with the evolution of dioecy in the Laboulbeniales (Benjamin 1986). This phenomenon can be compared to the occasional abnormal production, on damaged or aborted thalli, of antheridia-bearing branches as described by Tavares for the dioecious *Herpomyces paranensis* (Tavares 1965: Fig. 17–19) and Thaxter for the monoecious *Laboulbenia flagellata* Peyr. [as *L. elongata* Thaxt.] (Thaxter 1896: Pl. II, fig. 7, 8). Shift in the potential for certain cells or groups of cells in a thallus to form only female structures may be overridden by physiological changes brought on by trauma. Further study of the presumably dioecious species in genera like *Cryptandromyces*, *Euphoriomyces*, and *Nanomyces* may reveal similar anomalies for some of the taxa or that others, like *E. cioideus*, are misplaced generically (Tavares 1985).

Structure of males and females ranges from that seen in *Laboulbenia formicarum* and all of the taxa comprising the Dimorphomycetaceae, where in both sexes of each genus the primary appendages are similar and the receptacles differ only in the formation of either male or female reproductive structures, to those like members of Amorphomycetinae where the male is reduced to only two or three superposed cells bearing a single terminal antheridium. In the large genus *Laboulbenia*, with hundreds of typically hermaphroditic species, *L. formicarum* may be viewed as an early stage, possibly of recent origin, of the evolution of dioecy in the genus, wherein there has been only a loss of bisexuality without obvious reduction in size of the male as is seen in other dioecious species of *Laboulbenia* like *L. inflata* and *L. marina* (Santamaria 1996b). On the other hand, in genera of Dimorphomycetaceae like *Dimeromyces* with over a hundred known species dioecy must have evolved long ago with some subsequent reduction in size of the male but without other marked changes between the sexes in thalloid morphology.

The range of sexual plasticity in *Triceromyces* is the most remarkable yet found in Laboulbeniales and provides examples of at least two possible stages in the evolution of dioecy from monoecy in the order. The two species on Hebridae, *T. balazucii* and *T. hebri*, are known only as hermaphrodites. Monoecious-dioecious

dimorphism characteristic of *T. bullatus*, *T. biformis*, and *T. poissonii*, parasitic on Mesoveliidae, evidences the possibility for a shift from monoecy to dioecy where normal hermaphrodites and unisexuals, i.e., simple males and females with highly reduced appendages, still coexist. The dioecious condition in *T. terrestris* and *T. lithophilus*, on Hydrometridae, where relatively simple males are accompanied by ascomata (females) in which the appendage has undergone little morphological change save for the loss of sexual function, can be viewed as a transitional stage from monoecy to dioecy intermediate between that of a hermaphrodite like *T. hydrometrae*, also on Hydrometridae, and the dioecious morphs of a trioecious species like *T. biformis* where the appendage of the ascomata has become reduced to a few superposed cells.

Most of the strictly dioecious Stigmatomycetinae and Amorphomycetinae feature simple males consisting of a few superposed cells and a single terminal antheridium derived from the upper cell of the two-celled ascospore; some males are only a cell or two removed from the original spore from which they arose. Among Amorphomycetinae, *Amorphomyces*, *Corylophomyces*, *Dioicomyces*, and *Tetrandromyces* appear closely related based on morphological similarities. However, *Nanomyces* and *Rhizopodomyces* probably are not closely related either to these genera or to one another (Benjamin 1979, 1995). In the latter genera, the antheridium (or antheridia) of the male of some species may not be strictly terminal, being accompanied by a sterile branchlet(s), which in the case of *Rhizopodomyces* represents the terminal cell of the original ascospore, the antheridium(a) arising from the distal cell of the receptacle (Benjamin 1989).

Ascosporic dimorphism has been observed in dioecious species of at least three genera, i.e., *Aporomyces* (Bánhegyi 1944; Benjamin 1989), *Dioicomyces* (Thaxter 1908; Benjamin 1970), and *Nanomyces* (Tavares 1985). This presumably derived condition within Laboulbeniales is especially well marked in five species of *Aporomyces*, and the most extreme case of spore dimorphism yet known in the Laboulbeniales is found in *A. leutrochi* where the male spore, only about half the length and half the width of the female spore (Benjamin 1989), is \pm enveloped by the sheath surrounding the female spore.

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