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SYNANDROMYCES TELEPHANI (ASCOMYCETES: LABOULBENIALES) FROM ILLINOIS AND DEVELOPMENT OF ITS TRICHOGYNE

Richard K. Benjamin

Abstract.—*Synandromyces telephani,* originally described from Argentina and subsequently recorded (immature specimens only) from Guatemala, Jamaica, and Trinidad, is reported from Illinois, U.S.A. Characteristics of the genus *Synandromyces* are reviewed and compared with those of two nearly related genera, *Acompsomyces* and *Stemmatomyces.* A key to the nine known species of *Synandromyces* is presented. Development of the relatively gigantic, determinate, two-celled trichogyne of *S. telephani* is described and illustrated from the Illinois collections. Trichogyne morphology and other thallus characteristics are discussed in relation to their possible significance in assessing relationships among *Acompsomyces, Stemmatomyces, Synandromyces,* and other genera of Laboulbeniales.

Index words: Laboulbeniales, *Synandromyces,* trichogyne, *Telephanus.*

INTRODUCTION

Synandromyces Thaxter (1912) is one of 26 genera of Laboulbeniales with species known to parasitize cucujiform beetles (Order: Coleoptera; Suborder: Polyphaga; Series: Cucujiformia [Arnett 1962]), and its members are known on representatives of two superfamilies, Tenebrionoidea and Cucujoidea. Nine species have been described as follows: On Tenebrionoidea, Tenebrionidae: *S. amarygmi* Thaxter (1931) on species of *Amarygmus* Dalm. from Fiji and the Solomon Islands; *S. peltoidis* Thaxter (1931) on species of *Peltoides* Laporte from the Cameroons; *S. platydemae* Thaxter (1931) on a species of *Platydema* Laporte & Brullé from the Cameroons.—On Cucujoidea, Cucujidae: *S. geniculatus* Thaxter (1912) on species of *Telephanus* Erichson from Argentina; *S. javanus* Thaxter (1915) on a species of *Psammoecus* Latreille (syn.: *Psammoechus* Boudier) from Java; *S. psammoechi* Thaxter (1931) on species of *Psammoecus* from the Cameroons and Sumatra; *S. telephani* Thaxter (1912) on species of *Telephanus* from Argentina, Jamaica, Trinidad, and Guatemala.—On Cucujoidea, Nitidulidae: *S. floriformis* Thaxter (1931) on a species of *Platychora* Erichson from the Cameroons.—On Cucujoidea, Cryptophagidae: *S. tomari* Thaxter (1931) on a species of *Toramus* Grouvelle (syn.: *Tomarus* Le Conte) from the Cameroons.

Synandromyces is one of many seemingly allied genera which resemble

Stigmatomyces Karsten and can thus be referred to a separate tribe of the Laboulbeniaceae, Stigmatomyceteae, established by Thaxter (1908). All of these fungi have in common a simple, determinate, three-celled receptacle—derived from the lower segment of a two-celled ascospore—which consists of a basal cell (I) forming the foot, a subbasal cell (II) bearing a single, stalked perithecium, and a terminal cell (III) subtending the so-called primary appendage. The latter is developed from the upper segment of the spore and may form one or more phialidelike antheridia. *Synandromyces* probably is most closely related to *Acompsomyces* Thaxter (1901) and *Stemmatomyces* Thaxter (1931). These genera are distinguished from one another primarily by the nature of their primary appendages, and species of all three of them develop often greatly enlarged, determinate, two-celled (*Synandromyces, Stemmatomyces*) or three-celled (*Acompsomyces*) trichogynes bearing peculiar globoid or elongated outgrowths or prominences. In two species of *Synandromyces, S. telephani* and *S. psammoechi,* the trichogyne may be nearly as large as the rest of the young thallus.

From specimens of *Telephanus velox* Hald. collected in Illinois, I have obtained a *Synandromyces* that can readily be identified as *S. telephani,* and the objectives of this paper are (1) to extend the known distribution of *Synandromyces* well into temperate North America, (2) to discuss the genus briefly and compare it with its nearest relatives, (3) to provide a key to the known species, and (4) to describe development of the distinctive trichogyne of *S. telephani.*

I thank Dr. Isabelle I. Tavares, University of California, Berkeley, who kindly reviewed the manuscript and offered a number of helpful suggestions for improvement.

MATERIALS AND METHODS

Telephanus velox, a species known from Iowa to the east coast of the United States (Leng 1920), occurs in decomposing plant material and may be encountered on occasion in lawn, garden, and forest litter. All specimens of *T. velox* examined in this study were found in accumulations of miscellaneous beetles that had been collected in the field and preserved in 70% alcohol. Infected hosts were placed in a large drop of glycerine in a concavity slide (Maximov Tissue Culture) and manipulated with fine-pointed tweezers for easy examination. The fungi were removed with the aid of a minuten insect pin held in a small pin vise and mounted on slides in glycerine containing a trace of cotton blue or acid fuchsin dye.

The following collections of *Synandromyces telephani* were studied: On *Telephanus* sp. (as *T. cribratus* Grouv.). ARGENTINA. Temperley and Llavallol, near Buenos Aires (*Thaxter 1992,* authentic *Synandromyces telephani*) (*RKB 1536, 1634*).—On *Telephanus velox.* ILLINOIS. Champaign

County: Brownfield Woods, 3 mi NE of Urbana, R. K. Benjamin coll., 9 Oct. 1949 (*RKB 291*), 30 Oct. 1940 (*RKB 1752A*), 12 May 1950 (*RKB 3038A*); Trelease Woods, 4 mi E of Urbana, R. K. Benjamin coll., 21 Sept. 1950 (*RKB 1750B*); Champaign, R. K. Benjamin coll., 23 Oct. 1949 (*RKB 311B, 3039*); Urbana, M. W. Sanderson coll., Sept. 1958 (*RKB 2081A*).— Pope County: Herod, Sanderson & Leighton coll., 8 July 1948 (*RKB 3042*). (Note: Brownfield Woods and Trelease Woods are tracts of relatively undisturbed woodland controlled by the University of Illinois.) All slides are deposited in the Rancho Santa Ana Botanic Garden (RSA).

Other specimens cited by number in this work are in the author's collection at RSA.

Drawings were prepared with the aid of a camera lucida mounted on a Leitz Dialux microscope equipped with interference contrast optics. Kodak Tri-X Pan Professional Film 4164 (ASA 320) and Kodak Contrast Process Pan Film 4155 (ASA 80) were used for making the photographic illustrations.

Terminology relating to the thallus and perithecium of Laboulbeniales is based on Thaxter's system (Thaxter 1896) as modified by Benjamin (1979, 1983) and Tavares (1979, 1980).

RESULTS AND DISCUSSION

A. *The Genus* Synandromyces

Synandromyces Thaxter, Proc. Amer. Acad. Arts Sci. 48: 174, 1912; emend. Mem. Amer. Acad. Arts Sci. 16:101, 1931.

Receptacle consisting of three usually greatly elongate cells; the basal cell (I) centrally located, more or less surrounded anteriorly by the subbasal cell (II) and posteriorly by the terminal cell (III). Appendage, subtended by cell III, consisting of three or four superposed cells; the basal cell separating, on the inner side, a supernumerary cell bearing a single simple antheridium; the succeeding cells above the basal cell typically bearing single antheridia distally on the inner side; the terminal antheridium with or without a conspicuous spine. Immature perithecia bearing bicellular trichogynes; the upper cell simple or furcate and forming conspicuous receptive prominences. Mature perithecia with well-defined stalk and basal cells, five tiers of outer wall cells, and single ascogenic cells.

Type species: *Synandromyces telephani* Thaxter.

Up to now all information bearing on *Synandromyces* is due to the studies of Thaxter who described (Thaxter 1912, 1915, 1931) and illustrated (Thaxter 1931) the nine known species. It is likely that examination of large numbers of cucujiform beetles, especially from the tropics, will result in the discovery of additional species. Certainly anyone acquiring new collections will compare these with the descriptions and illustrations of Thaxter (1931)

for possible identification with the known species. Nevertheless, based on Thaxter's descriptions and drawings and on photographs of type or isotype specimens in my files, I am providing a key to the species of *Synandromyces* as a further aid in identifying these taxa.

A KEY TO THE SPECIES OF *SYNANDROMYCES*

A. Cells II and III of receptacle greatly elongated, reaching nearly to the base of cell I B
– Cells II and III of receptacle not greatly elongated, extending only slightly or part way downward along the sides of cell I H
B. Axis of appendage consisting of four cells *S. peltoidis*
– Axis of appendage consisting of three cells C
C. Thallus strongly geniculate, somewhat sigmoid *S. geniculatus*
– Thallus nearly straight or slightly curved D
D. Appendage forming only two antheridia, one each from supernumerary (produced by basal cell) and terminal cells *S. javanus*
– Appendage forming three antheridia, one each from supernumerary, median, and terminal cells E
E. Body of appendage relatively narrow, longer than broad; receptacle and appendage more or less strongly pigmented F
– Body of appendage nearly globose or only slightly elongate; receptacle and appendage not strongly pigmented G
F. Dark brown or blackish pigmentation nearly obscuring cells of appendage; venter of terminal antheridium forming a conspicuous external prominence *S. platydemae*
– Yellowish brown to olivaceous pigmentation not obscuring cells of appendage; terminal antheridium rounded externally but not forming a prominence *S. amarygmi*
G. Body of appendage yellowish to pale amber-brown, nearly globose or broader than long; upper ⅓ of perithecium abruptly distinguished from lower part, outer margins nearly parallel *S. telephani*
– Body of appendage pale brown, somewhat longer than broad; upper ⅓ of perithecium tapering gradually from lower part *S. psammoechi*
H. Apex of perithecium abruptly narrowed; terminal cells horizontally flattened distally, divergent, petallike *S. floriformis*
– Apex of perithecium tapered, broad, subtruncate *S. tomari*

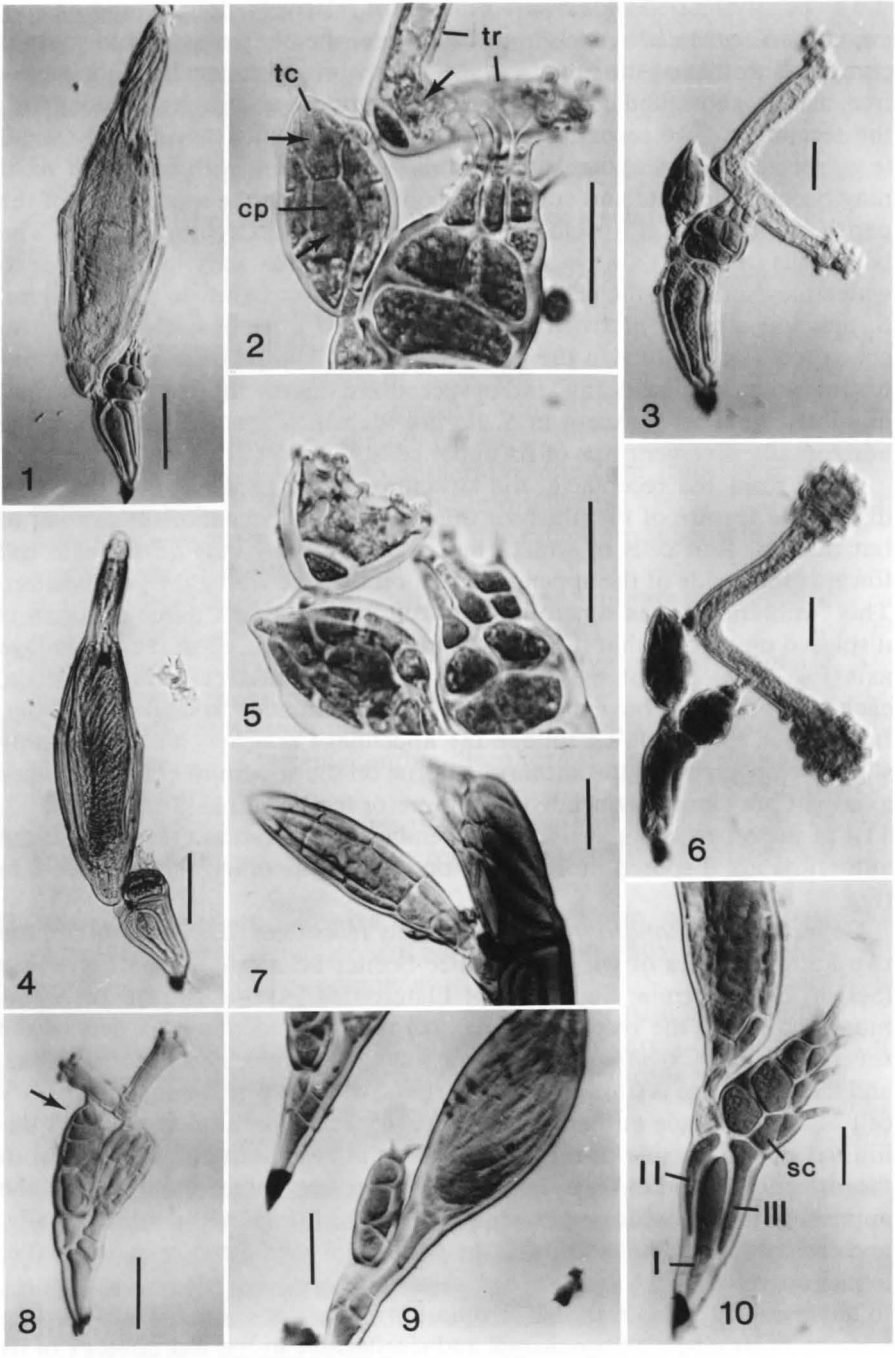
Seven species of *Synandromyces,* including *S. telephani,* i.e., those parasitizing Cucujidae and Tenebrionidae, are characterized by a distinctive type of receptacle (Fig. 1, 11) in which cells II and III extend downward on either side of cell I, often to just above the blackened foot. In two species, *S. floriformis* on a nitidulid and *S. tomari* on a cryptophagid, elongation of cells II and III is less pronounced, but the appendages and perithecia of these species are structurally like those of the others.

The perithecia of *Synandromyces* spp. are relatively elongate and narrow except in *S. geniculatus* and *S. javanus* where the body may be rather stout compared to that of the other species. The primary stalk cell (VI) is nearly free, usually short, and constricted near the middle or near its juncture with the receptacle. The secondary stalk cell (VII) too may be relatively small (e.g., species on Cucujidae and Nitidulidae) or, along with basal cell *m*, it may become elongate and contribute considerably to the total length of the perithecial stalk, (e.g., species on Tenebrionidae and Cryptophagidae). The basal cells (*m, n, n'*) always are well defined and may vary in the degree to which they surround the base of the perithecial cavity. Only in *S. amarygmi, S. peltoidis,* and *S. platydemae* are cells *n* and *n'* sufficiently elongate to contribute significantly to the perithecial stalk. The perithecial apex is undistinguished, i.e., lacks any kind of specialized upgrowths from the terminal or subterminal cells, except in *S. floriformis* which gets its name from the horizontally divergent tips of its upper cells.

Aside from the receptacle, the structure of the appendage is the most distinctive feature of members of this genus, in all instances consisting of but three or four cells of which the basal invariably cuts off a single cell towards the inside of the appendage, i.e., on the side facing the perithecium. This "antheridiiferous supernumerary cell," in Thaxter's parlance, often is displaced upward so that it lies alongside the subbasal cell of the appendage axis (Fig. 2, 11). Except in *S. javanus,* where the subbasal cell remains sterile, each cell of the axis above the basal cell gives rise directly to single antheridia. In the four species on Cucujidae the appendage is nearly globose or only slightly elongated and the antheridia borne on the supernumerary and other axis cells are closely associated in a more or less terminal group (Fig. 2, 5, 11). In the other four species, the appendage is somewhat elongate and the antheridia are disposed more nearly one above the other on the inner side (Fig. 7).

Generically, *Synandromyces* most closely resembles *Stemmatomyces,* the two known species of which parasitize beetles belonging to the Elateridae (Series: Elateriformia; Superfamily: Elateroidea [Arnett 1962]). In *Stemmatomyces* spp. the receptacle (Fig. 10) is nearly identical to that of the several species of *Synandromyces* parasitizing Cucujidae and Tenebrionidae, and the appendage is similar in that the basal cell also forms a supernumerary cell bearing a single antheridium. However, the supernumerary cell is delimited on the outside of the appendage as are the antheridia arising from the other cells above (Fig. 10). In addition, the subterminal cell of the appendage in *Stemmatomyces* usually forms additional antheridia laterally, and each of the four cells forming the perithecial apex develops a distinctive lobate upgrowth.

Thaxter (1931) also regarded *Acompsomyces* as very near *Synandromyces* because of its single ascogenic cell and similarities in the morphology of its appendage and trichogyne. This genus, like *Synandromyces,* parasitizes cu-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cujiform beetles (Cucujoidea) with two species, *A. brunneolus* Thaxt. and *A. corticariae* Thaxt., on Lathridiidae and two species, *A. atomariae* Thaxt. and *A. pauperculus* Thaxt., on Cryptophagidae. The appendage of these forms (Fig. 8, 9), three of which I have studied (Benjamin, unpubl.), consists of four superposed cells. The basal cell, as in *Synandromyces* spp., cuts off a supernumerary cell on the inside. This cell, however, gives rise usually to three antheridia in succession, one distally and one on each side. The next two cells above the basal cell remain sterile, whereas the terminal, spinose cell forms an antheridium directly and in one instance, *A. brunneolus,* cuts off a smallish cell on the outside (Fig. 8).

←

Fig. 1–10.—1–5. *Synandromyces telephani.*—1. Mature individual from Illinois (*RKB 1752A*), ×200 (bar = 50 μm).—2. Upper part of a young individual (*RKB 1750B*) showing primary appendage bearing a terminal group of three antheridia and an immature perithecium at the one wall-cell stage with a maturing trichogyne (*tr*). The latter is forming receptive prominences only at the tips of the divaricate upper cell. The nucleolus of the single nuclei in the carpogenic cell (*cp*), trichophoric cell (*tc*), and upper cell of the trichogyne are clearly visible (arrows), ×800 (bar = 20 μm).—3. Immature individual (*RKB 1752A*) with mature, divaricate trichogyne bearing terminal receptive prominences, ×315 (bar = 20 μm).—4. Mature type from Argentina (*Thaxter 1992*), ×185 (bar = 50 μm).—5. Upper part of immature authentic specimen (*Thaxter 1992*; *RKB 1634B*) showing upper cell of trichogyne that is forming receptive prominences along entire upper surface, ×800 (bar = 20 μm).—6. *Synandromyces psammoechi* (*?Thaxter 3333; RKB 1423*). Immature individual from Sumatra showing clublike arms of divaricate upper cell of trichogyne bearing large, globose receptive prominences terminally, ×315 (bar = 20 μm).—7. *Synandromyces peltoidis* (*Thaxter 2572; RKB 3405*). Immature individual from the Cameroons showing primary appendage bearing antheridia in a linear series on the inside. The young perithecium is at the four wall-cell stage, ×465 (bar = 20 μm).—8. *Acompsomyces brunneolus* (*RKB 2530*). Immature individual from California with mature primary appendage and immature perithecium bearing a tricellular, divergent trichogyne. The two elongate arms of the latter have developed several large, globose receptive prominences terminally. The basal cell of the appendage has cut off a supernumerary cell on the inside that has formed three successive antheridia; the next two cells above are sterile; and the terminal cell has formed a single spinose antheridium and a small cell on the outside (arrow), ×465 (bar = 20 μm).—9. *A. atomariae* (*RKB 2437*). Mature individual from Illinois showing primary appendage consisting of four superposed cells. The basal cell has delimited a supernumerary cell on the inside which has formed three successive antheridia; the next two cells above are sterile; and the terminal cell has formed a spinose antheridium directly, ×465 (bar = 20 μm).—10. *Stemmatomyces anoplischii* (*Thaxter 2038; RKB 1406*). Immature authentic specimen from Argentina showing receptacle and primary appendage. The receptacle is structurally like that of *Synandromyces* spp. in that the subbasal cell (II) and the upper cell (III) project downward along the sides of the basal cell (I). The basal cell of the appendage has cut off a supernumerary cell (*sc*) on the outside which bears a single antheridium. The subbasal cell has formed one antheridium on the outside; the subterminal cell has formed two antheridia, one on the outside, the other laterally; and the terminal cell has formed one spinose antheridium directly, ×465 (bar = μm).

B. Synandromyces telephani

Collections of *Synandromyces* from Illinois (Fig. 1) can be readily identified as *S. telephani* on the basis of comparisons with Thaxter's descriptions and drawing of this species (Thaxter 1912:175–176; emended 1931:103–104, Pl. XIX, Fig. 5), a photograph of the type specimen in my files (Fig. 4), and authentic specimens from duplicates of Thaxter's type-bearing host insects collected in Argentina (*Thaxter 1992*). The latter were obtained during my tenure as a National Research Fellow at Harvard University (1951–1952).

Dimensions of *S. telephani* accompanying Thaxter's description of the type collection were as follows: total length, 290–400 μm; perithecia, including stalk and basal cells, 235–310 × 45–58 μm; receptacle, 45–60 × 25–35 μm; appendage, 45–50 × 25–30 μm; ascospores, 40 × 6 μm. My measurements of 22 authentic specimens were: total length, (255–)340(–456) μm; perithecia, (214–)279(–388) × (54–)70(–80) μm; receptacle, (50–)64(–90) × (28–)39(–50) μm; appendage, (34–)41(–48) × (28–)33(–40) μm; ascospores, (39–)40(–41) × 5–6 μm. Measurements of 20 specimens from Illinois were: total length, (260–)320(–392) μm; perithecia, (200–)261(–328) × (49–)68(–83) μm; receptacle, (50–)71(–88) × (26–)34(–40) μm; appendage, (40–)43(–50) × (26–)31(–36) μm; ascospores, (38–)41(–45) × 5–6 μm.

The occurrence of *S. telephani* in the United States is not surprising, for the host genus, *Telephanus,* ranges from the eastern states southwest through Arizona (Arnett, 1962; Leng 1920), south on the mainland into Argentina in South America, and east to the West Indies (Blackwelder 1945). However, only two species, *T. velox* and *T. lecontei* Casey, have been reported in the U.S. (Leng 1920), the latter from Arizona and the former from Iowa to Connecticut. On the other hand, Bladkwelder (1945) reported 96 species and three varieties south of the U.S. border: Mexico, 17 spp.; West Indies, 28 spp.; Central America, 24 spp. and two var.; and South America, 27 spp. and one var. Thaxter described *S. telephani* from insects identified as *T. cribratus* collected in Argentina. Blackwelder lists this species only from Jamaica, and Thaxter's specimens may have been misidentified. Thaxter also reported immature specimens which he identified with *S. telephani* from Jamaica on *T. strictus* Grouv., from Trinidad on *T. paradoxus* Reitt. (listed by Blackwelder only for Grenada, Colombia, and Venezuela), and from Guatemala on *T. brontoides* Sharp. Careful examination of large series

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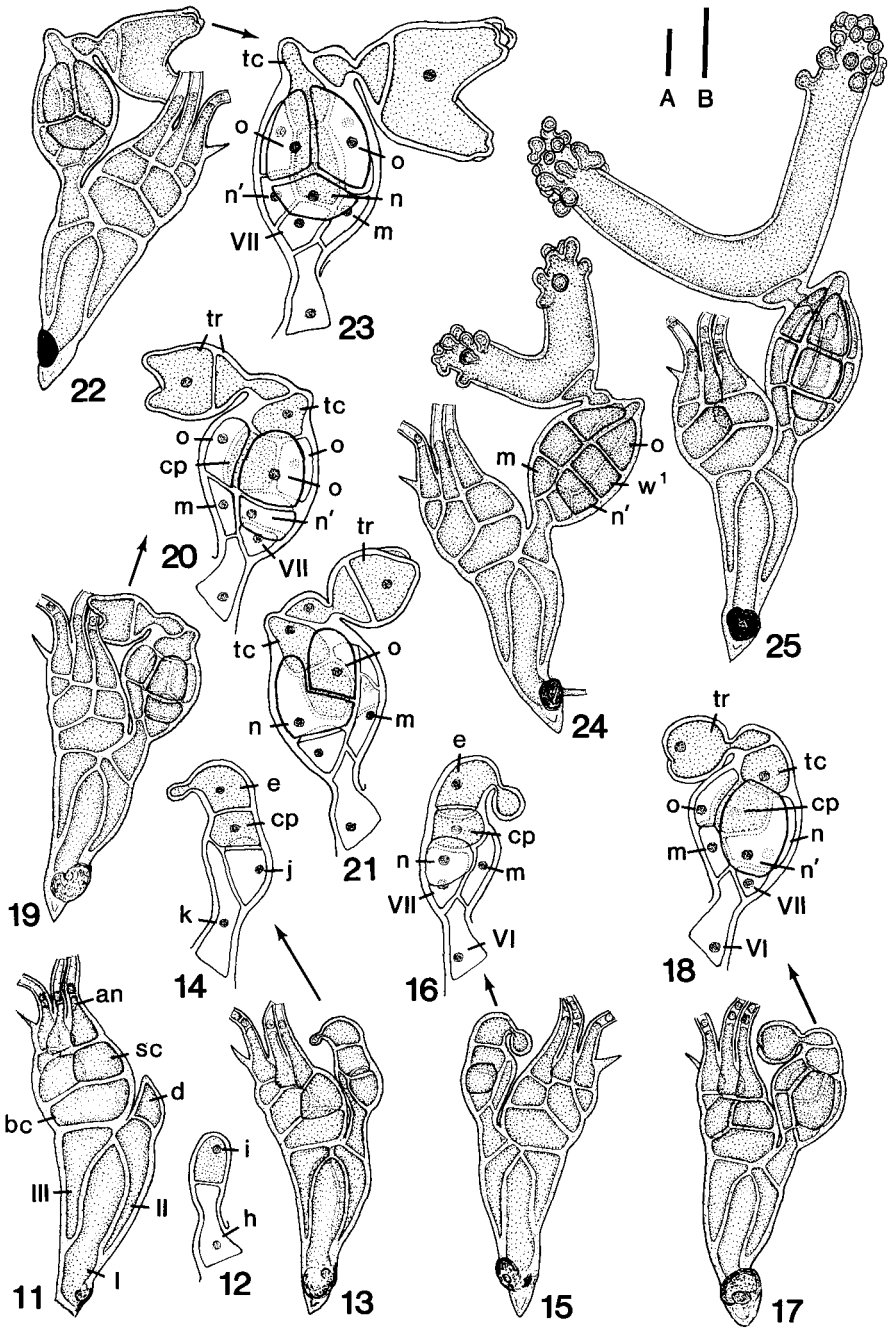
Fig. 11–25. *Synandromyces telephani.* All drawings are from specimens collected in Illinois (*RKB 1752A*). Early stages of development of the perithecium and formation of the trichogyne. Details and terminology are in the text. (Bars = 10 μm. A [×640]: Fig. 11, 13, 15, 17, 19, 22, 24, 25; B [×930]: Fig. 12, 14, 16, 18, 20, 21, 23.)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of collections of the many species of *Telephanus* reported from Mexico, the West Indies, and Central and South America would surely reveal the widespread occurrence of *S. telephani* in the Western Hemisphere.

C. *The Trichogyne of* Synandromyces *and Its Nearest Allies*

Thaxter (1931:101) called special attention to the distinctive trichogynes of *Synandromyces* spp. which he placed "among the most remarkable yet described." In two species, *S. telephani* and *S. psammoechi,* they reach truly gigantic proportions when compared to the rest of the young individual (Fig. 3, 6, 25). Thaxter (1931) provided drawings of the trichogyne of five of the nine species: *S. geniculatus* (Pl. XIX, Fig. 4); *S. telephani* (Pl. XIX, Fig. 6–7); *S. peltoidis* (Pl. XIX, Fig. 11); *S. amarygmi* (Pl. XIX, Fig. 14); and *S. platydemae* (Pl. XX, Fig. 8). He also illustrated the trichogyne borne by two young individuals of a taxon presumed to be a species of *Synandromyces* (Pl. XIX, Fig. 15–16) which he did not name for lack of mature individuals. The bicellular trichogyne of this form bore divergent, terminal, segmented outgrowths unlike the prominences on the other species; however, formal disposition of this taxon and its relationship to other *Synandromyces* spp. must await discovery of mature adults. I am including here a photograph of an immature, trichogyne-bearing individual of *S. psammoechi* (Fig. 6) found on a specimen of *Psammoecus* sp. from Sumatra salvaged from one of the insects accumulated by Thaxter (*?Thaxter 3333*).

The free part of the trichogyne of *Synandromyces* spp. consists of two cells and is reflexed so that during development of the young thallus it remains closely associated with the appendage and its complement of antheridia (Thaxter 1931). The upper cell may remain simple though sometimes larger and more elongate than the basal cell or it may become greatly enlarged and divaricate, as in *S. telephani* (Fig. 3; Thaxter 1931, Pl. XIX, Fig. 7) and *S. psammoechi* (Fig. 6), with the divergent lobes projecting backward past the sides of the appendage.

When Thaxter illustrated development of the perithecium of *Stigmatomyces baeri* Peyritsch he depicted what he thought were globose spermatia attached to the free part of the unicellular trichogyne (Thaxter 1896: Pl. I, Fig. 17–18). He later (Thaxter 1931:115) decided that these presumed spermatia were instead globoid vesicles formed on the trichogyne corresponding to those terminating the arms of the bifurcate, but tricellular, trichogynes of *Acompsomyces atomariae* and *A. brunneolus* (Fig. 8; Thaxter 1908:Pl. XLII, Fig. 8, 12); a like trichogyne has been found on *A. pauperculus* (Benjamin, unpubl.). *Stemmatomyces* also possesses a bicellular trichogyne. The latter, as yet observed in only one of the two known species, *Stemmatomyces anoplischi* Thaxt. (1931:Pl. XVIII, Fig. 10), has elongate, fingerlike, terminal outgrowths rather than the globoid terminal or lateral prominences of *Syn-*

andromyces spp. Further study is needed to clarify a possible relationship of *Hesperomyces* Thaxter (1891:264; 1931:109) to *Synandromyces* on the basis of trichogyne structure, although Thaxter did illustrate this organelle for three of the six species he described. In *H. virescens* Thaxt. (as *Stigmatomyces virescens* [Thaxt.] Thaxt.), one of his drawings (Thaxter 1896: Pl. VIII, Fig. 3) shows a small unicellular trichogyne which probably is immature. His drawing of a young individual of *H. coccinelloides* (Thaxt.) Thaxt. (1931:Pl. XVIII, Fig. 14) shows a two-celled trichogyne bearing terminal, rounded, pedicellate prominences resembling those of *Synandromyces*. However, his drawing of a young specimen of *H. catopii* Thaxt. (1931: Pl. XVIII, Fig. 21) shows a trichogyne, perhaps beginning to degenerate, which appears to have consisted of several cells. Similarities in trichogyne morphology coupled with appendage morphology among species of *Synandromyces, Stemmatomyces,* and *Acompsomyces* do indicate, as suggested by Thaxter in his writings, a close relationship of these genera with one another as well as a more distant alliance with *Stigmatomyces.*

D. *Trichogyne Development in* Synandromyces telephani

When Thaxter first illustrated *Synandromyces telephani* in 1931 he figured two young individuals. One specimen bore an immature, divaricate trichogyne growing backward past the antheridium-bearing extremity of the appendage "like the horns of a buffalo" (Thaxter 1931:Pl. XIX, Fig. 7), and the other bore a mature, divaricate trichogyne having the end and upper surface of each elongate lobe studded with globoid receptive prominences (Thaxter 1931:Pl. XIX, Fig. 6). The latter figure shows what is undoubtedly the largest trichogyne relative to the size of the immature perithecium yet known in the Laboulbeniales. Both of these specimens had been found on *Telephanus brontoides* from Guatemala in the absence of mature specimens, and their identity was not regarded as certain by Thaxter (1931:104). As shall be seen in the description of trichogyne development in *S. telephani* to follow, the mature trichogyne depicted by Thaxter differs in certain respects from that found on specimens collected in Illinois.

No specimens of *S. telephani* were found during this study which could give an adequate picture of early stages of development of the appendage and receptacle, and those showing even the beginning stage of formation of the perithecial initial (Fig. 11*d*) already had fully mature receptacles and appendages. Only the individual depicted in Fig. 11 is labelled to designate the relationship to one another of the elongate basal (I), subbasal (II), and terminal (III) cells of the receptacle and the position of the supernumerary cell (*sc*) relative to the basal (*bc*) and other two cells of the appendage. By the time the perithecial primordium (*d*) appears, the single antheridia (*an*), derived from the supernumerary, median, and terminal cells of the appen-

dage, are forming spermatia. Although the fungi studied were originally fixed only in 70% alcohol and nuclear and cytoplasmic preservation were poor, the position of the single nucleus in each cell of the young thallus was usually, but not always, readily seen with differential interference contrast microscopy. The relatively large nucleoli are often clearly resolved (Fig. 2, arrows) and are shown here in the semidiagrammatic figures (Fig. 12, 14, 16, 18, 20, 21, 23) where only cells derived from cell *i* are stippled. Accurate study of subsequent development of the carpogenic cell (*cp*) which gives rise to the ascogenous cell and its associated cells was not possible.

Figure 12 shows a two-celled perithecial primordium derived from cell *d* which consists of a lower cell *h*, the primordial cell of the perithecium (Thaxter 1896), and an upper cell *i*, the primordial cell of the procarp (Thaxter 1896). Cell *h* becomes divided distally by a diagonal septum (Fig. 13–14) and forms two cells *j* and *k* representing the first stage of formation of the perithecium proper. At about the same time cell *i* has divided transversely and formed the carpogenic cell (*cp*) below and the trichophoric-trichogynic initial (*e*) above, which already is developing a terminal bud directed toward the antheridia. This bud will enlarge and form the main body of the trichogyne. I should point out here that in two previous studies of perithecial development I incorrectly referred to this cell (*e*) as the trichophoric cell prior to delimitation of the trichogyne (Benjamin 1979:Fig. 2G; 1983:Fig. 14).

In the individual shown in Fig. 15–16 the stalk cells and two of the three basal cells of the perithecium have been delimited. Cell *k* (Fig. 14) has divided and formed the primary stalk cell (VI) and basal cell *m* which constitutes the posterior part of the young perithecium (Fig. 16). Cell *j* has divided and formed the secondary stalk cell (VII) and the laterally placed basal cell *n*. The carpogenic cell (*cp*) remains unchanged as it will during later stages of development up to maturity of the trichogyne (Fig. 2, 17–25). The trichogynic bud is enlarging but still is a part of cell *e* to which it is attached by a narrow isthmus.

Figures 17–18 show a slightly later stage of development of the young perithecium in which cell VII has cut off basal cell *n'*, here facing the viewer. This cell and basal cell *n*, on the opposite side, are growing upward and around the lateral and anterior faces of the carpogenic cell (*cp*). Basal cell *m* has divided distally and formed the first primordial wall cell (*o*) of the *m* row of outer wall cells. The trichogyne (*tr*), unicellular at this stage of development, has been delimited from cell *e* which now becomes the trichophoric cell (*tc*). The large trichogynic bud is beginning to show signs of divarication.

In the young perithecium shown in Fig. 19–20 basal cell *n'* has separated the first primordial wall cell (*o*) of the *n'* row of outer wall cells, and the young trichogyne has become bicellular through formation of a septum near

the base of the trichogynic bud shown in the previous figure. Bifurcation of the upper cell of the reflexed trichogyne is under way, and this would appear to be the stage of development of the thallus shown by Thaxter in his Plate XIX, Fig. 7 (Thaxter 1931). The trichophoric cell (*tc*) is beginning to grow upward past the base of the medianly constricted lower trichogynic cell. Figure 21 illustrates a perithecium at a stage of development comparable to that shown in Fig. 20 as viewed from the opposite side. Here basal cell *n* has cut off primordial wall cell (*o*) of its lateral row of outer wall cells and is growing upward anteriorly preparatory to delimiting the first primordial wall cell of the second row of outer wall cells it generates. The nucleolus in each cell of the trichogyne was well defined in the specimen depicted in this drawing.

In the perithecium shown in Fig. 22–23, all four of the first-formed primordial outer wall cells (*o*) are present and surround the carpogenic cell and the base of the elongating trichophoric cell (*tc*). The latter persists for a time during early development of the female organ from the carpogenic cell and appears to serve as a guide around which the upper inner and outer wall cells grow. The lower cell of the trichogyne undergoes no further significant enlargement unlike the upper bifurcate cell, the arms of which are elongating and beginning to form the characteristic prominences at their extremities.

As the upper cell of the trichogyne matures, the two arms elongate and form numerous globoid or ovoid outgrowths apically (Fig. 24, 25). At the same time, each of the first-formed primordial outer wall cells delimits a second primordial wall cell (*o*) distally. The lower cells then comprise the basal tier of true outer wall cells (w^1) which undergo no further changes save enlargement. Further development of the perithecium is like that in all members of suborder Laboulbeniineae (Tavares 1977, 1980; Benjamin 1983), and in *S. telephani* the four rows of outer wall cells ultimately consist of five cells each, the lower three tiers relatively long, the upper two comparatively short (Fig. 1, 4).

When the perithecium reaches stages of development much beyond that shown in Fig. 25, the free part of the trichogyne is missing, presumably falling away or degenerating following fertilization. The lower part of the basal cell of the trichogyne persists and forms a slightly rounded protrusion on the posterior wall of the growing perithecium. When the perithecium is mature, this trichogynic scar may be barely visible at the base of the third tier of outer wall cells at the juncture of the *m*- and posterior *n*-derived rows.

Thaxter (1931:103) commented on a possible near relationship of *S. telephani* and *S. psammoechi* which do occur on closely related hosts. He opted in favor of their being distinct from one another on the basis of differences in the shape of their appendages and perithecia. When one compares their trichogynes one notes a similarity in basic structure but a marked difference in certain dimensions. In *S. psammoechi* the apices of the two

arms of the upper cell become enlarged, somewhat ovoid, and bear very large globoid prominences (Fig. 6). In *S. telephani,* on the other hand, the arms of the upper cell do not become swollen distally, and bear smaller globid or slightly irregular prominences (Fig. 3, 25; Thaxter 1931:Pl. XIX, Fig. 6). I concur with Thaxter that the two taxa should be regarded as distinct but closely related species.

Thaxter's illustration of a mature trichogyne of *S. telephani* was based on a specimen removed from a host collected in Guatemala, distantly removed from the type locality of this species near Buenos Aires, Argentina. As already noted, the trichogyne he figured bore globoid prominences not only at the extremities but also all along the upper surface of the long, robust, divaricate upper cell. From a duplicate specimen of *Telephanus "cribratus"* (*Thaxter 1992*) from which Thaxter obtained his type material, I found and mounted a few immature specimens of *S. telephani* bearing young trichogynes at about the same stage of development as the one shown here in my Fig. 22–23. On these Argentine specimens, the early development of prominences along all of the upper surface (Fig. 5) indicates that Thaxter's immature specimens from Guatemala probably represent *S. telephani* much as it exists in Argentina.

Trichogyne morphology indicates that there are genetic differences between *S. telephani* populations occurring in Illinois and in Central and South America. Such differences would be expected in view of the apparent widespread distribution of the species in the Western Hemisphere, and subspecific diversification also could be expected. However, I believe that detailed study of many populations of the species from throughout its range would be needed to determine the nature and degree of variations within the taxon that one should have before proposing subspecific taxa. Ascospore dimensions in the collections from Illinois and the Argentine are essentially the same, and a comparison of mean values of total thallus length and length and width of perithecia and appendages fall well below significant *t* values at the 5% level. The receptacle shows a slightly significant degree of variation in linear dimensions, but not morphology. My comparison of the relatively limited number of mature individuals available to me from Illinois and Argentina lead me for the present to recognize a single species.

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