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A NEW SPECIES OF *PYXIDIOPHORA* AND ITS *THAXTERIOLA* ANAMORPH

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ABSTRACT

Nine genera of minute nonmycelial fungi characterized by a thallus of one to 15 cells in linear arrangement, a usually darkened holdfast, and often endospores cut off in succession are known from arthropod hosts. The taxonomic relationship of these minute fungi, including *Thaxteriola,* has been the subject of speculation, and morphological comparisons have been made to the Laboulbeniales. One genus has been synonymized with *Pyxidiophora* in the Hypocreales. The discovery of a new species of *Pyxidiophora* with a *Thaxteriola* anamorph on mites associated with the southern pine beetle gives new evidence of relationships and points out the importance of a mycological curiosity as a dispersal stage. This anamorph is nonmycelial, highly specialized, and unlike any known for an ascomycete.

Key Words: *Pyxidiophora, Thaxteriola, Dendroctonus,* entomogenous fungi, mites, taxonomy.

Spegazzini (**1918**) described the genus *Thaxteriola* and its species, *T. infuscata* Speg. and *T. subhyalina* Speg., from beetles in Argentina. Several years earlier Thaxter (**1914**) had illustrated a similar fungus of a type he found on a variety of insects and occasionally on the laboulbenialean fungi on the insects; no formal description was given because he knew nothing of its development. Thaxter (**1920**) later accepted Spegazzini's genus and described a third species, *T. nigromarginata,* on a staphylinid from Java. He cautioned that many species probably exist and that eventually "posterity will have become burdened with a horde of these uninteresting little plants." However, only one additional species, *T. moseri* Majewski *et* Wiśniewski (**1978a**), has been formally described from mites in Poland.

Other genera of morphologically similar fungi are known from insects, mites, and a centipede (TABLE I). Common features include morphological simplicity with thalli having one to four or fifteen cells in linear arrangement, a usually darkened holdfast, and endospores cut off in succession (except in *Laboulbeniopsis* and *Coreomycetopsis,* see under Discussion below). Haustoria have not been reported for any of the species, and the mode of nutrition of the fungi in the aerial environment is unknown. While these forms are not encountered by most mycologists they have been of interest from a phylogenetic point of view because they are so different from other fungi.

The resemblance of these fungi to the male thalli of some dioecious laboulbenialean species has been noted several times. Thaxter (**1914, 1920**) pointed out that the similarity of *Amphoromorpha, Thaxteriola,* and *Endosporella* to the male thallus of species of *Dimeromyces* and *Amphoromyces* was probably only superficial and did not indicate a relationship with the Laboulbeniaceae. However, Gäumann and Dodge (**1928**) believed that thalli of *Thaxteriola* and *Endosporella* were conidium-producing forms of the Laboulbeniales.

Benjamin (**1971**) found no evidence for or against the idea that species of *Thaxteriola* and *Endosporella* are imperfect Laboulbeniales. He expressed the belief that such forms could be the result of convergent evolution from fungi unrelated to precursors of the Laboulbeniales.

While Spegazzini thought the four genera he described (*Amphoropsis, Entomocosma, Myriapodophila,* and *Thaxteriola*) (TABLE I) were related to *Amphoromorpha* ("Anforomorfas," Spegazzini, **1918**), Thaxter (**1920**) suggested a relationship only between *Thaxteriola, Entomocosma, Endosporella,* and *Laboulbeniopsis* ("Thaxteriolae," Thaxter, **1920**). *Acariniola,* de-

TABLE I

NONMYCELIAL FUNGAL ECTOPARASITES OF ARTHROPODS

Species	Hosts	Locality	Reference
Acariniola subbasalipunctata Maj. et Wiśn.	Mites (*Dendrolaelaps, Proctolaelaps, Trichouropoda,* and *Pygmephorus*). Associated with beetles in *Pinus sylvestris* L. and *Abies alba* Mill.	Poland	Majewski and Wiśniewski, **1978a**
Acariniola basalipunctata Maj. et Wiśn.	Mites (*Dendrolaelaps* and *Proctolaelaps*). Associated with beetles in *Pinus sylvestris*	Poland	Majewski and Wiśniewski, **1978a**
Amphoromorpha entomophila Thaxt.	Staphylinid beetles (*Diochus,* others), earwig (*Labia* sp.)	Philippines	Thaxter, **1914**
Amphoromorpha blattina Thaxt.	Roaches	Grenada	Thaxter, **1920**
Amphoromorpha spp.	Mucoralean fungi	U.S.	R. K. Benjamin (pers. comm.)
	Laboulbenia leleupidiae W. Rossi et Cesari Rossi on carabid beetle host	Zaire	Rossi and Cesari Rossi, **1982**
	Laboulbenia biondii W. Rossi et Cesari Rossi on a chrysomelid beetle host	Italy	Rossi and Cesari Rossi, **1979**
	Diplopod (*Ophiiulus*)	Italy	Rossi and Balazuc, **1977**
	Termites	Sierra Leone	Blackwell and Rossi, **1986**
		Florida	J. W. Kimbrough (pers. comm.)
Amphoropsis minuta Speg.	Histerid beetle (*Hister*)	Argentina	Spegazzini, **1918**
Amphoropsis subminuta Speg.	Staphylinid beetle (*Echiaster*)	Argentina	Spegazzini, **1918**
Amphoropsis media Speg.	Carabid beetle (*Clivina*)	Argentina	Spegazzini, **1918**
Coreomycetopsis oedipus Thaxt.	Termites	Grenada	Thaxter, **1920**
		Florida	Blackwell and Kimbrough, **1978a**
		Georgia	Blackwell, **1980**
Endosporella diopsidis Thaxt.	Fly (*Diopsis*)	Cameroons	Thaxter, **1920**
Entomocosma laboulbenioides Speg.	Hydrophilid beetle (*Cercyon*). In cow dung	Argentina	Spegazzini, **1918**
Laboulbeniopsis termitarius Thaxt.	Termites	Worldwide, except Australia	Thaxter, **1920**; Blackwell and Rossi, **1986**
Myriapodophila argentinensis Speg.	Centipede (*Scolopendra*)	Argentina	Spegazzini, **1918**
Thaxteriola infuscata Speg.	Earwig (*Labia*), staphylinid beetles (*Philonthus, Belonuchus*)	Argentina	Spegazzini, **1918**
Thaxteriola subhyalina Speg.	Scarabid beetle (*Aphodius*), Nitudulid(?) beetle	Argentina	Spegazzini, **1918**
		Michigan	Povah, **1931**
Thaxteriola nigromarginata Thaxt.	Staphylinid beetle	Java	Thaxter, **1920**
Thaxteriola moseri Maj. et Wiśn.	Mites (*Dendrolaelaps, Proctolaelaps, Trichouropoda, Uroobovella*). Associated with beetles in *Pinus sylvestris,* and *Picea abies* Karst.	Poland	Majewski and Wiśniewski, **1978a**
Thaxteriola spp.	Mites (*Ameroseius, Dendrolaelaps, Lasioseius, Uroobovella*). Associated with beetles in *Pinus taeda* L.	Louisiana	Majewski and Wiśniewski, **1978b**
	Laboulbeniales	?	Taxter, **1914**

scribed more recently, is very similar to *Thaxteriola* (Majewski and Wiśniewski, **1978a**), and has been placed in the synonymy of the pyrenomycete genus *Pyxidiophora* Bref. *et* Tav. emend. Lundq. (Lundqvist, **1980**). Conidium formation by *Acariniola* was not observed and it was not recognized as an anamorph, but considered merely an ascospore (see Discussion, below).

Thaxter (**1920**) recommended that these minute fungi "must remain among the 'genera incertae sedis' until the discovery of further types which may possibly throw some light on their affinities." One of us (T.J.P.) has recently discovered an undescribed species of *Pyxidiophora* in the galleries of the southern pine beetle, *Dendroctonus frontalis* Zimmermann, which does throw light on the affinities of *Thaxteriola.*

The southern pine beetle is the most destructive pest of southern pine forests (Payne, **1980**). This beetle is only one member of a symbiotic complex that includes other insects, mites, and a variety of fungi. Several species of mites have phoretic stages that attach to the beetle (Kinn, **1976**), and an undescribed species of *Thaxteriola* is known on these mites in western Louisiana (Majewski and Wiśniewski, **1978b**). Ascospores of the newly discovered species of *Pyxidiophora* begin development into the *Thaxteriola* anamorph while still in the asci and ascocarp. The anamorph is highly specialized and nonmycelial. Its development is unlike any previously described anamorph.

In this paper the new species of *Pyxidiophora* is described and discussed. Phylogeny of the minute fungi on insects and mites is reevaluated in light of this discovery.

METHODS AND MATERIALS

The *Pyxidiophora* state was observed in 1985 on wood samples from southern pine beetle-infested loblolly pine trees (*Pinus taeda* L.) from Grant Parish, Louisiana, and Sabine County, Texas (4 June and 25 July). Wood samples beneath beetle-infested bark were removed with a chisel and examined for perithecia with a dissecting microscope at 60×.

Perithecia were mounted in lactophenol-cotton blue (Stephens, **1974**) or a glycerol-acid fuchsin solution (Benjamin, **1971**). Mounts were ringed with fingernail polish.

The *Thaxteriola* state was observed on *Tarsonemus krantzi* Smiley and Moser and *T. ips* Lindquist phoretic on southern pine beetles. Collections were made 16 July, 6 August, and 21 August 1984 from loblolly pine trees in Sabine and Shelby counties in east Texas, and in Winn Parish in central Louisiana. To collect beetles and mites, outer bark containing pupae or callow adult beetles was removed from trees, brought to the laboratory, and placed in rearing containers. Beetles were collected as they emerged from the bark. Mites were removed from beetles, cleared in lactophenol, and permanently mounted in Berlese's medium (Kinn, **1976**).

TAXONOMY

Pyxidiophora kimbroughii M. Blackwell *et* T. J. Perry *sp. nov.* FIGS. 1–9

Characteristicis generis; perithecium ampulliforme, hyalinum ad cremeum, basi 70–100 μm latissimo diam, rostrum rectum aut flexum, 85–155 μm longum; asci octospori, fusiformes, 70–106 × 19–33 μm; ascosporae hyalinae, unicellulares, mox bicellularascentes, aliquantum falcatae e latere visae, fusiformes a fronte visae, vagina hyalina gelatinosa, 50–75 × 6–8 μm exclusa vagina, ascospora recte evolvens ad Thaxteriolam anamorphem.

Hab. in ligno Pini taedae e Dendroctono frontale infecta.

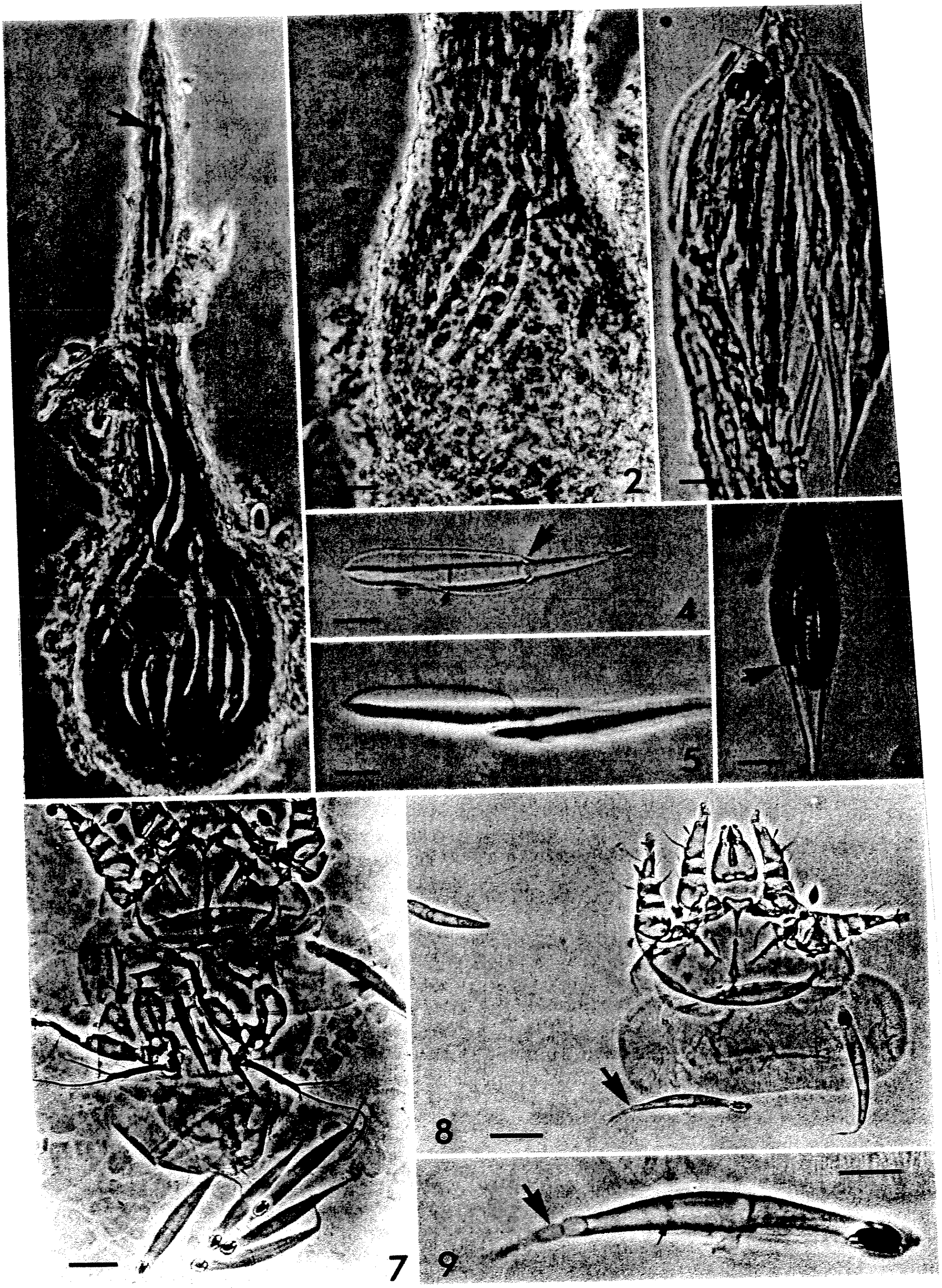
HOLOTYPUS: UNITED STATES: TEXAS; Sabine County, 25 July 1985. Blackwell No. 200 in FH. Isotypus in BPI (Blackwell No. 200). Paratypus in FH (J. Moser 31,087).

This species is named for James W. Kimbrough, a contemporary student of minute entomogenous fungi.

Ascocarps superficial or slightly immersed in substrate, flask shaped, hyaline to creme (FIGS. 1, 2); bases 70–100 μm diam at widest; outer peridium composed of polygonal, hyaline cells, 8–13 × 5–6 μm; necks straight or bent, 85–155 μm long including ostiolar hyphae, 35–57 μm wide at the base, 12–32 μm wide beneath the ostiolar hyphae, composed of parallel, relatively thin walled, multiseptate, fused filaments 10–16 × 2–4 μm that extend as ostiolar hyphae at the apex; ostiolar hyphae converging, 6–13 μm in length, parallel, little subulate.

Asci (FIG. 3) 8-spored, evanescent, fusiform; 70–100 × 19–33 μm.

Ascospores hyaline, at first 1-celled, soon becoming 2–3-celled, somewhat falcate with attenuated ends in side view, fusiform in face view, partially surrounded by a hyaline gelatinous sheath which leaves a scar on anamorph thallus (FIGS. 4, 5, 9), 50–75 × 5–8 μm excluding sheath; ascospores from each ascus extruded in a mass before maturation of next oldest ascus (FIG. 3);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end of distal cell of ascospore as positioned in ascocarp developing a darkly pigmented holdfast (FIGS. 1–3), proximal cell about 60–70% of total spore length sometimes becoming once septate, tip of proximal cell retaining its attenuated shape void of cytoplasm at tip (FIG. 6); entire spore enlarging somewhat during development, wall becoming thickened. Ascospore developing directly as a *Thaxteriola* anamorph (Majewski and Wiśniewski, **1978b**) with spherical to ovoid phialoconidia 2.0–2.5 × 2.0–2.5 μm (FIGS. 7–9).

DISCUSSION

The taxonomy of *Pyxidiophora* has been discussed most recently by Breton and Faurel (**1967**) (as *Mycorhynchus* Sacc.), Hawksworth and Webster (**1977**) (as *Mycorhynchus*), and Lundqvist (**1980**). Lundqvist considered *Mycorhynchus, Treleasia* Speg., *Copranophilus* Speg., *Ascolanthanus* Caill., and *Acariniola* Maj. et Wiśn. to be congeneric with *Pyxidiophora* and recognized about twenty species in the genus. *Pyxidiophora kimbroughii* is most similar morphologically to *P. grovei* (Hawksw. *et* Webst.) Lundq. (Hawksworth and Webster, **1977**; Lundqvist, **1980**). Ascospores of both species are similar in size and have a darkened holdfast with a pore at maturity. However, *P. grovei* has a light ochraceous perithecium, a longer perithecium neck, and 6-spored asci. *Pyxidiophora grovei* is known only from dung.

Most modern treatments have included *Pyxidiophora* in the Hypocreales (Breton and Faurel, **1967**; Rogerson, **1970**; Müller and von Arx, **1973**; Hawksworth and Webster, **1977**). Arnold (**1972**), however, considered the genus distinct from other hypocrealean genera and erected the monotypic family Pyxidiophoraceae. Lundqvist (**1980**) followed this arrangement and emended the family to include the cleistothecial genus *Mycorhynchidium* Malloch *et* Cain (Malloch and Cain, **1971**). While Arnold (**1972**) suggested a relationship between *Pyxidiophora* and *Melanospora* Corda, Lundqvist doubted this possibility, based on putative reports of a *Chalara* (Corda) Rabenh. anamorph for some species of *Pyxidiophora.* Parguey-Leduc and Janex-Favre (**1981**) proposed the relationship of *Lulworthia* Sutherland to *Ceratocystis* Ellis et Halstead, *Pyxidiophora,* and *Thielavia* Zopf based on the similarity of ascospores, *Chalara*-type anamorph, perithecium, and additional characters. While not all these relationships may seem reasonable, the comparison of *Ceratocystis* and *Pyxidiophora* is of interest to us. We have noted similarities between *P. kimbroughii* and certain species of *Ceratocystis* and *Ceratocystiopsis* Upadhyay et Kendrick (Upadhyay and Kendrick, **1975**; Upadhyay, **1981**) which occur in the bark beetle habitat. We feel that the possibility of these relationships should be investigated further.

Lundqvist (**1980**) was the first to recognize the similarity between ascospores of *Pyxidiophora* and the thalli of *Acariniola* spp. and *Thaxteriola* spp. on mites associated with bark beetles (Majewski and Wiśniewski, **1978a, b**) and placed these species in *Pyxidiophora.* The decision was based on the absence of endoconidia in Majewski and Wiśniewski's material which was reexamined by Lundqvist. Lundqvist decided that the specimens from mites were unrelated to *Thaxteriola* Speg. The discovery of endoconidia in thalli of *Thaxteriola* on mites leads us to conclude, however, that they are true anamorphs developed directly from ascospores. We maintain the placement of mite-associated species in *Thaxteriola.*

Thaxter used the term "endospores" for the propagules of *Thaxteriola.* Because *Thaxteriola* sp. is considered to be an anamorph of *Pyxidiophora kimbroughii* we use the term "endoconidia" for these structures. Endoconidium for-

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FIGS. 1–9. *Pyxidiophora kimbroughii* and its *Thaxteriola* anamorph. 1. Perithecium showing ascospores which have already begun development into the anamorph. Arrow indicates flattened holdfast end. Holotype. Phase contrast. 2. Perithecium with blackened holdfasts (arrow) of two fully developed anamorph thalli. 3. Mechanically expressed asci at perithecial neck. Contents of each ascus (brackets) are typically at different stages of development. Holotype. 4. Young ascospore showing septum (small arrow) and gelatinous membrane. Site of membrane attachment (large arrow) remains visible in mature anamorph. Isotype. 5. A second young ascospore. Isotype. Phase contrast. 6. Cytoplasm (arrow) of developing anamorph does not extend into the attenuated tip. Holotype. 7. *Tarsonemus ips* with six *Thaxteriola* sp. thalli. Thallus attachment is easily disrupted. J. Moser 31,052. 8. *Tarsonemus krantzi* with endoconidium-producing anamorph (arrow). Paratype. 9. Thallus (same as that indicated in FIG. 8) with endoconidia (large arrow). Remnant of ascospore membrane attachment visible at small arrow. Bar = 10 μm for FIGS. 1–6, 9; 20 μm for FIGS. 7, 8.

mation as viewed with the light microscope appears to be by enteroblastic phialidic conidiogenesis with the entire terminal cell of the thallus acting as a phialide and the attenuated tip breaking before conidium release. This is similar to the condition observed in *T. infuscata* (FH 9031) (unpublished observations, M.B.).

Endoconidium formation by the *Thaxteriola* anamorph is reminiscent of "microendospore" formation in ascospores of *Ceratocystis ulmi* (Buisman) C. Moreau (Ouellette and Gagnon, **1960**). Juzwik and Hinds (**1984**) found that some ascospores of the discomycete *Encoelia pruinosa* (Ell. et Everh.) Torkelson et Eckblad can function as phialides which give rise to microconidia. The morphological differentiation of the ascospore of *P. kimbroughii* which precedes endoconidium formation and the apparent obligate development of this state at a certain point in the life cycle, however, indicate that *Thaxteriola* is a true anamorph.

In their report of *Thaxteriola,* Majewski and Wiśniewski (**1978b**) pointed out that Louisiana specimens were different from Polish *T. moseri* because the thallus of Louisiana material was almost completely covered with minute verrucae, light brown in color, and somewhat larger than that of Polish specimens. We feel that they were correct in not describing an additional species of *Thaxteriola* and hope that the eventual discovery of additional teleomorphs associated with bark beetles will clarify the situation.

Of the other phylogenetically problematical genera of fungi listed in TABLE I, only two are relatively well known. *Laboulbeniopsis termitarius* and *Coreomycetopsis oedipus* are both restricted to termite hosts. They are morphologically more complex than species of the other genera listed. Although *C. oedipus* is known from three localities of the New World, *L. termitarius* has a much wider range including North and South America, Europe, Africa, and southeastern Asia (Blackwell and Rossi, **1986**). While Thaxter (**1920**) recognized their morphological similarity, he thought the two species were unrelated. He suggested a relationship between *Thaxteriola, Entomocosma, Endosporella,* and *Laboulbeniopsis* (see above). We do not believe *Laboulbeniopsis* is closely related to these genera. In two studies (Blackwell and Kimbrough, **1976a, b**) development of *C. oedipus* and *L. termitarius* was followed. Spores of *C. oedipus* were velop in a cavity formed within cells above the three basal cells of the thallus. Spores and young thalli of this species were observed on termite cuticle and gave assurance that spores of *C. oedipus* thalli did, in fact, develop into the same kind of thalli (Blackwell and Kimbrough, **1976a**). *Laboulbeniopsis termitarius* appears to produce ascospores. This is evidenced by simultaneous spore formation (Thaxter, **1920**) and spore development which apparently occurs within an ascus vesicle with epiplasm (Blackwell and Kimbrough, **1976b**). Ascospores and young thalli were recognizable on termite cuticle. No evidence was obtained that *L. termitarius* and *C. oedipus* were different stages of the same fungus. However, at the ultrastructural level the foot cells of each species were indistinguishable (Blackwell and Kimbrough, **1976a, b**). The ovoid cells with complex secretory canals and secreted adhesive pads are so similar that these species are almost certainly related to each other.

The other seven genera (TABLE I) are morphologically less complex than *C. oedipus* and *L. termitarius.* No additional information on *Entomocosma, Amphoropsis, Myriapodophila,* and *Endosporella* has become available since Spegazzini (**1918**) and Thaxter (**1920**) described the genera. We know of no casual observations of species of these genera. *Amphoromorpha* has been observed on several occasions, on termites, a diplopod, a pseudoscorpion, and mucoralean and laboulbenialean fungi (TABLE I).

Species of *Thaxteriola* and *Acariniola* are distinguished from *Myriapodophila, Amphoropsis, Amphoromorpha, Endosporella,* and *Entomocosma* by the slender 2–3-celled thallus with a darkened foot and, in some specimens, the presence of an easily observed pore at the proximal end of the basal cell (*Thaxteriola moseri*) or between the center and the distal end of the basal cell (*Acariniola* spp.). Majewski and Wiśniewski (**1978a, b**) speculated the pore might be a nutrient absorption site. We suspect a perithecial teleomorph will be discovered for *Acariniola.* Some species of the other genera may have perithecial teleomorphs, but we refrain from further speculation on phylogenetic relationships until we acquire additional information. Host habitats should be examined carefully for possible teleomorphs of all of these forms, especially *Acariniola* and *Endosporella,* which Thaxter (**1920**) believed closely related to *Thaxteriola.* These microscopic examination of alcohol-preserved hosts long removed from their habitat.

The mycota associated with a recent southern pine beetle population increase in western Louisiana and eastern Texas is still not characterized fully, and the cause of tree death after beetle invasion is not understood completely (Bridges, **1983**, **1985**). While the effect of *Pyxidiophora kimbroughii* on bark beetle-infested trees and the beetles themselves is unknown, this study does point out that it is possible that mites associated with the beetle and its habitat are necessary for the spread of a specialized anamorph that may be important in the symbiotic assemblage.

Fungal groups that cannot be cultured and that have simple morphologies have always been a problem to taxonomic mycologists. Benjamin (**1971**), especially, warned about the possibility of convergence in many cases where entomogenous fungi are involved. Reduction of the thallus, perhaps from mycelial ancestors or by development from a single ascospore, must have occurred on a number of occasions to allow the successful colonization of insect and other arthropod hosts which survive fungal infestation. The mobility afforded the fungi for dispersal and the habitat stability produced by the insect could have influenced selection of this life style for the fungi. The possibility that other species may have an unknown teleomorph offers some hope for their eventual classification in higher taxonomic categories.

Thaxteriola is certainly far more interesting than Thaxter ever considered it to be. It is fitting that the genus named in honor of this great student of entomogenous fungi is the first to be shown to have a perithecial teleomorph.

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