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Ascospores of *Pyxidiophora* on mites associated with beetles in trees and wood

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Records of *Pyxidiophora* ascospores attached to 116 collections of 35 species of mites associated with beetle habitats in trees and wood show that these associations are common and widespread. Range extensions include western North America, Asia and New Guinea. A large series from one Louisiana locality provides information on ontogenetic and interspecific differences. Although new species of *Pyxidiophora* are almost certainly present in beetle habitats, new species are not formally described here on the basis of the ascospores. Species of *Pyxidiophora*, previously known from dung and plant debris and as mycoparasites, are present and common in tree and wood habitats of beetles where phoretic mites are important for ascospore dispersal.

Key words: *Pyxidiophora, Thaxteriola, Acariniola*, Spore dispersal, Insect and mite association.

Pyxidiophora Bref. & Tav. is a perithecial ascomycete with long, slender, two-celled ascospores. Most species develop a darkened region at the distal end of the ascospore (as it is oriented at the perithecium neck). In *P. kimbroughii* Blackwell & Perry the darkened region develops into a holdfast for attachment of the ascospores to mites where the spores later develop into a *Thaxteriola* Speg. anamorph (Blackwell *et al.*, 1986*a, b*).

Species of *Pyxidiophora* are best known from dung and plant litter habitats (see Lundqvist, 1980). *Pyxidiophora kimbroughii* is the only species known to be associated with mites in bark beetle habitats (Blackwell *et al.*, 1986*a, b*). However, based upon previous reports of a variety of presumed *Pyxidiophora* ascospores on mites, we suspect the widespread occurrence of additional species associated with bark beetles (Majewski & Wiśniewski 1978*a, b*; Lundqvist, 1980; Simpson & Stone, 1987).

Pyxidiophora ascospores have been described as *Thaxteriola moseri* Maj. & Wiśn. and *Acariniola subbasalipunctata* Maj. & Wiśn. and *A. basalipunctata* Maj. & Wiśn. (Majewski & Wiśniewski, 1978*a, b*). *Acariniola* Maj. & Wiśn. was distinguished from *Thaxteriola* on the basis of the placement of a pore-like structure outside the darkened holdfast region. However, Lundqvist (1980) pointed out that these forms lack conidia and have no status as anamorphs.

Here we provide additional reports of *Pyxidiophora* ascospores from mites associated with beetles (Scolytidae, Brenthidae, Cerambycidae), and free-living mites in wood. Some of the ascospores are identical to those of *P. kimbroughii*; other types of spores cannot be referred to known species of *Pyxidiophora*.

We have not described new taxa because this is best done from the entire teleomorph. We hope that the information provided will encourage a search for additional species of *Pyxidiophora* which almost certainly exist in trees and wood.

METHODS AND MATERIALS

Mites known to bear ascospores of *Pyxidiophora* were obtained from a variety of collectors. They were usually mounted in Hoyer's solution or Berlese's modification (Kinn, 1976) and ringed with Glyptol (General Electric), or a similar sealant. The mites were collected from pheromone traps, beetles and insect galleries. Mite specimens examined are listed in Table 1 and 2 and are housed in the collection of J. C. Moser, Southern Forest Experiment Laboratory, USDA Forest Service, Pineville, Louisiana, U.S.A.

Ascospores were studied and photographed on mounted mites at × 1000. Original drawings were made using a drawing tube calibrated at × 1500.

Table 1. Geographical distribution, habitat, and arthropod associations of *Thaxteriola*-type ascospores

Mite species	Mite stage[1]	Habitat, arthropod associations	Locality
Dendrolaelaps neocornutus (Hurlbutt) (J. Moser 6027, 6222, 6240, 6241, 6243, 6249, 6253, 6254, 6258, 6262, 6266, 6267, 6269, 6303, 6351)	1, pn, dn[2], m, f	Galleries SPBB[3] in *Pinus taeda* L.	Louisiana: Elizabeth
Dendrolaelaps varipunctatus (Hurlbutt) (J. Moser 6083, 6107, 6389)	m, f	Galleries *Ips* spp.	Louisiana: Elizabeth
Dendrolaelaps quadrisetus (Berlese) (J. Moser 30215, 30320, 30348, 30353, 30361, 30389, 30404, 30427)	dn[2]	Reared adults *Ips confusus* (LeConte) in *P. edulis* Engelm.	California: 6 miles N. Fawnskin.
Dendrolaelaps quadrisetus (J. Moser 24552)	dn[2]	On *Ips typographus* L.	Sweden: 18 km E. Uppsala
Dendrolaelaps quadrisetosimilis (Hirschmann) (J. Moser 6640)	m	Galleries *Ips* spp. in *P. taeda*	Louisiana: Elizabeth
Dendrolaelaps neodisetus (Hurlbutt) (J. Moser 12465, 19188, 30308)	dn[2], f	Galleries *Ips* spp. in *P. taeda*; on *Ips grandicollis* Eichhoff	Louisiana: Elizabeth, Livingston, William
Dendrolaelaps rotoni (Hurlbutt) (J. Moser 10741, 10757, 10773, 10783, 10825, 10830, 10843)	m, f	Galleries SPB[4] in *P. taeda*	Louisiana: Elizabeth
Dendrolaelaps rostricornutus Hirschmann & Wiśniewski (Wiśniewski–no number)	f	Under bark *Abies alba* Mill.	Poland: Świętokrzyski National Park
Dendrolaelaps fukikoae Ishikawa (Canadian National Collection 81–888)	dn	On *Monochamus alternatus* Hope	Japan: Ibaraki Pref.
Longoseius brachypoda (Hurlbutt) (J. Moser 4649)	f	Galleries SPB in *P. taeda*	Louisiana: Elizabeth
Mucroseius sp. nov. (J. Moser 11537)	f[2]	Reared adult *Monochamus titilator* (Fabricius)	Louisiana: Elizabeth
Ameroseius longitrichus Hirschmann (J. Moser 4664, 4810, 4837, 4839, 4853, 5090)	f[2]	Galleries SPB in *P. taeda*	Louisiana: Elizabeth
Proctolaelaps fiseri Samšiňák	m, f[2]	Galleries in *P. taeda*	Louisiana: Elizabeth
Proctolaelaps hystricoides Lindquist & Hunter (J. Moser 6078)	f[2]	Galleries *Ips* spp. in *P. taeda*	Louisiana: Elizabeth
Proctolaelaps subcorticalis Lindquist (J. Moser 15922)	f[2]	Galleries SPB in *P. rudis* Endl.	Guatemala: Totonicapán
Vulgarogamasus lyriformis (McGraw & Farrier) (J. Moser 1629)	f	Galleries SPB in *P. taeda*	Mississippi: Bude
Gamasolaelaps subcorticalis (McGraw & Farrier) (J. Moser 4233)	m	Galleries *Ips* spp. in *P. taeda*	Louisiana: Elizabeth
Uroobovella orri Hirschmann (J. Moser 16442)	f	Galleries SPB in *P. taeda*	Louisiana: LaSalle Par.
Cercoleipus coelonotus Kinn (J. Moser 5659, 10057)	m[2], f[2]	Galleries SPB in *P. taeda*	Louisiana: Elizabeth
Histiogaster rotundus Woodring (J. Moser 5995, 6015, 6016, 6019, 6068, 6072, 6099, 6100, 6102, 6300, 6337, 16102)	m, f	Galleries *Ips* spp. in *P. taeda*	Louisiana: Elizabeth
Tarsonemus krantzi Smiley & Moser (J. Moser 31060, 31070, 32653)	f[2]	Reared SPBB in *P. taeda*	Louisiana: Winn Par., Grant Par.
Tarsonemus krantzi (J. Moser 30828, 31092, 31143)	f[2]	Reared SPB in *P. taeda*	Texas: Sabine National Forest
Tarsonemus ips Lindquist (J. Moser 31052)	f[2]	On SPB in *P. taeda*	Louisiana: Grant Par.
Heterotarsonemus lindquisti Smiley (J. Moser 30857)	f[2]	On SPB in *P. taeda*	Texas: San Jacinto Co.
Trichouropoda longiovalis Hirschmann & Zirngiebl-Nicol (Wiśniewski–no number)	f		Poland: Świętokrzyski National Park
Trichouropoda munroi Ryke (Wiśniewski–no number)	m	Under bark of *Entandrophragma cylindricum* Sprague imported to Poland	Central African Republic
Trichouropoda munroi (Wiśniewski U–555)	f	On *Entandrophragma cylindricum* logs imported to Poland	Congo

Mite species	Mite stage[1]	Habitat, arthropod associations	Locality
Trichouropoda szczecinensis Wiśniewski & Hirschmann (Wiśniewski U–558)	f	On *Entandrophragma cylindricum* logs imported to Poland	Congo
Nenteria nuciphila Hirschmann & Wiśniewski (Acad. of Agric. Poznań–no number)	dn	On *Elytracantha pogonocerus* Montrouzier	New Guinea: Sattelberg

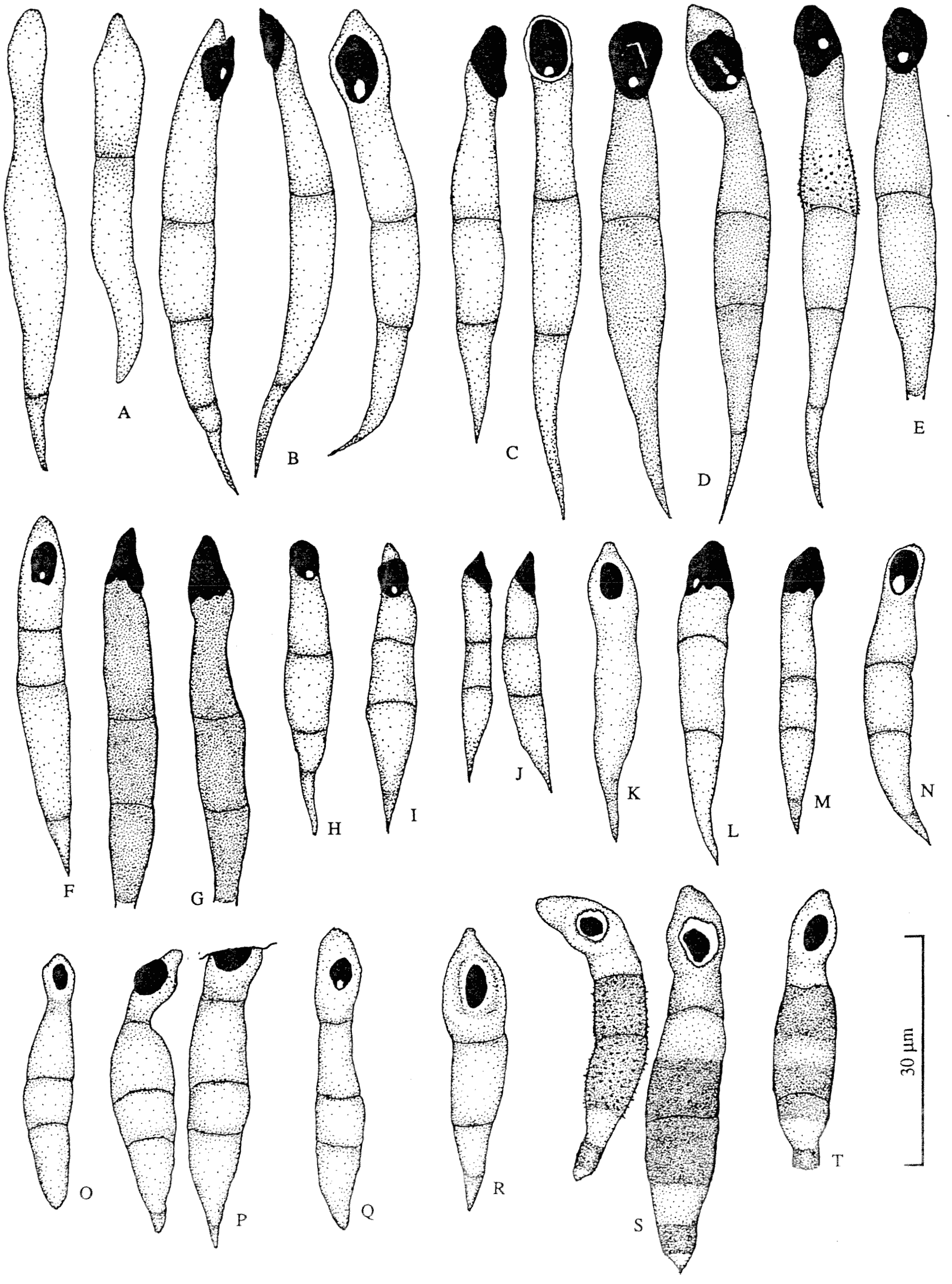
[1] l = larva; pn = protonymph; dn = deutonymph; m = male; f = female.
[2] Phoretic stages of mites.
[3] SPBB = Southern pine bark beetles (any of a number of bark beetles, mostly *Dendroctonus* spp. and *Ips* spp.) that infest southern pines.
[4] SPB = Southern pine dark beetle, *Dendroctonus frontalis* Zimm.

Table 2. Geographical distribution, habitat, and arthropod associations of *Acariniola*-type ascospores

Mite species	Mite stage[1]	Habitat, arthropod associations	Locality
Dendrolaelaps neocornutus (J. Moser 15754, 15762, 15834)	f	Galleries of *Ips* spp. in *Pinus rudis*	Guatemala: Totonicipán
Dendrolaelaps neocornutus (J. Moser 168, 303, 305, 311, 323, 329, 339, 342, 346)	dn[2], m, f	Galleries SPB[3]	Virginia: Accomac
Dendrolaelaps quadrisetus (J. Moser 30587, 30623)	dn[2]	Reared adults *Ips confusus* in *P. coulteri* D. Don	California: Lake Arrowhead
Dendrolaelaps quadrisetus (J. Moser 24552, 29930)	dn[2]	On *Ips typographus*	Sweden: 18 km E. Uppsala
Proctolaelaps sp. (J. Moser 275)	f[2]	Galleries SPB in *P. echinata* Miller	Virginia: Accomac
Proctolaelaps subcorticalis (J. Moser 2021)	f[2]	Reared adult *Dendroctonus ponderosae* Hopk. in *P. contorta* Loud.	British Columbia: Radium
Proctolaelaps subcorticalis (J. Moser 19782)	m	Galleries SPB	Guatemala: Puenta Tzaztzia Solata
Proctolaelaps xylotari Samšiňák (J. Moser 23041)	f[2]	On *Thanasimus formicarius* L.	Norway: Kongsberg
Proctolaelaps xylotari (J. Moser 24670, 24693)	f[2]	On *Trypodendron lineatum* Ol.	Germany: 25 km S.E. Freiburg
Lasioseius safroi (Ewing) (J. Moser 8598)	f[2]	Galleries *Dendroctonus pseudotsugae* Hopk. in *Pseudotsuga menziesii* (Mirb.) Franco	Idaho: Moscow
Histiostoma conjuncta Woodring & Moser (J. Moser 15850, 15897)	m, f	Galleries *Ips* spp. in *P. rudis*	Guatemala: Totonicipán
Histiostoma dryocoeti Scheucher (J. Moser 24682)	dn[2]	On *Trypodendron lineatum*	Germany: 25 km S.E. Freiburg
Trichouropoda polytricha (Vitzthum) (J. Moser 24119)	dn[2]	On *Ips typographus*	Germany: 70 km E. Freiburg
Uroobovella vinicolora (Vitzthum) (J. Moser 24470, 24494, 24696, 24910, 24911, 25007, 25021)	dn[2]	On *Trypodendron lineatum*, *Ips typographus*	Germany: 25 km S.E. Freiburg, 50 km S.E. Freiburg, 70 km E. Freiburg, Rhornkopf
Pediculaster sp. (J. Moser 18505)	m, f[2]	Galleries of *Hylurgops palliatus* (Gyllenhal)	Poland

[1] dn = deutonymph, m = male, f = female.
[2] phoretic stages of mites.
[3] SPB = Southern pine bark beetle, *Dendroctonus frontalis*.

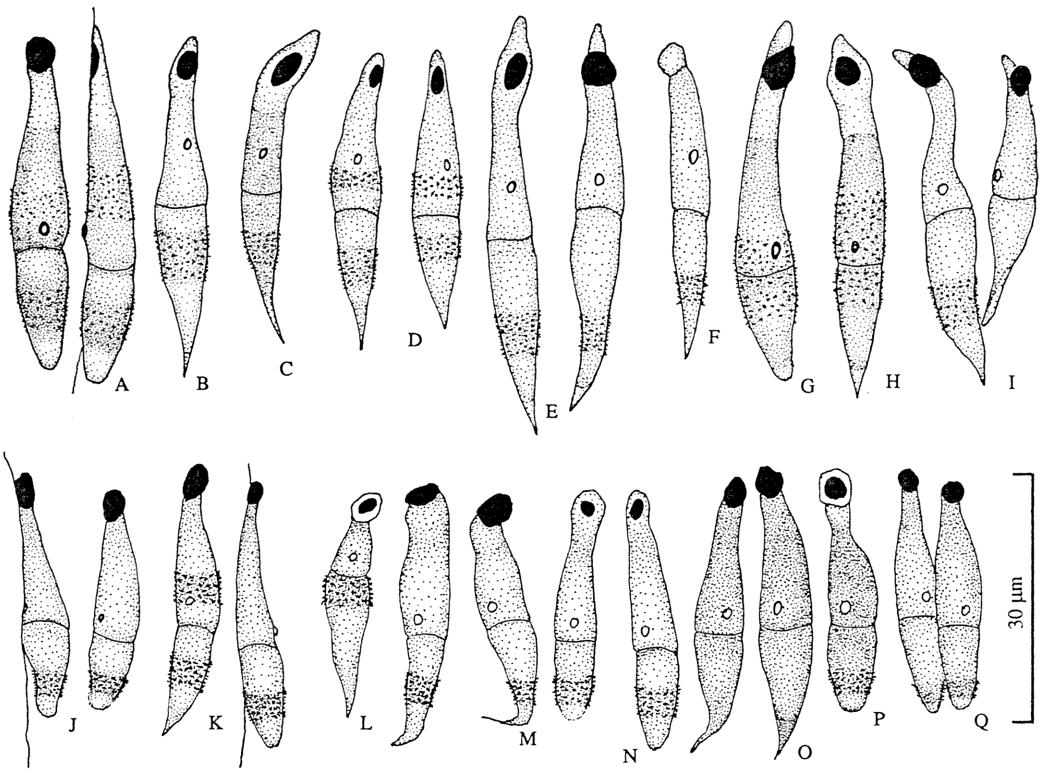
Fig. 1. A–T. *Thaxteriola*-type ascospores. All attached to mites except 1A. A, Immature ascospores of *Pyxidiophora kimbroughii*, Louisiana, holotype, Blackwell 200; B, *Thaxteriola* anamorph of *P. kimbroughii*, Texas, paratype, J. Moser 31087; C, Louisiana, J. Moser 4649; D, Louisiana, J. Moser 6249; E, Texas, J. Moser 31143; F, Louisiana, J. Moser 30308; G, California, J. Moser 30361; H, Louisiana, J. Moser 6019; I, Louisiana, J. Moser 6243; J, Louisiana, J. Moser 5995; K, Virginia, J. Moser 323; L, Guatemala, J. Moser 15922; M, Sweden, J. Moser 24522; N, New Guinea, Wiśniewski specimen; O, New Guinea, Wiśniewski specimen; P, Japan, Can. Nat. Collection 81–888; Q, Congo, Wiśniewski U–555; R, Central African Republic, Wiśniewski specimen; S, Poland, Wiśniewski specimen; T, Poland, Wiśniewski specimen.



RESULTS

All the ascospores were present on thirty five species of mites phoretic on wood-boring beetles, collected in bark beetle galleries, under bark or on logs (Tables 1, 2). Individual mites of the 116 collections had several, to well over 100, attached ascospores. Comparisons of the ascospores show variation in spore length, width, size and shape of the basal attachment region, pore location, color, wall ornamentation and number of septa. While some of the variation is almost certainly interspecific other variation is probably the result of ontogenetic differences.

Fig. 2. A–Q. *Acariniola*-type ascospores attached to mites. A, Norway, J. Moser 23041; B, Sweden, J. Moser 29930; C, Germany, J. Moser 24911; D, Germany, J. Moser 24494; E, Germany, J. Moser 25007; F, Germany, J. Moser 24470; G, Germany, J. Moser 24682; H, Germany, J. Moser 24670; I, Germany, J. Moser 24910; J, British Columbia, J. Moser 2021; K, Idaho, J. Moser 8598; L, Utah, J. Moser 18840; M, California, J. Moser 30623; N, Virginia, J. Moser 303; O, Virginia, J. Moser 168; P, Guatemala, J. Moser 15754; Q, Guatemala, J. Moser 15762.



Two basic types of ascospore were recognized on mite surfaces. The *Thaxteriola*-type (Spegazzini, 1918; Thaxter, 1914, 1920; Povah, 1931; Majewski & Wiśniewski, 1978*a*, *b*; Lundqvist, 1980; Blackwell *et al.*, 1986*a*, *b*) has a pore which is usually visible in the darkened attachment region and two, or rarely three, septa (Fig. 1). The *Acariniola*-type (Majewski & Wiśniewski, 1978*a*, *b*; Lundqvist, 1980) is distinguished by a pore outside the darkened attachment region nearer the septum of the basal cell; walls of one or both cells are usually finely spinulose (Fig. 2).

Both types of ascospores were found on a variety of mite species from geographically well-separated localities. The majority of the mite specimens were from the southern United States of America. *Thaxteriola*-type ascospores (55–75 µm long) on twelve species of mites from about 75 collections from the contiguous states of Louisiana, Texas and Mississippi, were identical with those of *Pyxidiophora kimbroughii* (Fig. 1 A–F). Specimens from California were similar in size and shape except that the ascospore walls were more darkly pigmented (Fig. 1 G).

A second *Thaxteriola*-type spore was found at one Louisiana locality, sometimes on the same mite with *P. kimbroughii* ascospores. It was clearly distinguished by its consistently shorter length (30–38 µm) and smaller dark basal region (Fig. 1 H-J).

Spores similar in appearance and size to this smaller Louisiana type were also found on mites from Virginia, U.S.A., Guatemala, Sweden and New Guinea (Fig. 1K-O). Louisiana specimens may be conspecific with those from Virginia and Guatemala; they were associated with *Dendroctonus frontalis* at all three localities. The Swedish mite was associated with the scolytid beetle, *Ips typographus* (L.), but the New Guinea specimens were associated with a brenthid beetle, *Elytracantha pogonocerus* Montrouzier.

A variety of other *Thaxteriola* spore types smaller than *P. kimbroughii* were present on mites from Japan, the Congo, Central African Republic and Poland (Fig. 1 P–T). The Polish specimens are distinctive in their banded pigmentation pattern, constricted spore tip, and in some spores, heavily spinulose walls. The Congo and Japanese specimens differed from others in this study by having three transverse septa. These mites were collected from diverse habitats: under fir bark (Poland), in sapela imported to Poland from the two African localities, and with a cerambycid beetle in pine (Japan).

Acariniola-type ascospores were found in several localities in North America and northern Europe (Table 2). These spores were 26–38 µm in length and one-septate; the cell adjacent to the attached cell and sometimes both cells were spinulose and usually more darkly pigmented in the spinulose area. European specimens were somewhat longer (Fig. 2 A–I) than North American specimens (Fig. 2 J–Q). All of these spores were collected on mites associated with scolytid beetles in pine. At two localities (Sweden, 18 km E. Uppsala, and Guatemala) the *Acariniola*-type spore was present with a small *Thaxteriola*-

type spore, sometimes on the same mite. Most ascospores had pores in the attached cell within 2–5 µm from the septum; however, specimens from Sweden (Fig. 2B) and some from Germany (Fig. 2C–F) had pores about mid-way between the darkened holdfast region and the septum. Pore placement was consistent within each collection. The deeply-pigmented holdfast region on North American (Fig. 2J–Q) spores was generally at the end of the spore; European specimens (Fig. 2A–I) usually had a darkened region several micrometers from the end of the spore. This may be due to ontogenetic differences. A single non-pigmented holdfast region was found in one of six normal spores from a German collection (Fig. 2F). There was no evidence of any pore structure in this region or in any normally darkened holdfast structures in the *Acariniola*-type spores.

DISCUSSION

Lundqvist (1980) recognized Polish specimens of *Thaxteriola moseri* and *Acariniola* spp. (Majewski & Wiśniewski, 1978*a*, *b*) as those of *Pyxidiophora*; because conidia were not present he included these species in the synonymy of *Pyxidiophora*. However, the discovery of conidia in the *Thaxteriola* anamorph of *P. kimbroughii* Blackwell & Perry (Blackwell *et al.*, 1986*a*, *b*) establishes a link between at least this one species of *Pyxidiophora* from bark beetle habitats and species of *Thaxteriola* producing conidia discussed by Spegazzini (1918) and Thaxter (1914, 1920) from dung beetle habitats and free insects. Whether the ability of *Pyxidiophora* ascospores to develop directly into a conidium-producing anamorph is a widespread phenomenon or not is unknown (Blackwell & Malloch, 1989).

We have assumed that the ascospores reported here are those of species of *Pyxidiophora*. However, discovery of complete teleomorphs is necessary to be certain. Our basis for considering the ascospores to be those of *Pyxidiophora* is similarity in spore shape and the presence of the unusual darkened holdfast region. *Thaxteriola*-type spores have a pore-like structure in the darkened region which we interpret as a secretory pore from light microscopic observations. In *Acariniola*-type spores no such pore was observed, although they were attached to the mite cuticle at the darkened region. The additional attachment structure found nearer the septum is similar to early attachment structures found in the laboulbenialean genus *Herpomyces* Thaxter (Blackwell & Malloch, 1989). While we refer to it as a 'pore', it may be a sucker-like pad. No haustoria were observed in either spore type.

Dramatic ontogenetic changes occur during ascospore development in *P. kimbroughii* culminating in release of ascospores to the perithecial neck, often before complete maturation (Blackwell *et al.*, 1986*a*, *b*; Blackwell & Malloch, 1989). At the perithecial neck the one-septate, smooth, hyaline spores begin to develop the darkened holdfast region and may become two-septate. These progressive changes may occur as long as several days after ascospore release. Ascospores with entire walls somewhat darkened and roughened have been observed only attached to mites. Amount of wall darkening cannot be used with confidence here as a taxonomic character because amount of pigment may have been affected by differences in the treatment of mite specimens which often are cleared in hot lactophenol. Ascospores of some species of *Pyxidiophora* are known to be three-septate (Breton & Faurel, 1967; Hawksworth & Webster, 1977; Lundqvist, 1980; Barrasa & Moreno, 1982), and two collections reported here have three-septate ascospores. Based on previous observations (Blackwell *et al.*, 1986*b*), ascospores of *P. kimbroughii* sometimes become two-septate late in development. Additional studies of maturing spores are needed to evaluate the use of septation as a taxonomic character.

The darkened holdfast region increases in area and apparently develops the pore after attachment to mites in the *Thaxteriola*-type spore. Although the darkened region may be subterminal in early stages of development, it eventually fills the terminal part of the spore in at least some specimens. Early development of the pore near the septum in *Acariniola*-type ascospores has not been observed in any species of *Pyxidiophora* which are known from the entire teleomorph. One additional change apparently occurs during ascospore maturation on mite substrates – the elongated, thickened spore tip often becomes broken. This fact must be taken into consideration when spore lengths are compared.

Observations on *P. kimbroughii* development, the large number of collections of *P. kimbroughii*, and the smaller ascospores from the Gulf of Mexico region have helped us to infer ontogenetic changes which may occur after ascospores become attached to mites. Other differences in *Thaxteriola*-type ascospore morphology are considered interspecific. Where a large series of specimens was examined from similar arthropod assemblages, non-overlapping ascospore length ranges were interpreted as evidence of different species. The conspicuous banding pattern and constriction of the spore tip in Polish *Thaxteriola*-type ascospores separate them from all others known. Pore placement near the septum or midway between darkened region and septum is consistent in *Acariniola*-type ascospores and has been used to distinguish species (Majewski & Wiśniewski, 1978*a*). Two trends in spore size are evident from the material we have examined: *Acariniola*-type spores are smaller than *Thaxteriola*-type spores in bark beetle habitats; *Thaxteriola*-type spores from bark beetle habitats are generally smaller than those of known species of *Pyxidiophora* from other habitats.

Limited material of the other *Thaxteriola*-type and the *Acariniola*-type ascospores and lack of information on development of the teleomorphs prevents recognition of additional species. Until teleomorphs are discovered in the beetle and mite habitats, the taxonomic questions raised by the presence of the ascospores cannot be answered.

The occurrence of *Pyxidiophora* ascospores reported here indicates that the genus is commonly associated with mites in trees and wood. Previous distribution records from Europe (Majewski & Wiśniewski, 1978*a*), Gulf Coast, U.S.A. (Majewski & Wiśniewski, 1978*b*; Blackwell *et al.*, 1986*a*, *b*), and Australia (Simpson & Stone, 1987) have been extended greatly to include New Guinea, Japan, Africa, Central America and western North America. Other species of *Pyxidiophora* known from the complete teleomorphs occur primarily in dung and plant debris habitats and sometimes as mycoparasites. Blackwell & Malloch (1989) speculated that most species may actually be mycoparasites. Mite dispersal and perhaps that of insects is probably extremely important to dispersal of many species. Mite dispersal has been observed in only two dung *Pyxidiophora* species, but is suspected in others (Blackwell & Malloch, 1989). In addition ascospores occur on a variety of mites from plant debris (Blackwell, unpubl.).

The recognition of the common widespread association of *Pyxidiophora* with tree- and wood-inhabiting mites, usually in beetle habitats, will be important in the consideration of evolution within the genus. Study of this assemblage has already led to a better understanding of the biology of other species by explaining the function of the darkened holdfast region and suggesting the general importance of arthropod dispersal in the genus.

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