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Commensal Nematodes in the Glands, Genitalia, and Brood Cells of Bees (Apoidea)[1]

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Abstract: Seven species of bees from the eastern United States, representing four families in the Apoidea, were dissected and examined for nematode associates. Dufour's glands in females of *Halictus ligatus, Augochlora pura mosieri,* and *Augochlorella gratiosa* (Halictidae) from Florida were infested with dauer juveniles of *Aduncospiculum halicti* (Diplogasteridae). The Dufour's glands of *Colletes thoracicus* (Colletidae) females from Maryland were infested with dauer juveniles of a new species of *Koerneria* sp. (Diplogasteridae), and abdominal glands of females of *Andrena alleghaniensis* (Andrenidae) from New York were infested with dauer juveniles of another new species of *Koerneria.* The lateral and median oviducts, Dufour's glands, and poison sacs in females of *Anthophora abrupta* (Anthophoridae) from Maryland and Alabama were infested with dauer juveniles of a new species of *Bursaphelenchus* sp. (Aphelenchoididae). Cross sections of the nematode-infested poison sacs of *A. abrupta* revealed two types of humoral host defense reactions.

Key words: Andrenidae, *Aduncospiculum halicti,* Anthophoridae, bees, *Bursaphelenchus* sp., Colletidae, commensal, Diplogasteridae, Halictidae, *Koerneria* spp.

Most commensal associations between nematodes and bees have been reported from the western United States (7,8). *Bursaphelenchus seani* Giblin and Kaya (Aphelenchoididae: Aphelenchida) has a highly synchronized phoretic association with the digger bee, *Anthophora bomboides stanfordiana* Cockerell (Anthophoridae: Hymenoptera), a univoltine species that nests gregariously along the California coast (6,7), and *B. kevini* Giblin et al. is associated with *Halictus ligatus* Say and *H. farinosus* Smith (Halictidae: Hymenoptera) in the Pacific Northwest (8,11). In addition, *Aduncospiculum halicti* Giblin and Kaya (Diplogasteridae: Diplogasterida) is phoretically associated with *H. ligatus* in four western states and in New Jersey and New York (8,9) and with *H. rubicundus* (Christ) in New Jersey (8). Batra (2) observed juveniles of unidentified rhabditid nematodes in the Dufour's glands of *Colletes thoracicus* Smith, *C. inaequalis* Say, *C. validus* Cresson (Colletidae: Hymenoptera), and *H. ligatus,* and juveniles of an unidentified aphelenchoidid nematode in the Dufour's glands of *Anthophora abrupta* (Say) from Maryland.

The purpose of this study was to expand the previous observations concerning the nematode associates of *A. abrupta* and *C. thoracicus* (2) and to examine *H. ligatus, Augochlora pura mosieri* Cockerell, *Augochlorella gratiosa* (Smith), *Augochloropsis anonyma* (Cockerell) (Halictidae: Hymenoptera), and *Andrena alleghaniensis* Viereck (Andrenidae: Hymenoptera) collected from various locations in the eastern United States for nematode associates.

MATERIALS AND METHODS

Halictidae: Adults of *Augochlora pura mosieri, Augochlorella gratiosa, Augochloropsis anonyma,* and *H. ligatus* were collected with a sweep net from the flowers of *Bidens bipinnata* L., and (or) *Momordica charantia* L. between 27 November 1985 and 6 October 1986 from Ft. Lauderdale and Davie, Broward County, Florida. Adult bees were transported to the laboratory where they were cooled in a refrigerator to 5 C, rinsed externally, dissected alive in deionized water, and examined for internal nema-

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tode associates (10). The location, stage, and number of nematodes infesting each bee were recorded, and culture attempts were made at 25 C on 5% (v/v) glycerol supplemented potato dextrose agar (GPDA) (5) or GPDA that had been previously inoculated with the yeast *Candida membranaefaciens* (Lodder & Kreger-Van Rij) (5). Adult nematodes from successful cultures were fixed in formalin-glycerin for morphological comparisons (17) and used for species identification.

Mating studies were conducted with isolates of *Aduncospiculum halicti* recovered from different hosts and locations. Isolates of *Aduncospiculum* from *H. ligatus, A. pura mosieri,* and *A. gratiosa* from Broward County, Florida, were crossed as previously described (8). Nematodes were recovered as juveniles from cultures of a specific host isolate and placed individually onto 16-mm-d cores of GPDA. These had been previously seeded with *C. membranaefaciens* in 12 separate wells of a sterile 24-multiwell tissue culture plate. Another juvenile from the same isolate (control) or from a different host isolate was then transferred to each well. Half of the wells in any given plate would arbitrarily have a male and a female allowing for comparisons in mating compatibility within and between different bee host isolates. Experimental crosses were observed for successful reproduction for 6 weeks at 27 ± 1 C. There were three replicates (12 cores per replicate) for each cross.

Augochlora pura mosieri differs from most species of halictids, which are soil-nesting, by nesting in rotting wood (18). A rotting *Casuarina* sp. log containing unopened brood cells of *A. pura mosieri* was discovered by R. Scheffrahn at Markham Park in Broward County, Florida. The brood cells had apparently been constructed within the frass and galleries of a large wood-boring beetle. Brood cells and bees of various stages from these cells were examined for nematodes, and bees were dissected and examined internally for nematodes. Adult nematodes from cells were heat killed and fixed in formalin-glycerin (17) for comparison with other *Aduncospiculum* isolates.

Colletidae: Flying adults of *Colletes thoracicus* were collected on 16 May 1986 from a nesting site in Clinton, Prince Georges County, Maryland, packed in moistened paper toweling in cardboard cartons and shipped overnight with an ice pack to Ft. Lauderdale, Florida. Bees were held in the refrigerator no longer than 3 days after arrival before being dissected and examined for nematodes. Recovered nematodes were placed on nutrient agar (NA), 10% tryptic soy broth agar (TSB), or GPDA for culture attempts at 25 C. Adult nematodes were killed and fixed for identification.

Andrenidae: Flying adults of *Andrena alleghaniensis* were collected on 29 May 1986 and 18 June 1987 from a nesting site in the central Adirondack mountains near Saranac Lake, Franklin County, New York (3). Living bees were shipped with ice packs to Ft. Lauderdale for examination and dissection. Culture attempts were done with nematode associates on NA, TSB, and GPDA.

Anthophoridae: Newly emerged adults of *Anthophora abrupta* were collected on 3 and 4 June 1986 from excavated portions of a gregarious nest that had been removed from a farm shed wall in Ownings Mills, Baltimore County, Maryland (14). Cells from this site were opened and examined for nematodes. Flying adults of *A. abrupta* were collected from a rock quarry nesting site in Prince Georges County, Maryland, on 6 June 1986 and from a nesting site in Montgomery County, Alabama, on 16 May 1988. Living bees were sent with ice packs to Ft. Lauderdale for examination and dissection. Culture attempts with nematode associates were done with GPDA or GPDA that had been seeded with the fungus *Monilinia fructicola* (Wint.) for 1 week (5).

Nematode-infested poison sacs from *A. abrupta* were isolated, heat treated at 60 C for 1 minute, fixed in 5% formalin, dehydrated into 95% ethanol, processed into glycol methylacrylate (JB-4 embedding kit; Polysciences, Warrington, PA), sectioned on an ultramicrotome with a glass knife to

produce 2–4-μm thick sections, and stained with Lee's Methylene-blue-basic fuchsin stain (10). Photomicrographs of nematode-infested organs and sections were made with an Olympus PM-10A photomicroscope attached to a Zeiss compound microscope.

Results and Discussion

Halictidae: Dauer juveniles (denoted JIII in contrast to J3 for third-stage juveniles from the propagative phase) of *Aduncospiculum halicti,* identified from adults in culture, were recovered from the Dufour's glands of females of *A. pura mosieri, A. gratiosa,* and *H. ligatus* from Florida (Table 1). Only the genital capsules of males of *A. pura mosieri* and *A. gratiosa* were infested with dauers of *A. halicti. Augochloropsis anonyma* was not infested with nematodes (Table 1).

Seven cells were recovered from a nest of *A. pura mosieri.* Two of these cells contained adult male bees which were ready to emerge. The aedeagus and genital capsule of each of these males were infested with 84–124 dauer juveniles of *Aduncospiculum halicti.* Each of the male cells contained ca. 150 *Aduncospiculum* of all stages, including dauer juveniles and a few wide stomatal (eurystomatous) female morphs. The nematodes were recovered from the feces and the top of these cells. Two cells contained pupae of *A. pura mosieri,* and ca. 50 dauer juveniles of *Aduncospiculum* were recovered from the cuticle of one of the pupae, but no nematodes were recovered internally. In both pupal cells, *Aduncospiculum* of all stages were recovered from the feces and fungal mycelia growing on them. No nematodes were recovered from a cell containing an egg or a cell containing a pharate adult. The pharate adult was not infested internally. One cell contained a larva and pollen provisions. No nematodes were recovered internally from the larva, but several propagating nematodes were found on the cell walls. In addition, two adult females and one adult male bee emerged from the log during examination. Each of these bees were infested with 50–60 dauer juveniles of *Aduncospiculum halicti* in their Dufour's glands or genital capsule.

These results suggest that the association between *Aduncospiculum halicti* and *A. pura mosieri* in the wood-nesting environment is very similar to that reported for *Aduncospiculum halicti* and the soil-dwelling halictids, *H. ligatus* and *H. farinosus* (8). Stockhammer (unpubl.) found nematodes in the Dufour's glands of *Augochlora pura* from Lawrence, Kansas, and also observed nematodes in the cell lining as soon as a female bee applied it in observation nests. The nematode observed by Stockhammer probably was *Aduncospiculum halicti* because this is the only species of nematode identified to date from the Dufour's glands of halictids. The observation of dauers in cells of pupae and adults of *A. pura mosieri,* but only propagative forms in the larval cell, supports the hypothesis that the life cycle of the nematode is synchronized with its bee transport host (8) (Fig. 1). Dauer juveniles of *Aduncospiculum halicti* probably persist in the Dufour's glands of overwintering female bees.

Aduncospiculum halicti produced dimorphic females in nests of *Halictus* and in old monoxenic cultures (8,9). In cultures less than 5 weeks old, almost all of the females observed were the narrow stomatal (stenostomatous) female morph which fed on bacteria or yeasts. In monoxenic cultures more than 6 weeks old, wide-mouthed (eurystomatous) females were observed in low proportions (9), and these were observed to cannibalize young conspecifics (R. Giblin-Davis, unpubl.). This morphological plasticity of the stoma probably allows for trophic niche divergence. The ecological significance of this phenomenon is not known, but it may be an important population survival strategy permitting efficient use of ephemeral food resources in bee cells.

Aduncospiculum halicti cultured from the different halictids in this study were very similar morphologically except for differences in tail length. A proposed character for the diagnosis of the monotypic genus *Aduncospiculum* was a conoid tail with an

TABLE 1. Survey of the internal association of nematodes with bees from the eastern United States.

Bee species	Collection location†	Date(s)	Sex	Bees infested with nematodes (%)	Bees examined (N)	Nemas/infested bee		Internal location of nematodes§	Nematode species
						Mean ± SD	Range		
Augochlora pura mosieri	Br	11/85–3/86	F	39	18	96 ± 105	25–269	DG	*Aduncospiculum halicti*
			M	20	5	7		GC	*A. halicti*
Augochlorella gratiosa	Br	11/85–10/86	F	80	15	48 ± 43	5–121	DG	*A. halicti*
			M	50	2	40		GC	*A. halicti*
Augochloropsis anonyma	Br	11/85–3/86	F	0	6				
			M	0	12				
Halictus ligatus	Br	11/85–5/86	F	12	68	12 ± 12	2–35	DG	*A. halicti*
			M	0	2				
Colletes thoracicus	PG	5/86	F	21	101	31 ± 59	1–270	DG	*Koerneria* n. sp.
			M	0	3				
Andrena alleghaniensis	Fr	5/86	F	81	31	22 ± 25	1–93	AG	*Koerneria* n. sp.
			M						
		6/87	F	55	11	12 ± 19	1–50	AG	*Koerneria* n. sp.
			M						
Anthophora abrupta	Ba	6/86	F	3	37	1		LO	*Bursaphelenchus* n. sp.
			M	3	33	68		GC	*Bursaphelenchus* n. sp.
	PG	6/86	F	79	29	170 ± 130	4–349	DG, LO, PS	*Bursaphelenchus* n. sp.
			M						
	Mo	5/88	F	82	28	92 ± 88	3–365	DG, LM, PS	*Bursaphelenchus* n. sp.
			M	41	17	7 ± 5	2–15	GC	*Bursaphelenchus* n. sp.

† Ba = Baltimore County, MD; Br = Broward County, FL; Fr = Franklin County, NY; Mo = Montgomery County, AL; PG = Prince Georges County, MD.
§ AG = abdominal glands; DG = Dufour's gland; GC = genital capsule and aedeagus; LO = lateral oviducts; LM = lateral and median oviducts; PS = poison sac.

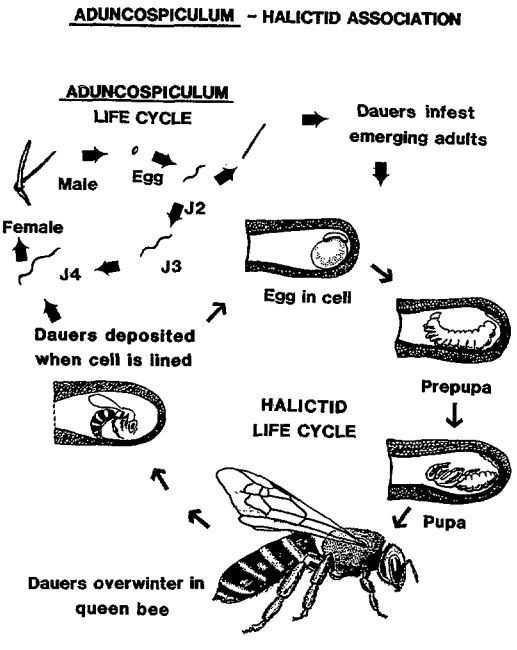

FIG. 1. Association between halictid bees and the nematode *Aduncospiculum halicti*. Dauer juveniles (JIII) are deposited into newly constructed bee cells during the lining of the cell. Dauers molt into propagative cycle and feed on yeasts and bacteria in the cell. Dauer juveniles are produced about the time of bee pupation and infest the adult bee prior to emergence from the cell. Dauers of *Aduncospiculum halicti* overwinter in Dufour's glands of mated females (queens).

acute terminus in adult females based upon cultured isolates and adults recovered from *H. ligatus* cells (9). *Aduncospiculum halicti* from *H. ligatus* had a c′ ratio value (tail length/anal body width) of less than 5.5 for both males and females (9). In this study, eurystomatous and stenostomatous females and stenostomatous males of the nematodes cultured from *A. pura mosieri* and *A. gratiosa* had long filiform tails with c′ ratios greater than 6. However, in *Aduncospiculum halicti* from the *A. pura mosieri* nest and from nematodes cultured from the nest, filiform tails with c′ ratios greater than 6 were noted in both stomatal morphs of females, but males had c′ ratios of less than 5.5. *Aduncospiculum halicti* cultured from *H. ligatus* from Broward County, Florida, were consistent with the original description; females of both morphotypes with uniformly conoid tails, and both sexes with c′ ratio values of less than 5.5. There is precedence for tail length variability between diplogasterid nematodes recovered from the environment and those from culture. First generation adults of *Eudiplogaster aphodii* (Bovien) cultured from their dung beetle host possessed short tails, whereas second generation adults subcultured from juveniles on agar had long filiform tails (16). The generic diagnosis for *Aduncospiculum* should be modified to account for the variability in tail shape observed.

We observed successful mating within *Aduncospiculum halicti* isolates from *A. pura mosieri* (36%), *A. gratiosa* (11%), and *H. ligatus* (19%), but no successful outcrosses between nematode isolates from the different bee hosts were observed. Giblin and Kaya (8) reported successful mating crosses between *Aduncospiculum halicti* populations isolated from *H. ligatus* from different geographical locations. The apparent lack of mating compatibility coupled with the slight morphological divergence in tail shape between populations suggests that gene flow between populations of *Aduncospiculum halicti* associated with *Halictus, Augochlora,* and *Augochlorella* may be restricted by differences in their hosts' nesting biology or other factors. Further work should be done to elucidate the taxonomic status of these different *Aduncospiculum* populations.

Lello (13) observed unidentified nematodes in the Dufour's glands of fixed specimens of *H. rubicundus* from Corvallis, Oregon, and *Megalopta genalis* Meade-Waldo from Barro Colorado Island, Panama, but not in the other halictids she examined, which included *Augochlora pura* and *Augochloropsis* sp. Since *M. genalis* nests in wood like *A. pura*, it would be interesting to see if the nematode in the Dufour's glands of *M. genalis* is *Aduncospiculum halicti.*

Nest sharing in sympatrically occurring bee species could be one way for the original infestation of a species of bee and could allow for subsequent gene flow in nematodes phoretically bound to different bee species. Three other routes for colonization

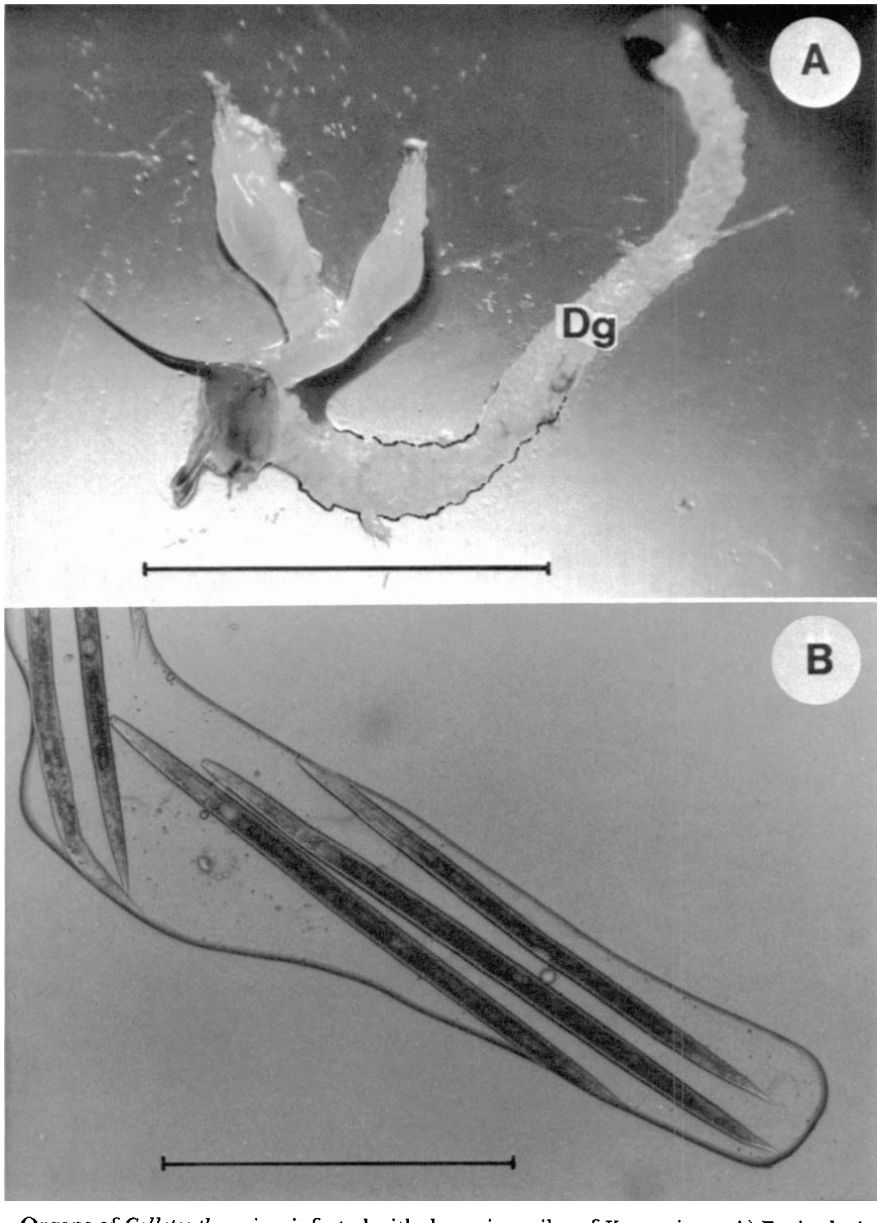

FIG. 2. Organs of *Colletes thoracicus* infested with dauer juveniles of *Koerneria* sp. A) Excised sting, ovaries, and Dufour's gland (Dg) of *Colletes thoracicus*. Scale bar = 5 mm. B) *Koerneria* sp. dauer juveniles (JIII) in a droplet of the macrocyclic lactone secretion from an infested Dufour's gland of *Colletes thoracicus*. Scale bar = 400 μm.

of a new host species and gene flow amongst *Aduncospiculum halicti* populations could occur: 1) by venereal transmission of nematodes during congeneric mating attempts, 2) by migration of nematodes through the substrate from infested nests to the nearby nests of different bee species, or 3) by cleptoparasitic "cuckoo" bees, such as *Sphecodes* spp. (Halictidae: Hymenoptera), which may lay their eggs in nests of bee host species different from that in which they developed.

Colletidae: Dauer juveniles (JIII) of a diplogasterid nematode that appears to be a new species of *Koerneria* was recovered from the Dufour's glands of 21% of *C. thoracicus*

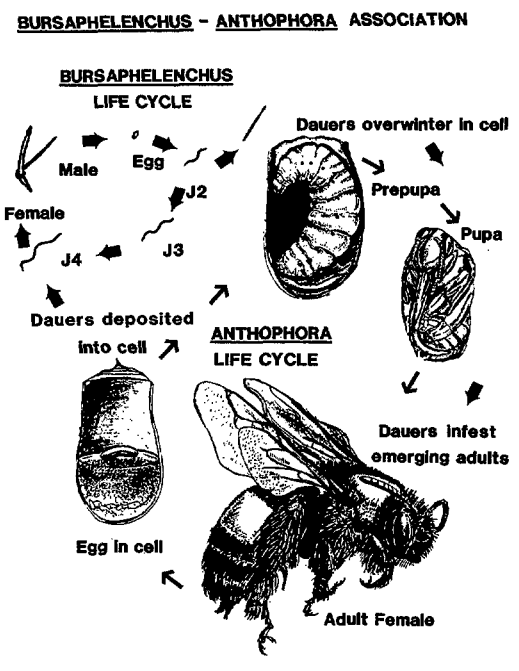

FIG. 3. Association between anthophorid bees and *Bursaphelenchus* spp. Dauer juveniles (JIII of *B. seani*, JIII and JIV of *Bursaphelenchus* sp.) are deposited in brood cells during oviposition (both *Anthophora bomboides stanfordiana* and *A. abrupta*) or cell lining (*A. abrupta* only). Dauer nematodes molt into the propagative phase and feed on fungi on cell walls or provisions. Dauer juveniles form when the bee larva defecates (prepupa), persist under frass in the cell with overwintering prepupa, and migrate into the newly emerged adult in its cell.

females (Table 1, Fig. 2). This nematode was easily cultured and maintained xenically on 10% TSB agar or NA, but it required subculturing every 2 weeks for maintenance. Stomatal dimorphism, as reported for *Aduncospiculum halicti*, was observed in cultured adults of both sexes of the *Koerneria* sp. from *C. thoracicus*, with the most common form being the stenostomatous morph.

The *Koerneria* sp. that we cultured and identified from the Dufour's glands of *C. thoracicus* in this study and the rhabditid reported from *C. thoracicus*, *C. validus*, and *C. inaequalis* (2) are probably the same nematode species. *Colletes thoracicus* from both studies were collected from the same location, and dauer juveniles of diplogasterid and rhabditid nematodes are nondescript and easily confused. Also, genera now classified within the order Diplogasterida were once considered members of the superfamily, Rhabditoidea. Observations concerning *Aduncospiculum halicti* and different halictid bee hosts suggest that sympatrically occurring congeneric species of *Colletes* could be phoretically associated with a single nematode species.

Colletes and *Halictus* bees spread the macrocyclic lactones released from the Dufour's glands onto cell walls (4,12). These compounds, or their w-hydroxyalkanoic acids, polymerize in *Colletes* spp. to form a highly hydrophobic laminester lining (12). Nematode deposition probably occurs during the cell lining process. Because *C. thoracicus* is univoltine and overwinters as a prepupa (2), the life cycle of the nematode is probably synchronized with the bee and similar to the generalized cycle presented for *Bursaphelenchus* nematodes and *Anthophora* bees (Fig. 3). Batra (2) did not observe nematodes in the provisions or nests of the *Colletes*. However, with only a 21% infestation level, this nematode would have been difficult to detect in arbitrarily collected cells. An extensive study over the course of the annual life cycle of *C. thoracicus* should be made to confirm the nature of the association between this *Koerneria* sp. and its host(s).

Andrenidae: Over 50% of females of *A. alleghaniensis* had one or more abdominal glands infested by dauer juveniles (JIII) of a diplogasterid nematode that appears to be another new species of *Koerneria* (Table 1, Fig. 4). Usually, about half of the six abdominal glands in any one infested bee contained nematodes, and each infested gland contained 6 ± 6 (range = 1–28) nematodes.

Dauer juveniles were easily extracted from ruptured abdominal glands and cultured xenically on TSB or NA as described for the *Koerneria* sp. isolated from *C. thoracicus*. As with the isolate from *C. thoracicus*, this *Koerneria* sp. exhibited stomatal di-

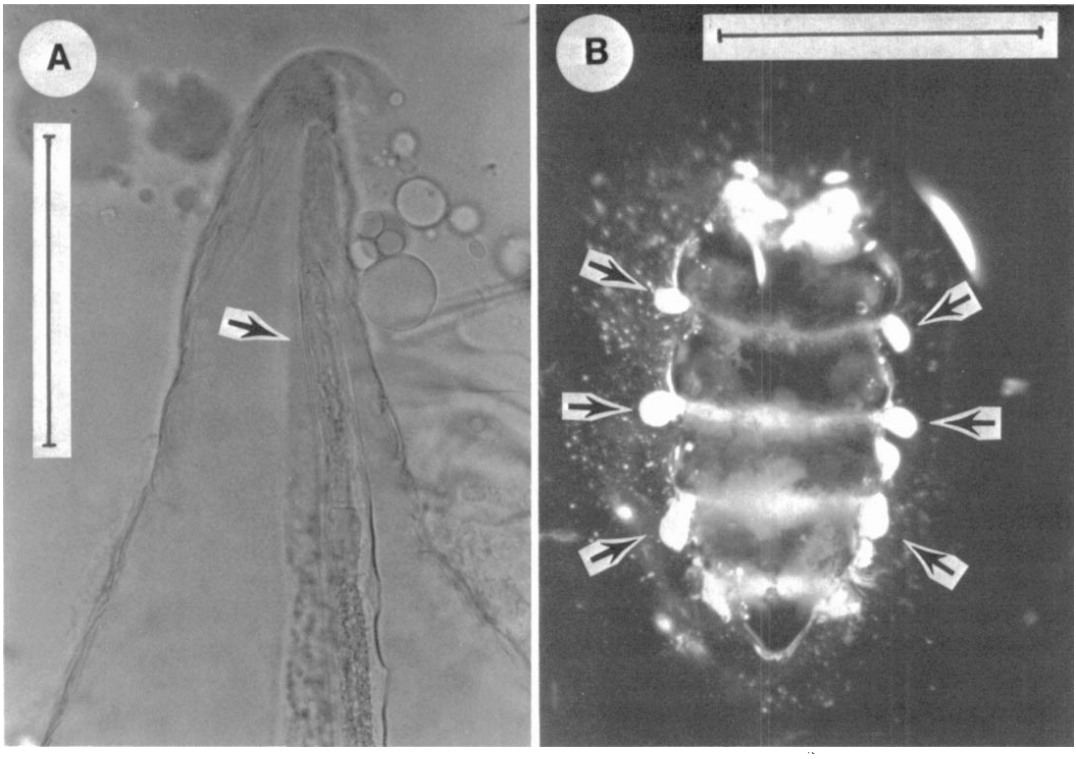

FIG. 4. Organs from *Andrena alleghaniensis* infested with dauer juveniles of *Koerneria* sp. A) Dauer juveniles (JIII) of *Koerneria* sp. (arrow) near the orifice of an abdominal gland of *Andrena alleghaniensis.* Scale bar = 100 μm. B) Dissected abdomen of *A. alleghaniensis* with sternites and viscera removed exposing abdominal glands (arrows). Scale bar = 4 mm.

morphism in females. This morphological feature, however, was rare and has not yet been observed in males. Although morphologically very similar to the isolate from *C. thoracicus,* the adults and dauer juveniles of the *A. alleghaniensis* isolate were consistently shorter in total body length.

An unidentified dauer diplogasterid was recovered by Altenkirch (1) from the abdominal glands of *Andrena vega* Panzer, *A. fulva* Schrank, and *A. albicans* Muller in Germany. There was an apparent correlation between the reduction in abdominal gland volume and the number of nematodes per gland, suggesting that the nematodes were transferred to the bee cells with the gland secretions. Adults and juveniles of the unidentified diplogasterid were recovered from the pollen balls and on the walls of cells with immature bees. In addition, nematodes were recovered from the scopal hairs of adult bees. Altenkirch (1) observed female andrenids stroking the sides of their abdomens with their hind legs and suggested that the abdominal glands in *Andrena* might provide a sticky material to hold pollen grains to the scopa. If this is so, nematodes could be transferred from one generation to the next when they were deposited into the bee cells with pollen loads. No volatile organic compounds were detected by gas chromatography in hexane-extracted abdominal glands of *A. alleghaniensis* (Scheffrahn and Giblin-Davis, unpubl.). This suggests that the abdominal glands secretions are not pheromones, and further work must be done to identify and ascribe a function for these secretions. These univoltine bees may have a synchronized nematode association similar to other univoltine bees, except that the nematodes overwinter in the abdominal

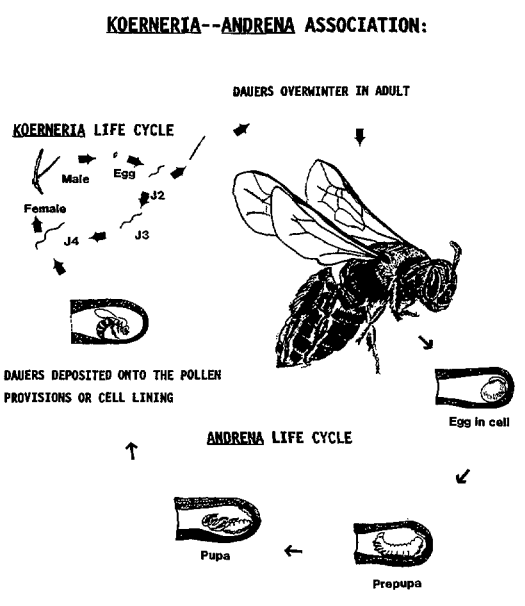

FIG. 5. Association between andrenid bees and *Koerneria* sp. Dauer nematodes (JIII) probably are deposited into bee's pollen load with abdominal gland secretions. Dauer nematodes molt into propagative phase and feed on bacteria. Dauers probably form at time of bee pupation and migrate into abdominal glands of the adult as it molts in its cell.

glands of adult females in their brood cells (Fig. 5).

Anthophoridae: Dauer juveniles (JIII and JIV) of a new species of *Bursaphelenchus,* very similar morphologically to the pinewood nematode, *B. xylophilus* (Steiner & Buhrer), were recovered from *A. abrupta* at all three locations surveyed (Table 1). Male bees were infested in the genital capsule and (or) aedeagus, whereas females were infested in the lateral and median oviducts, Dufour's glands, and (or) poison sacs (Table 1, Fig. 6). This association contrasts with that observed between *B. seani* and *A. bomboides stanfordiana* where dauer juveniles (JIII only) of the nematode were restricted to the lateral and median oviducts of female bees (10). No overt pathology was observed in the nematode-infested organs of *A. abrupta* males or females, but clear host defense reactions were observed in infested poison sacs (Fig. 6A). In cross-section these host reactions appeared to be humoral (noncellular) in nature (Fig. 7). In most cases, nematodes appeared to be enveloped in a sclerotized matrix (Fig. 7A). In a few cases, the nematodes were dead, vacuolated, and darkened (Fig. 7B). Possibly the nematodes were killed by the venom in the poison sacs followed by the host reaction in response to dead or dying nematodes.

Bursaphelenchus sp. was easily maintained xenically on fungi from the host bee or dixenically on *M. fructicola* on GPDA. There were no morphological differences among the different geographical isolates of *Bursaphelenchus* sp. examined. No nematodes were recovered from the cells, but this is probably because of the very low (3%) infestation level at the Baltimore County location and the relatively few cells examined. This association probably is similar to the one reported between *B. seani* and *A. bomboides stanfordiana* (7). Nematodes (JIII and JIV) in the lateral and median oviducts probably are deposited during oviposition, while those in the triglyceride secretions of the Dufour's gland (15) probably are deposited in cells during the cell lining phase. The life cycle of *Bursaphelenchus* sp. probably is highly synchronized with its univoltine host, as was shown for the association between *B. seani* and *A. bomboides stanfordiana* (7). *Bursaphelenchus* sp. probably overwinters as dauer juveniles (JIII and JIV) with the prepupa of *A. abrupta* and internally infests the newly molted adult bee before it chews its way out of the earthen cell (Fig. 3).

Infestations of *A. abrupta* usually numbered fewer than 400 nematodes per bee (Table 1) compared with as many as 10,000 *B. seani* per infested *A. bomboides stanfordiana* female (7). It is not clear why most of the nematode associates are organ specific in their respective female bee hosts, whereas *Bursaphelenchus* sp. is not. This lack of organ specificity during infestation and the host defense reactions observed in the poison sacs suggest that the association between *Bursaphelenchus* sp. and *A. abrupta* is relatively recent in origin.

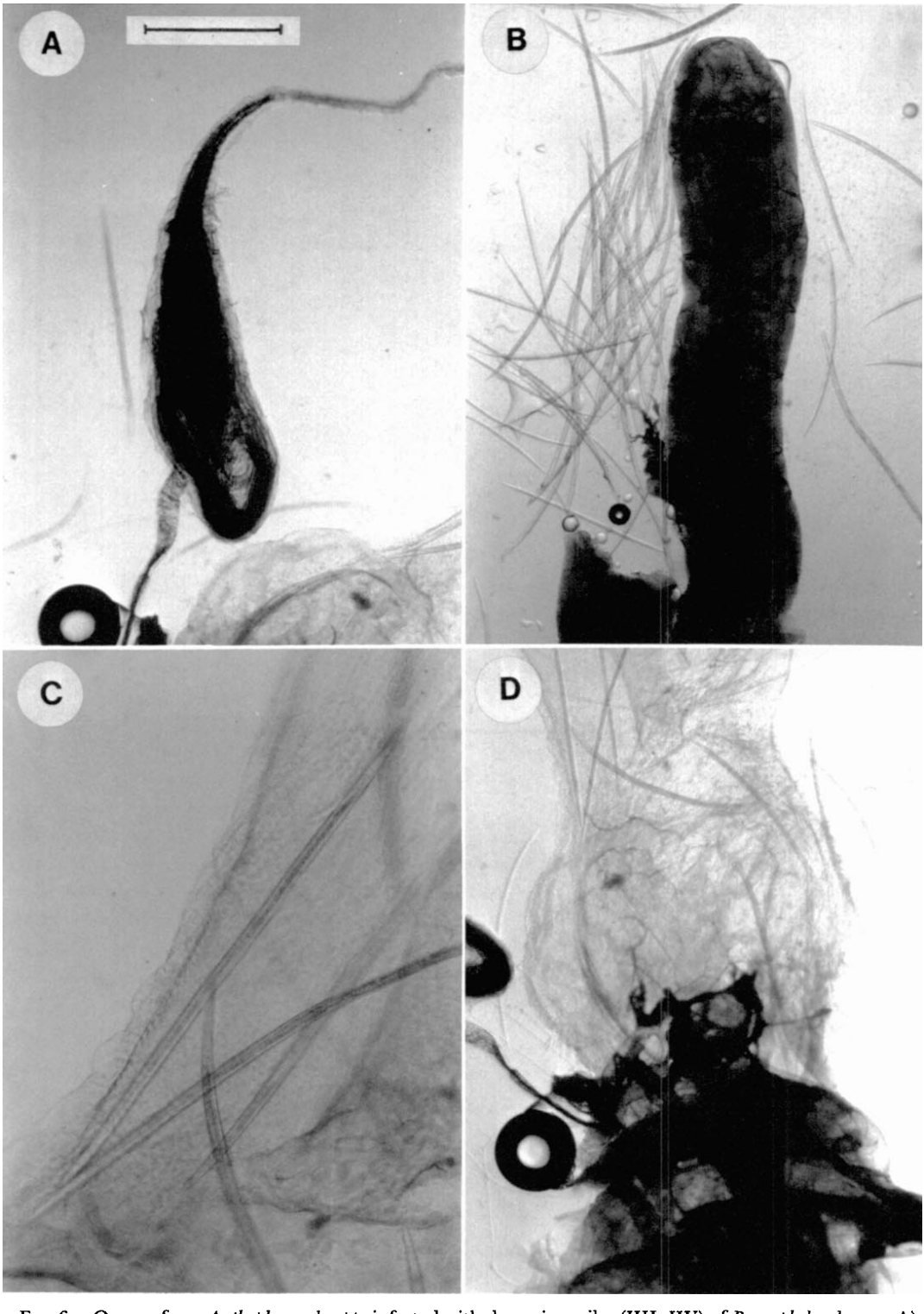

FIG. 6. Organs from *Anthophora abrupta* infested with dauer juveniles (JIII, JIV) of *Bursaphelenchus* sp. A) Poison sac. B) Dissected Dufour's gland. C) Median oviduct. D) Median and lateral oviducts. Scale bar for A, B, D = 500 μm; C = 200 μm.

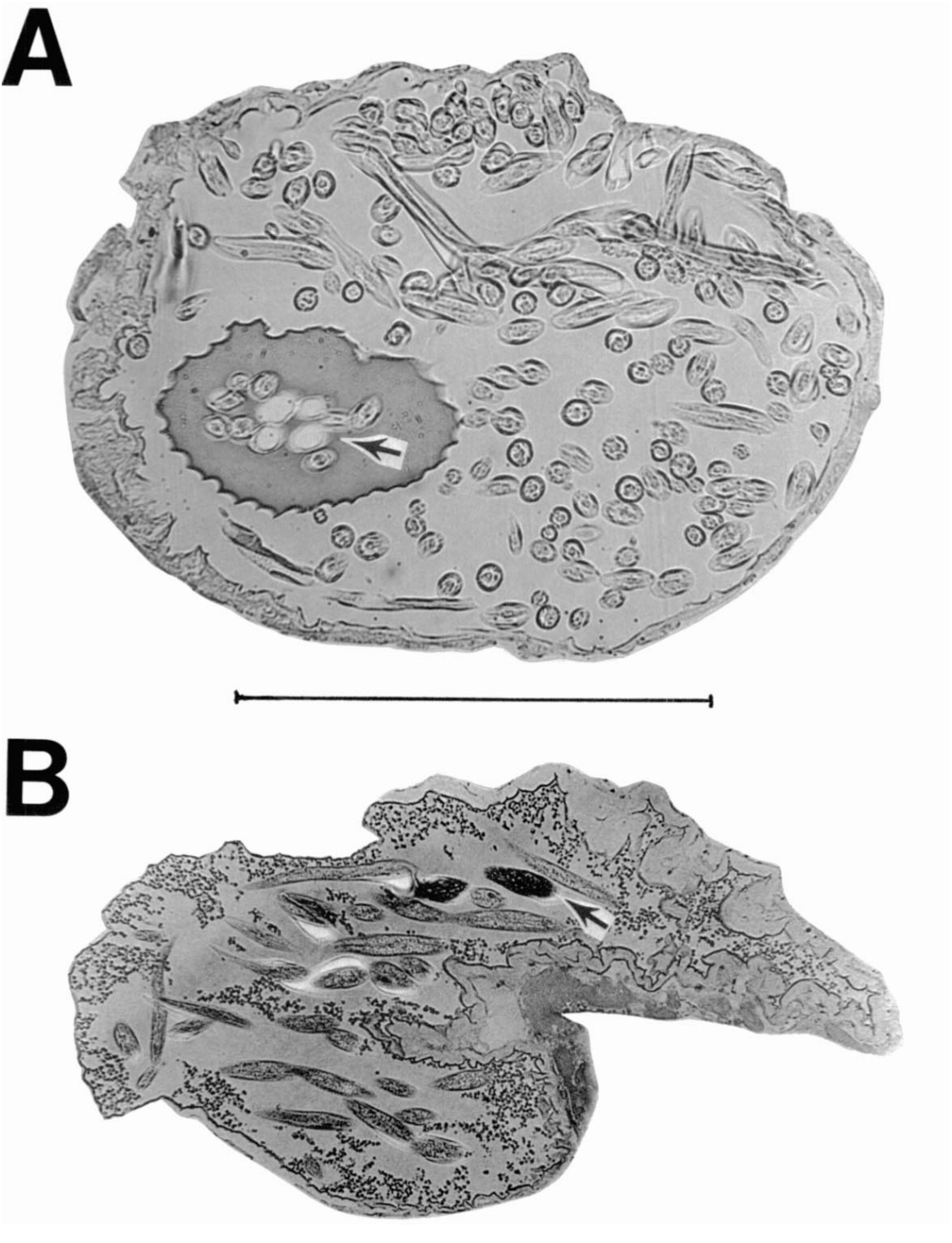

FIG. 7. Cross sections of poison sacs from *Anthophora abrupta* females infested with *Bursaphelenchus* sp. with two types of humoral host responses. Scale bar = 500 μm. A) Nematodes enveloped in sclerotized matrix (arrow). B) Darkly colored and vacuolated nematodes (arrow).

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