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Agamermis (Nematoda: Mermithidae) Infection in South Carolina Agricultural Pests

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Abstract: Native and invasive stink bugs (Hemiptera: Pentatomidae) and the closely related invasive *Megacopta cribraria* (Hemiptera: Plataspidae) are agricultural pests in the southeastern United States. Natural enemies, from various phyla, parasitize these pests and contribute to population regulation. We specifically investigated Nematoda infections in pentatomid and plataspid pests in one soybean field in South Carolina in 2015. Nematodes were identified through molecular and morphological methods and assigned to family Mermithidae, genus *Agamermis*. This study reports mermithid nematode infection in immature *M. cribraria* for the first time and provides the first mermithid host record for the stink bugs *Chinavia hilaris*, *Euschistus servus*, and another *Euschistus* species, and a grasshopper (Orthoptera: Acrididae) in South Carolina. The same *Agamermis* species infected all hosts. The broad host range and prevalence suggests that *Agamermis* may be an important contributor to natural mortality of pentatomid and plataspid pests. Previous mermithid host records for the Pentatomidae and Plataspidae worldwide are summarized. Further work is needed to assess the impact of infection on populations over a broader range of agricultural fields and geographic localities.

Key words: Agamermis, agricultural pests, detection, entomoparasitic nematode, hemipteran, Mermithidae, pentatomid, plataspid.

Over 200 pentatomid species are present in North America (Froeschner, 1988), of which three, the green stink bug, *Chinavia hilaris* (Say), the brown stink bug, *Euschistus servus* (Say), and the southern green stink bug, *Nezara viridula* (L.), are considered the main agricultural pests of economic importance in the southeastern United States (Jones and Sullivan, 1982; Barbour et al., 1990; Greene et al., 2001). In 2014, stink bugs infested 2.5 million ha of cotton, *Gossypium hirsutum* L., (approximately half of the area planted in the United States), destroying 135,000 bales and resulting in total damage estimated at $106 million (Williams, 2015). Damage was particularly severe in the southeastern United States, representing the majority of total insect damage to the crop in the region (Williams, 2015). Significant yield losses from the stink bug complex are also frequent in soybean, *Glycine max* (L.) Merr. (McPherson and McPherson, 2000). In 2014, stink bugs accounted for 20% ($370 million) of the reported yield losses and management costs for insect pests in the crop, in the southeastern United States (Musser et al., 2015). Recently, the invasion and establishment of the highly polyphagous brown marmorated stink bug, *Halyomorpha halys* Stål (Nielsen and Hamilton, 2009), the redbanded stink bug, *Piezodorus guildinii* (W.) (Temple et al., 2013a), and the kudzu bug, *Megacopta cribraria* (F.) (Plataspidae; closely related to the Pentatomidae family) (Ruberson et al., 2013), have added to the soybean pest complex. In Louisiana, *P. guildinii* was the most dominant stink bug species (54%) collected in soybean from 2008 to 2010 (Temple et al., 2013a). From 2011 to 2014, over $6.7 million in losses plus management costs were attributed to *M. cribraria* in the southern United States (Musser et al., 2012, 2013, 2014, 2015). Stink bugs can also be a pest in corn, *Zea mays* L. (Negrón and Riley, 1987), peaches, *Prunus persica* L. (Rings, 1957), sorghum, *Sorghum bicolor* L. (Young and Teetes, 1977), tomato, *Solanum lycopersicum* L. (Michelbacher et al., 1952), and wheat, *Triticum aestivum* L. (Viator et al., 1983).

The widespread pest status of stink bugs across multiple crops in the United States, and particularly in the southeast, often requires multiple applications of broad-spectrum pyrethroid or organophosphate insecticides to preserve yields. Populations of stink bugs with decreased sensitivity to a broad range of insecticides have been reported in the United States (Baur et al., 2010; Temple et al., 2013b). Furthermore, insecticide usage can result in pest resurgence or secondary pest outbreaks through elimination of beneficial natural enemies (Ruberson et al., 1998). To reduce these threats, research has historically been conducted on integrating control tactics, including the identification and use of natural enemies for biological control. Indeed, a complex of parasitoids and predators, traversing phyla, are known to attack populations of both stink bugs (Jones, 1988; Jones et al., 1996; Fuxa et al., 2000; Koppel et al., 2009; Esquivel, 2011) and *M. cribraria* (Gardner et al., 2013; Golec et al., 2013; Greenstone et al., 2014; Stubbins et al., 2015) in the United States.

Terrestrial mermithids are a large group of obligate entomoparasitic nematodes that are considered important regulators for some insect populations, including hemipteran pests (Kaburaki and Imamura, 1932; Choo and Kaya, 1990), because of their capacity to retard development, induce female sterility, and cause death on host emergence (Kaiser, 1991).

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Although characterized with a broad host range (Poinar, 1979; Nickle, 1981), research directed at terrestrial mermithids has often been carried out during sampling of only one insect species in a particular location (Esquivel, 2011; Tarla et al., 2012, 2015).

This study was prompted by observations of terrestrial mermithid nematodes in adult female and male *M. cribraria* in South Carolina in 2014 (Stubbins et al., 2015) and designed to develop our knowledge regarding mermithid host range and prevalence. Specifically, we aimed to (i) determine prevalence of mermithid nematodes in economically important hemipteran pests in soybean in South Carolina and (ii) identify mermithid nematodes using molecular tools.

Materials and Methods

Insect sampling and nematode collection: A soybean (variety AG6934) field (33.352723 N, −81.331518 W) at the Clemson University Edisto Research and Education Center near Blackville, SC (where mermithid nematode infection in adult male and female *M. cribraria* had been previously documented [Stubbins et al., 2015]), was selected for sweep-net sampling in 2015. Twenty sweeps (38-cm diameter sweep net) across two rows (planted on 97-cm rows) at four distances from the field edge (0, 10, 20, and 40 m) on three transects (240 sweeps per date) were carried out weekly from 6 June (soybean stage R1; when *M. cribraria* adults were first observed in the field) until 9 October (soybean stage R7; 13 wk). Samples were collected in plastic bags (30 × 50 cm) and frozen (−20°C) in the laboratory before enumeration of *M. cribraria* (from 6 June) and pentatomids (adults and fourth/fifth instars; from 21 July). An adult sex ratio shift from an expected 1:1 ratio was analyzed using the χ^2 goodness-of-fit test. Collected *M. cribraria* (females from 6 June, males and fifth instars from 21 July) were summed across the three transects for each distance, and 10 specimens (when available) of each life stage (up to 40 per field, per date) were partially dissected by removing the entire scutellum and pleural membrane (adults) or dorsum (nymphs) to expose the internal organs. Collected pentatomids were summed across field each week and the majority partially dissected (Table 1). Nematodes observed in the abdominal cavities of dissected insects were photographed with a zipScope 2M USB Digital Microscope (Aven Inc., Ann Arbor, MI), removed, and preserved in 80% ethanol. Nematode voucher specimens were deposited in the Clemson University Arthropod Collection. On 30 July, due to high lepidopteran pest abundance, an application of indoxacarb (0.065 kg [AI]/ha, Steward EC; Dupont Inc., Wilmington, DE) was made.

Nematode identification: Nematodes collected from *M. cribraria* (adult, n = 3; nymph, n = 3); *Acrididae* sp. (nymph, n = 2); *E. servus* (nymph, n = 2); other *Euschistus* sp. (adult, n = 1); and *C. hilaris* (nymph, n = 1) were examined for morphological features (Olympus BH2 light microscope). Genomic DNA was extracted from individual parasitic juvenile nematodes (Table 1 [all n = 1]; *M. cribraria* adult [n = 1]; *M. cribraria* nymph [n = 1]; *Acrididae* sp. nymph [n = 1]) using Sigma Extract-N-Amp kit (XNAT2) (Sigma, St. Louis, MO). A portion of the 18S small subunit rDNA (800 bp) was amplified using the forward primer 18S-5F (5′-GCGAAAGCATTTGCCAAGAA-3′) and 18S-9R (5′-GATCCTTCCGCAGGTTCACCT-3′) (Vandergast and Roderick, 2003). A portion of the mitochondrial *COI* gene (658 bp) was amplified using the primer pair LC01490 (5′-GGTCAACAAATCATAAAGATATTGG-3′) and HC02198 (5′-TAAACTTCAG GGTGACCAAAAA-ATCA-3′) (Folmer et al., 1994). For all primers, polymerase chain reaction (PCR) was performed in a final volume reaction of 25 μl final volume, adding 9 μl of PCR-grade water, 12 μl of ReadyMix Taq PCR Mix with $MgCl_2$ (Sigma), 2 μl of DNA template, and 1 μl of each primer. Thermal cycling conditions included initial denaturation at 94°C for 1 min, 35 cycles of 94°C for 30 sec, 50°C for 40 sec, 72°C for 1 min, and final extension at 72°C for 10 min. The amplified products were loaded onto a 1.5% agarose gel and visualized using GelRed™ (Biotium, San Francisco, CA) to confirm amplification.

Table 1. Collection, dissection, and infection information of pentatomid species collected in a soybean field in Blackville, SC, in 2015 by sweep-net sampling.

Pentatomid species	Life stage	Total number collected	Number of weeks collected	Total number dissected (total % dissected)	Number infected (% infected)
Chinavia hilaris	Adult	32	5	32 (100)	0 (0)
	Nymph	88	5	84 (95)	1 (1)
Euschistus servus	Adult	41	5	37 (90)	0 (0)
	Nymph	48	5	46 (86)	1 (2)
Other *Euschistus* sp.	Adult	5	4	5 (100)	2 (40)
	Nymph	0	–	–	–
Nezara viridula	Adult	2	2	2 (100)	0 (0)
	Nymph	16	1	7 (44)	0 (0)
Podisus maculiventris	Adult	8	4	4 (50)	0 (0)
	Nymph	0	–	–	–

PCR products were purified using Quantum Prep PCR Kleen Spin Columns (Bio-Rad Laboratories, Hercules, CA) and sequenced at the Clemson University Genomics Institute (Clemson, SC). All sequences were checked and edited manually, and contigs were assembled and aligned in Sequencher 5.2 (Genes Codes Corporation, Ann Arbor, MI). The 18S rDNA sequence was uploaded onto the GenBank database at the National Center for Biotechnology Information (http://www.ncbi.nlm.nih.gov).

Results

M. cribraria as nematode hosts: Over 13 sampling dates, 1,459 *M. cribraria* females were collected, of which 402 were dissected (28%), with 13 parasitized by nematodes (3.2%). The nematode infection rate peak (15%) was reached on 21 July when five *M. cribraria* females were sampled for every 20 sweeps. Out of 1,402 *M. cribraria* males collected, 273 were dissected (19%), with 7 parasitized by nematodes (2.6%). The peak of nematode infection of *M. cribraria* males (9%) was reached on 21 July, when *M. cribraria* males were sampled at four per 20 sweeps. The sex ratio of sampled adult *M. cribraria* over the course of the season did not differ from an expected 1:1 ratio (χ^2 = 1.136; df = 1; P = 0.2866). Mermithid infection was not affected by insect host sex (χ^2 = 0.529, df = 1; P = 0.4669). The last recorded adult *M. cribraria* infection was on 9 October, when densities averaged 31.1 *M. cribraria* adults per 20 sweeps (Fig. 1). All juvenile parasitic nematodes were found singly in the abdominal cavity.

Out of 808 fifth instars collected, 143 were dissected (18%) with 18 parasitized with a nematode (12.6%). The first nematode infection was recorded on 18 August. An infection peak of 20% was reached on 27 August, when *M. cribraria* nymphs were sampled at 25 per 20 sweeps (Fig. 1). Infection was recorded in all weeks that *M. cribraria* nymphs were dissected (n = 5, Fig. 1). The last recorded parasitism of a *M. cribraria* nymph was on 30 September, when fifth instars averaged 0.75 per 20 sweeps. Parasitic juvenile nematodes were always found in isolation in the abdominal cavity (Fig. 2).

Pentatomidae species as nematode hosts: Five pentatomid species from four genera were collected and dissected (Table 1). Overall, seasonal densities of pentatomids were much lower than those of *M. cribraria* (Table 1), with *C. hilaris* as the most abundant species, reaching over three adults and nymphs per 20 sweeps on 30 September. Individual nematodes were observed in an adult *Euschistus* sp. on 27 July (n = 1) and 3 August (n = 1). On 27 August, one nematode was observed in the abdominal cavity of an immature *E. servus*. On 9 October, one nematode was observed in a nymph of *C. hilaris*.

Orthoptera: Acrididae as nematode hosts: Nematodes were serendipitously discovered in three immature grasshoppers (Orthoptera: Acrididae) on 21 (n = 2) and 27 July (n = 1), when immatures were sampled at 0.66 and 0.25 per 20 sweeps, respectively, resulting in an infection rate of 50% and 33%, respectively. Further orthopteran dissections were not carried out after this date.

Nematode identification: Examination of parasitic juveniles under the microscope revealed well-developed stichosomes, a diagnostic characteristic of the family Mermithidae (Kaya and Stock, 1997). Genus and species identification requires adult samples and was, therefore, not possible through morphological

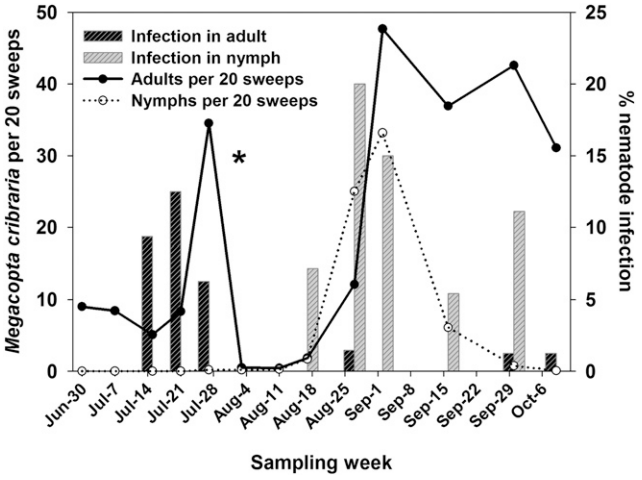

Fig. 1. Mean densities of *Megacopta cribraria* adults (male and female data combined) and nymphs per 20 sweeps and percentage of dissected (up to 40 when available) adults and nymphs infected with *Agamermis* sp. Asterisk indicates insecticide application.

Fig. 2. Parasitic juvenile nematode (*Agamermis* sp.) within abdomen of fifth instar *Megacopta cribraria* collected from a soybean field near Blackville, SC, during 2015.

TABLE 2. Worldwide mermithid host records for Pentatomidae (Hemiptera: Heteroptera) and Plataspidae (Hemiptera: Heteroptera).

Host species family	Host species	Host life stage	Genus	Molecular genus identification	Locality	Reference	GenBank accession number (18S, partial COI)
Pentatomidae	*Aelia acuminata*	?[a]	Undetermined	–	Uzbekistan	Sultanov et al., 1990	–
	Aelia rostrata	A[b]	*Hexamermis*	×	Turkey	Tarla et al., 2012	–
			Mermis	×	Turkey	Dikyar, 1981	–
	Chinavia hilaris	A/N[c]	*Hexamermis*	✓	United States	Kamminga et al., 2012	–
		N[d]	*Agamermis*	✓	United States	Present study	KX173336, KX853515
	Euschistus servus	A	Undetermined	-	United States	Esquivel, 2011	–
		N	*Agamermis*	✓	United States	Present study	KX173336
	Other *Euschistus* sp.	A	*Agamermis*	✓	United States	Present study	KX173336, KX853515
	Halys dentatus	?	*Hexamermis*	×	India	Dhiman and Yadav, 2004	–
	Nezara viridula	A	Undetermined	×	United States	Fuxa et al., 2000	–
		N[c]/?	*Pentatomermis*	×	India	Rubtsov, 1977; Bhatnagar et al., 1985	–
	Platynopus sp.	N	*Hexamermis*	×	India	Gokulpure, 1970	–
	Piezdorus guildinii	A	Undetermined	-	United States	Kamminga et al., 2012	–
		A/N[d]	*Hexamermis* or *Mermis*	×	Uruguay	Riberiro and Castiglioni, 2008	–
	Rhaphigaster nebulosa	?	*Hexamermis*	×	Italy	Manachini and Landi, 2003	–
Plataspidae	*Coptosoma mucronatum*	?	*Pentatomermis*	×	Slovakia	Rubtsov, 1977	–
	Megacopta cribraria	A/N	*Agamermis*	✓	United States	Present study	KX173336, KX853515

[a] Host life stage not recorded.
[b] Mermithid found in adult.
[c] Mermithid found in adult and nymph.
[d] Mermithid found in nymph.

examination. Sequencing of 18S rDNA ($n = 6$) and COI mDNA ($n = 5$) portions were successful. The COI amplicon from the *E. servus* host was not sequenced successfully and was removed from further analyses. All insect nematodes had identical 18S and COI sequences. A Basic Local Alignment Search Tool (BLAST) through GenBank noted the 18S sequence (703bp; KX173336; Table 2) had the closest match to *Agamermis changshaensis* Bao, Luo, and Luo 18S (DQ638908; 99% identity). The COI sequence (573bp, KX853515; Table 2) produced significant alignments with areas from the complete *Hexamermis agrotis* Wang, Bao, and Chan and *Agamermis* sp. mitochondrian genome (EF368011 and DQ665656; 79% identity). The absence of a tail appendage on parasitic juveniles and presence of a tail end ring provided robust evidence for an *Agamermis* genus identification (Kaiser, 1991).

DISCUSSION

We provide the first report worldwide of a mermithid nematode infecting the immature stages of *M. cribraria*. We also report the first South Carolina mermithid host record for *C. hilaris*, *E. servus*, other *Euschistus* sp., and an orthopteran. Previous pentatomid–mermithid infections in the United States have been reported in nymphs and adults of *C. hilaris* (as *Acrosternum hilare* [Say]) in Louisiana (Kamminga et al., 2012) and *E. servus* adults in Texas (Esquivel, 2011). Literature reporting mermithid infections in pentatomids and plataspids worldwide is scarce (Table 2). Records are often single observations, and specimens are frequently identified only to the family level due to lack of obvious morphological features. Furthermore, molecular analysis is rarely carried out; hence, few GenBank reference sequences are available for comparison. Only one pentatomid–mermithid infection study in the United States assigned genus identification to the collected mermithid (Kamminga et al., 2012). The presence of a tail appendage on the parasitic juvenile (Kaiser, 1991) confirmed the molecular identification of *Hexamermis* from GenBank available sequences. Availability of genomic sequences makes phylogenetic analyses and comparisons possible (Poinar et al., 2007). Observations that *Allomermis solenopsi*, a parasite of the fire ant, *Soleopsis invicta* Buren, requires standing water to emerge from its host was consistent with the placement of the species as sister taxa to *Mermis* Dujardin, in which some species cause their hosts to seek open water when they are ready to emerge. Genus identification through molecular techniques can, therefore, help predict and infer mermithid biology, which can ultimately assist in rearing protocols, essential if mermithids are to be used for future research and incorporation into current management protocols.

Through integration of morphological and molecular analyses, we provide evidence that a species of *Agamermis* infected insect hosts in South Carolina. The same *Agamermis* species was observed in three insect families across two orders, an observation consistent with the reported broad host range characteristic for

this genus (Poinar, 1979; Choo and Kaya, 1990). We did not observe mermithid infection in *Podisus maculiventris* (Say), a generalist predator of crop pests (O'Neil, 1988). It will be important to investigate whether this pentatomid and other beneficial predators can harbor mermithids, as this could counteract their valuable role in pest population regulation. Although not considered of primary importance in the southeastern United States, *Euschistus* spp. (comprising the "lesser" brown stink bug complex which excludes *E. servus*) can predominate populations in the Lower Gulf Coast region of Texas, contributing to cotton yield loss (Hopkins et al., 2010; Williams, 2015). Crop damage caused by the "lesser" complex in South Carolina is negligible, but, as a suitable host for *Agamermis*, it allows the nematode to propagate and presumably infect other pest species.

Agamermis species infecting insects have been reported in North America (Cobb et al., 1923; Christie, 1936; Weaver and King, 1954), Asia (Kaburaki and Imamura, 1932; Choo et al., 1995), Australasia (Baker and Poinar, 1995), Africa (Igbinosa, 1998), and Europe (Rubtsov, 1969). In Korea, *Agamermis unka* Kaburaki and Imamura is a major natural enemy of the brown planthopper, *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae), and to a lesser extent the whitebacked leafhopper, *Sogatella furcifera* (Horvath) (Hemiptera: Delphacidae), and has been widely studied regarding future inoculative releases and conservation approaches to manage populations in rice (Choo and Kaya, 1994). *Agamermis* species live in the soil and infect hosts from the soil directly or after short migration up a plant stem (Nickle, 1981; Choo et al., 1995). Stubbins et al. (2015) hypothesized two possible infection routes for mermithids infecting *M. cribraria* in South Carolina during (i) residency under leaf litter at overwintering or (ii) residency in soybean fields. Nematode infection in wingless, immobile nymphs provides strong evidence that infection occurs directly in the soybean field. Early season soybean colonization by adult *M. cribraria* (as observed in this study) can consist of the overwintered or first generation populations, hence, we cannot rule out nematode acquisition during plataspid overwintering. Although studies have reported mermithid infection from insects collected directly from cultivated crops (Bhatnagar et al., 1985; Kamminga et al., 2012) or traps surrounding crops (Esquivel, 2011), mermithids have also been found in hemipterans collected from overwintering sites (Tarla et al., 2012; Tarla et al., 2015). It is thought that infection is often higher during this period, as insects are present in one area for long periods of time.

Despite the pest status of pentatomids and *M. cribraria* in agriculture in the southeastern United States, the impact of mermithid nematodes on populations is under-explored and potentially undervalued. We observed high prevalence of nematode infection in *M. cribraria*, consistent with the previous year (Stubbins et al., 2015), and report pentatomid–mermithid infection for the first time in South Carolina. Sole use of chemicals for pest management is not sustainable, hence research into alternative strategies for incorporation into a chemical-based management system are required. Biological control research endeavors in the past, for pentatomid and plataspid pests, have generally focused on exploitation of macroscopically perceptible organisms (Orr et al., 1986; Leskey et al., 2012; Seiter et al., 2014). This study underlines the importance of considering more covert natural enemies as population regulators. Results provide a foundation for future studies into prevalence within agricultural systems. Baseline data from a larger sample of fields and further understanding of mermithid biology, ecology, and host–parasite interacting behavior will be essential to understand how valuable mermithid entomoparasitic are at regulating pest populations in southeastern farmscapes.

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