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Hairworm and nematode infections of North American Jerusalem crickets, field crickets, and katydids (Orthoptera: Stenopelmaticidae, Gryllidae and Tettigoniidae)

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Abstract

New records of hairworms (Gordioidea: Nematomorpha) and mermithid nematodes (Mermithidae: Nematoda) are reported from North American Orthoptera collected over the past 25 y. Several thousand Jerusalem crickets (Stenopelmaticidae: *Stenopelmatus* spp.), field crickets (Gryllidae: *Gryllus* sp.), and several hundred decticine katydids (Tettigoniidae: Tettigoniinae) were captured in the field and maintained alive, serving as potential hosts. A total of 36 specimens were found infected (most multiple), which resulted in the recovery of 19 hairworm lots associated with some 11 species of *Stenopelmatus*; 6 hairworm lots from 4 species of *Gryllus* and 2 decticine katydid genera, and 11 mermithid nematode lots associated with 5 species of *Stenopelmatus*, *Capnobotes fuliginosus* and a *Gryllus* sp. The present study identifies hosts of hairworms and mermithids collected from sites throughout central and western United States and much of Mexico.

Key words

parasites, hairworms, Nematomorpha, mermithid, Nematoda, *Stenopelmatus*, *Gryllus*, *Pediectes*, *Steiroxys*, *Capnobotes*

Introduction

Hairworms (also called horse hairworms) (Gordioidea: Nematomorpha) and mermithid nematodes (Mermithidae: Nematoda) are worldwide, enigmatic obligate parasites that have been little studied, mainly because of their general rareness, difficulty in rearing under laboratory conditions, and lack of economic importance. These 2 groups are often confused with one another since the mature forms are elongate, narrow worms, with invertebrates, especially insects, as developmental hosts. In fact, as shown here, some host species support the development of both hairworms and mermithids, although rarely in the same individual. Immature hairworms are white and usually die if removed from their hosts. They turn black or various shades of brown when mature and then leave the host. Mermithid nematodes are normally white or cream colored in both the immature and mature stages; however females of the genus *Mermis* can appear brown when gravid with eggs.

Little is known about the host diversity of these parasites. Hosts of most of the 18 described species of North American hairworms are unknown (Poinar & Chandler 2004). No mermithids are previously known from stenopelmaticids (Poinar 1975). The present study identifies orthopteran hosts of hairworms and mermithids collected from sites throughout central and western United States and much of Mexico. Host groups involved members of the Orthoptera: Stenopelmaticidae, Gryllidae and Tettigoniidae.

Methods

Orthopterans for this study were field collected and laboratory maintained for studies (see, e.g., Weissman 2001a,b) on communication and biology used in taxonomic investigations. Over the past 25 y, more than 2500 Jerusalem crickets (*Stenopelmatus* spp.), almost 5000 field crickets (*Gryllus* spp.) and several hundred decticine katydids have been so treated, providing an unparalleled variety of potential host data. Because worm-infected individuals typically do not molt or sing, yet appear healthy and active, hosts are unintentionally retained alive until their parasites mature and emerge.

Methods for preserving and preparing specimens for optical microscopic examination are reported elsewhere (Poinar 2001, Smith 2001). Generic and specific identification are based on keys presented in Poinar & Chandler 2004, with reference to earlier descriptions by Montgomery (1898a, 1898b, 1907), Ward & Whipple (1918), and Leidy (1851, 1856). All specimens are preserved in alcohol and deposited at the California Academy of Sciences, San Francisco, CA. Localities where host orthopterans were collected are tabulated in Tables 1, 2, and 3, with specific collection data presented in the Appendix.

Results

Thirty six identifiable hosts were parasitized, most multiple. Of these, 19 were hairworms associated with some 11, mostly undescribed, species of *Stenopelmatus* (Table 1), 6 were hairworms from 4 species of *Gryllus* and 2 decticine katydid genera (Table 2), and 11 were mermithid nematodes associated with 5 species of *Stenopelmatus*, *Capnobotes fuliginosus* (Thomas) and a *Gryllus* sp. (Table 3).

Discussion

Hairworms normally emerge from their hosts as adults and possess diagnostic characters for identification to species. Mermithid nematodes, in contrast, emerge as postparasitic juveniles and must undergo a final molt in the environment to reach the adult stage. This final molt may take weeks and since most specimens are fixed immediately upon exit from their hosts, the adult is not available. Since all of the basic diagnostic characters in mermithids occur in the adults, postparasitic juveniles cannot be confidently identified beyond family level. Many of our specimens probably represent new species.

Most if not all hairworms (as well as some mermithid species) utilize both a paratenic host (a host where encystment but no development occurs) as well as a developmental host, in their life cycle. In the present study, all of the hosts are developmental hosts, where the parasite grows to maturity in the body cavity.

The present study contributes significantly to our knowledge of orthopteran hosts of North American hairworms and mermithid nematodes. Up to the present, there have been no published records of mermithids infesting members of the Stenopelmatidae (Poinar 1975). Here, we report mermithids from 5 species of *Stenopelmatus*. No mermithids had been reported previously from members of the decicene genus *Capnobotes*. However, the mermithids *Mermis subnigrescens* Cobb and *Agamermis decaudata* Cobb, Steiner & Christie have been reported from other members of the Tettigoniidae (Poinar 1975). Only one location [Charmlee State Park, Los Angeles Co., CA, (S89-92 in Table 1 and S01-12 in Table 3)] in the present study contained a host species infected with both hairworms and mermithids: but not in the same individual.

Thus far, hairworm parasites of stenopelmatids and related anostomatids are known from North America, New Zealand and Australia (Poinar 1991, Wharton *et al.* 2001). Our knowledge is not complete enough to determine if any hairworm species is restricted to members of these families. However, on the basis of these results and what has been reported previously, it appears that certain species of North American hairworms definitely prefer Orthoptera as hosts.

One of these is *Gordius robustus* Leidy. In 1856, Leidy reported infestations in the tettigoniid *Xiphidium nemorale* Scudder (now *Conocephalus nemoralis*). Later, May (1919) found the tettigoniids *Orchelimum nigripes* Scudder, *O. vulgare* Harris and *Scudderella furcata* Brunner to be infected by *G. robustus*. Thorne (1940) studied this hairworm in the decicene katydid *Anabrus simplex* Haldeman, and Cappucci (1977) reported *G. robustus* from the stenopelmatid *Stenopelmatus longispina* Brunner. The present report (see Table 2) is the first case of this hairworm species infecting members of the decicene katydid genus *Steiroxys* and a *Gryllus* sp.

A second North American orthopteran hairworm is *Paragordius varius* Leidy. Ward & Whipple (1918) mentioned the gryllids *Acheta abbreviata* Serville (now *Gryllus pennsylvanicus* Burmeister) and *Nemobius fasciatus* De Geer as developmental hosts for *P. varius*. We confirm here that crickets may be a preferred host of *P. varius* as we also found them in 3 species of *Gryllus* (Table 2).

A third hairworm species that appears to prefer Orthoptera is *Neochordodes occidentalis* (Montgomery). The only previous report of a host of this species is by Ward & Whipple (1918) who state that an acridid grasshopper was parasitized. The present study reports the first case of this hairworm parasitizing members of the genus *Stenopelmatus* (5 species) (Table 1) and the decicene katydid genus *Pediocetes* (Table 2).

Our records of the hairworm *Parachordodes platycephalus* Montgomery from 2 species of *Stenopelmatus* (Table 1), are interesting since members of that genus normally develop in predatory beetles, especially members of the family Carabidae (Poinar *et al.* 2004).

A previous study dealing with hairworm parasites of Anostomatidae showed that an obligate paratenic host is involved in the life cycle (Poinar 1991). This paratenic host is usually an aquatic insect, especially a mayfly (Ephemeroptera) or caddisfly (Trichoptera). The larvae of these insects ingest hairworm eggs or first stage larvae from the stream bed. The ingested eggs hatch, and the larvae proceed to bore through the insect midgut and encyst in various tissues in the hemocoel. They do not grow or develop in this location, but simply enter a dormant stage that can be carried through the pupal and into the adult stages of the insect. Hosts become infected when they eat one of these insects containing hairworm cysts. The cysts are quite durable and it is possible for infection to occur even if the paratenic host is dying or already dead. In the

orthopteran gut, the hairworm larva leaves the cyst, penetrates the gut wall and enters the body cavity where it grows. When mature, hairworms somehow alter their host's behavior, causing them to seek a water source (most hosts do not live far from some supply of water, whether a permanent or temporary stream, pond, puddle or even a water trough). Upon emerging from the host, the hairworms enter the water, mate, and the female oviposits strings or masses of eggs in the aquatic habitat. Since they kill their hosts at the time of, or soon after, emergence, hairworms can be a significant mortality factor and were the major parasite of New Zealand wetas (Poinar 1991). In the present study, we found that hairworm-parasitized stenopelmatids usually did not molt. A notable exception was a nymph from S92-146 that molted several times over the 16-month period she was in captivity, only to ultimately die upon emergence of the hairworm. There may be other abnormalities in parasitized hosts, especially in relation to sexual behavior. Our paucity of worm records from Mexico, despite much collecting, probably reflects the few stenopelmatids recovered.

Acknowledgments

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Fig. 1. *Neochordodes occidentalis* emerging from the anus of its developmental host, *Stenopelmatus* sp.

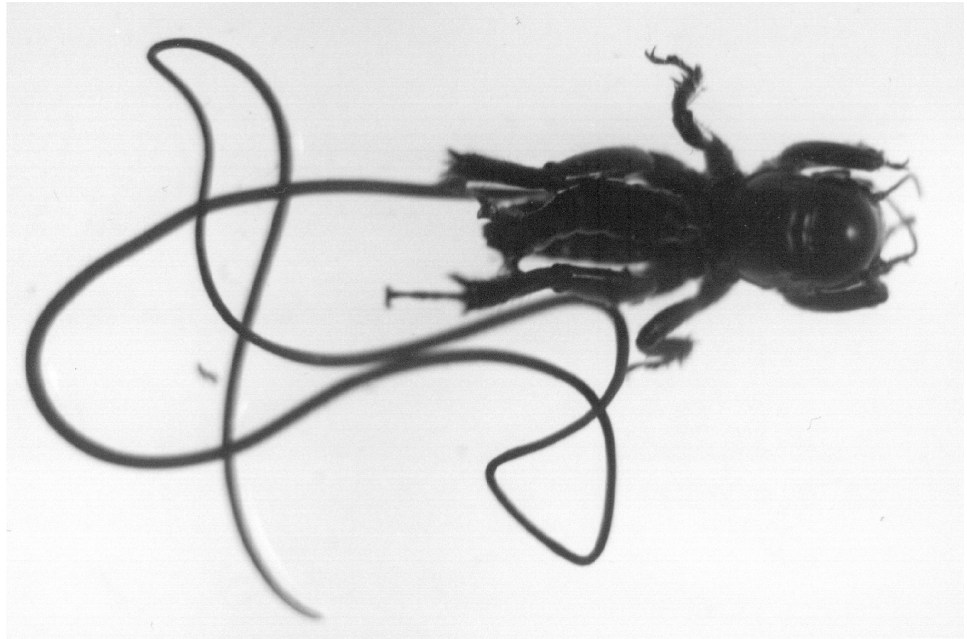


Fig. 2. *Paragordius varius* emerging from its developmental host, *Gryllus* sp.

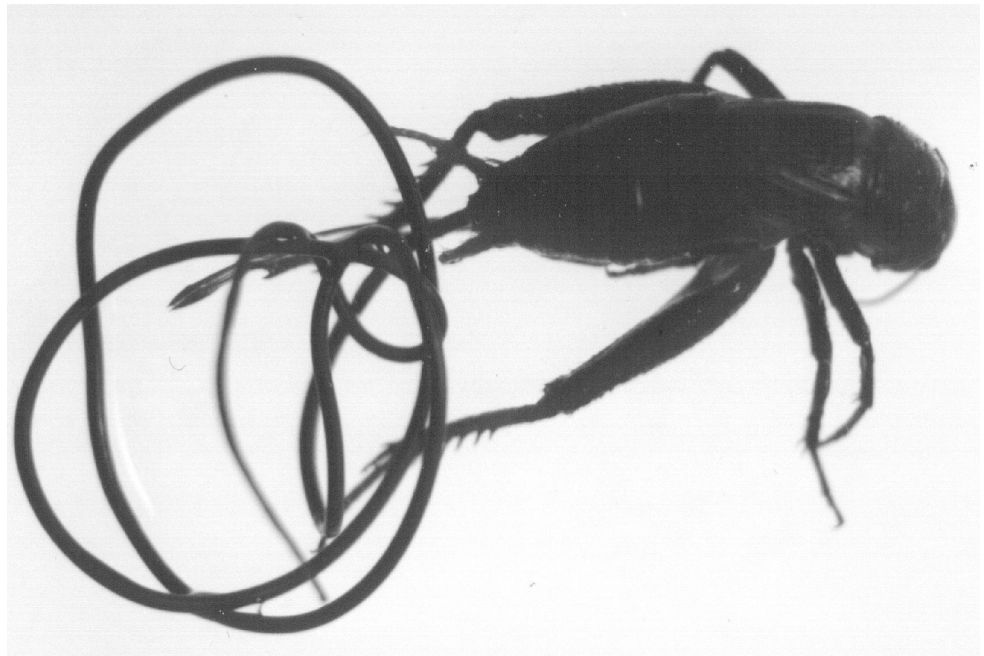


Table 1. New host records of hairworms for North American species of *Stenopelmatus*.

Accession No.	Locality	Hairworm	Collected:emerged
A	Los Angeles Co., CA	<i>N. occidentalis</i>	3/24/81: -
A	Los Angeles Co., CA	<i>N. occidentalis</i>	4/1/81: -
S83-159	Fresno Co., CA	<i>N. occidentalis</i>	12/14/83: 1/13/84
A	Los Angeles Co., CA	<i>N. occidentalis</i>	3/20/87: -
S87-126	Baja CA, Mexico	<i>G. robustus</i>	12/20/87: 2/9/88
S89-92	Los Angeles Co., CA	<i>G. robustus</i>	12/27/89: 3/10/90
S92-8	Monterey Co., CA	<i>N. occidentalis</i>	3/1/92: 4/15/92
S92-8	Monterey Co., CA	<i>N. occidentalis</i>	3/1/92: 4/30/92
S92-8	Monterey Co., CA	<i>N. occidentalis</i>	3/1/92: 5/11/92
S92-146	Monterey Co., CA	<i>N. occidentalis</i>	12/27/92: 4/6/94
S97-65	Navajo Co., AZ	<i>N. occidentalis</i>	6/26/97: 8/26/97
B	Santa Clara Co., CA	<i>G. robustus</i>	1/21/99: -
S99-161	Piute Co., UT	<i>P. platycephalus</i>	10/2/99: 7/15/00
S00-62	Santa Barbara Co., CA	<i>N. occidentalis</i>	10/9/00: 5/4/01
S01-25	Los Angeles Co., CA	<i>P. platycephalus</i>	4/29/01: 12/10/01
S02-66	Santa Barbara Co., CA	<i>G. robustus</i>	8/30/02: 12/15/02
S02-66	Santa Barbara Co., CA	<i>G. robustus</i>	8/30/02: 12/15/02
S02-66	Santa Barbara Co., CA	<i>G. robustus</i>	8/30/02: 4/20/03
C	Riverside Co., CA	<i>G. robustus</i>	—

Table 2. New host records of hairworms from North American gryllids and tettigoniids.

Accession No.	Locality	Host	Hairworm	Collected: emerged
S90-79	Santa Cruz Co., AZ	<i>Gryllus</i> sp.	<i>P. varius</i>	7/26/90: 7/26/90
S92-79	Josephine Co., OR	<i>Gryllus</i> sp.	<i>P. varius</i>	7/27/92: 8/16/92
S94-78	Nuevo Leon, Mexico	<i>Pediodes</i> sp.	<i>N. occidentalis</i>	8/3/94: 8/3/94
S97-83	Dawes Co., NE	<i>Gryllus</i> sp.	<i>G. robustus</i>	7/28/97: 7/28/97
S97-95	Richland Co., MT	<i>Gryllus</i> sp.	<i>P. varius</i>	7/31/97: 8/19/97
S00-36	Union Co., OR	<i>Steiroxys</i> sp.	<i>G. robustus</i>	8/29/00: 8/30/00

Table 3. New host records of mermithids from North American stenopelmatids, tettigoniids and gryllids.

Accession No.	Locality	Host	Collected: emerged
S89-51	Mesa Co., CO	<i>Capnobotes fuliginosus</i>	5/31/89: 7/27/89
S91-135	San Benito Co., CA	<i>Stenopelmatus</i> sp.	12/28/91: 1/26/92
S92-14	Orange Co., CA	<i>Stenopelmatus</i> sp.	3/2/92: 3/17/92
S92-14	Orange Co., CA	<i>Stenopelmatus</i> sp.	3/2/92: 3/21/92
S98-128	Humboldt Co., CA	<i>Stenopelmatus</i> sp.	12/14/98: 2/24/99
S98-128	Humboldt Co., CA	<i>Stenopelmatus</i> sp.	12/14/98: 3/10/99
S01-11	Ventura Co., CA	<i>Stenopelmatus</i> sp.	2/25/01: 5/5/01
S01-12	Los Angeles Co., CA	<i>Stenopelmatus</i> sp.	2/25/01: 4/16/01
D	Alameda Co., CA	<i>S. intermedius</i> D & S	—
E	Orange Co., CA	<i>Stenopelmatus</i> sp.	4/4/03: 5/15/03
S03-27	Tulare Co., CA	<i>Gryllus</i> sp.	5/4/03: 6/3/03

Appendix: Full collection citation for host specimens. Accession numbers are listed chronologically. Specimens without a S (stop = collection point) number in Tables 1 and 3, are given a letter designation and listed serially below.

- S83-159 USA. CA. Fresno Co., 5.5 mi NE Academy on Hwy 168. 14/xii/1983. 800' N.J. Smith, W. Peregrin.
 S87-126 Mexico. Baja California Norte. 27 km E Tecate on Mexico 2 at km 104. 20/xii/1987. 2900' D.B. Weissman.
 S89-51 USA. CO. Mesa Co., Colorado National Monument, Fruita entrance. 31/v/1989. 4700' R.S. Peigler, M.J. Weissmann.
 S89-92 USA. CA. Los Angeles Co., Santa Monica Mtns, Charmlee State Park. 27/xii/1989. 1200' D.B. Weissman.
 S90-79 USA. AZ. Santa Cruz Co., Madera Canyon Rec. Area, end of road. 26/vii/1990. 4900' D.B. Weissman, D.C. Lightfoot.
 S91-135 USA. CA. San Benito Co., Fremont Peak State Park, peak area. 28/xii/1991. 3100' D.B. Weissman.
 S92-8 USA. CA. Monterey Co., Arroyo Seco Rd 0.6 mi W intersection Arroyo Seco Rd and G16. 1/iii/1992. 700' D.B. Weissman, V.F. Lee.
 S92-14. USA. CA. Orange Co., O'Neill Regional County Park near Trabuco Creek Trail trailhead. 2/iii/1992. 1000' D.B. Weissman, V.F. Lee.
 S92-79 USA. OR. Josephine Co., 8 mi W Selma on road to Store Gulch Campground. 27/vii/1992. 800' D.B. Weissman, D.C. Lightfoot.
 S92-146 same data as S92-8, except 27/xii/1992.
 S94-78 Mexico. Nuevo Leon. Hwy 58 5.4 km E Iturbide at km 38.4. 3/viii/1994. 3980' D.B. Weissman, D.C. Lightfoot, V.F. Lee.
 S97-65 USA. AZ. Navajo Co., Keet Seel Canyon 2.5 mi S Keet Seel Ruin. 26/vi/1997. 1980-2040m. N 36.45 W 110.30. D.H. Kavanaugh, J. Schweikert, C. Drost.
 S97-83 USA. NE. Dawes Co., 4mi W, 4mi S Chadron. 28/vii/1997. 3100' D.B. Weissman, D.C. Lightfoot.
 S97-95 USA. MT. Richland Co., Sidney. 31/vii/1997. 1840' D.B. Weissman, D.C. Lightfoot.
 S98-128 USA. CA. Humboldt Co., Blue Lake, off Greenhill Rd. 14/xii/1998. 260' D.B. Weissman, M. Caterino.
 S99-161 USA. UT. Piute Co., Elbow Ranch 9 mi W Marysville. 2/x/1999. 6200' K.L. Waters.
 S00-36 USA. OR. Union Co., 8.2mi W La Grande 29/viii/2000. 3100' N 45.19688 W 118.13931. D.B. Weissman, D.C. Lightfoot.
 S00-62 USA. CA. Santa Barbara Co., Santa Rosa Island, Windmill Canyon. 9/x/2000. 75m J. Powell.
 S01-11 USA. CA. Ventura Co., Santa Monica Mtns., Hwy 23S 0.1 mi W Westlake Village. 25/ii/2001. 800' D.B. Weissman, V.F. Lee.
 S01-12. same as S89-92, except 25/ii/2001. D.B. Weissman, V.F. Lee.
 S01-25 USA. CA. Los Angeles Co., San Gabriel Mts., Monte Cristo Campground, 29/iv/2001. 3640' N 34.20685 W 118.06577. D.B. Weissman.
 S02-66 USA. CA. Santa Barbara Co., Montecito, 1781 Glen Oaks Dr., 30/viii/2002. 100' R. Doult.
 S03-27 USA. CA. Tulare Co., Hwy 190 0.5 m W Pierpoint Springs at House Way Ct. 4/v/2003. 4700' D.B. Weissman.
 A. USA. CA. Los Angeles Co., Santa Catalina Island. S Bennett.
 B. USA. CA. Santa Clara Co., San Jose. 1375 Box Canyon Rd. J Ryan.
 C. USA. CA. Riverside Co., San Jacinto Mtns., University of California James Reserve. W. Sakai.
 D. USA. CA. Alameda Co., Oakland. E. Miller.
 E. USA. CA. Orange Co., Allyso Woods Canyon. A. Vandergast.