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VENEREAL WORMS: SEXUALLY TRANSMITTED NEMATODES IN THE DECORATED CRICKET

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ABSTRACT: The nematode, *Mehdinema alii,* occurs in the alimentary canal of the decorated cricket *Gryllodes sigillatus.* Adult nematodes occur primarily in the hindgut of mature male crickets, whereas juvenile nematodes are found in the genital chambers of mature male and female crickets. Here, we present experimental evidence for the venereal transmission of *M. alii* in *G. sigillatus.* Infectivity experiments were conducted to test for transmission via oral–fecal contamination, same-sex contact, and copulation. The infective dauers of the nematode are transferred from male to female crickets during copulation. Adult female crickets harboring infective dauers subsequently transfer the nematode to their next mates. Thus, *M. alii* is transmitted sexually during copulation.

Sexually transmitted diseases (STDs) have received much attention in the last few decades (Holmes et al., 1990; Smith and Dobson, 1992; Sheldon, 1993; Able, 1996; Lockhart et al., 1996). STDs not only have medical and veterinary importance, but ecological and evolutionary implications as well. Sexually transmitted parasites may affect the evolution of host mating behavior, reproductive physiology, secondary sexual characters, and mate choice (Freeland, 1976; Hamilton, 1990; Sheldon, 1993). Thus, there is a potential for tight coevolution or coadaptation between host and parasite life history strategies, because sexually transmitted parasites rely on host reproduction for transmission.

STDs are transmitted during sexual contact, i.e., vertically via the zygote or horizontally via copulation. Most of the work on STDs has focused primarily on short-lived microparasites such as viruses, bacteria, and protozoa (Oriel and Hayward, 1974; Holmes et al., 1990; Smith and Dobson, 1992; Sheldon, 1993; Lockhart et al., 1996). Here, we use the term STDs to refer to diseases that are transmitted horizontally (within members of the same generation) and not to those that are transmitted vertically from parent to offspring. Modes of horizontal transmission include environmental contamination where infective stages are deposited into the environment, transferring (actively or passively) to naive individuals that come into contact with the contaminated environment (fecal–oral contamination [F-O]), casual physical contact between infected individuals and noninfected individuals (including same sex contact [S-S] and interstage contact), and copulation (C).

Lockhart et al. (1996) mention several sexually transmitted macroparasites, most commonly in pulmonate snails where the infectious agents are vertically transmitted (Conte and Bonnet, 1903; Anderson, 1960; Morand and Hommay, 1990). Only a few studies have critically examined venereally transmitted nematodes (Poinar, 1970, 1971; Marti et al., 1990), i.e., horizontal transmission of nematodes. Previous reports have speculated on the occurrence of a venereally transmitted nematode (*Oryctonema genitalis*) in the dynastid beetle *Oryctes monoceros* (Poinar, 1970). This and other accounts of sexual transmission were based primarily on anatomical evidence, i.e., locating adult and juvenile nematodes in the bursa copulatrix and phallus of the adult female and male beetles, respectively (Poinar, 1971). These studies did not experimentally demonstrate sexual transmission of a nematode. Here, we present experimental evidence for the venereal transmission of a macroparasite using the unusual endoparasitic nematode *Mehdinema alii* (Farooqui, 1967).

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MATERIALS AND METHODS

Crickets and nematodes

The decorated or Indian house cricket, *Gryllodes sigillatus* (Vickery and Kevin, 1983) is distributed throughout the tropics of the world (Herberd, 1952) and has been recorded from Australia, Cuba, Mexico, and Florida. This introduced tropical insect also occurs in more arid conditions and is widely distributed in southern California, southwest Arizona, and extreme northwest Mexico. *Gryllodes sigillatus* is well established in Riverside, California, and can be found in residential and business sites. This nocturnal cricket is light yellow with brown markings, ranging in size from 15 to 21 mm (Smith and Thomas, 1988). *Gryllodes sigillatus* has a polygamous mating system. Male crickets attract females by producing acoustic signals (Sakaluk, 1987).

This nematode, *M. alii,* occurs in the hindgut of the male *G. sigillatus.* The nematode is ovoviviparous and produces infective juveniles called dauers. Dauers can be recovered in the genital chambers of both male and female crickets in an infested population, suggesting that female crickets act to help redistribute dauers to uninfected males (Luong and Platzer, 1998; Luong et al., 1999).

Survey

Over 200 decorated crickets were sampled using a miniature vacuum and necropsied from local populations in Riverside, California between November 1996 and May 1998. About 70% of the males from these populations harbor *M. alii.* Males collected from these sites and used in transmission experiments were considered "infected." This status was confirmed by necropsy at the end of each experiment. Naive (sexually inexperienced and uninfected) crickets were reared in ventilated plastic containers and provided with water and cat food (9 Lives Plus®) ad libitum.

Transmission experiments

All crickets were maintained in an incubator at 25 C with water and cat food provided ad libitum. In the fecal–oral and sexual transmission experiments, 8–10 "infected" males collected from the field were used as the source of infection, with the expectation that 70% of the males harbor nematodes (see results of survey below). Because fielded-collected females were less likely to be infected with dauers (10%, see below), they were first housed with field-collected males to facilitate the transmission of dauers. These preliminary steps were taken to establish a status of "infected" for females in the same-sex and sexual transmission experiments. Both males and females in these groups were later necropsied to confirm the status of infection.

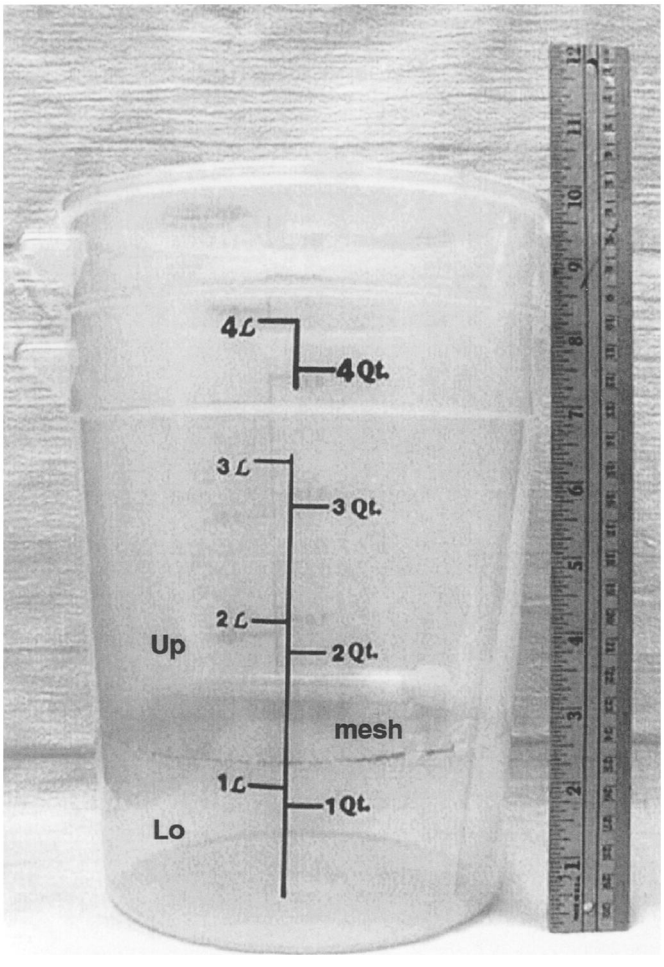

FIGURE 1. Set-up for transmission experiments consisting of 2 plastic containers stacked together, forming an upper (up) and lower (lo) compartment seperated by metal wire mesh.

Fecal-oral transmission: Transmission experiments were conducted for 5–7 days to test fecal–oral contamination (F-O), i.e., ingestion of infective eggs or dauers, using plastic containers (4.0 L) with 2 compartments, a top and bottom, separated by a wire mesh (Fig. 1). Infected male crickets were placed in the upper level so that fecal pellets fell to the bottom layer where the naive crickets resided in same sex groups. Naive males were tested in 4 groups of 4; 1 died during the experiment and was therefore eliminated from the trial (total n = 15). Naive females were tested in 4 groups of 3; 2 died (n = 10). In these experiments, naive crickets were exposed to the feces of the infected crickets only and could not contact the infected male crickets housed above.

Same-sex contact transmission: Infected and naive crickets of the same sex were marked for identification by infection status with liquid paper and placed in the upper level (Fig. 1) to allow physical contact while minimizing fecal contact for 5–7 days. In the male-to-male studies, naive males in 2 groups of 4 (n = 8), were housed with infected males. In female-to-female studies, females that had previously mated with infected males were marked and housed with naive females; 3 trials were conducted with naive females in groups of 4; 2 died (n = 10).

Sexual contact transmission: Infected male crickets were housed with 12 naive female crickets. Four trials were conducted with just 1 naive female at a time and 4 trials were conducted with 2 naive females at a time, for 5–7 days. Also, infected female crickets were housed with 15 naive males to test for sexual transmission. A total of 6 trials was conducted with n = 1, 1, 2, 2, 3, and 6 naive males, respectively. All trials were done in the top compartment (Fig. 1) with wire mesh as a floor to allow feces to fall through and reduce the chances for environmental contamination. All crickets were necropsied in 0.1 M saline at the end of each experiment. Females were also checked microscopically for the presence of sperm in the spermatheca to confirm that mating had occurred.

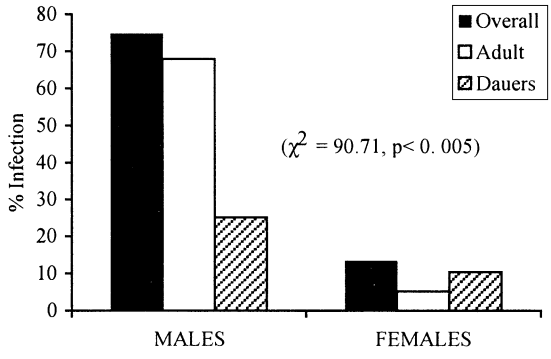

FIGURE 2. Prevalence of infection. Data from survey of adult male (n = 131) and female (n = 97) crickets showing a high male-biased infection (χ^2 = 90.71, $P < 0.005$). None of the nymphs (n = 30) sampled was infected. The percentage of adults harboring dauers is an underestimate because the genital chambers were not inspected for nematodes until later in the survey. ■ = overall level of infection; □ = proportion infected with adult nematodes; hatched bar = proportion harboring dauers in the genital chamber.

Scanning electron microscopy (SEM)

Phalli removed from infected male crickets were prepared for viewing with SEM. Specimens for SEM were fixed in 10% formalin and then postfixed by exposure to osmium-tetroxide (OsO_4) vapor for 24 hr. Specimens were then washed in buffered 0.1 M saline and deionized water and gradually dehydrated in a graded ethanol series. The phalli were then transferred to 100% ethanol and critical point dried using carbon dioxide (Eisenback, 1985). Dried specimens were mounted on stubs, sputter-coated with 20 nm of gold/palladium alloy, and examined with a Philips XL30-FEG SEM at 12 kV.

Histopathology

Live adult male and female crickets that were suspected to be naive or infected with *M. alii* were cut in half at the juncture between the thorax and the abdomen with the abdomen being retained in FAA (formalin, acetic acid, ethanol; 5:5:90). In several cases, the gut was excised and retained separately. After several days in FAA, the samples were dehydrated in a tertiary butyl alcohol series and embedded in paraffin (Johansen, 1940). Embedded cricket halves or guts were transversely sectioned 10–15 μm thick, mounted on slides treated with Mayer's albumin (50 ml fresh egg albumin, 50 ml glycerin, 1 g sodium salicylate), stained with 1% safranin in water and 0.5% fast green in clove oil and 100% ethanol (1:1), and examined and photographed with a compound photomicroscope.

RESULTS

Survey

The survey showed that male crickets were significantly more likely to be infected with adult nematodes than females (χ^2 = 90.71, $P < 0.005$) (Fig. 2). Of the adult males (n = 131), 68% were infected with adult nematodes in the hindgut and 25% harbored infective dauers in the genital chamber, in close association with the phallus. Only 5% of the females (n = 97) were infected with adult nematodes, whereas 10% of the females harbored dauers in the genital chamber (Fig. 2). The intensity of infection ranged from 1 to 112 in males and from 1 to 10 in females. None of the nymphs (n = 30) was infected.

The prevalence of dauer infections is an underestimate be-

TABLE I. Results from transmission experiments.*

	Naive					
	Fecal–oral		Same-sex		Venereal	
Infected	Males	Females	Males	Females	Males	Females
Males	0 (15)	0 (10)	0 (8)	n/a	n/a	12 (12)
Females	n/a	n/a	n/a	0 (10)	15 (15)	n/a

*We tested for transmission via fecal–oral contamination, same-sex contact, and copulation. Values indicate the number of successful transmissions out of (n) trials; n/a = not attempted.

cause we did not inspect the genital chamber of the adult crickets for nematodes until later in the survey. Genital chambers from 91 adult male crickets were examined, 36.3% harbored dauers. Whereas, the genital chamber of 50 adult females were inspected and 20% harbored dauers.

Transmission experiments

The infection status of all field-collected males and females presumed to be infected in these experiments were confirmed upon necropsy. At least 1 of the "infected" crickets used for each naive group was confirmed to be infected. In some cases, none of the "infected" crickets harbored nematodes; the data for these trials were discarded and are not reported here.

Fecal–oral transmission: When infected males were housed above naive males, nematodes were recovered only from the hindgut of infected crickets but not in the naive males (0 out of 15). Similarly, when infected males were housed above naive females, nematodes were found only in the hindgut of infected males but not in the naive females (0 out of 10) (Table I). Therefore, transmission did not occur through fecal–oral contamination from infected individuals under the conditions of this experimental design.

Same-sex transmission: None of the marked naive males (0 out of 8) acquired a nematode infection from the infected males. Likewise, none of the naive females (0 out of 10) acquired any nematodes via physical contact with the females harboring dauers (Table I). These results suggest that the nematode is not transmitted via same-sex contact.

Sexual contact transmission: When infected males were mated with naive females, larvae were recovered from the genital chambers of all the mated females (12 out of 12) (Table I). Subsequent developmental and adult stages of the nematode were never recovered from the hindgut of these female crickets or observed during histopathology of infected females. As we expected from the survey, infected males harbored both adult nematodes in the hindgut and dauers in the genital tract and on the phallus. These results strongly suggest that the dauers were transferred from males to females during copulation. However, dauers in females remained in the genital tract without developing into adults.

When females harboring dauers were mated with naive males, we recovered dauers from the genital tract and phallus (Fig. 3) of all the mated males (15 out of 15) (Table I). In addition, subsequent developmental stages of the nematodes were found in the posterior hindgut and adult nematodes were found in the anterior hindguts of these necropsied male crickets. Thus, female crickets successfully transferred dauers to males during copulation resulting in propagation of the next generation of nematodes.

The location of the developmental stage of the nematode in these males and in histological sections of infected males suggests that the dauers gain entrance via the posterior end of the cricket. These results further support the hypothesis that *M. alii* is sexually transmitted during copulation between adult crickets. Venereal transmission of the nematode is limited primarily to sexually mature, reproducing adults, which explains the lack of infections in juvenile crickets. The exact mechanical aspects of transmission, however, remain unclear.

Histopathology

Comparisons of sections from the same regions of naive and infected male and female crickets revealed no apparent pathology caused by this nematode association. Sectional work demonstrated that in infected male crickets dauers occurred only in the genital tract (Fig. 4a), propagative juveniles and adults were observed in the posterior gut (Fig. 4b), and adults were observed in the anterior gut (Fig. 4c). In females, dauers were only observed in the genital tracts (Fig. 4d–f).

DISCUSSION

The sex- and age-biased prevalence of infection can be attributed to several factors, the most likely being directly linked to the nematode's mode of transmission (see below).

During copulation, the epiphallus of the male cricket is hooked onto the female cricket's subgenital plate, and the copulatory papilla of the female then everts into a cavity enclosed by the epiphallus (Sakai et al., 1991). In infected male crickets, dauers reside primarily on the epiphallus (Fig. 3). The period of physical contact between host genitalia may allow the dauers to migrate into the genital chamber of the next host cricket. Subsequently, the male cricket transfers a spermatophore to the female's copulatory chamber by expansion of the ventral lobe (Sakai et al., 1991), also an attachment site on the phallus for the dauers. When the ventral lobe contacts the copulatory chamber of the female, dauers can again potentially move from host to host genitalia. Dauers recovered from a female cricket were observed actively migrating into the male genital chamber when mechanically placed on the outer rim of the genital opening. Further studies are needed to identify the exact mechanism of transmission.

The occurrence of venereal transmission in a phoretic nematode (*Bursaphelenchus* sp.) has been demonstrated in nitidulid beetles (Giblin, 1985). *Bursaphelenchus* is mycophagous and free living. The nematode–beetle association is purely phoretic, and nematodes were not observed outside of the host genital chamber. Giblin (1985) was able to establish venereal transmission from male to female but not vice-versa. In contrast, the ectoparasitic nematode *Noctuidonema guyanense* has been shown to be transmitted during copulation between adults of the fall armyworm, *N. guyanense* (Lepidoptera: Noctuidae) (Marti et al., 1990). These nematodes that occur primarily on the intersegmental membranes of the posterior abdomen could be transferred during copulation between adult moths (Rogers and Marti, 1994). However, other potential modes of transmission, e.g., via close association between nonmating individuals, were not tested.

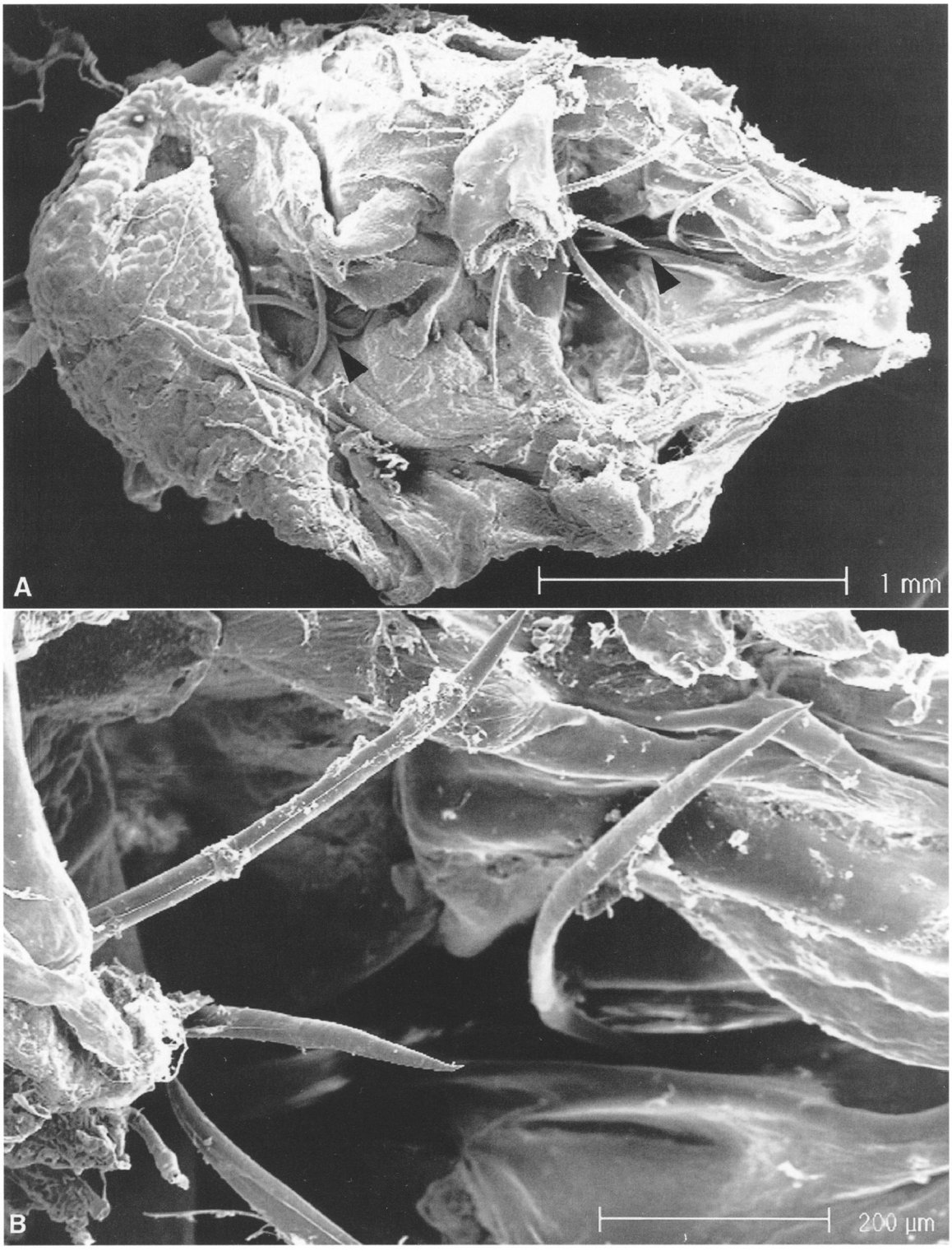

FIGURE 3. Scanning electron micrograph of male decorated cricket. (**A**) Dorsal view of phallus with infective dauers (*Mehdinema alii*). Arrowheads indicate several nematodes; 8 nematodes are present on the specimen, which was dissected out of an infected cricket (low magnification). (**B**) Epiphallus of infected male cricket with dauers attached (high magnification).

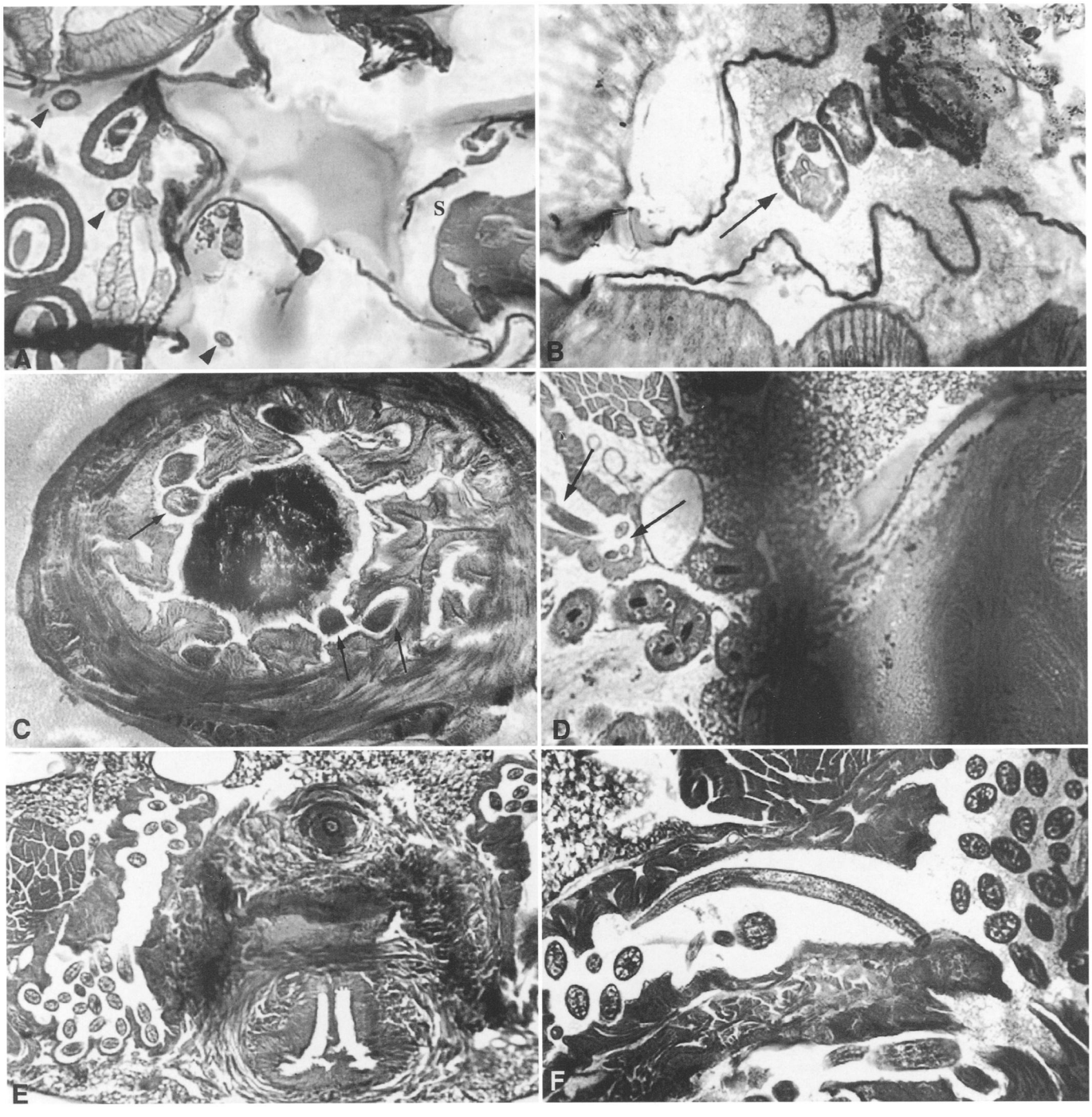

FIGURE 4. (**A–C**) Histological section of infected adult male cricket. (**A**) Genital tract with dauers (arrowhead); note spermatophylax (S); 100×. (**B**) Posterior hindgut/rectum with adult *M. alii*: note characteristic triradiated esophagus (arrow); 200×. (**C**) Anterior hindgut with adult nematodes (arrows); note spiny profile; 67×. (**D–F**) Histological sections of infected adult female cricket. (**D**) Anterior genital chamber with dauers (arrows) and spermatheca (lower right); 50×. (**E**) Posterior genital chamber with dauers and ovipositor (lower middle); 50×. (**F**) Genital chamber with dauers in cross and longitudinal section; 100×.

Our results support the hypothesis that *M. alii* dauers are neither transmitted via the fecal–oral route nor by same-sex contact, but rather during copulation (Table I). The dauers occurred only in the genital chamber of sexually mature crickets where they are transferred venereally (Figs. 3, 4). Moreover, the parasitic adult stage of the nematode primarily develops in the adult male host and cannot survive outside of its host on nutrient agar plates (preliminary observations). The infective dauers migrate into the male's hindgut and develop into the parasitic, propagative adult stage. Although adult female crickets also acquired dauer stages in this study, subsequent developmental stages of the nematode were never observed in the females. However, a small number of mature nematodes were recovered from field-collected female crickets in the survey;

this suggests that a small proportion of dauers can mature in the female host. This phenomenon was rarely observed and may not contribute significantly to the overall life history of *M. alii.*

The male-biased occurrence of the reproductive stage of *M. alii* can be attributed to several factors. First, the nematode may require specific nutrients for development that are available only in the male hosts. Alternatively, the bias may simply be due to the mechanism of transmission, i.e., the anatomy of the female host may inhibit dauers from gaining entrance to the intestine.

This parasite–host relationship is unique relative to other infectious diseases in several respects. Because the parasitic stage occurs, develops, and reproduces primarily in adult male crickets, females serve essentially as vectors. In most vectorborne diseases, an interspecific parasite vector serves as a refuge, providing an avenue for the evolution of high virulence (Ewald, 1990). However, an intraspecific vector and lack of refuges does not offer the same opportunities, which may partially explain the low pathogenicity of *M. alii* in *G. sigillatus.* The nematode appears to persist without eliciting any obvious clinical symptoms in the cricket. For a relatively long-lived parasite, low pathogenicity is an advantage for its own survival and transmission, because the parasite cannot persist if host mortality is too high. Therefore, the parasite should evolve to a level of pathogenicity that reflects a balance between parasite growth and reproduction versus dispersal to new hosts (Ewald, 1994; Lockhart et al., 1996), which in this case depends directly on host survival, fitness, and reproductive activity.

Because the parasite is venereally transmitted its reproductive success is directly linked to that of its host, in the sense that parasite transmission success depends on host mating success but not necessarily on increased host fertility. Thus STD transmission rates should increase if the parasite could induce sterility while increasing host sexual activity, resulting in repeated attempts at mating (Lockhart et al., 1996). These predictions have significant implications for a polygamous mating system, such as that of *G. sigillatus,* in which males attract multiple females by producing acoustic signals (Sakaluk, 1987). For example, the parasite could increase the attractiveness of its male host by affecting singing behavior.

Likewise, the parasite could in effect induce sterility by manipulating spermatophore production. Mating female decorated crickets receive a nutrient-rich spermatophylax, attached to a sperm-containing ampulla. The ampulla is removed after the spermatophylax is consumed. Females mate with multiple partners until enough sperm is obtained to fertilize and deposit eggs (Sakaluk, 1985). If the nematode decreases a male cricket's ability to produce a sufficiently large or nutritious spermatophylax, then his mate must copulate with additional males. This situation could increase the transmission rate of the nematode over a nonsexually transmitted parasite or one that does not affect the mating frequency of its host. Further studies are needed to determine the fitness cost of *M. alii* on *G. sigillatus,* if any, and whether the nematode affects host reproduction.

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