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Ecological Study of Nematode Parasitism in *Ips* Beetles from California and Idaho

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Abstract: Nematodes found in *Ips paraconfusus* from ponderosa pine in California were an undescribed species of *Parasitaphelenchus, Contortylenchus elongatus, C. reversus,* and *C. brevicomi. C. elongatus,* the most commonly found contortylenchid, was present in 98.2% of the contortylenchid-parasitized beetles. Only one nematode parasite of the gut, a *Parasitorhabditis* sp., was isolated. Although significant differences in parasitism were observed, they were by collection sites, rather than by elevation or bole sources (slash or standing). Significant changes in parasitism between fall and spring collections were observed but not at every site. Nematode parasitism in the F_1 generation of *I. paraconfusus* by *Parasitaphelenchus, Contortylenchus,* or *Parasitorhabditis* increased or decreased from the parent generation depending upon the experiment.

Nematode parasites from *I. pini* included an undescribed *Parasitaphelenchus* sp., two undescribed *Contortylenchus* spp., *C. reversus* and *Parasitylenchus* (= *Neoparasitylenchus*) *ovarius* from the hemocel, and *Parasitorhabditis ipini* from the gut. *Parasitaphelenchus* sp. was found in 99% and 45.3% of the beetles from Idaho and California, respectively. Of the 1,000 *I. pini* from Idaho and California, 157 were parasitized by the contortylenchid species or *P. ovarius.*

Key words: bark beetle, biological control, *Contortylenchus,* entomogenous nematode, *Ips,* parasitism, *Parasitaphelenchus, Parasitorhabditis, Parasitylenchus, Pinus.*

The California five-spined engraver, *Ips paraconfusus* Lanier, attacks nine species of *Pinus,* especially ponderosa pine, *P. ponderosa* Dougl. ex Laws., from southern Oregon to southern California west of the Cascade and Sierra Nevada Mountains (2). It breeds in fresh slash and recently downed trees and is one of the most destructive insects of young pine forests (16). *I. paraconfusus* closely resembles *I. confusus* (LeConte), but it differs in host trees attacked and geographical range. The pine engraver, *I. pini* (Say), widely distributed in North American with breeding habits similar to *I. paraconfusus,* is an important pest of ponderosa pine, lodgepole pine, *P. contorta* Dougl., and Jeffrey pine, *P. jefferyi* Grev. & Balf (14).

Endoparasitic nematodes are believed to be major factors in bark beetle population reduction (10). Generally, these nematodes do not kill their host, but they can alter host behavior, reduce fecundity, longevity, and flight, and delay emergence (3). Few studies have been conducted with endoparasitic nematodes from *I. paraconfusus* and *I. pini.* In those studies, *I. paraconfusus* was identified as *I. confusus.* It seems, however, that *I. paraconfusus* and *I. confusus* share the same nematode–parasite–species complex.

Two nematode parasites, a *Contortylenchus* sp. and a *Parasitaphelenchus* sp., found in the hemocoel of *I. confusus* did not affect mortality of adult beetles (11). *Contortylenchus elongatus* (Massey) and its biology was described in *I. confusus* from pinyon pine in New Mexico (8,9) and from ponderosa pine in California (12,13). *Parasitaphelenchus* sp. was recovered from the hemocoel and *Parasitorhabditis obtusa* (Fuchs), now called *P. subelongati* Slobodjanjuk (1,17), from the midgut of the beetle (8). *Parasitorhabditis* sp. has an adverse effect on the midgut cells of *I. confusus* (13).

Massey (7) described *Contortylenchus spi-*

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rus (Massey) from *I. pini* (= *I. oregoni* [Eichoff]), and later he (10) summarized the nematode parasites of *I. pini.* Included were the hemocoelic parasites, a *Contortylenchus* sp., *C. spirus,* a *Parasitylenchus* sp., *P.* (= *Neoparasitylenchus*) *ipinius* Massey, *P. ovarius* Massey, and a midgut parasite, *Parasitorhabditis ipini* Massey.

The objectives of our study were fourfold: 1) to determine the distribution and occurrence of nematode parasites in *I. paraconfusus* from various elevations in California and in *I. pini* from California and Idaho; 2) to compare the distribution of endoparasitic nematodes in *I. paraconfusus* and *I. pini* from infested slash and standing trees; 3) to identify to genus the nematodes in excavated frass from *I. paraconfusus*; and 4) to determine the effect of culturing *I. paraconfusus* in the greenhouse for one generation on nematode parasitism.

Materials and Methods

Ips paraconfusus: To study the effects of elevation on nematode parasitism, bole sections of ponderosa pine, 50–60 cm in length and 15–20 cm in diameter, were obtained from the Sierra National Forest, Madera County, California, collected between 17 and 24 September 1985 at 1,200, 1,280, and 1,650 m elevation. At 1,200 m, there were two collection sites 100 m apart at Pilot Peak Plantation where the bole sections were obtained from slash and one site at Point Sale where the bole sections, 2–5 m above ground, were taken from standing trees. Pilot Peak Plantation and Point Sale are located 14.5 km from each other. At 1,280 m, bole sections were taken from standing trees at two sites at Flume Sale 6.4 km apart. At Chilkoot Sale, 1,600 m, bole sections were obtained from slash. Boles were taken from two trees at each site, except from Chilkoot where only one infested tree was found. For comparison between fall and spring nematode parasitism, infested boles were collected again from the three sites at the 1,200 m elevation on 29 April 1986.

Boles were kept at 10 C until placed in emergence cages. One or two bole sections from each site were placed in a cage in a greenhouse at 20–26 C. A 500-ml Mason jar containing a paper towel was placed in a hole on the bottom of the cage. Upon eclosion, the adult bark beetles were attracted to the light and became trapped in the jar; they were removed daily for dissection.

Each adult beetle was identified to species, sexed, and examined externally under the elytra and on the rest of the body for phoretic nematodes. The elytra were removed, and the beetle was washed in 0.75% saline solution to remove the external phoretic nematodes. The beetle's head and prothorax were dissected and examined for endoparasitic nematodes, then the rest of the body was dissected and checked for endoparasitic nematodes in the hemocoel and alimentary canal. The species and number of endoparasitic nematodes were recorded. Voucher nematode specimens, killed and fixed in hot (80 C) 10% formalin and processed to pure glycerin (15), were used to confirm species identification. Adults of *Parasitaphelenchus* and *Parasitorhabditis* were obtained by placing immature stages from the bark beetles on sterilized bark beetle frass or malt agar (6) and then processed to glycerin.

Excavated bark beetle frass from the bottom of the cage was used to determine the nematode complex in the galleries. The nematodes were separated from frass by the modified Baermann funnel technique. The nematodes were processed to glycerin and identified to family and genera.

Nematode parasitism of the parent and F_1 generation was studied in the greenhouse. A bole from the Sierra National Forest, Madera County, was placed in an emergence cage, and beetle adults of the parent generation were dissected. Another bole from the same beetle-infested tree was placed in a screened cage (82.5 × 82.5 × 121.5 cm) with a freshly cut 1-m section of ponderosa pine bole. The freshly cut ends of the boles were coated with paraffin to reduce desiccation. After the parent beetle generation attacked the uninfested bole, it was placed in an emergence cage. Twenty

TABLE 1. *Ips paraconfusus* adults with internal nematodes from two sources at different elevations.

Elevation (m)	Collection site	Source of bole	Total dissected	Bark beetle parasitized (%)		
				Parasitaphelenchus†	*Contortylenchus*†	*Parasitorhabditis*‡
1,200	Pilot Peak 1	Slash	221	92.3 a	21.3 b	17.7 b
	Pilot Peak 2	Slash	168	92.9 a	12.5 cd	7.2 cd
	Point Sale	Standing	293	77.4 b	31.0 a	5.4 d
1,280	Flume Sale 1	Standing	219	92.2 a	25.5 ab	5.9 d
	Flume Sale 2	Standing	259	76.5 b	19.0 bc	10.1 c
1,650	Chilkoot	Slash	87	85.0 ab	9.2 d	45.9 a

Percentages followed by different letters in a column are significantly different ($P < 0.05$). Percentages add up to more than 100% because of multiple parasitism.

† Nematodes found in the hemocoel of bark beetle.

‡ Nematodes found in the alimentary canal of bark beetle.

to thirty days after attack, beetle adults emerged but were discarded because they could represent the parent generation. Only beetles emerging 5 days after the initial adults had emerged were considered to be F_1. Adults were collected daily and dissected. The experiment was repeated three times.

Ips pini: Prevalence of nematode parasitism on overwintering beetles collected in California and Idaho was compared. Bole sections from ponderosa pine slash, *P. ponderosa* var. *scopulorum* Engelm., in Boise National Forest, Glen County, Idaho, collected on 2 October 1985, and of Jeffery pine, *P. jefferyi* from Lassen National Forest, Lassen County, California, collected on 22 August 1985, were held in emergence cages as described for *I. paraconfusus*. Three hundred beetles from each state were dissected.

In addition, nematode parasitism of beetles from slash and standing Jeffery pine from Lassen National Forest was compared. Boles, cut 2–5 m above ground, from three standing trees and two slash trees were obtained at the 1,490 m elevation on 2 April 1986.

Voucher nematode specimens: Voucher specimens from this study are deposited in the Korean Bark Beetle Nematode Collection at Gyeongsang National University and in the University of California Davis Nematode Collection (UCDNC) at Davis. In most cases, nematodes were identified to species and (or) genus, but if only juvenile nematodes were collected, they were identified to family.

Data analysis: Data were analyzed by testing for equality of proportions (Z-values) between collection sites. Chi-square test was done for sex ratios. In all statistical tests, the level of significance is based at $P < 0.05$.

RESULTS

Ips paraconfusus: Four species of nematode parasites were recovered from the hemocoel of *I. paraconfusus*. In the elevation study the most common hemocoelic parasite was an undescribed species of *Parasitaphelenchus* found in 85.1% of the total sample (Table 1). Three other species found were *Contortylenchus elongatus, C. reversus* (Thorne), and *C. brevicomi* (Massey). *C. elongatus* comprised 98.2% of the total contortylenchid from parasitized beetles in the sample (n = 272). Three beetles were parasitized with *C. brevicomi* and two with *C. reversus*. *Parasitorhabditis* sp., the only internal gut parasite observed, was in 11.7% of the total sample (Table 1).

Significantly more females than males of *I. paraconfusus* emerged from the boles. Of 1,247 beetles dissected in the elevation study (Table 1), 65.2% were females. Similar results were observed in the fall versus spring study (Table 2), where 73.0% of the spring beetles (n = 419) were females, and in the generation study (Table 3), where 68.6% of the F_1 generation bark beetles (n = 414) emerging were females. Al-

TABLE 2. *Ips paraconfusus* from 1,200 m elevation with nematodes in September 1985 and April 1986.

Collection site	Time of collection	Source of bole	Total dissected	Parasitism (%)		
				Parasitaphelenchus†	*Contortylenchus*†	*Parasitorhabditis*‡
Pilot Peak 1	September	Slash	221	92.3 a	21.3 b	17.7 a
	April	Slash	100	90.0 a	36.0 a	5.0 b
Pilot Peak 2	September	Slash	168	92.9 a	12.5 b	7.2 b
	April	Slash	200	75.0 b	28.0 a	18.0 a
Point Sale	September	Standing	293	77.4 a	31.0 a	5.4 b
	April	Standing	90	60.0 b	31.1 a	15.6 a

Percentages followed by a different letter in a column for each collection site are significantly different ($P < 0.05$). Percentages add up to more than 100% because of multiple parasitism.
† Nematodes found in the hemocoel of bark beetle.
‡ Nematodes found in the alimentary canal of bark beetle.

though these were highly significant differences in the beetle's sex ratio, there were no significant differences in nematode parasitism according to sex and the parasitism data were combined.

Nematode parasitism from three different elevations and two different bole sources showed no obvious trends (Table 1). Parasitism by *Parasitaphelenchus* exceeded 76% for the three elevations, whereas parasitism by *Contortylenchus* varied from 9 to 31% and by *Parasitorhabditis* varied from 5 to 46%. There were significant differences, however, in nematode parasitism among beetles by collection sites. Parasitism by *Parasitaphelenchus* and parasitism by *Parasitorhabditis* were independent of each other.

At the 1,200 m elevation, *Parasitaphelenchus* parasitism decreased significantly from fall to spring at two of the three sites and remained about the same at the third (Table 2). Parasitism by *Contortylenchus* increased significantly from fall to spring at two sites and remained about the same at the third. Parasitism by *Parasitorhabditis* decreased significantly at one site and increased significantly at the other two.

In the elevation study the number of nematodes within a beetle host varied considerably, precluding significant difference in mean numbers among the various collection sites, and the data were combined. The mean number of *Contortylenchus* females infecting the bark beetle was 2.1 ± 2.0 SD (range 1–21), whereas the mean number of *Parasitaphelenchus* was 20.0 ± 27.2 SD (range 1–346) and of *Parasitorhabditis* was 16.1 ± 23.6 SD (range 1–145). Similar mean numbers were observed in the other studies.

Parasitaphelenchus parasitism decreased

TABLE 3. *Ips paraconfusus* from parent to F_1 generation parasitized by nematodes under laboratory conditions.

Experiment	Generation	Total dissected	Bark beetle parasitized (%)		
			Parasitaphelenchus†	*Contortylenchus*†	*Parasitorhabditis*‡
1	Parent	149	100.0 a	26.8 b	51.7 b
	F_1	252	89.3 b	38.1 a	65.5 a
2	Parent	149	100.0 a	26.8 a	51.7 a
	F_1	64	98.5 a	29.7 a	53.1 a
3	Parent	98	76.5 a	21.4 a	10.2 b
	F_1	98	56.1 b	20.4 a	97.0 a

Percentages followed by a different letter in a column between parent and F_1 generation are significantly different ($P < 0.05$). Percentages add up to more than 100% because of multiple parasitism.
† Nematodes found in the hemocoel of bark beetle.
‡ Nematodes found in the alimentary canal of bark beetle.

TABLE 4. Nematode parasitism of emerging adult bark beetle, *Ips paraconfusus*, over time under laboratory conditions.

Emergence intervals (days)	No. dissected	Bark beetle parasitized (%)		
		Parasitaphelenchus	*Contortylenchus*	*Parasitorhabditis*
1–5	76	93.4	21.0	27.6
6–10	49	85.7	26.5	73.5
11–15	31	83.8	32.2	58.1
16–20	39	66.7	41.0	60.0
21–25	88	71.6	29.5	80.7
26–30	72	97.2	40.3	95.8
31–35	28	75.0	39.3	100.0
36–40	15	73.3	46.7	100.0
41+	16	53.3	43.8	93.8
Overall parasitism		81.6	32.6	71.5

Combined data of three experiments from generation study.

from parent to F_1 generation beetles in all three experiments, significantly in two of them (Table 3). *Contortylenchus* parasitism increased significantly in experiment 1, but there was no significant difference in experiments 2 or 3. *Parasitorhabditis* parasitism increased in all three experiments; the increase was significant in experiments 1 and 3.

Early or late emerging beetles had equal chances of being parasitized by *Parasitaphelenchus* (Table 4). Parasitism by *Contortylenchus* showed a tendency toward higher percentages 10 days after the first beetles emerged, and *Parasitorhabditis* definitely parasitized more in late emerging beetles.

Multiple parasitism, defined as the presence of two or more species within the same host, was common (Table 5). It occurred frequently between *Parasitaphelenchus* and *Contortylenchus*, and one gut parasite and two hemocoelic parasites were occasionally found in the same beetle.

Nine nematode genera in six families were isolated from the excavated bark beetle frass. These included the following genera: *Aphelenchoides, Cryptaphelenchus, Laimaphelenchus,* and *Parasitaphelenchus* in the family Aphelenchoididae; *Panagrolaimus* in the family Cephalobidae; *Mikoletzkya* in the family Diplogasteridae; *Robleus* in the family Paurodontidae; and *Mesorhabditis* and *Parasitorhabditis* in the family Rhabditidae. An unidentified genus in the family Neotylenchidae was also isolated. However, no *Contortylenchus* was isolated from excavated frass.

Ips pini: I. pini had five different hemocoelic nematode parasites. Included were an undescribed species of *Parasitaphelenchus,* three species of *Contortylenchus,* and *Parasitylenchus ovarius. Parasitaphelenchus* was found in 99% and 45.3% of the dissected beetles from Idaho and California, respectively. The three contortylenchid species included *C. reversus* and two undescribed species referred to here as *Contortylenchus* sp. 1 and *Contortylenchus* sp. 2. Of 1,000 bark beetles dissected from Idaho and California (Table 6), 157 were parasitized by the four tylenchid species—the three contortylenchid species or *Parasitylenchus ovarius.* Of the 157, 71.3% were parasitized by contortylenchids, with *Contortylenchus* sp. 1 in 63.7% of the beetles,

TABLE 5. Single and multiple parasitism in *Ips paraconfusus* adults by entomogenous nematodes at different elevations.

Elev.	Collection site	Source of bole	Total dissected	Bark beetle parasitized (%)						
				Pa	Ct	Pr	Pa and Ct	Pa and Pr	Pa, Ct and Pr	Pr and Ct
1,200	Pilot Peak 1	Slash	221	62.4	0.5	0.9	13.1	9.1	7.7	0.0
	Pilot Peak 2	Slash	168	74.4	0.0	0.0	11.3	6.0	1.2	0.0
	Point Sale	Standing	293	47.1	2.7	1.7	26.6	2.0	1.7	0.0
1,280	Flume Sale 1	Standing	219	63.5	0.9	0.0	22.8	4.1	1.8	0.0
	Flume Sale 2	Standing	259	52.5	0.4	2.7	17.0	5.8	1.2	0.4
1,650	Chilkoot	Slash	87	44.8	0.0	10.3	4.6	31.0	4.6	0.0

Parasitaphelenchus (Pa) and *Contortylenchus* (Ct) are hemocoelic nematode parasites of bark beetles, and *Parasitorhabditis* (Pr) occurs in the alimentary canal of bark beetles.

TABLE 6. Nematode parasitism in *Ips pini* collected from Idaho and California.

Collection site	Source of bole	Date collected	Total dissected	Bark beetle parasitized (%)			
				Parasitaphelenchus†	*Contortylenchus*†	*Parasitylenchus*†	*Parasitorhabditis*‡
Idaho	Slash	10-2-85	300	98.6 a	13.7 a	7.7 a	80.6 a
California	Slash	8-22-85	300	66.7 b	14.7 a	5.4 a	83.7 a
California	Slash	4-2-86	100	60.0 b	6.0 b	4.0 ab	88.3 a
California	Standing	4-2-86	300	19.0 c	10.3 ab	2.4 b	62.7 b

Percentages followed by different letters in a column are significantly different ($P < 0.05$). Percentages add up to more than 100% because of multiple parasitism.
† Nematodes found in the hemocoel of bark beetle.
‡ Nematodes found in the alimentary canal of bark beetle.

C. reversus in 7%, and *Contortylenchus* sp. 2 in 2.5%. *Parasitylenchus ovarius* parasitized 31.8% of the beetles. Total parasitism of the contortylenchids and parasitylenchid exceeded 100% because of multiple parasitism (Table 7). *Parasitorhabditis ipini,* the only gut parasite isolated, represented 81% of the total sample from Idaho and 63–88% from California (Table 6).

The sex ratio of *I. pini* was significantly biased toward females, with 65% females (n = 300) from Idaho and 86.4% females (n = 700) from California. There was no significant difference in parasitism between males and females, and the parasitism data were combined.

I. pini collected from Idaho had significantly higher parasitism by *Parasitaphelenchus* than *I. pini* from California (Table 6). Parasitism of beetles by *Parasitaphelenchus* was not significantly different between the August and April collections from the same site in California, but there were significant differences between standing and slash trees. There were no significant differences in parasitism by *Contortylenchus* for the August and October collections between California and Idaho. There were significant differences, however, between the August and April slash collections from the same California site. No significant difference in parasitism by *Parasitylenchus* in the summer and fall collections from California or Idaho was observed. Parasitism by *Parasitylenchus* was generally low but was significantly different between slash and standing trees (Table 7), as was parasitism by *Parasitorhabditis* (Table 6).

Multiple parasitism between *Contortylenchus* and *Parasitaphelenchus* varied from 3 to 13%, and between *Parasitylenchus* and *Parasitaphelenchus* it varied from 0.7 to 6.3% (Table 7). Moreover, the occurrence of *Contortylenchus* sp. 1 with *C. reversus* was observed in one bark beetle from California and two from Idaho. The presence of hemocoelic nematode parasites and *Parasitorhabditis* in the alimentary canal in *I. pini* was common. Two bark beetles from Idaho had *Parasitorhabditis* in the alimentary canal and *Parasitaphelenchus, Parasitylenchus,* and *Contortylenchus* in the hemo-

TABLE 7. Single and multiple hemocoelic parasitism in *Ips pini* by entomogenous nematodes from Idaho and California.

Collection site	Date collected	Source of bole	Total dissected	Bark beetle parasitized (%)						
				Pa	Ct	Pt	Pa and Ct	Pa and Pt	Pa, Ct and Pt	Pt and Ct
Idaho	10-2-85	Slash	300	79.0	0.0	0.37	13.0	6.3	0.37	0.0
California	8-22-85	Slash	300	54.3	3.0	0.37	10.7	1.7	0.0	1.0
	4-2-86	Slash	100	52.0	0.0	1.8	6.0	1.0	0.0	0.0
	4-2-86	Standing	300	16.0	8.0	1.7	2.3	0.7	0.0	0.0

Parasitaphelenchus (Pa), *Contortylenchus* (Ct) and *Parasitylenchus* (Pt) are hemocoelic parasites of bark beetles.

coel. *Parasitorhabditis, Parasitaphelenchus,* and *Contortylenchus* were observed in the same bark beetle in 11.7% (35/300) of Idaho and in 5.4% (38/700) of California beetles. When *Parasitaphelenchus* and *Parasitylenchus* occurred in combination, *Parasitorhabditis* was not found in the same beetle.

The mean numbers of nematode parasites per bark beetle were similar in Idaho and California, and the data were combined. The mean number of *Contortylenchus* per *I. pini* was 2.4 ± 5.7 SD (range 1–46); *Parasitylenchus* 2.1 ± 2.3 SD (range 1–10); *Parasitaphelenchus* 47.6 ± 66.6 SD (range 1–439); and *Parasitorhabditis* 16.5 ± 18.0 (range 1–222).

Discussion

The recovery of *C. reversus* and *C. brevicomi* from *I. paraconfusus* and of *C. reversus* from *I. pini* are new host records. Parasitism by *C. brevicomi* was probably due to the overlapping of two bark beetle species because we observed *I. paraconfusus* and *Dendroctonus brevicomis* LeConte occurring sympatrically in the same bole. *D. brevicomis* adults were parasitized by *C. brevicomi* (unpubl.), and we hypothesize that gallery overlap between beetle species occurred. *C. reversus* from other bark beetle species may have parasitized *I. paraconfusus* and *I. pini* under similar circumstances as described for *C. brevicomi.*

Massey (10) listed the parasites of *I. pini* and reported the presence of an unidentified *Contortylenchus* sp. We have examined the available type specimens of *Contortylenchus* from the Massey Collection (Lincoln, Nebraska) and the Thorne Utah Collection (Beltsville, Maryland) and determined that both *Contortylenchus* sp. 1 and 2 are new; they will be described at a later date. Massey (10) did not list *Parasitaphelenchus* sp. in *I. pini* or *I. paraconfusus,* but this nematode was commonly found in both species.

Although significant differences in nematode parasitism were observed, there was no relationship to elevation, collection sites, source of bole (standing or slash), sex of bark beetle, time of collection, or generations. Longer term studies, more collection sites, and (or) different sampling procedures may show trends that were not apparent in this study. Massey (10), however, stated that percentages of individual bark beetle species infected by internal nematode parasites are quite variable. Thus, the percentage of infected beetles of a given species and population may vary considerably from year to year. Reasons for this variation are not known, but Massey (10) concluded that moisture is probably the most important environmental factor. He noted that nematode populations are extremely high and varied as to the species found in bark beetles from spruce and fir but are low with less species variation from ponderosa pine and pinyon pine where a lower moisture is required for survival of the tree.

Our study showed that multiple parasitism commonly occurs in *I. paraconfusus* and *I. pini.* Two or more genera of hemocoelic nematodes were found in the same bark beetle, and nematode parasitism appeared to be independent of other nematode species. Similar observations have been made in *Ips sexdentatus* (Boern) parasitized by two species of *Parasitaphelenchus* (5).

A number of phoretic and parasitic nematode species were recovered from the frass of *I. paraconfusus,* but *Contortylenchus* was absent. *Contortylenchus* may have been absent because of the extraction procedure, sample size, timing of sample, or its ability to avoid being excavated from frass. Interestingly, Massey (10) indicated that the free-living forms of contortylenchids do not persist very long in the galleries. Lieutier (4) also noted that *C. diplogaster* (v. Linstow) disappears from galleries very quickly.

Entomogenous nematodes are important parasites of bark beetles. More studies are needed to understand the role of entomogenous nematodes on the ecology, behavior, and physiology of their hosts and how these nematodes affect the population dynamics of the bark beetles.

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