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Teratorhabditis palmarum n. sp. (Nemata: Rhabditidae): An Associate of *Rhynchophorus palmarum* and *R. cruentatus*[1]

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Abstract: *Teratorhabditis palmarum* n. sp., an associate of the palm weevils *Rhynchophorus palmarum* and *R. cruentatus* is described. *Teratorhabditis palmarum* was isolated from newly emerged adults and cocoons of *R. palmarum* from red-ring diseased coconut palms, *Cocos nucifera,* in Trinidad and Ecuador, and from red-ring diseased oil palms, *Elaeis guineensis,* in Colombia. *Teratorhabditis palmarum* was also associated internally with newly emerged adults of *R. cruentatus* from mature transplanted cabbage palmettos, *Sabal palmetto,* in Florida. Dauer juveniles of *T. palmarum* infested the genital capsule and body cavity of newly emerged adult female and male palm weevils. Adult nematodes isolated from cocoons and dauer juveniles from newly emerged palm weevils were culturable on bacterial lawns on several solid media. Females of *T. palmarum* have a single anteriorly directed ovary; vulva at 93–96% of the body length; short, hemispherical spicate tail; three or four teeth in the metastom; cuticle with distinct transverse punctations that change abruptly at the level of the procorpus to indentations of alternating size and arrangement; and eggs with cuticular sculpturing. Males have a crenate, peloderan bursa with a 2 + 5 + 3 pattern of bursal rays (7 extend to the margin of bursa); spicules linear, completely fused at the distal tip and dorsally for 50% of the total spicule length.

Key words: coconut palm, *Cocos nucifera,* Colombia, Ecuador, *Elaeis guineensis,* entomophilic nematode, Florida, new species, oil palm, red ring disease, *Rhadinaphelenchus cocophilus, Sabal palmetto, Teratorhabditis palmarum* n. sp., Tobago, Trinidad.

During studies on the association between the palm weevil *Rhynchophorus palmarum* (L.) and the red ring nematode, *Rhadinaphelenchus cocophilus* (Cobb) Goodey, in coconut palm, *Cocos nucifera* L., in Trinidad, a new species of *Teratorhabditis* was found (4–6). All life stages of the nematode were extracted from the cocoons of *Rhynchophorus palmarum* in Trinidad and Tobago. Dauer juveniles of the new species were located in the genital capsule (ovipositor or aedeagus) and the body cavity of newly emerged palm weevils of both sexes (4). Dauer juveniles from weevils were cultured to adults and shown to be conspecific with the adults from cocoons (4). Experiments in Ecuador and Trinidad showed that surface disinfestation of pupae or larvae of *R. palmarum* diminished the internal association of *Teratorhabditis* with the resulting weevil adults but did not reduce the association between the red ring nematode and the weevils, suggesting that the association between *Teratorhabditis* and *R. palmarum* is commensal (5).

Adults of *Teratorhabditis* were discovered in a cocoon of *R. palmarum* from coconut palms with red ring disease in Ecuador, and dauer juveniles were extracted from adult *R. palmarum* attacking oil palm, *Elaeis guineensis* Jacquin, in Colombia (Gerber, unpubl.). Additionally, dauer juveniles of *Teratorhabditis* were found to be internally associated with the palmetto weevil, *Rhynchophorus cruentatus* (Fabricius) (Giblin-Davis, unpubl.), a pest of the cabbage palmetto, *Sabal palmetto* (Walter) Lodd., in Florida (8, 9).

Teratorhabditis palmarum n. sp. is described here with comparisons between isolates from different geographic loca-

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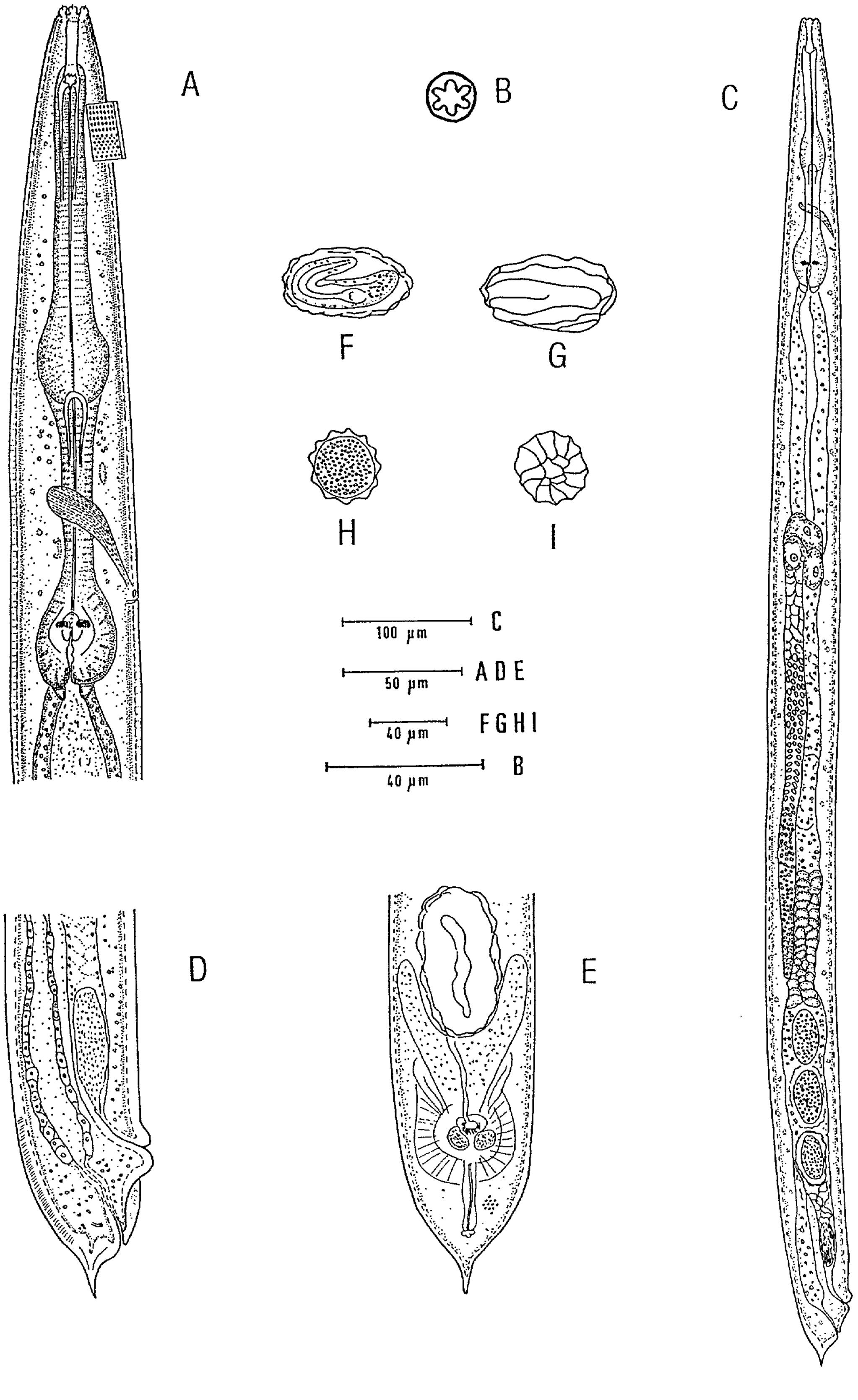
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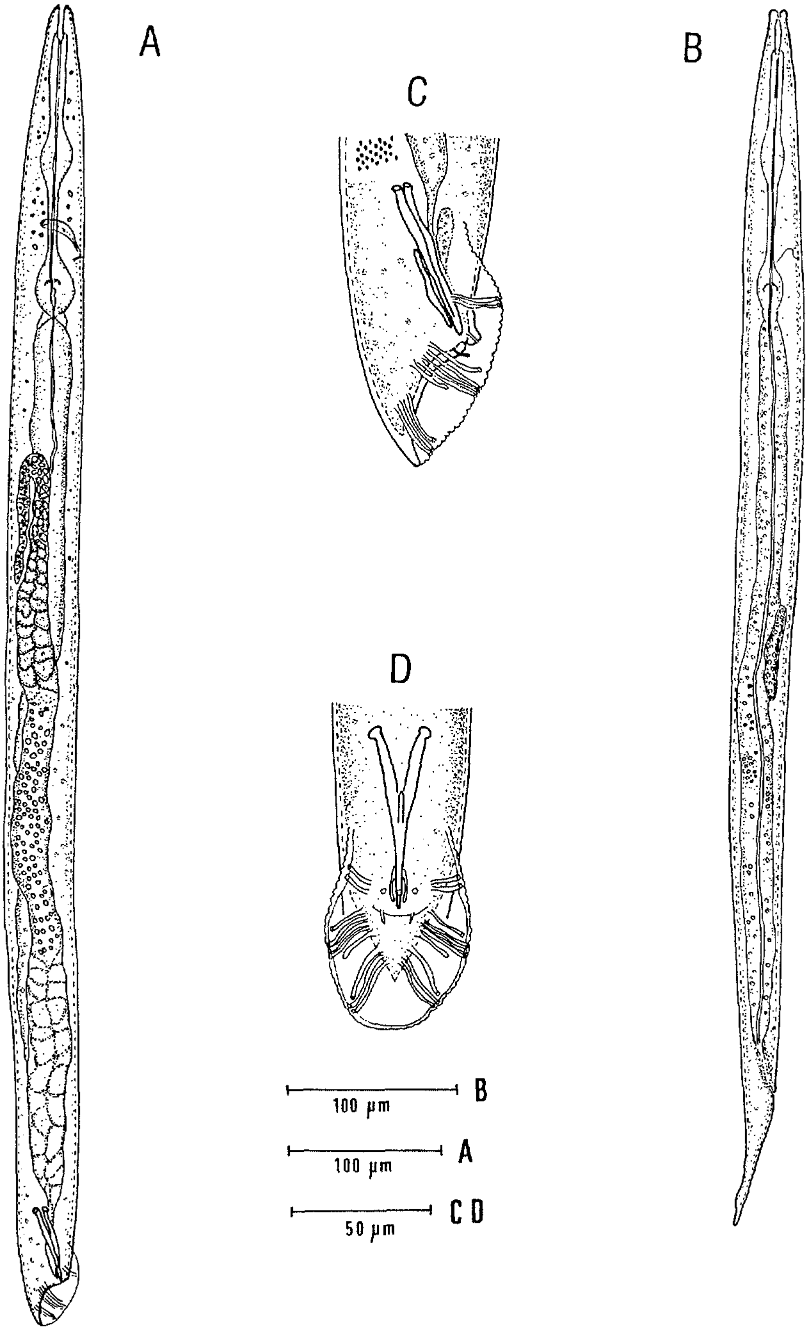

FIG. 2. *Teratorhabditis palmarum* n. sp. A) Male. B) Dauer juvenile from inside *Rhynchophorus palmarum.* C) Male tail, lateral view showing male characteristics including arrangement of bursal rays. D) Male tail, ventral view.

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FIG. 1. *Teratorhabditis palmarum* n. sp. A) Anterior region of adult female. Note abrupt change of cuticle ornamentation at anterior third of procorpus. B) En face view. C) Female. D) Female tail, lateral view. E) Female tail, ventral view with egg in uterus. F, G) Egg, lateral view showing typical cuticular ornamentation. H, I) Egg, dorsal or ventral view showing cuticular ridges.

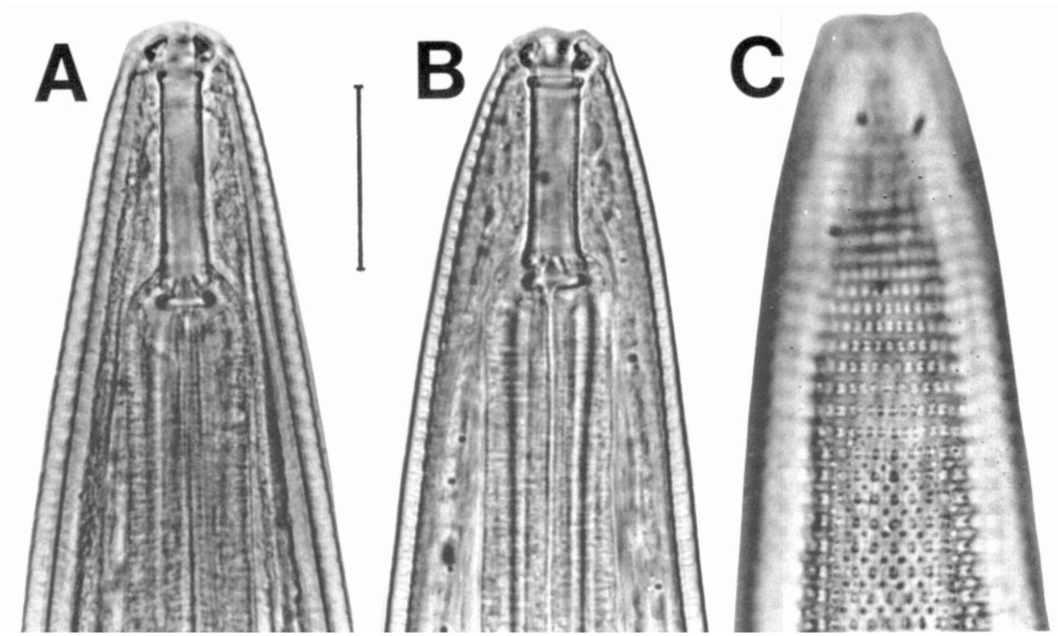

FIG. 3. Photomicrographs of anterior end of adult females of *Teratorhabditis palmarum* n. sp. A) Specimen from *Rhynchophorus cruentatus* from Florida showing stoma. B) Specimen from *Rhynchophorus palmarum* from Trinidad showing stoma. C) Specimen from Trinidad showing cuticular pattern at the procorpus level. Bar = 20 μm.

tions, host insects, and host plants. *Teratorhabditis palmarum* is the first species in the genus to be observed in an association with an insect.

MATERIAL AND METHODS

Cocoons of the palm weevil *R. palmarum* were collected from May 1987 to May 1988 at the Cocal plantation, Manzanilla, Trinidad, West Indies, and stored in separate containers in the laboratory until adults emerged. Newly emerged palm weevils were killed and dissected, and nematodes were extracted by a modified Baermann method. Dauer juveniles were cultured to adults on unidentified bacteria and fungi on glycerol-supplemented potato dextrose agar (GPDA) (7), nutrient agar (NA), or 10% tryptic soy broth agar (TSB). Cocoons, which are composed of the rough fibers of the coconut palm petiole or stem, were teased apart and soaked overnight in a pie pan for nematode extraction. Nematodes were killed by gentle heat, fixed in 4% formalin, processed, and mounted in glycerin.

Cocoons of *R. palmarum* from a coconut palm at Hacienda Las Penas, La Tola, Esmeraldas, Ecuador, were collected in January 1988 and extracted for nematodes. A few *T. palmarum* were harvested, killed with gentle heat, and processed to glycerin.

Two females of *R. palmarum* collected June 1988 from the oil palm plantation, Palmeras de la Costa, Copey-Cesar, Barranquilla, Colombia, were dissected and dauer juveniles were extracted and cultured on GPDA (7). Adult *T. palmarum* were harvested from culture and processed to glycerin.

Cocoons of *R. cruentatus* were collected from infested cabbage palmettos in Broward County, Florida, and adults were allowed to emerge separately. Dauer juveniles of *T. palmarum* were recovered from the excised genital capsules of newly emerged adult weevils and cultured on GPDA or TSB. Adult nematodes were harvested and fixed in 4% formalin. Measurements of the Florida population of *T. palmarum* were made in formalin according to previously depicted conventions (2).

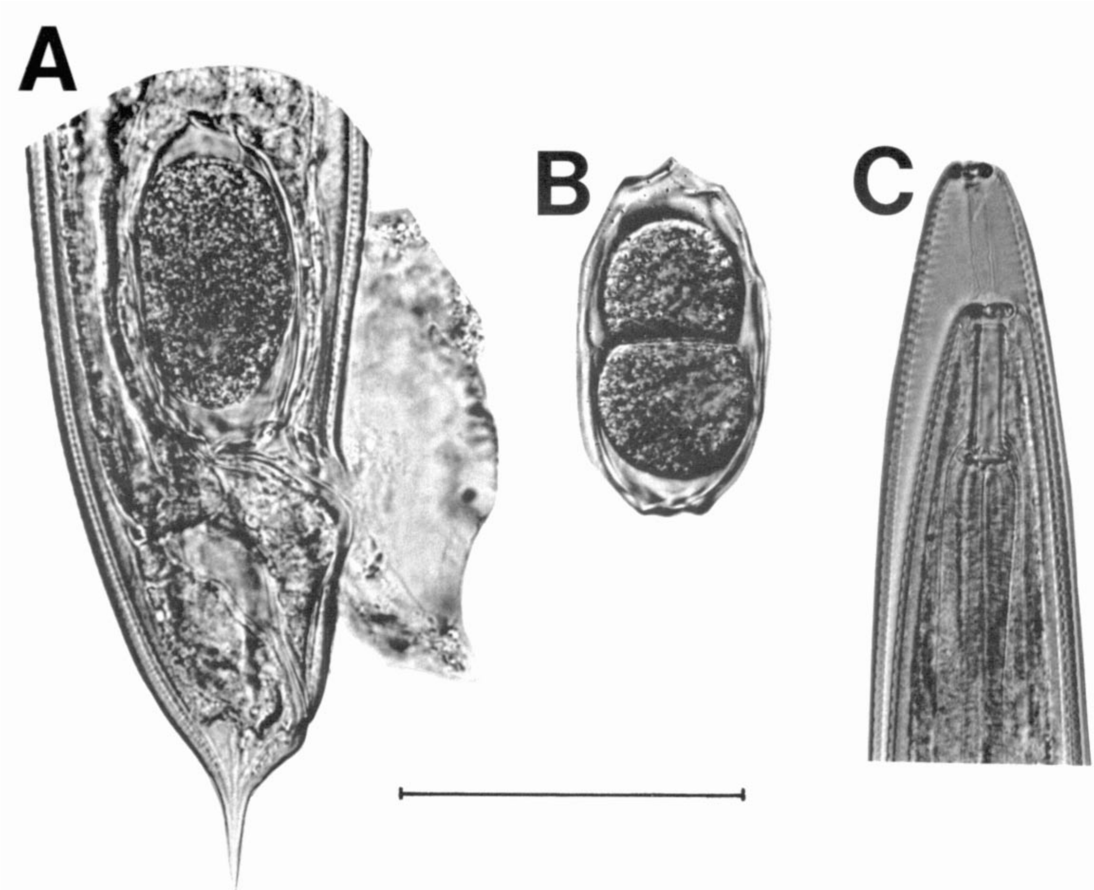

FIG. 4. Photomicrographs of *Teratorhabditis palmarum* n. sp. from *Rhynchophorus cruentatus* from Florida. A) Adult female tail. B) Egg. C) Molting of juvenile to adult. Bar = 50 μm.

SYSTEMATICS

Teratorhabditis palmarum n. sp.
(Figs. 1–7)

Description

Female: Measurements of holotype (female in glycerin), paratypes from Trinidad cocoon culture (n = 20), and female specimens from Ecuador, Colombia, and Florida in Table 1. Body straight to slightly curved ventrally after fixation (Fig. 1C). Cuticle with distinct plaques arranged in transverse rows from anterior end of body to anterior third of procorpus where there is an abrupt change of cuticular pattern posteriorly to alternating small and large punctations arranged in transverse rows around the body (Figs. 1A, 3C). Spicate tail-terminus lacks punctations. Lateral field distinct with two lines, 3 μm apart at midbody and terminating at vulva.

Six lips of uniform shape, each with one papilla and a short seta. Lip margins strongly cuticularized, refractive (Figs. 1A; 3A, B). En face view with six distinct indentations (Fig. 1B). Amphids not observed. Metarhabdions usually isomorphic, three or four small teeth in the metastom. Telorhabdions in the form of small dots. Esophageal collar starting at base of mesostom (Figs. 1A; 3A, B).

Procorpus 73 ± 5 μm (62–80) long, basal bulb 43 ± 2 μm (40–46) long and 32 ± 2 μm (29–35) wide (paratypes; n = 20). Valvular apparatus prominent with fringed bulb flaps, haustrulum prominent. Excretory pore usually obscure, 216 ± 10 μm (204–231) (paratypes; n = 10) from ante-

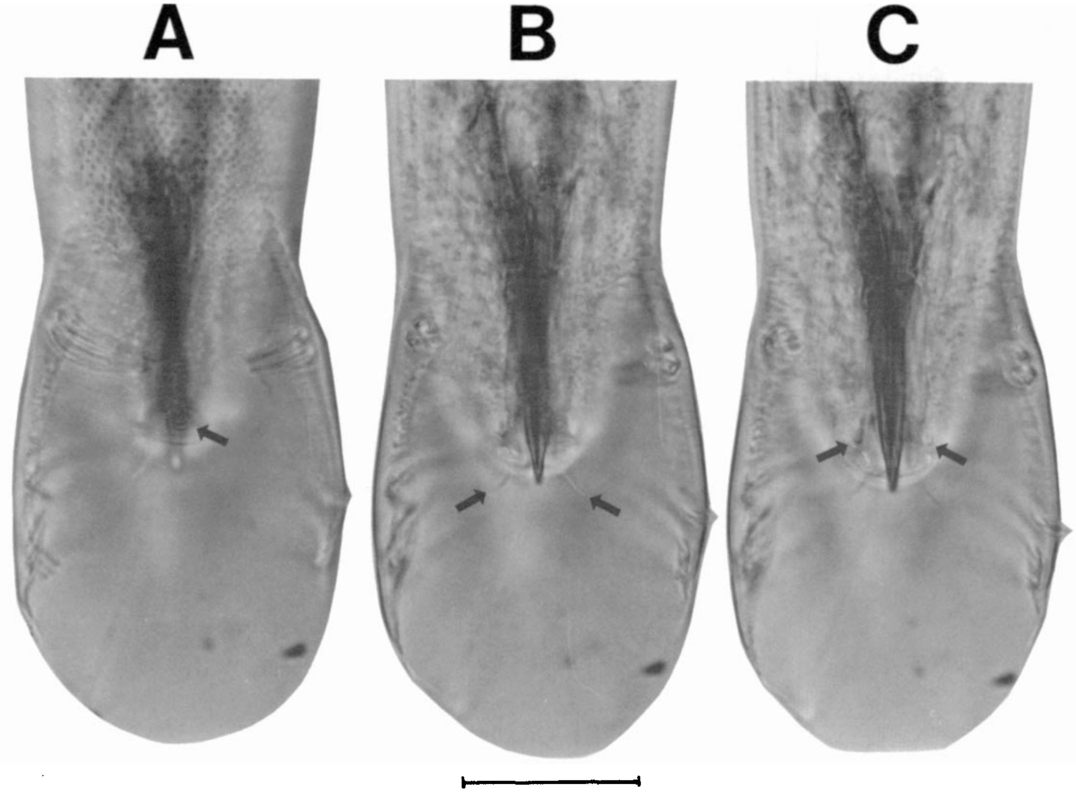

FIG. 5. Photomicrographs of male tail and cloacal region of *Teratorhabditis palmarum* n. sp. from *Rhynchophorus cruentatus* from Florida. A) Single preanal median papilla on protuberance (arrow). B) Two postanal subventral setae (arrows). C) Two preanal subventral papillae (arrows). Bar = 20 μm.

rior end, located between posterior third of isthmus and base of postcorpus. Hemizonid immediately anterior to excretory pore. Nerve ring position ranging from middle to posterior portion of isthmus (Fig. 1A).

Single, anteriorly directed ovary, reflexed dorsally (Fig. 1C); reflexed part 61 ± 4% (49–68%) of outstretched part of ovary (paratypes; n = 20). Vulval lips protuberant. Remains of copulatory cement commonly observed around vulval region (Fig. 4A). Vagina thick-walled, short; strong muscles acting as sphincter immediately anterior to short uterus. Spermatheca not clearly defined. Uterus usually with 1–3 eggs, occasionally up to five eggs. Distance between vulva and anus slightly greater than tail length. Tail rounded, spicate, with sharply pointed spine (Figs. 1D, E; 4A; 7A). Cuticular punctation ending before spine. Phasmids greater than 10 μm anterior to anus.

Male: Measurements of allotype (male in glycerin), paratypes from Trinidad cocoon culture (n = 20), and male specimens from Ecuador, Colombia, and Florida in Table 2. Similar to female in general appearance, but usually shorter and narrower (Fig. 2A). Single testis 504 ± 78 μm (325–652) long (paratypes; n = 20), dorsally reflexed for 16–35% of its length. Single median precloacal protuberance with papilla (Figs. 2C, D; 5A; 6B) and cement duct (Fig. 2C), two preanal subventral papillae, and a pair of postanal subventral setae (Figs. 2D; 5B, C). Spicules mostly linear (Figs. 2C, D; 3G–I); globular heads offset and curved laterally (Figs. 2D, 7B); spicules completely fused at distal ends and connected dorsally for 50% of the spicule length (Fig. 7B); gubernaculum linear (Figs. 2C, 6B, 7B). Bursa peloderan, open with crenated margins (Figs. 2C, D; 5A–C; 6A, C). Ten bursal rays in arrangement of 2, 5, and 3 pairs with variable width and shape (Figs. 2C, D; 6A, C);

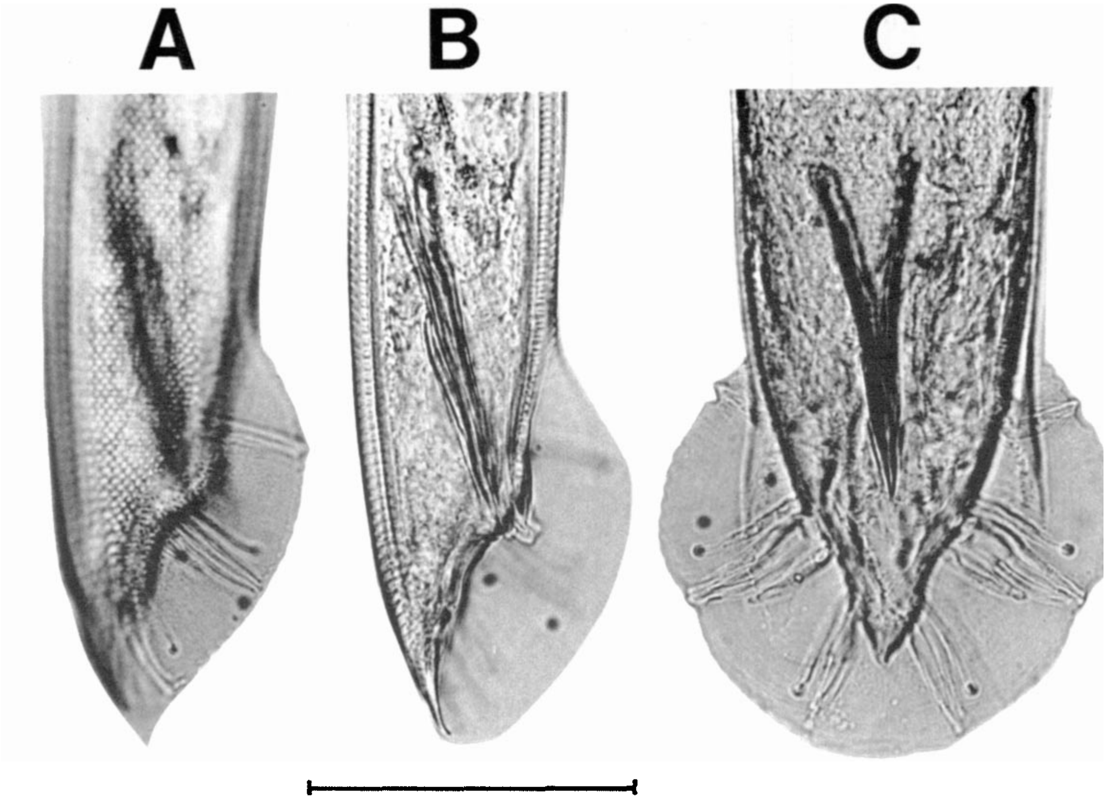

FIG. 6. Photomicrographs of the male tail of *Teratorhabditis palmarum* n. sp. A, B) Lateral view of specimens from Trinidad from *Rhynchophorus palmarum.* C) Ventral view of specimens from Florida from *Rhynchophorus cruentatus.* Bar = 50 μm.

all bursal rays except numbers 3, 7, and 8 (numbered consecutively starting from anterior bursal fringe) extend to the bursal margin (Figs. 6A, C).

Dauer juvenile: (n = 30) from R. palmarum from Trinidad (Fig. 2B): L = 623 ± 32 μm (549–713); a = 23.2 ± 1.7 (20.3–27.5); b = 3.8 ± 0.1 (3.5–4.4); c = 9.8 ± 0.7 (8.7–12.5); c′ = 4.2 ± 0.4 (3.3–5.4); stoma 19 ± 1 μm (18–20); excretory pore 126 ± 6 μm (108–140) from anterior end; distance of primordium from anterior end 155 ± 15 μm (128-185); primordium length 35 ± 12 μm (17–52); body width 27 ± 2 μm (22–30); tail 63 ± 4 μm (54–71). Dauer juveniles in the palm weevil have slightly offset head, distinct excretory pore, and conoid tail with a pointed terminus. All propagative stages have conoid tails.

Egg: Cuticular surface of eggs sculptured (Figs. 1F, G; 4B) in cross-section with up to 12 ridges (Fig. 1H, I).

Type host and locality

Cocal plantation, Manzanilla, Trinidad, West Indies; Cocoon of *R. palmarum* from the petiole of a red-ring diseased coconut palm.

Insect host affiliation

Dauer juveniles of *T. palmarum* associated internally with *R. palmarum,* from red-ring diseased coconut and oil palms. Dauer juveniles also extracted from the inside of *R. cruentatus* from infested cabbage palmettos.

Geographic distribution

Colombia, Ecuador, Tobago (King's Bay), Trinidad, United States (FL).

Type specimens

Holotype (female) and allotype (male) deposited in the USDA Nematode Collec-

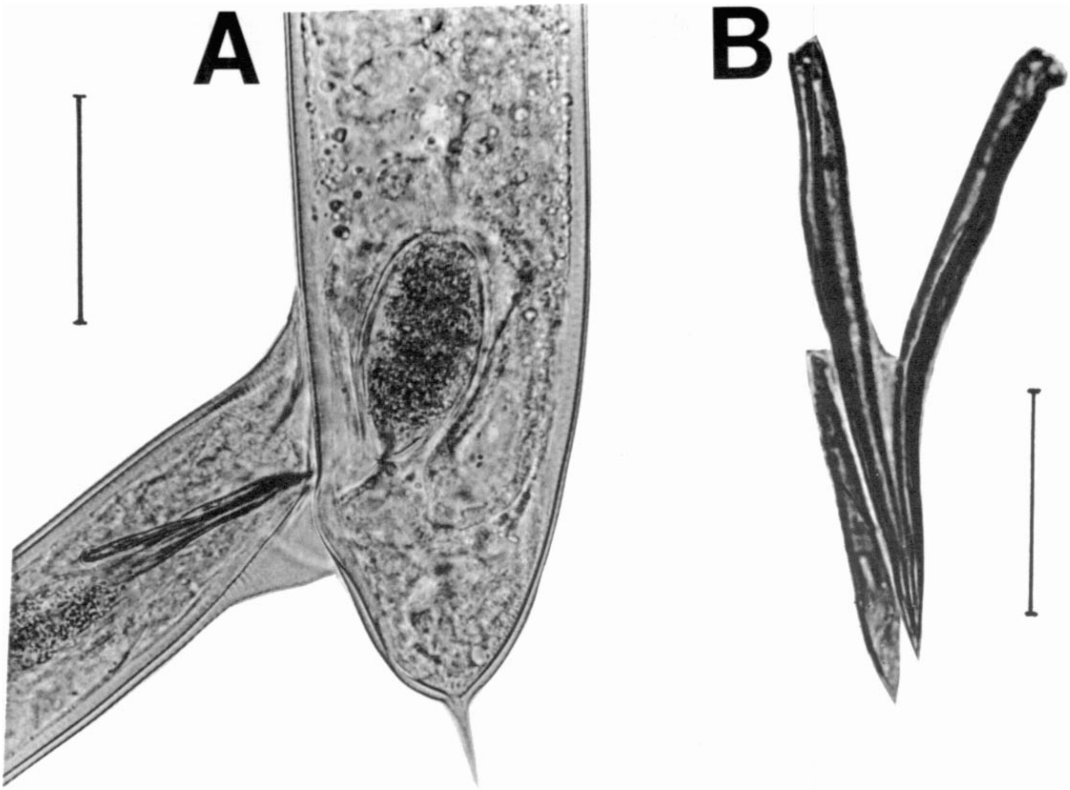

FIG. 7. Photomicrographs of *Teratorhabditis palmarum* n. sp. cultured from *Rhynchophorus cruentatus* from Florida. A) Typical antiparallel copulation position (bar = 50 μm). B) Dorsal view of fused spicules. Bar = 20 μm.

tion (USDANC) at Beltsville, Maryland, USA. Paratypes (four females, four males each location) deposited at USDANC, the Florida Nematode Collection, Gainesville, Florida, USA; University of California Nematode Collection (UCNC), Davis, California, USA; Department of Nematology, Agricultural University, Wageningen, The Netherlands. All type material from GPDA cultures started with nematodes from palm weevil cocoons from Cocal Plantation, Manzanilla, Trinidad.

Diagnosis and relationships

Anderson (1) emended the diagnosis of the genus *Teratorhabditis* (Osche, 1952) Dougherty, 1953, described *T. stiannula,* and listed six valid species. Andrassy (2,3) further emended the generic diagnosis, synonomized *T. vivipara* Gagarin 1977 with *Pelodera punctata* (Cobb, 1914) Dougherty, 1955 and considered *T. boettgeri* (Meyl, 1953) Dougherty, 1955 as a *species inquirenda.* He presented a key for the four remaining species in the genus: *T. dentifera* (Völk, 1950) Dougherty, 1953; *T. stiannula* Anderson, 1979; *T. mariannae* Farkas, 1973; and *T. rovinjensis* (Sudhaus, 1974) Andrassy, 1983.

Females of *T. palmarum* have a hemispherical spicate tail and differ from *T. dentifera* and *T. stiannula* which both possess conoid-attenuated tails. Males of both *T. dentifera* and *T. stiannula* have a 2 + 4 + 1 + 3 bursal ray arrangement compared with *T. palmarum* with a 2 + 5 + 3 arrangement. *Teratorhabditis rovinjensis* females have a c-ratio of 18.7 (12.7–25.7) (10) compared with *T. palmarum* paratypes with a c-ratio of 48.3 (37.0–60.7). Males of *T. rovinjensis* have a 2 + 1 + 5 + 2 bursal ray arrangement and no preanal protu-

TABLE 1. Measurements and ratios of females of *Teratorhabditis palmarum* n. sp. from palm weevils from four locations.†

	Cocoon host			Adult insect host	
	R. palmarum Coconut palm Trinidad		*R. palmarum* Coconut palm Ecuador	*R. palmarum* Oil palm Colombia	*R. cruentatus* *Sabal palmetto* Florida
	Paratypes (20)	Holotype (1)	(2)	(10)	(15)‡
L (μm)	1,230 ± 86 (1,080–1,397)	1,216	994 ± 65 (948–1,040)	1,136 ± 48 (1,049–1,199)	1,164 ± 81 (997–1,364)
a	20.1 ± 1.1 (17.6–22.1)	20.2	19.4 ± 1.3 (18.5–20.3)	21.6 ± 1.2 (19.8–23.0)	19.7 ± 1.4 (17.8–23.1)
b	5.1 ± 0.4 (4.4–6.0)	5.1	3.8 ± 0.1 (3.7–3.9)	3.7 ± 0.1 (3.6–4.0)	4.6 ± 1.4 (4.2–5.3)
c	48.3 ± 5.3 (37.0–60.7)	43.4	55.5 ± 8.0 (49.8–61.1)	33.3 ± 3.5 (26.5–38.6)	39.0 ± 3.1 (35.4–44.2)
c′	1.0 ± 0.1 (0.9–1.3)	1.1	0.9 ± 0.1 (0.8–0.8)	1.4 ± 0.1 (1.2–1.6)	1.2 ± 0.1 (1.0–1.4)
V	95.2 ± 0.4 (94.5–96.0)	95.0	94.8 ± 0.4 (94.5–96.0)	93.3 ± 0.3 (92.8–93.9)	93.8 ± 0.4 (93.0–94.5)
Greatest body width (μm)	61 ± 5 (53–68)	60	51 ± 0 (51–51)	52 ± 2 (50–55)	59 ± 4 (52–65)
Promesostom length (μm)	21 ± 1 (21–22)	21	23 ± 1 (22–23)	22 ± 1 (20–23)	22 ± 1 (20–24)
Prostom width (μm)	5 ± 1 (5–6)	5	5 ± 0 (5–5)	6 ± 1 (6–7)	5 ± 1 (5–6)
Esophagus length (μm)	236 ± 8 (221–248)	237	258 ± 7 (253–263)	299 ± 12 (279–314)	250 ± 12 (225–268)
V–anus distance (μm)	33 ± 3 (28–39)	32	34 ± 1 (33–35)	41 ± 3 (36–45)	41 ± 5 (35–55)
Tail length (μm)	26 ± 3 (21–31)	28	18 ± 1 (17–19)	35 ± 4 (29–44)	30 ± 2 (27–33)
Anal body width (μm)	23 ± 2 (20–25)	24	20 ± 0 (20–20)	24 ± 3 (20–27)	24 ± 2 (20–27)

Measurements and ratios are mean ± standard deviation (range).
† Nematodes were isolated from xenic cultures started with juveniles from adult weevils or cocoons.
‡ Measurements in 4% formalin; all others in glycerin.

berance, whereas *T. palmarum* has a 2 + 5 + 3 bursal ray arrangement and a preanal protuberance. The spicules of the males of *T. rovinjensis* are fused for about 35–40% of their length, whereas those in *T. palmarum* are fused completely at the distal ends and connected dorsally for 50% of the spicule length. *Teratorhabditis palmarum* differs from *T. mariannae* by its uniform lip shape and by the c-ratio of 48.3 (37.0–60.7) vs. lip shape not uniform and a c-ratio of 22–28 in *T. mariannae. Teratorhabditis palmarum* males can be distinguished from *T. mariannae* by the extent of fusion of the spicules (50% vs. 75% of spicule length, respectively) and by the arrangement of the bursal rays (2 + 5 + 3 vs. 2 + 5 + 2, respectively). The unusual cuticular sculpturing of eggs of *T. palmarum* separates it from *T. rovinjensis,* but more information is needed on the sculpturing of eggs of other species.

DISCUSSION

In Trinidad, 82% of cocoons of *R. palmarum* (n = 76) examined contained all stages of *T. palmarum* (4). Fifty-three percent of newly emerged females (n = 30) and 71% of newly emerged male palm weevils (n = 31) in Trinidad were infested internally with dauer juveniles of *T. palmarum* (4). Most newly emerged adult weevils

TABLE 2. Measurements and ratios of males of *Teratorhabditis palmarum* n. sp. from palm weevils from four locations.†

	Cocoon host			Adult insect host	
	R. palmarum Coconut palm Trinidad		*R. palmarum* Coconut palm Ecuador	*R. palmarum* Oil palm Colombia	*R. cruentatus* *Sabal palmetto* Florida
	Paratypes (20)	Allotype (1)	(3)	(10)	(10)‡
L (μm)	923 ± 80 (723–1,086)	830	796 ± 48 (762–851)	993 ± 71 (892–1,093)	1,001 ± 88 (827–1,093)
a	18.8 ± 1.7 (15.9–22.9)	16.6	20.2 ± 2.2 (18.9–22.8)	20.7 ± 1.8 (17.4–23.3)	18.2 ± 1.5 (15.6–20.9)
b	4.6 ± 0.4 (4.1–5.7)	4.3	3.4 ± 0.2 (3.2–3.4)	3.8 ± 0.2 (3.6–4.1)	4.6 ± 0.4 (3.9–5.5)
c	27.1 ± 4.1 (19.5–34.9)	24.4	24.4 ± 0.6 (23.8–25.0)	29.2 ± 2.8 (26.2–34.9)	25.4 ± 3.5 (20.6–33.3)
c	1.1 ± 0.1 (0.9–1.4)	1.4	1.3 ± 0.2 (1.2–1.5)	1.2 ± 0.1 (1.1–1.6)	1.2 ± 0.1 (1.1–1.4)
Spicule length (μm)	56 ± 3 (53–61)	56	55 ± 5 (51–61)	63 ± 2 (59–65)	64 ± 5 (55–67)
Gubernaculum length (μm)	29 ± 2 (26–31)	29	29 ± 3 (25–31)	31 ± 2 (28–35)	34 ± 3 (30–38)
Greatest body width (μm)	49 ± 5 (38–56)	41	40 ± 6 (34–45)	48 ± 2 (45–51)	55 ± 3 (51–60)
Promesostom length (μm)	23 ± 1 (21–24)	21	21 ± 1 (20–22)	21 ± 1 (20–23)	20 ± 1 (18–22)
Prostom width (μm)	5 ± 1 (4–6)	5	6 ± 1 (5–6)	6 ± 1 (5–6)	5 ± 1 (4–5)
Esophagus length (μm)	197 ± 9 (174–210)	190	232 ± 10 (220–239)	261 ± 17 (226–286)	214 ± 11 (196–233)
Tail length (μm)	34 ± 4 (27–39)	39	33 ± 2 (31–35)	34 ± 4 (30–41)	40 ± 4 (32–45)
Anal body width (μm)	28 ± 3 (22–32)	27	24 ± 4 (20–28)	27 ± 2 (24–31)	31 ± 3 (27–35)

Measurements and ratios are mean ± standard deviation (range).
† Nematodes were isolated from xenic cultures started with juveniles from adult weevils or cocoons.
‡ Measurements in 4% formalin; all others in glycerin.

were infested internally with less than 499 dauer juveniles of *T. palmarum* (4). A newly emerged adult of *R. palmarum* could also be infested with dauer juveniles of *Rhadinaphelenchus cocophilus, Diplogasteritus* sp., *Monochoides* sp., and *Bursaphelenchus* sp. (4).

Xenic cultures of *T. palmarum* were more easily established on GPDA with nematodes extracted from cocoons of *Rhynchophorus palmarum* from Trinidad than with juveniles isolated from the insect. However, *T. palmarum* juveniles extracted from *R. palmarum* from Colombia and from *R. cruentatus* from Florida were easily established. *Teratorhabditis palmarum* always exhibited antiparallel copulation (Fig. 7A) which lasted several hours and a cement was produced to seal and maintain the union. The life cycle on bacterial lawns was 5–6 days at 27 C. Dauer juveniles of *T. palmarum* were not observed to show a "winking" behavior.

Teratorhabditis palmarum is closely associated with *R. palmarum* and *R. cruentatus* and does not seem to adversely affect the palm weevils. It is highly probable that the biology of *T. palmarum* is synchronized with the life cycle of its weevil hosts to maximize the utilization of bacteria, yeasts, or other fungi growing on the dead and decaying palm host, while minimizing the risk of being left behind without a transport host.

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