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Meloidogyne haplanaria n. sp. (Nematoda: Meloidogynidae), a Root-knot Nematode Parasitizing Peanut in Texas

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Abstract: Meloidogyne haplanaria n. sp. is described and illustrated from specimens parasitizing peanut in Texas. The perineal pattern of the female is rounded to oval with a dorsal arch that is high and rounded except for striae near the vulva, which are low with rounded shoulders. The striae are distinctly forked in the lateral field, and punctations often occur as a small group near the tail tip and singly within the whole perineal pattern. The female stylet is 13–16 µm long and has broad, distinctly set-off knobs. The excretory pore opens 40–118 µm from the head, approximately halfway between the anterior end and the metacorpus. Males are 1.2–2.4 µm in length and have a high, wide head cap that slopes posteriorly. The labial disc and medial lips are partially fused to form an elongated lip structure. In some specimens the labial disk is distinctly separated from the lips by a groove. The stylet is 17–22 µm long and has wide knobs that are rounded and distinctly set off from the shaft. Mean second-stage juvenile length is 419 µm. The head region is not annulated, and the large labial disc and crescent-shaped medial lips are fused to form a dumbbell-shaped head cap. The stylet is 9–12 µm long and has rounded, posteriorly sloping knobs. The slender tail, 58–74 µm long, has a distinct, inflated rectum and a slightly rounded tip. The hyaline tail terminus is 11–16 µm long. The isozyme phenotypes for esterase and malic dehydrogenase do not correspond to any other recognized *Meloidogyne* species. Tomato and peanut are good hosts; corn and wheat are very poor hosts; and cotton, tobacco, pepper, and watermelon are nonhosts.

Key words: esterase phenotype, malate dehydrogenase phenotype, scanning electron microscopy, taxonomy.

Peanut (*Arachis hypogaea* L.) is a major crop in Texas with an annual production of 282,106 kg on 109,105 hectares. Collingsworth County, near the Oklahoma border, ranks eight in total production in Texas, producing 104,106 kg annually.

Root-knot nematodes are major pathogens of peanut in Texas and in other peanut production areas. *Meloidogyne arenaria* (Neal, 1889) Chitwood 1949 is the most common species attacking peanut in Texas (Wheeler and Starr, 1987). A population of *M. javanica* (Treub, 1885) Chitwood 1949 that attacks peanut was reported from one field in Texas in 1994 (Tomaszewski et al., 1994) and has now been found on peanut in three widely separated counties (Comanche, Frio, and Mason). The current known distribution of *M. hapla* Chitwood 1949 on peanut in Texas is limited to Collingsworth County. In 1993, a field of peanut in Collingsworth County was diagnosed with an infestation of root-knot nematodes. The field is located 6.4 km north of the intersection of Highway 204 and road FM 1547 (community of Quail) on the east side of the highway. Root-galling of infected plants was somewhat similar to that of *M. hapla,* with small galls and increased numbers of secondary roots. Examination of esterase and malate dehydrogenase phenotypes and reproduction on a standard set of host differentials, however, indicated that the population differed from previously described *Meloidogyne* species. Detailed morphological studies also supported the conclusion that this population was a new species. The common name "Texas peanut root-knot nematode" is suggested. Populations of this species have been found in other fields in Collingsworth County and in one field in Comanche County.

Materials and Methods

An isolate of *Meloidogyne haplanaria* n. sp. (NO. 93-13) was established by collecting egg masses from several different plants in the type locality and propagated on tomato (*Lycopersicon esculentum* Mill. cv. Rutgers) in a greenhouse at 22–28 °C. All nematode stages used in morphologic and morphometric studies were from these cultures.

Morphological studies: Males and second-stage juveniles (J2) were extracted from galled roots incubated in a moist chamber. Light microscopy (LM) observations were made from specimens that were killed by gentle heat, and fixed specimens were always compared to live specimens mounted in 0.9% saline. Females, males, and J2 were prepared for scanning electron microscopy (SEM) observations according to Eisenback (1985). The female perineal patterns were prepared for SEM according to Charchar and Eisenback, 2001. Eggs were measured in fresh tap water. All LM observations were made by using a bright field microscope and at least 100 specimens. Thirty randomly selected specimens were measured.

Isozyme patterns: Mature adult females were excised from infected tomato roots and individually macerated in 0.1 M phosphate extraction buffer (pH 7.4) with 20% sucrose, 2% Triton X-100, and 0.1% bromphenol tracking dye. Electrophoresis of macerates of individual females was accomplished on an automatic apparatus (PhastSystem, Pharmacia, Uppsula, Sweden) on 10% to 15% gradient polyacrylamide gels (Esbenshade and Triantaphyllou, 1986). Gels were first stained for malate dehydrogenase (MDH) activity and then counter-

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stained for nonspecific esterase activity (Esbenshade and Triantaphyllou, 1990).

Host range test: Eggs extracted from established cultures using 0.05% NaOCl (Hussey and Barker, 1973) were used as inoculum for a standardized host differential test (Hartman and Sasser, 1985). Maize (*Zea mays,* L.) and wheat (*Triticum aestivum* L.) were added to the standard set of differential plant species because they are widely grown in Collingsworth County. Seedlings of each test species were transplanted to 15-cm-diam. pots containing a sand-peat (6:1, V/V) potting medium. Each seedling was inoculated with 10,000 eggs of *M. haplanaria* n. sp. Additional plants were similarly inoculated with eggs of either *M. incognita* (Kofoid and White) Chitwood, 1949 race 3 (isolate no. 82-2) or with *M. arenaria* race 1 (isolate no. 82-4) for comparative purposes. All plants were maintained in a greenhouse with ambient temperatures of 26–34 °C. The plants were harvested at 8 weeks after inoculation and the roots washed in water to remove adhering soil. Roots were weighed and then treated with 1.0% NaOCl to extract eggs of the *Meloidogyne* species that were present.

Systematics

Meloidogyne haplanaria n. sp.
(Figs. 1–6)

Description

Holotype (female in glycerin): Body length including neck = 921.0 µm; body width 576.0 µm; neck length = 351.9 µm; stylet length = 14.5 µm; stylet knob height = 2.2 µm; stylet knob width = 4.9 µm; dorsal esophageal gland orifice to stylet base = 5.5 µm; excretory pore to head end = 69.9 µm. Females as in general description; perineal region not visible.

Female (n = 30, in 2% glutaraldehyde in 0.1 M cacodylic acid buffer pH 7.2 and perineal patterns in glycerin); measurements are listed in Table 1.

Body translucent white, variable in size, pear-shaped with short neck, posteriorly rounded, without tail protuberance. In SEM, stoma slit-like, located in ovoid prestoma, surrounded by pit-like openings of six inner labial sensilla. Labial disc fused with medial lips; dumbbell-shaped in face view. Medial lips crescent-shaped. Lateral lips large, triangular, separated from medial lips and head region. Head region not set off from regular body annules. In LM, cephalic framework distinct, hexaradiate; lateral sectors enlarged. Vestibule and extensions prominent. Cephalids and hemizonid not observed. Distance of excretory pore to head end variable in distance (30.9–118.2 µm); located in most specimens midway between anterior end and metacorpus; terminal excretory duct very long. Stylet long and robust; cone of same size as shaft, tip straight or slightly curved dorsally, widening gradually posteriorly; junction of cone and shaft uneven. Shaft cylindrical and same width throughout, or widening slightly near junction with knobs; knobs broad laterally, set off from shaft, distinctly separated from each other; knobs very slightly indented anteriorly. Distance between stylet base and dorsal esophageal gland orifice (DGO) moderately long (4.7–6.3 µm); gland orifice branched into three channels; dorsal gland ampulla large; subventral gland orifices branched, located posteriorly to enlarged triradiate lumen lining of metacorpus. Esophageal lumen lining with small rounded vesicles anterior to triradiate lumen lining. Esophageal glands large, trilobed; dorsal lobe largest, unicleate; two subventral nucleated lobes variable in size, shape, and position; located posterior to dorsal gland lobe. Esophago-intestinal cells two, small, rounded, nucleated, located between metacorpus and intestine. Two ovaries and six rectal glands as characteristic of genus.

Perineal patterns extremely rounded to oval-shaped. Dorsal arch high and rounded except for striae near vulva, which are low with rounded shoulders. Lateral field with distinctly forked striae. Ventral striae vary from wavy to coarse. Tail tip area well defined, free of striae; often with a few to several subcuticular punctations. Subcuticular punctations located randomly within the pattern area. Perivulval region not striated, rarely striae near lateral edges of vulva. Vulva located in depression, surrounded by wide cuticular ridge. Phasmidial ducts distinct, phasmid surface structure often obscured by striae in SEM. Anus distinct, surrounded by a thick cuticular layer.

Allotype (male in glycerin): Body length = 1,873 µm; body width = 38.2 µm; stylet length = 18.9 µm; stylet knob height = 3.3 µm; stylet knob width = 5.2 µm; dorsal esophageal gland orifice to stylet base = 5.8 µm; excretory pore to head end = 163.5 µm; tail length = 14.2 µm; gubernaculum length = 7.6 µm; testis length = 788.0 µm; a = 41.4 µm; c = 102.9 µm; and T = 44%. Male as in general description.

Males: (n = 30, in fresh tap water stored in refrigerator for at least 48 hours and killed by gentle heat) measurements are listed in Table 2.

Body translucent white, vermiform; body tapering anteriorly, bluntly rounded posteriorly; tail twisting through 90° in heat-killed specimens. Head cap high in lateral view, extending posteriorly onto distinctly set-off head region. Head region high in lateral view, tapering posteriorly, distinctly set off from body. Hexaradiate cephalic framework well sclerotized; vestibule and extension distinct. Prestoma large, hexagonal. Stoma slit-like, located in large, hexagonal prestomatal cavity, surrounded by pore-like openings of six inner labial sensilla. In SEM, labial disc rounded, very large; often separated from medial lips by a shallow groove. Medial lips very wide, outer margins crescent-shaped, sloping

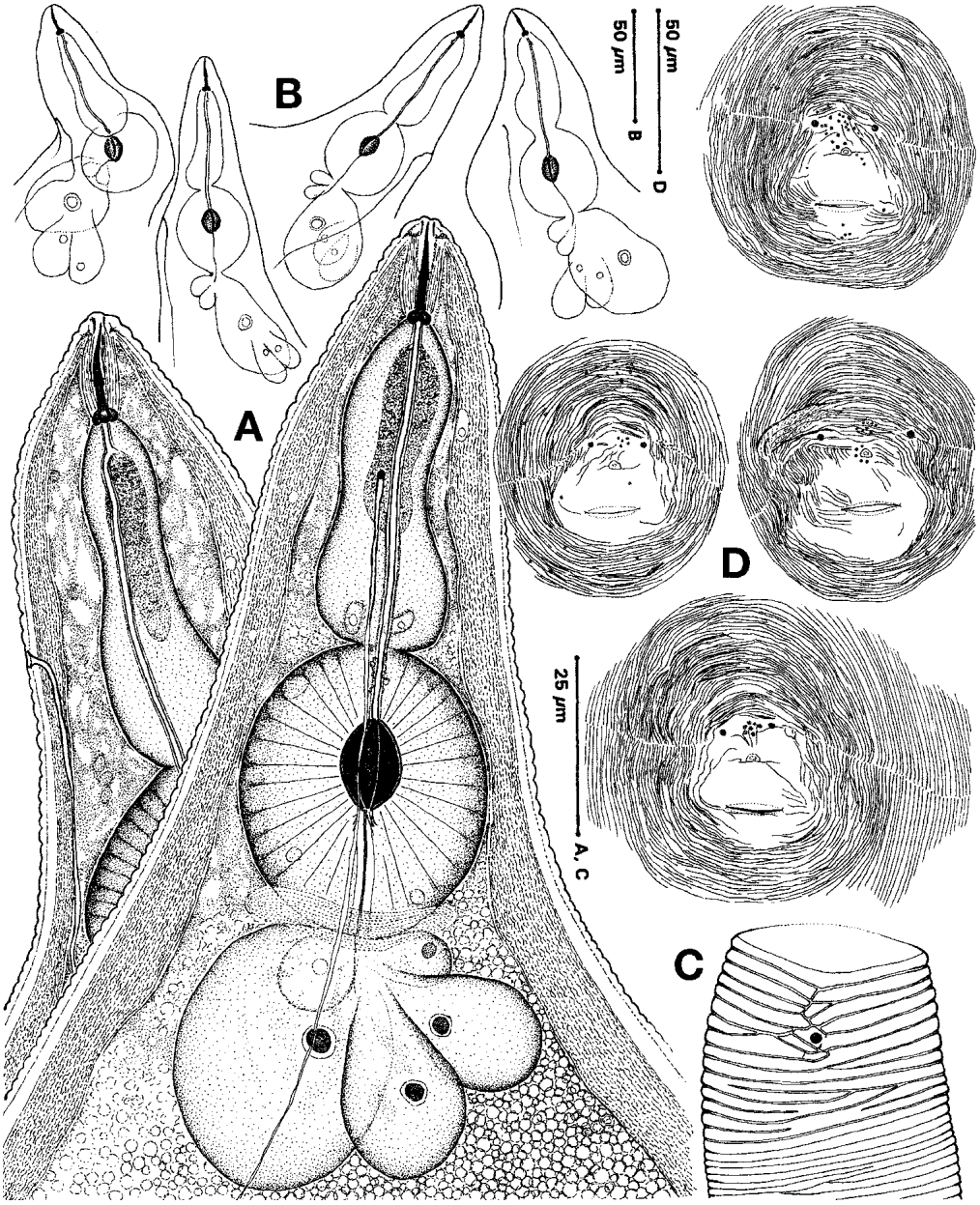

FIG. 1. Drawings of females of *Meloidogyne haplanaria* n. sp. A) Anterior end, lateral and ventral views, respectively. B) Outlines of anterior end and esophagus, lateral views. C) Annules in the region of the excretory-secretory pore, ventral view. D) Perineal patterns.

posteriorly. Labial disc and medial lips may or may not be fused to form elongate and wide lip structure extending posteriorly onto head region. Four cephalic sensilla marked on medial lips by shallow, elongated, ovoid, depressions. Amphidial apertures large, elongated, slit-like between labial disc and lateral sectors of head region. Lateral lips absent. Head region smooth, annulation absent. Body annules large, distinct. Lateral field with four incisures, two beginning near level of stylet knobs and two near level of metacorpus; lateral field areolated, encircling tail. Stylet robust, large; cone straight, pointed, gradually increasing in diameter posteriorly; opening located several micrometers from stylet tip; cone of same size as shaft. Shaft cylindrical, posterior end wider than anterior end. Knobs large, wide, rounded, set off from shaft. Dorsal esophageal gland orifice to stylet base variable in distance (3.7–6.4 µm), dorsal gland duct branched into three channels, gland ampulla indistinct. Procorpus indistinctly outlined, indistinctly outlined metacorpus elongated, oval-shaped with valve enlarged, triradiate cuticular lumen lining; subventral esophageal gland orifices branched, located posteriorly to metacorpus. Esophago-intestinal junction indistinct. Gland lobe variable in length, with indistinct nuclei rarely visible. Excretory pore distinct, variable in position (150.0–180.9 µm), terminal duct long. Hemi-

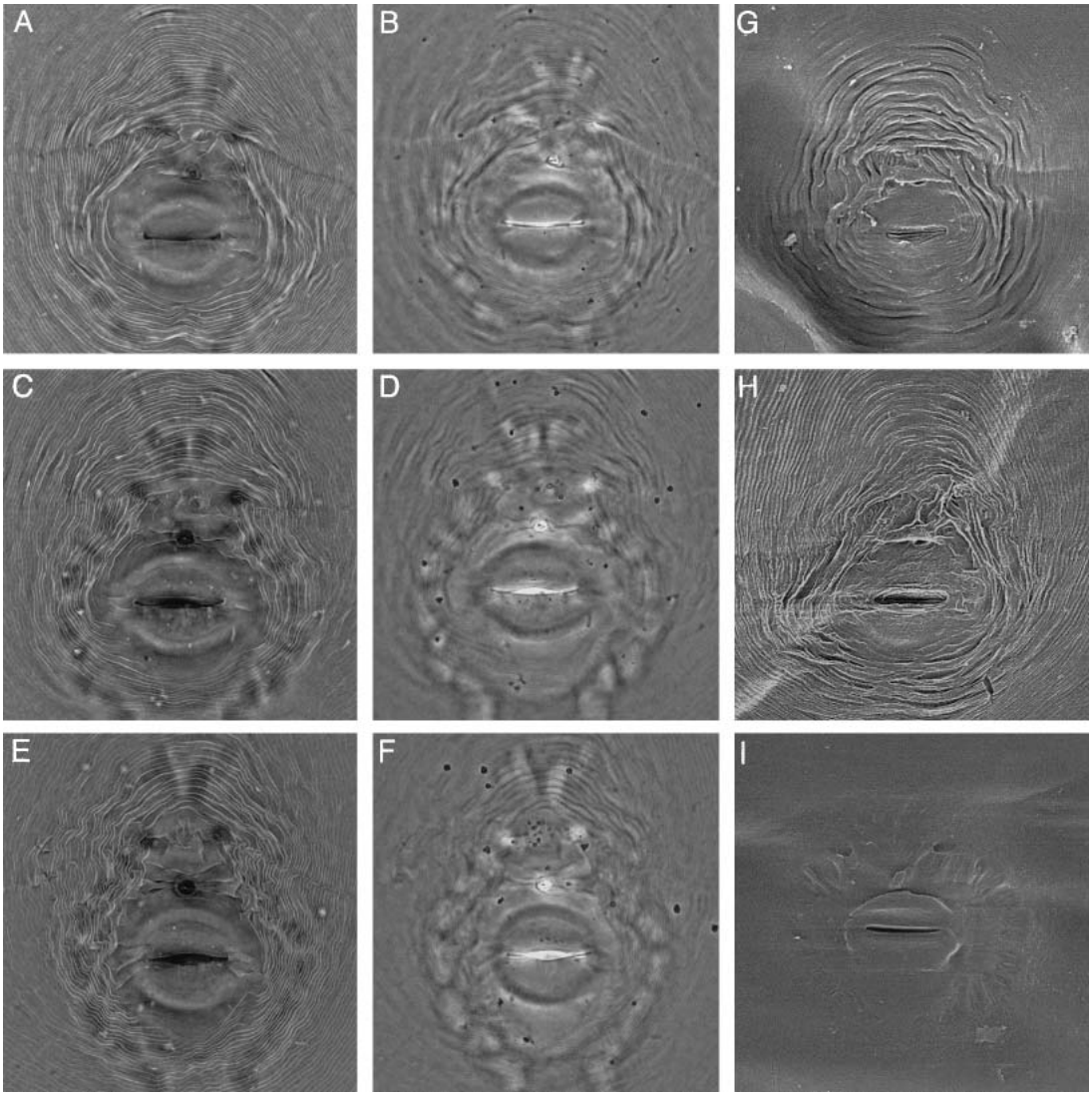

FIG. 2. Perineal patterns of females of *Meloidogyne haplanaria* n. sp. A, C, E) Light micrographs of the surface details. B, D, F) Light micrographs of the details below the surface of the pattern shown in the adjacent photograph. G–H) Scanning electron micrographs (SEM) of the outside surface. I) SEM of the internal surface.

zonid located anterior to excretory pore. Intestinal caecum short, extends anteriorly on dorsal side to base of metacorpus. Usually one testis, rarely two testes, outstretched, or reflexed anteriorly. Spicules long, slender, slightly arcuate with single tip, short head, wide vellum, and indistinct shaft. Gubernaculum distinct, crescent shaped. Tail short and rounded. Phasmids slit-like opening near level of cloaca.

Second-stage juveniles: (n = 30 J2 in fresh tap water killed by gentle heat) measurements are listed in Table 3.

Body translucent white, long, slender, tapering anteriorly but more so posteriorly. Body annules distinct, increase in size and become irregular in posterior tail region. Lateral field starts approximately at middle of procorpus and extends to near phasmids, with four incisures, areolated in some specimens. Stoma slit-like, located in oval-shaped prestomatal depression, surrounded by pore-like openings of six inner labial sensilla. Head cap high, narrower than head region. Labial disc elongated, round-shaped, completely fused with medial lips. Medial lips with outer margins crescent-shaped, smooth. Medial lips and labial disc dumbbell-shaped. Lateral lips distinct, lower than medial lips, margins crescent-shaped. Head region smooth without annulation. Amphidial apertures elongate, located between labial disc and lateral lips. Head region high, distinctly set off from body. Hexaradiate framework weakly sclerotized in LM, vestibule and vestibule extension distinct. Stylet moderately long (9.1–12.3 µm); but delicate, stylet cone sharply pointed, increases in width gradually posteriorly; shaft cylindrical, may widen slightly posteriorly; knobs rounded. Distance of dorsal esophageal gland orifice to stylet base moderately long (1.8–3.6 µm); orifice branched into three channels; ampulla poorly defined. Procorpus faintly outlined, meta-

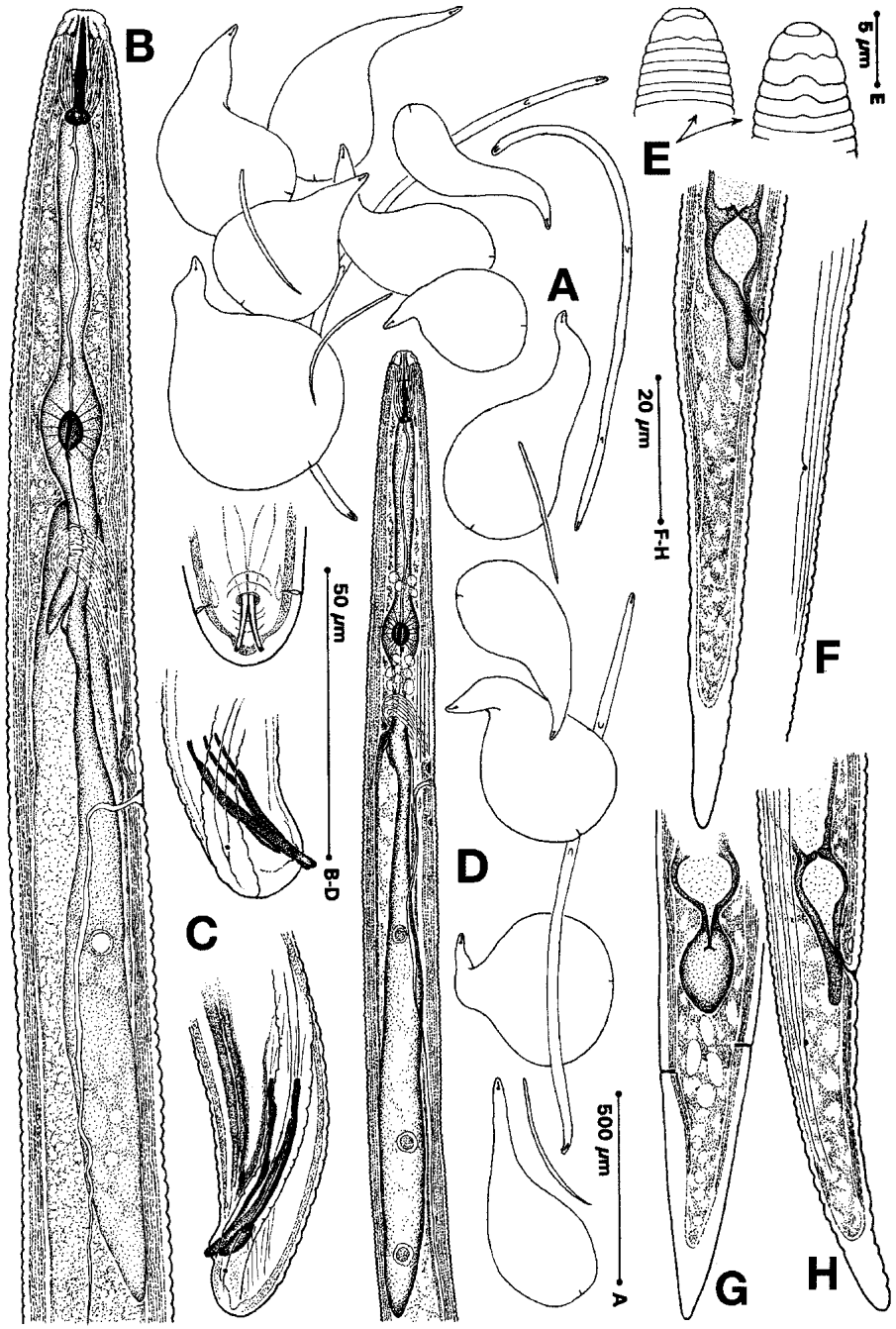

FIG. 3. Drawings of males, females, and second-stage juveniles of *Meloidogyne haplanaria* n. sp. A) Outlines of all three life stages. B) Anterior end of a male. C) Male tails, ventral and two lateral views, respectively. D) Anterior end of second-stage juvenile, lateral view. E) Anterior end of external morphology of second-stage juvenile, lateral and ventral view, respectively. F) Tail and lateral field of second-stage juvenile, lateral views. G) Tail of second-stage juvenile, ventral view. H) Tail of second-stage juvenile, sublateral view.

corpus ovoid with distinct valve; subventral esophageal gland orifices posterior to valve; ampulla distinct. Esophagus-intestinal junction indistinct, at the level of nerve ring. Esophageal gland lobe variable in length with three small nuclei of same size. Excretory pore distinct, variable in position (74.5–105.5 µm), terminal duct very long. Hemizonid distinct, located anteriorly to excretory pore. Tail slender, ending in slightly round tip; tail annules larger and irregular posteriorly. Hyaline tail end long, variable in size (10.9–16.4 µm). Rectal dilatation large. Phasmids small, indistinct, located at one edge of lateral field, below level of anus.

Eggs (n = 30 in fresh tap water): Length = 93–110 µm; (mean 98.8 µm + 4.45 standard, error of mean at 95% confidence interval); width = 51–57 µm (mean 53.4 µm + 2.99 standard); length/width ratio = 1.7–2.0 µm (mean 1.9 + 0.08 standard). Morphology similar to other *Meloidogyne* species.

Host test results (Table 4): Meloidogyne haplanaria n. sp. reproduced on tomato and peanut, but reproduction

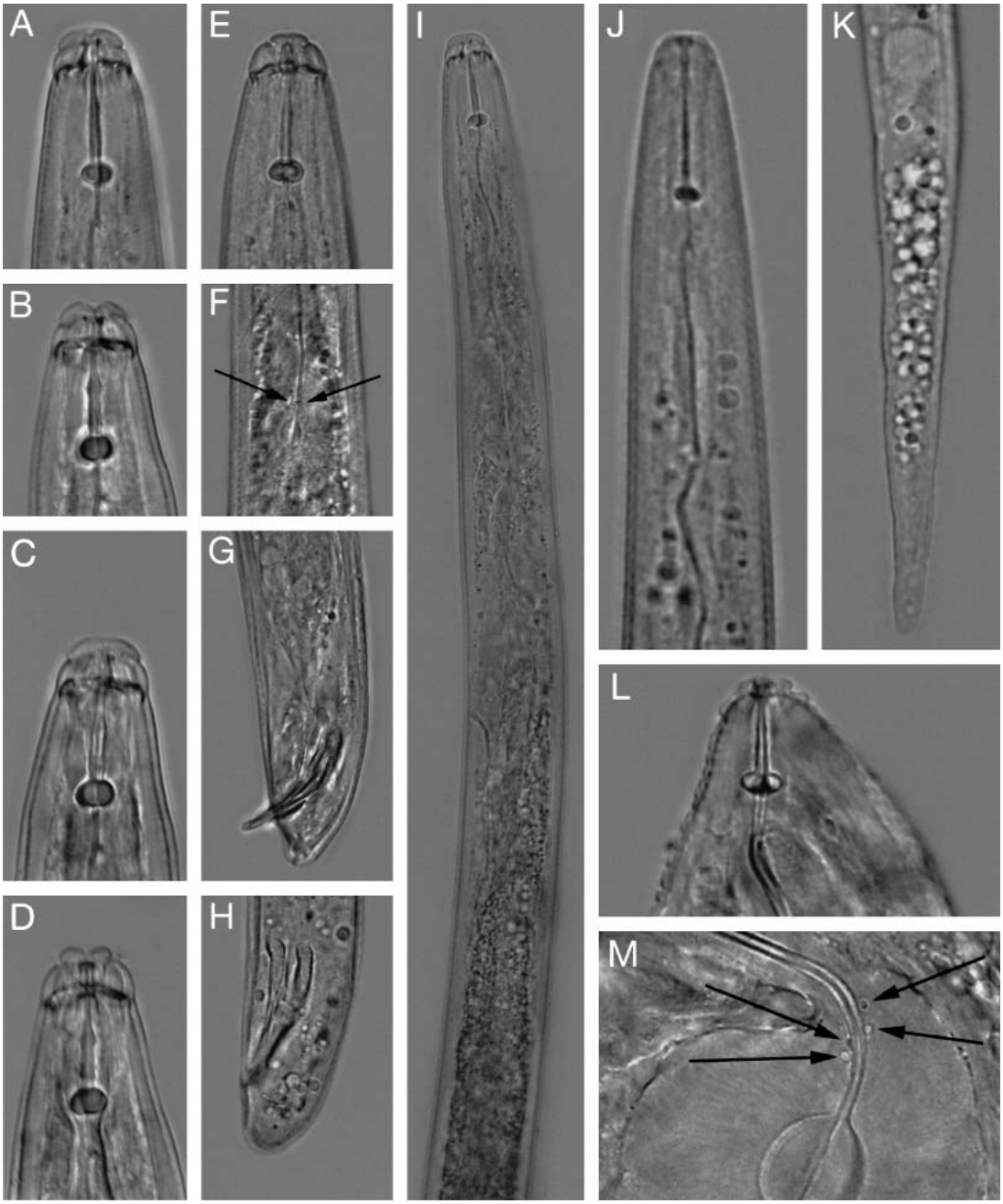

FIG. 4. Light micrographs of males, second-stage juveniles, and females of *Meloidogyne haplanaria* n. sp. A–C) Anterior end of the male (lateral views). D–E) Anterior end of the male (dorsal views). F) The metacorpus of the male showing vesicles near the lumen lining (arrows). G–H) LM of the tail of the male (lateral and nearly lateral views, respectively). I) LM of the anterior end of the male showing the indistinct outline of the esophagus. J) LM of the anterior end of the second-stage juvenile. K) LM of the tail of the second-stage juvenile. L) Anterior end of the female. M) Anterior portion of the metacorpus showing the vesicles near the lumen lining (arrows).

was low on maize and wheat. Cotton (*Gossypium hirsutum* L.), tobacco *Nicotiana tabacum* L.), pepper (*Capsicum frutescens* L.), and watermelon (*Citrullus vulgaris* Schard.) were nonhosts. The isolates of *M. incognita* and *M. arenaria* host-range test results were typical for the species and quite different from that of the new species.

Biochemical tests (Fig. 6): The esterase and MDH isozyme phenotypes for *M. hapla, M. incognita,* and *M. javanica* were identical to those characteristic of the species (Esbenshade and Triantaphyllou, 1990) and differed from that of the new species. The isozyme phenotypes of the new species did not correspond to any recognized *Meloidogyne* species. It was characterized by a single MDH isozyme (Rf = 0.44) and a single isozyme of esterase activity at Rf = 0.61. The esterase isozyme was further characterized by a low intensity of staining relative to that of other species and that of MDH. Use of

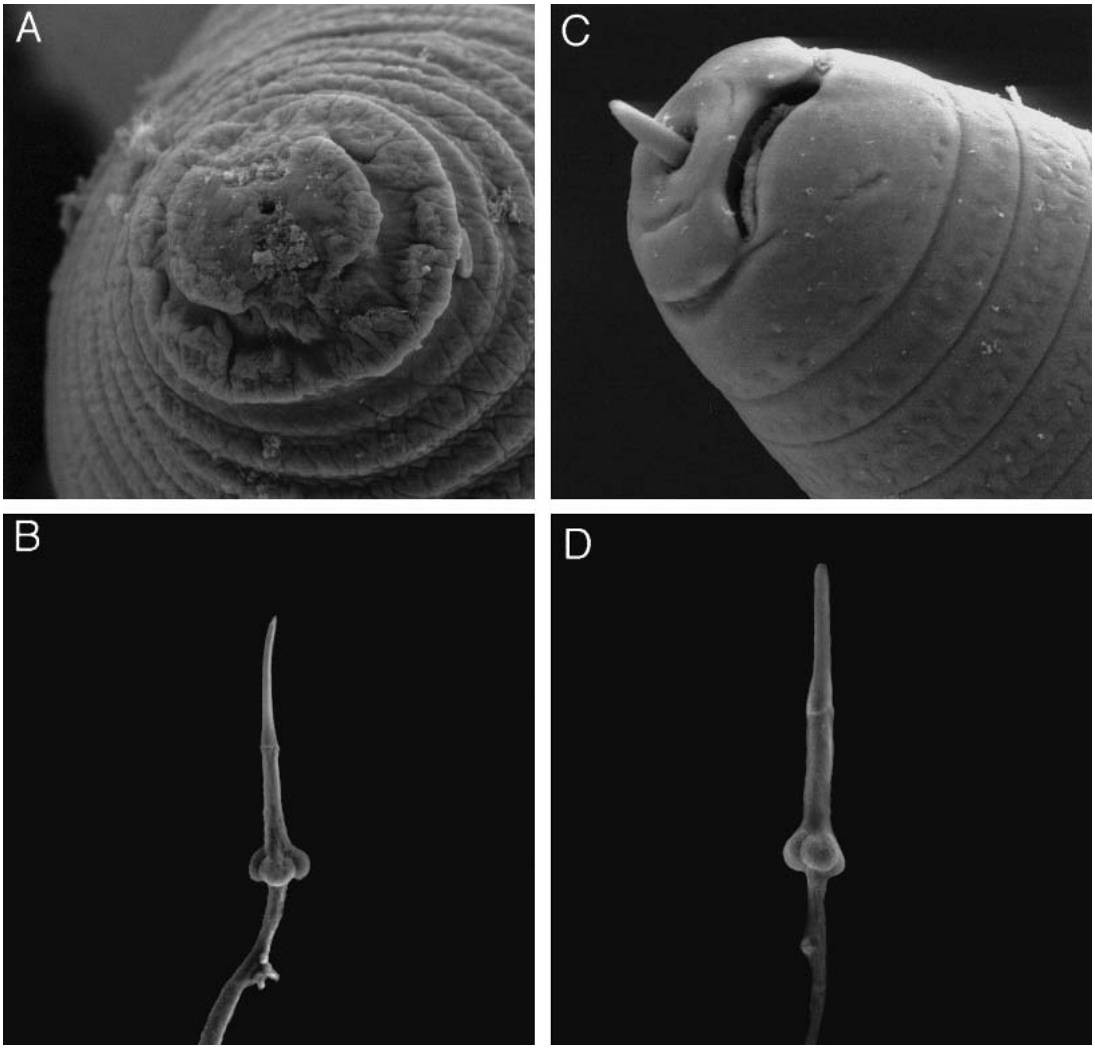

FIG. 5. Female and male of *Meloidogyne haplanaria* n. sp. A) Scanning electron micrographs of head of a female, face view. B) SEM of extracted stylet from a female. C) SEM of a male head, lateral view. D) SEM of extracted stylet from a male.

other esterase substrates did not result in increased intensity of the esterase isozyme (data not shown).

Molecular data (Powers, pers. commun.): Meloidogyne haplanaria n. sp. was sequenced for two mitochondrial markers from two individuals. First, at 18S, a relatively conserved marker, there was one nucleotide substitution difference from *M. arenaria, M. incognita,* and *M. javanica.* These three common species are identical in the 650-bp region of 18s. Fortunately, the one nucleotide affects a restriction site, making it a useful marker in

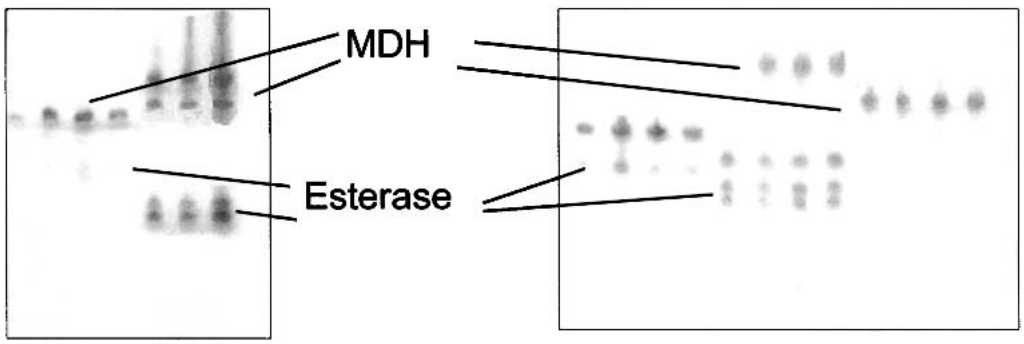

FIG. 6. Comparison of esterase and malate dehydrogenase (MDH) isozyme phenotypes of *Meloidogyne haplanaria* with those of other *Meloidogyne* species parasitic on peanut. A) *M. haplanaria* in lanes 1 to 4 and 8, and *M. arenaria* in lanes 5 to 7. B) *M. hapla* in lanes 1 to 4, *M. javanica* lanes 5 to 8, and *M. haplanaria* lanes 9 to 12.

TABLE 1. Measurements of 30 females of *Meloidogyne haplanaria* n. sp.

Character	Range	Mean	Standard error of mean	Std. deviation	Coef. of var. (%)
Linear (µm)					
Body length	675–1475	936.0	29.5	158.8	16.9
Body width	450–775	588.0	14.9	80.3	13.7
Neck length	125–725	294.0	22.2	119.4	40.6
Stylet length	12.9–16.2	14.3	0.4	0.9	8.2
Stylet knob height	1.8–2.6	2.4	0.1	0.5	9.5
Stylet knob width	3.7–5.4	4.7	0.2	0.9	9.7
DGO	4.7–6.3	5.4	0.2	0.8	11.2
Excretory pore to head end	30.9–118.2	69.1	4.5	24.3	35.1
Interphasmidial distance	18.6–25.5	18.8	0.7	3.7	9.9
Vulva length	16.4–25.5	23.3	0.8	4.3	8.4
Vulva-anus distance	17.3–28.9	19.6	0.8	4.5	24.3
Ratios					
a	1.0–2.2	1.6	0.1	0.3	17.6
Body length without neck/ body width	0.8–1.4	1.1	0.0	0.2	13.8

screening individuals to distinguish *M. haplanaria* n. sp. from these three species. Over these same 650 nucleotides, *M. hapla* differs by approximately a half a dozen sites and almost twice that by *M. chitwoodi* Golden et al., 1979.

Type host and locality

Roots of peanut were collected from Collingsworth, Texas, in a commercial field located 6.4 km north of the intersection of Highway 204 and road FM 1547 (community of Quail) on the east side of the highway.

TABLE 2. Measurements of 30 males of *Meloidogyne haplanaria* n. sp.

Character	Range	Mean	Standard error of mean	Std. deviation	Coef. of var. (%)
Linear (µm)					
Body length	1,350–2,425	1847	49.0	263.9	14.3
Body width	24.5–45.5	38.1	0.4	4.4	11.7
Tail length	7.0–16.8	10.8	2.7	2.5	23.3
Stylet length	16.6–21.8	18.1	0.3	1.6	8.1
Stylet knob height	2.7–3.5	3.2	0.1	0.5	8.3
Stylet knob width	4.5–6.3	5.5	0.1	0.8	8.3
DGO	3.7–6.4	5.2	0.2	0.9	21.5
Excretory pore to head end	150.0–180.9	137.4	6.2	33.3	8.2
Spicule length	36.4–41.8	38.5	0.6	3.3	9.1
Testis length	385–1284	830.0	259.0	30.1	20.7
Ratios					
a	32.8–54.6	43.8	4.8	4.8	10.9
c	545.6–159.7	102	21.9	21.3	18.2
Percentages					
T	30.0–56.2	44.2	5.2	5.8	11.8

TABLE 3. Measurements of 30 second-stage juveniles of *Meloidogyne haplanaria* n. sp.

Character	Range	Mean	Standard error of mean	Std. deviation	Coef. of var. (%)
Linear (µm)					
Body length	365–480	419.0	3.9	21.1	5.0
Body width	16.4–22.7	19.1	0.3	1.6	8.3
Tail length	58.2–73.6	65.0	2.0	10.7	18.1
Length of hyaline tail terminus	10.9–16.4	14.6	0.6	3.1	20.9
Excretory pore to head end	74.5–105.5	82.7	4.0	21.5	26.1
Stylet length	9.1–12.3	10.4	0.3	1.8	9.5
Stylet knob height	1.8–1.9	1.8	0.0	0.0	4.0
Stylet knob width	2.3–3.6	2.9	0.1	0.4	12.6
DGO	1.8–3.6	2.9	0.1	0.6	22.3
Ratios					
a	18.5–27.8	22.0	0.4	2.0	9.0
c	5.5–9.9	7.3	0.2	1.2	7.1

Type specimens

Holotype (female): Specimens were isolated from single egg mass of greenhouse cultures maintained on tomato cv. Rutgers. The original population was derived from type locality and host (U.S. Department of Agriculture Nematode Collection [USDANC], Beltsville, MD).

Allotype (male): Same data as holotype. USDANC, Beltsville, Maryland.

Paratypes (females, males, and J2): Same data as holotype. USDANC, University of California Davis. Nematode Collection (UCDNC), Davis California.

Diagnosis

Meloidogyne haplanaria n. sp. can be distinguished from the four most common species of root-knot nematodes (*M. arenaria, M. hapla, M. incognita,* and *M. javanica*) (Eisenback et al., 1981) by the unique form of

TABLE 4. Reproduction (egg/g root) of *Meloidogyne incognita* race 3, *M. arenaria* race 1, and *M. haplanaria* n. sp. on selected plant species.

Test plant	*M. haplanaria* n. sp.	*M. incognita*	*M. arenaria*
Tomato cv. Rutgers	4,100	22,200	24,000
Cotton cv. Rowden	0	7,500	0
Tobacco cv. NC 95	0	20	20
Pepper cv. California Wonder	200	1,200	20
Peanut cv. Florunner	4,300	70	10,700
Watermelon cv. Charleston Gray	0	1,460	10
Maize cv. Funk's G-90	0	330	600
Wheat cv. Tam 107	0	120	150

perineal pattern, shape, and morphology of head and stylet, shape and constitution of metacorpus, and position of excretory pore in females; and shape and morphology of head and stylet in males. The perineal pattern is similar to *M. arenaria* in overall shape but similar to *M. hapla* because of the punctations that are present in the tail tip area.

Meloidogyne haplanaria n. sp. can be easily diagnosed and separated from the four most common root-knot nematodes by the inability to infect cotton, tobacco, pepper, and watermelon. Pepper, watermelon, and cotton are good hosts for *M. incognita;* watermelon is also a good host for *M. javanica;* pepper is a good host for *M. arenaria* and *M. hapla* (Hartman and Sasser, 1985) but not *M. haplanaria* n. sp. Peanut is good host for *M. arenaria* and *M. hapla,* as well as *M. haplanaria* n. sp.

Relationships

Meloidogyne haplanaria n. sp. is similar to *M. arenaria* in the shape of the perineal pattern, shape of the male head and stylet, and shape of the stylet of the female. Punctations in the tail tip region of the perineal pattern are similar to those of *M. hapla.*

The mitochondrial markers show that with standard-size variable marker, *M. haplanaria* n. sp. gives a 550-bp fragment. This is approximately the same size as in *M. hapla, M. chitwoodi, M. fallax, M. graminis* (Sledge and Golden, 1964) Whitehead, 1968, and *M. partityla* Kleynhands, 1986. *Meloidogyne arenaria* typically produces a 1-kb fragment, *M. incognita* and *M. javanica* 1.6 kb, and *M. mayaguensis* Rammah and Hirschmann, 1988 700 kb. At this sequence level, *M. haplanaria* n. sp. is distinct, loosely grouping with *M. mayaguensis* but not tightly associated with any of the above species (Powers, pers. comm.).

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