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Evaluation of Morphological Variability in *Meloidogyne arenaria*[1]

GEAN M. CLIFF[2] AND HEDWIG HIRSCHMANN[3]

Abstract: Seven populations, representing cytological race A (triploid, 3n = 51–56) and the two host races (infective and noninfective on peanut) of *Meloidogyne arenaria* were studied with light microscopy (LM) and scanning electron microscopy (SEM). Characteristics of root-knot nematodes, recently recommended as useful taxonomic traits, were reexamined among these populations, and their variability both within and between populations was ascertained. We found that stylet morphology of females and head and stylet morphologies of males and second-stage juveniles were the most reliable characters for identification. The two host races of *M. arenaria* could not be distinguished morphologically. Two of the populations could be separated consistently from the remainder but were not sufficiently divergent to be considered new species. These two variant populations were similar; neither produced males in culture, and they differed from the typical populations in female perineal patterns (LM) as well as in cephalic structure (SEM) and tail shape (LM) of second-stage juveniles. In morphometric studies, most characters of the variant populations differed significantly from those of the typical *M. arenaria.*

Key words: root-knot nematodes, cytological races, host races, morphometrics, taxonomy, scanning electron microscopy, light microscopy.

The economic importance of certain members of the genus *Meloidogyne* Goeldi as pathogens of crop plants has led to intensive studies in an effort to clarify their taxonomy and biology. A great deal of information has accumulated over the years, revealing the biological complexity of these nematodes (15). However, species identification is still difficult and confusing (17). Many of the morphological characters used in the past to distinguish species, such as perineal patterns, number of annulations on the head region and many body measurements, have been found to be variable and unreliable (9,10,12,20), especially in the four most common and economically important species, *M. incognita* (Kofoid and White) Chitwood, *M. javanica* (Treub) Chitwood, *M. arenaria* (Neal) Chitwood, and *M. hapla* Chitwood. Recent work (7,13) discourages species determinations on the basis of a few morphological characteristics and emphasizes consideration of many characters. Additional information on physiology, biochemistry, cytology, and mode of reproduction should also be considered for accurate species identification.

The scanning electron microscope (SEM) has recently become a useful tool in the taxonomy of *Meloidogyne* (1–6,14). The morphological characters revealed by SEM made it possible to distinguish the four common species, the two cytological races of *M. hapla,* and the chromosomal forms within one of the races of *M. hapla* (1–6). Six populations of *M. hapla* were examined, but only one population each of *M. incognita, M. javanica,* and *M. arenaria* was studied. The extent of variation of these SEM characters must be assessed comparing several populations of the same species before their value in species identification can be determined.

Our objectives were to examine populations of *M. arenaria* from different geographic regions using SEM and light microscopy (LM), record the variability of morphological characters within and between populations, and amend the description to facilitate identification of this species.

M. arenaria reproduces by obligatory mitotic parthenogenesis and consists of two cytological races, a common triploid race (3n = 51–56) and a rare diploid race (2n = 34–37) (18,19). In addition, two host races are recognized: race 1 which infects peanut (*Arachis hypogaea* L.) and race 2 which does not (16). Populations representing cytological race A and the two host races were

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[2] Research Associate, Department of Zoology, University of Toronto, Toronto, Ontario, Canada M5S 1A1.

[3] Professor, Department of Plant Pathology, North Carolina State University, Raleigh, NC 27695.

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TABLE 1. Populations of *Meloidogyne arenaria*, race A (triploid), examined.

Population no.	Origin	Number of chromosomes	Host race
54	Virginia	51–53	1*
56	North Carolina	52–53	2†
256	Colombia	53	1
413	Nigeria	53–54	1
480	North Carolina	54	2
E5	Guadeloupe	53	2
392	Colombia	54	2

* Reproduces on peanut.
† Does not reproduce on peanut.

compared to determine the extent of morphological variability within this species.

MATERIALS AND METHODS

Seven populations tentatively identified as *M. arenaria*, cytological race A (verification by A. C. Triantaphyllou), with representatives of the two host races were selected from the *Meloidogyne* culture collection maintained by the International *Meloidogyne* Project at North Carolina State University (Table 1). All populations exhibited typical *M. arenaria* esterase and superoxide dismutase patterns as determined by Esbenshade and Triantaphyllou (8). Stock cultures of these populations were established and maintained on tomato (*Lycopersicon esculentum* Mill. cv. Rutgers) in the greenhouse at 22–28 C. All life stages for morphological and morphometric studies were obtained from these greenhouse cultures.

Egg masses and females were hand picked from infected tomato roots. Second-stage juveniles (J2) were hatched from egg masses incubated in moist chambers. Washed, infected root-systems were incubated in moist chambers to obtain males; roots were rinsed periodically and males were collected from the washings.

Light microscopy: Eggs were fixed and mounted in 2% formalin. Males and J2 were fixed with TAF at 100 C and mounted in TAF. Females were fixed in 2% glutaraldehyde for 1 week at 7 C. The anterior portions of females, including the esophageal region, were removed with an eye knife and mounted in 2% glutaraldehyde. Perineal patterns were cut from fresh, unfixed females in 45% lactic acid and were mounted in glycerin.

Scanning electron microscopy: Males, J2, perineal patterns, and stylets were prepared according to previously described methods (2–5). Specimens were observed and photographed with an ETEC Autoscan scanning electron microscope operating at 20 kV or a JEOL T200 operating at 25 kV.

Morphometrics: Measurements of females, males, and J2 of typical and variant populations were compared using analysis of variance.

RESULTS

Five populations of *M. arenaria* cytological race A (54-Va, 56-NC, 256-Colombia, 413-Nigeria, 480-NC) were within the range of morphological variability typical for *M. arenaria*. The remaining two populations (E5-Guadeloupe, 392-Colombia) differed consistently from the typical *M. arenaria* in several characters including female perineal patterns, head morphology, and J2 tail shape. The differences, however, were considered insufficient to designate new species, thus the populations are considered morphological variants of cytological race A of *M. arenaria*. These two variant populations were morphologically similar, and neither produced males in culture.

Distinct morphological or morphometric differences were not found between the two host races.

Females

Measurements of females of typical and variant populations are compared in Table 2.

Typical populations (54-Va, 56-NC, 256-Colombia, 413-Nigeria, 480-NC) (Figs. 1A–C, E, F, 4A, B): Body creamy-white, pyriform with prominent neck, without tail protuberance. Body annules fine. Head region slightly set off, very small relative to total body. Labial disc rounded, raised above medial lips in lateral view (Fig. 1B). Medial lips not extending posteriorly over head region, rounded, set off from labial disc by shallow indentations in lateral view. Cephalic framework delicate; vestibule and vestibule extension distinct (Fig. 1A–C). Stylet robust, cone curved dorsally, gradually tapering to blunt tip anteriorly; shaft broad, cylindrical, gradually widens posteriorly near junction with stylet knobs

TABLE 2. Morphometric comparison of females of typical populations of *Meloidogyne arenaria* with those of variant populations.

Character (μm)	Typical populations (N = 150)	Variant populations (N = 30)	
	54-Va, 56-NC, 256-Colombia, 413-Nigeria, 480-NC (pooled) Mean ± SE (range)	E5-Guadeloupe Mean ± SE (range)	392-Colombia Mean ± SE (range)
Stylet length	15.1 ± 0.05 (13.1–16.7)	14.8 ± 0.08 (14.1–15.8)	15.1 ± 0.07 (14.2–15.9)
Stylet knob height	2.8 ± 0.02 (2.0–3.8)	2.3 ± 0.03 (1.9–2.7)	2.5 ± 0.03 (2.1–2.7)
Stylet knob width	4.7 ± 0.03 (3.8–5.5)	4.5 ± 0.04 (4.2–4.9)	4.9 ± 0.04 (4.4–5.3)
DGO	4.8 ± 0.06 (3.1–6.6)	4.0 ± 0.07 (3.2–4.9)	4.2 ± 0.06 (3.6–5.0)
Excretory pore to head end	42.2 ± 0.94 (17.8–80.1)	30.0 ± 1.70 (17.8–53.4)	29.7 ± 1.01 (17.8–40.1)

(Figs. 1A–C, E, F, 4A, B). Stylet knobs large, rounded to tear-drop shaped, gradually merging with shaft; in some populations knobs more set off from shaft (Fig. 1A–C, E, F). Distance from base of stylet to branched dorsal esophageal gland orifice (DGO) 3.1–6.6 μm. Ampulla of dorsal esophageal gland large. Procorpus irregular in outline, widens posteriorly; median bulb round to oval, muscular with prominent valve. Branched subventral gland orifices posterior to bulb valve. Esophageal glands with one large dorsal lobe and two smaller subventral lobes. Two small, rounded esophago–intestinal cells near junction of median bulb and intestine. Excretory pore variable in position, usually between level of DGO and base of median bulb.

Perineal patterns variable, many exhibit features typical for *M. arenaria* (Figs. 2A–E, 3A–D, 4D, E). Entire pattern rounded to ovoid with fine to coarse striae. Dorsal arch low, flattened with striae smooth or slightly wavy, continuous or broken, slightly bent toward tail tip at lateral line; may form shoulders on lateral portion of arch. Ventral striae smooth or slightly wavy, usually continuous, forked or discontinuous near lateral line. Distinct, slightly irregular lateral lines visible where dorsal and ventral striae meet. Phasmidial canals visible but no phasmid surface structure observed. Vulval margins usually smooth.

Patterns more variable in some populations than in others. Overall shape of pattern variable. In some patterns dorsal striae crenate or discontinuous forming a zig-zag arrangement on one side of the pattern. Ventral striae extend laterally to form a wing on both sides or one side of pattern (Fig. 3A). Some patterns reminiscent of *M. hapla* or *M. incognita*.

Variant populations (E5-Guadeloupe, 392-Colombia) (Figs. 1D, G, 2F, G, 3E, F, 4C): Most features typical of *M. arenaria*. Head region and stylet morphologies similar (Fig. 1D, G) but perineal patterns different (Figs. 2F, G, 3E, F). Dorsal arch usually high, rounded to squarish in shape. Occasionally, dorsal striae form shoulders in lateral regions of pattern. Lateral lines near tail tip often widely spaced, with few broken, irregular striae between lines (Figs. 2G, 3E, F). Anteriorly from tail tip lines become finer. Widened lateral lines near tail tip occasionally present in patterns from typical *M. arenaria* populations. Dorsal and ventral striae wavy, irregular or forked near lateral lines but usually smooth throughout remainder of pattern, rarely forming zigzag pattern.

Males

Measurements of the typical populations are presented in Table 3. Males were not found for either variant population.

Typical populations (54-Va, 56-NC, 256-Colombia, 413-Nigeria, 480-NC) (Figs. 5A–G, 6A–F, 7A–C): Body of variable length, usually slender, tapering to bluntly rounded ends, posterior region twisted through 90 degrees. Lateral field with four incisures, areolated throughout. Size of head region variable, usually short. Head cap smoothly rounded, variable in height but usually low in lateral view (Figs. 5A–C, 6A–D). Medial lips extend a short distance posteriorly onto head region. In SEM, head morphology remarkably consistent among populations (Fig. 7A–C). In face view, stoma slit-like, prestoma hexagonal with six inner labial

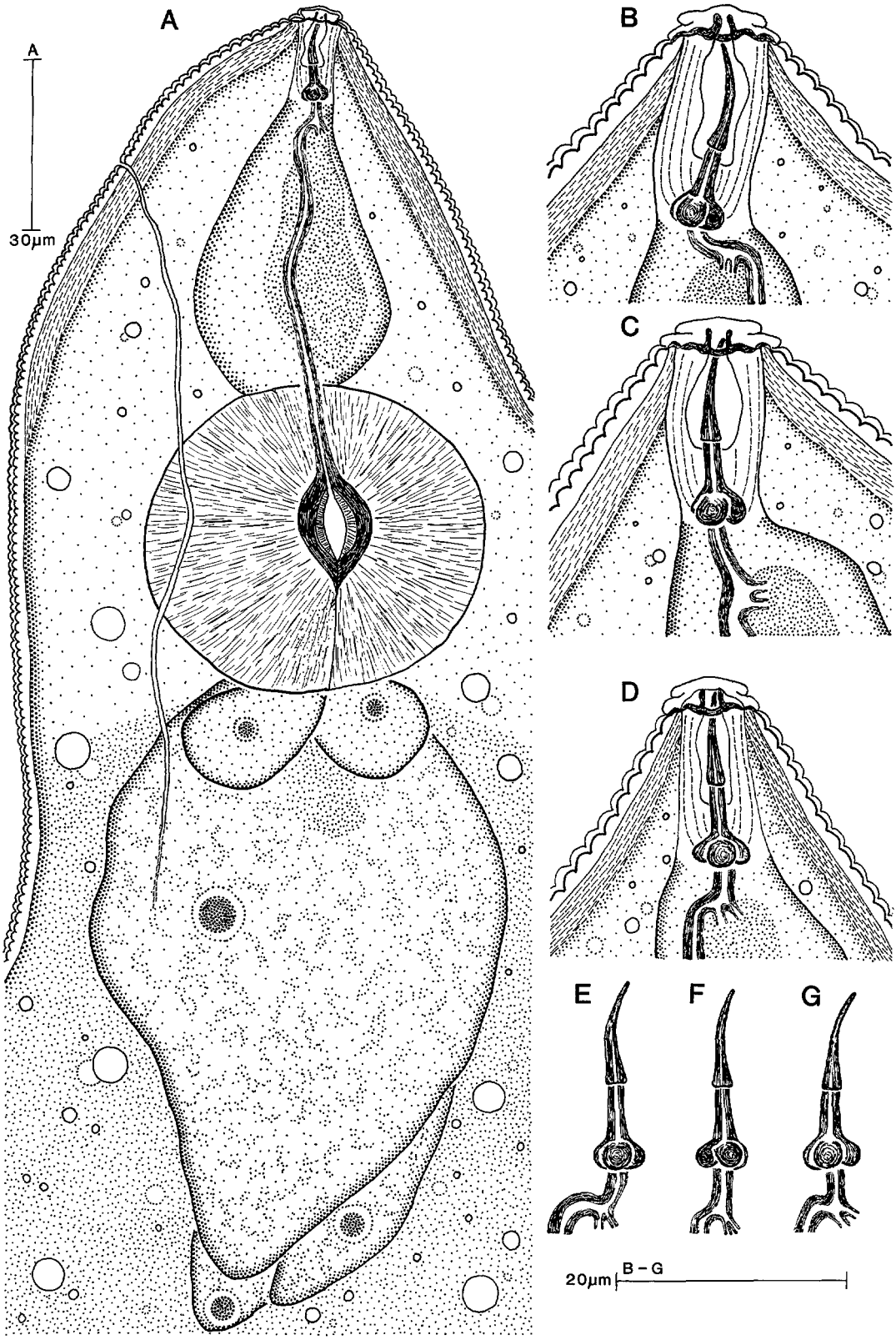

FIG. 1. Line drawings of females of *Meloidogyne arenaria*. A) Esophageal region (lateral). B–D) Cephalic region (lateral). E–G) Stylets (lateral). A–C, E, F) Typical populations. D) E5-Guadeloupe. G) 392-Colombia.

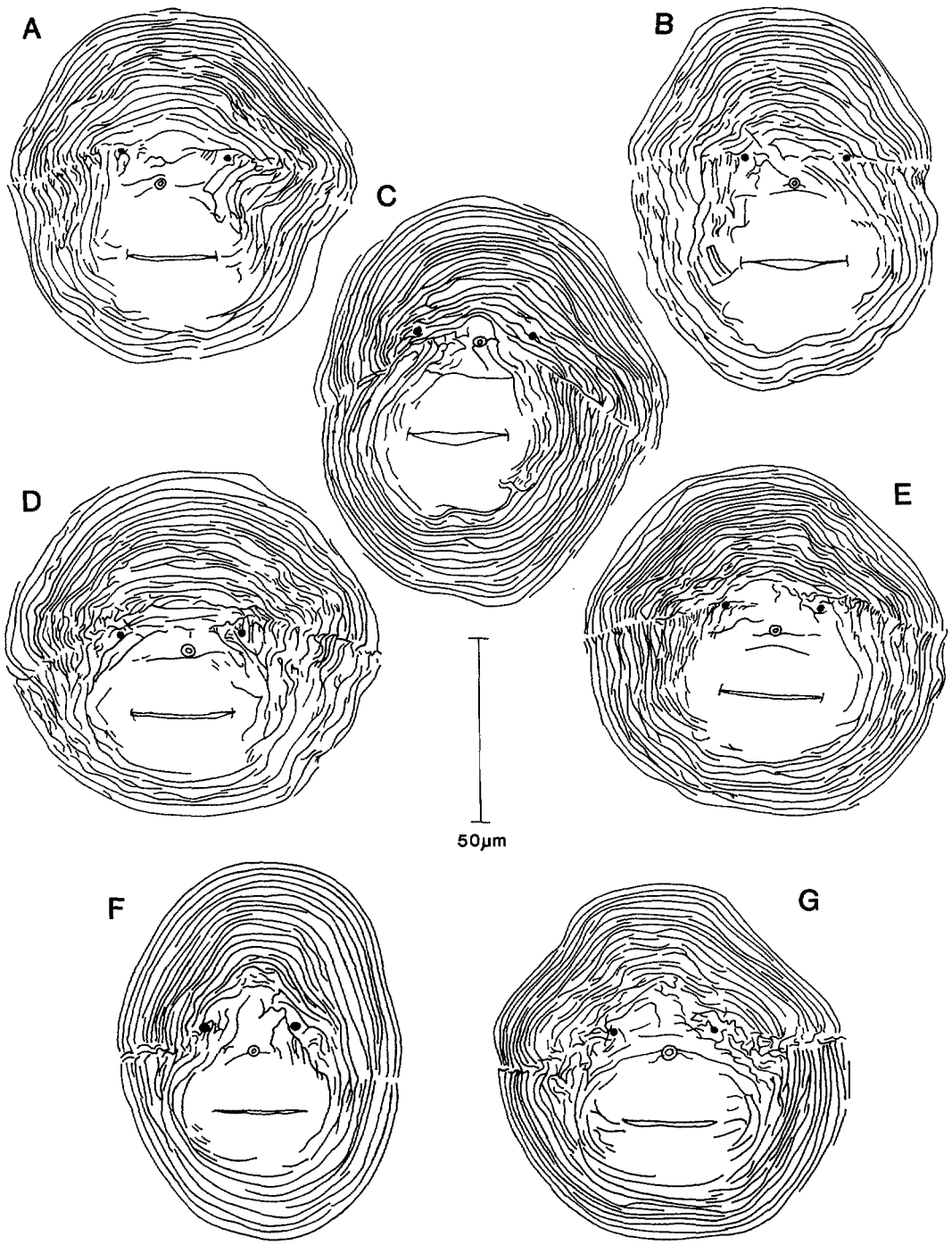

FIG. 2. Line drawings of perineal patterns of *Meloidogyne arenaria*. A–E) Typical populations. F) 392-Colombia. G) E5-Guadeloupe.

sensilla opening at edge onto labial disc (Fig. 7A, B). Labial disc more or less rounded, slightly raised above level of medial lips. Medial lips crescent shaped. Fused medial lips and labial disc form an elongate, roughly rectangular head cap. Indentations between labial disc and medial lips more or less pronounced. Four cephalic sensilla usually distinct. Lateral lips absent, occasionally remnants present. Head re-

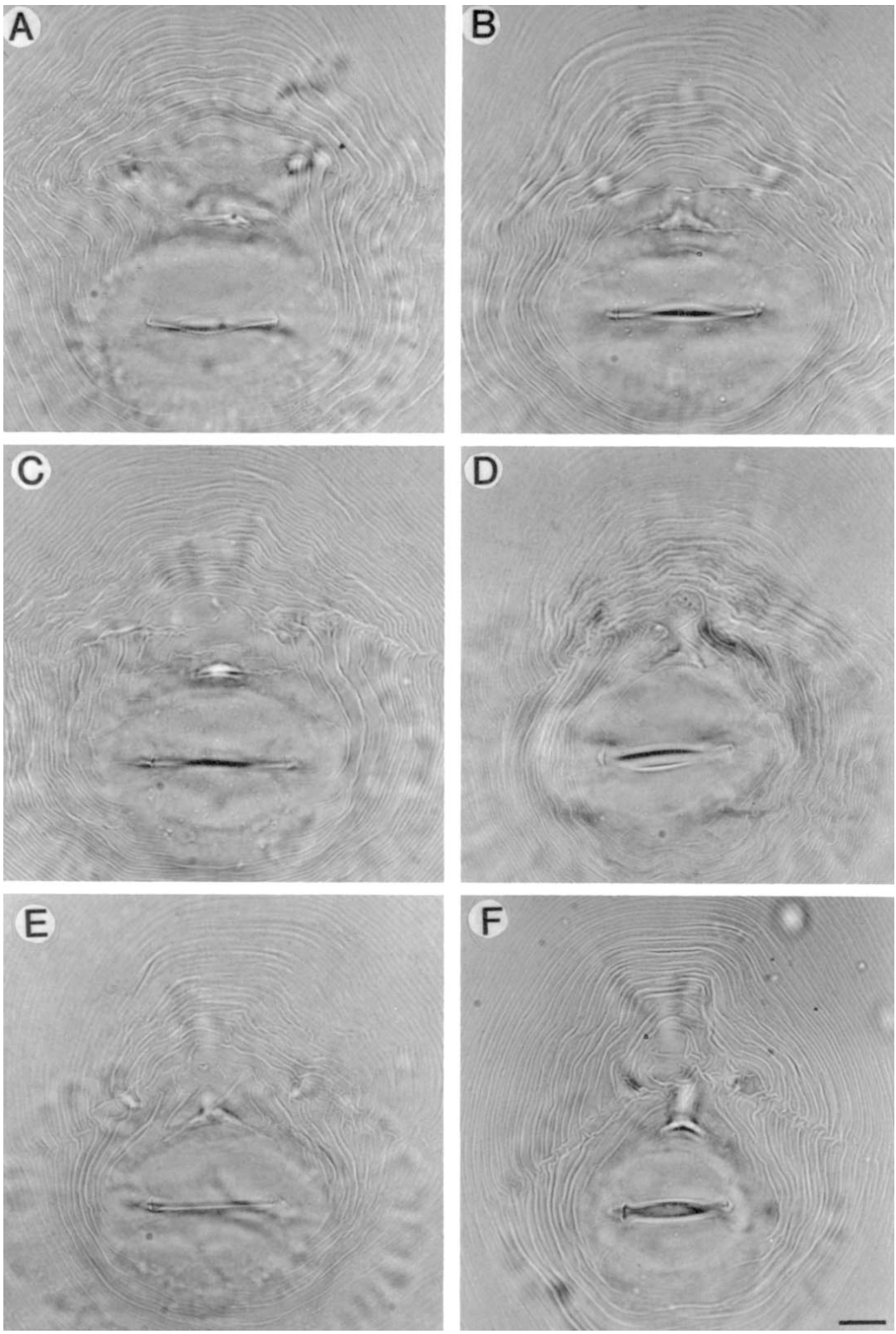

FIG. 3. LM photographs of perineal patterns of *Meloidogyne arenaria* showing typical variation. A–D) Typical populations. E) E5-Guadeloupe. F) 392-Colombia. A–E same scale as F, bar = 10 μm.

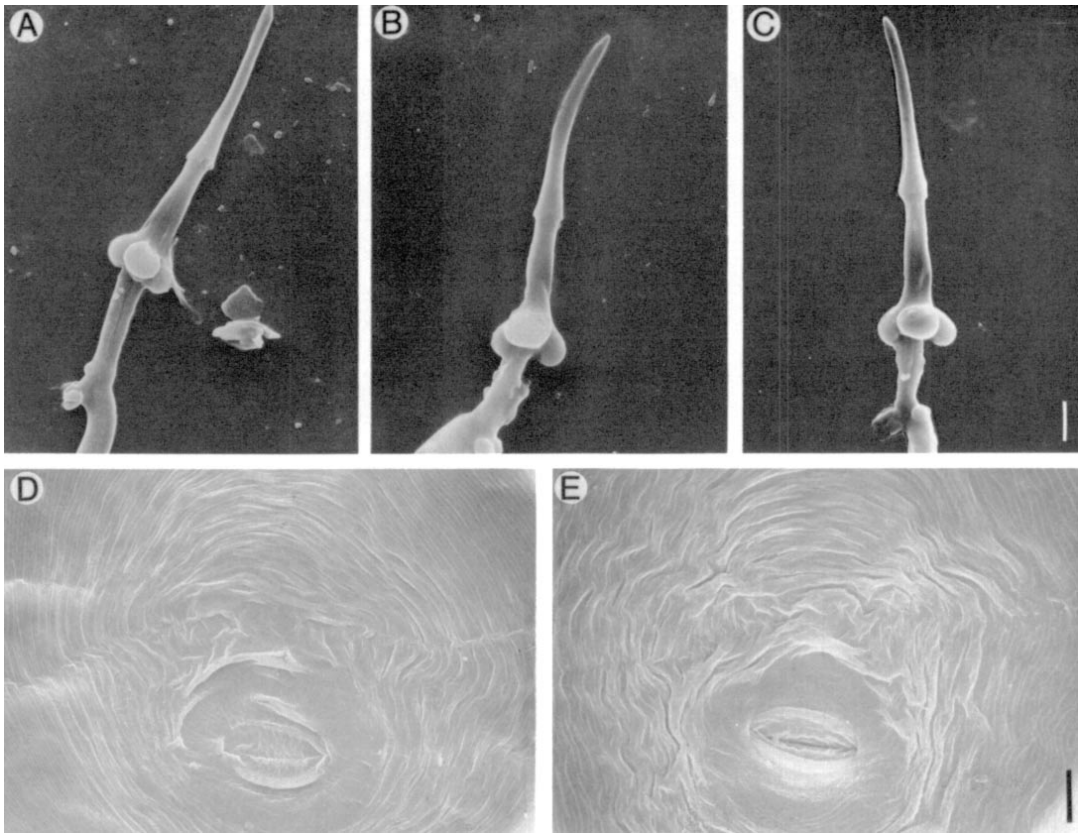

FIG. 4. SEM photographs of stylets and perineal patterns of females of *Meloidogyne arenaria.* A, B, D, E) Typical populations. C) 392-Colombia. A, B same scale as C, bar = 2 μm; D same scale as E, bar = 10 μm.

gion smooth, rarely with one or two incomplete annulations. Cephalic framework moderately well to very well developed, vestibule and vestibule extension distinct. Stylet morphology variable, stylet usually robust; cone straight, occasionally irregular or wavy in outline with wavy lumen (Figs. 5C, 6B) tapering anteriorly to pointed tip; shaft wide, frequently irregular in outline with wavy lumen (Figs. 5C, 6B); stylet knobs large, tear-drop shaped in lateral view, usually merging gradually with shaft, occasionally more offset. In some populations stylet knobs smaller, slightly angular, or more amalgamated. Stylet knob shape occasionally varies within populations. Distance between base of stylet and DGO usually long to very long (4–8 μm) (Fig. 6A–F). Esophageal procorpus cylindrical, slender; metacorpus distinct, oval, with prominent valve (Fig. 5A). Subventral gland openings posterior to valve. Esophageal gland long with two nuclei variable in position. Esophago–intestinal junction indistinct, between nerve ring and excretory pore. Intestinal caecum variable in size. Hemizonid 1–6 body annules anterior to excretory pore. One testis or two testes, outstretched. Sperm large, globular, granular. Spicules slender, arcuate (Fig. 5F, G); size of spicule head varies among populations. Gubernaculum small, slender, crescent shaped. Tail short, bluntly rounded. Phasmids prominent, located at level of cloaca.

Second-stage juveniles

Measurements of typical and variant populations are compared in Table 4.

Typical populations (54-Va, 56-NC, 256-Colombia, 413-Nigeria, 480-NC) (Figs. 8A–E, H–L, 9A–C, 10A–F): Body generally long, slender, tapering to bluntly rounded anterior and sharply pointed posterior ends. Body annulations fine becoming irregular and larger in tail region. Lateral field with four incisures. Head region slightly set off from body. Head cap low, not as wide as

TABLE 3. Measurements of males of *Meloidogyne arenaria*, typical populations (54-Va, 56-NC, 256-Colombia, 413-Nigeria, 480-NC).

Character	N	Range	Mean	Standard error of mean	Standard deviation	Coefficient of variability (%)
Linear (μm)						
Body length	150	979.0–2,279.0	1,720.0	23.45	287.22	17.0
Greatest body width	100	27.0–48.0	36.0	0.39	3.89	11.0
Body width at stylet knobs	150	15.0–22.0	19.0	0.13	1.57	8.0
Body width at excretory pore	150	22.0–40.0	29.0	0.26	3.17	11.0
Stylet length	150	20.0–28.0	23.0	0.12	1.46	6.0
Stylet knob height	100	3.0–5.0	4.0	0.04	0.36	11.0
Stylet knob width	150	4.0–6.0	5.0	0.04	0.45	9.0
DGO	150	4.0–8.0	6.0	0.08	0.96	17.0
Head end to metacorpus valve	100	83.0–121.0	105.0	0.91	9.09	9.0
Excretory pore to head end	150	119.0–213.0	173.0	1.59	19.53	11.0
Tail length	87	11.0–17.0	14.0	0.13	1.22	9.0
Spicule length	66	27.0–39.0	32.0	0.24	1.98	6.0
Gubernaculum length	25	7.0–10.0	9.0	0.16	0.82	9.0
Ratios						
a	100	30.0–64.0	48.0	0.78	7.77	16.0
Body length/head end to metacorpus valve	100	12.0–20.0	17.0	0.19	1.94	12.0
c	87	88.0–190.0	127.0	2.36	21.98	17.0

head region (Figs. 8A, B, D, E, 9A). In SEM, head morphology more variable than in males (Fig. 10A–F). In face view, labial disc rounded to elongate and slightly rectangular; slightly to distinctly raised above medial lips. Medial lips large, ovoid to triangular, outer margins occasionally irregular. Fused labial disc and medial lips form dumbbell-shaped to somewhat bowtie-shaped head cap in face view. Inner margins of medial lips usually perpendicular to lateral edge of labial disc (Fig. 10D), rarely junction of medial lips and labial disc forming a more obtuse angle (Fig. 10A). Lateral lips rounded to triangular, lower than medial lips, occasionally fused to head region (Fig. 10C, D). At junction of lateral lips and medial lips frequent irregularity in margins of medial lips (Fig. 10A). Head region usually smooth, occasionally with one or two incomplete annulations. Stoma slit-like. Prestoma oval. Six inner labial sensilla open onto labial disc, arranged symmetrically around prestoma. Prestoma and sensilla located in slight depression on labial disc. Cephalic sensilla faint. Cephalic framework very delicate, vestibule and vestibule extension distinct (Fig. 9A). Stylet delicate, but knobs fairly large and somewhat variable in shape among populations, distinctly separate, frequently rounded to slightly triangular in profile (Fig. 8B–E); knobs usually merge gradually with shaft (Fig. 8D), occasionally more set off in some populations (Figs. 8B, 9A). Distance from base of stylet to DGO 2.7–4.7 μm. Outline of procorpus indistinct, metacorpus oval with prominent valve plates, esophageal gland lobe long with three nuclei (Fig. 8A). Esophago–intestinal junction obscure. Hemizonid 1–3 annules anterior to excretory pore. Rectal dilation pronounced (Fig. 8H–L). Phasmids small, 8–12 annules posterior to anal opening. Tail length and shape variable among populations (Figs. 8H–L, 9C). Tail tip rounded to pointed, in very few specimens squarish in shape, with or without several distinct, large annulations. Hyaline tail terminus indistinct (Figs. 8H–L, 9C).

Variant populations (E5-Guadeloupe, 392-Colombia) (Figs. 8F–G, M, N, 9D–F, 10G–I): Second-stage juveniles appear more slender than those of typical populations of *M. arenaria*. Head region is shorter and head cap narrower in lateral view (Figs. 8F, G, 9D). In SEM, labial disc rounded but not as elongate, medial lips crescent shaped but narrower (Fig. 10G). Fused labial disc and medial lips form a more compact head cap than in most typical populations. Several to many incomplete head annulations are

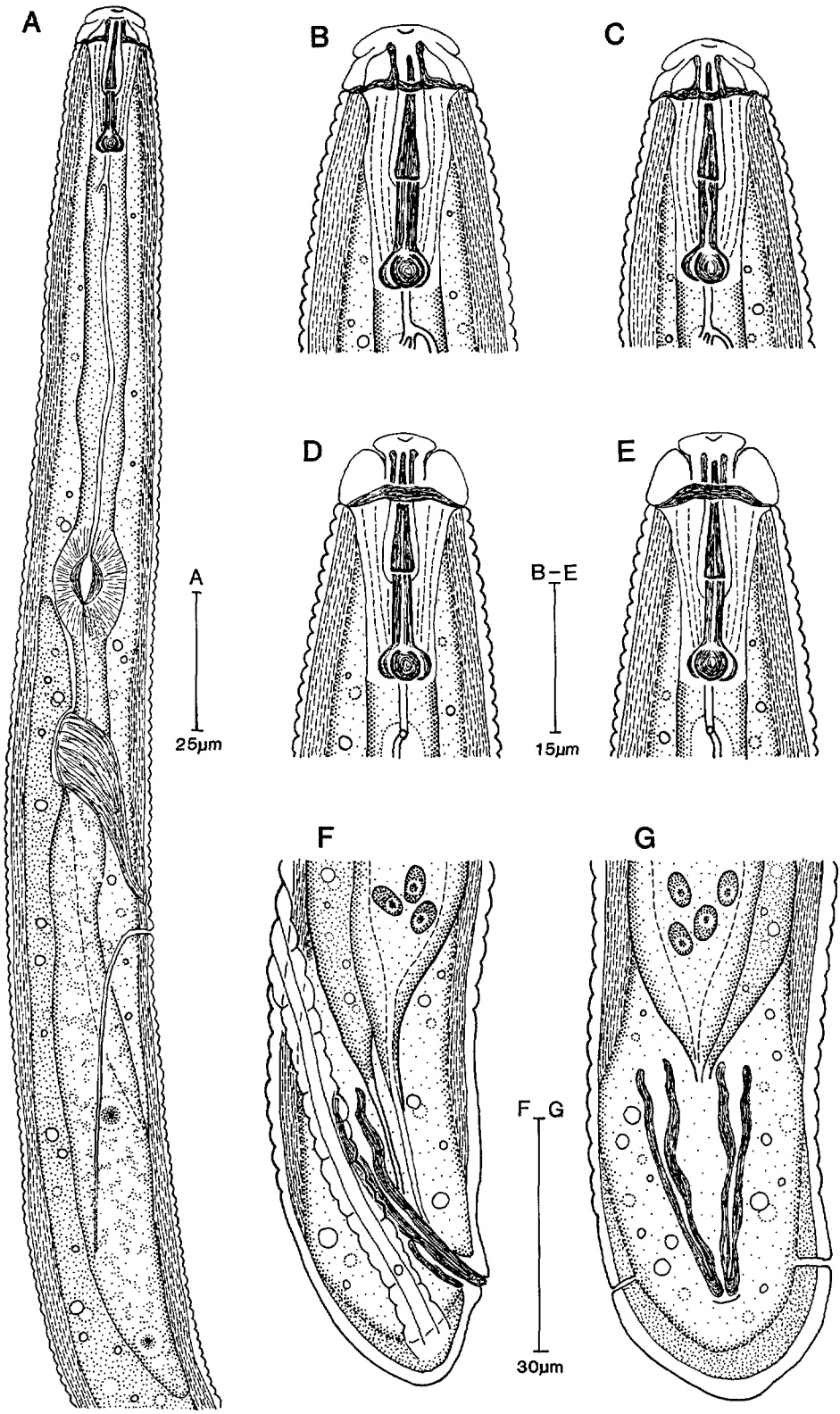

FIG. 5. Line drawings of males of *Meloidogyne arenaria,* typical populations. A) Esophageal region (lateral). B, C) Cephalic region (lateral). D, E) Cephalic region (dorsal). F) Tail (lateral). G) Tail (ventral).

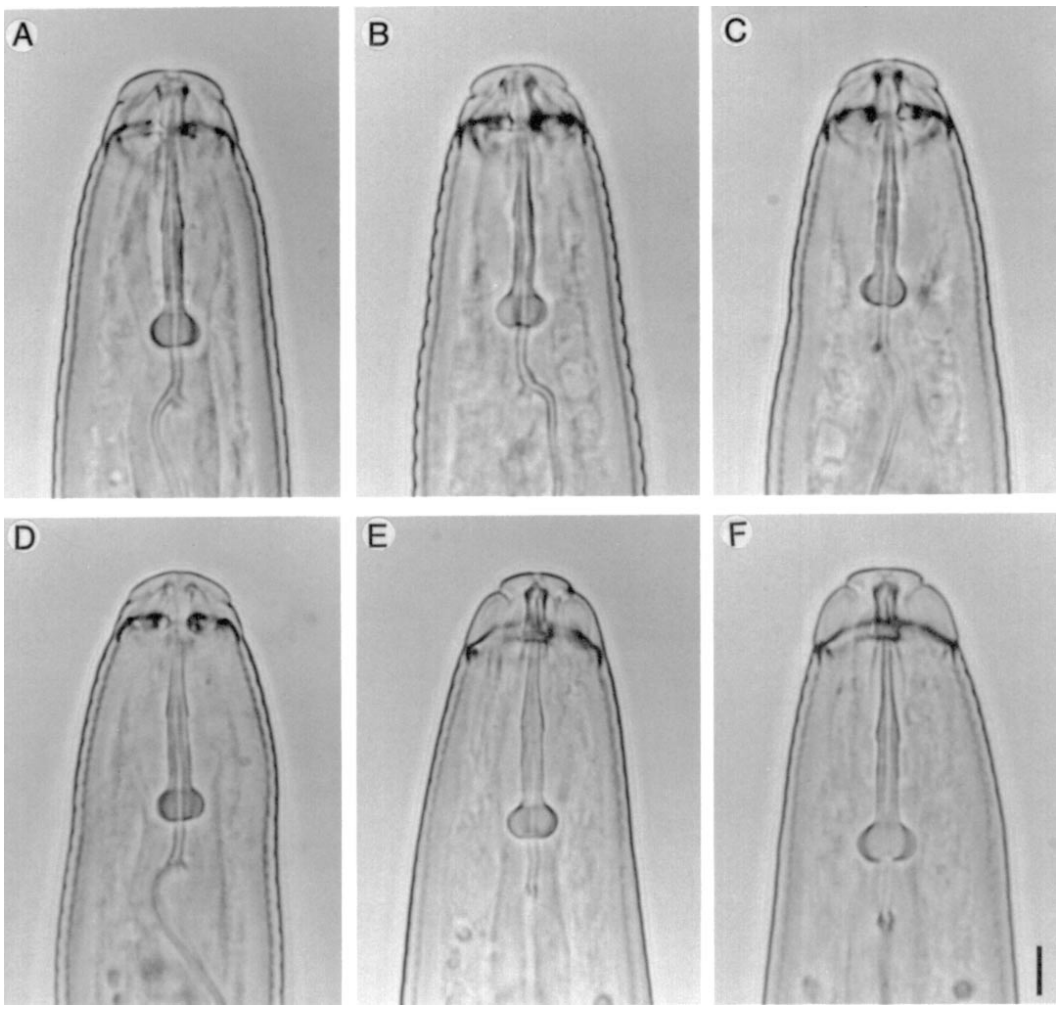

FIG. 6. LM photographs of the anterior portions of males of *Meloidogyne arenaria* showing variation in head cap and stylet morphology of typical populations. A–D) Lateral. E, F) Dorsal. A–E same scale as F, bar = 4 μm.

always present (Fig. 10G–I). Stylet morphology similar to that of typical populations, but stylet knobs slightly smaller and more rounded (Figs. 8F, G, 9D, E). Tail region distinctive, thinner, and tapers to finer point (Figs. 8M, N, 9F). Usually several pronounced annules near tail tip.

Morphometrics

A comparison of the variant populations E5-Guadeloupe and 392-Colombia with the typical populations of *M. arenaria* showed that values of most characters were significantly different (Tables 2, 4). In 392-Colombia, no differences were found in stylet length of females and the ratios c, and body length/head end to metacorpus valve of J2. Second-stage juveniles of E5-Guadeloupe were similar to the typical populations in tail length and ratios a, d. When populations E5-Guadeloupe and 392-Colombia were compared, values of most characters again were different. Similar values were found in the distance of excretory pore to head end of females and in stylet length, tail length, body width at anus, and ratio a of J2.

DISCUSSION

The present SEM and LM study of seven populations of *M. arenaria* revealed that the morphology of this species is quite variable.

Considerable variation in perineal pat-

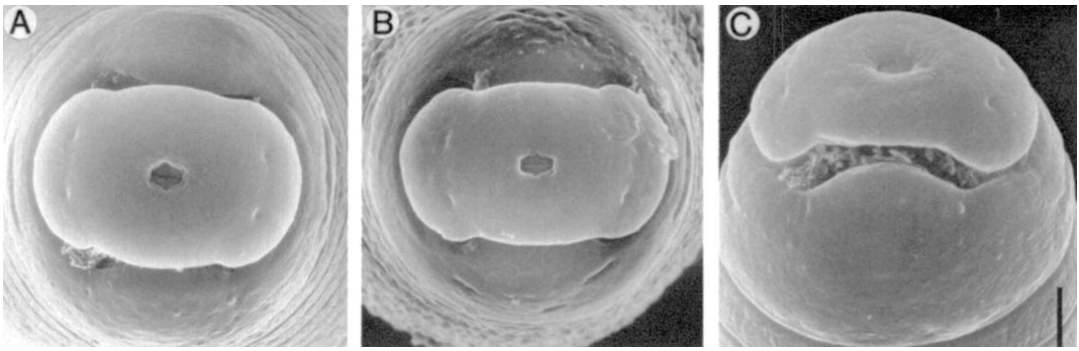

FIG. 7. SEM photographs of head region of males of *Meloidogyne arenaria,* typical populations. A, B) Face views. C) Lateral view. A, B same scale as C, bar = 2 μm.

terns was observed both within and among populations of *M. arenaria.* Although the majority of patterns possessed typical *M. arenaria* characteristics, many aberrant patterns were found. Perineal pattern morphology, therefore, cannot be relied upon as the sole criterion for identification of *M. arenaria.*

The stylet morphology of adult females of *Meloidogyne* is considered species specif-

TABLE 4. Morphometric comparison of second-stage juveniles of typical populations of *Meloidogyne arenaria* with those of variant populations.

Character (μm)	Typical populations (N = 150) 54-Va, 56-NC, 256-Colombia, 413-Nigeria, 480-NC (pooled) Mean ± SE (range)	Variant populations (N = 30) E5-Guadeloupe Mean ± SE (range)	Variant populations (N = 30) 392-Colombia Mean ± SE (range)
Body length	503.6 ± 4.26 (391.6–605.2)	525.9 ± 2.92 (494.8–557.1)	486.6 ± 3.70 (449.5–520.7)
Greatest body width	15.3 ± 0.09 (12.8–17.8)	15.7 ± 0.25 (13.4–18.3)	14.3 ± 0.11 (12.9–15.4)
Body width at anus	10.9 ± 0.05 (9.7–12.8)	10.1 ± 0.14 (8.8–12.2)	9.9 ± 0.09 (8.9–10.6)
Stylet length	11.1 ± 0.03 (10.1–11.9)	10.8 ± 0.03 (10.5–11.2)	10.8 ± 0.06 (10.3–11.3)
Stylet base to head end	14.8 ± 0.05 (13.4–16.2)	15.3 ± 0.10 (14.4–16.7)	14.5 ± 0.07 (13.8–15.2)
DGO	3.7 ± 0.04 (2.7–4.7)	4.1 ± 0.06 (3.5–4.8)	3.5 ± 0.04 (2.8–3.8)
Head end to metacorpus valve	60.9 ± 0.43 (49.4–71.2)	65.2 ± 0.58 (54.5–71.2)	58.6 ± 0.40 (54.9–65.1)
Excretory pore to head end	89.8 ± 0.56 (75.0–105.2)	91.5 ± 0.53 (82.9–97.0)	86.7 ± 0.61 (79.0–96.3)
Tail length	56.0 ± 0.53 (43.6–69.4)	54.9 ± 0.86 (44.5–62.3)	54.2 ± 0.47 (48.7–60.3)
a	33.1 ± 0.29 (22.4–40.5)	33.8 ± 0.57 (28.7–38.5)	34.1 ± 0.33 (29.5–38.2)
Body length/head end to metacorpus valve	8.3 ± 0.04 (7.3–9.6)	8.1 ± 0.08 (7.3–9.9)	8.3 ± 0.06 (7.7–8.8)
c	9.0 ± 0.05 (7.5–10.9)	9.6 ± 0.16 (8.4–11.4)	9.0 ± 0.07 (8.1–9.8)
d	5.1 ± 0.05 (3.8–6.6)	5.1 ± 0.10 (4.3–6.7)	5.5 ± 0.06 (4.7–6.4)

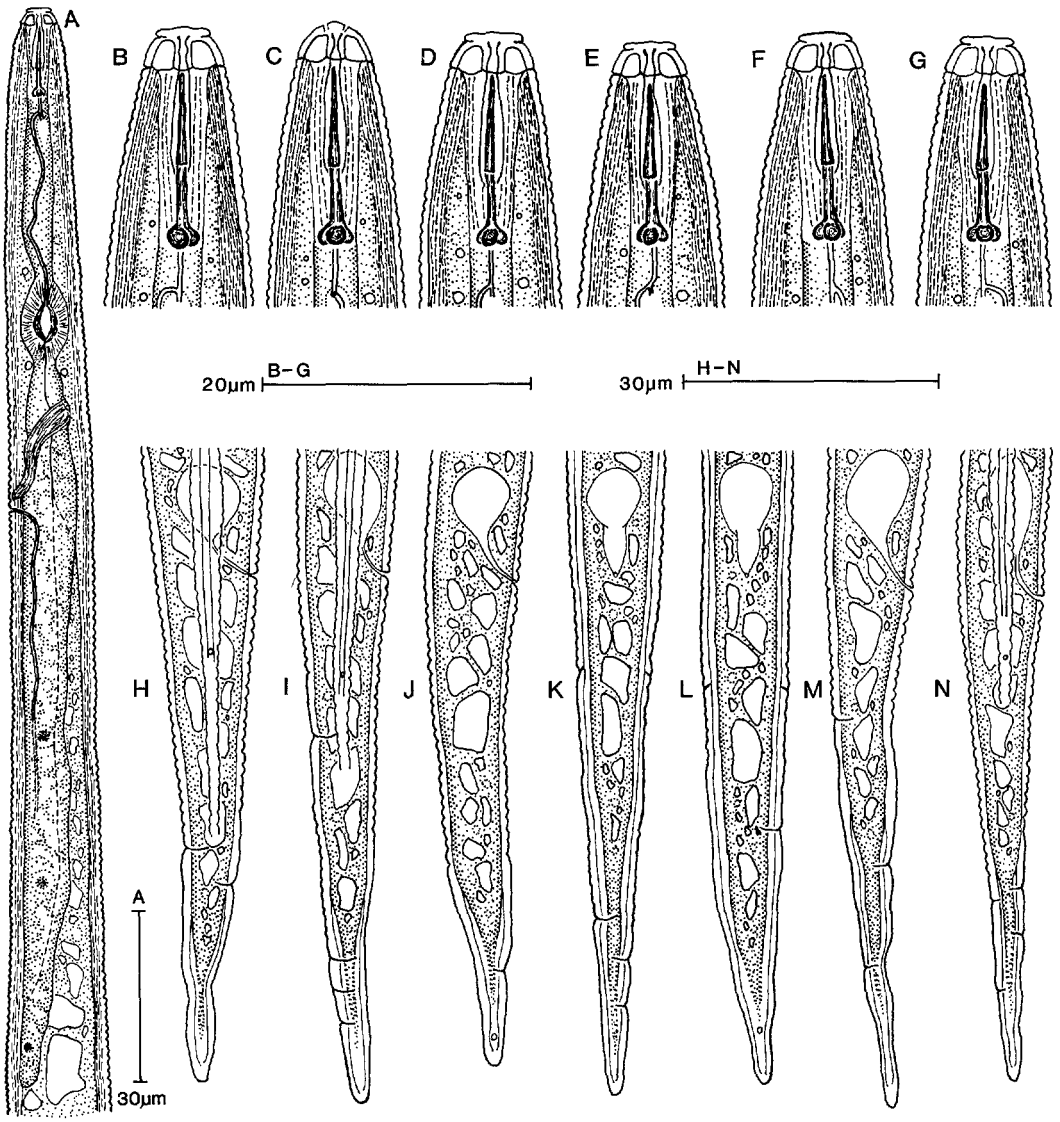

FIG. 8. Line drawings of second-stage juveniles of *Meloidogyne arenaria* showing variation in head cap, stylet, and tail morphologies. A, B, D–G, H–J, M, N) Lateral. C) Dorsal. K, L) Ventral. A–E, H–J, K, L) Typical populations. F, M) E5-Guadeloupe. G, N) 392-Colombia.

ic. Stylets of *M. arenaria* had been previously characterized as robust with rounded, posteriorly sloping knobs that gradually merge with the posteriorly widening shaft (6,14). Stylets of our populations often were not as robust and stylet knob shape was more variable.

Head and stylet morphologies of males have recently been recommended as reasonably reliable taxonomic characters for the identification of *Meloidogyne* spp. (3–5,12). Males of several populations of *M. arenaria* were characterized in the LM by a low, rounded, posteriorly sloping head cap which was nearly as wide as the head region (4,5,12). The stylet was robust with pointed cone and usually cylindrical shaft; the rounded knobs gradually merged with the shaft. In our LM studies, head and stylet morphologies of males were more variable than previously described. In some populations, the head cap was higher and slightly squarish. Cone and shaft were occasionally irregular in outline with wavy

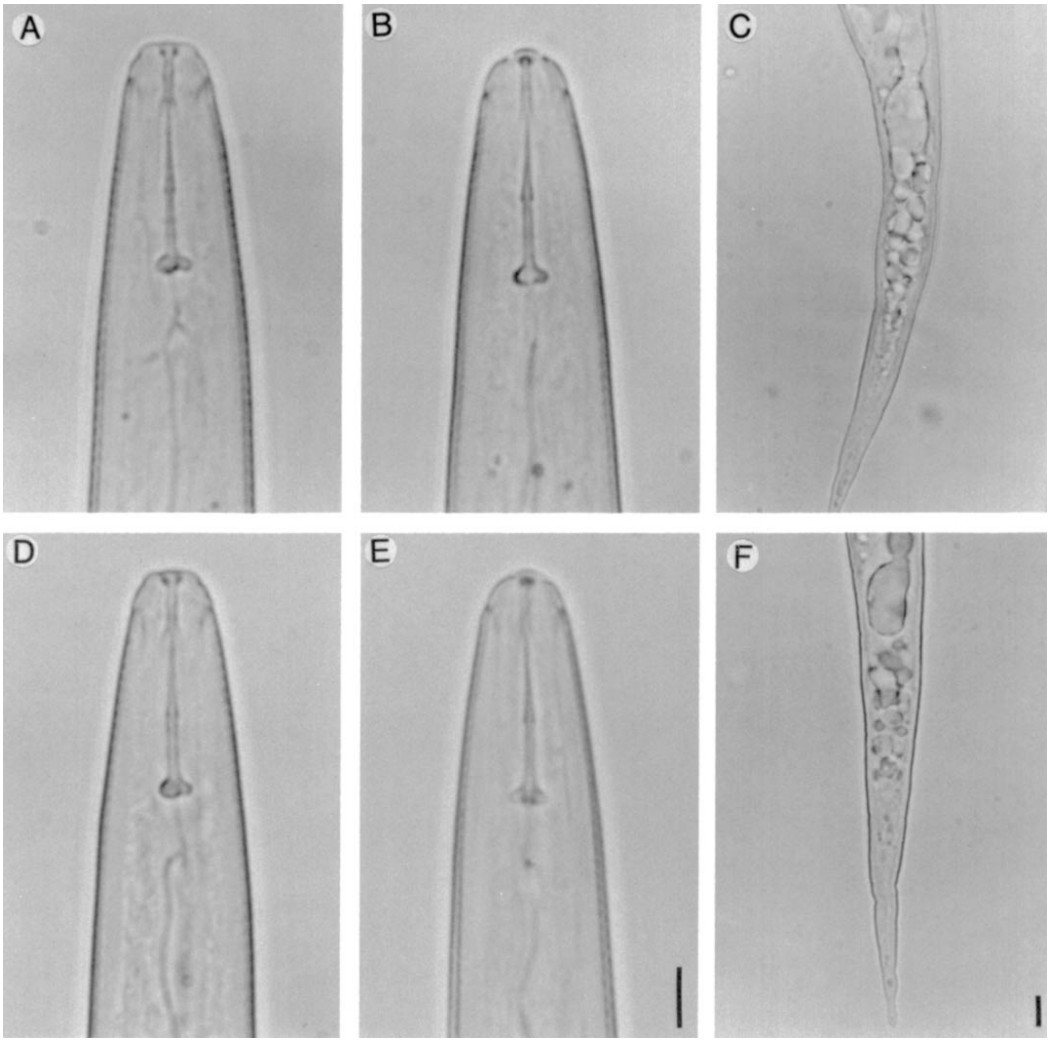

FIG. 9. LM photographs of second-stage juveniles of *Meloidogyne arenaria.* A, B, D, E) Anterior portion (A, D lateral; B, E dorsal). C, F) Tails (lateral). A–C) Typical populations. D–F) E5-Guadeloupe. A, B, D same scale as E, bar = 4 μm; C same scale as F, bar = 4 μm.

lumen. The stylet knobs were more set off in some populations, and their size and shape was more variable.

In previous SEM studies, males of a single population of *M. arenaria* could be distinguished from those of *M. incognita, M. javanica,* and *M. hapla* by the raised labial disc, crescent shaped medial lips, and 2–3 head annulations (3). Our SEM studies showed the cephalic morphology to be remarkably consistent within and among populations of *M. arenaria,* but the labial disc was only very slightly raised, and head annulations and remnants of lateral lips were rare. In spite of their morphologic variability, characteristics of *M. arenaria* males did not closely resemble those of the other three common species of *Meloidogyne.*

Head and styled morphologies of J2 also have been recommended as useful taxonomic characters (1,2). In previous LM studies, only *M. hapla* could be distinguished by head morphology (1). *M. arenaria* could be differentiated by its more robust stylet and by the stylet knobs which merged gradually with the shaft. In our LM studies, the J2 head region was not distinctive. The stylet was often slender, and occasionally the knobs were low and

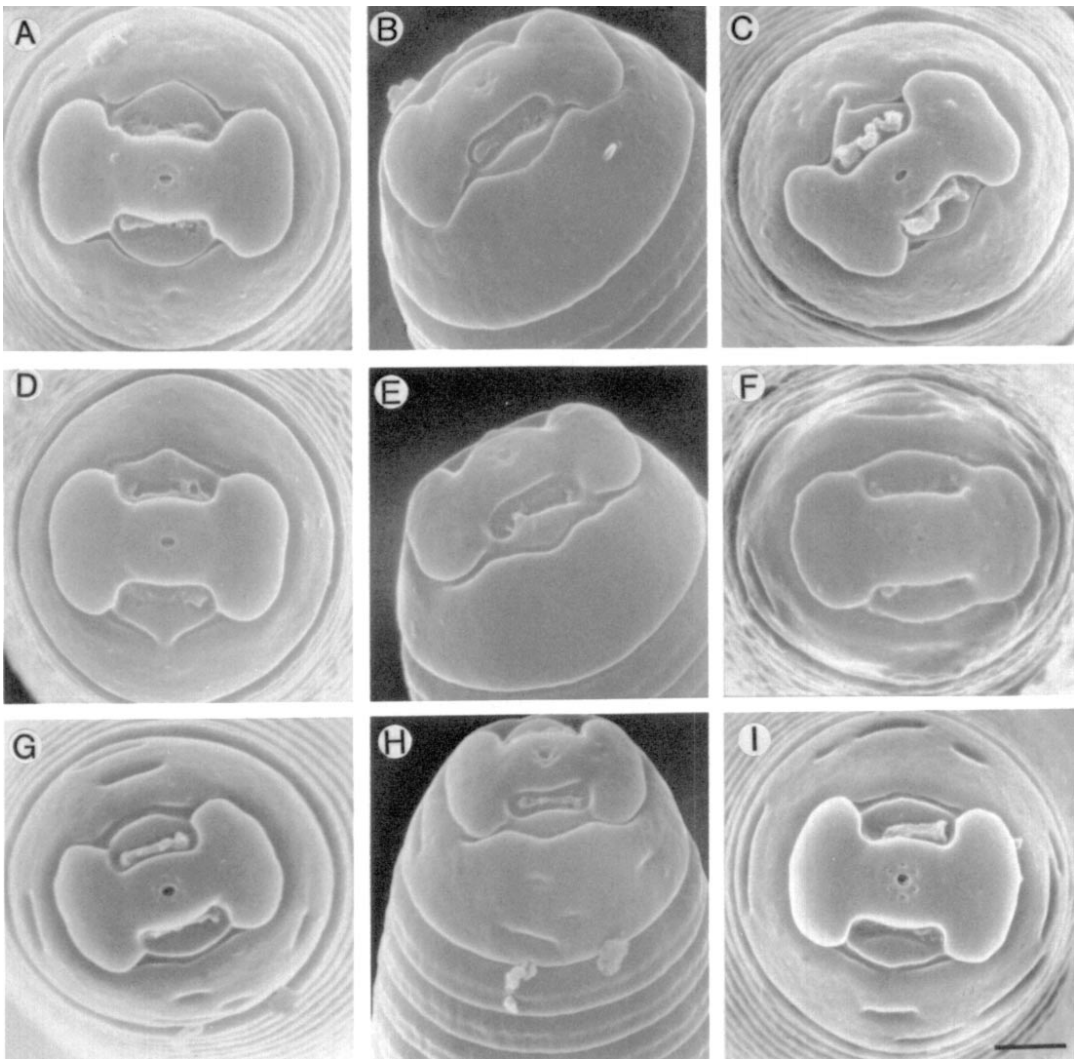

FIG. 10. SEM photographs of head regions of second-stage juveniles of *Meloidogyne arenaria*. A, C, D, F, G, I) Face views. B, E, H) Lateral views. A–F) Typical populations. G) 392-Colombia. H, I) E5-Guadeloupe. A–H same scale as I, bar = 1 μm.

wide and appeared more set off from the shaft. In general, juvenile head caps and stylets are very small and difficult to discern in the light microscope and thus should not be relied upon in species identification.

In recent SEM studies, the four common species differed in juvenile cephalic morphology (2); the typical features described for *M. arenaria* resemble those of our Fig. 10F. Our SEM observations revealed substantial variation in cephalic morphology of J2 of *M. arenaria* with respect to amount of elevation and shape of labial disc, shape of medial and lateral lips, and size of angle between labial disc and medial lips. Very rarely incomplete head annulations were present.

Consistent morphological differences were not found between the two host races of *M. arenaria*. In similar LM and SEM studies, comparison of the four host races of *M. incognita* also revealed no morphological differences (11).

The variant populations E5-Guadeloupe and 392-Colombia were morphologically similar. Their taxonomic status is uncertain. Although, many characters were examined, accurate identification of these populations was difficult. The majority of their morphological features, their cytol-

ogy, and host responses were similar to those of *M. arenaria,* but certain characteristics atypical in *M. arenaria* were consistently observed in each variant population. Frequently, unusual perineal patterns were found in females. Second-stage juveniles differed to some extent from the typical populations in tail shape and cephalic structures, including the presence of several to many incomplete head annulations, a rare trait in the typical *M. arenaria* populations. More information or new characters are needed before the proper taxonomic placement of these variants can be attempted.

The morphometric studies showed that most characters were significantly different when either E5-Guadeloupe or 392-Colombia were compared to the typical *M. arenaria.* The two variant populations also differed from each other in most morphometric characters. Measurements, however, can be affected by environmental conditions (9,10) and statistically significant differences have been reported among populations of the same species (20).

Although, the morphology of *M. arenaria* is variable, the characters described herein remain of taxonomic value and should facilitate the accurate identification of most *M. arenaria* populations. Caution should be exercised, however, when using these characters in taxonomic studies because the amount of variation in these characters among populations of *M. incognita* and *M. javanica* has not been documented.

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