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The Hoplolaiminae

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I. INTRODUCTION

The Hoplolaiminae *sensu* Fortuner (1987a) include eight genera: *Pararotylenchus, Rotylenchus, Scutellonema, Aorolaimus, Hoplolaimus, Helicotylenchus, Antarctylus,* and *Aphasmatylenchus*. They belong to the family Hoplolaimidae together with the forms in the related subfamily Rotylenchulinae. Some Hoplolaiminae, and particularly some species in the genera *Scutellonema* and *Helicotylenchus*, have a worldwide distribution and they are very common on many cultivated plants. Other hoplolaimids are found in more restricted areas: *Aphasmatylenchus* in a few sites in West Africa, *Pararotylenchus* in cool localities in the western United States and the Far East, *Antarctylus* on an island in Antarctica, etc.

Host specificity varies from species to species. Most Hoplolaiminae are found in many different plants: the list of hosts of *Helicotylenchus dihystera* includes grasses, rice, corn, soybean, sorghum, wheat, rye, sugarcane, Cyperaceae, potato, strawberry, peanut, cotton, vegetables, trees and bushes, tea, various ornamentals, and more.

Hoplolaimids accomplish part or all of their cycle in the soil. They are obligate plant parasites, and they are closely associated with plant roots. Some are migratory ectoparasites browsing the surface of roots, sometimes attacking the outer layers. Some are migratory semiendoparasites. They penetrate the cortex and remain there for long periods as semiendoparasites, but they can move out of the roots. A few species are true endoparasites, e.g., several *Hoplolaimus* species, *Scutellonema bradys*, etc.

Members of this family are often considered as second-class parasites. In California, all *Helicotylenchus, Hoplolaimus, Rotylenchus*, and *Scutellonema* are classified as parasites and organisms of little or no economic significance by the California Department of Food and Agriculture. However, some hoplolaimids have been shown to cause heavy damage. *Hoplolaimus columbus* is a major parasite of soybean and cotton in southern United States, *Scutellonema bradys* can cause severe damage on yams, *Helicotylenchus multicinctus* is an important parasite of banana, etc.

II. TAXONOMY OF HOPLOLAIMIDAE

A. Diagnosis of the Family

Hoplolaimidae Filip'ev,* 1934
syn. Nemonchidae Skarbilovich, 1959
Aphasmatylenchidae Sher, 1965
Rotylenchulidae Husain and Khan, 1967

Tylenchoidea. Females vermiform to kidney-shaped; when vermiform, habitus often spiral. Lip region high, typically higher than half the diameter of the basal lip annulus; anterior end with rounded or trapezoidal outline in lateral view, annulated, sometimes with longitudinal striae on basal lip annulus, rarely striae on other lip annuli. Lateral field typically with four lines, sometimes regressed (some *Hoplolaimus* and *Aorolaimus* spp.). Phasmids typically near anus level, rarely on tail, sometimes migrated far anteriorly (*Aorolaimus, Hoplolaimus*), generally small porelike structures, sometimes enlarged into scutella, rarely absent (*Aphasmatylenchus*). Tail typically short, less than two tail diameters long, rarely longer; generally more curved dorsally, sometimes regularly rounded, rarely conical. Caudalids and cephalids generally present; deirids absent.

Labial framework strong, with high arches. Stylet strong, its length typically equals to 2–1/2 to 3 times the diameter of the basal lip annulus. Stylet knobs strong, rounded to indented, sometimes anchor-shaped. Dorsal esophageal gland opening (DGO) at least 4 µm, sometimes more than 20 µm, from the stylet base. Median bulb strong, rounded. Esophageal glands arrangement variable but mostly overlapping the intestine. Esophagointestinal junction a small, triangular structure.

Two genital branches, opposed, outstretched or rarely flexed (*Rotylenchulus*); posterior branch may be degenerated or reduced to a PUS. Columned uterus with three rows of four cells. Epiptygmata and vulval flaps generally present but sometimes inconspicuous.

Males with secondary sexual dimorphism present, with anterior end less developed than in females, sometimes degenerated and nonfunctional. Caudal alae generally enveloping the tail end, rarely stopping short of it (*Rotylenchulus*). Gubernaculum often with titillae.

Type subfamily: Hoplolaiminae Filip'ev, 1934.

Members of the family Hoplolaimidae are recognized by the strong and long stylet, and by the high lip region.

Under the dissecting microscope, typical hoplolaimids are seen (Fig. 1) as medium to large nematodes, with a body elegant to robust, regularly cylindroid. Stylet is well visible with knobs appearing as clearly seen dots. Esophagointestinal junction is definitely not straight, but often it is not clearly defined, and it looks like a half-round bulge of the dark intestine. When clearly visible, the junction often shows a dorsal overlap of the intestine by the glands. Vulva at midbody, easy to see as a straight line in a clear area. Body remains very regularly cylindroid down to the short tail, often broadly rounded or quarter rounded.

When present, males are similar to females, but a little smaller and with a stylet less well defined. The tail has the typical conoid ventrally bent shape seen in many tylenchs,

*The Russian author Filip'ev used to transliterate his name as "Filipjev," and he is known in the West under this spelling. However, the Russian letter "b" should be transliterated as ' according to the International Standard ISO/R9 1968 (E)–Table 2. The correct transliteration Filip'ev is used in this chapter.

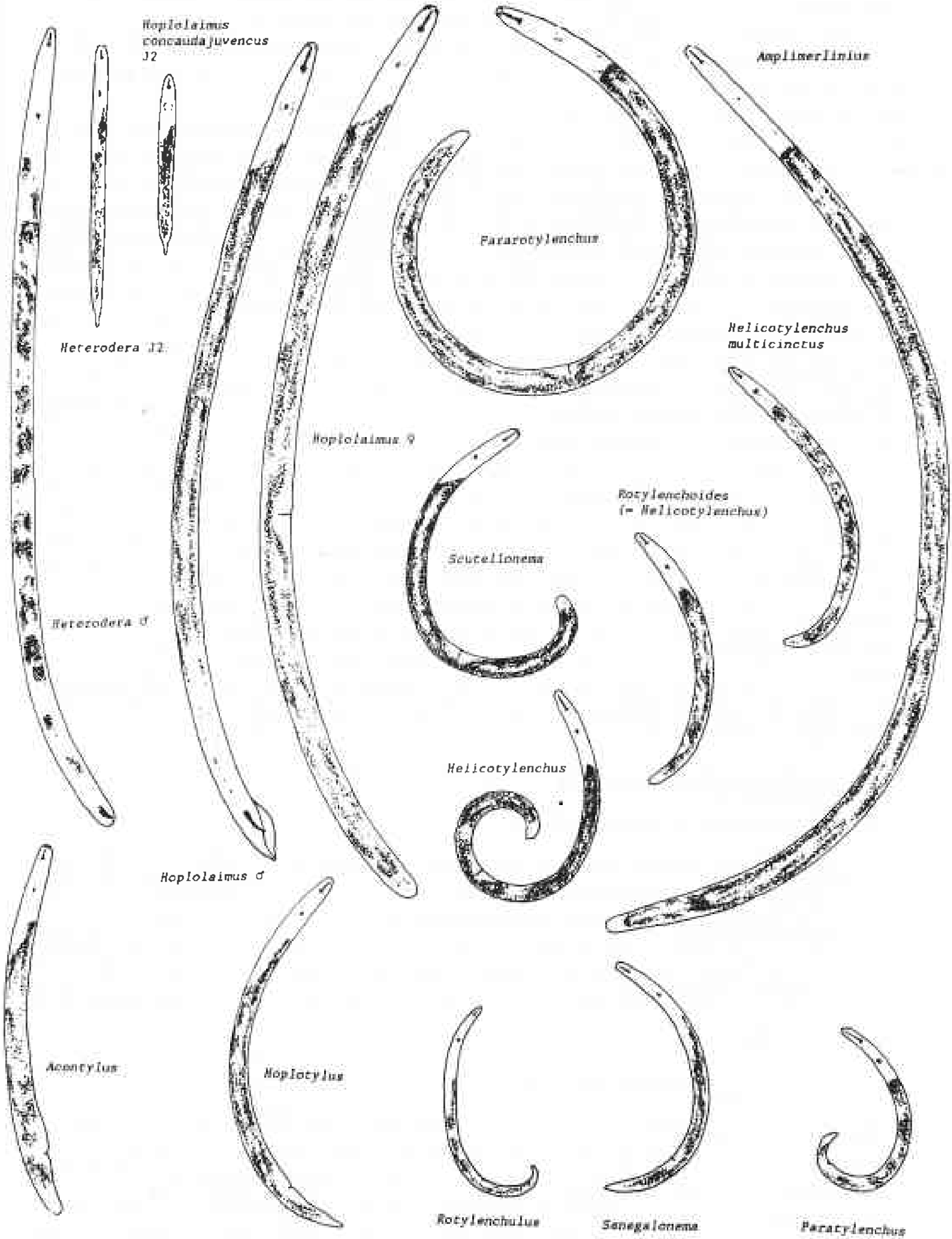

FIGURE 1 Hoplolaimids and phenetically similar forms, seen under the dissecting microscope.

with clearly visible caudal alae and spicules. The tail and alae region is shorter than in tylenchorhynchid males, and about the same as in pratylenchid males.

Some species in the genera *Pararotylenchus, Amplimerlinius, Pratylenchoides* (syn. *Hoplorihynchus*) have forms intermediate between tylenchorhynchids and hoplolaimids: robust cylindroid body with rounded end, strong stylet easy to see, vulva at midbody (like typical hoplolaimids) but junction straight (like typical tylenchorhynchids). Only a detailed examination with the compound microscope will reveal their true identity.

Some taxa, genera, or species of the family exhibit remarkable tendencies that can help in their identification: shortening of tail, posterior migration of DGO, enlargement and anterior migration of phasmids, etc. Enlargement of phasmids into scutella involves modification of both the phasmid opening and the phasmid duct. The opening enlarges from a typical diameter of 1 μm or less in, e.g., *Rotylenchus* or *Helicotylenchus* species to 3–5 μm in *Scutellonema* or *Hoplolaimus*. The phasmidial duct, which is a simple tube in *Rotylenchus*,enlarges in a wide chamber, the ampulla, generally even wider than the opening. As a consequence, reported measurement of a scutellum should include two values—the diameter of the opening, and that of the widest part of the ampulla, seen by focusing below the opening. For example, Germani et al. (1986) report measurements of 2.8 (2–3.5) μm for the opening and 4.1 (3.5–5) μm for the ampulla in *Scutellonema brachyurus*.

In the male genital system the gubernaculum is thickened both dorsally and ventrally. The dorsal cuticularized portion is often described as if it were the whole gubernaculum, and the ventral portion is named the capitulum. The capitulum sometimes has been called telamon, after a structure that exists in the strongylids. Both capitulum and telamon are seen in a ventral position in relation to the spicules but the telamon of strongylids is a cuticularization of the cloacal pouch whereas the capitulum, being a part of the gubernaculum, is a cuticularization of the spicular pouch. This is a good example of homoplasy with two structures of different origin having the same function and appearing equivalent at first. The gubernaculum bears distal projections named the titillae.

B. Systematic Relationships

1. Relationships with Belonolaimidae

The family Hoplolaimidae probably originated from tylenchorhychid-like ancestors, as demonstrated by *Pararotylenchus*. This genus exhibits a number of derived characters that are already hoplolaimid (short tail, phasmids near anus level, DGO more than 4 μm from stylet base, high labial region, strong stylet and labial framework, and spiral habitus), but the criterion traditionally given as the most characteristic for the family, the glandular overlap over the intestine, does not appear, or is little developed, as in the tylenchorhynchids in Belonolaimidae.

2. Relationships with Pratylenchidae

The Pratylenchidae followed a different evolutionary path and became endoparasites whereas generally speaking the Hoplolaimidae are semiendoparasites. Because of endoparasitism, the stylet of Pratylenchidae does not have to reach deep into the root, and this organ is generally shorter than in Hoplolaimidae. Some other characters are less derived than in Hoplolaimidae, e.g., in Pratylenchidae, the tail is generally longer than two body diameters at anus, and the phasmids are situated on the tail, as in Belonolaimidae.

Most pratylenchids are easy to differentiate from hoplolaimids by the lower lip region and the shorter, squat stylet, but some intermediate forms may be quite puzzling. For example, Andrássy recently described a new genus, *Hoplorhynchus*, with characteristics intermediate between hoplolaimids and tylenchorhynchids (hence the genus name). It was eventually shown by Luc (1986) to be a synonym of the genus *Pratylenchoides*, a pratylenchid.

3. Relationships with Heteroderidae

The Heteroderidae probably originated from Hoplolaimidae. They evolved into sedentary endoparasites by establishing very close relationships with their hosts. The host response resulting in specialized feeding structures allowed the female body to enlarge for increased egg production. In some aspects of their morphology, the two families are very close. The anterior end of an heteroderid male has a definite hoplolaimid appearance, and it may be difficult to differentiate under the dissecting microscope second-stage juveniles of *Heterodera* from, e.g., *Hoplolaimus concaudajuvencus* juveniles (Fig. 1).

Adults of heteroderids have unique characteristics that clearly differentiate the family, both for systematics and identification. Males have extremely short tails; females are typically enlarged.

C. Subfamilies in Hoplolaimidae

Hoplolaiminae Filip'ev, 1934
syn. Nemonchinae Skarbilovich, 1959
Rotylenchoidinae Whitehead, 1958
Aphasmatylenchinae Sher, 1965
Rotylenchinae Golden, 1971
Pararotylenchinae Baldwin and Bell, 1981

Hoplolaimidae. Adult females remain vermiform. Lateral field with four lines or less. Phasmids near anus or erratic, anteriorly migrated on body, rarely on tail, small or enlarged, rarely absent. Tail short, more curved dorsally with or without a ventral projection, or regularly rounded, rarely conoid. Caudalids and cephalids present, labial framework and stylet strong. DGO more or less far from stylet. Esophageal glands either of the same length and not overlapping the intestine, or variously enlarged and overlapping the intestine. Genital branches always outstretched, two of equal length or posterior branch smaller or reduced to a postuterine sac (PUS).

Males with anterior end smaller than females but still functional. Caudal alae enveloping tail end.

Migratory ecto- or semiendoparasites of higher plants. Eggs laid free in the soil and not deposited in a gelatinous matrix.

Type genus: *Hoplolaimus* von Daday, 1905
syn. *Nemonchus* Cobb, 1913
Hoplolaimoides Shakil, 1973
Basirolaimus Shamsi, 1979
Other genera: *Rotylenchus* Filip'ev, 1936
syn. *Anguillulina* (*Rotylenchus*) Filip'ev, 1936
Gottholdsteineria Andrássy, 1958
Orientylus Jairajpuri and Siddiqi, 1977
Calvatylus Jairajpuri and Siddiqi, 1977
Interrotylenchus Eroshenko, 1984
Scutellonemoides Eroshenko, 1984

Varotylus Siddiqi, 1986
Helicotylenchus Steiner, 1945
syn. *Rotylenchoides* Whitehead, 1958
Zimmermannia Shamsi, 1973
Scutellonema Andrássy, 1958
Aorolaimus Sher, 1963
syn. *Peltamigratus* Sher, 1964
Nectopelta Siddiqi, 1986
Aphasmatylenchus Sher, 1965
Antarctylus Sher, 1973
Pararotylenchus Baldwin and Bell, 1981

2. Rotylenchulinae Husain and Khan, 1967

Rotylenchulinae, including *Acontylus, Senegalonema,* and *Rotylenchulus* are studied in Chap. 11.

Rotylenchulinae differs from Hoplolaiminae in having body of mature females swollen or kidney-shaped, lip region not as high as in Hoplolaiminae, glandular overlap long and mostly lateral. Rotylenchulinae are sessile semiendoparasites and they lay their eggs in a gelatinous matrix.

III. *Pararotylenchus* Baldwin and Bell, 1981

A. Diagnosis

Hoplolaiminae. Females: Body spiral to C-shaped. Labial region annulated; oral opening slitlike; round labial disk present; amphid apertures elongate at lateral edge of disk; first lip annulus divided into six lip sectors; lateral sectors smaller than the others (SEM). Lateral field with four lines. Labial framework, stylet, and stylet knobs average-sized for the family; knobs round to indented. DGO about 4–7 μm from stylet base. Esophageal glands not overlapping intestine, symmetrically arranged around esophageal lumen. Two genital branches outstretched, equally developed. Two epiptygmata present. Tail short, of variable shape, usually more curved on dorsal side; phasmids small, porelike, near level of anus.

Males. Caudal alae enveloping tail. Gubernaculum flexed distally and with small titillae but no capitulum. Spicules trough-shaped. No secondary sexual dimorphism.

Type species: *Pararotylenchus hopperi* Baldwin and Bell, 1984, syn. *P. brevicaudatus* (Hopper, 1959) Baldwin and Bell, 1981.

Except for *P. pini,* known from Japan and Korea, all the species in this genus have been found in the western United States, in Utah and California. All occur in cool regions, either at high elevations or along the cool Pacific coast. They are associated with a wide range of plants, including various conifers, rose, aspen, *Veratrum* spp., and barley.

B. Systematic Relationships

Pararotylenchus belongs to Hoplolaimidae because of the short tail, phasmids near anus level, DGO more than 4 μm from the stylet base, high labial region, strong stylet and cephalic framework, and spiral habitus. The esophageal glands not overlapping the intestine are similar to the glands in *Tylenchorhynchus* and some other Belonolaimidae. In the hypothesis that hoplolaimids originated from tylenchorhynchid-like ancestral forms, *Pararotylenchus* can be seen as a relic of the intermediary forms where some but not all of the characters of Hoplolaimidae were present.

Pararotylenchus is very close to *Rotylenchus*, except for the arrangement of the glands and the presence of longitudinal striae on the lip annuli in some *Rotylenchus* species. Baldwin and Bell (1981) noted that a morphological continuum exists from *Pararotylenchus*, with glands of equal length, not overlapping the intestine, and esophageal lumen symmetrically arranged between the three glands, to *Rotylenchus fallorobustus* and *R. breviglans* that also have glands of equal length not overlapping the intestine but where the esophageal lumen is shifted ventrally between the subventral glands, and finally to the typical *Rotylenchus* species with dorsal overlap.

C. Representative Species

1. *Pararotylenchus hopperi* Baldwin and Bell, 1984 (Fig. 2)

Measurements (mean ± standard deviation, and range; after Baldwin and Bell, 1981): Females (n = 22): L = 1.413 mm ± 1.134 (1.24–1.61); a = 38.5 ± 2.954 (32.8–44); b' = 7.38 ±0.406 (6.7–8.3); c = 44.22 ± 4.938 (36.5–53.3); c' = 1.15 ± 0.180 (0.8–1.6); m = 51.1% ± 1.353 (49–54); V = 58.5% ± 2.029 (54–62); stylet = 38.3 μm ± 4.239 (36.5–41). Males (n = 21): L = 1.239 mm ± 0.767 (1.12–1.39); a = 42.06 ± 0.154 (38–46.3); b = 6.81 ± 0.989 (5.8–10.7); c = 33.95 ± 2.351 (28.9–39.4); c' = 1.81 ± 0.176 (1.5–2.1); stylet = 35.62 μm ± 0.857 (33–37); spicules = 36 μm ± 2.021 (32.5–39), gubernaculum = 15.9 μm ± 0.088 (14.5–18.5).

Description. Females: Body generally in loose spiral shape. Lip region slightly offset, flattened to slightly rounded anteriorly, usually with eight annuli. SEM face view shows round oral disk, and first annulus separated in six low sectors, the two lateral sectors smaller than the submedian ones. Labial framework sclerotized. Stylet massive with knobs anteriorly flattened. DGO 5.36 μm ± 1.082 (3.5–7.5) posterior to stylet base. Excretory pore at level of the middle portion of the esophageal glands. Hemizonid one to five annuli anterior to excretory pore. Two large epiptygmata, one inwardly, the other outwardly folded. Spermatheca oval, with round sperms. Tail dorsally convex conoid, 32.32 μm ± 4.239 (24.5–38) long, 28.3 μm ± 2.583 (20.5–32) wide at anus level, tail end rounded and coarsely annulated. Phasmids prominent, at anus level.

Males similar to females. Spicules arcuate; gubernaculum with titillae.

IV. *ROTYLENCHUS* FILIP'EV, 1936

A. Diagnosis

Hoplolaiminae. Females: Body spiral to C-shaped. Labial region offset or continuous with body contours, anteriorly rounded or flattened, generally annulated, with or without longitudinal striae on basal lip annulus. Lateral field with four lines, with or without scattered transverse striae. Labial framework, stylet, and stylet knobs average-sized for the family; knobs with rounded to indented anterior surface. DGO often close to stylet (6 μm) but with a tendency to posteriorly directed migration (up to 16 μm). Esophageal glands overlap intestine dorsally and laterally; dorsal gland more developed than subventral glands; intestine symmetrically arranged between the subventral glands. Two genital branches outstretched, equally developed; posterior branch rarely degenerated. One or two epiptygmata present.

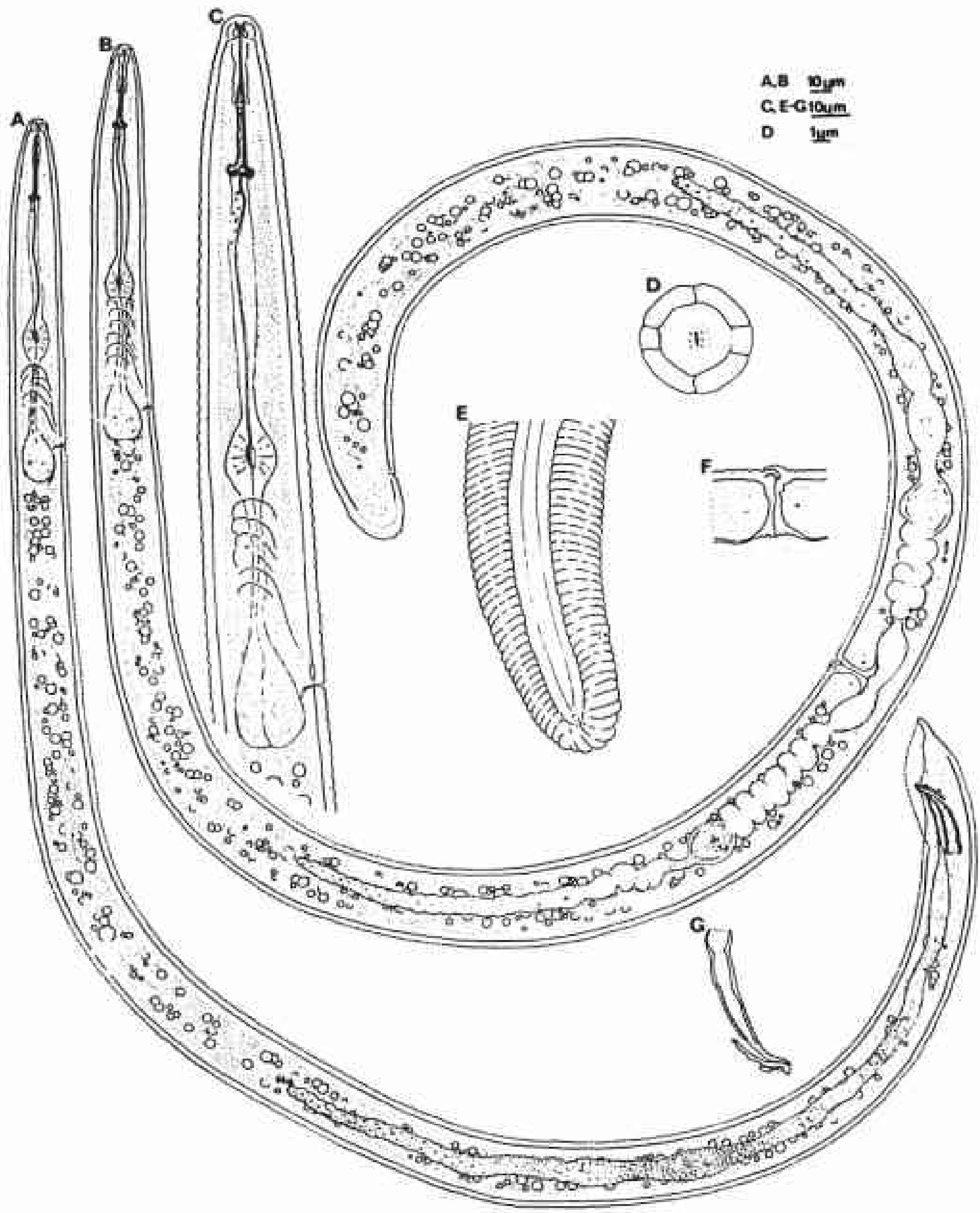

FIGURE 2 *Pararotylenchus hopperi* Baldwin and Bell, 1984. (A) Entire male. (B) Entire female (curvature of specimen slightly exaggerated for convenience of illustration). (C) Cephalic and esophageal region of female. (D) Face view as observed with SEM. (E) Female tail. (F) Vulva. (G) Spicule and gubernaculum. (Baldwin and Bell, 1981, courtesy *J. Nematol.*)

Tail short, hemispheric, rarely with small ventral projection; phasmids porelike, small, near anus level.

Males: Caudal alae enveloping tail, not lobed. Secondary sexual dimorphism not marked, sometimes anterior part of male body slightly smaller than that of female.

Type species: *Rotylenchus robustus* (de Man, 1876) Filip'ev, 1936.

B. Systematic Relationships

From a hypothetical ancestor resembling present-day *Pararotylenchus*, the most obvious synapomorphy in this genus is the development of the dorsal gland and its overlapping of the intestine, and the reduction in size of the ventral glands. However, at the difference of the genus *Helicotylenchus*, the esophageal lumen remains symmetrically situated between the two subventral glands.

The characters used by various authors to differentiate the genera *Orientylus* Jairajpuri and Siddiqi, 1977, *Calvatylus* Jairajpuri and Siddiqi, 1977, *Interrotylenchus* Eroshenko, 1984, *Scutellonemoides* Eroshenko, 1984, *Varotylus* Siddiqi, 1986 have been shown (Fortuner, 1987a; Maggenti et al., 1988) to be irrelevant at the genus level.

C. Representative Species

1. *Rotylenchus robustus* (de Man, 1876) Filip'ev, 1936 (Fig. 3)

Measurements (after Sher, 1965). Females (n = 20): L = 1.22–1.87 mm; a = 32–40; b = 8.1–10.1; b' = 6.0–8.1; c = 48–70; V = 54–58; stylet = 44–50 μm; o = 8–16. Males (n = 10): L = 1.06–1.30 mm; a = 35–42; b = 6.6–10.0; b' = 5.2–6.9; c = 33–41; stylet = 41–44 μm; o = 10–15; spicules = 34–40 μm; gubernaculum = 17–21 μm; capitulum = 9–12 μm.

Description. Females: Relaxed body usually forming a single spiral, sometimes C-shaped; annuli prominent, about 1.7 μm wide near middle. Lateral fields irregularly areolated on body, with four lines, about one-fifth wide as body. Lip region hemispheric, offset by a constriction, with six to seven distinct annuli; labial disk slightly raised above the lip outline; lip annuli longitudinally indented to give a tiled surface appearance; 24–30 such indentations on basal annulus. In SEM head view, round labial disk with first labial annulus in six sectors about equal in size; other labial annuli with characteristic tiled appearance; amphid apertures wide and kidney-shaped (De Grisse et al., 1974). Anterior and posterior cephalids distinct, at 2–3 and 9–10 annuli behind lip region. Spear well developed, cone 50–56% of its total length; basal knobs large, about 7 μm across, rounded but sometimes with flat or indented anterior surfaces. Median esophageal bulb ovate, very muscular, and with a prominent valvular apparatus in center. Esophageal glands extending over intestine dorsally and dorsolaterally as the two subventral glands are shifted from their normal to a subdorsal position; nuclei of subventral glands varying in position from slightly posterior to slightly anterior to that of dorsal gland. Excretory pore usually close to esophagointestinal valve. Hemizonid distinct, three annuli long, just anterior to the excretory pore. Hemizonion indistinct. Vulva a depressed, transverse slit; two short epiptygmata present, sometimes appearing as a single epiptygma in lateral view. Uterine sac formed by a few flattened cells; at the transition to the uterus not more than four larger cells are found; the columnar uterus consists of no more than 12 cells in three rows. Spermathecae formed by 12 cells in various spatial arrangements, rounded, usually packed with sperms; oviduct as two rows of four small, flattened cells forming a constriction between spermatheca and ovary. At the transition to the oviduct, the ovary sometimes contains eight nuclei lying at about the same level, sometimes slightly overlapping the oviduct (Geraert, 1981). Oocytes in a single row except

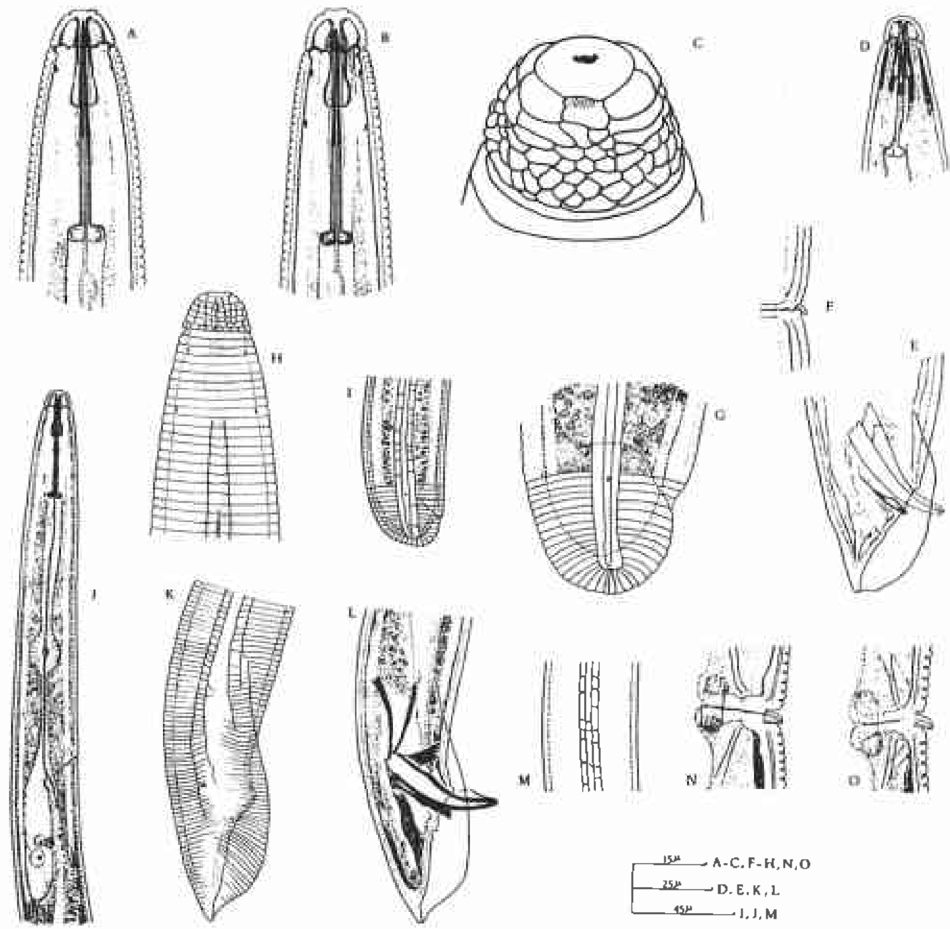

FIGURE 3 *Rotylenchus robustus* (de Man, 1876) Filip'ev, 1936. (A,C,H) Female, anterior ends. (B,D) Male, anterior ends. (F,N,O) Vulval region with epiptygmata. (G,I) Female, posterior ends. (E,K,L) Male, posterior ends. (J) Male, esophageal region. (M) Lateral fields. (H,K) Surface views. (Siddiqi, 1972, courtesy Commonwealth Agricultural Bureaux.)

for the multiplication area. Intestine partially overlapping rectum. Tail hemispheric, regularly annulated, with 8–17 annuli from anus to center of terminus. Phasmids distinct, porelike, usually just preanal but varying from three annuli posterior to seven annuli anterior to anal level.

Males: Body in open C-shape when relaxed. Lip region more distinctly offset and elevated than in female. Bursa crenate, enveloping tail. Spicules slightly cephalated and ventrally arcuate, with well-developed ventral flanges on distal third. Gubernaculum protruding, with prominent titillae.

Rotylenchus robustus is widely distributed in Europe, USSR, Egypt, Zaire, India, Canada, USA, and Brazil. It prefers light sandy soils and it parasitizes many grasses, ornamentals, vegetable crops, and forest trees. It is an ectoparasite of roots causing reduced growth, yellowing, and yield reduction.

Rotylenchus robustus is representative of a group of species within the genus *Rotylenchus* with phasmid not enlarged into scutella, and situated opposite each other, near the anus; lateral fields composed of four lateral lines, sometimes areolated near the phasmids; lip region including longitudinal striae in addition to the usual transverse lip annuli; and opening of the dorsal esophageal gland less than one-quarter stylet length behind stylet base. The females have two equally developed genital branches. The caudal alae of the males are not indented.

2. Species Formerly in the Genus "*Calvatylus*"

The species that were transferred to this genus are quite similar to those in typical *Rotylenchus* except that distinct lip annulation is lacking. Other minor differences include lip region slightly offset (offset in *Rotylenchus*), tail shorter than body width (often a little longer in *Rotylenchus*), and in the males, gubernaculum not protruding, lacking titillae (titillae present in *Rotylenchus*). The genus *Calvatylus* was accepted as valid by Siddiqi (1986), but it was considered a synonym of *Rotylenchus* by Ferraz (1980) and by Fortuner (1987a). It included only three species: *R. calvus, R. heredicus*, and *R. nexus*. None are economically important parasites, and they will not be described here.

3. *Rotylenchus orientalis* Siddiqi and Husain, 1964 (Fig. 4)

Measurements (after Siddiqi and Husain, 1964). Females (n = 5): Length = 0.72 mm (0.68–0.76); a = 29 (27–32); b = 6.4 (6.2–6.7); c = 42 (36–56); V = 69.5% (66–72); stylet = 25–28 μm. After Choi and Geraert, 1972. Females (n = 19): L = 570–690; a = 27–29; b = 5.8–7; c = 37–52; c' = 0.8–1.3; V = 67–73%; stylet = 23–26 μm; m = 43–47; o = 50–61.

Description. Females: Body spirally coiled. Cuticle with coarse striae, 1.7 μm apart near midbody. Lateral fields one-fourth as wide as body. Phasmids porelike, from four annuli anterior to three annuli posterior to anus level. Head conoid-rounded, with four or five annuli, continuous with body. Spear of medium built, with prominent, anteriorly cupped to flattened basal knobs. DGO 12–15.5 μm behind spear base. Corpus cylindrical, narrowed at its junction with median esophageal bulb which is oval in shape. Excretory pore a little behind level of nerve ring. Esophageal glands forming an elongate lobe, extending over dorsal and dorsolateral sides of the anterior end of the intestine; the subventral glands usually are elongated as in *Helicotylenchus*, but in some specimens the subventral glands were not as long giving the esophagus the appearance of a *Rotylenchus* esophagus (Geraert, 1976). Vulva a transverse slit. Reproductive system paired, opposed; posterior genital branch reduced, 50–60% of anterior branch; this difference in length is essentially caused by the lesser development of the ovary. Spermatheca empty, sometimes inconspicuous. Uterus at its distal end with a prominent swelling. Tail 11–18 μm long, dorsally convex, rounded, with 9–11 ventral annuli, about one anal body width long.

Males unknown.

The species is known from India to Korea, but its biology has not been studied. Its systematic position is very unsettled.

Rotylenchus orientalis is representative of the species formerly in the genus *Orientylus*. These species are quite similar to typical *Rotylenchus* except that the posterior genital branch is nonfunctional or absent, and the lip region does not have longitudinal striae. Other minor differences include DGO more posterior, and lip region smaller, narrower than in other *Rotylenchus*. Siddiqi (1986) accepted *Orientylus* as a valid genus in Rotylenchoidinae, a subfamily differentiated from Rotylenchinae by smaller lip region, smooth ba-

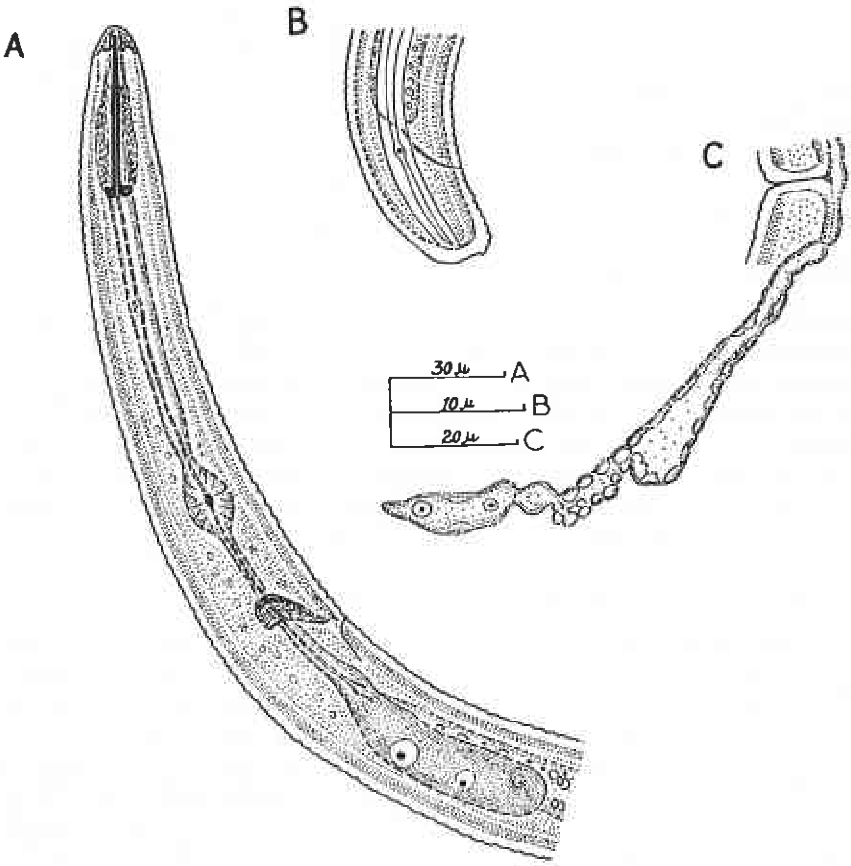

FIGURE 4 *Rotylenchus orientalis* Siddiqi and Husain, 1964. (A) Female, esophageal region. (B) Female, posterior end. (C) Female, regressed posterior genital branch. (Siddiqi and Husain, 1964, courtesy *Proc. Helm. Soc. Wash.*)

sal lip annulus, and DGO more than one-fourth of stylet length behind stylet base. Zancada and Lima (1986) and Fortuner (1987a) considered it a synonym of *Rotylenchus*.

4. *Rotylenchus varus* (Jairajpuri and Siddiqi, 1979) Zancada and Lima, 1986 (Fig. 5).

Measurements (after Jairajpuri and Siddiqi, 1979). Females (n = 20): L = 0.55 mm (0.47–0.61); a = 31 (29–33); b = 6.5 (6–7.5); b' = 4.3 (4–4.7); c = 45 (36–64); c' = 1.2 (0.9–1.5); V = 64% (62–68); stylet = 21 µm (20–23); m = 46 (44–50); o = 51 (49–55).

Description. Females: Heat relaxed body forming a tight double spiral of 1.5–2.5 turns. Cuticle annuli distinct, 1.2 µm wide at midbody. Lateral field with four lines, non-areolated, one-fourth to one-third of body width wide. Labial region narrow, almost hemispherical, continuous with body contours; three or four indistinct lip annuli; cephalic framework strongly sclerotized. Stylet cone 9–11 µm long; stylet knobs anteriorly rounded to indented. DGO 9–12 µm from stylet base. Excretory pore 76–89 µm from anterior end, opposite base of isthmus. Hemizonid zero to two annuli anterior to excretory pore, three annuli wide. Esophagointestinal junction ventral just posterior to the level of the excretory pore. Glands overlapping the intestine over two body widths; dorsal gland in a dorsal posi-

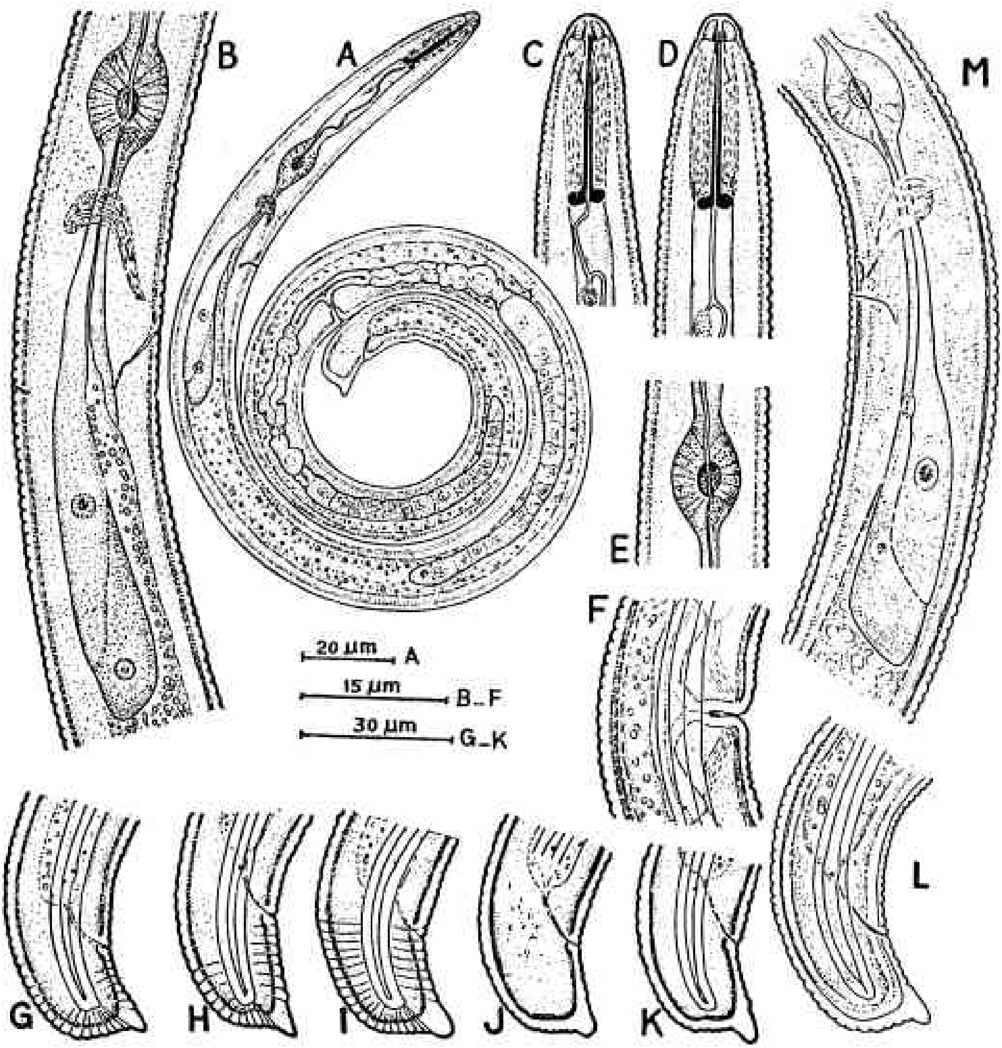

FIGURE 5 *Rotylenchus varus* (Jairajpuri and Siddiqi, 1979) Zancada Lima, 1986. (A) Female, entire body. (B,M) Median esophageal bulb and glandular region. (C,D) Anterior ends. (E) Median bulb. (F) Vulvar region. (G–L) Tails. (Jairajpuri and Siddiqi, 1979 and Siddiqi, 1986, courtesy *Ind. J. Nematol.* and CAB.)

tion, its nucleus about one body width behind intestinal junction; subventral glands in a dorsolateral position, extending past the dorsal gland; subventral gland nuclei posterior to the dorsal one. Vulva depressed, with two indistinct epiptygmata deep at the end of vagina vera. Two genital branches opposed. Spermatheca small, dorsally offset, empty; oocytes in one row except for multiplication area. Tail more rounded dorsally, with distinct terminal ventral projection; 6–10 ventral tail annuli, the terminal annuli are narrower than the other tail annuli. Phasmids dotlike, 3–10 annuli anterior to anus, on or near ventral inner lateral field line.

Males unknown.

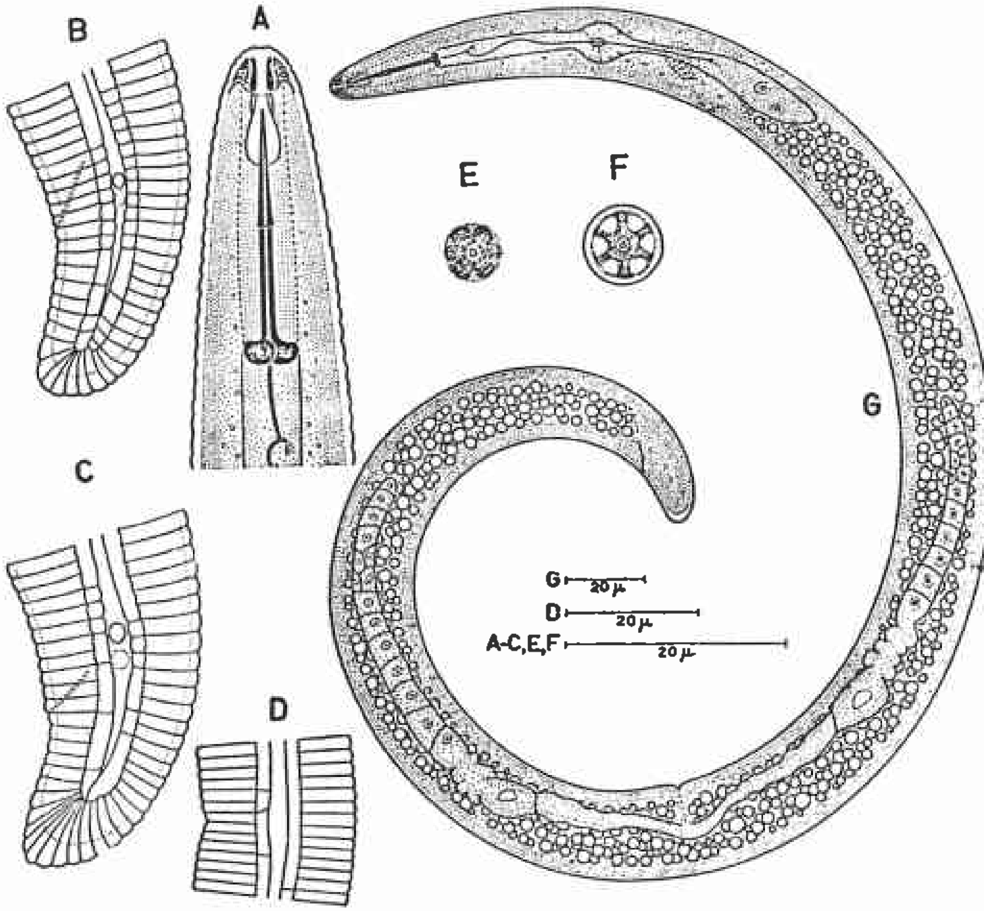

FIGURE 6 *Rotylenchus insularis* (Phillips, 1971) Germani, Baldwin, Bell, and Wu, 1986. (A) Female, anterior end. (B,C) Female, posterior ends. (D) Female, lateral fields near vulva. (E) Female, face view. (F) Female, cross-section through basal labial annulus. (G) Female, entire body. (After Phillips, 1971, courtesy *Qd. J. Agr. Anim. Sci.*)

Rotylenchus calvus has been found on grass in Malawi, and nothing is known of its biology. It is representative of the species formerly in the genus *Varotylus*. The subventral glands extend past the dorsal gland, whereas they are less developed in typical *Rotylenchus*. However, they remain in a symmetrical position, quite different from the asymmetrical arrangement found in *Helicotylenchus*. As in *Orientylus*, the lip region is smaller, narrower than in typical *Rotylenchus*, and it does not have longitudinal striae. The DGO is more posterior to stylet base. The posterior genital branch is well developed.

5. *Rotylenchus insularis* (Phillips, 1971) Germani, Baldwin, Bell, and Wu, 1986 (Fig. 6)

Measurements (after Phillips, 1971). Females (n = 7): L = 558 μm (515–596); a = 22 (22–23); b = 6.0 (5.3–6.7); b' = 4.6 (4.1–5.1); c = 37 (30–37); c' = 1.2 (0.9–1.5); V = 61% (57–65); stylet = 23 μm (22–24).

Description. Females: Body in spiral shape. Lip region hemispheric, not set off, with four annuli; basal lip annulus without longitudinal striae. Stylet knobs rounded, with flattened anterior surfaces. DGO 7 μm behind stylet. Hemizonid one annulus anterior to excretory pore. Spermathecae without sperms. Epiptygma not seen. Scutellum opening 1.9 μm (1.8–2.1) in diameter, three annuli anterior to anus. Lateral fields areolated in esophageal region and near scutella, occasional areolation of outer bands in midbody. Tail broadly rounded, slightly more curved dorsally, with 12 ventral annuli; terminal striations similar to other tail annuli.

Males unknown.

Rotylenchus minutus and four of the five *Scutellonema* species described by Phillips (1971) from Queensland have phasmid openings 1.2–2.1 μm in diameter. This is smaller than the diameter of the opening in typical *Scutellonema* (at least 3 μm, up to 9 μm), but larger than the phasmid opening in *Rotylenchus*, often less than 1 μm in diameter. The two phasmids are a little above anus level, and not quite opposed to each other, which is another difference from typical *Scutellonema*. The lateral field with four lines is areolated near the phasmids in at least three of the species (*R. minutus, R. insulare, R. impar*), and striae are seen near the phasmids in a few specimens of *R. laeviflexum*, a character at variance with typical *Rotylenchus*, but more frequent in *Scutellonema*. The basal lip annulus has no longitudinal striae. These four species seems somewhat intermediate between *Rotylenchus* and *Scutellonema*. They were placed in *Rotylenchus* by Germani et al. (1986) and Fortuner (1987a), but left in *Scutellonema* by Siddiqi (1986).

V. *SCUTELLONEMA* ANDRÁSSY, 1958

A. Diagnosis

Hoplolaiminae. Females: Body spiral to C-shaped or almost straight. Labial region narrow truncate to offset rounded; annulated, with or without longitudinal striae. First labial annulus divided into six sectors, lateral sectors smaller than the others (SEM). Amphid apertures oval between labial disk and lateral sectors. Lateral field with four lines usually areolated near phasmids and anteriorly, sometimes transverse striae scattered over whole field. Labial framework, stylet and stylet knobs average-sized for the family; knobs rounded to indented. DGO 4–8 μm from stylet base. Esophageal gland overlap dorsal and lateral. Two genital branches outstretched, equally developed. Epiptygmata present. Tail short, rounded. Phasmids enlarged (scutella) situated opposite each other, near anus level.

Males. Caudal alae enveloping tail tip, regular or rarely deeply lobed. No secondary sexual dimorphism.

Type species: *Scutellonema bradys* (Steiner and Le Hew, 1933) Andrássy, 1958.

B. Systematic Relationships

The species in *Scutellonema* are identified by the phasmids, enlarged into scutella, and opposite each other near the anus level. The development of scutella seems to be a valid apomorphy because it probably has some evolutionary advantage (a wide open scutellum may be a better chemoreceptor than a regular phasmid with a small opening). *Rotylenchus*, with a small phasmid opening and no phasmidial ampulla, is accepted and differentiated from *Scutellonema* and the genera with scutella.

C. Representative Species

1. *Scutellonema brachyurus** (Steiner, 1938) Andrássy, 1958 (Fig. 7)

Measurements: Females: Composite description from Steiner (1938), Williams (1960), Sher (1964a), van den Berg and Heyns (1973), Sharafat-Ali et al. (1973), Geraert et al. (1975), Ratanaprapa and Boonduang (1975), van den Berg and Kirby (1979), Khan and Nanjappa (1970: *S. bangalorensis*), and Sivakumar and Selvasekaran (1982: *S. conicaudatum*). For each measurement is given the average and standard deviation calculated from the mean values, and the range of individual values. Females (n = 11): L = 0.715 mm ± 0.0758 (0.5– 1); a = 26 ± 2.770 (16.7–36); b (n = 9) = 6.6 ± 0.780 (4.5–10.3); b' (n = 6) = 5.7 ± 0.451 (4–9.1); c = 70.6 ± 15.444 (37.2–127.7); c' (n = 4) = 0.55 ± 0.083 (0.4–0.9); V = 58.75% ± 1.636 (51.9–67); stylet = 27 µm ± 1.684 (21.7–31). Males after Sher, 1964a. (n = 8): L = 0.63–0.85 mm; a = 25–33; b = 6.1–7.5; b' = 4.5–6.6; c = 45–58; stylet = 24–27 µm; gubernaculum = 12–14 µm; capitulum = 7–9 µm. After van den Berg and Heyns, 1973 (n = 7): L = 0.7 mm (0.6–0.8); a = 34.3 (31.6–36.9); b = 7.3 (6.9–8.1); b' = 5.4 (5.3–5.6); c = 41.1 (37–39.8); stylet = 22.9 µm (22.4–24.3); spicules = 26.1 µm (25–27.2); gubernaculum = 12 µm (10.7–13.2); capitulum = 7.5 µm (7– 8.1).

Description. Females: Body forming a single spiral occasionally arcuate; annuli distinct, average annulus width 1.4 µm near midbody. Lateral fields about one-fourth as wide as body, areolated from the anterior end to the excretory pore and at phasmids, marked by four incisures. Lip region hemispheric, slightly set off by a constriction, with three to four (sometimes five) annuli of irregular width. In SEM face view, labial disk round to oval; first lip annulus divided into six sectors; lateral sectors slightly smaller than submedian ones (Germani et al., 1986). Basal annulus marked by six longitudinal striae. Labial framework strongly sclerotized, its basal ring extending posteriorly over one body annulus. Stylet well developed, cone almost as long as shaft (m = 48.1 ± 1.737; 43–52.3); basal knobs prominent, rounded with slightly flattened anterior surfaces, 4.5 µm across. DGO rather obscure, about 5 µm (2–7) behind spear knobs. Cephalids, hemizonid, and hemizonion indistinct. Esophagus with a slight constriction at base of isthmus. Median esophageal bulb ovoid, extending over 8 (8–10) body annuli. Excretory pore at level of esophageal glands, at 132 µm (115–150) or 88 (80–97) body annuli from the anterior end. Esophageal glands overlapping intestine dorsally and dorsolaterally. Hemizonid at level of, or up to eight annuli anterior to, excretory pore; hemizonion 5–10 body annuli posterior to hemizonid. Oocytes in a single row except in multiplication zone. No spermatheca or sperms in uterus. One or two epiptygmata indistinct, inwardly folded. Intestine slightly overlapping rectum. Tail broadly rounded; annuli following tail contour; annuli slightly irregular and coarser than adjacent body annuli; 12 (7–19) annuli between anus and tail tip; inner cytoplasmic core terminally flattened or with shallow depression. Phasmid opening 2–4 µm in diameter from two annuli behind to two annuli in front of anus; phasmid ampulla 3.5–5 µm in diameter, but according to Wang and Chen (1985), the volume of the ampulla is affected by the osmolarity of the environment.

Males: Absent from most populations. Rarely present in small numbers (one for several hundred females). Similar to female in most details. Spicules arcuate, with a swollen head, a crescentic shaft, and a blade composed of a central trunk with two winglike lateral vela. Gubernaculum completely embedded in the cuticle of the spicular pouch; the gub-

*The species name is often spelled "*brachyurum*"; however *urus* (= tail) is a substantive in apposition, and its ending does not change whatever the gender of the generic name with which it is combined [ICZN, Art. 31 (b) (ii)].

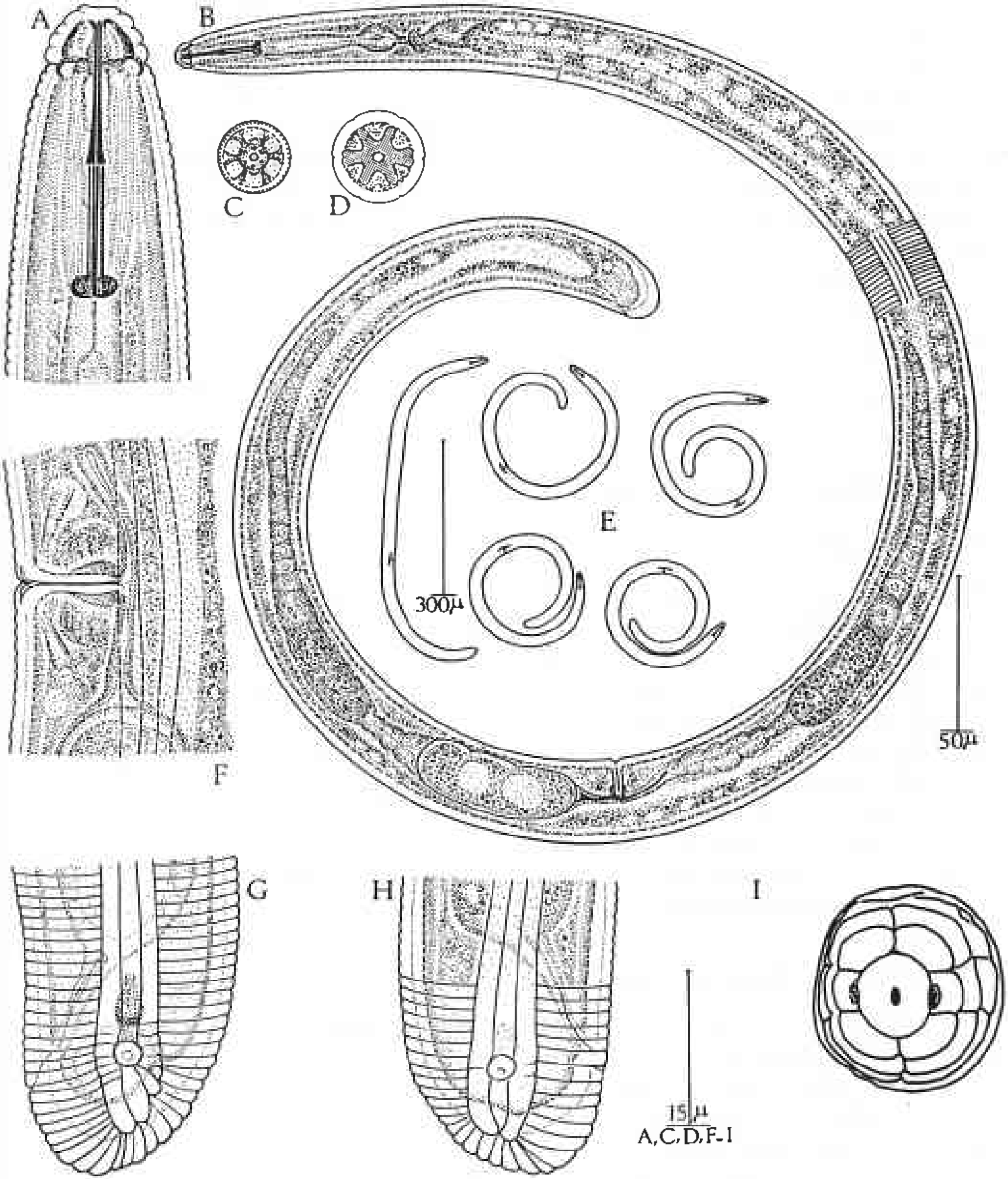

FIGURE 7 *Scutellonema brachyurus* (Steiner, 1938) Andrássy, 1958. (A) Head view. (B) Female, entire body. (C,I) Face view. (D) Cross-section through basal labial annulus. (E) Thermal death body posture. (F) Vulval region. (G,H) Posterior ends. (Siddiqi, 1974, courtesy Commonwealth Agricultural Bureaux.)

ernaculum proper is connected to a capitulum lying in the spicular pouch between the spicules; in the midregion the capitulum separates from the dorsal wall of the spicular pouch to form a bar tongue that bears the proximal titillae (Wang and Chen, 1985b).

Scutellonema brachyurus is widely distributed in the world. It occurs on a number of cultivated plants. It has been found in virgin soil in Natal, and Sher (1964a) infers from this fact that this species is native from southern Africa. It is primarily an ectoparasite, but it may also be found in the root cortex. It is a semiendoparasite on sycamore. High populations may build up on suitable hosts. Reports of injury to the plant are conflicting. No apparent injury was caused by *S. brachyurus* to red clover (Chapman, 1963); it caused a reduction in leaf growth of amaryllis but no concomitant destruction of bulb and roots although it was found in the epidermis and cortical tissues (Nong and Weber, 1964); it was found associated with stunted sugarcane in Malagasy (Luc, 1959). Root growth of pine seedlings increased rather than decreased with high inoculum of *S. brachyurus*, possibly because of parasitic stimulation (Ruehle, 1973).

VI. *AOROLAIMUS* SHER, 1963

A. Diagnosis

Hoplolaiminae. Females: Body spiral to C-shaped, medium-sized. Lip region slightly offset or continuous with body, with or without annuli and/or longitudinal striae. Lateral field with four or less incisures. Labial framework and stylet medium-sized; stylet knobs flattened to indented anteriorly. DGO 3–10 μm from stylet base. Esophageal glands with three nuclei, overlap intestine dorsally and laterally; intestine symmetrically arranged between the subventral glands. Two genital branches outstretched, equally developed. Tail short, rounded. Phasmids enlarged to scutella erratically situated on body, not opposite each other, anterior to anus level; sometimes one scutellum is anterior to vulva level.

Males. Caudal alae enveloping tail, lobed or regular. Secondary sexual dimorphism visible in labial region and esophageal structures smaller in males.

Type species: *Aorolaimus helicus* Sher, 1963.

B. Systematic Relationships

The position of the scutella (on tail vs. on body) may have some biological significance and *Aorolaimus* is accepted as a valid genus and differentiated from *Scutellonema*, with scutella on tail. However, the exact location of the scutella on the body (e.g., anterior or posterior to the vulva) cannot be accepted as a generic character in view of the variability of this character in this group and in *Hoplolaimus*. The synonymy of *Peltamigratus* and *Nectopelta* to *Aorolaimus* proposed by Fortuner (1987a) is upheld here.

The lateral lip sectors of the face view, as seen with SEM in *Rotylenchus* and *Scutellonema*, have either the ancestral arrangement (six sectors of about equal size) or the lateral sectors are smaller than the submedian sectors. Some species in *Aorolaimus* (syn. *Peltamigratus*) have one or the other of these two arrangements, or the lateral sectors are longer than the submedian ones, or the lateral sectors merge with the first labial annulus. The variability of this character makes it difficult to accept it as a valid criterion for evolutionary relationships. It is known only in a few species (particularly no *Aorolaimus stricto sensu* have been studied with SEM), and future studies may shed more light on its value and significance.

C. Representative Species

1. *Aorolaimus christiei* (Golden and Taylor, 1956) Fortuner, 1987 (Fig. 8)

Measurements (after Sher, 1964b). Females (n = 20): L = 0.67–0.87 mm; a = 25–31; b = 6.4–8.3; b' = 5.3–7.3; c = 45–80; V = 53–58%; stylet = 30–34 μm; o = 11–18; anterior phasmid = 76–85%; posterior phasmid = 82–90%. Males (n = 10): L = 0.66–0.81 mm; a = 26–33; b = 6.7–8.6; b' = 5.3–6.7; c = 39–58; stylet = 29–33 μm; o = 11–18; anterior phasmid = 76–84; posterior phasmid = 85–89; gubernaculum = 11–15 μm; spicules = 27–31 μm;

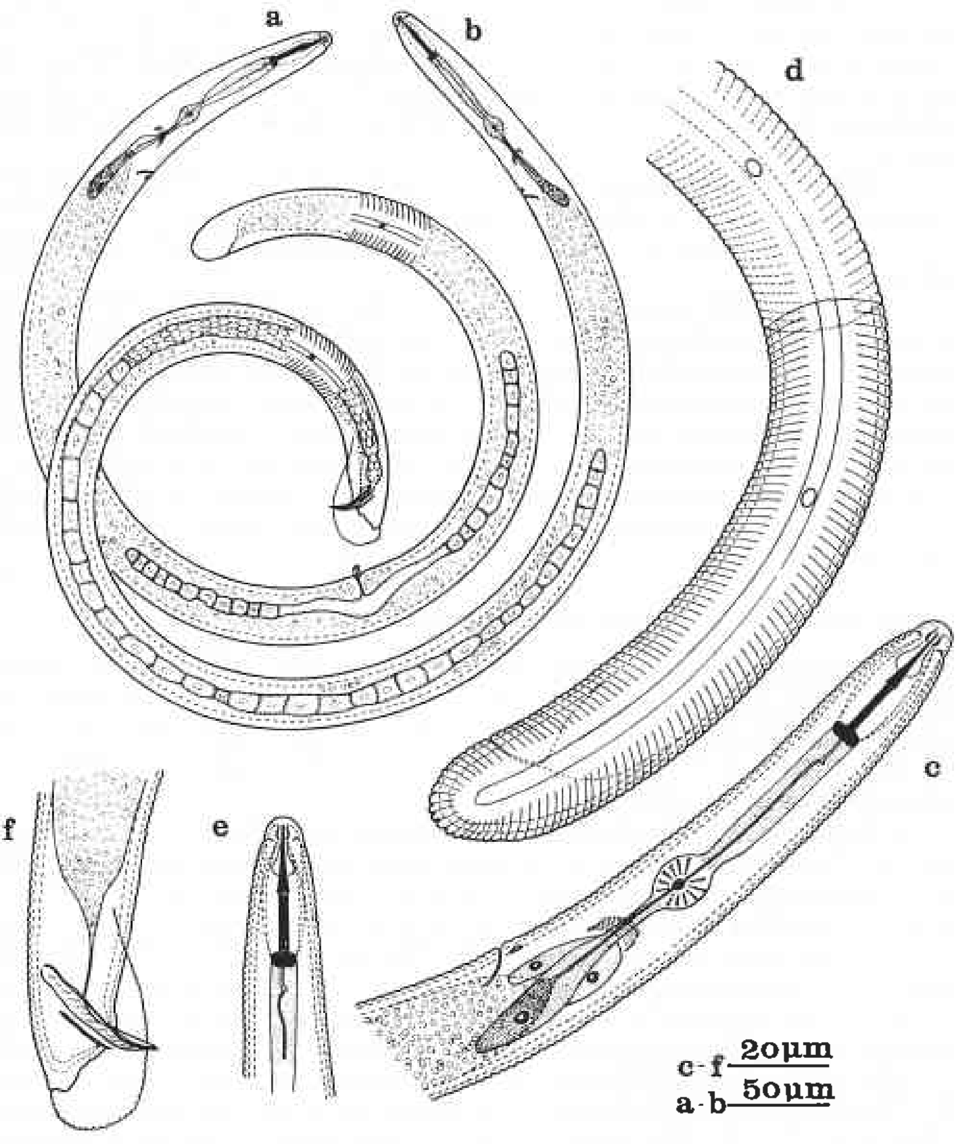

FIGURE 8 *Aorolaimus christiei* (Golden and Taylor, 1956) Fortuner, 1987. (a) Female, entire body. (b) Male, entire body. (c) Female, esophageal region. (d) Female, posterior end. (e) Male, anterior end. (f) Male, posterior end.(Bittencourt and Huang, 1986, courtesy *Rev. Nématol.*)

capitulum = 6–8 μm. After Bittencourt and Huang, 1986; Females (n = 5): L = 0.88 mm ± 0.08; a = 31.5 ± 2.7; b = 8.7 ± 0.9; b' = 6.7 ± 0.9; c = 53.8 ± 2.6; o = 19.9 ± 3.4; V = 57.3% ± 2.3; stylet = 29.6 μm ± 1; anterior phasmid = 80.4% ± 1.4; posterior phasmid = 88.1% ±1. Males (n = 2): L = 0.83–0.91; a = 34.7–39; b = 9.1; b' = 7.1–7.9; c = 56.2–61.3; stylet = 28 μm; spicules = 26–29 μm; gubernaculum = 11–12 μm.

Description. Females: Body usually in an open C-shape. Body annuli 1.3–1.4 μm wide at midbody. Lip region slightly offset or continuous with body, with three indistinct annuli. Stylet knobs often slightly flattened anteriorly. DGO about 5 μm posterior to stylet base. Excretory pore usually opposite anterior part of the esophageal glands. Hemizonid zero to two annuli anterior to excretory pore. Hemizonion about eight annuli below hemizonid. Spermatheca round, usually partially filled with sperms. Two epiptygmata, well developed, projecting outward. Lateral field usually with two lines, sometimes four lines on part of the body. Intestine slightly overlapping rectum. Tail rounded to slightly asymmetrical dorsally, shorter than body anal diameter, with 6–10 annuli; terminal annuli deeply marked.

Males: Similar to females except for sexual dimorphism. Caudal alae deeply indented. Gubernaculum with titillae. Capitulum present.

This species is known from Florida and Brazil. Its biology and pathogenicity have not been studied.

A. christiei and some of the species formerly in the genus *Peltamigratus* were placed by Eerens and Loof (1985) in a phenetic group, "Peltamigratus Group I." In this group of species, the scutella are not opposite each other, but they are both situated between vulva and anus. The lateral fields have two lines, or at least two lines in posterior part of the body even though there may be four lines anteriorly. There are no areolations near the scutella. The lip region is without longitudinal striae, and generally without lip annuli (rarely present). The male caudal alae generally are not indented (rarely indented). This group is represented by *P. christiei* and other species from Central and South America, Florida, and western Africa.

2. *Aorolaimus annulatus* (Mulk and Siddiqi, 1982) Fortuner, 1987

Measurements (after Mulk and Siddiqi, 1982). Females (n = 4): L = 0.75 (0.69–0.81) mm; a = 28 (26–29); b = 8 (6.4–8.6); c = 44 (32–63); c' = 0.8 (0.6–1.2); V = 55 (52–59); stylet = 26 μm (25–27). Males (n = 4): L = 0.69 mm (0.67–0.71); a = 30 (26–33); b = 7.5 (7–8); c = 35 (34–36); c' = 1.2–1.3; T = 53% (49–56); stylet = 26 μm (25–26.5); spicules = 30–31 μm; gubernaculum = 15–15.5 μm.

Description. Females: Body arcuate to C-shaped, maximum width 25–29 μm, annuli 1.6–1.7 μm wide at midbody. Lateral field with four smooth lines extending to near tail tip, areolated only anteriorly at phasmids. Scutella postvulval, anterior one at 64–70% and posterior one at 84–92% of body length. Lip region hemispheric, offset, with four to five distinct annuli. Stylet well developed, cone 11–12.5 μm long or 45% (43–47) of stylet length; knobs rounded, compact 4.5–5 μm across. DGO 7–8 μm from stylet base. Median esophageal bulb oval, about 11 × 9 μm. Esophageal gland lobe about one body width long. Excretory pore near base of gland lobe. Hemizonid indistinct, one to two annuli anterior to excretory pore. Vulva with two epiptygmata which may or may not be projecting beyond the body surface. Spermathecae with sperm. Rectum shorter than anal body width. Tail hemispheric to conoid-rounded, with 7–15 ventral annuli, terminal annuli roughly about the same width as adjacent annuli but slightly offset from them.

Males: Generally similar to females. Body C-shaped. Anterior and posterior phasmids at 60–70% and 84–88% of body from anterior end, respectively.

Siddiqi (1986) proposed a new genus, *Nectopelta* (syn. *Aorolaimus*), for species like *A. annulatus* with both scutella are posterior to vulva as above, but with lateral fields always with four lateral lines, and always areolated near scutella. The lip region always has annuli; labial longitudinal striae may be present or absent. The males have caudal alae indented or not indented. *Nectopelta* was rejected by Fortuner (1987a).

The species that were placed in the genus *Nectopelta* have the same geographic distribution as those in *Peltamigratus* (*sensu* Siddiqi). *A. indicus* has been reported in Iraq and India.

3. *Aorolaimus helicus* Sher, 1963 (Fig. 9)

Measurements (after Sher, 1963). Females (n = 20): L = 0.78–0.98 mm; a = 24–33; b = 7.9–9.9; b' = 6.2–7.8; c = 43–71; V = 54–60%; stylet = 24–29 μm; o = 16–24. Males (n = 10): L = 0.72–0.84 mm; a = 26–36; b = 6.2–9.7; b' = 4.7–6.5; c = 28–36; stylet = 23–28 μm; spicules = 27–32 μm; gubernaculum = 11–15 μm; capitulum = 10–14 μm.

Description. Females: Body in spiral shape. Lip region rounded, slightly set off from body, with four to five annuli; basal annulus with longitudinal striae. Stylet knobs rounded to oval-shaped. Excretory pore at level of esophagointestinal valve. Hemizonid just anterior to excretory pore, two annuli long. Hemizonion and caudalid not seen. Anterior phasmid 30–40%, and posterior phasmid 80–86% of body length from anterior end. One or two epiptygmata. Spermatheca round, partially filled with sperms. Intestine slightly overlapping rectum. Tail rounded to broadly rounded, more curved dorsally, with 9–13 ventral annuli.

Males: Generally similar to females. Lip region more broadly rounded, more set off from body. Anterior phasmid at 30– 39%, and posterior phasmid at 78–84% from anterior end. Gubernaculum with inconspicuous titillae.

Aorolaimus helicus represents a group of species that constituted the genus *Aorolaimus* when it was first described by Sher (1963). *Aorolaimus s. str.* has lateral fields always with four lateral lines, and always areolated near scutella; lip region always with annuli; labial longitudinal striae may be present or absent. The only difference with the taxa traditionally placed in *Peltamigratus* is that one phasmid is anterior to the vulva. These species differ from the genus *Hoplolaimus*, also with one phasmid anterior to vulva, in that they have stylet and cephalic framework not massive, and stylet knobs not tulip-shaped. The males have caudal alae not indented.

Species in *Aorolaimus s. str.* have been found in the USA (Great Plains, Maryland, South Carolina), the Mediterranean (Spain, Morocco, Israel), and India (Maharashtra). Their biology and pathogenicity is unknown.

VII. *HOPLOLAIMUS* VON DADAY, 1905

A. Diagnosis

Females: Body straight, large (1–2 mm long). Lip region offset from body, wide, anteriorly flattened, with clearly marked annuli, and with longitudinal striae. Lateral field with four lines or less, generally areolated at level of phasmids and anteriorly, sometimes with striae irregularly scattered over entire field, rarely not areolated. Labial framework and stylet massive; stylet knobs anchor or tulip-shaped. DGO 3–10 μm from stylet base. Esophageal glands overlap intestine dorsally and laterally; sometimes gland nuclei duplicated to a total of six nuclei; intestine symmetrically arranged between the subventral glands. Two genital

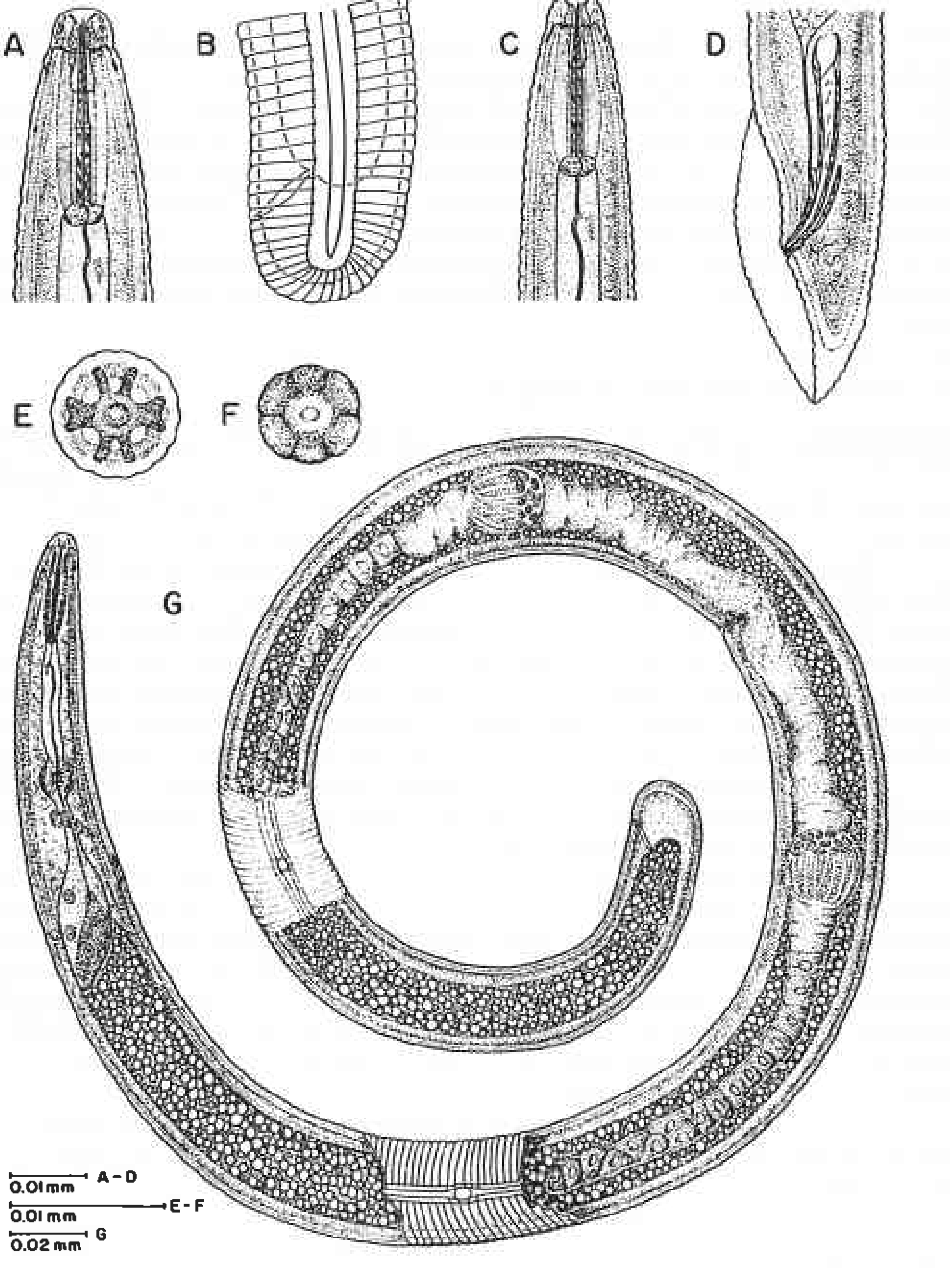

FIGURE 9 *Aorolaimus helicus* Sher, 1963. (A) Female, anterior end. (B) Female, posterior end. (C) Male, anterior end. (D) Male, posterior end. (E) Female, cross-section through basal labial annulus. (F) Female, face view. (G) Female, entire body. (Sher, 1963, courtesy *Nematologica*.)

branches outstretched, equally developed. Tail short, rounded, phasmids enlarged to scutella erratically situated on body, anteriorly to anus level, and sometimes anterior to vulva level, not opposite each other.

Males: Caudal alae enveloping tail, regular. Secondary sexual dimorphism visible in labial region and esophageal structures smaller in males.

Type species: *Hoplolaimus tylenchiformis* von Daday, 1905.

Members of the genus *Hoplolaimus* are easy to recognize under the dissecting microscope. Under the compound microscope they are seen to have scutella present, erratic on body (not on tail or near anus), and esophageal glandular overlap mostly dorsal. There is a possible confusion with *Aorolaimus* (syn. *Peltamigratus*) that also have erratic scutella. Differences exist in the shape of anterior end, cephalic framework, and stylet knobs. *Hoplolaimus* is more robust, and larger than *Aorolaimus*.

B. Systematic Relationships

All the species in the genus *Hoplolaimus* share a number of apomorphies as identified from an hypothetical *Scutellonema*-like ancestor: body always large, robust, straight, stylet large, strong, with tulip-shaped knobs, each knob with toothlike projection, massive cephalic framework, labial area clearly demarcated from body, with well-marked annuli, basal labial annulus wide, giving an almost trapezoidal outline to the lip region.

Four groups of species can be defined within the genus (Fortuner, 1974) depending on number of gland nuclei (ancestral state: three nuclei; derived state: six nuclei); the number of lateral lines (ancestral four lines, derived less than four lines); the position of the excretory pore below (ancestral) or above (derived) the hemizonid; and the presence of either regular or irregular striae on the basal lip annulus.

A separate genus name, *Basirolaimus*, was proposed by Shamsi (1979) for the species that have extra gland nuclei, regression of the lateral field, migration of the hemizonid above the excretory pore, and diminution of the number of striae on the basal lip annulus. However, *H. clarissimus* has all the characters of *Hoplolaimus sensu stricto*, except that it has six gland nuclei, as in *Basirolaimus*. The group of species including *H. pararobustus* has all the characters of *Basirolaimus* except that it has only three gland nuclei. The migration of the excretory pore above the hemizonid has been observed in several taxa, widely separated from hoplolaimids, such as *Sychnotylenchus* (Anguinidae) and *Meloidogyne* (Heteroderidae).

While the characters used to define *Basirolaimus* are useful for practical identification, they do not exhibit a clear evolutionary pattern. The genus was rejected by Luc (1981) and Fortuner (1987a).

C. Representative Species

1. *Hoplolaimus galeatus* (Cobb, 1913) Thorne, 1935 (Fig. 10)

Measurements (after Sher, 1963). Females (n = 20): L = 1.24–1.94 mm; a = 25–34; b = 7.6–10.8; b' = 6–8.8; c = 42–82; V = 52–60%; stylet = 43–52 µm; o = 10–17; anterior phasmid at 30–46% on body length; posterior phasmid at 75–88% of body length. Males (n = 10): L = 1.05–1.56 mm; a = 25–32; b = 8.3–10.3; b' = 6–8.4; c = 28–40; stylet = 40–48 µm; o = 10–17; anterior phasmid at 29–45% of body; posterior phasmid at 75–89% of body length; gubernaculum = 20–28 µm; spicules = 40–52 µm; capitulum = 16–20 µm. After Thorne and Malek (1968): Females: L = 1.1–1.5 mm; a = 22–26; b = 7.4–8.6; c = 48–54; V = 55%. Males: L = 0.9–1.3 mm; a = 27–30; b = 6.5–7; c = 28–32; T = 42–50%. After Doucet (1980).

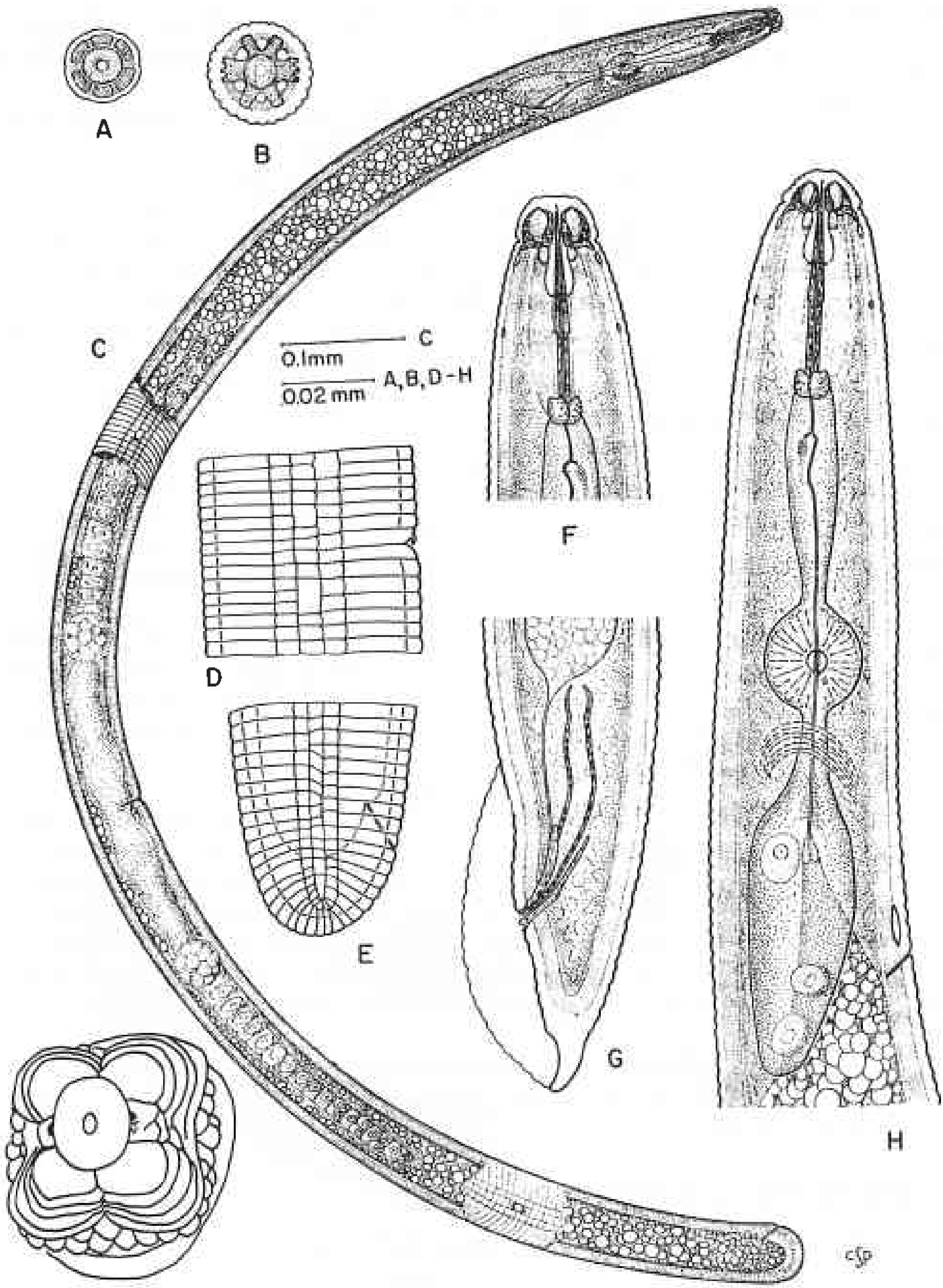

FIGURE 10 *Hoplolaimus galeatus* (Cobb, 1913) Thorne, 1935. (A) Female, face view. (B) Female, cross-section through the basal labial annulus. (C) Female, entire body. (D) Female, surface view at vulva. (E) Female, posterior end. (F) Male, anterior end. (G) Male, posterior end. (H) Female, anterior end. (Sher, 1961, courtesy *Nematologica*.)

Females ($n = 10$): L=1.4 mm, 0.07; a = 29.1, 1.42; b = 9.7, 0.59; b' = 6.9, 0.47; c = 55.1, 8.24; V = 0.84, stylet = 45.4 μm, 1.67; tail = 27.3 μm, 4.1. Males (n = 10): L = 1.2 mm, 0.07; a = 29.5, 2.53; b = 8.6, 0.89; b' = 6.5, 0.63; c = 33, 1.71; stylet = 43.2 μm, 0.57; tail = 38.2 μm, 3.03; spicules = 49 μm, 2.15; gubernaculum = 24.5 μm, 1.02; capitulum = 15.5 μm, 2.33.

Description. Females: Body slightly ventrally curved when relaxed. Cuticle consisting of six layers (Wen and Chen, 1972). Lateral field with four lines, usually areolated but occasionally only partly so. Cephalic region offset usually with five annuli, forming a low cone generally with flattened sides. All labial annuli divided into tilelike elements, and basal annulus with 32–36 regular longitudinal striations. In SEM face view, labial disk oval, well marked, first labial annulus divided into six sectors, the submedian sectors well developed, rounded, each with a papilla, the two lateral sectors visibly smaller. Amphidial apertures a long slit along the labial disk. Four labial annuli with a general quadrilobed shape, with two longitudinal lines in dorsal and ventral position. Basal annulus somewhat squarish, divided in many tilelike rounded parts, all more or less of the same size, most arranged regularly in a row, but occasionally in two rows (Hirschmann, 1983). Tail rounded, with 10–16 annuli. Cephalic framework massive. Spear knobs with anteriorly directed processes. Cephalic framework massive. Median bulb spheroid. Esophageal glands with three nuclei. Dorsal gland opening near spear base. Intestine overlapping rectum and usually extending into tail. Excretory pore near level of esophagointestinal valve. Hemizonid about two annuli long situated just anterior to excretory pore. Hemizonion about five annuli posterior to excretory pore. Caudalid about eight annuli anterior to anus. Ovaries outstretched, spermathecae round to oval. One or two epiptygmata, usually conspicuous.

Males: Body smaller and more slender than female. Cephalic region higher and less conoid than female, hemispheric with convex sides, without tiling or with striae only on basal annulus. Spicules slightly arcuate; the outer one with a distinct velum seen with SEM (Högger and Bird, 1974). Gubernaculum with two lateral titillae, bent distally in some specimens. The gubernaculum stays protruded out of the cloacal orifice, even when all the other male appendages are retracted. When this occurs, only the gubernaculum and its two lateral titillae are visible in a ventral SEM view (Högger and Bird, 1974). Capitulum present. Caudal alae broad, striated, enveloping tail.

The population described by Doucet (1980) has scutellum diameter 8–9 μm, always two epiptygmata, and intestine overlapping rectum but not continuing into tail.

Hoplolaimus galeatus is widely distributed in the USA. It has also been reported from Canada, Central and South America, and India. It has a large variety of hosts, particularly cotton, trees (pine, oak, sycamore, etc.), turf grasses, other graminaceous plants, etc. It lives as an endoparasite on cotton, causing considerable damage to cortex and vascular tissue. On pine, most of the cortex of infested roots was destroyed. In sycamore, *H. galeatus* causes extensive root necrosis but it is unable to penetrate completely within the roots and its body partly protrudes out of the root.

Hoplolaimus galeatus is representative of a group of *Hoplolaimus* species characterized by lateral field with four lines, and esophageal glands with three nuclei. This group includes *H. tylenchiformis*, *H. californicus*, *H. concaudajuvencus*, *H. galeatus*, and more.

2. *Hoplolaimus pararobustus* (Schuurmans Stekhoven and Teunissen, 1938) Coomans, 1963 (Fig. 11)

Measurements: Composite measurements from descriptions published in Andrássy (1961, *H. kittenbergeri*), Coomans (1963), Elmiligy (1980), Goodey (1957, *H. proporicus*), Maqbool and Ghazala (1988), Sher (1963), Suryawanshi (1971), van den Berg and Heyns (1970), Vovlas and Lamberti (1985), and Whitehead (1959, *H. angustalatus*).

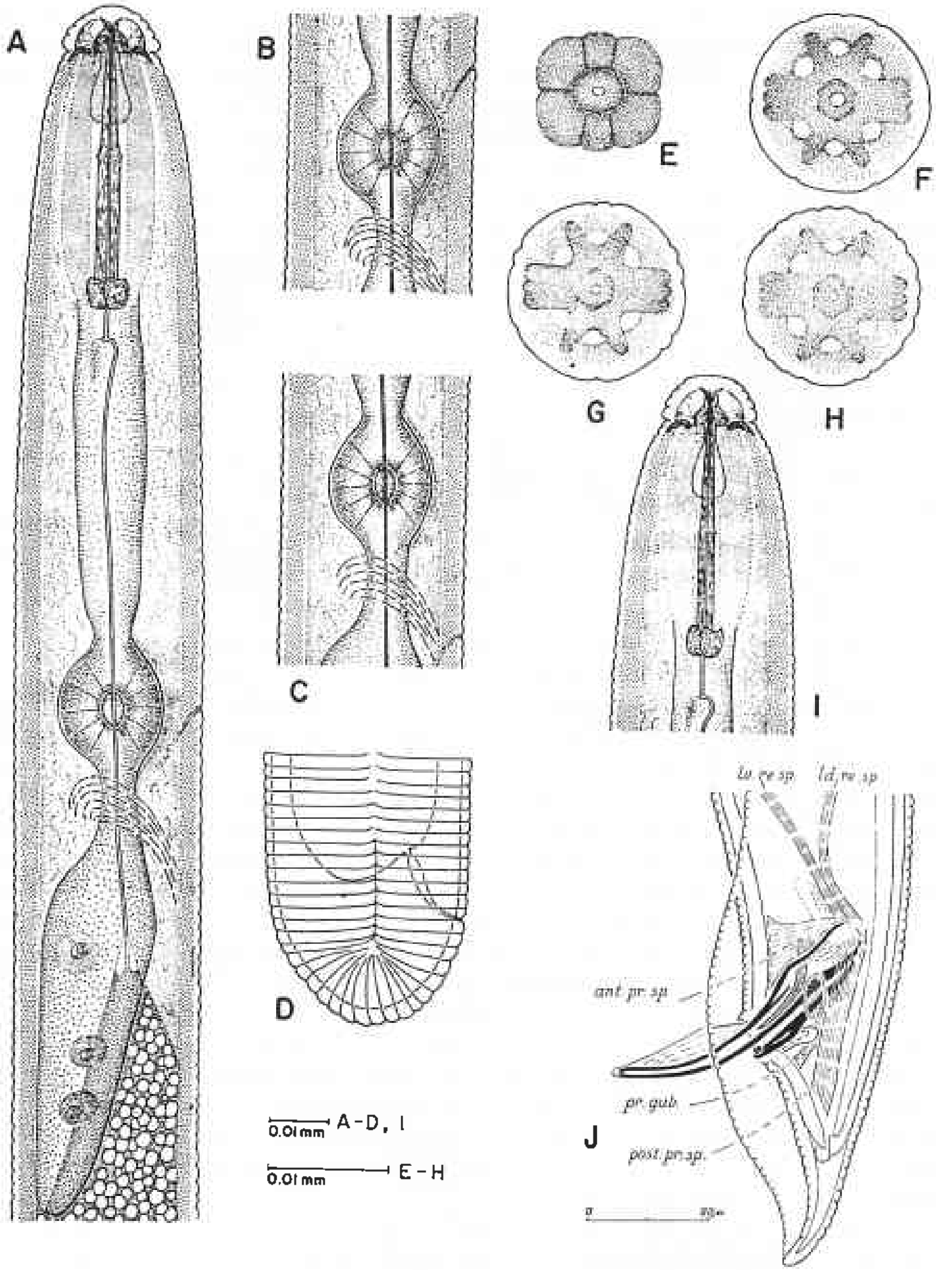

FIGURE 11 *Hoplolaimus pararobustus* (Schuurmans Stekhoven and Teunissen, 1938) Coomans, 1963. (A) Female, esophageal region. (B,C) Female, median esophageal bulb. (D) Female, posterior end. (E) Female, face view. (F–H) Female, cross-section through basal labial annulus. (I) Male, anterior end. (J) Male, posterior end; ant.pr.sp. = *anterior protractor spiculi*; post.pr.sp. = *posterior protractor spiculi*; lv. and ld. re.sp. = *lateroventral* and *laterodorsal retractor spiculi*; pr.gub. = *protractor gubernaculi*. (Sher, 1963; Coomans, 1963, courtesy *Nematologica*.)

Females (n = 17): L = 1.314 mm ± 0.127 (0.94–1.8); a = 27.3 ± 2.689 (20–39); b (n = 14) = 8.98 ± 1.361 (6–14.1); b' (n = 7) = 7.1 ± 0.682 (5.1–10); c = 60.8 ± 15.185 (40–164); c' (n = 7) = 0.67 ± 0.135 (0.4–0.9); V = 56.28% ± 2.6096 (51–62); stylet = 42.3 μm ± 2.378 (37.5–49). Males (n = 14): L = 1.158 mm ± 0.102 (0.93–1.5); a = 29.2 ± 2.227 (21–37.2); b = 8.5 ± 1.328 (6.2–13.8); b' (n = 7) = 6.6 ± 0.570 (5–8.7); c = 36.9 ± 6.605 (22.2–51.9); c' (n = 4) = 1.6 ± 0.206 (1.4–2.1); stylet (n = 11) = 40.8 μm ± 2.676 (35–46); spicules = 46.9 μm ± 3.318 (40–57), gubernaculum = 21.9 μm ± 2.4296 (15.4–31); capitulum (n = 10) = 16.1 μm ± 2.728 (10.3–20).

Description. Females: Body cylindrical, straight to slightly ventrally arcuate when heat-relaxed; cuticle annuli distinct, about 2 μm wide; subcuticular annuli about 1 μm wide. Lip region hemispheric, set off from body by a constriction, usually with four distinct annuli; sometimes with three on one side and four on the other; as many as six annuli may be present. Longitudinal striae on lip annuli variable in number, on basal annulus 7–25 striae may be seen in face views. SEM face views show a round/oval labial disk and six labial sectors; the lateral sectors are smaller than the submedian ones; longitudinal striae divide the basal annulus in irregular sections, triangular or rectangular in shape (Vovlas and Lamberti, 1985). Labial framework hexaradiate, heavily sclerotized; lateral sectors smaller than submedian ones. Lateral fields represented by an interruption of body annuli or by a single incisure toward the extremities or along the entire body length; or by two to three incomplete incisures especially in badly fixed specimens. Phasmids as enlarged scutella, scutellum opening diameter 5.3 μm (4.1–6), anterior one at 34% ± 5.725 (22–52) and posterior one at 79.5% ± 2.305 (58–89) of body length from anterior end; anterior one may be on right side and posterior one on the left, or vice versa. Excretory pore distinct, usually opposite the median esophageal bulb, but may be anterior or posterior to it. Hemizonid always posterior (sometimes by as much as 20 annuli) to the excretory pore, about two body annuli wide. Stylet cone about as long as shaft; basal knobs tulip-shaped, with two or more anterior projections. DGO 5.6 μm ± 1.377 (4–8) behind spear base. Esophagus typical of the genus; median bulb rounded, very muscular and with a distinct valvular apparatus in center; three uninucleate esophageal glands extending dorsally or dorsolaterally over the intestine; esophagointestinal junction indistinct. Intestine overlaps rectum. Vulva a transverse slit; one epiptygma anterior or posterior. Spermathecae spherical, axial, with sperms. Ovaries with oocytes in tandem. Eggs 78–96 ± 26–28 μm. Tail short, rounded, usually hemispheric and with 7–15 annuli.

Males: Common. Body ventrally arcuate. Lip region rounded, higher than in females, with three to five (usually four) annuli. Excretory pore near median esophageal bulb, 8–23 annuli in front of hemizonid. Stylet, esophagus, lateral field, and phasmids as in female. Spicules ventrally arcuate, slightly cephalated, with large distal flanges. Gubernaculum troughlike, with titillae. The gubernaculum is said to be protrusible through cloaca, and Coomans (1963) did draw *protractor gubernaculi* and *retractor gubernaculi* muscles, but actual outward movement of the gubernaculum has not been documented. In SEM observation of *H. galeatus* (Högger and Bird, 1974), the gubernaculum protrudes, but it is not protrusible. Bursa large, with crenate margins,enclosing the conoid tail.

Hoplolaimus pararobustus is found in Africa, mostly within the roots of banana, but it can also parasitize coffee, tea, sugarcane, palm trees, various tropical fruit trees, rice, yam, and other plants. It has been described from grass in Maharashtra, India (Suryawanshi, 1971) and various plants in Pakistan (Maqbool and Ghazala, 1988).

On banana, it feeds mostly endoparasitically, but it has occasionally been observed only partially embedded within the roots. On coffee, it feeds semiendoparasitically. Cortex penetration results in cavities and ruptured cells. Numerous irregular brown necrotic lesions develop on the roots of infested coffee plants (Vovlas and Lamberti, 1985).

In the group represented by *H. pararobustus*, the lateral field is degenerate and never shows the regular complement of four lines. The esophageal glands have three nuclei, as in typical *Hoplolaimus*. The group includes *H. pararobustus* and a few other species that have been synonymized by various authors to *H. pararobustus*. The species *H. capensis* that was listed by Siddiqi (1986) as a synonym of *H. pararobustus* is in fact a valid species with longer stylet and spicules.

3. *Hoplolaimus columbus* Sher, 1963 (Fig. 12)

Measurements (after Sher, 1963). Females (n = 20): L = 1.26–1.80 mm; a = 30–38; b = 9.1–12.4; b' = 6.3–9.7; c = 39–57; V = 51–60%; stylet = 40–48 µm; o = 9–13; anterior phasmid = 34–47%; posterior phasmid = 80–90%. After Fassuliotis (1974). Males (n = 8): L = 1.15–1.40 mm; a = 31.9 (25.9–39.2); b = 10.9 (9.58–12.18); c = 29.9 (26.8–33.1); stylet = 42 µm (40.2–43.7); o = 5.2 (4.8–5.2); anterior phasmid = 38% (35.4–42.2); posterior phasmid = 82% (79.7–83.2); spicules = 46.8 µm (36.6–52.5); gubernaculum = 21.3 µm (19.5–23.2). *H. chambus* (after Jairajpuri and Baqri, 1973). Females (n = 14): L = 1.40 (1.24–1.62) mm; a = 31 (28–35); b = 9.8 (8.4–11); b' = 8.1 (7–9.1); c = 58 (52–67); V = 55% (52–56) o = 12–14. Males unknown.

Description. Females: Cephalic region offset, usually with three annuli but a fourth annulus is often seen on one side of the cephalic region due to the division of one of the regular annuli. The basal annulus of the lip region has 10–15 irregular longitudinal striae (six striae in *H. chambus*). Basal plate with six arms, the dorsal and ventral ones being tripartite. Spear knobs with two anterior projecting processes. Esophageal glands with six nuclei, one or two often indistinct. Excretory pore behind the level of the esophagointestinal valve. Hemizonid two to five annuli posterior to excretory pore, two annuli long (9–11 annuli in *H. chambus*). Hemizonion usually not seen. Anterior phasmid 29–47%, posterior phasmid at 79–90% of body length from anterior end. Sher (1963) reported one specimen with both phasmids posterior to vulva. Ovaries outstretched; spermatheca absent (indistinct?). Two epiptygmata. Intestine overlaps rectum, extending partly into tail. Tail rounded with 16–22 annuli from anus to tail end (13 annuli in *H. chambus*). In a population from Georgia, Bird and Högger (1974) observed a peglike projection in the anal region of half of the 22 specimens studied under SEM. The peg was 4 µm long and 1–2 µm in diameter. An orifice of about 0.2 µm in diameter was present at the tip of the peg. Each specimen with anal peg lacked a normal anal opening, and the vulva was covered with cuticle and had no definite orifice. Caudalid usually not seen. Lateral field represented by one indistinct incisure.

The cuticle consists of six layers in four zones: cortical, with three sublayers, medial, striated, and granulated. The granular layer is unique to this nematode and it may explain its resistance to osmotic stress and desiccation (Lewis and Huff, 1976).

Males: Extremely rare. Reported only once from a soybean field in South Carolina present in the ratio of one male for 60 females (Fassuliotis, 1974). Body similar to female except for secondary sexual dimorphism. Cephalic region with three to four annuli with seven to eight irregular longitudinal striae on basal lip annulus. Basal plate with six arms, the lateral ones are tripartite. Excretory pore anterior or posterior to esophagointestinal valve. Hemizonid two to eight annuli posterior to excretory pore and hemizonion 10 annuli posterior to hemizonid. No longitudinal lines present. Gubernaculum troughlike, with distinct titillae. Spicules slightly arcuate with a very thin velum observed only when spicules

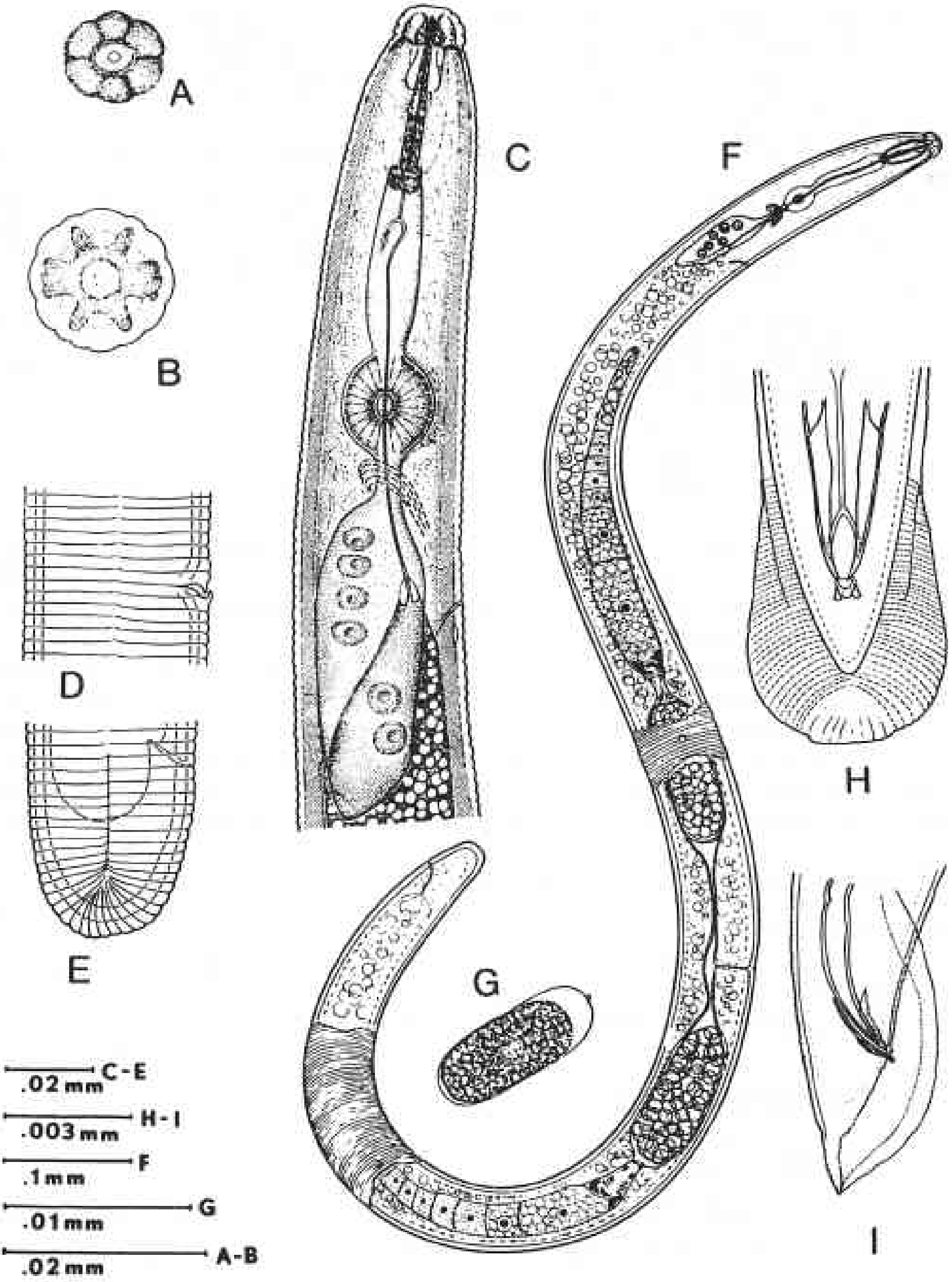

FIGURE 12 *Hoplolaimus columbus* Sher, 1963. (A) Female, face view. (B) Female, cross-section through basal labial annulus. (C) Female, esophageal region. (D) Female, surface view at vulval region. (E) Female, posterior end. (F) Female, entire body. (G) Egg in one-cell stage showing distal stalk. (H) Male, posterior end, ventral view. (I) Male, posterior end, lateral view. (Fassuliotis, 1976, courtesy Commonwealth Agricultural Bureaux.)

are extended. Capitulum distinct, lying between the spicules. Caudal alae begin at about the level of the anterior end of the spicules and extends around the tip of the tail.

Hoplolaimus columbus is known in Georgia, South Carolina, North Carolina. It has been reported in Pakistan. *H. chambus* has been described in India, and it has been reported in Vietnam (Eroshenko and Thanh, 1981). *H. columbus* is reported to be spreading in the USA, which would point to a recent introduction.

In the USA, *H. columbus* is an important parasite of soybean and cotton. It is an endoparasite on soybean roots, penetrating endodermis, pericycle, and phloem. On cotton, it is a semiendoparasite, and it penetrates the cortex but not the endodermis (Lewis et al., 1974).

Life cycle was investigated on alfalfa root and callus cultures by Fassuliotis (1975). Feeding was ectoparasitic on cortical cells in the maturation area of the root. High populations (more than 4000 per 100 cm^3 of soil) were found associated with the roots of dwarfed, chlorotic soybean plants. Few pods were produced. In infested cotton fields, the plants were dwarfed and with purple leaves, and the bolls were small or shedding. Very few other nematodes are found when medium to high populations of *H. columbus* are present (Fassuliotis et al., 1968).

Other crops, wheat, corn, millet (*Panicum miliaceum L.*), lima bean, common bean, watermelon, okra, and numerous weeds are excellent hosts of *H. columbus*. This makes carefully planned crop rotations and good control of weeds important factors for a successful control of the nematode (Stokes, 1977).

A number of species similar to *H. columbus* were grouped in the genus *Basirolaimus* because of degenerate lateral field with less than four lines and six esophageal gland nuclei. Siddiqi (1986) claims that this results from the presence of four nuclei in the dorsal gland instead on the usual single one, but he does not state the origin of this observation. Included in the genus *Basirolaimus* were *H. seinhorsti, H. columbus, H. indicus, H. puertoricensis,* and others, mostly from India. *Basirolaimus* is a synonym of *Hoplolaimus*.

4. *Hoplolaimus clarissimus* Fortuner, 1974

Hoplolaimus clarissimus is the only species in *Hoplolaimus s. l.* with six nuclei, as in *Basirolaimus*, but with a nondegenerated lateral field, with four well-marked lines as in *Hoplolaimus s. str.* This species has been found only in a limited area in Senegal. It has no agricultural importance and will not be described here.

VIII. *HELICOTYLENCHUS* STEINER, 1945

A. Diagnosis

Hoplolaiminae. Females: Body vermiform, spiral to straight. Labial region continuous to slightly offset, rounded or anteriorly flattened, generally annulated but never longitudinally striated; anterior lip annulus generally not divided into sectors, with elongate amphid apertures (SEM); rarely faint or well-marked lip sectors are present. Lateral field with four lines. Phasmids small, near anus; cephalids and caudalid present. Tail 1–2.5 body diameters long, typically more curved dorsally, with or without a terminal ventral process, sometimes rounded. Stylet and labial framework average-sized. DGO from 6 to 16 μm from stylet base. Median bulb rounded with average-sized valve. Glands overlap intestine dorsally and ventrally, all three glands of about the same length. Two genital branches, the posterior one sometimes degenerated or reduced to a PUS. Epiptygmata present but folded inward, into the vagina. Vulval flaps present, inconspicuous.

Males. Slight secondary sexual dimorphism seen in smaller anterior end. Caudal alae enveloping tail end.

Type species: *Helicotylenchus dihystera* (Cobb, 1893) Sher, 1961.

B. Systematic Relationships

Helicotylenchus is distinctive among hoplolaimids by the arrangement of its esophageal glands, overlapping the beginning of the intestine on all sides, and the position of the esophageal lumen, asymmetrically situated between the dorsal gland and one of the subventral glands. Most other hoplolaimids have a symmetrical arrangement, with the lumen between the two subventral glands (Seinhorst, 1971). The esophageal glands are sometimes described as fused together and forming a single structure around the intestine (Siddiqi, 1986), but this affirmation is not backed by any published observation of this region in cross-section.

Helicotylenchus most likely originated from ancestral forms close to *Pararotylenchus*, but the difference in glandular structure between *Helicotylenchus* (asymmetrical) and *Rotylenchus, Scutellonema, Aorolaimus*, and *Hoplolaimus* (symmetrical) is unexplained. It is not known whether *Helicotylenchus* and the other Hoplolaiminae are monophyletic.

The position of the dorsal esophageal gland opening is extremely variable in the subfamily. Its use, either for systematics or for identification, is very delicate. There is a definitive tendency among hoplolaimids for a posterior migration of the DGO. The opening, which is only 1 or 2 μm from the stylet in many tylenchs, is 3–10 μm in many hoplolaimids, up to 16 μm in *Helicotylenchus*, and up to 33 μm in *Rotylenchulus*.

The species in *Helicotylenchus* are identified within hoplolaimids by their peculiar glandular arrangement and by the fact that the DGO is often farther away from the stylet base than in other hoplolaimids. In addition, they are often smaller and slimmer, tail outline is often a quarter-round (instead of a half-round as in, e.g., *Rotylenchus*), and the body posture is often spiral. There are many exceptions to these latter characters and they can be best used to define some phenetic groupings within *Helicotylenchus*.

C. Representative Species

1. *Helicotylenchus dihystera* (Cobb, 1893) Sher, 1961 (Fig. 13)

Measurements (average of the mean values in 20 different populations, standard deviation, after Fortuner, 1987b). Females: L = 652 mm ± 44.4; stylet = 25 μm ± 0.7; esophagus length = 114 μm ± 7; esophageal glands length = 139 μm ± 7; DGO = 11.3 μm ± 1.5; distance to excretory pore = 107 μm ± 5; body diameter = 24.3 μm ± 1.9; tail length = 16.5 μm ± 1.8; tail diameter at anus = 14 μm ± 1; tail annuli = 9.6 annuli ± 1.4; ratios $a = 26.9 \pm 1.8$; $b = 5.7 \pm 0.3$; $b' = 4.7 \pm 0.2$; $c = 40.8 \pm 3.7$; $c' = 1.2 \pm 0.1$; $m = 46 \pm 2.5$; $V = 63.4\% \pm 0.6$.

Description. Females: Body spiral-shaped, spiral very variable, from loose one-turn spiral in the posterior half with anterior half almost straight to tight spiral of almost three turns. Lip region hemispheroid, outline hemispheric, or with anterior end very slightly flattened four to five labial annuli, more or less distinct. In SEM face view, labial disk oval, first lip annulus not divided into sectors, amphid apertures two longitudinal slits clearly marked at the limit of the labial disk. Stylet knobs anteriorly flattened to indented. Hemizonid always anterior to excretory pore, pore always anterior to esophagointestinal junction. Intestinal fasciculi (canals) absent. Lateral field areolated at the esophagus level; rarely some transverse striae scattered on rest of body. Inner lines of lateral field fusion at posterior end

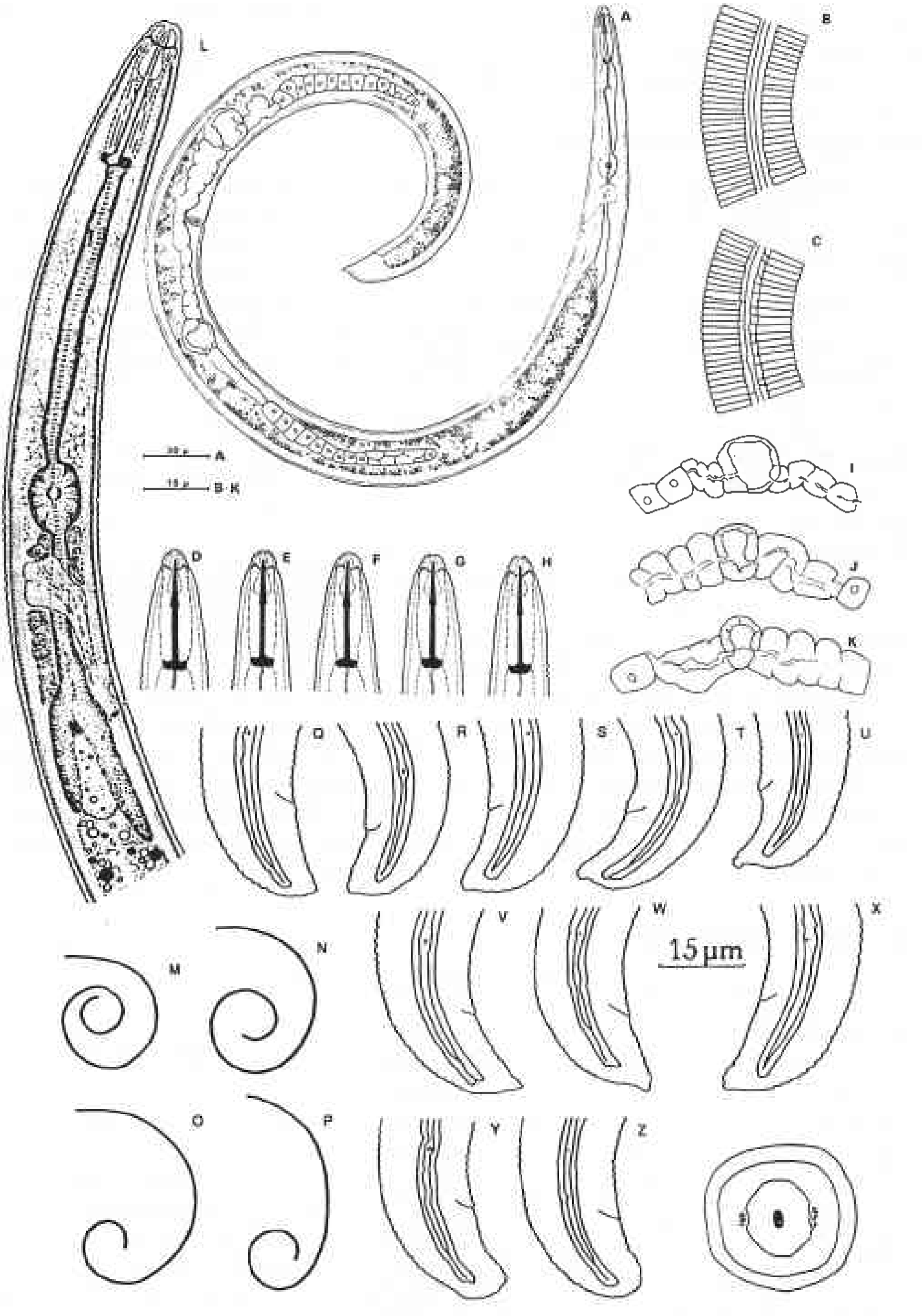

FIGURE 13 *Helicotylenchus dihystera* (Cobb, 1893) Sher, 1961. (A) Female, entire body. (B,C) Lateral fields. (D–H) Anterior ends. (I–K) Position of spermatheca in genital tract. (L) Esophageal region. (M–P) Body thermal death posture. (Q–Z) Tail ends. (Fortuner et al., 1984 and Fortuner, 1987b, courtesy *Rev. Nématol.* and Editions ORSTOM.)

in a Y or V pattern, the length of the leg of the Y varies from 0 to 5 μm. Phasmids 3–13 annuli anterior to anus, situated in the center of the lateral field or closer to one or the other of the inner lines. Tail more curved dorsally, with or without a short ventral terminal projection. Genital system with two branches, both functional, but posterior branch often slightly smaller than anterior one. Spermatheca offset, empty.

Males absent.

Helicotylenchus dihystera is a cosmopolitan species with a very large host list. It is an ecto- or semiendoparasite on the roots of many plants. Feeding behavior has been studied on wheat by Jones (1978a). Typically several cells are penetrated before feeding begins. The nematodes are partially or fully embedded in the root where they feed from a single cell during several days. Feeding resulted in cortical lesions of the roots (Jones, 1978b). Damage to crops was observed in the greenhouse on olive seedlings in Egypt where *H. dihystera* proved to be more damaging than *Xiphinema elongatum* and *Meloidogyne javanica*, with 78% reduction in top weight, and greatly reduced root system (Diab and El-Eraki, 1968). *H. dihystera* was found associated with unhealthy turf bowling greens in Australia (Wallace, 1971). In Nebraska, *H. dihystera* was one of the predominant nematode species found in unhealthy lawns, but attempts to demonstrate pathogenicity in vitro were unsuccessful (Sumner, 1967).

There are many species similar to *H. dihystera* in the genus *Helicotylenchus*, with body spiral, tail more curved dorsally (outline shaped as a quarter-round) with small or large ventral projection. In some species the tail is almost conoid pointed (e.g., *H. caudatus, H. craigi, H. issykkulensis, H. lissocaudatus, H. spicaudatus, H. thornei*, etc.). In *H. martini*, the tail is quite long for the genus, over two diameters long, and it looks like the tail of some *Tylenchorhynchus* species. In other species, the tail is indented dorsally (e.g., *H. crenacauda, H. curvicaudatus, H. digitatus, H. digitiformis, H. pteracercus*, etc.).

2. *Helicotylenchus africanus* Micoletzky, 1916 (Fig. 14)

Measurements (after Fortuner, Maggenti, and Whittaker, 1984). Females (n = 6): L = 0.856 ± 70); stylet = 29.9 μm ± 1.2; esophagus = 127 μm ± 7; esophageal glands = 174 μm ± 14; dorsal gland opening = 9.5 μm ± 1.9; excretory pore = 116 μm ± 4; body diameter = 24.3 μm ± 3.5; tail length = 30.9 μm ± 4.3; anal body diameter = 15.6 μm ± 1.3. Ratios: a = 35.8 ± 4.3; c = 28.2 ± 3.3; c' = 1.98 ± 2.5; m = 44 ± 0.6; V = 59.0% ± 1.42. Males (after Sher, 1966): (n = 4): L = 0.78–0.84 mm; a = 34–38; b = 4.8–5.6; c = 34–40; stylet = 25–28 μm; m = 46–49; o = 37–41; spicules = 21–25 μm; gubernaculum = 8–9 μm. After van den Berg and Heyns, 1975. Females (n = 43): L = 0.8 mm (0.7–1); a = 36.5 (29.5–42); b = 7.4 (6.2–8); b' = 5.2 (4.6– 7.3); c = 38.6 (32.6–43.5); c' = 1.6 (1.4–1.8); o = 36.6 (31–37.7); V = 60% (56–64); stylet = 27.6 μm (26.1–28.7). Males (n = 3): L = 0.8 mm (0.8–0.9); a = 35.4 (31.4–38.1); b = 6.7 (6.2–8.5); b' = 4.7 (4.4–5.3); c = 40 (38.8–41); stylet = 23.6 μm (23.5–23.9); spicules = 25 μm; gubernaculum = 9.2 μm (8.5–9.9).

Description. Females: Body posture C-shaped, annuli 1.5–2 μm wide at midbody. Lip region hemispheric not or slightly set off, with four or five well-marked annuli; labial disk not visible in lateral view. Basal ring of cephalic framework 2 μm deep. Anterior cephalid not seen, posterior cephalid 11–16 μm from the anterior end. Stylet knobs variable in shape, anteriorly indented, flattened or rounded, 5.9 μm (4.8–6.6) across and 2.4 μm (2.2–2.9) wide. Excretory pore anterior to the esophagointestinal junction. Hemizonid just anterior to the excretory pore; hemizonion indistinct, 9–10 annuli posterior to hemizonid. Fasciculi absent. Spermatheca apparently in line with the genital tract, full of rounded sperms. Epiptygmata not seen in most specimens, but two epiptygmata rarely present. Lat-

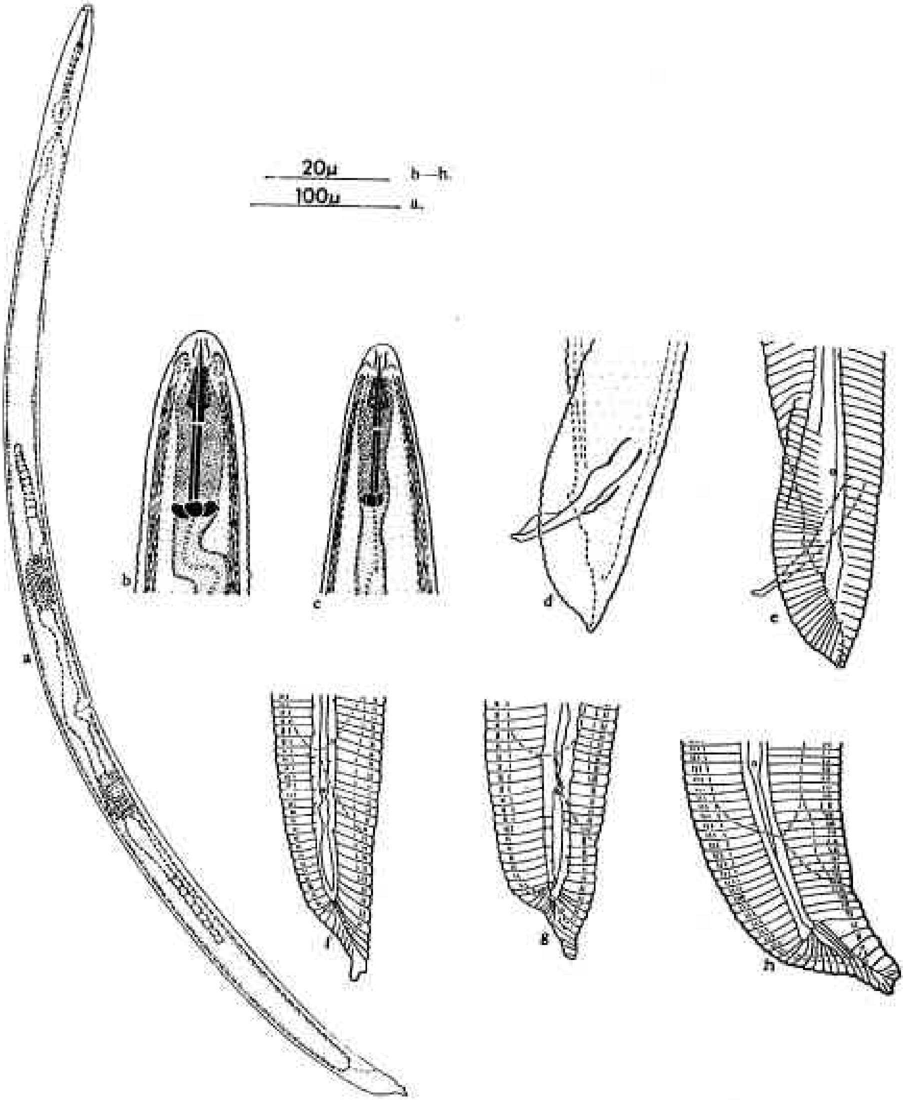

FIGURE 14 *Helicotylenchus africanus* Micoletzky, 1916. (a) Female, entire body. (b) Female, anterior end. (c) Male, anterior end. (d, e) Male, posterior end. (f–h) Female, posterior end. (van den Berg and Heyns, 1975, courtesy *Phytophylactica*.)

eral field 4.5–6.5 µm wide, with scattered transverse striae on body and tail; longitudinal inner lines join together on the tail in a U-shaped pattern, in a V-shaped pattern in one specimen. Phasmids from one annulus posterior to eight anterior to anus level, distinct, and in the center of the lateral field. Caudalid three to seven annuli anterior to anus. Tail with 9–18 ventral annuli, about two body diameters long, with a short nonannulated ventral section, and with dorsal terminal annuli smaller than other tail annuli. Tail dorsally curved with a rounded terminal projection, 2–4 µm long, annulated, rarely the projection is pointed.

Males present, similar to females except for sexual dimorphism.

H. africanus is known from southern Africa. This and some other species in the genus are similar to *H. dihystera*, mostly by the tail shape, but they have body weakly curved, C-shaped.

3. *Helicotylenchus multicinctus* (Cobb, 1893) Golden, 1956 (Fig. 15)

Composite description from Elmiligy (1970), Goodey (1940), Das (1960), Ratanaprapa and Boonduang (1975), Sher (1966), Sauer and Winoto (1975), van den Berg and Heyns (1975), van den Berg and Kirby (1979), and Vovlas (1984).

Measurements. Females (n = 12): L = 0.546 mm ± 0.054 (0.393–0.710); a = 26.9 ± 2.077 (18.5–35); b = 4.95 ± 0.650 (3.7–6.4); b' (n = 9) = 4.2 ± 0.293 (3.4–5); c = 48 ± 6.273

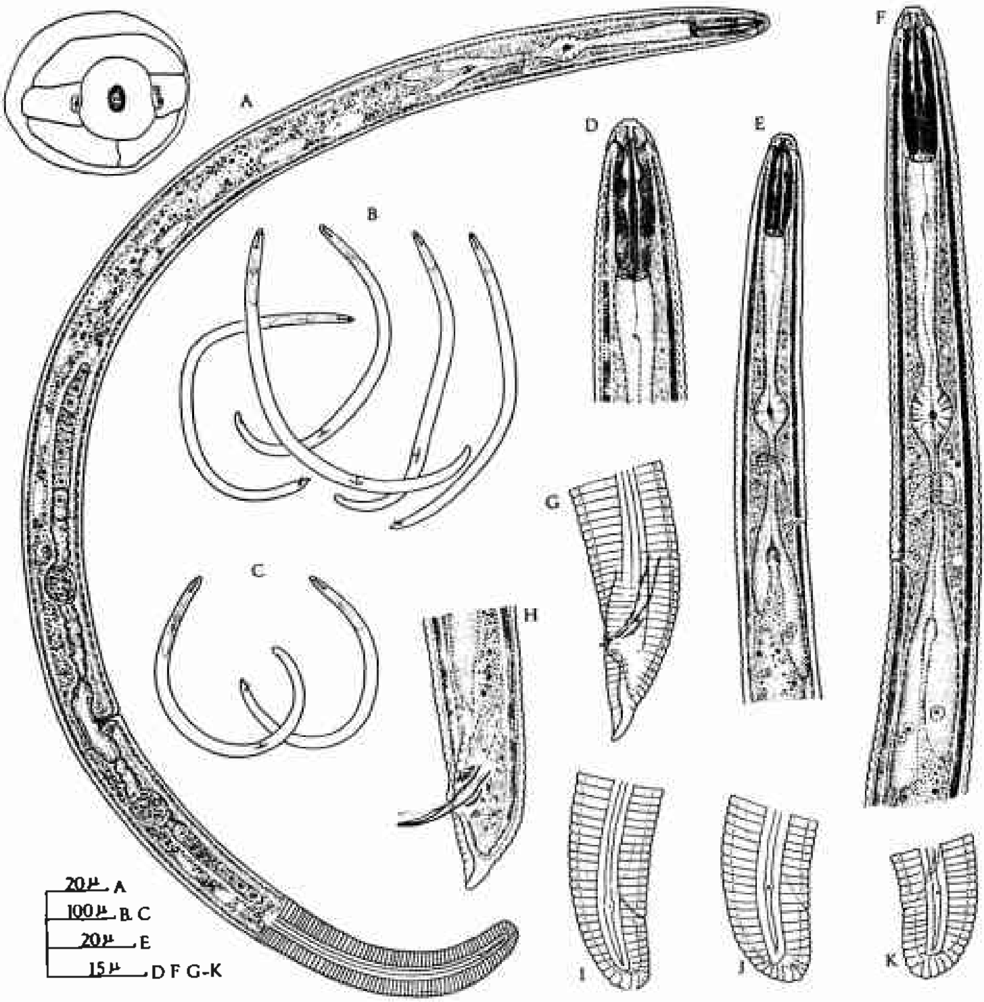

FIGURE 15 *Helicotylenchus multicinctus* (Cobb, 1893) Golden, 1956. (A) Females, entire body. (B,C) Males and females, thermal death posture. (D) Female, anterior end. (E) Female, esophageal region. (F) Male, esophageal region, (G,H) Male, tail ends. (I–K) Females posterior ends. (Siddiqi, 1973 and Vovlas, 1984, courtesy Commonwealth Agricultural Bureaux and *Rev. Nématol.*)

(31–70); c' (n = 9) = 1 ± 0.128 (0.7–1.5); V = 67.6% ± 1.622 (61–75.6); stylet = 23.6 μm ± 1.263 (19.8–28). Males (n = 11): L = 0.5 mm ± 0.065 (370–736); a = 30 ± 2.939 (22.5–40); b = 4.8 ± 0.543 (3.6–6.3); b' (n = 8) = 4.1 ± 0.423 (3.1–3.8); c = 33 ± 3.044 (25–41); stylet (n = 9) = 21.6 μm ± 1.277 (18–24); spicules = 18.4 μm ± 1.975 (15–26); gubernaculum = 5.8 μm ± 0.944 (4–8.5).

Description. Females: Body arcuate to C-shaped when relaxed; annuli distinct, about 1.5 μm wide at midbody; lateral fields not areolated, with four incisures, about one-fourth of the body width. Lip region hemispheric, slightly offset, with three to five (usually four) annuli; labial disk slightly raised above the first labial annulus. In SEM face view, labial disk rounded; first labial annulus with six sectors; submedian sectors low; lateral sectors rectangular, smaller than submedian sectors; amphid openings ovoid (Vovlas, 1985). Labial framework heavily sclerotized, with basal ring conspicuous extending posteriorly along three to four body annuli, which are much narrower at that region than on the rest of the body. Anterior and posterior cephalids usually indistinct, zero to one and four to six annuli posterior to cephalic framework respectively. Stylet well developed, with prominent basal knobs measuring 5–6 μm across, anteriorly flattened or concave. Procorpus usually expanded anteriorly; median esophageal bulb round to oval with small valvular apparatus in center; about six body annuli long; esophageal glands compact, wrapped round front end of intestine, dorsal gland anterior to subventral glands. Excretory pore level with or close to esophagointestinal junction. Hemizonid usually distinct, two to three annuli long, zero to three annuli anterior to excretory pore; hemizonion minute, six to eight annuli behind excretory pore. Posterior genital branch sometimes reduced. Spermathecae slightly offset, rounded, usually filled with sperms. Vulva prominent, a depressed transverse slit. Epiptygma not observed. Intestine not overlapping rectum. Tail slightly tapering, with a hemispheric annulated terminus, usually more curved dorsally than ventrally, devoid of any ventral projection or mucro (but ventral process present in second-stage larvae; Zuckerman and Strich-Harari, 1964), with 6–13 ventral annuli; inner lateral fields lines fusion U-or V-shaped on tail. Phasmids porelike, one to six annuli anterior to anus level.

Males: Similar to females except for sexual dimorphism. Body less curved than in females. Sperms small, rounded. Bursa short, not conspicuously projecting beyond body contour in lateral view, crenate and enclosing tail. Spicules cephalated with narrowed distal half bearing small ventral flanges; gubernaculum simple.

Helicotylenchus multicinctus is an important parasite of banana in all the banana-growing regions of the world. It is an endoparasite in the cortex of the roots where it feeds and produces small superficial lesions. It represents a group of species with body C-shaped, tail conoid/rounded, and vulva more posterior than usual in the genus *Helicotylenchus*.

4. *Helicotylenchus vulgaris* Yuen, 1964 (Fig. 16)

Composite description after Yuen (1964, 1966), d'Errico (1970), Mancini and Moretti (1977), and Ivan (1978).

Measurements. Females (n = 5): L = 0.935 mm ± 0.083 (0.706–1.180); a = 28.7 ± 1.662 (23.8–34); b = 7.3 ± 0.712 (5.8– 9.1); b' = 5.2 ± 0.189 (4.1–6.6); c = 79.4 ± 7.028 (52.5–115.5); c' (n = 2) = 0.7 (0.5–0.9); V = 59.8% ± 0.924 (55–65); stylet = 32.3 μm ± 0.609 (30–36).

Description. Females: Body slender C-shaped or coiled in 1–1/2 spirals. Anterior end continuous with body contour, anteriorly flattened, with four or five annuli. Cuticle annuli approximately 1.7 μm wide. Lateral field occupies about one-quarter body width at region of vulva, anteriorly areolated. Stylet strongly developed with cone and shaft approxi-

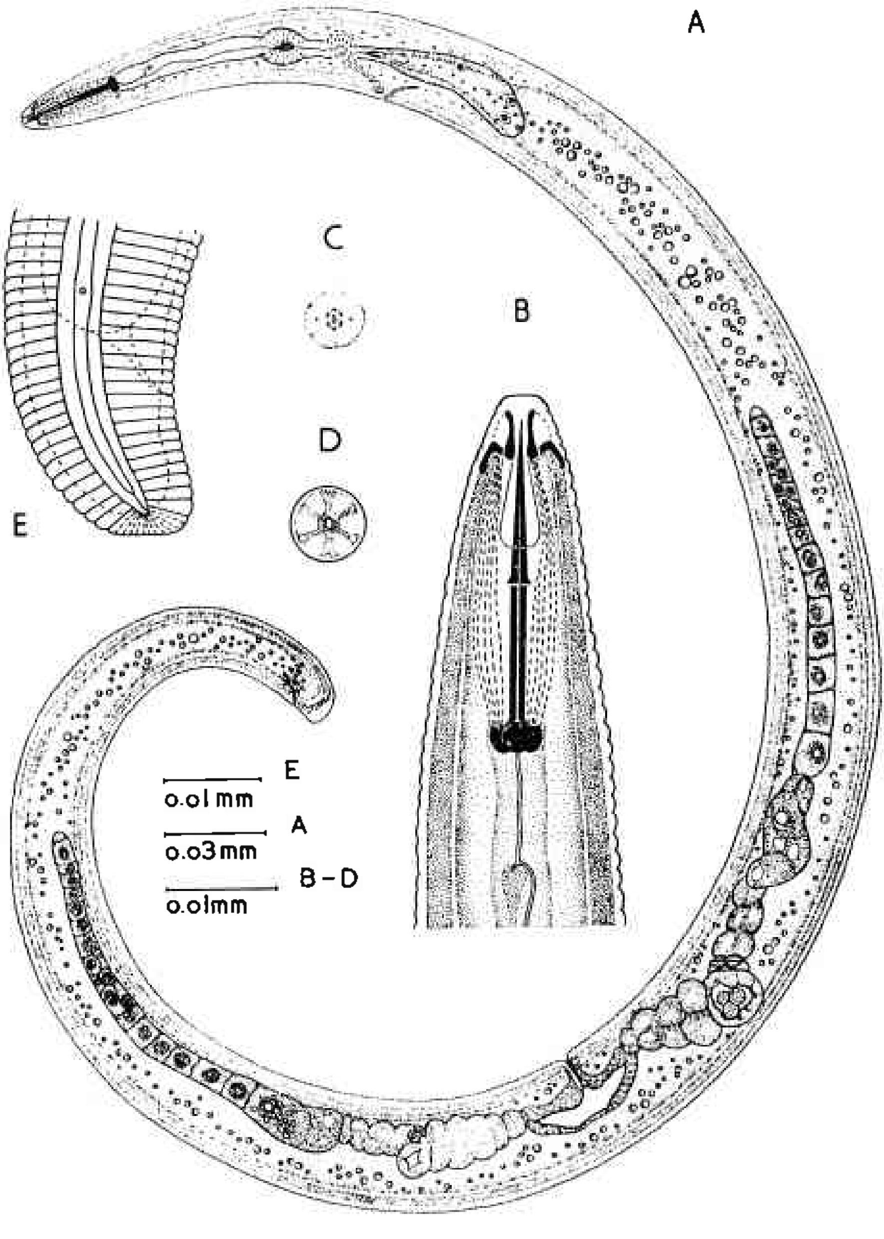

FIGURE 16 *Helicotylenchus vulgaris* Yuen, 1964. (A) Female, entire body. (B) Anterior end. (C) Face view. (D) Cross-section through basal lip annulus. (E) Tail. (Yuen, 1964, courtesy *Nematologica*.)

mately equal in length. Basal knobs massive and slightly concave anteriorly. DGO 9–12 μm behind spear base. Esophageal-intestinal junction close behind nerve ring and always anterior to excretory pore. The nerve ring and excretory pore are located at 104–120 and 120–138 μm from the anterior end, respectively. Hemizonid distinct two annuli wide, zero to one annulus anterior to excretory pore. Hemizonion 11–17 annuli posterior to excretory pore. Tail 8–15 μm long, rounded, with 4–10 ventral annuli. Annuli narrower at distal end. Tail end of second-stage juveniles with projection (Yuen, 1966). Phasmids small and porelike, 6–18 annuli anterior to anus. Tip of anterior or posterior ovary occasionally flexed. Vulva a transverse slit opening into the short, tubular, thick-walled vagina. Uterus consisting of the columned uterus and the thin-walled muscular portion between columned uterus and vagina. Spermatheca offset, occasionally with spherical granules. Oocytes arranged in a single row except at region of multiplication. Only a single egg matures at a time and is retained in the columned uterus before it is laid. Intestine contains dense spherical granules and does not overlap rectum. Rectal glands conspicuous.

Males unknown.

Helicotylenchus vulgaris is known from Europe (Great Britain, the Netherlands, Germany, France, Italy). It has been observed in USSR (Moldavia), Romania, Bulgaria, South Africa, and California. Possible damage to pea has been reported in Britain by Green and Dennis (1981), but according to Spaull (1982), it does not cause significant yield loss to sugar beet under normal conditions in the same country.

Helicotylenchus vulgaris and related species are easily confused with *Scutellonema* species under the dissecting microscope because of their body spiral and hemispheric tail.

5. *Helicotylenchus coomansi* Sharafat-Ali and Loof, 1975 (Fig. 17)

Measurements (after Sharafat-Ali and Loof, 1975). Females (n = 4): L = 1.17–1.30 mm; a = 35–40; b = 6.5–7.3; b' = 5.4–5.5; c = 43–67; c' = 0.7–1.1; V = 58–60; stylet = 39–42 μm; m = 48–50; o = 16–19. Males (n = 2): L = 1.19–1.26 mm; a = 39–41; b = 7.0–8.0; b' = 5.5–6.4; c = 33–35; c' = 2.0; T = 46–51; stylet = 35–36 μm; m = 51–52; o = 16–20; spicules = 34–36 μm; gubernaculum = 10–12 μm.

Description. Females: Body weakly ventrally curved when relaxed; tapering gradually toward both extremities. Cuticle with distinct transverse striae about 1.8 μm apart on middle of body. Lateral field marked by four longitudinal lines, the two outer ones slightly crenate except on the tail of the female; areolated anteriorly. Fusion of the two inner lines on tail mostly V-shaped. Lip region continuous, conoid-hemispheric to slightly truncate, with four to five fine annuli sometimes indistinct. Labial framework strongly sclerotized, with basal ring extending posteriorly over five to six annuli. Anterior and posterior cephalids conspicuous, respectively 5–7 and 12–15 annuli behind lip region. Spear guide massive. Spear knobs with flattened anterior surfaces. Excretory pore anterior to esophagointestinal junction. Hemizonid conspicuous, two to three annuli long, two to three annuli anterior to excretory pore. Vaginal walls thickened. Spermatheca axial, offset, oval to elongate, filled with sperm. Tail straight, tapering ventrally, almost straight dorsally, terminus irregularly hemispheric with a subventral unstriated area more than three annuli wide; the distal subdorsal annuli generally narrower than other annuli. Tail with hyaline distal area 7–13 μm wide. Ten to thirteen tail annuli. Phasmids prominent, five to eight annuli anterior to anus.

Males: Body almost straight when relaxed. Lip region broadly hemispheric, with five annuli. Tail tapering to a subacute terminus, somewhat ventrally offset. Spicules almost straight. Gubernaculum simple, slightly sinuate. Phasmids anterior to cloacal aperture.

Helicotylenchus coomansi was described from the Netherlands.

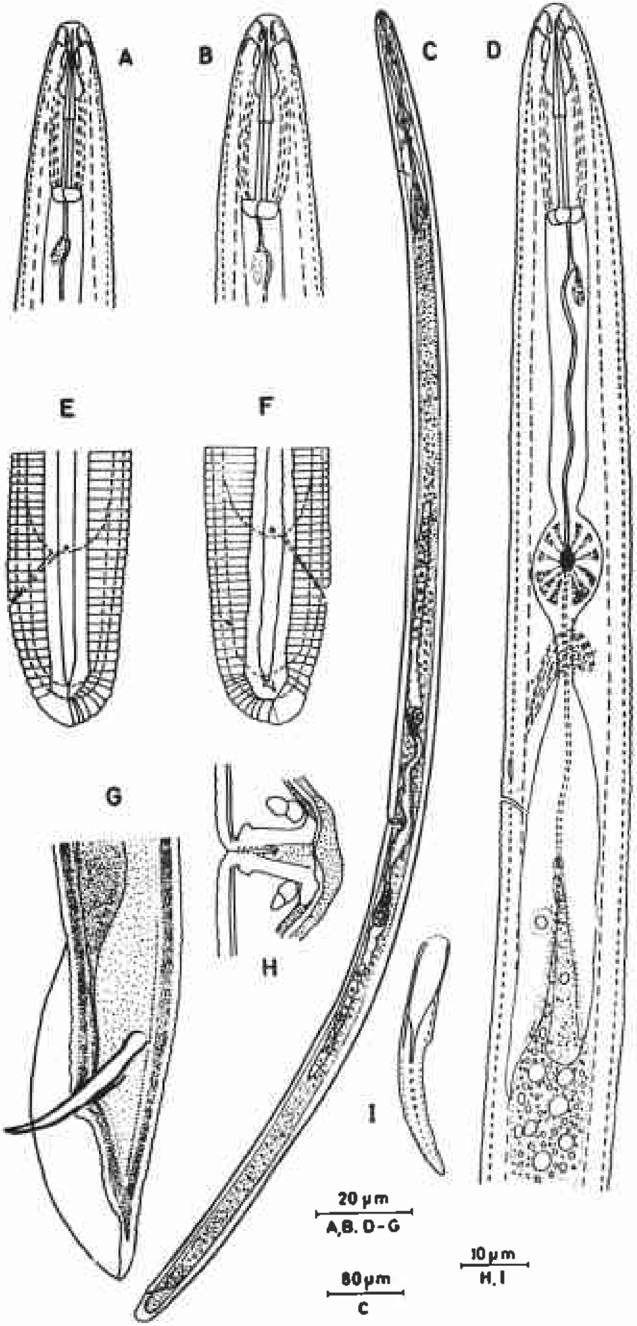

FIGURE 17 *Helicotylenchus coomansi* Sharafat-Ali and Loof, 1975. (A) Male, anterior end. (B) Female, anterior end. (C) Female, entire body. (D) Female, esophageal region. (E,F) Female, tail end. (G) Male, tail end. (H) Female, vaginal structure. (I) Male, spicule. (Sharafat-Ali and Loof, 1975, courtesy *Nematologica*.)

Helicotylenchus coomansi and related taxa have body weakly curved, almost straight, and hemispheric tail. Because of their general shape and large size, these species may be thought to be *Hoplolaimus* species under the dissecting microscope.

6. *Helicotylenchus intermedius* (Luc, 1960) Siddiqi and Husain, 1964 (Fig. 18)

Measurements (after Luc, 1960). Females (n = 6): L = 0.454 mm (0.394–0.523); a = 22.4–235.5; b = 3.9–4.7; c = 41.4–59.7; V = 78–83.2%; stylet = 26–27 µm. Males (n = 3): L = 0.372 mm (0.343–0.387); a = 25.4–29.7; b = 3.7–4.56; c = 25.7–32.2; stylet = 20.21 µm; spicules = 14.5–15 µm; gubernaculum = 4.5–5 µm.

Description. Females: Body almost straight or slightly bent, marked narrowing of the body at vulva level, narrowing less marked at anus level. Annuli 1.6 µm wide at mid-body. Lateral field with four lines, one-fourth of body diameter wide. Outer lines slightly crenated, anteriorly areolated. Inner lines fusion U-shaped. Lip region hemispheroid, non-offset, with four annuli. Cephalic framework well developed, basal ring three annuli deep.

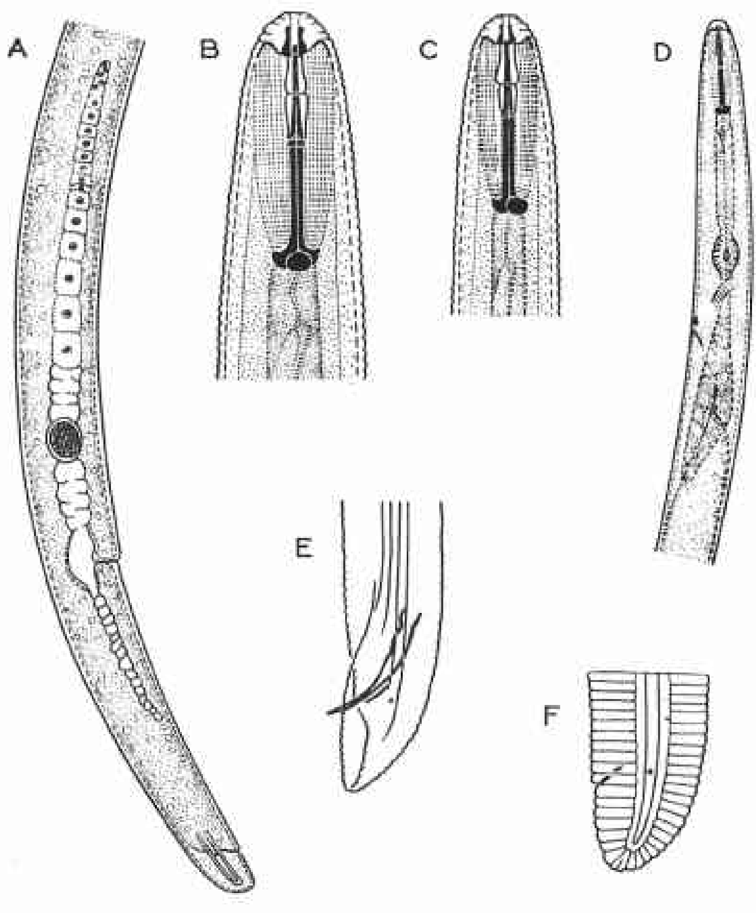

FIGURE 18 *Helicotylenchus intermedius* (Luc, 1960) Siddiqi and Husain, 1964. (A) Female, tractus genital and posterior end. (B) Female, anterior end. (C) Male, anterior end. (D) Male, esophageal region. (E) Male, posterior end. (F) Female, posterior end. (Luc, 1960, courtesy *Nematologica*.)

Stylet cone slightly shorted than shaft, basal knobs anteriorly indented. DGO at 7–9 μm from stylet base. Median bulb oval. Esophageal glands with three nuclei, overlapping the intestine ventrally or lateroventrally. Nerve ring immediately posterior to median bulb. Excretory pore at 78–98 μm from anterior end. Hemizonid just anterior to excretory pore, two annuli wide. Vulva posterior. Anterior genital branch 130 μm (111–162) long; oocytes in one row except in the multiplication area, spermatheca 10 μm in diameter, with thick wall, full of spherical sperms about 1 μm in diameter. Posterior genital branch regressed, 41–53 μm long, appearing as a row of small, degenerated cells. Tail 8–12 μm long, 0.8–1 μm wide at anus level, more rounded dorsally, with rounded end. Eight to ten tail annuli. Phasmids very small, at anus level.

Males: Similar to females. Stylet shorter than in females. Excretory pore at 67–69 μm from anterior end. Spicules 14.5–15 μm long, very slightly curved, cephalated. Small gubernaculum, slightly curved. Caudal alae enveloping tail end. Phasmids anterior to anus level.

Helicotylenchus intermedius is found in virgin forests in Ivory Coast. It was observed in the virgin forest of Taï. After the land was deforested for cultivation, this nematode disappeared from subsequent sampling (Fortuner and Couturier, 1983).

Helicotylenchus intermedius has vulva very posterior and posterior genital branch degenerate but still present. It is considered to belong to the genus *Rotylenchoides* by some authors (Luc, 1960; Sher, 1966, Siddiqi, 1986) and to the genus *Helicotylenchus* by others (Siddiqi and Husain, 1964; Fortuner, 1984).

7. *Helicotylenchus brevis* (Whitehead, 1958) Fortuner, 1984 (Fig. 19)

Measurements (after Whitehead, 1958). Females (n = 6): L = 0.43– 0.53 mm; a = 18–22; b = 3.6–4.4; c = 36–55; V = 89.7–92.1%; stylet = 26–29 μm. Males (n = 11): L = 0.37–0.44 mm; a = 24–30; b = 3.4– 4.3; c = 23–36; spicule = 21–25 μm; gubernaculum = 4–8 μm; capitulum = 11 μm.

Description. Females: Anterior end flattened, continuous with body, with three to four annuli. Lateral field with four lines, anteriorly areolated. Cephalic framework strongly developed; basal ring extending posteriorly over three body annuli. Stylet stout and about three head widths long. Stylet shaft slightly shorter than cone. Stylet knobs anteriorly flattened. DGO slightly less than one-third of stylet length behind stylet base. Precorpus long; valvular median bulb ovate; isthmus short; esophageal glands in a lobe of varying shape overlapping the anterior portion of the intestine. Esophagointestinal junction posterior to nerve ring. Nuclei of esophageal glands not observed. Excretory pore opposite middle of glandular lobe, hemizonid immediately anterior to excretory pore. Ovary short with oocytes in two rows. Spermatheca rounded. Postvulval uterine sac present, about one vulval body width long. Phasmids small at about anal level. Tail short, less than one anal body diameter long, rounded.

Males: Testis with double row of spermatocytes passing into a longer vas deferens, full of spermatozoa. Walls of vas deferens are composed of large squamous cells. Narrow ejaculatory duct passes between spicules to cloaca. Caudal alae arise just anterior to spicule heads and surround tail tip. Spicules are slightly cephalated, with strongly developed blades. Gubernaculum very thin. A capitulum was observed between the spicules in a single specimen.

Helicotylenchus brevis was found on cultivated plants (banana, mango) and uncultivated bush, ferns, and bulbous plants in southern Africa (Tanzania and South Africa).

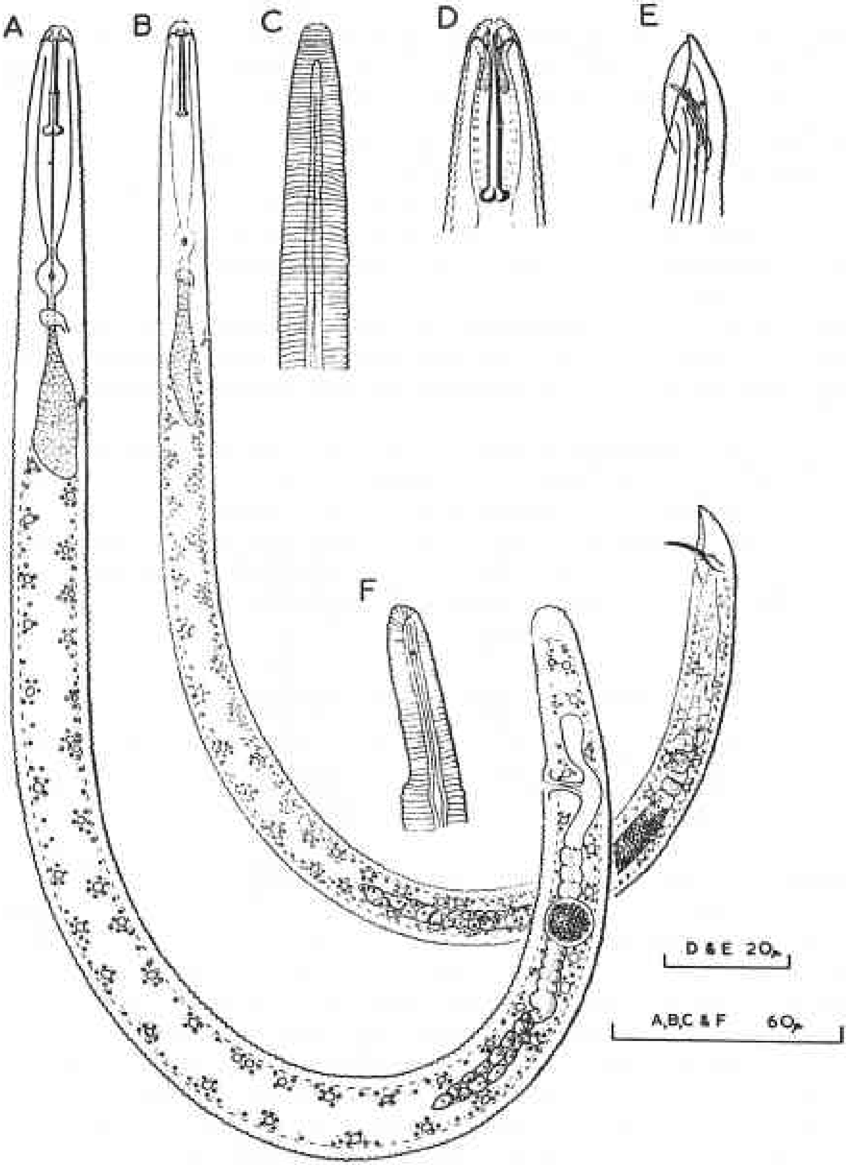

FIGURE 19 *Helicotylenchus brevis* (Whitehead, 1958) Fortuner, 1984. (A) Female, entire body. (B) Male, entire body. (C) Female, anterior end showing origin of lateral fields. (D) Female, anterior end. (E) Male, tail end. (F) Female, posterior end. (Whitehead, 1958, courtesy *Nematologica*.)

This species was the type species of the genus *Rotylenchoides*. It is similar to the species in the group *H. intermedius*, but here the regression of the posterior genital branch is complete, and it is represented only by a short postuterine sac. Fortuner (1984; 1987a) synonymized *Rotylenchoides* to *Helicotylenchus*.

IX. *ANTARCTYLUS* SHER, 1973

Hoplolaiminae. Females: Body vermiform, spiral to C-shaped. Labial region rounded, continuous, annulated; anterior lip annulus not divided into sectors (SEM, Sher and Bell, 1975). Lateral field with four lines. Phasmids small, near anus. Caudalids not described. Tail rather long (two to three body diameters long), conoid, pointed. Stylet and cephalic framework average-sized. DGO about 10 μm from stylet base in the only species known in this genus. Median bulb oval/rounded with average sized valve. Glands overlapping the intestine; the dorsal gland and one subventral gland overlap dorsally, the second subventral gland overlaps ventrally for a short distance. Both subventral glands are shorter than the dorsal one. Esophagointestinal junction a small triangular structure. Two equally developed genital branches. One or two epiptygmata present, inconspicuous. Vulval flap not described.

Males: Slight secondary sexual dimorphism seen in smaller anterior end. Tail with long hyaline end. Caudal alae said to envelop tail end, but seen stopping just short of tail tip in original figure. Gubernaculum not described; titillae not figured.

The type and only species, *A. humus* Sher, 1973 (Fig. 20), was found in forest peat soil in Auckland Island, Antarctica. Its pointed tail, rather long for a hoplolaimid ($c' = 2.5$), similar to some taxa in Telotylenchinae such as *Triversus*, and the arrangement of the esophageal glands, somewhat similar to that in *Helicotylenchus*, may indicate that this genus is a relic of the forms that evolved into present day *Helicotylenchus*.

X. *APHASMATYLENCHUS* SHER, 1965

A. Diagnosis

Hoplolaiminae. Females: Body vermiform, circle to C-shaped. Labial region slightly offset from body, annulated, but without longitudinal striae. First labial annulus divided into six equal sectors, elongate amphid apertures (SEM). Lateral field with four lines. Phasmids absent. Cephalids and caudalids not described. Tail 1.5–2 body diameters long, more curved dorsally, with rounded end. Stylet and labial framework well developed. DGO about 8 μm from stylet base. Median bulb rounded. Gland overlapping the intestine ventrally and laterally. Two genital branches equally developed. Epiptygmata and vulval flap not described.

Males: Slight secondary sexual dimorphism seen in the smaller anterior end. Tail conoid, elongate, with a hyaline end. Caudal alae enveloping tail end. Gubernaculum with titillae, but no capitulum.

Type species: *A. nigeriensis* Sher, 1965

B. Systematic Relationships

In this genus, the phasmids have disappeared, which is peculiar in a family where many species have over enlarged phasmids developed into scutella. The glands overlap is lateral, not like any other in Hoplolaiminae. The tail is often conoid rather than cylindroid, and it is rather long for the group. The male tail of *A. straturatus* has a definite tylenchorhynchid

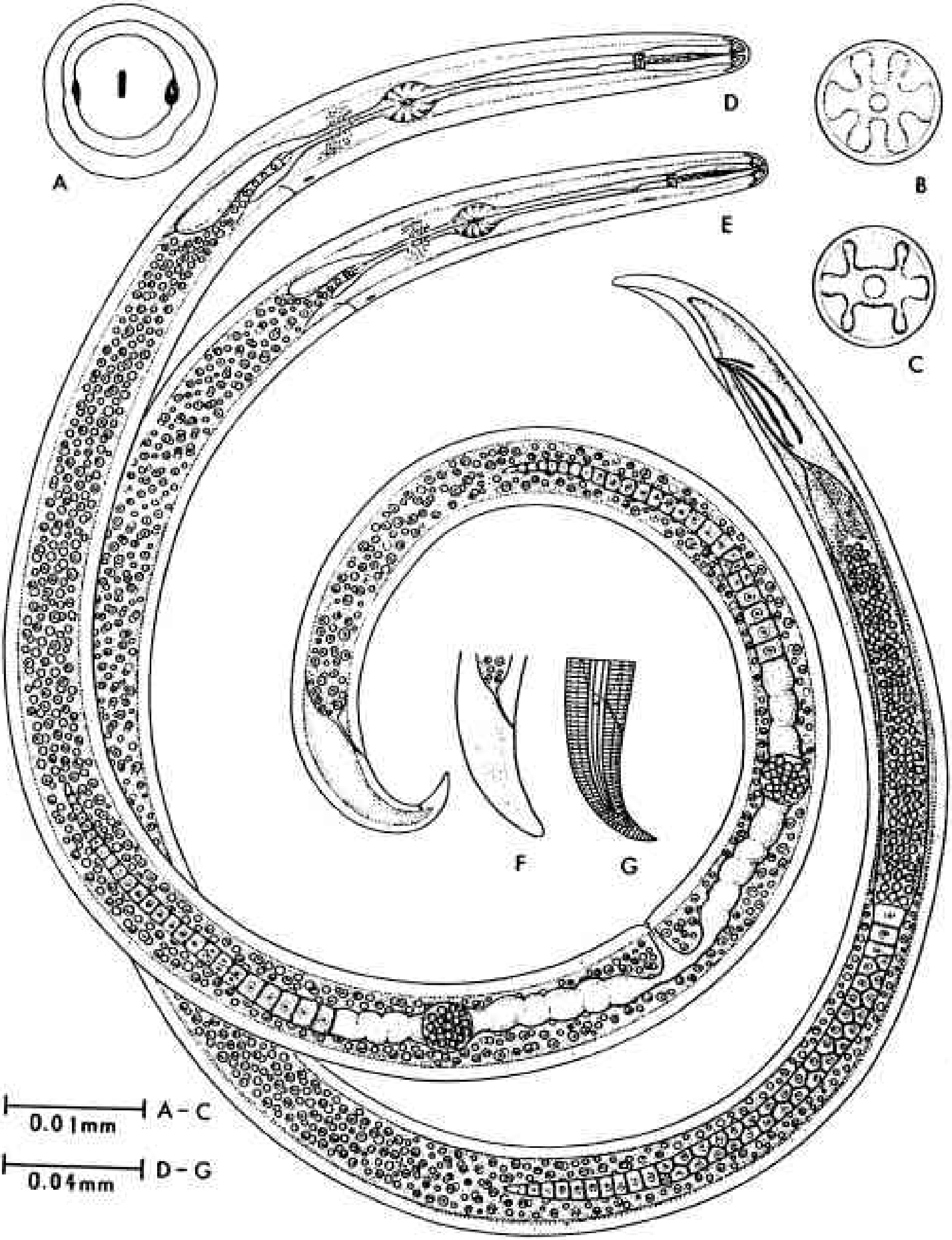

FIGURE 20 *Antarctylus humus* Sher, 1973. (A) Female, face view. (B) Female, cross-section through basal annulus of lip region. (C) Male, cross section through basal annulus of lip region. (D) Female. (E) Male. (F,G) Female, posterior ends. (Sher, 1973, courtesy *J. Nematol.*)

allure. The face pattern is ancestral and offers no clue to the systematic position of this genus. It is placed in Hoplolaiminae because of posterior DGO; junction esophagointestinal faint, without definite valve; sexual dimorphism (smaller anterior end in males); high lip region with well-developed cephalic framework.

This genus is known only from West Africa. *A. nigeriensis* was found in two localities in Nigeria, and a rain forest in Ivory Coast (Fortuner and Couturier, 1983), *A. variabilis* from Senegal and Mali, and *A. straturatus* is known only from southwest Burkina Faso.

C. Representative Species

Aphasmatylenchus straturatus Germani, 1970 (Fig. 21)

Measurements after Germani (1970). Females (n = 36): L = 1.43 mm (1.18–1.75); a = 31.1 (26–35.6); b' = 7.8 (6–9.1); c = 22.4 (18–27.5); V = 52.9% (50–56); stylet = 33 μm (30–36). Males (n = 6): L = 1.13 mm (0.99–1.26); a = 34.8 (29.1–38); b' = 6.8 (6.1–7.2); c = 16.4 (14.6–17.4); T = 28.7% (28–29.4); stylet = 29 μm (28–30).

Other population in Germani (1970): Females (n = 36): L = 1.6 mm (1.2–1.9); a = 33.9 (27.3–44); b = 8.1 (6.5–10); c = 24 (18.4–32.5); c' = 1.7(1.3–2.3); V = 54% (50.7–58.7); stylet = 35 μm (32–39). Males (n = 12): L = 1.3 mm (1.1–1.5); a = 37.9 (34–47.2); b' = 6.7 (5.7–7.6); c = 19.8 (16.5–30); T = 24.9% (19–32); stylet = 30 μm (25–33).

Description. Females: Body curved ventrally in an open C, sometimes a closed circle shape. Annuli 1.4–1.8 μm wide at center of body. Cuticle annuli divided by fine longitudinal striae giving it a corncoblike aspect. Lateral field occupying about one-fourth body width with four lines (three longitudinal bands), outer bands regularly areolated, central band irregularly areolated. Lip region slightly offset from body contour, generally rounded, with slight flattening on top; 8–11 labial annuli; the first annulus with the labial disk is conspicuously larger. In face view, with SEM, large oval oral disk present, but amphidial openings not observed; the first annulus is divided into six sectors, the two lateral sectors smaller than the submedian sectors. Cephalic framework massive (reminiscent of *Dolichodorus*). Esophagus: procorpus sometimes narrowing slightly at posterior end; dorsal esophageal gland duct opening 5–9 μm behind spear base; esophageal glands overlapping the intestine ventrally or lateroventrally. Postanal intestinal sac present. Fasciculi (canals) present over the entire length of the intestine including the postanal sac. Excretory pore at 138–208 μm from anterior end. Hemizonid one to three annuli anterior to excretory pore, two to three annuli wide. Spermatheca almost rectangular, containing spermlike bodies. Tail cylindroconical, tapering to a round or bluntly rounded terminus, 41–06 μm long or 1.3–2.5 times anal body width.

Males: Lip region more rounded than in female, distinctly set off. In SEM face view, well-developed, subhexagonal oral disk present. Amphidial openings narrow slits. Stylet and esophagus less well developed than in female. Only one esophageal gland nucleus observed. Excretory pore located 130–206 μm from anterior end. Testis single, outstretched. Spicules curved, 37–57 μm long; gubernaculum 14–21 μm long, with titillae. Caudal alae enveloping tail, with annulated edges. Tail 3–3.3 times body width at cloaca.

This species is known only from Niangoloko, Burkina Faso, where it is a major parasite of peanut and pigeon pea. The nematode seems to destroy the nitrogen-fixing nodules associated with leguminous plants. The normal host of the nematode is the karite tree (*Butyrospermum parkii*). The nematode spends the dry season in the soil, 40–50 cm deep, where it feeds on the tree roots. During the rainy season, the nematode is attracted toward the peanuts, and it moves near the surface (Germani and Luc, 1982).

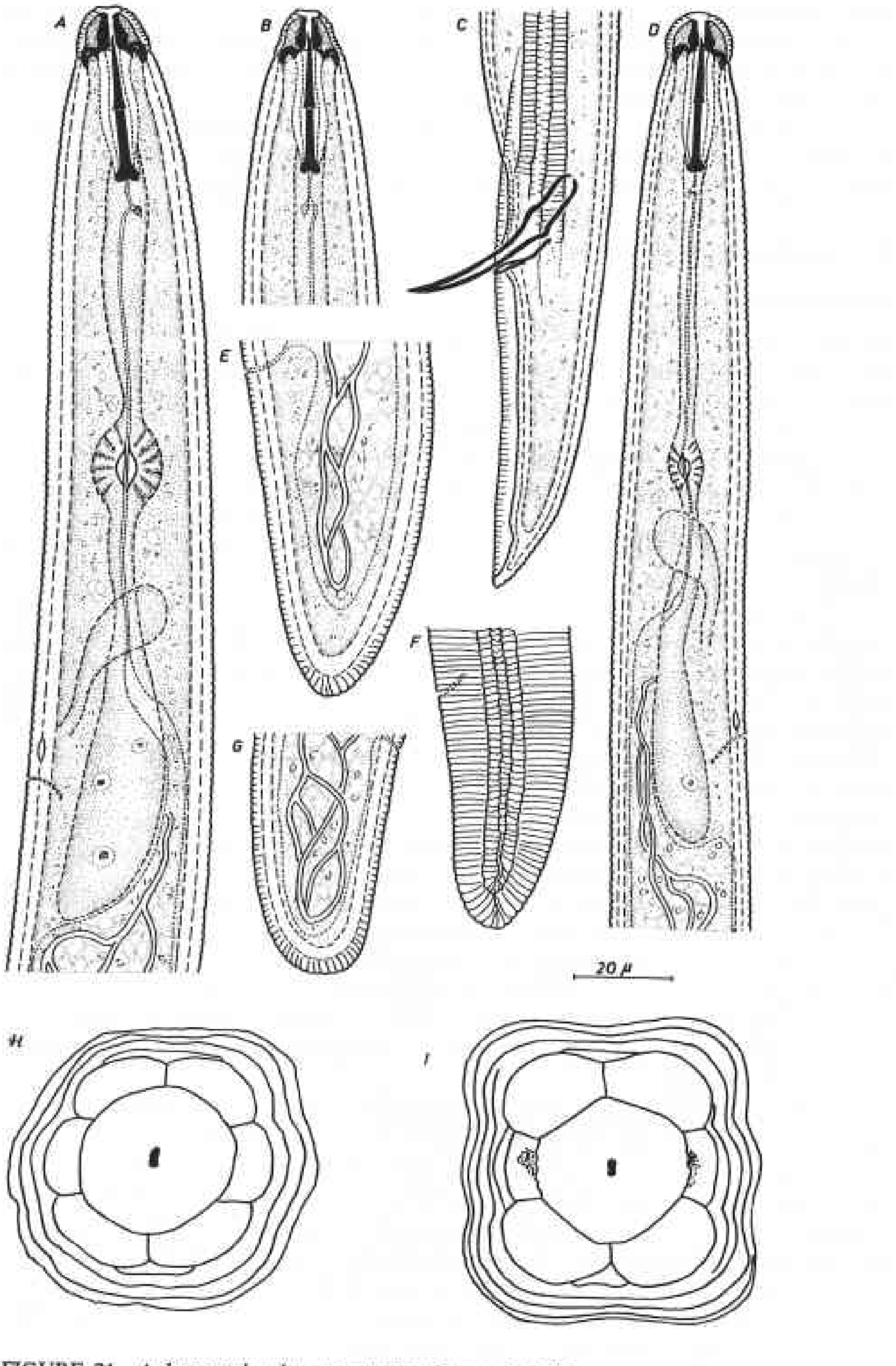

FIGURE 21 *Aphasmatylenchus straturatus* Germani, 1970. (A,B) Female, anterior end. (C) Male, posterior end. (D) Male, anterior end. (E–G) Female, posterior end. Bottom left, female, SEM face view. Bottom right, male, SEM face view. (Germany, 1977, courtesy Commonwealth Agricultural Bureaux.)

REFERENCES

Andrássy, I. 1961. Wissenschaftliche Ergbnisse der ersten ungarischen zoologischen Expedition in Ostafrika. 2. Nematoda. *Ann. Hist-Nat. Mus. Nat. Hung.* 53: 281–297.

Baldwin, J. G., and Bell, A. H. 1981. *Pararotylenchus* n.gen. (Pararotylenchinae n.subfam., Hoplolaimidae) with six new species and two new combinations. *J. Nematol.* 13: 111–128.

Bird, G. W., and Högger, C. 1974. Anal peg of *Hoplolaimus columbus. Nematologica* 20: 103 + plate XI.

Bittencourt, C., and Huang, C.S. 1986. Brazilian *Peltamigratus* Sher, 1964 (Nematoda: Hoplolaimidae) with description of six new species. *Rev. Nématol.* 9: 3–24.

Chapman, R. A. 1963. Population development of the plant parasitic nematode *Scutellonema brachyurum* on red clover. *Proc. Helm. Soc. Wash.* 30: 169–173.

Choi, Y. E., and Geraert, E. 1971. Some remarkable Tylenchida from Korea. *Nematologica* 18: 66–73.

Coomans, A. 1963. Observations on the variability of morphological structures in *Hoplolaimus pararobustus. Nematologica* 9: 241–254.

Das, V. M. 1960. Studies on the nematodes parasites of plants in Hyderabad (Andhra Pradesh, India). *Z. Parazitenkunde* 19: 553–605.

De Grisse, A. T., Lippens, P. L., and Coomans, A. 1974. The cephalic sensory system of *Rotylenchus robustus* and a comparison with some other tylenchids. *Nematologica* 20: 88–95.

D'Errico, F. P. 1970. Su alcuni nematodi fitoparassiti trovati in Italia. *Boll. Lab. Ent. Agr. Filippo Silvestri* 28: 183–189.

Diab, K. A., and El-Eraki, S. 1968. Plant-parasitic nematodes associated with olive decline in the United Arab Republic. *Plant Dis. Reptr.* 52: 150–154.

Doucet, M. E. 1980. Description de deux nouveaux *Peltamigratus* et d'une population d'*Hoplolaimus galeatus* (Nematoda: Tylenchida) de la Province de Cordoba, Argentine. *Nematologica* 26: 34–36.

Eerens, J. P. J., and Loof, P. A. A. 1985. Systematic observations on the genera *Scutellonema* Andrássy, 1958 and *Peltamigratus* Sher, 1964 (Nematoda, Hoplolaimidae). *Meded. Fac. LandbWettens. Gent* 50: 857–860.

Elmiligy, I. A. 1970. On some Hoplolaiminae from Congo and Egypt. *Meded. Fac. LandbWettens. Gent* 35: 1141–1153.

Eroshenko, A. S. 1984. [Plant nematodes of coniferous plants in the Primorsk Territory.] *Parazity zhivotnykh i rastenii*: 87–97.

Eroshenko, A. S., and N. V. Thanh 1981. [Ectoparasitic nematodes of pineapple plantations in the northern and central provinces of Vietnam.] In [*Freeliving and Plant Parasitic Nematodes in the Far East.*] Eroshenko, A. C., and O. I. Belogurov, eds., Dal'nev Nauch. Tsentr Akad. Nauk SSSR, Bio.-Poch. Inst., Vladivostok, pp. 28–34 and 93–98.

Fassuliotis, G. 1974. A description of males of *Hoplolaimus columbus. J. Nematol.* 6: 116–118.

Fassuliotis, G. 1975. Feeding, egg-laying, and embryology of the Columbia lance nematode, *Hoplolaimus columbus. J. Nematol.* 7: 152– 158.

Fassuliotis, G. 1976. *Hoplolaimus columbus*. C.I.H. descriptions of plant-parasitic nematodes, Set 6, No. 81.

Fassuliotis, G., Rau, G. J., and Smith, F. H. 1968. *Hoplolaimus columbus*, a nematode parasite associated with cotton and soybeans in South Carolina. *Plant Dis. Reptr.* 52: 571–572.

Ferraz, S. 1980. Description of *Rotylenchus nexus* n. sp. (Nematoda: Hoplolaiminae) from Brazil, with some observations on the nematode genus *Calvatylus. Syst. Parasitol.* 2: 21–24.

Fortuner, R. 1974. Description de *Pratylenchus sefaensis* n.sp. et de *Hoplolaimus clarissimus* n.sp. (Nematoda: Tylenchida). *Cah. ORSTOM, sér. Biol. No. 21* (1973): 25–34.

Fortuner, R. 1984. Morphometrical variability in *Helicotylenchus* Steiner, 1945. 6: Value of the characters used for specific identification. *Rev. Nématol.* 7: 245–264.

Fortuner, R. 1987a. A reappraisal of Tylenchina (Nemata). 8. The family Hoplolaimidae Filip'ev, 1934. *Rev. Nématol.* 10: 219–232.

Fortuner, R. 1987b. Variabilité et identification des espèces chez les nématodes du genre *Helicotylenchus*. *Etudes et Thèses*, ORSTOM, Paris.

Fortuner, R. 1989. A new description of the process of identification of plant-parasitic nematode genera. In *Nematode Identification and Expert System Technology*. Fortuner, R., ed., Plenum Press, New York, pp. 35–44.

Fortuner, R., and Couturier, G. 1983. Les nématodes parasites de plantes de la foret de Taï (Côte d'Ivoire). *Rev. Nématol.* 6: 3–10.

Fortuner, R., Maggenti, A. R., and Whittaker, L. M. 1984. Morphometrical variability in *Helicotylenchus* Steiner, 1945. 4: Study of field populations of *H. pseudorobustus* and related species. *Rev. Nématol.* 7: 121–135.

Geraert, E. 1976. Problems concerning the genera *Helicotylenchus* Steiner, 1945 and *Rotylenchus* Filipjev, 1936. *Nematologica* 22: 284– 288.

Geraert, E. 1981. The female reproductive system in nematode systematics. *Ann. Soc. R. Zool. Belg.* 110: 73–86.

Geraert, E., Zepp, A., and Borazanci, N. 1975. Some plant nematodes from Turkey. *Meded. Fac. LandbWettens. Gent* 40: 511–515.

Germani, G. 1970. *Aphasmatylenchus straturatus* sp. n. (Nematoda: Hoplolaimidae) from West Africa. *Proc. Helm. Soc. Wash.* 37: 48–51.

Germani, G. 1977. *Aphasmatylenchus straturatus*. C.I.H. descriptions of plant-parasitic nematodes, Set 7, No. 104.

Germani, G., Baldwin, J. G., Bell, A. H., and Wu, X. Y. 1986. Revision of the genus *Scutellonema* Andrássy, 1958 (Nematoda: Tylenchida). *Rev. Nématol.* 8(1985): 289–320.

Germani, G., and Luc, M. 1982. Etudes sur la "chlorose voltaïque" des légumineuses due au nématode *Aphasmatylenchus straturatus* Germani. II. *Rev. Nématol.* 5: 195–199.

Goodey, J. B. 1957. *Hoplolaimus proporicus* n. sp. (Hoplolaiminae: Tylenchida). *Nematologica* 2: 108–113.

Goodey, T. 1940. On *Anguillulina multicincta* (Cobb) and other species of *Anguillulina* associated with the roots of plants. *J. Helminthol.* 18: 21–38.

Green, C. D., and Dennis, E. B. 1981. An analysis of the variability in yield of pea crops attacked by *Heterodera goettingiana, Helicotylenchus vulgaris* and *Pratylenchus thornei*. *Plant Path.* 30: 65–71.

Hirschmann, H. 1983. Scanning electron microscopy as a tool in nematode taxonomy. In *Concepts in Nematode Systematics*. Stone, A. R., Platt, H. M., and Khalil, L. F., eds., Academic Press, London, pp. 95–111.

Högger, C., and Bird, G. W. 1974. Secondary male sex characteristics of *Hoplolaimus galeatus*. *J. Nematol.* 6: 12–16.

Ivan, M. 1978. Trei specii de namatode identificate in culturile de coacaz, noi pentru fauna Romaniei. *Studii si Cercetari de Biologie, Biologie Animala* 30: 13–15.

Jairajpuri, M. S., and Baqri, Q. H. 1973. Nematodes of high altitudes in India. I. Four new species of Tylenchida. *Nematologica* 19: 19–30.

Jairajpuri, M. S., and Siddiqi, M. R. 1979. Observations on the nematode genera *Orientylus* and *Calvatylus* (Rotylenchoidinae: Hoplolaimidae) with descriptions of three new species. *Ind. J. Nematol.* 7: 101–111.

Jones, R. K. 1978a. The feeding behavior of *Helicotylenchus* spp. on wheat roots. *Nematologica* 24: 88–94.

Jones, R. K. 1978b. Histological and ultrastructural changes in cereal roots caused by feeding of *Helicotylenchus* spp. *Nematologica* 24: 393–397.

Khan, E., and Nanjappa, C. K. 1970. Four new species in the superfamily Hoplolaimoidea (Tylenchida: Nematoda) from India. *Bull. Ent.* 11: 143–149.

Lewis, S. A., and Huff, T. F. 1976. Cuticle anatomy of *Hoplolaimus columbus*. *J. Nematol.* 8: 293.

Lewis, S. A., Smith, F. H., and Powell, W. M. 1974. Histopathology of infection by *Hoplolaimus columbus* on cotton and soybean and aspects of its pathogenicity. *J. Nematol.* 6: 145.

Luc, M. 1959. Nématodes parasites ou soupçonnés de parasitisme envers les plantes de Madagascar. *Bull. Inst. Res. Agron. Madagascar* 3: 89–101.

Luc, M. 1960. Trois nouvelles espèces du genre *Rotylenchoides* Whitehead, 1958 (Nematoda: Tylenchida). *Nematologica* 5: 7–17.

Luc, M. 1981. *Basirolaimus* Shamsi, 1979, a junior synonym of *Hoplolaimus* von Daday, 1905 (Nematoda: Tylenchida). *Nematol. Mediterranea* 9: 197–199.

Luc, M. 1986. *Hoplorhynchus* Andrássy, 1985, a junior synonym of *Pratylenchoides* Winslow, 1958 (Nemata: Pratylenchidae). *Rev. Nématol.* 9: 198.

Maggenti, A. R., Luc, M., Raski, D. J., Fortuner, R., and Geraert, E. 1988. A reappraisal of Tylenchina (Nemata). 11. List of generic and supra-generic taxa, with their junior synonyms. *Rev. Nématol.* 11: 177–188.

Mancini, G., and Moretti, F. 1977. Il genere *Helicotylenchus* Steiner, 1945 in piemonte e Valle d'Aosta, Nota 1. *Redia* 59: 225–228.

Maqbool, M. A., and Ghazala, P. 1988. Observation of some known species of *Hoplolaimus* von Daday, 1905 (Nemata: Hoplolaimidae) from Pakistan. *Pak. J. Nematol.* 6: 1–7.

Mulk, M. M., and Siddiqi, M. R. 1982. Three new species of hoplolaimid nematodes from South America. *Ind. J. Nematol.* 12: 124–131.

Nong, L., and Weber, G. F. 1964. Amaryllis diseases caused by two nematodes. *Phytopathology* 54: 902–903.

Phillips, S. P. 1971. Studies of plant and soil nematodes. 16. Eight new species of spiral nematodes (Nematoda: Tylenchoidea) from Queensland. *Qd. J. Agr. Anim. Sci.* 28: 227–242.

Ratanaprapa, D., and Boonduang, A. 1975. Identification of plant parasitic nematodes of Thailand. A second systematic study of Hoplolaimidae in Thailand. *Plant Prot. Serv. Tech. Bull.* (Bangkok) No. 27.

Ruehle, J. L. 1973. Influence of plant-parasitic nematodes on longleaf pine seedlings. *J. Nematol.* 5: 7–9.

Sauer, M. R., and Winoto, R. 1975. The genus *Helicotylenchus* Steiner, 1945 in West Malaysia. *Nematologica* 21: 341–350.

Seinhorst, J. W. 1971. The structure of the glandular part of the esophagus of Tylenchidae. *Nematologica* 17: 431–443.

Shamsi, M. A. 1979. *Basirolaimus* gen.n. (Nematoda: Hoplolaimidae) with the description of *Basirolaimus sacchari* n.sp. from India. *Nematol. Mediterranea* 7: 15–19.

Sharafat-Ali, S., Geraert, E., and Coomans, A. 1973. Some spiral nematodes from Africa. *Biol. Jaarb.* 41: 53–70.

Sharafat-Ali, S., and Loof, P. A. A. 1975. Two new species of *Helicotylenchus* Steiner, 1945 (Nematoda: Hoplolaiminae). *Nematologica* 21: 207–212.

Sher, S. A. 1961. Revision of the Hoplolaiminae (Nematoda). I. Classification of nominal genera and nominal species. *Nematologica* 6: 155–169.

Sher, S. A. 1963. Revision of the Hoplolaiminae (Nematoda). II. *Hoplolaimus* Daday, 1905 and *Aorolaimus* n.gen. *Nematologica* 9: 267–295.

Sher, S. A. 1964a. Revision of the Hoplolaiminae (Nematoda) III. *Scutellonema* Andrássy, 1958. *Nematologica* 9(1963): 421–443.

Sher, S. A. 1964b. Revision of the Hoplolaiminae (Nematoda) IV. *Peltamigratus* n.gen. *Nematologica* 9(1963): 455–467.

Sher, S. A. 1965. *Aphasmatylenchus nigeriensis* n.gen., n.sp. (Aphasmatylenchinae n. subfam.: Tylenchoidea, Nematoda) from Nigerian soil. *Proc. Helm. Soc. Wash.* 32: 172–176.

Sher, S. A. 1965. Revision of the Hoplolaiminae (Nematoda). V. *Rotylenchus* Filipjev, 1936. *Nematologica* 11: 173–198.

Sher, S. A. 1966. Revision of the Hoplolaiminae (Nematoda). VI. *Helicotylenchus* (Steiner, 1945). *Nematologica* 12: 1–56.

Sher, S. A. 1973. *Antarctylus humus* n.gen., n.sp. from the subantarctic (Nematoda: Tylenchoidea). *J. Nematol.* 5: 19–21.

Sher, S. A., and Bell, A. H., 1975. Scanning electron micrographs of the anterior region of some species of Tylenchoidea (Tylenchida: Nematoda). *J. Nematol.* 7: 69–83.

Siddiqi, M. R. 1972. *Rotylenchus robustus*. C.I.H. descriptions of plant-parasitic nematodes, Set 1, No. 11.

Siddiqi, M. R. 1972. *Helicotylenchus multicinctus*. C.I.H. descriptions of plant-parasitic nematodes, Set 2, No. 23.

Siddiqi, M. R. 1972. *Scutellonema brachyurum*. C.I.H. descriptions of plant-parasitic nematodes, Set 4, No. 54.

Siddiqi, M. R. 1986. Tylenchida parasites of plant and insects. Commonwealth Agricultural Bureaux, Slough, UK.

Siddiqi, M. R., and Husain, Z. 1964. Three new species of nematodes in the family Hoplolaimidae found attacking citrus trees in India. *Proc. Helm. Soc. Wash.* 31: 211–215.

Sivakumar, C. V., and Selvasekaran, E. 1982. Description of two new species of *Scutellonema* Andrássy, 1958 (Hoplolaimoidea: Nematoda). *Ind. J. Nematol.* 12: 118–123.

Spaull, A. M. 1982. *Helicotylenchus vulgaris* and its association with damage to sugar beet. *Ann. App. Biol.* 100: 501–510.

Steiner, G. 1938. Nematodes infesting red spiderlilies. *J. Agr. Res.* 56: 1–8.

Stokes, D. E. 1977. The Columbia lance nematode, *Hoplolaimus columbus* Sher, 1963. *Nematology Circular*, 34, Florida Depart. Agr. and Consumer Serv.

Sumner, D. R. 1967. Nematodes in bluegrass. *Plant Dis. Reptr.* 51: 457–460.

Suryawanshi, M. V. 1971. Studies on Tylenchida (Nematoda) from Marathwada, India, with descriptions of four new species. *Nematologica* 17: 393–406.

Thorne, G., and Malek, R. B. 1968. Nematodes of the Northern Great Plains. Part I. Tylenchida (Nemata: Secernentea). *South Dakota Agr. Exp. Stat. Tech. Bull.* No. 31.

Van den Berg, E., and Heyns, J. 1970. South African Hoplolaiminae. I. The genus *Hoplolaimus* Daday, 1905. *Phytophylactica* 2: 221–226.

Van den Berg, E., and Heyns, J. 1973. South African Hoplolaiminae. 2. The genus *Scutellonema* Andrássy, 1958. *Phytophylactica* 5: 23–39.

Van den Berg, E., and Heyns, J. 1975. South African Hoplolaiminae 4. The genus *Helicotylenchus* Steiner, 1945. *Phytophylactica* 7: 35– 52.

Van den Berg, E., and Kirby, M. F. 1979. Some spiral nematodes from the Fiji Islands (Hoplolaimidae: Nematoda). *Phytopathology* 11: 99– 109.

Vovlas, N. 1984. Morphology of a local population of *Helicotylenchus multicinctus* from southern Italy. *Rev. Nématol.* 6(1983): 327–329.

Vovlas, N. 1985. Head structure of five species in the subfamily *Hoplolaiminae* (Nematoda). *Nematol. Mediterranea* 12(1984): 163–168.

Vovlas, N., and Lamberti, F. 1985. Observations on the morphology and histopathology of *Hoplolaimus pararobustus* attacking coffee in Sao Tome. *Nematol. Mediterranea* 13: 73–80.

Wallace, H. R. 1971. The influence of the density of nematode populations on plants. *Nematologica* 17: 154–166.

Wang, K. C., and Chen, T. A. 1985a. Ultrastructure of the phasmids of *Scutellonema brachyurum*. *J. Nematol.* 17: 175–186.

Wang, K. C., and Chen, T. A. 1985b. Ultrastructure of male sexual apparatus of *Scutellonema brachyurum*. *J. Nematol.* 17: 435–444.

Wen, G. Y., and Chen, T. A. 1972. Fine structures of the cuticle of *Hoplolaimus galeatus*. *J. Nematol.* 4: 236–237.

Whitehead, A. G. 1958. *Rotylenchoides brevis* n.g., n.sp. (Rotylenchoidinae n.subfam.: Tylenchida). *Nematologica* 3: 327–331.

Whitehead, A. G. 1959. *Hoplolaimus angustalatus* n.sp. (Hoplolaiminae: Tylenchida). *Nematologica* 4: 99–105.

Williams, J. R. 1960. Studies on the nematode fauna of sugar cane fields in Mauritius. 4. Tylenchoidea (partim). *Mauritius Sug. Ind. Res. Inst. Occ. Pap.* No. 4.

Yuen, P. H. 1964. Four new species of *Helicotylenchus* Steiner (Hoplolaiminae: Tylenchida) and a redescription of *H. canadensis* Waseem, 1961. *Nematologica* 10: 373–387.

Yuen, P. H. 1966. Further observations on *Helicotylenchus vulgaris* Yuen. *Nematologica* 11(1965): 623–637.

Zancada, M. C., and Lima, M. B. 1986. Numerical taxonomy of the genera *Rotylenchus* Filipjev, 1936 and *Orientylus* Jairajpuri and Siddiqi, 1977 (Nematoda: Tylenchida). *Nematologica* 31: 44–61.

Zuckerman, B. M., and Strich-Harari, D. 1964. The life stages of *Helicotylenchus multicinctus* (Cobb) in banana roots. *Nematologica* 9(1963): 347–353.