Scanning Electron Micrographs of the Anterior Region of Some Species of Tylenchoidea (Tylenchida: Nematoda)

S. A. SHER and A. H. BELL[1]

Abstract: Micrographs of the anterior region of 42 species in 36 genera of Tylenchoidea obtained with a scanning electron microscope are presented. Greater detail, depth of focus, and structures not previously seen with the light microscope have been obtained in this study. Some of the implications of the morphology of the face view on the classification of the Tylenchoidea are discussed. *Key Words:* nematode morphology.

The anterior region of some Tylenchoidea was examined with a scanning electron microscope (SEM) to ascertain if additional information could be obtained to better understand their morphology, classification, and phylogeny. This paper presents micrographs of 42 species in 36 genera obtained in this survey and some comments on their classification.

Previous work (2, 5, 6, 7, 8, 9, 11, 22) has

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[1]Professor of Nematology and Staff Research Associate, Department of Nematology, University of California, Riverside 92502. Appreciation is expressed to D. J. Raski, W. M. Wouts, and S. D. Van Gundy for reviewing the manuscript and offering valuable comments, and to H. J. Jensen for providing the specimens of *Nacobbodera chitwoodi*.

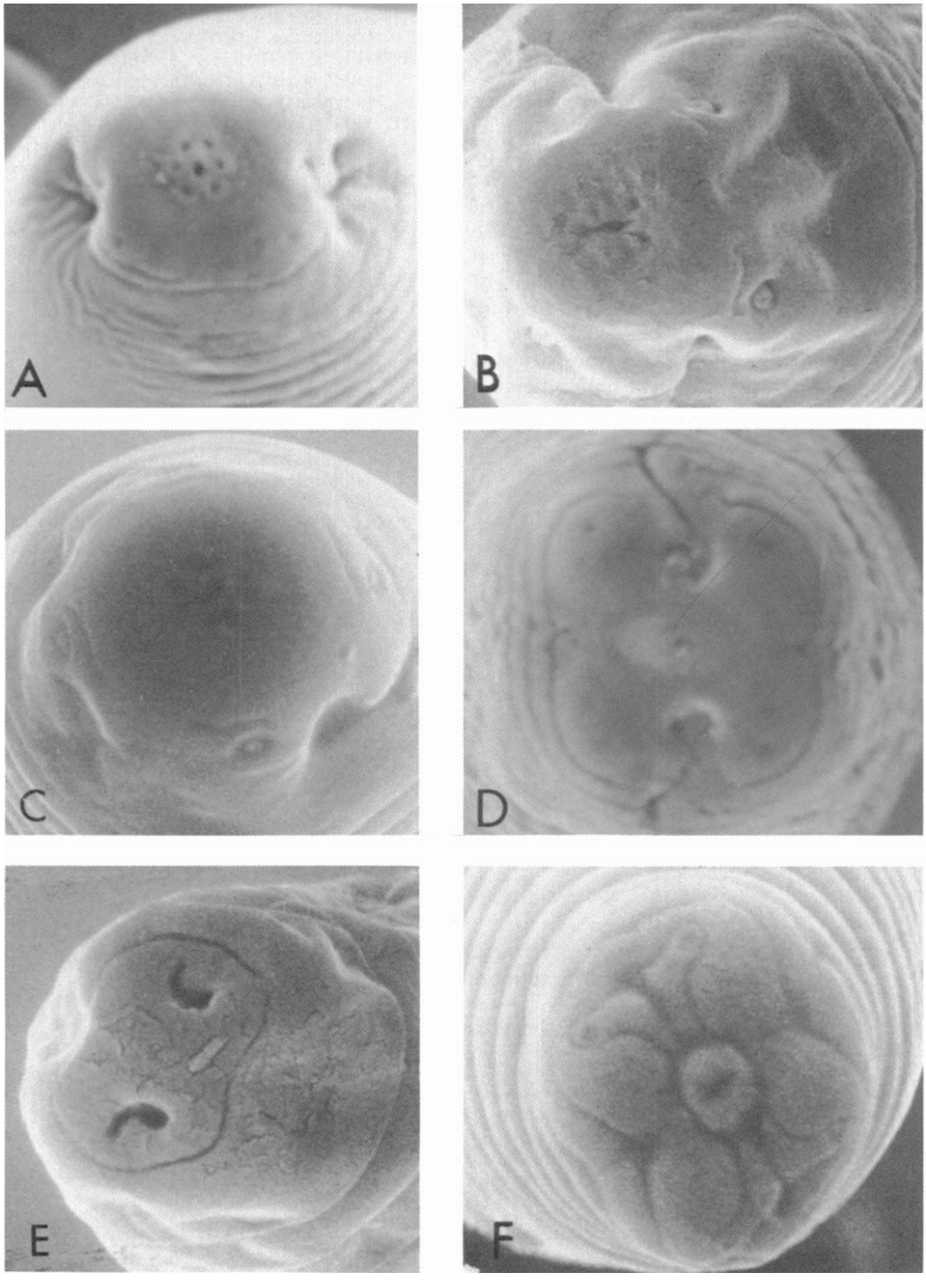

FIG. 1-(A-F). **A)** *Psilenchus* sp. female (New Zealand) × 7,500. **B)** *Neopsilenchus* sp. female (Israel) × 10,000. **C)** *Clavilenchus* sp. female (New Zealand) × 10,000. **D)** *Tylenchus davainii* female (California) × 7,500. **E)** *Aglenchus* sp. female (England) × 10,000. **F)** *Cephalenchus* sp. female (Australia) × 10,000.

shown that much greater detail and depth of focus can be obtained for surface structures of nematodes with the SEM. In recent papers (15, 16, 19, 21) SEM micrographs have been used to supplement light microscope drawings.

MATERIALS AND METHODS

Specimens used in our study were whole mounts in dehydrated glycerine placed on a glass chip with the anterior end protruding past the edge of the chip. Four to eight specimens of a single population usually were mounted on each chip. The body of the nematode was secured to the glass chip with a layer of thinned Zut. The chip then was glued to a SEM mounting stub with the specimens in a vertical position and coated with about 200×10^{-1} nm of gold. A JEOL JSM-U3 scanning electron microscope operating at an accelerating voltage of 5 to 15 KV was used to examine the specimens and micrographs were taken with a Polaroid type 55 camera and Polaroid 545 film holder.

RESULTS

Six populations of Psilenchinae representing three species in three genera were examined with the SEM [Fig. 1-(A-C)]. *Psilenchus* (Fig. 1-A) has a smooth lip region with six pits (papillae?) surrounding the round oral opening; eight pits (papillae?), two at each edge of the face view; and irregular U-shaped amphid apertures on the lateral sides of the lip region. *Neopsilenchus* and *Clavilenchus* (Fig. 1-B, C) are similar in appearance, having a smooth lip region with six pits surrounding the slit-to-oval oral opening. Four papillae are located in depressions equidistant from each other on the side of the lip region; an incomplete annule or slit is located above each papilla, and, elongated slit-like amphid apertures are located on the lateral sides of the lip region.

Fifteen populations of Tylenchinae identified as belonging to three genera *(Tylenchus, Aglenchus,* and *Cephalenchus)* were examined [Fig. 1-(D-F)]. Most of the specimens produced unsatisfactory results since they deteriorated under the electron beam. Micrographs of a fair quality were obtained for some of the specimens in seven populations. *Tylenchus davainii* (Fig. 1-D) has a rectangular-shaped face with slight indentations dorsally and laterally. Amphid apertures are a slit along the lateral side of the lip region terminating in a rounded area on the face. There is a single pit (papillae) in each corner of the face. One other population from New Zealand closely related to *T. davainii* showed a similar face view though the micrographs were not as clear as the California population.

Aglenchus (Fig. 1-E) shows a large rectangular area (oral disc?) clearly delimited on the face, and large comma-shaped to oval amphid apertures, but no pits or papillae are visible. A population of *Aglenchus* from Thailand had a similar face view, except for a less conspicuous oral disc and more rounded amphid apertures.

Four populations of *Cephalenchus* (probably *C. emarginatus)* from Canada and Australia were similar in morphology (Fig. 1-F). The face view is rectangular with an indentation dorsally and ventrally, a small round area (oral disc?) is seen clearly around the rectangular oral opening, four sectors are seen laterally, starting near the center of the face view and extending at right angles dorsally and laterally to form a boomerang-shaped structure. A conspicuous pit (papillae?) is located at the distal end of each of these structures. The amphid apertures are slit-like and located laterally between the proximal part of the previous structure (Fig. 1-F).

Dolichodoridae are represented in this survey by the genera *Tylodorus* and *Dolichodorus*. The face views are similar in having a conspicuous oral disc and elongated longitudinal amphid apertures. *Tylodorus acuminatus* (Fig. 2-A, B) has four papillae, one in each portion of the rounded slightly rectangular face view. *Dolichodorus nigeriensis* and *D. silvestris* (Fig. 2-C, D) have more conspicuous amphid apertures, the lip region is indented laterally, and there are no papillae. Three additional species of *Dolichodorus* have been examined with the SEM, and they are similar to Fig. 2-C, D.

A single population of *Tylenchorhynchus phaseoli* (Fig. 3-B) shows an oral disc (?) with two indentations laterally where the large rounded amphid apertures are located, with more pronounced indentations dorsally and ventrally; and six protuberances (papillae?) surrounding the oval oral aperture. The longitudinal ridges of the cuticle are prominent in the anterior part of the body

(Fig. 3-A). A single population of *T. lamelliferus* (Fig. 3-D) has a large irregular, squarish oral disc (?), a round oral opening surrounded by a small depressed area, and

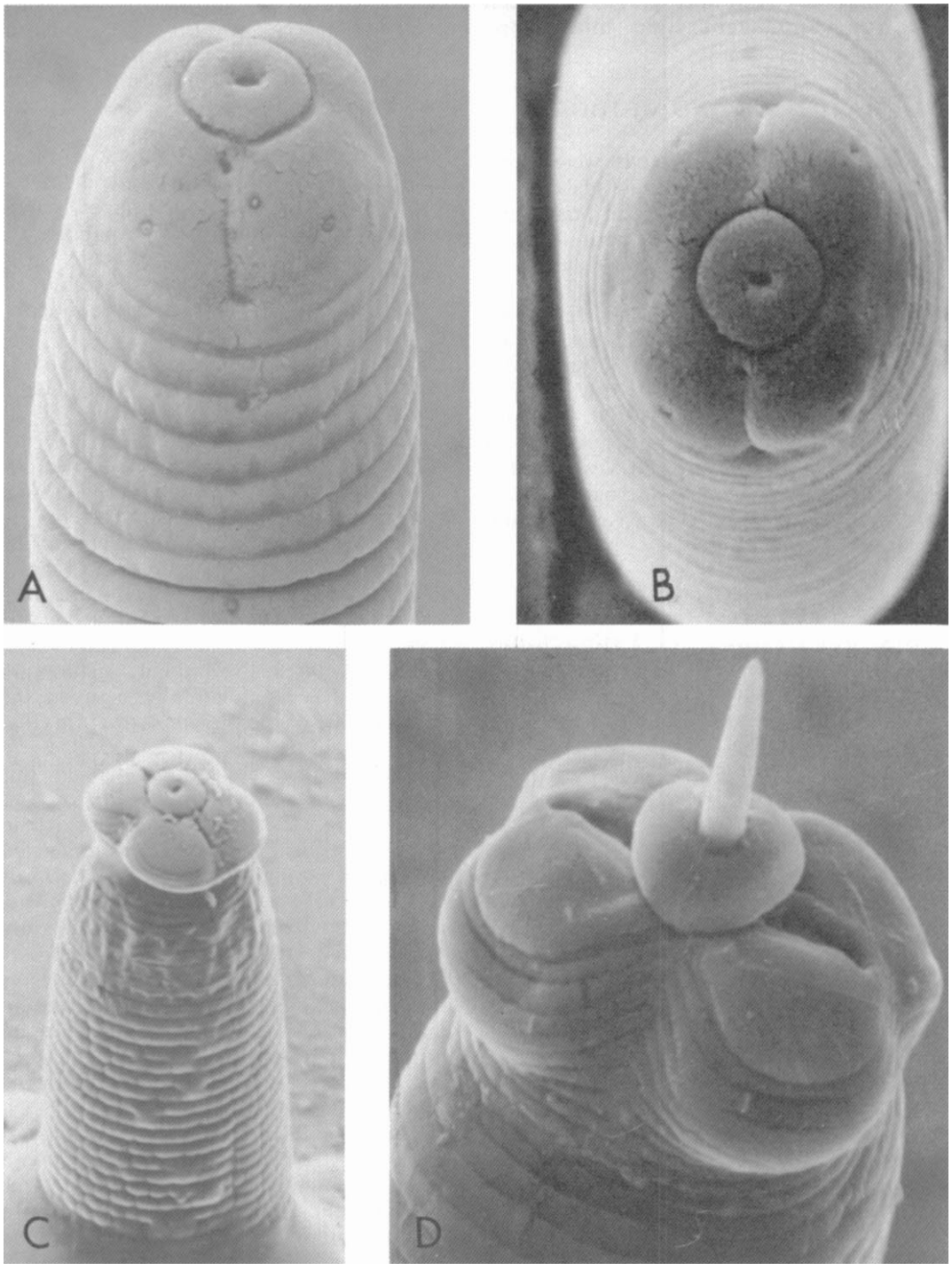

FIG. 2-(A-D). **A)** *Tylodorus acuminatus* female anterior region (Australia) × 5,000. **B)** *T. acuminatus* female face view × 5,000. **C)** *Dolichodorus nigeriensis* female anterior region (Nigeria) × 2,000. **D)** *Dolichodorus silvestris* female anterior region (topotype) × 4,000.

irregularly oval amphid apertures. Figure 3-C shows the longitudinal lines and the longitudinal ridges of the cuticle.

Four populations of *Quinsulcius* representing three species *(Q. capitatus, Q. curvus,* and *Q. acutus)* have been examined. They are all similar to the illustrations of *Q. acutus* (Fig. 4-A, B) and have a four-lobed oral disc (?) with two pits (papillae?) in each lobe, round amphid apertures with lip-region

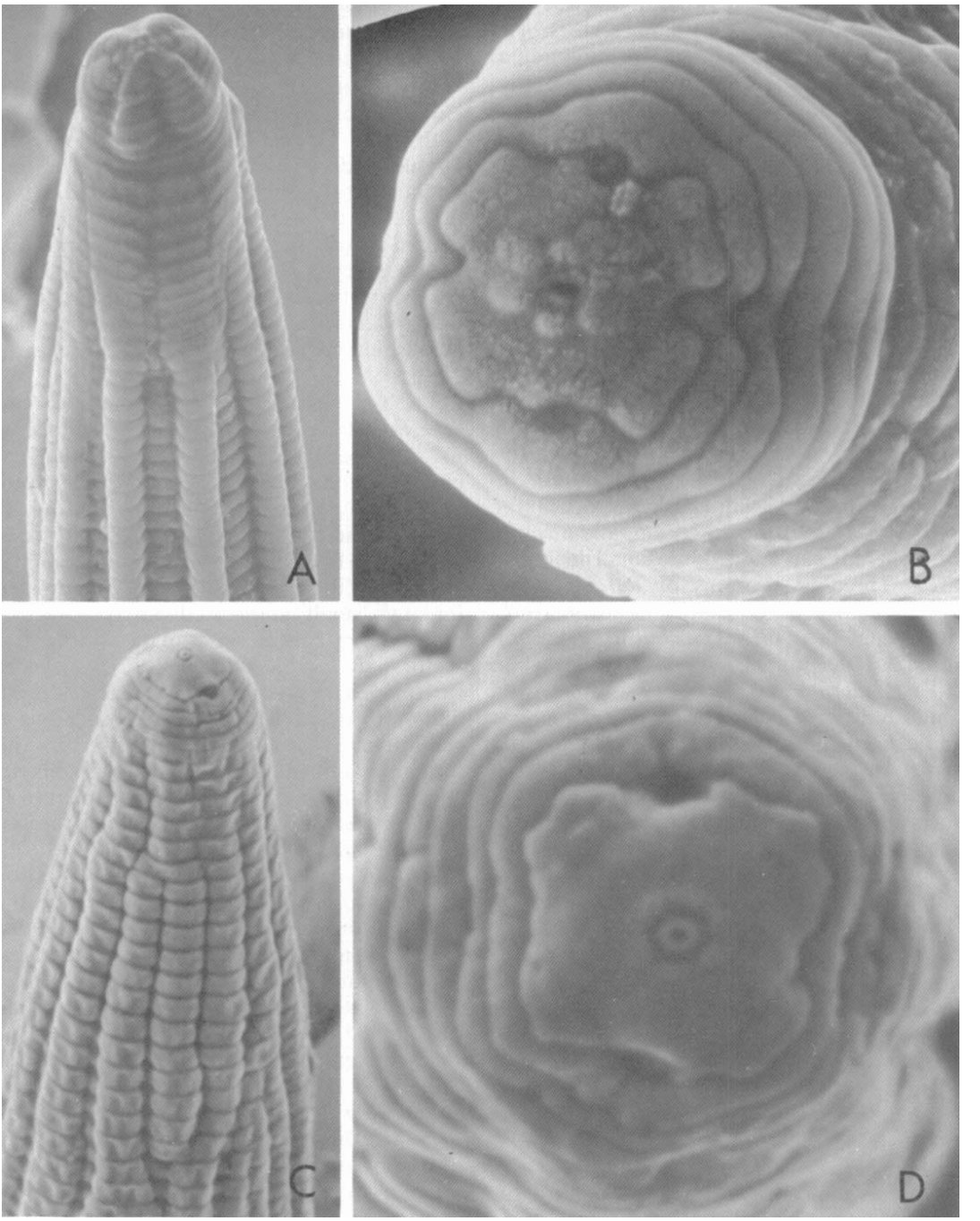

FIG. 3-(A-D). **A)** *Tylenchorhynchus phaseoli* female anterior region (Brazil) × 3000. **B)** *T. phaseoli* female face view (Brazil) × 10,000. **C)** *Tylenchorhynchus lamelliferus* female anterior region (England) × 3,000. **D)** *T. lamelliferus* female face view (England) × 10,000.

incisures directed toward them, and a slit-like oral opening with six pits (papillae?), three on each side of the oral opening.

Merlinius quadrifer (Fig. 4-C, D) (two populations) has a lip region with six longitudinal incisures, a distinct oral disc and almost oval amphid apertures near the anterior end of the lateral lip sectors. The anterior region clearly shows the longitudinal striations of the cuticle (Fig. 4-C).

Three populations of *Tylenchorhynchus cylindricus* (Fig. 5-A) show an irregular oral disc (?) with rounded amphid apertures at its edge, a slit-like oral opening, and six minute pits (papillae?), three on each side of the oral opening, and distinct lip region annules. *T. goffarti* (Fig. 5-B) (two populations) has a four-lobed oral disc (?) with two pits in each lobe (similar to *Quinsulcius);* a rounded oral opening surrounded by six raised areas (papillae?); round, usually obscure, amphid apertures; and a single distinct incisure laterally extending the length of the lip region.

A single population of *Macrotrophurus arbusticus* (Fig. 5-C) shows a smooth lip region with slit-like amphid apertures near the posterior area of the lip region, and a round oral opening surrounded by a small depressed area. Three populations of *Paratrophurus* (Fig. 5-D) have large round amphid apertures at the edge of an inconspicuous irregular oral disc (?). Three populations of *Trophurus* (Fig. 5-E) (Israel, Brazil, and England) show a smooth lip region with only the slightest indication of amphid apertures and oral opening. Four populations of *Uliginotylenchus rhopalocercus* (different locations in Nigeria) (Fig. 5-F) have an inconspicuous oral disc, elongated amphid apertures at the edge of the oral disc, and a round oral opening surrounded by a depressed area.

Aphasmatylenchus (Fig. 6-A) has a large conspicuous oral disc, slit-like amphid apertures at the edge of the oral disc, the anterior annule divided into six almost equal sectors, and a slit-like rectangular oral opening.

Telotylenchoides housei (Fig. 6-B) (two populations) face view morphology is similar to *Quinsulcius* except for the lip region annules which are not directed toward the amphid apertures. *Histotylenchus* sp. (Fig. 6-C) (one population) has a more rectangular oral disc (?), no indication of papillae on the oral disc, except for the six pits (papillae) around the oval oral opening, and incisures directed toward the oral disc. *Telotylenchus ventralis* (Fig. 6-D) (two populations) has an oral disc (?) similar to *Quinsulcius* and *Tylenchorhynchus goffarti,* but only one papilla in each lobe, six raised areas and pits (papillae?) surrounding the oval oral opening, and incisures directed toward the large, rounded amphid apertures.

Morulaimus (Fig. 6-E) has a large laterally elongated oral disc with an oval oral opening with three pits on each side. The anterior annule is divided into six sectors, the two lateral sectors being smaller than the two dorsal and two ventral sectors. *Belonolaimus* (Fig. 6-F) has a more set off round oral disc, the lip region is divided into four large sectors (two dorsal and two ventral) and two small lateral sections. The amphid apertures are inconspicuous and located at the lateral lip sectors.

Twelve populations belonging to five species of *Pratylenchus* were examined. Most of the specimens deteriorated under the electron beam, but useful micrographs were obtained for three species [Fig. 7-(A-C)]. *P. vulnus* and *P. zeae* micrographs (one population of each) were of very poor quality. *P. minyus* (Fig. 7-A) has the face view divided into two small lateral wedge-shaped sectors and a large continuous dorsal and ventral sector; the oral opening is oval, and surrounded by six pits, three on each side. An undescribed species from California has a smooth face view not divided into sectors and similar oral opening and pits as in *P. minyus* (Fig. 7-B). *P. thornei* (Fig. 7-C) is similar to *P. minyus,* but the lip region sectors are of different sizes and shapes.

Hoplotylus femina (Fig. 7-D) (one population) has a smooth face view with the anterior annules of the lip region divided irregularly and incompletely by incisures, slit-like amphid apertures with distal edges directed laterally, and an oval oral opening surrounded by six pits.

Two populations of *Radopholus similis* (Fig. 7-E) (Hawaii and Nigeria) have two lateral lip sectors the length of the lip region, with oval amphid apertures anteriorly, and an oval oral opening surrounded by six pits, three on each side.

Nacobbus aberrans (Fig. 7-F) has a large oval oral disc, the anterior annule shows four large rounded protuberances (sectors), a slightly oval oral opening surrounded by six

indistinct pits, and elongated amphid apertures.

The following additional Pratylenchidae genera were examined: *Hirschmanniella, Pratylenchoides, Apratylenchoides,* and *Zygotylenchus*. Most of the specimens

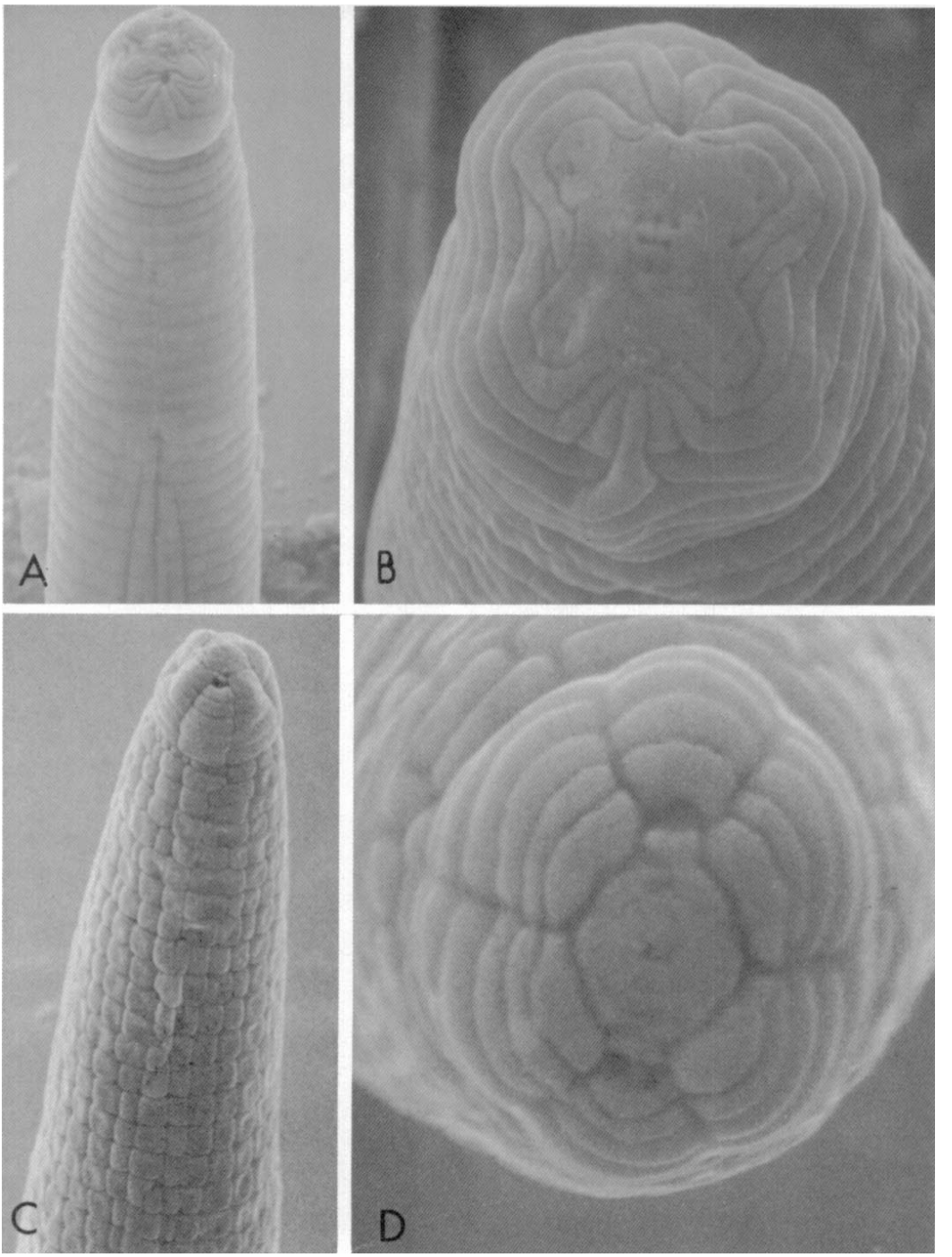

FIG. 4-(A-D). **A)** *Quinsulcius acutus* female anterior region (California) × 3000. **B)** *Q. acutus* female face view (California) × 10,000. **C)** *Merlinius quadrifer* female anterior region (England) × 3,000. **D)** *M. quadrifer* female face view (England) × 10,000.

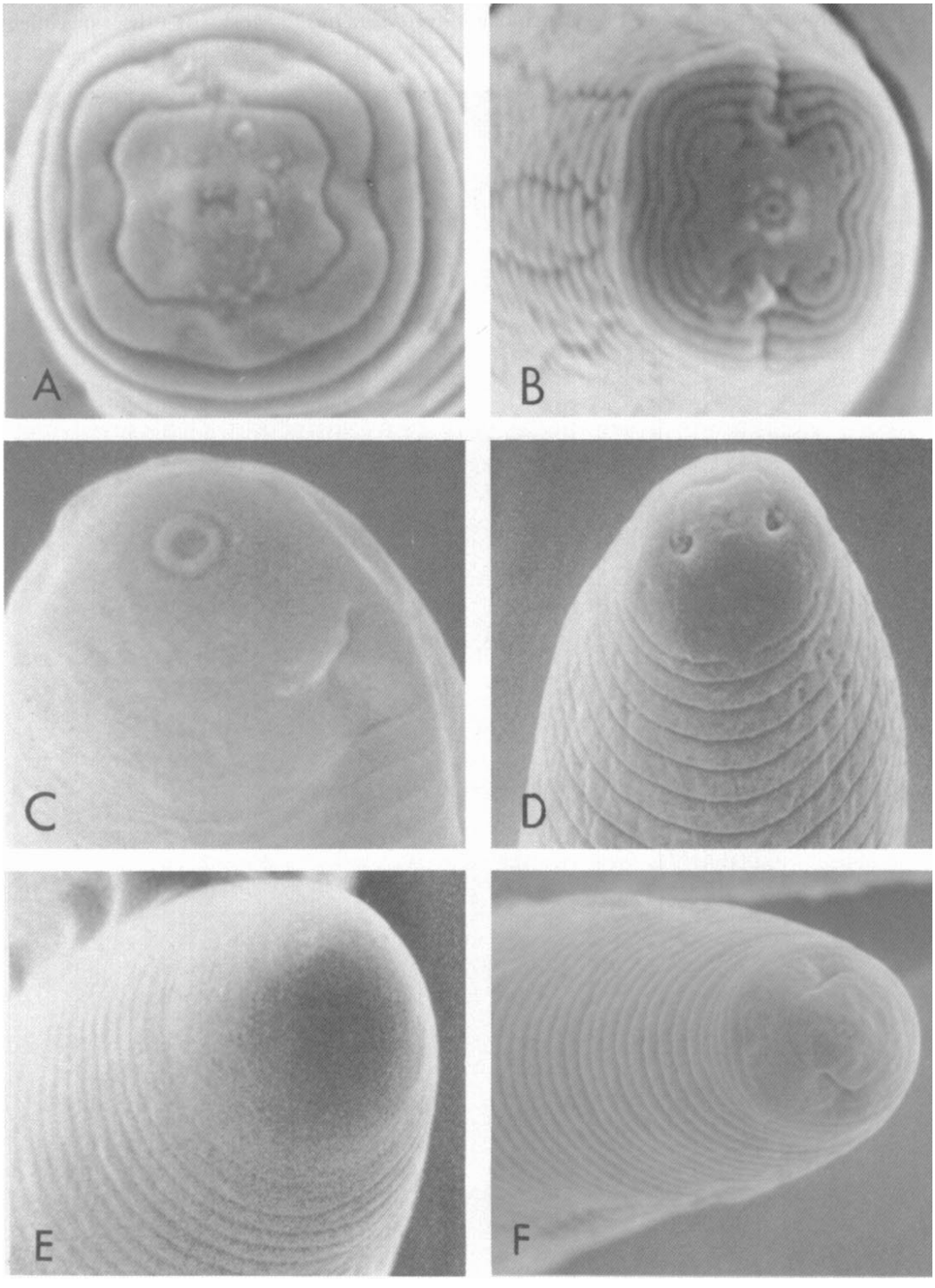

FIG. 5-(A-F). **A)** *Tylenchorhynchus cylindricus* female (California) × 10,000. **B)** *Tylenchorhynchus goffarti* female (Israel) × 7,500. **C)** *Macrotrophurus arbusticola* female (France) × 5,000. **D)** *Paratrophurus* sp. female (Thailand) × 5,000. **E)** *Trophurus* sp. female (Brazil) × 7,500. **F)** *Uliginotylenchus rhopalocercus* female (Nigeria) × 5,000.

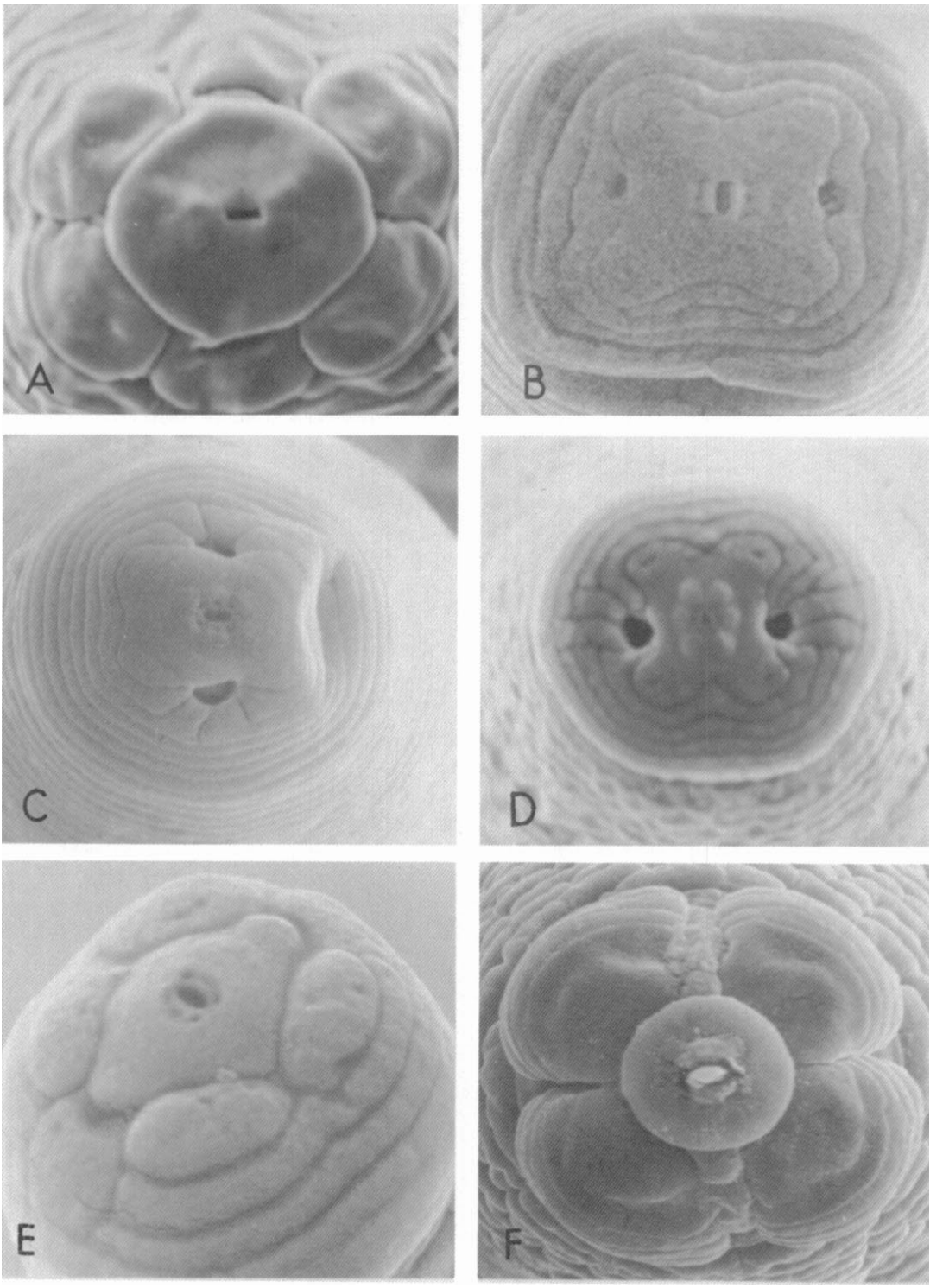

FIG. 6-(A-F). **A)** *Aphasmatylenchus nigeriensis* female (Nigeria) × 7,500. **B)** *Histotylenchus* sp. female (Kenya) × 7,500. **C)** *Telotylenchoides housei* juvenile (paratype) × 7,500. **D)** *Telotylenchus ventralis* female (Nigeria) × 7,500. **E)** *Morulaimus* sp. female (Australia) × 7,500. **F)** *Belonolaimus lineatus* female (paratype) × 5,000.

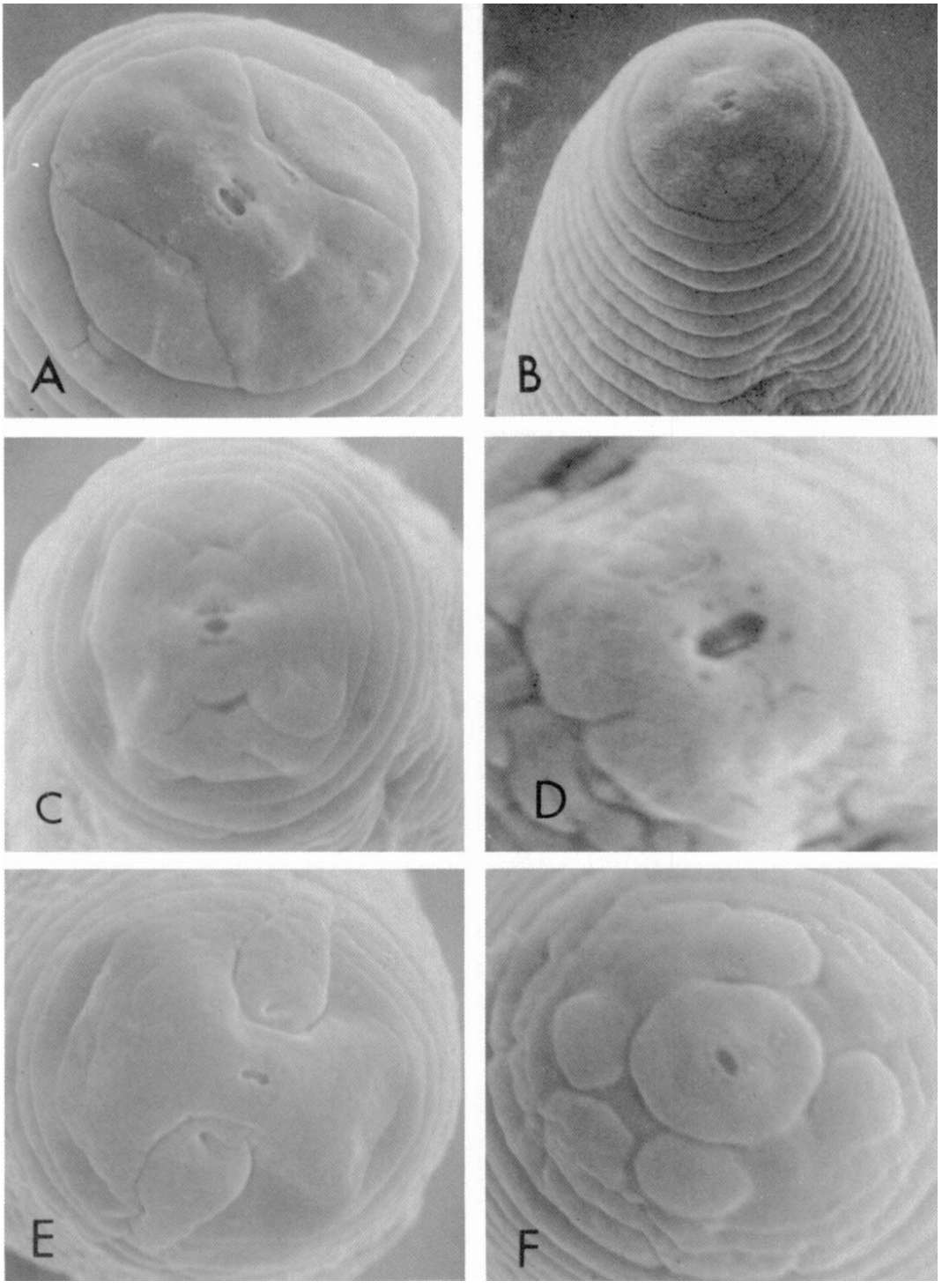

FIG. 7-(A-F). **A)** *Pratylenchus minyus* female (California) × 10,000. **B)** *Pratylenchus* sp. female (California) × 5,000. **C)** *Pratylenchus thornei* female (California) × 10,000. **D)** *Hoplotylus femina* female (New Jersey) × 10,000. **E)** *Radopholus similis* female (Nigeria) × 7,500. **F)** *Nacobbus aberrans* immature female (England) × 7,500.

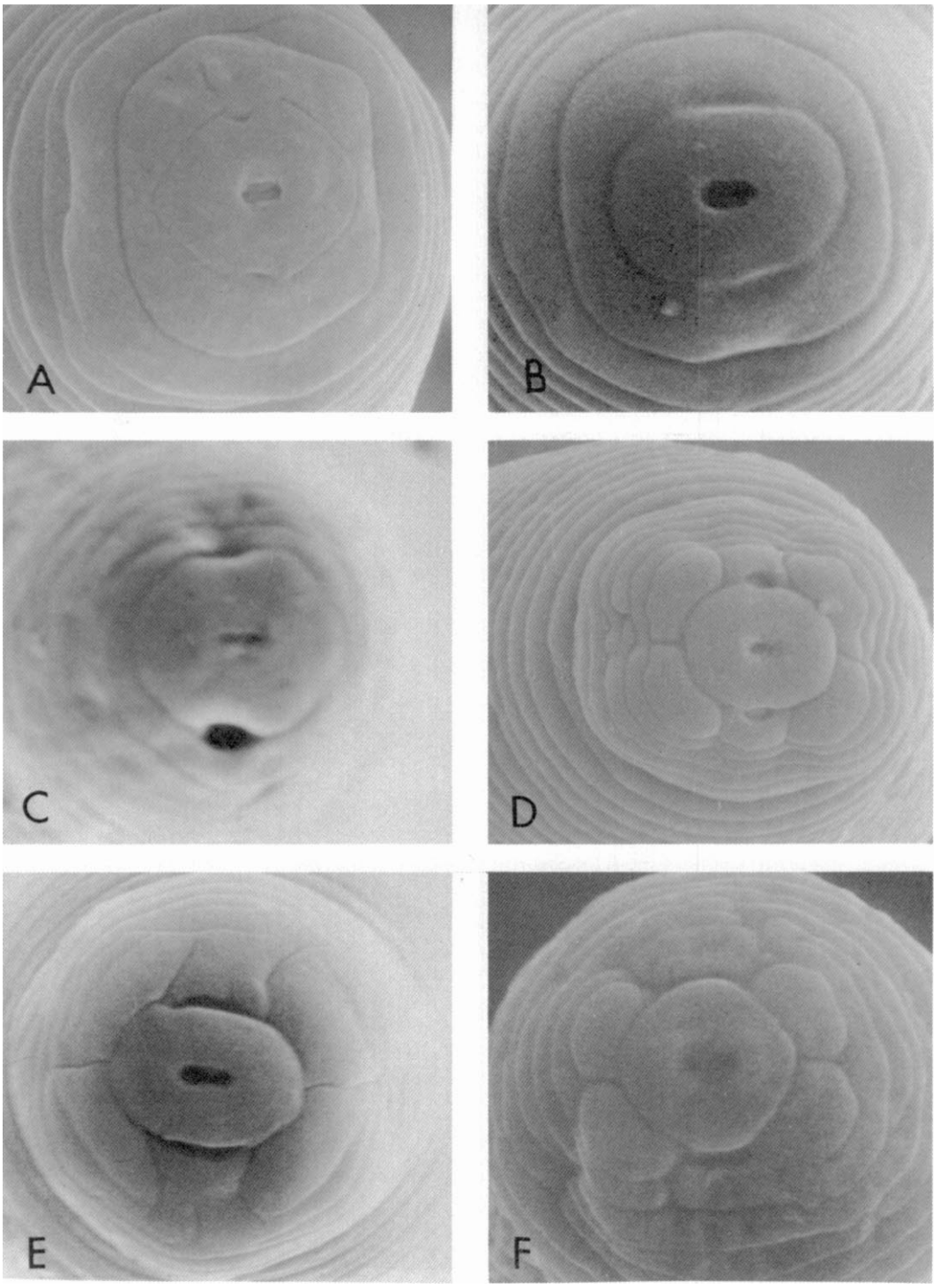

FIG. 8-(A-F). **A)** *Rotylenchoides intermedius* female (Nigeria) × 10,000. **B)** *Helicotylenchus hydrophilus* female (South Carolina) × 10,000. **C)** *Antarctylenchus humus* female (paratype) × 7,500. **D)** *Scutellonema bradys* female (Nigeria) × 5,000. **E)** *Peltamigratus* sp. female (Brazil) × 7,500. **F)** *Rotylenchulus reniformis* immature female (Hawaii) × 10,000.

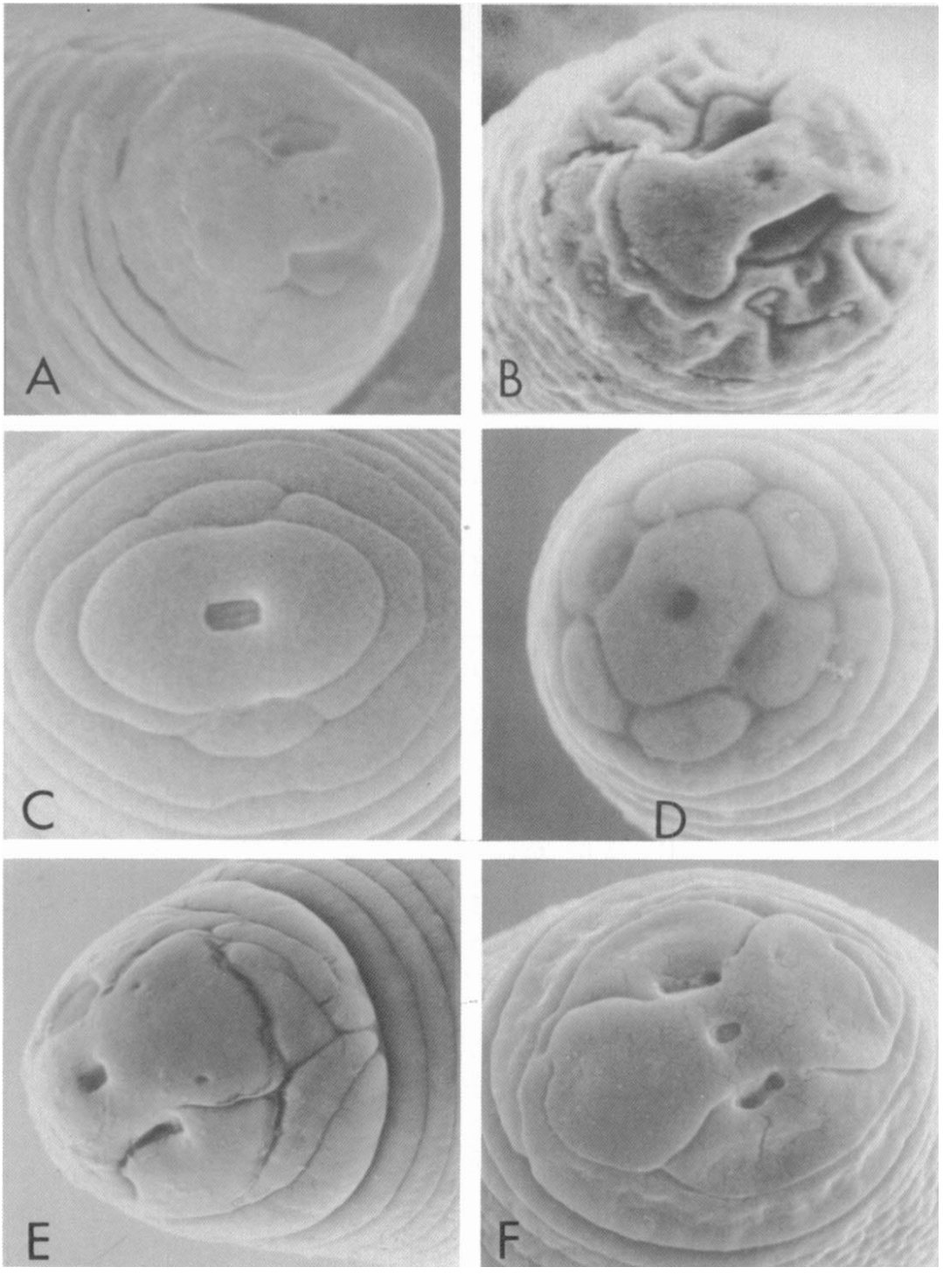

FIG. 9-(A-F). **A)** *Hypsoperine graminis* second-stage juvenile (topotype) × 12,000. **B)** *Meloidogyne javanica* second-stage juvenile (California) × 12,000. **C)** *Sarisodera hydrophila* second-stage juvenile (topotype) × 7,500. **D)** *Meloidodera belli* second-stage juvenile (topotype) × 7,500. **E)** *Nacobbodera chitwoodi* male (topotype) × 3,750. **F)** *N. chitwoodi* juvenile (topotype) × 5,000.

deteriorated under the electron beam, but the following structures of the face view were observed on some of the specimens in all of these genera: six pits around the oral opening and elongated slit-like amphid apertures similar to *Pratylenchus* [Fig. 7-(A-C)].

Hoplolaimidae (Fig. 8) show a pattern of slit-like to oval amphid apertures at the lateral edge of a large round to oval oral disc, and a conspicuous oval oral opening. Specimens usually did not deteriorate under the electron beam. *Helicotylenchus* (Fig. 8-A), *Rotylenchoides* (Fig. 8-B) and *Antarctylenchus* (Fig. 8-C) have no longitudinal incisures of the lip region. *Scutellonema* (Fig. 8-D), *Peltamigratus* (Fig. 8-E) and *Rotylenchulus* (Fig. 8-F) have the anterior lip annule divided into six sectors. No pits (papillae) are seen on the face view of these species, or any of the other Hoplolaimidae examined (19 species in eight genera) with the SEM.

Second-stage juveniles of six populations of *Meloidogyne* and one population of *Hypsoperine* representing four species were examined. Although most of the specimens deteriorated under the electron beam, micrographs of fair quality were obtained for three species of *Meloidogyne* (Fig. 9-B) and the *Hypsoperine* species (Fig. 9-A). They all showed a pattern of a large dumbbell-shaped oral disc (?) with elongated conspicuous amphid apertures at the lateral edges, and a round to oval oral opening surrounded by six pits.

In contrast to Meloidogynidae, second-stage juveniles of Heteroderidae withstood the same accelerating voltage used with *Meloidogyne* without deteriorating. One population each of two genera was examined. *Sarisodera* (Fig. 9-C) has a large oval labial disc, slit-like amphid apertures at the edge of the labial disc, conspicuous oval oral aperture, and the anterior annule of the lip region is divided into four sectors, the lateral sectors being considerably smaller. *Meloidodera belli* (Fig. 9-D) has a large irregularly oval labial disc, slit-like amphid apertures, a conspicuous rounded oral aperture, and the anterior annule of the lip region is divided into six, almost equal sectors.

The recently described genus *Nacobbodera* (Fig. 9-E, F) has a large dumbbell-shaped oral disc with four pits (papillae?), one each near the lateral edges of the oral disc; conspicuous slit-like to oval amphid apertures; and an oval to rectangular oral aperture.

Additional genera of Tylenchoidea *(Ditylenchus, Anguina, Trichotylenchus, Nagelus,* and *Geocenamus)* were examined with the SEM; but, because the micrographs were of such poor quality, they are not included. Genera which show some evidence of being closely related to some of these genera, but usually not included in the Tylenchoidea *(Nothanguina, Boleodorus, Nothotylenchus,* and *Deladanus)* also deteriorated under the electron beam in initial attempts to obtain micrographs.

DISCUSSION

The face view of Tylenchoidea as seen with the scanning electron microscope shows that the true surface morphology usually has not been seen with the light microscope. This study and some previous work (20) show that morphological structures of the face view appear to be constant for some taxa at the specific (20), generic, and higher categories. This additional morphological information provides some exciting material for understanding the morphology, classification, and relationships of the Tylenchoidea. The following discusses some implications of these preliminary studies for the Tylenchoidea.

The genera of Psilenchinae and Tylenchinae studied *(Psilenchus, Neopsilenchus, Tylenchus, Aglenchus,* and *Cephalenchus)* have distinctive face view patterns that can be distinguished by SEM micrographs. *Neopsilenchus* and *Clavilenchus* face view micrographs are similar and support the synonomy of these genera.

Tylodorus and *Dolichodorus* micrographs of the face view agree with the speculation proposed by Meagher (10) that "*Tylodorus* seems to occupy a systematic position between *Tylenchus* and *Dolichodorus*."

Six species of Tylenchorhynchinae, in three genera, all show a different pattern for the face view (Fig. 3; 4-A, B; 5-A, B, F). *Tylenchorhynchus goffarti* (Fig. 5-B) appears similar to *Telotylenchus ventralis* (Fig. 6-D) in the family Belonolaimidae. *Tylenchorhynchus cylindricus* (Fig. 5-A), *T. phaseoli* (Fig. 3-B) and *Quinsulcius acutus* (Fig. 4-B) also show some similarities to *Histotylenchus* sp. (Fig. 6-B),

Telotylenchoides housei (Fig. 6-C) and *Telotylenchus ventralis* (Fig. 6-D) in the family Belonolaimidae.

Aphasmatylenchus nigeriensis (Fig. 6-A) has a face view similar to the basic pattern seen in the Hoplolaimidae (Fig. 8). It is also one of the few species in which the face view pattern as seen with the light microscope (14) is similar to the SEM micrographs.

Merlinius quadrifer (Fig. 4-C, D) exhibits a pattern similar to micrographs previously reported for *Merlinius joctus* and *M. microdorus* (15).

The three genera in the subfamily Trophurinae all show different patterns [Fig. 5-(C-E)]. The four populations (Brazil, Israel and England) of *Trophurus* sp. examined were all similar in that they did not show any structures on the smooth lip region, not even the amphid apertures or oral opening (Fig. 5-E)!

Hoplolaimidae are considered to have a basic pattern of a conspicuous round to oval oral opening without associated pits (papillae) and a large round to oval oral disc with the amphid apertures at the edge of the oral disc (Fig. 8). A further division of the Hoplolaimidae can be made on the basis of the anterior lip annule. *Helicotylenchus, Rotylenchoides,* and *Antarctylenchus* [Fig. 8-(A-C)] have an undivided anterior annule (no longitudinal lines on the lip region) and the rest of the genera have the first annule divided into six sectors (longitudinal lines on the lip region) [Fig. 8-(D-F), 3, 7]. This supports the classification of Siddiqi (17) but not the classification of Golden (3).

The *Belonolaimus lineatus* face view (Fig. 6-F) appears similar to micrographs published for *Belonolaimus longicaudatus* (18). The papillae reported by Roman (12) on the lip region for *Belonolaimus lineatus, B. longicaudatus,* and *B. gracilis* are not seen with the scanning electron microscope.

Morulaimus micrographs of the face view are similar to those published for the original description of the genus (13) except for the six pits (papillae) surrounding the oral opening. This can be used as additional information to separate *Morulaimus* from *Belonolaimus.*

Pratylenchidae face views all have six pits (papillae) surrounding the oral opening, and this appears to be a good character to help define this taxon. This provides justification for the placement of *Hoplotylus* in the Pratylenchidae (3).

The face view of *Nacobbus* is not similar to other Pratylenchidae studied, which supports the recent transfer of this taxon from the Pratylenchidae (3).

The second-stage juvenile specimens of Meloidogynidae and Heteroderidae species appear to differ primarily in the presence of six pits (papillae?) around the oral opening in *Meloidogyne,* the shape of the oral disc, the segmentation of the anterior lip annule, and the reaction to the electron beam in the SEM. Further study of other stages and additional species are needed.

The two genera of Heteroderidae examined (Fig. 9-E, F) can be distinguished from *Heterodera* (21) by SEM micrographs. *Sarisodera* (Fig. 9-E) and *Meloidodera* (Fig. 9-F) micrographs are similar to Hoplolaiminae face view micrographs (Fig. 8) and support the theory of Wouts and Sher that Heteroderinae evolved from a Hoplolaiminae (23). They considered *Meloidodera* the most primitive Heteroderinae because of morphological characters that they have in common. The face view of *Meloidodera belli* (Fig. 9-F) appears to be, of all the Heteroderinae studied by SEM, the most closely related to Hoplolaiminae (Fig. 8).

The micrographs of *Nacobbodera* (Fig. 9-E, F) show a related, but different, pattern than Meloidogynidae or Heteroderidae. The face view shows no similarities to *Nacobbus,* and therefore does not support the classification of this genus as being most closely related to *Nacobbus* (4). *Meloinema* which appears to be similar to *Nacobbodera* (the latter may be a synonym of *Meloinema)* was placed by Choi and Geraert in the family Meloidogynidae (1). Specimens of *Meloinema* have not been available for study, but the results with *Nacobbodera* would support the placement of *Meloinema (=Nacobbodera?)* in the Meloidogynidae.

Additional comments and speculations on the morphology, classification and phylogeny of the Tylenchoidea are being postponed because additional SEM work is still in progress to confirm and expand these studies.

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