Journal of Nematology 17(3):297-309. 1985.

Comparative Morphology of *Meloidodera* spp. and *Verutus* sp. (Heteroderidae) with Scanning Electron Microscopy[1]

ABUBAKER A. OTHMAN AND J. G. BALDWIN[2]

Abstract: Scanning electron microscopy (SEM) of second-stage juveniles (J2), males, and females of *Meloidodera floridensis, M. charis, M. belli,* and *Verutus volvingentis* reveals detailed characteristics of the head region, lateral field, phasmid, body striae, vulva, and perineal region. In *M. charis* and *M. belli* the en face pattern conforms to a basic pattern in which the labial disc is surrounded by six lips (sectors) of the first head annulation. In J2 the head has additional annulations, whereas in males annulation is replaced by longitudinal blocks. Conversely, J2 and males of *M. floridensis* and *V. volvingentis* each have a unique derived face pattern with fusion of various lip components and with head annulation. All six lips of females of *M. charis* and *M. belli* are fused, whereas females of *M. floridensis* and *V. volvingentis* have distinct lateral lips. Lateral fields vary among species, with only slight differences at the anterior and posterior ends of the lateral lines and in the spatial relation of the lines to phasmid openings. Phasmid openings are present in adults of *Meloidodera* spp., but were not observed in adults of *V. volvingentis*; in this respect, the female perineal pattern of *Verutus* is different from *Meloidodera* spp. The very large vulva (± 48 μm long) of *V. volvingentis* is in sharp contrast to the minute vulva (± 6 μm long) in a population of *M. charis* from San Bernardino. Morphological characters revealed by SEM will be most informative when investigated throughout Heteroderidae and incorporated with additional characters for a phylogenetic analysis of the family.

Key words: en face patterns, perineal pattern, phasmids, phylogeny, SEM, systematics, vulva.

Meloidodera Chitwood et al., 1956 was introduced to accommodate a noncyst-forming heteroderid with annulated (i.e., striated) cuticle and subequatorial vulva, *M. floridensis* (5). These characters, which are believed to be primitive (i.e., plesiomorphic) (11), are shared by *Verutus* Esser, 1981 (10). Previous light microscope descriptions are inadequate to elucidate phylogenetic relationships within *Meloidodera,* between *Meloidodera* and *Verutus,* and among Heteroderidae in general. Detailed scanning electron microscopy (SEM) may reveal new shared derived characters which can be useful in testing hypotheses of phylogeny of *Meloidodera* and *Verutus* as a basis for systematics.

Meloidodera has six putative species and *Verutus* one; in the present study we examined en face patterns, lateral fields, tails, and sensory openings of juveniles (J2), males, and females of three *Meloidodera* spp. and *Verutus* sp. In addition, we examined annulation and the vulva and anus region of females. Terminology used here for en face patterns was proposed previously (2) for a basic pattern which occurs throughout Tylenchida. This pattern includes a rounded labial disc encircled by six lips (i.e., sectors) of the first lip annule: two subdorsal, two subventral, and two lateral. Since the subdorsal and subventral lips are identical, they are referred to as submedial lips. Interpretation of the combined lips as the first annule is consistent with classical light microscopy which counts this specialized annule with additional head annules for diagnoses of certain taxa (e.g., many *Pratylenchus* spp.).

MATERIALS AND METHODS

Second-stage juveniles, males, and females of *M. charis, M. belli, M. floridensis,* and *V. volvingentis* were collected from field sites or greenhouse cultures (Table 1). Specimens were isolated from roots and soil and processed for SEM using either the glycerin infiltration (gly) (14) or critical point drying (cpd) method. Results of these methods were compared to help identify possible artifacts. Some shrinkage occurred in cpd specimens, particularly in the tail region, but certain structures, such as phasmid openings, were more clearly observed in glycerin infiltrated than cpd specimens. Specimens prepared for cpd were

---

Received for publication 13 September 1984.

[1] A portion of the senior author's Ph.D. thesis. This research was supported in part by the Libyan people and by U.S. National Science Foundation Grant 84-15627.

[2] Graduate student and Associate Professor, respectively, Department of Nematology, University of California, Riverside, CA 92521.

The authors thank J. D. Eisenback (*M. floridensis*), D. T. Kaplan (*V. volvingentis*), and M. A. McClure (*M. charis*, Arizona population) for supplying specimens.

TABLE 1. Species, population, and numbers of *Meloidodera* and *Verutus* examined and their source.

Nematode	Host	Location	Number examined
Meloidodera floridensis Chitwood et al., 1956	loblolly pine *Pinus taeda* L.	North Carolina (greenhouse culture)	100 juveniles 12 males 50 females
M. charis Hooper, 1960	peony *Peonia californica* Nutt.	San Bernardino, California	100 juveniles 50 males 40 females
M. charis	honey mesquite *Prosopis juliflora* (Sw.) DC.	Arizona (greenhouse culture)	100 juveniles 9 males
M. belli Wouts, 1973	sage *Artemisia tridentata* Nutt.	German Flats near Salina, Utah	100 juveniles 10 males 6 females
Verutus volvingentis Esser, 1981	buttonweed *Diodia virginiana* L.	Orlando, Florida (greenhouse culture)	100 juveniles 20 males 30 females

placed in 0.025 M phosphate buffer at pH 7.2 and fixed in buffered glutaraldehyde. The concentration of fixative was gradually increased over a 30-minute period by adding 7% glutaraldehyde to the specimens in a known volume of buffer to a final concentration of 3.5%; after at least 2 hours, specimens were transferred to a processing chamber and washed repeatedly in buffer (8,9). The nematodes were postfixed for 2 hours in buffered 1% osmium tetroxide (OsO_4), washed in buffer, and treated with 1% thiocarbohydrazide (TCH) for 30 minutes (12). After thorough rinsing in buffer, they were again fixed in OsO_4 for 2 hours and rinsed in buffer. Specimens were dehydrated with a graduated acetone or ethanol series for 1.5 hours, infiltrated with Freon 113 for 1 hour, and critical point dried using carbon dioxide. Dried nematodes were mounted on stubs, sputter-coated with 20 nm gold palladium, and examined with a JEOL 35C SEM at 15 kV.

RESULTS

Head morphology: The en face patterns of J2, males, and females of *M. charis, M. belli, M. floridensis,* and *V. volvingentis* are modifications of the basic pattern (e.g., *M. charis;* Fig. 1B), including a rounded to hexagonal labial disc surrounded by six lips of the first head annule. Centrally located on the labial disc, the rectangular to ovoid prestoma leads to a slit-like stoma. Six pores of inner labial sensilla encircle the prestoma, and an amphid opening occurs between the labial disc and each lateral lip. The basic lip pattern is variously modified among species and life stages. These modifications may result from fusion of adjacent submedial lips with each other as well as with the lateral lips and the labial disc. In addition to the labial disc and first annule (including lips), the head usually includes other annules. Annules may be reduced in number, absent, or replaced by longitudinal blocks.

The labial disc of J2 of *M. charis* and *M. belli* is a dorso-ventrally elongate hexagon surrounded by six similar but separate lips. The head region includes one or two additional annulations (Fig. 1A–C, G–I). Although the lips of *M. charis* and *M. belli* males are similar to those of J2, other characters are different. The labial disc of males is round with a raised ring enclosing the prestoma (Fig. 1K). The head lacks additional annulation and is separated into 14–20 longitudinal blocks (Fig. 1D–F, J–L). In some individuals of *M. belli* and *M. charis* (Arizona population), each lateral lip may be fused with an adjacent longitudinal block.

The en face patterns of J2 and males of *M. floridensis* are different from other *Meloidodera* species (Fig. 2A–F). Adjacent submedial lips of J2 are fused (Fig. 2B) and in some cases are incompletely fused with the labial disc (Fig. 2A). Lateral lips are absent. In addition to the first annule, the head region includes one incomplete and one complete annulation (Fig. 2A, C). The en face pattern of males of *M. floridensis* con-

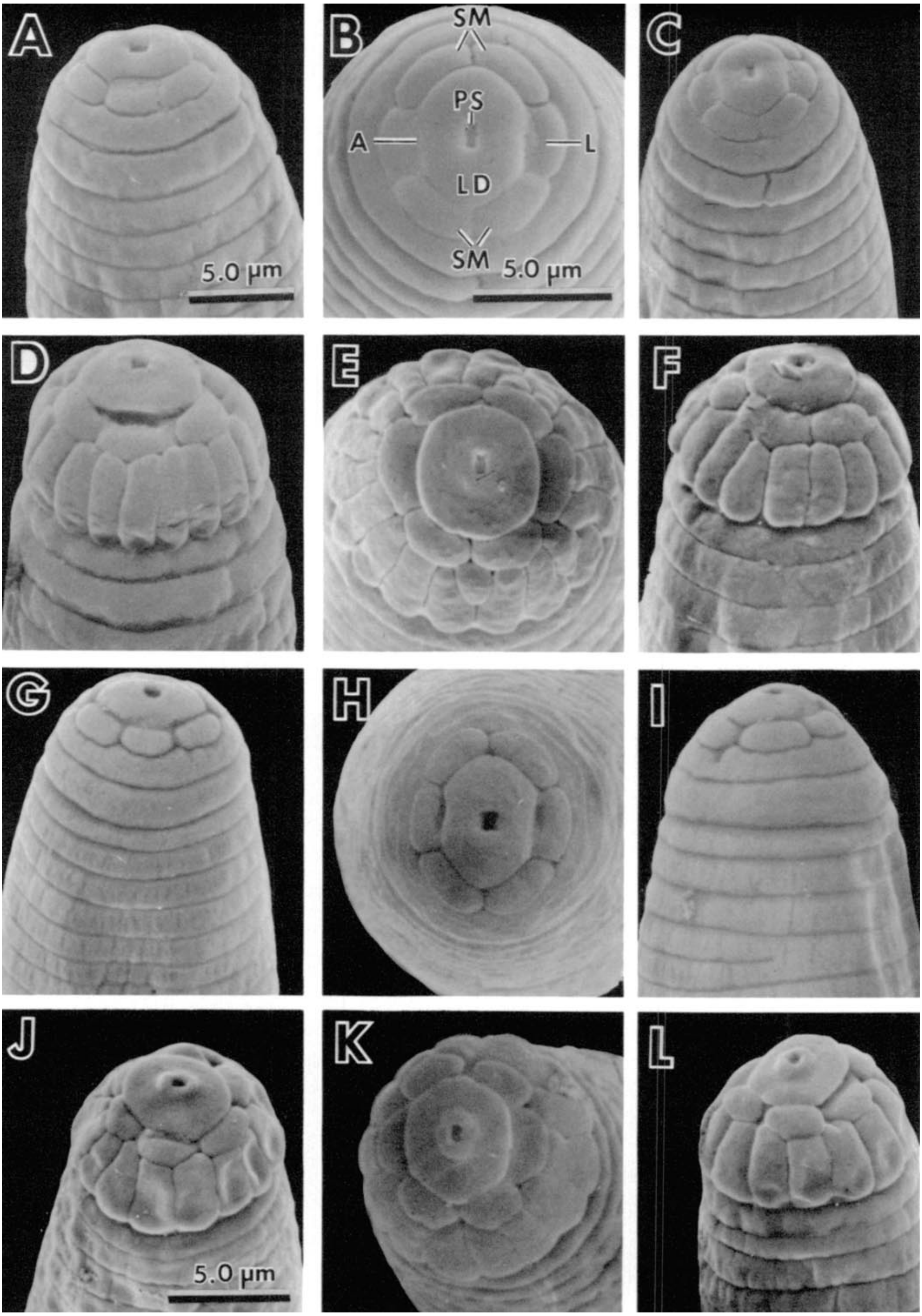


FIG. 1. Head region of vermiform stages of *Meloidodera charis* (A–F) and *M. belli* (G–L) prepared by glycerin (gly). A–C) Second-stage juveniles (J2) of *M. charis.* A) Lateral. B) En face showing basic pattern. Pattern includes hexagonal labial disc (LD) with prestoma (PS), surrounded by lateral (L) and submedial (SM) lip sectors. A = amphid opening. C) Medial. Scale as in A. D–F) Males of *M. charis.* D) Lateral. Scale as in B. E) En face. Scale as in B. F) Medial. Scale as in B. G–I) J2 of *M. belli.* G) Lateral. Scale as in A. H) En face. Scale as in B. I) Medial. Scale as in A. J–L) Males of *M. belli.* J) Lateral. K) En face. Scale as in B. L) Medio-lateral. Scale as in J.

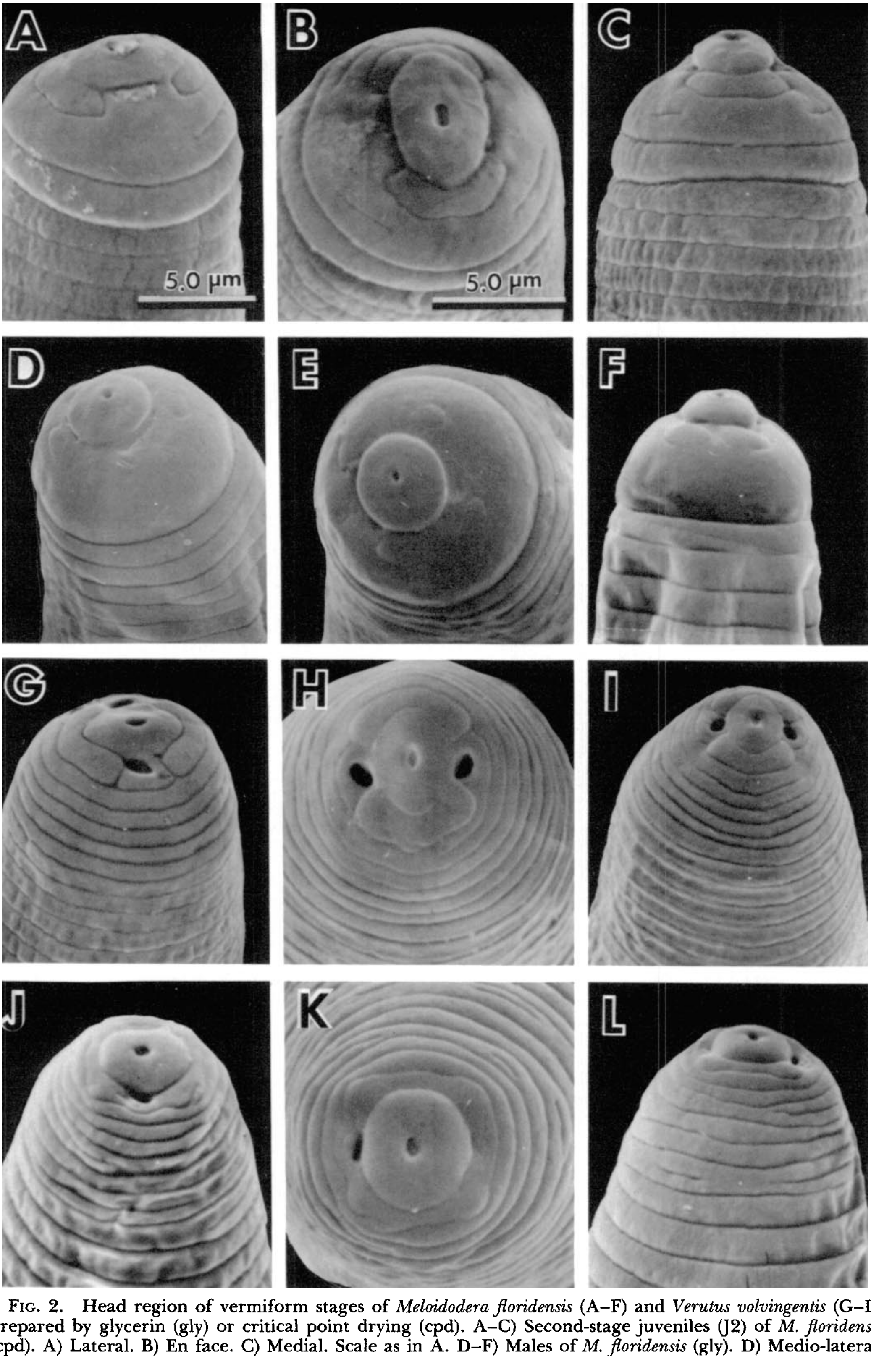


FIG. 2. Head region of vermiform stages of *Meloidodera floridensis* (A–F) and *Verutus volvingentis* (G–L) prepared by glycerin (gly) or critical point drying (cpd). A–C) Second-stage juveniles (J2) of *M. floridensis* (cpd). A) Lateral. B) En face. C) Medial. Scale as in A. D–F) Males of *M. floridensis* (gly). D) Medio-lateral.

sists of a round labial disc with four submedial lips (Fig. 2E) which are partially fused posteriorly with the remainder of the head region (Fig. 2F). Lateral lips are absent, and the head is without annulations (Fig. 2D–F).

The head region of J2 and males of *V. volvingentis* is very distinctive among Heteroderidae thus far examined (Fig. 2G–L). The labial disc of J2 is ovoid and tapers dorsally and ventrally. The disc is fused with the lateral lips which enclose unusually large amphid openings (Fig. 2G–I). Adjacent submedial lips are fused and broadened in the four medio-lateral positions (Fig. 2H). Posteriorly, the head region has five complete annulations (Fig. 2G, I). The en face pattern of males of *V. volvingentis* has a round labial disc enclosing a round prestoma, and all six lips are fused with each other to form a modified rectangle (i.e., broad in the four medio-lateral positions) (Fig. 2K). Posteriorly, the head region includes about seven complete and at least one incomplete annulations (Fig. 2J, L).

The en face patterns of females of *M. charis, M. belli, M. floridensis,* and *V. volvingentis,* however, all have an elevated labial disc with a raised ring at the periphery and the first annule does not include clearly demarcated lips (Fig. 3A–H). In *M. charis,* the labial disc is round and the peripheral ring occupies about one-third to one-half the diameter of the labial disc (Fig. 3A, B). The fused lips form a flat circular plate. Lateral lips adjacent to the pore-like amphid openings are obscure (Fig. 3A). The head region includes at least two additional incomplete annulations and one complete annulation which tend to anastomose (Fig. 3B).

Females of *M. belli* were limited to a few specimens infiltrated with glycerin in 1969; the en face pattern was similar to *M. charis* (Fig. 3C). The specimens of *Meloidodera belli* examined differ from *M. charis* by the presence of an incomplete second head annulation (limited to the lateral sides) and absence of anastomoses (Fig. 3D).

The en face pattern of *M. floridensis* females is similar to *M. charis* and *M. belli* (Fig. 3E, F). The submedial lips are fused dorsally and ventrally, but triangular lateral lips are each partially delimited at their apex by a large crescent-shaped groove (Fig. 3E). The submedial lips also fuse laterally, peripheral to the grooves and lateral lips. Posteriorly, the head region apparently includes two or three additional incomplete annulations with anastomoses; however, head annulations often are not clearly demarcated from body annulations (Fig. 3F).

The en face pattern of *V. volvingentis* females is distinctive. The labial disc and first head annule are broadest in the four medio-lateral positions, and the periphery of the disc is faintly elevated (Fig. 3G, H). The submedial lips are fused as in *M. floridensis,* but unlike *M. floridensis,* they do not quite join laterally (Fig. 3G). The triangular lateral lips each occur adjacent to an amphid opening. Posteriorly the head region includes one additional incomplete and five complete annulations (Fig. 3G, H).

Lateral lines and phasmids: The lateral field of J2 of *Meloidodera* and *Verutus* species, includes four incisures delineating three longitudinal bands of equal width with only the outer bands clearly areolated (Fig. 4). The lateral field of *Meloidodera* J2 originates about 7–8, 9–10, and 8 annules from the labial disc, respectively, in *M. belli, M. charis,* and *M. floridensis.* The lateral field generally begins with only two bands rarely preceded by a very short single band; the third, middle band appears about five annules further posteriorly in *M. charis* and *M. floridensis* and after only three annules in *M. belli* (Fig. 4A, D, G). In J2 of *V. volvingentis* two bands of the lateral field are barely visible 16 annules from the labial disc and the middle band begins about eight annules posterior to the beginning of the lateral field (Fig. 4J).

The lateral field of J2 of all species examined changes little throughout the length of the nematode (Fig. 4B, E, H, K). Posteriorly, they are closely associated with the phasmids. In *Meloidodera* the phasmid

---

←

Scale as in A. E) En face. Scale as in B. F) Medial. Scale as in A. G–I) J2 of *V. volvingentis* (gly). G) Lateral. Scale as in A. H) En face. Scale as in B. I) Medial. Scale as in A. J–L) Males of *V. volvingentis* (gly). J) Lateral. Scale as in A. K) En face. Scale as in B. L) Medial. Scale as in A.

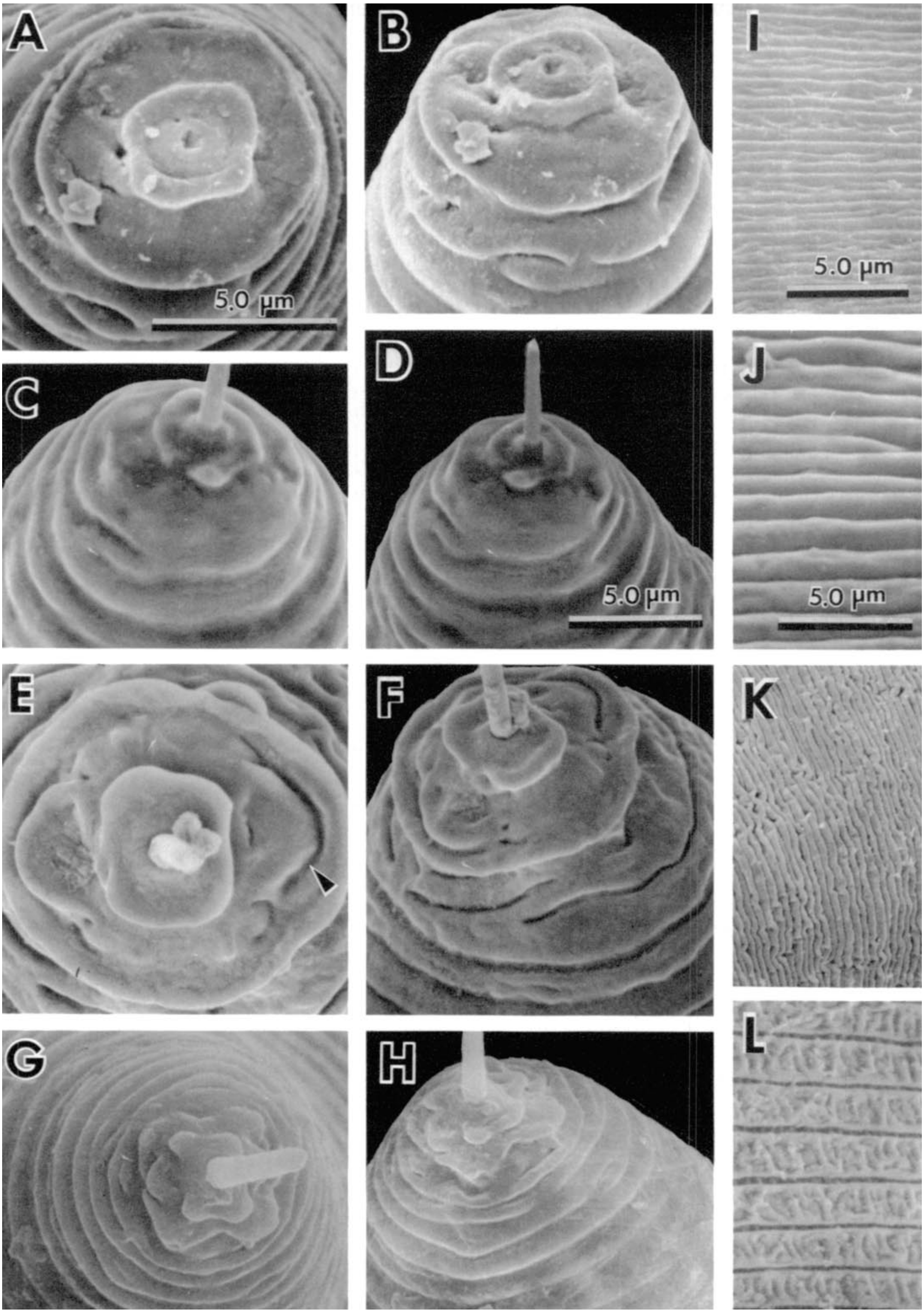


FIG. 3. Head region and body striae of females of *Meloidodera* spp. and *Verutus* sp. prepared by glycerin (gly) or critical point drying (cpd). A–B) *M. charis* (cpd). A) En face. B) Medio-lateral. Scale as in A. C–D) *M. belli* (gly). C) En face. Scale as in A. D) Medio-lateral. E–F) *M. floridensis* (gly). E) En face. Scale as in A. Arrow

pores are located in the middle longitudinal band, but in many specimens they are obscured by folds in the cuticle. The exact location of the phasmid openings varies among species. In *M. charis, M. belli,* and *M. floridensis* they occur, respectively, about 6–9, 4, and 7 annules anterior from the end of the lateral fields. In *M. floridensis* J2 the areolation is slightly closer together at the phasmid than elsewhere on the body (Fig. 4I), but in other species differences in areolation near the phasmid are less pronounced (Fig. 4C, F). In J2 of *V. volvingentis* the middle longitudinal band ends anterior to phasmids, so that the phasmid occurs as a small pit between or on either of the remaining two bands (Fig. 4L).

The lateral field of males in *Meloidodera* spp. and *V. volvingentis* also includes four incisures delineating three longitudinal bands (Fig. 5A, D, G, J). The anterior end of the three bands is about 5–8 annules posterior from the head, except in *M. charis* (San Bernardino population) where the middle band begins about two annules further posteriorly. Anteriorly, all the bands are generally areolated, except the middle band in *M. belli,* but further posteriorly the middle band is smooth in all the species (Fig. 5A, D, G, J). In some cases the middle band is about twice the width of the areolated outer bands (Fig. 5J). In *V. volvingentis* the anterior end of two bands is about 12 annules posterior from the lip annule and the middle band occurs eight annules further posteriorly.

The end view of the tail of *Meloidodera* spp. includes a pair of phasmid openings, one on each lateral side (Fig. 5B, C, E, F, H, I), but phasmids were not observed in males of *V. volvingentis* (Fig. 5K, L). In *M. charis* and *M. belli* the phasmid openings are located in the center of the middle longitudinal band, but in *M. floridensis* they occur in one of the inner two incisures. Although morphology of the phasmid openings is similar among species, the cuticle surrounding the pore is different. In the Arizona population of *M. charis* and in *M. floridensis* the openings are surrounded by numerous irregular lines (Fig. 5H). The lines in *M. floridensis* are separated from the opening by a small smooth area (Fig. 5H). Conversely, in the San Bernardino population of *M. charis* and in *M. belli* the middle band of the lateral field is smooth except for a few small protuberances encircling the opening in *M. belli* (Fig. 5E, F). In males of *V. volvingentis* the lateral lines terminate near the level of the spicules (Fig. 5L). The tail terminus (end view) is smooth except for four parallel incisures (Fig. 5K). Although phasmid openings were not observed in *V. volvingentis,* a pair of protuberances (sensory?) occur at the base of the spicule sheath (Fig. 5K).

Female striae: Although *Meloidodera* spp. and *V. volvingentis* females are similar in the subequatorial location of the vulva and in the striated (i.e., finely annulated) cuticle, surface markings are different (Fig. 3I–L). In *V. volvingentis* the striae are regular and most nearly resemble those of vermiform stages (Fig. 3L). The striae of *M. charis* and *M. belli* are more irregular and of variable width, whereas those of *M. floridensis* include wavy regions (Fig. 3I–K). Although striae tend to be widest in *M. belli* and *V. volvingentis,* this character is highly variable depending upon age of individuals and preparation methods.

Vulva and perineal regions: The vulva slit is also variable among species (Fig. 6B, E, G, I, J). In *M. charis* (San Bernardino population) it is relatively small (± 6 μm long) and encircled by a ridge, which, in turn is surrounded by a smooth area (Fig. 6B, J); we designate the ridge as the "inner lip" and the smooth area as the "outer lip." The vulva and lips appear to be located in a small depression.

The vulvas of *M. belli* and *M. floridensis* are much larger (± 35 μm long) than the *M. charis* vulva and tend to protrude (Fig. 6E, G). They are of similar size in the two species, and in both the vulval region is lenticular with the slit separating discrete anterior and posterior lips.

←

indicates groove delimiting lateral lip. F) Medio-lateral. Scale as in A. G–H) *V. volvingentis* (cpd). G) En face. Scale as in A. H) Medio-lateral. Scale as in A. I–L) Body striae. I) *M. charis* (cpd). J) *M. belli* (gly). K) *M. floridensis* (cpd). Scale as in I. L) *V. volvingentis* (gly). Scale as in I.

The vulva of *V. volvingentis* is strikingly different from that of *Meloidodera* spp. (Fig. 6I). In *V. volvingentis* it is very large (± 48 μm long) and the surrounding region is ellipsoidal and extends several micrometers beyond the slit; since the female is relatively narrow, the vulva occupies about two-thirds of the body width. The area around the vulva is not differentiated into inner and outer lips.

The female anus of *Meloidodera* and *Verutus* is subterminal and associated with a perineal region including the tail terminus and, in most cases, lateral fields and phasmids (Fig. 6A–D, F, H). In *M. charis* the entire perineal region is surrounded by circular striae which are interrupted by lateral fields that join at the terminus (Fig. 6A). Distinct phasmid openings occur on either side of the terminus, and the anus is situated ventrally in a round depression. The striae are irregular and anastomose in the region between the anus and phasmids. In *M. belli* the perineal region is similar to that of *M. charis,* except that striae encircle the anus rather than the entire perineal region and irregular striae rarely occur between the anus and tail terminus (Fig. 6C). In some specimens of *M. belli,* however, the pattern is asymmetrical with a smooth area surrounding one phasmid and a "wing" of striae extending dorsally between the phasmids (Fig. 6D). A similar asymmetric pattern with striae occurring between the phasmid openings characterizes *M. floridensis* (Fig. 6F).

The perineal patterns of *Verutus* and *Meloidodera* spp. are different. Phasmids are not visible in *Verutus* females, and about five striae tend to form a figure 8 which extends between the anus and tail terminus (Fig. 6H). The lateral field is delimited by interruptions in the striae.

DISCUSSION

Detailed SEM of J2, males, and females of *Meloidodera* spp. and *Verutus* sp. has revealed new characteristics of the head region, lateral field, phasmids, body striae, vulva, and perineal region. These characters may be useful in testing hypotheses of phylogenetic relationships, may indicate new features for identifying these nematodes, and may show changes with development. For example, in each species examined, the en face pattern changes from J2 to adults. Head annules in J2 of *M. charis* and *M. belli* are replaced by longitudinal blocks in males; yet the two stages are similar in the presence of a labial disc surrounded by six lips. In females, however, the six lips are fused and the head has annules.

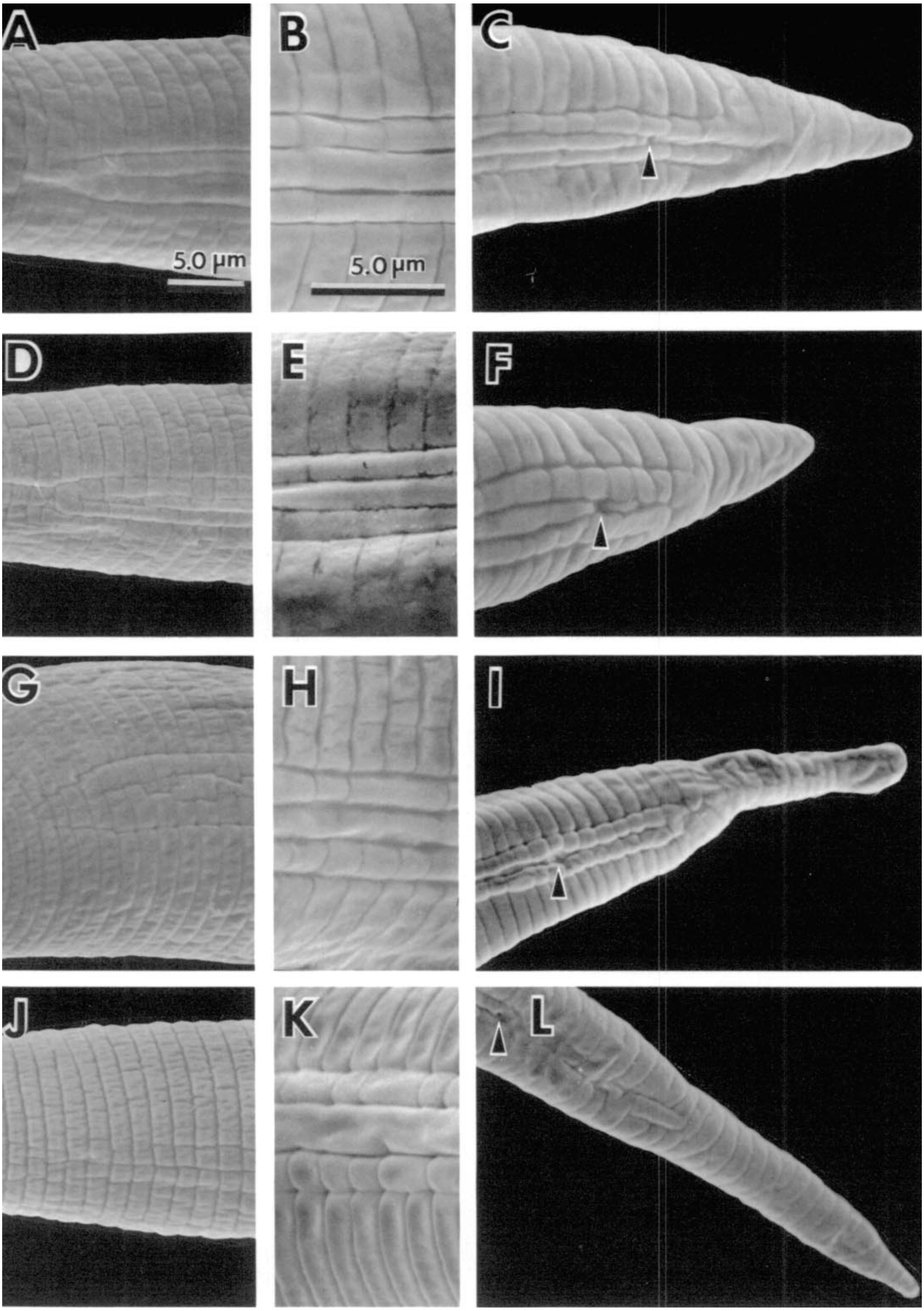
In *M. floridensis* the en face pattern of J2 contains fused submedial lips and the head region has annules. However, in males the

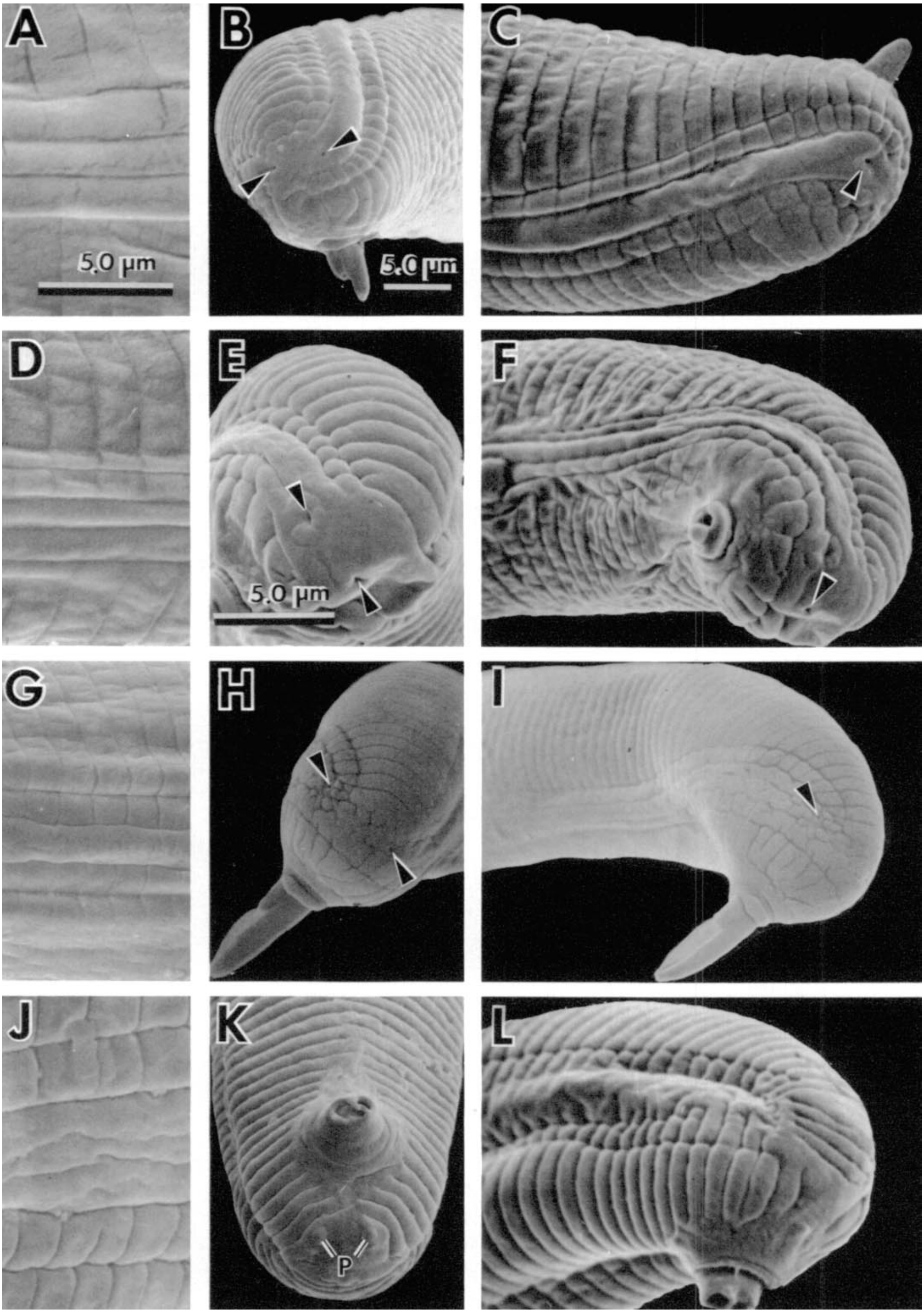
→

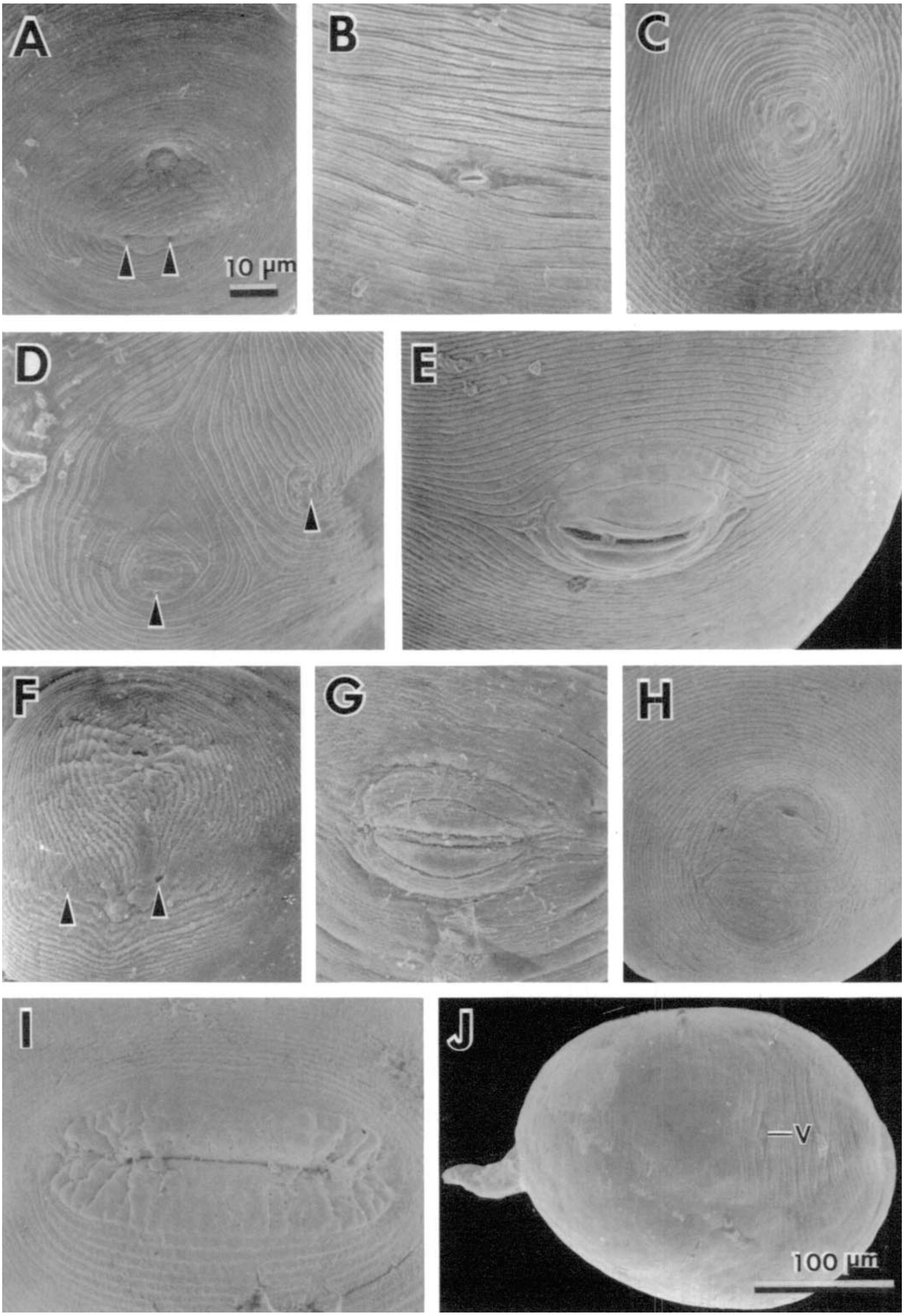
FIG. 4. Lateral field and tail region of second-stage juveniles of *Meloidodera* spp. and *Verutus* sp. prepared by glycerin (gly). A–C) *M. charis.* A) Anterior end of lateral field. B) Lateral field in midbody. C) Tail region. Scale as in A. D–F) *M. belli.* D) Anterior end of lateral field. Scale as in A. E) Lateral field in midbody. Scale as in B. F) Tail region. Scale as in A. G–I) *M. floridensis.* G) Anterior end of lateral field. Scale as in A. H) Lateral field in midbody. Scale as in B. I) Tail region (1,500 ×). J–L) *V. volvingentis.* J) Anterior end of lateral field. Scale as in A. K) Lateral field in midbody. Scale as in B. L) Tail region. Scale as in A. Arrows indicate positions of phasmids.

FIG. 5. Lateral field and tail region of *Meloidodera* spp. and *Verutus* sp. males prepared by glycerin (gly). A–D) *M. charis* (San Bernardino population). A) Lateral field in midbody. Scale as in B. B) End on view of tail. C) Tail region. Scale as in B. D–F) *M. belli.* D) Lateral field in midbody. Scale as in A. E) End on view of tail. F) Tail region. Scale as in B. G–I) *M. floridensis.* G) Lateral field in midbody. Scale as in A. H) End on view of tail. Scale as in E. I) Tail region. Scale as in B. J–L) *V. volvingentis.* J) Lateral field in midbody. Scale as in A. K) Ventral view of tail. Scale as in B. P = protuberances. L) Tail region. Scale as in B. Arrows indicate positions of phasmids.

FIG. 6. Vulva and perineal region of *Meloidodera* spp. and *Verutus* sp. females prepared by glycerin (gly) or critical point drying (cpd). A, B) *M. charis* (cpd). A) Anus and phasmids. B) Vulva. Scale as in A. C–E) *M. belli* (gly). C) Anus. Scale as in A. D) Anus and phasmids. Scale as in A. E) Vulva. Scale as in A. F, G) *M. floridensis* (cpd). F) Anus and phasmids. Scale as in A. G) Vulva. Scale as in A. H, I) *V. volvingentis* (gly). H) Anus. Scale as in A. I) Vulva. Scale as in A. J) Adult females of *M. charis.* V = vulva. Arrows indicate positions of phasmids.


A
B
C
5.0 µm
5.0 µm
D
E
F
G
H
I
J
K
L


A
5.0 µm
B
5.0 µm
C
D
E
5.0 µm
F
G
H
I
J
K
P
L


A
10 µm
B
C
D
E
F
G
H
I
J
V
100 µm

submedial lips are separate and the head region lacks annulation. Lateral lips are absent in both J2 and males, whereas females possess lateral lips and head annulation.

In *V. volvingentis* J2 and adults adjacent submedial lips are fused and thickened in the medio-lateral position. J2 and adults both have a relatively large number of head annulations posterior to the lip annule (5–7 versus 0–2 in *Meloidodera* spp.). Curiously, lateral lips are fused only with the labial disc in J2, but in males the lateral lips completely fuse with the other lips of the first head annule, and in females the lateral lips are only partially fused with other lips. Oval amphid openings are large in J2 and males but small in females.

New characters revealed in this study may be useful for testing phylogenetic relationships between *Verutus* and *Meloidodera.* We have noted, for example, that *Verutus* and *Meloidodera* share some characteristics (e.g., subequatorial vulva, striated cuticle of female) that are believed to be plesiomorphic; *Verutus* is primarily distinguished by a reniform or sausage-shaped (versus ovoid) female and large vulva (10). On the other hand, this study has shown that the en face pattern of J2, males, and females of *Verutus* is derived from the basic Tylenchid pattern (2) and is apparently unique to this genus. In addition, *Verutus* differs from *Meloidodera* spp. by the anterior origin and posterior termination of lateral lines in J2 and males, the apparent absence of phasmid openings in adults, and the unique terminal protuberances in males. Other characters which distinguish *Verutus* from *Meloidodera* include host response (respectively, syncytium versus single uninucleate giant cell) (7,13) and cuticle layering of females (1,6). In general, our findings support the present position of *Verutus* as a genus separate from *Meloidodera* spp.

New characters revealed by this study may also be useful in evaluating monophyly of *Meloidodera* spp. Previously, *M. charis* and *M. belli* were believed to be similar (15). Although we have shown that the vulva in the San Bernardino population of *M. charis* is uniquely small, the overall similarity to *M. belli* is generally confirmed by SEM observations of lip patterns and other surface structures. Conversely, *M. floridensis,* the type species, is highly distinctive. The en face pattern of J2 and males is unique and apparently derived from the plesiomorphic pattern in *M. charis* and *M. belli.* In addition, J2 of *M. floridensis* have a phasmid which is lens-like versus pore-like in some other *Meloidodera* spp. (15). *Meloidodera floridensis* is also distinct from *M. charis* and *M. belli* because it induces a giant cell with a single irregularly shaped nucleus, in comparison to a giant cell with inter-connected nuclear units in the other two species (13).

New characters we have disclosed may be useful in testing hypotheses of relationships of Heteroderidae to other Tylenchida. It was previously proposed, for example, that Heteroderidae and Hoplolaimidae share a common ancestor (16). This hypothesis is strengthened by the occurrence of longitudinal blocks in the head region of many species of both taxa. In Heteroderidae these include males of *M. charis, M. belli,* and *M. eurytyla* Bernard, 1981 (4) as well as some *Cryphodera* spp. (3). Similarly, J2 of certain Heteroderidae, including *M. floridensis* and *Cryphodera* spp. (3), have phasmids with enlarged ampulla (i.e., "lens-like") which may be homologous with the large phasmids of many Hoplolaiminae. The two groups may also share specialized features of cuticle layering (1). Unique characteristics common to both Heteroderidae and Hoplolaiminae strengthen the hypothesis that the taxa are sister groups. Furthermore, on the basis of outgroup comparisons with Hoplolaimidae, longitudinal blocks and enlarged phasmids might be interpreted as plesiomorphic, relative to other characteristics, within Heteroderidae.

Our SEM observations in *Meloidodera* spp. and *Verutus* sp. will be most informative when characters and their polarity are investigated throughout genera of Heteroderidae. Evaluation of the usefulness of characters for interpreting relationships at the generic level requires consideration of variability among species within each genus, as well as intraspecific variability. In the present study, for example, we found en face patterns to be particularly stable among individuals within species, but the usefulness of these characters must be further tested by examination of more individuals (e.g., females of *M. belli*) and additional populations. New useful characters can be incorporated with additional characters, including those obtained by light microscopy, for a phylogenetic analysis of Heteroderidae.

LITERATURE CITED

1. Baldwin, J. G. 1983. Fine structure of body wall cuticle of females of *Meloidodera charis, Atalodera lonicerae,* and *Sarisodera hydrophila* (Heteroderidae). Journal of Nematology 15:370–381.

2. Baldwin, J. G., M. Luc, and A. H. Bell. 1983. Contribution to the study of the genus *Pratylenchoides* Winslow (Nematoda: Tylenchida). Revue de Nematologie 6:111–125.

3. Baldwin, J. G., M. Mundo-Ocampo, and A. A. Othman. 1983. *Cryphodera utahensis* n. sp. (Heteroderidae): A new species from wild rose in Utah. Journal of Nematology 15:182–191.

4. Bernard, E. C. 1981. Three new species of Heteroderoidea (Nematoda) from the Aleutian Islands. Journal of Nematology 13:499–513.

5. Chitwood, B. G., C. I. Hannon, and R. P. Esser. 1956. A new nematode genus, *Meloidodera,* linking the genera *Heterodera* and *Meloidogyne.* Phytopathology 46:264–266.

6. Cliff, G., and J. G. Baldwin. 1985. Fine structure of body wall cuticle of females of eight genera of Heteroderidae. Journal of Nematology 17:286–296.

7. Cohn, E., D. T. Kaplan, and R. P. Esser. 1984. Observations on the mode of parasitism and histopathology of *Meloidodera floridensis* and *Verutus volvingentis* (Heteroderidae). Journal of Nematology 16:256–264.

8. De Grisse, A. T. 1973. A method for preparing nematodes and other soft tissues for scanning electron microscopy. Mededelingen Van de Faculteit. Landbouwwetenschappen Rijksuniversiteit (Gent) 38:1685–1695.

9. Eisenback, J. D., and H. Hirschmann. 1979. Morphological comparison of second-stage juveniles of six populations of *Meloidogyne hapla* by SEM. Journal of Nematology 11:5–16.

10. Esser, R. P. 1981. *Verutus volvingentis* n. gen., n. sp. (Heteroderidae: Tylenchida) in Verutinae n. subf., a phytoparasitic nematode infesting buttonweed in Florida. Proceedings of the Helminthological Society of Washington 48:220–240.

11. Ferris, V. R. 1979. Cladistic approaches in the study of soil and plant parasitic nematodes. American Zoologist 19:1195–1215.

12. Malick, L. E., and R. B. Wilson. 1975. Modified thiocarbohydrazide procedure for scanning electron microscopy: Routine use for normal, pathological, or experimental tissues. Stain Technology 50: 265–269.

13. Mundo-Ocampo, M., and J. G. Baldwin. 1983. Host response to *Meloidodera* spp. (Heteroderidae). Journal of Nematology 15:544–554.

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

15. Wouts, W. M. 1973. A revision of the family Heteroderidae (Nematoda: Tylenchoidea) II. The subfamily Meloidoderinae. Nematologica 19:218–235.

16. Wouts, W. M., and S. A. Sher. 1971. The genera of the subfamily Heteroderinae (Nematoda: Tylenchoidea) with a description of two new genera. Journal of Nematology 3:129–144.