Pararotylenchus **n. gen.** **(Pararotylenchinae n. subfam.,** Hoplolaimidae) **with Six New Species and Two New Combinations**

J. G. Baldwin and A. H. Bell[1]

Abstract: A new subfamily, Pararotylenchinae, (Hoplolaimidae) is described. It includes a single genus, *Pararotylenchus* n. gen., six new species, and two new combinations, *Pararotylenchus* (syn. *Tylenchorhynchus*) *brevicaudatus* (Hopper, 1959) n. comb. and *Pararotylenchus* (syn. *Rotylenchus*) *pini* (Mamiya, 1968) n. comb. Pararotylenchinae is similar to certain other Hoplolaimidae, such as Rotylenchinae, with respect to most characters including the short tail, the position of the phasmids near the anus, and the relatively great distance of the dorsal gland orifice from the base of the stylet knobs. The lip region, as observed with the scanning electron microscope, conforms to the basic pattern for Hoplolaimidae. The labial disc is round with slit-like amphidial openings at the lateral sides of the periphery of the disc. The distinctive anteriormost lip annule is segmented into six sectors. Unlike other Hoplolaimidae, however, the esophageal glands of Pararotylenchinae form a basal bulb similar to that of Tylenchorhynchidae; other characters do not resemble Tylenchorhynchidae. Specimens of *Pararotylenchus* have been recovered only from cool regions at high elevations and Pacific coastal areas in the Western United States, Japan, and Korea. *Key words:* taxonomy, scanning electron microscopy, esophageal glands, new species, new genera, new subfamily, morphology.

Preliminary examination of specimens of several nematode populations indicated that they represented at least six species requiring a common new genus to accommodate them, but their relationship among other Tylenchida Thorne, 1949 was not readily apparent. The esophageal glands of these specimens comprised a basal bulb similar to that of Tylenchorhynchidae (Eliava, 1964) Golden, 1971 (2,5,8,16,17,18), but additional characteristics such as tail length, positions of the phasmids and dorsal gland orifice, morphology of the head region, and strong ventral curvature of heat-killed specimens suggested a similarity to certain Hoplolaimidae (Filipjev, 1934) Wieser, 1953 (2,5,9,17). Specimens considered in the preliminary observations included material collected by Professor G. Thorne between 1924 and 1936 in Utah. Thorne labeled these specimens as *Rotylenchus* sp. but in most cases did not designate a species. Similar specimens have been collected by the junior author since 1962 from sites in Utah and California. The new species closely resemble two previously described species which also possess a glandular basal bulb, *Rotylenchus pini* Mamiya, 1968 (7) and *Tylenchorhynchus brevicaudatus* Hopper, 1959 (6). The original description of *T. brevicaudatus* is based on three females and four males. Paratypes are deposited in the University of California, Riverside (UCR) Nematode Slide Collection, but the holotype and allotype are no longer available from the collection originally designated for these specimens.

The present study was initiated to describe six new species of a genus, *Pararotylenchus* n. gen. (*para* Gr. near) in Pararotylenchinae n. subfam., of the Hoplolaimidae. Words used in forming specific epithets are Latinized from the Greek. The species are *P. blothrotylus* (*blothros* Gr. tall and *tylos* Gr. knob), *P. colocaudatus* (*kolos* Gr. stunted and *cauda* L. tail), *P. megastylus*

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[1]Assistant Professor of Nematology and Staff Research Associate, Department of Nematology, University of California, Riverside, CA 92521. The authors are grateful to Dr. Y. Mamiya of the Forestry and Forest Products Research Institute, Ushiku, Ibaraki, Japan, for supplying specimens of *Pararotylenchus* (syn. *Rotylenchus*) *pini*, n. comb. We also thank Dr. A. C. Bandy, Department of Literatures and Languages, University of California, Riverside, for assistance in the etymology of species nomenclature.

(*megas* Gr. large and *stylos* Gr. column), *P. sphaerocephalus* (*sphaira* Gr. ball and *kephale* Gr. head), *P. spiralis* (*speira* Gr. coil), and *P. truncocephalus* (*truncus* L. cut off and *kephale* Gr. head). We also evaluate the relationship of these new species to *R. pini* and *T. brevicaudatus*, redescribe the latter species, and examine the relationship of the new genus to certain other Tylenchida.

MATERIALS AND METHODS

Specimens from populations of *Pararotylenchus* were collected primarily during 1978 and 1979, from Farmington Flats, Soldier Canyon, Cedar Breaks, and Alta, Utah, as well as Cambria and San Jacinto, California. They were fixed in 5% formalin, slowly infiltrated with glycerin, and mounted as previously reported for examination with the light and scanning electron microscopes (SEM) (9,15). Additional specimens were available from the UCR slide collection, including type specimens designated *T. brevicaudatus* and *R. pini*. Specimens of *T. brevicaudatus* and *R. pini* were also collected from their respective type localities during 1978 and 1979. Attempts to establish stock cultures under greenhouse conditions were generally unsuccessful. More than 100 females and males (depending on availability) of each species were examined with the light microscope. Measurements and corresponding abbreviations included in descriptions are L = total body length, width = maximum body width, stylet = stylet length, DGO = distance of dorsal gland orifice from base of stylet, tail = length from anus to posterior terminus, ABW = body width at anus or cloaca opening, h = length of hyaline region of tail, TA = number of annules on tail, P = number of annules from anus to phasmid (+ indicates phasmid is anterior to anus), gubernaculum = gubernaculum length, and spicule = spicules length. Ratios included are a = L/width, b′ = L/distance from anterior end of nematode to posterior end of basal bulb, c = L/tail, c′ = tail/ABW, o = DGO/stylet, expressed as percent, m = stylet cone length/stylet, expressed as percent, and V = distance from anterior end of nematode to vulva/L, expressed as percent.

Examination with SEM included the head region of at least 15 females and the head and tail region of at least 10 males (depending on availability) of each species. The morphology of the head region was compared among species of *Pararotylenchus* and with previous observations among species of Tylenchorhynchidae and Hoplolaimidae, as well as additional Tylenchida (unpublished observations). Glycerin-infiltrated specimens were coated with about .02 μm gold using a Jeol J-4 vaccum evaporator and viewed with a Jeol JSM-U3 SEM operated at 7–10 Kv.

DESCRIPTIONS

Hoplolaimidae (Filipjev, 1934) Wieser, 1953

Diagnosis emended: Golden, 1971, Sher. 1961, Siddiqi, 1971, Andrássy, 1976 order Tylenchida Thorne, 1949, superfamily Hoplolaimoidea (Filipjev, 1934) Paramonov, 1967. Head with well-developed cephalic framework, sometimes showing slight sexual dimorphism. Distance of dorsal gland orifice from stylet knobs (DGO) typically more than 3 μm. Esophagus usually terminating in glandular lobes but forming basal bulb in Pararotylenchinae n. subfam. Phasmids small to large, absent in Aphasmatylenchinae Sher, 1965. Female tail short, two anal body widths or less in length (5). Bursa present.

Pararotylenchinae n. subfam.

Diagnosis: Hoplolaimidae. Lip region with well-developed framework in both sexes. Labial disc present, with elongate amphidial apertures at lateral sides of periphery. Anteriormost lip annule segmented with six sectors. Esophageal glands comprise basal bulb. Lateral field with four incisures. Cephalids in females generally occur near level of third and tenth body annules; hemizonid position variable relative to excretory pore; hemizonion seven to ten annules posterior to excretory pore; caudalid about five annules anterior to anus. Phasmids small, typically near level of anus. Female tail variably-shaped, usually more curved on dorsal side. Vulva with epiptygma. Gubernaculum reflexed distally and with small titillae.

Pararotylenchus n. gen.

Diagnosis: Pararotylenchinae n. subfam. Having characteristics of subfamily.

Type species: Pararotylenchus brevicaudatus (Hopper, 1959) n. comb.

SEM observations: The lip region, as observed *en face* with SEM, has a consistent pattern among females of *Pararotylenchus* spp. (Fig. 1A). The oral opening is slit-like with three conspicuous inner labial sensilla openings parallel to the slit, on each lateral side. The labial disc is large and round with obscure slit-like amphidial openings at the lateral side of its periphery. The anteriormost lip annule is divided into two subdorsal, two subventral, and two slightly smaller lateral sectors.

The lip region of males is similar to that of females. Protruded spicules, as observed with SEM, are each trough-shaped with the concave surfaces facing one another. The sides of the trough distally flange outward (Fig. 1B,C). Titillae of gubernaculum occur as double pairs (Fig. 1B,C).

Pararotylenchus brevicaudatus
(Hopper, 1959) n. comb.
(Figs. 1, 2)

Synonym, Tylenchorhynchus brevicaudatus Hopper, 1959. Measurements after Hopper, 1959 (6): (three females) L = 1.28–1.37 mm; a = 33.7–35.8; b = 6.7–6.9; c = 33.5–44; V = 57.5–58.6%; stylet = 37–38.4 μm. (four males) L = .99–1.17 mm; a = 33.6–36.6; b = 5.5–6.1; c = 29.4–30.8; stylet = 34.6–37 μm.

Type habitat and locality, after Hopper, 1959 (6): Soil around roots of quaking aspen (*Populus tremuloides* Michx.), Farmington Flats, Davis County, Utah.

Females (measurements of 22 topotypes): L = 1.24–1.61 mm (mean 1.413 mm, .95% confidence interval ± .503); width = 33.0–40.0 μm (36.70 μm ± .99); stylet = 36.5–41.0 μm (38.32 μm ± 1.88); DGO = 3.5–7.5 μm (5.36 μm ± .48); tail = 24.5–38.0 μm (32.32 μm ± 1.88); ABW = 20.5–32.0 μm (28.30 μm ± 1.19); h = 6.5–11.0 μm (9.09 μm ± .58); TA = 9–17 (12.6 ± .9); P = −3 to +7 (2.0 ± 1.1); a = 32.8–44.0 (38.50 ± 1.31); b′ = 6.7–8.3 (7.38 ± .18); c = 36.5–53.3 (44.22 ± 2.19); c′ = .8–1.6 (1.15 ± .08); o = 10–20% (14.0% ± 1.3); m = 49–54% (51.1% ± .6); V = 54–62% (58.5 ± .9).

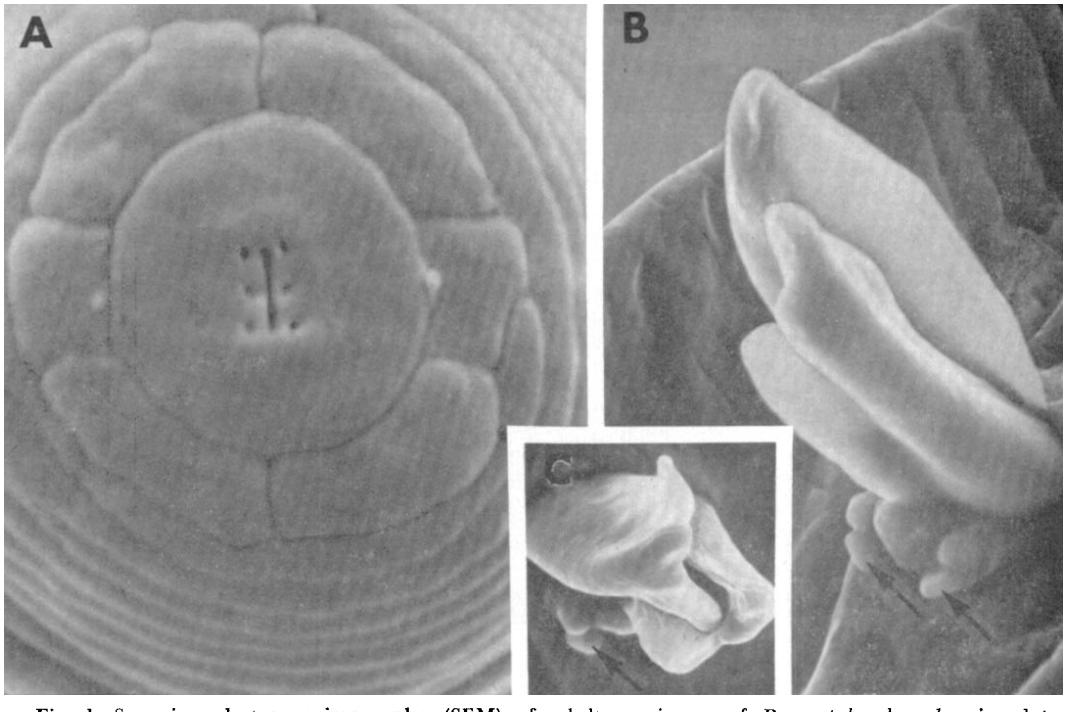

Fig. 1. Scanning electron micrographs (SEM) of adult specimens of *Pararotylenchus brevicaudatus* (Hopper, 1959) n. comb. A) *En face* view of lip region of female showing labial disc and anteriormost lip annule; 12,000×. B) Lateroventral view of protracted spicules, showing titillae of gubernaculum (arrows); 5,500×. C) Lateral view of spicules shown in B; 3,500×.

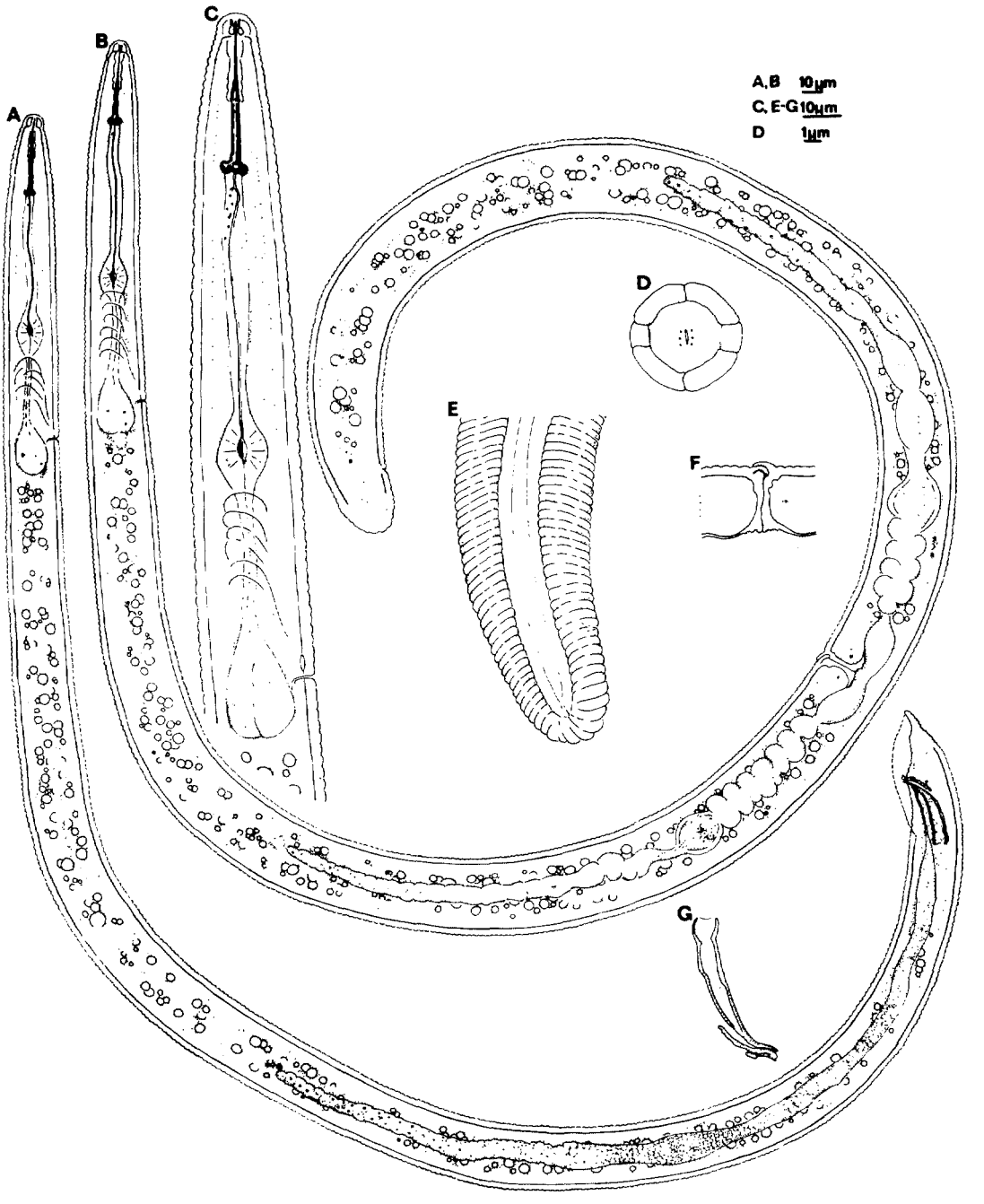

Fig. 2. Drawings of adults of *Pararotylenchus brevicaudatus* (Hopper, 1959) n. comb. A) Entire male (lateral). B) Entire female (lateral; curvature of specimen slightly exaggerated for convenience in illustrating). C) Cephalic and esophagus region of female (lateral). D) Labial region as observed with SEM (*en face*). E) Tail of female (lateral). F) Vulva (lateral). G) Spicule and gubernaculum (lateral).

Description (females): Body generally loosely coiled. Lip region slightly offset, flattened to slightly rounded anteriorly, usually with eight annules. Stylet massive with rounded knobs anteriorly flattened. Excretory pore at level of mid basal bulb. Hemizonid one to five annules anterior to excretory pore. Large double epiptygma.

Spermatotheca oval, containing round sperm. Tail terminus rounded and coarsely annulated.

Lectotype (female): L = 1.42 mm; width = 35.0 μm; stylet = 41.0μm; DGO = 5.0 μm; tail = 32.0 μm; ABW = 29.0 μm; h = 9.0 μm; TA = 14; P = +3; a = 35.0; b′ = 6.8; c = 41.0; c′ = 1.1; o = 12%; m = 50%; V = 59%. Female as in general description. Body coiled. Hemizonid two body annules anterior to excretory pore.

Males (measurements of 21 topotypes): L = 1.12–1.39 mm (1.239 mm ± .349); width = 27.0–32.0 μm (29.48 μm ± .75); stylet = 33.0–37.0 μm (35.62 μm ± .39); DGO = 3.5–7.5 μm (5.05 μm ± .41); tail = 31.5–41.5 (36.60 μm ± 1.18); ABW = 17.5–21.5 μm (20.24 ± .50); spicule = 32.5–39.0 μm (36.00 μm ± .92); gubernaculum = 14.5–18.5 μm (15.90 μm ± .04); a = 38.0–46.3 (42.06 ± .07); b′ = 5.8–10.7 (6.81 ± .45); c = 28.9–39.4 (33.95 ± 1.07); c′ = 1.5–2.1 (1.81 ± .08); o = 9–21% (14.2% ± 1.0); m = 48–54% (51.7% ± .6).

Description (males): Body slightly curved ventrally to loosely coiled. Lip region slightly offset, rounded with seven to nine annules. Stylet massive with rounded knobs. Excretory pore usually at level of mid basal bulb. Hemizonid as in female. Spicules arcuate.

Diagnosis: Pararotylenchus brevicaudatus is most similar to *P. sphaerocephalus* but differs with respect to the following: In the former, stylet of females typically slightly shorter (38.3 μm versus 41.3 μm), lip region slightly flattened anteriorly (versus hemispherical), tail terminus of females broadly rounded (versus strongly curved on dorsal side, often with dorsal indentation), and males present.

Lectotype (female): Selected from among paratypes. Collected by A. A. Foster, August 1957. Catalog number 36, Nematode Collection, Department of Nematology, University of California, Riverside.

Pararotylenchus blothrotylus n. sp. (Fig. 3)

Females (measurements of 20 paratypes): L = .86–1.14 mm (.967 mm ± .040); width = 27.0–35.0 μm (29.80 μm ± 1.05); stylet = 32.0–37.0 μm (34.18 μm ± .55); DGO = 3.5–7.0 μm (5.29 μm ± .37); tail = 21.0–31.0 μm (25.45 μm ± 1.26); ABW = 18.5–24.5 μm (21.10 μm ± .83); h = 4.0–8.5 μm (5.90 μm ± .67); TA = 8–13 (10.4 ± .7); P = −6 to −2 (−4.1 ± .5); a = 29.2–35.0 (32.44 ± .67); b′ = 5.8–7.5 (6.52 ± .20); c = 33.6–42.5 (38.19 ± 1.30); c′ = 1.0–1.4 (1.20 ± .05); o = 10–21% (15.5% ± 1.0); m = 49–52% (50.5% ± .4); V = 53–60% (56.9% ± .9).

Description (females): Body coiled. Lip region continuous with body contour, sometimes slightly flattened anteriorly, with seven to nine annules. Stylet robust with knobs typically higher than broad, often with slight indentation on anterior surface. Excretory pore at level from mid to anterior region of basal bulb. Hemizonid zero to two annules anterior to excretory pore. Epiptygma small. Spermathotheca rounded, containing round sperm. Tail tapering and more curved on dorsal surface with terminus rounded.

Holotype (female): L = 1.06 mm; width = 31.0 μm; stylet = 32.5 μm; DGO = 5.5 μm; tail = 33.0 μm; ABW = 22.0 μm; h = 1.0 μm; TA = 14; P = −6; a = 34.0; b′ = 6.8; c = 32.0; c′ = 1.5; o = 17%; m = 51%; V = 56%. Female as in general description. Lip region with nine annules. Excretory pore at level of mid basal bulb. Hemizonid one annule anterior to excretory pore.

Males (measurements of 20 paratypes): L = .75–.92 mm (.837 mm ± .022); width = 22.0–28.0 μm (24.91 μm ± .64); stylet = 31.5–34.5 μm (32.68 μm ± .33); DGO = 4.5–7.5 μm (6.03 μm ± .39); tail = 26.0–35.0 μm (29.83 μm ± 1.22); ABW = 15.5–19.0 μm (17.25 μm ± 1.40); spicule = 25.0–30.0 μm (28.00 μm ± .62); gubernaculum = 9.5–14.0 μm (12.10 μm ± .60); a = 28.6–37.2 (33.69 ± 1.02); b′ = 4.8–5.9 (5.46 ± .14); c = 24.8–31.9 (28.22 ± .99); c′ = 1.4–2.0 (1.73 ± .07); o = 14–23% (18.4% ± 1.0); m = 47–53% (51.0% ± .7).

Description (males): Body with slight ventral curvature to C-shaped. Lip region similar to female. Excretory pore at level of anterior basal bulb. Hemizonid zero to two annules anterior to excretory pore. Spicules arcuate, slightly cephalated.

Allotype (male): L = .91 mm; width = 24.0 μm; stylet = 32.0 μm; DGO = 4.5 μm; tail = 30.0 μm; ABW = 16.0 μm; spicule =

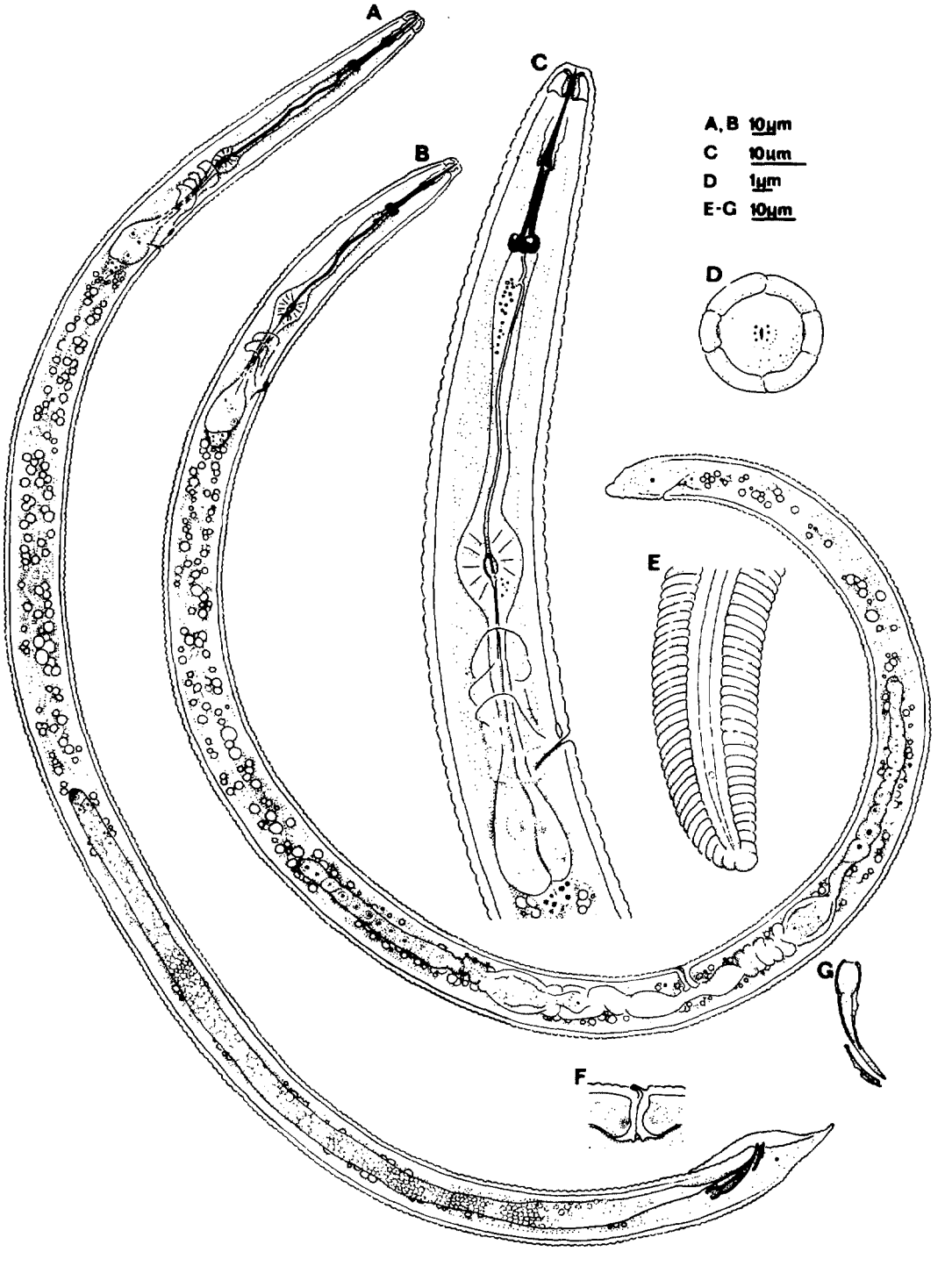

Fig. 3. Drawings of adults of *Pararotylenchus blothrotylus* n. sp. A) Entire male (lateral). B) Entire female (lateral). C) Cephalic and esophagus region of female (lateral). D) Labial region of female as observed with SEM (*en face*). E) Tail of female (lateral). F) Vulva (lateral). G) Spicule and gubernaculum (lateral).

28.0 μm; gubernaculum = 13.0 μm; a = 34.0; b′ = 5.5; c = 32.0; c′ = 1.5; o = 17%; m = 51%. Male as in general description. Excretory pore at base of isthmus. Hemizonid immediately anterior to excretory pore.

Diagnosis: Pararotylenchus blothrotylus differs from other species on the basis of a combination of characteristics. Although similar to *P. colocaudatus* with respect to short females (.967 mm versus .985 mm), it differs by its less offset head and longer more tapered tail. Stylet distinctively short with knobs typically higher than broad and anterior surface of knobs often indented.

Holotype: (female): Collected by H. E. McKinney and A. H. Bell on June 4, 1978. Catalog number 37, Nematode Collection, Department of Nematology, University of California, Riverside.

Allotype: (male): Catalog Number 38. Same data as holotype.

Paratypes (164 females, 96 males, 37 juveniles): Same data as holotype. Specimens distributed in nematode collections as follows: 8 females, 5 males, 1 juvenile, Division of Nematology, University of California, Davis; 8 females, 5 males, 3 juveniles, USDA Nematology Investigations, Beltsville, Maryland; 8 females, 4 males, 2 juveniles, Rothamsted Experimental Station, Harpenden, England; 140 females, 82 males, 31 juveniles, Department of Nematology, University of California, Riverside.

Type habitat and locality: Soil around roots of wild rose (*Rosa* sp. L.; blooms were not available for specific identification), Soldier Canyon, Sevier County, Utah.

Pararotylenchus colocaudatus n. sp. (Fig. 4)

Females (measurements of 20 paratypes): L = .85–1.08 mm (.985 mm ± .369); width = 33.0–46.0 μm (38.38 μm ± 1.70); stylet = 31.0–36.0 μm (34.08 μm ± .66); DGO = 3.0–6.5 μm (4.41 μm ± .57); tail = 18.0–24.5 μm (21.67 μm ± .79); ABW = 22.5–33.5 μm (26.55 μm ± 1.30); h = 3.5–10.0 μm (7.08 μm ± 1.00); TA: 6–10 (8.3 ± .5); P = −1 to +2 (.7 ± .6); a = 21.9–30.3 (25.79 ± 1.22); b′ = 5.2–6.6 (5.87 ± .17); c = 37.5–54.4 (45.6 ± 2.08); c′ = .7–1.0 (.82 ± .05); o = 8–20% (13.0% ± 2.8); m = 47–57% (51.9% ± 1.4); V = 58–63% (60.1% ± .5).

Description (females): Body C-shaped to coiled. Lip region slightly offset, hemispherical with six or seven annules. Stylet knobs rounded, anterior surface sloping. Excretory pore typically at level anterior to basal bulb. Hemizonid zero to three annules anterior to excretory pore. Epiptygma small. Spermatotheca oval, containing round sperm. Tail more curved dorsally, terminus broadly rounded.

Holotype (female): L = 89 mm; width = 33.0 μm; stylet = 33.5 μm; DGO = 3.5 μm; tail = 19.0 μm; ABW = 24.0 μm; h = 7.5 μm; TA = 7; P = +1; a = 28.0; b′ = 5.3; c = 46.0; c′ = .8; o = 10%; m = 51%; V = 60%. Female as in general description. Lip region with seven annules. Hemizonid two annules anterior to excretory pore.

Males (measurements of 20 paratypes): L = .78–1.00 mm (.901 mm ± .042); width = 25.5–35.5 μm (30.30 μm ± 2.00); stylet = 27.5–34.5 μm (32.12 μm ± 1.20); DGO = 2.5–4.5 μm (3.69 μm ± .62); tail = 21.0–33.5 μm (26.70 μm ± 2.00); ABW = 15.5–20.5 μm (18.70 μm ± 1.10); spicule = 31.0–39.0 μm (34.20 μm ± 1.00); gubernaculum = 12.5–17.0 μm (14.70 μm ± .75); a = 25.4–35.1 (30.0 ± 1.9); b′ = 4.1–6.4 (5.50 ± .33); c = 28.7–42.4 (34.10 ± 2.18); c′ = 1.2–1.8 (1.40 ± .66); o = 7–15% (11.4% ± 1.9); m = 51–58% (53.5% ± 1.5).

Description (males): Body C-shaped to loosely coiled, less curved anteriorly. Lip region slightly offset, rounded to slightly flattened anteriorly, with six or seven annules. Stylet knobs rounded, anterior surface sloping posteriorly from shaft. Excretory pore at level anterior to basal bulb. Hemizonid generally one or two annules anterior to excretory pore. Spicules arcuate, slightly cephalated.

Allotype (male): L = .90 mm; width = 27.0 μm; stylet = 33.0 μm; DGO = 4.5 μm; tail = 24.0 μm; ABW = 19.0 μm; spicule = 35.0 μm; gubernaculum = 17.0 μm; a = 33.0; b′ = 5.5; c = 37.0; c′ = 1.3; o = 14%; m = 53%. Male as in general description. Body C-shaped. Lip region slightly flattened with seven annules. Hemizonid one annule anterior to excretory pore.

Diagnosis: Pararotylenchus colocaudatus most closely resembles *P. pini,* but differs primarily by position of phasmids relative

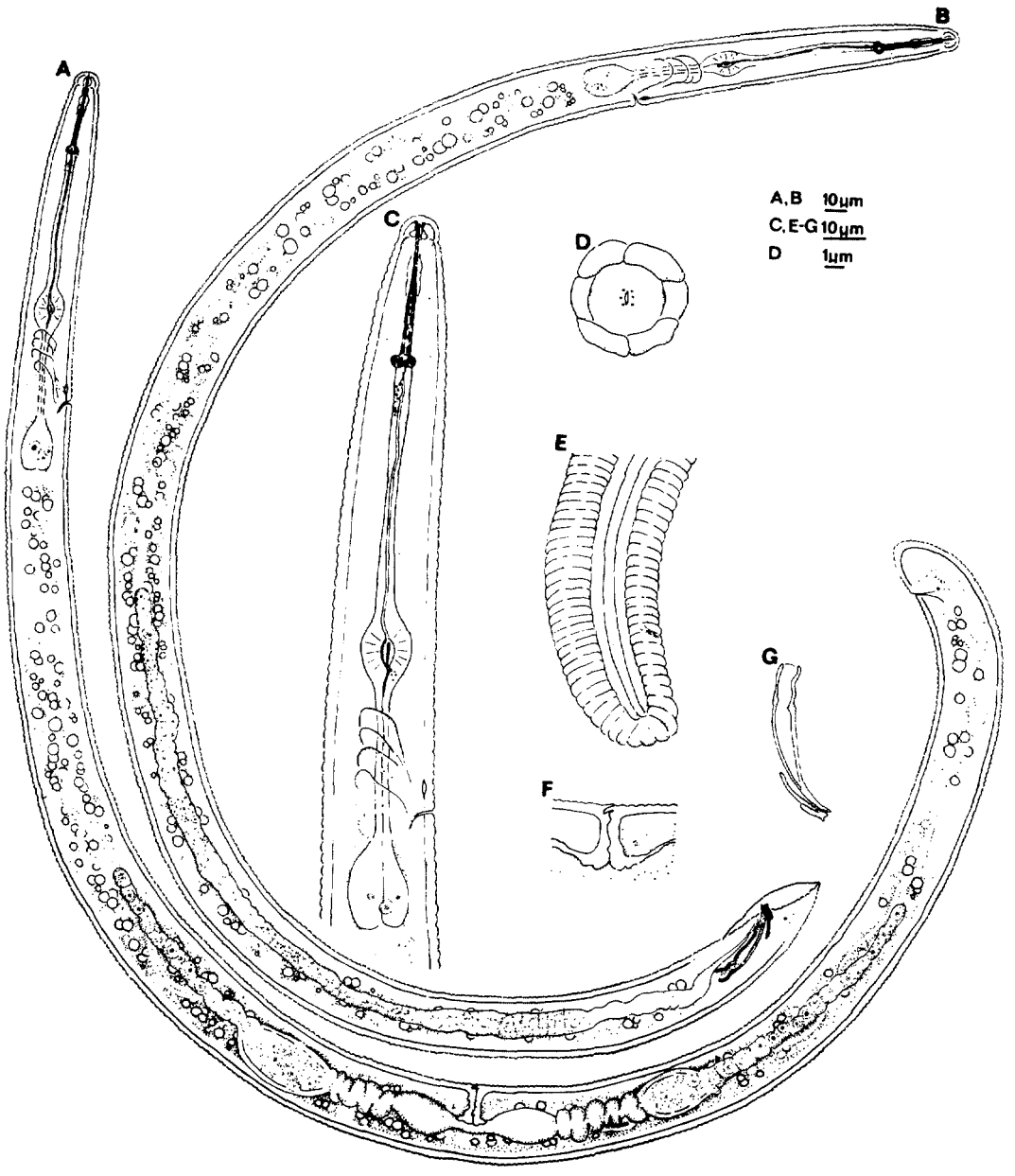

Fig. 4. Drawings of adults of *Pararotylenchus colocaudatus* n. sp. A) Entire female (lateral). B. Entire male (lateral). C) Cephalic and esophagus region of female (lateral). D) Labial region of female as observed with SEM (*en face*). E) Tail of female (lateral). F) Vulva (lateral). G) Spicule and gubernaculum (lateral).

to anus in females (P = −1 to +2 versus +11 to +30). In addition, esophagus of *P. colocaudatus* is longer (b′ = 5.9 versus 6.6). Measurements of *P. pini* after Mamiya (7).

Holotype (female): Collected by A. Cooper, July 1, 1971. Catalog number 39, Nematode Collection, Department of Nematology, University of California, Riverside.

Allotype (male): Catalog number 40. Same data as holotype.

Paratypes (24 females, 28 males, 25 juveniles): Same data as holotype, except some specimens collected by H. E. McKinney in 1979. Specimens distributed in nematode collections as follows: 2 females, 2 males, 1 juvenile, Division of Nematology, University of California, Davis; 4 females, 3

males, USDA Nematology Investigations, Beltsville, Maryland; 3 females, 3 males, 2 juveniles, Department of Nematology, Rothamsted Experimental Station, Harpenden, England; 15 females, 20 males, 22 juveniles, Department of Nematology, University of California, Riverside.

Type habitat and locality: Soil around roots of Monterey pine (*Pinius radiata* D. Don.), Cambria, California.

Specimens of *P. colocaudatus* n. sp. have also been collected from soil of the forest floor of *Sequoia sempervirens* (D. Don.) Endl. (redwoods), Woodside, California, and soil around roots of *Abies concolor* (Gord. and Glend.) Lindl. (white fir), Linn County, Oregon.

Pararotylenchus megastylus n. sp. (Fig. 5)

Females (measurements of 23 paratypes): L = 1.20–1.52 mm (1.367 mm ± .036); width = 34.0–44.0 μm (38.68 μm ± 1.22); stylet = 39.0–43.0 μm (41.35 μm ± .42); DGO = 3.5–6.5 μm (5.17 μm ± .31); tail = 28.0–45.0 μm (34.21 μm ± 1.68); ABW = 27.0–33.5 μm (29.80 μm ± .79); h = 6.5–11.5 μm (8.72 μm ± .59); TA = 13–22 (16.7 ± .9); P = −2 to +7 (3.4 ± 2.1); a = 32.0–40.4 (35.43 ± .78); b′ = 6.3–8.0 (7.20 ± .18); c = 32.8–48.4 (40.37 ± 1.85); c′ = 1.0–1.4 (1.14 ± .05); o = 8–15% (12.5% ± .8); m = 48–53% (50.3% ± .6); V = 53–59% (56.9% ± .7).

Description (females): Body coiled. Lip region broad, rounded on sides but flattened anteriorly, continuous with body contour and having eight or nine annules. Spear massive with large rounded knobs anteriorly flattened. Excretory pore usually located at level of mid basal bulb. Hemizonid one to four annules anterior to excretory pore. Spermatotheca relatively small, without sperm. Tail cylindrical with rounded terminus.

Holotype (female): L = 1.43 mm; width = 38.0 μm; stylet = 42.0 μm; DGO = 5.0 μm; tail = 38.0 μm; ABW = 29.0 μm; h = 8.5 μm; TA = 18; P = +2; a = 38.0; b′ = 7.2; c = 38.0; c′ = 1.3; o = 12%; m = 51%; V = 55%. Female as in general description. Body coiled. Lip region with nine annules. Hemizonid one annule anterior to excretory pore. Tail with 16 annules; phasmids at level of anus.

Males: Unknown.

Diagnosis: Pararotylenchus megastylus resembles *P. spiralis* but differs in that the lip region of the former is broader, lower, and slightly hemispherical (versus truncate); stylet knobs are distinctly massive. Tail terminus of *P. megastylus* is cylindrical (versus tapered).

Holotype (female): Collected by H. E. McKinney and A. H. Bell, June 4, 1978. Catalog number 41, Nematode Collection, Department of Nematology, University of California, Riverside.

Paratypes (79 females): Same data as holotype. Specimens distributed in nematode collections as follows: 6 females, Division of Nematology, University of California, Davis; 7 females, USDA Nematology Investigations, Beltsville, Maryland; 6 females, Department of Nematology, Rothamsted Experimental Station, Harpenden, England; 60 females, Department of Nematology, University of California, Riverside.

Type habitat and locality: Soil around roots of quaking aspen (*P. tremuloides*), Alta, Utah. Additional specimens of *P. megastylus* have been collected from soil around quaking aspen in Cedar Breaks, Farmington Flats, and Soldier Canyon, Utah; as well as Summit Lake, Alaska.

Pararotylenchus sphaerocephalus n. sp. (Fig. 6)

Females (measurements of 20 paratypes): L = 1.25–1.64 mm (1.405 mm ± .042); width = 38.0–48.0 μm (42.05 μm ± 1.31); stylet = 39.0–44.0 μm (41.25 μm ± .48); DGO = 3.5–7.0 μm (5.13 μm ± .35); tail = 29.0–39.5 μm (34.42 μm ± 1.43); ABW = 25.5–34.0 μm (29.18 μm ± .99); h = 6.5–10.0 μm (8.73 μm ± .44); TA = 12–16 (13.9 ± .6); P = −4 to +2 (−1.1 ± .8); a = 28.8–39.3 (33.48 ± 1.11); b′ = 6.3–8.5 (7.10 ± .23); c = 35.1–50.0 (41.0 ± 1.7); c′ = 1.0–1.4 (1.18 ± .05); o = 8–18% (12.5% ± .9); m = 51–55% (52.6% ± 1.0); V = 52–62% (56.7% ± 1.1).

Description (females): Body generally coiled. Lip region hemispherical and slightly offset with seven to nine annules. Labial disc often slightly protruding. Stylet knobs rounded with anterior surface flattened. Excretory pore at level of mid to

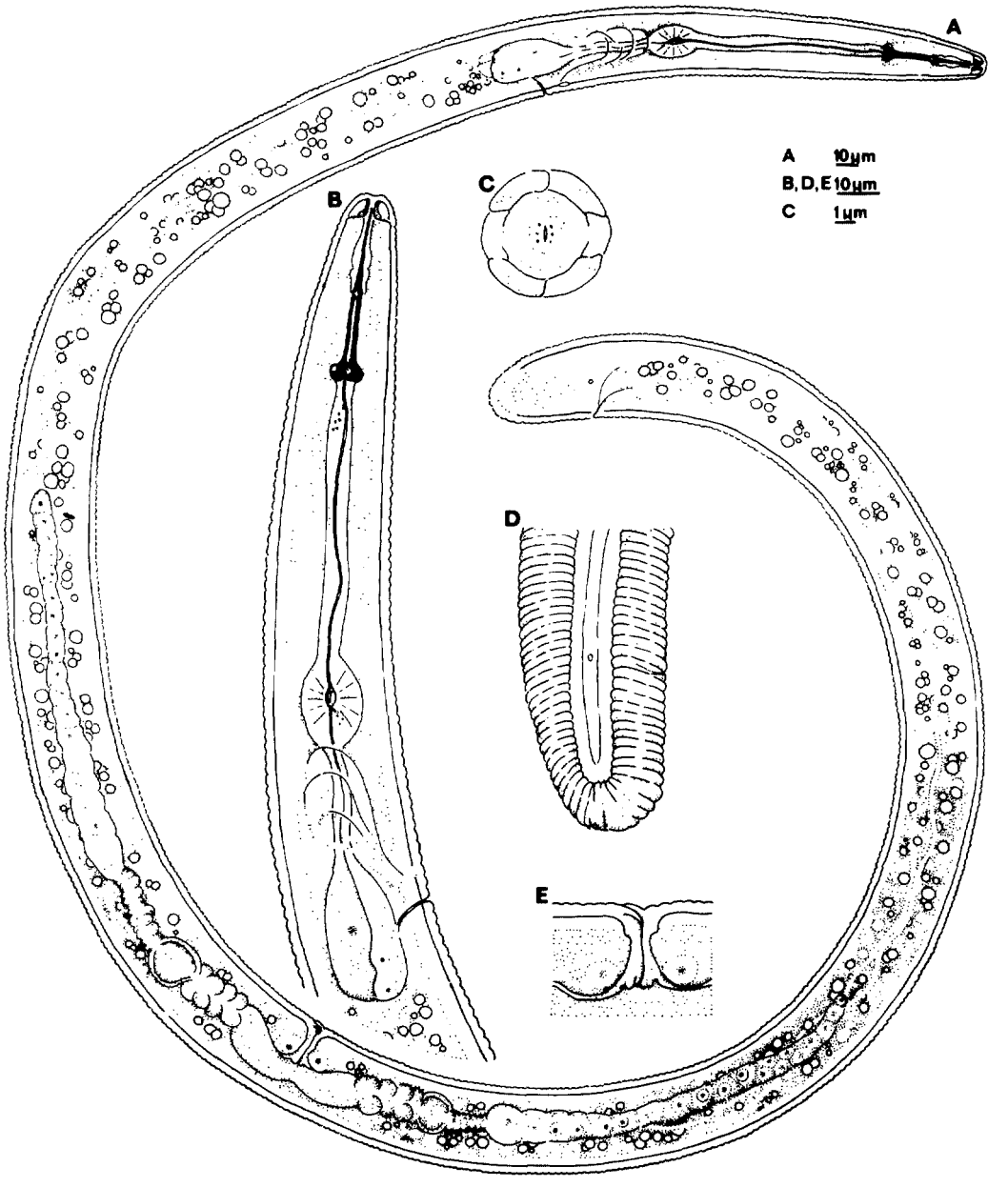

Fig. 5. Drawings of females of *Pararotylenchus megastylus* n. sp. A) Entire specimen (lateral). B) Cephalic and esophagus region (lateral). C) Labial region as observed with SEM (*en face*). D) Tail (lateral). E) Vulva (lateral).

posterior region of basal bulb. Hemizonid four or five annules anterior to excretory pore. Epiptygma typically large and conspicuous. Spermatotheca round, without sperm. Tail tapering, more curved on dorsal side and often slightly flattened or dorsally indented near terminus.

Holotype (female): L = 1.43 mm; width = 41.0 µm; stylet = 43.0 µm; DGO = 5.0 µm; tail = 39.5 µm; ABW = 30.5 µm; h = 9.0 µm; TA = 16; P = –4; a = 35.0; b′ = 6.7; c = 36.0; c′ = 1.3; o = 12%; m = 52%; V = 55%. Female as in general description. Lip region with nine annules and labial disc slightly protruding. Excretory pore at level of posterior region of basal bulb. Hemizonid five annules anterior to excretory pore.

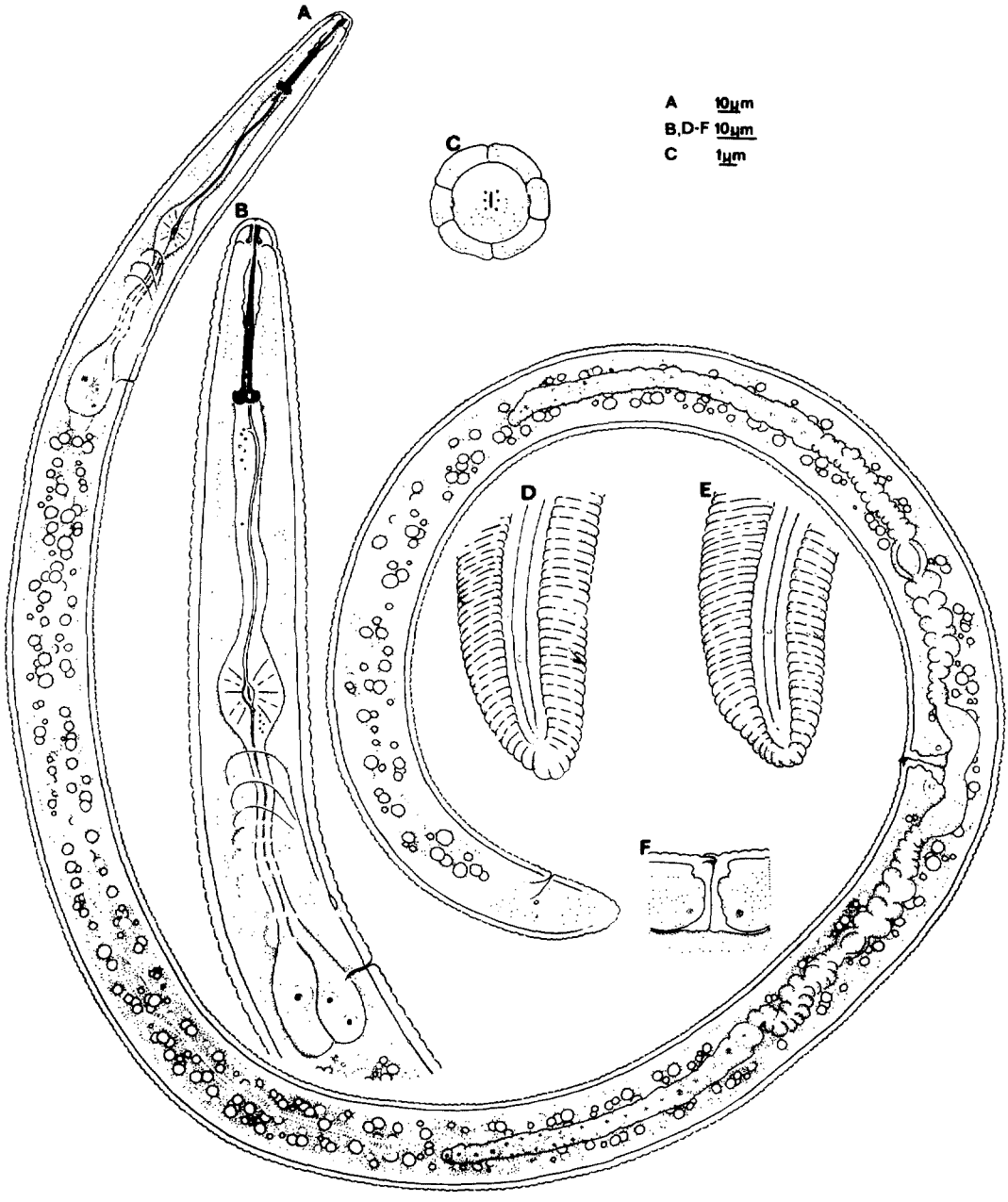

Fig. 6. Drawings of females of *Pararotylenchus sphaerocephalus* n. sp. A) Entire specimen (lateral; curvature slightly exaggerated for convenience in illustrating). B) Cephalic and esophagus region (lateral). C) Labial region as observed with SEM (*en face*). D) Tail tapering (lateral). E) Tail concave on dorsal side near terminus (lateral). F) Vulva (lateral).

Males: Unknown.

Diagnosis: Pararotylenchus sphaerocephalus is most similar to *P. brevicaudatus* but differs with respect to the following: In the former, the stylet is typically slightly longer (41.3 µm versus 38.3 µm), lip region hemispherical (versus slightly flattened anteriorly), tail terminus more strongly curved on dorsal side often with dorsal indentation (versus broadly rounded), and males are unknown.

Holotype (female): Collected by H. E. McKinney and A. H. Bell on June 5, 1978. Catalog number 42. Nematode Collection,

Department of Nematology, University of California, Riverside.

Paratypes (172 females, 10 juveniles). Same data as holotype. Specimens distributed in nematode collections as follows: 15 females, 1 juvenile, Division of Nematology, University of California, Davis; 11 females, USDA Nematology Investigations, Beltsville, Maryland; 11 females, Rothamsted Experimental Station, Harpenden, England; 135 females, 9 juveniles, Department of Nematology, University of California, Riverside.

Type habitat and locality: Soil around roots of *Veratrum* sp. L. (blooms were not available for specific identification), near Farmington Flats, Utah.

Pararotylenchus spiralis n. sp. (Fig. 7)

Females (measurements of 20 paratypes): L = 1.08–1.33 mm (1.245 mm ± .283); width = 34.0–42.0 μm (38.30 μm ± 1.08); stylet = 37.0–41.0 μm (39.10 μm ± .44); DGO = 2.5–6.0 μm (3.83 μm ± .40); tail = 23.5–43.0 μm (30.40 μm ± 1.94); ABW = 27.0–38.0 μm (29.18 μm ± .55); h = 6.0–9.5 μm (7.60 μm ± .38); TA = 12–17 (14.6 ± .7); P = −3 to +4 (.6 ± .9); a = 27.0–37.7 (32.67 ± 1.26); b′ = 6.2–7.6 (6.71 ± .15); c = 28.8–51.8 (41.56 ± 2.17); c′ = .9–1.4 (1.04 ± .06); o = 6–16% (10% ± 1.0); m = 47–53% (50.6 ± .8); V = 55–65% (58.3% ± 1.0).

Description (females): Body typically spiral. Lip region continuous or nearly continuous with contour of body, truncate, with seven to nine annules. Stylet with rounded knobs anteriorly flattened. Excretory pore near level of mid basal bulb. Hemizonid two to five annules anterior to excretory pore. Epiptygma large. Spermatotheca often obscure; sperm absent. Tail broad near terminus, strongly curved on dorsal side.

Holotype (female): L = 1.17 mm; width = 42.0 μm; stylet = 38.0 μm; DGO = 5.0 μm; tail = 33.0 μm; ABW = 30.0 μm; h = 7.0 μm; TA = 15; P = −3; a = 28.0; b′ = 6.4; c = 35.0; c′ = 1.1; o = 13%; m = 51%; V = 58%. Female as in general description. Lip region nearly continuous with body contour, seven annules. Hemizonid five annules anterior to excretory pore.

Males: Unknown.

Diagnosis: Pararotylenchus spiralis is most similar to *P. truncocephalus,* but females of former differ in that stylet is longer (39.1 μm versus 34.4 μm), tail terminus broad and slightly curved (versus tapered and often strongly curved), and epiptygma is typically larger.

Holotype: Female collected by O. F. Clarke, June 5, 1963. Catalog number 43, Nematode Collection, Department of Nematology, University of California, Riverside.

Paratypes (138 females, 25 juveniles): Same data as holotype, distributed in nematode collections as follows: 6 females, 2 juveniles, Division of Nematology, University of California, Davis; 7 females, 1 juvenile, USDA Nematology Investigations, Beltsville, Maryland; 5 females, 1 juvenile, Rothamsted Experimental Station, Harpenden, England; and 120 females, 21 juveniles, Department of Nematology, University of California, Riverside.

Type habitat and locality: Soil around roots of *Veratrum californicum* Durand., Wellman's Cienega, San Jacinto Mountains, Riverside County, California. Additional specimens of *P. spiralis* have been collected from soil around *Veratrum* sp. near Farmington Flats, Utah.

Pararotylenchus truncocephalus n. sp. (Fig. 8)

Females (measurements of 23 paratypes): L = 1.14–1.41 mm (1.267 mm ± .032); width = 31.0–41.0 μm (36.62 μm ± 1.21); stylet = 31.5–36.0 μm (34.37 μm ± .46); DGO = 3.5–9.0 μm (7.3 μm ± .62); tail = 28.5–41.0 μm (35.15 μm ± 1.64); ABW = 21.5–28.5 μm (24.48 μm ± .68); h = 5.0–12.5 μm (8.79 μm ± .89); TA = 9–14 (11.5 ± .7); P = −7 to −3 (−4.7 ± .5); a = 30.6–42.3 (34.72 ± 1.14); b′ = 7.1–8.5 (7.75 ± .15); c = 30.0–43.5 (36.36 ± 1.61); c′ = 1.1–1.7 (1.44 ± .07); o = 10–26% (21.2% ± 1.9); m = 44–50% (47% ± .7); V = 54–61% (57.7% ± .6).

Description (females): Body generally loosely coiled. Lip region continuous with body contour, angular, truncate, with seven or eight annules. Stylet massive with rounded knobs flattened anteriorly. Excretory pore located near level of esophagointestinal valve. Hemizonid two to six annules anterior to excretory pore. Epiptygma

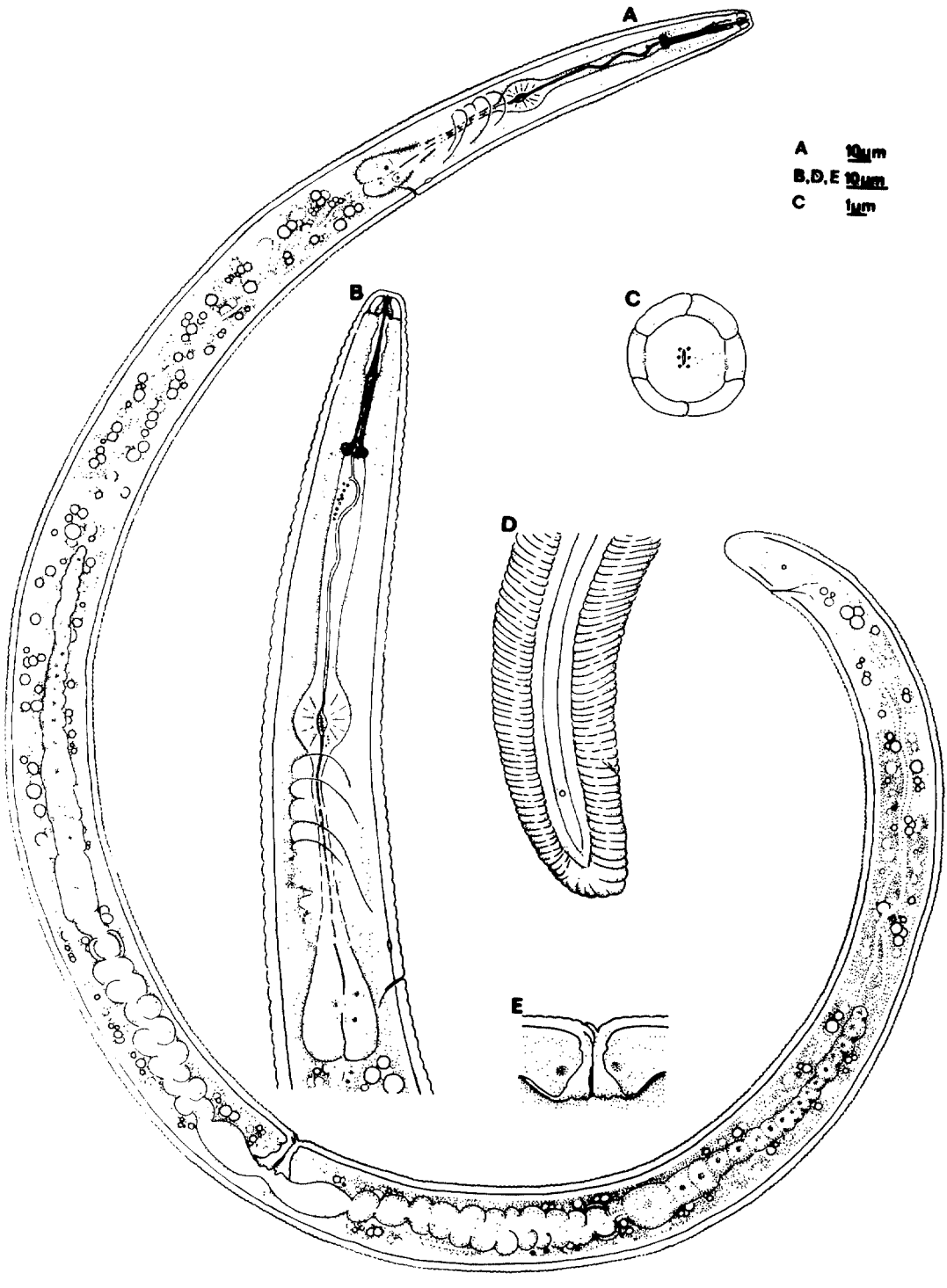

Fig. 7. Drawings of females of *Pararotylenchus spiralis* n. sp. A) Entire specimen (lateral). B) Cephalic and esophagus region (lateral). C) Labial region as observed with SEM (*en face*). D) Tail (lateral). E) Vulva (lateral).

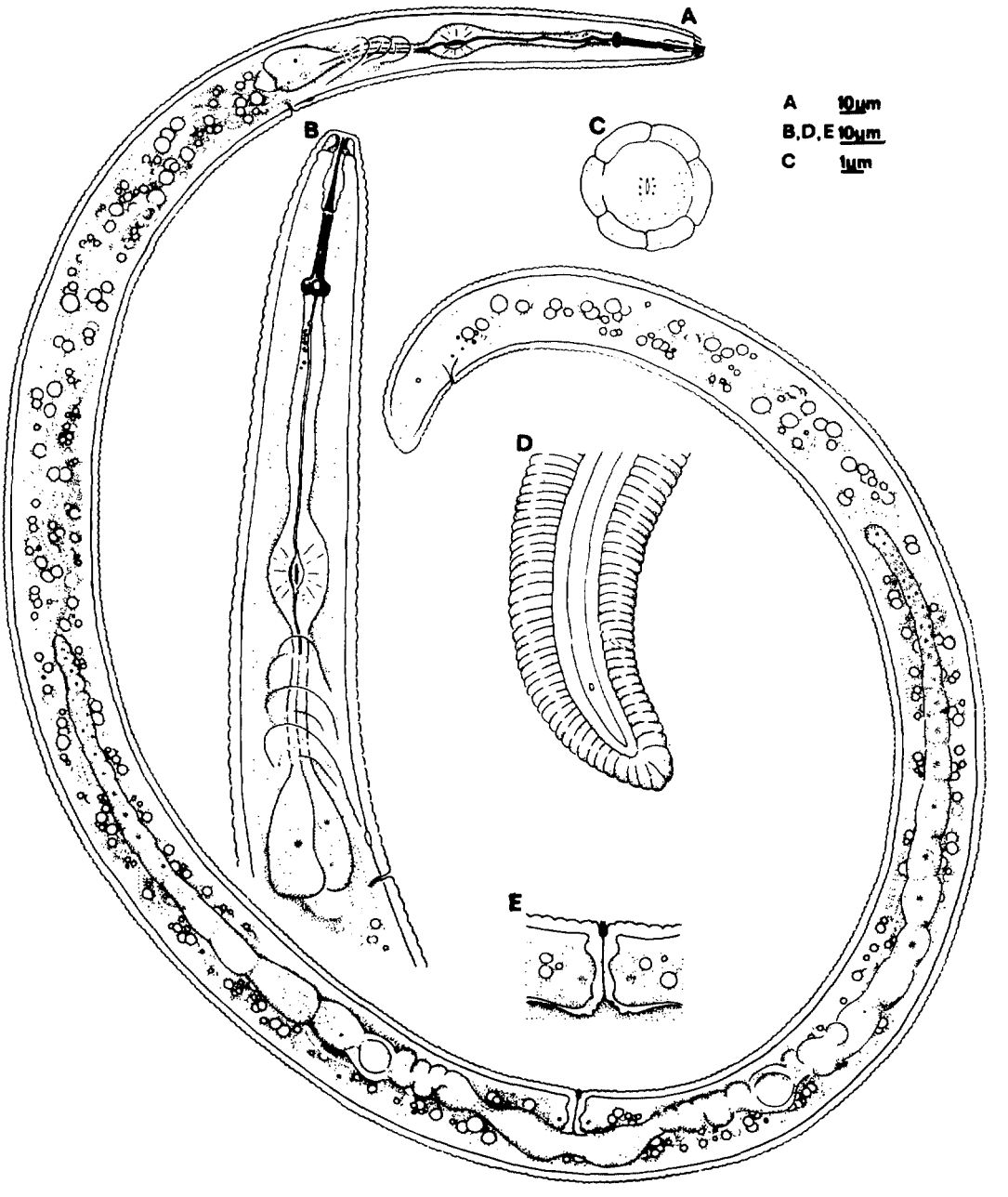

Fig. 8. Drawings of females of *Pararotylenchus truncocephalus* n. sp. A) Entire specimen (lateral; curvature slightly exaggerated for convenience in illustrating). B) Cephalic and esophagus region (lateral). C) Labial region as observed with SEM (*en face*). D) Tail (lateral). E) Vulva (lateral).

relatively small. Spermatotheca round and small without sperm. Tail tapering, curving ventrally with rounded terminus.

Holotype (female): L = 1.41 mm; width = 39.5 µm; stylet = 36.0 µm; DGO = 5.0 µm; tail = 41.0 µm; ABW = 28.0 µm; h = 9.0 µm; TA = 14; P = –7; a = 37.0; b′ = 8.0; c = 33.0; c′ = 1.6; o = 14%; m = 47%; V = 59%. Female as in general description. Body loosely coiled with seven annules on lip region. Hemizonid five annules anterior to excretory pore. Epiptygma protrudes at right angle to body axis.

Males: Unkonwn.

Diagnosis: Pararotylenchus truncocephalus is most similar to *P. spiralis,* but fe-

males of the former differ in that stylet is shorter (34.4 μm versus 39.1 μm), tail curved ventrally, sometimes forming weak hook and tapering to a rounded terminus (versus broad and slightly curved), and epiptygma is typically smaller.

Holotype (female): Collected by H. E. McKinney and A. H. Bell, June 5, 1978. Catalog number 44, Nematode Collection, Department of Nematology, University of California, Riverside.

Paratypes (167 females, 20 juveniles): Same data as holotype, distributed in nematode collections as follows: 12 females, 1 juvenile, Division of Nematology, University of California, Davis; 12 females, 2 juveniles, USDA Nematology Investigations, Beltsville, Maryland; 11 females, 3 juveniles, Rothamsted Experimental Station, Harpenden, England; 132 females, 14 juveniles, Department of Nematology, University of California, Riverside.

Type habitat and locality: Soil around roots of quaking aspen (*P. tremuloides*), Farmington Flats, Utah.

Additional species

Pararotylenchus pini (Mamiya, 1968) n. comb. (syn. *Rotylenchus pini*), described from Japanese red pine (*Pinus densiflora* Sieb. et Zucc.), Shimane, Japan. Measurements of paratypes and topotypes of *P. pini* were similar to those reported by Mamiya (7). Esophageal glands were previously described as short and compact. Although they were illustrated as forming a basal bulb, there was apparent uncertainty regarding a slight dorsal or ventral overlap (7). Our observations indicate that *P. pini* forms a basal bulb as in other *Pararotylenchus* spp. Additional specimens of *P. pini* in the UCR slide collection, as well as some reported by Choi (3), have been described associated with roots of several plants in Korea, including unidentified species of fir (*Abies* sp. Mill.), bamboo, chestnut (*Castanea* sp. Mill.), and barley (*Hordeum* sp. L.).

Key to species of *Pararotylenchus* n. gen.

1. Males present (sperm in spermatotheca) 2
   Males absent (no sperm in spermatotheca) 5
2. Stylet 37–41 μm long; 8–9 lip annules ..... *P. brevicaudatus* (Hopper) n. comb.
   Stylet 28–36 μm long; 6–7 lip annules 3
3. Phasmids 9–30 annules anterior to level of anus ..... *P. pini* (Mamiya) n. comb.
   Phasmids near level of anus 4
4. Stylet knobs flat to slightly indented on anterior surface; phasmids two to six annules posterior to level of anus ..... *P. blothrotylus* n. sp.
   Stylet knobs rounded; phasmids at or slightly anterior to level of anus ..... *P. colocaudatus* n. sp.
5. Lip region truncate, angular 6
   Lip region rounded on sides 7
6. Stylet 36 μm or less, tail curves ventrally ..... *P. truncocephalus* n. sp.
   Stylet 37 μm or more, ventral side of tail straight or curves dorsally ..... *P. spiralis* n. sp.
7. Lip region slightly offset, broadly flattened anteriorly; tail nearly cylindrical, broadly rounded at terminus ..... *P. megastylus* n. sp.
   Lip region hemispherical; tail tapering more on dorsal side ..... *P. sphaerocephalus* n. sp.

DISCUSSION

Species of *Pararotylenchus* n. gen. have presented difficulties in classification for many years. Thorne collected specimens of this genus more than 50 years ago and identified them as *Rotylenchus* spp. More recently, *P. pini* (syn. *Rotylenchus pini*) was classified in Hoplolaimidae, regardless of the presence of a basal bulb because according to Mamiya (7) it had so many characteristics typical of *Rotylenchus*. On the other hand, *P. brevicaudatus* (syn. *Tylenchorhynchus brevicaudatus*) was included in Tylenchorhynchidae, although its short tail and anterior location of phasmids were recognized as distinctive (6). A review of family diagnoses and numerous species descriptions indicates that *Pararotylenchus* spp. possess a combination of morphological characters which are shared with other Hoplolaimidae and are distinct from Tylenchorhynchidae (1,2,5,9,10,11,12,13,14,16,17,18). The cephalic framework of *Pararotylenchus* spp. is well developed as in Hoplolaimidae, in contrast to the weak framework of most

Tylenchorhynchidae (e.g. particularly, *Tylenchorhynchus).* The DGO of *Pararotylenchus* is within the range of other Hoplolaimidae and is greater than the DGO among Tylenchorhynchidae. The tail length of *Pararotylenchus* is short as in other Hoplolaimidae; the tail is much longer among Tylenchorhynchidae, particularly when considered in relation to body length. The phasmids are positioned similarly to other Hoplolaimidae, except Hoplolaiminae Filipjev, 1934 where they may occur far anterior to the anus. Phasmids consistently occur considerably posterior to the anus in Tylenchorhynchidae. Heat-killed specimens of *Pararotylenchus* spp. are decidedly curved or coiled, a character which is more strongly and consistently expressed in certain Hoplolaimidae (e.g. Rotylenchinae Golden, 1971) than in Tylenchorhynchidae.

The diagnostic value of the lip region, as viewed with SEM, for characterizing higher categories such as families of Tylenchida, has not yet been clearly established. However, Sher and Bell (15) observed that a consistent basic pattern occurs among Hoplolaimidae; this is, the labial disc is round to oval, amphidial openings are slit-like at the periphery of the disc, and the anteriormost lip annule is distinct from other annules. This basic pattern for Hoplolaimidae has been subsequently confirmed by SEM examination of 25 species in 11 genera of Hoplolaimidae and by comparison with a wide range of additional Tylenchida (unpublished observations). Sher and Bell (15) reported considerable variability among lip region patterns of Tylenchorhynchidae. This variability has been confirmed by SEM observations of 41 species and 14 genera (unpublished observations), and none of the patterns specifically resemble those of *Pararotylenchus* or other Hoplolaimidae. In many species of *Tylenchorhynchus,* including the type species *Tylenchorhynchus cylindricus* Cobb, 1913, the labial disc is cross-shaped or consists of four lobes, and the anteriormost lip annule is similar to other annules of the head region (15, unpublished observations). However, the lip region of *Pararotylenchus* has a consistent pattern among species and the surface morphology conforms to the basic pattern for Hoplolaimidae.

Although *Pararotylenchus* shares most characteristics of Hoplolaimidae, particularly *Rotylenchus,* its esophageal glands comprise a basal bulb which is morphologically identical to that of *Tylenchorhynchus* spp. Light microscope observations of hand-cut sections of *Pararotylenchus* spp. indicate that the narrow cylinder of tissue including the esophageal lumen is symmetrically surrounded by three glands (unpublished observations). The glands are typically of equal length and terminate anterior to the esophago-intestinal junction. The morphological relationship of this basal bulb esophagus to the various esophagi of *Rotylenchus* spp. may contribute to understanding possible phylogenetic relationships. Seinhorst (8) notes that a modification from the basal bulb may occur by a ventral shift of the lumen, as in *Rotylenchus* spp.; this is a symmetric arrangement. An asymmetric arrangement occurs by a lateral shift of the lumen. Furthermore, the esophago-intestinal junction may be displaced anteriorly and one or more glands may be elongate. Genera with a basal bulb (i.e. *Pararotylenchus* spp.) are often closely related to those with an overlap resulting from an elongate dorsal gland (8). Although this type of overlap is not usually associated with a symmetric esophagus, the two characteristics apparently are combined in *Rotylenchus eximius* Siddiqi, 1964 (8). The esophagi of *Rotylenchus fallorobustus* Sher, 1965 and *Rotylenchus breviglans* Sher, 1965 are most similar to the basal bulb esophagus, differing only by the ventral shift of the lumen (8). *Pararotylenchus pini* (syn. *Rotylenchus pini*) is similar to *R. breviglans* (7) except that, like other *Pararotylenchus* spp., the lumen is symmetrically surrounded by glands and is not ventrally displaced. Thus, the basal bulb of *Pararotylenchus* spp. could be interpreted as part of a morphological continuum with *Rotylenchus* spp. in Hoplolaimidae. We believe a phylogenetic relationship between Rotylenchinae and Pararotylenchinae is, therefore, plausible on the basis of a wide range of shared characters, and this relationship is not necessarily contradicted by the presence of a basal bulb in Pararotylenchinae.

The arrangement of esophageal glands is not only variable within Hoplolaimidae

but within many additional groups of Tylenchida. Triantaphyllou and Hirschmann (19) note that the DGO and structure of the procorpus and metacorpus are stable and useful in tracing major phylogenetic lines but that the posterior esophagus region is often of more limited value in interpreting relationships. The overlapping esophagus might have originated many times from the primitive basal bulb type (19). This parallel evolution is indicated in the Aphelenchinae Geraert, 1966, Anguinidae Nicoll, 1935, and Dolichodoridae Chitwood and Chitwood, 1950 with Belonolaimidae Whitehead, 1959 (4). Other groups, such as Pratylenchinae Thorne, 1949, while not including known species with a basal bulb, show a continuum of esophageal types (8,19). In the Tylenchorhynchidae, nearly all species have a basal bulb, but in *Tylenchorhynchus clarus* Allen, 1955, glands overlap slightly dorsally.

These observations suggest that *Pararotylenchus* spp. share a greater number of characters with Hoplolaimidae than with Tylenchorhynchidae. Although, Hoplolaimidae and Tylenchorhynchidae are generally characterized respectively by overlapping glands and a basal bulb, a broader base of characters should be considered in their diagnoses. On the basis of present information, we believe *Pararotylenchus* should be included in Hoplolaimidae. Additional studies, including comparative cytology, physiology, biochemistry, biology, and electron microscopy, especially of the esophagus region, will further elucidate the relationship of *Pararotylenchus* spp. to other Tylenchida. Investigations are particularly needed to better define Tylenchorhynchidae, since its species are primarily grouped together on the basis of relatively primitive characteristics (e.g. basal bulb). Further research may also clarify the phylogenetic significance of those characteristics which are shared between *Pararotylenchus* and other Hoplolaimidae.

Pararotylenchus spp. have only been recovered from Western United States, except *P. pini* which has been reported from Japan and Korea. All occur in cool regions, primarily at high elevations, although the type locality of *P. colocaudatus* is along the cool Pacific coast. Although host range tests have not yet been conducted, *Pararotylenchus* spp. have been found associated with a wide range of plants including redwood, fir, pine, rose, aspen, *Veratrum* spp., and barley.

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