Systematics of the Monodelphic Species of Trichodoridae (Nematoda: Diphtherophorina) With Descriptions of a New Genus and Four New Species

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Abstract: To show the relationship of the monodelphic species of Trichodoridae with the nominal taxa, the genus *Monotrichodorus* is redefined, with the addition of one new species. The new genus *Allotrichodorus* is proposed on the basis of new species found in Brazil; and one new species is described in the genus *Paratrichodorus*. *Key Words:* Taxonomy; Trichodoridae; *Monotrichodorus monohystera; M. vangundyi; Allotrichodorus campanullatus; A. guttatus; Paratrichodorus (N.) westindicus.*

The first monodelphic species of *Trichodorus* Cobb, 1913, described from Venezuela, was named *Trichodorus monohystera* Allen, 1957 (1). The female of this species was distinguished by a single outstretched anterior ovary, lower position of the vulva, and two pairs of lateral body pores near the vulval level (1). Loof (4) mentioned some discrepancies in Allen's description for specimens which he collected in Venezuela.

Siddiqi (8) tentatively excluded *T. monohystera* from the genus *Trichodorus*, although it was reinstated in Loof's comprehensive paper on the taxonomy of Trichodoridae (6). Andrassy (2), with abbreviated explanation, proposed the genus *Monotrichodorus* on the basis of *T. monohystera*. The uncertainty regarding the taxonomic position of this group and the incomplete description given by Andrassy provided the impetus for this work on the monodelphic species of this important plant-parasitic taxon.

The specimens used in this study are primarily from the nematode survey collection held at the University of California, Riverside and Davis, California, USA. All observations were made on specimens fixed in 5% formalin and permanently mounted in glycerin. Some observations were made with SEM following the technique of Sher and Bell (7).

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Monotrichodorus Andrassy, 1976

Diagnosis (Expanded): Trichodoridae. Cuticle not swollen after fixation. Dorsal esophageal gland nucleus anterior to, and the same size as, the posterior subventral gland nuclei. Esophagus not overlapping intestine.

Female: Gonad monodelphic, prodelphic, with flexure at the oviduct; postvulvar uterine sac present. Vagina anteriorly directed, more than one-half body-width, with strong musculature and prominent cuticularization. Lateral advulvar body pores present. Vulva a transverse slit at about 80% of body length. Single caudal pore present.

Male: Spicules long and slender, cylindrical, with bristles; a longitudinal septum running from the head-shaft junction to near the distal end, opening terminal; fine transverse striae present along most of spicule length. Copulatory muscles prominent, elongate to oval. Three ventromedian supplements, at least one anterior to retracted spicule, posterior supplement near cloaca. Paired ventrolateral postcloacal papillae present. Single subterminal caudal pore. Single ventral cervical papilla anterior to excretory pore.

Type species: Monotrichodorus monohystera (Allen, 1957) Andrassy, 1976.

Syn. *Trichodorus monohystera* Allen, 1957

Other species: Monotrichodorus vangundyi n. sp.

Diagnosis: Monotrichodorus can be distinguished from *Trichodorus*, the most closely related genus, by the anterior position of the dorsal esophageal gland nucleus, the monodelphic females with posterior vulva and anteriorly directed vagina; in the male by the long slender cephalated spicules, fusion of outlet of caudal pores, and prominent elongate to oval copulatory muscles.

Monotrichodorus monohystera (Allen, 1957) Andrassy, 1976

Syn. *Trichodorus monohystera* Allen, 1957

Fig. 1

Measurements: (After Allen, 1957) 10 ♀♀: L = 0.61-0.90 mm; a = 15-23; b = 4.2-4.5; c = anus subterminal; V = 77-83; onchiostyle = 45-52 μm.

9 ♂♂: L = 0.67-0.90 mm; a = 19-24; b = 4-5; c = 70-90; T = 60-68; onchiostyle = 43-48 μm; spicules = 51-59 μm; gubernaculum = 10-13 μm.

San Salvador 6 ♀♀: L = 0.82-0.94 (0.87) mm; a = 18-22 (20); b = 4.5-5.2 (4.8); c = anus subterminal; V = 80-83; onchiostyle = 48-53 μm.

Female: Body slightly curved ventrally. Cuticle not swollen after fixation. Postvulvar uterine sac less than one body-width in length. Gonad single, prodelphic, with flexure at oviduct. Spermatheca round, usually filled with round sperm. Paired lateral vulvar body pores; right pore slightly posterior to vulva, left pore less than one body-width anterior to vulva. Vagina elongated, slanted anteriorly with conspicuous cuticularization. Vulva a transverse slit. Anus subterminal. Caudal pore single, terminal.

Male: Body slightly curved ventrally. One ventral cervical papilla immediately anterior to excretory pore, absent in one specimen. Paired lateral cervical pores slightly posterior to excretory pore. Three ventromedian supplementary papillae, only one within range of retracted spicules. Spicules arcuated, cephalated, bearing bristles. Gubernaculum linear. Caudal pore subterminal.

In addition to paratypes that have been studied and illustrated, this species has been identified from soil around sugar cane, San Salvador; soil around banana, Esquinas, Costa Rica; and soil around *Solanum* sp. and *Allstroameria* sp., Cordillera Blanca (3,900 m), Peru. Only females and juveniles were present in the few specimens available from those localities.

Monotrichodorus vangundyi n. sp.
Fig. 2

Measurements: Paratypes 20 ♀♀: L = 0.65-0.81 (0.72) mm; a = 15.5-22.0 (19.5); b = 3.5-5.8 (4.6); c = anus subterminal; V = 82.3-85.6 (83.8); onchiostyle = 48-57 (53) μm.

Paratypes: 20 ♂♂: L = 0.67-0.83 (0.73) mm; a = 18-24 (22); b = 4.3-5.7 (4.6); c = 60-80 (66.6); T = 57-70 (62.2); onchiostyle = 49-56 (53) μm; spicules = 50-57 (54) μm; gubernaculum = 13-16 (14) μm.

Holotype ♂: L = 0.78 mm; a = 21.6; b = 4.9; c = 80; T = 57; onchiostyle =

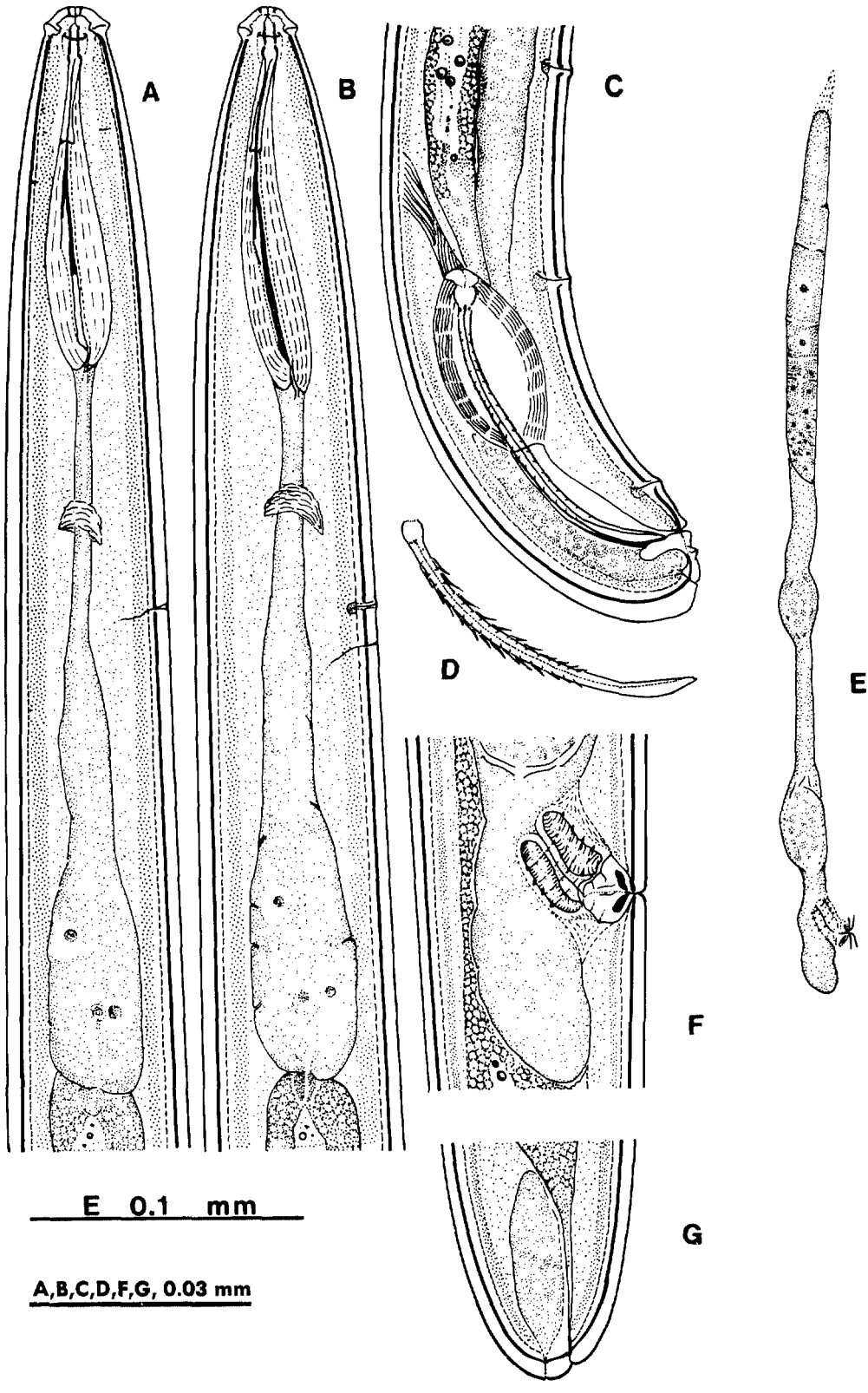
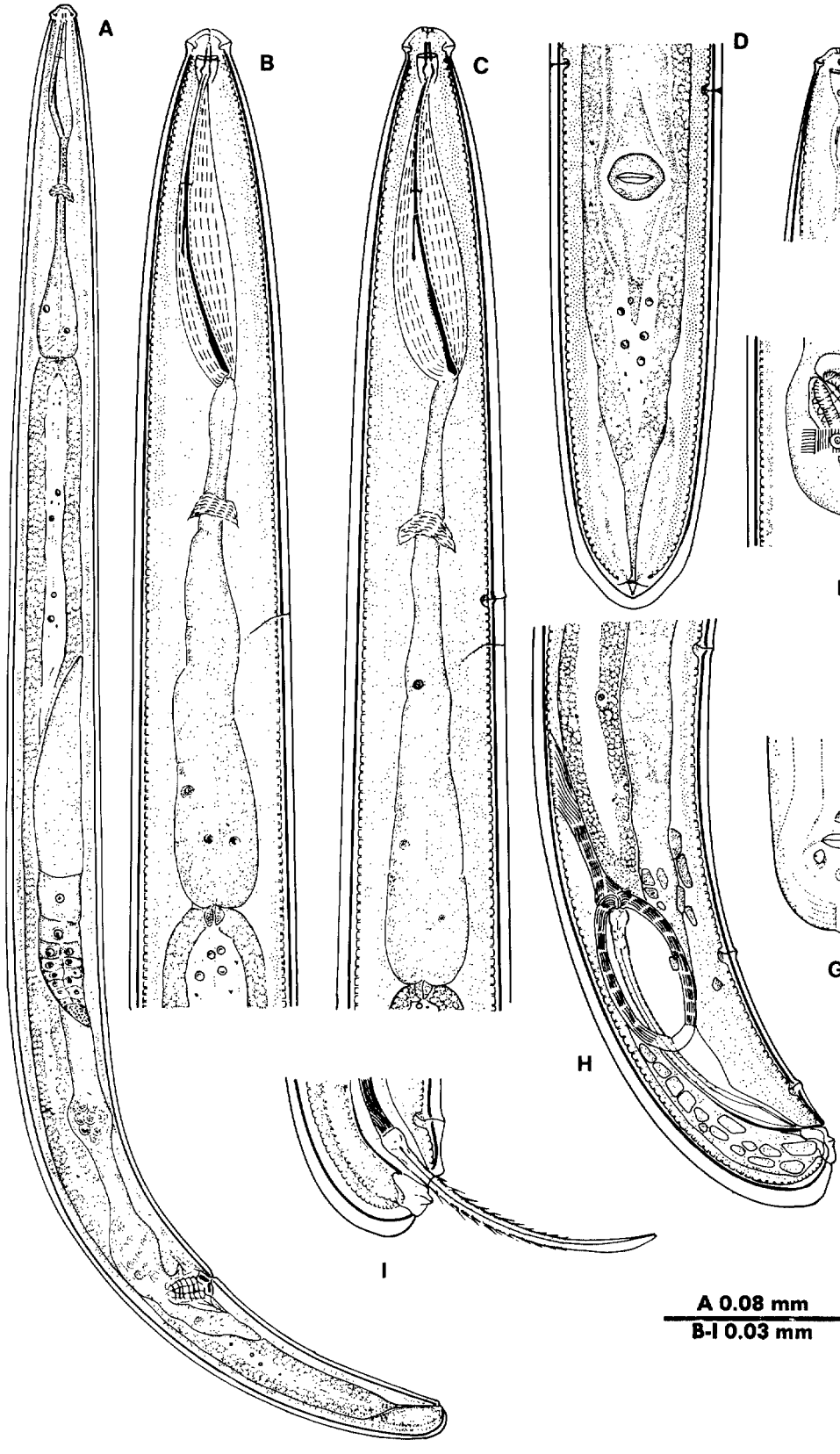


FIG. 1-(A-G). *Monotrichodorus monohystera. A)* Female esophageal region (Paratype). *B)* Male esophageal region (Paratype). *C)* Male posterior region (Paratype). *D)* Spicule *E)* Female gonad (Paratype). *F)* Vagina and related structures. *G)* Female posterior region.


A
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A 0.08 mm
B-I 0.03 mm

55 μm; spicule = 53 μm; gubernaculum = 17 μm. Body slightly curved ventrally, more abruptly curved posteriorly. Cuticle not swollen after fixation. Excretory pore at 95 μm (94 ± 5 μm in paratypes) from anterior end. Paired lateral cervical pores immediately posterior to excretory pore. Ventral cervical papilla 87 μm (89.3 ± 4.4 μm in paratypes) from anterior end. Onchiostyle tip 25 μm. Collar 30 μm from anterior end. Three ventromedian supplementary papillae, 55, 36, and 9 μm from cloaca. Spicules conspicuously cephalated, slender, slightly curved ventrally; protruding setae evident along the proximal two-thirds of protracted spicules, distal third smooth. Gubernaculum almost linear.

Allotype ♀: L = 0.76 mm; a = 20; b = 4.3; V = 86; onchiostyle = 55 μm. Body slightly curved ventrally. Cuticle, esophagus, and excretory pore as in male. Paired lateral cervical pores immediately behind amphid openings (Fig. 2-E). Gonad single, with flexure at oviduct; uterus elongated, directed anteriorly. Vaginal cuticularization conspicuous, rodlike. Vulva a large transverse slit. Postvulvar uterine sac about one body-width long. Paired lateral body pores within one vulvar-body-width anterior to vulva level. Anus and caudal pore subterminal.

Holotype: Male collected by S. D. Van Gundy; September 4, 1975. Catalogue No. 21, UCR Nematode Survey Collection, Riverside, California, USA.

Allotype: Female, same data as holotype. Catalogue No. 22.

Paratypes: 55 ♂♂, 67 ♀♀, 11 jj, same data as holotype, distributed as follows: 36 ♂♂, 43 ♀♀, 8 jj, Department of Nematology, University of California, Riverside, California; 8 ♂♂, 13 ♀♀, 1 j, Commonwealth Institute of Helminthology, St. Albans, England; 11 ♂♂, 11 ♀♀, 2 jj, Landbouwhogeschool, Wageningen, The Netherlands.

Type habitat and locality: Soil around roots of oil palm (*Elaeis guineensis*), Santa Gurtrudis Ranch, southeast of Rosa Zarate, Ecuador. Additional specimens also identified as *Monotrichodorus vangundyi* were found near the type locality around citrus and banana, and in native forest soils; in Rio Corutu riverbed soil, Puerto Armuelles, Panama; and around roots of *Ceiba pentandra* (L.) Gaert, Barro Colorado Island, Panama.

Diagnosis: Monotrichodorus vangundyi n. sp. can be recognized by the position of male supplementary papillae. *M. monohystera* has only the posterior supplement within the range of the retracted spicules, whereas *M. vangundyi* has the middle and posterior supplements within spicular range. Females of *M. vangundyi* differ by position of lateral cervical pores.

Allotrichodorus n. gen.

Diagnosis: Trichodoridae. Cuticle swollen after fixation. Dorsal esophageal gland nucleus the same size as subventral gland nuclei and located anterior to them. Intestine extending anteriorly into esophageal region dorsally and laterally.

Female: Gonad monodelphic, prodelphic, with flexure at oviduct. V = approximately 85%. Vagina more than half body-width in length, with conspicuous musculature and ventral cuticularization. Spermatheca conspicuous. Postvulvar uterine sac present. Anus subterminal and caudal pores almost terminal. Vulva a transverse slit.

Male: Caudal alae present. Lateral body pores present. Ventral cervical papilla, if present, anterior to excretory pore. Spicules transversely striated, elongate, slender, tubiform, with bristles; capitular extension having a dorsal groove or depression leading into proximal opening of spicule; lumen of spicule continuous with that of capitular extension (Fig. 3-G); longitudinal septa-like thickening present mainly in distal half of spicule. Gubernaculum not prominent. Three ventromedian supplementary papillae within range of retracted spicules. Large paired lateroventral postcloacal papillae present. Tail short with paired subterminal to terminal caudal pores.

FIG. 2-(A-I). *Monotrichodorus vangundyi* n. sp. *A)* Female lateral view. *B)* Female esophageal region. *C)* Male esophageal region (Holotype). *D)* Female posterior region, ventral view. *E)* Female anterior lateral body pore. *F)* Vagina and related structures. *G)* Male tail ventral view (Paratype). *H)* Male posterior region (Holotype). *I)* Protruding spicule (Paratype).

Type species: Allotrichodorus campanullatus n. sp.

Other species: A. guttatus n. sp.

Diagnosis: Allotrichodorus can be distinguished from the most closely related taxon, *Paratrichodorus (Atlantadorus)* Siddiqi, 1973, by the single ovary, posterior position of the vulva (V = 85%), prominent vaginal cuticularization, and in the male by spicule shape and the presence of three ventromedian supplementary papillae located within range of retracted spicules. The generic name is derived from the Greek word Allo, meaning other, or different, and retains the name *Trichodorus,* thus being masculine in gender.

Allotrichodorus campanullatus n. sp.
Fig. 3

Measurements: Paratypes 10 ♀♀: L = 0.63-0.68 (0.67) mm; a = 12-20 (15); b = 4.0-5.3 (4.5); c = anus subterminal; V = 83.3-86.4 (84.6); onchiostyle = 46-55 (52.4) μm.

Paratypes 10 ♂♂: L = 0.54-0.69 (0.62) mm; a = 11-20 (15.5); b = 3.6-5.5 (4.5); c = 60-100 (76); onchiostyle = 45-57 (50.3) μm; spicules = 46-59 (52) μm; gubernaculum = 14-17 (14.7) μm.

Holotype ♂: L = 0.69 mm; a = 16; b = 4.4; c = 98; T = 69; onchiostyle = 53 μm; spicules = 58 μm; gubernaculum = 16 μm. Body slightly curved ventrally. Cuticle swollen when fixed. Posterior labial papillae inconspicuous. Collar 25 μm from anterior end. Onchiostyle tip 25 μm long, basal portion slender. Nerve ring 12 μm posterior to onchiostyle. Dorsal esophageal gland nucleus anterior to posterior subventral gland nuclei. Excretory pore 90 μm from anterior end. Ventral cervical papilla 9 μm anterior to excretory pore. Paired lateral cervical pores posterior to onchiostyle base. Testis elongated, ending 42 μm from esophagus base. Spicules slender, arcuate, slightly swollen at distal end, with bristles; capitular extension 16 μm long, with dorsal groove or depression. Gubernaculum not prominent. Three ventromedian supplementary papillae, 60, 30, and 5 μm from cloaca, all within range of retracted spicules. Caudal alae inconspicuous in lateral view. Tail short, bluntly rounded. Caudal pores subterminal.

Allotype ♀: L = 0.75 mm; a = 12; b = 4.4; onchiostyle = 58 μm. Body slightly curved ventrally. Onchiostyle tip 30 μm long. Collar 25 μm from anterior end. Esophagus and nuclei as in male. Ovary single, flexed. Spermatheca well developed, 40 μm long, and 400 μm from vulva, filled with small round sperm. Vagina more than one-half body-width; vaginal cuticularization conspicuous, appearing as two small bells in lateral view (Fig. 3-E); vulva a transverse slit (Fig. 3-F). Postvulvar uterine sac about one body-width long, may contain a few sperm. Lateral body pores absent. Tail hemispheric, anus subterminal, caudal pores almost terminal.

Holotype: Male collected by R. D. Sharma, 1973; Catalogue No. 23, U.C.R. Nematode Survey Collection, Riverside, California, USA.

Allotype: Female, same data as holotype. Catalogue No. 24.

Paratypes: 10 ♂♂, 10 ♀♀, 15 jj, same data as holotype, distributed as follows: 8 ♂♂, 8 ♀♀, 10 jj, Department of Nematology, University of California, Riverside, California; 2 ♂♂, 2 ♀♀, 5 jj, Commonwealth Institute of Helminthology, St. Albans, England.

Type habitat and locality: Soil around roots of cocoa *(Theobroma cocao),* Cascata, Alcobaca, Brazil. Additional specimens also identified as *A. campanullatus* have been examined from cocoa and coffee soils, Itabuna, Bahia, Brazil.

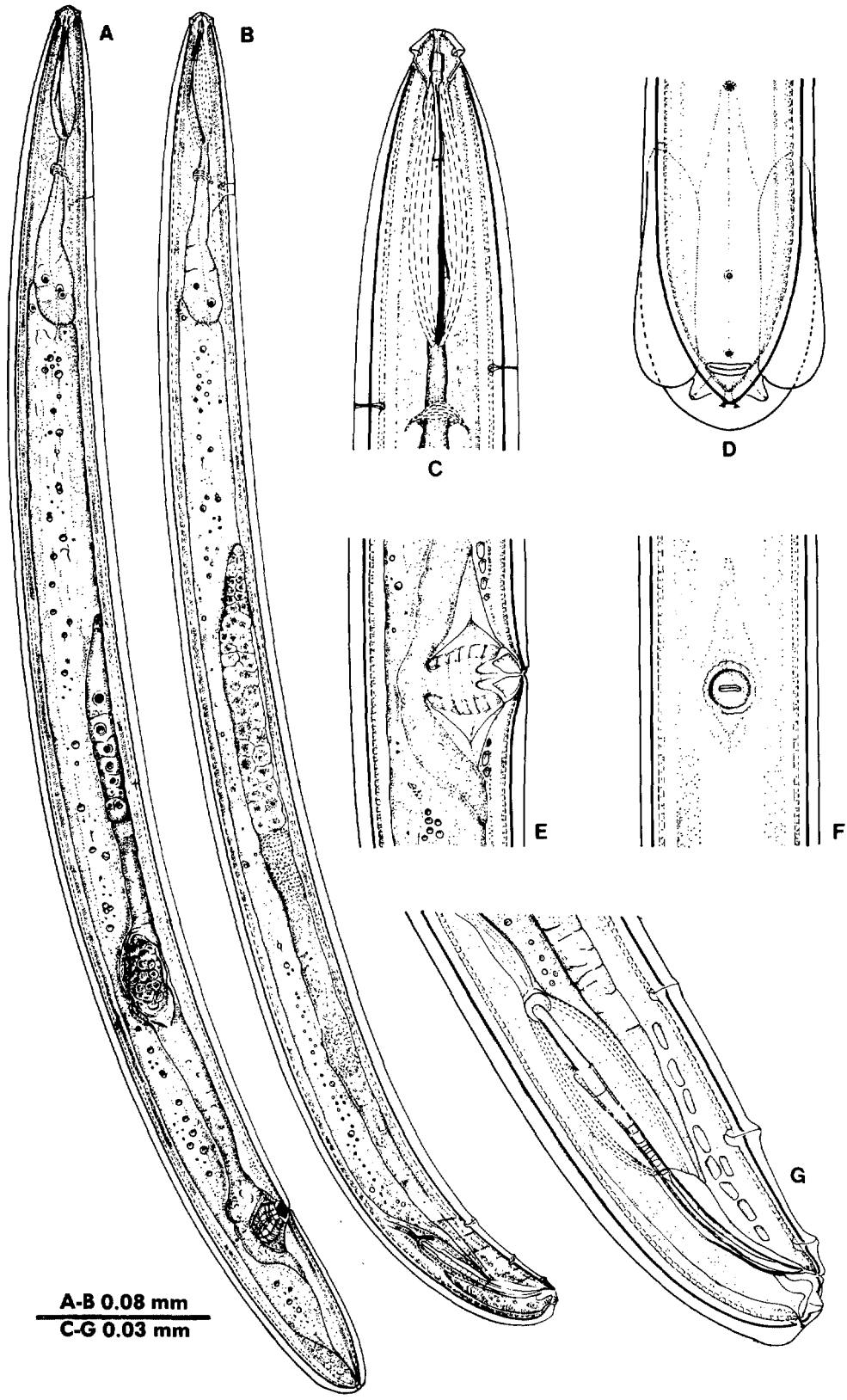
Diagnosis: This species can be recognized by a ventral cervical papilla anterior to the excretory pore, onchiostyle length, spicule shape, and campanulate vaginal cuticularization. The species name is derived from the Latin campanulla, meaning bell.

Allotrichodorus guttatus n. sp.
Fig. 4

Measurements: Paratypes 5 ♀♀: L =

➠

FIG. 3-(A-G). *Allotrichodorus campanullatus* n. sp. *A)* Female. *B)* Male (Holotype). *C)* Male anterior region, ventral view (Paratype). *D)* Male posterior region, ventral view (Paratype). *E)* Vagina and related structures. *F)* Vulva ventral view. *G)* Male posterior region (Holotype).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A-B 0.08 mm
C-G 0.03 mm

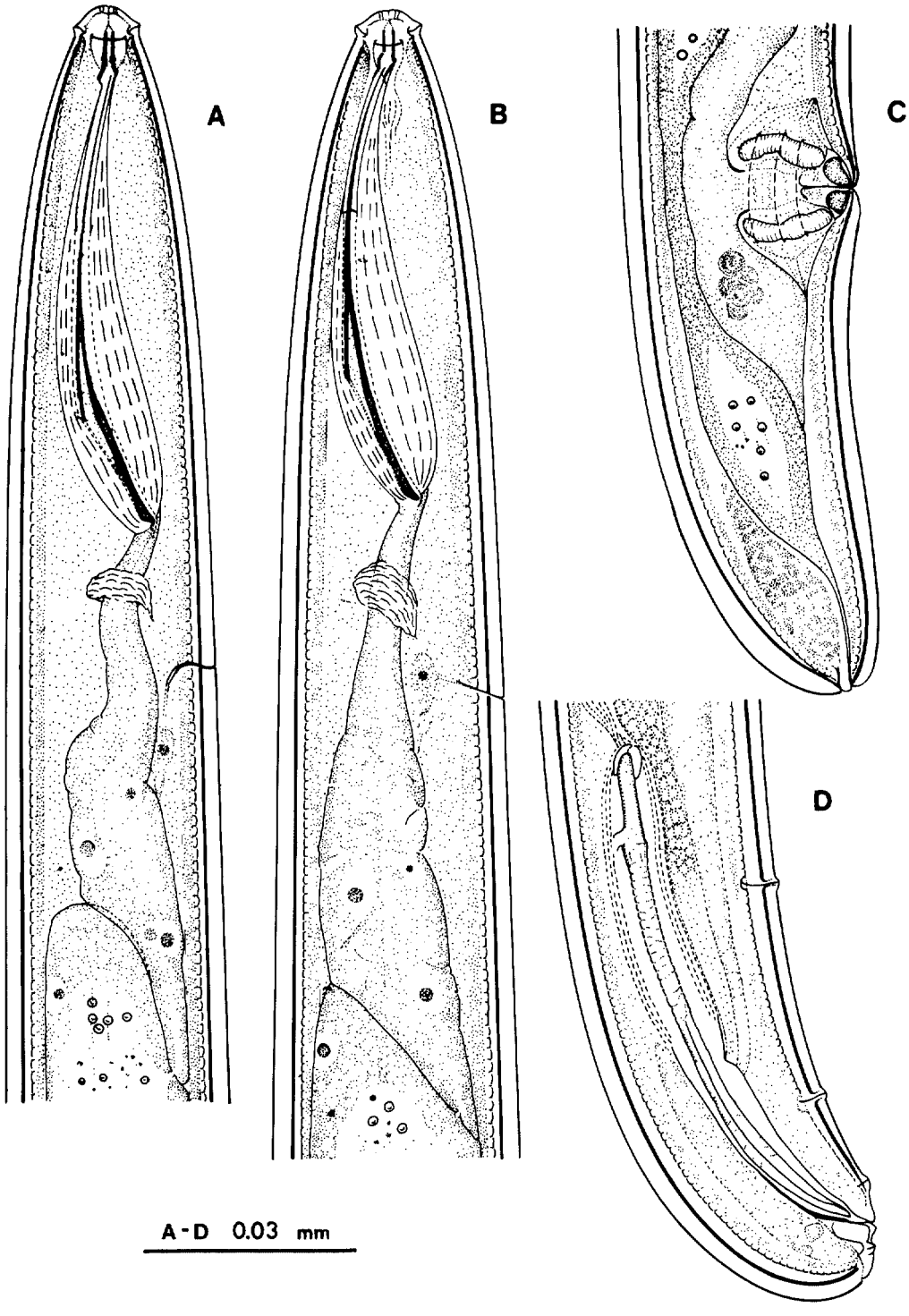

FIG. 4-(A-D). *Allotrichodorus guttatus* n. sp. *A)* Female anterior region. *B)* Male anterior region (Holotype). *C)* Female posterior region. *D)* Male posterior region (Holotype).

0.65-0.72 (0.69) mm; a = 12-15 (13); b = 4.1-5.2 (4.8); c = anus subterminal; V = 84-88 (86); onchiostyle = 63-71 (69) μm.

Paratypes 4 ♂♂: L = 0.67-0.74 (0.71) mm; a = 12-16 (14); b = 4.3-5.3 (5); c = 60-81 (71); T = 58-74 (64); onchiostyle = 65-72 (70) μm; spicules = 65-76 (70) μm; gubernaculum = 14-18 (16) μm.

Holotype ♂: L = 0.68 mm; a = 13; b = 4.3; c = 57; T = 58; onchiostyle = 67 μm; spicules = 76 μm; gubernaculum = 15 μm. Body almost straight except for slight ventral curve of the caudal region. Cuticle swells moderately after fixation. Lip region hemispheric, separated from body by small constriction. Paired lateral cervical pores slightly posterior to nerve ring. Ventral cervical papilla absent. Onchiostyle tip 33 μm long. Collar 30 μm from anterior end. Excretory pore 97 μm from anterior end, its duct ending in reniform cell. Slender portion of esophagus short, enlarged portion compressed dorsoventrally by intestine. Dorsal esophageal gland nucleus anterior to and same size as posterior subventral gland nuclei. Testis single, with large round sperm. Spicules slender, elongated, cylindrical, with transverse striations; capitular extension 15 μm long. Gubernaculum linear, inconspicuous. Three ventromedian supplementary papillae, 5-10 μm, 19-23 μm, and 40-70 μm from cloaca (ranges from paratypes). Paired sublateral postcloacal papillae prominent. Tail rounded with nearly terminal caudal pores. Caudal alae inconspicuous in lateral view.

Allotype ♀: L = 0.65 mm; a = 15; b = 4.1; V = 88; onchiostyle = 64 μm. Body slightly curved ventrally in posterior region. Gonad monodelphic, prodelphic, with flexure; short postvulvar uterine sac. Vagina and related structures prominent. Vagina more than half body-width, cuticularization appearing as two rather unequal drops in lateral view (Fig. 4-C). Vulva a wide transversal slit. No lateral body pores observed. Anus and caudal pores terminal. Tail terminus as illustrated (Fig. 4-C).

Holotype: Male collected by R. D. Sharma, 1973; Catalogue No. 25, U.C.R. Nematode Survey Collection, Riverside, California.

Allotype: Female, same data as holotype. Catalogue No. 26.

Paratypes: 4 ♂♂, 5 ♀♀, 13 jj, same data as holotype, distributed as follows: 2 ♂♂, 3 ♀♀, 10 jj, at Department of Nematology, University of California, Riverside, California; 2 ♂♂, 2 ♀♀, 3 jj, at Commonwealth Institute of Helminthology, St. Albans, England.

Type habitat and locality: Soil around cocoa *(Theobroma cacao),* San Francisco, Porto Seguro, Brazil.

Diagnosis: This species can be recognized by absence of ventral cervical papilla, onchiostyle length, characteristic spicules, single ovary, and drop-shaped vaginal cuticularization.

Paratrichodorus (Nanidorus) westindicus n. sp.
Fig. 5

Measurements: Paratypes 36 ♀♀: L = 0.40-0.50 (0.46) mm; a = 17-25 (22); b = 3.8-5.4 (4.6); c = 52-90 (72); V = 60-65 (64.7); onchiostyle = 32-37 (34.5) μm.

Holotype ♀: L = 0.46 mm; a = 23; b = 4.5; c = 86; V = 64; onchiostyle = 34 μm. Body slightly curved ventrally. Cuticle moderately swollen when fixed; subcuticle with coarse striations. Lip region rounded; amphid aperture small, at level of postlabial papillae. No lateral, ventral, or caudal pores observed. Excretory pore 98 μm from anterior end. Esophagus truncate, apparently overlapping intestine lateroventrally. Nucleus of dorsal esophageal gland larger than nuclei of posterior subventral glands, located near beginning of esophagus enlargement. Posterior subventral gland nuclei paired, near esophageal intestinal junction. Vulva inconspicuous, a transverse slit 1.5-2.0 μm long; vagina inconspicuous, less than half body-width, cuticularization appearing as two small rectangular pieces. Gonad monodelphic, prodelphic, with flexure; postvulvar uterine sac 23 μm long. Spermatheca with small cuneate sperm. Tail conoid, with subdigitate to obtusely rounded terminus, arched dorsally at anal level.

Male: Not found.

Holotype: Catalogue No. 27. Nematode Survey Collection, Department of Nematology, University of California, Riverside, California, USA. Collected by N. D. Singh; University of West Indies, Trinidad.

Paratypes: Same data as holotype. 28 ♀♀ at Nematology Department, University of

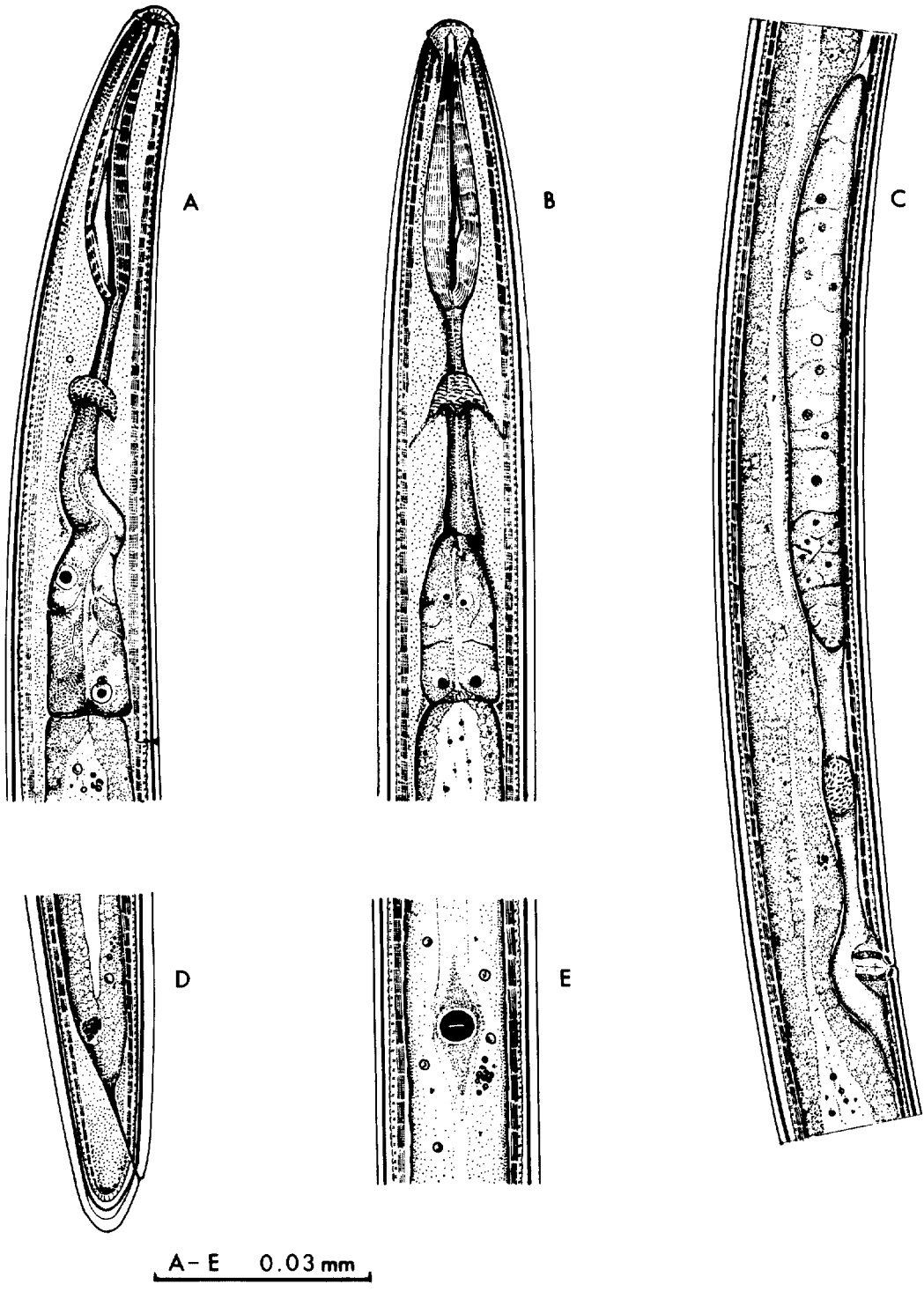

FIG. 5-(A-E). *Paratrichodorus (Nanidorus) westindicus* n. sp. *A)* Female anterior region. *B)* Female anterior region, ventral view. *C)* Female gonad, lateral view. *D)* Female posterior region, lateral view. *E)* Vulva ventral view. All drawings from holotype.

California, Riverside, California; 8 ♀♀ at Commonwealth Institute of Helminthology, St. Albans, England.

Type habitat and locality: Soil around roots of cocoa *(Theobroma cacao),* at Trinidad, West Indies. Additional specimens were also identified from soil around roots of sugar cane, same locality.

Diagnosis: P. (N.) westindicus is recognized by the single ovary and posterior position of vulva (60-65%), its relatively long onchiostyle, and typical tail, which arches dorsally at anal level.

DISCUSSION

Monodelphic nematodes are seen in many groups and are considered to have been derived from didelphic forms. One-ovaried forms are the usual condition in some large taxa (Aphelenchina, Criconematoidea, etc.). In some groups, such loss of an ovary is the single character separating genera. This situation is prevalent in Tylenchina, where monodelphic and didelphic species are placed in separate genera (e.g., this is the only character known to distinguish *Helicotylenchus* Steiner, 1945, from *Rotylenchoides* Whitehead, 1958; and *Radopholus* Thorne, 1949, from *Radopholoides* de Guiran, 1962).

In Dorylaimida, monodelphic and didelphic species are often in the same genus. In *Xiphinema* Cobb, 1913, most species are didelphic, although in some the anterior gonad appears in several stages of regression. This morphological character has been used in part to divide the genus into subgenera (3).

In monodelphic trichodorids, as in Tylenchina, the posterior gonad is lost, resulting in a posterior shift of the vulva. Both species of *Monotrichodorus* seem morphologically similar to *Trichodorus* because of the absence of caudal alae, unswollen condition of cuticle, similar arrangement of male copulatory muscles, and shape of the esophagus.

An important difference between *Trichodorus* and *Monotrichodorus* is the arrangement of the esophageal gland nuclei. In *Monotrichodorus* the dorsal gland nucleus is well anterior to the subventral gland nuclei, whereas in *Trichodorus* the dorsal esophageal gland nucleus lies at the same level as the posterior subventral gland nuclei. Arrangement of esophageal nuclei appears constant, and has been used to separate Dorylaimids at higher taxonomic levels (5).

Trichodorids normally have two caudal pores; *Monotrichodorus* is unique in having only one. The one-ovaried condition of females and the fusion of caudal pores indicate a different line of evolution of trichodorids, therefore substantiating the erection of a new genus to show phylogenetic relationships among this group of animals.

Allotrichodorus differs from *Monotrichodorus* because of the swollen condition of the cuticle and presence of caudal alae, though those same characters show a close similarity to *Paratrichodorus. Allotrichodorus* is similar to the subgenus *Atlantadorus* (8) in that both have paired lateral cervical pores at the level of the onchiostyle base and large paired postcloacal papillae; but it differs by the distinct spicule shape and presence of a capitular extension which is unique. Females of *Allotrichodorus* are also unique in having the vagina longer than a vulvar body-width with large cuticularization, and with the vulva appearing as a large transverse slit. Thus this group appears to form a line of evolution different from that of *Trichodorus, Paratrichodorus,* or *Monotrichodorus* and is proposed as the new genus *Allotrichodorus.*

Paratrichodorus (Nanidorus) westindicus n. sp., is tentatively described within the subgenus *Nanidorus.* The males of this species, when found, should substantiate this placement.

The finding of these new forms justifies a review of the entire systematics of Trichodoridae.

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