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Taxonomic Review of the Genera of the Aphelenchoidea
(Fuchs, 1937) Thorne, 1949 (Nematoda: Tylenchida)

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A Taxonomic Review of the Genera of the Aphelenchoidea (Fuchs, 1937) Thorne, 1949 (Nematoda: Tylenchida)

WILLIAM R. NICKLE¹

Abstract: This generic level taxonomic review of the nematode superfamily Aphelenchoidea is based upon a study of specimens from 24 of the 28 described genera. The diagnoses of these genera are presented, and some are emended with new information. One new genus, *Huntaphelenchoides*, and five new combinations are proposed. The families Paraphelenchidae and Anomyctidae are placed in synonymy with Aphelenchidae and Aphelenchoididae, respectively. The genera *Asteroaphelenchoides* and *Pseudaphelenchoides* are placed in synonymy under the genus *Aphelenchoides*. Rare male and/or female specimens of *Peraphelenchus*, *Anomyctus*, *Laimaphelenchus*, *Aphelenchus*, *Cryptaphelenchoides*, *Megadorus*, *Tylaphelenchus*, and *Entaphelenchus*, are redescribed and illustrated. Four plates, containing 106 original drawings of the males, females, stylets, and spicules of representatives of 22 aphelenchoid genera, are presented. *Key Words:* Taxonomic review, Aphelenchoidea.

The superfamily Aphelenchoidea (Fuchs, 1937) Thorne, 1949 is a large group of stylet-bearing nematodes that have adapted to a wide range of ecological relationships including phytoparasitism, predation, fungus feeding, both in soil and in association with insects, and obligate insect parasitism. Generally, aphelenchoid nematodes have their ecological counterparts in the Tylenchoidea with the possible exception of predators, which to date have not been reported among tylenchs. It is interesting that phytoparasitism has evolved to a higher level in the Tylenchoidea than in the Aphelenchoidea. For unknown reasons, aphelenchoid phytoparasites have colonized only leaves, stems, and buds. In nature they have not utilized fibrous roots of higher plants as a food source to any great degree. Tylenchoid nematodes have utilized the roots of higher plants and, therefore, gained more prominence in phytonematology.

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Gasparrini (12) was the first to describe an aphelenchoid nematode, *Schistonchus caprifici* (Gasparrini, 1864) Cobb, 1927. One year later Bastian (3) described two other basic forms, *Aphelenchus avenae* and *Aphelenchoides parietinus*. In 1890 the plant parasitic species, *Aphelenchoides fragariae*, was described by Ritzema Bos (28). However, it was not until 1923 (4) that the eminent USDA nematologist, Dr. N. A. Cobb, showed that both the dorsal and subventral esophageal gland orifices were contained within the large median esophageal bulb in specimens of the genus *Aphelenchus*; whereas, in the tylenchoid forms, only the subventral glands emptied near the middle of the esophagus, and the dorsal gland orifice was located anteriorly behind the stylet knobs. His observation thus provided a sound basis for separation of the aphelenchoid and the tylenchoid nematodes. The works of the German scientists, Fuchs (8, 9, 10, 11) and Rühm (29, 30, 31), illustrated the large numbers and diversity of aphelenchoid nematodes associated with bark beetles. The Soviet workers, Skarbilovich (34) and Paramonov (24, 25, 26, 27) have dealt with higher taxa. J. B. Goodey (13) and Franklin (7) in Great Britain made significant contributions to the advancement of our knowl-

edge; and Allen (1), Thorne (40), and Sanwal (32, 33) provided leadership in North America on the systematics of this group.

Specimens representing 24 of the 28 described aphelenchoid genera were studied in this project. Several attempts were made to obtain specimens of the nominal genera *Devibursaphelenchus*, *Paraphelenchoides*, *Neoseinura*, and *Ruehmaphelenchus*, without success. Little attempt was made to rationalize the ten or more subfamilies erected in recent literature, because I felt the genus is the best-defined and most objective taxonomic category in the aphelenchs at this time. Drawings of stylets, spicules, and the entire body of adults of each sex are provided, with all drawings on each plate at the same magnification for convenient comparison. All spicule drawings were made of the inside lateral view. Generic differences often seem evident from only the study of drawings of spicules published by over 50 different workers. Occasionally these differences disappear when all the spicules are compared and are illustrated using the same technique. In the diagnostic statements presented below, the most important differential characteristics of each genus are in *italics*.

Aphelenchoidea (Fuchs, 1937) Thorne, 1949

Syn. Aphelenchoidea Fuchs, 1937 (as a subdivision of Tylenchinae)

Definition.—Tylenchida. Stylet with or without basal knobs. Esophagus with large median esophageal bulb; dorsal esophageal gland outlet empties into lumen of median bulb just anterior to valve; with dorsally overlapping esophageal glands, except in *Paraphelenchus* which has posterior esophageal bulb. Female with prodelpic ovary and posteriorly located vulva. Male with or without caudal alae; gubernaculum or gubernaculum-like structure present or absent.

Type Family.—Aphelenchidae (Fuchs, 1937) Steiner, 1949

Aphelenchidae (Fuchs, 1937) Steiner, 1949

Syn. Paraphelenchidae (T. Goodey, 1951)
J. B. Goodey, 1960

Definition (emended).—Aphelenchoidea. Stylet with or without small basal thickenings. Esophagus with overlapping glands, or contained in posterior bulb. Spicules long, slender; gubernaculum V-shaped; peloderan caudal alae present or absent, when present supported by ribs. Mycophagous; soil inhabiting.

Type Genus.—*Aphelenchus* Bastian, 1865

Aphelenchus Bastian, 1865

(Fig. 11, 38, 60, 82)

Syn. *Isonchus* Cobb, 1913

Aphelenchus (Aphelenchus) Bastian, 1865. (Cobb, 1927)

Metaphelenchus Steiner, 1943

Definition.—Aphelenchidae. Lips slightly offset. Stylet without basal knobs. Esophageal glands overlap intestine dorsally. Hemizonid usually present, 3–8 annules posterior to excretory pore. Body narrowing abruptly behind vulva. Postuterine sac long. Female tail short, bluntly rounded. *Spicules paired, slender, not fused, with minute rostrum. Gubernaculum V-shaped*, (Fig. 82). *Male tail with well-developed caudal alae supported by prominent ribs*. Males often rare.

Bionomics.—Mycophagous, soil inhabiting.

Type Species.—*Aphelenchus avenae* Bastian, 1865

Paraphelenchus (Micoletzky, 1922)

Micoletzky, 1925

(Fig. 21, 33, 64, 83)

Syn. *Aphelenchus (Paraphelenchus)*
Micoletzky, 1922

Definition.—Aphelenchidae. Body usually large. Lips plump, forming flat cap, slightly offset. Stylet with or without small basal knobs. *Esophageal glands contained within spatulate posterior bulb*. Excretory pore posterior to median bulb; excretory duct leads

to prominent, ventrally located excretory cell. Hemizonid adjacent and posterior to excretory pore. Lumen of rectum widened considerably just behind sphincter. Postuterine sac well-developed. Female tail short, conical, sometimes with terminal mucron. *Spicules paired, slender, not fused; apex enlarged, rostrum short, with acute posteriorly directed terminus. Gubernaculum V-shaped* (Fig. 83). Male tail conoid, often mucronate or digitate, with 3–5 pairs of caudal papillae; with or without caudal alae.

Bionomics.—Mycophagous, soil inhabiting.

Type Species.—*Paraphelenchus pseudoparietinus* (Micoletzky, 1922)
Micoletzky, 1925

Aphelenchoididae (Skarbilovich, 1947)
Paramonov, 1953

Syn. Anomyctidae J. B. Goodey, 1960

Definition (emended).—Aphelenchoidea. Stylet with knobs ranging from absent, to slightly thickened, to well-developed. Esophagus with overlapping glands. Spicules characteristically rosethorn-shaped; gubernaculum-like structures present or absent; caudal alae absent or short, terminal. Phytophagous, mycophagous, predaceous; soil or marine inhabiting, also insect associate.

Type Genus.—*Aphelenchoides* Fischer, 1894

Aphelenchoides Fischer, 1894

(Fig. 4, 5, 8, 9, 14, 15, 17, 28, 31, 34, 35, 40, 41, 52, 73, 74, 75, 76, 77, 78, 90, 91, 92, 93, 94, 95, 96)

Syn. *Pseudaphelenchoides* Drozdovsky, 1967
Asteroaphelenchoides Drozdovsky, 1967

Definition.—Aphelenchoididae. Body slender, length variable. Lips often slightly offset. *Stylet with basal knobs.* Oocytes in one or more rows; postuterine sac usually well-developed, length variable. *Spicules paired, rosethorn-shaped, not fused, rostrum usually prominent.* Male tail without caudal alae or gubernaculum; with 3 pairs of ventro-

submedian papillae. Tails of both sexes never elongate-filiform, but usually more or less tapering, conical and frequently ending in one or more mucrons.

Bionomics.—Phytophagous, mycophagous, soil inhabiting.

Type Species.—*Aphelenchoides kuehnii*
Fischer, 1894

Bursaphelenchus Fuchs, 1937

(Fig. 3, 32, 69, 98)

Syn. *Aphelenchoides* (*Bursaphelenchus*)
(Fuchs, 1937) Rühm, 1956

Definition.—Aphelenchoididae. Usually long. Lips high, offset. Stylet with small rounded basal knobs. Excretory pore usually behind median bulb. Vulval lips sometimes protruding; postuterine sac usually long. Female tail rounded, conoid, or sharply pointed. *Spicules large, narrow, usually with prominent rostrum. Male tail strongly arcuate, variously pointed, with short, terminal caudal alae.* Usually 2 pairs of caudal papillae, 1 adanal, the other postanal. Gubernaculum absent.

Bionomics.—Mycophagous, insect associate.

Type Species.—*Bursaphelenchus piniperdae* Fuchs, 1937

Cryptaphelenchus (Fuchs, 1937)

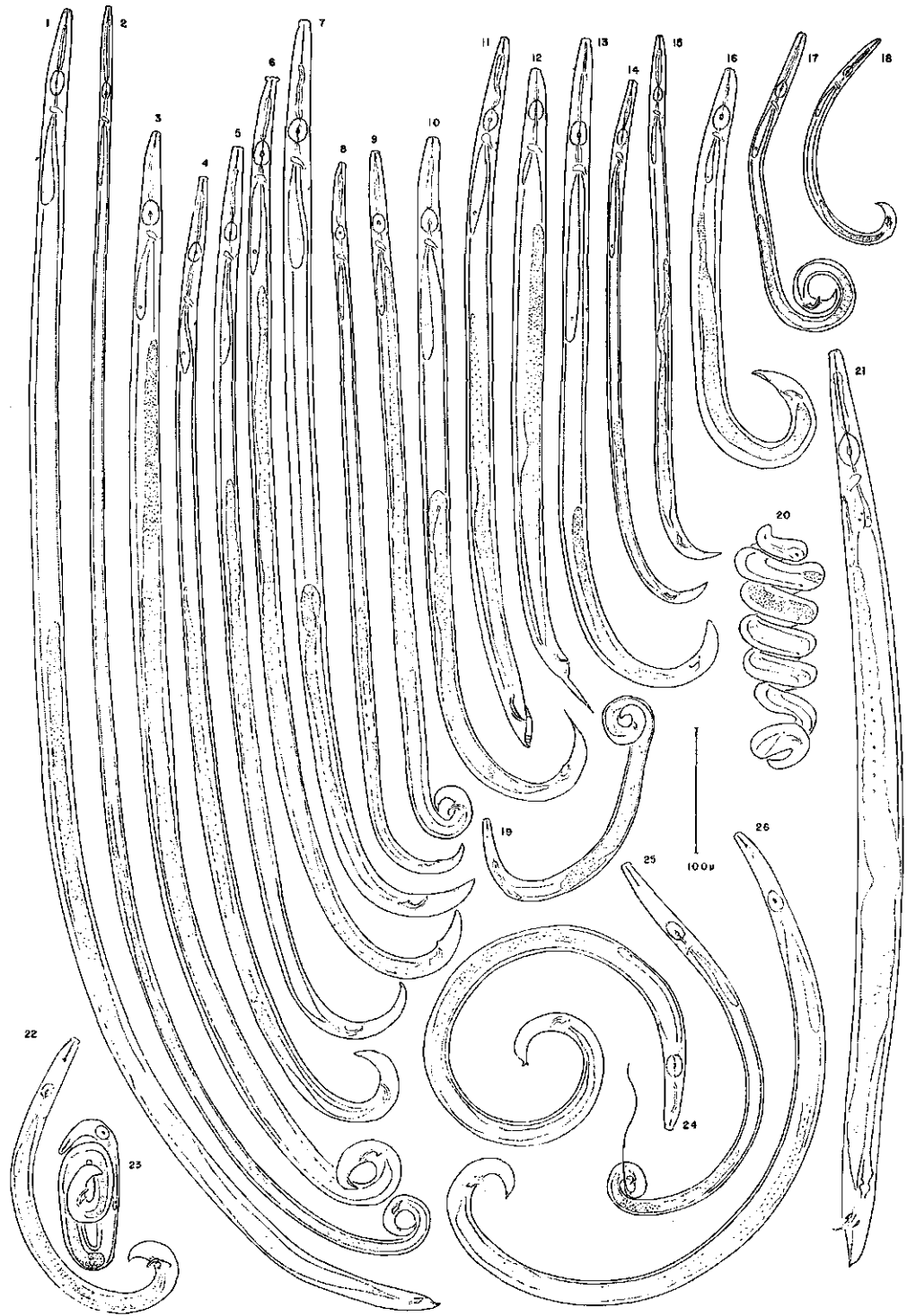
Rühm, 1954

(Fig. 18, 48, 71, 102)

Syn. *Parasitaphelenchus* (*Cryptaphelenchus*)
Fuchs, 1937

Parasitaphelenchus (*Steineria*) Fuchs, 1937
(nec *Steineria* Micoletzky, 1922)

Definition.—Aphelenchoididae. *Very small, 180–500 μ long, C-shaped, not particularly slender (a = about 20).* Lips rounded, forming cap, offset. Stylet delicate, shaft somewhat thickened with small rounded basal knobs. Ovary short; vulval lips not protruding; postuterine sac absent. Female tail conical. *Spicules paired, not fused, with prominent narrow rostrum.* Small gubernac-



ulum-like structure present. Male tail gradually attenuated to point; with at least 2 pairs of caudal papillae; caudal alae absent.

Bionomics.—Unknown, insect associate.

Type Species.—*Cryptaphelenchus macrogaster* (Fuchs, 1915) Rühm, 1956

Cryptaphelenchoides J. B. Goodey, 1960

(Fig. 13, 50, 55, 101)

Definition.—Aphelenchoidea. Cuticle strongly annulated. Lips offset, rounded, high. Stylet long, without basal knobs, similar to that of *Ektaphelenchus*. Esophageal valves large, usually located in posterior part of median bulb. *Vagina walls strongly cuticularized; postuterine sac short*. Female tail bluntly rounded. Spicules paired, not fused, with prominent rostrum and large, broad apex, ventral element continuing line of shaft. *Small, cuticularized, gubernaculum-like structure present; caudal alae absent*. Male tail bluntly rounded, with 3 pairs of caudal papillae.

Bionomics.—Unknown, insect associate.

Type Species.—*Cryptaphelenchoides macrobulbosus* (Rühm, 1956) J. B. Goodey, 1960

Ektaphelenchus (Fuchs, 1937) Skrjabin et al., 1954

(Fig. 6, 29, 58, 88)

Syn. *Parasitaphelenchus* (*Ektaphelenchus*)

Fuchs, 1937

Ectaphelenchus Rühm, 1956

Definition.—Aphelenchoidea. Long nematodes. *Lips large, offset, caplike, wider than neck region*. Stylet not less than 15 μ ,

shaft with or without basal knobs. Vulval lips not protruding; postuterine sac present, length variable. Tail conical to sharp or rounded point. *Spicules paired, not fused, scooped, trough-like, with delicate rostrum*, ventral element continuing line of shafts, caudal alae and gubernaculum absent. Tail short, conical, with 2–3 pairs of caudal papillae.

Bionomics.—Unknown, insect associate.

Type Species.—*Ektaphelenchus hylastophilus* (Fuchs, 1930) Skrjabin et al., 1954

Huntaphelenchoides n. gen.

(Fig. 16, 46, 66, 87)

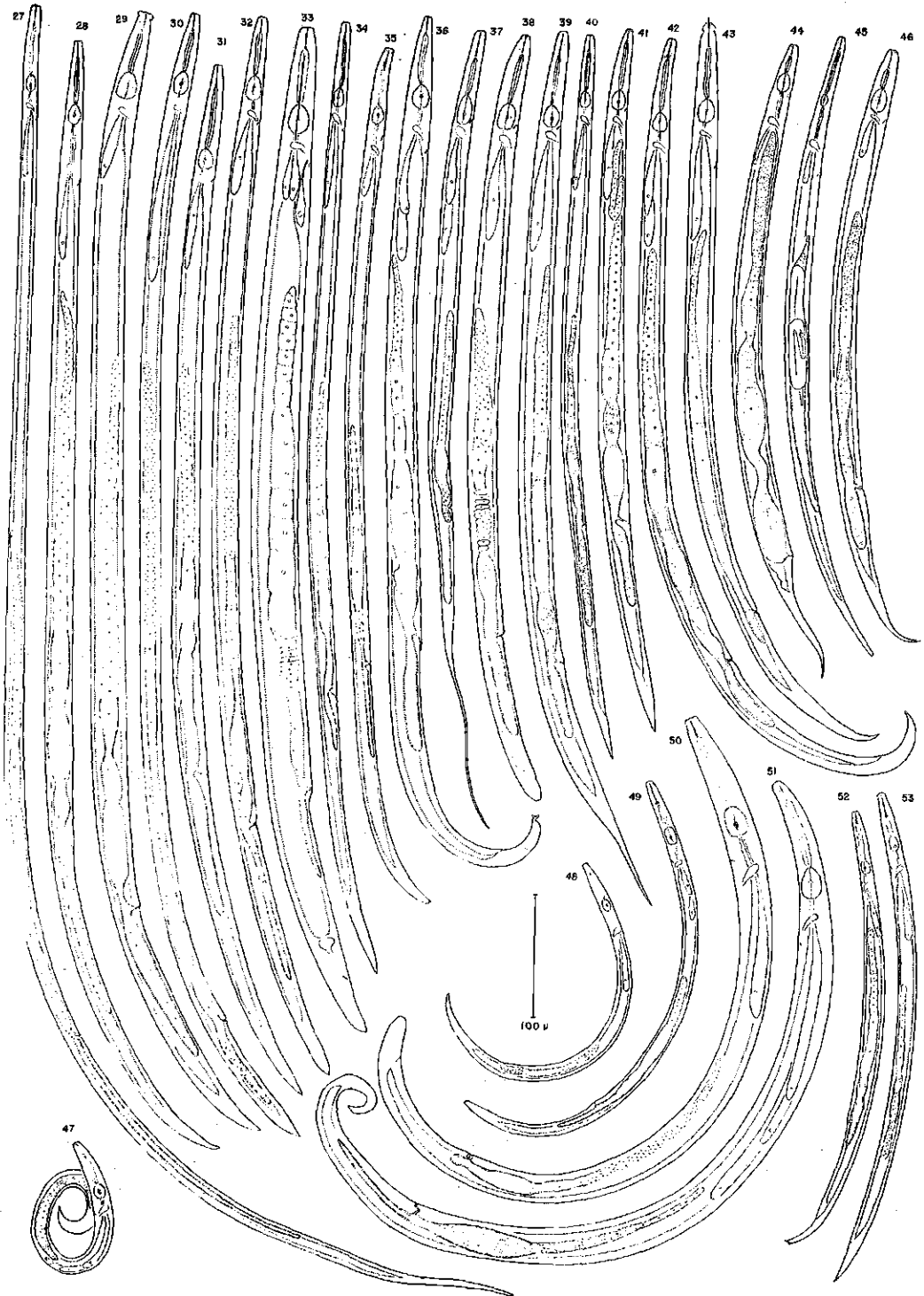
Definition.—Aphelenchoidea. Lips slightly offset. Stylet delicate, 11–14 μ long, with small basal knobs. Esophageal glands short. Postuterine sac long; may be ovoviparous. Female tail conical, tapering to rounded tip. *Spicules paired, not fused, wide, with prominent rostrum*. *Tip of sclerotized portion of ventral element appears to terminate some distance posterior to and separated from tip of dorsal element*, similar to that of *Parasitaphelenchus* and *Rhadinaphelenchus*. Male tail shorter than that of female, more conical, with 2 pairs of caudal papillae and with short terminal caudal alae. Gubernaculum absent.

Bionomics.—Unknown, probably mycophagous.

Type Species.—*Huntaphelenchoides huntii* (Steiner, 1935) n. comb.

Syn. *Aphelenchoides huntii* Steiner, 1935

←
PLATE 1, Fig. 1–26. Males of the Aphelenchoidea, full body (all drawings original). 1. *Parasitaphelenchus gallagheri*. 2. *Rhadinaphelenchus cocophilus*. 3. *Bursaphelenchus xylophilus*. 4. *Aphelenchoides ritzemabosi*. 5. *Aphelenchoides blastophthorus*. 6. *Ektaphelenchus brachycephalus*. 7. *Anomyctus xenurus*. 8. *Aphelenchoides subtennis*. 9. *Aphelenchoides saprophilus*. 10. *Seinura tenuicaudata*. 11. *Aphelenchus avenae*. 12. *Sheraphelenchus entomophagus*. 13. *Cryptaphelenchoides macrostylus*. 14. *Aphelenchoides besseyi*. 15. *Aphelenchoides fragariae*. 16. *Huntaphelenchoides huntii*. 17. *Aphelenchoides bicaudatus*. 18. *Cryptaphelenchus* sp. 19. *Roveaphelenchus jonesi*. 20. *Peraphelenchus* sp. 21. *Paraphelenchus* sp. 22. *Schistonchus caprifici*. 23. *Praecocilenchus raphidophorus*. 24. *Laimaphelenchus penardi*. 25. *Paraseinura musicola*. 26. *Tylaphelenchus* sp.



Male.—L = 0.360–0.740 mm; W = 18.9–21.4 μ ; Stylet = 11.8–13.4 μ ; a = 18.9–28.0; b = 6.8–11.1; c = 17.7–21.1; Spicule L = 15.9–16.8 μ .

Female.—L = 0.390–0.830 mm; W = 16.8–25.2 μ ; Stylet = 12.1–13.8 μ ; a = 21.1–29.0; b = 8.5–11.0; c = 9.2–13.2; V = 67.1–83.0%.

Male (Lectotype).—L = 0.452 mm; W = 21.4 μ ; Stylet = 13.0 μ ; a = 21.1; b = 7.2; c = 18.0; Spicule L = 16.0 μ .

Male received in 1934 by G. Steiner from diseased bulb of *Lilium tigrinum* intercepted by Plant Quarantine Inspector N. R. Hunt in a shipment from Japan. Slide T-152t (lecto) deposited in the USDA Nematode Collection, Beltsville, Maryland.

Paralectotypes.—3 males and 4 females, same data as lectotype. Slides T-752p (paralecto), T-753p (paralecto), T-754p (paralecto) deposited in USDA Nematode Collection, Beltsville, Maryland, USA; one male and one female paralectotypes deposited in University of California Nematode Survey Collection, Davis, California, USA and Canada National Nematode Collection, Ottawa, Canada.

Mass Collection Number 322 deposited in USDA Nematode Collection, Beltsville, Maryland.

Laimaphelenchus Fuchs, 1937

(Fig. 24, 36, 72, 89)

Definition.—Aphelenchoididae. Lips rounded, offset. Stylet with or without basal knobs. Excretory pore usually about 2 body

widths behind median bulb. *Vulva with flap*; vagina sloping forwards from vulva; postuterine sac long, about halfway to anus. *Tails of both sexes conical; terminus suddenly narrowing dorsally to short, narrow, cylindrical isthmus before ending in 4 stalked, fringed tubercles*. Males rare. Testis tip may be flexed slightly. Spicules paired, not fused, similar to that of *Aphelenchoides ritzemabosi*. Male tail with 3 pairs of caudal papillae; caudal alae and gubernaculum absent.

Bionomics.—Predaceous.

Type Species.—*Laimaphelenchus moro* Fuchs, 1937

Megadorus J. B. Goodey, 1960

(Fig. 49, 81)

Definition.—Aphelenchoididae. Small, 0.5 mm long. Body well annulated. Lips offset. Head skeleton, pharynx, guiding ring well cuticularized. *Stylet robust, with large rounded basal knobs*. Esophageal valve plates just posterior to middle of bulb. Nerve ring and excretory pore one body width behind median bulb. Vulval lips slightly protruded; postuterine sac long. Tail short, conical, tip rounded, without mucrons. Male unknown.

Bionomics.—Unknown, soil inhabiting.

Type Species.—*Megadorus megadorus* (Allen, 1941) J. B. Goodey, 1960

Parasitaphelenchus Fuchs, 1929

(Fig. 1, 30, 70, 85)

Syn. *Aphelenchoides* (*Parasitaphelenchus*) Fuchs, 1937

Definition.—Aphelenchoididae. Very long, slender. Lips clearly offset. Stylet

←
PLATE 2, Fig. 27–53. Females of the Aphelenchoidea, full body (all drawings original). 27. *Rhadinaphelenchus cocophilus*. 28. *Aphelenchoides ritzemabosi*. 29. *Ektaphelenchus brachycephalus*. 30. *Parasitaphelenchus gallagheri*. 31. *Aphelenchoidesblastophthorus*. 32. *Bursaphelenchus xylophilus*. 33. *Paraphelenchus* sp. 34. *Aphelenchoides besseyi*. 35. *Aphelenchoides subtenuis*. 36. *Laimaphelenchus penardi*. 37. *Paraseinura musicola*. 38. *Aphelenchus avenae*. 39. *Seinura tenuicaudata*. 40. *Aphelenchoides fragariae*. 41. *Aphelenchoides saprophilus*. 42. *Tylaphelenchus* sp. 43. *Anomyctus xenurus*. 44. *Sheraphelenchus entomophagus*. 45. *Roveaphelenchus jonesi*. 46. *Huntaphelenchoides huntii*. 47. *Praecocilenchus rhabdiphorus*. 48. *Cryptaphelenchus* sp. 49. *Megadorus megadorus*. 50. *Cryptaphelenchoides macrostylus*. 51. *Peraphelenchus* sp. 52. *Aphelenchoides bicaudatus*. 53. *Schistonchus caprifici*.

relatively long and slender, with small basal knobs. Vulva posterior 85–90%, body often narrowing abruptly posterior to vulva; postuterine sac long. Female tail short, conical. Spicules paired, apparently fused along shafts, rostrum prominent, ventral element well-developed continuing line of shaft. Tip of sclerotized portion of ventral element appears to terminate some distance from tip of dorsal element, similar to that of *Huntaphelenchoides* and *Rhadinaphelenchus*. Male tail short, conical, sometimes with offset tip and short terminal caudal alae; with 3 pairs of caudal papillae. Gubernaculum absent. Larvae usually with cuticular projections at anterior and posterior ends of body.

Bionomics.—Unknown, insect associate.

Type Species.—*Parasitaphelenchus uncinatus* (Fuchs, 1929) Fuchs, 1929

Rhadinaphelenchus J. B. Goodey, 1960

(Fig. 2, 27, 67, 86)

Definition.—Aphelenchoidea. Very long, very slender ($a =$ about 100). Lips high, slightly offset. Stylet with well-developed knobs. Median esophageal bulb about twice as long as wide, with valve posterior to center. Vulva with wide overlapping flap; postuterine sac very long, extending about $\frac{3}{4}$ distance to anus. Female tail elongated to small rounded terminus. Spicules paired, small, with elongated apex and prominent rostrum; tip of ventral element of spicule extending slightly back over posterior portion; tip of sclerotized portion of ventral element appears

to terminate some distance from tip of dorsal element, similar to that of *Parasitaphelenchus* and *Huntaphelenchoides*. Tail strongly arcuate, with 4 pairs of caudal papillae; with short terminal caudal alae.

Bionomics.—Phytophagous.

Type Species.—*Rhadinaphelenchus cocophilus* (Cobb, 1919) J. B. Goodey, 1960

Ruehmaphelenchus J. B. Goodey, 1963

Definition.—Aphelenchoidea. Body long, slender. Lips high, rounded, offset. Stylet with small basal knobs. Vulval lips protruding; postuterine sac long. Female tail short, dome-shaped, with terminal spike. Spicules paired, not fused, each with triangular ventral flange. Male tail with finer terminal spike, with 3 pairs of caudal papillae; caudal alae and gubernaculum absent.

Bionomics.—Unknown, insect associate.

Type Species.—*Ruehmaphelenchus martinii* (Rühm, 1955) J. B. Goodey, 1963

Schistonchus (Cobb, 1927) Fuchs, 1937

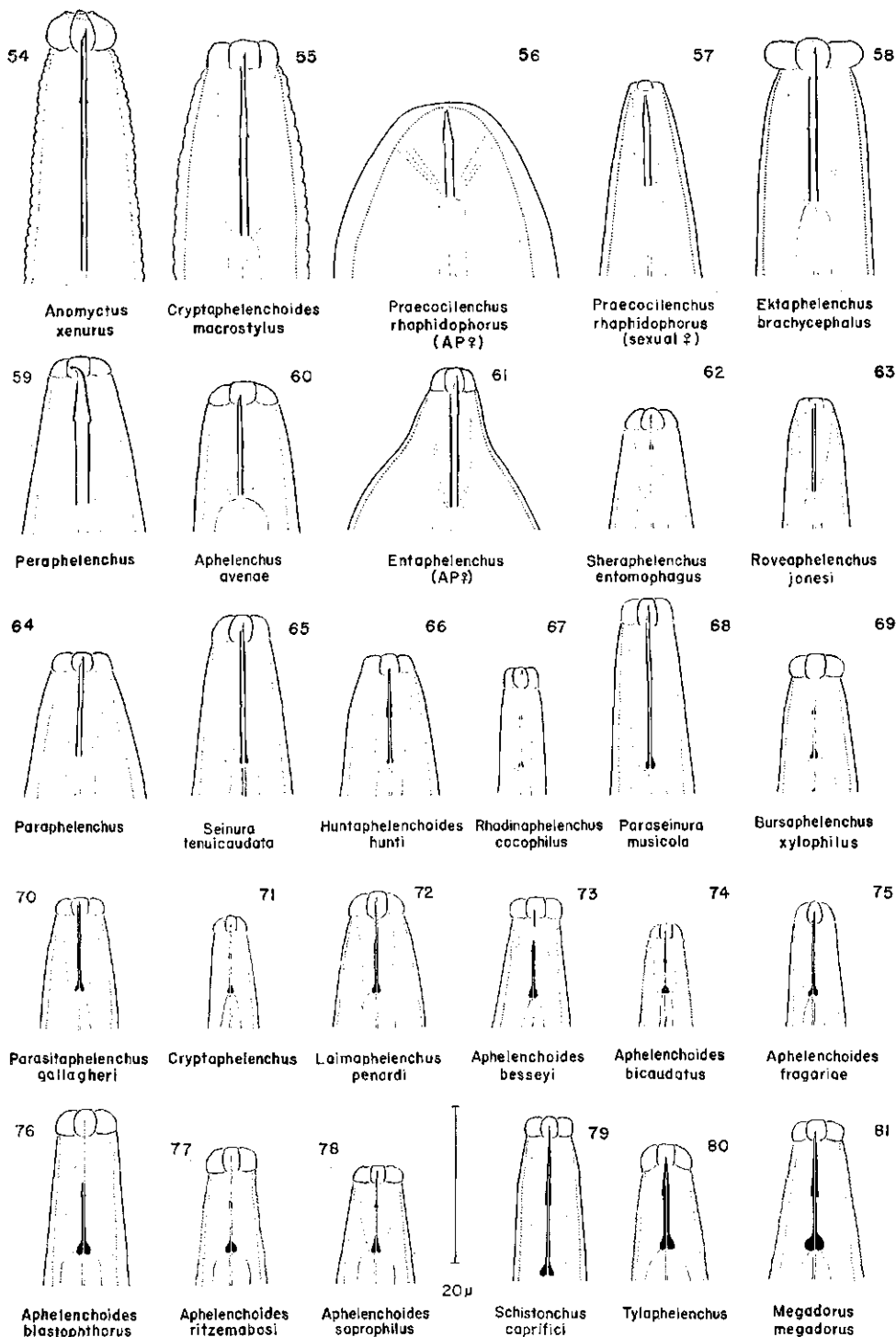
(Fig. 22, 53, 79, 100)

Syn. *Aphelenchus* (*Schistonchus*) Cobb, 1927

Definition.—Aphelenchoidea. Small. Male C-shaped, female slightly ventrally arcuate. Lips high, offset. Stylet long, robust, with well-developed basal knobs. Median esophageal bulb with valves just posterior to center. Uterus short; postuterine sac short. Tail conical, attenuated to sharp point. Spic-

→

PLATE 3, Fig. 54–81. Female stylets of the Aphelenchoidea (all drawings original). 54. *Anomyctus xenurus*. 55. *Cryptaphelenchoides macrostylus*. 56. *Praecocilenchus raphidophorus* (A. P. ♀). 57. *Praecocilenchus raphidophorus* (sexual ♀). 58. *Ektaphelenchus brachycephalus*. 59. *Peraphelenchus* sp. 60. *Aphelenchus avenae*. 61. *Entaphelenchus* sp. 62. *Sheraphelenchus entomophagus*. 63. *Roveaphelenchus jonesi*. 64. *Paraphelenchus* sp. 65. *Seinura tenuicaudata*. 66. *Huntaphelenchoides hunti*. 67. *Rhadinaphelenchus cocophilus*. 68. *Paraseinura musicola*. 69. *Bursaphelenchus xylophilus*. 70. *Parasitaphelenchus gallagheri*. 71. *Cryptaphelenchus* sp. 72. *Laimaphelenchus penardi*. 73. *Aphelenchoides besseyi*. 74. *Aphelenchoides bicaudatus*. 75. *Aphelenchoides fragariae*. 76. *Aphelenchoides blastophorus*. 77. *Aphelenchoides ritzemabosi*. 78. *Aphelenchoides saprophilus*. 79. *Schistonchus caprifici*. 80. *Tylaphelenchus* sp. 81. *Megadorus megadorus*.



ules paired, not fused, with wide elongated apex, prominent rostrum, dorsal element hooked. Gubernaculum-like structure present beneath spicules. Tail strongly arcuate; with 2–3 pairs of caudal papillae; caudal alae absent; terminus of male tail with ventral fingerlike projection.

Bionomics.—Unknown, insect associate.

Type Species.—*Schistonchus caprifici* (Gasparrini, 1864) Cobb, 1927

Seinura Fuchs, 1931

(Fig. 10, 39, 65, 104)

Definition.—Aphelenchoididae. *Tails* of both sexes usually variously elongate-filiform, not short-conical. Lips high. Stylet slender, 10–27 μ long, basal knobs absent or with small basal thickenings. Median esophageal bulb oblong to long-oval, with prominent posteriorly located valve plates. Postuterine sac present or absent. *Spicules* paired, not fused, similar to those of *Aphelenchoides*, but with elongated apex and prominent rostrum. Dorsal wall of spicule pouch thickened, cuticular. Male tail arcuate, with 2–4 pairs of caudal papillae; caudal alae absent.

Bionomics.—Predaceous.

Type Species.—*Seinura mali* Fuchs, 1931

Paraseinura Timm, 1960

(Fig. 25, 37, 68, 103)

Definition.—Aphelenchoididae. *Tails* of both sexes long, filiform, with exceedingly fine posterior portion. Lips somewhat rounded, not offset. Stylet long, anterior pointed part with prominent ventral slant, appearing jointed; shaft with slightly thickened basal knobs. Median esophageal bulb with posteriorly located valves. Postuterine sac short. Testis short. Spicules paired, not fused, with prominent rostrum and apex, more robust than that of *Seinura*. Gubernaculum-like structure small, posterior to cloacal wall, apex rounded, same refractivity as spicules. *Male tail* coiled once when relaxed;

with 3 pairs of caudal papillae; caudal alae absent. Otherwise similar to *Seinura*.

Bionomics.—Unknown, probably predaceous.

Type Species.—*Paraseinura musicola* Timm, 1960

Sheraphelenchus Nickle, 1970

(Fig. 12, 44, 62, 84)

Definition.—Aphelenchoididae. Lips slightly offset. Stylet without knobs. Esophageal glands short. Anterior part of gonad in both sexes usually with 3 cells across. *Uterus* often containing 2 or more eggs with embryos; postuterine sac absent. Female tail elongate, attenuates conically posterior to vulva, sharply pointed at tip. *Spicules* paired, apparently partially fused, slender with elongated apex and narrow rostrum, ventral element continuing less strongly along curve of shaft. *Male tail* spike-like, narrowing abruptly just posterior to spicule; 3 pairs of caudal papillae; caudal alae and gubernaculum absent.

Bionomics.—Mycophagous, insect associate.

Type Species.—*Sheraphelenchus entomophagus* Nickle, 1970

Tylaphelenchus Rühm, 1956

(Fig. 26, 42, 80, 97)

Definition.—Aphelenchoididae. Lips slightly offset, high. Stylet robust, with strongly developed tip and shaft, with strong basal knobs. Vulval lips not protruding; postuterine sac long. Spicules paired, not fused, similar to that of *Aphelenchoides*. Gubernaculum and caudal alae absent. *Tails* of both sexes conical, with ragged wedge-shaped terminus, sometimes with three pointed tips. Male with 2–4 pairs of caudal papillae.

Bionomics.—Unknown, found in moss, lichens, and bark beetle frass.

Type Species.—*Tylaphelenchus leichenicola* Rühm, 1956

Anomyctus Allen, 1940

(Fig. 7, 43, 54, 99)

Definition.—Aphelenchoidea. Rare. Cuticle strongly annulated. Lips offset; shallow, sclerotized, saucer-like frontal disc present. Six small projections surround oral opening. Stylet linear, without basal knobs, 35 μ long. Postuterine sac 1½ body widths long. Female tail conical to short terminal process. Male similar to female. Testis with anterior flexure. Spicules very large, paired, not fused, similar to those of *Aphelenchoides*. Tail conical, with short terminal process similar to that of female, with 3 pairs of caudal papillae; caudal alae and gubernaculum absent.

Bionomics.—Unknown, soil inhabiting.

Type Species.—*Anomyctus xenurus* Allen, 1940

Entaphelenchidae Nickle, 1970

Definition (emended).—Aphelenchoidea. Stylet with or without small basal knobs. Esophagus with overlapping glands. Spicules rosethorn-shaped; gubernaculum and caudal alae absent. Obligate insect parasites.

Type Genus.—*Entaphelenchus* Wachek, 1955

Entaphelenchus Wachek, 1955

(Fig. 61)

Definition.—*Entaphelenchidae*. Three adult forms; small males and females not found in insect body cavity. Cuticle smooth. Lips offset. Stylet 17–22 μ long, without basal knobs. Excretory pore behind median bulb. Median esophageal bulb with large valves, just posterior to center. **Female:** Ovary with only few cells; postuterine sac short. Female tail conical with rounded tip. **Male:** Spicules paired, not fused, with large, prominent rostrum; ventral element continuing line of shaft. Male tail short, conical to rounded point, usually with 3 pairs of caudal papillae; caudal alae and gubernaculum ab-

sent. **Adult parasitic female:** Occurring in insect body cavity. Body large, swollen, 1.2–2.5 mm long. Ovary long, convoluted; oviparous; perivaginal glandular cells present around vulva. Tail often dome-shaped, with spike-like tip.

Bionomics.—Obligate insect parasites (staphylinids).

Type Species.—*Entaphelenchus oxyteli* Wachek, 1955

Peraphelenchus Wachek, 1955

(Fig. 20, 51, 59)

Definition.—*Entaphelenchidae*. Rare. Three adult forms, all found in insect body cavity. Lips slightly offset. Stylet 17–18 μ long, with wide lumen, with ventral bend at anterior end. Excretory pore about 1 body width behind median bulb. **Female:** C-shaped ventrally when relaxed. Ovary few-celled; uterus filled with sperm (as in infective stage sphaerulariids); postuterine sac long. Tail short, conical. **Male:** Corkscrew-shaped. Spicules paired, possibly fused at tips, with prominent rostrum and apex. Tail bluntly rounded with 2 pairs of postanal caudal papillae; gubernaculum and caudal alae absent. **Adult parasitic female:** Ovary short; oviparous.

Bionomics.—Obligate insect parasites (*Necrophorus*: Silphidae).

Type Species.—*Peraphelenchus necrophori* Wachek, 1955

Praecocilenchus Poinar, 1969

(Fig. 23, 47, 56, 57, 105)

Definition.—*Entaphelenchidae*. Three adult forms, all found in insect body cavity. Female and male found in uterus of adult parasitic female. Cuticle with fine annulation. Lips small, low, not offset. Stylet short (8–10 μ) with wide lumen, without basal knobs. **Female:** Very small, less than .4 mm long. Esophageal glands long, extending to mid-body. Ovary short, postuterine sac



82
Aphelenchus
avenae



83
Paraphelenchus



84
Sheraphelenchus
entomophagus



85
Parasitaphelenchus
gallagheri



86
Rhadinaphelenchus
cocophilus



87
Huntaphelenchoides
hunti



88
Ektaphelenchus
brachycephalus



89
Laimaphelenchus
penardi



90
Aphelenchoides
ritzemabosi



91
Aphelenchoides
fragariae



92
Aphelenchoides
subtrenis



93
Aphelenchoides
besseyi



94
Aphelenchoides
saprophilus



95
Aphelenchoides
blastophthorus



96
Aphelenchoides
bicaudatus



97
Tylophelenchus



98
Bursaphelenchus
xylophilus



99
Anomyctus
xenurus



100
Schistonchus
caprifici



101
Cryptaphelenchoides
macrostylus



102
Cryptaphelenchus



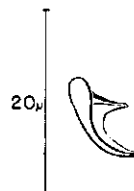
103
Paraseinura
musicola



104
Seinura
tenuicaudata



105
Praecocilenchus
raphidophorus



106
Roveaphelenchus
jonesi

short. Tail conical. *Male*: Small, .4–.5 mm long. *Spicules* paired, not fused, *rosethorn-shaped*, with prominent rostrum and apex. Tail curved, conical; caudal alae and gubernaculum absent. *Adult parasitic female*: Found in insect body cavity. Body large, swollen, C-shaped ventrally, uterus containing sexually mature males and females. Stylet short, with wide lumen, without basal knobs. Vulval lips protruding; postuterine sac absent; ovoviparous, larval nematodes reaching sexual maturity within uterus of swollen female. Tail bluntly rounded.

Bionomics.—Obligate insect parasites (*Rhynchoporus*: Cuculionidae).

Type Species.—*Praecocilenchus raphidophorus* Poinar, 1969

Roveaphelenchus Nickle, 1970

(Fig. 19, 45, 63, 106)

Definition.—Entaphelenchidae. *Three adult forms, all found in body cavity of insect*. Lips slightly offset. Stylet slender, without basal knobs. Esophageal glands short. *Female*: *Ovary with only one large larva in uterus*; postuterine sac absent. Tail cylindrical, ending in 4 mucronate points. *Male*: When relaxed, *tail remains in tight coil*. Testis flexed. Spicules paired, not fused, with prominent rostrum. Tail bluntly rounded. Caudal papillae not seen; gubernaculum and caudal alae absent. *Adult parasitic female*: Body swollen. Ovary convoluted, extending to neck region; vulva posterior (96%); ovoviparous, uterus contain-

ing pre-adult stage larvae. Tail short, digitate.

Bionomics.—Obligate insect parasites (staphylinids).

Type Species.—*Roveaphelenchus jonesi* Nickle, 1970

DISCUSSION OF MORPHOLOGY, BIOLOGY, AND TAXONOMY

Some unusual morphological and biological phenomena occur within the Aphelenchoidea which are not generally known and therefore will be discussed here. Perhaps the strangest looking member of the Aphelenchoidea is the male of *Peraphelenchus* (Fig. 20). Dr. H. E. Welch kindly sent me two male specimens and indeed they were corkscrew-shaped, as described by Wachek (42). Equally unusual, is the fact that the young of *Praecocilenchus* hatch, become adults, and mate, all within the uterus of their mother. Also, this superfamily may boast the smallest member of the Tylenchida in the genus *Cryptaphelenchus*, which ordinarily ranges from 180–360 microns in length. It obtains all its nourishment while living on excrement in the Malpighian tubules of small bark beetles.

The oldest described aphelench, *Schistonchus caprifici* (Gasparrini, 1864) Cobb, 1927, is perhaps one of the least known. It is found wrapped around the body of the small wasp, *Blastophaga psenes* (L.), which pollinates the Smyrna fig. Thorne's (40) description of this nematode is most accurate. The strong stylet, characteristic spicule, gubernaculum-like structure, fairly straight position

←

PLATE 4, Fig. 82–106. Spicules and gubernacula of the Aphelenchoidea (all drawings original). 82. *Aphelenchus avenae* (Note ventral view of gubernaculum). 83. *Paraphelenchus* sp. (Note ventral view of gubernaculum). 84. *Sheraphelenchus entomophagus*. 85. *Parasitaphelenchus gallagheri*. 86. *Rhadinaphelenchus cocophilus*. 87. *Huntaphelenchoides hunti*. 88. *Ektaphelenchus brachycephalus*. 89. *Laimaphelenchus penardi*. 90. *Aphelenchoides ritzemabosi*. 91. *Aphelenchoides fragariae*. 92. *Aphelenchoides subtenis*. 93. *Aphelenchoides besseyi*. 94. *Aphelenchoides saprophilus*. 95. *Aphelenchoides blastophthorus*. 96. *Aphelenchoides bicaudatus*. 97. *Tylaphelenchus* sp. 98. *Bursaphelenchus xylophilus*. 99. *Anomyctus xenurus*. 100. *Schistonchus caprifici*. 101. *Cryptaphelenchoides macrostylus*. 102. *Cryptaphelenchus* sp. 103. *Paraseinura musicola*. 104. *Seinura tenuicaudata*. 105. *Praecocilenchus raphidophorus*. 106. *Roveaphelenchus jonesi*.

of female when relaxed, and the unusual insect association with the fig-pollinating wasp are strong characters for a good genus. Though some workers tend to overlook this nematode systematically, the 1864 date for the species and the 1927 date for the genus give it indisputable priority. It should be considered on an equal basis with other aphelench genera.

Aphelenchs have a strong affinity for insect association. About two-thirds of the genera have either a phoretic or an obligate parasitic association with insects. The frass or borings of bark beetles may be teeming with several genera of aphelenchs and other groups. The author has collected frozen bark-beetle-infested *Ponderosa* pine logs in January in the Sierra Nevada Mountains. A day or two later, after the logs thawed, thousands of nematodes, including many aphelench genera, were collected from the frass. It is not uncommon to find a single bark beetle with several hundred larvae of *Parasitaphelenchus* in its body cavity, many specimens of a *Cryptaphelenchus* sp. in its Malpighian tubules, and some third stage larvae of *Bursaphelenchus* sp. and *Ektaphelenchus* sp. under its elytra and in the intersegmental folds. In the genera *Seinura* and *Laimaphelenchus* predation on other nematodes is known to occur [Linford (20), Hechler (16), and McBeth (21)]. There are probably others. Predation is not known to occur in the Tylenchoidea. Many aphelenchs feed on fungi associated with decaying plant material, insect frass, or on soil fungi. Nickle and McIntosh (22) showed the effect of aphelenchs on cultures of *Rhizoctonia*, *Fusarium* and *Verticillium*. *Rhadinaphelenchus cocophilus* is an internal phytoparasite of coconut palm trees in the Caribbean. The nematodes are found in large numbers in the trunks of infected trees. It is significant to note that the palm weevil may act as a carrier for this pest. *Aphelenchoides fragariae* is found in

large numbers destroying buds and young leaves of more than 40 genera of flowering plants, and is a well-known pest of strawberry, lily, fern, and peony. Two species of *Aphelenchoides* have also been found in a marine environment (41).

The aphelenchoid spicule, a very stable character, can be utilized by the systematist at both the generic and specific levels. Conceivably, the spicule may become as important in the systematics of aphelenchoid nematodes as is the male genitalia in certain insect groups. Figures 82–106 show the types of spicules of the aphelenchoid genera studied. They are all original drawings prepared at the same magnification (oil immersion) and from the same inside lateral view. The male of *Anomyctus xenurus* Allen, 1940, has the largest spicule (Fig. 99), a linear stylet, and many of the diagnostic characters which typify the female. This male, new to science, will be described in a later work. The spicule of *Rhadinaphelenchus cocophilus* is surprisingly small (Fig. 86). On the basis of the ecology of the nematodes and the morphology of the spicule and short, terminal caudal alae, the genera *Parasitaphelenchus*, *Rhadinaphelenchus*, and *Huntaphelenchoides* probably should be placed in the same subfamily instead of three different subfamilies as is the present situation.

The aphelench stylet (Fig. 54–81) is useful to the systematist at the generic and specific level because it is one of the most stable characters. Unlike the tylenchoid stylet, which is usually knobbed, aphelench stylets range, in the different genera, from unknobbed and linear (Fig. 54) to heavily knobbed and robust (Fig. 81). The anterior end of the stylet of *Peraphelenchus* (Fig. 59) is bent ventrally.

The size and shape of the median esophageal bulb are variable and are not recommended as taxonomic characters. Living aphelenchs often exhibited round median

bulbs, whereas, the same material when preserved, exhibited a rectangular shape. *Seinura* and *Roveaphelenchus* sometimes had a violin-shaped median bulb, which was a result of fixation. The location of the valves, either in the center of the bulb or posterior to the center, proved to be a fairly stable and useful character.

The overlapping esophageal glands of *Rhadinaphelenchus cocophilus* (Cobb, 1919) J. B. Goodey, 1960, are not ventrally located as illustrated by Goodey (14) but lie dorsally (Fig. 2, 27). Thorne (40) also illustrates dorsal glands for this nematode. All members of the Aphelenchoidea have dorsally overlapping esophageal glands except the genus *Paraphelenchus* in which the glands are contained within a posterior bulb.

Aphelenchus and *Paraphelenchus* have a V-shaped gubernaculum. *Schistonchus*, *Cryptaphelenchoides*, *Cryptaphelenchus*, and *Paraseinura* have cuticularized gubernaculum-like structures and *Rhadinaphelenchus* and *Seinura* have a thickening of the cuticle in this area.

Caudal alae are present in some aphelenchoid genera. Small terminal caudal alae are found in members of the genera *Rhadinaphelenchus*, *Bursaphelenchus*, *Huntaphelenchoides*, and *Parasitaphelenchus*. *Aphelenchus* has males with peloderan caudal alae with ribs resembling those of the diplogasterids and rhabditids. Baranovskaya (2) described *Paraphelenchus tritici* from the Soviet Union and illustrated narrow peloderan caudal alae and a V-shaped gubernaculum. She is correct in her observations because I too have seen these structures in various species of *Paraphelenchus*. The generic diagnosis is hereby changed from *caudal alae absent to with or without caudal alae*, and gubernaculum linear to V-shaped. Readers are referred to the excellent description of Baranovskaya.

Because the V-shaped gubernaculum, the

peloderan caudal alae with ribs, the long, slim spicules, the type of gonad in the female, and the feeding habits of both the genera *Aphelenchus* and *Paraphelenchus* are remarkably similar, I feel that the placement of these two forms in separate monotypic families hides this close relationship and serves no useful purpose. Paraphelenchidae is hereby placed in synonymy under Aphelenchidae. After studying the male of *Anomyctus*, I find that the spicule and stylet of this nematode are similar to *Aphelenchoides* and not unusual enough to warrant separate family status. Therefore the family Anomyctidae is hereby placed as a synonym of Aphelenchoididae.

The aphelenchs exhibit a wide range of tail tip shapes, which are relatively good taxonomic characters when used with moderation. They range from just ordinary tail tips to bizarre forms such as those found in the genera *Laimaphelenchus* (Fig. 36) and *Paraseinura* (Fig. 25). Nickle (23) described an unusual spike-like tail for *Sheraphelenchus entomophagus* (Fig. 12). The illustration of the female tail in Steiner's (35) description of *Parasitaphelenchus heterophallus* (Steiner, 1934) Rühm, 1956, which shows the vulva location near the anus, is not accurate; either it is incorrectly drawn, or it is not the female belonging to the figured male.

Studies of Steiner's (37) *Aphelenchoides hunti* and members of the genus *Bursaphelenchus* indicated the genus *Bursaphelenchus* contained species possessing two distinct spicule types, one of the true *Bursaphelenchus* type (Fig. 98) and the other was of *A. hunti* type (Fig. 87). For the latter group a new genus is proposed here: *Huntaphelenchoides*, with the type species *Huntaphelenchoides hunti* (Steiner, 1935) n. comb. Also included in the genus are *Huntaphelenchoides fungivorus* (Franklin and Hooper, 1962) n. comb., and *Huntaphelenchoides gonzalezi* (Loof, 1964) n. comb. These nematodes,

along with *H. hunti*, are probably transported by insects. Steiner's *A. hunti* material from tomatillo from Mexico appeared to be a different species than the one from lily from Japan. Specimens of *Huntaphelenchoides* have also been found in Great Britain, Venezuela, Peru, Hawaii, Africa, and New Zealand.

Observations on the original Steiner material of *Metaphelenchus rhopalocercus* and *M. micoletzkyi* support the action of J. B. Goodey and Hooper (15), which placed these taxa in synonymy with *Aphelenchus avenae*. These specimens have overlapping esophageal glands and, because males have never been found, Steiner's (39) hypothesis "Males, if present, with costate bursa" has no significance.

Khak (18) proposed the genus *Paraphelenchoides* to include his new species *P. capsuloplanus*, *Aphelenchoides xylophilus* Steiner and Buhner, 1934, and *Aphelenchoides limberi* Steiner, 1936. A study of the original Steiner and Buhner (36), and Steiner (38), material of *A. xylophilus* and *A. limberi*, indicates that the former should be *Bursaphelenchus xylophilus* (Steiner, 1934) n. comb. (See Fig. 3, 32, 69, 98). Due to a lack of males, *A. limberi* is difficult to place. Studies of the original female specimens indicate a close relationship with *Huntaphelenchoides hunti*. The diagnosis of *Paraphelenchoides*, as presented by Khak, contains characters common to most aphelenchs. Therefore, the status of this genus appears weak.

Studies of type material of Khan's (19) *Ektaphelenchus macrostylus* showed that this species is *Cryptaphelenchoides macrostylus* (Khan, 1960) n. comb. It has the gubernaculum-like structure (Fig. 101), the typical stylet (Fig. 55), (twice Khan's measurement), cuticularized vagina (Fig. 50), and spicule of *Cryptaphelenchoides*. The lips are not characteristic of *Ektaphelenchus*.

I find it difficult to accept the two genera of Drozdovsky (5), *Pseudaphelenchoides* and *Asteroaphelenchoides*; they are hereby placed as synonyms of *Aphelenchoides*. The first genus was proposed to include *Aphelenchoides ritzemabosi* and the other for *Aphelenchoides besseyi*. These two species fit well in the genus *Aphelenchoides*, and the character of the early embryonic divisions (up to 5 to 6 blastomeres) does not convince me that they require separate generic rank. The differences in the shape of the mucro, spicules, and the type of ovary can be accounted for within the genus *Aphelenchoides*. Drozdovsky (6) also set up the genus *Neoseinura* which is a *nomen nudum* and awaits a description and allocation of the type species.

Kakulia (17) described the genus *Devibursaphelenchus*, from the frass of *Ips typographus*. Though it looks very similar to *Cryptaphelenchoides*, specimens were not available for comparison. Unfortunately, the drawing of the spicule was rather poor.

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