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

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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 Aphelenchoidea, respectively. The genera Asteraphelenchoides 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, styles, 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.

Gasparrini (12) was the first to describe an aphelenchoid nematode, Schistonchus caprifichi (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 prodelphic ovary and posteriorly located vulva. Male with or without caudal alae; gubernaculum V-shaped; peloderan caudal alae present or absent, when present supported by ribs. Mycophagous; soil inhabiting.

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

Aphelenchidae (Fuchs, 1937) Steiner, 1949

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.**—Phytophagous, mycophagous, soil inhabiting.

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

*Aphelenchoidea* (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, 42, 73, 74, 75, 76, 77, 78, 90, 91, 92, 93, 94, 95, 96)

**Syn. Pseudaphelenchoides Drozdovskv, 1967**

*Aphelenchoides* Drozdovskv, 1967

**Definition.**—Aphelenchoidea. 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.**—Aphelenchoideidae. 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.**—Aphelenchoideidae. 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.**—Aphelenchoididae. 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

**Ektaphelenchus** Rühm, 1956

**Definition.**—Aphelenchoididae. 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.**—Aphelenchoididae. Lips slightly offset. Stylet delicate, 11–14 μ long, with small basal knobs. Esophageal glands short. Postuterine sac long; may be ooviviparous. 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 hunti (Steiner, 1935) n. comb.

**Syn.** Aphelenchoides hunti Steiner, 1935

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**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

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**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

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**Parasitaphelenchus** Fuchs, 1929

*(Fig. 1, 30, 70, 85)*

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

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

**Rhadinaphelenchus** J. B. Goodey, 1960


Bionomics.—Unknown, insect associate.

Type Species.—Rhadinaphelenchus martinitii (Rühm, 1955) J. B. Goodey, 1963

**Schistonchus** (Cobb, 1927) Fuchs, 1937

*Syn.* Aphelenchus (Schistonchus) Cobb, 1927


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 Riihm, 1956

(Fig. 26, 42, 50, 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 leicheniocola Riihm, 1956
Anomyctus Allen, 1940
(Fig. 7, 43, 54, 99)

Definition.—Aphelenchoideidae. 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 absent. 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
short. Tail conical. Male: Small, 0.4–0.5 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; ovoviviparous, larval nematodes reaching sexual maturity within uterus of swollen female. Tail bluntly rounded.

Bionomcs.—Obligate insect parasites (Rhynchoporus: Cuculionidae).

Type Species.—Praecocilenchus rhaphidophorus Poinar, 1969

Roveaphelenchus Nickle, 1970

(Fig. 19, 45, 63, 106)


Bionomcs.—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 capricorni (Gasparini, 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

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 cocoophilus 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 cocoophilus 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 Huntaphelenchoidea 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*, *Cryptaphelenchoïdes*, *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*, *Huntaphelenchoïdes*, 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 *Aphelenchoïdes* and not unusual enough to warrant separate family status. Therefore the family Anomyctidae is hereby placed as a synonym of Aphelenchoïdidae.

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) *Aphelenchoïdes huni* 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. huni* type (Fig. 87). For the latter group a new genus is proposed here: *Huntaphelenchoïdes*, with the type species *Huntaphelenchoïdes huni* (Steiner, 1935) n. comb. Also included in the genus are *Huntaphelenchoïdes fungivorus* (Franklin and Hooper, 1962) n. comb., and *Huntaphelenchoïdes 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 *Paraphelenchoids* to include his new species *P. capsuloplanus*, *Aphelenchoids xylophilus* Steiner and Buhrer, 1934, and *Aphelenchoids limberi* Steiner, 1936. A study of the original Steiner and Buhrer (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 *Paraphelenchoids*, 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 *Cryptaphelenchoids 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 *Cryptaphelenchoids*. The lips are not characteristic of *Ektaphelenchus*.

I find it difficult to accept the two genera of Drozdovsky (5), *Pseudaphelenchoids* and *Asteroaphelenchoids*; they are hereby placed as synonyms of *Aphelenchoids*. The first genus was proposed to include *Aphelenchoids ritzemabosi* and the other for *Aphelenchoids besseyi*. These two species fit well in the genus *Aphelenchoids*, 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 macro, spicules, and the type of ovary can be accounted for within the genus *Aphelenchoids*. Drozdovsky (6) also set up the genus *Neo-senura* which is a *nomen nudum* and awaits a description and allocation of the type species.

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

**Literature Cited**

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