On the Classification of the Insect Parasitic Nematodes of the Sphaerulariidae Lubbock, 1861 (Tylenchoidea: Nematoda)

W. R. NICKLE

Reprinted from PROCEEDINGS OF THE HELMINTHOLOGICAL SOCIETY OF WASHINGTON
Vol. 34, No. 1, January 1967, p. 72–94
Made in United States of America

On the Classification of the Insect Parasitic Nematodes of the Sphaerulariidae Lubbock, 1861 (Tylenchoidea: Nematoda)

W. R. NICKLE[1]

One of the first obligate tylenchid parasites of insects was described by Dufour in 1837 as *Sphaerularia bombi* from the bumblebees, *Bombus terrestris* and *Bombus hortorus*. In 1861, Lubbock proposed the family Sphaerulariaceae to contain the genus *Sphaerularia*. Other significant early contributions to the taxonomy of these forms include: Leuckart (1884), von Linstow (1890), zur Strassen (1892), Cobb (1920, 1921), Micoletzky (1922), T. Goodey (1930), Filipjev (1934), Thorne (1935), Fuchs (1915, 1929, 1933, 1938), Bovien (1937), Currie (1937), Chitwood and Chitwood (1937), Christie (1938) and Schneider (1939). More recent contributions include: T. Goodey (1953), Wachek (1955), Rühm (1956), Massey (1956, 1957, 1958, 1960, 1962), J. B. Goodey (1956, 1963), Khan (1957a, 1957b, 1960), Skarbilovich (1947, 1959), Welch (1959), and Nickle (1963a, 1963b). Fuchs, Wachek, and Rühm each published comprehensive works, and did much to clarify the systematics of this family. Bovien's publications on insect nematodes were outstanding and are classics today.

At present, 4 subfamilies, 21 genera, and 116 species are included in the Sphaerulariidae. Generally the classification is strong at the generic level, but at the specific level it is rather weak because detailed descriptions of free-living males and females are lacking. A tylenchid species can generally parasitize hosts in one genus, and unlike the mermithids, adults are found in adult hosts. Therefore, knowledge of the host aids in identification.

In several of the nematode genera the dorsal esophageal gland orifice is located at least one stylet length behind the base of the stylet or could not be found. The subventral esophageal glands may empty into the lumen of the esophagus a short distance behind the dorsal gland orifice. This led Wachek (1955) to place *Sphaerularia*, *Tripius*, and *Scatonema* in the Aphelenchoidea, though they lack the typical

[1] Research Nematologist, Crops Research Division, Agricultural Research Service, U. S. Department of Agriculture, Beltsville, Maryland. Some studies were made while the author was Research Assistant, University of California, Davis, California, and also Research Officer, Canada Department of Agriculture, Belleville, Ontario.

aphelenchoid median bulb and in all other respects appear to be tylenchoid.

Recently, I observed the dorsal esophageal gland orifice in the fourth stage female larva of *Sphaerularia bombi* and found that it was located behind the stylet in the normal tylenchoid position. Further, the presence of tylenchoid spicules and a gubernaculum in these forms also, supports their tylenchoid status. For these reasons I question the aphelenchoid status of these genera, and I now consider some of the genera placed in the Aphelenchoidea as belonging to the Tylenchoidea.

The problem inherent in making this change is that Sphaerulariaceae Lubbock, 1861 is an older family name than Allantonematidae (Pereira, 1931) Chitwood and Chitwood, 1937. In my opinion the insect parasitic Tylenchoidea merit only family rank along with the plant parasitic families; Tylenchidae, Heteroderidae, Criconematidae, Neotylenchidae, Hoplolaimidae, and Tylenchulidae. Future work in the group may necessitate the creation of a superfamily but at present, all insect-parasitic Tylenchoidea should be placed in the family Sphaerulariidae Lubbock, 1861; the Allantonematidae (Pereira, 1931) Chitwood and Chitwood, 1937 should be given the rank of subfamily.

Entaphelenchus Wachek, 1955 and *Peraphelenchus* Wachek, 1955 are endoparasitic tylenchids, having the typical aphelenchoid median bulb and spicules which are shaped like rose thorns. The gubernaculum is lacking, and in the writer's opinion, only these two genera are typical of the Aphelenchoidea.

During the last 8 years, I have studied representative specimens from 15 of the 22 genera belonging to the families Sphaerulariidae and Allantonematidae before making the revisions contained herein. It is hoped that this compilation will stimulate work in this interesting but neglected group.

Economically, insect parasitic nematodes of the Sphaerulariidae annually reduce insect populations by untold millions, and are indeed important self-perpetuating biological control agents. However, little effort has been made in manipulating, or exploiting these parasites for biological control, but the time is ripe for this type of endeavor.

Because of the brevity of the original description, the family diagnosis is emended. Brief diagnoses of the sub-families and genera are given and a new genus is established. Synonymies are presented along with my comments on the status of controversial groups.

The characters that typify the family include: absence of a valved median bulb; unique ovary of the free-living female; enlargement of female nematode in the body cavity of host, resulting in the nematode becoming a reproductive sac (heteromorphism), or female nematode with a prolapsed swollen uterus; obligate insect or mite parasitism.

FAMILY:

Sphaerulariidae Lubbock, 1861.

Syn. Sphaerulariaceae Lubbock, 1861.

DIAGNOSIS (Emended): Tylenchoidea. Usually with three distinct forms. Two free-living, slender, 0.5–1.0 mm long, often found in habitat of young host and one adult parasitic form found in haemocoel of insect or mite. (1) FL♀*: Stylet or pseudostylet rarely absent. Esophagus without median valvular bulb; ampullae near gland orifices often strongly developed; dorsal gland orifice not always found immediately behind spear, may be midway between spear and subventral gland orifices; esophageal glands long, overlap intestine. Gonad diagnostic; prodelphic; ovary small, finger-like with few oocytes; oviduct short; uterus prominent, temporarily packed with individual sperm after copulation. Becomes infective stage. Eggs absent. (2) FL♂: Usually slightly longer than female, not infective. Stylet may be absent. Esophagus weakly developed. Spicules usually tylenchoid, may be elaborate. Gubernaculum usually present. Caudal alae often present and peloderan. (3) AP♀: Obligate parasite in haemocoel of insects or mites. Large swollen reproductive sac, produced by expansion of free-living female; or, with uterus prolapsed, swollen. Stylet present or rarely absent, may be retracted. Esophagus and intestine usually degenerate at expense of reproductive system which often fills 80% of body. Oviparous or ovoviviparous; ovary usually flexed one or more times; rachis common.

* FL♀: Free-living female. FL♂: Free-living male. AP♀: Body cavity adult parasitic female.

PROPOSED CLASSIFICATION OF THE SPHAERULARIIDAE

Sphaerulariidae Lubbock, 1861.
Syn. Sphaerulariaceae Lubbock, 1861.
Sphaerulariinae (Lubbock, 1861) Pereira, 1931.
Sphaerularia Dufour, 1837.
Sphaerulariopsis Wachek, 1955.
Tripius Chitwood, 1935.
Syn. *Asconema* Leuckart, 1886.
Atractonema (Leuckart, 1886) Leuckart, 1887.
Proatractonema Bovien, 1944.
Allantonematinae Pereira, 1931. (Emended Chitwood, 1935).
Syn. Allantoneminae Pereira, 1931.
Allantonematidae (Pereira, 1931) Chitwood and Chitwood, 1937.
Contortylenchidae Rühm, 1956.
Allantonema Leuckart, 1884.
Syn. *Tylenchomorphus* Fuchs, 1915.
Aphelenchulus Cobb, 1920.
Bovienema Nickle, 1963.
Bradynema zur Strassen, 1892.
Chondronema Christie and Chitwood, 1931.
Contortylenchus Rühm, 1956.
Heterotylenchus Bovien, 1937.
Howardula Cobb, 1921.
Syn. *Tylenchinema* T. Goodey, 1930.
Prothallonema Christie, 1938.
Metaparasitylenchus Wachek, 1955. n. grad.
Neoparasitylenchus n. gen.
Parasitylenchoides Wachek, 1955.
Parasitylenchus Micoletzky, 1922.
Syn. *Polymorphotylenchus* Rühm, 1956.
Proparasitylenchus Wachek, 1955. n. grad.
Protylenchus Wachek, 1955.
Sulphuretylenchus Rühm, 1956. n. grad.
Scatonema Bovien, 1932.
Dotylaphus Andrassy, 1958. (genus inquirenda).
Fergusobiinae J. B. Goodey, 1963.
Syn. Fergusobiidae Siddiqi and J. B. Goodey, 1963.
Fergusobia Currie, 1937.
Syn. *Anguillulina* (*Fergusobia*) Currie, 1937.
Iotonchiinae T. Goodey, 1953.
Syn. Iotonchiidae (T. Goodey, 1953) Skarbilovich, 1959.
Iotonchium Cobb, 1920.

* Specimens of these genera were studied for this review.

SUBFAMILY:

Sphaerulariinae (Lubbock, 1861) Pereira, 1931.

DIAGNOSIS (Emended): Sphaerulariidae. FL♀: Stylet present, with or without knobs. Without eggs in uterus. FL♂: With tylenchoid anterior end. Stylet present, with or without knobs. Caudal alae present or absent. Spicules and gubernaculum tylenchoid. AP♀: Uterus everted partially or completely.

Genus *Sphaerularia* Dufour, 1837
(Figs. 2Z, 3V, 5A)

FL♀: Stylet present, without basal knobs. Dorsal gland orifice opens just behind stylet. FL♂: Stylet present, not prominent, without knobs. Caudal alae absent. Spicules and gubernaculum tylenchoid. AP♀: Uterus completely everted, greatly enlarged, larger and not as smooth as *Sphaerulariopsis*, becomes 15,000–20,000 times the volume of original female body which remains as a minute appendage to uterus, though often wrinkled and deformed. Oviparous.

HOST INSECTS:

Hymenoptera; *Bombus, Vespa, Psithyrus.*

TYPE SPECIES:

Sphaerularia bombi Dufour, 1837.
Syn. *Tylenchus bombi* (Dufour, 1837) Cobb, 1890.

Genus: *Sphaerulariopsis* Wachek, 1955
(Figs. 2W, 3W, 5A)

FL♀: Stylet present, well-developed, with basal knobs which may be irregular in size. Dorsal gland orifice opens anteriorly behind stylet. FL♂: Stylet present, with knobs. Caudal alae peloderan. Spicules and gubernaculum tylenchoid. AP♀: Uterus completely everted, greatly enlarged, smoother and not as large as *Sphaerularia*, original female body wrinkled and deformed, remains as an appendage to uterus. Oviparous.

HOST INSECTS:

Coleoptera; *Ernobius, Pissodes, Dendroctonus.* Hymenoptera; *Coeloides.*

TYPE SPECIES:

Sphaerulariopsis stammeri Wachek, 1955.
Syn. *Stictylus stammeri* (Wachek, 1955) Rühm, 1956.

OTHER SPECIES:

S. dendroctoni (Massey, 1956) Nickle, 1963.
Syn. *Sphaerularia dendroctoni* Massey, 1956.

S. hastatus (Khan, 1957) Nickle, 1963.
Syn. *Sphaerularia hastata* Khan, 1957.
Stictylus hastatus (Khan, 1957) Khan, 1960.

S. pini (Fuchs, 1929) Nickle, 1963.
Syn. *Tylenchus sulphureus pini* Fuchs, 1929.
Allantonema sulphureus pini (Fuchs, 1929) Filipjev, 1934.
Parasitylenchus sulphureus f. *pini* (Fuchs, 1929) Schneider, 1939.
Allantonema pini (Fuchs, 1929) Wachek, 1955.
Stictylus pini (Fuchs, 1929) Rühm, 1956.

S. piceae (Fuchs, 1929) n. comb.
Syn. *Tylenchus sulphureus piceae* Fuchs, 1929.
Allantonema sulphureus piceae (Fuchs, 1929) Filipjev, 1934.
Parasitylenchus sulphureus f. *piceae* (Fuchs, 1929) Schneider, 1939.
Stictylus sulphureus piceae (Fuchs, 1929) Rühm, 1956.

S. piniphili (Fuchs, 1929) Nickle, 1963.
Syn. *Tylenchus sulphureus piniphili* Fuchs, 1929.
Allantonema sulphureus piniphili (Fuchs, 1929) Filipjev, 1934.
Parasitylenchus sulphureus f. *piniphili* (Fuchs, 1929) Schneider, 1939.
Stictylus piniphili (Fuchs, 1929) Rühm, 1956.

S. ungulacaudus (Khan, 1957) Nickle, 1963.
Syn. *Sphaerularia ungulacauda* Khan, 1957.
Stictylus ungulacaudus (Khan, 1957) Khan, 1960.

This genus may eventually be placed under *Sphaerularia*, but is easily distinguished at this time by the smaller size of the prolapsed uterus, the knobbed stylet, the presence of the caudal alae. It is normally parasitic in bark beetles.

Fig. 1. Adult Parasitic Female Sphaerulariids. A. *Allantonema philonthi* (after Wachek, 1955); B. *Bovienema tomici* (after Nickle, 1963a); C. *Chondronema passali* (after Christie and Chitwood, 1931); D. *Fergusobia tumifaciens* (after Currie, 1937, in part); E. *Heterotylenchus bovieni* (after Wachek, 1955); F. *Allantonema mirabile* (after Leuckart, 1887); G. *Aphelenchulus mollis* (after Cobb, 1920, in part); H. *Bradynema rigidum*; I. *Contortylenchus elongatus* (after Nickle, 1963b); J. *Heterotylenchus stammeri* (after Wachek, 1955); K. *Protylenchus heteroceri* (after Wachek, 1955); L. *Howardula benigna*; M. *Howardula aptini* (after Nickle and Wood, 1964).

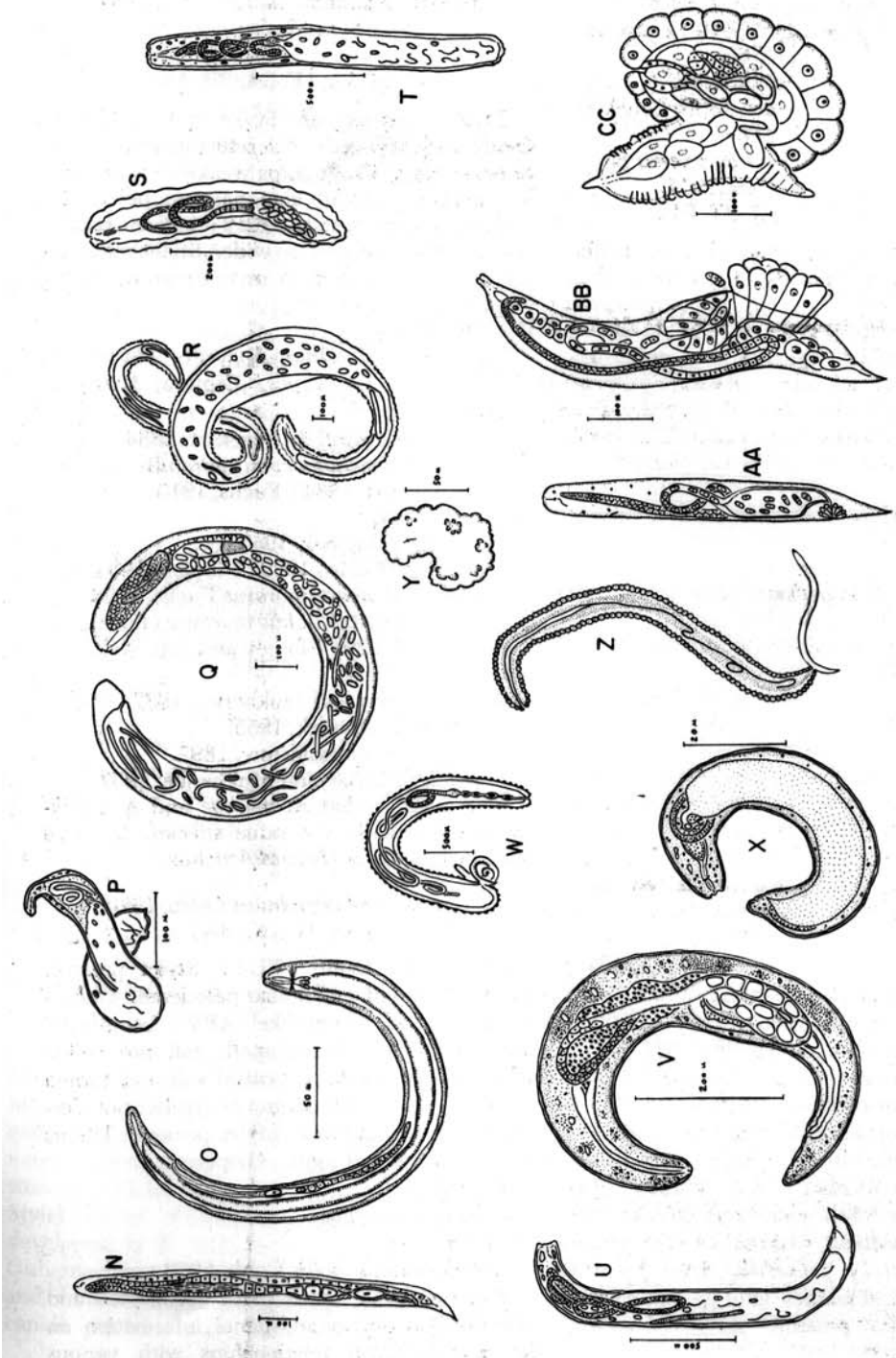

Fig. 2. Adult Parasitic Female Sphaerulariids. N. *Heterotylenchus aberrans* (after Bovien, 1937); O. *Heterotylenchus aberrans* (after Bovien, 1937); P. *Proparasitylenchus medonis* (after Wachek, 1955); Q. *Neoparasitylenchus* sp.; R. *Sulphuretylenchus* sp.; S. *Metaparasitylenchus mycetophagi* (after Wachek, 1955); T. *Metaparasitylenchus cryptophagi* (after Wachek, 1955); U. *Parasitylenchoides paromali* (after Wachek, 1955); V. *Parasitylenchus curvidentis* (after Rühm, 1956); W. *Sphaerulariopsis stammeri* (after Wachek, 1955); X. *Parasitylenchus typographi* (after Rühm, 1956); Y. *Parasitylenchus curvidentis* (after Rühm, 1956); Z. *Sphaerularia bombi* (after Leuckart, 1887); AA. *Scatonema wilkeri* (after Bovien, 1932); BB. *Tripius sciarae* (after Bovien, 1944); CC. *Tripius gibbosus* (after Leuckart, 1887).

Genus: *Tripius* Chitwood, 1935
Syn. *Asconema* Leuckart, 1886.
Atractonema (Leuckart, 1886) Leuckart, 1887.
Proatractonema Bovien, 1944.
(Figs. 2BB, 2CC, 3Q, 3Y, 5A)

FL♀: Stylet well-developed, with knobs. Two long esophageal glands. Ovary few-celled; walls of uterus with large cells; vulva posterior. FL♂: Stylet faintly developed, without knobs. Caudal alae absent. Spicules and gubernaculum small, tylenchoid. AP♀: Fusiform. Length up to 0.9 mm. Uterus partially prolapsed. Mouth cone and tail papilla present. Stylet present, not retracted. Oviparous.

HOST INSECTS:
Diptera; *Cecidomyia* or *Dasineura, Bradysia, Sciara.*

TYPE SPECIES:
Tripius gibbosus (Leuckart, 1886) Chitwood, 1935.
Syn. *Asconema gibbosum* Leuckart, 1886.
Atractonema gibbosum (Leuckart, 1886) Leuckart, 1887.

OTHER SPECIES:
Tripius sciara (Bovien, 1944) Wachek, 1955.
Syn. *Proatractonema sciara* Bovien, 1944.

Poinar (1965) has shown that the morphological basis for the genus *Proatractonema* may be just a stage in the development of a *Tripius* and he considers *Proatractonema* as a synonym of *Tripius*.

SUBFAMILY:
Allantonematinae Pereira, 1931. (Emended Chitwood, 1935).
Syn. Allantoneminae Pereira, 1931.
Allantonematidae (Pereira, 1931) Chitwood and Chitwood, 1937.
Contortylenchidae Rühm, 1956.

DIAGNOSIS (Emended): Sphaerulariidae. FL♀: With or without stylet. Without eggs in uterus. FL♂: With tylenchoid anterior end. Stylet usually present, with or without knobs. Caudal alae usually peloderan when present, not voluminous. Spicules and gubernaculum tylenchoid, when present. AP♀: Swollen, uterus not everted.

Genus: *Allantonema* Leuckart, 1884
Syn. *Tylenchomorphus* Fuchs, 1915.
(Figs. 1A, 1F, 3A, 3B, 4A)

FL♀: Lips set off. Stylet well-developed. Ovary with few cells. Excretory pore posterior to nerve ring. FL♂: Lips weakly set off. Stylet present. Caudal alae narrow, peloderan. Gubernaculum small. AP♀: Bean-shaped, only 2–3 times as long as wide. Stylet retracted into body. Oviparous or ovoviviparous. Vulva terminal.

HOST INSECTS:
Coleoptera; *Hylobius, Hylastes, Philonthus, Ochthebius, Geotrupes.* Diptera; *Musca.*

TYPE SPECIES:
Allantonema mirabile Leuckart, 1884.
Syn. *Tylenchomorphus mirabilis* (Leuckart, 1884) Fuchs, 1915.

OTHER SPECIES:
A. matthesi Wachek, 1955.
A. morosa (Fuchs, 1929) Filipjev, 1934.
Syn. *Tylenchus morosus* Fuchs, 1929.
Parasitylenchus morosus (Fuchs, 1929) Filipjev and Sch. Stek., 1941.
A. muscae Roy and Mukherjee, 1937.
A. philonthi Wachek, 1955.
A. silvaticum von Linstow, 1892.
A. stricklandi Roy and Mukherjee, 1937.

It is possible that *A. muscae* and *A. stricklandi* are actually the same species, i.e., two female stages of a *Heterotylenchus.*

Genus: *Aphelenchulus* Cobb, 1920
(Figs. 1G, 3C, 4A)

FL♀: Not found. FL♂: Stylet present. Length 1 mm. Caudal alae peloderan. Gubernaculum small, trough-like. AP♀: Length 2.6 mm. Swollen, worm-shaped; tail not coiled when relaxed by heat, ventral side not turned outward. Tail with diagnostic spike; not dorsally bent, papilliform. Stylet present. Uterus containing several eggs. Oviparous.

HOST INSECT:
Coleoptera; *Cyllene.*

TYPE SPECIES:
Aphelenchulus mollis Cobb, 1920.

This nematode needs to be recollected and restudied to obtain additional information on its morphological relationships with various

groups in the family. The shape of the AP♀, which aids in separating this genus from *Contortylenchus*, is shown in Fig. 1G.

Genus: *Bovienema* Nickle, 1963
(Figs. 1B, 3D, 4A)

FL♀: Small. Stylet well-developed. FL♂: Stylet present. With peloderan caudal alae. Gubernaculum present. AP♀: Length 0.5–0.75 mm. Body swollen, habit in the form of a tight circle, with externally turned ventral side, see *Contortylenchus*. Tail tip characteristically peg-like, directed dorsally. Stylet always present, well-developed, not retracted. Intestine not differentiated. Oviparous. Gonad with 2 or 3 flexures, one anterior in neck region, one posterior in vicinity of vulva; one to three eggs in uterus at one time.

HOST INSECT:
Coleoptera; *Pityogenes*.

TYPE SPECIES:
Bovienema tomici (Bovien, 1937) Nickle, 1963.
Syn. *Aphelenchulus tomici* Bovien, 1937.
Contortylenchus tomici (Bovien, 1937) Rühm, 1956.

OTHER SPECIES:
Bovienema chalcographi (Fuchs, 1938) n. comb.
Syn. *Parasitylenchus contortus chalcographi* Fuchs, 1938.
Parasitylenchus contortus f. *chalcographi* (Fuchs, 1938) W. Schneider, 1939.
Contortylenchus chalcographi (Fuchs, 1938) Rühm, 1956.

Genus: *Bradynema* zur Strassen, 1892
(Figs. 1H, 3E, 4A)

FL♀: With smooth cuticle. Lips faintly set off. Stylet absent. Stomal region faintly cuticularized. Esophageal glands well-developed, extending almost to the genital area. Intestine narrow-celled, used for storage. FL♂: With smooth cuticle. Lips not distinctly set off. Stylet absent. Caudal alae absent or faintly developed in *B. trixagi*. Spicules tylenchoid. Gubernaculum always present. AP♀: Cuticle and hypodermis traversed by small narrow canals. Metabolic products white. Head and tail drawn in by expansion. Stylet absent. Vulva with distinct lips; ovary and oviduct short; uterus occupies up to 85% of body. Ovoviviparous.

HOST INSECTS:
Coleoptera; *Aphodius, Spondylis, Throscus*. Hemiptera; *Gerris, Velia, Nepa*. Diptera; *Bibio*.

TYPE SPECIES:
Bradynema rigidum (von Siebold, 1836) zur Strassen, 1892.
Syn. *Filaria rigida* von Siebold, 1836.
Allantonema rigida (von Siebold, 1836) Moniez, 1891.

OTHER SPECIES:
B. bibionis Wachek, 1955.
B. gerridis Poisson, 1933.
B. nepal Poisson, 1933.
B. strasseni Wülker, 1923.
B. trixagi Wachek, 1955.
B. veliae Poisson, 1933.

Genus: *Chondronema* Christie and Chitwood, 1931
(Figs. 1C, 4D)

Head with 4 distinct papillae. Stylet small, tylenchoid. Dorsal esophageal gland present. Amphidial openings lateral, slightly nearer mouth than papillae; amphidial glands large. Esophagus without bulb-like swelling. A pair of large lateral pores on the tail. Male with small caudal alae; without gubernaculum. Testis reflexed. Body of female degenerating into nearly structureless sac filled with developing embryos. Body-cavity parasites throughout larval development, but free-living throughout adult stage.

HOST INSECT:
Coleoptera; *Passalus*.

TYPE SPECIES:
Chondronema passali (Leidy, 1852) Christie and Chitwood, 1931.
Syn. *Nematoideum passali* Leidy, 1852.

The life history of this nematode differs from the rest of the genera in the the family because only the larval stages are parasitic in the haemocoel of the insect. No AP♀'s could be found in the body cavity of the insect. Christie and Chitwood described the adult

forms as free-living, and found them in the frass of the beetles. Larval nematodes probably leave the host during oviposition. There is no reference to the type of gonad in the female, but a small tylenchoid stylet is present. The morphology and life history of the adult forms need more study.

Genus: *Contortylenchus* Rühm, 1956
(Figs. 1I, 3F, 4A)

FL♀: Stylet usually well-developed, tip symmetrical, lumen narrow, basal knobs variable, usually prominent. Small postuterine sac. Ovary with fewer cells than in neoparasitylenchs; vulva posteriorly located, with small opening, without projecting lips. FL♂: Stylet present, dimorphic. Testis with flexure. Tail bulkier, shorter than in neoparasitylenchs; rounded, always with peloderan caudal alae, usually narrow. Spicules small, tylenchoid. Gubernaculum small. AP♀: Sulphur to brown-yellow. Always sausage-shaped or worm-shaped; often coiled when relaxed by heat, with ventral side always turned outward; the "contortus" group of Fuchs. Body surface smooth, no body swellings; anterior end often wrinkled, narrower than rest of body in the form of a movable mouth cone with a stylet. Intestine retained, well defined from rest of tissue. Gonad may have 1 or 2 flexures; oviduct longer than in neoparasitylenchs; uterus narrow, not expanded to hypodermis; vulva subterminal, deeply recessed; vagina heavily cuticularized. Anus functionless. Tail rounded, or tapering to nipple-like papilla. Oviparous.

HOST INSECTS:

Coleoptera; *Ips, Dendroctonus, Cryphalus, Hylastes, Orthotomicus.*

TYPE SPECIES:

Contortylenchus diplogaster (von Linstow, 1890) Rühm, 1956.

Syn. *Allantonema diplogaster* von Linstow, 1890.
Tylenchus diplogaster (von Linstow, 1890) Fuchs, 1915.
Tylenchus contortus typographi Fuchs, 1914.
Parasitylenchus contortus typographi (Fuchs, 1915) Micoletzky, 1922.
Aphelenchulus contortus typographi (Fuchs, 1915) Micoletzky, 1925.
Anguillulina contortus typographi (Fuchs, 1915) Baylis and Daubney, 1926.
Aphelenchulus diplogaster (Fuchs, 1915) Filipjev, 1934.
Tylenchus contortus cembrae Fuchs, 1915.
Parasitylenchus contortus cembrae (Fuchs, 1915) Fuchs, 1929.

OTHER SPECIES:

C. acuminati Rühm, 1956.

C. amitini Rühm, 1956.

C. barberus (Massey, 1957) Rühm, 1960.
Syn. *Aphelenchulus barberus* Massey, 1957.

C. brevicomi (Massey, 1957) Rühm, 1960.
Syn. *Aphelenchulus brevicomi* Massey, 1957.

C. cryphali Rühm, 1956.
Syn. *Contortylenchus cryphali* Rühm, 1954. nomen nudum.

C. cunicularii (Fuchs, 1929) Rühm, 1956.
Syn. *Tylenchus contortus cunicularii* Fuchs, 1929.
Aphelenchulus cunicularii (Fuchs, 1929) Filipjev, 1934.
Parasitylenchus contortus f. *cunicularii* (Fuchs, 1929) W. Schneider, 1939.

C. elongatus (Massey, 1960) Nickle, 1963.
Syn. *Aphelenchulus elongatus* Massey, 1960.

C. grandicolli (Massey, 1957) Rühm, 1960.
Syn. *Aphelenchulus grandicolli* Massey, 1957.

C. laricis (Fuchs, 1929) Rühm, 1956.
Syn. *Tylenchus contortus laricis* Fuchs, 1929.
Aphelenchulus laricis (Fuchs, 1929) Filipjev, 1934.
Parasitylenchus contortus f. *laricis* (Fuchs, 1929) W. Schneider, 1939.

C. reversus (Thorne, 1935) Rühm, 1956.
Syn. *Aphelenchulus reversus* Thorne, 1935.

C. spirus (Massey, 1957) Rühm, 1960.
Syn. *Aphelenchulus spirus* Massey, 1957.

The contortylenchs have the type of ovary that is typical of the family and do not differ markedly from the rest of the genera. Therefore, Contortylenchidae Rühm, 1956, is considered a synonym of Allantonematinae.

Genus: *Heterotylenchus* Bovien, 1937
(Figs. 1E, 1J, 2N, 2O, 3I, 5B)

Four distinct forms. With alternation of gamogenetic and parthenogenetic generations. FL♀: Small, slender, about 0.5 mm long. Lips faintly set off. Stylet present, with knobs. Esophagus with overlapping glands and indistinct orifices. Anus vestigial. Vulva posterior, close to anus. FL♂: Slender, about 0.5 mm long. Stylet present, small, knobbed. Tail conical. Caudal alae absent. Spicules usually small, tylenchoid. Gubernaculum lacking or very small. *Gamogenetic female* (AP♀): Yellow-brown. Body swollen, curved, inert, much larger than the free-living stage (up to 3.00 mm); both ends rounded; or, tail with spike-like papilla. Stylet present, may be retracted into body. Intestine a syncytium. Anus vestigial. Ovary, oviduct and uterus of only moderate dimensions, outstretched; or, ovary and oviduct may lie in many convolutions. Oviparous. Eggs larger than those of parthenogenetic female. *Parthenogenetic female*: More slender (up to 1.00 mm long). Anterior end drawn in by expansion. Tail conical or dome-shaped. Stylet weakly developed. Esophagus degenerate. Ovary greatly developed, reaching into head region. Oviparous or ovoviviparous; when ovoviviparous, ovary and oviduct displaced anteriorly by uterus.

HOST INSECTS:

Diptera; *Hylemya, Musca.* Coleoptera; *Bembidion, Clivina.* Siphonaptera; *Coptopsylla, Ceratophyllus.*

TYPE SPECIES:

Heterotylenchus aberrans Bovien, 1937.

OTHER SPECIES:

H. bovieni Wachek, 1955.
H. stammeri Wachek, 1955.
H. wülkeri Wachek, 1955.
H. pawlowskyi Kurochkin, 1960.

Genus: *Howardula* Cobb, 1921
Syn. *Tylenchinema* T. Goodey, 1930.
Prothallonema Christie, 1938.
Acarinocola Warren, 1941.
(Figs. 1L, 1M, 3J, 3K, 3L, 4A)

FL♀: Stylet present. Lips faintly set off. FL♂: Stylet absent. Caudal alae narrow, peloderan. Gubernaculum present. AP♀: Length 1.2–7.0 mm. Stylet present. White, even in old age. Head and tail retracted. Oviparous or ovoviviparous. Ovary and oviduct in oviparous species coiled within body; in ovoviviparous species, crowded together in anterior section of body. Vulva posterior, almost terminal, lips protrude slightly.

HOST INSECTS AND MITES:

Coleoptera; *Diabrotica, Phyllotreta.* Diptera; *Oscinella.* Thysanoptera; *Aptinothrips, Taeniothrips, Frankliniella.* Acarina; *Parasitus, Poecilochirus, Haemogamasus, Euryparasitus, Cosmolaelaps, Acarinocola.*

TYPE SPECIES:

Howardula benigna Cobb, 1921.

OTHER SPECIES:

H. acarinorum Wachek, 1955.
H. aoronymphium Welch, 1959.
H. aptini (Sharga, 1932) Wachek, 1955.
Syn. *Tylenchus aptini* Sharga, 1932.
Anguillulina aptini (Sharga, 1932) Lysaght, 1936.
H. claviger (Warren, 1941) Wachek, 1955.
Syn. *Acarinocola claviger* Warren, 1941.
H. cuneifer (Warren, 1941) Wachek, 1955.
Syn. *Acarinocola cuneifer* Warren, 1941.
H. dubium (Christie, 1938) Nickle, 1965.
Syn. *Prothallonema dubium* Christie, 1938.
H. hirsuta (Warren, 1941) Wachek, 1955.
Syn. *Acarinocola hirsutus* Warren, 1941.
H. oscinellae (Goodey, 1930) Wachek, 1955.
Syn. *Tylenchinema oscinellae* Goodey, 1930.
H. phyllotretae Oldham, 1933.
H. terribilis (Warren, 1941) Wachek, 1955.
Syn. *Acarinocola terribilis* Warren, 1941.

This genus contains several diverse forms, and after more study it may be separated into

C. spirus (Massey, 1957) Rühm, 1960.
Syn. *Aphelenchulus spirus* Massey, 1957.

The contortylenchs have the type of ovary that is typical of the family and do not differ markedly from the rest of the genera. Therefore, Contortylenchidae Rühm, 1956, is considered a synonym of Allantonematinae.

Genus: *Heterotylenchus* Bovien, 1937
(Figs. 1E, 1J, 2N, 2O, 3I, 5B)

Four distinct forms. With alternation of gamogenetic and parthenogenetic generations. FL♀: Small, slender, about 0.5 mm long. Lips faintly set off. Stylet present, with knobs. Esophagus with overlapping glands and indistinct orifices. Anus vestigial. Vulva posterior, close to anus. FL♂: Slender, about 0.5 mm long. Stylet present, small, knobbed. Tail conical. Caudal alae absent. Spicules usually small, tylenchoid. Gubernaculum lacking or very small. *Gamogenetic female* (AP♀): Yellow-brown. Body swollen, curved, inert, much larger than the free-living stage (up to 3.00 mm); both ends rounded; or, tail with spike-like papilla. Stylet present, may be retracted into body. Intestine a syncytium. Anus vestigial. Ovary, oviduct and uterus of only moderate dimensions, outstretched; or, ovary and oviduct may lie in many convolutions. Oviparous. Eggs larger than those of parthenogenetic female. *Parthenogenetic female*: More slender (up to 1.00 mm long). Anterior end drawn in by expansion. Tail conical or dome-shaped. Stylet weakly developed. Esophagus degenerate. Ovary greatly developed, reaching into head region. Oviparous or ovoviviparous; when ovoviviparous, ovary and oviduct displaced anteriorly by uterus.

HOST INSECTS:
Diptera; *Hylemya, Musca.* Coleoptera; *Bembidion, Clivina.* Siphonaptera; *Coptopsylla, Ceratophyllus.*

TYPE SPECIES:
Heterotylenchus aberrans Bovien, 1937.

OTHER SPECIES:
H. bovieni Wachek, 1955.
H. stammeri Wachek, 1955.
H. wülkeri Wachek, 1955.
H. pawlowskyi Kurochkin, 1960.

Genus: *Howardula* Cobb, 1921
Syn. *Tylenchinema* T. Goodey, 1930.
Prothallonema Christie, 1938.
Acarinocola Warren, 1941.
(Figs. 1L, 1M, 3J, 3K, 3L, 4A)

FL♀: Stylet present. Lips faintly set off. FL♂: Stylet absent. Caudal alae narrow, peloderan. Gubernaculum present. AP♀: Length 1.2–7.0 mm. Stylet present. White, even in old age. Head and tail retracted. Oviparous or ovoviviparous. Ovary and oviduct in oviparous species coiled within body; in ovoviviparous species, crowded together in anterior section of body. Vulva posterior, almost terminal, lips protrude slightly.

HOST INSECTS AND MITES:
Coleoptera; *Diabrotica, Phyllotreta.* Diptera; *Oscinella.* Thysanoptera; *Aptinothrips, Taeniothrips, Frankliniella.* Acarina; *Parasitus, Poecilochirus, Haemogamasus, Euryparasitus, Cosmolaelaps, Acarinocola.*

TYPE SPECIES:
Howardula benigna Cobb, 1921.

OTHER SPECIES:
H. acarinorum Wachek, 1955.
H. aoronymphium Welch, 1959.
H. aptini (Sharga, 1932) Wachek, 1955.
Syn. *Tylenchus aptini* Sharga, 1932.
Anguillulina aptini (Sharga, 1932) Lysaght, 1936.
H. claviger (Warren, 1941) Wachek, 1955.
Syn. *Acarinocola claviger* Warren, 1941.
H. cuneifer (Warren, 1941) Wachek, 1955.
Syn. *Acarinocola cuneifer* Warren, 1941.
H. dubium (Christie, 1938) Nickle, 1965.
Syn. *Prothallonema dubium* Christie, 1938.
H. hirsuta (Warren, 1941) Wachek, 1955.
Syn. *Acarinocola hirsutus* Warren, 1941.
H. oscinellae (Goodey, 1930) Wachek, 1955.
Syn. *Tylenchinema oscinellae* Goodey, 1930.
H. phyllotretae Oldham, 1933.
H. terribilis (Warren, 1941) Wachek, 1955.
Syn. *Acarinocola terribilis* Warren, 1941.

This genus contains several diverse forms, and after more study it may be separated into