

7.19 Order Tylenchida Thorne, 1949

The order Tylenchida includes the largest and most economically important group of plant-parasitic nematodes. As plant parasites they have diverged to exploit all plant parts, including foliage, flowers and seeds, but mostly they attack roots. The order also includes mycophagous species, and a large group parasitizes the hemocoel of insects and mites. Several classifications and phylogenies have been proposed for tylenchids (Thorne 1949, Chitwood & Chitwood 1950, Maggenti 1971, 1981, Andr assy 1976, Skarbilovich 1978, 1980, Siddiqi 1980, 1986, 2000, Ryss & Krall 1981, Luc et al. 1987, Maggenti et al. 1987, Chizhov & Berezina 1988, Chizhov & Kruchina 1988, 1989, 1992, Ryss 1993, De Ley & Blaxter 2002, 2003, Chizhov 2004). At present, two prominent classifications of Tylenchida are in use. They differ by subdivision into suborders. Maggenti et al. (1987) recognized four suborders, the Tylenchina, Aphelenchina, Sphaerulariina and Hexatyliina; whereas Siddiqi (1980, 1986, 2000) recognized four suborders, the Tylenchina, Hoplolaimina, Criconematina and Hexatyliina but also regarded the Aphelenchida as a distinct order. In another recent classification of the phylum Nematoda proposed by De Ley & Blaxter (2002, 2004), the tylenchid nematodes are considered within the infraorder Tylenchomorpha in five superfamilies: Aphelenchoidea, Criconematoidea, Sphaerularioidea, Tylenchoidea and Myenchoidea and 16 families.

Diagnosis [embedded from Siddiqi (2000) and Andr assy (2007)]: *Secernentia*. Body shape predominantly vermiform, in females of some groups (Meloidogynidae, Heteroderidae, Tylenchulidae and others) obese or spheroid. Body size mainly ranging from 0.2 to 3 mm or longer. Cuticle usually clearly annulated, annuli occasionally wide or coarse, sometimes with short outgrowths. Amphidial apertures small, pore- or slit like (Fig. 7.192). Stylet composed of a conical and cylindrical part with three basal knobs. Orifice of dorsal pharyngeal gland located at base of stylet or immediately behind it. Pharynx typically divided into slender and cylindrical procorpus, bulb-like non-muscular or muscular, generally valvate matacorpus or median bulb, a slender isthmus crossed by a nerve ring and a basal glandular bulb with three pharyngeal glands. Males and juveniles of some parasitic genera may have a degenerate pharynx and degenerate or no stylet. Pharyngeal-intestinal valve present. Female genital trach amphidelphic or mono-prodelphic, rarely di-prodelphic. Glandular part of uterus, or custafomeria consists of three or four rows of cells. Vulva a transverse slit. Male with one

testis. Spicules paired, various in shape. Gubernaculum usually present. Bursa, or caudal alae generally present. Phasmids or phasmid-like structures present, punctiform, on or near tail or absent.

7.19.1 Origin of Tylenchida

The present classifications reflect controversy regarding the origin of Tylenchida and estimation of different evolutionary trends in this group (Baldwin et al. 2004). Filipjev (1934) was the first to propose that tylenchids originated from a rhabditid-diplogastrid ancestry. Paramonov (1962, 1970) pioneered more detailed work on phylogeny of Tylenchida, suggesting that, through a thorough study of ecological-morphological characters and ontogeny of contemporary nematodes, it is possible to deduce the phylogenetic relationships of various groups. Paramonov (1970) proposed, on the basis of evolutionary trends, that Tylenchida evolved from fungus feeding ancestors and suggested a hypothetical ancestor close to the modern *Psilenchus*. This point of view was later shared by Chizhov and Berezina (1988) and Ryss (1993). Another concept of tylenchid evolution was developed by Siddiqi (1980, 1986, 2000), who employed clado-evolutionary methods to understand the mutual relationships of the Tylenchida groups. He believed that tylenchids originated from a “Cephalobida-Oxyurida complex” and considered *Hexatylys* as being closest to the hypothetical ancestor of the Tylenchida. He also presented a cladogram that suggested relationships between tylenchid suborders. Although Chizhov and Kruchina (1988) and Ryss (1993) generally accepted Siddiqi’s classification, they differed in their proposal of phylogenetic relationships between the main tylenchid groups. Phylogenetic analysis using 18S rRNA gene sequences revealed Tylenchida and Aphelenchida as rooted within the Cephaloboidea and/or the Panagrolaimoidea (De Ley & Blaxter 2002).

In this chapter, the classification of Tylenchida is given as it has been proposed by Siddiqi (2000). The diagnoses of many taxa given here are made with some modifications from books on tylenchids by Brzeski (1998), Siddiqi (2000) and Andr assy (2007). The order Tylenchida contains 233 valid genera and 2828 valid species according to the second edition of Siddiqi’s (2000) book. Andr assy (2007) recognized 211 valid genera with a total of 2876 valid species.

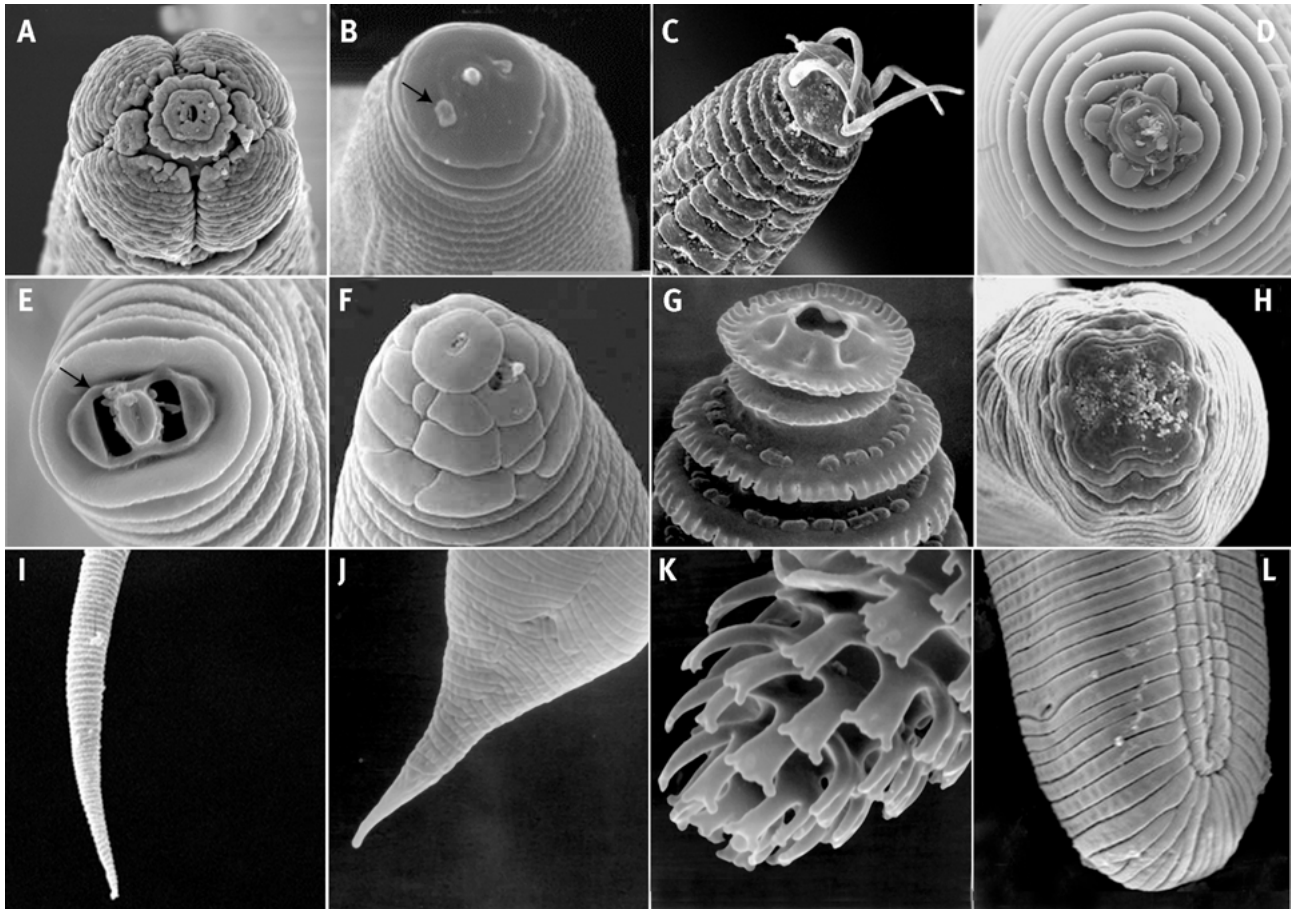


Fig. 7.192: Scanning electron microscopic photos. A–H, Head region. A, *Belonolaimus* sp. (Belonolaimidae); B, *Pratylenchus hippeastri* (Pratylenchidae); C, *Eutylenchus excretorius* (Atylenchidae); D, *Criconemoides* sp. (Criconematidae); E, *Caloosia longicaudata* (Caloosiidae); F, *Scutellonema* sp. (Hoplolaimidae); G, *Ogma* sp. (Criconematidae); H, *Ditylenchus gigas* (Anguinidae); I–L, Tail region; I, *Eutylenchus excretorius*; J, *Dolichodorus heterocephalus* (Dolichodoridae); K, *Ogma civellae* (Criconematidae); L, *Hoplolaimus stephanus* (Hoplolaimidae). Arrows point to amphid. Courtesy of Drs. I. Cid del Prado Vera (A), R. Inserra (B), P. Castillo (C, H, I), E. Van den Berg (D, E, F), J. Chitambar (G, J, K), X. Ma (L).

Key to suborders of Tylenchida

[after Siddiqi (2000)]

01a – Arthropod-parasitic cycle involving adult female in insect or mite hemocoel present; free-living mycetophagous or non-root phytoparasitic generation cycles may or may not be present; median pharyngeal bulb absent

..... **Hexatylinea**

01b – Arthropod-parasitic cycle absent; single generation cycle with only fungal or phytoparasitic form present; median pharyngeal bulb usually present

..... **2**

02a – Monodelphic with no postvulval uterine sac; phasmid or prophasid absent; spermatheca ventral to gonad axis; hypopytigma single; male pharynx degenerate

..... **Criconematina**

02b – Didelphic, if monodelphic then usually with a postvulval uterine sac; phasmid or prophasid present; spermatheca not ventral to gonad axis; hypopytigma double; male pharynx rarely degenerate

..... **3**

03a – Didelphic; phasmid present

..... **Hoplolaimina**

03b – Monodelphic; phasmid absent

..... **Tylenchina**

7.19.2 Suborder Tylenchina Chitwood in Chitwood and Chitwood, 1950

Diagnosis [After Siddiqi (2000)]: Tylenchida. Algal, fungal, moss and plant feeders. Adults without sexual dimorphism. Phasmids mainly absent. Cuticle without distinct outer and inner layers. Cuticle smooth or distinctly annulated, sometimes marked with longitudinal striae or grooves, Cephalic region smooth or annulated; framework with light, rarely heavy sclerotization. Labial plate with six inner labial sensilla, four cephalic sensilla on surface usually present. Stylet usually 10–15 µm knob small and rounded. Procorpus cylindroid or fusiform; median bulb usually muscular with refractive thickenings. Isthmus elongate, slender. Nerve ring circum-pharyngeal. Pharyngeal glands forming a basal bulb, rarely extending over intestine. Rectum and anus normally distinct. Tails elongate-tapering, filiform (Fig. 7.192 I) or short. Female reproductive system monodelphic, prodelphic, usually with a postvulval uterine sac. Crustaformeria normally with less than 20 cells arranged in a quadricolumella or tricolomella. Pharynx and stylet normally developed in male. Testis single, outstretched. Bursa simple or lobed, sometimes absent.

Two superfamilies: Tylenchoidea (Orley 1880) Chitwood & Chitwood, 1937 and Anguinoidea Nicoll, 1935

Key to superfamilies of Tylenchina

[after Siddiqi (2000), with modifications]

01a – Amphidial apertures minute
oblique slits on raised areas on
labial plate; cardia absent **Anguinoidea**

01b – Amphidial apertures not
minute oblique slits on raised
areas on labial plate but various,
modified from pore to large sinuate
slits; cardia present **Tylenchoidea**

7.19.2.1 Superfamily Tylenchoidea (Orley 1880) Chitwood & Chitwood, 1937

Diagnosis: Tylenchina. Small nematodes, usually less than 1 mm. Cephalic region variable from low flat to high. Amphidial apertures pore- or slit-like, usually extending along the lateral side of the cephalic region. Phasmids absent. Median bulb present or absent, smaller than basal

bulb, and not occupying entire body width. Tail similar between sexes, elongate-tapering, usually filiform. Bursa adanal. Postvulval uterine sac shorter than body width or, in some genera, absent. Algal and root feeders, not parasites of aboveground plant parts.

Four families: Tylenchidae Orley, 1880, Atylenchidae Skarbilovich, 1959 (Fig. 7.192 C), Ecphyadophoridae Skarbilovich, 1959, Tyldoridae Paramonov, 1967

7.19.2.1.1 Family Tylenchidae Orley, 1880

Diagnosis: Tylenchoidea. Small nematodes with annulated cuticle, with weak and slender stylet. Tails elongate, conoid to filiform, similar in both sexes. Bursa adanal and simple. More than 18% of known tylenchid species belong to this family. Associates of algae, mosses, lichens and plant roots. The family includes 29 genera grouped under five subfamilies: Tylenchinae Orley, 1880, Boleodorinae Khan, 1964, Duosulciinae Siddiqi, 1979, Thadinae Siddiqi, 1986, Tanzaniinae Siddiqi, 2000.

Genus *Tylenchus* Bastian, 1865 (Fig. 7.193 A–D)

Diagnosis: Tylenchidae, Tylenchinae. Body length 0.6–1.3 mm, often ventrally curved. Cuticle with distinct transverse striations, lateral field with four incisures, outer bands in some species areolated. Lip region may be narrower than adjacent body, finely annulated, not offset. Stylet moderately developed, mostly twice as long as labial width, with distinct knobs. Median bulb oval to spheroid, granular bulb offset from intestine. Gonad may extend anteriorly to isthmus, prodelphic. Vulval lips somewhat protruding, without lateral membranes. Males with adanal bursa. Tails similar in both sexes, elongate conoid, always curved ventrad; tail tip pointed or rounded.

Type species: *Tylenchus davainei* Bastian, 1865

Total number of species: 27

Tylenchus davainei is an abundant and widely distributed species of the genus. It is often found in the rhizosphere of many plants growing near water and also found in algae and mosses.

7.19.2.2 Superfamily Anguinoidea Nicoll, 1935

Diagnosis: Tylenchina. Small to large (0.4–3.5 mm) sized. Cephalic region low, cap-like, smooth. Small stylet less than 15 µm with small rounded knobs. Phasmids absent. Pharyngeal glands tend to be enlarged, forming a basal bulb. Cardia absent. Bursa moderately large, usually

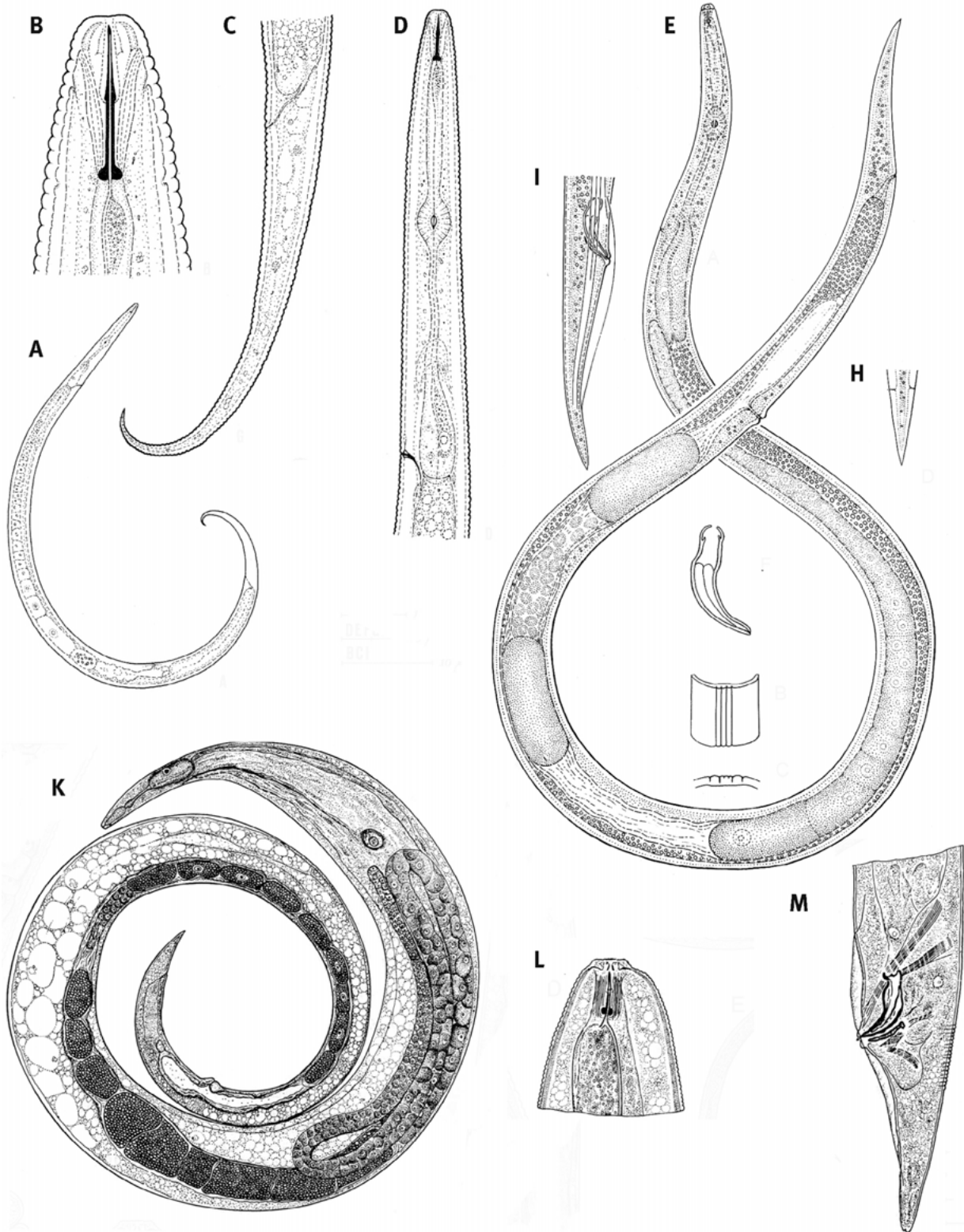


Fig. 7.193: *Tylenchulus davainei* (A–D). A, Entire female; B, Anterior end; C, Tail of females; D, Pharyngeal region. *Ditylenchus dipsaci* (E–I). E, Entire female; F, Section of cuticle at mid-body showing four incisures; G, Cross section of lateral field; H, Tail; I, Posterior portion of male; J, Spicules. *Anguina tritici* (K–M). K, Entire female; L, Head; M, Male tail. A–D after Andrassy (1977). E–J after Thorne (1945). K–M after T. Goodey (1932) with modifications.

subterminal, but may extend to terminus or be adanal. Tails usually elongate-conoid. Fungal feeders or parasites of lower and higher plants.

Two families: Anguinidae Nicoll, 1935, Sychnotylenchidae Paramonov, 1967

7.19.2.2.1 Family Anguinidae Nicoll, 1935

The family Anguinidae includes fungal feeders and parasites, attacking above ground parts of plants. Some representatives induce galls. This family differs from Tylenchidae by the mostly weak medial bulb and pharyngeal glands often overlapping intestine (Andrássy 2007). The family contains two subfamilies: Anguininae Nicoll, 1935 and Halenchinae Jairajpuri & Siddiqi, 1969.

Genus *Ditylenchus* Filipjev, 1936 (Figs 7.192 H and 7.193 E–J)

Diagnosis: Anguinidae, Anguininae. Body slender, not more than 2 mm, not curving strongly when relaxed, mature adults slender. Lateral field with four or six incisures, which may be indistinct. Median bulb muscular or non-muscular, with or without refractive thickenings. Basal bulb a thin elastic sac containing the pharyngeal glands. Ovary outstretched, oocytes in the zone of maturation in a single row. Crustaformeria in form of a quadricolumella, with four rows with four to seven cells per row; not longer than the spermatheca. Postvulval uterine sac present. Bursa adanal to subterminal, never enclosing tail tip. Tails elongate-conoid to subcylindrical or filiform. Fungal feeders and parasites of higher plants. Plant parasite species of *Ditylenchus* induce stunting and swelling in plants, but no galls.

Type species: *Ditylenchus dipsaci* (Kuhn 1957) Filipjev, 1936
Total number of species: 61

The stem and bulb nematode, *Ditylenchus dipsaci* is distributed worldwide, especially in temperate regions. It is known to attack over 450 different plant species and cause serious problems to onions, garlic, cereals, legumes, strawberries, sugar beet, carrot and many other agricultural crops as well as many horticultural plants, especially phlox, flower bulbs, such as narcissus, hyacinth and tulip. Several species of *Ditylenchus*: *D. dipsaci*, *D. africanus*, *D. angustus*, *D. destructor*, *D. myceliophagus* and *D. gigas* are among the phytonematodes of economic significance and are on the list of quarantine organisms of many countries around the world. The plant-parasitic *Ditylenchus* species completes multiple cycles within a season in plant tissues. *Ditylenchus myceliophagus* and *D. dipsaci* in a cryptobiotic state may remain viable more than 25 years and in a desiccated state they are heat and chemical resistant.

Genus *Anguina* Scopoli, 1777 (Fig. 7.193 K–M)

Diagnosis: Anguinidae, Anguininae. Females after heat relaxation are crescentic or spirally coiled. Ovary reflexed two or three times. Oocytes in the zone of maturation, usually in two or more rows (in the second-generation females of *A. agropyri*, in a single row). Crustaformeria gland is irregular and consists of 180–600 cells in 6–12 rows (20–60 cells in each of it). Up to 18 synchronous eggs present in crustaformeria gland. Infective second stage juveniles incite usually pigmented galls with an internal cavities on aboveground parts or sometimes on the rhizomes (underground stems) of monocotyledons of the family Poaceae (grasses), subfamilies Pooideae and Bambusoideae. The genus is the senior most genus in Tylenchida.

Type species: *A. tritici* (Steinbuch 1799) Filipjev, 1936

Total number of species: 21

Several species of this genus are economically important pathogens: *Anguina agrostis*, *A. funesta*, *A. pacificae*, *A. paludicola* and *A. tritici*. The wheat seed gall nematode, *A. tritici* has been recorded in major wheat-growing areas of all five continents, where it causes a disease in wheat and rye called “ear-cockle” or seed gall. This nematode reduces the yield of wheat and barley by replacing seed with galls. The ryegrass seed gall nematode, *A. funesta* is known in association with the species of coryneform bacteria of the genus *Rathayibacter*. The bacterium *R. toxicus* is responsible for a gumming disease and ryegrass toxicity resulting in an often fatal poisoning of livestock in Australia. The Pacific gall nematode, *A. pacificae* was found on grasses on *Poa annua* in several golf courses along the coast of central California, where it forms galls on the shoots of this plant and causes significant damage to golf course greens. The most species of the *Anguina* inducing a seed galls have a life cycle with one generation occurring within a growing season. The life cycle of *A. pacificae* is completed for near 32 days at a mean temperature of 20°C (McClure et al. 2008).

7.19.3 Suborder Hoplolaimina Chizhov & Berezina, 1988

Diagnosis: [after Siddiqi (2000)]. Tylenchida. This group represents the most advanced plant root parasites. Small to large nematodes approximately 0.5–2 mm long. Cuticle with distinct outer and inner layers, often strongly annulated. Lateral fields with one to six incisures reducing toward extremities. Cephalic framework well-developed, strongly sclerotized and refractive and usually with high arches. Labial disc with six labial sensilla in the form of papillae or pits present. Phasmids present. Stylet usually well developed; protractors tubular around stylet; basal

knobs prominent. Pharyngeal glands free in body cavity or enclosed in a basal bulb. Median bulb well-developed, muscular, with refractive inner thickenings. Rectum and anus distinct. Female reproductive system basically didelphic, amphidelphic; posterior branch may be reduced. Vulva a transverse slit, lip usually not modified, median or submedian, in swollen females may be located subterminally or terminally. Glandular part of uterus tri- or quadricolumellate. Ovaries outstretched in opposite direction, reflexed or coiled in obese forms. Tails usually dissimilar between sexes. Female tail generally short. Bursa usually enveloping tail, subterminal, adanal or rarely absent. Testis single, anteriorly outstretched.

Two superfamilies: Hoplolaimoidea (Filipjev 1934) Paramonov, 1967 and Dolichodoroidea Chitwood in Chitwood & Chitwood, 1950

Key to superfamilies of Hoplolaimina

[after Siddiqi (2000)]

01 – Subventral pharyngeal glands not enlarged and not extending past the dorsal gland; sexual dimorphism in anterior region present **Hoplolaimoidea**

02 – Subventral pharyngeal glands not enlarged, usually extending past the dorsal gland; sexual dimorphism in anterior region absent **Dolichodoroidea**

7.19.3.1 Superfamily Hoplolaimoidea (Filipjev 1934) Paramonov, 1967

Diagnosis: Hoplolaimina. Small to large nematodes. Sexual dimorphism in cephalic region present. Cuticle with distinct outer and inner layers. Cephalic sensilla not on surface. First cephalic annule generally divide into six sectors that may be modified. Pharyngeal glands lobed, overlapping intestine. Subventral glands enlarged, equal to or usually larger than dorsal glands; nuclei of one or both subventral glands lying posterior to that of the dorsal gland. Glandular part of uterus tricolumellate. Tails dissimilar between sexes (except for some Pratylenchidae). Male tail usually short and with a distinct hyaline terminal portion. Bursa enclosing all or most of tail, absent in forms with tail less than one anal body width long.

Families: Hoplolaimidae Filipjevi, 1934, Heteroderidae Filipjev & Schuurmans Stekhoven, 1941, Meloidogynidae

Skarbilovich, 1959, Pratylenchidae Thorne, 1949, Rotylenchulidae Husain & Khan, 1967

7.19.3.1.1 Family Hoplolaimidae Filipjevi, 1934

The Hoplolaimidae is one of the largest and economically important families. It includes migratory ectoparasites of roots. The main diagnostics characters of this family are a high labial region with a sclerotized framework, paired ovaries, phasmids either small and pore-like or large and scutellum-like; bursa large, enveloping tail, tail short.

Three subfamilies: Hoplolaiminae Filipjevi, 1934, Aphasmatylenchinae Sher, 1965, Rotylenchoidinae Whitehead, 1958

Genus *Scutellonema* Andrassy, 1958 (Figs. 7.192 F and 7.194 A–D)

Diagnosis: Hoplolaimidae, Hoplolaiminae. Small to moderately large, 0.5–1.3 mm. Lateral field with four incisures. Stylet of medium length, knob rounded. Pharyngeal glands forming short to large overlap on intestine dorsally and laterally. Phasmids enlarged, scutellum-like, located opposite or nearly opposite each other in or in close to the anal region. Bursa enveloping tail.

Type species: *Scutellonema bradys* (Steiner & LeHew 1933) Andrassy, 1958

Total number of species: 46

Scutellonema species are widely distributed in the tropical and subtropical regions of the world with the greatest species number in Africa (Sher 1963). These nematodes are primarily ectoparasites of roots and are associated with many agricultural and horticultural crops. With the exceptions of *S. bradys*, *S. cavenessi* and *S. brachyurus*, other species cause no or little economic losses to crops. The yam nematode *S. bradys* is responsible for significant yam tuber losses, especially, during storage, known as dry rot disease of yam. This nematode is considered a potential pathogen for potatoes in West Africa (Coyne et al. 2011).

Genus *Hoplolaimus* Daday, 1905 (Figs. 7.192 L and 7.194 K–N)

Diagnosis: Hoplolaimidae, Hoplolaiminae. Large sized, 1–2 mm. Labial disc distinct. Stylet massive, with compact tulip-shaped basal knobs. Phasmids large, scutellum-like, not opposite each other, one prevulval, another postvulval. Female tail hemispherical, annulated.

Type species: *Hoplolaimus tylenchiformis* Daday, 1905

Total number of species: 32

Lance nematodes parasitize a wide variety of hosts. *Hoplolaimus galeatus* is known primarily as a pest of turfgrasses in North and South America.

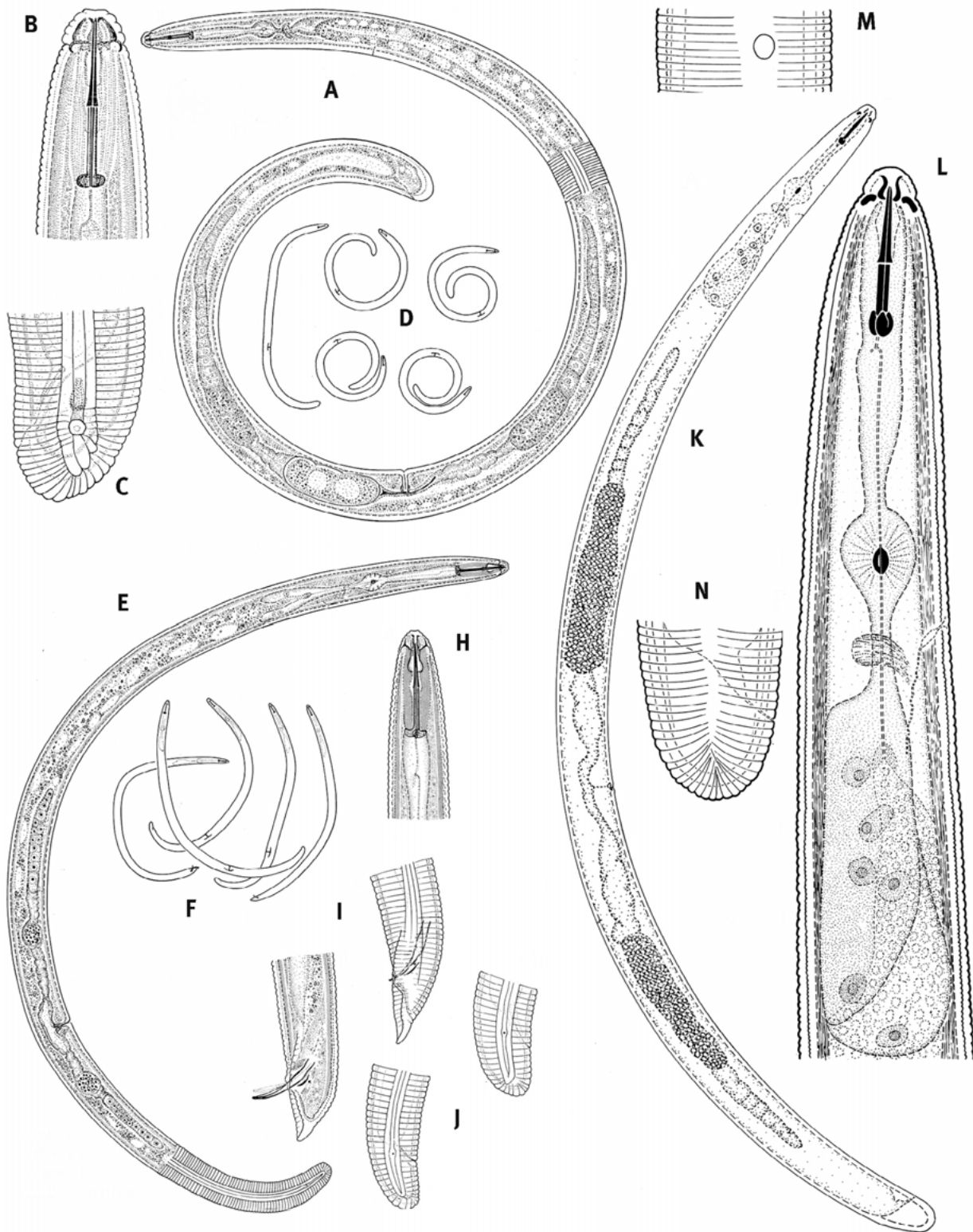


Fig. 7.194: *Scutellonema brachyurus* (A–D). A, D, Adults in relaxed body posture; B, Head; C, Tail. *Helicotylenchus multicinctus* (E–J). E, F, Adults in relaxed body postures. H, Head of female; I, Tails of males; J, Tails of females. *Hoplolaimus seinhorsti* (K–N). K, Adults in relaxed body posture; L, Pharyngeal region; M, Phasmid; N, Tail. A–D after Siddiqi (1974a); E–J after Siddiqi (1973); K–N after Van den Berg (1976) with modifications.

Genus *Helicotylenchus* Steiner, 1945 (Fig. 7.194 E–J)

Diagnosis: Hoplolaimidae, Rotylenchoidinae. Small nematodes between 0.4 and 1.2 mm long. Females generally spirally coiled. Cuticle well annulated; lateral field with four incisures. Labial region continuous or slightly offset. Stylet fairly robust. Orifice of dorsal pharyngeal gland a one-fourth to half of stylet length behind stylet. Median bulb strong. Pharyngeal glands overlapping intestine laterally and ventrally, the longest overlap on the ventral or lateral side of body. Female genital organ paired, branches opposite. Tail short, dorsally convex to hemispherical, often with terminal projection. Bursa enveloping tail.

Type species: *Helicotylenchus dihystra* (Cobb 1893) Sher, 1961

Total number of species: >190

The migratory ectoparasitic or semi-endoparasitic species of *Helicotylenchus* are globally distributed, spanning many climates, and are associated with the root system of diverse crops of agricultural importance. They are commonly called spiral nematodes because of their coiled *habitus mortis*. Five cosmopolitan species, *H. digonicus*, *H. dihystra*, *H. indicus*, *H. multicinctus* and *H. pseudorobustus*, are considered as parasites, causing growth suppression. The banana spiral nematode, *H. multicinctus*, is endoparasitic and polyphagous, but it is best known for suppressing growth and the yield of bananas in many regions of the world (De Waele & Elsen 2007).

7.19.3.1.2 Family Heteroderidae Filipjev & Schuurmans Stekhoven, 1941

The family Heteroderidae includes highly evolved plant parasites, and some of them are important agricultural pathogens. Nematodes with sexual dimorphism. The bodies of second-stage juveniles are slender and vermiform. Third- and fourth-stage juveniles and adult females are swollen and sedentary, with the anterior part of the body inside roots. Males are vermiform and free-living; however, they develop through metamorphosis within a swollen juvenile. The stylets of all juvenile stages and adults are robust. Feeding involves formation of a feeding site as a single giant cell or syncytium without gall formation. In several genera, the female body turns into a hard-walled protective cyst. Most of the eggs are generally retained within the swollen body, but also may be laid in a gelatinous matrix. In many species, the second stage juveniles remain dormant in the eggs for many years.

Three subfamilies: Heteroderinae Filipjev & Schuurmans Stekhoven, 1941 (cyst nematodes), Meloidoderinae Golden, 1971, Ataloderinae Wouts, 1973

Genus *Heterodera* Schmidt, 1871 (Figs. 7.195 E–G and 7.196 A–H)

Diagnosis: Heteroderidae, Heteroderinae. Mature female and cyst body more or less lemon-shaped, with a posterior cone (except apparently secondarily lost in *H. bamboosi*). Vulval slit terminal or sunken into cone, anus on dorsal vulval lip. Vulval slit 6–68 µm in length. Cuticle surface with zig-zag or lace-like pattern of ridges. Vulval fenestration ambifenestrate (Fig. 7.195 G), bifenestrate or absent. D-layer in cuticle rudimentary or absent. Subcrystalline layer present or absent. Anus without fenestration. Bullae and underbridge present or absent. Females are capable of producing usually up to 500 to 700 eggs. Eggs retained in body; in some cases, egg-sac also present. J2 with lateral field marked by three or four incisures, phasmids punctiform or lens-like. Several distinct morphological and molecular groups, *Afenestrata*, *Avenae*, *Cyperi*, *Goettingiana*, *Humuli*, *Sacchari* and *Schachtii*, are distinguished within this genus.

Type species: *Heterodera schachtii*

Total number of species: 81

The cyst nematode species of the genus *Heterodera* receive global attention because they have a wide distribution and impact the world's key agricultural regions. They are enormously diverse with respect to geographic and crop specialization and include several species (*H. avenae*, *H. cajani*, *H. filipjevi*, *H. goettingiana*, *H. glycines*, *H. latipons*, *H. medicaginis*, *H. schachtii* and others) that are recognized as the most important worldwide pathogens of particular key crops. The life cycle of cyst nematodes comprises the egg, four juvenile stages and the adult. The first-stage juvenile is limited to the egg; the J2 hatches from the egg while within the cyst or the gelatinous matrix that comprises egg-sacs. After penetrating into a root and establishing a feeding site, the J2 undergoes three moults to reach the adult stage. The life cycle, from egg to egg, varies depending on temperature and other environmental conditions but is usually completed in approximately 30 days. The number of generations per year also varies from one to several and depends on species.

Genus *Globodera* Skarbilovich, 1959 (Figs. 7.195 A, D and 7.196 I–O)

Diagnosis: Heteroderidae, Heteroderinae. Mature female and cyst spheroid, lacking terminal cone. Vulval area circumfenestrate. Vulva located in a cavity beneath outline of body, vulval slit <15 µm. No anal fenestra. Vaginal remnants, underbridge and bullae rarely present. Cuticle with distinct D-layer. All eggs retained in body; egg sac absent. Egg surface smooth. Male lateral field with four lines, spicules >30 µm, distally pointed. Second-stage juvenile with four incisures in lateral field. Tail conical, pointed, phasmids punctiform. *En face* pattern typically with six

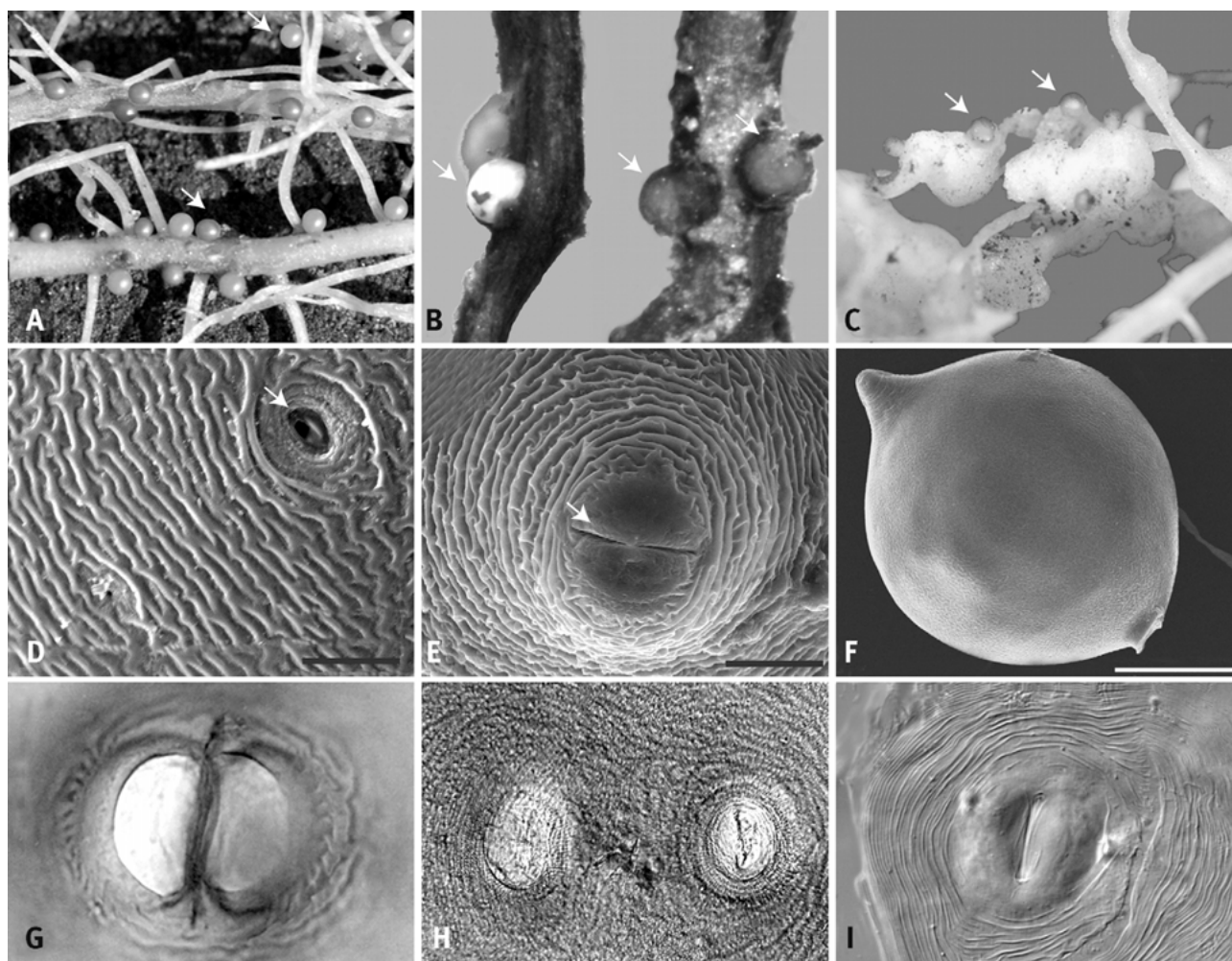


Fig. 7.195: A, Cysts of *Globodera rostochiensis* on potato roots; B, Females of *Meloidoderaalni* and *Sphaeronemaalni* on roots of *Alnusincana*; C, Females of *Meloidogyne* and root galls; D, Terminal region of *Globodera pallida*; E, Vulval cone of *Heterodera glycines* female; F, Cyst of *Heterodera zae*; G, Vulval plate of *Heterodera trifolii* (ambifenestrante); H, Vulval plate of *Punctodera punctata* (circumfenestrante); I, Perineal pattern of *Meloidogyne* sp. Arrows indicate cysts and females in A, B, C and vulval slit in D, E. Scale bars: D 15 µm; E 30 µm; F 200 µm. Courtesy of V. N. Chizhov (A–C, I) and T. Powers (D–F). G–H after Subbotin et al. (2010) with modifications.

separate lips, sometimes with fusion of adjacent submedial lips.

Type species: *Globodera rostochiensis* (Wollenweber 1923) Skarbilovich, 1959

Total number of species: 12

This genus includes potato cyst nematodes (PCN) (*G. rostochiensis* and *G. pallida*) that have been reported from many countries and are considered to be one of the most economically important pathogens of the potato. Hosts include potato, tomato, eggplant, many *Solanum* spp. and other Solanaceae. The PCN are native to South America and they have been introduced in many parts of the world, particularly in Europe, and also to the USA, Canada, New-Zealand and numerous other countries where potatoes are grown. The PCN are responsible for annual potato tuber losses of up to 9% in Europe (Evans & Stone 1977). Another species, *G. tabacum* is considered as a serious and

important pest of shade and broadleaf tobacco. It recorded from several countries in Europe, Asia, Africa, South and North America. *G. tabacum* is a polytypic species containing three subspecies: *G. tabacum tabacum*, *G. tabacum virginiae* and *G. tabacum solanacearum* (Subbotin et al. 2010).

Genus *Meloidodera* Chitwood, Hannon & Esser, 1956 (Figs. 7.195 B and 7.196 P–T)

Diagnosis: Heteroderidae, Meloidoderinae. Female oval, with a short neck. Cuticle annulated, except near vulva. Vulva median to submedian; no terminal cone. Eggs retained in body. Male slender with stylet of 20–25 µm in length. Bursa absent. Second-stage juvenile with four incisures. Tail conical, hyaline part under 36 µm long. Type species: *Meloidodera floridensis* Chitwood, Hannon & Esser, 1956

Total number of species: 9

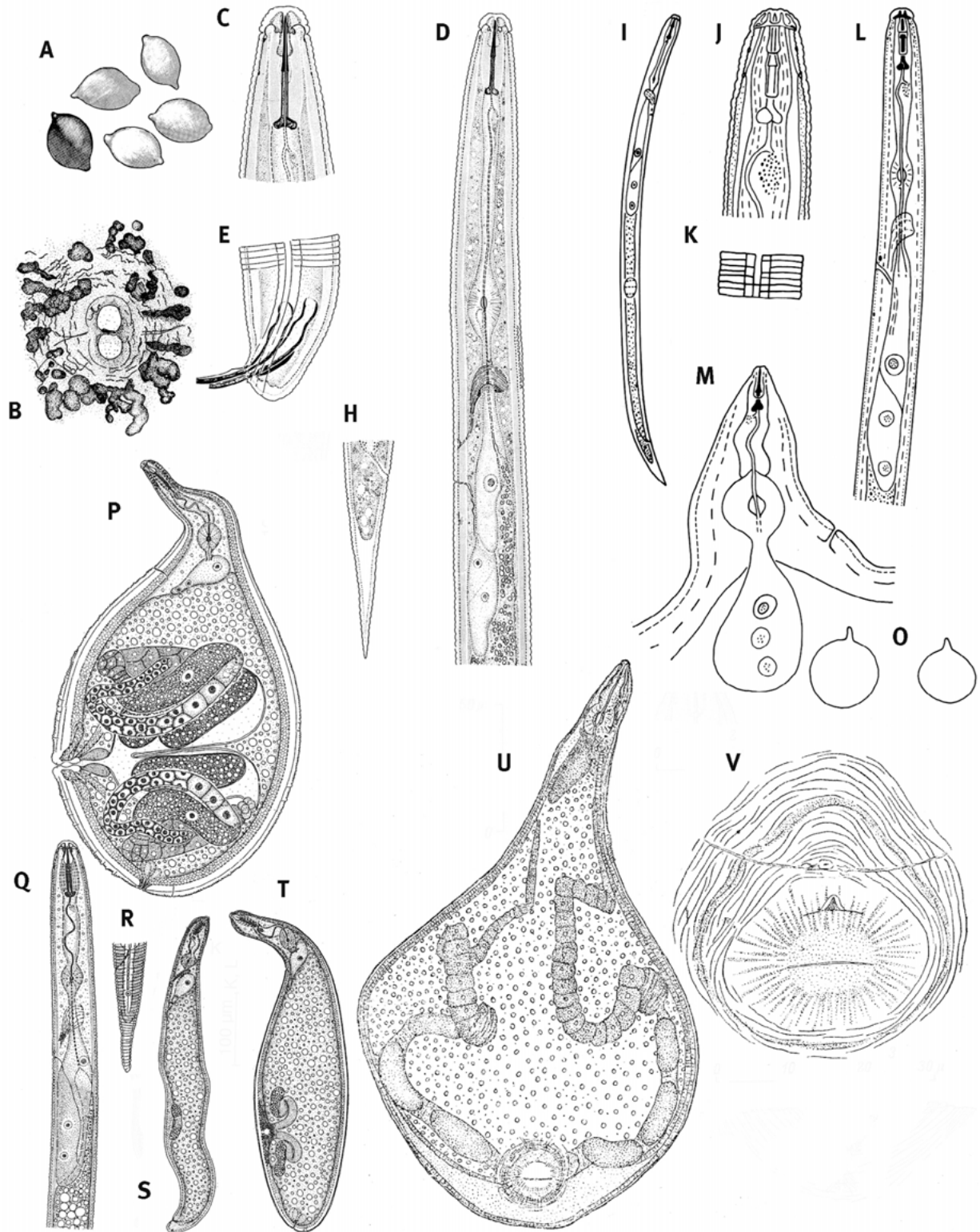


Fig. 7.196: *Heterodera avenae* (A–H). A, Cysts; B, Vulval cone; C, Anterior region of male; D, Pharyngeal region of male; E, Tail of male; F, Anterior region of J2; G, H, Tail of second-stage juvenile. *Globodera rostochiensis* (I–O). I–L, Second-stage juvenile. I, Entire body; J, Lip region; K, Lateral field; L, Pharyngeal region; M, Anterior region of female; O, Entire cysts. *Meloidodera floridensis* (P–T). P, Female; I, Pharyngeal region of second-stage juvenile; R, Tail of second-stage juvenile; S, Third-stage juvenile. T, Fourth-stage juvenile. *Meloidogyne* sp. (U, V). U, Female; V, Perineal pattern. A–G after Williams and Siddiqi (1972). I–O after Stone (1973). P–T after Hirschmann and Triantaphyllou (1973). U, V, after Kirjanova and Krall (1971), with modifications.

The non-cyst nematodes of the genus *Meloidodera* are morphologically similar to cyst and root knot nematodes, and they differ by the equatorial position of the vulva and wide distance vulva and anus. The nematode feeds from a single one-nuclear giant cell. In the Southeastern USA states *M. floridensis* is considered a pathogen of pine trees, especially, in nurseries.

7.19.3.1.3 Family Meloidogynidae Skarbilovich, 1959

The family Meloidogynidae contains very important agriculture pathogens. Nematodes induce root galls with multinucleate giant cells. Sexual dimorphism present. Mature female is swollen, sedentary, round, oval to pear-shaped with a projecting neck. No cyst stage. Vulva subterminal or terminal. Large rectal glands that secrete gelatinous matrix in which eggs are laid. Male vermiform, migratory. Tail short, lacking bursa.

Two subfamilies: Meloidogyninae Skarbilovich, 1959, Nacobboderinae Golden & Jensen, 1974

Genus *Meloidogyne* Goeldi, 1892 (Figs. 7.195 C, I and 7.196 U, V)

Diagnosis: Meloidogynidae, Meloidogyninae. Mature female white, rounded to pear-shaped body with protruding neck. Cuticle annulated posteriorly with a characteristic pattern around the anus and vulva: the perineal pattern. Mature females of root knot nematodes deposit eggs (up to 1000 or more) in an egg-sac. Male head cap with rounded labial disk, head region sometimes offset. Bursa absent. Second-stage juvenile, vermiform, infective. Body <0.6 mm with three or four incisures in the lateral field. Tail and hyaline region ranging from short to conical.

Type species: *Meloidogyne exigua* Goeldi, 1892

Total number of species: >80

Root-knot nematodes of the genus *Meloidogyne*, with the four major species being *M. javanica*, *M. arenaria*, *M. incognita* and *M. hapla*, are one of the most economically damaging genera of plant-parasitic nematodes on horticultural and field crops. They are distributed worldwide and parasitize the roots of thousands of plant species, including monocotyledonous and dicotyledonous. The second-stage juveniles penetrate into roots and cause development of root-knot galls. They undergo three moults prior to the adult stage. In roots, the second-stage juveniles induce feeding cells, coenocytes, which are hypertrophied multinucleate cells formed by repeated mitosis without cytokinesis. Root-knot nematodes exhibit a range of reproductive modes, including sexuality (amphimixis),

facultative sexuality, meiotic parthenogenesis (automixis) and mitotic parthenogenesis (apomixis). Species of *Meloidogyne* are differentiated by morphometrical and morphological characters including by the perineal pattern (Fig. 7.195 I), a unique and complex structure located in the posterior body region of females.

7.19.3.1.4 Family Pratylenchidae Thorne, 1949

Diagnosis: The family Pratylenchidae includes ecto- and endoparasitic vermiform nematodes; mature females of some genera become obese or spindle-shaped. Several genera also show a sexual dimorphism in the anterior body. Cephalic region is low. Cuticle distinctly annulated, lateral field with four or six incisures. Pharyngeal glands extending over intestine. Many species are important agriculture plant parasites.

Four subfamilies: Pratylenchinae Thorne, 1949, Hirschmanniellinae Fotedar & Handoo, 1978, Nacobbinae Chitwood in Chitwood & Chitwood, 1950, Radopholinae Allen & Sher, 1967

Genus *Pratylenchus* Filipjev, 1936 (Figs. 7.192 B and 7.197 A–F)

Diagnosis: Pratylenchidae, Pratylenchinae. Body stout, generally <1 mm, without marked sexual dimorphism in anterior region. Cuticle distinctly annulated, lateral field with four to six incisures. Lip region low, anteriorly flattened, continuous with body. Stylet massive, knobs large, rounded or anteriorly flattened. Medial bulb oval to spherical, pharyngeal glands overlapping intestine ventrally and laterally, the longest on ventral side. Genital organ prodelphic, posterior genital branch reduced to a postvulval sac with or without terminal cells. Female tail conoid to subcylindrical, terminus smooth or annulated. Bursa enveloping tail terminus.

Type species: *Pratylenchus pratensis* (de Man 1880) Filipjev, 1936

Total number of species: 85

The root lesion nematodes of the genus *Pratylenchus* (*P. brachyurus*, *P. coffeae*, *P. neglectus*, *P. penetrans*, *P. pratensis*, *P. scribneri*, *P. thornei* and others) are migratory root endoparasites that are among the most widespread and destructive phytopathogenic nematodes of agricultural crops, including bananas, cereals, coffee, corn, legumes, peanuts, potatoes and many fruits. They invade and migrate through root cortical parenchyma, producing necrotic lesions by direct feeding while providing avenues for secondary colonization by pathogenic microorganisms. The life cycle can be completed in three to four

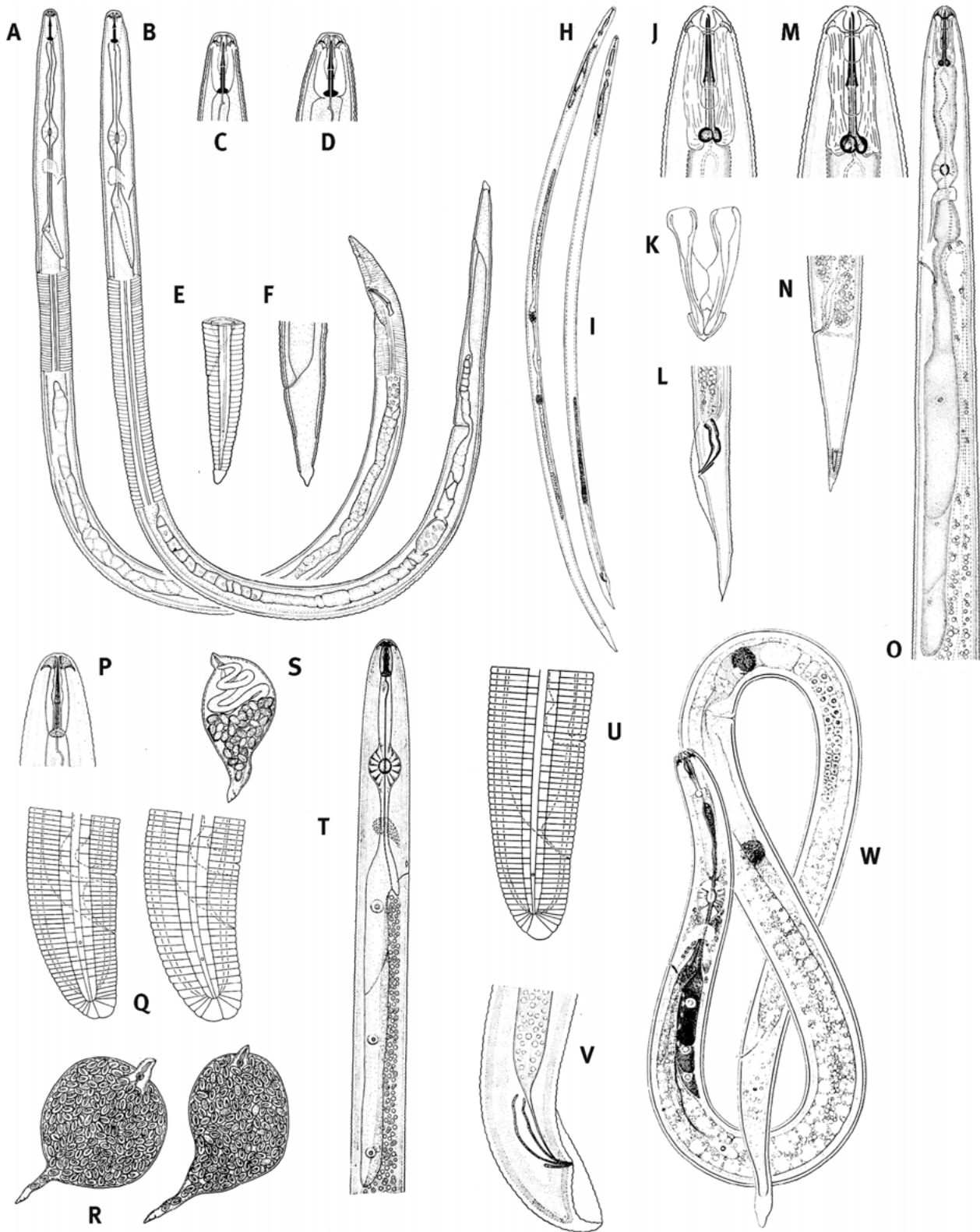


Fig. 7.197: *Pratylenchus vulnus* (A–F). A, Male; B, Female; C, Head of male; D, Head of female; E, F, Tails of females. *Hirschmanniella spinicaudata* (H–O). H, Female; I, Male; J, Head of male; K, Spicules; L, Tail of male; M, Head of female; N, Tail of female; O, Female pharyngeal region. *Nacobbus dorsalis* (P–V). P, Head of immature female; Q, U, Tails of immature females; S, R, Mature females; T, Pharyngeal region; V, Tail of male; *Radopholus similis* (W); W, Female. A–F after Corbett (1974). H–O after Luc and Fortuner (1975). P–V after Sher (1970). W after Cobb (1915), with modifications.

weeks, and nematodes can survive for several months without plant-hosts (Castillo & Vovlas 2007).

Genus *Hirschmanniella* Luc & Goodey, 1964 (Fig. 7.197 H–O)

Diagnosis: Pratylenchidae, Hirschmanniellinae. Body long, vermiform, slender, a = 40–79, from 0.9 to 4.2 mm, the longest tylenchids. Stylet strong, 15–46 µm. Cephalic region continuous, anteriorly flattened or hemispherical; framework heavily sclerotized. Cuticle finely annulated, lateral field with four incisures. Pharyngeal glands elongated, lying ventral to intestine; subventral glands asymmetrical, larger and much longer than the dorsal gland, nuclei of the three glands lying in a row, well separated from each other. Two branches of female reproductive organs equally developed and outstretched in opposite directions. Tail similar between sexes, conical, ending with small mucro. Bursa terminates shortly anterior to tail end.

Type species: *Hirschmanniella spinicaudata* (Schuurmans Stekhoven 1944) Luc & Goodey, 1964

Total number of species: 38

The genus *Hirschmanniella* has a worldwide distribution, with most of the species occurring in the warmer regions of the world but with five species described from Europe. More than 20 *Hirschmanniella* species are recognized as pathogens of rice, and nearly 60% of the world's rice fields are infected by these nematodes. *Hirschmanniella oryzae* is a well-known pathogen of rice. It causes heavy yield reductions in many paddy rice areas of the world (Bridge et al. 2005).

Genus *Nacobbus* Thorne & Allen, 1944 (Fig. 7.197 P–V)

Diagnosis: Pratylenchidae, Nacobbinae. Young female vermiform, elongate-slender, approximately 1 mm long, migratory in soil and roots. Lateral fields each with four incisures, irregularly areolated. Phasmid pore-like, anterior to middle of tail. Pharyngeal glands, extending for more than two body widths; subventral glands asymmetrical, extending past dorsal gland. Tail tapering to a broadly rounded terminus, one to two anal body widths long. Mature female body saccate tapering anteriorly, usually batatiform. Very long, tubular uterus, and a long, serpentine ovary reaching pharynx. Sedentary endoparasites inducing syncytium with root-galls. Male vermiform with well-developed cephalic sclerotization. Pharyngeal glands elongated, mostly dorsal to intestine. Male tail completely enveloped by a bursa.

Type species: *Nacobbus dorsalis* Thorne & Allen, 1944

Total number of species: 2

Nacobbus dorsalis was described from California, USA and is quite rare, whereas *N. aberrans* is an important pest of sugar beet in North America (Mexico and western USA) and of potatoes in South America.

Genus *Radopholus* Thorne, 1949 (Fig. 7.197 W)

Diagnosis: Pratylenchidae, Radopholinae. Sexual dimorphism in anterior region well observed. Cephalic framework, stylet and pharynx markedly reduced in males. Cephalic region low, continuous or slightly offset, framework strongly sclerotized in females. Lateral fields each with three to seven incisures, not areolated. Deirids absent. In females, vulva is 50%–70% of body length. Didelphic-amphidelphic. Female tail elongate-conoid to subcylindroid, usually two to four times and body width long. Endoparasites of roots.

Type species: *Radopholus similis* (Cobb, 1893) Thorne, 1949.

Total number of species: 30.

Burrowing nematode or banana-root nematode, *R. similis* is one of a few other species (*R. bridgei*, *R. duriophilus*, *R. arabocoffeae* and others) in the genus recognized as pathogens of widespread economic importance. This migratory endoparasitic nematode is an important parasite of fruit trees, banana plants, vegetables and other crops. It attacks more than 250 plant species from 16 families. *Radopholus similis* is widespread in tropical and subtropical regions of the world. All juvenile stages and adult females are infective and capable of penetrating roots. The nematode causes a lesion on the plant's root. The life cycle is completed in approximately 21 days at 25°C.

7.19.3.1.5 Family Rotylenchulidae Husain & Khan, 1967

The family includes ecto- or semi-endoparasites feeding on roots of various plants with distinct dimorphism between males and females. Mature females are swollen, immature females and males are vermiform. Males with reduced cephalic sclerotization, stylet and pharynx. Pharyngeal glands extending over intestine mainly ventrally. Female amphidelphic, rarely prodelphic. Tail in mature female short. Juveniles are vermiform with distinct or indistinct hyaline terminal portion of tail.

Three subfamilies: Rotylenchulinae Husain & Khan, 1967, Acontylinae Fotedar & Handoo, 1978, Verutinae Esser, 1981

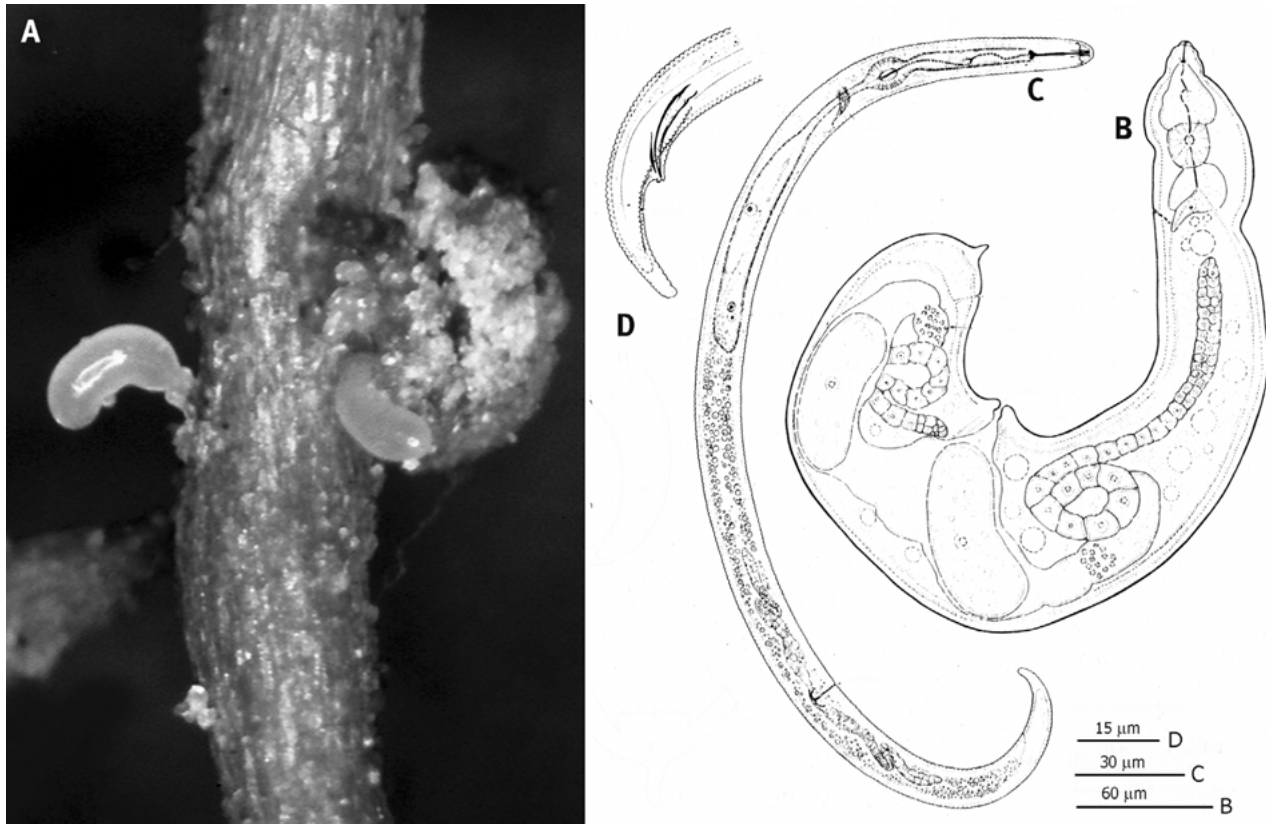


Fig. 7.198: *Rotylenchulus reniformis*. A, Mature female on root; B, Mature female; C, Immature female; D, Male tail end. A, Courtesy of C. Overstreet; B–D, after Siddiqi (1972) with modifications.

Genus *Rotylenchulus* Linford & Oliveira, 1940 (Fig. 7.198)

Diagnosis: Rotylenchulidae, Rotylenchulinae. Juveniles, males and young females vermiform, arcuate to spiral upon relaxation. Mature female kidney-shaped, with an irregular, less swollen neck, a postmedian vulva and a short, pointed tail. Orifice of dorsal pharyngeal gland usually about one stylet length behind stylet base. The female deposits eggs in a gelatinous matrix. Immature female vermiform, migratory. Ovaries paired, with double flexures. Male with weak stylet and reduced pharynx. Bursa not reaching tail tip.

Type species: *Rotylenchulus reniformis* Linford & Oliveira, 1940

Total number of species: 11

Reniform nematodes (*Rotylenchulus* spp.) are semi-endoparasites of roots of herbaceous and woody plants, mainly in tropical and subtropical regions throughout the world. *Rotylenchulus reniformis* is considered to be an agricultural pathogen that causes a major problem for cotton production in the mid-south and southeastern USA. It has been found associated with hundreds of species of plants. The life cycle is completed in 17 to 23 days under favorable temperatures.

**7.19.3.2 Superfamily Dolichodoroidea
Chitwood in Chitwood &
Chitwood, 1950**

Diagnosis: Hoplolaimina. Juveniles and adults vermiform; mature female not obese. No marked sexual dimorphism in anterior region. Lateral fields with one to six incisures. Deirids present only in Merliniinae and Psilenchidae. Phasmids small with pore-like aperture on tail.

Four families: Dolichodoridae Chitwood in Chitwood & Chitwood, 1950, Belonolaimidae Whitehead, 1960, Psilenchidae Paramonov, 1967, Telotylenchidae Siddiqi, 1960

**7.19.3.2.1 Family Dolichodoridae Chitwood in Chitwood &
Chitwood, 1950**

The family comprises ectoparasites of plant roots. These nematodes are named as awl nematodes, because they have long stylets. Generally, moderate-size nematodes. In the cephalic region, they are usually four-lobed with distinct labial distinct; framework well sclerotized. Pharyngeal glands do not overlap intestine. Tail dissimilar in

sexes. Spicules strong. Bursa enveloping tail, distinctly trilobed.

Two subfamilies: Dolichodorinae Chitwood in Chitwood & Chitwood, 1950; Brachydorinae Siddiqi, 2000.

Genus *Dolichodorus* Cobb, 1914 (Figs 7.192 J, 7.199 I–M)

Diagnosis: Dolichodoridae, Dolichodorinae. Body straight to arcuate when fixed. Stylet very long (50–170 μm). Lateral field with three incisures. Strong sclerotization of basal plate of framework. Median and basal bulbs well-developed. Female tail convex-conoid then conoid to filiform. Spicules and gubernaculum robust.

Type species: *Dolichodorus heterocephalus* Cobb, 1914

Total number of species: 16

Nematodes are distributed predominantly in subtropical and tropical regions and are considered to be pathogens. Usually, awl nematodes are found in moist to wet soil, low areas of fields and near irrigation ditches and other bodies of fresh water. *Dolichodorus heterocephalus* causes severe root damage and yield reductions for celery, corn, beans, tomatoes and other crops. The damage caused by awl nematodes leads to severe stunting of the entire plant, because of depletion of the root system.

7.19.3.2.2 Family Belonolaimidae Whitehead, 1960

The representatives of the family are known as sting nematodes, which are migratory ectoparasites of roots. Body length between 1 and 3 mm with very long stylet. Labial region usually four-lobed. Lateral field with one, two or four incisures. Pharyngeal glands overlapping intestine, bursa simple, not trilobed. The family contains one subfamily: Belonolaiminae Whitehead, 1960.

Genus *Belonolaimus* Steiner, 1949 (Figs 7.192 A, 7.199 N–Q)

Diagnosis: Belonolaimidae, Belonolaiminae. Large sized (2–3 mm) and slender ($a=50\text{--}80$). Lateral field with a single incisure from head to tail. Cephalic region large, rounded, offset, divided by longitudinal grooves into four well-separated sectors. Labial disc offset, rounded, conspicuous. Stylet very long, 90–160 μm . Median bulb round. Pharyngeal glands overlap intestine latero-ventrally. Tail elongate, in female cylindroid, three to six anal body widths long. Spicules robust, slightly arcuate.

Type species: *Belonolaimus gracilis* Steiner, 1949

Total number of species: 6

Sting nematodes are mainly found in sandy soils from southern states of North America. *Belonolaimus longica-*

datus is recognized as an important pathogen with a wide host plant range.

7.19.3.2.3 Family Telotylenchidae Siddiqi, 1960

Diagnosis: Small to medium sized (0.5–1.1 mm). Lateral fields with three to six incisures. Labial disc indistinct not marked off from cephalic annuli. Stylet usually under 45 μm . Pharyngeal glands enclosed in a basal bulb or extending over intestine laterally or latero-dorsally. Vagina not sclerotized. Ovaries paired.

Four subfamilies: Telotylenchinae Siddiqi, 1960, Fotedar & Handoo, 1978, Meiodorinae Siddiqi, 1976, Merliniinae Siddiqi, 1971

Genus *Tylenchorhynchus* Cobb, 1913 (Fig. 7.199 A–D)

Diagnosis: Telotylenchidae, Telotylenchinae. Body approximately 1 mm or less. Cuticle distinctly annulated, rarely divided by fine longitudinal striae; lateral fields with three or four incisures. Lip region continuous or offset, annulated or rarely smooth. Stylet well-developed, 15–25 μm with distinct knobs. Median bulb spheroid, basal bulb pyriform, offset from intestine or slightly extending over intestine. Ovaries paired and straight. Vulva generally near middle of body. Tail cylindrical to subcylindrical, conoid with blunt tip, pointed-conoid, conical to almost funnel-shaped, clavate to subclavate, or bluntly rounded; tail terminus hemispherical to subhemispherical, acutely pointed or bluntly pointed to bluntly rounded, conoid, or rounded; tail tip smooth or annulated. Bursa nearly always extending to tail tip; phasmids near middle of tail.

Type species: *Tylenchorhynchus cylindricus* Cobb, 1913

Total number of species: 130

These nematodes are migratory ecto- or semi-endoparasites. Some species (*T. claytoni*, *T. annulatus*, *T. nudus*, *T. cylindricus*, *T. capitatus* and others) can cause damage to turf grasses, tobacco, corn, azaleas and other plants in various climatic areas. Species of this genus are called as stunt nematodes because of inducing poor growth of affected plants.

Genus *Merlinius* Siddiqi, 1970 (Fig. 7.199 E–H)

Diagnosis: Telotylenchidae, Merliniinae. Small species up to 1 mm long. Cuticle finely but distinct annulated, without longitudinal striae. Lateral field with six incisures, normally not areolated. Cephalic region continuous or slightly offset. Stylet moderately long under 20 μm long. Basal bulb offset from intestine. Gonad paired. Vulval

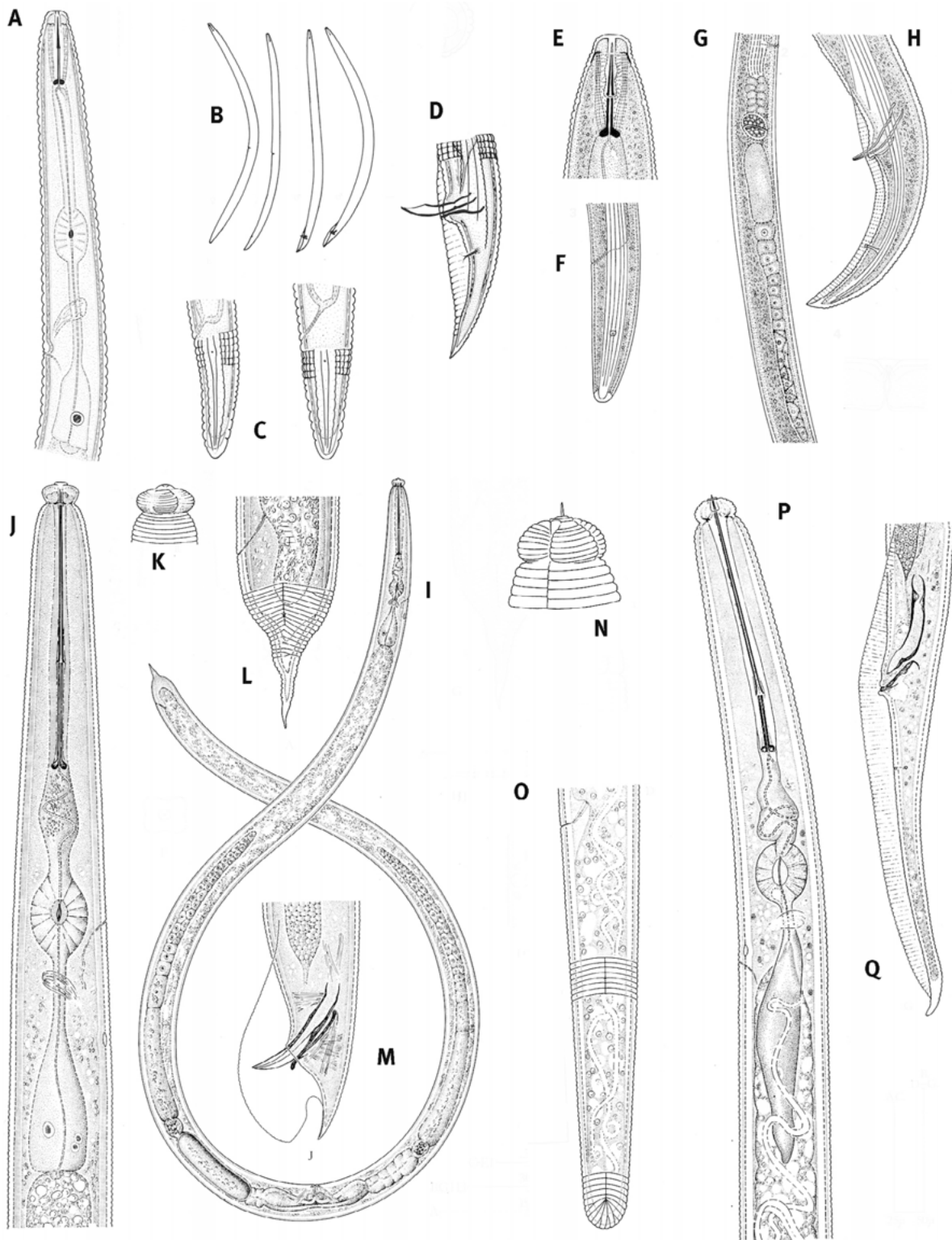


Fig. 7.199: *Tylenchorhynchus claytoni* (A–D). A, Anterior region of female; B, Entire body; C, Tails of female; D, Posterior end of male. *Merlinius microdorus* (E–H). E, Head of female; F, Tail of female; G, Reproductive tract; H, Tail of male; *Dolichodorus heterocephalus* (I–M). I, Female entire body; J, Female anterior region; K, Female head; L, Female tail; M, Male tail; *Belonolaimus longicaudatus* (N–Q). N, Female head; O, Female tail with annulation of phasmid region and terminus; P, Female anterior region; Q, Male tail. A–D after Loof (1974). E–H after Knobloch & Bird (1981). I–M after Williams (1974b). (N–Q) after Williams (1974a).

closed, slit-like; epiptygma indistinct. Bursa encircling tip. Female tail conoid to subcylindrical.

Type species: *Merlinius brevidens* (Allen, 1955) Siddiqi, 1970

Total number of species: 30

7.19.4 Suborder Criconematina Siddiqi, 1980

A large group of ecto- and endoparasitic nematodes that includes more than 750 species of ecto- and semi-endoparasitic soil-inhabiting nematodes. Several species, including the citrus nematode *Tylenchulus semipenetrans* and the ring nematode *Macroposthonia xenoplax* are considered to be of major agricultural importance for many countries. Based on the pharyngeal structure, Siddiqi (1980) stated that Criconematina might have originated from an ancestor with a broad corpus and strong stylet, as is found in infective females of some species in the suborder Hexatylna.

Diagnosis [after Siddiqi (2000)]: Tylenchida. Males and some juveniles lack a stylet or have a degenerate one. Marked sexual dimorphism in anterior region manifest. Cuticle either thin and finely annulated or thick and coarsely annulated; in later case may have retrorse annuli (Fig. 7.192 G), scales (Fig. 7.192 K), spines or an extra-cuticular body sheath. Lateral fields present or absent. Phasmids absent. Females: vermiform, sausage-shaped, or obese only in Tylenchuloidea, usually <1 mm long. Cephalic region smooth or usually with one to three coarse annuli; framework hexaradiate, with light to heavy sclerotization. Six lip areas, may be fused to form a labial disc. Stylet long or short, but shaft always approximately 8–10 µm. Basal stylet knobs well-developed. Pharynx criconematoid: corpus enormously developed; broad-cylindroid with muscular postcorpus amalgamated with precorpus; isthmus either slender and offset from basal bulb, or broad and amalgamated with it. Basal bulb small, containing three pharyngeal glands. Nerve ring circumpharyngeal. Excretory system may produce gelatinous matrix. Rectum obscure; anus a small round pore. Monodelphic, prodelphic. Vulva transversely oval or slit-like, located posteriorly, generally at more than 85% of body from anterior end. Postvulval uterine sac absent. Spermatheca small, offset, ventral or ventral-lateral to the axis of the gonoduct. Male vermiform with degenerate pharynx. Stylet also degenerates, or is lacking. Bursa weakly developed, rarely enveloping tail tip, absent in several groups. Spicules setaceous. Gubernaculum simple, linear or crescent-like.

Three superfamilies: Criconemoidea Taylor, 1936 (1914), Hemicycliophoroidea (Skarbilovich 1959) Siddiqi, 1980, Tylenchuloidea Skarbilovich, 1947

Key to superfamilies of Criconematina

[after Siddiqi (2000)]

- 01a** – Females and juveniles with thick cuticle bearing prominent annuli, pharynx with isthmus broad and amalgamated with basal bulb 2
- 01b** – Females and juveniles with thin cuticle bearing fine annuli; pharynx with isthmus not amalgamated with basal bulb **Tylenchoidea**
- 02a** – Females and juveniles elongate vermiform, usually over 0.6 mm long, annuli round, male with elongate tail and high bursa **Hemicycliophoroidea**
- 02b** – Females and juveniles spindle- or sausage shaped, usually under 0.5 mm long, annuli retrorse, male with short tail and low or no bursa **Criconematoidea**

7.19.4.1 Superfamily Criconemoidea Taylor, 1936

Diagnosis: Criconematina. Small nematodes. Female and juveniles sausage- to spindle-shaped with thick cuticle and coarse retrorse annuli, with or without scales, spines and other configuration. Male vermiform. Lateral field with incisures in males, absent in juveniles and females. Isthmus short, broad and amalgamated with a small reduced basal bulb offset from intestine. Male tail short with low bursa. Ectoparasites of roots.

One family: Criconematidae Taylor, 1936, which includes three subfamilies: Criconematinae Taylor, 1936, Hemicriconemoidinae Andrassy, 1979, Macroposthoniinae Skarbilovich, 1959

Genus *Macroposthonia* de Man, 1880 (Fig. 7.200 C–E)

Diagnosis: Criconematidae, Macroposthoniinae. Small- to medium-sized nematodes. Margins of annuli of female smooth, irregular or crenated, about 40–150 in number. First annulus smooth, without ornamentation or spines, retrorse to directed anteriorly. Stylet strong. Labial

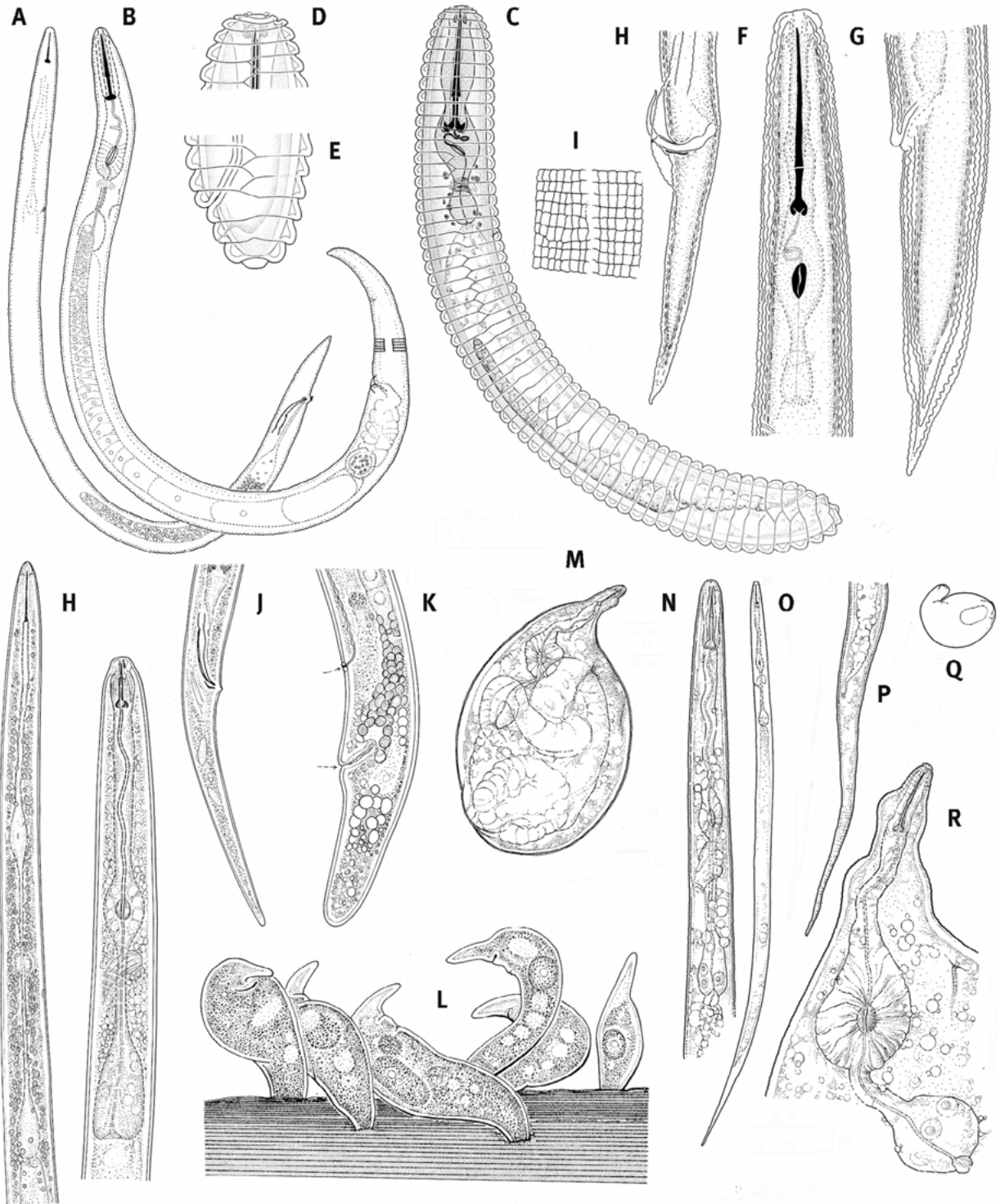


Fig. 7.200: *Paratylenchus bukowinensis* (A, B). A, Male; B, Female. *Macroposthonia sphaerocephala* (C–E). C, Entire body of female; D, Anterior end; E, Posterior end. *Hemicycliophora typica* (F–I). F, Head of female; G, Tail of female; H, Tail of male; I, Lateral field of female. *Tylenchulus semipenetrans* (H–L). H, Anterior end of male; I, Anterior end of young female; J, Posterior end of male; K, Posterior end of young female; L, Females on citrus roots. *Sphaeronema alni* (M–R). M, Q, Mature females; N, Pharyngeal region of second-stage juvenile; O, Entire body of second-stage juvenile; P, Tail region of second-stage juvenile; R, Pharyngeal region of mature female. A, B, after Brzeski (1976). D–E after Orton Williams (1973). F–I after Van Den Berg et al. (2010). H–L after Siddiqi (1974b). M–R after Palomares-Rius et al. (2010).

region with submedian lobes that are outgrowths of submedian pseudo-lips and usually present. Vulval lips not protruding, vulva open, anterior vulval lip may be ornamented by projections of various shapes. Male usually without lateral lines, bursa small.

Type species: *Macroposthonia annulata* de Man, 1880

Total number of species: 109

Macroposthonia xenoplax is one of agricultural important species of this genus with worldwide distribution and a wide host range, including grapevine, walnut, pine, grasses and other plants. It causes pruning and necrosis of fine feeder roots, especially on young plants.

7.19.4.2 Superfamily Tylenchuloidea Skarbilovich, 1947

Diagnosis: Criconematina. Body small, becoming obese in females of some genera. Cuticle thin, and finely annulated. Female has slender isthmus, not amalgamated with a small and rounded basal bulb. Vulva a large transverse slit. Uterine wall thick in obese females and it forms a cystoid body in *Meloidoderita*. Male with degenerate pharynx and stylet. Bursa usually absent.

Three families: Tylenchulidae Skarbilovich, 1947, Paratylenchidae (Thorne 1949) Raski, 1962, Sphaeronematidae Raski & Sher, 1952

7.19.4.2.1 Family Tylenchulidae Skarbilovich, 1947

Diagnosis: Tylenchuloidea. Adult female elongate obese, ventrally curved with a distinct postvulval region. Stylet about 15 μm or shorter. Excretory pore much behind pharyngeal region; excretory cell enormously developed, producing gelatinous matrix. Tail present, but short.

One subfamily: Tylenchulinae Skarbilovich, 1947

Genus *Tylenchulus* Cobb, 1913 (Fig. 7.200 H–L)

Diagnosis: Tylenchulidae, Tylenchulinae. Mature female elongate-obese, enlarging behind median bulb, mostly on dorsal side, ventrally arcuate; postvulval part elongate-tapering; maximum width up to 100 μm . Stylet 11–15 μm long. Excretory system well-developed, produced gelatinous matrix. Excretory pore 12–19 μm in front of vulva at 68%–85% of body length from the anterior end. Isthmus elongate slender. Basal bulb offset from intestine. Vulval lips thick, bulging. Male slender, straight or slightly arcuate ventrally. Stylet and pharynx degenerate. Bursa absent. Second-stage juvenile slender, straight to slightly

arcuate when relaxed. Deirids present. Excretory pore at 50%–60% of body length. Stylet 11–15 μm , knobs rounded. Rectum and anus obscure. Female feed on root inducing nurse cells, which have same size as normal cortical cells but with hypertrophied nuclei and dense cytoplasm.

Type species: *Tylenchulus semipenetrans* Cobb, 1913

Total number of species: 5

The citrus root nematode, *T. semipenetrans*, has a worldwide distribution and is one of the most common and important plant parasites of citrus in citrus groves. *Tylenchulus semipenetrans* parasitizes most *Citrus* species, *Poncirus trifoliata* and other citrus relatives from the Rutaceae. Several non-rutaceous plants, such as grape, olive and persimmon, are also reported as good hosts. The life cycle occurs during 6–8 weeks at 25°C. Female juveniles feed on root during every stage. The young females penetrate then deeper into the root and, after inducing a feeding site, the nematode's body becomes immobile. The nematodes can reach a high population level and cause a tree decline. Other *Tylenchulus* species were described from sugarcane, *Saccharum* hybrids from South Africa, native plants from Florida, USA and banana plants from Iran.

7.19.4.2.2 Family Paratylenchidae (Thorne 1949) Raski, 1962

Diagnosis: Tylenchuloidea. Vermiform, curving ventrally when relaxed. Cuticle thin, finely or moderately annulated. Stylet well-developed, occasionally long for some genera. Pharynx with strong muscular procorpus, slender isthmus and offset, usually spheroid basal bulb. One ovary, no postvulval sack. Male stylet and pharynx absent. Two subfamilies: Paratylenchinae Thorne, 1949, Tylenchocriconematinae Raski & Siddiqi, 1975

Genus *Paratylenchus* Micoletzky, 1922 (Fig. 7.200 A, B)

Diagnosis: Paratylenchidae, Paratylenchinae. Body very small, 0.2 to 0.5 mm, moderately slender, occasionally swollen in prevulval region. Cuticle finely annulated, lateral field with two to four incisures. Labial region narrow, not offset, round. Stylet 12–40 μm . Postvulval uterine sac absent. Tail conoid. Male with stylet degenerate or absent. Pharynx degenerate. Bursa absent.

Type species: *Paratylenchus bukowinensis* Micoletzky, 1922
Total number of species: 74

Pin nematodes of the genus *Paratylenchus* species are the smallest plant-parasitic nematodes that attack many plants and behave as migratory endoparasites.

Genus *Sphaeronema* Raski & Sher, 1952 (Figs. 7.195 B and 7.200 M–R)

Diagnosis: Sphaeronematidae, Sphaeronematinae. Obligate parasites of plant root. Sedentary female rounded with distinct neck. Cuticle thick, vulva cleft-like, terminal on cone-like protuberance of body. Male vermiform with degenerate pharynx without bursa. Second-stage juvenile vermiform with excretory pore in isthmus region and elongate tail.

Type species: *Sphaeronema californicum* Raski & Sher, 1952
Total number of species: 7

7.19.4.3 Superfamily Hemicycliophoroidea (Skarbilovich, 1959) Siddiqi, 1980

Diagnosis: Criconematina. Body moderate to large, vermiform with thick and coarse round; the number of annules is over 200. Stylet in juveniles and females elongated with rounded basal knobs. Males with degenerated pharynx, without stylet, an elongated tail and prominent bursa.

Two families: Hemicycliophoridae (Skarbilovich, 1959) Geraert, 1966, Caloosiidae Siddiqi, 1980

7.19.4.3.1 Family Hemicycliophoridae (Skarbilovich 1959) Geraert, 1966

Diagnosis: Criconematina, Hemicycliophoroidea. Females and juveniles with thick body sheath, usually have lateral field. Spicules arcuate, semicircular or U- or hook-shaped. One subfamily: Hemicycliophorinae Skarbilovich, 1959

Genus *Hemicycliophora* de Man, 1921 (Fig. 7.200 F–I)

Diagnosis: Hemicycliophorinae. Body varying from 0.6–1.8 mm in length, conspicuously narrowed behind vulva. Entire body surrounded by usually distinct, sheath-like second cuticle. Stylet long, often flexible, knobs rounded to sloping backwards. Female and juvenile tails elongate-conoid, filiform or cylindroid, rarely hemispherical. Vulva lips divergent, often modified. Spicules semicircular. Cloacal lips elongated to form a penial tube. Bursa adval, crenate.

Type species: *Hemicycliophora typica* de Man, 1921
Total number of species: 132

Sheath nematodes, *Hemicycliophora* species are ectoparasites, which are widely distributed throughout the world. These nematodes may cause stunting of root growth. *Hemicycliophora arenaria* induces gall-like formation on citrus roots.

7.19.5 Suborder Hexatylna Siddiqi, 1980

Diagnosis [after Siddiqi (2000)]: Tylenchida. Primarily entoparasitic, mostly with free-living mycetophagous or plant-parasitic generation. Entomoparasitic generation with only female parasitic in insect or mite hemocoel, other stages in host non-parasitic. Obese hemocoel inhabiting female uptakes food from the body surface. Lateral fields present and absent. Phasmids and prophasms not known. Cephalic region generally low, smooth or finely striated. Stylet generally <20 µm long, with or without basal knobs. esophagus in entomoparasitic forms not divisible into corpus, isthmus and basal region. Nerve ring circum-intestinal in insect-parasitic forms, circumpharyngeal in free-living stage. Anus pore-like, atrophied in saccate females. Tails of juveniles and adults over one anal body width long. Females are monodelphic, prodelphic. Free-living female with short slender stylet. Crustacean formeria in the form of a quadricolumella or with more than four rows of cells. Males with or rarely without a stylet. Pharynx as in free-living female, or rarely degenerated. Gubernaculum simple, fixed, may be lacking. Two superfamilies: Sphaerularioidea Lubbock, 1861, Iotonchioidea Goodey, 1953

7.19.5.1 Superfamily Sphaerularioidea Lubbock, 1861

Diagnosis: Hexatylna. Two types of generation, one free-living, fungus-feeding or plant-parasitic (or not known), another entomoparasitic hexerosexual female in insect or mite hemocoel. Spicules not angular.

Four families: Sphaerulariidae Lubbock, 1861, Allantone-matidae Pereira, 1931, Neotylenchidae Thorne, 1941, Paurodontidae (Thorne 1949) Massey, 1967 (*Familia dubia*)

7.19.5.1.1 Family Sphaerulariidae Lubbock, 1861

Diagnosis: Sphaerularioidea. Entomoparasitic female in host hemocoel everts uterus that often hypertrophies into a large sac. Pharyngeal glands of free-living females form a basal bulb or a short overlap over intestine. One subfamily: Sphaerulariinae Lubbock, 1861

Genus *Sphaerularia* Dufour, 1837 (Fig. 7.201)

Diagnosis [after Siddiqi (2000)]: Sphaerulariidae. Sphaerulariinae. Entomoparasitic form. Female. Upon entering the insect hemocoel, fertilized female everts its uterus,

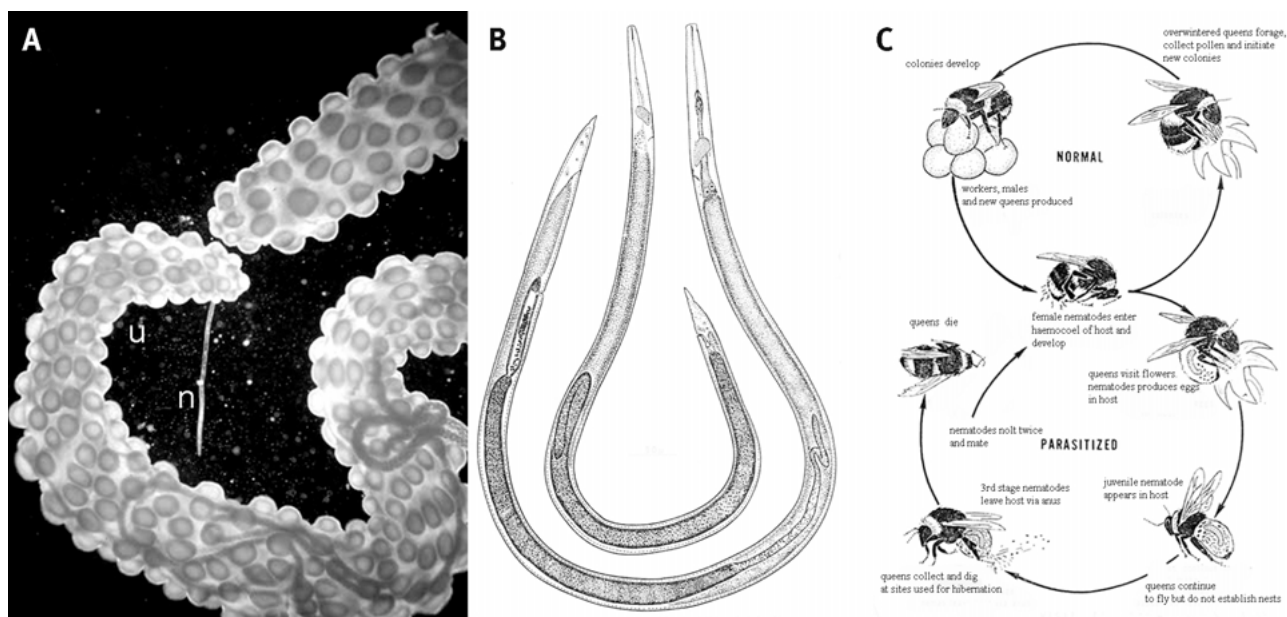


Fig. 7.201: *Sphaerularia bombi*. A, Parasitic female; B, Free-living adult male and female; C, Normal and *Sphaerularia*-parasitized cycles of *Bombus* spp. A, from <http://www.nematodes.org>. B, C after Poinar and van Der Laan (1972), with modifications. Abbreviations: n, body of female nematode; u, uterine sac.

oviduct and ovary through the vulva. The uterus becomes hypertrophied, forms egg-producing sac, or uterium, leading independent life. Uterium is sausage-shaped, 2–20 mm long, 1.2–1.5 mm wide; surface with rows of broadly based large rounded elevations. Third-stage juveniles are in insect hemocoel and soil. Body 0.9–1.5 mm long, C-shaped or straight when relaxed. Lateral field with up to eight incisures. Tail conoid, bluntly rounded. Partly free-living forms: No complete free-living generation known. Females, approximately 1–2 mm long, slender. Substylet gland orifice not seen. Vulva posterior but at more than two body widths from anus. Postvulval uterine sac present. Oviduct very long. Males, smaller than females but pharynx poorly developed. Tail similar to that of female. Bursa subterminal. Spicules arcuate, cephalated, 17–23 μm long.

Type species: *Sphaerularia bombi* Dufour, 1837

Total number of species: 2

The genus *Sphaerularia bombi* was described as an unusual parasite of bumblebees of the genera *Bombus* and *Psithyrus*. The parasitic nematode female everts its uterus and associated reproductive structures into the body cavity of its bumblebee host. This uterine sac then takes over the normal functions of the parasite and leads an independent existence. The life cycle of *S. bombi* is as follows: mated females invade bumblebee gynes that overwinter underground, parasitized gynes usually do not found colonies due to their undeveloped ovaries but repeatedly visit potential overwintering sites in spring and

early summer, where they disperse numerous parasitic juveniles. These juveniles grow into adults and mate, and wait for new hosts that happen to enter the overwintering sites in autumn (Poinar & van der Laan 1972).

7.19.5.1.2 Family Neotylenchidae Thorne, 1941

Diagnosis: Sphaerularioidea. Entomoparasitic female does not evert uterus. Pharyngeal glands of free-living female form a basal bulb or a long overlap over intestine. Free-living fungus feeding or plant-parasitic generation present. Four subfamilies: Neotylenchinae Thorne, 1941, Fergusobiinae Goodey, 1963, Gymnotylenchinae Siddiqi, 1980, Rubzovinematinae Slobodyanyuk, 1999

Genus *Fergusobia* (Currie 1937) Christie, 1941 (Fig. 7.202)

Diagnosis: Neotylenchidae, Fergusobiinae. Plant parasitic forms. Parthenogenetic female. Occur in plant galls. Semi-obese, usually dorsally curved when heat-killed but straight in some species. Less than 1 mm long (ca 250–700 μm long). Stylet knobbed, 5–20 μm long. Pharynx fusiform, non-muscular. Nerve ring just in front of dorsal pharyngeal gland. Vulva a transverse slit, at approximately 75%–90% of body length; may be depressed, flat or may have protuberant lips. Vagina anteriorly directed. No postvulval sac. Uterus extensile in some species; with a quadricolumell. Males, spicules slender to robust, approximately

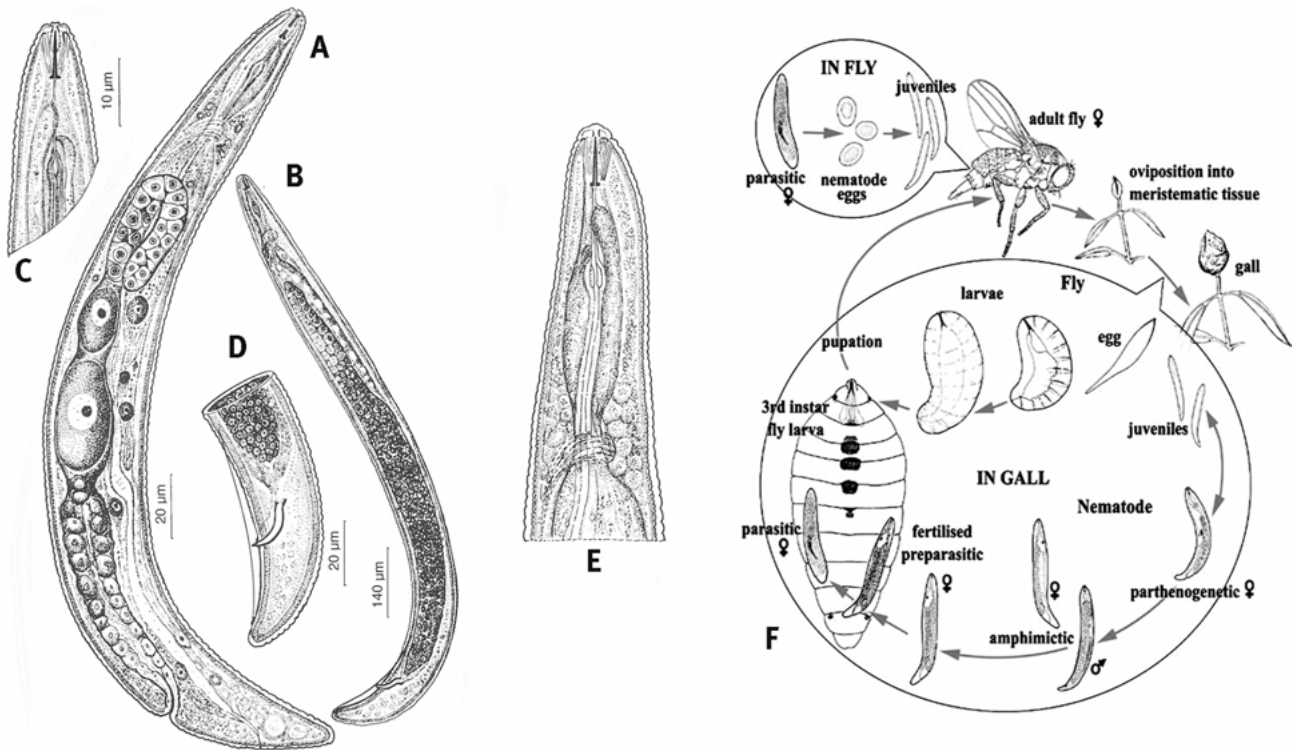


Fig. 7.202: *Fergusonobia tumifaciens* from *Eucalyptus* shoot-gall. A, Female; B, Male; C, Head of female; D, Tail of male; E, Anterior end of female; F, Annual cycle of a typical *Fergusonina* fly (Diptera: Fergusoninidae) and its associated *Fergusonobia* nematode (Nematoda: Neotylenchidae). A–E after Siddiqi (2000). F, Diagram prepared by Elise Head, Adelaide University, Australia.

10–40 μm long, usually angular but may be arcuate. No gubernaculum observed. Infective stage, pre-parasitic female. Similar in size but usually slightly larger and slimmer than parthenogenetic female. Vulva a transverse slit at 60%–85% of body length; may be surrounded by a cuticular plate, be depressed or have small lips. No post-vulval sac. Entomoparasitic female. Occurs in hemolymph in abdomen of adult female *Fergusonina* fly. Larger than other stages (ca 300–1400 μm long); non-motile. Straight, or slightly dorsally curved when heat-killed; stout. No stylet. Pharynx, intestine and rectum degenerate. Reproductive tract single, greatly hypertrophied, reflexed to coil along body length.

Type species: *Fergusonobia tumifaciens* (Currie 1937) Wachek 1955

Total number of species: 17 (based upon molecular analysis, more than 50 are predicted)

Nematodes of the genus *Fergusonobia* occur in a mutualistic association with flies of the genus *Fergusonina* Malloch, 1924 (Diptera: Fergusoninidae). Flies induce a variety of gall types in young meristematic, apical tissues of myrtaceous hosts in Australasia. *Fergusonobia* is dicyclic, with a parthenogenetic generation in a plant, followed by an amphimictic generation that begins in a plant and

ends with a parasitic, fertilized female in the hemolymph of (female only) flies. The parasitic female deposits eggs into the hemolymph of the fly, where they hatch and the juveniles move to the fly's oviducts. When the fly deposits her eggs in fresh meristematic tissue, she also deposits juvenile nematodes, thus beginning the next generation.

7.19.5.2 Superfamily Iotonchioidea Goodey, 1953

Diagnosis: Hexatylinea. Free-living feeding generation present. Two alternating entomoparasitic generations in host present; two or more types of adults found in host's hemocoel. Spicules large, may be angular.

Two families: Iotochiidae Goodey, 1953, Parasytylenchidae Siddiqi, 1986

7.19.5.2.1 Family Iotonchiidae (Goodey 1953) Skarbilovich, 1959

Diagnosis: Iotonchioidea. Two types of females occur in the host's body cavity. Alternation of heterosexual and

partthenogenetic generations present. Partially free-living forms with marked sexual dimorphism in anterior region, Vulva more than two body widths in front of anus.

One subfamily: Iotonchiinae Goodey, 1953

Genus *Skarbilovinema* Chizhov & Zakharenkova, 1991

Diagnosis: Iotonchiidae, Iotonchiinae. Only heterosexual stage known. Females, obese, elongate-tuboid with rounded ends, 3–16 mm long; old females yellow in color. Body wall with numerous hypodermal microvilli for food uptake. Genital branch reflexed several times, almost filling body cavity. Viviparous. Juveniles develop into bisexual stages. Fertilized infective stage female: body elongate slender ($L = 2.8\text{--}3.3$ mm; $a = 72\text{--}104$). Vulva at 92%–93% body length. Vulva lips prominent. Males, cephalic region pinhead-like. Stylet and pharynx degenerate. Gubernaculum absent. Bursa narrows, covers about two-thirds of tail. Parasites of flies, belonging to the genera *Helophilus*, *Eristalis* and *Myathropa* (family Syrphidae).

Type species: *Skarbilovinema laumondi* Chizhov & Zakharenkova, 1991

Total number of species: 2

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